Phylogenetic taxon definitions for Fungi, Dikarya, Ascomycota and Basidiomycota

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Abstract: Phylogenetic taxon definitions (PTDs) are explicit, phylogeny-based statements that specify clades. PTDs are central to the system of rank-free classification that is governed by the PhyloCode, but they can also be used to clarify the meanings of ranked names. We present PTDs for four major groups: Fungi, Dikarya, Ascomycota, and Basidiomycota.

INTRODUCTION

Phylogenetic taxon definitions (PTDs) are explicit, phylogeny-based statements that are used to describe clades in the rank-free approach to classification known as “phylogenetic taxonomy” (De Queiroz & Gauthier 1992). The principles and nomenclatural rules of phylogenetic taxonomy are described in the International Code of Phylogenetic Nomenclature (the PhyloCode), which is available on-line (https://www.ohio.edu/phylocode/) but is not yet published. The PhyloCode has encountered strident opposition (see the website for a comprehensive review of literature, both pro and con), but PTDs are not synonymous with the PhyloCode — they are simply devices for identifying clades with reference to phylogenies. PTDs can be used to describe ranked or unranked taxa. They can also be translated into Least Common Ancestor algorithms, which facilitate automated taxonomic data retrieval from phylogenies (Hibbett et al. 2005). Here, we present PTDs for four taxa that have been described in accordance with the Code (Turland et al. 2018): Fungi, Dikarya, Ascomycota, and Basidiomycota. The compositions of these clades, as defined here, are consistent with (most) current usage.

More than a decade has passed since the “AFTOL classification” momentarily unified the higher-level taxonomy of Fungi (Hibbett et al. 2007). Since then, mycology has witnessed the advent of phylogenomics and the recognition of groups such as Cryptomycota, Entorrhizomyctota, Mucoromycota, and Opisthosphorida, among others (Bauer et al. 2015, Jones et al. 2011, Karpov et al. 2014, Spatafora et al. 2016). However, there is still uncertainty about the higher-level placements of many clades, particularly those for which there are as yet no genomes available (like Entorrhizomyctota), which can destabilize classifications. There are also disagreements about the rankings of names that correspond to well-established monophyletic groups, such as Glomeromyctota/ Glomeromycota (Spatafora et al. 2016, Tedersoo et al. 2018). Even the delimitation of Fungi is controversial (Berbee et al. 2017, James et al. 2006, Karpov et al. 2014).

It is in the interests of the user community for fungal systematists to converge on a uniform set of names for well-supported clades. As genome sampling expands, many problematical nodes in the fungal phylogeny will be resolved, but improvements in phylogenetic resolution do not automatically translate into taxonomy. PTDs could promote taxonomic clarity and stability, by providing clear guidelines for representing phylogenetic trees in classifications based solely on tree topology, not arbitrary considerations, like phenotypic distinctiveness, or estimates of quantities with broad confidence intervals, such as taxonomic richness or ages of clades.

PTDs can take several forms. The PTDs for Fungi and Dikarya (below) are node-based definitions (also called minimum-crown-clade definitions), which consist of statements like “Taxon X is the least inclusive clade containing species A and species B”, while the PTDs for Ascomycota and Basidiomycota are stem-based definitions (also called maximum-crown-clade definitions), which take the form “the largest group containing species A but not species B”. In both kinds of definitions, species A and species B serve as “specifiers” (Fig. 1).
Carefully crafted PTDs can accommodate phylogenetic uncertainty. For example, the node-based PTD of Fungi includes *Rozella allomycis* as a specifier, because its position in the sister group to the rest of Fungi is strongly supported by genome data (James et al. 2013), but it does not use aphielsids, because there are no genomes yet available, or microsporidia because their placements are likely to remain controversial due to their high rates of molecular evolution (see the Comments for Fungi, below). Similarly, the stem-based PTD of Basidiomycota does not use a species of *Entorrhizomyces* as a specifier; *Entorrhizomyces* has been resolved as either (1) the sister group of Dikarya, or (2) more closely related to *Pucciniomycotina*, *Ustilaginomycotina*, and *Agaricomycotina* than to Ascomycota (Bauer et al. 2015).

