

Major clades of Agaricales: a multilocus phylogenetic overview

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Abstract: An overview of the phylogeny of the Agaricales is presented based on a multilocus analysis of a six-gene region supermatrix. Bayesian analyses of 5611 nucleotide characters of *rpb1*, *rpb1*-intron 2, *rpb2* and 18S, 25S, and 5.8S ribosomal RNA genes recovered six major clades, which are recognized informally and labeled the Agaricoid, Tricholomatoid, Marasmioid, Pluteoid, Hygrophoroid and Plicaturopsidoid clades. Each clade is discussed in terms of key morphological and ecological traits. At least 11 origins of the ectomycorrhizal habit appear to have evolved in the Agaricales, with possibly as many as nine origins in the Agaricoid plus Tricholomatoid clade alone. A family-based phylogenetic classification is sketched for the Agaricales, in which 30 families,

four unplaced tribes and two informally named clades are recognized.

Key words: Basidiomycota, fungi, phylogeny, mycorrhiza, systematics, *rpb1*, *rpb2*

INTRODUCTION

The Agaricales or euagarics clade (Basidiomycota, Agaricomycetidae) is the largest clade of mushroom-forming fungi and includes more than half of all known species of the homobasidiomycetes (Hibbett et al 1997, Hibbett and Thorn 2001). More than 9000 species and roughly 350 genera have been ascribed to the order, which contains 26 families (Kirk et al 2001). A consensus higher-level classification in the Agaricales has been difficult to achieve because competing systems circumscribe genera and families (or even orders) in different ways (Bas 1998, Jülich 1981, Kirk et al 2001, Kühner 1980, Singer 1986). Results from molecular phylogenetic studies have provided numerous fresh perspectives on the evolution and classification of the group, yet produced their own unique problems.

The foundation for a classification of mushrooms was built by Fries (1821–1832, 1828, 1857–1863, 1874), who emphasized macroscopic features, such as hymenophore type—gilled, poroid, ridged, veined, spinose, papillate, and smooth—to group the mushroom-forming fungi into higher-level taxa. Fries relied on spore deposit color—white, pink, brown, purple-brown and black—to divide the gilled mushrooms (agarics) into several series. Fries' macroscopic system, which initially recognized 12 genera of fleshy mushroom-forming fungi, was taxonomically practical. It was relatively unchallenged until Fayod (1889) surveyed the anatomy and microscopic features of many agarics and consequently recognized 108 genera.

Singer and Kühner, two recent influential agaric systematists, sustained Fayod's momentum in different ways. Each of their family-level classifications is depicted as a cladogram and illustrated opposite each other for comparison (SUPPLEMENTARY FIG. 1). Kühner (1980) investigated the utility of cytological characters and used these to help shape a notable departure from previous classifications. Singer (1986) primarily integrated anatomical characters and spore micromorphology but observed a greater diversity of agarics from the neotropics and the southern hemisphere. Many others have influenced higher-level classification of mushrooms and their allies or proposed various evolutionary hypotheses for the Agaricales during the past 50 y (e.g. Heim 1971; Horak 1968; Jülich 1981; Kühner and Romagnesi 1953; Moser 1983; Pegler and Young 1969, 1971; Petersen

1971). However, because of the synoptic scope found in Singer (1986) and Kühner (1980), and their opposing views, these systems are integral for a molecular phylogenetic evaluation of gilled mushrooms and their allies.

Singer (1986), whose legacy The Agaricales in Modern Taxonomy remains the most encompassing and detailed classification of agarics, employed a broad concept of the order. This treatment contained not only gilled mushrooms but also many elements of the Boletales and certain taxa (gilled and poroid) of the Russulales and Polyporales. He exercised a narrow generic concept in practice (Singer 1991) and as a result recognized 192 genera in the suborder Agaricineae alone, which roughly parallels the euagarics clade (Hibbett et al 1997; Moncalvo et al 2000, 2002), or what is referred to here as the Agaricales.

Kühner (1980) divided Singer's Agaricales into five orders: Tricholomatales (including some gilled taxa of the Polyporales), Agaricales *sensu stricto*, Pluteales, Russulales and Boletales. Three of the orders—Tricholomatales, Agaricales and Pluteales—conform mostly to our Agaricales (the euagarics clade) or Singer's Agaricineae. Kühner's treatment of multiple orders of agarics is not widely recognized, but neither has it been evaluated explicitly by molecular data. In contrast to Singer he employed a broad generic concept, recognizing 75 genera distributed across his three orders of euagaric fungi.

Overemphasis on spore deposit color, fruit body form and some anatomical and cytological traits, in hindsight, led to the establishment of many artificial groups and unexpected phylogenetic consequences. Molecular phylogenetic analysis of ribosomal RNA sequences has transfigured the circumscription of the Agaricales in the past decade, reaffirming some ideas of earlier workers while shattering others. Some of the important revelations of these studies showed that fruit body form and hymenophore type have been phylogenetically misleading (Hibbett et al 1997), that many families and genera of agarics were not monophyletic (Moncalvo et al 2000, 2002) and that ecological traits have been underused in diagnosis of natural groups (Moncalvo et al 2002). Other broad molecular phylogenetic studies (Bodensteiner et al 2004; Larsson, Larsson and Kõljalg 2004; Binder et al 2005) have demonstrated evolutionary relationships among nongilled basidiomycetes, such as resupinate and cyphelloid forms, with members of the Agaricales. Other molecular studies have united nongilled and gasteroid representative in various clades with gilled relatives (Binder et al 1997, Hallen et al 2003, Matheny and Bougher 2006, Peintner et al 2001). In some instances the priority of popular

family and generic level names has been contested (Norvell 2001; Redhead et al 2001a, 2001b). Some classification systems (Kirk et al 2001) began to incorporate findings of early research, but adjustments are necessary because more groups have been studied in detail and more molecules sequenced.

Here we present an analysis of 1090 DNA sequences for 146 genera and 238 species of euagarics and assemble them in a supermatrix of 5611 characters from six gene regions, *rpb1*, *rpb1*-intron2, *rpb2*, 18S, 25S and 5.8S rRNA, in an effort to assess the phylogeny of the Agaricales. We want to know (i) whether the phylogeny of the Agaricales can be resolved by analysis of multiple gene data, (ii) whether inclusive clades of Agaricales can be identified and what characters diagnose them, (iii) whether traditional family and ordinal level groupings are supported and (iv) whether insights can be gained into the evolution of the ectomycorrhizal (EM) habit, an important ecological trait of the mushroom-forming fungi.

MATERIALS AND METHODS

Taxon sampling, DNA isolation, PCR, sequencing and dataset assembly.—Ninety-four out of 192 genera (49%) of the Agaricineae *sensu* Singer (1986) are represented in this study (SUPPLEMENTARY TABLE I). However Singer's Agaricineae excludes numerous nongilled genera of the euagarics clade. Many resupinate and sequestrate taxa now are known to have evolved among the euagarics (Binder et al 2005, Hibbett et al 1997, Larsson et al 2004), so the number of genera (347) estimated by Kirk et al (2001) is a more reasonable figure at the moment. In this context our datasets are represented by 146 (42%) genera of euagaric fungi.

Standard protocols and published primers were used for extraction of DNA, PCR, sequencing and annotation of sequence chromatograms (Frøslev et al 2005, Matheny 2005, Matheny et al 2002, White et al 1990). Two hundred seventy-four taxa and their GenBank accession numbers are provided (SUPPLEMENTARY TABLE I). In total 1090 sequences were analyzed (284 25S, 274 18S, 266 5.8S, 136 *rpb2*, 130 *rpb1* and 129 *rpb1*-intron 2) with the vast majority (76%) generated as new. The bulk of the remaining 24% of sequences was presented previously in Aime and Phillips-Mora (2005), Binder et al (2005, 2006), Binder and Hibbett (2002), Matheny (2005) and Moncalvo et al (2000, 2002). Separate gene regions were aligned initially with Clustal X (Thompson et al 1997). Subsequent new sequences were aligned manually in MacClade 4.0 (Maddison and Maddison 2000). Separate partitions of each gene region were introduced into one nexus file via the PAUP* data editor (Swofford 2003) and put together in interleaved format for phylogenetic analysis. Taxa for which gene regions were not sequenced were coded as missing. Simulation studies show that the addition of taxa, despite large amounts of missing

data, can benefit phylogenetic reconstructions (Wiens 2006).

Phylogenetic analyses.—Three datasets were analyzed: (I) a nrDNA-only matrix of 274 taxa, (II) a six-gene region supermatrix of 250 taxa and (III) a six-gene region supermatrix of 175 taxa. Alignments are available from the lead author on request. For dataset III, 75 taxa with nrDNA regions only were excluded to ascertain any sensitivity to missing data. All datasets were analyzed with parallel and single-processor versions of MrBayes 3.1.1 (Altekar et al 2004, Ronquist and Huelsenbeck 2003). The parallel version operated on a Linux cluster with AMD Opteron 246 processors. We executed independent runs starting the analyses with random trees and sampling every 100 or 1000 generations, depending on the length of the analysis, and using six chains. Analyses were run 2 000 000–10 000 000 generations under a general-time-reversible (GTR) model plus a proportion of invariable sites and gamma distributed substitution rate heterogeneity parameters. Gene regions of dataset II also were partitioned by rRNA region, *rpb1*-intron 2 and codon position, allowing a GTR model and rate heterogeneity parameters to be optimized separately for 10 partitions.

A total of 1000 MP bootstrap replicates was performed with the subtree-pruning-regrafting (SPR) branch-swapping algorithm with the MULTREES option off. Five to 10 random additions of taxa were done holding one tree per step during stepwise addition. One tree was saved per bootstrap replicate. These parameters have been shown to reduce computational expense without a reduction in performance for large datasets (DeBry and Olmstead 2000, Salamin et al 2003). MP results refer to the MP bootstrap 50% majority rule consensus tree, plus other groups compatible with this tree.

Six-gene region dataset.—Analysis of nuclear rRNA gene sequences in dataset I (SUPPLEMENTARY FIG. 2) supported use of the Atheliales and Boletales as outgroups for a subsequent analysis of dataset II with a focus on relationships in the Agaricales. These taxa from the initial analysis were confirmed outside the Agaricales: *Epithele typhae* (Polyporales), *Waitea circinata* ("Corticiales") and *Clavaria purpurea*, *Cyphellostereum leave* and *Rickenella fibula* (Hymenochaetales). The generic composition of six clades of Agaricales plus a polyphyletic assortment of hygrophoroid taxa are summarized (SUPPLEMENTARY FIG. 2).

