

Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages

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Abstract The ectomycorrhizal (EcM) symbiosis involves a large number of plant and fungal taxa worldwide. During studies on EcM diversity, numerous misidentifications, and contradictory reports on EcM status have been published. This review aims to: (1) critically assess the current knowledge of the fungi involved in the EcM by integrating data from axenic synthesis trials, anatomical, molecular, and isotope studies; (2) group these taxa into monophyletic lineages based on molecular sequence data and published phylogenies; (3) investigate the trophic status of sister taxa to EcM lineages; (4) highlight other potentially EcM taxa that lack both information on EcM status and DNA sequence data; (5) recover the main distribution patterns of the EcM fungal lineages in the world. Based on critically examining original reports, EcM lifestyle is proven in 162 fungal genera that are supplemented by two genera based on isotopic evidence and 52 genera based on phylogenetic data. Additionally, 33 genera are highlighted as potentially EcM based on habitat, although their EcM records and DNA sequence data are lacking. Molecular phylogenetic

and identification studies suggest that EcM symbiosis has arisen independently and persisted at least 66 times in fungi, in the Basidiomycota, Ascomycota, and Zygomycota. The orders Pezizales, Agaricales, Helotiales, Boletales, and Cantharellales include the largest number of EcM fungal lineages. Regular updates of the EcM lineages and genera therein can be found at the UNITE homepage http://unite.ut.ee/EcM_lineages. The vast majority of EcM fungi evolved from humus and wood saprotrophic ancestors without any obvious reversals. Herbarium records from 11 major biogeographic regions revealed three main patterns in distribution of EcM lineages: (1) Austral; (2) Panglobal; (3) Holarctic (with or without some reports from the Austral or tropical realms). The holarctic regions host the largest number of EcM lineages; none are restricted to a tropical distribution with Dipterocarpaceae and Caesalpiniaceae hosts. We caution that EcM-dominated habitats and hosts in South America, Southeast Asia, Africa, and Australia remain undersampled relative to the north temperate regions. In conclusion, EcM fungi are phylogenetically highly diverse, and molecular surveys particularly in tropical and south temperate habitats are likely to supplement to the present figures. Due to great risk of contamination, future reports on EcM status of previously unstudied taxa should integrate molecular identification tools with axenic synthesis experiments, detailed morphological descriptions, and/or stable isotope investigations. We believe that the introduced lineage concept facilitates design of biogeographical studies and improves our understanding about phylogenetic structure of EcM fungal communities.

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Introduction

Since Frank's description and definition of mycorrhizas and ectomycorrhizas (EcM) in the 1880s (Frank 1885, 1887), numerous reports of the mycorrhizal status of both phyto- and mycobionts have been published. These reports involve various ecosystems on all continents (Trappe 1962; Wang and Qiu 2006; Brundrett 2009). Based on taxonomic and ecological extrapolation, an estimated 86% of terrestrial plant species acquire mineral nutrients via mycorrhizal root symbionts (Brundrett 2009). For the EcM symbiosis (where the fungus forms a mantle external to the plant root), the number of plant and fungal species involved is currently estimated to be ca. 6,000 and 20,000–25,000, respectively (Rinaldi et al. 2008; Brundrett 2009). Thus, the EcM symbiosis involves only a tiny fraction of the ca. 220,000–420,000 estimated plant species (ca. 2%; Scotland and Wortley 2003; Brundrett 2009) and the 1,500,000 fungal species (0.5–0.7%; Hawksworth 2001). Nevertheless, the ecologically and economically most important forest trees—Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, Leptospermoideae of Myrtaceae (incl. *Eucalyptus*), Dipterocarpaceae, and Amhersteae of Caesalpiniaceae—dominate woodland and forest communities in boreal, Mediterranean, and temperate forests of the Northern Hemisphere and parts of South America, seasonal savanna and rain forest habitats in Africa, India and Indo-Malay as well as temperate rain forest and seasonal woodland communities of Australia. Thus, EcM fungi play an important role in seedling establishment and tree growth in habitats across the globe.

Wide taxonomic distribution of EcM plants and fungi in all continents (except Antarctica) and large continental islands suggests an ancient evolution of the EcM symbiosis. Pinaceae is certainly the oldest extant plant family that is symbiotic with EcM fungi (Hibbett and Matheny 2009). The oldest Pinaceae fossils originate 156 Ma and the oldest EcM root fossils are dated to 50 Ma (LePage et al. 1997; LePage 2003). Because fungi are comprised of soft tissues, fungal fossils are extremely rare. Nevertheless, molecular tools have provided evidence for radiations of EcM-forming taxa, suggesting that orders of Agaricomycetes and families of Pezizales originated ca. 200 and 150 Ma, respectively (Berbee and Taylor 2001). Because of external calibrations and restricted taxon sampling, these values should be treated with caution, but they roughly correspond to the anticipated evolution of EcM in plants.

Unlike fungi that form arbuscular and ericoid mycorrhizas, most EcM fungi reproduce sexually and produce macroscopic fruit-bodies. These fruit-bodies are predominantly epigeous and stipitate, but substantial proportions are resupinate on the underside of debris or sequestrate, i.e., with a closed basidiome (inside soil or above the ground) that has no aerial dispersal mechanism. Not surprisingly,

fungi-producing hypogeous fruit-bodies in forest soil were the first suggested to be intimately associated with roots, either in the form of parasitism (e.g., Tulasne and Tulasne 1845; Reeß 1880) or mutualism (Frank 1885). Subsequently, various fungi with epigeous fruit-bodies commonly observed in forests were suspected to associate with tree roots in mycorrhizal symbiosis and demonstrated to do so via hyphal tracing (Noack 1889). Field observations of fruit-body occurrence as well as experimental synthesis trials since the 1920s (Melin 1921, 1923b) have revealed an amazing diversity of putatively EcM-forming fungi from many taxonomically unrelated genera (Trappe 1962). However, the reliability of many of the early studies suffered from: (1) ambiguous definition of EcM (Hatch and Hatch 1933; Brundrett 2009), (2) contamination of fungal cultures (Hutchison 1990), (3) misidentification of roots and fruit-bodies (Shemakhanova 1962), (4) the inability to axenically culture most EcM taxa (Modess 1941), and (5) naiveté of the real magnitude of fungal diversity belowground. Thus, ambiguous suggestions of EcM lifestyle have been attributed to numerous terrestrial, epigeous fungal genera (reviewed in Trappe 1962; Molina et al. 1992), and there is still great uncertainty in the trophic status of many fungal taxa (Rinaldi et al. 2008).

Data on decomposition capacity and culture characters complement those on the trophic status of some fungi, particularly basidiomycetes. With a few exceptions, EcM basidiomycetes lack enzymes for degradation of cellulose and lignin (Norkrans 1950; Hutchison 1990), and they do not produce conidia in pure culture (Hutchison 1989). Conversely, EcM or putatively EcM ascomycetes sometimes lack sexual reproduction, and they may produce lignolytic enzymes as well as conidia and chlamyospores (Caldwell et al. 2000; Egger 2006). In early studies, identification of mycobionts was attempted by comparing morphology of axenic cultures derived from field collected with that of isolates from fruit-bodies (Melin 1923b; Pachlewski 1967). However, many clades of EcM fungi have never been isolated into pure culture, rendering manipulative studies on their ecology and nutrition very difficult.

In the 1990s, a revolution of molecular tools partly ameliorated the “culturability problem” and substantially improved identification of EcM fungi in situ (Gardes et al. 1991; Egger 1995; Horton and Bruns 2001). With the advent of these techniques, many common yet unidentified EcM fungi on roots could be taxonomically assigned (Egger 1996; Kõljalg et al. 2000, 2002; Vrålstad et al. 2000). Not surprisingly, the EcM status of many additional fungal genera was discovered by comparing fungal DNA from root tips and fruit-bodies (Gehring et al. 1998; Palfner and Agerer 1998a, b; Tedersoo et al. 2006a; Smith et al. 2007). Unfortunately, a large number of described morpho-

and anatomotypes (Agerer 1987–2006) have not yet been identified with molecular techniques.

New molecular and bioinformatics tools have facilitated powerful phylogenetic analyses of fungi. These studies support the hypothesis of Malloch (1987) that EcM fungi have evolved multiple times from saprotrophic ancestors. Some studies (e.g., Hibbett et al. 2000) have also suggested reversals to a saprotrophic nutritional mode, but this hypothesis has been strongly challenged due to taxa sampling biased towards EcM-forming genera (see also Bruns and Shefferson 2004). At the other extreme, Weiß et al. (2004) hypothesized that all Agaricomycetes may have originated from EcM ancestors based on the discovery of EcM symbiosis in the Sebaciniales, a basal group of Agaricomycetes (Hibbett et al. 2007). However, this assertion is primarily attributable to the EcM lifestyle of a single clade within the Sebaciniales (Weiß et al. 2004, but see below).

Utilization of stable isotopes, particularly ^{15}N and ^{13}C has strongly enhanced understanding of energy flow from molecular to ecosystem levels (Dawson et al. 2002). Discrimination against heavier isotopes is common in many enzymatic, physiological, and physical processes, e.g., photosynthesis, respiration, and evaporation. EcM fungi are relatively enriched in ^{15}N and ^{13}C compared to autotrophs. Relative to saprobes, EcM fungi are enriched in ^{15}N but depleted in ^{13}C (Gebauer and Dietrich 1993; Gebauer and Taylor 1999; Mayor et al. 2009). This enrichment is due to different N and C sources as well as discrimination during nutrient transfer (Hobbie and Hobbie 2008). There is also a phylogenetic signal in the stable isotope concentrations of both plants (Delwiche et al. 1978) and fungi (Taylor et al. 2003). Inherent differences of ^{15}N isotope composition in EcM fungi derive from differences in nitrogen form (Lilleskov et al. 2002b), site (Kohzu et al. 1999; Taylor et al. 2003), soil horizons, the amount of extraradical mycelium produced (Trudell et al. 2004; Hobbie and Agerer 2009), season, part of fruit-body, host plant, N concentration, and efficiency of transportation (Taylor et al. 2003). Within EcM fungi, high ^{15}N values are attributable not only to uptake of protein N (Lilleskov et al. 2002b; Hobbie and Hobbie 2006) but also to ruderal strategy and low biomass of external hyphae (Trudell et al. 2004). The multifactorial nature of isotope signatures in fungal fruit-bodies acts to blur the differences between EcM and saprotrophic fungi and between “functional guilds” of EcM fungi. Accordingly, isotope data should be considered as circumstantial, suggestive evidence in studies of fungal trophic status and ecophysiology (Henn and Chapela 2001; Taylor et al. 2003).

The aims of the present review are fivefold: (1) to critically assess the current knowledge of the fungi involved in the EcM by integrating data from axenic

synthesis trials, anatomical, molecular, and isotope studies; (2) to group these taxa into monophyletic lineages based on molecular sequence data and published phylogenies; (3) to investigate the lifestyle of nonmycorrhizal sister taxa and evolution of fruit-body types to draw parallels in the development of EcM symbiosis in different lineages; (4) to highlight other potentially EcM taxa that lack both information on EcM status and DNA sequence data; (5) to recover the main distribution patterns of the EcM fungal lineages in the world based on the lineage concept and carefully revised fruit-body records.

Materials and methods

Definition of EcM

Here, we follow the basic concept of EcM as a balanced reciprocal parasitism between plant roots and fungi, where the symbiosis is beneficial (i.e., mutualistic) to both partners in natural conditions (Frank 1885; Melin 1923b; Egger and Hibbett 2004). This balance may dramatically differ in anthropogenic habitats and artificial conditions because of unnaturally elevated soil nutrient concentrations that enable one or the other partner to gain dominance. Plants provide photosynthetically fixed carbon and habitat for the fungi, whereas mycobionts provide dissolved and organically bound nutrients, particularly nitrogen and phosphorus to their hosts. Fungi may also provide other functions such as ameliorating environmental stress caused by chemicals, herbivory, pathogens, or drought (Smith and Read 2008). We agree with Brundrett (2004) and Smith and Read (2008) in distinguishing the EcM symbiosis from other putatively mutualistic plant–fungal interactions by morphological criteria, i.e., the presence of a fungal mantle covering the root tips and a Hartig net. The latter is a complex organ comprising cortical or epidermal cells of plant roots and fungal hyphae that have ramified intercellularly between the individual root cells to maximize the contact area for reciprocal nutrient transfer. Arbutoid, pyrolloid, and ectendomycorrhizas are considered subtypes of EcM because of the shared fungi and minor differences in the thickness of the fungal mantle and intracellular fungal colonization (Brundrett 2004). Orchid and liverwort mycorrhizas are not considered EcM because they are structurally unique and EcM fungal taxa appear only secondarily involved in the evolution of these symbioses. Root endophytes, i.e., more or less commensal root colonists that form no specialized interface for improved nutrient exchange are considered non-EcM, although they may develop mantle-like structures especially in axenic conditions (Jumpponen 2001; Peterson et al. 2008).

Sources of information

We studied and critically evaluated all available original literature reports where fungi were assigned EcM status based on (1) tracing of mycelium from fruit-bodies to EcM root tips; (2) direct microscopic comparisons between the hyphal morphology of fruit-bodies and the hyphal morphology of EcM; (3) pure culture synthesis experiments resulting in the development of EcM; and (4) in situ molecular identification by use of RFLP or DNA sequencing. As suggestive evidence, we also included data from (5) stable isotope studies aimed to distinguish EcM fungi from saprobes (Mayor et al. 2009 and references therein); and (6) well-resolved phylogenies involving closely related EcM genera. We paid particular attention to possible non-EcM taxa within EcM lineages as evidence for reversal to saprotrophic or other nutritional modes and to separate closely related EcM lineages. We disregarded superficial reports on fruiting habits with certain trees because all terrestrial fungi may grow in the vicinity of living plant roots by chance. The bulk of references for direct observations were obtained from reviews focusing on related aspects of fungal ecology (Shemakhanova 1962; Trappe 1962; Molina et al. 1992; Maia et al. 1996; de Roman et al. 2005; Agerer 2006; Rinaldi et al. 2008). In addition, we conducted blastN searches of ITS sequences from fruit-bodies and root tips of putatively EcM taxa against the INSD to confirm their trophic mode or to improve identification a posteriori. ITS sequences displaying >90% full-length similarity to identified taxa were conservatively considered congeneric, provided that other taxa were not more similar. We outline the discrepancies in EcM status of fungal taxa against Rinaldi et al. (2008) to explain and analyze different opinions and approaches.

Based on published and unpublished phylogenetic evidence, the EcM genera were assigned to monophyletic groups termed as “lineages” to avoid confusion and overlapping names with established clades of Agaricales and Agaricomycetes (sensu Binder and Hibbett 2002; Moncalvo et al. 2002). To avoid confusion, the names of lineages are based on the name of the dominant or characteristic genus (or genera) written in lower case, non-italicized font preceded with a slash (e.g., /inocybe) (Moncalvo et al. 2002). Due to taxonomic overlap, some names were adopted from Moncalvo et al. (2002). Whenever possible, names of tribes and families were not used because most of these taxonomic levels contain both EcM and nonmycorrhizal taxa. The higher-level taxonomy follows Hibbett et al. (2007) and Matheny et al. (2007). The online version of Index Fungorum (www.indexfungorum.org) was consulted to reveal synonymy and current generic names for EcM fungal species. Genera not included in *Index Fungorum* and synonyms (as of 20.07.2009) were

excluded. Regular updates of the EcM lineages and genera therein can be found at the UNITE homepage http://unite.ut.ee/EcM_lineages.

Literature searches in ecological and taxonomic publications revealed a number of genera that have been suggested as EcM but lack supporting evidence. For each of these genera, we searched the taxonomic literature and INSD for ITS or 28S rDNA sequence data and attempted to match these sequences with EcM root tip sequences by use of BLAST searches. When fruit-body and root tip sequences displayed high-sequence similarity, these taxa were considered molecularly supported as EcM fungi. In cases where sequence data were missing, these genera (many of which have sequestered fruit-bodies) are considered putatively EcM but not assigned to lineages, and their trophic mode is discussed with reference to their known habitat and possible host affiliations.

By use of published and unpublished phylogenies, we identified the successive sister taxa to EcM lineages to recover the trends in ancestral fruit-body type and nutritional mode among in EcM lineages. Fruit-body type (stipitate, resupinate, sequestrate, or asexual—with no known fruit-body) and nutritional mode (humus saprobe, wood saprobe, litter saprobe, pyrophilous saprobe, endophyte, parasite, other) were assigned to each of these sister taxa based on taxonomic literature and data on fruiting or isolation substrate. Uncertain cases were not considered.

Geographical distribution analysis

Many EcM fungal genera are non-monophyletic and may comprise saprotrophic members. To overcome these problems, we carried out geographical distribution analysis at the level of a lineage that represents a monophyletic, independently evolved EcM taxon. We anticipate that they differ substantially in their time of origin and rate of evolution. Since reliable estimates on the relative age of the lineages are lacking, we chose to give them equal weights but admit that this may blur the biogeographic pattern and the results cannot be interpreted in the context of evolutionary origin of EcM symbiosis. Data on distribution of lineages were retrieved from published and unpublished reports of fruit-bodies (and *Cenococcum sclerotia*) from major biogeographic regions of the world (Sanmartin et al. 2001; Sanmartin and Ronquist 2004). Despite potentially high diversity of EcM fungi, the large islands of New Guinea, New Caledonia, and Madagascar were excluded from the distribution dataset due to the small number of publications or collection records. We carefully excluded the numerous records of EcM fungi under introduced trees in gardens and plantations. In Northern South America, data on fungi under the Betulaceae, Fagaceae, and Salicaceae were excluded due to the relatively recently

arrival of these hosts. In addition to publications listed in Table 1, Corner (1969), Singer (1986), Trappe et al. (2009b), and herbarium records of TU, TAA, HUH, and MEL were studied on a global scale. The following regional sources were used: Hansen and Knudsen (1992, 1997); Pegler et al. (1993)(Europe); Arora (1986); Redhead (1989)(NE and NW America); Flore Iconographique des Champignons du Congo (1935–1970); Buyck et al. (1996); Härkönen et al. (2003); records in BR (Africa); Pegler (1986); Gunasekara and Wijekoon (2005); Natarajan et al. (2005); Butler (2008)(India and Sri Lanka); Sims et al. (1997); Lee et al. (2003)(SE Asia); Dennis (1970); Pegler (1983); de Meijer AAR (2001); Henkel et al. (2002); Lodge (2003); Læssøe and Petersen (2008)(Northern South America); Singer and Digilio (1951); Garrido (1988); Palfner (2001)(Southern South America); Warcup (1990a), Lepp (2009); May et al. (2009)(Australia); McKenzie et al. (2000), Orlovich and Cairney (2004); Auckland Fungus Group (2009)(New Zealand).

