

# 21st Century Guidebook to Fungi

## OUTLINE CLASSIFICATION OF FUNGI 2020

A trend in the last two or three decades has been the growing awareness of the enormous and numerous influences that fungi have exerted on the development of the biosphere of this planet. We have indicated above in the text of this book that animals and fungi are sister groups; they are each other's closest relatives and share a common ancestor which is known as the opisthokont clade. The name 'opisthokont' comes from the Greek and means 'posterior flagellum', so the common characteristic that gives them their name is that flagellate cells, when they occur, are propelled by a single posterior flagellum, and this applies as much to chytrid zoospores as to animal sperm. In contrast, other eukaryotic organisms that have motile cells propel them with one or more *anterior* flagella (these are the heterokonts). A recognisably fungal grade of organisation has been evident from the very earliest stages in evolution of higher organisms. And perhaps fungal pioneering goes further than this, because the idea that the very first terrestrial eukaryotes might have been fungal is increasingly gaining support. A couple of titles of scholarly articles will illustrate this: '*Terrestrial life - fungal from the start?*' (Blackwell, 2000); '*Early cell evolution, eukaryotes, anoxia, sulfide, oxygen, fungi first (?), and a Tree of Genomes revisited*' (Martin *et al.*, 2003) and '*Fungal biology in the origin and emergence of life*' (Moore, 2013a).

The evolution of fungi is ornamented with some of the most crucial mutualisms, or co-evolutions, of the living world. Lichens could be the most ancient; they have been found with certainty in some of the oldest fossils and are currently thought of as being able to flourish in the most extreme environments. Indeed, lichens can also survive 16 days open exposure to the space environment in orbit (Sancho *et al.*, 2007). Fully-formed mycorrhizas can also be found in the most ancient plant fossils, and today about 95% of all terrestrial plants depend on this fungal infection of their roots to provide the plant with phosphorus and other nutrients. Fungi may also have an impact on the aerial parts of plants today because endophytes (fungi that live in the spaces within the leaves and stems of living plants) '...are present in any healthy plant tissue...' (Sieber, 2007). Animal mutualisms also abound; from the dependence of leaf-cutter ants on their fungal gardens to make the ants the dominant herbivores of their tropical rain forests, to the dependence of even-toed ungulates on the chytrids in their rumens that make them the dominant herbivores of their savannah grasslands.

A possible explanation for fungal success throughout geological time is that their fundamental life style is to recycle the dead remains of other organisms. This means that extinction events of other organisms are just ways of providing additional nutritional resources for fungi. The Permian-Triassic extinction event that occurred approximately 250 million years ago is informally known as the Great Dying. It was the Earth's most severe extinction event (so far!), with about 96% of all marine species and 70% of terrestrial vertebrates becoming extinct. Plants suffered huge extinctions as well as animals, with such massive dieback of vegetation that terrestrial ecosystems destabilised and collapsed throughout the world. This global ecological catastrophe was caused by changes in atmospheric chemistry resulting from the volcanic eruption that formed what are now known as the Siberian Traps flood basalts. This eruption is thought to have covered an area of what is now Siberia equivalent to the current area of Australia. However, the result of all this death and destruction to the flora and fauna is that '...sedimentary organic matter preserved in the latest Permian deposits is characterised by unparalleled abundances of fungal remains, irrespective of depositional environment ... floral provinciality, and climatic zonation...' (Visscher *et al.*, 1996). The fungi were having a ball while the animals and plants were dying in unprecedented numbers.

Today, we humans depend on fungi for a great deal of our daily existence. Obviously, we depend on mycorrhizas to grow our crops, and chytrids to feed our farm animals to provide meat, dairy products, leather and woollen textiles. But we also depend on them for fungicides (strobilurins) to keep our farm crops healthy, enzymes to process our food and our textiles, and wonder drugs to keep ourselves and our animals healthy (penicillins, cephalosporins, cyclosporins, statins); and we've not even mentioned bread, cheese, wine and ale. After such a catalogue of the crucial

contributions of fungi to life on Earth (past and present), it is worrying to find that fungi are marginalised or totally ignored in schools around the world. Globally, school curricula call for comparisons only between animals and plants, leaving their pupils not only ignorant of the great Kingdom *Fungi*, but convinced that fungi are bacteria (Moore *et al.*, 2006)! An established spiral of ignorance seems to exist: learn little or nothing about fungi so that when you are old enough to teach, you can teach little or nothing about fungi. If this spiral continues uncorrected, mycologists will doubtless become extinct. At which point there will likely be an increase in populations of fungi digesting the carcasses of the few remaining previously eminent mycologists.

The taxonomy of the fungi is in continuous development as data about relationships accumulate and opinions change. At the time of writing, fungi are by far the best sampled eukaryotic kingdom, in terms of the number of complete genome sequences that are available. The recent deluge of genomic data available for the fungal kingdom (described as a tsunami by one author) emerging from the JGI's 1,000 Fungal Genomes Project provides genomic sequence data for an accelerating pace of taxonomic revisions. 1,000 genomes may sound a lot, and indeed sequencing this number of genomes represents several thousand person-years of effort; **BUT** it also represents only a tiny fraction of the 2 to 4 million species thought to exist on this planet (Hawksworth & Lücking, 2017). DNA sequencing, especially high-throughput sequencing, generates vast amounts of taxonomically-relevant data and it is inevitable that as such data accumulate the taxonomic framework of fungal classification will change (e.g. Tedersoo *et al.*, 2018) and anything we say now is bound to be quickly outdated.

It is with a degree of trepidation, therefore, that we present here a reasonably detailed list of taxa of Kingdom *Fungi*. We know that this Section will inevitably become outdated, perhaps even by the time you read this. However, we cannot claim to give you a Guidebook to the Kingdom without giving you some information about the population of that kingdom. ***Please accept the following as a snapshot of Kingdom Fungi, in this book at this time.***

The following classification is adapted from the 9th and 10th editions of *The Dictionary of the Fungi* (Kirk *et al.*, 2001, 2008), but it adopts the phylogenetic arrangement emerging from the AFTOL (*Assembling the Fungal Tree of Life*) project funded by the U.S. National Science Foundation (visit: <http://www.aftol.org/>; and see Blackwell *et al.*, 2006), as set out by Hibbett *et al.* (2007). AFTOL is a work in progress and uncertainties remain about the exact relationships of many groups. These are indicated in the annotated classification below with '*incertae sedis*', which means 'of uncertain position', this being the standard term for a taxonomic group of currently unknown or undefined relationship. Some of the material contained in this section is sourced from the '*Classification of the fungi*' entry (written by David Moore) in the *Encyclopaedia Britannica* and is used with permission, by courtesy of Encyclopaedia Britannica, Inc.© 2008.

The taxonomic arrangement shown here has been further adapted from that shown in the first edition to reflect the genome analyses of more recent times particularly the detailed reviews of phylogenetic analyses of McCarthy & Fitzpatrick (2017); as well as Choi & Kim (2017), Ren *et al.* (2016), Yarza *et al.* (2017), Zhang *et al.* (2017); and the two monographic volumes constituting the second edition of volume **VII** of *The Mycota* (McLaughlin & Spatafora (eds), 2014; 2015). Other publications (shown immediately below) are referenced in the taxonomic listings that follow. A cladogram (phylogenetic tree) showing the relationships of the five to seven 'Supergroups' into which the global tree of eukaryotes is currently subdivided has been shown above in Chapter 2 (Fig. 2.5). The taxonomically formal Kingdoms have been assigned to the deliberately informal supergroups by phylogenomic analysis, a method that reconstructs evolutionary histories using large alignments of tens to hundreds of genes, as well as whole genome sequences. The intention is to maintain flexibility as further work on phylogenomics resolves contentious relationships (Adl *et al.*, 2005, 2012; Burki, 2014; and see: <https://www.sciencenews.org/article/tree-life-gets-makeover>).

