Mycologia, 98(6), 2006, pp. 982–995.

Major clades of Agaricales: a multilocus phylogenetic overview

P. Brandon Matheny[1]
Judd M. Curtis
Biology Department, Clark University, 950 Main Street, Worcester, Massachusetts, 01610

Valérie Hofstetter
Department of Biology, Box 90338, Duke University, Durham, North Carolina 27708

M. Catherine Aime
USDA-ARS, Systematic Botany and Mycology Laboratory, Room 304, Building 011A, 10300 Baltimore Avenue, Beltsville, Maryland 20705-2350

Jean-Marc Moncalvo
Centre for Biodiversity and Conservation Biology, Royal Ontario Museum and Department of Botany, University of Toronto, Toronto, Ontario, M5S 2C6 Canada

Zai-Wei Ge
Zhu-Liang Yang
Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, P.R. China

Jason C. Slot
Biology Department, Clark University, 950 Main Street, Worcester, Massachusetts, 01609

Joseph F. Ammirati
University of Washington, Biology Department, Box 355325, Seattle, Washington 98195

Timothy J. Baroni
Department of Biological Sciences, SUNY Cortland, Box 2000, Cortland, New York 13045-0900

Neale L. Bougher
Department of Environment and Conservation, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia

Karen W. Hughes
Botany Department, 437 Hesler Biology Building, University of Tennessee, Knoxville, Tennessee 37996-1100

D. Jean Lodge
International Institute of Tropical Forestry, USDA Forest Service – FPL, PO Box 1377 Luqillo, PR 00773-1377

Richard W. Kerrigan
Sylvan Research, 198 Nolte Drive, Kittanning, Pennsylvania 16201

Michelle T. Seidl
Environmental Microbiology Laboratory Inc., 1400 12th Avenue SE, Bellevue, Washington 98004

Duur K. Aanen
Laboratory of Genetics, Arboretumlaan 4, 6703 BD, Wageningen, The Netherlands

Matthew DeNitis
127 Harrington Way, Worcester, Massachusetts 01604

Graciela M. Daniele
Instituto Multidisciplinario de Biología Vegetal, CONICET-Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina

Dennis E. Desjardin
Department of Biology, San Francisco State University, San Francisco, California 94132

Bradley R. Kropp
Department of Biology, Utah State University, Logan, Utah 84322

Lorelei L. Norvell
Pacific Northwest Mycology Service, 6720 NW Skyline Boulevard, Portland, Oregon 97229-1309

Andrew Parker
127 Raven Way, Metaline Falls, Washington 99153-9720

Else C. Vellinga
Department of Plant and Microbial Biology, 111 Koshland Hall, University of California, Berkeley, California 94720-3102

Rytas Vilgalys
Department of Biology, Box 90338, Duke University, Durham, North Carolina 27708

David S. Hibbett
Biology Department, Clark University, 950 Main Street, Worcester, Massachusetts, 01610

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,

Accepted for publication 1 August 2006.
[1] Corresponding author. E-mail: pmatheny@clarku.edu

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 partitoned 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 intial 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 merulioides*, 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, pilate-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, *Camarophyllopsis 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 *Camarophyllopsis* (= *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

