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Kjære leser

I denne utgaven gratulerer vi Thor Dybhave med 80 års dagen. Han er en av grunnleggerne av *Agarica* og fortsatt en viktig aktør i det mykologiske miljøet. En annen av grunnleggerne av *Agarica*, Roy Kristiansen, bidrar denne gangen med en beskrivelse av tre arter i slekten *Boubovia* fra Norge, samt et popularisert sammendrag angående den nye arten *Peziza nordica* fra Hallingskarvet. En annen nyhet fra arktisk-alpine og nordboreale områder er fra Gulden og Larsson, de presenterer en ny «traktsopp» for vitenskapen - *Atractosporocybe polaris*. Weholt og medforfattere presenterer en ny art for Norge – *Psathyrella jacobssonii*. Men *Agarica* handler ikke bare om nye arter, økt økologisk innsikt er svært viktig. Jordal og medforfattere presenterer en omfattende studie av habitatspesifisitet hos

utvalgte beitemarkssopp i Norge. Høiland og Botnen gir oss en sammenlikning av sporokarper over bakken og ektomykorrhizastrukturer for Agaricales, Boletales og Russulales under bakken i et sanddyneøkosystem. Det er fint å se at det er tilvekst av nye mykologer og to masteroppgaver som ser på nye aspekter av koblingene mellom barkbiller og sopp er presentert. Sist men ikke minst, en av Norges store mykologer, Halvor Gjærum gikk bort i desember 2015. Leif Sundheim gir oss en oversikt over Gjærum sitt omfattende virke gjennom et langt arbeidsliv.

God lesning!

Anders K. Wollan og Gry Alfredsen
Redaktører

Halvor B. Gjørøum; 1919-2015

Halvor B. Gjørøum passed away 30. December 2015, 96 years old. Gjørøum was a plant pathologist and mycologist at the Norwegian Plant Protection Institute (NPPI) during the period 1947-1986, with diseases on horticultural crops as his responsibility. Identification of pathogens in samples sent to the institute from growers and the extension services was an important part of his job. During the first ten years of his professional life, Gjørøum was



Halvor B. Gjørøum. Foto: E. Fløistad.

working closely with Government Mycologist Ivar Jørstad (1887-1967), who was familiar with all important groups of plant pathogens and had published extensively on powdery mildews and rust fungi. Jørstad became an important mentor in mycology for the young scientist. Gjørøum continued the research on microfungi on cultivated and wild plants initiated by Jørstad. During his traveling in Norway and abroad, Gjørøum collected microfungi, which he identified and placed in the Mycology Herbarium of previous NPPI, which is now merged into the Norwegian Institute of Bioeconomy Research (NIBIO).

Gjørøum was an ardent collector of microfungi wherever he travelled. In cooperation with botanists, he ensured that the hosts were correctly identified before he described new

species. He made accurate drawings of spores for his publications. His excellent memory was well known by all of us who were his colleagues. During most of his retirement, Gjørøum continued the collection of plant pathogens for the Herbarium.

Altogether he has collected and identified the majority of the 2.500 powdery mildews and the 13.000 rust specimen and a large number of microfungi from other taxonomic groups

in the Herbarium.

Nomenclature of rust fungi

The most important contribution of Gjørøum was his description of one new genus and 122 new species/combinations of rust fungi. The class Pucciniomycetes contains about 8000 species, which include many important plant pathogens. The black stem rust (*Puccinia graminis* Pers.) and the yellow rust (*Puccinia striiformis* Westend.) are causing two of the most serious diseases of wheat and other cereals, worldwide. In Norway, rust fungi is the best known group of microfungi. The botanist Axel Blytt (1843-1898) identified 205 species from his many excursions in the country. Jørstad started his studies of rust fungi while he was student, and he continued the

research on rust throughout his professional life and long into his retirement. He published monographs on rust fungi in Norway and Iceland. Gjørøum maintained this strong Norwegian position in the nomenclature of rust fungi.

Two years before his death, Gjørøum published his last description of a rust fungus, *Puccinia rhodosensis* Gjørøum, based on a specimen collected by Kåre A. Lye on *Tragopogon crocifolius* in Rhodos. During many years, Gjørøum collected rust fungi in Europe, East Africa, the Canary Islands, Madeira and the Azores archipelago. In addition, colleagues in several countries sent him material for identification of rust fungi. With his extensive collection of literature on rust nomenclature, Gjørøum was able to determine if the rust had been previously described. Not surprisingly, he frequently concluded that the rust was a new species, and Gjørøum described the species, illustrated with his accurate drawings and photos. When he published new species based on material sent to him, Gjørøum always included the collector as author of the paper. With his American colleague and friend George B. Cummins, Purdue University, Gjørøum described a new genus of rust fungi *Joerstadia* Gjørøum & Cummins 1982, honoring Ivar Jørstad.

The first checklist of the rust fungi in Macronesia was published in 1986 by Halvor B. Gjørøum and Per Sunding (Gjørøum and Sunding 1986). Both authors had done extensive field work in the very different climates of the islands Azores, Madeira, Canaries and Cape Verde. Research on the rust fungi in East Africa during the last three decades of the twentieth century was summarized in two important contributions. During that period the authors had described one new genus and 63 new species, and they presented a key to 11 genera with geographical distribution and host range of the 294 known species of rust fungi in Uganda (Gjørøum et al. 2000a, 2000b).

Gjørøum was well acquainted with the rust flora of the neighboring Nordic countries. Based on the work of his predecessors and colleagues and on his own collection, Gjørøum published “Nordiske rustsopper”, a flora of the rust fungi in the Nordic countries (Gjørøum 1974). This has been a very important handbook for both professionals, students and amateurs interested in this fascinating group of microfungi.

Ascomycota and smuts

Gjørøum described 6 species of Ascomycota from Norway and Denmark. He described the genus *Endoconospora* Gjørøum 1971 (anamorph Pezizomycetes), with the species *E. cerastii* Gjørøum 1971. The fungus produces leafspots on *Cerastium fontanum*. Based on a Danish specimen of *Vaccinium uliginosum*, in 1971 Gjørøum described the genus *Scopulariella* Gjørøum 1971 and the species *S. vaccinii* Gjørøum 1971, another anamorph Pezizomycetes. From *Carex pulicaris* Gjørøum described the anamorph *Arthrimum fuckelii* Gjørøum, with its unknown teleomorph in the genus *Apiospora* (Sordariomycetes). Also, he described the anamorph species *Ramularia albo-rosella* (Desm.) Gjørøum 1968 and *R. oxyriae-digynae* Gjørøum 1971. Their unknown teleomorphs belong to the genus *Mycosphaerella* (Dothideomycetes).

Fungi in the genus *Taphrina* are biotrophic parasites with a unique biology. Dicarvotic hyphae develop beneath the epidermis or cuticula. These fungi have no fruiting bodies and asci develop on the surface of leaves or fruits. The first collection in Norway was made by Axel Blytt in 1864, two years prior to the description of the genus by Tulasne in 1866. Altogether 26 species are known in Norway. An important disease is pocket plum caused by *T. pruni*, that causes unripe plums to grow abnormally large. Similar diseases are common in cherries and bird cherry. In peach, *T. deformans* causes the leaf curl disease. An

important contribution of Gjørøum was a monograph on the genus *Taphrina* in Norway (Gjørøum 1964).

Together with the Finnish mycologist, I.T.K. Kukkonen Gjørøum described two new species of smut fungi in the class Ustilaginomycetes, *Cintractia malawica* Kukkonen & Gjørøum 1977 and *C. retinospora* Kukkonen & Gjørøum 1977. Both smuts are pathogens on species of the sedge genus *Scleria* in East-Africa.

The genus *Gjaerumia* and the family Gjaerumiaceae

On the 7th International Mycology Congress in Oslo in 2002, Gjørøum was contacted by German mycologists, who asked for a location to look for a smut fungus on *Nartheceum ossifragum*. He informed them of a site in Møre and Romsdal County, and the mycologists were able to find the smut. They concluded that previously the fungus had not been correctly identified and published a description of a new smut genus, *Gjaerumia* R. Bauer, M. Lutz & Oberw. 2005 and a new family Gjaerumiaceae R. Bauer, M. Lutz & Oberw. 2005, both named in honor of the Norwegian mycologist. They changed the scientific name of the smut fungus on *Nartheceum ossifragum* to *Gjaerumia ossifragi* (Rostr.) R. Bauer, M. Lutz & Oberw. 2005. Previously, the bishop and botanist Johan Ernst Gunnerus (1718-1773) was the only Norwegian botanist who had

been honored with his name being used in creating a family name for fungi (Gunneraceae).

Leif Sundheim

A summary of new species and new combinations of rust fungi described by Halvor B. Gjørøum are given in the table below.

