Mycorrhiza (2008) 18:277–285
DOI 10.1007/s00572-008-0183-4

REVIEW

Morphological-anatomical characterization and identification of *Tomentella* ectomycorrhizas

Erzsébet Jakucs · Zsolt Erős-Honti

Received: 29 January 2008 / Accepted: 4 June 2008 / Published online: 12 July 2008

Abstract Over the last two decades, much information has been gathered on the ectomycorrhizal fungus community composition of plant associations of boreal, temperate, and tropical regions. Worldwide, *Tomentella* ectomycorrhizas (ECM) are often common and dominant in the mycorrhizosphere of coniferous and deciduous forests. They are present under different environmental conditions and associate with diverse plant hosts. *Tomentella* sporocarps, however, are rarely found aboveground, so *Tomentella* species are often missing from fungus community studies based on fruit-body presence. *Tomentella* is a resupinate genus of Thelephoraceae (Basidiomycota) forming black-brown, brown, yellow, or ochre ECM on the roots of gymnosperm and angiosperm trees, distinguished by typical morphological-anatomical characteristics (clamped hyphae, angular mantle, surface network, special rhizomorphs and cystidia). In this paper, we review the taxonomic position and morphological-anatomical characteristics of *Tomentella* ECM. A short summary of the microscopic features used for distinguishing tomentelloids during morphotyping and identification is presented in order to support molecular and ecological studies of ectomycorrhizal fungus communities.

Keywords *Tomentella* · Ectomycorrhiza · ECM · Morphology · Anatomy · Identification

E. Jakucs (✉) · Z. Erős-Honti
Department of Plant Anatomy,
Institute of Biology, Eötvös Loránd University,
1117 Budapest Pázmány Péter s. 1/c,
Budapest, Hungary
e-mail: jakucse@ludens.elte.hu

Introduction

The genus *Tomentella* (Thelephoraceae, Basidiomycota) forms ectomycorrhizas (ECM) with different plant hosts, and develops a well-defined, frequently found morphotype. Though *Tomentella* fruit-bodies are inconspicuous and rarely found, these fungi are among the most abundant and diverse mycobionts in ectomycorrhizal fungus communities from arctic regions to the tropics (Dahlberg et al. 1997; Trowbridge and Jumpponen 2004; Haug et al. 2005). Based on basidiocarp studies, *Tomentella* species are distributed mainly in temperate Eurasia (Köljalg 1996; Köljalg et al. 2000) and North America (Larsen 1974). However, they are reported from other continents and islands, e.g., the tropics of India (Thind and Rattan 1971), Korea (Jung 1994) and the Canary Islands (Larsen 1994), and the occurrence of their ECM in South America (Haug et al. 2005), Africa (Yorou et al. 2007) and Australia (Agerer and Bougher 2001a, b) indicates a worldwide distribution, with likely many as yet undetected species.

Host plants of *Tomentella* ectomycorrhizas belong to several families; however, the main hosts are gymnosperm (Wurzburger et al. 2001; Haug 2002; Burke et al. 2005; Cline et al. 2005; Douglas et al. 2005; Hibbett et al. 2005) and angiosperm trees (Brand 1991; Pritsch et al. 2000; Walker et al. 2005). Although tomentelloids mostly develop typical ectomycorrhizas with trees (Brand 1991; Taylor and Bruns 1999; Köljalg et al. 2000; Jakucs et al. 2005a, b; Tedersoo et al. 2007a), they may also form endomycorrhizas with herbaceous plants and shrubs belonging to the Orchidaceae, Ericaceae, Monotropaceae, and Pyrolaceae (Bidartondo et al. 2000, 2004; Bidartondo and Bruns 2001; Selosse et al. 2002; McCormick et al. 2004; Jun et al. 2005; Julou et al. 2005; Tedersoo et al. 2007b). Given their typically wide host ranges, *Tomentella* species may be important members of "common mycelial networks" (CMN, Selosse et al. 2006) by connecting different hosts, e.g., trees with photosynthetic and non-photosynthetic herbaceous plants (Shefferson et al. 2005). In the case of achlorophyllous partners, the monotropoid or orchid plant is totally or partially myco-heterotrophic, invading the ECM symbiosis as a "cheater", and carbon is transferred from ECM to the epiparasitic plant (Taylor and Bruns 1997; McKendrick et al. 2000; Taylor et al. 2003; Selosse et al. 2006).

Some authors suppose that the ECM of *Tomentella* are frequent in the mineral horizon of soils poor in organic material (Harrington and Mitchell 2005; Baier et al. 2006). This occurrence is characteristic of the smooth or weakly hairy "contact exploration type" ECM (Agerer 2001) to which the majority of tomentelloids belong. In contrast, in broad-leaved forests a significant portion of tomentelloid ECM occur in the organic horizon (Tedersoo et al. 2003), often attached to plant foliar debris; many species form slightly or highly differentiated rhizomorphs, indicating that these morphotypes belong to the "medium distance exploration type" (Agerer 2001). These ECM types generally occur in the organic layer of soils where they may also exhibit saprotrophic activity. Their mycelial networks may actively digest plant and insect remnants. Other fungal species in the Thelephorales (e.g., *Thelephora terrestris* Ehrh.) produce exocellular enzymes (cellulases, oxydases, polyphenoloxydases) (Burke and Cairney 2002). However, because it is difficult to obtain in vitro cultures of *Tomentella* species and their mycelia grow very slowly on agar media, experimental data on digestive enzyme production by *Tomentella* are lacking.

Although *Tomentella* ectomycorrhizas are common members of ECM communities, little information exists on the morphology, taxonomy, host specificity, geographic distribution, and ecology of most species. Few *Tomentella* ectomyorrhiza morphotypes are accurately identified in the literature and molecular databases contain a large number of tomentelloid DNA sequences from environmental samples without indicating their exact specification. More than 70 polymerase chain reaction (PCR)-based studies of ECM community structure report the presence of *Tomentella* ECM (e.g., Comandini et al. 1998; Buée et al. 2004; Kaldorf et al. 2004; De Román et al. 2005; Murat et al. 2005; O'Brien et al. 2005; Baier et al. 2006), but most of these studies lack morphological analysis of the ECM.

