

# Fungal Diversity

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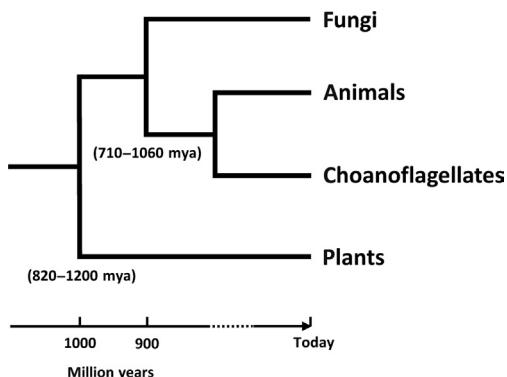
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## EVOLUTIONARY ORIGINS OF THE FUNGI AND THEIR RELATIONSHIPS TO OTHER EUKARYOTES

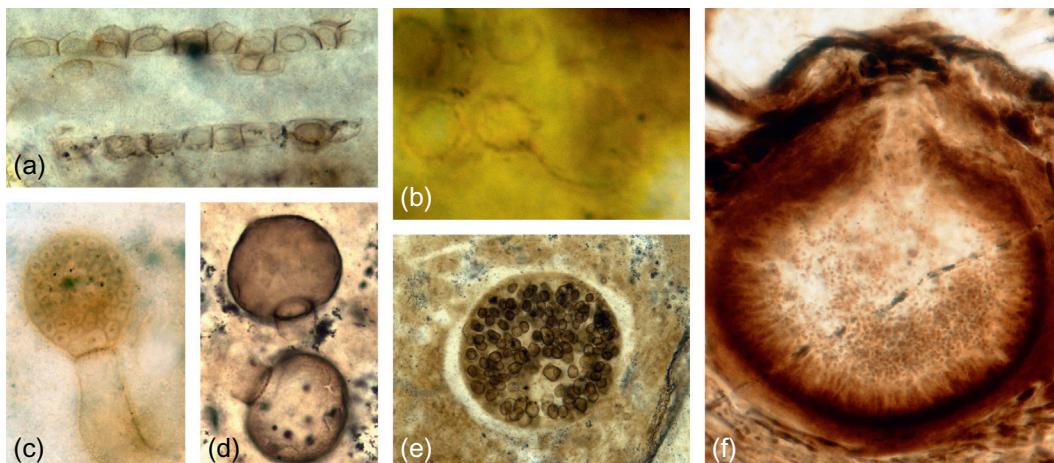
The fungi originated as a distinctive group of unicellular eukaryotes in the Precambrian. Recent estimates of the origin of the fungal kingdom based on the analysis of molecular clocks range from 760 million years ago to 1.06 billion years ago (Figure 1.1). The reliability of date estimates based on molecular clocks is dependent upon calibration points derived from the fossil record, which is far from satisfying for the fungi. The oldest unambiguous fossils of fungi are described from Lower Devonian Rhynie chert (400 million years old). These fossils show spectacular preservation and include chytrid sporangia and zoospores, zygomycete sporangia, and ascomycete fruit bodies (Figure 1.2). Spores and arbuscules of Glomeromycota are also found in the roots of plant fossils in the Rhynie chert and even older spores of these fungi are reported from 460 million-year-old rocks. These structures provide evidence for early symbioses that are thought to have been essential for the evolution of land plants. The oldest fossils of Basidiomycota are 330 million-year-old hyphae with clamp connections, but it seems likely that this phylum arose much earlier.

Evidence of an ancient origin for the prevailing fungal phyla leaves us with considerable uncertainty about the precise timing of the development of the ancestral species. Based on the structural simplicity of the chytrids and absence of flagella among other fungi, it is inferred that the earliest fungi may have been simple, unicellular organisms that propelled themselves through water using a flagellum anchored to the posterior of the cell. The signature of the posterior flagellum is common to fungi and animals and both groups are combined in the supergrouping of eukaryotes called the Opisthokonta. The cells of other kinds of motile eukaryotes are equipped with flagella connected to the anterior of the cell. The choanoflagellates are one of the basal groups of eukaryotes related to animals and their structural similarity to the chytrids is one of many lines of evidence of common ancestry (Figure 1.3).

## 1. FUNGAL DIVERSITY



**FIGURE 1.1** Evolutionary relationships between the fungi, animals, choanoflagellates, and plants with a timeline showing the emergence of the opisthokonts (fungi, animals, and choanoflagellates) approximately 1 billion years ago. The fungi are thought to have developed as a new kingdom of organisms between 710 and 1060 million years ago.



**FIGURE 1.2** Fossil fungi in Lower Devonian Rhynie chert. (a) Zoosporangia of a chytrid inside host cells. Note exit tubes in two of the sporangia, through which zoospores were expelled. (b) Chytrid zoospore with (putative) single flagellum. (c) Zoosporangium of *Palaeoblastocladia milleri* (Blastocladiomycota). (d) Sporangia of a zygomycete fungus. (e) Sporocarp of species of arbuscular mycorrhizal fungus containing numerous spores. (f) Perithecium of *Palaeopyrenomyces devonicus* (Ascomycota). Source: Thomas Taylor, University of Kansas.

## THE CLASSIFICATION OF FUNGI

Pioneers of mycology sought to organise fungi into groups with shared characteristics and this morphological approach was successful in carving out the ascomycetes and the basidiomycetes and identifying sub-groups of closely related genera. In some cases, these pre-Darwinian schemes reflected evolutionary relatedness because some broad structural similarities among the fungi do reflect kinship. In many instances, however, these early investigations lumped unrelated organisms into groups defined by shared

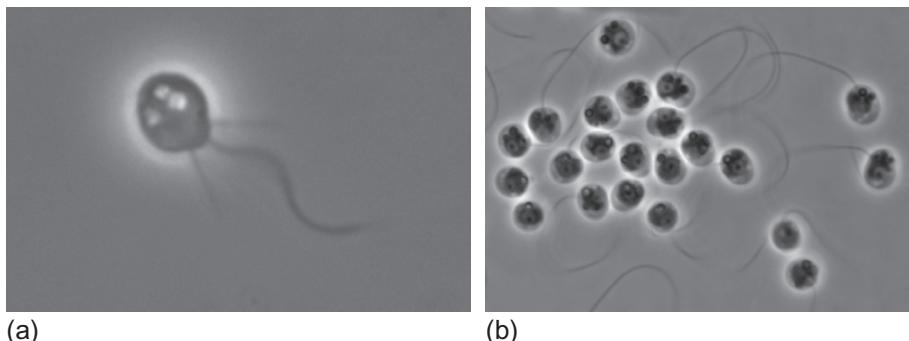
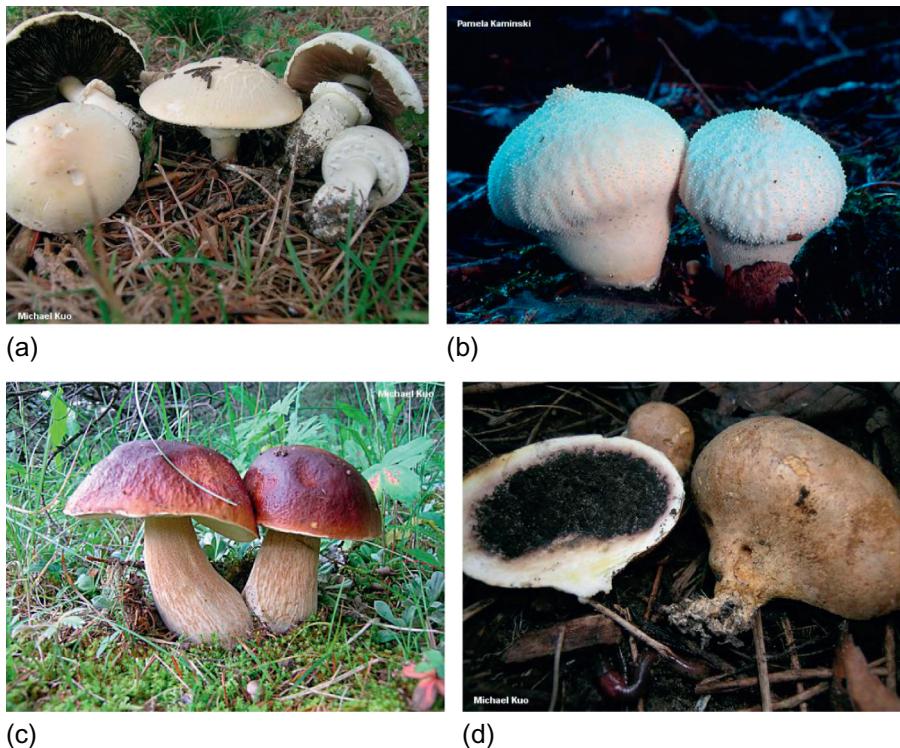


FIGURE 1.3 Similar morphology of single cells of a choanoflagellate and a chytrid fungus. (a) Marine choanoflagellate, *Monosiga brevicollis*. (b) Zoospore of freshwater chytrid, *Obelidium mucronatum*. Source: (a) Stephen Fairclough (Creative Commons) and (b) Joyce Longcore, University of Maine.

characteristics – such as spore colour – that held no evolutionary significance. Progress toward a natural classification of the fungi came with advances in microscopy and biochemistry in the twentieth century, but the advent of the polymerase chain reaction and other molecular genetic techniques in the 1980s transformed the study of fungal taxonomy. Since then, many of the traditional groups have been reorganised and renamed and the assignment of thousands of species remains in flux.

The study of fungal diversity spans the disciplines of taxonomy, classification, and systematics. Taxonomy concerns the identification, description, and naming of organisms; the assignment of these organisms to a hierarchy of groups – genus, family, order, and so on – is the task of classification; and systematics is the study of the evolutionary relationships between species and larger groupings of organisms. In theory, a fungal taxonomist might describe new species without considering their relationships to other fungi. She or he would proceed without any interest in systematics. In practice, modern taxonomists *are* concerned with evolutionary relationships between species, and fungal taxonomy has become synonymous with systematics. The goals of a field mycologist can be quite different. Classification is important to someone hunting for edible mushrooms: not recognising a death cap can be a fatal. The systematic position of the mushroom – its evolutionary relationship to other fungi – is immaterial to the collector. These differences in objectives have caused frustration among amateur mycologists who need reliable guides for identification (classification) but feel frustrated by frequent changes in scientific names. It probably makes sense for the amateur mycologist to ignore most academic research on systematics and concentrate on developing practical skills in identification. From the perspective of the biologist engaged in taxonomic research, however, the frequent name changes and adjustments to group assignments reflect the vibrancy of a field of inquiry that is benefiting from new technology and new ideas.

Thirty years ago, basidiomycetes including puffballs, earth-balls, earth-stars, stinkhorns, and bird's nest fungi, were placed in the Class Gasteromycetes. The only obvious shared characteristic among these fungi was their lack of the spore discharge mechanism found in the other mushroom-forming basidiomycetes and related rusts and smuts. In other words, this taxonomic entity was based upon the absence of a biomechanical character. Even then, however, mycologists who worked on these fungi were aware of many lines of evidence suggesting



**FIGURE 1.4** Surprising relatives. (a, b) Field mushroom, *Agaricus arvensis* and puffball, *Lycoperdon perlatum*. (c, d) Bolete, *Boletus pinophilus* and earth-ball, *Scleroderma michiganense*. Source: (a, c, d) Michael Kuo and (b) Pamela Kaminskyj.

that these organisms were not closely related. What we lacked, however, was proof of their relationships to other species. In the absence of this information, the Class Gasteromycetes was a convenient grouping for hundreds of distantly related basidiomycetes with an extraordinary range of fruit body types. With the introduction of molecular techniques for sequencing the genes of these fungi, and by comparing the similarity of these sequences with those of other basidiomycetes, the true relationships of the Gasteromycetes became clearer. The genetic data proves, for example, that puffballs are closely related to gilled mushrooms (Figure 1.4a, b). Additional information on the development of their spores suggests that puffballs evolved from ancestors with gills rather than vice versa. These findings are reflected in the modern classification that places the puffballs within the taxonomic Order Agaricales, which is the largest group of gilled mushrooms. Earth-balls produce fruit bodies that look similar to puffballs, but genetic comparisons show that these fungi are more closely related to mushrooms with tubes beneath their caps than to puffballs and their gilled relations. For this reason, the earth-balls are classified as members of the Order Boletales (Figure 1.4c, d).

The term gasteromycete remains a useful one for referring to the puffballs, earth-stars, and so on, but it is not a formal name of a taxonomic group today. The process of evolutionary convergence has often confused mycologists, as well as specialists in the taxonomy of other groups of organisms, leading them to guess at close phylogenetic affinities where none exist.

Mushrooms with gills offer another example of apparent kinship among fungi, whose fiction has been exposed by molecular phylogenetic studies. In addition to the Agaricales, fruit bodies with gills may have evolved independently within five other orders of basidiomycetes. There was no common gilled ancestor of gilled mushrooms. Molecular genetic analysis is the only objective method for sorting out who is related to whom.

## Molecular Phylogenetic Analysis of the Fungi

Evolutionary relationships between fungi have been examined by comparing the sequences of ubiquitous eukaryote genes. Scrutiny of the ribosomal gene cluster is the most common choice for this research. This cluster encodes three subunits of ribosomal RNA (18S [**small subunit (SSU)**], and 5.8S and 28S [**large subunit (LSU)**] rRNA) and intervening regions, or **internal transcribed spacers**, identified as ITS1 and ITS2. The two spacers plus the gene encoding the 5.8S subunit of the ribosome are called the **ITS region**. **External transcribed spacer sequences (ETS)** are located at the 5' and 3' ends of the cluster. ETS, ITS1, and ITS2 encode non-functional RNA molecules that are degraded when the functional rRNA is transcribed. Fungal genomes can contain more than 200 copies of the cluster organised in repeating sequences called **tandem repeats**. Individual copies are separated by a sequence called the **intergenic spacer region (IGS)** or **non-transcribed spacer region (NTS)**. The high copy number of the gene cluster simplifies amplification using PCR even when samples of fungal DNA are very small.