Taxon sampling of dataset I was reduced to 253 taxa in dataset II. Three taxa, *Pachylepyrium carbonicola*, *Volvariella volvacea* and *Rhodocybe aureicystidiata*, subsequently were omitted after initial analyses of dataset II. Thus a final total of 250 taxa were analyzed. Seventy-four euagaric taxa were maintained in dataset II despite representation by nrDNA regions only to maximize taxonomic coverage. This matrix was supplemented with 130 *rpb1* and 136 *rpb2* exon sequences between conserved domains A–C and 5–7, respectively. The conserved intron region of *rpb1*-intron 2 (Matheny et al 2002) also was included as a sixth gene region for 129 taxa. *Fibulorhizoctonia* sp. (Atheliales) was chosen to root the analyses.

Scoring of ectomycorrhizal character state.—Two hundred fifty taxa were scored for the presence or absence of an ectomycorrhizal (EM) state in MacClade 4.0 (Maddison and Maddison 2000). No attempt was made to distinguish between facultative versus obligatory formations. De Román, Claveria and De Miguel (2005) and Singer (1986) were used as primary references for character coding. In addition Bougher and Malajczuk (1985) and Norvell (1998) were referenced to score the EM status of *Descolea* and *Phaeocollybia*, respectively. Character states were mapped under parsimony on the Bayesian trees with the highest likelihood score produced from analyses of dataset II (uniform model and partitioned models) and charted in MacClade. The states of four taxa, *Neohygrophorus angelesianus*, *Clitocybe subvelosa*, *Lyophyllum* sp., *Cantharocybe gruberi* and *Boletinellus meruloides*, were coded ambiguously due to uncertainty over their EM status.

RESULTS AND DISCUSSION

Six major clades of Agaricales.—These clades are recovered in the combined Bayesian analysis of protein-coding and rRNA gene sequence data (FIG. 1). Representatives from each of the major clades are depicted (FIG. 2). After exclusion of introns and ambiguously aligned regions 5611 sites were included, of which 2108 were parsimony informative. A 50% majority rule consensus cladogram was produced from a stationary set of 6662 trees that had been estimated from a single model and sampled every 1000 generations from a run of 10 000 000 generations. In every analysis trees sampled from independent runs (<10 000 000 generations) failed to converge on a similar set of likelihood scores (the average standard deviation of split frequencies was more than 0.01). Future analyses of multilocus datasets of Agaricales with large numbers of taxa should consider running Bayesian analyses longer than 10 000 000 generations, fine-tune MCMC heating parameters or consider employing a user-specified starting tree. Despite this analytical challenge, runs from each analysis produced consistent results that are enumerated below. Attention is drawn to major inconsistencies where they occur.

Six major clades, 30 families, four tribes and two informally named clades are labeled (FIG. 1) and cross-referenced (SUPPLEMENTARY TABLE II) to traditional and phylogenetic classifications of Kirk et al (2001), Kühner (1980), Moncalvo et al (2002) and Singer (1986). The names of families and tribes applied in this study are intended to be provisional. A subordinal level classification might be suitable within the Agaricales, as in the Boletales (Binder and Bresinsky 2002), but at the moment we opt for an informal clade-based classification because three of the major clades (Plicaturopsidoid, Pluteoid and

Marasmioid) failed to receive consistent significant support. Two genera (FIG. 1) are unresolved with respect to these major lineages: *Infundibulicybe* and *Macrocystidia*. The former is the sister group of the Tricholomatoid clade, the latter lies in the Pluteoid clade based on the tree with the best likelihood score from the partitioned analysis of dataset II.

Plicaturopsidoid clade (I).—*early-diverging members of the Agaricales.* Bayesian analyses consistently recover this small cluster of six taxa with diverse fruit body morphology, including gilled, club, coralloid, pileate-stipitate and resupinate forms. The monophyly of the group receives significant support in Bayesian analysis of dataset III, which included all six representatives. All Bayesian analyses place the clade sister of the remaining Agaricales. Two supported subgroups are recovered. One (labeled the Atheliaceae *p. p.*) includes *Podoserpula* (the pagoda fungus), *Plicaturopsis* and *Sclerotium (Athelia) rolfsii*. *Podoserpula* has a club-like form but with interdigitated *Plicaturopsis*-like pileoli and a merulioid hymenial surface similar to *Plicaturopsis*. Donk (1964) considered *Podoserpula* allied to genera such as *Serpula* and *Coniophora* in the Coniophoraceae, taxa now shown to represent early diverging lineages in the Boletales (Binder and Bresinsky 2002). *Sclerotium rolfsii* is a resupinate anamorph of *Athelia rolfsii* and an important plant pathogen (Okabe and Matsumoto 2003). The second group includes a gilled member of the Hygrophoraceae, *Camarophylloopsis hymenocephala*, and club and coralloid elements of the Clavariaceae, which were shown to be related to the Agaricales in Pine et al (1999). The nuclear status of spores in the Clavariaceae is not known, but *Camarophylloopsis* (= *Hygrotrama*) (Arnolds 1986) has multinucleate spores, which is inferred as a derived condition (Kühner 1980). In the MP bootstrap tree the Clavariaceae is drawn into the Hygrophoroid clade but with weak support.

The ecologies of other members of the Plicaturopsidoid clade are obscure for the most part, yet no EM taxa are currently known. The group includes presumably mostly saprotrophic elements. *Podoserpula* is probably a saprotroph occurring on or near old rotting stumps (Bougher and Syme 1998).

Pluteoid clade (II).—The Pluteoid clade appears to include four agaric or gasteromycete families: the Pluteaceae, Amanitaceae, Pleurotaceae and Limnoperdonaceae, plus several orphan gilled genera. This grouping is poorly supported, and not all constituents are consistently resolved together. Analyses of datasets I and III place the Pleurotaceae and *Tricholomopsis* outside the Pluteoid clade. Nonetheless previous studies of rDNA placed the minute uniloculate

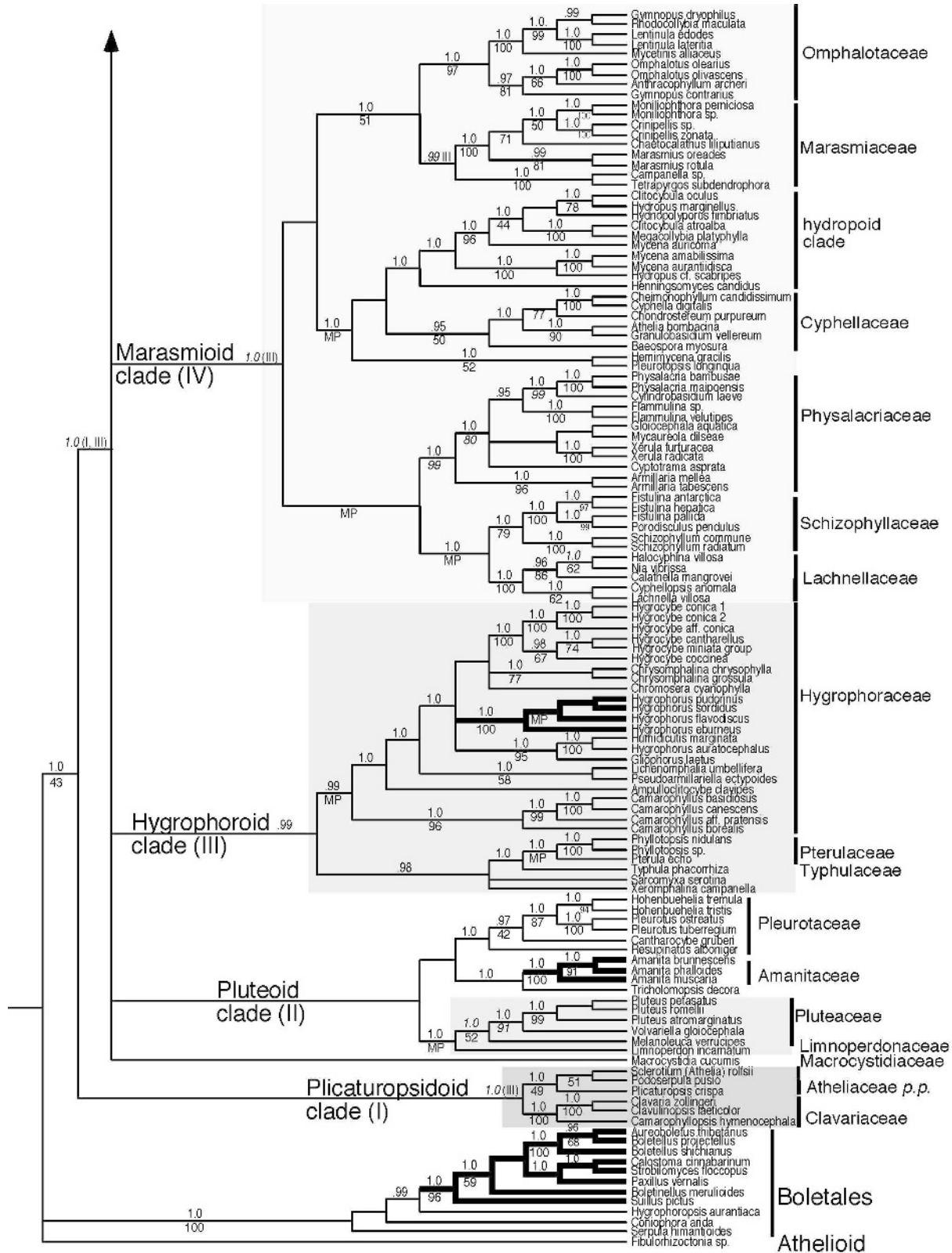


FIG. 1. Fifty percent majority-rule Bayesian cladogram of the Agaricales, six major clades and outgroups produced from combined *rpb1*, *rpb1*-intron2, *rpb2*, 18S, 25S and 5.8S nucleotide sequences for a supermatrix of 250 taxa (dataset II). Posterior probabilities ≥ 0.95 are indicated above branches. MP bootstrap values $\geq 40\%$ are shown below branches. Italicized support values are derived from analyses of datasets I and III and are indicated as such. MP refers to a branch that is present in

