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I **Pärtel K**, Baral H-O, Tamm H, Põldmaa K. 2016. Evidence for the polyphyly of *Encoelia* and *Encoelioideae* with reconsideration of respective families in Leotiomycetes. Fungal Diversity
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II **Pärtel K**. 2014. Ultrastructure of the ascus apical apparatus of *Encoelia furfuracea* (Helotiales). Mycological Progress 13: 981–986.

III **Leenurm K**, Raitviir A, Raid R. 2000. Studies on the ultrastructure of *Lachnum* and related genera (Hyaloscyphaceae, Helotiales, Ascomycetes). Sydowia 52(1): 30–45.

IV **Leenurm K**, Raitviir A. 2000. The ultrastructure of *Belonidium aeruginosum* Mont. & Durieu (Hyaloscyphaceae, Helotiales). Folia Cryptogamica Estonica 36: 57–63.

V **Leenurm K**, Raitviir A. 2001. The ultrastructure of *Lachnellula willkommii* (Hyaloscyphaceae, Helotiales, Ascomycetes). Folia Cryptogamica Estonica 38: 41–46.

VI **Pärtel K**, Raitviir A. 2005. The ultrastructure of the ascus apical apparatus of some Dermateaceae (Helotiales). Mycological Progress 4(2): 149–159.

The author's contribution to the publications

Kadri Pärtel was responsibile for developing the research ideas and writing all the manuscripts; where transmission electron microscopy (TEM) was used (II–VI), K. Pärtel conducted all laboratory work and analyses. A. Raitviir, K. Põldmaa and H.-O. Baral contributed to the conceptual aspects of the research questions and writing. K. Pärtel and H.-O. Baral contributed to the morphological studies in paper I. A. Raitviir participated in the identification of species, which ultrastructure was observed. H. Tamm contributed to the molecular laboratory work and phylogenetic analyses.

ABBREVIATIONS

DNA	deoxyribonucleic acid
DSE	dark septate endophyte
EcM	ectomycorrhiza
ErM	ericoid mycorrhiza
INSD	international nucleotide sequence databases
I+	ascus apex amyloid (blue/red in iodine solution)
I–	ascus apex inamyloid (not stained in iodine solution)
IR	ionomidotic reaction: fungal tissue extracting pigments in aqueous potassium hydroxide solution (KOH)
LM	light microscopy
LUG	Lugol's solution, aqueous solution of iodine and potassium iodide
MLZ	Melzer's solution, aqueous solution of chloral hydrate, potassium iodide, and iodine
PCR	polymerase chain reaction
rDNA ITS 18S 28S	regions coding for ribosomal RNA (ribonucleic acid): internal transcribed spacer: ITS1, ITS2 flanking 5.8 subunit in rDNA small subunit (SSU) large subunit (LSU)
rpb	RNA polymerase II subunit
tef	translation elongation factor
TEM	transmission electron microscopy
VB	vacuolar body

1. INTRODUCTION

Fungi represent a diverse group of eucaryotic organisms that were classified as a separate kingdom fifty plus years ago (Whittaker 1969). Mycology, initially a descriptive subdiscipline of botany, has increasingly been developed in terms of experimental and molecular science. Advances in methodology have allowed researchers to more precisely characterize and catalogue fungi, which remains an essential task of mycologists. The general principle of fungal systematics is based on the common origin of taxa, the hypotheses of evolutionary history, which are modeled using genetic data. The implementation of DNA-based methods of phylogenic classification has been especially important regarding ascomycetes (=phylum Ascomycota), the most species rich group of fungi.

Molecular studies are accumulating new evidence on the phylogenetic relationships of previously poorly explored lineages. This development is based not only on visible fruitbodies, but on data from analyses of their habitat, such as soil, water, and host plants. Although much regarding the life-histories of fungi remains unknown, DNA analysis has been confirmed as an important tool for providing essential information about the life of fungi, in addition to the traditional knowledge based on fruitbodies (Stajich 2015). However, many branches are missing or unnamed in the current Fungal Tree of Life (e.g. Fig. 4 in LoBuglio & Pfister 2010). The aim of this study was to investigate one of the "weak branches" of the Fungal Tree of Life, the helotialean fungi, which are mostly cupulate ascomycetes, that are as common as mushrooms. However, owing to their scattered growth and small size (often less than 2mm in fruitbody diameter), recording them in nature is difficult, despite the fact that some are brightly coloured.

The helotialean fungi belong to the class Leotiomycetes, where limitation of genera and higher taxa are not well agreed. Owing to the different interpretation of characteristics of these fungi, the morphological description of individual species often differ drastically, although some standard practise for describing species has been suggested (e.g. Huhtinen 1994). The search for information about species description often ends up in returning ambiguous information, especially where descriptions lack detailed illustrations and one must imagine the appearance of the fungus. Due to the scarcity of taxonomic keys, the process of species identification is often time-consuming and unproductive.

The molecular identification of helotialean fungi is critical, because the key users of taxonomic information (e.g. ecologists, evolutionary biologists, and plant pathologists) need DNA barcode markers for species identification. DNA-based methods will also help to characterise the biodiversity of helotialean fungi, especially their symbiotic relationships with plants. Current state, when several morphological criteria that once defined a taxon have been deposed, indicates the need for building a new classification based upon phylogenetic data. To ascertain new diagnostic characters, a critical revision of morphological characters using complemented technical possibilities (e.g. electron

micoscopy) is essential. The main research questions concern the delimitation of families and genera considering their phylogeny. In the following section, the selected groups of helotialean fungi with their main characters, are introduced. The original multigene phylogeny and electron microscopy results are then presented and discussed.

The current confusion regarding the order level delimitation of the studied fungi, necessitated using the informal name "helotialean fungi". This indicates that at present, Helotiales represents a polyphyletic group, largely circumscribed using characters that have evolved as a result of convergent evolution (e.g. Wang 2006a). The family names used in the original papers III–VI do not correspond to those in this thesis, because the classification of the studied genera was changed based upon the subsequently published data of other researchers and one's own results.

1.1. Overview of study groups and taxonomic problems

1.1.1. Class Leotiomycetes O.E. Erikss. & Winka 1997

The class Leotiomycetes includes over 1000 genera of inoperculate ascomycetes (Johnston et al. 2015). Their ascus apex lacks a lid or *operculum*, and they ejaculate spores via an alternative mechanism, which is mainly annular in structure. The sister class of the Leotiomycetes is the perithecial Sordariomycetes (Spatafora et al. 2006, Schoch et al. 2009a). Although these classes largely deviate morphologically, it has been presumed that they evolved from a common ancestor: a nonlichenized saprotroph with unitunicate inoperculate asci (Zhang & Wang 2015). The estimated time of diversification is about 300 million years ago, during the Permian-Carboniferous geological period, as there are no known fossil records of Leotiomycets (Beimforde et al. 2014).

The class Leotiomycetes was described by Eriksson and Winka (1997), and includes the orders Helotiales, Rhytismatales, Erysiphales, Thelebolales, Leotiales, Phacidiales, Cyttariales, and Medeolariales. The last two orders are monotypic, whereas several others contain numerous members (Kirk et al. 2008). The current classification of the Leotiomycetes (Lumbsch & Huhndorf (2010), public databases Mycobank and Index Fungorum) and its accepted orders, are based mainly on the traditional morphological characters of the teleomorph. Often these characters have not confirmed phylogenetically informative and the present Leotiomycetes classification is not congruent with recently presented phylogenies (Wang et al. 2006a, b; Schoch et al. 2009a; Hustad & Miller 2011; Lantz et al. 2011; Han et al. 2014; Crous et al. 2014). These phylogenies show both polyphyly or paraphyly among many of Helotiales taxa, intermixed between other orders, where monophyly is well supported for Cyttariales, Erysiphales, Rhytismatales, Phacidiales.

The proposed classifications are sometimes controversial and often very difficult to interpret when one compares morphology and phylogeny. For example, the Erysiphales (powdery mildews), which are chasmothecial epiphytic leaf parasites (Webster & Weber 2007), have very different morphology compared to apothecial Helotiales, but phylogenies (Wang et al. 2006a, b) have supported its placement among these. In contrast, members of *Geoglossaceae,* morphologically similar to Helotiales, have been excluded from this order, with a new class Geoglossomycetes created based on molecular phylogenies (Schoch et al. 2009b).

The biogeography of Leotiomycetes is also important to understand their diversity (Zhang & Wang 2015). In the Erysiphales, different lineages are geographically isolated, with two basal lineages diverged to South American and eastern Asia (Takamatsu 2004). The Cyttariales is restricted to the southern hemisphere, where *Cyttaria* spp. have coevolved with its host *Nothofagus* (Peterson et al. 2010).

1.1.2. Order Helotiales Nannf. 1932

Based on a macroscopial study of fungal fruitbodies, A. J. Retzius (1769) introduced the genus *Lachnum*; subsequently E. Fries (1822) established among many others, the genus names *Mollisia* and *Encoelia*. Based on micromorphology, during the second half of the 19th century the Friesian genera were divided into numerous smaller ones by Fuckel (1869), Karsten (1871), and Boudier (1885). At the beginning of the 20th century, J. A. Nannfeldt (1932) established the basis of generic level taxonomy in the order Helotiales.

Helotiales is an order with worldwide distribution, including approximately 300 genera and 3000 species (Baral 2016). The order is diverse both ecologically and regarding the "general habitus" of fruitbodies. The most common fruitbodies are non-stromatic sessile or stipitate cupulate-discoid apothecia, but other types include semi-immersed, turbinate, funnel-shaped, clavate (Baral 2016, Spooner 1987), or exceptionally cleistothecial (e.g. *Bicornispora,* see Galán et al. 2015). Stipes, if present, are mostly central and cylindrical. The apothecia may be scattered singly or variously aggregated, and be soft or leathery tough. Some examples of the different lineages studied for this thesis are illustrated in Fig. 1. The asci develop in the hymenium amongst the longitudinal sterile paraphyses, and the receptacle tissues are usually well developed.

Nannfeldt (1932) distinguished six families in the order Helotiales, of which the Geoglossaceae, Orbiliaceae and Phacidiaceae have been updated to a higher taxonomical rank today (Eriksson et al. 2003, Schoch et al. 2009b, Crous et al. 2014). The other three (Helotiaceae, Hyaloscyphaceae, and Dermateaceae) remain families within the Helotiales. However, the original concept of classifying these families based on their excipular structure, hairs, and ascus and paraphyses features (like introduced in Cannon & Kirk 2007), has been discredited by molecular phylogeny (Wang 2006a, Han et al. 2014, Crous et al.

2014), because members of these families have been divided into many separate lineages. Baral (2016) recently differentiated a total of 25 Helotiales families, many of which were resurrected from historical families. In the Helotiales, the classification of approximately 90 genera are *incertae sedis* (Lumbsch & Huhndorf 2010; Baral 2016).

a) Family Dermateaceae Fr. 1849

Members of the *Dermateaceae* (*sensu* Nannfeldt 1932) were defined by the parenchymatous cells of the outer excipulum and the sessile apothecia. Based on phylogenies globose excipular cells was considered to be homoplasious character. Wang (2006a, b) revealed two distinct lineages which form the *Dermateaceae* s. str and *Mollisia* complex. The first lineage includes the plant endophyte-parasites *Dermea* Fr., *Pezicula* Tul. & C. Tul., and *Neofabraea* H.S. Jacks., and the family name Dermateaceae should be restricted to those genera according to Verkley (1999) and Abeln (2000). This family is a quite well studied monophyletic group (Verkley 1999; Abeln et al. 2000; Jong et al. 2001; Chen et al. 2015).

The second of Wang's lineages (2006a) contained *Mollisia* in the larger clade *Loramyces-Mollisia-Vibrissea*. Mollisioids are soft (as indicated by their name), with mostly sessile discoid apothecium (Fig. 1e) and rounded or rectangular brown-walled excipular cells (Nauta 2010). The mollisioid fungi lack any modern revision based on morphology and there is also a shortage of molecular studies. *Mollisia*, with >120 species (Kirk et al. 2008), is "notorious" in terms of species misidendifications. Morphologically similar genera include the *Tapesia* (Pers.) Fuckel with the subiculum under the apothecia, and the septate-spored *Niptera* Fr. and *Belonopsis* (Sacc.) Rehm (Nannfeldt 1985; Nauta & Spooner 1999). *Pyrenopeziza* Fuckel is another species-rich genus, but with more erumpent apothecia than *Mollisia* (Greenleaf & Korf 1980, Gremmen 1958, Hütter 1958, Gminder 1996). Despite *Pyrenopeziza* and *Mollisia* being extremely similar macromorphologically, they are not genetically closely related. Anamorph features correspond to separate clades of the teleomorph of these fungi. *Cadophora*-like producing solitary phialids are related to *Mollisia dextrinospora* Korf (note: the morphology of this species is similar to *Pyrenopeziza*), and *Phialocephala*-like producing complex heads of multiple phialids are related to *Mollisia* spp. (Day et al. 2012). Baral (2016) resurrected the family Ploettnerulaceae Kirschst. which includes *Pyrenopeziza* and several other lineages traditionally connected with the Dermateaceae.

The Mollisiaceae comprises genera with high ecological plasticity, such as the *Phialocephala*, which includes species that are either frequent root endophytes, leaf endophytes, saprobes, or parasites (e.g. on grasses) (Zaffarano et al. 2010; Queloz et al. 2011, Wong et al. 2015, Tanney et al. 2016). Often the morphology is highly reduced and the lifecycle lacks the sexual state, such with in the *Phialocephala fortinii* complex as characterized by melanized septate hyphae (Grünig et al. 2008).

Fig. 1 Apothecia of helotialean fungi.
a *Ciboria batschii* with sclerotia, TU104222. **b** *Rutstroemia firma*, TU104493. **c** *Chlorencoelia versiformis*, TU107606. **d** *Encoelia furfuracea*, TU104599. **e** *Mollisia lividofusca*, TU104358. **f** *Calycina citrina*, TU109158. **g** *Lachnum brevipilosum*, TU109185. **h** *Capitotricha bicolor*, TU104600. **i** *Trichopeziza mollissima*, TU104372. **j** *Hymenoscyphus fraxineus*, TU104160. **k** *Ionomidotis irregularis,* TAAM198450. **l** *Chlorociboria aeruginascens*. Scale bar: a–d = 5mm, e–j, l = 1mm, k = 1cm. Authors of images V. Liiv: a, c, i, j, l; K. Põldmaa: d; H. Tamm: e,f; I. Zettur: k.

b) Family Helotiaceae Rehm 1892

Currently the Helotiaceae is the most heterogeneous family of the Helotiales in terms of morphology and ecology, and comprises 117 genera and 826 species (Kirk et. al. 2008). Previously, Nannfeldt (1932), Dennis (1978), and Korf (1973) distuingished up to 10 intrafamiliar subdivisions, but none have been systematically evaluated using molecular phylogenetics. Several lineages (Ascocoryne-Neobulgaria, Calycina, Chlorociboria, Cordierites, Hymenoscyphus-Cudoniella, Stamnaria, Strossmayeria, and Mitrula) have been recognized using phylogenies (Hustad & Miller 2011, Baral et al. 2013, Crous et al. 2014, Baral et al. 2015b). Chlorociboriaceae Baral & P.R. Johnst. has recently been described for the Chlorociboria lineage (Baral 2015a) and Pezizellaceae Velen. emended for Calycina-Calycellina-Mollisina lineage (Baral 2016). Some species-rich genera of the Helotiaceae, such as *Crocicreas* Fr. (Carpenter 1981) and *Hymenoscyphus* Gray (Lizoñ & Kučera 2014), have yet to be critically revised.

