Chapter 4

The Soil Fungi: Occurrence, Phylogeny, and Ecology

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Chapter Contents

I A PRIMER ON FUNGAL SYSTEMATICS

While Kingdoms were long recognized as the most encompassing categories in the taxonomic hierarchy of life, the landmark work of Karl Woese, showing that two groups of prokaryotes (microbial organisms without nuclei) were equally divergent from one another as from eukaryotes (single-celled and multicellular organisms with nuclei and usually additional organelles), led to the establishment of Domain as the deepest division (Woese and Fox, 1977). There are three domains: the prokaryotic domains of *Archaea* and *Bacteria*, and the *Eukaryota*. The formal Linnaean hierarchy thus proceeds as follows: Domain, Kingdom, Phylum (=Division for Animalia), Class, Order, Family, Genus, Species. However, this limited set of rankings does not allow recognition of all important groupings, hence informal rankings above (e.g., "superkingdom") and below (e.g. "subphylum") these formal levels are often used in systematics.

Bacteria and *Archaea* are subject to the International Code of Nomenclature of Bacteria (ICNB; www.the-icsp.org/), while formal taxonomy in the Kingdom Fungi falls under the International Code of Nomenclature for algae, fungi, and plants (ICN; www.iapt-taxon.org/nomen/main.php). Molecular, physiological, and ultrastructural data are increasingly useful in efforts to ascertain the boundaries of species and higher taxonomic ranks, but technical descriptions of the morphology of reproductive structures are still required in order to name (or rename) a fungal taxon. In most cases, these descriptions relate to structures produced in the sexual phase of the fungal lifecycle in which meiosis occurs (see

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Section II), such as mushrooms of the *Agaricomycetes* or morels of the *Ascomycota*. Species names based on a sexual sporocarp are called **teleomorphs**. If a fungus produces asexual reproductive structures (e.g., conidia and conidiophores, Fig. S4.1) and no sexual structures are known for this species, the Latin species description may be based upon these asexual forms; in this case, the species name is called the **anamorph**. Many fungi have been named based on sexual sporocarps collected in the wild, without any accompanying pure culture isolate. Many other fungi have been named based on isolates brought into pure culture; often these isolates produce asexual reproductive forms readily in culture, but rarely or never produce sexual structures (e.g., molds of the *Ascomycota*). As a consequence of these two strategies for naming new fungi, a number of species have both a teleomorphic and an anamorphic name attached to them. The connections between particular teleomorphs and anamorphs are slowly being discovered over time as more sterile fungi are induced to produce sexual structures in culture and molecular diagnostics are brought to bear. Furthermore, the sexual reproductive structures are historically the basis upon which fungi are placed in higher taxonomic ranks, e.g., class *Agaricomycetes* or phylum *Basidiomycota*. Hence, the asexual fungi known only by their anamorphs were traditionally placed in an artificial class, the ***Deuteromycetes***. It turns out that most members of the *Deuteromycetes* belong to the *Ascomycota* in terms of their shared evolutionary history; however, there are some anamorphic names spread among the other fungal phyla (e.g., *Rhizoctonia*, a widespread soil fungus in the *Basidiomycota*). These aspects of fungal systematics have caused great confusion for biologists from other disciplines

