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A phylogenetic overview of the Agaricomycotina

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Abstract: The Agaricomycotina contains about one-third of the described species of Fungi, including mushrooms, jelly fungi and basidiomycetous yeasts. Recent phylogenetic analyses by P. Matheny and colleagues combining nuclear rRNA genes with the protein-coding genes *rpb1, rpb2* and *tef1* support the division of Agaricomycotina into Tremellomycetes, Dacrymycetes and Agaricomycetes. There is strong support for the monophyly of the Tremellomycetes, and its position as the sister group of the rest of the Agaricomycotina. Dacrymycetes and Agaricomycetes also are supported strongly, and together they form a clade that is equivalent to the Hymenomycetidae of Swann and Taylor. The deepest nodes in the Agaricomycetes, which are supported only by Bayesian measures of confidence, suggest that the Sebacinales, Cantharellales and Auriculariales are among the most ancient lineages. For the first time, the Polyporales are strongly supported as monophyletic and are placed as the sister group of the Thelephorales. The Agaricales, Boletales and Atheliales are united as the Agaricomycetidae, and the Russulales might be its sister group. There are still some problematical nodes that will require more loci to be resolved. Phylogenomics has promise for reconstructing these difficult backbone nodes, but current genome projects are limited mostly to the Agaricales, Boletales and Polyporales. Genome sequences from other major lineages, especially the early diverging clades, are needed to resolve the most ancient nodes and to assess deep homology in ecological characters in the Agaricomycotina.

Key words: Basidiomycota, heterobasidiomycetes, hymenomycetes, phylogeny, taxonomy, *Wallemia*

Introduction.—The Agaricomycotina is a diverse clade of Basidiomycota that includes mushrooms, jelly fungi and basidiomycetous yeasts. There are about 20 000 described species of Agaricomycotina, which is 68% of the known Basidiomycota, or about a third of all Fungi (Kirk et al 2001). Molecular clock studies, reviewed by Taylor et al (2004), suggest that the Agaricomycotina could be anywhere from 380 000 000 to 960 000 000 y old.

The Agaricomycotina contains large concentrations of wood decayers, litter decomposers and ectomycorrhizal fungi, along with relatively small numbers of important pathogens of timber (e.g. *Phellinus weirii, Heterobasidion annosum*), vegetable crops (*Thanatephorus cucumeris*) and humans (*Filobasidiella neoformans*). Some Agaricomycotina are highly poisonous (*Amanita phalloides, Galerina autumnalis*), while others are hallucinogenic (*Psilocybe cubensis*) or edible. The latter include cultivated saprotrophs (*Agaricus bisporus, Lentinula edodes, Auricularia auricula-judae*) and field-collected mycorrhizal species (*Cantharellus cibarius, Boletus edulis, Tricholoma matsutake*). Certain members of the Agaricomycotina produce the largest fruiting bodies (*Bridgeoporus nobilissimus, Rigidoporus ulmarius*) and the most extensive, long-lived mycelial networks in the Fungi (*Armillaria gallica*).

This article presents an overview of the higher-level phylogeny of the Agaricomycotina, with particular reference to recent multilocus studies by Matheny and colleagues (2006b, c) and the emerging AFTOL classification (http://www.clarku.edu/faculty/dhibbett/AFTOL/AFTOL.htm). For detailed information on specific clades, the reader is referred to the articles in the present volume that discuss the Agaricales, Boletales, Cantharellales, Hymenochaetales, Russulales and Phallomycetidae (Matheny et al 2006a, Binder and Hibbett 2006, Moncalvo et al 2006, Larsson et al 2006, Miller et al 2006, Hosaka et al 2006) and other recent works that survey major assemblages of Agaricomycotina (Binder et al 2005, Fell et al 2001, Hibbett unpublished, Hibbett and Thorn 2001, Larsson et al 2004, Moncalvo et al 2002, Sampaio 2004, Weiss et al 2004, Wells and Bandoni 2001). Representatives of groups of Agaricomycotina that are not the subject of individual articles in this volume are illustrated (FIG. 1).