Morphological features of the family Helotiaceae, according to the original description (Rehm 1892) are sessile or stipitate, fleshy or cartilagineus apothecia, with most having ectal excipulum of the *textura oblita*. Korf (1973) emphasized long-celled excipulum, rarely of *t. prismatica* or *angularis*, gelatinized apothecia, and medullary excipulum of the *t. intricata* for the Helotiaceae. The subfamily Encoelioideae Nannf. was distinguished from the Ciborioideae by the former's longevity and the leathery consistency of their apothecia. The outside of the Encoelioideae apothecium seems mealy (Fig. 1d), because the outermost cells of the ectal excipulum are loosely aggregated. Several of these genera had previously been assigned to the family Cenangiaceae Rehm. Encoelioideae (*sensu* Korf 1973) was distinguished from other members of the Helotiaceae mainly by the characters of the excipulum.

Encoelia (Fr.) P. Karst. is a large heterogeneous genus with members that have tough apothecia with a coarse outside, and usually erumpent from bark (Korf 1973). Peterson and Pfister (2010) revealed that the genus *Encoelia* is polyphyletic, with three species included in their four gene phylogenetic analysis falling into two distinct groups: *E. heteromera* (Mont.) Nannf. with *E.helvola* (Jungh.) Overeem near the *Cordierites* Mont. (Helotiaceae); and *E.fascicularis* (Alb. & Schwein.) P. Karst. in the Sclerotiniaceae. However, *Encoelia furfuracea* (Roth) P. Karst., a type species of the genus, has been neglected in recent phylogenetic and morphological studies, despite being commonly found in Europe and North America.

c) Families Hyaloscyphaceae Nannf. 1932 **and Lachnaceae** (Nannf.) Raitv. 2004

The family Hyaloscyphaceae was established by Nannfeldt (1932) for taxa with hairy apothecia and was originally divided into tribes: 1) Arachnopezizeae: apothecia arising from the subiculum; 2) Hyaloscypheae: small-sized apothecia, mainly cylindrical paraphyses, hairs of various shape; and 3) Lachneae: relatively large apothecia, hairs multiseptate and granulated (Fig. 1g–h), lanceolate paraphyses. The first multigene phylogenetical work of hyaloscyphoid fungi–

based on Asian data–suggested this family is polyphyletic (Han et al. 2014). The Hyaloscyphaceae was emended by Raitviir (2004), who excluded genera of the Lachneae as a distinct family of its own (Lachnaceae), which was later supported by the multigene phylogenetic study of Hosoya et al. (2010).

Lachnum Retz. is a world-wide genus with approximately 250 species (Kirk et al. 2008). These have cupulate +/– stipitate apothecia with hyaline or pigmented hairs often bearing crystals in apices, and lanceolate paraphyses. Raitviir's (1970) idea that species with totally or partially smooth-walled hairs belonging to separate genera (*Albotricha* Raitv., *Belonidium* Mont. & Durieu, *Dasyscyphella* Tranzschel and *Trichopezizella* Dennis ex Raitv.), was confirmed by the exclusion of further taxa from *Lachnum*, based on morphological characters. New genera have been proposed for fungi with thick-walled hairs, e.g. *Capitotricha*, *Brunnipila*, and *Incrucipulum* by Baral (1985), and for those with thin-walled melanin-containing hairs (*Fuscolachnum* J.H. Haines, Haines 1989). *Albotricha* have hairs that bear amorphous reactive resinous matter that does not dissolve in Melzer reactive (MLZ) (Raitviir 1970). *Lachnellula* P.Karst. contains 40 species (Kirk et al. 2008) and is macromorphologically very similar to *Lachnum* segregates, in contrast to latter, *Lachnellula* asci arise from unique open croziers, the stipe is short, and the parahyses cylindrical. Baral (2000) emphasized the desiccation-tolerance of the apothecia in *Lachnellula* spp.

Trichopeziza (Fig. 1i) and *Trichopezizella* were assigned by Raitviir (1987) into a different subfamily (Trichopezizelloideae), which were also recently excluded from the emended Lachnaceae (Hosoya et al. 2010). In contrast to the Lachnaceae, the *Trichopeziza* spp. have long, smooth, densely septate, and relatively thick (up to 2µm) hairs of a yellow–reddish–brownish pigment.

1.2. Characters in systematics of Helotiales

1.2.1. Characters of apothecium

Traditional morphological characters used to identify the Helotiales are the shape and measurments of the hymenium components of apothecia: asci, ascospores, and paraphyses (Nannfeldt 1932, Korf 1973, Spooner 1987, Pfister & Kimbrough 2001). The structure that supports hymenial part of the apothecium is called the excipulum with layers of different hyphal types distinguished (*textura* type), and the presence of exudate or/and gel noted. The characters of hairs covering the external part of the apothecium of numerous helotialean taxa have been of important diagnostic value (hairs' density, length, shape, septation, presence of crystals or other external substances, and refractivness). The ornamented hairs, which seem punctate or granulate in LM, and the crystals in the central part of the hair apex have been observed under scanning electron microscopy (Hein 1980, Horner et al. 1983).

Baral (1992) has drawn the attention to the cell components, such as the amount of lipid bodies in ascospores, or vacuolar bodies in vegetative cells. The special components of vacuoles, the refractive vacuolar bodies, occurring on external parts of apothecia, contain a colloidal substance, which reflects the light during microscopical observations (Baral 1992).

Isolation of helotialean fungi into pure culture is not routinely applied and many of them do not produce conidiomata or any other asexual structures in culture, and/or the ascospores do not germinate on standard culture media.

1.2.2. Ascus and its apical apparatus

The ascus is the largest distinct cell in the fruitbodies of ascomycetes, resembles a fluid-filled sac, and its growth is determinate in contrast to unspecialized vegetative hyphae (Read & Beckett 1996). Asci develope from ascogenous hyphae growing out of an ascogonium (Wilson 1952). The essential biological processes karyogamy, meiosis, and mitosis, are conducted in the asci (Bellemère 1994). In Helotiales, the result of these processes, the ascospores, are forcibly ejected and carried via air to new substrata or habitats. For example, *Sclerotinia sclerotiorum* eject thousands of ascospores synchronistically, when a blast of air is created that carries the spores away (Roper et al. 2010).

At the top of the ascus is a strigger (a ring-shaped structure) and the structure of the ascus apex has been shown to be quite complex under TEM, and is called the ascus apical apparatus (Verkley 1992). This apparatus is responsible for the ejaculation of ascospores. This is very fast process, because it is important to cross the stagnant layer of air surrounding the fruitbodies, however the pressure is controlled to avoid rupture of the ascus (Fritz et al. 2013, Trail & Seminara 2014). It is assumed that glycose or glycerole provides the osmotically active solute responsible for the increase in turgor pressure just before discharge (Read & Beckett 1996). In helotialean fungi, the opening is in most cases via eversion of an apical ring (annulus) (Verkley 1995b).

Ascus characteristics have long been used in ascomycete systematics, first the shape and size, then the number of ascospores (mostly 8) per ascus, and the arrangement of spores (uniseriate, biseriate, or overlapping) (Bellemère 1994). The presence of croziers at the ascus base, next to the ascogeneous hyphae, is constant for a taxon (Huhtinen (1990). Boudier (1879) argued for use of iodine solution for studying the ascus apex in detail, as he found this method useful in classifiying apothecial ascomycetes (Discomycetes). The iodine reaction, however, has not become a standard component in all descriptions of taxa in the helotialean fungi.

The helotialean fungi differ in their ascus apices, with an apical ring not always present. When a ring is absent, the apical wall may be thickened (reviewed in Verkley 1995b). The annulus (the apical ring), usually reacts to iodine, and according to Baral (1987a) this species-specific reaction is either : 1) negative in iodine reagents = inamyloid, I–; 2) stains blue in Melzer (MLZ) and

Lugol (LUG) solution = euamyloid, I+ bb; 3) stains reddish in LUG = hemiamyloid, I+ rb (red at high, blue at low concentrations) or I+ rr (red); in addition, hemiamyloid apex stains blue in MLZ after KOH pretreatment. Ascus shapes change before the liberation of spores (Bellemère 1994). Mature asci are usually apically blunt, while the lateral wall becomes thinner and apical ring height decreases compared to juvenile asci. In some species, e.g. *Lachnellula occidentalis*, inamyloid and amyloid asci are intermixed in the hymenium of one apothecium (Baral & Matheis 2000). However, amyloidity type is mostly constant in a species, and the annulus shape and (approximate) type can be described using LM. Based on observations of different ascal apices, some taxa have been critically studied and taxonomic recombinations proposed (Triebel & Baral 1996, Johnston et al. 2014, Sandoval-Leiva 2014).

The pioneer of comparative TEM studies of the ascus appical apparatus in helotialean fungi was Bellemère (1977). Before him only single species of Sclerotiniaceae (*Ciboria acerina* by Corlett & Elliott 1974 and *Dumontinia tuberosa* by Schoknecht 1975) and Bulgariaceae (Bellemère 1969) had been studied. Later studies by G. J. M. Verkley revealed specific ascus apical apparatus in several families of Helotiales (Verkley 1992; 1993a, b; 1994; 1995a, b; 1996 and 2003). Verkley's comparative treatment of 26 genera (resulting in 14 different ascus types) in his doctoral thesis (1995b) suggested that ultrastructural studies offer a promising approach in refining the taxonomy of the Helotiaceae, Geoglossaceae and Sclerotiniaceae, via observing methodically each devepmental stage (juvenile, immature, and mature) of the ascus lateral wall structure and mode of dehiscence.

1.3. Ecology of Leotiomycetes

Leotiomycetes inhabit very different ecological niches, from marine to terrestrial, and from soil to the crowns of trees. A reference-based overview of substrata/hosts and putative lifestyles of this fungal class is presented in Table 1. Ecology has been neglected by most earlier taxonomists, and fruitbody specimens in fungal collections had often been detached from the substrate, and or the plant species upon which they were growing, was not identified. Teleomorphs and anamorphs of helotialean fungi are most frequently observed on different parts of plants, and the formers' lifestyle is either saprobic, parasitic, or symbiotic. In the case of foliicolous fungi, it has been shown with molecular and cultivating methods, that still attached senescent living leaves are hosts for endophytic Leotiomycetes, and that the same species later act as initial decomposers (Koukol & Baldrian 2012, Voříšková & Baldrian 2013) by producing extracellular enzymes (Korkama-Rajala et al. 2008, Žifčáková et al. 2011).

Table 1. Distribution of putative lifestyles and substrates among the lineages of the Leotiomycetes. Taxa are assigned into families according to the results of the phylogenetic analysis (**I**) and a recent classification by Baral (2016) in which old family names have been resurrected.

Life-style	Substrate/host	Examples	References	(Putative) lineage
Saprobes	dead leaves	*Heyderia*, Rutstroemiaceae, Lachnaceae, Pezizellaceae, Helotiaceae and many others	Hansen & Knudsen 2000, Dennis 1978	Various, see examples
	dead stems of herbaceous plants	*Crocicreas*, Lachnaceae, Mollisiaceae, Helotiaceae s.l., Hyaloscyphaceae and many others	Hansen & Knudsen 2000, Dennis 1978	Various, see examples
	decaying wood	Most families include lignicolous members	Hansen & Knudsen 2000, Dennis 1978	many
	algae, *Phaeofucaceae*	*Calycina maritima*	Baral & Rämä 2015	Pezizellaceae
	Fungi	*Hyphodiscus* spp.	Han et al. 2014	*Hyphodiscus*
		Moserella	Pöder & Scheuer 1994	unknown
		Ionomidotis pro parte	Zhuang 1988 a	Cordieritidaceae
		Unguicularіopsis, *Skyttea*	Suija et al. 2015	Cordieritidaceae
	Dung	*Coprotinia*	Dumont 1975	Sclerotiniaceae
		Thelebolales	Landvik et al. 1998	Thelebolales
	Soil	*Phaeohelotium geogenum*, *Discinella*	Hansen & Knudsen 2000	Helotiaceae
		Podophacidium xanthomelum		unknown
	Mosses	*Bryoscyphus, Hymenoscyphus, Mniaecia*	Stenroos et al. 2010	Pezizellaceae Helotiaceae, *Mniaecia*
		Hyaloscypha hepaticola	Baral et al. 2009	Hyaloscyphaceae
	submerged wood	*Vibrissea*	Hustad & Miller 2011	Vibrisseaceae
Parasites	leaves	*Hymenoscyphus fraxineus*	Baral & Bemmann 2014	Helotiaceae
		Kohninia linnaeicola	Holst-Jensen et al. 2004	Sclerotiniaceae
		Pyrenopeziza brassicae	Li et al. 2003	Ploettnerulaceae
		Rhytismatales	Lantz et al. 2011	Rhytismatales
		Erysiphales	Braun & Cook 2012	Erysiphales
	branches of trees	*Neofabraea*, *Pezicula*	Abeln et al. 2000	Dermateaceae s.str.
		Cyttaria	Peterson & Pfister 2010	Cyttariales
		Gremmeniella	Baral 2015a	Godroniaceae
	mosses	*Discinella*, *Pezoloma*	Kowal et al. 2015	Pezoloma
	plant roots	*Roesleria*	Kirchmair et al. 2008	Roesleria
	fruits, *Rosaceae* and others	*Monilinia*	Holst-Jensen et al. 1997	Sclerotiniaceae

Table 1. Continuation

Life-style	Substrate/host	Examples	References	(Putative) lineage
Parasites	herbs, Liliaceae	*Medeolaria*	LoBuglio & Pfister 2010	Medeolariales
	Equisetum	*Roseodiscus*, *Stamnaria*	Baral & Krieglsteiner 2006	Roseodiscus, Stamnaria
Symbionts, endophytes	Roots	*Leptodontidium orhidicola*	Walker et. al. 2011, Rodriques et al. 2009	Leptodontidium
		Oidiodendron, *Amorphotheca*, *Myxotrichium*	Wang 2006a	Myxotrichaceae
		Phaeomollisia, *Phialocephala*, *Acephala* *Leohumicola* *"Cadophora" finlandica*, *Phialophora*	Grünig et al. 2009 Day et al. 2012	Mollisiaceae Hyphodiscus Hyaloscyphaceae
		Meloniomyces variablis, *Pezoloma ericae*	Hambleton & Sigler 2005, Hambleton et al. 1999	Pezoloma
	Leaves	*Sarcotrochila, Cenangium, Rhabdocline*	Grünig et al. 2009	Cenangiaceae
		Phaeomollisia *Phialocephala*	Tanney et al. 2016	Mollisiaceae
		Rhytismataceae, Cryptomycetaceae	Lantz et al. 2011	Rhytismatales
Symbionts, mycorrhizal	arbutoid ErM subtype	*Leotia* cf. *lubrica*	Kühdorf et al. 2015	Leotiaceae
	ErM+DSE	*Acephala applanata* *Pezoloma ericae*	Lukešová et al. 2015, Hambleton & Sigler 2005, Walker et al. 2011	Mollisiaceae Pezoloma
	ECM with trees	*Meliniomyces* *„Cadophora" finlandica* *Phaeohelotium?* *Acephala macrosclerotiorum*	Reviewed in Tedersoo 2010 Baral et al. 2013 Münzenberger 2009	Hyaloscyphaceae Hyaloscyphaceae Helotiaceae Mollisiaceae
aeroaquatic		*Exochalara*, *Infundichalara*, *Brachychalara*, *Loramyces* *Hydrocina*, *Varicosporium* *Helicodendron* *Helicocentralis*	Réblová et al. 2011 Wang et al. 2006a Hustad & Miller 2011 Sri-indrasutdhi 2015	Hyphodiscus Loramycetaceae Pezoloma
aquatic		*Gyoerffyella*, *Tricladium, Ypsilina, Filosporella*, *Lemonierra* *Rhynchosporium* *Tetracladium* *Flagellospora*	All Baschien et al. 2013	Pezoloma ploettneruloid Tetracladium Phacidiales

Nowadays, fungal ecology is usually based on genetic data. Mycorrhizal or endophytic lifestyle, existence in soil or in aquatic environments, and either as mycelium or single conidia, are easily detected using modern DNA sequencing techniques, and such kinds of studies are increasing in number. DNA from the fruitbodies of numerous taxa are sequenced, though a large part of described taxa still lack molecular data. Therefore, it is difficult to refresh taxonomical information regarding the source organism of unidentified strains, resulting in them being named as "Leotiomycetes/Helotiales sp." or "uncultured ascomycetes" in international nucleotide sequence databases (INSD).

