



# Fungus Microbiology

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## Chapter 1

# Fungus



Clockwise from top left: *Amanita muscaria*, a basidiomycete; *Sarcoscypha coccinea*, an ascomycete; bread covered in mold; a chytrid; a *Penicillium* conidiophore.

### Scientific classification

Domain: Eukaryota  
(unranked): Opisthokonta  
Kingdom: **Fungi**  
(L., 1753) R.T. Moore, 1980

### Subkingdoms/Phyla/Subphyla

Blastocladiomycota  
Chytridiomycota  
Glomeromycota

Microsporidia  
Neocallimastigomycota

Dikarya (inc. Deuteromycota)

Ascomycota  
Pezizomycotina  
Saccharomycotina  
Taphrinomycotina  
Basidiomycota  
Agaricomycotina  
Pucciniomycotina  
Ustilaginomycotina

Subphyla Incertae sedis

Entomophthoromycotina  
Kickxellomycotina  
Mucoromycotina  
Zoopagomycotina

A **fungus** is a member of a large group of eukaryotic organisms that includes microorganisms such as yeasts and molds (British English: moulds), as well as the more familiar mushrooms. These organisms are classified as a kingdom, **Fungi**, which is separate from plants, animals, and bacteria. One major difference is that fungal cells have cell walls that contain chitin, unlike the cell walls of plants, which contain cellulose. These and other differences show that the fungi form a single group of related organisms, named the *Eumycota* (*true fungi* or *Eumycetes*), that share a common ancestor (a *monophyletic group*). This fungal group is distinct from the structurally similar myxomycetes (slime molds) and oomycetes (water molds). The discipline of biology devoted to the study of fungi is known as mycology, which is often regarded as a branch of botany, even though genetic studies have shown that fungi are more closely related to animals than to plants.

Abundant worldwide, most fungi are inconspicuous because of the small size of their structures, and their cryptic lifestyles in soil, on dead matter, and as symbionts of plants, animals, or other fungi. They may become noticeable when fruiting, either as mushrooms or molds. Fungi perform an essential role in the decomposition of organic matter and have fundamental roles in nutrient cycling and exchange. They have long been used as a direct source of food, such as mushrooms and truffles, as a leavening agent for bread, and in fermentation of various food products, such as wine, beer, and soy sauce. Since the 1940s, fungi have been used for the production of antibiotics, and, more recently, various enzymes produced by fungi are used industrially and in detergents. Fungi are also used as biological pesticides to control weeds, plant diseases and insect pests. Many species produce bioactive compounds called mycotoxins, such as alkaloids and polyketides, that are toxic to animals including humans. The fruiting structures of a few species contain

psychotropic compounds and are consumed recreationally or in traditional spiritual ceremonies. Fungi can break down manufactured materials and buildings, and become significant pathogens of humans and other animals. Losses of crops due to fungal diseases (e.g. rice blast disease) or food spoilage can have a large impact on human food supplies and local economies.

The fungus kingdom encompasses an enormous diversity of taxa with varied ecologies, life cycle strategies, and morphologies ranging from single-celled aquatic chytrids to large mushrooms. However, little is known of the true biodiversity of Kingdom Fungi, which has been estimated at around 1.5 million species, with about 5% of these having been formally classified. Ever since the pioneering 18th and 19th century taxonomical works of Carl Linnaeus, Christian Hendrik Persoon, and Elias Magnus Fries, fungi have been classified according to their morphology (e.g., characteristics such as spore color or microscopic features) or physiology. Advances in molecular genetics have opened the way for DNA analysis to be incorporated into taxonomy, which has sometimes challenged the historical groupings based on morphology and other traits. Phylogenetic studies published in the last decade have helped reshape the classification of Kingdom Fungi, which is divided into one subkingdom, seven phyla, and ten subphyla.

## ***Etymology***

The English word *fungus* is directly adopted from the Latin *fungus* (mushroom), used in the writings of Horace and Pliny. This in turn is derived from the Greek word *sphongos*/σφογγος ("sponge"), which refers to the macroscopic structures and morphology of mushrooms and molds; the root is also used in other languages, such as the German *Schwamm* ("sponge"), *Schimmel* ("mold"), and the French *champignon* and the Spanish *champiñon* (which both mean "mushroom"). The use of the word *mycology*, which is derived from the Greek *mykes*/μύκης (mushroom) and *logos*/λόγος (discourse), to denote the scientific study of fungi is thought to have originated in 1836 with English naturalist Miles Joseph Berkeley's publication *The English Flora of Sir James Edward Smith, Vol. 5*.

## ***Characteristics***

Before the introduction of molecular methods for phylogenetic analysis, taxonomists considered fungi to be members of the Plant Kingdom because of similarities in lifestyle: both fungi and plants are mainly immobile, and have similarities in general morphology and growth habitat. Like plants, fungi often grow in soil, and in the case of mushrooms form conspicuous fruiting bodies, which sometimes bear resemblance to plants such as mosses. The fungi are now considered a separate kingdom, distinct from both plants and animals, from which they appear to have diverged around one billion years ago. Some morphological, biochemical, and genetic features are shared with other organisms, while others are unique to the fungi, clearly separating them from the other kingdoms:

Shared features:

- With other eukaryotes: As other eukaryotes, fungal cells contain membrane-bound nuclei with chromosomes that contain DNA with noncoding regions called introns and coding regions called exons. In addition, fungi possess membrane-bound cytoplasmic organelles such as mitochondria, sterol-containing membranes, and ribosomes of the 80S type. They have a characteristic range of soluble carbohydrates and storage compounds, including sugar alcohols (e.g., mannitol), disaccharides, (e.g., trehalose), and polysaccharides (e.g., glycogen, which is also found in animals).
- With animals: Fungi lack chloroplasts and are heterotrophic organisms, requiring preformed organic compounds as energy sources.
- With plants: Fungi possess a cell wall and vacuoles. They reproduce by both sexual and asexual means, and like basal plant groups (such as ferns and mosses) produce spores. Similar to mosses and algae, fungi typically have haploid nuclei.
- With euglenoids and bacteria: Higher fungi, euglenoids, and some bacteria produce the amino acid L-lysine in specific biosynthesis steps, called the  $\alpha$ -aminoadipate pathway.
- The cells of most fungi grow as tubular, elongated, and thread-like (filamentous) structures and are called hyphae, which may contain multiple nuclei and extend at their tips. Each tip contains a set of aggregated vesicles—cellular structures consisting of proteins, lipids, and other organic molecules—called Spitzenkörper. Both fungi and oomycetes grow as filamentous hyphal cells. In contrast, similar-looking organisms, such as filamentous green algae, grow by repeated cell division within a chain of cells.
- In common with some plant and animal species, more than 60 fungal species display the phenomenon of bioluminescence.

#### Unique features:

- Some species grow as single-celled yeasts that reproduce by budding or binary fission. Dimorphic fungi can switch between a yeast phase and a hyphal phase in response to environmental conditions.
- The fungal cell wall is composed of glucans and chitin; while the former compounds are also found in plants and the latter in the exoskeleton of arthropods, fungi are the only organisms that combine these two structural molecules in their cell wall. In contrast to plants and the oomycetes, fungal cell walls do not contain cellulose.



*Omphalotus nidiformis*, a bioluminescent mushroom

Most fungi lack an efficient system for long-distance transport of water and nutrients, such as the xylem and phloem in many plants. To overcome these limitations, some fungi, such as *Armillaria*, form rhizomorphs, that resemble and perform functions similar to the roots of plants. Another characteristic shared with plants includes a biosynthetic pathway for producing terpenes that uses mevalonic acid and pyrophosphate as chemical building blocks. However, plants have an additional terpene pathway in their chloroplasts, a structure fungi do not possess. Fungi produce several secondary metabolites that are similar or identical in structure to those made by plants. Many of the plant and fungal enzymes that make these compounds differ from each other in sequence and other characteristics, which indicates separate origins and evolution of these enzymes in the fungi and plants.

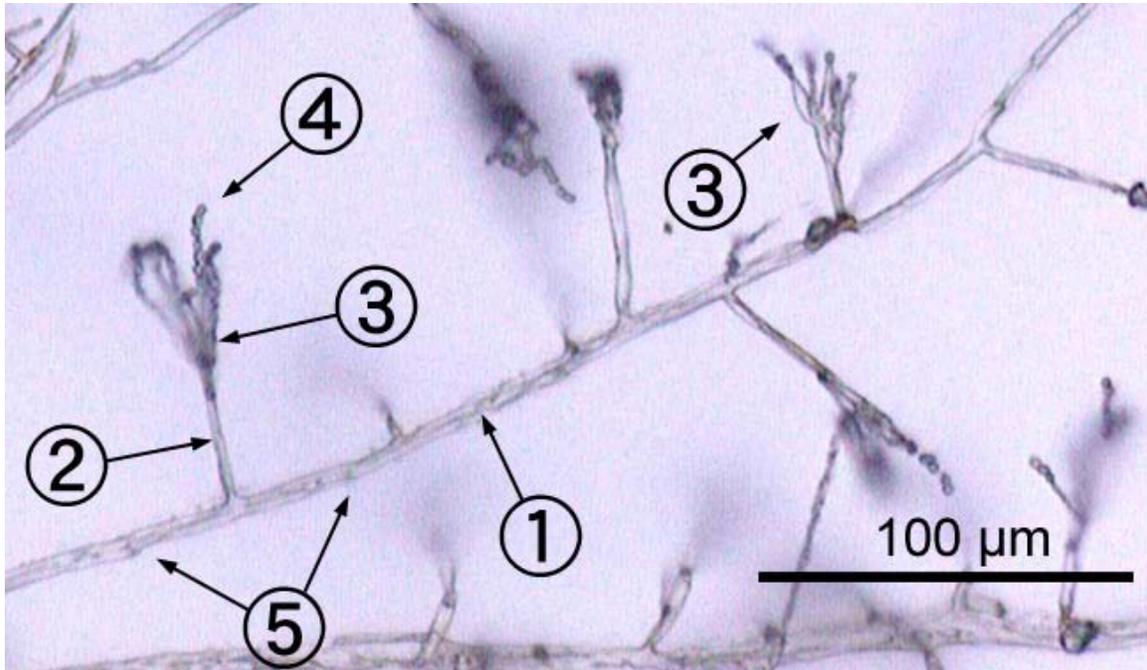
## **Diversity**

Fungi have a worldwide distribution, and grow in a wide range of habitats, including extreme environments such as deserts or areas with high salt concentrations or ionizing radiation, as well as in deep sea sediments. Some can survive the intense UV and cosmic radiation encountered during space travel. Most grow in terrestrial environments, though several species live partly or solely in aquatic habitats, such as the chytrid fungus *Batrachochytrium dendrobatidis*, a parasite that has been responsible for a worldwide decline in amphibian populations. This organism spends part of its life cycle as a motile zoospore, enabling it to propel itself through water and enter its amphibian host. Other examples of aquatic fungi include those living in hydrothermal areas of the ocean.

Around 100,000 species of fungi have been formally described by taxonomists, but the global biodiversity of the fungus kingdom is not fully understood. On the basis of observations of the ratio of the number of fungal species to the number of plant species in selected environments, the fungal kingdom has been estimated to contain about 1.5 million species. In mycology, species have historically been distinguished by a variety of methods and concepts. Classification based on morphological characteristics, such as the size and shape of spores or fruiting structures, has traditionally dominated fungal taxonomy. Species may also be distinguished by their biochemical and physiological characteristics, such as their ability to metabolize certain biochemicals, or their reaction to chemical tests. The biological species concept discriminates species based on their ability to mate. The application of molecular tools, such as DNA sequencing and phylogenetic analysis, to study diversity has greatly enhanced the resolution and added robustness to estimates of genetic diversity within various taxonomic groups.

## Morphology

### Microscopic structures



An environmental isolate of *Penicillium*

1. hypha 2. conidiophore 3. phialide 4. conidia 5. septa

Most fungi grow as hyphae, which are cylindrical, thread-like structures 2–10 μm in diameter and up to several centimeters in length. Hyphae grow at their tips (apices); new hyphae are typically formed by emergence of new tips along existing hyphae by a process called *branching*, or occasionally growing hyphal tips bifurcate (fork) giving rise to two parallel-growing hyphae. The combination of apical growth and branching/forking leads to the development of a mycelium, an interconnected network of hyphae. Hyphae can be either septate or coenocytic: septate hyphae are divided into compartments separated by cross walls (internal cell walls, called septa, that are formed at right angles to the cell wall giving the hypha its shape), with each compartment containing one or more nuclei; coenocytic hyphae are not compartmentalized. Septa have pores that allow cytoplasm, organelles, and sometimes nuclei to pass through; an example is the dolipore septum in the fungi of the phylum Basidiomycota. Coenocytic hyphae are essentially multinucleate supercells.

Many species have developed specialized hyphal structures for nutrient uptake from living hosts; examples include haustoria in plant-parasitic species of most fungal phyla, and arbuscules of several mycorrhizal fungi, which penetrate into the host cells to consume nutrients.

Although fungi are opisthokonts—a grouping of evolutionarily related organisms broadly characterized by a single posterior flagellum—all phyla except for the chytrids have lost their posterior flagella. Fungi are unusual among the eukaryotes in having a cell wall that, in addition to glucans (e.g.,  $\beta$ -1,3-glucan) and other typical components, also contains the biopolymer chitin.

### Macroscopic structures



*Armillaria solidipes*

Fungal mycelia can become visible to the naked eye, for example, on various surfaces and substrates, such as damp walls and on spoiled food, where they are commonly called molds. Mycelia grown on solid agar media in laboratory petri dishes are usually referred to as colonies. These colonies can exhibit growth shapes and colors (due to spores or pigmentation) that can be used as diagnostic features in the identification of species or groups. Some individual fungal colonies can reach extraordinary dimensions and ages as in the case of a clonal colony of *Armillaria solidipes*, which extends over an area of more than 900 ha (3.5 square miles), with an estimated age of nearly 9,000 years.

The apothecium—a specialized structure important in sexual reproduction in the ascomycetes—is a cup-shaped fruiting body that holds the hymenium, a layer of tissue containing the spore-bearing cells. The fruiting bodies of the basidiomycetes

(basidiocarps) and some ascomycetes can sometimes grow very large, and many are well-known as mushrooms.

### ***Growth and physiology***

The growth of fungi as hyphae on or in solid substrates or as single cells in aquatic environments is adapted for the efficient extraction of nutrients, because these growth forms have high surface area to volume ratios. Hyphae are specifically adapted for growth on solid surfaces, and to invade substrates and tissues. They can exert large penetrative mechanical forces; for example, the plant pathogen *Magnaporthe grisea* forms a structure called an appressorium which evolved to puncture plant tissues. The pressure generated by the appressorium, directed against the plant epidermis, can exceed 8 megapascals (1,200 psi). The filamentous fungus *Paecilomyces lilacinus* uses a similar structure to penetrate the eggs of nematodes.



Mold covering a decaying peach. The frames were taken approximately 12 hours apart over a period of six days.

The mechanical pressure exerted by the appressorium is generated from physiological processes that increase intracellular turgor by producing osmolytes such as glycerol. Morphological adaptations such as these are complemented by hydrolytic enzymes secreted into the environment to digest large organic molecules—such as polysaccharides, proteins, lipids, and other organic substrates—into smaller molecules that may then be absorbed as nutrients. The vast majority of filamentous fungi grow in a polar fashion—i.e., by extension into one direction—by elongation at the tip (apex) of the hypha. Alternative forms of fungal growth include intercalary extension (i.e., by longitudinal expansion of hyphal compartments that are below the apex) as in the case of some endophytic fungi, or growth by volume expansion during the development of mushroom stipes and other large organs. Growth of fungi as multicellular structures consisting of somatic and reproductive cells—a feature independently evolved in animals and plants—has several functions, including the development of fruiting bodies for dissemination of sexual spores and biofilms for substrate colonization and intercellular communication.

Traditionally, the fungi are considered heterotrophs, organisms that rely solely on carbon fixed by other organisms for metabolism. Fungi have evolved a high degree of metabolic versatility that allows them to use a diverse range of organic substrates for growth, including simple compounds such as nitrate, ammonia, acetate, or ethanol. For some species it has been shown that the pigment melanin may play a role in extracting energy from ionizing radiation, such as gamma radiation; however, this form of "radiotrophic" growth has only been described for a few species, the effects on growth rates are small, and the underlying biophysical and biochemical processes are not known. The authors speculate that this process might bear similarity to CO<sub>2</sub> fixation via visible light, but instead utilizing ionizing radiation as a source of energy.

## ***Reproduction***



*Polyporus squamosus*

Fungal reproduction is complex, reflecting the differences in lifestyles and genetic makeup within this kingdom of organisms. It is estimated that a third of all fungi reproduce by different modes of propagation; for example, reproduction may occur in two well-differentiated stages within the life cycle of a species, the teleomorph and the anamorph. Environmental conditions trigger genetically determined developmental states that lead to the creation of specialized structures for sexual or asexual reproduction. These structures aid reproduction by efficiently dispersing spores or spore-containing propagules.

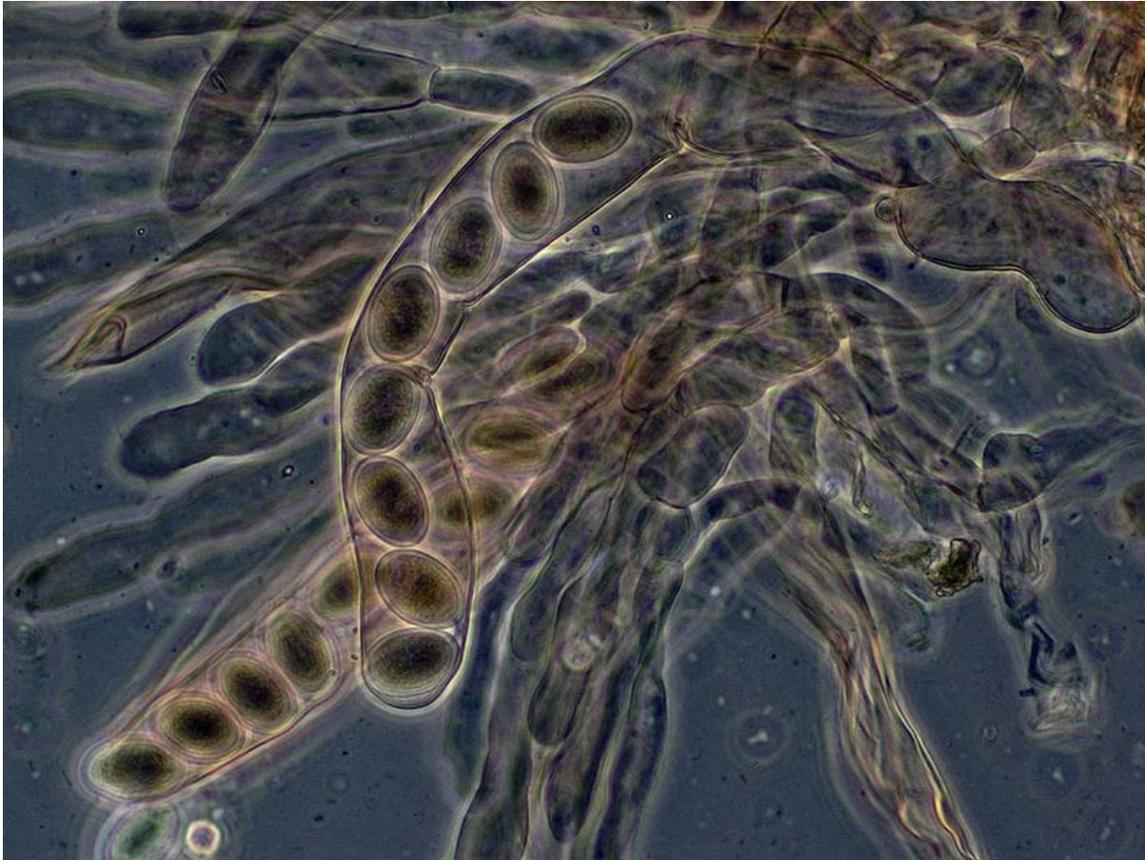
## **Asexual reproduction**

Asexual reproduction via vegetative spores (conidia) or through mycelial fragmentation is common; it maintains clonal populations adapted to a specific niche, and allows more rapid dispersal than sexual reproduction. The "Fungi imperfecti" (fungi lacking the perfect or sexual stage) or Deuteromycota comprise all the species which lack an observable sexual cycle.

## **Sexual reproduction**

Sexual reproduction with meiosis exists in all fungal phyla (with the exception of the Glomeromycota). It differs in many aspects from sexual reproduction in animals or plants. Differences also exist between fungal groups and can be used to discriminate species by morphological differences in sexual structures and reproductive strategies. Mating experiments between fungal isolates may identify species on the basis of biological species concepts. The major fungal groupings have initially been delineated based on the morphology of their sexual structures and spores; for example, the spore-containing structures, asci and basidia, can be used in the identification of ascomycetes and basidiomycetes, respectively. Some species may allow mating only between individuals of opposite mating type, while others can mate and sexually reproduce with any other individual or itself. Species of the former mating system are called heterothallic, and of the latter homothallic.

Most fungi have both an haploid and diploid stage in their life cycles. In sexually reproducing fungi, compatible individuals may combine by fusing their hyphae together into an interconnected network; this process, anastomosis, is required for the initiation of the sexual cycle. Ascomycetes and basidiomycetes go through a dikaryotic stage, in which the nuclei inherited from the two parents do not combine immediately after cell fusion, but remain separate in the hyphal cells.



The 8-spored asci of *Morchella elata*, viewed with phase contrast microscopy

In ascomycetes, dikaryotic hyphae of the hymenium (the spore-bearing tissue layer) form a characteristic *hook* at the hyphal septum. During cell division, formation of the hook ensures proper distribution of the newly divided nuclei into the apical and basal hyphal compartments. An ascus (plural *asci*) is then formed, in which karyogamy (nuclear fusion) occurs. Asci are embedded in an ascocarp, or fruiting body. Karyogamy in the asci is followed immediately by meiosis and the production of ascospores. After dispersal, the ascospores may germinate and form a new haploid mycelium.

Sexual reproduction in basidiomycetes is similar to that of the ascomycetes. Compatible haploid hyphae fuse to produce a dikaryotic mycelium. However, the dikaryotic phase is more extensive in the basidiomycetes, often also present in the vegetatively growing mycelium. A specialized anatomical structure, called a clamp connection, is formed at each hyphal septum. As with the structurally similar hook in the ascomycetes, the clamp connection in the basidiomycetes is required for controlled transfer of nuclei during cell division, to maintain the dikaryotic stage with two genetically different nuclei in each hyphal compartment. A basidiocarp is formed in which club-like structures known as basidia generate haploid basidiospores after karyogamy and meiosis. The most commonly known basidiocarps are mushrooms, but they may also take other forms.

In glomeromycetes (formerly zygomycetes), haploid hyphae of two individuals fuse, forming a gametangium, a specialized cell structure that becomes a fertile gamete-producing cell. The gametangium develops into a zygospore, a thick-walled spore formed by the union of gametes. When the zygospore germinates, it undergoes meiosis, generating new haploid hyphae, which may then form asexual sporangiospores. These sporangiospores allow the fungus to rapidly disperse and germinate into new genetically identical haploid fungal mycelia.

### Spore dispersal

Both asexual and sexual spores or sporangiospores are often actively dispersed by forcible ejection from their reproductive structures. This ejection ensures exit of the spores from the reproductive structures as well as travelling through the air over long distances.



The bird's nest fungus *Cyathus stercoreus*

Specialized mechanical and physiological mechanisms, as well as spore surface structures (such as hydrophobins), enable efficient spore ejection. For example, the structure of the spore-bearing cells in some ascomycete species is such that the buildup of substances affecting cell volume and fluid balance enables the explosive discharge of spores into the air. The forcible discharge of single spores termed *ballistospores* involves

formation of a small drop of water (Buller's drop), which upon contact with the spore leads to its projectile release with an initial acceleration of more than 10,000 g; the net result is that the spore is ejected 0.01–0.02 cm, sufficient distance for it to fall through the gills or pores into the air below. Other fungi, like the puffballs, rely on alternative mechanisms for spore release, such as external mechanical forces. The bird's nest fungi use the force of falling water drops to liberate the spores from cup-shaped fruiting bodies. Another strategy is seen in the stinkhorns, a group of fungi with lively colors and putrid odor that attract insects to disperse their spores.

### **Other sexual processes**

Besides regular sexual reproduction with meiosis, certain fungi, such as those in the genera *Penicillium* and *Aspergillus*, may exchange genetic material via parasexual processes, initiated by anastomosis between hyphae and plasmogamy of fungal cells. The frequency and relative importance of parasexual events is unclear and may be lower than other sexual processes. It is known to play a role in intraspecific hybridization and is likely required for hybridization between species, which has been associated with major events in fungal evolution.

### **Evolution**

In contrast to plants and animals, the early fossil record of the fungi is meager. Factors that likely contribute to the under-representation of fungal species among fossils include the nature of fungal fruiting bodies, which are soft, fleshy, and easily degradable tissues and the microscopic dimensions of most fungal structures, which therefore are not readily evident. Fungal fossils are difficult to distinguish from those of other microbes, and are most easily identified when they resemble extant fungi. Often recovered from a permineralized plant or animal host, these samples are typically studied by making thin-section preparations that can be examined with light microscopy or transmission electron microscopy. Compression fossils are studied by dissolving the surrounding matrix with acid and then using light or scanning electron microscopy to examine surface details.

The earliest fossils possessing features typical of fungi date to the Proterozoic eon, some 1,430 million years ago (Ma); these multicellular benthic organisms had filamentous structures with septa, and were capable of anastomosis. More recent studies (2009) estimate the arrival of fungal organisms at about 760–1060 Ma on the basis of comparisons of the rate of evolution in closely related groups. For much of the Paleozoic Era (542–251 Ma), the fungi appear to have been aquatic and consisted of organisms similar to the extant Chytrids in having flagellum-bearing spores. The evolutionary adaptation from an aquatic to a terrestrial lifestyle necessitated a diversification of ecological strategies for obtaining nutrients, including parasitism, saprobism, and the development of mutualistic relationships such as mycorrhiza and lichenization. Recent (2009) studies suggest that the ancestral ecological state of the Ascomycota was saprobism, and that independent lichenization events have occurred multiple times.

The fungi probably colonized the land during the Cambrian (542–488.3 Ma), long before land plants. Fossilized hyphae and spores recovered from the Ordovician of Wisconsin (460 Ma) resemble modern-day Glomerales, and existed at a time when the land flora likely consisted of only non-vascular bryophyte-like plants. Prototaxites, which was probably a fungus or lichen, would have been the tallest organism of the late Silurian. Fungal fossils do not become common and uncontroversial until the early Devonian (416–359.2 Ma), when they are abundant in the Rhynie chert, mostly as Zygomycota and Chytridiomycota. At about this same time, approximately 400 Ma, the Ascomycota and Basidiomycota diverged, and all modern classes of fungi were present by the Late Carboniferous (Pennsylvanian, 318.1–299 Ma).

Lichen-like fossils have been found in the Doushantuo Formation in southern China dating back to 635–551 Ma. Lichens were a component of the early terrestrial ecosystems, and the estimated age of the oldest terrestrial lichen fossil is 400 Ma; this date corresponds to the age of the oldest known sporocarp fossil, a *Paleopyrenomycites* species found in the Rhynie Chert. The oldest fossil with microscopic features resembling modern-day basidiomycetes is *Palaeoancistrus*, found permineralized with a fern from the Pennsylvanian. Rare in the fossil record are the homobasidiomycetes (a taxon roughly equivalent to the mushroom-producing species of the agaricomycetes). Two amber-preserved specimens provide evidence that the earliest known mushroom-forming fungi (the extinct species *Archaeomarasmius legletti*) appeared during the mid-Cretaceous, 90 Ma.

Some time after the Permian-Triassic extinction event (251.4 Ma), a fungal spike (originally thought to be an extraordinary abundance of fungal spores in sediments) formed, suggesting that fungi were the dominant life form at this time, representing nearly 100% of the available fossil record for this period. However, the relative proportion of fungal spores relative to spores formed by algal species is difficult to assess, the spike did not appear worldwide, and in many places it did not fall on the Permian-Triassic boundary.

## ***Taxonomy***

Although commonly included in botany curricula and textbooks, fungi are more closely related to animals than to plants and are placed with the animals in the monophyletic group of opisthokonts. Analyses using molecular phylogenetics support a monophyletic origin of the Fungi. The taxonomy of the Fungi is in a state of constant flux, especially due to recent research based on DNA comparisons. These current phylogenetic analyses often overturn classifications based on older and sometimes less discriminative methods based on morphological features and biological species concepts obtained from experimental matings.