Prior phylogenetic classifications.—Several higher-level classifications have been proposed for the Agaricomycotina since the advent of fungal molecular systematics (TABLE I). Swann and Taylor (1993, 1995) performed pioneering studies with nuclear small subunit rRNA genes and divided the Basidiomycota into three major groups, the Hymenomycetes, Ustilaginomycetes and Urediniomycetes, which are called the Agaricomycotina, Ustilaginomycotina and Pucciniomycotina in the AFTOL classification, as

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FIG. 1. Fruiting bodies of Agaricomycotina, emphasizing jelly fungi and resupinate forms. A. *Tremella mesenterica* (Tremellales). B. *Tremella fuciformis* (Tremellales). C. *Dacryopinax spathularia* (Dacrymycetales). D. *Tremellodendron pallidum* (Sebacinales). E. *Auricularia auricula-judae* (Auriculariales). F. *Exidiopsis sp.* (Auriculariales). G. *Trechispora sp.* (Trechisporales). H. *Tomentella sp.* (Thelephorales). I. *Athelia sp.* (probably Atheliales). J. *Veluticeps sp.* (Gloeophyllales).

recently formalized by Bauer et al (2006). Relationships among these three clades have proven difficult to resolve. The majority of analyses of nuclear rRNA genes have suggested that the Ustilaginomycotina is the sister group of the Agaricomycotina (e.g. Swann and Taylor 1995, Weiss et al 2004), which is consistent with ultrastructural characters (Lutzoni et al 2004, McLaughlin et al 1995), cell wall biochemistry (Prillinger et al 1993) and 5S rRNA secondary structure (Gottschalk and Blanz 1985). However, other analyses of rRNA genes as well as β-tubulin sequences have suggested that the Pucciniomycotina is the sister group of the Agaricomycotina or have produced an unresolved trichotomy among the three clades (Begerow, John and Oberwinkler 2004; Nishida et al 1995).

Swann and Taylor's classification was based on a small number of taxa and a single locus, but it has proven to be remarkably durable and influential (TABLE I). Nevertheless, their choice of the name Hymenomycetes was not ideal because this term was used by Fries (1874) to refer to fungi that bear their spores on an exposed hymenium, as opposed to Gasteromycetes, which bear their spores internally. Long before Swann and Taylor's publication it was well understood that the Hymenomycetes and Gasteromycetes of Fries are not monophyletic and these terms had come to be used in an informal, descriptive sense. The 9th edition of the *Dictionary of the Fungi* (Kirk et al 2001) referred to the Agaricomycotina as the Basidiomycetes, but this was also an unfortunate choice, because this term is used frequently to mean all fungi with a basidium (i.e. the Basidiomycota). In the AFTOL classification it was decided to use the name Agaricomycotina, because this name cannot be confused with informal terms and because it refers to *Agaricus bisporus*, which is perhaps the most widely recognized mushroom in the world.

The classification of major groups within the Agaricomycotina also has been unsettled. Taxa within the Agaricomycotina have been divided into heterobasidiomycetes (including species with mostly septate or tuning fork basidia, often with gelatinous fruiting bodies, yeast stages and spore repetition; approx. syn. Phragmobasidiomycetes; FIG. 1A–F) and homobasidiomycetes (mushroom-forming fungi, with undivided basidia; FIG. 1G–N). However, this basic division was shown to be artificial in the studies of Swann and Taylor (1995), who recognized two subclasses of Hymenomycetes, the Tremellomycetidae, containing Tremellales s.lat., and the Hymenomycetidae, containing homobasidiomycetes and the heterobasidiomycetous Auriculariales, Dacrymycetales and *Thanatephorus cucumeris* (Ceratobasidiales). Some workers recently have adopted the classification proposed by Swann and Taylor (e.g. Weiss et al 2004), but the classical heterobasidiomycete/homobasidiomycete dichotomy has remained influential. For example, the *Mycota* VIIb (McLaughlin et al 2001) contains separate chapters on heterobasidiomycetes (Wells and Bandoni 2001) and homobasidiomycetes (Hibbett and Thorn 2001) (although the latter chapter indicated that the homobasidiomycetes s.str. is not monophyletic). Similarly, the 9th edition of the *Dictionary of the Fungi* (Kirk et al 2001) contains two subclasses of ''Basidiomycetes'', the Tremellomycetidae, containing all the traditional heterobasidiomycetes, and the Agaricomycetidae, containing the homobasidiomycetes (TABLE I). The 16 orders within the Tremellomycetidae and Agaricomycetidae in the *Dictionary* classification largely parallel the orders of heterobasidiomycetes proposed by Wells and Bandoni (2001) and the informal clades of homobasidiomycetes proposed by Hibbett and Thorn (2001) (TABLE I). For the most part the orders recognized in the *Dictionary* are monophyletic based on current phylogenetic hypotheses, with the Polyporales and Tremellales being conspicuous exceptions.