Based on Tedersoo et al. (2014) the phylogenetic diversity of Leotiomycetes in soil is high. According to their analyses of global soil samples, Leotiomycetes represent 7.1% of all fungal groups detected in this environment, and are relatively more diverse in arctic tundra (approximately 25% from total sequences of that biome). In addition, proportions of Leotiomycetes in boreal and southern temperate forests, and grassland–shrublands, exceed the global average proportion, and are least abundant in tropical savannas (Tedersoo et al. 2014). Leotiomycetes can survive in extreme habitats, such as the acidotolerant anamorphic fungus *Soosiella minima* Hujslová & M. Kolařík recently discovered in acidic soil with a pH of <3 (Hujslová et al. 2014). The ectomycorrhizal helotialean fungi often lack latin names and known teleomorphs, and most probably have evolved independently in different geographical regions (Tedersoo 2010). In mycorrhizal symbiosis members of Leotiomycetes do not form the typical Hartig net, with the one exeption being *Leotia lubrica* that forms arbutoid mycorrhiza (Kühdorf et al. 2015).

Globally distributed root endophytes associated with ectomycorrhizae dominate among the soil-inhabiting Leotiomycetes. These are referred to as root associated fungi or dark septate endophytes (Queloz et al. 2011). Quite common among these are the *Phialocephala-Acephala* and *Rhizoscyphus-Meliniomyces* complexes, which are host generalists (Vrålstad et al. 2002, Tedersoo et al. 2009). Their effects upon the plant partner range from neutral to negative, and are strain-dependent (Tellenbach et al. 2011, Reininger et al. 2012). It has been shown that the fungi forming ericoid or orchidoid mycorrhiza largely overlap (Bergero 2000, Chambers et al. 2008, Kohout et al. 2012).

One important role of Leotiomycetes in plant communities is the decomposition of plant matter. This process involves many fungi, with early decomposers (in woody substrates often opportunistic basidiomycetes) are gradually replaced by ascomycetes. For instance, *Chlorociboria aeruginascens* causes soft rot while colonizing fallen trunks that have previously been degraded by white rot fungi (Richter & Glaeser 2015). The enzymatic activities of Leotiomycetes as wood-decomposers are not well known. *Calycina citrina* (Hedw.) Gray (Fig. 1f) and *Bulgaria inquinans*, have been associated with low levels of soft rot decay (Worrall et al. 1997), as has *Phialocephala dimorphospora* (Held 2013).

More than 100 Leotiomycetes species live in aquatic habitats. Many of these that live in freshwater also inhabit terrestrial habitats, such as waterlogged

wood (Dennis 1978, Pfister & Kimbrough 2001). Many species in the Loramycetaceae-Vibrisseaceae-Mollisiaceae clade, especially in an asexual state, are found on submerged wood or other substrate in aquatic environments (Baschien et al. 2013, Sandoval-Leiva et al. 2014).

Apothecia of encoelioid species mostly form on the bark or wood of various tree species (I Table S3) and saprotrophic or sometimes parasitic lifestyles have been suggested for these fungi (Torkelsen & Eckblad 1977). *Encoelia furfuracea* grows on recently died standing branches of *Corylus.*

1.4. Aims

The general aim of the present thesis was to contribute to establishing a phylogeny-based classification of the Leotiomycetes, especially of helotialean fungi.

In particular, the aims were following:

1) to evaluate the applicability of morphological and ultrastructural characters in the systematics of helotialean fungi (species, genus, family level) focusing on genera of the family Lachnaceae, as well as of mollisioid and encoelioid fungi;
2) to reveal the phylogenetic affinities of species included in the subfamily Encoelioideae, and particularly in the genus *Encoelia,* with a special focus on its type species, *E. furfuracea*;
3) to establish a phylogeny-based classification of the taxa previously incorporated to Encoelioideae;
4) to synthesize the information on the ecology of members of different helotialean lineages by analyzing together ITS rDNA sequences originating from fruitbodies, culture isolates and complex biological samples using sequences obtained in this study as well as those available in INSD.

2. MATERIALS AND METHODS

2.1. Materials

The studied fungal specimens for encoelioid phylogeny (**I**) were obtained from the fungaria (acronyms according to Thiers, 2015): BPI, C, CUP, DAOM, FH, K, LD, M, NY, O, OULU, QCNE, S, TAAM, TNS, and TU, and from the private collections of H.-O. Baral, G. Marson, J. H. Petersen, I. Wagner, and E. Rubio Domínguez. For the TEM research (**II**–**VI**), living apothecia were collected from nature and kept alive in plastic boxes until fixation. During winter, prefrozen substrates, such as dead *Rubus idaeus* canes and stems of *Filipendula ulmaria*, were incubated in vegetation chambers under artificial light and humid conditions (on wetted filter paper) at 20 °C, in order to obtain living apothecia for fixation. For original voucher specimens preserved in TAAM and TU collections, the exhaustive data were entered into the PlutoF platform (https://plutof.ut.ee/ Abarenkov et al. 2010) and data are partly accessable via the public website (https://natarc.ut.ee/en/seenekogud.php).

2.2. Methods

For identification purposes morphological characters were recorded in all studied specimens using LM. After the reconstruction of the multigene phylogeny (I), the features distinguishing monophyletic clades, were outlined for each taxon. The ascus apical apparatus and apothecial hair wall ultrastructure were selected for TEM observations because the resolution of LM was insufficient for characterising these and additional details were expected to be found in their ultrastructure.

2.2.1. Light microscopy

The morphology of the living apothecia and anamorphs was mostly studied with the specimens mounted in tap water. Dry specimens were rehydrated and mounted in a 3% aqueous potassium hydroxide solution (KOH). For staining specific structures, cotton blue (CB, in lactic acid), cresyl blue (CRB, in water), Melzer's regent (MLZ) and Lugol's solution (IKI) were used. Ionomidotic reaction (IR) was tested in encoelioid specimens (**I**) by applying a 3–10% aqueous KOH solution to a water mount of apothecial fragments. Microphotographs and measurements of structural elements were taken from freehand sections or squash mounts using a Nikon 80i microscope.

2.2.2. Transmission electron microscopy

For TEM analysis (II–VI), taxa were sampled from the Lachnaceae and Mollisiaceae, and *Encoelia furfuracea*, whose ultrastructure had not previously been included in comparative studies. The preparations followed Samuelson and Kimbrough's (1978), and Curry and Kimbrough's (1983).

- Fixation of apothecia: 2 hours using a 2% paraformaldehyde, 2.5% glutaraldehyde, and 2mM calcium chloride in a 0.1M sodium cacodylate buffer solution; post-fixation for 45 minutes in a 1% osmium tetroxide solution in the same buffer.
- Dehydration: through a graded ethanol series from 10–90 % and 3×100% solution of EtOH, followed by treatment with acetone.
- Embedding into Spurr's resin using an infiltration resin series and acetone in 1:3, 1:1 and 3:1 proportions for ≥4 hours each.
- Polymerization for 10–16 hours at 70°C.
- Ultramicrotomy: sections were made mostly using glass knives, except for some specimens when diamond knives were available.
- Staining of the sections: 2% uranyl acetate in 50% EtOH and 0.2% lead citrate solution.
- Examination: an electron microscope was used with magnifications from 5,000 × to 25,000×.

For more details, see the TEM methodologies in **II**–**VI**.

2.2.3. Molecular analysis

The methodological details of DNA extraction from fruitbodies of helotialean fungi, DNA amplification, and analysis of molecular data are given in **I**. Taxon sampling for multigene analysis was designed to cover the main Leotiomyces lineages, with an emphasis on the three lineages that were previously members of the Helotiaceae (the Encoelia furfuracea, Cordierites, and Chlorociboria lineages), and the families Hemiphacidiaceae, Rutstroemiaceae, and Sclerotiniaceae. For multigene phylogeny, genomic DNA was extracted from dried or fresh apothecia. In 70 specimens, selected regions of the nuclear 18S and 28S ribosomal subunits and three protein-coding genes (*tef1*, *rpb1* and *rpb2*) were amplified. The primers used in multigene (combined 18S and 28S rDNA) and ITS analysis are listed in **I** Table 1. For improving 18S rDNA and *rpb1* amplification, new primers were designed. DNA sequences obtained in **I** were submitted to the INSD (**I** Table S1).

Taxon sampling for ribosomal DNA (18S + 28 rDNA) focused on groups of helotialean fungi, members of which were used in the TEM analysis of this study. ITS rDNA taxon sampling included available public sequences with a certain percentage of similarity to the target species. This treshold value differed among studied families, the ITS sequences of which were analysed separately. DNA sequences used in Bayesian phylogeny of ITS rDNA

(Lachnaceae) and 18S+28S rDNA were submitted to UNITE via the PlutoF platform (https://plutof.ut.ee).

For constructing the Bayesian phylogeny of Leotiomycetes, a GTR+I+G evolutionary model was selected and constructed using MrModeltest (Nylander 2004) for most of the partitions. MrBayes v. 3.2.6 (Ronquist et al. 2012) was used to analyse the partitioned five-gene dataset for multigene analysis (**I**). The analyses were run for 50,000,000 generations using the CIPRES Science Gateway v. 3.3 (http://www.phylo.org), sampling each 1000th generation. By the end of the run, the average standard deviation of the split frequencies had reached 0.01. The first 25% of the trees were discarded as a burn-in, and the posterior probabilities (PP) calculated from the remaining trees.

ITS rDNA was used to test phylogenetic relationships among the members of Lachnaceae and encoelioid taxa. Due to the high variability in the ITS regions, the encoelioid sequences were aligned in separate matrices, conforming to the families studied (**I**). In addition to the original sequences, the most similar sequences were obtained from the INSD by applying a BLAST search for the target species, which were then added to the respective matrices. These resulting datasets were analysed using MrBayes v. 3.2.6 (Ronquist et al. 2012) in CIPRES. From 10,000,000 generations, 75% of trees were retained and used to calculate the PP. Species Hypothesis (SH) codes in the UNITE database (Kõljalg et al. 2013) were assigned to all ITS sequences generated in this study via the PlutoF platform.

3. RESULTS
3.1. Phylogenetic analyses

3.1.1. Multigene dataset

In the Bayesian phylogeny (**I**) based upon the analysis of five genes (Fig. 2), most of the terminal clades and many deeper branches, received strong posterior probability support (PP≥0.95). The results revealed the Helotiales to be paraphyletic. While Cyttariales, Thelebolales, Rhytismatales, Phacidiales, and Erysiphales were monophyletic, their relationships with various lineages of helotialean fungi remained unresolved. *Encoelia* (9 species) and Encoelioideae (28 species) appeared to be highly polyphyletic in all analyses. Members of Encoelioideae were dispersed among six families and three clades of unclear affiliation.

Encoelia fascicularis and *E. pruinosa* belonged to the Sclerotiniaceae, and these species were transferred to a new genus (*Sclerencoelia*), together with a new species, *S. fraxinicola*. The sister group of Sclerotiniaceae was Rutstroemiaceae, which included *Encoelia tiliacea* and *Dencoeliopsis johnstonii.* Due to their close relationship to the type species of *Rutstroemia* (*R. firma)* both species were accepted in *Rutstroemia*. *Piceomphale bulgarioides* and *Cenangium acuum*, whose taxonomy remained unsettled, formed the sister group of the Sclerotiniaceae and Rutstroemiaceae.

The type species of *Encoelia*, *E. furfuracea,* formed a strongly supported group with species of *Velutarina* and *Cenangiopsis* (Encoelioideae s. str.), as well as *Trochila* spp. and an undescribed taxon. The sister group of this clade comprised species of *Chlorencoelia* and *Heyderia*, *Sarcotrochila longispora* (a Hemiphacidium clade in Wang et al. 2006a), as well as *Crumenulopsis sororia*, and *Cenangium ferruginosum*. Altogether the E. furfuracea clade, the extended Hemiphacidium clade, and *Rhabdocline laricis*, were considered to represent Cenangiaceae, which thus includes the Hemiphacidiaceae.

Eleven encoelioids ("*Encoelia" fimbriata* and "*E." heteromera*, and species of *Ameghiniella*, *Cordierites*, *Diplocarpa*, *Ionomidotis*, *Llimoniella,* and *Unguiculariopsis*) formed a strongly supported clade with four non-encoelioid lichenicolous species. Altogether, the members of this clade were considered to constitute the family Cordieritidaceae Sacc. "*Encoelia" fimbriata* and "*E." heteromera* were not congeneric and *Ionomidotis* appeared to be polyphyletic.

The Chlorociboriaceae comprised *Chlorociboria* spp. and *Encoelia glauca,* witch was transferred to the former genus. Species of *Chaetomella*, *Pilidium*, and *Xeropilidium dennisii* (=*Encoelia fuckelii*), formed a strongly supported group representing the Chaetomellaceae. However, phylogenetic relationships of this family remained unresolved.