Supplementary material 1: The full list of all species and combinations are available via <http://www.agarica.no>.

Genus	Family	Number of species
<i>Puccinia</i>	Pucciniaceae	45
<i>Uredo</i>	Anamorphic	31
<i>Uromyces</i>	Pucciniaceae	20
<i>Aecidium</i>	Anamorphic	11
<i>Joerstadia</i>	Phragmidiaceae	4
<i>Elateracium</i>	Anamorphic	2
<i>Tranzchelia</i>	Uropyxidaceae	2
<i>Dicheirina</i>	Raveneliaceae	1
<i>Dietelia</i>	Puccinosiraceae	1
<i>Hemileia</i>	Anamorphic	1
<i>Maravalia</i>	Chaconiaceae	1
<i>Physopella</i>	Phakopsoraceae	1
<i>Ravenelia</i>	Raveneliaceae	1
<i>Trachyspora</i>	Phragmidiaceae	1
Total		122

Selected publications

- Bauer R, Lutz M, Oberw. 2005. *Gjaerumia*, a new genus in the Georfischeriales (Ustilaginomycetes). Mycological Research 109: 1250-1258.
- Gjørøum HB, 1964. The genus *Taphrina* Fr. in Norway. Nytt Magasin for Botanikk 11: 5-26.
- Gjørøum HB, 1974. Nordens Rustsopper. Fungiflora, 321 pp.
- Gjørøum HB, Sunding P, 1986. Flora of Macronesia. Checklist of rust fungi (Uredinales). Sommerfeltia 4: 1-42.
- Gjørøum HB, 1987. Rust fungi in the Canary Islands. Vieraea 17: 51-71.
- Gjørøum HB, Namaganda M, Lye KA 2000a. Ugandan rust fungi 1-4. Lidia 5: 9-24.
- Gjørøum HB, Namaganda M, Lye KA 2000b. Ugandan rust fungi 5-11. Lidia 5: 65-96.

Habitat specificity of selected grassland fungi in Norway

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KEY WORDS

Grassland fungi, seminatural grasslands, forests, other habitats, Norway

NØKKELOORD

Beitemarkssopp, seminaturlige enger, skog, andre habitater, Norge

SAMMENDRAG

132 taksa av sopp med regelmessig forekomst i seminaturlig eng av slektene *Camarophyllopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Hygrocybe*, *Microglossum*, *Porpoloma*, *Ramariopsis* og *Trichoglossum* er valgt ut. Habitatspesifisiteten deres er undersøkt basert på 39818 norske funn. Ca. 80% av funnene er gjort i seminaturlige enger, ca. 10% i andre åpne habitater som parker, hager og veikanter, rikmyrer, kystlyngheier, åpen grunnlendt mark, fosse-enger, rasmarksenger og alpine habitater, mens 13% er funnet i ulike skogtyper (enkelte funn har angitt mer enn én naturtype, derfor blir summen over 100%). Av funnene i skog er minst 85% gjort i rike skogtyper (både løvskog og barskog), mens relativt få funn er gjort i fattige skoger. Ulikheter mellom artene

er undersøkt når det gjelder habitatspesifisitet. 70 taksa (53%) har mindre enn 10% av sine funn i skog, mens 23 (17%) har mer enn 20% av funnene i skog. De som har høyest frekvens i skog i Norge er for det meste også vanligst i skog i Sverige.

ABSTRACT

132 taxa of fungi regularly found in seminatural grasslands from the genera *Camarophyllopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Hygrocybe*, *Microglossum*, *Porpoloma*, *Ramariopsis* and *Trichoglossum* were selected. Their habitat specificity was investigated based on 39818 records from Norway. Approximately 80% of the records were from seminatural grasslands, ca. 10% from other open habitats like parks, gardens and road verges, rich fens, coastal heaths, open rocks with shallow soil, waterfall meadows, scree meadows and alpine habitats, while 13% were found in different forest types (some records had more than one habitat type, the sum therefore exceeds 100%). Of all records in forests, at least 85% were from rich types (both deciduous and coniferous forests), while relatively few were from poor forests. Differences in habitat specificity between the taxa were analyzed. 70 taxa (53%) had less than 10% of their records in forests, while 23 (17%) had more than 20% of their records in forests. The taxa which had the highest frequency in forests in Norway are mostly the same as the most common species in forests in Sweden.

INTRODUCTION

The concept of grassland fungi could potentially be used about all fungi living in grasslands. However, here we use the term in a narrower sense, in accordance with several European authors (e.g. Nitare 1988, Griffith et al. 2013). According to this concept, grassland fungi are macrofungi confined to seminatural grasslands, which are regularly grazed (pastures) or mown (meadows), not or poorly manured, and not plowed (except possibly a long time ago). The concepts of “grassland fungi” and “waxcap grasslands” (used about seminatural grasslands rich in *Hygrocybe* species) were established a long time ago, and according to Griffith et al. (2013), they were given attention already in the 18th century. Grassland fungi form a taxonomically diverse group of seemingly ecologically related species from *Hygrocybe* (sensu lato), *Camarophylloopsis*, *Clavaria*, *Clavulinopsis*, *Dermoloma*, *Entoloma*, *Geoglossum*, *Microglossum*, *Porpoloma*, *Ramariopsis* and *Trichoglossum* (Nitare 1988, Noordeloos 1992, Jordal 1997, McHugh et al. 2000, Newton et al. 2003, Griffith et al. 2013). Here, we use the term grassland fungi to describe taxa from the genera mentioned above, often growing together in seminatural grasslands, and listed by at least two of the publications mentioned above. The genus *Tremellodendropsis* has been suggested to belong among the grassland fungi (Nitare 2014), but due to uncertainty about its ecology, we have chosen not to include this genus containing just one species in Norway, *T. tuberosa* (with 61 records). The group of grassland fungi comprises at least 150-160 species in Sweden and Norway (Nitare 1988, Jordal 2011, 2013); in the UK (also called “CHEGD” fungi - an acronym of group names) there are 180-200 species (Evans 2003, Griffith et al. 2013). Even small localities can be surprisingly rich in grassland fungi, with more than 50-60 species (Nitare 1988, Jordal 1997, McHugh et al. 2000, Evans

2003). The most species rich locality in the UK had 78 species, of which 34 were *Hygrocybe* spp. (Griffith et al. 2013). One Norwegian locality had 71 species, 32 of which were from *Hygrocybe* (Fadnes 2014), and one in Sweden had 76 species, 33 of these were *Hygrocybe* spp. (Pihl 1992). In one Swedish locality 36 species of *Hygrocybe* were recorded (Bergelin 2005). Additional 200-300 species of macrofungi from other genera occur in the same habitats (Arnolds and de Vries 1989, Aronsson and Hallingbäck 1995), but these species mostly seem to have other ecological preferences and are not treated here.

Different authors have pointed to the fact that many of the grassland fungi also can be found in other habitats, including forests (Boertmann and Rald 1991, Nitare 2000, Bendiksen et al. 2008, Boertmann 2010, Brandrud et al. 2015, Lorås and Eidissen 2011, Griffith et al. 2013). Outside Europe, e.g. in North America, the same (or closely related) species mostly occur in forests (both deciduous, coniferous and mixed), but can also be found in grasslands and swamps (e.g. Hesler and Smith 1963, Boertmann 2010, Lodge et al. 2013, Birkebak et al. 2013, Griffith et al. 2013).

Seminatural grasslands have declined dramatically in Norway. Since 1900, a loss of roughly 80-90% of the area is estimated for Norway (Jordal 2010). In Western Europe, a loss of 90% during the last 75 years is estimated (Griffith et al. 2013); in some countries the situation is even more dramatic (e.g. in the Netherlands; Arnolds 1988). Therefore it is important to know if the species living here can also survive in other habitats. Especially in the preparing of red lists (lists of threat status according to the IUCN classification) this information is important (Brandrud et al. 2015). Many of the grassland fungi are present on the red lists of several European countries (Griffith et al. 2013).

In Norway, public herbaria and NGOs have cooperated, especially during the last 20 years, to make records of fungi available in online databases. Now most data owners share records of fungi (and other groups of organisms) found in Norway in the same Internet solution, called "Species Map Service" (Artskart), comprising about 540000 fungal records (not including lichens) (Norwegian Biodiversity Information Centre and GBIF 2014).

The aim of this article is to compile information on known habitats of selected grassland fungi in Norway, and look for differences between species. By discussing the habitat specificity of the species we hope to improve the knowledge about them, which is also the basis for their conservation. However, we do not intend to emphasize in detail the response of the species to edaphic, climatic or other gradients beyond the habitats these gradients create (like calcareous forests or alpine snow beds).

