31

Fungi

▲ **Figure 31.1 Can you spot the largest organism in this forest?**

EVOLUTION

KEY CONCEPTS

31.1 Fungi are heterotrophs that feed by absorption
31.2 Fungi produce spores through sexual or asexual life cycles
31.3 The ancestor of fungi was an aquatic, single-celled, flagellated protist
31.4 Fungi have radiated into a diverse set of lineages
31.5 Fungi play key roles in nutrient cycling, ecological interactions, and human welfare

OVERVIEW

Mighty Mushrooms

Hiking through the Malheur National Forest in eastern Oregon, you might notice a few clusters of honey mushrooms (*Armillaria ostoyae*) scattered here and there beneath the towering trees **(Figure 31.1)**. The trees appear to dwarf the mushrooms, but as strange as it sounds, the reverse is actually true. All these mushrooms are just the aboveground portion of a single enormous fungus. Its subterranean network of filaments spreads through 965 hectares of the forest—more than the area of 1,800 football fields. Based on its current growth rate, scientists estimate that this fungus, which weighs hundreds of tons, has been growing for more than 1,900 years.

The inconspicuous honey mushrooms on the forest floor are a fitting symbol of the neglected grandeur of the kingdom Fungi. Most of us are barely aware of these eukaryotes beyond the mushrooms we eat or the occasional brush with athlete's foot. Yet fungi are a huge and important component of the biosphere. While about 100,000 species have been described, it is estimated that there are actually as many as 1.5 million species of fungi. Some fungi are exclusively single-celled, though most have complex multicellular bodies, which in many cases include the structures we know as mushrooms. These diverse organisms are found in just about every imaginable terrestrial and aquatic habitat; airborne spores have even been found 160 km above ground.

Fungi are not only diverse and widespread; they are also essential for the well-being of most ecosystems. They break down organic material and recycle nutrients, allowing other organisms to assimilate essential chemical elements. Humans make use of fungi as a food source, for applications in agriculture and forestry, and in manufacturing products ranging from bread to antibiotics. But it is also true that some fungi cause disease in plants and animals.

In this chapter, we will investigate the structure and evolutionary history of fungi, survey the major groups of fungi, and discuss their ecological and commercial significance.

CONCEPT **31.1**

Fungi are heterotrophs that feed by absorption

Despite their vast diversity, all fungi share some key traits, most importantly the way they derive nutrition. In addition, many fungi grow by forming multicellular filaments, a body structure that plays an important role in how they obtain food.

Nutrition and Ecology

Like animals, fungi are heterotrophs: They cannot make their own food as plants and algae can. But unlike animals, fungi do not ingest (eat) their food. Instead, a fungus absorbs nutrients from the environment outside of its body. Many fungi accomplish this task by secreting powerful hydrolytic enzymes into their surroundings. These enzymes break down complex molecules to smaller organic compounds that the fungi can absorb into their bodies and use. Other fungi use enzymes to penetrate the walls of cells, enabling the fungi to absorb nutrients from the cells. Collectively, the different enzymes found in various fungal species can digest compounds from a wide range of sources, living or dead.

This diversity of food sources corresponds to the varied roles of fungi in ecological communitities, with different species living as decomposers, parasites, or mutualists. Decomposer fungi break down and absorb nutrients from nonliving organic material, such as fallen logs, animal corpses, and the wastes of living organisms. Parasitic fungi absorb nutrients from the cells of living hosts. Some parasitic fungi are pathogenic, including many species that cause diseases in plants. Mutualistic fungi also absorb nutrients from a host organism, but they reciprocate with actions that benefit the host. For example, mutualistic fungi that live inside certain termite species use their enzymes to break down wood, as do mutualistic protists in other termite species (see Figure 28.26).

The versatile enzymes that enable fungi to digest a wide range of food sources are not the only reason for their ecological success. Another important factor is how their body structure increases the efficiency of nutrient absorption.

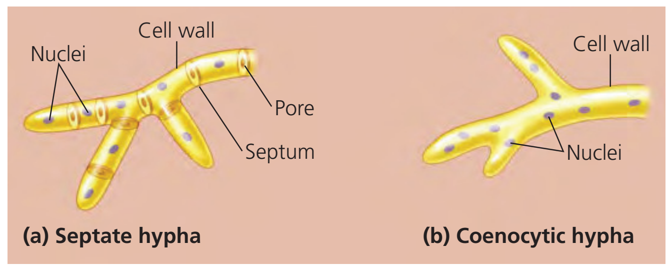
Body Structure

The most common fungal body structures are multicellular filaments and single cells (**yeasts**). Many species can grow as both filaments and yeasts, but even more grow only as filaments; relatively few species grow only as yeasts. Yeasts often inhabit moist environments, including plant sap and animal tissues, where there is a ready supply of soluble nutrients, such as sugars and amino acids. We'll discuss yeasts again later in the chapter.

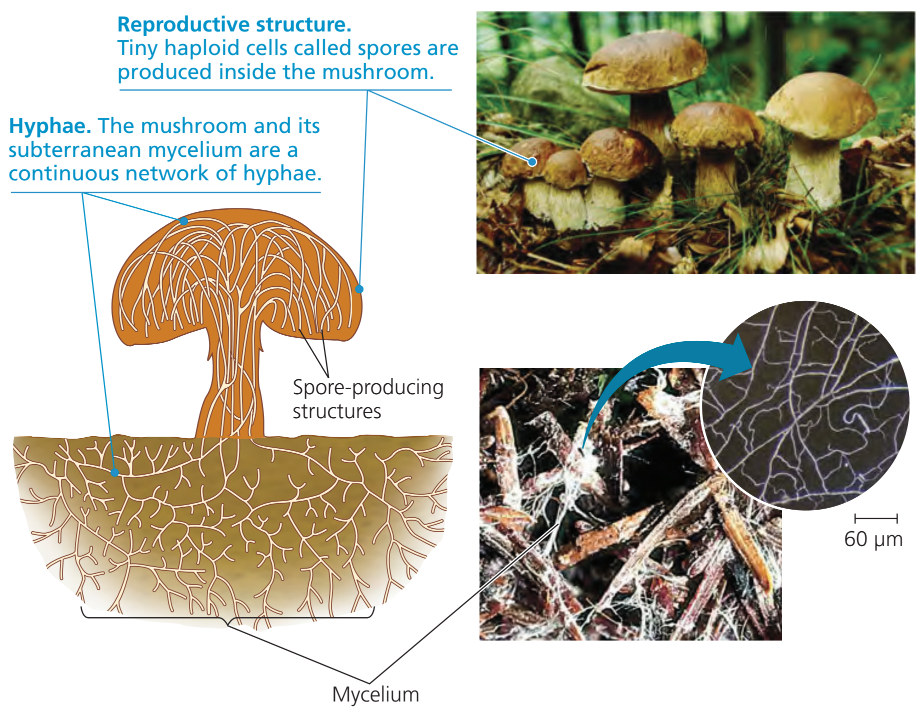
The morphology of multicellular fungi enhances their ability to grow into and absorb nutrients from their surroundings **(Figure 31.2)**. The bodies of these fungi typically form a network of tiny filaments called **hyphae** (singular, *hypha*). Hyphae consist of tubular cell walls surrounding the plasma membrane and cytoplasm of the cells. Unlike plant cell walls, which contain cellulose, fungal cell walls are strengthened by **chitin**. This strong but flexible nitrogen-containing polysaccharide is also found in the external skeletons of insects and other arthropods.

Fungal hyphae form an interwoven mass called a **mycelium** (plural, *mycelia*) that infiltrates the material on which the fungus feeds. A mycelium's structure maximizes its surface-to-volume ratio, making feeding very efficient. Just 1 cm^3 of rich soil may contain as much as 1 km of hyphae with a total surface area of 300 cm^2 in contact with the soil. A fungal mycelium grows rapidly, as proteins and other materials synthesized by the fungus are channeled through cytoplasmic streaming to the tips of the extending hyphae. The fungus concentrates its energy and resources on adding hyphal length and thus overall absorptive surface area, rather than on increasing hyphal girth. Fungi are not motile in the typical sense—they cannot run, swim, or fly in search of food or mates. However, as they grow, fungi can move into new territory, swiftly extending the tips of their hyphae.

In most fungi, the hyphae are divided into cells by crosswalls, or **septa** (singular, *septum*) **(Figure 31.3a)**. Septa generally have pores large enough to allow ribosomes, mitochondria, and even nuclei to flow from cell to cell. Some fungi lack septa **(Figure 31.3b)**. Known as **coenocytic fungi**, these organisms consist of a continuous cytoplasmic mass having hundreds or thousands of nuclei. The coenocytic condition results from the repeated division of nuclei without cytokinesis. This description



▲ **Figure 31.3 Two forms of hyphae.**



▲ **Figure 31.2 Structure of a multicellular fungus.** The top photograph shows the sexual structures, in this case called mushrooms, of the penny bun fungus (*Boletus edulis*). The bottom photograph shows a mycelium growing on fallen conifer needles. The inset SEM shows hyphae.

? *Although the mushrooms in the top photograph appear to be different individuals, could their DNA be identical? Explain.*

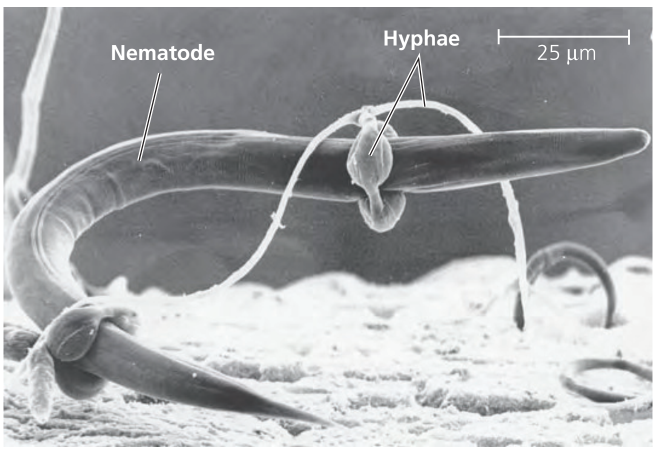
may remind you of the plasmodial slime molds you read about in Chapter 28, which also consist of cytoplasmic masses containing many nuclei. This similarity is one reason that slime molds were once classified as fungi; molecular data have since shown that slime molds and fungi belong to distinct clades.

