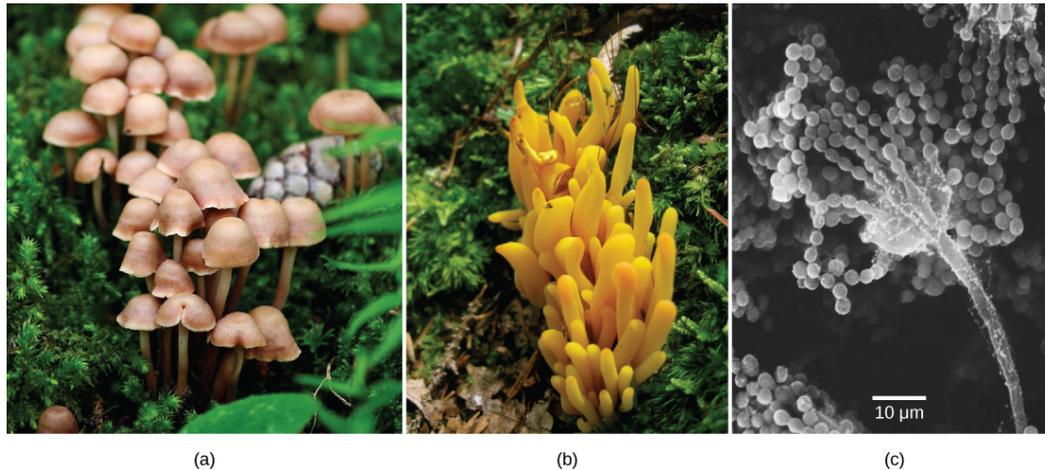


# 24 | FUNGI



**Figure 24.1** Many species of fungus produce the familiar mushroom (a) which is a reproductive structure. This (b) coral fungus displays brightly colored fruiting bodies. This electron micrograph shows (c) the spore-bearing structures of *Aspergillus*, a type of toxic fungi found mostly in soil and plants. (credit “mushroom”: modification of work by Chris Wee; credit “coral fungus”: modification of work by Cory Zanker; credit “*Aspergillus*”: modification of work by Janice Haney Carr, Robert Simmons, CDC; scale-bar data from Matt Russell)

## Chapter Outline

**24.1: Characteristics of Fungi**

**24.2: Classifications of Fungi**

**24.3: Ecology of Fungi**

**24.4: Fungal Parasites and Pathogens**

**24.5: Importance of Fungi in Human Life**

## Introduction

The word *fungus* comes from the Latin word for mushrooms. Indeed, the familiar mushroom is a reproductive structure used by many types of fungi. However, there are also many fungi species that don't produce mushrooms at all. Being eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles. The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eucomycota, or true Fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the 1.5 million species of fungus likely present on Earth. Edible mushrooms, yeasts, black mold, and the producer of the antibiotic penicillin, *Penicillium notatum*, are all members of the kingdom Fungi, which belongs to the domain Eukarya.

Fungi, once considered plant-like organisms, are more closely related to animals than plants. Fungi are not capable of photosynthesis: they are heterotrophic because they use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction with alternation of generations. Most fungi produce a large number of **spores**, which are haploid cells that can undergo mitosis to form multicellular, haploid individuals. Like bacteria, fungi play an essential role in ecosystems because they are decomposers and participate in the cycling of nutrients by breaking down organic materials to simple molecules.

Fungi often interact with other organisms, forming beneficial or mutualistic associations. For example most terrestrial plants form symbiotic relationships with fungi. The roots of the plant connect with the underground parts of the fungus forming **mycorrhizae**. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species. Alternatively, lichens are an association between a fungus and its photosynthetic partner (usually an alga). Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi*, is a particularly devastating type of fungal infestation that destroys many native species of elm (*Ulmus* sp.) by infecting the tree's vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree.

Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than American elms.

In humans, fungal infections are generally considered challenging to treat. Unlike bacteria, fungi do not respond to traditional antibiotic therapy, since they are eukaryotes. Fungal infections may prove deadly for individuals with compromised immune systems.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and cheese and wine making. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

## 24.1 | Characteristics of Fungi

By the end of this section, you will be able to:

- List the characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi

Although humans have used yeasts and mushrooms since prehistoric times, until recently, the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, arose mostly sessile and seemingly rooted in place. They possess a stem-like structure similar to plants, as well as having a root-like fungal mycelium in the soil. In addition, their mode of nutrition was poorly understood. Progress in the field of fungal biology was the result of **mycology**: the scientific study of fungi. Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome demonstrates that fungi are more closely related to animals than plants. They are a polyphyletic group of organisms that share characteristics, rather than sharing a single common ancestor.

### career CONNECTION

#### Mycologist

Mycologists are biologists who study fungi. Mycology is a branch of microbiology, and many mycologists start their careers with a degree in microbiology. To become a mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are minimally necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the world, or the deadly epidemic called white nose syndrome, which is decimating bats in the Eastern United States.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests. Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good understanding of fungal physiology routinely work in the food technology industry. Oenology, the science of wine making, relies not only on the knowledge of grape varieties and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

## Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches (Figure 24.2). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

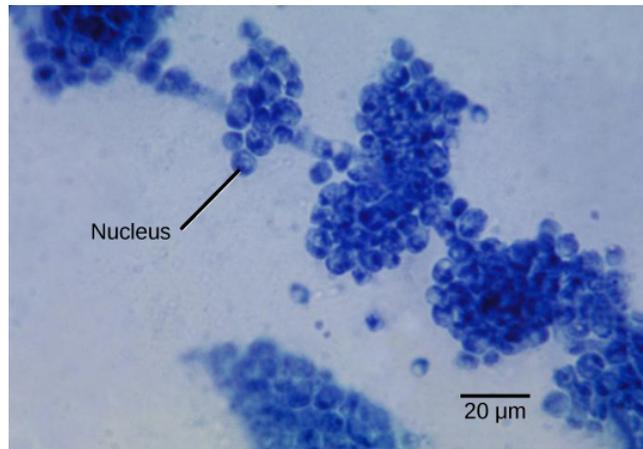


**Figure 24.2** The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America. (credit: Christine Majul)

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive Phylum Chytridiomycota.

### Growth

The vegetative body of a fungus is a unicellular or multicellular **thallus**. Dimorphic fungi can change from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi (Figure 24.3).