Similarity in EcM fungal distribution between biogeographic regions and among lineages was addressed by employing a two-way cluster analysis by use of the Euclidean distance and centroids as implemented in PC-Ord 5.04 (McCune and Mefford 2006). To reduce the impact of missing information, the occurrence data of 52 EcM fungal lineages in 11 regions were used for inferring the relatedness of regions and lineages. Based on the same dataset, we also performed an independent UPGMA analysis for biogeographical regions in PAUP 4.0 (Swofford 2002). Bootstrap support based on random resampling with replacement was calculated by use of 1,000 replications to demonstrate the robustness of clusters.

Results and discussion

Magnitude of EcM symbiosis in fungi

Based on critical examination of original reports on EcM synthesis trials and in situ identification, EcM lifestyle was recognized in 162 fungal genera (or a part of a genus, e.g., *Entoloma p. parte*). An additional 52 genera were considered EcM based on their phylogenetic positions nested within EcM-forming lineages (Table 1). *Sowerbyella* and *Catathelasma* were regarded as EcM based on stable isotope signatures and habitat in EcM vegetation. The attribution of EcM habit to 234 fungal genera by Rinaldi et al. (2008) closely matches our conclusions. We added 26 genera or provisional genera (11.1%) to the list of Rinaldi et al. However, after careful review of the primary literature and consideration of the fruiting habits of some taxa, we consider 25 of the genera (10.7%) suggested as EcM by Rinaldi et al. (2008) to be nonmycorrhizal and further 22

(9.4%) to have no direct evidence for EcM status. There were major discrepancies between our approach and that of Rinaldi et al. (2008) when interpreting the lifestyles of Ascomycota as well as Thelephorales and Sebaciales of the Basidiomycota (Table 2, see below).

Table 3 lists 33 genera of fungi that are probably EcM but lack unambiguous evidence. Due to lack of sequence data, most of these genera are only tentatively assigned to higher taxa based on morphological characters. Of these genera, 23 (69.7%) form sequestrate fruit-bodies; 16 (48.5%) belong to Boletales; and nine (27.3%) to Pezizales. Many of these genera are species-poor and are described from Austral or tropical realms. Sequencing of the ITS-28S rDNA region from herbarium specimens followed by phylogenetic analyses would greatly improve our understanding on the ecology and phylogenetic affinities of these taxa and facilitate comparison with root isolates (Brock et al. 2009).

Polyphyly or paraphyly of a large number of fungal genera constitutes a major problem in assigning trophic status to fungal species. Many poly- or paraphyletic genera of Ascomycota (*Humaria*, *Meliniomyces*, *Peziza*, *Tricharina*, and *Trichophaea*), Basidiomycota (*Amanita*, *Ceratobasidium*, *Clavariadelphus*, *Entoloma*, *Gyrodon*, *Lyophyllum*, *Ramaria*, *Sebacina*, *Sistotrema*, *Tomentella*, and *Tulasnella*), and Zygomycota (*Endogone*) comprise both EcM and saprotrophic species. Most of these genera contain a large number of species and have not been taxonomically revised since their description. Most of these genera have been retained due to a lack of good discriminating morphological characters. In particular, *Sebacina*, *Tulasnella*, and *Ceratobasidium* contain many cryptic species with contrasting lifestyles. In such heterogeneous genera, the EcM species are usually grouped within one or more monophyletic clades but phylogenetic treatments are not yet available for many of these taxa. The presence of different trophic modes within a genus strongly argues for reassessment of generic boundaries.

Phylogenetic diversity of EcM fungi

Integrating knowledge of EcM lifestyle and phylogenetic studies allowed us to hypothesize that EcM fungi evolved (and persisted) 66 times independently from non-EcM ancestors (Fig. 1; Table 1). This estimate substantially exceeds the previous estimates of 7–14 events (Hibbett et al. 2000; Bruns and Shefferson 2004). Our analysis indicates that 27 lineages of Ascomycota, 37 lineages of Basidiomycota, and two lineages of Zygomycota form EcM. Among these, the /sowerbyella and /catathelasma lineages were erected based on circumstantial isotopic evidence and remain to be confirmed experimentally or by use of molecular tools. The distinction of /densospora from

Table 1 Lineages (lower-case bold text) and genera (lower-case normal text) of confirmed and suspected ectomycorrhizal fungi based on original references to pure culture synthesis, molecular identification, stable isotope studies, anatomical description, and/or phylogeny arranged by phyla and orders

| Taxa of EcM fungi | References | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|---|---|---|-------------------|--|
| ASCOMYCOTA | | | | |
| DOTHIDEOMYCETES INCERTAE SEDIS | | | | |
| /cenococcium | | | | |
| <i>Cenococcium</i> | Hatch and Hatch 1933; Hatch 1934 (as <i>Mycelium radialis nigrostrigosum</i>); Lihnell 1942; Mikola 1948 | Ferdinandson and Winge 1925; Hatch 1934; Lihnell 1942; Dahlberg et al. 1997 ; Horton and Bruns 1998 ; Horton et al. 1999 | | LoBuglio et al. 1996 |
| EUROTIALES | | | | |
| /elaphomyces | | | | |
| <i>Elaphomyces</i> * | Warcup 1990c; Theodorou and Reddell 1991; Reddell et al. 1999 | Rees 1880; (Frank 1892); Fontana and Centrella 1967; Tedersoo et al. 2003 ; Smith et al. 2007 ; Courty et al. 2008 ; Henkel et al. 2006 | Mayor et al. 2009 | LoBuglio et al. 1996; Henkel et al. 2006 Miller et al. 2001 |
| <i>Pseudotulostoma</i> * | | | | |
| HELOTIALES | | | | |
| /acephala macrosclerotiorum | | | | |
| <i>Acephala</i> | Münzenberger et al. 2009 | Menkis et al. 2004 (as <i>Phialocephala</i> sp6); Münzenberger et al. 2009 | | |
| /macrosclerotiorum | | | | |
| /meliniomyces | | | | |
| <i>Cadophora</i> | Wilcox et al. 1974; Wang and Wilcox 1985; Wilcox and Wang 1987; Ursic and Peterson 1997 | Ursic and Peterson 1997; Tedersoo et al. 2003 ; Püttsepp et al. 2004 ; Korkama et al. 2006 | | Vrálstad et al. 2002a; Hambleton and Sigler 2005 |
| <i>finlandica</i> (incl. <i>Chloridium paucisporum</i>) | | | | |
| <i>Meliniomyces p. parte</i> (<i>M. bicolor</i> and <i>M. vvaolstadiae</i>) | Thomas and Jackson 1979 (as type 5); Vrálstad et al. 2002b | Gronbach 1988; Vrálstad et al. 2000 , 2002a; Tedersoo et al. 2008b | | Vrálstad et al. 2002a; Hambleton and Sigler 2005 |
| /unnamed | | | | |
| /helotiales1 | | | | |
| /helotiales2 | | | | |
| /unnamed | | | | |
| /helotiales3-6 | | | | |
| /unnamed | | | | |
| PEZIZALES | | | | |
| /galactinia | | | | |
| <i>Galactinia</i> (*) | | | | |
| (<i>Peziza p. parte</i>) | | Valentine et al. 2004 ; Tedersoo et al. 2006a ; Smith et al. 2007 | | Hansen et al. 2005; Tedersoo et al. 2006a |

- /genca-humaria
*Genabea**
- Genea**
- Gilkeya**
- Humaria*
- /geopora
Geopora(*)
- (*Hydnocystis p. parte*)*
*Picoa**
- Tricharina p. parte*
(*T. ochroleuca*)
/hydnotrya
*Hydnotrya**
- /leucangium
*Fischerula**
- (*Imaia*)*
*Leucangium**
- /marcelleina-peziza gerardii
*Hydnobolites**
- (*Marcelleina*)
Peziza gerardii
- /otidea
Otidea(*)
- /pachyphloeus-amylascus
(*Amylascus*)*
- Izzo et al. 2005b; Smith et al. 2006b; Morris et al. 2008
- Fontana and Centrella 1967; Jakucs et al. 1998; Liljeskov et al. 2002a; Tedersoo et al. 2006a; Smith et al. 2006b; Erös-Honti et al. 2008
- Moser et al. 2009
- Tedersoo et al. 2006a; Erös-Honti et al. 2008; Morris et al. 2009
- Gehring et al. 1998; Fujimura et al. 2005; Tedersoo et al. 2006a
- Trocha et al. 2006; Smith et al. 2009
- Peyronel 1929; Tedersoo et al. 2006a
- Palfner and Agerer 1998b
- Smith et al. 2007; Morris et al. 2008; Tedersoo et al. 2008b
- Smith et al. 2007; Morris et al. 2008 (as *Marcelleina*)
- Kennedy et al. 2003; Smith et al. 2004, 2007; Toijander et al. 2006
- Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007
- Smith et al. 2006b; Perry et al. 2007
- Smith et al. 2006b; Tedersoo et al. 2006a; Perry et al. 2007
- Smith et al. 2006b; Perry et al. 2007
- Smith et al. 2006b; Tedersoo et al. 2006a; Perry et al. 2007
- Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007
- M.E. Smith, unpubl.
- M.E. Smith, unpubl.
- Perry et al. 2007
- Hansen and Pfister 2006; Tedersoo et al. 2006a
- Hansen and Pfister 2006
- Kovács et al. 2008
- Hansen and Pfister 2006
- M.E. Smith, unpubl.
- Hansen et al. 2005
- Hansen et al. 2005
- Perry et al. 2007; Smith and Healy 2009
- Hansen et al. 2005; Tedersoo et al.

Table 1 (continued)

| Taxa of EcM fungi | References | Synthesis | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|---|--|-----------|--|-----------------------|---|
| <i>Chromelosporium</i> | | | | | 2006a |
| <i>p. parte</i> | | | Palmer et al. 2008 | | |
| (anamorph) | | | | | |
| <i>Glischroderma</i> | | | Tedersoo et al. 2006a; Morris et al. 2009 | | Tedersoo et al. 2006a |
| (anamorph) | | | Tedersoo et al. 2006a; Smith et al. 2007 | | Hansen et al. 2005; Tedersoo et al. 2006a |
| <i>Pachyphloeus*</i> | | | Smith et al. 2007; Morris et al. 2008 | | Hansen et al. 2005; Tedersoo et al. 2006a |
| <i>Scabropezia</i> | | | | | |
| /pulvinula | | | | | |
| <i>Pubinula p. parte</i> | Warcup 1990a | | Bencivenga et al. 1995 (cited in de Roman et al. 2005); Amicucci et al. 2001 | | Perry et al. 2007 |
| (<i>P. constellatio</i> , <i>P. tetraspora</i>) | | | | | |
| /sarcosphaera-hydnotryopsis | | | | | |
| <i>Hydnotryopsis*</i> | | | Frank et al. 2006; Smith et al. 2007 | | Hansen et al. 2005; Tedersoo et al. 2006a |
| <i>Sarcosphaera</i> | | | Tedersoo et al. 2006a | Tedersoo et al. 2007a | Hansen et al. 2005; Tedersoo et al. 2006a |
| (/soweryella) ^a | | | | | |
| <i>Soweryella</i> | | | | | |
| /sphaerosporella | | | | Hobbie et al. 2001 | Perry et al. 2007 |
| <i>Sphaerosporella</i> | Danielson 1984a; Egger and Paden 1986; Danielson and Visser 1988 | | Danielson 1984a; Danielson and Visser 1988 | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| <i>Trichophaea</i> | | | Tedersoo et al. 2006a; Mühlmann and Peintner 2008 (as Pezizales sp.) | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| <i>woolhopeta</i> | | | | | |
| /tarzetta | | | Tedersoo et al. 2006a; Smith et al. 2007; Mühlmann and Peintner 2008 | | Hansen and Pfister 2006; Tedersoo et al. 2006a |
| <i>Tarzetta</i> | | | | | |
| /terfezia-peziza depressa | | | INSD unpublished | | Hansen et al. 2005; |
| (<i>Cazia</i>) [*] | | | | | |

| | | | | |
|---|---|--|---|---|
| <i>Chromelosporium</i> | | | | Tedersoo et al. 2006a |
| <i>p. parte</i> | | | | INSD unpublished |
| <i>Hydnoplicata*</i> | Warcup 1990a (as <i>Peziza whitei</i>) | Palmer et al. 2008 | | INSD unpublished |
| (<i>Mycoclelandia</i>)* | | Smith et al. 2007; Morris et al. 2008 | | Trappe et al. 2009a |
| <i>Peziza p. parte</i> | Warcup 1990a | Cline et al. 2005; Tedersoo et al. 2006b, 2008b; Palmer et al. 2008 | | Hansen et al. 2005; Tedersoo et al. 2006a |
| (incl. <i>P. badia</i> , <i>P. depressa</i> , etc.)(*) | Warcup and Talbot 1989 (as <i>Muciturbo</i>); Warcup 1991a | | | Hansen et al. 2005; Tedersoo et al. 2006a |
| <i>Ruhlandiella*</i> | | | | |
| <i>Sphaerozone*</i> | | Shi et al. 2002; Tedersoo et al. 2006a | | |
| <i>Terfezia s. stricto*</i> | Dexheimer et al. 1985; Morte et al. 1994; Gutierrez et al. 2003 | (Pirota and Albini 1900) as cited in Melin 1923b; Ammarellou et al. 2007 | | Hansen et al. 2005; Tedersoo et al. 2006a |
| <i>Tirmania*</i> | Fortas and Chevalier 1992 | | | Hansen et al. 2005; Tedersoo et al. 2006a |
| (<i>Uturna</i>)* | | | | Trappe et al. 2009a |
| /tuber-helvella | | | | |
| <i>Balsamia*</i> | | (Ceruti and Bussetti 1962); Palfner and Agerer 1998a; Bidartondo and Read 2008 | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| <i>Barssia*</i> | | | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| <i>Choiromyces*</i> | | Izzo et al. 2005a, b | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| <i>Dingleya*</i> | | | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| (<i>Gymnohydnotrya</i>)* | | | | M.E. Smith unpublished |
| <i>Helvella</i> | | Weidemann 1998; Murat et al. 2005; Tedersoo et al. 2006a | Hobbie et al. 2001; Tedersoo et al. 2007a | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| <i>Labyrinthomyces*</i> | Warcup 1990a; (Warcup 1990c); Brundrett et al. 2005 | | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; |

Table 1 (continued)

| Taxa of EcM fungi | References | Synthesis | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|--|--|-----------|--|--|---|
| <i>Reddellomyces</i> * | Brundrett et al. 1996, 2005 | | | | O'Donnell et al. 1997; Hansen and Pfister 2006; |
| <i>Tuber</i> (l-type sensu Dominik 1959)* | Sappa 1940 (as cited in Trappe 1962); Fassi and Fontana 1967; Fontana and Fasolo-Bonfante et al. 1972; Giovanetti and Fontana 1980, 1982 | | (Matirolo 1887) as cited in Melin 1923b; (Frank 1892); (Peyronel 1929); Fontana and Centrella 1967; Palenzona et al. 1972; Horton et al. 1999; Baar et al. 1999; Taylor and Bruns 1999 | Hobbie et al. 2001; Zeller et al. 2008 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| (<i>Underwoodia</i>)* | | | | | O'Donnell et al. 1997; Hansen and Pfister 2006; |
| (<i>Wynnella</i>)* | | | | Hobbie et al. 2001 | O'Donnell et al. 1997; Hansen and Pfister 2006; Tedersoo et al. 2006a |
| /wilcoxina | | | | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| <i>Trichophaea hybrida</i> | | | Tedersoo et al. 2006a, 2008b | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| <i>Wilcoxina</i> (E-strain) | Laiho 1965; Mikola 1965; Danielson and Visser 1988 | | | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| SORDARIALES | | | | | |
| /sordariales | | | | | |
| Sordariales unnamed | Laiho 1965; Mikola 1965; Danielson and Visser 1988 | | Laiho 1965; Mikola 1965; Danielson and Visser 1988; Baar et al. 1999; Taylor and Bruns 1999; Grogan et al. 2000; Fujimura et al. 2005; Tedersoo et al. 2006a | | Hansen and Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007 |
| PEZIZALES INCERTAE SEDIS | | | | | |
| <i>Nothojafnea cryptotricha</i> (sensu J. Warcup)* | Warcup 1990a | | | | |
| <i>Lachnea vinosobrunnea</i> (sensu J. Warcup) | Warcup 1990a | | | | |
| BASIDIOMYCOTA | | | | | |
| AGARICALES | | | | | |
| /amanita | | | | | |
| <i>Amanita</i> | Melin 1923a, 1924; Hatch and Hatch 1933; (Doak 1934); Modess 1941; (Hacsckaylo and Palmer 1955); Vozzo and | | (Frank 1892); (Peyronel 1922); Gardes and Bruns 1996; Horton and Bruns 1998; Horton et al. 1999; | Gebauer and Dietrich 1993; Gebauer and Taylor 1999; Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; | Moncalvo et al. 2002; Hallen et al. 2004; Matheny et al. 2006 |
| | | | | | Tedersoo et al. 2007b |

- (*Amarrendia s. stricto*)*
(*Torrendia*)*
(*catathelasma*)^a
Catathelasma
/cortinarius
(*Amarrendia p. parte*)*
Cortinarius (incl. *Cuphocybe*, *Rapacea*, *Rozites*, *Thaxterogaster*) (*)
Dermocybe
*Protoglossum**
(*Quadrifora*)*
Stephanopus
/descolea
Descolea
*Descomyces**
*Setchelliogaster**
(*Tingrovea*)*
/entoloma
Entoloma s. str. (sections *Entoloma*, *Rhodopolia*) (*Rhodogaster*)*
(*Richoniella*)*
/hebeloma-almicola
Ahnicola
- Haskaylo 1961; Riffle 1973; Pachlewski and Chrusciak 1980; Malajczuk et al. 1982; Molina and Trappe 1982; Godbout and Fortin 1985
- (Hutchison 1992)
- Melin 1924, 1925; Ashton 1976; Antibus et al. 1981; Kropp and Trappe 1982; Godbout and Fortin 1985; Loree et al. 1989; van der Heijden and Kuyper 2003
- Malajczuk et al. 1987 (as *Cortinarius*)
- Burgess et al. 1993 (as *Hymenogaster*)
- Bougher and Malajczuk 1990; Lu et al. 1998; Brundrett et al. 2005
- Malajczuk et al. 1982 (as *Hymenogaster*); Burgess et al. 1993 (as *Hymenogaster*); Lu et al. 1998; Brundrett et al. 2005
- Burgess et al. 1993; Brundrett et al. 1996, 2005; Thomson et al. 1996
- Modess 1941; Zerova and Rozhenko 1966 (cited in Antibus et al. 1981); Antibus et al. 1981; Loree et al. 1989;
- Taylor and Bruns 1999**
- Trudell et al. 2004; Hart et al. 2006; Zeller et al. 2007, 2008
- Hallen et al. 2004
- Hallen et al. 2004
- Kohzu et al. 1999
- Moncalvo et al. 2002; Matheny et al. 2006
- Hallen et al. 2004
- Hobbie et al. 1999, 2001; Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Clemmensen et al. 2006; Zeller et al. 2007; Wilson et al. 2007; Mayor et al. 2009
- Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004;
- (Noack 1889); Kauffman 1906; McDougall 1914; Masui 1927; **Gardes and Bruns 1996**; **Dahlberg et al. 1997**; **Erland et al. 1999**; **Jonsson et al. 1999a**;
- Uhl and Agerer 1987; Gronbach 1988; **Cullings and Makhija 2001**; **Tedersoo et al. 2008a**
- Palfner 2001
- Bougher and Malajczuk 1985; Palfner 2001; **Tedersoo et al. 2008a, 2009a**
- Agerer et al. 2001; Tedersoo et al. 2008a, 2009a
- Tedersoo et al. 2008a, 2009a**
- Agerer 1997; **Avis et al. 2003**; **Walker et al. 2005**; **Smith et al. 2007**
- Kohzu et al. 1999; Trudell et al. 2004; see Taylor et al. (2003) for contrasting evidence
- D.L.V. Co, pers. comm. 2007
- D.L.V. Co, pers. comm. 2007
- D.L.V. Co, pers. comm. 2007
- Pritsch et al. 1997**; **Becerra et al. 2005b**
- Kohzu et al. 1999; Trudell et al. 2004
- Peintner et al. 2001; Moreau et al. 2006; Matheny et al. 2006; Garnica et al. 2007