Specialized Hyphae in Mycorrhizal Fungi

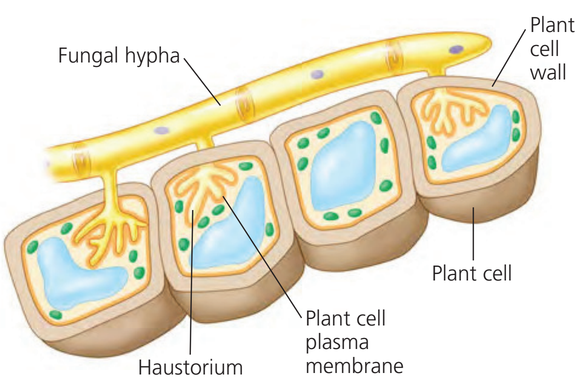
Some fungi have specialized hyphae that allow them to feed on living animals **(Figure 31.4a)**. Other fungal species have specialized hyphae called **haustoria**, which the fungi use to extract nutrients from, or exchange nutrients with, their plant hosts **(Figure 31.4b)**. Mutually beneficial relationships between such fungi and plant roots are called **mycorrhizae** (the term means "fungus roots").

Mycorrhizal fungi (fungi that form mycorrhizae) can improve delivery of phosphate ions and other minerals to plants because the vast mycelial networks of the fungi are more efficient than the plants' roots at acquiring these minerals from the soil. In exchange, the plants supply the fungi with organic nutrients such as carbohydrates. There are two main types of mycorrhizal fungi. **Ectomycorrhizal fungi** (from the Greek *ektos*, out) form sheaths of hyphae over the surface of a root and typically grow into the extracellular spaces of the root cortex (see Figure 37.13a). **Arbuscular mycorrhizal fungi** (from the Latin *arbor*, tree) extend branching hyphae through the root cell wall and into tubes formed by invagination (pushing inward) of the root cell plasma membrane (see Figure 37.13b).

Mycorrhizae are enormously important in natural ecosystems and agriculture. Almost all vascular plants have mycorrhizae and rely on their fungal partners for essential nutrients. Many studies have demonstrated the significance of mycorrhizae by comparing the growth of plants with and without them (see Figure 37.14). Foresters commonly inoculate pine seedlings with mycorrhizal fungi to promote growth. In the absence of human intervention, mycorrhizal fungi colonize soils by dispersing haploid cells called **spores** that form new mycelia after germinating. Spore dispersal is a key component of how fungi reproduce and spread to new areas, as we discuss next.



(a) Hyphae adapted for trapping and killing prey. In *Arthrobotrys*, a soil fungus, portions of the hyphae are modified as hoops that can constrict around a nematode (roundworm) in less than a second. The fungus then penetrates its prey with hyphae and digests the prey's inner tissues (SEM).



(b) Haustoria. Some mutualistic and parasitic fungi grow specialized hyphae called haustoria that can extract nutrients from living plant cells. Haustoria remain separated from a plant cell's cytoplasm by the plasma membrane of the plant cell (orange).

▲ **Figure 31.4 Specialized hyphae.**

CONCEPT CHECK 31.1

1. Compare and contrast the nutritional mode of a fungus with your own nutritional mode.
2. **WHAT IF?** Suppose a certain fungus is a mutualist that lives within an insect host, yet its ancestors were parasites that grew in and on the insect's body. What derived traits might you find in this mutualistic fungus?
3. **MAKE CONNECTIONS** Review Figure 10.4 (p. 186) and Figure 10.6 (p. 188). If a plant has mycorrhizae, where might carbon that enters the plant's stomata as CO_2 eventually be deposited: in the plant, in the mycorrhizal fungus, or in both? Explain.

For suggested answers, see Appendix A.

CONCEPT 31.2

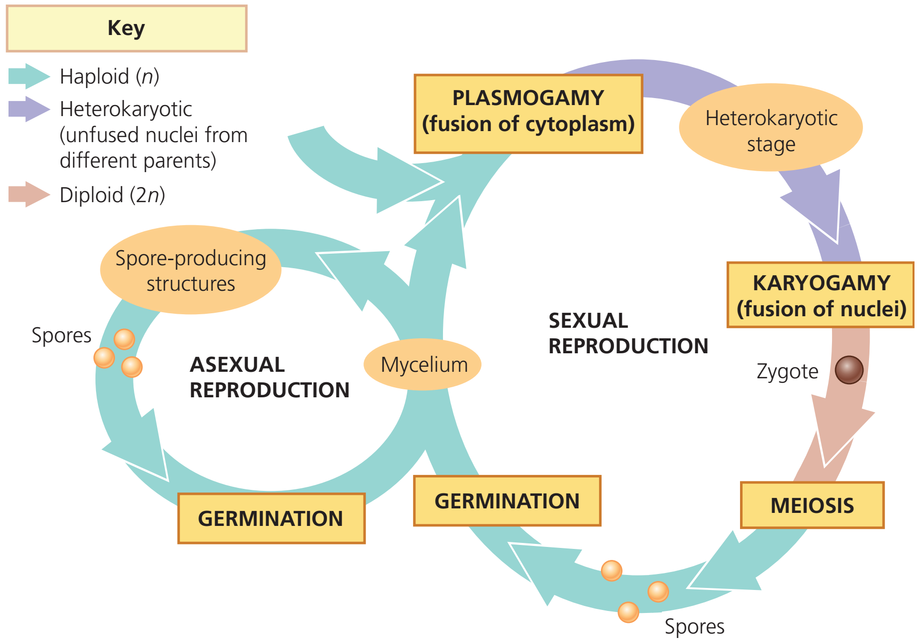
Fungi produce spores through sexual or asexual life cycles

Most fungi propagate themselves by producing vast numbers of spores, either sexually or asexually. For example, puffballs, the reproductive structures of certain fungal species, may release trillions of spores in cloud-like bursts (see Figure 31.18). Spores can be carried long distances by wind or water. If they land in a moist place where there is food, they germinate, producing new mycelia. To appreciate how effective spores are at dispersing, leave a slice of melon exposed to the air. Even without a visible source of spores nearby, within a week or so, you will likely observe fuzzy mycelia growing from the microscopic spores that have fallen onto the melon.

haploid nuclei, they differ from diploid cells, which have pairs of homologous chromosomes within a single nucleus.

Hours, days, or (in some fungi) even centuries may pass between plasmogamy and the next stage in the sexual cycle, **karyogamy**. During karyogamy, the haploid nuclei contributed by the two parents fuse, producing diploid cells. Zygotes and other transient structures form during karyogamy, the only diploid stage in most fungi. Meiosis then restores the haploid condition, leading to the formation of spores that enable the fungus to disperse.

The sexual processes of karyogamy and meiosis generate extensive genetic variation, a prerequisite for natural selection. (See Chapters 13 and 23 to review how sex can increase genetic diversity in a population.) The heterokaryotic condition also offers some of the advantages of diploidy in that one haploid genome may compensate for harmful mutations in the other.



▲ **Figure 31.5 Generalized life cycle of fungi.** Many—but not all—fungi reproduce both sexually and asexually. Some reproduce only sexually, others only asexually.

Figure 31.5 generalizes the many different life cycles that can produce fungal spores. In this section, we will survey general aspects of the sexual and asexual life cycles of fungi. Later, we'll examine more closely the life cycles of specific fungi.

Sexual Reproduction

The nuclei of fungal hyphae and the spores of most fungal species are haploid, although many fungi have transient diploid stages that form during sexual life cycles. In fungi, sexual reproduction often begins when hyphae from two mycelia release sexual signaling molecules called **pheromones**. If the mycelia are of different mating types, the pheromones from each partner bind to receptors on the other, and the hyphae extend toward the source of the pheromones. When the hyphae meet, they fuse. In species with such a "compatibility test," this process contributes to genetic variation by preventing hyphae from fusing with other hyphae from the same mycelium or another genetically identical mycelium.

The union of the cytoplasms of two parent mycelia is known as **plasmogamy**. In most fungi, the haploid nuclei contributed by each parent do not fuse right away. Instead, parts of the fused mycelium contain coexisting, genetically different nuclei. Such a mycelium is said to be a **heterokaryon** (meaning "different nuclei"). In some species, the different nuclei may even exchange chromosomes and genes in a process similar to crossing over (see Chapter 13). In other species, the haploid nuclei pair off two to a cell, one from each parent. Such a mycelium is **dikaryotic** (meaning "two nuclei"). As a dikaryotic mycelium grows, the two nuclei in each cell divide in tandem without fusing. Because these cells retain two separate

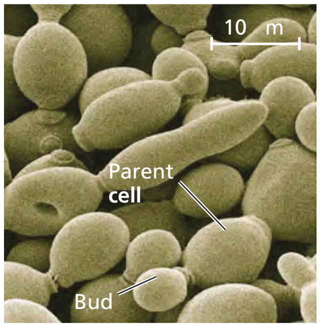
Asexual Reproduction

Many fungi can reproduce both sexually and asexually. Some 20,000 fungal species are only known to reproduce asexually. As with sexual reproduction, the processes of asexual reproduction vary widely among fungi.

Many fungi reproduce asexually by growing as filamentous fungi that produce (haploid) spores by mitosis; such species are known informally as **molds** if they form visible mycelia. Depending on your housekeeping habits, you may have observed molds in your kitchen, forming furry carpets on fruit, bread, and other foods **(Figure 31.6)**. Molds typically grow rapidly and produce many spores asexually, enabling the fungi to colonize new sources of food. Many species that produce such spores can also reproduce sexually if they happen to contact a member of their species of a different mating type.

▲ **Figure 31.6 *Penicillium*, a mold commonly encountered as a decomposer of food.** The bead-like clusters in the colorized SEM are conidia, structures involved in asexual reproduction.

Other fungi reproduce asexually by growing as single-celled yeasts. Instead of producing spores, asexual reproduction in yeasts occurs by ordinary cell division or by the pinching of small "bud cells" off a parent cell **(Figure 31.7)**. As already mentioned, some fungi that grow as yeasts can also grow as filamentous mycelia, depending on the availability of nutrients.



▲ **Figure 31.7 The yeast *Saccharomyces cerevisiae* in several stages of budding** (SEM).

Many yeasts and filamentous fungi have no known sexual stage in their life cycle. Since early mycologists (biologists who study fungi) classified fungi based mainly on their type of sexual structure, this posed a problem. Mycologists have traditionally lumped all fungi lacking sexual reproduction into a group called **deuteromycetes** (from the Greek *deutero*, second, and *mycete*, fungus). Whenever a sexual stage is discovered for a so-called deuteromycete, the species is reclassified in a particular phylum, depending on the type of sexual structures it forms. In addition to searching for sexual stages of such unassigned fungi, mycologists can now use genetic techniques to classify them.