Molecular methods are revolutionising our understanding concerning the extent of fungal diversity in nature and the definition of species among entities that are known only from the polynucleotides recovered from nature. Analysis of the phylogenetic and evolutionary ecological relationships among the fungal genomes (and partial genomes) so recovered are threatening to drastically alter

the morphology-based Linnaean classification system which is the basis for the classification scheme detailed below. In particular, there is a move towards recognising taxonomic ranks using phylogenetic divergence time as a universally standardised criterion (Zhao *et al.*, 2016; Tedersoo, *et al.*, 2018; He *et al.*, 2019; Varga *et al.*, 2019).

## Outline classification of fungi

**Supergroup** Opisthokonta

**Kingdom:** Fungi

Basal fungi

**Phylum** Cryptomycota

Also known as Rozellida and Rozellomycota but Cryptomycota is preferred and has been validly published. These organisms were first detected as DNA sequences retrieved from a fresh water pond and were found in samples taken from other freshwater environments, soils and marine sediments. Phylogenetic analysis of these sequences formed a unique terminal clade. The only formally described genera in the clade are *Rozella*, which was previously considered a primitive chytrid, *Nucleophaga* and *Paramicrosporidium*. The existence of related organisms is known from environmental DNA sequences. *Rozella* differs from classical fungi in lacking chitinous cell walls at any stage in their lifecycle, although chitin has been detected in the inner layer of resting spores and the organisms possess a fungal-specific chitin synthase gene. Cryptomycota are phagotrophic parasites that feed by attaching to, engulfing, or living inside other cells; although most fungi feed by taking in nutrients from outside the cell (osmotrophy) (Jones *et al.*, 2011).

**Phylum** Microsporidia

No formal subdivision is proposed yet because of the lack of well-sampled multi-gene phylogenies within the group. Microsporidia are unicellular parasites of animals and protists with highly reduced mitochondria. Microsporidia may be a sister group of the rest of the Fungi, but this suggestion may have arisen from incomplete sampling (Didier *et al.*, 2014).

## Traditional Chytridiomycota

**Phylum** Chytridiomycota

Water moulds that live as aquatic saprotrophs or parasites in fresh water and soils, a few are marine. Chytrids produce motile asexual zoospores (with a single posterior flagellum, both a kinetosome and non-functional centriole, nine flagellar procs, and a microbody-lipid globule complex) in zoosporangia. Golgi apparatus with stacked cisternae; nuclear envelope fenestrated at poles during mitosis. Thallus may be unicellular or filamentous, and holocarpic (where all the thallus is involved in formation of the sporangium) or eucarpic (where only part of the thallus is converted into the fruiting body, monocentric, polycentric, or filamentous. Sexual reproduction with zygotic meiosis where known; sometimes produce motile sexual zoogametes. Considered to be the most ancestral group of fungi (Powell & Letcher, 2014). Type: *Chytridium*.

**Class:** Chytridiomycetes

Reproducing asexually by zoospores bearing a single posteriorly-directed flagellum; zoospores containing a kinetosome and a non-flagellated centriole; thallus monocentric or rhizomycelial polycentric; sexual reproduction not oogamous. Type: *Chytridium*.

**Order:** Chytridiales

Thallus monocentric or polycentric. No mycelium formed, but produce short absorptive filaments called rhizoids that lack nuclei and may be sufficiently extensive to be described as a rhizomycelium. Zoospores typically with flagellar base containing an electron-opaque plug, microtubules extending from one side of the kinetosome in a parallel array, ribosomes aggregated near the nucleus, kinetosome parallel to non-flagellated centriole and connected to it by fibrous

material, nucleus not associated with kinetosome, fenestrated cisterna (rumposome) adjacent to lipid globule. Mostly freshwater saprotrophs or parasites of algae, other fungi and higher plants (e.g. *Synchytrium endobioticum*, cause of potato wart disease). Previously included the plant parasite *Olpidium* but this is now *incertae sedis*. Type: *Chytridium*; example genera: *Chytridium*, *Chytriomycetes*, *Nowakowskiella*.

**Order:** Rhizophydiales; example genus: *Rhizophyidium*.

**Order:** Spizellomycetales; example genera: *Spizellomyces*, *Powellomyces*.

#### **Phylum Monoblepharidomycota**

Thallus filamentous, either extensive or a simple unbranched thallus, often with a basal holdfast; asexual reproduction by zoospores or autospores; zoospores containing a kinetosome parallel to a non-flagellated centriole, a striated disk partially extending around the kinetosome, microtubules radiating anteriorly from the striated disk, a ribosomal aggregation, and rumposome (fenestrated cisterna) adjacent to a microbody; sexual reproduction oogamous by means of posteriorly uniflagellate antherozoids borne in antheridia and nonflagellate female gametes borne in oogonia (Powell & Letcher, 2014). Type: *Monoblepharis*.

**Order:** Monoblepharidales; example genus: *Monoblepharis*.

#### **Phylum Neocallimastigomycota**

Thallus monocentric or polycentric; anaerobic, found in digestive system of larger herbivorous mammals and possibly in other terrestrial and aquatic anaerobic environments; lacks mitochondria but contains hydrogenosomes of mitochondrial origin; zoospores posteriorly uniflagellate or polyflagellate, kinetosome present but non-functional centriole absent, kinetosome-associated complex composed of a skirt, strut, spur and circumflagellar ring, microtubules extend from spur and radiate around nucleus, forming a posterior fan, flagellar props absent; nuclear envelope remains intact throughout mitosis (Grüniger *et al.*, 2014; Powell & Letcher, 2014; Edwards *et al.*, 2017; Wang *et al.*, 2017).

**Class:** Neocallimastigomycetes

**Order:** Neocallimastigales; example genus: *Neocallimastix*.

#### **Phylum Blastocladiomycota**

Very like the chytrids, characteristically, the Blastocladiomycota have life cycles with what is described as a sporic meiosis; that is, meiosis results in the production of haploid spores that can develop directly into a new, but now haploid, individual. This results in a regular alternation of generations between haploid gametothallus and diploid sporothallus individuals. Members of this phylum were included in Chytridiomycota in older textbooks. Saprotrophs as well as parasites of fungi, algae, plants and invertebrates, and may be facultatively anaerobic in oxygen-depleted environments. All members of this phylum have zoospores with a distinct ribosome-filled cap around the nucleus. The thallus may be monocentric or polycentric and becomes mycelial in *Allomyces*. Other representative genera are: *Physoderma*, *Blastocladiella*, and *Coelomomyces*. *Physoderma* spp. are parasitic on higher plants, *Coelomomyces* is an obligate endoparasite of insects with alternating sporangia and gametangia stages in mosquito larvae and copepod hosts, respectively (James *et al.*, 2014).

**Class:** Blastocladiomycetes

**Order:** Blastocladales; Water moulds with a restricted thallus, characterised by the production of thick-walled, pitted, resistant sporangia; sexual reproduction by isogamous (equal in size and alike in form) or anisogamous (unequal in size but still similar in form) planogametes; *Allomyces* exhibits an alternation of two equal generations; most are saprotrophs, but various species of *Coelomomyces* are parasitic in mosquito larvae; uniquely, their hyphae are devoid of cell walls; more than 50 species. Example genera: *Allomyces*, *Coelomomyces*.

