The mushroom-forming fungus *Inocybe fastigiata,* a forest-dwelling species that commonly lives in close association with conifers and hardwood trees.

Fritz Polking/Peter Arnold, Inc.

28 Fungi

STUDY PLAN

28.1 General Characteristics of Fungi
- Fungi may be single-celled or multicellular
- Fungi obtain nutrients by extracellular digestion and absorption
- All fungi reproduce by way of spores, but other aspects of reproduction vary

28.2 Major Groups of Fungi
- Fungi were present on Earth by at least 500 million years ago
- Once they appeared, fungi radiated into at least five major lineages
- Chytrids produce motile spores that have flagella
- Zygomycetes form zygospores for sexual reproduction
- Glomeromycetes form spores at the ends of hyphae
- Ascomycetes, the sac fungi, produce sexual spores in saclike asci
- Basidiomycetes, the club fungi, form sexual spores in club-shaped basidia
- Conidial fungi are species for which no sexual phase is known
- Microsporidia are single-celled sporelike parasites

28.3 Fungal Associations
- A lichen is an association between a fungus and a photosynthetic partner
- Mycorrhizae are symbiotic associations of fungi and plant roots

WHY IT MATTERS

In a forest, decay is everywhere—rotting leaves, moldering branches, perhaps the disintegrating carcass of an insect or a small mammal. Each year in most terrestrial ecosystems, an astounding amount of organic matter is produced, cast off, broken down, and its elements gradually recycled. This recycling has a huge impact on world ecosystems; for example, each year it returns at least 85 billion tons of carbon, in the form of carbon dioxide, to the atmosphere. Chief among the recyclers are the curious organisms of the **Kingdom Fungi**—about 60,000 described species of molds, mushroom-forming fungi, yeasts, and their relatives **(Figure 28.1),** and an estimated 1.6 million more that are yet to be described.

Fungi are eukaryotes, most are multicellular, and all are heterotrophs, obtaining their nutrients by breaking down organic molecules that other organisms have synthesized. Molecular evidence suggests that fungi were present on land at least 500 million years ago, and possibly much earlier. In the course of the intervening millennia, evolution equipped fungi with a remarkable ability to break down organic matter, ranging from living and dead organisms and animal wastes to your groceries, clothing, paper and wood, even photographic

Sulfur shelf fungus, *Polyporus*

Big laughing mushroom, *Gymnopilus*

Baker's yeast cells, *Saccharomyces cerevisiae*

Robert C. Simpson/Nature Stock

Robert C. Simpson/Nature Stock

SciMAT/Photo Researchers, Inc.

Figure 28.1
Examples of fungi that hint at the rich diversity within the Kingdom Fungi.

film. Along with heterotrophic bacteria, they have become Earth's premier decomposers.

Fungi collectively also are the single greatest cause of plant diseases, and a host of species cause disease in humans and other animals. Some even produce carcinogenic toxins. On the other hand, 90% of plants obtain needed minerals by way of a symbiotic relationship with a fungus. Humans have harnessed the metabolic activities of certain fungi to obtain substances ranging from flavorful cheeses and wine to therapeutic drugs such as penicillin and the immunosuppressant cyclosporin. And, as you know from previous chapters, species such as the yeast *Saccharomyces cerevisiae* and the mold *Neurospora crassa* have long been pivotal model organisms in studies of DNA structure and function, and the yeast has also been important in the development of genetic engineering methods.

Despite their profound impact on ecosystems and other life forms, most of us have only a passing acquaintance with the fungi—perhaps limited to the mushrooms on our pizza or the invisible but annoying types that cause skin infections like athlete's foot. This chapter provides you with an introduction to mycology, the study of fungi (*mykes* = mushroom; *logos* = knowledge). We begin with general characteristics of this kingdom and then discuss its major divisions.

28.1 General Characteristics of Fungi

We begin our survey of fungi by examining how fungi differ from other forms of life, how fungi obtain nutrients, and the adaptations for reproduction and growth that enable fungi to spread far and wide through the environment.

Fungi May Be Single-Celled or Multicellular

Two basic body forms, single-celled and multicellular, emerged as the lineages of fungi evolved. Some fungi are single cells, a form called **yeast,** while others exist in a multicellular form made up of threadlike filaments. Still others alternate between yeast and multicellular forms at different stages of the life cycle. Whether a fungus is single-celled or multicellular, a rigid wall usually surrounds the plasma membrane of its cells. Generally the polysaccharide **chitin** provides this rigidity, the same function it serves in the external skeletons of insects and other arthropods.

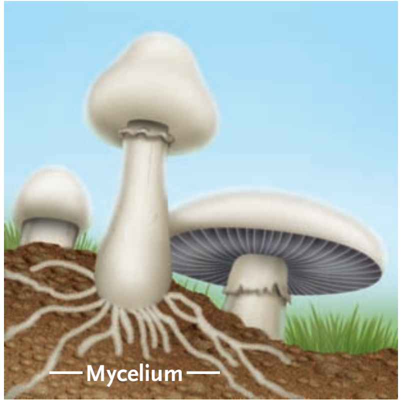
In a multicellular fungus, exploiting food sources is the province of a cottony mesh of tiny filaments that branch repeatedly as they grow over or into organic matter. Each filament is a **hypha** (*hyphe* = web; plural, hyphae); the combined mass of hyphae is a **mycelium** (plural, mycelia). Hyphae generally are tube-shaped **(Figure 28.2).** In most multicellular fungi the hyphae are partitioned by cross walls called **septa** (*saeptum* = partition; singular, septum). The septa create cell-like compartments that contain organelles. However, in one group, the zygomycetes described shortly, most hyphae are *aseptate*—they lack cross walls—although septa do arise to separate reproductive structures from the rest of the hypha.

The unusual features of fungal hyphae have led many mycologists to question whether "multicellular" is really an accurate description for most fungal architecture. For instance, depending on the species, hyphal cells may have more than one nucleus, and septa have pores that permit nuclei and other organelles to move between hyphal cells. These passages also allow cytoplasm to extend from one hyphal cell to the next, throughout the whole mycelium. By a mechanism called **cytoplasmic streaming,** cytoplasm containing nutrients can flow unimpeded through the hyphae, from food-absorbing parts of the fungal body to other, nonabsorptive parts such as reproductive structures.

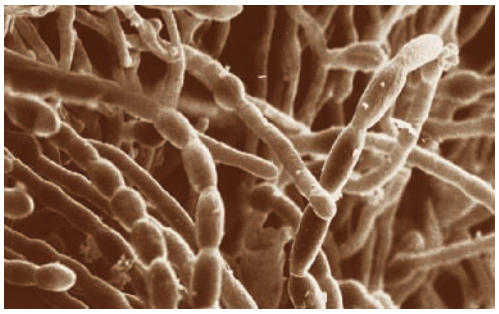
A multicellular fungus grows larger as its hyphae elongate and branch. Each hypha elongates at its tip as new wall polymers (delivered by vesicles) are incorporated and additional cytoplasm, including organelles, is synthesized. A hypha branches a few micrometers behind its tip, and as the new hyphae elongate, then branch themselves, an extensive mycelium can form quickly. Each forming branch fills with cytoplasm that includes new nuclei produced by mitosis. Although the rapid branching of hyphae is what allows multicellular fungi to grow aggressively—sometimes increasing in mass many times over within a few days—researchers have only recently gained the tools to explore the mechanisms that underlie this phenomenon. Studies spurred by the sequencing of the genome of *Neurospora crassa* suggest that multiple steps involving a variety of genes and their interacting protein products determine where and when a new branch arises. Given that the rapid growth of fungal mycelia has such a tremendous impact in nature, fungal diseases, and many other areas, this topic is a central focus of much mycological research.

Beyond their role in nutrient transport, aggregations of hyphae are the structural foundation for all other parts that arise as a multicellular fungus develops. For example, in many fungi a subset of hyphae interweave tightly, becoming prominent reproductive structures (sometimes called fruiting bodies). Grocery store mushrooms are examples. But while a mushroom or some analogous structure may be the most conspicuous part of a given fungus, it usually represents only a small fraction of the organism's total mass. The rest penetrates the food source the fungus is slowly digesting. In some fungi, modified hyphae called **rhizoids** anchor the fungus to its substrate. Most fungi that parasitize living plants produce hyphal branches called **haustoria** (*haustor* = drinker) that penetrate the walls of a host plant's cells and channel nutrients back to the fungal body.

a. Multicellular fungus



b. Fungal hyphae



Garry T. Cole, University of Texas, Austin/BPS

Figure 28.2 Fungal mycelia. **(a)** Sketch of the mycelium of a mushroom-forming fungus, which consists of branching septate hyphae. **(b)** Micrograph of fungal hyphae.

Fungi Obtain Nutrients by Extracellular Digestion and Absorption

Some major challenges have shaped the adaptations by which fungi obtain nutrients. As heterotrophs, fungi must secure nutrients by breaking down organic substances formed by other organisms. Nearly all fungi are terrestrial, but unlike other land-dwelling heterotrophs (such as animals), fungi are not mobile. They also lack mouths or appendages for seizing, handling, and dismantling food items. Instead, fungi have a very different suite of adaptations for obtaining nutrients.

To begin with, most species of fungi can synthesize nearly all their required nutrients from a few raw materials, including water, some minerals and vitamins (especially B vitamins), and a sugar or some other organic carbon source. For many species, carbohydrates in dead organic matter are the carbon sources, and fungi with this mode of nutrition are called **saprobes** (*sapros* = rotten). Other fungi are parasites, which extract carbohydrates from tissues of a living host, harming it in the process. Parasitic fungi include those responsible for many devastating plant diseases, such as wheat rust and Dutch elm disease. Still other fungi are nourished by plants with which they have a mutually beneficial symbiotic association.

Regardless of their nutritional mode, all fungi gain the raw materials required to build and maintain their cells by absorption from the environment. Fungi can absorb many small molecules directly from their surroundings, and gain access to other nutrients through extracellular digestion. In this process, a fungus releases enzymes that digest nearby organic matter, breaking down larger molecules into absorbable fragments. Fungal species differ in the particular digestive enzymes they synthesize, so a substrate that is a suitable food source for one species may be unavailable to another. Although there are exceptions, fungi typically thrive only in moist environments where they can directly absorb water, dissolved ions, simple sugars, amino acids, and other small molecules. When some of a mycelium's hyphal filaments contact a source of food, growth is channeled in the direction of the food source. Nutrients are absorbed only at the porous tips of hyphae; small atoms and molecules pass readily through these tips, and then transport mechanisms move them through the underlying plasma membrane.

Large organic molecules, such as the carbohydrate cellulose (see Section 3.3), *cannot* directly enter any part of a fungus. To use such substances as a food source, a fungus must secrete hydrolytic enzymes that break down the large molecules into smaller, absorbable subunits. Depending on the size of the subunit, further digestion may occur inside cells.

With their adaptations for efficient extracellular digestion, fungi are masters of the decay so vital to terrestrial ecosystems. For instance, in a single autumn one elm tree can shed 400 pounds of withered leaves; and in a tropical forest, a year's worth of debris may total 60 tons per acre. Without the metabolic activities of saprobic fungi and other decomposers such as bacteria, natural communities would rapidly become buried in their own detritus. As fungi digest dead tissues of other organisms, they also make a major contribution to the recycling of chemical elements those tissues contain. For instance, over time the degradation of organic compounds by saprobic fungi helps return key nutrients such as nitrogen and phosphorus to ecosystems. But the prime example of this recycling virtuosity involves carbon. The respiring cells of fungi and other decomposers give off carbon dioxide, liberating carbon that would otherwise remain locked in the tissues of dead organisms. Each year this activity recycles a vast amount of carbon to plants, the primary producers of nearly all ecosystems on Earth.

