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One hundred and seventeen clades of euagarics

Jean-Marc Moncalvo,^{a,*} Rytas Vilgalys,^a Scott A. Redhead,^b James E. Johnson,^a Timothy Y. James,^a M. Catherine Aime,^c Valerie Hofstetter,^d Sebastiaan J.W. Verduin,^{e,f} Ellen Larsson,^g Timothy J. Baroni,^h R. Greg Thorn,ⁱ Stig Jacobsson,^g Heinz Clémençon,^d and Orson K. Miller Jr.^c

^a Department of Biology, Duke University, Durham, NC 27708, USA

^b Systematic Mycology and Botany Section, Eastern Cereal and Oilseed Research, Agriculture and Agri-Food Canada, Ottawa, Ont., Canada K1A 0C6

^c Department of Biology, Virginia Tech, Blacksburg, VA 24061, USA

^d Department of Ecology, Lausanne University, Lausanne, Switzerland

^e Nationaal Herbarium Nederland, Universiteit Leiden branch, P.O. Box 9514, 2300 RA Leiden, The Netherlands

^f Centraal Bureau voor Schimmelcultures, P.O. Box 85167, 3508 AD Utrecht, The Netherlands

^g Botanical Institute, Göteborg University, SE 405 30 Göteborg, Sweden

^h Department of Biological Sciences, SUNY College at Cortland, Cortland, NY 13045, USA

ⁱ Department of Plant Sciences, University of Western Ontario, London, Ont., Canada N6A 5B7

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Abstract

This study provides a first broad systematic treatment of the euagarics as they have recently emerged in phylogenetic systematics. The sample consists of 877 homobasidiomycete taxa and includes approximately one tenth (ca. 700 species) of the known number of species of gilled mushrooms that were traditionally classified in the order Agaricales. About 1000 nucleotide sequences at the 5' end of the nuclear large ribosomal subunit gene (nLSU) were produced for each taxon. Phylogenetic analyses of nucleotide sequence data employed unequally weighted parsimony and bootstrap methods. Clades revealed by the analyses support the recognition of eight major groups of homobasidiomycetes that cut across traditional lines of classification, in agreement with other recent phylogenetic studies. Gilled fungi comprise the majority of species in the euagarics clade. However, the recognition of a monophyletic euagarics results in the exclusion from the clade of several groups of gilled fungi that have been traditionally classified in the Agaricales and necessitates the inclusion of several clavaroid, poroid, secotioid, gasteroid, and reduced forms that were traditionally classified in other basidiomycete orders. A total of 117 monophyletic groups (clades) of euagarics can be recognized on the basis on nLSU phylogeny. Though many clades correspond to traditional taxonomic groups, many do not. Newly discovered phylogenetic affinities include for instance relationships of the true puffballs (Lycoperdales) with Agaricaceae, of *Panellus* and the poroid fungi *Dictyopanus* and *Favolaschia* with *Mycena*, and of the reduced fungus *Caripia* with *Gymnopus*. Several clades are best supported by ecological, biochemical, or trophic habits rather than by morphological similarities. © 2002 Elsevier Science (USA). All rights reserved.

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"As soon as it will be possible to delimit 'mixed groups' of this order, we shall see the Agaricales fall apart [and it will be] extremely difficult to define the limits of the groups obtained" (Singer, 1951, pp. 127–128, footnote 51).

The rapid development of DNA sequencing techniques, phylogenetic theory, and bioinformatics has enabled systematists to envision a phylogenetic classification of all the branches of the tree of life. Notable examples include the recently published phylogenies of vascular plants (Chase et al., 1993; Qiu et al., 1999; Soltis et al., 1997, 1998, 1999; Savolainen et al., 2000)

^{*}Corresponding author. Present address: Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada.

E-mail address: jeanmarc@duke.edu (J.-M. Moncalvo).

and the "Deep Green" land plant phylogeny study (summarized in Brown, 1999). In fungi, the pace of discovery about natural relationships has also been greatly accelerated by new evidence from molecular systematics, mostly using ribosomal DNA sequence data. Based on molecular evidence, it is now believed that the Chytridiomycetes, Zygomycetes, Glomales, Ascomycetes, and Basidiomycetes form a monophyletic group sister to the Animals, whereas the myxomycetes and oomycetes, sometimes considered to be Fungi, should be classified outside the fungal kingdom (Bruns et al., 1992; Bowman et al., 1992; Wainright et al., 1993; Spiegel et al., 1995; Lipscomb et al., 1998; Tehler et al., 2000; James et al., 2000).

rDNA phylogenies support monophyly of many traditional basidiomycete taxa, but have also demonstrated the existence of several clades composed of members of disparate traditional groups (Swann and Taylor, 1993, 1995; Hibbett et al., 1997; Begerow et al., 1997; Bruns et al., 1998). In the homobasidiomycetes, gilled mushrooms appear to have evolved multiple times from morphologically diverse ancestors (Hibbett et al., 1997; Thorn et al., 2000; Hibbett and Thorn, 2000), making the Agaricales polyphyletic. It has also been demonstrated that gasteromycetes (e.g., puffballs and sequestrate or secotioid fungi) have evolved several times from gilled or poroid ancestors (Baura et al., 1992; Bruns et al., 1989; Kretzer and Bruns, 1997; Hibbett et al., 1997; Peintner et al., 2001). These and other findings open the way to deconstruct artificial taxa (e.g., the Gasteromycetes) and redefine others in a phylogenetic context. In a preliminary outline for a major revision of the classification of the homobasidiomycetes based on phylogenetic principles, Hibbett and Thorn (2000) recognized eight major clades. The largest of these (with ca. 8400 known species), the euagarics clade, is the focus of this study.

The core group of the euagarics clade is composed of gilled mushrooms. It corresponds largely to the Agaricineae of Singer (1986), but also includes taxa that were traditionally classified in the Aphyllophorales (e.g., *Clavaria, Typhula, Fistulina, Schizophyllum*, etc.) and several orders of Gasteromycetes (e.g., Hymenogastrales, Lycoperdales, Nidulariales). Phylogenetic relationships within the euagarics are still poorly known. However, an earlier molecular phylogenetic study that sampled rDNA sequences from 152 diverse agaricoid taxa showed that many families and genera of the Agaricales (e.g., Kühner, 1980; Singer, 1986) do not correspond to natural groups (Moncalvo et al., 2000).

In this study we expand our previous sampling (Moncalvo et al., 2000) for the nuclear large ribosomal subunit gene (nLSU; or 25-28S rDNA) to include about one tenth of the total number of known species of euagarics. The nLSU region has been shown to be most useful to infer phylogenetic relationships in basidiomycetous fungi and allies at genus and family levels (Moncalvo et al., 2000; Fell et al., 2000; Weiss and Oberwinkler, 2001). Representatives of each of the eight major clades of homobasidiomycetes (as defined by Hibbett and Thorn, 2000) were also included in the analyses. The purpose of this large-scale analysis is to identify monophyletic groups (clades) of euagarics.

1. Materials and methods

1.1. Sampling of nucleotide sequences

We sampled molecular data for 877 taxa representing 126 of the 192 Agaricineae genera recognized in Singer (1986) and members of each clade of homobasidiomycetes as defined in Hibbett and Thorn (2000). Nucleotide sequences produced in this study consist of about 1000 bp located at the 5' end of the nuclear large ribosomal subunit gene, which encompass divergent domains D1-D3 (Michot et al., 1984). Sequences were produced in different laboratories using a variety of standard molecular methods. A total of 491 new sequences were produced for this study and were combined into a single data set with previously published sequences (Vilgalys and Sun, 1994; Chapela et al., 1994; Lutzoni, 1997; Binder et al., 1997; Pegler et al., 1998; Johnson and Vilgalys, 1998; Drehmel et al., 1999; Hopple and Vilgalys, 1999; Larsson and Larsson, 1998; Mitchell and Bresinsky, 1999; Thorn et al., 2000; Hwang and Kim, 2000; Moncalvo et al., 2000). The data matrix employed in Moncalvo et al. (2000) was used as a template for manual alignment of the other sequences. A small number of sequences were recoded to fit the template alignment (these sequences are labeled with an asterisk in the data matrix, which is available at http://www.biology.duke.edu/fungi/mycolab/agaricphylogeny_start.html). Recoding generally consisted in the removal of autapomorphic inserts located in otherwise highly conserved regions (these were phylogenetically uninformative, and some may also possibly be PCR-sequencing or editing errors). A sequence from the heterobasidiomycete Auricularia polytricha was used to root the homobasidiomycete phylogeny, as suggested in Hibbett et al. (1997).

Collection data and GenBank accession numbers of the material used in this study are given in the Appendix. Authority names of the species used in this work can be found in the CABI Bioscience Database of Fungal Name (http://l94.131.255.3/cabipages/Names/ NAMES.ASP). Although a single sequence per species was used in the final analyses, taxonomic and sequence accuracy for several taxa were evaluated by sampling multiple collections from different sources. These taxa are identified in the Appendix A.

1.2. Phylogenetic analyses

The 877 sequences sampled in this study were aligned in approximately 1000 positions. Hypervariable, indelrich regions with problematic alignment were excluded from the analyses. Unambiguously aligned gaps were treated as missing data. Phylogenetic analyses were conducted in PAUP* (Swofford, 1998) with Power Macintosh computers using maximum-parsimony as the optimality criterion. Unequally weighted parsimony was employed to account for biases in base composition and nucleotide substitution rates, using a stepmatrix estimated from a smaller, but similar data set (Moncalvo et al., 2000). It has been shown that unequally weighted parsimony can recover correct phylogenies with fewer characters than required by equally weighted parsimony (Hillis et al., 1994).

Parsimony analyses of large data sets with high taxa/ characters ratio are impractical, and most parsimonious trees are not likely to be found (Rice et al., 1997). Therefore, only suboptimal searches could be conducted in this study. We performed an initial analysis using 100 heuristic searches of random addition sequence with TBR branch-swapping, MULPARS on, and MAX-TREES set to 10, saving all trees in each replicate (the other settings in PAUP* were as follows: multistate taxa were interpreted as uncertainty, the steepest descent option was not in effect, and branches were collapsed if minimum branch length was zero). The shortest trees found in the initial searches were used as starting trees for a recurrent search with TBR branch-swapping and MAXTREES set to 5000. The Templeton (1983) test was used to evaluate whether the trees found in the initial and final searches differed statistically. Branch robustness was evaluated using 100 bootstrap (BS) replicates (Felsenstein, 1985) with TBR branch-swapping and MULPARS off. Fast bootstrap searches have been shown to reveal robust branches in large-scale phylogenies within a reasonable amount of computation time (Moncalvo et al., 2000). Several other searches using smaller data sets were also conducted for empirical examination of the sensitivity of the tree topologies in relation to taxon sampling, to test the robustness of certain clades.

2. Results

2.1. Phylogenetic analyses

After removal of 123 redundant sequences (representing taxonomic duplicates) and regions with ambiguous nucleotide sequence alignment, the final data matrix was composed of 754 sequences and 781 characters: 211 characters were constant, 125 variable characters were parsimony uninformative, and 445 variable characters were parsimony informative. The initial search produced 1000 trees ranging in size from 43988.7 to 44185.9. These trees were not significantly different from each other (P > 0.05, Templeton test). When the shortest trees from the initial search were used as starting trees for TBR branch-swapping with MAX-TREES set to 5000, the analysis yielded 5000 equally parsimonious trees of score 43985.2 (consistency index = 0.1064, retention index = 0.6611). To facilitate the discussion, we will refer to the strict consensus tree of the 5000 equally parsimonious trees found in the final analysis as the most parsimonious trees found (MPF tree). The MPF tree was carefully compared with the bootstrap tree and with slightly longer (but statistically not significantly different) trees produced in the initial searches to identify branches that were consistently recovered by maximum-parsimony and branches that were not.

2.2. Phylogenetic relationships

Homobasidiomycetes clade. Both the MPF tree and the bootstrap tree support monophyly of six of the eight homobasidiomycetes clades recognized in Hibbett and Thorn (2000) and Binder and Hibbett (2002), i.e. (1) the euagarics clade, (2) the bolete clade, (3) the hymenochaetoid clade, (4) the thelephoroid clade, (5) the gomphoid-phalloid clade, and (6) the cantharelloid clade. The russuloid clade is recovered in the bootstrap tree (58% BS), but not in the MPF tree, whereas the polyporoid clade is recovered only in the MPF tree. A possible sister group relationship between the euagarics and the bolete clades (< 40% BS) and a basal position of the cantharelloid clade (< 41% BS) are also supported. Within the polyporoid clade, reciprocal monophyly of the polyporaceae and corticioid clades is supported in both the MPF and the bootstrap trees. These results are summarized in Figs. 1 and 2.

Euagarics clade. Basal relationships within the euagarics clade were poorly resolved and several taxa remained as "orphans" (incertae sedis). Many branches present in the MPF tree collapsed in the bootstrap trees (Fig. 1). These branches were also generally not supported in trees slightly longer than the MPF tree (data not shown). Conversely, some branches recovered in the bootstrap tree were absent from the MPF tree but these branches generally had low statistical support (<40%: data not shown). For instance, the placement of the Amanita clade was inconsistent between different analyses: it is nested in a derived position of the Agaricaceae clade in the MPF tree and as sister group to *Limacella* in both the bootstrap tree and most of the suboptimal trees examined. To best summarize the results of the diverse analyses, we have edited the tree depicted in Fig. 2, as follows: branches that were not present in both the MPF tree and the bootstrap tree were collapsed, with the exception of some branches

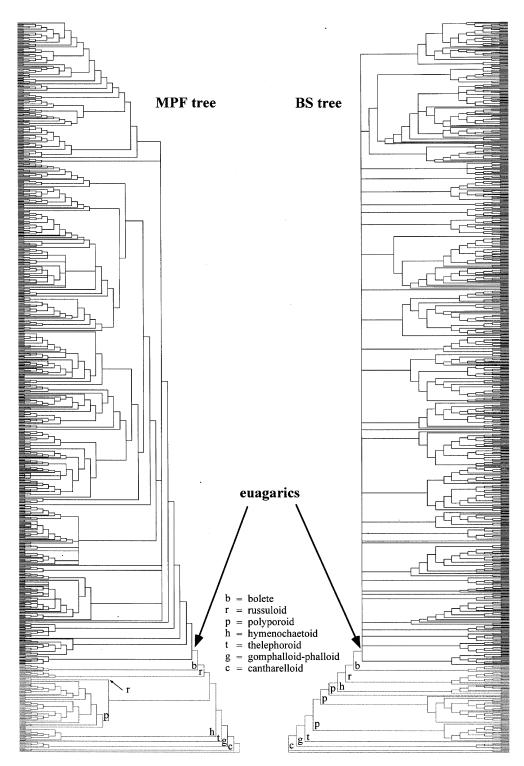


Fig. 1. Overall topologies of the strict consensus tree of 5000 equally most parsimonious trees found from heuristic searches (MPF tree) and the bootstrap 50% majority-rule consensus tree (BS tree). The placement in both trees of the eight major homobasidiomycetes groups (as defined in Hibbett and Thorn, 2000) is indicated by letters above corresponding branches. Trees are rooted with a sequence from the heterobasidiomycete *Auricularia polytricha*.

that were present in either tree (as indicated in Fig. 2) which are useful for discussion.

Within the euagarics, at least 117 clades revealed in the MPF tree (and generally also in slightly longer trees) have a bootstrap support >40% (Fig. 2) and/or are consistent with traditional groups based on morphology. Smaller clades often correspond to traditional genera (or part of them in cases of polyphyletic genera),

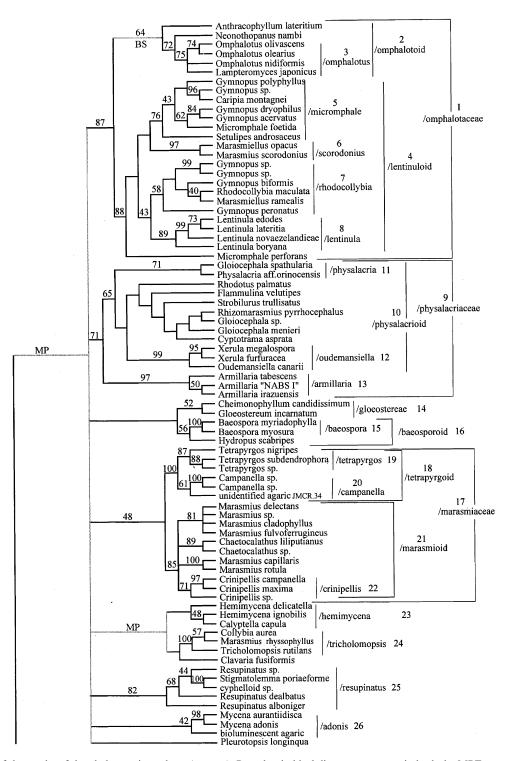


Fig. 2. Summary of the results of the phylogenetic analyses (see text). Branches in black lines were present in both the MPF tree and the bootstrap tree. Shaded branches were present in either the MPF (MP) or the BS tree, as indicated. Bootstrap values greater than 40% are shown above branches. In the tree depicted, *Armillaria irazuensis* should read *A. affinis*, *Poromycena gracilis* should read *Fibboletus gracilis*, and in /lichenomphalia *Omphalia viridis* should read *O. hudsoniana*.

whereas several larger clades correspond to the core genera of traditional families, tribes, or subfamilies. Therefore, it is sometimes possible to label clades with existing names. Other clades, however, are composed of taxa for which a natural relationship was never suspected before or have no evident name associated with them. These clades are labeled with provisional names. To distinguish between clade names and traditional taxonomic names, clade names are written in lowercase, never italicized, and preceded with the symbol "/."

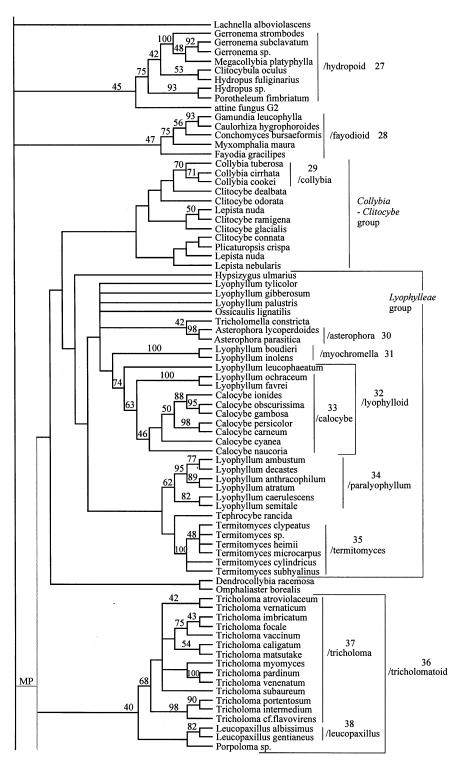


Fig. 2. (continued).