## Traditional ‘Zygomycotan’ (zygomycete) fungi

The traditional ‘Zygomycota’, being saprotrophs or parasites (especially of arthropods) that produce non-motile, asexual sporangiospores in sporangia and sexual spores known as zygospores. This grouping includes the common moulds such as *Mucor*, *Rhizopus*, and *Phycomyces*. At one time the Chytridiomycota, Oomycota (see below) and ‘Zygomycota’ were classified together in the class ‘Phycomycetes’. This is no longer valid although the word is often used still as a ‘catch-all’ phrase covering lower fungi. The problem with ‘Zygomycota’ is that the group of organisms is polyphyletic, and the name was first published without a Latin diagnosis and is invalid. When relationships among the constituent fungal lineages are resolved the name ‘Zygomycota’ could be resurrected and validated. It cannot be properly defined in this classification, so some of zygomycetes are left in an uncertain position (*incertae sedis*). The following listing reflects the consensus cladogram of Spatafora *et al.* (2016), which is based on genome-scale data.

Phylum Mucoromycota

### Subphylum Glomeromycotina

Until recently, arbuscular mycorrhizal (AM) fungi have generally been classified in the ‘Zygomycota’ (being placed in the Order Glomales), but they do not form the zygospores characteristic of zygomycetes, and all ‘glomalean’ fungi form mutualistic symbioses. Recent molecular studies have suggested separate subphylum status is appropriate for the AM fungi, the Glomeromycotina, and this is the position taken by the AFTOL study (Redecker *et al.*, 2013; Redecker & Schüßler, 2014; Spatafora *et al.* (2016)).

**Class:** Glomeromycetes

**Order:** Archaeosporales; example genera: *Archaeospora*, *Geosiphon*.

**Order:** Diversisporales; example genera: *Acaulospora*, *Diversispora*, *Pacispora*

**Order:** Glomerales; example genus: *Glomus*

**Order:** Paraglomerales; example genus: *Paraglomus*.

### Subphylum Mortierellomycotina

Previously included in the subphylum Mucoromycotina, the subphylum Mortierellomycotina comprises the single order, Mortierellales (Hoffmann *et al.*, 2011; Benny *et al.*, 2014).

**Order:** Mortierellales; example genera: *Mortierella*, *Dissophora*, *Modicella*.

### Subphylum Mucoromycotina

Fungi saprotrophs, or rarely gall-forming, nonhaustorial, facultative mycoparasites, or forming ectomycorrhiza. Mycelium branched, coenocytic when young, sometimes producing septa that contain micropores at maturity. Asexual reproduction by sporangia, sporangiola, or merosporangia, or rarely by chlamydospores, arthrospores, or blastospores. Sexual reproduction by more or less globose zygospores formed on opposed or apposed suspensors. This group includes the Mucorales, which is the core group of the traditional zygomycetes (Benny *et al.*, 2014).

**Order:** Mucorales; often called the bread moulds; saprotrophic, weakly parasitic on plants, or parasitic on humans and then causing mucormycosis (a pulmonary infection); asexual reproduction by sporangiospores, 1-spored sporangiola (a small deciduous sporangium), or conidia; in the genus *Pilobolus* the heavily cutinised sporangium is forcibly discharged; about 360 species, example genera: *Mucor*, *Parasitella*, *Phycomyces*, *Pilobolus*, *Rhizopus*.

**Order:** Endogonales; example genera: *Endogone*, *Peridiospora*, *Sclerogone*, *Youngiomyces*.

Phylum Zoopagomycota

### Subphylum Entomophthoromycotina

Obligate pathogens of animals (primarily arthropods), cryptogamic plants, or saprotrophs; occasionally facultative parasites of vertebrates. Somatic state consisting of a well-defined mycelium, coenocytic or septate, walled or protoplasmic, which may fragment to form multinucleate hyphal bodies; protoplasts either hyphoid or amoeboid and changeable in shape; cystidia or rhizoids formed by some taxa. Such nuclear characters as overall size, location and comparative size of nucleoli, presence or absence of granular heterochromatin in chemically unfixed interphasic nuclei, and mitotic patterns are important at the family level. Conidiophores branched or unbranched. Primary spores true conidia, uni-, pluri-, or multinucleate, forcibly discharged by diverse possible means or passively dispersed; secondary conidia often produced. Resting spores with thick bi-layered walls form as zygospores after conjugations of undifferentiated gametangia from different or the same hyphal bodies or hypha or as azygospores arising without prior gametangial conjugations (Benny *et al.*, 2014).

**Order:** Entomophthorales; insect parasites or saprotrophs, some implicated in animal or human diseases; asexual reproduction by modified sporangia functioning as conidia, forcibly discharged. About 150 species, example genera: *Entomophthora*, *Ballocephala*, *Conidiobolus*, *Entomophaga*, *Neozygites*.

### **Subphylum** Kickxellomycotina

Fungi saprotrophs, mycoparasites, or obligate symbionts. Thallus arising from a holdfast on other fungi as a haustorial parasite, or branched, septate, subaerial hyphae. Mycelium branched or unbranched, regularly septate. Septa with median, disciform cavities containing plugs. Asexual production by 1- or 2-spored merosporangia, trichospores, or arthrospores. Sexual reproduction by zygospores that are globose, biconical, or allantoid and coiled (Benny *et al.*, 2014).

**Order:** Kickxellales; example genera: *Kickxella*, *Coemansia*, *Linderina*, *Spirodactylon*.

**Order:** Dimargaritales; example genera: *Dimargaris*, *Dispira*, *Tieghemiomyces*.

**Order:** Harpellales; thallus simple or branched, septate; asexual reproduction by trichospores; sexual reproduction zygomycetous; about 35 species. These fungi are commensals (organisms living parasitically on another organism but conferring some benefit in return, or at least not harming the host) with their filamentous thallus attached by a holdfast or basal cell to the digestive tract or external cuticle of living arthropods. Taxa in this order have been referred to as ‘Trichomycetes’ but this is no longer a useful taxon because it describes a polyphyletic group and is more an ecological rather than a phylogenetic grouping, consequently, the term should not be capitalised, i.e. use as ‘trichomycetes’). Example genera: *Harpella*, *Furculomyces*, *Legeriomyces*, *Smittium*.

**Order:** Asellariales; thallus branched, septate, attached by a basal coenocytic cell; asexual reproduction by arthrospores; Asellariales are retained in the Fungi because of their ultrastructural characteristics. Six species, example genera: *Asellaria*, *Orchesellaria*.

### **Subphylum** Zoopagomycotina

Endo- or ectoparasites of microanimals and fungi. Vegetative body consisting of a simple, branched or unbranched thallus or more or less extensively branched mycelium. Ectoparasites forming haustoria inside the host. Asexual reproduction by arthrospores, chlamydospores or uni- or multispored sporangiola; sporangiospores of multispored sporangiola formed in simple or branched chains (merosporangia). Sexual reproduction by nearly globose zygospores; sexual hyphae like the vegetative hyphae or more or less enlarged (Benny *et al.*, 2014).

**Order:** Zoopagales; parasitic on amoebas, rotifers, nematodes, or other small animals, which they trap by various specialised mechanisms; asexual reproduction by conidia borne singly or in chains, not forcibly discharged. About 60 species, example genera: *Cochlonema*, *Rhopalomyces*, *Piptocephalis*, *Sigmoideomyces*, *Syncephalis*, *Zoopage*.

Subkingdom Dikarya

Subkingdom: Dikarya

Unicellular or filamentous Fungi, lacking flagella, often with a dikaryotic state; contains Ascomycota and Basidiomycota. The name alludes to the putative synapomorphy (being a derived, that is non-ancestral, character shared by the two constituent phyla) of *dikaryotic hyphae*.