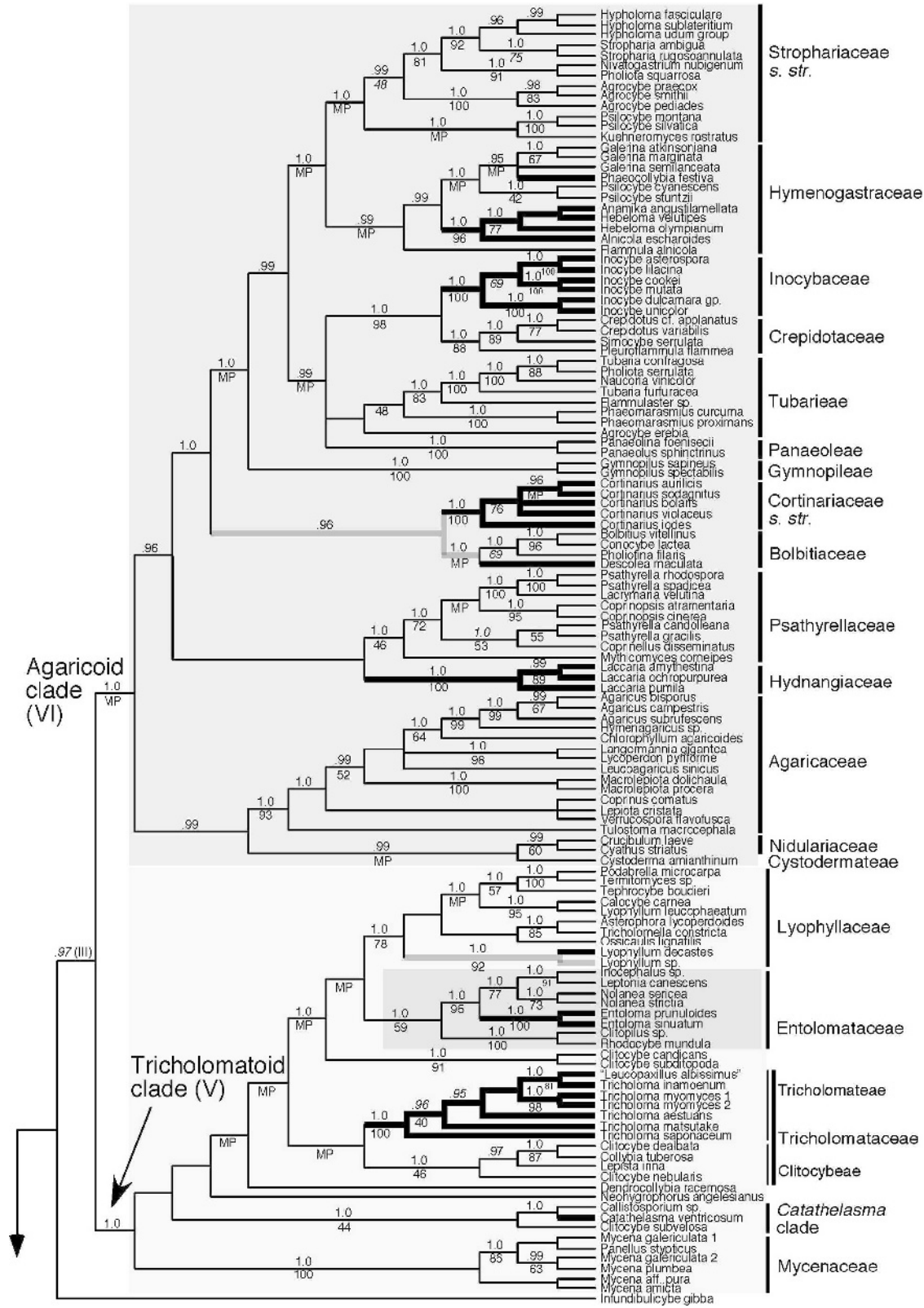


FIG. 1. Continued.

combined MP bootstrap consensus tree of dataset II, plus other groups compatible with that tree but with less than 40% bootstrap support. Thickened black branches refer to taxa with an EM habit; thickened gray branches represent an equivocal state; thin black branches represent the non-EM state.



FIG. 2. Representatives of the Agaricales. a. *Plicaturopsis crispa*. b. *Podoserpula pusio* (photo by Heino Lepp). c. *Pterula echo* (photo by Dave McLaughlin). d. *Camarophyllus borealis*. e. *Ampulloclitocybe clavipes*. f. *Resupinatus applicatus*. g. *Mycena* aff. *pura*. h. *Crucibulum laeve* (photo by Mark Steinmetz courtesy Mykoweb). i. *Nolanea* sp. j. *Volvariella gloiocephala*. k. *Crepidotus fimbriatus*. l. Basidiospores with germ pore of *Psilocybe squamosa* (photo by Roy Halling). m. *Camarophyllopsis hymenocéphala*.

gasteromycete, *Limnoperdon*, near the gilled genus *Melanoleuca* (Binder et al 2006, Bodensteiner et al 2004), while others placed *Melanoleuca* and *Pluteus* sister of Amanitaceae (Moncalvo et al 2000, 2002). Thus it is not surprising to see these taxa as part of a larger monophyletic group in analyses of more extensive character sampling (FIG. 1).

From an anatomical perspective many taxa of the Pluteoid clade exhibit conspicuous hymenial cystidia (*Pluteus*, *Volvariella*, *Hohenbuehelia*, *Cantharocybe*, *Tricholomopsis* and *Melanoleuca*) and others share salmon pink to reddish brown spores with complex spore walls (Pluteaceae and Limnoperdonaceae). Taxa with multinucleate spores are found in the Pluteaceae and Amanitaceae, but uninucleate spores appear to characterize the Pleurotaceae, *Tricholomopsis* and some Pluteaceae (Duncan and Galbraith 1972, Kühner 1980, Mueller and Ammirati 1993). Most taxa are decomposers except for the EM lineage *Amanita* and its sequestrate relatives. *Pleurotus* and *Hohenbuehelia* are characterized in part by their ability to attack and consume nematodes (Thorn et al 2000). Kühner (1980, 1984) predicted a close relationship between the Macrocystidiaceae and Pluteaceae based on similar spore characters (smooth complex spore wall, pigmentation and cyanophily) but distinguished the former by the noninverse lamellar trama. Kühner's prediction is supported by analysis of rRNA data alone (SUPPLEMENTARY FIG. 2) but unresolved by the combined analysis (FIG. 1). Only rRNA data are available for *Macrocystidia*. Future studies should address the monophyly of *Melanoleuca* and *Volvariella*.

Hygrophoroid clade (III).—Bayesian analysis of dataset II significantly supports this inclusive clade characterized by most members of the Hygrophoraceae (excluding *Neohygrophorus* and *Camarophylloopsis*) and several genera of the Tricholomataceae (Singer 1986) and Tricholomatales (Kühner 1980). Contrary to prior morphological-based classifications, club and coralloid fungi of the Pterulaceae and Typhulaceae are related to the Agaricales and nested in the Hygrophoroid clade. Most members of the Hygrophoroid clade exhibit slenderly clavate basidia and uninucleate spores, but some species of *Hygrocybe* and *Hygrophorus* possess multinucleate spores (Kühner 1977, 1980). The position of the Hygrophoroid clade (FIG. 1) is poorly resolved; however multilocus analyses of rRNA genes (Binder and Hibbett 2002) indicated a strongly supported position for the

Hygrophoraceae (two exemplars) as the group sister of 12 other Agaricales. The Plicaturopsidoid clade was not sampled in that study.

The Hygrophoraceae is monophyletic provided several genera of the Tricholomataceae are admitted and *Camarophylloopsis* and *Neohygrophorus* excluded. *Camarophylloopsis* (= *Hygrotrama*) has a hymeniform pileipellis, multinucleate spores and nonelongated basidia (Kühner 1980), while *Neohygrophorus* has amyloid spores and a unique reaction to weak potassium hydroxide solution (Hesler and Smith 1963, Redhead et al 2000), traits that are rare or absent in the Hygrophoraceae. Both *Chromosera* and *Chrysomphalina* are allied to a narrowly defined *Hygrocybe*. Both *Pseudoarmillariella* and *Chrysomphalina* exhibit thickened hymenia (Norvell, Redhead and Ammirati 1994), a trait similar to other Hygrophoraceae.

Ampulloclitocybe clavipes, formerly *Clitocybe clavipes* (Harmaja 2002 [syn. *Clavicybe*], Redhead et al 2002b) has unambiguous affinities with hygrophoroid taxa rather than with other clitocyboid species in the Tricholomatoid clade. Monophyletic groups of hygrophoroid taxa appear to correspond best to narrow generic concepts employed by Singer (1986) rather than the various broad concepts used by Hesler and Smith (1963), Kühner (1980), Arnolds (1990) and Boertmann (1996). For instance *Hygrocybe s. str.*, *Hygrophorus s. str.* and *Camarophyllus* all are supported as autonomous monophyletic groups.

The majority of Hygrophoraceae is saprotrophic. Many *Hygrocybe s. lat.* species are important indicators of habitat quality and are sensitive to application of fertilizers (Boertmann 1996). These species can be so prolific in grassland environments that Arnolds (1980) refers to such settings as “waxcap grasslands”. However other ecological traits are found in the family, such as the lichenized lineage *Lichenomphalia* (Oberwinkler 1984, Redhead et al 2002b) and the EM lineage *Hygrophorus s. str.* (Hesler and Smith 1963, Singer 1986, Horak 1990).

A second inclusive monophyletic group in the Hygrophoroid clade includes the families Pterulaceae and Typhulaceae, plus at least three gilled genera of the Tricholomataceae, *Phyllotopsis*, *Sarcomyxa* and *Xeromphalina*. This cluster of taxa receives significant support, but *Xeromphalina* is placed with weak support as the sister group of the Mycenaceae in the MP bootstrap tree. Nonetheless most agarics in this group are saprotrophic although several species of *Typhula* are grass pathogens (Hsiang and Wu 2000).

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(photo by D. Jean Lodge). n. inverse lamellar trama and pleurocystidia of *Pluteus* (photo from D.E. Stuntz slide teaching collection). o. *Clitocybe subditopoda*. p. *Cortinarius bolaris*. q. *Cylindrobasidium evolvens*. r. *Tricholoma columbetta*.

Fungal cultivars of the ant *Apterostigma pilosum* have been identified as relatives of *Pterula* and *Deflexula* (Munkacsi et al 2004). The approximately 200 species known in the Typhulaceae and Pterulaceae (Kirk et al 2001) warrant much more phylogenetic scrutiny.

Marasmioid clade (IV).—The Marasmioid clade is a taxonomically diverse group dominated by white-spored saprotrophic gilled fungi but also includes cyphelloid, resupinate and club-like forms. Almost one-third of the genera (43% or 30%) sampled in this study are concentrated in this clade. The Marasmioid clade is not strongly supported based on analyses of dataset II, but 39 taxa cluster together with a significant posterior probability (PP) in analysis of dataset III when 75 taxa with missing protein-coding data are excluded. Seven families and clades are recovered as monophyletic: the Omphalotaceae, Marasmiaceae, the hydropoid clade, Cyphellaceae, Physalacriaceae, Lachnellaceae (the *Nia* clade) and Schizophyllaceae. All receive significant support values. These families are consistently recovered together across Bayesian analyses with the exception of the Schizophyllaceae. Two genera, *Hemimycena* and *Pleurotopsis*, might represent a seventh lineage. Elements within the Marasmioid clade have been the target of much recent phylogenetic activity (Bodensteiner et al 2004, Mata et al 2004, Aime and Phillips-Mora 2005, Wilson and Desjardin 2005, Binder et al 2006).