MATERIAL AND METHODS

Taxonomy and nomenclature

Taxonomy and nomenclature follow the Norwegian taxon database (Norwegian Biodiversity Information Centre 2015), which for Basidiomycota largely follows Knudsen and Vesterholt (2012). The genus *Hygrocybe* s.l. was recently split into several genera (Lodge et al. 2013), but this is not yet implemented, awaiting more information and some species to be placed and combined in the appropriate genera. In many of the other genera there is also ongoing research by molecular methods (e.g. Arauzo and Iglesias 2014, Kautmanová et al. 2012, Morozova et al. 2014, Vila et al. 2013). Most new or recently redefined taxa are poorly known (with fewer than 10 records) and therefore excluded from this study.

Data extraction, processing and compilation

Data on records of taxa from the genera mentioned above have been extracted and downloaded from the Species Map Service (03.12.2014) and imported in a Microsoft Access database. Own unpublished data have been added. Records with information on uncertain determination were excluded. Records from before 1900 were removed because they were very few and had little information on habitats. Taxa not belonging among the grassland fungi (as defined above, e.g. many *Entoloma* spp.) were excluded. Ecological information on some of our own records has been added or improved. There has been searched for ecological information in five different fields (locality, ecology, habitat, substrate and notes). Records lacking ecological information, or with insufficient information, have been removed. Taxa with less than 10 records containing habitat information have been excluded from the study. We have included three varieties from *Hygrocybe* s.l., by some authors treated at species level.

Habitats are classified using nature types defined by Halvorsen et al. (2015) - called Nature in Norway (NiN 2.0), but some of the types had to be merged, e.g. grasslands which are not seminatural grasslands. The ecological information is used to classify each record in one of the following nature types: seminatural grassland, other grasslands (mostly lawns, parks, road verges), forests, sea shore meadows, heaths (oceanic *Calluna* heaths), rocks with shallow soil, waterfall meadows (created by spray from waterfalls), fens, scree meadows, and alpine habitats.

We made some criteria for handling insufficient habitat information. 'Forests' are sometimes actually seminatural grasslands in succession towards forest, but still with some grassland features intact. Halvorsen et al. (2015) define these cases to type by using degrees of "management intensity". 'Grazed



Figure 1. Some habitats treated in this study. A. In Holmvassdalen (Nordland: Grane) there is calcareous tall herb spruce forest with many grassland fungi. B. Calcareous low herb birch forest, Nordland: Hattfjelldal: Varnvatnet. C. Sea shore meadow between the sea and *Calluna* heath, grazed by sheep and with many grassland fungi, Hordaland: Bømlo Haverøya. D. Rocks with shallow soil, Oslo: Nakholmen. E. Scree meadow grazed by goats in Møre og Romsdal: Stranda: Norangsdalen. F. Dry seminatural grassland grazed by cows, Oppland: Vågå: Fellese. Photo B: GG, photos A and C-F: JBJ.



Figure 2. Grassland fungi in different habitats. A. *Hygrocybe lacmus* in poor, boreal birch forest, Møre og Romsdal: Sunndal: Bæverdalen. B. *Entoloma mougeotii* at the edge of a rich fen, Troms: Finnsnes. C. *Hygrocybe conica* in alpine snowbed 1450 m a.s.l., Møre og Romsdal: Sunndal: Råstu. D. *Hygrocybe aurantiosplendens* in calcareous birch forest, Nordland: Hattfjelldal: Raudvatnet. E. *Hygrocybe laeta* in a mossy spot in acid coastal *Calluna* heath, Møre og Romsdal: Smøla. F. *Porpoloma metapodium* in seminatural grassland, Sør-Trøndelag: Oppdal. Photo A, B, D: GG; photos C, E, F: JBJ.

forest' can be interpreted as forest, but can also be seminatural grassland with tree cover. If information was too scarce to make a final decision according to the definitions, we normally interpreted these cases as both forest and seminatural grassland. Half open pastures with some trees ("hagemark") were defined as seminatural grassland. In some cases of doubt we had to choose either the most probable nature type, two possible types where a final decision was difficult, or leave the record as "lacking sufficient ecological information" and thereby exclude it. Alpine habitats comprise more than one type in NiN 2.0, but the lack of detailed habitat information, combined with rather few records here, made us merge these types to one.

Statistical analysis

We wanted to investigate the habitat specificity of the different species and to look for differences between them. We assume that the probability of observing each species is equal among species and in all habitats, for a given sampling effort (but see discussion). Thus, if the habitat preferences of all species are similar, we would expect the frequency distribution of species records over all habitats to be equal among species. In order to test if this was the case, we used contingency tables and Chi-squared tests. For each species we compared the observed frequency in a given habitat (no. of records in the habitat/no. of records in total) with the expected frequency (no. of records in the habitat pooled over all species/no. of records in total pooled over all species and habitats). A significant test statistic (p -value < 0.050) suggests that the species has a higher/lower frequency of occurrence in the habitat than expected, i.e. than in the total dataset. Due to the low number of records in other habitats than seminatural grasslands and forests, analysis were only performed for these two habitats (with two exceptions; *Hygrocybe acutoconica*

and *H. conica*). When a record had two habitats given, we included two separate rows in the dataset for this record, one for each habitat.

RESULTS

Examples of habitats and species are shown in Figures 1-2.

Metadata

Totally about 43000 records from the mentioned genera were downloaded and about 4000 own, unpublished records were added. After the exclusion of species not belonging among the grassland fungi, rare and little known grassland species (< 10 records with habitat information), records from before 1900 (12 records) and records with uncertain determination, 42210 remained. Further, 2392 records lacking (sufficient) ecological information were excluded. Data from the remaining 39818 records of 132 taxa (129 species and 3 varieties) were analyzed and the results are presented in Tables 1-3 and in Figures 3-5. In *Hygrocybe* (sensu lato) there were 23773 records (59.7%) of 39 species and three varieties. There were 9117 records (22.9%) of 51 species of *Entoloma*. *Clavaria*, *Clavulinopsis* and *Ramariopsis* had totally 3829 records (9.6%) of 18 species. *Geoglossum*, *Microglossum*, and *Trichoglossum* had 2467 records (6.2%) of 14 species. Other genera (*Camarophylloopsis*, *Dermoloma*, *Porpoloma*) had 632 records (1.6%) of 7 species.

Table 1 shows the owners of the data used in this study. There were totally 28734 observations and 11084 herbarium collections. Two of the authors (JBJ, GG) have participated by the collecting of approximately 22500 of the records, 5500 of which are being stored as dried collections in the herbaria.

Table 1. Data owners with number of objects (dried specimens) and observations. N=total number of records. ¹3503 of the total number of records are unpublished. ²476 of the total number of records are unpublished. All other records were downloaded from Norwegian Biodiversity Information Centre & GBIF (2014).

Data owner	Objects	Observations	N
BioFokus	50	3468	3518
Ecofact		16	16
J.B. Jordal ¹		9090	9090
Miljøfaglig Utredning ²		6328	6328
Naturhistorisk Museum - UiO	9803	2943	12746
Norges sopp- og nyttevekstforbund		6785	6785
Norsk institutt for naturforskning		104	104
NTNU - Vitenskapsmuseet	743		743
Tromsø museum - Universitetsmuseet	339		339
Universitetsmuseet i Bergen - UiB	149		149
Total	11084	28734	39818

Figure 3 shows when the records have been collected. More than 96% were collected in/after 1990, i.e. the last 25 years. Therefore, e.g. conclusions on decline of the species over decades cannot be drawn based on the species records themselves, but have to depend on knowledge on decline of the habitats.