The aim of this paper is to review the present state of our knowledge about the morphological-anatomical characteristics of *Tomentella* ECM. In order to support extended molecular investigations on geographic distribution, ecological role and diversity of this common and widespread mycorrhizal group, we also present a short summary on microscopic features suitable for selecting tomentelloids during morphotyping of ECM root samples.

The taxonomic position of *Tomentella* ECM

Tomentella ECM are formed by aphyllophoraceous fungi positioned within the Thelephorales (Agaricomycetes, Basidiomycota) (Donk 1964; Corner 1968). The order was taxonomically revised by Stalpers (1993). The morphology of the often dark-colored basidiocarps is highly diverse, varying from resupinate to effused. A characteristic apomorphy (commonly derived phylogenetic character) of the order is the irregularly shaped, non-amyloid, ornamented, and often dark basidiospore with a large apiculus (Larsson et al. 2004). The presence of thelephoric acid, a blue cytoplasmatic pigment specific for the Thelephorales, is also a common character of the order (Agerer et al. 1995).

Stalpers recognized two families: the Bankeraceae Donk /Syn.: Boletopsidaceae Bond. & Singer ex Jülich/ and the Thelephoraceae Chev. /Syn.: Phylacteriaceae Maire; Tomentellaceae Bref.; Botryohypochnaceae (Parm.) Jülich; Lenztiopsidaceae Jülich/ (Stalpers 1993). According to recent molecular phylogenetic analyses, the Thelephorales form a monophyletic clade within the Agaricomycetes (Hibbett and Thorn 2001; Larsson et al. 2004; Lutzoni et al. 2004; Binder et al. 2005; Hibbett et al. 2007) as a sister group of the Polyporoid clade (Matheny et al. 2006). In the Thelephoraceae, Index Fungorum recognizes 72 valid species of *Tomentella,* in addition to 43 species of *Thelephora*, seven of *Pseudotomentella*, and four of *Amaurodon*, but more than 100 synonyms are indicated. Recent molecular studies show that the resupinate mycorrhizal genus *Tylospora*, previously positioned in the Thelephorales (Stalpers 1993), is closely related to *Piloderma*, *Amphinema*, and *Byssocorticium*, belonging to the Athelioid clade (Larsson et al. 2004). Surprisingly, though *Tomentellopsis* is generally accepted as the member of the thelephoroid clade (Larsson et al. 2004; Agerer 2006), Index Fungorum placed it also in the Atheliaceae.

Within the Thelephorales, there are several well-known ECM-forming genera in the Bankeraceae (*Hydnellum*, *Bankera*, *Phellodon*, *Sarcodon)* and the Thelephoraceae (*Thelephora)* with effused, clavarioid, flabelliform, or pileate basidiocarps (Agerer 2006). The ECM of *Thelephora* species, especially *T. terrestris* Ehrh., are common in pine forests and nurseries and are intensively studied as they are often used for seedling inoculation in reforestation programs (reviewed by Colpaert 1999). For general morphological characters of ECM within the thelephoroid clade, we refer to the recent summary of Agerer (2006).

The fruit-bodies of the genus *Tomentella* are resupinate, forming inconspicuous, spiderweb-like layers on the surface of soil, twigs, or other plant debris (Kõljalg 1996). Therefore, these species had been considered as rare, saprotrophic, wood-decaying fungi (Larsen 1974). However, in the 1980s *Tomentella* species were shown to form

Table 1 Identified and unidentified *Tomentella* ECM characterized morphologically in detail

Mycorrhiza	Host	Country	First description
Identified			
Tomentella brunneorufa Larsen	*Eucalyptus* sp.	Australia	Agerer and Bougher 2001a
Tomentella ferruginea (Pers.) Pat.	*Fagus sylvatica*	Germany	Raidl and Müller 1996 *
Tomentella galzinii Bourdot (sub nom *Quercirhiza fibulocystidiata*)	*Quercus* sp. *Populus alba*, *Fagus sylvatica*	Hungary	Jakucs et al. 1997 *
Tomentella pilosa (Burt) Bourdot & Galzin	*Populus alba*	Hungary	Jakucs and Agerer 1999 *
Tomentella stuposa (Link) Stalpers	*Quercus cerris*, *Picea abies*, *Populus alba*	Germany Hungary	Jakucs et al. 2005a
Tomentella sublilacina (Ellis & Holw.) Wakef. (sub nom *T. albomarginata*)	*Pinus sylvestris*	Germany	Agerer 1996 *
Tomentella subtestacea Bourdot & Galzin	*Populus alba*	Hungary	Jakucs and Agerer 2001 *
Unidentified			
Fagirhiza fusca	*Fagus sylvatica*	Germany	Brand 1991 *
Fagirhiza lanata	*Fagus sylvatica*	Germany	Brand 1991
Fagirhiza pallida	*Fagus sylvatica*	Germany	Brand 1991
Fagirhiza setifera	*Fagus sylvatica*	Germany	Brand 1991 *
Fagirhiza spinulosa	*Fagus sylvatica*	Germany	Brand 1991 *
Quercirhiza ateracusrugosa	*Quercus suber*	Portugal	Azul et al. 2006a *
Quercirhiza atrata	*Quercus robur*	Germany	Uhl 1988
Quercirhiza auraterocystidiata	*Quercus suber*	Portugal	Azul et al. 2006b *
Quercirhiza cumulosa	*Quercus ilex*	Spain	De Román et al. 2002a
Quercirhiza flavocystidiata	*Quercus suber*	Portugal	Azul et al. 2006c *
Quercirhiza squamosa	*Quercus robur*	Germany	Palfner and Agerer 1996 *
Quercirhiza stellata	*Quercus ilex*	Spain	De Román et al 2002b
Quercirhiza tomentellocystidiata	*Quercus suber*	Portugal	Azul et al. 2006d *
Quercirhiza tomentelloflexuosa	*Quercus suber*	Portugal	Azul et al. 2006e *
Quercirhiza tomentellofuniculosa	*Quercus suber*	Portugal	Azul et al. 2006f *
Piceirhiza cornuta	*Piecea abies*	Italy	Montecchio and Agerer 1997
Piceirhiza nigra	*Picea abies*	Germany	Gronbach 1988 *
Piceirhiza obscura	*Picea abies*	Germany	Gronbach 1988 *