The 9th edition of the *Dictionary of the Fungi* (Kirk et al 2001) contains the most comprehensive, detailed, and up-to-date classification of the Agaricomycotina in print. It represents a major overhaul of the classification in the 8th edition of the *Dictionary* (Hawksworth et al 1995) and is quite different from the classification currently employed by GenBank (http://www.ncbi.nlm.nih.gov/Taxonomy/; TABLE I). Nevertheless, there has been much recent progress in phylogenetic reconstruction that the current *Dictionary* classification does not reflect (Hibbett et al 2005). Many studies have reinforced the view that the Tremellomycetidae and Agaricomycetidae of the *Dictionary* are not monophyletic (Binder et al 2005, Moncalvo et al 2006, Weiss et al 2004) and the phylogenetic placements of many taxa formerly classified in the Polyporales, Tremellales and other orders have been resolved. In the process, five independent clades have been discovered that are not recognized in the *Dictionary* classification, in-

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K. *Phlebia sp.* (Polyporales). L. *Ganoderma australe* (Polyporales). M. *Hydnellum sp.* (Thelephorales). N. *Neolentinus lepideus* (Gloeophyllales). A–C and F–L © Heino Lepp, Australian National Botanical Gardens (http://www.anbg.gov.au/index.html). D, E © Pamela Kaminski (http://pkaminski.homestead.com/page1.html). Used with permission.

TABLE I. Recent classifications of Agaricomycotina to ordinal level

Swann and Taylor 1995	Wells and Bandoni 2001 excludes homobasidiomycetes	Hibbett and Thorn 2001 excludes most heterobasidiomycetes	Weiss et al 2004 excludes homobasidiomycetes
HYMENOMYCETES	HETEROBASIDIOMYCETES	HOMOBASIDIOMYCETES	HYMENOMYCETES
Tremellomycetidae	Heterobasidiomycetidae	Euagarics clade	Tremellomycetidae
Tremellales	Auriculariales	Bolete clade	Tremellales
Filobasidiales	Ceratobasidiales	Cantharelloid clade	Cystofilobasidiales
Trichosporon	Dacrymycetales	Gomphoid-phalloid clade	Hymenomycetidae
Hymenomycetidae	Tulasnellales	Hymenochaetoid clade	Auriculariales
Auriculariales	Tremellomycetidae	Polyporoid clade	Ceratobasidiales
Dacrymycetales	Tremellales	Russuloid clade	Dacrymycetales
Thanatephorus	Christianseniales	Thelephoroid clade	Sebacinales
homobasidio-mycetes	Filobasidiales	*Gloeophyllum*	Tulasnellales

GenBank 2006	Dictionary of Fungi 8th ed. 1995 (Pucciniomycotina)	Dictionary of the Fungi 9th ed. 2001	AFTOL
HYMENOMYCETES	BASIDIOMYCETES	BASIDIOMYCETES	AGARICOMYCOTINA
Heterobasidiomycetes	Phragmobasidiomycetidae	Tremellomycetidae	Tremellomycetes
Heterobasidio-mycetidae	Auriculariales	Auriculariales	Cystofilobasidiales
Auriculariales	(Agaricostilbales)	Ceratobasidiales	Filobasidiales
Dacrymycetales	(Atractiellales)	Christianseniales	Tremellales
Sebacinales	(Heterogastridiales)	Cystofilobasidiales	Dacrymycetes
Tremellomycetidae	Holobasidiomycetidae	Dacrymycetales	Dacrymycetales
Christianseniales	Agaricales	Filobasidiales	Agaricomycetes
Cystofilobasidiales	Boletales	Tremellales	Agaricomycetidae
Filobasidiales	Bondarzewiales	Tulasnellales	Agaricales
Tremellales	Cantharellales	Agaricomycetidae	Atheliales
Trichosporonales	Ceratobasidiales	Agaricales	Boletales
Homobasidiomycetes	Cortinariales	Boletales	Phallomycetidae
Agaricales	Dacrymycetales	Cantharellales	Geastrales
Aphyllophorales	Fistulinales	Hymenochaetales	Gomphales
Boletales	Ganodermatales	Phallales	Hysterangiales
Cantharellales	Gautieriales	Polyporales	Phallales
Ceratobasidiales	Gomphales	Russulales	Agaricomycetes inc sed.
Gautieriales	Hericiales	Thelephorales	Auriculariales
Geastrales	Hymenochaetales		Cantharellales
Hericiales	Hymenogastrales		Corticiales
Hymenochaetales	Lachnocladiales		Gloeophyllales
Hymenogastrales	Lycoperdales		Hymenochaetales
Lycoperdales	Melanogastrales		Polyporales
Melanogastrales	Nidulariales		Russulales
Nidulariales	Phallales		Sebacinales
Phallales	Poriales		Thelephorales
Stereales	Russulales		Trechisporales
Thelephorales	Schizophyllales		
Tulasnellales	Sclerodermatales		
Tulostomatales	Stereales		
Ramaria	Thelephorales		
	Tulasnellales		
	Tulostomatales		