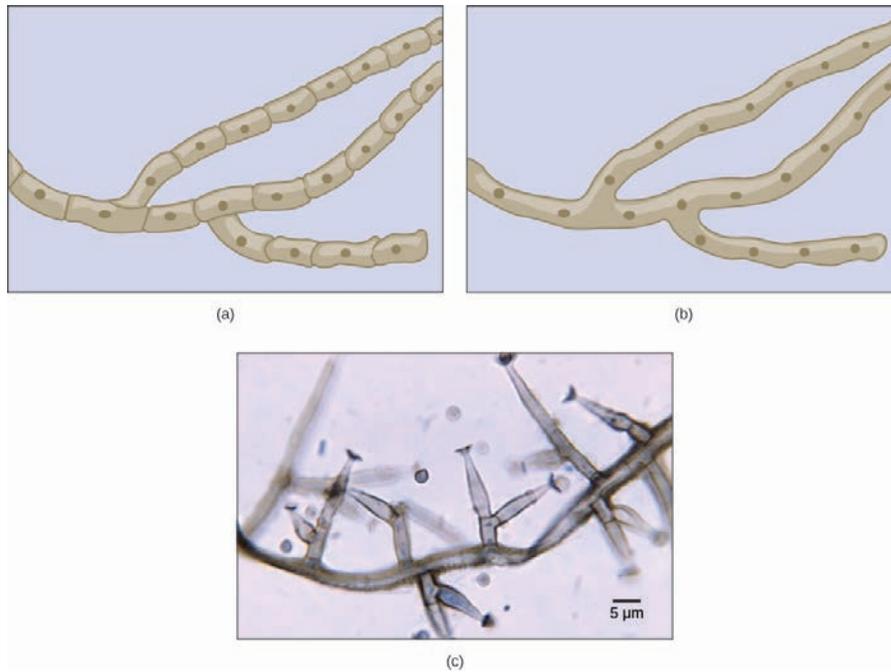
**Figure 24.3** *Candida albicans* is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

Most fungi are multicellular organisms. They display two distinct morphological stages: the vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, **hypha**), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a **mycelium** (**Figure 24.4**). It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being “the fungus humongous.” The giant *Armillaria solidipes* (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.



**Figure 24.4** The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC)

Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) (**Figure 24.5a, c**). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as **coenocytic hyphae** (**Figure 24.5b**).



**Figure 24.5** Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirement. Most fungi are **obligate aerobes**, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are **obligate anaerobes**, in that they only use anaerobic respiration because oxygen will disrupt their metabolism or kill them. Yeasts are intermediate, being **facultative anaerobes**. This means that they grow best in the presence of oxygen using aerobic respiration, but can survive using anaerobic respiration when oxygen is not available. The alcohol produced from yeast fermentation is used in wine and beer production.

### Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen, rather than starch, as found in plants.

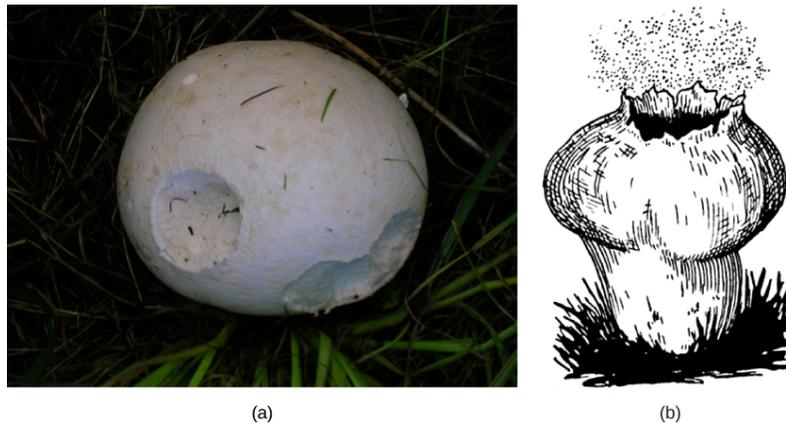
Fungi are mostly **saprobies** (saprophyte is an equivalent term): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and polycyclic aromatic hydrocarbons (PAHs). Other species take up heavy metals, such as cadmium and lead.

Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete's foot and candidiasis (thrush) are medically important fungal infections in humans. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called **haustoria**. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host, release digestive enzymes within the host's body, and absorb the digested nutrients.

## Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while the so-called imperfect fungi reproduce only asexually (by mitosis).

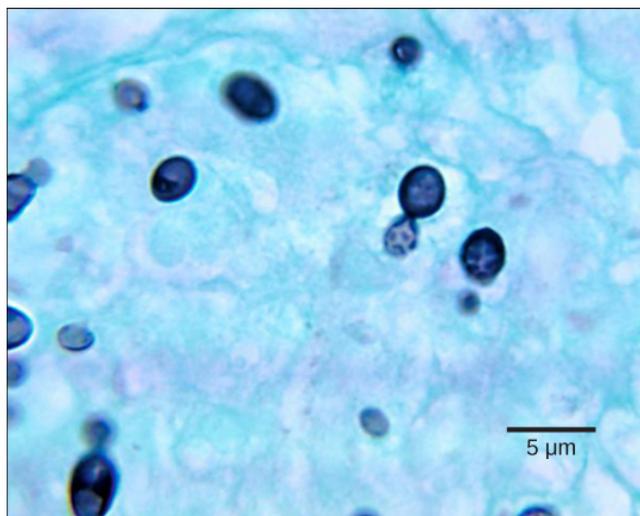
In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth (**Figure 24.6**).



**Figure 24.6** The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

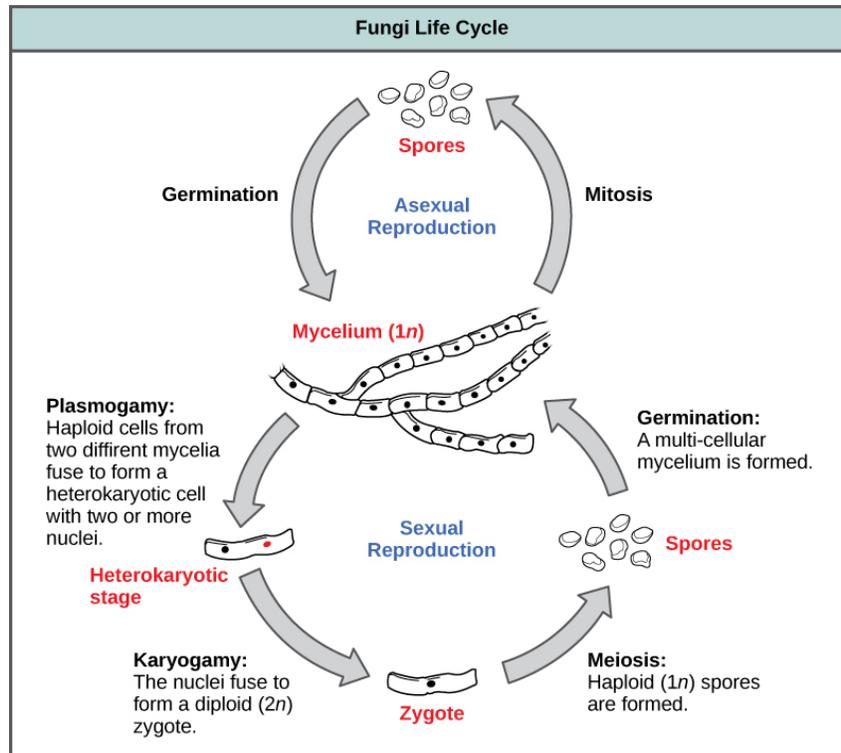
### Asexual Reproduction

Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell (**Figure 24.7**).



