

Taxonomy and Systematics of Thelephorales – Glimpses Into its Hidden Hyperdiversity

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Cover image: *Pseudotomentella alobata*, a newly described species in the *Pseudotomentella tristis* group.

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Många är långa och svåra att fånga

Många syns inte men finns ändå

Många är gula och fula och gröna

Och sköna och röda eller blå

Många är stora som hus eller så

Men de flesta är små, mycket små, mycket små

*– Olle Adolphson, från visan *Okända djur**

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ABSTRACT

The order Thelephorales is a widespread group of many thousands of species of ecologically important, ectomycorrhizal fungi, of which only a fraction have been described to date. Most species are corticioid (skin-like) and form complexes of morphologically similar, closely related species. At the same time the names that do exist are often old, have unclear synonymy and their common presence within such complexes often hinders the description of new species. For the comparatively few stipitate (with cap and stipe) Thelephorales species taxonomic knowledge is more complete but the phylogenetic relationships between taxa is largely unknown; most existing genera have been circumscribed based on macromorphology. Many stipitate species occurring in the Nordic countries are dependent on old growth forest and are hence included in the national Red Lists, while the conservational situation for nearly all corticioid species is unknown, due to their unclear taxonomy.

Pseudotomentella tristis s.l. is a seemingly common, widespread and ecologically very plastic, corticioid morphospecies with an old name and nine heterotypic synonyms. Through a combination of type studies, precise spore measurements, ecological data and a multi-gene phylogeny, three species are identified under already existing names and another ten are described as new. One species, *P. umbrina* is found to indeed be a common and widespread species with a wide ecological amplitude, while the remaining 12 are less common, possibly less widespread, have narrower ecological niches and in a few cases seem to be host-restricted. In similarity to stipitate species, a large proportion of the newly described species seem to only occur in old growth forest.

Three corticioid species from the Scandes mountains, two *Pseudotomentella* species and one *Tomentella*, are described as new, based on ITS-LSU phylogenies. The *Pseudotomentella* species belong to the *P. tristis* group, where they are more or less cryptic with another newly described species.

A new, stipitate species in the hitherto corticioid genus *Amaurodon* is described, the stipitate genera *Hydnellum* and *Sarcodon* are delimited against each other and the stipitate genus *Polyozellus* is delimited against the corticioid genus *Pseudotomentella* – the former two with phylogenies based on ITS and LSU sequences and the latter based on a multi-gene dataset. *Hydnellum* is found to make *Sarcodon* paraphyletic, as does *Polyozellus Pseudotomentella*. To amend this, twelve species are recombined from *Hydnellum* to *Sarcodon*, while all species, including the type, are moved from *Pseudotomentella* to *Polyozellus*.

In conclusion, this thesis demonstrates that corticioid species complexes in Thelephorales with many taxa and old names can be successfully disentangled and presents a method for doing so; it identifies molecular markers and sets a standard of measuring spores and collating ecological data that will facilitate further taxonomic work within the order. In addition, it shows that basidiomata shape is a poor predictor of generic affinity, even when derived from such striking differences as the separation of stipitate and corticioid forms. Consequently, the extinction threat previously documented for stipitate species is likely not restricted to such, and this is also tentatively shown for corticioid *Polyozellus* species.

Keywords: *Thelephorales*, *Tomentella*, *Polyozellus*, *Pseudotomentella*, *Amaurodon*, *Hydnellum*, *Sarcodon*, species delimitation, cryptic species, molecular systematics, ectomycorrhiza, basidiomata shape.

SVENSK SAMMANFATTNING

Ordningen Thelephorales är en vitt utbredd grupp svampar med många tusentals ekologiskt viktiga, ektomykorrhiza-bildande arter, varav endast en mycket liten del hittills är formellt beskrivna. De flesta arter är skinnlika och ingår ofta i artkomplex tillsammans med andra närbesläktade, morfologiskt lika arter. Samtidigt är de namn som beskrivits tidigare ofta gamla, har oklar synonymitet och förekommer ofta i sådana artkomplex, där de därmed hindrar beskrivningen av nya arter. Bland de jämförelsevis få stipitata (med hatt och fot) Thelephorales-arterna är den taxonomiska situationen mera fullständig men det fylogenetiska släktskapet mellan taxa är mestadels okänt; de flesta släkten är avgränsade baserade på makromorfologi. Många i Norden förekommande stipitata arter är beroende av gammelskog och är därmed nationellt rödlistade. Bevarandesituationen för de flesta skinnlika arter är okänd, på grund av sin oklara taxonomi.

Pseudotomentella tristis s.l. är en till synes vanlig, vitt utbredd och ekologiskt väldigt plastisk, skinnlik morfoart med ett gammalt namn och nio heterotypiska synonymer. Genom en kombination av typstudier, precisa spormått, ekologiska data och en multigensanalys identifieras tre arter till redan existerande namn och ytterligare tio beskrivs som nya. En art, *P. umbrina*, befins vara en mycket vanlig art med stor utbredning och ekologisk amplitud, medan de återstående tolv arterna är mindre vanliga, möjligen mindre utbredda, har mindre ekologiska nischer och verkar i ett fåtal fall vara värdspecifika. I likhet med många stipitata arter förefaller en stor del av de nybeskrivna arterna att vara begränsade till gammelskog.

Tre skinnlika arter från Skanderna, två i släktet *Pseudotomentella* och en i släktet *Tomentella*, beskrivs som nya, baserat på ITS-LSU-fylogener. *Pseudotomentella*-arterna tillhör *P. tristis*-gruppen, där de är mer eller mindre kryptiska med en annan nybeskriven art.

