FUNGI

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GLOSSARY

ectomycorrhiza (pl. ectomycorrhizae; adj., ectomycorrhizal) Part of a mutualistic relationship between a fungus (usually a basidiomycete, but sometimes an ascomycete) and a host plant in which hyphae aggregate as an extra surface around roots of the plant, aiding nutrient transfer between the plant and fungus.

endomycorrhiza (pl. endomycorrhizae; adj. endomycorrhizal) Part of a mutualistic relationship between a fungus (a zygomycete) and a host plant in which no sheath is formed. Nutrient transfer occurs with the aid of highly branched arbuscules.

exoenzymes Digestive enzymes excreted by fungi into the environment to digest materials externally.

fruiting body Sexual reproductive structure of a fungus.

fungus A member of the kingdom Fungi. Members of this kingdom are heterotrophic (requiring a preformed organic source, i.e., not able to make their own food), eukaryotic, have walls of chitin, and reproduce by means of spores.

karyogamy Fusion of nuclei.

mushroom Vernacular word for a large, fleshy fruiting body consisting of a cap with gills or pores on the undersurface (or sometimes flat or with teeth or folds), usually on a stalk, and producing sexual spores. The term is usually reserved for members of the Basidiomycota.

mutualism Two organisms living together for the mutual benefit of both.

mycelium (pl. mycelia) Vegetative filamentous body of a fungus; mass of hyphae from a single individual.

parasite Organism that obtains its nutrition from a living host, and in so doing harms the host.

plasmogamy Fusion of the cytoplasm of two cells.

spore One- to several-celled propagule of totipotent cytoplasm with cell walls, produced by cell division with concomitant meiosis or mitosis, that may serve for dispersal or overseasoning, but that does not contain an embryo.

substrate Material or host from which a fungus derives its nutrition.

toadstool vernacular name for a poisonous mushroom.

WHEN SOMEONE MENTIONS "FUNGI" you may think immediately of mushrooms on pizza or maybe

[1] www.wisc.edu/botany/fungi/volkmyco.html

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moldy food in your refrigerator. But in fact fungi are everywhere and affect our lives every day, from edible mushrooms to industrially important products to plant helpers, plant pathogens, and human diseases.

I. INTRODUCTION

Many fungi are detrimental in causing a large number of plant diseases that result in the loss of billions of dollars worth of economic crops each year. They also cause a number of animal diseases, including many human maladies. On the other hand, there is a long and rapidly growing list of useful fungi. Fungi have been used in the preparation of foods and beverages for thousands of years, and there are many mushrooms that are edible. Industry has used other fungi in the manufacture of many valuable organic compounds, including organic acids, vitamins, antibiotics, and hormones. They have been used in the research laboratory to study metabolic pathways, mineral nutrition, genetics, and a variety of other problems. But perhaps their greatest contribution has been, and continues to be, their role in recycling carbon and other essential elements in the ecosystem. Because all fungi are heterotrophic (see Section V), they rely on organic material, either living or dead, as a source of energy. Thus, many are excellent scavengers in nature, breaking down dead animal and vegetable material into simpler compounds that become available to other members of the ecosystem.

"Mycology" comes from the Greek words *mykos*, which means "fungi," and "-logy," which means "the study of." Mycologists study many aspects of the biology of fungi, usually starting with their systematics, taxonomy, and classification, and continuing on to their physiology, ecology, pathology, evolution, genetics, and molecular biology. There are quite a few aspects of applied mycology, such as plant pathology, human pathology, fermentation, mushroom cultivation, and many other fields.

II. WHAT ARE FUNGI?

A. Characteristics of Fungi That Separate Them from the Other Kingdoms

The most significant characteristics of fungi that place them apart from the plant, animal, and other kingdoms are the following:

- Fungi are eukaryotic.
- They are nonvascular organisms, meaning they have no specialized transport tissues.
- Most reproduce by means of spores, usually wind-disseminated, and occasionally by insects in some species.
- Both sexual (meiotic) and asexual (mitotic) spores may be produced, depending on the species and conditions.
- Fungi are typically not motile, although a few (e.g., chytrids) have a motile phase.
- Like plants, sexually reproducing fungi have an alternation of generations, although the generations may be different from those of plants.
- The fungal vegetative body may be unicellular (yeasts) or, more often, composed of microscopic threads called hyphae.
- Fungal cell walls are similar in structure to those of plants but differ in chemical composition—fungi cell walls are composed mostly of chitin, which are β-1,4 linkages of *n*-acetylglucosamine. In contrast, plant cell walls are composed mostly of cellulose, which are β-1,4 linkages of glucose. Many plants also contain lignin in their secondary walls.
- Fungal cytoplasmic ultrastructure is broadly similar to that of plant cells, but differs significantly in the kinds of organelles and their structures.
- Fungi are heterotrophic (i.e., "other feeding" in that they must feed on preformed organic material), not autotrophic (i.e., "self-feeding" in that they make their own food by photosynthesis, like most plants and algae).
- Unlike animals (which are also heterotrophic), which ingest and then digest, fungi first digest and then ingest. Fungi produce exoenzymes to accomplish this.
- Most fungi store their food as glycogen (like animals)—plants store food as starch.
- Fungal cell membranes have a unique sterol, ergosterol, which replaces the cholesterol found in mammalian cell membranes.
- The lysine biosynthesis pathway in fungi is different.
- The microtubule protein formed during nuclear division is different from that of all other organisms.
- Most fungi have very small nuclei, with little repetitive DNA, usually with few chromosomes.
- Mitosis and meiosis are generally accomplished without dissolution of the nuclear envelope.

There are about 70,000 named species of fungi and this is believed to be about 5% of the total number of species that exist in nature. If this is the case, 95% of all fungal species are unknown to science and do not yet have names!

In the outdated two-kingdom system, fungi were included in the plant kingdom, as were almost all walled organisms that are not motile. In almost all systematic schemes today, the heterotrophic and eukaryotic fungi are placed in their own kingdom, cleverly called the kingdom Fungi.

The eukaryotes, organisms with nuclei and membrane-bound organelles, can be divided into five kingdoms: Fungi, Plantae, Animalia, Protista, and Stramenopila. Recent DNA evidence suggests that fungi are more closely related to the animals than to plants. Prokaryotes, without nuclei and membrane-bound organelles, include the Bacteria and the Archaea.

As with all taxonomy, the names of various taxa of fungi each have a specific ending that refers to their taxonomic level. The fungal kingdom has its own endings for many taxa; these include the suffix -myc. It is of considerable advantage to be familiar with these endings so that one knows immediately what taxonomic level is being referred to when confronted with a particular name. The names of fungi are "regulated" by the International Code of Botanical Nomenclature, and thus endings for the order and family levels are the same as those of plants (Table I).

B. Fungal Roles in the Ecosystem

Lack of chlorophyll profoundly affects the lifestyle of fungi. Since they are not dependent on light, they can occupy dark habitats and can grow in any direction. The exoenzymes allow them to invade the interior of a substrate with absorptive filaments. Fungi may gain their nutrition from dead organisms, in which case they are called saprophytes. Some fungi derive their nutrition from living organisms; these are called symbionts. Symbionts can be further divided on the basis of whether or not they harm their host. Parasites cause harm to the host, whereas mutualists engage in a reciprocally beneficial association with their host. These categories are further described in Section V.

TABLE I

Taxonomic Endings for the Fungi

Taxonomic level	Taxonomic ending	White button pizza mushroom	The morel
Domain	Eukarya	Eukarya	Eukarya
Kingdom	Fungi	Fungi	Fungi
Phylum	-mycota	Basidiomycota	Ascomycota
Class	-mycetes	Hymenomycetes	Discomycetes
Order	-ales	Agaricales	Pezizales
Family	-aceae	Agaricaceae	Morchellaceae
Genus	—	*Agaricus*	*Morchella*
Species	—	*Agaricus bisporus*	*Morchella esculenta*

C. Importance of Studying Fungal Biodiversity

Fungi affect human lives in many and varied ways, so it is important to know something about the fungi to be able to control or exploit them for our own purposes. For example, more than 90% of known fungal species have never been screened for antibiotics or other useful compounds. However, even more important is the role that fungi play in the ecosystem. They are a vital part of the links in the food web as decomposers and pathogens and are important in grassland and forest ecosystems alike. Fungi have many different kinds of associations with other organisms, both living and dead. To learn more about the impact that fungi have on our lives, we must learn a lot more about them.

Many fungi are harmful to human interests. They can cause human disease, either directly or through their toxins, including mycotoxins and mushroom poisons. They can also cause diseases of plants and animals (e.g., crops, fruit trees, farm animals). Very often fungi cause rot and contamination of foods—most of us probably have something green and moldy in the back of our refrigerator right now. They can destroy almost every kind of manufactured good, with the exception of some plastics and some pesticides.

