Reviews, Critiques and New Ideas

Ectomycorrhizal fungal diversity: separating the wheat from the chaff

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Rinaldi, A.C., Comandini, O. and Kuyper, T.W. (2008). Ectomycorrhizal fungal diversity: separating the wheat from the chaff. Fungal Diversity 33: 1-45.

Thousands of ectomycorrhizal (ECM) fungal species exist, but estimates of global species richness of ECM fungi differ widely. Many genera have been proposed as being ECM, but in a number of studies evidence for the hypothesized ECM habit is lacking. Progress in estimating ECM species richness is therefore slow. In this paper we have retrieved studies providing evidence for the ECM habit of fungal species and for the identification of the mycobiont(s) in specific ECM associations, using published and web-based mycorrhiza literature. The identification methods considered are morpho-anatomical characterization of naturally occurring ECMs, pure culture synthesis, molecular identification, and isotopic evidence. In addition, phylogenetic information is also considered as a relevant criterion to assess ECM habit. Of 343 fungal genera for which an ECM status has been alleged, about two thirds have supportive published evidence or ECM status can be at least hypothesized. For the remaining taxa, currently no indication exists as for their ECM nutritional habit, besides field observations of associations with putative hosts. Our survey clearly indicates that current knowledge of ECM fungal diversity, as supported by experimental evidence, is only partly complete, and that inclusion of many fungal genera in this trophic and ecological category is not verified at this stage. Care must thus be used when compiling lists of ECM and saprotrophic fungi in community-level studies on the basis of published information only. On the basis of our literature search we conservatively estimate ECM species richness around 7750 species. However, on the basis of estimates of knowns and unknowns in macromycete diversity, a final estimate of ECM species richness would likely be between 20000 and 25000.

Key words: ecological role, ectomycorrhizal (ECM) fungi, diversity, host specificity, trophic status

Article Information
Received 4 June 2007
Accepted 30 September 2007
Published online 30 November 2008
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Introduction

The ectomycorrhizal (ECM) symbiosis represents one of the most prominent and ecologically crucial mutualistic associations in terrestrial habitats. This involves several thousands of species of fungi grouped within the phyla Basidiomycota, Ascomycota, and Zygomycota, and hundreds of mostly woody plant species worldwide; ectomycorrhizas (ECMs) occur in most of the temperate and boreal ecosystems and in large forested areas of tropical and subtropical regions (Smith and Read, 1997; Cairney and Chambers, 1999; Verbeken and Buyck, 2001; Comandini *et al*., 2006; Wang and Qiu, 2006).

One of the most active lines of ECM symbiosis research pursues the understanding of the causes and consequences of ECM fungal species diversity (richness, species composition) and of ECM fungal assemblages or communities. There is increasing support for the hypothesis that ECM fungal species composition affects the structure of plant communities. ECM fungal diversity is shaped by a complex mix of abiotic and biotic factors. One important biotic factor in this regard is that of host plant specificity or selectivity (Zhou and Hyde, 2001). The latter phenomenon can be considered from either a "phytocentric" or "mycocentric" point of view, i.e., emphasizing the fungal partners forming symbioses with a particular plant taxon (the fungus as a suitable and compatible partner for plants), or the diversity of plant species with which a fungal species can form mycorrhiza (the plant as a compatible host) (Molina *et al*., 1992; van der Heijden and Sanders, 2002). Given the ecological importance of host selectivity for plant communities and the associated fungal assemblages, studies describing such specificity or selectivity patterns in ecosystems are of particular significance, as they can contribute to a better understanding of the environmental factors that affect species diversity over ecological and evolutionary time scales.

Studies addressing ECM diversity and host selectivity in a detailed and reliable manner can only stem from basic information on the trophic status of fungi in a given ecosystem. Such knowledge is also needed for investigating wider aspects of community ecology in habitats where fungi play a major role, and for interpreting the evolutionary history of fungi and their associated hosts. In other words, it is important to know which fungi are ECM and which are saprotrophic or possess a mixotrophic life style (Taylor and Alexander, 2005; Koide *et al*., 2008). It might sound as a trivial matter, but it is not. Indeed, despite over 100 years of investigation on the subject, our knowledge of ECM-forming fungi is still rudimentary, and establishing the trophic status of fungal species in the field often remains a challenging task.

We present here a critical review of the evidence available about the ECM status of fungal genera. Five different types of evidence are considered: i) morpho-anatomical characterization of naturally occurring ECMs; ii) pure culture synthesis (including in microcosms); iii) molecular identification; iv) isotopic evidence; v) phylogenetic evidence. Owing to limitations of each method, we highlight those genera for which several methods produce mutually reinforcing evidence of ECM status. The types of evidence, and their accuracy and reliability are also discussed. We also reflect on the issues whether the generic level is the appropriate level for analysis and on the problem of mixotrophy (a combination of the ECM and saprotrophic life style). We conclude our paper with a revised estimate of the number of ECM fungal species.

Methods

Compilation of data on ECM associations

Our data set on the ECM fungi contains information collated from a variety of published and web-based sources. The primary list (Table 1) reports all fungal genera for which the ECM symbiosis has been alleged, regardless of putative or demonstrated plant host(s), which is not listed. Such information was retrieved either from reviews of the mycorrhizal status of fungal genera or from publications dealing with a limited number of taxa.

Our analysis focuses on those works that provide some kind of evidential information. In the list presented in Table 1, the fungal genera for which we conclude, on the basis of the information presented, that they have an ECM habit are reported in boldface. In these cases, the number of currently recognized species is reported, as retrieved from the *Dictionary of Fungi* (Kirk *et al*., 2001). Information for this section was collated by browsing (up to June 2008) web resources [Determination of Ectomycorrhizae (DEEMY), http://www.deemy.de; Database of Descriptions of Ectomycorrhizae (DDE), http://dde.forrex.org/biodiversity/ecto/index_e-html; UNITE, http://hermes.zbi.ee; Mycorrhiza Literature Exchange, http://mycorrhiza.ag.utk.edu], recent reviews (de Román *et al*., 2005; Agerer, 2006), specialized publications (e.g., *Descriptions of Ectomycorrhizae*), and the main mycological and botanical journals. For those fungal genera (e.g., *Lactarius*, *Rhizopogon*, *Russula*, *Suillus*) for which a plethora of data supporting ECM symbiosis are available, only representative articles are quoted.

Browsing the literature, one may encounter a number of other fungal genera for which the mycorrhizal status is strongly unlike quoted as ECM.

Results and Discussion

ECM fungal richness and diversity

Table 1 lists 343 genera in the Ascomycota (84 genera), Basidiomycota (252), Zygomycota (five) and Incertae Sedis (two) for which the ECM status has been alleged. The number of enlisted genera exceed that reported by other authors who have earlier summarized the diversity of ECM fungi (Molina *et al*., 1992; Bougher, 1995; Brundrett *et al*., 1996; Agerer, 2006). For 122 genera reported in Table 1 (in boldface), hosting a total of ~7200 species, evidence of ECM status by two or more approaches is available. For 114 genera, hosting ~550 species, relevant information on ECM-forming ability stems from application of a single criterion or ECM status can be at least hypothesized. Finally, for about one third of listed genera (107, hosting ~4200 species) no evidence was observed, although in many cases these genera have been repeatedly reported to have an ECM ecology (mostly on the ground of consistent association of fruitbodies with a potential plant host).

The data in Table 1 indicate that the most popular experimental method used so far to identify ECM mycobionts is morphotyping (105 cases, counting only the genera considered as ECM in this analysis), followed at a short distance by molecular tools (95 cases). Synthesis studies and, in particular, the recently-introduced isotope measurements lag well behind the other two methods (75 and 44 cases reported in Table 1, respectively). Because the use of isotopes is more controversial than morphological and molecular root tip-based methods, we discuss the isotopic method in more detail.

Malloch *et al.* (1980) were the first to produce a global estimate of ECM fungal species richness. They proposed a conservative estimate of 5000 species. Molina *et al.* (1992) who used essentially similar criteria, came to a slightly higher estimate, viz. 5400 species. Agerer (2006), on the basis of morphotyping only, recently calculated that about 5800 fungal species hosted in 184 genera form ECMs. Higher estimates have been published as well, e.g., Taylor and Alexander (2005) estimated that there are some 7000-10000 ECM fungal species; and Kuyper (in Brussaard *et al.,* 1997) suggested 10000 ECM fungal species globally. Our estimate, based on numbers of currently recognized species, amounts to about 7750 species. However, this is still a conservative estimate (see Conclusion).

Root tip evidence

Historically, knowledge of the associations between ECM plants and ECM fungi has been overwhelmingly based on field observation of sporocarp associations with potential hosts, a practice inherently exposed to a substantial degree of error (Trappe, 1962; 1969). More recently, the detailed study of the morpho-anatomical features of hundreds of ECMs has been conducted, in large part following the standardized guidelines by Reinhard Agerer (1986; 1987-2006; 1991a). Tracing mycelial connections between fruit-bodies and ectomycorrhizas is still the most reliable way of assessing in the field the trophic status of fungi. A recent survey by de Román and colleagues (2005) listed over 1200 ECM descriptions since 1961, with more than 800 different morphotypes described (the majority of them unidentified). Morphotyping is financially inexpensive, but it also needs well-trained personnel and it is very time-consuming. In our survey, the recent descriptions (summarized in de Román *et al*., 2005) have been accepted in almost all cases. Only in the case of *Rhodocollybia butyracea* and *Geastrum fimbriatum* (where the structure described was not clearly recognizable as ectomycorrhiza due to the lack of a Hartig net) we decided, based on phylogenetic and/or physiological considerations, that formation of ectomycorrhiza was unlikely. *Geastrum fimbriatum* was also mentioned as ECM by Noack (1889 – cited in Rayner, 1926), while *Geastrum*-like ectomycorrhizas were described by Ingleby *et al*., (1998). This latter paper, which also lists *Suillus*-like ectomycorrhizas in a tropical dipterocarp forest, highlights the problems associated with assignment of ECM morphotypes to known fungal genera in mycologically insufficiently explored regions.

In addition to the methods reported in Table 1, another possibility to identify the fungal partner of ECMs is the direct isolation of the fungus from the mycorrhiza, usually followed by matching the isolates with cultures obtained from fruitbodies. Although this has been successfully done in some cases, like for *Piloderma* (Kropp, 1982), *Hydnangium*, *Hysterangium*, *Paxillus*, *Scleroderma* (Chu-Chou and Grace, 1982), *Amphinema*, *Astraeus*, *Lactarius*, *Rhizopogon*, *Suillus*, *Tricholoma* (Danielson, 1984a), and *Sebacina* (Warcup, 1988), this method has been sparsely applied.

Table 1. Genera of proved and putative ectomycorrhizal fungi§.

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
ASCOMYCOTA									
Aleuria	Brundrett *et al*., 1996					**-** (Hansen and Pfister, 2006)	Sapro #		
Amylascus	Maia *et al*., 1996					+ (Hansen *et al*., 2005)	Ecto	2	
Balsamia	Trappe, 1969	+ (Palfner and Agerer, 1998)	+ (Palfner and Agerer, 1998)		+ (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	6	
Barssia	Trappe, 1969				+ (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	2	
Boudiera	Maia *et al*., 1996			+ (Warcup, 1990b)		**-** (Hansen *et al*., 2005)	Sapro		
Caloscypha	Breitenbach and Kränzlin, 1984				**-** (Hobbie *et al*., 2001)	**-** (Hansen and Pfister, 2006)	Sapro		*
Cazia	Agerer, 2006					+ (Hansen and Pfister, 2006)	Ecto	1	
Cenococcum	Trappe, 1962	+ (Harniman and Durall, 1996)	+ (Mahmood *et al*., 1999)	+ (Godbout and Fortin, 1983)			Ecto	1	
Chloridium	Wang and Wilcox, 1985	+ (Wang and Wilcox, 1985)		+ (Wilcox and Wang, 1987a)			Ecto	1	1
Choiromyces	Trappe, 1969		+ (Izzo *et al*., 2005a)		+ (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	5	
Cladophialophora	Izzo *et al*., 2005a		+ (Izzo *et al*., 2005a)				Sapro		2
Cudonia	Trappe, 1969					**-** (Wang *et al*., 2006)	Sapro		
Delastria	Agerer, 2006					? (Lumbsch and Huhndorf, 2007)	Ecto	1	3
Dingleya	Trappe, 1969				+ (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	7	
Elaphomyces	Trappe, 1969	+ (Agerer, 1999a)	+ (Tedersoo *et al*., 2003)	+ (Miller and Miller, 1984)			Ecto	20	
Eremiomyces	Brundrett, 2008					+ (Ferdman *et al*., 2005)	Ecto	1	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi§.