An important attribute of the ITS sequences for molecular phylogenetic research is that they show significant variations between closely related fungi, and sometimes between populations within a single species. These variations are caused by insertions, deletions, and point mutations, which are conserved because ITS1 and ITS2 encode non-functional RNA molecules. Genes encoding functional products are subjected to stronger evolutionary pressure, which tends to dampen variation. In addition to its usefulness in phylogenetic research, portions of the ITS region are also amplified using diagnostic kits for rapid identification of fungi causing human infections and plant disease, and contaminating water-damaged buildings. Other genes used for phylogenetic research on fungi encode RNA subunits of the ribosome (LSU and SSU), and genes that encode proteins including translation factor 1- $\alpha$ ,  $\beta$ -tubulin, actin, RNA polymerase II (*RPB1* and *RPB2*), and the minichromosome maintenance protein, *MCM7*.

### Phylogenetic Trees

Evolutionary relationships between fungi are represented in the form of **phylogenetic trees**. The tips of the branches of these trees are occupied by living fungi and internal branch points, or nodes, represent their ancestors. Phylogenetic trees can be constructed using any measure of kinship, including morphological data, protein sequences, single genes, groups of genes, or, most reliably, by comparing whole genomes. Evolutionary relationships among fungi are analysed by comparing the ITS regions of multiple taxa. Trees derived from this information can be **rooted** or **unrooted**. Unrooted trees show the relatedness of organisms without indicating ancestry. Rooted trees converge upon a single **node** (the root) that represents a hypothetical common ancestor. Trees are often organised by including an **outgroup** that is selected as a plausibly distant relative that unites everything else in the tree. Trees that are

displayed horizontally show close relatives one above the other on adjacent branches linked to a common ancestor. Connections between pairs of organisms, or groups of organisms, are discovered by following the branches back to shared branch points or internal nodes.

The passage of time is implicit in rooted trees, with the lengthiest pathways to an organism from the ancestor representing the longest evolutionary journeys. When fossils can be dated, actual time intervals can be estimated. Phylogenetic trees in which the lengths of the branches are scaled to evolutionary time are called **chronograms**. These are difficult to construct for fungi because the fossil record is so sparse. Nevertheless, the timing of the origins of some of the larger groupings has been estimated.

Once the necessary genetic sequences have been compiled and aligned with one another, phylogenetic trees can be constructed using a number of alternative methods. **Distance methods** organise sequences according to their overall similarity, computing the number of nucleotide substitutions between pairs of sequences. **Neighbour-joining** is the most popular of the distance methods and does not make any assumptions about evolutionary processes. **Character-based methods** are also used widely. These look at specific nucleotides and count insertions and deletions at each site. The advantage of these methods over neighbour-joining is that they can weigh the significance of changes in the nucleotide sequence differently. This is useful because some changes in a single sequence, relative to its comparison sequence, are uninformative. Neighbour-joining incorporates these changes into its trees; character-based methods can ignore these uninformative changes and focus on the more frequent and informative changes. **Maximum parsimony** is an example of a character-based method. This favours the simplest explanation for the similarities and differences between sequences. Parsimony looks at all possible trees and identifies the one that organises the sequences with the least evolutionary changes. **Maximum likelihood** is a more complicated character-based method that incorporates the lengths of branches into the tree that has the highest likelihood of being the correct representation of the phylogenetic relationships among the sequences. **Bayesian inference** is a third character-based method that generates a set of trees with roughly equal likelihoods.

When trees have been constructed, researchers can map various characteristics of the organisms represented in the tree onto its branches. This can inform us about the origin of particular features of cell biology, for example, or show how interactions between fungi and plant species evolved. Biogeographical patterns also emerge from these mapping exercises.

### *Operational Taxonomic Units and Environmental Sampling*

Sequencing of fungal DNA allows researchers to extend the traditional taxonomic work of generations of scientists who described the morphology of fungi collected in the field and cultured in the laboratory. Unlike morphological characters, genetic markers provide an objective measure of relatedness and, for the first time, mycologists are able to organize different groups of fungi into a robust natural system of classification that reflects their evolutionary history. Molecular techniques are also used to study fungi that have not been cultured. By amplifying fungal genes from soil, water, or decaying wood, scientists have discovered new species and, more importantly, new larger groupings of fungi. Because we do not know how to grow these fungi, it is difficult to study them microscopically. While we can determine, for example, that a sample of estuarine mud contains the genes of fungi related to known species of chytrid, we do not know which of the cells seen with a microscope belong to these enigmatic microorganisms. In some instances we can do better than this and identify particular

organisms in an environmental sample as the source of the amplified genes by hybridising genetic probes to the DNA inside their cells. These genetic probes are linked to a fluorescent dye so that the cells light up in the sample. This technique is called fluorescence in situ hybridization (**FISH**). Without this detailed investigation, we do not know whether genes that we have amplified have come from active fungi, from their inactive spores, or from remnants of the genome of damaged cells. Environmental sampling is a relatively new field of research for mycologists.

When we cannot determine whether a sequence has come from a distinctive species, we can describe the fungus as an **operational taxonomic unit (OTU)**. An OTU can refer to any stipulated level of the taxonomic hierarchy, ranging from populations of organisms to single genetic sequences. Other names include **ENAS**, for environmental nucleic acid sequence, and **eMOTU**, for environmental molecular operational taxonomic unit.

Mycologists face a difficult challenge in reconciling traditional taxonomy with the wealth of new molecular data and with the revelation of an incredible variety of fungi that, until very recently, we had no idea existed. We know that similarities in morphology do not necessarily indicate shared heredity and that the malleability of fungal growth in response to changes in nutrient availability can mislead researchers into thinking that they are looking at distinct species. Another problem is encountered in the complex life cycles of some fungi, in which one organism is remodelled when it encounters a compatible mate for sexual reproduction and develops in a different way when it engages in clonal reproduction. One species can be mistaken for two or more species. By ignoring structure, molecular phylogenetic analysis has been very effective in assigning ‘problematic’ fungi to natural taxonomic groups. The use of these techniques has been less helpful in distinguishing between individual species because we do not have any independent measure of the degree of genetic difference to anticipate between fungal species. Some investigators suggest that a 3% difference in ITS sequence between two fungal cultures, or collections of fruit bodies, is indicative of separate species, but this judgement is not founded on sound experimental evidence. The percentage differences in ITS sequences between species are certain to vary among different groups of fungi. Resolution of these profound uncertainties is the great challenge of modern taxonomic research.

### *Implications of Molecular Phylogeny*

Fungal classification is driven by the goal of producing a truly natural scheme that reflects evolutionary relationships between species. It is worth considering why this is viewed as an important objective. By recognising the evolutionary affinities of species, we immediately obtain useful information on the biology of a particular fungus by referring to what is known about its relatives. Interesting features of ecology, physiology, cell biology, and metabolism are often shared by related species, and so knowledge of a larger taxonomic group can inform research on a particular species. If, for example, two species in a fungal genus are capable of detoxifying oil-contaminated soil, it might be productive to study the biochemical attributes of other members of the genus. A second justification for investing time and money in this effort comes from the fundamental desire of biologists to understand nature. The pursuit of a natural classification of the fungi is revealing a wealth of information about the origins of these organisms, including estimates of the timing of the development of the major phyla. This is part of the story of life on Earth and there are few more interesting topics in science.

An important consideration in thinking about fungal classification is that the species with which we share our lives represent a tiny fraction of all of the fungi that have existed during the hundreds of millions of years of mycological history. This means that the closest relatives of many present-day species diverged from their common ancestor a very long time ago. In the intervening aeons of time, vast numbers of extinctions have pared away the majority of species, leaving huge gaps in the evolutionary tree. This makes it very difficult to unravel relationships between groups of fungi based on molecular analysis of living organisms. The scale of biological extinction is a huge challenge for phylogenetic studies on other groups of organisms, but the problem is alleviated when we look at the evolution of vertebrates, for example, by the availability of a rich fossil record. For these reasons, much of the evolutionary history of the fungi is obscure and this limits confidence in the details of the current natural, or evolutionary, classification of this diverse kingdom of microorganisms. With these shortcomings in mind, however, our picture of fungal diversity is incomparably richer than the textbook view of mycology even a generation ago. We turn now to the contemporary view of fungal classification.

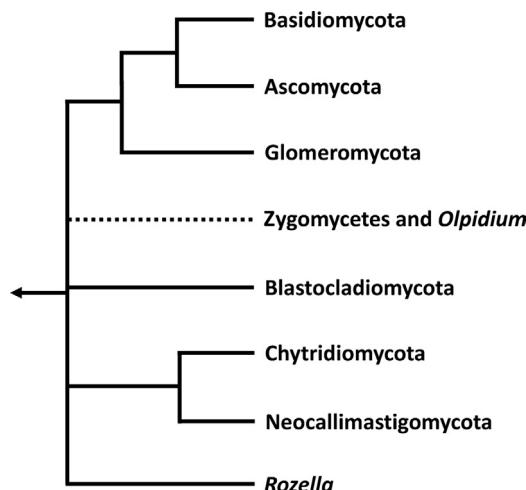
## FUNGAL PHYLA

Six phyla are recognised in the current taxonomic arrangement of the fungi:

### Kingdom Fungi

- Phylum Basidiomycota
- Phylum Ascomycota
- Phylum Glomeromycota
- Phylum Blastocladiomycota
- Phylum Chytridiomycota
- Phylum Neocallimastigomycota

The evolutionary relationships between these phyla is shown in [Figure 1.5](#). The name **Dikarya** has been proposed as a subkingdom that comprises the Basidiomycota and Ascomycota. The name refers to the formation of cells containing two nuclei during the process of sexual reproduction in these fungi (described later in this chapter). Genetic data indicate that some fungi do not fit neatly within any of the six phyla, but we do not have sufficient information to delineate additional phyla. These include 900 or more species of zygomycete, including *Mucor mucedo* that is used to illustrate simple sexual life cycles in laboratory classes. These organisms were identified as the Phylum Zygomycota in earlier classifications, but because these fungi do not seem to represent a cohesive phylogenetic assemblage, we will refer to them as zygomycetes in this book. Other fungi grouped in earlier classifications within the Zygomycota have been assigned to other phyla. In addition to the phyla listed above, there are more than 1000 species of animal parasite called microsporidians that many taxonomists regard as part of Kingdom Fungi. They are treated as a separate phylum called the Microspora in some classifications, but their evolutionary relationship to the other fungal phyla is not understood. In this portion of the book we will survey each of the major groups of fungi, describe their unifying characteristics, and provide examples of species.



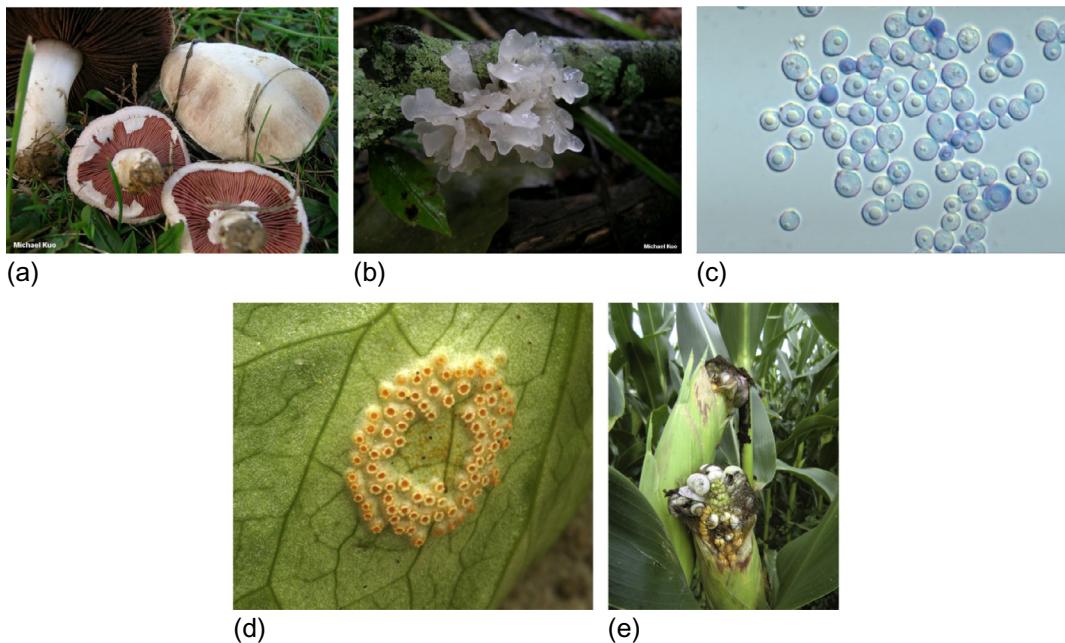
**FIGURE 1.5** Phylogenetic tree showing relationships within Kingdom Fungi. *Rozella* is a genus of aquatic fungi that does not fit into existing phyla. It is a representative of a diverse group of fungi identified using molecular genetic methods that has been proposed as a seventh phylum called the Cryptomycota.

## Phylum Basidiomycota

### Overview and Unifying Characteristics

The 30,000 described species of Basidiomycota include mushroom-forming fungi, jelly fungi, yeasts, rusts, and smuts (Figure 1.6). These fungi play a multitude of ecological roles. Many mushroom-forming species support forest ecology through the formation of mycorrhizal symbioses with trees and shrubs and others by decomposing wood and leaf litter (Chapters 5 and 7). Basidiomycetes partner with termites and leaf-cutter ants in complex symbioses in which the fungi are farmed by the insects, and other basidiomycetes feed upon scale insects that they protect under a crust. Basidiomycetes also cause animal diseases, including potentially lethal infections of humans and the rusts and smuts are among the most important pathogens of plants (Chapters 8 and 9).