En ny, stipitat art i det hittills skinnlika släktet *Amaurodon* beskrivs, de stipitata släktena *Hydnellum* och *Sarcodon* avgränsas gentemot varandra och det stipitata släktet *Polyozellus* avgränsas mot det skinnlika släktet *Pseudotomentella* – de två förstnämnda fylogenierna baserat på ITS- och LSU-sekvenser och den sistnämnda baserat på ett multigensdataset. *Hydnellum* visar sig göra *Sarcodon* parafyletiskt, liksom *Polyozellus* *Pseudotomentella*. För att åtgärda detta omkombineras tolv arter från *Hydnellum* till *Sarcodon*, medan alla arter i *Pseudotomentella*, inklusive typarten, flyttas till *Polyozellus*.

Sammanfattningsvis visar denna avhandling att artkomplex med skinnlika svampar i Thelephorales, innehållandes många arter och gamla namn, kan lösas upp på ett framgångsrikt sätt och presenterar en metod för detta; den pekar ut användbara molekylära markörer och sätter en standard för spormätning och sammanställning av ekologiska data som kommer att underlätta fortsatt systematiskt och taxonomiskt arbete inom ordningen. I tillägg visar den att fruktkroppsform är en dålig släktesavgränsare, även när det rör sig om så markanta skillnader som separationen av stipitata och skinnlika fruktkroppar. Således är den utrotningsrisk som tidigare dokumenterats för stipitata arter troligen inte begränsad till dem, och detta påvisas också preliminärt för skinnlika *Polyozellus*-arter.

PUBLICATIONS

- I **Svantesson S**, Larsson K-H, Kõljalg U, May TW, Cangren P, Nilsson RH, Larsson E (2019) Solving the taxonomic identity of *Pseudotomentella tristis* s.l. (Thelephorales, Basidiomycota) – a multi-gene phylogeny and taxonomic review, integrating ecological and geographical data. *MycKeys* 50: 1–77.
- II Larsson K-H, **Svantesson S**, Miscevic D, Kõljalg U, Larsson E (2019) Reassessment of the generic limits for *Hydnellum* and *Sarcodon* (Thelephorales, Basidiomycota). *MycKeys* 54: 31–47.
- III **Svantesson S**, Larsson K-H, Larsson E. *Pseudotomentella badjelanndana*, *Pseudotomentella sorjusensis* and *Tomentella viridibasidia* – three new corticioid Thelephorales species from the Scandes Mountains. Manuscript, submitted to *Phytotaxa*.
- IV **Svantesson S**, Syme K, Douch JD, Robinson RM, May TW. "The Mouldy Marshmallow" *Amaurodon caeruleocaseus* (Thelephorales, Basidiomycota) – the first stipitate species in the genus *Amaurodon*. Manuscript, submitted to *Sydowia*.
- V **Svantesson S**, Kõljalg U, Wurzbacher C, Saar I, Larsson K-H, Larsson E. *Polyozellus* vs *Pseudotomentella*: generic delimitation with a multi-gene dataset. Manuscript, submitted to *Fungal Systematics and Evolution*.

SS was responsible for the field work, the microscopy, the analyses and the manuscript, in Papers I, III and V. In Paper II SS was responsible for the analyses and wrote part of the manuscript. In Paper IV SS was responsible for the microscopy, the analyses and the manuscript.

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All papers are reproduced here for the purpose of academic procedure only. SS does not intend new names and combinations mentioned to be accepted as validly published in this

thesis (cf. the International Code of Nomenclature for Algae, Fungi and Plants, art. 36.1). The ISBN numbers refer to the thesis only, which per the Swedish definition does not include the attached papers.

Additional publications p.p., not included in this thesis

Spirin V, Nordén J, **Svantesson S**, Larsson K-H (2016) New records of intrahymenial heterobasidiomycetes (Basidiomycota) in North Europe. *Nordic Journal of Botany* 34(4): 475–477.

Nilsson RH, Wurzbacher C, Bahram M, Coimbra VRM, Larsson E, Tedersoo L, Eriksson J, Duarte C, **Svantesson S**, Sánchez-García, Ryberg MK, Kristiansson and Abarenkov K (2016) Top 50 most wanted fungi. *MycKeys* 12: 29–40.

Wurzbacher C, Larsson E, Bengtsson-Palme J, Wyngaert SVd, **Svantesson S**, Kristiansson S, Kagami M, Nilsson RH (2019) Introducing ribosomal tandem repeat barcoding for fungi. *Molecular Ecology Resources* 19(1): 118–127.

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, **Svantesson S**, et al. (2019) CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* 10(5): 744–751.

Wurzbacher C, Kreiling A-G, **Svantesson S**, Wyngaert SVd, Larsson E, Heeger F, Nilsson HR, Pálsson S (2020) Fungal communities in groundwater springs along the volcanic zone of Iceland. *Inland Waters* 10.

Nitare J, Ainsworth AM, Larsson E, Parfitt D, Suz LM, **Svantesson S**, Larsson K-H. Four new species of *Hydnellum* (*Thelephorales*, *Basidiomycota*) with a note on *Sarcodon illudens*. Manuscript.