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Fischerula	Molina *et al.*, 1992				+ (Hobbie *et al.*, 2001)	+ (Hansen and Pfister, 2006)	Ecto	2	
Genea	Trappe, 1969	+ (Jakucs *et al.*, 1998; Tedersoo *et al.*, 2006a)	+ (Tedersoo *et al.*, 2006a; Smith *et al.*, 2006)			+ (Hansen and Pfister, 2006)	Ecto	35	4
Geoglossum	Molina *et al.*, 1992					**-** (Wang *et al.*, 2006)	Sapro		
Geopora	Trappe, 1969	+ (Tedersoo *et al.*, 2006a)	+ (Tedersoo *et al.*, 2006a)			+ (Hansen and Pfister, 2006)	Ecto	12	
Geopyxis	Vrålstad *et al.*, 1998		+ (Vrålstad *et al.*, 1998)			+ (Hansen and Pfister, 2006)	Ecto	6	5; 6; see discussion
<u>Gilkeya</u>	Smith *et al.*, 2006					+ (Smith *et al.*, 2006)	Ecto	1	
<u>Glischroderma</u>	Tedersoo *et al.*, 2006b		+ (Tedersoo *et al.*, 2006b; Kjøller *et al.*, 2006)				Ecto	1	
GYMNOHYDNOTRYA	Brundrett *et al.*, 1996						Ecto	3	7
<u>Gyromitra</u>	Trappe, 1969				**-** (Hobbie *et al.*, 2001)	+ (Hansen and Pfister, 2006)	Ecto	15 (?)	*
Helvella	Trappe, 1969	+ (Tedersoo *et al.*, 2006a)	+ (Tedersoo *et al.*, 2006a); Kjøller *et al.*, 2006)		+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001)	+ (Hansen and Pfister, 2006)	Ecto	40	
Humaria	Molina *et al.*, 1992	+ (Ingleby *et al.*, 1990; Tedersoo *et al.*, 2006a)	+ (Tedersoo *et al.*, 2006a)			+ (Hansen and Pfister, 2006)	Ecto	15	
<u>Hydnobolites</u>	Molina *et al.*, 1992		+ (Tedersoo *et al.*, 2008a)				Ecto	2	
HYDNOCYSTIS	Molina *et al.*, 1992						Ecto	2	8
Hydnotrya	Trappe, 1969	+ (Tedersoo *et al.*, 2006a)	+ (Tedersoo *et al.*, 2006a)	+ (Lu *et al.*, 1998)	+/**-** (Hobbie *et al.*, 2001)	+ (Hansen and Pfister, 2006)	Ecto	12	*

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	**Reference †**	**Root tip morphology**	**Root tip molecular**	**Synthesis**	**Isotopic**	**Phylogeny**	**Conclusion**	**Species number (estim.d)‡**	**Notes**
Hydnotryopsis	Brundrett *et al*., 1996					+ (Hansen *et al*., 2005)	Ecto	2	
Kalaharituber	Brundrett, 2008					+ (Ferdman *et al*., 2005)	Ecto	1	
Labyrinthomyces	Molina *et al*., 1992			+ (Brundrett *et al*., 2005)		+ (Hansen and Pfister, 2006)	Ecto	7	
Lamprospora	Brundrett *et al*., 1996						Sapro		
Leotia	Molina *et al*., 1992					**-** (Wang *et al*., 2006)	Sapro		
Leptodontidium	Fernando and Currah, 1995	+ (Fernando and Currah, 1996)		+ (Fernando and Currah, 1995)			Ecto	1	
Loculotuber	Agerer, 2006					? (Lumbsch and Huhndorf, 2007)	Ecto	1	
Meliniomyces	Tedersoo *et al*., 2006b	+ (Brand *et al*., 1992)	+ (Tedersoo *et al*., 2006b; Twieg *et al*., 2007)				Ecto	3	9
Morchella	Maia *et al*., 1996	+ (Buscot, 1994)		+ (Dahlstrom *et al*., 2000)	+/- (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	? (Sapro, possibly mixotrophic)		*; 10
Muciturbo	Maia *et al*., 1996			+ (Warcup, 1990b)			Ecto	3	11
MYCOCLELANDIA	Brundrett *et al*., 1996						Ecto	2	
NEOCUDONIELLA	Maia *et al*., 1996						Ecto	2	
Nothojafnea	Maia *et al*., 1996			+ (Warcup, 1990b)			Ecto	2	
Otidea	Trappe, 1969		+ (Kennedy *et al*., 2003)		+ (Hobbie *et al*., 2001; 2002)	+ (Hansen and Pfister, 2006)	Ecto	15	12
Pachyphloeus	Molina *et al*., 1992	+ (Tedersoo *et al*., 2006a)	+ (Tedersoo *et al*., 2006a)			+ (Hansen *et al*., 2005)	Ecto	6	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
PARADOXA	Molina *et al*., 1992						Ecto	1	
Paurocotylis	Brundrett *et al*., 1996				+/- (Hobbie *et al*., 2001; 2002)	+ (Hansen and Pfister, 2006)	Ecto	1	*
Peziza	Molina *et al*., 1992	+ (Valentine *et al*., 2004; Tedersoo *et al*., 2006a)	+ (Valentine *et al*., 2004; Tedersoo *et al*., 2006a)	+ (Warcup, 1990b)	- (Hobbie *et al*., 2002)	+ (Hansen *et al*., 2005)	Ecto	84	*; 13
PHAEANGIUM	Maia *et al*., 1996						Ecto	1	
Phialocephala	Wang and Wilcox, 1985	+ (Wang and Wilcox, 1985)	+ (Menkis *et al*., 2005)	+ (Wilcox and Wang, 1987b)			Ecto	6	
Phialophora	Wang and Wilcox, 1985	+ (Wang and Wilcox, 1985)	+ (Vrålstad *et al*., 2002)	+ (Wilcox and Wang, 1987a)			Ecto	1	
Phillipsia	Brundrett *et al*., 1996					- (Hansen and Pfister, 2006; Lumbsch and Huhndorf, 2007)	Sapro		
Picoa	Trappe, 1969	+ (Palfner and Agerer, 1998b)	+ (Palfner and Agerer, 1998b)	+ (Gutiérrez *et al*., 2003)	+/- (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	4	*; 14; 15
Plectania	Molina *et al*., 1992						Sapro		
Plicaria	Maia *et al*., 1996			+ (Warcup, 1990b)		+ (Hansen *et al*., 2005)	Ecto	1 (?)	16
PSEUDALEURIA	Maia *et al*., 1996						Ecto	1	
Pseudoplectania	Molina *et al*., 1992						Sapro		
Pseudotulostoma	Miller *et al*., 2001	+ (Henkel *et al*., 2006)	+ (Henkel *et al*., 2006)				Ecto	1	
Pulvinula	Maia *et al*., 1996	+ (Amicucci *et al*., 2001)	+ (Amicucci *et al*., 2001)	+ (Warcup, 1990b)		+ (Hansen and Pfister, 2006)	Ecto	24	
Reddellomyces	Molina *et al*., 1992			+ (Brundrett *et al*., 2005)		+ (Hansen and Pfister, 2006)	Ecto	4	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi§.

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Rhizina	Hobbie *et al*., 2001				+/- (Hobbie *et al*., 2001)		Sapro		*; 17
Ruhlandiella	Molina *et al*., 1992			+ (Warcup, 1991)		+ (Hansen *et al*., 2005)	Ecto	1	see discussion
Sarcoscypha	Trappe, 1969					- (Hansen and Pfister, 2006)	Sapro		
Sarcosoma	Trappe, 1969						Sapro		
Sarcosphaera	Molina *et al*., 1992					+ (Hansen *et al*., 2005)	Ecto	1	
Scutellinia	Warcup, 1990a			+ (Warcup, 1990b)			Sapro		18
Sowerbyella	Hobbie *et al*., 2001				+ (Hobbie *et al*., 2001; 2002)		Ecto	14	17
Spathularia	Trappe, 1969						Sapro		
Sphaerosoma	Molina *et al*., 1992						Ecto	3	
Sphaerosporella	Molina *et al*., 1992	+ (Meotto and Carraturo, 1988; de Román and de Miguel, 2005b)		+ (Danielson, 1984b)		+ (Hansen and Pfister, 2006)	Ecto	2	19
Sphaerozone	Molina *et al*., 1992	+ (Brand, 1988)					Ecto	4	20
Stephensia	Molina *et al*., 1992			+ (Warcup, 1990b)	+ (Hobbie *et al*., 2001)		Ecto	6	21
Tarzetta	Tedersoo *et al*., 2006a	+ (Tedersoo *et al*., 2006a)	+ (Tedersoo *et al*., 2006a)			+ (Hansen and Pfister, 2006)	Ecto	8	
Terfezia	Trappe, 1969	+ (Gutiérrez *et al*., 2003)	+ (Walker *et al*., 2005)	+ (Kovács *et al*., 2003; Gutiérrez *et al*., 2003)		+ (Hansen *et al*., 2005)	Ecto	12	19; 22; 23
Tirmania	Trappe, 1969		+ (Walker *et al*., 2005)	+ (Fortas and Chevalier, 1992)		+ (Hansen *et al*., 2005)	Ecto	3	19; 22