Molecular phylogenetic analyses are effective at separating the majority of the Basidiomycota from other fungi and this genetic distinction is reflected in a handful of shared structural and developmental characteristics. The Basidiomycota produce spores called **basidiospores**. Basidiospores form on the outside of cells called **basidia**. Nuclear fusion and meiosis occur within the basidia and the resulting tetrad of haploid nuclei is transmitted into buds that differentiate into the basidiospores. There are many variations upon this typical life cycle, including the formation of basidiospores on the surface of individual haploid yeast cells following mitotic division of the nucleus. A second common feature of the group is the **dolipore septum** that partitions successive compartments along the length of the basidiomycete hyphae. This septum is perforated by a central canal (pore) that is defined by a barrel-shaped swelling of the septum cell wall. Structural details are provided in Chapter 2. Nuclei cannot migrate through unmodified dolipore septa and their distribution within the hyphae that develop after the fusion of sexually compatible colonies involves the formation of **clamp connections** (see next section). Clamp connections are a third characteristic of this phylum. All

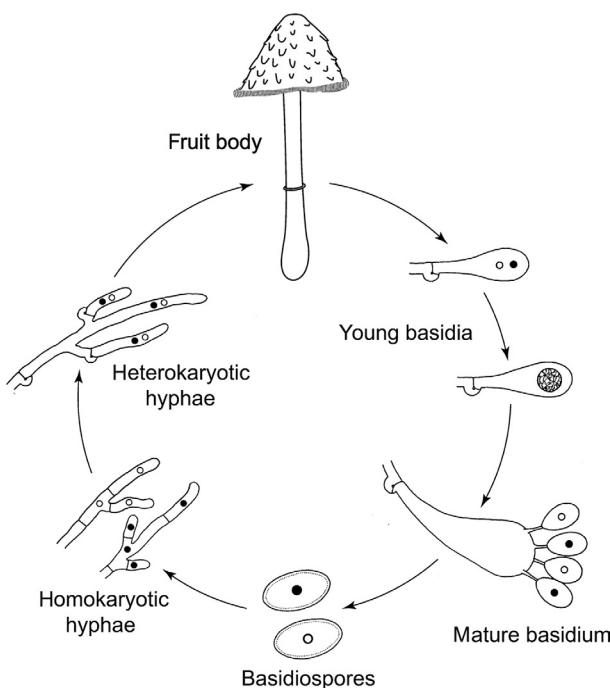


**FIGURE 1.6** Diversity of the Basidiomycota. (a) *Agaricus campestris*, the field mushroom. (b) *Tremella fuciformis*, a jelly fungus. (c) *Malassezia globosa*, yeast associated with dandruff. (d) *Puccinia sessilis*, a rust, on *Arum maculatum*. (e) *Ustilago maydis*, corn smut. Source: (a, b) Michael Kuo, (c) [http://www.pfdb.net/photo/nishiyama\\_y/box20010917/wide/024.jpg](http://www.pfdb.net/photo/nishiyama_y/box20010917/wide/024.jpg), (d) [http://upload.wikimedia.org/wikipedia/commons/ff8/Puccinia\\_sessilis\\_0521.jpg](http://upload.wikimedia.org/wikipedia/commons/ff8/Puccinia_sessilis_0521.jpg), and (e) [http://aktuell.ruhr-uni-bochum.de/mam/images/pi2012/begerow\\_maisbeulenbrand.jpg](http://aktuell.ruhr-uni-bochum.de/mam/images/pi2012/begerow_maisbeulenbrand.jpg)

basidiomycetes produce basidiospores, but basidiomycetes that grow exclusively as yeasts do not form them on basidia, nor do these fungi produce septa or clamp connections. But, any fungus with dolipore septa or clamp connections is a member of the Basidiomycota.

### *Basidiomycete Life Cycle*

There are some important differences among the life cycles of the Basidiomycota, but the following description of the developmental processes typical of a mushroom-forming species serves as a template for understanding the way that other basidiomycetes operate (Figure 1.7). A single basidiospore germinates to form a branching colony of filamentous hyphae. This young mycelium is composed of multiple compartments, separated by dolipore septa, each containing a single haploid nucleus in most species. These nuclei are formed by mitosis, beginning with the first division of the single nucleus within the founding spore. The resulting mycelium is termed a homokaryon because all of its nuclei are genetically identical clones. It is also called a monokaryon because the compartments contain single nuclei (see page 103–106). Homokaryotic mycelia expand through soil and wood, or other food materials. Some species can produce fruit bodies without mating, but the homokaryons of most mushroom-forming fungi fuse with other homokaryons before fruiting. When a pair of sexually compatible homokaryons merge they produce **heterokaryotic mycelia** in which each hyphal compartment contains a pair of nuclei, one derived from each mate. Compatibility is



**FIGURE 1.7** Life cycle of *Coprinus comatus*, the lawyer's wig. This is an example of a mushroom with a bipolar mating system that involves the fusion of homokaryotic colonies whose nuclei contain different alleles of a single mating type gene (open and closed circles). The resulting heterokaryon contains nuclei of both mating types. Fusion of these nuclei, followed by meiosis, occurs within basidia to produce four basidiospores.

determined by mating type genes (Chapter 4). The terms **dikaryon** and **dikaryotic mycelium** are also used to describe these colonies.

Clamp connections are crucial in the development of the heterokaryon (Figure 1.8). Consider an apical compartment of a heterokaryotic hypha: it contains two nuclei, one derived from each original mate. When these nuclei divide, a septum will form at a right angle across each mitotic spindle, creating three hyphal compartments; without the clamp connection, only one of the three compartments would be likely to contain nuclei of both mating types. Clamp connections are lateral branches that create bridges for nuclear movement between regions of the hypha that will become separate compartments. They allow the developing heterokaryon to populate each new compartment with nuclei of both mating types. This process of heterokaryon formation precedes the formation of fruit bodies in most Basidiomycota. It is regulated by interactions between the mating type genes within the cell that only permit clamp connections to form when the homokaryotic parents are sufficiently unrelated.

The elaboration of a mushroom from the colony of feeding filaments begins with the development of a knot of hyphae. As this pinhead-sized aggregate of cells enlarges, stem, cap, and gills become visible, priming the developing embryo, or button, for rapid expansion into the mature reproductive organ as soon as environmental conditions are conducive. **Basidia** form at the ends of hyphae whose tips stop growing at the surfaces of gills, spines, the interior of tubes, and other locations of spore production. These fertile tissue of a fruit

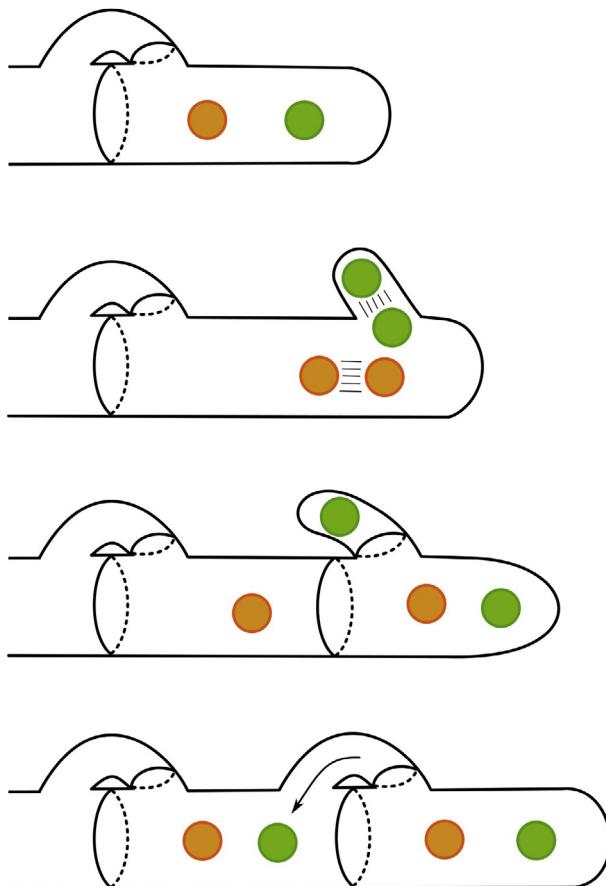


FIGURE 1.8 Formation of clamp connections on heterokaryotic basidiomycete hypha. Source: Creative Commons.

body is referred to as the **hymenium**. Like the billions of other cell compartments within the tissue of the mushroom, the young basidia are heterokaryotic, containing copies of the nuclei derived from the parent homokaryotic colonies. These fuse and then undergo meiosis to produce four haploid nuclei, each of which is packaged into one of the four basidiospores formed from the basidium. (Four is the usual number of spores per basidium, but some species produce single spores from each basidium, and pairs and multiple spores are also quite common configurations.) The spores are discharged from the gill surface by a mechanism described as a surface-tension catapult that is detailed in Chapter 3. Relative to spore production over a flat surface, gills achieve a maximum 20-fold increase in surface area, and the output of spores from some mushrooms is astonishing. A single basidiome of *Agaricus campestris* can discharge 2.7 billion microscopic spores per day, or 31,000 spores per second; 2 million tubes on the underside of a bracket of the wood-rotting basidiomycete *Ganoderma applanatum* can shed 30 billion spores per day, or more than 5 trillion in the 6 months that the perennial bracket is active each year!

### Taxonomic Groups Within the Basidiomycota

#### SUBPHYLUM: AGARICOMYCOTINA (MUSHROOMS, JELLY FUNGI, AND YEASTS)

The Agaricomycotina includes all of the Basidiomycota that form macroscopic fruit bodies, including mushrooms and jelly fungi, along with a variety of basidiomycete yeasts. There are three classes: **Agaricomycetes**, **Dacrymycetes**, and **Tremellomycetes**.

The Agaricomycetes contains the 16,000 species of identified mushroom-forming species. The variety of fruit body (**basidiome**) morphology in this group is remarkable: stalked umbrella-shaped mushrooms and brackets produce spores on the surface of gills or teeth, over flat or rippled surfaces, or over the inner surfaces of tubes; other species form branched basidiomes that resemble corals; basidiomes can form as gelatinous cushions or sticky, ear-shaped growths, and Agaricomycetes also produce vast numbers of basidiospores within closed fruit bodies, including puffballs and earth-stars (Figure 1.4). There are Agaricomycetes that develop underground, resembling ascomycete truffles, and others that form packets of spores in egg-like structures (peridioles) that are splashed from the cups of bird's nest fungi or propelled into the air by species of artillery fungus. As discussed in the '[The Classification of Fungi](#)' section, the morphology of the basidiome provides little guidance in understanding evolutionary affinity among the Agaricomycetes. Some individual orders contain species with all manner of mushroom types. Examples of the orders will be introduced here.

### Agaricales

This is the largest order within the Agaricomycotina, containing 8500 or more described species including the cultivated button mushroom, *Agaricus bisporus*, the ink caps (*Coprinus* and other genera), the lethal death cap, *Amanita phalloides*, hallucinogenic species of *Psilocybe*, and the world's largest organisms, *Armillaria gallica* and *Armillaria solidipes*. Most of these mushrooms are saprotrophs, feeding on plant debris in soils and rotting wood, or ectomycorrhizal fungi that absorb sugars from the roots of living trees and shrubs. A handful of species form mutualistic symbioses with ants and termites, and a few of the Agaricales are important plant pathogens. The first genome of a gilled mushroom, called *Laccaria bicolor*, was sequenced in 2008. This fungus forms mycorrhizas with pine, fir, birch, and poplar trees and is important in tree nurseries where it is added to soil to boost seedling growth. Its genome is quite large, containing 65 million base pairs (As and Ts, Gs and Cs), but is dwarfed by the 3 billion or so rungs on the ladder of the human genome. When we look at the number of genes that encode proteins, the comparison is more humbling: 20,000 for the mushroom, and between 20,000 and 25,000 for us. The fungus produces hundreds of enzymes that dissolve proteins, fats, and carbohydrates in the soil, but it lacks the usual catalysts for decomposing the cellulose and lignin of plant cell walls that are secreted by many other mushrooms. This is significant because it seems likely that *Laccaria* and other mycorrhizal fungi evolved from wood-rotting ancestors and must have lost these enzymes as they adopted their new lifestyle. In addition to fungi with umbrella-shaped mushrooms, the Agaricales encompasses species with clavarioid (cylindrical or club-shaped) fruit bodies, puffballs, and the bird's nest fungi with their extraordinary fluted fruit bodies from which spore-containing peridioles are ejected by raindrops.

## Boletales

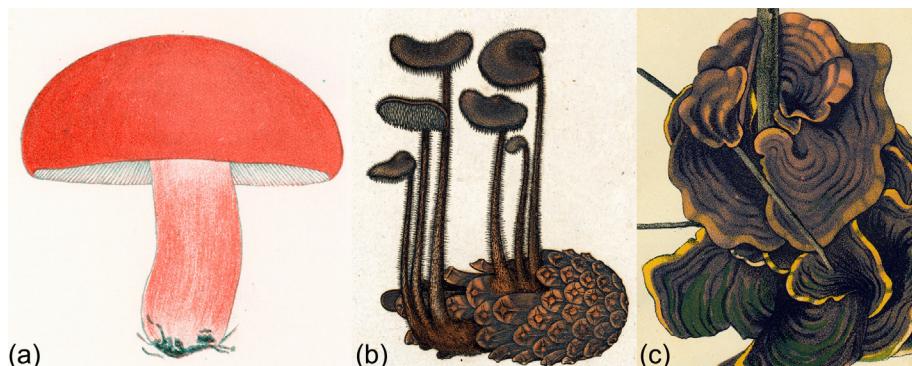
The Boletales include 300 species of *Boletus* whose spores are discharged from the surfaces of tubes beneath the mushroom cap. These fungi form ectomycorrhizas with the roots of forest trees. *Boletus edulis*, known as the king mushroom, cep or porcini, is a very important edible wild mushroom. It is harvested in Italy, Eastern Europe, China, Southern Africa, and North America. The dry rot fungus, *Serpula lacrymans*, is a saprotrophic member of the Boletales. This fungus is tremendously important as a cause of wood decomposition in buildings and is thought to have evolved from mycorrhizal ancestors. The cellar fungus, *Coniophora puteana*, is another member of the Boletales that damages buildings. There is some morphological diversity within the order, including the earth-balls (*Scleroderma* species, Figure 1.4d) that produce spherical fruit bodies superficially resembling puffballs, and the fruit bodies of *S. lacrymans* and *C. puteana* that take the form of crusts on the surface of the rotting wood.

## Russulales

Species form all kinds of fruit bodies in this order (Figure 1.9), including mushrooms with gills (*Russula* and *Lactarius* [milk caps]), teeth (*Auriscalpium*), and tubes (*Bondarzewia*), others forming little lozenges and flattened crusts (*Peniophora* and *Aleurodiscus*), and still others producing intricate coral shapes (*Clavicorona*). There are mycorrhizal, saprotrophic, and a few parasitic Russulales.