All Fungi Reproduce by Way of Spores, but Other Aspects of Reproduction Vary

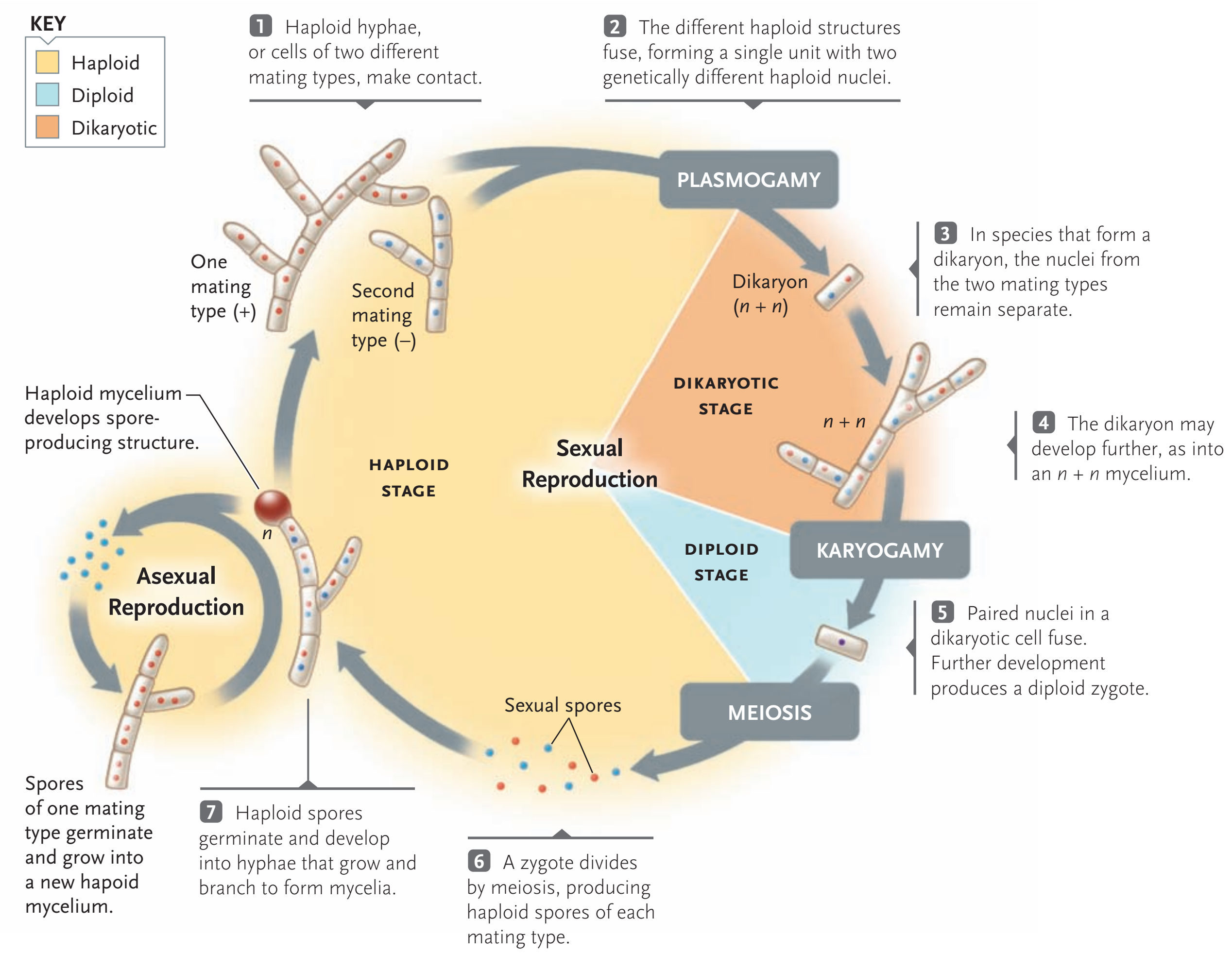
Biologists have observed a striking number of reproductive variations in fungi, differences that are part of what makes them fascinating to study. As you will learn in the next section, fungi have traditionally been classified on the basis of their reproductive characteristics, although today evidence from molecular analysis also plays a prominent role.

Overall, most fungi have the capacity to reproduce both sexually and asexually. Although no single diagram can depict all the variations, **Figure 28.3** gives an overview of the life cycle stages that mycologists have observed in several groups of fungi. The figure illustrates two general points. First, the life cycle of multicellular fungi typically involves a diploid stage ($2n$), a haploid stage (n), and a dikaryotic ("two nuclei") stage in which the fungus forms hyphae (and a mycelium) that are $n + n$—neither strictly haploid *nor* diploid. Depending on the type of fungus, this stage may be long lasting or extremely brief, and it is described more fully later in this section. Second, all fungi, whether they are multicellular or in a single-celled, yeast form, can reproduce via **fungal spores.** The spores are microscopic, and in all but one group they are not motile—that is, they are not propelled by flagella. Each spore is a walled single cell or multicellular structure that is dispersed from the parent body, often via wind or water. The spores of single-celled fungi form inside the parent cell, then escape when the wall breaks open. In multicellular fungi, spores arise in or on specialized hyphal structures and may develop thick walls that help them withstand cold or drying out after they are released.

Reproduction by way of spores is one of the crucial fungal adaptations. Most fungi are opportunists, obtaining energy by exploiting food sources that occur unpredictably in the environment. Having lightweight spores that are easily disseminated by air or water increases opportunities for finding food. And releasing vast numbers of spores, as some fungi do, improves the odds that at least a few spores will germinate and produce a new individual.

In nature generally, opportunistic organisms are adapted to reach new food sources quickly and utilize them rapidly. Fungi that are adept at degrading simple sugars and starches often are among the first decomposers to exploit a new source of food. They meet with keen competition from each other and from other decomposers. However, once fungal spores encounter potential food and favorable conditions, they can quickly develop into new individuals that simultaneously feed and rapidly make more spores.

Many opportunistic fungi develop rapidly, growing and reproducing before the food source is depleted. A common trade-off for speed, however, is small, even microscopic body size. Larger species of fungi are often adapted to move in later, exploiting food sources such as cellulose and lignin (a complex polymer in the walls of many plant cells), which their predecessors may have lacked the enzymatic machinery to digest efficiently. Some of these fungi may produce huge mycelia (and reproductive "fruiting bodies" such as mushrooms) by extracting nutrients from dead trees that



1 Haploid hyphae, or cells of two different mating types, make contact.

2 The different haploid structures fuse, forming a single unit with two genetically different haploid nuclei.

3 In species that form a dikaryon, the nuclei from the two mating types remain separate.

4 The dikaryon may develop further, as into an $n + n$ mycelium.

5 Paired nuclei in a dikaryotic cell fuse. Further development produces a diploid zygote.

6 A zygote divides by meiosis, producing haploid spores of each mating type.

7 Haploid spores germinate and develop into hyphae that grow and branch to form mycelia.

Figure 28.3
Generalized life cycle for many fungi. Overall, fungi are diploid for only a short time. The duration of the dikaryon stage varies considerably, being lengthy for some species and extremely brief in others. Some types of fungi reproduce only asexually while in others shifts in environmental factors, such as the availability of key nutrients, can trigger a shift from asexual to sexual reproduction or vice versa. For still others sexual reproduction is the norm.

contain enough organic material to sustain an extended period of growth.

Features of Asexual Reproduction in Fungi. When a fungus produces spores asexually (see Figure 28.3), it may disperse billions of them into the environment. Some fungi (including many yeasts) also can reproduce asexually by budding or fission, or, in multicellular types, when fragments of hyphae break away from the mycelium and grow into separate individuals. In still others, environmental factors may determine whether the fungus produces hyphal fragments *or* asexual spores. These asexual reproductive strategies all result in new individuals that are essentially clones of the parent fungus. They can be viewed as another adaptation for speed, because the alternative—sexual reproduction—requires the presence of a suitable partner and generally involves several more steps.

The asexual stage of many multicellular fungi—including the pale gray fuzz you might see on berries or bread—is often called a **mold.** The term can be confusing if you are attempting to keep track of taxonomic groupings; for example, the water molds and slime molds described in Chapter 26 are protists, although they were grouped with fungi until additional research revealed their true evolutionary standing. The mold visible on an overripe raspberry is actually a mycelium with aerial structures bearing sacs of haploid spores at their tips.

Features of Sexual Reproduction in Fungi. Although asexual reproduction is the norm, quite a few fungi shift to sexual reproduction when environmental conditions (such as a lack of nitrogen) or other influences dictate. As you may remember from Chapter 11, in sexual reproduction two haploid cells unite, and in most species fertilization—the fusion of two gamete nuclei to form a diploid zygote nucleus—soon follows. In fungi, however, the partners in sexual union can be two hyphae, two gametes, or other types of cells; the particular combination depends on the species involved. And in sharp contrast to other life forms, many days, months, or even years may pass between the time fertilization gets underway and when it is completed.

During the initial sexual stage, called **plasmogamy** (*plasma* = a formed thing; *gamos* = union), the cytoplasms of two genetically different partners fuse. The resulting new cell, a **dikaryon** (*di* = two; *karyon* = nucleus), contains two haploid nuclei, one from each parent. A dikaryon itself is not haploid (the condition of having one set of chromosomes) because it contains two nuclei. But neither is it diploid, because the nuclei are not fused. So, to be precise, we say that a dikaryon has an $n + n$ nuclear condition.

Plasmogamy can occur when hyphal cells of two different **mating type**, termed plus (+) and minus (−), fuse, a process that occurs in most fungi. The uniting hyphae belong to mycelia of different individuals of the same species that happen to grow near one another. The fusion of different mating types ensures genetic diversity in new individuals.

Once a dikaryon forms, the amount of time that elapses before the next stage begins depends on the type of fungus, as described in the next section. Sooner or later, however, a second phase of fertilization unfolds: The nuclei in the dikaryotic cell fuse to make a $2n$ zygote nucleus. This process is called **karyogamy** ("nuclear union"); in fungi that form mushrooms, it occurs in the tips of hyphae that end in the gills, which you may be able to see if you look closely at the underside of a mushroom cap (see Figure 28.1). In animals, a zygote is the first cell of a new individual, but in the world of fungi the zygote has a different fate. After it forms, meiosis converts the zygote nucleus into four haploid (n) nuclei. Those nuclei are packaged into haploid "sexual spores," which vary genetically from each parent. Then the spores are released to spread throughout the environment.

To sum up, in fungi both asexual and sexual spores are haploid, and both can germinate into haploid individuals. However, asexual spores are genetically identical products of asexual reproduction, while sexual spores are genetically varied products of sexual reproduction. We turn now to current ideas on the evolutionary history of fungi, and a survey of the major taxonomic groups in this kingdom.

STUDY BREAK

1. What features distinguish the two basic fungal body forms?
2. What is a fungal spore, and how does it function in reproduction?
3. Fungi reproduce sexually or asexually, but for many species the life cycle includes an unusual stage not seen in other organisms. What is this genetic condition, and what is its role in the life cycle?

28.2 Major Groups of Fungi

The evolutionary origins and lineages of fungi have been obscure ever since the first mycologists began puzzling over the characteristics of this group. With the advent of molecular techniques for research, these topics have become extremely active and exciting areas of biological research that may shed light on fundamental events in the evolution of all eukaryotes. Not surprisingly when so much new information is coming to light, mycologists hold a wide range of views on how different groups arose and may be related. Even so, there is wide agreement on five phyla of fungi, known formally as the Chytridiomycota, Zygomycota, Glomeromycota, Ascomycota, and Basidiomycota **(Figure 28.4).**

In a sixth group, termed conidial fungi, asexual reproduction produces spores called conidia. "Conidial" is not a true taxonomic classification, however. Rather, it serves as a holding station for fungal species that have not yet been assigned to one of the five phyla because no sexual reproductive phase has been observed. This is another instance in which the name for a fungal group can be confusing, because numerous species belonging to the Zygomycota, Ascomycota, and Basidiomycota also form conidia as part of their asexual reproductive cycle.

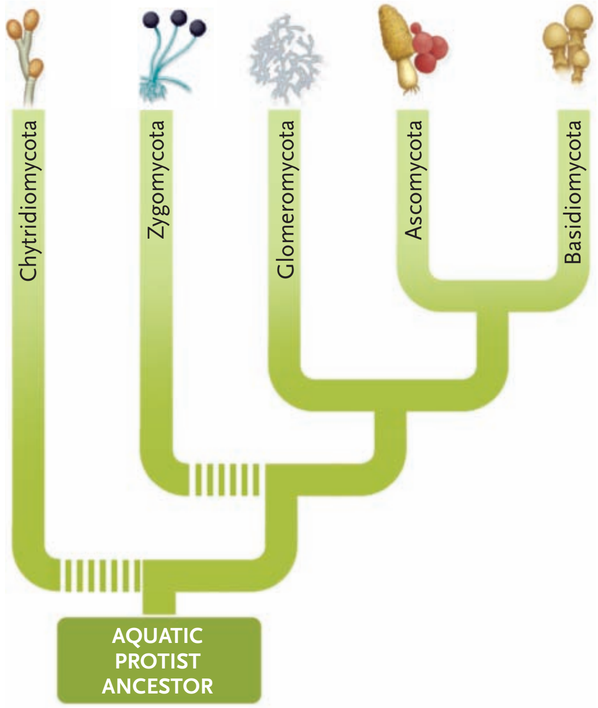


Figure 28.4

A phylogeny of fungi. This scheme represents a widely accepted view of the general relationships between major groups of fungi, but it may well be revised as new molecular findings provide more information. The dashed lines indicate that two groups, the chytrids and zygomycetes, are probably paraphyletic—they include subgroups that are not all descended from a single ancestor.