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	**Reference †**	**Root tip morphology**	**Root tip molecular**	**Synthesis**	**Isotopic**	**Phylogeny**	**Conclusion**	**Species number (estim.d)‡**	**Notes**
Tricharina	Agerer, 2006		+ (Trocha *et al*., 2006)			+ (Hansen and Pfister, 2006)	Ecto	12	5; 24
Trichoglossum	Molina *et al*., 1992					**-** (Wang *et al*., 2006)	Sapro		
Trichophaea	Molina *et al*., 1992	+ (Tedersoo *et al*., 2006a)	+ (Tedersoo *et al*., 2006a)			+ (Hansen and Pfister, 2006)	Ecto	20	5
Tuber	Trappe, 1969	+ (Comandini and Pacioni, 1997)	+ (Giomaro *et al*., 2002)	+ (Giomaro *et al*., 2002)	+ (Hobbie *et al*., 2001; 2002)	+ (Hansen and Pfister, 2006)	Ecto	63	
<u>***Underwoodia***</u>	Agerer, 2006					+ (Hansen and Pfister, 2006)	Ecto	1	
Urnula	Díez, 2005					- (Hansen and Pfister, 2006; Lumbsch and Huhndorf, 2007)	Sapro		
Verpa	Agerer, 2006				**-** (Hobbie *et al*., 2001)	**-** (Hansen and Pfister, 2006)	Sapro		*
Wilcoxina	Molina *et al*., 1992	+ (Ingleby *et al*., 1990; Tedersoo *et al*., 2006a)	+ (Tedersoo *et al*., 2006a)	+ (Scales and Peterson, 1991)		+ (Hansen and Pfister, 2006)	Ecto	3	19; 25
Wynnella	Agerer, 2006				+ (Hobbie *et al*., 2001)	+ (Hansen and Pfister, 2006)	Ecto	1	
BASIDIOMYCOTA									
Abstoma	Brundrett and Bougher, 2000			+ (Chu-Chou and Grace, 1982)			Sapro		
Aeruginospora	Molina *et al*., 1992						Sapro		26
AFROBOLETUS	Agerer, 2006						Ecto	5	
Agaricus	Malajczuk *et al*., 1982						Sapro		
Albatrellus	Molina *et al*., 1992	+ (Agerer, 1996)	+ (Bidartondo *et al*., 2000)		+ (Högberg *et al*., 1999)	+ (Miller *et al*., 2006)	Ecto	12	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Alnicola	Trappe, 1962	+ (Moreau *et al*., 2006a)	+ (Moreau *et al*., 2006a)			+ (Matheny *et al*., 2006)	Ecto	~30	27
Alpova	Molina *et al*., 1992	+ (Wiedmer *et al*., 2001)		+ (Molina, 1981)		+ (Binder and Hibbett, 2006)	Ecto	20	
Amanita	Trappe, 1962	+ (Mleczko, 2004a)	+ (Bidartondo *et al*., 2000)	+ (Cripps and Miller, 1995)	+ (Högberg *et al*., 1999; Hobbie *et al*., 2001; 2002)	+ (Zhang *et al.* 2004; Tulloss, 2008)	Ecto	~500	
AMARRENDIA	Bougher and Lebel, 2002						Ecto	1	28
Amaurodon	Agerer, 2006					+ (Larsson *et al*., 2004)	Ecto	6	
Amogaster	Castellano, 1995						?		
Amphinema	Molina *et al*., 1992	+ (Montecchio *et al*., 2002)	+ (Montecchio *et al*., 2002)	+ (Weiss, 1991)			Ecto	4	
Anamika	Agerer, 2006					+ (Matheny *et al*., 2006)	Ecto	3	29
Andebbia	Agerer, 2006					+ (Hosaka *et al*., 2006)	Ecto	1	
Antrodiella	Valentine *et al*., 2004	+ (Valentine *et al*., 2004)	+ (Valentine *et al*., 2004)				Sapro		30
Aphelaria	Brundrett *et al*., 1996						Sapro		
Arcangeliella	Molina *et al*., 1992	+ (Peter *et al*., 2001)	+ (Peter *et al*., 2001)			+ (Miller *et al*., 2006)	Ecto	12	31
Armillaria	Huai *et al*., 2003						Sapro		
Aroramyces	Dell *et al*., 2005					+ (Hosaka *et al*., 2006)	Ecto	2	
Astraeus	Molina *et al*., 1992	+ (Giraud, 1988)		+ (Molina, 1981)		+ (Binder and Hibbett, 2006)	Ecto	2	
Athelia	Kennedy *et al*., 2003		+ (Kennedy *et al*., 2003; Walker *et al*., 2005)			- (Matheny *et al*., 2006)	Sapro		

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Aureoboletus	Rinaldi *et al.*, this paper					+ (Binder and Hibbett, 2006)	Ecto	5	
Auritella	Matheny and Bougher, 2006					+ (Matheny and Bougher, 2006)	Ecto	7	32
Austroboletus	Molina *et al.*, 1992					+ (Binder and Hibbett, 2006)	Ecto	30	
AUSTROGASTER	Agerer, 2006						Ecto	3	
Austrogautieria	Molina *et al.*, 1992	+ (Thoen and Ba, 1989)		+ (Lu *et al.*, 1998)		+ (Hosaka *et al.*, 2006)	Ecto	6	
Austropaxillus	Agerer, 2006	+ (Palfner 2001)				+ (Binder and Hibbett, 2006)	Ecto	9	
Bankera	Molina *et al.*, 1992	+ (Agerer and Otto, 1997)		+ (Danielson, 1984a)			Ecto	2	
Boletellus	Trappe, 1962					+ (Binder and Hibbett, 2006)	Ecto	50	
BOLETOCHAETE	Brundrett *et al.*, 1996						Ecto	3	33
Boletopsis	Trappe, 1962	+ (Agerer, 1992a)	+ (Izzo *et al.*, 2005a)				Ecto	5	
Boletus	Trappe, 1962	+ (Hahn, 2001; Jakucs and Beenken, 2001)	+ (Jonsson *et al.*, 1999a; Jakucs and Beenken, 2001)	+ (Brunner *et al.*, 1992; Pera and Alvarez, 1995)	+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001)	+ (Binder and Hibbett, 2006)	Ecto	300	
Bothia	Halling *et al.*, 2007					+ (Halling *et al.*, 2007)	Ecto	1	
BOUGHERA	Brundrett *et al.*, 1996						Ecto	1	
Bovista	Malloch and Thorn, 1985						Sapro		
Buchwaldoboletus	Brundrett *et al.*, 1996					- (Binder and Hibbett, 2006)	Sapro		
Byssocorticium	Molina *et al.*, 1992	+ (Brand, 1991)	+ (Horton *et al.*, 2005)				Ecto	9	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Byssoporia	Molina *et al.*, 1992	+ (Zak and Larsen, 1978)		+ (Kropp, 1982)		+ (Miller *et al.*, 2006)	Ecto	1	
Calocybe						- (Matheny *et al.*, 2006)	Sapro		
Calostoma	Agerer, 2006	+ (Wilson *et al.*, 2007)	+ (Wilson *et al.*, 2007)		+ (Wilson *et al.*, 2007)	+ (Binder and Hibbett, 2006)	Ecto	15	
Calvatia	Trappe, 1962						Sapro		
Cantharellula	Brundrett *et al.*, 1996						Parasite (on moss)		
Cantharellus	Trappe, 1962	+ (Mleczko, 2004b)	+ (Countess and Goodman, 2000)	+ (Danell, 1994)	+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001; 2002)	+ (Moncalvo *et al.*, 2006)	Ecto	65	
Castoreum	Molina *et al.*, 1992			+ (Brundrett *et al.*, 2005)		+ (Hosaka *et al.*, 2006)	Ecto	2	
Catathelasma	Trappe, 1962					- ? (Matheny *et al.* 2006)	Sapro (?)		
<u>Chalciporus</u>	Brundrett *et al.*, 1996				**-** (Högberg *et al.*, 1999)	+ (Binder and Hibbett, 2006)	Ecto	15	*; see discussion
Chamonixia	Molina *et al.*, 1992	+ (Raidl, 1999)				+ (Binder and Hibbett, 2006)	Ecto	8	
<u>Chlorogaster</u>	Rinaldi *et al.*, this paper					+ (Binder and Hibbett, 2006)	Ecto	1	
Chlorophyllum	Trappe, 1962						Sapro		34
Chondrogaster	Molina *et al.*, 1992			+ (de Souza *et al.*, 2008)		+ (Hosaka *et al.*, 2006)	Ecto	1	
Chroogomphus	Molina *et al.*, 1992	+ (Agerer, 1990)	+ (Cullings *et al.*, 2000)		+ (Högberg *et al.*, 1999)	+/- (Binder and Hibbett, 2006)	Ecto	15	see discussion
Clathrus	Trappe, 1962					- (Hosaka *et al.*, 2006)	Sapro		
Clavaria	Trappe, 1962		+ (Burke *et al.*, 2005; 2006)				Sapro		
<u>Clavariadelphus</u>	Molina *et al.*, 1992	+ (Iosifidou and Raidl, 2006)				- (Hosaka *et al.*, 2006)	Ecto	18	35

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Clavicorona	Brundrett *et al*., 1996		+ (Izzo *et al*., 2005a)			**-** (Miller *et al*., 2006)	Sapro		36
Clavulina	Brundrett *et al*., 1996	+ (Tedersoo *et al*., 2003)	+ (Tedersoo *et al*., 2003)		**-** (Hobbie *et al*., 2002)	+ (Moncalvo *et al*., 2006)	Ecto	32	*
Clavulinopsis	Brundrett *et al*., 1996						Sapro		
Clitocybe	Trappe, 1962				+ (Högberg *et al*., 1999)	- (Matheny *et al*., 2006)	Sapro		
Clitopilus	Trappe, 1962				**-** (Högberg *et al*., 1999)	+/- (Matheny *et al*. 2006)	Sapro		*; 37
Collybia	Trappe, 1962				**-** (Hobbie *et al*., 2001)	- (Matheny *et al*. 2006)	Sapro		*
Coltricia	Agerer, 2006	+ (Thoen and Ba, 1989; Tedersoo *et al*., 2007b)	+ (Tedersoo *et al*., 2007b)	+ (Danielson, 1984a)		+ (Larsson *et al*. 2006)	Ecto	13	
Coltriciella	Tedersoo *et al*., 2007b	+ (Tedersoo *et al*., 2007b)	+ (Tedersoo *et al*., 2007b)			+ (Larsson *et al*. 2006)	Ecto	7	
Coprinopsis	Izzo *et al*., 2005a		+ (Izzo *et al*., 2005a)				Sapro		38
CORDITUBERA	Agerer, 2006						Ecto	5	
Corticium	Trappe, 1962						Sapro		39
Cortinarius	Trappe, 1962	+ (Kuss *et al*., 2004)	+ (Kuss *et al*., 2004)	+ (Godbout and Fortin, 1983)	+ (Högberg *et al*., 1999; Hobbie *et al*., 2001)	+ (Matheny *et al*., 2006)	Ecto	~2000	
<u>Craterocolla</u>	Selosse *et al*., 2002					+ (Weiß and Oberwinkler, 2001)	Ecto	2	
Craterellus	Trappe, 1962	+ (Fransson, 2004)	+ (Fransson, 2004)		+ (Högberg *et al*., 1999)	+ (Moncalvo *et al*., 2006)	Ecto	20	40
CRIBBEA	Brundrett *et al*., 1996						Ecto	4	
Cycloderma	Bougher, 1995						Sapro		

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Cystangium	Brundrett *et al*., 1996					+ (Miller *et al*., 2006)	Ecto	7	31
Cystoderma	Brundrett *et al*., 1996				**-** (Högberg *et al*., 1999)		Sapro		*
CYSTOGOMPHUS	Molina *et al*., 1992						Ecto	1	
Dermocybe	Molina *et al*., 1992	+ (Wurzburger *et al*., 2001)	+ (Wurzburger *et al*., 2001)				Ecto	15	41
Dermoloma	Orlovich and Cairney, 2004						Sapro		
Descolea	Trappe, 1962	+ (Palfner, 1997)	+ (Tedersoo *et al*., 2008b)	+ (Lu *et al*., 1998)		- ? (Matheny *et al*., 2006)	Ecto	10	
Descomyces	Brundrett *et al*., 1996	+ (Agerer *et al*., 2001)	+ (Agerer *et al*., 2001)	+ (Lu *et al*., 1998)			Ecto	3	
Destuntzia	Molina *et al*., 1992					+ (Albee-Scott, 2007b)	Ecto	5	
Diplocystis	Louzan *et al*., 2007					+ (Louzan *et al*., 2007)	Ecto	1	
Efibulobasidium	Selosse *et al*., 2002					+ (Weiß and Oberwinkler, 2001)	Ecto	2	
Entoloma	Trappe, 1962	+ (Agerer, 1997)	+ (Montecchio *et al*., 2006)	+ (Antibus *et al*., 1981)	**-** (Högberg *et al*., 1999)	+/- (Matheny *et al*., 2006)	Ecto	~100 (?)	*
FEVANSIA	Trappe and Castellano, 2000						Ecto	1	
Fistulinella	Brundrett *et al*., 1996					+ (Binder and Hibbett, 2006)	Ecto	15	42
Floccularia	Watling and Abraham, 1992						Sapro		
FUSCOGYROPORUS	Brundrett and Bougher, 2000						Ecto	1	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi§.