Table 1 (continued)

| Taxa of EcM fungi | References | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|---|---|--|--|--|
| | Synthesis | | | |
| <i>(Anamika)</i> | | | | Matheny et al. 2006 |
| <i>Hebeloma</i> | Shemakhanova 1956 (cited in Shemakhanova 1962); Trappe 1967; Haackaylo and Bruchet 1972; Antibus et al. 1981; Malajczuk et al. 1982; Godbout and Fortin 1985; Dunabeitia et al. 1996; van der Heijden and Kuypers 2003; | (Kljushnik 1952); Fontana 1961; Fassi and De Vecchi 1963; Fassi and Fontana 1966; Dahlberg et al. 1997; Hagerman et al. 1999; Jonsson et al. 1999a | Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Clemmensen et al. 2006 | Peintner et al. 2001; Moreau et al. 2006; Matheny et al. 2006; Garnica et al. 2007 |
| <i>Hymenogaster s. stricto*</i> | | Fontana and Centrella 1967; Kennedy et al. 2003; Izzo et al. 2006; Bidartondo and Read 2008 | | Peintner et al. 2001; Moreau et al. 2006; |
| <i>/hyrophorus</i> | | | | |
| <i>Hygrophorus</i> | Kropp and Trappe 1982 | (Frank 1888); (Noack 1889); (Peyronel 1922); Gronbach 1988; Dahlberg et al. 1997; Gehring et al. 1998; Stendell et al. 1999 | Hobbie et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Hart et al. 2006 | Moncalvo et al. 2002; Matheny et al. 2006 |
| <i>/inocybe</i> | | | | Matheny and Bougher 2006 |
| <i>(Auritella) (*)</i> | | | | |
| <i>Inocybe</i> (incl. <i>Astrosporina</i>) | Cripps and Miller 1995; van der Heijden and Kuypers 2003 | Zerova 1956; Schramm 1966; Ingleby et al. 1990; Horton et al. 1999; Magyar et al. 1999; Taylor and Bruns 1999; Cullings et al. 2000; Kernaghan 2001 | Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Abadie et al. 2005; Clemmensen et al. 2006; Hart et al. 2006; Zeller et al. 2008; Mayor et al. 2009 | Moncalvo et al. 2002; Matheny 2005; Matheny et al. 2006; Ryberg et al. 2008 |
| <i>/laccaria</i> | | | | |
| <i>Hydnangium*</i> | Malajczuk et al. 1982; Malajczuk and Hartney 1986; Burgess et al. 1993; Lu et al. 1998 | Chu-Chou and Grace 1981; Diez 2005 | | Mueller and Pine 1994; Matheny et al. 2006 |
| <i>Laccaria</i> | Bryan and Zak 1961 (as <i>Clitocybe</i>); Thomas and Jackson 1979; Molina and Trappe 1982; Godbout and Fortin 1985; Lu et al. 1998 | Fassi and Fontana 1966; Gardes et al. 1991; Horton and Bruns 1998; Kernaghan 2001 | Gebauer and Taylor 1999; Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Hart et al. 2006; Zeller et al. 2007 | Mueller and Pine 1994; Matheny et al. 2006 |
| <i>(Podohydangium)*</i> | | | | |
| <i>/paralyophyllum</i> | | | | |
| <i>Lyophyllum p. fusosum=shimeji; L. semitale</i>) | (Masui 1927); Norkrans 1950; Pera and Alvarez 1995; Kasuya and Igarashi 1996; Kawai 1997 | Agerer and Beenken 1998b; Bergemann and Garbelotto 2006 | Kohzu et al. 1999; Trudell et al. 2004 | Hofstetter et al. 2002; Moncalvo et al. 2002; Matheny et al. 2006 |
| <i>Tricholoma</i> | Melin 1923a, 1924, 1925; Modess 1941; Fries 1942; Norkrans 1950; Pachlewski and Chrusciak 1980; Kropp and Trappe 1982 | (Noack 1889); Masui 1927; Luppi and Gautero 1967 (cited in de Roman et al. 2005); Gehring et al. 1998; Horton et al. | Hobbie et al. 1999, 2001; Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Tedersoo et al. 2007a; Zeller | Moncalvo et al. 2002; Matheny et al. 2006 |

Table 1 (continued)

| Taxa of EcM fungi | References | Synthesis | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|---|---|--|--|--|--|
| <i>Heimioporus</i> (syn. <i>Heimiella</i>) (<i>Leccinellum</i>) | Bryan and Zak 1961 (as <i>Boletus</i>) | | | Kohzu et al. 1999 | M. Binder unpublished Binder and Hibbett 2006 |
| <i>Leccinum</i> | Melin 1923a (as <i>Boletus</i>); Molina and Trappe 1982; Dunabeitia et al. 2004 | McDougall 1914; (Peyronel 1920); Ingleby et al. 1990; Nara 2006; Tedersoo et al. 2006b; Courty et al. 2008 | | Kohzu et al. 1999; Taylor et al. 2003; Clemmensen et al. 2006 | Binder and Hibbett 2006 |
| (<i>Mackintoshia</i>)* | | | | | M.E. Smith unpublished |
| (<i>Mycosamaranthus</i>)* | | | | | M.E. Smith unpublished |
| <i>Octaviania p. parte*</i> (<i>Phylloboletellus</i>) | | | Chilvers 1968; Smith et al. 2007; Morris et al. 2008 | | Binder and Hibbett 2006 |
| <i>Phylloporus</i> | Vozzo and Hacsckaylo 1961 (as <i>Paxillus</i>) | | | Trudell et al. 2004; | Binder and Hibbett 2006 |
| <i>Porphyrellus</i> | | | Raidl and Hahn 2006 | | Binder and Hibbett 2006 |
| <i>Pseudoboletus</i> (<i>Pulveroboletus</i>) | Richter and Bruhn 1989 | | | | Binder and Hibbett 2006 |
| (<i>Retiboletus</i>) | | | | | Binder and Hibbett 2006 |
| (<i>Rhodactina</i>)* | | | | | Yang et al. 2006 |
| (<i>Royoungia</i>)* | | | | | M. Binder unpublished |
| (<i>Rubinoboletus</i>) | | | | | M. Binder unpublished |
| <i>Stribolomyces</i> | | | | Kohzu et al. 1999; | Binder and Hibbett 2006 |
| <i>Tyloporus</i> | (Doak 1934); Vozzo and Hacsckaylo 1961; Brundrett et al. 1996; Reddell et al. 1999 | (Peyronel 1920); Matsuda and Hijii 1999; Riviere et al. 2007; Sato et al. 2007 | Erland et al. 1999; Jonsson et al. 1999b; Dickie et al. 2002 | Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Mayor et al. 2009 | Binder and Hibbett 2006 |
| <i>Xanthoconium</i> | | | | Kohzu et al. 1999 | M. Binder unpublished |
| <i>Xerocomus</i> | Melin 1923b; Modess 1941; Bokor 1958; Bryan and Zak 1961; Vozzo and Hacsckaylo 1961; Dunabeitia | (Peyronel 1922); Ceruti and Bussetti 1962; Gronbach 1988; Gardes and Bruns 1996; Horton and Bruns 1998; | | Gebauer and Dietrich 1993; Gebauer and Taylor 1999; Taylor et al. 2003; Zeller et al. 2007, 2008 | Binder and Hibbett 2006 |

- et al. 1996; van der Heijden and Kuyper 2003
- Godbout and Fortin 1983; Danielson and Visser 1988; Massicotte et al. 1988
- (Godbout and Fortin 1985)
- Gyrodon s. stricto*
- Malajczuk et al. 1982; Molina and Trappe 1982; Pera and Alvarez 1995
- (*Paragyrodon*)
- Paxillus*
- Laiho 1970; Molina and Trappe 1982; Malajczuk et al. 1982
- /pisolithus-scleroderma
- Astraeus*
- Trappe 1967; Molina and Trappe 1982; Malajczuk et al. 1982
- Calostoma*
- (*Corditubera*)*
- (*Diplocystis*)(*)
- Gyroporus*
- Hatch and Hatch 1933; Vozzo and Haeskeylo 1961;
- Bryan and Zak 1961; Zak 1976; Marx et al. 1977
- Pisolithus*
- (Doak 1934); Modess 1941; Fries 1942; Bokor 1958; Vozzo and Haeskeylo 1961; Malajczuk et al. 1982; Dunabeitia et al. 1996; Lu et al. 1998; Reddell et al. 1999; van der Heijden and Kuyper 2003
- (*Tremellogaster*)(*)
- /suillus-rhizopogon
- (*Braunietillula p. parte*)*
- Chroogomphus*
- Horton et al. 1999; Jonsson et al. 1999b
- Massicotte et al. 1988; Miller et al. 1991; Taylor and Bruns 1999; Bergemann and Garbelotto 2006; Becerra et al. 2005a; Tedersoo et al. 2006b, 2009c
- Shi et al. 2002; Wiedmer et al. 2004; Cline et al. 2005; Bergemann and Garbelotto 2006; Tedersoo et al. 2006b;
- Laiho 1970; Lilleskov et al. 2002a; Korkama et al. 2006; Tedersoo et al. 2006b
- Schramm 1966; Dickie and Reich 2005
- Wilson et al. 2007
- Peyronel 1922 (as *Boletus*); Agerer 1999; Avis et al. 2008 (Kljushnik 1952); Schramm 1966; Tedersoo et al. 2007b
- McDougall 1914; (Peyronel 1920); Masui 1927; Zerova 1950; (Fassi 1957); Thoen and Ba 1989; Nara and Hogetsu 2004; Valentine et al. 2004; Murat et al. 2005
- Agerer 1990; Douglas et al. 2005
- Binder and Hibbett 2006
- Kretzer and Bruns 1999; Binder and Hibbett 2006; Yang et al. 2006
- Binder and Hibbett 2006; Yang et al. 2006
- Binder and Hibbett 2006
- Kretzer and Bruns 1999; Binder and Hibbett 2006; Yang et al. 2006
- Gebauer and Dietrich 1993; Gebauer and Taylor 1999; Taylor et al. 2003; Zeller et al. 2007
- Wilson et al. 2007
- M.E. Smith unpublished
- Binder and Hibbett 2006
- Binder and Hibbett 2006
- Binder and Hibbett 2006
- Binder and Hibbett 2006
- Binder and Hibbett 2006
- Wilson et al. 2007
- Kohzu et al. 1999
- Kohzu et al. 1999; Wilson et al. 2007; Zeller et al. 2007
- Binder and Hibbett 2006
- Miller 2003
- Binder and Hibbett 2006
- Kohzu et al. 1999; Taylor et al. 2003; see Trudell et al. (2004) for contrasting evidence

Table 1 (continued)

| Taxa of EcM fungi | References | Synthesis | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|--|--|-----------|--|---|-----------------------------------|
| <i>Gomphidius</i> | (Ohga and Wood 2000) | | Agerer 1991b; Olsson et al. 2000 | Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004 | Binder and Hibbett 2006 |
| <i>Rhizopogon</i> * | Young 1937 (cited in Trappe 1962); Modess 1941; (HacsKaylo 1953); HacsKaylo and Palmer 1955; Trappe 1967; Pachlewski and Chrusciak 1980; Malajczuk et al. 1982; Molina and Trappe 1982 | | (Fontana and Centrella 1967); Gardes and Bruns 1996 ; Gehring et al. 1998 ; Horton and Bruns 1998 ; Horton et al. 1999 | Kohzu et al. 1999; Taylor et al. 2003 | Binder and Hibbett 2006 |
| <i>Suillus</i> (incl. <i>Boletinus</i>) | Melin 1922, 1923b, 1924, 1925; Hammarlund 1923; Masui 1927; Hatch and Hatch 1933; Doak 1934; Fries 1942; Vozzo and HacsKaylo 1961; Trappe 1967; Pachlewski and Chrusciak 1980; Malajczuk et al. 1982; Molina and Trappe 1982 | | (Frank 1892); (Peyronel 1920, 1922); Peyronel 1929; Gardes and Bruns 1996 ; Dahlberg et al. 1997 ; Horton et al. 1999 ; Jonsson et al. 1999a | Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Hart et al. 2006; Tedersoo et al. 2007a | Binder and Hibbett 2006 |
| <i>Truncocolumella</i> * | Malajczuk et al. 1982; Molina and Trappe 1982; Massicotte et al. 2000 | | Goodman et al. 1996–2000; Cline et al. 2005 ; Horton et al. 2005 | | Binder and Hibbett 2006 |
| CANTHARELLES S. <i>LATO</i> | | | | | |
| /cantharellus | | | | | |
| <i>Cantharellus</i> | Doak 1934; Danell 1994 | | Goodman et al. 1996–2000; Agerer 1987–2006 | Gebauer and Dietrich 1993; Gebauer and Taylor 1999; Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Zeller et al. 2007; Mayor et al. 2009 | Moncalvo et al. 2006 |
| <i>Craterellus</i> | | | Goodman et al. 1996–2000; Jonsson et al. 2000 ; Shi et al. 2002 ; Walker et al. 2005 | Taylor et al. 2003; Zeller et al. 2007; Mayor et al. 2009 | Moncalvo et al. 2006 |
| <i>Hydnum</i> | Lu et al. 1998 | | Masui 1927; Agerer et al. 1996 ; Horton et al. 2005 ; Courty et al. 2008 (Verbeke and Walley 1999) | Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Zeller et al. 2007 | Moncalvo et al. 2006 |
| <i>Pterygellus</i> | | | Lian et al. 2001 ; Nilsson et al. 2006a ; Smith et al. 2007 | | INSD unpublished |
| <u><i>Sistotrema p. parte</i></u> | | | | | Moncalvo et al. 2006 |
| /clavulina | | | | | |
| <i>Clavulina</i> | | | Dickie et al. 2002 ; Kennedy et al. 2003 ; Tedersoo et al. 2003 | Gebauer and Taylor 1999 (misconsidered); Hobbie et al. 2001; Trudell et al. 2004; Zeller et al. 2008; Mayor et al. 2009 | Moncalvo et al. 2006 |
| <u><i>Membranomyces</i></u> | | | Tedersoo et al. 2003 (as <i>Clavulicium</i>) | | Moncalvo et al. 2006 |
| /tulasnella | | | | | |
| <u><i>Tulasnella p. parte</i></u> | (Bidartondo et al. 2003) | | (Haug and Oberwinkler 1987); Bidartondo et al. 2003 ; Tedersoo et al. 2008a, b | | Moncalvo et al. 2006 |
| /ceratobasidium1 | | | | | |

| | | | |
|---|--|--|--|
| <i>Ceratobasidium p. parte</i> | Warcup 1991b; Yagame et al. 2008; | Yagame et al. 2008 | Veldre 2009 |
| /ceratobasidium2 | | | |
| <i>Ceratobasidium p. parte</i> | | (Rosling et al. 2003); Wilson et al. 2007; unpublished INSD data | Veldre 2009 |
| GOMPHALES | | | |
| /clavariadelphus | | Izzo et al. 2005a; Iosifidou and Raidl 2006; Smith et al. 2007; Morris et al. 2008 | Hosaka et al. 2006 |
| <i>Clavariadelphus p. parte</i> (incl. <i>C. subfastigiatus</i> ; <i>C. truncatus</i> , <i>C. pistillaris</i>) | | | |
| /ramaria-gautieria | Dunabeitia et al. 1996; Reddell et al. 1999 | Griffiths et al. 1991; Douglas et al. 2005; Izzo et al. 2005b; Morris et al. 2008 | Hosaka et al. 2006 |
| <i>Gautieria*</i> | | | |
| (<i>Gloeocantharellus</i>) | | | |
| <i>Gomphus</i> | | Agerer et al. 1998b | Hosaka et al. 2006 |
| <i>Ramaria p. parte</i> | | Trudell et al. 2004 | Hosaka et al. 2006 |
| <i>Turbinellus</i> | | Kohzu et al. 1999; Hobbie et al. 2001; Trudell et al. 2004; Kohzu et al. 1999 | Hosaka et al. 2006 |
| HYMENOGHAEATALES | | | |
| /coltricia | | | |
| <i>Coltricia</i> | (Pachlewski and Chrusciak 1980); Danielson 1984b; Danielson and Visser 1988 | Danielson 1984b; Danielson and Visser 1988; Thoen and Ba 1989; Tedersoo et al. 2007c | Larsson et al. 2006; Tedersoo et al. 2007c |
| <i>Coltriciella</i> | | Tedersoo et al. 2007c, 2008a | Larsson et al. 2006; Tedersoo et al. 2007c |
| HYSTERANGIALES | | | |
| /hysterangium | | | |
| (<i>Andebbia</i>)* | | | Hosaka et al. 2006 |
| (<i>Aroramycetes</i>)* | | | Hosaka et al. 2006 |
| <i>Austrogautieria*</i> | | (Thoen and Ba 1989) | Hosaka et al. 2006 |
| <i>Castoreum*</i> | Brundrett et al. 2005 | (Dell et al. 1990) | Hosaka et al. 2006 |
| <i>Chondrogaster*</i> | Lupatini et al. 2008 | Lupatini et al. 2008 | Hosaka et al. 2006 |
| (<i>Gallacea</i>)* | | | |
| <i>Gummiglobus*</i> | Reddell et al. 1999 | | Hosaka et al. 2006 |
| (<i>Hallingea</i>)* | | | Hosaka et al. 2006 |
| <i>Hysterangium*</i> | Malajczuk et al. 1982; Molina and Trappe 1982; Theodorou and Reddell 1991; Brundrett et al. 2005 | Ceruti and Bussetti 1962; Fontana and Centrella 1967; Griffiths et al. 1991; Smith et al. 2007 | Hosaka et al. 2006 |
| (<i>Malajczukia</i>)* | | | Hosaka et al. 2006 |
| <i>Mesophellia*</i> | Lu et al. 1998; Reddell et al. 1999; Brundrett et al. 2005 | Ashton 1976; Dell et al. 1990 | Hosaka et al. 2006 |
| <i>Nothocastoreum*</i> | Reddell et al. 1999 | | Hosaka et al. 2006 |

