Mycologia, 98(6), 2006, pp. 982–995.
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Major clades of Agaricales: a multilocus phylogenetic overview

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Accepted for publication 1 August 2006.
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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 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

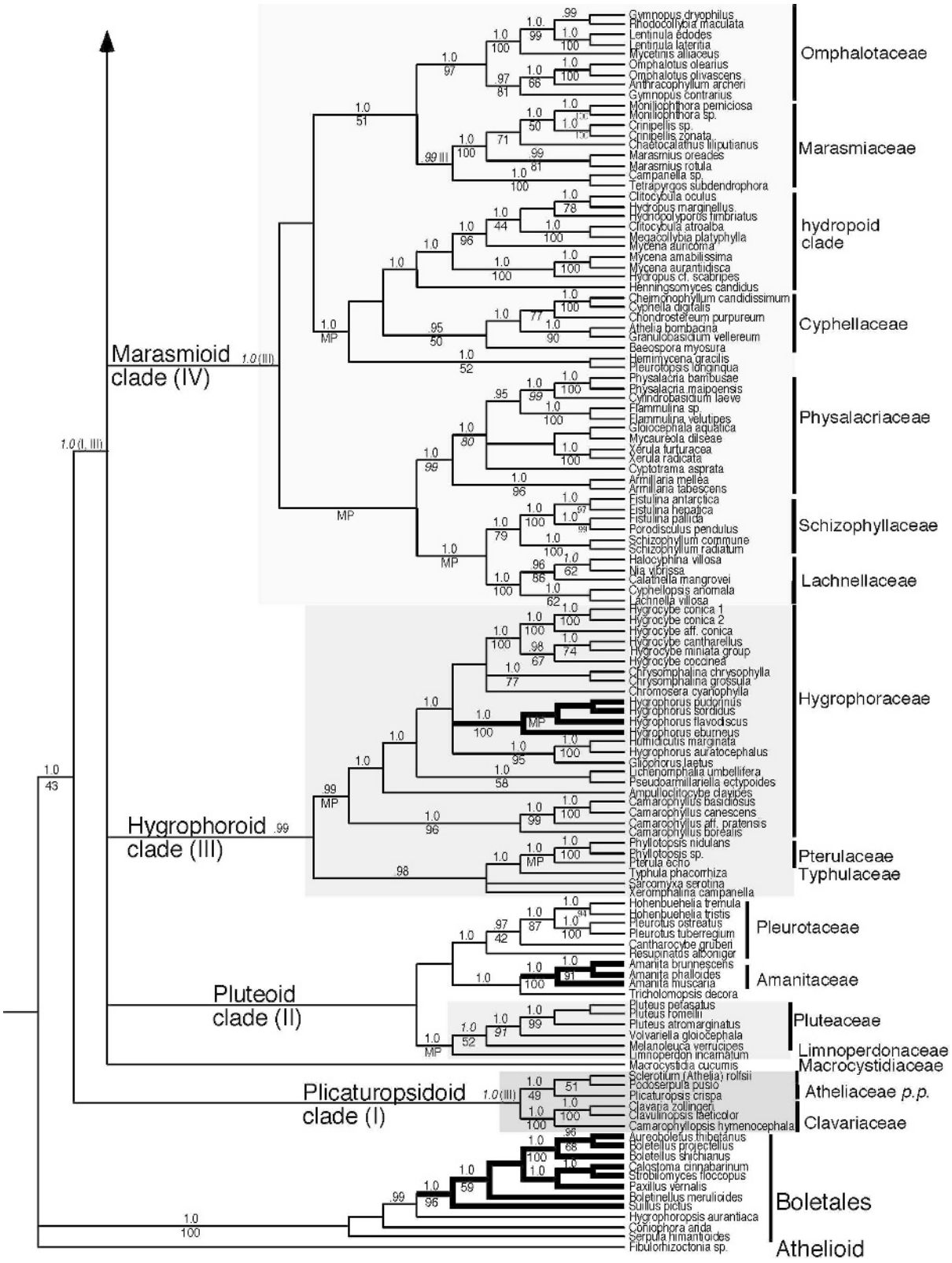

FIG. 1. Fifty percent majority-rule Bayesian cladogram of the Agaricales, six major clades and outgroups produced from combined *rpb1*, *rpb1*-intron2, *rpb2*, 18S, 25S and 5.8S nucleotide sequences for a supermatrix of 250 taxa (dataset II). Posterior probabilities ≥0.95 are indicated above branches.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