The vast majority of species decomposes wood or leaf litter. Some are primary colonizers of these substrates. Several are pathogens of green plants or algae (e.g. *Armillaria*, *Moniliophthora*, *Mycaureola*), and *Schizophyllum commune* can act as an infectious agent of humans (Rihs et al 1996, Sigler et al 1999). The EM habit appears not to have evolved in this group, although mycorrhizal formation has been attributed to *Rhodocollybia butyracea* (see De Román et al 2005) and *Armillaria*, in which endomycorrhizae are formed with orchids (Singer 1986).

Tricholomatoid clade (V).—The Tricholomatoid clade includes four families, the Tricholomataceae *s. str.*, Lyophyllaceae, Entolomataceae and Mycenaceae, plus the *Catathelasma* clade. The union of these five clades receives significant Bayesian support. Circumscription of the Tricholomataceae has been controversial and difficult to define based on gross morphological characters and 25S rRNA data (Smith et al 1979, Thorn et al 2000, Kirk et al 2001). The results (FIG. 1) suggest more narrow limits for the family. The Tricholomataceae *s. str.* appears to be composed of two monophyletic tribes, the Tricholomateae and Clitocybeae. Because *C. nebularis* appears widely accepted as lectotype of *Clitocybe* (e.g. Harmaja 2003, Kuyper 1995, Redhead et al 2002a), we accept

the clade composed of at least *Clitocybe s. str.*, *Collybia* and *Lepista* as the tribe Clitocybeae Fayod. The Entolomataceae is recovered as monophyletic. The unique spore form and pinkish spore deposit led early investigators to accept the Entolomataceae as a monophyletic entity (Pegler and Young 1979, Singer 1986), yet molecular studies using 25S rRNA data alone have not supported the monophyly of the family (Moncalvo et al 2000, 2002). Species that exhibit siderophilous granulated basidia (Cléménçon 1978, 2004) are restricted to the Tricholomatoid clade, which could be a synapomorphy for an inclusive Lyophyllaceae (Jülich 1981, Hofstetter et al 2002) plus Entolomataceae grouping. The genus *Mycena* is polyphyletic, as indicated in Moncalvo et al (2002), and represented by three separate lineages, the Mycenaceae *s. str.*, typified by *M. galericulata* (Redhead 1985), and at least two separate lines in the Marasmioid clade. Although data (FIG. 1) indicate the basal position of the Mycenaceae in the Tricholomatoid clade, other Bayesian analyses place it basal to the Marasmioid clade. The *Catathelasma* clade is poorly known but significantly supported. At present it includes the partial-veiled *Clitocybe subvelosa*, endemic to western North America (Smith and Stuntz 1950, Bigelow 1985), the EM genus *Catathelasma* and *Callistosporium*, a genus of decomposers. Analysis of only rRNA data place *Callistosporium* in the Entolomataceae. The genera *Dendrocollybia* and *Neohygrophorus* cannot be aligned with any existing family in the Tricholomatoid clade.

The ecologies of lineages in the Tricholomatoid clade are diverse. The group includes mycoparasites in the genera *Collybia*, *Dendrocollybia*, *Asterophora*, *Lyophyllum s. lat.*, and in the Entolomataceae (Vizzini and Girlanda 1997, Czederpiltz et al 2001, Hughes et al 2001, Hofstetter et al 2002). Some groups have unique nitrogen requirements, such as the ability to reduce nitrate (e.g. *Clitocybe nebularis*) or are associated with high concentrations of urea (e.g. *Nolanea*) (Bresinsky and Schneider 1975, Harmaja 1978, Largent 1994). Others (*Ossicaulis*, *Hypsizygus*) produce brown rot (Redhead and Ginns 1985) or are involved in bryophyte parasitism (*Lyophyllum s. lat.*) (Redhead 1981) or termite associations (*Termitomyces*) (Aanen et al 2002, Rouland-Lefevre et al 2002). Mycorrhizal formation by species of *Entoloma s. str.* also has been reported (Kobayashi et al 2005). Several species exhibit associations with rosaceous plants (Kobayashi et al 2003).

The Tricholomatoid clade appears sister of an inclusive group of mostly dark-spored taxa, the Agaricoid clade (see below). Analysis III produces a significant PP (0.97) for the union of these two inclusive clades. Of the 11 EM origins (FIG. 1) nine

are concentrated in the Tricholomatoid + Agaricoid clade alone. Gross morphologies in both groups are dominated by gilled pileate-stipitate forms but also include secotioid or truffle-like forms (sequestrate).

Agaricoid clade (VI).—Fourteen families and tribes of primarily dark-spored agarics and gasteromycetes cluster together in the Agaricoid clade with significant support from Bayesian analyses (FIG. 1). The same group also is resolved in the MP bootstrap tree but with poor support. The Agaricoid clade includes the Cystodermateae, Nidulariaceae, Agaricaceae, Hydnangiaceae, Psathyrellaceae, Bolbitiaceae, Cortinariaceae *s. str.*, Gymnopileae, Panaeoleae, Tubariaeae, Crepidotaceae, Inocybaceae, Strophariaceae *s. str.* and the Hymenogastraceae. The current configuration of lineages of the Cortinariaceae and Strophariaceae *sensu* Singer (1986) warrants the recognition of smaller monophyletic groups. Indeed Bayesian analyses of datasets II and III significantly support the sister relationship between *Cortinarius* and the Bolbitiaceae, a separate cluster of Inocybaceae and Crepidotaceae and the union of Hymenogastraceae and Strophariaceae *s. str.* Although not illustrated in our trees, the type of *Hymenogaster* (*H. builiiardii*) is nested within the Hymenogastraceae clade (Peintner et al 2001). A recent 25S rRNA only analysis suggested a rather inclusive treatment of the Strophariaceae (Gulden et al 2005).

Most members of the Agaricoid clade are characterized by pigmented, multinucleate basidiospores and an open-pore type of hilum (Pegler and Young 1969; Kühner 1980, 1984). The clade is essentially that of Kühner's narrow concept of the Agaricales but unequivocally includes the Hydnangiaceae (multinucleate, white-spored *Laccaria* and sequestrate allies), the gasteromycete groups, Nidulariaceae and Lycoperdales, and several other sequestrate forms (Krüger et al 2001, Peintner et al 2001). No links to resupinate taxa have been established, but a few cyphelloid lineages are included (*viz.* *Pellidiscus* [Crepidotaceae] and *Phaeosolenia*) (Bodensteiner et al 2004). Many taxa in the Agaricoid clade possess basidiospores with an apical germ pore (e.g. most Psathyrellaceae, many Agaricaceae, Panaeoleae, many Bolbitiaceae), but the phylogenetic distribution of these taxa is diffuse. A germ pore is not present among taxa in the other major clades of the Agaricales. In addition no members of the clade exhibit amyloid spores with the exception of some species of *Cystoderma*. Hallucinogenic compounds, namely psilocybin, can be found in several lineages of the Agaricoid clade—*Conocybe*, *Copelandia*, *Gymnopilus*, *Inocybe s. str.*, *Panaeolina*, *Panaeolus* (Benjamin 1995).

As many as six EM origins are inferred in the

Agaricoid clade and include the Hydnangiaceae, Cortinariaceae *s. str.*, Inocybaceae, the genera *Descolea* and *Phaeocollybia* and elements of the Hymenogastraceae. The remaining taxa are primarily saprotrophic (Vellinga 2004, Watling and Gregory 1987) but include some lineages in the Agaricaceae that are symbiotic with ants (Chapela et al 1994, Mueller et al 1998).

Independent origins of the ectomycorrhizal (EM) habit in the Agaricales.—At least 5000 species of Basidiomycota and some Ascomycota form a predominantly EM symbiosis with land plants (Malloch et al 1980). Hacskeylo (1971), Malloch (1987) and Bruns and Shefferson (2004) hypothesize the symbiosis evolved repeatedly. Others (*viz.* Hibbett et al 2000) also suggest independent origins have occurred but that subsequent losses (reversals) took place in some lineages. A third hypothesis (Weiss et al 2004) entails the ancient shared ancestry of the state followed by numerous losses. A parsimony reconstruction of evolution of the EM habit in the Agaricales suggests a minimum of 11 origins of the EM state with no unambiguous reversals (FIG. 1). Indeed all but two of the EM origins are concentrated in the Tricholomatoid/Agaricoid clade. These two separate origins occurred in *Hygrophorus s. str.* and in the Amanitaceae.

Maintenance of the EM state appears stable in diverse and species-rich EM lineages of Agaricales. For example *Amanita* (est. 500 spp.), *Cortinarius* (est. 2000 spp.), *Hebeloma* and allies (est. 280 spp.), Hydnangiaceae (est. 30 spp.), *Hygrophorus s. str.* (est. 100 spp.), Inocybaceae (est. 500 spp.), *Phaeocollybia* (est. 80 spp.) and *Tricholoma* (est. 200 spp.) represent species-rich lineages in which the EM state is maintained. The mechanisms of this stability are unexplored, but it seems that reversals to saprotrophy or biotrophy are constrained in these groups. However we caution that these results could be sensitive to outgroup choice, method of ancestral state reconstruction, character coding definition, incomplete knowledge of the life histories of many Agaricales and/or taxon sampling (Hibbett et al 2000, Hibbett and Binder 2002, Bruns and Shefferson 2004, Hibbett 2004).