On the other hand, many fungi are very useful to humans. Of course, there are many edible mushrooms. Yeasts have been used for baking and brewing for many millennia. Antibiotics such as penicillin and cephalosporin are produced by fungi. The immunosuppressive antirejection transplant drug cyclosporin is produced by the ascomycete *Tolypocladium inflatum*. Steroids and hormones—and even birth control pills—are commercially produced by various fungi. Many organic acids are also commercially produced with fungi, for example, citric acid in cola and other soda pop products is produced by an *Aspergillus* species. Some gourmet cheeses such as Roquefort and other blue cheeses, brie, and camembert are fermented with certain *Penicillium* species. Stone-washed jeans, strange as it sounds, are softened by *Trichoderma* species. There are likely many more potential uses that have not yet been explored.

Fungi are also important experimental organisms. They are easily cultured, occupy little space, multiply rapidly, and have a short life cycle. Since they are eukaryotes and more closely related to animals, their study is more applicable to human problems than is the study of bacteria. Fungi are used to study metabolite pathways, to study growth, development, and differentiation, for determining mechanisms of cell division and development, and for microbial assays of vitamins and amino acids. Fungi are also important genetic tools; the "one gene one enzyme" theory in *Neurospora* won George W. Beadle and Edward L. Tatum the Nobel Prize for Physiology or Medicine in 1958. The first eukaryotic genome to have its DNA sequenced was that of the bakers' and brewers' yeast, *Saccharomyces cerevisiae*.

III. HOW FUNGI GROW

A. Biology of Hyphae and Yeast Forms

A fungus is more than just the visible mushroom structure. In fact the mushroom, more properly called a fruiting body, is a very small portion of the individual life cycle and is mainly used for reproduction. The major portion of the life cycle, or the vegetative growth form, in the great majority of fungi consists of a system of threadlike, walled, more or less cylindrical hyphae (singular, hypha) making up what is called a mycelium (plural, mycelia) (Fig. 1). The Ascomycota and Basidiomycota have crosswalls called septa (singular, septum) separating compartments of the mycelium. An exceptional group is the yeasts, which consist of about 800 species that have a single-celled vegetative form. Note that yeast is a morphological term and has no taxonomic significance; yeasts and yeastlike forms can be found in all of the fungal phyla.

B. Exoenzymes and the Heterotrophic Lifestyle

Exoenzymes are the most important reason why fungi are so successful. Fungi excrete exoenzymes at the tips of the growing hyphae into their surrounding environment, where they play a major role in breaking down the substrate. Simpler molecules can then move into the hyphae by diffusion.

IV. REPRODUCTIVE BIODIVERSITY OF FUNGI

A. Fungal Life Cycles

The major events of any sexual life cycle are plasmogamy (cell and protoplast fusion), karyogamy (nuclear fusion), and meiosis (Fig. 2). In most other familiar types of organisms, such as plants and animals, plasmogamy and karyogamy occur in rapid succession and are usually referred to as the single event of fertilization. In the fungi, however, plasmogamy and karyogamy may be separated in time by several minutes, several hours, several days, several years, or even several centuries! Thus the dikaryon, the $n+n$ stage, is a major component of the life cycle of fungi, especially in the Basidiomycota and Ascomycota. Nuclear cycles of all the members of the various phyla can be placed within this generalized nuclear cycle, differing mainly in the amount of time spent in each of the phases.

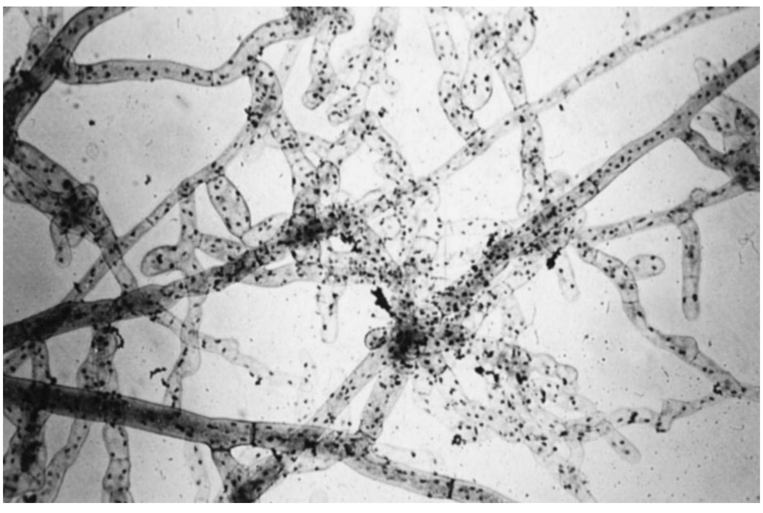

FIGURE 1 Hyphae with dark-stained nuclei.

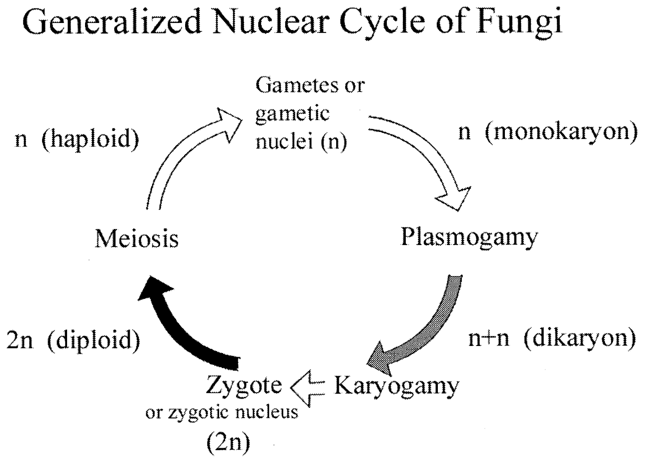

FIGURE 2 Generalized nuclear cycle for fungi.

Besides this sexual cycle, many fungi, commonly called molds, can also reproduce asexually (mitotically) in the absence of meiosis and karyogamy. Many of them produce specialized structures that bear the asexual spores. As in much of biology, there is some "competing" terminology here—the asexual state is also known as the anamorph or mitosporic state. Asexual reproduction can take place at any point in the life cycle (haploid, diploid, or dikaryon), depending on the species and conditions. The sexual state is also known as the teleomorph or meiosporic state.

B. Phyla of Fungi

Based primarily on variation in their sexual reproductive structures, the kingdom Fungi is usually divided into four major phyla.

- Chytridiomycota—sexual and asexual spores are motile, with posterior flagella.
- Zygomycota—sexual spores are thick-walled resting spores called zygospores, and asexual spores called sporangiospores (when present) are borne internally in structures called sporangia.

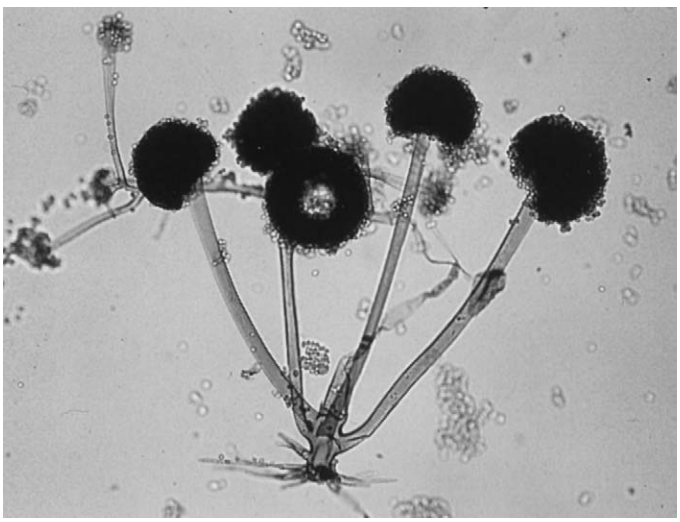

FIGURE 3 *Rhizopus* sporangia.

- Ascomycota—sexual spores (ascospores) are borne internally in a sac called an ascus, and asexual spores called conidia (when present) are borne externally on structures called conidiophores.
- Basidiomycota—sexual spores (basidiospores) are borne externally on a club-shaped structure called a basidium; most species do not have asexual spores, but when present they often take the form of conidia.

There is an additional group, the deuteromycetes, or "Fungi Imperfecti," for which there is no known sexual state. Its members have affinities to members of at least three of the phyla, especially the Ascomycota.

1. Chytridiomycota

The Chytridiomycota, commonly called the chytrids, are a group of mostly water-inhabiting organisms, although some are plant pathogens. In aquatic environments they mostly form scanty filaments with sporangia. Some examples of the Chytridiomycota are *Allomyces*, a water mold, *Synchytrium endobioticum*, a pathogen of potato, and *Neocallimastix*, a chytrid that lives symbiotically in the gut of herbivores, such as cattle. *Batrachochytrium dendrobatidis* and possibly other chytrids have been implicated as an infection associated with the worldwide decline in frog populations.

