

36

Fungi

Concept Outline

36.1 Fungi are unlike any other kind of organism.

A Fungus Is Not a Plant. Unlike any plant, all fungi are filamentous heterotrophs with cell walls made of chitin.

The Body of a Fungus. Cytoplasm flows from one cell to another within the filamentous body of a fungus.

How Fungi Reproduce. Fungi reproduce sexually when filaments of different fungi encounter one another and fuse.

How Fungi Obtain Nutrients. Fungi secrete digestive enzymes and then absorb the products of the digestion.

Ecology of Fungi. Fungi are among the most important decomposers in terrestrial ecosystems.

36.2 Fungi are classified by their reproductive structures.

The Three Phyla of Fungi. There are three phyla of fungi, distinguished by their reproductive structures.

Phylum Zygomycota. In zygomycetes, the fusion of hyphae leads directly to the formation of a zygote.

Phylum Ascomycota. In ascomycetes, hyphal fusion leads to stable dikaryons that grow into massive webs of hyphae that form zygotes within a characteristic saclike structure, the ascus. Yeasts are unicellular fungi, mostly ascomycetes, that play many important commercial and medical roles.

Phylum Basidiomycota. In basidiomycetes, dikaryons also form, but zygotes are produced within reproductive structures called basidia.

The Imperfect Fungi. Fungi that have not been observed to reproduce sexually cannot be classified into one of the three phyla.

36.3 Fungi form two key mutualistic symbiotic associations.

Lichens. A lichen is a mutualistic symbiotic association between a fungus and a photosynthetic alga or cyanobacterium.

Mycorrhizae. Mycorrhizae are mutualistic symbiotic associations between fungi and the roots of plants.



FIGURE 36.1

Spores exploding from the surface of a puffball fungus. The fungi constitute a unique kingdom of heterotrophic organisms. Along with bacteria, they are important decomposers and disease-causing organisms.

Of all the bewildering variety of organisms that live on earth, perhaps the most unusual, the most peculiarly different from ourselves, are the fungi (figure 36.1). Mushrooms and toadstools are fungi, multicellular creatures that grow so rapidly in size that they seem to appear overnight on our lawns. At first glance, a mushroom looks like a funny kind of plant growing up out of the soil. However, when you look more closely, fungi turn out to have nothing in common with plants except that they are multicellular and grow in the ground. As you will see, the more you examine fungi, the more unusual they are.

36.1 Fungi are unlike any other kind of organism.

A Fungus Is Not a Plant

The fungi are a distinct kingdom of organisms, comprising about 77,000 named species (figure 36.2). **Mycologists**, scientists who study fungi, believe there may be many more species in existence, as many as 1.2 million. Although fungi have traditionally been included in the plant kingdom, they lack chlorophyll and resemble plants only in their general appearance and lack of mobility. Significant differences between fungi and plants include the following:

- 1. Fungi are heterotrophs.** Perhaps most obviously, a mushroom is not green. Virtually all plants are photosynthesizers, while no fungi have chlorophyll or carry out photosynthesis. Instead, fungi obtain their food by secreting digestive enzymes onto the substrate, and then absorbing the organic molecules that are released by the enzymes.
- 2. Fungi have filamentous bodies.** Fungi are basically filamentous in their growth form (that is, their bodies consist of long slender filaments called hyphae), even though these hyphae may be packed together to form complex structures like the mushroom. Plants, in contrast, are made of several types of cells organized into tissues and organs.
- 3. Fungi have unusual reproductive modes.** Some plants have motile sperm with flagella. No fungi do.

Most fungi reproduce sexually with nuclear exchange rather than gametes.

- 4. Fungi have cell walls made of chitin.** The cell walls of fungi are built of polysaccharides (chains of sugars) and chitin, the same tough material a crab shell is made of. The cell walls of plants are made of cellulose, also a strong building material.
- 5. Fungi have nuclear mitosis.** Mitosis in fungi is different from that in plants or most other eukaryotes in one key respect: the nuclear envelope does not break down and re-form. Instead, mitosis takes place *within* the nucleus. A spindle apparatus forms there, dragging chromosomes to opposite poles of the *nucleus* (not the cell, as in most other eukaryotes).

You could build a much longer list, but already the take-home lesson is clear: fungi are not like plants at all! Their many unique features are strong evidence that fungi are not closely related to any other group of organisms. DNA studies confirm significant differences from other eukaryotes.

Fungi absorb their food after digesting it with secreted enzymes. This mode of nutrition, combined with a filamentous growth form, nuclear mitosis, and other traits, makes the members of this kingdom highly distinctive.



(a)



(c)



(b)

FIGURE 36.2

Representatives of the three phyla of fungi. (a) A cup fungus, *Cookeina tricholoma*, an ascomycete, from the rain forest of Costa Rica. (b) *Amanita muscaria*, the fly agaric, a toxic basidiomycete. In the cup fungi, the spore-producing structures line the cup; in basidiomycetes that form mushrooms, like *Amanita*, they line the gills beneath the cap of the mushroom. All visible structures of fleshy fungi, such as the ones shown here, arise from an extensive network of filamentous hyphae that penetrates and is interwoven with the substrate on which they grow. (c) *Pilobolus*, a zygomycete that grows on animal feces. Stalks about 10 millimeters long contain dark spore-bearing sacs.

The Body of a Fungus

Fungi exist mainly in the form of slender filaments, barely visible to the naked eye, which are called **hyphae** (singular, **hypha**). These hyphae are typically made up of long chains of cells joined end-to-end divided by cross-walls called **septa** (singular, **septum**). The septa rarely form a complete barrier, except when they separate the reproductive cells. Cytoplasm characteristically flows or streams freely throughout the hyphae, passing right through major pores in the septa (figure 36.3). Because of this streaming, proteins synthesized throughout the hyphae may be carried to their actively growing tips. As a result, fungal hyphae may grow very rapidly when food and water are abundant and the temperature is optimum.

A mass of connected hyphae is called a **mycelium** (plural, **mycelia**). This word and the term *mycologist* are both derived from the Greek word for fungus, *myketos*. The mycelium of a fungus (figure 36.4) constitutes a system that may, in the aggregate, be many meters long. This mycelium grows through and penetrates its substrate, resulting in a unique relationship between the fungus and its environment. All parts of such a fungus are metabolically active, continually interacting with the soil, wood, or other material in which the mycelium is growing.

In two of the three phyla of fungi, reproductive structures formed of interwoven hyphae, such as mushrooms, puffballs, and morels, are produced at certain stages of the life cycle. These structures expand rapidly because of rapid elongation of the hyphae. For this reason, mushrooms can appear suddenly on your lawn.