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SUPPLEMENTARY TABLE I. Species sampled and GenBank accession numbers used in this study. An asterisk next to an accession number indicates the sequence has been extended from its original length

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Agaricus</i> aff. <i>campestris</i>	DQ110871	DQ113914	DQ486682	—	DQ516068
<i>Agaricus bisporus</i>	AY635775	AY787216	DQ404388	AF107785	—
<i>Agaricus subrufescens</i> ^a	AJ244523	AJ012405	AJ133375	—	—
<i>Agrocybe erebia</i>	DQ457663	DQ440631	DQ484056	DQ472712	—
<i>Agrocybe pediades</i>	DQ110872	DQ113915	DQ484057	—	—
<i>Agrocybe praecox</i>	AY646101	AY705956	AY818348	DQ385876	DQ516069
<i>Agrocybe smithii</i>	DQ110873	DQ115779	DQ484058	—	—
<i>Alnicola escharoides</i>	AY380405	—	AJ585430	AY337411	AY351840 AY351841
<i>Amanita brunnnescens</i>	AY631902	AY707096	AY789079	AY780936	AY788847
<i>Amanita muscaria</i>	AF042643	AF026631	AB080787	AY218468	—
<i>Amanita phalloides</i>	AY380359	—	—	AY485609	AY485639
<i>Ampulloclitocybe clavipes</i>	AY639881	AY771612	AY789080	AY780937	AY788848
<i>Anamika angustilamellata</i>	AY575919	DQ092918	AY575919	—	—
<i>Anthracophyllum archeri</i>	AY745709	DQ092915	DQ404387	DQ385877	DQ435799
<i>Antrodia</i> sp.	DQ457649	DQ115778	DQ484059	—	—
<i>Armillaria mellea</i>	AY700194	AY787217	AY789081	AY780938	AY788849
<i>Armillaria tabescens</i>	AF042593*	DQ851572	AY213590	—	—
<i>Asterophora lycoperdoides</i>	AF223190	DQ367417	AF357037	DQ367431	DQ367424
<i>Athelia bombacina</i>	AF279377	M55638	DQ449026	AY641027	—
<i>Athelia rolfsii</i>			DQ484060 DQ484061 DQ484062	—	—
	AY635773	AY665774	DQ484062		
<i>Aureoboletus thibetanus</i>	AY700189	AY654882	DQ200917	DQ366279	DQ435800
<i>Baeospora myosura</i>	DQ457648	DQ435796	DQ484063	DQ470827	DQ435801
<i>Bolbitius vitellinus</i>	AY691807	AY705955	DQ200920	DQ385878	DQ435802
<i>Boletellus projectellus</i>	AY684158	AY662660	AY789082	AY787218	AY788850
<i>Boletellus shichianus</i>	AY647211	AY657011	DQ200921	DQ366280	—
<i>Boletinellus merulioides</i>	AY684153	AY662668	DQ200922	DQ366281	DQ435803
<i>Boletopsis leucomelaena</i>	DQ154112	DQ435797	DQ484064	—	—
<i>Bondarzewia montana</i>	DQ234539	U59063	DQ200923	—	—
<i>Calathella mangrovei</i>	AF426954	AF426948	AY571029	—	—
<i>Callistosporium</i> sp.	AY745702	AY752974	DQ484065	DQ825406	DQ825413
<i>Calocybe carnea</i>	AF223178	DQ367418	AF357028	DQ367432	DQ825423
<i>Calostoma cinnabarinum</i>	AY645054	AY665773	AY854064	AY780939	AY857979
<i>Camarophylloopsis hymenoccephala</i>	DQ457679	DQ444862	DQ484066	DQ472726	DQ516070
<i>Camarophyllus</i> aff. <i>pratensis</i>	DQ457650	DQ435798	DQ486683	—	DQ435804
<i>Camarophyllus basidiosus</i>	DQ457651	DQ435809	DQ486684	DQ470828	DQ435805
<i>Camarophyllus borealis</i>			DQ218307 DQ218308 DQ218309		
	AY70021	AY665782	DQ218309	—	DQ435806
<i>Camarophyllus canescens</i>	DQ457652	DQ435810	DQ486685	DQ470829	DQ435807
<i>Campanella</i> sp.	AY916668	AY916669	AY916670	—	AY916671
<i>Cantharocybe gruberi</i>		DQ234546	DQ234547		
	DQ234540	DQ234547	DQ200927	DQ385879	DQ435808
<i>Catathelasma ventricosum</i>	DQ089012	DQ435811	DQ486686	DQ470830	—
<i>Chaetocalathus liliputianus</i>	AY916680	AY916681	AY916682	—	AY916683
<i>Cheimonophyllum candidissimum</i>	DQ457654	DQ435812	DQ486687	DQ470831	DQ447888
<i>Chlorophyllum agaricoides</i>	AY700187	AY657010	DQ200928	—	DQ447889
<i>Chondrostereum purpureum</i>	AF518607	AF082851	DQ200929	AY218477	—
<i>Chromosera cyanophylla</i>	DQ457655	DQ435813	DQ486688	—	—
<i>Chrysomphalina chrysophylla</i>	DQ457656	DQ435814	DQ192180	—	DQ516071
<i>Chrysomphalina grossula</i>	U66444	AY752969	DQ486689	DQ470832	DQ516072
<i>Clavaria purpurea</i>	DQ457657	DQ437679	DQ486690	—	—
<i>Clavaria zollingeri</i>	AY639882	AY657008	AY854071	AY780940	AY857987

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Clavulinopsis laeticolor</i>	AY745693	DQ437680	DQ202267	DQ385880	DQ447890
<i>Clitocybe candicans</i>	AY645055	AY771609	DQ202268	DQ385881	DQ447891
<i>Clitocybe dealbata</i>	AF223175	DQ825431	AF357061	DQ825407	DQ825414
<i>Clitocybe nebularis</i>	DQ457658	DQ437681	DQ486691	DQ470833	DQ825415
<i>Clitocybe subditopoda</i>	AY691889	AY771608	DQ202269	AY780942	DQ447892
<i>Clitocybe subvelosa</i>	AY647208	DQ092913	DQ486692	—	—
<i>Clitocybula atroalba</i>	DQ457659	DQ437682	DQ192179	—	—
<i>Clitocybula oculus</i>	DQ151452	DQ440636	DQ192178	—	—
<i>Clitopilus</i> sp.	AY700181	AY771607	DQ202272	DQ825408	DQ825416
<i>Collybia tuberosa</i>	AY639884	AY771606	AY854072	AY787219	AY857982
<i>Coniophora arida</i>	AF098375	AY293123	DQ202271	DQ366282	—
<i>Conocybe lactea</i>	DQ457660	DQ437683	DQ486693	DQ470834	DQ447893
<i>Coprinellus disseminatus</i>	AF056456	—	AY461838	DQ056143	—
<i>Coprinopsis atramentaria</i>	DQ457661	DQ115781	DQ486694	—	—
<i>Coprinopsis cinerea</i>	AF041494	Genome ^b	AF345819	Genome ^b	Genome ^b
<i>Coprinus comatus</i>	AY635772	AY665772	AY854066	AY780934	AY857983
<i>Cortinarius aurilicis</i>	AY684152	AY705957	DQ083772	DQ083880	DQ083826
<i>Cortinarius bolaris</i>	AY293173	AY293125	AF389169	—	—
<i>Cortinarius iodes</i>	AY702013	AY771605	AF389133	AY536285	AY857984
<i>Cortinarius sodagnitus</i>	AY684151	AY752975	DQ083812	DQ083920	DQ083867
<i>Cortinarius violaceus</i>	DQ457662	AY705950	DQ486695	DQ470835	DQ447894
<i>Cotylidia</i> sp.	AY629317	AY705958	AY854079	—	—
<i>Crepidotus</i> cf. <i>applanatus</i>	AY380406	AY705951	DQ202273	AY333311*	AY333303
<i>Crepidotus variabilis</i>	AY293174	AY293126	—	—	—
<i>Crinipellis</i> sp.	AY916699	AY916700	AY916701	—	AY916702
<i>Crinipellis zonata</i>	AY916690	AY916691	AY916692	—	AY916693
<i>Crucibulum laeve</i>	AF336246	AF026624	DQ486696	DQ470836	—
<i>Cyathus striatus</i>	AF336247	AF026617	DQ486697	DQ472711	DQ447895
<i>Cylindrobasidium laeve</i>	DQ234541	AF518576	DQ205682	AY536283	DQ447896
<i>Cyphella digitalis</i> ^c	AY635771	AF334917	DQ486698	—	—
<i>Cyphellopsis anomala</i>	AF426955	AF426949	AY571034	—	—
<i>Cyphellostereum laeve</i>	AY745705	AY752973	DQ486699	—	—
<i>Cyptotrama asprata</i>	AF261353	DQ440637	DQ097355	—	—
<i>Cystoderma amianthinum</i>	DQ154108	DQ440632	DQ192177	—	DQ516073
<i>Dendrocollybia racemosa</i>	AF042598	DQ825432	DQ825425	DQ825409	DQ825417
<i>Descolea maculata</i>	DQ457664	DQ440633	DQ192181	—	DQ447897
<i>Echinodontium tinctorium</i>	AF393056*	AF026578	AY854088	—	—
<i>Entoloma prunuloides</i>	AY700180	AY665784	DQ206983	DQ385883	DQ447898
<i>Entoloma sinuatum</i>	AY691891	AY657007	DQ486700	—	DQ516074
<i>Epithele typhae</i>	DQ457665	DQ440638	DQ486701	—	—
<i>Fibulorhizoctonia</i> sp.	AY635779	AY654887	AY854062	AY885161	AY857985
<i>Fistulina antarctica</i>	AY293181	AY293131	DQ486702	DQ472713	DQ447899
<i>Fistulina hepatica</i>	AY293182	AF026591	AY571038	—	—
<i>Fistulina pallida</i>	AY293183	AY293132	AY571039	—	—
<i>Flammula alnicola</i>	DQ457666	DQ113916	DQ486703	DQ472714	DQ447900
<i>Flammulaster</i> sp.	AY380408	—	—	AY333315	AY333308
<i>Flammulina</i> sp.	DQ457667	—	DQ486704	—	—
<i>Flammulina velutipes</i>	AY639883	AY665781	AY854073	AY786055	AY858966
<i>Galerina atkinsoniana</i>	DQ457668	DQ440634	DQ486705	—	—
<i>Galerina marginata</i>	DQ457669	DQ440635	DQ192182	—	DQ4478901
<i>Galerina semilanceata</i>	AY038309	DQ440639	DQ486706	AY337357	AF389531
<i>Ganoderma tsugae</i>	AY684163	AY705969	DQ206985	—	—
<i>Gliophorus laetus</i>	DQ154109	DQ440640	—	—	—
<i>Gloeophyllum sepiarium</i>	AF393059	AF026608	AY497555	—	—
<i>Gloiocephala aquatica</i>	DQ097343	AY705968	DQ097356	DQ472715	—