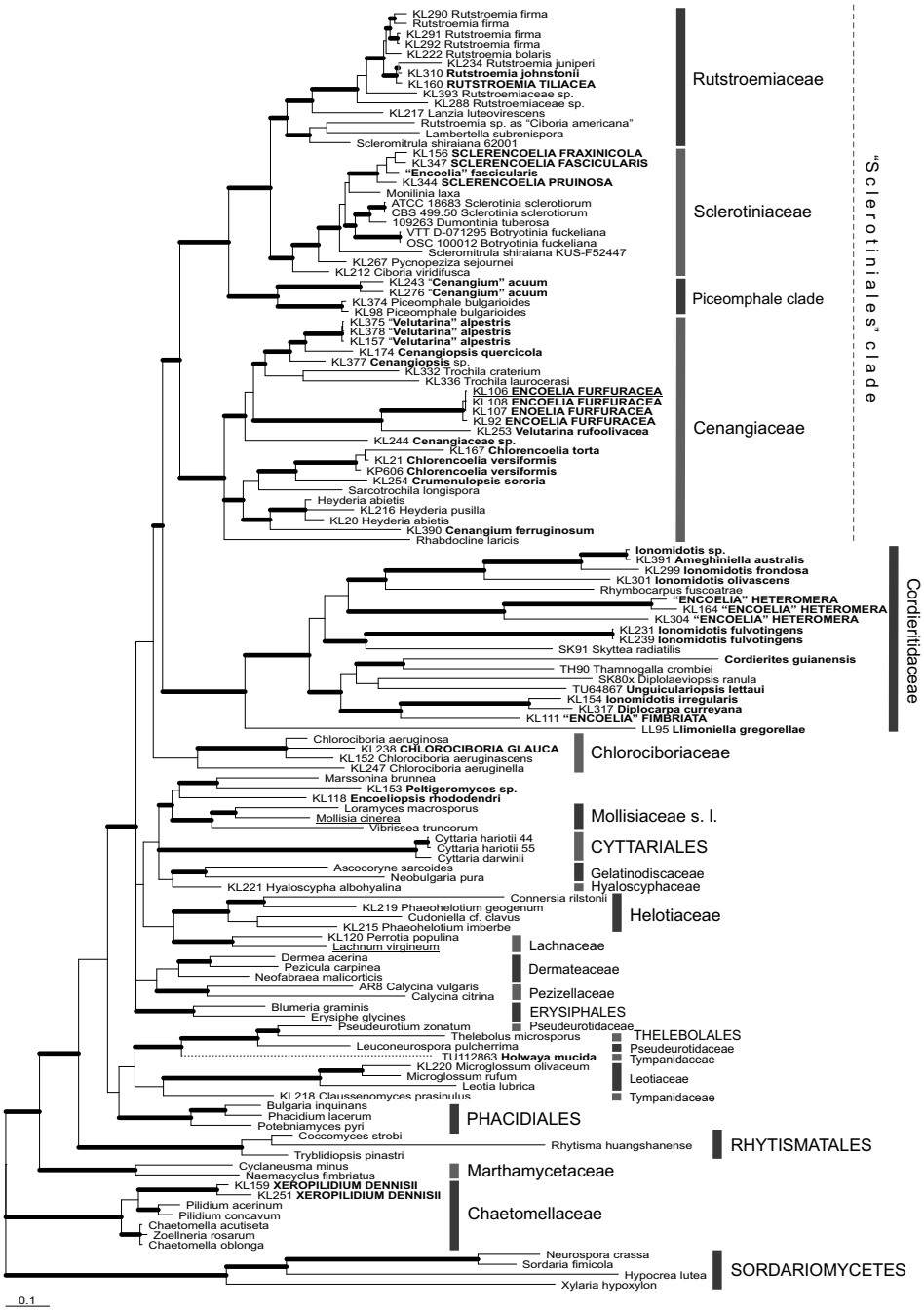


Fig. 2 Bayesian phylogeny of Leotiomycetes inferred from 5 genes (18S, 28S rDNA; *tef1*, *rpb1*, *rpb2*). Species traditionally recognised in Encoelioideae are presented in bold, with those of *Encoelia* in capital LETTERS. Species studied with TEM (in II, III,VI) are underlined. Taxa marked with „KL" are sequenced for this study. Sordariomycetes strains represent the outgroup. Branches with posterior probability scores ≥0.95 are presented in bold. Scale bar indicates substitutions per site.

3.1.2. 18S and 28S rDNA dataset

For rDNA (18S + 28S) dataset of Leotiomycetes, sequences of 90 genera, including newly sequenced *Encoelia furfuracea*, *Podophacidium xanthomelum*, the selected members of the Lachnaceae and the *Mollisia-Pyrenopeziza* complex, were merged into the matrix. Four species of Sordariomycetes were chosen to constitute an outgroup. *Mollisia revincta* and *Podophacidium xanthomelum* were represented with only 28S, and *Mollisia dilutella* with only 18S. The 18S + 28S rDNA dataset included 6797 characters; after removing ambiguously aligned nucleotids and long insertions, the matrix comprised 1480 bp from 18S and 1332 bp from 28S, of which 275 and 381 positions were, respectively, parsimony-informative. The Bayesian analysis was run using a partitioned gene dataset.

In the rDNA phylogeny the lineages of Helotiales were intermixed with those of Erysiphales, Rhytismatales, Phacidiales, and Cyttariales (Fig. 3), as in the multigene analysis (Fig. 2). Most of the Leotiomycetes lineages received low support. *Encoelia furfuracea* formed a clade with *Velutarina* spp., *Cenangiopsis quercicola*, *Trochila laurocerasi* and *Cenangium ferruginosum*. This clade formed together with the Chlorencoelia-Sarcotrochila clade, Piceomphale clade, Rutstroemiaceae and Sclerotoniaceae clades a well-supported large clade. Its sister group was formed of strongly supported Cordieritidaceae.

Lachnaceae was found to be monophyletic with *Phaeohelotium geogenum* as a poorly supported sister group. Within Lachnaceae, the close relationship of *Perrotia populina* to *Lachnellula willkommii* and L. *subtilissima* was strongly supported. *Incrucipulum ciliare* represented a sister group to these three species whereas *Lachnellula abietis* was not closely related to this group, but constituted a sister taxon of *Erioscyphella curvispora* and *Belonidium aeruginosum. Capitotricha bicolor, Dasyscyphella nivea* and *D. cassandrae* formed a sister clade to *Lachnum virgineum* and *L. arcticum*.

The Mollisiaceae- Loramycetaceae-Vibrisseaceae clade included *Belonopsis* spp., *Loramyces macrosporus*, *Mollisia cinerea*, *M. clavata*, *M. melaleuca*, *Tapesia fusca*, *Vibrissea truncorum,* and *Phialocephala fortinii*. Two analyzed strains of *Mollisia cinerea* most likely represent different species. The relationships of *Mollisia* species with other members of Mollisiaceae remained unresolved.

A clade corresponding to the family Ploettnerulaceae Kirschst. (fide Baral 2016) included three species of *Mollisia*, two *Pyrenopeziza* and *Peltigeromyces* sp. *Pyrenopeziza gentiana, Mitrula paludosa*, and *Encoeliopsis rhododendri* formed a separate clade. Thus, *Pyrenopeziza* was found to be not monophyletic and further studies are needed to ascertain the phylogenetic relationships of *Pyrenopeziza* species, including its type species, *P. chailletii* (Pers.) Fuckel.

The analysis confirmed the inclusion of *Pezicula carpinea, Dermea acerina* and *Neofabreae malicorticis* in Dermateaceae. The affinities of *Trichopezizella nidulus* and *Podophacidium xanthomelum* in the Leotimycetes remained unresolved.

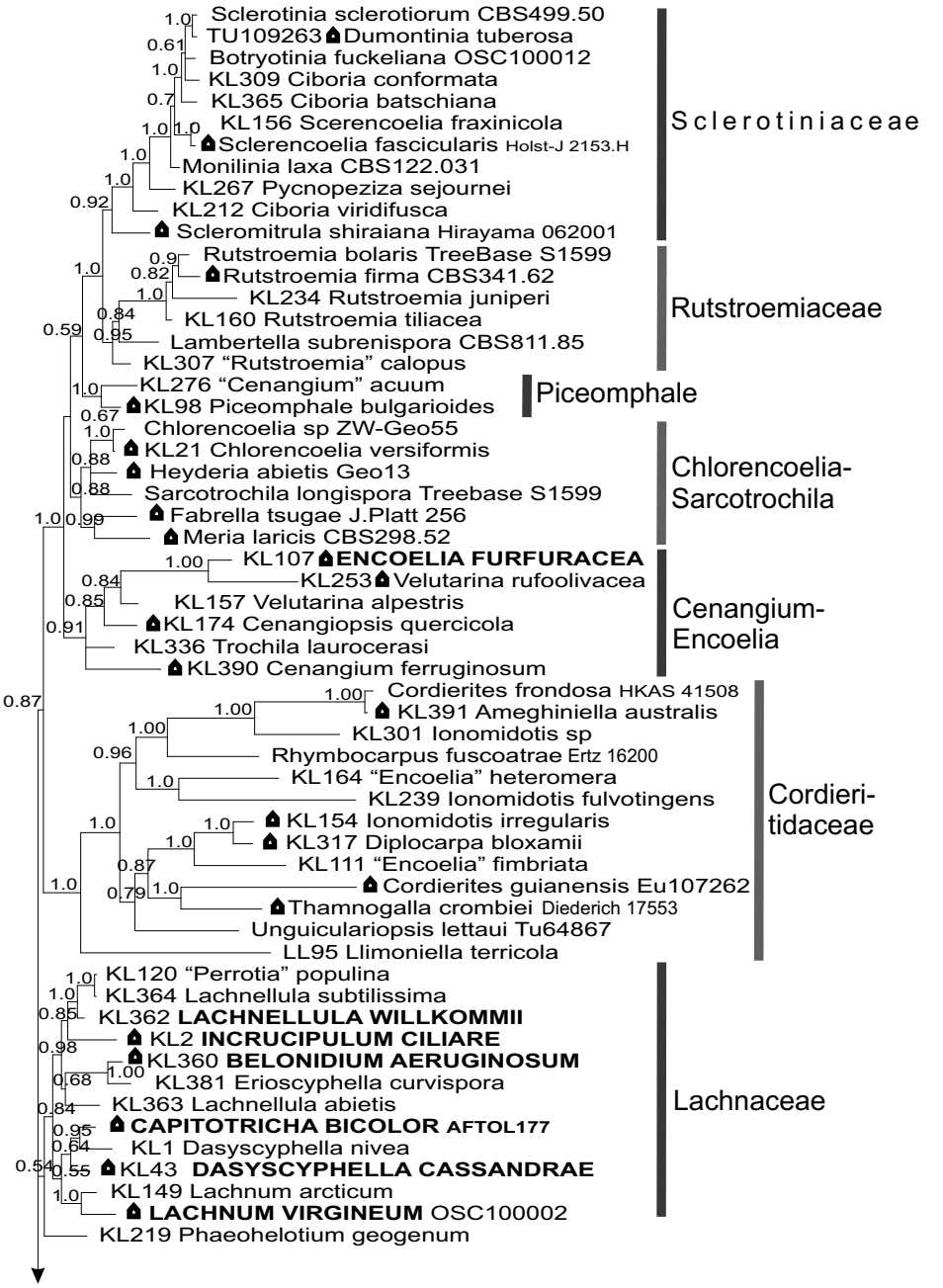
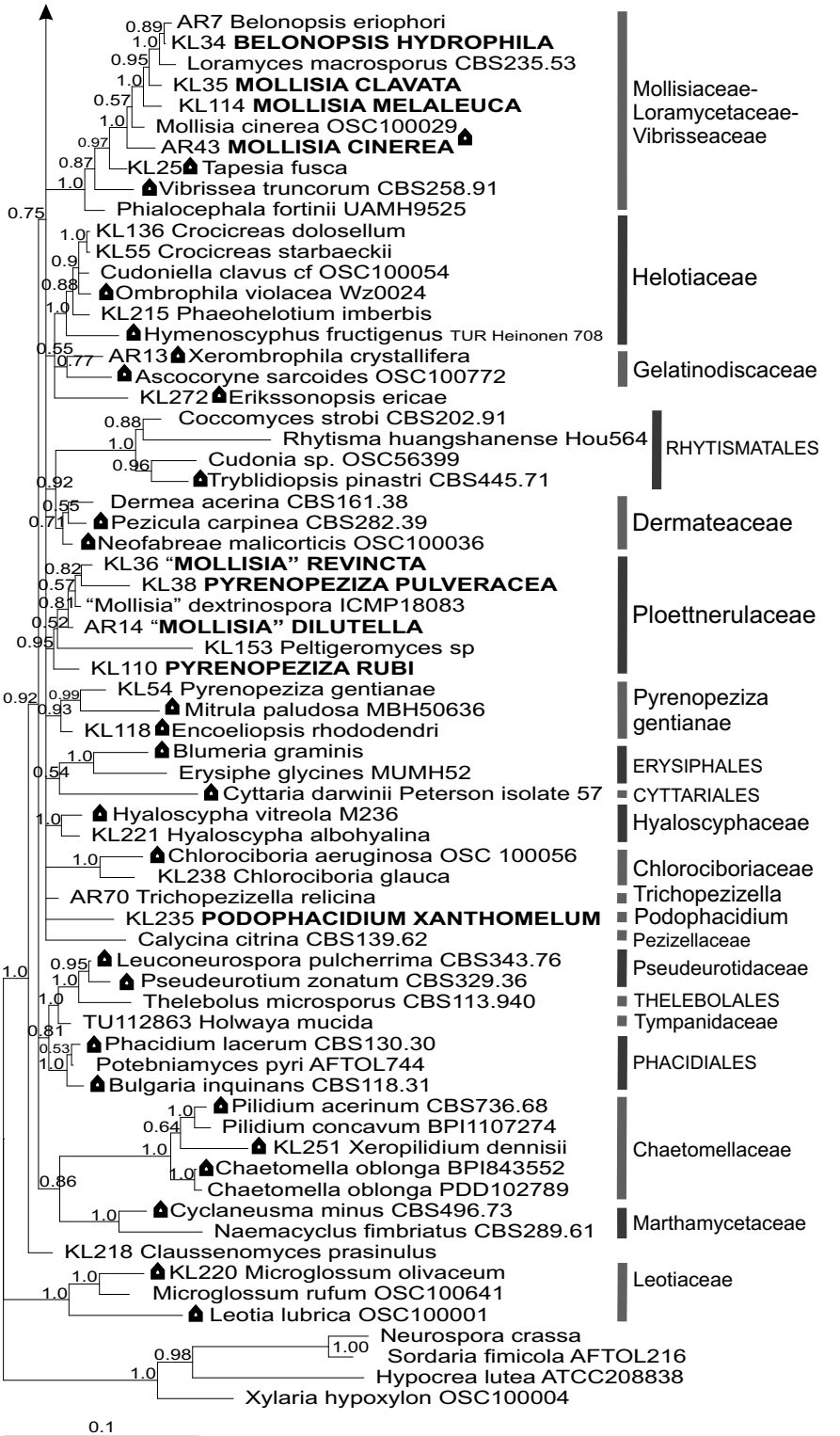


Fig. 3. Bayesian phylogeny inferred from rDNA 18S and 28S sequences of Leotiomycetes. Species studied with TEM (in II–VI) are presented in bold, in capital letters. Sordariomycetes strains represent the outgroup. Taxa marked with „KL" or „AR" are sequenced for this study. Generic types are marked with ♠. Scale bar indicates substitutions per site.