CONCEPT CHECK 31.2

1. **MAKE CONNECTIONS** Compare Figure 31.5 with Figure 13.6 (p. 252). In terms of haploidy versus diploidy, how do the life cycles of fungi and humans differ?
2. **WHAT IF?** Suppose that you sample the DNA of two mushrooms on opposite sides of your yard and find that they are identical. Propose two hypotheses that could reasonably account for this result.

For suggested answers, see Appendix A.

CONCEPT 31.3

The ancestor of fungi was an aquatic, single-celled, flagellated protist

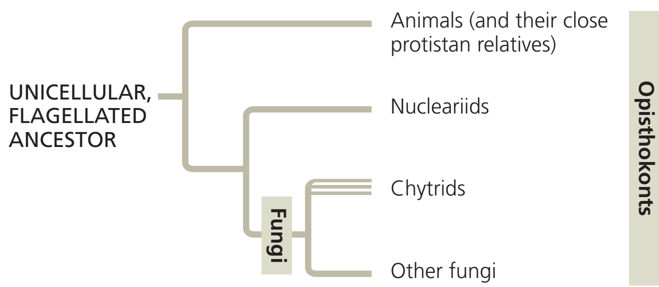
Data from both paleontology and molecular systematics offer insights into the early evolution of fungi. As a result, systematists now recognize that fungi and animals are more closely related to each other than either group is to plants or most other eukaryotes.

The Origin of Fungi

Phylogenetic systematics suggests that fungi evolved from a flagellated ancestor. While the majority of fungi lack flagella, some of the earliest-diverging lineages of fungi (the chytrids, discussed later in this chapter) do have flagella. Moreover, most of the protists that share a close common ancestor with animals and fungi also have flagella. DNA sequence data indicate that these three groups of eukaryotes—the fungi, the animals, and their protistan relatives—form a clade **(Figure 31.8)**. As discussed in Chapter 28, members of this clade are called **opisthokonts**, a name that refers to the posterior (*opistho-*) location of the flagellum in these organisms.

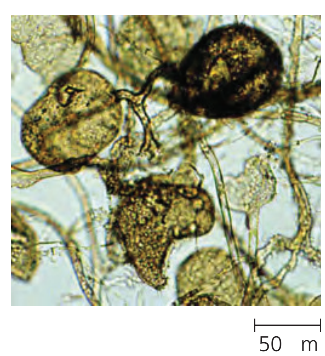
DNA sequence data also indicate that fungi are more closely related to several groups of single-celled protists than they are to animals, suggesting that the ancestor of fungi was unicellular. One such group of unicellular protists, the **nucleariids**, consists of amoebas that feed on algae and bacteria. DNA evidence further indicates that animals are more closely related to a *different* group of protists (the choanoflagellates) than they are to either fungi or nucleariids. Together, these results suggest that multicellularity must have evolved in animals and fungi independently, from different single-celled ancestors.

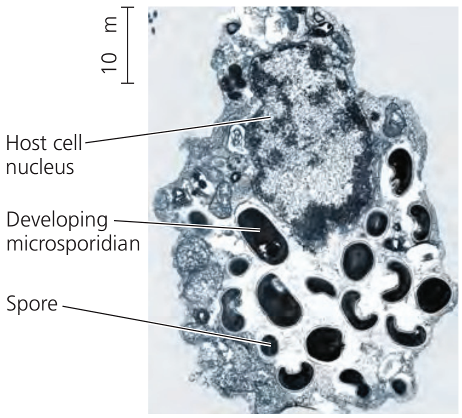
Based on molecular clock analysis (see Chapter 26), scientists have estimated that the ancestors of animals and fungi diverged into separate lineages about 1 billion years ago. However, the oldest undisputed fossils of fungi are only about 460 million years old **(Figure 31.9)**. One possible explanation for this discrepancy is that the microscopic ancestors of today's terrestrial fungi fossilized poorly.



▲ **Figure 31.8 Fungi and their close relatives.** Molecular evidence indicates that the nucleariids, a group of single-celled protists, are the closest living relatives of fungi. The three parallel lines leading to the chytrids indicate that this group may be paraphyletic.

► **Figure 31.9 Fossil fungal hyphae and spores from the Ordovician period (about 460 million years ago)** (LM).





▲ **Figure 31.10 A eukaryotic cell infected by microsporidia.** A large vacuole inside this host eukaryotic cell contains spores and developing forms of the parasite *Encephalitozoon intestinalis* (TEM).

Are Microsporidia Fungi?

In addition to animals and protists such as the nucleariids, another group of organisms, the microsporidia, are closely related to fungi—and may in fact be fungi. Microsporidia are unicellular parasites of animals and protists **(Figure 31.10)**. They are often used to control insect pests. While microsporidia do not normally cause illness in humans, they do pose a risk to people with AIDS and other immune-compromised conditions.

In many ways, microsporidia are unlike most other eukaryotes. They do not have conventional mitochondria, for example. As a result, microsporidia have been something of a taxonomic mystery, thought by some researchers to be a basal lineage of eukaryotes. In recent years, however, researchers have discovered that microsporidia actually have tiny organelles derived from mitochondria. In addition, most molecular comparisons indicate that microsporidia are fungi, suggesting that they are highly derived parasites. One such study, a 2006 analysis of DNA sequence data from six genes in nearly 200 fungal species, concluded that microsporidia are members of an early-diverging lineage of fungi. Additional genetic data from species belonging to early-diverging lineages of fungi are needed to fully resolve whether microsporidia are fungi or are a closely related but distinct group of organisms.

The Move to Land

Much of the fungal diversity we observe today may have originated during an adaptive radiation that began when multicellular plants and animals colonized land. For example, fossils of the earliest known vascular plants from the late Silurian period (420 million years ago) contain evidence of mycorrhizal relationships between plants and fungi. This evidence includes fossils of hyphae that have penetrated within plant cells and formed structures that closely resemble the haustoria of arbuscular mycorrhizae. Indeed, plants probably existed in beneficial relationships with fungi from the earliest periods of colonization of land.

CONCEPT CHECK 31.3

1. Why are fungi classified as opisthokonts despite the fact that most fungi lack flagella?
2. Explain the evolutionary significance of the presence of mycorrhizae in the earliest vascular plants.
3. **WHAT IF?** If fungi had colonized land before plants, where might the fungi have lived? What might they have used for food?

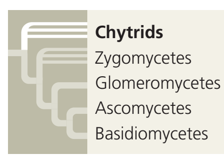
For suggested answers, see Appendix A.

CONCEPT 31.4

Fungi have radiated into a diverse set of lineages

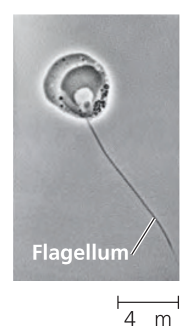
The phylogeny of fungi is currently the subject of much research. In the past decade, molecular analyses have helped clarify the evolutionary relationships between fungal groups, although there are still areas of uncertainty. **Figure 31.11**, on the next page, presents a simplified version of one current hypothesis. In this section, we will survey each of the major fungal groups identified in this phylogenetic tree.

Chytrids



The fungi classified in the phylum Chytridiomycota, called **chytrids**, are ubiquitous in lakes and soil. Some of the approximately 1,000 chytrid species are decomposers, while others are parasites of protists, other fungi, plants, or animals; as we'll see later in the chapter, one such chytrid parasite has likely contributed to the global decline of amphibian populations. Still other chytrids are important mutualists. For example, anaerobic chytrids that live in the digestive tracts of sheep and cattle help to break down plant matter, thereby contributing significantly to the animal's growth.

Molecular evidence supports the hypothesis that chytrids diverged early in fungal evolution. Like other fungi, chytrids have cell walls made of chitin, and they also share certain key enzymes and metabolic pathways with other fungal groups. Some chytrids form colonies with hyphae, while others exist as single spherical cells. But chytrids are unique among fungi in having flagellated spores, called **zoospores (Figure 31.12)**.

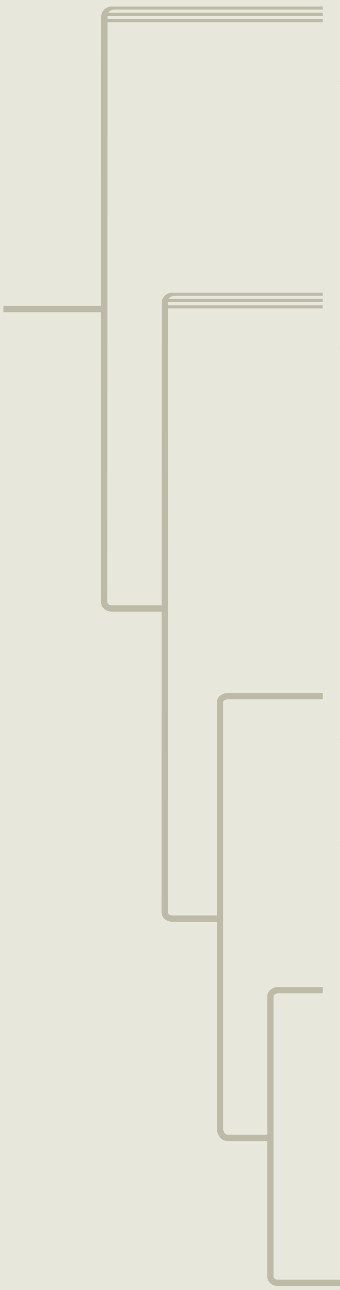


▲ **Figure 31.12 Flagellated chytrid zoospore** (TEM).

▼ **Figure 31.11**

Exploring Fungal Diversity

Most mycologists currently recognize five major groups of fungi, although the chytrids and zygomycetes are probably paraphyletic (as indicated by the parallel lines).

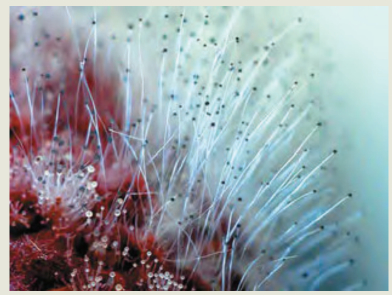


Chytrids (1,000 species)

In chytrids such as *Chytridium*, the globular fruiting body forms multicellular, branched hyphae (LM); other species are single-celled. Chytrids have flagellated spores and are thought to include some of the earliest fungal groups to diverge from other fungi.

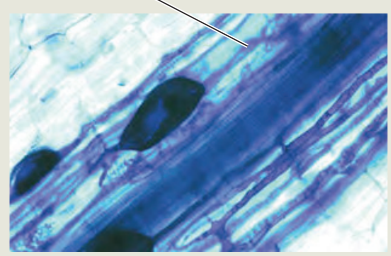
Zygomycetes (1,000 species)

The hyphae of some zygomycetes, including this mold in the genus *Mucor* (LM), grow rapidly into foods such as fruits and bread. As such, the fungi may act as decomposers (if the food is not alive) or parasites; other species live as neutral (commensal) symbionts. According to some recent analyses, the zygomycetes include the enigmatic group known as microsporidia; other studies have classified microsporidia as chytrids.



