21st Century Guidebook to Fungi
OUTLINE CLASSIFICATION OF FUNGI

Evolution and phylogeny

Until the latter half of the 20th century fungi were classified in the Plant Kingdom (strictly speaking into the subkingdom Cryptogamia, Division Fungi, subdivision Eumycotina) and were separated into four classes: the Phycomycetes, Ascomycetes, Basidiomycetes, and Deuteromycetes (the latter also known as Fungi Imperfecti because they lacked a sexual cycle). These traditional groups of 'fungi' were largely defined by the morphology of their sexual organs, whether or not their hyphae had cross-walls (septa), and the ploidy (degree of repetition of the basic number of chromosomes) of nuclei in their vegetative mycelium. The slime moulds, all grouped in the subdivision Myxomycotina, were also included in Division Fungi.

Around the middle of the 20th century the three major kingdoms of multicellular eukaryotes were finally recognised as being absolutely distinct; the crucial character difference being the mode of nutrition: animals (whether single cells or multicellular) engulf food; plants photosynthesise; and fungi excrete digestive enzymes and absorb externally-digested nutrients. Other differences can be added to these. For example: in their cell membranes animals use cholesterol, fungi use ergosterol; in their cell walls, plants use cellulose (a glucose polymer), fungi use chitin (a glucosamine polymer); recent genomic surveys show that plant genomes lack gene sequences that are crucial in animal development, and vice-versa, and fungal genomes have none of the sequences that are important in controlling multicellular development in animals or plants. This latter point implies that animals, plants and fungi separated at a unicellular grade of organisation.

The prokaryotic domains of bacteria and Archea, and the eukaryotic kingdoms (plants, animals, fungi, protozoa and algae), are the fundamental groupings of life on Earth. The prokaryote/eukaryote distinction recognises the 'higher organism' traits that eukaryotic organisms share, such as nuclei, cytoskeletons, internal membranes, and mitotic and meiotic division cycles. Eukaryotes must have evolved from prokaryotes and the most convincing endosymbiosis theory accounts for this through a sequence of symbiotic relationships being established between prokaryotic partners. The mitochondria of eukaryotes evolving from aerobic bacteria living within a host cell; chloroplasts of eukaryotes evolving from endosymbiotic cyanobacteria; eukaryotic cilia and flagella arising from endosymbiotic spirochetes, the basal bodies from which eukaryotic cilia and flagella develop being able to create the mitotic spindle and thus contribute to the cytoskeleton. However they evolved, molecular analyses indicate that eukaryotes and bacteria last shared a common ancestor about two billion years ago, and plants, animals and fungi diverged from one another just under one billion years ago.

In this section we will show the current classification of fungi, but will deal with a little terminology first. The basic rank of biological classification is the species (although there is no universally approved definition of a species) and species are then arranged (moving successively higher in rank) into genera, families (fungal family names end in …***aceae***), orders (names of fungal orders end in …***ales***), classes (names end in …***mycetes***), subphylum (names of fungal subphyla end in …***mycotina***) and phyla (singular = phylum, fungal names end in …***mycota***). Additional intermediate ranks are possible. A taxon (plural = taxa) is a taxonomic group of any rank. Although fungi are not plants, formal recognition of fungal nomenclature is governed by the International Code of Botanical Nomenclature (though the taxon 'phylum' has been adopted from animal taxonomy).