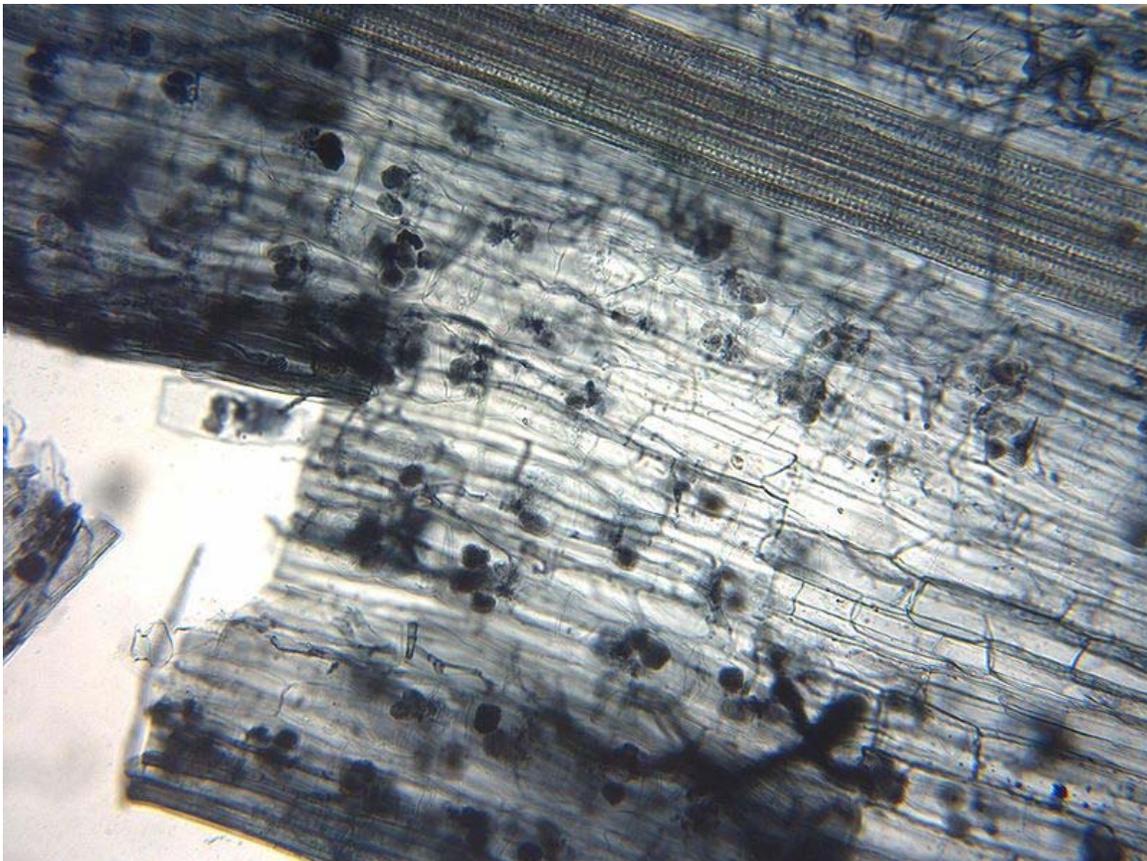
There is no unique generally accepted system at the higher taxonomic levels and there are frequent name changes at every level, from species upwards. Efforts among researchers are now underway to establish and encourage usage of a unified and more consistent nomenclature. Fungal species can also have multiple scientific names depending on their

life cycle and mode (sexual or asexual) of reproduction. Web sites such as Index Fungorum and ITIS list current names of fungal species (with cross-references to older synonyms).

The 2007 classification of Kingdom Fungi is the result of a large-scale collaborative research effort involving dozens of mycologists and other scientists working on fungal taxonomy. It recognizes seven phyla, two of which—the Ascomycota and the Basidiomycota—are contained within a branch representing subkingdom Dikarya. The below cladogram depicts the major fungal taxa and their relationship to opisthokont and unikont organisms. The lengths of the branches in this tree are not proportional to evolutionary distances.

### **Taxonomic groups**

The major phyla (sometimes called divisions) of fungi have been classified mainly on the basis of characteristics of their sexual reproductive structures. Currently, seven phyla are proposed: Microsporidia, Chytridiomycota, Blastocladiomycota, Neocallimastigomycota, Glomeromycota, Ascomycota, and Basidiomycota.



*Arbuscular mycorrhiza* seen under microscope. Flax root cortical cells containing paired arbuscules.

Phylogenetic analysis has demonstrated that the Microsporidia, unicellular parasites of animals and protists, are fairly recent and highly derived endobiotic fungi (living within the tissue of another species). One 2006 study concludes that the Microsporidia are a sister group to the true fungi, that is, they are each other's closest evolutionary relative. Hibbett and colleagues suggest that this analysis does not clash with their classification of the Fungi, and although the Microsporidia are elevated to phylum status, it is acknowledged that further analysis is required to clarify evolutionary relationships within this group.

The Chytridiomycota are commonly known as chytrids. These fungi are distributed worldwide. Chytrids produce zoospores that are capable of active movement through aqueous phases with a single flagellum, leading early taxonomists to classify them as protists. Molecular phylogenies, inferred from rRNA sequences in ribosomes, suggest that the Chytrids are a basal group divergent from the other fungal phyla, consisting of four major clades with suggestive evidence for paraphyly or possibly polyphyly.

The Blastocladiomycota were previously considered a taxonomic clade within the Chytridiomycota. Recent molecular data and ultrastructural characteristics, however, place the Blastocladiomycota as a sister clade to the Zygomycota, Glomeromycota, and Dikarya (Ascomycota and Basidiomycota). The blastocladiomycetes are saprotrophs, feeding on decomposing organic matter, and they are parasites of all eukaryotic groups. Unlike their close relatives, the chytrids, which mostly exhibit zygotic meiosis, the blastocladiomycetes undergo sporic meiosis.

The Neocallimastigomycota were earlier placed in the phylum Chytridomycota. Members of this small phylum are anaerobic organisms, living in the digestive system of larger herbivorous mammals and possibly in other terrestrial and aquatic environments. They lack mitochondria but contain hydrogenosomes of mitochondrial origin. As the related chytrids, neocallimastigomycetes form zoospores that are posteriorly uniflagellate or polyflagellate.

Members of the Glomeromycota form arbuscular mycorrhizae, a form of symbiosis where fungal hyphae invade plant root cells and both species benefit from the resulting increased supply of nutrients. All known Glomeromycota species reproduce asexually. The symbiotic association between the Glomeromycota and plants is ancient, with evidence dating to 400 million years ago. Formerly part of the Zygomycota (commonly known as 'sugar' and 'pin' molds), the Glomeromycota were elevated to phylum status in 2001 and now replace the older phylum Zygomycota. Fungi that were placed in the Zygomycota are now being reassigned to the Glomeromycota, or the subphyla incertae sedis Mucoromycotina, Kickxellomycotina, the Zoopagomycotina and the Entomophthoromycotina. Some well-known examples of fungi formerly in the Zygomycota include black bread mold (*Rhizopus stolonifer*), and *Pilobolus* species, capable of ejecting spores several meters through the air. Medically relevant genera include *Mucor*, *Rhizomucor*, and *Rhizopus*.

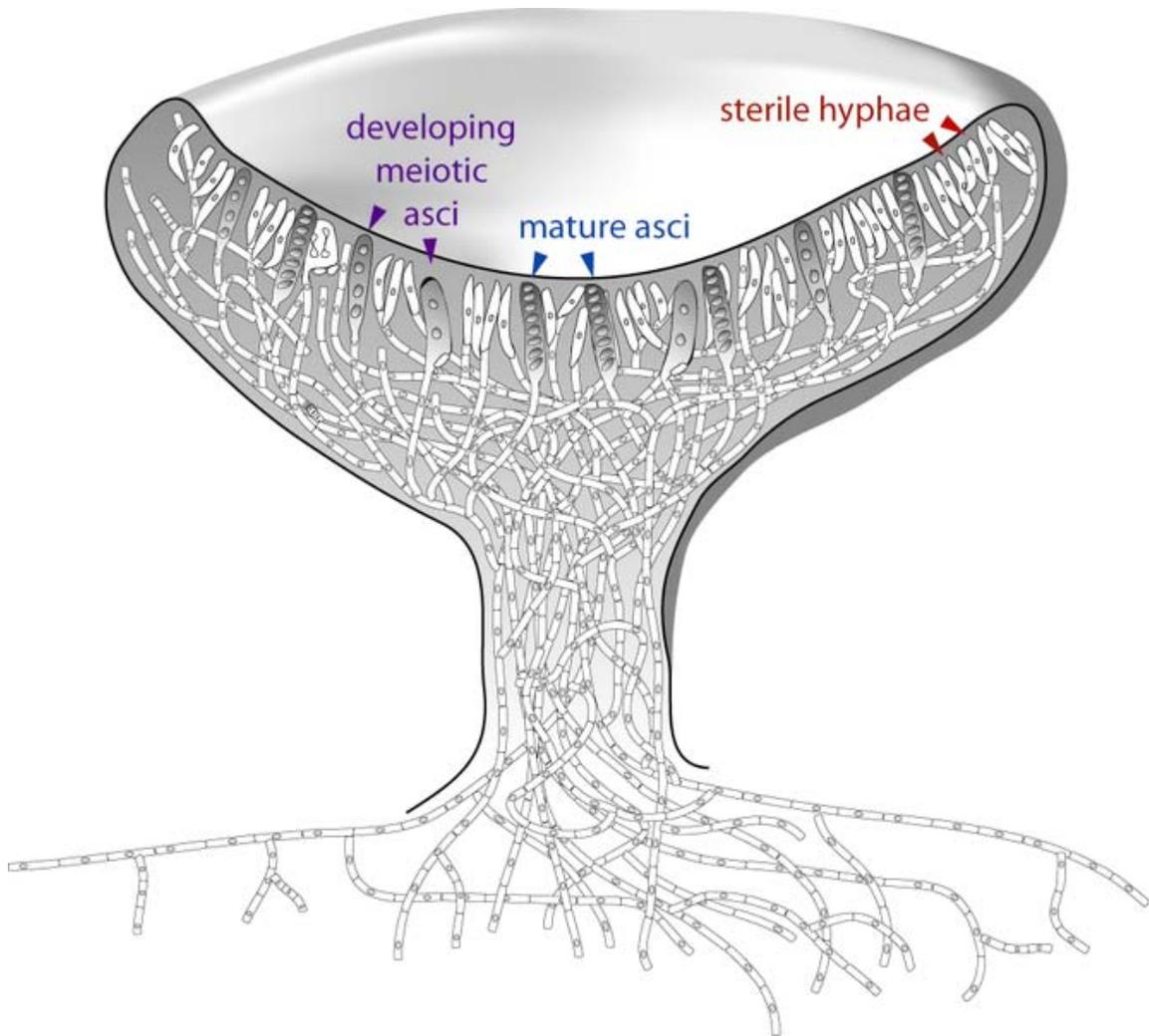


Diagram of an apothecium (the typical cup-like reproductive structure of Ascomycetes) showing sterile tissues as well as developing and mature asci.

The Ascomycota, commonly known as sac fungi or ascomycetes, constitute the largest taxonomic group within the Eumycota. These fungi form meiotic spores called ascospores, which are enclosed in a special sac-like structure called an ascus. This phylum includes morels, a few mushrooms and truffles, single-celled yeasts (e.g., of the genera *Saccharomyces*, *Kluyveromyces*, *Pichia*, and *Candida*), and many filamentous fungi living as saprotrophs, parasites, and mutualistic symbionts. Prominent and important genera of filamentous ascomycetes include *Aspergillus*, *Penicillium*, *Fusarium*, and *Claviceps*. Many ascomycete species have only been observed undergoing asexual reproduction (called anamorphic species), but analysis of molecular data has often been able to identify their closest teleomorphs in the Ascomycota. Because the products of meiosis are retained within the sac-like ascus, ascomycetes have been used for elucidating principles of genetics and heredity (e.g. *Neurospora crassa*).

Members of the Basidiomycota, commonly known as the club fungi or basidiomycetes, produce meiospores called basidiospores on club-like stalks called basidia. Most common mushrooms belong to this group, as well as rust and smut fungi, which are major pathogens of grains. Other important basidiomycetes include the maize pathogen *Ustilago maydis*, human commensal species of the genus *Malassezia*, and the opportunistic human pathogen, *Cryptococcus neoformans*.

### **Fungus-like organisms**

Because of similarities in morphology and lifestyle, the slime molds (myxomycetes) and water molds (oomycetes) were formerly classified in the kingdom Fungi. Unlike true fungi the cell walls of these organisms contain cellulose and lack chitin. Myxomycetes are unikonts like fungi, but are grouped in the Amoebozoa. Oomycetes are diploid bikonts, grouped in the Chromalveolate kingdom. Neither water molds nor slime molds are closely related to the true fungi, and, therefore, taxonomists no longer group them in the kingdom Fungi. Nonetheless, studies of the oomycetes and myxomycetes are still often included in mycology textbooks and primary research literature.

The nucleariids, currently grouped in the Choanozoa, may be a sister group to the eumycete clade, and as such could be included in an expanded fungal kingdom.

### **Ecology**

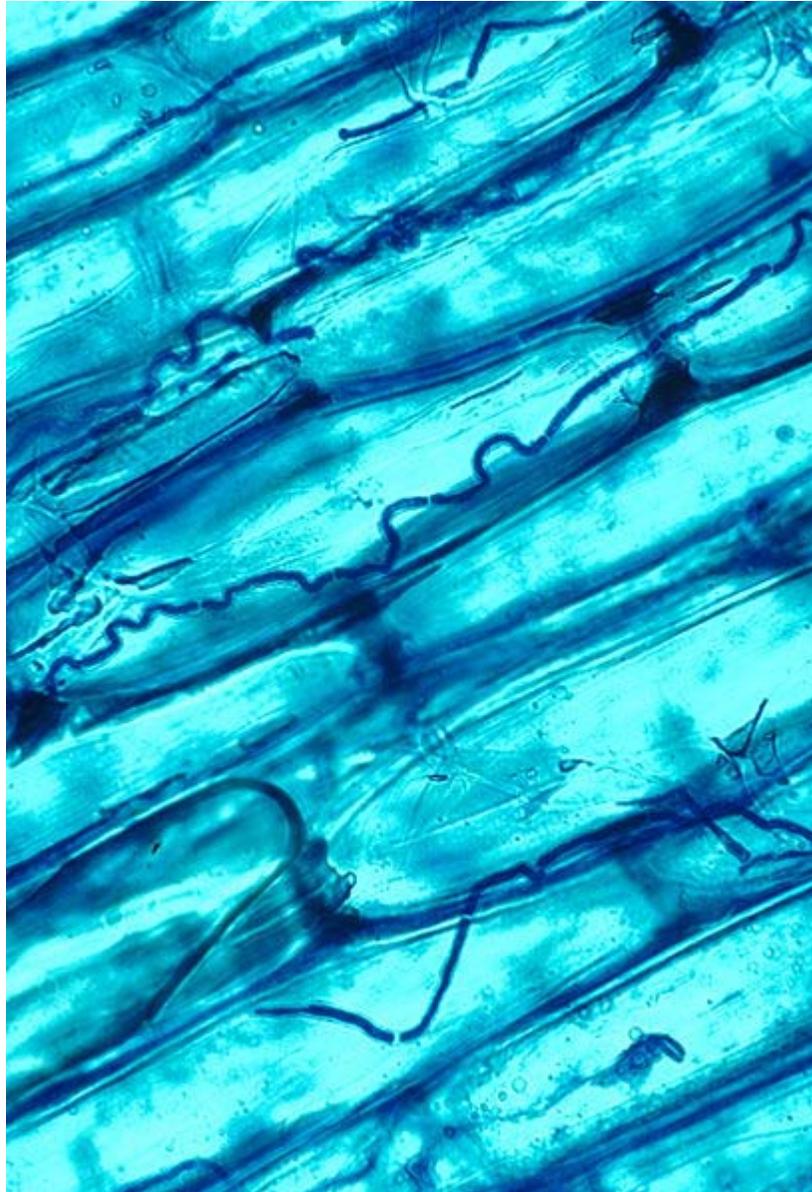
Although often inconspicuous, fungi occur in every environment on Earth and play very important roles in most ecosystems. Along with bacteria, fungi are the major decomposers in most terrestrial (and some aquatic) ecosystems, and therefore play a critical role in biogeochemical cycles and in many food webs. As decomposers, they play an essential role in nutrient cycling, especially as saprotrophs and symbionts, degrading organic matter to inorganic molecules, which can then re-enter anabolic metabolic pathways in plants or other organisms.

### **Symbiosis**

Many fungi have important symbiotic relationships with organisms from most if not all Kingdoms. These interactions can be mutualistic or antagonistic in nature, or in the case of commensal fungi are of no apparent benefit or detriment to the host.

### **With plants**

Mycorrhizal symbiosis between plants and fungi is one of the most well-known plant–fungus associations and is of significant importance for plant growth and persistence in many ecosystems; over 90% of all plant species engage in mycorrhizal relationships with fungi and are dependent upon this relationship for survival.



The dark filaments are hyphae of the endophytic fungus *Neotyphodium coenophialum* in the intercellular spaces of tall fescue leaf sheath tissue

The mycorrhizal symbiosis is ancient, dating to at least 400 million years ago. It often increases the plant's uptake of inorganic compounds, such as nitrate and phosphate from soils having low concentrations of these key plant nutrients. The fungal partners may also mediate plant-to-plant transfer of carbohydrates and other nutrients. Such mycorrhizal communities are called "common mycorrhizal networks". A special case of mycorrhiza is myco-heterotrophy, whereby the plant parasitizes the fungus, obtaining all of its nutrients from its fungal symbiont. Some fungal species inhabit the tissues inside roots, stems, and leaves, in which case they are called endophytes. Similar to mycorrhiza, endophytic colonization by fungi may benefit both symbionts; for example, endophytes of grasses

impart to their host increased resistance to herbivores and other environmental stresses and receive food and shelter from the plant in return.

### **With algae and cyanobacteria**



The lichen *Lobaria pulmonaria*, a symbiosis of fungal, algal, and cyanobacterial species

Lichens are formed by a symbiotic relationship between algae or cyanobacteria (referred to in lichen terminology as "photobionts") and fungi (mostly various species of ascomycetes and a few basidiomycetes), in which individual photobiont cells are embedded in a tissue formed by the fungus. Lichens occur in every ecosystem on all continents, play a key role in soil formation and the initiation of biological succession, and are the dominating life forms in extreme environments, including polar, alpine, and semiarid desert regions. They are able to grow on inhospitable surfaces, including bare soil, rocks, tree bark, wood, shells, barnacles and leaves. As in mycorrhizas, the photobiont provides sugars and other carbohydrates via photosynthesis, while the fungus provides minerals and water. The functions of both symbiotic organisms are so closely intertwined that they function almost as a single organism; in most cases the resulting organism differs greatly from the individual components. Lichenization is a common mode of nutrition; around 20% of fungi—between 17,500 and 20,000 described species—are lichenized. Characteristics common to most lichens include obtaining organic carbon by photosynthesis, slow growth, small size, long life, long-lasting (seasonal) vegetative reproductive structures, mineral nutrition obtained largely from

airborne sources, and greater tolerance of desiccation than most other photosynthetic organisms in the same habitat.

### **With insects**

Many insects also engage in mutualistic relationships with fungi. Several groups of ants cultivate fungi in the order Agaricales as their primary food source, while ambrosia beetles cultivate various species of fungi in the bark of trees that they infest. Similarly, females of several wood wasp species (genus *Sirex*) inject their eggs together with spores of the wood-rotting fungus *Amylostereum areolatum* into the sapwood of pine trees; the growth of the fungus provides ideal nutritional conditions for the development of the wasp larvae. Termites on the African savannah are also known to cultivate fungi, and yeasts of the genera *Candida* and *Lachancea* inhabit the gut of a wide range of insects, including neuropterans, beetles, and cockroaches; it is not known whether these fungi benefit their hosts.

### **As pathogens and parasites**

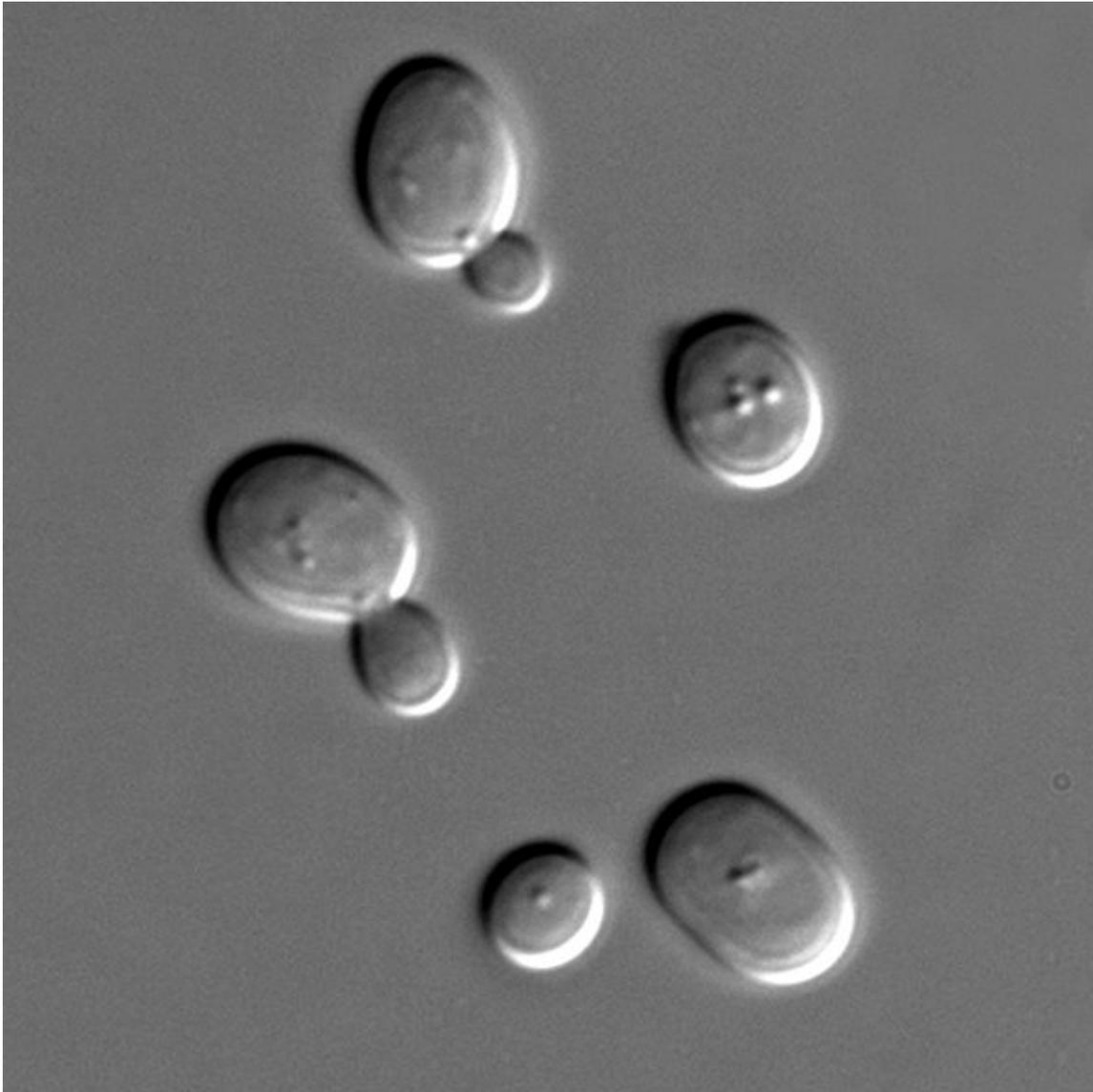


The plant pathogen *Aecidium magellanicum* causes calafate rust, seen here on a *Berberis* shrub in Chile.

Many fungi are parasites on plants, animals (including humans), and other fungi. Serious pathogens of many cultivated plants causing extensive damage and losses to agriculture and forestry include the rice blast fungus *Magnaporthe oryzae*, tree pathogens such as *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* causing Dutch elm disease, and *Cryphonectria parasitica* responsible for chestnut blight, and plant pathogens in the genera *Fusarium*, *Ustilago*, *Alternaria*, and *Cochliobolus*. Some carnivorous fungi, like *Paecilomyces lilacinus*, are predators of nematodes, which they capture using an array of specialized structures such as constricting rings or adhesive nets.

Some fungi can cause serious diseases in humans, several of which may be fatal if untreated. These include aspergilloses, candidoses, coccidioidomycosis, cryptococcosis, histoplasmosis, mycetomas, and paracoccidioidomycosis. Furthermore, persons with immuno-deficiencies are particularly susceptible to disease by genera such as *Aspergillus*, *Candida*, *Cryptococcus*, *Histoplasma*, and *Pneumocystis*. Other fungi can attack eyes, nails, hair, and especially skin, the so-called dermatophytic and keratinophilic fungi, and cause local infections such as ringworm and athlete's foot. Fungal spores are also a cause of allergies, and fungi from different taxonomic groups can evoke allergic reactions.

## **Human use**



*Saccharomyces cerevisiae* cells shown with DIC microscopy.

The human use of fungi for food preparation or preservation and other purposes is extensive and has a long history. Mushroom farming and mushroom gathering are large industries in many countries. The study of the historical uses and sociological impact of fungi is known as ethnomycology. Because of the capacity of this group to produce an enormous range of natural products with antimicrobial or other biological activities, many species have long been used or are being developed for industrial production of antibiotics, vitamins, and anti-cancer and cholesterol-lowering drugs. More recently, methods have been developed for genetic engineering of fungi, enabling metabolic engineering of fungal species. For example, genetic modification of yeast species—which are easy to grow at fast rates in large fermentation vessels—has opened up ways of

pharmaceutical production that are potentially more efficient than production by the original source organisms.

## Drugs

Many species produce metabolites that are major sources of pharmacologically active drugs. Particularly important are the antibiotics, including the penicillins, a structurally related group of  $\beta$ -lactam antibiotics that are synthesized from small peptides. Although naturally occurring penicillins such as penicillin G (produced by *Penicillium chrysogenum*) have a relatively narrow spectrum of biological activity, a wide range of other penicillins can be produced by chemical modification of the natural penicillins. Modern penicillins are semisynthetic compounds, obtained initially from fermentation cultures, but then structurally altered for specific desirable properties. Other antibiotics produced by fungi include: ciclosporin, commonly used as an immunosuppressant during transplant surgery; and fusidic acid, used to help control infection from methicillin-resistant *Staphylococcus aureus* bacteria. Widespread use of these antibiotics for the treatment of bacterial diseases, such as tuberculosis, syphilis, leprosy, and many others began in the early 20th century and continues to play a major part in anti-bacterial chemotherapy. In nature, antibiotics of fungal or bacterial origin appear to play a dual role: at high concentrations they act as chemical defense against competition with other microorganisms in species-rich environments, such as the rhizosphere, and at low concentrations as quorum-sensing molecules for intra- or interspecies signaling.

Other drugs produced by fungi include griseofulvin isolated from *Penicillium griseofulvum*, used to treat fungal infections, and statins (HMG-CoA reductase inhibitors), used to inhibit cholesterol synthesis. Examples of statins found in fungi include mevastatin from *Penicillium citrinum* and lovastatin from *Aspergillus terreus* and the oyster mushroom.

## Cultured foods

Baker's yeast or *Saccharomyces cerevisiae*, a single-celled fungus, is used to make bread and other wheat-based products, such as pizza dough and dumplings. Yeast species of the genus *Saccharomyces* are also used to produce alcoholic beverages through fermentation. Shoyu koji mold (*Aspergillus oryzae*) is an essential ingredient in brewing Shoyu (soy sauce) and sake, and the preparation of miso, while *Rhizopus* species are used for making tempeh. Several of these fungi are domesticated species that were bred or selected according to their capacity to ferment food without producing harmful mycotoxins, which are produced by very closely related *Aspergilli*. Quorn, a meat substitute, is made from *Fusarium venenatum*.

## Medicinal use



The medicinal fungi *Ganoderma lucidum* (left) and *Cordyceps sinensis* (right).

Certain mushrooms enjoy usage as therapeutics in folk medicines, such as Traditional Chinese medicine. Notable medicinal mushrooms with a well-documented history of use include *Agaricus subrufescens*,<sup>1</sup> *Ganoderma lucidum*, and *Cordyceps sinensis*. Research has identified compounds produced by these and other fungi that have inhibitory biological effects against viruses and cancer cells. Specific metabolites, such as polysaccharide-K, ergotamine, and  $\beta$ -lactam antibiotics, are routinely used in clinical medicine. The shiitake mushroom is a source of lentinan, a clinical drug approved for use in cancer treatments in several countries, including Japan. In Europe and Japan, polysaccharide-K (brand name Krestin), a chemical derived from *Trametes versicolor*, is an approved adjuvant for cancer therapy.

## Edible and poisonous species



*Amanita phalloides* accounts for the majority of fatal mushroom poisonings worldwide.

Edible mushrooms are well-known examples of fungi. Many are commercially raised, but others must be harvested from the wild. *Agaricus bisporus*, sold as button mushrooms when small or Portobello mushrooms when larger, is a commonly eaten species, used in salads, soups, and many other dishes. Many Asian fungi are commercially grown and have increased in popularity in the West. They are often available fresh in grocery stores and markets, including straw mushrooms (*Volvariella volvacea*), oyster mushrooms (*Pleurotus ostreatus*), shiitakes (*Lentinula edodes*), and enokitake (*Flammulina* spp.).

There are many more mushroom species that are harvested from the wild for personal consumption or commercial sale. Milk mushrooms, morels, chanterelles, truffles, black trumpets, and *porcini* mushrooms (*Boletus edulis*) (also known as king boletes) demand a high price on the market. They are often used in gourmet dishes.

Certain types of cheeses require inoculation of milk curds with fungal species that impart a unique flavor and texture to the cheese. Examples include the blue color in cheeses such as Stilton or Roquefort, which are made by inoculation with *Penicillium roqueforti*. Molds used in cheese production are non-toxic and are thus safe for human consumption; however, mycotoxins (e.g., aflatoxins, roquefortine C, patulin, or others) may accumulate because of growth of other fungi during cheese ripening or storage.



Stilton cheese veined with *Penicillium roqueforti*

Many mushroom species are poisonous to humans, with toxicities ranging from slight digestive problems or allergic reactions as well as hallucinations to severe organ failures and death. Genera with mushrooms containing deadly toxins include *Conocybe*, *Galerina*, *Lepiota*, and most infamously, *Amanita*. The latter genus includes the destroying angel (*A. virosa*) and the death cap (*A. phalloides*), the most common cause of deadly mushroom poisoning. The false morel (*Gyromitra esculenta*) is occasionally considered a delicacy when cooked, yet can be highly toxic when eaten raw. *Tricholoma*

*equestre* was considered edible until being implicated in serious poisonings causing rhabdomyolysis. Fly agaric mushrooms (*Amanita muscaria*) also cause occasional non-fatal poisonings, mostly as a result of ingestion for use as a recreational drug for its hallucinogenic properties. Historically, fly agaric was used by different peoples in Europe and Asia and its present usage for religious or shamanic purposes is reported from some ethnic groups such as the Koryak people of north-eastern Siberia.

As it is difficult to accurately identify a safe mushroom without proper training and knowledge, it is often advised to assume that a wild mushroom is poisonous and not to consume it.

