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Primer

The Fungi

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The Kingdom Fungi, home to molds, mushrooms, lichens, rusts, smuts and yeasts, comprises eukaryotes with remarkably diverse life histories that make essential contributions to the biosphere, human industry, medicine and research. With the aim of enticing biologists to include fungi in their research, we note that many fungi have haploid genetics, and that those in cultivation are essentially immortal, two features that make it easier to associate traits with genotype, even for complex traits, than with *Drosophila* or *Arabidopsis.* The typical fungal genome size of 30–40 Mb is small by eukaryotic standards, which is why fungi have led the way as models for eukaryote genome sequencing with over 100 assembled genome sequences available [1,2]. For some fungi, DNA transformations, gene knockouts and knockdowns are routine. Species of Ascomycota and Basidiomycota show simple, multicellular development with differentiated tissues. In many species these tissues are large enough to support studies of transcription and translation in the lab and even in nature.

About a billion years ago, give or take 500 million years [3], a population of aquatic, unicellular eukaryotes making sporangia containing zoospores each with a single posterior flagellum split into two lineages: one eventually gave rise to animals, the other to fungi. Here we shall summarize the major diversifications of the Fungi by introducing each major fungal branch in the order that it is thought to have diverged (Figure 1) and presenting salient facts about fungal modes of nutrition, reproduction, communication and interaction with other life. Our views are strongly influenced by the Fungal Tree of Life Project [4–6]. Readers interested in learning more about fungi are encouraged to consult any of a number of comprehensive texts [7,8].

The exact order of divergence in deep regions of the eukaryotic tree is controversial. On the lineage that leads to the Fungi there are thought to be two other groups; the first to diverge are the nucleariid amoebae, and the next the Microsporidia. Microsporidia are either the sister group to the Fungi, or lie within the Fungi (Figure 1), and they should be included in studies of fungi. They are unculturable, obligate parasites of animals, including humans. They have extremely reduced eukaryotic genomes — with a genome size of ~2.6 Mb and ~2000 genes [9] — remnant mitochondria, and unique morphologies related to parasitism, including a very frightening polar tube used to initiate infection [9].

Staying in the Kingdom Fungi, we next arrive at a divergence leading to *Rozella allomycis* [4] (Figure 2A), an intracellular parasite of the Blastocladiomycota fungus *Allomyces*. *Rozella* has a small body without a cell wall, which branches within the host and makes two types of sporangia: zoosporangia, which produce zoospores with posterior flagella that swim from the parent to find new hosts, and resistant sporangia, around which a thick cell wall develops to ensure persistence long after the host has died and decayed. Nothing is known about mating and meiosis in *Rozella*. Curiously, and like the Microsporidia, the lineage leading to *Rozella* diverged before that leading to its host, raising the worry that phylogenetic artifacts place parasite lineages at the base of phylogenies.

The next divergence leads to the Phylum Chytridiomycota, which constitute <1% of described fungi and, like *Rozella*, are presumed to retain key characters of the last common ancestor of Fungi and Animals [10]. These include a unicellular body bounded by a cell wall, which matures into a sporangium (Figure 2B), within which develop many posteriorly-uniflagellate zoospores (Figure 2C). The zoospores are cleaved from the sporangial cytoplasm by fusion of vesicles produced by a Golgi apparatus, and they swim to a fresh substrate, retract the flagellum, and secret a cell wall to encyst. The cyst germinates to start the life cycle anew. Although some Chytridiomycota have developed filamentous growth (hyphae), most have determinate development, and those living outside a substrate produce small, anucleate hyphae (rhizoids) that penetrate the food source. Species that live inside a host typically lack rhizoids, as does *Rozella*.

Chytriomyces hyalinus (Figure 2B) is the best studied Chytridiomycota species in terms of the morphology of sexual reproduction; however, no mating types are known. In this species, two individuals fuse at their rhizoids to form a thick-walled resistant spore. This fungus is a saprobe, but other Chytridiomycota, such as *Batrachochytrium*, are parasites, associated with amphibian decline, or like *Neocallimastix*, mutualists found in the stomachs of ruminate mammals. Another group member is one of the few fungi judged to be a weapon of terror, the agent causing potato black wart, *Synchytrium endobioticum*, infamous for making resting spores that can persist in soil for decades. Chytridiomycota have been thought to be haploid with zygotic meiosis, but DNA sequences of individual loci, as well as of the entire genome sequences of two *Batrachochytrium dendrobatidis* individuals (our unpublished data), raise the possibility that, like animals, these fungi can be diploid with gametic meiosis.