INTRODUCTION

The Thelephorales

Background

The order Thelephorales Corner ex Oberw. is a well-defined lineage of basidiomycetes (Larsson et al. 2004, Hibbett et al. 2007), distributed to all continents except Antarctica (Kõljalg et al. 2013, Nilsson et al. 2018). Its members are currently grouped into two families: Thelephoraceae Chevall. and Bankeraceae Donk (He et al. 2019). They vary greatly in the shape of basidiomata; Bankeraceae species are stipitate and hydroid (*Hydnellum* P. Karst., *Phellodon* P. Karst., *Sarcodon* Quél. ex P. Karst. and until recently also *Bankera* Coker & Beers ex Pouzar) or stipitate and poroid (*Boletopsis* Fayod), while most species in Thelephoraceae form corticioid, more or less smooth basidiomata (*Amaurodon* J. Schröt., *Odontia* Pers. p.p., *Pseudotomentella* Svrček, *Tomentella* Pers. ex Pat. p.p., *Tomentellopsis* Hjortstam; Stalpers 1993, Kõljalg 1996, Baird et al. 2013, He et al. 2019). A few Thelephoraceae species are corticioid but adorned with spines or protuberances (*Odontia* p.p., *Tomentella* p.p.), have smooth funnel- or rosette-shaped basidiomata (*Polyozellus* Murrill, *Thelephora* Ehrh. ex Willd. p.p.), smooth, finger-like basidiomata (*Thelephora* p.p.) or are lamellate (*Lenzitopsis* Malençon & Bertault; Stalpers 1993, Kõljalg 1996, He et al. 2019).

In contrast to the considerable macromorphological variation displayed among its species, the taxonomic affinity to the order is usually easily recognised under a light microscope; with the exception of *Amaurodon mustialaensis* (P. Karst.) Kõljalg & K.H. Larss., whose spores appear smooth, Thelephorales spores carry wart- to spine-like ornamentation, prominent apiculi and often have dark pigmentation in their walls or contents (Stalpers 1993, Kõljalg 1996). Another feature common to most species is the presence of thelephoric acid, a substance which is brown in water but turns blue in KOH.

Often collected on wood, the tomentelloid (corticioid Thelephorales) species were originally and until quite recently believed to be saprotrophs, with the taxonomic identity of the substrate they grew on often noted in their descriptions as an important feature (e.g. Fries 1828, Larsen 1968). In recent years, however, such a great majority of Thelephorales genera (*Boletopsis*, *Hydnellum*, *Phellodon*, *Sarcodon*, *Polyozellus*, *Pseudotomentella*, *Thelephora*, *Tomentella* and *Tomentellopsis*) have been shown to be ectomycorrhizal, that it has become the new null hypothesis (He et al. 2019). Two genera, *Odontia* and *Lenzitopsis*, have nevertheless been found to be saprotrophs and a third, *Amaurodon*, is believed to be as well

(Miettinen & Kõljalg 2007, Zhou & Kõljalg 2013, Tedersoo et al. 2014, He et al. 2019). Thelephoroid ectomycorrhiza is common in most habitats where ectomycorrhiza exists – for example forests in temperate, Mediterranean and subtropical climates, as well as on the arctic tundra, in coastal vegetation in the tropics, etc. – and in some environments it even co-dominates the rhizosphere (e.g. Kõljalg et al. 2000, Sønstebo 2002, Mühlmann & Peintner 2008, Ryberg et al. 2009, Botnen et al. 2015).

A study on *Tomentella sublilacina* Ellis & Holw. has found its spores to be dispersed by insects and given the similar growth habits of other tomentelloid species (on the underside of logs, turf and stones close to or under the ground) this may well be the case for most species (Lilleskov & Bruns 2005).

Taxonomy and diversity

Thelephorales comprises approximately 321 described species (He et al. 2019). The ITS sequence database UNITE, however, hosts 4305 Species Hypotheses (SHs) at 1.5 % minimum distance between sister species (2020-09-24; Kõljalg et al. 2013, Nilsson et al. 2018). Following this measure Thelephorales is of similar diversity to the more well-known, ectomycorrhizal orders Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David (4020 SHs) and Boletales E.-J. Gilbert (2106 SHs) but the overwhelming majority of its species are yet to be described. Out of the total number of Thelephorales SHs, 4095 belong in Thelephoraceae, thus likely indicating species with corticioid basidiomata.

Among tomentelloid species most names are old and their type material often in such bad condition that they cannot be reliably sequenced with currently available techniques (Index Fungorum 2020). The synonymy and genetic identity of these species is therefore often hard to establish without neo- or epitypification. In addition, the situation is further complicated by the fact that most commonly applied names (e.g. *Pseudotomentella tristis* (P. Karst.) M.J. Larsen, *Tomentella lapida* (Pers.) Stalpers and *Tomentellopsis echinospora* (Ellis) Hjortstam), when queried in UNITE, belong to groups of closely related species that include more than one old name and several to dozens of undescribed species (2020-09-01; Kõljalg et al. 2013, Nilsson et al. 2018).

Even though a lot of species remain to be described in Bankeraceae as well, taxonomic knowledge is considerably higher within the family. Through their remarkable appearance and importance in conservation, many species occurring in Europe and North America have been investigated more recently (e.g. Johannesson et al. 1999, Watling & Milne 2006, 2008,

Nitare & Högberg 2012, Baird et al. 2013) and although there are competing lineages for a lot of names there are usually only a few for each name and not dozens, even for more common species such as *Hydnellum ferrugineum* (Fr.) P. Karst and *Phellodon niger* (Fr.) P. Karst. (UNITE 2020-09-01; Kõljalg et al. 2013, Nilsson et al. 2018).