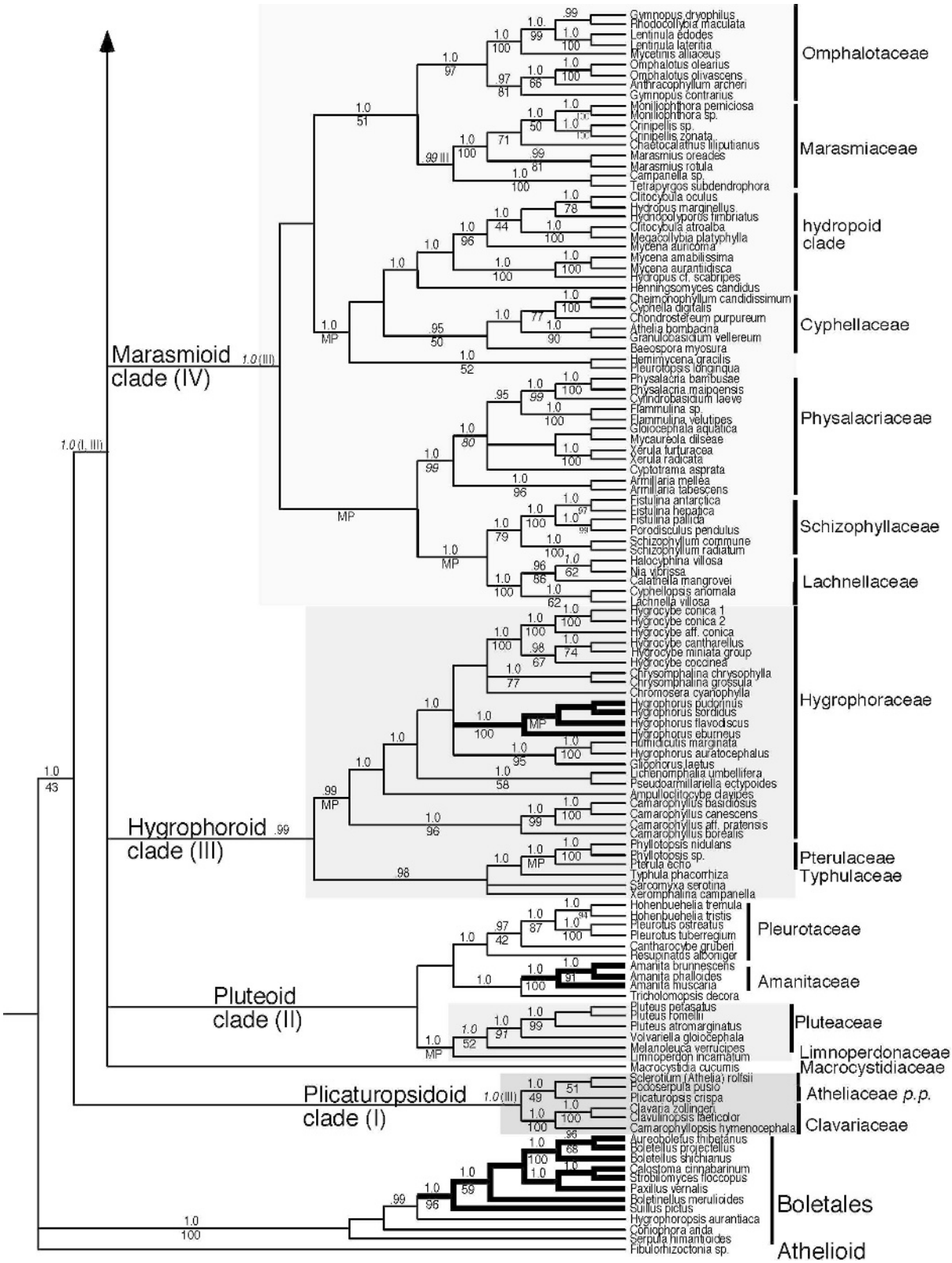


FIG. 1. Fifty percent majority-rule Bayesian cladogram of the Agaricales, six major clades and outgroups produced from combined *rpb1*, *rpb1*-intron2, *rpb2*, 18S, 25S and 5.8S nucleotide sequences for a supermatrix of 250 taxa (dataset II). Posterior probabilities ≥0.95 are indicated above branches. MP bootstrap values ≥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 the

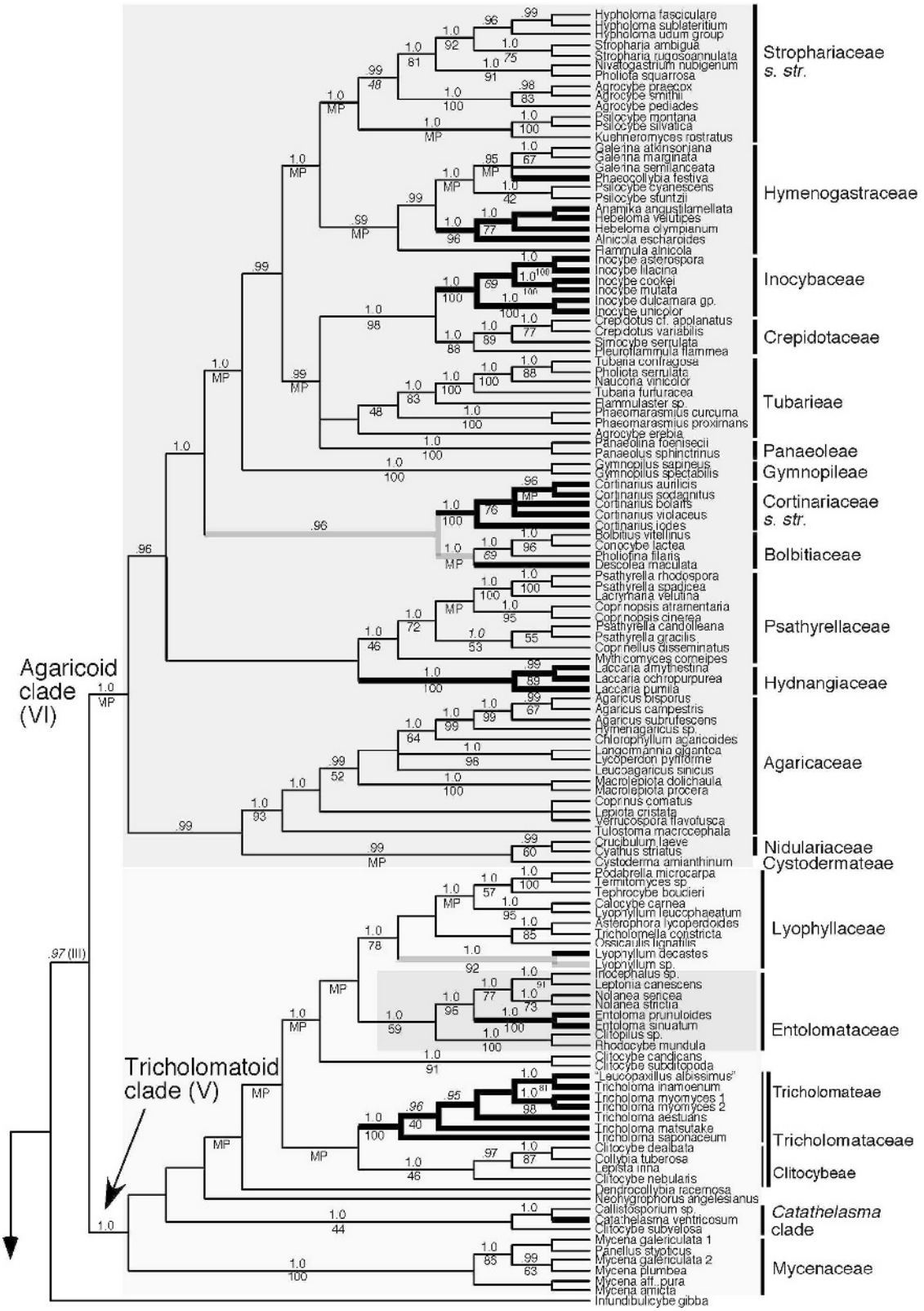


FIG. 1. Continued.

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 hymenocephala*

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 *Camarophyllopsis*) 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 *Camarophyllopsis* and *Neohygrophorus* excluded. *Camarophyllopsis* (= *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).

←
(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 (Clémençon 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, Tubarieae, 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. builliardii*) 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). Hacskaylo (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).

ACKNOWLEDGMENTS

We thank Shlomit Klopman and Ron McGuire for bioinformatic support at Clark University. We also thank Lisa Bukovnik and staff at Duke University for sequencing support, Manfred Binder, Zheng Wang, Maj Padamsee and David McLaughlin for donation of materials, Dennis Oliver of the WTU herbarium for curatorial support and Brian Perry for taxonomic assistance. We thank Roy Halling,

Heino Lepp, Dave McLaughlin, Mark Steinmetz and Mykoweb (http://www.mykoweb.com/) for use of photographs. Ideas about the historical classification of agarics were drawn from an unpublished paper titled ''Development of Classification of the Macrobasidiomycetes'' by D.E Stuntz (University of Washington no date). Financing was provided by National Science Foundation grants DEB 0228657 for the Assembling the Fungal Tree of Life project, DBI 0320875, NSF 0090301 Research Coordination Network: a phylogeny for kingdom fungi to M. Blackwell, J.W. Spatafora and J.W. Taylor, as well as numerous grants awarded to other co-authors.