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**Fig. 1.** Phylogenetic taxon definitions and specifiers for Fungi, Dikarya, Ascomycota and Basidiomycota. Capital letters following species names indicate the clade(s) for which they serve as specifiers (F for Fungi, and so on). There are two species of *Taphrina* in the tree: *T. wiesneri*, which was included in the reference phylogeny for Basidiomycota, and *T. neoformans*, which was used in the reference phylogeny for Ascomycota. 
A. Topology based on James et al. (2006: fig. 1) and Bauer et al. (2015: fig. 2).  
B. Topology based on Spatafora et al. (2016: fig. 1) and the alternative topology of Bauer et al. (2015), which was described but not illustrated.
Entorrhiza casparyana is a specifier in the node-based PTD for Dikarya, which ensures that Entorrhizomycota is retained in Dikarya, under either of the topologies reported by Bauer et al. (2015) (Fig. 1).

The history of phylogenetic taxonomy is long and tortuous. As reviewed in the Preface to the PhyloCode, the concept of phylogeny-based, rank-free classification had its origins in theoretical discussions of the 1980s, and a formal code began to take shape in the late 1990s. In 2002, a decision was made to tie the publication of the PhyloCode to a "Companion Volume" that would present PTDs for clades across the entire tree of life (or at least eukaryotes). Delays in preparation of the Companion Volume have forestalled its publication of the PhyloCode, but the project may be nearing completion. The PTDs and associated text presented here were first submitted for the Companion Volume in 2008, and revised and resubmitted in 2017. We anticipate that they will appear in the Companion Volume essentially in the form below, except that the references will be formatted differently, each entry will include an abbreviated form of the definition and a registration number.

Whether or not mycologists choose to publish names that follow the rules of the PhyloCode, PTDs have the potential to help resolve taxonomic disputes and focus attention on tree topology. PTDs have not been widely adopted by mycologists, although they are used for some taxa (including Ascomycota, Basidiomycota, and Dikarya). Phylogenetic, morphological, subcellular, or biochemical synapomorphies of Fungi, Most Fungi are filamentous, have chitinous cell walls, lack flagella, and have intranuclear mitosis with spindle pole bodies (instead of centrioles). However, there are also numerous unicellular forms (yeasts) scattered across the fungal phylogeny, thalli without hyphal growth developing from spores by cell division (Laboulbeniomyctes), and forms that develop centrioles and produce flagellated cells that lack cell walls during the motile part of their life cycles (the paraphyletic "chytrids": Chytridiomycota, Neocallimastigomycota, Blastocladiomycota, and Rozella allomycis). Rozella, Microsporida and Aphelida are intracellular parasites of diverse eukaryotes. Rozella and Aphelida produce both zoosporic stages and endoparasitic amoeboid forms that appear to ingest cytoplasm of their hosts by phagocytosis, whereas Microsporida lack a phagotrophic stage and infect hosts by a polar tube mechanism (Corsaro et al. 2014, James & Berbee 2012, Karpov et al. 2014, Powell et al. 2017). Rozella allomycis may also employ enzymatic degradation to penetrate the host cell wall (Held 1972). The R. allomycis genome encodes four division II chitin synthase genes, which are characteristic of other Fungi, including Microsporida (James et al. 2013). However, division II chitin synthase genes have also been found in the holozoan protists (Teretosporea), diatoms, and Metazoa, suggesting that they may be plesiomorphic in Opisthokonta (Torruella et al. 2015).

Synonym: Eumycota sensu Barr (1992) [approximate].

Comments: Application of the name Fungi to this clade, and the choice of this name rather than its approximate synonym Eumycota follows the phylogeny-based classification of Hibbett et al. (2007), which has been adopted in all editions of Ainsworth & Bisby's Dictionary of the Fungi since 1971 (Ainsworth et al. 1971, Kirk et al. 2008) and the GenBank taxonomy (http://www.ncbi.nlm.nih.gov/guide/taxonomy). The delimitation of Fungi by Hibbett et al. (2007) was based largely on the phylogenetic analysis of James et al. (2006), which used six genes and recovered a clade containing R. allomycis and Microsporida as the sister group of all other Fungi. Earlier analyses using α-tubulin and β-tubulin genes also placed Microsporida within Fungi (Edlund et al. 1996, Keeling 2003, Keeling & Doolittle 1996). Recent studies using data derived from whole genomes or transcriptomes have consistently supported monophyly of the clade containing Rozella plus Microsporida and have placed it as the sister group to the remaining Fungi (James et al. 2013, Ren et al. 2016, Torruella et al. 2015).