Genus	**Reference †**	**Root tip morphology**	**Root tip molecular**	**Synthesis**	**Isotopic**	**Phylogeny**	**Conclusion**	**Species number (estim.d)‡**	**Notes**
Galerina	Hobbie *et al.*, 2001				+ (Hobbie *et al.*, 2001)	- (Matheny *et al.*, 2006)	Sapro		17
Gallacea	McKenzie, 2006					+ (Hosaka *et al.*, 2006)	Ecto	5	
Gastroboletus	Molina *et al.*, 1992			+ (Molina and Trappe, 1982)		+ (Binder and Hibbett, 2006)	Ecto	10	
GASTROLECCINUM	Agerer, 2006						Ecto	1	43
Gastrosporium	Hallingbäck, 1994						Sapro		
GASTROTYLOPILUS	Agerer, 2006						Ecto	1	
Gautieria	Molina *et al.*, 1992	+ (Palfner, 2001)	+ (Walker *et al.*, 2005)	+ (Duñabeitia *et al.*, 1996)		+ (Hosaka *et al.*, 2006)	Ecto	25	
Geastrum	Trappe, 1962	+ (Agerer and Benken, 1998)	+ (Agerer and Benken, 1998)			- (Hosaka *et al.*, 2006)	Sapro		see discussion
Gelopellis	Brundrett *et al.*, 1996					- (Hosaka *et al.*, 2006)	Sapro		
GIGASPERMA	Brundrett *et al.*, 1996						Ecto	2	
Gloeocantherellus	Lee *et al.*, 2002					+ (Hosaka *et al.*, 2006)	Ecto	~6	
Gomphidius	Trappe, 1962	+ (Agerer, 1991b)	+ (Olsson *et al.*, 2000)	+ (Ohga and Wood, 2000)	+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001; 2002)	+/- (Binder and Hibbett, 2006)	Ecto	10	see discussion
GOMPHOGASTER	Molina *et al.*, 1992						Ecto	1	44
Gomphus	Molina *et al.*, 1992	+ (Agerer *et al.*, 1998a)	+ (Agerer *et al.*, 1998a)			+ (Hosaka *et al.*, 2006)	Ecto	10	
Gummiglobus	Brundrett *et al.*, 1996					+ (Hosaka *et al.*, 2006)	Ecto	2	
Gummivena	Trappe and Bougher, 2002					+ (Trappe and Bougher, 2002)	Ecto	1	
GYMNOGASTER	Bougher, 1995						Ecto	1	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Gymnomyces	Molina *et al.*, 1992		+ (Stendell *et al.*, 1999)	+ (Trappe and Castellano, 1986)		+ (Miller *et al.*, 2006)	Ecto	37	31; 45
Gymnopaxillus	Agerer, 2006					+ (Binder and Hibbett, 2006)	Ecto	2	
Gyrodon	Trappe, 1962	+ (Becerra *et al.*, 2005)	+ (Becerra *et al.*, 2005)			+ (Binder and Hibbett, 2006)	Ecto	10	
Gyroporus	Trappe, 1962	+ (Agerer, 1999b)				+ (Binder and Hibbett, 2006)	Ecto	10	
Hallingea	Rinaldi *et al.*, this paper					+ (Hosaka *et al.*, 2006)	Ecto	3	
Hebeloma	Trappe, 1962	+ (Jakucs *et al.*, 1999)	+ (Jakucs *et al.*, 1999)	+ (Brunner *et al.*, 1991)	+ (Clemmensen *et al.*, 2006)	+ (Matheny *et al.*, 2006)	Ecto	~150	
Heimioporus	Halling, 2007					+ (Binder and Hibbett, 2006)	Ecto	16	
HOEHNELOGASTER	Agerer, 2006						Ecto	1	
HORAKIELLA	Brundrett *et al.*, 1996						Ecto	1	
Humidicutis	Brundrett *et al.*, 1996						Sapro		
Hydnangium	Molina *et al.*, 1992			+ (Malajczuk *et al.*, 1982)		+ (Kropp and Mueller, 1999)	Ecto	3	
Hydnellum	Molina *et al.*, 1992	+ (Agerer, 1993; Kernaghan, 2001)	+ (Kernaghan, 2001)		**-** (Högberg *et al.*, 1999)		Ecto	38	*
Hydnum	Trappe, 1962	+ (Agerer *et al.*, 1996)	+ (Agerer *et al.*, 1996)	+ (Lu *et al.*, 1998)	+ (Högberg *et al.*, 1999)	+ (Moncalvo *et al.*, 2006)	Ecto	120	
Hygrocybe	Molina *et al.*, 1992					- (Matheny *et al.*, 2006)	Sapro		
Hygrophoropsis	Hallingbäck, 1994				**-** (Högberg *et al.*, 1999; Hobbie *et al.*, 2001)	- (Binder and Hibbett, 2006)	Sapro		*
Hygrophorus	Trappe, 1962	+ (Treu, 1990)	+ (Cullings *et al.*, 2000)	+ (Kropp and Trappe, 1982)	+ (Högberg *et al.*, 1999)	+ (Matheny *et al.*, 2006)	Ecto	~100	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Hymenogaster	Trappe, 1962	+ (Donnini and Bencivenga, 1995)		+ (Brundrett *et al*., 2005)			Ecto	~100	
Hypholoma	Malajczuk *et al*., 1982						Sapro		46
Hysterangium	Trappe, 1962	+ (Raidl and Agerer, 1998)		+ (Molina and Trappe, 1982)		+ (Hosaka *et al*. 2006)	Ecto	50	
Inocybe	Trappe, 1962	+ (Magyar *et al*., 1999)	+ (Magyar *et al*., 1999)	+ (Cripps and Miller, 1995)	+ (Högberg *et al*., 1999; Hobbie *et al*., 2001)	+ (Matheny *et al*., 2006)	Ecto	500	
Kavinia	Binder *et al*., 2005					- (Hosaka *et al*., 2006)	Sapro		
Kjeldsenia	Colgan *et al*., 1995					- (Hosaka *et al*., 2006)	Sapro		
Laccaria	Trappe, 1962	+ (Torres *et al*., 1995)	+ (Buée *et al*., 2005)	+ (Godbout and Fortin, 1983)	+ (Högberg *et al*., 1999; Hobbie *et al*., 2001)	+ (Matheny *et al*., 2006)	Ecto	25	
Lactarius	Trappe, 1962	+ (Eberhartd *et al*., 2000)	+ (Nuytinck *et al*., 2004)	+ (Flores *et al*., 2005)	+ (Högberg *et al*., 1999; Hobbie *et al*., 2001)	+ (Miller *et al*., 2006)	Ecto	~400	
<u>Leccinellum</u>	Binder and Hibbett, 2006					+ (Binder and Hibbett, 2006)	Ecto	~5	
Leccinum	Trappe, 1962	+ (Müller and Agerer, 1990)	+ (den Bakker *et al*., 2004)	+ (Molina and Trappe, 1982)	+ (Högberg *et al*., 1999)	+ (Binder and Hibbett, 2006)	Ecto	75	
Lentinula	Trappe, 1962						Sapro		47
<u>Lenzitopsis</u>	Agerer, 2006					+ (Stalpers, 1993)	Ecto	1	
Lepista	Trappe, 1962	+ (Fontana, 1961)		+ (Kasuya and Igarashi, 1996)		- (Matheny *et al*., 2006)	Sapro		48
Lepiota	Trappe, 1962				**-** (Hobbie *et al*., 2001; 2002)	- (Matheny *et al*., 2006)	Sapro		*

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Leucoagaricus	Lakhanpal, 2000						Sapro		
Leucocortinarius	Trappe, 1962						Sapro		
Leucogaster	Molina *et al*., 1992		+ (Izzo *et al*., 2005b)			+ (Miller *et al*., 2006)	Ecto	20	
Leucogyrophana	Hallingbäck, 1994					- (Binder and Hibbett, 2006)	Sapro		
Leucopaxillus	Trappe, 1962			+ (Lu *et al*., 1998)		+ (Matheny *et al*., 2006)	Ecto	15	
Leucophleps	Molina *et al*., 1992		+ (Izzo *et al*., 2005b)			+ (Albee-Scott, 2007a)	Ecto	5	
Limacella	Brundrett *et al*., 1996					- (Moncalvo *et al*., 2000)	Sapro		
<u>Lindtneria</u>	Rinaldi *et al*., this paper					+ (Martín *et al*., 2004)	Ecto	11	
Lycoperdon	Trappe, 1962				+ (Högberg *et al*., 1999)	- (Matheny *et al*., 2006)	Sapro		
Lyophyllum	Trappe, 1962	+ (Agerer and Benken, 1998)	+ (Agerer and Benken, 1998)	+ (Parladé *et al*., 1996a)		+/- (Matheny *et al*., 2006)	Ecto	50	
MACCAGNIA	Agerer, 2006						Ecto	1	49
MACKINTOSHIA	Agerer, 2006						Ecto	1	
Macowanites	Molina *et al*., 1992		+ (Kennedy *et al*., 2003)			+ (Miller *et al*., 2006)	Ecto	30	31
Macrolepiota	Trappe, 1962						Sapro		
Macrotyphula	Trappe, 1962						Sapro		50
<u>Malajczukia</u>	Molina *et al*., 1992					+ ? (Hosaka *et al*., 2006)	Ecto	8	
Marasmius	Trappe, 1962					- (Matheny *et al*., 2006)	Sapro		
MAYAMONTANA	Castellano *et al*., 2007						Ecto	1	
Melanogaster	Molina *et al*., 1992	+ (Wiedmer *et al*., 2004)	+ (Cline *et al*., 2005)	+ (Parladé *et al*., 1996b)		+ (Binder and Hibbett, 2006)	Ecto	25	
Melanoleuca	Trappe, 1962					- (Matheny *et al*., 2006)	Sapro		

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	**Reference †**	**Root tip morphology**	**Root tip molecular**	**Synthesis**	**Isotopic**	**Phylogeny**	**Conclusion**	**Species number (estim.d)‡**	**Notes**
Membranomyces	Tedersoo *et al.*, 2003	+ (Tedersoo *et al.*, 2003)	+ (Tedersoo *et al.*, 2003)			+ (Moncalvo *et al.*, 2006)	Ecto	3	51
Mesophellia	Molina *et al.*, 1992			+ (Lu *et al.*, 1998)		+ (Hosaka *et al.*, 2006)	Ecto	4	
Multifurca	Buyck *et al.*, 2008					+ (Buyck *et al.*, 2008)	Ecto	5	
Mutinus	Hallingbäck, 1994					- (Hosaka *et al.*, 2006)	Sapro		
MYCOAMARANTHUS	Bougher, 1995						Ecto	1	
Mycolevis	Molina *et al.*, 1992					+ (Miller *et al.*, 2006; Albee-Scott, 2007a)	Ecto	1	
Naucoria	Molina *et al.*, 1992	+ (Pritsch *et al.*, 1997a; 1997b; Becerra *et al.*, 2002)	+ (Pritsch *et al.*, 1997b; Becerra *et al.*, 2002)				Ecto	~30	52
Nothocastoreum	Brundrett *et al.*, 1996					+ (Hosaka *et al.*, 2006)	Ecto	1	
Notholepiota	McKenzie, 2006						Sapro		
Octaviania	Molina *et al.*, 1992	+ (Chilvers, 1968)	+ (Morris *et al.*, 2008)			+ (Binder and Hibbett, 2006)	Ecto	15	53
Paragyrodon	Binder and Hibbett, 2006					+ (Binder and Hibbett, 2006)	Ecto	1	
Paxillus	Trappe, 1962	+ (Mleczko, 1997)	+ (Lilleskov *et al.*, 2002)	+ (Molina, 1981)	+ (Högberg *et al.*, 1999)	+ (Binder and Hibbett, 2006)	Ecto	15	
PAXILLOGASTER	Agerer, 2006						Ecto	1	
Phaeocollybia	Orlovich and Cairney, 2004					- ? (Matheny *et al.*, 2006)	Biotrophic root parasite		see discussion
Phallus	Trappe, 1962					- (Hosaka *et al.*, 2006)	Sapro		

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Phellodon	Molina *et al.*, 1992	+ (Agerer, 1992b)			+/- (Högberg *et al.*, 1999)		Ecto	16	*
Phlebopus	Brundrett *et al.*, 1996					- (Binder and Bresinsky, 2002)	Sapro (?)		54
Phylloboletellus	Agerer, 2006					- ? (Binder and Hibbett, 2006)	Mycoparasite (?)		
Phylloporus	Trappe, 1962					+ (Binder and Hibbett, 2006)	Ecto	~50	
Piloderma	Molina *et al.*, 1992	+ (Goodman and Trofymow, 1996)	+ (Dahlberg *et al.*, 1997)	+ (Baxter and Dighton, 2001)			Ecto	6	
Pisolithus	Trappe, 1962	+ (de Román and de Miguel, 2005b)	+ (Moyersoen *et al.*, 2003)	+ (Baxter and Dighton, 2001)		+ (Binder and Hibbett, 2006)	Ecto	~12	
Pleurotopsis	Izzo *et al.*, 2005a		+ (Izzo *et al.*, 2005a)				Sapro		55
Pluteus	Trappe, 1962						Sapro		
Podaxis	Bougher, 1995						Sapro		56
Podohydnangium	Brundrett *et al.*, 1996					+ (Kropp and Mueller, 1999)	Ecto	1	
Podoserpula	Bougher, 1995					- (Matheny *et al.*, 2006)	Sapro		
Polyozellus	Kropp and Trappe, 1982					+ (Stalpers, 1993)	Ecto	1	
Polyporoletus	Agerer, 2006	+ (Agerer *et al.*, 1998b)	+ (Agerer *et al.*, 1998b)			+ (Miller *et al.*, 2006)	Ecto	1	
Polyporus	Trappe, 1962				- (Hobbie *et al.*, 2001)		Sapro		*
Porpoloma	Trappe, 1962						Sapro		
Protubera	Bougher, 1995					- (Hosaka *et al.*, 2006)	Sapro		
Pseudogymnopilus	Malajczuk *et al.*, 1982						Sapro		57

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi§.