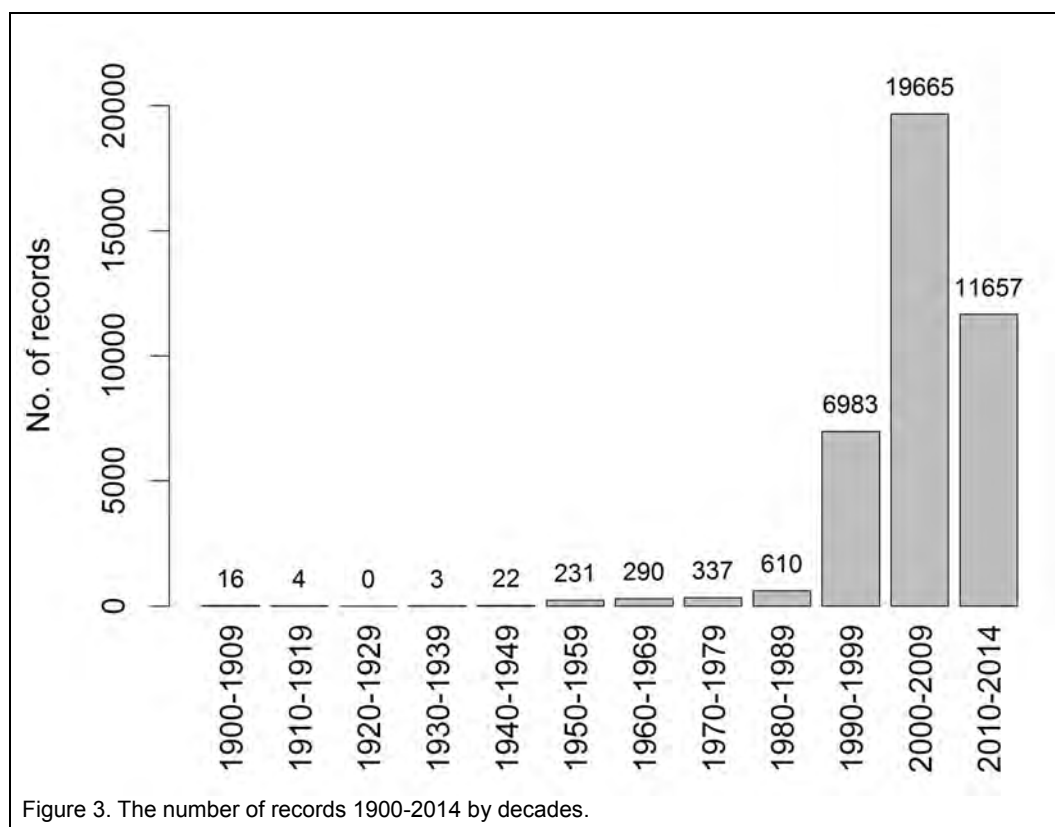
Habitats

Table 2 shows detailed information on the number of records of each species in the different habitats. For three records, three different habitats are given, whereas two different habitats are given for 1706 records. The remaining 38109 records have one habitat only. Some habitats are shown in Figure 1.

Seminatural grassland is generally the most important habitat, with 32034 records (80.5%) of (all) 132 species (Table 2). Most of the species also occur in other grasslands (*lawns*, *parks* and *road verges* which mostly are being mown). A total of 2147 records (5.4%) of 113 species are given from these habitats. *Sea shore meadows* (i.e. upper part, mostly the supralittoral zone which is only occasionally flooded by sea water) have 561 records (1.4%) of 88 species. *Sand dune meadows* have 188

records (0.5%) of 52 species. In *coastal Calluna heath* we find 351 records (0.9%) of 68 species. *Waterfall meadows* (created by the spray impact from waterfalls keeping trees away) are pretty rare, and have 24 records (0.1%) of 14 species. *Rocks with shallow soil*, often near the sea (and often grazed) have 487 records (1.2%) of 98 species. *Scree meadows* (kept open by snow avalanches in winter, often in combination with grazing in summer) have 64 records (0.2%) of 35 species. *Fens* (mostly at the edges of rich/calcareous fens) have 188 records (0.5%) of 52 species. In the *alpine region* most records are from different low alpine habitats, including seminatural grasslands, snowbeds and heaths (often described as grazed). The data include 240 records (0.6%) of 68 species from alpine habitats. *Forests* have 5246 records (13.2%) of 121 species. The term forest can include a wide variety of types, see below.

In summary, 91% of the records are found in open habitats – with 80.5% in seminatural grasslands. As 13% are from forests this sum up to 104%, due to some records coded for more than one habitat type.



Species occurrences in open habitats

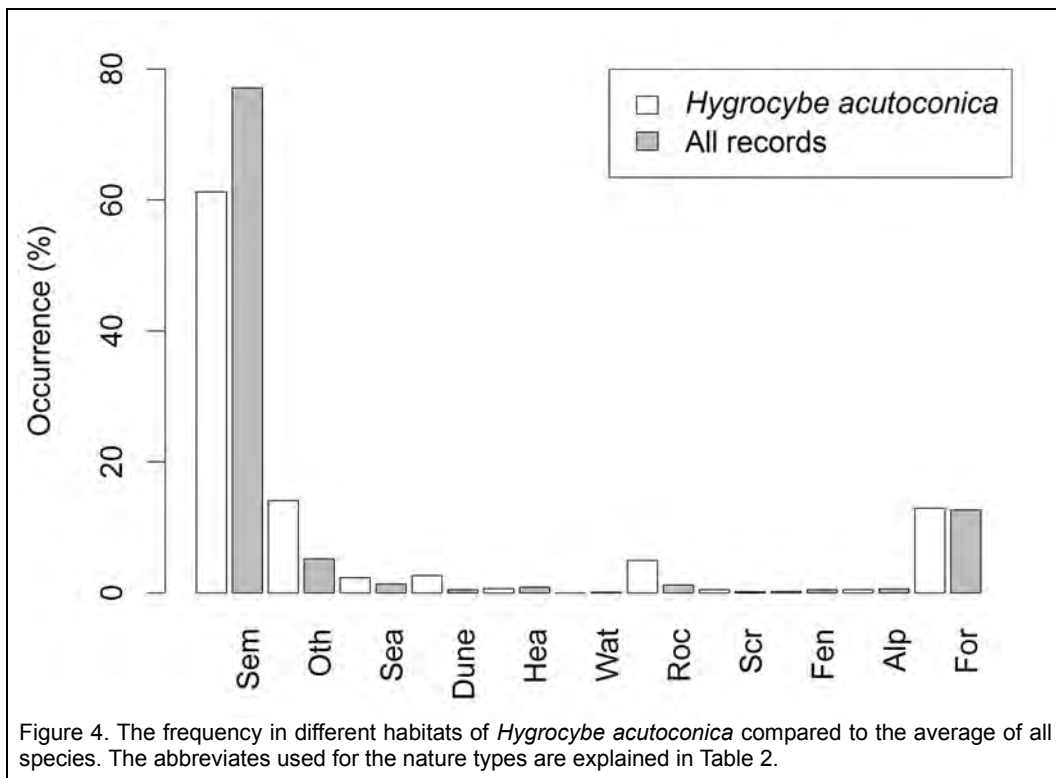
The most common species (both totally and in seminatural grasslands) were *Hygrocybe conica* (2516/1591), *H. pratensis* (1918/1593), *Hygrocybe virginea* (1724/1299) and *H. psittacina* (1408/1231), which is identical with the four most common species in the UK according to Griffith et al. (2013).

Table 3 shows the results of our statistical analysis of differences in habitat selection between the species. The species are grouped according to their frequency in forests.

Seminatural grasslands. A total of 11 species had significantly higher frequency ($p < 0.05$) of occurrence in seminatural grasslands than the total average: *Clavulinopsis helvola*, *Entoloma griseocyaneum*, *E. infula*, *Hygrocybe ceracea*, *H. flavipes*, *H. helobia*, *H. ingrata*,

H. laeta, *H. nitrata*, *H. psittacina* and *H. splendidissima* (Table 3). All were relatively common in the dataset, with > 300 records. 15 species had significantly lower frequency of occurrence in seminatural grasslands than the total average (Table 3). With one exception, all of these occurred more often in forests (see below).

Other grasslands. The majority of the investigated species can occur in grasslands like lawns, parks, gardens, old road verges etc. These habitats have much in common with seminatural grasslands if they are old and unmanured (not treated with fertilizer). *Hygrocybe acutoconica* was one of the most frequent species found in other grasslands. This species was significantly less frequent in seminatural grasslands ($p < 0.001$), but more



frequently observed than expected in other grasslands ($p < 0.001$), dune habitats ($p < 0.001$) and rocks with shallow soil ($p < 0.001$) (Figure 4).

Of the 88 species recorded in *sea shore meadows*, 14 had more than 10 records in this habitat. The most common were *Hygrocybe conica*, *H. virginea*, *H. russocoriacea*, *Entoloma sericeum*, *H. chlorophana*, *H. pratensis*, *H. ceracea*, *E. griseocyaneum*, *H. psittacina*, *H. coccinea*, *E. corvinum*, *Geoglossum cookeanum*, and *H. acutoconica* (Table 2). Some of these, like *H. russocoriacea*, *G. cookeanum* and *E. griseocyaneum* probably prefer calcareous shell bed areas. On the mostly acid rocks of western Norway, *H. russocoriacea* almost exclusively occurs on calcareous sandy soil near the sea.

The most common species recorded in *sand dune meadows* were *Entoloma corvinum*, *E. sericellum*, *E. sericeum*, *E. serrulatum*,

Geoglossum cookeanum, *Hygrocybe acutoconica*, *H. cantharellus*, *H. chlorophana*, *H. conica*, *H. psittacina*, *H. russocoriacea*, *H. virginea*, *Microglossum atropurpureum* and *Trichoglossum hirsutum*. Stabilized dunes have often been extensively grazed, and have many features in common with seminatural grasslands.