Glomeromycetes (160 species)

The glomeromycetes (arbuscular mycorrhizal fungi) are of great ecological importance. Many plants form mycorrhizal associations with these fungi. This LM shows glomeromycete hyphae (stained dark blue) within a plant root.



Ascomycetes (65,000 species)

Also called sac fungi, members of this diverse group are common to many marine, freshwater, and terrestrial habitats. The cup-shaped ascocarp (fruiting body) of the ascomycete shown here (*Aleuria aurantia*) gives this species its common name: orange peel fungus.

Basidiomycetes (30,000 species)

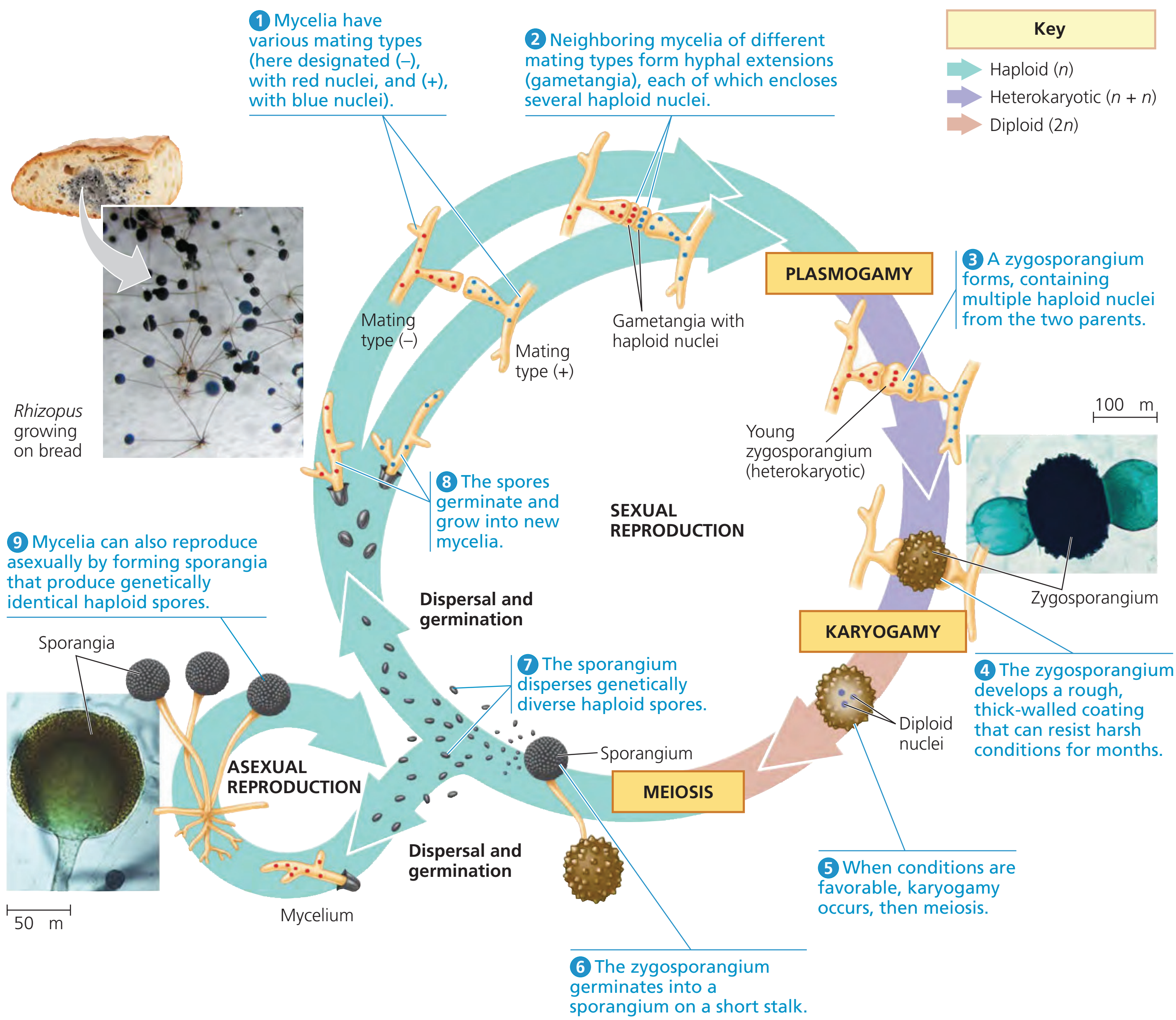
Often important as decomposers and ectomycorrhizal fungi, basidiomycetes, or club fungi, are unusual in having a long-lived, dikaryotic mycelium. The fruiting bodies—commonly called mushrooms—of this fly agaric (*Amanita muscaria*) are a familiar sight in coniferous forests of the Northern Hemisphere.

Zygomycetes

There are approximately 1,000 known species of **zygomycetes**, fungi in the phylum Zygomycota. This diverse phylum includes species of fast-growing molds responsible for causing foods such as bread, peaches, strawberries, and sweet potatoes to rot during storage. Other zygomycetes live as parasites or as commensal (neutral) symbionts of animals.

The life cycle of *Rhizopus stolonifer* (black bread mold) is fairly typical of zygomycete species (**Figure 31.13**). Its hyphae spread out over the food surface, penetrate it, and absorb nutrients. The hyphae are coenocytic, with septa found only where reproductive cells are formed. In the asexual phase, bulbous black sporangia develop at the tips of upright hyphae. Within each sporangium, hundreds of haploid spores develop and are dispersed through the air. Spores that happen to land on moist food germinate, growing into new mycelia.

If environmental conditions deteriorate—for instance, if the mold consumes all its food—*Rhizopus* may reproduce sexually. The parents in a sexual union are mycelia of different mating types, which possess different chemical markers but may appear identical. Plasmogamy produces a sturdy



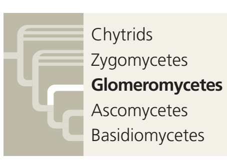
▲ **Figure 31.13 The life cycle of the zygomycete *Rhizopus stolonifer* (black bread mold).**

▲ **Figure 31.14** ***Pilobolus* aiming its sporangia.** This zygomycete decomposes animal dung. Its spore-bearing hyphae bend toward light, where there are likely to be openings in the vegetation through which spores may reach fresh grass. The fungus then launches its sporangia in a jet of water that can travel up to 2.5 m. Grazing animals ingest the fungi with the grass and then scatter the spores in feces, thereby enabling the next generation of fungi to grow.

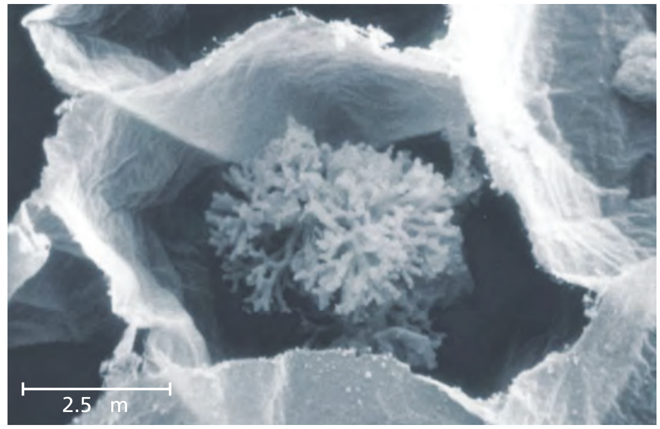
structure called a **zygosporangium**, in which karyogamy and then meiosis occur. Note that while a zygosporangium represents the zygote ($2n$) stage in the life cycle, it is not a zygote in the usual sense (that is, a cell with one diploid nucleus). Rather, a zygosporangium is a multinucleate structure, first heterokaryotic with many haploid nuclei from the two parents, then with many diploid nuclei after karyogamy.

Zygosporangia are resistant to freezing and drying and are metabolically inactive. When conditions improve, the nuclei of the zygosporangium undergo meiosis, the zygosporangium germinates into a sporangium, and the sporangium releases genetically diverse haploid spores that may colonize a new substrate. Some zygomycetes, such as *Pilobolus*, can actually "aim" and then shoot their sporangia toward bright light **(Figure 31.14)**.

Glomeromycetes



The **glomeromycetes**, fungi assigned to the phylum Glomeromycota, were formerly thought to be zygomycetes. But recent molecular studies, including a phylogenetic analysis of DNA sequence data from hundreds of fungal species, indicate that glomeromycetes form a separate clade (monophyletic group). Although only 160 species have been identified to date, the glomeromycetes are an ecologically significant group in that nearly all of them form arbuscular mycorrhizae **(Figure 31.15)**. The tips of the hyphae that push into plant root cells branch into tiny treelike arbuscules. About 90% of all plant species have such mutualistic partnerships with glomeromycetes.



▲ **Figure 31.15 Arbuscular mycorrhizae.** Most glomeromycetes form arbuscular mycorrhizae with plant roots, supplying minerals and other nutrients to the roots. This SEM depicts the branched hyphae—an arbuscule—of *Glomus mosseae* bulging into a root cell by pushing in the membrane (the root has been treated to remove the cytoplasm).

Ascomycetes

Mycologists have described 65,000 species of **ascomycetes**, fungi in the phylum Ascomycota, from a wide variety of marine, freshwater, and terrestrial habitats. The defining feature of ascomycetes is the production of spores in saclike **asci** (singular, *ascus*) during sexual reproduction; thus, they are commonly called *sac fungi*. Unlike zygomycetes, during their sexual stage most ascomycetes develop fruiting bodies, called **ascocarps**, which range in size from microscopic to macroscopic **(Figure 31.16)**. The ascocarps contain the spore-forming asci.

▼ The edible ascocarp of *Morchella esculenta*, the tasty morel, is often found under trees in orchards.

▼ *Tuber melanosporum* is a truffle species that forms ectomycorrhizae with trees. The ascocarp grows underground and emits a strong odor. These ascocarps have been dug up and the middle one sliced open.