Table 1 (continued)

| Taxa of EcM fungi | References | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|--|--|---|---|---|
| | Synthesis | | | |
| <i>(Protuberana p. parte: P. nothofagi)*</i> | | | | Hosaka et al. 2006 |
| RUSSULALES | | | | |
| /albatrellus | | | | |
| <i>Albatrellus</i> (incl. <i>Scutiger</i>) | Zak 1976 (as <i>Poria</i>), Kropp 1982 | (Pilat 1931 (as <i>Caloporus</i>)); Agerer 1996a; Izzo et al. 2005a; Walker et al. 2005 | Taylor et al. 2003; Trudell et al. 2004 | Miller et al. 2006; Albee-Scott 2007 |
| <i>Byssoporia</i> | | Zak 1969 (as <i>Poria</i>) | | Miller et al. 2006 |
| <i>Leucogaster*</i> | | Izzo et al. 2005b | | Miller et al. 2006; Albee-Scott 2007 |
| <i>Leucophleps*</i> | | Izzo et al. 2005b | | Albee-Scott 2007 |
| <i>(Mycolevis)*</i> | | | | Miller et al. 2006; Albee-Scott 2007 |
| <i>Polyporoletus</i> | | Agerer et al. 1998a | | Miller et al. 2006; Albee-Scott 2007 |
| /russula-lactarius | | | | |
| <i>Arcangeliiella*</i> | | Luppi and Gautero 1967 (cited in de Roman et al. 2005); Peter et al. 2001; Izzo et al. 2005b | | Peter et al. 2001; Miller et al. 2006; Lebel and Tonkin 2007 |
| <i>(Cystangium)*</i> | | Izzo et al. 2005a (as <i>Arcangeliiella</i>) | | Miller et al. 2006 |
| <i>Gastrolactarius*</i> | | Stendell et al. 1999; Douglas et al. 2005; Izzo et al. 2005b; Smith et al. 2006a | | Peter et al. 2001; Miller et al. 2006; Lebel and Tonkin 2007 |
| <i>Gymnomyces*</i> | | | | Peter et al. 2001; Miller et al. 2006; Lebel and Tonkin 2007 |
| <i>Lactarius</i> | Melin 1924, 1925; Hatch and Hatch 1933; Modess 1941; Riffle 1973; Zak 1976; Antibus et al. 1981; Kropp and Trappe 1982; Malajczuk et al. 1982; Godbout and Fortin 1985; Lu et al. 1998 | (Noack 1889); (Peyrone 1922); Luppi and Gautero 1967; Gronbach 1988; Kraigher et al. 1995; Gardes and Bruns 1996; Dahlberg et al. 1997; Kernaghan et al. 1997 | Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Mayor et al. 2009; Clemmensen et al. 2006; Zeller et al. 2007; Wilson et al. 2007 | Peter et al. 2001; Miller et al. 2006; Lebel and Tonkin 2007; Buyck et al. 2008 |
| <i>Macowanites*</i> | | Kennedy et al. 2003; Izzo et al. 2005a, b | | Peter et al. 2001; Miller et al. 2006; Lebel and Tonkin 2007 |
| <i>Martellia*</i> | Trappe and Castellano 1986 | Trappe and Castellano 1986; Horton et al. 2005; Izzo et al. 2005b | | Peter et al. 2001; Miller et al. 2006 |
| <i>(Multifurca)</i> | | | | Buyck et al. 2008 |
| <i>Russula</i> | Melin 1924, 1925; (Doak 1934); Bokor 1985; Lu et al. 1998 | (Frank 1892); (McDougall 1914); | Hobbie et al. 1999, 2001; Kohzu et al. | Peter et al. 2001; |

Table 1 (continued)

| Taxa of EcM fungi | References | Synthesis | In situ identification (first reports; bold, molecular data) | Stable isotopes | Phylogeny (to define the lineage) |
|---|--|-----------|---|---|--|
| /tomentella-thelephora | | | | | |
| <i>Thelephora</i> | Haaskaylo 1965; Zak 1976; Thomas and Jackson 1979 | | Fassi and Fontana 1966; Gardes et al. 1991 ; Jonsson et al. 1999b ; Stendell et al. 1999 | Abadie et al. 2006; Tedersoo et al. 2007a; Mayor et al. 2009 (unreplicated) | U. Kõljalg et al. unpublished |
| <i>Tomentella</i> (incl. <i>Riessia raditicicola</i> , <i>Riessella</i> spp.) | Danielson and Visser 1988; (Warcup 1990c); (Kõljalg 1992); Cairney et al. 1994 | | Danielson and Visser 1988; Danielson and Pruden 1989; Gardes and Bruns 1996 ; Horton and Bruns 1998 ; Taylor and Bruns 1999 ; Kõljalg et al. 2000 | Mayor et al. 2009 (unreplicated) | U. Kõljalg et al. unpublished |
| /tomentellopsis | | | | | |
| <i>Tomentellopsis</i> | Erland et al. 1990 | | Kõljalg et al. 2002 ; Rosling et al. 2003 ; Walker et al. 2005 | | Kõljalg et al. 2002; U. Kõljalg et al. unpublished |
| THELEPHORALES INCERTAE SEDIS | | | | | |
| <i>Boletopsis</i> | | | Agerer 1992b; Izzo et al. 2005a ; Bergemann and Garbelotto 2006 | Trudell et al. 2004 | U. Kõljalg et al. unpublished |
| ZYGOMYCOTA | | | | | |
| ENDOGONALES | | | | | |
| /endogone | | | | | |
| <i>Endogone p. parte</i> * | Warcup 1990b | | (Fassi et al. 1969); Walker 1985; Warcup 1990b; Tedersoo et al. 2008a, 2009a | | White et al. 2006 |
| <i>Sclerogone</i> * | Warcup 1990b | | Warcup 1990b | | |
| (/densospora) ^b | | | | | |
| <i>Densospora</i> (sporocarpic <i>Glomus</i> spp.)* | Warcup and McGee 1983; Warcup 1985; McGee 1996 | | (Warcup 1985) | | |

Genera that are suspected to be ectomycorrhizal based on phylogeny are indicated in parentheses. Asterisks denote sequestrate genera (asterisk in parentheses where only some species are sequestrate). Genera including members with resupinate fruit-bodies are underlined. References in parentheses indicate that the EcM association was not anyhow illustrated or described for proper evaluation

^a Direct proof for EcM status is lacking, but the taxon is phylogenetically distinct

^b Phylogenetic relations of this taxon are unknown

Table 2 Discrepancies between the present treatment of EcM genera and that of Rinaldi et al. (2008)

| Genus | This study | Rinaldi et al. (2008) |
|--|------------|-----------------------|
| <i>Acephala</i> (Helotiales) | NM (EcM) | nd |
| <i>Amaurodon</i> (Thelephorales) | NM | EcM |
| <i>Boughera</i> (unknown) | na | EcM |
| <i>Brauniellula</i> (Boletales) | EcM | nd |
| <i>Catathelasma</i> (Agaricales) | EcM | NM |
| <i>Ceratobasidium</i> 1,2 (Cantharellales) | EcM | nd |
| <i>Chalciporus</i> (Boletales) | NM | EcM |
| <i>Chromelosporium</i> (Pezizales) | EcM | nd |
| <i>Craterocolla</i> (Sebacinales) | NM | EcM |
| <i>Cribbea</i> (Agaricales) | NM | EcM |
| <i>Densospora</i> (Zygomycota) | EcM | NM |
| <i>Durianella</i> (Boletales) | EcM | nd |
| <i>Efibulobasidium</i> (Sebacinales) | NM | EcM |
| <i>Eremiomyces</i> (Pezizales) | NM | EcM |
| <i>Galactinia</i> (Pezizales) | EcM | nd |
| <i>Gastrolactarius</i> (Russulales) | EcM | nd |
| <i>Genabea</i> (Pezizales) | EcM | nd |
| <i>Geopyxis</i> (Pezizales) | NM | EcM |
| <i>Gyromitra</i> (Pezizales) | NM | EcM |
| Helotiales unnamed 1-6 (Helotiales) | EcM | nd |
| <i>Hoehnelogaster</i> (unknown) | na | EcM |
| <i>Hydnoplicata</i> (Pezizales) | EcM | nd |
| <i>Kalaharituber</i> (Pezizales) | NM | EcM |
| <i>Lenzitopsis</i> (Thelephorales) | NM | EcM |
| <i>Leptodontidium</i> (Helotiales) | NM | EcM |
| <i>Leucangium</i> (Pezizales) | EcM | nd |
| <i>Leucopaxillus</i> (Agaricales) | NM | EcM |
| <i>Lindtneria</i> (Agaricales) | NM | EcM |
| <i>Marcelleina</i> (Pezizales) | EcM | nd |
| <i>Martellia</i> (Russulales) | EcM | nd |
| <i>Neocudoniella</i> (Helotiales) | NM | EcM |
| <i>Nothojafnea</i> (Pezizales) | EcM | nd |
| <i>Paurocotylis</i> (Pezizales) | NM | EcM |
| <i>Peridiospora</i> (Zygomycota) | NM | EcM |
| <i>Phialocephala</i> (Helotiales) | NM | EcM |
| <i>Phylloboletellus</i> (Boletales) | EcM | NM |
| <i>Plicaria</i> (Pezizales) | NM | EcM |
| <i>Porphyrellus</i> (Boletales) | EcM | nd |
| <i>Protuberia</i> (Hysterangiales) | NM (EcM) | NM |
| <i>Pseudaleuria</i> (Pezizales) | NM | EcM |
| <i>Pseudoboletus</i> (Boletales) | EcM | nd |
| <i>Pseudohysterangium</i> (unknown) | na | EcM |
| <i>Riessia</i> (unknown) | NM (EcM) | EcM |
| <i>Scabropezia</i> (Pezizales) | EcM | NM |
| <i>Serendipita</i> (Sebacinales) | NM (EcM) | nd |
| Sordariales unnamed (Sordariales) | EcM | nd |
| <i>Stephanospora</i> (Agaricales) | NM | EcM |
| <i>Stephensia</i> (Pezizales) | NM | EcM |
| <i>Tricharina</i> (Pezizales) | NM (EcM) | EcM |
| <i>Trechispora</i> (Trechisporales) | NM | EcM |

Table 2 (continued)

| Genus | This study | Rinaldi et al. (2008) |
|-----------------------------------|------------|-----------------------|
| <i>Tremellogaster</i> (Boletales) | EcM | nd |
| <i>Trichophaea</i> (Pezizales) | NM (EcM) | EcM |
| <i>Xerocomus</i> (Boletales) | EcM | nd |
| <i>Youngiomyces</i> (Zygomycota) | NM | EcM |

Discrepancies are discussed in the section “Ecology and distribution of EcM lineages”

NM (EcM) only a single unrelated species is EcM, *na* absent from Index Fungorum, *nd* not determined

/endogone relies on anatomical differences due to the lack of molecular data. EcM taxa belong to five orders of Ascomycota and ten orders of Basidiomycota. Based on accumulating sequence data from fruit-bodies and EcM root tips, the order Pezizales comprises the greatest number of EcM lineages (16). This figure may expand when representative species from more genera (particularly sequestrate and Austral taxa) are sequenced, cultured, and detected below ground on EcM root tips. In particular, the ecology and phylogenetic relationships among the Austral members of Pezizales are almost unknown. Yet, Pezizales are common in arid and semiarid Australia (Trappe et al. 2008b) and many of the post-fire pezizalean taxa readily form EcM on a variety of hosts (e.g., Warcup 1990a). Helotiales is another order of Ascomycota, where additional EcM lineages await discovery (Tedersoo et al. 2009b). Thus far, records of any sexual structures are lacking for seven out of eight helotialean lineages that strongly hamper their formal description, isolation into pure culture, and subsequent manipulative studies.

Evolutionary ecology of EcM fungi

Based on the putative ecology of nonmycorrhizal sister and successive sister taxa (Table 4), the EcM lineages evolved mostly from saprotrophic fungi (94.7% of the resolved cases), confirming earlier suggestions (Hibbett et al. 2000). Among the saprotrophic sisters, humus saprobes predominated (61.1%), followed by wood (30.6%) and pyrophilous saprobes (8.3%). Among wood-decay fungi, EcM lineages appear to have evolved from white rot, brown rot, and soft rot specialists. Our analysis suggests that no EcM lineages evolved from litter decay fungi. Other sister ecologies included “other biotrophic” for the /pisolithus-scleroderma lineage and putatively endophytic for the /meliniomyces lineage. The ecology of sister taxa to 28 EcM lineages (42.4%) was considered unresolved.

The dominance of humus saprobes among sister groups of EcM lineages suggests that a shared soil habitat is a strong precondition for the evolution of EcM symbiosis in fungi. Most of the putative wood saprobe ancestors are secondary wood decayers that often share their habitat with

Table 3 Ancestral fruit-body types of ectomycorrhizal fungal lineages and lifestyle of their nonmycorrhizal sister taxa

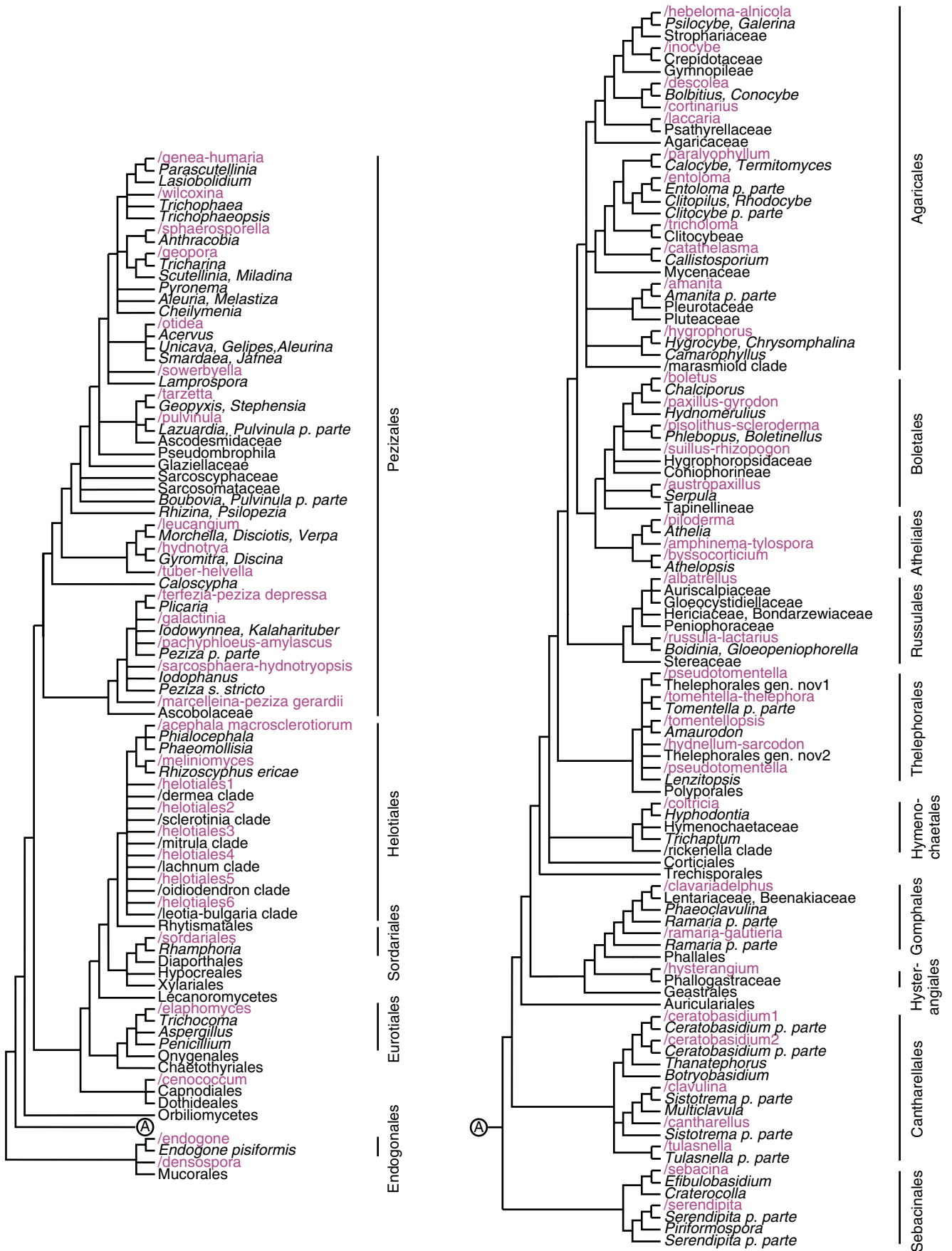
| Ectomycorrhizal taxon | Nonmycorrhizal sister taxon | | | Reference |
|-----------------------------|---|------------------------------|--------------------------------------|---|
| | Sister taxon | Putative ecology | Fruit-body | |
| /cenococcum | Unresolved | Unresolved | Unresolved | LoBuglio et al. 1996 |
| /elaphomyces | <i>Trichocoma</i> | Wood saprobe | Brush-like ascostroma | Miller et al. 2001; Geiser et al. 2006 |
| /acephala macrosclerotiorum | <i>Acephala</i> , <i>Phialocephala</i> , <i>Phaeomollisia</i> | Unresolved | Asexual | Münzenberger et al. 2009 |
| /meliniomyces | <i>Meliniomyces</i> , <i>Rhizoscyphus</i> | Root endophyte, (saprotroph) | Asexual | Hambleton and Sigler 2005 |
| /helotiales1 | Unresolved | Unresolved | Unresolved | Vrålstad et al. 2002 |
| /helotiales2–6 | Unresolved | Unresolved | Unresolved | Tedersoo et al. 2009b |
| /sordariales | <i>Rhizophoria delicatula</i> , unresolved | Wood saprobe | Cleistotheceum (muriform ascospores) | Tedersoo et al. 2007b |
| /galactinia | Unresolved | Unresolved | Unresolved | Hansen et al. 2005 |
| /genea-humaria | <i>Parascutellinia</i> | Humus saprobe | Apothecial | Perry et al. 2007 |
| /geopora | <i>Tricharina s. stricto</i> , (<i>Scutellinia-Ramsbottomia</i> group) | Humus saprobe | Apothecial | Perry et al. 2007 |
| /hydnotrya | <i>Gyromitra</i> , <i>Discina</i> , <i>Pseudorhizina</i> | Humus/wood saprobe | Apothecial | Hansen and Pfister 2006 |
| /leucangium | <i>Verpa</i> , <i>Morchella</i> , <i>Disciotis</i> | Humus saprobe | Apothecial | Hansen and Pfister 2006 |
| /marcellina-peziza gerardii | The rest of Pezizaceae | Unresolved | Unresolved | Hansen et al. 2005 |
| /otidea | unresolved | unresolved | unresolved | Hansen and Pfister 2006; Perry et al. 2007 |
| /pachyphloeus-amyloascus | Unresolved | Unresolved | Apothecial | Hansen and Pfister 2006 |
| /pulvinula | <i>Pulvinula archeri</i> | Pyrophilous saprobe | Apothecial | Perry et al. 2007 |
| /sarcosphaera-hydnotryopsis | Unresolved | Unresolved | Unresolved | Hansen et al. 2005 |
| /sowerbyella | Unresolved | Unresolved | Unresolved | Perry et al. 2007 |
| /sphaerosporella- | <i>Anthracoia</i> | Pyrophilous saprobe | Apothecial | Perry et al. 2007 |
| /tarzetta | <i>Geopyxis</i> , <i>Paurocotylis</i> , <i>Stephensia</i> | Unresolved | Unresolved | Perry et al. 2007 |
| /terfezia-peziza depressa | <i>Plicaria</i> | Pyrophilous saprobe | Apothecial | Hansen et al. 2005 |
| /tuber-helvella | Unresolved | Unresolved | Unresolved | Hansen and Pfister 2006; Læssøe and Hansen 2007 |
| /wilcoxina | <i>Trichophaea</i> , <i>Trichophaeopsis</i> . | Humus saprobe | Apothecial | Perry et al. 2007 |
| /amanita | <i>Amanita</i> subg. <i>Lepidella</i> ; (<i>Limacella</i>) | Humus saprobe | Stipitate | B.E. Wolfe & A. Pringle unpublished |
| /catathelasma | <i>Callistosporium</i> | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /cortinarius | Bolbitiaceae | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /descolea | <i>Bolbitis</i> , <i>Conocybe</i> , <i>Pholiotina</i> | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /entoloma | <i>Entoloma</i> (subg. <i>Nolanea</i> , <i>Leptonia</i>) | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /hebeloma-almicola | <i>Galerina</i> , <i>Psilocybe</i> | Humus (wood) saprobe | Stipitate | Matheny et al. 2006; Moreau et al. 2006 |
| /hygrophorus | <i>Hygrocybe</i> , <i>Chrysomphalina</i> , <i>Humidicutis</i> | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /inocybe | Crepidotaceae | Wood (humus) saprobe | Various | Matheny et al. 2006 |
| /laccaria | Psathyrellaceae | Humus saprobe | Stipitate | Mueller and Pine 1994; Matheny et al. 2006 |
| /paralyophyllum | <i>Calocybe</i> , <i>Lepista</i> , <i>Termitomyces</i> | Humus saprobe | Stipitate | Hofstetter et al. 2002; Matheny et al. 2006 |
| /tricholoma | <i>Clitocybe</i> , <i>Lepista</i> | Humus saprobe | Stipitate | Matheny et al. 2006 |
| /amphinema-tylospora | Unresolved | Unresolved | Resupinate | Binder and Hibbett 2006 |