3. Discussion

This study is the first broad systematic treatment of the "euagarics" as they have recently emerged in phylogenetic systematics (summarized in Hibbett and Thorn, 2000). For the first time, this work presents the unambiguous systematic placement among the euagarics of many Gasteromycetes (Table 1) and reduced forms (Table 2) and reveals natural relationships of several taxa for which taxonomic position has been controversial in the past. Some clades revealed in this work correspond in full or in part with taxonomic groups recognized in the last century

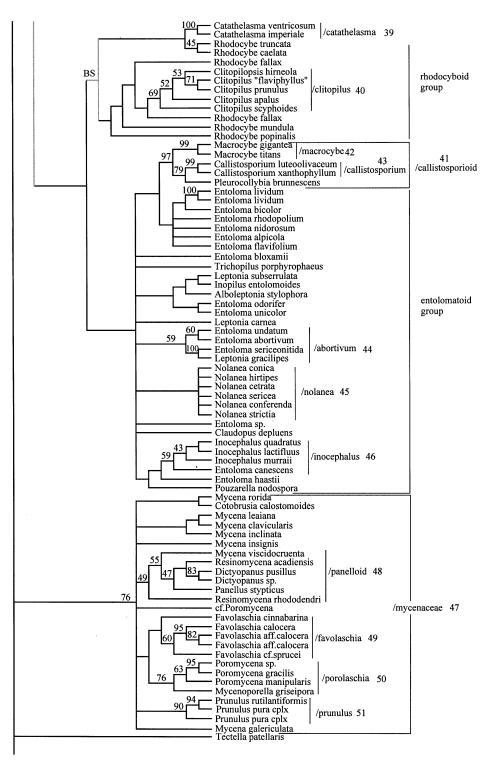


Fig. 2. (continued).

(e.g., in Kühner, 1980; Singer, 1986; Pegler, 1983; Bas et al., 1988; Jülich, 1981); however, many do not. The global taxonomic sampling of this study has allowed the identification of many distinct natural groups from which exemplar taxa could be selected to best represent both the euagarics and the homobasidiomycetes diversity in future phylogenetic studies. Data from other genes are still necessary both to examine to what extent the nLSU phylogeny shown in Figs. 1 and 2 does reflect organismal phylogeny (Doyle, 1992; Maddison, 1997) and to better resolve phylogenetic relationships both among and within clades. By sampling about one tenth of the total number

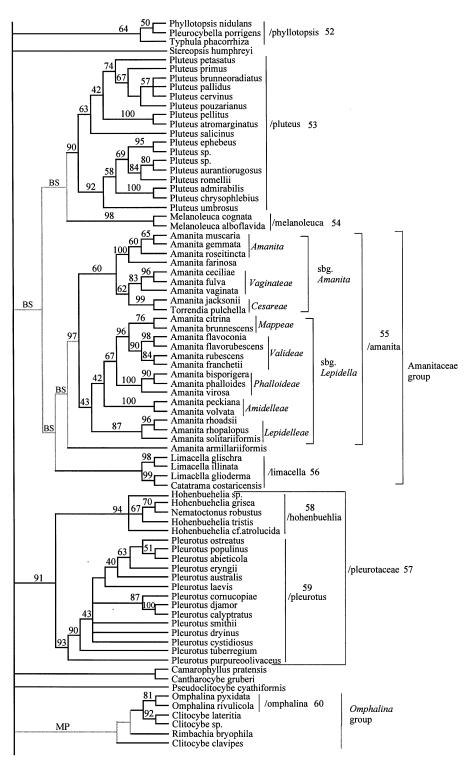


Fig. 2. (continued).

of known species of euagarics (Hawksworth et al., 1995; Hibbett and Thorn, 2000) and many other homobasidiomycetes taxa, this work should also significantly contribute to the development of a molecular database for the identification of new taxa and fungi from environmental samples (Bruns et al., 1998).

3.1. Large-scale phylogenies and higher clades of homobasidiomycetes

A common question in molecular systematics concerns optimization of the sampling ratio between the number of taxa vs characters and the number of char-

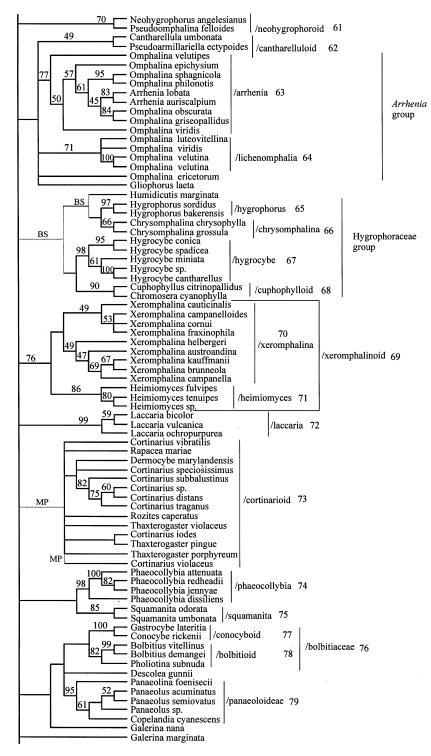


Fig. 2. (continued).

acters that are necessary to recover a correct phylogeny (Lecointre et al., 1994; Berbee et al., 2000). Both theoretical and empirical studies have demonstrated that increasing the taxa/characters ratio generally results in a decrease of statistical support in phylogenetic trees, especially at deeper nodes. However, it has also been shown that increasing taxon sampling increases accuracy of phylogenetic reconstruction (Hillis, 1996, 1998). In this study, the number of taxa sampled (877) was about twice higher than the number of parsimony-informative characters sampled (445). Therefore, high statistical support for deeper nodes was unlikely to be attainable. In contrast, the recent homobasidiomycetes phylogeny of Binder and Hibbett (2002) used a much

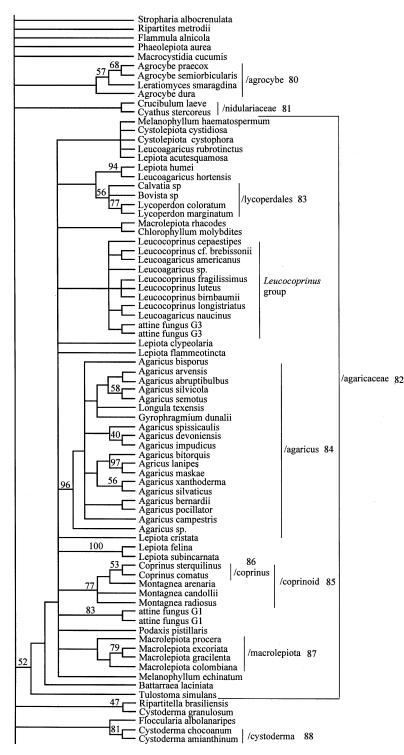


Fig. 2. (continued).

lower taxa/characters ratio, consisting of 83 taxa and 1114 parsimony-informative characters (produced from sequence data from four ribosomal genes). It is therefore helpful to compare results from these two studies.

Our analyses recover six of the eight homobasidiomycetes clades revealed in Binder and Hibbett (2002), but with lower bootstrap support. Both studies poorly resolve basal relationships between the homobasidiomycetes lineages, but both suggest a more basal position of the cantharelloid, gomphales-phallales, and thelephoroid clades. A major result in Binder and Hibbett (2002) was the strong bootstrap statistical support for a sister group relationship between the euagarics and the boletes (90% BS). This relationship

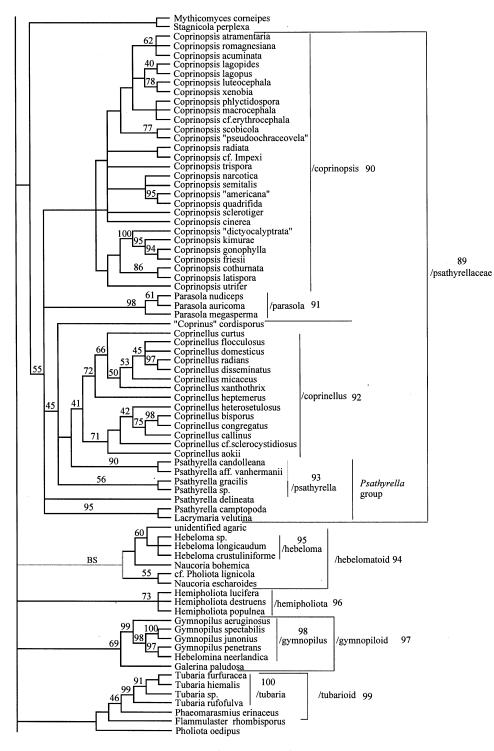


Fig. 2. (continued).

was only weakly suggested in earlier studies that sampled fewer characters (Hibbett et al., 1997; Fig. 5 in Moncalvo et al., 2000) and in the large-scale analysis presented here (< 40% BS; Fig. 2). Another significant result in Binder and Hibbett (2002) was the well-supported placement of *Hygrocybe* and *Humidicutis* (Hygrophoraceae) at the base of the euagarics (85% BS), which in other studies were found either inside (Moncalvo et al., 2000) or outside (Bruns et al., 1998) the euagarics in phylogenetic reconstructions. Based on nLSU evidence, support for a monophyletic Hygrophoraceae is still lacking, and there is no indication of a possible placement of *Hygrophorus/Humidicutis* at the base of the euagarics clade.

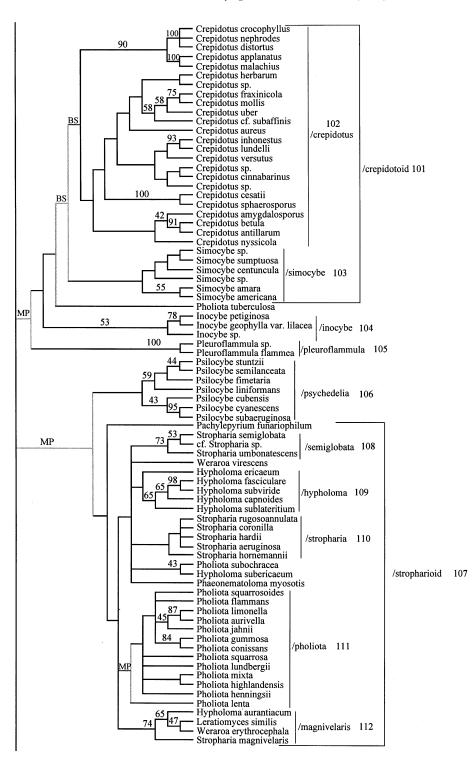


Fig. 2. (continued).

At least three conclusions with regard to homobasidiomycetes phylogeny can be drawn from these and earlier studies: (1) a dense taxon sampling using a limited number of phylogenetic characters—as conducted here—can still recover deeper nodes in the phylogeny and reveal many terminal clades with high bootstrap statistical support; (2) a higher character/taxa ratio—as conducted in Binder and Hibbett (2002)—can boost bootstrap statistical support at deeper nodes, but not always; and (3) ribosomal genes alone are not sufficient to fully resolve natural relationships among higher clades of homobasidiomycetes.

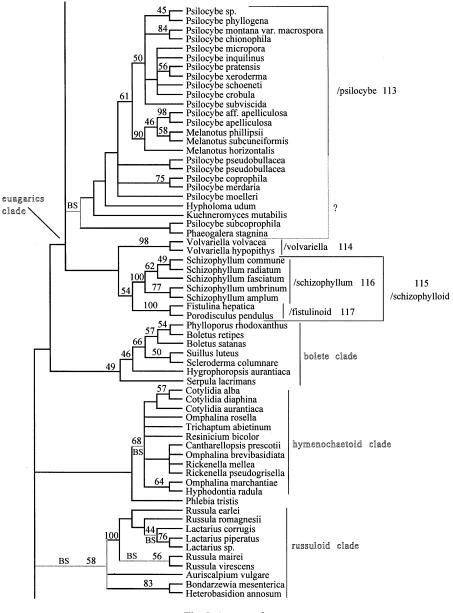


Fig. 2. (continued).

3.2. Morphological and ecological insights derived from the euagarics phylogeny

Gasteromycetization. The nesting of gasteromycetes taxa (e.g., puffballs and allies) among various groups of homobasidiomycetes was already indicated in earlier works (e.g., Baura et al., 1992; Bruns et al., 1989; Kretzer and Bruns, 1997; Hibbett et al., 1997; Peintner et al., 2001). However, as summarized in Table 1, this study is the first to unambiguously place several orders, families, and genera of gasteromycetes within the euagarics. Some of these relationships were already suggested by morphotaxonomists, including affinities between *Torrendia* and *Amanita*, between *Thaxterogaster* and *Cortinarius*, and between *Longula* and *Agaricus*

(Malencon, 1931, 1955; Savile, 1955, 1968; Heim, 1971; Smith, 1973; Bas, 1975; Thiers, 1984; Miller and Walting, 1987; Reijnders, 2000), but others were not. For instance, the placement of the true puffballs (/lycoperdales; clade 83 in Fig. 2) and *Tulostoma* and *Battarraea* in /agaricaceae (clade 82) was not previously suspected by morphotaxonomists. However, it has already been shown that *Agaricus* mushrooms have many biochemical features in common with members of the Lycoperdales (see below). Gasteromycetization appears to have occurred more frequently in certain clades, in particular in /agaricaceae and brown-spored groups.

Cyphelloid and reduced forms. Another syndrome of agaricoid fungi is the reduction of form or cyphellization, which has also occurred multiple times (Fig. 2 and

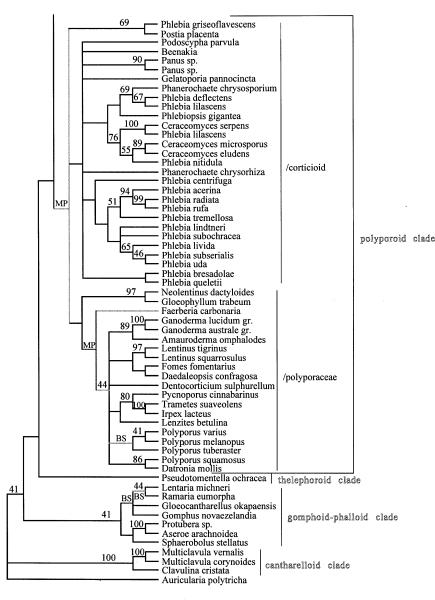


Fig. 2. (continued).

Table 2). For instance, we have identified *Caripia* as a reduced *Gymnopus* (in clade 5), *Stigmatolemma* as a cyphelloid *Resupinatus* (in clade 25), and *Porotheleum* as a cyphelloid member of /hydropoid (clade 27). Reduction and cyphellization are not unique to the euagarics, however, as shown by the placement of *Podoscypha* within the polyporoid clade and of *Cotylidia* within the hymenochaetoid clade.

Polyphyletic origin and instability of the lamellate hymenium. Results from this study support earlier findings that demonstrate the multiple origins of the lamellate hymenium within the basidiomycetes (Hibbett et al., 1997; Thorn et al., 2000; Moncalvo et al., 2000) and reveal for the first time that the hymenochaetoid clade might also include gilled fungi (*Rickenella, Cantharellopsis*, and *Omphalina* pro parte; Fig. 2). A lamellate hymenium is also known in the bolete clade (*Phylloporus*; Bruns et al., 1998, Fig. 2), the polyporoid clade (*Lentinus, Neolentinus, Heliocybe*, and *Faerberia*; Hibbett and Vilgalys, 1993; Hibbett et al., 1997; Thorn et al., 2000, Fig. 2), the russuloid clade (Russulaceae; Hibbett et al., 1997; Moncalvo et al., 2000, Fig. 1), and the cantharelloid clade (Hibbett et al., 1997). Fig. 2 also indicates that transition from a gilled ancestor to a poroid hymenophore architecture has occurred at least three times within the euagarics: /fistulinoid (clade 117) in clade 115 and two times within /mycenaceae (clade 47). In the latter clade, *Dictyopanus* is in a derived position in /panelloid (clade 48), and /favolaschia and /porolaschia (clades 49 and 50) have probably both been derived from a common gilled ancestor.

Ectomycorrhizal vs saprophyte habit. Most clades revealed in this study are only composed of either

Table 1 Classification of gasteromycetoid taxa among the euagarics clade as indicated by molecular data

Gasteromycete taxa	Euagarics clade	References
Lycoperdales	/agaricaceae	This work
Tulostoma	/agaricaceae	This work
Battarraea	/agaricaceae	This work
Podaxis	/agaricaceae	Hopple and
		Vilgalys, 1999
		This work
Montagnea	/agaricaceae/coprinus	This work
Longula	/agaricaceae/agaricus	This work
Gyrophragmium	/agaricaceae/agaricus	This work
Torrendia	/amanita/caesareae	This work
Thaxterogaster	/cortinarioid	This work; Peintner
0		et al., 2001
Protoglossum	/cortinarioid	Peintner et al., 2001
Hymenogaster pro	/cortinarioid	Peintner et al., 2001
parte		,
Quadrispora	/cortinarioid	Peintner et al., 2001
Setchelliogaster	Descolea spp.	Martin and Rac-
Ũ		cabruna, 1999
		Peintner et al., 2001
Descomyces	Descolea spp.	Peintner et al., 2001
Hymenogaster pro	/hebelomatoid	Peintner et al., 2001
parte		,
Gastrocybe	/conocyboid	Hallen and Adams,
		2000; this work
Leratiomyces	/agrocybe	This work
smaragdina	0	
Leratiomyces similis	/stropharioid/	Binder et al., 1997;
	magnivelaris	This work
Weraroa	/stropharioid	Binder et al., 1997;
	· · · · r	this work
Nia	/schizophylloid	Binder et al., 2001
Nidulariales	unresolved position	Hibbett et al., 1997;
		this work

Table 2

Classification of reduced forms among the euagarics clade as indicated by molecular data

Reduced taxa	Euagarics clade	References
Caripia	/omphalotaceae/micromphale	This work
Physalacria	/physalacriaceae/physalacria	This work
Lachnella	euagarics	This work
Gloeostereum	/gloeostereae	This work
Calyptella	/hemimycena	This work
Clavaria fusiformis	? /tricholomopsis	This work
Stigmatolemma	/resupinatus	This work
Porotheleum	/hydropoid	This work
Typhula phacorrhiza	/phyllotopsis	This work
Stereopsis humphreyi	euagarics	This work
Porodisculus	/fistulinoid	This work
Plicaturopsis	euagarics; Clitocybe group?	This work

obligatory saprophytic or ectomycorrhizal taxa. For instance, all members of the larger /agaricaceae (clade 82), /mycenaceae (clade 47), /psathyrellaceae (clade 89), / stropharioid (clade 107), and the possibly monophyletic larger group that includes clades 1–26 are saprophytic. Clades composed only of putatively obligatorily ecto-

mycorrhizal taxa (Singer, 1986; Clémençon, 1997; Norvell, 1998) include /tricholoma (clade 37), /amanita (clade 55), /hygrophorus (clade 65), /cortinarioid (clade 73), /phaeocollybia (clade 74), /hebeloma (clade 95), and /inocybe (clade 104). The existence of numerous, relatively large clades composed of either saprophytic or ectomycorrhizal fungi indicates that these two ecological habits have been relatively stable at least during the more recent radiation of the euagarics. Because of a lack of resolution of basal relationships, our phylogeny can neither fully support nor contradict results from a recent study by Hibbett et al. (2000) suggesting that the ancestor of the euagarics was ectomycorrhizal and that there have been multiple reversals to the saprophytic habit within this clade. However, there are several cases in our phylogeny that suggest that a transition from a saprophyte to a mycorrhizal habit is also possible. For instance, the putatively obligatorily ectomycorrhizal genus Descolea (Horak, 1971) is nested among saprophyte genera of clades 76-79, and both /amanita (clade 55) and /tricholoma (clade 37) also appear to be in derived, rather than basal, positions. All taxa in the Lyophylleae group are known to be saprophytes (Singer, 1986); therefore, the facultative mycorrhizal habit in Lyophyllum shimeji (Ohta, 1994; Agerer and Beenken, 1998), an ally to L. decastes (Moncalvo et al., 1993) in clade 34, is likely to be derived.