The highest formally accepted taxon is the Kingdom, the name of which must be a Latinised plural. Five Kingdoms of eukaryotes are now generally recognised as being the minimum number worthy of recognition: these are Kingdom Protozoa (which includes slime moulds); Kingdom Chromista (mostly algae, but including some fungus-like organisms); Kingdom Fungi; Kingdom Plantae; and Kingdom Animalia. The main aim of a phylogenetic classification is to group organisms on the basis of their ancestral relationships (their 'phylogeny'); the genes possessed by organisms in the present day have come to them through the lineage of their ancestors. Consequently, finding relationships between those lineages is the only way of establishing the natural relationships between living organisms. Phylogenetic relationships can be inferred from a variety of data, traditionally including fossils and comparative morphology and biochemistry, but most modern phylogenetic trees (evolutionary trees or cladograms) depend on molecular data. The fossil record of fungi is scanty. Fungal hyphae are evident within the tissues of the oldest plant fossils, showing that fungi are an extremely ancient group. Indeed some of the oldest terrestrial plant-like fossils known, called *Prototaxites*, which are common in all parts of the world in the mid-Devonian period (400 to 350 million years ago) are now being interpreted as either lichens or large saprotrophic fungi (possibly even Basidiomycota). In the absence of an extensive fossil record, biochemical characters have been useful markers to map the probable evolutionary relationships of fungi. Fungal groups can be related by their common cell wall composition (presence of both chitin and alpha-1,3 and alpha-1,6-glucan), the same pattern of organisation of tryptophan enzymes, and synthesis of lysine by the same, unique, aminoadipic acid pathway. However, the molecular phylogenetic analyses that became possible during the 1990s has contributed most to our understanding of fungal origins and evolution. At first, evolutionary trees were generated by comparing a single gene sequence, usually the small subunit ribosomal RNA gene (SSU rRNA). Addition of information from several protein-coding genes helped correct initial discrepancies, and phylogenetic trees are currently built using a wide variety of data largely, but not entirely, molecular in nature.

Kingdom Fungi is a monophyletic group (meaning that all modern fungi can be traced back to a single ancestral organism) that diverged from a common ancestor with the animals about 800 to 900 million years ago. The most recently published classification divides the kingdom into seven phyla, ten subphyla, 36 classes, 12 subclasses, and 140 orders. We will only give a summarised outline of this scheme, but it may be helpful to start by emphasising the more recent major changes.

The kingdom of true fungi is now recognised as one of the oldest and largest groups of living organisms. Many organisms included within the first paragraph of this section (particularly among the phycomycetes and slime moulds) are no longer considered to the true fungi, even though mycologists might study them. This applies to many of the water moulds, like the Oomycota (which include the plant pathogen *Phytophthora*, cause of potato late blight), all of which have been removed from the fungi to be classified with brown algae and diatoms in the Kingdom Chromista. Similarly, the Amoebidales, which are parasitic or commensal on living arthropods and were previously thought to be fungi, are now considered to be protozoan animals. None of the slime moulds are now placed in Kingdom Fungi and their relationship to other organisms, especially animals, is still in dispute. Kingdom Fungi has also gained a few recruits on the basis of molecular phylogenetic analysis, notably *Pneumocystis*, the Microsporidia, and *Hyaloraphidium*. *Pneumocystis carinii* (= *P. jirovecii*) is a pathogen causing pneumonia in mammals, including humans with weakened immune systems; pneumocystis pneumonia or PCP is the most common opportunistic infection in people with HIV and has been a major killer of patients infected with HIV. *Pneumocystis* was initially described as a trypanosome, but evidence from sequence analyses of several genes places it in the Taphrinomycotina in the Ascomycota (see below). The Microsporidia are obligate intracellular parasites of animals. They are extremely reduced organisms that lack mitochondria. Most infect insects, but they are also responsible for common diseases of crustaceans and fish, and have been found in most other animal groups, including humans (probably transmitted through contaminated food and/or water). They were thought to be a unique phylum of protozoa for many years. Recent molecular studies show that these organisms are fungi and Microsporidia is given phylum status. *Hyaloraphidium curvatum*, was previously classified as a colourless green alga but is now recognised as a fungus on the basis of molecular sequence data, which show it is a member of the Monoblepharidales in the Chytridiomycota.

Outline classification of fungi

The following classification is adapted from the 9th and 10th editions of *The Dictionary of the Fungi* (Kirk *et al*., 2001, 2008), but it has been amended to adopt 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/; 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 the abbreviation '*inc. sed*.', which stands for *incertae sedis*, meaning 'of uncertain position', this being the standard term for a taxonomic group of currently unknown or undefined relationship.

Dramatic changes have been made to the understanding of relationships of fungi that have traditionally been placed in the phyla Chytridiomycota and Zygomycota. The Chytridiomycota is retained, but in a much more restricted sense. For one thing, one of its traditional orders, the Blastocladiales, has been raised to phylum status as the Blastocladiomycota. Similarly, the group of anaerobic rumen chytrids previously known as order Neocallimastigales has also been recognised as a distinct phylum, the Neocallimastigomycota. The phylum Zygomycota is not accepted in the most recent classification because of remaining doubts about relationships between the groups that have traditionally been placed in this phylum. The consequences of this decision are the recognition of the phylum Glomeromycota and of four subphyla *inc. sed*.: Mucoromycotina, Kickxellomycotina, Zoopagomycotina and Entomophthoromycotina.