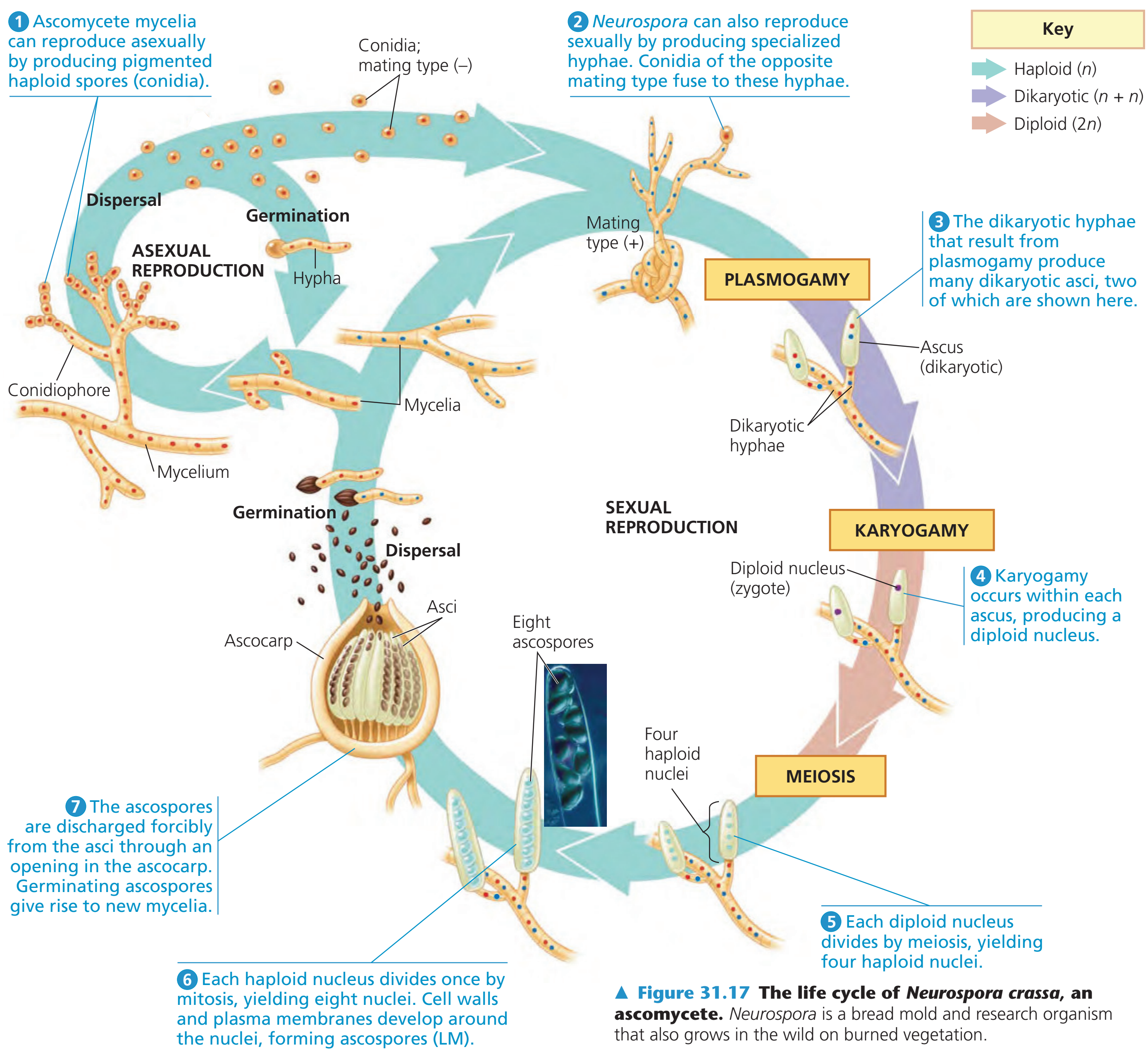
▲ **Figure 31.16 Ascomycetes (sac fungi).**

? *Ascomycetes vary greatly in morphology (see also Figure 31.11). How could you confirm that a fungus is an ascomycete?*

Ascomycetes vary in size and complexity from unicellular yeasts to elaborate cup fungi and morels (see Figure 31.16). They include some of the most devastating plant pathogens, which we will discuss later. However, many ascomycetes are important decomposers, particularly of plant material. More than 25% of all ascomycete species live with green algae or cyanobacteria in beneficial symbiotic associations called lichens. Some ascomycetes form mycorrhizae with plants. Many others live between mesophyll cells in leaves; some of these species release toxic compounds that help protect the plant from insects.

Although the life cycles of various ascomycete groups differ in the details of their reproductive structures and processes, we'll illustrate some common elements using the bread mold *Neurospora crassa* **(Figure 31.17)**. Ascomycetes reproduce asexually by producing enormous numbers of asexual spores called **conidia** (singular, *conidium*). Conidia are not formed inside sporangia, as are the asexual spores of most zygomycetes. Rather, they are produced externally at the tips of specialized hyphae called conidiophores, often in clusters or long chains, from which they may be dispersed by the wind.

Conidia may also be involved in sexual reproduction, fusing with hyphae from a mycelium of a different mating type, as occurs in *Neurospora*. Fusion of two different mating types is followed by plasmogamy, resulting in the formation of dikaryotic cells, each with two haploid nuclei representing



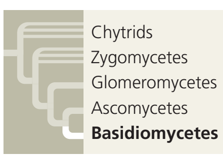
▲ **Figure 31.17 The life cycle of *Neurospora crassa*, an ascomycete.** *Neurospora* is a bread mold and research organism that also grows in the wild on burned vegetation.

the two parents. The cells at the tips of these dikaryotic hyphae develop into many asci. Within each ascus, karyogamy combines the two parental genomes, and then meiosis forms four genetically different nuclei. This is usually followed by a mitotic division, forming eight ascospores. The ascospores develop in and are eventually discharged from the ascocarp.

In contrast to the life cycle of zygomycetes, the extended dikaryotic stage of ascomycetes (and also basidiomycetes) provides increased opportunity for genetic recombination. In *Neurospora*, for example, many dikaryotic cells can develop into asci, recombining genomes during meiosis and resulting in a multitude of genetically different offspring from one mating event (see steps 2 and 3 in Figure 31.17).

Neurospora has a significant history in biological research. As we discussed in Chapter 17, biologists in the 1930s used *Neurospora* in research that led to the one gene–one enzyme hypothesis. Today, this ascomycete continues to serve as a model research organism. In 2003, its entire genome was published. With 10,000 genes, this tiny fungus has about three-fourths as many genes as the fruit fly *Drosophila* and about half as many as a human. The *Neurospora* genome is relatively compact, having few of the stretches of noncoding DNA that occupy so much space in the genomes of humans and many other eukaryotes. In fact, there is evidence that *Neurospora* has a genomic defense system that prevents noncoding DNA such as transposons from accumulating.

Basidiomycetes



Approximately 30,000 species, including mushrooms, puffballs, and shelf fungi, are called **basidiomycetes** and are classified in the phylum Basidiomycota **(Figure 31.18)**. This phylum also includes mutualists that form mycorrhizae and two groups of destructive plant parasites: rusts and smuts. The name of the phylum derives from the **basidium** (Latin for "little pedestal"), a cell in which karyogamy occurs, followed immediately by meiosis. The club-like shape of the basidium also gives rise to the common name *club fungus*.

Basidiomycetes are important decomposers of wood and other plant material. Of all the fungi, certain basidiomycetes are the best at decomposing the complex polymer lignin, an abundant component of wood. Many shelf fungi break down the wood of weak or damaged trees and continue to decompose the wood after the tree dies.

The life cycle of a basidiomycete usually includes a long-lived dikaryotic mycelium **(Figure 31.19)**. As in ascomycetes, this extended dikaryotic stage provides opportunities for many genetic recombination events, in effect multiplying the result of a single mating. Periodically, in response to environmental stimuli, the mycelium reproduces sexually by producing elaborate fruiting bodies called **basidiocarps**. The common white mushrooms in the supermarket are familiar examples of a basidiocarp.