Relationships with other cryptogams. Transition from a free-living to an obligatory lichenized habit has occurred at least three times independently within the homobasidiomycetes, as indicated from both anatomical (Oberwinkler, 1984; Redhead and Kuyper, 1987) and molecular (Gargas et al., 1995) evidence. It occurred at least once in the euagarics, with the radiation of /lichenomphalia (clade 64) from within the Arrhenia group. A second group of lichenized basidiomycetes, Dictyonema, may also possibly belong to the euagarics (Gargas et al., 1995); however, this taxon has not been sampled here and its phylogenetic affinities still remain unclear. The third known lichenization event in the homobasidiomycetes has occurred in the cantharelloid clade (Multiclavula), as indicated in both Fig. 2 and Hibbett et al. (1997). A suspected lichen parasite, Gamundia leucophylla (Bigelow, 1979), belongs to the euagarics and nests in a derived position in /fayodioid (clade 28).

The biology of the association between agaric fungi and bryophytes is still not well known, but has been documented in several studies (e.g., Redhead, 1981, 1984). The phylogeny depicted in Fig. 2 reveals that transition to a facultative or an obligatory bryophilous habit has occurred several times independently, apparently always from a saprophyte ancestor. For instance, *Lyophyllum palustris* (parasite on *Sphagnum*; Redhead, 1981) is derived from within the *Lyophylleae* group (which encompasses clades 30–35). *Galerina paludosa* (also a parasite on *Sphagnum*; Redhead, 1981, 1984) is possibly sister group to /gymnopilus (clade 98). The bryophilous or peat-inhabiting species Hypholoma ericaeum, Pholiota myosotis, and Pholiota henningsii (Noordeloos, 1999) are all independently derived from within /stropharioid (clade 107). Hypholoma uda and Phaeogalera stagnina (Redhead, 1979) are independently derived from psilocyboid taxa (at the base of clade 113 in Fig. 2). The fungus-bryophyte association does not appear to be evolutionarily very successful, judging from the limited radiation of bryophyte-associated clades. We observe only four instances of such radiations. (1) Psilocybe montana and P. chionophila are both often associated with mosses (Lamoure, 1977) and are uniquely derived from within /psilocybe (clade 113). (2) The / omphalina (clade 60) is composed of bryophilous species (Omphalina pyxidata and O. rivulicola; Lamoure, 1974) that are possibly a sister group of saprophytic species of *Clitocybe* and monophyletic with another bryophilous taxon, Rimbachia (Redhead, 1984) (Omphalina group in Fig. 2), hence representing one to two independent origins. (3) Nearly all members of /arrhenia (clade 63) are associated with bryophytes (Redhead, 1984). (4) All gilled taxa of /hymenochaete (Omphalina rosella, O. brevibasidita, O. marchantiae, Cantharellopsis prescottii, Rickenella mellea, and R. pseudogrisella) are bryophilous as are some Cotylidia species (S.A. Redhead et al., unpublished), and all may have a single origin (Fig. 2).

Relationships with insects. Chapela et al. (1994) identified three groups of ant-associated fungi (labeled G1–G3). The phylogeny depicted in Fig. 2 indicates that two groups, G1 and G3, are independently derived from within /agaricaceae (clade 82), G3 being possibly monophyletic with members of the Leucocoprinus group (Johnson and Vilgalys, 1998). Group G2 is weakly supported (45% BS) as a sister group of /hydropoid (clade 27). The relatively large, obligatory termite-associate genus Termitomyces (Heim, 1977) forms clade 35 within the Lyophylleae group. The association between euagarics and insects has therefore developed independently several times. These associations appear to be evolutionarily stable, as indicated in our phylogeny by taxonomic radiation of the fungal partner and lack of observed reversal to a free-living habit.

Overall, it appears that ecology supports many natural groups of euagarics better than morphology. It is therefore striking to observe that all earlier major treatments of the Agaricales focused primarily on morphology and microanatomy (e.g., Kühner, 1980; Singer, 1986; Pegler, 1983; Bas et al., 1988; Jülich, 1981; Clémençon, 1997), with limited attention being given to the taxonomic significance of physiological and ecological traits. This might explain why several taxonomic groups erected in the past are not natural. Redhead and Ginns (1985) were the first to introduce the idea of defining agaric genera based in part on their nutritional mode, but also supported by anatomical data, mating strategies, and nuclear status. Based upon wood rot capability, mycorrhizal formation, and nematophagy these authors refined several generic concepts (e.g., in *Lentinula, Lentinus, Pleurotus, and Hypsizygus*) and created new genera (e.g. *Neolentinus* and *Ossicaulis*) that are also supported by the molecular data presented here. For instance, our results support the distinction between *Lentinula* (in clade 8), *Lentinus, and Neolentinus* (the latter two being in /polyporaceae in the polyporoid clade; Fig. 2), in agreement with Thorn et al. (2000), and the segregation of *Ossicaulis* and *Hypsizygus* (both in the *Lyophylleae* group) from *Pleurotus* (in clade 59).

3.3. Clades of euagarics

The reconstruction of a monophyletic euagarics results in the exclusion from that clade of several groups of gilled fungi traditionally classified in the Agaricales (e.g., the Russulaceae and *Rickenella*) and necessitates the inclusion in the clade of several clavaroid, poroid, secotioid, gasteroid, and reduced forms (Tables 1 and 2) that were traditionally classified in other orders of basidiomycetes or else controversially classified. Morphological, physiological, or ecological synapomorphies for the euagarics clade are unknown.

Below, we list and briefly discuss the 117 euagarics clades recognized in Fig. 2. Many clades are directly rooted to the euagarics node. When a clade is not directly rooted to the euagarics node, its containing clade(s) is (are) indicated. For instance, to indicate that clade 3 (/omphalotus) nests in clade 2 (/omphalotoid), which is contained in clade 1 (/omphalotaceae), the following notation is used: /omphalotaceae/omphalotoid/omphalotus. These notations are practical. In future studies, it might be possible to reconcile phylogenetic systematic and traditional taxonomy.

Clade 1 (87% BS): lomphalotaceae. Representative taxa: /lentinuloid and /omphalotoid. This clade includes several genera that were traditionally classified in various families or tribes of Agaricales (Singer, 1986) and one reduced form (*Caripia montagnei*) that was generally placed in the Stereales (Hawksworth et al., 1995). All / omphalotaceae are saprophytic or necrotrophic on wood or litter and have nonamyloid basidiospores that lack a germ pore.

Clade 2 (64% BS): lomphalotoid. Containing clade: / omphalotaceae. Representative taxa: Anthracophyllum, Omphalotus, Lampteromyces, and Neonothopanus. The MPF tree indicates that /omphalotoid is possibly paraphyletic, but monophyly is relatively well supported by bootstrapping (64% BS) and by equally weighted parsimony analysis (data not shown). All members of this clade are lignicolous and have basidiomata with decurrent lamellae or that lack a well-formed central stipe. In general, the context tissues of the basidiomata are poorly differentiated and cystidia are absent. Anthraco-

phyllum, Lampteromyces, and Omphalotus species have all been shown to contain atromentin, as do other unrelated taxa (e.g., several boletes; Gill and Steglich, 1987). Lampteromyces and Omphalotus species also contain illudins and are luminescent and toxic (Singer, 1986). Neonothopanus nambi (reported as Pleurotus eugrammus; see Petersen and Krisai-Greilhuber, 1999) has also been reported to be luminescent (Corner, 1981), but this report needs confirmation.

Clade 3 (75% BS): lomphalotus. Containing clades: / omphalotaceae/omphalotoid. Representative taxa: *Omphalotus* spp. and *Lampteromyces japonicus.* The tree topology in Fig. 2 suggests that these two generic names are possibly synonymous.

Clade 4 (88% BS): Ilentinuloid. Containing clade: / omphalotaceae. Representative taxa: Caripia, Gymnopus, Lentinula, Marasmiellus pro parte, Marasmius pro parte [excl. type], Micromphale, Rhodocollybia, and Setulipes. Close affinities between members of this clade have not been previously suggested. However, members of /lentinuloid share several characteristics. They all have pale, nonamyloid spores with a thin or secondarily thickened wall and no germ pore. Hyphae in the basidiomata often thicken and subsequently impart revivability to the carpophores. Several lentinuloideae taxa produce glutamyl-peptides which are precursors of compounds with a polysulfide smell (Gmelin et al., 1976).

Clade 5 (76% BS): *micromphale*. Containing clades: /omphalotaceae/lentinuloid. Representative taxa: Gymnopus pro parte, Caripia, Setulipes, and Micromphale. The type species of both Setulipes (S. androsaceus) and Micromphale (M. foetida) nest in this clade. Our results support segregation of Setulipes from Marasmius (Antonin, 1987) since the type of the latter genus, M. rotula, is in Clade 21. Micromphale is polyphyletic since *M. perforans*, although also belonging to this clade, does not cluster with M. foetida. Gymnopus sensu Halling (1983) and Antonin et al. (1997) is also polyphyletic, with its members nesting in both this clade and clade 7. Caripia, which produces highly reduced basidiomata, is apparently derived from *Gymnopus* species, which has not been previously suspected.

Clade 6 (97% BS): *lscorodonius*. Containing clades: / omphalotaceae/lentinuloid. Representative taxa: *Marasmius scorodonius* and *Marasmiellus opacus*. A possible relationship between these two species has never been suspected before and is difficult to explain based on morphological or anatomical characters.

Clade 7 (58% BS): Irhodocollybia. Containing clades: /omphalotaceae/lentinuloid. Representative taxa: Rhodocollybia maculata, Marasmiellus ramealis, and Gymnopus pro parte. Marasmiellus is polyphyletic, with M. ramealis clustering in /rhodocollybia and M. opacus in / scorodonius. It still remains unknown where its type species, M. juniperinus, belongs. *Clade 8 (89% BS): llentinula*. Containing clades: / omphalotaceae/lentinuloid. This clade corresponds to the genus *Lentinula* Earle.

Clade 9 (71% BS): *lphysalacriaceae*. Representative taxa: /physalacrioid and *Armillaria*. Although Physalacriaceae was originally conceived for clavaroid fungi (Corner, 1970), inclusion of *Physalacria* in the Agaricales in the vicinity of *Gloiocephala* by Singer (1951, 1986) is congruent with nLSU phylogeny. Physalacriaceae is apparently the oldest available family name for clade 9; however, it still remains to be demonstrated if the type species of *Physalacria P. inflata* belongs to this clade.

Clade 10 (65% BS): lphysalacrioid. Containing clade: /physalacriaceae. Representative taxa: Cyptotrama, Flammulina, Gloiocephala, Oudemansiella, Physalacria aff. orinocensis, Rhizomarasmius, Strobilurus, Xerula, and Oudemansiella. Several morphological similarities exist among these taxa. Most members of /physalacrioid have a hymeniform pileipellis composed of smooth and clavate cells that are often embedded in a gel, and several are characterized by the abundance of secretory, large, presumably multinucleate cystidia either in the hymenium, lamellar edges, pilear, and/or stipe surfaces. Strobilurins (antibiotics) are produced by Oudemansiella, Strobilurus, and Xerula, but also occur in other lineages (Anke, 1997). /Physalacrioid are primary colonizers of dead wood or leaves and do not demonstrate competitive ability of the mycelium to proliferate in soils and heavily colonized or rotten substrates. Flammulina, Rhizomarasmius, Strobilurus, and Xerula are also adapted for colonization of subterranean material. Our results also support the segregation of Marasmius pyrrhocephalus into Rhizomarasmius, as proposed by Petersen (2000), and indicate polyphyly of Gloiocephala sensu Singer (1986).

Clade 11 (65% BS): lphysalacria. Containing clades: *l* physalacriaceae/physalacrioid. Representative taxa: *Physalacria* aff. *orinocensis* and *Gloiocephala spathularia*. Both taxa are reduced agarics.

Clade 12 (95% BS): loudemansiella. Containing clades: /physalacriaceae/physalacrioid. Representative taxa: *Oudemansiella* and *Xerula.* The two names are sometimes considered synonyms (Singer, 1986). A close relationship of these two taxa is confirmed here.

Clade 13 (97% BS): larmillaria. Containing clade: / physalacriaceae. This clade corresponds to the genus Armillaria (Fr.) Staude.

Clade 14 (52% BS): /gloeostereae. Representative taxa: *Gloeostereum* and *Cheimonophyllum.* Both taxa are lignicolous, have fleshy and conchate pilei and inamyloid and white spores, and produce sequiterpene-based antibiotics (Takazawa and Kashino, 1991; Stadler et al., 1994). They have been classified together in the tribus Gloeostereae Ito & Imai (Parmasto, 1968) in the Stereales. *Cheimonophyllum*, but not *Gloeostereum*, was

placed in the Agaricales by Singer (1986). It was recently debated whether *Gloeostereum* is closer to *Phlebia* (/corticioid, in the polyporoid clade) or to the agarics (Petersen and Parmasto, 1993): this study indicates that it is phylogenetically related to the latter group.

Clade 15 (56% BS): /baeosporoid. Representative taxa Baeospora and Hydropus scabripes. Both taxa have amyloid spores, cheilocystidia, dermatocystidia, and sarcodimitic tissues (Redhead, 1987) and form masses of simple conidia in culture (S.A. Redhead, pers. observ.). Hydropus scabripes was originally described in Mycena but based on nLSU data it is phylogenetically unrelated to either the type of Hydropus (H. fuliginarius, in clade 27) or Mycena (M. galericulata, in clade 47). /Baeosporoid is difficult to separate morphologically from /hydropoid (clade 27).

Clade 16 (100% BS): /baeospora. Containing clade: / baeosporoid. This clade corresponds to the genus Baeospora Singer.

Clade 17 (48% BS): Imarasmiaceae. Representative taxa: /tetrapyrgoid and /marasmioid. All members of this clade have pale spores and are saprophytes.

Clade 18 (100% BS): *Itetrapyrgoid*. Containing clade: /marasmiaceae. Representative taxa: *Campanella* and *Tetrapyrgos*. /Tetrapyrgoid is mostly composed of tropical species growing on woody debris. Basidiospores are hyaline, thin walled, smooth, inamyloid, and acyanophilous; the pilear trama is gelatinized (at least partly), inamyloid, with clamp connections; the epicutis has a well-developed or imperfect Rameales structure.

Clade 19 (87% BS): /tetrapyrgos. Containing clades: / marasmiaceae/tetrapyrgoid. This clade corresponds to the genus *Tetrapyrgos* Horak. It differs from its sister group, /campanella, by having tetraradiate basidiospores and a centrally or laterally attached pileus.

Clade 20 (61% BS): /campanella. Containing clades: / marasmiaceae/tetrapyrgoid. Representative taxa: Campanella spp. and an unidentified agaric. The two unidentified collections sampled from the mostly tropical genus Campanella exhibit the typical characters of the genus, as described in Singer (1986). The sister taxon (100% BS) of these two collections is another tropical, unidentified, centrally stipitate fungus with distant but well-developed gills connected with lower ridges or anastomoses (collection JMCR.34). Following Singer (1986), this collection would be classified as a Marasmiellus sensu lato, but its trama is similar to that of Campanella species.

Clade 21 (85% BS): Imarasmioid. Containing clades: Imarasmiaceae. Representative taxa: Chaetocalathus, Crinipellis, Marasmius (incl. Hymenogloea).

Clade 22 (71% BS): /crinipellis. Containing clades: / marasmiaceae/marasmioid. This clade corresponds to the genus *Crinipellis* Pat., which can be distinguished from other members of marasmioid by the presence of pseudoamyloid hairs on the pileus.

Clade 23 (100% BS): *lhemimycena*. Representative taxa: *Hemimycena* spp. and *Calyptella copula*. Our results support the segregation of *Hemimycena* Singer from the bulk species of *Mycena* (clade 47) and indicate that the cyphelloid fungus *Calyptella capula* is derived from *Hemimycena*.

Clade 24 (100% BS): Itricholomopsis. Representative species: Tricholomopsis rutilans, Collybia aurea, and Marasmius rhyssophyllus. A close relationship between the taxa of this clade has never been suspected before. All are saprophytic.

Clade 25 (82% BS): Iresupinatus. Representative taxa: Resupinatus and Stigmatolemma. Molecular data are in agreement with Singer (1986), who indicated a close relationship between Resupinatus and the reduced fungus Stigmatolemma. Our results additionally show that Stigmatolemma is derived from within Resupinatus, making the latter paraphyletic.

Clade 26 (42% BS): ladonis. Representative species: Mycena aurantiidisca, M. adonis, and an unidentified marasmielloid, bioluminescent fungus from the neotropics. These species differ from Mycena sensu stricto (clade 47) by having inamyloid spores.

Clade 27 (75% BS): *lhydropoid*. Representative taxa: *Hydropus* sensu stricto, *Gerronema* pro parte, *Megacollybia*, *Clitocybula*, and *Porotheleum fimbriatum*. The type of the genus *Hydropus*, *H. fuliginarius*, clusters here, whereas *H. scabripes* is in clade 16. Therefore, *Hydropus* sensu Singer (1986) is polyphyletic and should probably be restricted to species with amyloid spores, lacking pleurocystidia, and producing latex, as originally conceived by Kühner (1938). Our results also support Kühner's (1980) placement of *Megacollybia* and *Clitocybula* close to *Hydropus* and indicate that the reduced fungus *Porotheleum fimbriatum* is derived from *Hydropus* species. *Gerronema* sensu Singer (1986) is polyphyletic (Lutzoni, 1997; Moncalvo et al., 2000), but is monophyletic as restricted by Norvell et al. (1994).

Clade 28 (47% BS): Ifayodioid. Representative taxa: Gamundia leucophylla, Caulorhiza hygrophoroides, Conchomyces bursaeformis, Myxomphalia maura, and Fayodia gracilipes. Although the presence of the latter taxon in this clade is moderately supported, there is good statistical support for the monophyly of the other taxa (75% BS). Singer (1986) already recognized affinities between some members of this clade as he considered Gamundia and Myxomphalia synonyms of Fayodia. However, a possible relationship between these taxa and Caulorhiza and Conchomyces has never been suspected before.

Possible monophyly of clades 29–46. The MPF and slightly longer trees and trees produced with reduced data sets (data not shown) all consistently indicate the possible monophyly of a larger clade that includes the *Collybia–Clitocybe* (pro parte) group, the *Lyophylleae* group, /tricholomatoid, and Entolomataceae. However,

there is presently no statistical support to formally recognize this putative clade. Natural relationships between *Tricholoma*, *Lyophylleae*, and Entolomataceae have been speculated by Clémençon (1978, 1997) from similarities in the cell walls of basidiospores and the presence of siderophilous granules in the basidia in *Lyophylleae* and some Entolomataceae taxa.