Systematics

Phylogenetic studies in Thelephorales are scarce to date, and most serve to publish only one or a small number of species (e.g. *Amaurodon*, *Tomentella* and *Polyozellus*; Miettinen & Kõljalg 2007, Kuhar et al. 2016, Voitk et al. 2017). A few phylogenies have nevertheless been made with the objective of delimiting a genus: *Odontia* (Tedersoo et al. 2014), *Phellodon* vs. *Bankera* (Baird et al. 2013) and *Lenzitopsis* (Zhou & Kõljalg 2013). A small number of articles, based on nuclear, ribosomal DNA, have also hinted at the internal structure of the order, but they have thus far not been conclusive (Zhou and Kõljalg 2013, Tedersoo et al. 2014, Vizzini et al. 2016). The study including the most taxa is probably Vizzini et al. (2016), who pointed to taxonomical problems regarding the delimitation of *Polyozellus* vs. *Pseudotomentella*, *Hydnellum* vs. *Sarcodon*, *Bankera* vs. *Phellodon* and *Thelephora* vs. *Tomentella* – in each case making one genus paraphyletic.

Conservation

The species in *Bankeraceae* are to a large part rare and restricted to old growth forest. In accordance with the IUCN guidelines many are Nationally Red Listed in the Scandinavian countries, due to threat of extinction (Henriksen & Hilmo 2015, SLU ArtDatabanken 2020). They often occur on ground with high pH and are used as indicators of forests with high nature values (Nitare & Hallingbäck 2000, Ainsworth et al. 2005, Nitare 2019).

In Thelephoraceae the level of conservation knowledge is considerably poorer, due to its unclear taxonomy. Several *Amaurodon* species are, however, Red Listed in Norway and Sweden (Henriksen & Hilmo 2015, SLU ArtDatabanken 2020) and the species complex of *Polyozellus multiplex* (Underw.) Murrill was before its splitting (and presumably afterwards too) considered to be a good indicator of old growth forest in northern North America (United States Forest Service 1994, Baroni 2017). Preliminary data for both described and undescribed species, suggest that this might be the case also for many *Pseudotomentella* species.

Inferring systematics and taxonomy

The species problem

There are many competing definitions of the term “species”. Mayden (1997) lists 22, while Wilkins (2006) includes 26. Some, for example de Queiroz (1998) with his General Lineage Concept, have sought to reconcile existing concepts under yet other concepts. In current mycological, taxonomic practice though, there are mainly four that are prevalent: the morphological, ecological, phylogenetic and biological species concepts. According to the morphological and ecological concepts, individuals are referred to as different species if they differ in certain aspects of their morphology or ecology that are deemed important and viewed as stable within species but changing among them (Simpson 1961, Ruse 1969). The biological species concept is the idea that individuals belong to different species if they are reproductively separated (Mayr 1942), while the phylogenetic concept characterises species as spatially and chronologically, evolutionarily distinct lineages or the smallest possible group of individuals that share a unique evolutionary history (Wheeler & Platnick 2000, Giraud et al. 2008). Often combinations are employed, whereby phylogenetically or biologically delimited species are only accepted if they can also be distinguished morphologically or ecologically. In practice the user of the phylogenetic and biological definitions employs computer programs to delimit species according to the evolutionary relationships inferred by the individuals of a certain dataset. Gene or species trees are generated according to likelihood algorithms, which, following different theories, e.g. Bayesian, Maximum Likelihood, Maximum Parsimony etc., calculate the most likely route evolution has taken, and thus the most plausible relationship between individuals. The taxonomist then makes a decision about delimitation based on his or her choice of the amount of support needed to regard a lineage as a species and the amount of conflict allowed between such in order for them to still be accepted as separate. Implicit in the choice is also the set of genetic markers used.

Gene trees ≠ species trees

When inferring the phylogenetic relationship between species the interest, per definition, lies with the species tree. This relationship is inferred from one or several genetic regions. There are, however a number of reasons why different DNA regions might be unsuitable for this purpose or display conflict.

Incomplete lineage sorting (ILS)

One of the most common causes of conflict between gene trees in all diploid organisms is a phenomenon called Incomplete Lineage Sorting or Deep Coalescence (Rogers & Gibbs 2014). Instances of ILS arise when time between speciation events is short and population sizes are large. Several alleles of a gene can then persist between speciation events, where they “do not have time” to be sorted between different, emerging species, but instead coalesce past the second event, looking backwards in time (Maddison 1997). A situation is hence created where some genes have a phylogeny that do not agree with that of most others in the species tree (Fig. 1).

Paralogy

Paralogy occurs when genes are duplicated, through processes such as retrotransposition and replication slippage and persist through speciation events but remain so similar that they are not distinguished as different genes, but merely copies of the same gene (Koonin 2005). Within an individual, one copy of a certain gene will then be more closely related to the same copy within another individual of the same or another species than it will be to the other copy of the same gene within the same or any other individual (Fig. 2). A phylogeny correctly inferring the relationship

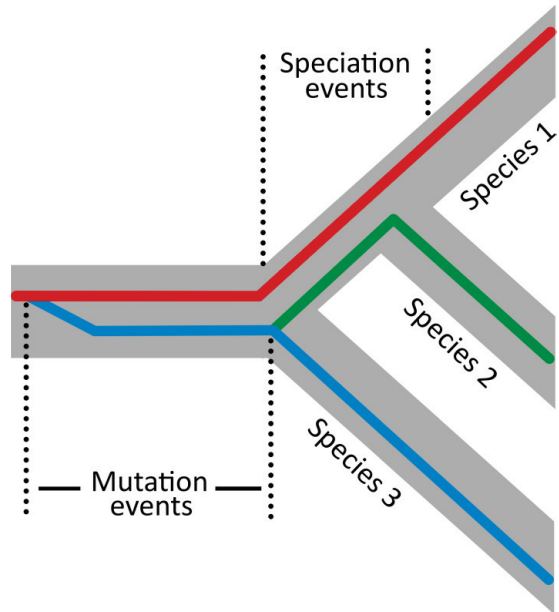


Figure 1. Divergence between the alleles of a gene tree (coloured) and a species tree (grey), caused by Incomplete Lineage Sorting. Modified from Thomas Shafee [CC BY 4.0](https://creativecommons.org/licenses/by/4.0/).

