

Kingdom Fungi



FUNGI: FRIENDS AND FOES

TRAITS OF TRUE FUNGI

True Fungi Are Eukaryotic, Spore-producing Heterotrophs with Chitinous Walls
Most Fungi Have Bodies Called Mycelia
Mycelia Compete Well with Bacteria

ECOLOGICAL STRATEGIES OF FUNGI

REPRODUCTIVE STRATEGIES

FUNGAL ORIGIN, CLADES, AND GRADES

True Fungi Are a Monophyletic Kingdom of Life
Sexual Reproduction and Flagellation Define Traditional Phyla
Fungal Systematics Is a Work in Progress
Dikaryomycetes and Coenomycetes Are Grades of Fungal Evolution

PHYLUM CHYTRIDIOMYCOTA

PHYLUM ZYGOMYCOTA

PHYLUM GLOMEROMYCOTA

PHYLUM ASCOMYCOTA

Ascomycetes Make Septate Hyphae and Conidia
Ascomycetes Have a Short but Powerful Dikaryotic Stage
There Are Three Main Types of Ascomata
Many Ascomycetes Engage in Symbiosis
Most Mitosporic and Dimorphic Fungi Are Ascomycetes

PHYLUM BASIDIOMYCOTA

Hymenomycetes Make Long-lived Dikaryons
Hymenomycetes Make varied Fruiting Bodies
Ballistospore Release Aids in Dispersing Basidiospores
Many Ustilaginomycetes Cause Smut Diseases
Urediniomycetes Cause Rust Diseases

SUMMARY

IN DEPTH: *Microsporidia: Fungi in Disguise?*

IN DEPTH: *The Hat Thrower*

KEY CONCEPTS

1. Kingdom Fungi (the true fungi) is a monophyletic group of eukaryotic heterotrophs that reproduce with spores and have chitinous cell walls. The most familiar fungi are kitchen molds and mushrooms. The kingdom may include 1.5 million species, of which about 80,000 species have been named and described.
2. Some fungi destroy crops and stored food. Others are valuable decomposers or symbionts that cohabit with algae and cyanobacteria or assist plant growth. Baker's yeast is a fungus, and penicillin is a fungal product.
3. Most fungi develop a mycelium, composed of branching threads (hyphae) that collect nutrients and produce reproductive structures. Some fungi have a simpler thallus or live as microscopic unicells (yeasts). Dimorphic fungi make both mycelia and yeasts.
4. Many fungi make asexual spores to multiply and sexual spores for diversity. Exceptions include mushroom fungi, which use sexual spores to multiply, and mitosporic fungi, which have not been observed to reproduce sexually. However, nearly all tested fungi show signs of recent genetic recombination.
5. Two large phyla (Ascomycota and Basidiomycota) contain 95% of named species in kingdom Fungi and are informally called dikaryomycetes because their sexual life cycle has a unique dikaryotic stage. The remaining 5% of named species are divided between three phyla (Glomeromycota, Zygomycota, and Chytridiomycota) and are informally called coenomycetes because their hyphae lack the regular septation found in dikaryomycetes.
6. Kingdom Fungi excludes some organisms that traditionally are called fungi, and adds other organisms that were previously left out. New studies are changing classification within the kingdom.

20.1 FUNGI: FRIENDS AND FOES

Everyone has met the fungi, for better or worse (Fig. 20.1). We all know about mushrooms and moldy food, but fungi are much more important than that. Many fungi reduce human hunger by aiding the growth of plants. Others attack crop plants, farm animals, and humans with costly results. Many fungi are valuable decomposers that break down wastes and release the elements for reuse. But this function takes a dark side when fungi attack stored food, lumber, and clothing.

We make bread, beer, and wine with the help of yeast fungi. We also use common baker's yeast, *Saccharomyces cerevisiae*, as a model in the quest for cancer cures, and its genome was the first among eukaryotes to be sequenced. Another fungus yielded the first evidence of how genes act. In medicine, countless lives have been saved by antibiotics that were first discovered in fungi, and organ transplants were made possible by fungal molecules that suppress the immune system. All in all, fungi have a remarkable diverse set of relationships with humankind.



Figure 20.1. A mushroom, the reproductive body of a fungus. Made of filaments highly packed together, the mushroom is only part of the body. The rest consists of branching, underground filaments. This fungus may be living in symbiosis with a forest tree.

20.2 TRAITS OF TRUE FUNGI

Members of kingdom fungi vary immensely in size, body form, and life patterns. Judging from details of their DNA, they share a common ancestry and form a monophyletic clade. Not all organisms commonly called fungi belong to the kingdom, and we reserve the term **true fungi** for those that do belong.

Kingdom Fungi may have branched off from the rest of the eukaryotes a billion years ago. With all that time to evolve, it makes sense that they would be highly diverse today. Still, they retain several traits that must have come from their common ancestor.

True Fungi Are Eukaryotic, Spore-producing Heterotrophs with Chitinous Walls

Like plants and animals, fungi are eukaryotes; their cells have true nuclei. In fact, their cells have all the organelles that occur in animal cells. But fungal cells lack the one organelle that is most characteristic of plants: they have no chloroplasts and cannot perform photosynthesis. Lacking photosynthesis, fungi are **chemoheterotrophs**: they get energy and carbon as animals and most bacteria do, by taking organic molecules from the environment.

Fungal cells are surrounded by a **chitinous cell wall**, a protective coating that contains the substance **chitin** and other molecules. The cell walls led early biologists to

view fungi as plants, for in both fungi and plants, cell wall precluded the evolution of muscles and nervous systems by limiting mobility.

Cell walls have advantages and disadvantages. Like a rubber tire, the wall is flexible but resists expansion, so it gives shape to the pressurized cell. Fungi depend on cell shape to hold reproductive structures aboveground. The strength of cell walls limits invasion by other organisms, and it prevents the cell from bursting under pressure. Offsetting those benefits, walls prevent the fungus from engulfing solid foods as animals do; nutrient molecules must pass one by one through the wall to enter the cell, giving all fungi **absorptive nutrition**. The wall also limits growth and must be softened locally for a cell to expand. To explore new territory without the help of muscles, fungi rely on growth and abundant reproduction.

To reproduce, fungi release **spores**--units consisting of only one or a few cells (Fig. 20.2). Spores are not unique to fungi; plants and some bacteria and protists also make them. A fungal spore can resist dehydration and is light enough to drift in a gentle breeze, remaining dormant until it reaches a moist environment that contains food. The most productive fungi release trillions of spores per year, and in the height of allergy season, a cubic meter of air may contain thousands of spores. The ever-present spores make it likely that a sandwich or a pile of manure will soon become moldy.

To summarize, members of kingdom Fungi are spore-making, chitin-walled, eukaryotic chemoheterotrophs. Keep this in mind if you see a mold and wonder if it is a true fungus. Everyone recognizes molds as furry, colored patches on decaying organic matter--but not all molds are true fungi. For example, slime molds (see Chapter 21) do not have chitin in their walls. The absence of chitin is one of many small clues that slime molds came from different ancestors. Hence, slime molds are not included in kingdom Fungi.

Most Fungi Have Bodies Called Mycelia

Fungi are simpler than animals and plants. A body as simple as that of a fungus often is called a **thallus** (plural, *thalli*)--a multicellular body without specialized conducting tissue.

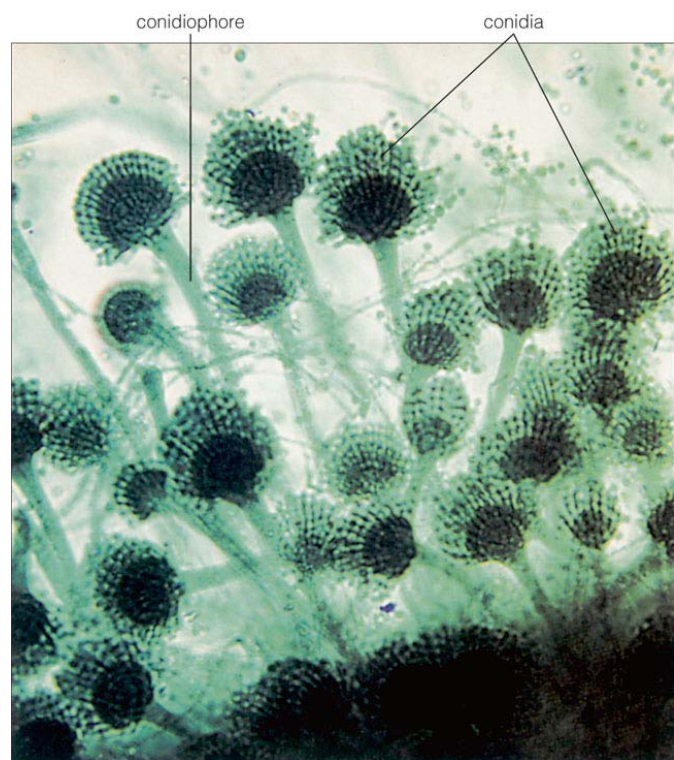


Figure 20.2. Spore production by *Aspergillus*, a common kitchen mold. Tiny spores, called conidia, form in chains at the tips of stalks called conidiophores. They often form black patches on moldy bread. X300

To explore, feed, and make reproductive structures, most fungi grow a unique type of thallus known as a **mycelium** (Fig. 20.3), composed of slender, branching tubes called **hyphae** (singular, *hypha*). Individual hyphae are extremely slender and almost colorless, making them hard to see. But at the surface of a food mass such as bread, countless exploratory hyphae grow into the air and make a visible fuzz. When reproduction starts,

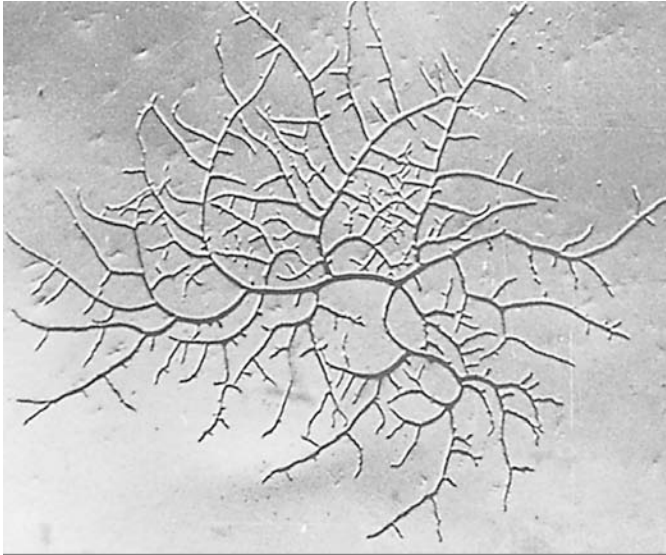


Figure 20.3. Hyphae making up a young mycelium of *Phycomyces blakesleeanus*, a zygomycete fungus. X400.

colored spores may cover the surface.

Hyphal growth begins when a spore absorbs water, swells, and germinates. The enclosed cell softens the spore wall, allowing it to expand. As the hypha grows, soft wall material is added to the tip, while older material stiffens along the sides of the hypha. The result is a tube that expands only at the tip. Sensing chemicals that diffuse from a food mass, hyphae grow toward the source. This orientation response to chemicals is called **chemotropism**. As the hypha lengthens, at intervals the tip lays down the beginnings of branch hyphae, small bumps that are left behind as the tip grows forwards. Later, some of the bumps become branch hyphae, which can form more branches. In this way, a single hypha quickly branches into a mycelium.

The mycelium may also form cross-bridges by the fusion of hyphae, creating a web.

A mycelium is well equipped to exploit a food mass such as a rotting peach. Pushed through the food by internal pressure that causes growth, each hyphal tip secretes digestive enzymes into the food mass, breaking proteins and other large food molecules into small molecules such as amino acids and sugars (Fig. 20.4). The small molecules pass through the cell wall and meet the cell membrane. In the membrane, proteins spend energy to pull food molecules into the cell, an example of *active transport* (see Chapter 11). Accumulation of food causes water to enter by osmosis. The added water exerts pressure that stretches the cell wall, elongating the hypha and driving it deeper into the food mass. Because these events require water, mycelia become inactive when the substrate dries.

Injured mycelia have remarkable powers of regeneration. If you cut a mycelium into fragments, the cut hyphae seal their broken ends and continue growing as separate fungi. Thus, injury can multiply the number of growing mycelia. But hyphae can distinguish self from nonself, and if hyphae from two genetically identical mycelia touch, they may fuse to make the two mycelia into a single unit.

The level of coordination between parts of a mycelium is much less than between parts of the animal body, but hyphae do share materials. A pressure-driven mass transport of material, like the flow of water in a pipe, runs from feeding hyphae to sites of reproduction. In addition, high magnification shows a slower, more controlled movement of particles along cytoskeletal elements in the hyphae. This controlled flow, called

cytoplasmic streaming, can either oppose or augment the mass transport. Such movements carry food and organelles to hyphae that can make the best use of them.

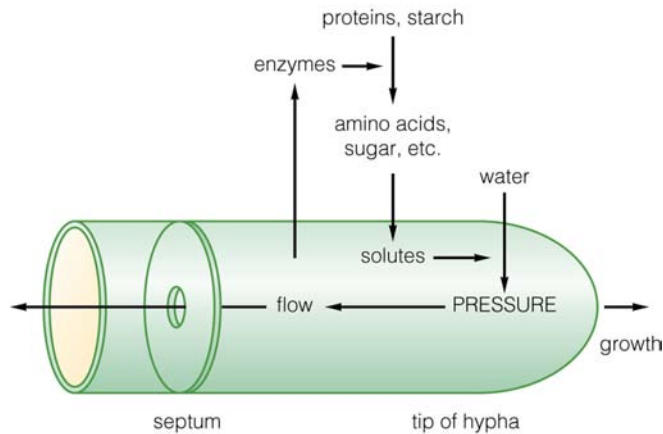


Figure 20.4. The act of feeding pushes a hypha into a food mass and drives food through the mycelium. The hypha secretes enzymes that break up large molecules. Proteins in the cell membrane carry small solute molecules into the hypha, causing water to enter. The added volume creates pressure that expands the soft tip, pushing forward. Pressure and cytoplasmic streaming create a flow that carries food to older parts of the mycelium. Cross walls (septa) may occur, but they have perforations that allow a flow of material.

The simplest fungi, yeasts, lack mycelia and live as microscopic, rounded cells (Fig. 20.5). Each time the growing cell doubles in size, it divides into two independent cells. In baker's yeast (*Saccharomyces cerevisiae*), the parent cell forms a bud that is cut off and released when it equals the parent cell's size. Some other yeasts simply double their size and split crosswise. Some fungi exhibit **dimorphism**, the occurrence of two growth forms. Dimorphic fungi can switch between mycelial and yeast growth, depending on the growing conditions.

Most fungi can make nearly all the molecules they need from a few environmental raw materials. They need water, a few minerals, and an organic compound for carbon and energy. Many fungi also need a few vitamins, including the same vitamin B₁ that humans need. Almost any organic material can be food for one or more fungi, including wood, paper, glue, leather, manure, and so on.

Mycelia Compete Well with Bacteria

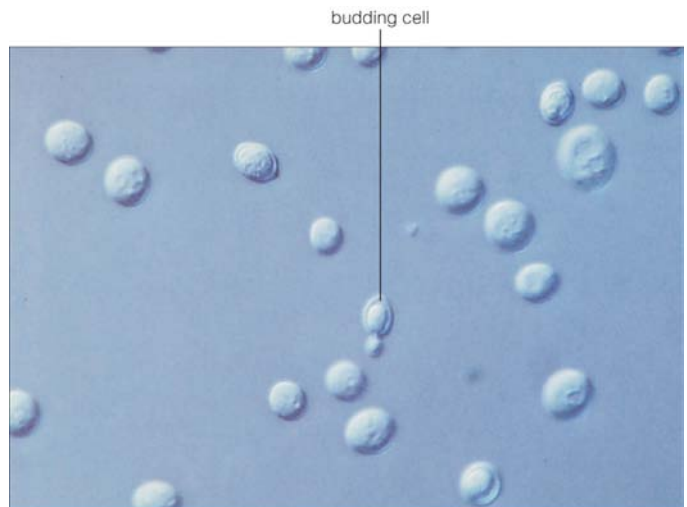


Figure 20.5. Cells of baker's yeast (*Saccharomyces cerevisiae*). One cell is reproducing by budding. X1,700.