## Pest control



Grasshoppers killed by *Beauveria bassiana*

In agriculture, fungi may be useful if they actively compete for nutrients and space with pathogenic microorganisms such as bacteria or other fungi via the competitive exclusion principle, or if they are parasites of these pathogens. For example, certain species may be used to eliminate or suppress the growth of harmful plant pathogens, such as insects, mites, weeds, nematodes and other fungi that cause diseases of important crop plants. This has generated strong interest in practical applications that use these fungi in the biological control of these agricultural pests. Entomopathogenic fungi can be used as biopesticides, as they actively kill insects. Examples that have been used as biological insecticides are *Beauveria bassiana*, *Metarhizium* spp, *Hirsutella* spp, *Paecilomyces* (*Isaria*) spp, and *Lecanicillium lecanii*. Endophytic fungi of grasses of the genus *Neotyphodium*, such as *N. coenophialum*, produce alkaloids that are toxic to a range of invertebrate and vertebrate herbivores. These alkaloids protect grass plants from herbivory, but several endophyte alkaloids can poison grazing animals, such as cattle and sheep. Infecting cultivars of pasture or forage grasses with *Neotyphodium* endophytes is one approach being used in grass breeding programs; the fungal strains are selected for producing only alkaloids that increase resistance to herbivores such as insects, while being non-toxic to livestock.

## **Bioremediation**

Certain fungi, in particular "white rot" fungi, can degrade insecticides, herbicides, pentachlorophenol, creosote, coal tars, and heavy fuels and turn them into carbon dioxide, water, and basic elements. Fungi have been shown to biomineralize uranium oxides, suggesting they may have application in the bioremediation of radioactively polluted sites.

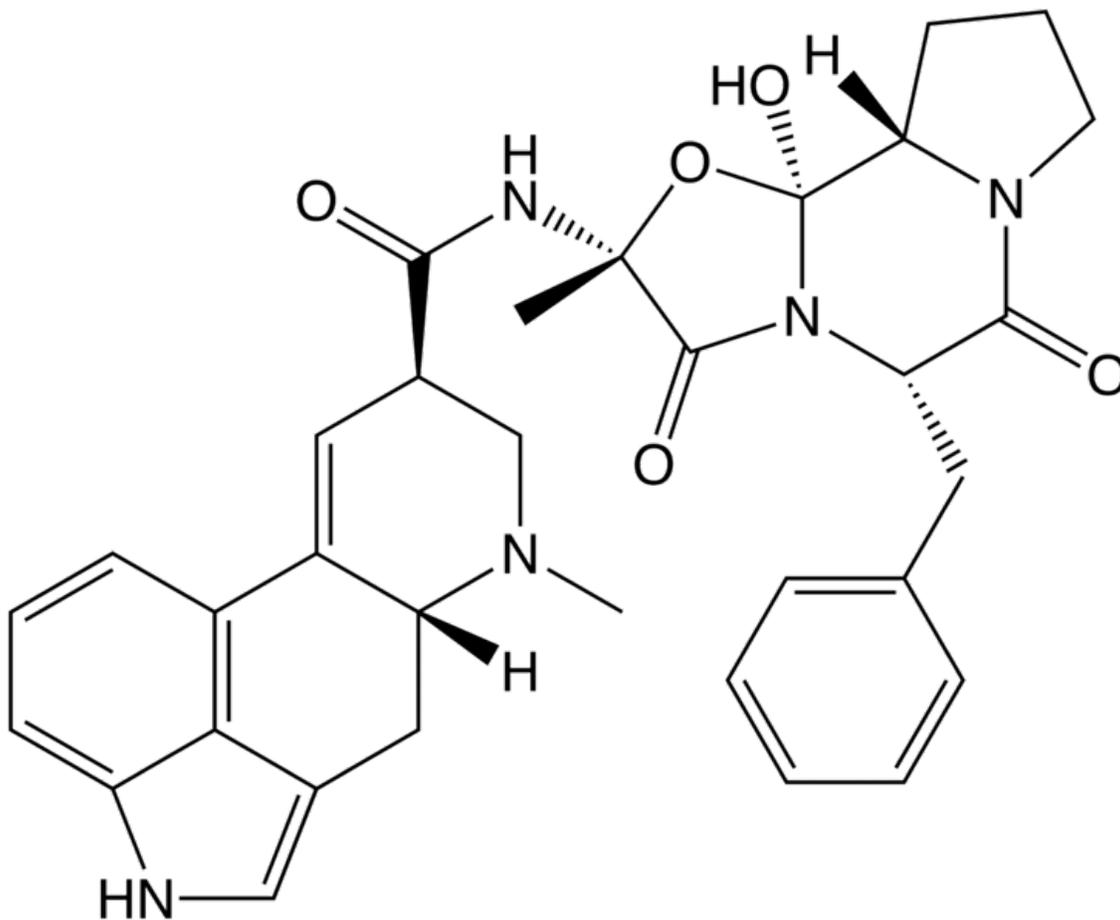
## **Model organisms**

Several pivotal discoveries in biology were made by researchers using fungi as model organisms, that is, fungi that grow and sexually reproduce rapidly in the laboratory. For example, the one gene-one enzyme hypothesis was formulated by scientists who used the bread mold *Neurospora crassa* to test their biochemical theories. Other important model fungi are *Aspergillus nidulans* and the yeasts, *Saccaromyces cerevisiae* and *Schizosaccharomyces pombe*, each of which has a long history of use to investigate issues in eukaryotic cell biology and genetics, such as cell cycle regulation, chromatin structure, and gene regulation. Other fungal models have more recently emerged that each address specific biological questions relevant to medicine, plant pathology, and industrial uses; examples include *Candida albicans*, a dimorphic, opportunistic human pathogen, *Magnaporthe grisea*, a plant pathogen, and *Pichia pastoris*, a yeast widely used for eukaryotic protein expression.

## **Others**

Fungi are used extensively to produce industrial chemicals like citric, gluconic, lactic, and malic acids, and industrial enzymes, such as lipases used in biological detergents, cellulases used in making cellulosic ethanol and stonewashed jeans, and amylases, invertases, proteases and xylanases. Several species, most notably *Psilocybin mushrooms* (colloquially known as *magic mushrooms*), are ingested for their psychedelic properties, both recreationally and religiously.

## Mycotoxins



Ergotamine, a major mycotoxin produced by *Claviceps* species, which if ingested can cause gangrene, convulsions, and hallucinations

Many fungi produce biologically active compounds, several of which are toxic to animals or plants and are therefore called mycotoxins. Of particular relevance to humans are mycotoxins produced by molds causing food spoilage, and poisonous mushrooms. Particularly infamous are the lethal amatoxins in some *Amanita* mushrooms, and ergot alkaloids, which have a long history of causing serious epidemics of ergotism (St Anthony's Fire) in people consuming rye or related cereals contaminated with sclerotia of the ergot fungus, *Claviceps purpurea*. Other notable mycotoxins include the aflatoxins, which are insidious liver toxins and highly carcinogenic metabolites produced by certain *Aspergillus* species often growing in or on grains and nuts consumed by humans, ochratoxins, patulin, and trichothecenes (e.g., T-2 mycotoxin) and fumonisins, which have significant impact on human food supplies or animal livestock.

Mycotoxins are secondary metabolites (or natural products), and research has established the existence of biochemical pathways solely for the purpose of producing mycotoxins and other natural products in fungi. Mycotoxins may provide fitness benefits in terms of

physiological adaptation, competition with other microbes and fungi, and protection from consumption (fungivory).

## **Mycology**

Mycology is the branch of biology concerned with the systematic study of fungi, including their genetic and biochemical properties, their taxonomy, and their use to humans as a source of medicine, food, and psychotropic substances consumed for religious purposes, as well as their dangers, such as poisoning or infection. The field of phytopathology, the study of plant diseases, is closely related because many plant pathogens are fungi.

Use of fungi by humans dates back to prehistory; Ötzi the Iceman, a well-preserved mummy of a 5,300 year old Neolithic man found frozen in the Austrian Alps, carried two species of polypore mushrooms that may have been used as tinder (*Fomes fomentarius*), or for medicinal purposes (*Piptoporus betulinus*). Ancient peoples have used fungi as food sources—often unknowingly—for millennia, in the preparation of leavened bread and fermented juices. Some of the oldest written records contain references to the destruction of crops that were probably caused by pathogenic fungi.

## **History**

Mycology is a relatively new science that became systematic after the development of the microscope in the 16th century. Although fungal spores were first observed by Giambattista della Porta in 1588, the seminal work in the development of mycology is considered to be the publication of Pier Antonio Micheli's 1729 work *Nova plantarum genera*. Micheli not only observed spores, but showed that under the proper conditions, they could be induced into growing into the same species of fungi from which they originated. Extending the use of the binomial system of nomenclature introduced by Carl Linnaeus in his *Species plantarum* (1753), the Dutch Christian Hendrik Persoon (1761–1836) established the first classification of mushrooms with such skill so as to be considered a founder of modern mycology. Later, Elias Magnus Fries (1794–1878) further elaborated the classification of fungi, using spore color and various microscopic characteristics, methods still used by taxonomists today. Other notable early contributors to mycology in the 17th–19th and early 20th centuries include Miles Joseph Berkeley, August Carl Joseph Corda, Anton de Bary, the brothers Louis René and Charles Tulasne, Arthur H. R. Buller, Curtis G. Lloyd, and Pier Andrea Saccardo. The 20th century has seen a modernization of mycology that has come from advances in biochemistry, genetics, molecular biology, and biotechnology. The use of DNA sequencing technologies and phylogenetic analysis has provided new insights into fungal relationships and biodiversity, and has challenged traditional morphology-based groupings in fungal taxonomy.

## Chapter 2

# Ascomycota

### Ascomycota



*Sarcoscypha coccinea*

### Scientific classification

Domain: Eukarya

Kingdom: Fungi

Subkingdom: Dikarya

Phylum: **Ascomycota**  
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### Subphyla/Classes

Pezizomycotina  
Arthoniomycetes  
Dothideomycetes  
Eurotiomycetes  
Geoglossomycetes  
Laboulbeniomycetes  
Lecanoromycetes  
Leotiomycetes

Lichinomycetes  
Orbiliomycetes  
Pezizomycetes  
Sordariomycetes  
"Unplaced orders"  
Lahmiales  
Medeolariales  
Triblidiales  
Saccharomycotina  
Saccharomycetes  
Taphrinomycotina  
Neoelectomycetes  
Pneumocystidomycetes  
Schizosaccharomycetes  
Taphrinomycetes

The **Ascomycota** are a Division/Phylum of the kingdom Fungi, and subkingdom Dikarya. Its members are commonly known as the **Sac fungi**. They are the largest phylum of Fungi, with over 64,000 species. The defining feature of this fungal group is the "ascus" (from Greek: *ἄσκος* (*askos*), meaning "sac" or "wineskin"), a microscopic sexual structure in which nonmotile spores, called ascospores, are formed. However, some species of the Ascomycota are asexual, meaning that they do not have a sexual cycle and thus do not form asci or ascospores. Previously placed in the Deuteromycota along with asexual species from other fungal taxa, asexual (or anamorphic) ascomycetes are now identified and classified based on morphological or physiological similarities to ascus-bearing taxa, and by phylogenetic analyses of DNA sequences.

The ascomycetes are a monophyletic group, i.e., all of its members trace back to one common ancestor. This group is of particular relevance to humans as sources for medicinally important compounds, such as antibiotics and for making bread, alcoholic beverages, and cheese, but also as pathogens of humans and plants. Familiar examples of sac fungi include morels, truffles, brewer's yeast and baker's yeast, Dead Man's Fingers, and cup fungi. The fungal symbionts in the majority of lichens (loosely termed "ascolichens") such as *Cladonia* belong to the Ascomycota. There are many plant-pathogenic ascomycetes, including apple scab, rice blast, the ergot fungi, black knot, and the powdery mildews. Several species of ascomycetes are biological model organisms in laboratory research. Most famously *Neurospora crassa*, several species of yeasts, and *Aspergillus* species are used in many genetics and cell biology studies. *Penicillium* species on cheeses and those producing antibiotics for treating bacterial infectious diseases are examples of taxa that belong to the Ascomycota.

### ***Ascomycetes versus Ascomycota***

Before the recognition of the fungal kingdom, the sac fungi were considered to be a *Class*, not a *Phylum*. The original collective term for these taxa was "Ascomycetes", which was first coined in the 1800s for a rankless nonlichenized taxon that possessed

asci. The names Ascomycota, Ascomycetes, and others with the same root are based upon the term "ascus". "Ascomycetes" was soon used to include lichenized taxa, and became the standard term, at the class level, for all ascus-bearing species, just as the term "Basidiomycetes" became used for their basidium-bearing counterparts. Elevation of the taxonomic rank of the Ascomycetes resulted in the names Ascomycetae, Ascomycotina, and finally Ascomycota. Together, the Ascomycota and the Basidiomycota form the subkingdom Dikarya. The more familiar term, Ascomycetes, is still loosely used, e.g. at fungal forays it is often said of a fungus, such as *Peziza*, "It is an ascomycete, not a basidiomycete" in reference to their sexual reproductive mode. The terms are further abbreviated to "ascos" and "basidos" which are not officially sanctioned technical names.

### **Modern classification of Ascomycota**

There are three subphyla that are described and accepted:

- The *Pezizomycotina* is the largest subphylum and contains all ascomycetes that produce ascocarps (fruiting bodies), except for one genus, *Neolecta*, in the Taphrinomycotina. It is roughly equivalent to the previous taxon, *Euascomycetes*. The *Pezizomycotina* includes most macroscopic "ascos" such as truffles, ergot, ascolichens, cup fungi (discomycetes), pyrenomycetes, lorchels, and caterpillar fungus. It also contains microscopic fungi such as powdery mildews, dermatophytic fungi, and Laboulbeniales.
- The *Saccharomycotina* comprises most of the "true" yeasts, such as baker's yeast and *Candida* which are single-celled (unicellular) fungi, which reproduce vegetatively by budding. Most of these species were previously classified in a taxon called *Hemiascomycetes*.
- The *Taphrinomycotina* includes a disparate and basal group within the Ascomycota that was recognized following molecular (DNA) analyses. The taxon was originally named *Archiascomycetes* (or *Archaeascomycetes*). It includes both hyphal fungi (*Neolecta*, *Taphrina*), fission yeasts (*Schizosaccharomyces*), and the mammalian lung parasite, *Pneumocystis*.

Ribosomal RNA gene sequencing of soil suggests that there may be a fourth subphylum of Ascomycota (termed Soil Clone Group I or SCGI), that has not been described in cultures or based on fruiting bodies. SCGI organisms are only known from DNA sequences found in soils worldwide and are placed between the Taphrinomycotina and the Saccharomycotina.

### **Outdated taxon names**

Several outdated taxon names—based on morphological features—are still occasionally used for species of the Ascomycota. These include the following sexual (teleomorphic) groups, defined by the structures of their sexual fruiting bodies: the Discomycetes, which included all species forming apothecia; the Pyrenomycetes, which included all sac fungi that formed perithecia or pseudothecia, or any structure resembling these morphological structures; and the Plectomycetes, which included those species that form cleistothecia.

Hemiascomycetes included the yeasts and yeast-like fungi that have now been placed into the Saccharomycotina or Taphrinomycotina, while the Euascomycetes included the remaining species of the Ascomycota which are now in the Pezizomycotina, and the Neolecta which are in the Taphrinomycotina.

Some ascomycetes do not reproduce sexually or are not known to produce asci and are therefore anamorphic species. Those anamorphs that produce conidia (mitospores) were previously described as Mitosporic Ascomycota. Some taxonomists placed this group into a separate artificial phylum, the Deuteromycota (or "Fungi Imperfecti"). Where recent molecular analyses have identified close relationships with ascus-bearing taxa, anamorphic species have been grouped into the Ascomycota, despite the absence of the defining ascus. Sexual and asexual isolates of the same species commonly carry different binomial species names, as, for example, *Aspergillus nidulans* and *Emericella nidulans*, for asexual and sexual isolates, respectively, of the same species.

Species of the Deuteromycota were classified as Coelomycetes if they produced their conidia in minute flask- or saucer-shaped conidiomata, known technically as *pycnidia* and *acervuli*. The Hyphomycetes were those species where the conidiophores (*i.e.*, the hyphal structures that carry conidia-forming cells at the end) are free or loosely organized. They are mostly isolated but sometimes also appear as bundles of cells aligned in parallel (described as *synnematal*) or as cushion-shaped masses (described as *sporodochial*).

## **Morphology**

Most species grow as filamentous, microscopic structures called hyphae. Many interconnected hyphae form a mycelium, which—when visible to the naked eye (macroscopic)—is commonly called mold (or, in botanical terminology, thallus). During sexual reproduction, many Ascomycota typically produce large numbers of asci. The ascus is often contained in a multicellular, occasionally readily visible fruiting structure, the ascocarp (also called an *ascoma*). Ascocarps come in a very large variety of shapes: cup-shaped, club-shaped, potato-like, spongy, seed-like, oozing and pimple-like, coral-like, nit-like, golf-ball-shaped, perforated tennis ball-like, cushion-shaped, plated and feathered in miniature (Laboulbeniales), microscopic classic Greek shield-shaped, stalked or sessile. They can appear solitary or clustered. Their texture can likewise be very variable, including fleshy, like charcoal (carbonaceous), leathery, rubbery, gelatinous, slimy, powdery, or cob-web-like. Ascocarps come in multiple colors such as red, orange, yellow, brown, black, or, more rarely, green or blue. Some ascomycetous fungi, such as *Saccharomyces cerevisiae*, grow as single-celled yeasts, which—during sexual reproduction—develop into an ascus, and do not form fruiting bodies.



The "candlesnuff fungus", *Xylaria hypoxylon*

In lichenized species, the thallus of the fungus defines the shape of the symbiotic colony. Some dimorphic species, such as *Candida albicans*, can switch between growth as single cells and as filamentous, multicellular hyphae. Other species are pleomorphic, exhibiting asexual (anamorphic) as well as a sexual (teleomorphic) growth forms.

Except for lichens, the non-reproductive (vegetative) mycelium of most ascomycetes is usually inconspicuous because it is commonly embedded in the substrate, such as soil, or grows on or inside a living host, and only the ascoma may be seen when fruiting. Pigmentation, such as melanin in hyphal walls, along with prolific growth on surfaces can result in visible mold colonies; examples include *Cladosporium* species, which form black spots on bathroom caulking and other moist areas. Many ascomycetes cause food spoilage, and, therefore, the pellicles or moldy layers that develop on jams, juices, and other foods are the mycelia of these species or occasionally Mucoromycotina and almost never Basidiomycota. Sooty molds that develop on plants, especially in the tropics are the thalli of many species.



The ascocarp of a morel contains numerous apothecia.

Large masses of yeast cells, asci or ascus-like cells, or conidia can also form macroscopic structures. For example, *Pneumocystis* species can colonize lung cavities (visible in x-rays), causing a form of pneumonia. Asci of *Ascospaera* fill honey bee larvae and pupae causing mummification with a chalk-like appearance, hence the name "chalkbrood". Yeasts for small colonies in vitro and in vivo and excessive growth of *Candida* species in the mouth or vagina causes "thrush", a form of candidiasis.

The cell walls of the ascomycetes almost always contain chitin and  $\beta$ -glucans, and divisions within the hyphae, called "septa", are the internal boundaries of individual cells (or compartments). The cell wall and septa give stability and rigidity to the hyphae and may prevent loss of cytoplasm in case of local damage to cell wall and cell membrane.

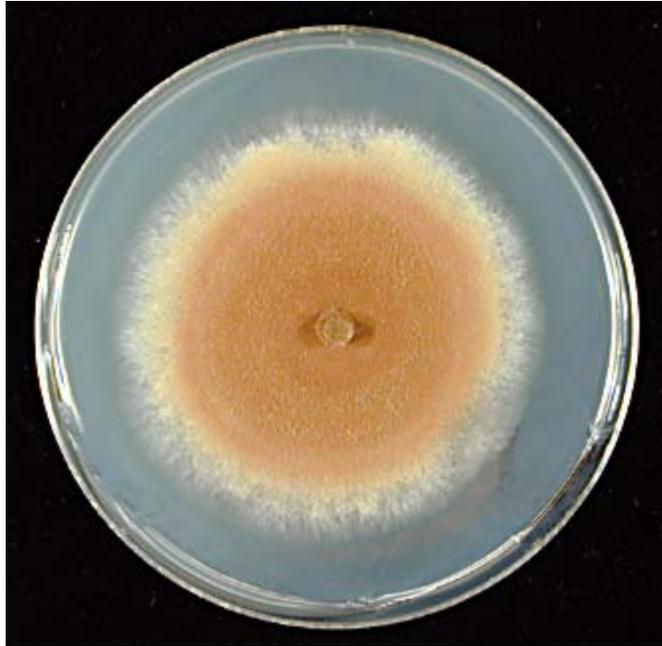
The septa commonly have a small opening in the center, which functions as a cytoplasmic connection between adjacent cells, also sometimes allowing cell-to-cell movement of nuclei within a hypha. Vegetative hyphae of most ascomycetes contain only one nucleus per cell (*uninucleate* hyphae), but multinucleate cells—especially in the apical regions of growing hyphae—can also be present.

## **Metabolism**

In common with other fungal phyla, the Ascomycota are heterotrophic organisms that require organic molecules as energy sources. These are obtained by feeding on a variety of organic substrates including dead matter, foodstuffs, or as symbionts in or on other living organisms. To obtain these nutrients from their surroundings, ascomycetous fungi secrete powerful digestive enzymes which break down organic substances into smaller molecules, which are then taken up into the cell. Many species live on dead plant material such as leaves, twigs, or logs. Several species colonize plants, animals, or other fungi as parasites or mutualistic symbionts and derive all their metabolic energy in form of nutrients from the tissues of their hosts.

Owing to their long evolutionary history, the Ascomycota have evolved the capacity to break down almost every organic substance. Unlike most organisms, they are able to use their own enzymes to digest plant biopolymers such as cellulose or lignin. Collagen, an abundant structural protein in animals, and keratin—a protein that forms hair and nails—, can also serve as food sources. Unusual examples include *Aureobasidium pullulans*, which feeds on wall paint, and the kerosene fungus *Amorphotheca resinae*, which feeds on aircraft fuel (causing occasional problems for the airline industry), and may sometimes block fuel pipes. Other species can resist high osmotic stress and grow, for example, on salted fish, and a few ascomycetes are aquatic.

The Ascomycota is characterized by a high degree of specialization; for instance, certain species of Laboulbeniales attack only one particular leg of one particular insect species. Many Ascomycota engage in symbiotic relationships such as in lichens—symbiotic associations with green algae or cyanobacteria—in which the fungal symbiont directly obtains products of photosynthesis. In common with many basidiomycetes and Glomeromycota, some ascomycetes form symbioses with plants by colonizing the roots to form mycorrhizal associations. The Ascomycota also represents several carnivorous fungi, which have developed hyphal traps to capture small protists such as amoebae, as well as roundworms (*Nematoda*), rotifers, tardigrades, and small arthropods such as springtails (*Collembola*).



*Hypomyces completus* on culture medium

### ***Distribution and living environment***

The Ascomycota are represented in all land ecosystems worldwide, occurring on all continents including Antarctica. Spores and hyphal fragments are dispersed through the atmosphere and freshwater environments, as well as ocean beaches and tidal zones. The distribution of species is variable; while some are found on all continents, others, as for example the white truffle *Tuber magnatum*, only occur in isolated locations in Italy and Eastern Europe. The distribution of plant-parasitic species is often restricted by host distributions; for example, *Cyttaria* is only found on *Nothofagus* (Southern Beech) in the Southern Hemisphere.

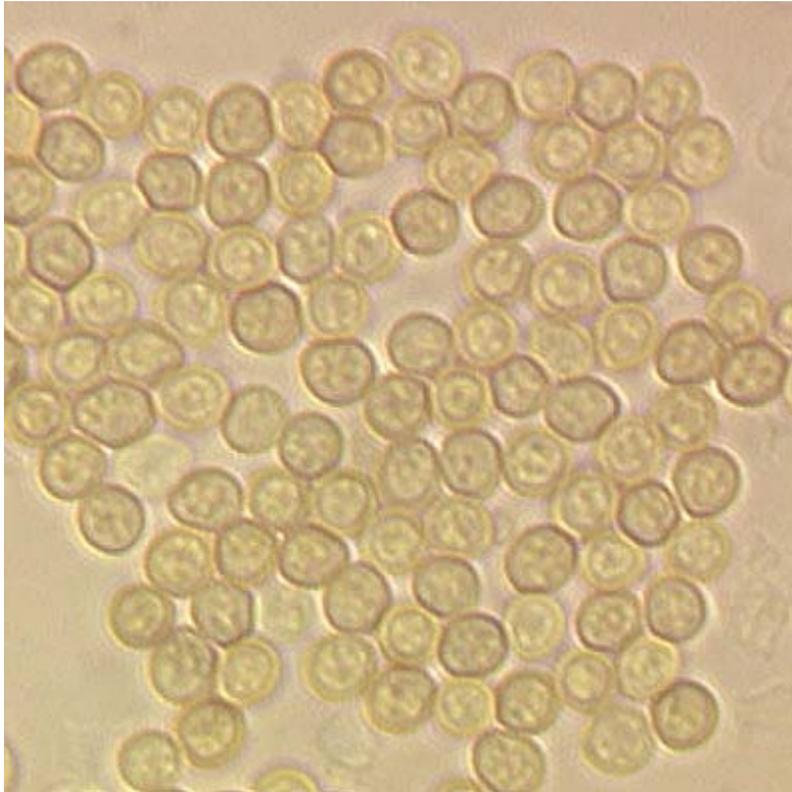
### ***Reproduction***

#### **Asexual reproduction**

Asexual reproduction is the dominant form of propagation in the Ascomycota, and is responsible for the rapid spread of these fungi into new areas. It occurs through vegetative reproductive spores, the conidia. The conidiospores commonly contain one nucleus and are products of mitotic cell divisions and thus are sometimes called mitospores, which are genetically identical to the mycelium from which they originate. They are typically formed at the ends of specialized hyphae, the *conidiophores*. Depending on the species they may be dispersed by wind or water, or by animals.

## Asexual spores

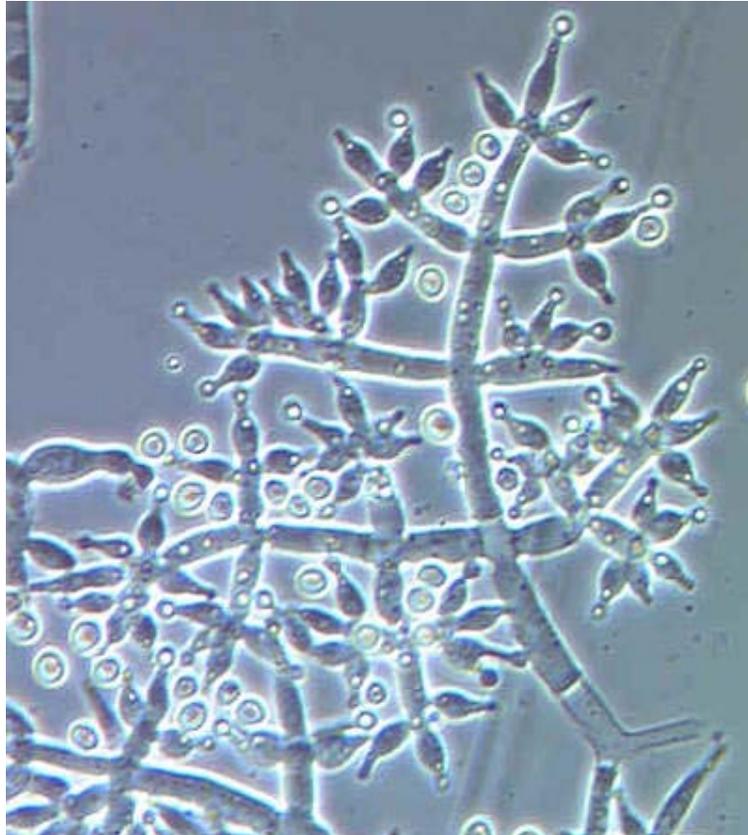
Different types of asexual spores can be identified by colour, shape, and how they are released as individual spores. Spore types can be used as taxonomic characters in the classification within the Ascomycota. The most frequent types are the single-celled spores, which are designated *amerospores*. If the spore is divided into two by a cross-wall (septum), it is called a *didymospore*.



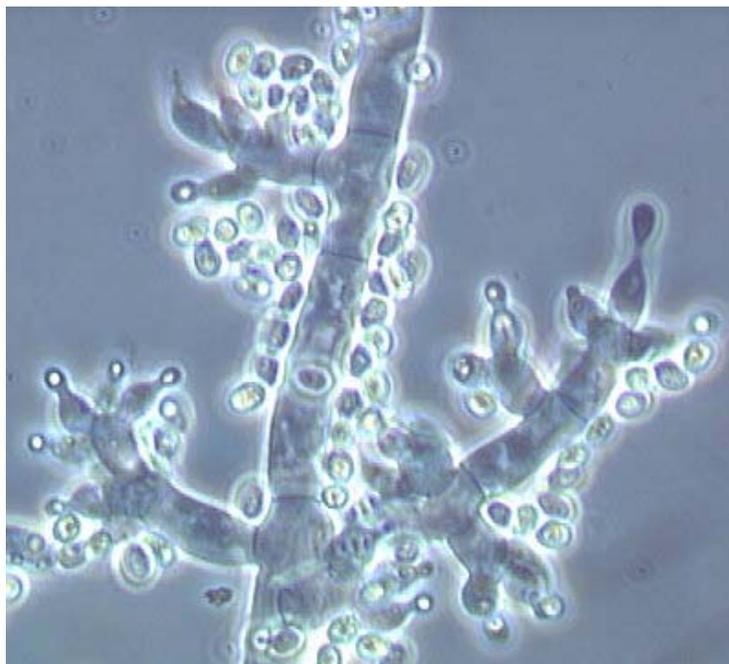
Conidiospores of *Trichoderma aggressivum*, Diameter approx. 3 $\mu$ m



Conidiophores of molds of the genus *Aspergillus*, conidiogenesis is blastic-phialidic



Conidiophores of *Trichoderma harzianum*, conidiogenesis is blastic-phialidic



Conidiophores of *Trichoderma fertile* with vase-shaped phialides and newly formed conidia on their ends (bright points)

When there are two or more cross-walls, the classification depends on spore shape. If the septa are *transversal*, like the rungs of a ladder, it is a *phragmospore*, and if they possess a net-like structure it is a *dictyospore*. In *staurospores* ray-like arms radiate from a central body; in others (*helicospores*) the entire spore is wound up in a spiral like a spring. Very long worm-like spores with a length-to-diameter ratio of more than 15:1, are called *scoleospores*.