## **Phylum: Ascomycota**

This is the largest group of fungi, and the life styles adopted cover the complete range from saprotrophs, to symbionts (notably lichens), and to parasites and pathogens (plant pathogens are particularly numerous, but there are many important human pathogens in this group also). The Ascomycota are characterised by having sexual spores (ascospores) formed *endogenously* within an ascus (indeed the original Latin diagnosis consisted of only two words: ‘*sporae intracellulares*’ and while it is questionable that this description is truly diagnostic for the Ascomycota, as a validating diagnosis it is acceptable under the Code). A layered hyphal wall with a thin relatively electron-dense outer layer and a thicker electron-transparent inner layer also appears to be diagnostic. Except for the ascosporegenous yeasts (such as *Saccharomyces* and *Schizosaccharomyces*, which are only distantly related), asci are usually produced in complex fruit bodies (ascomata). The phylum comprises at least 64,000 species in 6,355 genera. In the past, these fungi were grouped based on fruit body shape and ascus arrangement. For example, Hemiascomycetes = no fruit bodies, asci naked; Euascomycetes = asci contained within ascomata, of which there are three main sorts, cleistothecia being closed, usually globose, but may be rudimentary or may consist of loosely interwoven hyphae, perithecia are flask-shaped, and in apothecia the asci are contained within saucer- or disc-shaped ascomata. The arrangement given below reflects the impact of molecular sequence data, but it is important to emphasise that further data are bound to change this interpretation (Prieto *et al.*, 2013; Wijayawardene *et al.*, 2018). Basic type genus: *Peziza*.

**Subphylum:** Taphrinomycotina (Kurtzman & Sugiyama, 2015)

**Class:** Taphrinomycetes

**Order:** Taphrinales; parasites on vascular plants; asci produced from binucleate ascogenous (ascus-producing) cells formed from the hyphae in the manner of chlamydospores (thick-walled spores). Example genera: *Taphrina*, *Protomyces*.

**Class:** Neoelectomycetes

**Order:** Neoelectales; example genus: *Neoelecta*.

**Class:** Pneumocystidomycetes

**Order:** Pneumocystidales; example genus: *Pneumocystis*.

**Class:** Schizosaccharomycetes

**Order:** Schizosaccharomycetales; example genus: *Schizosaccharomyces*.

**Subphylum:** Saccharomycotina (Kurtzman & Sugiyama, 2015)

**Class:** Saccharomycetes

**Order:** Saccharomycetales

Growth usually by individual yeast cells, often accompanied by pseudohyphae and/or true hyphae. Cell walls predominately of  $\beta$ -glucan. Ascomata not formed; one to many ascospores formed in asci that often are converted from individual cells or borne on simple ascophores. Mitotic and meiotic nuclear divisions within an intact nuclear membrane. Enveloping membrane system in ascospore delimitation associated independently with postmeiotic nuclei. Asexual reproduction by holoblastic budding, conidia or fission (arthrospores). Example genera: *Saccharomyces*, *Candida*, *Dipodascopsis*, *Metschnikowia*.

**Subphylum:** Pezizomycotina (Pfister, 2015)

**Class:** Arthoniomycetes

**Order:** Arthoniales; example genera: *Arthonia*, *Dirina*, *Roccella*.

**Class:** Dothideomycetes (Schoch & Grube, 2015).

**Subclass:** Dothideomycetidae

**Order:** Capnodiales; example genera: *Capnodium*, *Scorias*, *Mycosphaerella*.

**Order:** Dothideales; asci borne in fascicles (clusters) in a locule without sterile elements. About 350 species, example genera: *Dothidea*, *Dothiora*, *Sydowia*, *Stylodothis*.

**Order:** Myriangiales; example genera: *Myriangium*, *Elsinoe*.

**Subclass:** Pleosporomycetidae

**Order:** Pleosporales; asci borne in a basal layer among pseudoparaphyses. More than 4,705 species, example genera: *Pleospora*, *Phaeosphaeria*, *Lophiostoma*, *Sporormiella*, *Montagnula*.

**Dothideomycetes incertae sedis** (not placed in any subclass)

**Order:** Botryosphaeriales; example genera: *Botryosphaeria*, *Guignardia*.

**Order:** Hysteriales; stroma boat-shaped, opening by a longitudinal slit, which renders it apothecium-like; asci borne among pseudoparaphyses. About 110 species, example genera: *Hysterium*, *Hysteropatella*.

**Order:** Patellariales; example genus: *Patellaria*.

**Order:** Jahnulales; example genera: *Aliquandostipite*, *Jahnula*, *Patescospora*.

**Class:** Eurotiomycetes; three subclasses, Chaetothyriomycetidae, Eurotiomycetidae, and Mycocaliciomycetidae, are defined to represent the major lineages within Eurotiomycetes (Geiser *et al.*, 2015).

**Subclass:** Chaetothyriomycetidae

Lichenised, parasitic, and saprotrophic ascomycetes with mostly bitunicate/fissitunicate to evanescent asci, produced in perithecial ascomata arranged superficially or immersed in a thallus. Thalli often produced on the surfaces of rocks, lichens, decaying plant material and other substrata. Ascospores variable, from colourless to pigmented, simple to muriform. Hamathecium, when present, consisting of pseudoparaphyses. Pigments, when present, generally related to melanin. Asexual stages with phialidic and annellidic anamorphs observed in non-lichenised taxa.

**Order:** Chaetothyriales; example genera: *Capronia*, *Ceramothyrium*, *Chaetothyrium*.

**Order:** Pyrenulales; example genera: *Pyrenula*, *Pyrgillus*.

**Order:** Verrucariales; example genera: *Agonimia*, *Dermatocarpon*, *Polyblastia*, *Verrucaria*.

**Subclass:** Eurotiomycetidae

Saprotrophic, parasitic and mycorrhizal. Ascomata, when present, usually cleistothecial/gymnothecial, globose, often produced in surrounding stromatic tissue and brightly coloured; hamathecial elements lacking; gametangia usually undifferentiated and consisting of hyphal coils. Asci usually evanescent, sometimes bitunicate, scattered throughout the ascoma, rarely from a hymenium. Ascospores usually single-celled, lenticular, sometimes spherical or elliptical. Anamorphs variable, including phialidic and arthroconidial forms. Type: *Eurotium*.

**Order:** Coryneliales; asci in ascostromata with funnel-shaped ostioles at maturity. About 46 species, example genera: *Corynelia*, *Caliciopsis*.

**Order:** Eurotiales; asci globose to broadly oval, typically borne at different levels in cleistothecia (completely closed ascoma or fruiting structure); most of the human and animal dermatophytes belong here, also many saprotrophic soil or coprophilous fungi. Up to 930 species, example genera: *Eurotium*, *Emericella*, *Talaromyces*, *Elaphomyces*, *Trichocoma*, *Byssochlamys*.

**Order:** Onygenales; asci formed in a mazaedium (a fruiting body consisting of a powdery mass of free spores interspersed with sterile threads, enclosed in a peridium or wall structure), evanescent,



and liberating the ascospores as a powdery mass among sterile threads. About 270 species, example genera: *Onygena*, *Gymnoascus*, *Arthroderma*.

**Subclass:** Mycocaliciomycetidae

Parasites or commensals on lichens or saprotrophs. Ascomata disciform, stalked or sessile. Excipulum cupulate, and like the stalk hyphae at least in part sclerotised. Spore dispersal active, more rarely passive and ascomata then with a moderately developed mazaedium. Asci unitunicate, cylindrical, mostly with a distinctly thickened apex, 8-spored. Ascospores pale to blackish brown, ellipsoidal or spherical to cuboid, non-septate or transversely 1–7-septate. Spore wall pigmented, smooth or with an ornamentation formed within the plasmalemma. Vulpinic acid derivatives occur in a few species. A variety of coelomycetous and hyphomycetous anamorphs occur in the group. Type genus: *Mycocalicium*.

**Order:** Mycocaliciales; example genera: *Mycocalicium*, *Chaenothecopsis*, *Stenocybe*, *Sphinctrina*.

**Class:** Laboulbeniomycetes

**Order:** Laboulbeniales; minute parasites of insects and arachnids with mycelium represented only by haustoria and stalks. About 2,050 species, example genera: *Laboulbenia*, *Rickia*, *Ceratomyces*.