The cell walls of fungi are formed of polysaccharides and chitin, not cellulose like those of plants and many groups of protists. Chitin is the same material that makes up the major portion of the hard shells, or exoskeletons, of arthropods, a group of animals that includes insects and crustaceans (see chapter 46). The commonality of chitin is one of the traits that has led scientists to believe that fungi and animals share a common ancestor.

Mitosis in fungi differs from that in most other organisms. Because of the linked nature of the cells, the cell itself is not the relevant unit of reproduction; instead, the nucleus is. The nuclear envelope does not break down and re-form; instead, the spindle apparatus is formed *within* it. Centrioles are lacking in all fungi; instead, fungi regulate the formation of microtubules during mitosis with small, relatively amorphous structures called **spindle plaques**. This unique combination of features strongly suggests that fungi originated from some unknown group of single-celled eukaryotes with these characteristics.

Fungi exist primarily in the form of filamentous hyphae, typically with incomplete division into individual cells by septa. These and other unique features indicate that fungi are not closely related to any other group of organisms.



FIGURE 36.3
A septum (45,000 \times). This transmission electron micrograph of a section through a hypha of the basidiomycete *Inonotus tomentosus* shows a pore through which the cytoplasm streams.



FIGURE 36.4
Fungal mycelium. This mycelium, composed of hyphae, is growing through leaves on the forest floor in Maryland.

How Fungi Reproduce

Fungi are capable of both sexual and asexual reproduction. When a fungus reproduces sexually it forms a diploid zygote, as do animals and plants. Unlike animals and plants, all fungal nuclei except for the zygote are haploid, and there are many haploid nuclei in the common cytoplasm of a fungal mycelium. When fungi reproduce sexually, hyphae of two genetically different mating types come together and fuse. In two of the three phyla of fungi, the genetically different nuclei that are associated in a common cytoplasm after fusion do not combine immediately. Instead, the two types of nuclei coexist for most of the life of the fungus. A fungal hypha containing nuclei derived from two genetically distinct individuals is called a **heterokaryotic** hypha. If all of the nuclei are genetically similar to one another, the hypha is said to be **homokaryotic**. If there are two distinct nuclei within each compartment of the hyphae, they are **dikaryotic**. If each compartment has only a single nucleus, it is **monokaryotic**. Dikaryotic hyphae have some of the genetic properties of diploids, because both genomes are transcribed. These distinctions are important in understanding the life cycles of the individual groups.

Cytoplasm in fungal hyphae normally flows through perforated septa or moves freely in their absence. Reproductive structures are an important exception to this general pattern. When reproductive structures form, they are cut off by complete septa that lack perforations or have perforations that soon become blocked. Three kinds of reproductive structures occur in fungi: (1) **sporangia**, which are involved in the formation of spores; (2) **gametangia**, structures within which gametes form; and (3) **conidiophores**, structures that produce **conidia**, multinucleate asexual spores.

Spores are a common means of reproduction among fungi. They may form as a result of either asexual or sexual processes and are always nonmotile, being dispersed by wind. When spores land in a suitable place, they germinate, giving rise to a new fungal hypha. Because the spores are very small, they can remain suspended in the air for long periods of time. Because of this, fungal spores may be blown great distances from their place of origin, a factor in the extremely wide distributions of many kinds of fungi. Unfortunately, many of the fungi that cause diseases in plants and animals are spread rapidly and widely by such means. The spores of other fungi are routinely dispersed by insects and other small animals.

Fungi reproduce sexually after two hyphae of opposite mating type fuse. Asexual reproduction by spores is a second common means of reproduction.



FIGURE 36.5
A carnivorous fungus. The oyster mushroom, *Pleurotus ostreatus*, not only decomposes wood but also immobilizes nematodes, which the fungus uses as a source of nitrogen.

How Fungi Obtain Nutrients

All fungi obtain their food by secreting digestive enzymes into their surroundings and then absorbing back into the fungus the organic molecules produced by this **external digestion**. The significance of the fungal body plan reflects this approach, the extensive network of hyphae providing an enormous surface area for absorption. Many fungi are able to break down the cellulose in wood, cleaving the linkages between glucose subunits and then absorbing the glucose molecules as food. That is why fungi so often grow on dead trees.

It might surprise you to know that some fungi are predatory (figure 36.5). For example, the mycelium of the edible oyster fungus, *Pleurotus ostreatus*, excretes a substance that anesthetizes tiny roundworms known as nematodes (see chapter 44) that feed on the fungus. When the worms become sluggish and inactive, the fungal hyphae envelop and penetrate their bodies and absorb their nutritious contents. The fungus usually grows within living trees or on old stumps, obtaining the bulk of its glucose through the enzymatic digestion of cellulose from the wood, so that the nematodes it consumes apparently serve mainly as a source of nitrogen—a substance almost always in short supply in biological systems. Other fungi are even more active predators than *Pleurotus*, snaring, trapping, or firing projectiles into nematodes, rotifers, and other small animals on which they prey.

Fungi secrete digestive enzymes onto organic matter and then absorb the products of the digestion.

FIGURE 36.6

World's largest organism?

Armillaria, a pathogenic fungus shown here afflicting three discrete regions of coniferous forest in Montana, grows out from a central focus as a single circular clone. The large patch at the bottom of the picture is almost 8 hectares in diameter. The largest clone measured so far has been 15 hectares in diameter—pretty impressive for a single individual!



Ecology of Fungi

Fungi, together with bacteria, are the principal decomposers in the biosphere. They break down organic materials and return the substances locked in those molecules to circulation in the ecosystem. Fungi are virtually the only organisms capable of breaking down lignin, one of the major constituents of wood. By breaking down such substances, fungi release critical building blocks, such as carbon, nitrogen, and phosphorus, from the bodies of dead organisms and make them available to other organisms.

In breaking down organic matter, some fungi attack living plants and animals as a source of organic molecules, while others attack dead ones. Fungi often act as disease-causing organisms for both plants (figure 36.6) and animals, and they are responsible for billions of dollars in agricultural losses every year. Not only are fungi the most harmful pests of living plants, but they also attack food products once they have been harvested and stored. In addition, fungi often secrete substances into the foods that they are attacking that make these foods unpalatable, carcinogenic, or poisonous.

The same aggressive metabolism that makes fungi ecologically important has been put to commercial use in many ways. The manufacture of both bread and beer depends on the biochemical activities of **yeasts**, single-celled fungi that produce abundant quantities of ethanol and carbon dioxide. Cheese and wine achieve their delicate flavors because of the metabolic processes of certain fungi, and others make possible the manufacture of soy sauce and other fermented foods. Vast industries depend on the biochemical manufacture of organic substances such as citric

acid by fungi in culture, and yeasts are now used on a large scale to produce protein for the enrichment of animal food. Many antibiotics, including the first one that was used on a wide scale, penicillin, are derived from fungi.