As walled heterotrophs, fungi compete with bacteria for food--and bacteria evolved superb scavenging abilities a billion years before the first fungi. How could fungi succeed against the fierce bacterial competition? The answer relates partly to mycelial growth. To reach new food sources, a fungus or bacterium must feed quickly, reproduce abundantly, and disperse offspring widely. Bacteria excel in fast feeding and reproduction; their tiny cells can double in number every half hour, and each cell is a reproductive unit. But if bacteria live deep within a food source, they can be slow to reach the surface for dispersal. Even at the food surface, bacteria are slow to reach new regions after they exhaust the food in their immediate vicinity. A single bacterium quickly forms a small colony, but most colonies remain small after that. By contrast, fungal hyphae rapidly grow into new territory. A mycelium can expand without limit--its size is indeterminate. Furthermore, the mycelium is a system of connected pipes in which pressure can rapidly move nutrients from buried feeding hyphae to aerial hyphae that make and disperse spores.

Rapid transport through a mycelium is possible because hyphae are not divided into distinct cells. Most fungi make cross walls known as **septa** (singular, *septum*) at regular intervals along the hyphae (Fig. 20.4). But the middle of each new septum has a hole or **septal pore** (also called a perforation) that allows material to move between compartments. Thus, most of the mycelium is a single giant cell.

Given that septa are perforated, you might wonder what value they have. Don't septa slow down transport, reducing the mycelium's advantage over bacteria? Why do hyphae make septa at all? Part of the answer may be that septa aid in damage control. Some of the fastest-growing fungi lack septa and are said to be *aseptate*. Their fast growth may derive partly from having wide-open pipelines for transport. But if an aseptate hypha is cut through, much material leaks out before repair mechanisms seal the break. Septate hyphae leak less when broken.

In addition to reaching and transporting food quickly, fungi exploit several chemical tools to compete with bacteria. All fungi secrete acid (H^+) as part of their feeding system. A side benefit is that acid slows bacterial growth. Acidic soils, such as those beneath conifers or heaths, are rich in fungal decomposers and poor in soil bacteria. Some fungi also secrete specific antibiotics that poison bacteria. Penicillin was the first fungal antibiotic to be recognized as such in science. It causes bacteria to burst by inhibiting the enzymes that build the bacterial cell wall--an effect that leaves fungi (and humans) unharmed because eukaryotes do not have the enzyme that penicillin blocks. The alcohol made by baker's and brewer's yeasts also is an antibiotic that slows bacterial growth. Alcohol is a fine antiseptic that was used in medicine long before the discovery of penicillin, and yeast cells tolerate it more readily than do bacteria.

Finally, some fungi outcompete bacteria with the help of superior food-digesting systems. Fungi that attack wood are an important example. Wood contains cellulose, a valuable nutrient, which is protected by a coating of the hardening agent lignin. Lignin resists attack by most organisms, but some fungi have enzymes that degrade lignin to expose the cellulose.

20.3 ECOLOGICAL STRATEGIES OF FUNGI

Fungi have several lifestyles that make them vital agents in the world ecosystem. To get food from living host organisms, many fungi engage in symbiotic relationships

comparable to those in the bacteria (see Chapter 19): there is mutualism, which benefits both the fungus and its host; and there is parasitism, in which the fungus benefits while its host is harmed. Some fungi take a step further, killing the host organism as they feed. This is true of fungi that kill insects and nematode worms.

Many fungi are adept at mutualism, where they partner with organisms from every kingdom of life. The most important fungal mutualisms involve photosynthetic organisms--plants, algae, and bacteria. Every plant has fungi living in its leaves or stems. These opportunists may harm the plant, or they may aid the plant by secreting chemicals that deter predators or parasites. More organized and important associations are **mycorrhizae**, in which fungi colonize roots. Mycorrhizal fungi take organic nutrients from the plant, in exchange for minerals and water that hyphae get from soil. In lichens (Fig. 20.6), fungi partner with green algae or cyanobacteria. The fungus shelters the algae or bacteria and provides minerals and water, taking energy-rich carbon compounds in return.

Fungi also form mutualistic symbioses with animals. Cows depend on tiny fungi to help them digest grass. The fungi dwell in one of the cow's several stomachs (the rumen), where they break down cellulose and other substances that the cow's own enzymes cannot attack. A more complex symbiosis involves leaf-cutter ants, tropical fungi, and bacteria. The ants cut leaves into small pieces and carry them underground where they infect the leaves with small bits of mycelium. The ants carefully tend their fungal gardens, and feed on bits of the mycelium. When the ants move to a new location and start a new nest, they carry tiny bits of the fungus with them to establish new fungal colonies. The ants may also carry bacteria that inhibit the growth of competing fungi--a form of biological pest control.

Among the many species of fungi that live as parasites, some attack other fungi or animals, but the great majority attack plants. Rust and smut fungi are especially notable because some of them attack crop plants such as corn and wheat.

Not all fungi get food from living hosts; many species live all or part of the time as **saprobies**, organisms that feed on dead organic matter. In ecological terms, saprobic fungi are *decomposers*--organisms that recycle chemical elements by breaking down organic molecules. Without decomposers, the nitrogen, carbon, and phosphorus needed for life would be increasingly tied up in wastes and dead bodies.

Most saprobic fungi are *opportunists*: they survive by exploiting temporary opportunities, such as a fallen fruit. Many opportunistic fungi are small organisms



Figure 20.6. An Alaskan forest lichen occupies most of the photograph. In this lichen symbiosis, an ascomycete fungus (genus *Peltigera*) shelters photosynthetic green algae or cyanobacteria.

because they have little time for growth before the food is gone. But saprobic mycelia may grow large in a forest or grassland, where fallen leaves and dead branches regularly replenish the food supply. Other saprobes are less opportunistic and grow large and old by attacking dead trees that contain enough food to support years of growth.

20.4 REPRODUCTIVE STRATEGIES

Fungi rely on spore production to reach distant food sources. More than 1,000 species have swimming spores that actively seek out food. But the great majority of fungi lack swimming cells; the spores drift passively in air or water. Spores that travel through air have walls that limit water loss by means of waxy or oily molecules. Some spores have extensions that catch air currents; other attach to animals by means of hooks or glue.

Only a tiny percentage of spores reach food sources; therefore, a fungus must build huge numbers of spores as fast as possible. Most fungi meet the challenge with *asexual reproduction*, releasing tiny parts of the parental body as *mitospores* (Fig 20.7).

Mitospores are made in a variety of ways, some of which will be shown later in the chapter. Those in Figures 20.2 and 20.7 show variations of the most common method, in which spores form one by one at the tips of hyphae. Such spores are called **conidia** (singular, *conidium*), and hyphae that make them are called **conidiophores**. Masses of conidia often give moldy food vivid colors.

Asexual reproduction is the fastest, most economical way to multiply because it does not require a partner. However, all the mitospores are genetically identical to the parent. This uniformity limits the capacity of asexual reproduction to exploit new opportunities.

To make genetically diverse spores, most fungi also have *sexual reproduction*. When compatible cells or hyphae meet, they fuse and bring their nuclei together. Then the nuclei fuse and go through *meiosis*, a division process in which chromosomes trade parts (see Chapter 12). Nuclei emerge from meiosis with varied combinations of genes from the two parents and are made into *meiospores*. The meiospores grow into mycelia with new traits, some of which may be useful in new habitats.



Figure 20.7. Mitospore production by *Penicillium*, the kind of fungus in which penicillin was discovered. Masses of these spores often make green patches on moldy oranges and cheese. Called conidia, the spores are produced one by one at the tips of specialized hyphae (conidiophores). X550.

Thousands of fungal species have never been seen to reproduce sexually and are informally termed **mitosporic fungi**. But in wild populations of mitosporic fungi, studies of DNA nearly always show evidence of recent recombination. Either these fungi do reproduce sexually on occasion, or they recombine genes in other ways. One such method, which has been seen only in the laboratory, is referred to as the **parasexual cycle** because it lacks the meiosis that typifies sexual reproduction. The cycle begins when hyphae of two haploid mycelia fuse together, permitting nuclei of both to mingle. Such a mycelium, with nuclei of more than one genotype in uncontrolled proportions, is said to be **heterokaryotic**. Nuclei of the two kinds sometimes fuse, trade parts of chromosomes, and return to the haploid state by losing chromosomes. The result is a recombinant nucleus that has a mixture of genes from the original nuclei.

20.5 FUNGAL ORIGIN, CLADES, AND GRADES

Before biologists invented molecular phylogenetics (see Chapter 18), organisms were classified mainly by visible characters such as details of body form. This classification obscured the real diversity among the simpler organisms such as fungi, which have many fewer visible characters than animals and plants. Currently, mycologists—scientists who study fungi—are updating fungal classification with molecular phylogenetic methods that provide many more characters for comparison. These methods reveal that there are many more species of fungi than previously thought. Some estimates suggest that the kingdom may include as many as 1.5 million species, of which the current 80,000 named species is just a small sample. As discussed below, other findings help to revise the way fungi are subdivided.

True Fungi Are a Monophyletic Kingdom of Life

After centuries of classifying fungi with plants, systematists in the early twentieth century decided that fungi should be viewed as a separate kingdom. Their view emphasized differences in cell structure and nutrition. Both plants and fungi have cell walls, but the walls differ radically in composition. And whereas green plants are photosynthetic autotrophs, fungi never perform photosynthesis and are chemoheterotrophs.

The current emphasis on molecular characters has shown that the original kingdom Fungi included some organisms that did not belong there and excluded some members that did belong. In so doing, the original kingdom violated a demand of modern systematics: all named groups must be *monophyletic*—that is, they must include one originating ancestor, all of its descendants and nothing else.

To see the problem with the original kingdom Fungi, it must be viewed in the context of other kingdoms. Figure 20.8 uses shades of blue for all the groups that were in the original kingdom Fungi. They come from varied origins, so a monophyletic clade that includes all of them would also include the animal and plant kingdoms. With this information, mycologists saw that the only way to make kingdom Fungi monophyletic was to remove the three small groups in the middle of the cladogram. That has now been done, leaving the modern kingdom Fungi monophyletic like the plant and animal kingdoms.

The three omitted groups are still studied by mycologists, for they have many similarities to organisms of kingdom Fungi. In fact, most of them are still informally called "fungi." To avoid confusion, mycologists often refer to members of the monophyletic kingdom as *true fungi*.

Like true fungi, all three omitted groups are spore-producing, eukaryotic chemoheterotrophs that have cell walls at some stage of life. The group that most resembles modern fungi still bears a fungal name--*Oomycota*, meaning "egg fungi." Its members have mycelia and other structures that closely resemble true fungi, but differences in detail suggested a separate origin even before DNA comparisons were possible. Figure 20.8 suggests that the similarities to true fungi came about by convergent evolution, a conclusion that is currently well accepted. The other two groups that traditionally were included in kingdom Fungi are *slime molds*--organisms that spend most of their lives without walls, moving about and engulfing solid foods as amoebae do. They were originally classified with fungi because they make spores like true fungi. Again, the molecular differences suggest that slime molds evolved spores independently. In Figure 20.8, the slime molds are label Acrasids and Mycetozoa. Chapter 21 discusses Oomycota and slime molds.

The DNA comparisons of figure 20.8 suggest that the closest relatives of kingdom Fungi are animals. These studies confirm earlier suspicions on the basis of other traits. The chitinous cell walls of fungi differ too much from the cellulose/lignin walls of plants to have come from a common ancestor; and elsewhere in the living world, only animals make chitin. Moreover, some fungi have swimming cells with a single trailing flagellum like animal sperm, unlike the paired lateral flagella of plant sperm. Other similarities include storage products and various enzymes that occur in animals and fungi but not in plants. These facts strongly suggest that kingdom Fungi is a sister clade to the animal kingdom and that its relation to plants is much more distant.

Sexual Reproduction and Flagellation Define Traditional Phyla

Mycologists group the members of kingdom Fungi into phyla (also called divisions), with names ending in *-mycota* (derived from the Greek word *mykes*, mening "fungus"). Within

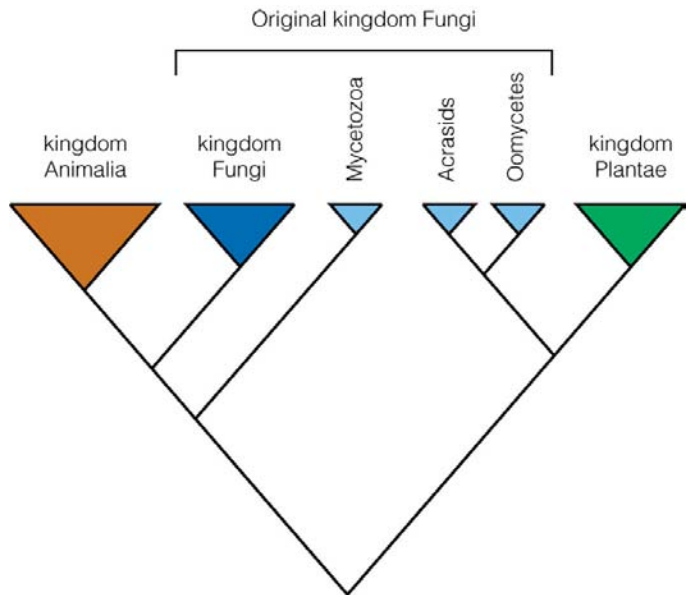


Figure 20.8. Evolutionary relationships between kingdom fungi and other eukaryotic groups, based on comparisons of the DNA that specifies ribosomal RNA. As originally defined, kingdom fungi was not monophyletic. Since then, systematists made the kingdom monophyletic by excluding the groups shown in light blue. Kingdom Fungi is a sister group to animals.

a phylum, class names end in *-mycetes*; other ranks have the same endings as in plants (Table 18.1).

To define phyla of terrestrial fungi, early mycologists emphasized the details of sexual reproduction. This defined three phyla that differ in the way they make sexual spores (Fig. 20.9). Members of phylum **Basidiomycota** extrude sexual spores from the surface of a cell called a **basidium** (Fig. 20.9a), much as children blow bubbles from a pipe. The walls of the resulting spores come from stretching and thickening a local part of the basidial wall. Phylum Basidiomycota contains more than 26,000 named species. In contrast, members of phylum **Ascomycota** make sexual spores inside a cell called an **ascus** (Fig. 20.9b). The spores get their walls by dividing the contents of the ascus into cells and making a completely new wall around each cell. Phylum Ascomycota includes more than 32,000 named species. Members of phylum **Zygomycota**, numbering only 1,100 named species, have a third way of making sexual spores: when parental hyphae meet in sexual reproduction, they fuse at the tips to form a large cell called a **zygosporangium**, which hardens its wall and goes to rest as a **zygospore** (Fig. 20.9c).

Details of sexual reproduction are not adequate for classifying all terrestrial fungi, because thousands of fungal species have never been seen to reproduce sexually. Early mycologists classified these fungi by details of mitospore formation and other nonsexual traits and grouped them into an artificial phylum called **Deuteromycota**.

When mycologists studied aquatic forms of life, they found organisms that resemble terrestrial fungi enough to suggest descent from common ancestors. Many of these aquatic fungi have never been seen to reproduce sexually, but one feature sets them apart from all other true fungi: they make reproductive cells that swim by means of a flagellum. They were assigned to a fourth phylum, the **Chytridiomycota**.