cluding the heterobasidiomycetous Sebacinales (FIG. 1D) and four clades of homobasidiomycetes, the Atheliales, Corticiales, Gloeophyllales and Trechisporales (Binder et al 2005, Hibbett and Binder 2002, Larsson et al 2004, Lim 2001, Weiss et al 2004; FIG. 1G, I, J, N). These discoveries were based on analyses of rRNA genes, which generally provide weak bootstrap support for many deep nodes in the Agaricomycotina

(Binder and Hibbett 2002). One of the major goals of the AFTOL project (http://aftol.org/) was to create multilocus datasets to resolve the deep nodes of the Agaricomycotina and other Fungi (Lutzoni et al 2004; Matheny et al 2006b, 2006c).

Multilocus perspectives.—The tree (FIG. 2A) represents a synthesis of recent studies of Agaricomycotina phylogeny and includes the 21 orders of Agaricomycotina in the forthcoming AFTOL classification as terminal taxa (some are not yet formally published, e.g. Gloeophyllales, Trechisporales). The backbone for the tree is taken from a study of higher-level phylogenetic relationships of Basidiomycota by Matheny and colleagues (2006c), which used sequences of *rpb2*, *tef1* and nuclear 18S, 25S and 5.8S rRNA genes from 146 taxa, including 125 Agaricomycotina. The topology shown is from a Bayesian analysis of nucleotide characters (6603 positions, including 3318 parsimony informative positions). Sixteen orders of Agaricomycotina were represented in the dataset of Matheny et al, but the Cystofilobasidiales, Filobasidiales, Geastrales, Gloeophyllales and Hysterangiales were not included. Placements of these taxa (FIG. 2A) were based on other studies (Fell et al 2001, Hibbett and Donoghue 2001, Lutzoni et al 2004, Hosaka et al 2006). The trees (FIG. 2B) are derived from another study by Matheny et al (2006b), which used the three nuclear rRNA genes along with *rpb1*, *rpb2* and *tef1*, and that was focused on the phylogenetic placement of Wallemia, an enigmatic group of apparently mitosporic Basidiomycota that has dolipore septa and colonizes dried and salted foods, and which is the sole genus of the Wallemiomycetes (Moore 1986, Zalar et al 2005).

In both studies of Matheny et al (2006b, c) the Ustilaginomycotina was resolved as being more closely related to the Agaricomycotina than the Pucciniomycotina (FIG. 2). It is too early, however, to state with confidence that the sister group of the Agaricomycotina has been identified, because analyses of protein-coding genes suggest that the closest relative of the Agaricomycotina might be *Wallemia* (FIG. 2B). This result appears to be driven primarily by the *rpb2* data partition (Matheny et al 2006b). In contrast analyses that include rRNA genes place *Wallemia* as the sister group of the Ustilaginomycotina or as the sister group of *Entorrhiza*, which is a small group of root-inhabiting fungi that has been classified in the Entorrhizomycetidae, Ustilaginomycotina (Bauer et al 2001, Piepenbring 2004). Combined 18S, 25S and 5.8S rRNA gene sequences, which are the only molecular data currently available for *Entorrhiza*, consistently place this taxon as the sister group of the rest of the Basidiomycota, separate from other Ustilaginomycotina (FIG. 2B). However, additional loci are needed to resolve the phylogenetic placements of both *Entorrhiza* and *Wallemia*.

