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Front cover
Hemileucoglossum pusillum
Photo: P. Fadnes

Kjære leser,

Det har vært et spesielt år, også i Agarica-sammenheng, med to flotte spesialvolum , volum 40 og 41, og det har formelig rent inn manus til vol 42.

Det er selvfølgelig overveiende positivt med mange manus, men vi fikk mange manus omtrent samtidig, sent oktober til tidlig desember, og fikk litt kapasitetsproblemer. Kanskje er 12-måneders intervall for Agarica for langt? Vi får la tilgang på manus styre når vi trykker, men benytter her anledningen til å oppfordre dere til å sende inn manus når som helst på året. Får vi inn mange manus tidlig på året, kan vi sette strek for inntak for ett volum og utgi dette, samtidig som vi fortsetter arbeidet med å ta inn manus og bygge opp det neste.

Vi har fått inn mange gode bidrag fra både nye, for oss, og mer erfarne forfattere, og ønsker nye bidragsytere i Agarica velkommen. Manus i vol. 42 spenner fra beskrivelse av enkeltfunn nye for Norge til en større gjennomgang av en hel slekt, slik som artikkelen om reddiksopper i Norge. Nybeskrivelser i Agarica er muligens en ny trend, som gjenspeiles i antallet artikler i dette nummeret. Takk til alle bidragsytere til dette særdeles fyldige vol. 42!

Vi ønsker også å benytte anledningen til igjen å takke Edvin Johansen og Per Vetlesen for spesialvolumet om slimsopp (Agarica 40: *Special issue on slime moulds (myxomycetes) in Norway)* og Trond Schumacher for spesialvolumet om Pezizomyceter (Agarica 41: *Special issue on Pezizomycetes in Grimsdalen)*. Vi i redaksjonen har ikke drevet frem disse spesialvolumene. De er blitt til etter mange års arbeid av forfatterne, men er gjerne blitt diskutert med oss i redaksjonen flere år før de var klare for trykking. Hva vil det neste spesialvolumet omhandle mon tro?

Oslo, 7. april 2021

Ella Thoen & Anders K. Wollan

Dear reader,

It has been a special year, also in the Agarica context, with two great special volumes, volume 40 and 41, and we have received plenty of manuscripts for vol. 42.

It is of course predominantly positive with many manuscripts, but we received most of them at about the same time, late October to early December, and had some capacity problems. Maybe the 12-month interval for Agarica is too long? We let the influx of manuscripts decide when to publish a volume, and will use this opportunity to encourage you to submit manuscripts at any time of the year. If we receive many manuscripts early in the year, we can draw a line for intake for one volume and publish this, at the same time as we continue to receive new manuscripts and work on the next volume.

We have received many excellent contributions from, for us, both new and more experienced authors, and welcome new contributors to Agarica. The manuscripts in vol 42. ranges from description of finds new to Norway to a larger review of an entire genus, such as the article on *Hebeloma* in Norway. Publishing descriptions of new species in Agarica is possibly a new trend, which is reflected in the number of articles in this issue. Thanks to all the contributors to this particularly voluminous vol. 42!

We would also like to take this opportunity to thank Edvin Johansen and Per Vetlesen once again for the special volume on slime molds (Agarica 40: *Special issue on slime molds (myxomycetes) in Norway)* and Trond Schumacher for the special volume on Pezizomycetes (Agarica 41: *Special issue on Pezizomycetes in Grimsdalen)*. We in the editorial staff have not played an important part for these special volumes. They are the results of many years of work by the authors, and they have discussed with us in the editorial board several years before they were ready for printing. What will be the topic for the next special volume, we wonder?

Hebeloma of Norway

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Norsk tittel: *Hebeloma* i Norge

Ursula Eberhardt, Øyvind Weholt, Morten Pettersen, Nicole Schütz, Henry J. Beker *Hebeloma* of Norge. Agarica 2021 vol. 42: 3-29

KEYWORDS
Agaricales; Basidiomycota; ectomycorrhizal fungi; boreal woodland

NØKKELORD
Agaricales; Basidiomycota; sopp med ektomykorrhiza; boreal skog

SAMMENDRAG
Hebeloma er hattsopper med ektomycorrhiza, vanlige i skog og arktisk-alpine habitater på den nordlige halvkule. Inntil nylig var bestemmelse av arter innen denne slekten enormt vanskelig på grunn av manglende klarhet om artsavgrensning, og navnene som ble brukt på funn, observasjoner og sekvenser var svært upålitelige. Basert på nylige revisjoner, inkludert morfologiske og molekylære teknikker, er 85 arter av *Hebeloma* nå bekreftet i Europa. I denne gjennomgangen er det blitt analysert 296 herbariekollekter av *Hebeloma* fra Norge, og det er utarbeidet en sjekkliste for Norge som bekrefter tilstedeværelsen av 49 *Hebeloma*-arter. Denne listen er sammenlignet med eksisterende lister for Norge fra Norsk mykologisk database (NMD) og Global Biodiversity Information Facility (GBIF). De 36 *Hebeloma*-artene i disse listene som vi ikke har kunnet bekrefte for Norge, blir diskutert og gitt en kommentar med hensyn til deres sannsynlige eksistens i landet i forhold til Norges nordlige beliggenhet.

ABSTRACT
Hebeloma are ectomycorrhizal fungi, common in woodlands and arctic-alpine habitats of the northern hemisphere. Until recently determination of species within this genus was hugely difficult due to the lack of clarity on species delimitation and thus names applied to collections, observations and sequences were highly unreliable. Based on recent revisions, including morphological and molecular techniques, 85[1] species of *Hebeloma* are now confirmed within Europe. In this review 296 vouchered records of *Hebeloma* from Norway have been analysed and a check-list has been generated for Norway, confirming the

1 "Note added in proof: L.C. Monedero and P. Alvarado recently described an additional new species and section from Spain, *Hebeloma adherens, H.* sect. *Adherentia*, in YESCA 32: 56-67 (2020)."

presence of 49 species of *Hebeloma.* This list is compared to existing lists for Norway from the Norwegian Mycological Database (NMD) and the global biodiversity information facility (GBIF). The 36 *Hebeloma* species not currently confirmed for Norway are discussed and acommentary provided, with regard to those which might exist within the country, and those for which Norway is beyond their current northern limits.

INTRODUCTION

Hebeloma is a genus of ectomycorrhizal fungi that is well represented in a wide range of different habitats, including temperate and boreal woodlands, and is particularly common in arctic and alpine environments (Beker et al. 2016). Its members associate with a wide variety of host trees and are often encountered in disturbed habitats. Mainland Norway that is located on the Scandinavian Peninsula, exhibiting a long latitudinal extension ranging from almost 58°N to just over 71°N, has many diverse habitats. Consequently, this territory is likely to house *Hebeloma* species with a number of different ecologies and distribution patterns. Svalbard, also part of Norway, was excluded from this study; the *Hebeloma* of Svalbard were discussed in detail in Beker et al. (2018).

The aim of this project is to review the occurrence of *Hebeloma* in mainland Norway and to provide an up-to-date check list of the species of *Hebeloma* that we have confirmed as growing in the country. By "confirmed", we mean that a voucher exists in a recognized herbarium and that the material has been (re-)identified using modern species concepts. This check list is compared with the lists of species generated by the Norwegian Mycological Database (NMD) and the Global Biodiversity Information Facility (GBIF). The review also addresses those species not yet confirmed to occur in Norway in order to assess whether they are to be expected to exist in Norway or whether Norway is beyond their current northern limits.

Hebeloma collections are usually correctly identified as *Hebeloma* but regarded as difficult to determine to species level. A huge part of the problem was the lack of definition of species limits, and, as a consequence, different interpretations of species and unreliable naming of collections, observations and sequences. Different authors had different species concepts resulting in the publication of contradictory species descriptions. The molecular analyses that existed were confusing as it appeared that every clade could contain every species and every species might come up in several different clades!

In May 2016, Beker, Eberhardt and Vesterholt published a monograph on the genus *Hebeloma* in Europe which used both morphological and molecular techniques. The monograph was based on the study of all the European names that had been published and all the type material that could be located. Following the exclusion of names that could not be interpreted and the synonymy of species names that were shown to be conspecific, 84 species of *Hebeloma* were described that were known to occur in Europe. In Grilli et al. (2020) one more species was added to that list, bringing the total number of species recorded in Europe to 85.

Determining the *Hebeloma* section

For the sake of consistency, the following paragraphs and keys are taken almost unchanged from this monograph (Beker et al., 2016) and from Beker et al. (2017). While keys to the individual species, known to occur in Norway, could have been included here, by adapting the keys in Beker et al. (2016), there is little to gain and much to lose as a number of the species, for which no confirmed Norwegian records yet exist, might well occur in Norway. Instead, we discuss below both the species now confirmed to exist

in Norway as well as those not yet recorded in Norway.

The determination of *Hebeloma* spp. is difficult, not only morphologically but also in many cases molecularly. There are several possible reasons for this, for example: recent speciation, morphological stasis after speciation, morphological plasticity within species, reticulate evolution or incomplete lineage sorting. Whatever the reason, it is true that a number of species are macroscopically similar and even enjoy the same habitats. It is not unusual to find '*Hebeloma* hotspots' where several different species may be growing together. Despite this difficulty, many *Hebeloma* species can be recognised in the field, with reasonable certainty; examples, which occur in Norway, include: *H. incarnatulum, H. laterinum, H. pusillum, H. radicosum* and *H. sinapizans.*

The first step to identify a *Hebeloma* is to determine the section to which it belongs. With a small amount of microscopy, and a certain amount of experience, this is relatively straightforward. Determination at this level depends on just a few characters: smell, number of full-length lamellae (lamellae reaching from the edge of the stipe to the edge of the pileus), habitat, whether there are remnants of a veil, the shape and dextrinoidity of the spores and the shape of the cheilocystidia.

The '*Hebeloma sacchariolens* smell' is usually clearly identifiable and places the collection into *H.* sect. *Sacchariolentia*; a strong smell of marzipan places the collection in *H.* sect. *Myxocybe* (which in Europe has only the one species, *H. radicosum*). A raphanoid smell is common in *Hebeloma* and does rule out certain sections like *H.* sect. *Naviculospora* and *H.* sect. *Scabrispora*; a raphanoid smell plus the remains of a cortina do imply *H.* sect. *Hebeloma*. Similarly, the presence of a cortina and ventricose (lageniform) cheilocystidia also implies the collection belongs to *H.* sect. *Hebeloma*.

The number of full-length lamellae is a very useful character. If the number of full-length lamellae is at least 80 and the spores are strongly dextrinoid then the species belongs to *H.* sect. *Sinapizantia*. The habitat can provide many clues. For example, if the collection is from burnt ground and the spores are strongly dextrinoid and very small (at most 10 × 6 µm) and most of the cheilocystidia are swollen at the base and the apex (clavate-ventricose), then the collection is from *H.* sect. *Pseudoamarescens* (which in Europe has only one species, *H. pseudoamarescens*).

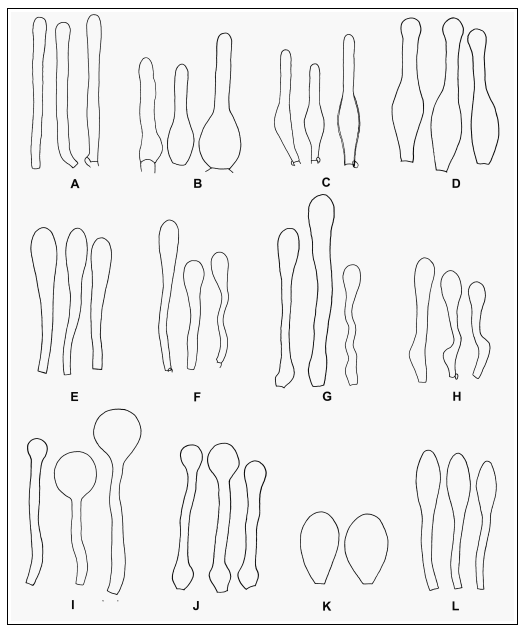

Figure 1. Shape of cystidia. **A**. Cylindrical. **B**. Lageniform. **C**. Ventricose. **D**. Ventricose or lageniform with capitate or clavate apex (tibiiform, usually indistinguishable from capitate-ventricose, capitate-lageniform, clavate-ventricose, clavate-lageniform; see also **H**). **E**. Gently clavate. **F**. Clavate-stipitate. G. Clavate-stipitate with widened base. **H**. Clavate-ventricose (clavate-lageniform, hourglass). **I**. Capitate-stipitate. **J**. Capitate-stipitate with widened base. **K**. Broadly clavate (balloon shaped, particularly when stipitate it resembles a balloon on a string). **L**. Spathulate-stipitate. Drawing J. Vesterholt.

If none of the above characters have already led to a specific section, then it is necessary to

look at the shape of the cheilocystidia (Fig. 1). If the shape of most of the cheilocystidia is cylindrical then the specimen belongs in either *H.* sect. *Naviculospora* or *H.* sect. *Scabrispora*. Members of the latter section have a tendency to root and the cheilocystidia can be very rudimentary. For the former section, the cheilocystidia are more distinct and can be rather irregular. If the cheilocystidia are gently clavate at the apex and tapering towards the base or the cheilocystidia are ventricose and the spores are strongly dextrinoid then the specimen belongs to *H.* sect. *Velutipes*. If the cheilocystidia are clavate-ventricose but very short (on average less than 40 µm) then the collection belongs to *H.* sect. *Theobromina*. And finally, if the cheilocystidia are not so short and are relatively abruptly clavate or capitate at the apex and either tapering towards the base (clavate-stipitate) or swollen towards the base (clavate-ventricose) then the collection belongs to *H.* sect. *Denudata*, which is the largest section of *Hebeloma*, at least in Europe, with one third of the species. This discussion is expressed more formally in the key below.

Key to *Hebeloma* sections

The key, essentially reproduced from Beker et al. (2016), includes all sections of *Hebeloma*, that are known to occur in Europe.

An important character in the genus, is the evaluation of the dextrinoidity of the spores (Vesterholt, 2005). The colour of the endospore mounted in Melzer's reagent is observed after 1–2 minutes or more in mature and undamaged spores floating at a distance from the hymenium. Spores on or near the lamellar tissue usually show a less distinct dextrinoid reaction or none at all. Often it is necessary to use exsiccates or spore deposits for the examination. In a few cases, it has been observed that the dextrinoid reaction can be stronger when studied from fresh material. Crushed or immature spores often show a stronger reaction and they should therefore be ignored. The apex of the spores is typically almost indextrinoid and this often gives the dextrinoid spores a bicoloured appearance in Melzer's reagent. All mature and normally developed spores within a preparation show almost the same colour in Melzer's reagent. In some cases, the spores are completely indextrinoid, in other cases a deep red-brown colour develops. However, intermediate reactions are frequent and therefore, a scale from 0 to 4 has been used in order to quantify this character (Fig. 2):

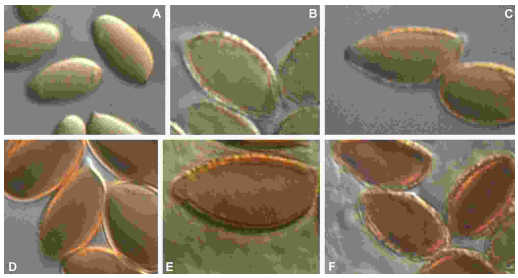

Figure 2. Examples of spore dextrinoidity in *Hebeloma*. **A**. *H. mesophaeum* (HJB12794) D0. **B**. *H. geminatum* (HJB11801) D1. **C**. *H. fragilipes* (HJB11737) D2. **D**. *H. velutipes* (HJB11951) D3. **E**. *H. nauseosum* (HJB10848) D3,D4. **F**. *H. birrus* (HJB11830) D4. Photos H.J. Beker, assembled 2016.

D0: spores completely indextrinoid
D1: spores with an indistinct brownish tint in Melzer's reagent
D2: spores weakly but distinctly dextrinoid, becoming pale brown
D3: spores rather strongly dextrinoid, becoming medium brown
D4: spores strongly dextrinoid, immediately becoming deep and intensely red-brown

MATERIALS AND METHODS

The set of 296 collections studied consists of specimens collected by the authors (particularly MP and ØW) and loans from herbaria (particularly O and TROM; herbarium abbreviations follow Index Herbariorum, Thiers

The key

1a Lamellae with distinct pinkish tinge, fresh spore deposit with distinct reddish hues ..... **sect. *Porphyrospora* (*H. porphyrosporum*)**

1b Lamellae without a pinkish tinge, spore deposit Isabella or brownish olive or umber to sepia or whitish **2**

2a Basidiomes with very sweet smell, the '*Hebeloma sacchariolens* smell' .....**sect. *Sacchariolentia***

2b Basidiomes without strong distinctive sweet smell **3**

3a Growing on burnt ground with spores strongly dextrinoid on ave. ≤ 10.0 × 6.0 µm and ave. cheilocystidium ratio basal width/median width ≥ 1.25 ..... **sect. *Pseudoamarescens* (*H. pseudoamarescens*)**

3b Not growing on burnt ground or if on burnt ground then not satisfying all other conditions **4**

4a Basidiomes with cortina (sometimes persistent, sometimes fugacious), most cheilocystidia distinctly ventricose .....**sect. *Hebeloma***

4b Basidiomes without cortina or if cortina present then most cheilocystidia not ventricose **5**

5a With any of the following distinctive features: i) basidiomes rooting; ii) membranous annulus; iii) cylindrically shaped spores; iv) pruinose pileus and growing with *Cistaceae*; v) most cheilocystidia more or less cylindrical; vi) cheilocystidia very irregular in shape; vii) cheilocystidia with ave. length less than 40 µm **6**

5b With none of the above distinctive features; cheilocystidia normally consistently gently clavate or clavate-stipitate or clavate-ventricose or ventricose or a mixture of these shapes **7**

6a With any of the following distinctive features and not associated with *Cistus*: i) basidiomes rooting; ii) membranous annulus; iii) cylindrically shaped spores; iv) most cheilocystidia more or less cylindrical; v) cheilocystidia very irregular in shape.....**sects. *Duracinus*, *Myxocybe*, *Naviculospora*, *Scabrispora* & *Syrjense***

6b With none of the above distinctive features; cheilocystidia distinctly clavate-ventricose and either ave. length ≤ 40 µm or associated with *Cistaceae*..... .....**sect. *Theobromina***

7a Most cheilocystidia gently clavate or ventricose or number of full-length lamellae (L) at least 80 and spores strongly dextrinoid (D3 or D4)..... .....**sects. *Sinapizantia* & *Velutipes***

7b Most cheilocystidia clavate-stipitate or clavate-ventricose, if number of full-length lamellae (L) at least 80 then spores at most weakly dextrinoid (at most D2) ....**sect. *Denudata***

2016 [continuously updated]). Only material from mainland Norway was considered.

Further, the Norwegian Mycological Database (NMD, Larsson et al. 2010) and the Global Biodiversity Information Facility (GBIF) were accessed to obtain lists of *Hebeloma* records from mainland Norway. In the case of the NMD, this list refers to records of fungal collections from the herbaria at O (Oslo), BG (Bergen), TRH (Trondheim), TROM (Tromsø) and NFRI (Norwegian Forest and Landscape Institute, NIBIO). It is acknowledged that not all information from these herbaria is yet digitised so the information obtained may

underestimate the number of *Hebeloma* collections in these herbaria. For GBIF, our focus is on the records of observations, normally not supported by voucher material in public collections. Sequence databases UNITE (Kõljalg et al. 2013) and NCBI (GenBank) through PlutoF (Abarenkov et al. 2010) were searched for *Hebeloma* records of species from mainland Norway that likely represent taxa not yet confirmed here.

For those collections examined, that were obtained when still fresh, in situ photographs were usually obtained and full macroscopic descriptions. For the herbarium loans, the level of information, accompanying the collections, was hugely variable. Photographs and macroscopic descriptions were often unavailable and some parameters (e.g. number of full-length lamellae) had to be estimated from the exsiccata. For the great majority of the 296 collections, ITS sequence data (barcodes) were generated to assist species identification. In rare cases data from other loci were used to confirm identifications.

Data processing in the *Hebeloma* project database follows Beker et al. (2016), using Biolomics version 12 (Bioaware SA NV, Hannut, Belgium), a commercially available database system catering for natural history collections. At the time of writing there are data from almost 10 000 collections of *Hebeloma* on the database, collected mainly in Europe and North America, including types. It also includes the 296 collections from Norway.

As described in detail by Beker et al. (2016), all collections are entered on the database where, as well as the collection details, their morphological description (as far as it is available) is held as a number of parameters describing the collection both macroscopically and microscopically.

In short, to address the morphology, given the similarity of many species, a set of parameters was developed that could describe a *Hebeloma*, both macroscopically and microscopically. The description of any collection could then be registered on the database. This enables the collections to be searched based on any set of parameters. Thus, for example, collections with similar properties may be clustered, the parameters of collections that fall into the same phylogenetic clades may be compared, keys may be built, as queries on the database, which are continually tested against all the database collections. The parameters used have been refined from the character set that various authors (for example Bruchet 1970, Romagnesi 1965, 1983, Favre 1955, 1960, Boekhout 1982, Smith et al. 1983, Vesterholt 1995), had developed over a period of years. Details of morphological analyses were provided in Beker et al. (2016). These characters include, but are not restricted to, pileus and stipe measures, number of full-length lamellae, presence or absence of cortina and universal veil, spore measures, including Q value and other spore characters (perispore loosening, ornamentation and dextrinoidity) as well as cheilocystidia shape, defined by length and width (apex, median and base) and the corresponding ratios.

Species identification follows Beker et al. (2016), Cripps et al. (2019) and Grilli et al. (2020). Beker et al. (2016) lists 84 species of *Hebeloma* known to occur in Europe; Grilli et al. (2020) added another one, *H. alpinicola*, described in detail by Cripps et al. (2019). Barcode identification is achieved through BLAST (Basic Local Alignment Search Tool) searches against the *Hebeloma* sequence project database (*i.e.* sequences of collections in the *Hebeloma* project database, see Beker et al. 2016), using the standalone version of the Basic Local Alignment Search Tool (BLAST+), version 2.9.0 (NCBI, Bethesda). All taxa with at least some sequences with at most 0.5% (1%) p-distance difference to a query sequence are considered. This corresponds to at most 4 (7) positions with unambiguous transitions or transversions in a

pairwise alignment of *Hebeloma* full length ITS sequences. Doubts on species identity left after sequence analysis are resolved by morphology and vice versa. Ecology and habitat are also considered for achieving species determination.

RESULTS

Table 1 lists the 49 species for which we have confirmed Norwegian material among the 296 collections examined. These species fall into the (sub)sections shown in Table 1. Here are also numbers of records for each species given and a herbarium reference for one of the verified records. The distribution of these collections is illustrated in Fig. 3.

According to the Norwegian Mycological Database (NMD, accessed on 31 July 2020) there are 871 *Hebeloma* collections in these herbaria, as shown in Table 2, representing 40 named species. Table 2 is turned into Table 3 by (a) renaming those species that have been synonymised with one of the 85 recognised species, and (b) removing those collections that were named as "sp." and (c) removing those names that were deemed not possible to interpret by Beker et al. (2016). Table 3 includes 686 collections and 33 species. The NMD data have four species listed which are not included in Table 1, *i.e.* have not been

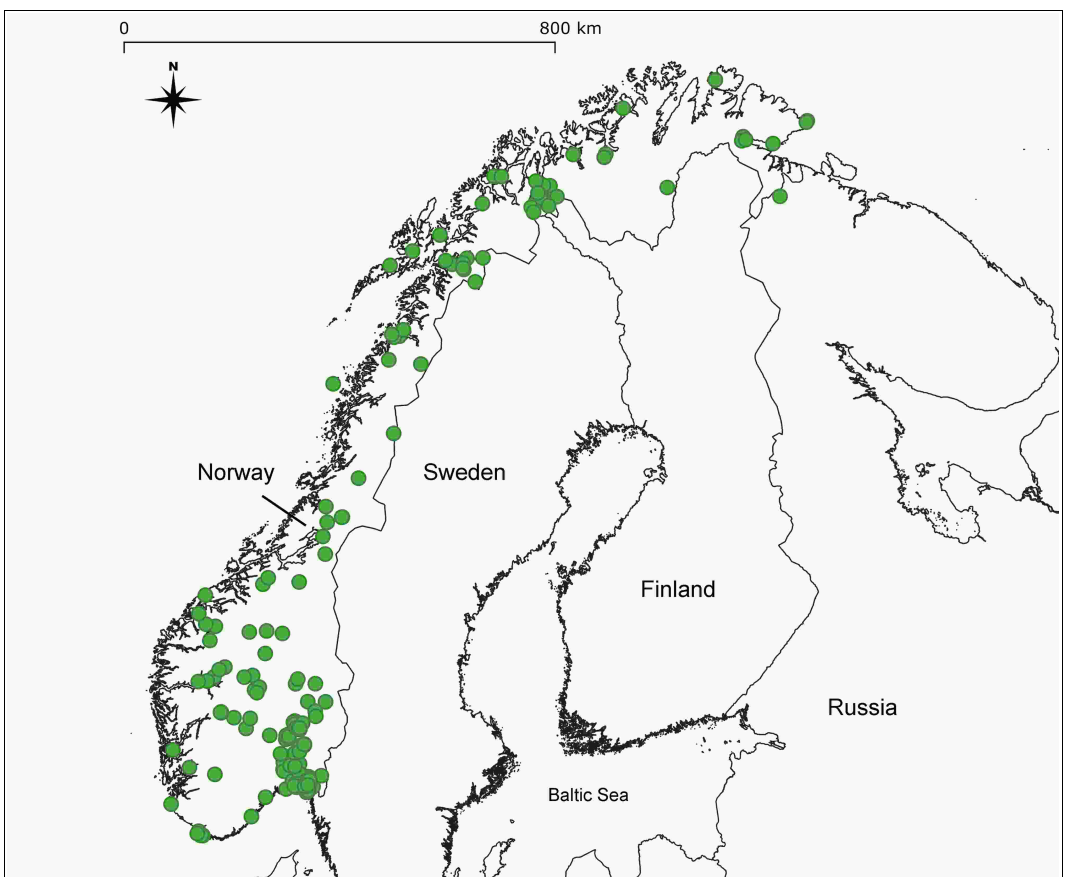

Figure 3. Collection sites of the 296 Norwegian *Hebeloma* collections on the *Hebeloma* project database. The map was compiled with QGIS v. 3.14.16 'Pi', WGS84/World Mercator, EPSG:3395, using shapefiles from www.gadm.org.

Table 1. List of species of *Hebeloma* from the *Hebeloma* project database, with one example each of a verified record from Norway given, referred to by the accession code of public collection. # – number of records in the *Hebeloma* project database. Species are listed by (sub)section.

Species	#	Herb. Ref.
Denudata – Crustuliniformia		
H. aanenii	12	O-F-70069
H. alpinum	9	O-F-154650
H. aurantioumbrinum	2	IB 19980462
H. eburneum	1	O-F-256942
H. geminatum	14	TROM-F-17325
H. helodes	9	O-F-248325
H. lutense	1	O-F-256945
H. pusillum	2	O-F-168159
H. salicicola	2	O-F-253108
Denudata – Clepsydroida		
H. cavipes	11	O-F-256949
H. fragilipes	2	O-F-256943
H. ingratum	1	TROM-F-4752
H. pseudofragilipes	13	O-F-249615
H. vaccinum	4	O-F-253033
Denudata – Echinospora		
H. rostratum	1	O-F-256948
Denudata – Hiemalia		
H. hiemale	30	O-F-253102
Hebeloma (non-dextrinoid spores)		
H. alpinicola	10	TROM-F-26579
H. dunense	8	O-F-252381
H. marginatulum	6	O-F-73832
H. mesophaeum	6	TROM-F-8958
H. subtortum	1	O-F-256948
Hebeloma – (dextrinoid spores)		
H. clavulipes	2	O-F-154758
H. hygrophilum	1	TROM-F-16849
H. monticola	16	O-F-75306
H. nigellum	7	O-F-304988
H. oreophilum	1	O-F-256947
H. sordescens	10	O-F-254041
H. spetsbergense	1	O-F-154755
Myxocybe		
H. radicosum	1	O-F-305051
Naviculospora		
H. islandicum	2	O-F-73849
H. nanum	1	TRH-F-21146
Pseudoamarescens		
H. pseudoamarescens	1	O-F-304836
Sinapizantia		
H. sinapizans	3	O-F-253839
Sacchariolentia		
H. fusisporum	6	O-F-251542
H. ischnostylum	3	O-F-256944
H. nauseosum	1	O-F-256946
H. odoratissimum	1	O-F-340667
H. sacchariolens	4	O-F-253852
Theobromina		
H. theobrominum	3	O-F-75223
Scabrispora		
H. birrus	6	O-F-254038
H. circinans	9	O-F-75302
H. laterinum	3	O-F-248253
H. pumilum	2	O-F-70583
Scabrispora		
H. syrjense	3	O-F-248508
Velutipes		
H. celatum	6	O-F-248534
H. incarnatulum	9	TROM-F-31436
H. leucosarx	15	TROM-F-26556
H. subconcolor	1	O-F-154867
H. velutipes	33	O-F-252921
Total	296	

Table 2. List of Norwegian *Hebeloma* records by herbarium according to Norwegian Mycological database (NMD, accessed 31 July 2020).

Species	O	BG	TRH	TROM	NIBIO	Totals
H. alpinum	16			4		20
H. birrus	18	1	1	3	1	24
H. candidipes			1			1
H. cavipes	1					1
H. circinans	14		5	2		21
H. clavulipes	1					1
H. collariatum	23					23
H. crustuliniforme	72	1	8	37	1	119
H. cylindrosporum			1			1
H. dunense	1					1
H. fastibile	2		1	1		4
H. fragilipes	2					2
H. fusisporum	1					1
H. helodes	1					1
H. hetieri	1					1
H. hiemale	4		4			8
H. incarnatulum	3		2	1		6
H. laterinum	20		11	1		32
H. longicaudum	14	1	3	42		60
H. marginatulum	6			2		8
H. mesophaeum	118	1	7	36	3	165
H. minus	2					2
H. monticola	11			1		12
H. nigellum	13		3			16
H. perpallidum	1					1
H. polare	6					6
H. populinum	1					1
H. pseudoamarescens	1		2	5		8
H. punctatum				1		1
H. pusillum	21		4	9		34
H. radicosum	8	1				9
H. sacchariolens	27		1			28
H. sarcophyllum	1					1
H. sinapizans	32		3	2		37
H. sordescens	16		3	1		20
H. subconcolor	1					1
H. syrjense	7		2			9
H. theobrominum	21		1			22
H. velutipes	41				2	43
H. versipelle			1	1		2
Hebeloma sp.	75	7	8	28		118
Totals	**603**	**12**	**72**	**177**	**7**	**871**

verified during this study; they are marked with an * in Table 3 and will be discussed further below.

The Global Biodiversity Information Facility (GBIF.org, accessed 14 Sept. 2020) also provides information with regard to records of *Hebeloma* in Norway. Table 4 summarises those collections which are unvouchered observations. Table 4 lists the species names encountered, followed by the number of records. Table 5 is generated from the renaming of those names synonymised and the removal of those not unambiguously interpretable; this has 1054 records and 28 species. Table 5 includes just one species which is not included within the check list generated by this study (Table 1), namely *H. crustuliniforme*. Additionally, GBIF lists two further species for Norway that are not included in the NMD database and are not included in our check list: *H. anthracophilum* with a voucher at BG and *H. quercetorum* with an extracted DNA sample in the NHMO DNA Bank at the Natural History Museum in Oslo and a voucher at the herbarium (O).

As mentioned above, the NMD data had four species listed which are not included in Table 1, *i.e.* have not been verified during this study and on GBIF we found three species not verified during this study, one of which overlapped with the NMD data. These six species are: *H. anthracophilum*, *H. crustuliniforme*, *H. minus*, *H. populinum*, *H. quercetorum* and *H. sarcophyllum*, and will be discussed below.

Table 3. List of Norwegian *Hebeloma* records by herbarium according to Norwegian Mycological database (NMD, accessed 31 July 2020) after removal of dubious names and applying synonyms. * indicates species that have not been verified within this study.

Species	O	BG	TRH	TROM	NIBIO
H. alpinum	16			4	
H. birrus	18	1	1	3	1
H. cavipes	1				
H. circinans	14		5	2	
H. clavulipes	1		1		
*H. crustuliniforme**	72	1	8	37	1
H. cylindrosporum			1		
H. dunense	24				
H. eburneum	1				
H. fragilipes	2				
H. fusisporum	1				
H. helodes	1				
H. hiemale	4		4		
H. incarnatulum	3		2	1	
H. laterinum	20		11	1	
H. marginatulum	12			2	
H. mesophaeum	118	1	7	36	3
*H. minus**	2				
H. monticola	11			1	
H. nigellum	13		3		
H. odoratissimum	1				
*H. populinum**	1				
H. pseudoamarescens	1		2	5	
H. pusillum	21		4	9	
H. radicosum	8	1			
H. sacchariolens	27		1		
*H. sarcophyllum**	1				
H. sinapizans	32		3	2	
H. sordescens	16		3	1	
H. subconcolor	1				
H. syrjense	7		2		
H. theobrominum	21		1		
H. velutipes	41				2
Totals	**512**	**4**	**59**	**104**	**7**

Table 4. List of Norwegian *Hebeloma* observation records according to Global Biodiversity Information Facility (GBIF.org (14 September 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.e62j64).

Species	# Records	Species	# Records
H. alpinum	9	*H. marginatulum*	1
H. birrus	14	*H. mesophaeum*	215
H. cavipes	5	*H. monticola*	5
H. circinans	20	*H. nigellum*	10
H. collariatum	1	*H. pseudoamarescens*	1
H. crustuliniforme	346	*H. pseudofragilipes*	5
H. dunense	2	*H. pusillum*	12
H. fragilipes	1	*H. radicosum*	7
H. fusisporum	1	*H. saccharіolens*	21
H. geminatum	2	*H. sinapizans*	108
H. gigaspermum	1	*H. sordescens*	8
H. helodes	8	*H. syrjense*	3
H. hiemale	20	*H. theobrominum*	36
H. incarnatulum	43	*Hebeloma* sp.	76
H. laterinum	88		
H. leucosarx	61	**Total**	**1130**

Table 6 lists in order of frequency the 15 species with most records on the NMD database, the GBIF observations database and the *Hebeloma* project data, respectively.

UNITE and GenBank include 23 ITS sequences from mainland Norway that refer to material we have not seen. Of these, two did not produce clear BLAST results owing to quality reasons. The remaining sequences were not unambiguously identifiable based on the sequences alone, but all had matches with species that are confirmed for Norway.

DISCUSSION

Species confirmed for Norway

Given the huge disagreement with regard to species interpretations and limits in the past, we believe that, at this point, it is better to depend on records that have been verified according to the species delimitations established in Beker et al. (2016) rather than risk misinformation through using records where the determiner may have had a different species concept in mind. Thus, here we list only species that have been confirmed by us. Full descriptions of 48 species confirmed for Norway can be found in Beker et al. (2016). Descriptions of *H. alpinicola* can be found in Cripps et al. (2019) and Grilli et al. (2020).

There are sixteen species from *Hebeloma* sect. *Denudata*, confirmed in Norway. Determination of the correct subsection is based on the properties of the spores and the cheilocystidia (for full descriptions and a dichotomous key, see Beker et al. 2016).

Strongly ornamented, very dextrinoid spores, with the perispore loosening around almost every spore, indicates the species is from *H.* subsect. *Echinospora,* named to emphasise the very warty spores that characterise this section. To date, the only species from this subsection that has been verified within Norway is *H. rostratum*. The only confusion might occur with *H. vaccinum,* the

Table 5. List of Norwegian *Hebeloma* observation records according to Global Biodiversity Information Facility (GBIF.org (14 September 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.e62j64) after removal of dubious names and applying synonyms following Beker et al. (2016). * indicates species that have not been verified within this study.

Species	# Records	Species	# Records
H. alpinum	9	*H. mesophaeum*	215
H. birrus	14	*H. monticola*	5
H. cavipes	5	*H. nauseosum*	1
H. circinans	20	*H. nigellum*	10
*H. crustuliniforme**	346	*H. pseudoamarescens*	1
H. dunense	3	*H. pseudofragilipes*	5
H. fragilipes	1	*H. pusillum*	12
H. fusisporum	1	*H. radicosum*	7
H. geminatum	2	*H. sacchariolens*	21
H. helodes	8	*H. sinapizans*	108
H. hiemale	20	*H. sordescens*	8
H. incarnatulum	43	*H. syrjense*	3
H. laterinum	88	*H. theobrominum*	36
H. leucosarx	61		
H. marginatulum	1	**Total**	**1054**

spores of which are also rather dextrinoid but not as strongly warty as those of members of *H.* subsect. *Echinospora.* In addition, in *H. vaccinum*, although some spores do have a clearly and strongly loosening perispore, this does not occur on almost all spores.

Hebeloma subsect. *Crustuliniformia* is characterised by the cheilocystidia that are clavate to capitate at the apex but little swollen in their basal part. This subsection has nine confirmed species in Norway. Four of these (*H. aanenii, H. alpinum, H. eburneum, H. geminatum*) are representatives of the alpinum-complex, a set of five species molecularly very closely related. *Hebeloma aurantioumbrinum* and *H. helodes* are also closely related species. *Hebeloma aurantioumbrinum* is restricted to alpine and arctic regions. The two are easily distinguished, macroscopically by the colour of the pileus (orange-brown for *H. aurantioumbrinum* and pale cream to whitish for *H. helodes*) and microscopically by the conspicuous wall thickening of the apex of the cheilocystidia in *H. helodes*, which is absent for *H. aurantioumbrinum. Hebeloma lutense, H. pusillum* and *H. salicicola,* all appear to be confined to *Salicaceae* as ectomycorrhizal partner. *Hebeloma lutense* has a bicoloured pileus, significantly darker in the centre and characteristic sinuous cheilocystidia with a rather narrow apex. *Hebeloma pusillum* is also bicoloured but has far smaller basidiomes. The only confusion may be with *H. luteicystidiatum,* not yet recorded for Norway. *Hebeloma salicicola,* also bicoloured, is most common in dunes and arctic habitats.

Hebeloma subsects. *Hiemalia* and *Clepsydroida* both have cheilocystidia that are clearly and consistently swollen in their basal part. In Norway, five members of *H.* subsect. *Clepsydroida* are confirmed. *Hebeloma cavipes* and *H. vaccinum* are molecularly very close,

Table 6. The 15 most frequently recorded *Hebeloma* species in Norway according to NMD, GBIF.org and the *Hebeloma* project Database, the number of records (#) and percentages of total number of records in the respective dataset (%).

NMD (686 collections)			**GBIF (1054 observations)**			***Hebeloma* project (296 collections)**		
Species	#	%	Species	#	%	Species	#	%
H. mesophaeum	165	24	*H. crustuliniforme*	346	33	*H. velutipes*	33	11
H. crustuliniforme	119	17	*H. mesophaeum*	215	20	*H. hiemale*	30	10
H. velutipes	43	6	*H. sinapizans*	108	10	*H. monticola*	16	5
H. sinapizans	37	5	*H. laterinum*	88	8	*H. leucosarx*	15	5
H. pusillum	34	5	*H. leucosarx*	61	6	*H. geminatum*	14	5
H. laterinum	32	5	*H. incarnatulum*	43	4	*H. pseudofragilipes*	13	4
H. sacchariolens	28	4	*H. theobrominum*	36	3	*H. aanenii*	12	4
H. birrus	24	3	*H. sacchariolens*	21	2	*H. cavipes*	11	4
H. dunense	24	3	*H. circinans*	20	2	*H. alpinicola*	10	3
H. theobrominum	22	3	*H. hiemale*	20	2	*H. sordescens*	10	3
H. circinans	14	3	*H. birrus*	14	1	*H. alpinum*	9	3
H. alpinum	16	3	*H. pusillum*	12	1	*H. circinans*	9	3
H. sordescens	16	3	*H. nigellum*	10	1	*H. helodes*	9	3
H. nigellum	13	2	*H. alpinum*	9	1	*H. incarnatulum*	9	3
H. marginatulum	12	2	*H. helodes*	8	1	*H. dunense*	8	3

indeed their ITS sequences are indistinguishable. But *H. vaccinum* normally has larger, less fusoid spores with a more conspicuous loosening perispore. *Tef1a* is the most consistent locus to separate these taxa (Beker et al. 2016, Eberhardt et al. 2016). *Hebeloma fragilipes*, *H. ingratum* and *H. pseudofragilipes,* all present in Norway, form the fragilipes-complex. *Hebeloma ingratum* is easily separated from the other two taxa with its distinctly coloured pileus and smaller spores. The separation of the other two taxa, both with very pale whitish to yellowish pilei, is rather more difficult. Generally, if the ratio of the average apical width of the cheilocystidia and the average basal width of the cheilocystidia is at least 1.4 this indicates *H. fragilipes;* the mitochondrial locus V6 will distinguish these two species reliably, (Beker et al. 2016, Eberhardt et al. 2016).

Hebeloma subsect. *Hiemalia*, with just one species (*H. hiemale,* present in Norway) has indextrinoid spores with low ornamentation and always has some brown or buff tones in the pileus.

With regard to the 33 species confirmed from Norway and outside *H.* sect. *Denudata*, *H.* sects. *Myxocybe, Pseudoamarescens, Sinapizantia, Syrjense* and *Theobromina* each contain just a single species, so determination to section is equivalent to determination to species.

Hebeloma sect. *Velutipes* has five representatives recorded so far in Norway. Four of

these species (*H. incarnatulum, H. leucosarx, H. subconcolor, H. velutipes)* belong to the velutipes-complex. *Hebeloma celatum,* also confirmed in Norway, is distinguished from the members of the velutipes-complex by having a far bigger proportion of ventricose cheilocystidia, resulting in a ratio of average basal width to average median width greater than 1.35 (always lower for members of the velutipes-complex). Within the velutipes-complex *H. subconcolor* is readily separable given its alpine/arctic habitat and the number of full-length lamellae, at most 32. *Hebeloma incarnatulum* is usually recognisable in the field, growing in association with conifers and usually deeply embedded in *Sphagnum* moss. Its slender appearance, an almost conical pileus and a bulbous base are good characters. Microscopically, the slender cheilocystidia with average width at the apex less than 6.5 µm, will distinguish this taxon from the other members of this complex. Separating *H. leucosarx* and *H. velutipes* is rather more difficult as microscopically they are very similar. However, macroscopically the slenderer appearance of *H. leucosarx* together with the much darker brown pileus usually allow these two taxa to be separated, even in the field.

Hebeloma sect. *Scabrispora* has four representatives known to exist in Norway. The strongly and consistently loosening perispore separates *H. birrus* and *H. pumilum* from *H. circinans* and *H. laterinum.* The first two can then be separated from each other on spore size. The *H. pumilum* average spore length is always less than 9 µm, while *H. birrus* has an average spore length between 9 µm and 11 µm (and *H. anthracophilum* which also has a consistently loosening perispore has average spore length at least 11 µm, not yet confirmed from Norway). *Hebeloma circinans* and *H. laterinum* may be separated by counting the number of full-length lamellae; the former never has more than 65, while the latter always has in excess of 65. *Hebeloma laterinum* also has a stipe that discolours strongly when bruised or dried.

There are two species from *H.* sect. *Naviculospora* confirmed in Norway: *H. islandicum* and *H. nanum.* Distinguishing these two species is straightforward. *Hebeloma nanum* is commonly found in boreal coniferous woodland, with sandy soil following a burn while *H. islandicum* grows in more arctic-alpine habitats, usually with *Salix*. Also, they have very different spores and cheilocystidia. At the time of the monograph by Beker et al. (2016), the authors had seen only a single collection of *H. islandicum.* Since that time a number of collections have been discovered, including these two from Norway.

Weholt (1985) provided a first overview of *H.* sect. *Sacchariolentia* in Norway. Based on modern species concepts, within Norway, there are verified records of all five recognised European members of the section (Beker et al. 2016). The key to these species is primarily based on spore size and detailed in Beker et al. (2016).

Vesterholt and Weholt (1985) gave an overview of the state of knowledge of *H.* sect. *Hebeloma* in Scandinavia at the time. Within the section there are now twelve species confirmed within Norway. These can be separated into two groups. The first group, containing *H. alpinicola, H. dunense, H. marginatulum, H. mesophaeum* and *H. subtortum,* all have mainly non-dextrinoid ellipsoid to ovoid spores. For three of these species (*H. alpinicola, H. mesophaeum* and *H. subtortum*) the average spore size is generally less than 10 x 6 µm. *Hebeloma subtortum* can be distinguished from the other two species as it always has more than 50 full-length lamellae, while the others never have that many lamellae. With regard to separating *H. mesophaeum* and *H. alpinicola* the situation is more difficult. *Hebeloma alpinicola* was described by Smith et al. (1983) from northern America. This

species appears relatively common in subalpine and subarctic habitats as well as arctic and alpine habitats. It was only recently acknowledged that this species can also occur in Europe in similar habitats (Grilli et al. 2020). In such situations it may easily be confused with *H. mesophaeum*. It is now evident that in Beker et al (2016) these two species were confused. They are clearly very closely related although an ITS sequence will usually provide separation (Cripps et al. 2019). *Hebeloma dunense* and *H. marginatulum* are another pair of closely related species. The latter is restricted to arctic and alpine habitats, but the former can also occur in these habitats. While morphological separation based on spore morphology is usually possible, an ITS sequence is a more reliable way of separating these two taxa (Beker et al. 2016, Cripps et al. 2019).

The second group of this section (*H. clavulipes, H. hygrophilum, H. monticola, H. nigellum, H. oreophilum, H. sordescens* and *H. spetsbergense*) all have mainly amygdaloid, distinctly dextrinoid spores. *Hebeloma sordescens* does not occur in arctic or alpine habitats and is usually recognisable by the blackening of the stipe that almost always occurs on drying. *Hebeloma monticola* appears to prefer subalpine, subarctic habitats and always has at least 50 full-length lamellae. *Hebeloma clavulipes* and *H. oreophilum* both have between 36 and 50 full-length lamellae; the latter having larger spores and being restricted to alpine and arctic habitats; neither of them is well represented in our sample. *Hebeloma hygrophilum, H. nigellum* and *H. spetsbergense* all exhibit at most 36 full-length lamellae. *Hebeloma nigellum* and *H. spetsbergense* can both be found in alpine and arctic habitats but the latter has significantly larger spores. When *H. nigellum* occurs in habitats that are more subalpine or subarctic then it may be confused with *H. hygrophilum,* but the latter has smaller spores.

Further details to separate all these taxa and detailed keys can be found in Beker et al. (2016).

Species allegedly occurring in Norway

These are the six species that are listed in the NMD database or by GBIF that are not confirmed, *i.e.* which could not be verified by collections. These are:

Hebeloma anthracophilum: According to GBIF, there is one collection recorded, namely BG-F-1096 (collected by D.O. Øvstedal on 14 Aug. 1992 near Lygra in Vestland. Unfortunately, this collection appears to have been lost and hence cannot be verified.

Hebeloma crustuliniforme: This species is one of the most often recorded *Hebeloma* species worldwide (GBIF, accessed 31 July 2020), and certainly this is true for Norway, as evidenced in Tables 2 and 4. As described in Eberhardt et al. (2015), the crustuliniforme-complex comprises five closely related species from *H.* sect. *Denudata* subsect. *Crustuliniformia* that have long been confused. Indeed, given the chaos surrounding species delimitation within the genus, numerous different taxa have, in the past, been referred to *H. crustuliniforme*. Weholt examined a further approx. 100 collections labelled *H. crustuliniforme* morphologically (a subset of the specimens at O and all available at TROM), without finding any true member of this species. During this study more than 20 collections labelled *H. crustuliniforme,* from various Norwegian herbaria, have been studied and sequenced. Most collections sequenced were either *H. geminatum* or *H. velutipes*. Thus far not a single specimen representing *H. crustuliniforme* has been discovered, although it might be expected that *H. crustuliniforme* would be present in Norway.