Back on the main fungal lineage, the next divergence leads to the Blastocladiomycota [10], the second phylum of Fungi with single, posterior flagella and home to *Allomyces*, the host for *Rozella allomycis*. Blastocladiomycota, once considered members of the Chytridiomycota, also account for <1% of described Fungi. Indeterminate, hyphal growth is better developed in Blastocladiomycota than in Chytridiomycota, although the hyphae often sprout rhizoids. Blastocladiomycota are unusual in alternating their haploid and diploid generations. Gametes in Blastocladiomycota resemble zoospores and, in *Allomyces*, female gametes produce a sesquiterpene pheromone, sirenin, that attracts male gametes. In these organsisms, meiosis occurs in thick-walled, resistant sporangia, but, as in Chytridiomycota, mating types are

unknown. Blastocladiomycota may be saprobic or parasitic on plants or animals; the best-studied animal parasite, *Coelomomyces*, kills mosquito larvae and copopods as it alternates generations.

Travelling back to the main branch, again, we encounter one of the major shifts in fungal form, the loss of the flagellum [3,4]. This loss is associated with two other major changes: from this point in evolution forward, all stages of fungal life cycles have cell walls, and the microtubule organizing centers of nuclear division no longer are centrioles. Released from the constraint of organizing both flagella and spindles, the microtubule organizing centers associated with spindles, known as spindle pole bodies, have diversified morphologically and probably functionally, as is likely to become apparent when genomes of fungi with and without flagella are compared.

The next five major clades on our march through the fungi, subphyla Mucoromycotina, Entomophthoromycotina, Zoopagomycotina, and Kickxellomycotina, and the phylum Glomeromycota, formerly constituted the phylum Zygomycota [11], and together account for <1% of described fungi. These taxa are organized into three clades, Mucoromycotina, Entomophthoromycotina + Zoopagomycotina + Kickxellomycotina and Glomeromycota, whose composition and relationships are not strongly supported.

Mucoromycotina, the best studied of this group, will be familiar to all who have found their fresh berries rendered inedible by enveloping wefts of white mycelium. These fungi are saprobes, commonly growing on damaged fruit but also on mammal dung. Among them are two genera of model fungi, for example *Rhizopus* and *Phycomyces*. These fungi grow primarily as hyphae, or as yeasts where oxygen is scarce and carbon dioxide is abundant. As in all the hyphal fungi encountered so far, septa are rare, apart from adventitious septa defining reproductive structures. Mitotic spores are formed in sporangia in a process very similar to zoospore formation within chytrid sporangia, but without flagella and with cell walls.