Some fungi are used to convert one complex organic molecule into another, cleaning up toxic substances in the environment. For example, at least three species of fungi have been isolated that combine selenium, accumulated at the San Luis National Wildlife Refuge in California's San Joaquin Valley, with harmless volatile chemicals—thus removing excess selenium from the soil.

Two kinds of mutualistic associations between fungi and autotrophic organisms are ecologically important. **Lichens** are mutualistic symbiotic associations between fungi and either green algae or cyanobacteria. They are prominent nearly everywhere in the world, especially in unusually harsh habitats such as bare rock. **Mycorrhizae**, specialized mutualistic symbiotic associations between the roots of plants and fungi, are characteristic of about 90% of all plants. In each of them, the photosynthetic organisms fix atmospheric carbon dioxide and thus make organic material available to the fungi. The metabolic activities of the fungi, in turn, enhance the overall ability of the symbiotic association to exist in a particular habitat. In the case of mycorrhizae, the fungal partner expedites the plant's absorption of essential nutrients such as phosphorus. Both of these associations will be discussed further in this chapter.

Fungi are key decomposers and symbionts within almost all terrestrial ecosystems and play many other important ecological and commercial roles.

36.2 Fungi are classified by their reproductive structures.

The Three Phyla of Fungi

There are three phyla but actually four groups of fungi: phylum Zygomycota, the **zygomycetes**; phylum Ascomycota, the **ascomycetes**; phylum Basidiomycota, the **basidiomycetes**, and the imperfect fungi (figure 36.7 and table 36.1). Several other groups that historically have been associated with fungi, such as the slime molds and water molds (phylum Oomycota; see chapter 35), now are considered to be protists, not fungi. Oomycetes are sharply distinct from fungi in their (1) motile spores; (2) cellulose-rich cell walls; (3) pattern of mitosis; and (4) diploid hyphae.

The three phyla of fungi are distinguished primarily by their sexual reproductive structures. In the zygomycetes, the fusion of hyphae leads directly to the formation of a zygote, which divides by meiosis when it germinates. In the other two phyla, an extensive growth of dikaryotic hyphae may lead to the formation of structures of interwoven hyphae within which are formed the distinctive kind of reproductive cell characteristic of that particular group. Nuclear fusion, followed by meiosis, occurs within these cells. The imperfect fungi are either asexual or the sexual reproductive structures have not been identified.

Sexual reproductive structures distinguish the three phyla of fungi.

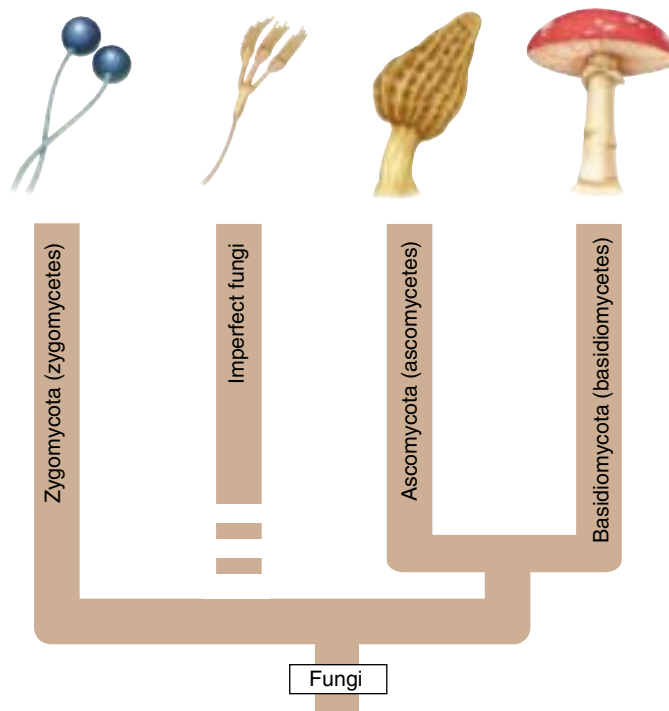






FIGURE 36.7
The four major groups of fungi. The imperfect fungi are not a true phylum, but rather a collection of fungi in which sexual structures have not been identified.

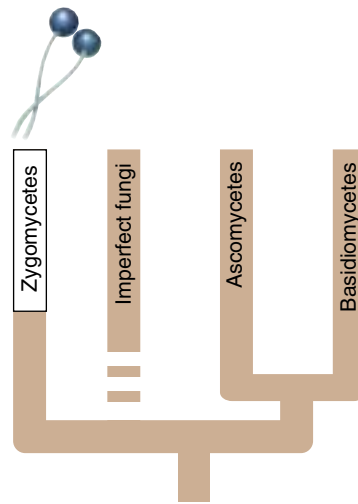
Table 36.1 Fungi

| Phylum | Typical Examples | Key Characteristics | Approximate Number of Living Species |
|-----------------|---|--|--------------------------------------|
| Ascomycota | Yeasts, truffles, morels  | Develop by sexual means; ascospores are formed inside a sac called an ascus; asexual reproduction is also common | 32,000 |
| Imperfect fungi | <i>Aspergillus</i> , <i>Penicillium</i>  | Sexual reproduction has not been observed; most are thought to be ascomycetes that have lost the ability to reproduce sexually | 17,000 |
| Basidiomycota | Mushrooms, toadstools, rusts  | Develop by sexual means; basidiospores are borne on club-shaped structures called basidia; the terminal hyphal cell that produces spores is called a basidium; asexual reproduction occurs occasionally | 22,000 |
| Zygomycota | <i>Rhizopus</i> (black bread mold)  | Develop sexually and asexually; multinucleate hyphae lack septa, except for reproductive structures; fusion of hyphae leads directly to formation of a zygote, in which meiosis occurs just before it germinates | 1050 |

Phylum Zygomycota

The zygomycetes (phylum Zygomycota) lack septa in their hyphae except when they form sporangia or gametangia. Zygomycetes are by far the smallest of the three phyla of fungi, with only about 1050 named species. Included among them are some of the more common bread molds (figure 36.8), as well as a variety of other microscopic fungi found on decaying organic material. The group is named after a characteristic feature of the life cycle of its members, the production of temporarily dormant structures called **zygosporangia**.

In the life cycle of the zygomycetes (figure 36.8b), sexual reproduction occurs by the fusion of gametangia, which contain numerous nuclei. The gametangia are cut off from the hyphae by complete septa. These gametangia may be formed on hyphae of different mating types or on a single hypha. If both + and - mating strains are present in a colony, they may grow together and their nuclei may fuse. Once the haploid nuclei have fused, forming diploid zygote nuclei, the area where the fusion has taken place develops into an often massive and elaborate zygosporangium. A zygosporangium may contain one or more diploid nuclei and acquires a thick



coat. The zygosporangium helps the species survive conditions not favorable for growth. Meiosis occurs during the germination of the zygosporangium. Normal, haploid hyphae grow from the haploid cells that result from this process. Except for the zygote nuclei, all nuclei of the zygomycetes are haploid.

Asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae grow over the surface of the bread or other material on which the fungus feeds and produce clumps of erect stalks, called **sporangiophores**. The tips of the sporangiophores form **sporangia**, which are separated by septa. Thin-walled haploid spores are produced within the sporangia. Their spores are thus shed above the substrate, in a position where they may be picked up by the wind and dispersed to a new food source.

Normal, haploid hyphae grow from the haploid cells that result from this process. Except for the zygote nuclei, all nuclei of the zygomycetes are haploid.

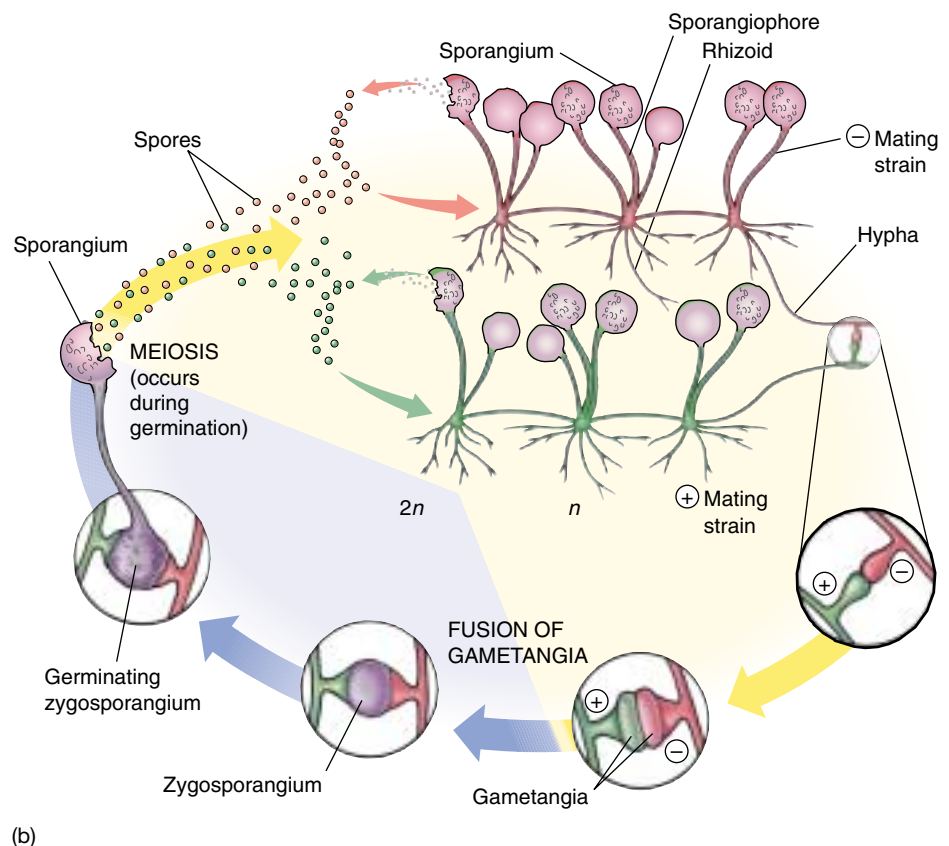
Zygomycetes form characteristic resting structures, called zygosporangia, which contain one or more zygotic nuclei. The hyphae of zygomycetes are multinucleate, with septa only where gametangia or sporangia are separated.



(a)

FIGURE 36.8

Rhizopus, a zygomycete that grows on moist bread and other similar substrates. (a) The dark, spherical, spore-producing sporangia are on hyphae about a centimeter tall. The rootlike hyphae anchor the sporangia. (b) Life cycle of *Rhizopus*, a zygomycete. This phylum is named for its characteristic zygosporangia.



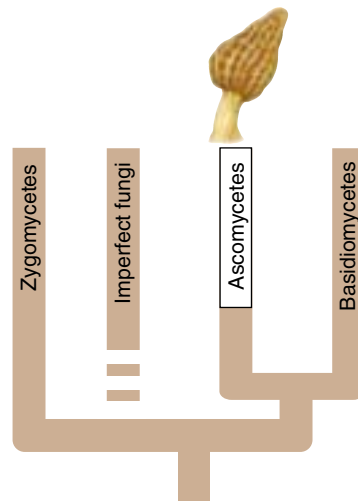
(b)

Phylum Ascomycota

The second phylum of fungi, the ascomycetes (phylum Ascomycota), is a very large group of about 32,000 named species, with more being discovered each year. Among the ascomycetes are such familiar and economically important fungi as yeasts, common molds, morels (figure 36.9a,b), and truffles. Also included in this phylum are many serious plant pathogens, including the chestnut blight, *Cryphonectria parasitica*, and Dutch elm disease, *Ophiostoma ulmi*.

The ascomycetes are named for their characteristic reproductive structure, the microscopic, saclike **ascus** (plural, **asci**). The zygotic nucleus, which is the only diploid nucleus of the ascomycete life cycle (figure 36.9c), is formed within the ascus. The asci are differentiated within a structure made up of densely interwoven hyphae, corresponding to the visible portions of a morel or cup fungus, called the **ascocarp**.

Asexual reproduction is very common in the ascomycetes. It takes place by means of **conidia** (singular,



conidium), spores cut off by septa at the ends of modified hyphae called **conidiophores**. Conidia allow for the rapid colonization of a new food source. Many conidia are multinucleate. The hyphae of ascomycetes are divided by septa, but the septa are perforated and the cytoplasm flows along the length of each hypha. The septa that cut off the asci and conidia are initially perforated, but later become blocked.