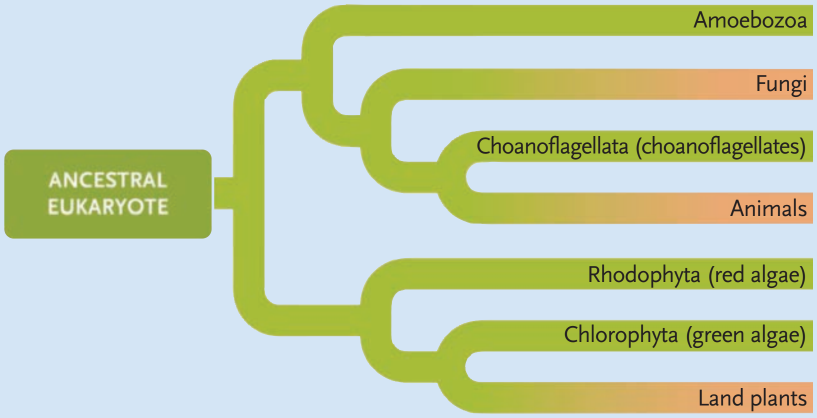
Insights from the Molecular Revolution

There Was Probably a Fungus among Us

The relationships of the fungi to protists, plants, and animals are buried so far back in evolutionary history that they have proved difficult to reconstruct. On the basis of morphological comparisons, for a long time taxonomists classified fungi as more closely related to the protists or plants than to animals. However, an investigation of ribosomal RNA (rRNA) sequences led to the conclusion that fungi and animals are more closely related to each other than either group is to protists or plants.

Patricia O. Wainwright, Gregory Hinkle, Mitchell L. Sogin, and Shawn K. Stickel of Rutgers University and the Woods Hole Marine Biology Laboratory carried out the analysis by comparing sequences of 18S rRNA, an rRNA molecule that forms part of the small ribosomal subunit in eukaryotes (see Section 15.4). The investigators began their work by sequencing the 18S rRNA molecules of species among the sponges, ctenophores, and cnidarians (see Chapter 29), which had never been sequenced before. These sequences were then compared with the 18S rRNA sequences of fungi, plants, and several protists, including protozoans and algae, which had been previously obtained by others. For the comparisons, the investigators used a computer program that sorts the rRNA sequences into related groups under the assumption that species with the greatest similarities in 18S rRNA sequence are most closely related. The sequence information was entered into the program in several different combinations; each time the analysis came up with the same family tree (see **figure**).

The family tree placed animals as the branch most closely related to fungi, and indicates that the two groups share a common ancestor not shared with any of the other groups. Other investigators have cited similarities in biochemical pathways in fungi and animals, such as pathways that make the amino acid hydroxyproline, the protein ferritin (which combines with iron atoms), and the polysaccharide chitin, which is a primary constituent of both fungal cell walls and arthropod exoskeletons. Studies of fungi called chytrids (p. 612) also are providing provocative insights on this topic.



Finally, we will briefly consider a particular odd group of single-celled parasites called **microsporidia.** Based on genetic studies, many mycologists believe they make up a possible sixth phylum within the Kingdom Fungi.

Fungi Were Present on Earth by at Least 500 Million Years Ago

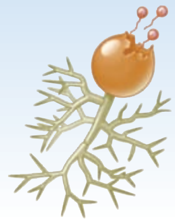
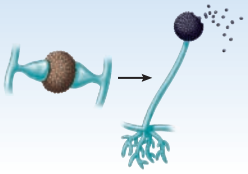
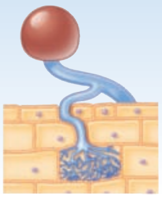
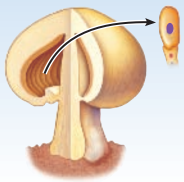
Many fungi look plantlike, and for many years fungi were classified as plants. As biologists learned more about the distinctive characteristics of fungi, however, it became clear that fungi merited a separate kingdom. The discovery of chitin in fungal cells, and recent comparisons of DNA and RNA sequences, all indicate that fungi and animals are more closely related to each other than they are to other eukaryotes (see *Insights from the Molecular Revolution*). Analysis of the sequences of several genes suggests that the lineages leading to animals and fungi may have diverged around 965 million years ago. Whenever the split developed, phylogenetic studies indicate that fungi first arose from a single-celled, flagellated protist—the sort of organism that does not fossilize well. Although traces of what may be fossil fungi exist in rock formations nearly 1 billion years old, the oldest fossils that we can confidently assign to the modern Kingdom Fungi appear in rock strata laid down about 500 million years ago.

Once They Appeared, Fungi Radiated into at Least Five Major Lineages

Most likely, the first fungi were aquatic. When other kinds of organisms began to colonize land, they may well have brought fungi along with them. For example, researchers have discovered what appear to be mycorrhizae—symbiotic associations of a fungus and a plant—in fossils of the some of the earliest known land plants (see Chapter 27). The final section of this chapter examines the nature of mycorrhizae more fully.

Over time, fungi diverged into the strikingly diverse lineages that we consider in the rest of this section **(Table 28.1).** As the lineages diversified, different adaptations associated with reproduction arose. For this reason, mycologists traditionally assigned fungi to

Table 28.1 Summary of Fungal Phyla

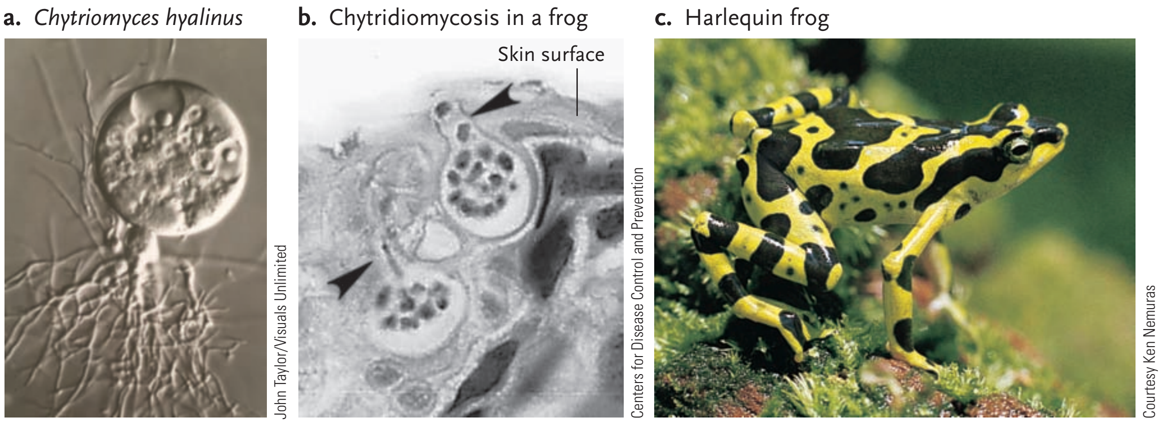
Phylum	Body Type	Key Feature	
Chytridiomycota (chytrids)	One to several cells	Motile spores propelled by flagella; usually asexual	
Zygomycota (zygomycetes)	Hyphal	Sexual stage in which a resistant zygospore forms for later germination	
Glomeromycota (glomeromycetes)	Hyphal	Hyphae associated with plant roots, forming arbuscular mycorrhizae	
Ascomycota (ascomycetes)	Hyphal	Sexual spores produced in sacs called asci	
Basidiomycota (basidiomycetes)	Hyphal	Sexual spores (basidiospores) form in basidia of a prominent fruiting body (basidiocarp)	

phyla according to the type of structure that houses the final stages of sexual reproduction and releases sexual spores. These features can still be useful indicators of the phylogenetic standing of a fungus, although now the powerful tools of molecular analysis are bringing many revisions to our understanding of the evolutionary journey of fungi. Our survey begins with chytrids, which probably most closely resemble the fungal kingdom's most ancient ancestors.

Chytrids Produce Motile Spores That Have Flagella

The phylum Chytridiomycota includes about a thousand species, referred to simply as chytrids. Chytrids are the only fungi that produce motile spores, which swim by way of flagella. Nearly all chytrids are microscopic **(Figure 28.5a)**, and mycologists have recently begun paying significant attention to them, in part because their characteristics strongly suggest that the group arose near the beginning of fungal evolution. Another reason for research interest is the discovery that the chytrid *Batrachochytrium dendrobatis* is responsible for a disease epidemic that recently has wiped out an estimated two-thirds of the species of harlequin frogs *(Atelopus)* of the American tropics **(Figure 28.5b)**. The epidemic has correlated with the rising average temperature in the frogs' habitats, an increase credited to global warming. Studies show that the warmer environment provides optimal growing temperatures for the chytrid pathogen.

Most chytrids are aquatic, although a few live as saprobes in soil, feeding on decaying plant and animal matter; as parasites on insects, plants, and some animals or even as symbiotic partners in the gut of cattle


a. *Chytriomyces hyalinus*

John Taylor/Visuals Unlimited

b. Chytridiomycosis in a frog

Centers for Disease Control and Prevention

c. Harlequin frog

Courtesy Ken Nemuras

Figure 28.5
Chytrids. **(a)** *Chytriomyces hyalinus,* one of the few chytrids that reproduces sexually. **(b)** Chytridiomycosis, a fungal infection, shown here in the skin of a frog. The two arrows point to flask-shaped cells of the parasitic chytrid *Batrachochytrium dendrobatis,* which has devastated populations of harlequin frogs **(c)**.

and some other herbivores. Wherever a chytrid lives, reproduction requires at least a film of water through which the swimming spores can move.

A chytrid may advance though its entire life cycle within a matter of days, and for most species, much of this brief lifetime is spent in asexual reproduction. Although individuals initially exist as a vegetative (nonreproductive) phase, the fungus soon shifts into a reproductive mode. First, one or more spore-forming chambers called **sporangia** (*angeion* = vessel; singular, sporangium) develop, each containing one or more haploid nuclei. More developmental steps package the nuclei one by one in flagella-bearing spores. The spores are released to the environment through a pore or tube, and each swims briefly until it comes to rest on a substrate and a tough cyst forms around it. Under proper conditions, it will soon germinate and launch the life cycle anew.

A few chytrids reproduce sexually. Mycologists have observed a remarkable variety of sexual modes, but in all of them spores of different mating types unite. Karyogamy directly follows plasmogamy to produce a $2n$ zygote. This cell may form a mycelium that gives rise to sporangia, or it may directly give rise to either asexual or sexual spores.

Zygomycetes Form Zygospores for Sexual Reproduction

The phylum Zygomycota—fungi that reproduce sexually by way of structures called *zygospores*—contains fewer than a thousand species. What zygomycetes lack in numbers, however, they make up for in impact on other organisms. Many zygomycetes are saprobes that live in soil, feeding on plant detritus. There, their metabolic activities release mineral nutrients in forms that plant roots can take up. Some zygomycetes are parasites of insects (and even other zygomycetes), and some wreak havoc on human food supplies, spoiling stored grains, bread, fruits, and vegetables such as sweet potatoes. Others, however, have become major partners in commercial enterprises, where they are used in manufacturing products that range from industrial pigments to pharmaceuticals.

Most zygomycetes have aseptate hyphae, a feature that distinguishes them from the other multicellular fungi. Like other fungi, however, zygomycetes usually reproduce asexually, as shown at the lower left in **Figure 28.6.** When a haploid spore lands on a favorable substrate, it germinates and gives rise to a branching mycelium. Some of the hyphae grow upward, and saclike, thin-walled sporangia form at the tips of these aerial hyphae. Inside the sporangia the asexual cycle comes full circle as new haploid spores arise through mitosis and are released.