2. Zygomycota

Commonly called the bread molds, the Zygomycota are terrestrial fungi whose fruiting bodies are mostly microscopic in nature, although their asexually produced sporangia can reach greater than 5 cm tall in some species (Fig. 3). Under certain conditions they may sexually produce thick-walled resting spores called zygospores (Fig. 4). Some, such as *Rhizopus, Mucor*, and *Phycomyces*, can grow on a wide variety of substrates, and a few can act as human pathogens. Most importantly, members of one order, the Glomales, are responsible for forming mutualistic associations called endomycorrhizae with the roots of about 70% of the world's plants. Ectomycorrhizae (from Basidiomycota and Ascomycota) form with another 20% of plant species. See Section V,D,1 for further discussion of mycorrhizae.

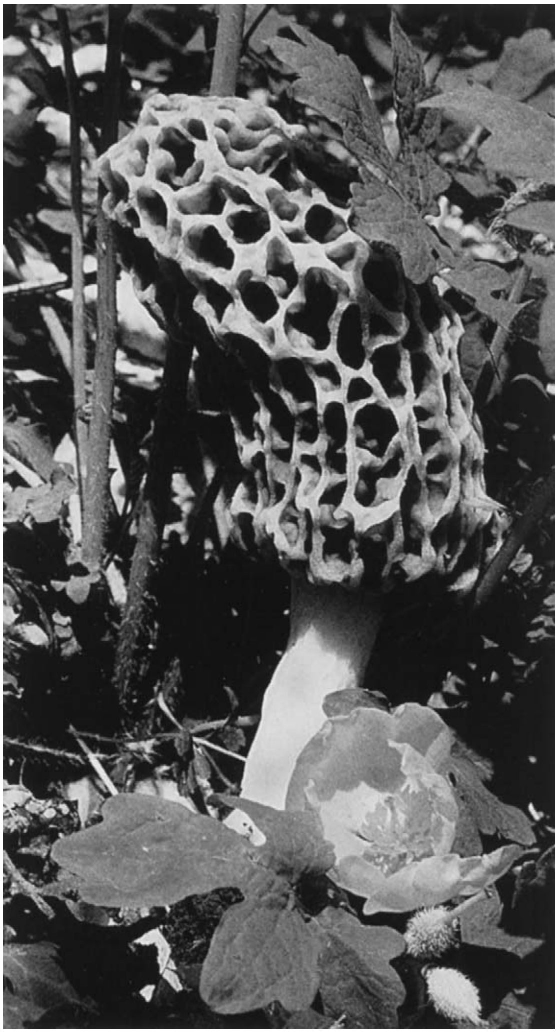

FIGURE 5 *Morchella esculenta*, the morel, a prime edible mushroom. See also color insert, Volume 1.

FIGURE 4 *Syzygites* zygospore between suspensors.

3. Ascomycota

The Ascomycota bear their sexual spores (ascospores) in sacs called asci, which are usually cylindrical. Many

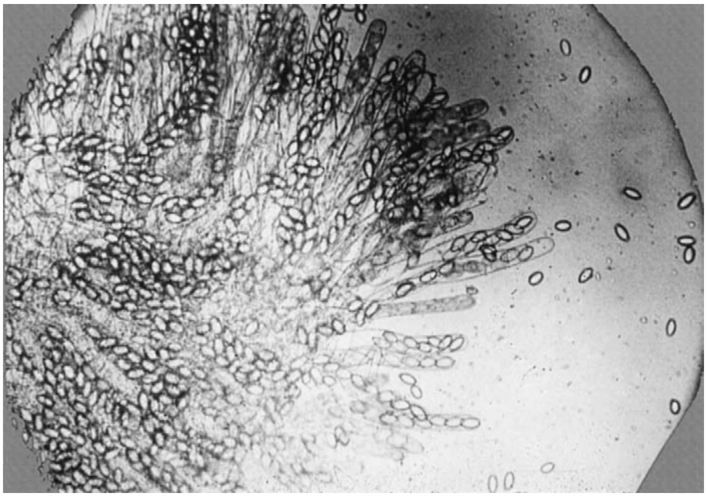

FIGURE 6 Morel asci containing ascospores.

members also form conidia as asexual spores. Familiar members of this phylum include the morels and other cup and saddle fungi, powdery mildews, the industrial yeast *Saccharomyces cerevisiae*, the incitant of chestnut blight (*Cryphonectria parasitica*,) the cause of Dutch elm disease (*Ophiostoma ulmi*), and a variety of other plant pathogens (Figs. 5 and 6).

4. Basidiomycota

The Basidiomycota bear their sexual spores externally on a usually club-shaped structure called a basidium, which is often borne on or in a fruiting body called a basidiocarp or basidiome (Fig. 7). This phylum includes the well-known mushrooms, both edible and poisonous, as well as puffballs, shelf fungi, jelly fungi, and coral fungi (Fig. 8). These species that produce fruiting bodies exhibit various methods of increasing their surface area, as discussed in Section IV,C.

The Basidiomycota also contain perhaps the most important plant pathogens, the rusts and the smuts. These fungi do not produce macroscopic fruiting bodies, but instead bear their spores on the stems, leaves, and flowers of host plants. However, remember that the mycelium is internal and "sucks" the nutrients out of the plant. Effects on the plant range from a reduced yield to death. Rusts in particular have very complicated life cycles, often requiring two unrelated host species to complete their growth stages.

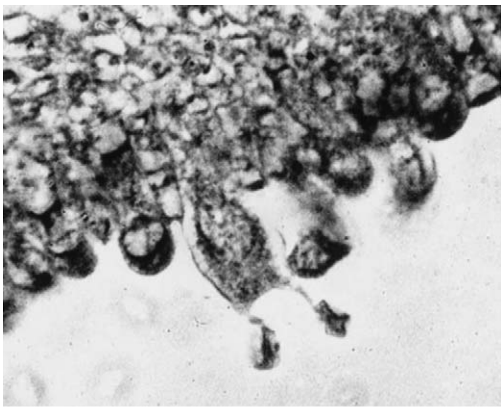

FIGURE 7 Basidium showing two of the four basidiospores produced by meiosis and pinching off of the spores from the basidium.

5. "Deuteromycetes," the Fungi Imperfecti

The deuteromycetes, commonly called molds, are "second-class" fungi that have no known sexual state in their life cycle, and thus reproduce only by producing spores via mitosis. About 90% of these have affinities to the Ascomycota. Most food spoilage and fungal human diseases are caused by members of this group (Figs. 9 and 10). They are also known as the fungi imperfecti, because of their "imperfect" lack of sex. When the "perfect state" of one of these organisms is discovered, as happens every year, the fungus is more properly classified with the teleomorph name. Notice that this group is not classified as one of the phyla. It is just a loose assemblage of organisms that we are not sure where to place accurately in the taxonomic order.

FIGURE 8 (A) *Armillaria nabsnona*, (B) *Tremella reticulata*, (C) *Trametes versicolor*, (D) *Pulcherricium caeruleum*. See also color insert, Volume 1.

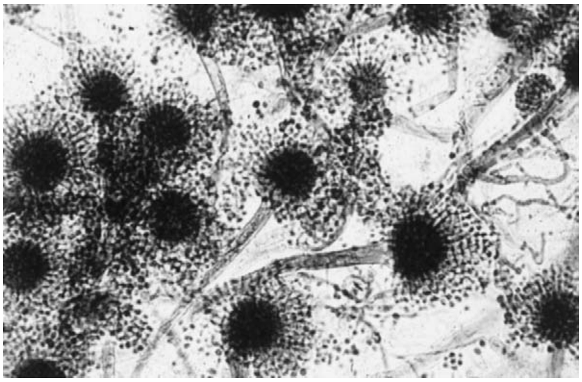

FIGURE 9 *Aspergillus* conidia. See also color insert, Volume 1.