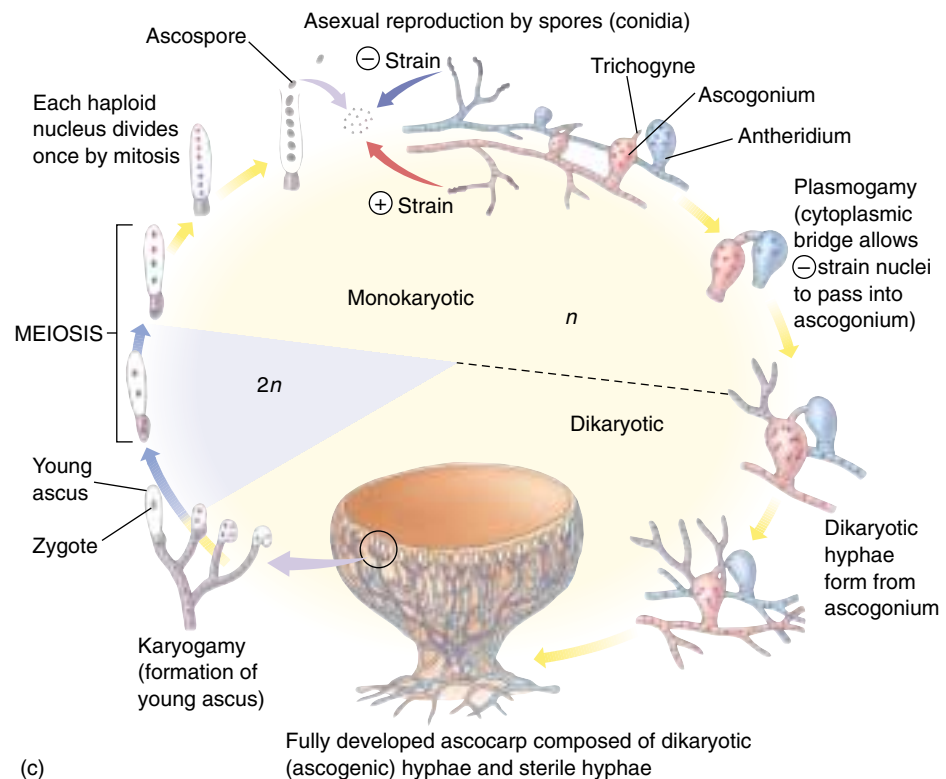
The cells of ascomycete hyphae may contain from several to many nuclei. The hyphae may be either homokaryotic or heterokaryotic. Female gametangia, called **ascogonia**, each have a beaklike outgrowth called a **trichogyne**. When the **antheridium**, or male gametangium, forms, it fuses with the trichogyne of an adjacent ascogonium. Initially, both kinds of gametangia contain a number of nuclei. Nuclei from the antheridium then migrate through the trichogyne into the ascogonium and pair with nuclei of the opposite mating type. Dikaryotic hyphae then arise from the area of the fusion. Throughout such hyphae,



(a)



(b)



(c)

FIGURE 36.9

An ascomycete. (a) This morel, *Morchella esculenta*, is a delicious edible ascomycete that appears in early spring. (b) A cup fungus. (c) Life cycle of an ascomycete. The zygote forms within the ascus.

nuclei that represent the two different original mating types occur. These hyphae are thus both dikaryotic and heterokaryotic.

Asci are formed at the tips of the dikaryotic hyphae and are separated by the formation of septa. There are two haploid nuclei within each ascus, one of each mating type represented in the dikaryotic hypha. Fusion of these two nuclei occurs within each ascus, forming a zygote. Each zygote divides immediately by meiosis, forming four haploid daughter nuclei. These usually divide again by mitosis, producing eight haploid nuclei that become walled **ascospores**. In many ascomycetes, the ascus becomes highly turgid at maturity and ultimately bursts, often at a preformed area. When this occurs, the ascospores may be thrown as far as 30 centimeters, an amazing distance considering that most ascospores are only about 10 micrometers long. This would be equivalent to throwing a baseball (diameter 7.5 centimeters) 1.25 kilometers—about 10 times the length of a home run!

Yeasts

Yeasts, which are unicellular, are one of the most interesting and economically important groups of microscopic fungi, usually ascomycetes. Most of their reproduction is asexual and takes place by cell fission or budding, when a smaller cell forms from a larger one (figure 36.10).

Sometimes two yeast cells will fuse, forming one cell containing two nuclei. This cell may then function as an ascus, with syngamy followed immediately by meiosis. The resulting ascospores function directly as new yeast cells.

Because they are single-celled, yeasts were once considered primitive fungi. However, it appears that they are actually reduced in structure and were originally derived from multicellular ancestors. The word *yeast* actually signifies only that these fungi are single-celled. Some yeasts have been derived from each of the three phyla of fungi, although ascomycetes are best represented. Even yeasts that were derived from ascomycetes are not necessarily directly related to one another, but instead seem to have been derived from different groups of ascomycetes.

Putting Yeasts to Work. The ability of yeasts to ferment carbohydrates, breaking down glucose to produce ethanol and carbon dioxide, is fundamental in the production of bread, beer, and wine. Many different strains of yeast have been domesticated and selected for these processes. Wild yeasts—ones that occur naturally in the areas where wine is made—were important in wine making historically, but domesticated yeasts are normally used now. The most important yeast in all these processes is *Saccharomyces cerevisiae*. This yeast has been used by humans throughout recorded history. Other yeasts are important pathogens and cause diseases such as thrush and



FIGURE 36.10

Scanning electron micrograph of a yeast, showing the characteristic cell division method of budding (19,000 \times). The cells tend to hang together in chains, a feature that calls to mind the derivation of single-celled yeasts from multicellular ancestors.

cryptococcosis; one of them, *Candida*, causes common oral or vaginal infections.

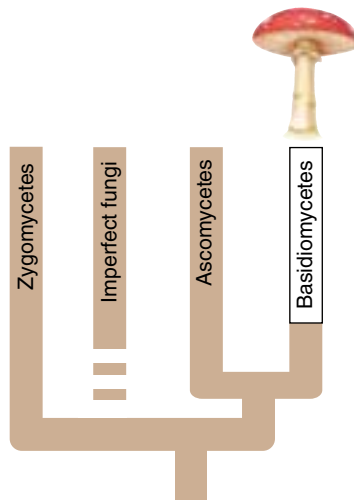
Over the past few decades, yeasts have become increasingly important in genetic research. They were the first eukaryotes to be manipulated extensively by the techniques of genetic engineering, and they still play the leading role as models for research in eukaryotic cells. In 1983, investigators synthesized a functional artificial chromosome in *Saccharomyces cerevisiae* by assembling the appropriate DNA molecule chemically; this has not yet been possible in any other eukaryote. In 1996, the genome sequence of *S. cerevisiae*, the first eukaryote to be sequenced entirely, was completed. With their rapid generation time and a rapidly increasing pool of genetic and biochemical information, the yeasts in general and *S. cerevisiae* in particular are becoming the eukaryotic cells of choice for many types of experiments in molecular and cellular biology. Yeasts have become, in this respect, comparable to *Escherichia coli* among the bacteria, and they are continuing to provide significant insights into the functioning of eukaryotic systems.

Ascomycetes form their zygotes within a characteristic saclike structure, the ascus. Meiosis follows, resulting in the production of ascospores. Yeasts are unicellular fungi, mainly ascomycetes, that have evolved from hypha-forming ancestors; not all yeasts are directly related to one another. Long useful for baking, brewing, and wine making, yeasts are now becoming very important in genetic research.

Phylum Basidiomycota

The third phylum of fungi, the basidiomycetes (phylum Basidiomycota), has about 22,000 named species. These are among the most familiar fungi. Among the basidiomycetes are not only the mushrooms, toadstools, puffballs, jelly fungi, and shelf fungi, but also many important plant pathogens including rusts and smuts (figure 36.11). Many mushrooms are used as food, but others are deadly poisonous.