LITERATURE CITED

Aanen DK, Eggleton P, Rouland-Lefevre C, Guldberg-Frøslev T, Rosendahl S, Boomsma J. 2002. The evolution of fungus-growing termites and their mutualistic fungal symbionts. Proc Nat Acad Sci, USA 99: 14887–14892.

Aime MC, Phillips-Mora. 2005. The causal agents of witches' broom and frosty pod rot of cacao (chocolate, *Theobroma cacao*) form a new lineage of Marasmiaceae. Mycologia 97:1012–1022.

Altekar GS, Dwarkadas S, Huelsenbeck JP, Ronquist F. 2004. Parallel metropolis-coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. Bioinformatics 20: 407–415.

Arnolds E. 1980. De oecologie en sociologie van Wasplaten (*Hygrophorus* subgenus *Hygrocybe sensu lato*). Natura 77:17–44.

———. 1986. Notes on Hygrophoraceae IX *Camarophyllopsis* Herink, an older name for *Hygrotrama* Sing. Mycotaxon 25:639–644.

———. 1990. Tribus Hygrocybeae. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC, eds., Rotterdam: A.A. Balkema. p 70–111.

Bas C. 1998. Orders and families in agarics and boleti. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC, eds. Flora agaracina neerlandica: critical monographs on families of agarics and boletii occurring in the Netherlands. Vol. 1. Rotterdam: A.A. Balkema. p 40–49.

Benjamin DR. 1995. Mushrooms: poisons and panaceas. New York: W.H. Freeman & Co. 422 p.

Bigelow HE. 1985. North American species of *Clitocybe*. Part II. Beih Nova Hedwigia 81:281–471.

Binder M, Besl H, Bresinsky A. 1997. Agaricales oder Boletales? Molekularbiologische Befunde zur Zuordnung einiger umstrittener Taxa. Z Mykol 63:189–196.

———, Bresinsky A. 2002. Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. Mycologia 94:85–98.

———, Hibbett DS. 2002. Higher-level Phylogenetic relationships of Homobasidiomycetetes (mushroom-forming fungi) inferred from four rDNA regions. Mol Phylogenet Evol 22:76–90.

———, ———, Larsson KH, Larsson E, Langer E, Langer G. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Syst Biodivers 3:113–157.

———, ———, Wang Z, Farnham W. 2006. Evolutionary relationships of *Mycaureola dilseae* (Agaricales), a basidiomycete pathogen of a subtidal rhodophyte. Am J Bot 93:547–556.

Bodensteiner P, Binder M, Moncalvo JM, Agerer R, Hibbett DS. 2004. Phylogenetic relationships of cyphelloid homobasidiomycetes. Mol Phylogenet Evol 33:501–515.

Boertmann D. 1996. The genus *Hygrocybe*. Fungi of Northern Europe 1:5–184.

Bougher NL, Malajczuk N. 1985. A new species of *Descolea* (Agaricales) from Western Australia, and aspects of its ectomycorrhizal status. Aust J Bot 33:619–627.

———, Syme K. 1998. Fungi of southern Australia. Perth: University of Western Australia Press. 391 p.

Bresinsky A, Schneider G. 1975. Nitratreduktion durch Pilze und die Verwertbarkeit des Merkmals für die Systematik. Biochem System Ecol 3:129–135.

Bruns TD, Shefferson RP. 2004. Evolutionary studies of ectomycorrhizal fungi: recent advances and future directions. Can J Bot 82:1122–1132.

Chapela IH, Rehner SA, Schultz TR, Mueller UG. 1994. Evolutionary history of the symbiosis between fungus-growing ants and their fungi. Science 266:1691–1694.

Clémençon H. 1978. Siderophilous granules in the basidia of Hymenomycetes. Persoonia 10:83–96.

———. 2004. Cytology and plectology of the Hymenomycetes. Bibliothec Mycol 199:iii–488.

Czederpiltz DLL, Volk TJ, Burdsall HH. 2001. Field observations and inoculation experiments to determine the nature of the carpophoroids associated with *Entoloma abortivum* and *Armillaria*. Mycologia 93:841–851.

DeBry RW, Olmstead RG. 2000. A simulation study of reduced tree-search effort in bootstrap resampling analysis. Syst Biol 49:171–179.

De Román M, Claveria V, De Miguel AM. 2005. A revision of the descriptions of ectomycorrhizas published since 1961. Mycol Res 109:1063–1104.

Donk MA. 1964. Conspectus of the families of Aphyllophorales. Persoonia 3:199–324.

Duncan EG, Galbraith MH. 1972. Post-meiotic events in the Homobasidiomycetidae. Trans Br Mycol Soc 58:387–392.

Fayod V. 1889. Prodrome d'une histoire naturelle des Agaricinées. Annls Sci Nat Bot Sér 7,9:181–411.

Fries E. 1821–1832. Systema mycologicum, sistens fungorum ordines, genera et species hucusque cognitas. Gryphiswaldiae.

———. 1828. Elenchus fungorum. Vols. I & II. Germany: Greifswald.

———. 1857–63. Monographia hymenomycetum sueciae. Vols. I & II. Uppsala: C.A. Leffler.

———. 1874. Hymenomycetes europaei. Uppsala: Berling. 755 p.

Frøslev TG, Matheny PB, Hibbett DS. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2, and ITS phylogenies. Mol Phylogenet Evol 37: 602–618.

Gulden G, Stensrud Ø, Shalchian-Tabrizi K, Kauserud H.

2005. *Galerina* Earle: a polyphyletic genus in the consortium of dark-spored agarics. Mycologia 97:823–837.

Hacskaylo E. 1971. The role of mycorrhizal associations in the evolution of the higher basidiomycetes. In: Petersen RH, ed. Evolution in the higher basidiomycetes: an international symposium. Knoxville: University of Tennesee Press. p 217–237.

Hallen HE, Watling R, Adams GC. 2003. Taxonomy and toxicity of *Conocybe lactea* and related species. Mycol Res 107:969–979.