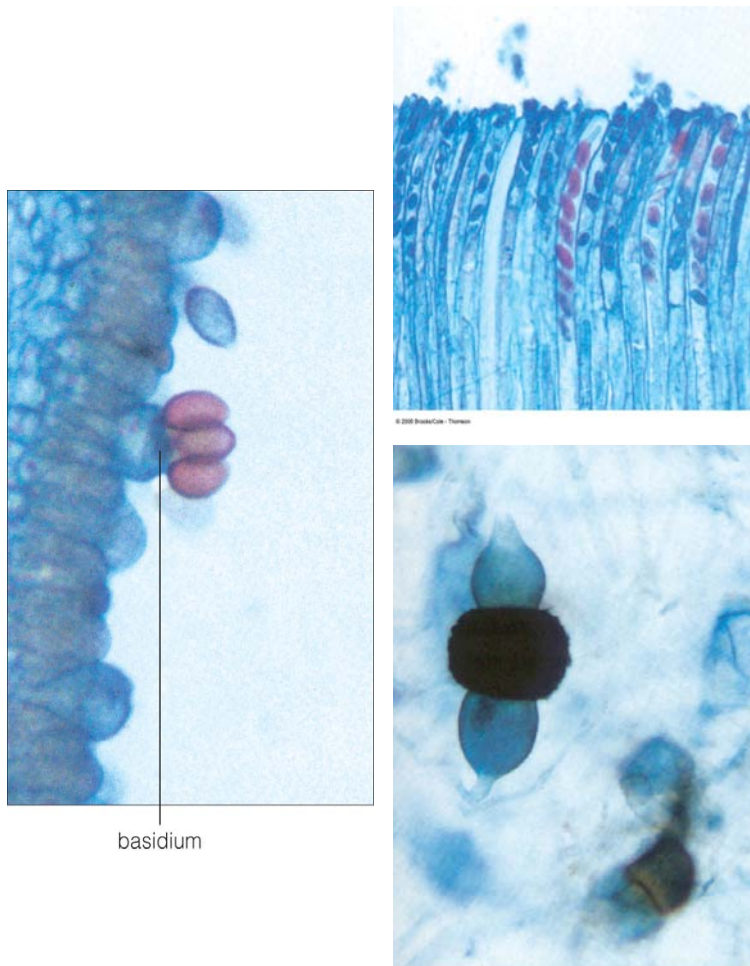


Figure 20.9. Sexual structures that were used to define three traditional phyla of fungi. (a) A basidium of *Coprinus*, phylum Basidiomycota, with extruded spores. (b) Asci of *Peziza*, phylum Ascomycota. Each elongated bag is an ascus with eight spores. (c) A zygospore of *Rhizopus*, phylum Zygomycota. The dark object between the two parental hyphae is the resting zygospore formed by their fusion.

Fungal Systematics Is a Work in Progress

Molecular phylogenetics is having a major impact on the way true fungi are grouped within the kingdom. One result was to eliminate the artificial phylum Deuteromycota. On the basis of similarities in mitospore formation, scientists had always suspected that most asexual fungi were ascomycetes that had lost or severely reduced their sexual function. DNA comparisons confirm the suspicion, and the great majority of mitosporic fungi have now been placed in phylum Ascomycota. Others have been placed in phylum Basidiomycota.

Numerous molecular phylogenetic studies agree that the traditional Ascomycota and Basidiomycota are monophyletic (Fig. 20.10). but the same studies agree that Zygomycota and Chytridiomycota are probably *not* monophyletic. If figure 20.10a is correct, the only way to make all fungal phyla monophyletic is to put groups 1 and 2 into new phyla and reverse the assignments of groups 3 and 4.

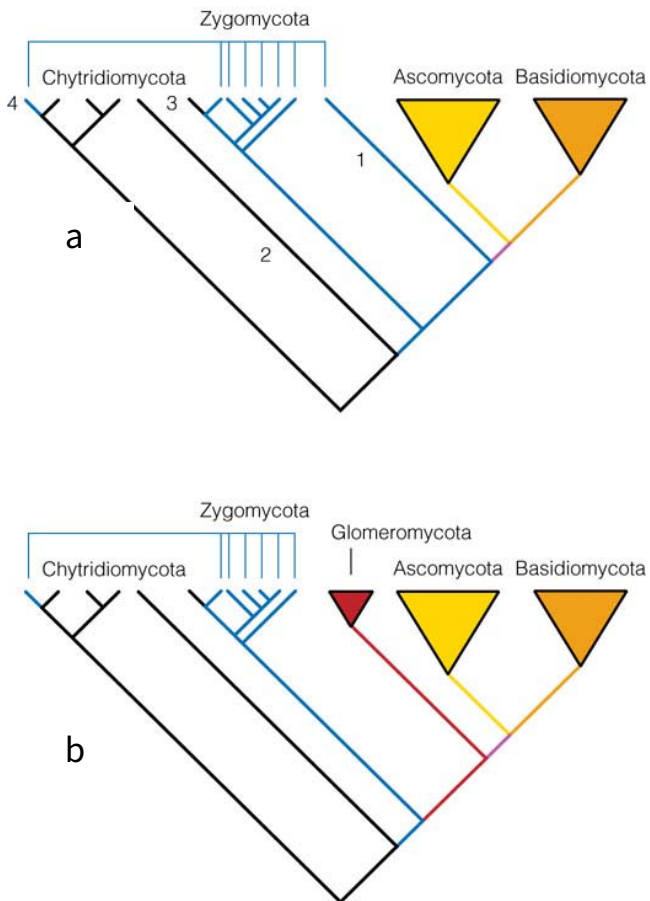


Figure 20.10. Cladograms based on rDNA, showing probable evolutionary relationships among phyla of Fungi. (a) If the inferred relationships are correct, the traditional Ascomycota and Basidiomycota are monophyletic, and the other two phyla are not. Zygomycota and Chytridiomycota are shown in blue and black, respectively. (b) The same cladogram, relabeled to establish lineage 1 in (a) as a fifth phylum, the Glomeromycota.

A step toward making Zygomycota monophyletic occurred in 2001 when the German mycologist Arthur Schüssler and colleagues proposed moving the group designated 1 in Figure 20.10a from Zygomycota to a new monophyletic phylum, the **Glomeromycota** (Fig.

20.10b). This text adopts that proposal, as do many mycologists. Phylum Glomeromycota has few named species but is immensely important--its members assist the growth of about 80% of green plants through symbiotic associations with roots. As you consider the problems posed by Figure 20.10, keep in mind that the cladogram is just one hypothesis, based on one set of genes (rDNA, the genes that specify RNA molecules found in ribosomes). Other studies, using different genes, reach broadly similar conclusions but differ in detail. Thus, like all systematics, the classification of fungi is still a work in progress. Currently, we must simply accept that the evolutionary relationships among zygomycete and chytrid fungi are still uncertain. This is true partly because these fungi branched off from common ancestors in ancient times--perhaps 1.6 billion years ago, by some estimates. It is difficult to find the true sequence of branching when it happened so long ago. Perhaps further studies with additional characters will resolve the uncertainties.

Dikaryomycetes and Coenomycetes Are Grades of Fungal Evolution

If some members of a clade are far more successful than the rest because of special traits they share, the successful members are said to be at a higher **grade of evolution**. So it is with some of the true fungi (Fig. 20.11). The Ascomycota and Basidiomycota are sister clades that include more than 95% of named fungal species. All the large and complex fungi are found here. They include mushrooms, many common molds, and most fungi that cause human disease. Their success suggests that they inherited something useful from their immediate ancestor--new traits that placed them at a higher grades of evolution. Reflecting that idea, mycologists once called Ascomycota and Basidiomycota *higher fungi*, leaving the rest of the kingdom as *lower fungi*.

What made higher fungi so successful? Two relevant traits are named in Figure 20.11, with a red tick mark to show when they probably arose. One trait is a unique **dikaryotic stage** in the sexual life cycle--a stage in which hyphae have paired haploid nuclei of two genotypes. To emphasize the dikaryotic stage, the informal term **dikaryomycetes** was coined for fungi that have it. The second relevant trait is the presence of **septate hyphae**--hyphae that have septa at regular intervals.

In contrast, lower fungi never have a dikaryotic stage, and their hyphae are usually **aseptate**, with few or no septa. An aseptate mycelium is said to be **coenocytic**, meaning that the many nuclei are not walled off into separate compartments. To emphasize their coenocytic hyphae, the informal term **coenomycetes** was coined for all fungi that are not dikaryomycetes. This textbook uses the terms dikaryomycetes and coenomycetes rather than higher and lower fungi.

Figure 20.12 illustrates a sexual life cycle that includes a dikaryotic stage. As in other sexual cycles, plasmogamy brings $1n$ nuclei of two parents into a single cell. But instead of fusing, the two kinds of $1n$ nuclei form pairs that multiply by mitosis and guide the growth of new hyphae. The result is a **dikaryotic mycelium**, or **dikaryon**, so named because each of its septate compartments contains paired nuclei of two kinds (*di-*, "two"; *karyon* is derived from Greek meaning "nucleus"). The dikaryon's genetic constitution is called $n + n$, because both kinds of nuclei are $1n$. The dikaryon is the dikaryotic stage in the life cycle (the green sector in Fig. 20.12).

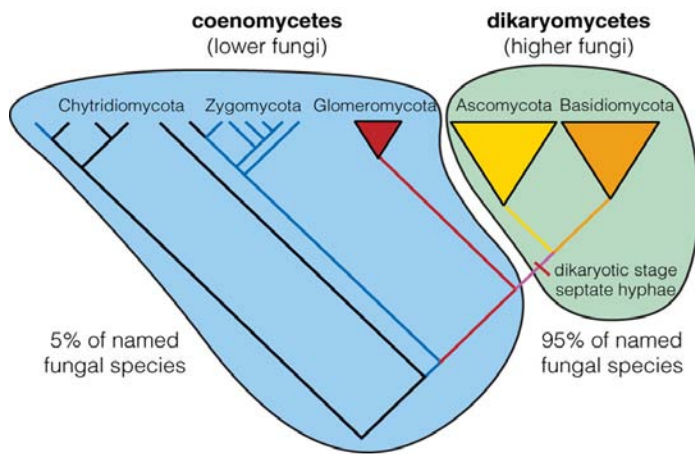


Figure 20.11. Two evolutionary grades of true fungi (dikaryomycetes and coenomycetes). Mycelial dikaryomycetes have a dikaryotic stage and regularly septate hyphae. Coenomycetes usually have aseptate hyphae and never have a dikaryotic stage.

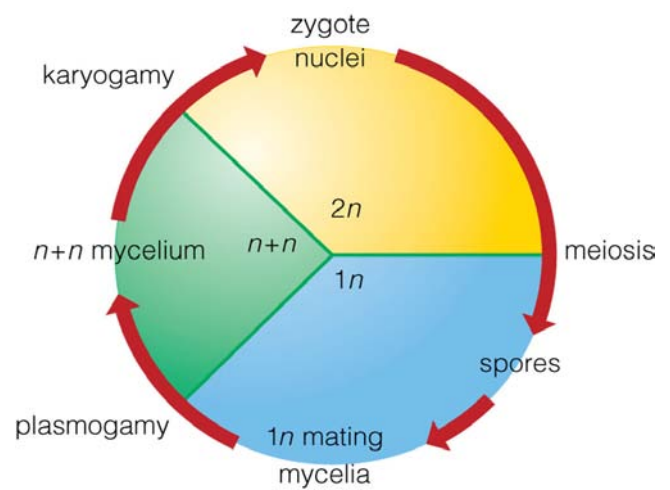


Figure 20.12. a sexual life cycle with a dikaryotic ($n+n$) stage (green sector). After plasmogamy, the fusion cells grows a septate mycelium in which mitotic divisions give each compartment a pair of $1n$ nuclei from each of the two parents.

A dikaryon can produce spores with immense genetic diversity. Such diversity can greatly increase the formation of new species by improving the chance that some offspring will thrive in new environments. Figure 20.13 shows how a dikaryon increases spore diversity. Focus on meiosis, the source of diversity. From one $2n$ nucleus, meiosis makes four $1n$ nuclei with new combination of genes. The gene combinations differ in every meiosis, because crossovers at random points trade parts of paired homologous chromosomes. Therefore, the number of genetically different spores that come from a mating depends on how many $2n$ nuclei go through meiosis.

One way to get more $2n$ nuclei is to divide them by mitosis, as the human body does. But few fungi do that. *Allomyces* (a coenomycete) and *Armillaria* (a basidiomycete) are among the small minority of fungi that build a $2n$ mycelium. The vast majority of fungi put $2n$ nuclei directly through meiosis. Thus, to get more $2n$ nuclei, most fungi depend on events that occur before parental $1n$ nuclei fuse.

Some coenomycetes bring many $1n$ nuclei together when tips of mating hyphae fuse. But this yields very limited spore diversity, for the tiny fusion cell has room for only a few hundred nuclei. Karyogamy converts them to hundreds of $2n$ nuclei; hence, no more than a few hundred genetically different spores are produced.

A dikaryotic mycelium is immensely more effective. Its growing hyphae can multiply a single pair of $1n$ nuclei into *trillions* of pairs that fuse to make $2n$ nuclei. In this way, a large dikaryon such as a mushroom fungus can produce trillions of spores, each with a different combination of parental genes.

A dikaryotic stage may also promote the evolution of complex bodies by reducing the impact of harmful mutations. The more complex a body is, the more genes are needed to build it, and the more points exist where failure of a gene can be fatal. In a body with nuclei of two genotypes, even if one kind of nucleus has a bad copy of a gene, the other kind will probably have a good copy. This may explain why the largest, most

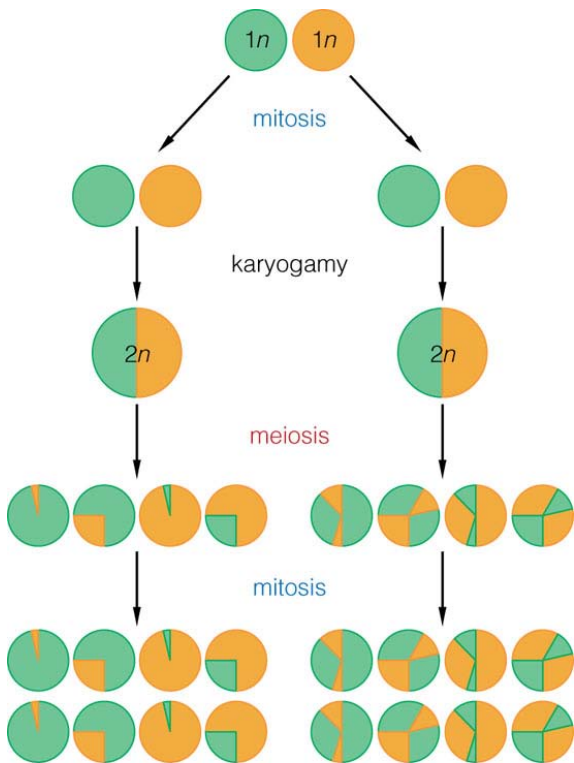


Figure 20.13. The dikaryotic stage increases spore diversity by increasing the number of $2n$ nuclei formed by karyogamy and thus the number of independent meiotic divisions. Green and orange represent the contributions from different parents.

complex structures in fungi are dikaryotic. Coenomycetes, with haploid mycelia, have only one version of each gene, and they have much simpler bodies.

Regular septation may also be important in making complex bodies. To construct such differentiated parts as a mushroom's cap and stalk, nuclei in different parts of the body must follow different genetic programs. This may be hard to achieve if nuclei wander freely, as they can do in a coenomycete mycelium.

20.6 PHYLUM CHYTRIDIOMYCOTA

With about 1,000 named species, phylum Chytridiomycota contains all the fungi that have swimming cells at some point in their life cycle. None are familiar in everyday life--they are too small to study without a microscope, none cause human disease, and few are significant pests. Nevertheless, they merit attention because they are part of the natural world and because they give clues to the origin of kingdom Fungi.

If you have a microscope, chytrids are not hard to find. Simply add a pinch of pine pollen to a container of either pond water or soil in tap water. In a day or two, you may see microscopic chytrid thalli on the pollen grains. Chytrids are common in ponds and wet soil, where they decompose organic matter or attack algae, pollen grains, and plant roots. Sometimes they cause "swimmer's itch" in people who bathe in lakes. One parasitic chytrid became a pest when it attacked potatoes in the ground, but currently farmers grow potato strains that resist chytrids.

A few chytrids make highly branched aseptate mycelia, but most have a simpler thallus composed of just one or a few tiny cells. Figure 20.14 diagrams traits that are common to most simple chytrids. The cycle starts with a haploid meiospore that is called a

zoospore because it swims. The zoospore has no cell wall and it swims with a single trailing flagellum, much like a human sperm cell. Reaching a food source, the zoospore drops or retracts its flagellum, forms a cell wall, and grows into a thallus. Often, slender extensions called **rhizoids** anchor the thallus to a food mass and absorb food. Eventually, part of all of the thallus differentiates into one or more **mitosporangia**, enclosures in which mitospores form. A mitosporangium contains cytoplasm and nuclei that divide by mitosis, then differentiate into many swimming mitospores. Most of the mitospores function in asexual reproduction, making new thalli that are genetically identical to the original meiospore.