Several studies, including combined analyses of genes encoding ribosomal RNA (rRNA) and RNA polymerase II (rpb1 and rpb2), have suggested that the clade containing Rozella and Microsporida also contains the endoparasitic Aphelida (Corsaro et al. 2014, Karpov et al. 2013, Letcher et al. 2015), collectively termed the "ARM clade" (Karpov et al. 2014).
However, other analyses using rRNA genes only have placed *Aphelida* as the sister group of a clade containing *Rozella*, *Microsporidia*, and all other *Fungi* (Corsaro et al. 2016). The minimum-crown-clade definition of *Fungi* proposed here employs multiple specificers, but *R. allomyces* is the only specifier in the ARM clade. *Microsporidia* were not used as specificers, because they have a dramatically elevated rate of molecular evolution (Corradi 2015), and *Aphelida* were not used, because they are still represented only by a handful of genes. Nevertheless, current best estimates of the phylogeny suggest that *Microsporidia* and *Aphelida* are members of *Fungi* as defined here.

The sister group of *Fungi* (including *Aphelida*) appears to be a clade containing nucleariids and *Fonticula alba* (Brown et al. 2009, Paps et al. 2013, Torruella et al. 2015). The former are phagotrophic, non-flagellated, amoeboid protists that lack a cell wall, and the latter is a kind of cellular slime mold with aggregative, multicellular reproductive structures that produces spores with cell walls lacking chitin. Berbee et al. (2017) suggested that the nuclearid-*F. alba* clade should be included in *Fungi*. However, most studies refer to the group containing *Fungi* and the nuclearid-*F. alba* clade as Holomycota (Corsaro et al. 2014, Karpov et al. 2014, Liu et al. 2009, Paps et al. 2013, Torruella et al. 2015), or, less often, Nucleomycina (Adl et al. 2012, Brown et al. 2009).

Karpov et al. (2014) named the ARM clade Opisthosphoridia and suggested that it should be excluded from *Fungi*. However, *Rozella* has traditionally been considered a fungus based on morphological and ecological similarities to other chytrids, and *Microsporidia* have been widely regarded as members of *Fungi* ever since the early analyses using tubulin genes (Edlind et al. 1996, Keeling & Doolittle, 1996). Thus, the present definition preserves the composition of *Fungi* as it has come to be understood since the mid-1990s (e.g., Hibbett et al. 2007, James et al. 2006, Kirk et al. 2008, Spatafora et al. 2017), with the likely addition of *Aphelida* and other recently discovered members of the ARM clade (Jones et al. 2011). Moreover, evidence from comparative genomics and ultrastructural studies supports the view that members of the ARM clade are highly reduced and that their common ancestor may have been free-living and possessed many traits typically associated with *Fungi*, including chitinous cell walls and possibly osmoheretrophy (Berbee et al. 2017, Held 1972, James et al. 2013, Keeling & Corradi 2011, Quandt et al. 2017).

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**Dikarya**

D. S. Hibbett et al., *Mycol. Res.* 111: 518 (2007).

**Definition:** The smallest crown clade containing *Coprinopsis cinerea* (Schaeff.) Redhead et al. 2001 (*Basidiomycota*), *Saccharomyces cerevisiae* Meyen 1838 (*Ascomycota*), and *Entorrhiza casparyana* (Magnus) Lagerb. 1888 (*Entorrhizomycota*). This is a minimum-crown-clade definition.

**Etymology:** Derived from the Greek di- (two) and karyon (nut or kernel, interpreted by biologists to refer to nuclei).

**Reference phylogeny:** The primary reference phylogeny is Bauer et al. (2015: fig. 2). See also James et al. (2006: fig. 1), Ebersberger et al. (2011: fig. 3), Chang et al. (2015: fig. 1), and Ren et al. (2016: fig. 5).