▶ Shelf fungi, important decomposers of wood

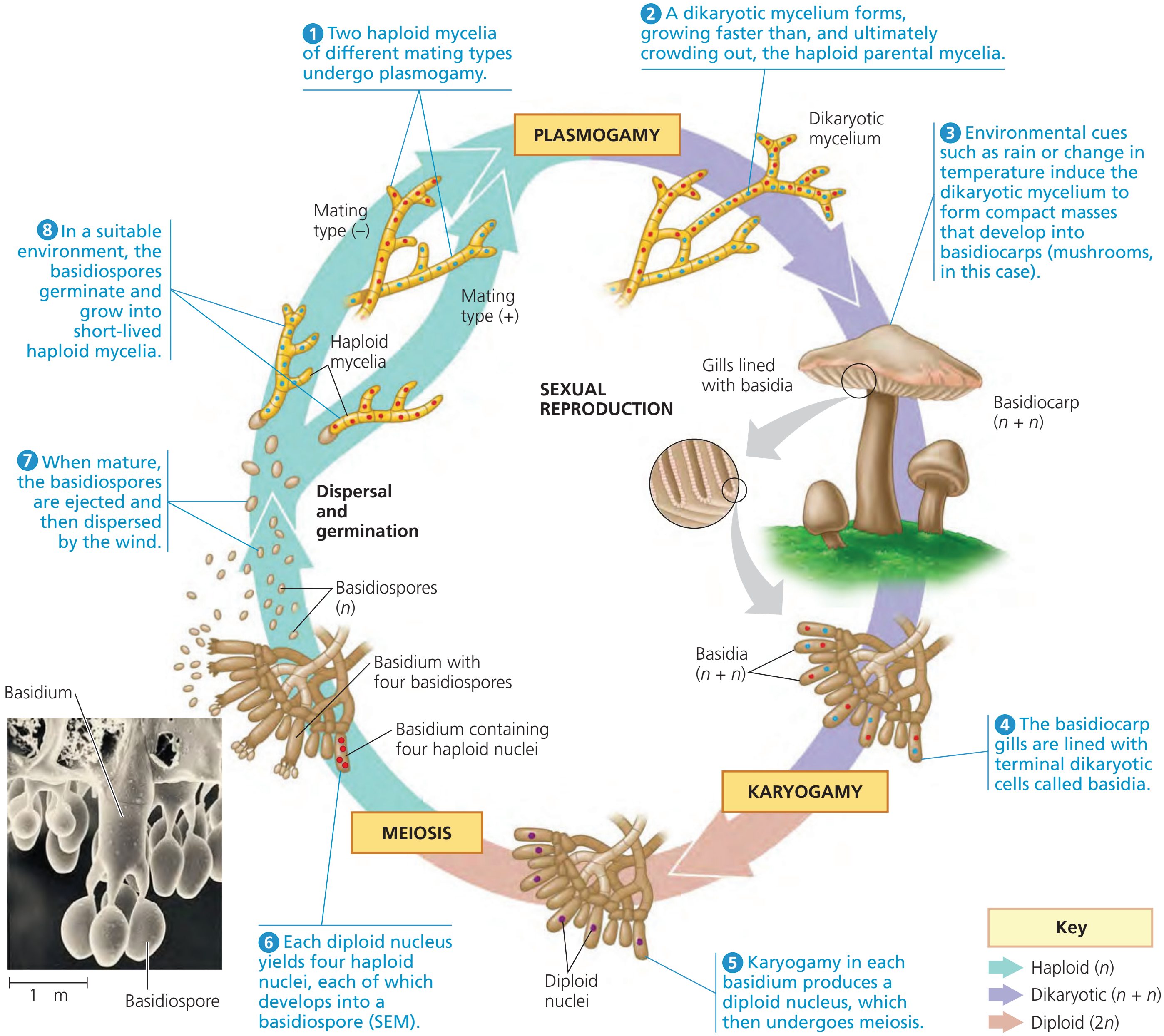
◀ Puffballs emitting spores

▶ Maiden veil fungus (*Dictyphora*), a fungus with an odor like rotting meat

▲ **Figure 31.18 Basidiomycetes (club fungi).**

By concentrating growth in the hyphae of mushrooms, a basidiomycete mycelium can erect its fruiting structures in just a few hours; a mushroom pops up as it absorbs water and as cytoplasm streams in from the dikaryotic mycelium. By this process, a ring of mushrooms, popularly called a "fairy ring," may appear literally overnight **(Figure 31.20)**. The mycelium below the fairy ring expands outward at a rate of about 30 cm per year, decomposing organic matter in the soil as it grows. Some giant fairy rings are produced by mycelia that are centuries old.

The numerous basidia in a basidiocarp are the sources of sexual spores called basidiospores. After a mushroom forms,



▲ **Figure 31.19 The life cycle of a mushroom-forming basidiomycete.**

its cap supports and protects a large surface area of dikaryotic basidia on gills. During karyogamy, the two nuclei in each basidium fuse, producing a diploid nucleus (see Figure 31.19). This nucleus then undergoes meiosis, yielding four haploid nuclei. The basidium then grows four appendages, and one haploid nucleus enters each appendage and develops into a basidiospore. Large numbers of basidiospores are produced: The gills of a common white mushroom have a surface area of about 200 cm^2 and may release a billion basidiospores, which drop from the bottom of the cap and are blown away.

▲ **Figure 31.20 A fairy ring.** According to legend, these mushrooms spring up where fairies have danced in a ring on a moonlit night. (The text provides a biological explanation of how fairy rings form.)

CONCEPT CHECK 31.4

1. What feature of chytrids supports the hypothesis that they represent an early-diverging fungal lineage?
2. Give examples of how form fits function in zygomycetes, glomeromycetes, ascomycetes, and basidiomycetes.
3. **WHAT IF?** Suppose that the mutation of an ascomycete changed its life cycle so that plasmogamy, karyogamy, and meiosis occurred in quick succession. How might this affect the ascospores and ascocarp?

For suggested answers, see Appendix A.

CONCEPT 31.5

Fungi play key roles in nutrient cycling, ecological interactions, and human welfare

In our survey of fungal classification, we've touched on some of the ways fungi influence other organisms. We will now look more closely at these impacts, focusing on how fungi act as decomposers, mutualists, and pathogens.

Fungi as Decomposers

Fungi are well adapted as decomposers of organic material, including the cellulose and lignin of plant cell walls. In fact, almost any carbon-containing substrate—even jet fuel and house paint—can be consumed by at least some fungi. As you might expect, researchers are developing ways to use a variety of fungal species in bioremediation projects. In addition, fungi and bacteria are primarily responsible for keeping ecosystems stocked with the inorganic nutrients essential for plant growth. Without these decomposers, carbon, nitrogen, and other elements would remain tied up in organic matter. Plants and the animals that eat them could not exist because elements taken from the soil would not be returned (see Chapter 55). Without decomposers, life as we know it would cease.

Fungi as Mutualists

Fungi may form mutualistic relationships with plants, algae, cyanobacteria, and animals. All of these relationships have profound ecological effects, often affecting the growth, survival, or reproduction of many species in a community.

Fungus-Plant Mutualisms

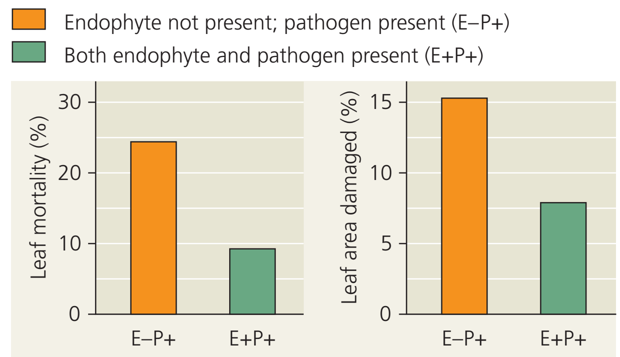
We've already considered the enormous importance of the mutualistic associations that most vascular plants form with mycorrhizal fungi. In addition, all plant species studied to date appear to harbor symbiotic **endophytes**, fungi that live inside leaves or other plant parts without causing harm. Most endophytes identified to date are ascomycetes. Endophytes have been shown to benefit certain grasses and other nonwoody plants by making toxins that deter herbivores or by increasing host plant tolerance of heat, drought, or heavy metals. Seeking to discover how endophytes affect a woody plant, researchers tested whether leaf endophytes benefit seedlings of the cacao tree, *Theobroma cacao* (**Figure 31.21**). Their findings show that the endophytes of woody flowering plants can play an important role in defending against pathogens.

▼ **Figure 31.21** INQUIRY

Do endophytes benefit a woody plant?

EXPERIMENT Endophytes are symbiotic fungi found within the bodies of all plants examined to date. A. Elizabeth Arnold, at the University of Arizona, Tucson, and colleagues tested whether endophytes benefit the cacao tree (*Theobroma cacao*). This tree, whose name means "food of the gods" in Greek, is the source of the beans used to make chocolate, and it is cultivated throughout the tropics. Endophytes were added to the leaves of some cacao seedlings, but not others. (In cacao, endophytes colonize leaves after the seedling germinates.) The seedlings were then inoculated with a virulent pathogen, the protist *Phytophthora* (see Chapter 28).

RESULTS Fewer leaves were killed by the pathogen in seedlings with endophytes than in seedlings without endophytes. Among leaves that survived, pathogens damaged less of the leaf surface area in seedlings with endophytes than in seedlings without endophytes.



CONCLUSION The presence of endophytes appears to benefit cacao trees by reducing the leaf mortality and damage caused by *Phytophthora*.

SOURCE A. E. Arnold et al., Fungal endophytes limit pathogen damage in a tropical tree, *Proceedings of the National Academy of Sciences* 100:15649–15654 (2003).

WHAT IF? Arnold and colleagues also performed control treatments. Suggest two controls they might have used, and explain how each would be helpful in interpreting the results described here.

Fungus-Animal Mutualisms

As mentioned earlier, some fungi share their digestive services with animals, helping break down plant material in the guts of cattle and other grazing mammals. Many species of ants take advantage of the digestive power of fungi by raising them in "farms." Leaf-cutter ants, for example, scour tropical forests in search of leaves, which they cannot digest on their own but

▲ **Figure 31.22 Fungus-gardening insects.** These leaf-cutting ants depend on fungi to convert plant material to a form the insects can digest. The fungi, in turn, depend on the nutrients from the leaves the ants feed them.

carry back to their nests and feed to the fungi **(Figure 31.22)**. As the fungi grow, their hyphae develop specialized swollen tips that are rich in proteins and carbohydrates. The ants feed primarily on these nutrient-rich tips. The fungi break down plant leaves into substances the insects can digest, and they also detoxify plant defensive compounds that would otherwise kill or harm the ants. In some tropical forests, the fungi have helped these insects become the major consumers of leaves.

The evolution of such farmer ants and that of their fungal "crops" have been tightly linked for over 50 million years. The fungi have become so dependent on their caretakers that in many cases they can no longer survive without the ants, and vice versa.

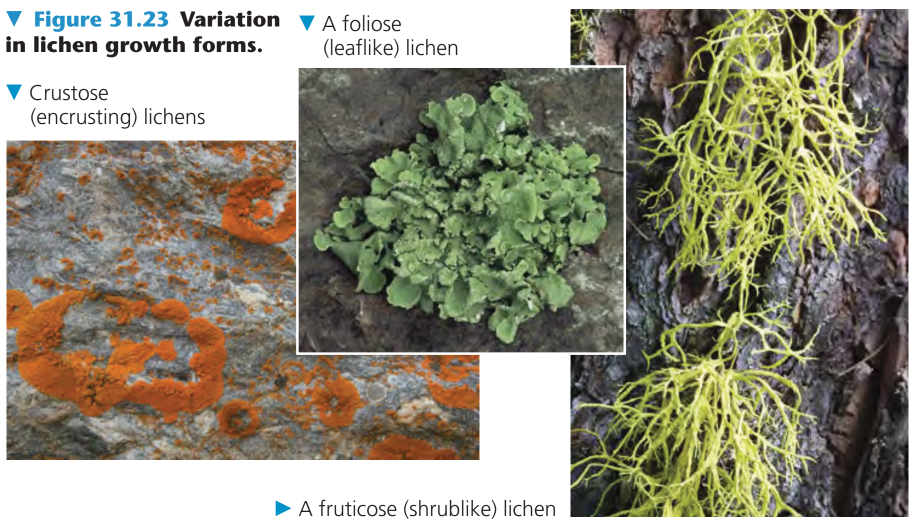
Lichens

A **lichen** is a symbiotic association between a photosynthetic microorganism and a fungus in which millions of photosynthetic cells are held in a mass of fungal hyphae. Lichens grow on the surfaces of rocks, rotting logs, trees, and roofs in various forms **(Figure 31.23)**. The photosynthetic partners are unicellular or filamentous green algae or cyanobacteria. The fungal component is most often an ascomycete, but one glomeromycete and 75 basidiomycete lichens are known. The fungus usually gives a lichen its overall shape and structure, and tissues formed by hyphae account for most of the lichen's mass. The algae or cyanobacteria generally occupy an inner layer below the lichen surface **(Figure 31.24)**.