between species can thus not be made from paralogous genes (= of different copy numbers), but needs to only employ orthologous genes (= of the same copy number). A complication arises when Sanger sequencing and PCR is used, since this method is designed to only capture the most prevalent copy of each gene targeted. Through the random amplification of the different gene copies genes of unknown orthology may then result in phylogenies that come across as orthologous, when they are not. Paralogy is known from the fungal kingdom (e.g. Walther et al. 2019) but its extent is poorly known.

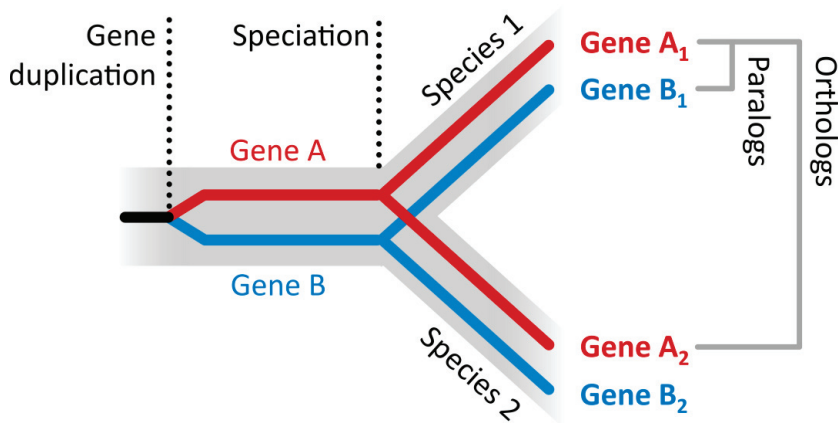


Figure 2. Paralogy and orthology of a duplicated gene (coloured) within a species tree (grey).

Modified from Thomas Shafee [CC BY 4.0](https://creativecommons.org/licenses/by/4.0/).

Hybridisation, introgression and horizontal gene transfer

The formation of a new species from the DNA of two parental ones is termed hybridisation and transfer of genes from one species to another, usually mediated through a hybrid, is referred to as introgression. In both of these instances affected individuals would display two distinct relatives as the closest for different sets of genes. Events of hybridisation and introgression do not seem to be uncommon in some groups of Ascomycota but only a handful of cases appear to be known among Basidiomycota (Brasier 2000, Baumgartner et al. 2012, Zhang et al. 2018a, Matute & Sepúlveda 2019, Steenwyk et al. 2020).

Horizontal gene transfer is the transfer of genetic material between individuals of the same or different species by other means than sexual reproduction, e.g. through viral or bacterial infections. The existence of such transfers have been documented for fungi (Hall et al. 2005), but its prevalence among basidiomycetes is even less known than for paralogy and hybridisation.

Micromorphological descriptions and measurements

Tomentelloid fungi usually lack cystidia and other sterile organs in their hymenia and their micromorphological descriptions are therefore often limited to measurements of subicular and subhymenial hyphae, as well as the size and shape of basidia (tend to be featureless) and spores (Kõljalg 1996). The spores often have an intricate shape that is hard to perceive; the basic shape varies from nearly round to ellipsoid, egg-, pear- or heart-shaped, is often

regularly to irregularly lobed and the lobes are in turn adorned with warts or spines, the latter referred to as echinuli. The echinuli can be singularly or plurally attached. To complicate the picture further the different sides of tomentelloid spores do not look alike; the adaxial side (facing the basidium Fig 3a) is different to the abaxial side (facing away from the basidium Fig 3b), while the lateral sides are similar (Fig 3c). The polar (top and bottom) sides look different again, but are not usually described. All of the above features vary markedly within some species but not in others and when viewed through a light microscope most spores display faces that are somewhere in between the ones needing description. Needless to say

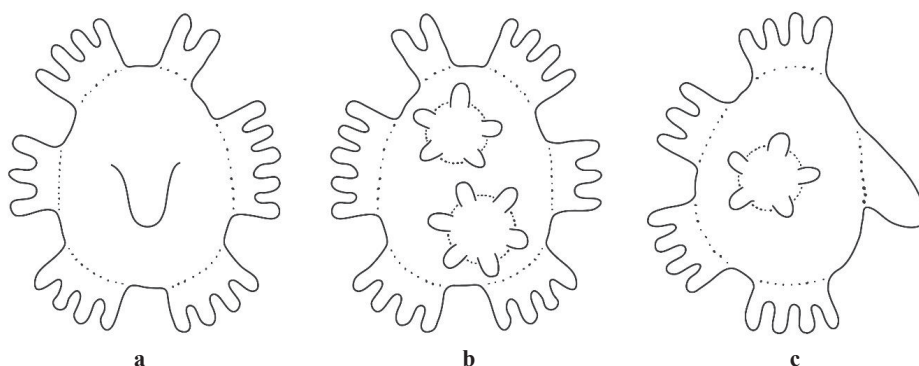


Figure 3. A stylised, tomentelloid spore in face view, showing its a) adaxial, b) abaxial and c) lateral sides. © Mirjam Korn

this part of the descriptive work constitutes an interesting but time-consuming test of spatial ability and requires a reasonably good microscope. In older descriptions, by for example Larsen (1968), the spore shape is often stated as “lobed” or simply “irregularly globose to irregular” and a single **measurement** for the general diameter is given. Stalpers (1993) provided measurements in two dimensions but did not separate between the different sides of spores, while Kõljalg (1996) described the shape of both the adaxial and lateral sides of spores in face view (in his work termed “frontal” and “lateral face” and from here on used for consistency). He supplemented these descriptions with a length measurement (which is the same for both sides).