Hebeloma minus: The two collections present on GBIF are O-F-154755 (collected by J. Stordal on 5 Sep. 1981 near Øyer: Øvre Moksjø) and O-F-243280 (recorded by G.

Strømsøe, Ø. Weholt, B. Sunde, I.-L. Walter on 19 Aug. 2011 in Sør-Varanger: near Skrukkebukta Fjellheim on roadside gravel). The first of these is now confirmed as *H. spetsbergense* and the second as *H. nigellum.* Hence there is no confirmed record for *H. minus.*

Hebeloma populinum: There is one collection on GBIF: O-F-70069 (collected by G. Gulden on 23 Sep. 1994 near Ryggsetra, Viken in an unfertilized hay meadow on lime, 5-10 m from *Betula, Populus, Salix* and *Alnus*). This collection has been studied and confirmed as *H. aanenii*; thus, there is no confirmed collection of *H. populinum* for Norway.

Hebeloma quercetorum: This single record refers to a DNA sample held at the NHMO DNA Bank Fungi and Lichens collection, based on material collected near Botnermyr in Østfold by E.W. Hanssen and R. Braathen on 22 Aug. 2008, for which a voucher is kept at O with accession number O-F-287257. This collection has been examined and is confirmed as *H. hiemale*. It would be unlikely that *H. quercetorum* would exist in Norway, as it is a southern European species and from data of 81 records, all collections were at latitudes below 45°N. The closely related *H. celatum* has been recorded in Norway at latitudes up to 69°N.

Hebeloma sarcophyllum: There is one collection on the NMD: O-F-175051 (collected by P. Marstad on 11 Jul. 1998 near Kjellelia, Vestfold and Telemark with *Quercus,* on a urea plot). *Hebeloma sarcophyllum* was originally described as *Agaricus sarcophyllus* by Peck (1873) and, to date, there are no verified collections for this taxon in Europe (Beker et al. 2016, Eberhardt et al. 2020). *Hebeloma sarcophyllum* belongs to *H.* sect. *Porphyrospora* which is characterised by lamellae that turn pink to reddish-brown, as the spores mature, and a spore print that is reddish-brown when fresh, albeit the redness disappears with age. *Hebeloma sarcophyllum* is unusual, being the only known member of this section in northern America. The closely related *H. porphyrosporum* is the only member of this section known in Europe. For many years it was believed that these two taxa were conspecific; it is now clear that they are not. *Hebeloma porphyrosporum* is primarily known from southern Europe and the most northerly verified record is from approximately 49°N in France (Beker et al. 2016). Collection O-F-175051 has been examined and confirmed as representing *H. birrus.*

Critical comparison of databases examined

Considering the figures for the species most commonly recorded in different databases (Table 6), at first glance it appears that there is quite good correlation between the NMD and GBIF databases, but little similarity with the *Hebeloma* project database. Focusing first on the NMD and GBIF databases, the two most recorded species are *H. crustuliniforme* and *H. mesophaeum* in both cases accounting for more than 40% of records (53% in the case of the GBIF Observations database). In practice, based on many man-years of experience examining *Hebeloma* collections, and because of the historical problems of delimiting species, these two taxa were the 'buckets' for collections with large, pale basidiomes with drops on the lamellae, and smallish basidiomes with veils, respectively. In the case of *H. crustuliniforme*, based on our examination of herbarium material and collections sent to us, this could represent some 15 different taxa! The NMD database has the common *H. velutipes* high on its list, but *H. leucosarx* is not featured at all; for the GBIF database it is the reverse situation. Until the publication of the *Hebeloma* monograph (Beker et al. 2016), there was much confusion between these two species and for a time they were regarded as synonyms. Looking further down the list, it must be noted that species like *Hebeloma alpinum, H. circinans, H. incarnatulum, H. laterinum, H. pusillum, H. sinapizans, H. sordescens* and *H. theobrom-*

Table 7. Species of *Hebeloma* not yet confirmed in Norway, listed by (sub)section: °primarily from southern Europe, *primarily arctic-alpine, "may be present in Norway.

Denudata –Crustuliniformia	***Duracinus***	***Sinapizantia***
H. crustuliniforme"	*H. duracinoides°*	*H. bulbiferum°*
*H. louiseae**	***Hebeloma* (non-dextrinoid spores)**	***Theobromina***
H. luteicystidiatum"		*H. alboerumpens°*
*H. minus**	*H. cistophilum°*	*H. erumpens°*
*H. pallidolabiatum**	*H. psammophilum"*	*H. griseopruinatum°*
*H. perexiguum**	*H. pubescens**	*H. parvicystidiatum°*
Denudata – Clepsydroida	***Hebeloma* (dextrinoid spores)**	*H. plesiocistum°*
H. ammophilum°	H. fuscatum*	*H. vesterholtii°*
H. laetitiae°	*H. grandisporum**	***Scabrispora***
H. limbatum°	***Naviculospora***	*H. anthracophilum"*
H. matritense°	*H. catalaunicum°*	*H. cylindrosporum"*
Denudata – Echinospora	*H. naviculospora"*	*H. danicum"*
H. echinosporum"	***Porphyrospora***	*H. lindae°*
H. populinum"	*H. porphyrosporum°*	*H. melleum"*

inum will tend to be recorded more often because they are easier to identify and *H. sacchariolens* is the 'bucket' for all collections with the 'sacchariolens smell'.

With regard to our database, as already discussed, *H. crustuliniforme* remains elusive, and certainly is not common in Norway; indeed, as explained below, Norway may be beyond the northern limit for this species. *Hebeloma mesophaeum* is probably rather more common than would appear to be the case from our database, but is probably rarely referred for confirmation of identity. *Hebeloma aanenii* and *H. geminatum* are both members of the crustuliniforme-complex and would most likely, in the past, have been recorded as *H. crustuliniforme*. *Hebeloma cavipes* is a common, ubiquitous species that in the past was also probably lumped in with *H. crustuliniforme* and rarely recorded in its own right.

Species of *Hebeloma* not yet recorded in Norway

There are 36 species recognised in Europe but not yet recorded in Norway; these are listed, by section, in (Table 7). Seventeen of these species, marked with a ° in Table 7 are species primarily from southern Europe (some of which are normally associated with *Cistus*); the most northerly records for any of these taxa are for *H. vesterholtii* in Denmark at approximately 55°N. It would be surprising to find any of these species growing naturally in Norway. Of the remaining nineteen species, seven (marked with an * in Table 7) are primarily arctic/alpine species (although some may occur rarely in subarctic or subalpine habitats) and might exist in Norway at high altitude; photographs may be found in Beker et al. (2016). The remaining twelve species (marked with a " in Table 7) are likely to occur in Norway, in the right habitat, although some,

Figure 4. *Hebeloma psammophilum* JV91-873 (HJB10943). Photo: J. Vesterholt 1991.

Figure 5. *Hebeloma echinosporum* holotype BR BR-MYCO174907-16 (HJB13524). Photo: H.J. Beker 2010.

Figure 6. *Hebeloma populinum* EG-091116.02 (HJB16492). Photo: M. Maletti 2009.

Figure 7. *Hebeloma luteicystidiatum* holotype BR BR-MYCO166233-72 (HJB11837). Photo: P. Derboven 2006.

Figure 8. *Hebeloma crustuliniforme* HJB14077. Photo: H.J. Beker 2011.

Figure 9. *Hebeloma erebium* HJB12624. Photo: H.J. Beker 2008.

Figure 10. *Hebeloma aestivale* HJB10487. Photo: H.J. Beker 2004.

Figure 11. *Hebeloma naviculosporum* LB11081701 (HJB14211). Photo: L. Ballester 2011.

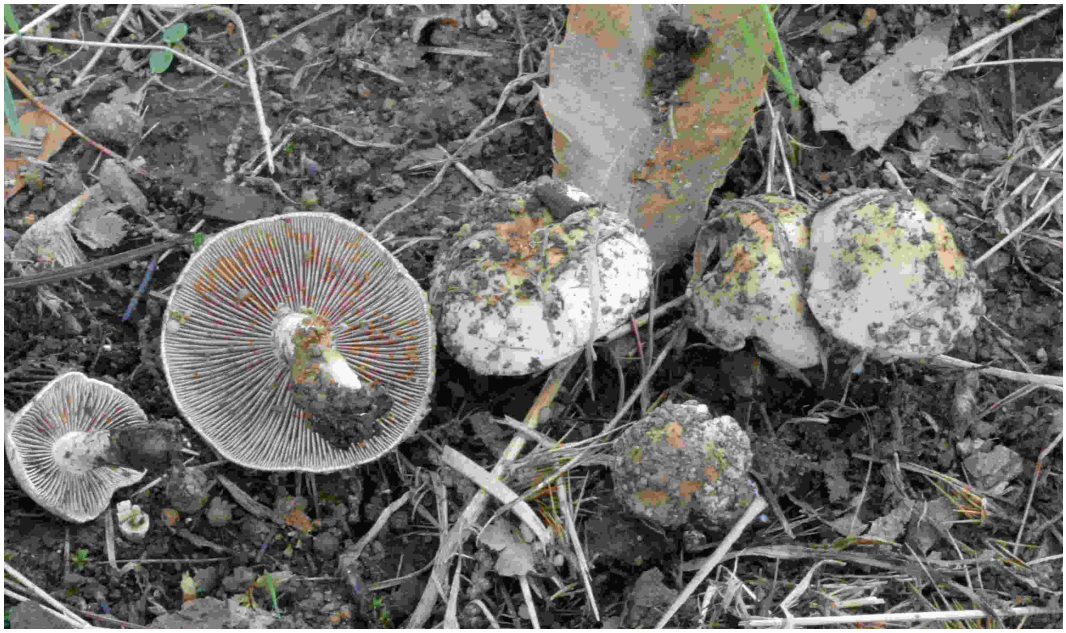

Figure 12. *Hebeloma anthracophilum* HJB13673. Photo: H.J. Beker 2010.

Figure 13. *Hebeloma cylindrosporum* HJB13859. Photo: H.J. Beker 2011.

Figure 14. *Hebeloma danicum* 7381F (HJB10807). Photo: J. Vauras 1992.

as described below, may have their current northern limits south of mainland Norway. Photographs of these 12 species are given in Figs. 4–15. We give a brief commentary of these twelve non arctic/alpine species below; full descriptions can be found in Beker et al. (2016).

Hebeloma* section *Hebeloma – *Hebeloma psammophilum* (Fig. 4): This is a sand dune species that appears to be quite uncommon. Currently, verified records only exist from Denmark, France and Wales. It normally grows in the shifting sands in the dunes (not from the pans), usually with the stipe deeply buried in sand and often with a sand ball around the base of the stipe giving the appearance of a bulbous base. Existing records have either pine or *Salix repens* as the most likely host. This species is most likely to be confused with *H. dunense*, but the latter is far more slender, has a discolouring stipe and less than 50 full length lamellae, whereas *H. psammophilum* is far more robust (stipe width at least 8 mm), the stipe does not significantly discolour and the number of full-length lamellae is at least 50. Confusion, in the field at least, may also occur with *H. ammophilum,* but this has totally different spores and cheilocystidia, and appears to be primarily a Southern European species. See Beker et al. (2016).

Hebeloma* section *Denudata – *Hebeloma echinosporum* (Fig. 5). This taxon is known only from the type collection and, hence, it is difficult to be sure of the species delimitation. The single collection was from a deciduous woodland near Boulogne in France. The strongly dextrinoid, very warty spores, with the perispore loosening in a conspicuous fashion for almost every spore, place this species within *H.* subsect. *Echinospora.* It can be distinguished from *H. rostratum*, known to occur in Norway, on the apical width of the cheilocystidia and from *H. populinum* based on the spore size. See Beker et al. (2016) and Eberhardt et al. (2016).

Hebeloma populinum (Fig. 6), like *H. echinosporum* is also from *H.* subsect. *Echinospora* and hence also has strongly dextrinoid, very warty spores, with the perispore loosening in a conspicuous fashion for almost every spore. It can be separated from other members of the section based on the spore size and the apical width of the cheilocystidia. The most northerly verified record of this taxon, to date, is at 55°N, so it is possible that this species as well as *H. echinosporum* do not occur as far north as Norway. See Beker et al. (2016) and Eberhardt et al. (2016). As mentioned above, the single collection found on the databases we explored, with this name, turned out to be *H. aanenii.*

Hebeloma luteicystidiatum (Fig. 7). All records of this rarely recorded species are from wet boggy areas in association with *Salix*. The small stature of the basidiomes means it is likely to have often been overlooked. In the field, it is most likely to be confused with *H. pusillum*. However, microscopically it is easily distinguished from *H. pusillum* by the apical thickening of the cheilocystidium, often looking yellow under the light microscope, which does not occur with *H. pusillum*. The spores are also differently shaped. See Eberhardt et al. (2015), Beker et al. (2016) and Grilli et al. (2020).

Hebeloma crustuliniforme (Fig. 8 and above). A member of the crustuliniformecomplex, *H. crustuliniforme* is relatively easy to identify, owing to the epitypification by Vesterholt et al. (2014). It always has at least 60 full-length lamellae, the average spore size is usually greater than 11 x 6 µm and the average apical width of the cheilocystidia is less than 8 µm. Within more than 110 verified collections on the *Hebeloma* project database the most northerly are from Denmark at c. 56°N, so it is possible that this taxon does not exist in Norway. See also Eberhardt et al. (2015), Beker et al. (2016) and Grilli et al. (2020).

Figure 15. *Hebeloma melleum* IB 19920061 (HJB 11592). Reproduced from Moser and Jülich (1998) by M. Candusso 2016.

Hebeloma* section *Velutipes – *Hebeloma erebium* (Fig. 9). A member of the quercetorum-complex, this species appears widespread, but uncommon, across Northern Europe at latitudes between 48°N and 59°N. The most northerly records are from Estonia so it may well be present in the south of Norway. It has a preference for base-rich soils in deciduous woodland (usually *Fagaceae* but there exist records with other deciduous trees); the holotype was collected in a dune. It can be distinguished from *H. celatum* through its less robust basidiomes. As discussed above, the third member of this complex, *H. quercetorum,* is unlikely to exist as far north as Norway. See Grilli et al. (2016) and Beker et al. (2016).

Hebeloma aestivale (Fig. 10). This is another taxon which may have its northerly boundary south of Norway. Among 72 verified collections, the most northerly is in Denmark at approx. 57°N. *Hebeloma aestivale* with its long slender cheilocystidia and its strongly ornamented and strongly dextrinoid spores with a strongly loosening perispore make this species readily distinguishable. See Grilli et al. (2016, 2020) and Beker et al. (2016).

Hebeloma* section *Naviculospora – *Hebeloma naviculosporum* (Fig. 11). This species favours base-poor soils, often grassy, near the edge of conifer woodland. Although uncommon, it is widespread across Europe in subalpine habitats. It is easy to recognise, macroscopically from the orange-brown pileus and microscopically through the navicular spores with an average spore Q (length to width ratio) over 2.1. While macroscopically it may resemble *H. nanum,* the latter has spores that are smaller and with a smaller average Q. See Beker et al. (2016).

Hebeloma* section *Scabrispora – *Hebeloma anthracophilum* (Fig. 12). This species always occurs on burnt ground. It is closely related to *H. birrus* and *H. pumilum,* both of which occur in Norway. It is separated from these other two taxa based on spore size, as discussed above. At present, the most northerly verified collection is from England at 54°N. So, it is possible that it does not occur in Norway. See Beker et al. (2016) and Grilli et al. (2020). Again, as discussed above, a record with this name does exist but the material appears to be lost, so this species remains unconfirmed for Norway.

Hebeloma cylindrosporum (Fig. 13). This species is easy to distinguish based on its cylindrical, strongly dextrinoid spores. A single record of this taxon existed on the databases we explored, and this collection turned out to be *H. nanum.* The material described by Weholt (1983) from Kirkøy Island, collected by the author 10 Oct. 1982, allows the conclusion that the species is present in Norway. However, this material is lost, and, since no voucher material exists, we must include this species among those unconfirmed for Norway.

Hebeloma danicum (Fig. 14). This taxon is normally deeply and conspicuously rooting and usually has conspicuous veil remnants on the stipe. Microscopically, the spore characters distinguish the species from others within *H.* sect. *Scabrispora*. There do exist verified collections from Finland, in excess of 60°N. See Beker et al. (2016) and Grilli et al. (2020).

Hebeloma melleum (Fig. 15). The single collection of this taxon, on which the description was based, was from a subalpine area in Austria with conifer. It is similar to *H. pumilum*, from which it can be separated, macroscopically by the more honey, saffron yellow coloured pileus and microscopically by its longer spores. Recently, a second collection of this species has been discovered in Finland at over 62°N, so this species may well be present in Norway.

CONCLUSION

Of the 85 species of *Hebeloma* known to occur in Europe, 49 are confirmed as being

present within mainland Norway. It appears that the most common species in Norway are *H. velutipes* and *H. hiemale,* while the presence of most of the European species known to have a preference for boreal woodland are confirmed as present in Norway. Of the 36 species not recorded within Norway, 17 are only known from Southern Europe, some of them in association with *Cistus.* Seven species are normally restricted to arctic or alpine habitats (or very rarely in subalpine/subarctic habitats) so might occur in alpine habitats in Norway. The remaining 12 taxa could well exist in Norway, although some of these currently have no confirmed records above 56°N.

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Psathyrella confundens (Psathyrellaceae, Agaricales) — a moist growing new species from Europe

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KEY WORDS
Drosophila albidula, molecular systematics, new species, taxonomy

NØKKELORD
Drosophila albidula, molekylær systematikk, ny art, taksonomi

SAMMENDRAG
Basert på fylogenetiske analyser og morfologi er den nye arten *Psathyrella confundens* beskrevet. Det er så langt kjent fra Frankrike, Tyskland og Sverige. Den tvetydige bruken av navnet *Drosophila albidula* blir diskutert. Arten gjenkjennes av små basidiomata, sparsomt slør, spisse cystidier, store sporer og et fuktig habitat. Karakterer som skiller den fra nært beslektede arter er gitt.

ABSTRACT
Based on phylogenetic analyses and morphology the new species *Psathyrella confundens* is described. It is so far known from France, Germany and Sweden. The ambiguous use of the name *Drosophila albidula* is discussed. The species is recognised by small basidiomata, scanty veil, acute cystidia, large spores, and a moist habitat. Separating characters of closely related species are given.

INTRODUCTION

Romagnesi (1952) gave the diagnosis of *Drosophila albidula* Romagn. without description: '*Drosophila albidula* nom. nov. (= *Ps. subatomata* Lange nec Karsten)' (Table 1). Kühner and Romagnesi (1953) provided a short description of *Drosophila albidula* (= *Psathyrella potteri* A.H. Sm.) with 13–16 × 7–8 µm large spores and a habitat 'on wilted grasses'. The cap was 5–20 mm broad and 'at first dull ochre brown or pale brownish'. Nothing was said about striation. According to Lange (1940) his *Psathyra subatomata* J.E. Lange (= *Psathyrella potteri*) was characterized by small basidiomata, pale ochre clay cap without striations. The gills were broadly adnate with white edge and the spores were given to 14–15.5 × 7.5 µm. The species grew on naked ground in stack-yard among rotten straw. Kühner and Romagnesi (1953) recognised *Drosophila atomata* ss. Bres. and *D. albidula* as two separate species, both in our view conspecific with *Psathyrella potteri*.

On our request Romagnesi sent on loan what he called the type of *Drosophila albidula*, collected in 1940 'on muddy soil of a shady path', herbarium number 233'. The material

was in a bad condition. The gill edge was collapsed and it was only possible to discern the shape and size of the cystidia. The spores measured 12–13.2 × 5.8–7.2 µm, compared with 13–16 × 7–8 µm given by Kühner and Romagnesi (1953) for their *D. albidula*, thus an indication of two different taxa. Romagnesi (1975) gave a complete description of *D. albidula* with 'barely chocolate brown' cap when young, 11.5–14.7 × 6.7–7.5 µm large spores, and a white gill edge. It is likely to believe that *Drosophila albidula* sensu Romagnesi 1975 represents *D. albidula* sensu Romagnesi 1952 (= coll. 233 above) while *D. albidula* sensu Kühner and Romagnesi (1953) most certainly is identical with *Psathyrella atomata* sensu Romagnesi 1975 (= *Psathyrella potteri*). Romagnesi (1975: 215) admits that collections of *Drosophila albidula*, not the ones based on the description from 1953, incorrectly were determined to *D. atomata* sensu Bres.

The validly published name *Psathyra subatomata* (Lange 1940) is not a later homonym of *Psathyrella subatomata* P. Karst. (Karsten, 1885). Romagnesi (1952) created the superfluous but legitimate name *Drosophila albidula* to replace *Psathyra subatomata*. He should have combined the epithet *subatomata* in *Drosophila*. *Psathyrella albidula* (Romagn.) n. c. made by Moser (1967) should not be considered as a new combination but as the new name *Psathyrella albidula* M.M. Moser nom. nov. The type goes back via *Drosophila albidula* Romagn. to Lange's material of *Psathyra subatomata*. The names *Drosophila albidula* Romagn., 1952, *Psathyrella albidula* M.M. Moser, 1967 and *Psathyrella prona* f. *albidula* (M.M. Moser) Kits van Wav., 1972, are all nomenclatural synonyms to *Psathyra subatomata* J.E. Lange, 1940. From a taxonomical point of view *Psathyrella albidula* sensu Moser is a misapplication lacking Latin diagnosis and type. The greater part of the text above is written in collaboration with professor Nils Lundqvist who thought that the epithet *confundens* would be a suitable name for a new species.

In the large molecular phylogenetic study of psathyrelloid species (Örstadius et al. 2015) a collection of the new species was included, named *Psathyrella* sp LÖ312-92. In the phylogenetic analyses it came out as a distinct species together with *P. orbitarum* (Romagn.) M.M. Moser in the /prona clade. Due to the taxonomical confusion around the species name it was not further dealt with in that study.

MATERIALS AND METHODS

Colour names follow the Munsell soil colour charts (Munsell 1975), cited as Mu. in the text.

Micromorphological characters were observed using a Nikon Eclipse E200 light microscope equipped with phase contrast. Digital images were recorded with a Nikon Infinity 2 camera. For each collection, 10 to 20 mature spores were measured in water at ×1.000 magnification. Abnormally large or small spores were not considered. Other microscopic characters were studied in a 10 % NH_4OH solution and measured to nearest micron. To observe the hymenial cystidia, a complete lamella was cut off with a razor blade and soaked for a while. The gill edge was removed in order to check the cheilocystidia. The middle portion of the gill was cut out, crush-mounted, and pleurocystidia, basidia, subhymenium, and hymenophoral trama studied. The layers of the pileus were observed halfway from the margin by cutting tangential to the pileus, called a 'scalp'. The presence of clamps were checked. As for the shape of spores and cystidia the terminology of Vellinga (1988) was followed. Spores were mounted in a solution of ammonia before capturing digital images. Scale bars in figures of spores and cystidia represent 10 µm while scale bar in figure of basidioma represents 10 mm.

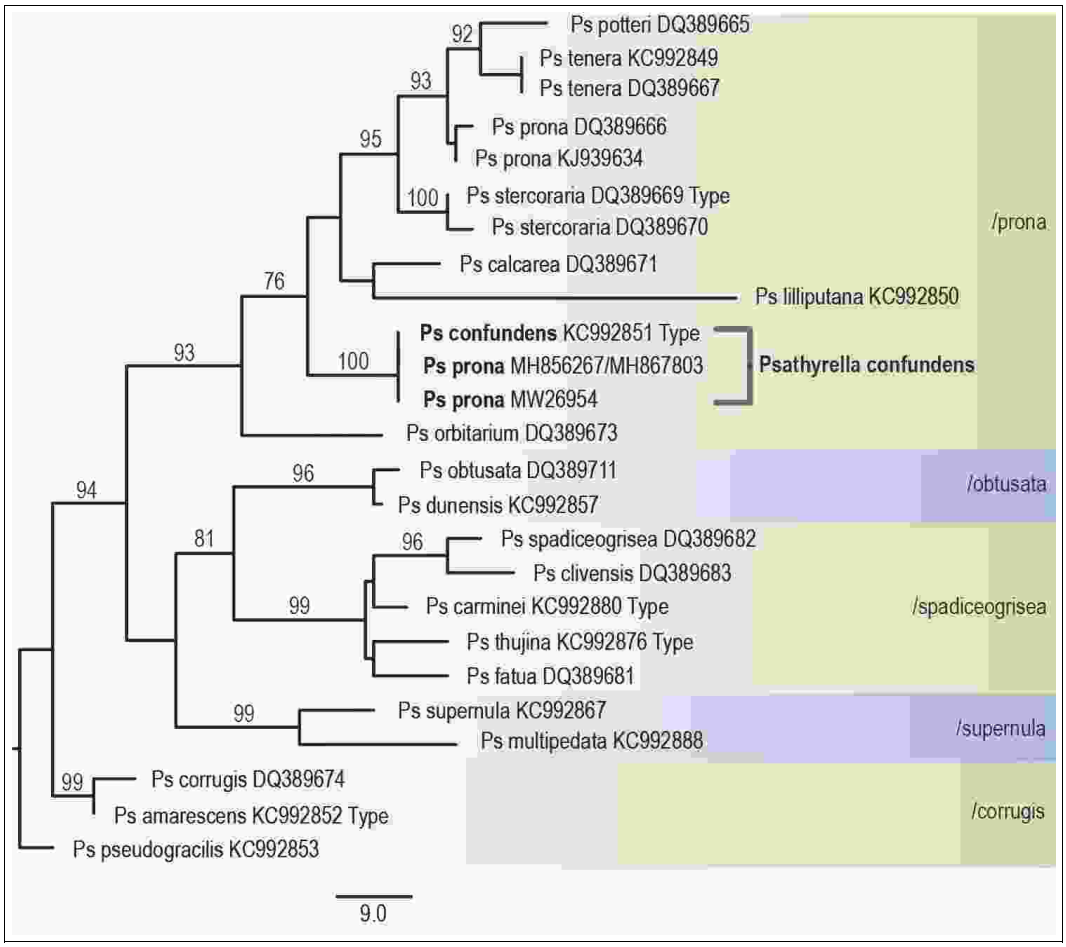

Figure 1. Phylogram showing the position of *Psathyrella confundens* in the /prona clade based on ITS and LSU sequence data. Bootstrap values are indicated on branches, the major supported clades are marked with names. Sequences originating from type specimens are indicated.

A nuc rDNA ITS and LSU data set to present *P. confundens* in a phylogenetic context was compiled based on the results from the multi gene analysis of Psathyrellaceae in Örstadius et al (2015). Representatives from the /prona, /spadiceogrisea, /obtusata and /supernula clades were selected. Rooting of trees are made with representatives from the /corrugis clade. In addition, the ITS sequence of *P. confundens* was blasted in GenBank (Clark et al. 2016) to seek additional available sequence data of similar and closely related taxa. Two sequences deposited as *Ps. prona* (Fr.) Gillet, one originating from Belgium (MH867803) and one from Portugal (MW269541) were found and added to the data set.

Alignment of the data set was performed using the L-INS-i strategy implemented in MAFFT 7.017 (Katoh and Standley 2013). The alignment was adjusted using ALIVIEW 1.17.1 (Larsson 2014). For inference of phylogenetic relationships of the dataset, heuristic searches for the most parsimonious trees were performed using PAUP* under the maximum parsimony (MP) criterion (Swofford 2003).

Table 1. An overview of names, spore sizes, etc.

Year	Name and author	L. Örstadius and E. Larsson	Spores
1940	*Psathyra subatomata* J.E. Lange	*Psathyrella potteri*	14-15.5 x 7.5 µm
1952	*Drosophila albidula* Romagnesi nom. nov.	*P. potteri* and/or *P. confundens*	The author refers to Lange 1940
1953	*Drosophila albidula* ss. Kühner and Romagnesi	*P. potteri*	13-16 x 7-8 µm
1953	*D. atomata* ss. Kühner and Romagnesi who refer to Bresadola	*P. potteri*	12-16 x 6.5-8 µm
1967	*Psathyrella albidula* (Romagn.) M.M. Moser n. c.	*P. potteri*	14-15.5 x 7.5 µm
1972, 1985	*Psathyrella prona* f. *albidula* Kits van Waveren	*P. potteri* and/or *P. confundens*	13-16 x 7-8 µm
1975	*Drosophila albidula* Romagnesi	*P. confundens*	11.5-14.7 x 6.7-7.5 µm
1975	*Drosophila atomata* ss. Romagnesi	*P. potteri*	14-16-(17) x 7-8.2 µm
-	Coll. 233 from 1940, type of *D. albidula* examined by Örstadius	*P. confundens*	12-13.2 x 5.8-7.2 µm

All transformations were considered unordered and equally weighted and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed. Relative robustness of clades was assessed by the bootstrap (BT) method using 1000 heuristic search replicates with 10 random taxon addition sequence replicates and TBR branch swapping, saving 100 trees in each replicate.

MOLECULAR RESULTS

The aligned ITS and LSU dataset consisted of 25 sequences and 1628 characters. After exclusion of ambiguous data, mainly from the beginning and the end of the data set, 1552 characters remained for the analysis. Of these, 1370 were constant, 78 were variable but parsimony uninformative, and 104 were parsimony informative. The MP analysis yielded 6 equally most parsimonious trees (length = 317 steps, CI = 0.6593, and RI = 0.7818). One of these trees is presented in Fig. 1. Bootstrap analysis recovered four supported clades corresponding to /prona (93%), /obtusata (96%), */spadiceogrisea* (99%) and /supernula (99%). The three sequences of *C. confundens* form a terminal strongly supported clade (100%) within / prona, with *P. orbitarum* as a sister species.

TAXONOMY

Psathyrella confundens Örstadius & E. Larss. sp. nov. – Figs. 2-5.

MycoBank: MB838658

Etymology: The epithet refers to the ambiguous use of the name *Drosophila albidula* Romagn.

Holotype: Sweden: Skåne: Nosaby, Eknabben, on moist soil in a rich deciduous wood, 12. September 1992, leg. L. Örstadius, LÖ312-92 (Herb. GB-0131144, ITS and LSU sequence GenBank KC992851).

Basidiomata small, psathyrelloid. *Cap* 5–15 mm diam, at first conical, campanulate, conico-convex, then convex with a low umbo and a regular margin, when old sometimes with

conspicuously distant furrows, dark reddish brown (Mu. 5YR 3/3, Munsell 1975), dark brown, rusty brown, rather dull, ochraceous brown, drying to dirty pale, grey, cream, or pink tinges, slightly to distinctly hygrophanous, when moist striate at margin or further towards centre; *veil* fibrillose, covering almost entire primordium, when mature only scattered fibrils remaining, evanescent. *Gills* distant to medium spaced, L = 14–20, adnate, ventricose, when young ochraceous grey, becoming grey (Mu. 5YR 6/1), when old blackish brown; *edge* white pruinose, sometimes red underlined. *Stipe* 15–120 × 0.5–2 mm, cylindrical, often slightly flexuous, with a small bulb at base, pale brown, pulverulent at apex, lower part with fibrils from veil. *Smell* not distinctive; *taste* mild. *Spores* 11.5–13.5 × 6–7.5 µm (av. 12.2–12.8 × 6.5–6.9 µm, Qav. = 1.9–2), oblong, subcylindrical, subovoid, in profile sometimes with a slight suprahilar depression, hardly amygdaliform, in water red (Mu. 2.5YR 4/8); germ pore distinct. *Basidia* 4-spored, 20–36 × 10–12 µm. *Pleurocystidia* 35–80 × 9–16 µm, lageniform, sometimes flexuous, scattered to numerous, pale. *Cheilocystidia* of two types: A: 25–65 × 7–16 µm, similar in shape and frequency to pleurocystidia, B: 16–40 × 10–20 µm, clavate, numerous especially close to cap margin (Fig. 5). Scalp cap ½-way from margin: *pileipellis* made up of subglobose to ellipsoid 10–40 µm wide cells; *pileitrama* with strongly incrusted hyphae. *Hymenophoral trama* made up of rather strongly pigmented hyphae. *Veil cells* 30–60 × 4–12 µm. *Clamp connections* seen at stem base mycelium.

Figure 2. Basidioma from the type locality, Sweden: Skåne: Nosaby, Eknabben, LÖ294-01. Scale bar 10 mm.

Figure 3. Type locality of *Psathyrella confundens*, Sweden: Skåne: Nosaby, Eknabben.

Habit and habitats: Solitary to gregarious, moist to wet, 'on very wet clay soil' (Romagnesi 1975, as *Drosophila albidula*), among leaves, on sticks or twigs, on moss, fruits in autumn September - October.
Distribution: The species is confirmed from Sweden, Portugal and Belgium, but rarely recorded from France, Germany and Sweden. Kits van Waveren (1972, 1985) reported *Psathyrella prona* f. *albidula* (Table 1) from the Netherlands and Switzerland. Exact distribution is unknown due to confusion with related species.

Specimens examined
France: Bourgogne-Franche-Comté: Yonne, Sens, 'on the muddy earth of a shady path', 18. Sept. 1940, H. Romagnesi 233 (PC, type of *Drosophila albidula*), (Fig 4).
Germany: Bayern: Leipheim, by Donau-Brücke, down by the poplars, 22. Oct. 1996, M. Enderle (KR).
Sweden: Skåne: Nosaby, Eknabben, on moist soil in a rich deciduous wood, 2. Oct. 1986, L. Örstadius, LÖ168-86 (GB) (Fig. 2); 12. Sept. 1992, L. Örstadius, LÖ312-92, HOLOTYPUS (GB), (Fig 2, 5); 16. Oct. 2001, L. Örstadius, LÖ294-01 (GB), (Figs 2, 3).

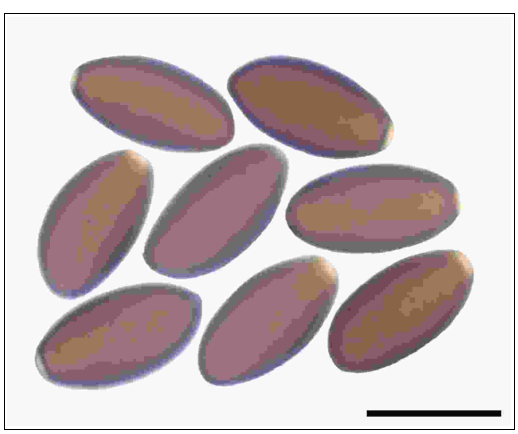

Figure 4. Spores from the type of *Drosophila albidula,* France: Bourgogne-Franche-Comté: Yonne, Sens, Romagnesi. 233. Scale bar 10 µm.

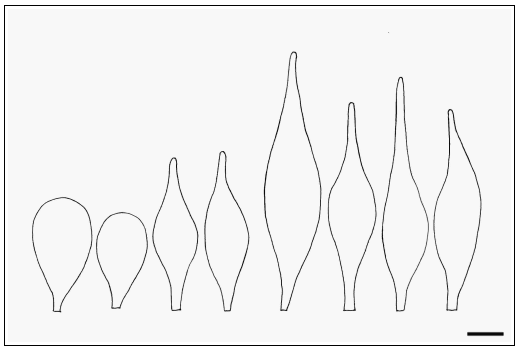

Figure 5. Hymenial cystidia from the holotype (cheilocystidia to the left, pleurocystidia to the right), Sweden: Skåne. Nosaby, Eknabben, LÖ312-92. Scale bar 10 µm.

Notes: The description is partly taken from Romagnesi (1975) as *Drosophila albidula* and our examination of material from France, Germany and Sweden. Romagnesi always found a white gill edge. The Swedish and German material varied from a pure white to a slightly or distinctly pigmented edge. *Psathyrella confundens* is recognised by small basidiomata, a fibrillose veil when young, acute ending cystidia, large spores, and a moist habitat. *Psathyrella prona* (Fr.) Gillet is separated by 2-spored basidia and slightly larger spores that often are limoniform with a more or less pronounced suprahilar depression. *Psathyrella potteri* differs in an early drying and hardly striate cap, a preference of growing on manured soil, and broader spores. The separating morphological features between *P. orbicularis* (Romagn.) Kits van Wav. and *P. confundens* are not convincing but the former can have a pseudorrhiza and it grows not only moist but also in dry forests or open grassland. Moreover, the spores are slightly narrower (av. 5.1–6.5 µm) and the cheilocystidia of type B are scattered close to cap margin opposite to *P. confundens* that often has a deep layer of cells. *Psathyrella orbitarum* (Romagn.) M.M. Moser differs in having smaller spores (av. 10.1–11.6 × 5.1–6 µm). Genetically *P. confundens* is closely related to *P. orbitarum* but the two differ by

15 substitutions in the ITS1 region, and 9 substitutions and one 2bp insertion/deletion event in the ITS2 region.

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Cuphophyllus atlanticus (Hygrophoraceae, Agaricales) — a new sister species to the North American *C. canescens*

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Norsk tittel:
Cuphophyllus atlanticus (Hygrophoraceae, Agaricales) – en ny søsterart til den nordamerikanske *C. canescens*

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KEYWORDS
Cuphophyllus canescens, molecular systematics, new species, taxonomy

NØKKELORD
tinnvokssopp, molekylær systematikk, ny art, taksonomi

SAMMENDRAG
Cuphophyllus canescens er en art som opprinnelig ble beskrevet fra Nord-Carolina, USA. Det vitenskapelige navnet er også blitt brukt om europeisk materiale rapportert fra Norge, Sverige og Storbritannia. I forbindelse med studier av materiale av tinnvokssopp fra Norge avdekket molekylære undersøkelser at vår art har ITS-sekvens som er forskjellig fra isotypen av *C. canescens* og derfor bør beskrives som en ny art. *Cuphophyllus atlanticus* er foreslått som navn for den nye arten, som viser seg å ha en interkontinental utbredelse. Utbredelsen av *Cuphophyllus canescens* synes å være begrenset til Nord-Amerika.

ABSTRACT
Cuphophyllus canescens is a species originally described from North Carolina, USA. The name has been applied to specimens collected in Europe, and the species has been reported from Norway, Sweden and Great Britain. In connection with an inventory and study of *C. canescens* in Norway, the molecular investigations revealed that the Scandinavian specimens differ in ITS sequence data from the isotype of *C. canescens* and therefore should be described as a new species. *Cuphophyllus atlanticus* is proposed as a new name for this species, which is shown to have an intercontinental distribution range while *Cuphophyllus canescens* seems to be restricted to North America.

INTRODUCTION

Cuphophyllus (Donk) Bon is a genus of Hygrophoraceae Lotzy, with species globally distributed in the northern and southern hemispheres. In the systematic review of Hygrophoraceae, Lodge et al. (2014) it was found that *Cuphophyllus* occupied a relatively isolated phylogenetic position in the family. Several species in the genus are shown to have a broad distribution range and to occur from the nemoral to the arctic-alpine zones in Europe (Boertmann 2010). Most European species differ from the ones occurring in North America, but there are exceptions. These are

especially found among species having a northern boreal to arctic-alpine distribution range, for example *C. hygrocyboides* (Kühner) Bon (Voitk et al. 2020).

The species in *Cuphophyllus* are characterized by having clitocyboid basidiomata with thick decurrent lamellae and a white spore print. In micro-morphology they have an interwoven or rarely almost subregular lamellar trama, with or without a regular or subregular central strand; smooth, hyaline, inamyloid basidiospores; very long basidia relative to spore length (usually 7–8, rarely 5–6 times the spore length), and a basal clamp on the basidia (Lodge et al. 2014). An interwoven lamellar trama, together with large basidia to spore length ratio are the most reliable characters for separating *Cuphophyllus* from other white-spored agaric genera. Species of *Cuphophyllus* are now regarded to have a biotrophic mode of nutrition, but the nature of the fungus-plant association is largely unknown (e. g. Halbwachs et al. 2018).

Cuphophyllus canescens (A.H. Sm. and Hesler) Bon was originally described from the Great Smoky Mountains National Park, North Carolina, USA by Smith and Hesler (1942). It has been described as a rare species in Europe, occurring in semi-natural grasslands of Norway, Sweden and Great Britain (Boertmann 2010). In connection with a study and inventory of *C. canescens* in Norway (Jordal 2019a), investigations with molecular methods were also undertaken and revealed that the ITS sequence data of the Norwegian specimens differ from the isotype of *C. canescens*. *Cuphophyllus atlanticus* is therefore proposed here as a new name for this species, which is so far identified from Norway, Sweden, South Europe and also from USA and Canada.

MATERIAL AND METHODS

Morphological methods

Fresh basidiomata were photographed *in situ* and the habitat was noted and described. Information from other collectors like photos and habitat data has been compiled (Jordal 2019a). Detailed observations of macromorphological characters were made on fresh and photographed material together with field notes. Micro-morphological characters were observed and measured from dried material dehydrated in 3% KOH and ammoniacal Congo red solution at 1000× magnifications using a Zeiss Axioskop 2 microscope and ZEN imaging software (Zeiss). A minimum of 20 spores were measured from each basidioma, abnormally large or small spores were not considered. Spore measurements exclude apical appendage. Basidial measurements exclude sterigmata, and the sterigmata were measured separately. The measurements in the description below are based on five sequenced collections with mature and well developed basidiomata (GB-0076131, OF241128, OF288790, OF288304, OF287870).

Molecular methods

Nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) sequence data of 14 specimens of *C. atlanticus* were newly generated for this study.

DNA was extracted using DNeasy Plant Mini Kit (Qiagen, Hilden), and for the PCR reactions Illustra PuReTaq Ready to go PCR beads (GE Healthcare, Buckinghamshire) were used with 0.5 μM of each primer and 1-3μL of DNA solution. PCR clean-up was made with QIAquick PCR purification kit (Qiagen, Hilden). Primers used to amplify the ITS region were ITS1F (Gardes and Bruns 1993) and LR21 (Hopple and Vilgalys 1999). Sequences were generated by Macrogen Europe (Amsterdam, The Netherlands) using primers ITS1, ITS4 (White et al. 1990). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor,

Michigan). The sequences have been deposited in GenBank (MW332281 – MW332294), see also material studied below.

The ITS data set was compiled based on the results from the ITS analysis of *Cuphophyllus* and data presented in Voikt et al. (2020). ITS sequence data of two collections of the *Cuphophyllus hygrocyboides* complex were used for rooting of trees. The ITS of the target species in this study was blasted in GenBank (Clark et al. 2016) and the UNITE database (Kõljalg et al. 2013) to seek additional available sequence data of similar and closely related taxa. Seven additional sequences deposited as *Cuphophyllus* sp., *C. canescens* and *C. basidiosus* (Peck) Lodge & Matheny were found and added to the data set, among them the ITS1 of the isotype of *C. canescens* (HQ185699).

Alignment of the data set was performed using the L-INS-i strategy implemented in MAFFT 7.017 (Katoh and Standley 2013). The alignment was adjusted using ALIVIEW 1.17.1 (Larsson 2014). For inference of phylogenetic relationships of the dataset, heuristic searches for the most parsimonious trees were performed using PAUP* under the maximum parsimony (MP) criterion (Swofford 2003). All transformations were considered unordered and equally weighted and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed. Relative robustness of clades was assessed by the bootstrap (BT) method using 1000 heuristic search replicates with 10 random taxon addition sequence replicates and TBR branch swapping, saving 100 trees in each replicate.

RESULTS

The aligned ITS dataset consisted of 37 sequences and 873 characters. After exclusion of ambiguous data, mainly from the beginning and the end of the data set, 838 characters remained for the analysis. Of these, 269 were constant, 21 were variable but parsimony uninformative, and 548 were parsimony informative. The MP analysis yielded 6 equally most parsimonious trees (length = 939 steps, CI = 0.8427, and RI = 0.9597). One of these trees is presented in Fig. 1. Bootstrap analysis recovered nine supported terminal clades, corresponding to *C. flavipes* (Britzelm.) Bon (100%), *C. pseudopallidus* (Hesler and A.H. Sm.) Lodge, Boertm. & E. Larss. (84%), *C. cinerellus* (Kühner) Bon (99%), *C. esteriae* Voitk, I. Saar and E. Larss. (97%), *C. colemannianus* (A. Bloxam) Bon (100%), *C. lacmus* (Schumach.) Bon (93%), *C. atlanticus* (94%), *C. canescens* (91%) and *C. basidiosus* (100%). A BT value greater that 70% is considered strong.

The *C. canescens* group formed a well-supported clade with 100% BT value, Fig 1. Within the clade the ITS 1 sequence of the isotype of *C. canescens* come together with two other sequences originating from North America. Of the three sequences representing *C. basidiosus* originating from North America are two identical and form a supported clade and one rather divergent from the others that merge on a single branch, suggesting that there may be more taxa involved here. However, sequence data of the type is not available. The 17 sequences in the *C. atlanticus* clade are homogenous. The sequences originate from Norway, Sweden, South Europe and North America, suggesting a broad an intercontinental distribution range.

TAXONOMY

Cuphophyllus atlanticus J.B. Jordal & E. Larss. sp. nov. – Figs. 2-3.

MycoBank: MB838472

Etymology: the epithet refers to the occurrence of the species on both the European and the North American side of the Atlantic Ocean, and its main European distribution in the northwestern, atlantic parts.

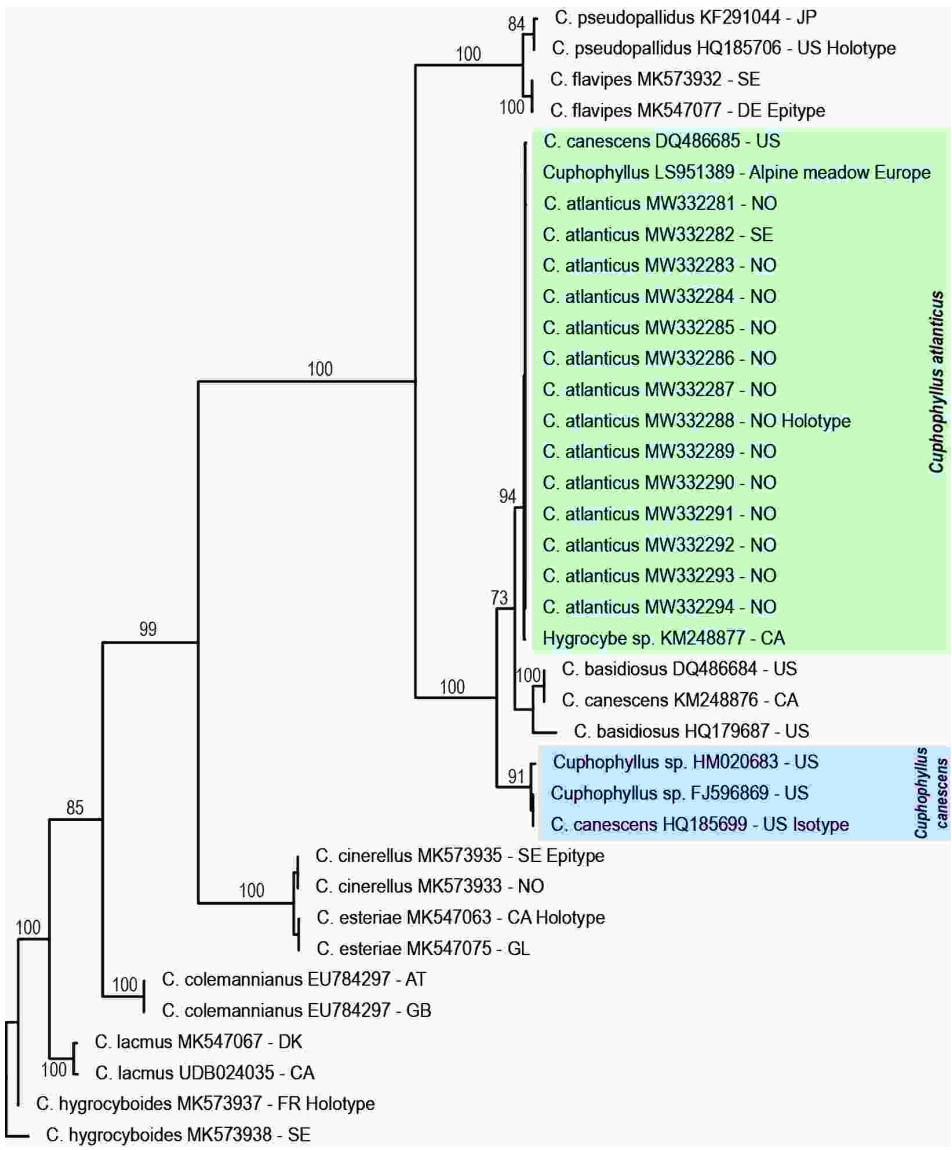

Figure 1. Phylogram showing the phylogenetic position of *Cuphophyllus atlanticus* based on ITS sequence data, placed as a supported clade together with *C. basidiosus* and *C. canescens* as sister species. Bootstrap values are indicated on branches. Sequences originating from type specimens are marked.