6. Excluded Taxa: Former Members of the Kingdom Fungi

The organisms included here were once considered to be true fungi, but have been excluded because they do not exactly fit our modern classification scheme of the true fungi. They are now considered to belong in other kingdoms, such as Protista or Stramenopila.

a. Oomycota: Water Molds and Downy Mildews

The Oomycota have been excluded from the kingdom Fungi primarily because their cell walls are made of cellulose rather than chitin. They also have swimming zoospores, large nuclei, large egglike oospores, and various other unfungal-like features. They are closely related to the algae, simply lacking chloroplasts, and are now placed in the kingdom Stramenopila (or Protista according to some authors). Ecologically many of its members act like fungi, especially the plant pathogens. *Phytophthora infestans* causes a disease called late blight of potato, which was the cause of the Irish potato famine in the 1840s, in which more than a million Irish people perished and another million emigrated. The downy mildews *Peronospora parasitica* and *Plasmopara viticola* cause diseases of members of the cabbage family and of grapes, respectively. *Pythium* species cause damping-off disease of seedlings in agricultural practice. However, many other species are innocuous saprophytes that decompose debris in water. A few of these so-called water molds (some species of *Saprolegnia* and *Achlya*) are opportunistic fish parasites, especially in aquariums and fish hatcheries (Figs. 11 and 12). They are a particular problem in trout and salmon hatcheries.

b. Myxomycota: True Slime Molds

The Myxomycota are the true slime molds, also known as the plasmodial slime molds, and are considered members of the kingdom Protista. They exist in nature as a plasmodium—a blob of protoplasm without cell walls and only a cell membrane to keep everything in (Fig. 13). It is really nothing but a large amoeba and feeds much the same way, by engulfing its food (mostly bacteria) with pseudopodia, in a process called phagocytosis. So the slime mold ingests its food, then digests it. True fungi have a cell wall and digest their food with exoenzymes before ingesting it. When the plasmodium runs out of food it can form fruiting bodies. Most slime mold fruiting bodies are quite small, 1–4 mm in height, but

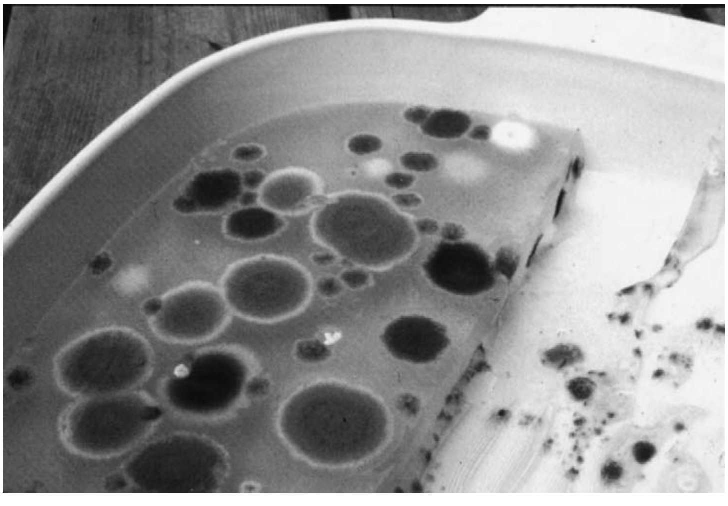

FIGURE 10 Jello mold, a favorite dish for picnics.

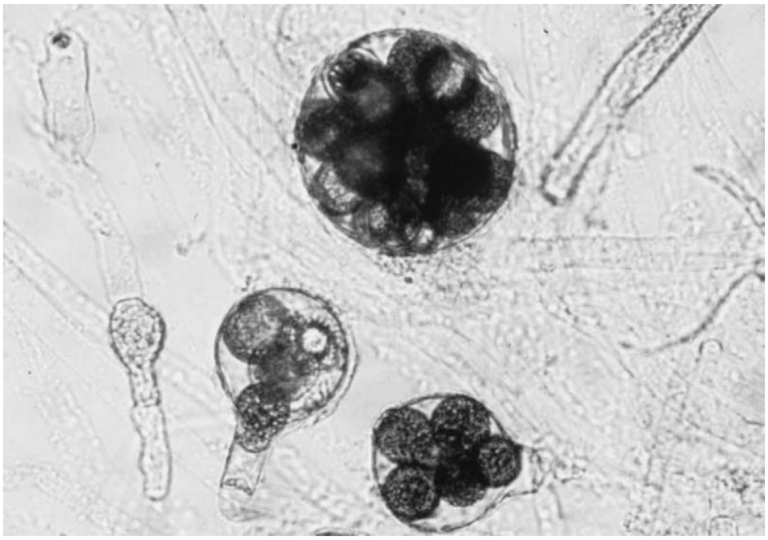

FIGURE 11 *Saprolegnia* oogonium containing oospores.

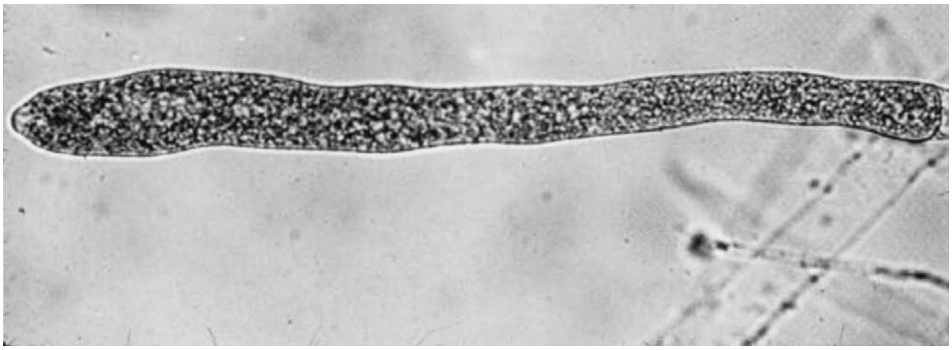

FIGURE 12 *Saprolegnia* sporangium containing small zoospores.

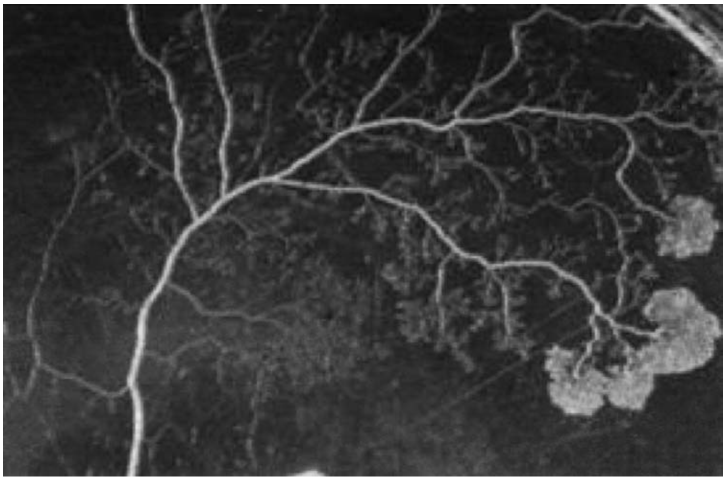

FIGURE 13 Plasmodium of a slime mold. See also color insert, Volume 1.

some can be up to 25 cm in diameter (Fig. 14). In such cases a large plasmodium may be seen crawling along the ground, inspiring science fiction movies such as "The Blob." These slime molds have been traditionally studied by mycologists because their small, delicate fruiting bodies tend to be fungal in appearance. Most slime mold fruiting bodies are quite beautiful.

c. Dictyosteliomycota: Cellular Slime Molds

The Dictyosteliomycota are the cellular slime molds or "social amoebae" and are among the most bizarre of microorganisms. These members of the Protista are free-living amoebae with no cell walls, indistinguishable from garden-variety amoebae until they begin to run out of food. At that point they signal to one another using cyclic AMP (a small nucleotide molecule) and begin to aggregate to form a "slug" or pseudoplasmodium. This slug, composed of hundreds of amoebae, acts as a single organism and can actually migrate along a light or temperature gradient. Eventually the slug stops migrating, rounds up, and forms a sorus, a kind of sporangium containing spores on a stalk. Not all of the cells become spores; some of them "sacrifice" themselves to become stalk cells to raise the spores up into the air for a better position for wind dispersal. So formerly free-living organisms act like a single organism for the good of the species. Very strange indeed!

d. Plasmodiophoromycota: Endoparasitic Slime Molds

The Plasmodiophoromycota are an odd group of endoparasites that live almost their entire life cycle inside a cell of another organism. They lack cell walls in the assimilative state and reproduce by means of swimming spores, the only part of their life cycle that does not occur inside a cell. *Plasmodiophora brassicae* causes club root in crucifers, and *Spongospora subterranea* causes powdery scab of potatoes. Scientists really do not know where to place these organisms taxonomically; they have been allied with the Oomycota, the Myxomycota, or various other protists, but in reality they are not closely related to any other known group of organisms. No one is even sure what kingdom to place them in!