Genus	**Reference †**	**Root tip morphology**	**Root tip molecular**	**Synthesis**	**Isotopic**	**Phylogeny**	**Conclusion**	**Species number (estim.d)‡**	**Notes**
PSEUDOHYSTERANGIUM	Brundrett *et al*., 1996						Ecto	1	
Pseudotomentella	Agerer, 2006	+ (Di Marino *et al*., 2007)	+ (Kõljalg *et al*., 2000; Di Marino *et al*., 2007)				Ecto	9	
PSILOBOLETINUS	Trappe, 1962						Ecto	1	
PTERYGELLUS	Verbeken and Walleyn, 1999						Ecto (?)	5	
<u>Pulveroboletus</u>	Molina *et al*., 1992					+ (Binder and Hibbett, 2006)	Ecto	25	
Pyrenogaster	Molina *et al*., 1992					- (Hosaka *et al*., 2006)	Sapro		
Radiigera	Molina *et al*., 1992					- (Hosaka *et al*., 2006)	Sapro		
Ramaria	Trappe, 1962	+ (Nourha *et al*., 2005)	+ (Nourha *et al*., 2005)		+/- (Hobbie *et al*., 2001; 2002)	+ (Hosaka *et al*., 2006)	Ecto	~60 (?)	*
Ramaricium	Binder *et al*., 2005					- (Hosaka *et al*., 2006)	Sapro		
Ramariopsis	Brundrett *et al*., 1996						Sapro		
<u>Retiboletus</u>	Binder and Hibbett, 2006					+ (Binder and Hibbett, 2006)	Ecto	6	
Rhizopogon	Trappe, 1962	+ (Jakucs *et al*., 1998b)	+ (Jakucs *et al*., 1998b)	+ (Massicotte *et al*., 1999)	+ (Högberg *et al*., 1999)	+ (Binder and Hibbett, 2006)	Ecto	~150	
<u>Rhodactina</u>	Yang *et al*., 2006					+ (Yang *et al*., 2006)	Ecto	2	
Rhodocollybia	Agerer, 2006	+ (Mleczko, 2004c)	+ (Mleczko, 2004c)	+ (Pera and Alvarez, 1995)		- (Matheny *et al*., 2006)	Sapro		58; see discussion
Rhodocybe	Brundrett *et al*., 1996				- (Högberg *et al*., 1999)	+/- (Matheny *et al*., 2006)	Sapro		*
RHODOGASTER	Brundrett *et al*., 1996						Ecto (?)	2	59
<u>Rhopalogaster</u>	Rinaldi *et al*., this paper					+ (Hosaka *et al*., 2006)	Ecto	1	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
RICHONIELLA	Molina *et al.*, 1992						Ecto (?)	5	59
Riessia	Lee *et al.*, 1997	+ (Lee *et al.*, 1997)					Ecto	4	60; see discussion
Riessiella	Lee *et al.*, 1997	+ (Lee *et al.*, 1997)					Ecto	2	60; see discussion
Royoungia	Brundrett *et al.*, 1996					+ ? (Binder and Hibbett, 2006)	Ecto	1	
Rozites	Trappe, 1962					+ (Peintner *et al.*, 2002a; 2002b)	Ecto	20	61
Rubinoboletus	Brundrett *et al.*, 1996					+ (Binder and Hibbett, 2006)	Ecto	10	
Russula	Trappe, 1962	+ (Benken, 2001a; 2001b)	+ (Benken, 2001a; 2001b)	+ (Taylor and Alexander, 1989)	+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001)	+ (Miller *et al.*, 2006)	Ecto	~750	
Sarcodon	Agerer, 2006	+ (Agerer, 1991c)	+ (Izzo *et al.*, 2005a)				Ecto	36	
Scleroderma	Trappe, 1962	+ (Ingleby, 1999)	+ (Valentine *et al.*, 2004)	+ (Mohan *et al.*, 1993b)		+ (Binder and Hibbett, 2006)	Ecto	25	
Sclerogaster	Molina *et al.*, 1992					- ? (Hosaka *et al.*, 2006)	Sapro (?)		
SCUTIGER							Ecto	1	62
Scytinostroma	de Román and de Miguel, 2005a	+ (de Román and de Miguel, 2005a)				**-** (Miller *et al.*, 2006)	Sapro		
Sebacina	Selosse *et al.*, 2002	+ (Urban *et al.*, 2003)	+ (Urban *et al.*, 2003)	+ (Warcup, 1988)			Ecto	6	
Secotium	Bougher, 1995						Sapro		
Sedecula	Molina *et al.*, 1992						Sapro		

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Setchelliogaster	Molina *et al*., 1992			+ (Brundrett *et al*., 2005)			Ecto	6	
SETOGYROPORUS	Buyck *et al*., 1996						Ecto	1	
Simocybe	Grgurinovic and Simpson, 2001					- (Matheny *et al*., 2006)	Sapro		63
SINOBOLETUS	Dell *et al*., 2005						Ecto	5	
Sistotrema	Nilsson *et al*., 2006a	+ (Di Marino *et al*., 2008)	+ (Nilsson *et al*., 2006a)			+ (Moncalvo *et al*., 2006)	Ecto	4 (?)	see discussion
Stephanopus	Molina *et al*., 1992	+ (Palfner, 2001)					Ecto	5	
Stephanospora	Brundrett *et al*., 1996		+ (Bastias *et al*., 2006)				Ecto	4	
Strobilomyces	Trappe, 1962	+ (Matsuda and Hijii, 1999)	+ (Matsuda and Hijii, 1999)			+ (Binder and Hibbett, 2006)	Ecto	20	
Stropharia	Lakhanpal, 2000						Sapro		
Suillus	Trappe, 1962	+ (Treu, 1990)	+ (Horton *et al*., 2005)	+ (Samson and Fortin, 1988)	+ (Högberg *et al*., 1999)	+ (Binder and Hibbett, 2006)	Ecto	50	
Thanatephorus	Brundrett, 2008						Sapro		
Thelephora	Trappe, 1962	+ (Agerer and Weiss, 1989)	+ (Mahmood *et al*., 1999)	+ (Mohan *et al*., 1993a)			Ecto	49	
TIMGROVEA	Brundrett *et al*., 1996						Ecto	5	
Tomentella	Agerer, 2006	+ (Jakucs *et al*., 2005)	+ (Jakucs *et al*., 2005)	+ (Kõljalg, 1992)			Ecto	75	
Tomentellopsis	Agerer, 2006	+ (Agerer, 1998)	+ (Kõljalg *et al*., 2002)	+ (Kõljalg *et al*., 2002)			Ecto	5	
Torrendia	Brundrett *et al*., 1996					+ (Zhang *et al*. 2004; Tulloss, 2008)	Ecto	2	

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi§.

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Trappea	Molina *et al.*, 1992					- (Hosaka *et al.*, 2006)	Sapro		
Trechispora	Dunham *et al.*, 2007		+ (Dunham *et al.*, 2007)			- (Larsson *et al.*, 2004)	Ecto (?)	46	
Tremellodendron	Selosse *et al.*, 2002		+ (Walker, 2003; Tedersoo *et al.*, 2006b)				Ecto	8	
Tremelloscypha	Selosse *et al.*, 2002					+ (Weiß and Oberwinkler, 2001)	Ecto	1	
Tricholoma	Trappe, 1962	+ (Comandini *et al.*, 2004)	+ (Comandini *et al.*, 2004)	+ (Brunner *et al.*, 1992)	+ (Högberg *et al.*, 1999; Hobbie *et al.*, 2001)	+ (Matheny *et al.*, 2006)	Ecto	~200	
Tricholomopsis	Brundrett *et al.*, 1996					- (Matheny *et al.*, 2006)	Sapro		
Truncocolumella	Trappe, 1962	+ (Eberhart and Luoma, 1996)	+ (Horton *et al.*, 2005)	+ (Massicotte *et al.*, 2000)		+ (Binder and Hibbett, 2006)	Ecto	3	
Tubaria	Hallingbäck, 1994					- (Matheny *et al.*, 2006)	Sapro		
Tubosaeta	Agerer, 2006					+ (Binder and Hibbett, 2006)	Ecto	5	
Tubulicrinis	Kernaghan, 2001	+ (Kernaghan, 2001)					Sapro		64
Tulasnella	Bidartondo *et al.*, 2003		+ (Bidartondo *et al.*, 2003)	+ (Bidartondo *et al.*, 2003)		+ (Moncalvo *et al.*, 2006)	Ecto	46	
Turbinellus	Hosaka *et al.*, 2006					+ (Hosaka *et al.*, 2006)	Ecto	5	
Tylopilus	Trappe, 1962	+ (Uhl, 1989; Raidl and Hahn, 2006)	+ (Jonsson *et al.*, 1999b; Burke *et al.*, 2005; 2006)		+ (Högberg *et al.*, 1999)	+ (Binder and Hibbett, 2006)	Ecto	~75	65

Table 1 (continued). Genera of proved and putative ectomycorrhizal fungi[§].

Genus	Reference †	Root tip morphology	Root tip molecular	Synthesis	Isotopic	Phylogeny	Conclusion	Species number (estim.d)‡	Notes
Tylospora	Agerer, 2006	+ (Eberhardt *et al*., 1999)	+ (Eberhardt *et al*., 1999)	+ (Taylor and Alexander, 1990)			Ecto	2	
Vascellum	Malloch and Thorn, 1985						Sapro		
VELOPORPHYRELLUS	Agerer, 2006						Ecto	2	
Volvariella	(Trappe, 1962)					- (Matheny *et al*., 2006)	Sapro		
Wakefieldia	Molina *et al*., 1992						Sapro		
<u>***Xanthoconium***</u>	Brundrett *et al*., 1996					+ (Binder and Hibbett, 2006)	Ecto	7	
Zelleromyces	Molina *et al*., 1992			+ (Molina and Trappe, 1982)		+ (Miller *et al*., 2006)	Ecto	17	31
ZYGOMYCOTA									
Endogone	Molina *et al*., 1992	+ (Chu-Chou and Grace, 1983)	+ (Chu-Chou and Grace, 1984)	+ (Warcup, 1990a)			Ecto	~20	
Densospora	McGee, 1996			+ (Warcup, 1985)			Sapro		66
PERIDIOSPORA	Brundrett, 2008						Ecto	4	67
<u>***Sclerogone***</u>	Brundrett *et al*., 1992			+ (Warcup, 1990a)			Ecto	1	
YOUNGIOMYCES	Brundrett, 2008						Ecto	2	67
INCERTAE SEDIS									
Noahmyces	Bougher, 1995								68
Occultogaster	Orlovich and Cairney, 2004								68