Basidiomycetes are named for their characteristic sexual reproductive structure, the **basidium** (plural, **basidia**). A basidium is club-shaped. Karyogamy occurs within the basidium, giving rise to the zygote, the only diploid cell of the life cycle (figure 36.11*b*). As in all fungi, meiosis occurs immediately after the formation of the zygote. In the basidiomycetes, the four haploid products of meiosis are incorporated into **basidiospores**. In most members of this phylum, the basidiospores are borne at the end of the basidia on slender projections called **sterigmata** (singular, **sterigma**). Thus the structure of a basidium differs from that of an ascus, although functionally the two are identical. Recall that the ascospores of the ascomycetes are borne internally in asci.



The life cycle of a basidiomycete continues with the production of homokaryotic hyphae after spore germination. These hyphae lack septa at first. Eventually, septa form between the nuclei of the monokaryotic hyphae. A basidiomycete mycelium made up of monokaryotic hyphae is called a **primary mycelium**. Different mating types of monokaryotic hyphae may fuse, forming a dikaryotic or **secondary mycelium**. Such a mycelium is heterokaryotic, with two nuclei, representing the two different mating types, between each pair of septa. The maintenance of two genomes in the heterokaryon allows for more genetic plasticity than in a diploid cell with one nucleus. One genome may compensate for mutations in the other. The **basidiocarps**, or mushrooms, are formed entirely of secondary (dikaryotic) mycelium. Gills on the underside of the cap of a mushroom form vast numbers of minute spores. It has been estimated that a mushroom with a cap that is 7.5 centimeters across produces as many as 40 million spores per hour!

Most basidiomycete hyphae are dikaryotic. Ultimately, the hyphae fuse to form basidiocarps, with basidia lining the gills on the underside. Meiosis immediately follows syngamy in these basidia.

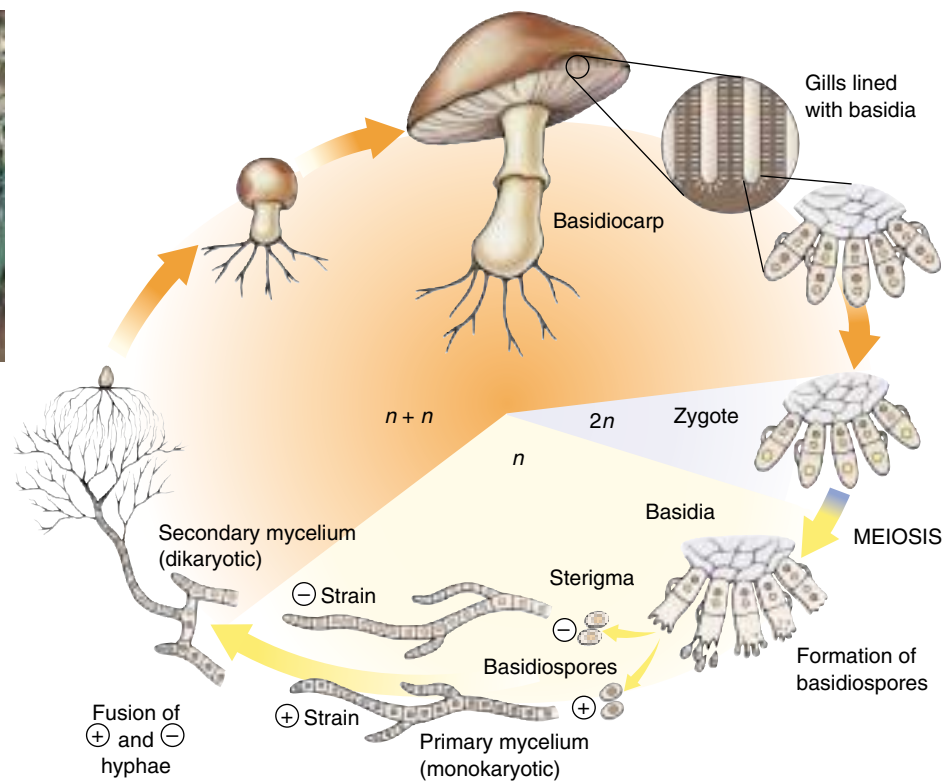
Most basidiomycete hyphae are dikaryotic. Ultimately, the hyphae fuse to form basidiocarps, with basidia lining the gills on the underside. Meiosis immediately follows syngamy in these basidia.



(a)

FIGURE 36.11

Basidiomycetes. (a) Death cap mushroom, *Amanita phalloides*. When eaten, these mushrooms are usually fatal. (b) Life cycle of a basidiomycete. The basidium is the reproductive structure where syngamy occurs.

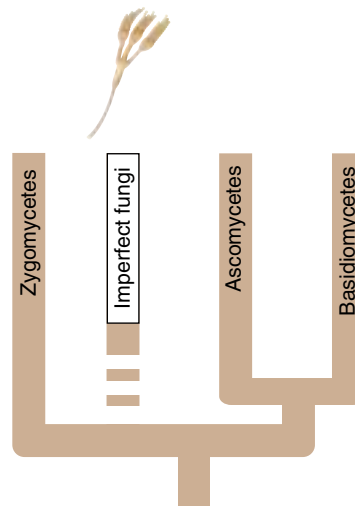


(b)

The Imperfect Fungi

Most of the so-called imperfect fungi, a group also called deuteromycetes, are those in which the sexual reproductive stages have not been observed. Most of these appear to be related to ascomycetes although some have clear affinities to the other phyla. The group of fungi from which a particular nonsexual strain has been derived usually can be determined by the features of its hyphae and asexual reproduction. It cannot, however, be classified by the standards of that group because the classification systems are based on the features related to sexual reproduction. One consequence of this system is that as sexual reproduction is discovered in an imperfect fungus, it may have two names assigned to different stages of its life cycle.

There are some 17,000 described species of imperfect fungi (figure 36.12). Even though sexual reproduction is absent among imperfect fungi, a certain amount of genetic recombination occurs. This becomes possible when hyphae of different genetic types fuse, as sometimes happens spontaneously. Within the heterokaryotic hyphae that arise from such fusion, a special kind of genetic recombination called **parasexuality** may occur. In parasexuality, genetically distinct nuclei within a common hypha exchange portions of chromosomes. Recombination of this sort also occurs in other groups of fungi and seems to be responsible for some of the new pathogenic strains of wheat rust.



Economic Importance

Among the economically important genera of the imperfect fungi are *Penicillium* and *Aspergillus*. Some species of *Penicillium* are sources of the well-known antibiotic penicillin, and other species of the genus give the characteristic flavors and aromas to cheeses such as Roquefort and Camembert. Species of *Aspergillus* are used to ferment soy sauce and soy paste, processes in which certain bacteria and yeasts also play important roles. Citric acid is produced commercially with members of this genus under highly acidic conditions. Some species of both *Penicillium* and *Aspergillus* form ascocarps, but the genera are still classified primarily as imperfect fungi because the ascocarps are found rarely in only a few species. Most of the fungi that cause skin diseases in humans, including athlete's foot and ringworm, are also imperfect fungi.