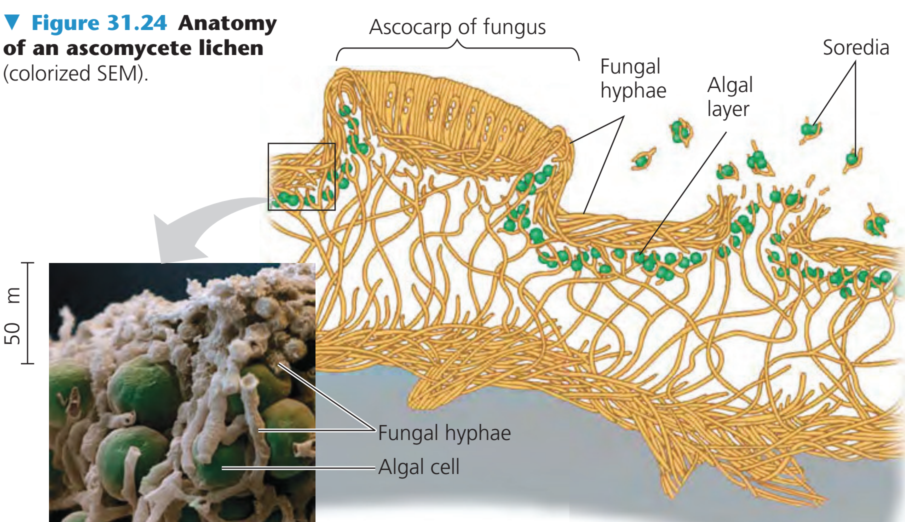
The merger of fungus and alga or cyanobacterium is so complete that lichens are given scientific names as though they were single organisms; to date, 17,000 lichen species have been described. As might be expected of such "dual organisms," asexual reproduction as a symbiotic unit is common. This can occur either by fragmentation of the parental lichen or by the formation of **soredia**, small clusters of hyphae with embedded algae (see Figure 31.24). The fungi of many lichens also reproduce sexually, and lichen algae can reproduce independently of the fungus by asexual cell division.

In most lichens, each partner provides something the other could not obtain on its own. The algae provide carbon compounds; the cyanobacteria also fix nitrogen (see Chapter 27) and provide organic nitrogen compounds. The fungi provide their photosynthetic partners with a suitable environment for growth. The physical arrangement of hyphae allows for gas

▼ **Figure 31.23 Variation in lichen growth forms.**



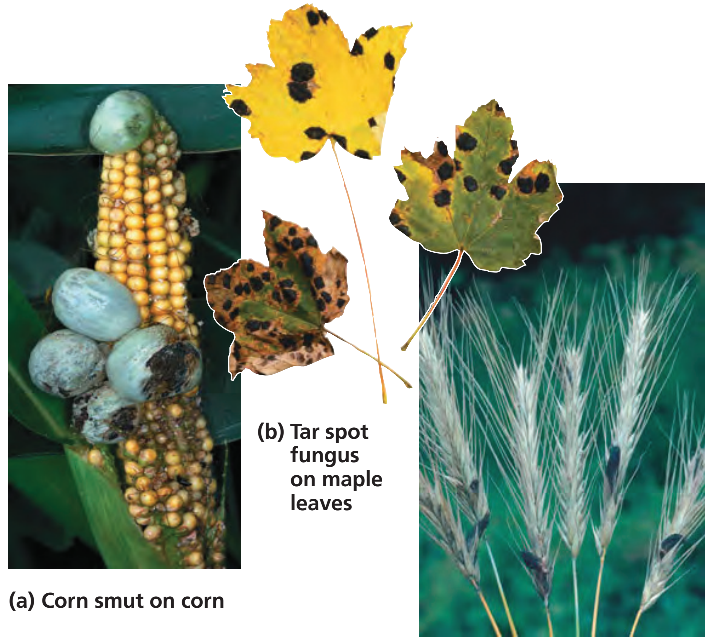
▼ **Figure 31.24 Anatomy of an ascomycete lichen** (colorized SEM).



exchange, protects the photosynthetic partner, and retains water and minerals, most of which are absorbed either from airborne dust or from rain. The fungi also secrete acids, which aid in the uptake of minerals.

Lichens are important pioneers on cleared rock and soil surfaces, such as volcanic flows and burned forests. They break down the surface by physically penetrating and chemically attacking it, and they trap windblown soil. Nitrogen-fixing lichens also add organic nitrogen to some ecosystems. These processes make it possible for a succession of plants to grow (see Chapter 54). Lichens may also have aided the colonization of land by plants. Fossils of lichens or lichen-like organisms date to 550–600 million years ago, long before plants grew on land. Early lichens may have modified rocks and soil much as they do today, helping pave the way for plants.

As tough as lichens are, however, many do not stand up well to air pollution. Their passive mode of mineral uptake from rain and moist air makes them particularly sensitive to sulfur dioxide and other airborne poisons.


(a) Corn smut on corn

(b) Tar spot fungus on maple leaves

(c) Ergots on rye

▲ **Figure 31.25 Examples of fungal diseases of plants.**

Fungi as Pathogens

About 30% of the 100,000 known species of fungi make a living as parasites or pathogens, mostly of plants **(Figure 31.25)**. For example, *Cryphonectria parasitica*, the ascomycete fungus that causes chestnut blight, dramatically changed the landscape of the northeastern United States. Accidentally introduced on trees imported from Asia in the early 1900s, spores of the fungus enter cracks in the bark of American chestnut trees and produce hyphae, killing the tree. The once-common chestnuts now survive mainly as sprouts from the stumps of former trees. Another ascomycete, *Fusarium circinatum*, causes pine pitch canker, a disease that threatens pines throughout the world. Between 10% and 50% of the world's fruit harvest is lost annually due to fungi, and grain crops also suffer major losses each year.

Some fungi that attack food crops produce compounds that are toxic to humans. Certain species of the ascomycete *Aspergillus* contaminate grain and peanuts by secreting compounds called aflatoxins. Another example is the ascomycete *Claviceps purpurea*, which grows on rye plants, forming purple structures called ergots. If infected rye is milled into flour, toxins from the ergots can cause ergotism, characterized by gangrene, nervous spasms, burning sensations, hallucinations, and temporary insanity. An epidemic of ergotism around 944 CE killed more than 40,000 people in France. One compound that has been isolated from ergots is lysergic acid, the raw material from which the hallucinogen LSD is made.

Although animals are less susceptible to parasitic fungi than are plants, about 500 fungi are known to parasitize animals. One such parasite, the chytrid *Batrachochytrium dendrobatidis*, has been implicated in the recent decline or extinction of about 200 species of frogs and other amphibians **(Figure 31.26)**. This chytrid can cause severe skin infections, leading to massive die-offs. Field observations and studies of museum specimens indicate that *B. dendrobatidis* first appeared in frog populations shortly before their declines in Australia, Costa Rica, the United States, and other countries. In addition, in regions where it infects frogs, this chytrid has very low levels of genetic diversity. These findings are consistent with the hypothesis that *B. dendrobatidis* has emerged recently and spread rapidly across the globe, decimating many amphibian populations.

The general term for an infection caused by a fungal parasite is **mycosis**. In humans, skin mycoses include the disease ringworm, so named because it appears as circular red areas on the skin. The ascomycetes that cause ringworm can infect almost any skin surface. Most commonly, they grow on the feet, causing the intense itching and blisters known as athlete's foot. Though highly contagious, athlete's foot and other ringworm infections can be treated with fungicidal lotions and powders.

Systemic mycoses, by contrast, spread through the body and usually cause very serious illnesses. They are typically caused by inhaled spores. For example, coccidioidomycosis is a systemic mycosis that produces tuberculosis-like symptoms in the lungs. Each year, hundreds of cases in North America require treatment with antifungal drugs, without which the disease would be fatal.

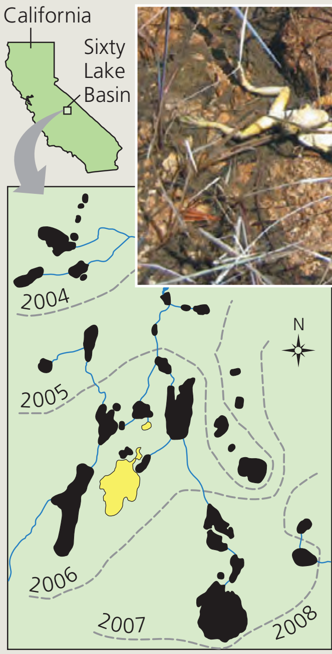
Some mycoses are opportunistic, occurring only when a change in the body's microorganisms, chemical environment, or immune system allows fungi to grow unchecked. *Candida albicans*, for example, is one of the normal inhabitants of moist epithelia, such as the vaginal lining. Under certain circumstances, *Candida* can grow too rapidly and become pathogenic, leading to so-called "yeast infections." Many other opportunistic mycoses in humans have become more common in recent decades, due in part to AIDS, which compromises the immune system.

▼ **Figure 31.26**

IMPACT

Amphibians Under Attack

Could a fungal parasite have caused the hundreds of amphibian population declines and extinctions during the last three decades? While habitat losses resulting from human activities have often been the culprit, the underlying causes have been unknown for nearly half the declining species. However, recent studies have implicated the global spread of a parasitic fungus, the chytrid *Batrachochytrium dendrobatidis*. For example, Vance Vredenburg, at San Francisco State University, and colleagues showed that the number of yellow-legged frogs (*Rana muscosa*) plummeted after the chytrid reached the Sixty Lake Basin area of California. Prior to the chytrid's 2004 arrival, on average there were 2,325 frogs in these lakes. By 2009, only 38 frogs remained. All the surviving frogs were in two lakes (yellow) where researchers had applied a fungicide to reduce the chytrid's impact.



▲ Yellow-legged frogs killed by *B. dendrobatidis* infection

Key

--- Boundary of chytrid spread

Lake status in 2009:

■ Frog population extinct

■ Treatment lake: frogs treated with fungicides and released

WHY IT MATTERS Worldwide, over one-third of amphibian species are suffering serious population declines. Information about the causes of these declines is essential if we are to protect these animals from extinction. Furthermore, because about 60% of human diseases originate from diseases in other animals, it is in our best interest to understand emerging diseases in amphibians.

FURTHER READING V. T. Vredenburg, et al., Large-scale amphibian die-offs driven by the dynamics of an emerging infectious disease, *Proceedings of the National Academy of Sciences* 107:9689-9694 (2010).

WHAT IF? Do the data depicted indicate that the chytrid *caused* or *is correlated to* the drop in frog numbers? Explain.