C. Surface Area and Reproduction

Many fungi have very specialized habitats. For example, the basidiomycete *Suillus americanus* can grow only in association with the eastern white pine, *Pinus strobus*. To infect a new white pine, the immobile mycelium of the fungus must produce spores to move to a new host. These spores are carried by the wind, not by some specific insect or other animal vector. Thus the fungus must produce enormous numbers of spores so that a few of them will land on the "correct" substrate. The underside of the *Suillus* mushroom has small pores that are lined with microscopic spores. This increases the surface area for bearing spores by more than 100 times. More commonly, mushrooms have gills underneath the cap to increase surface area. Other fungi increase their surface area by forming upright coral-like branches, whereas others form downward-pointing teeth or spines

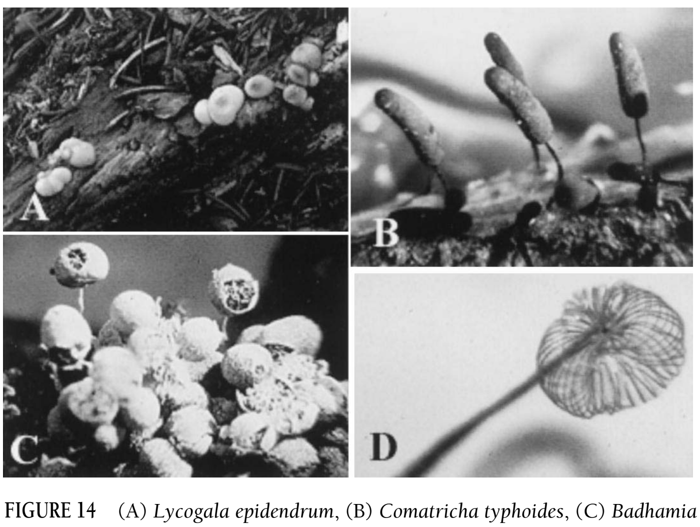

FIGURE 14 (A) *Lycogala epidendrum*, (B) *Comatricha typhoides*, (C) *Badhamia utricularia*, (D) *Dictydium cancellatum*.

FIGURE 15 Different ways of increasing the surface area for bearing spores. Clockwise from upper left: pores, upright branches (coral), teeth, and gills.

(Fig. 15). Others (not shown) have blunt ridges and some have folds, and some increase the time of sporulation rather than the spore-bearing physical space. Analogous surface area modifications are made by members of other phyla of fungi.

V. FUNGI IN THE ENVIRONMENT

Fungi occupy many different niches in the environment, although any one species usually occupies only a single niche. Many niches have not yet been explored for fungi, which is the major reason why mycologists believe there are high number of fungi yet to be discovered. Fungi can be divided into groups based on their nutritional status and the nature of their relationship with their host. Saprophytes use nonliving organic material and are important scavengers in ecosystems. Along with bacteria, fungi are important in recycling carbon, nitrogen, and essential mineral nutrients. Parasites use organic material from living organisms, harming them in some way. Their hosts range from single-celled diatoms to other fungi, plants, animals, and humans. Fungi are the major parasites (pathogens) of plants. Mutualists are fungi that have a reciprocally beneficial relationship with other living organisms, in which both organisms benefit. The two main types of mutualistic associations involving fungi are mycorrhizae, which are associations of fungi with plants roots, and lichens, which are associations of fungi with algae or cyanobacteria There are also a few commensal fungi that use other organisms as merely a place to live; these fungi derive no nutrition from their host.

A. Fungi as Saprophytes

Along with bacteria, fungi are the major decomposers and recyclers in the environment. For every sort of dead material present, there is usually at least one fungus that can degrade that material. A few exceptions include some pesticides and some types of plastics; no fungi have yet developed exoenzymes capable of digesting these synthetic materials. Fungi are important in breaking down carbon- and nitrogen-containing compounds into components that they and other organisms can use. Fungi are especially important in the breakdown of the wood components cellulose and lignin (discussed in Section VI,F).

B. Fungi as Plant Parasites

About 90% of plant diseases are caused by fungi, resulting in billions of dollars in crop and forest losses each year. A parasite is referred to as a pathogen if it elicits a recognizable and persistent disease. The most severe pathogens are those that are imported accidentally from other continents and that cause severe problems with the native populations and cultivated plants. The severity of any plant disease is determined by three factors, known as the disease triangle, consisting of the interaction of the host (conditions favoring susceptibility), pathogens (conditions affecting virulence), and the environment (conditions favoring disease)(Fig. 16). All three factors must work in conjunction to produce a disease and determine its harshness.

1. Fungi in Crop Pathology

The science of plant pathology deals mostly with organisms, especially fungi, that cause plant disease. Plant diseases are generally classified on the basis of what kinds of symptoms occur in which part(s) of the plant (Table II). Some important fungal pathogens of crop plants include *Puccinia graminis* (black stem rust of wheat), *Erysiphe graminis* (powdery mildew of grasses), *Claviceps purpurea* (ergot), and *Ustilago maydis* (corn smut).

2. Fungi in Forest Pathology

There have been a number of fungal diseases of forest trees that have caused great problems in North America (Table III). Forest pathogens often need a longer time to kill their larger, perennial hosts, sometimes living inside the tree for several decades before the host finally succumbs.

Cryphonectria parasitica, Ophiostoma ulmi, and *Discula destructiva* are introduced pathogens that have dev-

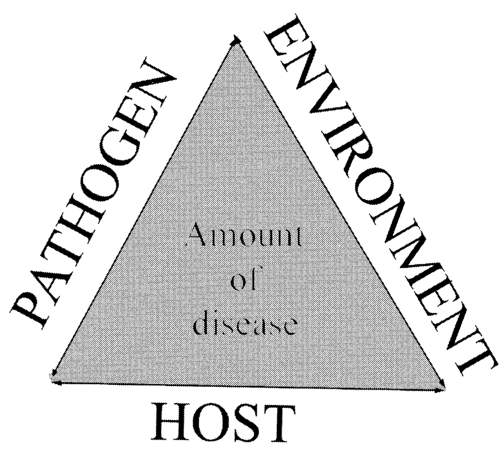

FIGURE 16 The disease triangle, showing the three factors that determine the disease severity.

TABLE II

Types of Plant Diseases

Type of disease	Symptoms
Blight	Extensive necrosis and rapid death
Dieback	Dead branches protruding from apparently healthy tissue
Lesion	Localized cell death
Canker	Lesion on a woody stem
Rot	Extensive decay of tissue
Vascular wilt	Blockage of the vascular transport system, resulting in starvation or disiccation
Gall	Localized tumorlike growth
Stunting	Reduction in overall growth size
Rusts	Rust-colored lesions on various parts of the plant
Smuts	Drastic malformations, usually of reproductive parts

astated their hosts in North America. In their native Asia, these pathogens coevolved with their hosts and caused them only minor annoyance. However, when they were accidentally introduced into North America, either on live plants or on logs for sawing, the fungus escaped and subsequently devastated the North American tree species because there was not enough time for the host to develop resistance. *Cronartium ribicola, Ceratocystis fagacearum*, and *Armillaria* species are native American fungi, but they cause severe diseases nonetheless. A good pathogen does not kill its host right away, but keeps it alive as long as possible to continue deriving nutrients from it.

C. Fungi as Animal Parasites

1. Fungi Affect Humans

Fungal effects on humans are classified by whether they can grow on the body (mycoses) or whether they cause problems by their ingestion. Mycetismus refers to the eating of poisonous mushrooms, and mycotoxicosis refers to the ingestion of toxins produced by the fungus, not involving eating the fungus itself. Mycoallergies may be a separate category.

a. Mycosis: Fungi Growing Directly on Human Tissues

There are a number of fungi that can grow directly on human tissue. Most of them require some debilitation of host defenses, especially the immune system. Fungal diseases have gained in importance over the last couple of decades because of increases in the numbers of such patients, including those with AIDS, people on corticosteroid therapy or immunosuppressive drugs (such as the transplant drug cyclosporin), diabetics, and people undergoing chemotherapy treatment for cancers.

About 175 human pathogens are recognized among the approximately 70,000 known species of fungi. Around 20 are regularly isolated from cutaneous infections (dermatophytes and yeasts), a dozen are associated with severe subcutaneous localized disease, and

TABLE III

Some Important Forest Pathogens

Pathogen	Disease
Cryphonectria parasitica	Chestnut blight
Ophinostoma ulmi	Dutch elm disease
Discula destructiva	Dogwood anthracnose
Cronaritum ribicola	White pine blister rust
Ceratocystis fagacearum	Oak wilt
Armillaria spp., especially *A. mellea* and *A. ostoyae*	*Armillaria* root rot

about 20 may cause systemic infections (Table IV). In addition, there are many opportunistic pathogens that cause disease in debilitated or immunosuppressed patients.