## Polyporales

Most of the 1800 or so species of Polyporales (shelf fungi) cause rot in standing trees and fallen logs. Their activity as wood decomposers is vital to the health of forest ecosystems. Many species are saprotrophs and grow exclusively on standing dead wood, logs, and other woody debris. Others, including species of *Ganoderma* and *Fomes*, attack living tissues and



**FIGURE 1.9** Diversity of fruit body morphology in the Russulales, Agaricomycotina. (a) Gilled mushroom, *Russula lepida*; (b) hydnoid or toothed fruit body of *Auriscalpium vulgare*; (c) flattened fruit body of *Stereum ostrea*, the false turkey tail. Source: (a) Lange, J.E., 1940. *Flora Agaricina Danica*, vol. 5. Recato, Copenhagen; (b) Bulliard, P., 1791. *Histoire des Champignons de la France*. Chez L'auteur, Barrois, Belin, Croullebois, Bazan, Paris; (c) Inzenga, G., 1869. *Funghi Siciliani Studii*, vol. 2. Di Francesco Lao, Palermo.

continue to decompose the wood of their dead hosts. *Ganoderma lucidum* (reishi) and other Polyporales have been used as natural medicines in traditional Chinese medicine. Purified cell wall polysaccharides from these fungi have a wide range of pharmacological activities. The majority of the bracket fungi that shed spores from tubes beneath their caps are Polyporales, but the order also includes hundreds of **corticoid** species whose fruit bodies are flattened crusts on the surface of logs.

## Phallales

Stinkhorns and their relatives are among the minority of Basidiomycota that have lost the catapult mechanism of spore discharge (ballistospory) and interact with animals that disperse their spores. The common stinkhorn, *Phallus impudicus*, expands an epigaeous (above ground) fruit body with a slime covered head in which the spores are embedded. A variety of volatile compounds diffuse from the slime (gleba) and attract carrion flies and other invertebrates. These animals act as vectors for stinkhorn dispersal when they carry the basidiospores on their bodies as well as consuming and defecating them some distance from the parent fruit body. The order includes other species whose foul-scented glebal slime is exposed on the surface of fruit body tissues that expand into cages (*Clathrus*) and star shapes (*Anthurus*).

## Auriculariales

The edible Judas ear mushroom, *Auricularia auricula-judae*, is the best known fungus in this order. Its ear-shaped fruit bodies develop from mycelia on elder (*Sambucus*) and other woody plants. Basidiospores form on elongated basidia that are partitioned into four compartments by transverse septa. These form on the lower surface of the 'ears' and the spores are catapulted into the air beneath the fruit body. The fruit bodies have a rubbery texture and have been cultivated for centuries in Asia. *Exidia glandulosa*, witches' butter, is another species in this order that forms black fruit bodies on decaying wood. Its basidia are divided lengthwise into four compartments.

## Jelly Fungi: Dacrymycetes and Tremellomycetes

Like the Auriculariales, jelly fungi in this pair of taxonomic classes form distinctive basidia. The basidium of the Dacrymycetales is shaped like a tuning fork and forms one spore at the tip of each of its two branches (epibasidia). In the Tremellomycetes, the basidium is divided into four separate compartments by septa that run through the cell longitudinally. Basidiospores develop at the tips of epibasidia that extend from each of the compartments. The fruit bodies of some species of both classes of jelly fungus are brightly coloured. In the Dacrymycetes, *Dacrymyces stillatus* forms tiny orange cushions on wet decomposing wood and *Calocera* species sprout orange spikes in similar locations. Colourful Tremellomycetes include the bright yellow or orange membranous fruit bodies of *Tremella mesenterica*. Its relative *Tremella fuciformis* is cultivated in China and is called the silver ear fungus. The life cycles of the Tremellomycetes involve switching between hyphal and yeast phases. This process occurs in *Cryptococcus neoformans* that adopts a budding unicellular morphology in the human nervous system where it causes life-threatening infections (Chapter 9). Species of *Tremella* are

mycoparasites that feed on the colonies of other fungi in decomposing wood and some species form their gelatinous fruit bodies on the basidiomata of their hosts.

### ***Subphylum: Ustilaginomycotina (Smuts)***

The smuts are obligate pathogens of plants that cause devastating diseases of cereal crops including common bunt or stinking smut of wheat, caused by *Tilletia caries*, and corn smut (of maize), caused by *Ustilago maydis* (Chapter 8). The majority of the more than 1000 species of smut fungi infect flowering plants, but some cause diseases in conifers, ferns, and lycopophytes. Related fungi within the Ustilaginomycotina include the yeast *Malassezia globosa* that is part of the natural microbial community on the human scalp and is associated with dandruff.

*U. maydis* has been studied in greater detail than other smuts. Genetic manipulation of this fungus, and the sequencing of its genome, has allowed researchers to use the smut as a model system for understanding interactions between pathogens and host plants. The fungus has also been used in cancer research. Disruption of a gene in the smut called *brh2*, which is related to the human tumour suppressor gene *BRCA2*, results in a deficiency in DNA repair mechanisms. This is consistent with a mechanistic link between mutations in the human gene and an increased risk of developing breast cancer.

The life cycle of *U. maydis* differs greatly from the mushroom life cycle in its details, but it shares the heterokaryotic phase with other members of the phylum (Figure 1.10). The smut alternates between a budding yeast phase and a filamentous mycelium; the yeast phase is saprotrophic and can be cultured in the lab, but the mycelium grows only within the tissues of the host plant. The yeast cells contain single haploid nuclei and mating, to form the heterokaryon, is controlled by two genetic loci, *a* and *b* (Chapter 4). The *a* locus contains genes that encode the precursors of sex hormones and receptors to these hormones. There are two versions of these loci, *a1* and *a2*, and the fungus can mate only with a strain of the opposite mating type; the *a1* pheromone docks with the *a2* receptor, and vice versa. When compatible strains are paired, they form conjugation tubes that grow toward one another and fuse at their tips. Fusion produces a dikaryon but this is stable and capable of infecting the host only when mating occurs between strains that differ in their *b* locus alleles. The *b* locus contains a pair of genes that encode transcription factors. There are more than 25 different *b* locus alleles, which means that there are hundreds of different combinations of compatible mating types that produce pathogenic heterokaryons.

As the heterokaryon penetrates the tissues of its host plant, it causes the development of tumours or galls. Tumour development within the flowers of *Zea mays* results in the formation of masses of swollen kernels. The mycelium within these galls is converted into blackened spores (the source of the name ‘smut’), called **teliospores**, and nuclear fusion occurs during this process so that each spore contains a single diploid nucleus. The teliospores are dispersed by wind, but they can also lie dormant during winter months. Under appropriate environmental conditions, the diploid nucleus divides by meiosis and the spore germinates to produce a filamentous **promycelium** that forms haploid buds, or **sporidia**, on its surface. These sporidia are the source of the yeast phase that proliferates on the surface of the host plant before mating, dikaryon formation, and infection. The teliospore plays a comparable role to the basidium in the mushroom life cycle, as the site for nuclear fusion and subsequent meiosis. The spore-filled galls or tumours on maize are a Mexican delicacy called huitlacoche, which is used in soups, as a flavourful filling in tamales, in ice cream, and many other dishes.

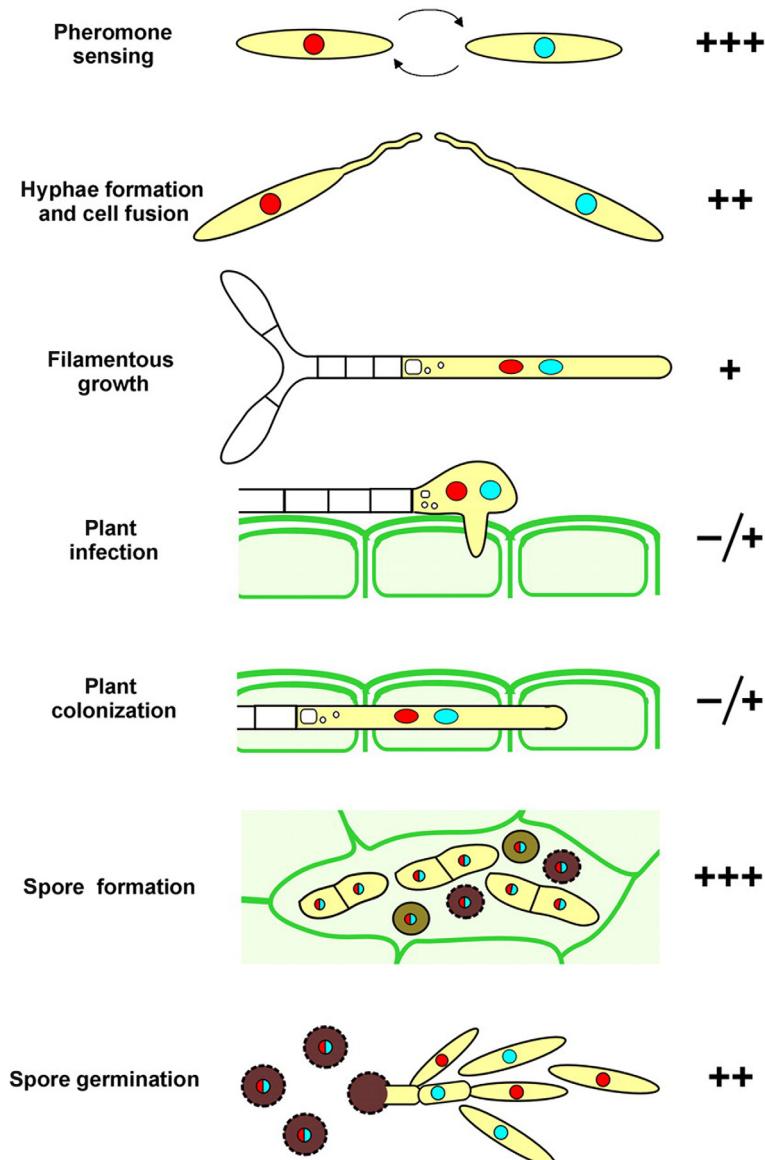


FIGURE 1.10 Life cycle of corn smut, *Ustilago maydis*. Source: Fuchs, U. et al., 2006. Endocytosis is essential for pathogenic development in the corn smut fungus *Ustilago maydis*. *Plant Cell* 18, 2066–2081.

The fungus has been eaten for centuries and was part of Aztec, Hopi, and Zuni cuisine long before the Spanish conquests in the sixteenth century.

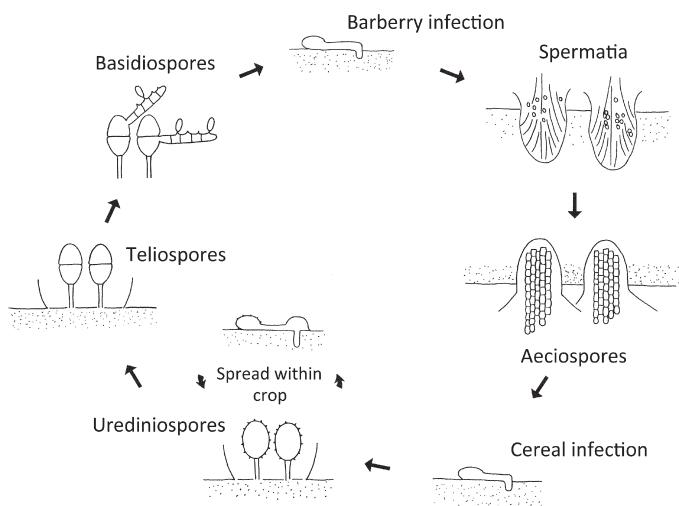
The basidiomycete affinity of *U. maydis* is evident from its genome and is reflected in the dikaryotic phase of its life cycle. Like other basidiomycetes, the dikaryotic hyphae of the smut are partitioned by septa, but these are relatively simple structures compared with the dolipore

septa of mushroom-forming species. *Ustilago* species also lack the ballistospore discharge mechanism that is emblematic of the phylum Basidiomycota. The mechanism does operate, however, in other smut fungi, including *T. caries*. There are many variations among the life cycles of the smut fungi. *Microbotryum violaceum* has a much simpler mating system than corn smut, with sexual compatibility controlled by a single genetic locus with a pair of alleles. This fungus infects the anthers of campion species (Caryophyllaceae), *Silene dioica* and *Silene alba*, that produce separate male and female plants (i.e. they are dioecious species). When the fungus infects the female flowers, it suppresses the formation of the ovaries and stimulates the production of stamens. The infected anthers fill with teliospores, completely subverting plant reproduction, and butterflies and other insect pollinators disperse the parasite's teliospores.

### *Subphylum Pucciniomycotina (Rusts and Allies)*

Most of the more than 7000 species within this subphylum are rust fungi that are obligate parasites of plants. Septobasidiaceae form mutualistic symbioses with scale insects are closely related to the rusts. More distantly related Pucciniomycotina include plant pathogens that were classified originally as smuts. The basidiomycete affinities of the rusts are indicated by the formation of a dikaryotic phase in the life cycle that precedes nuclear fusion and meiosis. The rusts produce septa, but not the dolipore type of other basidiomycetes. They do, however, release ballistospores using the same catapult mechanism characteristic of the mushroom-forming species. The life cycle of many rusts is exceedingly complicated, involving as many as four distinct types of spore.

*Puccinia graminis* causes black stem rust of wheat and is often used to illustrate the processes of infection and dispersal utilised by rusts to move between two species of host plant and to recombine genes by sexual reproduction (Figure 1.11). Rusts often have alternate hosts and this cereal pathogen infects barberry, *Berberis vulgaris* and *Berberis canadensis*. *Puccinia* forms four types of spores: **urediniospores**, **teliospores**, and **basidiospores** on wheat, and **aeciospores** on barberry. Sexual reproduction is achieved by the transfer of gametes, called



**FIGURE 1.11** Life cycle of the rust, *Puccinia graminis*. Source: Money, N.P., 2002. *Mr. Bloomfield's Orchard. The Mysterious World of Mushrooms, Molds, and Mycologists*. Oxford University Press, New York.