**Composition:** *Ascomycota* and *Basidiomycota*, including *Entorrhizomycetes* (Hibbett et al. 2007).

**Diagnostic apomorphies:** The dikaryotic condition, which results from cytoplasmic fusion of two haploid, monokaryotic hyphae, is the putative synapomorphy for which the group is named. Clamp connections of *Basidiomycota* and croziers of *Ascomycota*, which are cellular structures that function in the apportioning of nuclei to daughter cells following mitosis in dikaryotic hyphae, may be homologous and could represent an additional synapomorphy. Regularly septate hyphae are also probably a synapomorphy, because members of the candidate sister taxon, *Mucoromycota* (Spatafora et al. 2016, 2017), have predominantly coenocytic hyphae (Benny et al. 2014, Hibbett et al. 2007, Redecker & Schüßler 2014). If clamps/croziers and septate hyphae of *Basidiomycota* and *Ascomycota* are homologous, then the ancestor of *Dikarya* must have been filamentous, and the unicellular forms (yeasts) that occur in multiple major clades of both *Ascomycota* and *Basidiomycota* were derived by reduction (Nagy et al. 2014).

**Synonyms:** *Carpomycetaceae* Bessey 1907 [approximate], *Dikaryomycota* W. B. Kendr. 1985 [approximate], *Neomycota* Caval.-Sm. 1998 [approximate].

**Comments:** Application of the name *Dikarya* to this clade, and the choice of this name rather than one of the infrequently used synonyms *Dikaryomycota* and *Neomycota*, follow the phylogeny-based classification of Hibbett et al. (2007), which has been adopted in Ainsworth & Bisby’s *Dictionary of the Fungi* (Kirk et al. 2008) and the GenBank taxonomy (http://www.ncbi.nlm.nih.gov/guide/taxonomy). James et al. (2006) used the name *Dikarya* in the same sense as that proposed here, but the name was first validly published (according to the ICN; Turland et al. 2018) by Hibbett et al. (2007). Monophyly of *Dikarya* is strongly supported by independent and combined analyses of nuclear ribosomal RNA genes, RNA polymerase II subunits, and whole genomes (Chang et al. 2015, James et al. 2006, Ren et al. 2016). The position of *Entorrhizomycetes* within *Dikarya* is not well resolved (see Comments under *Basidiomycota*).

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**Ascomycota**

Caval.-Sm., *Biol. Rev.* 73: 247 (1998).

**Definition:** The largest crown clade containing *Taphrina deformans* (Berk.) Tul. 1866, but not *Puccinia graminis* Pers. 1794, *Ustilago tritici* (Berk.) Rostr. 1890, *Agaricus bisporus* (J.E. Lange) Imbach 1946, and *Entorrhiza casparyana* (Magnus) Lagerb. 1888. This is a maximum-crown-clade based definition.


Etymology: Derived from the Greek askos (sac) + mykes (fungus).

Reference phylogeny: The primary reference phylogeny is Bauer et al. (2015: fig. 2). See also Lutzoni et al. (2004: fig. 2), Liu et al. (2008: fig. 1), James et al. (2006: fig. 1), Schoch et al. (2009: fig. S6), Carbone et al. (2017: fig. 1), and Spatafora et al. (2017: fig. 1).

Composition: Taphrinomycota, Saccharomycotina and Pezizomycotina (Hibbett et al. 2007).

Diagnostic apomorphies: Morphological synapomorphies of Ascomycota include the formation of meiospores (ascospores) within sac-shaped meiosporangia (asci) by the process of free cell formation. Free cell formation involves the production of an enveloping membrane system, which is derived from either the ascus plasmalemma or the nuclear envelope and delimits ascospore initials. Meiotic reproduction is unknown in many species and may have been lost in some. All Ascomycota lack flagellia and exhibit intranuclear mitosis with spindle pole bodies instead of centrioles (Kumar et al. 2011). Most Ascomycota are filamentous with simple septa, but there are numerous yeasts ( unicellular forms) especially in the Taphrinomycotina (Healy et al. 2013) and Saccharomycotina and dimorphic species (capable of both yeast and filamentous growth) in Pezizomycotina, Taphrinomycotina and Saccharomycotina. A multicellular thallus lacking filamentous growth is formed in Laboulbeniales (Pezizomycotina) (Blackwell 1994).

Synonyms: Ascomycetes sensu Whittaker (1959) [approximate], Ascomycota sensu Ainsworth et al. (1971) and Ainsworth (1973) is a partial synonym because the asexual ascomycetes were excluded and assigned instead (along with other asexual fungi) to Deuteromycotina. Following extensive discussions the General Committee on Nomenclature endorsed the view that Cavalier-Smith's two-word diagnosis in Latin ("sporae intracellulares") was acceptable as a validating diagnosis and this was ratified by the 2011 International Botanical Congress (Turland et al. 2018: Art. 38 Ex. 8).