Harmaja H. 1978. The division of the genus *Lepista*. Karstenia 18:49–54.

———. 2002. *Amylolepiota*, *Clavicybe* and *Cystodermella*, new genera of Agaricales. Karstenia 42:39–48.

———. 2003. Notes on *Clitocybe s. lato* (Agaricales). Ann Bot Fennici 40:213–218.

Heim R. 1971. The interrelationships between the Agaricales and Gasteromycetes. In: Petersen RH, ed. Evolution in the higher basidiomycetes. Knoxville: University of Tennessee Press. p 505–534.

Hesler LR, Smith AH. 1963. North American species of *Hygrophorus*. Knoxville: University of Tennessee Press. 416 p.

Hibbett DS, Pine EM, Langer E, Langer G, Donoghue MJ. 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc Natl Acad Sci USA 94:12002–12006.

———, Gilbert LB, Donoghue MJ. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature 407:506–508.

———, Thorn RG. 2001. Basidiomycota: Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA, eds. The Mycota. VIIB. Systematics and Evolution. Berlin: Springer-Verlag. p 121–168.

———, Binder M. 2002. Evolution of complex fruiting-body morphologies in homobasidiomycetes. Proc R Soc Lond B 269:1963–1969.

———. 2004. Trends in morphological evolution in homobasidiomycetes inferred using maximum likelihood: a comparison of binary and multistate approaches. Syst Biol 53:889–903.

Hofstetter V, Clémençon H, Vilgalys R, Moncalvo JM. 2002. Phylogenetic analyses of the Lyophylleae (Agaricales, Basidiomycota) based on nuclear and mitochondrial rDNA sequences. Mycol Res 106:1043–1059.

Horak E. 1968. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Beiträge zur Kryptogamenflora der Schweiz 13:1–741.

———. 1990. Monograph of the New Zealand Hygrophoraceae (Agaricales). NZ J Bot 28:255–309.

Hsiang T, Wu C. 2000. Genetic relationships of pathogenic *Typhula* species assessed by RAPD, ITS-RFLP and ITS sequencing. Mycol Res 104:16–22.

Hughes KW, Petersen RH, Johnson JE, Moncalvo JM, Vilgalys R, Redhead SA, Thomas T, McGhee LL. 2001. Infrageneric phylogeny of *Collybia s. str.* based on sequences of ribosomal ITS and LSU regions. Mycol Res 105:164–172.

Jülich W. 1981. Higher taxa of basidiomycetes. Bibliothec Mycol 85:5–485.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's dictionary of the fungi. 9th ed. Surrey, UK: CAB International. 655 p.

Kobayashi H, Degawa Y, Yamada A. 2003. Two new records of entolomatoid fungi associated with rosaceous plants from Japan. Mycoscience 44:331–333.

———, Yamada A, Tokumasu S, Kakishima M. 2005. Mycorrhizal morphology in Rosaceae and Ulmaceae produced by entolomatoid fungi in Japan. Abstract from the Mycological Society of American and Mycological Society of Japan Joint Meeting, Hilo, Hawaii, 30 Jul–5 Aug 2005. 144 p.

Krüger D, Binder M, Fischer M, Kreisel H. 2001. The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia 93:947–957.

Kühner R. 1977. Variation of nuclear behaviour in the homobasidiomycetes. Trans Br Mycol Soc 68:1–16.

———. 1980. Les Hyménomycètes agaricoïdes. Bull Soc Linn Lyon 49: Numéro spécial. 1027 p.

———. 1984. Some mainlines of classification in the gill fungi. Mycologia 76:1059–1074.

———, Romagnesi H. 1953. Flore analytique des champignons supérieurs (agarics, bolets, chanterelles). Paris: Masson. 556 p.

Kuyper TW. 1995. 5. *Clitocybe*. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC, eds. Flora agaricina neerlandica. Vol. 3. Rotterdam: A.A. Balkema. p 42–62.

Largent DL. 1994. Entolomatoid fungi of the western United States and Alaska. Eureka, California: Mad River Press. 277 p.

Larsson KH, Larsson E, Kõljalg U. 2004. High phylogenetic diversity among corticioid basidiomycetes. Mycol Res 108:983–1002.

Maddison DR, Maddison WP. 2000. MacClade 4: analysis of phylogeny and character evolution. Sunderland, Massachusetts: Sinauer Associates.

Malloch DW. 1987. The evolution of mycorrhizae. Can J Plant Path 9:398–402.

———, Pirozynski KA, Raven PH. 1980. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). Proc Natl Acad Sci USA 77: 2113–2118.

Mata JL, Hughes KW, Petersen RH. 2004. Phylogenetic placement of *Marasmiellus juniperinus*. Mycoscience 45:214–221.

Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). Mol Phylogenet Evol 35:1–20.

———, Bougher NL. 2006. The new genus *Auritella* from Africa and Australia (Inocybaceae, Agaricales): molecular systematics, taxonomy and historical biogeography. Mycol Prog 5:2–17.

———, Liu YJ, Ammirati JF, Hall BD. 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). Am J Bot 89:688–698.

Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based

on nuclear large subunit ribosomal DNA sequences. Syst Biol 49:278–305.

———, Vilgalys R, Redhead SA, Johnson JE, Jame TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémençon H, Miller Jr OK. 2002. One hundred seventeen clades of euagarics. Mol Phylogenet Evol 23:357–400.

Moser MM. 1983. Keys to agarics and boleti. London: Roger Phillips. 535 p.

Mueller GM, Ammirati JF. 1993. Cytological studies in *Laccaria* (Agaricales). II. Assessing phylogenetic relationships among *Laccaria*, *Hydnangium* and other Agaricales. Am J Bot 80:322–329.

Mueller UG, Rehner SA, Schultz TR. 1998. The evolution of agriculture in ants. Science 281:2034–2038.

Munkacsi AB, Pan JJ, Villesen P, Mueller UG, Blackwell M, McLaughlin DJ. 2004. Convergent coevolution in the domestication of coral mushrooms by fungus-growing ants. Proc R Soc Lond B 271:1777–1782.

Norvell LL. 1998. Observations on the development, morphology and biology of *Phaeocollybia*. Mycol Res 102:615–630.