The combined rRNA, *rpb2, tef1* dataset (Matheny et al 2006c) provides strong support for the earliest divergences in the Agaricomycotina. The Tremellomycetes are strongly supported as the sister group of the rest of the Agaricomycotina but are represented by only two isolates of *Cryptococcus*. Prior analyses with much more extensive sampling of Tremellomycetes using rRNA genes have found weak support for the monophyly of this group (Swann and Taylor 1995, Weiss et al 2004), or have resolved it as paraphyletic (Sampaio 2004) (Fell et al 2001 also sampled Tremellomycetes intensively, but their analyses did not test the monophyly of the Tremellomycetes because they did not include other groups of Agaricomycotina). Monophyly of Tremellomycetes was addressed in the second study by Matheny et al (2006b), which included representatives of Cystofilobasidiales, Filobasidiales and Tremellales. In analyses of rRNA genes alone the Tremellomycetes was resolved as a paraphyletic assemblage, with the Cystofilobasidiales placed as the sister group of the rest of the Agaricomycotina (FIG. 2B). These results are similar to those of Sampaio (2004), who analyzed partial 25S rRNA gene sequences. However analyses that used *rpb1, rpb2*, and *tef1*, either alone or in combination with the rRNA genes, provided strong support for the monophyly of Tremellales plus Cystofilobasidiales (Filobasidiales were not sampled for the protein-coding loci). These results highlight the importance of obtaining data from multiple loci for analyses of deep nodes in Agaricomycotina.

The Dacrymycetes (including only the Dacrymycetales) was strongly supported as monophyletic by both bootstrap and Bayesian criteria in the studies of Matheny and colleagues (2006b, c) as in other studies (Binder et al 2005, Weiss et al 2004). In addition, the Dacrymycetes was strongly supported as the sister group of the Agaricomycetes, which conflicts with placements of this group based on rRNA genes alone (Weiss et al 2004). The Dacrymycetes/Agaricomycetes clade is equivalent in composition to the Hymenomycetidae of Swann and Taylor (1995). Many Dacrymycetes and Tremellomycetes (as well as Auriculariales) form gelatinous, translucent fruiting bodies (FIG. 1A–C), and it is plausible that this could be the plesiomorphic condition of the Agaricomycotina as a whole. These two early diverging clades have very different ecological strategies, however. The Dacrymycetes are saprotrophs that produce a brown rot type of wood decay, whereas the Tremellomycetes include mycoparasites and pathogens of mammals (Wells and Bandoni 2001). Many Tremellomycetes