AR7 Belonopsis eriophori
KL34 BELONOPSIS HYDROPHILA
Loramyces macrosporus CBS235.53
KL35 MOLLISIA CLAVATA
KL114 MOLLISIA MELALEUCA
Mollisia cinerea OSC100029
AR43 MOLLISIA CINEREA
KL25 Tapesia fusca
Vibrissea truncorum CBS258.91
Phialocephala fortinii UAMH9525
Mollisiaceae-Loramycetaceae-Vibrisseaceae
KL136 Crocicreas dolosellum
KL55 Crocicreas starbaeckii
Cudoniella clavus cf OSC100054
Ombrophila violacea Wz0024
KL215 Phaeohelotium imberbis
Hymenoscyphus fructigenus TUR Heinonen 708
Helotiaceae
AR13 Xerombrophila crystallifera
Ascocoryne sarcoides OSC100772
Gelatinodiscaceae
KL272 Erikssonopsis ericae
Coccomyces strobi CBS202.91
Rhytisma huangshanense Hou564
Cudonia sp. OSC56399
Tryblidiopsis pinastri CBS445.71
RHYTISMATALES
Dermea acerina CBS161.38
Pezicula carpinea CBS282.39
Neofabreae malicorticis OSC100036
Dermateaceae
KL36 "MOLLISIA" REVINCTA
KL38 PYRENOPEZIZA PULVERACEA
"Mollisia" dextrinospora ICMP18083
AR14 "MOLLISIA" DILUTELLA
KL153 Peltigeromyces sp
KL110 PYRENOPEZIZA RUBI
Ploettnerulaceae
KL54 Pyrenopeziza gentianae
Mitrula paludosa MBH50636
KL118 Encoeliopsis rhododendri
Pyrenopeziza gentianae
Blumeria graminis
Erysiphe glycines MUMH52
ERYSIPHALES
Cyttaria darwinii Peterson isolate 57
CYTTARIALES
Hyaloscypha vitreola M236
KL221 Hyaloscypha albohyalina
Hyaloscyphaceae
Chlorociboria aeruginosa OSC 100056
KL238 Chlorociboria glauca
Chlorociboriaceae
AR70 Trichopezizella relicina
Trichopezizella
KL235 PODOPHACIDIUM XANTHOMELUM
Podophacidium
Calycina citrina CBS139.62
Pezizellaceae
Leuconeurospora pulcherrima CBS343.76
Pseudeurotium zonatum CBS329.36
Pseudeurotidaceae
Thelebolus microsporus CBS113.940
THELEBOLALES
TU112863 Holwaya mucida
Tympanidaceae
Phacidium lacerum CBS130.30
Potebniamyces pyri AFTOL744
Bulgaria inquinans CBS118.31
PHACIDIALES
Pilidium acerinum CBS736.68
Pilidium concavum BPI1107274
KL251 Xeropilidium dennisii
Chaetomella oblonga BPI843552
Chaetomella oblonga PDD102789
Chaetomellaceae
Cyclaneusma minus CBS496.73
Naemacyclus fimbriatus CBS289.61
Marthamycetaceae
KL218 Claussenomyces prasinulus
KL220 Microglossum olivaceum
Microglossum rufum OSC100641
Leotia lubrica OSC100001
Leotiaceae
Neurospora crassa
Sordaria fimicola AFTOL216
Hypocrea lutea ATCC208838
Xylaria hypoxylon OSC100004
0.1

3.1.3. ITS rDNA dataset

The high interspecific variation hampered unambiguous alignment of ITS sequences from different genera and higher level taxa. ITS phylograms, as examplified in Fig. 4 and in **I**, resulted in partly/largely unresolved phylogenies with limited support to deeper nodes. In particular, Bayesian analyses of original ITS sequences of nine species of Cenangiaceae from different genera along with ≥90% similar INSD sequences for each of these, resulted in a largely unresolved tree (**I** Fig. S1). However, the monophyly of genera and species was strongly supported in case of *Heyderia*, *Rhabdocline*, *Sarcotrochila* and *Trochila*. Also in Sclerotiniaceae, a clade comprising three encoelioid species of newly described genus, *Sclerencoelia* was well supported, but the relationships among many sclerotiniaceous genera remained unsettled. The same analysis also supported the idea about the lack of extant close relatives of *E. furfuracea* (note: the sequence of *Velutarina rufoolivacea*, the most similar taxon based on morphology, was unavailable). While the sequences of *E. furfuracea* from Europe and North America were almost identical, these showed only 87% overlap with the most similar INSD sequence, and 88.3 % and to 88 % with *Cenangiopsis quercicola* and *Cenangium ferruginosum*, respectively.

The ITS phylogenetic tree of Lachnaceae was poorly resolved, too. INSD BLAST searches were conducted using nine sequences of putatively distinct genera of Lachnaceae. ITS sequences of ≥95% similarity to the queries were added to the matrix including sequences obtained from apothecia. The dataset contained 65 sequences and the Lachnaceae were represented by 46 species and 13 genera. In the phylogenetic tree (Fig. 4) *Brunnipila* and *Lachnellula* appeared monophyletic. Most species of *Lachnum* formed a strongly supported clade, including the type species, *L. virgineum*. Relationship of *Albotricha* spp. and *Perrotia flammea,* type species of *Perrotia,* remained unresolved. *Belonidium aeruginosum* formed a clade with "*Lachnum*" *euterpes* which was a lineage in a clade including septate-spored seggregates of previous *Lachnum* with 4 species of *Erioscyphella* (as resurrected by Perić & Baral 2014) and "*Lachnum*" *pteridophyllum*. *Lasiobelonium spp.*, *Trichopezizella nidulus*, and *Trichopeziza* spp. formed a well-supported clade.

Differences in ITS rDNA sequences among members of one genus and family varied considerably. At family level, widest range of sequence variation (15–16%) was observed among Cenangiaceae as delimited in I, Chlorociboriaceae and Chaetomellaceae. ITS analyses revealed several genera not to be monophyletic, these including *Ciboria*, *Chlorencoelia, Chlorociboria*, *Rutstroemia, Lanzia, Dasyscyphella, Incrucipulum, Perrotia* and others. In contrast, ITS data supported the distinction of a newly described species, *Sclerencoelia fraxinicola*, the ITS sequence of which differed from that of its closest relative, *S. fascicularis*, at 15 positions.

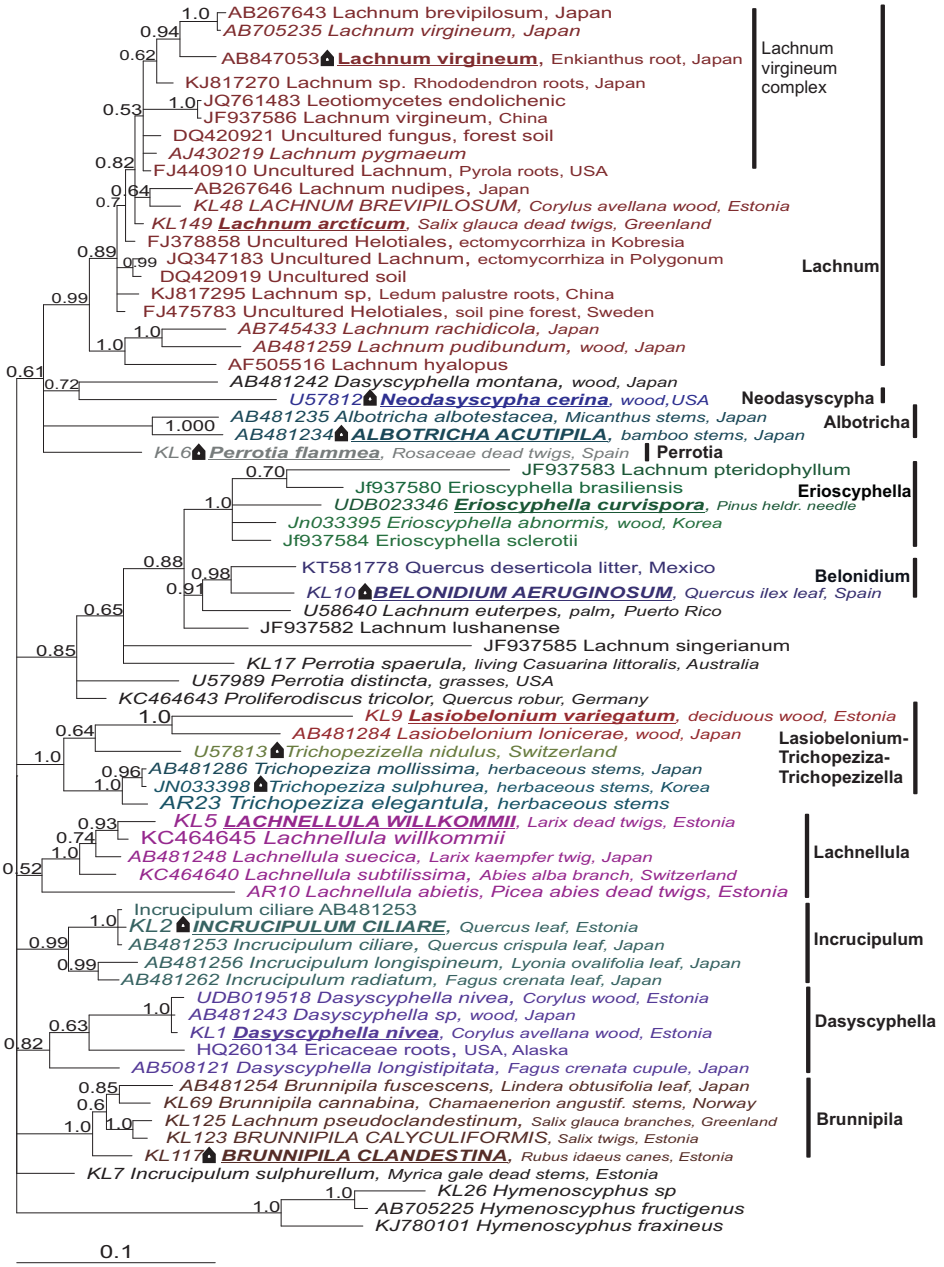


Fig. 4. Bayesian phylogeny based on rDNA ITS sequences of *Lachnaceae* with *Hymenoscyphus* spp. as the outgroup. The datamatrix included sequences obtained from fruitbodies in this study (marked with „KL" or „AR"), with those studied with TEM (in capital letters) and available sequences originating from fruitbody or culture of INSD (all in italics). INSD environmental sequences with ≥95% similarity to one of the 12 reference sequences (underlined, in bold) were added to the analysis. Taxa marked with ♠ are generic types. Scale bar indicates substitutions per site.

Incorporation of public sequences from various biological samples (labelled as 'uncultured Helotiales/Leotiomycetes/Ascomycota/fungus' in the INSD) in ITS rDNA analyses allowed to identify sequenced organisms at species, genus, or family level and added information on the ecology of several taxa. For example, INSD sequences originating from needles or twigs of *Pinus spp*. and *Viscum album* parasitizing these, could be identified as belonging to *Cenangium ferruginosum*. Endophytic isolates were also included in *Sclerencoelia fascicularis*, *S. fraxinicola*, *Xeropilidium dennisii*, *Heyderia abietis*, *Rhabdocline laricis*, *R. parkeri*. An INSD sequence obtained from the European elm bark beetle (*Scolytus multistriatus*), the vector of Dutch elm disease, was shown to belong to *Xeropilidium dennisii*. An isolate from *Quercus* leaf-litter was congeneric with *Belonidium*. The genus *Lachnum* comprised unnamed members sampled from soil, from roots of *Pyrola*, *Rhododendron* and *Ledum*, and from ectomycorrhizae.

The ITS sequences of helotialean fungi generated in this study were assigned to 41 Species Hypotheses (SH, Kõljalg et al. 2013) according to the 1.5% distance treshold. More than half of the ITS sequences generated in **I** (40 out of unique 73 sequences) had also no >97% similar sequences available. New SHs were generated for these sequences in the 7.1 version of UNITE SHs (https://unite.ut.ee).

In several cases ITS sequences from biological samples formed lineages devoid from, but closely related to groups including apothecia-derived sequences. For example, sequences from EcM root tips or litter of conifers were closely related to *C. versiformis* and *C. torta*. Cenangium ferruginosum clade comprised sequences from surface sterilised tissues of conifers, a forest grass, a liverwort and a lichen. Sclerotiniaceae and "Rutstroemia" calopus clade included lineages of INSD sequences originating mostly from soil samples. In addition, three strongly supported groups with unresolved relationships in Cenangiaceae comprised sequences only from endophytes, mostly originating from roots or soil.

3.2. Evaluation of characters

Delimitation of monophyletic lineages comprising encoelioid fungi revealed the importance of observing the complex of morphological characters of apothecia, and of avoiding the overestimation of the importance of one or a few characters when aiming at a natural classification. The members of each studied lineage could be delimited according to a typical combination of characters (**I** Table S3). Namely, most of the monophyletic groups observed in the multigene analysis (Fig. 2) differ with respect of the type of the ascus apical structure, the presence/absence of an ionomidotic reaction, the characteristics of the asexual state (if the anamorph was studied), and vacuolar bodies (VB) in living vegetative cells. However, in some lineages one or a few characteristics varied among closely related species/genera.

3.2.1. The ascus apical apparatus

The ascus apical apparatus was studied in 21 species of Lachnaceae, mollisioids, and *Encoelia*. As a result, five main types of ascus ultrastructure were distinguished (Table 2). In general, taxa that were closely related in the 18S and 28S rDNA phylogeny (Fig. 3) and available for TEM studies, shared the general structure of ascus apex. These could be assigned to the types distinguished by Verkley (1995b). Type VIII, (*Chlorociboria-Pezizella-Calycina* ascus type) included members of the Lachnaceae except for *Lachnellula* (**III–IV** and Fig. 5b, c), and *Mollisia* spp., *Pyrenopeziza* spp., *Belonopsis hydrophila* (Fig. 5e and **VI**). However, the latter three genera sharing a morphologically similar mollisioid subtype of ascal apex, were distributed among three lineages (Fig. 3). *Encoelia* (Fig. 5a), *Lachnellula* (Fig. 5d), and *Podophacidium* (Fig. 5g), belonging to three lineages (Fig. 3), each represented an unique type of ascus apex ultrastructure (**II**, **V**, **VI**), not described in previous literature. The *Pezicula* type was published by Bellemère (1977), and specific ontogenesis and annulus (Fig. 5f) were described in **VI**. *Pezicula* is placed in Dermateaceae clade (Fig. 3).

Table 2. The ascus apical apparatus characteristics of the studied fungal species in comparision with Baral's (1987b, LM) and Verkley's (1995b, TEM) typifications. Lineages of taxa are presented according to rDNA phylogenetic analysis (Figs. 3–4).

Species; lineage	Ascus shape/ apex shape (LM)	Annulus type/ amyloidity in LUG (LM)	Ascus apical apparatus (TEM) Comparative type according to Verkley in Roman numerals	paper
Encoelia furfuracea; Cenangiaceae/ Encoelia	cyl cl with long narrow stipe/ ro–tr	*Calycina*-like/ I+, bb	*Encoelia* type. Apical thickening increases gradually, annular protrusion absent, annulus is homogenous, relatively broad, narrowing downwards.	II
Lachnum brevipilosum; Lachnaceae/ Lachnum	cyl cl/ co–subpapillate	*Calycina*-like/ I+, bb	t VIII, *Lachnum* st. Apical thickening moderal, disctinct annular protrusions, tapering and becoming more electron-dense toward lower end. Apical chamber quite high.	III
Dasyscyphella cassandrae; Lachnaceae	cyl cl/ co–ro	*Calycina*-like/ I+, bb		
Brunnipila clandestinum; Lachnaceae/ Brunnipila	cyl cl/ co–tr to subpapillate	*Calycina*-like/ I+, bb	As in the t VIII, *Lachnum* st, but annular protrusion more blunt	
Albotricha acutipila; Lachnaceae	cyl cl/ subpapillate	*Calycina*-like/ I+, bb		
Capitotricha bicolor; Lachnaceae	cyl cl/ co–tr	*Calycina*-like/ I+, bb		
Incrucipulum ciliare; Lachnaceae/ Incrucipulum	cyl cl/ ro	*Calycina*-like/ I+, rb	t VIII, similar to *Lachnum*, but annulus broadening upwards and electron-dense apical cap (*nasse apicale*). Apical chamber more rounded than those of Lachnum	
Belonidium aeruginosum; Lachnaceae/ Belonidium	cyl cl / co–tr	*Calycina*-like/ I+, bb		IV

Table 2. Continuation

Species; lineage	Ascus shape/ apex shape (LM)	Annulus type/ amyloidity in LUG (LM)	Ascus apical apparatus (TEM) Comparative type according to Verkley in Roman numerals	paper
Lachnellula willkommii; Lachnaceae/ Lachnellula	cyl cl/ blunt, tr–ro	NA/ I–	*Lachnellula* t. Apical thickening abruplty becomes to annulus. Annular protrusion incurved, apical camber and central cylinder wide.	V
Belonopsis hydrophila; Mollisiaceae/ Belonopsis	cyl cl/ co–tr	*Calycina*-like/ I+, bb	t VIII, mollisioid st. Moderal, at first gradual beside the annulus abrupt apical thickening. Annulus a bit narrowing on lower part. The annular protrusions points straight downwards and apical chamber present.	VI
Mollisia clavata; Mollisiaceae				
Mollisia stromaticola; NA				
Mollisia revincta; Ploettnerulaceae?[1]				
Mollisia dilutella; Ploettnerulaceae				
Pyrenopeziza millegrana; NA				
Pyrenopeziza pulveracea; Ploettnerulaceae				
Pyrenopeziza rubi; Ploettnerulaceae				
Mollisia melaleuca; Mollisiaceae	cyl cl/ co–tr,	*Calycina*-like/ I+, bb	t VIII, mollisioid st: annulus broader, electron-density lower	
Mollisia ramealis; Cenangiaceae? [2]	cyl cl/ co–tr	*Calycina*-like/ I+, rb	t VIII, mollisioid st: more abrupt apical thickening, annulus broader. Apical chamber more prominent.	
Pezicula cinnamomea; Dermateaceae/Pezicula (Verkley 1999)	cyl cl/ ro	*Pezicula*-like/ I+, rr	*Pezicula* t, wide central cylinder, broad annular protrusions points strongly inwards. Apical chamber flattened.	
Podophacidium xanthomelum; Helotiales inc. sedis	cyl cl/ tr–ro	NA/ strongly I+; bb	*Podophacidium* t, aff. Verkley t XIII, *Phaeohelotium sub-carneum*. Apical thickening gradual. Very narrow highly electron-dense annulus. Apical chamber absent.	