Table 3 (continued)

| Ectomycorrhizal taxon EcM fungal lineage | Nonmycorrhizal sister taxon | | | Reference |
|---|---|---------------------------------|------------------------|---|
| | Sister taxon | Putative ecology | Fruit-body | |
| /byssocorticium | Unresolved | Unresolved | Resupinate | Binder and Hibbett 2006 |
| /piloderma | Unresolved | Unresolved | Resupinate | Binder and Hibbett 2006 |
| /austropaxillus | <i>Serpula</i> | Wood (brown-rot) saprobe | Resupinate | Binder and Hibbett 2006 |
| /boletus | <i>Chalciporus</i> | Unknown | Stipitate | Kretzer and Bruns 1999; Binder and Hibbett 2006 |
| /paxillus-gyrodon | <i>Hydnomerulius pinastri</i> | Wood (brown-rot) saprobe | Resupinate | Binder and Hibbett 2006 |
| /pisolithus-scleroderma | <i>Boletinellus merulioides</i> , (<i>Gyrodon rompelii</i>) | Aphid, root biotroph (see text) | Stipitate | Binder and Hibbett 2006 |
| /suillus-rhizopogon | Unresolved | Unresolved | Stipitate | Binder and Hibbett 2006 |
| /cantharellus | <i>Sistotrema p. parte</i> | Wood saprobe | Resupinate | Moncalvo et al. 2006; Nilsson et al. 2006 |
| /ceratobasidium1 | <i>Ceratobasidium</i> | Unresolved | Resupinate | Veldre 2009 |
| /ceratobasidium2 | <i>Ceratobasidium</i> | Unresolved | Resupinate | Veldre 2009 |
| /clavulina | <i>Sistotrema p. parte</i> | Wood saprobe | Resupinate | Moncalvo et al. 2006 |
| /tulasnella | <i>Tulasnella p. parte</i> | Various | Resupinate | Moncalvo et al. 2006 |
| /clavariadelphus | Lentariaceae, Beenakiaceae, <i>Ramaria p. parte</i> | Humus (wood) saprobe | Stipitate (clavarioid) | Hosaka et al. 2006 |
| /ramaria-gautieria | Lentariaceae, Beenakiaceae, (<i>Phaeoclavulina</i> , <i>Ramaria p. parte</i>) | Humus (wood) saprobe | Stipitate (clavarioid) | Hosaka et al. 2006 |
| /coltricia | <i>Hyphodontia</i> , unresolved | Wood saprobe | Resupinate | Larsson et al. 2006 |
| /hysterangium | Phallogastraceae | Humus saprobe | Sequestrate | Hosaka et al. 2006 |
| /albatrellus | <i>Gloeocystidiellum</i> , Auriscalpiaceae, Hericiaceae | Wood saprobe (parasite) | Various | Larsson and Larsson 2003; Miller et al. 2006 |
| /russula-lactarius | <i>Boidinia</i> , <i>Gloeocystidiellum</i> | Wood saprobe | Resupinate | Larsson and Larsson 2003; Miller et al. 2006 |
| /sebacina | <i>Efibulobasidium</i> , <i>Craterocola</i> | Wood saprobe | Tremelloid | Weiss et al. 2004 |
| /serendipita | <i>Sebacina vermifera s. lato</i> | Unresolved | Unresolved | L. Tedersoo unpublished |
| /hydnellum-sarcodon | unresolved | Unresolved | Unresolved | U. Kõljalg unpublished |
| /phellodon-bankera | unresolved | Unresolved | Unresolved | U. Kõljalg unpublished |
| /pseudotomentella | Thelephorales gen. nov | Humus saprobe | Resupinate | U. Kõljalg unpublished |
| /tomentella-thelephora | <i>Tomentella p. parte</i> | Humus (wood) saprobe | Resupinate | U. Kõljalg unpublished |
| /tomentellopsis | <i>Amaurodon</i> | Humus saprobe | Resupinate | U. Kõljalg unpublished |
| /endogone | <i>Endogone pisiformis</i> , (Mucorales) | Humus saprobe | Sequestrate | White et al. 2006 |
| /densospora | Unresolved | Unresolved | Unresolved | No sequence data |

tree roots penetrating soft wood. Depleting nutrient resources in decaying wood may exert a strong pressure on decay fungi to exploit alternative energy sources. Indeed, some wood decay fungi can form thin, undifferentiated mantle-like structures and penetrate fine roots intercellularly without obvious disease symptoms (Vasiliauskas et al. 2007). Among the Pezizales, pyrophilous and disturbance-adapted saprobes were the sister taxa to EcM lineages with more or less pyrophilous and disturbance-adapted lifestyles (/sphaerosporella and /pulvinula). This suggests that certain ecological affinities may persist in fungal taxa even after the development of the EcM habit.

Except for a few ambiguous cases in Helotiales, Sebacinales, and Cantharellales, the paucity of root endophytes among sister groups to EcM fungi indicates that endophytic and EcM lifestyles are mostly evolutionarily unrelated and alternative ways of biotrophic root interactions. The high frequency of the EcM lifestyle in Pezizales and the root endophytic lifestyle in Helotiales is particularly striking. Although many members of Pezizales form a variety of biotrophic interactions with roots (Egger 2006), they are very seldom recovered during molecular identification studies of roots. Except for *Melinomyces bicolor* (/meliniomyces), EcM lifestyle is phylogenetically distinct



◀ **Fig. 1** Simplified schematic tree demonstrating the phylogenetic position of EcM lineages (in purple) based on various studies (Table 1). Note that known sister taxa to EcM lineages are included, but other intervening non-EcM taxa are usually omitted for simplicity

from endophytic and ericoid mycorrhizal habits, despite the fact that the two latter guilds are strongly linked in the Helotiales (Tedersoo et al. 2009b).

We found no evidence for the reversal to non-EcM nutrition (Hibbett et al. 2000) in the evolutionary patterns of EcM lineages. However, it is highly probable that at least some EcM fungal species have become exploitative on their partners (see discussion on stable isotopes and tripartite associations) (Egger and Hibbett 2004). Order-level multigene phylogenies with inclusive taxon sampling have strongly improved our understanding of the evolution of ecological and morphological traits in fungi (e.g., Hansen et al. 2005; Hosaka et al. 2006; Matheny et al. 2006; Moncalvo et al. 2006) and emphasized the strong evidence for the independent evolution of EcM-forming taxa with no clear evidence for reversals. The present-limited taxon sampling and knowledge of the phylogeny does not allow to reject the possibility of regains of saprotrophic or other modes of nutrition in Atheliales, Boletales, and Thelephorales.

Sequestrate fruit-body forms have arisen in at least 30 lineages (45.5%) of EcM fungi. This has occurred independently multiple times in many taxa (e.g., Peintner et al. 2001; Peter et al. 2001; Hansen et al. 2005; Perry et al. 2007). Respectively in Ascomycota and Basidiomycota, at least 37 and 57 genera of EcM fungi include or are totally comprised of sequestrate members. Despite their wide distribution, sequestrate fruit-bodies prevailed in non-EcM sister groups to *Hydangium* and *Endogone* lineages only. Stipitate (including apothecial, clavarioid, and agaricoid forms) and resupinate fruit-body types were predominant in sister species to 24 (36.4%) and 14 (21.2%) lineages, respectively (Table 4). The fruit-body types of sisters to 20 lineages (30.3%) remain uncertain. Interestingly, EcM lineages with resupinate-fruiting sister species have never developed sequestrate fruit-bodies.

The majority of sequestrate fungi form EcM and are considered mammal-dispersed (Trappe and Claridge 2005). Although dispersal of spores of sequestrate EcM fungi by mammals certainly contributes to long-distance dispersal in some species (e.g., Grubisha et al. 2007), deposition, and persistence of spores directly in the rooting zone may also be an important advantage of hypogeous vs. epigeous fruiting form (Miller et al. 1994). Although the majority of taxa with sequestrate fruit-bodies form EcM, there are still many species in several genera whose ecology and/or phylogenetic placement suggests that they are saprotrophs or non-EcM root biotrophs. These genera include *Carbotomyces*, *Elderia*, *Eremiomyces*, *Kalaharituber*, *Mattiolomy-*

ces, *Paurocotylis*, and *Stephensia* (Pezizales); *Agrogaster*, *Barcheria*, *Cribbea*, *Endoptychum*, *Notholepiota*, *Stephanospora*, *Tympanella*, and *Weraroa* (Agaricomycetidae); *Claustula*, *Gelopellis*, *Kjeldsenia*, *Kobayasia*, *Phallobata*, *Phelbogaster*, *Protuberata*, *Radiigera*, *Schenella* (syn. *Pyrrenogaster*), *Sclerogaster*, and *Trappea* (Phallomycetidae); *Endogone p. parte*, *Peridiospora*, and *Youngiomyces* (Zygomycota). In contrast to many sequestrate EcM taxa, the putatively saprotrophic sequestrate genera are often monospecific or species-poor, and their ecology remains poorly understood. Many of these non-EcM taxa associate with roots of various non-EcM plants (e.g., Yao et al. 1995; Wu and Lin 1997; Kovács et al. 2007).

Tripartite interactions among EcM fungi

Certain fungal taxa within EcM lineages are routinely observed fruiting in association with other EcM fungi and even co-infect EcM roots. *Chroogomphus* and *Gomphidium* spp. are commonly observed with *Suillus* and *Rhizopogon* spp. (Miller 2003) and may form EcM in bi- or tripartite associations with a host tree. Similarly, *Russula pulchella* always fruits in the presence of *Lactarius pubescens*, but its own EcM have not been found (Beenken 2004). In some tripartite associations, haustoria of one fungus can be seen inside the other fungus, suggesting exploitative interactions (Agerer 1990, 1991b).

Fruit-bodies of *Pseudoboletus* (syn. *Xerocomus*) *parasiticus* are attached to those of *Scleroderma citrinum*; therefore, *P. parasiticus* has been considered a mycoparasite. However, Richter and Bruhn (1989) convincingly demonstrated EcM formation between *P. parasiticus* and *Pinus resinosa* in pure culture, with abundant production of well-developed EcM characteristic of Boletaceae. Fruit-bodies of *Chalciporus piperatus* display significant spatial affinity towards fruit-bodies of *Amanita muscaria* (L. Tedersoo unpublished), further suggesting *Chalciporus* may have a biotrophic interaction. A similar association is described between fruit-bodies of *A. muscaria* and *Boletus edulis* in New Zealand (Wang and Hall 2004). *C. piperatus* has not been identified from EcM in situ or demonstrated forming EcM in vitro despite relatively rapid mycelial growth and numerous synthesis attempts (e.g., Modess 1941; Godbout and Fortin 1985; Yamada and Katsuya 1995; Kasuya and Igarashi 1996). Although Garrido (1988) reported a successful EcM synthesis with *C. piperatus* and *Pinus* sp., many of his illustrations document endophytic or superficial hyphal formations rather than true EcM associations. Accordingly, his reports on EcM status and host specificity for both plants and fungi should be treated with caution. *Chalciporus* is phylogenetically a sister taxon to the putatively non-EcM fungus *Buchwaldoboletus lignicola* (Pantidou 1962; Pilat 1965; M. Binder unpublished),

Table 4 Suspected EcM fungi that lack published ITS sequence data and are not treated in phylogenetic studies

| Genus | Putative affiliation | Remarks |
|--|--|---|
| <i>Aleurina</i> (syn. <i>Jafneadelphus</i>) | <i>Unicava-Gelinipes</i> , Pezizales | <i>Aleurina</i> is polyphyletic. <i>A. argentina</i> is common on soil in Chilean <i>Nothofagus</i> forests and is clustered with EcM species (M.E. Smith & D.H. Pfister unpublished) |
| <i>Amogaster</i> ^a | Agaricales | Found in California under <i>Populus</i> spp. (Castellano 1995) |
| <i>Austrogaster</i> ^{a,b} | Boletales | Found exclusively in Chilean <i>Nothofagus</i> vegetation (Singer 1962) |
| <i>Boletochaete</i> ^b | /boletus, Boletales | Found in African EcM forests (Singer 1944, 1986) |
| <i>Chlorogaster</i> ^a | /pisolithus-scleroderma, Boletales | Found in Asian dipterocarp forests (Watling 2006) |
| <i>Delastria</i> ^{a,b} | Pezizales | Found in the Mediterranean region associated with Cistaceae (Moreno-Arroyo et al. 2000) |
| <i>Destuntzia</i> ^{a,b} | Phallomycetidae | Found in North American EcM vegetation (Fogel and Trappe 1985) |
| <i>Fevansia</i> ^{a,b} | Boletales | Always found in EcM vegetation (Trappe and Castellano 2000) |
| <i>Gastroleccinum</i> ^{a,b} | /boletus, Boletales | Thiers (1989) suggested it to be a secotioid <i>Leccinum</i> ; found in association with EcM trees |
| <i>Gelinipes</i> , nom. prov. ^a | Pyronemataceae, Pezizales | found from Australian EcM vegetation (Perry et al. 2007) |
| <i>Gigasperma</i> ^{a,b} | Agaricales | <i>Gigasperma</i> is probably polyphyletic. Found with EcM <i>Cercocarpus</i> (Kropp and Hutchison 1996) in Utah or with <i>Nothofagus</i> in New Zealand (Horak 1971) |
| <i>Gomphogaster</i> ^{a,b} | /suillus-rhizopogon, Boletales | Miller (1973) suggested it to be a secotioid <i>Gomphidius</i> |
| <i>Gummivena</i> ^{a,b} | /hysterangium, Hysterangiales | Found in Australian EcM vegetation (Trappe and Bougher 2002) |
| <i>Gymnohydnotrya</i> ^{a,b} | /tuber-helvella, Pezizales | Found in Australian EcM vegetation (Zhang and Minter 1989) |
| <i>Horakiella</i> ^{a,b} | /pisolithus-scleroderma, Boletales | Found with Australian EcM Myrtaceae (Castellano and Trappe 1992) |
| <i>Loculotuber</i> ^{a,b} | /tuber-helvella, Pezizales | Found with Cistaceae and Fagaceae in the Mediterranean region (Alvarez and Parladé 1992) |
| <i>Mayamontana</i> ^{a,b} | Agaricales (Larsson 2007) | Suggested to associate with EcM Nyctaginaceae in Central America (Castellano et al. 2007) |
| <i>Neopaxillus</i> | Agaricales (based on ITS sequences in INSD) | Found with South American EcM trees (Singer 1986) |
| <i>Paradoxa</i> ^{a,b} | /tuber-helvella, Pezizales | Found with European deciduous trees (Montechi and Sarasini 2000) |
| <i>Paxillogaster</i> ^{a,b} | /austropaxillus, Boletales | Found in South American <i>Nothofagus</i> vegetation (Horak and Moser 1965) |
| <i>Phyllobolites</i> | Agaricomycetes | Found with South American EcM trees (Singer 1986) |
| <i>Protogautieria</i> ^a | /ramaria-gautieria, Gomphales | Found in Californian mixed forests (Thiers 1979) |
| <i>Psiloboletinus</i> ^b | /suillus-rhizopogon, Boletales | Found always in association with <i>Larix</i> and very closely related to <i>Boletinus</i> (<i>Suillus</i>) according to Smith (1966) |
| <i>Rhopalogaster</i> ^{a,b} | /suillus-rhizopogon, Boletales (Hosaka et al. 2006) | Found in coniferous and mixed forests with EcM hosts |
| <i>Setogyroporus</i> ^b | Boletales | Found in African EcM vegetation (based on herbarium records) |
| <i>Singeromyces</i> ^a | Boletales | Found in Chilean <i>Nothofagus</i> vegetation (Horak and Moser 1965) |
| <i>Sinoboletus</i> ^b | /boletus, Boletales | Found mostly in forests of Fagaceae in East Asia (based on herbarium records) |
| <i>Sphaerosoma</i> ^{a,b} | Pezizales | <i>Sphaerosoma</i> is polyphyletic. The type, <i>S. fuscescens</i> is found in EcM vegetation (Dissing and Korf 1980) |
| <i>Trichophaeopsis</i> | Pyronemataceae, Pezizales | <i>T. eguttulispora</i> is found on soil in Chilean <i>Nothofagus</i> forests and its ITS sequence matches 88% to EcM root sequences (M.E. Smith & D.H. Pfister unpublished) |
| <i>Tubosaeta</i> ^b | Boletales | Found in African EcM forests (Singer 1944, 1986) |
| <i>Unicava</i> nom. prov. ^a | Pyronemataceae, Pezizales; close to <i>Gelinipes</i> and <i>Aleurina</i> (Perry et al. 2007) | Found in Australian EcM vegetation (Perry et al. 2007) |
| <i>Veloporphyrellus</i> ^b | /boletus, Boletales | Found in Mexican <i>Quercus</i> forests (Singer 1986) |
| <i>Wakefieldia</i> ^{a,c} | Boletales | <i>Wakefieldia</i> may be polyphyletic. <i>W. macrospora</i> is found beneath <i>Quercus</i> in Europe whereas <i>W. striaespora</i> is found in Malaysian forests (Hawker 1954). |

^a Taxa with sequestrate fruit-bodies^b Considered EcM in Rinaldi et al. (2008)^c Considered saprotrophic in Rinaldi et al. (2008)

providing further suggestion that *Chalciporus* may be non-EcM. High ^{13}C values and %N values also (Taylor et al. 2003; Zeller et al. 2007) indicate that *C. piperatus* may be a non-EcM fungus. The ecology and potential multitrophic interactions of *Chalciporus* warrant further investigation.