The Collybia–Clitocybe group. In all our analyses / collybia, Clitocybe spp., Lepista spp., Dendrocollybia, Omphaliaster, and the reduced form Plicaturopsis crispa are recovered as a mono- or paraphyletic group attached to either the Lyophylleae group or /tricholomatoid.

Clade 29 (70% BS): lcollybia. This clade includes the type species of *Collybia* Kummer, *C. tuberosa. Collybia* should be restricted to its type and closely related taxa (including *C. cirrhata* and *C. cookei*; Fig. 2; Hughes et al., 2001).

The Lyophylleae group. Both the MPF tree and the bootstrap tree produced in this study (Fig. 2) are in agreement with earlier studies that place *Termitomyces* in the Lyophylleae (Moncalvo et al., 2000; Hofstetter, 2000). Here we show that Ossicaulis may possibly also belong to this group (a sequence labeled Ossicaulis (GenBank Accession No. AF042625) that clustered with Macrocybe in Moncalvo et al. (2000) has been reidentified as a sequence of Callistosporium).

However, statistical support for recognizing a larger, monophyletic *Lyophylleae* is weak. In particular, the exact positions of *Ossicaulis* (the only taxon of this clade lacking siderophilous granules) and *Hypsizygus* (which clusters outside the group in several suboptimal trees examined) remain unclear. The clades recognized below in the *Lyophylleae* group are in agreement with results of a broader, multigene systematic study of the *Lyophylleae* (Hofstetter, 2000).

Clade 30 (98% BS): lasterophora. This clade belongs to the Lyophylleae group and corresponds to Asterophora Ditmar ex. Link (Redhead and Seifert, 2001). In Fig. 2, the sister group of lasterophora is Tricholomella constricta.

Clade 31 (100% BS): Imyochromella. This clade belongs to the Lyophylleae group. Representative species: Lyophyllum boudieri and L. inolens. /Myochromella is composed of small, collybioid species formerly classified in either Lyophyllum or Tephrocybe, which can be separated from these genera by having a striate and hygrophanous cap (Hofstetter, 2000).

Clade 32 (74% BS): Ilyophylloid. This clade belongs to the Lyophylleae group. Representative taxa: Lyophyllum leucophaeatum (type of Lyophyllum Karst.), L. favrei, L. ochraceum, and Calocybe spp.

Clade 33 (63% BS): *lcalocybe*. Containing clade: *l* lyophylloid, in the *Lyophylleae* group. This clade corresponds to the genus *Calocybe* sensu Singer (1986) with the exclusion of *C. constricta* and the inclusion of *Lyophyllum favrei* and *L. ochraceum*. Therefore, our results

support both the segregation of *C. constricta* in *Tricholomella* (Kalamees, 1992) and a close relationship between *L. favrei* and *L. ochraceum* with *Calocybe* species as indicated in Kühner and Romagnesi (1953).

Clade 34 (62% BS): /paralyophyllum. This clade belongs to the Lyophylleae group. Representative taxa: Lyophyllum ambustum, L. decastes, L. semitale, L. caerulescens, L. anthracophilum, and L. atratrum.

Clade 35 (100% BS): Itermitomyces. This clade belongs to the Lyophylleae group. It corresponds to the termite-associated genus Termitomyces Heim (including Podabrella Singer), which is sister group to the type species of Tephrocybe (T. rancida) in Fig. 2.

Clade 36 (40% BS): Itricholomatoid. Representative taxa: *Tricholoma, Leucopaxillus*, and *Porpoloma.* This clade is composed of fungi with a tricholomatoid habit and a white spore deposit. Our sampling of *Porpoloma* was restricted to a single, unidentified species; therefore a closer examination of this genus is still necessary to fully address its phylogenetic affinities. *Tricholoma* is held to be obligatorily ectomycorrhizal, whereas it is still controversial whether *Porpoloma* and *Leucopaxillus* are ectomycohrizal or saprophytic (Singer, 1986; Clémençon (1997; G. Thorn, pers. obs.)).

Clade 37 (68% BS): Itricholoma. Containing clade: *I* tricholomatoid. This clade corresponds to *Tricholoma* (Fr.) Staude, which is monophyletic only when restricted to ectomycorrhizal taxa (Pegler et al., 1998; Moncalvo et al., 2000).

Clade 38 (82% BS): *lleucopaxillus*. Containing clade: /tricholomatoid. This clade corresponds to the genus *Leucopaxillus* Boursier as described in Singer (1986). In Fig. 2, *Leucopaxillus* is phylogenetically distinct from *Tricholoma* in contrast to a previous report (Moncalvo et al., 2000) that used a mislabeled sequence (*L. albissimus* SAR1-2-90, GenBank Accession No. AF042592, excluded from this study). *Porpoloma* is weakly supported as sister group of *l*leucopaxillus (Fig. 2).

Clade 39 (100% BS): /catathelasma. This clade corresponds to *Catathelasma* Lovejoy, a taxon with problematic classification (Kühner, 1980; Singer, 1986). Analyses of nLSU sequence data consistently place it with two *Rhodocybe* species (Fig. 2), although without significant statistical support. We are not aware of any obvious anatomical, physiological, or ecological similarity between these taxa. Therefore, we consider /catathelasma to have unknown phylogenetic affinity in the euagarics.

Entolomataceae (rhodocyboid and entolomatoid groups in Fig. 2). Modern agaricologists have agreed that the angular-pink-spored agarics (Entoloma sensu lato, Clitopilus, and Rhodocybe) represent a natural group, Entolomataceae (Singer, 1986; Kühner, 1980; Horak, 1980; Baroni, 1981; Baroni and Lodge, 1998). However, there is virtually no molecular support for a monophyletic Entolomataceae in our analyses, but this hypothesis cannot be rejected from our data. In Fig. 2, the Entolomataceae segregates into two statistically weakly supported groups: a rhodocyboid group (*Rho-docybe* and *Clitopilus*) and an entolomatoid group (*Entoloma* sensu lato). Consistently nested in the former group is /catathelasma (clade 39), and frequently nested within the latter group is /callistosporoid (clade 41).

Clade 40 (69% BS): lclitopilus. This clade belongs to the rhodocyboid group in the Entolomataceae. Representative taxa: *Clitopilus* spp. (including the type, *C. prunulus*) and *Clitopilopsis hirneola.*

Clade 41 (97% BS): lcallistosporoid. Representative taxa: *Callistosporium, Macrocybe*, and *Pleurocollybia*. This clade has not previously been recognized. All / callistosporoid are saprophytic and have a white spore print and hyaline, smooth, and inamyloid spores. Pigments are intracellular when present, and the epicutis is composed of filamentous hyphae that are either repent (*Callistosporium* and *Pleurocollybia*) or strongly interwoven (*Macrocybe*).

Clade 42 (99% BS): Imacrocybe. Containing clade: / callistosporoid. This clade corresponds to *Macrocybe* Pegler.

Clade 43 (99% BS): *lcallistosporium*. Containing clade: *lcallistosporoid*. This clade corresponds to *Callistosporium* Singer. Its sister group is *Pleurocollybia brunnescens* (79% BS).

Clade 44 (59% BS): labortivum. This clade belongs to the entolomatoid group in the Entolomataceae. Representative species: Entoloma undatum, E. abortivum, E. sericeonitida, and Leptonia gracilipes.

Clade 45 (< 40% BS): *Inolanea*. This clade belongs to the entolomatoid group in the Entolomataceae. It corresponds to the genus *Nolanea* (Fr.) Quélet, which may therefore warrant distinction from *Entoloma*.

Clade 46 (59% BS): linocephalus. This clade belongs to the entolomatoid group in the Entolomataceae. It corresponds to the genus *Inocephalus* (Noordeloos) P.D. Orton (Baroni and Hailing, 2000), with the inclusion of *Entoloma canescens.*

Clade 47 (76% BS): Imycenaceae. Representative taxa: Mycena pro parte (including its type, M. galericulata), Resinomycena, Panellus stypticus (type of Panellus,) Dictyopanus, Favolaschia, Poromycena and Filoboletus spp., Prunulus, and Mycenoporella griseipora. Members of this clade of pale-spored agarics are morphologically very diverse, but amyloid spores are nearly always formed and dextrinoid tissues are frequent. Nearly all are primary colonizers of wood or leaves (they are rarely found on humus). Mycena sensu Singer (1986) is a polyphyletic genus with members clustering both in this clade and /adonis (clade26). It should therefore be restricted to taxa around its type species, M. galericulata. This study reveals a previously unsuspected relationship between Mycena and Panellus (including *Dictyopanus*). It also unambiguously places

the tropical, poroid genus *Favolaschia* among the euagarics.

Clade 48 (49% BS): *lpanelloid*. Containing clade: / mycenaceae. Representative taxa: *Resinomycena*, *Panellus*, *Dictyopanus*, and *Mycena viscidocruenta*. A natural relationship between these taxa has never been suspected before.

Clade 49 (<50% BS): Ifavolaschia. Containing clade: /mycenaceae. This clade corresponds to the genus Favolaschia (Pat.) Pat.

Clade 50 (76% BS): *porolaschia*. Containing clade: / mycenaceae. Representative taxa: *Poromycena* and *Filoboletus* spp. and *Mycenoporella griseipora*. All members of this clade have a poroid hymenium. However, it also appears that additional sampling of mycenaceae from the tropics breaks down generic distinction between poroid and gilled mycenoid taxa (J. M. Moncalvo, pers. obs.).

Clade 51 (90% BS): prunulus. Containing clade:/ mycenaceae. This clade corresponds to Mycena sect. Purae in Singer (1986), for which the generic name Prunulus S.F. Gray is available (Redhead et al., 2001).

Clade 52 (64% BS): lphyllotopsis. Representative taxa: *Phyllotopsis nidulans, Pleurocybella porrigens*, and *Typhula phacorrhiza. Typhula* was previously classified in the Cantharellales (Hawksworth et al., 1995), but shown to be among the euagarics by Hibbett et al. (1997). Relationships between taxa of this clade have not been previously suspected, and we are still unaware of any morphological or anatomical character that could unify them.

Clade 53 (90% BS): lpluteus. This clade corresponds to *Pluteus* Fries. At least two well-supported clades can be distinguished within this genus: one clade (63% BS) includes only species of section *Pluteus*, and one clade (92% BS) is composed of members of both sections *Hispidoderma* Fayod and *Celluloderma* Fayod.

Clade 54 (98% BS): Imelanoleuca. This clade corresponds to Melanoleuca Pat. This genus can be distinguished by several unique characters, but its relationships with other pale-spored agarics have never been clear (see for instance Singer, 1986). In our analyses, Melanoleuca clusters with Pluteus but with weak bootstrap support (<40%). The two taxa share similar stature and pigments, but differ significantly in their microanatomy.

Clade 55 (97% BS): lamanita. This clade corresponds to the genus Amanita Persoon. Monophyly of the ectomycorrhizal Amanita taxa is strongly supported (97% BS); a potentially nonectomycorrhizal species, A. armillariformes (Miller et al., 1990), clusters weakly with / amanita in the bootstrap tree and is not monophyletic with other Amanita species in the MPF tree. There is a good agreement between molecular and morphological data for infrageneric segregation of the genus, as shown in Fig. 2 and in earlier studies (Drehmel et al., 1999; Weiss et al., 1998; Moncalvo et al., 2000b). This work shows for the first time that the secotioid fungus *Torrendia* belongs to *Amanita* subsection *Caesareae* (99% BS).

Clade 56 (<40% BS): llimacella. This clade corresponds to the genus *Limacella* Earle, with inclusion of the monotypic genus *Catatrama* (Franco-Molano, 1991). The two taxa share a bilateral lamellar trama. viscid pilei, and amyloid spores. A sister group relationship between *Limacella* and *Amanita* (Amanitaceae) is weakly supported in our analyses.

Clade 57 (91% BS): lpleurotaceae. Representative taxa: *Hohenbuehlia* (including its *Nematoctonus* anamorphs) and *Pleurotus.* The production of nematode-trapping organs and nematophagy are synapomorphies for this clade (Moncalvo et al., 2000; Thorn et al., 2000).

Clade 58 (94% BS): *Ihohenbuehlia*. Containing clade: /pleurotaceae. This clade corresponds to the genus *Hohenbuehlia* Schulzer, including its *Nematoctonus* anamorphs.

Clade 59 (93% BS): *lpleurotus*. Containing clade: / pleurotaceae. This clade corresponds to the genus *Pleurotus* (Fr.) Quélet.

Omphalinoid and hygrophoroid taxa. Most members of *Omphalina* sensu lato and Hygrophoraceae sensu singer (1986) are intermixed in clades 60–71 and related groups. These taxa have white, generally smooth, thinwalled spores; pilei are generally brightly pigmented and often have attached or decurrent gills. Many omphalinoid and hygrophoroid taxa form obligatory or facultative association with bryophytes or algae (see above). Three groups can be recognized in Fig. 2, although statistical support for each group remains weak: they are the *Omphalina* group, the *Arrhenia* group, and the Hygrophoraceae group.

Clade 60 (81% BS): lomphalina. Representative taxa: Omphalina pyxidata and O. rivulicola. Both species are bryophilous (Lamoure, 1974). The former species is the conserved type for Omphalina (Greuter et al., 2000). Omphalina s.s. Singer (1986) has already been shown to be polyphyletic (Lutzoni, 1997; Moncalvo et al., 2000). In Fig. 2, Omphalina species sensu lato are in this clade and in the Arrhenia group and the hymenochaetoid clade. Both the MPF tree and the bootstrap (<50% BS) tree indicate possible monophyly of /omphalina with another bryophyte-associate taxon, Rimbachia (see above), and saprophyte Clitocybe species (Omphalina group; Fig. 2).

Clade 61 (70% BS): Ineohygrophoroid. Representative taxa: Neohygrophorus angelesianus and Pseudoomphalina felloides. A close phylogenetic relationship between these two species has never been suspected before.

The Arrhenia group (clades 61–64). Both the MPF tree and the bootstrap (<50% BS) tree indicate possible monophyly of the core *Omphalina* (excluding the type species) with members of *Arrhenia, Cantharellula*,

Pseudoarmillariella, and *Gliophorus*. Several taxa in this group are associated with cryptogams (see above).

Clade 62 (49% BS): lcantharelluloid. This clade belongs to the Arrhenia group. Representative taxa: Cantharellula umbonata and Pseudoarmillariella ectypoides. Affinities between these two taxa were already suspected by Singer, who first recognized Pseudoarmillariella as a subgenus of Cantharellula before recognizing it at the genus level (Singer, 1986).

Clade 63 (77% BS): larrhenia. This clade belongs to the Arrhenia group. Representative taxa: Arrhenia auriscalpium, A. lobata, Omphalina velutipes, O. epichysium, O. sphagnicola, O. philonotis, O. obscurata, O. griseopallidus, and O. viridis. Clade 63 includes the type species of Arrhenia (A. auriscalpium) and the core of the nonlichenized Omphalina species.

Clade 64 (71% BS): llichenomphalia. This clade belongs to the Arrhenia group. Representative taxa: Omphalina luteovitellina, O. hudsoniana, O. velutina, and O. grisella. Lichenization is a synapomorphy for this clade. Monophyly of /lichenomphalia with another lichenized fungus, O. ericetorum, is not evident in Fig. 2 but has been shown in Lutzoni (1997). These species correspond to "Phytoconis" sensu Redhead and Kuyper (1987).

The Hygrophoraceae group (clades 65–68). There is virtually no support for a monophyletic Hyrophoraceae sensu auth. in our analyses, as indicated by the placement of *Gliophorus laeta* in the *Arrhenia* group and the possible relationship between *Hygrophorus* and *Chrysomphalina* species (the latter being traditionally classified in the Tricholomataceae). However, the core genera of Hygrophoraceae (*Hygrophorus, Hygrocybe, Humidicutis*, and *Cuphophyllus*) cluster together in the bootstrap tree (<40% BS).

Clade 65 (97% BS): lhygrophorus. This clade belongs to the Hygrophoraceae group and corresponds to *Hygrophorus* Fr., a genus that can be distinguished by its ectomycorrhizal habit and the presence of a bilateral lamellar trama.

Clade 66 (66% BS): *lchrysomphalina*. This clade belongs to the Hygrophoraceae group. It corresponds to the genus *Chrysomphalina* Clémençon. Our results support the segregation of this genus from both *Gerronema* and *Omphalina*, as discussed in Clémençon (1982).

Clade 67 (98% BS): *Ihygrocybe*. This clade belongs to the Hygrophoraceae group. It corresponds to the genus *Hygrocybe* Kummer, including *Pseudohygrocybe* Kovalenko. In Fig. 2, species of *Pseudohygrocybe* (61% BS) are separated from *Hygrocybe* sensu stricto (95% BS).

Clade 68 (90% BS): /cuphophylloid. This clade belongs to the Hygrophoraceae group. Representative taxa: *Chromosera cyanophylla* and *Cuphophyllus citrinopallidus.* These two genera were segregated from *Hygrocybe* (see Redhead et al., 1995). Results of our analysis indicate that /cuphophylloid could be sister group of / hygrocybe, but statistical support is weak (<40% BS).

Clade 69 (76% BS): /xeromphalinoid. Representative taxa: Xeromphalina and Heimiomyces. A close relationship between these two genera was already recognized by Singer (1986), who considered Heimiomyces a subgenus of Xeromphalina.

Clade 70 (<40% BS): /xeromphalina. Containing clade: /xeromphalinoid. This clade corresponds to *Xeromphalina* Kühner & Maire.

Clade 71 (86% BS): /heimiomyces. Containing clade: /xeromphalinoid. This clade corresponds to *Heimiomyces* Singer.

Clade 72 (99% BS): llaccaria. This clade corresponds to *Laccaria* Berk. & Br. Monophyly of this ectomycorrhizal, white-spored genus is strongly supported by nLSU sequence data. However, its phylogenetic relationships are still unresolved. In earlier studies (Bruns et al., 1998; Moncalvo et al., 2000) *Laccaria* clustered with brown-spored taxa, but statistical support was weak.

Clade 73 (0% BS): /cortinarioid. Representative taxa: Cortinarius, Rozites, Dermocybe, Rapacea, and the gasteromycete Thaxterogaster. All members of this clade are obligatorily ectomycorrhizal. Monophyly of these taxa is weakly supported in our analyses. However, the MPF tree is consistent with the multigene phylogeny of U. Peintner et al. (unpublished).

Clade 74 (98% BS): lphaeocollybia. This clade corresponds to *Phaeocollybia* Heim.

Clade 75 (85% BS): lsquamanita. This clade corresponds to *Squamanita* Imbach.

Clade 76(<40% *BS*): */bolbitiaceae*. Representative taxa: /bolbitioid and /conocyboid. This clade corresponds in part to the family Bolbitiaceae in Singer (1986). It is possibly a sister group of /panaeoloideae. *Descolea*, included in Bolbitiaceae by Singer (1986), nests in an unresolved position between /bolbitiaceae and /panaeoloideae (Fig. 2).

Clade 77 (100% BS): /conocyboid. Containing clade: / bolbitiaceae. Representative taxa: Gastrocybe and Conocybe. Gastrocybe appears to be a secotioid Conocybe (Hallen and Adams, 2000; Fig. 2).

Clade 78 (82% BS): *Ibolbitioideae*. Containing clade: /bolbitiaceae. Representative taxa: *Bolbitius* and *Pholiotina subnuda*. *Pholiotina* has an overall morphology closer to *Conocybe* (Singer, 1986) but *P. subnuda* appears to be phylogenetically closer to *Bolbitius*.