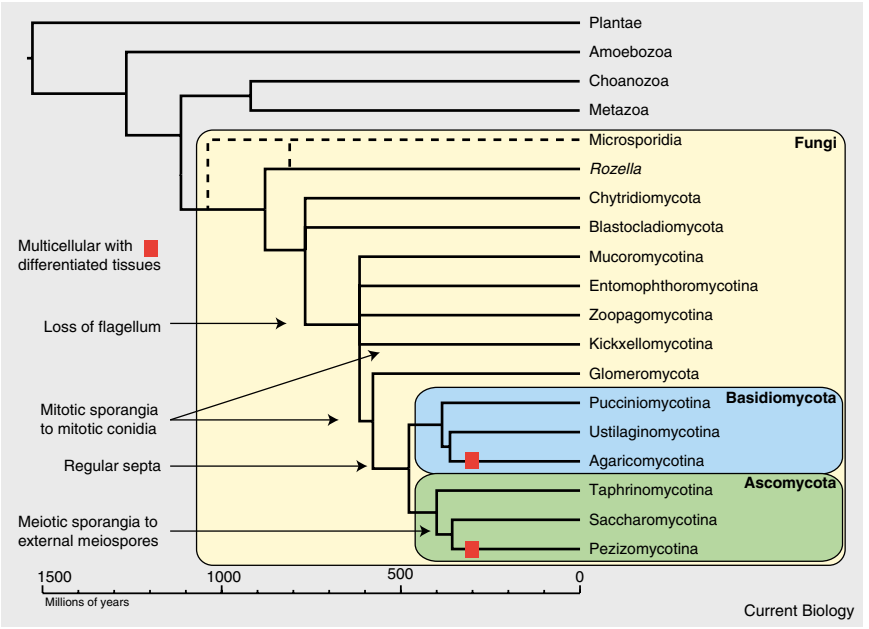

Figure 1. The Fungi.

Phylogenetic tree, based on [4], showing relationships of many of the fungal lineages fit to geologic time using the program r8s and considering *Paleopyrenomycites* to be a member of the Ascomycota [3]. Arrows depict changes in morphology including the major loss of the flagellum, transition of mitotic sporangia to mitotic conidia, invention of regular septa, and meiotic sporangia to external meiospores. The blocks indicate branches where most members have multicellular differentiated tissues. The phylogenetic position of the Microsporidia is not confidently resolved as indicated by the dotted line.

These fungi are haploid with zygotic meiosis. Sexual spores (zygospores) result when differentiated gametangia form and fuse, in a process involving pheromones derived from the carotenoid pathway. Mating compatibility is regulated by one mating locus with two alleles that encode a high mobility group (HMG) domain transcription factor related to the product of the human sex-determining gene *SRY*. Zygospores show little variation among members of the subphylum, but the diversity of mitospore morphology and dispersal is staggering. For example, *Pilobolus* launches its sporangium by water pressure (recently captured by high-speed videography [12]), *Gilbertella* presents its mitospores to insect vectors in a drop of liquid held between halves of the sporangial wall and *Phycomyces* perches the sporangium on a 10 cm stalk that, as it elongates, responds to light and can sense and avoid obstructions without the need for physical contact. The tremendous potential for developmental studies in these fungi has been given a boost by genome sequencing of several Mucoromycotina, among them *Phycomyces*, *Rhizopus* and *Mucor* [13].

Entomophthoromycotina, Zoopagomycotina and Kickxellomycotina form a single clade of Fungi that, like Mucoromycotina, are hyphal, produce thick-walled, sexual zygospores [11] and are haploid with zygotic meiosis. The best-studied of these clades is Entomophthoromycotina, aptly named parasites of insects that manipulate host behavior to promote the transmission of their mitospores. *Entomophthora muscae*, for example, induces its fly host, just before death, to attach itself to elevated vegetation while enlarging its abdomen to increase sexual attractiveness, all the better to lure males for spore transmission during pointless copulation. The large, multispored sporangia typical of Mucoromycotina are not the rule in this subphylum. Instead, what appear to be multispored sporangia are often single, multinucleate spores, termed conidia.

Zoopagomycotina comprise fungi that are parasites on animals or other fungi and that form haustoria, hyphae that are specialized to promote

nutrient transfer from host to fungus (Figure 2E). One likely member of Zoopagomycotina, *Zoophagus*, traps rotifers, amoebae or nematodes by attracting the tiny animals to feed on short, lateral hyphae that are covered with adhesives, so called 'lethal lollipops'. Kickxellomycotina comprise saprobes, mycoparasites of Mucoromycotina and animal parasites and, as with Entomophthoromycotina and Zoopagomycotina, they show reduced reliance on multispored sporangia and increased reliance on conidia (Figure 2E). With each mitosis in their hyphae, Kickxellomycotina produce septa containing central pores that, with age, become plugged (Figure 2D). The development of regular septa may have helped initiate the shift from spores cleaved from inside sporangia by fusion of vesicles to conidia formed by hyphal septation. This shift in the method of spore formation might have been a key evolutionary event, because conidia are well developed not only in Kickxellomycotina and Zoopagomycotina, but also in the two dominant groups of fungi, Ascomycota and Basidiomycota.