**spermatia** (singular **spermantium**), which are transferred between pustules on barberry leaves by insects. The name rust refers to the reddish lesions that develop on wheat leaves and shed the reddish urediniospores. Urediniospores are dikaryotic, containing a pair of nuclei. They are dispersed by wind and germinate on leaf surfaces under humid conditions when the stomata are likely to be open. When the germ tube locates a stoma it inflates over the opening, forming an **appressorium**, and penetrates the leaf. The infectious mycelium develops between the leaf cells and produces branches called **haustoria** that penetrate the host cell walls. The haustoria form a tight connection with the host cell without destroying its plasma membrane, supporting sustained nutrient absorption from the living plant. This is characteristic of **biotrophic pathogens**. The rust can complete multiple rounds of urediniospore production, release, and cereal infection, allowing the disease to spread as an epidemic among susceptible hosts over a wide region. Toward the end of the growing season, uredial lesions are converted into black streaks producing teliospores. These telial lesions are responsible for the black stem reference in the common name for the disease. Teliospores of *P. graminis* have two cells supported on a stalk. Initially, each of the cells contains a pair of haploid nuclei, but these fuse to form a single diploid nucleus. In this condition, the thick-walled teliospores can survive within stubble during cold winter months. The teliospores germinate in the spring to produce a short septate hypha or promycelium from each cell. The single diploid nucleus in each cell of the teliospore divides by meiosis and the resulting haploid nuclei are packaged in four basidiospores. These spores are discharged into the air by the same catapult mechanism described in mushrooms and they infect barberry leaves.

Within the barberry leaf, the rust produces feeding haustoria again and forms flask-shaped structures on the upper leaf surface, called **spermagonia** that exude spermatia in a sugar-rich fluid. This nectar attracts flies and other insects that transfer spermatia between spermagonia on the same plant and to neighbouring plants. Each spermatium acts as a gamete, its single haploid nucleus fertilising a compatible spermagonium. There are two mating types (+) and (-) and cross fertilisation between these mating types converts the existing mycelium in the barberry leaf into a dikaryon. The final spore type, the aeciospore, is formed in pustules called **aecia** on the underside of the leaf. The dikaryotic aeciospores are spread by wind and infect susceptible wheat plants.

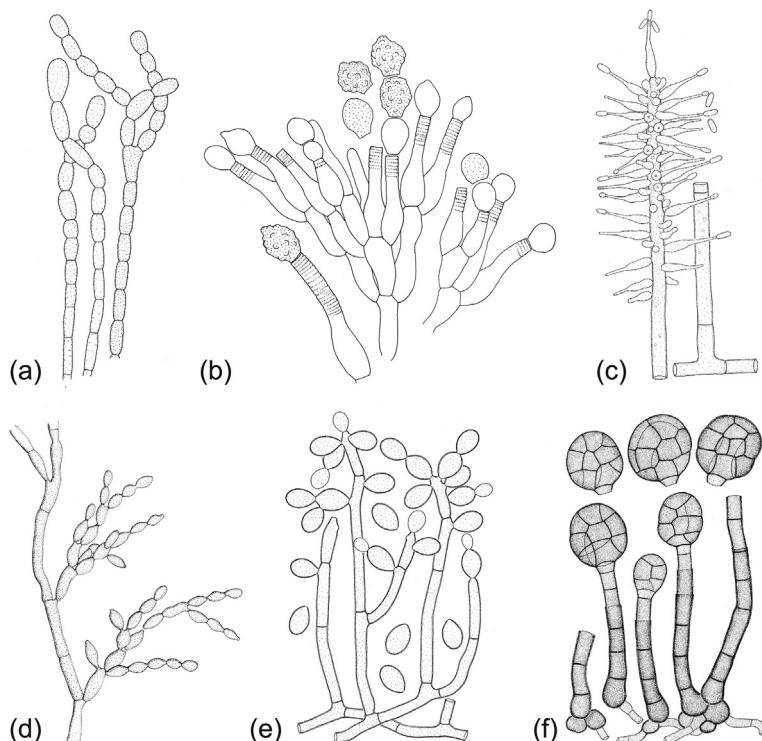
Other rusts have less complex life cycles missing one or more of the spore-producing stages described for *P. graminis*, or complete their life cycles on a single host species. *Gymnosporangium globosum*, which causes hawthorn rust, produces its spermatia and aeciospores on hawthorn (*Crataegus*) and its teliospores and basidiospores on evergreens. It lacks the urediniospore stage of the life cycle. Coffee rust is caused by *Hemileia vastatrix* that produces urediniospores, teliospores, and basidiospores on coffee (*Coffea*). The function of the basidiospores is unknown because a second host has not been identified. *Uromyces viciae-fabae*, which causes rust of faba bean (broad bean, *Vicia faba*), produces all four of the spore types and spermatia on the same species of host plant.

## Phylum Ascomycota

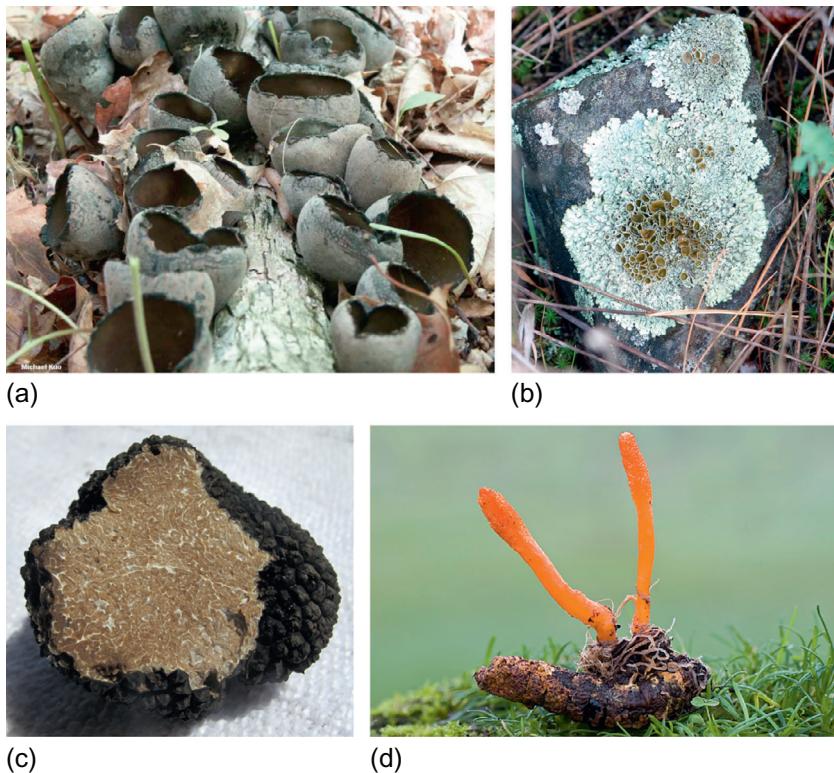
### *Overview and Unifying Characteristics*

The Ascomycota is the largest phylum of fungi encompassing more than 33,000 named species and a vast number of undescribed fungi. The phylum includes yeasts and filamentous fungi, fungi that partner with algae and cyanobacteria to form **lichen symbioses**, mycorrhizal

species, saprotrophs, and pathogens of plants and animals. Ascomycetes are utilised in industrial applications, in food production and flavouring, and the fruit bodies of morels and truffles are prized edible fungi. Many species are known only as asexual fungi (**anamorphs**) that produce asexual spores (**conidia**) on stalks called **conidiophores** (Figure 1.12), but sexual phases (**teleomorphs**) have been identified in the life cycles of most ascomycetes that have been studied in detail. The sexual organs formed by ascomycetes are called **ascomata** (s. **ascoma**, Figure 1.13). Ascomata include open cup-shaped fruit bodies (**apothecia**), flask-shaped structures with a single vent for spore release (**perithecia**), and fruit bodies that develop as closed structures that open in a variety of ways to release spores (**cleistothecia**). Ascomata contain the characteristic spore-producing cells of the phylum called **asci** (s. **ascus**).



**FIGURE 1.12** Selection of conidial stages, or anamorphs, of ascomycetes. (a) *Basipetospora variabilis*, a soil fungus. (b) *Scopulariopsis brevicaulis*, a saprotroph that grows in soil and causes opportunistic infections of humans. (c) *Harziella (Lepisticola) capitata*, which grows on fruit bodies of *Lepista nuda* (blewits). (d) *Tyrannosorus pinicola*, isolated from rotting wood. (e) *Haplodichthium chilense*, isolated from wood. (f) *Junewangia globulosa*, isolated from rotting plant stems. Source: (a) Minter, D.W., Kirk, P.M., Sutton, B.C., 1983. Thallic phialides. *Trans. Br. Mycol. Soc.* 80, 39–66; (b) Minter, D.W., Kirk, P.M., Sutton, B.C., 1983. Holoblastic phialides. *Trans. Br. Mycol. Soc.* 79, 75–93; (c) Gams, W., Seifert, K.A., Morgan-Jones, G., 2009. New and validated hyphomycete taxa to resolve nomenclatural and taxonomic issues. *Mycotaxon* 110, 89–108; (d) Müller, E., et al., 1987. Taxonomy and anamorphs of the Herpotrichellaceae with notes on generic synonymy. *Trans. Br. Mycol. Soc.* 88, 63–74; (e) Partridge, E.C., Baker, W.A., Morgan-Jones, G., 2001. Notes on Hyphomycetes. LXXXII. A further contribution toward a monograph of the genus *Haplodichthium*. *Mycotaxon* 78, 127–160; (f) Baker, W.A., Partridge, E.C., Morgan-Jones, G., 2002. Notes on Hyphomycetes. LXXXV. *Junewangia*, a genus in which to classify four *Acrodicrys* species and a new taxon. *Mycotaxon* 81, 293–319.



**FIGURE 1.13** Examples of fruit bodies, or ascocarps, produced by Ascomycota in Subphylum Pezizomycotina. (a) Goblet shaped apothecia of *Urnula craterium*, the Devil's urn. (b) Flattened discoid apothecia on the thallus of a species of the lichen *Xanthoparmelia*. (c) Highly modified apothecium of the summer truffle, *Tuber aestivum*. (d) Perithecial stroma of *Cordyceps militaris* fruiting from parasitized caterpillar. Source: (a) Michael Kuo, (b) [http://en.wikipedia.org/wiki/Lichen#/media/File:Lichen\\_reproduction1.jpg](http://en.wikipedia.org/wiki/Lichen#/media/File:Lichen_reproduction1.jpg), (c) [http://upload.wikimedia.org/wikipedia/commons/8/89/Tuber\\_aestivum\\_Valnerina\\_018.jpg](http://upload.wikimedia.org/wikipedia/commons/8/89/Tuber_aestivum_Valnerina_018.jpg), (d) [http://upload.wikimedia.org/wikipedia/commons/4/44/2008-12-14\\_Cordyceps\\_militaris\\_3107128906.jpg](http://upload.wikimedia.org/wikipedia/commons/4/44/2008-12-14_Cordyceps_militaris_3107128906.jpg)

The sexual spores of ascomycetes, called **ascospores**, form inside asci. This internal development of ascospores contrasts with the production of basidiospores on the outside of basidia in the Basidiomycota (compare Figure 1.14 with Figure 1.7). The hyphae of ascomycetes lack the dolipore septa and clamp connections of basidiomycetes; their septa have a single, central pore. Mobile organelles (microbodies) with dense protein cores, called **Woronin bodies**, plug the septal pores and isolate damaged hyphal compartments from the rest of the colony. These organelles are found in the largest subphylum, the Pezizomycotina, which contains 90% of the Ascomycota, but are absent from the other members of the phylum (whose groups are detailed below).

### Ascomycete Life Cycle

Like the Basidiomycota, it is impossible to detail a single life cycle that is applicable to all species within the Ascomycota. The perithecial ascomycete, *Neurospora crassa*, is used to illustrate the life cycle here and a few of the variations in other species are discussed when the

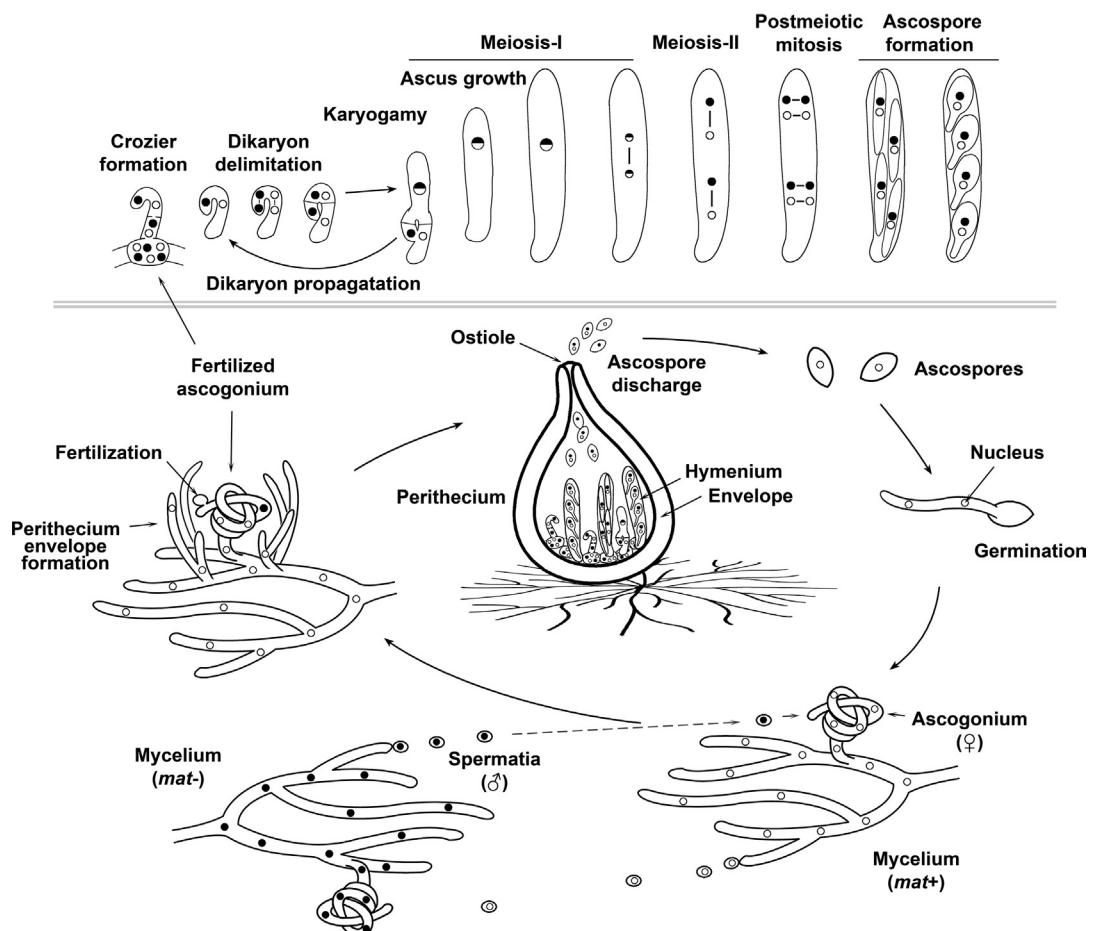


FIGURE 1.14 Sexual cycle of a filamentous ascomycete. Source: Peraza-Reyes, L., Berteaux-Lecellier, V., 2013. Peroxisomes and sexual development in fungi. *Front. Physiol.* 4, 244.

sub-phyla are introduced (Figure 1.14). Ascospores of *Neurospora* contain haploid nuclei that are replicated by mitosis when the spore germinates and distributed within the developing colony. The colony expands by hyphal extension and repeated branching, and septa form between multinucleate compartments. *N. crassa* is a heterothallic species with two mating types called *MAT A* and *MAT a*. All of the nuclei in a colony derived from a single ascospore are of the same mating type; the colony is homokaryotic. Sexual reproduction requires the formation of a heterokaryon that contains nuclei of both mating types. Unlike the basidiomycetes, ascomycetes do not form the extensive heterokaryotic colony or dikaryon. In *Neurospora*, a short-lived heterokaryon is formed within the developing ascoma. Colonies produce airborne **microconidia** (also called **spermatia**) that act as gametes, and these fuse with hyphae called **trichogynes** that project from the developing ascomata. The young ascoma is called the **protoperithecium**. Fusion between a microconidium and trichogyne of opposite mating

type produces a heterokaryotic or ascogenous hypha. Different mating processes in other ascomycetes include (i) fusion of swollen male and female gametangia, and (ii) fusion of undifferentiated hyphae.