Sexual reproduction is unknown in most chytrids. Where it has been seen, rhizoids sometimes fuse to transfer nuclei between thalli. In other cases, some of the swimming mitospores serve as gametes. Two gametes fuse (plasmogamy) to become a single cell with two nuclei and two flagella. The fusion cell expands, forming a thick-walled **meiosporangium**--an enclosure in which meiospores are made. The meiosporangium may lie inert for months. Then its nuclei fuse (karyogamy) and divide by meiosis to make genetically diverse meiospores, completing the life cycle.

Every chytrids species has its own unique traits, and most have more complex bodies than shown in Figure 20.14. Some chytrids have branching aseptate hyphae. The largest is the much-studied genus *Allomyces*, which can be collected from soil and may grow into a fuzzy mycelium around decaying seeds. *Allomyces* makes alternating haploid and diploid mycelia--a rare trait among fungi.

In tracing the origins of fungi, chytrids are of interest because they have flagellated swimming cells. Eukaryotic flagella are complex; therefore, it is unlikely that more than one group evolved them independently. Similar flagella occur in plants and animals; therefore flagella probably evolved in the common ancestor of plant, animal, and fungi. This means that the first true fungi had flagella. Chytrids retained them. The lack

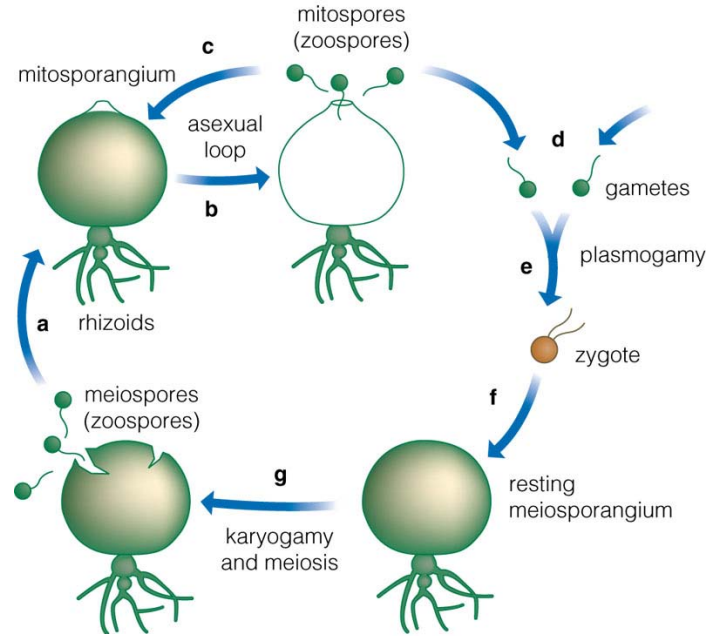


Figure 20.14. Life cycle of a simple chytrid. (a) A $1n$ meiospore swims to a food source, loses the flagellum, and grows into a thallus with a mitosporangium. (b) Mitotic divisions in the mitosporangium create many cells that become swimming mitospores. (c) Some mitospores make new $1n$ thalli, achieving asexual reproduction. (d) Other mitospores serve as gametes. (e) Plasmogamy results in a swimming zygote. (f) A zygote grows into a $2n$ thallus with a meiosporangium. (g) Karyogamy and meiosis occur to make cells that become new $1n$ meiospores, completing the cycle.

of flagella in other true fungi means that the ability to make them was lost after chytrids branched off. Perhaps the loss happened when fungi moved from water to land, where flagella are easily damaged and less useful.

20.7 PHYLUM ZYGOMYCOTA

Of all land fungi, zygomycetes have the most in common with aquatic chytrids. The similarities make these fungi important in studies of the way fungi moved from water to land more than 400 million years ago.

Only about 1,100 zygomycete species have been named and described, but the members are extremely diverse in lifestyle, and some are quite important as pests in food storage facilities. You may have seen their coarse, cottony mycelia on aging strawberries. Not many zygomycetes attack humans. However, a few cause dangerous diseases called *mucormycoses*, which can be contracted when farm workers inhale spores from dusty fields. Many zygomycetes are saprobes that recycle waste products such as dung and fallen fruits. One of them, *Rhizopus stolonifer*, is used here to illustrate the life history of these important decomposers (Fig. 20.15).

The life history begins when a passively drifting meiospore settles on food and grows into a large, aseptate mycelium (Fig. 20.15a). Burrowing deep into the food mass, hyphae collect food and transport it to numerous reproductive hyphae called **sporangiophores** that grow into the air. Each sporangiophore swells at the tip to form a mitosporangium, where the contents divide into many mitospores inside the sheltering parental wall (Fig. 20.15b). The mature sporangium breaks open, releasing the spores to drift in the air, settle on food, and make mycelia—an act of asexual reproduction (Fig. 20.15c).

If two compatible *Rhizopus* mycelia meet, they engage in sexual reproduction. To be compatible, mycelia must be of plus and minus *mating types*. First, they grow special hyphae that meet at the tips (Fig. 20.15d). Then cross walls form behind the tips, walling off two cells called *gametangia*, which play the part of gametes (Fig. 20.15e). Next, plasmogamy fuses the gametangia as the walls between them dissolve. The fusion cell, called a zygosporangium, is a meiosporangium (Fig. 20.15f). These events bring nuclei from two parents into the same cell without risking dehydration.

Inside the zygosporangium, the two kinds of nuclei fuse in pairs and produce $2n$ zygote nuclei. The wall of the zygosporangium grows thick and hard. With these events the zygosporangium becomes a zygospore, which rests for months (Fig. 20.15g). Eventually, meiosis converts the $2n$ nuclei into recombinant $1n$ nuclei, and a hypha grows out of the zygospore (Fig. 20.15h). Its tip swells to form a *germ sporangium* where the recombinant nuclei are incorporated into meiospores, completing the life cycle.

The life of *Rhizopus*—which is typical of saprobic zygomycetes—shares many features with chytrids, suggesting that these features were present in the common ancestor of all fungi.

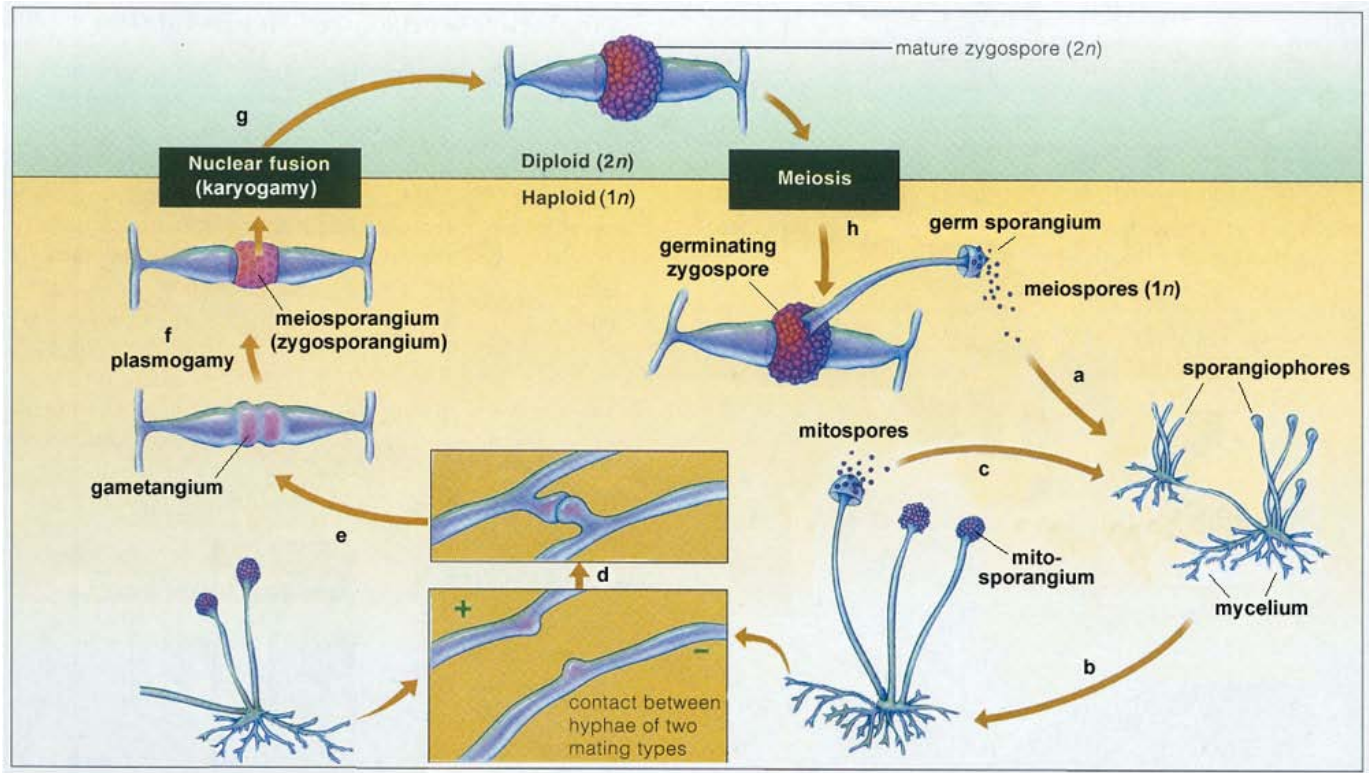


Figure 20.15. Life cycle of a zygomycete (*Rhizopus stolonifer*). (a) A nonmotile meiospore grows into a $1n$ mycelium from which sporangiophores grow into the air. (b) Tips of sporangiophores swell to become mitosporangia with mitospores. (c) The sporangium wall breaks open. Released mitospores grow into new mycelia for asexual reproduction. (d) Compatible + and - mycelia grow sexual hyphae that meet at the tips. (e) Septa form behind the tips of touching + and - hyphae, making gametangia. (f) Plasmogamy occurs when the walls between gametangia dissolve, making a meiosporangium (zygosporangium). (g) Inside the zygosporangium, karyogamy creates $2n$ zygote nuclei, and the zygosporangium wall thickens and hardens to form a zygospore. (h) Meiosis converts the $2n$ nuclei into $1n$ nuclei. A hypha grows out and makes a germ sporangium, where recombinant nuclei are packaged into meiospores.

The shared ancestral traits include making both meiospores and mitospores inside sporangia, putting meiosporangia to rest, and making aseptate hyphae. The chief differences are adaptations to life on land. Swimming spores are replaced by passive spores with water-retaining walls, and swimming gametes are replaced by hyphal tips that deliver gamete nuclei directly to the mating partner.

Rhizopus belongs to a small but important order (the Mucorales) with about 130 named species. Other zygomycetes vary immensely. Many attack insects such as flies, termites, and aphids. If you see a fly walking slowly as if nearly paralyzed, a zygomycete mycelium may be consuming the fly from within. These fungi make tiny mycelia or even simpler thalli inside the body of an insect. Efforts have been made to control insect pests with such fungi, but thus far the results are too variable for commercial use. These also are zygomycetes that parasitize other fungi and small animals such as microscopic nematode worms in the soil.

Large zygomycetes such as *Rhizopus* make extensive aseptate mycelia. But small zygomycetes may have septa, and some have a tiny thallus without hyphae. Some small zygomycetes have never been seen to reproduce sexually. And although most make asexual sporangia, some make conidia. The great diversity among zygomycetes may result from multiple origins, making this phylum artificial (not monophyletic). However, the early branching that gave rise to zygomycetes occurred too long ago for the relationships to be clear.

Despite their simplicity, some zygomycetes have been studied in great detail because their reproductive hyphae are large and easy to observe, and they are very sensitive to environmental stimuli. Some of them use light and gravity to guide their growth (see end note "IN DEPTH: The Hat Thrower"). This helps them release spores where wind and animals are likely to occur. Zygomycetes can be as sensitive to light as the human eye. Scientists who study sensory systems have used these responses as models to guide their thinking. Other experiments showed that zygomycetes find mating partners by exchanging chemical signals called *pheromones*, which differ between species and mating types. We know now that chytrids, ascomycetes, and basidiomycetes also find mating partners by exchanging pheromones.

20.8 PHYLUM GLOMEROMYCOTA

In some ways, the most important fungi may not be mushrooms or molds, but fungi that partner with green plants in the symbiotic associations known as mycorrhizae. More than 80% of wild plants are estimated to have such fungal partners, and the relationship may have begun even before primitive plants emerged from water to begin the conquest of dry land. Some of the oldest plant fossils, in rocks that are 400 million years old, contain mycorrhizal fungi.

Until recently, these mycorrhizal fungi were classified in phylum Zygomycota, as the order Glomales. But DNA comparisons have shown them to be a distinct clade, a sister group to the ancestor of dikaryomycetes (Fig. 20.11). They are currently being considered for phylum status with the title Glomeromycota, and are treated as such in this chapter.

The Glomeromycota live in soil, where their coarse, aseptate hyphae enter roots or thalli of rootless plants such as liverworts. In roots, the symbiotic associations are called **endomycorrhizae** because hyphae penetrate inside root cells (*endo-* means "within"). In a root, hyphae grow along intercellular spaces between plant cell walls (Fig. 20.16). At intervals, a hyphal tip punches through a cell wall of the host root, to branch repeatedly in the space shared with the plant cell. The result is a characteristic structure called an **arbuscule** ("little tree").

The fungus does not penetrate through the plant cell membrane; therefore, the arbuscule is not actually inside the living plant cell. Instead, the plant cell surrounds and coats every hypha in the arbuscule, much as a glove fits each finger of a hand. With this close contact, nutrients can move rapidly between the fungus and the plant. The fungus takes carbon-containing nutrients from the plant cell. In some species, hyphae store excess nutrients in swollen hyphal tips called vesicles, which form either in spaces between plant cells or in the space enclosed by the wall of a single plant cell. The fungus pays the plant for nutrients by bringing in water, phosphate, and sometimes nitrogen compounds from the soil.

To the plant, the value of having a fungal partner depends on how well the root system could collect water and phosphate on its own. Experiments show that plants benefit most if they have sparse root systems or grow in soils where phosphate is scarce. Thus the symbiosis can be either mutualistic or parasitic, depending on circumstances. But for many plants, the partnership is vital--the plant grows poorly without its mycorrhizal partner. Perhaps the fungus also helps the plant by repelling parasites and predators.

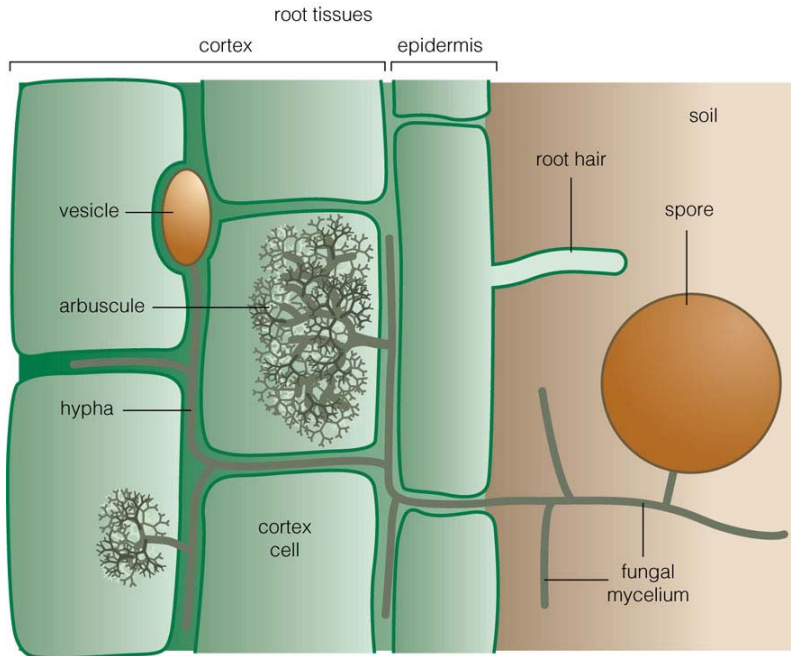


Figure 20.16. Diagram of an arbuscular endomycorrhiza, showing a section through the epidermis and two cortical cell layers of an infected root. Spaces between cells are exaggerated for easier viewing. A mycelium in the soil has grown branching hyphae into the root, where they grow between cells. Hyphae have penetrated through the wall of two cortical cells. They branch repeatedly to form arbuscules. One hyphal tip between root cells has swollen into a food-storing vesicle. A hyphal tip in the soil has swollen to become a spore.