———. 2001. An informal poll for MSA members: should the type of *Coprinus* be changed? Inoculum 52:5.

———, Redhead SA, Ammirati JF. 1994. *Omphalina sensu lato* in North America 1–2. 1: *Omphalina wynniae* and the genus *Chrysomphalina*. 2: *Ompahlina sensu* Bigelow. Mycotaxon 50:379–407.

Oberwinkler F. 1984. Fungus-alga interactions in basidiolichens. Beih Nova Hedwig 79:739–774.

Okabe I, Matsumoto N. 2003. Phylogenetic relationships of *Sclerotium rolfsii* (teleomorph *Athelia rolfsii*) and *S. delphinii* based on ITS sequences. Mycol Res 107:164–168.

Pegler DN, Young TWK. 1969. Ultrastructure of basidiospores in Agaricales in relation to taxonomy and spore discharge. Trans Br Mycol Soc 52:491–513.

———, ———. 1971. Basidiospore morphology in the Agaricales. Beih Nova Hedwig 35:1–210.

———, ———. 1979. Spore form and phylogeny of Entolomataceae (Agaricales). Sydow Beih. 8:290–303.

Peintner U, Bougher NL, Castellano MA, Moncalvo JM, Moser MM, Trappe JM, Vilgalys R. 2001. Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). Am J Bot 88:2168–2179.

Petersen RH, ed. 1971. Evolution in the higher basidiomycetes. Knoxville: University of Tennessee Press. 562 p. 13 pl.

Pine EM, Hibbett DS, Donoghue MJ. 1999. Phylogenetic relationships of cantharelloid and clavarioid Homobasidiomycetes based on mitochondrial and nuclear rDNA sequences. Mycologia 91:944–963.

Redhead SA. 1981. Parasitism of bryophytes by agarics. Can J Bot 59:63–67.

———. 1985. Proposal to conserve *Mycena* (Tricholomataceae, Agaricales). Taxon 34:303–307.

———, Ginns JH. 1985. A reappraisal of agaric genera associated with brown rots of wood. Trans Mycol Soc Jap 26:349–381.

———, Ammirati JF, Norvell LL, Seidl MT. 2000. Notes on western North American snowbank fungi. Mycotaxon 76:321–328.

———, Vilgalys R, Moncalvo JM, Johnson J, Hopple JS. 2001a. *Coprinus* Pers. and the disposition of *Coprinus* species *sensu lato*. Taxon 50:203–241.

———, ———, ———, ———, ———. 2001b. Proposals to conserve or reject. Proposals to conserve *Psathyrella* (Fr.) Quél. with a conserved type and to reject the name *Pselliophora* P. Karst. (Basidiomycetes: Psathyrellaceae). Taxon 50:275–277.

———, Moncalvo JM, Vilgalys R, Lutzoni F. 2002a. Phylogeny of agarics: partial systematics solutions for bryophilus omphalinoid agarics outside of the Agaricales (euagarics). Mycotaxon 82:151–168.

———, Lutzoni F, Moncalvo JM, Vilgalys R. 2002b. Phylogeny of agarics: partial systematics solutions for core omphalinoid genera in the Agaricales (euagarics). Mycotaxon 83:19–57.

Rihs JD, Padhye AA, Good CB. 1996. Brain abscess caused by *Schizophyllum commune*: an emerging basidiomycete pathogen. J Clin Microbiol 34:1628–1632.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Rouland-Lefevre C, Diouf MN, Brauman A, Neyra M. 2002. Phylogenetic relationships in *Termitomyces* (family Agaricaceae) based on the nucleotide sequence of ITS: a first approach to elucidate the evolutionary history of the symbiosis between fungus-growing termites and their fungi. Mol Phylogenet Evol 22:423–429.

Salamin N, Chase MW, Hodkinson TR, Savolaine V. 2003. Assessing internal support with large phylogenetic matrices. Mol Phylogenet Evol 27:528–539.

Sigler L, Bartley JR, Parr DH, Morris AJ. 1999. Maxillary sinusitis caused by medusoid form of *Schizophyllum commune*. J Clin Microbiol 37:3395–3398.

Singer R. 1986. The Agaricales in modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books. 981 p. 88 pl.

———. 1991. Toward a definition of the genus in mycological taxonomy. Mycol Helvetica 6:92–94.

Smith AH, Smith HV, Weber NS. 1979. How to know the gilled mushrooms. Dubuque, Iowa: Wm. C. Brown Publishers. 334 p.

———, Stuntz DE. 1950. New or noteworthy fungi from Mt Rainier National Park. Mycologia 62:80–134.

Swofford DL. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The Clustal X Windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucl Acid Res 25:4876–4882.

Thorn RG, Moncalvo JM, Reddy CA, Viglays R. 2000. Phylogenetic analysis and the distribution of nematophagy support a monophyletic Pleurotaceae within the polyphyletic pleurotoid-lentinoid fungi. Mycologia 92:241–252.

Vellinga EC. 2004. Ecology and distribution of lepiotaceous fungi (Agaricaceae)—a review. Nova Hedwig 78:273–299.

Vizzini A, Girlanda M. 1997. *Squamanita umbonata* (Sums.) Bas, a mycoparasite of *Inocybe oblectabilis* (Britz.) Sacc.—preliminary note. Allionia 35:171–175.