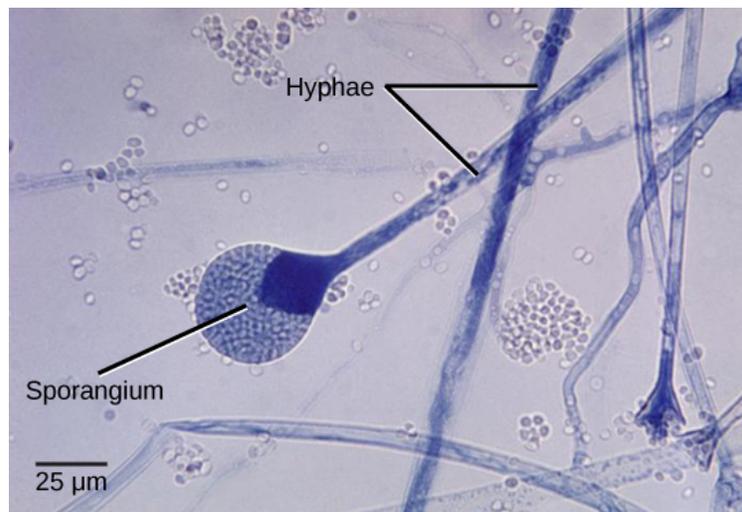
**Figure 24.7** The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. *Histoplasma* primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

The most common mode of asexual reproduction is through the formation of asexual spores, which are produced by one parent only (through mitosis) and are genetically identical to that parent (**Figure 24.8**). Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus either outside or within a special reproductive sac called a **sporangium**.



**Figure 24.8** Fungi may have both asexual and sexual stages of reproduction.

There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium (**Figure 24.9**).



**Figure 24.9** This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

### Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages (**Figure 24.8**). First, during **plasmogamy** (literally, “marriage or union of cytoplasm”), two haploid cells fuse, leading to a dikaryotic stage where two haploid nuclei coexist in a single cell. During **karyogamy** (“nuclear marriage”), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.



Review the characteristics of fungi by visiting this **interactive site** ([http://openstaxcollege.org/l/fungi\\_kingdom](http://openstaxcollege.org/l/fungi_kingdom)) from Wisconsin-online.

## 24.2 | Classifications of Fungi

By the end of this section, you will be able to:

- Classify fungi into the five major phyla
- Describe each phylum in terms of major representative species and patterns of reproduction

The kingdom Fungi contains five major phyla that were established according to their mode of sexual reproduction or using molecular data. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, are placed for convenience in a sixth group called a “form phylum”. Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a part of RNA) continue to show new and different relationships between the various categories of fungi.

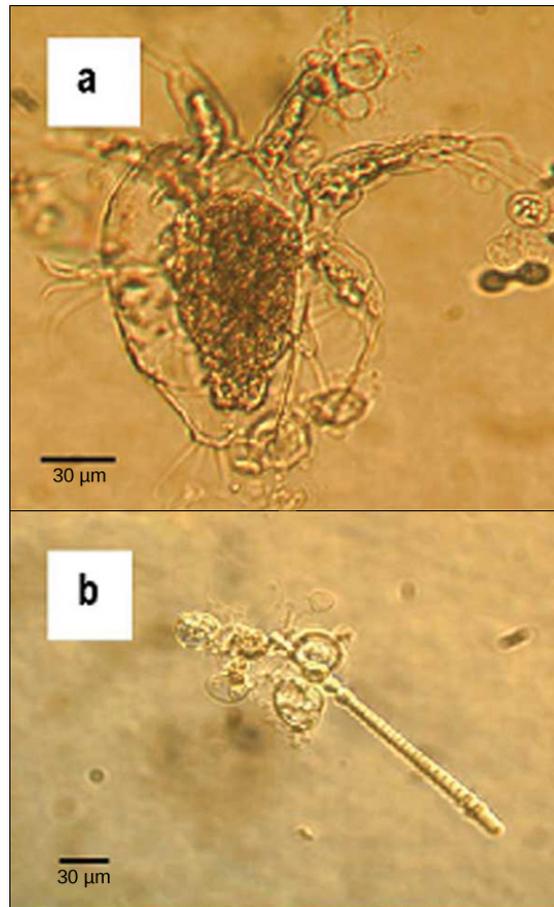
The five true phyla of fungi are the Chytridiomycota (Chytrids), the Zygomycota (conjugated fungi), the Ascomycota (sac fungi), the Basidiomycota (club fungi) and the recently described Phylum Glomeromycota. An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use.

Note: “-mycota” is used to designate a phylum while “-mycetes” formally denotes a class or is used informally to refer to all members of the phylum.

### Chytridiomycota: The Chytrids

The only class in the Phylum Chytridiomycota is the **Chytridiomycetes**. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They produce gametes and diploid zoospores that swim with the help of a single flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians (**Figure 24.10**), while others are saprobes. The chytrid species *Allomyces* is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.