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Granulobasidium vellereum</i>	AY745729	DQ440641	DQ205683	—	—
<i>Gymnopilus sapineus</i>	AY380362	—	AF501560	AY337358	AY351789
<i>Gymnopilus spectabilis</i>	AY700186	DQ440642	DQ486707	—	—
<i>Gymnopus contrarius</i>	DQ457670	DQ440643	DQ486708	DQ472716	DQ447902
<i>Gymnopus dryophilus</i>	AY640619	AY665779	DQ241781	DQ472717	DQ447903
<i>Halocyphina villosa</i>	AF426957	AF426951	AY571042	—	—
<i>Hebeloma olympianum</i>	AY038310	—	—	AY337359	AF389532
<i>Hebeloma velutipes</i>	AY745703	AY752972	AY818351	DQ472718	DQ447904
<i>Hemimycena gracilis</i>	DQ457671	DQ440644	DQ490623	DQ472719	DQ447905
<i>Henningsomyces candidus</i>	AF287864	AF334916	AY571043	AY218513	AY860521
<i>Hericium americanum</i>	DQ411538	AY665778	DQ206987	—	—
<i>Heterobasidion annosum</i>	AF287866*	AF026576	DQ206988	—	—
<i>Hohenbuehelia tremula</i>	DQ156129	DQ440645	DQ182504	—	—
<i>Hohenbuehelia tristis</i>	AF042602*	DQ851573	—	—	—
<i>Humidicutus marginata</i>	AF042580	AF287833	DQ490625	—	—
<i>Hydnellum geogenium</i>	AY631900	AY752971	DQ218304	—	—
<i>Hydnochaete duportii</i>	AY635770	AY662669	DQ404386	—	—
<i>Hydnopolyporus fimbriatus</i>	DQ457673	DQ444854	DQ490626	DQ472721	DQ447907
<i>Hydropus</i> cf. <i>scabripes</i>	DQ411536	DQ444855	DQ404389	DQ457634	DQ447908
<i>Hydropus marginellus</i>	DQ457674	DQ444856	DQ490627	DQ472722	—
<i>Hygrocybe</i> aff. <i>conica</i>	AY684167	AY752965	AY854074	AY803747	AY860522
<i>Hygrocybe cantharellus</i>	DQ457675	DQ444857	DQ490628	—	DQ447909
<i>Hygrocybe coccinea</i>	DQ457676	DQ444858	DQ490629	DQ472723	DQ447910
<i>Hygrocybe conica</i> 1	AF261450	AF184198	—	—	—
<i>Hygrocybe conica</i> 2	AF261450	DQ851574	—	—	—
<i>Hygrocybe miniata</i> group	DQ457677	DQ444859	DQ490630	DQ472724	—
<i>Hygrophoropsis aurantiaca</i>	AY684156	AY662663	AY854067	AY786059	AY858961
<i>Hygrophorus auratocephala</i>	DQ457672	DQ440646	DQ490624	DQ472720	DQ447906
<i>Hygrophorus eburneus</i>	AF430279	AF184199	AY242855	—	—
<i>Hygrophorus flavodiscus</i>	AY635769	DQ444860	DQ249276	—	DQ447911
<i>Hygrophorus pudorinus</i>	DQ457678	DQ444861	DQ490631	DQ472725	DQ447912
<i>Hygrophorus sordidus</i>	AF042562	AF287834	DQ490632	—	—
<i>Hymenagaricus</i> sp.	DQ457680	DQ089016	DQ490633	—	—
<i>Hyphoderma praetermissum</i>	AY700185	AY707094	AY854081	—	—
<i>Hypholoma fasciculare</i>	AY380409	—	AY354216	AY337413	AY351829
<i>Hypholoma sublateralium</i>	AY635774	AY787215	AY818349	—	—
<i>Hypholoma udum</i> group	DQ457681	DQ444863	DQ490634	—	—
<i>Infundibulicybe gibba</i>	DQ457682	DQ115780	DQ490635	DQ472727	DQ447913
<i>Inocephalus</i> sp.	DQ457683	DQ457622	DQ490636	DQ472728	—
<i>Inocybe asterospora</i>	AY70215	AY654889	DQ404390	—	DQ447914
<i>Inocybe cookei</i>	AY70214	AY752967	DQ404391	DQ385884	DQ447915
<i>Inocybe dulcamara</i> group	AY700196	AY657016	DQ221106	AY803751	DQ447916
<i>Inocybe lilacina</i> ^a	AY380385	AF287835	—	AF390020	AF390020
<i>Inocybe mutata</i>	AY732212	DQ457623	—	DQ472729	DQ447917
<i>Inocybe unicolor</i>	AY380403	AF287836	DQ490637	AY337409	AY351827
<i>Kuehneromyces rostratus</i>	DQ457684	DQ457624	DQ490638	DQ472730	DQ447918
<i>Laccaria amythestina</i>	AF393062	AF287837	AF440665	—	—
<i>Laccaria ochropurpurea</i>	AY700200	AY654886	AF006598	DQ472731	—
<i>Laccaria pumilla</i>	AF287869	AF287838	—	—	—
<i>Lachnella villosa</i>	DQ097362	AY70595	DQ097362	DQ472732	—
<i>Lachnocladium</i> sp.	DQ154110	DQ457625	DQ192176	—	—
<i>Lacrymaria velutina</i>	AY700198	AY654885	DQ490639	DQ472733	—
<i>Lactarius deceptivus</i>	AY631899	AY707093	AY854089	—	—
<i>Lactarius lignyotus</i>	AY631898	DQ457626	DQ221107	—	—

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Langemannia gigantea</i>	AF518603	AF026622	AJ617492	—	—
<i>Lentinula edodes</i>	AF261557	AF082686	AY636053	—	—
<i>Lentinula lateritia</i>	AF287872	AF026596	U33070	AY218492	—
<i>Lepiota cristata</i>	DQ457685	DQ457627	AF391041	—	—
<i>Lepista irina</i>	DQ234538	AY705948	DQ221109	DQ385885	DQ447919
<i>Leptonia canescens</i>	AF261307	DQ851575	—	—	—
<i>Leucoagaricus sinicus</i> ined,	DQ457653	DQ089019	DQ182505	—	—
“ <i>Leucopaxillus albissimus</i> ” ^c	AF042592	AF287839	—	—	—
<i>Lichenomphalia umbellifera</i>	AF261445	U23543	AY293961	—	—
<i>Limnoperdon incarnatum</i>	AF426958	AF426952	DQ097363	—	—
<i>Lycoperdon pyriforme</i>	AF287873	AF026619	AY854075	AY218495	AY860523
<i>Lyophyllum decastes</i>	AF042583	DQ367419	AF357059	DQ367433	DQ825418
<i>Lyophyllum leucophaeatum</i>	AF223202	DQ367420	AF357032	DQ367434	DQ825419
<i>Lyophyllum</i> sp.	DQ094785	DQ457628	DQ182502	—	DQ516075
<i>Macrocyttidia cucumis</i>	DQ094787	DQ089014	DQ490640	—	—
<i>Macrolepiota dolichaula</i>	DQ411537	AY771602	DQ221111	DQ385886	DQ447920
<i>Macrolepiota procera</i>	U85304	L36659	AF482848	—	—
<i>Marasmius oreades</i>	DQ156126	DQ457644	DQ490641	—	DQ447921
<i>Marasmius rotula</i>	DQ457686	DQ113912	DQ182506	DQ474118	DQ447922
<i>Megacollybia platyphylla</i>	AY635778	AY786053	DQ249275	DQ385887	DQ447923
<i>Melanoleuca verrucipes</i>	DQ457687	DQ457645	DQ490642	DQ474119	DQ447924
<i>Moniliophthora pernicioso</i>	AY916738	AY916739	AY317136	—	AY916740
<i>Moniliophthora</i> sp.	AY916752	AY916753	AY916754	—	AY916755
<i>Mycaureola dilseae</i>	DQ097348	DQ097342	DQ097364	—	—
<i>Mycena</i> aff. <i>pura</i>	DQ457688				
	DQ457689				
	DQ457690	DQ457646	DQ490643	DQ474120	DQ447925
<i>Mycena amabilissima</i>	DQ457691	DQ457647	DQ490644	DQ474121	DQ447926
<i>Mycena amicta</i>	DQ457692	DQ457693	DQ490645	—	—
<i>Mycena aurantiidisca</i>	DQ470811	DQ457694	DQ490646	DQ474122	DQ447927
<i>Mycena auricoma</i>	DQ470812	DQ457695	DQ490647	—	—
<i>Mycena galericulata</i> 1	AY647216	DQ457696	DQ404392	DQ385888	—
<i>Mycena galericulata</i> 2	AF042636*	DQ851576	—	—	—
<i>Mycena plumbea</i>	DQ470813	DQ457697	DQ494677	—	DQ447928
<i>Mycetinis alliaceus</i>	AY635776	AY787214	AY854076	AY786060	AY860525
<i>Mythicomycetes corneipes</i>	AY745707	DQ092917	DQ404393	DQ408110	DQ447929
<i>Naucoria vinicolor</i>	DQ536415	DQ536416	DQ536417	DQ536418	DQ536419
<i>Neohygrophorus angelesianus</i>	DQ470814	DQ457698	DQ494678	—	—
<i>Nia vibrissa</i>	AF334750	AF334754	AY571053	DQ408111	—
<i>Nivatogastrium nubigenum</i>	DQ470815	DQ459373	DQ494679	—	—
<i>Nolanea sericea</i>	DQ367423	DQ367421	DQ367430	DQ367435	DQ825424
<i>Nolanea stricta</i>	AF042620	AF287832	DQ494680	AY218483	—
<i>Omphalotus olearius</i>	DQ470816	DQ459374	DQ494681	—	—
<i>Omphalotus olivascens</i>	AF261325*	DQ851577	AF525063	—	—
<i>Ossicaulis lignatilis</i>	AF261396	AF334923	DQ825426	DQ825410	DQ825420
<i>Panaeolina foeniseccii</i>	AF041537*	DQ851578	—	—	—
<i>Panaeolus sphinctrinus</i>	DQ470817	DQ459375	DQ182503	—	—
<i>Panellus stypticus</i>	AF518634	AF026589	AB084488	—	—
<i>Paxillus vernalis</i>	AY645059	AY662662	DQ267128	—	—
<i>Peniophora nuda</i>	AF287880	AF026586	DQ411533	—	—
<i>Phaeocollybia festiva</i>	AY509119	DQ462516	DQ494682	AY509118	AY509117
<i>Phaeomarasmius proximans</i>	AY380410	AY752970	DQ404381	AY333314*	AY333307
<i>Phanerochaete chrysosporium</i>	AF287883	AF026593	AY854086	—	—
<i>Phlebia radiata</i>	AF287885*	AF026606	AY854087	—	—
<i>Pholiota serrulata</i>	DQ156128	DQ462517	DQ182507	—	DQ447930