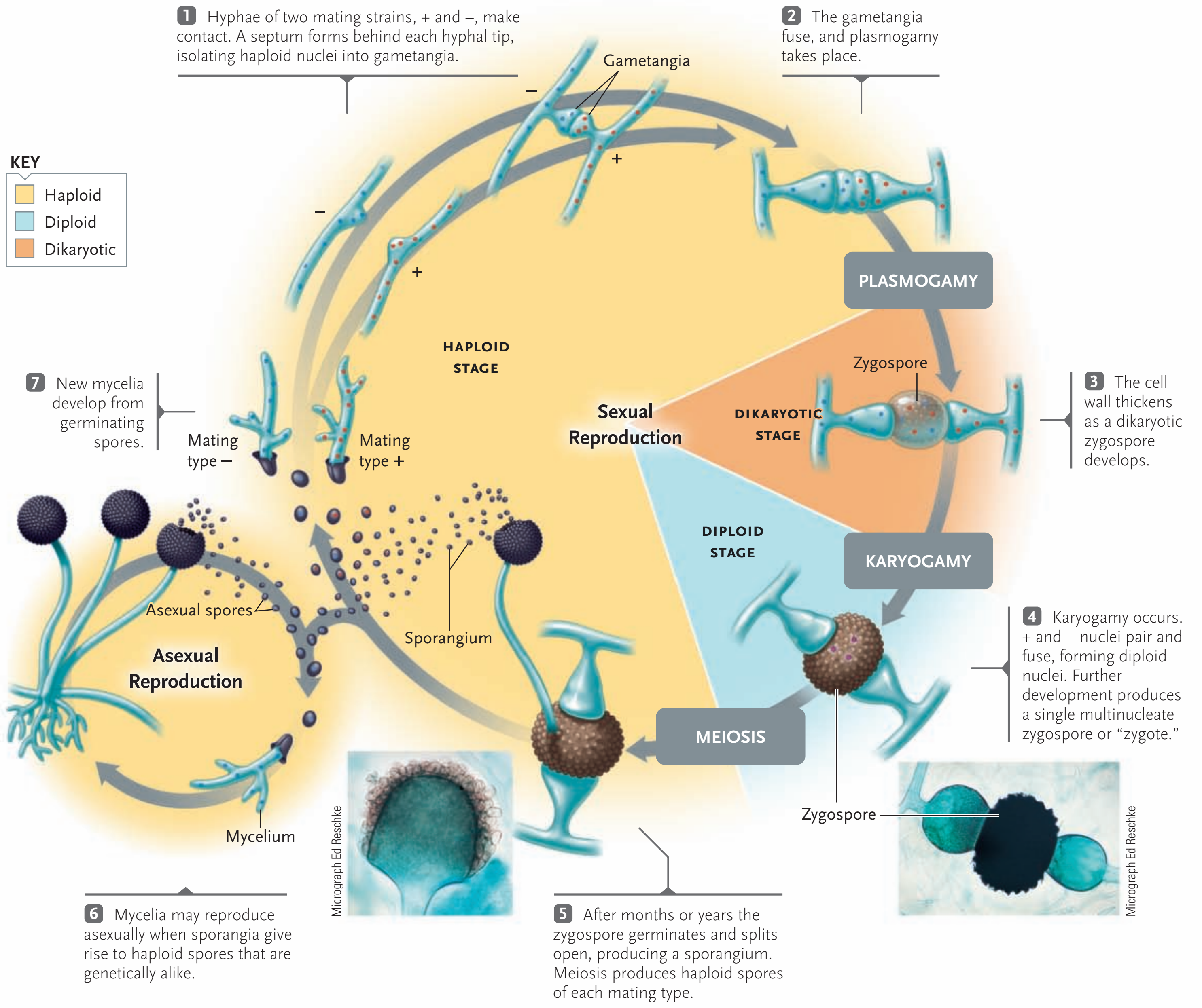
The black bread mold, *Rhizopus stolonifer,* may produce so many charcoal-colored sporangia **(Figure 28.7a)** that moldy bread looks black. The spores released are lightweight, dry, and readily wafted away by air currents. In fact, winds have dispersed *R. stolonifer* spores just about everywhere on Earth, including the Arctic. Another zygomycete, *Pilobolus* **(Figure 28.7b),** forcefully spews its sporangia away from the dung in which it grows. A grazing animal may eat a sporangium on a blade of grass; the spores then pass through the animal's gut unharmed and begin the life cycle again in a new dung pile.

Mycelia of many zygomycetes may occur in either the + or − mating type, and the nuclei of the different mating types are equivalent to gametes. Each strain secretes steroidlike hormones that can stimulate the development of sexual structures in the complementary strain and cause sexual hyphae to grow toward each other. When + and − hyphae come into close proximity, a septum forms behind the tip of each hypha, producing a terminal **gametangium** that contains several haploid nuclei (see Figure 28.6). When the gametangia of the two strains make contact, cellular enzymes digest the wall between them, yielding a single large, thin-walled cell that contains many nuclei from both parents. In other words, plasmogamy has occurred, and this new cell is a dikaryon. Gradually a second, inner wall forms, thickens, and hardens. This structure, with the multinucleate cell inside it, is a **zygospore,** the structure that gives this fungal group its scientific name. It becomes dormant and sometimes stays dormant for months or years.

Karyogamy follows plasmogamy, but the timing varies in different groups of zygomycetes. The exact trigger is unknown, but eventually the diploid zygospore ends its dormancy. The cell undergoes meiosis and produces a stalked sporangium (see Figure 28.6, step 5). The sporangium contains haploid spores of each mating type, which are released to the outside world. When a spore later germinates, it produces either a + or a − mycelium, and the sexual cycle can continue.

Zygomycetes that have aseptate hyphae are structurally simpler than the species in most other fungal groups. Although septa wall off the reproductive structures, in effect the branching mycelium of each fungus is a single, huge, multinucleate cell—the same body structure as found in some algae and certain protists. Because such zygomycetes have numerous nuclei in a common cytoplasm, these fungi are said to be **coenocytic,** which means "contained in a shared vessel." By contrast, in other fungal groups septa at least partially divide the hyphae into individual cells, which typically contain two or more nuclei.

Presumably, having hyphae that lack septa confers some selective advantages. One benefit may be that without septa to impede the flow, nutrients can move freely from the absorptive hyphal tips to other hyphae where reproductive parts develop. Hence the fungus may be able to reproduce faster.



1 Hyphae of two mating strains, + and –, make contact. A septum forms behind each hyphal tip, isolating haploid nuclei into gametangia.

2 The gametangia fuse, and plasmogamy takes place.

3 The cell wall thickens as a dikaryotic zygospore develops.

4 Karyogamy occurs. + and – nuclei pair and fuse, forming diploid nuclei. Further development produces a single multinucleate zygospore or "zygote."

5 After months or years the zygospore germinates and splits open, producing a sporangium. Meiosis produces haploid spores of each mating type.

6 Mycelia may reproduce asexually when sporangia give rise to haploid spores that are genetically alike.

7 New mycelia develop from germinating spores.

Figure 28.6
Life cycle of the bread mold *Rhizopus stolonifer*, a zygomycete. Asexual reproduction is common, but different mating types (+ and –) also reproduce sexually. In both cases, haploid spores form and give rise to new mycelia.

In zygomycetes, aggregations of "cooperating" hyphae may form body structures specialized for certain functions. However, such structures are more common in the three groups of more complex fungi that we consider next.

Glomeromycetes Form Spores at the Ends of Hyphae

The 160 known members of the phylum Glomeromycota are all specialized to form the associations called mycorrhizae with plant roots. It would be hard to overestimate their ecological impact, for Glomeromycota collectively make up roughly half of the fungi in soil and form mycorrhizae with an estimated 80% to 90% of all land plants. Virtually all glomeromycetes reproduce asexually, by way of spores that form at the tips of hyphae. The hyphae also secrete enzymes that allow them to enter plant roots, where their tips branch into treelike clusters. As you will read in the next section, the clusters, called arbuscules, nourish the fungus by taking up sugars from the plant and in return supply the plant roots with a steady supply of dissolved minerals from the surrounding soil.

Ascomycetes, the Sac Fungi, Produce Sexual Spores in Saclike Asci

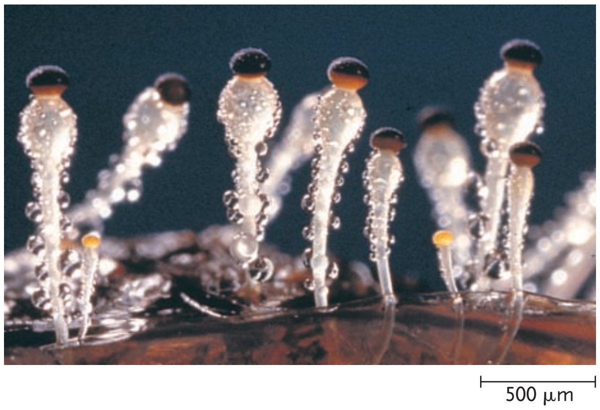
The phylum Ascomycota includes more than 30,000 species that produce reproductive structures called *asci* **(Figure 28.8).** A few ascomycetes prey upon various agricultural insect pests and thus have potential for use as "biological pesticides." Many more are destructive plant pathogens, including *Venturia inaequalis,* the fungus responsible for apple scab, and *Ophiostoma ulmi,* which causes Dutch elm disease. Several ascomycetes can be serious pathogens of humans. For example, *Claviceps purpurea,* a parasite on rye and other grains, causes ergotism, a disease marked by vomiting, hallucinations, convulsions, and in severe cases, gangrene and even death. Other ascomycetes cause nuisance infections such as athlete's foot and ringworm. Strains of *Aspergillus* grow in damp grain or peanuts; their metabolic wastes, known as aflatoxins, can cause cancer in humans who eat the poisoned food over an extended period. A few ascomycetes even show trapping behavior, ensnaring small worms that they then digest **(Figure 28.9a).** Yet some ascomycetes are valuable to humans: one species, the orange bread mold *Neurospora crassa,* has been important in genetic research, including the elucidation of the one gene–one enzyme hypothesis (see Section 15.1). And certain species of *Penicillium* **(Figure 28.9b)** are the source of the penicillin family of antibiotics, while others produce the aroma and distinctive flavors of Camembert and Roquefort cheeses. This multifaceted division also includes gourmet delicacies such as truffles *(Tuber melanosporum)* and the succulent true morel *Morchella esculenta.*

Although yeasts and filamentous fungi with a yeast stage in the life cycle occur in all fungal groups except chytrids, many of the best-known yeasts are ascomycetes. The yeast *Candida albicans* **(Figure 28.10)** infects mucous membranes, especially of the mouth (where it causes a disorder called thrush) and the vagina. *Saccharomyces cerevisiae,* which produces the ethanol in alcoholic beverages and the carbon dioxide

a. Sporangia of *Rhizopus stolonifer*

J. D. Cunningham/Visuals Unlimited

b. Sporangia (dark sacs) of *Pilobolus*



John Hodgin

Figure 28.7
Two of the numerous strategies for spore dispersal by zygomycetes. **(a)** The sporangia of *Rhizopus stolonifer,* shown here on a slice of bread, release powdery spores that are easily dispersed by air currents. **(b)** In *Pilobolus,* the spores are contained in a sporangium (the dark sac) at the end of a stalked structure. When incoming rays of sunlight strike a light-sensitive portion of the stalk, turgor pressure (pressure against a cell wall due to the movement of water into the cell) inside a vacuole in the swollen portion becomes so great that the entire sporangium may be ejected outward as far as 2 m—a remarkable feat, given that the stalk is only 5 to 10 mm tall.


a. Ascocarp

b. Asci

c. Asci within ascocarp

d. Morel

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Figure 28.8
A few of the ascomycetes, or sac fungi. The examples shown are multicellular species that form mushrooms as reproductive structures. **(a)** A cup-shaped ascocarp, composed of tightly interwoven hyphae. The spore-producing asci occur inside the cup. **(b)** Asci on the inner surface of an ascocarp. **(c)** Scarlet cup fungus *(Sarcoscypha).* **(d)** A true morel *(Morchella esculenta),* a prized edible fungus.

a. A penicillium species

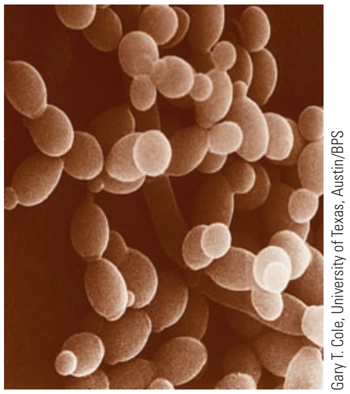
b. A trapping ascomycete

N. Allin and G. L. Barron

© Dennis Kunkel Microscopy, Inc.