Photodocumentation of the descriptions marked by * were published in Agerer (ed.) The Colour Atlas of Ectomycorrhizae (1987–2006)

ECM (Danielson and Pruden 1989). The Thelephoraceae species with resupinate sporocarps are often mentioned as “resupinate thelephoroid” or “tomentelloid” fungi (Köljalg et al. 2000), including also *Pseudotomentella*, *Amaurodon*, and even some resupinate *Thelephora* species (e.g., *Thelephora caryophyllea* (Schaeff.) Pers.) in addition to *Tomentella*. The ECM of resupinate ECM taxa is reviewed by Erland and Taylor (1999). On the phylogenetic trees constructed on the basis of ITS-rDNA (internal transcribed spacer region of the ribosomal DNA), *Tomentella* species are often intermingled within a common clade with *Thelephora* species of resupinate and erect fruit bodies (Köljalg et al. 2000; Binder et al. 2005), but based on microscopic ECM-characters, *Thelephora* and *Tomentella* species can be easily distinguished.

In his review on *Tomentella* and related genera in temperate Eurasia, Köljalg (1996) described 43 species and presented a phylogenetic tree based on morpho-anatomical fruit-body characteristics. However, his tree contradicts the phylogenetic trees that resulted from DNA analyses (Köljalg et al. 2000; Jakucs et al. 2005b). Within *Tomentella* ECM, the microscopic characteristics of ECM seem to correspond better to molecular results than to sporocarp morphology, as also observed in other taxa (Agerer 2006).

Our present review is restricted only to the ECM of the genus *Tomentella* because they are more common, they form a distinguished morphotype group, and differ significantly in microscopic characters from the ECM of the remaining resupinate taxa in the Thelephoraceae.

Morphological-anatomical characterization of *Tomentella* ECM

In the case of *Tomentella* ECM, microscopic investigation is particularly useful in community studies because these species can be separated relatively easily by morphotyping, and the majority of them have specific characteristics.

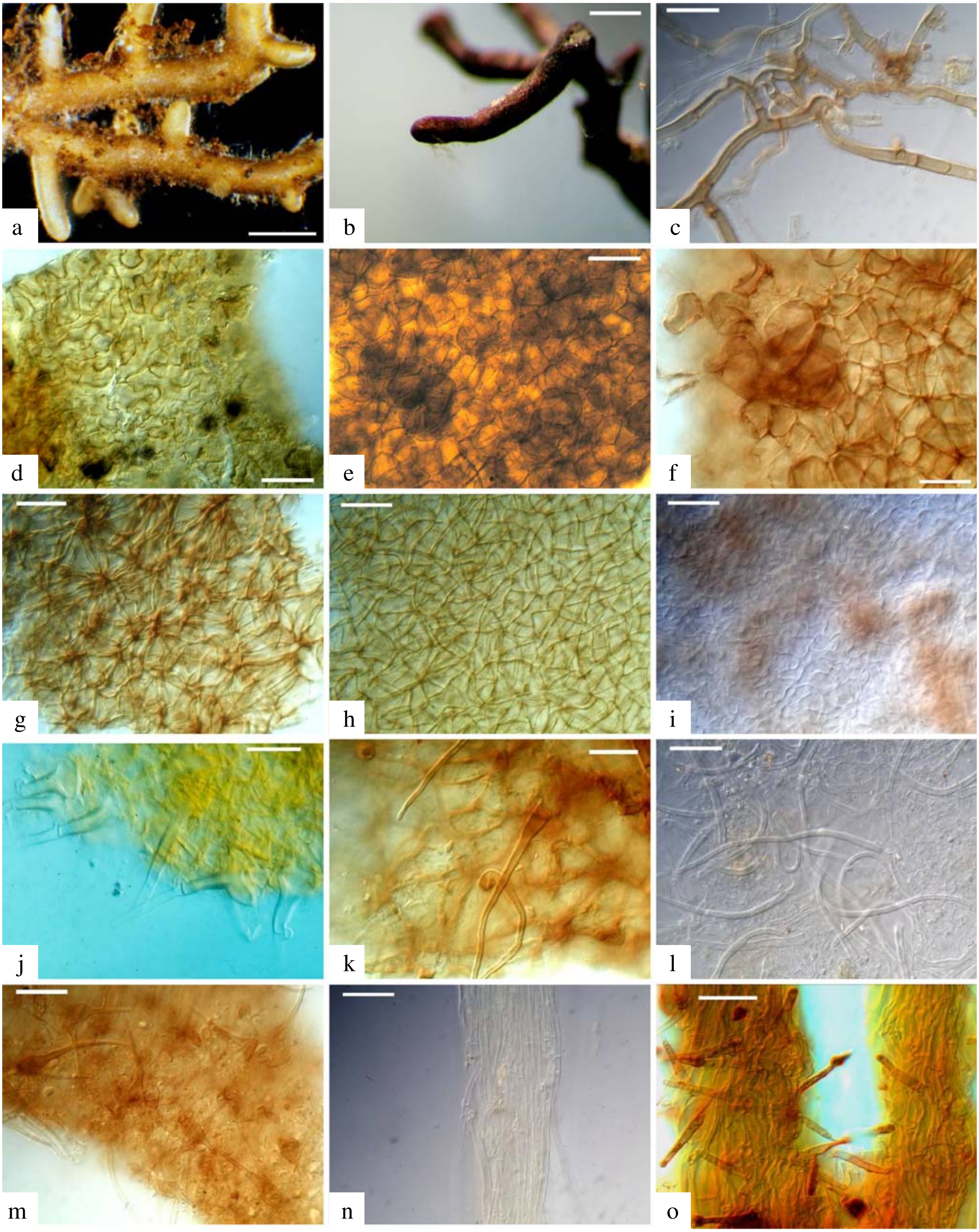
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o