Probably the most common fungal infection in North America is yeast infection, caused by *Candida albicans*. This yeast can grow on outside portions of the skin or in any area of the body that is moist and warm. It is especially prevalent in the genital area of women. Oddly enough *Candida* is part of the normal flora of the body and can be isolated from almost everyone at any time. Only when conditions get out of balance does the yeast flourish and cause disease. However, the systemic true pathogens are the most feared, since they do not require a debilitation of the host defenses to become pathogenic. These dimorphic fungi get around host defenses by changing their form from a mycelium to a yeast upon change in temperature, thus evading even the healthiest of immune systems. Fortunately they are all geographically restricted. (see also Rippon, 1988.)

b. Mycetismus: Eating Poisonous Mushrooms

Of the 70,000 species of fungi, there are about 250 species of delicious edible mushrooms and about 250 species that will kill you. Most of the other species are innocuous or unpleasant tasting. Some people call poisonous mushrooms "toadstools," a word probably derived from the old German *Todstuhle* for death chair. But how can you tell the difference? There is no easy way to tell if a mushroom is poisonous. Old wives' or old husbands' tales about silver spoons or whether it grows on wood or whether animals eat the mushrooms do not work! The only way to be sure if a mushroom is edible is to identify it to species by consulting books or knowledgeable persons. The old saying is "there are old mushroom hunters, and there are bold mushrooms hunters, but there are no old, bold mushroom hunters." The best way to learn about edible mushrooms is to join a local mushroom club. Do an internet web search for the North American Mycological Association for a list of these clubs. (NOTE: The pictures and descriptions in this article are NOT adequate to identify mushrooms for eating. We have a report of a woman who nearly died from eating wild mushrooms that she identified only from an encyclopedia drawing. Don't let this be you! Be absolutely sure of your identifications!)

As shown in Table V, unrelated species in various genera may contain the same toxin, and one or more toxin groups may be found in the same genus. To complicate things further, many genera contain both poisonous and nonpoisonous species, although several genera are more or less homogeneous with respect to poisoning ability. Most species of fungi have not yet been analyzed for toxins. Evidence suggests that mushroom toxins have not evolved for protection. For example, what good does it do a mushroom such as *Amanita virosa*, known as the death angel, if an animal eats the mushroom and then dies two days later? The toxins

TABLE IV

Mycoses Can Be Characterized by Their Location on the Body

Type of mycosis	Location	Some diseases	Some fungi causing disease
Superficial mycoses	Infections of the hair shaft or dead outer layer of skin (stratum corneum)	Pityriasis versicolor, tinea nigra palmaris, piedra	*Malassezia furfur, Trichosporon beigelii, Cladosporium, Piedraia hortae*
Cutaneous mycoses	Dermatophytes—infections of skin, hair, and nails	Ringworm, jock itch, athlete's foot, tinea corporis, tinea capitis, and many others	*Microsporum, Trichophyton,* and *Epidermophyton* spp., occasionally a *Candida* sp.
Subcutaneous mycoses	Chronic localized infections of the skin and subcutaneous tissues	Sporotrichosis, chromoblastomycosis, phaeohyphomycosis	*Sporothrix schenckii, Phialophora, Cladosporium*
Systemic mycoses (deep mycoses), true human pathogens	Fungal infections of the body caused by dimorphic fungal pathogens, usually entering through the lungs	Histoplasmosis Blastomycosis Coccidiodomycosis Paracoccidioidomycosis	*Histoplasma capsulatum* *Blastomyces dermatitidis* *Coccidiodes immitis* *Paracoccidioides brasiliensis*
Systemic mycoses, opportunistic pathogens	Fungal infections of the body caused by common fungi becoming pathogenic owing to patient debilitation	Aspergillosis Cryptococcosis Candidiasis Zygomycosis *Pheumocystis* pneumonia Penicillosis	*Aspergillus* spp. *Cryptococcus neoformans* *Candida* spp. *Mucor, Rhizopus* *Pneumocystis carinii* *Penicillium marneffei*

TABLE V

Seven Major Classes of Mushroom Toxins

Class of toxin	Fungi where found	Main symptoms	Mode of action
Cyclopeptides (amatoxins and phallotoxins)	*Amanita virosa* (Death angel), *A. phalloides* destroying angel), *A. verna, A. ocreata, Galerina autumnalis*	Violent cramps, diarrhea, nausea, jaundice, coma, death; it normally takes about 12–36 hours for symptoms to appear	Attacks RNA polymerase in the liver, eventually destroys liver
Monomethyl hydrazine (gyromitrin)	*Gyromitra* species (false morels)	Nausea, vomiting, diarrhea, cramps, jaundice, convulsions, coma, death; cancers produced in mice	Similar in structure to solid rocket fuel, destroys red blood cells, attacks central nervous system
Coprine (tippler's bane)	*Coprinus atramentarius*	Hot, flushed, metallic taste, palpitation, vertigo, vomiting headache like a bad hangover	Blocks alcohol dehydrogenase so alcohol cannot be completely metabolized; similar in structure and function to Antabuse
Muscarine	*Inocybe* spp., *Clitocybe dealbata* (the "sweater")	Induces PSL (perspiration, salivation, lacrimation) symptoms, cramps, blurred vision; contraction of pupils, hypotension	Anticholinergic—antagonist to action of parasympathetic nerve fibers
Ibotenic acid, muscimol	*Amanita muscaria* and *A. pantherina*	Rusults in "expanded perception," talking to God, macropsia (perceiving objects as enlarged), rapid heartbeat, dry mouth	Hallucinogenic, psychoactive, action on nervous system, acts as a neuropeptide receptor
Psilocybin, psilocin, psychedelic mushrooms	Many *Psilocybe* spp., some *Panaeolus* spp.	Trancelike state induced, hallucinations	Serotonin (neurotransmitter) analog
Gastrointestinal irritants	Many different kinds, found in hundreds of species	Nausea, vomiting, no effect on other organs, most just cause discomfort or distress to varying degrees	Various, depending on the species of mushroom

appear to be merely waste products, usually from nitrogen metabolism, that happen to be poisonous to animals or humans.

c. Mycotoxicosis: Eating Toxins Produced by Fungi, not Necessarily from Eating the Fungi Themselves

Mycotoxins are usually produced by molds growing on foods. As the molds grow, they metabolize the food product and excrete their waste products back into the substrate. Some of these waste products happen to be highly toxic, and when a person eats the toxin (even after cutting the mold off), there is usually some harm to the person. The common contaminants *Aspergillus flavus* and *A. parasiticus* can produce aflatoxins, especially in peanuts. If you have ever eaten a whole peanut that tastes so bitter that you spat it out, it was probably contaminated with aflatoxin. This compound is highly carcinogenic at about 10–20 parts per billion, and kills very rapidly at higher concentrations. There are legal limits for the amount of aflatoxin allowed in peanut butter sold in the United States.

2. Fungi Affect Other Animals

Nonhuman animals are affected by fungi in much the same way that humans are, with some differences in certain species. For example, dogs are susceptible to cyclopeptide poisoning while cats apparently are not. There are numerous other examples of this discrepancy—so do not pick and eat a mushroom just because you see an animal eat it. Another important point to consider is that you do not know what happened to that squirrel after it ate that mushroom.

Animals are also affected by many of the same fungal diseases as are humans. For example, dogs are particularly susceptible to blastomycosis and are often used as a warning sentinel, like a canary in a mine, for alerting humans to possible risk.

D. Fungi as Mutualists with Other Organisms

Rather than being harmful, some fungi benefit their host in some way while receiving nutrients from them.

The two most common mutualistic associations are mycorrhizae, an association between a fungus and the roots of a plant, and lichens, an association between a fungus and either an alga or a cyanobacterium or both.

1. Mycorrhizae

According to Harley and Smith (1983), a mycorrhiza is defined as "an association between a fungus and a host plant in which destructive disintegration of the host does not occur and which is a prevalent and usual condition of the host plant in natural habitats and as such is very common and widespread." *Myco*, of course, means "fungus," and *rhiza* is "root," so mycorrhiza literally means "fungus root." More than 90% of plants in nature have a mycorrhizal symbiont. The only groups of plants that regularly lack mycorrhizae are some crucifers, sedges, and some legumes.

There are several types of mycorrhizae. In ectomycorrhizae, the fungus, usually a Basidiomycota or sometimes an Ascomycota, forms a sheath outside the root (Fig. 17). Exchange of nutrients takes place in transfer cells called a Hartig net, which penetrates between the cells of the root cortex, but does not penetrate the cells themselves. In endomycorrhizae, also called vesicular-arbuscular mycorrhizae (VAM) or sometimes simply arbuscular mycorrhizae, no sheath is formed. This fungus is always a member of the Zygomycota. Nutrient exchange takes place in highly branched hyphae called arbuscules, which penetrate into the cortical cells, but do not penetrate the cell membrane. Orchid mycorrhizae and ericoid mycorrhizae are special types that are found with plants in the Orchidaceae and the Ericaceae, respectively, and they differ significantly in their structure and life strategies.