## Conidiogenesis and dehiscence

Important characteristics of the anamorphs of the Ascomycota are *conidiogenesis*, which includes spore formation and dehiscence (separation from the parent structure). Conidiogenesis corresponds to Embryology in animals and plants and can be divided into two fundamental forms of development: *blastic* conidiogenesis, where the spore is already evident before it separates from the conidiogenic hypha, and *thallic* conidiogenesis, during which a cross-wall forms and the newly created cell develops into a spore. The spores may or may not be generated in a large-scale specialized structure which helps to spread them.

These two basic types can be further classified as follows:

- *blastic-acropetal* (repeated budding at the tip of the conidiogenic hypha, so that a chain of spores is formed with the youngest spores at the tip),
- *blastic-synchronous* (simultaneous spore formation from a central cell, sometimes with secondary acropetal chains forming from the initial spores),
- *blastic-sympodial* (repeated sideways spore formation from behind the leading spore, so that the oldest spore is at the main tip),
- *blastic-annellidic* (each spore separates and leaves a ring-shaped scar which is inside the scar left by the previous spore),
- *blastic-phialidic* (the spores arise and are ejected from the open ends of special conidiogenic cells called phialides which remain constant in length),
- *basauxic* (where a chain of conidia, in successively younger stages of development, is emitted from the mother cell),
- *blastic-retrogressive* (spores separate by formation of crosswalls near the tip of the conidiogenic hypha, which thus becomes progressively shorter),
- *thallic-arthric* (double cell walls split the conidiogenic hypha into cells which develop into short, cylindrical spores called *arthroconidia*; sometimes every second cell dies off, leaving the arthroconidia free),
- *thallic-solitary* (a large bulging cell separates from the conidiogenic hypha, forms internal walls, and develops to a *phragmospore*).

Sometimes the conidia are produced in structures visible to the naked eye, which help to distribute the spores. These structures are called "conidiomata" (singular: conidioma), and may take the form of *pycnidia* (which are flask-shaped and arise in the fungal tissue) or *acervuli* (which are cushion-shaped and arise in host tissue).

Dehiscence happens in two ways. In *schizolytic* dehiscence, a double-dividing wall with a central lamella (layer) forms between the cells; the central layer then breaks down thereby releasing the spores. In *rhizolytic* dehiscence, the cell wall which joins the spores on the outside degenerates and releases the conidia.

### **Heterokaryosis and parasexuality**

Several Ascomycota species are not known to have a sexual cycle. Such asexual species may be able to undergo genetic recombination between individuals by processes involving *heterokaryosis* and *parasexual* events.

Parasexuality refers to the process of heterokaryosis, caused by merging of two hyphae belonging to different individuals, by a process called *anastomosis*, followed by a series of events resulting in genetically different cell nuclei in the mycelium. The merging of nuclei is not followed by meiotic events, such as gamete formation and results in an increased number of chromosomes per nuclei. *Mitotic crossover* may enable recombination, i.e., an exchange of genetic material between homologous chromosomes. The chromosome number may then be restored to its haploid state by nuclear division, with each daughter nuclei being genetically different from the original parent nuclei. Alternatively, nuclei may lose some chromosomes, resulting in aneuploid cells.

### **Sexual reproduction**



Ascus of *Hypocrea virens* with eight two-celled Ascospores

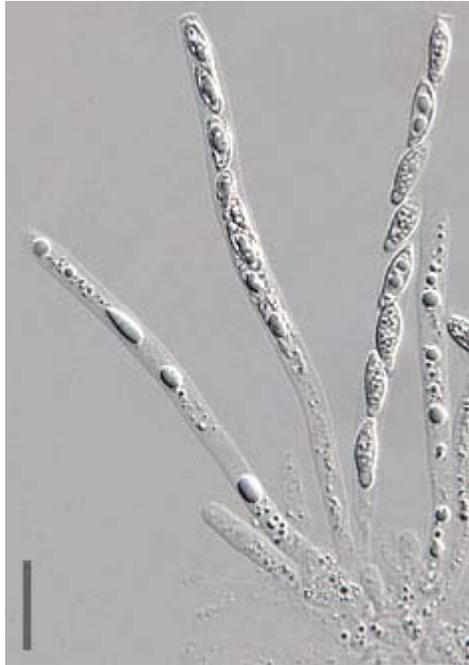
Sexual reproduction in the Ascomycota leads to the formation of the *ascus*, the structure that defines this fungal group and distinguishes it from other fungal phyla. The ascus is a tube-shaped vessel, a *meiosporangium*, which contains the sexual spores produced by meiosis and which are called *ascospores*.

Apart from a few exceptions, such as *Candida albicans*, most ascomycetes are haploid, i.e., they contain one set of chromosomes per nuclei. During sexual reproduction there is a diploid phase which commonly is very short, and meiosis restores the haploid state.

### **Formation of sexual spores**

The sexual part of the life cycle commences when two hyphal structures mate. In the case of *homothallic* species, mating is enabled between hyphae of the same fungal clone, whereas in *heterothallic* species, the two hyphae must originate from fungal clones that differ genetically, i.e., those that are of a different mating type. Mating types are typical of the fungi and correspond roughly to the sexes in plants and animals; however one species may have more than two mating types, resulting in sometimes complex vegetative incompatibility systems.

Gametangia are sexual structures formed from hyphae, and are the generative cells. A very fine hypha, called trichogyne emerges from one gametangium, the *ascogonium*, and merges with a gametangium (the *antheridium*) of the other fungal isolate. The nuclei in the antheridium then migrate into the ascogonium, and plasmogamy—the mixing of the cytoplasm—occurs. Unlike in animals and plants, plasmogamy is not immediately followed by the merging of the nuclei (called *karyogamy*). Instead, the nuclei from the two hyphae form pairs, initiating the *dikaryophase* of the sexual cycle, during which time the pairs of nuclei synchronously divide. Fusion of the paired nuclei leads to mixing of the genetic material and recombination and is followed by meiosis. A similar sexual cycle is present in the red algae (Rhodophyta).



Unitunicate-inoperculate Asci of *Hypomyces chrysospermus*

From the fertilized ascogonium, *dinucleate* hyphae emerge in which each cell contains two nuclei. These hyphae are called *ascogenous* or fertile hyphae. They are supported by the vegetative mycelium containing uni- (or mono-) nucleate hyphae, which are sterile. The mycelium containing both sterile and fertile hyphae may grow into fruiting body, the *ascocarp*, which may contain millions of fertile hyphae.

The sexual structures are formed in the fruiting layer of the ascocarp, the hymenium. At one end of ascogenous hyphae, characteristic U-shaped hooks develop, which curve back opposite to the growth direction of the hyphae. The two nuclei contained in the apical part of each hypha divide in such a way that the threads of their mitotic spindles run parallel, creating two pairs of genetically different nuclei. One daughter nucleus migrates close to the hook, while the other daughter nucleus locates to the basal part of the hypha. The formation of two parallel cross-walls then divides the hypha into three sections: one at the hook with one nucleus, one at the basal of the original hypha that contains one nucleus, and one that separates the U-shaped part which contains the other two nuclei.

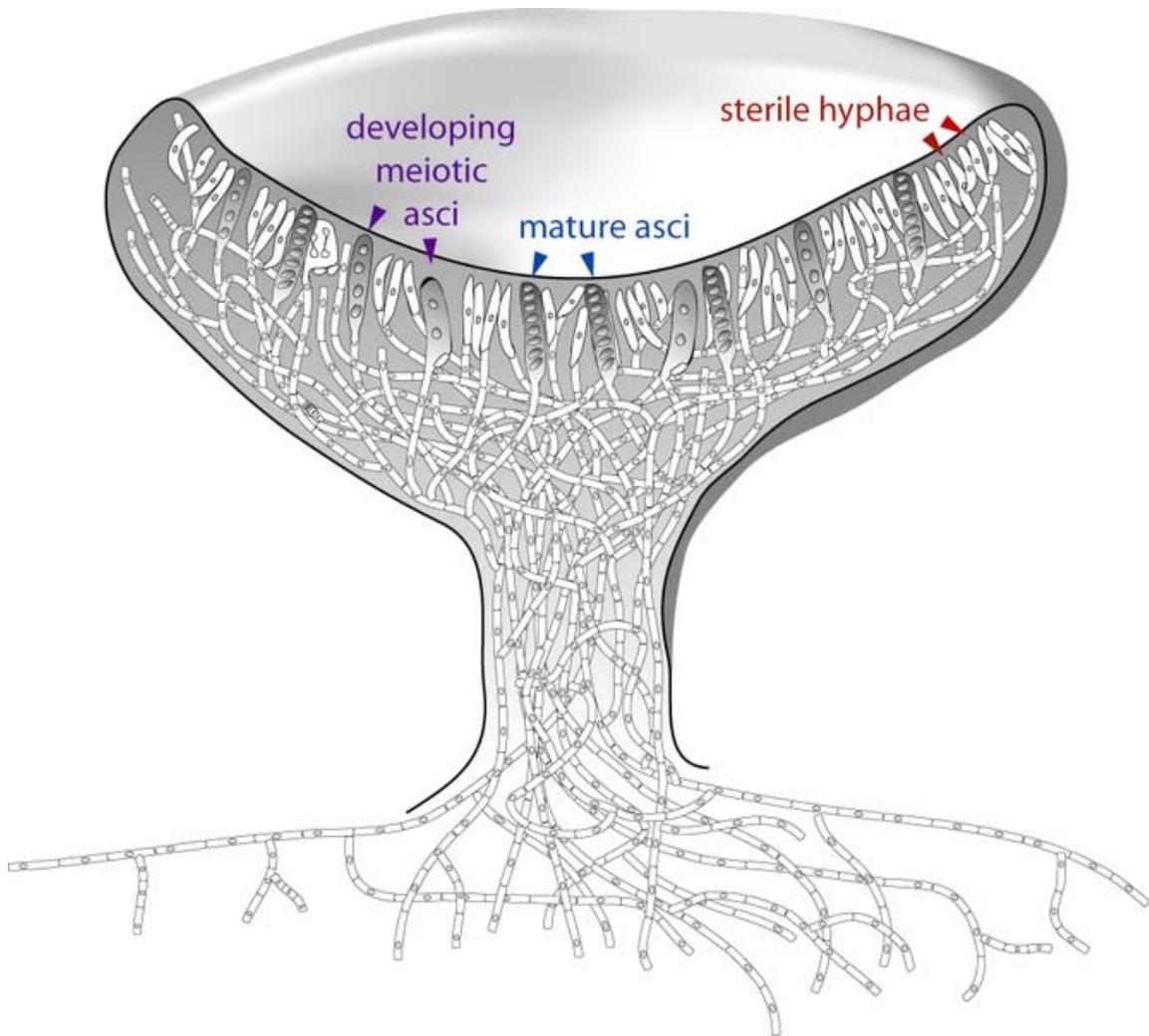


Diagram of an apothecium (the typical cup-like reproductive structure of Ascomycetes) showing sterile tissues as well as developing and mature asci.

Fusion of the nuclei (karyogamy) takes place in the U-shaped cells in the hymenium, and results in the formation of a diploid zygote. The zygote grows into the ascus, an elongated tube-shaped or cylinder-shaped capsule. Meiosis then gives rise to four haploid nuclei, usually followed by a further mitotic division that results in eight nuclei in each ascus. The nuclei along with some cytoplasm become enclosed within membranes and a cell wall to give rise to ascospores that are aligned inside the ascus like peas in a pod.

Upon opening of the ascus, ascospores may be dispersed by the wind, while in some cases the spores are forcibly ejected from the ascus; certain species have evolved spore cannons, which can eject ascospores up to 30 cm. away. When the spores reach a suitable substrate, they germinate, form new hyphae, which restarts the fungal life cycle.

The form of the ascus is important for classification and is divided into four basic types: unitunicate-operculate, unitunicate-inoperculate, bitunicate, or prototunicate.

## **Ecology**

The Ascomycota fulfil a central role in most land-based ecosystems. They are important decomposers which break down organic materials, such as dead leaves and animals, and help the detritivores (animals which feed on decomposing material) to obtain their nutrients. Ascomycetes along with other fungi can break down large molecules such as cellulose or lignin, and thus have important roles in nutrient cycling such as the carbon cycle.

The fruiting bodies of the Ascomycota provide food for many animals ranging from insects and slugs and snails (*Gastropoda*) to rodents and larger mammals such as deer and wild boars.

Many ascomycetes also form symbiotic relationships with other organisms, including plants and animals.

## **Lichens**

Probably since early in their evolutionary history, the Ascomycota have formed symbiotic associations with green algae (*Chlorophyta*), and other types of algae and cyanobacteria. These mutualistic associations are commonly known as lichens, and can grow and persist in terrestrial regions of the earth that are inhospitable to other organisms and characterized by extremes in temperature and humidity, including the Arctic, the Antarctic, deserts, and mountaintops. While the photoautotrophic algal partner generates metabolic energy through photosynthesis, the fungus offers a stable, supportive matrix and protects cells from radiation and dehydration. Around 42% of the Ascomycota (about 18,000 species) form lichens, and almost all the fungal partners of lichens belong to the Ascomycota.

## **Mycorrhizal fungi and endophytes**

Members of the Ascomycota form two important types of relationship with plants: as mycorrhizal fungi and as endophytes. Mycorrhiza are symbiotic associations of fungi with the root systems of the plants, which can be of vital importance for growth and persistence for the plant. The fine mycelial network of the fungus enables the increased uptake of mineral salts that occur at low levels in the soil. In return, the plant provides the fungus with metabolic energy in the form of photosynthetic products.

Endophytic fungi live inside plants, and those that form mutualistic or commensal associations with their host, do not damage their hosts. The exact nature of the relationship between endophytic fungus and host depends on the species involved, and in some cases fungal colonization of plants can bestow a higher resistance against insects, roundworms (nematodes), and bacteria; in the case of grass endophytes the fungal symbiont produces poisonous alkaloids, which can affect the health of plant-eating (herbivorous) mammals and deter or kill insect herbivores.

## Symbiotic relationships with animals

Several ascomycetes of the genus *Xylaria* colonize the nests of leafcutter ants and other fungus-growing ants of the tribe Attini, and the fungal gardens of termites (Isoptera). Since they do not generate fruiting bodies until the insects have left the nests, it is suspected that, as confirmed in several cases of Basidiomycota species, they may be cultivated.

Bark beetles (family Scolytidae) are important symbiotic partners of ascomycetes. The female beetles transport fungal spores to new hosts in characteristic tucks in their skin, the *mycetangia*. The beetle tunnels into the wood and into large chambers in which they lay their eggs. Spores released from the mycetangia germinate into hyphae, which can break down the wood. The beetle larvae then feed on the fungal mycelium, and, on reaching maturity, carry new spores with them to renew the cycle of infection. A well-known example of this is Dutch elm disease, caused by *Ophiostoma ulmi*, which is carried by the European elm bark beetle, *Scolytus multistriatus*.

## Importance for humans



Tree attacked by the Bluestain fungus, *Ophiostoma minus*

Ascomycetes make many contributions to the good of humanity, and also have many ill effects.

## Harmful interactions

One of their most harmful roles is as the agent of many plant diseases. For instance:

- Dutch Elm Disease, caused by the closely related species *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, has led to the death of many elms in Europe and North America.



*Claviceps purpurea* on rye (*Secale cereale*)

- The originally Asian *Cryphonectria parasitica* is responsible for attacking Sweet Chestnuts (*Castanea sativa*), and virtually eliminated the once-widespread American Chestnut (*Castanea dentata*),
- A disease of Maize (*Zea mays*), which is especially prevalent in North America, is brought about by *Cochliobolus heterostrophus*.
- *Taphrina deformans* causes leaf curl of peach.
- *Uncinula necator* is responsible for the disease Powdery mildew, which attacks grapevines.
- Species of *Monilia* cause brown rot of stone fruit such as peaches (*Prunus persica*) and sour cherries (*Prunus cerasus*).

- Members of the Ascomycota such as *Stachybotrys chartarum* are responsible for fading of woollen textiles, which is a common problem especially in the tropics.
- Blue-green, red and brown moulds attack and spoil foodstuffs - for instance *Penicillium italicum* rots oranges.
- Cereals infected with *Fusarium graminearum* contain mycotoxins like deoxynivalenol (DON), which can lead to skin and mucous membrane lesions when eaten by pigs.
- Ergot (*Claviceps purpurea*) is a direct menace to humans when it attacks wheat or rye and produces highly poisonous and carcinogenic alkaloids, causing ergotism if consumed. Symptoms include hallucinations, stomach cramp, and a burning sensation in the limbs ("Saint Anthony's Fire").
- *Aspergillus flavus*, which grows on peanuts and other hosts, generates aflatoxin, which damages the liver and is highly carcinogenic.
- *Candida albicans*, a yeast which attacks the mucous membranes, can cause an infection of the mouth or vagina called thrush or candidiasis, and is also blamed for "yeast allergies".
- Fungi like *Epidermophyton* cause skin infections but are not very dangerous for people with healthy immune systems. However if the immune system is damaged they can be life-threatening; for instance, *Pneumocystis jiroveci* is responsible for severe lung infections which occur in AIDS patients.

### Positive effects

On the other hand, ascus fungi have brought some important benefits to humanity.

- The most famous case may be that of the mould *Penicillium chrysogenum* (formerly *Penicillium notatum*), which, probably to attack competing bacteria, produces an antibiotic which, under the name of Penicillin, triggered a revolution in the treatment of bacterial infectious diseases in the 20th century.
- The medical importance of *Tolypocladium niveum* as an immunosuppressor can hardly be exaggerated. It excretes Cyclosporin, which, as well as being given during organ transplants to prevent rejection, is also prescribed for auto-immune diseases such as multiple sclerosis, although there is some doubt over the long-term side-effects of the treatment.



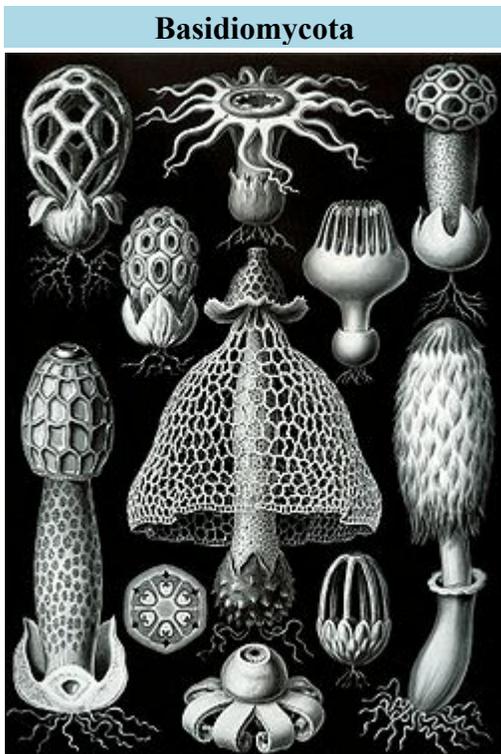
Stilton cheese veined with *Penicillium roqueforti*

- Some ascomycete fungi can be altered relatively easily through genetic engineering procedures. They can then produce useful proteins such as insulin, human growth hormone, or TPA, which is employed to dissolve blood clots.
- Several species are common model organisms in biology, including *Saccharomyces cerevisiae*, *Schizosaccharomyces pombe*, and *Neurospora crassa*. The genomes of a number of ascomycete fungi have been fully sequenced.
- Baker's Yeast (*Saccharomyces cerevisiae*) is used to make bread, beer and wine, during which process sugars such as glucose or sucrose are fermented to make ethanol and carbon dioxide. Bakers use the fungus for the carbon dioxide production, causing the bread to rise, with the ethanol boiling off during cooking. Most vintners use it for the ethanol production, with the carbon dioxide being released into the atmosphere during fermentation. Brewers and traditional producers of sparkling wine use both, with a primary fermentation for the alcohol and a secondary one to produce the carbon dioxide bubbles that provide the drinks with "sparkling" texture in the case of wine and the desirable foam in the case of beer.
- Enzymes of *Penicillium camemberti* play a role in the manufacture of the cheeses Camembert and Brie, while those of *Penicillium roqueforti* do the same for Gorgonzola, Roquefort and Stilton.

- In Asia *Aspergillus oryzae* is added to a pulp of soaked soya beans to make soy sauce.
- Finally, some members of the Ascomycota are eaten with relish; morels (*Morchella*) and truffles (*Tuber*) are some of the most sought-after fungus delicacies.

## Chapter 3

# Basidiomycota



Basidiomycetes from Ernst Haeckel's 1904  
*Kunstformen der Natur*

### Scientific classification

Domain:	Eukarya
Kingdom:	Fungi
Subkingdom:	Dikarya
Phylum:	<b>Basidiomycota</b> R.T. Moore, 1980

### Subphyla/Classes

Agaricomycotina

Pucciniomycotina  
Ustilaginomycotina  
*Incertae sedis* (no phylum)

Wallemiomycetes

**Basidiomycota** is one of two large phyla that, together with the Ascomycota, comprise the subkingdom Dikarya (often referred to as the "**higher fungi**") within the Kingdom Fungi. More specifically the Basidiomycota include mushrooms, puffballs, stinkhorns, bracket fungi, other polypores, jelly fungi, boletes, chanterelles, earth stars, smuts, bunts, rusts, mirror yeasts, and the human pathogenic yeast *Cryptococcus*. Basically, Basidiomycota are filamentous fungi composed of hyphae (except for those forming yeasts), and reproducing sexually via the formation of specialized club-shaped end cells called basidia that normally bear external meiospores (usually four). These specialized spores are called basidiospores. However, some Basidiomycota reproduce asexually, and may or may not also reproduce sexually. Asexually reproducing Basidiomycota (discussed below) can be recognized as members of this phylum by gross similarity to others, by the formation of a distinctive anatomical feature, cell wall components, and definitively by phylogenetic molecular analysis of DNA sequence data.

### **Classification**

The most recent classification adopted by a coalition of 67 mycologists recognizes three subphyla (Pucciniomycotina, Ustilaginomycotina, Agaricomycotina) and two other class level taxa (Wallemiomycetes, Entorrhizomycetes) outside of these, among the Basidiomycota. As now classified, the subphyla join and also cut across various obsolete taxonomic groups previously commonly used to describe various Basidiomycota. According to a 2008 estimate, Basidiomycota comprises three subphyla (including six unassigned classes) 16 classes, 52 orders, 177 families, 1,589 genera, and 31,515 species.

The Basidiomycota had traditionally been divided into two obsolete classes, the Homobasidiomycetes (including true mushrooms); and the Heterobasidiomycetes (the jelly, rust and smut fungi). Previously the entire Basidiomycota were called **Basidiomycetes**, an invalid class level name coined in 1959 as a counterpart to the **Ascomycetes**, when neither of these taxa were recognized as phyla. The terms basidiomycetes and ascomycetes are frequently used loosely to refer to Basidiomycota and Ascomycota. They are often abbreviated to "basidios" and "ascos" as mycological slang.

### **Agaricomycotina**

The Agaricomycotina include what had previously been called the Hymenomycetes (an obsolete morphological based class of Basidiomycota that formed hymenial layers on their fruitbodies), the Gasteromycetes (another obsolete class that included species mostly lacking hymenia and mostly forming spores in enclosed fruitbodies), as well as

most of the jelly fungi. The three classes in the Agaricomycotina are the Agaricomycetes, the Dacrymycetes, and the Tremellomycetes.

## **Pucciniomycotina**

The Pucciniomycotina includes the rust fungi, the insect parasitic/symbiotic genus *Septobasidium*, a former group of smut fungi (in the Microbotryomycetes, which includes mirror yeasts), and a mixture of odd, infrequently seen or seldom recognized fungi, often parasitic on plants. The eight classes in the Pucciniomycotina are Agaricostilbomycetes, Atractiellomycetes, Classiculomycetes, Cryptomycocolacomycetes, Cystobasidiomycetes, Microbotryomycetes, Mixiomycetes, and Pucciniomycetes.

## **Ustilaginomycotina**

The Ustilaginomycotina are most (but not all) of the former smut fungi and along with the Exobasidiales. The classes of the Ustilaginomycotina are the Exobasidiomycetes, the Entorrhizomycetes, and the Ustilaginomycetes.

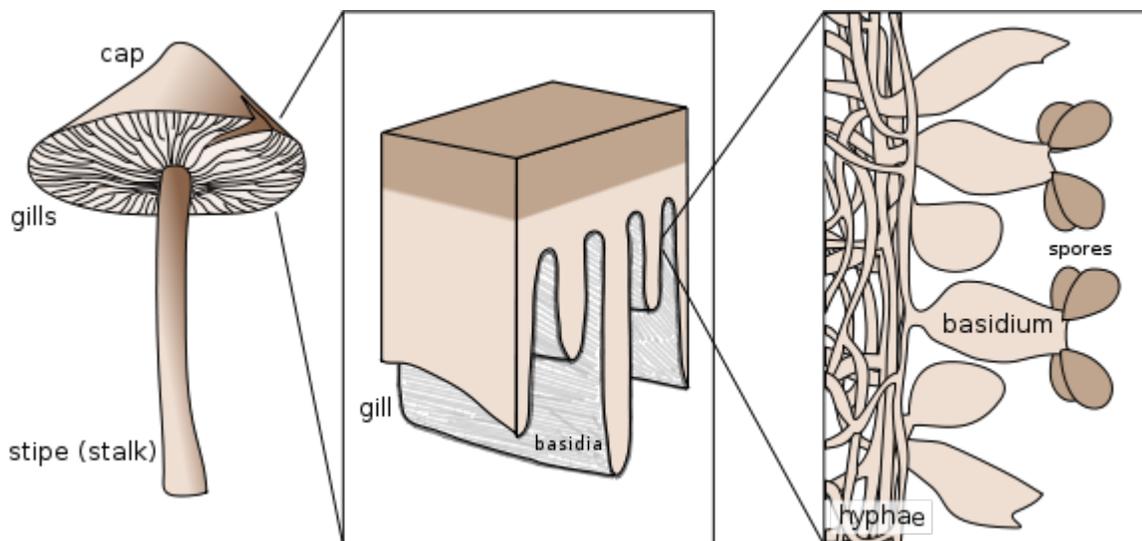
The class Wallemiomycetes is not yet placed in a subphylum.

## **Typical life-cycle**

Unlike higher animals and plants which have readily recognizable male and female counterparts, Basidiomycota (except for the Rust (Pucciniales)) tend to have mutually indistinguishable, compatible haploids which are usually mycelia being composed of filamentous hyphae. Typically haploid Basidiomycota mycelia fuse via plasmogamy and then the compatible nuclei migrate into each other's mycelia and pair up with the resident nuclei. Karyogamy is delayed, so that the compatible nuclei remain in pairs, called a **dikaryon**. The hyphae are then said to be **dikaryotic**. Conversely, the haploid mycelia are called **monokaryons**. Often, the dikaryotic mycelium is more vigorous than the individual **monokaryotic** mycelia, and proceeds to take over the substrate in which they are growing. The dikaryons can be long-lived, lasting years, decades, or centuries. *The monokaryons are neither male nor female.* They have either a **bipolar (unifactorial)** or a **tetrapolar (bifactorial)** mating system. This results in the fact that following meiosis, the resulting haploid basidiospores and resultant monokaryons, have nuclei that are compatible with 50% (if bipolar) or 25% (if tetrapolar) of their sister basidiospores (and their resultant monokaryons) because the mating genes must differ for them to be compatible. However, there are many variations of these genes in the population, and therefore, over 90% of monokaryons are compatible with each other. It is as if there were multiple sexes.

The maintenance of the dikaryotic status in dikaryons in many Basidiomycota is facilitated by the formation of clamp connections that physically appear to help coordinate and re-establish pairs of compatible nuclei following synchronous mitotic nuclear divisions. Variations are frequent and multiple. In a typical Basidiomycota lifecycle the long lasting dikaryons periodically (seasonally or occasionally) produce

basidia, the specialized usually club-shaped end cells, in which a pair of compatible nuclei fuse (karyogamy) to form a diploid cell. Meiosis follows shortly with the production of 4 haploid nuclei that migrate into 4 external, usually apical basidiospores. Variations occur, however. Typically the basidiospores are ballistic, hence they are sometimes also called ballistospores. In most species, the basidiospores disperse and each can start a new haploid mycelium, continuing the lifecycle. Basidia are microscopic but they are often produced on or in multicelled large fructifications called basidiocarps or basidiomes, or fruitbodies), variously called mushrooms, puffballs, etc. Ballistic basidiospores are formed on **sterigmata** which are tapered spine-like projections on basidia, and are typically curved, like the horns of a bull. In some Basidiomycota the spores are not ballistic, and the sterigmata may be straight, reduced to stubbs, or absent. The basidiospores of these non-ballistosporic basidia may either bud off, or be released via dissolution or disintegration of the basidia.



Schematic of a typical basidiocarp, the diploid reproductive structure of a basidiomycete, showing fruiting body, hymenium and basidia.

In summary, meiosis takes place in a diploid basidium. Each one of the four haploid nuclei migrates into its own basidiospore. The basidiospores are ballistically discharged and start new haploid mycelia called monokaryons. There are no males or females, rather there are compatible thalli with multiple compatibility factors. Plasmogamy between compatible individuals leads to delayed karyogamy leading to establishment of a dikaryon. The dikaryon is long lasting but ultimately gives rise to either fruitbodies with basidia or directly to basidia without fruitbodies. The paired dikaryon in the basidium fuse (i.e. karyogamy takes place). The diploid basidium begins the cycle again.