Fig. 1 Typical morphological-anatomical characteristics of tomentelloid ectomycorrhizas. **a** Monopodial-pyramidal ECM system with yellow-ochre mantle (*Tomentella pilosa*); **b** ECM tip with woolly emanating hyphae and dark-brown mantle (*T. stuposa*); **c** typical brown, clamped tomentelloid emanating hyphae*; **d** pseudoparenchymatous-epidermoid mantle with thelephoric-acid-containing cells, stained dark-blue in KOH*; **e** brown, pseudo-parenchymatous-angular mantle*; **f** groups of globular cells on the surface of mantle*; **g** pseudoparenchymatous mantle with star-like pattern*; **h** yellow, pseudoparenchamatous mantle composed of angular-triangular cells*; **i** pseudoparenchymatous-epidermoid mantle*; **j** clamped "fibulocystidium-type"cystidia with large basal cells (*T. galzinii*); **k** unclamped, awl-shaped cystidia*; **l** long, curved, unclamped, thick-walled cystidia*; **m** spiny cystidia with broad basal parts*; **n** undifferentiated rhizomorph with clamped hyphae*; **o** typical tomentelloid rhizomorph with a rind formed by thin, densely entwined, multi-branched, clamped marginal hyphae and cystidia containing black pigment in apical part (*T. subtestacea*). *Asterisk* Identified as *Tomentella* ECM by sequence analysis. **a**, **b** Stereomicroscopy, *bar* = 0.1 mm; **c**–**o** Nomarski-DIC, *bar* = 10 µm

Anatomical features of the identified tomentelloid ECM are included in the recent comparative review of Agerer (2006). However, for the approximately 70 known *Tomentella* species, only seven have been accurately identified and their ECM characterized in detail (De Román et al. 2005). In addition to these, several precise descriptions and image documentations of unidentified ECM appeared in *Descriptions of Ectomycorrhizae* and the *Colour Atlas of Ectomycorrhizae*. These ECM lack DNA-based identification but belong certainly to *Tomentella*, based on microscopic similarities. Table 1 summarizes the hitherto published, detailed morphological-anatomical descriptions of seven identified and 18 unidentified but likely *Tomentella* ECM. Several other tomentelloid ECM morphotypes have been described or documented in the literature, but we consider those descriptions to lack sufficient detail so we restrict our review only to detailed descriptions with complete image documentation.

According to Kõljalg et al. (2000), tomentelloid ECM mycobionts encompass species characterized by melanized hyphae and contain one or more of the following three criteria: presence of clamp connections, presence of cystidia, or of a greenish-blue color reaction in KOH indicating the presence of thelephoric acid. However, positive KOH reaction, observed in mantle cells (Fig. 1d) or the presence of cystidia (Fig. 1o) is quite infrequent within *Tomentella*. ECM of the genus are generally characterized by brown or brown-black mantles, or the color may be yellow, pale ochre, or whitish (Fig. 1a, b), depending on the concentration of cell wall pigments. In most cases, emanating hyphae of the mantle and hyphae of the rhizomorphs are clamped (Fig. 1c, 2e). In contrast to *Thelephora*, *Tomentellopsis*, and *Pseudotomentella* mycorrhizas, which have plectenchymatous mantles, most *Tomentella* ECM show a mainly angular, pseudoparenchymatous outer layer in their mantle. In some species, the angular cells are organized in a star-like pattern (Fig. 1f), or in others the cells are epidermoid (Fig. 1d, h). Cell wall

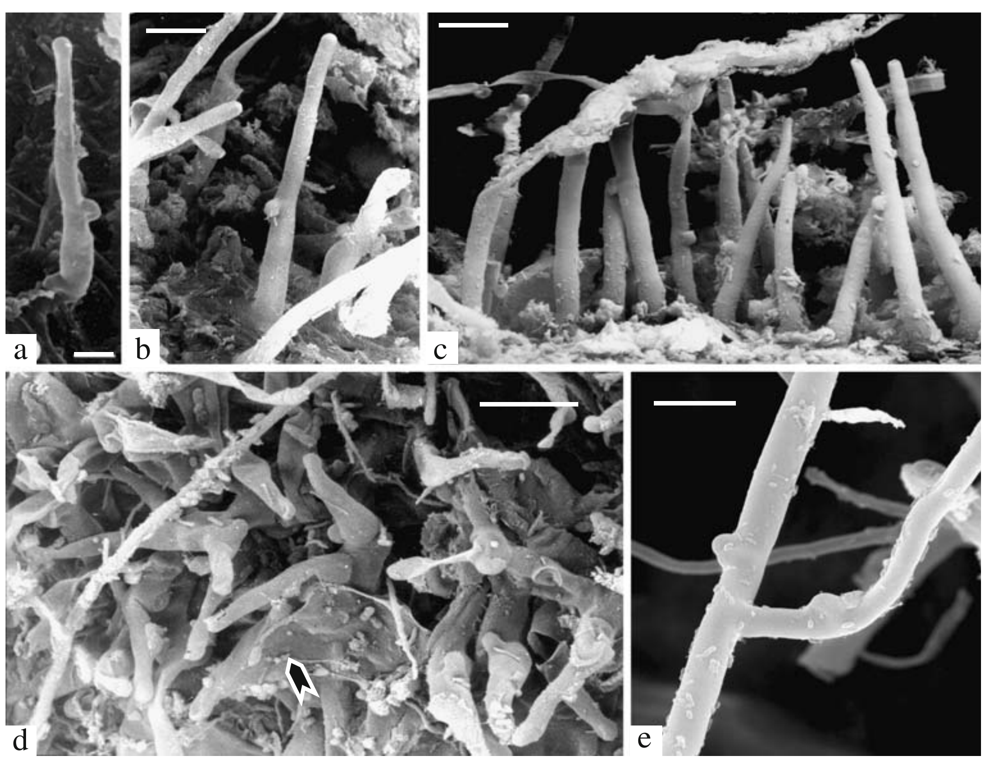

Fig. 2 Emanating elements of *Tomentella* ECM. **a**–**c** Clamped cystidia ('fibulocystidia') of *T. galzinii* emerging from the mantle covered by amorphous gelatinous matrix; **d** cystidia of *T. subtestacea* originating from a surface network formed by horn-shaped cells (arrow); **e** ramification of clamped hypha of *T. pilosa*. SEM, *bars* = 10 µm. Photo: K. Bóka (with permission)