OBJECTIVES

The main purposes of this thesis are to increase knowledge on the biodiversity, systematics and taxonomy of the mainly ectomycorrhizal, fungal order Thelephorales, primarily in Scandinavia/Sweden and in particular among corticioid species.

Paper I aimed at taxonomically resolving the many names and species thus far residing under the name *Pseudotomentella tristis*, with the support of a multi-gene phylogeny, and revising the taxonomy accordingly.

Paper II focused on delimiting the genera *Hydnellum* and *Sarcodon* against each other, based on an ITS-LSU phylogeny and making the taxonomic changes warranted.

Paper III aimed at describing two new *Pseudotomentella* species and one new *Tomentella* species from the Scandinavian Mountains, with the support of ITS and LSU phylogenies.

Paper IV focused on describing the first stipitate species in the genus *Amaurodon*, based on an ITS-LSU phylogeny.

Paper V had the objective of identifying genetic regions useful in inferring the phylogenetic relationship between the stipitate genus *Polyozellus* and the corticioid genus *Pseudotomentella*, inferring this relationship with the multiple regions identified and revising the taxonomy accordingly.

METHODS

Taxon sampling

The project had access to ca 1500 basidiomata collections from Norway, mostly collected in nemoral, deciduous forest 2010–2014, partly by the author and determined by the same. To complement this dataset, extensive field work was carried out seasonally in Sweden 2015–2018. Collecting was then focused on the mycologically understudied mountain regions in the northern part of the country (Lule Lappmark, Lycksele Lappmark and Västerbotten) and calcareous forests with documented high diversity of other ectomycorrhizal fungi, in the same areas and in the south (Bohuslän, Dalsland, Öland, Östergötland and Västergötland). A trip was also made to USA and Canada to collect material for epitypes. In total the field work generated ca 550 collections. Approximately 150 collections from herbaria GB and TU were also studied and determined. Loans of type material were made from herbaria ARIZ, BPI, H, PERTH, S, TUR and in situ studies were conducted at UPS and MEL.

For the majority of the Swedish and Norwegian specimens the vegetation type of each collection was recorded, following Fremstad (1997) and Pålsson (1998). This information was sorted into the soil pH types “low”, “intermediate” and “high”, following Fremstad (1998) and Halvorsen (2015) and for Paper I also into the habitats “tundra”, “coniferous forest”, “deciduous forest” and “mixed forest”. In addition, the potential hosts of each specimen, as indicated by nearby ectomycorrhiza-forming plants, was noted. The Swedish specimens were photographed, weather permitting. Taxonomic author abbreviations follow IPNI and herbarium codes follow Index Herbariorum (Thiers 2020).

Morphological and ecological data

All specimens were studied macroscopically, at 20× magnification under a dissecting microscope and at 400× and 1000× under a light microscope. Measurements were made on dried material, mounted in 3% (potassium hydroxide) KOH and in Melzer’s reagent. A minimum of three specimens per species were examined, whenever the total number of specimens allowed it and 20–30 micromorphological structures of each type were measured. To utilise all available morphological features in groups of closely related species, Kõljalg’s (1996) method of spore description, stating the shape and length of spores in frontal and lateral face, is here complemented with width measurements in both faces as well as more detailed descriptions of shape. The shape is thus described both in terms of the basic shape of spores, excluding lobes, and through specifying the outline of the same, including lobes. The

number and shape of lobes observed are also stated. An exception was made for *Amaurodon*, since the species of this genus have structurally much simpler spores and most previous descriptions only provide length measurements; spore dimensions of the new species in Paper IV was only provided for the lateral face. The precise instrument specifications and measurement methodology is described in the papers.

Molecular data

In order to screen the Scandinavian material of tomentelloid fungi all collections were first identified to morphospecies and then 2–3 specimens of each were sequenced for the complete ITS region, including the 5.8S gene. For morphospecies that included several ITS-genotypes further collections were sequenced. Additional genetic regions targeted varied between papers and included: ca 1200–2500 bases of the nrLSU gene (I–V), ca 1500 bases of SSU (V), ca 600 bases of Tef1 α (I, V), ca 700 bases of mtSSU (I, V), ca 1100 bases of RPB2 (V) and ca 500 bases of Betatubulin (V). PCR reactions with marker-specific primers were used in all papers in order to increase the amount of sequenceable DNA. The resulting DNA concentrations were often very low. The method of sequencing was Sanger. In addition, Paper V included sequences of the complete nrDNA tandem repeat, generated through Nanopore sequencing, as well as RPB1 sequences generated through whole genome sequencing with Illumina HiSeq. A trial with Nanopore sequencing of whole genome DNA from very large basidiomata was also attempted but failed due to large amounts of contaminating substances. The precise DNA extraction, PCR and sequencing methods used are described in the papers.