In *coastal Calluna heaths* the most common species was *Hygrocybe laeta* (25 records), which is sometimes also seen in burnt heath, where the vegetation the first years after burning is rather grass rich. Other species (8-17 records) were *Clavulinopsis helvola*, *C. luteoalba*, *Geoglossum difforme*, *Hygrocybe cantharellus*, *H. ceracea*, *H. chlorophana*, *H. coccinea*, *H. conica*, *H. flavipes*, *H. irrigata*, *H. pratensis*, *H. psittacina*, *H. punicea*, *H. reidii*, *H. splendidissima*, *H. virginea* and *Trichoglossum walteri*.

Many of the records on *rocks with shallow soil* were made on rocks near the sea shore. These habitats are sometimes grazed and occur in mosaic with pastures on deeper soil. Commonly found are e.g. *Hygrocybe acutoconica*, *H. conica*, *H. virginea*, *Entoloma prunuloides*, *H. coccinea*, *H. russocoriacea*, *H. pratensis*, *H. psittacina* and *E. mougeotii*. In the Oslofjord area there are many calcareous rocks with shallow soil and a rich flora and funga. These areas seem to stay open without overgrowing for a long time even without grazing or mowing (Halvorsen et al. 2015). A considerable amount of the records on rocks are from the Oslofjord area, and many of the species preferring strongly calcareous rocks are found here, like *Camarophylloopsis* spp., *Entoloma bloxamii*, *E. excentricum*, *E. incanum*, *Hygrocybe calciphila*, *H. colemaniana*, *H. mucronella* and *Microglossum olivaceum*. Some species with less than 10 Norwegian records (not included in our data) were also found here, like *Camarophylloopsis atropuncta* and *Entoloma fridolfingense*. Similar habitats also occur in some other parts of the country, like the coast of Nordland.

Records from *fens* with detailed habitat information were especially found at the edges of rich or intermediate fens. Most common was *Entoloma mougeotii* (23 records), regularly found at the edges of rich fens (Figure 2). Other species (4-11 records) are e.g. *Entoloma asprellum*, *E. caesiocinctum*, *E. formosum*, *E. poliopus*, *E. serrulatum*, *Geoglossum simile*, *Hygrocybe cantharellus*, *H. coccinea*, *H. conica*, *H. helobia*, *H. miniata*, *H. russocoriacea*, *H. virginea* and *Trichoglossum hirsutum*. Many of the fungi found in rich fens belong to the genus *Entoloma*. Species which are often also found in moist to wet places in seminatural grassland are e.g. *Geoglossum simile*, *Hygrocybe helobia* and *Trichoglossum hirsutum*.

The number of species recorded in *waterfall meadows* was low, due to the rarity of the

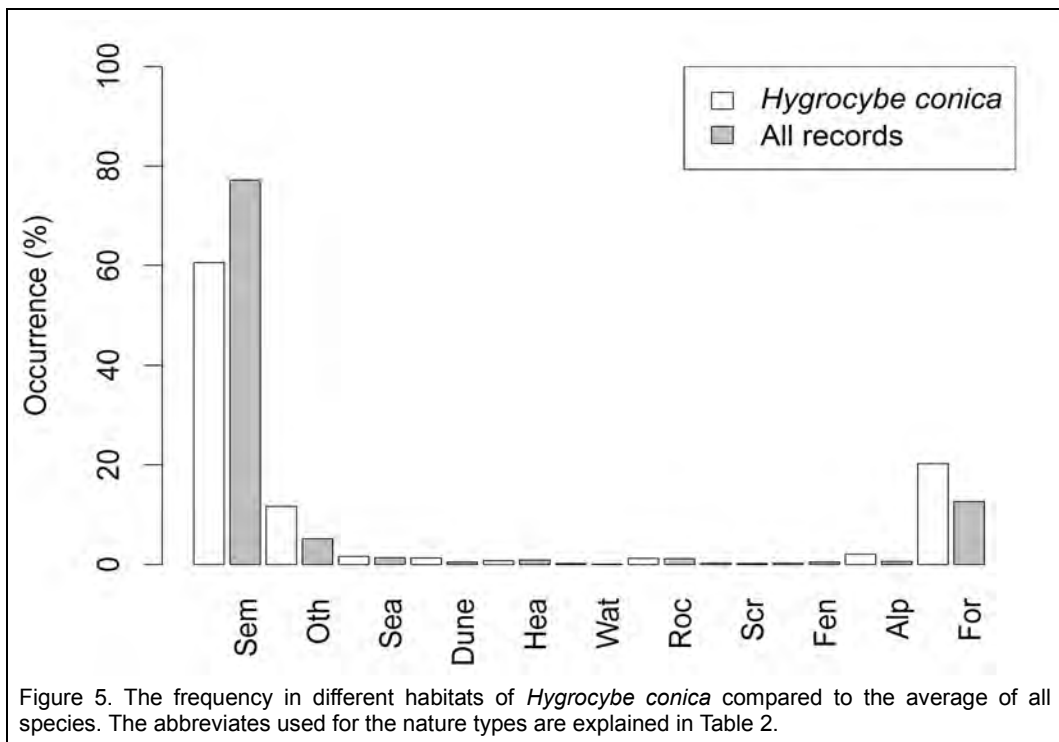
habitat. Species with >1 record were *Entoloma caesiocinctum*, *E. poliopus*, *Hygrocybe conica* and *H. reidii*, which all are widespread species.

The most abundant species in *scree meadows* were generally common species like *Hygrocybe conica*, *H. acutoconica*, *H. coccinea*, *Entoloma poliopus*, *E. serrulatum* and *E. sericeum*. Scree meadows – often grazed by domestic animals – differ only slightly from other pastures, but the soil layer may be interrupted or destroyed more often due to snow avalanches which often bring with them stones, trees, ice and gravel. The instability of the soil is a possible reason why scree habitats are generally poor in grassland fungi.

In *alpine habitats* the far most common species was *Hygrocybe conica* (49 records), which is rather frequent in snowbeds, and found up to 1450 m a.s.l in the middle alpine zone (Figures 2 and 5). Other species (4-11 records) were *Entoloma asprellum*, *E. caesiocinctum*, *E. corvinum*, *E. papillatum*, *E. prunuloides*, *E. sericellum*, *E. sericeum*, *E. serrulatum*, *E. turci*, *E. xanthochroum*, *Hygrocybe pratensis* and *H. virginea*. Grazed, rich snowbeds have many features in common with seminatural grasslands, and true seminatural grasslands can also occur in the low alpine zone (Moen 1999, Senn-Irlet et al. 1990).

Species occurrences in forests

A total of 121 species were recorded in forests, with 5246 records. In *Hygrocybe* (sensu lato), 3260 records (13.8%) were from forests. In *Entoloma*, 1067 records (11.7%) were from forests; in *Clavaria*, *Clavulinopsis* and *Ramariopsis* 508 records (13.9%); *Geoglossum*, *Microglossum*, and *Trichoglossum* had 234 records (9.5%) in forests, while other genera (*Camarophylloopsis*, *Dermoloma*, *Porpoloma*) had 51 records (8.3%) from forests. *Porpoloma* is rare in forests, the two other genera more frequent. For 33 species,



the frequency of occurrence in forest was lower than expected (Table 3). Some species were never found in forests, like *Entoloma velenovskyi* and *Geoglossum difforme*, whereas several species had < 5% of their records in forests, such as *Entoloma griseocyaneum*, *E. infula*, *E. papillatum*, *Geoglossum glutinosum*, *Hygrocybe flavipes*, *H. helobia*, *H. ingrata*, *H. nitrata*, *H. ovina*, *H. turunda*, *H. vitellina*, *Porpoloma metapodium* and *Trichoglossum walteri*.

On the other hand, there were species with a considerable part of their records in forests. E.g. *Entoloma incanum*, *Hygrocybe cantharellus*, *Ramariopsis subtilis* and *Microglossum olivaceum* had more than 30% of their records in forests (Table 3). In the interval of 20-30% of the records in forest there were both species preferring calcareous soil like *Clavulinopsis umbrinella*, *Dermoloma cuneifolium*, *Entoloma bloxamii*, *E. mougeotii* and *H. mucronella*, and more indifferent species like *Hygrocybe*

coccinea, *H. conica* and *H. miniata*. Notable is for instance the difference in habitat preference between the closely related *H. flavipes* (0.6% in forests, less frequent than expected, $p < 0.001$) and *H. lacmus* (19.7% in forests, not significantly different from expected).