Abbreviations: cylindrical = cyl; clavate = cl; conical = co; I+, bb = euamyloid; I+, rb/rr = hemiamyloid; I– inamyloid; NA = data not available; st = subtype; rounded = ro; truncate = tr; type of ascus = t

[1] Based on the phylogeny in Crous & Groenewald (2003), *M. revincta* is a member of the Mollisiaceae.

[2] Based on BLAST search of ITS rDNA, this species is likely a member of Cenangiaceae.

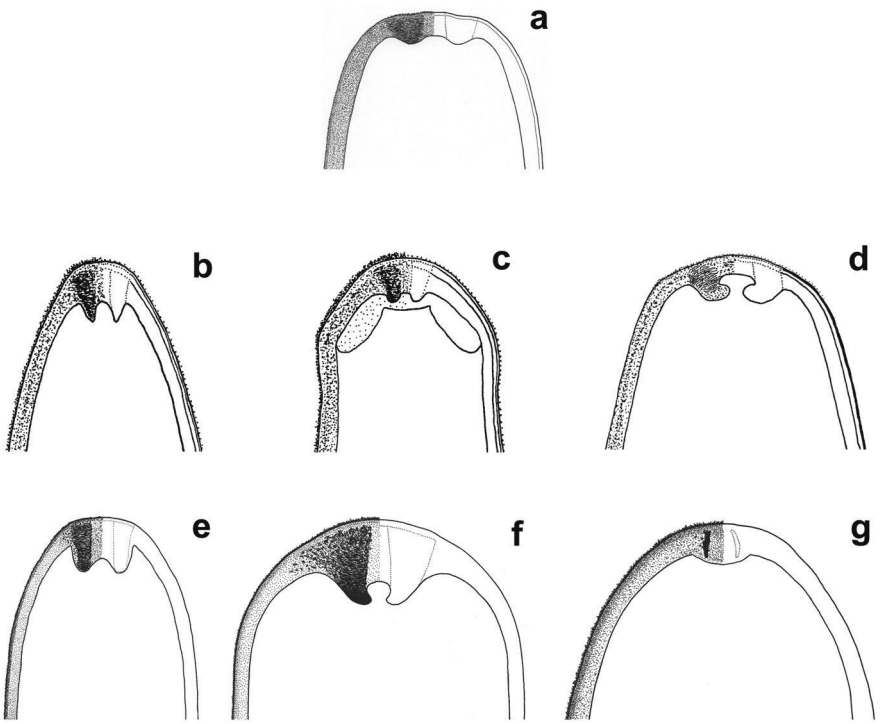


Fig. 5. Studied types of ascus apical apparatus, the schematic representation
a *Encoelia furfuracea*. **b** *Lachnum virgineum*. **c** *Belonidium aeruginosum.* **d** *Lachnellula willkommii.* **e** *Belonopsis hydrophila*. **f** *Pezicula cinnamomea*. **g** *Podophacium xanthomelum.*

3.2.2. Apothecial hair ultrastructure

Owing to the increased magnification, the micrographs of the hairs obtained using TEM, in particular complemented the characteristics of the ornamentation of walls. This allowed for better comparison with related taxa than is possible using LM. The hair ultrastructure in each lineage was characterized by a similar thickness, stratification, and ornamentation of the wall. The refracted or pigmented areas seen in LM, differed in electron density under TEM. This allowed to refine the description of hair ultrastructure in the following lineages of Leotiomycetes:

Hyaloscyphaceae, *sensu* Han et al. (2014)
The hair walls of *Hyaloscypha aureliella* (Nyl.) Huhtinen, *Olla millepunctata* (Lib.) Svrček and *Unguiculella hamulata* (Feltgen) Höhn. (Fig. 6 a–c), were thin and unclearly stratified, and the refractive parts of the hairs (under LM, *Olla* and *Unguiculella*) were electron-transparent under TEM.

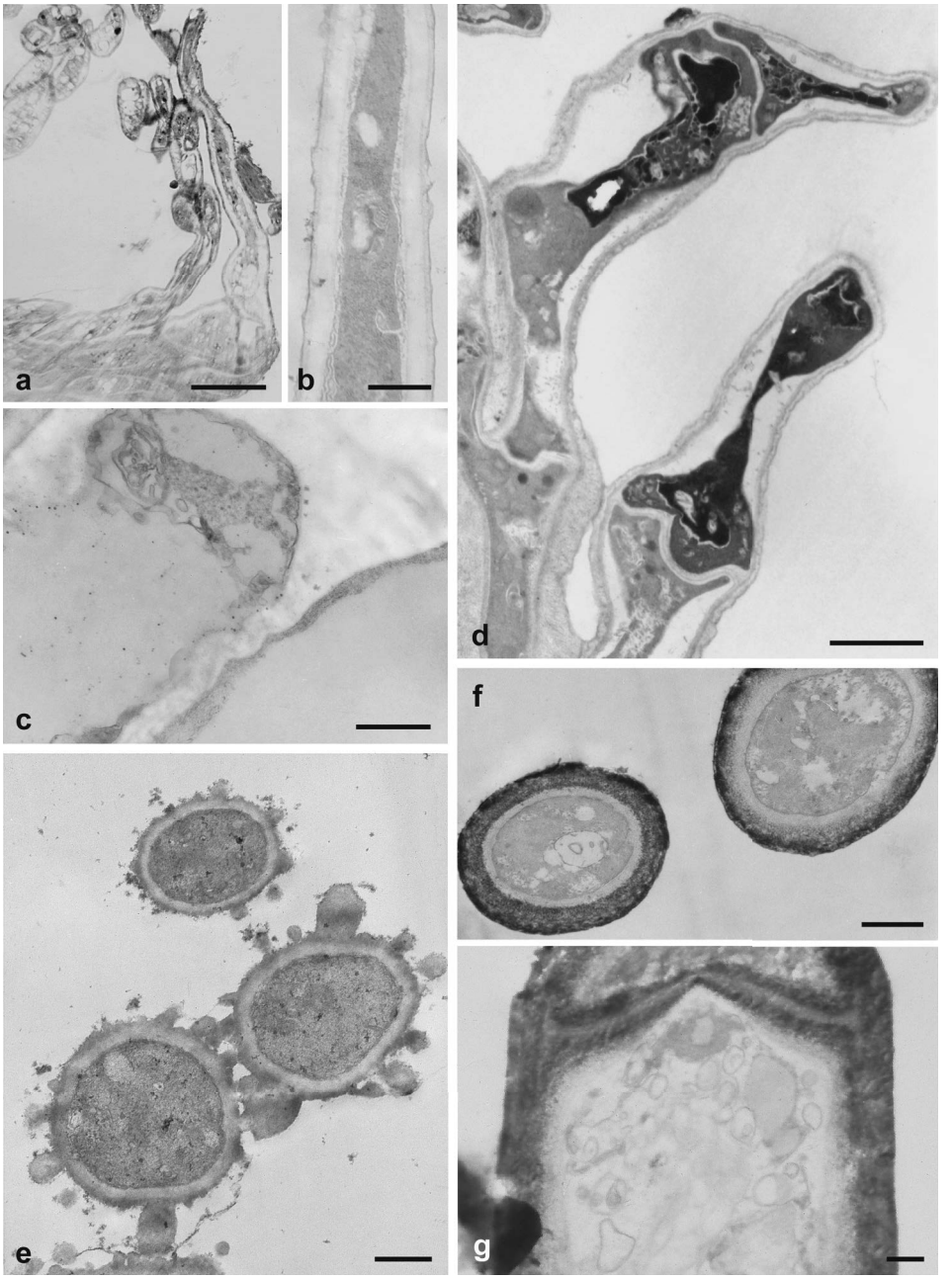


Fig. 6. Hairs of helotialean species, as observed under TEM
a–c Hyaloscyphaceae s.str.: a *Hyaloscypha aureliella* TAAM165603. b *Unguiculella hamulata* TAAM165350. c Glassy apex of hair. *Olla millepunctata* TAAM164053. **d** *Pezizellaceae*: *Phialina ulmariae* TAAM165353. **e** *Lachnaceae*: *Lachnellula calyciformis* TAAM165524, **f–g** Trichopeziza lineage: f *Lasiobelonium variegatum* TAAM165343. g *Trichopezizella nidulus* TAAM165352. b, e, f–cross-sections, a, c, d, g–longitudinal sections. Bar = 1µm, except for a 5µm.

The Pezizellaceae lineage (according to Baral & Rämä 2015)
Phialina ulmariae (Lasch) Dennis, which based on morphology belongs (the DNA barcode was unavailable) to the recently resurrected *Pezizellaceae* Velen., showed under TEM very homogeneous electron dense regions (Fig. 6d) in the apical part of hairs, where yellow vacuolar bodies were observed under LM.

The Lasiobelonium-Trichopeziza-Trichopezizella lineage (Fig. 3)
In contrast to the Lachnaceae, in the *Trichopeziza* lineage the outer layer of the hair wall was very electron dense, as examplified by *Lasiobelonium variegatum* (Fuckel) Raitv. and *Trichopezizella nidulus* (J.C. Schmidt & Kunze) Raitv. (Fig. 6 f–g).

Lachnaceae (**III**–**V**)
Seven genera and nine species of warty members of the monophyletic Lachnaceae clade (Fig. 3), had more complex hair walls than members of the Hyaloscyphaceae that were available for comparision. The studied Lachnaceae members also differed in hair wall thickness, stratification, warts' shape, electron-density, and erodibilty. The hair ultrastructure of *Lachnum brevipilosum* and *L. virgineum*, as well *Brunnipila clandestinum* and *B. calyculiformis* were highly similar in respective genera. Although sampling was restricted, a genus-specific pattern can be suggested, because the genera *Albotricha*, *Belonidium*, *Brunnipila*, *Capitotricha*, *Dasyscyphella*, and *Incrucipulum* were all represented by their type species (Fig. 6e and Figs. in III–V).

3.2.3. Vacuolar bodies

Vacuolar bodies (VB, as introduced by Baral 1992) in the apical part of the paraphyses or outer excipulum cells occured in some helotialean groups. VBs of studied taxa were either hyaline, bright yellow or greenish, globose or elongated. These were affirmed as taxonomically informative and represented the main synapomorph in the resurrected family Cenangiaceae (**I**). The morphology of the mostly elongated VBs were lineage-specific, e.g. pigmented in Cenangiaceae and hyaline in *Mollisia* spp., but in the latter group vacuolar bodies turned yellow in KOH. According to Baral (2016), cylindrical refractive VBs in the paraphyses apex occur in *Mollisia* but are absent in *Pyrenopeziza* and *Pirottaea*.

3.2.4. Anamorphs and stromata

The anamorphs clearly indicated the previous misplacement of following species of *Encoelia* (**I**): a) *Chlorociboria glauca* apothecia were observed with *Dothiorina* asexual morphs on the same substrate, and b) *Xeropilidium dennisii* synanamorphs (sporodochial conidiomata in culture and pycnidial conidiomata on bark along the apothecia).

Sclerotium-like structures of the genus *Sclerencoelia*, were described here for two previous *Encoelia* members, *E. fascicularis* and *E. pruinosa* and a new species (**I**). These structures were hidden under the apothecia in the substratum under the bark of trees. This fact pointed to an additional reason to accept these taxa, whose apothecia emerge from sclerotia or stromatized plant debris, into the Sclerotiniaceae. Typical for Rutstroemiaceae, the stipe base of apothecia of *Rutstroemia tiliacea* was blackish brown, and arose from indeterminate dark substratal stroma. The latter was visible as a black line in wood cross-section under the apothecia.

3.2.5. Ionomidotic reaction

Studying the genus *Ionomidotis*, Korf (1958) introduced the term ionomidotic reaction (IR) for a chemical reaction whereby aqueous potassium hydroxide solution (KOH) extracts pigments from fungal tissues. The pigments are released into the medium seconds after adding KOH to a microscope slide of fungal preparate. IR can be detected also in the dried fungal specimens of collections. However, the chemical background of this reaction has yet to be studied among the Leotiomycetes. In the current work, IR was observed in most members of the monophyletic Cordieritidaceae (**I**). IR can be considered as the main synapomorph in this family, where morphological characteristics are quite deviating. The colour resulting IR, however, differed among the members of Cordieritidaceae. For example, in species of *Ionomidotis irregularis* and *Diplocarpa curreyana*, the extracted pigments were purple, wheras the IR of taxa related to *Ameghiniella* was ochraceous. However, "*Encoelia" heteromera* and "*E". fimbriata*, belonging to different lineages, had a golden-yellow reaction. It can be concluded that among the Cordieritidaceae, IR is a valuable characteristic for discriminating genera. However, solitary IR+ exceptions in generally IR- families were observed, e.g. in Lachnaceae (*Brunnipila calyciformis,* pinkish IR) and Cenangiaceae (*Cenangium ferruginosum,* peach-colored IR). The basal part of *Belonidium aeruginosum* (Lachnaceae) hairs and outer excipulum turn lilac in KOH, distinguishing it from the morphologically similar genus *Incrucipulum*. Based on references, IR is known to occur in *Godronia* spp. and members of Dermateaceae s. str. (Baral 2016).

3.2.6. Ecology

The rDNA ITS phylogeny of Leotiomycetes allowed to make the following observations (compare with Table 1):

An endophytic lifestyle is quite common in the Cenangiaceae, wheras it is almost entirely absent among its sister families Rutstroemiaceae and Sclerotiniaceae (**I** Figs. S1–S4). Many INSD sequences of Cenangiaceae originated from the leaves and roots of coniferous trees (**I** Fig. S1). ITS analysis provided strong evidence for the occurrence of *Cenangium ferruginosum* as an endophyte

in pine needles and twigs, as well in as *Viscum album* parasitizing pines. ITS phylogeny supported the distinction of the endophytic *Rhabdocline parkeri* from the pathogenic *R. pseudotsugae, R. epiphylla, R. oblonga,* and *R. obovata*.

In the Sclerotiniaceae, the inclusion of the newly described genus *Sclerencoelia* expanded the concept of the ecology of this family to include lignicolous members. A sequence originating from the shoots of *Fraxinus* spp. was assigned to *Sclerencoelia fraxinicola* (**I** Fig. 2), providing additional evidence for the distinction of this supposedly *Fraxinus*-restricted species from its siblings that grow mainly on *Populus spp*. The apothecia of *Sclerencoelia fraxinicola* grew on recently dead branches. *S. pruinosa* was found to act as a intensive parasite (Anonymous 2011), whereas own observations about *S. fascicularis* pointed only saprotrophic occurrence.

Inclusion of *Rutstroemia* (=*Dencoeliopsis) johnstonii* expanded the Rutstroemiaceae to include a fungicolous species. Rutstroemiaceae split into two groups: a) the *Rutstroemia firma* clade comprising species growing on fallen branches and leaves of trees, or on fruits, which also includes *R. johnstonii*; and b) the clade of species related to *Rutstroemia calopus*, whose apothecia form on monocot stems; this group included many DNA sequences obtained from soil in various habitats (**I** Fig. S4).

