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Review

Lineages of ectomycorrhizal fungi revisited: Foraging strategies and novel lineages revealed by sequences from belowground[☆]



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ABSTRACT

In the fungal kingdom, the ectomycorrhizal (EcM) symbiosis has evolved independently in multiple groups that are referred to as lineages. A growing number of molecular studies in the fields of mycology, ecology, soil science, and microbiology generate vast amounts of sequence data from fungi in their natural habitats, particularly from soil and roots. However, as the number and diversity of sequences has increased, it has become increasingly difficult to accurately identify the fungal species in these samples and to determine their trophic modes. In particular, there has been significant controversy regarding which fungal groups form ectomycorrhizas, the morphological “exploration types” that these fungi form on roots, and the ecological strategies that they use to obtain nutrients. To address this problem, we have synthesized the phylogenetic and taxonomic breadth of EcM fungi by using the wealth of accumulated sequence data. We also compile available information about exploration types of 143 genera of EcM fungi (including 67 new reports) that can be tentatively used to help infer the ecological strategies of different fungal groups. Phylogenetic analyses of ribosomal DNA ITS and LSU sequences enabled us to recognize 20 novel lineages of EcM fungi. Most of these are rare and have a limited distribution. Five new lineages occur exclusively in tropical and subtropical habitats. Altogether 46 fungal genera were added to the list of EcM fungal taxa and we anticipate that this number will continue to grow rapidly as taxonomic works segregate species-rich genera into smaller, monophyletic units. Three genera were removed from the list of EcM groups due to refined taxonomic and phylogenetic information. In all, we suggest that EcM symbiosis has arisen independently in 78–82 fungal lineages that comprise 251–256 genera. The EcM fungal diversity of tropical and southern temperate ecosystems remains significantly understudied and we expect that these regions are most likely to reveal additional EcM taxa.

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1. Introduction

The ectomycorrhizal (EcM) symbiosis has evolved multiple times both in plants and fungi. The fungal kingdom includes at least 66 independent lineages of EcM fungi, mostly members of the Basidiomycota and Ascomycota (Tedersoo et al., 2010). In the past it has been challenging to unambiguously determine whether some fungal groups are ectomycorrhizal or not because of limited or ambiguous evidence and alternative interpretations (Rinaldi et al., 2008; Tedersoo et al., 2010; Comandini et al., 2012; Ryberg and Matheny, 2012). However, community studies of ectomycorrhizal fungi have become more sophisticated over the past two decades and a variety of techniques have been used to determine EcM status and to delimit groups of EcM taxa, including experimental synthesis trials, field observations combining anatomical and molecular techniques, stable nitrogen and carbon isotope signatures, and phylogenetic analyses. Unfortunately, many EcM fungal taxa detected as environmental sequences do not match sequences of fruit-body vouchers or pure cultures (Tedersoo et al., 2010). Although reference sequences from fruit-bodies are accumulating at an exponential rate, many sequences from EcM root tips remain unmatched to their sexual stages. This suggests that much of the EcM fungal diversity is indeed cryptic. Nevertheless, many described species and even genera lack publicly available sequence data (Tedersoo et al., 2010) and this underscores the need to produce DNA sequences from identified herbarium specimens (Brock et al., 2009).

The rapidly growing DNA sequence data in public repositories, in conjunction with recently developed sequence annotation tools (e.g. PlutoF workbench – Abarenkov et al., 2010; Tedersoo et al., 2011a), provide an invaluable source of metadata about the host plants, isolation sources, and geographic origin of EcM fungal isolates. By using the data in public sequence databases, Hynson et al. (2013), Tedersoo et al. (2013a) and Veldre et al. (2013) recently detected additional putative EcM lineages within the Serendipitaceae (Sebacinales group B), Pyronemataceae and Ceratobasidiaceae. These fungal lineages were previously considered root endophytes, saprotrophs or parasites. The limited number of sequences from these lineages suggests that they are uncommon in EcM fungal communities or were considered root contaminants in the original studies (e.g. Oberwinkler et al., 2013).

It is important to understand which fungal taxa are EcM and which are not. EcM fungi play fundamentally different roles in forest communities and in ecosystems compared to other functional guilds such as fungal root endophytes and decomposers. For example, EcM fungi are uniquely adapted to facilitate mineral nutrition of plants and to distribute recent photosynthates into the mycorrhizosphere soil (Buee et al., 2009). Mycorrhizal fungi have mostly lost the powerful enzymes used for attacking plant cell walls and degrading organic compounds such as lignin (Eastwood et al., 2011). Furthermore, since EcM fungi are often the most abundant organisms in forest soils, it is important to understand their ecology for the purposes of management and conservation. This is particularly relevant for taxa in the Ceratobasidiaceae, since this group includes beneficial orchid and

ectomycorrhizal symbionts as well as devastating fungal plant pathogens (Veldre et al., 2013). Several lineages within Pezizales are associated with tree roots in truffières where they compete for space and resources with the valuable truffle “crop” species (Bonito et al., 2011, 2012; Rubini et al., 2011). However, most species of Pezizales are saprotrophic and a few are pathogenic (Hansen and Pfister, 2006). The rapid shift from root tip-based studies to soil fungal community studies necessitates discriminating between mycorrhizal and non-mycorrhizal fungi. Molecular studies of soil increasingly use sophisticated second and third generation sequencing technologies to generate millions of reads. In contrast to EcM roots and fruit-bodies that can be stored as vouchers and morphologically examined in the future, soil-based studies cannot provide morphological or ultrastructural information to infer ecological interactions. These high-throughput sequencing methods are an easy and cost-effective way to study mycorrhizal ecology *in situ* but currently our ability to adequately identify fungal DNA sequences and interpret the ecological role of these species is lagging behind our ability to produce sequence data. The phylogenetic and functional breadth of fungi in soil and other complex substrates poses a great challenge for taxonomic identification as well as functional characterization. Because of the large volume of sequence data and the large number of fungal taxa involved in the EcM symbiosis, researchers would benefit from a well-annotated reference database from which they can automatically extract information on ecology and taxonomy of fungal taxa (Köljalg et al., 2013).

Within EcM fungi, there are major differences in ecological strategies of dispersal (Ishida et al., 2008), metabolic activity (Trocha et al., 2010) and in relative benefits to plant hosts (van der Heijden and Kuyper, 2003; Nara, 2006). This is at least partly ascribed to differences in the relative carbon cost to plants and efficiency in enzymatic access to organically bound nutrients, nutrient uptake and nutrient transfer (Courty et al., 2010). Species of EcM fungi differ strongly in their potential enzymatic capacity, which is a function of both the substrate and climatic conditions (Courty et al., 2010). Evidence suggests that key enzyme functions are highly variable between (and within) EcM lineages and are partly predictable based on phylogenetic relationships among the EcM fungi (Tedersoo et al., 2012b). Not surprisingly, the abundance and morphology of the extraradical mycelial system is the single most important variable in determining enzymatic capacity (Tedersoo et al., 2012b). The presence and characteristics of extraradical hyphae and rhizomorphs serve as proxies for foraging strategies referred to as “exploration types” (Agerer, 2001, 2006). Species of medium-distance and long-distance exploration types tend to exhibit similar responses to climatic gradients (Ostonen et al., 2011), N fertilization or pollution (Lilleskov et al., 2011; Kjøller et al., 2012) and carbon influx (Markkola et al., 2004). Most fungi with long-distance exploration strategies appear specialized in N uptake from organic sources and they apparently expend significant carbon resources on rhizomorphs so they appear to lose their relative benefits or competitive abilities in disturbed systems (Lilleskov et al., 2011). In contrast, smooth and short-distance exploration types are more frequently detected in

mineral soils and these types are more resilient in response to disturbance, apparently because they can easily regenerate their reduced system of extraradical hyphae. So far, in-depth studies of EcM morphology and examination of subterranean foraging strategies cover only the most common genera and species (reviewed in Agerer, 2006). Based on these studies it appears that EcM morphology and exploration types are mostly phylogenetically conserved (Eberhardt, 2002; Agerer, 2006), but that there are variations in foraging strategy within the largest and most well studied genera (e.g. *Russula*, *Lactarius* and *Tomentella*). This information is increasingly referred to in fruit body, root tip and soil mycelium-based community analyses (e.g. Deslippe et al., 2011; Ostonen et al., 2011), but most studies do not determine these types *in situ*.

We have three main purposes in this review. First, we gather and interpret information about cryptic EcM lineages from environmental sequences in public databases and we give these lineages formal names and designated reference sequences. Second, we revise the lineage concept in several groups of EcM fungi based on newly available taxonomic and ecological information. Third, we compile existing published and unpublished information about the exploration types of all EcM fungal genera by lineages. Information about all of the EcM lineages detailed in this paper and by Tedersoo et al. (2010) are provided in Table S1 and regularly updated in the UNITE homepage (<http://unite.ut.ee/EcMlineages.php>).

2. Methods

We searched the fungal ITS sequence data deposited in International Nucleotide Sequence Database consortium (INSDc) and UNITE (as of 01.12.2012) using the PlutoF workbench, an online tool that allows users to permanently annotate sequence quality and metadata (Abarenkov et al., 2010). We updated the metadata on EcM fungi (source of isolation, host or substrate, and geographical origin) in PlutoF by searching in the published studies or directly consulting the authors of the studies. We primarily focused on sequences with the term “ectomycorrhiza” listed as the “isolation source” in PlutoF. All of the sequences with this designation were assigned to EcM fungal lineages or given a status “non-ectomycorrhizal” or “uncertain” based on sequence alignments and phylogenetic analyses following the protocols of Tedersoo et al. (2011a). We also consulted recent publications to evaluate the opinion of other authors on previously unrecognized EcM taxa. We downloaded sequences and associated metadata for all these EcM groups and their non-EcM relatives (out-group sequences) as determined by blastN searches against INSDc and UNITE. We used multiple outgroup taxa when possible, because this improved our ability to evaluate the EcM status and monophyly of the ingroup taxa. All of the analyses used ITS rDNA alignments but in several cases we were also able to use the flanking LSU alignments in order to enhance the phylogenetic signal. In one group of EcM-associated Agaricomycetes (/agaricomycetes1), LSU sequences were used separately to determine their broad placement among Basidiomycota. Briefly, all downloaded sequences were aligned with MAFFT 7 (Katoh and Strandley, 2013), trimmed and manually corrected in SeaView 4 (Gouy

et al., 2010), and subjected to RaXML Maximum Likelihood analyses with the GTR + G + I evolutionary model and 1000 fast bootstrap replicates (Stamatakis et al., 2008). We used a series of Fisher’s Exact tests to investigate the null hypothesis that sequences derived from EcM root tips are non-randomly distributed in the target lineage and its sister groups. We anticipate that *a posteriori* selection of the ingroup and outgroup, presence of redundant sequences (i.e. similar sequences from the same study) and multiple testing may introduce biases to these results.

We evaluated all EcM-associated sequences and mycorrhizal literature published since our previous review (Tedersoo et al., 2010) in order to determine EcM fungal lineages that may be present in the database but have not been formally recognized. In order to be considered EcM symbionts, a fungal lineage had to meet at least one of the three following criteria: 1) the EcM-derived sequences form a well-supported monophyletic clade that includes all or mostly EcM fungal sequences and does not include sequences from non-EcM habitats (e.g. sequences from roots of non-EcM plants, agricultural soil, etc.); 2) EcM root tip vouchers (obtained directly from the study authors) exhibited typical EcM morphology and the morphological features were both consistent among different vouchers and also consistent with the phylogenetic position of the fungal lineage (cf. Agerer, 2006); and 3) a phylogenetic test statistic indicating that there is a greater probability of association with EcM root tips in the ingroup taxa as compared to outgroup taxa.

To determine exploration types of fungi, we relied on an extensive online database about morphological and anatomical descriptions of EcM at www.deemy.de (see also Agerer, 2006). For groups for which no exploration type data are available, we studied the publications that included brief EcM descriptions or directly contacted study authors to obtain additional information on EcM morphology. Lastly, we used light microscopy to re-analyze the EcM morphology of vouchered EcM root tips from our own community studies.

3. Novel lineages of ectomycorrhizal fungi

Based on ITS sequence data, together with updated metadata and findings from previous studies, we identified 20 previously unrecognized EcM lineages (11 in Basidiomycota, 7 in Ascomycota and 2 in Zygomycota) (Table 1). Eight lineages are derived from separating previously described lineages into two groups in light of accumulated sequence and phylogenetic information. We also briefly describe what is known about the EcM exploration types of these new lineages. Information about the exploration types of all EcM lineages and genera are given in Table S1.

Basidiomycota

The /agaricales1 lineage is known from fruit body collections (representative specimen TH9235; INSDc accession KC155374) and associated root tips from *Dicymbium jenmanii* (under the same accession; Smith et al., 2013a) and *Dicymbium cymbosum* (M.E. Smith and T.W. Henkel, unpublished) from Guyana. The ITS region of this group is short compared with

Table 1 – Information about the newly described EcM lineages

Lineage	Number of sequences in UNITE (as of 01.05.2013)	Representative sequence in INSDc or UNITE	P-value from Fisher's exact test (total n)
/agaricales1	1	KC155374	nd
/agaricomycetes1	8	UDB008409	0.003 (16)
/atheliales1	10	UDB014265	nd
/atheliales2	10	JN168682	0.015 (12)
/boletopsis	23	UDB016630	nd
/hydropus	4	JN168774	0.071 (8)
/serendipita1	66	UDB002608	<0.001 (153)
/serendipita2	21	EU909214	<0.001 (43)
/sordariales1	41	UDB017246	<0.001 (50)
/sordariales2	33	UDB008982	<0.001 (42)
/tulasnella1	53	AY192445	nd
/tulasnella2	15	UDB002679	nd
/xenasmatella	10	JN168733	<0.001 (24)
/aleurina	33	KC905032	nd
/pustularia	52	EU649088	nd
/rhodoscypha	2	FJ236854	nd
/pyronemataceae1	11	JN569352	<0.001 (31)
/pyronemataceae2	3	AY702741	0.012 (9)
/endogone1	1	AY977045	nd
/endogone2	2	UDB002714	nd

most other species of Agaricales (ITS1: 111 bp; ITS2: 149 bp), which may partly explain why this taxon has no close matches in the INSDc and UNITE databases. Nuclear and mitochondrial LSU sequences and nuclear SSU sequences indicate that this fungus has evolutionary affinities with pink-spored or white-spored Agaricales, but it is distinct from any previously recognized EcM lineage. This fungus forms dense clusters of white ectomycorrhizas of the medium-distance fringe exploration type beneath fruit-bodies in sandy soils (see Fig 4 of Smith et al., 2013a).

The /agaricomycetes1 lineage comprises a monophyletic group of eight sequences (BS = 70) that were obtained from healthy EcM root tips. This lineage is split into two strongly supported clades (BS = 100; Fig 1a), a Southern temperate group (Horton et al., 2013; Nouhra et al., 2013) and a Northern temperate group (Bergemann and Garbelotto, 2006; Ishida et al., 2007). Both the ingroup and its sister clade form a deep branch among the Agaricomycetes and cannot be placed into any of the currently recognized orders (Fig 1b). We have examined four Argentinean EcM root tip vouchers that represent two distinct species. Both species exhibit short-distance exploration types with narrow, thin-walled hyphae and an EcM mantle anatomy that is intermediate between the pseudoparenchymatous and plectenchymatous types. One of the species has long, unicellular, needle-like cystidia, while the other species lacks cystidia.