The DNA sequences generated through Sanger sequencing were assembled with Sequencher 5.1 (Gene Codes, Ann Arbor, MI, USA). Alignments were made in AliView (Larsson 2014), utilising the MAFFT L-INS-i algorithm (Katoh et al. 2005, Katoh & Standley 2013), since it is one of the most accurate methods available (Carroll et al. 2007). The nrDNA datasets of Papers I–IV were then enriched with ITS sequences from UNITE. In Papers I–III the alignments were manually adjusted, while in Papers IV and V Gblocks 0.91b (Castresana 2000, Talavera & Castresana 2007) was used to excise regions with unclear homology. This switch in methods reflects the simplicity of the alignments used – with more “messy” alignments the need for a more objective procedure of removing regions with unclear homology was deemed necessary.

Molecular analyses

RDP4 (Martin et al. 2015) was used to test for recombination. In addition, SplitsTree 4 (Huson & Bryant 2006) was employed in Paper I to explore the amount of intragenic conflict present.

Bayesian Inference (BI) gene trees were estimated using BEAST 2 (Bouckaert et al. 2014, 2019) in all papers. Maximum Likelihood (ML) gene trees were inferred with PhyML (Guindon et al. 2010) in Papers I-III and W-IQ-TREE (Trifinopoulos et al. 2016) in Paper IV. STACEY (Jones et al 2015, Jones 2017; Papers I and V) and ASTRAL III (Zhang et al. 2018b; Paper I) were employed to infer species trees. Both algorithms infer trees under the multispecies coalescent model – STACEY concurrently with estimating gene trees and ASTRAL with gene trees as input (i.e. a summary method). Both methods have been shown to perform well in empirical settings (e.g. Jones 2017, Nute et al. 2018).

Substitution models and alignment partitions were evaluated using the automated best-fit tests implemented in PAUP 4.0a. (Swofford 2002) or, in the case of W-IQ-TREE, the associated ModelFinder software (Kalyaanamoorthy et al. 2017).

In this thesis a phylogenetic/biological concept has been adopted – species are considered to be divergent evolutionary lineages, among which no or very limited transfer of genetic information is expected. Differences in morphology and ecology have been searched for but were not considered requirements of species separation.

MAIN RESULTS

Paper I

Pseudotomentella tristis is an ectomycorrhizal, corticioid fungus whose name is frequently assigned to collections of basidiomata, root tips and soil from a wide range of habitats and hosts, across the northern hemisphere. Specimens determined to *P. tristis* or its nine morphologically similar, heterotypic names were studied morphologically, ecologically and through gene and species trees of four genetic regions, generated in BEAST 2, PhyML, STACEY and ASTRAL III. They were shown to correspond to 13 molecularly and morphologically distinct species. A more precise method of measuring and describing spores was developed, as well as careful collection and collation of ecological data. This enabled the separation of species morphologically and in some cases ecologically. Through type studies, three species, *P. tristis*, *Pseudotomentella atrofusca* and *Pseudotomentella umbrina*, were found to belong to existing names, while the remaining ten species were described as new. One genetic region, Tef1 α , was indicated to be paralogous. All species, except *P. atrofusca*, were shown to form a monophyletic clade. Two names, *Hypochnus rhacodium* and *Pseudotomentella longisterigmata* were regarded as doubtful taxa and another three were excluded from *Pseudotomentella*. *Pseudotomentella umbrina* was found to be a common species with a wide, Holarctic distribution, forming ectomycorrhiza with a large number of host species in habitats ranging from tropical forests to the Arctic tundra. The remaining 12 species are less common, possibly less widespread, occur on ground with intermediate to high pH and in a smaller variety of forests types. A few of them also seem to be host-restricted.

Paper II

Hydnellum and *Sarcodon* are two genera of stipitate, ectomycorrhizal species that are considered threatened by extinction in many countries and are frequently used in nature conservation. Both have a nearly worldwide distribution but are described from Fennoscandia, and have thus far been separated based on the consistency of their basidiomata. Phylogenies based on ITS and LSU sequences were inferred with BEAST 2 and PhyML. The current delimitation was shown to make *Sarcodon* paraphyletic with regard to *Hydnellum*. To make *Sarcodon* monophyletic 12 species were recombined to *Hydnellum*. Spore size was found to be the most reliable character in separating the two genera. Neotropical species were found to represent a third, as yet unnamed, lineage.

Paper III

One *Toментella* and two *Pseudotomentella* species are described from alpine areas of Sweden and Norway, based on ITS and LSU sequences. *Toментella viridibasidia nom. prov.* is genetically closely related to *Toментella bryophila* (Pers.) M.J. Larsen, but is morphologically most similar to *Toментella olivascens* (Berk. & M.A. Curtis) Bourdot & Galzin.

Pseudotomentella badjelanndana nom. prov. and *Pseudotomentella sorjusensis nom. prov.* belong to the *P. tristis* group. At least *P. sorjusensis* is regarded as morphologically cryptic with the previously described *Pseudotomentella rotundispora nom. prov.* Basidiomata of the new species have only been encountered in the Scandes Mountains, but root-tip and soil sequences indicate that all three are geographically widespread. An updated key to the *P. tristis* group is provided.

Paper IV

Amaurodon constitutes a small but globally distributed genus that is thought to be saprotrophic. Previously described species are soft and corticioid, with a smooth or hydroid, blue to green hymenium which turns green after drying and have spores with a purple reaction in KOH. Based on ITS and LSU sequences, *Amaurodon caeruleocaseus nom. prov.* is described from Western Australia. It has all the morphological features common to the genus, with the interesting exception of forming a stipitate basidiome with a marshmallow-like consistency. Its closest relative is shown to be *A. mustialaensis*. The two species are unique within Thelephorales in having spores that appear smooth rather than ornamented under a light microscope.