Sexual reproduction is unknown in the Glomeromycota. They make asexual mitospores in the part of the mycelium that extends into the soil, and some species make mitospores inside the root, either between cells or in the space enclosed by the wall of one plant cell. Unlike chytrids and most zygomycetes, the spores are not made in sporangia. Instead, each spore is simply the swollen tip of a hypha, full of cytoplasm and stored food. The spore may reach a millimeter in diameter--a colossal size compared with spores of other fungi. Sometimes the spores are found in the gut of soil insects, suggesting a possible dispersal mechanism.

Because some of the oldest plant fossils contain similar fungal structures, botanists have postulated that plants and glomeromycetes moved from water to land as partners. If so, these fungi could have been important in helping plants make the transition to land. Early plants would have lacked roots, as algae and nonvascular plants do today. Fungal hyphae, reaching into soil, would have been a great help in collecting water and minerals. Partnerships continued as plants diversified on land. Perhaps this is why arbuscular mycorrhizae are so widespread among modern plants.

Despite their importance, phylum Glomeromycota includes only about 157 named species. But the low total may result from the simplicity of glomeromycetes; they have few structural characters that can be used to distinguish species. Many more species may emerge as systematists analyze the DNA of these important fungi.

20.9 PHYLUM ASCOMYCOTA

Every time you eat bread, drink wine or beer, take penicillin, or throw out a moldy orange, you cross paths with an ascomycete. With more than 32,000 named species, ascomycetes impact our lives in more ways than any other group of fungi.

At least 58 genera of ascomycetes have members that cause human disease. That is a tiny fraction of the 3,409 ascomycete genera, but they threaten the health of many people. Athlete's foot, jock itch, and ringworm are ascomycete infections that the immune system cannot defeat because the fungi grow in dead layers of skin beyond the bloodstream. The immune system blocks most deeper fungal infections, but a few ascomycetes occasionally get into the bloodstream and do great damage and can even cause death. *Coccidioides immitis* is such a species. Dwelling in soil in the western United States, this species can infect farm workers who breathe contaminated dust. The resulting lung infections may spread to the joints, central nervous system, adrenal glands, and skin. About 95% of patients eventually throw off the fungus; however, in others the infection can be fatal.

Pathogenic ascomycetes are especially dangerous in individuals with a compromised immune system, such as patients with acquired immune deficiency syndrome (AIDS) and patients whose immune system is suppressed to permit an organ transplant. *Pneumocystis carinii* (also called *Pneumocystis jiroveci*) and *Candida albicans* are particular problems. *Candida* is a common yeast that dwells in the human mouth and vagina, where bacteria and the immune system normally hold it in check. But when the immune system is weak or antibiotics kill the bacteria, *Candida* can cause a painful condition called *thrush*. In patients with human immunodeficiency virus (HIV), thrush often signals the transition to full-blown AIDS. *Pneumocystis* lung infections are more serious, causing fatal pneumonia in many patients with AIDS. At one time about half of all patients with AIDS died of fungal disease. New medicines have decreased the proportion, but fungal diseases are still lethal to many patients with a compromised immune system.

Ascomycetes also cause most fungal disease in animals and plants. In plants, the most familiar example is the dusty white deposit on leaves called **powdery mildew**, which often is seen on rose bushes, grape vines, barley, and other plants. On grape vines, the infection can seriously reduce the harvest.

On the positive side, ascomycetes have been valuable partners of humankind in the kitchen, laboratory, and hospital. Four kinds of ascomycetes helped scientists win Nobel prizes: studies of the mold *Neurospora crassa* first revealed that genes control protein synthesis; *Penicillium notatum* gave us penicillin, launching a revolution in medicine; and the yeasts *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* vastly improved our understanding of cell division. In the kitchen, morels (*Morchella*) and truffles (*Tuber*) are prized by gourmets, and several ascomycete yeasts are used to bake bread; ferment beer, wine, and soy sauce; and flavor cheeses.

The most valuable fungi of all--*Saccharomyces cerevisiae* and related species, the yeasts of baking and brewing--are ascomycetes. When grown without oxygen, *Saccharomyces* get energy by alcoholic fermentation, releasing carbon dioxide and alcohol as byproducts. When this happens in bread dough, the carbon dioxide make the bread rise. In beer and wine, both alcohol and gas bubbles are valued products. The alcohol made by yeast is also an important disinfectant and a fuel.

Ascomycetes Make Septate Hyphae and Conidia

Why did the ascomycota evolve into such a huge and important phylum, with more than 10 times as many species as all coenomycetes put together? Although some ideas were presented in discussing dikaryomycetes, the full answer is uncertain. For additional ideas, the whole life cycle of a typical ascomycete must be considered (Fig. 20.17).

A mycelial ascomycetes begins life as a $1n$ spore, which drifts in space until it lands on a food mass. The spore initiates a branching, septate mycelium (Fig. 20.17a).

Ascomycetes spread mainly by making asexual conidia on hyphae at the surface of a food mass (Fig. 20.17b). The green color of moldy oranges and cheese comes from conidia of *Penicillium* (Fig. 20.7). If infected food is exposed to open air in the kitchen, the spores

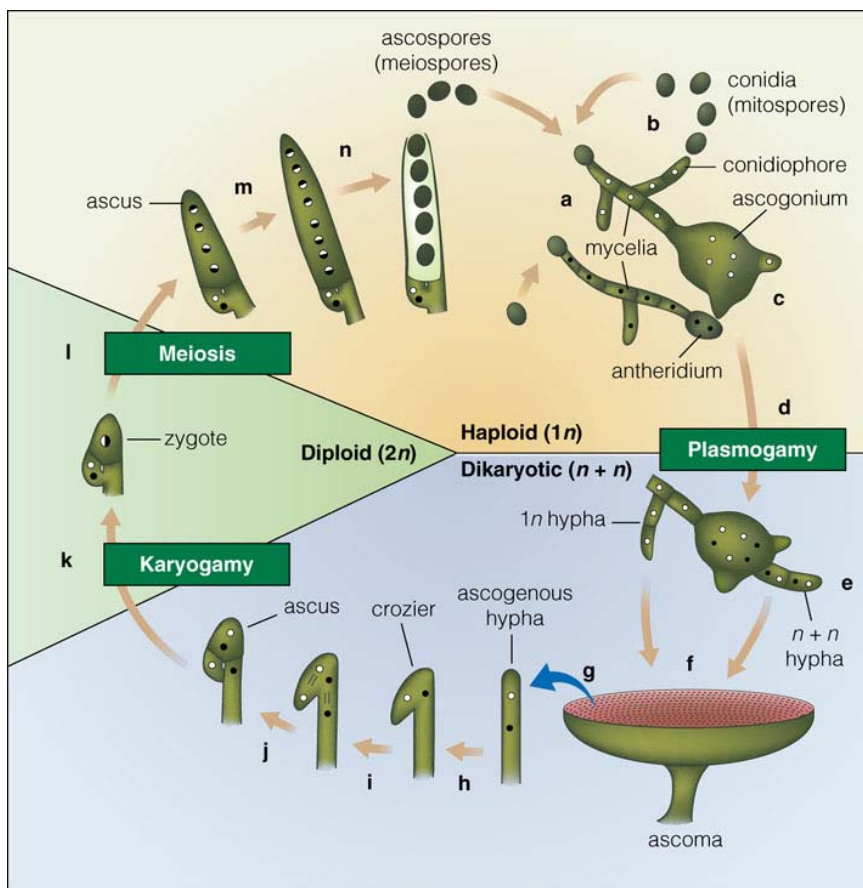


Figure 20.17. Life cycle of a mycelial ascomycete. (a) Septate $1n$ mycelia grow from $1n$ spores. (b) Conidia (mitospores) are released, making new $1n$ mycelia. (c) If $1n$ mycelia are compatible, they grow female ascogonia and male antheridia. (d) In plasmogamy, an antheridium delivers nuclei to an ascogonium. (e) $n+n$ hyphae grow from the fertilized ascogonium. (f) $n+n$ hyphae and $1n$ hyphae from the ascogonial parent make an ascoma. (g) One of many $n+n$ ascus-making hyphae in the ascoma is enlarged to show ascus formation. (h) The tip of hypha grows laterally to make a crozier. (i) Nuclei divide by mitosis. (j) Two septa divide off cells at the end of the crozier. The penultimate cell is the ascus. (k) Nuclei fuse to make a $2n$ zygote. (l) Meiosis makes four $1n$ nuclei in the ascus. (m) $1n$ nuclei divide by mitosis. (n) $1n$ nuclei are incorporated into meiospores (ascospores) that are released, often forcefully.

quickly spread to other rooms (a good reason to dispose of infected food while conidial patches are still tiny).

Conidia are made in several ways--some of them so different that they must have evolved independently. For example, some fungi make conidia like blowing bubbles from a pipe, whereas others make them by splitting the conidiophore into short segments.

Ascomycetes Have a Short but Powerful Dikaryotic Stage

If ascomycete mycelia meet and are compatible, which usually means of plus and minus mating types, they engage in sexual reproduction (Fig. 20.17c). A meeting usually causes both mycelia to make female structures called **ascogonia** and smaller male structures called **antheridia**. In plasmogamy, antheridia of each mycelium can fuse with ascogonia of the other mycelium. Nuclei move from the antheridium to the ascogonium (Fig. 20.17d).

The fertilized ascogonium grows $n + n$ hyphae (Fig. 20.17e). The $n + n$ hyphae usually weave together with $1n$ hyphae from the ascogonial parent to build a fruiting structure called an **ascoma** (plural, *ascomata*; Fig. 20.17f). Ascomata are discussed more fully later in this chapter.

On one side of the ascoma (the upper surface here) many $n + n$ hyphae produce meiosporangia called **asci**. Such an ascus-making hypha is said to be *ascogenous*. One such hypha is enlarged in Figure 20.17g. To make an ascus, the tip of the hypha bends as it grows, making a **crozier** (hook) that contains a nucleus from each parent (Fig. 20.17h). Next the two nuclei divide mitotically, and walls form to divide the crozier into three cells (Fig. 20.17i,j). The second or *penultimate* cell has two nuclei of opposite types. This cell is the young ascus. Within it, karyogamy occurs to make a $2n$ zygote nucleus (Fig. 20.17k). Also, the tipmost cell of the crozier fuses with the hyphal stalk, regaining the $n + n$ state. This sets the stage for making more asci from the same hypha (Fig. 20.18). Next the zygote nucleus goes through meiosis to make four recombinant $1n$ nuclei (Fig. 20.17l). A mitotic division usually follows, and the resulting nuclei are packaged with cytoplasm into eight meiospores, which are called **ascospores** (Fig. 20.17m,n).

Ascomycetes vary widely in how they release ascospores. Some species release ascospores passively. In other species, each ascus shoots off its spores, either one spore at a time or all at once in a sticky mass. The shooting force comes from pressure that builds up inside the ascus until it ruptures the tip.

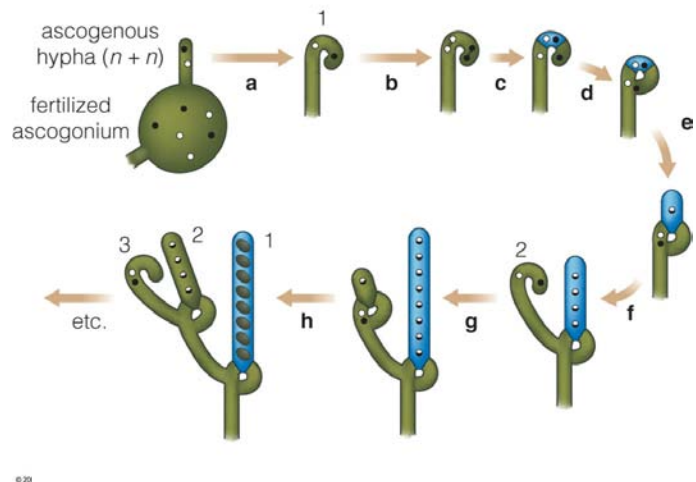


Figure 20.18. One $n + n$ hypha can make many asci. The first ascus (*blue*) is followed to maturity. Two more asci (*green*) will follow the same steps as the first.

There Are Three Main Types of Ascomata

Most ascomycetes make complex fruiting bodies (*ascomata*) in which both $1n$ hyphae and $n + n$ hyphae take part. An ascoma makes asci and spores, shelters the immature spores, and assists in dispersing mature spores. This is a step beyond anything that occurs in coenomycetes, where sexual spores are made individually with little supporting structure from other hyphae. There are three main types of ascomata, which are variations on a theme: a protective layer of nonreproductive hyphae provides a shelter or platform, and

multiple asci form in a layer called the **hymenium** on one side of the supporting layer (Fig. 20.19). An ascoma is an *apothecium* if it resembles an open cup (Figs. 20.9b, 20.17, and 20.19a,b). Apothecia range from a millimeter to several centimeters in diameter. Asci line the upper surface of the ascoma, pointing upward or outward. The alignment aids in dispersal when spores are shot away shooting the spores upward helps disperse spores because air is stagnant near the face of the ascoma (a region called the *boundary layer*). The ascus shoots spores through the boundary layer to a height where spores may encounter a breeze.

An ascoma is a *perithecium* if it is nearly closed, like a tiny flask. A pore at the small end opens to release the spores (Fig. 20.19c,d). Here the spores may be either shot off or not shot off, depending on the fungal species. Dutch elm disease is caused by a perithecial fungus, *Ophiostoma ulmi*. The spores spread with the help of beetles that burrow into tree bark. When a spore-carrying beetle makes a tunnel in the bark, spores rub off and grow mycelia into the bark tissue. Ascospores are not shot off. Instead, perithecia open into

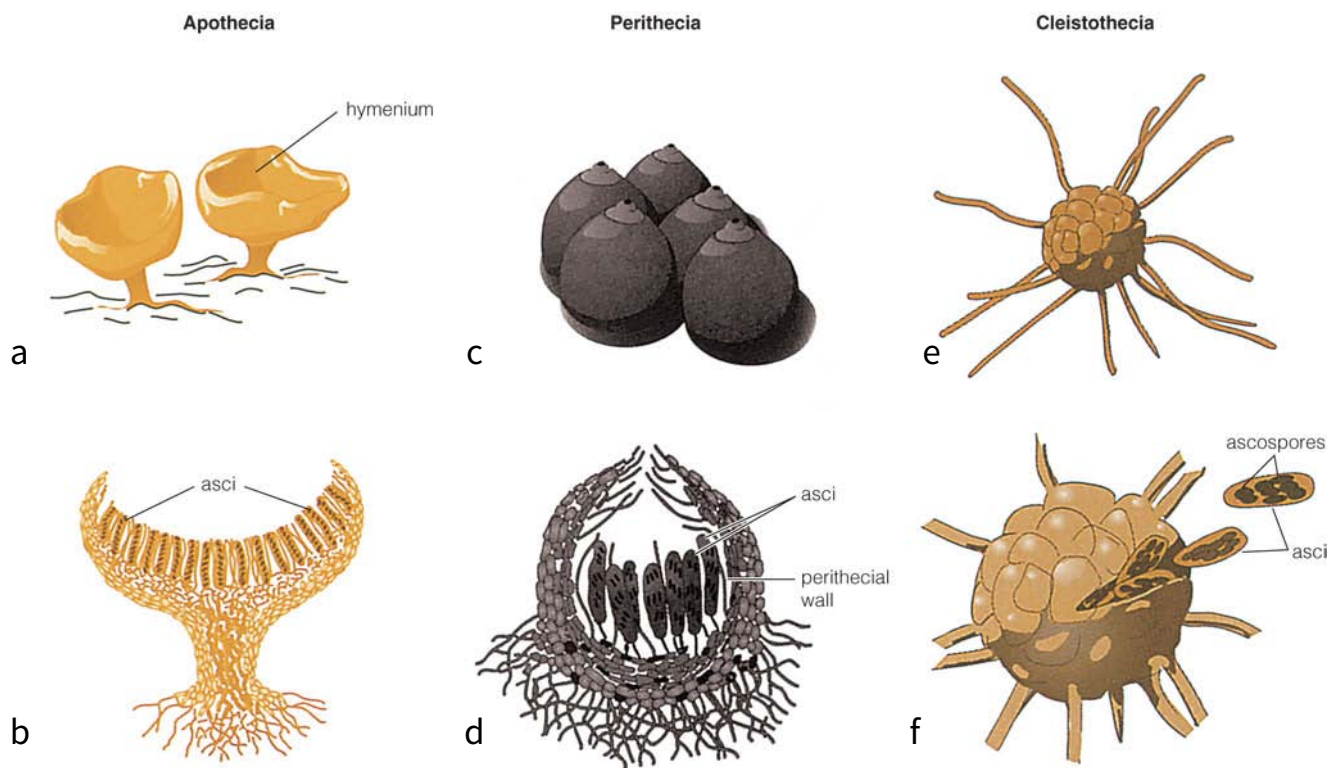


Figure 20.19. Ascomata. (a) Two apothecia. (b) a cross section through an apothecium. X10. (c) Five perithecia. (d) Diagram of a perithecium in cross section. X150. (e) A cleistothecium that is still closed. (f) A cleistothecium of a mildew that has opened to release asci. Each ascus contain eight spores. X500. Most cleistothecia do not actively discharge asci or ascospores.

burrows and extrude a jelly that contains spores. Beetles accidentally pick up the jelly when they pass and carry spores to other trees. In this way, Dutch elm disease has all but eliminated the elm forests that once existed all across the eastern United States.