The /atheliales1 lineage represents a monophyletic group (BS = 96) of tropical EcM root tip isolates and unidentified fruit body specimens. Phylogenetic analysis was unable to resolve a sister group (Fig 2). An unpublished sequence from a fruit body collected in a Cuban *Coccoloba uvifera* stand and an EcM isolate from dry dipterocarp forest in Thailand (Phosri et al., 2012) are relatively similar and they form a monophyletic clade (BP = 100) that is basal to the rest of the lineage. Other sequences in this group are derived from EcM roots of Dipterocarpaceae in Malaysia (Peay et al., 2010), India (L. Tedersoo

and M. Bahram, unpublished), Cameroon, Gabon and Madagascar (Tedersoo et al., 2011b). In Indian and African sites, members of the /atheliales1 EcM lineage were locally abundant. Species in this fungal lineage form EcM of a medium-distance mat exploration type characterized by abundant mycelium, rhizomorphs and binding of soil

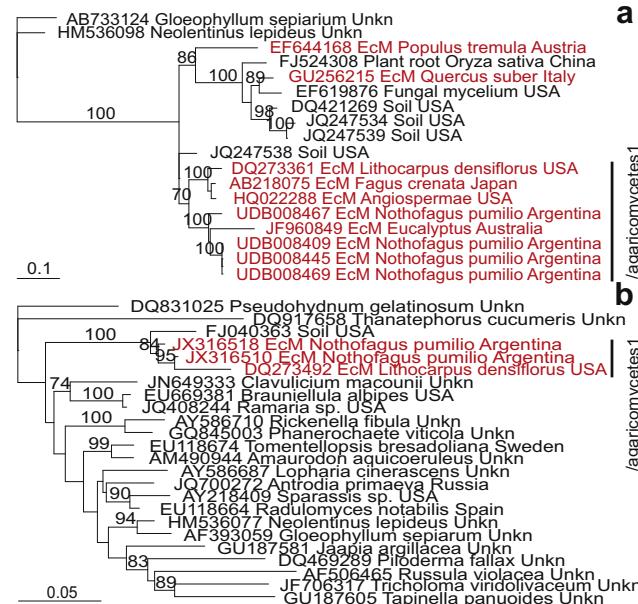


Fig 1 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of sequences in the /agaricomycetes1 lineage based on a) ITS sequences; and b) LSU sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

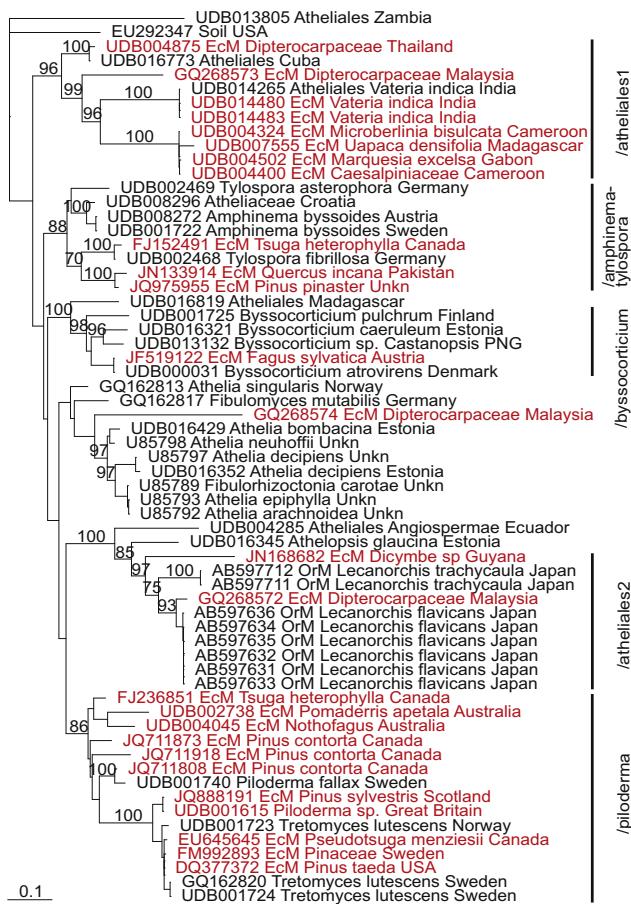


Fig 2 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of sequences in the Atheliales based on combined ITS and LSU sequences. The /piloderma, /amphinema-tylospora and /byssocorticium lineages are represented by a few divergent sequences for illustration purposes. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

particles. Taxa in this lineage were found to exhibit strong leucine aminopeptidase enzyme activity, whereas members of other EcM lineages from the same site did not (Tedesco et al., 2012b).

The /atheliales2 lineage constitutes a monophyletic group (BS = 97) that has been recovered only from EcM root tips and the roots of orchids in tropical and subtropical ecosystems. An unidentified Atheliales sp. from Ecuador (BP = 100) and the non-EcM taxon *Athelopsis glaucina* from Estonia (BP = 85) form successive sister groups to this EcM lineage (Fig 2). An isolate from a *Dicymybe* root tip (Smith et al., 2011) forms a basal group within the /atheliales2 lineage (BP = 97). Another EcM root tip from a Dipterocarpaceae host (Peay et al., 2010) is nested within uncultured isolates from non-photosynthetic orchids (*Lecanorchis* spp.) from Shikoku, a subtropical island of Japan (Okayama et al., 2012). We consider the orchid association to be strongly indicative of EcM habit since *Lecanorchis* spp. are mycoheterotrophic and their sister taxa

associate with well-known EcM fungi in *Quercus-Castanopsis* forests (Okayama et al., 2012). The /atheliales1 and /atheliales2 lineages are phylogenetically distinct from the previously known EcM lineages within Atheliales (e.g. /piloderma, /amphinema-tylospora and /byssocorticium), but the relative positions of these different groups within the order remain unclear.

The /boletopsis lineage is erected in this study based on sequences of *Boletopsis* fruit-bodies and mycorrhizas that form a strongly supported monophyletic group with no close relatives (Cooper and Leonard, 2012; U. Köljalg et al., unpublished). *Boletopsis* is well-known for its conspicuous fruit-bodies with a poroid hymenium but this group has been recovered only twice in EcM community studies (Izzo et al., 2005; Bergemann and Garbelotto, 2006) suggesting that this lineage is rare on EcM roots. This lineage is distributed in the temperate and boreal zone of the Northern hemisphere as well as in *Nothofagus* forests in New Zealand. It is possible that *Boletopsis nothofagi* was introduced to New Zealand from the Northern Hemisphere, but more data are needed (Cooper and Leonard, 2012).

The putative /hydropus lineage represents a small monophyletic group of sequences derived from EcM root tips in Malaysia (Peay et al., 2010) and Guyana (Smith et al., 2011), and from leaf litter in a *Dicymybe*-dominated forest in Guyana (K. McGuire, unpublished). This group is nested within the genus *Hydropus* (Agaricales) that comprises putative saprobes (Fig 3). Compared to the outgroup taxa, the association with EcM roots was not significant in the ingroup sequences (Fisher's Exact test: P = 0.071) leaving open the possibility that /hydropus lineage is a parasitic or saprotrophic taxon that invades EcM roots.

The /serendipita lineage as defined in Tedesco et al. (2010) is re-considered here based on new information. In a series of publications, Warcup (1988, 1990b) suggested that certain strains of *Serendipita vermicifera* (Sebacinales clade B sensu Weiss et al., 2004) isolated from orchid roots are able to form EcM in axenic conditions. However, subsequent field and experimental studies have failed to confirm these findings in Australia and elsewhere. Notably, Warcup (1988) reported on EcM formation in arbuscular mycorrhizal herbs and EcM Myrtaceae, but the mantle was usually fragmentary and only one or two cell layers deep. This suggests that he used an overly relaxed definition for ectomycorrhizas that probably included any root endophytes and saprobes that attach to roots (Brundrett, 2009). To the best of our knowledge, the isolates Warcup considered EcM have not been sequenced (M. Weiss and P. McGee, pers. comm March, 2013). More recently, however, molecular studies have identified species of *Serendipita* from EcM root tips in temperate, boreal, and subarctic communities throughout the Northern hemisphere (Ryberg et al., 2009; Stefani et al., 2009). In northern boreal and temperate forests, fungi identified as *Serendipita* spp. are dominant on roots of *Pyrola japonica* seedlings, indicating their substantial role in both carbon and mineral nutrition of the ericoid plant (Hashimoto et al., 2012). Although these fungi also occur on adult *Pyrola rotundifolia* (Vincenot et al., 2009), Hynson et al. (2013) were the first to suggest that several *Serendipita* spp. associating with Pyroleae are actually ectomycorrhizal based on their tight clustering in phylogenetic trees. Based on full-

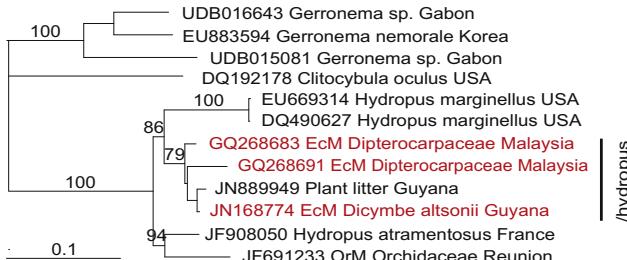


Fig 3 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of sequences in the /hydropus lineage based on ITS sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

length ITS sequences of the Sebacinales clade B, it appears that EcM taxa fall into two major monophyletic clades (Figs 4, S1), hereafter referred to as the /serendipita1 and /serendipita2 EcM lineages. In both of these groups, the sebacinalean taxa were also recovered from non-EcM roots by specifically targeting these taxa using lineage-specific primers and sometimes cloning (Weiss et al., 2011; Garnica et al., 2013). Use of specific primers may result in detection of species that are not necessarily prevalent; we suggest that this incidental detection of these taxa from non-EcM root systems does not exclude them as EcM symbionts.

The /serendipita1 lineage forms a monophyletic group (BS = 97). Species of this group associate with Salicaceae, Fagaceae, Betulaceae, Pinaceae, Tiliaceae and Pyroleae in temperate, boreal, subalpine and subarctic habitats of the Northern Hemisphere (Fig 4). We have been able to study the anatomy of only a single root tip isolate, UDB002608, that is characterized by a plectenchymatous mantle and smooth surface with no hyphae. In another isolate, JX316811, sparse extraradical hyphae were observed (C. Andrew, pers. comm. March, 2013). Thus, the examined species of the /serendipita1 lineage belong to either contact or short-distance exploration types.

The /serendipita2 lineage is phylogenetically distinct and it forms a monophyletic group (BS = 98; Fig 4). Members of this lineage associate predominantly with Pinaceae, but to a lesser extent with Fagaceae and Pyroleae in subtropical and temperate forest ecosystems. Although no root tips were available to us for study, species of this group probably fall into the contact or short-distance exploration types described for other Sebacinales (Urban et al., 2003; Agerer, 2006).

The /tulasnella lineage (sensu Tedersoo et al., 2010) is similarly split into two groups. These two lineages are monophyletic, but distantly related to one another within the Tulasnellaceae phylum (J. Oja, unpublished).

The /tulasnella1 lineage comprises a deeply diverging monophyletic clade of closely related fungal species that colonize both the rhizoids of hepatic (Bidartondo et al., 2003; Bidartondo and Duckett, 2010) and EcM root tips of *Betula pendula* and *Pinus sylvestris* (Bidartondo et al., 2003; I. Ostonen et al., unpublished) in temperate forests of Europe. In addition, sequences from *Betula nana*-dominated tundra soil in Alaska

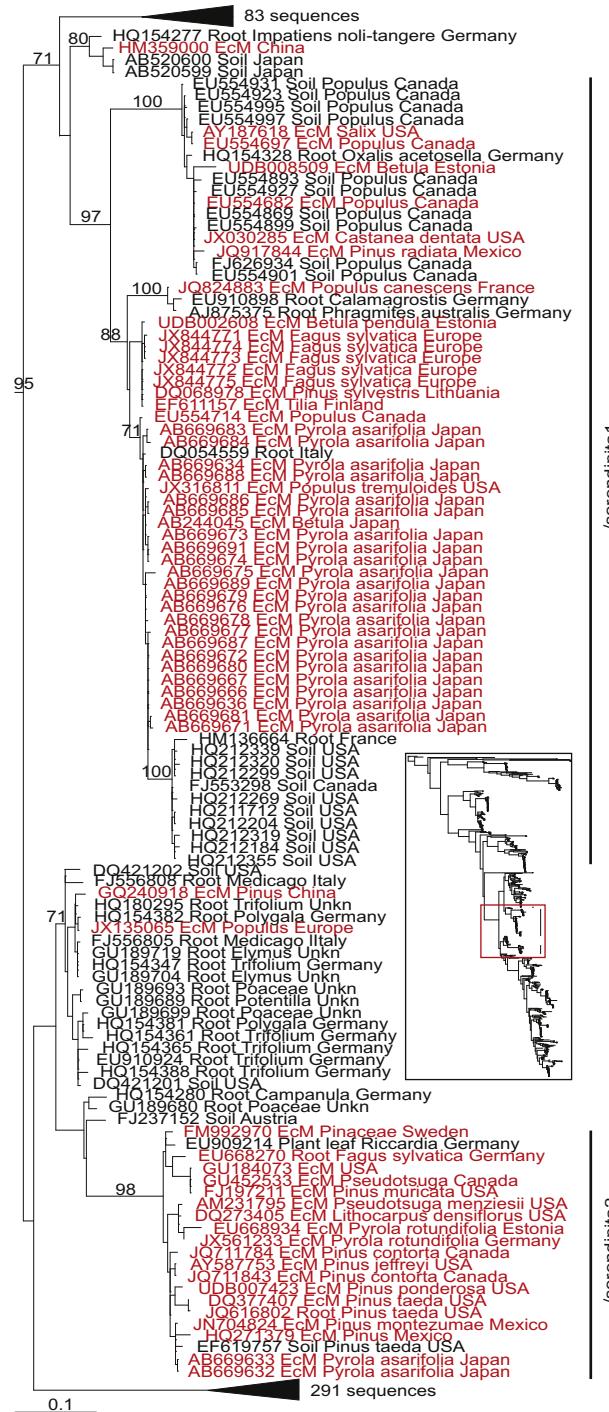


Fig 4 – Cut-out of an unrooted maximum likelihood phylogram demonstrating phylogenetic placement of EcM lineages in the Serendipitaceae family (Sebacinales clade B) based on ITS sequences. The inclusive tree (in the rectangle) is given in Fig S1. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

(Deslippe et al., 2011) fall into this group, but the sequences were recently withdrawn from INSDc. The EcM formed by *Tulasnella* are smooth with no extraradical mycelium and correspond to the contact exploration type.