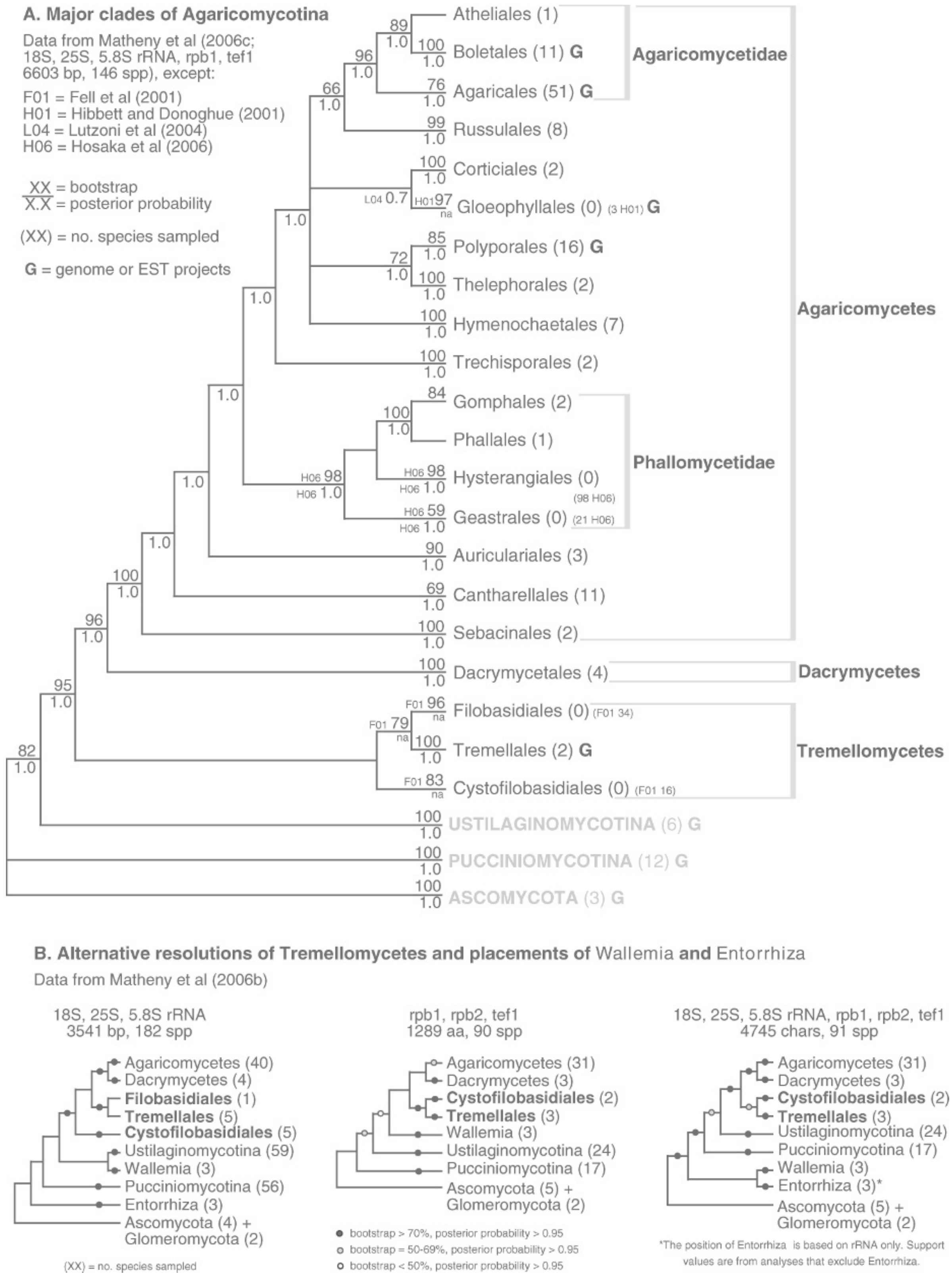

FIG. 2. Higher-level phylogenetic relationships of Agaricomycotina. A. Bayesian majority-rule consensus topology based on 6603 bp of 18S, 25S, and 5.8S rRNA, *rpb2*, and *tef1*. Backbone based on analyses by Matheny et al (2006c), with placements of Gloeophyllales, Hysterangiales, Geastrales, Filobasidiales and Cystofilobasidiales based on studies by Fell et al (2001), Hibbett

have been cultured, but it is not known to what extent they are able to function saprotrophically in nature.

The Agaricomycetes also was supported strongly as monophyletic by both bootstrap and Bayesian measures (FIG. 2). Most of the terminal clades in the Agaricomycetes (FIG. 2A) have been discussed in previous studies and require little comment here (see the later articles in this volume). However, several nodes are resolved with confidence for the first time in the multilocus analyses of Matheny et al (2006c). One of these is the node that unites the Agaricales, Boletales and Atheliales, which is being proposed as the Agaricomycetidae in the AFTOL classification. The Atheliales is a small group of ephemeral resupinate forms (FIG. 1I), whereas the Agaricales and Boletales contain major concentrations of large pileate-stipitate forms. The positioning of the Atheliales as the sister group of the Boletales, and the occurrence of resupinate taxa within early diverging clades of Boletales (Binder and Hibbett 2006) and Agaricales (Binder et al unpublished), is consistent with the view that resupinate forms make up a paraphyletic assemblage that has given rise to more elaborate forms many times within the Agaricomycetes (Hibbett and Binder 2002).

The Russulales is resolved as the sister group of the Agaricomycetidae, with strong Bayesian support and weak (66%) bootstrap support. If the Agaricales, Boletales and Russulales were found to form a monophyletic group, then that would be partly consistent with Singer's (1986) conception of the Agaricales, which he divided into the suborders Agaricineae, Boletineae, and Russulineae. Of course, Singer's suborders did not include many of the ''aphyllophoraceous'' and gasteroid taxa that are now known to be in the Agaricales, Boletales and Russulales.