Comments: Application of the name Ascomycota to this clade, and the choice of this name rather than the synonyms Ascomycetes (class) and Ascomycotina (subphylum), follow the phylogeny-based classification of Hibbett et al. (2007), which has been adopted in Ainsworth & Bisby’s Dictionary of the Fungi (Kirk et al., 2008) and the GenBank taxonomy (http://www.ncbi.nlm.nih.gov/guide/taxonomy). In rank-based classifications (e.g. Kirk et al. 2008, Spatafora et al. 2017), the clade Ascomycota is the largest phylum of Fungi. It is supported in molecular phylogenetic analyses (Lutzoni et al. 2004, James et al. 2006, Schoch et al. 2009) and comprises three mutually exclusive subclades (Carbone et al. 2017, Schoch et al. 2009, Spatafora et al. 2006). Taphrinomycotina is sister group to a well-supported clade comprising Saccharomycotina and Pezizomycotina. Pezizomycotina includes all ascma-producing taxa with the exception of Neoleotiomycetes of Taphrinomycotina. The monophyly of Taphrinomycotina was not supported by early analyses of ribosomal data (reviewed in Sugiyama et al. 2006), but sampling of protein coding loci (RPB1, RPB2, and TEF) and mitochondrial DNA in multi-gene analyses provided support for its monophyly (James et al. 2006, Liu et al. 2008, Spatafora et al. 2006). Saccharomycotina (Riley et al. 2016, Shen et al. 2016) and Pezizomycotina (Carbone et al. 2017, Kumar et al. 2012, Schoch et al. 2009, Spatafora et al. 2006) are both well-supported clades. The sister group of Ascomycota is Basidiomycota (James et al. 2006). The fossil record of Ascomycota dates to at least the Devonian, with Paleopyrenomycites (Taylor et al. 2005), and the enigmatic Prototaxites taitii (Honegger et al. 2018) identified as part of the Rhynie Chert fossil fungi, but putative ascomycete fossils have been reported from the Silurian (Sherwood-Pike & Gray, 1985). Efforts to fit molecular phylogenies to the fossil record have estimated the origin of Ascomycota to be between 0.40 to 1.3 billion years before present (Heckman et al. 2001, Lücking et al. 2009, Taylor & Berbee 2006).

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Basidiomycota

R.T. Moore, Bot. Marina 23: 371 (1980).

Definition: The largest clade containing Coprinopsis cinerea (Schaeff.) Redhead et al. 2001, but not Taphrina wiesneri (Ráthay) Mix 1954, Saccharomyces cerevisiae Meyen 1838, and Peziza vesiculosa Bull. 1790. This is a maximum-clade definition.

Etymology: Derived from the Latin basis (base, support) plus diminutive suffix -idi-um, referring to the basidium, a “little pedestal”, on which the basidiospores develop, plus the Greek mykes (fungus).

Reference phylogeny: The primary reference phylogeny is James et al. (2006: fig. 1). See also Bauer et al. (2015: fig. 2), Nagy et al. (2016: fig. 1), and Zhao et al. (2017: fig. 3).

Composition: Pucciniomycotina, Ustilaginomycotina, Agaricomycotina (Hibbett et al. 2007). Entorrhizomycetes may also be in Basidiomycota (Bauer et al. 2015, see Comments).

Diagnostic apomorphies: A prolonged, free-living dikaryotic mycelium and the production of meiospores on basidia are putative synapomorphies, although Basidiomycota also includes asexual taxa and unicellular forms (yeasts).

Synonyms: Basidiomycetes sensu Whittaker (1959) [approximate], Basidiomycotina sensu Ainsworth et al. (1971) and Ainsworth (1973) is a partial synonym because the asexual basidiomycetes were excluded and assigned instead (along with other asexual fungi) to Deuteromycotina.