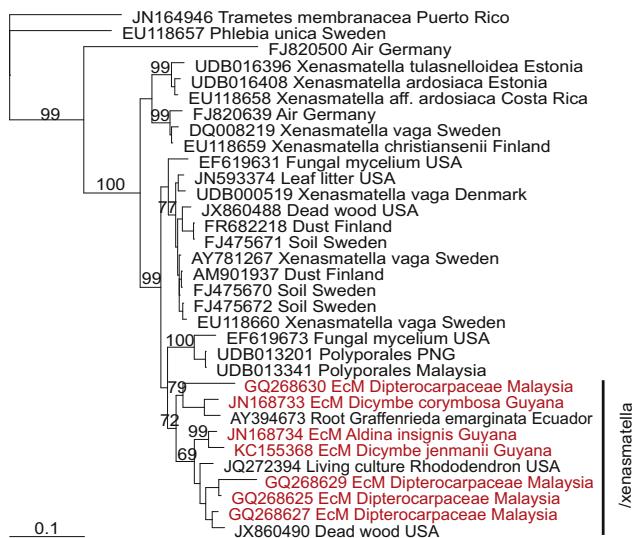


Fig 5 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of sequences in the /xenasmatella lineage based on combined ITS and LSU sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

The /tulasnella2 lineage is restricted to southern temperate habitats. The isolates have been found from *Nothofagus* spp. in Argentina (Nouhra et al., 2013) and *Nothofagus cunninghamii*, *Eucalyptus regnans*, and *Pomaderris apetala* in Tasmania (Tedesco et al., 2008a, 2009a). Individual species of the /tulasnella2 lineage share a gelatinous mantle; some species possess long, thick-walled cystidia, whereas others do not. Extraradical mycelium is absent or scarce. This group belongs to the contact exploration type.

The putative /xenasmatella lineage forms a strongly supported monophyletic group that is nested within the genus *Xenasmatella* (Fig 5). The EcM-associated groups originate from roots of Dipterocarpaceae and Caesalpinoideae in Malaysia and Guyana (Peay et al., 2010; Smith et al., 2011, 2013). Although taxa in this group have been regularly encountered on EcM root tips and form apparently normal EcM morphology (as /polyporales1 in Smith et al., 2011), the phylogeny provides conflicting evidence about the trophic mode of this group. EcM-forming isolates are phylogenetically placed alongside sequences from dead wood, a non-EcM tree (contrary to the assertions of Haug et al. (2004) we consider Graffenreida to be non-EcM), and cultures from ericoid mycorrhizal plants. Considering these features and the conflicting data, we suggest that the /xenasmatella lineage may represent a non-mycorrhizal, opportunistic, facultative root association that colonizes mycorrhizas of other species. Another possibility is that fungi in this group form extensive rhizomorphs similar to those in temperate *Xenasmatella* spp. and they are tightly bound to roots and preferentially amplified during PCR. Further work is definitely needed to clarify the nutritional mode and ecology of the putative /xenasmatella lineage.

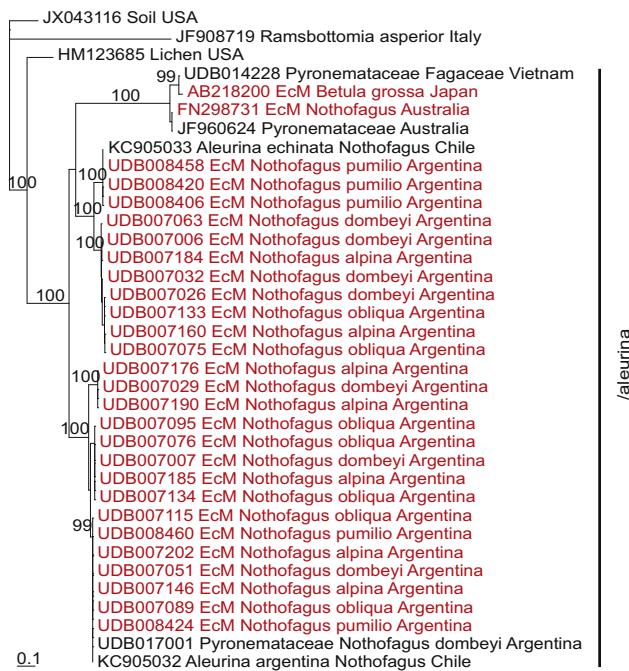


Fig 6 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of sequences in the /aleurina lineage based on ITS sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

Several other Basidiomycota species have been suggested as EcM symbionts since 2010. For example, Walker et al. (2012) consistently recovered *Alloclavaria purpurea* and a related species from EcM root tips of *Pseudotsuga menziesii* in Canada and considered these to be EcM fungi. However, the ¹³C and ¹⁵N stable isotope signatures were equivocal and could not definitively determine the likely source of nutrients for these fungi. Because the root tips had contrasting morphology, ranging from cream and hairy (Amphinema-type) to black and rough (Tomentella-type; J.K.M. Walker, pers. comm. January, 2013), *Alloclavaria* probably functions as an endophyte or saprobe and should not be considered ectomycorrhizal. Nouhra et al. (2013) similarly found that a *Rickenella* sp. and a *Tulasnella* sp. (closely related to *Cypripedium* symbionts) frequently colonized root tips of *Nothofagus* spp. at several study sites in Argentina. Based on the high variation in EcM mantle anatomy, both groups were considered saprotrophic or endophytic. Besides these groups, EcM root tips are commonly colonized by basidiomycetous yeasts such as *Atractiellales* and *Cryptococcus* based on INSDc records and our own results. These are common soil fungi and their function on the surface and inside roots is not clear. However, certain tropical orchids have evolved mutualistic associations with *Atractiellales* (Kottke et al., 2010) and some species in this group are frequently isolated as root endophytes from EcM trees. Among Agaricomycetes, species of *Gymnopus*, *Rhodocollybia*, *Trechispora*, *Bjerkandera*, *Mycena* and *Pleurotus* have all been occasionally recovered from EcM root tips based on the



Fig 7 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of EcM lineages in the Scutellinia-Trichophaea clade of Pyronemataceae (sensu Hansen et al., 2013) based on combined ITS and LSU sequences. The /wilcoxina, /geopora and /sphaerospora lineages are represented by a few divergent sequences for illustration purposes. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

records in INSDc. However, these are not concentrated in specific clades nor do they form monophyletic groups of EcM isolates, leading us to treat them as parasitic, endophytic or saprotrophic root colonizers rather than true EcM symbionts.

Ascomycota

The /aleurina lineage is comprised of species of *Aleurina*, *Geli-nipes* nom. prov. and *Unicava* nom. prov. (J.M. Trappe et al.,

unpublished; Perry et al., 2007; Tedersoo et al., 2013a). Based on LSU, the /aleurina lineage is nested within the Pyronemataceae family and it has Southern Hemisphere distribution (Tedersoo et al., 2013a). However, the more inclusive ITS dataset of this ECM lineage suggests that the distribution involves both the Southern Hemisphere and Eastern Asia. In particular, this group has been found in natural forests in Japan (Ishida et al., 2007) and Vietnam (L. Tedersoo and co-workers, unpublished). In Argentina, the /aleurina lineage is divided into five

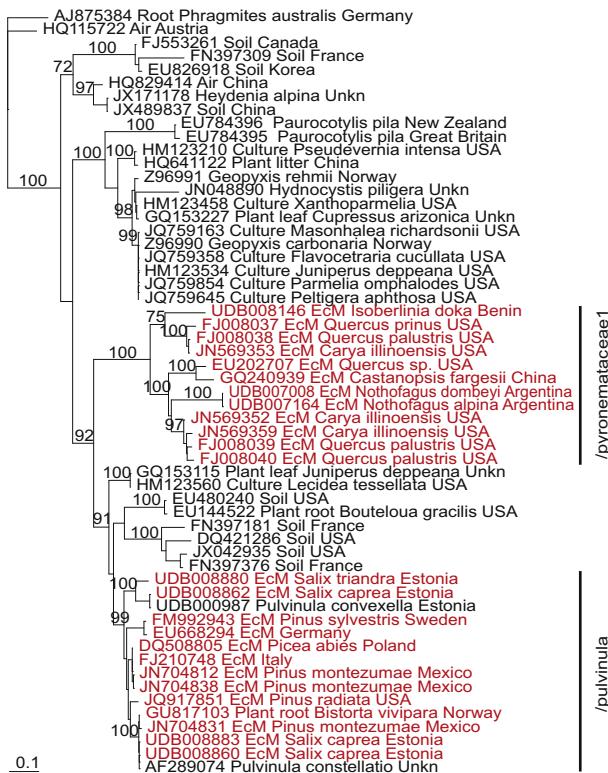


Fig 8 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of the /pulvinula and /pyronemataceae1 lineages based on combined ITS and LSU sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

species based on ITS sequences from EcM roots (Nouhra et al., 2013) and at least two of these taxa correspond to named species (*Aleurina echinata* KC905033 and *Aleurina argentina* KC905032; Pfister & Smith, unpublished). In Australia, this group is thus far represented by a single species (Tedessoo et al., 2008a; Horton et al., 2013; Fig 6). We studied several EcM root tips from this group and all had a typical coarse pseudoparenchymatous mantle and either thick-walled hyphae or no hyphae. Thus, species of this lineage belong to either contact or short-distance exploration types.

The /pustularia lineage was recovered based on an LSU match between a *Pustularia patavina* fruit body and sequences of EcM root tips (Tedessoo et al., 2013a). Based on ITS sequences, this is a monophyletic group (BS = 100) of closely related isolates that have been found throughout the boreal and temperate forests of the Northern Hemisphere. This lineage is most commonly recovered from EcM roots of Pinaceae, but they are occasionally identified from Fagaceae, Tiliaceae, Salicaceae and Rosaceae (Fig 7). Members of this group exhibit mantle structure similar to that of *Geopora* (Tedessoo et al., 2006) and sparse extraradical hyphae that correspond to the short-distance exploration type. The genus name *Pustularia* had a very wide use and its type species, *Pustularia cupularis*, has been

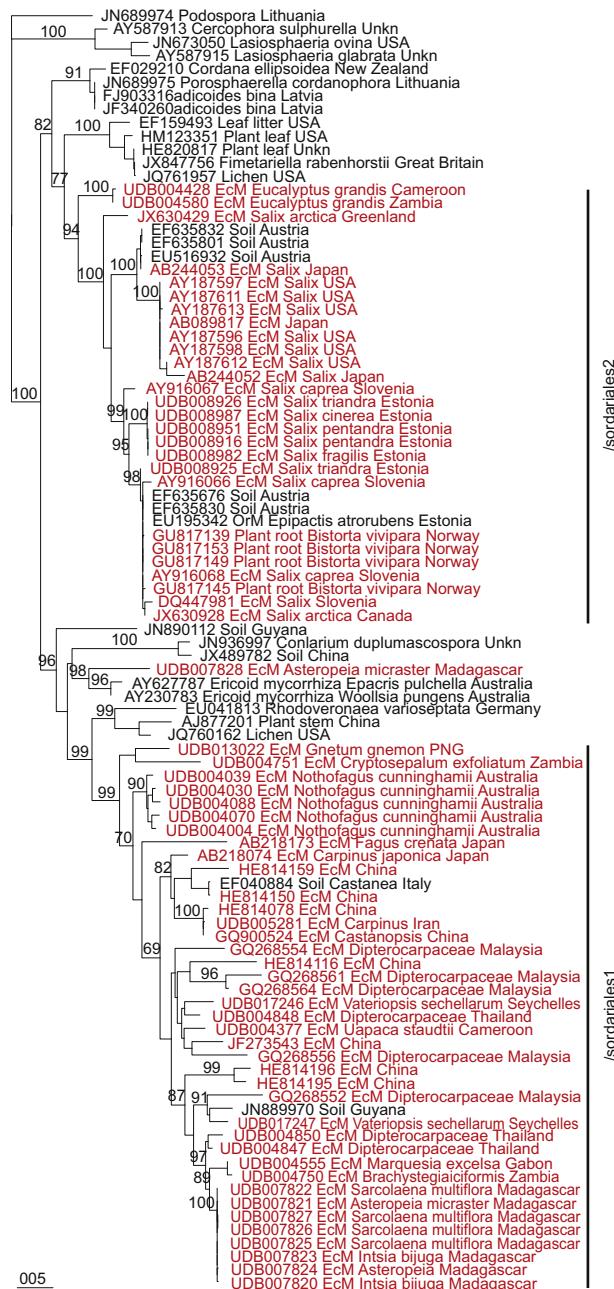


Fig 9 – Unrooted maximum likelihood phylogram demonstrating phylogenetic placement of EcM lineages within Sordariales based on combined ITS and LSU sequences. Significant bootstrap support (>70) is indicated above branches. Abbreviations: EcM, ectomycorrhiza; ErM, ericoid mycorrhiza; OrM, orchid mycorrhiza; Unkn, unknown country.

transferred to Tarzetta; therefore the genus name of *P. patavina* may change.

The /rhodoscypha lineage comprises a small monophyletic group of sequences that was discerned based on LSU (Tedessoo et al., 2013a). There are only two EcM-derived ITS sequences available in INSDc and both originated from Pinaceae in SW Canada (Jones et al., 2008; S. Lim, unpublished).

The monotypic genus *Rhodoscypha* is distributed in the boreal and temperate forests of the Northern Hemisphere and is rare throughout its range. Unfortunately no root tips were available from the authors for microscopy.

The /pyronemataceae1 lineage comprises a heterogeneous group of EcM root-derived sequences that have no fruit body representatives. This group displays affinities to the *Pulvinula-Lazuardia* group, but is distinct from the /pulvinula EcM fungal lineage (Tedersoo et al., 2013a; Fig 8). ITS sequences of this group were derived from EcM roots of Fagaceae and Juglandaceae in the USA (Cavender-Bares et al., 2009; Bonito et al., 2012), Nothofagaceae in Argentina (Nouhra et al., 2013) and from Caesalpinioideae in Benin (L. Tedersoo and N.S. Yorou, unpublished). The Argentinean root tip vouchers have sparse hyphae and have a mantle structure that is intermediate between the pseudoparenchymatous and plectenchymatous types. We believe that this lineage is best characterized by short-distance exploration type.

The /pyronemataceae2 lineage is a monophyletic group (BS = 100) of three sequences recovered exclusively from EcM root tips of Pinaceae in California (Izzo et al., 2005; Smith et al., 2009) and Northern Mexico (Hoeksema et al., 2012; Fig 7). This small group is closely related to but clearly distinct from the /geopora lineage. Based on 97 % ITS similarity, each sequence could be recognized as a distinct taxon. No root tips were available for microscopy.

The /sordariales lineage of Tedersoo et al. (2010) is divided into two groups based on additional sequence data and phylogenetic analyses of combined ITS and LSU sequences (Fig 9).

The /sordariales1 lineage encompasses sequences from various angiosperm hosts in tropical (Tedersoo et al., 2007, 2011b; Peay et al., 2010; Phosri et al., 2012), southern temperate (Tedersoo et al., 2009a) and warm northern temperate (Ishida et al., 2007; Bahram et al., 2012) biomes, and forms a well-supported monophyletic group (BS = 99; Fig 9). Based on descriptions of EcM roots from the Seychelles (Tedersoo et al., 2007) as well as material from Australia and Africa, members of the /sordariales1 lineage form short-distance exploration type.

The /sordariales2 lineage represents a monophyletic group of sequences (BS = 94; Fig 9). While the bulk of the sequences originates from arctic, alpine and temperate habitats in association with *Salix* (Trowbridge and Jumpponen, 2004; Nara, 2006b; Timling et al., 2012; Tedersoo et al., 2013b) and *Bistorta vivipara* (Brevik et al., 2010), species in the basal clade of this lineage are EcM symbionts of *Eucalyptus* introduced to Africa. This group was common on eucalypts but absent on indigenous trees, suggesting their co-introduction to Africa (Jairus et al., 2011). Root tip vouchers from Estonia and Africa have a thin mantle and abundant hyphae, pointing to a short-distance exploration type.