Paper V

Polyozellus and *Pseudotomentella* are two genera of closely related, ectomycorrhizal fungi, the former stipitate and the latter corticioid. Both are widespread on the Northern Hemisphere and many species from both genera seem to be restricted to old growth forest. With the aim of resolving the intergeneric relationship of *Polyozellus* and *Pseudotomentella*, partial *Betatubulin*, *Tef1 α* , *RPB1*, *RPB2*, *mtSSU*, as well as nearly full-length *LSU* and *SSU* genes were evaluated for their usability as molecular markers. The latter four were found to be comparatively easy to sequence and provided a strong phylogenetic signal. A *STACEY* species tree revealed that *Polyozellus* makes *Pseudotomentella* paraphyletic. As a result, nearly all species currently placed in *Pseudotomentella*, including its type, were recombined to *Polyozellus*. *Pseudotomentella larsenii* Kõljalg & Dunstan was found to be closer to

Tomentellopsis than *Polyozellus*, but its placement needs further study and it was hence not recombined. For many resupinate *Polyozellus* species several contenders exist for the names in current use. The synonymy of many old names also remains unclear.

Additional remarks

Among the ca 2000 collections of Scandinavian corticioid Thelephorales determined within the project, sequencing of the ITS region has revealed approximately 250 hypothetical species, based on clustering in the UNITE sequence database. Some of the species hypotheses that the Nordic material clusters to have been assigned taxonomic names but most have not. In the cases where a name exists the situation is in most cases similar to that of *P. tristis* prior to review; a large number of closely related possible species share one or several old names, whose meaning today is unknown. In other cases, the situation is worse – a species name has clearly been applied to a large number of very distantly related species.

DISCUSSION

Paper I investigated the taxonomy of *P. tristis* s.l. – a species complex with many old names of unclear synonymy and a large number of possibly undescribed species. Through a combination of a multi-gene phylogeny, ecological data and a new, more precise way of measuring spores of types as well as extensive, recently collected material, this proved fruitful in disentangling old names and linking them to gene regions and morphological and ecological features, thus catalysing the description of many new species (Papers I and III). Most species could be well separated based on morphology and ecology, while a few are more cryptic. Most other corticioid Thelephorales names in use are also part of species complexes with several old names and many undescribed species (Kõljalg et al. 2013, Nilsson et al. 2018, Index Fungorum 2020). The present papers hence demonstrate a method for studying this group of fungi through a synergy of molecular, morphological and ecological methods and the descriptive potential of doing so.

Basidiome shape and texture were revealed to be poor predictors of generic affiliation in Thelephorales (Papers II, IV and V). The descriptions of two genera, *Polyozellus* and *Amaurodon* were emended to include both corticioid and stipitate basidiomata, while the distinction of another two, *Hydnellum* and *Sarcodon* was shown to correspond to spore size rather than basidiome consistency. In similarity to for example Trechisporales K.H. Larss., basidiome evolution is evidently still very much ongoing in Thelephorales; corticioid and stipitate forms have in several cases not yet become separated into different genera (Ryvarden 2002, Birkebak et al. 2013).

While the RPB, mtSSU, LSU, SSU regions were found to be reliable molecular markers on genus level, and also ITS on species level, the *Tef1 α* gene was indicated to constitute a paralogous region for *Pseudotomentella* and possibly beyond (Papers I and V). The latter is a well-studied genetic region that has proven to be a qualitative molecular marker for many other groups of fungi (Roger et al. 1999, Stielow et al. 2015). This shows that the orthology of molecular markers should never be assumed and underscores the importance of including multiple genetic regions in phylogenies.

The use of additional DNA regions would have been preferable for inferring the phylogenetic relationships studied, but the use of such was hampered by low amounts of DNA and the presence of contaminating compounds, effectively limiting sequencing options to Sanger. Whole genome sequencing was attempted but for the latter reason unsuccessful.

While priority in this thesis, given the time-frame, was given to descriptive taxonomy and systematics rather than molecular methodology, this or similar options should indeed be explored in more depth in order to further improve the accuracy of the field.

The probably most important implication of the close relationship between species with stipitate and corticioid basidiomata is for conservation; the stipitate *Polyozellus* species are considered to be rare and restricted to old growth, coniferous forest. Current knowledge for the corticioid members of the genus (previously *Pseudotomentella*) is poorer, but based on data from Paper I a number of them are now Red Listed as DD in Sweden, since they too seem to be rare and restricted to old growth forest, in their case on ground with higher pH (SLU Artdatabanken 2020), but sufficient data to list them in other categories is not yet available. It is not unreasonable to believe that this situation may exist also for other genera in Telephorales and that among the masses of currently undescribed, corticioid species a considerable amount may be of conservation concern.

CONCLUSIONS AND OUTLOOK

This thesis has made a minuscule dent in the enormous mountain of undescribed species that currently constitutes the order Thelephorales. It has demonstrated that such is possible in the face of small morphological differences and plenty of old names, as well as laid the ground for further taxonomic and systematic work in terms of morphological and ecological methodology and molecular markers. It has shown that circumscriptions of genera based on morphology cannot be taken for granted and may need reevaluation, even when previously based on such striking differences as the separation of stipitate and corticoid basidiomata. Consequently, the extinction threat previously documented for stipitate species is likely not restricted to such, which is also tentatively shown. Given this incitement, it is hoped and believed that the work put down in this thesis will facilitate the description and amendment of many future Thelephorales taxa.

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