The Polyporales (FIG. 1K–L) has been a particularly challenging group for basidiomycete systematists and were something of a garbage can taxon in the 9th edition of the *Dictionary of the Fungi* (Kirk et al 2001). Members of the Polyporales have been sampled in numerous studies, but the group has received weak bootstrap support (Binder and Hibbett 2002, Hibbett and Donoghue 2001) or has been resolved as paraphyletic (Binder et al 2005) or polyphyletic (Larsson et al 2004). The multilocus dataset of Matheny et al (2006c) included a diverse sample of 16 Polyporales, including white-rot and brown-rot species that represent the ''core polyporoid clade'', ''phlebioid clade'', ''*Antrodia* clade'' and ''residual polyporoid clade'', as delimited by Binder et al (2005). For the first time, the Polyporales was strongly supported as monophyletic, and the Thelephorales (FIG. 1H, M) was placed as its sister group, with moderately strong support (FIG. 2A). It is surprising to find that these two groups are closely related because the Thelephorales are exclusively mycorrhizal, as far as is known, whereas the Polyporales all are saprotrophic and include many decayers of large woody substrates. Evidently there was a transformation between saprotrophic and mycorrhizal life strategies early in the evolution of this clade.

Remaining problems.—The promise of phylogenomics. Through combined analyses of rRNA and protein-coding genes, the backbone of the phylogeny of Agaricomycotina is finally coming into focus, and strong support is being obtained for terminal clades that previously had not been resolved with confidence, such as the Polyporales. However, five of the backbone nodes in the Agaricomycetes are supported only by Bayesian measures and the relationships among the Agaricomycetidae/Russulales, Polyporales/Thelephorales, Hymenochaetales, Gloeophyllales and Corticiales are not resolved at all (FIG. 2A). This topological uncertainty will hinder efforts to understand the evolution of morphological and ecological characters or to localize shifts in diversification rates.

To resolve the remaining major phylogenetic questions in the Agaricomycotina it will be necessary to assemble and analyze large-scale molecular datasets that go far beyond the handful of loci that are the focus of the current AFTOL project. Complete genome sequences will be important to this effort because they can be used directly in phylogenomic analyses (e.g. Robbertse et al in press) and because they can guide the development of degenerate primers for amplifying orthologous genes across large numbers of taxa (e.g. Rokas et al 2005). Complete genomes also will be necessary to understand the genetic bases of ecological and physiological evolution, including switches between mycorrhizal and decayer life strategies, and the diversification of mechanisms for degradation of lignocellulose. Understanding the latter has potential applications in green technologies such as the production of

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and Donoghue (2001), Lutzoni et al (2004) and Hosaka et al (2006). B. Alternative resolutions of Tremellomycetes and placements of *Wallemia* and *Entorrhiza*, inferred with 18S, 25S, and 5.8S rRNA, *rpb1, rpb2* and *tef1*. Based on analyses by Matheny et al (2006b).

alternative energy sources and therefore should be a priority.

Comparative genomics of Agaricomycotina is a young, rapidly expanding discipline. As of this writing, complete genome sequences have been produced for only four species, including multiple isolates of the human pathogen *Cryptococcus neoformans*, but there are at least nine other genome and expressed sequence tag (EST) sequencing efforts pending or in progress (a partial list of ongoing projects, with varying levels of activity, is listed in SUPPLEMENTARY TABLE I). Individually, a strong case can be made for each of the genome targets, but in aggregate they represent a phylogenetically skewed sample. Thus, in addition to the *Cryptococcus* projects, there are multiple projects in the Agaricales, Boletales and Polyporales and one ongoing project in the Gloeophyllales (which is important because *Gloeophyllum trabeum* is a model system for studies of brown-rot decay mechanisms). Having multiple genome sequences within these groups will be valuable because that will allow studies of genome evolution over a relatively short time. Nevertheless to resolve the backbone nodes of the Agaricomycotina phylogeny and to assess deep homology in ecological characters it will be necessary to obtain complete genome sequences from ecologically diverse species in clades that have yet to be sampled, including the Dacrymycetes, Sebacinales, Cantharellales, Auriculariales, Hymenochaetales and Russulales. (A dozen candidates, with brief rationales, are listed in SUPPLEMENTARY TABLE II).

Even if all the species in the supplementary information were sequenced, the available genomes still would represent a tiny fraction of the extant diversity of Agaricomycotina. Fortunately, as the articles in this volume attest, there has been tremendous recent progress in developing detailed phylogenetic hypotheses for terminal clades of Agaricomycotina. These studies increasingly are based on intensively sampled multilocus datasets (e.g. Hosaka et al 2006, Matheny et al 2006a) but there is still an excess of taxa for which there are only rRNA sequences, including those of the rapidly evolving ITS region. To achieve a comprehensive view of the phylogeny of Agaricomycotina, it will be necessary to integrate genome-scale information with the ever growing database of ITS and other highly variable regions, including sequences generated in molecular studies of fungal ecology.