As the perithecium of *Neurospora* develops, the ascogenous hyphae form hook-shaped tips, called **croziers**. A pair of nuclei at the end of the crozier divides by mitosis and septum formation isolates two of the resulting four nuclei, one of each mating type, in the crook of the crozier. This cell extends to form the ascus. Its pair of nuclei fuse, and then divide by meiosis to produce four haploid nuclei. In *N. crassa*, each of these nuclei divides by mitosis and each of the resulting eight nuclei is packaged into a separate ascospore. A second mitotic division occurs within each developing ascospore so that it is equipped with an identical pair of nuclei. Additional divisions may occur so that the ascospore becomes multinucleate. After the formation of the ascus, the ascogenous hypha can form additional croziers and generate a cluster of asci within the fruit body.

The nuclear events that take place in the crozier are comparable to those within the young basidium of the Basidiomycota. (The process of spore formation in both groups involves the differentiation of cells containing pairs of nuclei, which is the characteristic that unites these phyla in the subkingdom Dikarya.) The subsequent development of the spores is very different in the pair of largest phyla in Kingdom Fungi and, currently, there is no evidence of evolutionary homology between the crozier and basidium. There are a lot of variations among the ascosporogenesis process in the Ascomycota, but in all cases nuclei along with portions of cytoplasm are separated within the ascus and packaged within individual cell walls. In most species, this is achieved by the formation of a cylinder of two membranes inside the ascus cytoplasm. This double membrane lies inside the plasma membrane that lines the inner surface of the ascus cell wall and is called the **ascospore-delimiting membrane**. The ascospore-delimiting membrane folds and fuses around the developing spores, and their cell walls are deposited in the sandwich formed by this structure. The cytoplasm that remains around the spores is called the epiplasm. This develops a mucilaginous consistency in some species and, in others, forms a watery fluid. The epiplasm is expelled with the spores during the discharge process (Chapter 3).

### Taxonomic Groups Within the Ascomycota

#### SUBPHYLUM: PEZIZOMYCOTINA

Ten or more classes are designated within the Pezizomycotina. The subphylum includes saprotrophs that grow on woody and non-woody plant tissues, and on herbivore dung, parasites of plants and animals (particularly invertebrates), and partners in lichen and mycorrhizal symbioses. The variety of fruit bodies in the Pezizomycotina is remarkable. The cup fungi, with various types of apothecia, include the morels and truffles, many of the lichenized ascomycetes, species of *Rhytisma* whose apothecia are embedded in tar spots on leaves, and earth-tongues with club-shaped apothecia. The asci in these fungi open via lids in operculate species and by fracture of the ascus tip in inoperculate species. The asci are highly modified in the truffles and do not discharge spores into the air. Perithecial ascomycetes show comparable morphological diversity, ranging from species of *Neurospora*, *Sordaria*, and *Podospora* that form individual perithecia with a diameter of a few tenths of one millimetre, to *Xylaria*, *Daldinia*, and *Nectria* species whose multiple perithecia are embedded in the surface of larger fruit bodies called **perithecial stromata**. These fungi are ubiquitous in forest habitats where their colonies blacken decaying wood and their stromata develop as finger-like projections

from the ground, and tiny antlers, single or multiple spheres, and crusts on the surfaces of logs. Perithecial stromata are also produced by *Cordyceps*, *Metarrhizium*, and other arthropod pathogens, the cereal pathogen *Claviceps purpurea* (ergot), and *Epichloë* and related endophytes in grasses (Chapter 7). Tiny elongated perithecia formed by Laboulbeniales develop on the surface of insects and other arthropods, attached to the cuticle via a foot structure. These ascomycetes are regarded as parasites, but do not appear to incapacitate their hosts.

Cleistothelial ascomycetes include species of *Aspergillus* and *Penicillium* whose conidial phases are crucial in biotechnological applications including fermentation and food production, and the production of enzymes and antibiotics (Chapter 12). *Aspergillus* species are also significant as a source of carcinogenic aflatoxins in contaminated food and as pathogens of immune-compromised human patients where they cause **aspergillosis** (Chapter 9). Spore release from cleistothecia involves the release of ascospores by disintegration of the fruit body wall. In a different type of ascoma, called a **chasmothecium**, the ascospores are exposed to the air when the fruit body opens along a preformed line of weakness. *Erysiphe*, *Blumeria*, and other genera of powdery mildews form chasmothecia. Further structural diversity is seen in ascomycetes with **fissitunicate** ascospores in which spore release entails the splitting of the outer wall of the ascus, followed by inflation of the inner ascus wall before forcible discharge of the spores (Chapter 3). The fissitunicate ascospores develop inside distinctive types of ascocarps called **pseudothecia** and **hysterothecia**. Ascomycetes with fissitunicate ascospores include many important plant pathogens including species of *Pleospora*, and the sexual stages of *Cochliobolus*, *Venturia*, and *Cladosporium*. *Alternaria* species are saprotrophs and plant pathogens, whose abundant airborne conidia are a significant contributors to asthma. Sexual stages are not known in these fungi, but molecular data show that *Alternaria* species are related to *Pleospora*. *Sporormiella* is another of the ascomycetes that produces fissitunicate ascospores. *Sporormiella* species grow on herbivore dung. Their spores are so prevalent in the palynological record that changes in their abundance identify the mass extinction of large herbivores in North America at the end of the Pleistocene.

#### SUBPHYLUM: SACCHAROMYCOTINA

Fungi in this group produce budding yeast cells. Morphological diversity is limited, but pseudohyphae, consisting of short bud-producing filaments, are formed under certain conditions, and some of the species produce tip-growing hyphae and elongated ascospores. In nature, the yeast *Saccharomyces cerevisiae* thrives on the sugar-rich diet available in ripened fruits. Its ability to metabolise glucose under conditions of low oxygen availability and produce carbon dioxide and alcohol has allowed humans to brew beer, make bread, and ferment wine and other alcoholic beverages for thousands of years. The yeast cell reproduces as a haploid cell by budding. When the single nucleus divides by mitosis, one of the daughter nuclei is shifted into the bud. A single cell may produce a series of buds and each leaves a scar on the surface of the mother cell upon separation. There are two mating types in *Saccharomyces*, designated  $\alpha$  and  $\alpha$ . Cells of opposite (compatible) mating type fuse to produce a single diploid cell and meiosis converts this cell into an ascus containing four haploid ascospores.

*Candida* is a large genus of saprotrophic yeast species that grow on many different foods including soil and rotting wood. *Candida* species have been isolated from seawater and fish guts, but the best known of these yeasts is *Candida albicans* that is a resident in 80% of human population where it grows in the gut. *C. albicans* can also cause infections ranging from

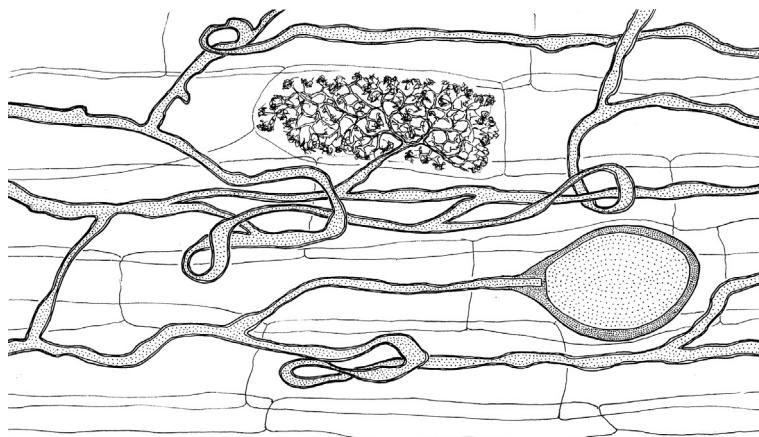
proliferation of the fungus in the oral or vaginal mucosa (thrush), to life-threatening invasive growth of the hyphal phase of the fungus (**invasive candidiasis**) in patients with debilitated immune systems. Yeast cells of *C. albicans* are diploid and mating produces a tetraploid zygote. A parasexual programme of chromosome loss is responsible for restoring the normal diploid complement of chromosomes. *Dipodascus* is another genus within the Saccharomycotina. Species of *Dipodascus* switch between a yeast and hyphal phase, and their haploid cells conjugate to produce elongated ascospores that contain multiple spores.

### SUBPHYLUM: TAPHRINOMYCOTINA

This subphylum contains five classes: Schizosaccharomycetes, Pneumocystidiomycetes, Neolectomycetes, Taphrinomycetes, and Archaeorhizomycetes. The Class Schizosaccharomycetes contains only three species of **fission yeast**, including *Schizosaccharomyces pombe*. Fission yeasts differ from budding yeasts in their mechanism of cell division: fission yeasts divide through the formation of a septum in the middle of the cell. This yeast is a saprotroph that grows on sugar-rich foods (e.g. fruits and honey). It is used as a model organism for research on the eukaryotic cell cycle and was the subject of investigations that were recognised by the award of the Nobel Prize for Medicine and Physiology in 2001 to Paul Nurse and colleagues. *Pneumocystis jirovecii* (Pneumocystidiomycetes) is an opportunistic pathogen of humans that causes pneumonia in patients with damaged immune systems. Species of *Neolecta* (Neolectomycetes) are the only members of this subphylum that produce a macroscopic fruit body: the other species are yeasts, although the plant parasitic Taphrinomycetes also form colonies of tip-growing hyphae within their host plants. The Archaeorhizomycetes were described in 2011 as an assemblage of hundreds of species of filamentous fungi whose rDNA was amplified from soil samples. These ascomycetes are associated with roots without forming typical mycorrhizal or endophytic structures. Although some of the Archaeorhizomycetes have been cultured, little is known about their biology.

### Phylum Glomeromycota

Ninety percent of all plants form mycorrhizal associations with fungi. The most widespread of these are arbuscular mycorrhizas produced by fewer than 200 species of fungi within the Phylum Glomeromycota. Genera include *Glomus*, *Acaulospora*, and *Gigaspora*. Nutrient transfer between the fungus and host plant occurs through intricately branched microscopic structures called **arbuscules** (meaning ‘dwarf trees’) that develop inside the living root cells (Figure 1.15). The mycorrhizal symbiosis is obligate for the fungi and they cannot be cultured in isolation from their hosts. Cellular characteristics that help identify these fungi include the development of non-septate hyphae and large spores (up to 800 µm in diameter) with multilayered walls. The spores are formed individually or in clusters. In some species, spore clusters are surrounded by a rind of hyphae forming a fruit body called a **sporocarp**. Each spore contains hundreds or thousands of nuclei. Sexual reproduction does not occur within these fungi but mixed populations of genetically distinct nuclei coexist within individual spores. It seems likely that these multi-genomic fungi have evolved through the accumulation of mutations without recombination (or with very infrequent recombination). New symbioses are formed from hyphal fragments in the soil, or when spores germinate close to the root surfaces, and fungi can also spread from a colonised plant to neighbouring hosts.

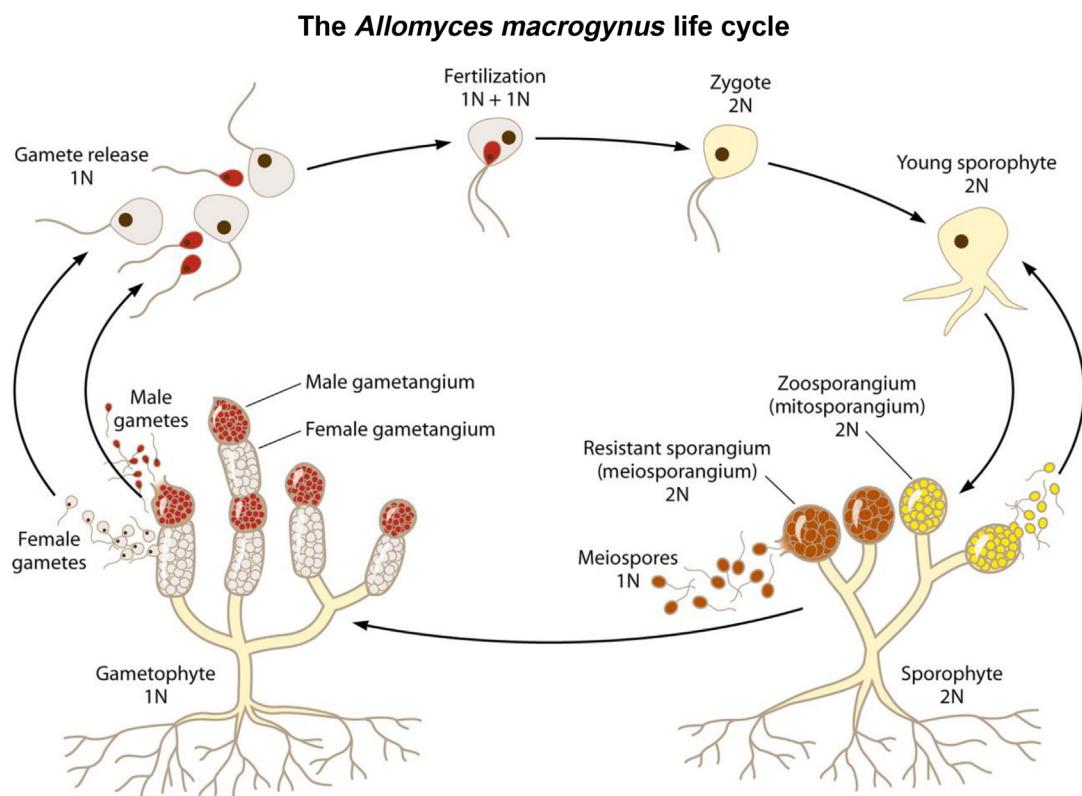


**FIGURE 1.15** Arbuscular mycorrhizal fungus, Phylum Glomeromycota. Mycelium within plant root is connected to a single arbuscule and thick-walled spore. *Source: Roo Vandegrift.*

*Geosiphon pyriforme* is the only example of a non-mycorrhizal species within the Glomeromycota. It produces inflated bladder cells that contain endosymbiotic nitrogen-fixing cyanobacteria (*Nostoc punctiforme*). *Geosiphon* may be a member of an ancestral group within the phylum from which the mycorrhizal species evolved.