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Pholiota squarrosa</i>	DQ470818	DQ465337	DQ494683	—	DQ447931
<i>Pholiotina filaris</i>	DQ470819	DQ465338	DQ494684	—	DQ447932
<i>Phyllotopsis nidulans</i>	AF042578	DQ851579	—	—	—
<i>Phyllotopsis</i> sp.	AY684161	AY707090	DQ404382	AY786061	DQ447933
<i>Physalacria bambusae</i>	DQ097349	AY705953	DQ097367	DQ474123	DQ447934
<i>Physalacria inflata</i> ^f	AY293201	AY293146	—	—	—
<i>Physalacria maipoensis</i>	AF426959	AF426953	—	—	—
<i>Pleuroflammula flammea</i>	AF367962	DQ089021	DQ494685	DQ474124	DQ447935
<i>Pleurotopsis longinqua</i>	AF042604*	DQ851580	AF012195	—	—
<i>Pleurotus ostreatus</i>	AY645052	AY657015	AY85407	AY786062	AY862186
<i>Pleurotus tuberregium</i>	AF135180	AF026595	AY450344	—	—
<i>Plicaturopsis crispa</i>				DQ474125	—
	DQ470820	AY293148	DQ494686	DQ474126	—
<i>Pluteus atromarginatus</i>	DQ094788	DQ092912	DQ494687	—	—
<i>Pluteus petasatus</i>	AF042611	AF026634	AF085495	—	—
<i>Pluteus romellii</i>	AY634279	AY657014	AY854065	AY786063	AY862187
<i>Podabrella microcarpa</i>	AF042587*	DQ851581	—	—	—
<i>Podoserpula pusio</i>	DQ470821	—	DQ494688	—	—
<i>Polyporus squamosus</i>	AY629320	AY705963	DQ267123	—	—
<i>Porodisculus pendulus</i>	AY293204	AY293150	AY572009	—	—
<i>Psathyrella candolleana</i>	DQ110874	DQ465339	DQ494689	—	—
<i>Psathyrella gracilis</i>	AF041533*	DQ851582	—	—	—
<i>Psathyrella rhodospora</i>	AY645058	DQ089018	DQ267129	—	—
<i>Psathyrella spadicea</i>	DQ470822	DQ465340	DQ494690	—	—
<i>Pseudoarmillariella ectypoides</i>	DQ154111	DQ465341	DQ192175	DQ474127	DQ516076
<i>Psilocybe cyanescens</i>	AF261620	AY705949	DQ494691	—	—
<i>Psilocybe montana</i>	DQ470823	DQ465342	DQ494692	—	—
<i>Psilocybe silvatica</i>	AF042618	DQ851583	AY129362	—	—
<i>Psilocybe stuntzii</i>	AF042567*	DQ851584	—	—	—
<i>Pterula echo</i>	AY629315	DQ092911	DQ494693	—	—
<i>Punctularia strigosozonata</i>	AF518642	AF518586	DQ398598	—	—
<i>Pycnoporus</i> sp.	AY684160	AY705970	DQ411525	—	—
<i>Respuinatus alboniger</i>	AF042600*	DQ851585	AY571059	—	—
		DQ851586			
<i>Rhodocollybia maculata</i>	AY639880	AY752966	DQ404383	AY787220	DQ447936
<i>Rhodocybe mundula</i>	AY700182	DQ089017	DQ494694	DQ474128	DQ447937
<i>Rickenella fibula</i>	AY700195	AY771599	DQ241782	—	—
<i>Sarcomyxa serotina</i>	AY691887	AF026590	DQ494695	DQ859892	DQ447938
<i>Schizophyllum commune</i>	AF334751	X54865	AF249390	AY218515	—
<i>Schizophyllum radiatum</i>	AY571023	AY705952	AY571060	DQ484052	DQ447939
<i>Serpula himantioides</i>	AF518648	AF518589	AJ536025	DQ366283	—
<i>Simocybe serrulata</i>	AY745706	DQ465343	DQ494696	DQ484053	DQ447940
<i>Stereum hirsutum</i>	AF393078	AF026588	AY854063	AY218520	AY864885
<i>Strobilomyces floccopus</i>	AY684155	AY662661	AY854068	AY786065	AY858963
<i>Stropharia ambigua</i>	AY646102	DQ092924	AY818350	DQ484054	DQ447941
<i>Stropharia rugosoannulata</i>	AF041544	AF026635	DQ494697	—	—
<i>Suillus pictus</i>	AY684154	AY662659	AY854069	AY786066	AY858965
<i>Tephroclype boudieri</i>	DQ825430	DQ825433	DQ825427	DQ825411	DQ825421
<i>Termitomyces</i> sp.	DQ110875	DQ092922	DQ494698	—	DQ447942
<i>Tetrapyrgos subdendrophora</i>	AY445115	AY445118	AY445121	—	—
<i>Thelephora</i> sp	AF287890	AF026627	AY456370	—	—
<i>Trametes versicolor</i>	AY684159	AY706965	AY354226	—	—
<i>Tricholoma aestuans</i>	AY700197	AY757267	DQ494699	DQ484055	—
<i>Tricholoma inamoenum</i>	AY293215	AY293161	AF377246	—	—
<i>Tricholoma matsutake</i>	U62964	U62538	AB188557	—	—

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	<i>rpb2</i>	<i>rpb1</i>
<i>Tricholoma myomyces</i> 1	AF518660	AF287841	AF377210	—	—
<i>Tricholoma myomyces</i> 2	U76459	DQ367422	DQ825428	DQ367436	DQ842013
<i>Tricholoma saponaceum</i>	AY647209	AY654883	DQ494700	—	—
<i>Tricholomella constricta</i>	AF223188	DQ825434	DQ825429	DQ825412	DQ825422
<i>Tricholomopsis decora</i>	AY691888	DQ092914	DQ404384	DQ408112	DQ447943
<i>Tubaria confragosa</i>	AY700190	AY665776	DQ267126	DQ408113	DQ447944
<i>Tubaria furfuracea</i>	AF205710*	DQ851587	—	—	—
<i>Tulostoma macrocephala</i>	AF518663	AF026625	—	—	—
<i>Typhula phacorrhiza</i>	AF393079	AF026630	AF134710	AY218525	—
<i>Vararia</i> sp.	DQ470824	AF334939	DQ241775	—	—
<i>Verrucospora flavofusca</i>	DQ470825	AY665783	DQ241779	—	—
<i>Volvariella gloiocephala</i>	AY745710	DQ089020	DQ494701	—	DQ447945
<i>Volvariella volvacea</i>	AF261531	DQ851588	AY632077	—	—
<i>Vuilleminia comedens</i>	AF518666	AF518594	DQ398959	—	—
<i>Waitea circinata</i>	AY885164	D85647	AJ000195	—	—
<i>Xeromphalina campanella</i>	DQ470826	DQ465344	DQ494702	—	DQ516077
<i>Xerula furfuracea</i>	AY691890	DQ089015	DQ494703	—	—
<i>Xerula radicata</i>	AY645051	AY654884	DQ241780	AY786067	DQ447946

^a 18S and 25S GenBank accessions are mislabeled as *Agaricus sylvaticus*.

^b Sequences obtained from the fungal genome initiative at the Broad Institute, Cambridge, Massachusetts.

^c 18S accession is mislabeled as *Laetiporus portentosus*.

^d 18S accession is mislabeled as *Inocybe geophylla*.

^e This accession represents a *Tricholoma* sp.

^f This accession represents a *Trametes* sp.

SUPPLEMENTARY TABLE II. Family-level phylogenetic classification systems for the Agaricales compared to selected references

Kirk et al (2001)	Singer (1986)	Kühner (1980)	Moncalvo et al (2002)	This study (family/tribe/clade)	This study (major clade)	
Agaricaceae =Podaxaceae	Agaricaceae	Agaricaceae	/adonis	Hydropoid clade	Marasmioid	
			/agaricaceae	Agaricaceae	Agaricoid	
Bolbitiaceae Broomeiaceae ^b Clavariaceae Plicaturopsidoid	Bolbitiaceae	Amanitaceae	/agrocybe ^a	Strophariaceae	Agaricoid	
				<i>s. str.</i>		
			Amanitaceae group	Tubarieae	Agaricoid	
			<i>Arrhenia</i> group	Amanitaceae	Pluteoid	
			Hygrophoraceae	Hygrophoroid		
			<i>s. lat.</i>			
			/baeosporoid	<i>Incertae sedis</i>	Marasmioid	
			/bolbitaceae (<i>s. str.</i>)	Bolbitiaceae	Agaricoid	
			unsampled	unsampled	unsampled	
			<i>Insertae sedis</i>	Clavariaceae		
Hymenochaetales						
			<i>Collybia-Clitocybe</i> group	Tricholomataceae	Tricholomatoid	
				<i>s. str.</i>		
				<i>Atheliaceae p. p.</i>		
Plicaturopsidoid						
Coprinaceae	Coprinaceae	Coprinaceae	/psathyrellaceae	Psathyrellaceae	Agaricoid	
Cortinariaceae= Crepidotaceae	Cortinariaceae	Cortinariaceae	/cortinarioid (<i>s. str.</i>)	Cortinariaceae <i>s. str.</i>	Agaricoid	
	Crepidotaceae		/crepidotoid	Crepidotaceae	Agaricoid	
Entolomataceae	Entolomataceae	Rhodophyllaceae	not monophyletic (/rhodocyboid, /callistosporoid, entolomatoid group)	Entolomataceae	Tricholomatoid	
			/fayodioid	unsampled	unsampled	
Fistulinaceae			/fistulinoid	Schizophyllaceae	Marasmioid	
Gigaspermaceae ^c			unsampled	unsampled	unsampled	
			/gloeostereae	Cyphellaceae	Marasmioid	
			/gymnopileoid	Gymnopileae	Agaricoid	
			/hebelomatoid	Hymenogastraceae	Agaricoid	
Hemigasteraceae			unsampled	unsampled	unsampled	
			/hemimycena	Hydropoid clade	Marasmioid	
Hydnangiaceae		Hydnangiaceae	/laccaria	Hydnangiaceae	Agaricoid	
			/hydropoid	Hydropoid clade	Marasmioid	
	Hygrophoraceae	Hygrophoraceae	Hygrophoraceae group	Hygrophoraceae <i>s. lat.</i>	Hygrophoroid	
Lycoperdaceae			/lycoperdales (nested within /agaricaceae)	Agaricaceae	Agaricoid	
			/lyophylleae	Lyophyllaceae	Tricholomatoid	
		Macrocystidiaceae	unsampled	Macrocystidiaceae	Pluteoid?	
Marasmiaceae= Macrocystidiaceae		Macrocystidiaceae	/marasmiaceae	Marasmiaceae	Marasmioid	
Mesophelliaceae ^d			unsampled	unsampled	unsampled	
			/mycenaceae (<i>s. str.</i>)	Mycenaceae	Tricholomatoid	
Mycenastraceae ^e			unsampled	unsampled	unsampled	
Niaceae			unsampled	Lachnellaceae	Marasmioid	