Comments: Application of the name Basidiomycota to this clade, and the choice of this name rather than the synonyms Basidiomycetes (class) and Basidiomycotina (subphylum), follow the phylogeny-based classification of Hibbett et al. (2007), which has been adopted in Ainsworth & Bisby’s Dictionary
have been classified in
1, rpb RNA genes, alone or in combination with RNA polymerase
fungi, and relatives), are resolved in most analyses (Aime et al., Ainsworth GC, James PW, Hawksworth DL (1971)
including genome-based datasets (Nagy et al. 2016, Zhao et al. 2017), and was also corroborated in an analysis of non-
molecular characters (Tehler 1988). Three major subclades, Pucciniomycotina (rusts and relatives), Ustilaginomycotina
(smuts and relatives), and Agaricomycotina (mushrooms, jelly fungi, and relatives), are resolved in most analyses (Aime et al. 2014, Begerow et al. 2014, Hibbett et al. 2014).

The relationship of Entorrhizymycetes to Basidiomycota is controversial (Bauer et al. 2015, Matheny et al. 2006, Zhao et al. 2017). Entorrhizymycetes includes root-gall fungi with similarities to certain Basidiomycota, including dolipore septa, dikaryotic vegetative cells, and teliospores with cruciate septation (Bauer et al. 2015). Entorrhizymycetes have been classified in Ustilaginomycotina (Begerow et al. 2006), but phylogenetic analyses of nuclear ribosomal RNA genes, alone or in combination with RNA polymerase II subunits 1 and 2 (rpb1, rpb2), suggest that it could be the sister group of all other Basidiomycota or of Dikarya (Bauer et al. 2015, Matheny et al. 2006, Zhao et al. 2017). Bauer et al. (2015) classified Entorrhizymycetes in its own phylum, Entorrhizymycota. There are still no whole-genome sequences available for Entorrhizymycetes.

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REFERENCES

Adl SM, Simpson AG, LaneCE, Lukeš J, Bass D, et al. (2012) The revised classification of eukaryotes. Journal of Eukaryotic Microbiology 59: 429–493.

Aime MC, Toome M, McLaughlin DJ (2014) Pucciniomycotina. In: The Mycota. Vol. VIIA. Systematics and Evolution (McLaughlin DJ, Spatafora JW, eds.): 271–294. 2nd edn. Berlin: Springer-Verlag.

Ainsworth GC (1973) Introduction and keys to higher taxa. In: The Fungi: an advanced treatise (Ainsworth GC, Sparrow FK, Sussman AS, eds) 4A: 1–7. New York: Academic Press.

Ainsworth GC, James PW, Hawksworth DL (1971) Ainsworth & Bisby’s Dictionary of the Fungi. 6th edn. Kew: Commonwealth Mycological Institute.

Barr DJS (1992) Evolution and kingdoms of organisms from the perspective of a mycologist. Mycologia 84: 1–11.

Bauer R, Garnica S, Oberwinkler F, Riess K, Weiß M, Begerow D (2015) Entorrhizymycota: a new fungal phylum reveals new perspectives on the evolution of Fungi. PLOS One 10: e0128183.

Begerow D, Schäfer AM, Kellner R, Yurkov A, Kemler M, et al. (2014) Ustilaginomycotina. In: The Mycota. Vol. VIIA. Systematics and Evolution (McLaughlin DJ, Spatafora JW, eds): 295–329. 2nd edn. Berlin: Springer-Verlag.

Begerow D, M Stoll, R Bauer (2006) A phylogenetic hypothesis of Ustilaginomycotina based on multiple gene analyses and morphological data. Mycologia 98: 906–916.

Benny GL, Humber RA, Voigt K (2014) Zygomycetous fungi: phylum Entomophthoromycota and subphyla Kickxellomycotina, Mortierellomycotina, Mucoromycotina, and Zoopagomycotina. In: The Mycota. Vol. VIIA. Systematics and Evolution (McLaughlin DJ, Spatafora JW, eds): 209–250. 2nd edn. Berlin: Springer-Verlag.

Berbee ML, James TY, Strullu-Derrien C (2017) Early-diverging fungi: diversity and impact at the dawn of terrestrial life. Annual Reviews of Microbiology 71: 41–60.

Bessey CE (1907) A synopsis of the plant phyla. University Studies, University of Nebraska 7: 275–373.

Blackwell M (1994) Minute mycological mysteries: the influence of digesting cell walls of algal ancestors of land plants. Molecular Biology and Evolution 26: 2699–2708.