### Phylum Blastocladiomycota

Blastocladiomycota, along with the Chytridiomycota and Neocallimastigomycota, are aquatic fungi that produce flagellate zoospores. It is important to underscore the absence of flagella in the majority of the fungi. No flagella are produced by the Basidiomycota, Ascomycota, Glomeromycota, and filamentous zygomycetes. Some molecular phylogenetic studies have concluded that the loss of flagella occurred once in the fungal lineage, suggesting that there was a single common ancestor for all of the non-flagellate groups. Blastocladiomycota live in freshwater habitats, mud, and soil where they operate as saprotrophs, decomposing plant and animal debris, or parasitize arthropods. Less than 200 species have been described. *Allomyces* species are saprotrophs that form separate haploid and diploid colonies with an unusual morphology. When *Allomyces* is grown on agar medium, it forms branched colonies of broad hyphae that lack septa. In liquid medium, or in samples of pond water, the hyphae are often stunted, producing short colonies attached to surfaces by a basal network of fine filaments referred to as **rhizoids**. Haploid and diploid colonies look the same, but when nutrients become limited, the hyphae stop extending and produce different types of reproductive structures at their tips (Figure 1.16). The diploid colony is called the **sporophyte** (drawing upon botanical nomenclature). This forms two different types of sporangia: **zoosporangia** and **meiosporangia**. The zoosporangia release diploid zoospores. Each spore has a single flagellum that pushes the spore through the water like a miniature tadpole. The single diploid nucleus in the spore contains a large nucleolus and is surrounded by a membrane-bound assemblage of ribosomes called the **nuclear cap**. This spore structure is one of the distinguishing features of the Blastocladiomycota. The



**FIGURE 1.16** Life cycle of *Allomyces* (Blastocladiomycota). Source: Lee, S.C., 2010. *Microbiol. Mol. Biol. Rev.* 74, 298–340.

spores are chemotactic and direct their motion toward sources of dissolved amino acids. If they locate suitable food, the zoospores attach to the surface of the target, encyst, and form rhizoids that penetrate the underlying material. Branching hyphae of the new colony develop from the opposite side of the cyst and extend into the water. The importance of nutrient absorption by the rhizoids versus the hyphae is unclear, but may be determined by the relative concentrations of nutrients in the food base and within the surrounding water. Hyphal cultures on solid medium probably function like the cultured mycelia of other fungi, with most of the absorption of nutrients occurring at the hyphal apices as the colony periphery extends into fresh medium.

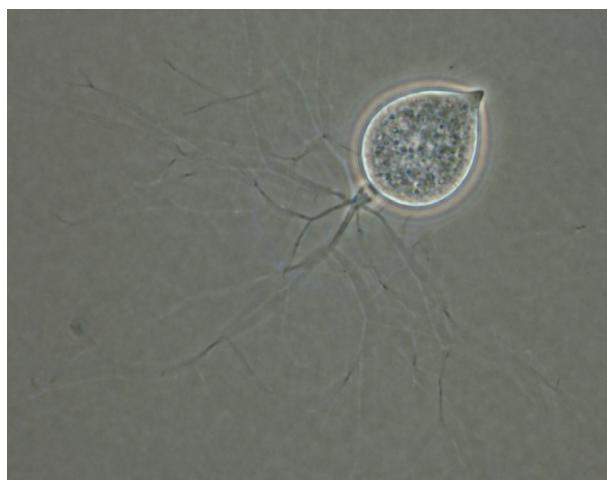
The second type of sporangium, the meiosporangium, also releases swimming spores, but these are formed by meiosis and give rise to haploid or **gametophyte** colonies. These colonies develop in the same fashion as the sporophytes, but produce terminal structures, which look like sporangia that release motile gametes rather than zoospores. The gamete-releasing structures are called **gametangia**. In *Allomyces macrogynus*, the male gametangia are formed at the ends of the hyphae, with the female gametangia directly behind them. The opposite arrangement occurs in *Allomyces arbusculus*. The male gametangia are coloured bright orange with gamma-carotene. The female gametangia and gametes release a sexual attractant, or pheromone, called **sirenin** to which the male gametes respond. After their release, male gametes

swarm around the female gametangia and fuse with the emerging female gametes. The fused gametes produce a biflagellate zygote that swims through the water until it locates a suitable food source and encysts. Upon germination, the cyst produces a new sporophyte colony and the life cycle processes can be repeated.

The zoospores of *Blastocladiella emersonii* have a very similar structure to those of *Allomyces*, but this fungus produces an ovoid thallus rather than the more extended colony of branched hyphae characteristic of *Allomyces*. Nutrient limitation triggers the transformation of the thallus into a sporangium from which zoospores are discharged into the water. Species of a third genus in the Blastocladiomycota, *Coelomomyces*, are parasites of arthropods. *Coelomomyces psorophorae* has a complicated life cycle, reminiscent of the biology of some rusts, which involves the infection of mosquito larvae and copepods. Prospects for the development of *Coelomomyces* species as biocontrol agents against mosquito-borne infectious diseases seemed bright after the elucidation of its life cycle in the 1970s, but attempts to implement control methods have been unsuccessful.

## Phylum Chytridiomycota

Chytridiomycota (true chytrids) are aerobic zoosporic fungi that operate as saprotrophs and pathogens in freshwater, brackish, and marine habitats, and are also abundant in soil. The host range of pathogenic chytrids includes other fungi, algae, plants, and amphibians. Pathogenic species include *Synchytrium endobioticum*, that causes wart disease in potatoes, and *Batrachochytrium dendrobatidis*, which causes amphibian **chytridiomycosis** that is implicated in the global decline in amphibian populations and extinction of multiple species. Like the Blastocladiomycota, the Chytridiomycota produce uniflagellate zoospores ([Figure 1.3b](#)). They do not form colonies of branched hyphae (mycelia) like non-flagellate fungi, but produce multinucleate, spheroidal bodies referred to as thalli ([Figure 1.17](#)). These are the



**FIGURE 1.17** Thallus of the chytrid *Obelidium mucronatum* in process of differentiation into a sporangium from which zoospores will be released. Thin rhizoids spread from the base of the thallus. Source: Joyce Longcore, University of Maine.

feeding structures that absorb nutrients from their surroundings, and are transformed into sporangia that release zoospores when nutrients become limiting. Zoospore release occurs through discharge tubes that expand from the thalli (Chapter 3). The presence or absence of a lid at the tip of the discharge tube (**operculate** and **inoperculate** conditions) is a diagnostic feature for these fungi. The thalli of many chytrids are anchored to solid materials by finely branched rhizoids. The thalli of some parasitic species develop inside the cells of their hosts, others on the host surface, and multiple thalli of chytrids with the most complex morphology can be connected together in chains via a system of rhizoids to resemble the colonies of non-flagellate fungi. Chytrid zoospores are haploid and it is not clear whether sexual reproduction occurs in the life cycles of most chytrids. Sexual reproduction may involve fusion of haploid zoospores. If it does occur, sexual reproduction is followed by the development of a resting spore or sporangium and meiosis produces a new generation of recombinant haploid zoospores.

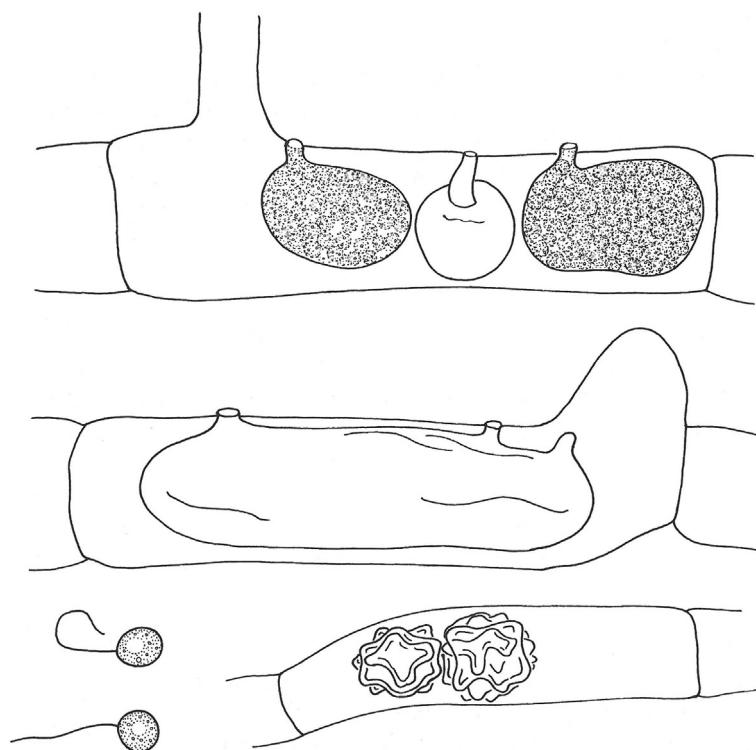
## Phylum Neocallimastigomycota

The 20 species in this highly specialised phylum are anaerobic fungi that grow in the digestive tracts of herbivores. Their metabolism is fuelled by the decomposition of polysaccharides in the fibre of the host diet to produce sugars: the Neocallimastigomycota are **fibrolytic**. These fungi lack mitochondria. In the absence of oxygen, pyruvate oxidation is catalysed by pyruvate:ferredoxin oxidoreductase in hydrogenosomes with electron donation to a [Fe]-hydrogenase that produces hydrogen. Uniflagellate zoospores are produced by these fungi but multiflagellate spores are also described in some species.

## Where Do *Olpidium* and *Rozella* Fit?

Two zoosporic genera that were originally assigned to the Chytridiomycota fall outside this phylum according to molecular phylogenetic analysis: *Olpidium* and *Rozella*. *Olpidium brassicae* infects the epidermal cells of cabbage roots, forming ovoid thalli that develop into zoosporangia (Figure 1.18). The zoospores are released into the surrounding soil water via exit tubes. They infect susceptible hosts by encysting on their root surface (epidermal cells/root hairs), penetrating the host cell wall, and transferring their cytoplasm from the cyst into the plant. The zoospores act as vectors for a number of different plant viruses. Other species of *Olpidium* infect nematodes and rotifers. *Olpidium* may be more closely related to the zygomycetes than other zoosporic species within the Chytridiomycota.

*Rozella allomycis* is an obligate parasite of *Allomyces* species (Blastocladiomycota) that infects both the haploid and diploid stages in its life cycle (Figure 1.19). Other *Rozella* species infect Oomycota (see the section '[Miscellaneous Microorganisms Studied by Mycologists](#)'). The infection process resembles the mechanism of *Olpidium*: the fungus produces infectious zoospores that attach to the host colony, encyst, and penetrate the cell wall via a germ tube. The contents of the cyst pass through the germ tube and enter the host cell. Within its host, *Rozella* produces spherical thalli that absorb nutrients from the cytoplasm. These thalli are transformed into zoosporangia or thick-walled resting spores with a spiny surface. Molecular analysis shows that *Rozella* is a member of a large clade of fungi referred to as the **Cryptomycota**. Very little is known about the biology of species of Cryptomycota



**FIGURE 1.18** *Olpidium brassicae*, an aquatic fungus that infects cabbage roots using zoospores. Source: Webster, J., Weber, R.W.S., 2007. *Introduction to Fungi*, third ed. Cambridge University Press.