SUPPLEMENTARY TABLE II. Continued

Kirk et al (2001)	Singer (1986)	Kühner (1980)	Moncalvo et al (2002)	This study (family/tribe/clade)	This study (major clade)
Nidulariaceae			/nidulariaceae <i>Omphalina</i> group	Nidulariaceae <i>Incertae sedis</i> Hygrophoraceae <i>s. lat.</i>	Agaricoid <i>Incertae sedis</i> Hygrophoroid
Phelloriniaceae			/omphalotaceae /panaeoloideae unsampled	Omphalotaceae Panaeoleae unsampled	Marasmioid Agaricoid unsampled
Pleurotaceae	Polyporaceae p.p.	Pleurotaceae	/physalacriaceae /pleurotaceae (<i>s. str.</i>)	Physalacriaceae Pleurotaceae	Marasmioid Pluteoid
Pluteaceae =Amanitaceae	Pluteaceae	Pluteaceae	/pluteus (/volvariella excluded)	Pluteaceae (including <i>Volvariella p. p.</i> , excluding Amanitaceae)	Pluteoid
Pterulaceae			/psilocybe (<i>s. str.</i>)	Strophariaceae <i>s. str.</i>	Agaricoid
Schizophyllaceae			unsampled /resupinatus	Pterulaceae Pleurotaceae	Hygrophoroid Pluteoid
Strophariaceae	Strophariaceae	Strophariaceae =Crepidotaceae =Bolbitiaceae =Cortinariaceae <i>p.p.</i>	/schizophyllum /stropharioid (<i>s. str.</i>)	Schizophyllaceae Strophariaceae <i>s. str.</i>	Marasmioid Agaricoid
Tricholomataceae =Hygrophoraceae =Rhodotaceae	Tricholomataceae	Tricholomataceae	/tricholomatoid (<i>s. str.</i>)	Tricholomataceae	Tricholomatoid
Tulostomataceae			/tricholomopsis /tubaroid	<i>Incertae sedis</i> Tubarieae	Pluteoid Agaricoid
Typhulaceae			/agaricaceae /phyllotopsis	Agaricaceae Typhulaceae	Agaricoid Hygrophoroid
		Rhodotaceae	/physalacriaceae /xeromphalinoïd	Physalacriaceae <i>Incertae sedis</i>	Marasmioid Hygrophoroid

^a *Agrocybe* is polyphyletic (FIG. 1).

^b *Diplocystis* (Broomeiaceae) is a member of the Boletales (Binder and Hibbett 2006, Louzan R, unpub).

^c *Gigasperma clelandii* is allied to the Sclerodermataceae and treated in the genus *Horakiella* (Boletales) (Castellano and Trappe 1992). *Gigasperma cryptica* and *G. americanum* are nested within the euagarics (Kropp and Trappe 2005).

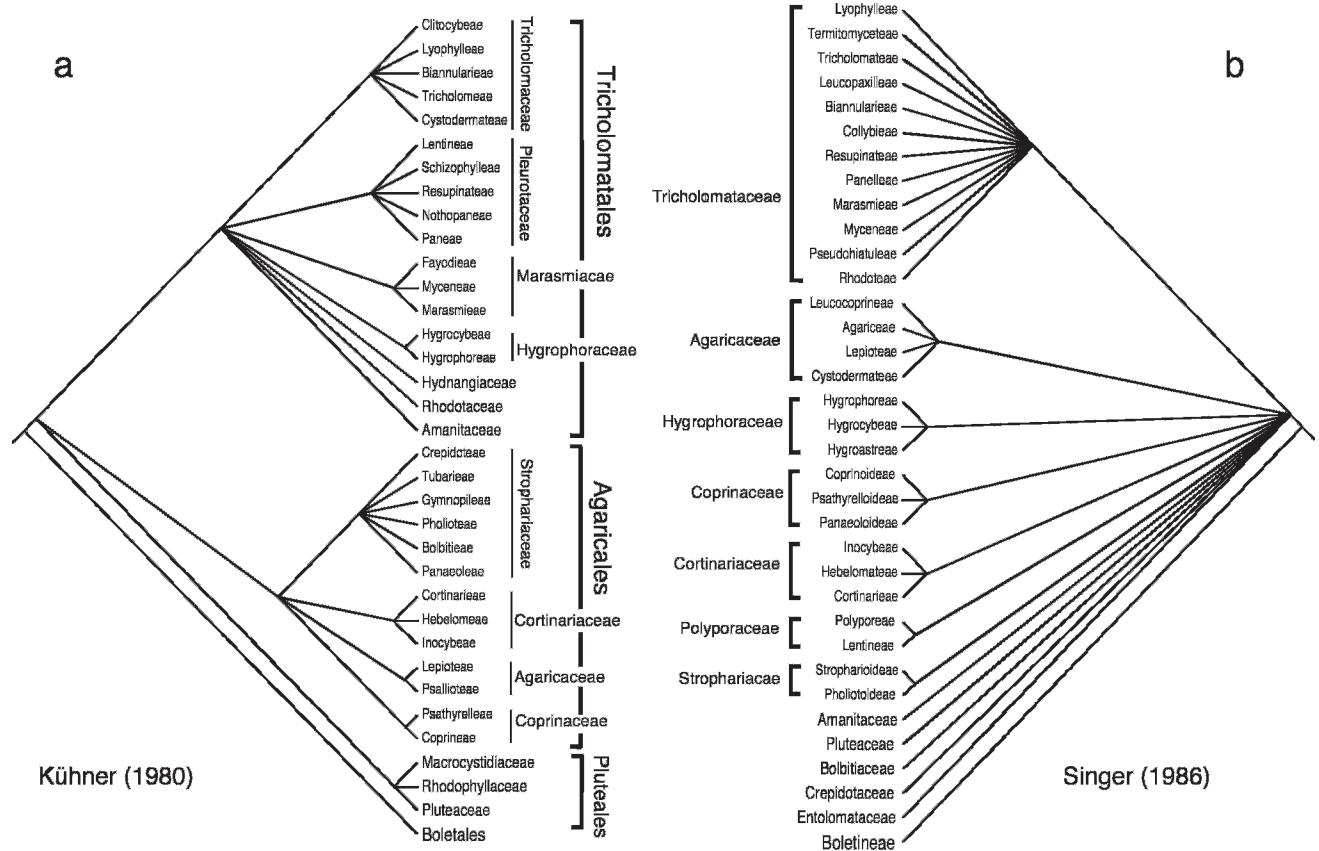
^d *Mesophellia* is a constituent of the gomphoid-phalloïd clade (Hosaka et al 2006).

^e Mycenastraceae is nested within the Lycoperdaceae per Krüger et al (2001), which we treat as a synonym of the Agaricaceae.

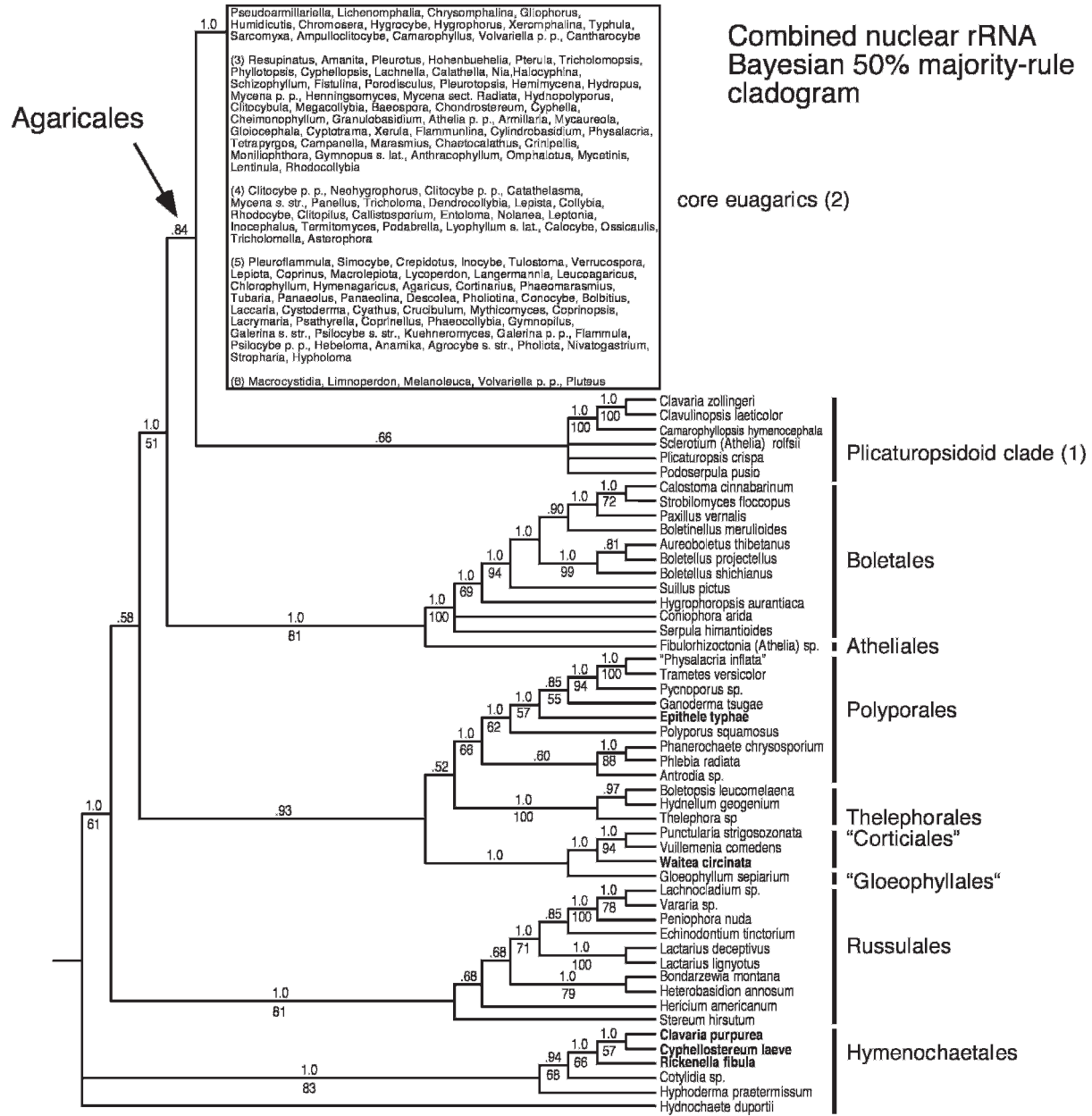
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SUPPLEMENTARY FIG. 1. Two higher-level competing classification systems of the euagarics depicted as cladograms. (a) Family and order-level classification of euagarics in Kühner (1980); (b) Tribe (subfamily) and family level classification of the Agaricineae in Singer (1986).



SUPPLEMENTARY FIG 2. 50% majority-rule Bayesian cladogram of the Agaricales and outgroup taxa inferred from nuclear ribosomal RNA gene regions (18S, 25S, 5.8S). The tree is summarized to show the generic composition of at least six major rRNA clades, which are numbered. Values above nodes reflect posterior probabilities, those below parsimony bootstrap proportions. Taxa in bold font indicate species previously believed to be allies of euagarics or members of the Agaricineae sensu Singer.