**Order:** Pyxidiophorales; example genus: *Pyxidiophora*.

**Class:** Lecanoromycetes (Gueidan *et al.*, 2015).

**Subclass:** Acarosporomycetidae

**Order:** Acarosporales

Lichen-forming ascomycetes with chlorococcoid photobiont. Ascomata immersed or sessile, disciform or perithecioid. True exciple hyaline, annulate. Hymenium non-amyloid. Paraphyses moderately to poorly branched, septate, moderately to poorly anastomosing. Asci functionally unitunicate, lecanoralean, non-amyloid or with slightly amyloid tholi, polyspored, generally with more than 100 ascospores per ascus. Ascospores hyaline, small, non-septate, non-halonate. The members of this order were formerly classified within the Lecanorales, but Acarosporaceae diverged earlier than the Lecanoromycetidae and Ostropomycetidae. example genera: *Acarospora*, *Pleopsidium*, *Sarcogyne*.

**Subclass:** Lecanoromycetidae

Lichen-forming ascomycetes with green algal or cyanobacterial photobiont. Ascomata immersed, sessile or stalked, usually disciform. True exciple hyaline or pigmented, annulate or cupulate. Hymenium amyloid or non-amyloid. Paraphyses simple or moderately to richly branched, septate, anastomosing or not. Asci bitunicate, functionally unitunicate, or prototunicate, lecanoralean, non-amyloid or amyloid, mostly 8-spored, but varying from 1-to poly-spored. Ascospores hyaline or brown, non-septate, trans-septate or muriform, halonate or non-halonate. This subclass includes the bulk of lichenised discomycetes.

**Order:** Lecanorales; example genera: *Cladonia*, *Lecanora*, *Parmelia*, *Ramalina*, *Usnea*.

**Order:** Peltigerales; example genera: *Coccocarpia*, *Collema*, *Nephroma*, *Pannaria*, *Peltigera*.

**Order:** Teloschistales; example genera: *Caloplaca*, *Teloschistes*, *Xanthoria*.

**Subclass:** Ostropomycetidae

**Order:** Agyriales; example genera: *Agyrium*, *Placopsis*, *Trapelia*, *Trapeliopsis*.

**Order:** Baeomycetales

Lichen-forming ascomycetes with chlorococcoid photobiont. Ascomata sessile or rarely stalked, disciform. True exciple hyaline or pigmented, annulate or cupulate. Hymenium non-amyloid. Paraphyses moderately to richly branched, septate. Asci unitunicate, non-amyloid or with slightly amyloid tholi, 8-spored. Ascospores hyaline, non-septate or trans-septate, halonate or non-halonate. Type genus: *Baeomyces*.

**Order:** Ostropales; ascoma an apothecium (an open, often cuplike ascoma); asci inoperculate (without a terminal pore); ascospores septate, threadlike. This order includes taxa formerly classified in separate orders, such as Gomphillales, Graphidales, Gyalectales and Trichotheliales; example genera: *Ostropa*, *Stictis*, *Gyalecta*, *Gomphillus*, *Graphis*, *Odontotrema*, *Porina*, *Thelotrema*.

**Order:** Pertusariales (this order may not be monophyletic as currently circumscribed, with Ochrolechiaceae and some groups of the heterogeneous *Pertusaria* clustering in a separate clade, but without support. Nonetheless, a cluster of taxa in a ‘core’ group of Pertusariales has been strongly supported as monophyletic in phylogenetic analyses. Example genera: *Coccotrema*, *Icmadophila*, *Ochrolechia*, *Pertusaria*.

**Lecanoromycetes *incertae sedis*** (not placed in any subclass):

**Order:** Candelariales

Lichen-forming ascomycetes with chlorococcoid photobiont, predominantly nitrophilous. Thallus of various morphology, yellow to orange (pulvinic acid derivatives). Ascomata apothecial, sessile, with or without a distinct margin, yellow to orange. The ascomatal wall formed from densely septate twisted hyphae. paraphyses mostly simple. Excipulum hyaline, hymenium amyloid. Asci unitunicate of Candelariatype with the amyloid lower part of the apical dome and broad apical cushion, often multispored. Ascospores hyaline, aseptate, rarely 1-septate. Type: *Candelaria*. Example genera: *Candelaria*, *Candelariella*.

**Order:** Umbilicariales

Lichen-forming ascomycetes with chlorococcoid photobiont. Ascomata sessile, or rarely immersed or stalked, mostly black, irregular, disciform. True exciple pigmented, annulate. Hymenium amyloid. Paraphyses simple or slightly branched, septate, apically thickened. Asci unitunicate, with slightly amyloid tholi, 1–8-spored. Ascospores hyaline or brown, non-septate to muriform. Type: *Umbilicaria*. Example genera: *Lasallia*, *Umbilicaria*.

**Class:** Leotiomyces (Zhang & Wang, 2015).

**Order:** Cyttariales; example genus: *Cyttaria*.

**Order:** Erysiphales; Obligate parasites on flowering plants causing powdery mildews; mycelium white, superficial in most, feeding by means of haustoria sunken into the epidermal cells of the host; one to several asci in a cleistothecium, if more than one, in a basal layer at maturity; asci globose to broadly oval; cleistothecia with appendages. About 150 species, example genera: *Erysiphe*, *Blumeria*, *Uncinula*.

**Order:** Helotiales; ascoma an apothecium bearing inoperculate asci exposed from an early stage; some important plant diseases are caused by members of this group. Monophyly of Helotiales *sensu lato* is not well supported by current data. There exists a minimum of five helotialean lineages that are intermixed with other leotiomyces taxa (e.g. Cyttariales, Erysiphales) and relationships are poorly resolved, thus preventing accurate phylogenetic classification at this time. Example genera: *Mitrula*, *Hymenoscyphus*, *Ascocoryne*.

**Order:** Rhytismatales; example genera: *Rhytisma*, *Lophodermium*, *Cudonia*.

**Order:** Thelebolales; example genera: *Thelebolus*, *Coprotus*, *Ascozonus*.

**Class:** Lichinomycetes

**Order:** Lichinales; example genera: *Heppia*, *Lichina*, *Peltula*.

**Class:** Orbiliomycetes

**Order:** Orbiliales; example genera: *Orbilina*, *Hyalorbilia*.

**Class:** Pezizomycetes

**Order:** Pezizales; ascoma an apothecium bearing operculate (with a hinged cap) asci above the ground; apothecia often large, cup- or saucer-shaped, spongy, brain-like, saddle-shaped, etc.; this

group includes morels, false morels, saddle fungi and cup fungi among others. About 1 700 species, example genera: *Peziza*, *Glaziella*, *Morchella*, *Pyronema*, *Tuber*.

**Class:** Sordariomycetes (Zhang & Wang, 2015; Hyde *et al.*, 2017).

**Subclass:** Hypocreomycetidae

**Order:** Coronophorales; asci in ascostromata with irregular or round, never funnel-shaped, openings. About 90 species, example genera: *Nitschkia*, *Scortechinia*, *Bertia*, *Chaetosphaerella*.

**Order:** Hypocreales; perithecia and stromata when present, often brightly coloured; asci in a basal layer among apical paraphyses; perithecia immersed in a stroma formed from a sclerotium (a hard-resting body resistant to unfavourable environmental conditions); asci with a thick apex penetrated by a central canal through which the septate, threadlike ascospores are ejected. The ergot fungus (*Claviceps purpurea*), cause of ergotism in plants, animals, and humans, and the original source of LSD, belongs to this order; *Cordyceps* spp. parasitise insect larvae. About 2 700 species, example genera: *Hypocrea*, *Nectria*, *Cordyceps*, *Claviceps*, *Niesslia*.