Still other ascocarps are tiny closed spheres, or *cleistothecia*, which dry up and shelter the enclosed asci until the cleistothecium is crushed (Fig. 20.19e,f). Then the spores may be shot away or released passively. Powdery mildews make cleistothecia that remain through winter on dead leaves.

Many Ascomycetes Engage in Symbiosis

Many ascomycetes form symbiotic associations with other organisms. Some form mycorrhizae with tree roots. Truffles, the delight of French chefs, are underground ascomata of the genus *Tuber* that live in mycorrhizal association with tree roots. The hyphae in these and other ascomycete mycorrhizae do not enter plant cells, but rather coat the root tip and grow between root cells. Such external associations are called **ectomycorrhizae**. They assist the plant by bringing in nitrogen compounds and water.

A great many ascomycetes engage in symbiotic associations called **lichens**, where they partner with algae, cyanobacteria, or both. More than 42% of named ascomycetes--more than

13,500 species--take part in lichens. Only a few dozen other fungal species, all of them basidiomycetes, form lichens.

Figure 20.6 illustrated a leaflike of *foliose* lichen. But there also are branching or *fruticose* lichens, and most familiar of all are crusty or *crustose* lichens that form green, yellow, red, or orange patches on bark, posts, and rocks (Fig. 20.20).

Lichens are important pioneers in rock areas without soil, such as newly exposed volcanic islands and alpine cliffs. Secreting acid, lichens break down the rock to release minerals. As their bodies collect dust and finally decay, they build up soil that other organisms can exploit. Lichens with cyanobacteria are important in the nitrogen economy of some conifer forests, because the cyanobacteria convert atmospheric nitrogen to organic forms (the process of *nitrogen fixation*). When the lichen dies and drops from a tree branch to the forest floor, its decomposition releases nitrogen compounds to the soil.

Fruticose lichens of the genus *Usnea* are particularly beautiful, hanging from tree branches near the west coast of the United States as long, gray-green

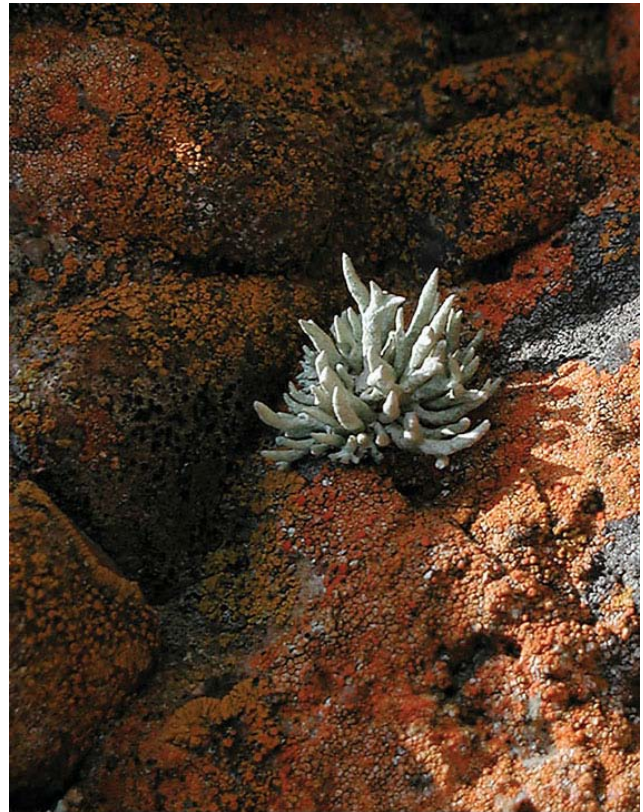


Figure 20.20. Fruticose and crustose lichens growing on rocks above the ocean at Pt. Lobos, CA. The branching grey-green lichen in the center is fruticose; the orange crust on the rocks are crustose lichens.

streamers. They often are mistaken for the flowering plant of the South called Spanish moss and can reach 10 m in length.

Lichens are named for the fungal component, but both partners influence the body form. (When each partner grows alone, it bears little resemblance to the lichen.) The fungus encloses the photosynthetic partners, holding them in place by peg-like hyphae that indent the algal cell wall but usually do not penetrate healthy algal cells. In some lichens, the fungus secretes water-repellant proteins called **hydrophobins** on its exposed surfaces, sealing the contact between hypha and alga. Water flows through the underlying hyphal walls to the alga.

Scientists debate whether lichen symbiosis is mutualistic or parasitic. When the partners are artificially separated, the algal partner usually grows better than the fungus, and many fungi that form lichens are never found growing alone in nature. These facts have led some researchers to view a lichen fungus as parasitic on the photosynthetic partners. However, the fungus also provides a moist, mineral-rich shelter that permits algae and cyanobacteria to grow in habitats where they could not live alone. Thus, whether the symbiosis is mutualistic or parasitic may depend on the environment.

Most lichens reproduce asexually, often by releasing tiny units called **soredia** (singular, *soredium*) in which a few hyphae tightly wrap around one or more photosynthetic cells. Soredia can drift far in air or water. Other reproductive structures are simple fragments of a lichen or outgrowths that pinch off. The most common of these are called **isidia** (singular, *isidium*). The fungus may produce conidia as well. For sexual reproduction, the fungal partner makes typical asci, and the algal partners also undergo genetic recombination.

For a fungal spore to initiate a new lichen, it must find a partner. Some spores land on existing lichens, grow mycelia, kill the lichen's fungal partner, and take over the algae for themselves. But the lichen symbiosis requires a close match between partners. Thus, a fungus growing among free algae will form only loose associations until it meets an alga with compatible genetic traits.

How did so many ascomycetes gain the ability to form lichens? One view is that lichen symbiosis is easy to evolve and has arisen many times in separate fungal groups. If this is true, many groups gained their lichen-forming ability recently. But a recent statistical study supports the opposite view. The ability to make lichens may be very hard to gain, and it may have evolved no more than two or three times--or perhaps just once, early in the evolution of ascomycetes. If this study's views are accepted, then many modern free-living ascomycetes had lichen-forming ancestors. Those fungi include the common kitchen molds *Penicillium* and *Aspergillus*.

Most Mitosporic and Dimorphic Fungi Are Ascomycetes

The great majority of mitosporic fungi are now recognized as ascomycetes. They include the important genera, *Penicillium* and *Aspergillus*, which are among the most useful and most dangerous mitosporic fungi. *Penicillium* has been discussed several times in this chapter. The black-spored kitchen mold *Aspergillus* (Fig. 20.2) also causes food decay and may cause a respiratory disease called aspergillosis. *Aspergillus flavus* makes cancer-producing compounds called *aflatoxins* when it attacks nuts and grains. But some *Aspergillus* species are valuable, contributing to the production of soy sauce and industrial

chemicals as well as the citric acid used in soft drinks. These and other mitotic fungi are extremely widespread, traveling by conidia and growing as molds on organic products as diverse as book bindings and bread.

Hundreds of ascomycete species are dimorphic, switching between mycelial and yeast form in response to environmental conditions. Even baker's yeast sometimes makes hypha-like filaments. Some dimorphic ascomycetes are dangerous human pathogens. *Histoplasma capsulatum* is an example: it grows a mycelium at 25°C, but is a yeast at 37°C, the human body temperature. In the yeast form it can invade the lungs and enter the bloodstream, where its presence can be fatal. *Candida*, by contrast, is a yeast in the environment and a mycelium in the human body.

20.10 PHYLUM BASIDIOMYCOTA

At last we arrive at fungi that make the largest and most complex structure, for example, mushrooms. They occur in phylum Basidiomycota, a group of fungi that is second only to ascomycetes in number of named species (the current total is more than 26,000).

Hymenomycetes Make Long-lived Dikaryons

There are three classes within phylum Basidiomycota. The largest class, the **Hymenomycetes**, contains more than 14,000 species, including all the basidiomycetes that make complex structures. The other two classes are much less conspicuous but include costly crop parasites.

Mushrooms, which make us all familiar with hymenomycetes, are sexual fruiting bodies, or **basidiomata** (singular, *basidioma*). The largest mushrooms are about 1 m in diameter. By contrast, ascomata never exceed a few centimeters in size. Yet ascomycetes and basidiomycetes are sister clades; both are dikaryomycetes. Why, then, do basidiomata get so much larger? A look at the life cycle of a mushroom fungus provides some clues (Fig. 20.21).

Like any fungus, a hymenomycete usually begins life as a spore (Fig. 20.21a). But the spores are nearly always of sexual origin, because mushroom fungi defy the usual rules of fungal life and make few asexual spores. They use meiospores to multiply as well as diversify. The haploid meiospore grows into a small $1n$ mycelium. With luck, the $1n$ mycelium soon meets a compatible partner, usually of a different mating type, and mating occurs.

The first events in mating are simple: compatible hyphae fuse at their tips (plasmogamy), making a fusion cell with one nucleus from each parent (Fig. 20.21b). In many cases, nuclei from each parent slip through septa to other compartments in the partner's mycelium, dividing mitotically as they go, so the joined haploid mycelia become a single $n + n$ mycelium. In other cases, the fusion cell simply begins to make branching $n + n$ hyphae. Either way, the result is an $n + n$ mycelium (Fig. 20.21c).

Eventually, basidiomata--fruiting bodies--form at various points on the $n + n$ mycelium (Fig. 20.21d). To make a basidioma, $n + n$ hyphae branch repeatedly and grow together. Signals must be exchanged between the hyphae, because they develop differently depending on their location in the basidioma. In a gilled mushroom, some hyphae make up a stalk, or stipe. Others make up a protective cap, within which still other

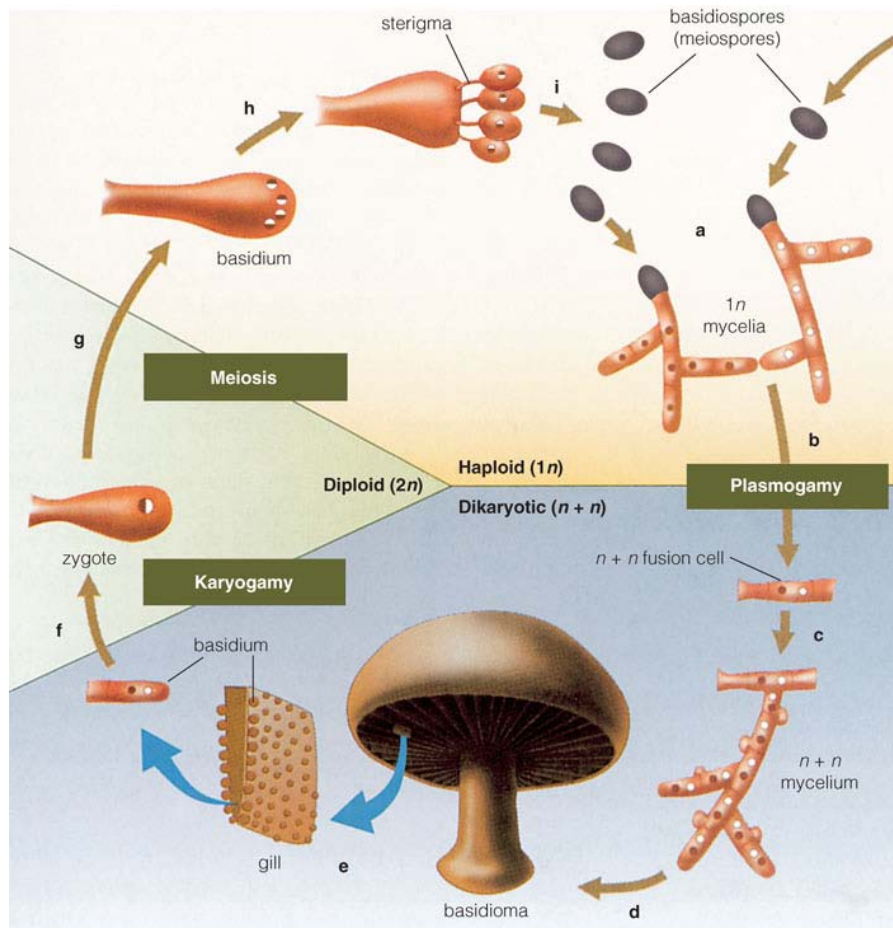


Figure 20.21. Life cycle of a mushroom fungus (class Hymenomycetes). Reproduction is entirely sexual. (a) Basidiospores from two compatible fungi germinate and form $1n$ mycelia. (b) The tips of two hyphae fuse to make an $n + n$ fusion cell. (c) The $n + n$ cell grows into an $n + n$ mycelium. (d) Many $n + n$ hyphae join to build a basidioma, with spore-producing gills under the cap. (e) Enlargement of a small part of a gill. Young basidia (tips of $n + n$ hyphae) jut out over the gill's surface. (f) The basidium swells, and its two nuclei fuse (karyogamy) to make a $2n$ zygote nucleus. (g) Meiosis creates four recombinant $1n$ nuclei in the basidium. (h) The $1n$ nuclei and cytoplasm are forced through sterigmata to make four basidiospores (meiospores). (i) With hardened walls, the basidiospores are released from the gill.

hyphae make gills, the spore-producing part of the basidioma (Fig. 20.21e). All these hyphae are dikaryotic.

Spores are made all over the surface of each gill, from tips of $n + n$ hyphae that face the air between the gills. The tipmost cell in each of these hyphae is a basidium. As the basidium swells, the paired nuclei fuse (karyogamy) to make a $2n$ zygote nucleus (Fig. 20.21f). Meiosis divides the $2n$ nucleus into four $1n$ nuclei, each with a different combination of chromosomes from the two parents (Fig. 20.1g). Next, pressure in the basidium creates spores: the wall of the basidium near each $1n$ nucleus grows a slender stalk or **sterigma**; then the tip of the sterigma balloons into a spore, similar to a person blowing a bubble from a pipe. As pressurized cytoplasm floods through the sterigma, a nucleus is carried with it. This creates four meiospores called basidiospores (Fig. 20.21h), each with a different $1n$ genotype. The spore walls harden, and the spores are released (Fig. 20.21i).

Hymenomycetes lengthen the dikaryotic stage of life far longer than ascomycetes, and this may help explain how basidiomata can grow much larger than ascomata. In ascomycetes, the dikaryon is short-lived and serves only to make a fruiting body; the feeding mycelium is haploid. By contrast, hymenomycetes make dikaryons that may feed and live for many years. During its long life, the dikaryon may create basidiomata many times--typically in the warm, wet spring and autumn.