Clade 79 (95% BS): lpanaeoloideae. Representative taxa: *Panaeolina, Panaeolus,* and *Copelandia*. This clade corresponds to Panaeoloideae Singer (1986) in Coprinaceae (= Psathyrellaceae; Redhead et al., 2001), but our results indicate that it is possibly closer to /bolbitiaceae.

Clade 80 (<40% BS): lagrocybe. This clade corresponds to the genus *Agrocybe* Fayod with the inclusion of the gasteromycete *Leratiomyces smaragdina. Leratiomyces* appears to be polyphyletic, with *L. similis* nesting in clade 113.

Clade 81 (<40% BS): Inidulariaceae. Representative taxa: Crucibulum laeve and Cyathus stercoreus. The placement of the bird nest fungi (Nidulariales) in the euagarics was first demonstrated by Hibbett et al. (1997) and is supported in this study. However, its exact position among the euagarics remains unknown.

Clade 82 (52% BS): lagaricaceae. Representative taxa: /lycoperdales, /agaricus, /leucocoprinus, /coprinoid, /macrolepiota, Podaxis, Lepiota, Leucoagaricus, Melanophyllum, Chlorophyllum, Cystolepiota, Battarraea, Tulostoma, and two groups of attine fungi. This clade represents a morphologically highly diverse assemblage of taxa, including traditional orders and genera of gasteromycetes and hymenomycetes. However, virtually all the taxa in the clade occur on the soil (none are primary wood decay organisms and none are known to be ectomycorrhizal) and fairy ring formation is a common feature in the Agaricaceae. The true puffballs (Lycoperdales) have many biochemical features in common with Agaricus, such as formation of urea, concentration of silver, mercury, selenium, and arsenic, and biosynthesis of methylmercury and arsenobetaine (Byrne et al., 1979; Slejkovec et al., 1997; Tjakko Stijve, pers. comm. to H.C.).

Clade 83 (56% BS): llycoperdales. Containing clade: / agaricaeae. This clade corresponds to the traditional gasteromycete order Lycoperdales.

Clade 84 (96% BS): lagaricus. Containing clade: / agaricaeae. This clade corresponds to Agaricus Fries, with the inclusion of the secotioid genera Gyrophragmium and Longula.

Clade 85 (77% BS): /coprinoid. Containing clade: / agaricaeae. Representative taxa: /coprinus and Montagnea. A close affinity between Coprinus sensu stricto (Redhead et al., 2001) and the secotioid genus Montagnea is established here.

Clade 86 (53% BS): lcoprinus. Containing clade: *l* agaricaeae. This clade corresponds to *Coprinus* Persoon as emended by Redhead et al. (2001).

Clade 87 (<40% BS): /macrolepiota Containing clade: /agaricaeae. This clade corresponds to *Macrolepiota* Singer.

Clade 88 (81% BS): lcystoderma. Containing clade: / agaricaeae. Representative taxa: Cystoderma amianthinum (type of Cystoderma Fayod) and C. chocoanum. The separate placement of Cystoderma granulosum, which clusters with Ripartitella (Johnson and Vilgalys, 1998; Fig. 2) remains unexplained and needs further scrutiny. The placement of Floccularia as sister group to /cystoderma is weakly supported by bootstrapping (<50% BS), and there is no obvious morphological character to explain this relationship.

Clade 89 (55% BS): /psathyrellaceae. Representative taxa: *Psathyrella, Lacrymaria,* /coprinopsis, /coprinellus, and /parasola. This clade corresponds to the family Psathyrellaceae as defined in Redhead et al. (2001).

Clade 90 (<40% BS): lcoprinopsis. Containing clade: /psathyrellaceae. This clade corresponds to the genus *Coprinopsis* as described in Redhead et al. (2001).

Clade 91 (98% BS): |parasola. Containing clade: / psathyrellaceae. This clade corresponds to the genus *Parasola* as described in Redhead et al. (2001).

Clade 92 (41% BS): lcoprinellus. Containing clade: / psathyrellaceae. This clade corresponds to the genus Coprinellus as described in Redhead et al. (2001).

Clade 93 (56% BS): lpsathyrella. Containing clade: / psathyrellaceae. Representative species: Psathyrella gracilis (type species of Psathyrella). The results in Fig. 2 question monophyly of the large genus Psathyrella.

Clade 94 (<40% BS): *lhebelomatoid*. Representative taxa: *Naucoria*, and *l*hebeloma. This large-scale analysis supports a close relationship between the ectomy-corrhizal genera *Hebeloma* and *Naucoria* and indicates that the latter genus is probably not monophyletic. These results are in agreement with other molecular studies (Aanen et al., 2000; E. Horak et al., unpublished; U. Peintner et al., unpublished). The placement in this clade of *Pholiota lignicola* is suspect and needs confirmation.

Clade 95 (60% BS): *lhebeloma*. Containing clade: *l* hebelomatoid. This clade corresponds to *Hebeloma* Kummer.

Clade 96 (73% BS): *lhemipholiota*. This clade corresponds to *Hemipholiota* (Singer) Romagn. ex Bon.

Clade 97 (69% *BS*): */gymnopiloid*. Representative taxa: */gymnopilus* and *Galerina paludosa*. *Galerina* appears to be a polyphyletic genus, with its members clustering here and close to /panaeolideae (clade 79).

Clade 98 (99% BS): /gymnopilus. Containing clade: / gymnopiloid. This clade corresponds to the saprophytic genus Gymnopilus Karsten with the inclusion of Hebelomina Maire. Hebelomina was erected for taxa that resemble Hebeloma but are distinguished by having smooth and hyaline spores (Singer, 1986). This study confirms a close affinity of Hebelomina with dark-spored taxa, but indicates that the taxon is derived from within Gymnopilus rather than being close to Hebeloma (in clade 95). The ecology of *Hebelomina* is unclear. Singer (1986) wrote that the taxon is "probably ectomycorrhizal." Because natural groups revealed by rDNA phylogenies are generally largely congruent with ecology and Gymnopilus is known not to be ectomycorrhizal, our results would suggest that Hebelomina is probably not ectomycorrhizal.

Clade 99 (46% BS): Itubarioid. Representative taxa: Tubaria and Phaeomarasmius. Singer (1986) classified the former genus in Crepidotaceae and the latter in Strophariaceae; however, a close relationship between these two taxa was already indicated by Kühner (1980).

Clade 100 (99% BS): /tubaria. Containing clade: / tubarioid. This clade corresponds to *Tubaria* (W.G. Smith) Gillet, as described in Singer (1986).

Clade 101 (<40% BS): lcrepidotoid. Representative taxa: *Crepidotus* and *Simocybe.* These two genera are reciprocally monophyletic in the bootstrap analysis, but not in the MPF tree. Reciprocal monophyly is also supported from an independent phylogenetic analysis in Aime (2001). A close relationship between *Crepidotus* and *Simocybe* is also apparent from morphology (Singer, 1986; Kühner, 1980).

Clade 102 (<40% BS): /crepidotus. Containing clade: /crepidotoid. This clade corresponds to *Crepidotus* Kummer.

Clade 103 (<40% BS): /simocybe. Containing clade: / crepidotoid. This clade corresponds to *Simocybe* Karsten.

Clade 104 (53% BS): linocybe. This clade corresponds to the genus *Inocybe* Fries. In both the MPF tree and the bootstrap tree linocybe comes close to /crepidotoid, but with weak statistical support (<40% BS).

Clade 105 (100% BS): lpleuroflammula. This clade corresponds to Pleuroflammula Singer.

Clade 106(<40% BS): /psychedelia. Representative taxa: Psilocybe cubensis, P. semilanceata, P. stuntzii, P. flmetaria, P. liniformans, P. cyanescens, and P. subaeruginosa. This clade is composed only of psilocybincontaining (hallucinogenic) species of Psilocybe, whereas nonhallucinogenic Psilocybe species are in clade 112. Psilocybin is also produced in other mushrooms, for instance in Copelandia and Panaeolus (in clade 79) and several Pluteus species (in clade 53) (Stijve and Bonnard, 1986; Stamets, 1996). /Psychedelia is monophyletic with /stropharioid in the MPF tree, but this relationship is not supported by bootstrapping.

Clade 107 (<40% BS): Istropharioid. Representative taxa: Istropharia, Ipholiota, Isemiglobata /magnivelaris, Phaeonematoloma, Hypholoma spp, and the secotioids Weraroa spp. and Leratiomyces similis. Chrysocystidia are present in all members of this clade, except in some species in /magnivelaris (e.g., in Stropharia magnivelaris). They are also absent in Pachylepyrium, the putative sister group of /stropharioid (Fig. 2).

Clade 108 (73% BS): lsemiglobata. Containing clade: lstropharioid. Representative taxa: Stropharia semiglobata and S. umbonatescens. These two Stropharia species may not be monophyletic with the type of the genus, S. aeruginosa.

Clade 109 (<40% BS): /hypholoma. Containing clade: /stropharioid. Representative taxa: Hypholoma sublateritium. H. capnoides, H. subviride, H. fasciculare, and H. ericaeum. This clade is composed of the core species of Hypholoma Kummer. However, this genus is probably polyphyletic: in our analyses H. subericaeum clusters with Pholiota subochracea, H. aurantiacum is in clade 111, and H. udum is basal to Psilocybe spp. in clade 113. H. udum is the only species with chrysocystidia that classifies outside /stropharioid; the placement of this species therefore needs further scrutiny. Clade 110 (<40% BS): /stropharia. Containing clade: /stropharioid. Representative taxa: Stropharia aeruginosa, S. rugosoannulata, S. coronilla, S. hardii, and S. hornemannii. This clade includes the type of the genus Stropharia, S. aeruginosa, and closely related species. Our results suggest that Stropharia magnivelaris (in clade 112), S. albocrenulata (in an isolated position outside /stropharioid), and possibly also S. semiglobata and S. umbonatescens (both in clade 108) should be excluded from this genus.

Clade 111 (<40% BS): lpholiota. Containing clade: / stropharioid. This clade corresponds to the core of the genus Pholiota Kummer, including its type species (P. squarrosa). Our results support the separation of Hemipholiota (clade 96) from Pholiota and suggest the exclusion from Pholiota of P. oedipus (close to clade 99), P. tuberculosa (in an isolate position between clades 103 and 104 in Fig. 2), and possibly P. subochracea (which clusters with Hypholoma subericaeum in /stropharioid) and P. lignicola (in a doubtful position in clade 94).

Clade 112 (74% BS): Imagnivelaris. Containing clade: Istropharioid. Representative taxa: Stropharia magnivelaris, Hypholoma aurantiacum, and the secotioids Leratiomyces similis and Weraroa erythrocephala.

Clade 113 (61% BS): *Ipsilocybe*. Representative taxa: *Psilocybe montana* (type of *Psilocybe* in Singer, 1986) and related non-psilocybe-containing species (as listed in Fig. 2), including *Melanotus*. Monophyly of *Psilocybe* is questioned by nLSU data: hallucinogenic species are separated in clade 106, and *Psilocybe subcoprophila* clusters with *Phaeogalera stagnina* at the base of clade 113. Based on Fig. 2, *Ipsilocybe may possibly also in*clude *Kuehneromyces, Phaeogalera*, and *Hypholoma udum*.

Clade 114 (98% BS): lvolvariella. This clade corresponds to *Volvariella* Spegazzini. In the results depicted in Fig. 2 and other analyses (data not shown) /volvariella consistently clusters with /schizophylloid but always with a weak statistical support.

Clade 115 (54% BS): lschizophylloid. Representative taxa: Schizophyllum, Fistulina, and Porodisculus pendulus. This study supports the findings by Hibbett et al. (1997) showing that Schizophyllum and Fistulina are closely related and belong to the euagarics.

Clade 116 (100% BS): /schizophyllum. Containing clade: /schizophylloid. Clade 116 corresponds to Schizophyllum Fr.

Clade 117 (100% BS): *Ifistulinoid*. Containing clade: / schizophylloid. Representative taxa: *Fistulina* and the reduced fungus *Porodisculus pendulus*. A possible affinity of *Fistulina* with both agarics and reduced forms was already indicated by Singer (1986, p. 843) who stated that "the gelatinizing of the trama of *Fistulina* and the acanthophysoid hairs of *Pseudofistulina* suggest [...] strong similarities with cyphelloid reduced agarics [...]. I am not at present ready to introduce Fistulinaceae as a

family of the Agaricales, because I believe that additional studies will be required to substantiate this position."

Euagarics Incertae Sedis. Natural relationships of several species included in this study remain unresolved. However, our results support the placement in the euagarics of the following taxa: Clavaria fusiformis (possibly related to Tricholomopsis in clade 24), Pleurotopsis longinqua, Lachnella alboviolascens, Tectella patellaris, Stereopsis humphreyi, Cantharocybe gruberi, Camarophyllus pratensis, Pseudoclitocybe cyathiformis, Stropharia albocrenulata, Ripartites, Flammula alnicola, Phaeolepiota aurea, Macrocystidia cucumis, Floccularia albolanaripes, Pholiota oedipus, Pholiota tuberculosa, Laccaria, Squamanita, Phaeocollybia, Descolea, Galerina spp. (this genus does not appear to be monophyletic), Agrocybe, Cystoderma, Ripartitella, Mythicomyces, Stagnicola, Hemipholiota, Flammulaster, Inocybe, Pleuroflammula, and Nidulariaceae.

4. Conclusions

Ribosomal DNA systematics has become a standard method in fungal taxonomy. It is therefore expected that in the coming years rDNA sequence data for the large majority of homobasidiomycetes will be produced. In nearly all studies published to date, rDNA data have been useful but not entirely sufficient for reconstructing fully resolved, well-supported phylogenies, for at least two reasons: (1) rDNA genes cannot always resolve relationships at every taxonomic level (Bruns et al., 1991) and (2) rDNA cannot provide the number of molecular characters needed to provide statistical support at all taxonomic levels (Berbee et al., 2000). In consequence, several laboratories are beginning to develop primers for PCR amplification and sequencing of additional mitochondrial and nuclear protein-coding genes in fungi (e.g., Thon and Royse, 1999; Kretzer and Bruns, 1999). Eventually, combining phylogenetic data from this work and others into a "supertree" (Sanderson et al., 1998) may boost our understanding of evolutionary relationships in the euagarics and other fungi and contribute to Darwin's dream (as cited in Burkhardt and Smith, 1990;, p. 456): "The time will come [...] though I shall not live to see it, when we shall have fairly true genealogical trees of each kingdom of nature."

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Appendix A. List of strains used with their sources and GeneBank accession numbers

Taxon	GenBank Accession No.	Source: Strain No. ^a
Anthracophyllum lateritium	AF261324	This work: (T) CULTENN4419
Neonothopanus nambi	AF042577	Moncalvo et al., 2000 (as Nothopanus eugrammus)
-	AF135175*	This work: (D) RVPR27
Omphalotus olivascens	AF261325	This work: (V) VT645.7
Omphalotus nidiformis	AF042621	Moncalvo et al., 2000
Omphalotus olearius	AF042010	Binder et al., 1997
Lampteromyces japonicus	AF135172	Moncalvo et al., 2000
	AF042008*	Binder et al., 1997
Gymnopus polyphyllus	AF042596	Moncalvo et al., 2000 (as Collybia)
Gymnopus dryophilus	AF042595	Moncalvo et al., 2000 (as Collybia)
Gymnopus acervatus	AF223172	This work: CBS174.48
Gymnopus sp.	AF261326	This work: (J) JEJ.PR.213
Caripia montagnei	AF261327	This work: (D) JMCR.143
Setulipes androsaceus	AF261585	This work: (D) HN4730
Micromphale foetidum	AF261328	This work: (J) JEJ.VA.567
Marasmiellus opacus	AF261329	This work: (J) JEJ.574
-	AF261330*	This work: (D) HN2270
Marasmius scorodonius	AF261331	This work: (J) JEJ.586
	AF261332*	This work: DAOM175382
Gymnopus sp	AF261333	This work: (D) RVPR98.46
	AF261334*	This work: (D) RV.PR.98.08
Gymnopus sp.	AF261335	This work: (D) RVPR98.13
Gymnopus biformis	AF261336	This work: (D) RV98/32
Rhodocollybia maculata	AF042597	Moncalvo et al., 2000 (as Collybia)
Marasmiellus ramealis	AF042626	Moncalvo et al., 2000
	AF042650*	Moncalvo et al., 2000
Gymnopus peronatus	AF223173	This work: CBS426.79
Lentinula edodes	AF042579	Moncalvo et al., 2000
	AF261557*	This work: (G) TMI1941
Lentinula boryana	AF261558	This work: (G) RGT960624
·	AF261559*	This work: (D) HN2002
	AF261560*	This work: (D) R38
Lentinula novaezelandieae	AF261561	This work: (G)TMI1172
Lentinula lateritia	AF261562	This work: (G) TMI1485
Micromphale perforans	AF042628	Moncalvo et al., 2000
	AF042651*	Moncalvo et al., 2000
Tetrapyrgos nigripes	AF261337	This work: DAOM186918
Tetrapyrgos subdendrophora	AF042629	Moncalvo et al., 2000 (as Campanella)
Tetrapyrgos sp.	AF261338	This work: (T) TENN7373
<i>Campanella</i> sp.	AF261339	This work: (D) RV-PR075
<i>Campanella</i> sp.	AF261340	This work: (D) RV98/79
Unidentified agaric	AF261341	This work: (D) JMCR.34