Holotype: NORWAY. Vestland (former Hordaland) county, Austevoll municipality, island of Møgster (northern part), in semi-natural grassland grazed by sheep, 6 Oct 2008, 60.0700°N, 5.0902°E (± 7 m), leg. Asbjørn Knutsen, John Bjarne Jordal, OF287870 (holotype O, isotype GB), ITS sequence GenBank No. MW332288.

Figure 2. *In situ* photo of the basidiomata of the holotype of *C. atlanticus* in Norway, county of Vestland (Hordaland), Austevoll municipality, Møgster (OF287870). Photo J.B. Jordal.

Diagnosis: Macroscopically similar to *C. canescens* but differ in pileus colour, where that of *C. atlanticus* as young and fresh is grey, often with a weak bluish tint (grey-blue or tin-coloured) and with paler greyish white areas, without any brown, while *C. canescens* is described as «benzo brown» to «drab grey». Also, the stipe of *C. atlanticus* is pale greyish to almost white without any longitudinally streakes, while the stipe of *C. canescens* is described as near «pallid purplish gray» somewhat longitudinally streaked and white at base. The spores in *C. atlanticus* are slightly larger and subglobose to broadly ellipsoid (5.4–5.9 × 4.4–4.8 µm, average 5.6 × 4.5 µm, Q = 1.2–1.3) than those given in the original diagnosis of *C. canescens* (4-5 µm and globose). The two differ in ITS1 sequence data, by 7 substitutions and one 4bp, two 2bp and 6 single bp insertion/deletion events.

Pileus 15 − 40(45) mm in diameter, obtuse to convex sometimes with a broad and blunt umbo and margin long remaining incurved, later becoming more plane, sometimes slightly depressed and with a lobed or irregular incurved margin, dry or weakly greasy (never slimy), matt, greyish, tin-coloured with a bluish tint and with paler greyish white areas, with age pale greyish. Not translucently striate or hygrophanous. *Lamellae* adnate to decurrent, sometimes deeply decurrent, distant to subdistant, lamellae that reach the stipe = 30 − 40(50), interspaced with lamellulae, a few furcate, intervening, pale grey, to grey with a weak bluish tint, with age pale

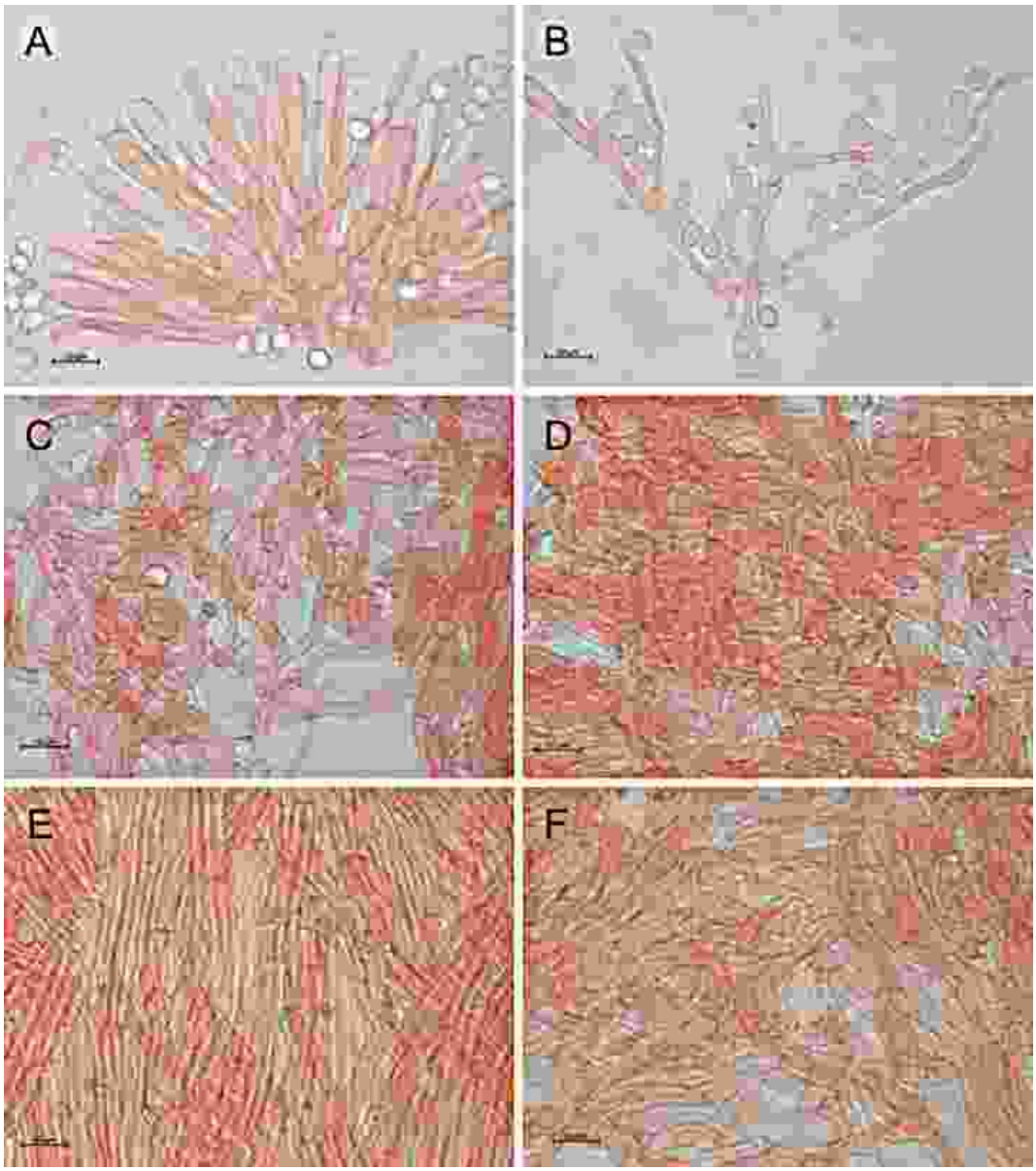

Figure 3. Micromorphological characters of the holotype of *C. atlanticus* (OF287870). A – Hymenium with basidia. B – Basidiospores among hyphae and basidia. C – Hymenophoral trama. D – Pileipellis. E – Stipetipellis. F – Subpileus trama. Scale bars 10µm. Photo E. Larsson.

greyish. *Stipe* 25–65 × 3–7 mm, cylindrical and thickest at the apex, often twisted, tapering and often bending towards the base, with age hollow, dry, matt with a whitish felty covering, pale greyish to almost white towards apex and mostly whitish below. Context concolourous. The smell is weak and indistinct, taste not observed.

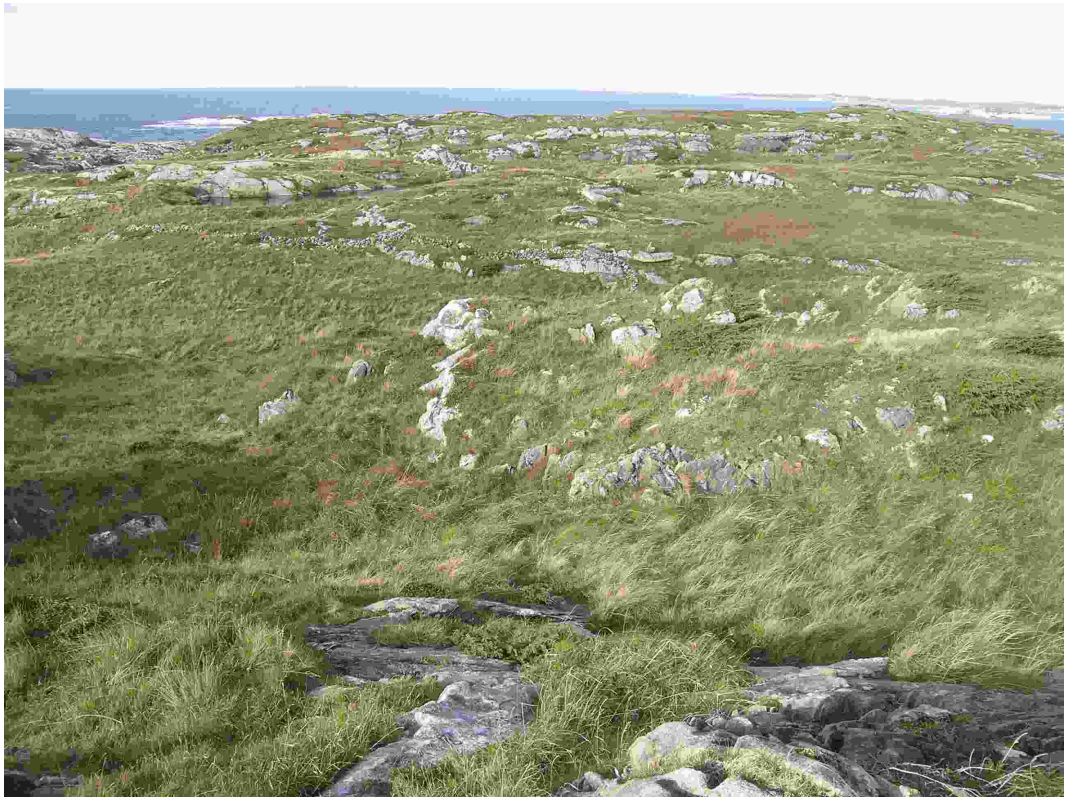

Figure 4. Habitat view from the type locality of *C. atlanticus* in Austevoll, Møgster. The species was found in the middle of the picture, in old semi-natural grassland that has been grazed, mostly by sheep, for centuries. Photo J.B. Jordal.

Spores [161] (4.7–)5.4–5.9(–6.8) × (3.3–)4.4–4.8(–5.4) µm, average 5.6 × 4.5 µm, Q = 1.2–1.3, globose to subglobose, hyaline, white in deposit, non-amyloid.

Basidia 40–55 × 5–7 µm, four-spored, two-spored observed, sterigmata 6–8 µm.
Lamellar trama interwoven, made up of cylindrical hyphae 3–7 µm wide and 30–60 µm long. *Pileipellis* a cutis with radially interwoven hyphae 3.5–6 µm wide, 30–50 µm long, upper layer with few repent to erect hyphae. Subcutical hyphae interwoven 4–7 µm wide. *Stipetipellis* with parallel and finely interwoven hyphae 3.5–5.5 µm wide and 30–70 µm long. Incrusted, finely granular pigmented hyphae observed. *Clamp* connections frequent in all tissues.

Habitat: The species is associated with semi-natural grasslands, among mosses, herbs and grasses, with the soil ranging from rather acid to moderately calcareous (Fig 4.) Most localities are situated in the boreonemoral (hemiboreal) to southern boreal vegetation zones.

Distribution: The species is shown to have an intercontinental distribution range and is confirmed from Norway, Sweden, USA (NC), Canada and with one sequence originating from soil sample from an alpine meadow area in the European Alps or Carpathian Mountains.

Specimens studied:
NORWAY**.** Vestland (Hordaland): Austevoll, Møgster northern part, semi-natural grassland (grazed by sheep), 6 Oct 2008, A. Knutsen, J. B. Jordal, OF287870 (ITS GenBank MW332288) Holotype. Bømlo, Brandasund, old grassy road (semi-natural grassland, grazed by livestock), 22 Sept 2012, Per Fadnes, OF245811 (ITS GenBank MW332284). Bømlo, Spyssøya: Myra, semi-natural grassland (grazed by sheep), 2 Oct 2009, A. Knutsen, J. B. Jordal, OF291300 (ITS GenBank MW332281). Bømlo, Tverrborgvika, semi-natural grassland (grazed by sheep), 29 Sept 2013, A. Vatten, P. Fadnes, J. B. Jordal, OF247485 (ITS GenBank MW332286). Alver (Lindås), Lygra, Bløddalen nord, small spot of semi-natural grassland surrounded by *Calluna* heath (grazed by sheep), 26 Sept 2018, J. B. Jordal, JB18-041 OF257333 (ITS GenBank MW332283). Masfjorden, Hopsdalen, semi-natural grassland (pasture), 2 Oct 2008, G. Gaarder, OF288790 (ITS GenBank MW332292). Masfjorden, Vågset, semi-natural grassland (pasture), 2 Oct 2008, G. Gaarder, OF288698 (ITS GenBank MW332293). Alver (Radøy), Bøøyna, semi-natural grassland (grazed by sheep), 18 Sept 2013, G. Gaarder, OF245904 (ITS GenBank MW332285). Vestland (Sogn og Fjordane): Solund, Gåsvær: Fiskholmen, semi-natural grassland/coastal *Calluna* heath (grazed by sheep), 12 Oct 2006, B. H. Larsen, OF288304 (ITS GenBank MW332294). Møre og Romsdal: Aure, Husfest, semi-natural grassland (grazed by sheep), 22 Sept 1995, J. B. Jordal, OF241128 (ITS GenBank MW332290). Herøy (Møre og Romsdal), Skorpa, semi-natural grassland (grazed by goat), 27 Sept 1994, G. Gaarder, J. B. Jordal, OF241127 (ITS GenBank MW332289). Fjord (Norddal), Valldal, Heimsetra, semi-natural grassland on summer farm (grazed by cows), 3 Sept 2009, J. B. Jordal, OF291137 (ITS GenBank MW332287). Fjord (Stordal), Dyrkorn, Indresæter, Josætra, semi-natural grassland, 10 Sept 2002, J. B. Jordal, OF178756 (ITS GenBank MW332291). SWEDEN. Värmland: Svanskog, Mosserud, Yttre Hedane, semi-natural grassland (hayfield), 17. Aug 2002, L. Gustavsson, GB-0076131 (ITS GenBank MW332282).

DISCUSSION

Based on the original description of *C. canescens* (Smith and Hesler 1942) and the somewhat emended description in Hesler and Smith (1963) it is easy to understand that the name in Northern Europe (Boertmann 2010) has been applied to the species we now describe as *C. atlanticus*. They are indeed very similar. We have shown that both *C. canescens s.str.* and *C. atlanticus* occur in North America, and both species even in North Carolina. Therefore, we cannot be sure what species are included in the emended description of *C. canescens* in Hesler and Smith (1963), and we rely on the original description by Smith and Hesler (1942), which is based on the type. For instance, the spore form and measurements differ in the two publications. The type is said to have globose spores 4-5 µm in Smith and Hesler (1942); while later the spores of *C. canescens* are described as, at times globose, more often subovoid, 4-5.5(6)x 4-4.5 µm (Hesler and Smith 1963). This is based on more collections where no further sequence data are available, and a mixture of species cannot be excluded.

In the phylogenetic analysis *C. basidiosus* comes out as a sister species to *C. atlanticus* and *C. canescens* in a strongly supported clade, Fig. 1. The species is also similar in morphology but differ and can be distinguished by the greyish-brown colour of pileus and stipe, and striations on the pileus. The species is not so far known from Europe.

Due to the red-listing the species *C. canescens* has been given attention and inventories have been undertaken, especially in Norway. This has improved our knowledge of occur-

rence and habitat preferences (Jordal 2019a).

In Norway, all finds have been done in open, semi-natural grasslands mainly without trees or bushes, with the soil ranging from rather acid to moderately calcareous. One find was on a grassy road surrounded by old cultural landscape. Most localities were within the hemiboreal to southern boreal vegetation zones (Moen 1999), except one (OF291137) that was found in the mid boreal zone near a summer farm. Along the coast-inland gradient, it occurred mostly in the strongly oceanic vegetation section (along the outer coast), but also sometimes in the markedly oceanic, and once in the weakly oceanic section. In Sweden the records available also suggest that it is associated to nutrient poor open semi-natural grassland, both on grazed and mown localities (SLU ArtDatabanken 2020). Most records are from the coast or inland of south Sweden and associated with the old cultural landscape.

The species *C. canescens s. l.* seems to be rare in North America and GBIF (2020) lists only about 20 records from eastern USA and eastern Canada. The habitat information is scarce, but waxcaps are generally found in forests or forest margins, preferably under trees that don't form ectomycorrhiza (Lodge et al. 2014, Halbwachs et al. 2018). Grasslands could be an underestimated waxcap habitat in North America due to limited attention (Griffith et al. 2013). On the label of the type of *C. canescens* it is said to be collected under *Fagus* and Hemlock in the Great Smoky Mts. National Park, North Carolina, suggesting a forest habitat. Due to the lack of information, it is hard to decide if habitat is a key factor for discrimination of the two species.

Cuphophyllus atlanticus is on the red list and evaluated as endangered (EN) in both Sweden (SLU ArtDatabanken 2020) and Norway (Artsdatabanken 2015) because its habitat of nutrient poor semi-natural grassland, is rapidly decreasing. *Cuphophyllus atlanticus* is in Europe an indicator of mycologically rich but nutrient-poor, semi-natural grasslands, and a member of the waxcap grassland assemblage. As a whole, most waxcap grasslands are among the habitat types that are listed as VU, EN or CR in the EU Red List of habitats (Janssen et al. 2016).

We conclude that *C. atlanticus* is the name to be applied to the red-listed and strongly threatened species in Norway and Sweden. *Cuphophyllus canescens* has been evaluated as vulnerable (VU) on the global red list (Jordal 2019b), and as endangered (EN) regionally in Europe (Jordal 2019c). The assessment for Europe should from now be applied to *C. atlanticus,* and the global assessment should be applied to *C. canescens s. l.*, including both *C. atlanticus* and *C. canescens s. s*. until a new assessment is done.

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Coprinellus dilectus versus *Coprinellus aquatilis* (Psathyrellaceae, Agaricales)

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Norsk tittel: *Coprinellus dilectus* versus *Coprinellus aquatilis* (Psathyrellaceae, Agaricales)

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Coprinellus dilectus, C. aquatilis, description, holotype

NØKKELORD
Coprinellus dilectus, C. aquatilis, beskrivelse, holotype

SAMMENDRAG
Den sjelden rapporterte *Coprinellus dilectus* (Fr.) Redhead, Vilgalys and Moncalvo sensu auct. og *Coprinus aquatilis* Peck anses å være den samme arten. Beskrivelser er gitt. Arten kan gjenkjennes på den lyse oransje brune hatten, et granulose slør, lageniform cystidia, ganske store sporer med en eksentrisk spirepore og et fuktig habitat. Den originale beskrivelsen av *Coprinus dilectus* Fr. samt noen rapporter om artene fra Europa blir diskutert. Typematerialet til *Coprinus aquatilis* Peck er undersøkt og status diskuteres. Fylogenetiske analyser plasserte arten nær *Coprinellus silvaticus*.

ABSTRACT
The rarely reported *Coprinellus dilectus* (Fr.) Redhead, Vilgalys and Moncalvo sensu auct. and *Coprinus aquatilis* Peck are considered to be the same species. Descriptions are given. The species can be recognized by the bright orange brown cap, a granulose veil, lageniform cystidia, rather large spores with an eccentric germ pore, and a moist habitat. The original description of *Coprinus dilectus* Fr. as well as some reports of the species from Europe are discussed. The type of *Coprinus aquatilis* Peck is examined and its status discussed. Phylogenetic analyses placed the species close to *Coprinellus silvaticus*.

INTRODUCTION

It frequently happens that descriptions by Fries (e.g. 1821) and contemporary authors lack information of characters important for us today. Examples can be microscopic characters or pubescent covering on cap or stem hard to see with the naked eye. *Coprinus dilectus* is one such species, for which the original description by Fries (1838) reads like:
"C. DILECTUS, pileo tenuissimo campanulato obtuso furfuraceo-floccoso, dein fisso revoluto nudo, stipite attenuato glabrello *basi squamuloso-volvato*, lamellis liberis sublanceolatis confertis rubrofuscis demum nigris. Locis adustis umbrosis in fagetis. Est quasi A. *obleclus* diminutus, volva obliterata, stipite 2—3 unc. l., 1—2 lincr. albo, pileo ½—¾ unc. lato albido-roseo, disco livido."

In the last 80 years the species now and then has been described by authors as Lange (1939-1940), Heinemann and Josserand (1941), Orton and Watling (1979), Krieglsteiner et al. (1982), Uljé and Bas (1991), Gerault (2005), Ludwig (2007), Schmidt-Stohn (2012), and Gierczyk et al. (2014). Despite several descriptions, the exact identity of the species remained unresolved and the name has not been typified by modern materials. Schmidt-Stohn considers the squamulose stem base given by Fries (1838) to deviate from today's view of the species. Fries writes in italics *basi squamuloso-volvato* that excludes the possibility to be a species of subsection Setulosi (Uljé and Bas 1991, Uljé 2005). Moreover, Schmidt-Stohn refers to Heinemann and Josserand who believes *Coprinus dilectus* sensu Lange to agree with *C. erythrocephalus* (Lév.) Fr. (= today´s *Coprinopsis erythrocephala* (Lév.) Redhead, Vilgalys and Moncalvo). Schmidt-Stohn further points out that the important feature of the germ pore position, if central or eccentric, differs by the authors. He noted that *Coprinellus dilectus* sensu auct. are found seven times in Europe, four of which from Germany. Schafer (2009) reported the species with informative illustrations from the British Isles.

Last year the species was collected in Skåne, the southernmost province of Sweden. We consider the Friesian species to be misapplied by mentioned European authors and below we provide a description using Peck´s name.

MATERIALS AND METHODS

Colour names follow the Munsell soil colour charts (Munsell 1975), cited as Mu. in the text.

Micromorphological characters were observed using a Nikon Eclipse E200 light microscope equipped with phase contrast. Digital images were recorded with a Nikon Infinity 2 camera. For each collection, 10 to 20 mature spores were measured in water at ×1.000 magnification. Abnormally large or small spores were not considered. Other microscopic characters were studied in a 10 % NH4OH solution and measured to nearest micron. To observe the hymenial cystidia, a complete lamella was cut off with a razor blade and soaked for a while. The gill edge was removed in order to check the cheilocystidia. The middle portion of the gill was cut out, crush mounted, and pleurocystidia, basidia, subhymenium, and hymenophoral trama studied. The layers of the pileus were observed halfway from the margin by cutting tangential to the pileus, called a ‘scalp’. The presence of clamps were checked. As for the shape of spores and cystidia the terminology of Vellinga (1988) was followed. Spores were mounted in a solution of ammonia before capturing digital images. All scale bars in the figures represent 10 µm.

Molecular protocols and phylogenetic analyses followed Nagy et al. 2012 (Mycologia). The combined Internal Transcribed Spacer (ITS) and 28S ribosomal subunit dataset from our previous paper was supplemented with new sequences from *C. aquatilis*. A maximum likelihood analysis with 1000 bootstrap replicates under a partitioned GTR+G model was performed in RAxML 8.2.12 (Stamatakis 2014).

RESULTS

Coprinus aquatilis Peck is reported as occurring in Finland and Norway (Vesterholt 2012). The description reminds of *Coprinellus dilectus* sensu auct. We obtained the type collection on loan from NYS. The scanty material only permitted to examine the spores that agreed in size and shape and the eccentric position of the germ pore with *C. dilectus* sensu auct.

We made the following observations on the type of *Coprinus aquatilis*: Spores 11.4-12.8 x 6.6-7.5 x 5.8-6.6 µm, av. 12.1 x 7.1 x 6.2 µm, Qav. 1.7 (in front view), 2 (in profile),

ellipsoid, ovoid, subfusoid, sometimes slightly irregular in outline, in profile distinctly flattened on one side, oblong, amygdaloid, or with a suprahilar depression, in water red (Munsell 2.5YR 4/6); germ pore strongly eccentric (Fig. 1).

Peck's original description does not contradict today's view of *C. dilectus*.

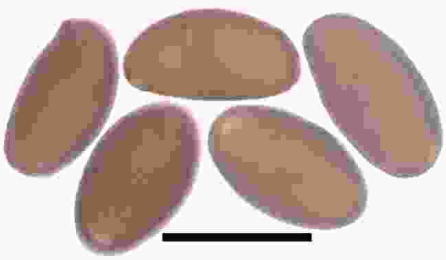

Figure 1. Spores of *Coprinus aquatilis*. type NYS 300.1

"COPRINUS AQUATILIS *n. sp*.
Pileus membranaceous, campanulate, sulcate-plicate almost to the apex, furfuraceous, yellowish-brown; lamellae subdistant, reaching the stem, brownish then black; stem slender, equal, hollow, furfuraceous, whitish; spores . 0005' long, .0003' broad.

Plant fragile, 2'-2.5' high, pileus 6"-8" broad. Sticks and twigs partly submerged or lying in wet mossy places. Adirondack Mts. Aug.

The young plant is more yellow than the mature one. The species is related to *C. silvaticus*" (Fig. 2).

***Coprinellus aquatilis* (Peck) Voto**

Coprinus aquatilis Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 27: 96, 1875 (1874); *Coprinellus aquatilis* (Peck) Voto, Boll. Assoc. Micol. Ecol. Romana 107(2): 94, 2019. Holotype: USA: New York, Adirondack Mts (NYS). Fig. 3A-E.

Synonym: *Coprinellus neodilectus* Voto, Boll. Assoc. Micol. Ecol. Romana 107(2): 95, 2019.

Misapplied name: *Coprinellus dilectus* (Fr.) Redhead, Vilgalys and Moncalvo sensu auct.

Pileus when closed ellipsoid, then slightly expanded, 8 mm high and 7 mm wide, orange-yellow to orange-brown, becoming paraboloid, 11 mm wide, reddish yellow (Munsell 5YR 6/8), covered by a flocculose to granulose veil, copious at apex and margin, plicate-striate. Gills free, medium spaced, L = c. 36, when young whitish, darkening and becoming blackish. Stem 25 x 1.8-2 mm, whitish, granulose, pubescent. Smell not distinctive.

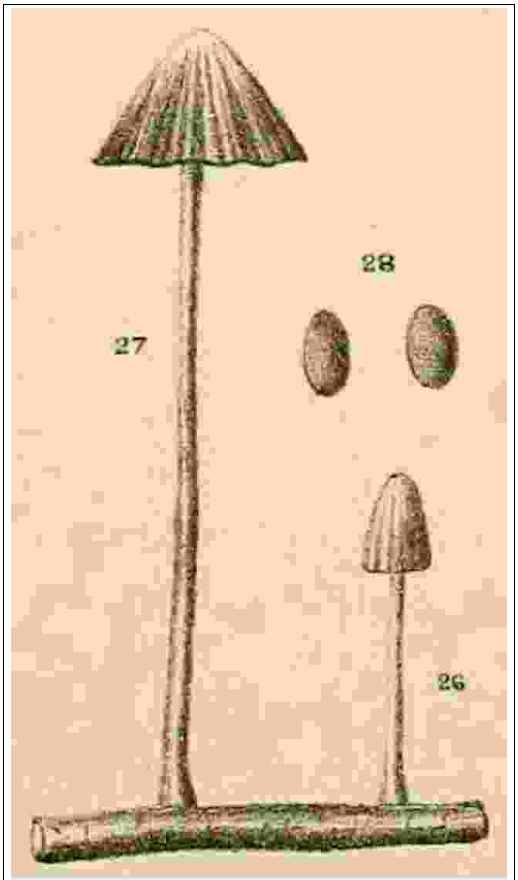

Figure 2. Illustration from the original description of *Coprinus aquatilis* Peck. Fig. 26. A young plant. Fig. 27. A mature plant. Fig. 28. Two spores x 400.

Spores 11-12.6 x 6.8-7.2 x 6.2-6.8 µm, av. 12.2 x 7.1 x 6.3 µm, Qav. = 1.7 (in front view), 1.9 (in profile), ellipsoid, ovoid, subfusoid, in profile flattened on one side, sometimes amygdaloid or with a suprahilar depression, in water red (Munsell 2.5YR 4/8); germ pore distinct, strongly eccentric. Basidia 4-spored, 22-42 x 10-11 µm, surrounded by 5-6 pseudoparaphyses. Pleurocystidia absent.

Cheilocystidia of two types: A: 35-80 x 12-30 µm, lageniform, rather numerous, B: 16-30 µm wide, spheropedunculate to subglobose, numerous. Caulocystidia 70-95 x 15-24 µm, lageniform, rather numerous.

Pileocystidia not seen. Scalp cap surface half-way from centre: pileipellis with spheropedunculate, subglobose to clavate, yellow brown, 15-30 µm wide cells, indicating a hymeniderm. Veil from cap surface: subglobose, ellipsoid, 20-40 µm wide, also otherwise shaped, smooth, incrusted or granulose. Clamps not seen on stem hyphae and stem base, 125 septa checked.

Habitat: Single growing on a branch in a small, slowly floating stream, surrounded by a moist, herb rich forest with *Alnus glutinosa, Corylus avellana, Anemone nemorosa, A. ranunculoides* and *Ficaria verna.*

Collection examined: Sweden: Skåne, Linderöd, Tågarp, west of Lindemölla, 21.V.2018, R. Tillgren (SZMC, Örstadius 3/18, Fig. 3).

Additional specimen examined: USA, New York, Adirondack Mts, August 1874, C.H. Peck (NYS f 300.1, holotype of *Coprinus aquatilis*).

Remarks: The description is based on one specimen. The species is recognized by the beautiful orange-brown cap, the granulose veil, the pubescent stem, spore size and shape, strongly eccentric germ pore, lageniform cheilo- and caulocystidia, and the lentic habitat on a branch in a small stream.

We tried to find pileocystidia without success. Krieglsteiner et al. (1982) and Schmidt-Stohn (2012) found them, but the latter author also stated that pileocystidia can not always be found.

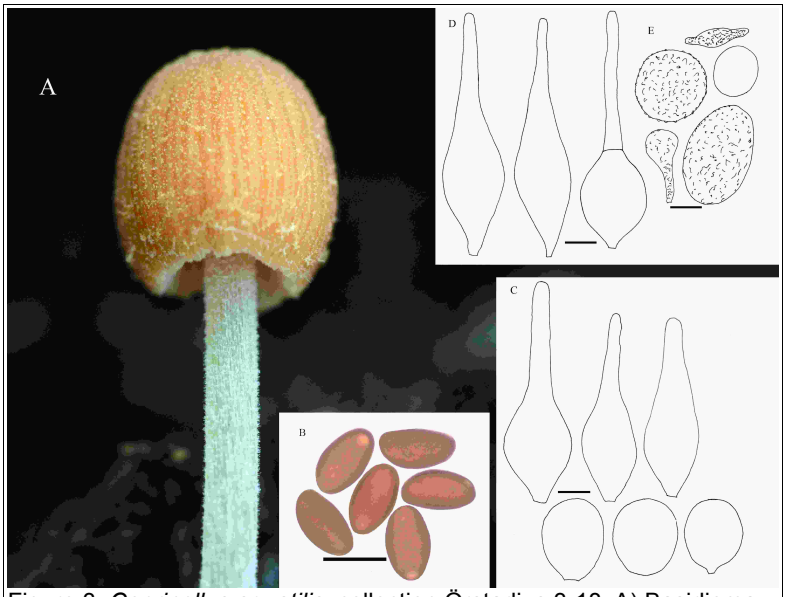

Figure 3. *Coprinellus aquatilis,* collection Örstadius 3-18. A) Basidioma. Photo L. Örstadius. B) Spores. C) Cheilocystidia. D) Caulocystidia. E) Veil cells. (scale bars = 10 µm B-E)

DISCUSSION Uljé and Bas (1991) placed their *Coprinus dilectus* in subsection Setulosi and considered it closely related to *C. pyrrhanthes*. The latter species differs in having vesiculose cheilocystidia and smaller spores. Nagy et al. (2012) did not obtain specimens for sequencing of *Coprinellus dilectus* sensu auct. PCR amplification or sequencing

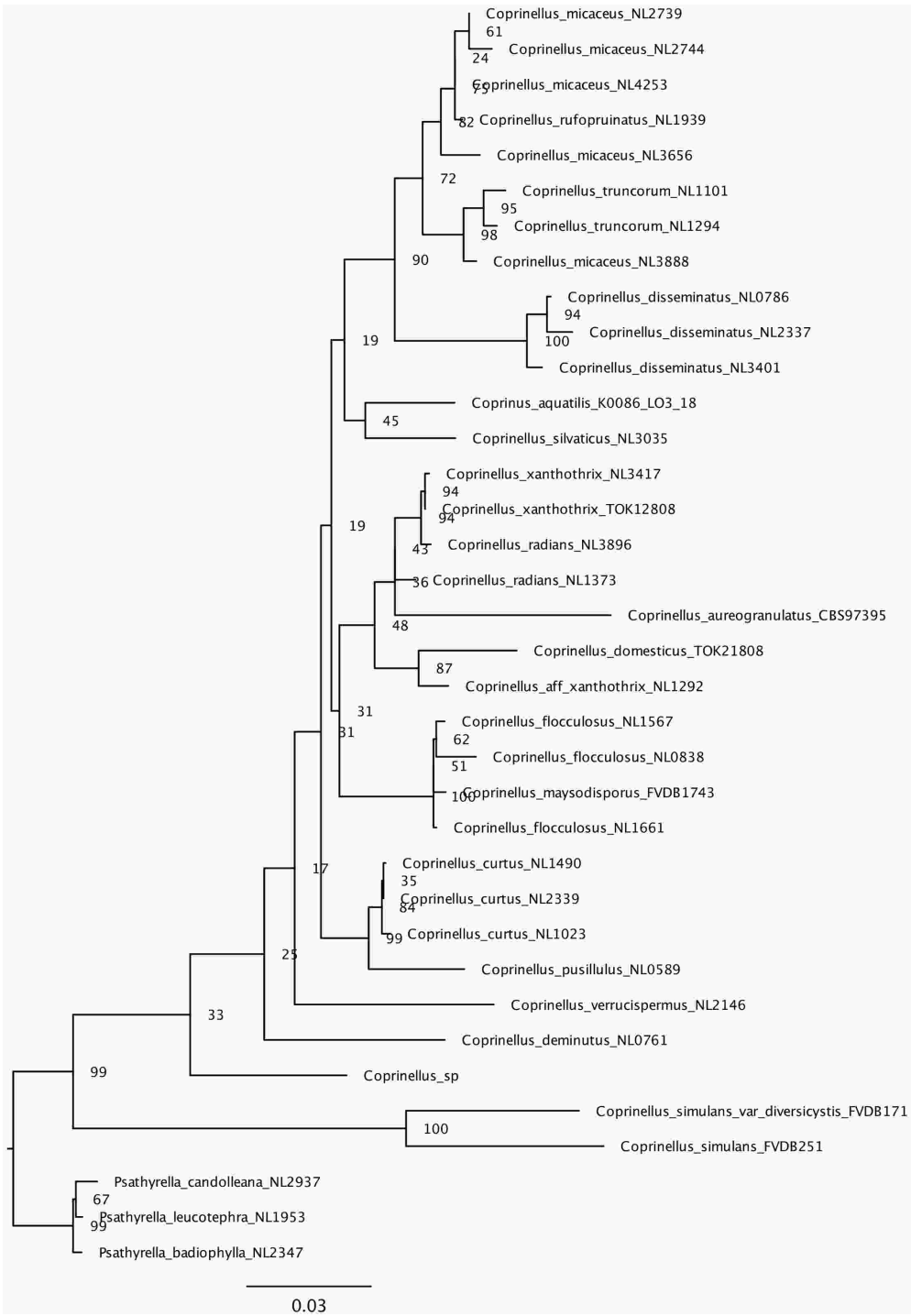

Figure 4. Maximum likelihood bootstrap analysis of section Domestici.

failed for *C. pyrrhanthes*. In their phylogenetic tree *Coprinellus* is represented by the clades Core Setulosi, eurysporoid, sabulicola, Domestici, and Micacei. Phylogenetic analyses (Fig. 4) placed our material of *Coprinellus aquatilis* close to *C. silvaticus* in the clade Domestici sensu Nagy et al. (2012).

Morphologically, the latter species differs in having larger basidiomata, a dry habitat, ornamented spores and central germ pore.

It must become a later task to investigate material of *C. aquatilis* from Norway and Finland. The species is also reported from Herrljunga in Sweden by Hernqvist (2018).

In the same paper Voto (2019) described the new species *Coprinellus neodilectus* and proposed new combinations of many species including *Coprinellus aquatilis*. It is not clear whether type material was examined. We consider *Coprinellus neodilectus* to be a later synonym of *Coprinellus aquatilis*.

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The genus *Morchella* section *Morchella* in Norway

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Norsk tittel: Rundmorkler (*Morchella* sect. *Morchella*) i Norge

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Ascomycetes, *Morchella* sect. *Morchella*, clade Esculenta, yellow morels, molecular systematics

NØKKELORD
Askomyceter, *Morchella* sect. *Morchella*, klade Esculenta, rundmorkler, molekylær systematikk

SAMMENDRAG
Ved å studere ITS rDNA sekvenser i 46 kollekter av rundmorkler i norske museumssamlinger og i nyere tilsendt materiale har vi påvist to arter og en varietet av rundmorkler i Norge: *Morchella esculenta* (rundmorkel), *M. vulgaris* og *M. vulgaris* var. *dunensis,* de to siste uten norsk navn. *Morchella esculenta* er desidert den vanligste av disse.

ABSTRACT
By studying ITS rDNA sequences of 46 yellow morel collections deposited in Norwegian fungaria or sent us by amateur mycologists, we discovered that two species and one variety of yellow morels occur in Norway, *i. e*. *Morchella esculenta, M. vulgaris*, and *M. vulgaris* var. *dunensis*. *Morchella esculenta* is by far the most common of these.

INTRODUCTION

This is a follow-up of our previous review dealing with the black morels, *Morchella* section *Distantes* ('spissmorkler'), in Norway (Weholt et al. 2020). The present review deals with the other section of *Morchella* occurring in Norway, section *Morchella* (yellow morels, 'rundmorkler'). Both reviews are based on molecular analyses and our main purpose is to report on which morel species occur in Norway, their geographic distribution and specific niche.

The genus *Morchella* Dill. ex Pers., which is theorised to have originated early in the Cretaceous period (O'Donnell et al. 2011), has more than 75 phylogenetically distinct species worldwide (Du et al. 2019) and about 37 species in Europe (Clowez and Moreau 2020). It has three sections of which the oldest one, section *Rufobrunnea* Clowez & Courtecuisse, has only two extant species. They both occur in Mediterranean habitats; one of them, *M. rufobrunnea*, was the first morel to be cultivated (Clowez and Moreau 2020). Section *Distantes* Boud., with about 26 European species is the largest section, and has at least 10 species in Norway (Weholt et al. 2019).

The third section, section *Morchella* (yellow morels), is represented by at least 11 species

in Europe; however, members of this sectionare rarely documented in Norway. Ascomata of yellow morels typically possess greyish to ochraceous caps that are ovoid to round and with ridges that tend to turn reddish and develop a white crust. They are saprotrophsor form biotrophic relationships with trees and plants that translocate carbon rich nutrients.

It is generally agreed that *Morchella* species are extremely difficult to discriminate from each other using morphological features. However, distinguishing between black and yellow morels is generally not problematic based on the cap shape and colour change from young to old specimens. With the publication of a new *Morchella* monograph (Clowez and Moreau 2020) identifying morels to species has been made much easier. The book conveys results from a life-long devotion to the genus combined with molecular expertise, and provides useful descriptions, photographs, and an identification key. We refer to this important presentation of the genus *Morchella* for identification of Norwegian finds.

MATERIALS AND METHODS

Materials

The study is based on 46 collections of putative yellow morels deposited in the Norwegian public fungaria in Oslo (O) and Trondheim (TRH) and newly collected material sent to Øyvind Weholt from amateur mycologists. Among them is one sample from Mallorca (Spain) of *M. vulgaris* var. *dunensis* collected by the Norwegian mycologist Sigmund Sivertsen (1929-2019) while the other 45 collections are from Norway, see Table 1 and 2. Until recently, most preserved specimens were collected by one of us, Roy Kristiansen (RK) in the Fredrikstad region (SE Norway) and accordingly, the geographical representation of our material is somewhat biased.

Methods

Total DNA was extracted from dry specimens employing a modified protocol based on Murray and Thompson (1980). Primers ITS1F and ITS4 (White et al. 1990, Gardes and Bruns 1993) were employed to amplify the ITS rDNA region. PCR products were checked in 1% agarose gels, and amplicons were sequenced with one or both PCR primers. Once sequence chromatograms were corrected to remove errors, text files of these were used to conduct BLASTn (Altschul et al. 1990) searches of the International Nucleotide Sequence Database Collaboration (INSDC, Cochrane et al. 2011) public database. Morel sequences in INSDC were mainly from studies conducted by Du et al. (2012a, b, 2020), Clowez et al. (2014), Richard et al. (2015), and Petrželová and Sochor (2019). Sequences first were aligned in MEGA 5.0 (Tamura et al. 2011) software with its Clustal W application and then realigned manually as needed to establish positional homology. The final alignment, which included 376/1123 variable/total sites, was loaded in MrBayes 3.2.6 (Ronquist et al. 2012), where a Bayesian analysis was performed using the GTR-G model (single partition, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after 0.27 M generations. Finally, a full search for the best-scoring maximum likelihood tree was performed in RAxML 8.2.12 (Stamatakis 2014) using the standard search algorithm (same partitions, GTRGAMMA model, 2000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70% bootstrap proportions (BP).

RESULTS AND DISCUSSION

Fig. 1 shows a phylogenetic tree of sect. *Morchella* with the Norwegian collections and the collection from Mallorca. The samples analysed grouped in two distinct clades: one

Table 1. Data for collections sequenced by Kerry O'Donnell

Voucher number in Herb O	ID Roy Kristiansen	ID Kerry O'Donnell	Original idenification (det. E. Jacquetant)	Sequence results	Location	Voucher number in Herb O	Habitat	Date of collection
O-257284	RK 81.01	M485	*M. pseudoumbrina*	failed	Østfold, Fredrikstad, Kråkerøy, Holte	O-257284	Black soil under *Ulmus*	26-May-1981
O-257285	RK 87.11	M490	*M. pseudoumbrina*	failed	Østfold, Fredrikstad, Onsøy, Østre Vikane	O-257285	Black soil under *Ulmus*	5-June-1987
O-257286	RK 89.12	M484	*M. pseudoumbrina*	failed	Østfold, Fredrikstad, Onsøy, Østre Vikane	O-257286	Black soil under *Ulmus*	19-May-1989
O-257288	RK 97.09	M493	*M. pseudoumbrina*	*M .esculenta*	Østfold, Fredrikstad, Kråkerøy, Holt	O-257286	Black soil under *Ulmus*	20-May-1997
O-257289	RK 98.26	M491	*M. pseudoumbrina*	*M. esculenta*	Østfold, Fredrikstad, Kråkerøy, Holt	O-257289	Black soil under *Ulmus*	20-May-1998
O-257290	RK 98-27	M497A/B	*M. pseudoviridis*	*M. esculenta*	Østfold, Fredrikstad, Kråkerøy, Holt	O-257290	Black soil under *Ulmus*	20-May-1998
O-257292	RK 01.01	M498	*M. pseudoviridis*	*M. esculenta*	Østfold, Fredrikstad, Kråkerøy, Holt	O-257292	Under *Ulmus*, calcareous soil	20-May-2001
O-257291	RK.98.28	M486	*M. rotunda*	*M. esculenta*	Buskerud, Øvre Eiker, Vestfossen, Hamre Nature Reserve	O-257291	Deciduous forest, calcareous soil	May-1998
O-257287	RK 95.60	M488	*M. vulgaris*	*M. esculenta*	Buskerud, Nedre Eiker, Krokstadelva, Enga 5	O-257287	In garden, sandy, *Pinus mugo*	3-June-1995

Table 2. Data for collections sequenced by Pablo Alvarado Garcia, ALVALAB

Voucher number in Herb O/Artskart*	**Isolate**	**Sequence results**	**Location**	**Habitat**	**Date of collection**	**ITS rDNA**
O-309188 / 14382065	ALV8015	*M. esculenta*	Vestfold, Tønsberg, Nordbyen 24	In old garden	8-May-2016	MW307504
Material lost	ALV12016	*M. esculenta*	Telemark, Bamble, Tangvall	In deciduous forest with *Ulmus* and *Corylus*	12-May-2017	MW307505
O-257281 / 21696867	ALV21092	*M. esculenta*	Telemark, Porsgrunn, Klepp	Deciduous forest, *Corylus, Picea,* calcareous	13-June-2019	MW307506
O-257283	ALV21226	*M. esculenta*	Telemark, Porsgrunn, Versvika	Forest, under *Pinus* etc., calcareous ground	2-June-2019	MW307507
O-257282 / 2269899	ALV21674	*M. esculenta*	Telemark, Tokke, Rui-Nord	Rich deciduous forest, probably calcareous groud	3-June-2019	MW307508
O-65772	ALV24920	*M. esculenta*	Hedmark, Ringsaker, Ringsaker church	Bark in garden	5-March-2003	MW307509
O-66421	ALV24921	*M. esculenta*	Oslo, Tåsen	Edge of flowerbed with bark and gravel	12-May-2003	MW307510
O-71623	ALV24922	*M. esculenta*	Oslo, Hovedøya	Under *Corylus*, barren soil and dry leaves	1-June-1997	MW307511
O-86558	ALV24924	*M. esculenta*	Vestfold, Sande Bjerkøya	Open, bushy site	13-May-1989	MW307512
O-90177	ALV24927	*M. esculenta*	Oslo, Hovedøya	Close to shore, on lawn	19-May-1988	MW307513
O-270132	ALV24929	*M. esculenta*	Oslo, Ekeberg, Sjømannskolen	Lawn, near large tree stump, tall grass	15-May-2000	MW307514
O-291103	ALV24930	*M. esculenta*	Buskerud, Nedre Eiker, Mjøndalen, Vikkollveien 34	Bark in garden	21-May-2010	MW307515
O-257280	ALV25125	*M. esculenta*	Buskerud, Lier, S of Gjellebekk nature protection area	Deciduous forest, *Alnus, Betula, Fraxinus*	28-May-2020	MW307516
O-370360	ALV24931	*M. esculenta*	Telemark, Porsgrunn	Lawn close to apple tree	5-July-2007	MW307517
TRH-3181	ALV25409	*M. esculenta* (noisy or cont.)	Nordland, Rana, Hammanes	Under *Ulmus*	10-June-1979	No sequence
TRH-3184	ALV25411	*M. esculenta* (noisy or cont.)	Sør-Trøndelag, Trondheim, Byåsen, Steinbeget	Newly repared lawn	26-May.1964	No sequence
No material/ 21792572	ALV21016	*M. vulgaris var. vulgaris*	Rogaland, Karmøy, Åkra, Støvegen 12	Old carrot field covered with cloth, bark, gravel and sand	31-March-2019	MW307518
O-222387	ALV24928	*M. vulgaris var. dunensis*	Rogaland, Hå, Holmasanden	In sandy meadow under *Salix repens*	23-April -2002	MW307519
TRH-12910	ALV25415	*M. vulgaris var. dunensis*	Mallorca, Alcudia, S' Oberta	Ruderate area	3-March-1985	MW307520

* Number in the Norwegian Biodiversity Information Centre (https://artskart1.artsdatabanken.no/default.aspx)

Figure 1. 50% majority rule ITS rDNA consensus phylogram obtained using MrBayes from 2025 sampled trees. For each sample, species name or an informal ad hoc 'Mes' code that was assigned in previous studies is provided. Nodes were annotated if they were supported by ≥ 0.95 Bayesian PP (left) or ≥ 70% ML BP (right).

with high identity to sequences of *M. esculenta* in public databases, and another sharing high identity to sequences of *M. vulgaris* and *M. dunensis*. While no significant differences were observed within *M. esculenta*, significant genetic structure was detected within the clade containing *M. vulgaris* and *M. dunensis*, although these were not resolved as reciprocally monophyletic. Twenty samples turned out to be black morels (*M. norvegiensis* (10) and *M. importuna* (1)), or useful DNA sequence data were not obtained (9).