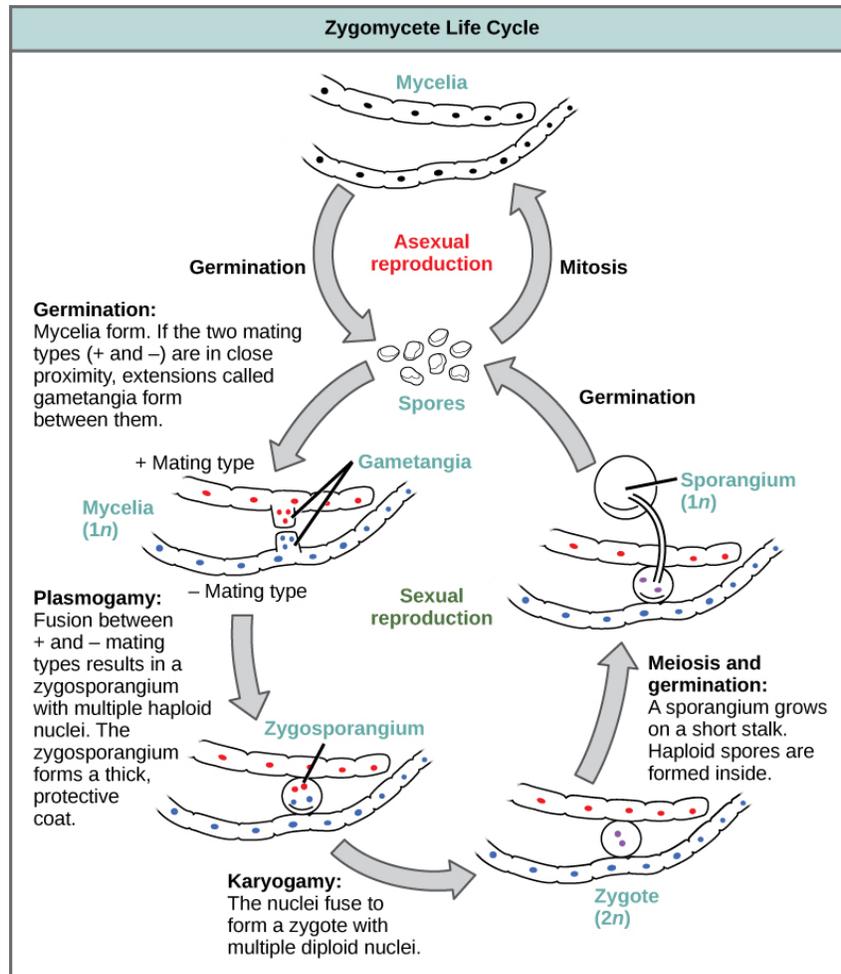


**Figure 24.10** The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work by Johnson ML, Speare R., CDC)

## Zygomycota: The Conjugated Fungi

The zygomycetes are a relatively small group of fungi belonging to the Phylum **Zygomycota**. They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. Most species are saprobes, living off decaying organic material; a few are parasites, particularly of insects. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores (**Figure 24.11**). The black tips of bread mold are the swollen sporangia packed with black spores (**Figure 24.12**). When spores land on a suitable substrate, they germinate and produce a new mycelium. Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia from the hyphae to be produced and fuse, leading to karyogamy. The developing diploid **zygospores** have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi”.



**Figure 24.11** Zygomycetes have asexual and asexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.



**Figure 24.12** Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

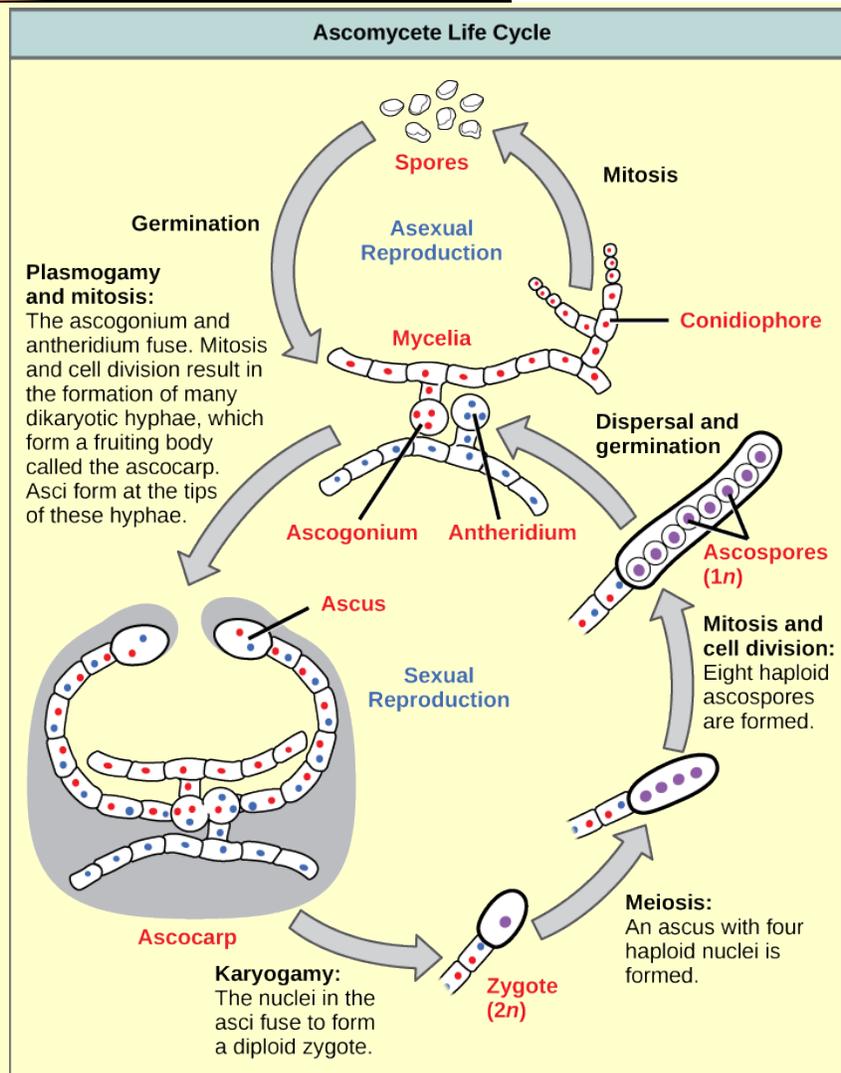
## Ascomycota: The Sac Fungi

The majority of known fungi belong to the Phylum **Ascomycota**, which is characterized by the formation of an **ascus** (plural, asci), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly; they also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce

hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores (**Figure 24.13**). Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains (**Figure 24.13**). The “male” strain produces an antheridium and the “female” strain develops an ascogonium. At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the “male” strain and one from the “female” strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy. During sexual reproduction, thousands of asci fill a fruiting body called the **ascocarp**. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia (**Figure 24.14**).

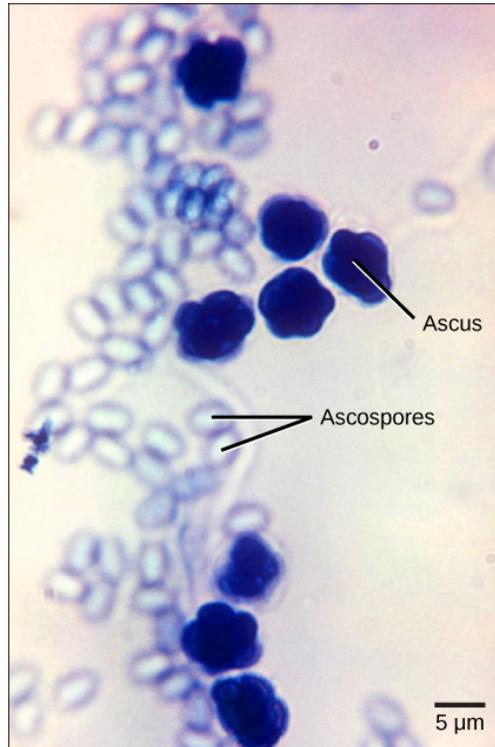
# art CONNECTION



**Figure 24.13** The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Which of the following statements is true?

- A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
- A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
- A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
- A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.