Figure 28.9
Other ascomycete representatives. **(a)** *Eupenicillium.* Notice the rows of conidia (asexual spores) atop the structures that produce them. **(b)** Hyphae of *Arthrobotrys dactyloides,* a trapping ascomycete, form nooselike rings. When the fungus is stimulated by the presence of a prey organism, rapid changes in ion concentrations draw water into the hypha by osmosis. The increased turgor pressure shrinks the "hole" in the noose and captures this nematode. The hypha then releases digestive enzymes that break down the worm's tissues.

Yeast cells



Gary T. Cole, University of Texas, Austin/BPS

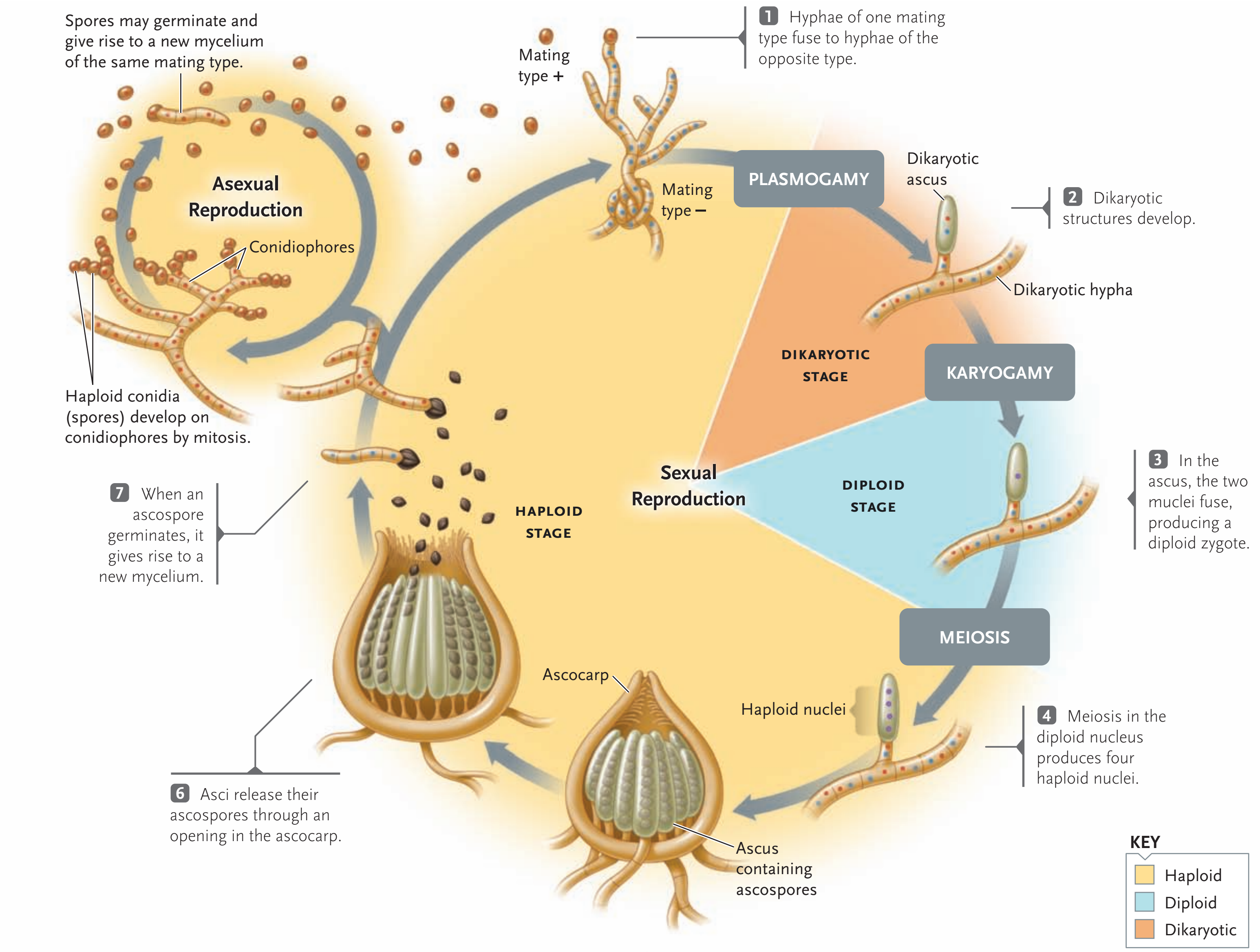
Figure 28.10
Candida albicans, cause of yeast infections of the mouth and vagina.

that leavens bread, has also been a model organism for genetic research. By one estimate it has been the subject of more genetic experiments than any other eukaryotic microorganism. Yeasts commonly reproduce asexually by fission or budding from the parent cell, but many also can reproduce sexually after the fusion of two cells of different mating types (analogous to the mating types described earlier). Many ascomycete yeasts are found naturally in the nectar of flowers and on fruits and leaves. At least 1500 species have been described, and mycologists suspect that thousands more are yet to be identified.

Tens of thousands of ascomycetes, however, are not yeasts. They are multicellular, with tissues built up from septate hyphae. Although septa do slow the flow of nutrients (which, recall, can cross septa through pores), they also confer advantages. For example, septa present barriers to the loss of cytoplasm if a hypha is torn or punctured, whereas in an aseptate zygomycete, fluid pressure may force out a significant amount of cytoplasm before a breach can be sealed by congealing cytoplasm. In ways that are not well understood, septa can also limit the damage from toxins that are secreted by competing fungi.

As with zygomycetes, certain hyphae in ascomycetes are specialized for asexual reproduction. Instead of making spores inside sporangia, however, many ascomycetes produce asexual spores called **conidia** ("dust"; singular, conidium). In some of the species, the conidia form in chains that elongate from modified hyphal branches called **conidiophores.** In other ascomycetes, the conidia may pinch off from the hyphae in a series of "bubbles," a bit like a string of detachable beads. Either way, an ascomycete can form and release spores much more quickly than a zygomycete can. Each newly formed conidium contains a haploid nucleus and some of the parent hypha's cytoplasm. Conidia and conidiophores of some ascomycete species are visible as the white powdery mildew that attacks grapes, roses, grasses, and the leaves of squash plants.

Ascomycetes can also reproduce sexually, and are commonly termed sac fungi because the meiotic divisions that generate haploid sexual spores occur in saclike cells called **asci** (*askos* = bladder; singular, ascus). In *Neurospora crassa* **(Figure 28.11)** and other complex ascomycetes, reproductive bodies called **ascocarps** bear or contain the asci. Some ascocarps resemble globes, others flasks or open dishes. An ascocarp begins to develop when two haploid mycelia of $+$ and $-$ mating types fuse (step 1). Plasmogamy then takes place, with the details differing from species to species. (In some species, hormonal signals cause the tip of one hypha to enlarge and form a "female" reproductive organ called an ascogonium, while the other hyphal tip develops into a "male" antheridium.) Paired nuclei, one from each mating type, migrate into the hyphae. During plasmogamy, the fused sexual structures give rise to dikaryotic hyphae, which develop inside the ascocarp. Asci form at the hyphal tips. Inside them, karyogamy takes place, producing a diploid zygote nucleus. It divides by meiosis, producing four haploid nuclei. In yeasts and some other ascomycetes cell division stops at this point, but in *N. crassa* and in many other species a round of mitosis ensues and results in eight nuclei. Regardless, the nuclei, other organelles, and a portion of cytoplasm then are incorporated into ascospores that may germinate on a suitable substrate and continue the life cycle.



Spores may germinate and give rise to a new mycelium of the same mating type.

Haploid conidia (spores) develop on conidiophores by mitosis.

1 Hyphae of one mating type fuse to hyphae of the opposite type.

2 Dikaryotic structures develop.

3 In the ascus, the two muclei fuse, producing a diploid zygote.

4 Meiosis in the diploid nucleus produces four haploid nuclei.

5 The four nuclei now divide by mitosis; then cell walls form around each of the resulting eight nuclei. These cells are ascospores. Asci develop inside an ascocarp, which began to form soon after sexual reproduction began.

6 Asci release their ascospores through an opening in the ascocarp.

7 When an ascospore germinates, it gives rise to a new mycelium.

Figure 28.11 Life cycle of the ascomycete *Neurospora crassa.*

Basidiomycetes, the Club Fungi, Form Sexual Spores in Club-Shaped Basidia

The 25,000 or so species of fungi in the phylum Basidiomycota include the mushroom-forming species, shelf fungi, coral fungi, bird's nest fungi, stinkhorns, smuts, rusts, and puffballs **(Figure 28.12).** The common name for this group is club fungi, so named because the spore-producing cells, called **basidia** (meaning base or foundation), usually are club shaped. Some species have enzymes for digesting cellulose and lignin and are important decomposers of woody plant debris. A surprising number of basidiomycetes, including the prized edible oyster mushrooms (*Pleurotus ostreatus*), also can trap and consume bacteria and small animals such as rotifers and nematodes by secreting paralyzing toxins or gluey substances that immobilize the prey. This adaptation gives the fungus access to a rich source of molecular nitrogen, an essential nutrient that often is scarce in terrestrial habitats.

Many basidiomycetes take part in vital mutualistic associations with the roots of forest trees, as discussed later in this chapter. Others, the rusts and smuts, are parasites that cause serious diseases in wheat, rice, and other plants. Still others produce millions of dollars' worth of the reproductive structures commonly called mushrooms.

Amanita muscaria, the fly agaric mushroom (see Figure 28.12d), has been used as a fly poison, from

a. Coral fungus

Robert C. Simpson/Nature Stock

b. Shelf fungus

Robert C. Simpson/Nature Stock

c. White-egg bird's nest fungus

Jeffrey Lepore/Photo Researchers, Inc.

d. Fly agaric mushroom

Jane Burton/Bruce Coleman Ltd.

e. Scarlet hood

Robert C. Simpson/Nature Stock

Figure 28.12

Representative basidiomycetes, or club fungi. **(a)** The light red coral fungus *Ramaria*. **(b)** The shelf fungus *Polyporus*. **(c)** The white-egg bird's nest fungus *Crucibulum laeve*. Each tiny "egg" contains spores. Raindrops splashing into the "nest" can cause "eggs" to be ejected, thereby spreading spores into the surrounding environment. **(d)** The fly agaric mushroom *Amanita muscaria*, which causes hallucinations. **(e)** The scarlet hood *Hygrophorus*.