Table 2 Differential characters of identified and unidentified *Tomentella* ECM

Mycorrhiza	Color	Outer mantle				Surface network		Surface		Clamps	Cystidia	Rhizomorph	
		Plect	Ang	Star-like	Epid	Hyphal	Angular-triangular	Gelatinous	Surface cells			Undiff	Diff
Tomentella brunneorufa	W	+	–	–	–	–	–	–	–	+	–	–	+
Tomentella ferruginea	B	–	+	–	–	+	–	–	S	+	–	–	+
Tomentella galzinii	Y	–	+	–	–	–	–	+	–	+	+	+	–
Tomentella pilosa	Y	–	+	–	–	–	+	–	–	+	+	–	+
Tomentella stuposa	B	–	+	–	–	–	–	+	G	+	–	+	–
Tomentella sublilacina	B (L)	–	+	–	–	+	–	+	–	+	–	+	–
Tomentella subtestacea	Y	–	+	–	–	–	+	–	–	+	+	–	+
Fagirhiza fusca	B	–	+	–	–	–	–	–	–	+	–	+	–
Fagirhiza lanata	B	+	–	–	–	+	–	–	–	+	–	–	+
Fagirhiza pallida	W (B)	–	–	–	+	–	–	–	–	+	+	–	–
Fagirhiza setifera	B	–	+	+	–	–	–	–	G	+	+	–	–
Fagirhiza spinulosa	B	–	+	–	–	–	–	–	G	+	+	–	–
Quercirhiza ateracusrugosa	B	–	+	–	–	–	–	–	–	+	+	–	–
Quercirhiza atrata	B	–	+	+	–	–	–	–	–	–	–	–	–
Quercirhiza auraterocystidiata	B	–	+	–	–	–	–	–	–	+	+	+	–
Quercirhiza cumulosa	B	–	+	–	–	–	–	–	G	+	–	–	+
Quercirhiza flavocystidiata	B	+	–	–	–	–	–	–	–	+	+	–	+
Quercirhiza squamosa	B	–	+	–	–	–	–	–	S	+	–	–	–
Quercirhiza stellata	B	–	+	+	–	–	–		–	+	–	–	–
Quercirhiza tomentellocystidiata	B	–	+	+	–	–	+	–	–	+	+	–	–
Quercirhiza tomentelloflexuosa	B	–	+	–	–	–	–	+	–	+	–	–	+
Quercirhiza tomentellofuniculosa	B	+	–	–	–	+	–	–	–	+	–	–	+
Piceirhiza cornuta	Y (B)	–	–	–	+	+	–	–	–	+	+	–	–
Piceirhiza nigra	B	–	+	–	–	–	–	–	G	+	+	–	–
Piceirhiza obscura	B	–	–	–	+	–	–	–	–	–	+	–	–

Abbreviations: Color: *W* whitish, *B* brown, *Y* yellow, *L* lilac; Outer mantle: *Plect* plectenchymatous, *Ang* angular, *Epid* epidermoid: surface cells: *G* groups of globular cells, *S* scales; Rhizomorph: *Undiff* undifferentiated, *Diff* differentiated

thickness and the size and shape of cells are highly variable both among and within the species. Plectenchymatous ECM mantles are considered phylogenetically ancient compared to pseudoparenchymatous mantles (Agerer 1995). The presence of both types within the family may lead to the conclusion that the recent representatives of Thelephoraceae have a long evolutionary history (or accelerated evolution) and the pseudoparenchymatous mantle of the typical *Tomentella* ECM is the apomorphic state within this group.

The mantle surface may be covered by a gelatinous matrix in some *Tomentella* species (Fig. 2b, c) or may bear a hyphal net or a network of angular-triangular, horn-shaped cells on the surface of the mantle (Fig. 2d). In some species (e.g. *T. stuposa*), groups of globular cells are formed on the mantle (Fig 1e, f). "*Quercirhiza squamosa*" and some other morphotypes have scales of dead cell remnants on the mantle. Many species also have rhizomorphs or cystidia (Agerer 1995; Jakucs et al. 2005b). The structure of rhizomorphs of some *Tomentella* species is undifferentiated (like those of *Thelephora*), but some *Tomentella* ECM have differentiated rhizomorphs (Fig 1n, o). As rhizomorphs are functional organs involved in water and mineral transport, their morphology and structure indicates different transport mechanisms and exploration types (Agerer 2001**)**. The typical *Tomentella* rhizomorph is characterized by bilateral, nodal ramifications and a rind formed by thin, clamped, densely entwined, multi-branched marginal hyphae as seen in *T. subtestacea*, *T. pilosa*, and *T. ferruginea* (Fig. 1o). The structural heterogeneity of rhizomorphs and the presence of highly specialized rhizomorph types also presume a long evolution history of the genus. Most *Tomentella* ECM have characteristic cystidia. A special, clamped cystidium-type ("fibulocystidium") is regarded as an apomorphic character in the group formed by *Tomentella galzinii*, *T. pilosa*, and T. *subtestacea* (Kõljalg et al. 2001) (Fig. 1j, 2a–e). The apical part of cystidia of *T. subtestacea* contains blackish-blue drops of the pigment thelephoric acid (Fig. 1o). In other (unidentified) species, unclamped, awl-shaped cystidia can be observed (Fig. 1k–m).

Specific features of *Tomentella* ECM

Table 2 contains a comparison of morphological-anatomical characteristics suitable for differentiation within the recently described *Tomentella* ECM.

To aid morphotyping of unknown ECM in root samples, we summarize the most important distinctive characteristics of *Tomentella* ECM. The presence of more than three of the following common features in any combination typically indicates a *Tomentella* ectomycorrhiza.

1. Color of the ECM black-brown, brown
2. Hyphae clamped
3. Structure of the outer mantle layer angular
4. Cells of mantle organized in star-like pattern
5. Surface network on mantle composed of hyphae or angular-triangular, horn-shaped cells
6. Groups of globular cells on mantle surface
7. Rhizomorphs with bilateral, nodal ramifications and a rind formed by thin, clamped, densely entwined, multi-branched marginal hyphae
8. Clamped cystidia

Because in this group molecular results highly correlate with mycorrhizal characters, further detailed descriptions of *Tomentella* ECM would contribute to solving taxonomic and phylogenetic problems in the Thelephoraceae. Accurate identification and precise microscopic investigations of *Tomentella* ECM would allow construction of a key to identify species of the genus for future diversity studies. Although morphological and anatomical analyses of ECM is time-consuming and requires experience (Agerer 1991), combining microscopy with DNA-based analyses is the most effective way to obtain valuable information on ECM community structure. Extending microscopic investigations of *Tomentella* ECM from new localities would highly support ecological studies on their role in different geographic regions and plant communities.