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Marasmius delectans	U11922	Chapela et al., 1994
Marasmius sp.	AF261342	This work: (J) JEJ.PR.256
Marasmius cladophyllus	AF261343	This work: (D)JMCR. 121
Hymenogloea papyracea	AF261344*	This work: HALLING.5013
Marasmius capillaris	AF042631	Moncalvo et al., 2000
Marasmius rotula	AF261345	This work: (J) JEJ.VA.595
Marasmius fulvoferrugineus	AF261584	This work: (D) HN2346
Chaetocalathus liliputianus	AF261346	This work: DAOM175886
Chaetocalathus sp.	AF261347	This work: (T) TENN3572
Crinipellis campanella	U11916	Chapela et al., 1994
Crinipellis maxima	AF042630	Moncalvo et al., 2000
Crinipellis sp.	AF261348	This work: (D) RV.PR98/75
Gloiocephala spathularia	AF261349	This work: (D) JMCR.115
Physalacria aff.orinocensis	AF261350	This work: (T) TENN9134
Rhodotus palmatus	AF042565	Moncalvo et al., 2000
Xerula megalospora	AF042649	Moncalvo et al., 2000
Xerula furfuracea	AF042566	Moncalvo et al., 2000
Oudemansiella canarii	AF261351	This work: (D) RV.PR100
Flammulina velutipes	AF042641	Moncalvo et al., 2000
Strobilurus trullisatus	AF042633	Moncalvo et al., 2000
Rhizomarasmius pyrrhocephalus	AF261352	This work: (J) JEJ.596
	AF042605*	Moncalvo et al., 2000 (as Marasmius)
Cyptotrama asprata	AF261353	This work: (D) RV98/78
	AF042642*	Moncalvo et al., 2000
Gloiocephala menieri	AF042632	Moncalvo et al., 2000
<i>Gloiocephala</i> sp.	AF261354	This work: (T) TENN7573
Armillaria tabescens	AF042593	Moncalvo et al., 2000
Armillaria "NABS1"	AF261355	This work: (B) GC17
Armillaria affinis	AF261356	This work: (D) JMCR.126
Cheimonophyllum candidissimum	AF261357	This work: DAOM187959
Gloeostereum incarnatum	AF141637	Hallenberg and Parmasto (GenBank)
Hemimycena delicatella	AF261358	This work: DAOM187554
Hemimycena ignobilis	AF261359	This work: DAOM214662
Calyptella capula	AF261379	This work: (J) JAN.SW.21835
Mycena aurantiidisca	AF261360	This work: DAOM216791
Mycena adonis	AF261361	This work: DAOM174885
bioluminescent agaric	AF261362	This work: (D) JMCR.32
Pleurotopsis longinqua	AF042604	Moncalvo et al., 2000
Baeospora myriadophylla	AF042634	Moncalvo et al., 2000
Baeospora myosura	AF261363	This work: (T) TENN4256
Hydropus scabripes	AF042635	Moncalvo et al., 2000
Gerronema strombodes	U66433	Lutzoni, 1997
	AF261364*	This work: (J) JEJ580
Gerronema subclavatum	U66434	Lutzoni, 1997
Gerronema sp.	AF261365	This work: (V) OKM27143
Megacollybia platyphylla	AF261366	This work: DAOM195782
Clitocybula oculus	AF261367	This work: DAOM195995
Hydropus fuliginarius	AF261368	This work: DAOM196062
<i>Hydropus</i> sp.	AF261369	This work: (D) RV98/43
Porotheleum fimbriatum	AF261370	This work: (D) HC.10/11/98.C
= Stromatoscypha fimbriata	AF261371*	This work: (J) FP102067
attine fungus G2	U11901	Chapela et al., 1994

Taxon	GenBank Accession No.	Source: Strain No. ^a
	U11905*	Chapela et al., 1994
Resupinatus sp.	AF042599	Moncalvo et al., 2000
Resupinatus alboniger	AF042600	Moncalvo et al., 2000
Resupinatus dealbatus	AF139944	Thorn et al., 2000 (as Asterotus)
Stigmatolemma poriaeforme	AF261372	This work: (J)RLG1156sp
cyphelloid sp.	AF261373	This work: HHB3534sp
Phyllotopsis nidulans	AF042578	Moncalvo et al., 2000
Pleurocybella porrigens	AF042594	Moncalvo et al., 2000
Typhula phacorrhiza	AF261374	This work: DAOM195241
Gamundia leucophylla	AF261375	This work: DAOM192749
Caulorhiza hygrophoroides	AF042640	Moncalvo et al., 2000
Conchomyces bursaeformis	AF042603	Moncalvo et al., 2000
	AF261376*	This work: (D) RV95/695
Fayodia gracilipes	AF261377	This work: DAOM187531
Myxomphalia maura	AF261378	This work: DAOM187839
Floccularia albolanaripes	AF261380	This work: DAOM214667
Mythicomyces corneipes	AF261381	This work: DAOM178138
Stereopsis humphreyi	AF261382	This work: DAOM185795
Pseudoclitocybe cyathiformis	AF261383	This work: DAOM191063
Collybia tuberosa	AF261384	This work: (D) DUKE1424
	AF261385*	This work: DAOM191061
	AF261386*	This work: (T) TENN53630
Collybia cirrhata	AF261387	This work: (T) TENN53540
Collybia cookei	AF261388	This work: (T) TENN55143
Dendrocollybia racemosa	AF042598	Moncalvo et al., 2000 (as <i>Collybia</i>)
Clitocybe dealbata	AF042589	Moncalvo et al., 2000 (us conjota) Moncalvo et al., 2000
emocyse acaisaia	AF223175*	This work: (S) HC95/cp3
Clitocybe connata	AF042590	Moncalvo et al., 2000
Lepista nuda	AF042624	Moncalvo et al., 2000 (as <i>Clitocybe</i>)
Lepista nuda	AF139963	Thorn et al., 2000
Clitocybe ramigena	AF042648	Moncalvo et al., 2000
Clitocybe glacialis	AF261389	This work: DAOM208590
Clitocybe odorata	AF261390	This work: (D) RV98/145
Lepista nebularis	AF223217	This work: CBS362.65
Plicaturopsis crispa	AF261586	This work: (D) RV98/1
Omphaliaster borealis	AF261391	This work: DAOM189775
Tricholoma atroviolaceum	U76457	Shank and Vilgalys (GenBank)
Tricholoma imbricatum	U76458	Shank and Vilgalys (GenBank)
Tricholoma focale	U76460	Shank and Vilgalys (GenBank)
Tricholoma myomyces	U76459	Shank and Vilgalys (GenBank)
Tricholoma vernaticum	U76461	Shank and Vilgalys (GenBank)
Tricholoma pardinum	U76462	Shank and Vilgalys (GenBank)
Tricholoma venenatum	U76463	Shank and Vilgalys (GenBank)
Tricholoma portentosum	U76464	Shank and Vilgalys (GenBank)
Tricholoma intermedium	U76465	Shank and Vilgalys (GenBank)
Tricholoma subaureum	U76466	Shank and Vilgalys (GenBank)
Tricholoma caligatum	U76467	Shank and Vilgalys (GenBank)
inchoioma cauguran	AF261392*	This work: (D) SAR1/2/88
Tricholoma matsutake	U62964	Hwang and Kim, 2000.
	U86672	
Tricholoma cf. flavovirens Tricholoma vaccinum		Pegler et al., 1998 Nakasana and Pantmaastar (CanBank)
	U86443-4	Nakasone and Rentmeester (GenBank) This work: DAOM182713
Leucopaxillus albissimus Leucopaxillus gentianeus	AF261393	
Leuconaxших gentlaneus	AF261394	This work: (T) TENN5616

Taxon	GenBank Accession No.	Source: Strain No. ^a
Porpoloma sp.	AF261395	This work: JLPR3395
Hypsizygus ulmarius	AF042584	Moncalvo et al., 2000
Ossicaulis lignatilis	AF261396	This work: DAOM188196
	AF261397*	This work: (D, V) D604
	n.a.*	This work: DAOM211765
Lyophyllum tylicolor	AF139964	Thorn et al., 2000
	AF223193*	This work: (S) SAG5/271yo9
	AF223194*	This work: (S) SAG5/27.11
	AF223192*	This work: CBS362.80
	AF223195*	This work: BSI92/245
Lyophyllum gibberosum	AF223198	This work: CBS320.80
	AF223196*	This work: CBS321.80
	AF223197*	This work: CBS328.50
Lyophyllum palustris	AF223200	This work: CBS717.87
	AF223199*	This work: CBS714.87
Tephrocybe rancida	AF223203	This work: CBS204.47
Tricholomella constricta	AF223187	This work: (S) HC80/148
	AF223186*	This work: CBS660.87
	AF223189*	This work: CBS320.85
	AF223188*	This work: (S) HC84/75
Lyophyllum boudieri	AF223206	This work: (S) HC78U
Lyopnymun oouden	AF223205*	This work: CBS379.88
	AF223204*	This work: BSI96/84
Lyophyllum inolens	AF223201	This work: CBS330.85
Lyophyllum ambustum	AF223215	This work: CBS451.87
Lyophynam amoustam	AF223216*	This work: CBS452.87
	AF223210	This work: CBS452.07 This work: CBS450.87
Lyophyllum anthracophilum	AF223211	This work: BSI94/88
Lyopnynum unin acopnnum	AF223212*	This work: (S) HC79/132
	AF223212 AF223213*	This work: CBS156.44
Lyophyllum atratum	AF042582	Moncalvo et al., 2000
	AF223210*	This work: CBS709.87
Lyophyllum decastes	AF042583	Moncalvo et al., 2000
Lyophyllum caerulescens	AF223209	This work: (S) HC80/140
Lyophyllum sykosporum	AF223209 AF223208	This work: IFO30978
Lyophyllum sykosporum Lyophyllum semitale	AF042581	Moncalvo et al., 2000
Termitomyces cylindricus	AF042585	Moncalvo et al., 2000
Termitomyces clypeatus	AF261398	This work: (D) JMleg.MUID
Termitomyces heimii	AF042586	Moncalvo et al., 2000
Termitomyces microcarpus	AF042587	Moncalvo et al., 2000
Termitomyces sp.	AF261399	This work: (D) JJs.n.
Termitomyces subhyalinus	AF223174	This work: BSI93/3
Lyophyllum leucophaeatum	AF223202	This work: (S) HAe251/97
Lyophyllum ochraceum	AF223185	This work: BSI94/cp1
Lyophyllum favrei	AF223183	This work: (S) HAe.251.97
	AF223184*	This work: (S) HC96/cp4
	AF223182*	This work: BSI94/cp2
Calocybe ionides	AF223179	This work: (S) HC77/33
Calocybe naucoria	AF223180	This work: (S) HC80/103
Calocybe obscurissima	AF223181	This work: (S) HC79/181
Calocybe cyanea	AF261400	This work: (D) RVPR10 June 97
Calocybe persicolor	AF223176	This work: (S) HC80/99
Calocybe gambosa	AF223177	This work: (S) HC78/64

Faxon	GenBank Accession No.	Source: Strain No. ^a
	U86441/2*	Nakasone and Rentmeester (GenBank)
Calocybe carneum	AF223178	This work: CBS552.50
Asterophora lycoperdoides	AF223190	This work: CBS170.86
Asterophora parasitica	AF223191	This work: CBS683.82
Catathelasma ventricosa	AF261401	This work: DAOM221514
Catathelasma imperialis	AF261402	This work: DAOM225247
Rhodocybe fallax	AF223166	This work: CBS129.63
	AF223165*	This work: CBS605.79
	AF261283	This work: (V) OKM25668
Rhodocybe truncata	AF223168	This work: CBS604.76
	AF223167*	This work: CBS482.50
Rhodocybe caelata	AF261282	This work: (C) TB5890
Rhodocybe mundula	AF261284	This work: (C) TB4698
Rhodocybe popinalis	AF261285	This work: (C) TB6378
Clitopilus ''flaviphyllus''	AF261286	This work: (C) TB8067
Clitopilus apalus	AF261287	This work: (C) M536
Clitopilus scyphoides	AF261288	This work: (C) T777
Clitopilus prunulus	AF042645	Moncalvo et al., 2000
Clitopilopsis hirneola	AF223164	This work: CBS576.87
	AF223163*	This work: CBS577.87
Entoloma bloxamii	AF261289	This work: (C) TB6117
Trichopilus porphyrophaeus	AF261290	This work: (C) TB6957
Leptonia subserrulata	AF261291	This work: (C) TB6993
Alboleptonia stylophora	AF261292	This work: (C) TB8475
nopilus entolomoides	AF261293	This work: (C) TB8507
Entoloma lividum	AF261294	This work: (C) TB5034
	AF261295	This work: (C) TB6807
Entoloma nidorosum	AF261296	This work: (C) TB6263
Entoloma bicolor	AF261297/8	This work: (C) TB4967
Entoloma rhodopolium	AF261299	This work: (C)TB6221
Entoloma flavifolium	AF261301	This work: (C) TB6215
Entoloma alpicola	AF261302	This work: (C) TB6415
Inocephalus quadratus	AF261303	This work: (C) TB7695
Inocephalus lactifluus	AF261304	This work: (C) TB7962
Inocephalus murraii	AF261305/6	This work: (C) TB6038
Entoloma canescens	AF261307	This work: (C) TB5657
Pouzarella nodospora	AF261308	This work:(C) TB5716
Entoloma haastii	AF261309	This work: (C) BY21
Entoloma odorifer	AF261310	This work: (C) TB6366
Entoloma unicolor	AF261311/2	This work: (C) TB5520
Leptonia carnea	AF261313	This work: (C) TB5812
Entoloma undatum	AF261314	This work: (C) TB6398
Entoloma abortivum	AF223169	This work: CBS143.34
Entoloma sericeonitida	AF261315	This work: (C) TB7144
Leptonia gracilipes	AF261316	This work: (C) TB6033
<i>Nolanea conica</i>	AF261317	This work: (C) MB6
Volanea cetrata	AF261319	This work: (C) TB7382
Nolanea hirtipes	AF261320	This work: (C) K1171992
Nolanea conferenda	AF261321	This work: (C) TB7660
Nolanea strictia	AF042620	Moncalvo et al., 2000 (as <i>Entoloma</i>)
Nolanea sericea	AF261318	This work: (C) TB6506
, omnen bernett	AF223170*	This work: CBS237.50
	111 2231/0	11115 WOLK, CB(22)1.00

51322 This work: (D) JM98/123 51323 This work: (C) TB7522 51403 This work: (D) RV.PR98/27 51404 This work: DAOM225484 This work: (D) RV.98.143 This work: (D) RV.98.143 7 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: DAOM34832 51407 This work: DAOM34832 51408 This work: DAOM167618 51408 This work: TO TENN7495 51411 This work: (T) TENN7495 51424 This work: (D) JM08/128 51424 This work: (D) JM98/128 51424 This work: (D) JM08/128 51425 This work: (D) JM28/128 51426 This work: (D) JM28/128
51403 This work: (D) RV.PR98/27 51404 This work: DAOM225484 This work: JLPR5831 This work: (D) RV.98.143 7 Pegler et al., 2000 37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM167618 51411 This work: CT) TENN7495 51424 This work: (T) TENN7495 51424 This work: (D) JM98/128 51414 This work: (D) JM98/128 51415 This work: (D) JM98/128 51414 This work: (D) JM98/128 51425 This work: (D) RV.PR98/36
51404 This work: DAOM225484 This work: JLPR5831 This work: (D) RV.98.143 42591 Moncalvo et al., 2000 37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM167618 51408 This work: OAOM167618 51411 This work: (T) TENN7495 51412 This work: (T) TENN7495 51413 This work: DAOM208539 51424 This work: (D) JM98/128 51414 This work: DUKE3411 51415 This work: (J) JEJ.VA.599 51415 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
This work: JLPR5831 This work: (D) RV.98.143 V2591 Moncalvo et al., 2000 37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM167618 50408 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51411 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D) JMCR.100 51429 This work: DUKE3411 51414 This work: DUKE3411 51415 This work: (J) JEJ.VA.599 51426 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
This work: (D) RV.98.143 42591 Moncalvo et al., 2000 37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM167618 51411 This work: DAOM167618 51412 This work: (T) TENN7495 51413 This work: (D) JMCR.100 51424 This work: (D) JM98/128 51414 This work: DUKE3411 51425 This work: (D) RV.PR98/36 51415 This work: (T) CULTENN7699
42591 Moncalvo et al., 2000 37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM167618 51411 This work: OD (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 51424 This work: DAOM208539 51424 This work: (D) JM98/128 51414 This work: OJ JM98/128 51415 This work: (J) JEJ.VA.599 51425 This work: (T) CULTENN7699
37 Pegler et al., 1998 51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM15019 51411 This work: DAOM167618 52636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D) JMCR.100 51429 This work: DUKE3411 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51405 This work: (D) JM99/124 51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM15019 51411 This work: DAOM167618 42636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 42637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D) JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51406 This work: IB19770276 51407 This work: DAOM34832 51408 This work: DAOM15019 51411 This work: DAOM167618 52636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D) JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 52638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51426 This work: (T) CULTENN7699
51407 This work: DAOM34832 51408 This work: DAOM15019 51411 This work: DAOM167618 52636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D) JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 52638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51426 This work: (T) CULTENN7699
51408 This work: DAOM215019 51411 This work: DAOM167618 52636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 52638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51411 This work: DAOM167618 42636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 42637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
#2636 Moncalvo et al., 2000 (as <i>M. galericulata</i>) 51412 This work: (T) TENN7495 #2637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 #2638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51412 This work: (T) TENN7495 52637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 52638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
42637 Moncalvo et al., 2000 51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51413 This work: DAOM208539 51424 This work: (D)JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 12638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51424 This work: (D) JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51424 This work: (D) JMCR.100 51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51429 This work: (D) JM98/128 51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51414 This work: DUKE3411 42638 Moncalvo et al., 2000 51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51415 This work: (J) JEJ.VA.599 51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
51425 This work: (D) RV.PR98/36 51426 This work: (T) CULTENN7699
This work: (T) CULTENN7699
51427 This work: (J) CMC5
51416 This work: (D) RVPR82
51417 This work: (J) SR.KEN.346
51418 This work: (D) JM98/186
51419 This work: (D) JM98/372
51420 This work: (D) TH6418
51421 This work: (D) RV.PR114
51422 This work: (J) JEJ.PR.253
51423 This work: (D) JM98/217
51428 This work: (D) JM98/156
2606 Moncalvo et al., 2000 (as <i>Mycena</i>)
51409 This work: (D) JMCR.101
51410 This work: (D) JM98/136
51430 This work: (D) TH6346
51431 This work: DAOM181084
39960 Thorn et al., 2000
42603 Moncalvo et al., 2000
39954/5 Thorn et al., 2000
39956* Thorn et al., 2000
39957/8* Thorn et al., 2000
3995/78 Thorn et al., 2000 39950/1* Thorn et al., 2000
39950/1 Thorn et al., 2000 39959* Thorn et al., 2000
39952/3 Thorn et al., 2000
2602 Moncalvo et al., 2000
35171* Thorn et al., 2000 40 Vilgelys and Sym 1004
40 Vilgalys and Sun, 1994
126 199 199 199 199 199 199

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
	U04147*	Vilgalys and Sun, 1994
	U04142*	Vilgalys and Sun, 1994
Pleurotus pulmonarius	U04157*	Vilgalys and Sun, 1994
	U04152*	Vilgalys and Sun, 1994
	U04141*	Vilgalys and Sun, 1994
	U04151*	Vilgalys and Sun, 1994
	U04153*	Vilgalys and Sun, 1994
Pleurotus populinus	U04159	Vilgalys and Sun, 1994
Pleurotus eryngii	U04136	Vilgalys and Sun, 1994
	U04137*	Vilgalys and Sun, 1994
	U04155*	Vilgalys and Sun, 1994
	U04154*	Vilgalys and Sun, 1994
Pleurotus abieticola	AF135176	Thorn et al., 2000
Pleurotus australis	AF261432	This work: (D) RV95/568
Pleurotus cornucopiae	U04146	Vilgalys and Sun, 1994
Ĩ	U04135*	Vilgalys and Sun, 1994
Pleurotus djamor	AF042575	Moncalvo et al., 2000
	U04139*	Vilgalys and Sun, 1994
	U04138*	Vilgalys and Sun, 1994
Pleurotus calyptratus	AF135177	Thorn et al., 2000
Pleurotus cystidiosus	U04148	Vilgalys and Sun, 1994
i icui orus cystiaiosus	U04149*	Vilgalys and Sun, 1994
Pleurotus smithii	U04150	Vilgalys and Sun, 1994
Pleurotus laevis	U04156	Vilgalys and Sun, 1994
Tienotus incois	U04158*	Vilgalys and Sun, 1994
	AF139968*	Thorn et al., 2000
Pleurotus dryinus	AF135178	Thorn et al., 2000
Pleurotus tuberregium	AF135180	Thorn et al., 2000
Pleurotus purpureoolivaceus	AF042576	Moncalvo et al., 2000
Tieurotus purpurcoonouceus	AF135179*	Thorn et al., 2000
Pluteus petasatus	AF042611	This work: (S) JB91/21
Pluteus primus	AF042610	This work: (S) JB94/24
Pluteus brunneoradiatus	AF261567	This work: (S) JB97/3
Pluteus pouzarianus	AF261568	This work: (S) JB94/26
Pluteus pallidus	AF261569	This work: (S) JB90/27
Pluteus cervinus	AF261570	This work: (S) JB97/19
Pluteus pellitus	AF261570	This work: (S) JB97/19 This work: (S) JB93/3
Pluteus atromarginatus	AF261572	This work: (S)JB97/14
Pluteus salicinus	AF261573	This work: (S) JB97/6
Pluteus ephebeus	AF261574	This work: (S) JB97/23
Pluteus "white"	AF042612	
	AF261576	Moncalvo et al., 2000 This work: (S) JMCR.124
Pluteus sp. Pluteus romellii	AF261575	
		This work: (S) JB97/26
Pluteus admirabilis	AF261577	This work: DAOM193532
	AF261578*	This work: DAOM197226
Pluteus aurantiorugosus	AF261579	This work: DAOM197369
Pluteus umbrosus	AF261580	This work: DAOM197235
Pluteus chrysophlebius	AF261581	This work: DAOM 190194
Melanoleuca cognata	AF261433	This work: DAOM210221
Melanoleuca alboflavida	AF261434	This work: DAOM215874
	AF139965*	Thorn et al., 2000
Amanita muscaria	AF042643	Moncalvo et al., 2000
Amanita roseitincta	AF097369	Drehmel et al., 1999