### ***Variations in life-cycles***

Many variations occur. Some are self compatible and spontaneously form dikaryons without a separate compatible thallus being involved. These fungi are said to be *homothallic*, versus the normal *heterothallic* species with mating types. Others are

**secondarily homothallic**, in that two compatible nuclei following meiosis migrate into each basidiospore, which is then dispersed as a pre-existing dikaryon. Often such species form only two spores per basidium, but that too varies. Following meiosis, mitotic divisions can occur in the basidium. Multiple numbers of basidiospores can result, including odd numbers via degeneration of nuclei, or pairing up of nuclei, or lack of migration of nuclei. For example, the chanterelle genus *Craterellus* often has 6-spored basidia, while some corticioid *Sistotrema* species can have 2-, 4-, 6-, or 8-spored basidia, and the cultivated button mushroom, *Agaricus bisporus*, can have 1-, 2-, 3- or 4-spored basidia under some circumstances. Occasionally monokaryons of some taxa can form morphologically fully formed basidiomes and anatomically correct basidia and ballistic basidiospores in the absence of dikaryon formation, diploid nuclei, and meiosis. A rare few number of taxa have extended diploid life-cycles, but can be common species. Examples exist in the mushroom genera *Armillaria* and *Xerula*, both in the Physalacriaceae. Occasionally basidiospores are not formed and parts of the "basidia" act as the dispersal agents, e.g. the peculiar mycoparasitic jelly fungus, *Tetragoniomyces* or the entire "basidium" acts as a "spore", e.g. in some false puffballs (*Scleroderma*). In the human pathogenic genus *Cryptococcus*, 4 nuclei following meiosis remain in the basidium but continually divide mitotically, each nucleus migrating into synchronously forming nonballistic basidiospores that are then pushed upwards by another set forming below them, resulting in 4 parallel chains of dry "basidiospores".

Other variations occur, some as standard life-cycles (that themselves have variations within variations) within specific orders.

## **Rusts**

Rusts (Pucciniales, previously known as Uredinales) at their greatest complexity produce five different types of spores on two different hosts in two unrelated host families. Such rusts are heteroecious (requiring 2 hosts) and macrocyclic (producing all 5 spores types). Wheat stem rust is an example. By convention the stages and spore states are numbered by Roman numerals. Typically, basidiospores infect host one, the mycelium forms pycnidia, called spermagonia, which are miniature, flask-shaped, hollow, submicroscopic bodies embedded in host tissue (such as a leaf). This stage, numbered "0", produces single-celled, minute spores that ooze out in a sweet liquid and that act as nonmotile spermatia, and also protruding receptive hyphae. Insects and probably other vectors such as rain carry the spermatia from spermagonia to spermagonia, cross inoculating the mating types. Neither thallus is male or female. Once crossed, the dikaryons are established and a second spore stage is formed, numbered "I" and called aecia, which form dikaryotic aeciospores in dry chains in inverted cup-shaped bodies embedded in host tissue. These aeciospores then infect the second host genus and cannot infect the host on which they are formed (in macrocyclic rusts). On the second host a repeating spore stage is formed, numbered "II", the urediospores in dry pustules called uredinia. Urediospores are dikaryotic and can infect the same host that produced them. They repeatedly infect this host over the growing season. At the end of the season, a fourth spore type, the teliospore, is formed. It is thicker-walled and serves to overwinter or to survive other harsh conditions. It does not continue the infection process, rather it

remains dormant for a period and then germinates to form basidia (stage "IV"), sometimes called a promycelium. In the Pucciniales, the basidia are cylindrical and become 3-septate after meiosis, with each of the 4 cells bearing one basidiospore each. The basidiospores disperse and start the infection process on host 1 again. Autoecious rusts complete their life-cycles on one host instead of two, and **microcyclic** rusts cut out one or more stages.

## Smuts

The characteristic part of the life-cycle of smuts is the thick-walled, often darkly pigmented, ornate, teliospore that serves to survive harsh conditions such as overwintering and also serves to help disperse the fungus as dry diaspores. The teliospores are initially dikaryotic but become diploid via karyogamy. Meiosis takes place at the time of germination. A promycelium is formed that consists of a short hypha (equated to a basidium). In some smuts such as *Ustilago maydis* the nuclei migrate into the promycelium that becomes septate, and haploid yeast-like conidia/basidiospores sometimes called sporidia, bud off laterally from each cell. In various smuts, the yeast phase may proliferate, or they may fuse, or they may infect plant tissue and become hyphal. In other smuts, such as *Tilletia caries*, the elongated haploid basidiospores form apically, often in compatible pairs that fuse centrally resulting in "H"-shaped diaspores which are then dikaryotic. Dikaryotic conidia may then form. Eventually the host is infected by infectious hyphae. Teliospores form in host tissue. Many variations on these general themes occur.

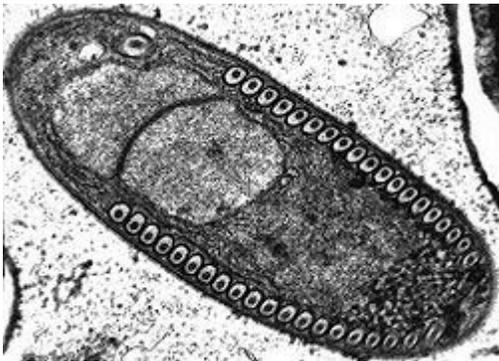
Smuts with both a yeast phase and an infectious hyphal state are examples of dimorphic Basidiomycota. In plant parasitic taxa, the saprotrophic phase is normally the yeast while the infectious stage is hyphal. However, there are examples of animal and human parasites where the species are dimorphic but it is the yeast-like state that is infectious. The genus *Filobasidiella* forms basidia on hyphae but the main infectious stage is more commonly known by the anamorphic yeast name *Cryptococcus*, e.g. *Cryptococcus neoformans* and *Cryptococcus gattii*.

The dimorphic Basidiomycota with yeast stages and the pleiomorphic rusts are examples of fungi with anamorphs, which are the asexual stages. Some Basidiomycota are only known as anamorphs. Many are yeasts, collectively called basidiomycetous yeasts to differentiate them from ascomycetous yeasts in the Ascomycota. Aside from yeast anamorphs, and uredinia, aecia and pycnidia, some Basidiomycota form other distinctive anamorphs as parts of their life-cycles. Examples are *Collybia tuberosa* with its apple-seed-shaped and coloured sclerotium, *Dendrocollybia racemosa* with its sclerotium and its *Tilachlidiopsis racemosa* conidia, *Armillaria* with their rhizomorphs, *Hohenbuehelia* with their *Nematoctonus* nematode infectious, state and the coffee leaf parasite, *Mycena citricolor* and its *Decapitatus flavidus* propagules called gemmae.

## Chapter 4

# Microsporidia

### Microsporidia



Sporoblast of  
*Fibrillanosema crangonycis*

### Scientific classification

Kingdom: Fungi  
Division: **Microsporidia**

### Classes and orders

Dihaplophasea  
Dissociodihaplophasida  
Meiodihaplophasida  
Haplophasea  
Chyridiopsida  
Glugeida

The **microsporidia** constitute a phylum of spore-forming unicellular parasites. They were once thought to be protists but are now known to be fungi. Loosely 1500 of the probably more than one million species are named now. Microsporidia are restricted to animal hosts, and all major groups of animals host microsporidia. Most infect insects, but they are also responsible for common diseases of crustaceans and fish. The distinguished species of microsporidia usually infect one specific host or a related group of hosts. Several species, most of which are opportunistic, also infect humans.

Approximately 10 percent of the species are parasites of vertebrates, including in humans.

After infection they influence their hosts in various ways and all organs and tissues are invaded. Some species are lethal, and a few are used in biological control of insect pests. Parasitic castration, gigantism, change of host sex are effects of microsporidian parasitism. In the most advanced cases of parasitism the microsporidium rules the host cell completely and controls its metabolism and reproduction, forming a xenoma. .

Replication takes place within the host's cells, which are infected by means of unicellular spores. These vary from 1-40  $\mu\text{m}$ , making them some of the smallest eukaryotes. They also have the smallest eukaryotic genomes.

Microsporidium was once the vernacular name for a member of the class Microsporea.



Xenoma on flatfish caused by *Glugea stephani*

### **Anatomy**

Microsporidia lack mitochondria and possess, instead, mitosomes. They also lack motile structures such as flagella.

Microsporidia produce highly resistant spores to survive outside the host for up to several years. Spore morphology is useful in distinguishing between different species. Spores of

most species are oval or pyriform, but rod-shaped or spherical spores are not unusual. A few genera produce spores of unique shape for the genus.

The spore is protected by a wall, consisting of three layers:

- an outer electron-dense *exospore*
- a median, wide and seemingly structureless *endospore*, containing chitin
- a thin internal *plasma membrane*

In most cases there are two closely associated nuclei, forming a *diplokaryon*, but sometimes there is only one.

The anterior half of the spore contains a harpoon-like apparatus with a long thread-like *polar filament*, which is coiled up in the posterior half of the spore. The anterior part of the polar filament is surrounded by a *polaroplast*, a lamella of membranes. Behind the polar filament there is a posterior *vacuole*.

## ***Infection***

In the gut of the host the spore germinates. It builds up osmotic pressure until its rigid wall ruptures at its thinnest point at the apex. The posterior vacuole swells, forcing the polar filament to rapidly eject the infectious content into the cytoplasm of the potential host. Simultaneously the material of the filament is rearranged to form a tube which functions as a hypodermic needle and penetrates the gut epithelium.

Once inside the host cell, a sporoplasm grows, dividing or forming a multinucleate plasmodium, before producing new spores. The life cycle varies considerably. Some have a simple asexual life cycle, while others have a complex life cycle involving multiple hosts and both asexual and sexual reproduction. Different types of spores may be produced at different stages, probably with different functions including autoinfection (transmission within a single host).

## ***Medical implications***

The microsporidia often cause chronic, debilitating diseases rather than lethal infections. Effects on the host include reduced longevity, fertility, weight, and general vigor. Vertical transmission of microsporidia is frequently reported. In the case of insect hosts, vertical transmission often occurs as transovarial transmission, where the microsporidian parasites pass from the ovaries of the female host into eggs and eventually multiply in the infected larvae. *Amblyospora salinaria* n. sp. which infects the mosquito *Culex salinarius* Coquillett, and *Amblyospora californica* which infects the mosquito *Culex tarsalis* Coquillett, provide typical examples of transovarial transmission of microsporidia.

Microsporidia, specifically the mosquito-infecting *Vavraia culicis*, are being explored as a possible 'evolution-proof' malaria-control method. Microsporidian infection of *Anopheles gambiae* (the principal vector of *Plasmodium falciparum* malaria) reduces malarial infection within the mosquito, and shortens the mosquito lifespan. As the

majority of malaria-infected mosquitoes naturally die before the malaria parasite is mature enough to transmit, any increase in mosquito mortality through microsporidian-infection may reduce malaria in humans.

## **Classification**

For some time microsporidia were considered as very primitive eukaryotes, especially because of the lack of mitochondria, and placed along with the other protozoa *diplomonads*, *parabasal* and *archamoebae* in the protist-group "**Archezoa**". More recent research has falsified this theory of early origin (for all of these). Yet microsporidia are proposed to be highly developed and specialized organisms, which just dispensed functions that are needed no longer, because they are supplied by the host. Furthermore, spore-forming organisms in general do have a complex system of reproduction, both sexual and asexual, which look far from primitive.

Nowadays microsporidia are placed within the Fungi or as a sister-group of the Fungi with a common ancestor.

Forming of clades is largely based on habitat and host. Three classes of Microsporidia are proposed by Vossbrinck and Debrunner-Vossbrinck, based on the habitat: Aquasporidia, Marinosporidia and Terresporidia.

One classification could be:

### 1. Subclass: *Dihaplophasea*

- - Order: *Meiodihaplophasida*
    - Superfamily *Thelohaniioidea*
      - Family *Thelohaniidae*
      - Family *Duboscqiidae*
      - Family *Janacekiidae*
      - Family *Pereziidae*
      - Family *Striatosporidae*
      - Family *Cylindrosporidae*
    - Superfamily *Burenelloidea*
      - Family *Burenellidae*
    - Superfamily *Amblyosporoidae*
      - Family *Amblyosporidae*
  - Order *Dissociodihaplophasida*
    - Superfamily *Nosematoidea*
      - Family *Nosematidae*
      - Family *Ichthyosporidiidae*
      - Family *Caudosporidae*
      - Family *Pseudopleistophoridae*
      - Family *Mrazekiidae*

- Superfamily *Culicosporoidea*
  - Family *Culicosporidae*
  - Family *Culicosporellidae*
  - Family *Golbergiidae*
  - Family *Spragueidae*
- Superfamily *Ovavesiculoidea*
  - Family *Ovavesiculidae*
  - Family *Tetramicridae*

## 2. Subclass *Haplophasea*

- - Order *Glugeida*
    - 
    - Family *Glugeidae*
    - Family *Pleistophoridae*
    - Family *Encephalitozoonidae*
    - Family *Abelsporidae*
    - Family *Tuzetiidae*
    - Family *Microfilidae*
    - Family *Unikaryonidae*
  - Order *Chytridiopsida*
    - 
    - Family *Chytridiopsida*
    - Family *Buxtehudiidae*
    - Family *Enterocytozoonidae*
    - Family *Burkeidae*

## Chapter 5

# Glomeromycota and Chytridiomycota

## Glomeromycota

**Glomeromycota** (informally **glomeromycetes**) is one of seven currently recognized phyla within the kingdom Fungi, with approximately 200 described species. Members of the Glomeromycota form arbuscular mycorrhizas (AMs) with the roots or thalli (e.g. in bryophytes) of land plants. *Geosiphon pyriformis* forms an endocytobiotic association with *Nostoc* cyanobacteria. AM formation has not yet been shown for all species. The majority of evidence shows that the Glomeromycota are obligate biotrophs, dependent on symbiosis with land plants (*Nostoc* in the case of *Geosiphon*) for carbon and energy, but there is recent circumstantial evidence that some species may be able to lead an independent existence. The arbuscular mycorrhizal species are terrestrial and widely distributed in soils worldwide where they form symbioses with the roots of the majority of plant species (>80%). They can also be found in wetlands, including salt-marshes, and associated with epiphytic plants.

### **Reproduction**

The Glomeromycota have generally coenocytic (occasionally sparsely septate) mycelia and reproduce asexually through blastic development of the hyphal tip to produce spores (Glomerospores) with diameters of 80-500 $\mu$ m. In some, complex spores form within a terminal saccule.

### **Phylogeny**

Initial studies of the Glomeromycota were based on the morphology of soil-borne sporocarps (spore clusters) found in or near colonized plant roots. Distinguishing features such as wall morphologies, size, shape, color, hyphal attachment and reaction to staining compounds allowed a phylogeny to be constructed. Superficial similarities led to the initial placement of genus *Glomus* in the unrelated family Endogonaceae. Following broader reviews that cleared up the sporocarp confusion, the Glomeromycota were first proposed in the genera *Acaulospora* and *Gigaspora* before being accorded their own

order with the three families Glomaceae (now Glomeraceae), Acaulosporaceae and Gigasporaceae.

With the advent of molecular techniques this classification has undergone major revision. An analysis of small subunit (SSU) rRNA sequences indicated that they share a common ancestor with the Dikarya.

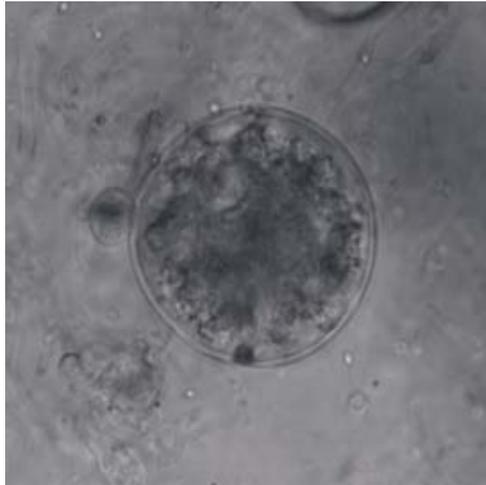
Several species which produce glomoid spores (i.e. spores similar to *Glomus*) in fact belong to other deeply divergent lineages and were placed in the orders, Paraglomerales and Archaeosporales. This new classification includes the Geosiphonaceae, which presently contains one fungus (*Geosiphon pyriformis*) that forms endosymbiotic associations with the cyanobacterium *Nostoc punctiforme* and produces spores typical to this phylum, in the Archaeosporales.

Work in this field is incomplete, and members of *Glomus* may be better suited to different genera or families.

### ***Molecular biology***

The biochemical and genetic characterization of the Glomeromycota has been hindered by their biotrophic nature, which impedes laboratory culturing. This obstacle was eventually surpassed with the use of root cultures. The first mycorrhizal gene to be sequenced was the small-subunit ribosomal RNA (SSU rRNA). This gene is highly conserved and commonly used in phylogenetic studies so was isolated from spores of each taxonomic group before amplification through the polymerase chain reaction (PCR). A molecular clock approach, based on the substitution rates of SSU sequences, was used to estimate the time of divergence of the fungi. The molecular analysis found that they are between 462 and 353 million years old. The data enforces the long-held theory that they were instrumental in the colonization of land by plants.

# Chytridiomycota



**Chytridiomycota** is a division of the Fungi kingdom. The name is derived from the Greek *chytridion*, meaning "little pot", describing the structure containing unreleased spores. In older classifications, chytrids (except the recently established order Spizellomycetales) were placed in the Class Phycomycetes under the subdivision Myxomycophyta of the Kingdom Fungi. Also, in an older and more restricted sense (not used here), the term "chytrids" referred just to those fungi in the order Chytridiales. The chytrids have also been included among the Protista, but are now regularly classed as fungi.

The chytrids are the most primitive of the fungi and are mostly saprobic (degrading chitin and keratin). The thalli are coenocytic and usually form no true mycelium (having rhizoids instead). Some species are unicellular. As with other fungi, the cell wall in chytrids is composed of chitin.

Many chytrids are aquatic (mostly found in fresh water). There are approximately 1,000 chytrid species, in 127 genera, distributed among 5 orders.

## ***Reproduction***

Both zoospores and gametes of the chytrids are mobile by their flagella, one whiplash per individual.

An example of a Chytrid species is the water mold - *Allomyces* sap, it is a saprotroph found in water or wet soil. The species has an interesting life cycle. The thallus (body) is attached by rhizoids, and has an erect trunk on which reproductive organs are formed at the end of branches. The life cycle has the ability to change from haploid and diploid generations. The haploid thallus forms male and female gametangia from which flagellated gametes are released and merge to form a Zygote. Gametes and female gametangia attract the opposite sex by producing pheromones. The germinated zygote

produces a diploid thallus with two sorts of sporangia; thin-walled zoosporangia which release diploid zoospores resulting in a diploid thalli and thick-walled sporangia which after meiosis release haploid zoospores which form haploid thalli.

### ***As a parasite***

The chytrid *Batrachochytrium dendrobatidis* (itself commonly known as "Chytrid") is responsible for a recently discovered disease of amphibians, chytridiomycosis. Discovered in 1998 in Australia and Panama this disease is known to kill amphibians in large numbers, and has been suggested as a principal cause for the worldwide amphibian decline. In one example an outbreak of the fungus was found responsible for killing much of the Kihansi Spray Toad population in its native habitat of Tanzania. The actual process leading to mortality is, however, unknown. A popular theory is the fungus hardens the skin of amphibians which hinders respiration.

Chytrids may also infect plant species; in particular, maize-attacking and alfalfa-attacking species have been described. *Synchytrium endobioticum* is an important potato pathogen.

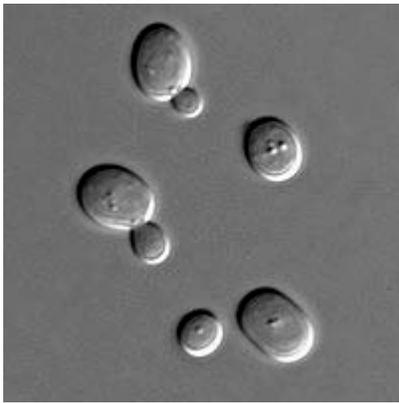
### ***Fossil record***

The earliest fossils of chytrids are from the Scottish Rhynie chert, a Devonian-age locality with anatomical preservation of plants and fungi. Among the microfossils are chytrids preserved as parasites on rhyniophytes. These fossils closely resemble the genus *Allomyces*.

## Chapter 6

# Yeast

### Yeast



Yeast of the species *Saccharomyces cerevisiae*

### Scientific classification

Domain: Eukaryota

Kingdom: Fungi

### Phyla and Subphyla

#### Ascomycota

- Saccharomycotina (true yeasts)
- Taphrinomycotina
  - Schizosaccharomycetes (fission yeasts)

#### Basidiomycota

- Agaricomycotina
  - Tremellomycetes
- Pucciniomycotina
  - Microbotryomycetes

**Yeasts** are eukaryotic micro-organisms classified in the kingdom Fungi, with the 1,500 species currently described estimated to be only 1% of all yeast species. Most reproduce asexually by budding, although a few do so by mitosis. Yeasts are unicellular, although some species with yeast forms may become multicellular through the formation of a string of connected budding cells known as pseudohyphae, or false hyphae, as seen in most molds. Yeast size can vary greatly depending on the species, typically measuring 3–4  $\mu\text{m}$  in diameter, although some yeasts can reach over 40  $\mu\text{m}$ .

The yeast species *Saccharomyces cerevisiae* has been used in baking and in fermenting alcoholic beverages for thousands of years. It is also extremely important as a model organism in modern cell biology research, and is one of the most thoroughly researched eukaryotic microorganisms. Researchers have used it to gather information about the biology of the eukaryotic cell and ultimately human biology. Other species of yeast, such as *Candida albicans*, are opportunistic pathogens and can cause infections in humans. Yeasts have recently been used to generate electricity in microbial fuel cells, and produce ethanol for the biofuel industry.

Yeasts do not form a single taxonomic or phylogenetic grouping. The term "yeast" is often taken as a synonym for *Saccharomyces cerevisiae*, but the phylogenetic diversity of yeasts is shown by their placement in two separate phyla, the Ascomycota and the Basidiomycota. The budding yeasts ("true yeasts") are classified in the order Saccharomycetales.

## **History**

The word "yeast" comes to us from Old English *gist*, *gyst*, and from the Indo-European root *yes-*, meaning *boil*, *foam*, or *bubble*. Yeast microbes are probably one of the earliest domesticated organisms. People have used yeast for fermentation and baking throughout history. Archaeologists digging in Egyptian ruins found early grinding stones and baking chambers for yeasted bread, as well as drawings of 4,000-year-old bakeries and breweries. In 1680, the Dutch naturalist Anton van Leeuwenhoek first microscopically observed yeast, but at the time did not consider them to be living organisms, but rather globular structures. In 1857, French microbiologist Louis Pasteur proved in the paper "*Mémoire sur la fermentation alcoolique*" that alcoholic fermentation was conducted by living yeasts and not by a chemical catalyst. Pasteur showed that by bubbling oxygen into the yeast broth, cell growth could be increased, but fermentation was inhibited – an observation later called the "Pasteur effect".

By the late 18th century, two yeast strains used in brewing had been identified: *Saccharomyces cerevisiae*, so called top fermenting yeast, and *S. carlsbergensis*, bottom fermenting yeast. *S. cerevisiae* has been sold commercially by the Dutch for bread making since 1780; while around 1800, the Germans started producing *S. cerevisiae* in the form of cream. In 1825 a method was developed to remove the liquid so the yeast could be prepared as solid blocks. The industrial production of yeast blocks was enhanced by the introduction of the filter press in 1867. In 1872, Baron Max de Springer developed a manufacturing process to create granulated yeast, a technique that was used

until the first World War. In the United States, naturally occurring airborne yeasts were used almost exclusively until commercial yeast was marketed at the Centennial Exposition in 1876 in Philadelphia, where Charles L. Fleischmann exhibited the product and a process to use it, as well as serving the resultant baked bread.

## **Nutrition and growth**

Yeasts are chemoorganotrophs, as they use organic compounds as a source of energy and do not require sunlight to grow. Carbon is obtained mostly from hexose sugars, such as glucose and fructose, or disaccharides such as sucrose and maltose. Some species can metabolize pentose sugars like ribose, alcohols, and organic acids. Yeast species either require oxygen for aerobic cellular respiration (obligate aerobes), or are anaerobic, but also have aerobic methods of energy production (facultative anaerobes). Unlike bacteria, there are no known yeast species that grow only anaerobically (obligate anaerobes). Yeasts grow best in a neutral or slightly acidic pH environment.

Yeasts vary in what temperature range they grow best. For example, *Leucosporidium frigidum* grows at -2 to 20 °C (28 to 68 °F), *Saccharomyces telluris* at 5 to 35 °C (41 to 95 °F) and *Candida slooffi* at 28 to 45 °C (82 to 113 °F). The cells can survive freezing under certain conditions, with viability decreasing over time.

Yeasts are generally grown in the laboratory on solid growth media or in liquid broths. Common media used for the cultivation of yeasts include potato dextrose agar (PDA) or potato dextrose broth, Wallerstein Laboratories nutrient (WLN) agar, yeast peptone dextrose agar (YPD), and yeast mould agar or broth (YM). Home brewers who cultivate yeast frequently use dried malt extract (DME) and agar as a solid growth medium. The antibiotic cycloheximide is sometimes added to yeast growth media to inhibit the growth of *Saccharomyces* yeasts and select for wild/indigenous yeast species. This will change the yeast process.

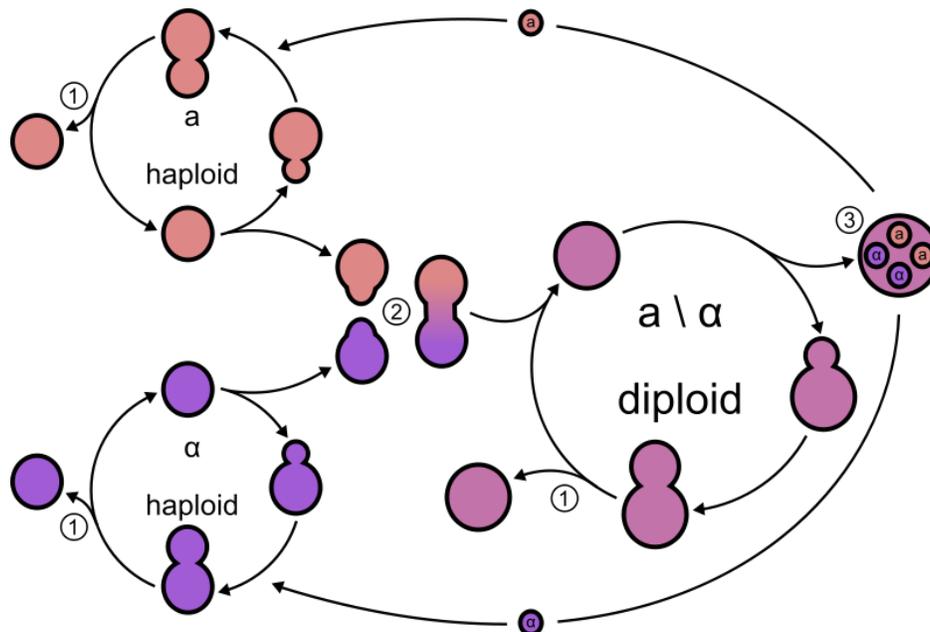
The appearance of a white, thready yeast, commonly known as kahm yeast, is often a byproduct of the lactofermentation (or pickling) of certain vegetables, usually the result of exposure to air. Although harmless, it can give pickled vegetables a bad flavour and so must be removed regularly during fermentation.

## **Ecology**

Yeasts are very common in the environment, but are usually isolated from sugar-rich material. Examples include naturally occurring yeasts on the skins of fruits and berries (such as grapes, apples or peaches), and exudates from plants (such as plant saps or cacti). Some yeasts are found in association with soil and insects. The ecological function and biodiversity of yeasts are relatively unknown compared to those of other microorganisms. Yeasts, including *Candida albicans*, *Rhodotorula rubra*, *Torulopsis* and *Trichosporon cutaneum*, have been found living in between people's toes as part of their skin flora. Yeasts are also present in the gut flora of mammals and some insects and even deep-sea environments host an array of yeasts.

An Indian study of seven bee species and 9 plant species found 45 species from 16 genera colonise the nectaries of flowers and honey stomachs of bees. Most were members of the *Candida* genus; the most common species in honey stomachs was *Dekkera intermedia* and in flower nectaries, *Candida blankii*. Yeast colonising nectaries of the stinking hellebore have been found to raise the temperature of the flower, which may aid in attracting pollinators by increasing the evaporation of volatile organic compounds. A black yeast has been recorded as a partner in a complex relationship between ants, their mutualistic fungus, a fungal parasite of the fungus and a bacterium that kills the parasite. The yeast have a negative effect on the bacteria that normally produce antibiotics to kill the parasite and so may affect the ants' health by allowing the parasite to spread.

## Reproduction



The yeast cell's life cycle:

1. Budding
2. Conjugation
3. Spore

Yeasts have asexual and sexual reproductive cycles. The most common mode of vegetative growth in yeast is asexual reproduction by budding. Here a small bud, or daughter cell, is formed on the parent cell. The nucleus of the parent cell splits into a daughter nucleus and migrates into the daughter cell. The bud continues to grow until it separates from the parent cell, forming a new cell. Some yeasts, including *Schizosaccharomyces pombe*, reproduce by mitosis instead of budding.

Under high stress conditions, haploid cells will generally die; under the same conditions, however, diploid cells can undergo sporulation, entering sexual reproduction (meiosis) and producing a variety of haploid spores, which can go on to mate (conjugate), reforming the diploid.

## Uses

The useful physiological properties of yeast have led to their use in the field of biotechnology. Fermentation of sugars by yeast is the oldest and largest application of this technology. Many types of yeasts are used for making many foods: baker's yeast in bread production; brewer's yeast in beer fermentation; yeast in wine fermentation and for xylitol production. So-called red rice yeast is actually a mold, *Monascus purpureus*. Yeasts include some of the most widely used model organisms for genetics and cell biology.

## Alcoholic beverages

Alcoholic beverages are defined as beverages that contain ethanol ( $C_2H_5OH$ ). This ethanol is almost always produced by fermentation – the metabolism of carbohydrates by certain species of yeast under anaerobic or low-oxygen conditions. Beverages such as wine, beer, or distilled spirits all use yeast at some stage of their production. A distilled beverage is a beverage containing ethanol that has been purified by distillation. Carbohydrate-containing plant material is fermented by yeast, producing a dilute solution of ethanol in the process. Spirits such as whiskey and rum are prepared by distilling these dilute solutions of ethanol. Components other than ethanol are collected in the condensate, including water, esters, and other alcohols, which account for the flavour of the beverage.