**Figure 24.14** The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

## Basidiomycota: The Club Fungi

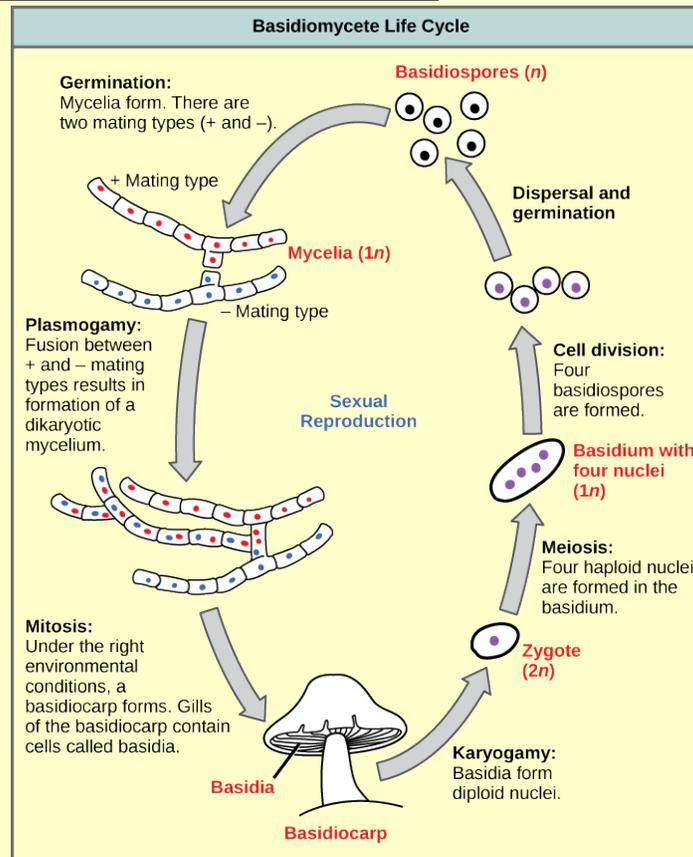
The fungi in the Phylum **Basidiomycota** are easily recognizable under a light microscope by their club-shaped fruiting bodies called **basidia** (singular, **basidium**), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn (**Figure 24.15**). These mushroom-producing basidiomycetes are sometimes referred to as “gill fungi” because of the presence of gill-like structures on the underside of the cap. The “gills” are actually compacted hyphae on which the basidia are borne. This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens; toadstools, and shelf fungi stacked on tree trunks. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.



**Figure 24.15** The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring.” The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center and leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen. (Credit: "Cropcircles"/Wikipedia Commons)]

The lifecycle of basidiomycetes includes alternation of generations (**Figure 24.16**). Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomycetes lifecycle and it is the dominant stage. Eventually, the secondary mycelium generates a **basidiocarp**, which is a fruiting body that protrudes from the ground—this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

# art CONNECTION



**Figure 24.16** The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

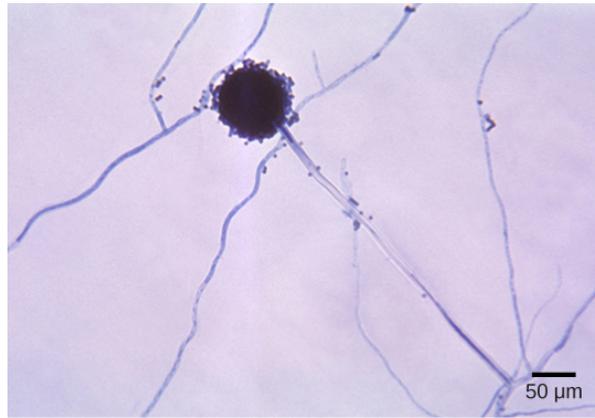
Which of the following statements is true?

- A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
- The result of the plasmogamy step is four basidiospores.
- Karyogamy results directly in the formation of mycelia.
- A basidiocarp is the fruiting body of a mushroom-producing fungus.

## Asexual Ascomycota and Basidiomycota

Imperfect fungi—those that do not display a sexual phase—use to be classified in the form phylum **Deuteromycota**, a classification group no longer used in the present, ever-developing classification of organisms. While Deuteromycota use to be a classification group, recent molecular analysis has shown that the members classified in this group belong to the Ascomycota or the Basidiomycota classifications. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other members. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.

Reproduction of the fungi in this group is strictly asexual and occurs mostly by production of asexual conidiospores (**Figure 24.17**). Some hyphae may recombine and form heterokaryotic hyphae. Genetic recombination is known to take place between the different nuclei.



**Figure 24.17** *Aspergillus niger* is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

The fungi in this group have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi killed the bacterial growth surrounding it. Other fungi in this group cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

## Glomeromycota

The **Glomeromycota** is a newly established phylum which comprises about 230 species that all live in close association with the roots of trees. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that all members of this family form **arbuscular mycorrhizae**: the hyphae interact with the root cells forming a mutually beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

## 24.3 | Ecology of Fungi

By the end of this section, you will be able to:

- Describe the role of fungi in the ecosystem
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms
- Describe the beneficial relationship between some fungi and insects

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Fungi are not obvious in the way large animals or tall trees appear. Yet, like bacteria, they are the major decomposers of nature. With their versatile metabolism, fungi break down organic matter, which would not otherwise be recycled.

### Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich

in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

## Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter (**Figure 24.18**). Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



**Figure 24.18** Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk. (credit: Cory Zanker)

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways (**Figure 24.19**).



**Figure 24.19** Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. (credit: Cory Zanker)

## Mutualistic Relationships

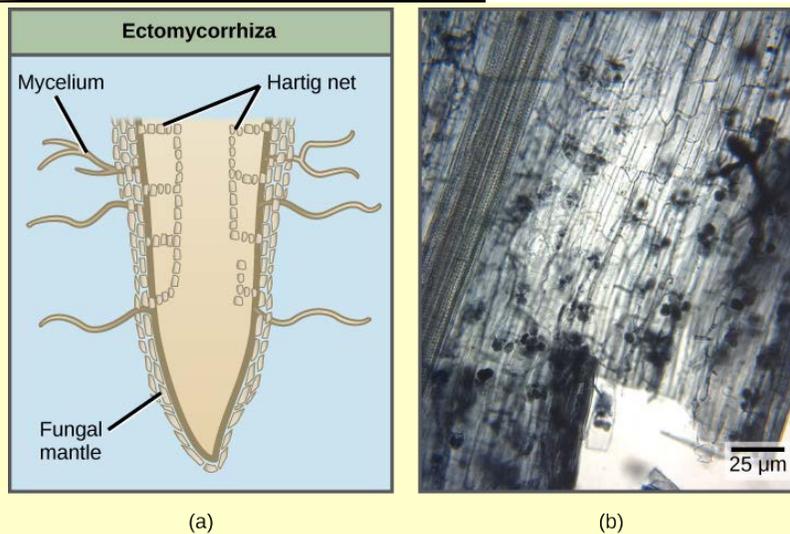
Symbiosis is the ecological interaction between two organisms that live together. The definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

