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# 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*.

**Key words:**  
classification  
PhyloCode  
rank-free taxonomy  
systematics

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## 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*, *Entorrhizomycota*, *Mucoromycota*, and *Opisthosporidia*, 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 *Entorrhizomycota*), which can destabilize classifications. There are also disagreements about the rankings of names that correspond to well-established monophyletic groups, such as *Glomeromycota*/*Glomeromycotina* (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).

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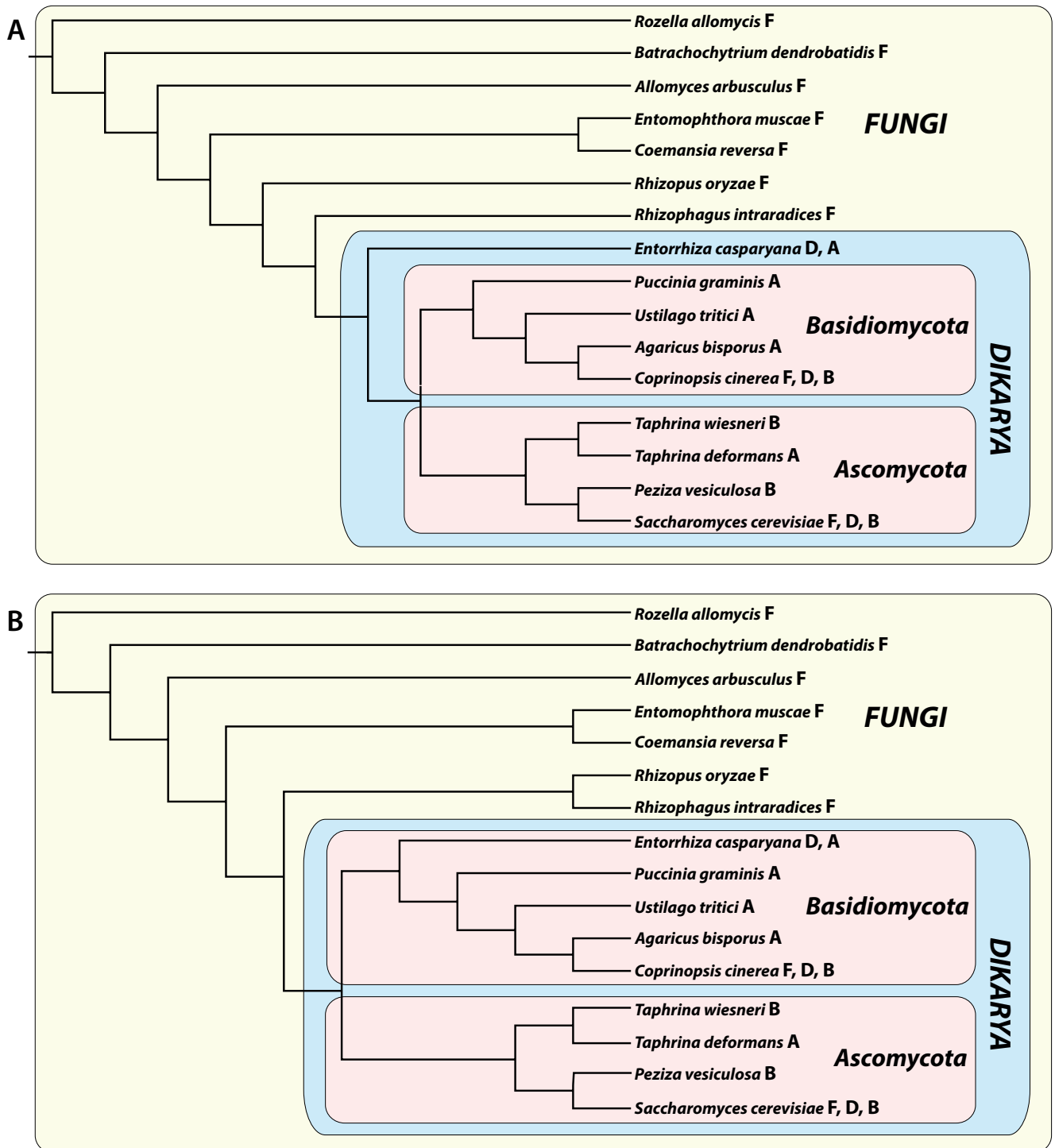
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**Fig. 1.** Phylogenetic taxon definitions and specifiers for *Fungi*, *Dikarya*, *Ascomycota* and *Basidiomycota*. Capital letters following species names indicate the clade(s) for which they serve as specifiers (F for *Fungi*, and so on). There are 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.