Another group of boletes with ambiguous trophic status includes the closely related genera *Phlebopus* and *Phylloboletellus*. *Phylloboletellus* is found in South American ‘anectotrophic forests’ (Singer 1986) and *Phlebopus sudanicus* fruits in various African habitats that include non-EcM vegetation. No EcM structures of *P. sudanicus* have been observed in nature, but pure culture synthesis trials with Australian *Acacia* spp. resulted in the formation of well-developed EcM (Thoen and Ducouso 1989). On *Pinus* spp., however, only a thin hyphal mantle (with no Hartig net) developed, despite the abundant formation of characteristic sclerotia. Because (1) sclerotia were not observed on *Acacia* inoculations, (2) the authors did not include uninoculated controls, and (3) the yellow EcM typical of *Scleroderma* developed in open containers in a greenhouse, we suspect that the *Acacia* seedlings may have been contaminated by a *Scleroderma* species. Goncalves (1940) demonstrated the tripartite association of *Phlebopus tropicus*, *Pseudococcus* aphids, and *Citrus* species. Singer (1986) and Watling (2006) assumed that many other members of *Phlebopus* form biotrophic associations with root aphids. The non-EcM *Boletinellus merulioides* (Gruhn et al. 1992) interacts similarly with root aphids (Brundrett and Kendrick 1987). These observations suggest that *Phlebopus*, *Boletinellus*, and *Phylloboletellus* are non-EcM but facultatively or obligately biotrophic taxa.

Stable isotopes

Stable isotopes, expressed as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, usually confirm the mycorrhizal status of EcM fungi, particularly in relation to humus, wood, and litter saprobes provided that samples are collected without spatial and temporal bias (Taylor et al. 2003). Because multiple factors affect the stable isotope composition of plants and fungi (see Introduction), the isotope values of certain EcM fungal taxa differ from the general pattern. These differences may either represent random deviations or suggest preferential uptake of certain nitrogen compounds or alternative modes of nutrition. EcM fungi with notably low $\delta^{15}\text{N}$ values include *Chroogomphus tomentosus* (Kohzu et al. 1999); *C. rutilus* (Taylor et al. 2003; Trudell et al. 2004); *Hygrophorus olivaceo-albus* (Taylor et al. 2003, but see Trudell et al. 2004); *Gomphidius subroseus*, *Clavulina cristata*, *Phylloporus rhodoxanthus* (Trudell et al. 2004); and *Helvella* spp. (Tedersoo et al. 2007a). Except for *Helvella* spp., most aforementioned taxa have a relatively low N concentration that often positively

correlates with $\delta^{15}\text{N}$ values (Hobbie et al. 2001; Taylor et al. 2003) and suggests including %N as a third factor explaining differences between EcM and saprotrophic fungi. Alternatively, similar $\delta^{15}\text{N}$ values in an EcM fungus and a host may indicate the presence of different transport molecules or the lack of N transfer from fungi to host trees. These processes are considered the main sources of isotope discrimination in EcM symbiosis (Hobbie and Hobbie 2008). In contrast, EcM fungi with very high $\delta^{15}\text{N}$ values include *Lyophyllum fumosum*, *Hebeloma radicosoides*, *H. vinosophyllum* (Kohzu et al. 1999); *Phellodon tomentosa*, *Hydnellum ferrugineum*, *H. peckii* (with high %N; Taylor et al. 2003); *Boletopsis leucomelaena*, and *Lyophyllum semitale* (%N not reported; Trudell et al. 2004). Several members of *Hebeloma* section *Myxocybe* are well-known for use of readily available animal-derived nitrogen forms (Sagara 1995). Apart from *Hebeloma*, these species produce great amounts of extraradical mycelium and rhizomorphs that correlates with high $\delta^{15}\text{N}$ (Trudell et al. 2004; Hobbie and Agerer 2009).

Remarkably high $\delta^{13}\text{C}$ values are described in *Entoloma* sp., *Hydnellum caeruleum*, *Catathelasma ventricosum*, *L. fumosum* (Kohzu et al. 1999); *Entoloma nitidum*, *H. ferrugineum*, *H. peckii*, and *Phellodon niger* (coupled with high %N; Taylor et al. 2003). The high $\delta^{13}\text{C}$ values of these fungi remain unexplained but may be, again, associated with the %N, great amounts of mycelium, or partial utilization of soil carbon.

While the EcM and saprotrophic Basidiomycota can mostly be distinguished by their isotope composition, Ascomycota pose a greater challenge. Isotope patterns of several taxa strongly contradict their anticipated lifestyle. For example, the putatively non-EcM taxa *Pseudoplectania nigrella* (Trudell et al. 2004), *Paurocotylis pila*, *Morchella* sp., *Aleuria aurantia*, *Rhizina undulata* (Hobbie et al. 2001), and *Leotia lubrica* (Zeller et al. 2007) all have isotope patterns consistent with EcM lifestyle. It appears that many Pezizales and Helotiales form other types of root-associated biotrophic relations with plants that serve to blur their isotope signals (Egger and Paden 1986; Egger 2006; Kovács et al. 2007; Tedersoo et al. 2009b).

The grouping of plant parasites such as *R. undulata* (Hobbie et al. 2001), *Bryoglossum gracile*, and *Cantharellopsis prescottii* (Clemmensen et al. 2006) with EcM fungi based on $\delta^{13}\text{C}$ values reflects their use of relatively recent plant-derived carbon. However, these taxa are usually highly depleted in $\delta^{15}\text{N}$ or their $\delta^{15}\text{N}$ signatures are highly variable intraspecifically, suggesting that their N is probably derived from plants and further fractionated during this process. Members of *Phaeocollybia* (Trudell et al. 2004), *Hygrocybe*, *Clavulinopsis*, *Clavaria*, *Trichoglossum*, and *Geoglossum* (Griffith et al. 2002) have extremely high $\delta^{15}\text{N}$ values. Unculturability, extreme isotope values,

and association with other organisms (e.g., *Hygrocybe* spp. with mosses—Griffith et al. 2002) suggest the possibility of unknown biotrophic lifestyles in many of these fungi. Accumulation of heavy isotopes is characteristic of higher levels in food webs (Vanderklift and Ponsard 2003). Extremely low $\delta^{13}\text{C}$ values, however, may indicate strong discrimination during parasitic C acquisition from hosts rather than use of energy sources inaccessible to other saprobes.

Notes on EcM lineages and related nonmycorrhizal taxa

Dothideomycetes incertae sedis

Sister relations of the */cenococcum* lineage among the Dothideomycetes remain undescribed. Based on INSD searches, several foliar endophytes and isolates from ericoid mycorrhiza displayed high ITS sequence similarity (95% to 96% full-length sequence similarity) to *Cenococcum* isolates. This suggests that the ubiquitous, asexual *Cenococcum* may be ecologically more variable as compared to other EcM fungi. For reasons that are unclear, *Cenococcum* is uncommon in tropical regions.

Eurotiales

Elaphomyces and *Pseudotulostoma* form a monophyletic */elaphomyces* lineage (Henkel et al. 2006) that has a nearly cosmopolitan distribution. Based on some morphological structural resemblance in the fungal mantle of *Cenococcum geophilum* and ascocarp peridium of *Elaphomyces* spp., Trappe (1971b: 22, 31) suggested that “*C. graniforme* is unquestionably related to the genus *Elaphomyces*....It is anatomically analogous to several *Elaphomyces* species and possibly is the vegetative stage of *E. anthracinus*.” Surprisingly, this hypothesis is still cited in EcM literature, despite a clear demonstration by use of molecular data that *Elaphomyces* and *Cenococcum* belong to phylogenetically distinct classes of ascomycetes (LoBuglio et al. 1996).

Members of *Cladophialophora*, *Capronia*, and *Exophiala* (Chaetothyriomycetidae) are often identified from EcM root tips. Because they are more commonly described as root endophytes and occasionally detected as ericoid mycorrhizal fungi, they probably represent secondary colonizers of EcM root tips (Tedersoo et al. 2009b). This is similar to many taxa within Helotiales (see below).

Helotiales

So far, only three species of EcM-forming Helotiales from the *Meliniomyces–Rhizoscyphus* complex have been confirmed in pure culture synthesis trials, viz. *Cadophora*

finlandica, *M. bicolor* and one of the two strains of *M. vraolstadae* (INSD accession AJ292200—Vrålstad et al. 2002a, b; Hambleton and Sigler 2005). These taxa constitute the */meliniomyces* lineage. Hambleton and Sigler (2005) recognized three additional species of *Meliniomyces* (species 2–4) that were nested within a clade including *C. finlandica*, *M. bicolor*, and *M. vraolstadae*, but their EcM status remains to be verified. INSD included only EcM-derived sequences with >96% ITS sequence similarity to *M. vraolstadae* (Menkis et al. 2006; INSD unpublished), supporting an EcM lifestyle of this taxon. Other sister taxa such as *M. variabilis* are saprotrophic, ericoid mycorrhizal with the Ericaceae or endophytic in the roots of trees and herbs (Vrålstad et al. 2002a, b; Hambleton and Sigler 2005). However, the monophyly of *M. bicolor*, *M. vraolstadae*, and other putatively EcM taxa remains to be proven. Haug et al. (2004) suggested that certain members of the *Meliniomyces–Rhizoscyphus* complex form EcM with arbuscular mycorrhizal *Graffenrieda emarginata* (Melastomataceae). However, in our opinion this interaction clearly lacks a Hartig net and root epidermal cells including junctions are covered with a single layer of hyphae (Haug et al. 2004:343–345; L. Tedersoo pers. obs.) that is typical of dark septate root endophytes (Jumpponen 2001; Peterson et al. 2008).

Based on consistent molecular identification of an identical phylotype from black EcM morphotypes of *Pinus sylvestris* (INSD accession AJ430411 and AJ292197), Vrålstad et al. (2002a) suggested the presence of another, unrelated EcM taxon (treated here as */helotiales1*). This suggestion is supported by the detection of */helotiales1* DNA sequences from arbutoid mycorrhizal roots of Pyroleae (Tedersoo et al. 2007a). Tedersoo et al. (2008b) found a distinct yellowish EcM morphotype with ascomycete mantle anatomy on *Picea abies* that was consistently identified as a member of Helotiales from several samples (UNITE accession UDB002570) and is designated as */helotiales2*. Tedersoo et al. (2008a, 2009a) also recovered eight species of Helotiales that form EcM with Australian hosts. These species are grouped into four well-supported lineages (*/helotiales3–6*) which are distantly related to the EcM taxa in the Northern Hemisphere and to any root endophytes (Tedersoo et al. 2009b).

Early studies of Elias Melin revealed frequent root colonization by black ascomycete mycelium that was easily cultured and usually inhibited seedling growth (Melin 1923b). These isolates were named “*Mycelium radicis atrovirens*” (MRA) and considered “pseudomycorrhizal” due to their biotrophic habit. The isolates of MRA mostly belong to the *Phialocephala–Acephala* and *Meliniomyces–Rhizoscyphus* complexes (Peterson et al. 2008). These taxa are frequently identified as secondary colonizers of EcM root tips by use of molecular tools (Rosling et al. 2003). The EcM-like

structures of *P. fortinii* have been synthesized and described on *Salix* sp. (Fernando and Currah 1996) and *Pinus* sp. (Peterson et al. 2008). Because both the mantle and Hartig net are poorly developed and *P. fortinii* forms endophytic associations with many non-EcM plants, we consider this taxon non-EcM (Jumpponen 2001). In studies on *Phialocephala*–*Acephala* complex in various habitats, Menkis et al. (2004) identified a monophyletic clade of mycobionts exclusively from conifer EcM. Recently, Münzenberger et al. (2009) demonstrated that phylogenetically closely related mycobionts form “*Pinirhiza sclerotia*” anatomotypes are able to form normally developed EcM in axenic conditions and named. This taxon was named *Acephala macrosclerotiorum*, and it is the only EcM taxon in the *Phialocephala*–*Acephala* complex (Münzenberger et al. 2009). In contrast to the interpretation of Rinaldi et al. (2008), we found no evidence for EcM formation in the interaction between *Leptodontidium orchidicola* and species of *Betula* and *Picea* (Fernando and Currah 1995). Rinaldi et al. (2008) also suggested that *Neocudoniella* forms EcM. *Neocudoniella albiceps* fruits on dead wood, whereas *N. radicella* forms apothecia on long roots of *Picea mariana* (Kohn et al. 1986). A very thin and patchy mantle-like structure comprised of inter- and intracellular hyphae penetrating the cortical cells and extending to the outer wall of endodermis are characteristic of the axenically synthesized biotrophic interaction (Kohn et al. 1986). This nonmycorrhizal association resembles other incompatible in vitro interactions between ascomycetes and EcM trees. Stable isotope values suggest that *L. lubrica* has an EcM lifestyle (Zeller et al. 2007). *Leotia* aff. *lubrica* was sometimes identified from EcM roots formed by Basidiomycota and Australian trees, suggesting that *Leotia* species may secondarily colonize roots (Tedersoo et al. 2009b).

Pezizales

The /galactinia lineage comprises a group of *Peziza* species that contain a whitish or yellowish milky substance that is exuded from cut fruit-bodies (*Peziza succosa* clade—Hansen et al. 2005). *Peziza infossa* and several undescribed hypogeous species (M.E. Smith et al. unpublished) are nested within an otherwise epigeous clade. A few morphological species of /galactinia are known from the Holarctic and Southern South America.

The /genea-humaria lineage comprises mostly sequestrate taxa. This lineage has been reliably identified only from the Holarctic realm and Southern South America (Perry et al. 2007). *Genea eucalyptorum* is described from Australia but probably represents an *Amylascus* species.

The /geopora lineage comprises several sequestrate genera in addition to the predominately epigeous *Geopora*. Of the large, polyphyletic genus *Tricharina*, only *T.*

ochroleuca seems to be EcM (Trocha et al. 2006); this species is nested within *Geopora* species in the /geopora lineage (Hansen et al. 2005). Several other INSD reports of *Tricharina* EcM actually match closest to *Geopora*. The /geopora lineage is known only from the Holarctic realm.

The /hydnotrya and /leucangium lineages comprise a few sequestrate taxa. Both lineages are found solely in the Holarctic realm. Based on some phylogenies, *Fischerula* is non-monophyletic with *Leucangium* and *Imaia* (Kovács et al. 2008) and may represent an independent EcM lineage.

The /marcelleina-peziza gerardii lineage includes both apothecial and sequestrate taxa. This group is known from the Holarctic realm and New Zealand, where it may be introduced with roots of exotic trees.

The predominately apothecial /otidea lineage includes a single sequestrate taxon (Smith and Healy 2009). The lineage is reliably known only from the Holarctic realm with a few additional records from Malaysia (Perry et al. 2007).

The /pachyphloeus-amylascus lineage includes both apothecial and sequestrate taxa. Several species form *Glischroderma* and *Chromelosporium* anamorphs (Hansen et al. 2005). This lineage is relatively species-rich and is distributed in both the Holarctic and Austral realms, but reports are lacking from New Zealand.

The /pulvinula lineage includes a few pyrophilous taxa with epigeous fruit-bodies. *Pulvinula archeri* does not form EcM-like structures (Warcup 1990a), but *P. constellatio* is a common EcM “contaminant” in greenhouse studies of *Tuber* EcM (Amicucci et al. 2001). *P. archeri* forms a sister taxon to the /pulvinula lineage, but only a few species of this heterogeneous genus are included in the phylograms (Perry et al. 2007). The distribution and systematics of the /pulvinula lineage are poorly understood, but species are reported from the Holarctic realm and Australia.

The /sarcosphaera-hydnotryopsis lineage comprises both semihypogeous and fully hypogeous sequestrate taxa that are known only from the Holarctic realm.

The /sowerbyella lineage has only circumstantial isotope evidence for being EcM (Hobbie et al. 2001). *Sowerbyella* includes rare species fruiting predominately in the forest floor of undisturbed, mature coniferous, and mixed forests of the Holarctic realm and *Nothofagus*-dominated forests in Southern South America (M.E. Smith and D.H. Pfister unpublished). The growth habit of *Sowerbyella* in conjunction with the fact that this genus cannot be grown in axenic culture supports the putative consideration as an EcM lineage.