## Beer



Beer being fermented by brewers yeast

Brewing yeasts may be classed as "top cropping" (or "top fermenting") and "bottom cropping" (or "bottom-fermenting"). Top cropping yeasts are so called because they form a foam at the top of the wort during fermentation. An example of a top cropping yeast is *Saccharomyces cerevisiae*, sometimes called an "ale yeast". Bottom cropping yeasts are typically used to produce lager-type beers, though they can also produce ale-type beers. These yeasts ferment more sugars, creating a dryer beer, and grow well at low temperatures. An example of bottom cropping yeast is *Saccharomyces pastorianus*, formerly known as *S. carlsbergensis*.

The most common top cropping brewer's yeast, *S. cerevisiae*, is the same species as the common baking yeast. However, baking and brewing yeasts typically belong to different strains, cultivated to favour different characteristics: baking yeast strains are more aggressive, to carbonate dough in the shortest amount of time possible; brewing yeast strains act slower, but tend to produce fewer off-flavours and tolerate higher alcohol concentrations (with some strains, up to 22%).

*Brettanomyces* is a genus of wild yeast important in brewing lambic, a beer produced not by the deliberate addition of brewer's yeasts, but by spontaneous fermentation by wild yeasts and bacteria. *Brettanomyces lambicus*, *B. bruxellensis* and *B. claussenii* are native to the Senne Valley region of Belgium, where lambic beer is produced.

## Wine



Fresh grapes with visible bloom.

Yeast is used in winemaking, where it converts the sugars present in grape juice (must) into ethanol. Yeast is normally already present on grape skins (the white powder called "the bloom"). Fermentation can be done with this endogenous "wild yeast," but this procedure gives unpredictable results, which depend upon the exact types of yeast species present. For this reason, a pure yeast culture is usually added to the must; this yeast quickly dominates the fermentation. The wild yeasts are repressed, which ensures a reliable and predictable fermentation.

Most added wine yeasts are strains of *S. cerevisiae*, though not all strains of the species are suitable. Different *S. cerevisiae* yeast strains have differing physiological and fermentative properties, therefore the actual strain of yeast selected can have a direct impact on the finished wine. Significant research has been undertaken into the development of novel wine yeast strains that produce atypical flavour profiles or increased complexity in wines.

The growth of some yeasts, such as *Zygosaccharomyces* and *Brettanomyces*, in wine can result in wine faults and subsequent spoilage. *Brettanomyces* produces an array of metabolites when growing in wine, some of which are volatile phenolic compounds. Together, these compounds are often referred to as "*Brettanomyces* character", and are often described as "antiseptic" or "barnyard" type aromas. *Brettanomyces* is a significant contributor to wine faults within the wine industry.

Researchers from University of British Columbia, Canada, have found a new strain of yeast that has reduced amines. The amines in red wine and Chardonnay produce off-flavors and cause headaches and hypertension in some people. About 30 percent of people are sensitive to biogenic amines, such as histamines.

## **Baking**

Yeast, most commonly *S. cerevisiae*, is used in baking as a leavening agent, where it converts the fermentable sugars present in dough into the gas carbon dioxide. This causes the dough to expand or rise as gas forms pockets or bubbles. When the dough is baked, the yeast dies and the air pockets "set", giving the baked product a soft and spongy texture. The use of potatoes, water from potato boiling, eggs, or sugar in a bread dough accelerates the growth of yeasts. Most yeasts used in baking are of the same species common in alcoholic fermentation. Additionally, *Saccharomyces exiguus* (also known as *S. minor*), a wild yeast found on plants, fruits, and grains, is occasionally used for baking. Sugar and vinegar provide the best conditions for yeast to ferment. In bread making, the yeast initially respire aerobically, producing carbon dioxide and water. When the oxygen is depleted, anaerobic respiration begins, producing ethanol as a waste product; however, this evaporates during baking.



A block of fresh yeast

It is not known when yeast was first used to bake bread. The first records that show this use came from Ancient Egypt. Researchers speculate a mixture of flour meal and water was left longer than usual on a warm day and the yeasts that occur in natural contaminants of the flour caused it to ferment before baking. The resulting bread would have been lighter and tastier than the normal flat, hard cake.



Active dried yeast, a granulated form in which yeast is commercially sold

Today, there are several retailers of baker's yeast; one of the best-known in North America is Fleischmann's Yeast, which was developed in 1868. During World War II, Fleischmann's developed a granulated active dry yeast, which did not require refrigeration and had a longer shelf life than fresh yeast. The company created yeast that would rise twice as fast, reducing baking time. Baker's yeast is also sold as a fresh yeast compressed into a square "cake". This form perishes quickly, and must therefore be used soon after production. A weak solution of water and sugar can be used to determine if yeast is expired. In the solution, active yeast will foam and bubble as it ferments the sugar into ethanol and carbon dioxide. Some recipes refer to this as proofing the yeast as it "proves" (tests) the viability of the yeast before the other ingredients are added. When using a sourdough starter, flour and water are added instead of sugar; this is referred to as proofing the sponge.

When yeast is used for making bread, it is mixed with flour, salt, and warm water or milk. The dough is kneaded until it is smooth, and then left to rise, sometimes until it has doubled in size. Some bread doughs are knocked back after one rising and left to rise again. A longer rising time gives a better flavour, but the yeast can fail to raise the bread in the final stages if it is left for too long initially. The dough is then shaped into loaves, left to rise until it is the correct size, and then baked. Dried yeast is usually specified for use in a bread machine, however a (wet) sourdough starter can also work.

## **Bioremediation**

Some yeasts can find potential application in the field of bioremediation. One such yeast, *Yarrowia lipolytica*, is known to degrade palm oil mill effluent, TNT (an explosive material), and other hydrocarbons, such as alkanes, fatty acids, fats and oils. It can also tolerate high concentrations of salt and heavy metals, and is being investigated for its potential as a heavy metal biosorbent.

## **Industrial ethanol production**

The ability of yeast to convert sugar into ethanol has been harnessed by the biotechnology industry to produce ethanol fuel. The process starts by milling a feedstock, such as sugar cane, field corn, or other cereal grains, and then adding dilute sulfuric acid, or fungal alpha amylase enzymes, to break down the starches into complex sugars. A glucoamylase is then added to break the complex sugars down into simple sugars. After this, yeasts are added to convert the simple sugars to ethanol, which is then distilled off to obtain ethanol up to 96% in concentration.

*Saccharomyces* yeasts have been genetically engineered to ferment xylose, one of the major fermentable sugars present in cellulosic biomasses, such as agriculture residues, paper wastes, and wood chips. Such a development means ethanol can be efficiently produced from more inexpensive feedstocks, making cellulosic ethanol fuel a more competitively priced alternative to gasoline fuels.

## Nonalcoholic beverages



A Kombucha culture fermenting in a jar

Root beer and other sweet carbonated beverages can be produced using the same methods as beer, except the fermentation is stopped sooner, producing carbon dioxide, but only trace amounts of alcohol, and a significant amount of sugar is left in the drink. *Kvass*, a fermented drink made from rye, is popular in Eastern Europe; it has a recognizable, but low alcoholic content. Yeast in symbiosis with acetic acid bacteria is used in the preparation of *kombucha*, a fermented sweetened tea. Species of yeast found in the tea can vary, and may include: *Brettanomyces bruxellensis*, *Candida stellata*, *Schizosaccharomyces pombe*, *Torulasporea delbrueckii* and *Zygosaccharomyces bailii*. *Kombucha* is a popular beverage in Eastern Europe and some former Soviet republics

under the name *chajnyj grib* (Чайный гриб). *Kefir* and *kumis* are made by fermenting milk with yeast and bacteria.

## Nutritional supplements

Yeast is used in nutritional supplements popular with vegans and the health conscious, where it is often referred to as "nutritional yeast". It is a deactivated yeast, usually *S. cerevisiae*. It is an excellent source of protein and vitamins, especially the B-complex vitamins, whose functions are related to metabolism, as well as other minerals and cofactors required for growth. It is also naturally low in fat and sodium. Some brands of nutritional yeast, though not all, are fortified with vitamin B<sub>12</sub>, which is produced separately by bacteria. Nutritional yeast, though it has a similar appearance to brewer's yeast, is very different and has a very different taste.

Nutritional yeast has a nutty, cheesy, creamy flavor which makes it popular as an ingredient in cheese substitutes. It is often used by vegans in place of Parmesan cheese. Another popular use is as a topping for popcorn. It can also be used in mashed and fried potatoes, as well as in scrambled eggs. It comes in the form of flakes, or as a yellow powder similar in texture to cornmeal, and can be found in the bulk aisle of most natural food stores. In Australia, it is sometimes sold as "savory yeast flakes". Though "nutritional yeast" usually refers to commercial products, inadequately fed prisoners have used "home-grown" yeast to prevent vitamin deficiency.

## Probiotics

Some probiotic supplements use the yeast *S. boulardii* to maintain and restore the natural flora in the gastrointestinal tract. *S. boulardii* has been shown to reduce the symptoms of acute diarrhea in children, prevent reinfection of *Clostridium difficile*, reduce bowel movements in diarrhea-predominant IBS patients, and reduce the incidence of antibiotic, traveler's, and HIV/AIDS associated diarrheas.

## Aquarium hobby

Yeast is often used by aquarium hobbyists to generate carbon dioxide (CO<sub>2</sub>) to nourish plants in planted aquariums. A homemade setup is widely used as a cheap and simple alternative to pressurized CO<sub>2</sub> systems. While not as effective as these, the homemade setup is considerably cheaper for less demanding hobbyists.

There are several recipes for homemade CO<sub>2</sub>, but they are variations of the basic recipe: Baker's yeast, with sugar, baking soda and water, are added to a plastic bottle. A few drops of vegetable oil at the start reduces surface tension and speeds the release of CO<sub>2</sub>. This will produce CO<sub>2</sub> for about 2 or 3 weeks; the use of a bubble counter determines production. The CO<sub>2</sub> is injected in the aquarium via a narrow hose and released through a diffuser that helps dissolve the gas in the water. The CO<sub>2</sub> is used by plants in the photosynthesis process.

## Science

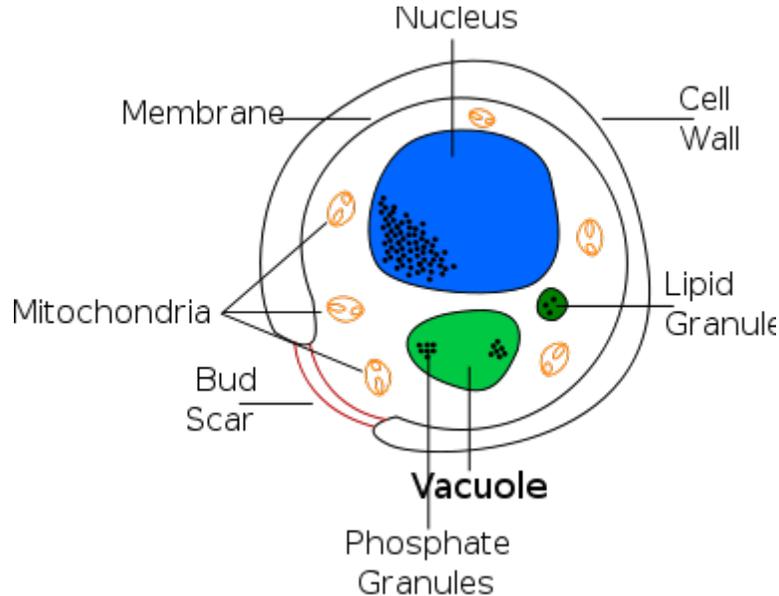


Diagram showing a yeast cell

Several yeasts, particularly *S. cerevisiae*, have been widely used in genetics and cell biology. This is largely because *S. cerevisiae* is a simple eukaryotic cell, serving as a model for all eukaryotes, including humans for the study of fundamental cellular processes such as the cell cycle, DNA replication, recombination, cell division and metabolism. Also, yeasts are easily manipulated and cultured in the laboratory, which has allowed for the development of powerful standard techniques, such as yeast two-hybrid, synthetic genetic array analysis and tetrad analysis. Many proteins important in human biology were first discovered by studying their homologues in yeast; these proteins include cell cycle proteins, signaling proteins, and protein-processing enzymes.

On 24 April 1996 *S. cerevisiae* was announced to be the first eukaryote to have its genome, consisting of 12 million base pairs, fully sequenced as part of the Genome project. At the time, it was the most complex organism to have its full genome sequenced, and took seven years and the involvement of more than 100 laboratories to accomplish. The second yeast species to have its genome sequenced was *Schizosaccharomyces pombe*, which was completed in 2002. It was the sixth eukaryotic genome sequenced and consists of 13.8 million base pairs.

## Yeast extract



Marmite and Vegemite have a distinctive dark colour

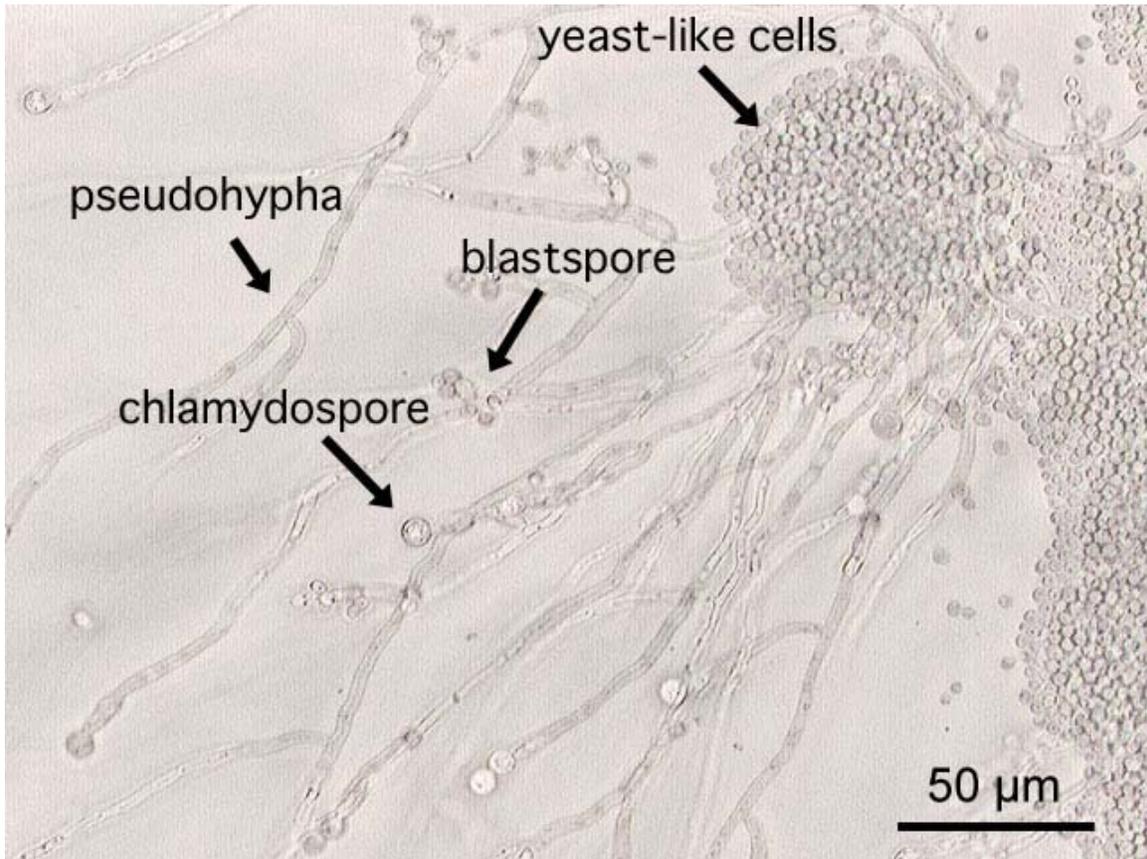


Marmite and Vegemite, products made from yeast extract

Yeast extract is the common name for various forms of processed yeast products that are used as food additives or flavours. They are often used in the same way that monosodium glutamate (MSG) is used, and like MSG, often contain free glutamic acid. The general method for making yeast extract for food products such as Vegemite and Marmite on a commercial scale is to add salt to a suspension of yeast making the solution hypertonic, which leads to the cells shrivelling up. This triggers *autolysis*, where the yeast's digestive enzymes break their own proteins down into simpler compounds, a process of self-

destruction. The dying yeast cells are then heated to complete their breakdown, after which the husks (yeast with thick cell walls which would give poor texture) are separated. Yeast autolysates are used in Vegemite and Promite (Australia); Marmite, Bovril and Oxo (the United Kingdom, Republic of Ireland and South Africa); and Cenovis (Switzerland).

### **Pathogenic yeasts**



A photomicrograph of *Candida albicans* showing hyphal outgrowth and other morphological characteristics.

Some species of yeast are opportunistic pathogens where they can cause infection in people with compromised immune systems.

*Cryptococcus neoformans* is a significant pathogen of immunocompromised people causing the disease termed cryptococcosis. This disease occurs in about 7–9% of AIDS patients in the USA, and a slightly smaller percentage (3–6%) in western Europe. The cells of the yeast are surrounded by a rigid polysaccharide capsule, which helps to prevent them from being recognised and engulfed by white blood cells in the human body.

Yeasts of the *Candida* genus are another group of opportunistic pathogens which causes oral and vaginal infections in humans, known as candidiasis. *Candida* is commonly found

as a commensal yeast in the mucus membranes of humans and other warm-blooded animals. However, sometimes these same strains can become pathogenic. Here the yeast cells sprout a hyphal outgrowth, which locally penetrates the mucosal membrane, causing irritation and shedding of the tissues. The pathogenic yeasts of candidiasis in probable descending order of virulence for humans are: *C. albicans*, *C. tropicalis*, *C. stellatoidea*, *C. glabrata*, *C. krusei*, *C. parapsilosis*, *C. guilliermondii*, *C. viswanathii*, *C. lusitaniae* and *Rhodotorula mucilaginosa*. *Candida glabrata* is the second most common *Candida* pathogen after *C. albicans*, causing infections of the urogenital tract, and of the bloodstream (candidemia).

### **Food spoilage**

Yeasts are able to grow in foods with a low pH, (5.0 or lower) and in the presence of sugars, organic acids and other easily metabolized carbon sources. During their growth, yeasts metabolize some food components and produce metabolic end products. This causes the physical, chemical, and sensible properties of a food to change, and the food is spoiled. The growth of yeast within food products is often seen on their surface, as in cheeses or meats, or by the fermentation of sugars in beverages, such as juices, and semi-liquid products, such as syrups and jams. The yeast of the *Zygosaccharomyces* genus have had a long history as a spoilage yeast within the food industry. This is mainly due to the fact that these species can grow in the presence of high sucrose, ethanol, acetic acid, sorbic acid, benzoic acid, and sulfur dioxide concentrations, representing some of the commonly used food preservation methods. Methylene blue is used to test for the presence of live yeast cells.

## Chapter 7

# Mold

**Molds** are fungi that grow in the form of multicellular filaments called hyphae. In contrast, microscopic fungi that grow as single cells are called yeasts. A connected network of these tubular branching hyphae has multiple, genetically identical nuclei and is considered a single organism, referred to as a colony or in more technical terms a mycelium.

Molds do not form a specific taxonomic or phylogenetic grouping, but can be found in the divisions *Zygomycota*, *Deuteromycota* and *Ascomycota*. Some molds cause disease or food spoilage, others play an important role in biodegradation or in the production of various foods, beverages, antibiotics and enzymes.

### **Biology**

There are thousands of known species of molds which include opportunistic pathogens, saprotrophs, aquatic species, and thermophiles. Like all fungi, molds derive energy not through photosynthesis but from the organic matter in which they live. Typically, molds secrete hydrolytic enzymes, mainly from the hyphal tips. These enzymes degrade complex biopolymers such as starch, cellulose and lignin into simpler substances which can be absorbed by the hyphae. In this way, molds play a major role in causing decomposition of organic material, enabling the recycling of nutrients throughout ecosystems. Many molds also secrete mycotoxins which, together with hydrolytic enzymes, inhibit the growth of competing microorganisms.

Molds reproduce through small spores, which may contain a single nucleus or be multinucleate. Mold spores can be asexual (the products of mitosis) or sexual (the products of meiosis); many species can produce both types. Mold spores may remain airborne indefinitely, may cling to clothing or fur, or may be able to survive extremes of temperature and pressure.

Although molds grow on dead organic matter everywhere in nature, their presence is only visible to the unaided eye when mold colonies grow. A mold colony does not comprise

discrete organisms, but an interconnected network of hyphae called a mycelium. Nutrients and in some cases organelles may be transported throughout the mycelium. In artificial environments like buildings, humidity and temperature are often stable enough to foster the growth of mold colonies, commonly seen as a downy or furry coating growing on food or other surfaces.

Many molds can begin growing at 4 °C (39 °F), the temperature within a typical refrigerator, or less. When conditions do not enable growth, molds may remain alive in a dormant state depending on the species, within a large range of temperatures before they die. The many different mold species vary enormously in their tolerance to temperature and humidity extremes. Certain molds can survive harsh conditions such as the snow-covered soils of Antarctica, refrigeration, highly acidic solvents, and even petroleum products such as jet fuel.

Xerophilic molds use the humidity in the air as their only water source; other molds need more moisture. Mold has a musty odor.

### ***Common molds***

- Acremonium
- Aspergillus
- Cladosporium
- Fusarium
- Mucor
- Penicillium
- Rhizopus
- Stachybotrys
- Trichoderma

### ***Uses***

#### **Food production**

Cultured molds are used in the production of foods, including:

- cheese (*Penicillium* spp.)
- tempeh (*Rhizopus oligosporus*)
- oncom (*Neurospora sitophila*)
- Quorn (*Fusarium venenatum*)
- bread
- beer
- some sausages
- soy sauce

The *koji* molds are a group of *Aspergillus* species, notably *Aspergillus oryzae*, that have been cultured in eastern Asia for many centuries. They are used to ferment a soybean and

wheat mixture to make soybean paste and soy sauce. They are also used to break down the starch in rice (saccharification) in the production of *sake* and other distilled spirits.

Red rice yeast is a product of the mold *Monascus purpureus* grown on rice, and is common in Asian diets. The yeast contains several compounds collectively known as monacolins, which are known to inhibit cholesterol synthesis. According to a study published in the journal *Mayo Clinic Proceedings* by Dr. David Becker, red rice yeast used as a dietary supplement, combined with fish oil and healthy lifestyle changes, may help reduce "bad" cholesterol as effectively as certain commercial statin drugs.

## **Drug creation**

Alexander Fleming's famous discovery of the antibiotic penicillin involved the mold *Penicillium chrysogenum*.

Several cholesterol-lowering drugs (such as Lovastatin, from *Aspergillus terreus*) are derived from molds.

The immunosuppressant drug cyclosporine, used to suppress the rejection of transplanted organs, is derived from the mold *Tolypocladium inflatum*.

## **Health effects**

Molds are ubiquitous in nature, and mold spores are a common component of household and workplace dust. However, when mold spores are present in large quantities, they can present a health hazard to humans, potentially causing allergic reactions and respiratory problems.

Some molds also produce mycotoxins that can pose serious health risks to humans and animals. Some studies claim that exposure to high levels of mycotoxins can lead to neurological problems and in some cases death. Prolonged exposure, e.g. daily workplace exposure, may be particularly harmful. Research on the health effects of mold has not been conclusive. The term "toxic mold" refers to molds that produce mycotoxins, such as *Stachybotrys chartarum*, and not to all molds in general.

Mold in the home can usually be found in damp, dark or steam filled areas e.g. bathroom or kitchen, cluttered storage areas, recently flooded areas, basement areas, plumbing spaces, areas with poor ventilation and outdoors in humid environments. Symptoms caused by mold allergy are watery, itchy eyes, a chronic cough, headaches or migraines, difficulty breathing, rashes, tiredness, sinus problems, nasal blockage and frequent sneezing.

## **Growth in buildings and homes**

Mold growth in buildings can lead to a variety of health issues. Various practices can be followed to mitigate mold issues in buildings, the most important of which is to reduce

moisture levels that can facilitate mold growth. Removal of affected materials after the source of moisture has been reduced and/or eliminated may be necessary for remediation.



Bread mold is one of the most common types of mold, and can cover a loaf of bread in less than three days.



Mold covering a decaying peach over a period of six days. The frames were taken approximately 12 hours apart. There are 12 frames of changes.



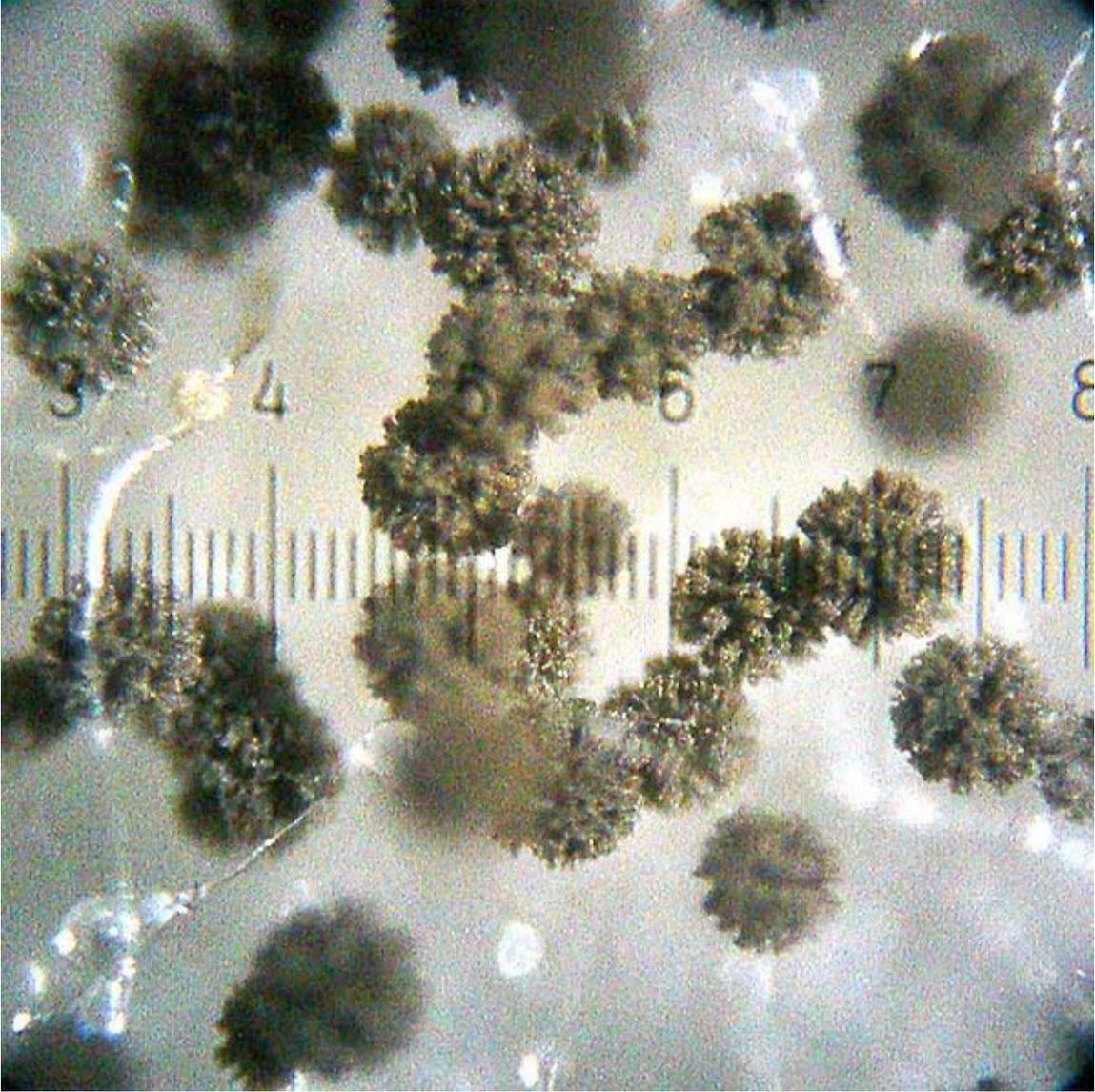
Moldy nectarines that were in a refrigerator. The nectarine with black mold is also affecting the nectarine underneath.



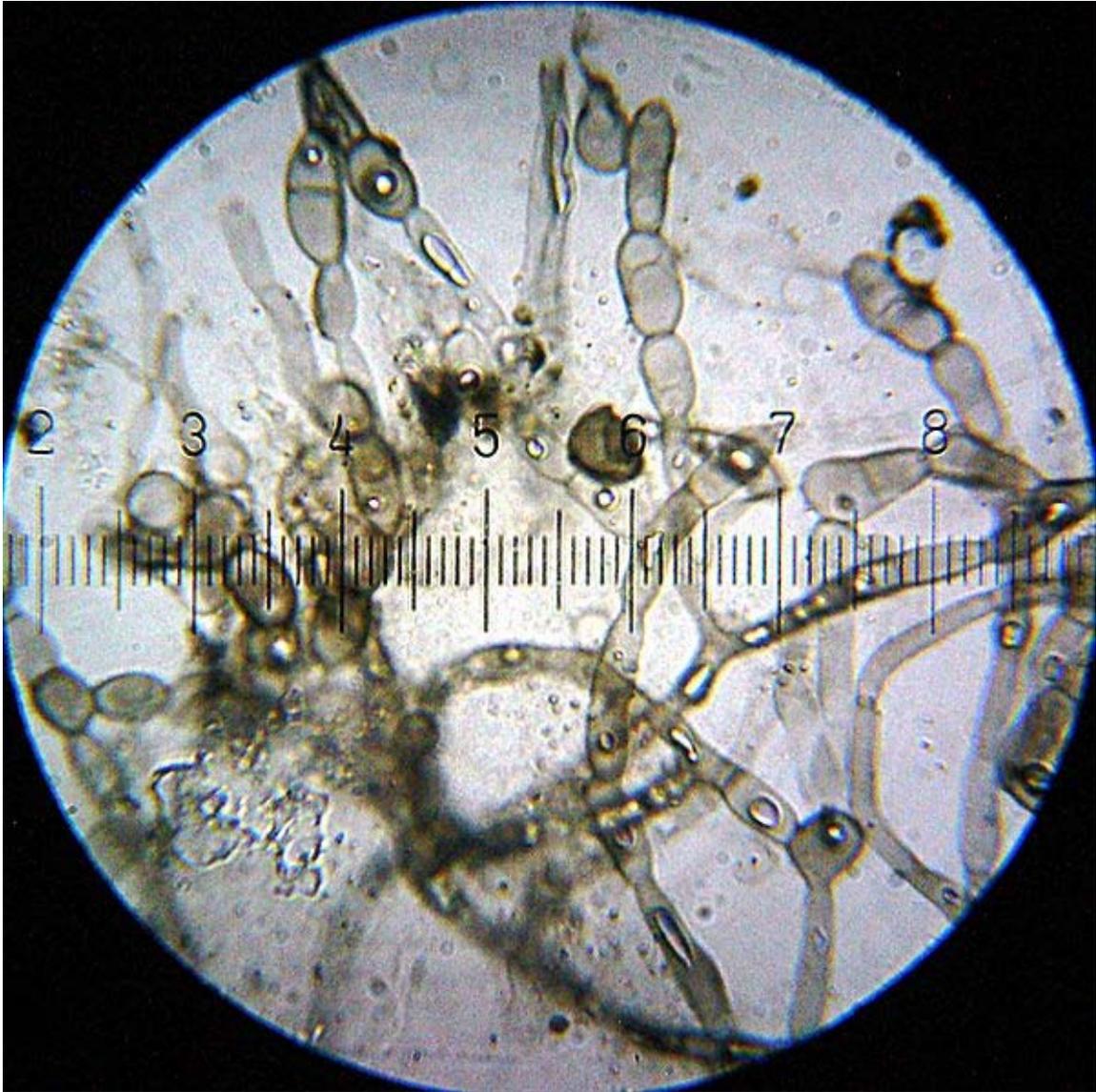
A bowl of moldy strawberries after being left in a room for several days.