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 aphelids, 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 *Entorrhizomycota* as a specifier; *Entorrhizomycota* 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).

*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 torturous. 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 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 name will be identified as a “converted clade name”, and 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 *Dikarya*) in the classification of protists and other eukaryotes by Adl *et al.* (2012). It is hoped that the PTDs presented below will clarify and stabilize application of the names *Fungi*, *Dikarya*, *Ascomycota*, and *Basidiomycota*, and provide a model for other mycologists who wish to name clades, ranked or otherwise.

The authors of the entries for each of the higher taxon names treated here are indicated at the end of each entry.

## TAXONOMY

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

**Definition:** The smallest crown clade containing *Rozella allomycis* F.K. Faust 1937, *Batrachochytrium dendrobatidis* Longcore *et al.* 1999, *Allomyces arbusculus* E.J. Butler 1911, *Entomophthora muscae* (Cohn) Fresen. 1856, *Coemansia reversa* Tiegh. & G. Le Monn. 1873, *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler 2010, *Rhizopus oryzae* Went & Prins. Geerl. 1895, *Saccharomyces cerevisiae* Meyen 1838, and *Coprinopsis cinerea* (Schaeff.) Redhead *et al.* 2001. This is a minimum-crown-clade definition.

**Etymology:** Derived from the Latin *fungus* (mushroom).

**Reference phylogeny:** The primary reference phylogeny is James *et al.* (2006: fig. 1). See also James *et al.* (2013: fig. 2), Karpov *et al.* (2013: fig. 3), Paps *et al.* (2013: fig. 1), Chang *et al.* (2015: fig. 1), Torruella *et al.* (2015: fig. 1), and Spatafora *et al.* (2016: fig. 1).

**Composition:** *Rozella*, *Microsporidia*, *Aphelida*, *Chytridiomycota*, *Neocallimastigomycota*, *Blastocladiomycota*, *Mucoromycota*, *Zoopagomycota*, *Ascomycota* and *Basidiomycota* (Hibbett *et al.* 2007, Karpov *et al.* 2014, Spatafora *et al.* 2016).

**Diagnostic apomorphies:** There are no unambiguous 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 (*Laboulbeniomyces*), 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*, *Microsporidia* and *Aphelida* are intracellular parasites of diverse eukaryotes. *Rozella* and *Aphelida* produce both zoospore stages and endoparasitic amoeboid forms that appear to ingest cytoplasm of their hosts by phagocytosis, whereas *Microsporidia* 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 *Microsporidia* (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 *Microsporidia* as the sister group of all other *Fungi*. Earlier analyses using  $\alpha$ -tubulin and  $\beta$ -tubulin genes also placed *Microsporidia* within *Fungi* (Edlind *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 *Microsporidia* 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 *Microsporidia* 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 specifiers, but *R. allomycis* is the only specifier in the ARM clade. *Microsporidia* were not used as specifiers, 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 nucleariid-*F. alba* clade should be included in *Fungi*. However, most studies refer to the group containing *Fungi* and the nucleariid-*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, *Nucleomycea* (Adl *et al.* 2012, Brown *et al.* 2009).

Karpov *et al.* (2014) named the ARM clade *Opisthospordia* 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 osmoheterotrophy (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:** *Carpomyceteae* 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* (Bjerk.) 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:** *Taphrinomycotina*, *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 flagella 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]. *Ascomycotina 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 subclasses (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 ascoma-producing taxa with the exception of *Neoelectromycetes* 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 crown 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-crown-clade definition.

**Etymology:** Derived from the Latin *basis* (base, support) plus diminutive suffix *-idium*, 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*

of the *Fungi* (Kirk *et al.* 2008) and the GenBank taxonomy (<http://www.ncbi.nlm.nih.gov/guide/taxonomy>). Monophyly of *Basidiomycota* has been strongly supported in phylogenetic analyses of multi-locus molecular data (James *et al.* 2006), 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 *Entorrhizomycetes* to *Basidiomycota* is controversial (Bauer *et al.* 2015, Matheny *et al.* 2006, Zhao *et al.* 2017). *Entorrhizomycetes* includes root-gall fungi with similarities to certain *Basidiomycota*, including dolipore septa, dikaryotic vegetative cells, and teliospores with cruciate septation (Bauer *et al.* 2015). *Entorrhizomycetes* 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 *Entorrhizomycetes* in its own phylum, *Entorrhizomycota*. There are still no whole-genome sequences available for *Entorrhizomycetes*.

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