Glomeromycota [14], another species-poor group, is one of most ecologically-important groups of fungi, because of its mutualisms with the roots of ~90% of plant species, known as arbuscular mycorrhizae [15]. Arbuscular mycorrhizae, which are seen in below-ground parts of the earliest plant fossils, facilitate nutrient acquisition by plants in exchange for photosynthate; they are vital to plant fitness, and may drive the composition of plant communities. Arbuscular mycorrhizal fungi are hyphal and produce highly branched haustoria that promote nutrient exchange with host root cells. They also produce asexual, thick-walled multinucleate spores defined by adventitious septa. The fragmentary knowledge about most aspects of Glomeromycota biology belies their importance, because they cannot be cultivated apart from the host plant. For example, controversy clouds their ploidy, their genome size, and whether or not they reproduce sexually. Evidence for recombination has been provided, but whether mating and meiosis are involved is unknown. There might be no more important contribution to mycology than discovering how to axenically cultivate arbuscular mycorrhizae fungi.

We now arrive at the Dikarya, a subkingdom embracing the two largest fungal phyla, Ascomycota and Basidiomycota, home to ~98% of described fungi. The name Dikarya emphasizes an amazing feature of mating in these fungi: nuclear fusion does not follow directly from gamete fusion, so that hyphae with two nuclei (a dikaryon), one from each parent, constitute a significant (in Ascomycota), or the most significant (in Basidiomycota), part of the life cycle. The role of the dikaryon in adaptation will be revisited when we get to Basidiomycota, but one advantage applies to all Dikarya: a dramatic increase in the diversity of recombined progeny. In earlier diverging phyla, most matings lead to one zygote and one meiotic event. In Dikarya, one mating can lead to zygotes and independent meioses that number in the tens of thousands (as in a *Neurospora* colony) or even hundreds of trillions (in long-lived Basidiomycota with large or perennial fruiting bodies, such as the puffballs of *Calvatia*, false truffles of *Rhizopogon*, or shelf fungi of *Ganoderma*).

Morphologically, species with hyphae or unicellular yeasts, or both, are common throughout Dikarya. In hyphae, mitosis is followed by septum formation to produce regular septa, as opposed to the adventitious septa found in most earlier-branching groups. These regular septa form centripetally and have central pores, most often with a means of regulating the passage of cytoplasm and organelles, including nuclei, between hyphal segments. Filters involve membranes in Basidiomycota (Figure 2G) or modified microbodies (Woronin bodies) in most Ascomycota (Figure 2H). The advent of regular septa is also correlated with the evolution of macroscopic, multicellular fungi where different hyphal segments evolve to perform different functions, for example, the stalk, cap and gills of an *Agaricus* mushroom (Basidiomycota) or the stalk, cup and ascus layer of a morel (Ascomycota). Remarkably, it appears that multicellularity with differentiated tissues evolved independently in each phylum.

Ascomycota is the larger taxon of Dikarya, with ~64% of described fungi, including species in four genera that helped researchers win Nobel Prizes (*Penicillium*, *Neurospora*, *Saccharomyces* and *Schizosaccharomyces*). Although each of these fungi is best known from laboratory studies, Ascomycota in nature earn their livings in all possible ways, as saprobes, as mutualists (forming lichens with algae or ectomycorrhizae with woody plants in Pinaceae, Fagales, Dipterocarpaceae, Fabaceae and Ericaceae), and as parasites. Pathogenic Ascomycota pose as great a threat to agriculture as any group of organisms, and parasitic Ascomycota adapted to animals account for almost all the severe, systemic human mycoses as well as athlete's foot and similar fungal skin diseases [16].

These fungi are typically haploid with one mating locus occuring as two alleles. The alleles are so diverged that they are termed idiomorphs and they code for homeodomain, alpha box and HMG-domain transcription factors. Potential partners communicate by oligopeptide pheromones. In hyphal species, mating leads to a short dikaryotic stage that produces a multitude of zygotes and meiocytes (asci) as previously mentioned. Sporangia with internal mitospores are not found in Ascomycota. Instead conidia are the means of asexual reproduction. Within asci, however, meiotic spores (ascospores) form as membranous vesicles fuse to delimit uninucleate portions of cytoplasm (Figure 2F) in a process reminiscent of sporangiospore formation in early-diverging fungi. The hypothesis that internal spore formation by cytoplasmic cleavage seen in mitotic sporangia of Chytridiomycota or Zygomycota homologous to meiotic ascospore formation in Ascomycota would be worth testing with transcriptional genomic approaches. In most Ascomycota, turgor pressure generated in the mature ascus forcibly ejects the ascospores.