### Fungus/Plant Mutualism

One of the most remarkable associations between fungi and plants is the establishment of mycorrhizae. **Mycorrhiza**, which comes from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80 and 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are a number of types of mycorrhizae. **Ectomycorrhizae** (“outside” mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells (**Figure 24.20**). The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with **arbuscular mycorrhiza** (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant (**Figure 24.20** and **Figure 24.21**). The arbuscules (from the Latin for little trees) have a shrub-like appearance. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

## art CONNECTION



**Figure 24.20** (a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?



**Figure 24.21** The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The *Amanita* hyphae cover these small roots with a white mantle. (b) Spores (round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza between a fungus and the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

Other examples of fungus–plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

## evolution CONNECTION

### Coevolution of Land Plants and Mycorrhizae

Mycorrhizae are the mutually beneficial symbiotic association between roots of vascular plants and fungi. A well-accepted theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most primitive plants and the first to survive on dry land, do not have a true root system; some have vesicular–arbuscular mycorrhizae and some do not. They depend on a simple rhizoid (an underground organ) and cannot survive in dry areas. True roots appeared in vascular plants. Vascular plants that developed a system of thin extensions from the rhizoids (found in mosses) are thought to have had a selective advantage because they had a greater surface area of contact with the fungal partners than the mosses and liverworts, thus availing themselves of more nutrients in the ground.

Fossil records indicate that fungi preceded plants on dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae; up to about 90 percent of today's vascular plants have associations with fungi in their rhizosphere. The fungi involved in mycorrhizae display many characteristics of primitive fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats because of increased uptake of nutrients, and this gave them a selective advantage over plants that did not establish symbiotic relationships.

### Lichens

**Lichens** display a range of colors and textures (**Figure 24.22**) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.



Explore the world of lichens using this [site \(http://openstaxcollege.org/l/lichenland\)](http://openstaxcollege.org/l/lichenland) from Oregon State University.



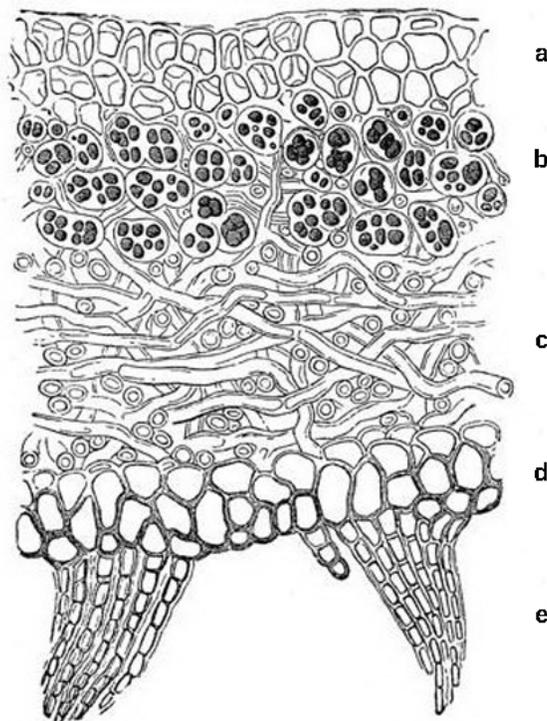
(a)

(b)

(c)

**Figure 24.22** Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djmappleferryman"/Flickr; credit c: modification of work by Cory Zanker)

Lichens are not a single organism, but rather an example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium) (**Figure 24.23**). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.



**Figure 24.23** This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce **soredia**, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogen and sulfur. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes.



Lichens are used to monitor the quality of air. Read more on this [site \(http://openstaxcollege.org/l/lichen\\_monitrng\)](http://openstaxcollege.org/l/lichen_monitrng) from the United States Forest Service.

### **Fungus/Animal Mutualism**

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: jointed, legged invertebrates. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens (**Figure 24.24**). Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced

and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.



**Figure 24.24** A leaf cutting ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

## Fungivores

Animal dispersal is important for some fungi because an animal may carry spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some dung fungi actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground mushroom. Almost all truffles are ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles. Female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.

## 24.4 | Fungal Parasites and Pathogens

By the end of this section, you will be able to:

- Describe fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is hampered by the similarity between fungal and animal cells

**Parasitism** describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, the pathogen causes a disease, whereas the parasite usually does not. **Commensalism** occurs when one member benefits without affecting the other.

### Plant Parasites and Pathogens

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host (**Figure 24.25**). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.



**Figure 24.25** Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea*, the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes by *Botrytis* results in noble rot, a condition that produces strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA-ARS; credit b: modification of work by Stephen Ausmus, USDA-ARS; credit c: modification of work by David Marshall, USDA-ARS; credit d: modification of work by Joseph Smilanick, USDA-ARS)

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

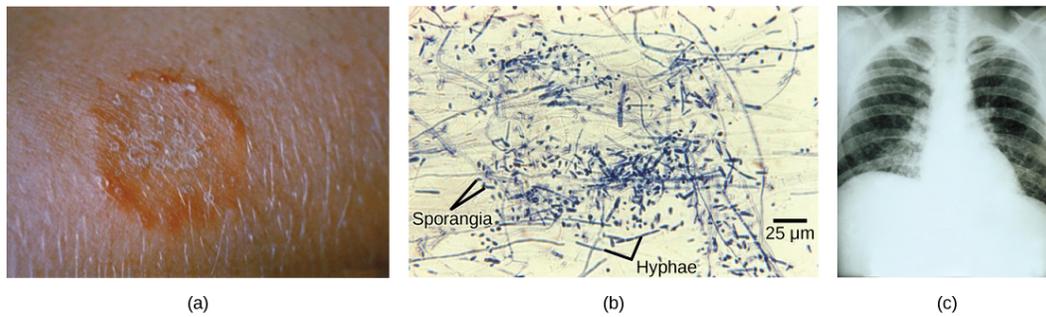
## Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A **mycosis** is a fungal disease that results from infection and direct damage. Fungi attack animals directly by colonizing and destroying tissues. **Mycotoxicosis** is the poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). **Mycetismus** describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are superficial; that is, they occur on the animal's skin. Termed cutaneous ("skin") mycoses, they can have devastating effects. For example, the decline of the world's frog population in recent years may be caused by the chytrid fungus *Batrachochytrium dendrobatidis*, which infects the skin of frogs and presumably interferes with gaseous exchange. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Pseudogymnoascus destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *P. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue (**Figure 24.26**). These fungi are often misnamed "dermatophytes", from the Greek words *dermis* meaning skin and *phyte* meaning plant, although they are not plants. Dermatophytes are also called "ringworms" because of the red ring they cause on skin. They secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing conditions

such as athlete's foot and jock itch. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent superficial mycoses may require prescription oral medications.