Morchella esculenta (L.: Fr.) Pers. – Figs. 2-3. Synonyms: *M. rotunda* (Pers.) Boud., *M. pseudoviridis* Jacqet. (invalid name), *M. pseudoumbrina* Jacqet. (invalid name).

Typical features of *Morchella esculenta* are an ovoid to round cap, regular, polygonal pits, and ridges with white crests. In contrast to the somewhat similar *M. norvegiensis* of section *Distantes* the cap colour is dark in young ascomata and becomes paler with age. It is by far the most common of the yellow morels in Norway. Our 20 sequenced collections were from nemoral and hemiboreal regions in SE Norway. There are, however, two interesting

Figure 2. *Morchella esculenta*, Nordland, Rana, Hammarnes, S-exposed hill, under *Ulmus*, 10 June 1979, leg. H. Dissing & S. Sivertsen. Photo: Sigmund Sivertsen.

Figure 3. **A**. "*M. pseudoumbrina*." Holte, Kråkerøy, 10 May 2015, leg. Roy Kristiansen. **B**. "*M. pseudoviridis*", Holte, Kråkerøy, 22 May 2003, leg. Roy Kristiansen. Photo: Roy Kristiansen.

collections in TRH, which were identified as *M. esculenta* by S. Sivertsen, one of these is from Trondheim and one from N Norway (see Tab. 1). These yielded no sequence data due to contamination. The northernmost of these was collected by the Danish mycologist H. Dissing and S. Sivertsen in 1979 under *Ulmus* in the hemiboreal region in Rana municipality, Nordland, and has an ascomata morphology matching our concept of *M. esculenta* (Fig. 2). This collection may represent the northern most distribution of this species. Most of the Norwegian collections of *M. esculenta* were from disturbed or manmade habitats, often gardens with lawns and bark-covered flowerbeds. The rest are from mostly natural sites with deciduous trees such as *Alnus* sp., *Betula* sp., *Fraxinus excelsior*, *Salix* sp. and *Ulmus glabra*, apparently always in base rich sites.

Morchella esculenta is also one of the most common yellow morels in central and northwestern Europe, occurring in the lowlands and, less frequently, in the mountains. It has a wide Eurasian distribution from Europe to China (Loizides 2017, Clowez and Moreau 2020).

In the late 1970s and early 1980s RK collaborated with the French mycologist E. Jacquetant by posting him dried specimens of morels from the Fredrikstad region accompanied by colour photographs, among them specimens that Jacquetant identified as *M. pseudoviridis* sp. nov. and *M. pseudoumbrina*, a species he had described earlier on material from Central Europe. IT sequences from several of these collections show that all belong in *M. esculenta* (see Table 1, Richard et al. 2015).

Morchella vulgaris* var. *vulgaris (Pers.: Fr.) Gray. Fig. 4.
This is an extremely polymorphic species with more inflated ridges than those of *M. esculenta*, forming irregular pits giving the cap a labyrinth-like to cerebriform appearance. It also has a distinctive odor when fresh that is not present in *M. esculenta*. This is a common morel in temperate Europe, known as far east as Ukraine (Clowez and Moreau 2020). Our single voucher collection of this species is from Karmøy, Rogaland situated on the Atlantic coast of S Norway where it was growing in an old carrot field on soil covered by bark, gravel and sand as a top layer.

Morchella vulgaris* var. *dunensis (Castañera, J.L. Alonso & G. Moreno) Weholt & P. Alvarado comb. nov.
Basionym: *M. esculenta* f. *dunensis* Castañera, J.L. Alonso & G. Moreno, Yesca 8: 27 (1996)
= *Morchella andalusiae* Clowez & L. Romero in Clowez, Bull. Soc. Mycol. France 126: 255. 2012
= *Morchella dunensis* (Castañera, J.L. Alonso & G. Moreno) Clowez
= *Morchella spongiola* var. *dunensis* R. Heim, Les Champignons d'Europe, 1 Généralités. Partie Descriptive: Ascomycètes (Paris): 260 (1957). [nom. inval., Art. 39.1]
Mycobank: MB838153

Loizides et al. (2016) considered *M. esculenta* f. *dunensis* a distinct species closely related to *M. vulgaris* based on their reciprocal monophyly, unique ecology, and subtle diagnostic morphological features. The ITS sequences

Figure 4. *Morchella vulgaris,* Rogaland, Karmøy, Åkra, 31 March 2019, leg. Terje Mikkelsen. Photo: Terje Mikkelsen.

analysed by them differed in 7/1000 bp, while no evident apomorphic sites were present in three other genetic markers (*RPB1*, *RPB2*, *TEF1*). Intermediate ITS sequences between both taxa are known (AJ539473 from Kellner et al. 2007, GQ228476 from Kanwal et al. 2011, MN513757 and MN513758 from Du et al. 2020). Future studies are needed to more accurately determine the taxonomic status of these collections.

Partial reproductive isolation can be driven by multiple factors, including specialised habitat, a feature employed by Loizides et al. (2016) to separate *M. dunensis* from *M. vulgaris*. However, collections identified as *M. dunensis* occur in a variety of habitats, including the original coastal sandy soils with *Ammophila* (Castañera and Moreno 1996, Clowez 1997, Snabl et al. 2019), as well as other habitats associated with *Fraxinus*, *Castanea*, and *Ranunculus* (Clowez 2012), *Pinus* forests (Taşkin et al. 2012, Kaygusuz et al. unpubl., Bozok et al. 2020), and *Malus* orchards (Loizides et al. 2016). These habitats appear to be shared by *M. vulgaris* (Petrželová and Sochor 2019). In the present work, the sequenced Norwegian collection of this taxon, collected by J. I. Johnsen, was from a sand dune meadow in Hå, Rogaland on the Atlantic coast of S Norway. Two additional collections were from sand dunes in Hå collected by the same person and accessioned in O, but not sequenced. A collection from Mallorca (Balearic Islands, Spain) was analysed as well to provide further information about this taxon. According to Clowez and Moreau (2020), *M. esculenta* occasionally occurs in sand dunes, suggesting that this habitat alone is not enough to enforce complete reproductive isolation in these species. Finally, *M. dunensis* does not appear to occupy a particular geographical area, as it has been found in the Mediterranean region, but also in Xinjiang province of China (MK321872, MK321873), and now in Norway coastlands. These results suggest that *M. dunensis* does not have a significantly distinct habitat or distribution. Therefore, both names probably refer to partially isolated populations that occasionally occur in the same habitats and interbreed, so we here choose to consider *M. dunensis* a variety of *M. vulgaris*.

Morphologically, *M. vulgaris* var. *dunensis* has a labyrinth-like or somewhat spongy appearance and a remarkable odor similar to *M. vulgaris* var. *vulgaris,* but it is smaller and rounder (Clowez and Moreau 2020). The noted differences between the two (Loizides et al. 2016) could have a genetic basis, especially if *M. vulgaris* var. *dunensis* is a partially isolated population, but these differences could also be due to the influence of sandy environments. A more complete study including collections from other habitats and geographical regions is needed to further investigate these issues.

Summary

In Norway, three taxa of yellow morels are currently known: *M. esculenta, M. vulgaris* var. *vulgaris* and *M. vulgaris* var. *dunensis*. They produce ascomata from primo March to primo July. The relatively common *Morchella esculenta* occurs mainly in the SE part of the country, in temperate and hemiboreal regions, but possibly as far north as 66º in N Norway, almost at the Arctic Circle. The other two taxa were found on the Atlantic West coast of S Norway. Yellow morels are by far less common than black morels in Norway. In general, yellow and black morels are readily distinguished, but our study indicates that especially the black morel *M. norvegiensis* easily may be mistaken for a yellow morel when only the shape of the cap is considered - which has been the traditional way in Norway to distinguish between ‘rundmorkler’ and ‘spissmokler’.

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Hemileucoglossum pusillum, an earthtongue new to Norway

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NØKKELORD
Geoglossaceae, *Hemileucoglossum*, jordtunger, Norge

SAMMENDRAG
Hemileucoglossum pusillum ble første gang beskrevet fra Slovakia i 2017, og den er ellers kjent fra Spania. Første funn i Norge ble gjort allerede i 2010, og er seinere gjenfunnet de fleste år frem til i dag på samme lokalitet. På den tiden var det gjort lite med revisjon av slektene innenfor Geoglossaceae, og funnet forble ubestemt helt frem til i dag. Ved hjelp av mikroskopi og DNA analyser er det nå bekreftet at arten er *Hemileucoglossum pusillum*, som er første registrering av denne arten i Norge. *Pusillum* betyr liten og puslete, så et forslag til norsk navn kan være puslejordtunge.

ABSTRACT
Hemileucoglossum pusillum was first described from Slovakia in 2017 and is also known from Spain. The first record in Norway was collected as early as 2010 and is later found almost every year since on the same spot. At that time, little was done concerning revision of the genera in Geoglossaceae, and the fungus has remained undetermined until today. By microscopy and molecular studies, it was confirmed that the species was *Hemileucoglossum pusillum*, which is the first record of this species in Norway.

INTRODUCTION

The family Geoglossaceae (*sensu lato*) is very well represented in unfertilized grassland in the Southwestern part of Norway. At least 15 different species are known from the area, from the genera *Geoglossum* (*sensu lato*), *Trichoglossum* and *Microglossum* (Fadnes 2011) (*Microglossum* is now excluded from Geoglossaceae (*sensu stricto*)). The family Geoglossaceae is currently undergoing great changes, demonstrated by different molecular studies (Hustad et al. 2011 and 2013, Arauzo & Iglesias, 2014, Fedosova et al. 2018). New genera have been proposed like *Glutinoglossum* including the former *Geoglossum glutinosum, Sabuloglosum* including *Thuemenidium (Geoglossum) arenarium (Hustad et al. 2013), and Hemileucoglossum* to accommodate the

species *Geoglossum littorale* and allies (Arauzo & Iglesias 2014). Before these revisions took place, already in 2010, a new unknown earthtongue was found in SW-Norway. With available keys, it was not easy to determine. However, there were some similarities with *Geoglossum lineare* described by Hakelier (1967). Especially the form of the paraphyses was similar as well as the spores. However, *G. lineare* should have viscid stipe, and pale brown spores, while the stipe of this species was squamulose and the spores are hyaline. It therefore until now remained an unknown species.

The article by Arauzo & Iglesias (2014) brought new information on the revision of the Geoglossaceae, but an exact determination requires molecular studies.

After ten years of uncertainty, it was microscopically identified by one of the authors (VK) and later confirmed by molecular studies. According to DNA (ITS and LSU) this was *H. pusillum,* and therefore a new species of earthtongues in Norway. This taxon is previously only known from Spain (five locations) and Slovakia (two locations).

MATERIAL AND METHODS

Fresh material of the ascocarp was studied microscopically after soaking in water using a LEICA DM750 microscope and LEICA EZ4W stereo binocular. Spores, asci, paraphyses and setae hair were photographed by an integrated microscope-camera, LEICA ICC50 W and measured by LEICA application Suite (LAS) EZ software.

Molecular studies have been performed, and the fungus has been found identical with the type material. The DNA extraction, amplification and sequencing of the internal transcribed spacer region of the nuclear ribosomal DNA (nrITS1–5.8S–ITS2, ITS) and the 28S nuclear ribosomal large subunit region (nrLSU, LSU) were provided on commercial base in Alvalab (Spain).

Newly generated sequences were submitted in NCBI GenBank (http://www.ncbi.mlm.nih.gov, accession numbers: MW295710, MW295713)

Individual ITS and LSU datasets were created in MEGA7 (Kumar et al. 2016) and then were aligned in MAFFT v.7 Web tool (Katoh et al. 2019). Ambiguous regions were eliminated from individual alignments using TrimAl v.1.2b (Capella-Gutiérrez et al. 2009). The best-fit AICc-selected model of evolution (SYM+I+G for ITS and GTR+I+G for LSU) was calculated by PartitionFinder 2 (Lanfear et al. 2017).

The maximum likelihood (ML) phylogenetic analysis was run in RAxML v.7.2.6 (Stamatakis 2006). The Bayesian analyses (BA) was performed using MrBayes v.3.2.7 (Ronquist et al. 2012). Four independent chains were run one million generations with trees sampled every 100 generations. To evaluate the quality of a sample from the posterior and the continuous parameters, effective sample size (ESS) was estimated in Tracer v.1.7.1 (Rambaut et al. 2018). The clades with bootstrap support (BS) value $\geq$ 80% for ML analysis and posterior probability (PP) value > 0.95 for BA analysis were considered significant.

Individual alignments of ITS and LSU were concatenated into a single dataset. Further ML and BA analyses were performed on the combined dataset as described above except for four independent chains were run ten million generations. Alignments with obtained phylogenies were deposed in TreeBASE (http://treebase.org) under the submission ID 27328.

TAXONOMICAL PART

Original description

The original description is cited from Crous, PW, et al. (2017).

Ascocarps scattered to gregarious, clavate, stipitate, 0.8–3.5 cm tall, 0.1–0.5 cm wide, black throughout. Ascigenous part clavate,

broadly clavate or compressed, c. 1/4–1/2 of the total ascocarp length, 0.2–1.1 cm long, black, concolorous with the stipe, compressed or oval in cross section, sharply delimited from the stipe, smooth both in fresh and dry conditions. Stipe terete, cylindrical, oval in cross section, slender to robust, conspicuously hairy with dark brown setose hairs in tufts in upper part of the stipe when fresh, rough to squamulose when dry.

Asci clavate to broadly clavate, (135–)141.5–181.5(–187) × (14–)15.5–23.5(–25) µm (measured in water), Q = (6.3–)6.8–8.7(–9.5), 8-spored, with euamyloid apical ring and inamyloid wall in MLZ and IKI.

Ascospores elongate-clavate, subfusiform to fusiform, narrowed to the base, sometimes slightly curved, (41–)50–76.5(–82) × (5–)5.5–7.5(–8) µm (in water), Q = (8.5–)12.6(–15.2), hyaline, finally in some asci becoming brown, predominantly 3–4-septate, rarely with 0–5(–6) septa. Ascoconidia not observed.

Paraphyses cylindrical, sparsely septate, 2–3 µm diam, straight to slightly curved and inflated at the apex, hyaline at basal part to pale brown at the apex, embedded in a dense brown amorphous matter, extending beyond the asci. Apical cells usually inflated and constricted or pyriform, sometimes proliferating (12.5–)18.5–46(–54) × (4.5–)6–8.5(–11) µm.

Stipe surface squamulose of protruding paraphysal elements forming scales and with tufts of dark brown setose septate hairs (85–)90–120(–144) µm long, straight, moderately septate, basal cell usually inflated, (7–)10–13 (–17.5) µm, medial part (4.5–)5.5 –7(–9.5) µm and apical part (2–)3 µm with rounded apex.

Description of the Norwegian material

Specimen molecular studied:
Location: Hovaneset, Stord municipality, Vestland county.
Date of collecting: 10.09.2017
Coordinates: 32V LM 05902,34580
Collector: Per Fadnes
Herbarium number: O-F-257329.

Macro- and micromorphological studies are in addition based on several collections from the same spot from different years. These collections are stored in a private herbarium by one of the authors (PF).

Locality

Specimens of *H. pusillum* were found during several years from 2010 to 2020. The locality is a semi natural calcareous grassland (grazed by sheeps) in a peninsula (Hovaneset) in Stord municipality, SW-Norway. Grassland fungi on this locality have been studied since 2003, the last 11 years weekly during the season. Results from the 11 first years were published in 2014 (Fadnes 2014), and a number of totally 71 different grassland fungi, among them ten earthtongues have been found in the locality. During the last seven years, the number has raised to 90 different species, making it the most species rich locality of grassland fungi in Norway known today. *H. pusillum* grows in a north facing hill only a few meters from the seashore. It is heavily embedded in a dense moss-carpet, and due to its very small size it can be difficult to spot. However, it has been found eight times during the last 11 years, appearing on the same spot (Fig. 1).

Macromorphology

Ascocarps are black throughout, mostly scattered, clavate, stipitate, 1.0–3.5 cm tall – they vary in size but are relatively small compared to other earthtongues (Fig. 2). Ascigenous part is clavate, sometimes compressed, twisted and folded, spatuliform, sometimes irregularly lobed and sometimes with longitudinal groove(s), 0.4–0.8 cm wide, 0.6–1.0 cm long, smooth, round to oval, normally sharply delimited from the stipe.

Stipe cylindrical sometimes curved, slender to robust depending on size of the ascocarp,

Figure 1. Locality where *H. pusillum* grows in Hovaneset, Stord mnucipality, SW-Norway. Photo: PF

1–2.3 cm long, 0.13–0.17 cm wide. Squamulose, rough due to tufts of setose hair especially in the upper part.

Micromorphology

Asci clavate to broadly clavate, (127–)140–180(–220) × 17–22 µm, Q = 7.2–9.0 (–9.5) (measured in water), eight spored (Figure 3).

Figure 2. Ascocarps of *H. pusillum* from Hovaneset, SW-Norway. Photo: PF

Ascospores elongate, clavate, fusiform often tapering to one base, often curved, normally hyaline, 0-4 septate. Septa often difficult to spot, seldom more than four septa, (41–) 52 – 70 (–75) × (4.5–) 5.5–7.5 (–8.2) µm, Q = 7.0–12.2. (Fig. 4A and B)

Paraphyses cylindrical, sparsely septate, 2–4 µm in diameter, up to 7–8 µm at the terminal cell, which is some inflated, constricted or pyriform at the apex. Paraphyses are hyaline but brown at apex, embedded in a dense brown amorphous matter and extending beyond the asci (Fig. 3).

Stipe surface squamulose due to tufts of brown septate setae hairs extending from the surface. Basal cell normally inflated, broader then the rest of the setae hair. Size of hair (70–) 90–140 (–160) µm with rounded apex (Fig. 5).

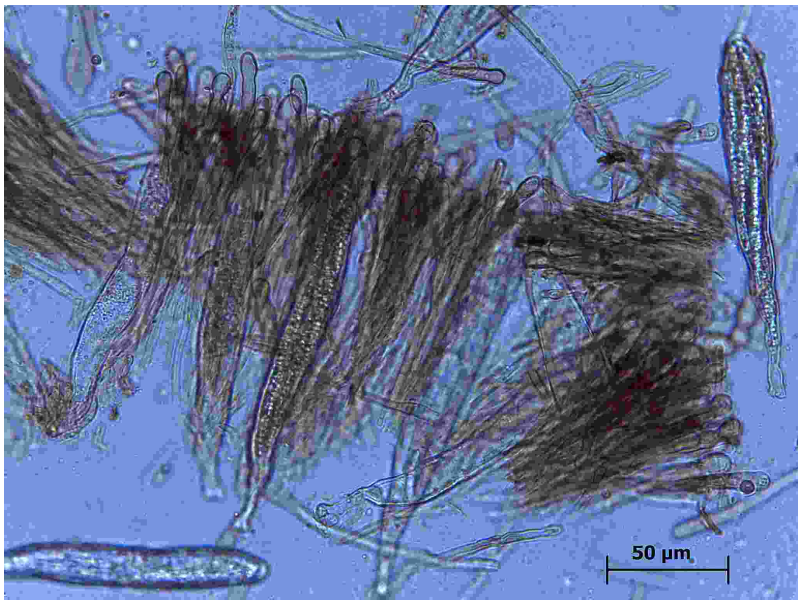

Figure 3. Asci and paraphyses of *H. pusillum* with dense brown amorphous matter from Hovaneset, SW-Norway. Photo: PF

Molecular study

Table 1 represents 25 specimens involved in the phylogenetic analysis. Five type specimens including holotype of *H. pusillum* were used in the analyses. *Graddonia coracina* (Bres.) Dennis was taken as an outgroup. Two newly generated sequences (one ITS and one LSU) were obtained for this study. In total 25 ITS and 23 LSU sequences were analyzed.

The concatenated ITS-LSU data matrix had an aligned length 1521 bp, which was reduced to 1321 bp after elimination of 200 bp by TrimAl. To remove the prestationary posterior probability distribution burn-in of 19% (ESS = 10672.1) was estimated with Tracer to be sufficient. The most likely tree topology produced by the ML analysis of the combined ITS-LSU dataset is illustrated (Fig. 6).

The phylogenetic analyses confirmed identity of the Norwegian specimen and specimens of *H. pusillum* from Slovakia and Spain.

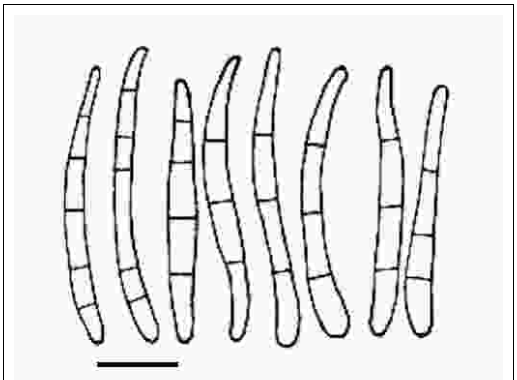

FIgure 4A. Spores from *H. pusillum* from Hovaneset SW-Norway. Drawings showing some of the variability among the spores of *H. pusillum*. Bar. 20 µm

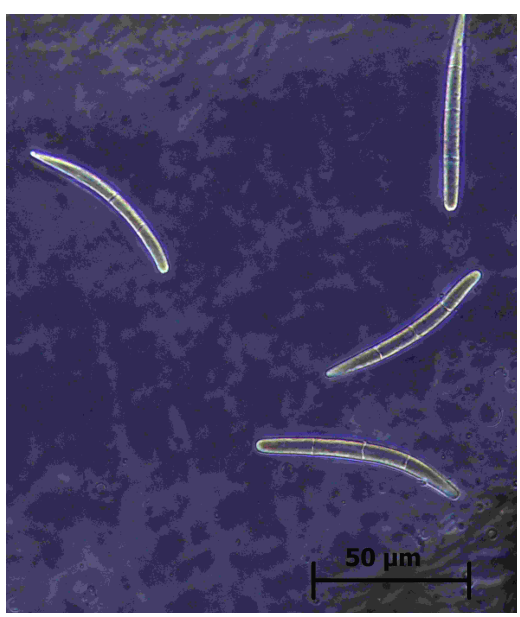

Figure 4B. Spores from *H. pusillum* from Hovaneset, SW-Norway. Photo: PF

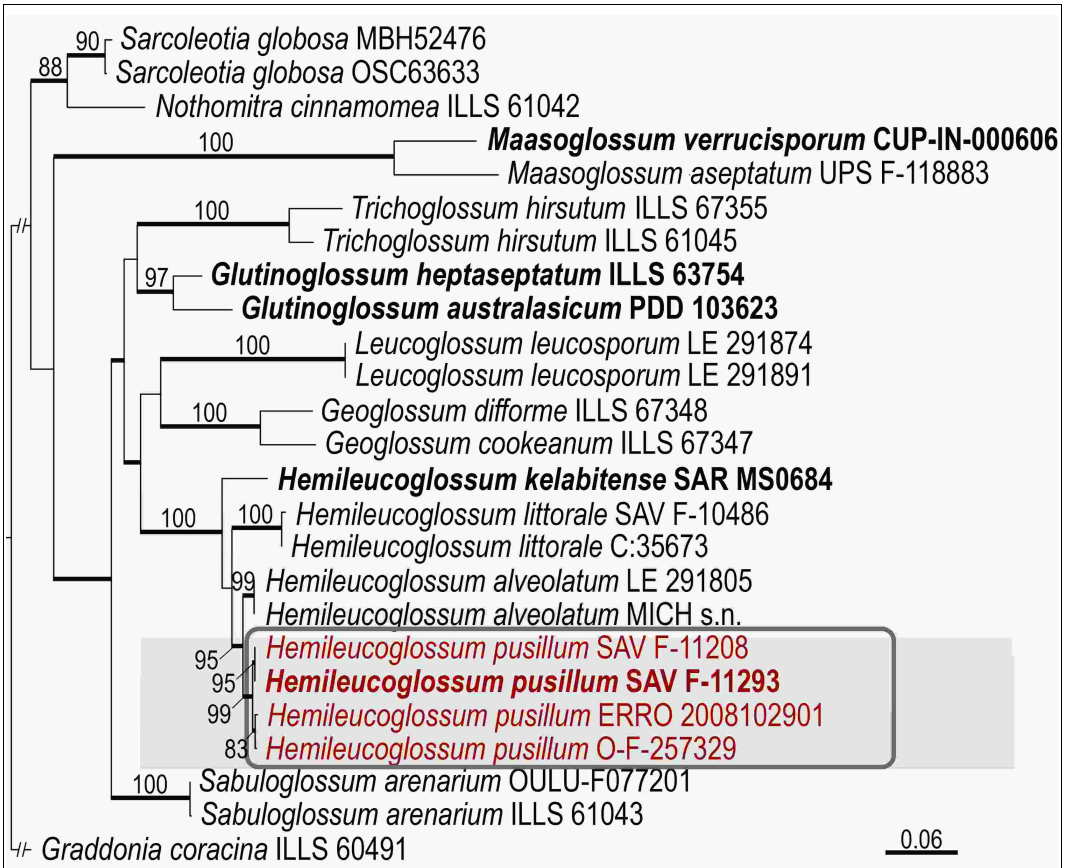

Figure 6. Phylogenetic tree generated from maximum likelihood analysis based on ITS–LSU sequence data. Numbers above branches indicate BS values > 80%, thickened branches indicate PP value > 0.95. Holotypes and isotype are in bold. The clade *H. pusillum* is indicated with box and color. Affiliation to the genus *Hemileucoglossum* is highlighted. Scale bar represents the number of nucleotide changes per site.

Sequences from all these specimens formed a strongly supported clade of *H. pusillum* (BS=99%, PP=1). A sister clade to *H. pusillum* was *H. alveolatum*.

COMMENTS

The taxonomy of Geoglossaceae has historically been difficult due to lack of good morphological characters to distinguish the different species. The group includes species mostly with black or blackish color and generally stipitate, claviform or capitate form. The ascocarps of most earthtongues genera and species show a great variation both in size and in form, and microscopic characters are therefore important. The genus *Trichoglossum* is the easiest one, because it is densely covered with long setae hairs all over the ascocarp, and in Norway, we have until now, only recognized three different species. The genus *Geoglossum* (sensu latu) is the most difficult genus and have recently been revised by many authors. Schoch et. al. (2009) reduced the family only to include the genera *Sarcoleotia*, *Geoglossum* and *Trichoglossum*. *Microglossum,* which has earlier been included in

Table 1. Specimens and NCBI GenBank accession numbers of DNA sequences used in phylogenetic analysis.

Species	Country	Voucher No.	GenBank accession No.		Notes
			ITS	LSU	
Geoglossum cookeanum	Czech Republic	ILLS 67347	KC222122	KC222135	
G. difforme	USA	ILLS 67348	KC222123	KC222136	
Glutinoglossum australasicum	New Zealand	PDD 103623	KP690088	KP690100	holotype
G. heptaseptatum	Czech Republic	ILLS 63754	KC222130	KC222143	holotype
Graddonia coracina	USA	ILLS 60491	JQ256423	JN012009	outgroup
Hemileucoglossum alveolatum	USA	MICH s.n.	KP657560	KP657565	
H. alveolatum	Russia	LE 291805	MF353087	—	
H. littorale	Denmark	C:35673	KP657561	KP657566	
H. littorale	Slovakia	SAV F-10486	MF353089	MF353092	
H. kelabitense	Borneo	SAR MS0684	MT021979	MT021912	holotype
H. pusillum	Norway	O-F-257329	MW295710*	MW295713*	
H. pusillum	Slovakia	SAV F-11293	MF353090	MF353093	holotype
H. pusillum	Slovakia	SAV F-11208	MF353088	MF353091	
H. pusillum (as *H. littorale*)	Spain	ERRO 2008102901	KP144108	—	
L. leucosporum	Russia	LE 291891	KP272112	KP272113	
L. leucosporum	Russia	LE 291874	KP272114	KP272115	
Maasoglossum aseptatum	Sweden	UPS F-118883	KP657562	KP657567	
M. verrucisporum	Bhutan	CUP-IN-000606	KP657563	KP657568	isotype
Nothomitra cinnamomea	France	ILLS 61042	JQ256424	JQ256439	
Sabuloglossum arenarium (as *Thuemenidium arenarium*)	Netherlands	ILLS 61043	JQ256426	JQ256440	
S. arenarium (as *T. arenarium*)	Finland	OULU-F077201	GU324765	GU324764	
Sarcoleotia globosa		OSC63633	AY789410	AY789409	
S. globosa		MBH52476	AY789429	AY789428	
Trichoglossum hirsutum	Czech Republic	ILLS 61045	JQ256428	JQ256442	
T. hirsutum	USA	ILLS 67355	KC222132	KC222145	

* – sequences obtained in this study.

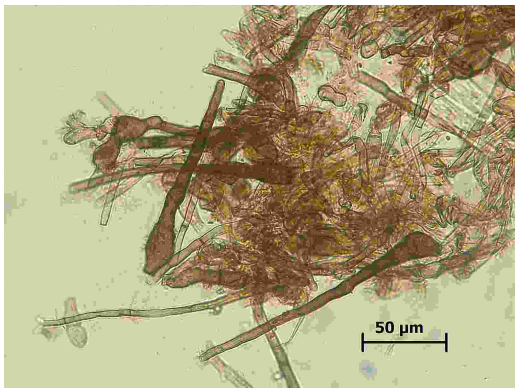

Figure 5. Setose hairs from stipe of *H. pusillum* from Hovaneset, SW-Norway. Photo: PF

Geoglossaceae, is now excluded, and shown to be very distant related based on molecular methods (Schoch et al 2009, Sandnes 2006). Hustad et al. (2011 and 2013) also included the genus *Nothomitra* in Geoglossaceae and created a new genus *Sabuloglossum* (including the former *Geoglossum arenarium*) and *Glutinoglossum* (including the former *Geoglossum glutinosum)*. Studies of Fedosova et al. (2018) have later proposed 13 species in the genus *Glutinoglossum* by molecular studies, where seven species are known from Europe.

The studies of Arauzo & Iglesias (2014) confirmed the genus *Leucoglossum* proposed by Imai in 1942. They also proposed a new genus *Hemileucoglossum,* which includes species with hyaline spores and setae on the stipe showing resemblance with those of the genus *Trichoglossum*.

The type species of the genus *Hemileucoglossum, H. littorale* differs from *H. pusillum* in having smaller asci and spores, and maybe the best distinguishing character is the presence of long brown branched hyphae on the stipe resembling a mesh. The ecology is also different since *H. littorale* is growing on annually exposed sandy shores of oligotrophic lakes and on soil in a fen-meadow.

There are some small differences in the microscopic data between the Norwegian collect of *H. pusillum* and the holotype, but it should be within the variation to be expected. Spores are in average a little bit smaller, the asci are in the same range but have a lager maximum size, and the same is for the setose hairs. We have data from the Norwegian species going back ten years in time, and they are all showing the same pattern. Pictures of the ascocarp from all those years shows a great variety both in form and in size, but are all within the stated data, the same is for the microscopic data.

The location where it was found has been surveyed intensively since 2003, so it is no surprise that it was found already in 2010. The area contains at least 10 different earthtongues from different genera, so it was clear early that this was a new unidentified species.

The article by Arauzo and Iglesias (2014) contains very good pictures and drawings of microscopic characters of *Hemileucoglossum pusillum* (misinterpreted as *H. littorale*) so it is possible to get a long way just by the pictures and illustrations in the article. However, it was first in 2020 that the unnamed earthtongue was identified both microscopically and by molecular investigation. This is so far the only known occurrence of *Hemileucoglossum pusillum* in Norway.

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Caesiodiscus populicola gen. et sp. nov. (Leotiomycetes, Helotiales), a remarkable new corticolous ascomycete from Norway

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Norsk tittel: *Caesiodiscus populicola*, en bemerkesesverdig ny barklevende sekksporesopp fra Norge

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KEYWORDS
Caesiodiscus, Helotiales, new species, phylogeny, taxonomy

NØKKELORD
Caesiodiscus, fylogeni, Helotiales, ny art, taksonomi

SAMMENDRAG
Den nye sekksporesoppen *Caesiodiscus populicola* Holien og Suija blir her beskrevet basert på morfologiske, anatomiske og molekylære karakterer. Artens systematiske plassering innenfor orden Helotiales er uklar, men analyser av nuLSU-sekvenser tyder på at de nærmeste slektningene er *Connersia rilstonei* og *Pleuroascus nicholsonii*. Den nye arten har distinkte karakterer både habituelt og mikroskopisk. Den vokser på stammer av løvtrær med rik bark og det viktigste vertstreet er osp. Arten er så langt bare kjent fra Norge hvor den hovedsakelig er funnet langs kysten.

ABSTRACT
A new ascomycete genus and species *Caesiodiscus populicola* Holien and Suija is herein described based on morphological, anatomical and molecular characteristics. Its systematic position within the Helotiales is unclear, but analysis of nuLSU sequences indicated that the closest relatives are *Connersia rilstonei* and *Pleuroascus nicholsonii*. The species is distinct both macroscopically and microscopically and is corticolous on deciduous trees with a high bark-pH. The most common phorophyte is *Populus tremula*. It is at present only known from Norway, mainly along the west coast.

INTRODUCTION

During the last decade of fieldwork along the west coast of Norway we have come across a distinct, corticolous ascomycete. The species has pruinose, bluish grey to greyish apothecial disc, distinct greyish white excipulum, 4-spored asci and eumuriform ascospores, and it grows mainly on old trunks of living *Populus tremula* L. With such distinct combined microscopic, macroscopic and ecological characters, we optimistically searched for its name.

Surprisingly, we were not able to find neither a name nor a genus, not even a family, for this species. We first thought the species could belong in the family Triblidiaceae (Leotiomycetes), which was recently revised (Karakehian et al. 2019), but preliminary studies indicated that this was probably not true. In the present study, we address the taxonomic affinity of this new species using morphological, anatomical and molecular data.

MATERIALS AND METHODS

Material

This study is based on material collected by the first author. In addition, we have received collections from several other persons. The material is deposited in the herbarium in Trondheim (TRH) with duplicates to O, TUF and UPS.

Microscopy

We examined dried herbarium specimens by standard techniques, using Leica MZ8 and Leica S4E stereomicroscopes, and Zeiss Axio A1 and Leica DM750 light microscopes. For examination of details of the ascomata we used razor-blade-cut sections mounted in tap water, in 10 % aqueous solution of potassium hydroxide (KOH, K), c. 50% nitric acid (HNO_3, N), Cresyl Blue (CRB) and in Lugol's iodine solution (I). For observation of amyloid reactions of the ascus apical apparatus, Lugol's solution both with (denoted as K/I) and without pretreating with KOH were used.

Measurements were made in water and the sizes are presented as (minimum-)average (-maximum) value.

DNA extraction, PCR amplification and DNA sequencing

DNA extraction, amplification and purification were carried out at Tartu University (TU). Genomic DNA was extracted from ascomata of five specimens (Table 1) using High pure PCR Template Preparation Kit (Roche Applied Science®, Penzberg, Germany) following the protocol provided by the manufacturer. We amplified four ribosomal loci. These include three nuclear (internal transcribed spacer (nuITS), large subunit (nuLSU), and small subunit (nuSSU)) and one mitochondrial (small subunit (mtSSU)) DNA regions. To amplify these four loci, we used the following primer pairs, respectively: ITS0F-LA-W (Tedersoo et al. 2008), LROR-LR7 (Vilgalys and Hester 1990), SSU1-SSU3R (Pärtel et al. 2017), and mrSSU1-mrSSU3R (Zoller et al. 1999). Sample preparation, polymerase chain reaction (PCR) amplification and DNA purification are described in detail in Suija et al. (2017). Both strands were Sanger sequenced at Macrogen Inc. (Amsterdam, the Netherlands). The nuITS sequences were sequenced with primer pair ITS4 and ITS5 (White et al. 1990),

Table 1. Voucher information and GenBank accession codes corresponding to sequences generated for this study. Sequences from type specimen are marked in bold.

Laboratory code	Fungarium	Collector and collection number	nuITS	nuLSU	nuSSU	mtSSU
AS364	TRH-F-17978	Holien 17/18	MW298844	MW298855	-	MW298850
AS443	**TUF-087471**	**Holien 15910**	**MW298848**	**MW298857**	-	**MW298854**
TR391	TUF-091126	Olsen OO-L-19.02	MW298845	MW298856	-	MW298851
TR392	TRH-F-17225	Jordal s.n.	MW298846	-	-	MW298852
TR393	TRH-F-17224	Jordal s.n.	MW298847	-	MW298849	MW298853

Table 2. GenBank accession codes of nuLSU sequences used for building phylogeny. The taxonomy of species follows Jaklitsch et al. (2016) and Johnston et al. (2019).

GenBank acc. code	Species name	Taxonomy
MK226457	*Alatospora acuminata*	Leotiales, incertae sedis
AB481317	*Albotricha acutipila*	Lachnaceae, Helotiales
JN086746	*Arachnopeziza obtusipila*	Arachnopezizeaceae, Helotiales
MK226456	*Articulospora tetracladia*	Discinella-Pezoloma lineage, Helotiales
JN086709	*Ascocoryne cylichnium*	Gelatinodiscaceae , Helotiales
JN086695	*Brunnipila fuscescens*	Lachnaceae, Helotiales
EU940107	*Bryoscyphus dicrani*	Helotiaceae, Helotiales
KJ663870	*Bulgaria inquinans*	Phacidiaceae, Phacidiales
KR094163	*Calycellinopsis xishuangbanna*	Helotiales, incertae sedis
KX090811	*Cenangiopsis quercicola*	Cenangiaceae, Helotiales
KX090822	*Cenangium acuum*	Cenangiaceae, Helotiales
AY487083	*Chaetomella oblonga*	Chaetomellaceae, Helotiales
AY544669	*Chlorociboria cf. aeruginacens*	Chlorociboriaceae, Helotiales
MH729335	*Chlorosplenium chlora*	Mollisiaceae, Helotiales
JN086732	*Cistella albidolutea*	Stamnaria lineage/Han Clade 9
KX090815	*Claussenomyces prasinulus*	Tympanidaceae
AY544657	*Coccomyces dentatus*	Rhytismataceae
GQ154611	*Collophorina paarla*	Tympanidaceae
MK314598	*Collophorina rubra*	Tympanidaceae
FJ176866	*Connersia rilstonei*	Helotiales, incertae sedis
AY544680	*Crinula caliciiformis*	Leotiomycetes, incertae sedis
MH985296	*Cryptohymenium pycnidiophorum*	Helotiales sclerotinioid clade
DQ470944	*Cudoniella clavus*	Helotiaceae, Helotiales
EU107207	*Cyttaria darwinii*	Cyttariaceae
EU107223	*Cyttaria hariotii*	Cyttariaceae
DQ247801	*Dermea acerina*	Dermateaceae, Helotiales
AB570319	*Dictyocatenulata alba*	Ostropomycetidae
AB570320	*Dictyocatenulata alba*	Ostropomycetidae
KX090834	*Diplocarpa bloxamii*	Cordieritidaceae, Helotiales
EU940116	*Discinella schimperi*	Discinella-Pezoloma lineage, Helotiales
KX090798	*Encoelia furfuracea*	Cordieritidaceae, Helotiales
KX090809	*Encoelia heteromera*	Cordieritidaceae, Helotiales
EU940128	*Epiglia gloeocapsae*	Mniaeciaceae
KC834021	*Filosporella fistucella*	Helotiales, incertae sedis
MH485386	*Gelatinopsis fungicola*	Helicogoniaceae, Phacidiales

GenBank acc. code	Species name	Taxonomy
KC834029	*Gyoerffyella rotula*	Discinella-Pezoloma lineage, Helotiales
JN086755	*Hamatocanthoscypha laricionis*	Pezizellaceae, Helotiales
MH870940	*Haplographium delicatum*	Hyaloscyphaceae, Helotiales
JN086748	*Hyalopeziza pygmaea*	Hyaloscyphaceae, Helotiales
JN086705	*Hymenoscyphus caudatus*	Helotiaceae, Helotiales
NG66420	*Hymenoscyphus ohakue*	Helotiaceae, Helotiales
HM140528	*Hypoderma rubi*	Rhytismataceae
HQ609479	*Infundichalara microchona*	Pezizellaceae, Helotiales
KX090833	*Ionomidotis olivascens*	Cordieritidaceae, Helotiales
MH748087	*Lachnellula subtilissima*	Lachnaceae, Helotiales
JN086698	*Lachnum abnorme*	Lachnaceae, Helotiales
DQ470978	*Lambertella subrenispora*	Rutstroemiaceae, Helotiales
AB481319	*Lasiobelonium lonicerae*	Lachnaceae, Helotiales
DQ267627	*Lemonniera aquatica*	Discinella-Pezoloma lineage, Helotiales
AY544644	*Leotia lubrica*	Leotiaceae, Leotiales
FJ176884	*Leuconeurospora pulcherrima*	Pseudeurotiaceae, Phacidiales
KX090842	*Llimoniella terricola*	Cordieritidaceae, Helotiales
DQ470957	*Loramyces macrosporus*	Loramycetaceae, Helotiales
MK599207	*Marthamyces dracophylla*	Marthamycetaceae, Marthamycetales
DQ470954	*Meria laricis*	Cenangiaceae, Helotiales
KX090817	*Microglossum olivaceum*	Leotiaceae, Leotiales
DQ470981	*Microglossum rufum*	Leotiaceae, Leotiales
JN086721	*Microscypha ellisii*	Pezizellaceae, Helotiales
JN086706	*Microscypha sp*	Pezizellaceae, Helotiales
EU940115	*Mniaeciaceae nivea*	Tympanidaceae, Phacidiales
AB926162	*Moellerodiscus pinicola*	Rutstroemiaceae, Helotiales
DQ470942	*Mollisia cinerea*	Mollisiaceae, Helotiales
JN086707	*Mollisina uncinata*	Mollisiaceae, Helotiales
KC834033	*Mycofalcella calcarata*	Helotiaceae, Helotiales
AY541491	*Myxotrichum deflexum*	Myxotrichaceae , Helotiales
FJ176867	*Naemacyclus fimbriatus*	Marthamycetaceae, Marthamycetales
FJ176865	*Neobulgaria pura*	Gelatinodiscaceae , Helotiales
JN086683	*Olla millepunctata*	Pezizellaceae, Helotiales
DQ470967	*Pezicula carpinea*	Dermateaceae, Helotiales
DQ470976	*Phacidium lacerum*	Phacidiaceae, Phacidiales
AB926130	*Phaeohelotium epiphyllum*	Helotiaceae, Helotiales
JN086727	*Phialina lachnobrachyoides*	Pezizellaceae, Helotiales
MH869755	*Phialocephala dimorphospora*	Mollisiaceae, Helotiales

GenBank acc. code	Species name	Taxonomy
KR859069	*Phlyctema vagabunda*	Dermateaceae, Helotiales
MH870939	*Pilidium acerinum*	Chaetomellaceae, Helotiales
MH872404	*Pleuroascus nicholsonii*	Helotiaceae, Helotiales
AB926136	*Poculum pseudosydowia*	Rutstroemiaceae, Helotiales
JN086753	*Polydesmia pruinosa*	Helotiales sclerotinioid clade
MG719709	*Polyphilus frankenii*	Stamnaria lineage/Han Clade 9
DQ470949	*Potebniamyces pyri*	Phacidiaceae, Phacidiales
HM140560	*Propolis versicolor*	Marthamycetaceae, Marthamycetales
DQ470988	*Pseudeurotium zonatum*	Pseudeurotiaceae, Phacidiales
KR859074	*Pseudofabraea citrica*	Dermateaceae, Helotiales
JN086699	*Psilachnum staphyleae*	Stamnaria lineage/Han Clade 9
AF356696	*Rhytisma acerinum*	Rhytismataceae
JN086717	*Rodwayella citrinula*	Pezizellaceae, Helotiales
AB628056	*Roesleria subterranea*	Helotiaceae, Helotiales
KT972712	*Roseodiscus formosus*	Helotiales, incertae sedis
KX090797	*Rutstroemia bulgarioides*	Rutstroemiaceae, Helotiales
DQ470963	*Rutstroemia firma*	Rutstroemiaceae, Helotiales
MH748088	*Sclerotinia pseudotuberosa*	Sclerotiniaceae, Helotiales
MH872858	*Sordaria fimicola*	Sordariomycetes (outgroup)
FJ176895	*Thelebolus ellipsoideus*	Thelebolaceae
JQ256441	*Thuemenidium atropurpureum*	Leotiaceae, Leotiales
MN540636	*Triblidium caliciiforme*	Triblidiaceae
JN086701	*Trichopeziza sulphurea*	Lachnaceae, Helotiales
AB481307	*Trichopezizella otani*	Lachnaceae, Helotiales
GQ477333	*Tricladium splendens*	Helotiaceae, Helotiales
EU940114	*Trizodia acrobia*	Mniaeciaceae
KX090835	*Trochila laurocerasi*	Cenangiaceae, Helotiales
DQ470983	*Tryblidiopsis pinastri*	Rhytismataceae
JN086682	*Urceolella crispula*	Stamnaria lineage/Han Clade 9
KC834036	*Varicosporium delicatum*	Discinella-Pezoloma lineage, Helotiales
AB546954	*Venturiocistella japonica*	Helotiales - Han Clade 4
FJ176874	*Vibrissea truncorum*	Vibrisseaceae, Helotiales
KX090824	*Xeropilidium dennisii*	Chaetomellaceae, Helotiales
AY544648	*Xylaria hypoxylon*	Sordariomycetes (outgroup)

nuLSU with CTB6 (Garbelotto et al. 1997) and LR7, and mtSSU and nuSSU with same primers as amplified. Sequencher 4.10.1. (GeneCodes Corp®, Ann Arbor, Michigan, USA) was used to check, assemble and manu-

The consensus sequences were compared with those publicly available in National Center for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih.gov/) and

Table 3. The results of *blastn* comparison of different genes (accessed October 2020). Per id % = identity percent. The taxonomy follows *Index Fungorum.*

Gene	Closest match	Per id %	Taxonomy	Family / Order	Reference
nuITS	GU055726	86.88–88.32	Uncultured Helotiales	Incertae sedis, Helotiales	Klaubauf et al. 2010
nuLSU	AY541491	94.37–94.49	*Myxotrichum deflexum*	Amorphothecaceae, Erysiphales	Lumbsch et al. 2005
nuSSU	AB570321	91.88	*Dictyocatenulata alba*	Incertae sedis, Ostropomycetidae	An et al. 2012
mtSSU	FJ713604	91.66–91.93	*Cudoniella clavus*	Helotiaceae, Helotiales	Schoch and Sung, unpubl.