§ The nomenclature used in this paper is that adopted by Kirk *et al*. (2001) in the *Dictionary of the Fungi*, integrated following various additional sources (see the notes to specific taxa). To improve readability, taxa are listed alphabetically within their phylum, regardless of the class, order and family. Genera for which two or more different lines of evidence support an ECM habit are reported in boldface, whereas those for which a single type of experimental evidence is available are in boldface and underlined. In both these cases, the number of currently recognized species is reported, as retrieved from the *Dictionary of Fungi*, or from more recent taxonomic monographs of specific genera. An entry does not necessarily imply that all species of that genus are ECM (see main text). Genera for which no experimental or phylogenetic evidence is currently available, but for which ECM status can be hypothesized based on habitat features and/or our personal experience, are in boldfaced small caps. Synonimized genera are not listed;

† a reference (not necessarily the first one in chronological terms) alleging or quoting the ECM status of each listed genus, is reported;

‡ for those genera where both mycorrhizal and non mycorrhizal species are thought to occur, only the species believed or proved to form ECMs are reported;

Sapro = saprotrophic, Ecto = ectomycorrhizal;

* asterisk means that radioisotope measurements suggested either a saprotrophic life style or gave non conclusive indications as for the trophic status of the relevant taxon;

1 The status of several Dark Septate Endophytes (e.g., *Chloridium*, *Leptodontidium*, *Phialocephala*, *Phialophora*, *Meliniomyces*) as mycorrhizal fungi is contested. We follow Jumpponen (2001) and assign it to the mycorrhizal fungi. In the case of *Phialocephala fortinii*, at least 6 cryptic species exist in this complex (Grünig *et al*., 2008). See also comment under *Meliniomyces*;

2 a root tip in Izzo *et al*. (2005a) was assigned to *Cladophialophora* through BLAST searches. A recent *emerencia* search (22 May 2008) indicated that the sequence could either belong to *Cladophialophora* or *Phialocephala*. Considering that *Cladophialophora* is regarded as saprotrophic, and *Phialocephala* as a root endophyte, we consider that latter assignment more likely;

3 although sometimes considered as members of the ECM family Terfeziaceae, the real taxonomic position of *Delastria* and *Loculotuber* is still debated (Lumbsch and Huhndorf, 2007);

4 some authors consider *Genea* and *Genabea* as synonyms, others as separate genera (e.g., Smith *et al*., 2006);

5 according to Egger and Paden (1986), synthesised biotrophic interactions of isolates of *Tricharina*, *Trichophaea* and *Geopyxis* on *Pinus contorta* showed some features of pathogenicity;

6 isolated from mycorrhiza and isolate DNA sequenced;

7 it shares the habitat of many other hypogeous fungi, ECM symbionts of *Eucalyptus* (see Claridge *et al*., 2000);

8 possibly a synonym of *Gymnohydnotrya*;

9 Several strains of *Meliniomyces* (3 spp.) have been reported to form ectomycorrhizas, while other strains are unspecified root endophytes (Hambleton and Sigler, 2005). It is likely that several other members of the *Rhizoscyphus ericae* clade also form ectomycorrhizas, described as *Piceirhiza bicolorata* (see Alberton, 2008). Recent in vitro resynthesis study confirmed that an isolate of *Meliniomyces variabilis* (LtVB3) could form ericoid mycorrhizal structures in an axenically reared host, but did not form typical mycorrhizal structures in an ectomycorrhizal host (Ohtaka and Narisawa, 2008).

10 features of both ECM and ectendomycorrhizal colonization generally observed, together with an often poor or incomplete development of Hartig net and mantle;

11 possibly a synonym of *Ruhlandiella*;

12 in Hobbie *et al*. (2001; 2002), as *Otidia*;

13 in Hobbie *et al*., 2002, as *Aleuria*;

14 as *Leucangium* in Palfner and Agerer, 1998b, and Hobbie *et al*., 2001;

15 in Gutiérrez *et al*., 2003, both inter- and intracellular colonization observed;

16 as *Scabropezia* in Hansen *et al*., 2005;

17 these taxa, although not previously alleged as being ECM, were isotopically tested by Hobbie *et al*. (2001; 2002);

18 as *Lachnea* in Warcup, 1990b;

19 these taxa have been reported to form also ectendomycorrhizas, and in some cases even endomycorrhizas (see also Bratek *et al*., 1996; Zaretsky *et al*., 2006; Yu *et al*., 2001).

20 in Brand 1988, as '*Fagirhiza tubulosa*' (see DEEMY, www.deemy.de);

21 in Warcup, 1990b, as *Labyrinthomyces*;

22 tentatively identified in Walker *et al*., 2005;

23 the status of *Mattirolomyces* (not listed) is debated. The *Dictionary of Fungi* lists it as a synonym of *Terfezia*, whereas some authors believe it should be reinstated as a valid genus (e.g., Percudani *et al*., 1999; Kovács *et al*., 2007);

24 according to Yang and Korf (1985), anamorphs of several species assigned to *Tricharina* should be grouped in the genera *Ascorhizoctonia* (believed to be saprotrophic in soils) and *Complexipes* (mycorrhizal);

25 in Ingleby *et al*., 1990, misidentified as *Tricharina* (see DEEMY, www.deemy.de);

26 in Molina *et al*., 1992, as *Camarophyllus*;

27 = *Naucoria, pro parte* (see Moreau, 2005; Moreau *et al*., 2006b);

28 many genera of sequestrate fungi would under a phylogenetic classification have to be reduced to synonymy (e.g. *Amarrendia* = *Amanita*, *Torrendia* = *Amanita*, *Hydnangium* = *Laccaria*);

29 see Thomas *et al*., 2002;

30 Valentine *et al*. (2004) reported a root tip whose sequence was claimed to be identical to that of *Antrodiella*, a confirmed saprotrophic genus. No sequence for the root tip was available. See also http://mor.clarku.edu/equences.php?acc=

0&sort=reason for information why the *Antrodiella* sequence in GenBank is problematical;

31 these gasteroid genera are currently considered valid, although several independent studies seem to suggest that their synonomy with *Russula* (*Macowanites*, *Gymnomyces*, *Cystangium*) and *Lactarius* (*Arcangeliella*, *Zelleromyces*) might be taxonomically justifiable (e.g., Miller *et al*., 2001; Desjardin, 2003; Nuytinck *et al*., 2003);

32 recently separated from *Inocybe* on the basis of molecular systematic studies (Matheny and Bougher, 2006). Ectomycorrhizal habit suspected but not yet proved;

33 possibly a synonym of *Tylopilus* (see http://www.nybg.org/bsci/res/all/boletes/tylopilus_digest.html);

34 in Trappe, 1962, as *Lepiota*;

35 position of *Clavariadelphus* in phylogeny seems a bit problematical and could allow both ECM and sapro status. In this case, we decided to rely on similarity between *Gomphus* and *Clavariadelphus*, and the work by Agerer *et al*. (1998a) to treat it as ECM;

36 in Izzo *et al*., 2005a, as *Artomyces*;

37 *Clitopilus* has been mentioned as forming ectomycorrhizas by Lindeberg, 1948 (see also Koide *et al*., 2008, on ECM – sapro divide), but we believe there is no good modern evidence. That's why we prefer to treat it as sapro;

38 in Izzo *et al*., 2005a, as *Coprinus*;

39 under older taxonomic concepts the name *Corticium* refers to a very large diversity of corticioid fungi, and some of these form indeed ectomycorrhiza. *Corticium* in its restricted sense is a saprotroph, however;

40 in Högberg *et al*., 1999, as *Cantharellus*;

41 possibly a synonym of *Cortinarius* (see Hawksworth *et al*., 1983; Peintner *et al*., 2004);

42 apparently a synonym of *Gastrotylopilus*;

43 it is likely that all the 'Gastroboletes' are to be reduced to 'true' bolete genera, like *Gastrosuillus* (not mentioned in the Table) which is just a gastroid form of *Suillus grevillei*;

44 possibly a synonym of *Gomphidius* (see Miller, 2003);

45 in Trappe and Castellano, 1986, as *Martellia*;

46 as *Nematoloma*. *Hypholoma* and *Stropharia* are considered as synonyms of *Psilocybe* by some authors;

47 in Trappe, 1962, as *Lentinus*;

48 in Fontana, 1961, as *Rhodopaxillus*;

49 possibly a synonym of *Hydnangium*;

50 as *Clavariadelphus*;

51 in Tedersoo *et al*., 2003, as *Clavulicium*;

52 Nomenclatural complications surround this genus, with the result that it is often synonymized with either the ectomycorrhizal *Alnicola* (see relevant note) or under the saprotrophic *Simocybe*, depending on the typification. According to Moreau (2005), *Naucoria escharioides* (Fr. : Fr.) P. Kumm. and *N. subconspersa* Kühner, i.e. the species whose mycorrhizae were characterized by Pritsch *et al*. (1997a; 1997b) and Becerra *et al*. (2002), should be classified in the genus *Alnicola* (synonimizing *N. subconspersa* with *A. luteolofibrillosa* Kühner). Moreover, Agerer (2006) has recently questioned the identification of the ECM described by Becerra *et al*. as *N. escharioides*, noting that its features recall more the ECMs formed by some *Entoloma* species;

53 in Chilvers, 1968, as *Octavianina*;

54 there are reports of *Phlebopus* forming ectomycorrhiza (see Thoen and Ducousso, 1990) with exotic acacias in Africa. Indigenous *Phlebopus* in Cameroon was consistently found in vegetation without ectomycorrhizal trees (Th.W. Kuyper, unpublished), which fits with its phylogenetic position;

55 based on a root tip where the Blast search by Izzo *et al*. (2005a) suggested *Pleurotopsis*. A recent *emerencia* search also pointed to a member of the mycenoid clade (*Mycena*, *Hydropus*). No ectomycorrhizal fungi are known in that clade. We treat the occurrence of this sequence as similar to the occurrence of a *Mycena epipterygia* sequence by Rosling *et al*., 2003 (see discussion). The genus *Pleurotopsis* is sometimes synonymized with *Resupinatus* or *Hohenbuehelia*;

56 as *Chainoderma*;

57 as *Gymnopilus*;

58 in Pera and Alvarez, 1995, as *Collybia*;

59 there is no complete phylogeny available of *Entoloma* in a large sense, so the position of these sequestrate entolomataceous taxa cannot be evaluated from that phylogeny. Considering that in many cases sequestrate derived species form ectomycorrhizas, we accept the claims by Brundrett *et al*. and Molina *et al*.;

60 anamorphic genera; Hartig net absent; currently it is not sure this is a functional ECM; *Riessiella* was recently shown to be nested within *Tomentella* on the ground of molecular evidence (see Tedersoo *et al*., 2007a);

61 Phylogenetically just a *Cortinarius*, (see Peintner *et al*., 2002a);

62 A taxonomic synonym or closely related genus to *Albatrellus*,

63 in Grgurinovic and Simpson, 2001, as *Ramicola*;

64 ECMs tentatively identified on the basis of their amyloid lyocystidia;

65 in Raidl and Hahn, 2006, as *Porphyrellus*;

66 originally reported as *Glomus* (see Dunstan *et al*., 1998);

67 belong to the Endogonaceae (see to http://www.zygomycetes.org/);

68 both names have apparently never been validly published.

The results confirm those of morphology-based root tip methods. This information derived from isolation experiments is therefore not included in our Table. The only exceptions are ascomycetes *Geopyxis* (Vrålstad *et al.*, 1998) and *Ruhlandiella* (Warcup, 1991), for which no other evidence supporting ECM formation is available.

Molecular evidence

Molecular tools are relatively simple to apply and can rapidly screen an ecosystem-wide ECM community. Data coming from this source are being released at a growing pace, and will presumably surpass those originated by morphotyping quite soon. Molecular identification of root tips is generally considered a very reliable way of assessing the status as ECM fungus (Kõljalg *et al.*, 2005; Nilsson et al., 2006b). However, like every method it is not free from pitfalls. Such problems may either reside in the database (according to Bridge *et al.* (2003) some 20% of sequences deposited as *Amanita* do belong to different fungi) or in inherent weaknesesses of programmes such as BLAST (see Nilsson *et al.*, 2005 for an alternative tool, *emerencia*, at http://emerencia.math.chalmers.se/). Improved possibilities for (third-party) annotation of published sequences makes a contribution to reduce the unreliable information that is inherent in such large databases. Even the nature of the root tip evidence itself may in some cases be ambiguous. Root tips could show double bands, indicating the presence of secondary colonizers on ectomycorrhizas. Such secondary colonizers can be quite common. Rosling *et al.* (2003) suggested that around 25% of the root tips yielded double bands. Often the second species belongs to ascomycete groups, and interpretation of such species as secondary colonizers is relatively unproblematical. However, in exceptional cases even saprotrophic basidiomycetes could be encountered on such root tips. This is our interpretation of the record of a basidiomycete on a *Cenococcum*-like root tip (Rosling *et al.*, 2003). This basidiomycete belongs to the *Mycena epipterygia* group, as evident through BLAST and *emerencia* searches. We do not consider this molecular identification of a root tip as evidence that *Mycena* species form ectomycorrhizas.