In Ascomycota, there are many EcM fungal lineages that are comprised of only a few species (e.g. /cenococcum and several lineages in the Helotiales). Many of these species-poor lineages apparently are either limited in their distribution or are infrequently detected in EcM community studies, perhaps due to their specific ecological requirements. The lineages within Helotiales have remained challenging to accurately detect and identify, because they are closely related to

common root endophytes that are frequently detected by molecular (Tedersoo et al., 2009a,c) and culture-based surveys (Vrålstad et al., 2002; Kernaghan and Patriquin, 2011; Menkis and Vasaitis, 2011) of EcM tissues. Phylogenetic analyses of subgroups of Helotiales indicate that endophytic, ericoid mycorrhizal, soil-derived and EcM-associated isolates occur throughout the phylogeny (Vrålstad et al., 2002; Hambleton and Sigler, 2005). Without statistical approaches or information about EcM morphology and behavior in culture, it is difficult to assign a nutritional mode to an individual species in this group. An additional problem is the thin mantle and sometimes poorly developed Hartig net in these helotialean EcM (Yu et al., 2001; Tedersoo et al., 2008b; Münenberger et al., 2009). These anatomical features have led to many ambiguous reports on EcM formation between Helotiales and various plants (Kohn et al., 1986; Haug et al., 2004; Peterson et al., 2008; Comandini et al., 2012). In Pezizales, where root endophytes have rarely been recovered in molecular and culture-based surveys, assignment of nutritional mode to particular taxa is more straightforward (Tedersoo et al., 2013a). In only one of the pezizalean families, the Pyronemataceae, we documented five novel lineages. Previous recognition of these groups was hampered by the lack of ITS sequences from sporocarps, because molecular taxonomic work has mostly utilized LSU and protein-encoding genes (Hansen et al., 2013). However, recent ecological studies have started to routinely sequence both ITS and partial LSU to improve biogeographic and taxonomic resolution (e.g. Smith et al., 2007). Matching LSU genes from fruit-bodies and EcM root tips can prove useful to assign nutritional mode to pezizalean groups (Tedersoo et al., 2006, 2013a; Smith et al., 2007).

Zygomycota

There is only limited phylogenetic information available for EcM fungal lineages in Zygomycota (Desiro et al., 2013). The /endogone lineage has been separated into two parts based on phylogenetic information from SSU, ITS and LSU genes (L. Tedersoo et al., unpublished data). Of species studied by Warcup (1990a), the Pinaceae-associated *Endogone flammicrona* and *Endogone lactiflua* constitute the /endogone1 lineage, whereas the Australian *Endogone aggregata*, *Endogone tuberculosa* and *Sclerogone eucalypti* form the /endogone2 lineage. Probably numerous sequenced EcM root tips from the Australian Myrtaceae, Nothofagaceae and Rhamnaceae (Tedersoo et al., 2008a, 2009a) also fall into the latter group. Notably, the type species of *Endogone*, *Endogone pisiformis*, is non-EcM (e.g. Berch, 1983). Sequences from old collections of *Densospora* spp., associated with Myrtaceae (McGee 1996), are phylogenetically distinct from the /endogone1 and /endogone2 lineages (L. Tedersoo et al., unpublished data).

Doubtful groups

Several EcM lineages such as /catathelasma, /sowerbyella, /endogone1 and /densospora have never been recovered in EcM community studies. Root tips of the /catathelasma lineage have been documented only once, when specifically searching for them under a fruit body of *Catathelasma*

imperiale (L. Tedersoo, unpublished). Although *Sowerbyella* is suggested to form EcM based on its habitat and the ^{15}N isotopic signature (Hobbie et al., 2001), there are still no direct observations on EcM in this group. Of novel lineages, /*hydropus* and /*xenasmatella* require further support for their EcM status (see above).

4. New EcM fungal genera

Since taxonomists continually lump, split, and create new genera, the list of EcM groups is subject to change. There is still substantial controversy as to whether monophyletic lineages that contain different fruit body types should be treated as monogeneric or multigeneric groups. In particular, sequestrate fungi have traditionally been named in separate genera, but since these truffle-like taxa are often nested within groups of epigeous species, the nomenclature has become problematic. For example, the polyphyletic sequestrate fungi within the /*cortinarius* lineage were previously treated within the genus *Thaxterogaster*, but have now all been synonymized within the genus *Cortinarius*. In contrast, the sequestrate fungi within the /*boletus* and /*russula-lactarius* lineage have mostly been retained as separate genera (but see Desjardin (2003) and Lebel and Tonkin (2007) for exceptions). Within the /*boletus* lineage, many new genera of both epigeous and hypogeous taxa have been erected in recent years. *Peziza* *sensu lato* represents the opposite scenario and this genus is still treated as a large, paraphyletic group even though it includes several well-defined lineages that include sequestrate and epigeous species as well as both EcM and non-EcM taxa.

For 14 previously recognized lineages, we provide updated information about the genera that are currently included. In total, we add 47 genera to the list of EcM fungi, most of which have been described very recently. We also remove three genus-level taxa (*Hydnocystis piligera*, *Tricharina ochroleuca*, *Rubinoboletus rubinus*; see below). The updated list of EcM fungal genera is found in Table S1.

From matching fruit body and EcM root tip LSU sequences, there is good evidence that the Pezizalean genus *Parascutellinia* is ectomycorrhizal with *Salix* spp. in various habitats in Estonia (Tedersoo et al., 2013b). Unfortunately, no ITS sequences of *Parascutellinia* fruit-bodies are available in INSDC. Although *Parascutellinia* was considered a saprotrophic sister group to the /*genea-humaria* lineage in Tedersoo et al. (2010), recent phylogenetic analyses support its placement within this group (Hansen et al., 2013; Tedersoo et al., 2013b).

In previous reports by Tedersoo et al. (2010) and Comandini et al. (2012), the fungus *T. ochroleuca* was reported as an EcM-forming member of the /*geopora* lineage. However, all reports of EcM formation by *T. ochroleuca* are apparently based on partial ITS matches to sequences from cultures that are phylogenetically placed outside the /*geopora* lineage (Fig 7; see also Stielow et al., 2013). We find no credible evidence that any *Tricharina* species form EcM. Similarly, *H. piligera* (type species) forms a sister group to the non-EcM genus *Stephensia* and therefore we consider the genus *Hydnocystis* to be non-EcM. However, at least one species of *Hydnocystis* s. lato, *Hydnocystis clausa*, is an EcM member of the /*geopora* lineage. However, we

suggest that it should be treated as *Geopora clausa* (Tul. and C. Tul.) Burds. (Burdsall 1968; M.E. Smith, unpublished).

The /*leucangium* lineage is appended with the recently erected, monophyletic genus *Kalapuya* that is nested within this group (Trappe et al., 2010). While the genus *Fischerula* is distantly placed in some phylogenetic studies (Healy et al., 2013), most studies with more focused taxonomic sampling or inclusive ingroup sampling support placement of *Fischerula* within the /*leucangium* lineage (Trappe et al., 2010; Alvarado et al., 2011).

Several recently sequenced and/or newly described genera are accommodated in the /*marcelleina-peziza gerardii* lineage. *Delastria rosea*, a rare sequestrate species was recently placed as a sister group to species of *Hydnobolites* (Alvarado et al., 2011; Healy et al., 2013). *D. rosea* isolate JN102449 exhibits 99.5 % ITS sequence similarity with an EcM root tip isolate FJ013057 from Portugal (Rincon and Pueyo, 2010) and slightly less to many other root tip isolates, indicating that *Delastria* spp. are ectomycorrhizal. Kovacs et al. (2011) described the new sequestrate fungal genera *Temperantia* and *Stouffera* that are nested within the /*marcelleina-peziza gerardii* lineage (Kovacs et al., 2011; Healy et al., 2013), suggesting that these genera are ectomycorrhizal.

The /*tuber-helvella* lineage includes the Southern Hemisphere genera *Gymnohydnomyia* and *Nothojafnea* in addition to previously reported taxa (Bonito et al., 2013). The genus *Underwoodia* appears to be split into two distinct groups that likely constitute one genus for the Northern Hemisphere and one for the Southern Hemisphere (Bonito et al., 2013, M.E. Smith, unpublished). *Loculotuber* and *Paradoxa* also belong to this group, but these taxa will probably be synonymized with *Tuber* (Kinoshita et al., 2011; Alvarado et al., 2012; Bonito et al., 2013). In contrast to most *Tuber* species, the basal Southern Hemisphere species in *Gymnohydnomyia* and *Underwoodia* *sensu lato* exhibit a contact exploration type that is similar to species in the Helvellaceae.

A recently sequenced isolate of *Discinella terrestris* from New Zealand (GU222294) has 96–97 % ITS match to multiple species within the /*helotiales4* lineage that has so far only documented from Australia (Tedersoo et al., 2008a; Horton et al., 2013). The core group of *Discinella* *sensu stricto* is probably non-ectomycorrhizal, because the type species *Discinella boudieri* has a Northern Hemisphere distribution and it has not been sequenced thus far.

The /*hebeloma-alnicola* lineage is widened by the addition of the genus *Psathylooma* (nom. prov.; P.B. Matheny, pers. comm. January 2013) that has been found mostly in New Zealand as fruit-bodies, but also as EcM root tips in Tasmania (Tedersoo et al., 2009a; Horton et al., 2013) and Argentina (Nouhra et al., 2013). In contrast to other members of this lineage, EcM of *Psathylooma* spp. exhibit a short-distance exploration type with abundant dark brown hyphae but no rhizomorphs. At least one species from the genus *Wakefieldia* (*Wakefieldia macrospora*) also belongs to the /*hebeloma-alnicola* lineage, because it is phylogenetically placed among species of *Alnicola*, *Hebeloma* and *Hymenogaster* (Kaounas et al., 2011). Sequences from EcM root tips (isolates HQ204662, HQ204659) of *Quercus ilex* in France (Richard et al., 2011) are 99.8 % similar to *W. macrospora*. However, the type species, *Wakefieldia striaespora* was described from SE Asian

dipterocarp forests and it may belong to a different group based on the combination of morphology and habitat (M.E. Smith, unpublished).

In the /inocybe lineage, *Tubariomyces* has been erected from *Inocybe* (Alvarado et al., 2010). *Tubariomyces* is inferred to associate with Cistaceae. However, since relatively few studies have focused on EcM communities of Cistaceae there are currently no available root-derived sequences that correspond to *Tubariomyces*.

The /piloderma lineage includes a recently erected genus *Tretomyces* that has been recorded only from boreal and temperate Pinaceae forests (Kotiranta et al., 2011; Fig 2).

Destuntzia fusca was considered putatively EcM (Tedersoo et al., 2010) and is now a confirmed member of the /ramaria-gautieria lineage based on ITS sequence data. The isolate EU697269 matches a group of ectomycorrhizal *Ramaria* species (not shown).

DNA sequences of ITS and LSU from the genus *Fevansia* indicate that this genus belongs to the EcM/albatrellus lineage (Smith et al., 2013b). Although *Fevansia* does not match closely with any EcM root tip sequences, this species is consistently found among EcM roots of Pinaceae and all of its closest relatives form EcM.

The /boletus lineage has been enriched with several recently described genera or genera with newly generated molecular data (Nuhn et al., 2013). The LSU sequences of the sequestrate *Gymnogaster boletoides* falls into the /boletus lineage (Halling et al., 2012b). The monotypic *Heliogaster* was segregated from *Octaviania* and it represents a sequestrate *Xerocomus* species (Orihara et al., 2010). No EcM root tips are matched to *Heliogaster columellifera*, but the phylogenetic position indicates that it is ectomycorrhizal. *Tubosaeta* belongs to the /boletus lineage based on ITS sequences (Brock et al., 2009). However, none of the sequenced specimens match ITS sequences from EcM root tips. *Rossbeevera* was erected to accommodate a monophyletic group of sequestrate fungi from Australia and Japan (Lebel et al., 2012). Sequences corresponding to this group have been found from EcM root tips in Australia (Tedersoo et al., 2009a; Horton et al., 2013). *Turmalinea* is a recently described sequestrate genus that is sister to *Rossbeevera*; this group is phylogenetically related to other EcM-forming members of the /boletus lineage and *Turmalinea* species are consistently found with EcM trees (Orihara et al., 2013). *Spongiforma* represents a recently described sequestrate genus that is related to *Porphyrellus* (Desjardin et al., 2009). The pileate genus *Borofutus* has been described to accommodate a sister species to *Spongiforma* (Hosen et al., 2013). No EcM isolates correspond to these two genera but both groups are inferred as EcM. *Zangia* has been erected from *Tylopilus* and this group is currently represented only by Chinese species (Li et al., 2011). No EcM root tip sequences correspond to *Zangia roseola*, the only species for which an ITS sequence is available. The recently described sequestrate genus *Soliocasus* is phylogenetically allied with *Bothia* and is inferred as EcM as it is always encountered among ECM Myrtaceae and *Allocasuarina* in Northern Queensland and Papua New Guinea (Trappe et al., 2013). *Corneroboletus* has been described to accommodate *Boletus indecorus* (Zeng et al., 2012). No EcM root isolate corresponds to *Corneroboletus*. *Hemileccinum* was described to accommodate *Boletus impolitus* and *Boletus depilatus*

(Sutara, 2008). *Australopilus* and *Harrya* are Australian genera that have been erected as segregates of the Northern Hemisphere genus *Tylopilus* (Halling et al., 2012b). The genus *Sutorius* has been erected from *Boletus* (Halling et al., 2012a). For some reason, no ITS sequences exist for *Australopilus*, *Gymnogaster*, *Harrya*, *Phyllobolotellus*, *Royoungia* and *Sutorius*, and therefore root tip matches to these genera cannot be evaluated. The type species of *Rubinoboletus*, *R. rubinus* is nested within the non-EcM *Chalciporus*, but a few other species are nested among EcM taxa within the /boletus lineage (Nuhn et al., 2013). Nuhn et al. (2013) listed a number of genera that belong to the Boletaceae (*Boletochaete*, *Gastroleccinum*, *Paxillogaster*, *Sinoboletus*) or Paxillaceae (*Austrogaster*, *Hoehnelogaster*, *Meiorganum*) based on morphological characters, but they lack ITS or LSU sequence data to evaluate their phylogenetic position and their EcM status.

Rhopalogaster belongs to the /suillus-rhizopogon lineage based on LSU sequence data (Hosaka et al., 2006). *Rhopalogaster transversarium* isolate DQ218599 has 96.6 % LSU sequence identity with *Suillus hirtellus* fruit body AY612828. ITS sequences of this genus are lacking from sequence databases.

5. Confirmed non-EcM genera

The genus *Amogaster* that produces sequestrate fruit-bodies was originally considered a member of Boletales. However, this species is nested within the saprotrophic genus *Lepiota* and does not form EcM (Ge and Smith, 2012). Similarly, American species of *Gigasperma* are nested within *Lepiota* and are currently treated in the sequestrate, non-EcM genus *Cryptolepiota* (Kropp et al., 2012). Sequestrate forms have evolved multiple times in Lepiotaceae (Ge and Smith, 2012), which is a common phenomenon in Basidiomycota. The type species of *Gigasperma*, *Gigasperma cryptica* is found exclusively in New Zealand and is nested within the /cortinarius EcM lineage (Kropp et al., 2012). The fruit body sequence generated by Kropp et al. (2012) has 93.7 % ITS sequence match with *Corticarius elaiops* (JX000369). *Neopaxillus* forms a monophyletic sister group to *Crepidotus* and *Simocybe* and no EcM-derived ITS sequences fall into this group so *Neopaxillus* is therefore considered non-ectomycorrhizal (Vizzini et al., 2012).