Acknowledgment We thank Dr. Gábor M. Kovács for contribution to the revision of the literature. The kind help of Dr. Károly Bóka in preparing the SEM images is highly appreciated. This study was supported by the Hungarian Research Fund (OTKA, no. K60887).

References

Agerer R (1991) Characterization of ectomycorrhiza. Methods Microbiol 23:27–72

Agerer R (1995) Anatomical characteristics of identified ectomycorrhizas: an attempt towards a natural classification. In: Varma A, Hock B (eds) Mycorrhiza. Springer Verlag, Heidelberg

Agerer R (1996) Ectomycorrhizae of Tomentella albomarginata (Thelephoraceae) on Scots pine. Mycorrhiza 6:1–7 doi:10.1007/s005720050098

Agerer R (ed) (1987–2006) Colour atlas of ectomycorrhizae. 1st–13th del. Einhorn Verlag, Schwabisch Gmünd

Agerer R (2001) Exploration types of ectomycorrhizae. A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance of ectomycorrhiza. Z Mykol 60:143–158

Agerer R (2006) Fungal relationships and structural identity of their ectomycorrhizae. Mycol Prog 5:7–107 doi:10.1007/s11557–006–0505-x

Agerer R, Bougher NL (2001a) Tomentella brunneorufa MJ Larsen + Eucalyptus spec. Descriptions of Ectomycorrhizae 5:205–212

Agerer R, Bougher NL (2001b) Tomentella subamyloidea sp. nov. and T. radiosa (Thelephoracee, Hymenomycetes, Basidiomycota) from Australia. Aust Syst Bot 14:607–614 doi:10.1071/SB00031

Agerer R, Klostermeyer D, Steglich W (1995) "Piceirhiza nigra", an ectomycorrhiza on Picea abies formed by a species of Thelephoraceae. New Phytol 131:377–380 doi:10.1111/j.1469–8137.1995.tb03074.x

Azul AM, Agerer R, Freitas H (2006a) "Quercirrhiza ateracusrugosa" + Quercus suber L. Descriptions of Ectomycorrhizae 9:75–79

Azul AM, Martín MP, Agerer R, Freitas H (2006b) "Quercirrhiza auraterocystidiata" + Quercus suber L. Descriptions of Ectomycorrhizae 9:81–86

Azul AM, Martín MP, Agerer R, Freitas H (2006c) "Quercirrhiza flavocystidiata" + Quercus suber L. Descriptions of Ectomycorrhizae 9:93–97

Azul AM, Agerer R, Freitas H (2006d) "Quercirrhiza tomentellocystidiata" + Quercus suber L. Descriptions of Ectomycorrhizae 9:115–119

Azul AM, Agerer R, Freitas H (2006e) "Quercirrhiza tomentelloflexuosa" + Quercus suber L. Descriptions of Ectomycorrhizae 9:121–126

Azul AM, Martín MP, Agerer R, Freitas H (2006f) "Quercirrhiza tomentellofuniculosa" + Quercus suber" L. Descriptions of Ectomycorrhizae 9:127–134

Baier R, Ingenhaag J, Blaschke H, Göttlein A, Agerer R (2006) Vertical distribution of an ectomycorrhizal community in upper soil horizons of a young Norway spruce (Picea abies [L.] Karst.) stand of the Bavarian Limestone Alps. Mycorrhiza 16:197–206 doi:10.1007/s00572–006–0035-z

Bidartondo MI, Bruns TD (2001) Extreme specificity in epiparasitic Monotropoideae (Ericaceae): widespread phylogenetic and geographical structure. Mol Ecol 10:2285–2295 doi:10.1046/j.1365–294X.2001.01358.x

Bidartondo MI, Burghardt B, Gebauer G, Bruns TD, Read DJ (2004) Changing partners in the dark: isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. Proc R Soc Lond B Biol Sci 271:1799–1806 doi:10.1098/rspb.2004.2807

Bidartondo MI, Kretzer AM, Pine EM, Bruns TD (2000) High root concentration and uneven ectomycorrhizal diversity near Sarcodes sanguinea (Ericaceae): a cheater that stimulates its victims? Am J Bot 87:1783–1788 doi:10.2307/2656829

Binder M, Hibbett DS, Larsson K-H, Larsson E, Langer E, Langer G (2005) The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Syst Biodivers 3:113–157 doi:10.1017/S1477200005001623

Brand F (1991) Ektomykorrhizen an Fagus sylvatica. Charactersisierung und Identifizierung, ökologische Kennzeichnung und unsterile Kultivierung. Libri Botanici 2. IHW-Verlag

Buée M, Vairelles D, Garbaye J (2004) Year-round monitoring of diversity and potential metabolic activity of the ectomycorrhizal community in a beech (Fagus silvatica) forest subjected to two thinning regimes. Mycorrhiza 15:235–245 doi:10.1007/s00572–004–0313–6

Burke RM, Cairney JWG (2002) Laccases and other polyphenol oxidases in ecto- and ericoid mycorrhizal fungi. Mycorrhiza 12:105–116

Burke DJ, Martin KJ, Rygiewicz PT, Topa MA (2005) Ectomycorrhizal fungi identification in single and pooled root samples: terminal restriction fragment length polymorphism (TRFLP) and morphotyping compared. Soil Biol Biochem 37:1683–1694 doi:10.1016/j.soilbio.2005.01.028

Cline ET, Ammirati JF, Edmonds RL (2005) Does proximity to mature trees influence ectomycorrhizal fungus communities of Douglas-fir seedlings?. New Phytol 166:993–1009, doi:10.1111/j.1469–8137.2005.01387.x

Colpaert JV (1999) Thelephora. In: Cairney JWG, Chambers SM (eds) Ectomycorrhizal fungi. Key genera in profile. Heidelberg, Springer Verlag, pp 325–345