The Chaetomellaceae was expanded by the inclusion of desiccation-tolerant species with a xylicolous lifestyle, transferred to a new genus *Xeropilidium.* The others members of this family are desiccation-sensitive and parasitic or saprobic on leaves, stems, or fruits of dicots (**I** Fig. S6).

Analysis of Lachnaceae revealed an INSD sequence from *Quercus deserticola* leaf-litter, closely related to *Belonidium aeruginosum*, which also inhabits oak leaves. The *Lachnum* clade included sequences from soil, roots of Ericaceae, and from ectomycorrhizae of herbaceous plants (Fig. 4).

3.3. Taxonomical novelties

Resurrected families. The phylogenetic analyses in **I** distinguished two monophyletic groups of helotialean fungi without a name in current use at the family rank. However, as old family names were available for some members of these groups, two names were resurrected and applied to these groups while expanding the concept of respective families.

1. Cenangiaceae Rehm 1888 was the sister group of Sclerotiniaceae and Rutstroemiaceae, and was emended by Baral & Pärtel, using additional information regarding neglected morphological characteristics, e.g. refractive vacuolar bodies of the vegetative cells. Beside *Velutarina*, *Encoelia*, *Cenangium* and *Cenangiopsis* (Rehm's original genera *Cenangiaceae*), relationships with members of the family *Hemiphacidiaceae* (Korf 1962) were affirmed in the current work. The hymenium in the premature apothecia of many taxa of Cenangiaceae s. str. and former Hemiphacidiaceae is initially protected in unsuitable dry conditions by inrolled margins or by a

membraneous lid (**I** Fig. 3). Members of the Cenangiaceae grow as endophytes, saprobes, or parasites, and inhabit wood or needles of conifers.

2. Cordieritidaceae Sacc. 1889 was originally described to include helotialean fungi with leathery, carbonaceous apothecia developing from a common or branched and often excentric stipes. The current work, howewer, showed more extended morphological variation. Many members of this group have an ionomidotic reaction or change the colour of their excipulum in KOH. Cordieritidaceae species are lignicolous, lichenicolous, fungicolous on ascomycetes, or co-occur with certain fungi.

New species and genera, and new combinations

Chlorociboria glauca (Dennis) Baral & Pärtel (Chlorociboriaceae)
Basionym: *Encoelia glauca* Dennis 1975

Genus *Sclerencoelia* Pärtel & Baral (Sclerotiniaceae)
Sclerencoelia fraxinicola Baral & Pärtel
Sclerencoelia fascicularis (Alb. & Schwein.) Pärtel & Baral (neotype selected)
Basionym: *Peziza fascicularis* Alb. & Schwein. 1805
Sclerencoelia pruinosa (Ellis & Everh.) Pärtel & Baral
Basionym *Dermatea pruinosa* Ellis & Everh. 1888

Genus *Xeropilidium* Baral & Pärtel (Chaetomellaceae)
Xeropilidium dennisii Baral, Pärtel & G. Marson

4. DISCUSSION

4.1. Distinction of monophyletic groups of helotialean fungi

The results of this study showed that the taxonomy of studied helotialean fungi has suffered from reliance on convergent morphological characters. Evidence on this was provided by the genus *Encoelia,* members of which were distributed across major lineages of Leotiomycetes based on the multigene phylogeny. One of such lineages, representing the family Chaetomellaceae, might even not belong to the Leotiomycetes as its phylogenetic relationship remained unresolved in the multigene phylogeny. The sampling used for multigene analysis was more extended in terms of genes and taxa than in previously published phylogenies of the Leotiomycetes, despite it being uneven for various lineages due to the focus on encoelioids. Hibbett et al. (2007) commented in their fungal classification, that Leotiomycetes is one of the most undersampled higher taxa among the Ascomycota, and predicted the creation of additional orders after more extensive molecular sampling. Until now, the situation has not changed much and the polyphyletic Helotiales is used *sensu lato*.

The present work contributed to establishing a phylogeny-based taxonomy of Leotiomycetes by accumulating molecular data of the genera thus far classified in the Helotiaceae. Moreover, a distinct clade of Leotiomycetes was found that could be described as a new order, the Sclerotiniales. This lineage includes members of the Sclerotiniaceae, Rutstroemiaceae, the Piceomphale clade), and Cenangiaceae. The Sclerotiniales lineage was affirmed as clearly unrelated to the Helotiaceae s.s., the core group of the Helotiales. However, we preferred to postpone describing the new order until experts of different taxa will contribute additional DNA sequences from well studied voucher specimens that would enable to construct a new order-level classification for the major part of Leotiomycetes.

4.2. Ultrastructural characters of helotialean fungi

Phylogenetic analyses and morphological observations, including ascus ultrastructure, enabled to re-evaluate the diagnostic characters thus far used for the delimitation of the families Helotiaceae, Hyaloscyphaceae, and Dermateaceae. It can be summarized that for completing historical taxon descriptions of helotialean fungi it is necessary to study the type of the ascus apex. Whenever possible, living specimens should be used for detecting characters that may disappear in dried vouchers and for obtaining the anamorph stage in culture.

Distinct patterns of ascus apical apparatus characters were detected in families/lineages of Helotiales, and in general these proved to be informative for the taxonomy. Some types of the ascus apical apparatus were distributed

among many lineages, whereas others were unique. Ascus apparatus type VIII (Verkely's (1995b) appeared to be widely distributed in unrelated lineages, such as the Lachnaceae (**III**–**IV**, Verkley 1996), Chlorociboriaceae (Verkley 1993b), Pezizellaceae (*Calycina*, "*Hymenoscyphus*" *herbarum*, and *Pezizella*, Verkley 1993b), Mollisiaceae, and Ploettnerulaceae (**VI**). This work supported the conclusion of Verkley (1995b) that the ascus annulus amyloidity of the Helotiales observed in LM correspond to the most electron-dense structurally differentiated areas in the TEM micrographs. This enables one to compare the general apical apparatus morphology obtained by TEM and LM. However, owing to the size of the annulus (approximately 3 µm wide), light microscopy has limitations for observing details, especially in cases when the amyloid reaction is absent/very weak or very strong (overshadow). For example, the ascus apical apparatus of *Encoelia furfuracea* could not be distinguished from that of *Calycina* until using TEM. LM can be useful for characterizing the ascus apex, if illustrations are presented along indication which chemicals have been used for testing the amyloidity (see e.g. Baral 1987b). Without figures of ascus apex it is nearly impossible to compare the ascus apex characters of different helotialean taxa.

a) Cenangiaceae

Encoelia furfuracea placement in the Cenangiaceae was in accordance with the morphological similarity of related fungi, especially *Velutarina rufoolivacea*. In general, the fruitbody's macroscopical depiction, as illustrated in **I** Fig. 3, can vary largely among the Cenangiaceae. Under LM, the ascus apices showed different amyloidity among genera. Many Cenangiaceae members were with euamyloid annulus, but some were hemiamyloid or inamyloid. For example, *Velutarina rufoolivacea* is hemiamyloid whereas *V. bertiscensis* is inamyloid (Baral & Perić 2014). Such variation has also been observed in the genera *Sarcotrochila* and *Rhabdocline* (Stone & Gernandt 2005). *Encoelia furfuracea* had a well-developed ascus apparatus (**II**), whereas *Cenangium ferruginosum* has a strongly reduced apical apparatus (Verkley 1995a), with a recognisable apical chamber and annulus, but which do not function during dehiscence. According to Verkley (1995a), the ejaculation of the ascospores instead occurs via an irregular slit next to the apical apparatus, which is unique among the helotialean fungi.

In the sister families Sclerotiniaceae and Rutstroemiaceae, the characters of the ascus apex were similar in these groups under LM and TEM. The asci were mostly euamyloid, with one ascus apical type characterized thus far (Verkely 1993a). Spooner (1987) has proposed a correlation between the presence of stromatic tissues, and a long and narrow ascus pore. In support of this idea, the length of ascus apical thickening was observed as relatively short in Cenangiaceae, a closely related family, whose members are non-stromatic. Howewer, the extent of the variation of the apical apparatus among the Cenangiaceae and its differences from those in Sclerotiniaceae and Rutstroemiaceae remain unknown.

b) Cordieritidaceae

The Cordieritidaceae lineage is one of the few monophyletic lineages (beside Ascocorticiaceae, Chaetomellaceae, and Loramyces and Roesleria lineages), whose known members have inamyloid asci that lack the observable ascus apical apparatus due the absence of annulus. This is significant variation comparing to their sister clade, Sclerotiniales lineage. In this family, the asci were observed to be apically rounded, and with thickened apical wall in some taxa. Verkley (1995a) has shown unique ascus dehiscence by the lid for "*Encoelia" fimbriata*, the only member of the Cordieritidaceae studied with TEM. The thickened ascus wall structure is probably caused by the repeated desiccation and rehydration of the longeval apothecia in nature according to Verkley (1995a). *Encoelia furfuracea* shares the longevity and retracting of apothecia in unsuitable conditions with "*E.*" *fimbriata,* but has a different ascus lateral wall and opening mechanism (**II**), which indicates that the ascus ultrastructure of helotialean fungi apparently do not show direct adaptation to the xero-tolerance. Besides the ascus characters, the ionomidotic reaction in Cordieritidaceae was observed as unique. Baral et al. (2015) noticed that the presence of vacuolar bodies is negatively correlated with IR, and VBs are never seen together in the same taxa/lineage. Further studies could detect how Cordieritidaceae species eject spores, and whether the discharge is more passive compared to taxa with a well-developed ascal apparatus.

The family Cordieritidaceae includes genera in which apothecia vary from tiny immersed perithecioids to apothecia 10 cm in diam (Fig. 1k), and that are lignicolous, fungicolous or lichenicolous. The type genus *Cordierites* is comprised of tropical species with cupulate brownish apothecia that arise from branched stipes; it is lignicolous, but associated with Xylariales (Zhuang 1988). In phylogenetic analyses (**I**, Peterson & Pfister 2010, Suija et al. 2015), Cordieritidaceae has been distinguished as a strongly supported group. It is likely that adaptation to a possible fungicolous lifestyle has created the morphological diversity in this group.

c) Lachnaceae

In this family, the ascus apical apparatus was represented by two types, one in the *Lachnellula* (**V**) and the second in *Lachnum*-related taxa (**III**–**IV**, Verkley 1996), but intergeneric variation was described for hair walls using TEM (**III**). The ITS rDNA phylogeny of Hyaloscyphaceae s.l. (Cantrell & Hanlin, 1997) and subsequent works with extended gene-sampling (Hosoya et al. 2010, Han et al. 2014), have demonstrated different hyaloscyphaceous lineages and multiple origins of the hairs among the Helotiales. Until now, molecular sampling has been quite occasional among hairy helotialean fungi. Here (**III**–**IV**), additional evidence was offered to support the distinctness of the family Lachnaceae and Hyaloscyphaceae based on the TEM characters of hairs. All studied members of Lachnaceae formed a monophyletic group (Fig. 3), and monophyly of most of the studied genera (*Lachnum*, *Lachnellula*, *Brunnipila*, *Incrucipulum* and *Albotricha*) was supported by ITS phylogeny (Fig. 4, compare Hosoya et al.

2010, Perić & Baral 2014). As congruent with TEM studies, *Brunnipila* species with unique pigmented hair wall formed a distinct clade. More extensive sampling with molecular methods is needed for the delimitation of *Albotricha*, *Capitotricha*, and *Dasyscyphella*. TEM studies of the excipular hairs in Lachnaceae offered a more detailed view of the cell wall stratification and ornamentation compared with studies published based on scanning electron microscopy (Hain 1980).

Belonidium aeruginosum was not closely related to *Incrucipulum* according to the rDNA phylogenetic analysis (Figs. 3–4). This fact rejected the hypotheses proposed in **IV**, which was based on hair wall and ascus ultrastructural characters of the type species in both genera, *Belonidium aeruginosum* (**IV**) and *Incrucipulum ciliare* (**III**). Based on phylogeny, *B. aeruginosum* belonged to a complex of species having elongated ascospores. The apical cap (*nasse apicale sensu* Bellemére 1977) was present in *Belonidium aeruginosum* and *Incrucipulum ciliare* as shown under TEM. *Vibrissea* (Vibrisseaceae) is the only other genus that has this structure of the helotialean fungi, as illustrated in a micrograph of *V. decolorans* (Bellemère, 1977: 244) and the LM figure of *V. truncata* (Baral 1987b, Fig. 17). Our results on *B. aeruginosum* and *I. ciliare* provide new evidence of homoplasy of ultrastructural characters in Lachnaceae, complementing those of Hosoya et al. (2010: Table 4) aquired using LM. Further sampling is needed for taxa with elongated spores like *Erioscyphella* species, to establish monophyletic lineages and delimit genera in Lachnaceae.

d) Dermateaceae compared to Mollisiaceae and Ploettnerulaceae

Dermateaceae s. str. was monophyletic, and characterized by mostly a hemiamyloid ascus apex of a specific structure (**VI**). The *Mollisia*-like fungi, even though sharing a similar ascus apparatus among *Belonopsis*, *Pyrenopeziza*, and *Mollisia* (**VI**), appeared to belong to not closely related groups based on their rDNA (Fig. 3). Taxon sampling of mollisioid species was limited in this work, and further phylogenetic studies are needed to reveal their phylogenetic relationships. However, the species of Mollisiaceae studied in this work were distinct from those in the Ploettnerulaceae. *Mollisia pro parte* and two *Belonopsis* species were related to the Loramycetaceae-Vibrisseaceae-Mollisiaceae (Fig. 3) clade, as shown for *Mollisia* in other published phylogenies (Wang et al. 2006b, Grünig et al. 2009).

In the Plottnerulaceae, some original strains of *Pyrenopeziza* spp., "*Mollisia*" *dilutella* and "*M*." *revincta*, complemented the list of members of this lineage. Designation of reference sequences from well-studied voucher specimens is critical for identification of mollisioids species. At present many misidentified entries from this group occur in INSD. For example, *Mollisia cinerea* is represented by several deviating ITS rDNA sequences. In the mollisioid complex, epitypification and neotypification of generic types is needed to introduce meaningful names for the phylogenies at higher levels.

The diagnostic importance of the content of the paraphyses, as introduced by Baral (1992), was confirmed for certain lineages. According to Beckett et al.

(1974), the cell vacuoles may have many functions, and these organelles have been mentioned as having the most variable structure in cells (Riquelme et al. 2011). The published descriptions of helotialean fungi often miss out this characteristic, because it is only visible in living material. This can be a reason for misidentication of macroscopically similar taxa throughout the mollisioids.

4.3. Ecological patterns

The role of helotialean fungi in nature is complex. Different lifestyles alternate during the life of a fungus, the switches are likely determined by senescence or weakening of the host the mycelium is living in. The host range of an ascomycete can be broader in the endophytic than in the saprotrophic stage when fruitbodies are formed (Sieber 2007). This work offered some examples of this trend: a common aspen-dwelling species, *Sclerencoelia fascicularis*, was found from pine needles based on an INSD sequence. Similarly, Tanney et al. (2016) described the life history of *Phialocephala* spp.: a vegetative endophytic stage occurs in *Picea* leaves, followed by a saprotrophic anamorphic stage on non-foliar substrates (angiosperm fallen branches, intact to decayed), and the formation of a teleomorph on the same substrate. A common toolbox of genes in Sclerotiniaceae, necessary for plant symbiosis, was shown to be selectively expressed during these different lifestyle stages (Andrew et al. 2012).