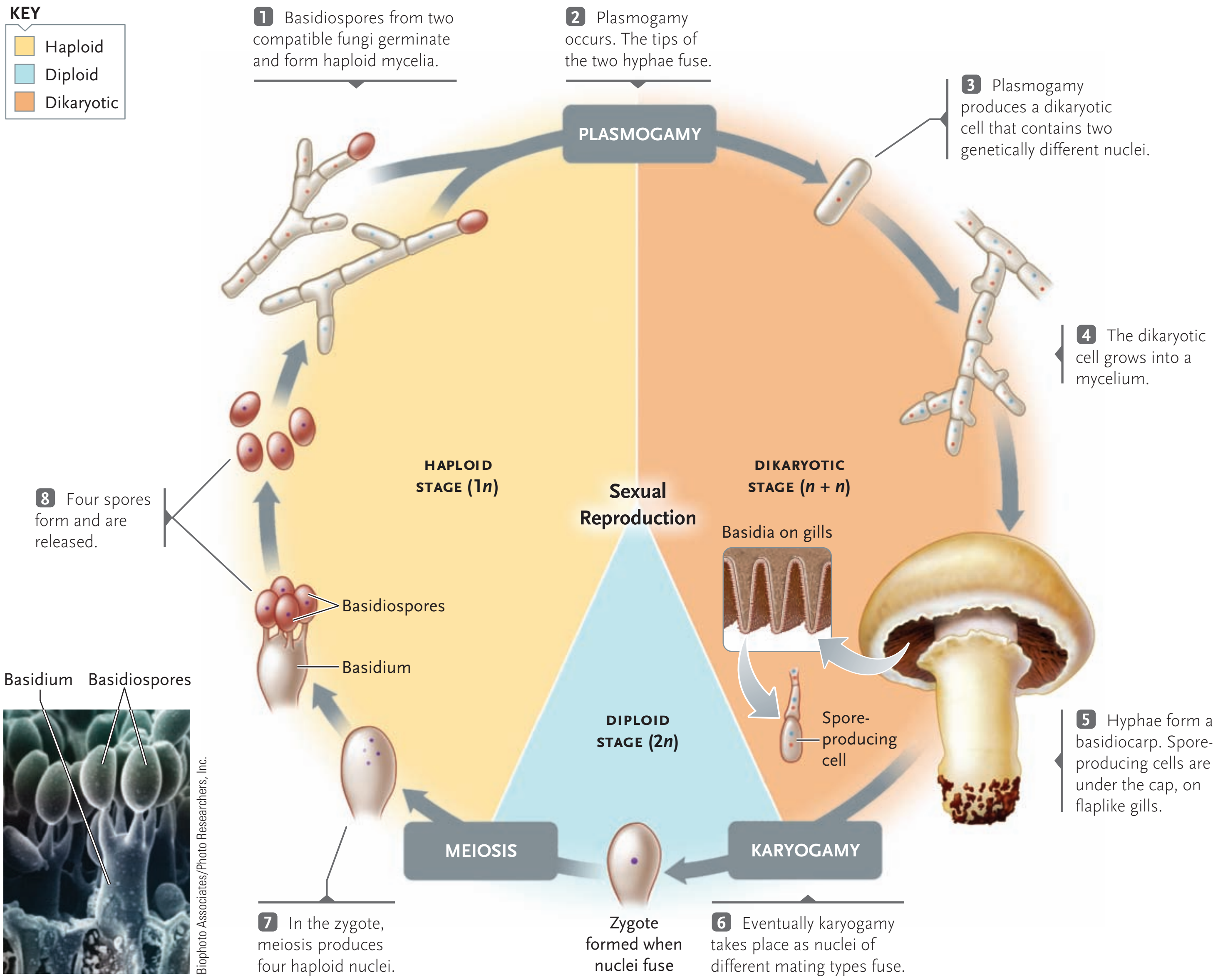
which it gets its common name. Due to its hallucinogenic effects, *A. muscaria* also is used in the religious rituals of ancient societies in Central America, Russia, and India. Other species of this genus, including the death cap mushroom *Amanita phalloides*, produce deadly toxins. The *A. phalloides* toxin, called α-amanitin, halts gene transcription, and hence protein synthesis, by inhibiting the activity of RNA polymerase. Within 8 to 24 hours of ingesting as little as 5 mg of the toxin, vomiting and diarrhea begin. Later, kidney and liver cells start to degenerate; without intensive medical care, death can follow within a few days.

A few basidiomycetes generally reproduce only by asexual means, by budding or shedding a fragment of a hypha. One is *Cryptococcus neoformans*, which causes a form of meningitis in humans. In general, however, basidiomycetes do reproduce sexually, producing large numbers of haploid sexual spores. **Figure 28.13** shows the life cycle of a typical basidiomycete.

Basidia typically develop on a **basidiocarp**, which is the reproductive body of the fungus. A basidiocarp consists of tight clusters of hyphae; the feeding mycelium is buried in the soil or decaying wood. The shelflike bracket fungi visible on trees are basidiocarps, and about 10,000 species of club fungi produce the basidiocarps we call mushrooms. Each is a short-lived reproductive body consisting of a stalk and a cap. Basidia develop on "gills," which are the sheets of tissue on the underside of the cap. The basidia undergo meiosis to produce microscopic, haploid **basidiospores** (Figure 28.13, inset) that disperse throughout the environment.

When a basidiospore lands on a suitable food source, it germinates and gives rise to a haploid mycelium. Two compatible mating types growing near each other may undergo plasmogamy. The resulting mycelium is dikaryotic, its cells containing one nucleus from each mating type. The dikaryotic stage of a basidiomycete is the feeding mycelium that can grow for years—a major departure from an ascomycete's short-lived dikaryotic stage. Accordingly, a basidiomycete has many more opportunities for producing sexual spores, and the mycelium can give rise to reproductive bodies many times.

After an extensive mycelium develops, and when environmental conditions such as moisture are favorable, basidiocarps grow from the mycelium and develop basidia. At first, each basidium in the mushroom or other reproductive body is dikaryotic, but then the two



1 Basidiospores from two compatible fungi germinate and form haploid mycelia.

2 Plasmogamy occurs. The tips of the two hyphae fuse.

3 Plasmogamy produces a dikaryotic cell that contains two genetically different nuclei.

4 The dikaryotic cell grows into a mycelium.

5 Hyphae form a basidiocarp. Spore-producing cells are under the cap, on flaplike gills.

6 Eventually karyogamy takes place as nuclei of different mating types fuse.

7 In the zygote, meiosis produces four haploid nuclei.

8 Four spores form and are released.

Figure 28.13
Generalized life cycle of the basidiomycete *Agaricus bisporus*, a species known commonly as the button mushroom. During the dikaryotic stage, cells contain two genetically different nuclei, shown here in different colors. Inset: Micrograph showing basidia and basidiospores.

nuclei undergo karyogamy, fusing to form a diploid zygote nucleus. The zygote exists only briefly; meiosis soon produces haploid basidiospores, which are wafted away from the basidium by air currents. Basidia can produce huge numbers of spores—for many species, estimates run as high as 100 million spores *per hour* during reproductive periods, day after day.

Squirrels and many other small animals may eat mushrooms almost as soon as they appear, but in some species the underlying mycelium can live for many years. For example, U.S. Forest Service scientists have found that the mycelium of a single individual of *Armillaria ostoyae* covers an area equivalent to 1665 football fields in an eastern Oregon forest. By one estimate, it measures an average of 1 m deep and nearly 6000 m across, making it perhaps one of the largest organisms on Earth. As such a mycelium grows, specialized mechanisms during cell division maintain the dikaryotic condition and the paired nuclei in each hyphal cell.

Conidial Fungi Are Species for Which No Sexual Phase Is Known

As noted earlier, fungi generally are classified on the basis of their structures for sexual reproduction. When a sexual phase is absent or has not yet been detected, the fungal species is said to be anamorphic ("no related form") and is lumped into a convenience grouping, the conidial fungi (recall that conidia are asexual spores). This classification is the equivalent of "unidentified." Other names for this grouping are "imperfect fungi" and deuteromycetes.

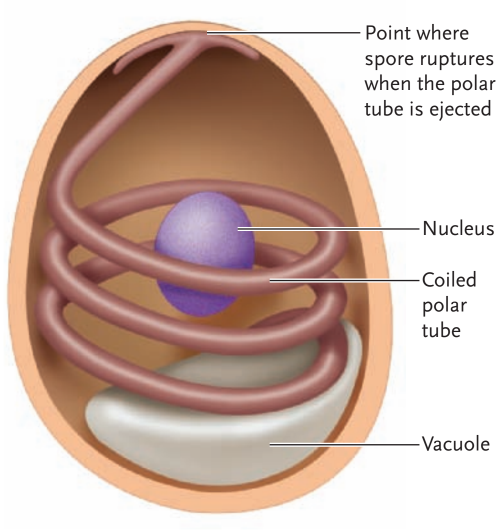


Figure 28.14

Structure of microsporidia. When a spore germinates, its vacuole expands and forces the coiled "polar tube" outward and into a nearby, soon-to-be host cell. The nucleus and cytoplasm of the parasite enter the host through the tube, launching developmental steps that lead to the development of more microsporidia inside the host.

When researchers discover a sexual phase for a conidial fungus, or when molecular studies establish a clear relationship to a sexual species, the conidial fungus is reassigned to the appropriate phylum. Thus far, some have been classified as basidiomycetes, but most conidial fungi have turned out to be ascomycetes.

Microsporidia Are Single-Celled Sporelike Parasites

There are more than 1200 species of the single-celled parasites called **microsporidia.** They are known to infect insects including honeybees and grasshoppers, and vertebrates including fish and humans—especially individuals with compromised immune systems such as people with AIDS. Microsporidia are rather mysterious organisms. Physically they resemble spores **(Figure 28.14),** but they lack mitochondria and have several other puzzling characteristics. Molecular studies suggest that they are related to zygomycetes, and some researchers have proposed that the group may have lost many typical fungal features as it evolved a highly specialized parasitic lifestyle.

STUDY BREAK

1. Name the five phyla of the Kingdom Fungi and describe the reproductive adaptations that distinguish each one.
2. In terms of structure, which are the simplest fungal groups? The most complex?
3. Describe some ways, positive or negative, that members of each fungal phylum interact with other life forms.

28.3 Fungal Associations

Many fungi are partners in mutually beneficial interactions with photosynthetic organisms, and these associations play major roles in the functioning of ecosystems. A **symbiosis** is a state such as parasitism or mutualism in which two or more species live together in close association. Chapter 50 discusses general features of symbiotic associations more fully; here we are interested in some examples of the symbioses fungi form with photosynthetic partners—cyanobacteria, green algae, and plants.

A Lichen Is an Association between a Fungus and a Photosynthetic Partner

You may be familiar with one type of lichen, the leathery patches of various colors growing on certain rocks. Technically, a **lichen** is a single vegetative body that is the result of an association between a fungus and a photosynthetic partner. The fungal partner in a lichen, called the **mycobiont**, usually makes up only about 10% of the whole. The other 90% is the photosynthetic partner, called the **photobiont.** Most frequently, these are green algae of the genus *Trebouxia* or cyanobacteria of the genus *Nostoc*. Thousands of ascomycetes and a few basidiomycetes form this kind of symbiosis, but only about 100 photosynthetic species serve as photobionts.

Lichens often live in harsh, dry microenvironments, including on bare rock and wind-whipped tree trunks. Yet lichens have vital ecological roles and important human uses. Lichens secrete acid that eats away at rock, breaking it down and converting it to soil that can support larger plants. Some paleobiologists have suggested that lichens may have been some of the earliest land organisms, covering bare rocks during the Ordovician period (roughly 500 million to 425 million years ago). In this scenario, millennia of decaying lichens would have created the first soils in which the earliest land plants could grow. Today, lichens continue to enhance the survival of other life forms. For instance, in arctic tundra, where plants are scarce, reindeer and musk oxen can survive by eating lichens. Insects, slugs, and some other invertebrates also consume lichens, and they are nest-building materials for many birds and small mammals. People have derived dyes from lichens; they are even a component of garam masala, an ingredient in Indian cuisine. Some environmental chemists monitor air pollution by observing lichens, most of which cannot grow in heavily polluted air (see *Focus on Research*).

Because lichens are composite organisms, it may seem odd to talk of lichen "species." Biologists do give lichens binomial names, however, based on the characteristics of the mycobiont. More than 13,500 lichens are recognized, each one a unique combination of a

Focus on Research

Applied Research: Lichens as Monitors of Air Pollution's Biological Damage

Lichens have become reliable pollution-monitoring devices all over the world—in some cases, replacing costly electronic monitoring stations. Different species are vulnerable to specific pollutants. For example, *Ramalina* lichens are damaged by nitrate and fluoride salts. Elevated levels of sulfur dioxide (a major component of acid rain) cause old man's beard *(Usnea trichodea)* to shrivel and die, but strongly promote the growth of a crusty European lichen, *Lecanora conizaeoides*. The sensitivity of yellow *Evernia* lichens to SO_2 enabled the scientist who discovered its damage at remote Isle Royale in Michigan to point the finger northward to coal-burning furnaces at Thunder Bay, Canada. Conversely, healthy lichens on damaged trees of Germany's Black Forest lifted suspicion from French coal-burning power plants and allowed investigators to identify the true source of the tree damage: nitrogen oxides from automobile exhausts. The result was Germany's first auto emission standards, which went into effect in the 1990s.

Mark Mattock/Planet Earth Pictures

Usnea (old man's beard), a pendent (hanging) lichen.

particular species of fungus and one or more species of photobiont. The relationship often begins when a fungal mycelium contacts a free-living cyanobacterium, algal cell, or both. The fungus parasitizes the photosynthetic host cell, sometimes killing it. If the host cell can survive, however, it multiplies in association with the fungal hyphae. The result is a tough, pliable body called a **thallus**, which can take a variety of forms **(Figure 28.15a).** Short, specialized hyphae penetrate algal cells of the thallus, which become the fungus's sole source of nutrients. Often, the mycobiont of a lichen absorbs up to 80% of the carbohydrates the photobiont produces.