Comandini O, Pacioni G, Rinaldi AC (1998) Fungi in ectomycorrhizal associations of silver fir (Abies alba Miller) in Central Italy. Mycorrhiza 7:323–328 doi:10.1007/s005720050200

Corner E, JH (1968) A monograph of Thelephora (Basidiomycetes). Beih Nova Hedwig 27:1–110

Dahlberg A, Jonsson L, Nylund J-E (1997) Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old-growth Norway spruce forest in south Sweden. Can J Bot 75:1323–1335

Danielson RM, Pruden M (1989) The ectomycorrhizal status of urban spruce. Mycologia 81:335–341 doi:10.2307/3760071

De Román M, Agerer R, De Miguel A (2002a) “Quercirhiza cumulosa” + Quercus ilex L. subsp. ballota (Desf.) Samp. Descriptions of Ectomycorrhizae 6:13–18

De Román M, Agerer R, De Miguel A (2002b) “Quercirhiza stellata” + Quercus ilex L. ssp. ballota (Desf.) Samp. Descriptions of Ectomycorrhizae 6:19–24

De Román M, Claveria V, De Miguel AM (2005) A revision of the descriptions of ectomycorrhizas published since 1961. Mycol Res 109:1063–1104 doi:10.1017/S0953756205003564

Donk MA (1964) A conspectus of the families of the Aphyllophorales. Persoonia 3:199–324

Douglas RB, Parker TV, Cullings KW (2005) Belowground ectomycorrhizal community structure of mature lodgepole pine and mixed conifer stands in Yellowstone National Park. For Ecol Manag 208:303–317

Erland S, Taylor AFS (1999) Resupinate ectomycorrhizal fungi. In: Cairney JWG, Chambers SM (eds) Ectomycorrhizal fungi. Heidelberg, Key genera in profile. Springer Verlag, pp 347–363

Gronbach E (1988) Characterisierung und identifizierung von ektomycorrhizen in einem fichtenbestand mit untersuchungen zur merkmalsvariabilität in sauer beregneten flächen. Bibl Mycol 125:35–45

Haug I (2002) Identification of Picea-ectomycorrhizae by comparing DNA-sequences. Mycol Prog 1:167–178 doi:10.1007/s11557–006–0016–9

Haug I, Weiss M, Homeier J, Oberwinkler F, Kottke I (2005) Russulaceae and Thelephoraceae form ectomycorrhizas with members of the Nyctaginaceae (Caryophyllales) in the tropical mountain rain forest of southern Ecuador. New Phytol 165:923–936 doi:10.1111/j.1469–8137.2004.01284.x

Harrington TJ, Mitchell DT (2005) Ectomycorrhizas associated with a relict population of Dryas octopetala in the Burren, western Ireland. I. Distribution of ectomycorrhizas in relation to vegetation and soil characteristics. Mycorrhiza 15:425–433 doi:10.1007/s00572–005–0347–4

Hibbett DS, Thorn RG (2001) Basidiomycota: Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The Mycota VII. B., Springer, pp 121–16

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE et al (2005) Douglas-fir ectomycorrhizae in 40-and 400-year-old stands: mycobiont availability to late successional western hemlock. Mycorrhiza 15:393–403 doi:10.1007/s00572–004–0339–9

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE et al (2007) A higher-level phylogenetic classification of the Fungi. Mycol Res 111:504–548

Jakucs E, Agerer R (1999) Tomentella pilosa (Burt.) Bourdot & Galzin + Populus alba L. Descriptions of Ectomycorrhizae 4:121–126

Jakucs E, Agerer R (2001) Tomentella subtestacea Bourdot& Galzin + Populus alba L. Descriptions of Ectomycorrhizae 5:213–219

Jakucs E, Agerer R, Bratek Z (1997) “Quercirhiza fibulocystidiata” + Quercus spp. Descriptions of Ectomycorrhizae 2:67–72

Jakucs E, Kovács GM, Agerer R, Romsics C, Erős Z (2005a) Morphological-anatomical characterization and molecular identification of Tomentella stuposa ectomycorrhizae and related anatomotypes. Mycorrhiza 15:247–258 doi:10.1007/s00572–004–0326–1

Jakucs E, Kovács GM, Szedlay G, Erős-Honti Z (2005b) Morphological and molecular diversity and abundance of tomentelloid ectomycorrhizae in broad-leaved forests of the Hungarian Plain. Mycorrhiza 15:459–470 doi:10.1007/s00572–005–0351–8

Julou T, Burghardt B, Gebauer G, Berveiller D, Damesin C, Selosse M-A (2005) Mixotrophy in orchids: insights from a comparative study of green individuals and nonphotosynthetic individuals of Cephalanthera damasonium. New Phytol 166:639–653 doi:10.1111/j.1469–8137.2005.01364.x

Jun Y, Tatsuya F, Hirokazu T (2005) Molecular identification of the mycorrhizal fungi of the epiparasitic plant Monotropastrum humile var. glaberrimum (Ericaceae). J Plant Res 118:53–56 doi:10.1007/s10265–004–0188–9

Jung HS (1994) Floral studies on Korean wood-rotting fungi II: on the flora of the Aphyllophorales (Basidiomycotina). Korean Journal of Mycology 22:62–99

Kaldorf M, Renker C, Fladung M, Buscot F (2004) Characterization and spatial distribution of ectomycorrhizas colonizing aspen clones released in an experimental field. Mycorrhiza 14:295–306 doi:10.1007/s00572–003–0266–1

Kõljalg U (1996) Tomentella (Basidiomycota) and related genera in Temperate Eurasia. Synopsis Fungorum. Oslo, Fungiflora

Kõljalg U, Dahlberg A, Taylor AFS, Larsson E, Hallenberg N, Stenlid J et al (2000) Diversity and abundance of resupinate thelephoroid fungi as ectomycorrhizal symbionts in Swedish boreal forests. Mol Ecol 9:1985–1996 doi:10.1046/j.1365–294X.2000.01105.x

Kõljalg U, Jakucs E, Bóka K, Agerer R (2001) Three ectomycorrhizae with cystidia formed by different Tomentella species as revealed by rDNA IST sequences and anatomical characteristics. Folia Cryptogam Est 38:27–39