Hygrocybe conica constituted the majority of records in several habitat types. Figure 5 shows the observed frequency distribution of *H. conica* compared with the frequency distribution of all species over all habitats. Although the species was commonly found in semi-natural grasslands (ca. 60% of the records, significantly lower than expected, $p < 0.001$), it was overrepresented in other habitats, such as other grasslands, alpine habitats, sand dunes and forests (all $p < 0.001$). *H. conica* alone constituted about 10% of all records in forests, and about 20% of the records of this species was from different forest types.

Among the records from forests, we did a descriptive analysis of information on forest type. There was information on 1324 records said to be found in calcareous forests, that means 25.2% of all records in forests. There was information on 2273 (43.3%) records said to be found in broadleaved forests (mainly forests with *Ulmus*, *Fraxinus*, *Tilia* or *Corylus* as important trees). We also searched for the terms "rich" and "low herb" and for some plant species occurring in rich forests like *Hepatica nobilis* and *Galium odoratum*. Adding this to the information above, we got totally 4375 (83.4%) records found in calcareous or rich/low herb forest types including rich broadleaved forests (and exclusive poor oak forests). For grassland fungi growing in forests, these rich forest types are obviously important. In addition, a total of 489 records (9.3% of forest records) were from "grazed forests", which possibly in many cases also could have been counted as "rich".

There was also a smaller group of records found in more acid forests, like poor boreal deciduous forests and poor oak forests. The species diversity here seems to be rather low, mainly with widespread species, like *Hygrocybe cantharellus*, *H. conica* and *H. reidii* (see also Bendiksen et al. 2008, pp. 60-61). One of the rarer species repeatedly encountered in poor forests was *Hygrocybe lacmus* (Figure 2). *H. cantharellus* has occasionally been found on strongly decayed wood. This substrate has similarities with soil, containing humus and plant roots.

DISCUSSION

Data quality

Our data are based on collections and observations without comprehensive quality control, and there are obviously many possible sources of error. The quality of output data is never better than the quality of input data, and the data should be used with caution. Nevertheless,

many authors point to the big possibilities if such data are used carefully. The availability of open data sources like Species Map Service has made it possible to extract information that may be very useful in scientific work (e.g. Kauserud 2012). The amount of data from Norway can also be compared to 95585 records of 'CHEGD species' in a similar database in the UK according to Griffith et al. (2013), also used for extracting data.

Representativity of sampling

The majority of records in our data were from seminatural grasslands. This could be due to either higher sampling effort (more time spent searching) in seminatural grasslands than in other habitats, to higher detectability of the species in seminatural grasslands, or to higher occurrence of the species in seminatural grasslands. These factors probably influence the observed pattern, but their relative importance is difficult to entangle. We do not know the relative effort of sampling in different habitats. What we know is that there has been a considerable effort investigating seminatural grasslands during the last 25 years. The people sampling in grasslands also collect or note these fungi when searching in other habitats, like forests, but the sampling effort might be lower. The sampling effort in fens may have been lower than in grasslands and forests (Tor Erik Brandrud pers. comm.). Other examples of undersampled habitats might be rocks with shallow soils and scree meadows. However, as a whole we believe that the bias created by different sampling effort between habitats is rather similar between species. Therefore we think that the frequency in different habitats can be compared among species. However, non-significant results of habitat distribution for a species does not mean that a species does not prefer seminatural grassland, but that its distribution is not significantly different

from the overall average of all species in the dataset. This could partly be due to low sampling size (i.e. a low number of records). Knowledge on sampling effort in different habitats would be required to get more solid data on habitat specificity, although the results give some clear indications of relative habitat preferences for several species.

Another bias is related to differences in detectability due to size, colors and presence/lifetime of the carpophores. *Hygrocybe* spp. constitute 59.7% of the records, but only 31.8% of the taxa. These fungi are both big, colourful and possibly more frequently present (long lived, often with fruit bodies) compared to many other genera, and are probably oversampled due to this. Many *Entoloma*'s are smaller, brown, short lived and difficult to determine, while many taxa from *Clavaria*, *Clavulinopsis*, *Ramariopsis*, *Geoglossum*, *Trichoglossum* and *Microglossum* are small and easily overlooked. We think that the bias due to different detectability is rather similar between habitats and therefore not seriously affects the relative frequency between habitats when we compare the species.

Identification

An obvious source of error in the input data is the possibility of misidentifications. We have used a large amount of observations (72.5% of all data) where no control of the determination is possible. On the other hand, collections sent to herbaria are often not controlled either and may have a similar quality as the observations – the difference is only the possibility to control them. *Hygrocybe* s.l. is regarded as a rather well-known group with some exceptions (Boertmann 2010, Lodge et al. 2013). An ongoing Norwegian project on *Entoloma* spp. will probably contribute to changes in species limitations within this genus and even species new to science, but the results are not yet published

or used here. In this situation we have chosen a pragmatic approach. Some poorly understood and rarely collected taxa were initially excluded from the study. All records with information on uncertain determination (cf./aff.) were also excluded. Records of the selected species where the determination is considered valid by the providers of data were included. As two of the authors (GG, JBJ) are responsible for 56.5% of the records, we take our part of the responsibility for this. Generally, data on easily determined species can be trusted more than data on difficult ones.

Habitat information

Another kind of quality is related to the ecological information given in each record. We often had to make an interpretation of what was the meaning in the text describing the habitats, and there is still a potential of improving and standardizing the methods used. Generally, the quality is assumed to be quite good for our purpose. This is partly due to efforts by herbaria and NGOs during the last 20 years to improve the methods of people collecting fungi. As our own data comprise more than a half of the records used here, we were also able to control and improve the quality of the habitat data especially for the aim of this article. Nevertheless the results create many new questions. Based on our own observations, the typical habitat labelled "*Calluna* heath" is in fact often grassy or mossy spots in the heaths, a vegetation type with many features in common with pastures, but detailed information on this is often lacking. So "which species can actually grow in *Calluna* dominated vegetation?" is an example of many questions which may not be properly answered here.

Taxonomic notes

In most genera, several taxonomic problems are not yet solved, but this will not be discussed in detail here. The variation in/around e.g.

Hygrocybe virginea, *H. acutoconica* and *H. conica* is still not completely understood. What has been called *Hygrocybe pratensis* var. *pallida* is probably at least two separate species different from *H. pratensis* (Ellen Larsson pers. comm.). The genus *Entoloma* is very species rich, with sometimes subtle characters separating the species, which can also be variable depending on age of basidiomata and weather conditions (Noordeloos 1992, 2004). The subgenus *Cyanula*, which is important in grasslands, still awaits a comprehensive analysis by molecular methods. The same is the case in parts of Clavariaceae, where some groups have been treated recently (e.g. Kautmanová et al. 2012, Birkebak et al. 2013, Olariaga et al. 2015). In spite of some recent publications on earth tongues (e.g. Arauzo and Iglesias 2014), there are still unsolved problems in *Geoglossum*, *Trichoglossum* and *Microglossum*. Many of the new taxa and redefined species are not yet well understood or investigated in Norway. For example we use *Microglossum olivaceum* in a broad sense including *M. nudipes* which is recently discovered in Norway and Sweden (Kristiansen and Marstad 2015, Persson 2013). The problems with the delimitation of species should generally lead us to be careful about conclusions on ecological differences between closely related taxa. What we believed was one species or even a variety can turn out to comprise two or more species with ecological differences. On the other hand, seemingly separable species can turn out to be one species.

Selection of species

The selection of species is based on the definition of grassland fungi (see Introduction) and some criteria related to data quality (see Material and methods). Several poorly known species have been excluded from our analysis. Some of them are probably belonging among the grassland fungi, supported by data from

other European countries. Here we have to wait for more Norwegian data.

Notes on species and habitats

Generally, the selected species are regarded as grassland species all over Northern Europe (see Introduction). Our results (Tables 2 and 3) show that 83% of the species have less than 20% of their records from forests. For these species, open grassy habitats by far seem to be the most important in Norway. Only for the species with a high number of records, however, we can say this with more confidence. We have also included species with a considerable part of their known Norwegian population in forests. When living in seminatural grasslands, these species seem to have a similar ecology as the other species, also supported by these species listed among grassland fungi in other countries. But these species have a lower degree of habitat specificity. As a conclusion, we can regard the majority of species as having a rather high degree of habitat specificity, preferring seminatural grasslands and similar open, mostly grass- or herb-dominated habitats.

Hygrocybe acutoconica is deviating by having a higher frequency than expected in other grasslands (like road verges) and rocks with shallow soil (Figure 4). This pattern may be due to a preference for calcareous, mineral rich soil poor in humus (sand/clay), and may be shared by more species, e.g. some *Camarophylloopsis* spp., *Clavaria* spp. and *Entoloma incanum*. These species, however, have too few records to give significant results.