There are three deep clades of Ascomycota: Taphrinomycotina, Saccharomycotina and Pezizomycotina. The subphylum Pezizomycotina is home to almost all Ascomycota that protect their asci with multicellular structures, ranging from microscopic fruiting bodies to 25 cm tall morels. The subphylum Saccharomycotina contains the industrial yeasts,

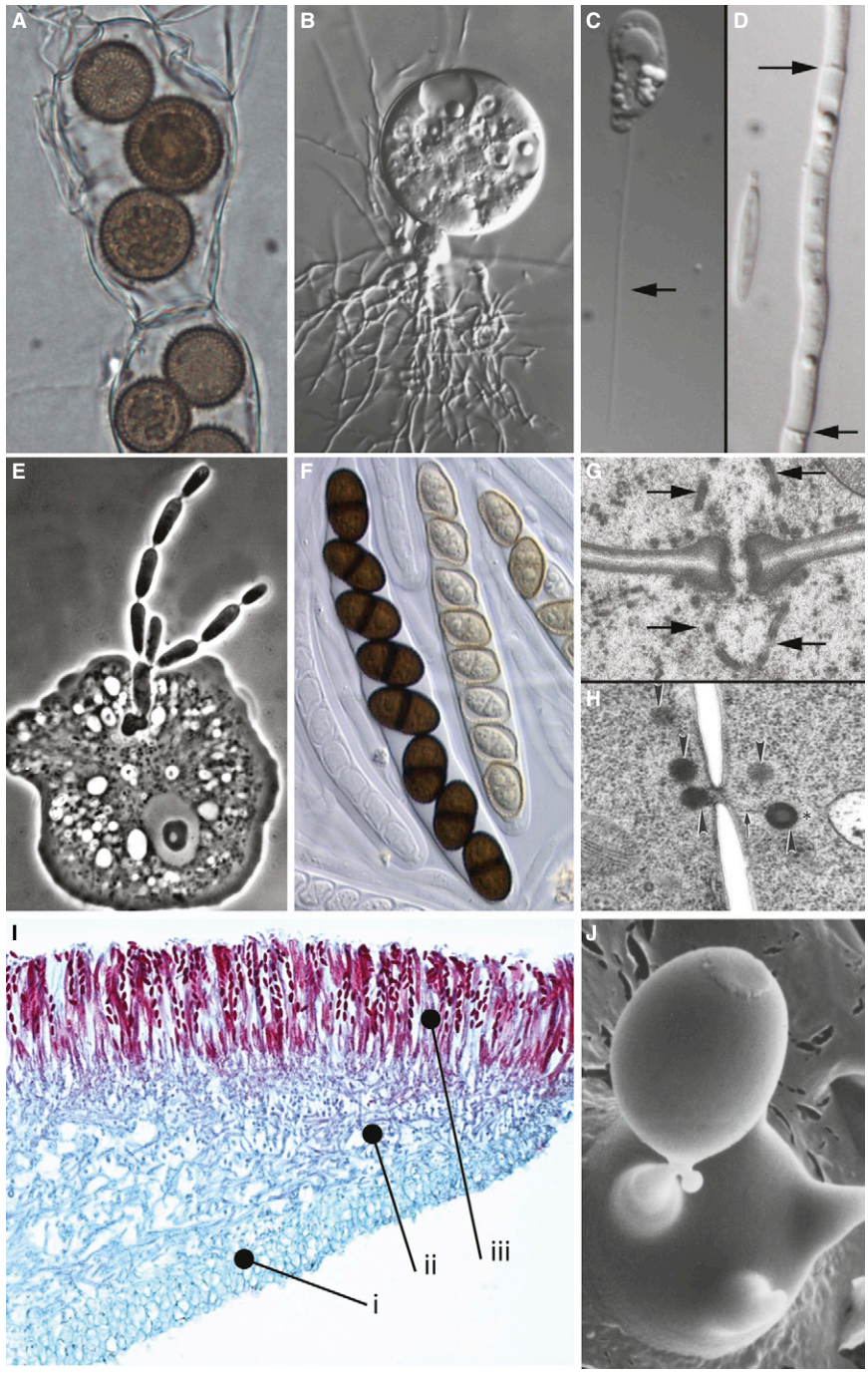

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Figure 2. Cellular structures of unicellular and multicellular fungi.