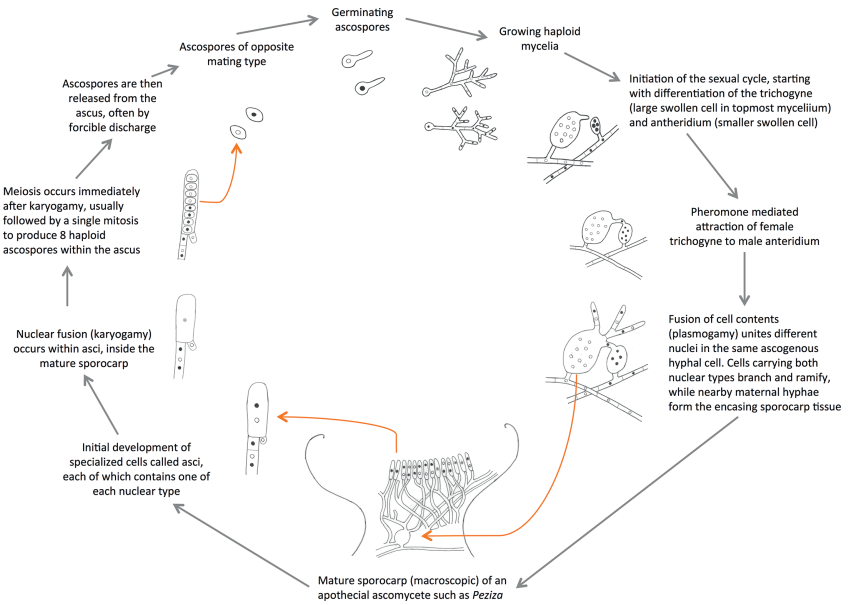

FIG. S4.1 A typical life cycle for a fungus in the *Ascomycota*.

seeking to use or interpret fungal names. Recently, a movement under the banner "one fungus, one name" was successful in their lobbying to abolish the two name, anamorph-teleomorph system (Taylor, 2011). Every fungus will now have only one formally recognized name. In addition, non-phylogenetic classifications, such as *Deuteromycetes*, are no longer recognized. These changes will help make fungal systematics more digestible for ecologists, soil scientists, evolutionary biologists, and others. However, some familiarity with these outdated terms may be helpful, since they will be widely encountered in the literature. Some additional terms that are fading from use are **hyphomycete**, which is a synonym for *Deuteromycetes*, and **microfungi**, which refers to fungi that only produce very small sexual or asexual reproductive structures, i.e., filamentous soil fungi other than mushroom-forming *Basidiomycota*. Microfungi are mostly members of the Ascomycota; the term encompasses common soil molds, such as *Trichoderma, Aspergillus*, and *Penicillium*.

Table S4.1 Exemplar taxonomic classifications downloaded from the NCBI taxonomy pages for two soil dwelling fungi (www.ncbi.nlm.nih.gov/taxonomy). The ranks at the top are the broadest and proceed through successively narrower groupings until reaching the species. Formal taxonomic ranks

TABLE S4.1 Two examples of formal fungal classification

Taxonomic Rank	Classification for *Tuber melanosporum*	Classification for *Agaricus bisporus*
Superkingdom	*Eukaryota*	*Eukaryota*
Unranked	Opisthokonta	Opisthokonta
Kingdom	*Fungi* (=*Eumycota*)	*Fungi* (=*Eumycota*)
Subkingdom	*Dikarya*	*Dikarya*
Phylum	*Ascomycota*	*Basidiomycota*
Unranked	*Saccharomyceta*	
Subphylum	*Pezizomycotina*	*Agaricomycotina*
Class	*Pezizomycetes*	*Agaricomycetes*
Subclass		*Agaricomycetidae*
Order	*Pezizales*	*Agaricales*
Family	*Tuberaceae*	*Agaricaceae*
Genus	*Tuber*	*Agaricus*
Species	*Tuber melanosporum*	*Agaricus bisporus*
Common name	Perigord truffle	button mushroom

should be capitalized and italicized. Notice that several unranked taxonomic groupings have been used for these fungi. A number of previous formal classification terms, such as the class "*Basidiomycete*," have been replaced as systematics has progressed (this taxon was elevated to phylum, as *Basidiomycota*). Older terms are still often used in a less formal sense, in which case they should be non-italic and non-capitalized, e.g., "a basidiomycete fungus."