The isotopic evidence

The measurement of stable isotopes of carbon and nitrogen at their natural abundances has enabled improved assessment of pathways and rates of nutrient fluxes. It has been proposed that stable isotopes of carbon and nitrogen could also provide decisive information in separating and quantifying the roles of saprotrophic and mycorrhizal fungi in forest ecosystems. And finally, the suggestion has been made that an assessment of the isotopic signatures of fruitbodies of macromycetes would help in assigning trophic status to that fungal species.

Henn and Chapela (2001) coined the term ectomycorrhiza – saprotrophic divide (EM – SAP divide), to indicate that within an ecosystem the groups of ECM and saprotrophic fungi were significantly different in their ^{13}C and ^{15}N signal. They also suggested that a combination of both isotopes allowed an even better separation of both trophic groups. On average ECM fungi were more enriched in (had a higher value of) ^{15}N and more depleted in (had a more negative value of) ^{13}C than saprotrophic fungi. A graph where both parameters are plotted shows a significant correlation, and a dividing line can then be drawn with (almost) all ECM fungi above that divide, and saprotrophic fungi below that divide. However, within each trophic group ^{13}C and ^{15}N signatures are not correlated, so the general correlation is technically spurious. There were also large site-specific effects in the carbon and nitrogen signatures. Henn and Chapela (2001) also mentioned that there is no underlying mechanism in physiology that determines a simultaneous impact on both stable isotopes.

Statistically significant differences between both trophic groups can be caused by different isotope signals of the source and / or different fractionation processes by the biochemical pathways of the fungus.

For nitrogen isotopes early work on plants with different kinds of mycorrhizal associations (non-mycorrhizal, arbuscular, ericoid, and ECM plants) had indicated different ^{15}N signatures, consistent with different ^{15}N signals of the source (ammonium, nitrate, organic nitrogen). However, it soon became clear that ^{15}N signals in plants and fruitbodies were unlikely be determined exclusively or mainly by the source signal. Fractionation processes after uptake had therefore to be taken into account, and in the case of ECM fungi also the fractionation of the ^{15}N that stayed in the fungus and that was transferred to the plant. The importance of this latter fractionation was evident considering large differences in the ^{15}N signal of ECM root tips and fruitbodies.

While the average ^{15}N signals of ECM and saprotrophic fungi were significantly different in most studies, the values for individual species showed substantial overlap. This overlap makes the ^{15}N isotopic signature of fruitbodies alone insufficient to assign trophic status. A further analysis of the ^{15}N values casts even more doubts on its validity as a marker for trophic status. This analysis indicated that:

1) There is a large range within ECM fungi. According to Lilleskov *et al*. (2002) high ^{15}N signatures occur in species with better proteolytic capacities. Similarly, species with the highest ^{15}N signal (*Hydnellum*, *Cortinarius*, *Tricholoma*) are species most sensitive to N deposition (Arnolds, 1991). A study by Hobbie *et al*. (2005) indicated higher ^{15}N enrichment in ECM fungi that show high selectivity compared to generalist ECM fungi. While Hobbie *et al*. (2005) suggested that the higher signature was due to the fact that in host-specific fungi fitness of plant and fungus was more intimately linked (resulting in a higher transfer of N to the host tree), the data are also consistent with the observation by Arnolds (1991) that ECM fungi that associate exclusively with conifers are more sensitive to nitrogen enrichment. That nitrophobic species differ in their N metabolism (leading to this enrichment) is also suggested by the very high ^{15}N signals of various saprotrophic grassland fungi such as clavarioid fungi, Geoglossaceae and *Hygrocybe* species (Griffiths *et al*. 2002). In fact, their ^{15}N signal would indicate that these species are unambiguously ECM! Interestingly their ^{13}C signal would similarly support classification as ECM fungi, although they were even more depleted in ^{13}C than ECM fungi.

2) Within the saprotrophic fungi wood-decomposing fungi had lower ^{15}N signals than litter decomposers. Species characteristic for old humus (*Agaricus* species) tended to have high N values (Taylor *et al*., 2003; Hart *et al*., 2006). As a consequence, the discriminatory power between different trophic modes based on ^{15}N is affected by the extent to which wood-inhabiting, litter decomposing and humus decomposing fungi are represented among the decomposers.

3) Parasitic fungi also possess high ^{15}N signals. The values reported by Hart *et al*. (2006) for *Pholiota squarrosa* would fit better with an ECM trophic mode. Isotopic signatures for species that combine an ECM / parasitic lifestyle (Gomphidiaceae) were quite variable. The study by Trudell *et al*. (2004) found very low ^{15}N signatures, whereas Taylor *et al*. (2003) found high signatures.

4. The ^{15}N source signal depends to a large extent on ecosystem nitrogen availability. Under conditions of high N input or even N-saturation the source ^{15}N signal increases, affecting the fungal N concentration and ^{15}N signal. Because N concentration is positively correlated with ^{15}N in saprotrophic fungi (but not in ECM fungi) N enrichment tends to elevate the ^{15}N signal of saprotrophic fungi. In ECM fungi N concentration and ^{15}N signature are not correlated. Because the fungal species with the highest ^{15}N signal are also most sensitive to N enrichment, the ^{15}N signature of ECM fungi declines with increasing N availability. Consequently, overlap becomes larger and the discriminatory power of the method becomes weaker.

Because ^{15}N reflects both the source and subsequent fractionation processes of N, the relative importance of which is unknown, and because there is no underlying theory that suggests fundamentally different biochemical processes of N metabolism between both trophic groups, we question the use of ^{15}N signature of sporocarps as an independent indicator, in agreement with Henn and Chapela (2001). At best ^{15}N signatures can be interpreted as additional assignment of a trophic mode – but then data on many other fungal species need to be available and the important N fluxes for that ecosystem need to be quantitatively known too.

Most studies also reported statistically different ^{13}C signals between ECM and saprotrophic fungi. On average ^{13}C is around 2‰ more negative in sporocarps of ECM fungi than of saprotrophs, but again the values partly overlap. Henn and Chapela (2001) analysed ^{13}C of both fungal groups and their substrates (green leaves and needles versus shed litter and wood) and noted that the difference in ^{13}C signal between both trophic modes was almost completely explained by the difference in the ^{13}C source signal, with no additional role for different physiological mechanisms. They did not observe additional fractionation processes between both groups. These observations would make ^{13}C a much more reliable indicator for trophic status. However, this method too is not without difficulties because:

1. The ^{13}C signals of conifers is usually about 1-2‰ lower than that of broad-leaved trees, and a similar difference is visible in the fruitbodies of ECM fungi (Taylor *et al*., 2003).

2. A biotrophic lifestyle may also cause a ^{13}C signal that is similar to that of ECM fungi – due to the fact that both life styles depend on simple hexoses provided by the tree. *Phaeocollybia*, a fungal genus that is likely a biotrophic root parasite (Norvell, 1998) has a ^{13}C (and ^{15}N) signal similar to ECM fungi (Trudell *et al*., 2004).

3. The strong ^{13}C depletion of species of the *Geoglossaceae*, clavarioid fungi and members of the genus *Hygrocybe* suggests other nutritional modes that could result in the same pattern.

4. The ^{13}C signal of saprotrophic fungi differs –again– between litter and wood-decomposing fungi. In general the ^{13}C signal of organic remains increases (becomes less negative) during decomposition (Hobbie *et al*., 2001). As a consequence the ^{13}C signal of fungi that live on rather undecomposed material can be rather close to the signal of ECM fungi.

5. Uptake of organic N also results in uptake of some carbon from the soil. The amount is usually less than 10% of total carbon demand, so the effects on the fungal signal should be rather limited except for species with strong proteolytic activities.

6. A few strongly deviating ^{13}C signals have been reported. While the very high ^{13}C values for *Cortinarius variosimilis* (Trudell *et al*., 2004) and *C. paleaceus* (Zeller *et al*., 2007) have just been accepted as anomalies and not as suggestive that the species are facultatively saprotrophic, the similarly high signal for *Chalciporus piperatus* (Taylor *et al*., 2003) has raised doubts whether this species forms ectomycorrhiza or whether the species is better classified as saprotrophic. However, in the absence of supporting evidence, we consider the ^{13}C evidence alone as insufficient, the more so because in the same study the confirmed ECM genera *Hydnellum* and *Phellodon* also had relatively high ^{13}C values. *Chalciporus piperatus* also had a very high ^{15}N value.

Again, we agree with Henn and Chapela (2001) that the isotopic signature alone is insufficient to establish a fungal trophic mode. The ^{13}C signal could provide suggestions for trophic modes that should be backed up with further research. In that way it has been successfully applied in genera like *Sowerbyella* and *Clavulina*.

Because the ^{13}C signature in fungal fruitbodies mainly reflects the carbon source (without major fractionation processes through fungal metabolism) the possibility has been raised whether the radioactive isotope ^{14}C could be used as a tracer for fungal trophic mode. The atmospheric levels of ^{14}C have very substantially increased in the 1960s due to the testing of nuclear weapons. After such above-ground tests were banned, the atmospheric levels have fairly rapidly gone down. The ^{14}C signal could therefore provide a fairly accurate signal of the age of the fungal carbon used. Hobbie *et al*. (2002) applied the method and noted, after correction for fractionation against ^{14}C, being approximately twice that against ^{13}C, significantly different carbon ages for four ECM genera than for saprotrophic genera. However, for species of as-yet-unknown life histories the ^{14}C data were more difficult to interpret and partly at variance with ^{13}C data that were simultaneously assessed. *Otidea* and *Sowerbyella* were ECM according to both carbon signatures, whereas *Aleuria Clavulina*, *Paurocotylis* and *Ramaria* had a ^{13}C signal that suggested an ECM status but a ^{14}C signal that suggested that its carbon was between 3 and 12 years old. A complicating issue is that the ^{14}C signal is not always accurate to indicate carbon less than 1 year and very young carbon (1-2 years), so interpretation of the signal for fungi that grow on fresh organic material is more difficult. A further complicating issue is that the ^{14}C signal could also be affected by uptake of old organic nitrogen in proteolytic ECM fungi, which leads to an enrichment of ^{14}C in fruitbodies and hence an overestimate of the carbon age. This could also make the method not very robust, especially with carbon ages of only a few years. No recent work employing the ^{14}C method to infer mycorrhizal status has come to our attention.

Phylogenetic evidence

Inclusion in the list reported in Table 1 does not automatically imply that all species of that genus form ECMs. Because we analyse the (putative) nutritional mode as ECM on generic level, the assumption then is that the genus level is the adequate analytical level, and hence that nutritional modes within a genus are essentially constant. That assumption has not been unchallenged and should therefore be critically evaluated. Criticism of this assumption has mentioned three, partly unrelated elements, viz.:

1. The evolution of the ECM habit (and / or its secondary loss) occurred repeatedly within lineages;
2. Several (or even many) genera known as ECM are not monophyletic, and therefore scaling up from species level to genus level introduces errors;
3. Our table pigeonholes fungi as either forming ECM or possessing a saprotrophic life style, not allowing for mixotrophy on species or generic level.