Presently, then, the true fungi which make up this monophyletic clade called kingdom Fungi comprises the seven phyla:

- **Chytridiomycota,**
- **Blastocladiomycota,**
- **Neocallimastigomycota,**
- **Microsporidia,**
- **Glomeromycota,**
- **Ascomycota and**
- **Basidiomycota.**

The latter two phyla are combined in the subkingdom Dikarya. All of these are described in more detail below.

The ancestral group is thought to be represented by the present day Chytridiomycota, or water moulds (though the Microsporidia may be an equally ancient sister-group). The first major steps towards higher fungi were loss of the chytrid flagellum and the development of branching, aseptate fungal filaments; this occurred as terrestrial fungi diverged from water moulds 600-800 million years ago. Septate filaments evolved by divergence from the Glomeromycota as a combined 'pre-basidiomycota/pre-ascomycota' clade about 500 million years ago. Hyphae with the characteristic appearance of modern Basidiomycota can be seen in some of the earliest known specimens of plant fossils, so Ascomycota and Basidiomycota probably diverged (as so-called 'sister groups' which are now placed together in subkingdom Dikarya) about 300 million years ago. Mushroom fungi, with all the characteristics and readily-recognisable morphology of today, probably diversified 130-200 million years ago, soon after flowering plants became an important part of the flora and well before the age of dinosaurs. Another noteworthy diversification is the relatively recent evolutionary radiation, perhaps 60-80 million years ago, of anaerobic Chytridiomycota as grasses and grazing mammals became more abundant; the chytrid fungi serving as symbionts within the rumen of such animals, enabling the grazing mammals to digest their grassy diet.

Summarised classification of Kingdom Fungi

Members of Kingdom Fungi are eukaryotic organisms (that is, they have true nuclei with nuclear membranes, chromosomes and a cytoskeletal division apparatus); they may be acellular (a characteristic of a few highly adapted parasites), unicellular ('yeast-like', a growth strategy of species adapted to life in small volumes of fluid and/or used by parasites to spread through fluid channels of the host) or multicellular, typically apically-elongating filamentous organisms (the growth form of the great majority), in which the filaments are called hyphae and have cell walls composed of chitin and alpha-glucans. The yeasts can be individually microscopic in size, but filamentous hyphae make up the commonly encountered mould mycelium, as well as mildews, rusts, smuts, cup fungi, mushrooms, puffballs, truffles and morels. At least 98,000 species of fungi have been described, but estimates of the total number that exist on Earth range between 0.5 and 9.9 million. The best estimate is approximately 1.5 million species (Hawksworth, 2001).

The most recently-published phylogenetic classification of Fungi (Hibbett *et al*., 2007)

Kingdom: Fungi

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 props, 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 of 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. 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 *inc. sed*. Type: *Chytridium*; example genera: *Chytridium*, *Chytriomyces*, *Nowakowskiella*.

Order: Rhizophydiales; example genus: *Rhizophydium*.

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

Class: Monoblepharidomycetes
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. 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 unflagellate 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.

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 anerobic 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.

Class: Blastocladiomycetes

Order: Blastocladiales; 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*

Phylum: Microsporidia

No subdivision of the group 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.

Phylum: Glomeromycota

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 zygomycota, and all ‘glomalean’ fungi form mutualistic symbioses. Recent molecular studies have suggested a separate phylum is appropriate for the AM fungi, the Glomeromycota, and this is the position taken by the AFTOL study. The International Code of Botanical Nomenclature requires the name of a family or order to be formed from the genitive singular of a legitimate name of an included genus. The genitive of the type genus *Glomus* is Glomeris, and so the name of the family should be Glomeraceae and order Glomerales (rather than ‘Glomales’).

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*

Subphyla incertae sedis (not assigned to any phylum, but representing the traditional ‘Zygomycota’, being saprotrophs or parasites (especially of arthropods) that produce non-motile, asexual sporangiospores in sporangia and sexual spores known as zygospores. The taxon 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 it 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, perhaps including subphylum Mucoromycotina. As yet it cannot be properly defined in this classification so the subphyla listed below are left in an uncertain position.