A number of imperfect fungi occur widely on food. *Fusarium* species growing on spoiled food produce highly toxic substances such as trichothecenes. Aflatoxins, among the most carcinogenic compounds known, are produced by some *Aspergillus flavus* strains growing on corn, peanuts, etc. Most developed countries have legal limits on the concentration of aflatoxin permitted in different foods.

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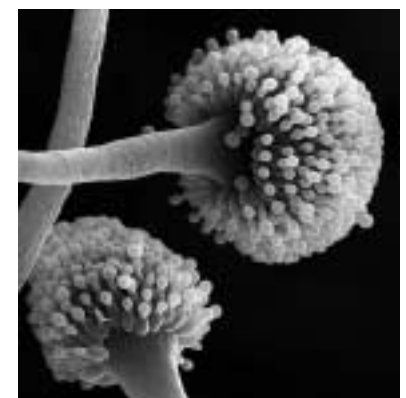
Imperfect fungi are fungi in which no sexual reproduction has been observed. For this reason, they cannot be classified by the standards applied to the three phyla of fungi. The great majority of the imperfect fungi are clearly ascomycetes.



(a)



(b)



(c)

FIGURE 36.12

The imperfect fungi. (a) *Verticillium albo-atrum* (1350 \times), an important pathogen of alfalfa, has whorled conidiophores. The single-celled conidia of this member of the imperfect fungi are borne at the ends of the conidiophores. (b) In *Tolypocladium inflatum*, the conidia arise along the branches. This fungus is one of the sources of cyclosporin, a drug that suppresses immune reactions and thus assists in making human organ grafts possible; the drug was put on the market in 1979. (c) This scanning electron micrograph of *Aspergillus* shows conidia, the spheres at the end of the hyphae.

36.3 Fungi form two key mutualistic symbiotic associations.

Lichens

Lichens (figure 36.13) are symbiotic associations between a fungus and a photosynthetic partner. They provide an outstanding example of mutualism, the kind of symbiotic association that benefits both partners. Ascomycetes (including some imperfect fungi) are the fungal partners in all but about 20 of the approximately 15,000 species of lichens estimated to exist; the exceptions, mostly tropical, are basidiomycetes. Most of the visible body of a lichen consists of its fungus, but within the tissues of that fungus are found cyanobacteria, green algae, or sometimes both (figure 36.14). Specialized fungal hyphae penetrate or envelop the photosynthetic cells within them and transfer nutrients directly to the fungal partner. Biochemical “signals” sent out by the fungus apparently direct its cyanobacterial or green algal component to produce metabolic substances that it does not produce when growing independently of the fungus. The photosynthetic member of the association is normally held between thick layers of interwoven fungal hyphae and is not directly exposed to the light, but enough light penetrates the translucent layers of fungal hyphae to make photosynthesis possible. The fungi in lichens are unable to grow normally without their photosynthetic partners and the fungi protect their partners from strong light and desiccation.

The durable construction of the fungus, combined with the photosynthetic properties of its partner, has enabled lichens to invade the harshest habitats at the tops of mountains, in the farthest northern and southern latitudes, and on dry, bare rock faces in the desert. In harsh, exposed areas, lichens are often the first colonists, breaking down the rocks and setting the stage for the invasion of other organisms.

Lichens are often strikingly colored because of the presence of pigments that probably play a role in protecting the photosynthetic partner from the destructive action of the sun’s rays. These same pigments may be extracted from the lichens and used as natural dyes. The traditional method of manufacturing Scotland’s famous Harris tweed used fungal dyes.

Lichens are extremely sensitive to pollutants in the atmosphere, and thus they can be used as bioindicators of air quality. Their sensitivity results from their ability to absorb substances dissolved in rain and dew. Lichens are generally absent in and around cities because of automo-



(a)



(b)

FIGURE 36.13

Lichens are found in a variety of habitats. (a) A fruticose lichen, *Cladonia evansii*, growing on the ground in Florida. (b) A foliose (“leafy”) lichen, *Parmotrema gardneri*, growing on the bark of a tree in a mountain forest in Panama.

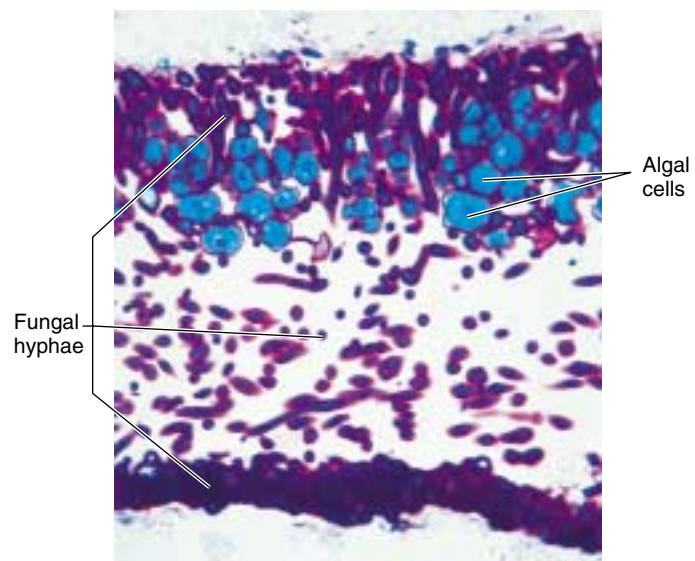


FIGURE 36.14

Stained section of a lichen (250×). This section shows fungal hyphae (purple) more densely packed into a protective layer on the top and, especially, the bottom layer of the lichen. The blue cells near the upper surface of the lichen are those of a green alga. These cells supply carbohydrate to the fungus.

bile traffic and industrial activity, even though suitable substrates exist.

Lichens are symbiotic associations between a fungus—an ascomycete in all but a very few instances—and a photosynthetic partner, which may be a green alga or a cyanobacterium or both.

Mycorrhizae

The roots of about 90% of all kinds of vascular plants normally are involved in mutualistic symbiotic relationships with certain kinds of fungi. It has been estimated that these fungi probably amount to 15% of the total weight of the world's plant roots. Associations of this kind are termed **mycorrhizae** (from the Greek words for “fungus” and “roots”). The fungi in mycorrhizae associations function as extensions of the root system. The fungal hyphae dramatically increase the amount of soil contact and total surface area for absorption. When mycorrhizae are present, they aid in the direct transfer of phosphorus, zinc, copper, and other nutrients from the soil into the roots. The plant, on the other hand, supplies organic carbon to the fungus, so the system is an example of mutualism.