**Order:** Melanosporales

Ascoma perithecial or secondarily cleistothecial, peridium derived from base of an ascogonial coil, translucent; centrum pseudoparenchymatous, paraphyses absent in development; asci unitunicate, evanescent; ascospores dark, with germ pores at both ends; anamorphs hyphomycetous; often mycoparasitic. Example genus: *Melanospora*.

**Order:** Microascales; example genera: *Microascus*, *Petriella*, *Halosphaeria*, *Lignincola*, *Nimbospora*.

**Subclass:** Sordariomycetidae

**Order:** Boliniales; example genera: *Camarops*, *Apiocamarops*.

**Order:** Calosphaeriales; example genera: *Calosphaeria*, *Togniniella*, *Pleurostoma*.

**Order:** Chaetosphaeriales; example genera: *Chaetosphaeria*, *Melanochaeta*, *Zignoëlla*, *Striatosphaeria*.

**Order:** Coniochaetales; example genera: *Coniochaeta*, *Coniochaetidium*.

**Order:** Diaporthales; perithecia immersed in plant tissue or in a stroma with their long ostioles protruding; ascial stalks gelatinising, freeing the asci from their basal attachment; paraphyses lacking. The chestnut blight fungus (*Endothia parasitica*) belongs here. Close to 1 200 species, example genera: *Diaporthe*, *Gnomonia*, *Cryphonectria*, *Valsa*.

**Order:** Ophiostomatales; example genera: *Ophiostoma*, *Fragosphaeria*.

**Order:** Sordariales; example genera: *Sordaria*, *Podospora*, *Neurospora*, *Lasiosphaeria*, *Chaetomium*.

**Subclass:** Xylariomycetidae

**Order:** Xylariales; perithecia with dark, membranous or carbonous (appearing as black burned wood) walls, with or without a stroma (a compact structure on or in which fructifications are formed); asci persistent, borne in a basal layer among paraphyses (elongate structures resembling asci but sterile), which may ultimately gelatinise and disappear; example genera: *Xylaria*, *Hypoxylon*, *Anthostomella*, *Diatrype*, *Graphostroma*.

**Sordariomycetes *incertae sedis*** (not placed in any subclass)

**Order:** Lulworthiales (this order includes members formerly placed in the Spathulosporales). Example genera: *Lulworthia*, *Lindra*.

**Order:** Meliolales; mycelium dark, superficial on leaves and stems of vascular plants, typically bearing appendages (termed hyphopodia or setae); asci in basal layers in ostiolate perithecia without appendages; mostly tropical fungi. More than 1 900 species, example genus: *Meliola*.

**Order:** Phyllachorales; example genus: *Phyllachora*.

**Order:** Trichosphaeriales; example genus: *Trichosphaeria*.

*Pezizomycotina incertae sedis* (not placed in any class)

**Order:** Lahmiales; example genus: *Lahmia*.

**Order:** Medeolariales; example genus: *Medeolaria*.

**Order:** Triblidiales; example genera: *Huangshania*, *Pseudographis*, *Triblidium*.

## **Phylum: Basidiomycota**

Saprotrophic or parasitic on plants or insects; filamentous; hyphae septate, the septa typically inflated (dolipore) and centrally perforated; mycelium of two types, primary (homokaryotic) of uninucleate cells, succeeded by secondary (heterokaryotic), consisting of dikaryotic cells, this often bearing bridge-like clamp connections over the septa; asexual reproduction by fragmentation, oidia (thin-walled, free, hyphal cells behaving as spores), or conidia; sexual reproduction by fusion of hyphae with each other or with hyphal fragments or with germinating spores (somatogamy), resulting in dikaryotic hyphae that eventually give rise to basidia, either singly on the hyphae or in variously shaped basidiomata. The meiospores (sexual spores) are basidiospores borne exogenously on basidia; many are ballistospores that are actively discharged from the small hyphal branches (sterigmata) on which they arise. This is a large phylum of fungi containing the rusts, smuts, jelly fungi, club fungi, coral and shelf (bracket) fungi, mushrooms, puffballs, stinkhorns, and bird's-nest fungi. Known Basidiomycota comprise about 1-600 genera and 32,000 species. The majority of these are in the subphylum Agaricomycotina; about 250 genera (8,400 species) occur in the Pucciniomycotina, and 62 genera (1,200 species) are assigned to the Ustilaginomycotina.

Subdivision of the Basidiomycota is based on the form of the basidium and, traditionally, the shape and morphology of the mature fruit body. Developmental comparisons show that apparently similar structures and shapes can arise in different ways; for example, there are several ways of creating the folded spore-bearing surface that we call gills. Since they arise in different ways such features are only superficially similar because they have evolved in different ways (like, for example, the wings of butterflies and birds); they are described as analogous organs (as distinct from homologous organs, which are those that have a shared evolutionary ancestry). Shape and morphology of mature fruit bodies, even though these are the easiest to find in the field, can be misleading because they do not contribute to a natural classification. The introduction of molecular sequence comparisons is prompting major, and many surprising, revisions of the classification scheme originally constructed based on shape and morphology. Some of these revisions are reflected in the arrangement shown below. But this is far from being the final story (Zhao *et al.*, 2016; Tedersoo, *et al.*, 2018; He *et al.*, 2019; Varga *et al.*, 2019).

**Subphylum:** Pucciniomycotina (equivalent to the traditional Urediniomycetes) (Aime *et al.*, 2014).

**Class:** Pucciniomycetes

**Order:** Septobasidiales; example genera: *Septobasidium*, *Auriculoscypha*.

**Order:** Pachnocybales; example genus: *Pachnocybe*.

**Order:** Helicobasidiales; example genera: *Helicobasidium*, *Tuberculina*.

**Order:** Platygloeales; example genera: *Platygloea*, *Eocronartium*.

**Order:** Pucciniales; example genera: *Puccinia*, *Uromyces*.

**Class:** Cystobasidiomycetes

**Order:** Cystobasidiales; example genera: *Cystobasidium*, *Occultifur*, *Rhodotorula*.

**Order:** Erythrobasidiales; example genera: *Erythrobasidium*, *Rhodotorula*, *Sporobolomyces*, *Bannoa*.

**Order:** Naohideales; example genus: *Naohidea*.

**Class:** Agaricostilbomycetes

**Order:** Agaricostilbales; example genera: *Agaricostilbum*, *Chionosphaera*.

**Order:** Spiculogloeales; example genera: *Mycogloea*, *Spiculogloea*.

**Class:** Microbotryomycetes

**Order:** Heterogastridiales; example genus: *Heterogastridium*.

**Order:** Microbotryales; example genera: *Microbotryum*, *Ustilentyloma*.

**Order:** Leucosporidiales; example genera: *Leucosporidiella*, *Leucosporidium*, *Mastigobasidium*.

**Order:** Sporidiobolales; example genera: *Sporidiobolus*, *Rhodosporidium*, *Rhodotorula*.

**Class:** Atractiellomycetes

**Order:** Atractiellales; example genera: *Atractiella*, *Saccoblastia*, *Helicogloea*, *Phleogena*.

**Class:** Classiculomycetes

**Order:** Classiculales; example genera: *Classicula*, *Jaculispora*.

**Class:** Mixiomycetes

**Order:** Mixiales; example genus: *Mixia*.

**Class:** Cryptomycocolacomycetes

**Order:** Cryptomycocolacales; example genera: *Cryptomycocolax*, *Colacosiphon*.

**Subphylum:** Ustilaginomycotina (equivalent to the traditional Ustilaginomycetes) (Begerow *et al.*, 2014; Kijpornyongpan *et al.*, 2018).