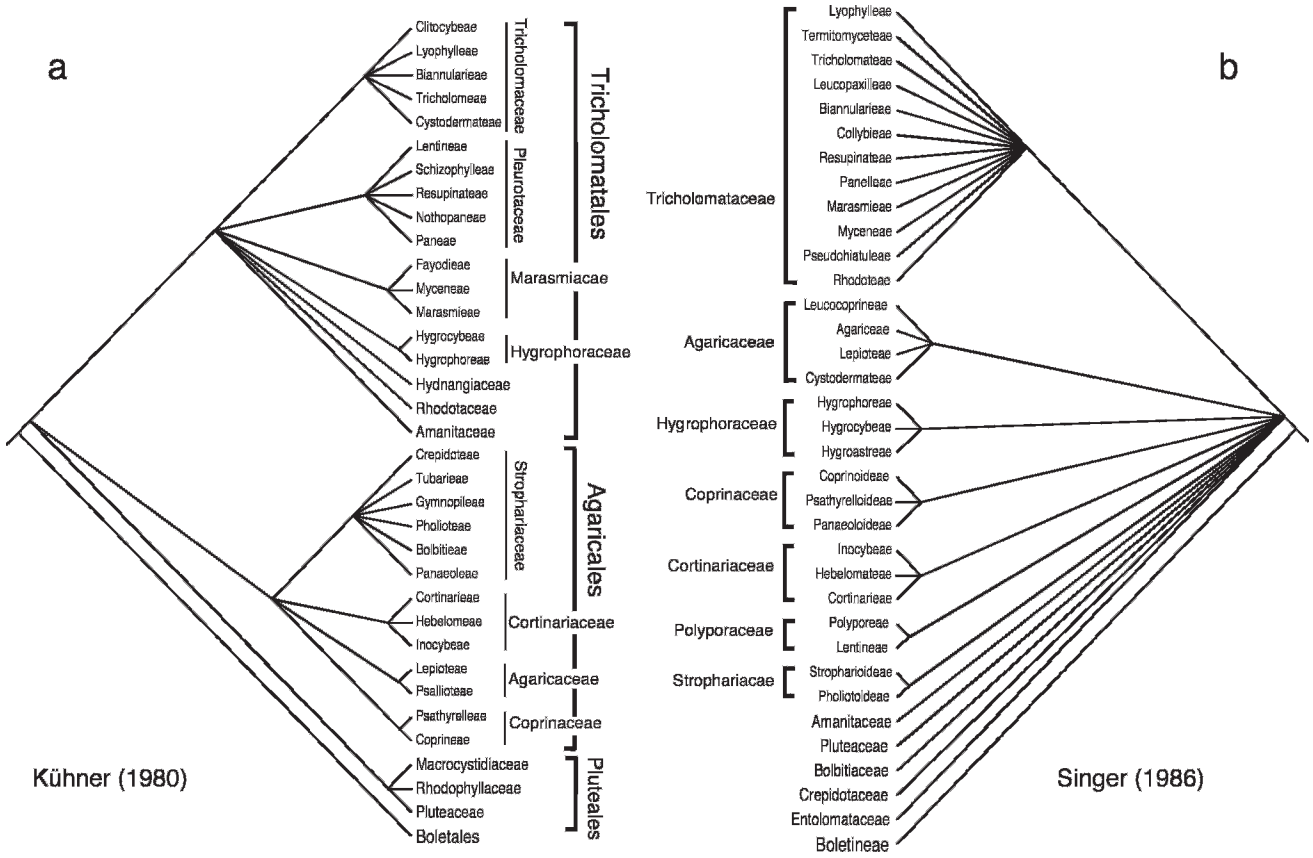
Watling R, Gregory NM. 1987. 5 / Strophariaceae & Coprinaceae pp. In: Gregory NM, Watling R, eds. British fungus flora: agarics and boleti. Edinburgh: Royal Botanic Garden. p 1–121.

Weiss M, Selosse MA, Rexer KH, Urban A, Oberwinkler F. 2004. Sebacinales: a hitherto overlooked cosm of heterobasidiomycetes with a broad mycorrhizal potential. Mycol Res 108:1003–1010.

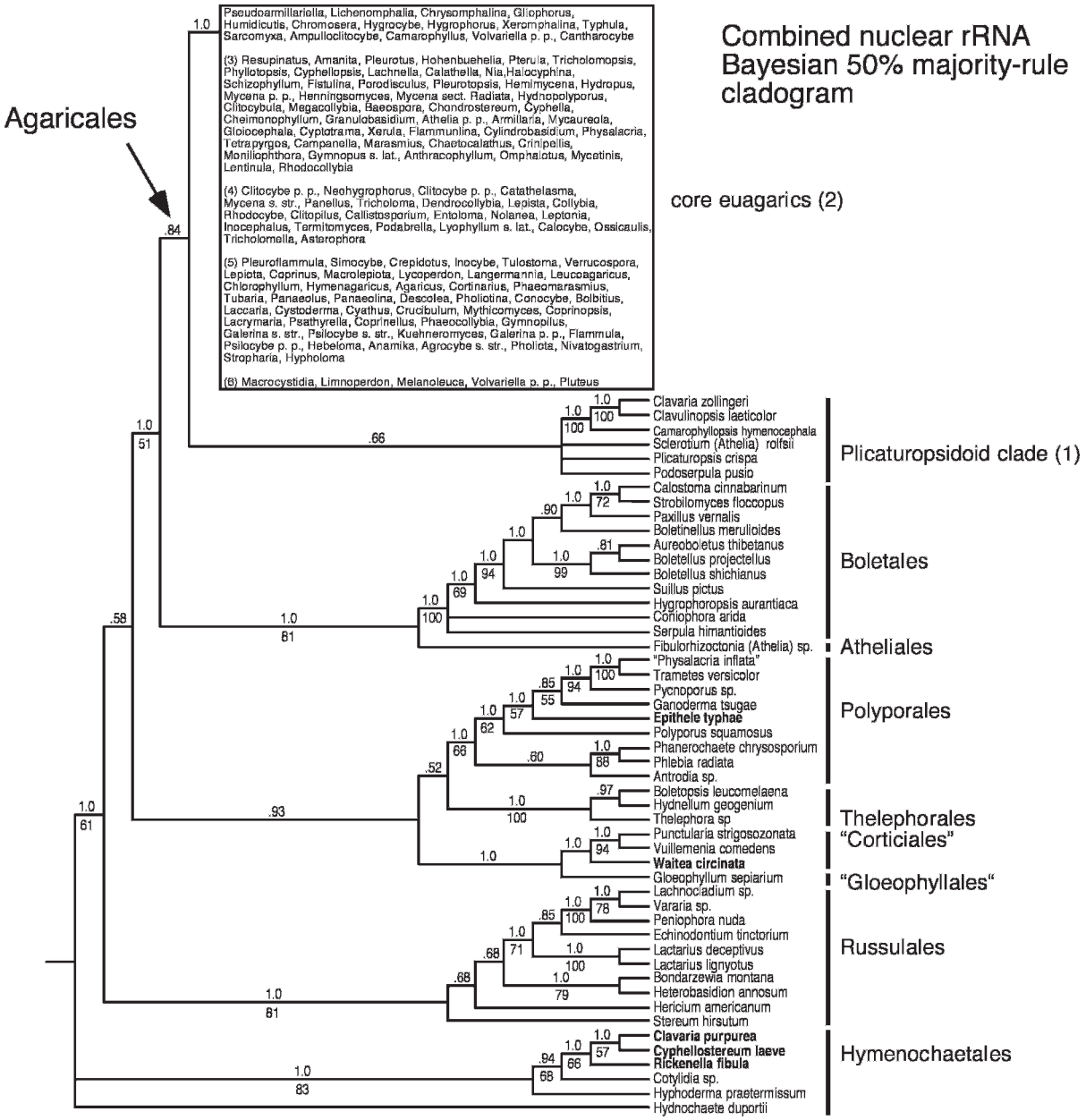
White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenies. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds. PCR protocols: a guide to methods and applications. San Diego: Academic Press. p 315–322.