Larsen MJ (1974) A contribution to the taxonomy of the genus Tomentella. Mycol Mem 4:1–145

Larsen MJ (1994) Tomentella oligofibula sp. nov. (Aphyllophorales, Thelephoraceae s. str.) from the Canary Islands. Mycotaxon 63:1–8

Larsson K-H, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycol Res 108:983–1002 doi:10.1017/S0953756204000851

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B et al (2004) Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. Am J Bot 91:1446–1480 doi:10.3732/ajb.91.10.1446

Matheny PB, Curtis JC, Hofstter V, Aime MC, Moncalvo JM, Ge ZW et al (2006) Major clades of Agaricales: a multi-locus phylogenetic overview. Mycologia 98:982–995 doi:.3852/mycologia.98.6.982

McCormick MK, Whigham DF, O'Neill J (2004) Mycorrhizal diversity in photosynthetic terrestrial orchids. New Phytol 163:425–438 doi:10.1111/j.1469–8137.2004.01114.x

McKendrick SL, Leake JR, Read DJ (2000) Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal Salix repens and Betula pendula to the orchid Corallorhiza trifida through hyphal connections. New Phytol 145:539–548 doi:10.1046/j.1469–8137.2000.00592.x

Montecchio L, Agerer R (1997) Piceirhiza cornuta + Picea abies (L.) Karst. Descr Ectomyc 2:31–35

Murat C, Vizzini A, Bonfante P, Mello A (2005) Morphological and molecular typing of the below-ground fungal community in a natural Tuber magnatum truffle-ground. FEMS Microbiol Lett 245:307–313 doi:10.1016/j.femsle.2005.03.019

O'Brien HE, Parrent JL, Jackson JA, Moncalvo JM, Vilgalys R (2005) Fungal community analysis by large-scale sequencing of environmental samples. Appl Environ Microbiol 71:5544–5550 doi:10.1128/AEM.71.9.5544–5550.2005

Palfner G, Agerer R (1996) "Quercirhiza squamosa" eine nichtidentifizierte Ektomykorrhiza an Quercus robur. Sendtnera 3:137–145

Pritsch K, Munch JC, Buscot F (2000) Identification and differentiation of mycorrhizal isolates of black alder by sequence analysis of the ITS region. Mycorrhiza 10:87–93 doi:10.1007/s005720000063

Raidl S, Müller WR (1996) Tomentella ferruginea (Pers.) Pat. + Fagus sylvatica L. Descr Ectomyc 1:161–166

Selosse M-A, Weiß M, Jany J-L, Tillier A (2002) Communities and populations of sebacinoid basidiomycetes associated with the achlorophyllous orchid Neottia nidus-avis (L.) L.C.M. Rich. and neighbouring tree ectomycorrhizae. Mol Ecol 11:1831–1844 doi:10.1046/j.1365–294X.2002.01553.x

Selosse M-A, Richard F, He X, Simard SW (2006) Mycorrhizal networks: des liaisons dangereuses? Trends Ecol Evol 21:621–628 doi:10.1016/j.tree.2006.07.003

Shefferson RP, Weiß M, Kull T, Taylor DL (2005) High specificity generally characterizes mycorrhizal association in rare lady's slipper orchids, genus Cypripedium. Mol Ecol 14:613–626 doi:10.1111/j.1365–294X.2005.02424.x

Stalpers JA (1993) The Aphyllophoraceous fungi I. Keys to the species of the Thelephorales. Stud Mycol 35:1–168

Taylor DL, Bruns TD (1997) Independent, specialized invasions of ectomycorrhizal mutualism by two nonphotosynthetic orchids. Proc Natl Acad Sci U S A 94:4510–4515 doi:10.1073/pnas.94.9.4510

Taylor DL, Bruns TD (1999) Community structure of ectomycorrhizal fungi in a Pinus muricata forest: minimal overlap between the mature forest and resistant propagule communities. Mol Ecol 8:1837–185 doi:10.1046/j.1365–294x.1999.00773.x

Taylor DL, Bruns TD, Szaro TM, Hodges SA (2003) Divergence in mycorrhizal specialization within Hexalectris spicata (Orchidaceae), a nonphotosynthetic desert orchid. Am J Bot 90:1168–1179 doi:10.3732/ajb.90.8.1168

Tedersoo L, Kõljalg U, Hallenberg N, Larsson K-H (2003) Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytol 159:153–165 doi:10.1046/j.1469–8137.2003.00792.x

Tedersoo L, Suvi T, Beaver K, Kõljalg U (2007a) Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native Vateriopsis seychellarum (Dipterocarpaceae) and Intsia bijuga (Caesalpiniaceae) to the introduced Eucalyptus robusta (Myrtaceae), but not Pinus caribea (Pinaceae). New Phytol 175:321–333 doi:10.1111/j.1469–8137.2007.02104.x

Tedersoo L, Pellet P, Kõljalg U, Selosse M-A (2007b) Parallel evolutionary paths to mycoheterotrophy in understorey Ericaceae and Orchidaceae: ecological evidence for mixotrophy in Pyroleae. Oecologia 151(2):206–217 doi:10.1007/s00442–006–0581–2

Thind KS, Rattan SS (1971) The Thelephoraceae of India. Part 4. The genus Tomentella. Indian Phytopathol 24:32–42

Trowbridge J, Jumpponen A (2004) Fungal colonization of shrub willow roots at the forefront of a receding glacier. Mycorrhiza 14:283–293 doi:10.1007/s00572–003–0264–3

Uhl M (1988) Identifizierung und Charakterisierung von Ektomykorrhizen an Pinus silvestris und von Ektomykorrhizen aus der Gattung Tricholoma. Diss. Univ. München

Walker JF, Miller OK , Horton JL (2005) Hyperdiversity of ectomycorrhizal fungus assemblages on oak seedlings in mixed forests in the southern Appalachian Mountains. Mol Ecol 14:829–838 doi:10.1111/j.1365–294X.2005.02455.x

Wurzburger N, Bidartondo MI, Bledsoe CS (2001) Characterization of Pinus ectomycorrhizas from mixed conifer and pygmy forests using morphotyping and molecular methods. Can J Bot 79:1211–1216 doi:10.1139/cjb-79–10–1211