UNITE (https://unite.ut.ee) databases. The newly generated DNA sequences are available in NCBI (Table 1) and UNITE databases.

The phylogenetic analyses

We compiled DNA alignments for each gene, using taxon sampling that encompassed as many of the segregate of Leotiomycetes as possible (Table 2). The DNA sequences were aligned with the on-line version of Mafft ver. 7 (Katoh et al. 2019) using default options and corrected manually with SeaView ver. 4.6 (Gouy et al. 2010). These single gene alignments were analysed using the one-click mode in NGPhylogeny (Lemoine et al. 2019). After that we selected nuLSU dataset (110 sequences, including three new sequences; see Table 1 and 2) to analyse it further because the nuLSU dataset was the most comprehensive. The ambiguous regions were identified and eliminated with on-line version of Gblocks ver. 0.91b (Talavera and Castresana 2000), adjusting relaxed filtering parameters (smaller final blocks; gap positions within the final blocks). The resulting new alignment consisted of 768 nucleotide positions (121 variable, 96 informative) i.e., 23% of the original alignment. The best-fit nucleotide substitution model according to AIC criterion – GTR + I + G – was calculated with jModeltest ver. 2.1.6. (Darriba et al. 2012). The alignment was analysed using Markov Chain Monte Carlo (MCMC) and Maximum Likelihood (ML) approaches. The Bayesian analysis was performed with MrBayes ver. 3.2.1. (Ronquist et al. 2012) using the following settings: two parallel simultaneous runs over 8 million generations starting with a random tree and employing four simultaneous chains; sampling after 1000 steps. The average standard deviation of split frequencies across runs reached 0.01, and the potential scale reduction factor (PSRF) for all models and parameters was close to 1. The first 25 % of saved data was discarded as 'burnin'; the consensus tree and posterior probabilities (PP) were calculated from the rest. The ML analysis was run with RAxML ver. 8.2.12 and inferred assuming GTR + G as the nucleotide substitution model. Branch support was calculated by rapid bootstrapping over 1000 pseudoreplicates. All analyses were implemented at the CIPRES Science Gateway ver. 3.3 (Miller et al. 2010). The clades with posterior probabilities (PP) $\geq$ 0.95 and bootstrap values (BS) $\geq$ 0.75 have been regarded as significantly supported. The phylogenetic tree was visualized and edited using FigTree ver. 1.4.2 (Rambaut 2014) and Adobe Illustrator CS3® was used for artwork.

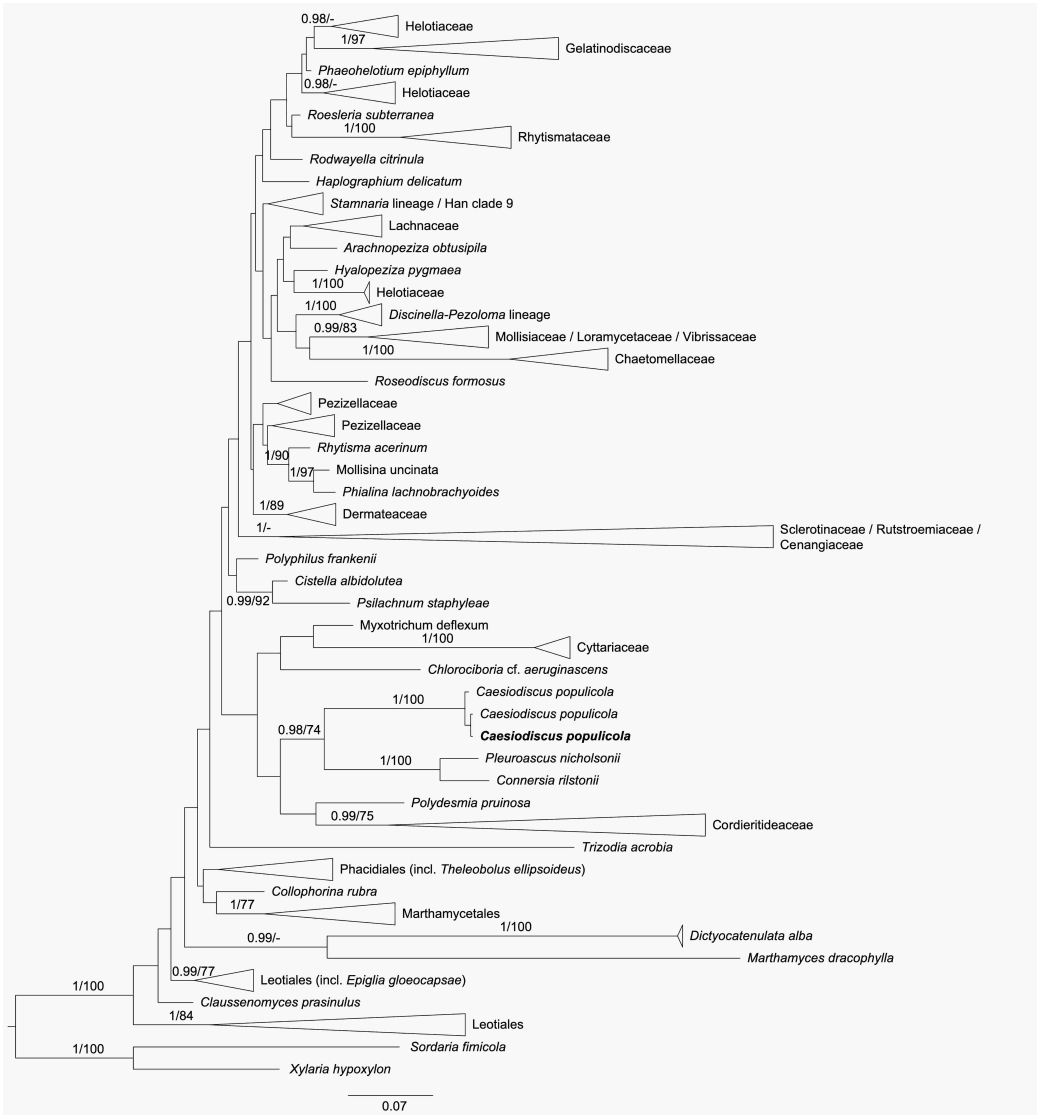

Figure 1. The nuLSU-based Bayesian phylogeny showing the position of *Caesiodiscus populicola* (type specimen in bold) within Helotiales, Leotiomycetes. The branches with posterior probabilities (PP) ≥ 0.95 and bootstrap values (BS) ≥ 75 % (given above branches) are considered as supported; the clades corresponding to higher taxonomic or informal units according to Jaklitsch et al. (2016) and Johnston et al. (2019) are collapsed.

RESULTS

Phylogenetic analyses

Based on *blastn* (Altschul et al. 1990) search in NCBI and UNITE nucleotide databases, no identical or similar sequences were found, and the percentage of identity of different genes ranged from 87.37% (nuITS) to 94.49% (nuLSU) (Table 3). Moreover, the closest matches of different genes pointed to different taxonomic groups in Leotiomycetes, except nuSSU which closest match belonged to Ostropomycetidae, Lecanoromycetes (Table 3). The initial analyses of single-gene alignments using one-click option (data not shown) gave ambiguous results, mainly due to differences in sequence data coverage. This made the exact phylogenetic arrangement of the species impossible, but still allowed placement among Leotiomycetes. In the analysis of the most comprehensive nuLSU dataset, the sister clade of the specimens was formed by *Pleuroascus nicholsonii* Massee and E.S. Salmon and *Connersia rilstonei* (C. Booth) Malloch (Fig. 1; PP=0.98, BS=74), both Helotiales, Helotiaceae (Johnston et al. 2019).

Taxonomy

***Caesiodiscus* Holien and Suija gen. nov.**

MycoBank: MB838686

Diagnosis: Non-lichenized. Ascomata apothecial, marginate, erumpent; asci cylindrical, inoperculate, without croziers, but with long leg separated by septum, with distinct, hemiamyloid ascus apical apparatus; paraphyses filiform, distantly septate, mostly unbranched, apically not thickened; ascospores arranged uniseriately in asci, hyaline, inamyloid, eumuriform.

Typus generis: *Caesiodiscus populicola* Holien and Suija

***Caesiodiscus populicola* Holien and Suija sp. nov.**

MycoBank: MB838687

Diagnosis: *Caesiodiscus populicola* is characterized by the bluish grey to greyish (lead-grey) ascomata covered with greyish white pruina, up to 1.5 mm in diameter, the pale swollen margin and the more or less roundish shape, with 4-spored (more rarely 6–8-spored)

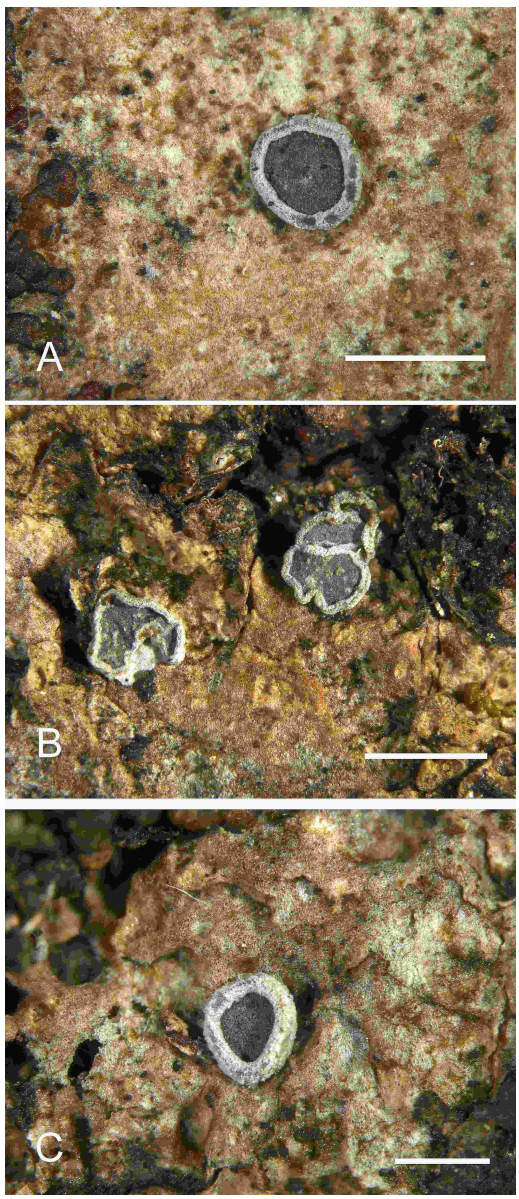

Figure 2. *Caesiodiscus populicola*, the holotype (TRH-F-17665). Scales: A-B= 2 mm; C= 1 mm. Photo: A. Frisch.

Figure 3. *Caesiodiscus populicola* with associate green algal film (TRH-F-17688). Photo: K. Mandal.

asci, eumuriform ascospores and the corticolous habit on deciduous trees with calcium rich bark.

Type: NORWAY: Nord-Trøndelag, Flatanger, between Hylla and Innervika, W side of Utvordveien, 64.55456°N, 11.07011°E, alt. ca 30 m, on trunk of *Populus tremula* in boreal rainforest, 2019-10-24, Holien 15910 (TRH-F-17665 − Holotype; O, TUF-087471 and UPS−Isotypes)
NCBI accession nos. from isotype (TUF-087471): MW298848 (nuITS; DNA barcode/ reference sequence), MW298857 (nuLSU), MW298854 (mtSSU)

Ascomata apothecia, solitary, sometimes gregarious, two or more apothecia in clusters, sessile, narrowed at base, (0.7-)1.0(-1.5) mm (n=18) in diameter (Figs. 2 and 3), outline of the apothecia roundish to somewhat irregular in shape, disc plane to concave, bluish grey (Fig. 4A-C), pruinose, giving the frosty impression; apothecia with distinct, swollen and almost white margin, (0.1-)0.2(-0.3) mm (n=18) in diameter; in young ascomata the margin is slightly turned inwards. All microscopical structures hyaline, except the outermost layers which are greyish, K– or K+ slightly olive green, N+ violet (reaction disappears quickly), with granular pigments, granules insoluble in K–, but stain in CRB; no crystals. **Hymenium** hyaline, c. 150 µm thick, I–, K–, K/I–, the uppermost part greyish to dark greenish; subhymenium hyaline to slightly beige, c. 30 µm, composed of elongated interwoven cells (*textura intricata* type). **Ectal exciple** distinct, hyaline in central part, of *textura intricata* type, greyish in outer part, composed of angular, irregular cells (*textura angularis* type); excipular hairs and setae missing, however, the tips of hyphae extend from the exciple (well-visible after treatment with K), (Fig. 4I) the tips of hyphae somewhat coiled. **Medullary exciple** (hypothecium) multilayered, hyaline in upper part, *textura intricata* type, c. 50 µm thick, the layer below *textura angularis* type, hyaline in upper part,

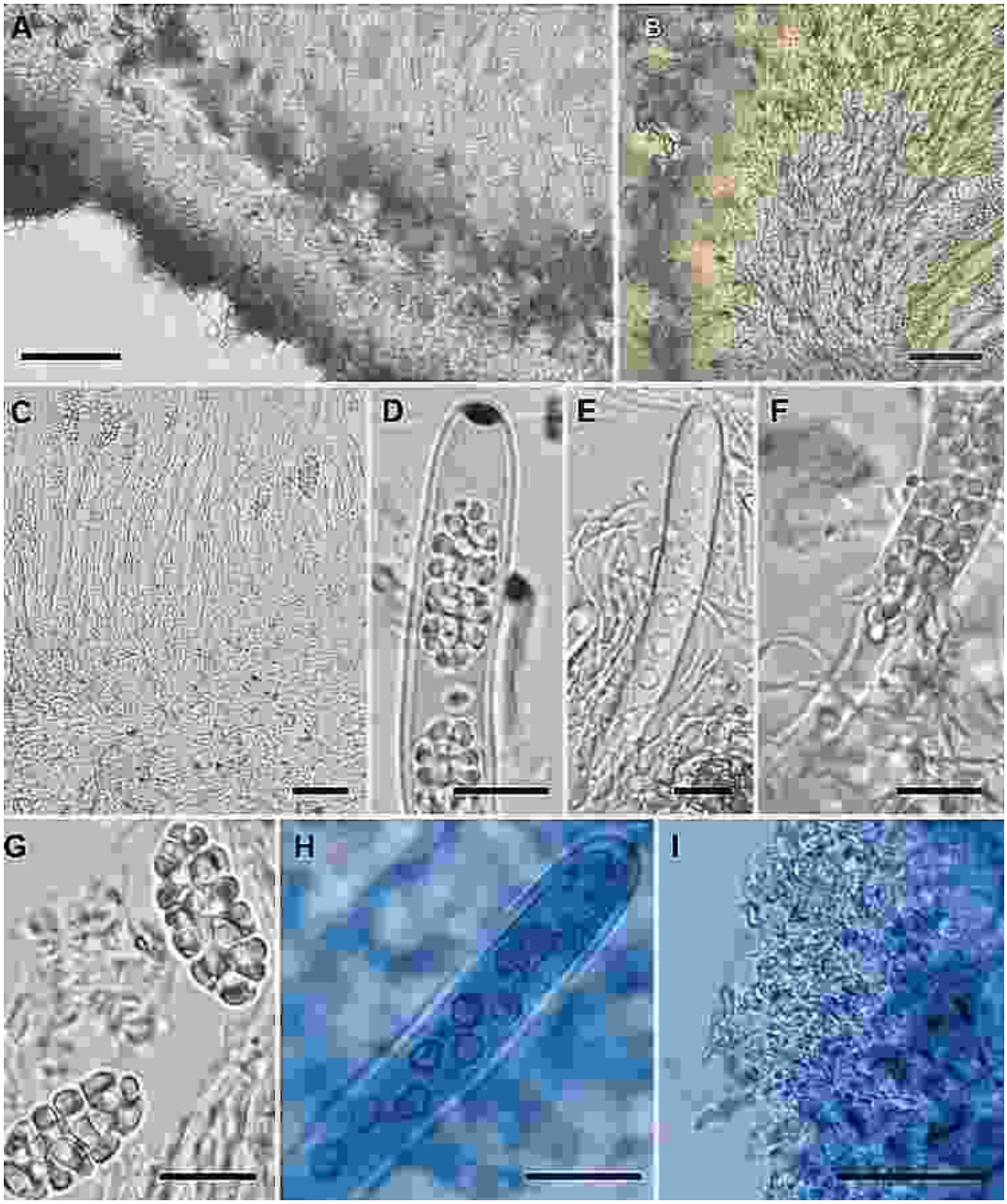

Figure 4. *Caesiodiscus populicola* (TUF-087471, isotype). A, section through ascomata, multilayered medullary exciple and lower part of hymenium (in water); B, section of ectal exciple (in water); C, lower part of the hymenium with asci and paraphyses, and upper part of medullary exciple (in K); D, mature ascus with mature ascospores (in K/I); E, young ascus with 1-celled ascospores (in K); F, base of the ascus (in K/I); G, ascospores (in K/I); H, young ascus with eight 1-celled ascospores (in CRB); I, tips of hyphae extending from the exciple (in CRB). Scales: A= 50 µm; B, C=20 µm; D, E, F, G, H=10 µm; I= 5 µm. Photos: A. Suija.

the outermost part greyish, c. 50 µm wide. **Asci** inoperculate, mostly 4-spored, more rarely 6- to 8-spored; the young asci contain eight 1-celled ascospores; asci narrow cylindrical (Fig. 4E, H) (125-)135(-150) × (10-)11(-13) µm, narrowed towards the base forming a long leg (Fig. 4F), c. 15–20 µm long and c. 5 µm wide, separated by septum; without croziers; asci with apical thickening c. 5 µm wide, ascus apical ring structure detectable already in water, hemiamyloid, I+ red, IKI+ blue (Fig. 4D); ascus wall c. 1 µm thick, wall surface CRB+ light blue in dead state. **Ascospores** uniseriate, hyaline, eumuriform, with 20-28 cells on surface view, broadly ellipsoid, with rounded ends, inamyloid, (20-)25(-30) × (9-)11(-13) µm (n=50) (Fig. 4G), with thick, c. 1 µm wide wall, wall surface CRB+ light blue in dead state; young spores 1-celled, globose to ellipsoid, the first spore division in transverse direction (Fig. 4E, H). **Paraphyses** narrow, filiform, distantly septate, unbranched or occasionally forked, apically not thickened, c. 1 µm wide, slightly exceeding asci. **Anamorph** not observed. **Photobiont** usually absent, but present in one specimen as a thin green algal film (Fig 3).

Etymology: Caesiodiscus from latin caesius = bluish, and populicola = growing on *Populus*.

Substrate and habitat: The species grows on deciduous trees with calcium-rich bark, mainly on old trunks of *Populus tremula*, more rarely on trunks of *Fraxinus excelsior* and dead stems of *Sambucus racemosa*. The epiphytic community on the host trees is dominated by small bryophytes. On the type locality the most common bryophyte on the host trees was *Frullania fragillifolia* (Taylor) Gottsche et al. with additional *Barbilophozia barbata* (Schmidel ex Schreb.) Loeske, *Lophozia longidens* (Lindb.) Macoun, *Sanionia uncinata* (Hedw.) Loeske and *Ulota phyllantha* Brid. Other associated species include the corticolous ascomycete *Lasiobelonium corticale* (Pers.: Fr.) Raitv. and small amounts of the cyanolichens *Pannaria rubiginosa* (Ach.) Bory and *Parmeliella triptophylla* (Ach.) Müll. Arg. *Caesiodiscus populicola* was not found on trunks rich in foliose lichens. Other associate species found in the other localities include the liverwort *Radula complanata* (L.) Dumort., the fungi *Amphisphaerella dispersella* (Nyl.) O.E. Erikss. and *Stictis radiata* (L.) Pers. and the lichens *Megalaria grossa* (Pers. Ex Nyl.) Hafellner, *Normandina acroglypta* (Norman) Aptroot and *Pectenia plumbea* (Lightf.) P.M. Jørg. et al.

The habitat in the type locality (Fig. 5) can be characterized as a rather open boreal rainforest with *Picea abies* and deciduous trees i.e. *Betula pubescens*, *Populus tremula*, *Salix caprea* and *Sorbus aucuparia*. On *Sorbus* close to the host trees interesting redlisted rainforest lichens i.e. *Pseudocyphellaria citrina* (Gyeln.) Lücking et al. and *Rinodina disjuncta* Sheard and Tønsberg were present.

Distribution: So far, the species has been recorded only from Norway where it has been found in humid coastal areas from Agder in the south to Hamarøy in Nordland county. An additional record from Akershus in the Oslofjord region is locally humid and can be characterized as suboceanic. Its altitudinal range is from just above sea level to about 280 m in the south. The known localities are situated within the south and middle boreal vegetation zones (Moen 1999).

Additional specimens examined: NORWAY: Akershus, Rælingen, Mørkåstjerna N, 59.85978°N, 11.05262°E, on *Populus tremula*, alt. ca. 260 m, 2014-05-10, Klepsland JK14-S004 (TRH-F-17671). Vest-Agder, Søgne, Øygardsbekken, 58.11110°N, 7.65085°E, on *Fraxinus excelsior*, alt. ca. 90 m, 2008-06-23, Klepsland JK08-S016 (TRH-F-17669). Møre og Romsdal, Aure, Vik,

Figure 5. The type locality for *Caesiodiscus populicola* in Flatanger. The host tree, *Populus tremula*, along with *Betula pubescens*, *Picea abies* and *Sorbus aucuparia*. 24th October 2019. Photo: H. Holien.

63.1297°N, 8.6127°E, on *Populus tremula*, alt. 67 m, 2018-11-18, Jordal s.n. (TRH-F-17224); Aure, Vik, 63.1926°N, 8.6124°E, on *Populus tremula*, alt. 61 m, 2018-11-18, Jordal s.n. (TRH-F-17225); Molde, Vikvatnet SE, Vass-skaret, 62.70120°N, 7.49900°E, on *Populus tremula*, alt. ca. 200 m, 2020-01-26, Olsen OOL-20.01 (TRH-F-17582); Molde, Høystakkliåsen, 62.8207°N, 7.7042°E, on *Populus tremula*, alt. ca. 200 m, 2020-10-12, Lorentzen s.n. (TRH-F-17703); Skodje, Liafjellet, 62.4832°N, 6.7361°E, on *Populus tremula*, alt. ca. 140 m, 2019-05-21, Olsen OOL-19.02 (TRH-F-17238 and 17239, TUF-091126); Surnadal, Hjellnes, 62.8395°N, 8.6593°E, on *Populus tremula*, alt. ca. 90 m, 2020-10-13, Lorentzen s.n. (TRH-F-17702); Volda, Bjørkedalsvatnet, 62.0257°N, 6.0417°E, on *Populus tremula*, alt. ca. 30 m, 2019-10-29, Olsen OOL-19.09 (TRH-F-17668). Sør-Trøndelag, Ørland (Bjugn), Fagerenget, 63.87250°N, 9.88810°E, on *Sambucus racemosa*, alt. ca. 20 m, 2020-10-09, Mandal s.n. (TRH-F-17688). Nord-Trøndelag, Flatanger, between Hylla and Innervika, W side of Utvordveien, 65.55454°N, 11.07019°E, on *Populus tremula*, alt. ca. 30 m, 2018-08-08, Holien 17/18 (TRH-F-17239); Flatanger, between Hylla and Innervika, W side of Utvordveien, 65.55444°N, 11.07036°E, on *Populus tremula*, alt. ca. 30 m, 2019-10-24, Holien 15909 (TRH-F-17666). Nordland, Rødøy, Esvikelva, 66.70025°N, 13.39650°E, on *Populus tremula*, alt. ca. 30 m, 2013-06-07, Klepsland JK13-S005 (TRH-F-17670); Hamarøy, Dragskrysset nord, Kvannvatnet, 68.0556°N, 15.9538°E, on *Populus tremula*, alt. ca 30 m, 2016-07-19, Gaarder 6808 (TRH-F-17667); Hamarøy, Buktaelva øvre, 67.9952°N, 15.9056°E, on *Populus tremula*, alt. ca. 65 m, 2020-07-15, Lorentzen s.n. (TRH-F-17631).

DISCUSSION

In this study, we wanted to determine the identity of some distinct specimens found along the Norwegian west coast. These specimens had the remarkable combination of bluish grey ascomata with 4-spored asci and eumuriformic ascospores.

Eumuriform ascospores are uncommon within Leotiomycetes. The only family in which such type of ascospores are common is the Triblidiaceae (Jaklitsch et al. 2016) that in the recent phylogeny by Karakehian et al. (2019) was proven to belong to Rhytismatales. Searching for similar DNA sequences in databases and rough analyses did not confirm the affiliation of *Caesiodiscus* neither with this family nor order. Another taxon having muriform spores is *Mellitiosporium* (Jaklitch et al. 2016), that is currently placed in Marthamycetaceae, Marthamycetales (Jaklitsch et al. 2016, Johnston et al. 2019). However, DNA sequences of this genus are not available in public databases. *Mellitiosporium* differs from *Caesiodiscus* by having erumpent ascomata and non-amyloid asci (Senn-Irlet 2014, Jaklitsch et al. 2016, Johnston et al. 2019). *Connersia* and *Pleuroascus*, that showed up to be the closest genera according to nuLSU sequence analysis, have reduced, cleistothecial ascomata and single-celled hyaline ascospores within globose, evanescent asci (Malloch 1974, Plishka et al. 2008, Johnston al. 2019). Thus, the affiliation of *Caesiodiscus* within Helotiales, Leotiomycetes remains unclear. This can probably, at least partly, be attributed to the fact that Leotiomycetes remains a poorly studied taxonomic group within the Ascomycota, as a high proportion of unsettled taxa are lacking molecular data and recent collections (Jaklitsch et al. 2016, Johnston et al. 2019). On the other hand, many helotialean taxa are known by environmental DNA sequences only (e.g. Johnston et al. 2019) without association of reliable taxon names.

In one specimen of *C. populicola* (TRH-F-17688), see Fig. 3, we observed a thin green algal film close to the apothecia. We believe that the species is non-lichenized, but it may be an example of a saprotrophic species that can be facultatively weakly lichenized. This is in need of further study.

Our observations indicate that the fruitbodies of *Caesiodiscus populicola* most often develop in late autumn. They are often browsed by herbivores (possibly molluscs) that remove the hymenium, as seen in nearly all collections so far.

Caesiodiscus populicola seems to have a strong preference for large, living trees of *Populus tremula* which is generally considered a tree species with calcium-rich bark, consequently with a high bark-pH (DuRietz 1945, Barkman 1958). However, the variation in bark-pH is considerable in *Populus*, mostly reflecting soil chemistry (Gustafsson and Eriksson 1995). The other known phorophytes, *Fraxinus excelsior* and *Sambucus racemosa* have normally even higher bark-pH and the latter could be classified as extremely calcium rich with a bark-pH about 7 (Poncet et al. 2015).

Old trees of *Populus tremula* have the highest diversity of red-listed species among the boreal deciduous trees in Norway (Bendiksen et al. 2008). The amount of old *Populus* is declining in Norway due to clear-cut logging and transformation of deciduous forest to spruce plantations (Bendiksen et al. 2008, Lorentzen 2020), but probably even more due to browsing by herbivores, red deer and moose in particular (Speed et al. 2020).

Among relevant red-listed species with a preference for *Populus* in Norway, the lichen *Staurolemma omphalarioides* (Anzi) P.M. Jørg. and Henssen and the fungus *Caliciopsis calicioides* (Ellis and Everh.) Fitzp. are the most interesting (see e.g. Holien and Jørgensen 2010, Holien 2011, Bendiksby et al. 2014, Jordal et al. 2014). It seems that *Caesiodiscus*

populicola shares the same habitat as the two species mentioned above and even the same host trees in several localities from Møre and Romsdal to Nordland (Lorentzen 2020). *Caesiodiscus populicola* should therefore be considered for the Norwegian red list of species.

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Psathyrella dondlii, a so far misunderstood species

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NØKKELORD
Agaricales, Psathyrellaceae, *Psathyrella*, *Psathyrella dondlii*, *Psathyrella fibrillosa*

SAMMENDRAG
Psathyrella dondlii er beskrevet som en ny art, makro- og mikrofunksjonene er beskrevet og illustrert med bilder og strektegninger. Plassering i Psathyrellaceae er vist i et fylogram, forskjellene fra nærstående eller lignende arter er diskutert.

ABSTRACT
Psathyrella dondlii is presented as a new species, the macro- and micro-features are described and illustrated with photos and line drawings. The position within the Psathyrellaceae is highlighted by a phylogram, the differences to similar species are discussed.

INTRODUCTION

In October 2016, the German mycologist Matthias Dondl discovered a *Psathyrella* species in the vicinity of Passau (Germany, Bavaria), which in the absence of an alternative was tentatively referred to as *Psathyrella* cf. *fibrillosa* (Pers.: Fr.) Maire. However, already the habit aroused some doubts; this increased after the study of microscopic features, which in many respects signaled a proximity to *P. fibrillosa* but showed some slightly differences. The find was examined by the first author, but there was no exact assignment, only the statement that it could be an aberrant form or a previously unknown species. Therefore, sequencing was initiated in order to gain further information. In the same period the second author made numerous collections in Norway, which turned out to be identical to the German mushrooms.

MATERIAL AND METHODS

Morphology

The fruiting bodies were photographed in situ and the macro-characteristics were documented by the collector. The description of the microscopic characters is based on the dried specimen. Cystidia, veil and other structures were studied in pure water or in ammonia solution (NH_4OH 10 %) stained with Congo Red. Spores were measured in water; 20 mature spores found on the apex of the stipe were used for this per measurement series. The colour of the spores was examined in water, ammonia solution (10 %) and potassium hydroxide (KOH 5 %). Specified color codes refer to Küppers (2007).

Molecular analysis

DNA extraction, amplification and sequencing of the fungus was performed by Alvalab (Oviedo, Spain), the phylogenetic analysis

Table 1: List of used relevant sequences, taken from NCBI or Unite.

Designation	**voucher**	**ITS**
Psathyrella atomatoides (Peck) A.H. Sm.	LO249-82	KC992930.1
Psathyrella atomatoides (as *Psathyrella obtusata* (Pers.) A.H. Sm.)	MICH65721	MF326013.1
Psathyrella conica T. Bau & J.Q. Yan	HMJAU:37846	NR_160507.1
Psathyrella conica	HMJAU 22096	MG734713.1
Psathyrella conica	HMJAU 37905	MG734745.1
Psathyrella cortinarioides P.D. Orton	LO77-00	KC992936.1
Psathyrella cortinarioides	MCVE28713	MF326010.1
Psathyrella dondlii n. sp. (as *Psathyrella borealis* A.H. Sm.)	HMJAU 37911	MG734746.1
Psathyrella dondlii n. sp. (as *Psathyrella borealis*)	HMJAU 37924	MG734743.1
Psathyrella dondlii n. sp. (as Uncultured Basidiomycota)	BF-OTU563	FR682306.1
Psathyrella fibrillosa (Pers.: Fr.) Maire	LO138-00	DQ389686.1
Psathyrella fibrillosa	SZMC-NL-0201	FN396137.1
Psathyrella fibrillosa (as *Psathyrella artemisiae* (Pass.) Konrad & Maubl.)	K70570	AM712248.1
Psathyrella fibrillosa (as *Psathyrella artemisiae*)	BRNM705610	AM712249.1
Psathyrella flexispora T.J. Wallace & P.D. Orton	LO228-00	KC992929.1
Psathyrella flexispora	ALG 1/12	MK045306.1
Psathyrella flexispora	AH33720	MF966494.1
Psathyrella flexuosipes A.H.Sm.	MICH:32961	NR_161024.1
Psathyrella incondita A.H.Sm.	MICH36450	MF325975.1
Psathyrella jilinensis T. Bau & J.Q. Yan	HMJAU 37822	NR_160504
Psathyrella jilinensis	HMJAU 37822	MG734717.1
Psathyrella jilinensis	HMJAU 37824	MG734721.1
Psathyrella longistriata (Murrill) A.H. Sm.	JLF1949	MK996313.1
Psathyrella longistriata	JLF2470	MK996315.1
Psathyrella pennata (Fr.) A. Pearson & Dennis	Deckerova	AM712259.1
Psathyrella pennata	LO216-84	KJ939633.1
Psathyrella pennata	LO206-03	DQ389710.1
Psathyrella pennata	BRNM705608	AM712258.1
Psathyrella rostellata Örstadius	LO228-85	DQ389693.1
Psathyrella rostellata	BRNM705632	AM712246.1
Psathyrella sabuletorum Örstadius & E. Larss.	LO196-98	KC992919.1
Psathyrella sabuletorum (as *Psathyrella* spec.)	JV90-77	KC992918.1
Psathyrella septentrionalis A.H. Sm.	MICH12045	MF326014.1
Psathyrella sphagnicola (Maire) J. Favre	TU117154	UDB024323
Psathyrella sphagnicola	LO233-99	KC992937.1
Psathyrella spintrigeroides	WU17247	AM712251.1
Psathyrella spintrigeroides	BRNM705639	AM712252.1
Psathyrella spintrigeroides	HMJAU37821	MG367204.1
Psathyrella squamosa (P. Karst.) M. M. Moser ex A.H. Sm.	BRNM705611	AM712250.1
Psathyrella vesterholtii Örstadius & E. Larss.	HMJAU37833	MG367202.1
Psathyrella vesterholtii	JHP10.086	KC992938.1
Psathyrella sp.	ACS1811	MK855482.1

was done by Alexander Karich (Zittau, Germany). The genomic DNA was extracted from dried fruiting bodies, amplification was carried out with the ITS4 primer (White et al. 1990). The following molecular phylogenetic markers were used for the phylogenetic analysis: ITS1, 5.8S, ITS2, LSU, β-tub, ef-1α. The nucleotide sequences for the tree inference were taken from NCBI (https://www.ncbi.nlm.nih.gov) and Unite (Kõljalg et al. 2013), essential ones see Table 1. The names used in the databases have been retained. As outgroup, sequence sets of the genus *Lacrymaria* Pat. were selected.

The initial alignment of the ITS region was performed with Mafft (Katoh 2013) using the L-INS-i method and corrected manually. The final maximum likelihood analysis was done with PhyML3.320180621 (Guindon et al. 2010), applying the GTR substitution model. 1000 ML bootstrap inferences were calculated. Of these, 1000 trees were sampled and the best tree was labeled with the ML bootstrap support values over 60 % (compare Fig. 4).

DESCRIPTION

Psathyrella dondlii Weholt & A. Melzer, spec. nova - Figs. 1-3

Mycobank no.: MB 829651
Genbank accession no.: MG010483

Diagnosis: Similar *Psathyrella fibrillosa* (Pers.: Fr.) Maire but the pleurocystidia are predominantly obtuse, almost never acute.

Etymology: Named after the discoverer of the German collection.

Holotype: Germany, Bavaria, Passau, Ziegelreuth, forest Steinbichel, MTB 7347/333, 13.507728°E, 48.60439°N, approx. 395 m s. m.,

Figure 1. *Psathyrella dondlii* (holotype) in situ. Photo: M. Dondl.

08.X.2016, leg. M. Dondl (Herbarium Senckenbergianum Görlitz GLM-F117716).

Description: based on all available collections.

Pileus up to approx. 30 mm broad, young conical, then convex to flat convex, in the center red brown (approx. $S_{80}Y_{30}M_{80}$), brighter towards the edge (approx. $S_{40}Y_{80}M_{70}$), veil to half the height as scattered white fibrils, on the margin as a tight hem or as protruding denticles. *Lamellae* adnate, normally close to somewhat crowded, old grey brown, edges white. *Stipe* up to 60 x 5 mm, cylindrical, hollow, white, flocculose over its entire length, without a pseudorrhiza. *Odor* inconspicuous. *Taste* not tested.

Spores (7.3-) 7.5-10 (-10.5) x (4-) 4.5-5 (-5.5) µm, on the average = 8.53 x 4.65 µm, Q =1.52-2.06, on the average =1.86, frontally ellipsoid to somewhat ovoid, laterally sometimes with a slightly suprahilar depression or weakly phaseoliform, mostly with a round or ellipsoid oil drop, germ pore truncate, 1-1.5 µm broad. In water and ammonia solution reddish brown, in KOH dark grey brown, not opaque. *Basidia* 15-22 x 8-9.5 µm, clavate, sphaeropedunculate, 4-spored. *Pleurocystidia* 43-77 x 11-22 (-24.5) µm, very numerous, fusoid to

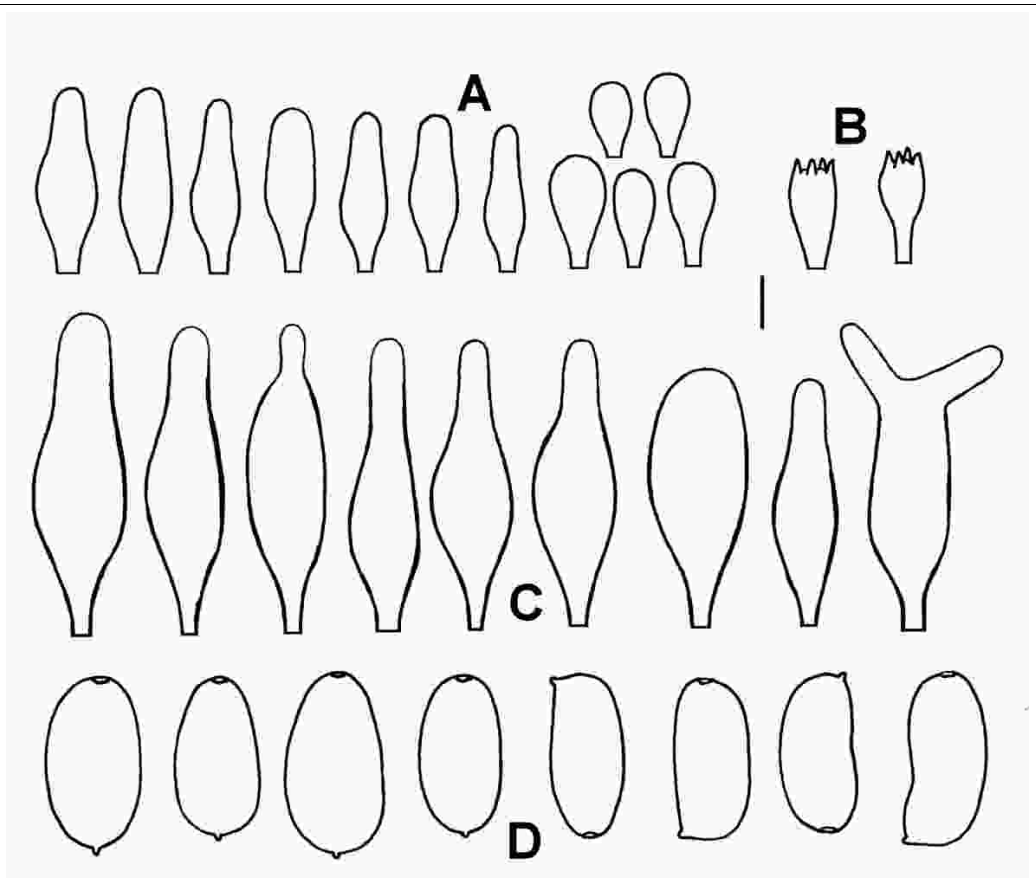

Figure. 2. *Psathyrella dondlii*, Microcharacters (from holotype), A = cheilocystidia, B = basidia, C = pleurocystidia, D = spores; bar: 5 µm (spores), 10 µm (other). Drawing: A. Melzer.

sublageniform, only exceptionally ellipsoid or utriform, apically predominantly broadly rounded, occasionally with a small protuberance, rarely forked, sometimes with inconspicuous grainy deposits, wall below the apex sometimes slightly refractive to thickened. *Cheilocystidia* 24.5-50 x 8-15 µm, quite close, mostly fusoid and utriform, less common sublageniform or subcylindrical, colorless, thin-walled, mixed with moderately frequent clavate and sphaeropedunculate cells, these 18-22 x 9.5-15 µm. *Clamp connections* present.

Habitat: Solitary or or in small numbers in coniferous forests (*Picea* A. Dietr., *Pinus* L.), interspersed with deciduous trees, in fairly humid areas, on half-buried mossy wood oder immediately between moss, especially *Sphagnum*. The Chinese collections grew on the moss layer in mixed birch forest, the Spanish find grew „en turbera entre *Sphagnum*“ [in a peat bog between *Sphagnum*], the French record comes from „dans les grandes mousses humides … des plantationes de *Pinus sylvestris* et *pinaster*“ (in big, wet mosses ... in *Pinus sylvestris* and *pinaster* plantations). It should be mentioned briefly that the voucher BF-OTU563 was found in a dust sample from a building in central Finland (Pitkäranta et al 2011).

Distribution: China, Germany, Finland, France, Norway, and Spain, perhaps Danmark.

Sequenced collections (beside the type and the Spanish collection H.AH 14230): Norway, Viken, Fredrikstad, Hystad, 28.09.2014, leg. Morten Pettersen (MP-1-280914), Viken, Fredrikstad, Hystad, 15.09.2016, leg. Morten Pettersen (MP-12-150916), Viken, Fredrikstad, Hystad, 29.09.2018, leg. Morten Pettersen

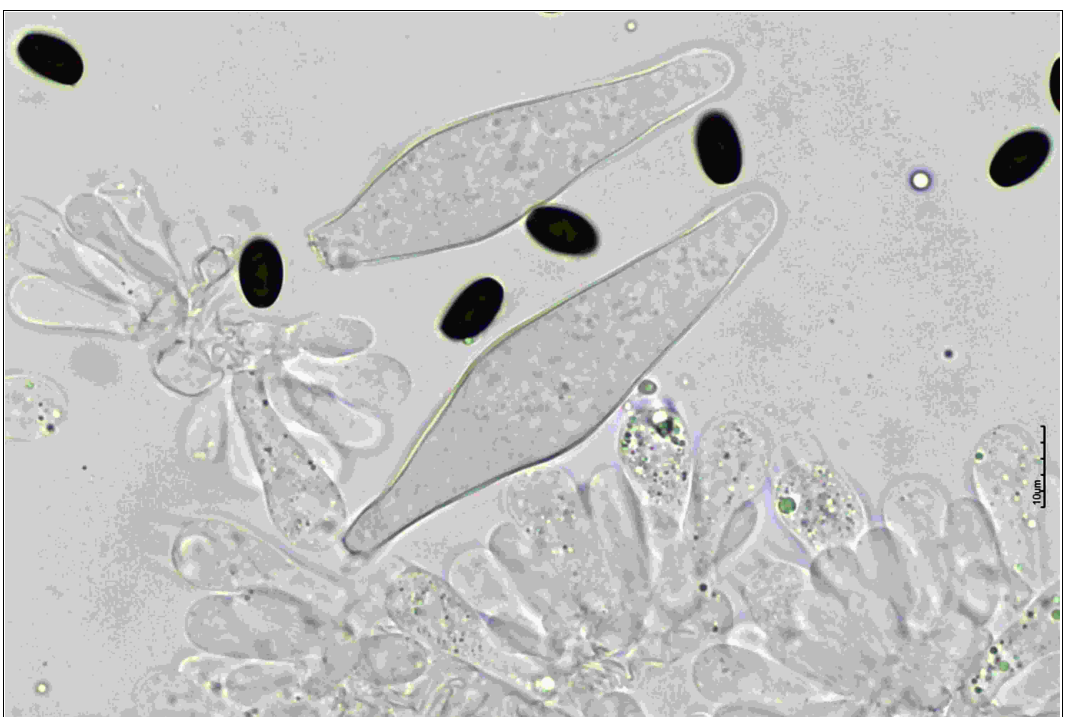

Figure 3. *Psathyrella dondlii*, pleurocystidia (from holotype). Photo: M. Dondl.

(Morten Petersen), Viken, Fredrikstad, near Vetatoppen, 28.06.2017, leg. Øyvind Weholt (OW-23-17), Viken, Fredrikstad, Tofteberg, 13.09.2018, leg. Morten Petersen (MP-5-130918), Viken, Fredrikstad, Storhaug, near Vetatoppen, 12.09.2018, leg. Morten Petersen (MP-1-120918), Viken, Fredrikstad, Blåkoll, near Stordal-anlegget, 03.09.2018, leg. Morten Petersen (MP-2-030919), Viken, Fredrikstad, Prestemyra, 17.06.2019, leg. Øyvind Weholt (OW-33-19), Hedmark, Sel, Otta, 19.09.2015, leg. Tor Erik Brandrud (teb-100-15, teb-139-15). In addition several collections from Norway has only been identified by microscopy.

Notes: It is very likely that the species was often overlooked or misinterpreted. The main problem is probably a confusion with *P. fibrillosa* (Pers.: Fr.) Maire. A delimitation is not easy, even with a good knowledge of the genus, although both species are not directly related (compare Fig. 4). The pileus veil of *P. fibrillosa* seems to be stronger, in addition, a fibrous annular zone is often formed on the stipe. However, these features are not constant or are very much subject to external influences. A differentiation can therefore (apart from the genetic procedure) only be done microscopically. There is an agreement in the literature that the pleurocystidia of *P. fibrillosa* below the apical region are slightly thick-walled and predominantly more or less pointed, at least not broadly rounded or even capitate (Breitenbach and Kränzlin 1995, Enderle 1996, Kits van Wav. 1985, Gröger 1984, Gröger 2014, Kits van Waveren 1985, Krieglsteiner and Gminder 2010, Ludwig 2007, Muñoz and Caballero 2012, Örstadius and Knudsen 2008). A detailed presentation is included in Örstadius (2007). There, too, the pleurocystidia are usually drawn and described with a relatively narrow apex („acute fusiform to lageniform and rarely even to subutriform“). According Smith and Stuntz (1950) the pleurocystidia have „acute apices“ and Fig. 20a perfectly illustrates this statement; Smith (1972) also affirms „with acute apex“.

The interpretation of the original *Agaricus fibrillosus* Pers. and a historical derivation of *P. fibrillosa* is nearly impossible. As one of the more modern authors, Smith (1972) wrote „However, the species apparently does not have a clear and widely accepted concept in Europa by present-day mycologist. Hence the name is used here tentatively.“ Kits van Waveren (1977) was also confronted with this problem. He wrote "… *A. fibrillosus* Pers. ex Fr. cannot be conspecific with *P. fibrillosa* sensu Lange..." and established as a new species *P. friesii* Kits van Wav. Also in Kits van Waveren (1985) *P. fibrillosa* is mentioned as a dubious name. However, *P. friesii* is possibly a synonym of *P. senex* (Peck) A.H. Sm. (Örstadius 2007).

Romagnesi (1976) pointed out „Il ne nous parait pas possible de savoir ce qu'est exactement l'*Agaricus* fibrillosus de Persoon ni de Fries, ni même de Quelét...“ [It does not seem to be possible for us to know exactly what the *Agaricus fibrillosus* of Persoon or Fries or of Quelet is...]. An interesting fact should be mentioned in this context. Romagnesi (1976) wrote to his collections of *Drosophila* (*Psathyrella*) *fibrillosa*: „…forèt d'Ermenonville (Oise), notamment au Bois de la Pisselote, … le 15 octobre 1970 près de la Butte aux Gendarmes (n° 959) (recolte type)…" The number 959 is archived today as MNHN-PC-FUSION104610; actually this could be the neotype of *Psathyrella fibrillosa*! In this case a new name would be necessary for the current *P. fibrillosa*. But such a consequence is not desirable, because Romagnesii was just writing "ss. Lange", and both Lange's description and the original diagnosis leave a lot of leeway for interpretation (see below).