Wiens JJ. 2006. Missing data and the design of phylogenetic analyses. J Biomed Inform 39:34–42.

Wilson AW, Desjardin DE. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (Basidiomycetes, euagarics clade). Mycologia 97:667–679.



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.

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)
			/adonis	Hydropoid clade	Marasmioid
Agaricaceae =Podaxaceae	Agaricaceae	Agaricaceae	/agaricaceae	Agaricaceae	Agaricoid
			/agrocybe[a]	Strophariaceae *s. str.*	Agaricoid
				Tubarieae	Agaricoid
	Amanitaceae	Amanitaceae	Amanitaceae group	Amanitaceae	Pluteoid
			Arrhenia group	Hygrophoraceae *s. lat.*	Hygrophoroid
			/baeosporoid	*Incertae sedis*	Marasmioid
Bolbitiaceae	Bolbitiaceae		/bolbitaceae (*s. str.*)	Bolbitiaceae	Agaricoid
Broomeiaceae[b]			unsampled	unsampled	unsampled
Clavariaceae			*Insertae sedis*	Clavariaceae	
Plicaturopsidoid					
Hymenochaetales					
			Collybia-Clitocybe group	Tricholomataceae *s. str.*	Tricholomatoid
				Atheliaceae *p. p.*	
Plicaturopsidoid					
Coprinaceae	Coprinaceae	Coprinaceae	/psathyrellaceae	Psathyrellaceae	Agaricoid
Cortinariaceae= Crepidotaceae	Cortinariaceae	Cortinariaceae	/cortinarioid (*s. str.*)	Cortinariaceae *s. str.*	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
			/gymnopiloid	Gymnopileae	Agaricoid
			/hebelomatoid	Hymenogastraceae	Agaricoid
Hemigasteraceae			unsampled	unsampled	unsampled
			/hemimycena	Hydropoid clade	Marasmioid
Hydnangiaceae		Hydnangiaceae	/laccaria	Hydnagniaceae	Agaricoid
			/hydropoid	Hydropoid clade	Marasmioid
	Hygrophoraceae	Hygrophoraceae	Hygrophoraceae group	Hygrophoraceae *s. lat.*	Hygrophoroid
Lycoperdaceae			/lycoperdales (nested within /agaricaceae)	Agaricaceae	Agaricoid
			/lyophylleae	Lyophyllaceae	Tricholomatoid
		Macrocystidiaceae	unsampled	Macrocystidiaceae	Pluteoid?
Marasmiaceae= Macrocystidiaceae		Marasmiaceae	/marasmiaceae	Marasmiaceae	Marasmioid
Mesophelliaceae[d]			unsampled	unsampled	unsampled
			/mycenaceae (*s. str.*)	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	Nidulariaceae	Agaricoid
			Omphalina group	*Incertae sedis*	*Incertae sedis*
				Hygrophoraceae *s. lat.*	Hygrophoroid
			/omphalotaceae	Omphalotaceae	Marasmioid
			/panaeoloideae	Panaeoleae	Agaricoid
Phelloriniaceae			unsampled	unsampled	unsampled
			/physalacriaceae	Physalacriaceae	Marasmioid
Pleurotaceae	Polyporaceae p.p.	Pleurotaceae	/pleurotaceae (*s. str.*)	Pleurotaceae	Pluteoid
Pluteaceae =Amanitaceae	Pluteaceae	Pluteaceae	/pluteus (/volvariella excluded)	Pluteaceae (including *Volvariella p. p.*, excluding Amanitaceae)	Pluteoid
			/psilocybe (*s. str.*)	Strophariaceae *s. str.*	Agaricoid
Pterulaceae			unsampled	Pterulaceae	Hygrophoroid
			/resupinatus	Pleurotaceae	Pluteoid
Schizophyllaceae			/schizophyllum	Schizophyllaceae	Marasmioid
Strophariaceae	Strophariaceae	Strophariaceae =Crepidotaceae =Bolbitiaceae =Cortinariaceae *p.p.*	/strophariod (*s. str.*)	Strophariaceae *s. str.*	Agaricoid
Tricholomataceae =Hygrophoraceae =Rhodotaceae	Tricholomataceae	Tricholomaceae	/tricholomatoid (*s. str.*)	Tricholomataceae	Tricholomatoid
			/tricholomopsis	*Incertae sedis*	Pluteoid
			/tubarioid	Tubarieae	Agaricoid
Tulostomataceae			/agaricaceae	Agaricaceae	Agaricoid
Typhulaceae			/phyllotopsis	Typhulaceae	Hygrophoroid
		Rhodotaceae	/physalacriaceae	Physalacriaceae	Marasmioid
			/xeromphalinoid	*Insertae sedis*	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 consituent of the gomphoid-phalloid 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.

LITERATURE CITED

Binder M, Hibbett DS. 2006. Molecular systematics and biological diversification of Boletales. Mycologia (see this issue).

Castellano MA, Trappe JM. 1992. Australian truffle-like fungi. VI. *Gigasperma* (Basidiomycotina, Tricholomataceae) and *Horakiella* gen. nov. (Basidiomycotina, Sclerodermataceae). Aust Syst Bot 5:631–638.