The /sphaerosporella lineage includes the mostly pyrophilous *Sphaerosporella* and non-pyrophilous *Trichophaea woolhopeia*. Their putative ecology and EcM anatomy differs strongly, suggesting that the close relationship of these taxa may be an artifact of incomplete taxon sampling

and long branch attraction (Perry et al. 2007). Both species are known only from the Holarctic realm.

The /tarzetta lineage comprises apothecial taxa. The /tarzetta lineage is reliably known from the Holarctic realm, New Zealand and Southern South America (M.E. Smith and D.H. Pfister unpublished); the reports from Australia require confirmation.

The /terfezia-peziza depressa lineage includes both epigeous and sequestrate taxa as well as the anamorphic genus *Chromelosporium* (*p. parte*). Several members of the /terfezia-peziza depressa lineage are pyrophilous. This species-rich group is distributed both in Holarctic and Austral realms, although its presence in New Zealand remains uncertain.

The /tuber-helvella lineage includes a large number of sequestrate taxa. While *Tuber* is known only from the Holarctic realm, other members of the /tuber-helvella lineage are widely distributed in the Austral regions.

The /wilcoxina lineage comprises a few epigeous taxa, *Wilcoxina* spp. and *Trichophaea hybrida* that form ectendomycorrhiza on *Pinus* and *Larix*, and EcM with other host trees (Yu et al. 2001). These pioneer fungi are known only from the Holarctic realm.

Warcup (1990a) obtained typical EcM in pure culture synthesis with *Nothofajnea cryptotricha*, *Lachnea vinosobrunnea*, and the host plants *Eucalyptus* sp. and *Melaleuca* sp. Unfortunately, the phylogenetic position of these taxa is unknown.

Tedersoo et al. (2006a) suggested that EcM symbiosis is a precondition for the development of sequestrate hypogeous fruiting in Pezizales. A more thorough literature review, however, suggests that this may not be true for all lineages. Nevertheless, many of the nonmycorrhizal sequestrate Pezizales taxa form a biotrophic interaction with arbuscular mycorrhizal plants that is distinct from the endophytic interactions displayed by members of the Helotiales. For example, the putatively nonmycorrhizal genus *Carbomyces*, a hypogeous taxon found in deserts of New Mexico, is suggested to be EcM but no EcM hosts have been identified in its natural habitat (Trappe 1971a). Similarly, *Eremiomyces echinulatus*, a hypogeous member of Pezizales, fruits in the South African Republic where no EcM hosts are known. *Kalaharituber* is suggested to form EcM with African plants including *Acacia* spp. However, none of the studied African *Acacia* spp. form EcM and the fungus was found infecting root systems of *Citrullus vulgaris*, a non-EcM plant. Moreover, there are no known EcM plants found in the natural habitat of *Kalaharituber* in Namibia, Botswana and the South African Republic (Trappe et al. 2008a). *Mattiolomyces terfezioides* forms a biotrophic association with *Robinia pseudoacacia* and several other arbuscular mycorrhizal plants (Bratek et al. 1996; Kovács et al. 2007). *Mattiolomyces* and an Australian desert truffle

Elderia are probably nested within *Peziza s. stricto*, a clade with no known EcM species (Læssøe and Hansen 2007; Trappe et al. 2009a).

Geopyxis is probably a facultatively parasitic genus. *Geopyxis carbonaria* weakly parasitizes *Pinus* sp. in axenic synthesis trials (Egger and Paden 1986) and often fruits on elevated pieces of burnt wood with no close connection to roots. Warcup (1990a) observed no EcM-like features when species of *Eucalyptus* and *Melanoleuca* were inoculated with *G. carbonaria*. Vrålstad et al. (1998) observed an abundant fruiting of *G. carbonaria* on root mounds of fallen *Picea* and identified the fungus from moribound root tips, characterized by a thin mantle-like structure. *Geopyxis* sp. formed a thin mantle, but no Hartig net on nonmycorrhizal roots of *Alnus* spp. and secondarily colonized EcM formed by species of Basidiomycota (Tedersoo et al. 2009c). An unidentified *Geopyxis* sp. has also been isolated from surface-sterilized seeds of *Pinus* (Ganley and Newcombe 2007). The closely related genus *Paurocotylis* is suggested to be EcM based on stable isotope signatures (Hobbie et al. 2001). However, *Paurocotylis* produces sequestrate hypogeous fruit-bodies in flowerbeds and greenhouses associated with arbuscular mycorrhizal herbs or trees, suggesting a non-EcM but potentially biotrophic lifestyle (Dennis 1974; Læssøe and Hansen 2007). *Stephensia* is a closely related truffle genus that is also probably non-EcM. Ascospores of *S. shanorii* readily germinate on various media (Uecker 1967), a feature uncharacteristic of most EcM fungi. Fontana and Giovanetti (1980) failed to establish EcM symbiosis between *S. bombycina* and *Quercus*. It should be noted, however, that *Stephensia* encompasses species from several continents and it may be polyphyletic with some EcM and some non-EcM taxa.

Several other species of Pezizales that were suggested as EcM based on isotope signatures are instead probably facultative biotrophs or pathogens (e.g., *Morchella* sp., *A. aurantia*, and *R. undulata*—Hobbie et al. 2001). *R. undulata* is a root pathogen of conifers and inhibits seedling growth in vitro (Egger and Paden 1986). *A. aurantia* usually fruits on disturbed, sandy, or bare clayey soil and has not been identified from EcM roots. The paraphyletic *Gyromitra* and *Discina* sometimes act as weak parasites and fail to form EcM in synthesis trials (Godbout and Fortin 1985; Egger and Paden 1986). Similarly, *Pseudaleuria* did not form EcM in synthesis trials involving several potential host trees (Lusk 1987). *Morchella* spp. may associate with plant roots as weak, probably facultative biotrophs. For example, *M. rotunda* co-occurs with an unknown basidiomycete EcM fungus on suberized long roots of *P. abies* (Buscot and Kottke 1990), the arbuscular mycorrhizal *Fraxinus excelsior* and various other plants (Wipf 1997 as cited in Dahlström et al. 2000). Dahlström et al. (2000) observed an ectendomycorrhiza-like structure with a patchy

mantle, poorly developed Hartig net and some intracellular colonization in pure culture synthesis trials between *Morchella* spp. and Pinaceae. In contrast, there was no evidence for EcM relationships in synthesis experiments involving *M. conica* (Godbout and Fortin 1985), *M. elata* (Warcup 1990a), or *M. esculenta* (Yamada and Katsuya 1995).

Boudiera tracheia (sensu Warcup 1990a) forms a thin and patchy mantle on *Melaleuca uncinata*. Since *B. tracheia* was originally described as a European species that fruits on damp soil, it is likely that Warcup's specimens of "*B. tracheia*" actually represent a morphologically similar *Ruhlandiella* species. Similarly, *Muciturbo reticulatus* and *Plicaria alveolata* probably represent *Ruhlandiella* spp. (Dissing and Korf 1980; Hansen et al. 2005). Species retained in *Plicaria* (*s. stricto*) did not form EcM in aseptic synthesis trials (Warcup 1990a).

Sordariales

The ITS sequences of the /sordariales lineage from *Salix* spp. in USA, Japan, and Slovenia (Trowbridge and Jumpponen 2004; Nara 2006; INSD unpublished) are closely related to each other. More distant members of the /sordariales lineage are found from *Vateriopsis* (Dipterocarpaceae) in Seychelles (Tedersoo et al. 2007b) and *Nothofagus* in Australia (Tedersoo et al. 2009a).

Brundrett et al. (2005) reported EcM formation of ascomycetes producing either tiny cleistothecia or muriform conidia that are unknown in Helotiales and Pezizales but common in other ascomycetes such as Sordariomycetes. Based on the illustrations, it is impossible to judge the taxonomic similarity between these taxa, but these reports suggest that the importance and diversity of ascomycete EcM may be currently underestimated. Integration of molecular and morphological–anatomical techniques in studies of EcM roots will likely detect more of these divergent EcM Ascomycota and reduce the possibility of misinterpretation of the secondary root endophytic fungi that is common in EcM literature.

Agaricales

The panglobal /amanita lineage is only partly EcM. Its basal members of section *Lepidella* are saprobes in various ecosystems (B.E. Wolfe and A. Pringle unpublished). *Amarrendia s. stricto* and *Torrendia* are small more or less hypogeous and sequestrate taxa nested within *Amanita*.

Catathelasma is a genus with just a few rare species restricted to coniferous forests of the Northern Hemisphere. Its rarity may account for the apparent lack of molecular detection below ground. *Catathelasma imperiale* forms poorly developed EcM-like structures with a bi-seriate Hartig

net in pure culture synthesis trials with *Pinus* sp. Incomplete and slow development of EcM is attributed to the apparent late-successional ecological strategy (Hutchison 1992).

The globally distributed /cortinari lineages comprise multiple mono- or paraphyletic stipitate and sequestrate genera nested within *Cortinarius* (Peintner et al. 2001, 2002). While /cortinari is one of the most species-rich taxa in Holarctic and Austral realms, only a few species are known from tropical forests dominated by Caesalpinaceae and Dipterocarpaceae.

The /descolea lineage is most common in the Austral *Nothofagus* area (Australia, Southern South America, New Zealand, New Guinea), with a single species found in temperate Asia. The sequestrate *Descomyces*, *Setcheliogaster*, and *Timgrovea* have evolved from stipitate taxa.

Entoloma s. lato is a huge panglobal genus. EcM members, i.e., the /entoloma lineage, comprise a minor part of the genus, viz. sections *Entoloma* and *Rhodopolia*. Sequestrate taxa, *Richoniella*, and *Rhodogaster* are most probably members of the EcM lineage, although their exact phylogenetic position and EcM habit is unconfirmed (D. L. V. Co, pers. comm. 2007). The Rosaceae-associated members of *Entoloma* (section *Nolanidea*) are considered weak, obligate parasites because of abnormal Hartig net-like structures and the destruction of the root cap region in arbuscular mycorrhizal species of Rosaceae (Agerer and Waller 1993).

The /hebeloma-alnicola lineage is distributed in all regions except Northern South America. The sequestrate *Hymenogaster* has probably evolved several times from epigeous ancestors within this group (Peintner et al. 2001).

The /hygrophorus lineage corresponds to the genus *Hygrophorus s. stricto* and is found in both Holarctic and Austral regions. Phylogenetic relationships and EcM status of the Austral species remain unknown. No sequestrate taxa are described in the /hygrophorus lineage.

The globally distributed /inocybe lineage comprises *Inocybe* and *Auritella* and includes a few sequestrate species (Matheny and Bougher 2006).

The /laccaria lineage is widespread in the Holarctic realm and Austral *Nothofagus* area. *Hydnangium* and *Podohydnangium* are nested within *Laccaria* and form sequestrate fruit-bodies (Mueller and Pine 1994).

The /paralyophyllum lineage (Moncalvo et al. 2002) comprises EcM members of the polyphyletic genus *Lyophyllum*. The saprotrophic clades of *Lyophyllum* appear closely related to *Calocybe*, *Termitomyces*, and other genera (Hofstetter et al. 2002). The EcM status of *Lyophyllum* spp. has been debated due to polyphyly, the habitat similar to humus and litter saprobes, somewhat deviating stable isotope signatures (see above), formation of fruit-bodies in pure culture (Kawai 1997) and cellulase activities (Norkrans 1950). Nevertheless, *Lyophyllum shimeji* and *L. semitale* form EcM in pure culture (Yamada et al. 2001). In the same

study, *L. fumosum* failed to form EcM because of poor mycelium growth, whereas *L. decastes* formed a thin mantle-like structure but no Hartig net. However, synthesis of typical EcM between *L. decastes* and *Pinus* sp. was reported in Pera and Alvarez (1995). Similarly, *L. fumosum* formed well-developed EcM in pure culture synthesis trials (Norkrans 1950). The enzymatic properties and ^{15}N values suggest that the EcM habit in the /paralyophyllum lineage may be exploitative.

The /tricholoma lineage is a globally distributed EcM taxon with no known sequestrate forms.

Saprotrophic or other biotrophic taxa are commonly treated as EcM in the Agaricales (Trappe 1962). Of these non-mycorrhizal taxa, “*Chlorophyllum* (syn. *Macrolepiota*) *rhacodes*” forms well-developed pale EcM and numerous stringy rhizomorphs in pure culture synthesis with *Pinus virginiana* (Hacskeylo 1953). However, Modess (1941) was unable to establish an EcM symbiosis between *C. rhacodes* and three conifer species. Since the origin of the Hacskeylo (1953) culture is unknown, it is possible that he used a culture of another species from E. Melin’s laboratory. Despite this anomalous report, species of *Chlorophyllum*, *Macrolepiota*, and related genera are widely accepted as humus saprobes; they often grow far from EcM hosts and resemble saprotrophs in their stable isotope values (Kohzu et al. 1999; Trudell et al. 2004; Hart et al. 2006). *Clitopilus prunulus* forms a poorly developed EcM-like association with *Pinus* sp. in pure culture synthesis trials (Modess 1941) that was not supported based on other hosts (Modess 1941; Pera and Alvarez 1995) or stable isotopes (Zeller et al. 2007).

Cribbea forms sequestrate fruit-bodies often on dead wood and rDNA sequences (Lebel and Catcheside 2009) and place it in the Physalacriaceae alongside *Xerula* and *Oudemansiella*, which are saprobes or root parasites. *Lepista nuda* EcM is described from natural conditions by Fontana (1961), and EcM of *L. nuda* and *L. graveolens* were synthesized with *Picea* (Kasuya and Igarashi 1996). However, the yellow EcM and hyphae described by Kasuya and Igarashi (1996) were probably formed by a contaminant because *Lepista* species are characterized by whitish or bluish mycelium. Norkrans (1950) found no EcM formation by *L. nuda* or *L. inversa*, and both taxa had high decomposing abilities characteristic of saprobes. Stable isotopes suggest saprotrophic nutrition for *Lepista* sp. (Tedersoo et al. 2007a). Bryan and Zak (1961) reported on EcM synthesis between *Leucopaxillus albissimus* var. *piceina* and *Pinus* sp. but with poorly developed mantle and Hartig net. This taxon probably represents a *Tricholoma* sp. (Matheny et al. 2006). Stable isotopes (Kohzu et al. 1999; Hart et al. 2006) and synthesis experiments (Yamada et al. 2001) suggest that *Leucopaxillus* spp. are nonmycorrhizal. *Phaeocollybia* spp. fruit in EcM vegetation and group with EcM fungi based on stable isotope values (Trudell et al.

2004). *Phaeocollybia* spp. form pseudorhizas that extend deep into mineral soil but are attached directly to suberized long roots, suggesting a root parasitic lifestyle (Redhead and Malloch 1985). By use of PCR-RFLP, *Rhodocollybia butyracea* EcM were identified and characterized in the field (Mieczko 2004). This supports the EcM synthesis report involving *R. maculata* and *Pinus* sp. in vitro (Pera and Alvarez 1995). However, despite rapid mycelial growth, other attempts to synthesize EcM with *Rhodocollybia* spp. have failed (Yamada and Katsuya 1995), and stable isotope data suggest the saprotrophic nature of *R. butyracea* (Gebauer and Dietrich 1993; Zeller et al. 2007) and *R. maculata* (Trudell et al. 2004). Molecular tools sometimes detect *Rhodocollybia* spp. as secondary colonizers of moribund EcM root tips (L. Tedersoo unpublished). Despite contradictory evidence, we consider *Rhodocollybia* as a non-EcM, facultatively biotrophic saprobe. The sequestrate genera *Mayamontana* and *Stephanospora* are related to the resupinate *Lindtneria*, forming the family *Stephanosporaceae* (Agaricales) (Castellano et al. 2007; Larsson 2007). There is no evidence for EcM formation in these taxa, despite searching EcM root tips below the fruit-bodies of *Lindtneria* and *Stephanospora* (L. Tedersoo and M.E. Smith unpublished). The monotypic semi-hypogeous *Mayamontana*, however, is found consistently with neotropical EcM trees *Coccoloba* and *Neea* in Belize (Castellano et al. 2007). *Stephanospora* sometimes fruits in non-EcM vegetation and produces abundant mycelium in agricultural soil (Lynch and Thorn 2006).

Atheliales

Published phylogenies addressing the Atheliales are currently lacking, and the affinities of many saprotrophic and parasitic taxa remain uncertain. *Amphinema* and *Tylospora* are closely related based on morphological and molecular characters but distantly related to *Piloderma* and *Byssocorticium* (Binder and Hibbett 2006). The /amphinema-tylospora and /byssocorticium lineages are known only from the Holarctic realm, whereas /piloderma is distributed also in Australia and Africa. Atheliales lineages produce only resupinate fruit-bodies.

Boletales

Boletales is a rich order in terms of genera and ecological functions. Inclusive phylogenies have been constructed based on 28S rDNA and to a lesser extent the *atp6* locus (Kretzer and Bruns 1999; Binder and Hibbett 2006; M. Binder, pers. comm. 2008). Representative ITS sequences are not publicly unavailable for many genera of Boletales. Thus, the phylogeny of Boletales is largely unresolved and only the /austropaxillus lineage is well defined. The segregation

of the crown group of Boletales into four lineages is somewhat tentative, but multigene phylogenies generally support a monophyletic Boletineae, Sclerodermatineae, and Suillineae (Binder and Hibbett 2006). Despite the lack of resolution provided by the LSU, the distinction between the /boletus and /paxillus-gyrodon lineages is also strongly supported by *atp6* sequence data (Kretzer and Bruns 1999; Yang et al. 2006), and all five Boletales lineages are morphologically, ecologically, and biogeographically well-defined groups (Agerer 2006; Binder and Hibbett 2006). The /austropaxillus lineage is known only from the Austral realm, while /paxillus-gyrodon and /suillus-rhizopogon have Holarctic distribution. Neglecting ambiguous or anamalous reports, the entire /suillus-rhizopogon lineage appears specific to Pinaceae and individual species to different genera of Pinaceae (Molina et al. 1992). The /boletus and /pisolithus-scleroderma lineages have panglobal distribution with a likely center of diversity in tropical areas.

Cantharellales

Cantharellales includes at least five EcM lineages, all except /cantharellus being recently discovered by use of molecular tools. Fruit-bodies of the /ceratobasidium1, /ceratobasidium2, and /tulasnella lineages have not yet been discovered or taxonomically characterized. This is probably due to their rarity or to a cryptic fruiting habit. Alternatively, some of these lineages may reproduce exclusively via conidia (asexual spores) because anamorphs are abundant in the closely related saprotrophic and orchid mycorrhizal taxa. The distribution of the /ceratobasidium1, /ceratobasidium2, and /tulasnella lineages remains poorly known, but the larger /cantharellus and /clavulina lineages are globally distributed. Phylogenetic analyses suggest that the Japanese /ceratobasidium1 isolates are phylogenetically closely related to isolates from SE Asia, Africa, and Australia but distant from the European and North American /ceratobasidium2 lineage (Veldre 2009, V. Veldre unpublished). The same may be true for the European and Australian members of the /tulasnella lineage.