Hygrocybe species found by us to occur also in alpine habitats (but which are not true alpine species) are very much the same as reported from the alpine, subarctic or low arctic zone in Greenland, Scandinavia and the Alps (Boertmann 2010, Borgen and Arnolds 2004, Senn-Irlet et al. 1990), like *H. conica*, *H. nitrata*, *H. pratensis* and *H. virginea*.

The same is the case in *Entoloma*, compared with information from Northern Europe in Noordeloos (1992, 2004). As mentioned earlier, true seminatural grasslands can also occur in the low alpine zone (Moen 1999).

Nitare (2014) gives semi-quantitative information on the occurrence of 50 grassland fungi in forests in Sweden. In about 30-35 species there is a good to very good compliance between his results and ours, e.g. regarding most of the *Hygrocybe* spp. However, in some few species the results differ. Species not often observed in forests in Sweden are e.g. *H. miniata* (Table 3: 24.0% in forests in Norway) and *H. punicea* (29.6%). *H. punicea* is on the red list in Sweden but not in Norway, due to the seemingly different habitat specificity between the countries. On the other hand some species are more frequently found in Swedish than in Norwegian forests, like *Geoglossum fallax* (forest records in Norway: 6.3%), *G. glutinosum* (4.0%) and *Hygrocybe fornicata* (7.2%). Nitare (2000) lists 'grassland fungi' used to evaluate management priority of forests in Sweden. He mentions 20 *Hygrocybe* species. Most of these have more than 10% of their records in forests in our data. We find that there are striking similarities between Swedish and Norwegian data, indicating that there are real differences between species of grassland fungi with regard to their occurrence in forests in Scandinavia. Differences in available habitats, habitat quality or climate could possibly explain the observed differences between the two countries within some species.

In the literature, many forest localities with records of grassland fungi are described as moist and shady, often with naked soil (Nitare 2000, Hesler and Smith 1963), in strong contrast to open grassland habitats which are frequently sun exposed and with a dense layer of mosses, grasses and herbs. In our dataset, only 227 of the forest records

were noted on naked soil and additional 140 records on naked soil in tall herb vegetation. Many forest records were from sun exposed forests, but certainly often in regions with a moist climate. Generally, our data on forest vegetation are not very detailed, but the preference in most species for rich forest types seems to be clear (see results).

Boertmann (2010) also describes *Alnus* swamps as a *Hygrocybe* habitat. We found only 16 records of 10 common species (*Clavaria*, *Entoloma*, *Hygrocybe*) in our material describing wetland forests as habitat. The most abundant was *Hygrocybe cantharellus* with 7 records. This is probably a habitat of minor importance in Norway. The same is the case in Sweden (Johan Nitare pers. comm.).

Implications for nature management

The survival of these species is strongly influenced by the decline in seminatural grasslands, a habitat listed as vulnerable (VU) on the Norwegian red list for nature types (Lindgaard and Henriksen 2011). Forest constitutes an important habitat for 23 species (17.0%) having more than 20% of their records in forests. These species are less vulnerable to the loss of seminatural grasslands. This is taken into consideration in the revision of the Norwegian red list, and should be considered in general nature management. However, the forest types most important for these fungi – calcareous or rich/low herb forests – have also declined and cover limited areas, and some of these are also present on the Norwegian red list for nature types (as NT or VU, Lindgaard and Henriksen 2011). Some other open habitats of grassland fungi have also declined during the last decades. Sea shore meadows are exposed to regrowth or habitat destruction and are near threatened (NT, Lindgaard and Henriksen 2011). Coastal heaths (endangered – EN), sand dunes (VU) and waterfall meadows (NT) can also be

subject to regrowth or other changes in land use (Lindgaard and Henriksen 2011). Continued grazing of these habitats is probably important for the fungi. Rich fens have declined in many regions, and are classified as EN in the lowlands (Lindgaard and Henriksen 2011). Grassland fungi in Norway thus seem to have experienced more decline in their populations during the last 50-100 years than most other fungi (Jordal 2010), and therefore deserve high attention when it comes to management measures, like in other European countries (e.g. Arnolds 1988, Griffith et al. 2013, Newton et al. 2003, Nitare 1988).

Is habitat specificity influenced by nutritional strategy?

Knowledge on the nutritional strategy of the grassland fungi treated here could contribute to the understanding of their habitat selection and habitat specificity. This topic has been debated for a long time, some authors arguing that they must have some kind of mycorrhiza (e.g. Nitare 1988, 2014), while others think they are saprotrophs (e.g. Arnolds 1982). These fungi are very difficult to cultivate in the laboratory (Griffith et al. 2013, Lodge et al. 2013). Recent studies have shown that many of them have isotopic signatures indicating that they are neither ectomycorrhizal nor saprotrophic, but could have some kind of biotrophy (Griffith et al. 2002, Seitzman et al. 2011, Birkebak et al. 2013). There are further some recent observations of *Hygrocybe* hyphae, verified by DNA analysis, inside plant tissues and even inside plant cells, like in roots of herbaceous plants, and leaves and seeds of *Plantago lanceolata* (Halbwachs et al. 2013, Tello et al. 2014), indicating endophytic growth and suggesting a close biotrophic relation between grassland fungi and plants. *Hygrocybe coccinea* was also detected in pine trees and mistletoes in Germany and Austria (Persoh 2013), which is interesting in trying to answer the question why 'grassland

fungi' occur in forests. Most questions about their ecology are still unanswered (Lodge et al. 2013, Birkebak et al. 2013). Differences in habitat specificity between species of fungi shown in this paper might be due to differences in nutritional strategy, for instance which plant species they are able to make biotrophic relations to. This will be an exciting topic in the future.

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Table 2. Selected grassland fungi in Norway with ≥ 10 records, collected 1900-2014. RL=Norwegian red list status 2015, Loc=number of localities (calculated for redlisted species only), N=number of records, Sem=seminatural grasslands, Oth=other grasslands (e.g. lawns, parks, road verges), Sea=sea shore meadows, Dun=sand dune meadows, Hea=coastal heath, Wat=waterfall meadows, Roc=rocks with shallow soil, mostly near the sea, Scr=open scree meadows, Fen=fens, Alp=alpine habitats, For=different forest types, TOT=sum of records in all habitats; can exceed N because one record can contain information about more than one type of habitat, % For=the percent of records in forests in relation to N.

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Camarophyllopsis foetens</i>	VU	38	56	42	2	0	1	0	0	4	0	0	0	9	58	16.1
<i>Camarophyllopsis hymenoccephala</i>	EN	9	11	3	3	1	0	0	0	2	0	0	0	2	11	18.2
<i>Camarophyllopsis micacea</i>	EN	8	16	3	0	0	0	0	0	3	0	0	0	10	16	62.5
<i>Camarophyllopsis schulzeri</i>	NT	204	274	253	7	2	0	0	0	1	1	0	0	16	280	5.8
<i>Clavaria amoenoides</i>	VU	71	95	85	10	0	0	0	0	0	1	0	0	7	103	7.4
<i>Clavaria falcata</i>	LC		256	167	26	2	0	0	0	19	2	1	0	47	264	18.4
<i>Clavaria flavipes</i>	VU	92	103	94	6	0	0	0	0	1	0	0	0	8	109	7.8
<i>Clavaria fragilis</i>	LC		264	203	25	0	0	2	0	6	1	0	0	38	275	14.4
<i>Clavaria fumosa</i>	NT	144	191	161	5	0	0	0	0	2	0	0	0	31	199	16.2
<i>Clavaria greletii</i>	VU	9	11	6	2	0	1	0	0	1	0	0	0	2	12	18.2
<i>Clavaria pullei</i>	VU	11	15	12	1	0	0	0	0	0	0	0	0	2	15	13.3
<i>Clavaria rosea</i>	VU	19	24	11	14	0	1	0	0	0	0	0	0	1	27	4.2
<i>Clavaria zollingeri</i>	VU	162	235	206	7	1	0	0	0	2	0	0	0	26	242	11.1
<i>Clavulinopsis corniculata</i>	LC		625	462	40	10	0	0	1	14	1	3	2	114	647	18.2
<i>Clavulinopsis fusiformis</i>	VU	18	21	18	1	0	1	2	0	1	0	0	0	2	25	9.5
<i>Clavulinopsis helvola</i>	LC		848	757	30	11	2	10	1	3	0	0	0	64	878	7.5
<i>Clavulinopsis laeticolor</i>	LC		328	261	11	10	0	2	0	9	0	0	2	48	343	14.6
<i>Clavulinopsis luteoalba</i>	LC		440	377	14	4	0	8	0	3	0	0	2	48	456	10.9
<i>Clavulinopsis umbrinella</i>	NT	60	83	62	3	0	0	0	0	3	0	0	0	20	88	24.1
<i>Dermoloma cuneifolium</i>	VU	35	66	41	9	1	0	0	0	2	0	0	0	16	69	24.2
<i>Dermoloma pseudocuneifolium</i>	VU	14	21	15	1	0	0	0	0	1	2	0	0	5	24	23.8