Hosaka K, Bates ST, Beever RE, Castellano MA, Colgan W, Dominguez LS, Giachini AJ, Kenney SR, Nouhra ER, Simpson NB, Spatafora JW, Trappe JM. 2006. Molecular phylogenetics of the gomphoid-phalloid fungi with an establishment of the new subclass Phallomycetidae and two new orders. Mycologia (see this issue).

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's dictionary of the fungi. 9th ed. Surrey, UK: CAB International. 655 p.

Kühner R. 1980. Les Hyménomycètes agaricoïdes. Bull Soc Linn Lyon 49:Numéro spécial. 1027 p.

Kropp BR, Trappe JM. 2005. Phylogenetics of *Gigasperma* based on partial nuclear large subunit rDNA se-

quences. Abstract from the Mycological Society of American and Mycological Society of Japan Joint Meeting, Hilo, Hawaii, 30 Jul–5 Aug 2005: p. 145.

Krüger D, Binder M, Fischer M, Kreisel H. 2001. The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia 93:947–957.

Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, Jame TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémençon H, Miller OK Jr. 2002. One hundred and seventeen clades of euagarics. Mol Phylogenet Evol 23:357–400.

Singer R. 1986. The Agaricales in modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books. 981 p., 88 pl.

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

SUPPLEMENTARY TABLE I. Continued

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

SUPPLEMENTARY TABLE I. Continued

Species	25S	18S	ITS/5.8S	*rpb2*	*rpb1*
Granulobasidium vellereum	AY745729	DQ440641	DQ205683	—	—
Gymnopilus sapineus	AY380362	—	AF501560	AY337358	AY351789
Gymnopilus spectabilis	AY700186	DQ440642	DQ486707	—	—
Gymnopus contrarius	DQ457670	DQ440643	DQ486708	DQ472716	DQ447902
Gymnopus dryophilus	AY640619	AY665779	DQ241781	DQ472717	DQ447903
Halocyphina villosa	AF426957	AF426951	AY571042	—	—
Hebeloma olympianum	AY038310	—	—	AY337359	AF389532
Hebeloma velutipes	AY745703	AY752972	AY818351	DQ472718	DQ447904
Hemimycena gracilis	DQ457671	DQ440644	DQ490623	DQ472719	DQ447905
Henningsomyces candidus	AF287864	AF334916	AY571043	AY218513	AY860521
Hericium americanum	DQ411538	AY665778	DQ206987	—	—
Heterobasidion annosum	AF287866*	AF026576	DQ206988	—	—
Hohenbuehelia tremula	DQ156129	DQ440645	DQ182504	—	—
Hohenbuehelia tristis	AF042602*	DQ851573	—	—	—
Humidicutus marginata	AF042580	AF287833	DQ490625	—	—
Hydnellum geogenium	AY631900	AY752971	DQ218304	—	—
Hydnochaete duportii	AY635770	AY662669	DQ404386	—	—
Hydnopolyporus fimbriatus	DQ457673	DQ444854	DQ490626	DQ472721	DQ447907
Hydropus cf. *scabripes*	DQ411536	DQ444855	DQ404389	DQ457634	DQ447908
Hydropus marginellus	DQ457674	DQ444856	DQ490627	DQ472722	—
Hygrocybe aff. *conica*	AY684167	AY752965	AY854074	AY803747	AY860522
Hygrocybe cantharellus	DQ457675	DQ444857	DQ490628	—	DQ447909
Hygrocybe coccinea	DQ457676	DQ444858	DQ490629	DQ472723	DQ447910
Hygrocybe conica 1	AF261450	AF184198	—	—	—
Hygrocybe conica 2	AF261450	DQ851574	—	—	—
Hygrocybe miniata group	DQ457677	DQ444859	DQ490630	DQ472724	—
Hygrophoropsis aurantiaca	AY684156	AY662663	AY854067	AY786059	AY858961
Hygrophorus auratocephala	DQ457672	DQ440646	DQ490624	DQ472720	DQ447906
Hygrophorus eburneus	AF430279	AF184199	AY242855	—	—
Hygrophorus flavodiscus	AY635769	DQ444860	DQ249276	—	DQ447911
Hygrophorus pudorinus	DQ457678	DQ444861	DQ490631	DQ472725	DQ447912
Hygrophorus sordidus	AF042562	AF287834	DQ490632	—	—
Hymenagaricus sp.	DQ457680	DQ089016	DQ490633	—	—
Hyphoderma praetermissum	AY700185	AY707094	AY854081	—	—
Hypholoma fasciculare	AY380409	—	AY354216	AY337413	AY351829
Hypholoma sublateritium	AY635774	AY787215	AY818349	—	—
Hypholoma udum group	DQ457681	DQ444863	DQ490634	—	—
Infundibulicybe gibba	DQ457682	DQ115780	DQ490635	DQ472727	DQ447913
Inocephalus sp.	DQ457683	DQ457622	DQ490636	DQ472728	—
Inocybe asterospora	AY70215	AY654889	DQ404390	—	DQ447914
Inocybe cookei	AY70214	AY752967	DQ404391	DQ385884	DQ447915
Inocybe dulcamara group	AY700196	AY657016	DQ221106	AY803751	DQ447916
Inocybe lilacina[d]					AF390020
	AY380385	AF287835	—	AF390020	AY351834S2
Inocybe mutata	AY732212	DQ457623	—	DQ472729	DQ447917
Inocybe unicolor	AY380403	AF287836	DQ490637	AY337409	AY351827
Kuehneromyces rostratus	DQ457684	DQ457624	DQ490638	DQ472730	DQ447918
Laccaria amythestina	AF393062	AF287837	AF440665	—	—
Laccaria ochropurpurea	AY700200	AY654886	AF006598	DQ472731	—
Laccaria pumilla	AF287869	AF287838	—	—	—
Lachnella villosa	DQ097362	AY70595	DQ097362	DQ472732	—
Lachnocladium sp.	DQ154110	DQ457625	DQ192176	—	—
Lacrymaria velutina	AY700198	AY654885	DQ490639	DQ472733	—
Lactarius deceptivus	AY631899	AY707093	AY854089	—	—
Lactarius lignyotus	AY631898	DQ457626	DQ221107	—	—

SUPPLEMENTARY TABLE I. Continued

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

Supplementary Table I. Continued

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

SUPPLEMENTARY TABLE I. Continued

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