Gomphales

The genus *Clavariadelphus* is nonmonophyletic (Hosaka et al. 2006) comprising both EcM and saprotrophic members. EcM have been identified in the monophyletic *Clavariadelphus s. stricto* that comprises species that produce large fruit-bodies (*C. subfastigiatus*, *C. truncatus*, *C. pistillaris*, and *C. occidentalis*). Other taxa such as *C. sachalinensis* are probably non-EcM, because they fruit abundantly on dead wood and are phylogenetically more closely related to the basal, non-EcM *Ramaria* spp. (Hosaka et al. 2006; L. Tedersoo, unpublished).

The globally distributed /ramaria-gautieria lineage comprises taxa with ramarioid, clavarioid, and sequestrate fruit-bodies, but the latter form a minority.

Hymenochaetales

The core Hymenochaetales comprises a diverse group of white rot polypores. The globally distributed /coltricia lineage has been long considered saprotrophic despite some early reports on EcM formation in *Coltricia perennis* and *Coltricia cinnamomea*, but is confirmed as EcM (Table 1).

There is no evidence for EcM formation in *Tubulicrinis* (Hymenochaetales) and *Trechispora* (Trechisporales). ITS sequences from the latter are available in INSD, but these are recovered from mycelial mats rather than EcM root tips.

Hysterangiales

The globally distributed /hysterangium lineage comprises only sequestrate taxa. Many of the subclades and genera have Australian or Austral distribution (Hosaka et al. 2008) and lack available ITS sequences in INSD. Hysterangiales and Gomphales are closely related to non-EcM Phallales and Geastrales, forming a subclass Phallomycetidae (Hosaka et al. 2006). The genus *Geastrum* has often been suggested to be EcM. In particular, *Geastrum fimbriatum* is suggested to form a thin mantle and a poorly developed Hartig net (Agerer and Beenken 1998a). Noack (1889) established mycelial connection between fruit-bodies of *G. fimbriatum* and *G. coronatum* with EcM root tips of *Pinus* and *Abies* sp., but the illustrated mycorrhiza belongs to *Tuber* based on the characteristic cystidia. There are no such cystidia in the description of a biotrophic interaction in Agerer and Beenken (1998a). Kasuya and Igarashi (1996) synthesized a morphologically similar association between *G. mirabile* and *Picea* with no Hartig net, whereas Modess (1941) failed to synthesize EcM of *G. minus* with *Picea* and *Pinus*. *Geastrum* spp. are sometimes reported in tropical forests where no EcM trees or other EcM fungi are found. Mycelium of *Geastrum* sp. is abundant in agricultural soil (Lynch and Thorn 2006), suggesting a facultatively biotrophic lifestyle.

Russulales

The /albatrellus lineage is widely distributed predominantly with coniferous hosts in the Holarctic realm, with a few additional reports from Africa and Australia. The lineage contains stipitate, sequestrate, and resupinate fruit-body types. A few distantly related, saprotrophic *Albatrellus* spp. are placed in the Polyporales but should be transferred to a new genus in the Polyporales (Binder and Hibbett 2002).

The /russula-lactarius lineage is globally distributed and includes numerous sequestrate taxa that have independently evolved from epigeous ancestors (Peter et al. 2001).

Sebacinales

Based on fruit-body taxonomy, Sebacinales has been considered a taxon of low species richness and marginal importance. Although the EcM status of *Serendipita* (syn. *Sebacina*) *vermifera* was confirmed more than 20 years ago (Warcup 1988), recent molecular studies have highlighted the diversity of Sebacinales and its mycorrhizal associations (Weiß et al. 2004). The EcM-forming, globally distributed, yet unculturable /sebacina lineage forms only a part of the Sebacinales clade A (sensu Weiß et al. 2004). The genus *Tremelloscypha* is also probably EcM since many root tip DNA sequences fall close to *T. gelatinosa* (Weiß et al. 2004). Here, we consider *Craterocolla* and *Efibulobasidium*, the sister taxa of /sebacina, saprotrophic because they produce tremelloid fruit-bodies on herbaceous stems or standing sound wood. The range of *Efibulobasidium* includes Pacific coral islands (Wells 1975) that host no EcM trees besides *Pisonia grandis*. The /sebacina lineage is phylogenetically unrelated to the readily culturable *Serendipita vermifera* (clade B—Weiß et al. 2004). Recent molecular sequence data from EcM, orchid, and arbutoid mycorrhizal roots revealed members of Sebacinales clade B. These isolates form a monophyletic /serendipita lineage that is a sister group to the root endophytic, saprotrophic, ericoid, and orchid mycorrhizal clades (Ryberg et al. 2009; L. Tedersoo unpublished). We believe that the EcM-forming isolates of Warcup (1988) belong to this lineage.

Thelephorales

Based on 28S rDNA sequence data, the paraphyletic *Tomentella* and *Thelephora* form a distinct, well-supported /tomentella-thelephora lineage that is globally distributed (U. Kõljalg, unpublished). It includes also *Riessia radicola* and probably *Riessiella* spp. (see discussion in Tedersoo et al. 2007b). These taxa were erroneously concluded to be anamorphs of *Tomentella* (Rinaldi et al. 2008:33), but in fact represent capitate cystidia on the surface of EcM mantle. Other species of *Riessia* are probably phylogenetically distantly related anamorphic states of saprobes (e.g., Noetzi et al. 2008). The /hydnum-sarcodon, /tomentellopsis, and /phellodon-bankera lineages are widely distributed, whereas the /pseudotomentella lineage is found only in the Holarctic realm, predominately with Pinaceae. The phylogenetic placement of *Boletopsis* remains unclear. The thelephoralean EcM lineages are interspersed with rare and species-poor non-EcM genera that are occasionally found fruiting

in living tree canopies (e.g., *Lenzitopsis*) or decaying wood in tropical forests with no EcM hosts nearby. Attempts to find EcM of the putatively nonmycorrhizal *Amaurodon* have consistently failed (L. Tedersoo unpublished) and some specimens fruit on tree trunks ca. 2 m above the forest floor (U. Kõljalg, pers. comm.).

Endogonales

Because no published phylogenies of Endogonales are available, the taxonomic affiliations of the EcM lineages /endogone and /densospora remain unknown. Both *Endogone* and *Densospora* include non-EcM taxa and the recently described genera *Youngiomyces* and *Peridiospora* are putative non-EcM biotrophs (Yao et al. 1995; Wu and Lin 1997).

Global distribution of EcM fungi

Biogeographic regions

On a global scale, the distribution of fungal lineages revealed three main clusters of geographic regions (Fig. 2). The northern temperate regions in Europe, America, and Asia are strongly related and support the greatest richness of fungal lineages, with all but /austropaxillus and /descolea present in all regions. In the Northern Hemisphere, the /descolea lineage occurs only in Temperate Asia, where it has probably recently extended its range from Australia via the Sunda Islands of Indonesia (Wallacea; Horak 1983). All Holarctic regions harbor Pinaceae, probably the oldest extant EcM host (LePage 2003), as well as Arbutoideae, Betulaceae, Fagaceae, Salicaceae, and Cistaceae (Table 5). Most of these plant groups also occur in SE Asia.

The three Austral regions (Australia, New Zealand, and Southern South America) formed a second cluster, sharing the /descolea and /austropaxillus lineages but entirely lacking 11 lineages and having representation of 18 other lineages only in some regions (Fig. 2). *Nothofagus* is the only EcM host in Southern South America and occurs in other Austral regions as well. Hosts characteristic of Australia, such as Casuarinaceae, Leptospermoideae (incl. *Eucalyptus*), Bossiidae, Pomaderreae, and *Acacia* are absent from or recently migrated to other Austral or tropical regions. Similarly, the dominant EcM families of the Holarctic (Pinaceae, Betulaceae, Fagaceae) and tropical (Caesalpiniaceae and Dipterocarpaceae) realms are lacking in the Austral regions (except the genus *Intsia* of the Caesalpiniaceae in Queensland). Despite the very low overlap in EcM plant hosts, all the Austral fungal lineages with the two exceptions occur widely in the Northern Hemisphere.

The neo- and paleotropical regions formed the third cluster. These regions differ widely in the occurrence of

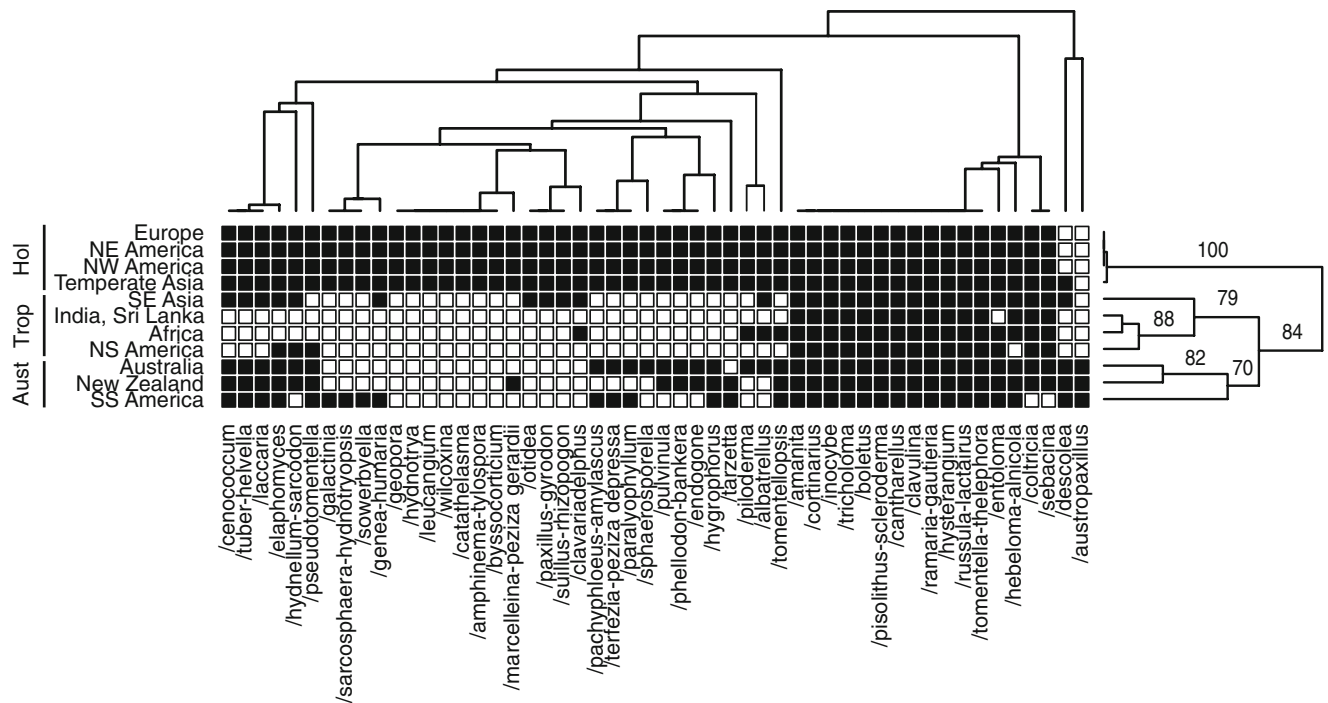


Fig. 2 Reciprocal cluster analysis of EcM fungal lineages and the 11 biogeographic regions. UPGMA-based bootstrap values are shown for clusters of regions. *Closed squares* indicate the presence of EcM

fungal lineages in particular regions. *Hol* Holarctic realm; *Trop* tropical realm; *Aust* Austral realm

Table 5 Distribution of major host taxa in biogeographic realms

| Host taxon | Holarctic | | | | Tropical | | | | Austral | | | |
|----------------------------|-----------|------------|------------|-----------------|----------|-------------------|--------|------------------|------------------|------------------|-----------|-------------|
| | Europe | NE America | NW America | Tempe-rate Asia | SE Asia | India & Sri Lanka | Africa | Northern America | Southern America | Southern America | Australia | New Zealand |
| Arbutioideae | x | x | x | x | x | | | (x)* | | | | |
| Betulaceae | x | x | x | x | x | | | | | (x)* | | |
| Fagaceae | x | x | x | x | x | | | (x)* | | | | |
| Pinaceae | x | x | x | x | x | | | (x)* | | | | |
| Salicaceae | x | x | x | x | x | | | (x)* | | (x)* | | |
| Cistaceae | x | x | x | x | | | | | | | | |
| Caesalpinioideae | | | | | (x) | (x) | x | x | | | (x) | |
| Dipterocarpaceae | | | | | x | x | x | x | | | | |
| Uapacaceae | | | | | | | x | | | | | |
| Pisoniae | | | | | | | | x | | | (x) | |
| <i>Coccoloba</i> | | | | | | | | x | | | | |
| Nothofagaceae | | | | | | | | | | x | | x |
| <i>Acacia (s. stricto)</i> | | | | | | | | | | | x | |
| Bossiaeeae | | | | | | | | | | | x | |
| Casuarinaceae | | | | | (x) | | | | | | x | |
| Leptospermoideae | | | | | (x) | | | | | | x | x |
| Pomaderreae | | | | | | | | | | | x | (x) |

X indicates presence of a taxon. Parentheses denote recent spread or low abundance. Asterisks indicate taxa that are not considered in comparisons of fungal lineage distribution

EcM fungal and plant lineages. In all tropical regions, the plant families Dipterocarpaceae and Caesalpiniaceae are present. Southeast Asia has the highest diversity of EcM host lineages because this region shares the Arbutioideae, Betulaceae, Fagaceae, Pinaceae, and Salicaceae with the north temperate regions and Leptospermoideae with Australia. The Austral and tropical regions were linked due to the shared absence of many fungal lineages that were present in the Holarctic realm.

The grouping of the austral regions (Australia, Southern South America, and New Zealand) on the basis of their EcM lineages is in agreement with geological, plant, and animal area cladograms that link Gondwanan regions (Sanmartin and Ronquist 2004). However, methodological differences and simplicity of the present analysis, which involved no phylogenetic data, caution against further interpretation of biogeographic relationships.

Distribution of fungal lineages

Based on specimen records in the 11 biogeographic regions, the EcM fungal lineages were clustered into three broad groups. The */descolea* and */austropaxillus* lineages formed a cluster characterized by distribution and highest diversity in Austral regions. Austral realm was suggested as a center of origin for the */descolea* lineage (Horak 1983). The second cluster was formed by 16 lineages of globally distributed EcM fungi that have been reported from at least 10 out of 11 regions. These panglobal lineages, such as */tomentella-thelephora* and */russula-lactarius*, are the most species-rich and abundant and also associate with all major plant host taxa in a variety of ecosystems (Buyck et al. 2008; U. Kõljalg et al. unpublished). Interestingly, none of the EcM fungal lineages are restricted to tropical regions, a pattern that is common in many animal and plant taxa, including EcM plant hosts (Sanmartin and Ronquist 2004).

The third cluster of fungal lineages consists of a subcluster of */piloderma* and */albatrellus* (linked by their co-occurrence in Australia and Africa) and also two main subclusters comprising taxa with either Holarctic distribution (many pezizalean lineages) or disjunct Holarctic–Austral distribution (e.g., */cenococcum*, */laccaria*). The Holarctic lineages occur in regions that coincide with the natural habitat of Pinaceae. Some lineages, such as */suillus-rhizopogon*, are restricted to this host family, hence, explaining their geographic distribution, but most Holarctic lineages have a broad host range. The disjunct Holarctic–Austral distribution matches the distribution of Fagales, which comprises EcM Fagaceae, Betulaceae, and Corylaceae in the Holarctic realm, Nothofagaceae in the Austral realm, and Casuarinaceae in Australia.

A major shortfall of our analysis is lack of fine detail about the correlation between fungal lineages, biogeograph-

ic regions, and associated host plants. The main reason for this is that data are limited about the vegetation where most fungal specimens were collected. Even in cases where the plants and habitat are well documented, it is often impossible to accurately determine which EcM plant is the host of a given EcM fungus without use of molecular tools (but see den Bakker et al. 2004). Missing distribution data (particularly false negatives) may further bias the results, although ongoing below ground EcM community surveys (L. Tedersoo and coworkers unpublished data from three tropical regions) generally agree with the present data on fruit-body distribution. Nevertheless, the broad pattern of distribution of the main EcM fungal lineages demonstrates certain biogeographic trends among the lineages and regions that can be further tested by use of phylogeographic analyses. Our data also highlight areas where further collection of distributional data on EcM lineages is needed, such as to confirm the absence of */hebeloma-anicola* in Northern South America and */coltricia* and */sebacina* from Southern South America. Macrofungal surveys should include various fruit-body types. Unfortunately, epigeous, hypogeous, and resupinate taxa are rarely collected at the same site (Tedersoo et al. 2006b), thus biasing the biogeographical datasets and contributing to the myth of contrasting above- and belowground views at the fungal community level (Smith et al. 2007).

Substantial biogeographic information of EcM fungi is contained within EcM lineages (Martin et al. 2002; Hosaka et al. 2008; Jeandroz et al. 2008; Matheny et al. 2009). However, caution is needed when interpreting distribution patterns on a species or genus level, because several morphologically well-defined species or genera, such as *Rozites*, are polyphyletic based on molecular data (Peintner et al. 2002). Thus, selection of a suitable monophyletic group (i.e., the entire */cortinarius* lineage in this case) is critical for addressing biogeographic and phylogenetic hypotheses.

Conclusions

EcM lifestyle has evolved multiple times independently from humus and wood saprotrophic ancestors in 16 orders of fungi. Several monophyletic EcM lineages cannot be, thus far related to any fruit-bodies due to the lack of sequenced collections (Brock et al. 2009). The presence of many uncharacterized lineages suggests that Ascomycota and basal groups of Agaricomycetes may reveal additional EcM taxa solely based on DNA sequence data. However, morphological studies and physiological experiments should also be performed to avoid considering ubiquitous root endophytes and saprobes as mycorrhizal (Brundrett 2009).

The Holarctic realm provides a habitat for the largest number of EcM lineages, but this can only be partly

ascribed to the high intensity of mycological exploration relative to the Austral and tropical regions. While tropical regions have low lineage-level diversity, they are of great importance in the evolution of EcM symbiosis for some key fungal lineages (Buyck et al. 2008; Matheny et al. 2009). Further taxonomic and belowground biodiversity studies should focus on recording host data and providing sequence data from at least the ITS region and partial 28S rDNA (Smith et al. 2007). Lineage-level phylogenetic analyses coupled with molecular clock dating (Matheny et al. 2009) and community-level belowground studies offer promising opportunities to improve our understanding on the biogeography and evolution of EcM fungi.

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