While the conclusion that the ECM symbiosis evolved more than once among the fungi is uncontroversial, because ECM fungal genera occur in the Zygomycota (*Endogone*), Ascomycota and Basidiomycota, the issue of multiple gains and/or losses of the ECM habit on lower levels is less straightforward. The issue of evolutionary stability of the ECM symbiosis from a fungal viewpoint has been addressed by Hibbett *et al*. (2000). They used a basidiomycete phylogeny in which they plotted cases of ECM and saprotrophic nutritional modes and used parsimony to evaluate the question of multiple losses of the ECM habit. They compared two scenarios, one in which secondary losses of the ECM habit was impossible, and one in which gains and losses were equally likely. While the first scenario put no constraints on the number of convergent gains, the second scenario can partly reduce the number of independent origins. An important argument for minimizing independent origins is the complex character of the trait of the ECM morphology and nutritional mode (evolution of sheath and Hartig net, while not allowing intracellular colonization, impact on root morphology, an interface where nutrients and carbon are exchanged in a regulated fashion). Because the evolution of complex traits seems less likely than its loss, a model with secondary losses seems a plausible alternative. This model initially did gain additional support when Chen *et al*. (2001) claimed widespread occurrence of genes involved in ligninolysis among ECM Basidiomycota, suggesting that these fungi have retained a substantial saprotrophic ability. However, Cairney *et al*. (2003) subsequently retracted their initial claim and there is little corroborated evidence to date that suggests significant saprotrophic ability among ECM Basidiomycota.

Bruns and Shefferson (2004) re-analysed the data by Hibbett *et al*. (2000). They noted that with a 1:2 weighting (considering the transition saprotrophic – ECM twice as likely as the reversal ECM - saprotrophic) the most parsimonious explanation was that all transformations, except one, consisted of gains of the ECM habit. Only one likely case of secondary loss in their phylogeny remained, the evolution of saprotrophy in *Lentaria byssoides* from an ECM gomphoid clade. However, recent analyses of that gomphoid lineage (Humpert *et al*., 2001; Hosaka *et al.,* 2006) have shown that even this case is only very weakly supported. These recent analyses indicated that *Lentaria* is part of the basal clade within the gomphoid lineage, so even here a gain of the ECM habit within that lineage is a plausible alternative. One further instance of secondary loss of the ECM habit could refer to the Boletinellaceae (the clade of *Boletinellus* and *Phlebopus*). This clade was part of the ECM Boletineae + Paxillineae + Sclerodermatineae lineage in Binder and Hibbett (2006) but other classifications have resolved it as a basal lineage (Hughey *et al*., 2000; Binder and Bresinsky 2002), so support for secondary loss of the ECM habit is ambiguous.

Of course the choice for a 1:2 weighting as an alternative for a 1:1 weighting needs argumentation. We would argue that ECM fungi, while retaining some limited saprotrophic ability that allows them, in temperate regions, to survive winter in the absence of a carbon flow and during the dying off of fine roots, are competitively inferior to saprotrophic fungi (Taylor and Alexander, 2005; but cf Koide *et al.,* 2008). Their levels of cellulolysis must be downregulated in order to prevent the killing of the host tree. Many species are also deficient in one or more B vitamins such as thiamine and biotin, relying on the host tree. Even when grown in the laboratory, in the absence of competitors and supplied with large amounts of simple carbohydrates and externally supplied vitamins, they need to be regularly 'rejuvenated' through ECM synthesis, as the physiological performance over time declines. Bruns and Shefferson (2004) further noted that many radiations occurred during episodes of major climatic change, especially the Oligocene – Eocene transition when ECM plants co-evolved, and that this evolutionary scenario strongly argues against secondary saprotrophic ability.

On the basis of these data we accept that there are no strongly supported circumstances of secondary reversal from the ECM habit to a saprotrophic mode. Because of this phylogenetic conservatism, phylogenetic data could also provide additional support for (or refutation of) an ECM habit. We have used this reasoning to argue against the ECM habit for *Rhodocollybia butyracea* and *Geastrum fimbriatum*, despite descriptions of ectomycorrhizas as indicated in Table 1. Similarly we have used this reasoning to include *Chalciporus piperatus*, which belongs to an exclusively ECM clade (Binder and Hibbett 2006) despite stable isotope evidence that potentially suggests a saprotrophic lifestyle.

However, it could still be possible that the genus level is not adequate for our analysis, because the genus is not monophyletic (and therefore combines unrelated members with different lifestyles). Genera, morphologically based, that apparently combine species with ECM and saprotrophic life styles are for instance *Paxillus*, *Amanita*, *Ramaria*, *Entoloma, Peziza*. In the case of *Paxillus* molecular methods (Binder and Hibbett 2006) have demonstrated that the genus consists of two separate and not very closely related lineages (that are not even sister groups), *Paxillus* (containing ECM species) and *Tapinella* (containing saprotrophic species). Similarly *Ramaria* was demonstrated polyphyletic by Humpert *et al*. (2001). A closer look at their phylogeny (and also the newer phylogeny of that complex by Hosaka *et al*., 2006) suggests that some basal lineages (including the lineage with *R. stricta*, and also with *Beenakia* and *Lentaria*) are likely saprotrophic, whereas the larger part of *Ramaria* forms ectomycorrhiza. The estimate by Agerer (2006) of 60 ECM *Ramaria* species of a total of 221 described is, however, considered too conservative (Agerer, 2006). Of some 1000 recognized species of *Entoloma,* only five have been reported to be ECM. Agerer (2006) estimated that about 10% (~100) of *Entoloma* species might be ECM. In *Amanita* non-mycorrhizal species occur in sect. *Lepidella*, the basal clade in *Amanita* phylogenies published by Zhang *et al*. (2004) and Tulloss (2008). Note that the sister groups of *Amanita* are also non-ECM. *Peziza* contains both ECM and saprotrophic species. The phylogeny of *Peziza* and allied genera published by Hansen *et al*. (2005) suggested that the ECM habit evolved at least twice, viz. in the clades of *P. depressa* and *Sarcosphaera coronaria*. *Sistotrema* is a further polyphyletic genus that contains both saprotrophic and ECM fungi (Larsson *et al*., 2004; Nilsson *et al*., 2006a). The phylogeny of the cantharelloid clade (Moncalvo *et al*., 2006) confirmed that *Sistotrema* is polyphyletic and showed that *S. muscicola* and *S. alboluteum* (and likely *S. confluens*) belong to the same clade as the ECM genera *Hydnum*, *Cantharellus*, and *Craterellus* – again providing strong support for our claim that there is sufficient phylogenetic conservatism in nutritional mode to use phylogenetic information for our evaluation. Similarly the two sister genera *Membranomyces* and *Clavulina* are both ECM (Tedersoo *et al*., 2003). We treat *Geastrum* as non-mycorrhizal The phylogeny of *Geastrum*

(Hosaka *et al*., 2006) puts it together with *Sphaerobolus* as a separate saprotrophic clade in the phalloid lineage.

Mixotrophic lifestyles

Another assumption made in this paper is that species can be rather unambiguously classified as possessing either an ECM or a saprotrophic life style, and that mixotrophy (a combination of both life styles) is rare at best. It is an empirical issue whether pigeonholing life styles in mutually exclusive classes reflects some underlying fundamental principles of fungal metabolism or only human convention. Hering (1982) proposed that both categories were mutually exclusive. However, Hering's view has recently been criticized by Koide *et al.* (2008) who came to the opposite conclusion that the distinction was arbitrary. While it is clear that ECM fungi are evolutionarily derived from saprotrophic fungi and have retained saprotrophic capacities (which is essential for survival in a seasonal climate after root death), we have not encountered evidence that an ECM fungus can complete its life cycle in the absence of a host plant. Evolutionary considerations would, in our opinion, also make such a putative organism unlikely. A fungus that can exist as facultative ECM fungus and as saprotroph would outcompete both obligate ECM fungi (because of more extensive saprotrophic capabilities during periods that trees are physiologically inactive) and saprotrophs (because of access to easily degradable carbon sources). To the best of our knowledge, such species have never been reported.

On the other hand, several instances have been reported where a biotrophic mutualistic life style is combined by a biotrophic antagonistic life style. Members of the Gomphidiaceae (*Chroogomphus* and *Gomphidius*) engage in peculiar three-way associations with species of *Rhizopogon* and *Suillus*. In these mixed ECMs, haustoria produced by the Gomphidiaceae penetrate the root cortical cells of *Rhizopogon* and *Suillus*, suggesting that, at least in this case, *Chroogomphus* and *Gomphidius* may act as parasites, on either the fungal or the plant host, or both (Olsson *et al*., 2000; Agerer, 2006). We have classified these fungi among the ECM fungi. Other examples of possibly mixed lifestyles are known, not necessarily involving exploitation of one partner on the other(s) (Brand, 1992; Buscot, 1994). Agerer and Wallander (1993) observed that *Entoloma saepium* acts more as a parasite than as a symbiont on *Rosa* sp., as it invades and almost completely destroys the root meristem and young root cells. A similar behavior is shown by members of the genus *Morchella* (Buscot, 1993; Dahlstrom *et al*., 2000) These taxa have been excluded from our list. In the ECMs formed by anamorphic Basidiomycetes *Riessia* and *Riessiella* (now known to be an anamorphic state of *Tomentella*, see Tedersoo *et al.,* 2007a) on the dipterocarpaceous host *Shorea leprosula*, both inter- and intracellular colonization were observed (Lee *et al*., 1997 (Table 1).

Conclusion: ECM fungi - the known and the unknown

As we show in this paper, part of our knowledge of global ECM diversity is based on unsubstantiated observations. In other words, together with a lot of good wheat, previous studies (some of which date back to over 40 years) have bequeathed us with a non-negligible amount of chaff, which, if not recognized and eliminated, can be detrimental to the quality of the dough and to the taste of the bread we are preparing.

On the basis of this evaluation of trophic status and the information on species richness of the genera listed in Table 1, we estimate the number of ECM fungal species as around 7750. However, it should be emphasised that this is still a conservative estimate. Probably some of the genera listed here for which no evidence supporting an ECM status exists today belong to the ECM guild, and work in this direction should be continued. To assist this process, Table 1 can be considered as a guide, to check which gaps need to be eventually filled.

While new ECM genera continue to be described (see Tedersoo *et al*. 2007a for ECM members of the Sordariales observed in the Seychelles), we believe it is not so much the list of ECM genera, but the estimated species numbers per genus that show the larger uncertainty. Species numbers of many genera are still inadequately known, and the increased taxonomic efforts especially in ECM rain forests of west and central Africa, south-east Asia and the Amazon, in savanna vegetation in east Africa, and in eucalypt forests in Australia will certainly further (substantially) raise this number(e.g. see Nuytinck *et al.,* 2006; Ortiz-Santana *et al*., 2007). In Australia only, there could be some 6500 ECM fungi, probably endemic in large part (Bougher, 1995). Mueller *et al.* (2007) tried to produce an estimate of global macromycete diversity. Their analysis suggests that less than half of macromycete species are known. Assuming that the ratio known : unknowns is similar for ECM and saprotrophic fungi, these data would result in an estimated ECM fungal species richness [multiply by 2.614] of 20000-25000 species.

Our estimate of around 25000 ECM species raises a major question regarding fungal diversity and biology. In the ECM symbiosis the ratio of mycorrhizal fungi to mycorrhizal plants is well above 1 (there are about 8000 species of ECM plants). However, in the other mycorrhizal symbioses the ratio is much smaller than one (around 200 species of AM fungi associate with 200000 plants; around 10 species of orchid mycorrhizal fungi associate with 25000 orchids; and around 15 species of ericoid mycorrhizal fungi associate with 3000 members of the Ericales). Understanding the causes and consequences of fungal diversity will continue to be the major challenge for mycologists.

Acknowledgements

We dedicate this paper to Dr. Cornelis Bas (Rijksherbarium, Leiden, the Netherlands) on the occasion of his 80th birthday. His revision of *Amanita* sect. *Lepidella* has been a major source of inspiration for the issue of evolutionary relations between mycorrhizal and saprotrophic habits in the *Agaricales*.

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Note added in proof: Considering the polyphyly of *Lyophyllum*, it is interesting to note that also *L. semitale* forms ECMs in synthesis experiments, as reported by Yamada *et al*., Mycorrhiza 11: 67-81.