The currently accepted concept of *P. fibrillosa* was created by Örstadius (2007), including the selection of a neotype. At the same time

the name used by recent authors *Psathyrella artemisiae* was discarded, because *Agaricus artemisiae* Pass. is a species „In looghi arenosi...tru i cespi di *Artemisia camphorata* …“ (Passerini 1872).

RESULTS AND DISCUSSION

The analysis showed that the sequence was inserted into a clade, which includes some taxa of the section *Pennatae* Romagn. ex Romagn. (see Fig. 4), also the type species *Psathyrella pennata* (Fr.) A. Pearson & Dennis. The vast majority of these species have pleurocystidia with more or less thickened, yellowish to brownish pigmented walls. The spores are medium-sized (usually no more than 10 µm long) and at least partially phaseoliform. The true cheilocystidia are always mixed with clavate or sphaeropedunculate cells, which never dominate. Moreover, there is always a good to very strongly developed veil present, often also as a stipe ring. But even though the resulting subclade was well demarcated and already had a few members, it was impossible to immediately find a correct name.

The vouchers H6008328, H6038511 and BF-OTU563 initially proved to be phylogenetically identical with *P. dondlii,* but unfortunately, no morphological data are available. The latter voucher is evidence in a dust sample from a building in central Finland (Pitkaränta et al. 2011). The origin of the other two vouchers is also Finland.

In Heykoop and Esteve-Raventos (1994: 41-43) is presented a collection (voucher H.AH 14230) of *P. fibrillosa*, which in all the important matters match very well. About the pleurocystidia is written „… más o menos lageniformes a fusiforme-ventricosos, con el ápice más o menos obtuso (algunos ligeramente utriformis), con las paredes ligeramente refringentes (da color amarillento)“ [more or less lageniform to fusiform-ventricose, with a more or less obtuse apex (some slightly utriform), with slightly refractive walls (yellowish colored)]. Also, the attached drawing shows striking resemblance of the contours, although the walls are shown thin.

Heykoop and Esteve-Raventos (1994) expressly point out that the record has been determinated in the sense of Romagnesi (1976). There the pleurocystidia are described as „… plutôt lagéniformes, à cod d'épaisseur moyenne obtus, parfois flexueux … souvent avec exsudat incolore“ [rather lageniform, dull on average, sometimes bent ... often with a colorless exudate]. The latter is difficult to evaluate, because such deposits are hardly found in dried material. However, an indication of thickened walls is missing, but these are mentioned in the cheilocystidia as „mais á parois réfringentes“ [but with refractive walls]. Romagnesi (1976) incidentally, refers to Lange (1939). Its watercolor (Plate 152, Fig. D) is in good agreement, but the description lacks an indication of thick or at least refractive walls of the pleurocystidia. Moreover, the statement „... face of gill sparingly set with roundish, about 12 microns broad cystidia“ is strange. Whether the fungus of Romagnesi and that of Lange are in fact the same taxon can not be clearly answered. It is not completely excluded, but very unlikely due to the very different micro features. The Spanish record of *P. fibrillosa* was kindly provided for further investigation, and a sequencing was commissioned. The result was a perfect genetic match with the Bavarian and Norwegian finds. Nevertheless, a correct name could not be given at this time.

Somewhat later, the sequences of HMJAU 37911 and HMJAU 37822 from China (Yan and Bau unpubl.) were available, provisionally named *Psathyrella borealis* A.H. Sm. The description was sent for review (Yan by mail). Again, a relatively good agreement of the morphological features could be stated. Indeed, the description in Smith (1972) has many similarities, but also some notable differences. The cap is referred to as „margin

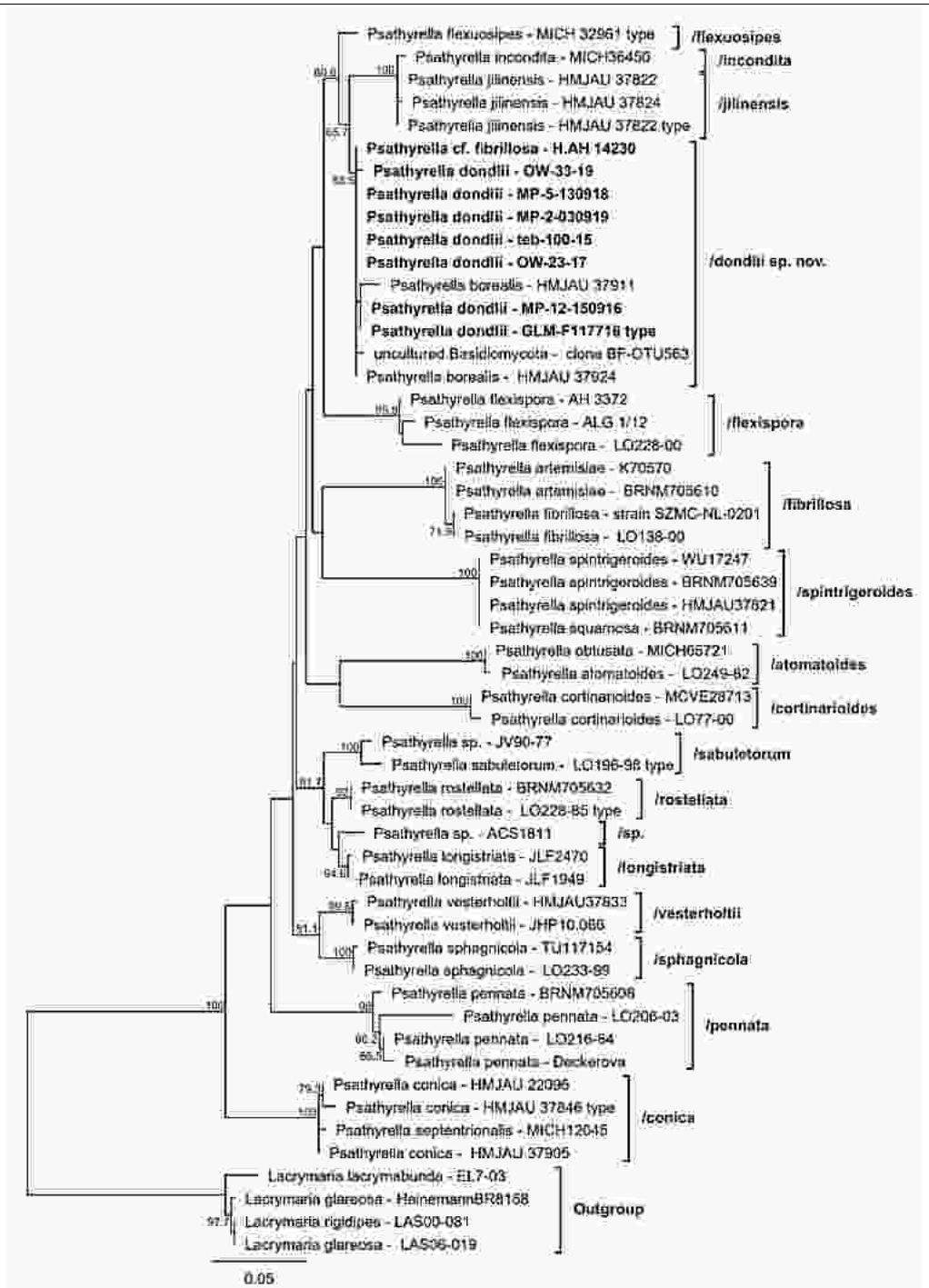

Figure 4: Maximum likelihood consensus phylogram; on the branches ML bootstrap values are indicated. Bold: personally examined collections.

naked or practically so at all times“, the pleurocystidia are characterized by „apex subacute and thin-walled“. For this reason, the name *P. borealis* was not without considerable doubt. The problem was finally solved when the type of *P. borealis* was sequenced, and the evaluation showed that this species occupies a position outside the *Pennatae* and is probably identical to *P. senex* (Peck) A.H. Sm. (NCBI Blast: 99%, Mycobank, pairwise sequence alignment: 99.5 %). In any case, the Chinese collections are definitely not *P. borealis*.

P. fibrillosa is also in a different clade, partly with the older *Psathyrella artemisiae* (Pass.) Konr. & Maubl.; the sources of the sequences (Larsson and Örstadius 2008, Nagy et al. 2011, Vašutová et al. 2008) are trustworthy and the determinations can be considered accurate.

Closely related is *Psathyrella jilinensis* T. Bau & J. Q. Yan, described from China (Yan and Bau 2018). Their spores are also much smaller (up to 7.8 x 4.4 µm). Another phylogenetic neighbor is the voucher MICH36450 which was designated as *Psathyrella incondita* A.H. Sm., but is an unknown species (Voto et al. 2019). The deviations from *P. dondlii* are clear; the spores are smaller (up to 8.7 x 4.4 µm), and the growth is "gregarious on alm wood". From a phylogenetic point of view, this species and *P. jilinensis* could be conspecific.

Finally, as seen from the phylogram (Fig. 4) *Psathyrella flexuosipes* A.H. Sm. (Smith 1972) comes close to *P. dondlii*. However, Smith places the species in Subsection *Largae* and the shape differs from *P. dondlii* by a much larger species (stipe 12-14 cm long), and it has a more yellowish brown pileus colour. Both the spore shape and the pleurocystida depicted in Smith (1972: 469), are different, and especially the cystidia are somewhat more acute than is the case for *P. dondlii*. Habitat given as “debris along roads through alder stands” differs substantially from what is observed for *P. dondlii* as well.

None of the European species can be considered. The majority of species has characteristics, which allow a doubtless determination already using the morphological features. On a superficial look, confusion with the few species is possible because some characteristics (e.g. spore size, cystidia shape) match.

Psathyrella magnispora Heykoop and G. Moreno has a different habitat (dry calcareous grasland), less veil, broadly adnate and somewhat distant lamellae. *P. senex* is larger on average and has often a long, silky shiny stem, the veil is very fugacious, the spores are smaller. *P. impexa* (Romagn.) Bon is usually slightly larger, has a well-developed veil, shows mostly pink colors when it dries out. *Psathyrella squamosa* (P. Karst) M.M. Moser ex A.H. SM. has smaller and paler spores, the veil of fresh mushrooms is well present. *Psathyrella sphagnicola* (Maire) J. Favre, which prefers sphagnum, has a stem with a ring.

However, there seems to be some similarity to *Psathyrella laurentiana* A. H. Sm., whose description is based on a single specimen from Canada. The ecology is comparable („on *Sphagnum* on bogs“), but the mushroom is much smaller (pileus up to 15 mm wide, stem approx. 1 mm thick). The spores are similar in size (8-10 x 4-5 µm), but Smith (1972) mentions another shape, neither ovoid (in font view) nor phaseoliform (in side view). In addition, the presence of brachybasidioles is pointed out. The walls of the pleurocystidia are usually thin and colorless, only after remaining in KOH should they swell and become ochraceous. Such a phenomenon could not be observed in *P. dondlii*. It is doubtful that *P. laurentiana* belongs to the *Pennatae*, because at least refractive walls of the pleurocystidia would be expected. Unfortunately, the type of *P. laurentiana*, preserved in MICH, is very fragile and not permitted to have on loan for further examination.

It is therefore considered justified to describe a new species.

ACKNOWLEDGMENTS
Special thanks to Matthias Dondl (Munich, Germany) for the delivery of his interesting find, information and photos. Regarding the Norwegian collection thanks go to Morten Pettersen who has provided large part of the collections. We would like to thank Pablo Alvarado (Oviedo, Spain) for the sequencing and Alexander Karich (Technical University Dresden - International Institute Zittau, Germany) for the phylogenetic analysis, Gabriel Moreno and Michel Heykoop (both University of Alcalá, Spain) for sending the Spanish voucher, Jun-Qing Yan (Jilin University, China) for the transmission of information on the Asian finds.

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Two species of *Octosporella* (Pezizales) new to Norway

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Norsk tittel: To arter av *Octosporella* (Pezizales) nye for Norge

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NØKKELORD: Ascomycetes, Pezizomycetes, bryosymbiotisk, *Octosporella*, nye for Norge

SAMMENDRAG

To arter av den bryosymbiotiske slekten *Octosporella* (Pezizomycetes) er karakterisert med mikroskopiske data og illustrasjoner. *O. erythrostigma* er registrert både i Møre og Romsdal og Østfold, mens *O. ornithocephala* kun er funnet i Møre og Romsdal. Begge artene er nye for Norge.

ABSTRACT

Two species of the bryosymbiotic genus *Octosporella* (Pezizomycetes) are provided with microscopic data and illustrations. *O. erythrostigma* are recorded from both Møre and Romsdal and Østfold, while *O. ornithocephala* was found only in Møre and Romsdal. Both are new to Norway.

INTRODUCTION

Octosporella is a bryophilous genus, and cover both mosses and liverworts, and one of the smallest discomycetes genera within Pezizomycetes, appearing with perithecioid-like ascomata, mostly less than 0.3 mm in diameter, of orange to orange-red in color due to carotene in the paraphyses. It is only exceeded in smallness by the coprophilous genus *Ascodesmis* Tiegh. (*Ascodesmidaceae*), see Kristiansen (2011)

Species of *Octosporella* are likely ectoparasitic on species of liverworts, and does not kill the host, and today we know twelve species (Yao et al. 2006, 2019); the majority are found in Europe, while only four outside Europe (Döbbeler 2011, Döbbeler et al. 2018). *Octosporella* produces its minute apothecia directly on its hepatic hosts.

Octosporella differs from the bryophilous genera *Lamprospora, Octospora* and *Neottiella* in the shape of the apothecium (Kristiansen 2006, 2018), which has evolved into a closed structure that resembles a perithecium (Döbbeler 1979). This was already interpreted by Corner (1929) by his statement: "a persistently juvenile form of apothecium consequent on depauperation and xerophily". Corners illustration from his paper 1929 shows the fine structure and anatomy in the median section of the apothecium of *Neottiella crozalsiana* Grelet, now *Octosporella jungermanniarum*. (Fig. 1).

The genus was erected by Döbbeler (1979), with its type species *Octosporella jungermanniarum* (Cr.) Döbb., which occurs on the liverwort *Plagiochila asplenioides* s.l., and found at Rambjøllen near Bergen, Norway in March 1977. Montagne (1842) was, however, one of the very first to describe a bryophilous fungi, but assigned it to *Peziza erythrostigma*.

A large phylogenetic study of the bryosymbiotic species was published by Stenroos et al (2010), which included two species of the

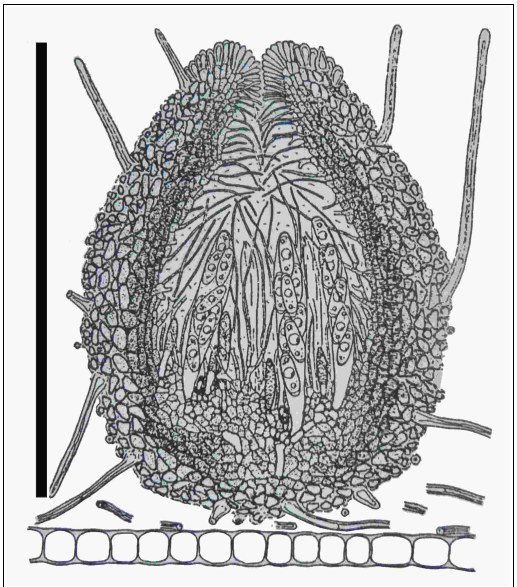

Figure 1. *Octosporella jungermanniarum*. Medium section shows the anatomy of the ascomata. After Corner (1929). Scale bar: 0.25 mm

genus *Octosporella* (see below), and a *Lamprospora* sp. was included in their analyses.

Their investigation showed that *Lamprospora* sp. was nested to *Octosporella*. That implies that *Octosporella* belongs to the bryosymbiotic clade of the *Octospora* lineage. That questions the monophyly of the genus (*loc.cit.*). Bryosymbionts of this group are likely evolved from saprobic ancestors (Gargas and Taylor 1995).

O. erythrostigma is parasitic on *Frullania dilatata* whereas *O. jungermanniarum* parasitizes several different species of liverworts. All octosporaceous taxa are characterized by an infection structure consisting of an appressorium and an intracellular haustorium. Döbbeler (1979) illustrates and describes the infection mechanism and behaviour.

Discovery of the species in Norway

Late fall 2019 one of us, Oddvar Olsen (OO), found a very small orange subglobular fungi growing on the liverwort *Frullania dilatata* on a living tree of *Populus tremula* near Volda

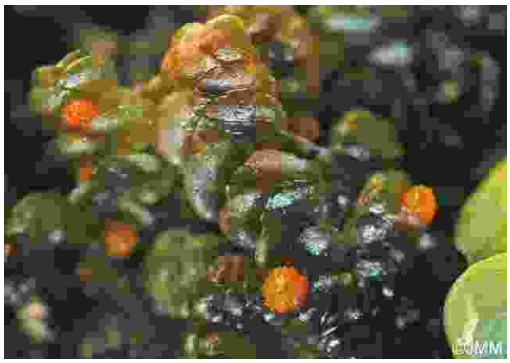

Figure 2. *O. erythrostigma*. Ascomata *in situ* on *Frullania dilatata*. Scale bar: 2 mm. Photo: R. Kristiansen

in Møre and Romsdal, western Norway. The material was sent to Roy Kristiansen (RK), and identified as *O. erythrostigma*, a species not reported from Norway before.

Inspired by the finding in Volda, RK was tempted to look his own local area, and early December 2019 the first author collected *Frullania dilatata* on living *Populus tremula* in the Hvaler archipelago in the SE part of the Østfold county, and upon examination found a species of *Octosporella*, which also turned out to be *O. erythrostigma* (Mont.) Döbbeler like in Volda, but far away from the new occurence, some 430 km SE.

Several more excursions were carried out in the area of Hvaler and on the main land, with mild temperatures and without snow, during January and February resulting in the documentation of even more collection sites. The first discovery in Østfold was reported in the local newspaper (Lågbu 2020).

In January 2020 OO found another *Octosporella*, although very sparse, but it turned out to be the much rarer, namely *O. ornithocephala* Döbbeler an obligate on *Radula complanata* (L.) Dumort., about 18 km east of the other (OOL-19.1), also new to Norway.

MATERIAL AND METHODS

Samples were examined on living material in different reagents, as Cotton blue in lactic

Figure 3. *O. erythrostigma*. Ascomata in situ. Scale bar: 1 mm. Photo: R. Kristiansen

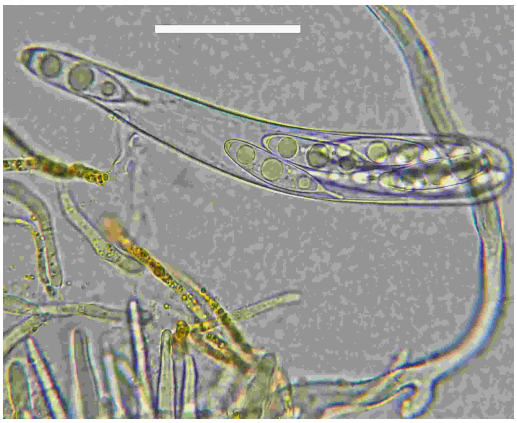

Figure 4. *O. erythrostigma*. Asci with spores, showing appendage and oil droplets. Scale bar: 50 µm. Photo: O. Olsen

acid, methyl blue, Melzer's reagent, and water on squashed mounts.

Octosporella erythrostigma

(Mont.)Döbbeler – Figs. 2, 3, 4, 5, 6, 7, 8.

Basionym: *Peziza erythrostigma* Mont. Ann-Sci. Nat. Bot., 2, sër. 18: 246, no. 47 (1842). Syll.gen. sp. crypt p. 186, no. 628 (1856), non *Peziza erythrostigma* Berk. & Broome, Ann. Mag. Nat. Hist. ser. 3, 18: 126. no.1168, pl. 4, Fig. 34 (1866).

Syn.:

Nectria erythrostigma (Mont.)Tul. & C.Tul., Select. fung. carpol 3: 196 (1865).

Orbilia erythrostigma (Mont.)Quel.. Enchir. fung (Paris):298 (1886)

Orbilia erythrostigma (Mont.) Sacc., Syll. fung. 8: 632 (1889).

Nectriella erythrostigma (Mon.) Sacc. Syll. fung. 9: 942 (1891).

Octosporella urosperma Döbbeler. Mitt. Bot. Staatsamml. München. 16:477. Figs. 3, 4 (1980).

Characteristics

Ascomata perithecioid, 250 - 350 x 200 - 300 µm, ellipsoid or ovoid, rarely barrel-shaped, orange red. Setae up to c. 100 x 8 µm, uncolored, curved or straight, thick-walled densely formed in the upper part of the ascomata.

Outer excipular cells 18 - 28 µm in diameter, thick -walled.

Asci. 8-spored, sometimes with some spores aborted, irregular biseriate, J-, clavate with a short foot, 130 - 150 x 18 - 22 µm. This is slightly longer than reported by Döbbeler (2004).

Paraphyses filimentous, containing numerous yellow reddish droplets, 2 - 4 µm diam.

Ascospores: (without appendage) (25) 28 - 35 x 7 - 10 µm, narrowly ellipsoid, slightly asymmetric, colorless, with often three yellowish oil droplets, two larger and one smaller, but variable (see Fig. 6); spore wall in both ends thickened inside. Episporium weakly cyanophilic. Spores have a filamentous appendage in one end, c. 4 - 6 x 1 µm; appendage directed against the ascus apex.

Material examined

Møre and Romsdal, Volda municipality, south of Straumshamn, in the northern end of Bjørkedalsvatnet, growing in between the dorsal lobes of *Frullania dilatata* on bark of standing living *Populus tremula*, c. 25 m above sea-level. OOL-19.1, 29. October 2019. UTM 32V LP 45221,80571.

Møre and Romsdal, Volda municipality, east of Fyrde at Hjellane, on a partly overgrown

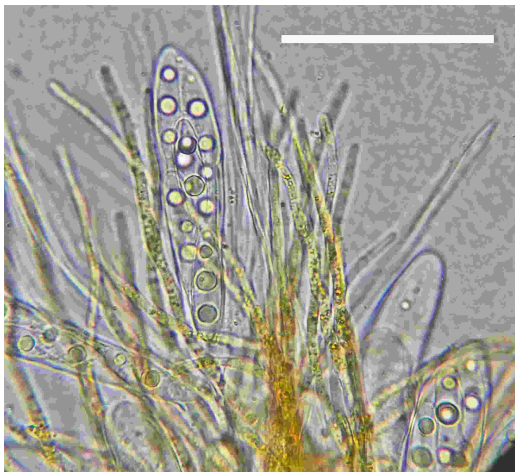

Figure 5. *O. erythrostigma*. Asci with spores and paraphyses with yellow droplets. Scale bar: 50 μm. Photo: O. Olsen

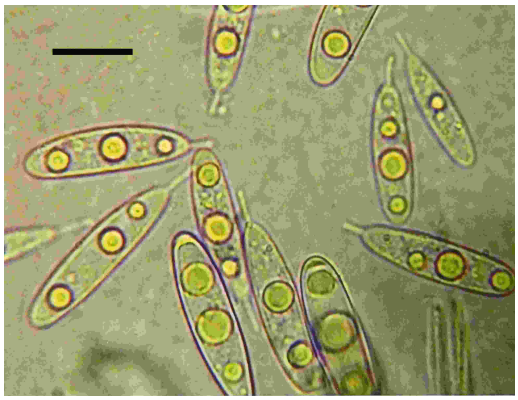

Figure 6. *O. erythrostigma*. Ascospores showing oil drops and appendages. Scale bar: 15 μm. Photo: R. Kristiansen

pasture in deciduous wood with standing *Populus tremula* on *Frullania dilatata*, 7. January 2020. UTM 32V LP 63569,82607.
Møre and Romsdal, Sunndal municipality, NW of Sunndalsøra at Jordalsgrenda, Dalan. East-turned hill, deciduous wood with living *Populus tremula*, on *Frullania dilatata* 25. January 2020. UTM 32 V MQ 64909,58484.
Østfold, Hvaler municipality, Kirkøy, close to Rødshuet, at Stallane, close to the sea, growing on *Frullania dilatata* on bark of living *Populus tremula* in a shallow spot along a track among a large population of living *Populus tremula* and *Pices alba*. RK 21.19, 7. December 2019; Ibid. 11. December 2019; Ibid. 16. January 2020; Ibid. 30. January 2020; Ibid. 16. February 2020; Ibid. 11.November 2020. 59.03658 N 10.99010E.
Østfold, Hvaler municipality, Vesterøy, Vauerkilen, Barm, growing on *Frullania dilatata* on a living *Populus tremula* in a dense stand of *Populus tremula, Alnus glutinosa, Quercus rubra* along a small rivulet on calcareous ground, at sea level. RK 04.20, 12. February 2020. 6557169.36N 262704.99E.
Østfold, Hvaler municipality, Kirkøy, close to Storefjellveien at Stallane 39 occurring on *Frullania dilatata* on an old large *Populus tremula* with several mosses and lichens in mixed pine and spruce forest. RK 06.20. 21. February 6550811.41N 270221E.

Comments

Döbbeler (1979) emphasize the wide variability in morphological characters among *Octosporella* and doubt the unity of the genus. Probably one need to examine all the species to see if the perithecium-like ascomata is not as unique as it may appear as a delimiting character at generic level. *Lamprospora*, however, seems to be monophyletic, while *Octospora* and *Neottiella* seems polyphyletic (Perry et al. 2007).

No doubt that this small fungus should be looked for on *Frullania dilatata* on populations of *Populus tremula* in other places in Norway. We have examined several hundred samples of *Frullania dilatata* from many places in different districts without further findings of *O. erythrostigma*. The species is obviously not common. The appendaged ascospores are a unique character within Pezizomycetes, which makes identification easy.

Peter Döbbeler wrote in a personal communication 21. November 2019 to RK: *"Octosporella erythrostigma* is very distinct by having short setae and a filamentous appendage at the spores. The species is un-

Figure 7. *O. erythrostigma*. Squashed ascomata with asci with spores, paraphyses and setae. Scale bar: 150 μm. Photo: O. Olsen

mistakable. I would be happy to receive a copy (file) of your paper dealing with that new record for Norway. *Filicupula suboperculata* occurs very sporadically on *Frullania tamarisci* in Europe, but does not have hairs and other deviating characters."

Döbbeler (2004a) noted an interesting phenomenon that freshly collected ascomata remain alive for some months in the dried state. However, with time they gradually become discolored, and coloration and oil guttules in the ascospores disappear. Based on our experience of findings the number of ascomata varies from place to place, usually less than a dozen. On the other hand, the population from Kirkøy in Østfold counted more than hundred ascomata.

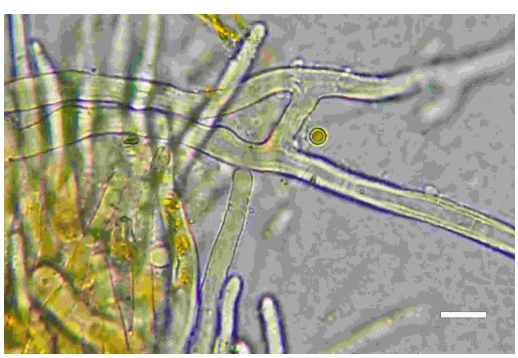

Figure 8. *O. erythrostigma.* Thick-walled setae. Scale bar: 10 μm. Photo: O. Olsen

The fungus is distributed in several countries in Europe (Döbbeler 2004a). One should be aware of (sometimes) that another associated very small (0.1 mm) orange-colored perithecioid ascomata occurs on the lobes of *Frullania*, but belongs to the hypocrealean genus *Bryocentria* (Döbbeler 2004b) with the species *B. brongniartii* (P.Crouan & H.Crouan) Döbbeler, but easily distinguished by its microscopic features. It is identified on some of the material from both Møre and Romsdal and Østfold.

Note on the ecology at Stallane, Kirkøy, Hvaler. Figs. 9, 10.

The locality at Stallane, Kirkøy in the Hvaler archipelago is inside the border of the Ytre Hvaler National Park (Ryvarden 2020), and protected by law, and all intervention is prohibited. The ground comprises of boulders and shell beds covered by a loose layer of debris of rotten leaves and needles from spruce, *Populus tremula, Juniperus communis, Sorbus aucuparia, Salix spp*., herbs and ferns. Rocks and pebbles are overgrown by a number of mosses, and the most abundant are *Dicranum scoparium, Plagiomnium cuspidatum, Pleurozium schreberi*, and lots of *Metzgeria furcata* on *Populus tremula*. The population of *Populus tremula* are well sheltered by a dense stands

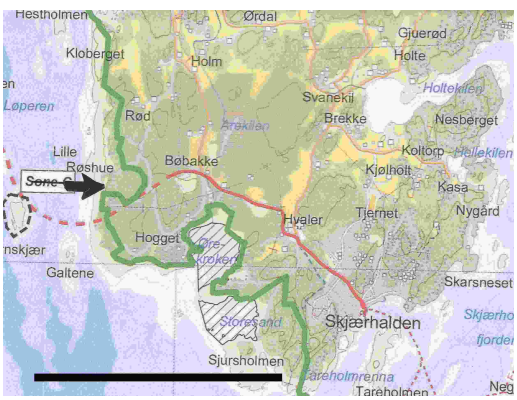

Figure 9. Location of *O. erythrostigma* inside the border-line (green) of Ytre Hvaler National park at Stallane, Kirkøy. Scale bar: 2.5 km.

Figure 10. Kåre Lye standing next to a population of aspen covered by the liverworts *Metzgeria furcata and Frullania dilatata* (above his head), at Stallane, Kirkøy, in the Ytre Hvaler National Park. Photo: R. Kristiansen

of spruces in front, which protects from large waves from the sea in stormy weather during the winter. Distance to the sea < 20 meter. The area of *P. tremula* are approx. 100 m^2, and consists of ca 30 trees, most of them inhabited by liverworts, like *Frullania dilatata, Radula complanata, Metzgeria furcate* and the common *Pylaisa polyantha.*

Octosporella ornithocephala Döbbeler – Figs. 11, 12, 13, 14, 15.

Characteristics

Ascomata perithecioid, 250 x 200 µm in diameter, almost globule, reddish orange, beset with distinct setae, stiff or curved, thick-walled, c. 130 x 7 µm.

Asci: mostly 2-(3-)-spored, uniseriate, J^- , which agrees with the original (Döbbeler 1980),

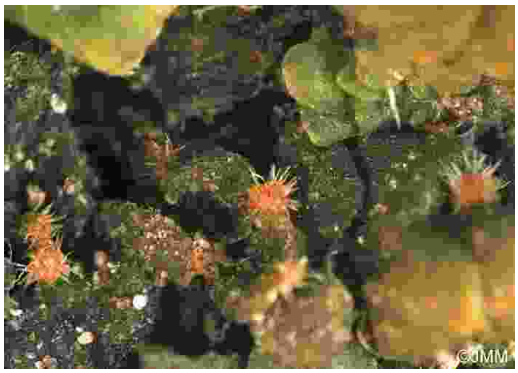

Figure 11. *Octosporella ornithocephala*. Ascomata with setae in situ on *Radula complanata*. Field of view: 10 mm. Photo by permission of Gilbert Moyne.

cylindric with a short foot, , c. 120 x 15 µm.

Paraphyses: straight, filamentous, contains numerous yellow droplets, 2 - 3 µm.

Ascospores: variable dimensions, 29 x 10; 45 x 12; 46 x 11; 51 x 11 µm, or simply 29 - 51 x

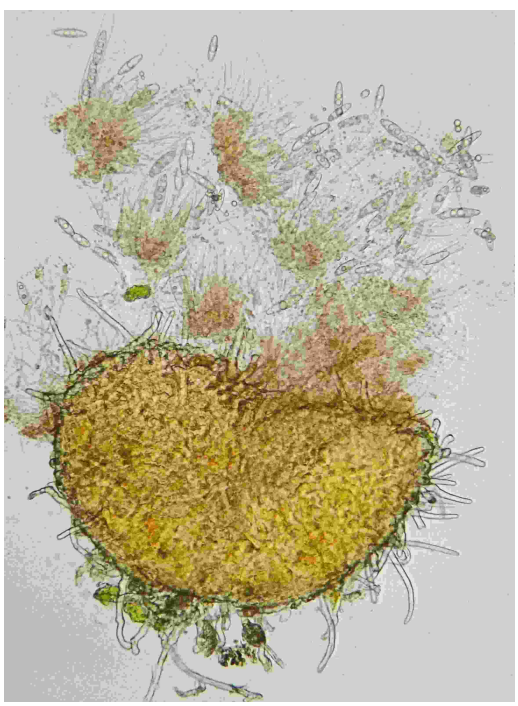

Figure 12. *O. ornithocephala*. Squashed mount of ascomata showing asci, setae and spores. Field of view: 0.3 mm. Photo: O. Olsen

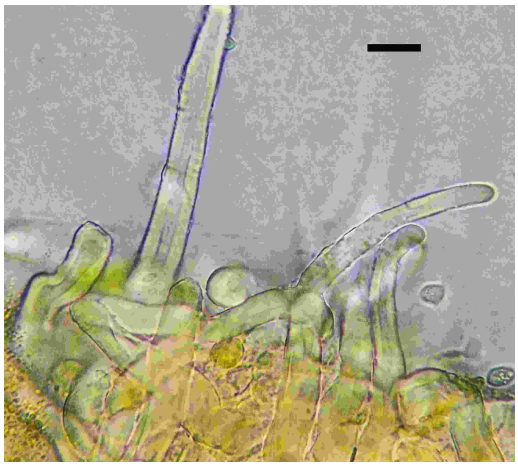

Figure 13. *O. ornithocephala*. Thick-walled setae on the margin. Scale bar: 10 μm. Photo: O. Olsen

10 - 12 μm, ellipsoidal – subfusoid, 3 - 4 oil guttules. Spore-wall thickened inside each pole, c. 4 μm thick, smooth or minutely verruculose. Episporium with very small cyanophilic warts. The ascomata are usually submersed and develops between the lobes.

Material examined.
Møre and Romsdal, Vestnes municipality, south of Indre Tresfjorden, close to Rypdal near Urdelva, 140 m asl, west-turned hill with mixed wood, with some coarse living *Populus tremula* and *Corylus avellana.* Collected on *Radula complanata* on bark of

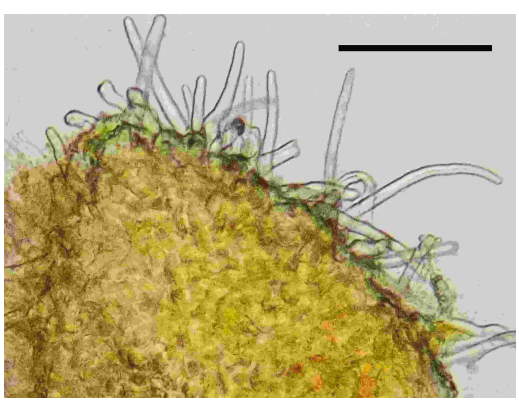

Figure 14 *O. ornithocephala*. Marginal setae. Scale bar: 100 μm. Photo: O. Olsen

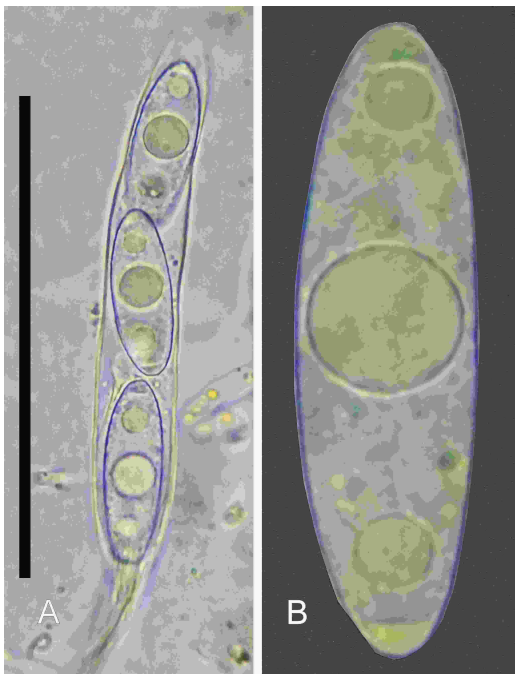

Figure 15 a. *O. ornithocephala*. Asci with 3 ascospores Scale bar: 100 μm. Photo: O. Olsen

standing *Populus tremula*, 23. January 2020. UTM 32V MQ 04910,31834.

Comments
Unfortunately, the material from Møre and Romsdal consisted of only one ascomata, which prevented us from making many photos or to collect detailed microscopical notes, but the identity is distinct. It is typical with large spores, and 2-spored, rarely 3-spored; the only *Octosporella* species with less than four spores in asci.

We have noted some variations compared to the original with slightly smaller setae, 130 versus 150 μm, slightly longer asci, and variable number of guttules. The type material was collected at Lemland, Åland in Finland 1962 (Döbbeler 1980).

The species have been reported from Germany (Döbbeler 1980, von Bracel 2011), and France (Moyne et al. 2011a). The find in Western Norway is the second finding in

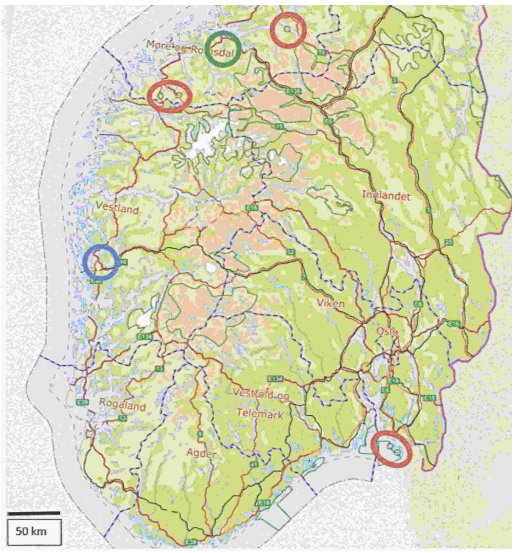

Figure 16. Distribution of *Octosporella* species in Norway.
Red circles: *O. erythrostigma*
Green circle: *O. ornithocephala*
Blue circle: *O. jungermanniarum*

Scandinavia. There are no record of *Octosporella* in Sweden (Eriksson 2014). It is striking that the findings in France were all collected in January-February, but the climate may be less risky regarding desiccation at that time of the year.

EPILOGUE

There are numerous species of very small fungi, which inhabit mosses and hepatics, and they are mostly overlooked because of the size. The majority are Ascomycota distributed among many genera. Based on the published references it seems that *O. ornithocephala* is much less distributed than *O. erythrostigma*. There are three species of *Octosporella* in Norway, viz. *O. jungermanniarum, O. erythrostigma* and *O. ornithocephala*. Fig. 16 indicates the distribution of Octosporellas in Norway.

Another small bryophilous fungus is *Neottiells ricciae* (Cr.) Le Gal, which infect species of the liverworth *Riccia*, and reported from two locations in Norway (Kristiansen 2018), both within the Hvaler archipelago. There are a total fifteen localities in the world, twelve of them in Europe (Németh et al. 2017, Moyne et al. 2011b), on both *R. sorocarpa* and *R. glauca*.

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Key to hysterioid fungi on bark and wood in Scandinavia

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NØKKELORD
Tykksekksopper, forsømte taksa, identifiseringsnøkkel

KEYWORDS
Dothideomycetes, neglected taxa, identification key

ABSTRACT
The lack of useful determination keys is often a major obstacle for naming species of Ascomycota, especially for the amateur mycologist. One group of fungi in need of a key are species of Dothideomycetes with hysterioid ascomata on bark and wood in Scandinavia, and we present such a key encompassing 31 species in 14 genera. Hysterothecia are commonly found on bark and wood, and most species with hysterothecia are saprophytes. Since several lichenized, doubtfully lichenized, and other species have ascomata resembling hysterothecia we also mention several such cases of possible misidentification.

SAMMENDRAG
Mangelen på nyttige bestemmelsesnøkler er ofte et stort hinder for å navngi arter av Ascomycota, spesielt for amatørmykologen. En gruppe sopper som har behov for en nøkkel er arter av Dothideomycetes med hysterioide ascomata på bark og tre i Skandinavia, og vi presenterer en slik nøkkel som omfatter 31 arter i 14 slekter. Hysterioide ascomata finnes ofte på bark og tre, og de fleste arter med hysterioide ascomata er saprofytter. Siden flere licheniserte, tvilsomt licheniserte og andre arter har ascomata som ligner på hysterioide ascomata, nevner vi også flere slike tilfeller av mulig feilidentifisering.

INTRODUCTION

Most fungal species are Ascomycota, and most of them belong to the class Dothideomycetes. Non–lichenized Dothideomycetes are poorly known regarding taxonomy, ecology and distribution, largely because of the lack of comprehensive and recent literature. Another reason is that microscopic identification is often needed to identify a fungus as belonging to the Dothideomycetes rather than to the Sordariomycetes, making surveys more difficult to perform. However, some groups within the dothideomycetes have easily recognizable ascomata and a limited number of species, and one such morphological group consist of species with hysterioid ascomata (hysterothecia). The hysterothecium is a strongly carbonized and thick–walled, elongated, lip–shaped ascoma with a central slit. The ascospores are released through the slit rather than through a pore as in perithecioid ascomata. Hysterothecia have developed independently several times within the Dothideomycetes (Boehm et al. 2009, Jayasiri et al. 2018); in the Hysteriales, Acrogenosporaceae (Minutisphaerales), Anteagloniaceae

(Pleosporales), Gloniaceae (currently in Mytilinidiales), Patellariales (Boehm et al. 2015), and Stigmatodiscales (Voglmayr et al. 2016), as well as in *Glyphium* (Patellariales) and Mytilinidiaceae (Mytilinidiales), which have upright, shell–, ax–, or chisel–shaped, thin–walled, laterally compressed hysterothecia.

Hysterothecia are commonly found on bark and wood, and most species are probably saprophytes. Many species also occur as endophytes within living trees, and one of the most common ectomycorrhizal fungi (Peter et al. 2016), *Cenococcum geophilum*, belong to the Gloniaceae. Many hysteriothecia are long-lived and capable of surviving periods of drought.

We here provide a key to the non–lichenized species with hysteriothecia in Scandinavia. Several lichenized, doubtfully lichenized, and saprophytic species of other taxa on wood and bark have ascomata resembling hysterothecia, often referred to as lirellate apothecia. Fungi with lirellate apothecia may sometimes strongly resemble hysterioid fungi.

A possible case of confusion is species of the lichen genus *Opegrapha* (Arthoniales, Arthoniomycetes), e.g. *O. atra, herbarum, ochrocheila* and *varia*. These species are mainly found on the bark of deciduous trees and the sessile lirellate apothecia have a black true exciple, continuous under the hypothecium, which is not as thick and hard as in a true hysterothecium. Further, the disc is often somewhat exposed, and in some species bear yellow–green, orange or white pruina. The hamathecium consists of septate and branched paraphysoids and the ascospores are multiseptate, fusiform or acicular, hyaline or become ornamented and red–brown when old.

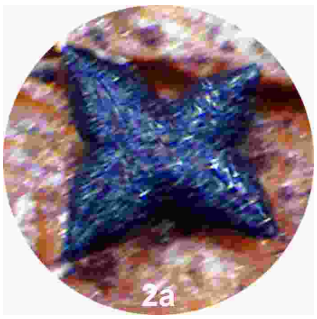
On dead wood, some lichenized fungi with a sometimes indistinct thallus and black lirellate apothecia such as *Xylographa* spp. (Baeomycetales), and *Ptychographa xylographoides* (Trapeliales; Nordén et al. 2019) may also cause confusion. *Xylographa* spp. have unbranched, linear apothecia, while *P. xylographoides* have sometimes branching ascomata. The exciple of *Xylographa* is brown and the hypothecium is colourless, while the exciple is black and friable and the hypothecium is dark brown in *P. xylographoides*. Both have simple or sparingly branched paraphyses, with brown apices and simple, hyaline ascospores. It may also be possible to confuse ascomata of Rhytismatales (Leotiomycetes) with hysteriothecia at a quick glance, for instance ascomata of *Colpoma crispum,* but these are soft–textured apothecia, with filiform paraphyses and hyaline, rod–shaped to filiform ascospores.

Another taxon not included in the key is *Melaspilea lentiginosula* (Dothideomycetes, Eremithallales; Jordal et al. 2017). This doubtfully lichenized species occurs on the bark of old pine trees and has small, black, lirelliform, and sometimes branched apothecia with exposed or slit–like discs. The hamathecium consists of sparsely branched paraphyses and the ascospores are 1–septate, sole–shaped, brown and ± warted. In addition, *Wadeana minuta* (Ascomycota incertae sedis) has lirellate apothecia with glossy margins and simple spores in multispored, non–fissitunicate asci. It occurs on rough bark of old deciduous trees. The mentioned species are all stated to be lichenized with *Trentepohlia* as photobiont in the literature but the thallus can be hard to discern, or is indeed lacking.

Further hysterioid fungi occur on other substrates, for example *Hypoderma* (Rhytismatales; on herbs etc.), *Hysteropeltella* (Patellariales; on ferns), *Leptopeltis* (Microthyriales; on ferns), *Lophodermium* (Rhytismatales; on herbs, needles etc.).