6. Biodiversity and biogeography

The lack of randomly obtained sequences from certain lineages suggests that, despite our good overall understanding of EcM fungal communities, several EcM groups still await discovery due to their natural rarity. Based on fruit body records, we previously suggested that tropical-endemic EcM lineages were either rare or absent (Tedersoo et al., 2010). However, here we report four putatively EcM groups that are hitherto known only from tropical habitats (/agaricales1, /atheliales1, /hydropsy, /xenasmatella) as well as one lineage that is found in both tropical and subtropical ecosystems (/atheliales2). All these lineages are relatively rare and species-poor except for the /atheliales1 lineage (see above). Given that four of these groups are distributed on multiple continents, it is reasonable to assume that these lineages are either relatively old or have excellent capacity for dispersal. However, given the rarity of

these taxa, we hypothesize that vicariance is probably more important than long-distance dispersal in explaining the distribution of these EcM groups. Nonetheless, we acknowledge that the present data are too scanty to generate any realistic biogeographic scenarios to explain their origins. In addition, several common groups of EcM fungi such as the /inocybe and /clavulina lineages may have evolved in tropical regions based on molecular data (Matheny et al., 2009; Smith et al., 2011; Kennedy et al., 2012). These groups have effectively spread to both temperate and arctic ecosystems, suggesting that long-term migration from tropical to temperate climates is possible for some EcM groups with tropical origins. We deduce that the rare tropical lineages described here may not have been able to expand beyond the tropics because of inefficient dispersal capacities or due to an inability to withstand cold temperatures. Based on large-scale biogeographic distribution patterns of EcM taxa (Geml et al., 2012; Tedersoo et al., 2012a; Timling et al., 2012; Bahram et al., 2013), we suggest that intolerance of low temperature may have limited migration of many lineages to subarctic and arctic ecosystems.

7. Concluding remarks

Based on accumulated ITS sequences and associated metadata, we describe 20 new lineages of EcM fungi. Thus, the number of distinct EcM lineages is elevated to 78–82 and the number of EcM fungal genus-level taxa is elevated to 251–256. However, several putative lineages require further morphological or ultrastructural proof, because saprotrophic Ascomycota, Basidiomycota and Zygomycota are all commonly detected as saprotrophs or endophytes with EcM root tips (Morris et al., 2008; Lindner and Banik, 2009; Tedersoo et al., 2009c; Nouhra et al., 2013). Given the rarity of many lineages in EcM community studies, we suggest that continued research will reveal new EcM lineages, especially in tropical and Southern Hemisphere ecosystems where fewer EcM community studies have been conducted. This synthesis of new data from our own studies and from the INSDC indicates that several uncommon, species-poor lineages may indeed be limited to tropical and subtropical ecosystems.

Information about EcM morphology allowed us to determine the main exploration types for both the novel groups and poorly studied taxa that have not been addressed in previous in-depth studies. Although most EcM fungal lineages (and genera therein) possess a single exploration type, the most common and species-rich genera exhibit multiple exploration types (Agerer, 2006). Based on these findings, we caution that exploration type cannot be consistently extrapolated from a few species to the entire genus or lineage. Therefore, we strongly encourage researchers to determine foraging strategies based on original experimental material. To be able to seek further molecular or morphological proof and to study the morphology in more detail in future, researchers should keep voucher root tips. A large number of in-depth morphological and anatomical descriptions of unidentified EcM is also available online (www.deemy.de). Molecular identification of these well-described EcM samples would further our understanding of EcM fungal community ecology.

Nevertheless, we believe that our summary of current knowledge on exploration types will be useful for analysis and interpretation of results from molecular studies that rely on fungal DNA from hyphal mesh bags and soil.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.fbr.2013.09.001>.

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Table S1. Exploration types of EcM fungal genera that have been sorted to lineages based on evidence from pure culture synthesis, morphological and molecular identification, stable isotope analysis, anatomical description and/or phylogeny. Genera that are EcM based on only phylogenetic evidence are indicated in parentheses. Asterisks denote genera with sequestrate fruit-bodies. Genera including members with resupinate fruit-bodies are underlined. Genera that were treated as EcM in Tedersoo et al. (2010a), but proven non-EcM are indicated in strikethrough. Exploration type abbreviations: C, conact; SD, short-distance; MDF, medium-distance fringe; MDM, medium-distance mat; MDS, medium-distance smooth; LD, long-distance (sensu Agerer 2001). References to exploration types in parentheses indicate origin of re-studied material. Modified and updated from Tedersoo et al. (2010a).

Taxa and lineages of EcM fungi	References				
	Synthesis	In situ identification (first reports; bold, molecular data)	Stable isotopes	Phylogeny (for lineage definition)	Exploration type
BASIDIOMYCOTA					
AGARICALES					
/agaricales 1					
unnamed		Smith et al. 2013a		Smith et al. 2013a	MDF: (Smith et al. 2013a)
/amanita					
<i>Amanita</i>	Melin 1923a; Melin 1924; Hatch & Hatch 1933; (Doak 1934); Modess 1941; (Hacskaylo & Palmer 1955); Vozzo & Hacskaylo 1961; Riffle 1973; Pachlewski & Chrusciak 1980; Malajczuk et al. 1982; Molina & Trappe 1982; Godbout & Fortin 1985	(Frank 1892); (Peyronel 1922); Gardes & Bruns 1996; Horton & Bruns 1998; Horton et al. 1998; Horton et al. 1999; Taylor & Bruns 1999	Gebauer & Dietrich 1993; Gebauer & 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; Zeller et al. 2008	Moncalvo et al. 2002; Hallen et al. 2004; Matheny et al. 2006; Wolfe et al. 2012	C/SD/MDS: Agerer 2006 ; (Tedersoo et al. 2011)
(<i>Amarrendia s. stricto</i>)*				Hallen et al. 2004	unknown
(<i>Torrendia</i>)*				Hallen et al. 2004	unknown
/cataethelasma					
<i>Cataethelasma</i>	(Hutchison 1992)	L. Tedersoo unpublished	Kohzu et al. 1999	Moncalvo et al. 2002; Matheny et al. 2006	MDM: L. Tedersoo unpublished
/cortinarius					
<i>Cortinarius</i> (incl. <i>Cuphocybe</i> , <i>Rapacea</i> , <i>Rozites</i> , <i>Thaxterogaster</i>) (*)	Melin 1924; Melin 1925; Ashton 1976; Antibus et al. 1981; Kropp & Trappe 1982; Godbout & Fortin 1985; Loree et al. 1989; van der Heijden & Kuyper 2003	(Noack 1889); Kauffman 1906; McDougall 1914; Masui 1927; Gardes & Bruns 1996; Dahlberg et al. 1997; Erland et al. 1999; Jonsson et al. 1999a	Hobbie et al. 1999; Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Clemmensen et al. 2006; Zeller et al. 2007; Wilson et al. 2007; Mayor et al. 2009	Hoiland & Holst-Jensen 2000; Peintner et al. 2002; Peintner et al. 2004; Matheny et al. 2006	MDF: Agerer 2006 ; rarely SD: Agerer 2006 ; (Tedersoo et al. 2008a ; Nouhra et al. 2013)
<i>Dermocybe</i>	Malajczuk et al. 1987 (as <i>Cortinarius</i>)	Uhl & Agerer 1987; Gronbach 1988; Cullings & Makhija 2001; Tedersoo et al. 2008a	Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004;	Hoiland & Holst-Jensen 2000; Peintner et al. 2001	MDF: Agerer 2006
(<i>Gigasperma p. parte</i> : <i>G. cryptica</i>)*				Kropp et al. 2012	MDF (SD) ³
<i>Protoglossum</i> *	Burgess et al. 1993 (as <i>Hymenogaster</i>)			Peintner et al. 2001	MDF (SD) ³
(<i>Quadruplicaria</i>)*				Peintner et al. 2001	MDF (SD) ³
<i>Stephanopus</i>		Palfner 2001			MDF: Agerer 2006

/desclea					
<i>Descolea</i>	Bougher & Malajczuk 1990; Lu et al. 1998; Brundrett et al. 2005	Bougher & Malajczuk 1985; Palfner 2001; Tedersoo et al. 2008a; Tedersoo et al. 2009a		Peintner et al. 2001; Matheny et al. 2006	SD: Agerer 2006
<i>Descomyces</i> *	Malajczuk et al. 1982 (as <i>Hymenogaster</i>); Burgess et al. 1993 (as <i>Hymenogaster</i>); Lu et al. 1998; Brundrett et al. 2005	Agerer et al. 2001; Tedersoo et al. 2008a; Tedersoo et al. 2009a		Peintner et al. 2001; Matheny et al. 2006	SD: (Tedersoo et al. 2008a)
<i>Setchellilogaster</i> *	Burgess et al. 1993; Brundrett et al. 1996; Thomson et al. 1996; Brundrett et al. 2005	Tedersoo et al. 2008a; Tedersoo et al. 2009a		Peintner et al. 2001; Matheny et al. 2006	SD: (Tedersoo et al. 2008a)
(<i>Tingmuroea</i>)*		Tedersoo et al. 2008a			SD: (Tedersoo et al. 2008a)
/entoloma					
<i>Entoloma s. str.</i> (sections <i>Entoloma</i> , <i>Rhodopolia</i> ; i.e. the rhodopolioid clade sensu Co-David et al. 2009)	Modess 1941; Zerova & Rozhenko 1966 (cited in Antibus et al. 1981); Antibus et al. 1981; Loree et al. 1989;	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	Co-David et al. 2009; Kinoshita et al. 2012	MDS: Agerer 2006; (Tedersoo et al. 2008b, 2013b)
/hebeloma-alnicola					
<i>Alnicola</i>		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	SD: Agerer 2006 ; (Pöhlme et al. 2013)
<i>Anamika</i>		L. Tedersoo & M. Bahram unpublished		Matheny et al. 2006 ; Ryberg & Matheny 2011	SD: (L. Tedersoo & M. Bahram unpublished)
<i>Hebeloma</i>	Shemakhanova 1956 (cited in Shemakhanova 1962); Trappe 1967; Hacsaylo & Bruchet 1972; Antibus et al. 1981; Malajczuk et al. 1982; Godbout & Fortin 1985; Dunabeitia et al. 1996; van der Heijden & Kuyper 2003;	(Kljushnik 1952); Fontana 1961; Fassi & De Vecchi 1963; Fassi & 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 ; Ryberg & Matheny 2011	SD/MDF: Agerer 2006
<i>Hymenogaster s. stricto</i> *		Fontana & Centrella 1967; Kennedy et al. 2003; Izzo et al. 2006; Bidartondo & Read 2008		Peintner et al. 2001; Moreau et al. 2006; Ryberg & Matheny 2011	SD: (Tedersoo et al. unpublished)
<i>Psathyromyces nom. prov.</i>		Tedersoo et al. 2009a ; Horton et al. 2013 ; Nouhra et al. 2013		P.B. Matheny and M. Ryberg, pers. comm., L. Tedersoo, unpublished	SD: (Tedersoo et al. 2009a ; Nouhra et al. 2013)
<i>Wakefieldia</i> (<i>p. parte</i>)		Richard et al. 2011			SD ³
(<i>hydropus</i>)					
<i>Hydropus p. parte</i>		Peay et al. 2010; Smith et al. 2011		This study	Probably MDF or MDS

/hygrophorus					
<i>Hygrophorus</i>	Kropp & 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	C/SD: Agerer 2006
/inocybe					
<i>Auritella</i> (*)		Tedersoo et al. 2011		Matheny & Bouger 2006	C: (Tedersoo et al. 2011)
<i>Inocybe</i> (incl. <i>Astrosporina</i> , <i>Mallocybe</i>)	Cripps & Miller 1995; van der Heijden & Kuyper 2003	Zerova 1956; Schramm 1966; Ingleby et al. 1990; Horton et al. 1999; Magyar et al. 1999; Taylor & 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	SD (C/MDF): Agerer 2006 ; (Tedersoo et al. 2006b, 2011)
(<i>Tuberiomycetes</i>)				Alvarado et al. 2010	SD (C/MDF) ³
/laccaria					
<i>Hydnangium</i> *	Malajczuk et al. 1982; Malajczuk & Hartney 1986; Burgess et al. 1993; Lu et al. 1998	Chu-Chou & Grace 1981; Diez 2005		Mueller & Pine 1994; Matheny et al. 2006	SD ³
<i>Laccaria</i>	Bryan & Zak 1961 (as <i>Clitocybe</i>); Thomas & Jackson 1979; Molina & Trappe 1982; Godbout & Fortin 1985; Lu et al. 1998	Fassi & Fontana 1966; Gardes et al. 1991; Horton & Bruns 1998; Kernaghan 2001	Gebauer & 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 & Pine 1994; Moncalvo et al. 2002; Matheny et al. 2006	SD: Agerer 2006
(<i>Podohydnangium</i>)*				Mueller & Pine 1994	SD ³
/paralyophyllum					
<i>Lyophyllum p. parte</i> (<i>L. decastes</i> , <i>L. fumosum</i> , <i>L. shimeji</i> , <i>L. semitale</i>)	(Masui 1927); Norkrans 1950; Pera & Alvarez 1995; Kasuya & Igarashi 1996; Kawai 1997 ; Yamada et al. 2001	Agerer & Beenken 1998b; Bergemann & Garbelotto 2006	Kohzu et al. 1999; Trudell et al. 2004	Hofstetter et al. 2002; Moncalvo et al. 2002; Matheny et al. 2006; Larsson et al. 2012	MDF/MDS: Yamada et al. 2001 ; Agerer 2006
/tricholoma					
<i>Tricholoma</i>	Melin 1923a; Melin 1924; Melin 1925; Modess 1941; Fries 1942; Norkrans 1950; Pachlewski & Chrusciak 1980; Kropp & Trappe 1982	(Noack 1889); Masui 1927; Luppi & Gautero 1967 (cited in de Roman et al. 2005); Gehring et al. 1998; Horton et al. 1999; Lilleskov et al. 2002a; Shi et al. 2002	Hobbie et al. 1999; Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004; Tedersoo et al. 2007a; Zeller et al. 2007	Moncalvo et al. 2002; Matheny et al. 2006	MDF: Agerer 2006
ATHELIALES					
/amphinema-tylospora					
<i>Amphinema</i>	Danielson & Visser 1988	Fassi & De Vecchi 1963; Hagerman et al. 2001; Kernaghan 2001; Lilleskov et al. 2002a		Binder & Hibbett 2006	MDF: Agerer 2006
<i>Tylospora</i>	Taylor & Alexander	Dahlberg et al. 1997; Eberhart		Binder & Hibbett 2006	SD: Agerer 2006