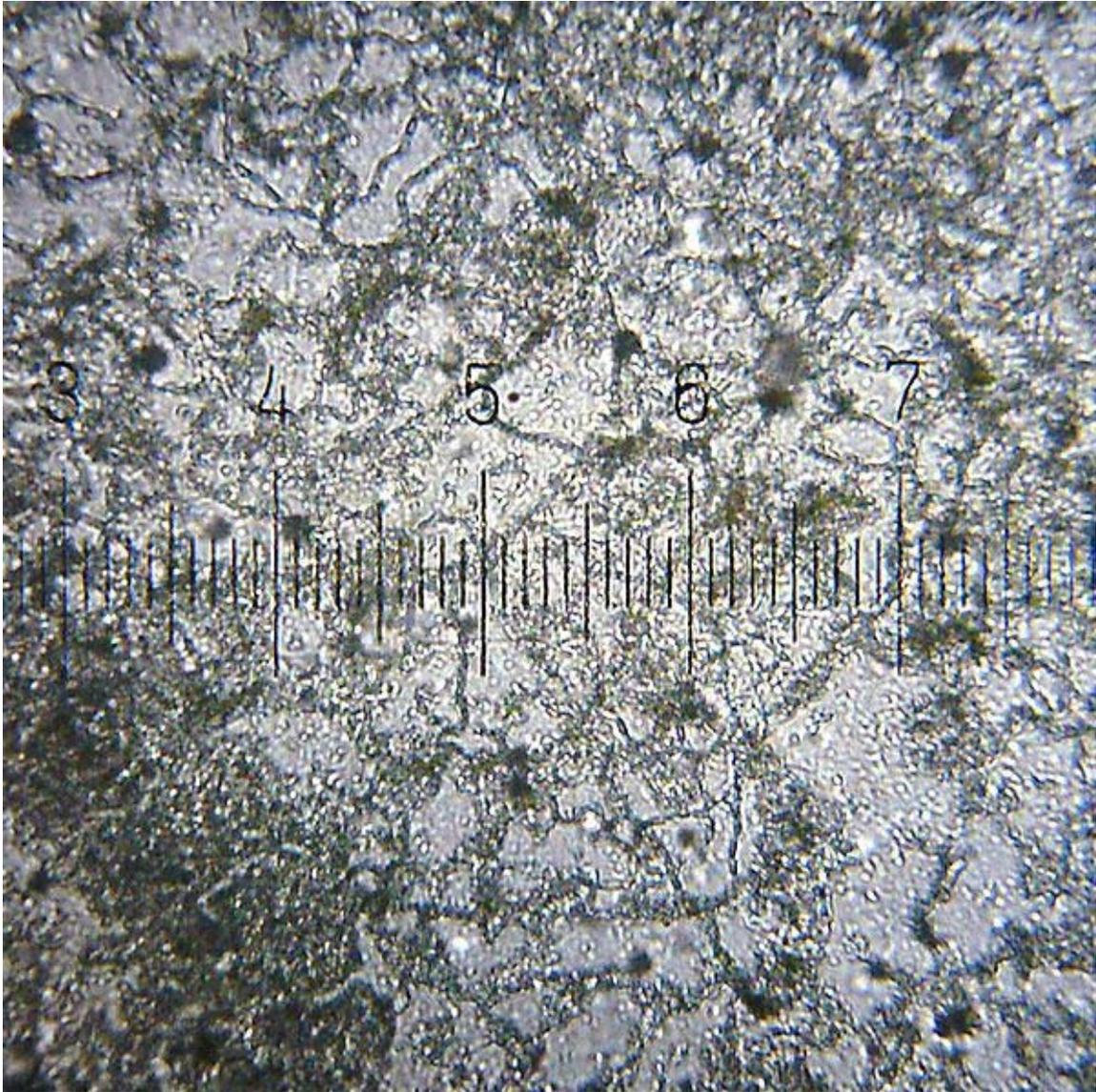
Mold cultured from dust shaken from an automotive cabin air filter



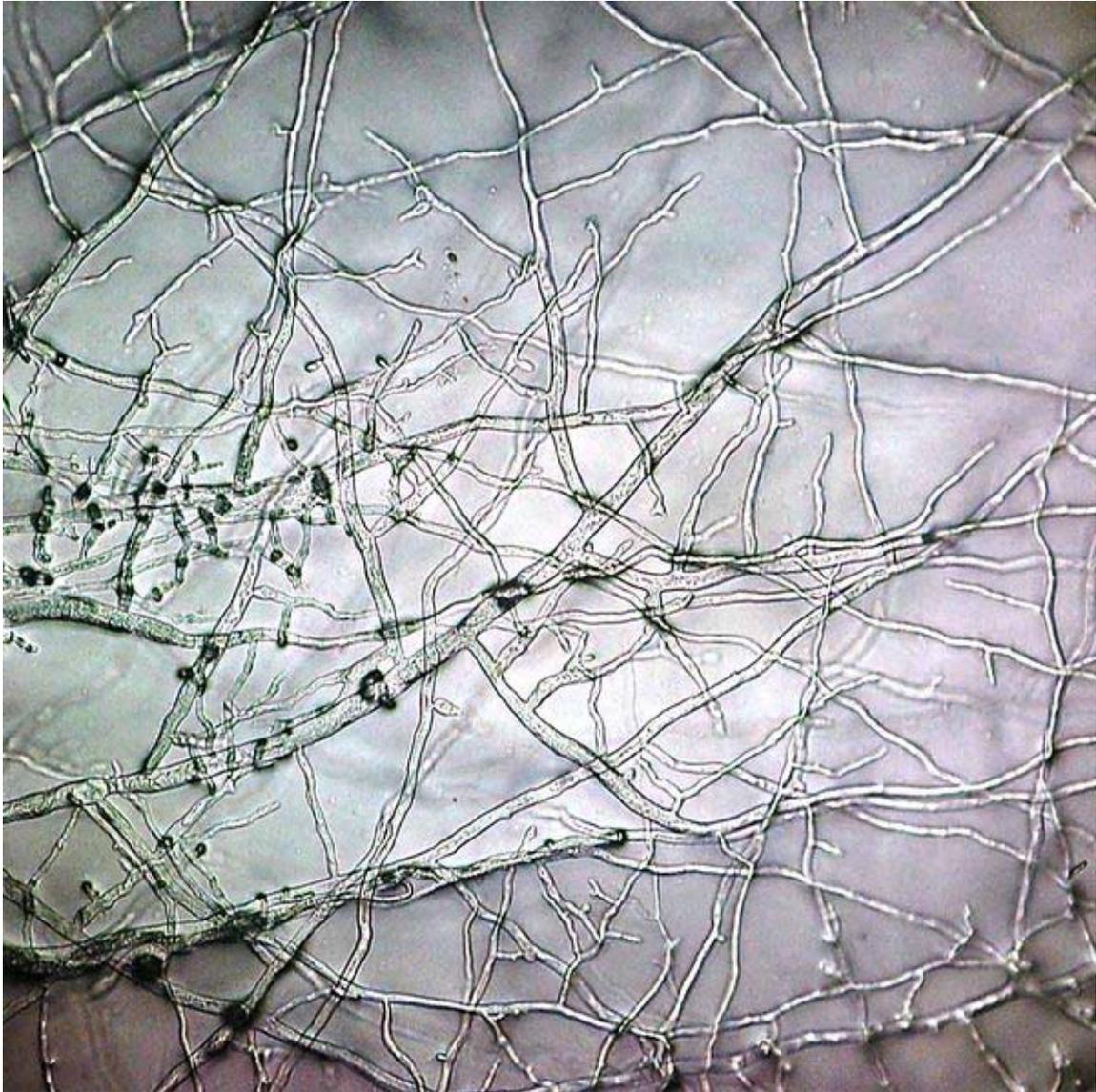
Mold grown from a nasal mucus sample.



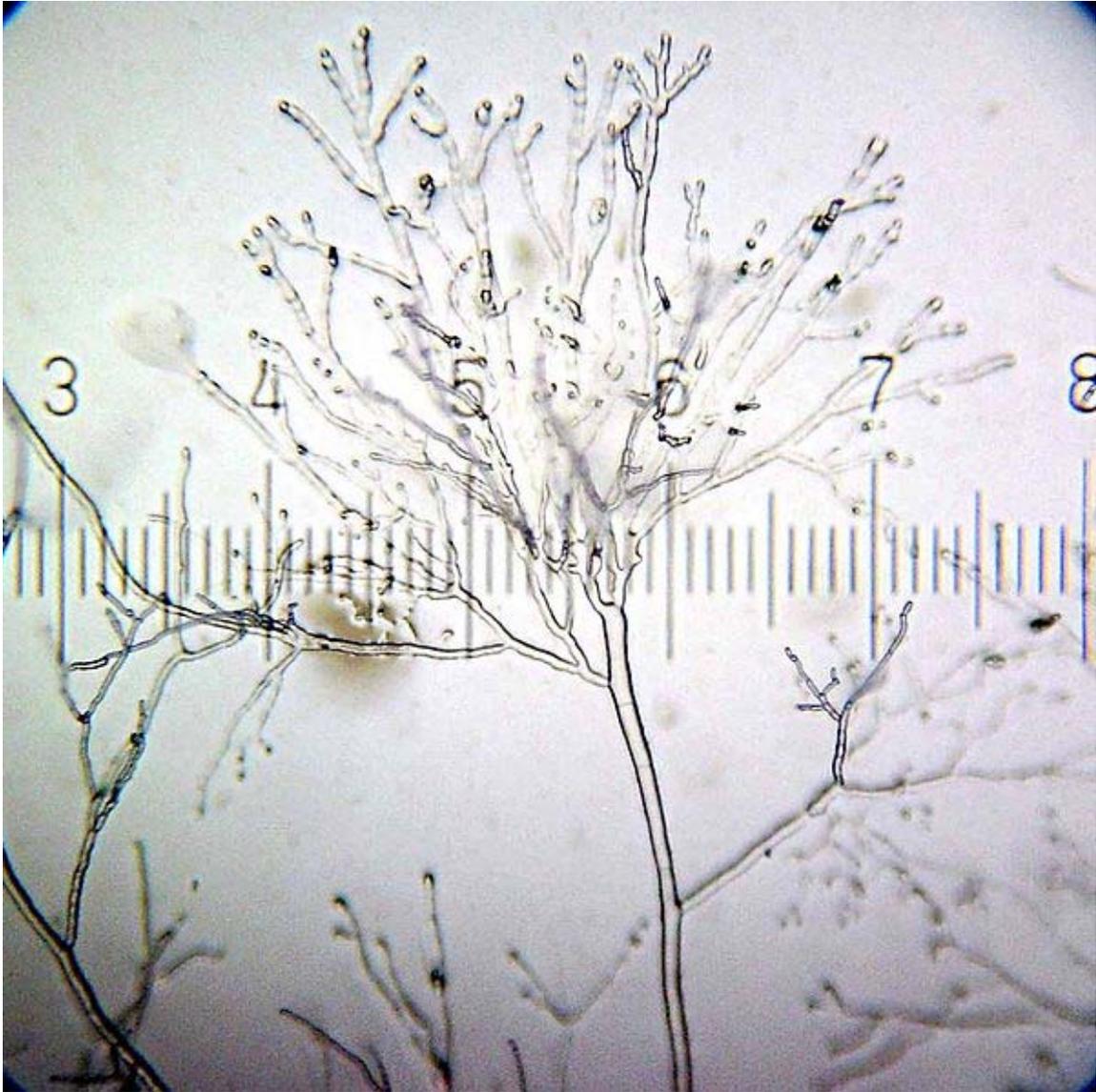
Mildew from a wooden soap holder.



Mildew growing on a plastic shower curtain.



Mycelium of unidentified mold. This image covers a one-millimeter square.



Another mycelium, of another mold.



A moldy tomato



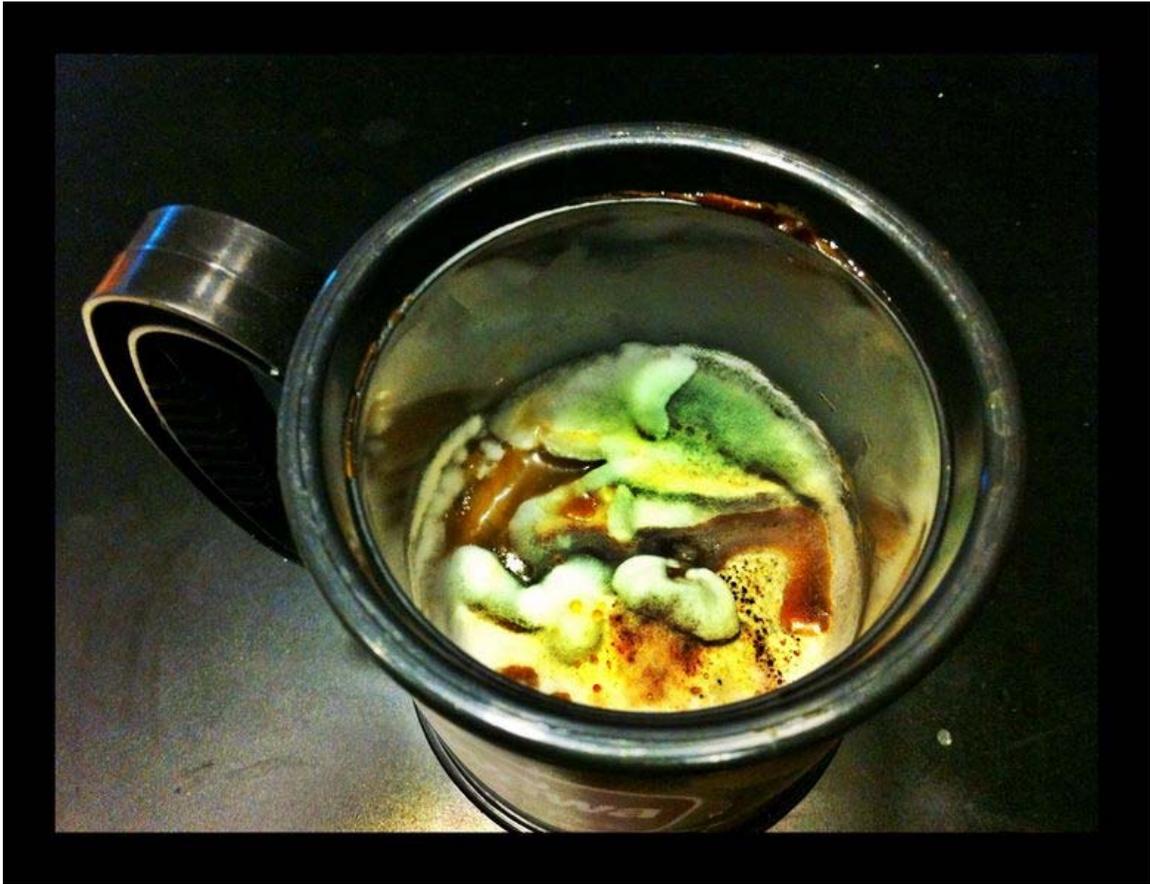
Moldy bread



Detailed picture of mold on tomato



Moldy peach



Moldy coffee

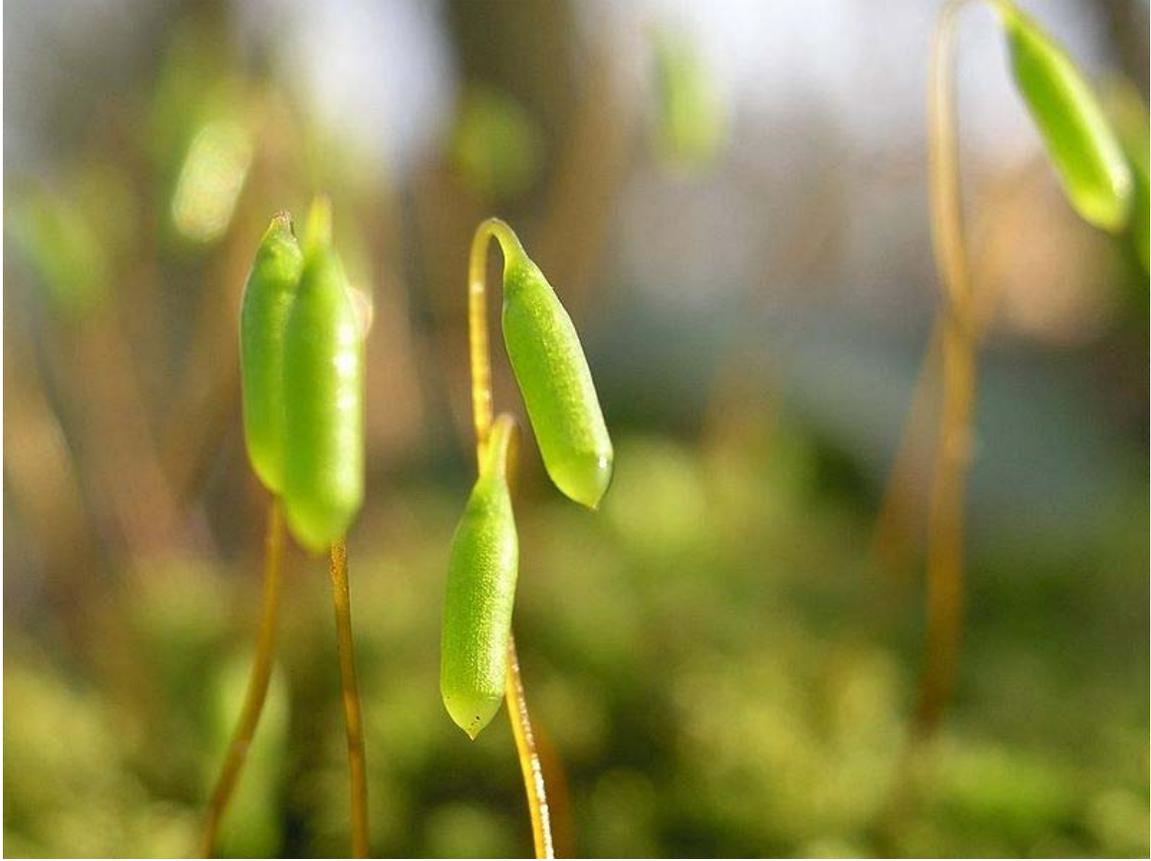
## Chapter 8

# Sporangium, Conidium and Ascospore

## Sporangium



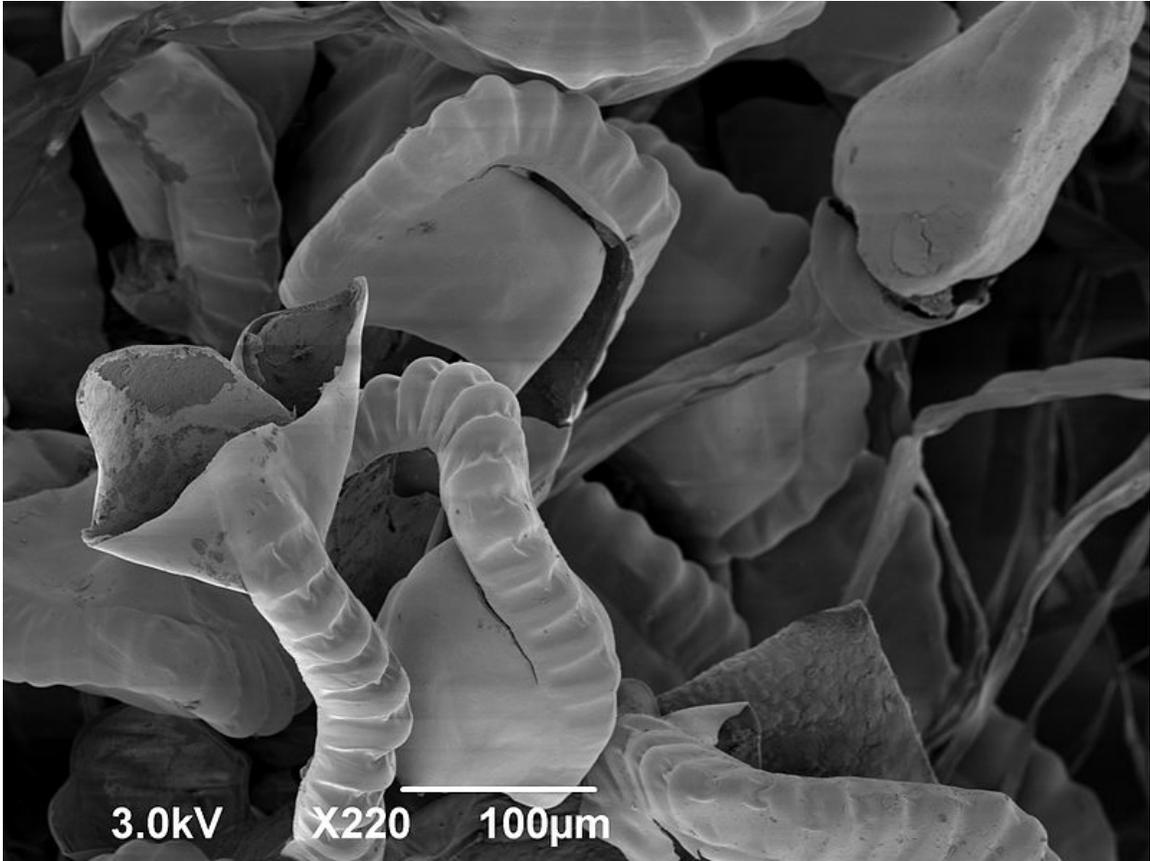
Mature sporangium of a *Absidia* mold



Moss sporangia (capsules)



Sporangia (sori) on a fern leaf



Scanning electron micrograph of fern sporangia



*Equisetum arvense* strobilus cut open to reveal sporangia

A **sporangium** (pl., **sporangia**) (modern Latin, from Greek spora ‘spore’ + angeion ‘vessel.’) is an enclosure in which spores are formed. It can be composed of a single cell or can be multicellular. All plants, fungi, and many other lineages form sporangia at some point in their life cycle. Sporangia, also known as sporanges (sing., sporange), can produce spores by mitosis, but in nearly all land plants and many fungi, sporangia are the site of meiosis and produce genetically unique haploid spores.

### ***Land Plants***

In mosses, liverworts and hornworts, an unbranched sporophyte produces a single sporangium, which may be quite complex morphologically. Most non-vascular plants, as

well as many lycophytes and most ferns, are homosporous (only one kind of spore is produced). Some bryophytes, most lycophytes, and some ferns are heterosporous (two kinds of spores are produced). These plants produce **microspores** and **megaspores**, which give rise to gametophytes that are functionally male or female, respectively. In some cases, both kinds of spores are produced in the same sporangium, and may even develop together as part of a spore tetrad. However, in most heterosporous plants there are two kinds of sporangia, termed **microsporangia** and **megasporangia**. A few ferns (Salviniaceae and Marsileaceae) and most lycophytes (the genera *Selaginella* and *Isoetes* and the extinct lepidodendrids) are heterosporous with two kinds of sporangia, as are all the seed plants.

Sporangia can be terminal (on the tips) or lateral (placed along the side) of stems or associated with leaves. In ferns, sporangia are typically found on the abaxial surface (underside) of the leaf and are densely aggregated into clusters called sori. Sori may be covered by a structure called an indusium. Some ferns have their sporangia scattered along reduced leaf segments or along (or just in from) the margin of the leaf.

Lycophytes, in contrast, bear their sporangia on adaxial surface (the upper side) of leaves or laterally on stems.

Leaves that bear sporangia are called sporophylls. If the plant is heterosporous, the sporangia-bearing leaves are distinguished as either microsporophylls or megasporophylls.

In seed plants, sporangia are typically located within strobili or flowers.

Cycads place their microsporangia on microsporophylls which are aggregated into strobili. Megasporangia are similarly found on megasporophylls, which are aggregated into strobili on separate plants (all cycads are dioecious). Conifers typically bear their microsporangia on microsporophylls aggregated into papery pollen strobili while megasporangia are inside ovules which are located on modified stem axes forming compound ovuliferous cone scales. Flowering plants contain microsporangia in the anthers of stamens (typically four microsporangia per anther) and megasporangia inside ovules inside ovaries. In all seed plants, spores are produced by meiosis and develop into gametophytes while still inside the sporangium. The microspores become microgametophytes (pollen). The megaspores become megagametophytes (embryo sacs).

### **Eusporangia and leptosporangia**

Categorized based on developmental sequence, *eusporangia* and *leptosporangia* are differentiated in the vascular plants.

- In a leptosporangium, found only in ferns, development involves a single initial cell that becomes the stalk, wall, and spores within the sporangium. There are around 64 spores in a leptosporangium.

- In a eusporangium, characteristic of all other vascular plants and some primitive ferns, the initials are in a layer (i.e., more than one). A eusporangium is larger (hence contain more spores), and its wall is multi-layered. Although the wall may be stretched and damaged, resulting in only one cell-layer remaining.

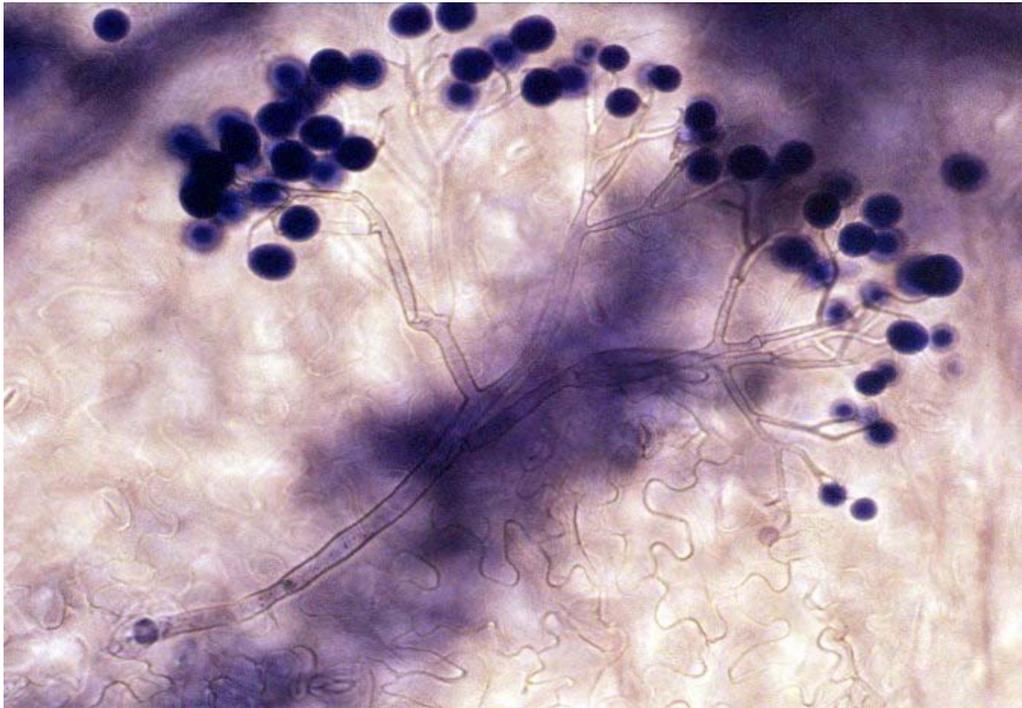
## Synangium

A cluster of sporangia that have become fused in development is called a **synangium**. This structure is most prominent in *Psilotum* and Marattiaceae such as *Christensenia*, *Danaea* and *Marattia*.