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Amanita farinosa	AF097370	Drehmel et al., 1999
Amanita gemmata	AF097371	Drehmel et al., 1999
Amanita ceciliae	AF097372	Drehmel et al., 1999
Amanita fulva	AF097373	Drehmel et al., 1999
Amanita vaginata	AF097375	Drehmel et al., 1999
Amanita jacksonii	AF097376	Drehmel et al., 1999
Torrendia pulchella	AF261566	This work: G.Platas
Amanita citrina	AF041547	Hopple and Vilgalys, 1999
Amanita brunnescens	AF097379	Drehmel et al., 1999
Amanita flavoconia	AF042609	Moncalvo et al., 2000
Amanita rubescens	AF042607	Moncalvo et al., 2000
Amanita flavorubescens	AF042609	Moncalvo et al., 2000
Amanita franchetii	AF097381	Drehmel et al., 1999
Amanita bisporigera	AF097384	Drehmel et al., 1999
Amanita phalloides	AF261435	This work: UPS2701
Amanita virosa	AF097386	Drehmel et al., 1999
Amanita rhoadsii	AF097391	Drehmel et al., 1999
Amanita solitariiformis	AF097390	Drehmel et al., 1999
Amanita peckiana	AF042608	Moncalvo et al., 2000
1	AF097387*	Drehmel et al., 1999
Amanita volvata	AF097388	Drehmel et al., 1999
Amanita rhopalopus	AF097393	Drehmel et al., 1999
Amanita armillariiformis	AF261436	This work: DAOM216919
internet a miner of ormals	AF261437*	This work: DAOM184734
Limacella glischra	U85301	Johnson and Vilgalys, 1998
Limacella glioderma	AF261438	This work: (V) VT(L18)
Limacella illinata	AF261439	This work: (V) VT8.9.96
Catatrama costaricensis	AF261440	This work: DAOM211663
Neohygrophorus angelesianus	AF261441	This work: DAOM208569
Pseudoomphalina felloides	AF261442	This work: DAOM11115
Cantharellula umbonata	AF261443	This work: DAOM198740
Pseudoarmillariella ectypoides	AF261444	This work: DAOM191921
Omphalina velutipes	U66455	Lutzoni, 1997
Omphalina epichysium	U66442	Lutzoni, 1997
Omphalina sphagnicola	U66453	Lutzoni, 1997
Omphalina philonotis	U66449	Lutzoni, 1997
Omphalina viridis	U66456	Lutzoni, 1997
Arrhenia lobata	U66429	Lutzoni, 1997
Arrhenia auriscalpium	U66428	Lutzoni, 1997
Omphalina obscurata	U66448	Lutzoni, 1997
Omphalina griseopallidus	U66436	Lutzoni, 1997 (as <i>Phaeotellus</i>)
Omphalina luteovitellina	U66447	Lutzoni, 1997 (as 1 nueotenus) Lutzoni, 1997
Omphalina velutina	U66454	Lutzoni, 1997
Omphalina velutina Omphalina velutina	U66443	Lutzoni, 1997 Lutzoni, 1997 (as <i>O. grisella</i>)
Omphalina hudsoniana	U66446	Lutzoni, 1997 (as <i>O. grisena</i>) Lutzoni, 1997
Omphalina ericetorum	U66445 AF261445*	Lutzoni, 1997 This work: DAOM180811
Gliophorus laeta	AF261446	This work: DAOM186394
Omphalina pyxidata	U66450	Lutzoni, 1997
Omphalina rivulicola	U66451	Lutzoni, 1997 Lutzoni, 1997
Clitocybe lateritia	U66431	
•		Lutzoni, 1997 Moncelvo et al. 2000
Clitocybe clavipes	AF042564	Moncalvo et al., 2000
	AF261447*	This work: (J) JEJ.VA.587

Taxon	GenBank Accession No.	Source: Strain No. ^a
	U86439/40*	Nakasone et al., (GenBank)
<i>Clitocybe</i> sp.	AF261448	This work: (J) JEJ.VA.581
Rimbachia bryophila	AF261449	This work: DAOM192811
Humidicutis marginata	AF042580	Moncalvo et al., 2000
Hygrophorus sordidus	AF042562	Moncalvo et al., 2000
Hygrophorus bakerensis	AF042623	Moncalvo et al., 2000
Chrysomphalina chrysophylla	U66430	Lutzoni, 1997
Chrysomphalina grossula	U66444	Lutzoni, 1997 (as Omphalina)
	U66457*	Lutzoni, 1997 (as Omphalina wynniae)
Hygrocybe conica	AF261450	This work: DAOM190581
Hygrocybe spadicea	AF261451	This work: DAOM171030
Hygrocybe miniata	AF261452	This work: DAOM169729
Hygrocybe sp.	AF261453	This work: (D) JM98/368
Hygrocybe cantharellus	AF261454	This work: (D) JM98/369
Cuphophyllus citrinopallidus	U66435	Lutzoni, 1997 (as Hygrocybe)
Chromosera cyanophylla	AF261455	This work: DAOM208603
= Mycena lilacifolia	AF261456	This work: (D) DUKE1645
Camarophyllus pratensis	AF261457	This work: DAOM215543
Cotylidia alba	AF261458	This work: (D) RV.PR98/28
Cotylidia diaphina	AF261459	This work: DAOM182136
Cotylidia aurantiaca	AF261460	This work: (D) JMCR.33
Cantharellopsis prescotii	AF261461	This work: DAOM225483
Omphalina brevibasidiata	U66441	Lutzoni, 1997
Omphalina rosella	U66452	Lutzoni, 1997
Rickenella mellea	U66438	Lutzoni, 1997
Rickenella pseudogrisella	U66437	Lutzoni, 1997
Omphalina marchantiae	U66432	Lutzoni, 1997 (as Gerronema)
Xeromphalina cauticinalis	AF042639	Moncalvo et al., 2000
Xeromphalina campanelloides	AF261462	This work: (T) TENN6368
Xeromphalina cornui	AF261463	This work: (T) TENN6397
Xeromphalina fraxinophila	AF261464	This work: (T) TENN6398
Xeromphalina helbergeri	AF261465	This work: (T) TENN6255
Xeromphalina austroandina	AF261466	This work: (T) TENN7392
Xeromphalina kauffmanii	AF261467	This work: (T) TENN6906
Xeromphalina kaujjmanii Xeromphalina brunneola	AF261468	Thiswork: (T)TENN1179
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Xeromphalina campanella Usimismussa fulsinga	AF261469	This work: (T) TENN7250
Heimiomyces fulvipes	AF261470	This work: (T) TENN5864
Heimiomyces tenuipes	AF261471	This work: (T) TENN6908
Heimiomyces sp.	AF261472	This work: (D) RV95/396
Ripartitella brasiliensis	U85300	Johnson and Vilgalys, 1998
Cystoderma granulosum	U85299	Johnson and Vilgalys, 1998
Cystoderma chocoanum	U85302	Johnson and Vilgalys, 1998
Cystoderma amianthinum	AF261473	This work: DAOM188121
Phaeolepiota aurea	AF261474	This work: DAOM178195
Lachnella alboviolascens	AF261475	This work: DAOM223321
Melanophyllum haematospermum	AF261476	This work: DAOM197183
Melanophyllum echinatum	AF059231	Mitchell and Bresinsky, 1999
Lepiota clypeolaria	U85291	Johnson and Vilgalys, 1998
Lepiota acutesquamosa	U85293	Johnson and Vilgalys, 1998
Lepiota cristata	U85292	Johnson and Vilgalys, 1998
Lepiota humei	U85284	Johnson and Vilgalys, 1998
Lepiota flammeotincta	U85296	Johnson and Vilgalys, 1998
Lepiota felina	U85295	Johnson and Vilgalys, 1998

Taxon	GenBank Accession No.	Source: Strain No. ^a
Lepiota subincarnata	U85294	Johnson and Vilgalys, 1998
Cystolepiota cystidiosa	U85298	Johnson and Vilgalys, 1998
Cystolepiota cystophora	U85297	Johnson and Vilgalys, 1998
Macrolepiota caperatus	U85277	Johnson and Vilgalys, 1998
	U11923*	Chapela et al., 1994
Macrolepiota procera	U85304	Johnson and Vilgalys, 1998
	U85275*	Johnson and Vilgalys, 1998
Macrolepiota excoriata	U85278	Johnson and Vilgalys, 1998
Macrolepiota gracilenta	U85279	Johnson and Vilgalys, 1998
Macrolepiota colombiana	U85276	Johnson and Vilgalys, 1998
Leucocoprinus cepaestipes	U85286	Johnson and Vilgalys, 1998
	U85305*	Johnson and Vilgalys, 1998
	U85306*	Johnson and Vilgalys, 1998
Leucocoprinus fragilissimus	AF041540	Hopple and Vilgalys, 1999
I J 3	U85289*	Johnson and Vilgalys, 1998
Leucocoprinus luteus	U11920	Chapela et al., 1994
Leucocoprinus birnbaumii	U85288	Johnson and Vilgalys, 1998
<i>F</i>	AF041541*	Hopple and Vilgalys, 1999
Leucocoprinus cf. brebissonii	U85290	Johnson and Vilgalys, 1998
Leucocoprinus longistriatus	U85287	Johnson and Vilgalys, 1998
Leucoagaricus rubrotinctus	U85281	Johnson and Vilgalys, 1998
Leucoagaricus naucinus	U11921	Chapela et al., 1994
Leucouzur ieus nuueinus	U85280*	Johnson and Vilgalys, 1998
Leucoagaricus sp.	U85285	Johnson and Vilgalys, 1998
Leucoagaricus sp. Leucoagaricus hortensis	U85283	Johnson and Vilgalys, 1998
Leucoagaricus americanus	U85282	Johnson and Vilgalys, 1998
Chlorophyllum molybdites	U11915	Chapela et al., 1994
Chiorophylian morybailes	U85274*	Johnson and Vilgalys, 1998
	U85303*	Johnson and Vilgalys, 1998
attine fungus G1	U11902	Chapela et al., 1994
attine fungus G1	U11893	Chapela et al., 1994
attine fungus G3	U11895	Chapela et al., 1994
attine fungus G3	U11906	Chapela et al., 1994
Agaricus bisporus	U11911	Chapela et al., 1994
Aguricus Disporus	AF059227*	Mitchell and Bresinsky, 1999
	AF059218*	Mitchell and Bresinsky, 1999
Agaricus spissicaulis	AF059218 AF059220	Mitchell and Bresinsky, 1999
Agaricus spissicaulis Agaricus devoniensis	AF059225	Mitchell and Bresinsky, 1999
-	AF059225 AF059226	Mitchell and Bresinsky, 1999
Agaricus impudicus	AF059220 AF059217	Mitchell and Bresinsky, 1999
Agaricus bitorquis		•
Agaricus bernardii	AF059215	Mitchell and Bresinsky, 1999
Agaricus pocillator	AF041542	Hopple and Vilgalys, 1999
Agaricus campestris	U85273	Johnson and Vilgalys, 1998
	AF059221*	Mitchell and Bresinsky, 1999
Agaricus xanthoderma	AF059222	Mitchell and Bresinsky, 1999
Agaricus silvaticus	AF059219	Mitchell and Bresinsky, 1999
Agaricus arvensis	U11910	Chapela et al., 1994 Mitchell and President 1000
Agaricus silvicola	AF059223	Mitchell and Bresinsky, 1999
Agaricus abruptibulbus	AF059228	Mitchell and Bresinsky, 1999
Agricus lanipes	AF059229	Mitchell and Bresinsky, 1999
Agaricus maskae	AF059230	Mitchell and Bresinsky, 1999
Agaricus semotus Agaricus sp.	AF059224	Mitchell and Bresinsky, 1999
	AF261477	This work: (D) JMCR.50

Appendix A. (continued)

GenBank Accession No.	Source: Strain No. ^a
AF261478	This work: leg.CALLAC
AF261479	This work: (V) OKM19301
AF208534	This work: (V) OKM22810
AF041530	Hopple and Vilgalys, 1999
AF041529	Hopple and Vilgalys, 1999
AF041538	Hopple and Vilgalys, 1999
AF261480	This work: (V) EK13
AF261481	This work: (V) EK7
AF041539	Hopple and Vilgalys, 1999
AF261482	This work: (J) JRT008
AF261483	This work: (D) DUKE2395
AF261484	This work: (D) TYJ
AF261485	This work: (J) JEJ.NC.60
AF261486	This work: (D) DUKE3733
AF261582	This work: (G) T816
AF261583	This work: (G) T815
AF041484	Hopple and Vilgalys, 1999 (as Coprinus)
AF041485	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
AF041486	Hopple and Vilgalys, 1999 (as Coprinus)
AF041488	Hopple and Vilgalys, 1999 (as Coprinus)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
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	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Thorn et al., 2000 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as Coprinus)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprinus</i>)
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	Hopple and Vilgalys, 1999 (as <i>Coprimus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprimus</i>)
	Hopple and Vilgalys, 1999 (as <i>Coprimus</i>)
AF041528	Hopple and Vilgalys, 1999 (as <i>Coprimus</i>)
	\mathbf{U}
	AF261478 AF261479 AF208534 AF041530 AF041529 AF041538 AF261480 AF261481 AF041539 AF261482 AF261482 AF261483 AF261484 AF261485 AF261485 AF261582 AF261582 AF041486 AF041485 AF041485 AF041488 AF041490 AF041490 AF041505 AF041498 AF041499 AF041499 AF041492 AF041492 AF041493 AF041495 AF041495 AF041504 AF041504 AF041505 AF041508 AF041497 AF041509 AF041509 AF041507 AF041507 AF041507 AF041517 AF041527 AF041521 AF041523

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Coprinellus callinus	AF041524	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus aokii	AF041526	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus flocculosus	AF041515	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus xanthothrix	AF041512	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus micaceus	AF041513	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus domesticus	AF041514	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus radians	AF041516	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus disseminatus	AF041525	Hopple and Vilgalys, 1999 (as Coprinus)
Coprinellus heptemerus	AF041522	Hopple and Vilgalys, 1999 (as Coprinus)
Psathyrella gracilis	AF041533	Hopple and Vilgalys, 1999
Psathyrella sp.	AF261488	This work: (D) JMCR.119
Psathyrella candolleana	AF041531	Hopple and Vilgalys, 1999
Psathyrella delineata	AF041532	Hopple and Vilgalys, 1999
Psathyrella aff. vanhermanii	AF261487	This work: (D) JMCR.31
Psathyrella camptopoda	AF261489	This work: DAOM214256
Lacrymaria velutina	AF041534	Hopple and Vilgalys, 1999
	AF139972*	Thorn et al., 2000
Crepidotus crocophyllus	AF139946	Thorn et al., 2000
Crepidotus nephrodes	AF205670	This work: (V) MCA 189
	AF205672*	This work: (V) OKM27048
Crepidotus distortus	AF205671	This work: (V) MCA386
Crepidotus applanatus v. globigera	AF205673	This work: (V)MCA188
Crepidotus malachius	AF205674	This work: (V) MCA343
Crepidotus herbarum	n.a.	This work: DAOM196391
Crepidotus sp.	AF205675	This work: (V) MCA258
Crepidotus fraxinicola	AF205676	This work: (V) OKM26739
Crepidotus mollis	AF205677	This work: (V) OKM26279
Crepidotus uber	AF205702	This work: (V) MCA672
Crepidotus cf. subaffinis	AF205703	This work: (V) MCA604
Crepidotus inhonestus	AF205704	This work: (V) MCA638
Crepidotus lundelli	AF205705	This work: (V)MCA163
Crepidotus amygdalosporus	AF205678	This work: (V) OKM26
Crepidotus versutus	AF205683	This work: (V)MCA381
Crepidotus sp.	AF205684	This work: (V) OKM26899
Crepidotus aureus	AF205685	This work: (V) OKM27300
Crepidotus cesatii	AF205681	This work: (V) OKM26976
Crepidotus sphaerosporus	AF205682	This work: (V) OKM270
Crepidotus cinnabarinus	AF205686	This work: (V) MCA387
Crepidotus sp.	AF205669	This work: (V) OKM27270
Crepidotus betula	AF205679	This work: (V) MCA384
Crepidotus antillarum	AF205680	This work: (V) OKM26827
Crepidotus nyssicola	AF205690	This work: (V) TJB8699
Simocybe sp.	AF205687	This work: (V) MCA424
Simocybe sumptuosa	AF205688	This work: (V) OKM27046
Simocybe amara	AF205708	This work: (V) MCA682
Simocybe americana	AF205709	This work: (V) VTMH3760
Simocybe centuncula	AF205707	This work: (V) MCA393
Simocybe sp.	AF205706	This work: (V) MCA750
Pleuroflammula sp.	AF208533	This work: (V) OKM24609
Pleuroflammula flammea	AF261490	This work: DAOM194781
	AF261491*	This work: DAOM198223
Tubaria furfuracea	AF205710	This work: (V) MCA391
Tubaria hiemalis	AF205689	This work: (V) MCA385