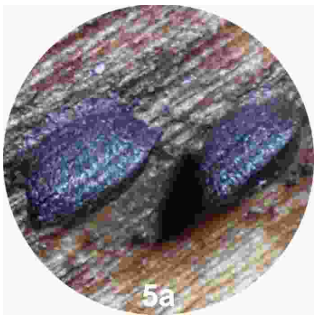
Determination key to hysterioid fungi on bark and wood in Scandinavia

1a. Hysteriothecia higher than broad, shell–, ax–, or chisel–shaped. Peridium thin, almost papery. Ascospores 1–9–septate, or filiform. On conifers, or in the case of *Glyphium*, on deciduous trees.....2
1b. Hysteriothecia broader than high, *either* short ellipsoid, elongated or beanshaped *or* repeatedly dichotomously branched, forming patches. Exciple thick, often hard and brittle. Ascospores 1–3–septate, or muriform. On deciduous trees or conifers.....13



2a. Hysterothecia in star–like configuration (Fig. 1). Ascospores 1–septate, symmetric, light olive– to reddish–brown, 11–14 × 2–3 µm.....***Actidium hysterioides***
2b. Ascomata not in star–like configuration, ascospores different.....3

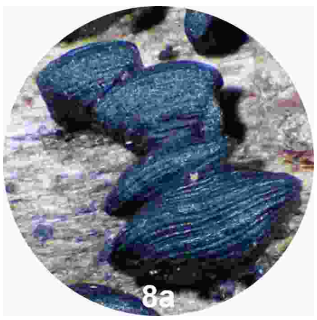
3a. Ascomata shell–shaped, <1 mm high. Ascospores not filiform. On conifers.....4
3b. Ascomata ax–, or chisel–shaped, 1–2 mm high. On deciduous trees. Ascospores filiform. On dead branches etc. of deciduous trees.....11



4a. Ascospores filiform.....5
4b. Ascospores 1– 9– septate.....6

5a. Ascospores parallel in ascus; 170–250 × 1–2 µm.....
.....***Lophium mytilinum***
5b. Ascospores spirally arranged in ascus; 260–280 × 2 µm.....
.....***Lophium elegans***

6a. Ascospores 1–septate, on *Juniperus* and other conifers.....
.....***Actidium nitidum***
6b. Ascospores with more than one septum.....7

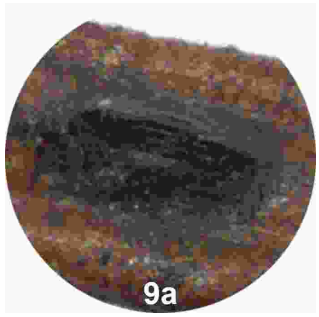


7a. Ascomata low. Ascospores 3–septate, shorter than <16 µm. On small branches and needles of *Juniperus*.....
.....***Mytilinidion decipiens***
7b. Ascomata high. Ascospores with 3 or more septate, longer than 16 µm. On various conifers.....8

8a. Ascospores 3–septate, 16–22 × 3–4 µm.....
.....***Mytilinidion mytilinellum***
8b. Ascospores with more septa, or longer than 22 µm.....9

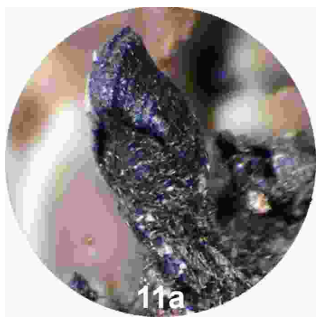
9a. Ascomata low, ascospores 3–5 septate. On small branches and needles of *Juniperus*.....***Mytilinidion acicola***
9b. Ascomata higher, standing on edge. On various conifers...10

10a. Ascospores 3–5–septa, 30–42 × 3–5 µm.....
.....***Mytillinidion rhenanum***
10b. Ascospores slightly bent and assymetric, 7–9–septate, 32–38 × 5–6 µm.....***Mytilinidion gemmigenum***



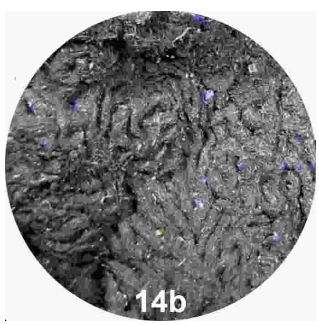
11a. Ascomata obpyriform in outline (Fig. 4). Asci 340–460 × 12–19 µm. Known from North Norway on *Salix*, and from the Swiss alps on *Betula*.....***Glyphium grisonense***
11b. Ascomata narrow (Fig. 3). Asci narrower.....12

12a. Asci 7–9 µm broad. Ascospores disarticulating into part–spores within the ascus. (Not yet recorded from the Nordic countries).....***Glyphium schizosporum***
12b. Asci 9–10 µm broad. Ascospores not disarticulating into part–spores in the ascus. On dead branches of deciduous trees in the lowland.....***Glyphium elatum***



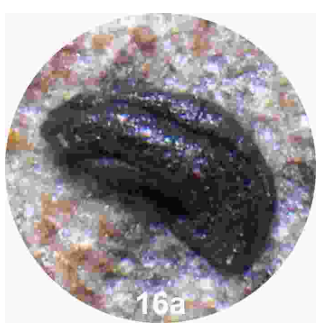
13a. Hysterothecia progressively dichotomously branched, with or without brown subiculum, forming patches of several cm^2 (Fig. 2). Peridium thick and three–layered, fragile. Ascospores 1–septate, hyaline.....14
13b. Hysterothecia not progressively dichotomously branched. Peridium thick and three–layered, hard. Ascospores varying. 15

14a. Ascospores 15–18 × 5–6 µm.....***Glonium graphicum***
14b. Ascospores 21–26 × 5–6 µm.....***Glonium stellatum***



15a. Ascospores 1–septate.....16
15b. Ascospores with more than one septum.....20

16a. Ascomata somewhat upright, mytilinidiform (Fig. 12). Asci obovoid. Ascospores brown, with median septum.....
.....***Poetschia buellioides***
16b. Ascomata not upright, mytilinidiform. Asci not obovoid. Ascospores with one large brown cell and one much smaller hyaline cell, or hyaline.....17



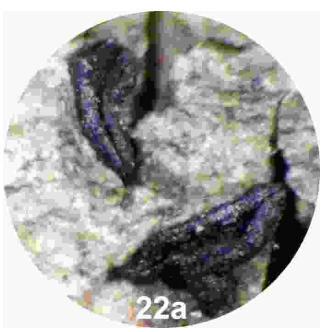
17a. Ascospores with one large brown cell and one much smaller hyaline cell.....***Acrogenospora carmichaeliana***
17b. Ascospores with two slightly unequally sized hyaline cells, +/– constricted at the septum.....18

18a. Ascospores fusiform, with both ends acuminate ca 45 × 9 µm .....***Psiloglonium hysterinum***
18b. Ascospores obovoid, with at least one, often both, ends obtuse.....19

19a. Ascomata in parallel rows, semi–immersed to erumpent. Ascospores with rounded ends 12–14 × 5–7 µm..... .....***Psiloglonium lineare***
19b. Ascomata scattered to closely aggregated, superficial. Ascospores with pointed ends, 22–27 × 7–10 µm..... .....***Psiloglonium araucanum***

20a. Ascospores 3–septate, or 5–7–septate.....21
20b. Ascospores muriform.....24

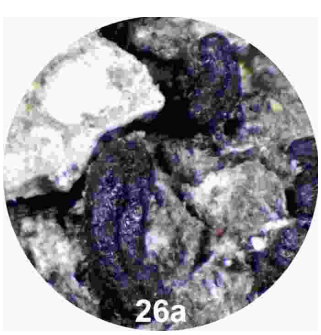
21a. Ascospores 3–septate.....22
21b. Ascospores with 5–7 septa and bulging epispore/gelatinous coating, 25–30 × 7–9 µm. On dead branches and bark of living *Taxus baccata*.....***Hysterium* sp**



22a. Hysterothecia partly open, exposing a disc (Fig. 8). Exciple two–layered, the outer layer of black and thick–walled cells and the inner layer of thin–walled, pallid and compressed cells..... ***Hysteropatella elliptica***
22. Hysterothecia closed. Exciple three–layered, the outer layer bblack and thick–walled and often, the middle layer lighter in pigmentation, and the inner layer distinctly thin–walled, with pallid and compressed cells.....23

23a. Ascospores 20–40 × 6–12 µm, usually with inner spore cells brown and end cells hyaline.....***Hysterium pulicare***
23b. Ascospores 14–21 × 4–8 µm, all cells usually brown..... .....***Hysterium acuminatum***

24a. Ascospores hyaline to yellowish.....25
24b. Ascospores brown.....27



25a. Ascospores 20–32 x 9–12 µm long, with obtuse ends, 5–7–septate.....***Gloniopsis praelonga***
25b. Ascospores 17.5 –25 x 7.5–8.75 µm, 4–6–septate.....26

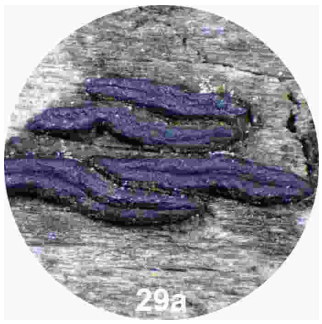
26a. Ascomata oblong, often sinuouse with narrow ends (Fig. 5). Ascospores ellipsoid (or narrower in one end) but with constricted septa, 'bumpy' in outline..... .....***Hysterobrevium curvatum***

26b. Ascomata fusiform with pointed ends. Ascospores obovoid to subfusiform, not clearly constricted at septa and not 'bumpy' in outline.....***Hysterobrevium smilacis***

27a. Ascospores usually shorter than 30 µm.....28
27b. Ascospores usually longer than 30 µm.....29

28a. Ascospores with 3–5 transverse septa and 1–2 vertical septa, 14–22 x 7–10 µm.....***Hysterobrevium mori***
28b. Ascomata without striation. Ascospores with 7–9 transverse septa, 32–45 × 12–15 µm.....***Hysterographium fraxini***

29a. Ascospores with 9–12 transverse septa, 37–56 × 13–20 µm .....***Hysterographium elongatum***
29b. Ascospores with ca 15 transverse septa, 45–65 × 11–17 µm… .....***Hysterographium flexuosum***



Other genera not yet found in Scandinavia include *Actidiographium, Anteaglonium, Ericboehmia, Gloniella, Hysterocarina, Oedohysterium, Ostreichnion, Rhytidhysteron* and *Stigmatodiscus*.

Notes on the species
Acrogenospora carmichaeliana (Berk.) Rossman & Crous.
Important synonyms: *Hysterium carmichaelianum* Berk, *Farlowiella carmichaeliana* (Berk.) Sacc.
Substrate: deciduous wood.
Distribution in Scandinavia: a few finds in SW Norway, Denmark, Sweden.
Selected descriptions: Zogg (1962): 85, Dennis (1981): 473, Ellis and Ellis (1997): 28, Læssøe and Petersen (2019): 1617. Wergen (2017a): 367, as *F. carmichaeliana.*

Actidium hysterioides Fr.
Substrate: coniferous wood.
Distribution Scandinavia: Rather common in SE, SW and N Norway, Sweden.
Selected descriptions: Zogg (1962): 124, Dennis (1981): 477, Ellis and Ellis (1985): 185.

Figure 1. *Actidium hysterioides* (O-F-88600). Photo: M. Andreasen.

Gloniopsis praelonga (Schwein.) Underw. & Earle
Important synonyms: *Hysterium praelongum* Schwein., *Hysterographium praelongum* (Schwein.) Sacc.
Substrate: Deciduous wood.
Distribution in Scandinavia: Rare in Norway (SW), Denmark, Sweden.
Selected descriptions: Zogg (1962): 50, Ellis and Ellis (1985): 238, Mathiassen and Granmo (2012): 22, Læssøe and Petersen (2019): 1619, Wergen (2017b): 707.

Glonium graphicum (Fr.) Duby
Important synonyms: *Hysterium graphicum* Fr.: Fr.
Substrate: Coniferous wood.
Distribution in Scandinavia: Rare in Norway (SE), Denmark, Sweden.
Selected descriptions: Zogg (1962): 69.

Glonium stellatum Muhl.
Substrate: Old wood.
Distribution in Scandinavia: Rare in Norway (SE), Sweden.
Selected descriptions: Zogg (1962): 71, Boehm et al. (2009): 466.

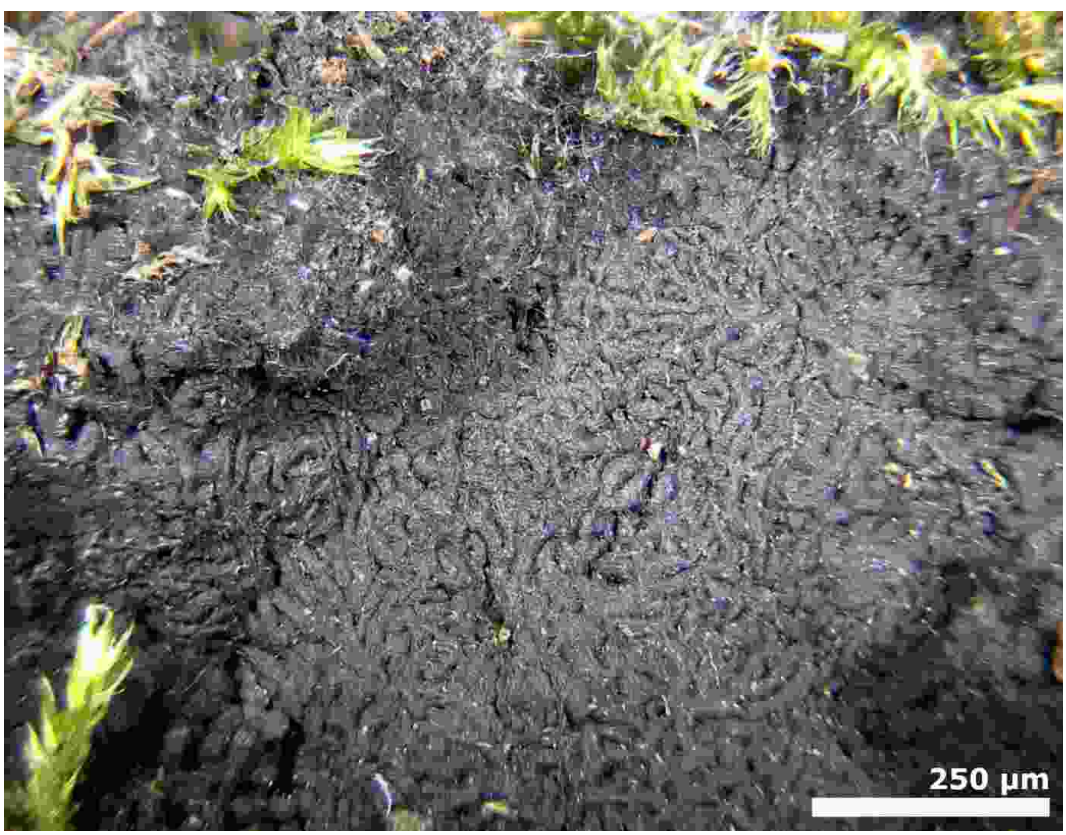


Figure 2. *Glonium stellatum* on decayed wood of *Quercus* sp. Photo: Mathias Andreasen.

Glyphium elatum (Grev.) H. Zogg
Important synonyms: *Lophium elatum* Grev.: Fr.
Substrate: Decideous wood, mostly on branches.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Ellis and Ellis (1985): 160, Boehm et al. (2015): 8, Læssøe and Petersen (2019): 1619, Wergen (2017b): 700.

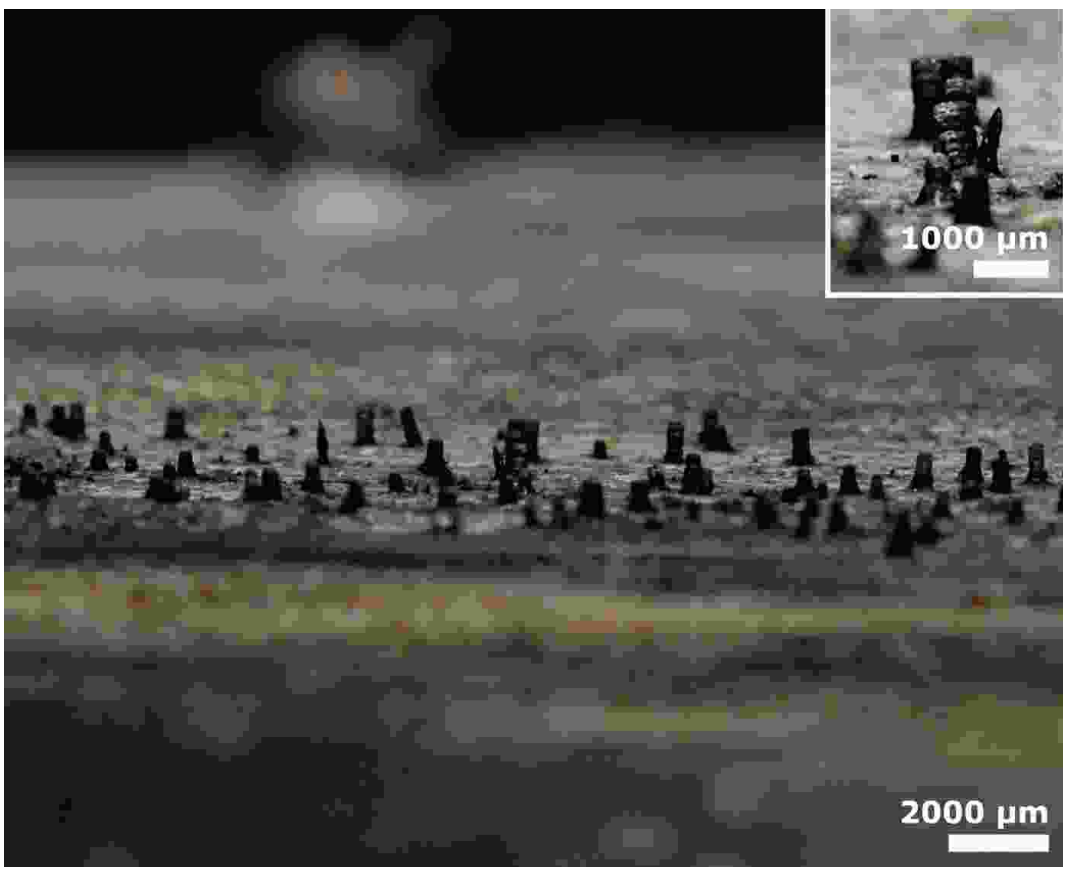


Figure 3. *Glyphium elatum* on *Fraxinus excelsior* branch. Photo: Leif Andersson.

Glyphium grisonense Math.
Substrate: Deciduous wood.
Distribution in Scandinavia: Quite common in N Norway.
Selected descriptions: Boehm et al. (2015): 9, Mathiassen 1993: 89

Glyphium schizosporum (Maire) H. Zogg
Important synonyms: *Lophium schizosporum* Maire
Substrate: Deciduous wood.
Distribution in Scandinavia: Not yet found in the Scandinavian countries.
Selected descriptions: Boehm et al. (2015): 8.

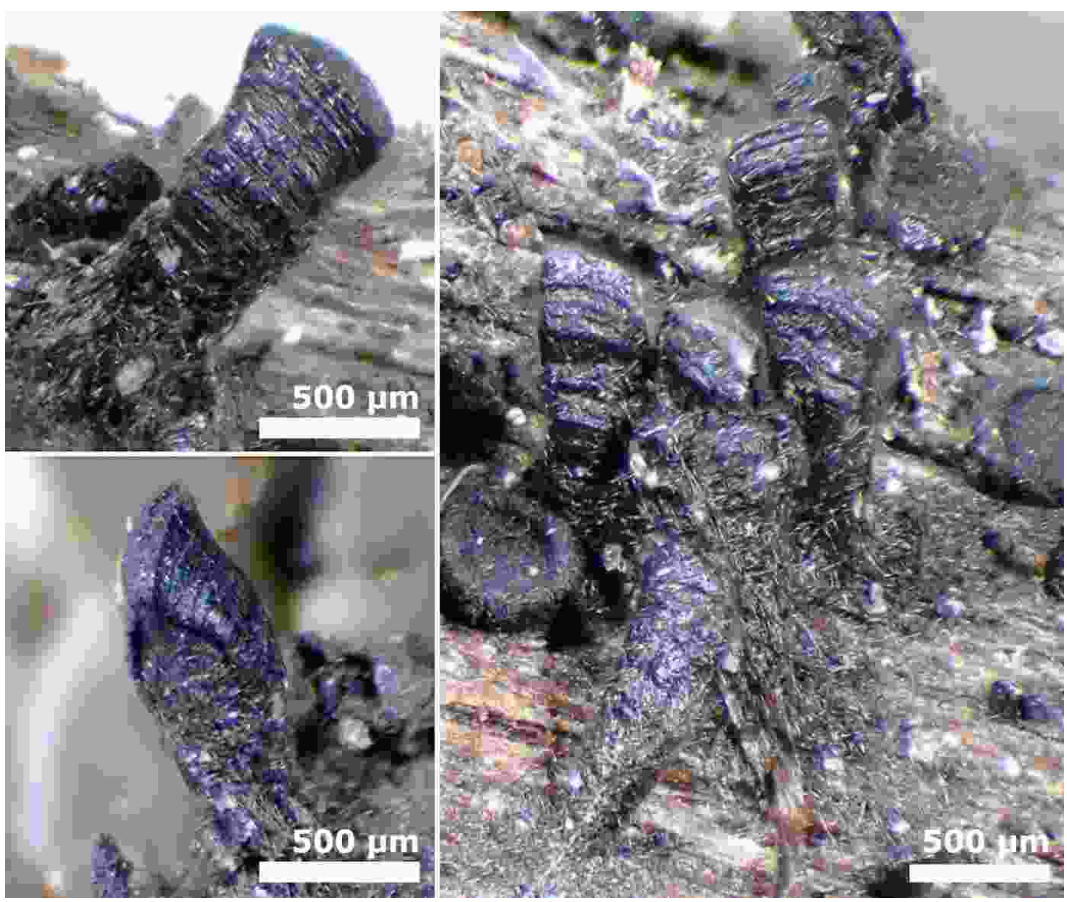


Figure 4. *Glyphium grisonense* on *Salix* sp. Photo: Mathias Andreasen.

Hysterium acuminatum Fr.
Important synonyms: *Hysterium angustatum* Alb. & Schwein.
Substrate: Bark of living deciduous trees.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Zogg (1962): 26 (as *H. angustatum*), Dennis (1981): 475 (as *H. angustatum* and *H. acuminatum*, Ellis and Ellis (1985): 31, Læssøe and Petersen (2019): 1617, Wergen (2017b): 495, as *H. angustatum*.

Hysterium pulicare Pers.: Fr.
Important synonyms: *Hysterium biforme* Fr.
Substrate: Bark of living deciduous trees.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Zogg (1962): 22, Dennis (1981): 475, Breitenbach and Kränzlin (1981): 300, Ellis and Ellis (1985): 31, Læssøe and Petersen (2019): 1617, Wergen (2017b): 482.

Hysterium sp.
This probably undescribed species resembles *H. pulicare* in macroscopic appearance. It was found by us a few times in the SW part of Norway. We would be grateful to receive more material of this species. It may or may not be specific to yew *Taxus baccata*.

Hysterobrevium curvatum (Fr.: Fr.) Math. & Granmo
Important synonyms: *Hysterium curvatum* (Fr.).
Substrate: Deciduous wood.
Distribution in Scandinavia: Rare in Norway (SE, SW), Denmark, Sweden.
Selected descriptions: Mathiassen and Granmo 2012: 25, Wergen (2017b): 708, as *H. smilacis*.

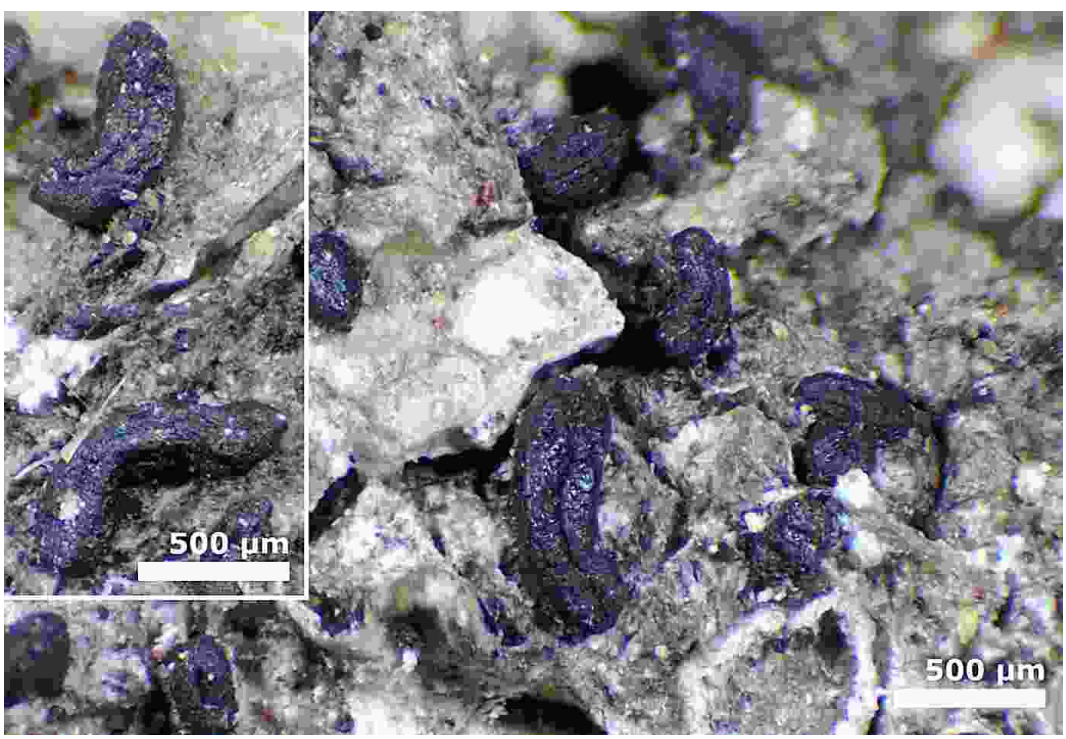


Figure 5. *Hysterobrevium curvatum* on *Populus tremula*. Photo: Mathias Andreasen.

Hysterobrevium mori (Schwein.) E.W.A. Boehm & C.L. Schoch
Important synonyms: *Hysterographium mori* (Schwein.) Rehm, *Hysterium mori* Schwein.
Substrate: Wood.
Distribution in Scandinavia: Rare in Norway, Denmark, Sweden.
Selected descriptions: Zogg (1962): 41, Barr (1990): 14, Ellis and Ellis (1985): 31, Læssøe and Petersen (2019): 1616.

Hysterobrevium smilacis (Schwein.) E.W.A. Boehm & C.L. Schoch
Important synonyms: *Hysterium smilacis* Schwein., *Gloniopsis smilacis* (Schwein.) Underw. & Earle.
Substrate: Deciduous wood.
Distribution in Scandinavia: Uncertain.
Selected descriptions: Boehm et al. (2009): 63.

Hysterographium elongatum (Wahlenb.: Fr.) Corda
Important synonyms: *Hysterium elongatum* Wahlenb.: Fr.
Substrate: Deciduous wood.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Sweden.
Selected descriptions: Mathiassen (1993): 101, Ellis and Ellis (1985): 251.

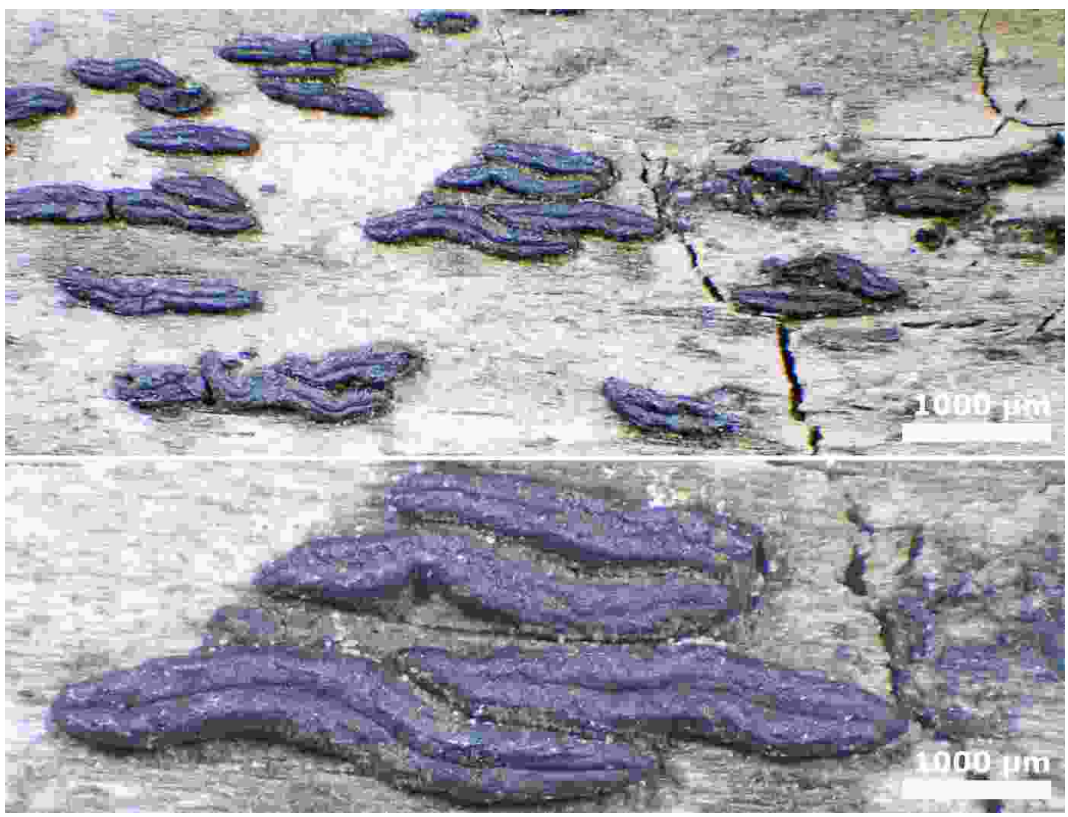


Figure 6. *Hysterographium elongatum* on wood of *Populus tremula*. Photo: Mathias Andreasen.

Hysterographium flexuosum (Schwein.: Fr.) Sacc.
Important synonyms: *Hysterium flexuosum* Schwein.: Fr.
Substrate: Deciduous wood.
Distribution in Scandinavia: Rare in Norway(SW), Sweden.
Selected descriptions: Zogg (1962): 39.

Hysterographium fraxini (Pers.: Fr.) De Not.
Important synonyms: *Hysterium fraxini* Pers.: Fr.
Substrate: Deciduous wood.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Zogg (1962): 35, Dennis (1981): 476, Breitenbach and Kränzlin (1981): 302, Barr (1990): 12, Ellis and Ellis (1985): 141. Læssøe and Petersen (2019): 1615, Wergen (2017b): 768.

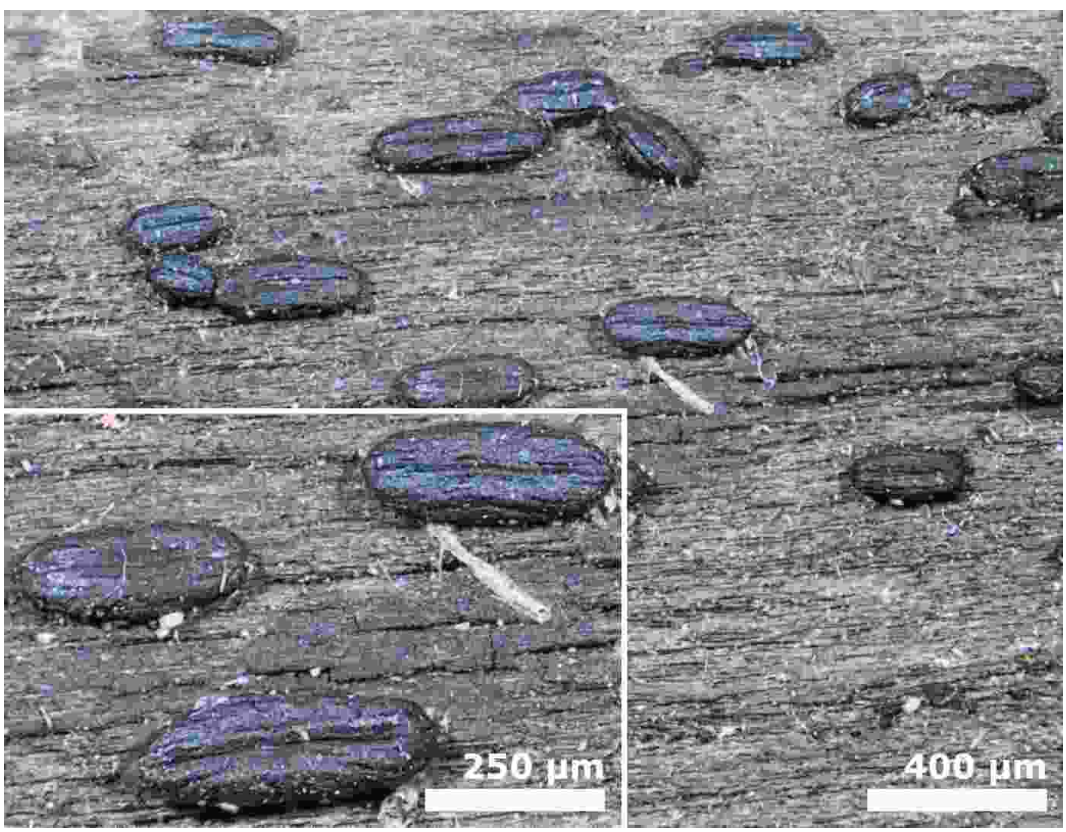


Figure 7. *Hysterographium flexuosum* on *Quercus* sp. Photo: Mathias Andreasen.

Hysteropatella elliptica (Fr.: Fr.) Rehm
Important synonyms: *Hysterium ellipticum* Fr.: Fr.
Substrate: Wood.
Distribution in Scandinavia: Rare in Norway (SE), Sweden.
Selected descriptions: Sherwood-Pike (1986): 267.

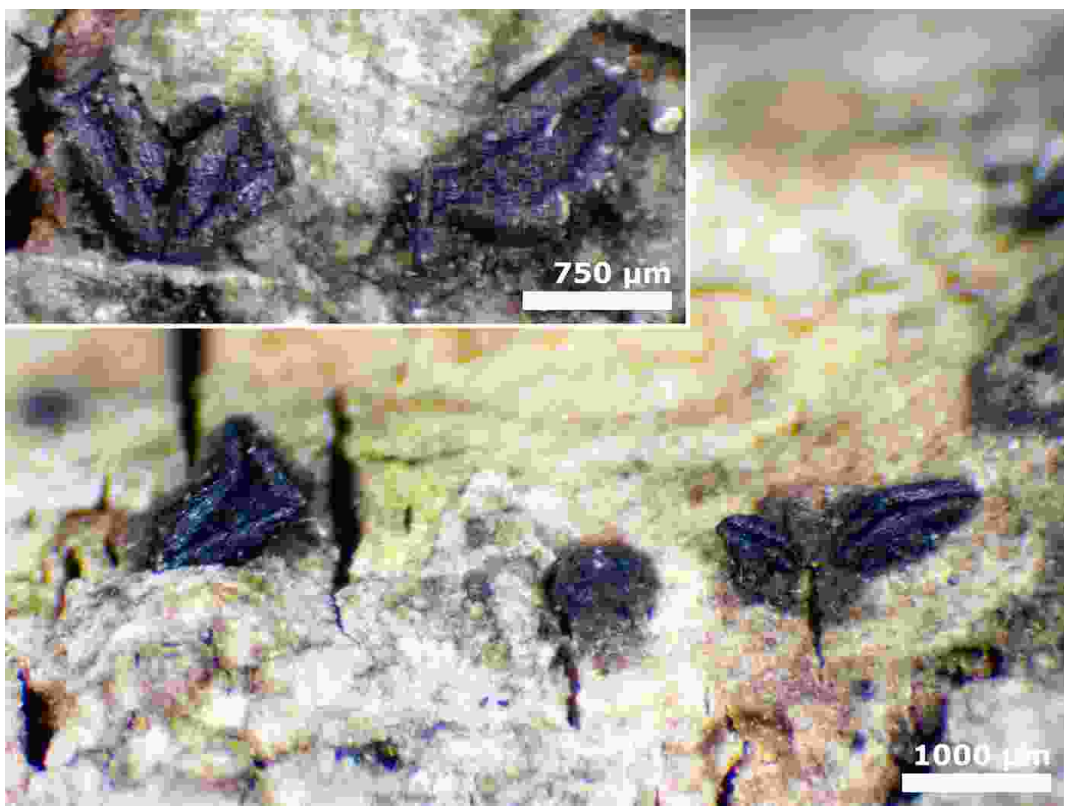


Figure 8. *Hysteropatella elliptica* on *Salix caprea*. Photo: Mathias Andreasen.

Lophium elegans H. Zogg
Substrate: branches of coniferous trees.
Distribution in Scandinavia: Uncommon in Norway (SE, SW, N).
Selected descriptions: Zogg (1954): 141.

Lophium mytilinum Pers.: Fr.
Important synonyms: *Hysterium mytilinum* Pers.
Substrate: Branches of coniferous trees.
Distribution in Scandinavia: Common in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Zogg (1962): 92, Dennis (1981): 477, Schmid (1990): 43, Ellis and Ellis (1985): 186, Læssøe and Petersen (2019): 1618, Wergen (2017b): 699.

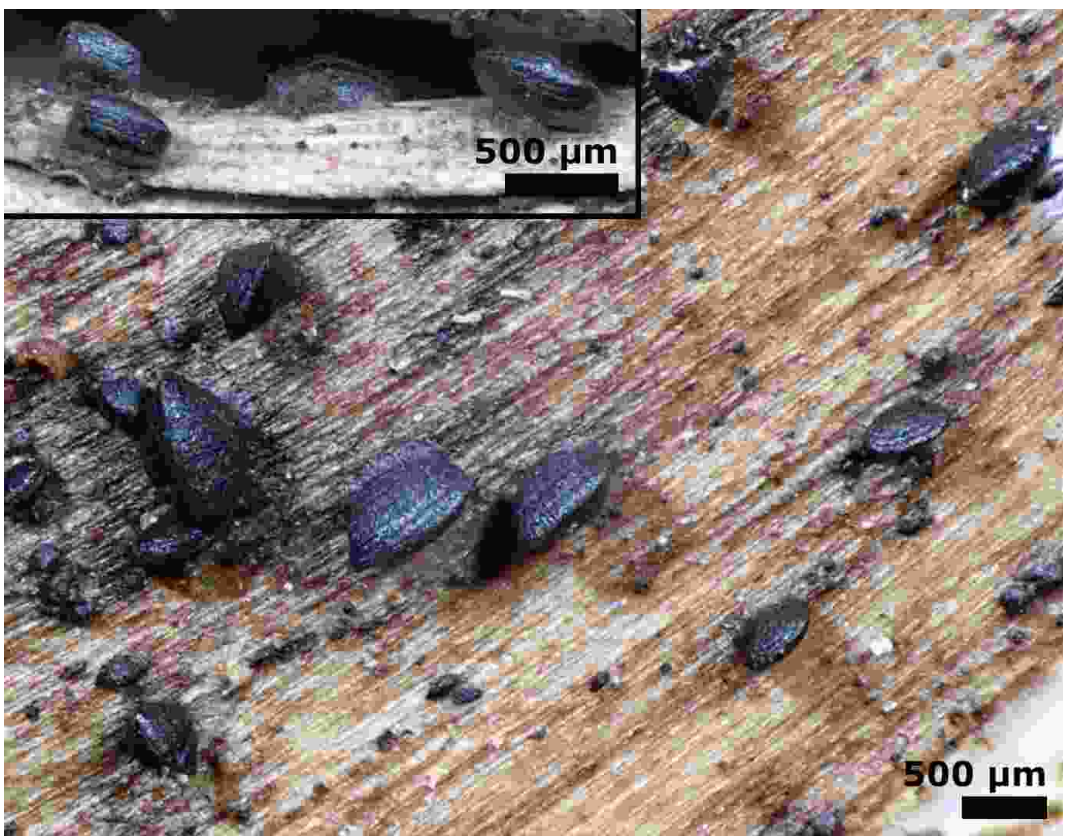


Figure 9. *Lophium mytilinum* on *Picea abies*. Top: on needles; Bottom: on decaying wood. Photo: Mathias Andreasen.

Mytilinidion acicola G. Winter
Substrate: Needles and bark on coniferous trees including *Juniperus communis*.
Distribution in Scandinavia: Rather common in Norway (SE, SW, N), Sweden.
Selected descriptions: Zogg (1962): 119, Holm and Holm (1977): 44, Ellis and Ellis (1985): 152, Læssøe and Petersen (2019): 1618, Wergen (2017b): 492.

Mytilinidion decipiens (P. Karst.) Sacc.
Important synonyms: *Lophium decipiens* P. Karst.
Substrate: Coniferous bark, wood.
Distribution in Scandinavia: Rare in Norway (SE, N), Denmark.
Selected descriptions: Boehm et al. (2009): 77, Læssøe and Petersen (2019): 1618.

Mytilinidion gemmigenum Fuckel
Substrate: Coniferous bark, wood.
Distribution in Scandinavia: Rare in Norway (SE, SW), Sweden.
Selected descriptions: Zogg (1962): 111, Mathiassen and Granmo (2012): 77.

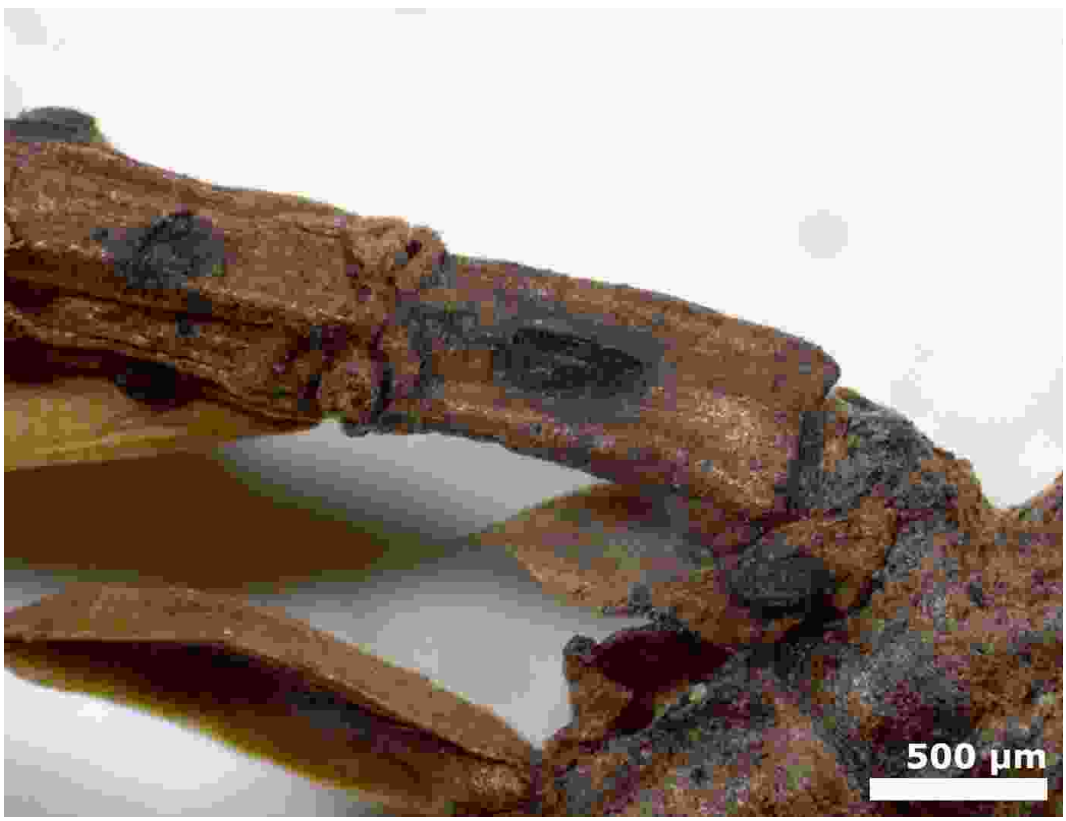


Figure 10. *Mytilinidion acicola* on *Juniperus communis* needles. Photo: Mathias Andreasen.

Mytilinidion mytilinellum (Fr.: Fr.) H. Zogg
Important synonyms: *Lophium mytilinellum* Fr.: Fr.
Substrate: Coniferous bark, wood.
Distribution in Scandinavia: Rare in Norway (SW), Sweden.
Selected descriptions: Zogg (1962): 106, Breitenbach and Kränzlin (1981): 302, Ellis and Ellis (1985): 186, Wergen (2017b): 493.

Mytilinidion rhenanum Fuckel
Important synonyms: *Mytilinidion karstenii* Sacc.
Substrate: Coniferous bark, wood.
Distribution in Scandinavia: Rare in Norway (two collections from 1840 by Nils Green Moe), Sweden.
Selected descriptions: Zogg (1962): 109, Ellis and Ellis (1985): 186.

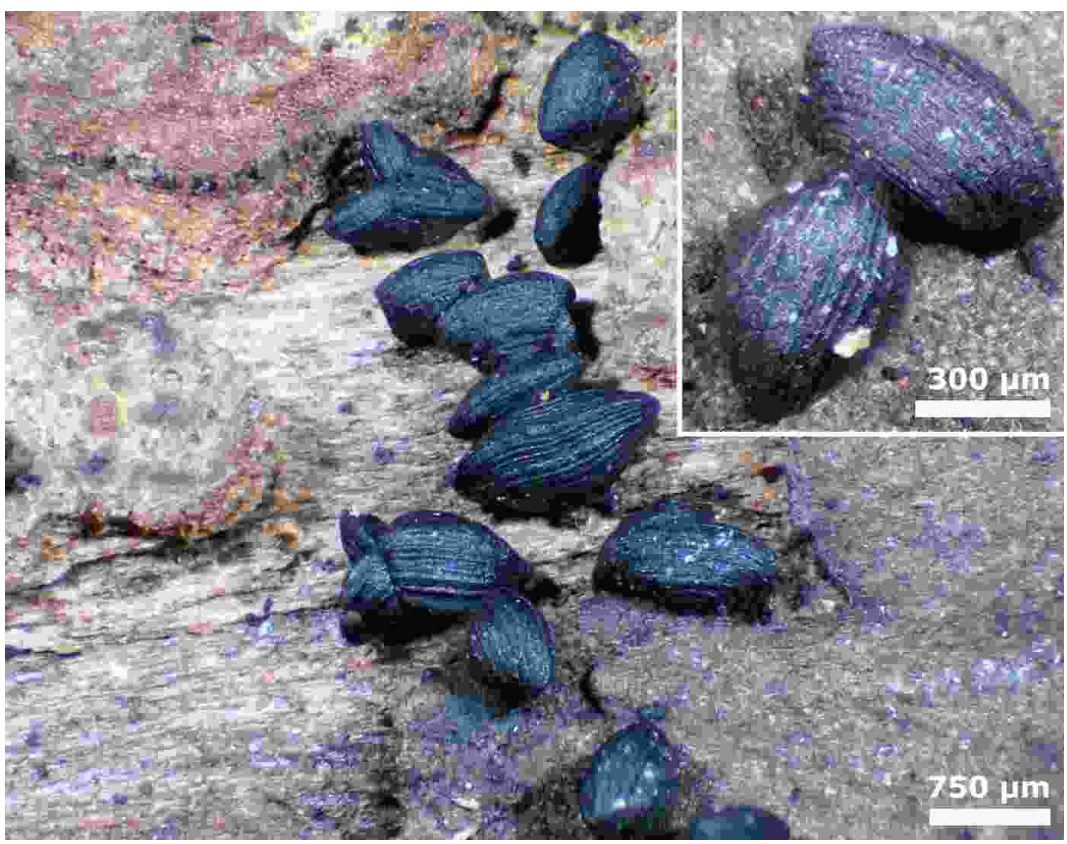


Figure 11. *Mytilinidion mytilinellum* on bark of *Pinus sylvestris*. Photo: Mathias Andreasen.

Poetschia buellioides Körb.
Substrate: Bark of *Pinus silvestris*.
Distribution in Scandinavia: Probably rather common in Norway (SE, SW).
Selected descriptions: Yacharoen et al. (2015): 311, Wergen (2017a): 402.

Poetschia buellioides Körb.
Substrate: Bark of *Pinus silvestris*.
Distribution in Scandinavia: Probably rather common in Norway (SE, SW).
Selected descriptions: Yacharoen et al. (2015): 311, Wergen (2017a): 402.

Psiloglonium araucanum (Speg.) E.W.A. Boehm, Marinc. & Schoch
Important synonyms: *Glonium araucanum* Speg.
Substrate: Bark of coniferous tree.
Distribution in Scandinavia: Found once in Denmark.
Selected descriptions: Boehm et al. (2009): 71.

Psiloglonium hysterinum (Rehm) E.W.A. Boehm & Schoch
Important synonyms: *Glonium hysterinum* Rehm
Substrate: Old wood.
Distribution in Scandinavia: Rare in Sweden.
Selected descriptions: Zogg (1962): 68.

Psiloglonium lineare (Fr.: Fr.) Petr.
Important synonyms: *Hysterium lineare* Fr.: Fr., *Glonium lineare* (Fr.: Fr.) De Not.
Substrate: Old wood.
Distribution in Scandinavia: Rather uncommon in Norway (SE, SW, N), Denmark, Sweden.
Selected descriptions: Zogg (1962): 63, Dennis (1981): 474, Ellis and Ellis (1985): 28, Boehm et al. (2009): 68.