There are two principal types of mycorrhizae (figure 36.15): **endomycorrhizae**, in which the fungal hyphae penetrate the outer cells of the plant root, forming coils, swellings, and minute branches, and also extend out into the surrounding soil; and **ectomycorrhizae**, in which the hyphae surround but do not penetrate the cell walls of the roots. In both kinds of mycorrhizae, the mycelium extends far out into the soil.

Endomycorrhizae

Endomycorrhizae are by far the more common of these two types. The fungal component in them is a zygomycete. Only about 100 species of zygomycetes are known to be involved in such relationships throughout the world. These few species of zygomycetes are associated with more than 200,000 species of plants. Endomycorrhizal fungi are being studied intensively because they are potentially capable of increasing crop yields with lower phosphate and energy inputs.

The earliest fossil plants often show endomycorrhizal roots. Such associations may have played an important role in allowing plants to colonize land. The soils available at such times would have been sterile and completely lacking in organic matter. Plants that form mycorrhizal associations are particularly successful in infertile soils; considering the fossil evidence, the suggestion that mycorrhizal associations found in the earliest plants helped them succeed on such soils seems reasonable. In addition, the most primitive vascular plants surviving today continue to depend strongly on mycorrhizae.

Ectomycorrhizae

Ectomycorrhizae (figure 36.15*b*) involve far fewer kinds of plants than do endomycorrhizae, perhaps a few thousand. They are characteristic of certain groups of trees and shrubs, particularly those of temperate regions, including pines, oaks, beeches, and willows. The fungal components in most ectomycorrhizae are basidiomycetes, but

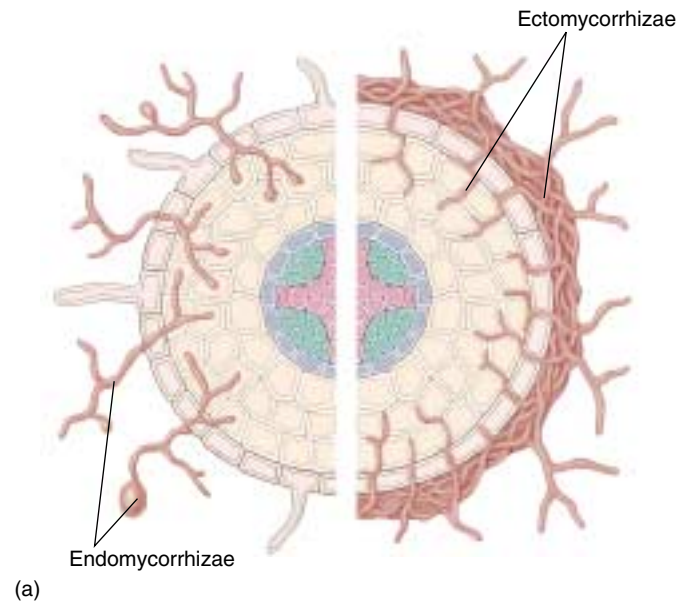


FIGURE 36.15
Endomycorrhizae and ectomycorrhizae. (a) In endomycorrhizae, fungal hyphae penetrate and branch out in the root cells of plants. In ectomycorrhizae, fungal hyphae do not penetrate root cells but grow around and extend between the cells. (b) Ectomycorrhizae on roots of pines. From left to right are yellow-brown mycorrhizae formed by *Pisolithus*, white mycorrhizae formed by *Rhizopogon*, and pine roots not associated with a fungus.

some are ascomycetes. Several different kinds of ectomycorrhizal fungi may form mycorrhizal associations with one plant. Different combinations have different effects on the physiological characteristics of the plant and its ability to survive under different environmental conditions. At least 5000 species of fungi are involved in ectomycorrhizal relationships, and many of them are restricted to a single species of plant.

Mycorrhizae are symbiotic associations between plants and fungi.



Summary

Questions

Media Resources

36.1 Fungi are unlike any other kind of organism.

- The fungi are a distinct kingdom of eukaryotic organisms characterized by a filamentous growth form, lack of chlorophyll and motile cells, chitin-rich cell walls, and external digestion of food by the secretion of enzymes.
- Fungal filaments, called hyphae, collectively make up the fungus body, which is called the mycelium.
- In many fungi, the two kinds of nuclei that will eventually undergo syngamy occur together in hyphae for a long period before they fuse. Meiosis occurs immediately after the formation of the zygote in all fungi; the zygote, therefore, is the only diploid nucleus of the entire life cycle in these organisms.

1. What is a hypha? What is the advantage to having incomplete septa?
2. What is the composition of the fungal cell wall? Why is this composition an advantage to the fungi?
3. Which fungal nuclei are diploid? Which are haploid? To what do the following terms refer: *heterokaryotic*, *homokaryotic*, *dikaryotic*, and *monokaryotic*?



- Characteristics of Fungi

36.2 Fungi are classified by their reproductive structures.

- There are three phyla of fungi: Zygomycota, the zygomycetes; Ascomycota, the ascomycetes; and Basidiomycota, the basidiomycetes.
- Zygomycetes form septa only when gametangia or sporangia are cut off at the ends of their hyphae; otherwise, their hyphae are multinucleate. Most hyphae of ascomycetes and basidiomycetes have perforated septa through which the cytoplasm, but not necessarily the nuclei, flows freely.
- Cells within the heterokaryotic hyphae of ascomycetes are multinucleate; those within the heterokaryotic hyphae of the basidiomycetes are dikaryotic. Zygotes in ascomycetes form within sac-like structures known as asci, and those in basidiomycetes form within structures known as basidia.
- Asexual reproduction in zygomycetes takes place by means of spores from multinucleate sporangia; in ascomycetes, it takes place by means of conidia. Asexual reproduction in basidiomycetes is rare.

4. What are the three reproductive structures that occur in fungi? How do they differ?
5. Fungi are nonmotile. How are they dispersed to new areas?
6. What are the ascomycete asexual spores called? Do the nonreproductive hyphae of this division have septa?
7. To what phyla do the yeasts belong? How do they differ from other fungi? Is it more likely that this characteristic is primitive or degenerate?
8. What are the imperfect fungi? Which phylum seems to be best represented in this group? By what means can individuals in this group be classified?



- Diversity of Fungi



- Student Research: Mushroom Spore Germination

36.3 Fungi form two key mutualistic symbiotic associations.

- Lichens are mutualistic symbiotic systems involving fungi (almost always ascomycetes), which derive their nutrients from green algae, cyanobacteria, or both.
 - Mycorrhizae are mutualistic symbiotic associations between fungi and plants. Endomycorrhizae, more common, involve zygomycetes, while ectomycorrhizal fungi are mainly basidiomycetes.
9. What are lichens? Which fungal phylum is best represented in the lichens?
 10. What are mycorrhizae? How do endomycorrhizae and ectomycorrhizae differ?