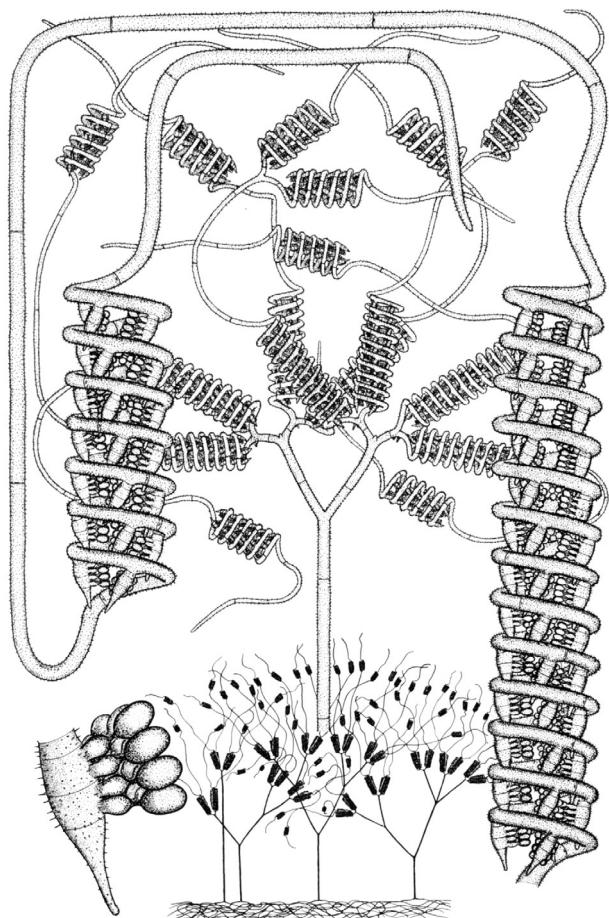
**FIGURE 1.19** Brown resting sporangia of *Rozella allomycis* inside infected cells of *Allomyces* (Blastocladiomycota). Source: Creative Commons.

besides *Rozella*. They have not been cultured, but they have been detected, using molecular techniques, in soil samples, and in freshwater and marine ecosystems. Zoospores have been observed, along with cysts, and the cells of some species are attached to diatoms. Studies show that none of these cell types produce the cell wall chitin characteristic of other fungi. The diversity of these microorganisms may be as extensive as the genetic diversity of all of

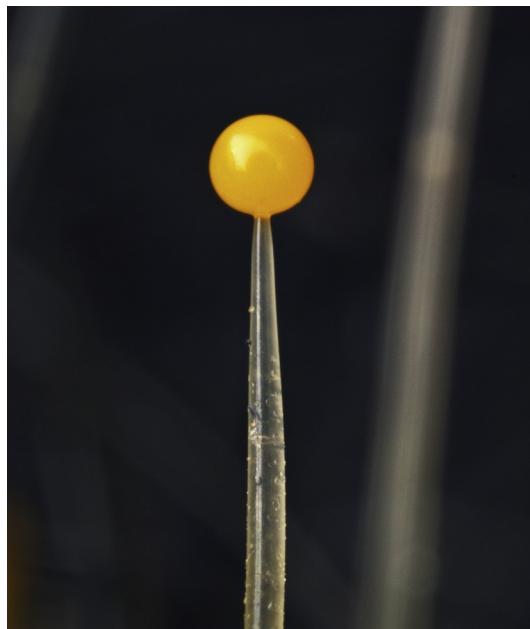
the other phyla of Kingdom Fungi. The Cryptomycota has been introduced as a new seventh phylum within the fungi.

## Zygomycetes

Molecular phylogenetic studies have disrupted the assemblage of fungi that had been placed within the Phylum Zygomycota. These include *Mucor* and related genera (Order Mucorales) that assimilate sugars from diverse food sources, specialised insect pathogens (Entomophthorales), species that form asexual spores on elaborately branched stalks (Kickxellales, Figure 1.20), and predators and parasites of other fungi, amoebae, and soil invertebrates (Zoopagales). Species in another order, the Endogonales, produce coiled hyphae inside the cells of liverworts, hornworts, and at least one species of fern. It has been suggested that these fungi, rather than the



**FIGURE 1.20** *Spirodactylon aureum*, a zygomycete fungus that grows on rodent dung and forms its spores on sporangiophores with a spectacular coiled structure. The fungus is shown in a variety of magnifications in this illustration. The spores are formed within the coils and are exposed in the drawing at bottom left. Source: *Spirodactylon is classified in the family Kixecellaceae*. Benjamin, K., 1959. *The merosporangiferous Mucorales*. Also 4, 321–433.



**FIGURE 1.21** Sporangium of the zygomycete *Phycomyces blakesleeanus*. The wall of the sporangium will blacken as it matures and then split open to release the sporangiospores. Source: Ron Wolf Photography.

Glomeromycota, may have produced the earliest endomycorrhizal relationships that supported the evolution of land plants. Together, more than 900 species of these zygomycetes have been described but the relationship between the Mucorales and the other orders is unresolved. Nevertheless, many of these fungi share some important characteristics. The most familiar zygomycetes are food-spoilage microorganisms that proliferate on fruit and food scraps, producing fluffy growths of white aerial **sporangiophores** that develop bulbous tips called **sporangia** filled with spores (Figure 1.21). Sporangia of some species contain tens of thousands of these spores, called **sporangiospores**, which are dispersed in air currents. Zygomycetes are also common on less sugary matter including herbivore dung, forming the first phase of a succession of fungi that decomposes different substances within this abundant material. *Pilobolus* species are common examples of dung fungi and their mechanism of spore discharge is described in Chapter 3. Species of Mucorales are also encountered as opportunistic pathogens of humans and other animals (Chapter 9). Patients suffering from severe burns or uncontrolled diabetes are particularly susceptible to tissue invasion by colonies of these fungi. These rare infections are referred to as **mucomycoses** and can be exceedingly difficult to treat. The food-spoilage fungi and the coprophilous species have been called **primary saprotrophs** because they assimilate low-molecular-weight compounds, including sugars, rather than breaking down cellulose and other more complex macromolecules like the basidiomycetes. The metabolic properties of the Mucorales have been utilised in the production of Asian foods including the Indonesian (Javan) staple tempeh, in which *Rhizopus oligosporus* is used to ferment soybeans to produce a solid protein-rich cake. A number of other species of Mucorales are used to produce fermented bean curd from dried tofu in East Asian cuisine (Chapter 12).

Most of these fungi produce colonies of large, multinucleate, non-septate hyphae (the septate mycelia of the Kickxellales and some closely related fungi are an exception) and produce sexual spores called **zygospores** by a process called **conjugation** or **gametangial fusion** (Figure 1.22). Conjugation occurs between colonies of opposite mating type, designated plus and minus. There are a number of steps in this process that are controlled by pheromones. Colonies release precursor molecules that are converted by compatible colonies to trisporic acid. One strain (the minus strain) produces trisporol and the other strain (plus strain) produces 4-dehydrotrisporic acid. The minus strain produces the enzyme necessary to convert 4-dehydrotrisporic acid into trisporic acid, but lacks the enzyme needed to convert its own trisporol to trisporic acid. The plus strain carries out the complementary reaction, so that compatible colonies become suffused with trisporic acid, while the concentration of trisporic acid remains very low in interactions between colonies of the same mating type. This collaborative synthesis of trisporic acid causes the formation of aerial branches from the mycelia called **zygophores**. The zygophores grow toward one another, fuse at their tips, and swell. The swollen tips (**progametangia**) are separated from their mycelia by the formation of septa. At this stage, the pair of multinucleate swellings are termed **gametangia**; the contact region between these cells is then dissolved allowing nuclei of both mating types to mingle in a shared cytoplasm. The fused gametangia constitute the **zygosporangium**. A thick, heavily pigmented zygospore forms inside the zygosporangium; the available evidence suggests that nuclei of different mating types fuse to produce diploid nuclei in the zygospore. The process of zygospore germination is not observed easily under laboratory conditions, but the development of sporangiophores and sporangia (one per zygospore) has been reported in the literature. Meiosis occurs during the germination process and the **germ sporangia** release spores of a single mating type or of both mating types. This means that the post-meiotic abortion of nuclei of one of the mating types occurs in some species. The spores are dispersed in air currents and have the potential to establish haploid colonies on fresh food sources. There is considerable variation among the zygomycete life cycles, but the formation of some type of zygospore is a common feature of this unnatural assemblage of fungi.

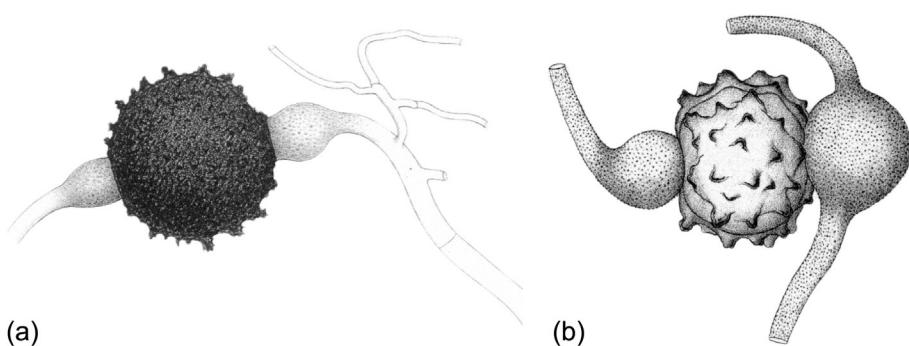


FIGURE 1.22 Mature zygospores formed between compatible strains of (a) *Mucor mucedo* and (b) *Chaetocladium jonesii*. Source: Brefeld, O., 1872. *Botanische Untersuchungen über Schimmelpilze*, vol. 1. Verlag von Arthur Felix, Leipzig.

## MICROSPORIDIA

Molecular studies showing the consensus between microsporidian and fungal genes suggest that these obligate parasites are nested within Kingdom Fungi and may share a common ancestor with zygomycetes. Other work indicates that they are a closely related sister group to the fungi. Irrespective of their precise evolutionary relationships, the microsporidia are sufficiently close relatives of the fungi to be considered part of the purview of fungal biology. All of the 1300 described species parasitize animals, particularly insects, crustaceans, and fish, and some cause opportunistic infections in humans. Microsporidia are obligate parasites that grow and reproduce only inside host cells; they lack functional mitochondria and are dependent upon their hosts for their energetic needs. The genomes of some microsporidians are diminutive, smaller even than some prokaryote genomes, but others possess genomes as large as those of other fungi. But, in all cases, a relatively small subset of protein-encoding genes is encoded: 2000-3000 genes for microsporidia, compared with the 6000 genes of *S. cerevisiae* and 10,000 genes in *N. crassa*. The larger microsporidian genomes are filled with non-coding sequences. Some species lack many of the genes that control primary metabolism in other eukaryotes. Even the genes for glycolytic enzymes are missing from one species, *Enterocytozoon bieneusi*, suggesting that it is entirely dependent upon its mammalian hosts for ATP and NADPH. Within the animal, some microsporidians become surrounded by host mitochondria and the combined host-parasite cell is transformed into a giant spore-producing structure called a **xenoma** (Figure 1.23). The spores are highly resistant and can remain infectious for years. The spore contains a harpoon-like infection apparatus consisting of a coiled polar filament that unravels and penetrates the host plasma membrane. The filament provides a conduit for the rapid migration of the spore cytoplasm into the host cell.



**FIGURE 1.23** Xenoma produced by microsporidian (*Glugea stephani*) infection of dab (*Limanda limanda*). Fish caught at the Vlakte van de Raan on the Belgian continental shelf (southern North Sea). *Photograph by Hans Hillewart (Source: Creative Commons).*

## MISCELLANEOUS MICROORGANISMS STUDIED BY MYCOLOGISTS

Water moulds within the **Oomycota** (a phylum in the eukaryote supergrouping called the Stramenopila) have been studied by mycologists since the nineteenth century. These micro-organisms are more closely related to diatoms and brown algae than they are to fungi, but they produce branched colonies of tip-growing hyphae, reproduce by spore formation, and operate as saprotrophs and pathogens (Figure 1.24). In other words, they are fungi in operational terms, but do not share close evolutionary affinity with species within Kingdom Fungi. Because mycologists have studied these microorganisms for so long, a significant part of our understanding of the way that hyphal organisms work has come from experiments on species within the Order **Saprolegniales** (e.g. *Saprolegnia ferax*, *Achlya bisexualis*) and Order **Pythiales** (e.g. species of *Phytophthora* and *Pythium*). These organisms will be discussed elsewhere in the book.

Mycologists have also studied slime moulds (Figure 1.25). The **Acrasiomycetes** (acrasid cellular slime moulds) and the **Dictyosteliomycetes** (dictyostelid cellular slime moulds) are groups of protists with an amoeboid feeding phase. *Dictyostelium discoideum* is viewed as a model for understanding cell–cell communication and the evolutionary origins of multicellularity. **Myxomycetes**, or ‘true slime moulds’, are the familiar slime moulds whose multinucleate plasmodia flow over the surface of rotting wood, before releasing spores from a variety of beautiful fruiting structures. The mechanism of cytoplasmic streaming (shuttle streaming) within the plasmodia of *Physarum polycephalum* has been the subject of intensive cell biological research. **Protosteliomycetes** are related to the Myxomycetes but form phagocytic amoebae and, in some species, small plasmodia. Finally, the **Plasmodiophoromycota** is a group of parasitic microorganisms that are related to the Myxomycota. The group includes *Plasmodiophora brassicae* that causes club root of cabbage. Finally, the **Labyrinthulomycota** are aquatic microorganisms that grow as networks of branched ‘slime tubes’ (slime nets) containing motile cells (Labyrinthulales), or as zoospore-producing thalli (Thraustochytriales) that

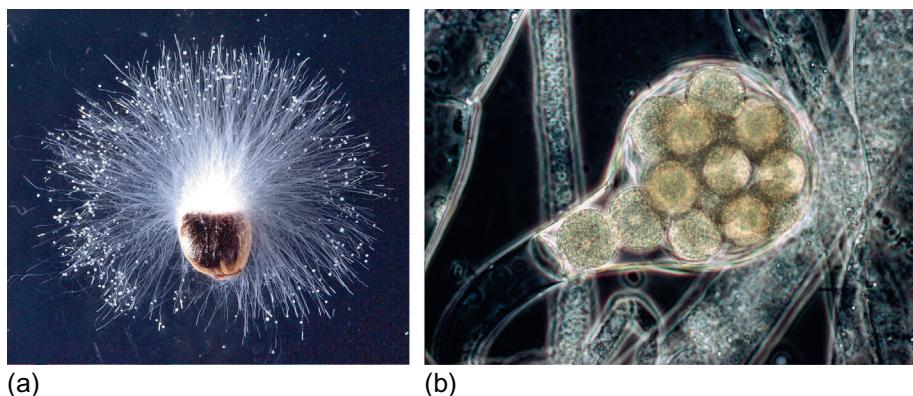


FIGURE 1.24 Oomycete water moulds, which are stramenopiles rather than fungi. (a) Filamentous hyphae of an *Achlya* species growing from a hemp seed immersed in water. (b) Sexual oospores of a *Saprolegnia* species within a structure called an oogonium. Source: George Barron, University of Guelph <https://dspace.lib.uoguelph.ca/xmlui/handle/10214/3955>



**FIGURE 1.25** Plasmodium of a slime mould *Leucocarpus fragilis*. *Source:* <http://curbstonevalley.com/wp-content/uploads/2010/02/LfragilisNet.jpg>

resemble the thalli of chytrids. The Labyrinthulomycota are stramenopiles, distantly related to the Oomycota. The biology of these diverse groups of slime moulds is not featured in this third edition of 'The Fungi'.

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## Weblinks

- <http://tolweb.org/tree/> offers a wealth of up-to-date information on fungal phylogeny as well as detailed descriptions of the major groupings of the fungi.
- <http://eol.org/pages/5559/overview>
- <http://genome.jgi.doe.gov/programs/fungi/1000fungalgenomes.jsf>