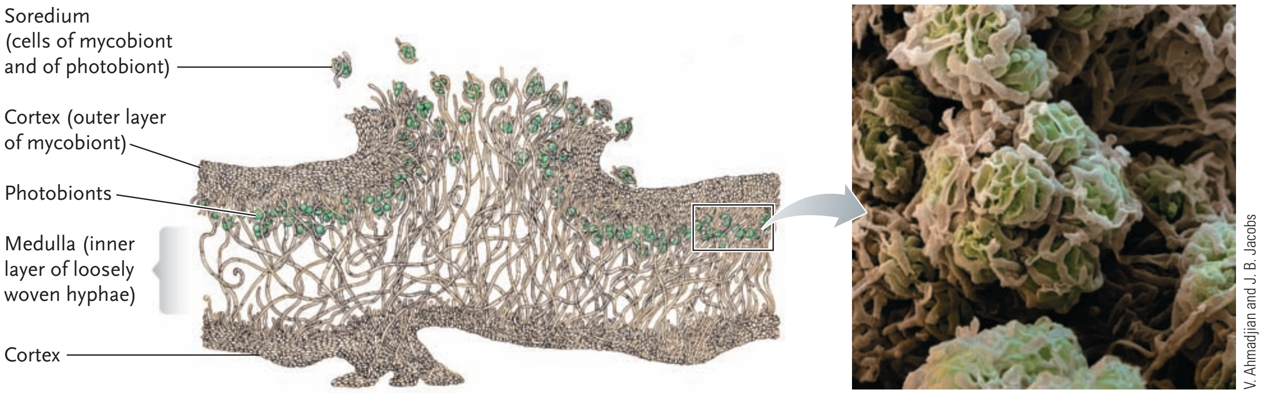
Benefits for the photobiont are less clear-cut, in part because the drain on nutrients hampers its growth and reproduction. In one view, many and possibly most lichens are parasitic symbioses in which the photobiont does not receive equal benefit. On the other hand, it is relatively rare to find a lichen's photobiont species living independently in the same conditions under which the lichen survives, whereas as part of a lichen it may eke out an enduring existence; some lichens have been dated as being more than 4000 years old! Studies have also revealed that at least some green algae do clearly benefit from the relationship. Such algae are sensitive to desiccation and intense ultraviolet radiation. Sheltered by a lichen's fungal tissues, a green alga can thrive in locales where alone it would perish. Clearly, we still have quite a bit to learn about the physiological interactions between lichen partners.

As you might expect with such a communal life form, reproduction has its quirky aspects. In lichens that involve an ascomycete, the fungus produces ascospores that are dispersed by the wind. The spores germinate to form hyphae that may colonize new photosynthetic cells and so establish new symbioses. A lichen itself can also reproduce in at least two ways. In some types, a section of the thallus detaches and grows into a new lichen. In about one-third of lichens, specialized regions of the thallus give rise asexually to reproductive cell clusters called **soredia** (*soros* = heap; singular, soredium). Each cluster includes both algal and hyphal cells **(Figure 28.15b).** As the lichen grows, the soredia detach and are dispersed by water, wind, or passing animals.

Mycorrhizae Are Symbiotic Associations of Fungi and Plant Roots

A **mycorrhiza** ("fungus-root") is a mutualistic symbiosis in which fungal hyphae associate intimately with plant roots. Mycorrhizae greatly enhance the plant's ability to extract various nutrients, especially phosphorus and nitrogen, from soil (see Chapter 33).

In **endomycorrhizae,** the fungal hyphae penetrate the cells of the root. This kind of association occurs on the roots of nearly all flowering plants, and in most



a. Thallus cross section

b. Soredia

V. Ahmadjian and J. B. Jacobs

c. Encrusting lichens

Jane Burton/Bruce Coleman Ltd.

d. Branching lichen

Eye of Science/SPL/Photo Researchers, Inc.

Figure 28.15
Lichens. **(a)** Sketch of a cross section through the thallus of the lichen *Lobaria verrucosa*. The soredia **(b),** which contain both hyphae and algal cells, are a type of dispersal fragment by which lichens reproduce asexually. **(c)** Encrusting lichens. **(d)** Erect, branching lichen, *Cladonia rangiferina*.

cases a glomeromycete is the fungal partner. The treelike, branched hyphae of endomycorrhizae are called arbuscules **(Figure 28.16),** and glomeromycetes are sometimes referred to as arbuscular fungi.

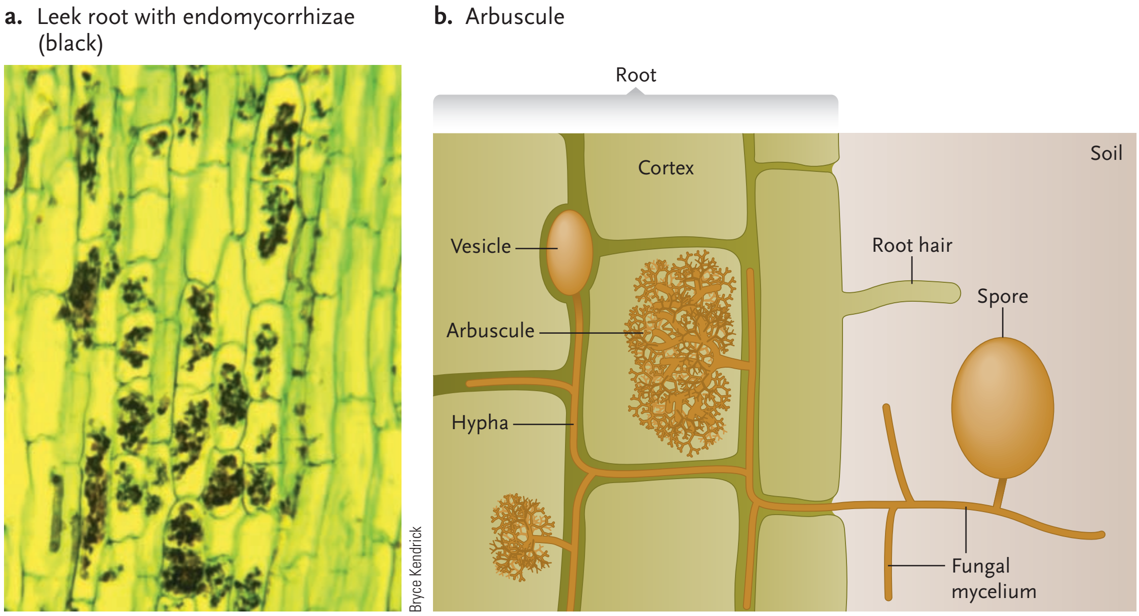
Basidiomycetes are the usual fungal partners in **ectomycorrhizae (Figure 28.17),** in which hyphal tips grow between and around the young roots of trees and shrubs but never enter the root cells. Ectomycorrhizal associations—often several of them—are very common with trees. For instance, the extensive root system of a mature pine may be studded with ectomycorrhizae involving dozens of fungal species. The musky-flavored truffles *(Tuber melanosporum)* prized by gourmets are ascomycetes that form ectomycorrhizal associations with oak trees (genus *Quercus*).

Orchids are partners in a unique mycorrhizal relationship. The fungal partner, usually a basidiomycete, lives inside the orchid's tissues and provides the plant with a variety of nutrients. In fact, seeds of wild orchids germinate, and seedlings survive, only when such mycorrhizae are present.

In general, mycorrhizae represent a "win-win" situation for the partners. The fungal hyphae absorb carbohydrates synthesized by the plant, along with some amino acids and perhaps growth factors as well. The growing plant in turn absorbs mineral ions made accessible to it by the fungus. Collectively, the fungal hyphae have a tremendous surface area for absorbing mineral ions from a large volume of the surrounding soil. Dissolved mineral ions accumulate in the hyphae when they are plentiful in the soil, and are released to the plant when they are scarce. This service is a survival boon to a great many plants, especially species that cannot readily absorb mineral ions, particularly phosphorus **(Figure 28.18).** For plants that inhabit soils poor in mineral ions, such as in tropical rain forests, mycorrhizal associations are crucial for survival. Likewise, in temperate forests, species of spruce, oak, pine, and some other trees die unless mycorrhizal fungi are present. Plants that live in dry habitats often rely on specialized mycorrhizal hyphae that serve as conduits for water into the root. Like lichens, mycorrhizae are highly vulnerable to damage from pollutants, especially acid rain.

Mycorrhizae have a long evolutionary history. Fossils show that endomycorrhizae were common among ancient land plants, and some biologists have speculated they might have been key for enhancing

Figure 28.16
Endomycorrhizae. (a) In this instance, the roots of leeks are growing in association with the glomeromycete *Glomus versiforme* (longitudinal section). Notice the arbuscules that have formed as the fungal hyphae branched after entering the leek root **(b).**



a. Leek root with endomycorrhizae (black)

Bryce Kendrick

b. Arbuscule

a. Lodgepole pine

Prof. D. J. Read, University of Sheffield

b. Mycorrhiza

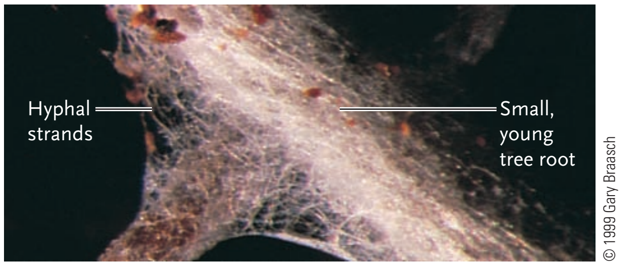


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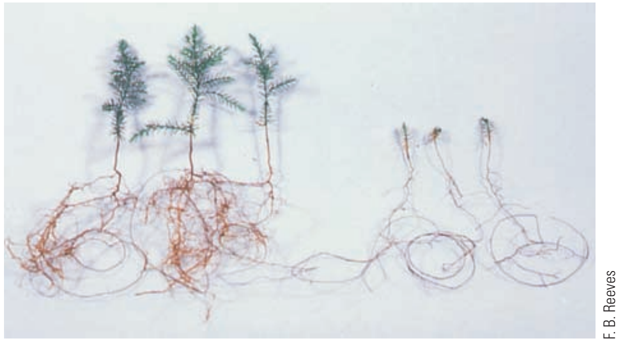
Figure 28.17
Ectomycorrhizae. (a) Lodgepole pine, *Pinus contorta,* seedling, longitudinal section. Notice the extent of the mycorrhiza compared with the above-ground portion of the seedling, which is only about 4 cm tall. **(b)** Mycorrhiza of a hemlock tree.



F. B. Reeves

Figure 28.18
Effect of mycorrhizal fungi on plant growth. The six-month-old juniper seedlings on the left were grown in sterilized low-phosphorus soil inoculated with a mycorrhizal fungus. The seedlings on the right were grown under the same conditions but without the fungus.

the transport of water and minerals to the plants. In that scenario, endomycorrhizae may have played a crucial role in allowing plants to make the transition to life on land.

STUDY BREAK

1. Explain what a lichen is, and how each partner contributes to the whole.
2. Describe the biological and ecological roles of mycorrhizae.
3. How do endomycorrhizae and ectomycorrhizae differ?

UNANSWERED QUESTIONS

How do plant pathogenic fungi invade plants?

Many species of fungi are pathogenic to plants. Of particular interest to humans are the pathogenic fungi that invade crop plants. In general, to invade a plant the pathogenic fungus must first break down any form of natural resistance that the plant has, and then establish an infection. Moreover, each pathogenic fungus has specificity—it invades only a particular set of plants, not all plants. For a number of pathogenic fungi, scientists are beginning to gain an understanding of the cellular and molecular events involved in invasion and the spread of the infection through the plant. A complete understanding of these processes will open the way to developing approaches that protect crop plants from fungal invasion, or at least reduce the extent of damage to the plants.

One example of the research being done in this area concerns the ascomycete fungus *Cochliobolus carbonum*. This fungus is pathogenic to maize, causing leaf blight (early drying of the leaves) and ear rot disease. *C. carbonum* secretes a toxin called HC-toxin to infect maize hosts. Guri Johal of Purdue University is studying the infection process, in particular investigating the molecular mechanisms by which HC-toxin leads to fungal colonization of maize tissues. Currently, little is known about those mechanisms.