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 Zygomycota.

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*.

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

Subphylum: Entomophthoromycotina
Obligate pathogens of animals (primarily arthropods), cryptogamic plants, or saprotrophs; occasionally facultative parasites ofvertebrates. Somatic state consisting of a well-defined mycelium, coenocytic or septate, walled or protoplastic, which may fragment to form multinucleate hyphal bodies; protoplasts either hyphoid or amoeboid and changeable in shape; cystidia or rhizoids formedby 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.

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: Zoopagomycotina
Endo-or ectoparasites of microanimals and fungi. Vegetative body consisting of a simple, branched or unbranched thallus or more of 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 similar to the vegetative hyphae or more or less enlarged.

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*.

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.

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*.

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 ascosporogenous 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 on the basis of 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. Basic type genus: *Peziza*.

Subphylum: Taphrinomycotina
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: Neolectomycetes
Order: Neolectales; example genus: *Neolecta*.
Class: Pneumocystidomycetes
Order: Pneumocystidales; example genus: *Pneumocystis.*
Class: Schizosaccharomycetes
Order: Schizosaccharomycetales; example genus: *Schizosaccharomyces.*
Subphylum: Saccharomycotina
Class: Saccharomycetes
Order: Saccharomycetales
Growth usually by individual yeast cells, often accompanied by pseudohyphae and/or true hyphae. Cell walls predominately of β-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
Class: Arthoniomycetes
Order: Arthoniales; example genera: *Arthonia*, *Dirina*, *Roccella*.
Class: Dothideomycetes
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)
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 producedinsurroundingstromatictissueand brightlycoloured; 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
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: Leotiomycetes

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* (*s. lat.*) is not well supported by current data. There exists a minimum of five helotialean lineages that are intermixed with other leotiomycetan 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: *Orbilia*, *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, brainlike, 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

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; ascal 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 bridgelike 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 on the basis of shape and morphology. Some of these revisions are reflected in the arrangement (dated 2007) shown below. But this is far from being the final story.
Subphylum: Pucciniomycotina (equivalent to the traditional Urediniomycetes)
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)
Class: Ustilaginomycetes
Order: Urocystales; example genera: *Urocystis*, *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*, *Phragmotaenium*, *Tilletiaria*, *Tilletiopsis*.
Order: Microstromatales; example genera: *Microstroma*, *Sympodiomycopsis*, *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
Order: Cystofilobasidiales; example genera: *Cystofilobasidium*, *Mrakia*, *Itersonilia*.
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

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

Class: Agaricomycetes

Subclass: Agaricomycetidae

Order: Agaricales; example genera: *Agaricus*, *Coprinus*, *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-refiexed or dimidiate, with smooth, wrinkled, dentate, lamellate or regularly poroid hymenophore, or pileate-stipitate with lamellae. (Aborted, coralloid or fiabelliform 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 suballantoid, 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, grandinioid, hydnoid 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*.

The fungi studied by mycologists include organisms from two other **Kingdoms**, the Chromista and the Protozoa.

Kingdom 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 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.
Order Labyrinthulales; e.g. *Labyrinthula*
Order Thraustochytriales; e.g. *Thraustochytrium*

Phylum Oomycota
Cosmopolitan and widespread 'water moulds' occurring in freshwater, soil-water and marine habitats, some being economically important pathogens such as *Saprolegnia*, *Pythium*, and *Phytophthora*. About 1 000 species in 110 genera.
Order Leptomitales; example genera: *Apodachlyella*, *Ducellieria*, *Leptolegniella*, *Leptomitus*
Order Myzocytiopsidales; 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 Anisolpidiales; example genus: *Anisolpidium*
Order Lagenismatales; example genus: *Lagenisma*
Order Rozellopsidales; example genera: *Pseudosphaerita*, *Rozellopsis*
Order Haptoglossales; example genera: *Haptoglossa*, *Lagena*, *Electrogella*, *Eurychasma*, *Pontisma*, *Sirolpidium*

Kingdom Protozoa

Protozoa are diverse unicellular organisms that descend from different unicellular ancestors. The organisms known as slime moulds all belong to this kingdom. They do not form hyphae, and they generally lack cell walls because they are capable of ingesting food particles by phagocytosis. The slime moulds fail to meet normal definitions of the fungi, but they produce fruiting bodies which have a superficial resemblance to those of fungi, and this is why they have been called 'moulds' and have been studied by mycologists and included in most textbooks on mycology.