Taxon	GenBank Accession No.	Source: Strain No. ^a
Tubaria rufo-fulva	AF205712	This work: (V) OKM24681
<i>Tubaria</i> sp.	AF205711	This work: (V) OKM24351
Phaeomarasmius erinaceus	AF261492	This work: DAOM153741
	AF261594*	This work: (L) $SV.H4 = ECV934$
Flammulaster rhombisporus	AF261493	This work: DAOM182559
Laccaria bicolor	AF042588	Moncalvo et al., 2000
Laccaria ochropurpurea	AF261494	This work: (D) JM96/46
Laccaria vulcanica	AF261495	This work: (D)JMCR.127
Rapacea mariae	AF261496	This work: ZT4339
Rozites caperatus	AF261497	This work: (D) G96/3
Dermocybe marylandensis	AF042615	Moncalvo et al., 2000
Cortinarius subbalustinus	AF195592	This work: SJ940
Cortinarius iodes	AF042613	Moncalvo et al., 2000
Cortinarius sp.	AF042614	Moncalvo et al., 2000
Cortinarius distans	AF261595	This work: (D) SV.S6
Cortinarius vibratilis	AF261498	This work: DAOM209287
Cortinarius violaceus	AF261499	This work: DAOM216796
Cortinarius traganus	AF261500	This work: DAOM212213
Cortinarius speciosissimus	AF261501	This work: DAOM174626
Thaxterogaster pingue	AF261550	This work: DAOM225303
matter og aster pingue	AF261549*	This work: IB19951102
Thaxterogaster porphyreum	AF261551	This work: (D) HN3036
Thaxterogaster violaceus	AF261552	This work: DAOM198883
Phaeocollybia attenuata	AF261502	This work: NORVELL1981111.C2.5
Phaeocollybia redheadii	AF261503	This work: DAOM215609
Phaeocollybia kauffmanii	AF261504*	This work: NORVELL1981104.01.3
Phaeocollybia dissiliens	AF261505	This work: NORVELL1981104.01.5
Phaeocollybia jennyae	AF261506	This work: DAOM221500
Squamanita odorata	AF261507	This work: DAOM221300 This work: DAOM225481
Squamanita umbonata	AF261508	This work: DAOM1223481 This work: DAOM199323
Stagnicola perplexa	AF261509	This work: DAOM199323
	AF261510	This work: DAOM191293 This work: DAOM174733
Inocybe petiginosa Inocybe geophylla yor lilaeeg	AF042616	Moncalvo et al., 2000
Inocybe geophylla var. lilacea	AF042617	
Inocybe sp.		Moncalvo et al., 2000 Moncalvo et al., 2000 (ag. $B_{\rm e}$ silverties)
Psilocybe sp.	AF042618	Moncalvo et al., 2000 (as <i>P. silvatica</i>)
Psilocybe phyllogena	AF261596	This work: (L) $v220 = CBS102746$
Psilocybe micropora	AF261597	This work: (L) $v226 = CBS101990$
Psilocybe inquilinus	AF261598	This work: (L) $v188 = CBS102740$
Psilocybe subviscida	AF261599	This work: (D) D580
Psilocybe pratensis	AF261600	This work: (L) $v189 = CBS101972$
Psilocybe xeroderma	AF261601	This work: (L) $v221 = CBS101989$
Psilocybe schoeneti	AF261602	This work: (L) $v200 = CBS101979$
Psilocybe crobula	AF261603	This work: (L) $v078 = CBS101835$
Psilocybe montana v. macrospora	AF261604	This work: (L) $v212 = CBS101983$
Psilocybe montana	n.a.*	This work: (L) $v069 = CBS101829$
Psilocybe chionophila	AF261605	This work: $c659 = CBS659.87$ (type)
Psilocybe aff. apelliculosa	AF261606	This work: (L) $v026 = CBS101811$
Psilocybe apelliculosa	AF261607	This work: (L) $v113 = CBS101867$
Melanotus phillipsii	AF261608	This work: (L) $v077 = CBS101833$
Melanotus subcuneiformis	AF261511	This work: (D) RV.PR64
Melanotus horizontalis	AF261609	This work: (L) $v208 = CBS101982$
Psilocybe pseudobullacea	AF261610	This work: (L) v145 = CBS101873
Psilocybe pseudobullacea	AF261611	This work: (D) D2402 (AnnePringle)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Psilocybe coprophila	AF139971	Thorn et al., 2000
	AF261612*	This work: (L) v254 = CBS101998
Psilocybe merdaria	AF261613	This work: (L) $v121 = CBS101859$
Psilocybe moelleri	AF261614	This work: (L) $v120 = CBS101858$
Psilocybe subcoprophila	AF261615	This work: (L) v135
Phaeogalera stagnina	AF261512	This work: DAOM187559
Kuehneromyces mutabilis	AF042619	This work: (S) DSM1684
Psilocybe stuntzii	AF042567	This work: (V)VT 1263
	U11917*	Chapela et al., 1994
Psilocybe semilanceata	AF261616	This work: (L) $v112 = CBS101853$
Psilocybe fimetaria	AF261617	This work: (L) $v051 = CBS101814$
Psilocybe liniformans	AF261618	This work: (L) v185
Psilocybe cubensis	AF261619	This work: (L) v141
Psilocybe cyanescens	AF261620	This work: (L) $v199 = CBS10197$
Psilocybe subaeruginosa	AF261621	This work: (D) RV95/502 (=HN2883)
· · · · · · · · · · · · · · · · · · ·	AF261622*	This work: (D) $RV95/448$ (= HN3408)
Pachylepyrium funariophilum	AF261513	This work: (T) TENN6030
Unidentified agaric	AF261623	This work: (L) SV.S2
Hebeloma sp.	AF261514	This work: AANEN540
Hebeloma crustuliniforme	U11918	Chapela et al., 1994
Hebeloma longicaudum	AF261515	This work: DAOM176597
f. Pholiota lignicola	AF195594	This work: SJ90025
Flammula alnicola	AF195588	This work: SJ86071
Vaucoria escharoides	AF261516	This work: AANEN-M29
tarcorta esenta otaes	AF261517*	This work: DAOM174734
Stropharia semiglobata	AF261624	This work: (L) v253
ni opnana semigiobala	AF261625*	This work: (L) $v166 = CBS102729$
Stropharia umbonatescens	AF261626	This work: (D) D602
f. Stropharia	AF261518	This work: (D) JMCR.99
Pholiota subochracea	AF195598	This work: SJ85066
Phaeonematoloma myosotis	AF195599	This work: SJ97002
Hypholoma udum	AF261627	This work: (L) v038 (as <i>Psilocybe uda</i>)
Typholoma uuum Typholoma ericaeum	AF261628	This work: (L) H16(HB7) = CB6321
Typholoma subericaeum	AF261629	This work: (L) $H15(HB8) = GHP996$
Typholoma subericaeum Typholoma fasciculare	AF261630	This work: (E) 1113(11B8) = 0117990 This work: CBS810.87
Typholoma subviride	AF042570	Moncalvo et al., 2000
Typholoma subtinue	AF261631*	
Junholoma cannoidea		This work: (L) SV.S4 This work: SJ84170
Hypholoma capnoides	AF195595	
Hypholoma sublateritium	AF042569	Moncalvo et al., 2000
Stropharia rugosoannulata	AF041544	Hopple and Vilgalys, 1999
	AF139976	Thorn et al., 2000
	AF261632	This work: (L) $v001 = CBS101784$
Hypholoma aurantiacum	AF261633	This work: (L) $H17(HB5) = Daams$
Stropharia magnivelaris	AF195600	This work: SJ85098
eratiomyces similis	AF042009	Binder et al., 1997
Veraroa erythrocephala	AF261634	This work: (D) $RV95/656 = HN3037$
Stropharia coronilla	AF261635	This work: (L) v073
~	AF059232*	Mitchell and Bresinsky, 1999
Stropharia hardii	AF261636	This work: (L) SV.S3
~	AF261637*	This work: (L) SV.S7
Stropharia aeruginosa	AF195597	This work: SJ76247
Stropharia hornemannii	AF195596	This work: SJ92047
	AF261638*	This work: CBS838.87

Appendix A. ((continued)
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Taxon	GenBank Accession No.	Source: Strain No. ^a
Weraroa virescens	AF042013	Binder et al., 1997
	AF261639*	This work: (D) RV95/669 = HN3050
Pholiota squarrosoides	AF042568	Moncalvo et al., 2000
	AF261641*	This work: (L) SV.S1
Pholiota squarrosa	AF261642	This work: (L) $H24(HB17) = MEN$
Pholiota lenta	AF195608	This work: SJ12894
	AF261643*	This work: CBS185.53
Pholiota mixta	AF195609	This work: SJ96022
Pholiota highlandensis	AF261644	This work: (L) v027
Pholiota henningsii	AF261645	This work: CBS710.84
Pholiota lundbergii	AF195607	This work: (E) LL950724
Pholiota limonella	AF195602	This work: (E) NH9200
Pholiota aurivella	AF195603	This work: SJ84131
Pholiota jahnii	AF195604	This work: SJ83118
Pholiota gummosa	AF195605	This work: SJ84095
Pholiota conissans	AF195606	This work: SJ96017
Pholiota flammans	AF195601	This work: SJ86074
Hemipholiota lucifera	AF261646	This work: (L) H26(HB12) = GHP1817
Hemipholiota destruens	AF261647	This work: (L) $H18(HB16) = CB$
Hemipholiota populnea	AF195593	This work: SJ94086
Agrocybe praecox	AF042644	Moncalvo et al., 2000
-0	AF041545*	Hopple and Vilgalys, 1999
	AF139941*	Thorn et al., 2000
Agrocybe semiorbicularis	AF139942	Thorn et al., 2000
Agrocybe dura	AF261648	This work: (L) v228
Gastrocybe lateritia	AF261519	This work: DAOM167564
Bolbitius vitellinus	U11913	Chapela et al., 1994
	AF041543*	Hopple and Vilgalys, 1999
Bolbitius demangei	AF261520	This work: (D) JMCR.137
Conocybe rickenii	AF041546	Hopple and Vilgalys, 1999
Pholiotina subnuda	AF261521	This work: DAOM208660
Naucoria bohemica	AF261522	This work: DAOM174734
Descolea gunnii	AF261523	This work: (D) DUKE3001
Leratiomyces smaragdina	AF042011	Binder et al., 1997
Galerina marginata	AF195590	This work: (E) RM3225
Galerina nana	AF261524	This work: DAOM208552
Panaeolina foenisecii	U11924	Chapela et al., 1994
anaeonna joenisecu	AF041537*	Hopple and Vilgalys, 1999
Panaeolus acuminatus	AF041537	Hopple and Vilgalys, 1999
	AF261525	This work: (D) JM98/6
Panaeolus sp.		
Panaeolus semiovatus	AF041536	Hopple and Vilgalys, 1999
Copelandia cyanescens	AF261526	This work: (D) JM98/10
Pholiota oedipus Stropharia alboerenulata	AF261649	This work: (L) $H19(HB6) = GHP1469$
Stropharia albocrenulata	AF195589	This work: (E) KGN94
Pholiota tuberculosa Dimentitas matuadii	AF195587	This work: SJ86019 Binder et al. 1007
Ripartites metrodii	AF042012	Binder et al., 1997 This work, CBS206.26
Gymnopilus aeruginosus	AF261650	This work: CBS296.36
Gymnopilus spectabilis	AF261651	This work: CBS489.90
Gymnopilus junonius	AF195591	This work: SJ84074
Gymnopilus penetrans	AF261652	This work: CBS168.79
Hebelomina neerlandica	AF261527	This work: CBS169.79
Galerina paludosa	AF261528	This work: DAOM197244
	AF261653*	This work: CBS388.88

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Cantharocybe gruberi	AF261529	This work: DAOM225482
	AF261530*	This work: DED6609
Volvariella volvacea	AF261531	This work: (D) JMleg.SRL
Volvariella hypopithys	AF261532	This work: (D) JMleg.AIME
Schizophyllum commune	AF261587	This work: (D) TYJ.Belize1
Schizophyllum radiatum	AF261588	This work: CBS301.32
Schizophyllum fasciatum	AF261589	This work: CBS267.60.
Schizophyllum umbrinum	AF261590	This work: (D) FL02.1
Schizophyllum amplum	AF261591	This work: (D) RGT-970618/01
Fistulina hepatica	AF261592	This work: (D) DSH93-183
Porodisculus pendulus	AF261593	This work: DAOM198417
Phylloporus rhodoxanthus	U11925	Chapela et al., 1994
Boletus retipes	U11914	Chapela et al., 1994
Suillus luteus	AF042622	Moncalvo et al., 2000
Hygrophoropsis aurantiaca	AF042007	Binder et al., 1997
Boletus satanas	AF042015	Binder et al., 1997
Scleroderma columnare	AF261533	This work: (D) JMCR.77
Russula earlei	AF042571	Moncalvo et al., 2000
Russula mairei	U11926	Chapela et al., 1994
Russula virescens	AF041548	Hopple and Vilgalys, 1999
Russula romagnesii	AF042572	Moncalvo et al., 2000
Lactarius corrugis	U11919	Chapela et al., 1994
Lactarius piperatus	AF042573	Moncalvo et al., 2000
Lactarius sp.	AF042574	Moncalvo et al., 2000 Moncalvo et al., 2000 (as <i>L. volemus</i>)
Bondarzewia mesenterica	AF042646	Moncalvo et al., 2000 (as L. totemus) Moncalvo et al., 2000
Heterobasidion annosum	AF139949	Thorn et al., 2000
Auriscalpium vulgare	AF261281	This work: (E) F799
Faerberia carbonaria	AF139947	Thorn et al., 2000
		Thorn et al., 2000
Neolentinus dactyloides Rodogowyka narwyla	AF135174	
Podoscypha parvula Basenalsia an	AF261534	This work: DAOM171399
Beenakia sp.	AF261535	This work: (D) PR10 june 97
Ganoderma lucidum gr.	X78776	Moncalvo et al., 1995
Ganoderma australe gr.	X78780	Moncalvo et al., 1995
Amauroderma omphalodes	n.a.	This work: (D) MUCL4027
Pycnoporus cinnabarinus	AF261536	This work: DAOM72065
Lentinus tigrinus	AF135173	Thorn et al., 2000
Lentinus squarrosulus	AF261563	This work: (D) Neda C500
Panus sp.	AF261564	This work: (D) E.Kay88/65
Panus sp.	AF261565	This work: (D) RV95/37
Trametes suaveolens	AF261537	This work: (H) DAOM196328
Fomes fomentarius	AF261538	This work: (H) DAOM129034
Polyporus squamosus	AF135181	Thorn et al., 2000
Dentocorticium sulphurellum	AF261539	This work: (H) FPL11801
Polyporus varius	AF261540	This work: (H) DSH93/195
Datronia mollis	AF261541	This work: (H) DAOM211792
Daedaleopsis confragosa	AF261542	This work: (H) DAOM180 496
Lenzites betulina	AF261543	This work: (H) DAOM180504
Polyporus tuberaster	AF261544	This work: (H) DAOM79978
Polyporus melanopus	AF261545	This work: (H) DAOM212269
Gloeophyllum trabeum	AF139948	Thorn et al., 2000
Irpex lacteus	AF139961	Thorn et al., 2000
Phanerochaete chrysorhiza	AF139967	Thorn et al., 2000
Phanerochaete chrysosporium	AF139966	Thorn et al., 2000

Appendix A. (continued)

Taxon	GenBank Accession No.	Source: Strain No. ^a
Ceraceomyces serpens	AF090882	Larsson and Larsson, 1998
Ceraceomyces microsporus	AF090874	Larsson and Larsson, 1998
Ceraceomyces eludens	AF090881	Larsson and Larsson, 1998
Phlebia lilascens GR.2	AF141621	Hallenberg and Parmasto (GenBank)
Phlebia nitidula	AF141625	Hallenberg and Parmasto (GenBank)
Phlebia centrifuga	AF141618	Hallenberg and Parmasto (GenBank)
Phlebia acerina	AF141615	Hallenberg and Parmasto (GenBank)
Phlebia lindtneri	AF141623	Hallenberg and Parmasto (GenBank)
Phlebia livida	AF141624	Hallenberg and Parmasto (GenBank)
Pseudotomentella ochracea	AF092847	Hallenberg and Parmasto (GenBank)
Phlebiopsis gigantea	AF141634	Hallenberg and Parmasto (GenBank)
Gelatoporia pannocincta	AF141612	Hallenberg and Parmasto (GenBank)
Hyphodontia radula	AF141613	Hallenberg and Parmasto (GenBank)
Phlebia bresadolae	AF141617	Hallenberg and Parmasto (GenBank)
Phlebia deflectens	AF141619	Hallenberg and Parmasto (GenBank)
Phlebia griseoflavescens	AF141620	Hallenberg and Parmasto (GenBank)
Phlebia lilascens GR.3	AF141622	Hallenberg and Parmasto (GenBank)
Phlebia queletii	AF141626	Hallenberg and Parmasto (GenBank)
Phlebia radiata	AF141627	Hallenberg and Parmasto (GenBank)
Phlebia rufa	AF141628	Hallenberg and Parmasto (GenBank)
Phlebia subochracea	AF141630	Hallenberg and Parmasto (GenBank)
Phlebia subserialis	AF141631	Hallenberg and Parmasto (GenBank)
Phlebia tremellosa	AF141632	Hallenberg and Parmasto (GenBank)
Phlebia tristis	AF141633	Hallenberg and Parmasto (GenBank)
Phlebia uda	AF141614	Hallenberg and Parmasto (GenBank)
Resinicium bicolor	AF141635	Hallenberg and Parmasto (GenBank)
Trichaptum abietinum	AF141636	Hallenberg and Parmasto (GenBank)
Postia placenta	AF139970	Thorn et al., 2000
Lentaria michneri	AF261546	This work: (D) RV98/147
Ramaria eumorpha	AF139973	This work: (G) T798
Gomphus novaezelandia	AF261547	This work: ZT68-657
Gloeocantharellus okapaensis	AF261548	This work: ZT7135
Protubera sp.	AF261555/233	This work: (D) JM98/351
Aseroe arachnoidea	AF139943	This work: (G) TMI50070
Multiclavula vernalis	U66439	Lutzoni, 1997
Multiclavula corynoides	U66440	Lutzoni, 1997
Clavulina cristata	AF261553	This work: (D) RV98/144
Serpula lacrimans	AF139974	Thorn et al., 2000
Sphaerobolus stellatus	AF139975	This work: (G) T800
Auricularia polytricha	AF261554	This work: (D) HN4076
		This work: (D) HN4076

^a Origin of material as follows: AANEN, Duur Aanen, Netherlands; (B), Jean Bérubé, Canada; BSI, Béatrice Senn-Irlet, Switzerland; (C), SUNY Cortland, U.S.A.; CALLAC, Philippe Callac, France; CBS, Centraalbureau voor Schimmelcultures, Netherlands; (D), Duke University, U.S.A.; DAOM, National Mycological Herbarium, Canada; DED, Dennis Desjardin, San Franciso State University, U.S.A.; (E), Ellen Larsson; (G), Greg Thorn; G. Platas, sequence provided by Gonzala Platas, MERK, Spain; (H), DNA provided by David Hibbett, Clark University, U.S.A.; HAL-LING, Roy Halling, New York Botanical Garden, U.S.A.; HHB, Hal Burdsall, U.S.A.; IB, University of Innsbruck, Austria; IFO, Institute for fermentation, Japan; (J), James Johnson; JLPR, Jean Lodge, Puerto Rico; (L), University of Leiden, Netherlands; NORVELL, Lorelei Norvell, Portland, U.S.A.; (S), University of Lausanne, Switzerland; SJ, Stig Jacobsson; (T), University of Tennessee, U.S.A.; UPS, Uppsala Herbarium Sweden; (V), Virginia Tech, U.S.A.; ZT, ETH Zürich, Switzerland.

* Strain not used in the final analysis (cluster with the taxon listed above in preliminary analyses).

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