In all types of mycorrhizae, hyphae extend from the root into the surrounding soil, greatly increasing the surface area for absorption of nutrients, particularly phosphate, nitrogen, and potassium. In return for shunting some of these nutrients into the plant, the fungus receives some sugars from plant photosynthesis. Thus both organisms benefit. Mycorrhizal fungi are abundantly represented in fossils from the Devonian and later periods and apparently coevolved with their hosts. It has been hypothesized that these fungi were necessary for the movement of water plants onto land.

As an interesting sidelight, there are also several hundred species of nonphotosynthetic plants (such as *Monotropa uniflora*, the Indian pipe) that get their energy as parasites of fungi that are mycorrhizal with photosynthetic plants. Radioactive carbon has been used to trace nutrient flow from the host plant through the mycorrhizal fungus and into the achlorophyllous plant.

2. Lichens

A lichen is a dual organism that consists of a mutualistic relationship between a fungus (the mycobiont) and an alga or cyanobacterium (the photobiont). Usually neither can survive on its own. Most of the fungi involved are Ascomycota, though a few are Basidiomycota. There are about 16,000 species of lichens, many of which can grow in very inhospitable environments—on rocks, sides and branches of trees, and gravestones, from the tropics to deserts to the Arctic (Fig. 18). Lichens are

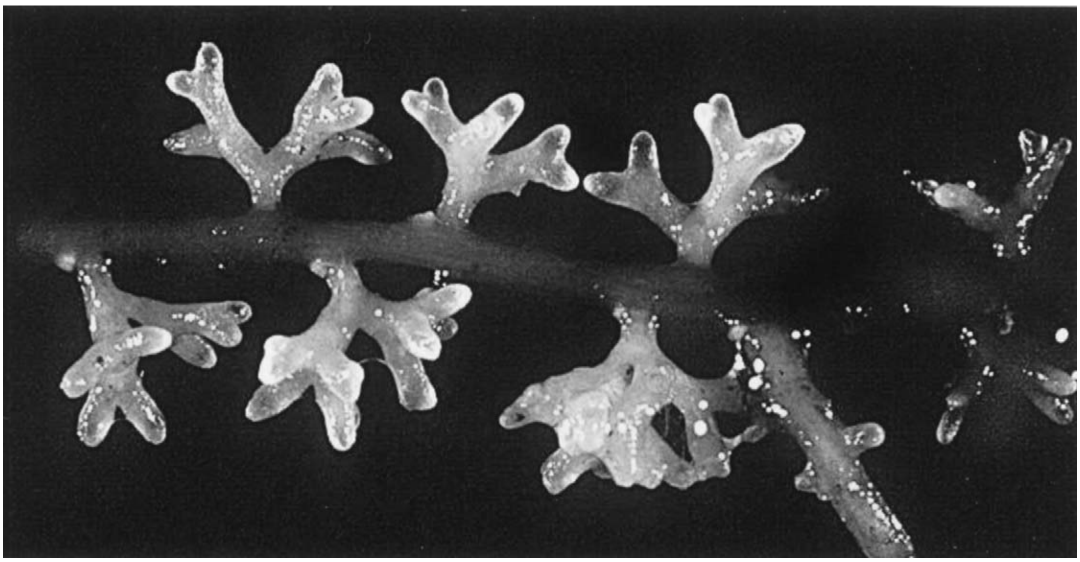

FIGURE 17 Ectomycorrhizae on pine roots.

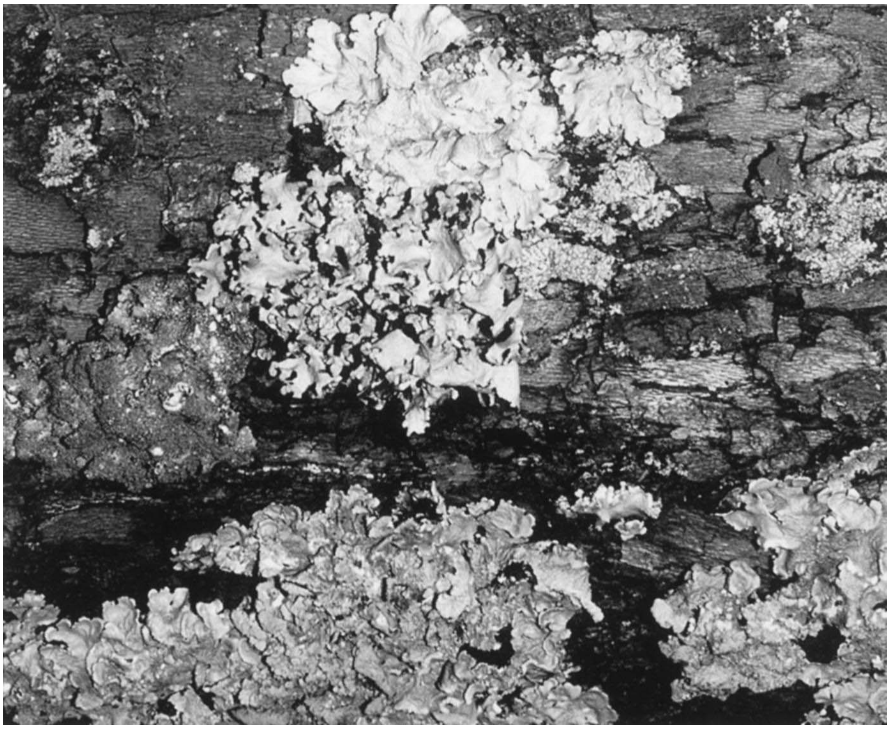

FIGURE 18 Some foliose lichens.

very sensitive to air pollution, especially sulfur and nitrogen, and so they are natural indicators of air quality. However, even under optimal conditions, lichens grow extremely slowly, usually 1–2 mm per year. The main ecological importance of lichens is their capacity to break down rocks into soil. They are an important food source for caribou and reindeer on the tundra. One of the first indications to the outside world that there had been a nuclear accident at Chernobyl, then in the Soviet Union, was the accumulation of radioactivity first in the lichens in Scandinavia, then in the milk given by the reindeer. There is significant evidence that the manna referred to in the Bible was actually a lichen, *Lecanora esculenta*, a loosely attached lichen that was blown down from the mountains into the lowlands. Some lichens have been used as natural dyes, such as tweed. In less enlightened times, a bright yellow lichen called *Letharia vulpina* was used by "pioneers" as a wolf poison.

VI. INDUSTRIAL USES FOR FUNGI

A. Mushroom Cultivation

The most widely available mushroom produced in the United States is the white button mushroom, *Agaricus bisporus* (Table VI). Commonly used on pizza and at salad bars, this mushroom is a secondary decomposer that is grown on composted cow or horse manure. Some brown forms of *A. bisporus* are currently being cultivated; brown buttons are sold as crimini and opened mushrooms are sold as portabella mushroom.

There are a number of steps in the commercial production of *Agaricus bisporus:*

- Manure is placed in large concrete "runways."
- Composting (breakdown of the substrate into simpler components) occurs with the bacteria and fungi naturally present in the manure.
- Large machines turn the compost weekly, otherwise the center of the pile gets too hot because of metabolic heat and kills the composting bacteria and fungi. This also ensures even composting. The different species present naturally shift as composting progresses.
- After a couple weeks, the odorless compost is ready and is placed into large trays, 6 ft. × 6 ft. × 2 ft.
- Mycelium of *Agaricus* is inoculated into the composted substrate and allowed to grow for a few weeks.
- When the substrate is colonized, a sterile layer of

TABLE VI

Some Commonly Cultivated Edible Mushrooms

Common name	Scientific name
White button pizza mushroom, crimini, portabella	*Agaricus bisporus* (a.k.a. *A. brunnescens*)
Shiitake, shiang-gu	*Lentinula edodes*
Oyster mushrooms	*Pleurotus* spp.
Enoki, velvet stem, winter mushroom	*Flammulina velutipes*
Maitake, hen-of-the-woods, sheepshead	*Grifola frondosa*
Cloud ear, wood ear, black mushroom	*Auricularia auricula,* available only dried
Chinese paddy straw mushroom	*Volvariella volvacea,* available only canned
Pom-pon or Lion's Mane	*Hericium erinaceus*
Reishi	*Ganoderma lucidum*
Wine cap	*Stropharia rugoso-annulata*
Morels	*Morchella* spp.

nutrient-poor casing soil is placed over the top of the substrate.

A few weeks later, the mycelia send up rhizomorphs (hyphal aggregations) through the casing layer and form mushrooms. Contrary to popular belief, most mushrooms require light to initiate fruiting body formation. Light is often used as a signal to the mycelium that it is outside the substrate and that fruiting bodies can be formed. Some fungi form fruiting bodies in response to reaching outside air, where the concentration of carbon dioxide is lower. A few fungi fruit only when they run out of available nutrients. *Agaricus bisporus* has been bred so that it requires no light for fruiting.