**Class:** Ustilaginomycetes

**Order:** Urocystales; example genera: *Urocystic*, *Ustacystis*, *Doassansiopsis*.

**Order:** Ustilaginales; example genera: *Ustilago*, *Cintractia*.

**Class:** Exobasidiomycetes

**Order:** Doassansiales; example genera: *Doassansia*, *Rhamphospora*, *Nannfeldtiomyces*.

**Order:** Entylomatales; example genera: *Entyloma*, *Tilletiopsis*.

**Order:** Exobasidiales; example genera: *Exobasidium*, *Clinoconidium*, *Dicellomyces*.

**Order:** Georgefischeriales; example genera: *Georgefischeria*, *Phragmotaeonium*, *Tilletiaria*, *Tilletiopsis*.

**Order:** Microstromatales; example genera: *Microstroma*, *Sympodiomyces*, *Volvocisporium*.

**Order:** Tilletiales; example genera: *Tilletia*, *Conidiosporomyces*, *Erratomyces*.

Ustilaginomycotina incertae sedis (not placed in any class):

**Order:** Malasseziales; example genus: *Malassezia*.

**Subphylum:** Agaricomycotina (equivalent to the traditional Hymenomycetes or Basidiomycetes)

**Class:** Tremellomycetes (Weiss *et al.*, 2014).

**Order:** Cystofilobasidiales; example genera: *Cystofilobasidium*, *Mrakia*, *Itersonia*.

**Order:** Filobasidiales; example genera: *Filobasidiella*, *Cryptococcus*.

**Order:** Tremellales; (jelly fungi) fruiting bodies (basidiomata) usually bright-coloured to black gelatinous masses; a few are parasitic on mosses, vascular plants, or insects; most are saprotrophs. About 350 species, example genera: *Tremella*, *Trichosporon*, *Christiansenia*.

**Class:** Dacrymycetes (Oberwinkler, 2014).

**Order:** Dacrymycetales; example genera: *Dacrymyces*, *Calocera*, *Guepiniopsis*.

**Class:** Agaricomycetes (Hibbett *et al.*, 2014)

**Subclass:** Agaricomycetidae

**Order:** Agaricales; example genera: *Agaricus* (Kerrigan, 2016; Zhao *et al.*, 2016), *Coprinopsis* (Moore, 2013b), *Pleurotus*.

**Order:** Atheliales; example genera: *Athelia*, *Piloderma*, *Tylospora*.

**Order:** Boletales; example genera: *Boletus*, *Scleroderma*, *Coniophora*, *Rhizopogon*.

**Subclass:** Phallomycetidae

**Order:** Geastrales; example genera: *Geastrum*, *Radiigera*, *Sphaerobolus*.

**Order:** Gomphales; example genera: *Gomphus*, *Gautieria*, *Ramaria*.

**Order:** Hysterangiales; example genera: *Hysterangium*, *Phallogaster*, *Gallacea*, *Austrogautieria*.

**Order:** Phallales; example genera: *Phallus*, *Clathrus*, *Claustula*.

**Agaricomycetes *incertae sedis*** (not placed in any subclass):

**Order:** Auriculariales; example genera: *Auricularia*, *Exidia*, *Bourdotia*.

**Order:** Cantharellales; example genera: *Cantharellus*, *Botryobasidium*, *Craterellus*, *Tulasnella*.

**Order:** Corticiales; basidiomycetes with effused or discoid (*Cytidia*) basidiomata, a smooth hymenophore, and a monomitic hyphal system with clamped, rarely simple-septate, hyphae. Dendrohyphidia common. Species with or without cystidia. A probasidial resting stage is present in many species. Spores smooth, in masses white to pink. Saprotrophic, parasitic, or lichenicolous. Type: *Corticium*. Example genera: *Corticium*, *Vuilleminia*, *Punctularia*.

**Order:** Gloeophyllales; fruiting bodies perennial or annual and long-lived, with hymenium maturing and thickening over time. Stature resupinate, effused-reflexed or dimidiate, with smooth, wrinkled, dentate, lamellate or regularly poroid hymenophore, or pileate-stipitate with lamellae. (Aborted, coralloid or flabelliform fruiting bodies may be formed under conditions of darkness or high carbon dioxide concentration). Leptocystidia or hyphoid hairs originating in the context and extending into or protruding from the hymenial layer (or lamellar margin in *Neolentinus*) are common; these often with thick brown walls and brownish incrustation. Context brown (but pallid in *Neolentinus*) and generally darkening in potassium hydroxide (the brownish incrustation in *Boreostereum* turning green in potassium hydroxide). Monomitic (if so, with sclerified generative hyphae), dimitic, or trimitic; generative hyphae with or without clamp connections. Basidiospores hyaline, ellipsoid to cylindrical or subballantoid, with thin, smooth walls, and neither amyloid, dextrinoid nor cyanophilous. Where this is known, basidiospores are binucleate and sexuality is heterothallic and bipolar (but tetrapolar in *V. berkeleyi*). Type: *Gloeophyllum*. Causing brown rots (*Gloeophyllum*, *Neolentinus*, *Veluticeps*) or stringy white rot (*Boreostereum*, *Donkioporia*) of wood of gymnosperms, monocots and dicots. Occurrence on 'wood in service' (e.g. railway ties, paving blocks, wooden chests) seems to be common (in *Donkioporia*, *Gloeophyllum*, *Heliocybe* and *Neolentinus*); often on charred wood (*Boreostereum* and *Veluticeps*). Example genera: *Gloeophyllum*, *Neolentinus*, *Veluticeps*.

**Order:** Hymenochaetales; example genera: *Hymenochaete*, *Phellinus*, *Trichaptum*.

**Order:** Polyporales; example genera: *Polyporus*, *Fomitopsis*, *Phanerochaete*.

**Order:** Russulales; example genera: *Russula*, *Aleurodiscus*, *Bondarzewia*, *Hericium*, *Peniophora*, *Stereum*.

**Order:** Sebacinales; example genera: *Sebacina*, *Tremellodendron*, *Piriformospora*.

**Order:** Thelephorales; example genera: *Thelephora*, *Bankera*, *Polyozellus*.

**Order:** Trechisporales (basidiomycetes with effused, stipitate or clavarioid basidiomata. Hymenophore smooth, granular (grandinioid), hydroid or poroid. Hyphal system monomitic, hyphae clamped, subicular hyphae with or without ampullate septa. Cystidia present in some species, mostly lacking. Basidia with four to six sterigmata. Spores smooth or ornamented. On wood or soil. Type: *Trechispora*. Example genera: *Trechispora*, *Sistotremastrum*, *Porpomyces*.

**Basidiomycota incertae sedis** (not placed in any subphylum):

**Class:** Wallemiomycetes

**Order:** Wallemiales; example genus: *Wallemia*.

**Class:** Entorrhizomycetes:

**Order:** Entorrhizales; example genus: *Entorrhiza*.

## Taxonomic outline for Fungi and fungus-like organisms

Kingdom Fungi is a member of one of the six ‘**Supergroups**’ into which the Domain Eukaryota is currently subdivided; these being (Adl *et al.*, 2005; 2012):

**Excavata:** flagellate protozoa; containing free-living, symbiotic forms, and some important parasites of humans. Classified on the basis of flagellar structures and considered to be the basal lineage of flagellated organisms.

**Amoebozoa:** amoeba-like protists, many with blunt, finger-like, lobed pseudopods and tubular mitochondrial cristae. Contains many of the best-known amoeboid organisms, including the genus *Amoeba* itself, as well as several varieties of slime moulds. Amoebozoa is a monophyletic clade, often shown as the sister group to Opisthokonta.

**Opisthokonta:** a broad group of eukaryotes, including both Kingdom Animalia and Kingdom Fungi, together with some eukaryotic microorganisms (choanoflagellates) that are sometimes grouped in the phylum Choanozoa.