II FUNGAL LIFE CYCLES

In general, fungi spend the majority of their life cycle in a haploid state. Haploid spores produced by meiosis or mitosis disperse. If conditions are conducive, the spore will then germinate and a hypha will begin to grow (unless the fungus is a yeast). A fungal body or thallus develops through progressive growth and branching of this original hypha (Fig. S4.1). In many fungi, asexual reproduction by mitotic production of conidia or other mitospores can occur at any time during growth of the mycelium (usually triggered by particular growth conditions). For sexual reproduction to occur, karyogamy to generate a transient diploid stage must take place. Most fungi are 'heterothallic' meaning that they cannot mate with themselves, but must instead mate with a different individual of an opposing mating type. When a haploid hypha encounters a hypha or conidium of another individual of the same species, but different mating type, it may engage in a series of steps leading to sexual reproduction. In brief, the cytoplasms fuse by anastomosis – a process called plasmogamy. This places the two different nuclei within the same cell (see Fig. S4.1). Next a complex developmental process unfolds, often involving synchronized mitotic replication of the two nuclei within the developing sporocarp. Finally, the two different nuclei fuse (karyogamy) within a specialized reproductive cell (e.g., the ascus in *Ascomycota* and the basidium in *Basidiomycota*). Meiosis and production of haploid spores usually follows quickly. There are exceptions to immediate meiosis; for example, the zygospore in members of the former *Zygomycota* remains diploid until this resting spore is triggered to germinate. The exception to dominance of the haploid stage occurs in the *Basidiomycota* in which mycelia are more likely to be dikaryotic. Here, the difference is that compatible hyphae of opposing mating types anastomose early in the life cycle, rather than late in the life cycle immediately before sexual reproduction. However, as with other fungi, these nuclei do not fuse until immediately before meiosis. Hence, cells of the 'vegetative' hyphae of most *Basidiomycota* contain pairs of unfused haploid nuclei from the two parents, a situation that is termed 'dikaryotic' (Fig. S4.1). Many basidiomycete fungi have bumps (actually a small hyphal loop) over the septa that separate cells called 'clamp connections.' Clamp connections are involved in maintaining exactly one nucleus of each type per cell. A third exception to the life cycle patterns described above concerns so called 'homothallic' species. These are species that do not require nuclei to have opposing mating types, and so are able to mate with themselves and undergo sexual reproduction.

III GLOSSARY OF TERMS

-ales	Ending for taxa at the ordinal level.
-cetes	Ending for taxa at the class level.
-eae	Ending for taxa at the familial level.
-ota	Ending for taxa at the phylum level.
-otina	Ending for taxa at the subphylum level.
Anamorph	The asexual phase of the life cycle of a fungus. Can also refer to the Latin name for a fungal species based on a description of the asexual stage; e.g., anamorph = *Fusarium moniliforme*, teleomorph = *Gibberella fujikuroi*.
Anastomosis	The fusion of two fungal hyphae to form a unified cytoplasm. Occurs often within the mycelium of a single fungal individual; can sometimes occur among different genotypes within a species.
Ascocarp	A conglomeration of asci and surrounding tissue forming the sexual reproductive structure of fungi in the *Ascomycota*.
Ascospore	A single-celled haploid spore produced by meiosis within an ascus of a fungus in the *Ascomycota*.
Ascus (singular), Asci (plural)	A specialized sack-shaped reproductive cell of fungi in the *Ascomycota* in which meiosis occurs and ascospores are produced.
Basal fungal lineages = early-diverging fungal lineages	Refers to major evolutionary lineages at the class to phylum level toward the base of the fungal tree of life. Most of these lineages were once placed within either the *Chytridiomycota* or the *Zygomycota*, but now stand on their own due to the polyphylly of the aforementioned phyla. Relationships among these lineages remain to be resolved.
Basidiocarp	A conglomeration of basidia and surrounding tissue forming the sexual reproductive structure of fungi in the *Basidiomycota*.
Basidiospore	A single-celled haploid spore produced by meiosis within a basidium of a fungus in the *Basidiomycota*.
Basidium (singular), Basidia (plural)	A specialized club-shaped reproductive cell of fungi in the *Basidiomycota* in which meiosis occurs and basidiospores are produced.
Black yeasts = microcolonial yeasts = meristematic yeasts	A polyphyletic assemblage of darkly pigmented extremophilic yeasts.
Brown rot	A type of wood decay in which lignin is only partially depolymerized and its C is not consumed. The cellulose and hemi-cellulose are attacked using hydrogen peroxide and the cellulosic C is mostly consumed. This type of decay leaves behind blocky brown material. Carried out by a spectrum of fungi in the *Basidiomycota*.