There are a number of other specialty mushrooms being grown throughout the world that are just becoming available in North American supermarkets. Almost all the others are primary decomposers of wood or other cellulose-containing substrates. These have gained in popularity in the past 10 to 20 years as consumers discover that these specialty mushrooms have great flavor and other interesting qualities. In Japan, China, and Korea, very little *Agaricus* is being grown; growers concentrate on mushrooms with more robust flavor and interesting texture, such as shiitake (Fig. 19). Most of these specialty mushrooms are now grown on artificial sawdust logs by the following method:

- Place sawdust or wood chips with supplementary bran and millet and the appropriate amount of water into clear polypropylene bags. Autoclave or sterilize the filled bags, then allow to cool.
- Inoculate spawn (usually grain or sawdust with mycelium of the fungus growing on it) into medium. Mix thoroughly by hand or mechanically.
- Place bags in growth room. Allow spawn to grow rapidly through the substrate. Fungus colonizes bag in 30–60 days; sawdust is easier than solid wood to colonize because of increased surface area-to-volume ratio, abundance of air spaces, and uniform distribution of nutrients.
- During this period the loose medium is joined together into a coherent synthetic log.
- Depending on the species, at this time the plastic is removed, and the synthetic log can be handled like a natural log. Fruiting usually occurs within 90–120 days after inoculation.

B. Antibiotics and Other Drugs

Penicillin is the first antibiotic that was discovered to fight the bacteria that cause human disease. It is naturally produced by *Penicillium chrysogenum* and related species as way of killing bacterial competitors in their environment. Cephalosporins are another class of antibiotics produced by *Acremonium* and related species. For a fungal infection of the fingernails and toenails, one prescribed drug is griseofulvin, produced by *Penicillium griseofulvum*. Ergotamine, produced by *Claviceps purpurea*, is used to facilitate the delivery of babies and can also be used to relieve migraine headaches. Another chemical found in *Claviceps* is a precursor to the hallucinogen LSD (lysergic acid diethylamide) that has the same effects as that illegal drug. The steroids in birth control pills are produced industrially by the fungus *Rhizopus nigricans*, as are the steroids cortisone and

FIGURE 19 Shiitake mushrooms fruiting on an artificial log.

prednisone. People who have had an organ transplant usually take the antirejection drug cyclosporin, which is produced by the fungus *Tolypocladium inflatum*. The pharmaceutical industry is constantly searching for new antibiotics and drugs to counteract microbes that become resistant to frequently used medications.

C. Wine and Beer Making

Yeasts, especially *Saccharomyces cerevisiae*, have played an important role in the development of human culture. Since brewing is an ancient art going back for millennia, yeasts have been our allies for many years. Virtually anything that contains simple sugars is fermentable by yeasts. In wine making, the grapes are pressed and yeast is added. Fermentation breaks the sugars down into carbon dioxide and ethyl alcohol. Since barley is the main carbohydrate source in beer making, there is an added step before fermentation, that of allowing the barley to germinate to produce sugar from its starch. Various other ingredients, such as hops, oatmeal, and flavorings, are added to make the wide variety of beers that are available. The aging process in alcoholic beverages also adds to their distinct flavors.

D. Bread Baking

Bread making also uses *Saccharomyces cerevisiae* to ferment sugars into carbon dioxide and ethyl alcohol. However, bakers are only interested in the carbon dioxide, which makes the bread rise. The alcohol evaporates rapidly on baking.

E. Fermentation Products for Food Use

Fungi are often used in the large-scale fermentation of liquid or solid substrates. Fermentation vats can sometimes be several hundred thousand liters in size. For example, citric acid in cola drinks is produced by large-scale vat fermentation of the deuteromycete *Aspergillus niger*. Yeasts are sometimes grown in large fermenters and used directly as food supplements. Vitamin B_2 (riboflavin) in enriched flour is produced by the ascomycete *Ashbya gossypii*. Cocoa beans are processed by a "fermentation" (sensu food scientists) of *Candida krusei* and *Geotrichum*. Authentic soy sauce is fermented in a three-step process with the fungi *Aspergillus oryzae* and *Zygosaccharomyces rouxii*, as well as the bacterium *Pediococcus halophilus*. Tempeh, a soybean product popular in Indonesia, is partially fermented with a species of *Rhizopus*. Many good cheeses, such as blue cheese, camembert, and brie, are ripened through the action of fungi to obtain their distinctive flavors. Blue cheeses such as Roquefort, Gorgonzola, and Stilton are ripened by *Penicillium roquefortii*—the blue color is caused by sporulation of the fungus! The white crust on the outside of brie and camembert is the mycelium of *Penicillium camembertii*.

F. Biopulping and Bioremediation

Several important industrial process, which have the potential to be great boons to ecosystem health, are in the pilot stage: biopulping and bioremediation. The lignin-degrading enzyme system of *Phanerochaete chrysosporium* is special for these two uses. One of the biggest energy and pollution expenditures in paper making comes from removal of the brown lignin from wood so that the white cellulose is all that is left to make paper. What if paper companies could use the enzymes of a fungus to remove the lignin? This could result in a savings in both energy and time and avoid the polluting wastes that are commonly dumped out of the mills. This process is known as biopulping. There are several products in the pilot stage, but no large-scale biopulping is yet being done.

To understand this system, you must know that wood consists primarily of cellulose, which is white, and lignin, which is brown. *Phanerochaete* species cause a white rot of wood. That is, the fungus decays the lignin and leaves the cellulose behind. There are also fungi that cause a brown rot, digesting the cellulose and leaving the lignin behind. Many kinds of fungi cause a white rot, but *P. chrysosporium* has several features that might make it very useful. First of all, unlike

FIGURE 20 The author with *Bridgeoporus nobilissimus* on a large host tree of *Abies procera*.

some white rotters, it leaves the cellulose of the wood virtually untouched. Second, it has a high optimum temperature (about 40°C), which means it can grow on wood chips in compost piles, which attain a high temperature. These characteristics point to some possible roles for this fungus in biotechnology applications.

Some of the lignin-degrading enzymes of *P. chrysosporium* will also degrade toxic wastes, such as PCBs (polychlorinated biphenyls), PCPs (phencyclidines), and TNT (trinitrotoluene). The structure of these chemicals is similar to that of lignin, and the ligninase enzymes will work on them. The fungus performs well on the laboratory bench, but as with many industrial bioprocesses, there are difficulties in scaling up the process. Nonetheless, this procedure has the potential to clean up some industrial and toxic waste sites.

VII. THREATENED OR ENDANGERED FUNGI

Like the proverbial canary in the coal mine, fungi may be the first indicators of things going wrong in ecosystems. Remember that fungi are the thread that tie the whole food web together, since they are the primary decomposers and aid most plants as mycorrhizae in the absorption of minerals and water. Thus if something goes wrong with the fungi—if they disappear—there may be dire consequences for any plants and animals that are dependent on them. Lichens have already been proven to be accurate indicators of air quality, in both their quantity and diversity.

Several European countries maintain "red lists" of threatened or endangered fungi. One fungus that may be a candidate for the endangered species list in the United States is *Bridgeoporus nobilissimus*, a polypore fungus with a very large, perennial fruiting body (Fig. 20). For a long time this fungus was in the *Guinness Book of World Records* as the largest known fruiting body of a fungus, at over 160 kg (300 pounds)! There are just six known sites in Washington and Oregon at which *B. nobilissimus* is now known to occur. It is considered by many to be a rare and probably endangered fungus. The main reason for this designation is that it is restricted to very large specimens of noble fir (*Abies procera*) and occasionally Pacific silver fir (*Abies amabilis*) with a diameter at breast height (dbh) of 1–2 meters. Trees of this diameter are not very common. This fungus is considered endangered because its habitat is endangered. Unfortunately, it is not clear whether the U.S. Endangered Species Act applies to fungi. In this zoocentric world, most people are more interested in the "charismatic megafauna" than in some lowly fungus. However, the fungi have many important roles to play in the ecosystem and should not be ignored. No ecosystem could exist for long without fungi!

Two states have thus far recognized the importance of fungi by naming a state mushroom. Minnesota was the first, naming the morel (*Morchella* species) as their state mushroom. Some ten years later, Oregon declared the Pacific golden chanterelle (*Cantharellus formosus*) as their state mushroom. Surprisingly, some forests yield more income annually from wild mushroom harvesting than from lumber harvesting. Moreover, intact forests continue to produce edible mushrooms yearly, whereas lumber harvesting can occur only once every 50 years or so. Mushrooms for human food is only one of the many contributions that fungi make to our lives, for their fundamental decomposer role supports almost all ecosystems and so helps to provide the essential ecological services that we take for granted, as well as the recreational opportunities of enjoying nature. Fungi have contributed a great deal to our standard of living by making most of the living world possible.

See Also the Following Articles

EUKARYOTES, ORIGIN OF • PARASITISM

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