Practical Uses of Fungi

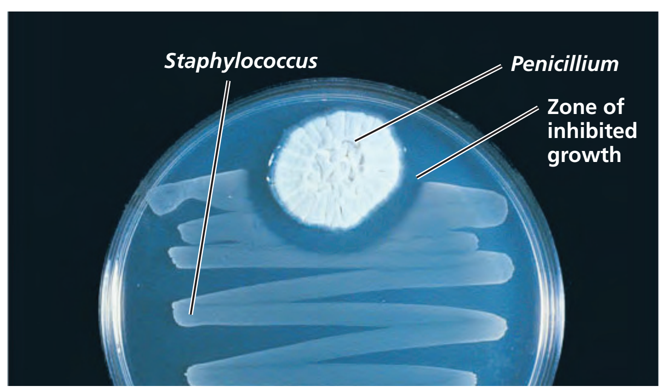
The dangers posed by fungi should not overshadow their immense benefits. We depend on their ecological services as decomposers and recyclers of organic matter. And without mycorrhizae, farming would be far less productive.

Mushrooms are not the only fungi of interest for human consumption. Fungi are used to ripen Roquefort and other blue cheeses. A species of *Aspergillus* produces citric acid used in colas. Morels and truffles, the edible fruiting bodies of various ascomycetes, are highly prized for their complex flavors (see Figure 31.16). These fungi can sell for hundreds to thousands of dollars a pound. Truffles release strong odors that attract mammals and insects, which in nature feed on them and disperse their spores. In some cases, the odors mimic the pheromones (sex attractants) of certain mammals. For example, the odors of several European truffles mimic the pheromones released by male pigs, which explains why *female* pigs are used to help find these delicacies.

Humans have used yeasts to produce alcoholic beverages and bread for thousands of years. Under anaerobic conditions, yeasts ferment sugars to alcohol and CO_2, which causes dough to rise. Only relatively recently have the yeasts involved been separated into pure cultures for more controlled use. The yeast *Saccharomyces cerevisiae* is the most important of all cultured fungi (see Figure 31.7). It is available as many strains of baker's yeast and brewer's yeast.

Many fungi have great medical value as well. For example, a compound extracted from ergots is used to reduce high blood pressure and to stop maternal bleeding after childbirth. Some fungi produce antibiotics that are effective in treating bacterial infections. In fact, the first antibiotic discovered was penicillin, made by the ascomycete mold *Penicillium* **(Figure 31.27)**. Other examples of pharmaceuticals derived from fungi include cholesterol-lowering drugs and cyclosporine, a drug used to suppress the immune system after organ transplants.

Fungi also figure prominently in research. For example, the yeast *Saccharomyces cerevisiae* is used to study the molecular genetics of eukaryotes because its cells are easy to culture and manipulate. Scientists are gaining insight into the genes involved in Parkinson's disease and other human diseases by examining the functions of homologous genes in *S. cerevisiae*.



▲ **Figure 31.27 Fungal production of an antibiotic.** The mold *Penicillium* produces an antibiotic (penicillin) that inhibits the growth of *Staphylococcus* bacteria, resulting in the clear area between the mold and the bacteria.

Genetically modified fungi hold much promise. Although bacteria such as *Escherichia coli* can produce some useful proteins, they cannot synthesize glycoproteins because they lack enzymes that can attach carbohydrates to proteins. Fungi, on the other hand, do produce such enzymes. In 2003, scientists succeeded in engineering a strain of *S. cerevisiae* that produces human glycoproteins, including insulin-like growth factor. Such fungus-produced glycoproteins have the potential to treat people with medical conditions that prevent them from producing these compounds. Meanwhile, other researchers are sequencing the genome of the wood-digesting basidiomycete *Phanerochaete chrysosporium*, one of many "white rot" fungi. They hope to decipher the metabolic pathways by which white rot breaks down wood, with the goal of harnessing these pathways to produce paper pulp.

Having now completed our survey of the kingdom Fungi, we will turn in the remaining chapters of this unit to the closely related kingdom Animalia, to which we humans belong.

CONCEPT CHECK 31.5

1. What are some of the benefits that lichen algae can derive from their relationship with fungi?
2. What characteristics of pathogenic fungi result in their being efficiently transmitted?
3. **WHAT IF?** How might life on Earth differ from what we know today if no mutualistic relationships between fungi and other organisms had ever evolved?

For suggested answers, see Appendix A.

31 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 31.1

Fungi are heterotrophs that feed by absorption (pp. 636–638)

- All **fungi** (including decomposers and symbionts) are heterotrophs that acquire nutrients by absorption. Many fungi secrete enzymes that break down complex molecules to smaller molecules that can be absorbed.
- Most fungi grow as thin, multicellular filaments called **hyphae**; relatively few species grow only as single-celled **yeasts**. In their multicellular form, fungi consist of **mycelia**, networks of branched hyphae adapted for absorption. Mycorrhizal fungi have specialized hyphae that enable them to form a mutually beneficial relationship with plants.

? *How does the morphology of multicellular fungi affect the efficiency of nutrient absorption?*

CONCEPT 31.2

Fungi produce spores through sexual or asexual life cycles (pp. 638–640)

- The sexual cycle involves cytoplasmic fusion (**plasmogamy**) and nuclear fusion (**karyogamy**), with an intervening heterokaryotic stage in which cells have haploid nuclei from two parents. The diploid cells resulting from karyogamy are short-lived and undergo meiosis, producing haploid **spores**.
- Many fungi can reproduce asexually as filamentous fungi or yeasts. DNA sequence data now allow mycologists to classify all fungi, even those lacking a known sexual cycle.

DRAW IT *Draw a fungal life cycle, labeling asexual and sexual reproduction, meiosis, plasmogamy, karyogamy, and the points in the cycle when spores and the zygote are produced.*

CONCEPT 31.3

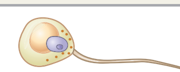
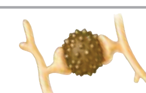
The ancestor of fungi was an aquatic, single-celled, flagellated protist (pp. 640–641)

- Molecular evidence supports the hypothesis that fungi and animals diverged from a common ancestor that was unicellular and had a flagellum.
- Unicellular parasites called microsporidia appear to be an early-diverging fungal lineage.
- Fungi were among the earliest colonizers of land, including species that were symbionts with early land plants.

? *Did multicellularity originate independently in fungi and animals? Explain.*

CONCEPT 31.4

Fungi have radiated into a diverse set of lineages (pp. 641–648)

Fungal Phylum	Distinguishing Features of Morphology and Life Cycles	
Chytridiomycota **(chytrids)**	Flagellated spores	
Zygomycota **(zygote fungi)**	Resistant zygosporangium as sexual stage	
Glomeromycota **(arbuscular mycorrhizal fungi)**	Arbuscular mycorrhizae formed with plants	
Ascomycota (**ascomycetes**, or **sac fungi**)	Sexual spores (ascospores) borne internally in sacs called asci; vast numbers of asexual spores (conidia) produced	
Basidiomycota **(basidiomycetes**, or **club fungi**)	Elaborate fruiting body (basidiocarp) containing many basidia that produce sexual spores (basidiospores)	

DRAW IT *Draw a phylogenetic tree showing relationships among the five major groups of fungi.*

CONCEPT 31.5

Fungi play key roles in nutrient cycling, ecological interactions, and human welfare (pp. 648–652)

- Fungi perform essential recycling of chemical elements between the living and nonliving world.
- Some **endophytes** help protect plants from herbivores and pathogens, while other fungi help certain animals digest plant tissue. **Lichens** are highly integrated symbiotic associations of fungi and algae or cyanobacteria.
- About 30% of all known fungal species are parasites, mostly of plants. Some fungi also cause disease in animals.
- Humans eat many fungi and use others to make cheeses, alcoholic beverages, and bread. Antibiotics produced by fungi treat bacterial infections. Genetic research on fungi is leading to applications in biotechnology.

? *Summarize how fungi are important as decomposers, mutualists, and pathogens.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. *All* fungi share which of the following characteristics?
   a. symbiotic
   b. heterotrophic
   c. flagellated
   d. pathogenic
   e. act as decomposers

2. Which feature seen in chytrids supports the hypothesis that they diverged earliest in fungal evolution?
   a. the absence of chitin within the cell wall
   b. coenocytic hyphae
   c. flagellated spores
   d. formation of resistant zygosporangia
   e. parasitic lifestyle

3. Which of the following cells or structures are associated with *asexual* reproduction in fungi?
   a. ascospores
   b. basidiospores
   c. zygosporangia
   d. conidiophores
   e. ascocarps

4. The photosynthetic symbiont of a lichen is often
   a. a moss.
   b. a green alga.
   c. a brown alga.
   d. an ascomycete.
   e. a small vascular plant.

5. Among the organisms listed here, which are thought to be the closest relatives of fungi?
   a. animals
   b. vascular plants
   c. mosses
   d. brown algae
   e. slime molds

LEVEL 2: APPLICATION/ANALYSIS

6. The adaptive advantage associated with the filamentous nature of fungal mycelia is primarily related to
   a. the ability to form haustoria and parasitize other organisms.
   b. avoiding sexual reproduction until the environment changes.
   c. the potential to inhabit almost all terrestrial habitats.
   d. the increased probability of contact between different mating types.
   e. an extensive surface area well suited for invasive growth and absorptive nutrition.

7. **SCIENTIFIC INQUIRY**
   DRAW IT The grass *Dichanthelium languinosum* lives in hot soils and houses fungi of the genus *Curvularia* as endophytes. Regina Redman, of Montana State University, and colleagues performed field experiments to test the impact of *Curvularia* on the heat tolerance of this grass. They grew plants without (E−) and with (E+) *Curvularia* endophytes in soils of different temperatures and measured plant mass and the number of new shoots the plants produced. Draw a bar graph of the results for plant mass versus temperature and interpret it.

Soil Temp.	*Curvularia* Presence	Plant Mass (g)	Number of New Shoots
30°C	E−	16.2	32
	E+	22.8	60
35°C	E−	21.7	43
	E+	28.4	60
40°C	E−	8.8	10
	E+	22.2	37
45°C	E−	0	0
	E+	15.1	24

Source: R. S. Redman et al., Thermotolerance generated by plant/fungal symbiosis, *Science* 298:1581 (2002).

LEVEL 3: SYNTHESIS/EVALUATION

8. **EVOLUTION CONNECTION**
   The fungus-alga symbiosis that makes up a lichen is thought to have evolved multiple times independently in different fungal groups. However, lichens fall into three well-defined growth forms (see Figure 31.23). What research could you perform to test the following hypotheses?

   Hypothesis 1: Crustose, foliose, and fruticose lichens each represent a monophyletic group.

   Hypothesis 2: Each lichen growth form represents convergent evolution by taxonomically diverse fungi.

9. **WRITE ABOUT A THEME**
   Emergent Properties As you read in this chapter, fungi have long formed symbiotic associations with plants and with algae. In a short essay (100–150 words), describe how these two types of associations may lead to emergent properties in biological communities.

For selected answers, see Appendix A.