**Figure 24.26** (a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an ascomycete that infects airways and causes symptoms similar to influenza. (credit a: modification of work by Dr. Lucille K. Georg, CDC; credit b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M. Renz, CDC; scale-bar data from Matt Russell)

Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause symptoms similar to those of tuberculosis. Histoplasmosis is caused by the dimorphic fungus *Histoplasma capsulatum*. It also causes pulmonary infections, and in rarer cases, swelling of the membranes of the brain and spinal cord. Treatment of these and many other fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments, or part of the normal biota. They mainly affect individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses that can be life threatening. The yeast *Candida* sp., a common member of the natural biota, can grow unchecked and infect the vagina or mouth (oral thrush) if the pH of the surrounding environment, the person's immune defenses, or the normal population of bacteria are altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during mushroom-picking season. Many edible fruiting bodies of fungi resemble highly poisonous relatives, and amateur mushroom hunters are cautioned to carefully inspect their harvest and avoid eating mushrooms of doubtful origin. The adage "there are bold mushroom pickers and old mushroom pickers, but are there no old, bold mushroom pickers" is unfortunately true.

# scientific method CONNECTION

## Dutch Elm Disease

**Question:** Do trees resistant to Dutch elm disease secrete antifungal compounds?

**Hypothesis:** Construct a hypothesis that addresses this question.

**Background:** Dutch elm disease is a fungal infestation that affects many species of elm (*Ulmus*) in North America. The fungus infects the vascular system of the tree, which blocks water flow within the plant and mimics drought stress. Accidentally introduced to the United States in the early 1930s, it decimated shade trees across the continent. It is caused by the fungus *Ophiostoma ulmi*. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible to the disease than are American elms.

**Test the hypothesis:** A researcher testing this hypothesis might do the following. Inoculate several Petri plates containing a medium that supports the growth of fungi with fragments of *Ophiostoma* mycelium. Cut (with a metal punch) several disks from the vascular tissue of susceptible varieties of American elms and resistant European and Asiatic elms. Include control Petri plates inoculated with mycelia without plant tissue to verify that the medium and incubation conditions do not interfere with fungal growth. As a positive control, add paper disks impregnated with a known fungicide to Petri plates inoculated with the mycelium.

Incubate the plates for a set number of days to allow fungal growth and spreading of the mycelium over the surface of the plate. Record the diameter of the zone of clearing, if any, around the tissue samples and the fungicide control disk.

Record your observations in the following table.

### Results of Antifungal Testing of Vascular Tissue from Different Species of Elm

Disk	Zone of Inhibition (mm)
Distilled Water	
Fungicide	
Tissue from Susceptible Elm #1	
Tissue from Susceptible Elm #2	
Tissue from Resistant Elm #1	
Tissue from Resistant Elm #2	

**Table 24.1**

Analyze the data and report the results. Compare the effect of distilled water to the fungicide. These are negative and positive controls that validate the experimental set up. The fungicide should be surrounded by a clear zone where the fungus growth was inhibited. Is there a difference among different species of elm?

**Draw a conclusion:** Was there antifungal activity as expected from the fungicide? Did the results support the hypothesis? If not, how can this be explained? There are several possible explanations for resistance to a pathogen. Active deterrence of infection is only one of them.

## 24.5 | Importance of Fungi in Human Life

By the end of this section, you will be able to:

- Describe the importance of fungi to the balance of the environment
- Summarize the role of fungi in food and beverage preparation
- Describe the importance of fungi in the chemical and pharmaceutical industries
- Discuss the role of fungi as model organisms

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they are part of the nutrient cycle in ecosystems. They have other ecosystem roles as well. As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack, and do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia and Maryland (**Figure 24.27**).



**Figure 24.27** The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus that holds promise as a biological insecticide. The parasitic fungus appears as white fuzz on the body of the insect. (credit: Houping Liu, USDA Agricultural Research Service)

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land. Without the fungal partner in root systems, 80–90 percent of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and are promoted by supporters of organic agriculture.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies (**Figure 24.28**). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked in order to capture the molds responsible for the blue veins and pungent taste of the cheese.



**Figure 24.28** The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO<sub>2</sub> and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer’s yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. This was one of the first examples of biotechnology patenting.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, are isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe semilanceata* and *Gymnopilus junonius*, which have been used for their hallucinogenic properties by various cultures for thousands of years.

As simple eukaryotic organisms, fungi are important model research organisms. Many advances in modern genetics were achieved by the use of the red bread mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli*, which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.

## KEY TERMS

**arbuscular mycorrhiza** mycorrhizal association in which the fungal hyphae enter the root cells and form extensive networks

**Arbuscular mycorrhizae** mycorrhizae commonly involving Glomeromycetes in which the fungal hyphae penetrate the cell walls of the plant root cells (but not the cell membranes)

**ascocarp** fruiting body of ascomycetes

**Ascomycota** (also, sac fungi) phylum of fungi that store spores in a sac called ascus

**basidiocarp** fruiting body that protrudes from the ground and bears the basidia

**Basidiomycota** (also, club fungi) phylum of fungi that produce club-shaped structures (basidia) that contain spores

**basidium** club-shaped fruiting body of basidiomycetes

**Chytridiomycota** (also, chytrids) primitive phylum of fungi that live in water and produce gametes with flagella

**coenocytic hypha** single hypha that lacks septa and contains many nuclei

**commensalism** symbiotic relationship in which one member benefits while the other member is not affected

**Deuteromycota** former form phylum of fungi that do not have a known sexual reproductive cycle (presently members of two phyla: Ascomycota and Basidiomycota)

**ectomycorrhiza** mycorrhizal fungi that surround the roots with a mantle and have a Hartig net that extends into the roots between cells

**Ectomycorrhizae** mycorrhizae in which the fungal hyphae do not penetrate the root cells of the plant

**facultative anaerobes** organisms that can perform both aerobic and anaerobic respiration and can survive in oxygen-rich and oxygen-poor environment

**Glomeromycota** phylum of fungi that form symbiotic relationships with the roots of trees

**haustoria** modified hyphae on many parasitic fungi that penetrate the tissues of their hosts, release digestive enzymes, and/or absorb nutrients from the host

**heterothallic** describes when only one mating type is present in an individual mycelium

**homothallic** describes when both mating types are present in mycelium

**hypha** fungal filament composed of one or more cells

**karyogamy** fusion of nuclei

**lichen** close association of a fungus with a photosynthetic alga or bacterium that benefits both partners

**mold** tangle of visible mycelia with a fuzzy appearance

**mycelium** mass of fungal hyphae

**mycetismus** ingestion of toxins in poisonous mushrooms

**mycology** scientific study of fungi

**mycorrhiza** mutualistic association between fungi and vascular plant roots

**mycorrhizae** a mutualistic relationship between a plant and a fungus. Mycorrhizae are connections between fungal hyphae, which provide soil minerals to the plant, and plant roots, which provide carbohydrates to the fungus

**mycosis** fungal infection

**mycotoxicosis** poisoning by a fungal toxin released in food

**obligate aerobes** organisms, such as humans, that must perform aerobic respiration to survive

**obligate anaerobes** organisms that only perform anaerobic respiration and often cannot survive in the presence of oxygen