Clamp connection	A hump-shaped outgrowth forming a channel from one cell to the next, bypassing a septum; found only in some species of *Basidiomycota*.
Codenitrification	A process in which additional amines react with intermediates in normal denitrification, resulting in N-N compounds with each N atom coming from a different source. This process can alter the dynamics of N turnover and loss from soil systems, but is poorly understood or quantified.
Conidium (singular), Conidia (plural)	A single-celled dispersal unit produced mitotically (i.e., not a sexual product).
Cryptic species	A situation in which multiple phylogenetic or biological species occur within a single morphologically demarcated species.
Deuteromycete = Fungi Imperfecti	An outdated taxonomic term to encompass asexual, anamorphic fungal species of uncertain evolutionary affiliation.
Dikaryon	A fungal individual that contains two types of haploid nuclei, one from each parent.
Dimorphic	A fungus that is able to switch between a single-celled yeast growth form and a multicellular filamentous growth form.
Dissimilatory denitrification	The reduction of nitrate or nitrite to gaseous forms (N_2O, N_2), resulting in loss of N back to the atmosphere. Nitrate is used in place of oxygen as the electron acceptor to carry out respiration.
DSE: Dark septate endophyte	Melanized fungi growing inside of roots; may also extend beyond the root and may be mildly beneficial or mildly harmful to the plant.
Extracellular enzyme	An enzyme that is targeted for export across the cell membrane and cell wall so that it can function outside the cytoplasm; often involved in degradation of organic polymers, such as starch, cellulose, proteins, or lignin.
Glomalin	A complex glycoprotein compound found in soil thought to be secreted by arbuscular mycorrhizal fungi. Glomalin contributes to aggregate formation and soil stabilization.
Glycosidase = glycosyl hydrolase	A hydrolytic enzyme that contributes to depolymerization of sugar polymers, such as cellulose and chitin. This is a very large group containing many families of enzymes; in fungi many are secreted (i.e., extracellular). This class includes xylanases, chitinases, beta-glucosidases, cellobiohydrolases, and endo-glucanases, among others.

Heterothallic	A species of fungus that requires the joining of nuclei from different mating types in order for sexual reproduction to occur.
Homothallic	A species of fungus in which identical nuclei (i.e., not from different mating types) can fuse and undergo sexual reproduction.
Hypha (singular), Hyphae (plural)	An individual filament or thread formed of tube-like cells attached end to end. Hyphae are the basic building blocks of all multi-cellular fungal structures, such as mushrooms.
Hyphomycete = soil microfungi	An umbrella term for asexual filamentous fungi in soils, particularly ascomycetous molds.
Karyogamy	The fusion of two different haploid nuclei from compatible mating types to form the diploid stage; followed immediately by meiosis in the vast majority of fungi.
Laccase	Copper-containing oxidative enzymes that may function inside the cytoplasm as part of various developmental processes or may be secreted to attack polyphenolics, such as lignin.
Mold = mould	An evolutionarily heterogeneous group of fast-growing fungi that rapidly produce masses of asexual spores soon after colonizing a high-energy substrate, such as bread, fruit, or dung.
Monophyletic	A group that encompasses all taxa descended from a single common ancestor; synonymous with 'natural evolutionary group' and 'clade.'
Mycelium	A constellation of interconnected hyphae belonging to a single fungal individual.
Mycoparasite	A fungus that preys upon (i.e., infects) other living fungi.
Phosphatase	A hydrolytic enzyme that cleaves phosphoric acid monoesters to release phosphate; secreted by many fungi to aid in P scavenging.
Phytase	A type of phosphatase that cleaves phosphate groups from phytic acid.
Plasmogamy	The fusion of cytoplasmic material by the joining of the cell walls of two compatible fungal individuals; usually precedes karyogamy and meiosis.
Polyphyletic	An assemblage of taxa that does not include all descendents from a single common ancestor; rather, taxa derived from different common ancestors are placed in the same grouping, such as 'yeasts.'
Psychrophile	Cold-loving organisms that are able to grow below 5°C and have a maximum growth rate below 20°C.
Psychrotolerant	Cold-tolerant organisms that are able to grow below 5°C, but have a maximum growth rate above 20°C.