(A) *Rozella allomycis* resistant sporangia formed inside hyphae of the host *Allomyces* sp. (Photomicrograph from T.Y. James.) (B) *Chytriomyces hyalinus* (Chytridiomycota) sporangium showing the anucleate hyphae (rhizoids) essential for feeding the growing, spherical sporangium. (C) *Blastocladiella simplex* (Blastocladiomycota) zoospore with flagellum (arrow). (D) *Coemansia* sp. (Kickellomycotina) hypha with regular septa (arrows). (E) *Amoebophilus simplex* (Zoopagomycotina) on its amoeba host. Note the haustorium below the primary attack spore that initiated the infection. The primary attack spore and haustorium become the body from which chains of spores develop. (Photomicrograph from G.L. Barron.) (F) *Valsaria rubricosa* (Pezizomycotina) asci (meiocytes) at various stages of maturity, indicated by the increasing melanization of the ascospores. (Photomicrograph from S.M. Huhndorf.) (G) *Auriscalpium vulgare* (Agaricomycotina) hyphal septum with associated membranes (arrows) that regulate the flow of cytoplasm and organelles through the central pore. (TEM reproduced with permission from Celio *et al*. 2007, Septal pore apparatus and nuclear division of *Auriscalpium vulgare*. Mycologia *99*, 644–654.) (H) *Aspergillus nidulans* (Pezizomycotina) hyphal septum with Woronin bodies that can plug the pore when hyphae are damaged. (TEM reproduced with permission from Momany *et al.* 2002, Mapping Woronin body position in *Aspergillus nidulans*. Mycologia *94*, 260–266.) (I) *Sclerotinia sclerotiorum* (Pezizomycotina) fruiting body showing the capacity of fungi to make a multicellular structure with differentiated tissues: Pseudoparenchymatous cortex (i), hyphal medulla (ii) and meiocytes (asci) and supporting hyphae in the hymenium (iii). (Photomicrograph from J. Rollins.) (J) *Coprinopsis cinerea* (Agaricomycotina) basidium with a mature basidiospore developing on one of four sterigma that emerge from the basidium. This partially frozen-hydrated specimen shows Buller's drop of liquid developing at the base of the basidiospore, which is essential to spore discharge. (SEM reproduced with permission from McLaughlin *et al.* 1985, Ultrastructure and evolution of ballistosporic basidiospores. Bot. J. Linn. Soc. *91*, 253–271.)

parasitic *Candida* species and, at the base of the clade, filamentous forms. No members of this subphylum, however, protect their asci with a fruiting body. The third subphylum, Taphrinomycotina [17], actually diverged before the other two. It contains species that have both yeasts and hyphae (*Taphrina*), species with just yeasts (*Schizosaccharomyces*, *Pneumocystis*), and one remarkable filamentous fungus, *Neolecta*, which makes a macroscopic fruitbody to support its asci. Both filaments and yeasts are found in Taphrinomycotina (and Mucoromycotina), suggesting that both morphologies are ancestral in Ascomycota and that hyphae were lost early in the evolution of Saccharomycotina. Multicellular species with differentiated tissues are seen in Taphrinomycotina and Pezizomycotina, so this trait may have evolved early in the Ascomycota, only to be lost in the Saccharomycotina and all extant Taphrinomycotina, except *Neolecta*, or it may have evolved independently in *Neolecta* and Pezizomycotina.