Carbone I, White JB, Miadlikowska J, Arnold AE, Miller MA, et al. (2017) T-BAS: Tree-Based Alignment Selector toolkit for phylogenetic-based placement, alignment downloads and metadata visualization: an example with the Pezizomycotina tree of life. Bioinformatics 33: 1160–1168.

Cavalier-Smith T (1998) A revised six-kingdom system of life. Biological Reviews 73: 203–266.

Chang Y, Wang S, Sekimoto S, Aerts AL, Choi C, et al. (2015) Phylogenetic analyses indicate that early fungi evolved digesting cell walls of algal ancestors of land plants. Genome Biology and Evolution 7: 1590–1601.

Corradi N (2015) Microsporida: eukaryotic intracellular parasites shaped by gene loss and horizontal gene transfers. Annual Review of Microbiology 69: 167–183.

Corsaro D, Walochnik J, Venditti D, Steinmann J, Müller K-D, Michel R (2014) Microsporidia-like parasites of amoebae belong to the early fungal lineage Rozellomycota. Parasitology Research 113: 1909–1918.

Corsaro D, Michel R, Walochnik J, Venditti D, Müller K-D, et al. (2016) Molecular identification of Nucleophaga terricola sp. nov (Rozellomycota), and new insights on the origin of the Microsporida. Parasitology Research 115: 3003–3011.

De Queiroz K, Gauthier J (1992) Phylogenetic taxonomy. Annual Reviews of Ecology and Systematics 23: 449-480.

Ebersberger I, de Matos Simoes R, Kupczok A, Grube M, Kothe E, et al. (2016) T-BAS: Tree-Based Alignment Selector toolkit for phylogenetic-based placement, alignment downloads and metadata visualization: an example with the Pezizomycotina tree of life. Bioinformatics 33: 1160–1168.

Healy RA, Kumar TK, Hewitt DA, McLaughlin DL (2013) Functional and phylogenetic implications of septal pore ultrastructure in the ascoma of Neolecta vitellina. Mycologia 105: 802–813.

Held AA (1972) Host-parasite relations between Allomyces and Rozella. Archiv für Mikrobiologie 82: 128–139.
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Letcher PM, Powell MJ, Lopez S, Lee PA, McBride RC (2015) Phylogenomic analyses support the monophyly of Taphrinomycotina, including Schizosaccharomycyzes fission yeasts. Molecular Biology and Evolution 26: 27–34.

Liu Y, Yeigh JW, Brinkmann H, Cushion MT, Rodriguez-Ezpeleta N, et al. (2008) Phylogenomic analyses support the monophyly of Taphrinomycotina, including Schizosaccharomycyzes fission yeasts. Molecular Biology and Evolution 26: 27–34.

Liu Y, Steenkamp ET, Brinkmann H, Forget L, Philipe H, Lang BF (2009) Phylogenomic analyses predict sister group relationship of nuclearids and Fungi and paraphyly of zymogycetes with significant support. BMC Evolutionary Biology 9: 272.

Lücking R, Huhndorf S, Pfister D, Plata ER, Lumbsch H (2009) Fungi evolved right on track. Mycologia 101: 810–822.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Cello G, et al. (2004) Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. American Journal of Botany 91: 1446–1480.

Matheny PB, Gossman JA, Zalar P, Arun Kumar TK, Hibbett DS (2006) Resolving the phylogenetic position of the Walliomyctes: an enigmatic major lineage of Basidiomycota. Canadian Journal of Botany 84: 1794–1805.

Nagy LG, Oth RA, Kovačs GM, Floudas D, Riley R, et al. (2014) Phylogenomics reveals latent homology behind the convergent evolution of yeast forms. Nature Communications 5: 4471 DOI: 10.1038/ncomms5471.

Nagy LG, Riley R, Tritt A, Adam C, Daum C, et al. (2016) Comparative genomics of early-diverging mushroom-forming fungi provides insights into the origins of lignocellulose decay capabilities. Molecular Biology and Evolution 33: 959–970.

Paps J, Medina-Chacón LA, Marshall W, Suga H, Ruiz-Trillo I (2013) Molecular phylogeny ofunikonts: new insights into the position ofapsomonomads and ancyromonomads and the internal relationships ofopisthokonts. Protist 164: 2–12.