	1991	et al. 1999; Jonsson et al. 2000			
/atheliales1					
<u>unnamed</u>		Peay et al. 2010 ; Tedersoo et al. 2010, 2011 ; Phosri et al. 2012		This study	MDM: (Tedersoo et al. 2011 ; L. Tedersoo & M. Bahram unpublished)
/atheliales2					
<u>unnamed</u>		Peay et al. 2010 ; Smith et al. 2011		This study	unknown
/byssocorticium					
<i>Byssocorticium</i>		Peyronel 1922 (as <i>Hypochnus cyanescens</i>); Shi et al. 2002; Bergemann & Garbelotto 2006; Tedersoo et al. 2008b		Binder & Hibbett 2006	SD/MDF: Agerer 2006 ; Tedersoo et al. unpublished
/piloderma					
<i>Piloderma</i>	Melin 1936; Zak 1976; Kropp 1982; Erland et al. 1990	Melin 1936; Dahlberg et al. 1997; Erland et al. 1999; Jonsson et al. 2000		Binder & Hibbett 2006	SD/MDF: Agerer 2006 ; Tedersoo et al. unpublished
<i>Tretomyces</i>		Parrent et al. 2006		Kotiranta et al. 2011	SD/MDF ³
BOLETALES					
/austropaxillus					
<i>Austropaxillus</i>	Garrido 1988; Burgess et al. 1993 (as <i>Paxillus</i>)	Palfner 2001 ; Nouhra et al. 2013		Binder & Hibbett 2006 ; Skrede et al. 2011	LD: Agerer 2006
(<i>Gymnopaxillus</i>)*				Binder & Hibbett 2006	LD ³
/boletus					
<i>Afroboletus</i>		Tedersoo et al. 2011		Binder & Hibbett 2006	LD ³
<i>Aureoboletus</i>		Walker et al. 2005	Kohzu et al. 1999	Binder & Hibbett 2006	LD ³
(<i>Australopilus</i>)				Halling et al. 2012a	LD ³
(<i>Astroboletus</i>)				Binder & Hibbett 2006	LD ³
<i>Boletellus</i>		Tedersoo et al. 2007b; Morris et al. 2009	Kohzu et al. 1999; Mayor et al. 2009	Binder & Hibbett 2006	LD: Tedersoo et al. 2007b
<i>Boletus</i>	(Doak 1934); Ferreira dos Santos 1941 (cited in Trappe 1962); (Hacsckaylo & Palmer 1955); Vozzo & Hacsckaylo 1961; Malajczuk et al. 1982; Molina & Trappe 1982; Dunabeitia et al. 1996	(Peyronel 1920); Horton et al. 1999; Jonsson et al. 2000; Dickie et al. 2002	Kohzu et al. 1999; Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004	Binder & Hibbett 2006	LD: Agerer 2006
(<i>Borofutus</i>)				Hosen et al. 2013	LD ³
(<i>Bothia</i>)				Halling et al. 2007	LD ³
<i>Chamonixia</i> *		Raidl 1999 ; Jones et al. 2008 ; Horton et al. 2013		Binder & Hibbett 2006	LD: Agerer 2006
(<i>Corneroboletus</i>)				Zeng et al. 2012	LD ³
(<i>Durianella</i>)*				Desjardin et al. 2008	LD ³
(<i>Fistulinella</i>)				Binder & Hibbett 2006	LD ³
<i>Gastroboletus</i> *	Molina & Trappe 1982			Dentinger et al. 2010	LD: (Molina & Trappe 1982)
(<i>Gymnogaster</i>)*				Halling et al. 2012a	LD ³

<i>(Harrya)</i>				Halling et al. 2012a	LD ³
<i>Heimioporus</i> (syn. <i>Heimiella</i>)	Bryan & Zak 1961 (as <i>Boletus</i>)		Kohzu et al. 1999	M. Binder unpublished	LD ³
<i>(Heliogaster)*</i>				Orihara et al. 2010	LD ³
<i>(Hemileccinum)</i>				Halling et al. 2012a	LD ³
<i>(Leccinellum)</i>				Binder & Hibbett 2006	LD ³
<i>Leccinum</i>	Melin 1923a (as <i>Boletus</i>); Molina & 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 & Hibbett 2006	LD: Agerer 2006
<i>(Mackintoshia)*</i>				M.E. Smith unpublished	LD ³
<i>Mycoamaranthus*</i>		Yomyart et al. 2007		Yomyart et al. 2007	LD ³
<i>Octaviania p. parte*</i>		Chilvers 1968; Orihara et al. 2012		Binder & Hibbett 2006; Orihara et al. 2012	LD: Agerer 2006
<i>(Phyllobotellus)</i>				Binder & Hibbett 2006	LD ³
<i>(Phyllobolites)</i>				Nuhn et al. 2013	LD ³
<i>Phylloporus</i>	Vozzo & Hacskaylo 1961 (as <i>Paxillus</i>)	Lian et al. 2006 ; Burke et al. 2009	Trudell et al. 2004	Binder & Hibbett 2006	LD ³
<i>Porphyrellus</i>		Raidl & Hahn 2006		Binder & Hibbett 2006	LD: Agerer 2006
<i>Pseudoboletus</i>	Richter & Bruhn 1989			Desjardin et al. 2009	LD: Richter & Bruhn 1989
<i>(Pulveroboletus)</i>				Binder & Hibbett 2006	LD ³
<i>(Retiboletus)</i>				Binder & Hibbett 2006	LD ³
<i>(Rhodactina)*</i>				Yang et al. 2006; no ITS available	LD ³
<i>Rossbeevera*</i>		Tedersoo et al. 2009a; Horton et al. 2013		Lebel et al. 2012	LD ³
<i>(Royoungia)*</i>				Halling et al 2012a	LD ³
<i>(Rubinoboletus p. parte)</i>				Nuhn et al. 2013	LD ³
<i>(Soliocasus)*</i>				(Trappe et al. 2013)	LD ³
<i>(Spongiforma)*</i>				Desjardin et al. 2009	LD ³
<i>Strobilomyces</i>		(Peyronel 1920); Matsuda & Hijii 1999; Riviere et al. 2007; Sato et al. 2007	Kohzu et al. 1999	Binder & Hibbett 2006	LD: Matsuda & Hijii 1999
<i>(Sutorius)</i>				Halling et al. 2012b	LD ³
<i>(Turmalinea)</i>				Orihara et al. submitted	LD ³
<i>Tylopilus</i>	(Doak 1934); Vozzo & Hacskaylo 1961; Brundrett et al. 1996;	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 & Hibbett 2006	LD: Agerer 2006

	Reddell et al. 1999				
<i>Xanthoconium</i>			Kohzu et al. 1999	Denting et al. 2010	LD ³
<i>Xerocomellus</i>		Aponte et al. 2010		Halling et al. 2012a	LD ³
<i>Xerocomus</i>	Melin 1923b; Modess 1941; Bokor 1958; Bryan & Zak 1961; Vozzo & Hacskaylo 1961; Dunabeitia et al. 1996; van der Heijden & Kuyper 2003	(Peyronel 1922); Ceruti & Bussetti 1962; Gronbach 1988; Gardes & Bruns 1996; Horton & Bruns 1998; Horton et al. 1999; Jonsson et al. 1999b	Gebauer & Dietrich 1993; Gebauer & Taylor 1999; Taylor et al. 2003; Zeller et al. 2007; Zeller et al. 2008	Binder & Hibbett 2006	LD: Agerer 2006
(<i>Zangia</i>)				Li et al. 2011	LD ³
/ <i>paxillus-gyrodon</i>					
<i>Alpova</i> *	Godbout & Fortin 1983; Danielson & Visser 1988; Massicotte et al. 1988	Massicotte et al. 1988; Miller et al. 1991; Taylor & Bruns 1999; Bergemann & Garbelotto 2006;		Binder & Hibbett 2006	LD: Agerer 2006
<i>Gyrodon s. stricto</i>	(Godbout & Fortin 1985)	Becerra et al. 2005a; Tedersoo et al. 2006b; Tedersoo et al. 2009c		Kretzer & Bruns 1999; Binder & Hibbett 2006; Yang et al. 2006	LD: Agerer 2006
<i>Melanogaster</i> *	Malajczuk et al. 1982; Molina & Trappe 1982; Pera & Alvarez 1995	Shi et al. 2002; Wiedmer et al. 2004; Cline et al. 2005; Bergemann & Garbelotto 2006; Tedersoo et al. 2006b;		Binder & Hibbett 2006; Yang et al. 2006	LD: Agerer 2006
(<i>Paragyrodon</i>)				Binder & Hibbett 2006	LD ³
<i>Paxillus</i>	Laiho 1970; Molina & Trappe 1982; Malajczuk et al. 1982	Laiho 1970; Lilleskov et al. 2002a; Korkama et al. 2006; Tedersoo et al. 2006b	Gebauer & Dietrich 1993; Gebauer & Taylor 1999; Taylor et al. 2003; Zeller et al. 2007	Kretzer & Bruns 1999; Binder & Hibbett 2006; Yang et al. 2006	LD: Agerer 2006
/ <i>pisolithus-scleroderma</i>					
<i>Astraeus</i>	Trappe 1967; Molina & Trappe 1982; Malajczuk et al. 1982	Schramm 1966; Dickie & Reich 2005		Binder & Hibbett 2006	LD: Agerer 2006
<i>Calostoma</i>		Wilson et al. 2007	Wilson et al. 2007	Binder & Hibbett 2006	LD: Wilson et al. 2007
(<i>Corditubera</i>)*				Smith & Schmull 2011	LD ³
(<i>Diplocystis</i>)(*)				Binder & Hibbett 2006	LD ³
<i>Gyroporus</i>	Hatch & Hatch 1933; Vozzo & Hacskaylo 1961;	Peyronel 1922 (as <i>Boletus</i>); Agerer 1999a; Avis et al. 2008	Wilson et al. 2007	Binder & Hibbett 2006	LD: Agerer 2006
(<i>Horakiella</i>)*				M.E. Smith & J.M. Trappe unpublished	LD ³
<i>Pisolithus</i>	Bryan & Zak 1961; Zak 1976; Marx et al. 1977	(Kljushnik 1952); Schramm 1966; Tedersoo et al. 2007b	Kohzu et al. 1999	Binder & Hibbett 2006	LD: Agerer 2006
<i>Scleroderma</i> (*)	(Doak 1934); Modess 1941; Fries 1942; Bokor 1958; Vozzo & Hacskaylo 1961; Malajczuk et al. 1982; Dunabeitia et al. 1996;	McDougall 1914; (Peyronel 1920); Masui 1927; Zerova 1950; (Fassi 1957); Thoen & Ba 1989; Nara & Hogetsu 2004; Valentine et al. 2004; Murat et al. 2005	Kohzu et al. 1999; Wilson et al. 2007; Zeller et al. 2007	Binder & Hibbett 2006	LD: Agerer 2006

	Lu et al. 1998; Reddell et al. 1999; van der Heijden & Kuyper 2003				
(<i>Tremellogaster</i>) ^(*)				Binder & Hibbett 2006	LD ³
/ <i>suillus-rhizopogon</i>					
(<i>Brauniellula p. parte</i>) [*]				Miller 2003	C ³
<i>Chroogomphus</i>		Agerer 1990; Douglas et al. 2005	Kohzu et al. 1999; Taylor et al. 2003; see Trudell et al. (2004) for contrasting evidence	Binder & Hibbett 2006	C: Agerer 2006
<i>Gomphidius</i>	(Ohga & Wood 2000)	Agerer 1991b; Olsson et al. 2000	Hobbie et al. 2001; Taylor et al. 2003; Trudell et al. 2004	Binder & Hibbett 2006	MDS: Agerer 2006
<i>Rhizopogon</i> [*]	Young 1937 (cited in Trappe 1962); Modess 1941; (Hacskeylo 1953); Hacskeylo & Palmer 1955; Trappe 1967; Pachlewski & Chrusciak 1980; Malajczuk et al. 1982; Molina & Trappe 1982	(Fontana & Centrella 1967); Gardes & Bruns 1996; Gehring et al. 1998; Horton & Bruns 1998; Horton et al. 1999	Kohzu et al. 1999; Taylor et al. 2003	Binder & Hibbett 2006	LD: Agerer 2006
(<i>Rhopalogaster</i>) [*]				Hosaka et al. 2006 ; M.E. Smith unpublished	LD ³
<i>Suillus</i> (incl. <i>Boletinus</i>)	Melin 1922; Hammarlund 1923; Melin 1923b; Melin 1924; Melin 1925; Masui 1927; Hatch & Hatch 1933; Doak 1934; Fries 1942; Vozzo & Hacskeylo 1961; Trappe 1967; Pachlewski & Chrusciak 1980; Malajczuk et al. 1982; Molina & Trappe 1982	(Frank 1892); (Peyronel 1920); (Peyronel 1922); Peyronel 1929; Gardes & 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 & Hibbett 2006	LD: Agerer 2006
<i>Truncocolumella</i> [*]	Malajczuk et al. 1982; Molina & Trappe 1982; Massicotte et al. 2000	Goodman et al. 1996-2000; Cline et al. 2005; Horton et al. 2005		Binder & Hibbett 2006	MDS: Agerer 2006
CANTHARELLALES S. LATO					
/ <i>cantharellus</i>					
<i>Cantharellus</i>	(Doak 1934); Danell et al. 1994	Goodman et al. 1996-2000; Agerer et al. 1987-2006	Gebauer & Dietrich 1993; Gebauer & 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	MDS: Agerer 2006
<i>Craterellus</i>		Goodman et al. 1996-2000; Jonsson et al. 2000b; Shi et al.	Taylor et al. 2003; Zeller et al. 2007; Mayor et al. 2009	Moncalvo et al. 2006	SD: Agerer 2006

		2002; Walker et al. 2005			
<i>Hydnnum</i>	Lu et al. 1998	Masui 1927; Agerer et al. 1996; Horton et al. 2005; Courty et al. 2008	Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004; Zeller et al. 2007	Moncalvo et al. 2006	MDS: Agerer 2006
<i>Pseudocraterellus</i>		Bahram et al. 2011, 2012			SD: T. Naadel & L. Tedersoo unpublished
<i>Pterygellus</i>		(Verbeke & Walleyn 1999)		INSDc unpublished data	
<i>Sistotrema p. parte</i>		Lian et al. 2006; Nilsson et al. 2006a; Smith et al. 2007		Moncalvo et al. 2006	MDF: Agerer 2006 ; Münzenberger et al. 2012
<i>/clavulina</i>					
<i>Clavulina</i>		Dickie et al. 2002; Kennedy et al. 2003; Tedersoo et al. 2003	Gebauer & Taylor 1999 (misconsidered); Hobbie et al. 2001; Trudell et al. 2004; Zeller et al. 2008; Mayor et al. 2009	Moncalvo et al. 2006	C: (Tedersoo et al. 2003, 2011)
<i>Membranomyces</i>		Tedersoo et al. 2003 (as <i>Clavulicium</i>); Ishida et al. 2007		Moncalvo et al. 2006; Uehling et al. 2012	C: (Tedersoo et al. 2003)
<i>/tulasnella1</i>					
<i>Tulasnella p. parte</i>	(Bidartondo et al. 2003)	(Haug & Oberwinkler 1987); Bidartondo et al. 2003; Tedersoo et al. 2008b;		Moncalvo et al. 2006	C: Bidartondo et al. 2003 ; I. Ostonen & L. Tedersoo unpublished
<i>/tulasnella2</i>					
<i>Tulasnella p. parte</i>		Tedersoo et al. 2008a ; Nouhra et al. 2013		L. Tedersoo unpublished	C: (Tedersoo et al. 2008a ; Nouhra et al. 2013)
<i>/ceratobasidium1</i>					
<i>Ceratobasidium p. parte</i>	Warcup 1991b; Yagame et al. 2008, 2012	Yagame et al. 2008, 2012; Tedersoo et al. 2011		Veldre 2009 ; Veldre et al. 2013	C: (Tedersoo et al. 2011)
<i>/ceratobasidium2</i>					
<i>Ceratobasidium p. parte</i>		(Rosling et al. 2003); Wilson et al. 2007		Veldre 2009 ; Veldre et al. 2013	C: (L. Tedersoo unpublished)
GOMPHALES					
<i>/clavariadelphus</i>					
<i>Clavariadelphus p. parte</i> (incl. <i>C. subfastigiatus</i> ; <i>C. truncatus</i> , <i>C. pistillaris</i>)		Izzo et al. 2005a; Iosifidou & Raidl 2006; Smith et al. 2007; Morris et al. 2008		Hosaka et al. 2006	MDM: Agerer 2006
<i>/ramaria-gautieria</i>					
<i>(Destuntzia)*</i>				INSDc, unpublished data	MDM³
<i>Gautieria*</i>	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	MDM: Agerer 2006
<i>(Gloeocantharellus)</i>				Hosaka et al. 2006	MDM³
<i>Gomphus</i>		Agerer et al. 1998b	Trudell et al. 2004	Hosaka et al. 2006	MDM: Agerer 2006
<i>Ramaria p. parte</i>		Agerer 1996b; Dickie et al. 2002; Smith et al. 2004; Horton et al. 2005	Kohzu et al. 1999; Hobbie et al. 2001; Trudell et al. 2004;	Hosaka et al. 2006	MDM: Agerer 2006
<i>Turbinellus</i>		Masui 1927 (as <i>Cantharellus</i>)	Kohzu et al. 1999	Hosaka et al. 2006	MDM³