In case of encoelioid fungi that form tough apothecia on still attached, recently dead branches, the sequence-based discovery of mycelium in their substrates seems rather predictable. In the Cenangiaceae, INSD data revealed that its members commonly grow as endophytes or parasites in leaves and roots of coniferous trees. An endophytic lifestyle is widely distributed among the Leotiomycetes (Wang et al. 2006a), however the current study concluded that it does not define the morphology of associated apothecia, as suggested by Wang et al. (2009). We do not know whether the ability to inroll the apothecia of Cenangiaceae is an adaptation to survive in arid conditions or it has rather evolved to protect the structures, related to reproduction and dissemination, from insects.

The sequences from roots and soil, including ectomycorrhizal samples, were found in lineages related to genera *Lachnum* and *Chlorencoelia*. Many species of these genera form apothecia on decorticated branches, that lie on the ground, in close contact with soil. It is unknown how many of these fungi lack reproductive structures or whether these have not yet been discovered or sequenced. Based on this study, the mycorrhizal symbiosis is uncommon in Cenangiaceae and *Chlorencoelia* represents an atypical member of this family in respect of ecology.

This work detected a wider substrate range than previously known in some of the helotialean lineages. One example was the addition of the caulicolous saprobe *Chlorociboria aeruginella* to the well-known lignicolous Chlorociboriaceae (**I**, compare with Johnston & Park 2005). According to Johnston &

Park, *Chlorociboria* is more diverse in the southern hemisphere, but further evidence is needed regarding whether a shift to a herbicolous substrate occurred in the northern hemisphere.

The substrate spectrum of all helotialean fungi is quite wide and is yet randomly sampled with molecular methods. Most probably hyphae inside the substratum precede fruitbodies in the majority of the helotialean fungi, and that could be detected by molecular methods. It seems that sequences from living deciduous trees are currently less represented than those from conifers in public databases. The search for similar sequences for taxa forming fruitbodies on deciduous substrates (*Encoelia furfuracea*, *Dasyscyphella* spp., *Incrucipulum* spp., *Lasiobelonium* spp., *Trochila* spp.) did not result in finding close matches from endophytic organisms in INSD. However, the studied group of fungi may play an important role in the decay of plant material in natural environments, but their task in the living plant tissues could be similarly important.

4.4. Methodological suggestions for the future

- The incubation of substrates (mostly decaying plant material) is useful to be able to study living fungi, especially in case of ephemeral apothecia. In this way the apothecia can easily be initiated to observe their morphology. For temperate and boreal zones, the substrate should be frozen before incubation to follow natural seasonality necessary for formation of apothecia.
- Chemotaxonomy should be given more attention as biochemical differences are likely to provide additional synapomorphies for distinguishing taxa of Leotiomycetes. Determination of KOH soluble pigments should be useful for taxonomic analysis of the members of Leotiomycetes, as has been done in studies of Sordariomycetes (see the review by Stadler 2011). Cell wall components should be investigated in the Cyttariales related lineages to find out whether these lack chitin like *Cyttaria* (Oliva et al. 1986).
- TEM provides informative characters for taxonomy, but its relevance is currently limited owing to a lack of comparative studies at larger taxonomic scale. It is quite unrealistic to suppose that usage of this method will increase much in the future because of the time, resource, and skill demands. Therefore, more precise LM observations, including those of the ascus apex, are recommended for refining the taxonomy of helotialean fungi.
- Due to the taxonomic value of vacuoles in paraphyses and excipular tissues, it would be very important to study their ultrastructure, chemical content, and function(s).
- Specific primers should be designed for amplification of genes containing insertions (e.g. 18S rDNA in Leotiomycetes).
- For species identification, rDNA ITS sequencing should be more extensively used among the helotialean fungi. This method is independent of specimen alteration during drying (loss of original apothecium shape and

colour, disappearance of some micromorphological characters). It also allows one to compare sequences from complex biological samples, deposited in public databases in order to complement the fruitbody-based information on the ecology lifecycle for these fungi.

- The UNITE (https://unite.ut.ee/) platform should be used to develop further ITS rDNA barcode-based Species Hypothesis in a large and intricate group as Leotiomycetes. It is critical to increase the number of reference sequences from holotypes or designated epitypes to serve as name anchors in public DNA databases.
- Isolation of pure cultures from ascospores should be increasingly used for characterizing asexual stages and obtaining pure DNA for molecular studies. This is especially important in case of rare species, or those with tiny solitary apothecia, and the vouchers of new taxa.

5. CONCLUSIONS

Revisions of classifications should first and foremost rely on the reconstruction of phylogenies. Special attention to type species is inevitable for linking phylogenies with traditional taxonomy. Integration of phylogenetic analyses with morphological and ecological observations on helotialean fungi led to the following conclusions:

1) A complex of several characters, rather than individual features, defined the studied taxa. High diagnostive value was ascribed to the ascus apex features, refractive vacuolar bodies in living paraphyses, ionomidotic reaction of apothecial tissues, morphology of anamorphs, presence of stromata/sclerotia, and the features of excipulum and hymenial parts of apothecia. TEM studies alone are insufficient for drawing taxonomic conclusions, but can offer additional details for describing the morphology of specimens under LM.
2) Phylogenetic hypotheses offer a new point of view regarding the delimination of helotialean taxa. Based on the phylogenetic analyses of multigene data, the subfamily Encoelioideae and the genus *Encoelia* appeared to be polyphyletic, with species distributed among eight major lineages of Leotiomycetes. A large extent of homoplasy of morphological characters was confirmed. The type species of *Encoelia, E. furfuracea*, was shown to belong to the Cenangiaceae. Considering its morphological uniqueness and isolated position in phylogenetic trees, it likely represents an early diverged species with no extant siblings. The ascus apparatus of *E. furfuracea* differs considerably from species previously accepted in *Encoelia*.
3) Based on ultrastructure, the wall of apothecial hairs in Lachnaceae varies at the genus level. Despite the ascus apical apparatus being largely similar among the segregates of *Lachnum*, it is unique in *Lachnellula*. *Lachnum* should be used *sensu stricto*, because the phylogeny and ultrastructural data endorse the distinction of the genera *Albotricha, Brunnipila*, *Belonidium*, *Capitotricha, Dasyscyphella,* and *Incrucipulum*, merged in *Lachnum* by some earlier authors. *Belonidium aeruginosum* is not congeneric with *Incrucipulum* as proposed based on ultrastructure.
4) To improve the taxonomy of mollisioid fungi further studies are needed to ascertain the synapomorphies characterising members of phylogenetic lineages. Based on their ascus apical apparatus, mollisioids are clearly distinct from Dermateaceae s. str.
5) For detecting helotialen fungi in diverse habitats, DNA-based methods are valuable, enabling to accumulate information about their distribution, substrata and lifestyle. Phylogenetic analyses combining ITS rDNA sequences from fruitbodies and complex biological samples enabled to provide a name to the unidentified source organisms of many INSD ITS sequences, and indicated that members of each lineage mostly share a

common lifestyle. Members of the Cenangiaceae frequently grow as endophytes in various host tissues, a feature thus far ascribed to Hemiphacidiaceae, here merged in the Cenangiaceae. This study highlights the potential of DNA-based identification methods in studies on the ecology of cryptic fungi in a phylogenetic context.

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KOKKUVÕTE

Ultrastruktuuri ja molekulaarsete andmete rakendused tiksikseente taksonoomias

Tänapäeva süstemaatika järgib põhimõtet, et ühte taksonisse kuuluvad ühisest eellasest pärinevad organismid. Klassifikatsiooni aluseks olevaid evolutsioonihüpoteese püstitatakse geneetiliste andmete alusel. DNA-põhiste meetodite kasutamine on iseäranis oluline väikesemõõtmeliste organismide taksonoomias, kuivõrd nende morfoloogilised kriteeriumid on raskemini tuvastatavad. Sarnane on olukord kottseente hulgas, kõige liigirikkamas seenehõimkonnas, kus siiani osutub taksonite piiritlemine paljudes rühmades keeruliseks.

Doktoritööga püütakse anda panus fülogeneesipõhise klassifikatsiooni loomisesse ühes molekulaarselt vähe uuritud kottseente rühmas, tiksikseened. Need kuuluvad klassi Leotiomycetes, mille liigirikkaim selts – tiksikulaadsed (Helotiales) (~300 perekonda, 3000 liiki) – on heterogeenne nii morfoloogia kui ökoloogia poolest. Nende lehtereoslad on valdavalt ketasjas-peekerjad, pruunikad, valkjad või eredavärvilised ning läbimõõduga alla 2 mm. Eluviisilt on tiksikseened kas saproobid, parasiidid või sümbiondid (endofüüdid, mükoriisaseened), keda leidub mitmesugustel taimsetel substraatidel, aga ka mullas ja vees. Viimasel aastakümnel on selgunud, et traditsiooniliselt tiksikulaadsete seltsi arvatud sugukonnad ei moodusta monofüleetilist rühma, mistõttu kasutatakse siinses töös uuritavate seente puhul mitteformaalset nimetust *tiksikseened*.

Doktoritöö eesmärk oli 1) hinnata morfoloogiliste ja ultrastruktuuri tunnuste sobivust taksonite eristamiseks nii liigi, perekonna kui ka sugukonna tasandil; sugukonna Lachnaceae ja alamsugukonna Encoelioideae esindajatel ning *Mollisia* rühma seentel; 2) selgitada välja alamsugukonna Encoelioideae ja perekonna lõhkik liikide sugulussuhted; 3) esitada perekonna lõhkik ja sellega lähisuguluses olevate liikide fülogeneesile tuginev klassifikatsioon; 4) värskendada infot uuritud rühmade ökoloogia kohta, kasutades ITS geenijärjestusi viljakehadest, seenekultuuridest ja keskkonnaproovidest avalikes andmebaasides.

Põhimeetodid püstitatud ülesannete lahendamisel olid valgus- ja transmissioon-elektronmikroskoopia, DNA sekveneerimine ning fülogeneesi rekonstrueerimine molekulaarsete tunnuste põhjal. Peaaegu kõigil uuritud taksonitel määrati DNA ITS nukleotiidne järjestus – seente triipkoodistamise marker, millest koostatud andmemaatriksitesse kaasati avalikes geeniandmebaasides talletatud keskkonnaproovidest pärit sekventsid. Et hinnata ultrastruktuuri tunnuste kasutatavust liikide ja perekondade piiritlemisel, rekonstrueeriti klassi Leotiomycetes fülogeneesipuu rDNA 18S ja 28S põhjal, haarates valimisse võimalikult palju taksoneid, mille ultrastruktuur oli kirjeldatud. Multigeenianalüüsi jaoks sekveneeriti 5 geenilõiku (rDNA 18S ja 28S ning valke kodeerivad geenid rpb1, rpb2 ja tef1) 70 taksonil, kaasates kättesaadavaid Encoelioideae taksoneid.

Multigeenianalüüsil osutus perekond lõhkik polüfüleetiliseks, kuna selle liigid jagunesid kuu sugukonna vahel. Perekonna tüüpliik, Eestiski sarapuudel

tavaline sametlõhkik (*Encoelia furfuracea*), eristus eoskoti tipustruktuuri poolest selgelt sinna perekonda varem arvatud liikidest ning paigutus sugukonna Cenangiaceae hulka. Selles sugukonnas kirjeldati vakuoolikehi elusate viljakehade parafüüsides. Cenangiaceae sisaldab puidusaproobe ning okaspuude parasiite-endofüüte, hõlmates varasema sugukonna Hemiphacidiaceae. ITS analüüsil leidis kinnitust perekonna *Cenangium* liikide esinemine endofüütidena nii mändides kui ka männi puuvõõrikus.

Sugukonda Sclerotiniaceae kuuluvad kobarlõhkik (*Encoelia fascicularis*) ja *E. pruinosa*, vastavalt saproob ja parasiit haavapuude koorel, neile lisaks kirjeldati uus liik saarepuul. Kõigi kolme jaoks kirjeldati uus prk. *Sclerencoelia*, mida iseloomustavad peremeespuu koore all moodustuvad sklerootsiumilaadsed struktuurid. Eestis uus liik *E. tiliacea* leiti olevat lähisuguluses perekonna *Rutstroemia* tüüpliigiga sugukonnas Rutstroemiaceae. Sclerotiniaceae, Rutstroemiaceae ja Piceomphale klaad ning Cenangiaceae moodustavad fülogeneesipuul tugeva toetusega monofüleetilise rühma, mis võib olla uus tiksikseente selts.

Kaks endist lõhkiku liiki ning mitmed Encoelioideae liikmed paigutusid taaselustatud sugukonda Cordieritidaceae, kuhu kuuluvad samblikel ja teistel seentel kui ka puidul saprotroofidena kasvavad seened. Sealhulgas on Eesti suurim tiksikseen *Ionomidotis irregularis*, millel esineb oma sugukonnale iseloomulik tugev ionomidootiline reaktsioon kaaliumhüdroksiidi lahuses. Suurest rühmasisesest morfoloogilisest varieeruvusest hoolimata oli Cordieritidaceae monofüleetilisus tugevalt toetatud. *Encoelia glauca* tõsteti rohetiksiku (*Chlorociboria*) perekonda sugukonnas Chlorociboriaceae. *Encoelia fuckelii* põhjal kirjeldati uus perekond *Xeropilidium* (Chaetomellaceae).

Lachnaceae oli rDNA fülogeneesi põhjal monofüleetiline rühm ning perekonnast *Lachnum* saab eristada mitmeid väiksemaid perekondi, mis erinevad üksteisest lehtereoslate karvade seinte ultrastruktuuri poolest. Lachnaceae esindajate eoskoti tipustruktuur oli sugukonna piires küllalt sarnane, v.a. perekond *Lachnellula.*

Mollisia rühma seentel osutus perekondade *Belonopsis*, *Mollisia* ja *Pyrenopeziza* eoskoti tipustruktuur vähe varieeruvaks ning perekonnad selle tunnuse alusel ei eristanud. Neil seentel on taksonoomiliselt olulised anamorfide ja parafüüside vakuoolikehade tunnused, olles kooskõlas perekondade asetsemisega fülogeneesipuul.

Fülogeneesianalüüsil ilmnes mitmete traditsiooniliselt eristatud sugukondade/perekondade para- ja polüfüleetilisus. Leiti, et uuritud seente liike ja kõrgemaid taksoneid eristab mitme tunnuse kombinatsioon, kus üksiku tunnuse seisundit ei või üle tähtsustada. Klassifikatsiooni korrastamisel on iseäranis oluline sugukondade ja perekondade tüüptaksonite analüüsimine. Paljude tiksikseente taksonite kohta saadi olulist ökoloogilist lisateavet, analüüsides koos viljakehadest ja keskkonnaproovidest pärit DNA järjestusi. Samas võimaldas viljakehade sekventside võrdlus identifitseerida mitmeid avaliku geeniandmebaaside määramata keskkonnasekvente (annoteeritud kui *kultiveerimata seen*, *Leotiomycetes sp.* vms). Siinse töö näitel võib julgustada taksonoome DNA triipkoodi rohkem kasutama ning tegema ökoloogidega tõhusamalt koostööd.

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PUBLICATIONS

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Pärtel K, Baral H-O, Tamm H, Põldmaa K. 2016. Evidence for the polyphyly of *Encoelia* and *Encoelioideae* with reconsideration of respective families in Leotiomycetes. Fungal Diversity DOI 10.1007/s13225-016-0370-0 (published online)

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Baral H-O, Haelewaters D, **Pärtel K**. 2015. A new attempt to classify the families of the Helotiales. The Second International Workshop of Ascomycete Systematics. 22–24 Apr 2015 Amsterdam, stendiettekanne

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