**parasitism** symbiotic relationship in which one member of the association benefits at the expense of the other

**plasmogamy** fusion of cytoplasm

**saprobe** organism that derives nutrients from decaying organic matter; also saprophyte

**septa** cell wall division between hyphae

**soredia** clusters of algal cells and mycelia that allow lichens to propagate

**sporangium** reproductive sac that contains spores

**spore** a haploid cell that can undergo mitosis to form a multicellular, haploid individual

**thallus** vegetative body of a fungus

**yeast** general term used to describe unicellular fungi

**Zygomycota** (also, conjugated fungi) phylum of fungi that form a zygote contained in a zygospore

**zygospore** structure with thick cell wall that contains the zygote in zygomycetes

## CHAPTER SUMMARY

### 24.1 Characteristics of Fungi

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophyll, nor organelles such as chloroplasts. Because fungi feed on decaying and dead matter, they are saprobes. Fungi are important decomposers that release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus, which is called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts, or develop a network of filaments called a mycelium, which is often described as mold. Most species multiply by asexual and sexual reproductive cycles and display an alternation of generations. Another group of fungi do not have a sexual cycle. Sexual reproduction involves plasmogamy (the fusion of the cytoplasm), followed by karyogamy (the fusion of nuclei). Meiosis regenerates haploid individuals, resulting in haploid spores.

### 24.2 Classifications of Fungi

Chytridiomycota (chytrids) are considered the most primitive group of fungi. They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called zoospores. Zygomycota (conjugated fungi) produce non-septated hyphae with many nuclei. Their hyphae fuse during sexual reproduction to produce a zygospore in a zygosporangium. Ascomycota (sac fungi) form spores in sacs called asci during sexual reproduction. Asexual reproduction is their most common form of reproduction. Basidiomycota (club fungi) produce showy fruiting bodies that contain basidia in the form of clubs. Spores are stored in the basidia. Most familiar mushrooms belong to this division. Fungi that have no known sexual cycle were classified in the form phylum Deuteromycota, which the present classification puts in the phyla Ascomycota and Basidiomycota. Glomeromycota form tight associations (called mycorrhizae) with the roots of plants.

### 24.3 Ecology of Fungi

Fungi have colonized nearly all environments on Earth, but are frequently found in cool, dark, moist places with a supply of decaying material. Fungi are saprobes that decompose organic matter. Many successful mutualistic relationships involve a fungus and another organism. Many fungi establish complex mycorrhizal associations with the roots of plants. Some ants

farm fungi as a supply of food. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium. The photosynthetic organism provides energy derived from light and carbohydrates, while the fungus supplies minerals and protection. Some animals that consume fungi help disseminate spores over long distances.

### 24.4 Fungal Parasites and Pathogens

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas systemic mycoses spread through the body. Fungal infections are difficult to cure.

### 24.5 Importance of Fungi in Human Life

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms, and also as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used as medicines, such as antibiotics and anticoagulants. Fungi are model organisms for the study of eukaryotic genetics and metabolism.

## ART CONNECTION QUESTIONS

- Figure 24.13** Which of the following statements is true?
  - A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
  - A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
  - A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
  - A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.
- Figure 24.16** Which of the following statements is true?
  - A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
  - The result of the plasmogamy step is four basidiospores.
  - Karyogamy results directly in the formation of mycelia.
  - A basidiocarp is the fruiting body of a mushroom-producing fungus.
- Figure 24.20** If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

## REVIEW QUESTIONS

- Which polysaccharide is usually found in the cell wall of fungi?
  - starch
  - glycogen
  - chitin
  - cellulose
- Which of these organelles is not found in a fungal cell?
  - chloroplast
  - nucleus
  - mitochondrion
  - Golgi apparatus
- The wall dividing individual cells in a fungal filament is called a
  - thallus
  - hypha
  - mycelium
  - septum
- During sexual reproduction, a homothallic mycelium contains
  - all septated hyphae
  - all haploid nuclei
  - both mating types
  - none of the above
- The most primitive phylum of fungi is the \_\_\_\_\_.
  - Chytridiomycota
  - Zygomycota
  - Glomeromycota
  - Ascomycota
- Members of which phylum produce a club-shaped structure that contains spores?
  - Chytridiomycota
  - Basidiomycota
  - Glomeromycota
  - Ascomycota

**10.** Members of which phylum establish a successful symbiotic relationship with the roots of trees?

- Ascomycota
- Deuteromycota
- Basidiomycota
- Glomeromycota

**11.** The fungi that do not reproduce sexually use to be classified as \_\_\_\_\_.

- Ascomycota
- Deuteromycota
- Basidiomycota
- Glomeromycota

**12.** What term describes the close association of a fungus with the root of a tree?

- a rhizoid
- a lichen
- a mycorrhiza
- an endophyte

**13.** Why are fungi important decomposers?

- They produce many spores.
- They can grow in many different environments.
- They produce mycelia.
- They recycle carbon and inorganic minerals by the process of decomposition.

**14.** A fungus that climbs up a tree reaching higher elevation to release its spores in the wind and does not

receive any nutrients from the tree or contribute to the tree's welfare is described as a \_\_\_\_\_.

- commensal
- mutualist
- parasite
- pathogen

**15.** A fungal infection that affects nails and skin is classified as \_\_\_\_\_.

- systemic mycosis
- mycetismus
- superficial mycosis
- mycotoxicosis

**16.** Yeast is a facultative anaerobe. This means that alcohol fermentation takes place only if:

- the temperature is close to 37°C
- the atmosphere does not contain oxygen
- sugar is provided to the cells
- light is provided to the cells

**17.** The advantage of yeast cells over bacterial cells to express human proteins is that:

- yeast cells grow faster
- yeast cells are easier to manipulate genetically
- yeast cells are eukaryotic and modify proteins similarly to human cells
- yeast cells are easily lysed to purify the proteins

## CRITICAL THINKING QUESTIONS

**18.** What are the evolutionary advantages for an organism to reproduce both asexually and sexually?

**19.** Compare plants, animals, and fungi, considering these components: cell wall, chloroplasts, plasma membrane, food source, and polysaccharide storage. Be sure to indicate fungi's similarities and differences to plants and animals.

**20.** What is the advantage for a basidiomycete to produce a showy and fleshy fruiting body?

**21.** For each of the four groups of perfect fungi (Chytridiomycota, Zygomycota, Ascomycota, and

Basidiomycota), compare the body structure and features, and provide an example.

**22.** Why does protection from light actually benefit the photosynthetic partner in lichens?

**23.** Why can superficial mycoses in humans lead to bacterial infections?

**24.** Historically, artisanal breads were produced by capturing wild yeasts from the air. Prior to the development of modern yeast strains, the production of artisanal breads was long and laborious because many batches of dough ended up being discarded. Can you explain this fact?