HYMENOCHAETALES					
/coltricia					
<i>Coltricia</i>	(Pachlewski & Chrusciak 1980); Danielson 1984b; Danielson & Visser 1988	Danielson 1984b; Danielson & Visser 1988; Thoen & Ba 1989; Cullings et al. 2001; Tedersoo et al. 2007c; Morris et al. 2008a	Tedersoo et al. 2007a	Larsson et al. 2006; Tedersoo et al. 2007c	SD: Tedersoo et al. 2007c
<i>Coltriciella</i>		Taniguchi et al. 2007; Tedersoo et al. 2007c; Tedersoo et al. 2008a	Mayor et al. 2009	Larsson et al. 2006; Tedersoo et al. 2007c	SD: Tedersoo et al. 2007c
HYSTERANGIALES					
/hysterangium					
<i>(Andebbia)*</i>				Hosaka et al. 2006	MDM³
<i>(Aroramycetes)*</i>				Hosaka et al. 2006	MDM³
<i>Austrogautieria*</i>		(Thoen & Ba 1989)		Hosaka et al. 2006	MDM³
<i>Castoreum*</i>	Brundrett et al. 2005	(Dell et al. 1990)		Hosaka et al. 2006	MDM³
<i>Chondrogaster*</i>	Lupatini et al. 2008	Lupatini et al. 2008			MDM³
<i>(Gallacea)*</i>				Hosaka et al. 2006	MDM³
<i>Gummiglobus*</i>	Reddell et al. 1999			Hosaka et al. 2006	MDM³
<i>(Hallingea)*</i>				Hosaka et al. 2006	MDM³
<i>Hysterangium*</i>	Malajczuk et al. 1982; Molina & Trappe 1982; Theodorou & Reddell 1991; Brundrett et al. 2005	Ceruti & Bussetti 1962; Fontana & Centrella 1967; Griffiths et al. 1991; Smith et al. 2007		Hosaka et al. 2006	MDM: Agerer 2006
<i>(Malajczukia)*</i>				Hosaka et al. 2006	MDM³
<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	MDM³
<i>Nothocastoreum*</i>	Reddell et al. 1999			Hosaka et al. 2006	MDM³
<i>(Protubera p. parte: P. nothofagi)*</i>				Hosaka et al. 2006	MDM³
POLYPORALES					
(/xenasmatella)					
<i>Xenasmatella p.parte</i>		Peay et al. 2010; Smith et al. 2011, 2013a		This study	LD³ (<i>X. vaga</i>: Cairney & Clipson 1991).
RUSSULALES					
/albatrellus					
<i>Albatrellus</i> (incl. <i>Scutiger</i>)		(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	MDS: Agerer 2006
<i>Byssoporia</i>	Zak 1976 (as <i>Poria</i>); Kropp 1982	Zak 1969 (as <i>Poria</i>)		Miller et al. 2006	MDS: Agerer 2006
<i>(Fevansia)*</i>				Smith et al. 2013b	MDS³
<i>Leucogaster*</i>		Izzo et al. 2005b		Miller et al. 2006; Albee-Scott 2007	MDS³
<i>Leucophleps*</i>		Izzo et al. 2005b		Albee-Scott 2007	MDS³

(<i>Mycolevis</i>)*				Miller et al. 2006; Albee-Scott 2007	MDS ³
<i>Polyporoletus</i>		Agerer et al. 1998a		Miller et al. 2006; Albee-Scott 2007	MDS: Agerer 2006
/ <i>russula-lactarius</i>					
<i>Arcangeliella</i> *		Luppi & 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 & Tonkin 2007	C: Agerer 2006
(<i>Cystangium</i>)*				Miller et al. 2006	C ³
<i>Gastrolactarius</i> *		Izzo et al. 2005a (as <i>Arcangeliella</i>)			C/MDS ³
<i>Gymnomyces</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 & Tonkin 2007	C ³
<i>Lactarius</i>	Melin 1924; Melin 1925; Hatch & Hatch 1933; Modess 1941; Riffle 1973; Zak 1976; Antibus et al. 1981; Kropp & Trappe 1982; Malajczuk et al. 1982; Godbout & Fortin 1985; Lu et al. 1998	(Noack 1889); (Peyronel 1922); Luppi & Gautero 1967; Gronbach 1988; Kraigher et al. 1995; Gardes & 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 & Tonkin 2007; Buyck et al. 2008	C/MDS: Agerer 2006
<i>Macowanites</i> *		Kennedy et al. 2003; Izzo et al. 2005a; Izzo et al. 2005b		Peter et al. 2001; Miller et al. 2006; Lebel & Tonkin 2007	C ³
<i>Martellia</i> *	Trappe & Castellano 1986	Trappe & Castellano 1986; Horton et al. 2005; Izzo et al. 2005b		Peter et al. 2001; Miller et al. 2006	C ³
(<i>Multifurca</i>)				Buyck et al. 2008	unknown
<i>Russula</i>	Melin 1924; Melin 1925; (Doak 1934); Bokor 1958; Vozzo & Hacsaylo 1961; Pachlewski & Chrusciak 1980; Kropp & Trappe 1982; Taylor & Alexander 1989; Dunabeitia et al. 1996	(Frank 1892); (McDougall 1914); (Peyronel 1922); Peyronel 1929; Gardes & Bruns 1996; Dahlberg et al. 1997; Kernaghan et al. 1997; Gehring et al. 1998; Horton & Bruns 1998; Horton et al. 1998	Hobbie et al. 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; Zeller et al. 2008; Mayor et al. 2009 ; for contrasting evidence, see Gebauer & Taylor (1999)	Peter et al. 2001; Miller et al. 2006; Lebel & Tonkin 2007; Buyck et al. 2008	C (SD/MDS/MDF): Agerer 2006 ; Tedersoo et al. 2011
<i>Zelleromyces</i> *	Molina & Trappe 1982; Reddell et al. 1999			Peter et al. 2001; Miller et al. 2006; Lebel & Tonkin 2007	C: Molina & Trappe 1982 ; Reddell et al. 1999
SEBACINALES					
/ <i>sebacina</i>					

<i>Sebacina</i> (clade A sensu Weiβ et al. p. parte)		Glen et al. 2002; Selosse et al. 2002; Urban et al. 2003; Tedersoo et al. 2003		Walker & Parrent 2004; Weiβ et al. 2004; Selosse et al. 2007	SD (C): Agerer 2006 ; L. Tedersoo unpublished
<i>Tremellodendron</i>		Walker & Parrent 2004	Mayor et al. 2009	Walker & Parrent 2004; Weiβ et al. 2004; Selosse et al. 2007	SD ³
<i>(Tremelloscypha)</i>				Weiβ et al. 2004; Selosse et al. 2007	C/SD ³
<i>/serendipita1</i>					
<i>Serendipita</i> p. parte (<i>Sebacina</i> clade B sensu Weiβ et al. 2004)		Trowbridge & Jumpponen 2004 ; Menkis et al. 2005 ; Nara 2006		This study	C/SD: (Tedersoo et al. 2008b ; C. Andrew, pers. comm.)
<i>/serendipita2</i>					
<i>Serendipita</i> p. parte (<i>Sebacina</i> clade B sensu Weiβ et al. 2004)		Izzo et al. 2006 ; Bergemann & Garbelotto 2006; Ryberg et al. 2009		This study	C/SD: D. Southworth, pers. comm.
THELEPHORALES					
<i>/boletopsis</i>					
<i>Boletopsis</i>		Agerer 1992c ; Izzo et al. 2005 ; Bergemann & Garbelotto 2006	Trudell et al. 2004	U. Köljalg et al. unpublished	MDM: Agerer 2006
<i>/hydnellum-sarcodon</i>					
<i>Hydnellum</i>		Agerer 1993; Kernaghan 2001; Walker et al. 2005; Bergemann & Garbelotto 2006;	Kohzu et al. 1999; Taylor et al. 2003; Trudell et al. 2004	U. Köljalg et al. unpublished	MDM: Agerer 2006
<i>Sarcodon</i>		(Masui 1927 as <i>Hydnus</i>); Agerer 1991a; Kernaghan 2001; Izzo et al. 2005a	Taylor et al. 2003; Trudell et al. 2004	U. Köljalg et al. unpublished	MDM: Agerer 2006
<i>/phellodon-bankera</i>					
<i>Bankera</i>	Danielson 1984b	Masui 1927 (as <i>Polyporus</i>); Agerer & Otto 1997; Bergemann & Garbelotto 2006		U. Köljalg et al. unpublished	MDM: Agerer 2006
<i>Phellodon</i>		Agerer 1992a; (Bergemann & Garbelotto 2006)	Kohzu et al. 1999; Taylor et al. 2003	U. Köljalg et al. unpublished	MDM: Agerer 2006
<i>/pseudotomentella</i>					
<i>Pseudotomentella</i> s. <i>stricto</i>		Agerer 1994; Köljalg et al. 2000; Smith et al. 2004; Cline et al. 2005; Izzo et al. 2005a		U. Köljalg et al. unpublished	MDS: di Marino et al. 2007 ; L. Tedersoo unpublished
<i>(Polyozellus)</i>				U. Köljalg et al. unpublished	MDS ³
<i>/tomentella-thelephora</i>					
<i>Thelephora</i>	Hacskeylo 1965; Zak 1976; Thomas & Jackson 1979	Fassi & 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. Köljalg et al. unpublished	SD/MDS: Agerer 2006 ; L. Tedersoo, unpublished
<i>Tomentella</i> (incl. <i>Riessia</i> <i>radicicola</i> , <i>Riessiella</i> spp)	Danielson & Visser 1988; (Warcup 1990c); Cairney et al. 1994	Danielson & Visser 1988; Danielson & Pruden 1989; Gardes & Bruns 1996; Horton & Bruns 1998; Taylor & Bruns 1999; Köljalg et al. 2000	Mayor et al. 2009 (unreplicated)	U. Köljalg et al. unpublished	C/SD/MDS: Agerer 2006 ; L. Tedersoo unpublished
<i>/tomentellopsis</i>					

<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	MDS: Agerer 2006
BASIDIOMYCOTA INCERTAE SEDIS					
/agaricomycetes1					
Unnamed		Bergemann & Garbelotto 2006; Ishida et al. 2007; Horton et al. 2013; Nouhra et al. 2013		This study	SD: (Nouhra et al. 2013)
ASCOMYCOTA					
DOTHIDEOMYCETES INCERTAE SEDIS					
/cenococcum					
<i>Cenococcum</i>	Hatch & Hatch 1933; Hatch 1934 (as <i>Mycelium radicis nigrostrigosum</i>); Lihnell 1942; Mikola 1948	Ferdinandsen & Winge 1925; Hatch 1934; Lihnell 1942; Dahlberg et al. 1997; Horton & Bruns 1998; Horton et al. 1999		LoBuglio et al. 1996; Spatafora et al. 2012	SD: Agerer 2006
EUROTIALES					
/elaphomycetes					
<i>Elaphomycetes</i> *	Warcup 1990c; Theodorou & Reddell 1991; Reddell et al. 1999	Reeß 1880; (Frank 1892); Fontana & Centrella 1967; Tedersoo et al. 2003; Smith et al. 2007, 2011; Courty et al. 2008		LoBuglio et al. 1996; Henkel et al. 2006	SD: Reddell et al. 1999; Agerer 2006
<i>Pseudotulostoma</i> *		Henkel et al. 2006; Smith et al. 2011	Mayor et al. 2009	Miller et al. 2001	SD: Henkel et al. 2006
HELOTIALES					
/acephala macrosclerotiorum					
<i>Acephala macrosclerotiorum</i>	Münzenberger et al. 2009	Menkis et al. 2004 (as <i>Phialocephala</i> sp6); Münzenberger et al. 2009		Münzenberger et al. 2009	SD: Münzenberger et al. 2009
/meliniomyces					
<i>Cadophora finlandica</i> (incl. <i>Chloridium paucisporum</i>)	Wilcox et al. 1974; Wang & Wilcox 1985; Wilcox & Wang 1987; Ursic & Peterson 1997	Ursic & Peterson 1997; Tedersoo et al. 2003; Püttsepp et al. 2004; Korkama et al. 2006		Vrålstad et al. 2002a; Hambleton & Sigler 2005	SD: Wilcox et al. 1974
<i>Meliomyces p. parte</i> (<i>M. bicolor</i>)	Thomas & Jackson 1979 (as type 5); Vrålstad et al. 2002b	Gronbach 1988; Vrålstad et al. 2000; Vrålstad et al. 2002a; Tedersoo et al. 2008b		Vrålstad et al. 2002a; Hambleton & Sigler 2005	SD: Vrålstad et al. 2002b
/helotiales1					
Unnamed		Clade III (Fig. 1) in Vrålstad et al. 2002a; Smith et al. 2004		Vrålstad et al. 2002a	SD ³
/helotiales2					
Unnamed		Tedersoo et al. 2008b; Kjoller et al. 2009; Jarvis et al. 2013		Tedersoo et al. 2009b	SD: (Tedersoo et al. 2008b)
/helotiales3					
Unnamed		Tedersoo et al. 2008a;		Tedersoo et al. 2009b	SD: (Tedersoo et al. 2008a)