Another example of research with pathogenic fungi concerns the ascomycete *Magnaporthe grisea,* the fungus that causes rice blast (lesions on leaves and other parts of the plant). The genome of this fungus has been sequenced, making possible the use of genomic/proteomic tools and approaches for studying pathogenesis. Dan Ebbole at Texas A&M University is using those tools and approaches to analyze proteins secreted by *M. grisea* with the aim of understanding their roles in the interaction of the pathogen with rice plants. Specifically, Ebbole and his group are looking at 300 proteins that, based on analysis of the genome, are predicted to be secreted. They produce tagged versions of the proteins by expressing the genes for them in fungal cultures. Then they test the purified proteins directly on plants one by one to see if any elicits a specific response by the host plant. They anticipate that this approach will serve as a screen to identify proteins that play significant roles in the pathogen–plant interaction. Those proteins will then be analyzed more completely, with the objective of developing cellular and molecular models for pathogenesis.

What are the interactions between all the molecular components of a fungus?

As you learned in Section 18.3, the study of the interactions between all of the molecular components of a cell or organism is systems biology. Over the years, significant advances have been made toward a molecular understanding of many processes in fungi, particularly in model fungi such as the yeast *Saccharomyces cerevisiae* and the mold *Neurospora crassa*. In addition, genome sequences have been obtained for a number of fungi, including the two species just mentioned as well as some pathogenic species. For a number of fungi, then, researchers are poised for systems biology studies. To that end, scientists from around the world have established the Yeast Systems Biology Network (YSBN) to coordinate research efforts in the systems biology of *S. cerevisiae*. The researchers argue that this yeast is a particularly appropriate model system for a concentrated effort to obtain a systems-level understanding of biological processes. Indeed, yeast has been a model system for eukaryotic cell structure and function, and for a number of aspects of fungal biology (see Chapter 10's *Focus on Research*). It was also one of the original model eukaryotes chosen for genome sequencing in the Human Genome Project (see Chapter 18).

Peter J. Russell

Review

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28.1 General Characteristics of Fungi

- Fungi are key decomposers contributing to the recycling of carbon and some other nutrients. They occur as single-celled yeasts or multicellular filamentous organisms.
- The fungal mycelium consists of filamentous hyphae that grow throughout the substrate the fungus feeds upon (Figure 28.2). A wall containing chitin surrounds the plasma membrane, and in most species septa partition the hyphae into cell-like compartments. Pores in septa permit cytoplasm and organelles to move between hyphal cells. Aggregations of hyphae form all other tissues and organs of a multicellular fungus.
- Fungi gain nutrients by extracellular digestion and absorption. Saprobic species feed on nonliving organic matter. Parasitic types obtain nutrients from tissues of living organisms. Many fungi are partners in symbiotic relationships with plants.
- All fungi may reproduce via spores generated either asexually or sexually (Figure 28.3). Some types also may reproduce asexually by budding or fragmentation of the parent body. Sexual reproduction usually has two stages. First, in plasmogamy, the cytoplasms of two haploid cells fuse to become a dikaryon containing a haploid nucleus from each parent. Later, in karyogamy, the nuclei fuse and form a diploid zygote. Meiosis then generates haploid spores.

Animation: Mycelium

28.2 Major Groups of Fungi

- The main phyla of fungi are the Chytridiomycota (which have motile spores), Zygomycota (zygospore-forming fungi), Glomeromycota, Ascomycota (sac fungi), and Basidiomycota (club fungi) (Figure 28.4). The phyla traditionally have been distinguished mainly on the basis of the structures that arise as part of sexual reproduction. When a sexual phase cannot be detected or is absent from the life cycle, the specimen is assigned to an informal grouping, the conidial fungi.
- Chytrids usually are microscopic. They are the only fungi that produce motile, flagellated spores. Many are parasites (Figure 28.5).
- Zygomycetes have aseptate hyphae and are coenocytic, with many nuclei in a common cytoplasm. They sometimes reproduce sexually by way of hyphae that occur in + and − mating types; haploid nuclei in the hyphae function as gametes. Further development produces the zygospore, which may go dormant

for a time. When the zygospore breaks dormancy it produces a stalked sporangium containing haploid spores of each mating type, which are released (Figures 28.6 and 28.7).

- Glomerulomycetes form a distinct type of endomycorrhizae in association with plant roots. They reproduce asexually, by way of spores that form at the tips of hyphae.
- Most ascomycetes are multicellular (Figure 28.9). In asexual reproduction, chains of haploid asexual spores called conidia elongate or pinch off from the tips of conidiophores (modified aerial hyphae; Figure 28.10). In sexual reproduction, haploid sexual spores called ascospores arise in saclike cells called asci. In the most complex species, reproductive bodies called ascocarps bear or contain the asci. Ascospores can give rise to a new haploid mycelium (Figures 28.8 and 28.11).
- Most basidiomycete species reproduce only sexually. Club-shaped basidia develop on a basidiocarp and bear sexual spores on their surface. When dispersed, these basidiospores may germinate and give rise to a haploid mycelium (Figure 28.13).
- Microsporidia are single-celled sporelike parasites of arthropods, fish, and humans (Figure 28.14).

Animation: Zygomycete life cycle

Animation: Sac fungi

Animation: Club fungus life cycle

28.3 Fungal Associations

- Many ascomycetes and a few basidiomycetes enter into symbioses with cyanobacteria or green algae to produce the communal life form called a lichen, which has a spongy body called a thallus. The algal cells supply the lichen's carbohydrates, most of which are absorbed by the fungus. In some lichens a section of the thallus may detach and grow into a new individual. In others, specialized regions of the thallus give rise asexually to reproductive soredia that include both algal and hyphal cells (Figure 28.15).
- In the symbiosis called a mycorrhiza, fungal hyphae make mineral ions and sometimes water available to the roots of a plant partner. The fungus in turn absorbs carbohydrates, amino acids, and possibly other growth-enhancing substances from the plant (Figures 28.16–28.18). In endomycorrhizae, the fungal hyphae (usually of a glomeromycete) penetrate the cells of the root. With ectomycorrhizae, hyphal tips grow close to young roots but do not enter roots cells; the usual fungal partner is a basidiomycete.

Animation: Lichens

Animation: Mycorrhiza

Questions

Self-Test Questions

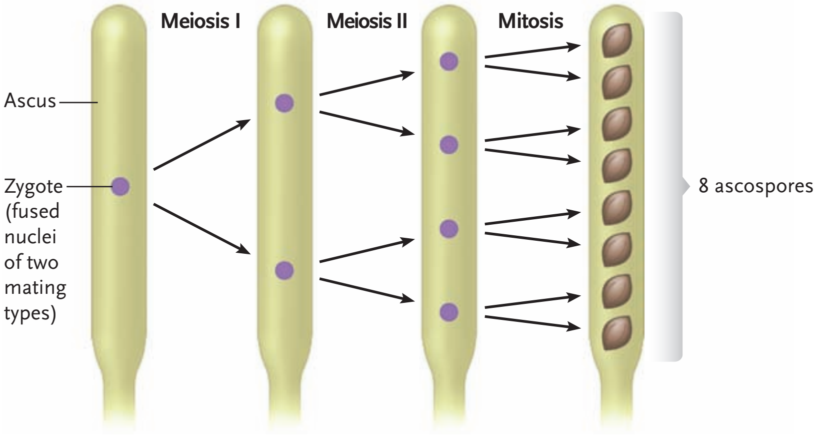
1. Which of the following attributes best exemplifies a filamentous saprobic fungus?
   a. reproduction by spores on week-old bread
   b. metabolic by-products that make bread rise
   c. extracellular digestion of tissues in a fallen log
   d. extracellular digestion of a living leaf's cellulose with hydrolytic enzymes
   e. aggressive expansion of the fungal mycelium into the tissues of a living elm tree
2. Which of the following events is/are *not* part of a typical fungal life cycle involving asexual reproduction?
   a. formation of a dikaryon
   b. hyphae developing into a mycelium
   c. formation of a diploid zygote
   d. plasmogamy, which occurs when hyphae fuse at their tips
   e. production and release of large numbers of spores
3. A trait common to all fungi is:
   a. reproduction via spores.
   b. parasitism.
   c. septate hyphae.
   d. a dikaryotic phase inside a zygospore.
   e. plasmogamy after an antheridium and ascogonium come into contact.
4. The chief characteristic used to classify fungi into the major fungal phyla is:
   a. nutritional dependence on nonliving organic matter.
   b. recycling of nutrients in terrestrial ecosystems.
   c. adaptations for obtaining water.
   d. features of reproduction.
   e. cell wall metabolism.
5. At lunch George ate a mushroom, some truffles, a little Camembert cheese, and a bit of moldy bread. Which of the following groups was *not* represented in the meal?
   a. Basidiomycota
   b. Ascomycota
   c. conidial fungi
   d. chytrids
   e. Zygomycota
6. Which of the following fungal reproductive structures is diploid?
   a. basidiocarps
   b. ascospores
   c. conidia
   d. gametangia
   e. zygospores
7. A mushroom is:
   a. the food-absorbing region of an ascomycete.
   b. the food-absorbing region of a basidiomycete.
   c. a reproductive structure formed only by basidiomycetes.
   d. a specialized form of mycelium not constructed of hyphae.
   e. a collection of saclike cells called asci.
8. A zygomycete is characterized by:
   a. aseptate hyphae.
   b. mostly sexual reproduction.
   c. absence of + and − mating types.
   d. the tendency to form mycorrhizal associations with plant roots.
   e. a life cycle in which karyogamy does not occur.
9. Which best describes a lichen?
   a. It is a fungus that breaks down rock to provide nutrients for an alga.
   b. It colonizes bare rocks and slowly degrades them to small particles.
   c. It spends part of the life cycle as a mycobiont and part as a fungus.
   d. It is an association between a basidiomycete and an ascomycete.
   e. It is an association between a photobiont and a fungus.
10. In a college greenhouse a new employee observes fuzzy mycorrhizae in the roots of all the plants. Destroying no part of the plants, he carefully removes the mycorrhizae. The most immediate result of this "cleaning" is that the plants cannot:
    a. carry out photosynthesis.
    b. absorb water through their roots.
    c. transport water up their stems.
    d. extract phosphorus and nitrogen from water.
    e. store carbohydrates in their roots.

Questions for Discussion

1. A mycologist wants to classify a specimen that appears to be a new species of fungus. To begin the classification process, what kinds of information on body structures and/or functions must the researcher obtain in order to assign the fungus to one of the major fungal groups?
2. In a natural setting—a pile of horse manure in a field, for example—the sequence in which various fungi appear illustrates ecological succession, the replacement of one species by another in a community (see Chapter 50). The earliest fungi are the most efficient opportunists, for they can form and disperse spores most rapidly. In what order would you expect representatives from each division of fungi to appear on the manure pile? Why?
3. As the text noted, conifers, orchids, and some other types of plants cannot grow properly if their roots do not form associations with fungi, which provide the plant with minerals such as phosphate and in return receive carbohydrates and other nutrients synthesized by the plant. In some instances, however, the plant receives proportionately more nutrients than the fungus does. Even so, biologists still consider this to be a mycorrhizal association. Explain why you agree or disagree.
4. Humans are fundamentally diploid organisms. Explain how this state of affairs compares with the fungal life cycle, then compare the two general life cycles in light of the two groups' overall reproductive strategies.

Experimental Analysis

Experiments on the orange bread mold *Neurospora crassa,* an ascomycete, were pivotal in elucidating the concept that each gene encodes a single enzyme. As *N. crassa* ascospores arise through meiosis and then mitosis in an ascus, each ascospore occupies a particular position in the final string of eight spores the ascus contains:



This quirk of ascospore development was extremely useful to early geneticists, because it vastly simplified the task of figuring out which alleles ended up in particular ascospores following meiosis. Recalling genetics topics discussed in Chapter 11, why was the analysis easier?

Evolution Link

The hypothesis that fungi are more closely related to animals than to plants has receive support from studies of fungus genomes. For instance, scientists have documented striking similarities in the structure of many fungal and human genes—similarities that may be especially important in medicine. One mycologist, John Taylor of the University of California at Berkeley, suggests that a close biochemical relationship between fungi and animals may explain why fungal infections are typically so resistant to treatment, and why it has proven rather difficult to develop drugs that kill fungi without damaging their human or other animal hosts. About 100 fungal genomes have been or soon will be sequenced, including genomes of several medically important species. If you are a researcher working to develop new antifungal drugs, how could you make use of this growing genetic understanding? Using Web resources, can you find examples of antifungal drugs that exploit biochemical differences between animals and fungi?

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? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.