Phylum Plasmodiophoromycota

Obligate intracellular symbionts or parasites of plant, algal or fungal cells living in freshwater or soil habitats. Multinucleate, unwalled plasmodia. About 15 genera with 50 species. *Plasmodiophora* and *Spongospora* cause serious plant diseases.

Class Plasmodiophoromycetes
Order Plasmodiophorales; example genera: *Plasmodiophora*, *Polymyxa*

Phylum Myxomycota

Free-living unicellular or plasmodial amoeboid slime molds. A total of 1 020 species assigned to 82 genera, but the majority (888 species) are placed in the Myxomycetes.

Class Dictyosteliomycetes
Order Dictyosteliales; example genera: *Actyostelium*, *Dictyostelium*
Class Myxomycetes
Order Echinosteliales; example genera: *Clastoderma*, *Echinostelium*
Order Liceales; example genera: *Cribraria*, *Licea*, *Reticularia*
Order Physarales; example genera: *Didymium*, *Physarum*, *Fuligo*
Order Stemonitales; example genus: *Stemonitis*
Order Trichiales; example genera: *Arcyria*, *Dianema*, *Trichia*, *Calonema*
Class Protosteliomycetes
Order Protosteliales; example genera: *Cavostelium*, *Ceratiomyxa*, *Echinosteliopsis*, *Protostelium*

Phylum Acrasiomycota

Amoeboid slime molds; generally saprotrophic, found on a very wide range of decaying plant material. A total of 14 species assigned to 6 genera.

Class Acrasiomycetes

Order Acrasiales; example genera: *Acrasis*, *Copromyxa*, *Guttulinopsis*, *Fonticula*

Phylum Choanozoa

Amoebidiales and Eccrinales, previously misclassified as trichomycete fungis, are now placed in the protozoan group Choanozoa

Class Mesomycetozoea

Order Amoebidiales

Thallus coenocytic (without cross walls, with numerous freely distributed nuclei) arising from a holdfast; amoeboid cells formed; about 12 species. Example genera: *Amoebidium*, *Paramoebidium*

Order Eccrinales

Thallus coenocytic, attached by a holdfast to the digestive tract of arthropods; aplanosporangia produced in succession; more than 50 species. *Eccrina*, *Trichella*, *Palavascia*, *Parataeniella*

Critical appraisal

An interesting trend in the last decade of the 20th century and first few years of the 21st, 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 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). So 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) and 'Early cell evolution, eukaryotes, anoxia, sulfide, oxygen, fungi first (?), and a Tree of Genomes revisited' (Martin *et al*., 2003).

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. Interestingly, 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 in 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 some kind of 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 previously eminent mycologists.

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Websites to visit

The **Index Fungorum** is the world standard database of fungal names coordinated and supported by the Index Fungorum Partnership. Visit: http://www.indexfungorum.org/

The US equivalent is the **Systematic Botany and Mycology Laboratory Fungal Database** operated by the USDA and ARS. Visit: http://nt.ars-grin.gov/fungaldatabases/

BioLib, at http://www.biolib.cz/en/main/, is an international encyclopedia of plants, fungi and animals.

For useful background discussion, try the **Biodiversity pages** at the University of Paisley. Visit: http://www-biol.paisley.ac.uk/bioref/index2.html

The Taxonomicon is a biodiversity information system with further Links to the literature and the Internet. Visit: http://www.taxonomy.nl/taxonomicon/Default.aspx

MycoBank is an on-line database aimed as a service to the mycological and scientific society by documenting mycological nomenclatural novelties (new names and combinations) and associated data. Visit: http://www.mycobank.org/DefaultPage.aspx

Although primarily aimed at medically important fungi, the **Doctor Fungus** website maintains an excellent range of information and an extensive species names index and image bank. Visit: http://www.doctorfungus.org/index.htm.

For general information visit the **Encyclopaedia Britannica Online** at this URL: http://www.britannica.com/bps/home (it's ***far better*** than Wikipedia because it is rigorously edited).