		Tedersoo et al. 2009a			
/helotiales4					
(<i>Discinella p. parte (D. terrestris group)</i>)		Tedersoo et al. 2008a; Tedersoo et al. 2009a; Horton et al. 2013		Tedersoo et al. 2009b	SD: (Tedersoo et al. 2008a)
/helotiales5					
Unnamed		Tedersoo et al. 2008a; Tedersoo et al. 2009a		Tedersoo et al. 2009b	SD: (Tedersoo et al. 2008a)
/helotiales6					
Unnamed		Tedersoo et al. 2008a; Tedersoo et al. 2009a		Tedersoo et al. 2009b	C: (Tedersoo et al. 2008a)
PEZIZALES					
/aleurina					
<i>Aleurina</i>		Ishida et al. 2007 ; Tedersoo et al. 2008a; Nouhra et al. 2013		Perry et al. 2007 ; Tedersoo et al. 2013	C/SD: (Nouhra et al. 2013)
(<i>Gelinipes, nom. prov.</i>)*				Perry et al. 2007	C/SD ³
<i>Unicava*, nom. prov.</i>				Perry et al. 2007 ; Tedersoo et al. 2013	C/SD ³
/galactinia					
<i>Galactinia(*) (Peziza p. parte)</i>		Valentine et al. 2004; Tedersoo et al. 2006a; Smith et al. 2007		Hansen et al. 2005; Tedersoo et al. 2006a	C: Tedersoo et al. 2006a
/genea-humaria					
<i>Genabea*</i>		Izzo et al. 2005b; Smith et al. 2006b; Morris et al. 2008		Smith et al. 2006b; Perry et al. 2007	SD: McDonald et al. 2010; (Tedersoo et al. 2013b)
<i>Genea*</i>		Fontana & Centrella 1967; Jakucs et al. 1998; Lilleskov et al. 2002a; Tedersoo et al. 2006b; Smith et al. 2006b; ErösHonti et al. 2008		Smith et al. 2006b; Tedersoo et al. 2006a; Perry et al. 2007	SD: Tedersoo et al. 2006a
<i>Gilkeya*</i>		Moser et al. 2009; McDonald et al. 2010		Smith et al. 2006b; Perry et al. 2007	SD: Moser et al. 2009
<i>Humaria</i>		Tedersoo et al. 2006b; ErösHonti et al. 2008; Morris et al. 2009		Smith et al. 2006b; Tedersoo et al. 2006a; Perry et al. 2007	SD: Tedersoo et al. 2006a
<i>Parascutellinia</i>		Tedersoo et al. 2013b		Perry et al. 2007; Tedersoo et al. 2013a	(SD: Tedersoo et al. 2013b)
/geopora					
<i>Geopora</i> (incl. <i>Sepultaria</i> , <i>Hydnocystis clausa</i>)(*)		Gehring et al. 1998; Fujimura et al. 2005; Tedersoo et al. 2006b		Hansen & Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007; Stielow et al. 2013; This study	SD: Tedersoo et al. 2006a
<i>Picoa*</i>	Gutierrez et al. 2003			Sbissi et al. 2010; Stielow et al. 2013; This study	SD: Gutierrez et al. 2003; A. Morte, pers. comm.
<i>Tricharina p. parte (T. ochroleuca)</i>		Trocha et al. 2006; Smith et al., 2009		Perry et al. 2007	
/hydnotrya					
<i>Hydnotrya*</i>	Lu et al. 1998	Peyronel 1929; Tedersoo et al.	Hobbie et al. 2001	Hansen & Pfister 2006;	C: Tedersoo et al. 2006a ;

		2003; Izzo et al. 2005b		Tedersoo et al. 2006a	T. Leski, pers. comm.
<i>/leucangium</i>					
<i>Fischerula</i> *			Hobbie et al. 2001	Hansen & Pfister 2006	C ³
<i>(Imia)</i> *				Kovács et al. 2008	C ³
<i>Leucangium</i> *		Palfner & Agerer 1998b	Hobbie et al. 2001	Hansen & Pfister 2006	C: Agerer 2006
<i>(Kalapuya)</i> *				Trappe et al. 2010	C ³
<i>/marcelleina-peziza gerardii</i>					
<i>Hydnobolites</i> *		Smith et al. 2007; Morris et al. 2008; Tedersoo et al. 2008b		Tedersoo et al. 2010NP; Healy et al., 2013	SD/C (Tedersoo et al. 2008b, 2012, unpublished)
<i>Delastria</i>		Rincon & Pueyo 2010; Buscardo et al. 2012		Alvarado et al. 2011 ; Kovacs et al. 2011 ; Healy et al. 2013	SD/C ³
<i>(Marcelleina)</i>				Hansen et al. 2005	
<i>Peziza gerardii</i>		Smith et al. 2007; Morris et al. 2008 (as Marcelleina)		Hansen et al. 2005	
<i>(Stouffera)</i> *				Kovacs et al. 2011	SD/C ³
<i>(Temperantia)</i> *				Kovacs et al. 2011	SD/C ³
<i>/otidea</i>					
<i>Otidea(*)</i>		Kennedy et al. 2003; Smith et al. 2004; Toljander et al. 2006; Smith et al. 2007	Hobbie et al. 2001	Perry et al. 2007; Smith & Healy 2009	SD: Southworth et al. 2009; (Tedersoo et al. 2013b)
<i>/pachyphloeus-amyłascus</i>					
<i>Amyłascus</i> *		Nouhra et al. 2013		Hansen et al. 2005; Tedersoo et al. 2006a ; Healy et al. 2013	SD: (Nouhra et al. 2013)
<i>Chromelosporium p. parte (anamorph)</i>		Palmer et al. 2008		Healy et al. 2013	SD: (Tedersoo et al. 2008b)
<i>Glischroderma (anamorph)</i>		Tedersoo et al. 2006a; Morris et al. 2009		Tedersoo et al. 2006a; Healy et al. 2013	SD: Tedersoo et al. 2006a
<i>Pachyphloeus</i> *		Tedersoo et al. 2006a; Smith et al. 2007		Hansen et al. 2005; Tedersoo et al. 2006a ; Healy et al. 2013	SD: Tedersoo et al. 2006a
<i>Scabropezia</i>		Morris et al. 2008 ; Tedersoo et al. 2009c		Hansen et al. 2005; Tedersoo et al. 2006a ; Healy et al. 2013	SD: (Tedersoo et al. 2009c)
<i>/pulvinula</i>					
<i>Pulvinula p. parte (P. constellatio, P. tetraspora)</i>	Warcup 1990a	Bencivenga et al. 1995 (cited in de Roman et al. 2005); Amicucci et al. 2001		Perry et al. 2007; Tedersoo et al. 2013 ; This study	SD: Amicucci et al. 2001 ; (Tedersoo et al. 2013b)
<i>/pustularia</i>					
<i>Pustularia patavina</i>		Kennedy et al. 2003 ; Menkis et al. 2005 ; Izzo et al. 2006 ; Trocha et al. 2006		Perry et al. 2007 ; Tedersoo et al. 2013a; This study	SD: (Bahram et al. 2012 ; D. Southworth, pers. comm)
<i>/pyronemataceae1</i>					
Unnamed		Pruett et al. 2008 ; Cavender-Bares et al. 2009 ; Bonito et al. 2012 ; Nouhra et al. 2013		Tedersoo et al. 2013a; This study	SD: (Nouhra et al. 2013)

/pyronemataceae2					
unnamed		Izzo et al. 2005b; Smith et al. 2009 ; Hoeksema et al. 2012		Tedersoo et al. 2013a ; This study	Probably SD
/rhodoscypha					
<i>Rhodoscypha</i>		Jones et al. 2008		Perry et al. 2007 ; Tedersoo et al. 2013a	Probably SD
/sarcosphaera-hydnotryopsis					
<i>Hydnotryopsis</i> *		Frank et al., 2006; Smith et al. 2007		Hansen et al. 2005; Tedersoo et al. 2006a	SD ³
<i>Sarcosphaera</i>		Tedersoo et al. 2006a	Tedersoo et al. 2007a	Hansen et al. 2005; Tedersoo et al. 2006a	SD: Tedersoo et al. 2006a
(<i>sowerbyella</i>) ¹					
<i>Sowerbyella</i>			Hobbie et al. 2001	Perry et al. 2007	Probably SD
/sphaerosporella					
<i>Sphaerosporella</i>	Danielson 1984a; Egger & Paden 1986; Danielson & Visser 1988	Danielson 1984a; Danielson & Visser 1988; Rincon et al. 2007; Stefani et al. 2009		Hansen & Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007; This study	SD: Agerer 2006
<i>Trichophaea woolhopeia</i>		Tedersoo et al. 2006a; Mühlmann & Peintner 2008 ; Rubini et al. 2011		Hansen & Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007; This study	SD: Tedersoo et al. 2006a; Rubini et al. 2010
/tarzetta					
<i>Tarzetta</i>		Tedersoo et al. 2006a; Smith et al. 2007; Mühlmann & Peintner 2008		Hansen & Pfister 2006; Tedersoo et al. 2006a	C/SD: (Nouhra et al. 2013; Tedersoo et al. 2013b)
/terfezia-peziza depressa					
<i>Cazia</i> *		Frank et al. 2009 ; Bahram et al. 2011		Hansen et al. 2005; Tedersoo et al. 2006a	SD ³
<i>Chromelosporium p. parte</i>		Palmer et al. 2008			SD: Barroetavena et al. 2010
<i>Hydnoplicata</i> *	Warcup 1990a (as <i>Peziza whitei</i>)	Smith et al. 2007; Morris et al. 2008			SD ³
(<i>Mycoclelandia</i>)*				Trappe et al. 2009a	SD ³
<i>Peziza p. parte</i> (incl. <i>P. badia</i> , <i>P. depressa</i> , etc.)(*)	Warcup 1990a	Cline et al. 2005; Tedersoo et al. 2006b; Tedersoo et al. 2008b; Palmer et al. 2008		Hansen et al. 2005; Tedersoo et al. 2006a	SD: Tedersoo et al. 2006a
<i>Ruhlandiella</i> *	Warcup & Talbot 1989 (as <i>Muciturbo</i>); Warcup 1991a	Jairus et al. 2011		Hansen et al. 2005; Tedersoo et al. 2006a ; Healy et al. 2013	SD: (Jairus et al. 2011)
<i>Sphaerozone</i> *		Shi et al. 2002; Tedersoo et al. 2006a			SD: Tedersoo et al. 2006a
<i>Terfezia s. stricto</i> *	Dexheimer et al. 1985; Morte et al. 1994; Gutierrez et al. 2003	(Pirotta & Albini 1900) as cited in Melin 1923b; Ammarellou et al. 2007		Hansen et al. 2005; Tedersoo et al. 2006a	SD: Gutierrez et al. 2003, A. Morte, pers. comm.
<i>Tirmania</i> *	Fortas & Chevalier 1992			Hansen et al. 2005; Tedersoo et al. 2006a	SD ³

<i>(Ultrua)*</i>				Trappe et al. 2009a	SD ³
/tuber-helvella					
<i>Balsamia*</i>		(Ceruti & Bussetti 1962); Palfner & Agerer 1998a; Bidartondo & Read 2008; Frank et al. 2009	Hobbie et al. 2001	O'Donnell et al. 1997; Bonito et al. 2013	C: Agerer 2006
<i>Barssia*</i>			Hobbie et al. 2001	O'Donnell et al. 1997; Bonito et al. 2013	C ³
<i>Choiromyces*</i>		Izzo et al. 2005a; Izzo et al. 2005b	Hobbie et al. 2001	O'Donnell et al. 1997; Bonito et al. 2013	C ³
<i>Dingleya*</i>			Hobbie et al. 2001	O'Donnell et al. 1997; Hansen & Pfister 2006;	C ³
<i>Gymnohydnomyces*</i>		Nouhra et al. 2013		Bonito et al. 2013	C: (Nouhra et al. 2013)
<i>Helvella</i>		Weidemann 1998; Murat et al. 2005; Tedersoo et al. 2006a,b	Hobbie et al. 2001; Tedersoo et al. 2007a	O'Donnell et al. 1997; Hansen & Pfister 2006; Tedersoo et al. 2006a	C: Tedersoo et al. 2006a
<i>Labyrinthomyces*</i>	Warcup 1990a; (Warcup 1990c); Brundrett et al. 2005		Hobbie et al. 2001	O'Donnell et al. 1997; Bonito et al. 2013	C ³
<i>(Nothojafinea)</i>				Bonito et al. 2013	C ³
<i>Reddellomyces*</i>	Brundrett et al. 1996; Brundrett et al. 2005			O'Donnell et al. 1997; Hansen & Pfister 2006;	C ³
<i>Tuber</i> (I-type sensu Dominik 1959)*	Sappa 1940 (as cited in Trappe 1962); Fassi & Fontana 1967; Fontana & Fasolo Bonfante 1971; Palenzona et al. 1972; Giovanetti & Fontana 1980; Giovanetti & Fontana 1982	(Mattiolo 1887) as cited in Melin 1923b; (Frank 1892); (Peyronel 1929); Fontana & Centrella 1967; Palenzona et al. 1972; Horton et al. 1998; Baar et al. 1999; Taylor & Bruns 1999	Hobbie et al. 2001; Zeller et al. 2008	O'Donnell et al. 1997; Bonito et al. 2013	SD (C): Agerer 2006
<i>Underwoodia p. parte*</i>		Nouhra et al. 2013		O'Donnell et al. 1997; Bonito et al. 2013	C: (Nouhra et al. 2013)
<i>(Wynnella p. parte: W. silvicola)*</i>			Hobbie et al. 2001	O'Donnell et al. 1997; Hansen & Pfister 2006; Tedersoo et al. 2006a	C ³
/wilcoxina					
<i>Trichophaea p. parte: T. hybrida, T. gregaria</i>		Tedersoo et al. 2006a; Tedersoo et al. 2008b		Hansen & Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007	SD: (Tedersoo et al. 2008b)
<i>Wilcoxina</i> (E-strain)	Laiho 1965; Mikola 1965; Danielson & Visser 1988	Laiho 1965; Mikola 1965; Danielson & Visser 1988; Baar et al. 1999; Taylor & Bruns 1999; Grogan et al. 2000; Fujimura et al. 2005; Tedersoo et al. 2006a		Hansen & Pfister 2006; Tedersoo et al. 2006a; Perry et al. 2007	SD: Agerer 2006
SORDARIALES					
/sordariales1					

unnamed		Ishida et al. 2007; Tedersoo et al. 2007b, 2009a, 2011b; Peay et al. 2010		Tedersoo et al. 2007b; This study	SD: Tedersoo et al. 2007b
/sordariales2					
unnamed		Trowbridge & Jumpponen 2004; Nara 2006; Brevik et al. 2010; Timling et al. 2012		This study	SD: (Jairus et al. 2011 ; Tedersoo et al. 2013b)
PEZIZALES INCERTAE SEDIS					
<i>Lachnea vinosobrunnea</i> (sensu J. Warcup)	Warcup 1990a				unknown
ZYGOMYCOTA					
ENDOGONALES					
/endogone1					
<i>Endogone p. parte*</i> (<i>E. flammicorona</i> , <i>E. lactifluva</i>)	Warcup 1990b	(Fassi et al. 1969); Walker 1985; Warcup 1990b		White et al. 2006; Desiro et al. 2013	unknown
/endogone2					
<i>Endogone p. parte</i> (<i>E. aggregata</i> , <i>E. tuberculosa</i>)	Warcup 1990b	Warcup 1990b; Tedersoo et al. 2008a; Tedersoo et al. 2009a ²			SD: (Tedersoo et al. 2008a, 2009b)
<i>Sclerogone*</i>	Warcup 1990b	Warcup 1990b			unknown
/densospora					
<i>Densospora*</i>	Warcup & McGee 1983; Warcup 1985; McGee 1996	(Warcup 1985)			unknown

¹Direct proof for EcM status is lacking, but the taxon is phylogenetically distinct

²Not certain if these Australian taxa belong to the same group

³Estimated based on phylogenetic relationships

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