Rhizomorph	A developmentally complex tube structure formed through the coordinated growth of a large number of hyphae. Similar to cords, but includes a cap that resembles a root cap rather than a diffuse mycelial front. Most common in *Basidiomycota*.
Rust	Common name for plant pathogens of the order *Pucciniales*, *Basidiomycota*. Rusts typically have complex life cycles that may include five different spore stages and alternation between two unrelated host species. The common name comes from the typical orange-brown color of the telial spore stage.
Sclerotium (singlular), Sclerotia (plural)	A conglomeration of thick-walled, resistant cells produced by mitosis.
Septum (singular), Septa (plural)	Cell wall material laid down within a hypha to divide the filament into discrete cells; has a septal pore in the middle that controls movement of structures, such as nuclei from cell to cell.
Smut	Common name for a class of fungi in the *Basidiomycota*, most of which are plant pathogens. The life cycles of smuts are not as complex as those of rusts, with completion of the life cycle usually requiring only one host. The common name comes from the gray-black, moldy teliospore stage produced within the flowering tissue of hosts, such as maize (corn).
Soft rot	A type of wood decay in which lignin is only partially depolymerized and its C is not consumed. Hyphae secrete cellulase, leading to microcavities in the wood. Carried out primarily by members of the *Ascomycota*.
Sporocarp	A conglomeration of fungal cells in which meisosis occurs and from which spores are released, e.g., a mushroom. Analogous to a plant flower.
Strand = cord	An aggregation of hyphae into a larger-diameter tube-like transport structure. Similar to rhizomorphs, but with a diffuse mycelial front. Most common in *Basidiomycota*.
Teleomorph	The sexual phase of the life cycle of a fungus. Can also refer to the Latin name for a fungal species based on a description of the sexual stage; e.g., teleomorph = *Talaromyces spiculisporus;* anamorph = *Penicillium lehmanii*.
Thermophile	Heat-loving organisms that are able to grow at 45–60°C.
Truffle	Species of fungi that produce macroscopic sexual sporocarps below ground. Divided into the 'true truffles' (e.g., *Tuber*) that belong to the Ascomycota and the 'false truffles' that belong to other phyla, especially the Basidiomycota.
White rot	A type of wood decay in which lignin is completely broken down and its C is consumed. This type of decay

	leaves behind a stringy/powdery white residue primarily composed of crystalline cellulose. Carried out by a limited number of species in the *Basidiomycota*.
Yeast	Any fungus with cells that separate after budding (e.g., *Saccharomyces*) or splitting (e.g., *Schizosaccharomyces*). Note that the term does not describe a phylogenetically united group of fungi.
Zygospore	A single-celled diploid resting spore resulting from fusion of compatible nuclei of opposite mating types that is produced within a Zygosporangium; characteristic of fungi that were once placed in the Zygomycota. Meiosis occurs when the zygospore is triggered to germinate.