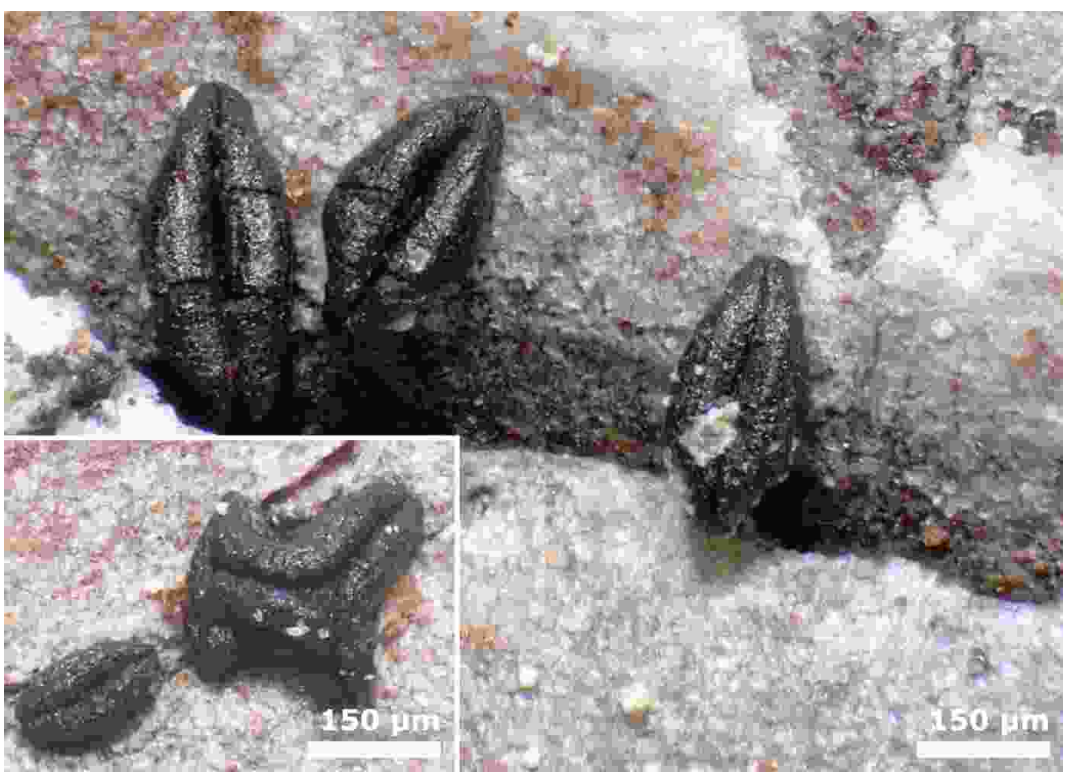


Figure 12. *Poetschia buellioides* on bark of *Pinus sylvestris*. Photo: Mathias Andreasen.

ACKNOWLEDGMENT

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Neozygites sminthuri (Entomophthoromycota, Neozygitales) a fungal pathogen on springtails new to Norway

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Norsk tittel: *Neozygites sminthuri* (Entomophthoromycota: Neozygitales) en ny patogen sopp på spretthaler i Norge

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KEYWORDS
Entomophthoromycota, Neozygitales, *Neozygites*, Entomopathogenic fungi, fungi on Collembola

NØKKELORD
Insektmuggsopper, Insektmuggordenen, insektspatogener, sopp på spretthaler (Collembola)

SAMMENDRAG
På en feltekskursjon utenfor Oslo ble det samlet en spretthale av familien Isotomidae. Denne ble videre mikroskopisk undersøkt og vi fant at eksemplaret var infisert av *Neozygites sminthuri* (Neozygitales: Neozygitaceae). Arten er ny for Norge og den er lite undersøkt internasjonalt. I tillegg har soppen ikke tidligere blitt registrert på en vert fra denne sprettthalefamilien. Funnet presenteres med bilder og kommentarer på dens anatomi, økologi og forekomst i Skandinavia.

ABSTRACT
During a field trip outside of Oslo, a springtail of the family Isotomidae was collected and microscopically investigated. We found the specimen to be infected with the fungal species *Neozygites sminthuri* (Neozygitales: Neozygitaceae). The species is new to Norway and is rarely investigated internationally. Also, it has not been registered on a host species of this family of springtails earlier. The collection is presented with photos and notes on its anatomy, ecology and occurrence in Scandinavia.

INTRODUCTION

Fungal pathogens are rarely recorded from springtails in Scandinavia (e.g. Visser et al. 1987; Balazy 1993; Keller and Steenberg 1996; Keller and Steenberg 1997; Dromph et al. 2001), and there is yet an enormous diversity to be investigated within the field of entomopathogenic fungi (e.g. Araújo and Hughes 2016). A fungus of the order Neozygitales (earlier Entomophthorales) was, however, found and investigated by Steenberg et al. (1996) in Danish populations of the lucerne flea *Sminthurus viridis* (Linnaeus, 1758) (Collembola: Symphypleona: Sminthuridae) collected from three separate locations. The species infecting the springtails was recognised to belong to genus *Neozygites* Witlaczil (1885) and later published as the new species *Neozygites sminthuri* (Keller and Steenberg 1997). The genus belongs to the family Neozygitaceae (Entomophthoromycota: Neozygitomycetes: Neozygitales) (acc. Humber 2012, Gryganskyi et al. 2012, 2013). They are

widely distributed and are obligate parasites of insects, mites and springtails (Keller and Steenberg 1997, Humber 2012).

On a field trip arranged through the course "Fungal Diversity and Evolution" by the Nordic Academy of Biodiversity and Systematics studies (NABiS) and the University of Uppsala, a springtail of the family Isotomidaewas collected. The specimen was found to be infected by a fungal parasite of the genus *Neozygites*. The finding represents the first Norwegian record of a *Neozygites* species infecting springtails. The only described *Neozygites* species known to infect springtails is *N. sminthuri* (e.g. Keller and Steenberg 1997, Dromph et al. 2001). We report *N. sminthuri* as new to Norway and make notes on its anatomy, ecology and distribution.

MATERIALS AND METHODS

A springtail from the family Isotomidae (Collembola: Entomobryomorpha), most likely from the genera *Desoria* Nicolet, 1841, *Isotoma* Bourlet, 1839 or *Isotomurus* Boerner, 1903, was found in a water sample collected from a small pond in temperate, boreal forests on an excursion from Oslo. The locality (59.9731806, 10.8856528) is situated in the Røverkollen nature reserve about 260 meters above sea level with bedrock in partly Basalt and partly Syenite. The water sample was collected from a small swamp area of type V2-C1 according to the national Nature in Norway (NiN) system surrounded by a spruce forest of type T4-C1 in the west and blockfields (T27) in the east (Halvorsen and Bratli 2019, Halvorsen et al. 2020). The water sample was initially collected to study species of Chytridiomycota on spruce pollen.

The springtail was first incubated in pond water and exposed to daylight for five days at varying temperatures from 20–30 °C and subsequently transferred into a sterile water droplet on a micro slide for morphological investigation. The first row of measurements and photos were then taken. Ten days later, the specimen was again investigated and photographed in lactophenol cotton blue solution and precise measurements made under a NIKON Eclipse Ci-L compound microscope using a Tucsen DigiRetina 16 camera. The software Lite Helicon Focus 7 v. 7.5.6 was used for precise measurements, higher depth resolution and scale bar ratios. Images were processed in GIMP v. 2.8.22 (Kimball and Mattis 1996).

DISTRIBUTION

Members of *Neozygites* are widely distributed (e.g. Keller 1991, Delalibera et al. 2004c, Montalva et al. 2016, 2018, Zhou et al. 2017) and have been recorded in Scandinavia (Steenberg and Bresciani 1996, Keller and Steenberg 1997, Dromph et al. 2001, Klingen et al. 2002, Nordengen and Klingen 2006, Klingen et al. 2008, Castilho et al. 2015). *Neozygites* species with collembolan hosts are rarely observed, and only one species, *Neozygites sminthuri*, is currently described (Keller and Steenberg 1997). The species is recorded from a few localities in Denmark (Stenberg and Bresciani 1996, Keller and Steenberg 1997, Dromph et al. 2001) and one locality in Norway (current study).

TAXONOMY

The genus *Neozygites* Witlaczil (1885) includes species with spherical or rod-shaped hyphal bodies; unbranched conidiophores; spherical to obovate primary conidia with 3–8 nuclei; presence of capilliconidia with typically bent capillary tubes; spherical or ellipsoidal, binucleate, dark brown to black zygospores, rarely azygospores; cystidia always absent, rhizoids usually absent (Keller 1997). This genus comprises species with relatively narrow host ranges, all of which have been found in small arthropods such as aphids (Homoptera), thrips (Thysanoptera) and mites (Acari) (Keller 1991, Keller and Steenberg 1997).

Neozygites sminthuri S. Keller & Steenberg (1997) Fig. 1

Etymology: Suggesting the host (*Sminthurus viridis*) from which the fungus was collected originally.
Description of Norwegian material: *Rhizoids* absent. *Hyphal bodies* spherical, 12–17 µm (n = 10), sometimes slightly subspherical, containing 4, rarely 3 nuclei. *Conidiophores* unbranched. *Primary conidia* 12–16x6–12 µm (n = 30), ovoid to pyriform, with apex rounded. *Papilla of primary conidia* rounded, rarely flat, with a diameter of 5–7 µm (n = 25). *Secondary conidia*, *capilliconidia*, *cystidia* and *resting spores* not observed.

Material examined: Norway, Oslo County and municipal, Ammerud, Røverkollen Naturreservat, 59.9731806, 10.8856528, 256 m a.s.l, on collembolan of the family Isotomidae, in a pond, 17 March 2020. O-F-256950.

Notes: The fungal structures present are typical for the genus *Neozygites*, especially the number of nuclei. The size of hyphal bodies and primary conidia, together with the collembolan host, distinguishes this species from other resembling species. The key by Keller (1997) was used together with subsequent literature to confirm the identification. Senior researcher Tove Steenberg at Aarhus University, Department of Agroecology and coauthor of the species, indicated a possible correct identification of *Neozygites sminthuri* based on photos of primary conidia, specifying the absolute need of microscopy imaging and measurements of dyed hyphal bodies for verification of the identification. These specifications, alongside additional taxonomical details, are presented in this article.

DISCUSSION

We observed the following asexual structures: hyphal bodies, young conidiophores stunting below the host's cuticle, conidiophore after penetration of the host's cuticle containing primary conidia and projected primary conidia. We did not observe any structures from the sexual stage. Since we also lack molecular data, it is difficult to determine the species confidently. A study by Dromph et al. (2001) reported four undescribed species of *Neozygites* on collembolans in Denmark. Our specimen fits the most with *N. smithuri* when comparing conidial measurements conducted in that study, but there is most likely unknown diversity in the genus in Scandinavia.

Our specimen was found on Isotomidae, a different family in a different order than *Sminthurus viridis* (Xiong et al. 2008, Leo et al. 2019), on which the species was initially described, which must also be taken into account. Conidiophores and hyphal bodies that closely resembled those found on the springtail were also observed on a spider carcass that had been soaked in the same water sample, suggesting that some life cycle stages of the fungus are more generalistic.

Increased levels of sampling followed by cultivation and sequencing are crucial for future investigation of neozygitoid systematics. Progress in sampling and molecular methods made by Jensen et al. (2001a,b, 2008) and cryopreservation and culturing by Delalibera Jr. et al. (2004a,b, 2006) have contributed to pushing research in entomopathogenic fungi forward. The potential for more novel methods of diversity measures through, e.g. environmental sequencing techniques should increase with the assemblage of genetic data.

The authors hope that this article gives inspiration for increased interest and activity, and we call for a joint effort to sample these exciting and beautiful fungi. The authors' interest and enthusiasm have indeed, been awakened.

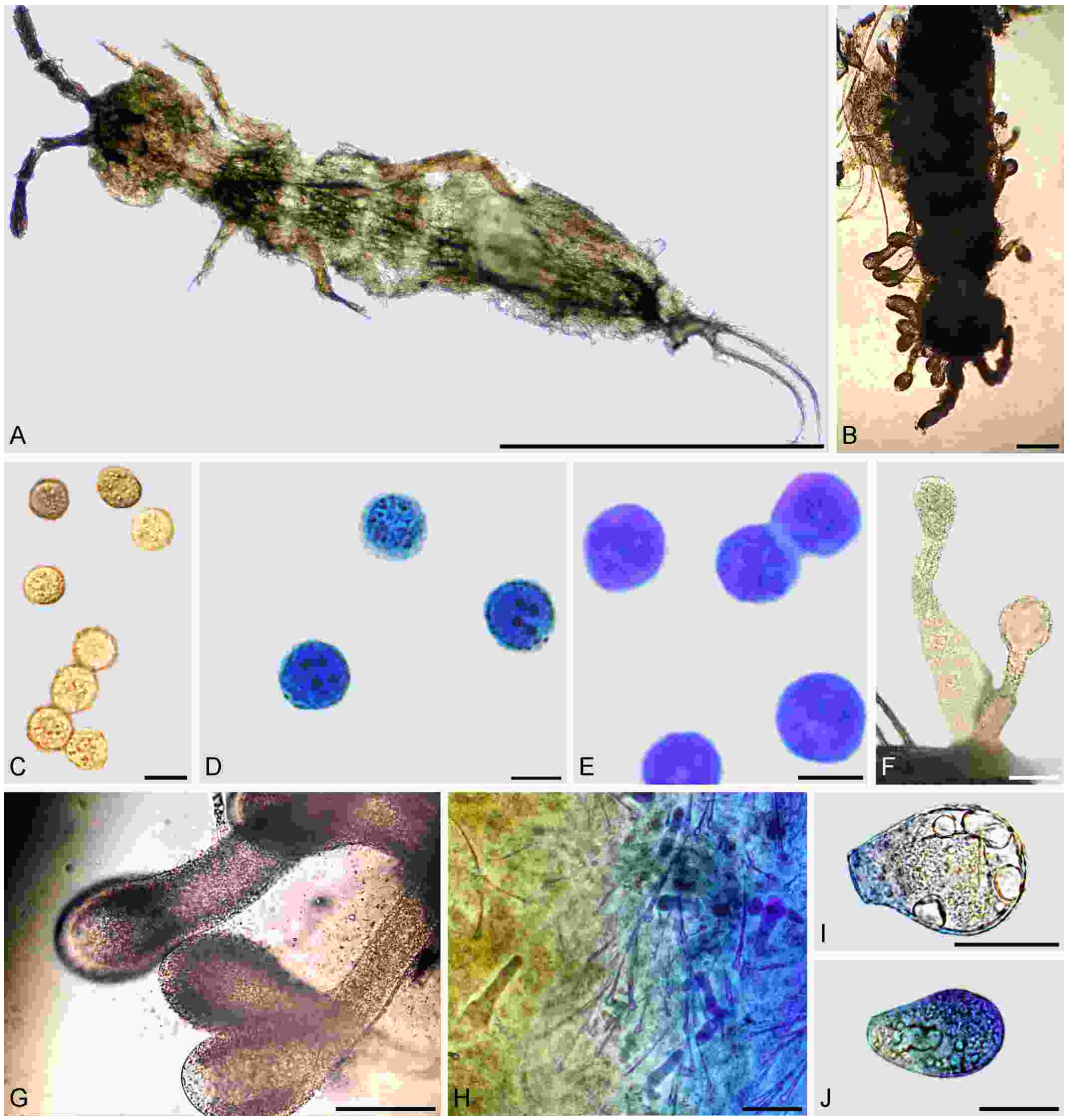

Figure 1. **A-B** Springtail. **C-K** *Neozygites sminthuri*. **A** Springtail under cover slip, without visible conidiophores fifteen days after incubation. **B** Conidiophores on the host, five days after incubation. **C** Hyphal bodies. **D**, **E** Hyphal bodies with nuclei (lactophenol cotton blue). **F** Conidiophore (on the left) and shells of hyphal bodies with developing conidiophores (on the right). **G**, **H** Conidiophores (H in lactophenol cotton blue). **I**, **J** Projected primary conidia (lactophenol cotton blue). Scale bars: **A** = 400 µm, **B** = 50 µm, **H** = 20 µm, **C**-**G**, **I**, **J** = 10 µm. Photo: **A**, **C**-**F**, **H**-**J** Mathias Andreasen, **B**, **G** Erik Möller.

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24th Nordic Mycological Congress 2019 Stord, Sunnhordland: into the wet wild west

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The 3. to 8. of September 2019, the 24. Nordic Mycological Congress (NMC) was arranged in the Stord-Bømlo-Tysnes island archipelago of Sunnhordland (Vestland), south-western-most Norway. This was the second, international mycological congress held in Norway 2019 (report on *Cortinarius* congress in Valdres august 2019, Brandrud et al. 2020a, b). Fortunately, we managed to set sails and land safe to shore these two congresses, just before the outbreak of the corona pandemic!

The NMCs are arranged every second year, and circulates in the Nordic countries. It has been held in Norway five times before; in Mo i Rana (Nordland) in 1976 (See Sivertsen 1978), Nymoen, Søndre Land (Oppland (Innlandet)) in 1984 (Bendiksen 1986), Skibotn 1992 (Mathiassen, and Granmo, 1995), Sogndal (Sogn og Fjordane (Vestland)) in 2000 and Steinkjer (Nord-Trøndelag (Trøndelag)) in 2009 (Brandrud et al. 2001, 2010). The NMCs are fieldwork focused forays and congresses, traditionally arranged mainly by and for the Nordic, professional (University) mycologists. Nowadays, this family of Nordic university and institute mycologist is becoming smaller, and fewer of the professional mycologists are field study focused. So the attendance of such mycologists on the NMC's has decreased, and we see that our "sister congress" in Central Europe, the "Dreiländer Tagung" in Germany-Austria-Switzerland is for the time being dormant. However, we have seen a renewal of the NMCs by involving (i) more amateur mycologists or citizens scientists, including the national mycological associations, and (ii) guests from outside the Nordic

Figure 1. The participants at NMC in Sunnhordland 2019. Photo: P. Karlsen.

Table 1. Species on the Norwegian Redlist for 2015 that was found during NMC, in the municipalitys visited.
*Redlist category for 2021 is to be considered as likely, not confirmed. The Norwegian Redlist for 2021 is not yet published.
Camarophyllopsis atrovelutina was found new for Norway, while *Cortinarius olidoamethysteus* was the second found globally.

Species	Norwegian species name	Norwegian Redlist category		Municipality			
		2015	2021*	Stord	Bømlo	Tysnes	Fitjar
Albatrellus subrubescens	Furufåresopp	NT	NT	X			
Boletopsis grisea	Furugråkjuke	VU	VU	X			
Camarophyllopsis atrovelutina	Fløyelsnarrevokssopp	DD	DD	X			
Cantharellus melanoxeros	Svartnede kantarell	NT	NT		X		
Clavaria atrofusca	Brunsvart køllesopp	DD	EN	X			
Cortinarius olidoamethysteus	Grønnbelteslørsopp	-	DD	**X**			
C. russulaespermus	Kremlesporeslørsopp	-	NT	**X**			
C. tofaceus	Løveslørsopp	VU	NT	**X**			
Cystolepiota hetieri	Rødnende melparasollsopp	EN	EN	X		**X**	
Entoloma allospermum = *caeruleum* s. auct		DD	-	**X**	**X**		
E. carneogriseum	Gråblå rødspore	DD	DD		**X**		
E. jubatum	Semsket rødspore	NT	NT		X		
E. luteobasis	Linderødspore	VU	VU	X			
E. nordeloosii	Machiels rødspore	-	NT	X		**X**	
E. ochromicaceum	Beige rødspore	DD	VU	X			
E. queletii	Fagerrødspore	NT	VU	X			
Hydnellum spongiosipes	Filtbrunpigg	EN	EN		X		

Species	Norwegian species name	Norwegian Redlist category		Municipality			
		2015	2021*	Stord	Bømlo	Tysnes	Fitjar
Lactarius azonites	Eikerøykriske	VU	VU			X	
*L. pterosporus**	Rosakjøttriske	VU	VU	X			
Lycoperdon echinatum	Piggsvinrøyksopp	EN	VU			X	
L. mammiforme	Flasset slørsopp	EN	EN			**X**	
Mycena cyanorhiza	Blåfothette	DD	DD		X		
M. latifolia	Alvehette	NT	NT		X		
Mycenella trachyspora	Rødflekket frøkenhette	DD	DD			**X**	
Polyporus badius	Kastanjestilkkjuke	VU	VU	X	X		
Pseudotricholoma (*Porpoloma*) *metapodium*	Grå narremusserong	EN	EN				X
Ramaria flavobrunnescens	Solkorallsopp	NT	NT	X			
Ramariopsis subtilis	Elegant småfingersopp	NT	NT		X		
Russula anthracina	Kokskremle	NT	NT		X		
Tremellodendropsis tuberosa	Buskgelésopp	NT	NT	X			
Tubulicrinis regificus		DD	DD	X			
SUM (31 species tot.)				18	10	6	1

range. In the 24. NMC at Stord, we had participants from 11 countries; from Denmark, Estonia, Finland, Iceland, Norway and Sweden, and involving guests from Germany, Hungary, Japan, Russia and The Netherlands. The congress was arranged by the University of Oslo in cooperation with the Norwegian association of Mycology and Foraging.

To get the participants in the correct Western Norway mood, the weather Gods had provided us with (continuously) wet weather, but hopefully the participants have already forgotten the most extreme weather and will remember the nice places, nice people and the interesting fungus-finds.

For some obscure reasons, it is difficult to get a really good, productive fungal season in the most rain-soaked, oceanic parts of Norway, but we were rather lucky, finding a rich funga in many of the localities, rich enough to fill a very long table at the study hall in the Grand Hotel at Leirvik, Stord.

Altogether, we recorded well above 400 species, probably closer to 450, which is a high number in the ultra-oceanic W Norway (an official species list is in progress, and will soon be distributed to all participants and published online). Many species were new for the region, for instance we recorded 31 new red-list species new for Sunnhordland (Stord-Bømlo-Tysnes; Table 1). The most species rich genus was *Cortinarius*, with altogether 50 species recorded.

Two persons (Gunnhild Marthinsen, Siri Rui) were the whole week devoted to obtain samples for ITS-DNA barcoding, and altogether 203 specimens were subsequently attempted barcoded through NorBOL (norbol.org). 181 specimens gave successful ITS sequences. This extensive ITS-DNA sequencing documented a number of rare and interesting finds, in groups which are otherwise difficult to identify. For instance a number of little known cortinarii and entolomas were documented, such as *Cortinarius aurantiocaeruleum* (*Obtusi* group) and *C. russulaespermus* (*Hinnulei* group) from oak forests, and *Entoloma carneogriseum* and *E. cuboidealbum* (in *Sericellum* group) from grasslands.

We wanted to show the participants the special, rich and partly very old habitat-types of the regions; the ancient, seminatural grasslands and pastures, the oceanic oak forests, the calcareous hazel, pine and Taxus(yew) forests, and the grazed pine forests. The Stord-Bømlo-Tysnes island archipelago stands out with a very varied bedrock, including rich, easy weathered shales, and strips of karstic marble and limestone rocks, as well as well-developed boreonemoral rainforest conditions.

Figure 2. Rich, oceanic oak forest visited at Agdestein, Stord. Photo: T.E. Brandrud.

Figure 3. Rich oak-lime forest at Eikåsen, Heie, Tysnes. Photo: T.E. Brandrud.

Rich, oceanic oak(-hazel-lime) forests

Our southernmost oak forests along the coast of Sørlandet, has been rather extensively studied for "oak-fungi", but our (north-) westernmost flank of strongly oceanic oak forests, having a concentration at Sunnhordland is less surveyed. We really hoped to reveal some of the secrets of these ancient western woodland remnants during the NMC.

Rich oak forests (low-herb oak forest), oak-hazel-lime forests or more pure hazel forests were mainly visited at SE part of the Stord island, (Agdestein (Fig. 2), Digernes, Lønning and Store Gullberg), but also at Tysnes (Eikåsen at Heie (Fig. 3)). These sites appeared to harbor outposts of a southern oak forest element. A number of these species reach their north-western limit in Norway or Norden in the present region (Sunnhordland-Hardanger), and the localities at Stord-Tysnes represent the westernmost occurrences in Scandinavia. Altogether seven redlisted oak forest species were found here, all being mycorrhizal species associated with *Quercus*, *Corylus* and *Tilia*. Six of these species were found at Agdestein. The southern *Quercus* (-*Corylus*) element included the following (*marking those that reaches their world north-westermost outposts in Sunnhordland-Hardanger):

Cortinarius russulaespermus NT*
Entoloma noordeloosii NT
Hydnellum compactum VU*
Lactarius azonites VU*
Lactarius pterosporus NT*
Ramaria botrytis NT
Ramaria flavobrunnescens NT

Entoloma noordeloosii was published new to Norway in 2018 (Brandrud et al. 2018), and *Cortinarius russulaespermus* is published new to Norway here. These are both under evaluation for the new Norwegian red-list 2021, and they are both preliminary assessed as NT.

All maps showing Norwegian registered finds are downloaded from The Norwegian Biodiversity Information Centre (NBIC) and Artsdatabanken (ADB) – Species distribution map (Artskart). All maps showing the species European or Global registrations are downloaded from The Global Biodiversity Information Facility (GBIF).

Figure 4A and B shows the registered Norwegian and European distribution, respectively, of *Hydnellum compactum*, a representative example of this element (for Scandinavian distribution, see Nitare et al. 2015). *Ramaria flavobrunnescens* seems to have one of its Norwegian core areas at Sunnhordland, but this is also distributed somewhat further north along the west coast of Norway, apparently

Figure 4. **A**) The Norwegian distribution of *Hydnellum compactum,* a representative example of the southern *Quercus*(-*Corylus*) element and **B**) the European registered distribution. GBIF records are probably equally representative for Norway, Sweden, Denmark and the UK.

with the global northernmost locality at Tingvoll, Møre & Romsdal (maps Fig. 5A and B). *Entoloma noordeloosii* seems also to have a core area in Sunnhordland (Fig. 6A), as it was found both at Digernes, near Leirvik and at Eikåsen and Heie (formerly known only from one site in Møre og Romsdal, and two sites in Oslofjord-Ringerike; Brandrud et al. 2019), and it has a limited distribution in Europe, according to (GBIF) (Fig. 6B).

Also other thermophilous deciduous forest species were found in the rich *Quercus-Corylus* forests, such as *Cantharellus melanoxeros* (NT) and *Amanita phalloides*.These have a wider distribution, reaching further north along the coast (Figs. 7 and 8). Maps of known localities of *A. phalloides* in the timespan from 1940, via 1980 until 2010 (Fig. 8C) and the status in 1980 as published by Eckblad (1981). In 1980 the species was not known from Western Norway north of Rogaland, except for one find of Blytt 1904 S of Bergen. The second find from Hordaland was in 1983 (Hardangerfjord) and from Sogn og Fjordane in 1990 (Sognefjord). Since 2010 there has

Figure 5. **A**) The Norwegian distribution of *Ramaria flavobrunnescens,* a representative example of the southern *Quercus*(-*Corylus*) element, and **B**) the European registered distribution. GBIF records are probably equally representative for Norway, Sweden, Denmark and the UK.

Figure 6. **A**) The Sunnhordland distribution of *Entoloma noordeloosii,* a representative example of the southern *Quercus*(-*Corylus*) element, and **B**) the European registered distribution. GBIF records are not representative for the European distribution, but confirms that the species is rare.

Figure 7. **A**) The Norwegian distribution of *Cantharellus melanoxeros,* a representative example of the southern *Quercus*(-*Corylus*) element, and **B**) the European registered distribution. GBIF records are not representative for all European countries.

been a number of new localities, but the distributional pattern has hardly changed. In NMC we did, however, register the first find of the species in Stord (Digerneset), and the second in Tysnes (Eikåsen and Heie). This is a good illustration of the gradual, time-consuming process of learning to know a species, its environmental preferences (correlations) and its distribution. But this also indicates how far we have come with mapping of distinct and enigmatic macrofungi in Norway per 2020; now showing apparently the true distributional pattern of some well-mapped species such as *Amanita phalloides*. The present, word northernmost limit, Gylhamran nature reserve, Tingvoll is based on a record from 2003 by Geir Gaarder, and it is approximately the same northern limit as for other *Quercus-Tilia-Corylus* associated species such as *Ramaria flavobrunnescens*. It is unlikely that the species at present occurs much further north. However, with climate change, there might be a different picture in the future.

Calcareous hazel(-pine-yew) forests

Calcareous hazel woodlands, calcareous hazel-yew(*Taxus*) sites, or calcareous pine-hazel forests, occur on marble, limestone strips and ridges in Sunnhordland along the islands of Huglo, Storsøy (Stord), Skorpo and Aanuglo Tysnes) (Figs. 9 and 10). These marble areas were previously hardly investigated mycologically, and a number of interesting taxa were found during the NMC. Most exotic was probably Storsøy nature reserve, a small marble island of karstic limestone, with rugged topography including cracks and wholes. This island is dominated by calcareous pine forest with much yew and climbing Hedera, but also hazel dominated patches, where most of the calciphilous fungi were found at NMC.

Many of the calciphilous fungi found at NMC were new to Sunnhordland or new to Western Norway, and the few known to the

region had previously been recorded in (calcareous) grasslands, and not in woodlands.

Figure 8. **A**) The Norwegian distribution of *Amanita phalloides,* a representative example of the southern *Quercus*(-*Corylus*) element, **B**) the European registered distribution.

Most of the rare and redlisted ones were non-mycorrhizal, soil saprotrophs (or some kind of biotrophic), associated with more or less open calcareous woodlands (or equivalent grasslands). The following red-listed taxa (all new to Sunnhordland woodlands; those completely new to Sunnhordland indicated with*) were recorded:

Camarophyllopsis schulzeri NT
Cystolepiota aff. hetieri EN
Entoloma linkii DD*
Entoloma luteobasis VU*
Entoloma ochromicaceum VU
Entoloma queletii NT
Entoloma querquedula DD*
Lycoperdon echinatum VU*
Lycoperdon mammiforme EN*
Mycenella trachyspora DD

Altogether five redlisted *Entoloma* species were found in these calcareous forests, and all of them were collected in the karstic hazel-pine forest at Storsøy. The entolomas are revised in Norway since last red-list, and there will be some changes in the new 2021 redlist. Their preliminary, new red-list categories are indicated. For instance, *Entoloma ochromicaceum*, is now proposed as VU, due to rarity and association with threatened and declining calcareous grassland and ditto forest habitats. The Storsøy NMC-record is the only verified west coast find from forests so far. The species registered Norwegian and European distribution, respectively, is shown in

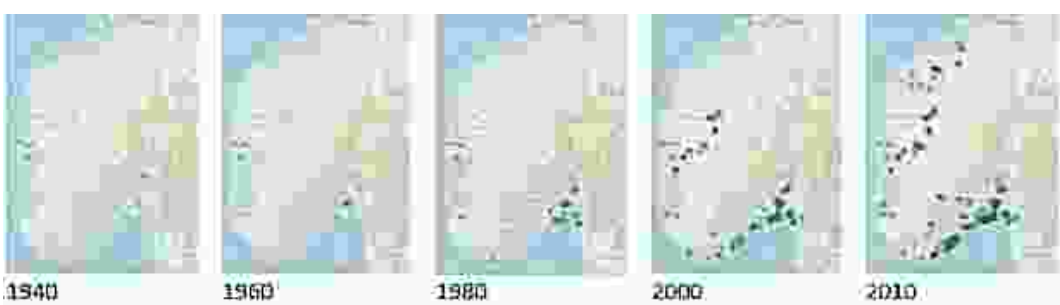

Figure. 8. **C.** A time series showing the progressive registration of the *Amanita phalloides* distribution in Norway from 1940 to 2010 (and 2020 in Fig. 8 A).

(Fig. 11A and B). *Lycoperdon mammiforme* (EN) was formerly known only from calcareous *Tilia-Corylus* forests of the Oslofjord-Mjøsa region, and was found new to Western Norway in the NMC. It was collected in hazel-yew forest on karstic marble at Brandvik protection area (landskapsvernområde) The species registered Norwegian and European distribution, respectively, is shown in (Fig. 12A and B). Along the marble and limestone strip at Skorpetveit, under hazel and some limes, *Lycoperdon echinatum* (VU) was found new to Sunnhordland, as was the calciphilous *Cystoderma aff. hetieri* (otherwise known from the Oslofjord-Mjøsa district). Some of the calcareous hazel-pine-yew forests were poor in fungi when visited during NMC, and there is certainly many more secrets to reveal in this strange, karstic landscape. It is interesting to note, that up to date, hardly any strictly calciphilous, mycorrhizal species of *Tilia-Corylus* or *Pinus* forests, have been found in Sunnhordland or more generally in Southwestern Norway, and maybe they are completely absent from this region. A possible explanation could be (i) too small and fragmented, calcareous habitat patches, combined with (ii) regional dispersal barriers.

Semi-natural grasslands and pastures

Sunnhordland still has many old unfertilized grasslands, mostly grazed by sheep, and can to some extent be called "hot spots" for fungi growing in such localities. Some areas have man-made traces going back to the bronze age and can therefore have been used by man for a very long time.

Compared to other nature types, seminatural grasslands have been intensively surveyed the last two decades. Very few grassland fungi were known from the area before the millennium, but today more than 100 different species are found here. The most intensively examined location is Hovaneset in Stord municipality, which has been investigated several times each year from 2003 until today. The total number of recorded grassland fungi has increased from 71 in 2013 (Fadnes 2014) to 90 in 2020, and is until now the most species-rich grassland known in Norway. A new earthtongue for Norway, *Hemileucoglossum pusillum* is reported from the area, in the present volume of Agarica (Fadnes et. al. 2021).

Because of the extensively surveys of grassland fungi in all municipalities in Sunnhordland, the expectation to find new species in semi-natural grassland during the days of the NMC was relatively low. However, one new species was found; *Camarophyllopsis*

Figur 9. Calcareous hazel woodlands from the karst area at Laukhammar, Skorpo. Photo: T. E. Brandrud.

Figur 10. Calcareous pine-hazel forests from the karst area at Storsøy, Stord. Photo: T. E. Brandrud.

atrovelutina (DD) on Nautøya, Stord; the first find in Norway. In addition, *Clavaria atrofusca* (DD) was found on Nautøya; the third find in Norway and second find in Sunnhordland. The registered global finds for *C. atrovelutina* and *C. atrofusca*, is shown in (Figs. 13 and 14), respectively. Figure 15 shows the semi natural grasslands at Nautøya.

Figure 11. Figure 10. **A**) The Norwegian distribution of *Entoloma ochromicaceum,* and **B**) the European. GBIF records are probably equally representative for Norway, Denmark and the UK.

Other NMC-records from semi-natural grasslands worth mentioning (none of them new for Sunnhordland), (Figs. 16 a – e) are:

Hygrocybe citrinovirens (EN) from Skorpeneset, Tysnes.

Pseudotricholoma metapodium (EN) from Øvrebygda, Fitjar (new to Fitjar)

Clavaria zollingeri (VU), from Aanuglo, Tysnes (new to Aanuglo)

Hygrocybe subpappilata (VU) from Hovaneset, Stord

Neohygrocybe ingrata (VU), Litlabø, Stord

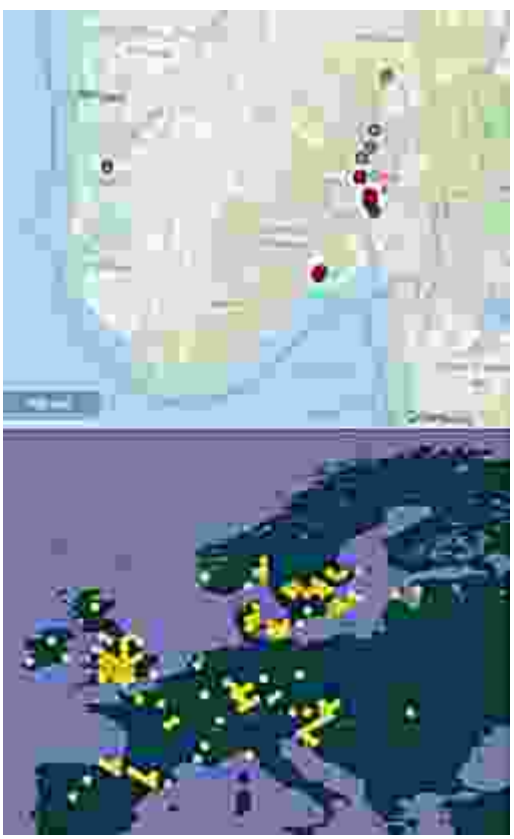

Figure 12. **A**) The Norwegian distribution of *Lycoperdon mammiforme*, and **B**) the European. GBIF records are probably equally representative for Norway, Sweden, Denmark and the UK.

Figure 13. The global finds for *Clavaria atrofusca* with the Norwegian locality at Nautøya, Stord, marked red.

Figure 14. The global finds for *Camarophyllopsis atrovelutina* with the Norwegian locality at Nautøya, Stord, marked red.

Finally – Thanks to all participants for making the NMC in Sunnhordland 2019 such a great experience, and for all the valuable finds and registrations you made!

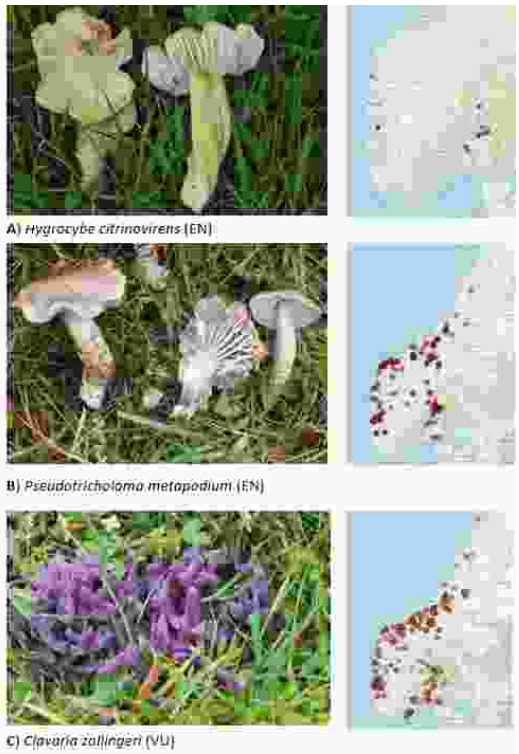

Figure 16 A - C. The Norwegian distribution of five other typical species from semi-natural grasslands found during the congress (none of them new for Sunnhordland): **A**) *Hygrocybe citrinovirens* (EN), **B**) *Pseudotricholoma metapodium* (EN), **C**) *Clavaria zollingeri* (VU),

Figure 15. The semi-natural grassland and pasture locality at Nautøya, Stord, with Anna Fedosova searching for earth-tongues and other grassland fungi. Photo: P Karlsen.

D) *Hygrocybe subpapillata* (VU)

E) *Neohygrocybe ingrata* (VU)

Figure 16 D - E. The Norwegian distribution of five other typical species from semi-natural grasslands found during the congress (none of them new for Sunnhordland): **D**) *Hygrocybe subpapillata* (VU), and **E**) *Neohygrocybe ingrata* (VU). Photo: all by P. Fadnes.

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Doktorgrad

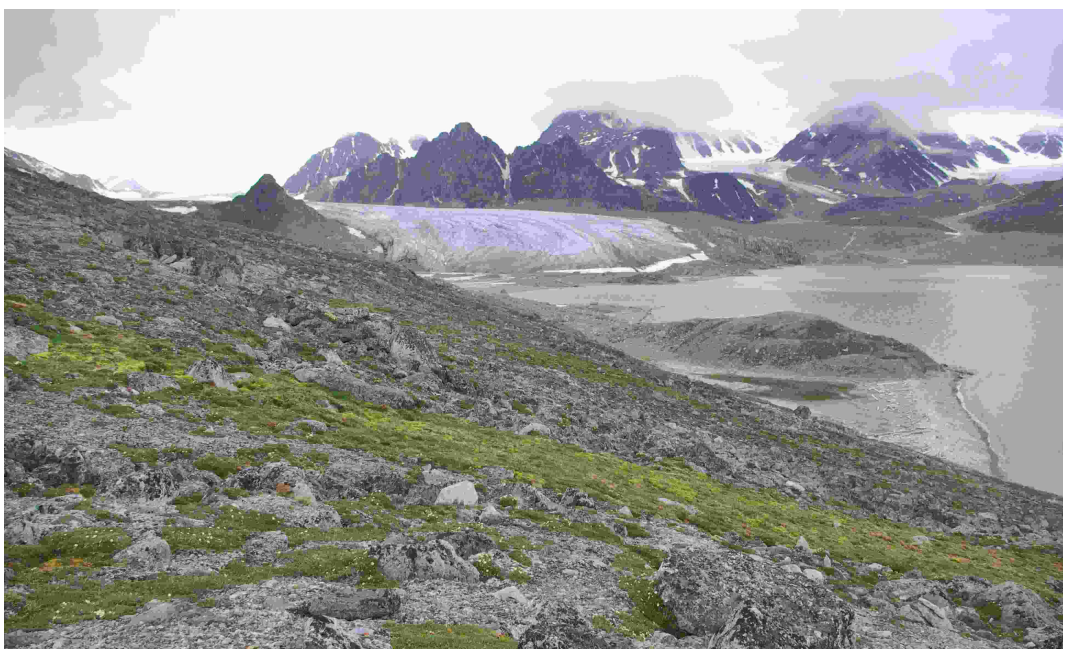
Biodiversity in the dark: root-associated fungi in the Arctic
Synnøve Botnen Philosophiae Doctor (PhD) Avhandling ved Universitetet i Oslo (UiO), nr. 2241, 2020. Det matematisk-naturvitenskapelige fakultet

I sin doktorgradsavhandling undersøkte Synnøve Smebye Botnen mangfoldet og økologien hos arktiske sopp. Dette er en gruppe organismer som tidligere er dårlig studert. Klimaendringer vil ha store innvirkninger på arktiske økosystemer, og vi trenger derfor grunnleggende informasjon om det eksisterende og mulig unike arktiske biologiske mangfoldet.

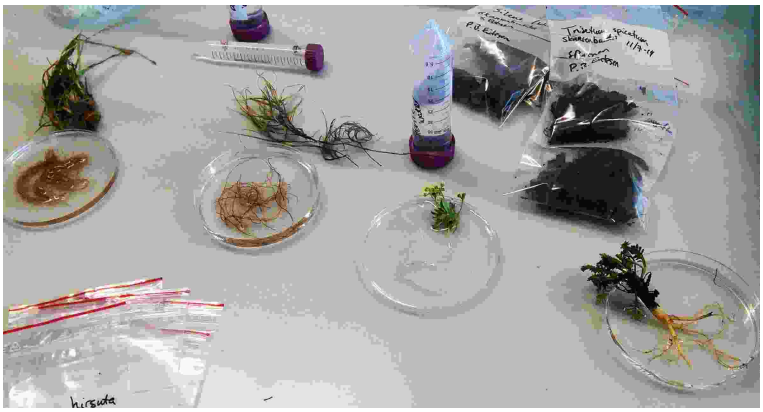
Arktiske planter lever, som andre steder, i symbiose med forskjellige rot-assosierte sopp som f.eks. gir essensielle næringsstoffer til vertsplanten. For å undersøke mangfoldet hos disse arktiske soppene, og hvilke miljøfaktorer (omgivelser) som påvirker dem, brukte Botnen en teknikk kalt DNA-metastrekkoding. Dette er en moderne DNA-sekvenseringsmetode. Hennes viktigste studieområde var Svalbard.

De DNA-baserte metodene avdekket et stort mangfold av sopp som lever i planterøtter i Arktis, der mesteparten fremdeles mangler vitenskapelige navn. For å illustrere dette: et enkelt rotsystem på Svalbard kan være vert for så mange sopp som det totale antall plantearter på hele Svalbard. Bare en liten andel av disse soppene produserer et overjordisk, lett synlig fruktlegeme, noe som gjør at det er vanskelig å studere dem uten DNA-baserte metoder. Videre avslørte Botnen at klimaforholdene, i tillegg til andre faktorer i omgivelsene, har en betydelig innvirkning på utbredelsen av arktiske sopper. Dette betyr at de pågående klimaendringene vil påvirke og føre til endringer i soppsamfunnene.

Det er ikke bare det fysiske miljøet påvirker hvordan soppsamfunnene er; Botnen



Figur 1. Friedrichbreen bockfjorden. Foto: P. Convey.



Figur 2. Planteprøver. Foto: S. Botnen.

avslørte at noen typer rotassosierte sopp kan være svært spesifikke når det gjelder hvilken planteart de lever sammen med. På den andre siden, når det gjelder ektomykorrhiza-sopper - en spesifikk gruppe med rotassosiert sopper - avslørte Botnen imidlertid at de typisk lever i røttene til flere forskjellige plantearter og viser liten gard av vertsspesifisitet.

I tillegg til disse empiriske studiene, gjennomførte Botnen også et metodestudie, der spesifikke elementer i fremgangsmåten ved DNA-metastekkoding ble evaluert. Disse analysene avdekket at DNA-metastrekkodemetoden gir et svært robust rammeverk for å studere endringer i artssammensetning hos sopp og mikroorganismer.

Botnens avhandling gir grunnleggende informasjon om det store mangfoldet av arktiske sopp. Denne grunnleggende informasjonen er svært nødvendig for å bedre forstå forventede endringer i arktiske økosystemer. Dog illustrerer avhandlingen, mest av alt, at vi knapt har skrapt på overflaten til dette stort sett, ukjente soppmangfoldet, og understreker behovet for en intensiv forskningsinnsats innenfor dette området.

Figur 3. Keilhaubukta, Egdeøya. Foto: S. Botnen.

Kuulo Kalamees, Vello Liiv. Heinikud. The genus Tricholoma in Estonia

Tartu 2019. Eesti elurikkus – 3. 158 pages. ISBN 978-9985-4-1160-5. Boken koster Ca 20 euro fra forlaget.

This book describes all species of *Tricholoma* that are found in Estonia, 43 altogether. In addition, 22 species that may occur in Estonia are included. The text is both in Estonian and English making the book very useful for people outside this country. There are two keys, one for each language. At the right side of the keys there are small photographs of the actual species, making the keys very useful, since we then immediately can see if we have the right species before going into the detailed description of the suggested species.

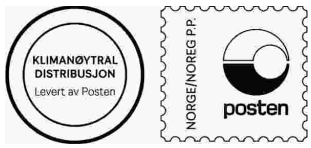
The species are treated alphabetically on two lookup pages. Under the now accepted scientific name (following Index Fungorum) are facts on nomenclature, including the original described name, synonyms, and references to illustrations. The descriptions are given in both Estonian and English and mainly based on original material. Here we find morphology, spore features, confusing species, ecology, and distribution. The photographs are presented on the right lookup page, or sometimes using the following two pages for more photographs. They are all photographed on their growing places, giving an idea of the ecology. The photographs are excellent, showing several basidiocarps in various ages and colouration. They also show important details that sometimes can be difficult to spot on photographs, for instance the droplets on *T. pessundatum* and the reddish stipe base of *T. saponaceum*. The latter species, which is extremely variable, is portrayed in five different photographs showing the variation cap colour and stipe surface (smooth or scaly), mentioned here as an example of the accuracy of the treatments.

Most species are sequenced for ITS, and the code in the UNITE-database is given if ITS-sequence exist. Herbarium number is stated for all species investigated.

This book is a valuable supplement to the Danish book on *Tricholoma* written by Christensen and Heilmann-Clausen. For mycologists in more northern countries, several species in boreal coniferous and deciduous forests are included. Species that may be rare or even lacking in Denmark.

I will warmly recommend this book, especially because of its excellent photos and thorough and precise descriptions.

Klaus Høiland



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