The diameter of a dikaryon can show how old it is. As time passes, the mycelium grows in diameter, until it may cover hectares of meadowland or forest floor. Mushrooms form near the growing edge of the mycelium. Because the mycelium grows in all directions from its point of origin, its perimeter often is more or less circular. Thus, in fruiting season, the mycelium will produce mushrooms in a ring-shaped array, which is called a fairy ring from an ancient notion that fairies dance on the forest floor and use mushrooms as stools. Each year's fairy ring is somewhat larger than the last one, permitting estimates of how fast the mycelium grows. On the basis of that and the current diameter, some $n + n$ mycelia appear to be hundreds of years old.

For the $n + n$ mycelium to last so long, it needs a way to give each compartment a dikaryotic pair of nuclei. Both nuclei must divide at the same time, and the four resulting nuclei must be sorted into proper pairs (Fig. 20.22). Some fungi solve the sorting problem by lining up the two dividing nuclei side by side and making the septum in the plane of the spindle equators (Fig. 20.22a).

Other species maintain the dikaryotic condition in a more complex way (Fig. 20.22b). As the nuclei begin to divide, a backward-pointing branch hypha forms beside the leading nucleus, and mitosis places one product nucleus into the branch. Then septa form at the equators of both spindles, so the leading compartment gets a proper pair of nuclei. The branch tip fuses with the trailing cell, delivering its nucleus so that the second compartment also has a proper pair. The fused lateral branch remains as a lump on the side of the hypha, positioned at a septum. The fused branch resembles

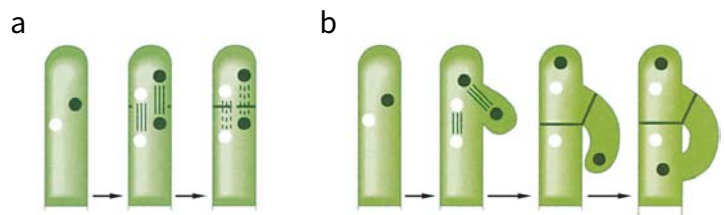


Figure 20.22. Two ways in which basidiomycetes maintain the $n + n$ nuclear condition during the growth of long-lived dikaryotic mycelia. (a) Overlapping mitotic spindles. (b) The formation of a clamp connection.

a carpenter's clamp, so mycologists call it a **clamp connection**. The occurrence of clamp connections in a feeding hypha is a sure sign that the hypha was made by an $n + n$ basidiomycete, because no other feeding mycelia have them. However ascomycetes go through similar steps to make many asci from one $n + n$ hypha. Perhaps both phyla inherited genes for maintaining the dikaryotic condition from their common ancestor.

Was it the long dikaryotic stage that enabled hymenomycetes to evolve their impressive reproductive structures? Perhaps. More mitotic divisions result in more pairs of nuclei that can fuse and make meiospores with unique genotypes. By maintaining the dikaryon for many years, a single hymenomycete can produce immensely more recombinant spores than any other fungus. Such diversity is a source of raw material on which natural selection can operate to produce new body forms.

Hymenomycetes have yet another feature that helps keep the mycelium dikaryotic and may also promote the evolution of complex body forms: their $n + n$ hyphae have unique septa called a **dolipore septum** (Fig. 20.23). Like the simpler septa of the $1n$ mycelium in ascomycetes, the dolipore septum is perforated, with an opening in the center for transport. The dolipore septum thickens around the opening, and a cup-shaped cap called a **parenthesome** forms on each side of the septum. Made of fused layers of

endoplasmic reticulum (ER) membranes held together by proteins, parenthesesomes have openings that let small particles and molecules pass, but not nuclei. Thus, dolipore septa assure that each compartment will keep both of its paired nuclei. This may promote the formation of complex basidiomata. To make complex structures, cells must follow different paths of development in different parts of the mycelium. Such local differentiation can be accomplished more easily if nuclei are kept in defined locations.

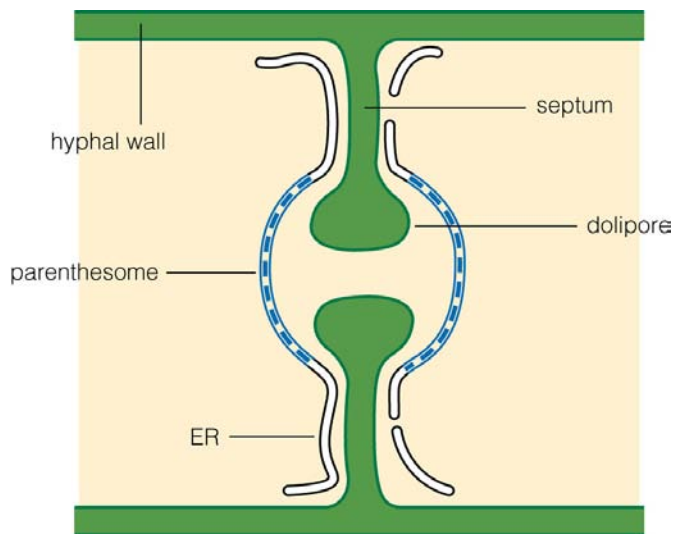


Figure 20.23. A diagram of a dolipore septum, as it appears in a thin section of a hypha. The septum has a ring-shaped thickening (dolipore) around the central opening. Parenthesomes on each side are made from fused layers of ER. Holes through parenthesomes allow passage of molecules and particles, but not nuclei.

Hymenomycetes Make Varied Fruiting Bodies

In addition to mushrooms with gills, the Hymenomycetes make several other kinds of basidiomata (Fig. 20.24). Many mushrooms replace the gills with thousands of vertical pores under the cap. Basidia line the pores. *Bracket* or *shelf fungi* (Fig. 20.24a), found on tree trunks and logs, have caps like mushrooms, but they omit the stipe and connect the cap directly to the food source. Brackets depend on a host tree trunk or log to hold the cap aboveground. Some brackets have pores and grow for many years, becoming woody and adding to the ends of the pores every year.

Puffballs (Fig. 20.24b), common on meadows and the forest floor, make spores inside a leathery bag and rely on raindrops and animals to disperse spores. While internal cells make basidiospores, the outer covering becomes leathery with a hole on top, or it may flake off. When a raindrop hits a mature puffball or an animal steps on it, spores puff into the air.

A *bird's-nest fungus* (Fig. 20.24c) makes basidiomata that look like tiny nests with eggs. The "eggs" are spore-bearing, football-shaped units. *Coral fungi* (Fig. 20.24d) make basidiomata that resemble certain reef corals and release spores all over the surface. In jelly fungi (not shown in fig. 20.24), the basidioma has supporting tissues with a delicate gelatinous texture.

Basidiomata may produce huge number of spores. The common grocery store mushroom, *Agaricus bisporus*, makes about 40 million spores per hour for 2 days. *Ganoderma applanatum*, a shelf fungus that attacks trees, can make 3 billion spores per

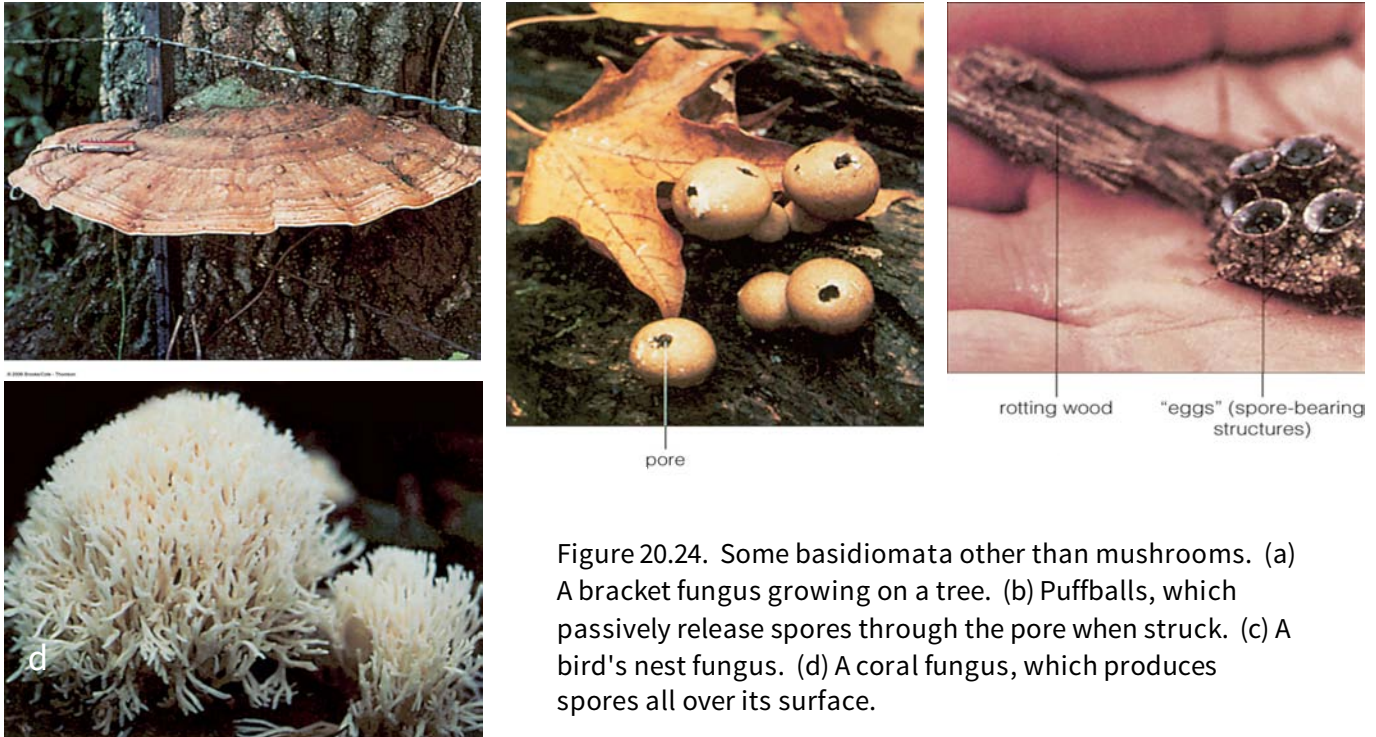


Figure 20.24. Some basidiomata other than mushrooms. (a) A bracket fungus growing on a tree. (b) Puffballs, which passively release spores through the pore when struck. (c) A bird's nest fungus. (d) A coral fungus, which produces spores all over its surface.

day for 6 months of each year. A large puffball, made by *Calvatia gigantea*, may produce 7 trillion spores.

The order of fungi that makes edible mushrooms also contains the most poisonous kinds. The genus *Amanita* is especially dangerous. Although poisonous mushrooms are less common than benign ones, mycologists advise enthusiasts to consult an expert before eating mushrooms they have gathered in nature. Deadly species are easily mistaken for edible ones.

Some basidiomycetes are important mycorrhizal partners of forest trees. Many mushrooms on the forest floor are fruiting bodies of an underground mycelium that draws its main nourishment from tree roots. In return, the fungus brings water, nitrogen compounds, and perhaps phosphates from the soil. These associations, like those made by ascomycetes, are ectomycorrhizae. Unlike those made by glomeromycetes, the basidiomycete hyphae do not invade cells of the host plant's roots, but lay down a dense mesh of hyphae around the tips of roots and grow between root cells.

Many basidiomycetes are saprobes that decompose dead wood and leaves. Even mycorrhizal fungi may do that. In decomposing wood, no other organisms can match these basidiomycetes, because they have superior enzymes to degrade the lignin that hardens wood. Lignin--the second most abundant organic compound on Earth--resists decay because few enzymes can attack it, and its breakdown products are somewhat toxic. Some basidiomycete decomposers make the required enzymes and resist toxicity. Without these fungi, most of the world's carbon could be locked up in dead wood.

Unfortunately, the same ability to decompose wood can be expensive for homeowners. To a basidiomycete, exposed wood in a house is just more food, and fungal attack on it causes damage called **dry rot**. The name is misleading, because the fungus

only grows and feeds when wood is wet. In dry conditions, the fungus lies dormant. You can protect against dry rot by keeping wood dry.

Ballistospore Release Aids in Dispersing Basidiospores

Mushrooms and brackets drop spores downward to reach open air for dispersal, but gills are closely spaced and pores are narrow. How can a fungus prevent spores from landing on

surfaces inside the cap? Basidiomata avoid collisions between spores and walls partly by sensing gravity and orienting growth so that the pores or gills stay nearly vertical. But even with vertical alignment, how can spores be pushed off just hard enough to clear nearby surfaces? The ascomycete way of shooting spores would be far too forceful.

Basidiomycetes evolved a gentler way to push off spores, called **ballistospore release** (Fig. 20.25). Each spore has a small projection where its base connects with a sterigma. When the spore matures, the projection secretes sugars that attract water from the air. A water droplet forms on the projection and grows larger with time. Water also condenses to make a separate thin film elsewhere on the spore. When the droplet grows large enough to touch the film, surface tension pulls the droplet into the film. The movement of the droplet pulls the spore toward the sterigma. As a result, the sterigma is compressed. Being elastic, the sterigma immediately rebounds to its original length, pushing the spore away. The spore moves about halfway to the opposite pore wall or gill before air resistance stops its horizontal motion, leaving the spore to drift slowly downward.

Ballistospore release occurs in members of all the major groups of Basidiomycota; therefore, it probably evolved in the common ancestor of all basidiomycetes.

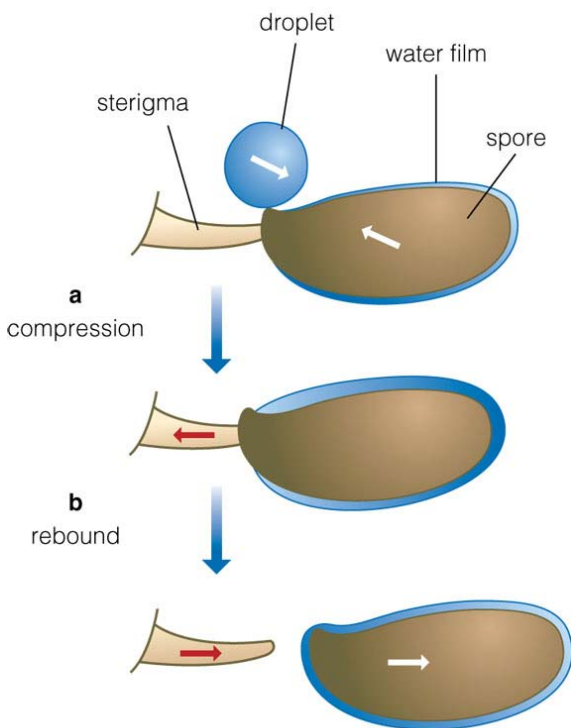


Figure 20.25. Ballistospore release. (a) Water from the air condenses, making a film on the spore and a droplet at the base of the spore. When the growing droplet contacts the film, surface tension pulls the droplet onto the spore, pulling the spore to the left, compressing the sterigma. (b) The elastic sterigma rebounds, pushing the spore away.

Many Ustilaginomycetes Cause Smut Diseases

In addition to Hymenomycetes, phylum Basidiomycota includes two quite different classes without large fruiting bodies. One class, the Ustilaginomycetes, includes 1,064 named species, most of which attack green plants. Most of the resulting diseases are called **smuts**, because black, greasy masses of spores erupt from infected plants, as in corn smut (Fig. 20.26). Some smut fungi infect only seedlings, others infect flowers, and still others form localized infections wherever they land on the plant. In flowers, smut spores may be spread by pollinating insects that come for nectar. Fortunately, each smut fungus attacks only one host species and can be controlled by breeding varieties of the host that resist the fungus.

Ustilago maydis causes a costly smut disease in corn (*Zea mays*). In an average year, *U. maydis* may attack up to 5% of the plants in a cornfield. If conditions are especially good for the fungus, most of the plants may be infected. When the mycelium invades a corn kernel, it takes over control of the kernel's development and stimulates great expansion, converting the kernel to a large gall that combines fungal and corn tissues. The galls drain energy from the rest of the plant and reduce the crop. However, the galls are considered a delicacy in parts of Mexico.