Saccharomycotina [18] harbors a fungus that is famous and atypical, the baking and brewing yeast, *Saccharomyces cerevisiae*. It is primarily unicellular, although capable of polarized growth resembling hyphae. Natural isolates are diploid and meiosis leads to naked asci with ascospores that are not

forcibly ejected. Most often, sibling ascospores mate to reestablish the diploid. If haploid colonies establish from single ascospores, they rapidly switch mating types, allowing them to essentially self-fertilize and become diploid. Rare mating with other genotypes is sufficient to maintain an outbred population. Yeast genomes are small, introns were lost early in Saccharomycotina evolution, and these fungi do not appear to contain genes involved in RNA interference (RNAi)-like gene regulation. In short, *S. cerevisiae* is an excellent model for the basic features of eukaryotes and for experimentation, but a poor model for other fungi. Although genomes of many Saccharomycotina have been sequenced, those of the very basal, filamentous taxa with forcible ascospore discharge, such as *Dipodascopsis*, have not. A *Dipodascopsis* genome sequence would stimulate studies of genome reduction and the loss of morphological complexity.

In Pezizomycotina [19], the largest and most diverse group of Ascomycota, hyphae are the rule. Mating of haploid partners results in short-lived, dikaryotic hyphae in which karyogamy and meiosis occur to produce asci and ascospores. The ancestral, widespread fruiting body in Pezizomycotina is a multicellular cup (apothecium) filled with asci (Figure 2I) and forcibly discharged ascospores. Apothecia have evolved into more enclosed fruiting bodies by narrowing the broad cup's surface to a pore — apparently independently in Sordariomycetes (*Neurospora*, *Ophiostoma*), Dothidiomycetes (*Cochliobolus*), Chaetothyriomycetidae (*Capronia*) and others — or by closing the cup completely — independently in Eurotiomycetes (*Emericella/Aspergillus*), Erysiphales (powdery mildews), Pezizales (truffles) and others. In most cases, closed fruiting bodies correlate with loss of forcible ascospore discharge, features that could only evolve after development of an alternative dispersal mechanism, for example, *Tuber* ascospores are dispersed by mammals attracted to truffles by fungal pheromones that mimic mammalian reproductive sterols.

Many Pezizomycotina, like truffles or the *Penicillium* species responsible for cheeses (Camembert, Brie and Roquefort), are socially-celebrated fungi. Alas, the socially-despised species are probably better known: *Ophiostoma,* worldwide devastator of elms; *Cryphonectria,* killer of four billion chestnuts in Eastern North America; *Fusarium*, principal pathogen of wheat, rice and banana and instrument of economic collapse in rural communities; or the agents of the potentially fatal human mycoses histoplasmosis, blastomycosis, paracoccidioidomycosis and coccidioidomycosis. (*Coccidioides* species are also on the US government list of select terrorist agents.)

Basidiomycota account for 34% of described fungi and comprise three subphyla, Pucciniomycotina, Ustilaginomycotina and Agaricomycotina, groups that are best known as containing the rusts, smuts and mushrooms, respectively. In all three groups, the growth form can be a yeast, a hypha or dimorphic. There can be one or two mating loci (one coding for a homeodomain transcription factor, the other for pheromone and receptor) each with from two to many alleles. Mating is by fusion of yeast cells or hyphae with the involvement of oligopeptide mating pheromones similar to those seen in Ascomycota. Cell fusion produces a dikaryon that can grow for days, years, or even centuries before karyogamy and meiosis occur. Recent research delving into dikaryons has shown that proportions of the two nuclei in a colony can vary as the environment changes [20] and that dikaryons are quicker to adapt to changed environments than their constituent haploids [21].

In dikaryotic hyphae, karyogamy and meiosis take place in terminal meiocytes (basidia). The meiotic spores (basidiospores) are not formed within the meiocyte, but develop on stalks that emerge from the surface of the basidium (Figure 2J). In all three subphyla, basidiospores are launched from the basidium by the shifting mass of a water drop (also a subject of high speed videography [22]). However, this ingenious process has often been lost wherever other means of spore discharge and dispersal have evolved. Pucciniomycotina (with the possible exception of *Septobasidium*) and Ustilaginomycotina lack the multicellularity and differentiation of tissues seen in Agaricomycotina, indicating that multicellularity with differentiation of tissues developed independently in Ascomycota and Basidiomycota. Among the best-known Basidiomycota are wheat rust (*Puccinia graminis*), maize smut (*Ustilago maydis*), and any of ~8,000 described mushrooms. Among the best model systems for genetics, development, and sexual reproduction are *U. maydis* and the mushroom *Coprinopsis cinerea*.