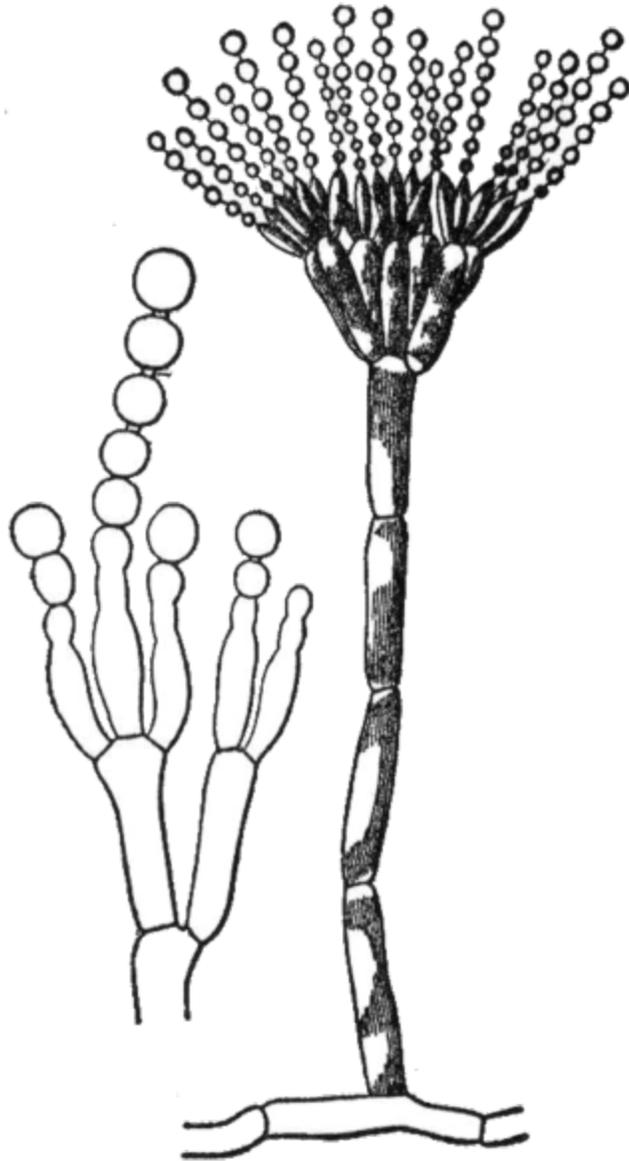
## Internal structures

A **columella** (pl. columellae) is a sterile (non-reproductive) structure that extends into and supports the sporangium. In fungi, the columella, which may be branched or unbranched, may be of fungal or host origin. *Secotium* species have a simple, unbranched columella, while in *Gymnoglossum* species, the columella is branched. In some *Geastrum* species, the columella appears as an extension of the stalk into the spore mass (gleba).

## Conidium



Conidiophore of *Hyaloperonospora parasitica* harboring several conidia



Conidia on conidiophores



Chain of conidia of *Alternaria*



Conidiomata of Cypress canker (probably *Seiridium cardinale*) erupting on a *Thuja* twig

**Conidia**, sometimes termed **conidiospores**, are asexual, non-motile spores of a fungus; they are also called **mitospores** due to the way they are generated through the cellular process of mitosis. The two new haploid cells are genetically identical to the haploid parent, and can develop into new organisms if conditions are favorable, and serve in biological dispersal.

Asexual reproduction in Ascomycetes (the Phylum Ascomycota) is by the formation of conidia, which are borne on specialized stalks called **conidiophores**. The morphology of these specialized conidiophores is often distinctive of a specific species and can therefore be used in identification of the species.

The terms "microconidia" and "macroconidia" are sometimes used.

## **Conidiogenesis**

There are two main types of conidium development:

- *Blastic* conidiogenesis, where the spore is already evident before it separates from the conidiogenic hypha which is giving rise to it, and
- *Thallic* conidiogenesis, where first a cross-wall appears and then the thus created cell develops into a spore.

## **Conidia germination**

A conidium may form germ tubes (germination tubes) and/or conidial anastomosis tubes (CATs) in specific conditions. These two are some of the specialized hyphae that are formed by fungal conidia. The germ tubes will grow to form the hyphae and fungal mycelia. The conidial anastomosis tubes are morphologically and physiologically distinct from germ tubes. After conidia are induced to form conidial anastomosis tubes, they grow homing toward each other, and they fuse. Once fusion happens, the nuclei can pass through fused CATs. These are events of fungal vegetative growth and not sexual reproduction. Fusion between these cells seems to be important for some fungi during early stages of colony establishment. The production of these cells has been suggested to occur in 73 different species of fungi.

## **Structures for release of conidia**

Conidiogenesis is an important mechanism of spread of plant pathogens. In some cases, specialized macroscopic fruiting structures perhaps 1mm or so in diameter containing masses of conidia are formed under the skin of the host plant and then erupt through the surface and allow the spores to be distributed by wind and rain. One of these structures is called a **conidioma** (plural: **conidiomata**).

Two important types of conidiomata, distinguished by their form, are:

- **pycnidia**, (singular: **pycnidium**) which are flask-shaped, and
- **acervuli** (singular: **acervulus**), which have a simpler cushion-like form.

Pycnidial conidiomata or *pycnidia* form in the fungal tissue itself, and are shaped like a bulging vase. The spores are released through a small opening at the apex, the **ostiole**.

Acervular conidiomata, or *acervuli*, are cushion-like structures that form within the tissues of a host organism:

- *subcuticular*, lying under the outer layer of the plant (the cuticle),
- *intraepidermal*, inside the outer cell layer (the epidermis),
- *subepidermal*, under the epidermis, or deeper inside the host.

Mostly they develop a flat layer of relatively short conidiophores which then produce masses of spores. The increasing pressure leads to the splitting of the epidermis and cuticle and allows release of the conidia from the tissue.

### ***Health issues***

Conidia are always present in the air, but levels fluctuate from day to day and with the seasons. An average person inhales 40 conidia per hour.

Conidia are often the method by which some normally harmless but heat-tolerating (thermotolerant), common fungi establish infection in certain types of severely immunocompromised patients (usually acute leukemia patients on induction chemotherapy, AIDS patients with superimposed B-cell lymphoma, bone marrow transplantation patients, or major organ transplant patients suffering from graft versus host disease). Their immune system is not strong enough to fight off the fungus, and it may, for example, colonise the lung, resulting in a pulmonary infection.

# Ascospore



Asci of *Morchella elata*, containing ascospores

An **ascospore** is a spore contained in an ascus or that was produced inside an ascus. This kind of spore is specific to fungi classified as ascomycetes (Ascomycota).

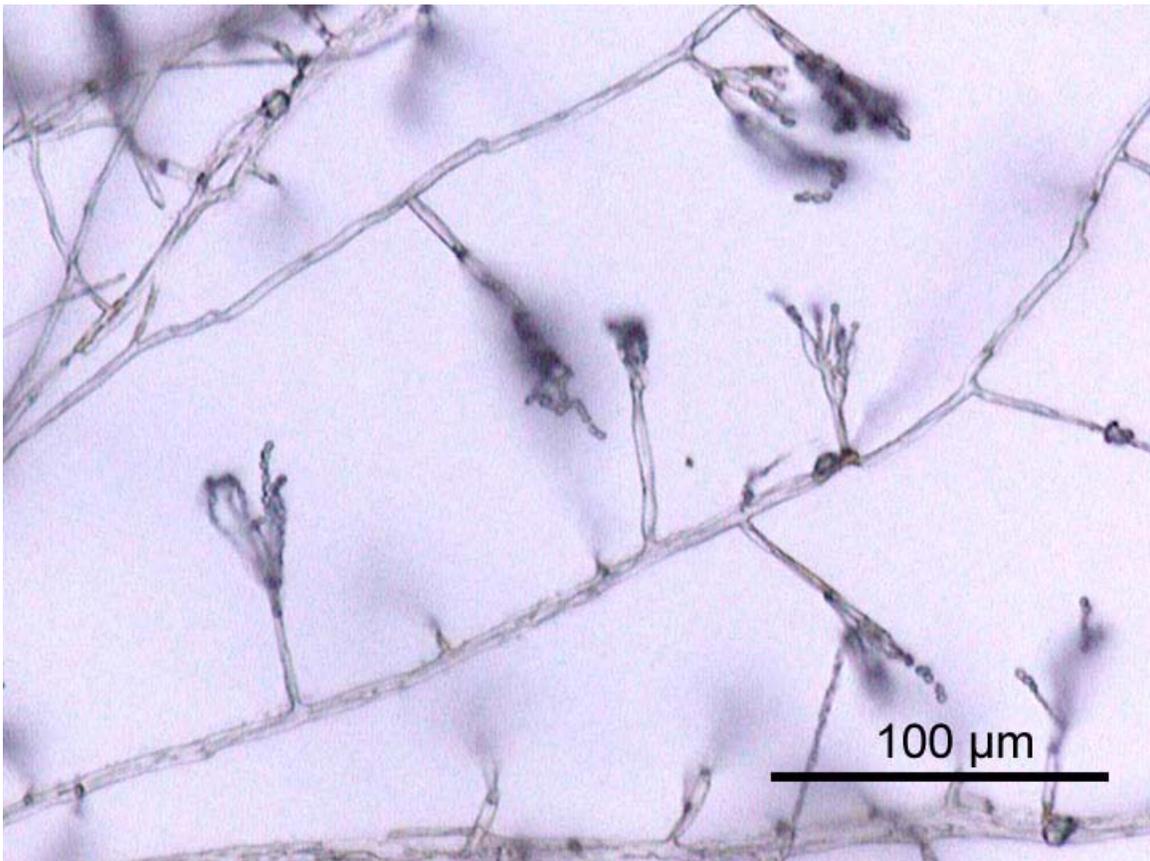
Typically, a single ascus will contain eight ascospores. The eight spores are produced by a combination of a meiotic division followed by a mitotic division. The meiosis division turns the original diploid zygote nucleus into four haploid ones. That is, the single original cell from which the whole process begins contains two complete sets of chromosomes. In preparation for meiosis, all the DNA of both sets is duplicated, to make a total of four sets. The nucleus that contains the four sets divides in two stages, separating into four new nuclei – each of which has one complete set of chromosomes. Following this process, each of the four new nuclei duplicates its DNA and undergoes a division by mitosis. As a result, the ascus will contain four pairs of spores.

The Fungi *Saccharomyces* produces ascospores when grown on V-8 medium, acetate ascospore agar, or Gorodkova medium. These ascospores are globose and located in asci. Each ascus contains one to four ascospores. The asci do not rupture at maturity. Ascospores are stained with Kinyoun stain and ascospore stain. When stained with Gram stain, ascospores are gram-negative while vegetative cells are gram-positive.

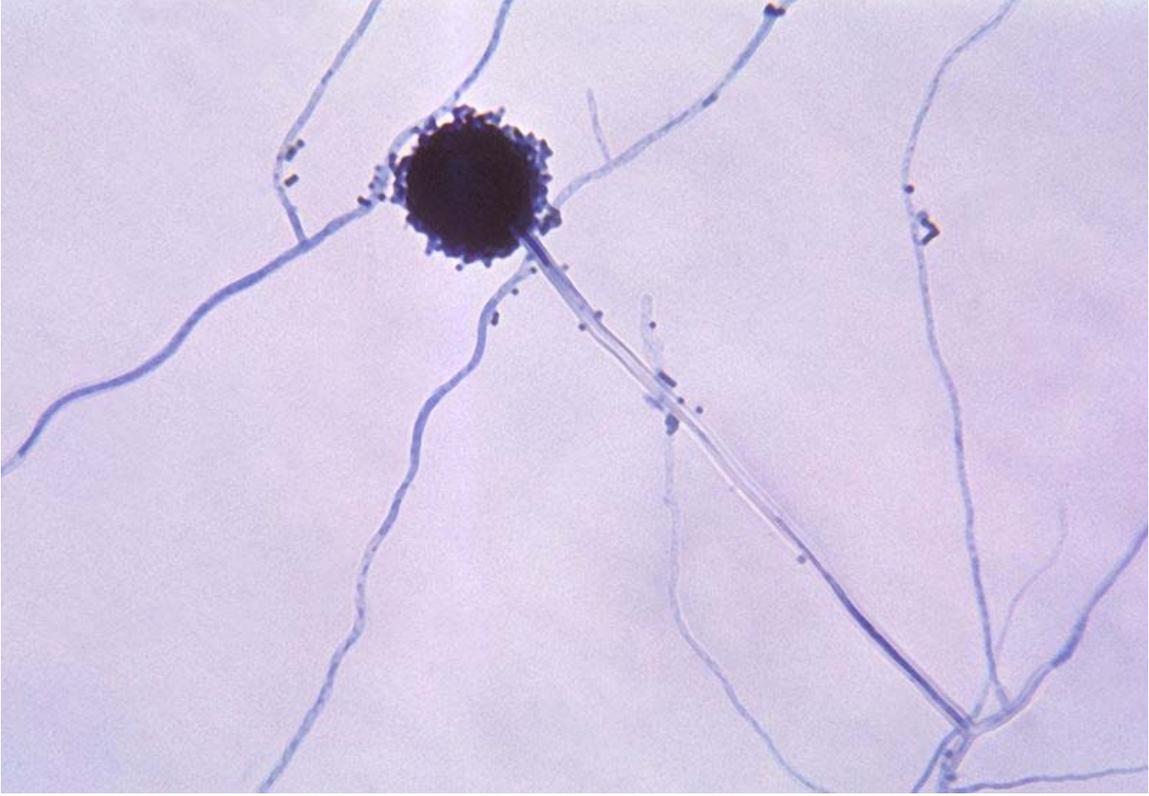
## Chapter 9

# Hypha and Mycelium

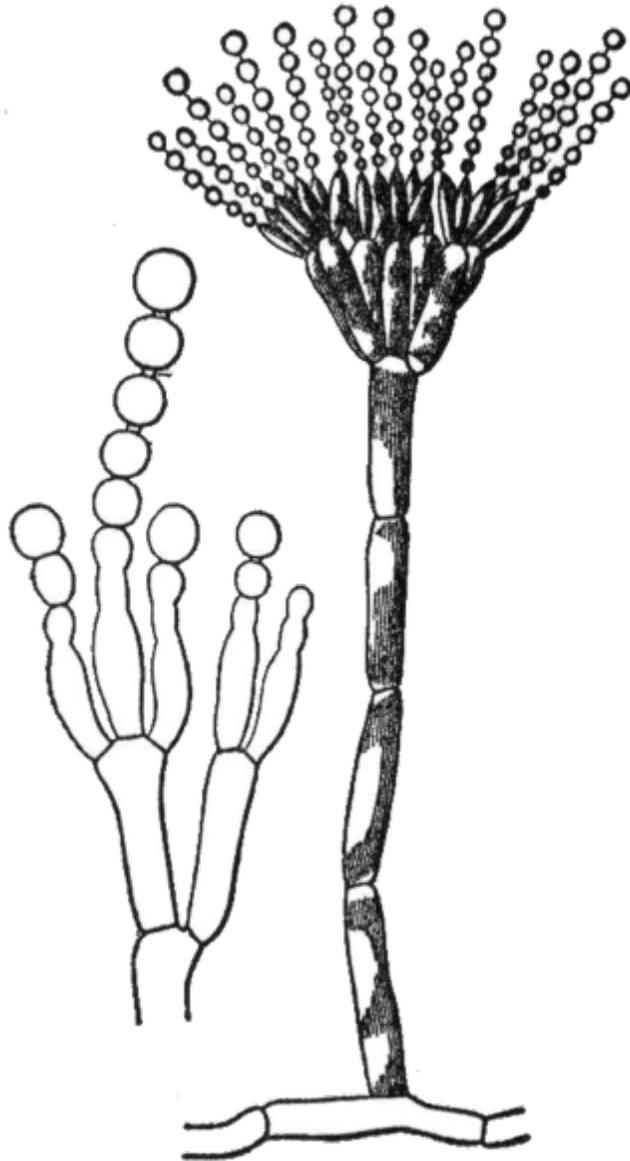
## Hypha



Hyphae of *Penicillium*



*Aspergillus niger*



Conidia on conidiophores

A **hypha** (plural **hyphae**) is a long, branching filamentous structure of a fungus, and also of unrelated Actinobacteria. In most fungi, hyphae are the main mode of vegetative growth, and are collectively called a mycelium; yeasts are unicellular fungi that do not grow as hyphae.

### **Structure**

A hypha consists of one or more cells surrounded by a tubular cell wall. In most fungi, hyphae are divided into cells by internal cross-walls called "septa" (singular septum). Septa are usually perforated by pores large enough for ribosomes, mitochondria and sometimes nuclei to flow between cells. The major structural polymer in fungal cell walls

is typically chitin, in contrast to plants that have cellulosic cell walls. Some fungi have aseptate hyphae, meaning their hyphae are not partitioned by septa.

## **Growth**

Hyphae grow at their tips. During tip growth, cell walls are extended by the external assembly and polymerization of cell wall components, and the internal production of new cell membrane. The Spitzenkörper is an intracellular organelle associated with tip growth. It is composed of an aggregation of membrane-bound vesicles containing cell wall components. The Spitzenkörper is part of the endomembrane system of fungi, holding and releasing vesicles it receives from the Golgi apparatus. These vesicles travel to the cell membrane via the cytoskeleton and release their contents outside the cell by the process of exocytosis, where it can then be transported to where it is needed. Vesicle membranes contribute to growth of the cell membrane while their contents form new cell wall. The Spitzenkörper moves along the apex of the hyphal strand and generates apical growth and branching; the apical growth rate of the hyphal strand parallels and is regulated by the movement of the Spitzenkörper.

As a hypha extends, septa may be formed behind the growing tip to partition each hypha into individual cells. Hyphae can branch through the bifurcation of a growing tip, or by the emergence of a new tip from an established hypha.

## **Modifications**

Hyphae may be modified in many different ways to serve specific functions. Some parasitic fungi form haustoria that function in absorption within the host cells. The arbuscules of mutualistic mycorrhizal fungi serve a similar function in nutrient exchange, so are important in assisting nutrient and water absorption by plants. Hyphae are found enveloping the gonidia in lichens, making up a large part of their structure. In nematode-trapping fungi, hyphae may be modified into trapping structures such as constricting rings and adhesive nets. Mycelial cords can be formed to transfer nutrients over larger distances.

## **Types**

### **Classification based on cell division**

- Septate (with septa)
  - *Aspergillus* and many other species have septate hyphae.
- Aseptate or coenocytic (without septa)
  - Non-septate hyphae are associated with *Mucor*, some zygomycetes, and other fungi.
- "Pseudohyphae" are distinguished from true hyphae by their method of growth, relative frailty and lack of cytoplasmic connection between the cells.

- Yeast can form pseudohyphae. They are the result of a sort of incomplete budding where the cells remain attached after division.

### Classification based on cell wall and overall form

Characteristics of hyphae can be important in fungal classification. In basidiomycete taxonomy, hyphae that comprise the fruiting body can be identified as generative, skeletal, or binding hyphae.

- **Generative** hyphae are relatively undifferentiated and can develop reproductive structures. They are typically thin-walled, occasionally developing slightly thickened walls, usually have frequent septa, and may or may not have clamp connections. They may be embedded in mucilage or gelatinized materials.
- **Skeletal** hyphae are of two basic types. The classical form is thick-walled and very long in comparison to the frequently septate generative hyphae, which are unbranched or rarely branched, with little cell content. They have few septa and lack clamp connections. Fusiform skeletal hyphae are the second form of skeletal hyphae. Unlike typical skeletal hyphae these are swollen centrally and often exceedingly broad, hence giving the hypha a fusiform shape.
- **Binding** hyphae are thick-walled and frequent branched. Often they resemble deer antlers or defoliated trees because of the many tapering branches.

Based on the generative, skeletal and binding hyphal types, in 1932 E. J. H. Corner applied the terms monomitic, dimitic, and trimitic to hyphal systems, in order to improve the classification of polypores.

- Every fungus must contain generative hyphae. A fungus which only contains this type, as do fleshy mushrooms such as agarics, is referred to as **monomitic**.
- Skeletal and binding hyphae give leathery and woody fungi such as polypores their tough consistency. If a fungus contains all three types (example: *Trametes*), it is called **trimitic**.
- If a fungus contains generative hyphae and just one of the other two types, it is called **dimitic**. In fact dimitic fungi almost always contain generative and skeletal hyphae; there is one exceptional genus, *Laetiporus* that includes only generative and binding hyphae.

Fungi that form fusiform skeletal hyphae bound by generative hyphae are said to have **sarcodimitic** hyphal systems. A few fungi form fusiform skeletal hyphae, generative hyphae, and binding hyphae, and these are said to have **sarcotrimitic** hyphal systems. These terms were introduced as a later refinement by E. J. H. Corner in 1966.

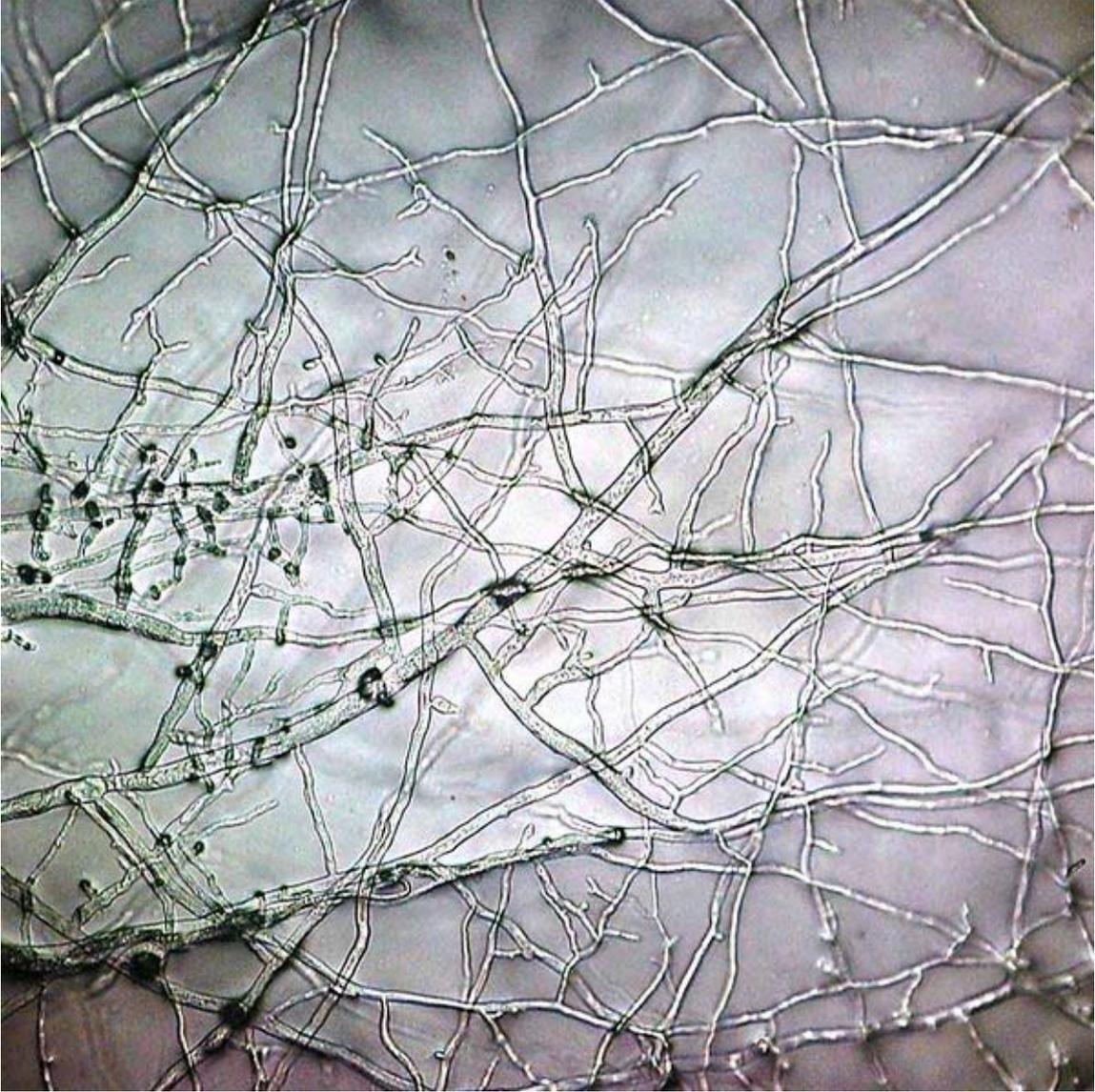
## **Classification based on refractive appearance**

Hyphae are described as "gloeoplerous" ("gloeohyphae") if their high refractive index gives them an oily or granular appearance under the microscope. These cells may be yellowish or clear (hyaline). They can sometimes selectively be coloured by sulphovanillin or other reagents. The specialized cells termed cystidia can also be gloeoplerous.

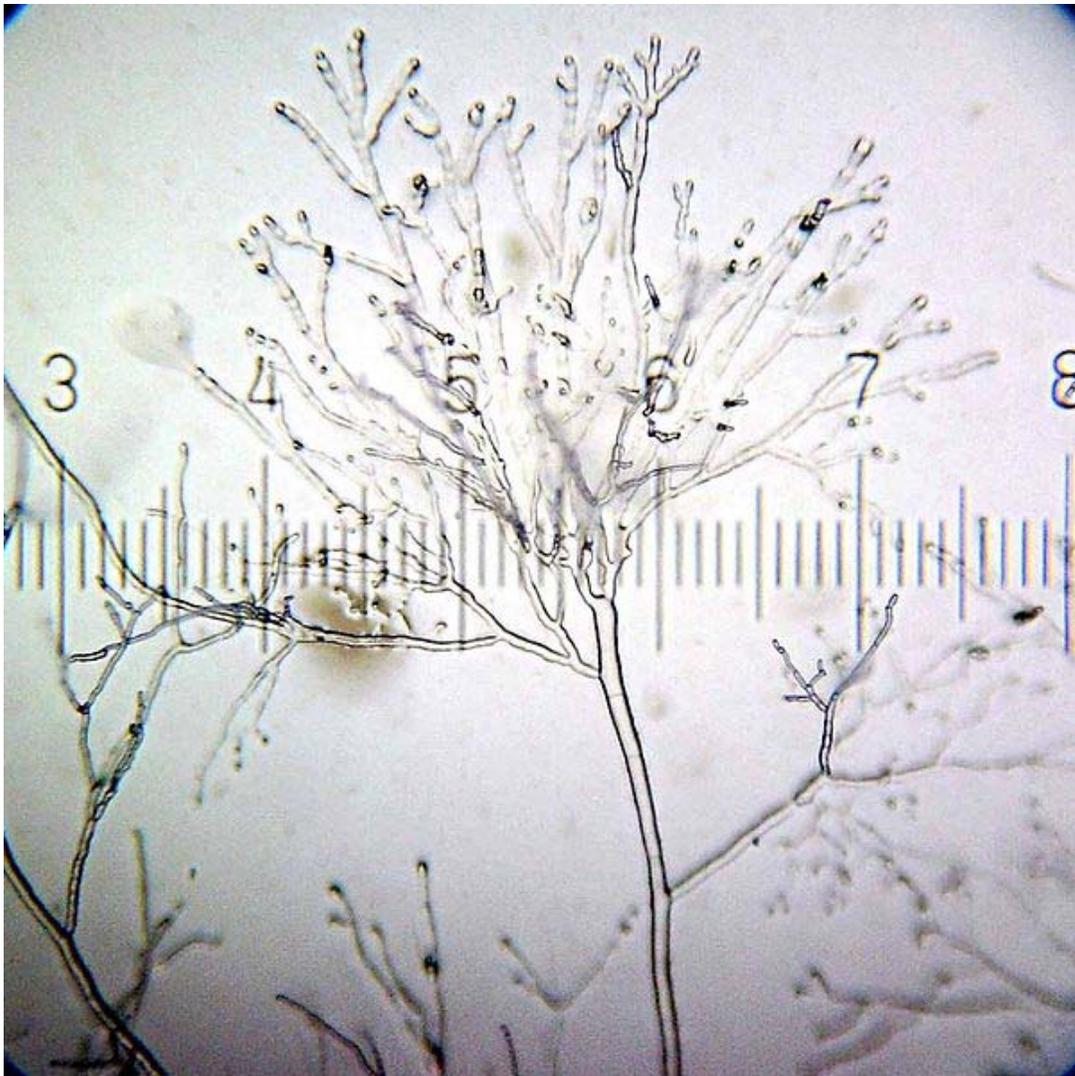
## **Mycelium**



Fungal mycelia



Microscopic view of a mycelium. This image covers a one-millimeter square.



Another microscopic view of a mycelium. Numbered ticks are 230  $\mu\text{m}$  apart.

**Mycelium** (plural **mycelia**) is the vegetative part of a fungus, consisting of a mass of branching, thread-like hyphae. The mass of hyphae is sometimes called **shiro**, especially within the fairy ring fungi. Fungal colonies composed of mycelia are found in soil and on or within many other substrates. A typical single spore germinates into a homokaryotic mycelium, which cannot reproduce sexually; when two compatible homokaryotic mycelia join and form a dikaryotic mycelium, that mycelium may form fruiting bodies such as mushrooms. A mycelium may be minute, forming a colony that is too small to see, or it may be extensive:

Is this the largest organism in the world? This 2,400-acre (9.7  $\text{km}^2$ ) site in eastern Oregon had a contiguous growth of mycelium before logging roads cut through it. Estimated at 1,665 football fields in size and 2,200 years old, this one fungus has killed the forest above it several times over, and in so doing has built deeper soil layers that allow the

growth of ever-larger stands of trees. Mushroom-forming forest fungi are unique in that their mycelial mats can achieve such massive proportions.

—Paul Stamets, *Mycelium Running*

It is through the mycelium that a fungus absorbs nutrients from its environment. It does this in a two-stage process. First, the hyphae secrete enzymes onto or into the food source, which break down biological polymers into smaller units such as monomers. These monomers are then absorbed into the mycelium by facilitated diffusion and active transport.

Mycelium is vital in terrestrial and aquatic ecosystems for its role in the decomposition of plant material. It contributes to the organic fraction of soil, and its growth releases carbon dioxide back into the atmosphere. The mycelium of mycorrhizal fungi increases the efficiency of water and nutrient absorption of most plants and confers resistance to some plant pathogens. Mycelium is an important food source for many soil invertebrates.

Sclerotia are compact or hard masses of mycelium.

## **Uses**

One of the primary roles of fungi in an ecosystem is to decompose organic compounds. Petroleum products and pesticides that can be contaminants of soil are organic molecules. Therefore, fungi should have potential to remove such pollutants from the soil environment, a process known as bioremediation.

Mycelial mats have been suggested as having potential as biological filters, removing chemicals and microorganisms from soil and water. The use of fungal mycelia to accomplish this has been termed "mycofiltration".

Knowledge of the relationship between mycorrhizal fungi and plants suggests new ways to improve crop yields.

When spread on logging roads, mycelium can act as a binder, holding new soil in place and preventing washouts until woody plants can be established.

Mycelium has been used to bind agricultural by-products to form products dubbed Greensulate and Ecocradle, which are alternatives to plastic styrofoam for packaging and insulation. Two inventors, Eben Bayer and Gavin McIntyre, and their company Ecovative Design, developed the method to manipulate a network of mycelia into desirable shapes, with properties comparable to its plastic counterpart. The invention has won two awards and is now in use commercially by Steelcase as packaging for furniture. This use of mycelium has been discussed in Time Magazine, Popular Science and other media, as well as being the subject of a TED Talk "Are Mushrooms the New Plastic?" by Eben Bayer.