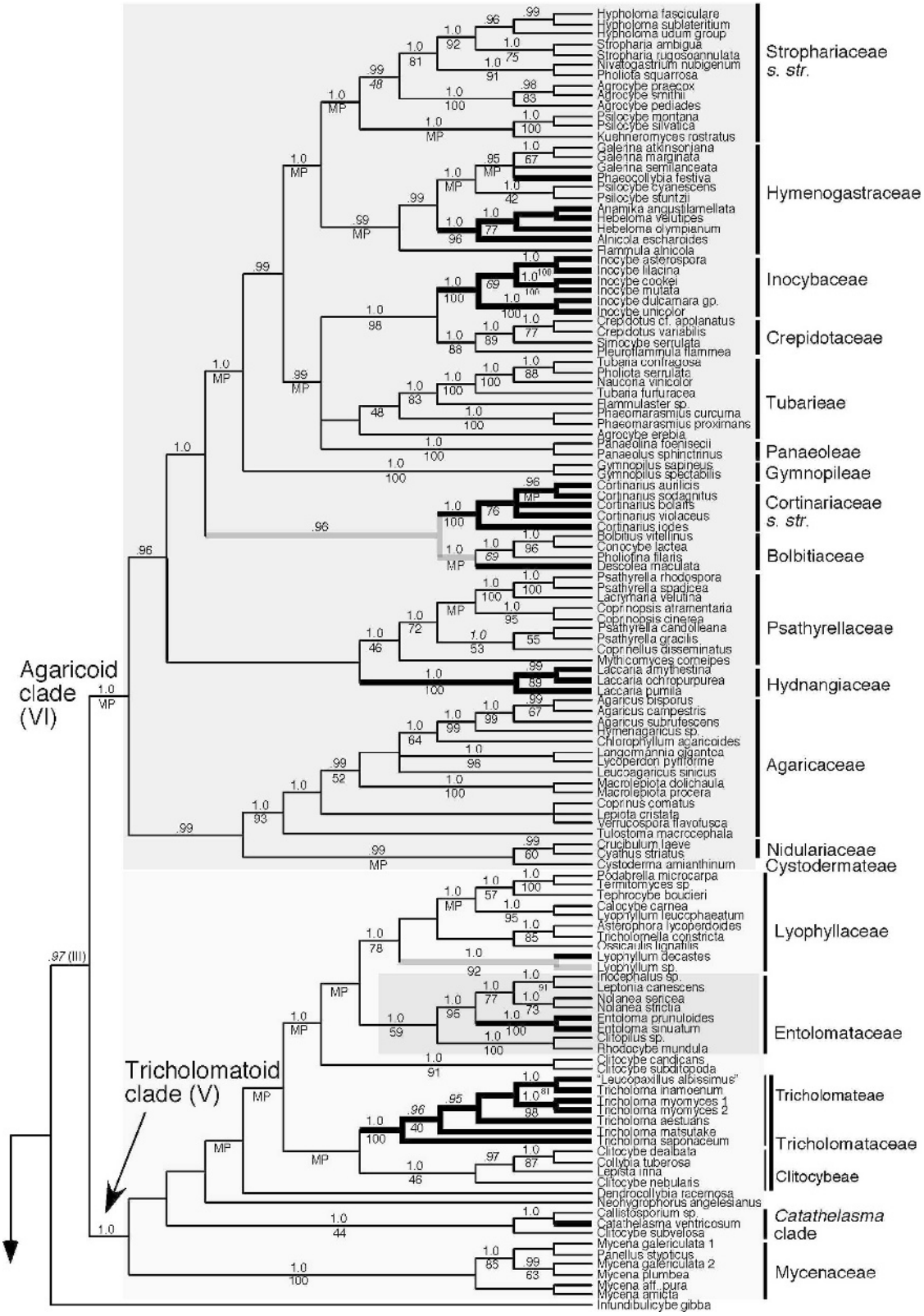

FIG. 1. Continued.

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.

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