Powell MJ, Letcher PM, James TY (2017) Ultrastructural characterization of the host-parasite interface between Allomyces anoma-lus (Blastocladiomycota) and Rozella allomycys (Cryptomycota). Fungal Biology 121: 561–572.

Quandt CA, Beaudet D, Corsaro D, Walochkin J, Michel R, et al. (2017) The genome of an intranuclear parasite, Paramicrosporidium saccamoebae, reveals alternative adaptations to obligate intracellular parasitism. eLife 2017;6:e29594 DOI: 10.7554/ eLife.29594.

Redecker D, Schüßler A (2014) Glomeromycota. In: The Mycota. Vol. VIIA. Systematics and Evolution (McLaughlin DJ, Spatafora JW, eds): 373-429. 2nd edn. Berlin: Springer-Verlag.

Ren R, Sun Y, Zhao Y, Geiser D, Ma H, Zhou X (2016) Phylogenetic resolution of deep eukaryotic and fungal relationships using highly conserved low-copy nuclear genes. Genome Biology and Evolution 8: 2683–2701.

Ren R, Sun Y, Zhao Y, Geiser D, Ma H, Zhou X (2016) Phylogenetic resolution of deep eukaryotic and fungal relationships using highly conserved low-copy nuclear genes. Genome Biology and Evolution 8: 2683–2701.

Riley R, Haridas S, Wolfe KH, Lopes MR, Hittinger CT, et al. (2016) Comparative genomics of biotechnologically important yeasts. Proceedings of the National Academy of Sciences, USA 113: 9882–9887.

Schöch CL, Sung G-H, López-Giráldez FL, Townsend JP, Miadlikowska J, et al. (2009) The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Systematic Biology 58: 224–239.

Shen XX, Zhou X, Kominic J, Kurtzman CP, Hittinger CT, Rokas A (2016) Reconstructing the backbone of the Saccharomycotina.
yeast phylogeny using genome-scale data. G3: Genes, Genomes, Genetics 6: 3927–3939.
Sherwood-Pike MA, Gray J (1985) Silurian fungal remains: probable records of the class Ascomycetes. Lethaia 18: 1–20.
Spatafora JW, Benny GL, Lazarus K, Smith ME, Berbee ML, et al. (2016) A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108: 1028–1046.
Spatafora JW, Aime MC, Grigoriev IV, Martin F, Stajich JE, Blackwell M (2017) The fungal tree of life: from molecular systematics to genome-scale phylogenies. Microbiology Spectrum 5: FUNK-0053-2016 doi:10.1128/microbiolspec.FUNK-0053–2016.
Spatafora JW, Johnson D, Sung GH, Hosaka K, O’Rourke B, et al. (2006) A five-gene phylogenetic analysis of the Pezizomycotina. Mycologia 98: 1018–1028.
Sugiyama J, Hosaka K, Suh S-O (2006) Early diverging Ascomycota: phylogenetic divergence and related evolutionary enigmas. Mycologia 98: 998–1007.
Taylor TN, Hass H, Kerp H, Krings M, Hanlin RT (2005) Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphisms. Mycologia 97: 269–285.
Taylor JW, Berbee ML (2006) Dating divergences in the fungal tree of life: review and new analyses Mycologia 98: 838–849.
Tedersoo L, Sánchez-Ramírez S, Kölijalg U, Bahram M, Döring M, et al. (2018) High-level classification of the Fungi and a tool for evolutionary ecological analyses. Fungal Diversity https://doi.org/10.1007/s13225-018-0401-0
Tehler A (1988) A cladistic outline of the Eumycota. Cladistics 4: 227–277.
Torruella G, De Mendoza A, Grau-Bové X, Antó M, Chaplin MA, et al. (2015) Convergent evolution of lifestyles in close relatives of animals and fungi. Current Biology 25: 2404–2410.
Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, et al. (eds) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. [Regnum Vegetabile No.159.] Glashütten: Koeltz Botanical Books.
Whittaker RH (1959) On the broad classifications of organisms. Quarterly Review of Biology 34: 210–226.
Zhao RL, Li G-J, Sánchez-Ramírez S, Stata M, Yang Z-L, et al. (2017) A six-gene phylogenetic overview of Basidiomycota and allied phyla with estimated divergence times of higher taxa and a phyloproteomics perspective. Fungal Diversity 84: 43–74.