**Rhizaria:** a species-rich supergroup of mostly unicellular eukaryotes, defined mainly from ribosomal-DNA sequences as they vary considerably in morphology. The three main groups of Rhizaria are Cercozoa (amoebae and flagellates common in soil); Foraminifera (amoeboids with reticulose pseudopods, common as marine benthos); and Radiolaria (amoeboids with axopods, common as marine plankton). Many produce shells or skeletons of complex structure, which form the bulk of protozoan fossils.

**Chromalveolata:** a varied assemblage divided into four major subgroups, **Cryptophyta** (cryptomonad algae), **Haptophyta** (coccoliths and other phytoplankton, some of which form toxic algal blooms), **Stramenopiles** (brown algae, kelps, diatoms, and water moulds) and **Alveolata** (includes ciliates, dinoflagellates, photosynthetic protozoa and parasitic protozoa). The emerging consensus is that the Chromalveolata is not monophyletic (Adl *et al.*, 2012; Cavalier-Smith *et al.*, 2015). The four original subgroups fall into at least two categories: one comprises the **Stramenopiles** and the **Alveolata**, to which the **Rhizaria** are now usually added to form the **SAR supergroup** (see below), whilst the other comprises the Cryptophyta and the Haptophyta.

**Archaeplastida** or **Primoplantae** (the latter name avoids confusion with an obsolete name once applied to cyanobacteria). This supergroup comprises red algae (Rhodophyta), green algae, and all land plants, together with a small group of freshwater unicellular algae called glaucophytes. In all these organisms, chloroplasts are surrounded by two membranes, suggesting they developed directly from endosymbiotic cyanobacteria (as opposed to other photosynthetic protists where chloroplasts are surrounded by three or four membranes, suggesting they were acquired secondarily from red or green algae).

Other than Kingdom Fungi in the Opisthokonta, mycologists might study organisms assigned to several of the supergroups into which eukaryotes are currently divided.

## **Slime moulds are assigned to several supergroups:**

Supergroup Amoebozoa

The superphylum **Mycetozoa** includes:

**Class Myxogastria** of syncytial or plasmodial slime moulds, such as *Physarum*, *Fuligo*, and *Stemonitis*.

**Class Dictyostelia** of cellular slime moulds like *Dictyostelium* and *Polysphondylium*.

**Class Protostelia**, an intermediate group that form much smaller fruit bodies than the rest, such as *Protostelium*.

Supergroup Rhizaria

This includes the plasmodiophorids, which are obligate intracellular symbionts or parasites of plant, algal or fungal cells living in freshwater or soil habitats. They form multinucleate, unwalled plasmodia and so are traditionally considered slime moulds, because of the plasmodial stage. Previously classified as fungi (and called Plasmodiophoromycota), genetic and ultrastructural studies place them in a diverse group of protists called the Cercozoa.

**Class Phytomyxea** a group of about 15 genera with 50 species of parasites of plants. The genera Plasmodiophora and Spongospora cause serious plant diseases (cabbage club root disease and powdery scab potato tuber disease, respectively).

Supergroup Excavata

Includes cellular slime moulds that have a similar life style to dictyostelids, but their amoebae behave differently, having temporary projections called pseudopods (false feet).

Class Heterolobosea, Order Acrasida; example genus *Acrasis*.

Supergroup SAR

The superphylum **Heterokonta** includes a class of marine protists that produce a network of filaments or tubes (slime nets) that form labyrinthine networks of tubes in which amoeba without pseudopods can travel and absorb nutrients. Commonly found as parasites on algae and seagrasses or as decomposers on dead plant material; they also include some parasites of marine invertebrates.

**Class Labyrinthulomycetes** (Botanical Nomenclature) or **Labyrinthulea** (Zoological Nomenclature) in two main groups, labyrinthulids (slime nets) and thraustochytrids. Example genera are *Labyrinthula*, *Pseudoplasmodium* and *Thraustochytrium*. **Included in the Kingdom Straminipila, Phylum Labyrinthulomycota, below; this reflects the border-line nature of these organisms.**

Supergroup Opisthokonta

*Fonticula* is a genus (with only one species, *Fonticula alba*) of cellular slime mould which forms a fruiting body in a volcano shape. It is not closely related to other well-established groups of cellular slime moulds (dictyostelids or acrasids) but molecular phylogenetics found homologies with members of the Opisthokonta as a sister taxon to *Nuclearia*, which is an opisthokont protist thought to be close to the animal-fungus boundary.

Finally, there is a collection of '**fungus-like**' organisms or **water moulds**, currently placed in **Supergroup SAR**, which have a long tradition of being studied by mycologists. These are placed in **Kingdom Straminipila** (Beakes *et al.*, 2014).

## **Kingdom Straminipila**

We follow Beakes *et al.* (2014) in the use of this name **and** this spelling. There are alternative spellings (Stramenopila, Straminopila) and arguments for the use of the kingdom name **Chromista**. A total of approximately 126 genera and 1,040 species; the majority being in the **Oomycota**. These are common microorganisms and include important plant pathogens such as the cause of potato



blight (*Phytophthora*). They have motile spores which swim by means of two flagella and grow as hyphae with cellulose-containing walls.

## Phylum Oomycota

About 1,000 species in 110 genera of cosmopolitan and widespread ‘water moulds’ occurring in freshwater, soil-water and marine habitats, some being economically **very** important pathogens such as *Saprolegnia*, *Pythium*, and *Phytophthora*. *Phytophthora* species are serious pathogens of native vegetation, commercial forests, agricultural and horticultural crops, and cultivated landscapes worldwide. Over 100 species of *Phytophthora* have been described and it has been estimated that there may be up to 500 yet to be discovered. A disturbing recent trend has been the rapid dispersal of new *Phytophthora* species around the world by international movement of nursery stocks and other plant material.

**Order** Leptomitales; example genera: *Apodachlyella*, *Ducellieria*, *Leptolegniella*, *Leptomitus*.

**Order** Myzocytiosidales; example genus: *Crypticola*.

**Order** Olpidiopsidales; example genus: *Olpidiopsis*.

**Order** Peronosporales; example genera: *Albugo*, *Peronospora*, *Bremia*, *Plasmopara*.

**Order** Pythiales; example genera *Pythium*, *Phytophthora*, *Pythiogeton*

**Order** Rhipidiales; example genus: *Rhipidium*.

**Order** Salilagenidiales; example genus: *Haliphthoros*.

**Order** Saprolegniales; example genera: *Leptolegnia*, *Achlya*, *Saprolegnia*.

**Order** Sclerosporales; example genera: *Sclerospora*, *Verrucalvus*.

**Order** Anisopidiales; example genus: *Anisopidium*.

**Order** Lagenismatales; example genus: *Lagenisma*.

**Order** Rozellopsidales; example genera: *Pseudosphaerita*, *Rozellopsis*.

**Order** Haptoglossales; example genera: *Haptoglossa*, *Lagena*, *Electrogella*, *Eurychasma*, *Pontisma*, *Sirolpidium*.

## Phylum Hyphochytriomycota

Microscopic organisms that form a small thallus, often with branched rhizoids, which occur as parasites or saprotrophs on algae and fungi in freshwater and in soil. The whole of the thallus is eventually converted into a reproductive structure. Only 24 species (in 6 genera) are known.

**Order** Hyphochytriales, example genera: *Hyphochytrium*, *Rhizidiomyces*.

## Phylum Labyrinthulomycota

Feeding stage comprises an ectoplasmic network and spindle-shaped or spherical cells that move within the network by gliding over one another. Occur in both salt- and freshwater in association with algae and other chromists. About 56 species in 12 genera. *Included in superphylum Heterokonta in the discussion of slime moulds above. This reflects the border-line nature of these organisms.*

**Order** Labyrinthulales; e.g. *Labyrinthula*.

**Order** Thraustochytriales; e.g. *Thraustochytrium*.

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