Pucciniomycotina [23] probably diverged first among subphyla of Basidiomycota and shares some ancestral traits with Ascomycota, including regular septa with simple pores and mating loci with typically just two alleles. Most Pucciniomycotina species are obligate parasites of plants (rusts), but there are also parasites of insects (*Septobasidium*) and even parasites of fungi (including a remarkable fungus, *Helicobasidium,* which is parasitic on rust fungi as a haploid and on plant roots as a dikaryon). Pucciniomycotina can grow as hyphae, yeasts, or both, and the yeasts are often saprobic. The dikaryotic phase can be dominant, and basidia and basidiospores develop without protecting fruiting bodies. Many species can manipulate host behavior; *Microbotryum*, for example, reproduces in the anthers of its dioecious host and, if the plant is female, causes its flowers to switch to male.

The majority of Ustilaginomycotina [24] are parasitic on plants (smuts), almost exclusively on just two angiosperm families, grasses and sedges. The model organism in this group is *Ustilago maydis*, which grows as a saprobic yeast when haploid, and after mating as a dikaryotic, parasitic mycelium. Mating is controlled by two loci, in contrast to the one-locus system in the previously described fungal phyla; one of the loci has two alleles, but the other has many. Partners must have different alleles at both loci to mate, an arrangement that restricts inbreeding to 25% of siblings. Smuts are amazingly sneaky parasites, often lying in wait as endophytes before commandeering the plant's developing ovaries for their own reproduction. One Ustilaginomycotina, *Malassezia*, is among the few Basidiomycota

parasitic on humans, albeit mildly; it causes dandruff.

The final clade, Agaricomycotina [25], is home to the most iconic of fungi: mushrooms and their allies. Different species of Agaricomycotina can grow as yeasts, as hyphae or as both. Species can have two mating loci and each locus can have many alleles, both restricting inbreeding and promoting outbreeding. In spite of this elegant control of mating, there are many self-fertile species. Multicellular fruiting bodies are the norm in Agaricomycotina and they come in seemingly endless variation. If basidiospores are forcibly launched, fruiting body form is evolved to increase the surface area for basidia, whether gills or tubes of a mushroom, branches of a coral fungus, or cerebriform folds of a jelly fungus. Where alternative methods of spore dispersal have evolved, fruitbody forms can only be described as bizarre: tiny bird-nest-shaped splash cups containing tiny 'eggs'; phallic columns topped by foul smelling ooze that attracts flies; small, pear-shaped bellows that puff spores, either perched on the soil or raised on columns or hygroscopic arches; soccer ball sized fungal tumble weeds filled with trillions of spores that gradually disperse; and small mortars that launch tiny cannonballs when turgid layers of the fruitbody separate catastrophically. Agaricomycotina are socially important as food (*Agaricus* mushrooms), as agents of wood decay (dry rot fungi now starring in the biofuels field), as the human pathogen now causing an outbreak of potentially-fatal cryptococcosis in Canada, and as ectomycorrhizae with most of the woody plants listed for Ascomycota [15].

We have been coy about the numbers of fungi, referring only to percentages of described fungi throughout. No one knows how many fungal species exist, although as many as 100,000 have been described and as many as 1.5 million have been estimated to exist in nature. Population genetic studies of described species invariably find that one morphological species is actually several phylogenetic species, and metagenomic studies of alpine soils or cultivation studies from beetles find new or greatly expanded clades; 1.5 million species may be an underestimate. We can be far more concrete about the number of sequenced fungal genomes [1,2], which is at more than 100 for different species and at 70 for individuals of just two sibling species of yeast. Comparative genomics at all levels is now the norm in fungi and has become an essential tool to help frame testable hypotheses in all fields of biology. The next decade of mycological research is going to be even more amazing than the last because next-generation sequencing will enable individual researchers to bring genomics to almost any fungus. Our challenge will be to maximize possible comparisons by making it possible for all of the data soon to be harvested in individual labs available to the community.

Acknowledgments

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