Most smut fungi live as yeasts in the haploid stage and parasitic mycelia in the dikaryotic stage. When compatible haploids meet on a plant, they fuse to make a parasitic $n + n$ mycelium. Later, karyogamy and meiosis generate new $1n$ basidiospores for the next generation.



Figure 20.26. *Ustilago maydis*, the common corn smut, infecting a cob of sweet corn (*Zea mays*). Each gray lump is an infected kernel, converted to a gall by the mycelium inside. The black masses at the top are mature galls that have opened to expose the smut spores.

Urediniomycetes Cause Rust Diseases

The Urediniomycetes are the third class of basidiomycetes. There are more than 8,000 named species. Here are found more complex life cycles and more costly pests. The diseases they cause are called **rusts** because their spores often give host leaves a rusty color. You may see rust on lawn grass when spring weather is especially damp.

Some rusts that attack cereal grains belong to the species *Puccinia graminis*. Their host preference is very specific, and taxonomists recognize several forms within the same species on the basis of host preferences. For example, *P. graminis* form *avenae* attacks only oats, whereas *P. graminis* form *tritici* attacks only wheat.

It is difficult to eradicate rust fungi because many of them have two hosts. In the case of wheat rust, one host is wheat and the second host is a wild shrub called barberry. The two hosts have different roles in the life of the fungus. On wheat, the rust is entirely dikaryotic. Its mycelia make $n + n$ conidia (mitospores) that attack more wheat plants. Being asexual, this reproduction on wheat spreads the parental genotypes through a wheat field. With several generations in a growing season, a single rust spore can start a widespread epidemic. Draining nutrients from the wheat plant without killing them, the rust infection reduces the harvest and may cost billions of dollars during a bad year.

Winter ends the epidemic by killing mycelia and summer conidia. But as the growing season ends, dikaryotic mycelia make special $n + n$ conidia called **teliospores** that survive the winter. In spring, teliospores germinate, go through karyogamy and meiosis, and release $1n$ basidiospores with new genotypes. Basidiospores are pushed away by the same ballistic mechanism as in a mushroom. The basidiospores attack barberry plants. But on barberry, the rust is gentler than on wheat and does not harm the host. The resulting haploid mycelia mate sexually in barberry leaves. Flies assist in the mating by carrying gamete cells between haploid mycelia. The mating results in dikaryotic mycelia with new genotypes. Conidia made by these dikaryotic mycelia attack wheat, launching new epidemics.

Biologists use two approaches to control wheat rust. One approach is to breed new varieties of wheat that resist the common strains of rust. However, new strains of rust fungi arise every year because of sexual recombination on the barberry hosts. Among them are strains that can attack the new varieties of wheat. Within a decade, existing varieties of wheat cannot be planted without risking a rust epidemic. Thus breeders must continually introduce new wheat varieties to keep ahead of the fungus.

The second approach to controlling wheat rust is to eliminate barberry plants. If successful, it would stop the formation of new rust strains. Unfortunately, barberry still survives our efforts to eradicate it.

In the battle for the wheat fields, rust fungi prove the value of sexual reproduction. Without sex to introduce new rust genotypes, we could eliminate wheat rust in a single year by planting only the latest resistant wheat varieties.

KEY TERMS

absorptive nutrition	heterokaryotic
antheridia	hydrophobins
arbuscule	hymenium
ascogonia	Hymenomycetes
ascoma	hyphae
Ascomycota	isidia
ascus, asci	meiosporangium
aseptate hypha	mitosporangia
ballistospore release	mitosporic fungi
basidiomata	mycelium
Basidiomycota	mycorrhizae
basidium	parasexual cycle
chemoheterotrophs	parenthesome
chemotropism	pheromones
chitinous cell wall	powdery mildew
Chytridiomycota	rhizoids
clamp connection	rusts
coenocytic	saprobies
coenomycetes	septa
conidia	septal pore
conidiophores	septate hyphae
crozier	smuts
cytoplasmic streaming	soredia
Deuteromycota	sporangiophores
dikaryomycetes	spores
dikaryon	sterigma
dikaryotic mycelium	teliospores
dikaryotic stage	thallus
dimorphism	true fungi
dolipore septum	zoospore
dry rot	Zygomycota
ectomycorrhizae	zygosporangium
endomycorrhizae	zygospore
Glomeromycota	
grade of evolution	

SUMMARY

1. Kingdom Fungi is a monophyletic group of eukaryotic chemoheterotrophs that reproduce with spores and have chitinous cell walls. About 80,000 species have been named, but 1.5 million species may exist. Kingdom Fungi excludes some organisms that are commonly called fungi (mycetozoa, acrasids, and oomycota) because they evolved from different ancestors.

2. Saprobiic fungi compete with bacteria as decomposers. Other fungi live symbiotically with algae and cyanobacteria (in lichens) or green plants (in mycorrhizae). Others are parasites on various hosts.
3. Some fungi cause human diseases, particularly in immunocompromised patients. These fungi include *Candida*, *Aspergillus*, *Histoplasma*, and *Coccidioides*. Microsporidia parasitize animals and humans and may be highly specialized fungi. Other fungi produce such useful chemicals as alcohol and penicillin, and some (most notable baker's yeast, *Saccharomyces cerevisiae*) are used in medical research.
4. The fungal body can be a microscopic yeast cell or a thallus, usually a mycelium made of branching hyphae. Growing hyphae secrete enzymes to digest foods. Food absorption leads to water uptake, driving growth and transport within the mycelium. Hyphae provide fast collection of food and fast internal transport of nutrients, and they secrete acids and antibiotics. These features, in addition to superior ability to decompose lignin in wood, enable fungi to compete with bacteria.
5. Most fungi reproduce both asexually and sexually, releasing mitospores to multiply the parental genotype and meiospores to produce new genotypes. However, many fungi have little asexual reproduction, and others, called mitosporic fungi (previously deuteromycetes), have little or no sexual reproduction. Mitosporic fungi achieve genetic recombination by occasional sexual reproduction, a parasexual process, or other means.
6. Traditional taxonomy defined four phyla in kingdom Fungi on the basis of details of sexual reproduction and the presence or absence of swimming cells. The two largest traditional phyla (Basidiomycota and Ascomycota) are monophyletic sister groups, whereas the two other traditional phyla (Zygomycota and Chytridiomycota) are not monophyletic. A fifth monophyletic phylum, the Glomeromycota, recently has been recognized.
7. Two grades of evolution--dikaryomycetes and coenomycetes--are informally recognized in kingdom Fungi. A dikaryotic stage and regular septation distinguish dikaryomycetes from coenomycetes. Dikaryomycetes belong to phyla Ascomycota and Basidiomycota and include all fungi that make complex fruiting structures.
8. Members of phylum Chytridiomycota (about 1,000 named species) have swimming reproductive cells. Primarily aquatic, the chytrids sometimes make small mycelia but more often have simpler thalli.
9. Phylum Zygomycota (about 1,100 named species) is named for producing zygospores during sexual reproduction, but some have not been seen to reproduce sexually. The phylum includes important decomposers, parasites of insects and small soil animals, and a few mycorrhizal symbionts. Some have large aseptate mycelia; others have simpler thalli. Mitospores usually are made in sporangia.

10. Members of phylum Glomeromycota (157 named species) nearly always partner with plants to make arbuscular endomycorrhizae. These mutualistic associations may involve more than 80% of plant species. The Glomeromycota have not been seen to reproduce sexually.

11. Members of phylum Ascomycota (more than 32,000 named species) make sexual spores in asci. Most are mycelial, but some are yeasts and others are dimorphic. Mycelia are septate and multiply by releasing mitospores (conidia). Sexual reproduction includes a short-lived dikaryon, usually with complex fruiting bodies (ascomata). Many have not been seen to reproduce sexually. About 42% of named ascomycetes pair with green algae or cyanobacteria in lichens. Others form ectomycorrhizae. Some are parasitic on plants, animals, or humans, and some are saprobes that include food storage pests. Most medically important fungal infections involve ascomycetes. Several ascomycetes are sources of antibiotics and other chemicals or are used in biological research.

12. Members of phylum Basidiomycota (more than 26,000 named species) extrude sexual spores from basidia. A few are yeasts, but most species make septate mycelia. Those in class Hymenomycetes make dikaryons that may last for centuries and also make complex basidiomata such as mushrooms. Some hymenomycetes live as saprobes, including the causal agent of dry rot in houses. Some partner with trees in ectomycorrhizae. A few cause human disease. Basidiomycetes in the phylum's other two classes make short-lived dikaryons, produce no basidiomata, and cause costly rust and smut diseases in plants.

Questions

1. French chefs flavor foods with truffles, underground fruiting bodies of fungi that are mycorrhizal partners of trees. Each fruiting body contains many unicellular sacs, each containing four or eight meiospores. The hyphae are septate. To what phylum of fungi do truffles belong? Which listed items are clues?

2. Most fungi compete with bacteria as decomposers. What traits allow fungi to compete effectively, and why do the traits help?

3. Offer a hypothesis as to the costs and benefits of regular septation in hyphae. How does your idea explain why dikaryomycetes make complex fruiting bodies and coenomycetes do not?

4. In your job as a farm advisor, a farmer shows you a handful of grain that is infected with a fungus. What is the easiest method to determine whether the fungus is an ascomycete, basidiomycete, zygomycete, chytridiomycete, or glomeromycete?

5. Why would a strict phylogenetic systematist object to calling Zygomycota a phylum?

6. Why did early biologists view fungi as plants, and why do modern biologists view fungi as being more closely related to animals?
7. Two phyla of fungi contribute to a slice of pizza. Name the phyla, and explain how they contribute.
8. The feeding process in fungi automatically leads to growth. Why?
9. What is a dikaryon? Which organisms have it? How long does it last? What is its value?
10. How do mitospores and meiospores contribute to fungal life?
11. Fill in the missing information in the table:

Common Features of the Five Phyla in Kingdom Fungi					
Trait	Chytridio- mycota	Zygomycota	Glomero- mycota	Ascomycota	Basidio- mycota
Swimming cells?		No	No		
Grade of evolution	Coeno- mycete			Dikaryo- mycete	
Dikaryotic stage?		No	Unknown		Yes
Septation	Aseptate		Aseptate	Simple perforate	
Characteristic asexual structure		Sporangium	Simple spore		Conidium
Characteristic sexual structure	Resting sporangium			Ascus	
Fruiting body	None				Basidioma
Main habitat		Terrestrial		Terrestrial	

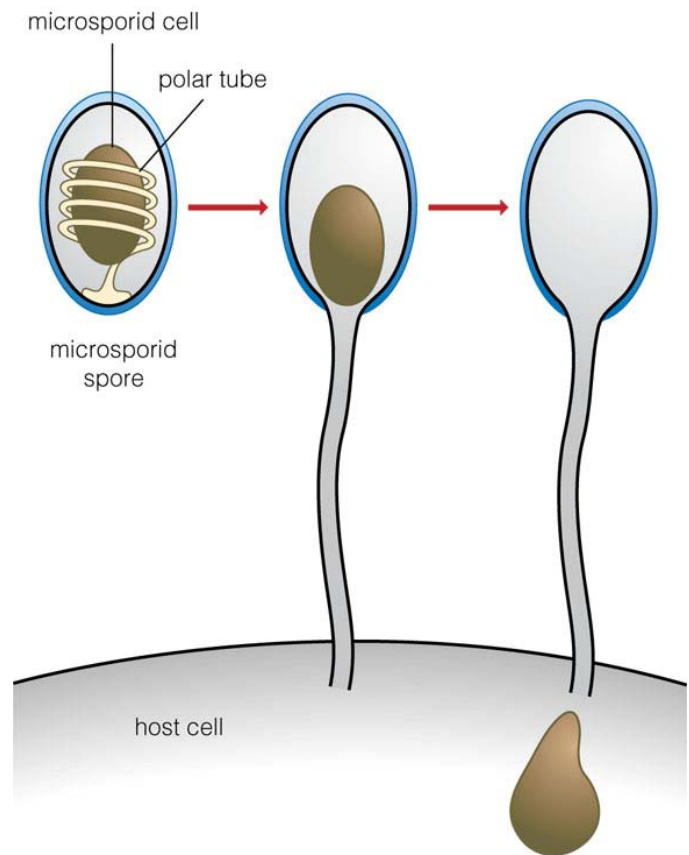
IN DEPTH: *Microsporidia: Fungi in Disguise?*

The widespread human and animal parasites called microsporidia may turn out to be highly modified fungi. Although long known to attack animals, microsporidia were ignored as human pests until 1985, when they were found to cause chronic diarrhea in patients with AIDS. Since then, many microsporidia have been found to infect humans.

Microsporidia are unicellular eukaryotes that attack as shown in the figure. Between hosts, they are spores that contain one cell with a long membranous tube coiled around it. When the spore senses a host cell, the tube is rapidly thrust out. If it penetrates the host cell, the microsporidian cell moves through the tube into the host. There the microsporidian cell multiplies and makes new spores.

Microsporidia are eukaryotes, but they lack mitochondria. In cladograms made from rDNA data, microsporidia branch off at the base of the cladogram, far from the plant, animal, and fungal kingdoms. These facts once suggested that microsporidia are relics of a time before eukaryotes acquired mitochondria. But studies based on other genes suggest a more recent origin of microsporidia, either from the base of the fungal clade or from a group of parasitic zygomycete fungi. If so, they once had mitochondria but lost them.

Evidence for recent loss of mitochondria is that two microsporidians have a gene for a protein called HSP70, which is widespread among eukaryotes and serves only to carry other proteins into mitochondria. The basal position of microsporidia in rDNA cladograms occurs because rDNA evolves more rapidly in microsporidia than other organisms. Finding that microsporidia are related to fungi may be a help in the quest for effective medication against them.



IN DEPTH: *The Hat Thrower*

Many zygomycetes let wind, water, or animals carry away spores, but a few are far more active. An example is *Pilobolus*, whose name means "hat thrower." With a hand lens, you may see it growing on dung in a horse pasture. Its tiny golden sporangiophores, a few millimeters in length, look like jewels. They mature in the morning and adjust their growth to point at the rising sun. A swelling under the sporangium focuses light on a sensitive region, causing fine adjustments in growth. Pressure mounts until the swelling bursts, throwing the sporangium several meters through the air. With luck, it sticks to a blade of grass and is

swallowed by a grazing animal. The spores survive passage through the animal's intestine and are excreted in manure. Most sporangia are shot away when the sun is about 45 degrees above the horizon--the angle at which projectiles travel the farthest. You can see this effect if you enclose *Pilobolus* in a foil-covered jar with a small hole in the foil to let in light. A day later, look for sporangia on the glass near the hole.

This is just one of many ways in which even the simplest fungi sense and adjust to the environment.

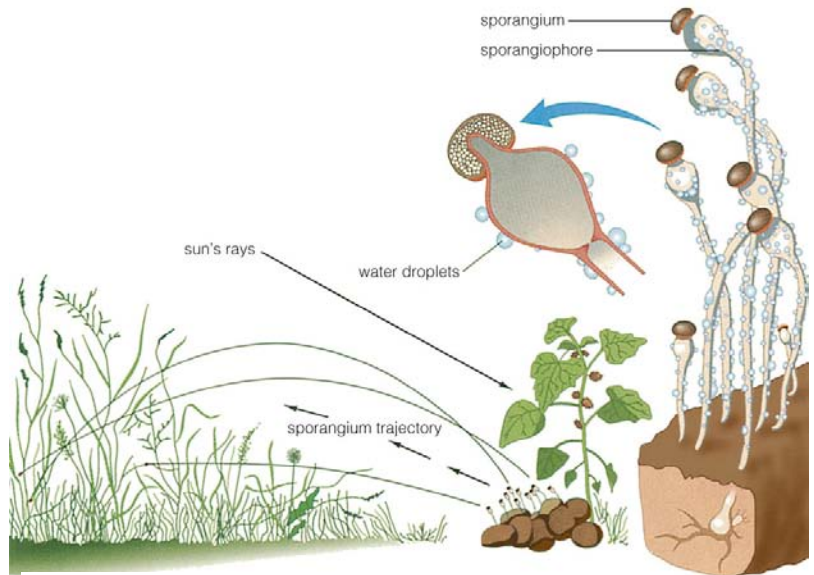


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