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SUPPLEMENTARY TABLE I. Agaricomycotina genome and EST projects as of Jun 2006

Species/Clade	Ecology	Status	Main laboratories/organizations/URL
Agaricales			
Amanita bisporigera	Ectomycorrhizal	EST	Walton laboratory, Michigan State University: http://www.prl.msu.edu/walton/amanita.htm
Coprinopsis cinerea	Coprophilic saprobe	Genome completed	Broad Institute: http://www.broad.mit.edu/annotation/genome/coprinus_cinereus/Home.html
Hebeloma cylindrosporum	Ectomycorrhizal	EST	International Mycorrhiza Genome Consortium: http://mycor.nancy.inra.fr/ectomycorrhizadb/
Laccaria bicolor	Ectomycorrhizal	Genome completed	DOE Joint Genome Institute: http://genome.jgi-psf.org/Lacbi1/Lacbi1.home.html
Lentinula edodes	White rot	EST	Fungal Genomics Project, Concordia University: https://fungalgenomics.concordia.ca/fungi/Ledo.php
Schizophyllum commune	White rot	EST, Genome pending	Lilly and Gathman laboratories, Southeast Missouri State University: http://biology.semo.edu/agathman/lab/est.htm DOE Joint Genome Institute: http://www.jgi.doe.gov/sequencing/DOEmicrobes2006.html
Boletales			
Paxillus involutus	Ectomycorrhizal	EST	International Mycorrhiza Genome Consortium: http://mycor.nancy.inra.fr/ectomycorrhizadb/
Pisolithus microcarpus	Ectomycorrhizal	EST	International Mycorrhiza Genome Consortium: http://mycor.nancy.inra.fr/ectomycorrhizadb/
Gloeophyllales			
Gloeophyllum trabeum	Brown rot	EST	Fungal Genomics Project, Concordia University: https://fungalgenomics.concordia.ca/fungi/Gtra.php
Polyporales			
Phanerochaete chrysosporium	White rot	Genome completed	DOE Joint Genome Institute: http://genome.jgi-psf.org/whiterot1/whiterot1.home.html
*Postia (Oligoporus) placenta(us)**	Brown rot	Genome in progress	DOE Joint Genome Institute: http://www.jgi.doe.gov/sequencing/DOEmicrobes2005.html
Trametes versicolor	White rot	EST	Fungal Genomics Project, Concordia University: https://fungalgenomics.concordia.ca/fungi/Tver.php
Tremellales			
Cryptococcus neoformans	Human pathogen	Genomes completed	Duke University Center for Applied Genomics and Technology http://cneo.genetics.duke.edu/ TIGR: http://www.tigr.org/tdb/e2k1/cna1/ Stanford Genome Technology Center: http://www-sequence.stanford.edu/group/C.neoformans/index.html Broad Institute: http://www.broad.mit.edu/annotation/genome/cryptococcus_neoformans/Home.html

* syn. *Rhodonia placenta*

Supplementary Table II. Potential genome sequencing candidates in Agaricomycotina

Clade	Species	Rationale
Dacrymycetales	*Dacrymyces sp.*	Brown rot, early-diverging lineage, no genomes from this clade.
Sebacinales	*Piriformospora indica*	Root symbiont, emerging model system for plant-fungal sysmbiosis, early-diverging lineage, no genomes from this clade.
Auriculariales	*Auricularia auricula-judae*	White rot, cultivated, no genomes from this clade.
Cantharellales	*Cantharellus cibarius*	Ectomycorrhizal, no genomes from this clade.
	Thanatephorus cucumeris	Important plant pathogen, no genomes from this clade.
Phallomycetidae	*Sphaerobolus stellatus*	White rot, no genomes from this clade.
Hymenochaetales	*Phellinus weirii*	White rot, timber pathogen, no genomes from this clade.
Thelephorales	*Thelephora terrestris*	Ectomycorrhizal, sister group to Polyporales, no genomes from this clade.
Russulales	*Heterobasidion annosum*	White rot, timber pathogen, no genomes from this clade.
	Russula sp.	Ectomycorrhizal, no genomes from this clade.
Boletales	*Serpula lacrymans*	Brown rot, destructive decayer of structural wood.
Agaricales	*Fistulina hepatica*	Brown rot.