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Entoloma aethiops</i>	VU	9	14	12	0	0	0	0	0	0	1	0	0	2	17	14.3
<i>Entoloma ameides</i>	NT	25	34	25	3	1	0	0	0	0	0	0	0	9	38	26.5
<i>Entoloma anatinum</i>	VU	10	12	10	0	0	0	2	0	1	0	0	0	1	14	8.3
<i>Entoloma asprellum</i>	LC		340	270	9	4	4	0	2	0	1	0	5	6	357	17.6
<i>Entoloma atrocoeruleum</i>	NT	133	195	169	4	5	0	1	0	7	0	2	1	15	204	7.7
<i>Entoloma bloxamii</i>	VU	76	115	77	5	0	0	12	0	5	0	2	1	31	133	27.0
<i>Entoloma caeruleopolitum</i>	VU	63	77	75	1	0	0	0	0	0	0	0	1	1	78	1.3
<i>Entoloma caeruleum</i>	DD	13	20	12	0	0	0	0	0	0	0	2	0	6	20	30.0
<i>Entoloma caesiocinctum</i>	LC		364	243	11	0	4	2	5	1	3	10	5	110	394	30.2
<i>Entoloma chalybeum</i>	NT	166	209	174	9	4	2	2	0	5	0	0	1	22	219	10.5
<i>Entoloma cocles</i>	VU	39	45	43	0	0	0	1	0	1	0	0	0	3	48	6.7
<i>Entoloma coeruleofoculosum</i>	VU	8	16	9	0	0	0	0	0	0	0	0	2	7	18	43.8
<i>Entoloma corvinum</i>	NT	234	289	239	11	14	3	3	0	1	0	2	5	30	308	10.4
<i>Entoloma cremeoalbum</i>	EN	4	11	11	0	0	0	0	0	0	0	0	0	0	11	0.0
<i>Entoloma cruentatum</i>	VU	10	13	12	0	0	0	0	0	0	0	0	0	1	13	7.7
<i>Entoloma cuspidiferum</i>	DD	9	16	15	0	0	0	0	0	0	0	0	0	1	16	6.3
<i>Entoloma cyanulum</i>	DD	10	12	8	1	0	0	0	0	0	0	1	0	2	12	16.7
<i>Entoloma excentricum</i>	VU	17	20	12	3	1	0	0	0	3	1	0	0	1	21	5.0
<i>Entoloma exile</i>	LC		269	237	8	3	0	2	1	1	1	1	3	2	279	7.8
<i>Entoloma formosum</i>	LC		234	169	22	2	1	3	0	1	0	4	2	44	248	18.8
<i>Entoloma fuscotomentosum</i>	NT	20	21	17	0	2	0	0	0	1	0	0	0	1	21	4.8
<i>Entoloma griseocyanum</i>	NT	390	549	518	17	17	1	1	0	7	1	0	3	10	575	1.8
<i>Entoloma incanum</i>	NT	49	75	24	15	1	2	0	0	8	1	1	1	33	86	44.0
<i>Entoloma infula</i>	LC		328	302	4	2	0	1	0	1	1	2	2	18	333	5.5
<i>Entoloma jubatium</i>	NT	132	188	156	5	2	1	1	0	0	0	2	3	25	195	13.3

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For	
<i>Entoloma kervinii</i>	VU	21	32	30	1	1	0	1	0	0	0	0	0	1	0	34	0.0
<i>Entoloma lividocyanulum</i>	LC		127	100	6	1	0	2	1	1	0	2	3	21	137	16.5	
<i>Entoloma longistriatum</i>	LC		215	176	6	2	0	2	0	2	0	3	3	26	220	12.1	
<i>Entoloma melanochroum</i>	VU	25	30	26	0	0	0	0	0	0	0	1	0	4	31	13.3	
<i>Entoloma mougeotii</i>	NT	190	243	149	15	5	1	3	0	10	2	23	3	56	267	23.0	
<i>Entoloma neglectum</i>	VU	12	13	8	3	0	0	0	0	0	1	0	0	1	13	7.7	
<i>Entoloma papillatum</i>	LC		513	460	21	7	2	3	0	9	0	1	4	21	528	4.1	
<i>Entoloma poliopus</i>	LC		561	472	8	7	2	6	3	8	3	5	5	55	574	9.8	
<i>Entoloma polito flavipes</i>	NT	15	16	15	0	0	1	0	0	0	0	0	0	0	16	0.0	
<i>Entoloma porphyrophaeum</i>	VU	81	100	93	3	1	1	0	0	0	0	0	1	9	108	9.0	
<i>Entoloma pratulense</i>	VU	92	110	103	6	2	0	0	0	2	0	0	3	7	123	6.4	
<i>Entoloma prunulooides</i>	NT	338	548	485	8	8	1	10	0	18	0	1	5	33	569	6.0	
<i>Entoloma pseudocoelestinum</i>	VU	28	33	30	0	0	0	0	0	1	0	1	1	1	34	3.0	
<i>Entoloma pseudoturci</i>	DD	23	27	25	0	1	0	0	0	0	1	0	1	1	29	3.7	
<i>Entoloma queletii</i>	NT	24	37	26	0	0	0	0	0	5	0	1	2	7	41	18.9	
<i>Entoloma rhombisporum</i>	VU	128	178	155	8	2	0	0	0	5	1	1	3	15	190	8.4	
<i>Entoloma sacchariolenis</i>	VU	9	12	11	0	0	1	0	0	0	0	0	2	0	14	0.0	
<i>Entoloma scabropellis</i>	DD	13	15	12	1	1	1	0	0	1	0	0	0	1	16	6.7	
<i>Entoloma sericellum</i>	LC		896	688	51	12	5	7	0	16	1	3	5	145	933	16.2	
<i>Entoloma sericeum</i>	LC		954	803	73	25	10	6	0	5	3	1	7	53	986	5.6	
<i>Entoloma serrulatum</i>	LC		543	399	24	12	4	3	0	12	3	8	7	100	572	18.4	
<i>Entoloma sodale</i>	VU	13	18	13	2	0	0	0	0	1	0	2	2	2	22	11.1	
<i>Entoloma turci</i>	NT	117	169	136	9	1	0	0	0	12	0	1	8	13	180	7.7	
<i>Entoloma undatum</i>	LC		164	98	12	4	2	2	0	4	0	2	2	41	167	25.0	
<i>Entoloma velenovskyi</i>	VU	31	38	36	2	0	0	0	0	1	0	0	1	0	40	0.0	

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Entoloma xanthochroum</i>	LC		60	55	1	0	0	0	0	0	0	1	6	3	66	5.0
<i>Geoglossum cookeanum</i>	NT	49	97	61	10	12	16	0	0	1	0	0	1	5	106	5.2
<i>Geoglossum difforme</i>	EN	22	77	74	1	4	1	8	0	0	0	0	0	0	88	0.0
<i>Geoglossum fallax</i>	LC		498	387	71	8	2	2	0	7	0	0	1	32	510	6.4
<i>Geoglossum glutinosum</i>	LC		339	284	36	4	0	4	0	5	0	0	0	14	347	4.1
<i>Geoglossum hakelieri</i>	EN	3	11	11	0	0	0	0	0	0	0	0	0	0	11	0.0
<i>Geoglossum simile</i>	NT	43	65	50	5	0	1	2	0	1	0	4	0	2	65	3.1
<i>Geoglossum starbaeckii</i>	LC		144	111	15	0	0	0	0	1	0	0	1	19	147	13.2
<i>Geoglossum uliginosum</i>	VU	15	28	26	1	0	0	0	0	0	0	1	0	1	29	3.6
<i>Geoglossum umbratile</i>	LC		379	265	71	5	2	1	0	4	0	0	1	35	384	9.2
<i>Hygrocybe acutoconica</i>	LC		567	370	85	14	16	4	0	30	3	1	3	78	604	13.8
<i>Hygrocybe aurantiosplendens</i>	NT	110	162	131	12	3	2	0	0	1	0	1	0	32	182	19.8
<i>Hygrocybe calciphila</i>	VU	27	31	20	3	2	0	0	0	8	0	0	1	0	34	0.0
<i>Hygrocybe calyptriformis</i>	EN	8	10	10	0	0	0	0	0	0	0	0	0	0	10	0.0
<i>Hygrocybe canescens</i>	EN	18	24	23	1	2	0	1	0	0	0	0	0	0	27	0.0
<i>Hygrocybe cantharellus</i>	LC		840	523	48	8	3	9	0	7	2	13	0	276	889	32.9
<i>Hygrocybe ceracea</i>	LC		1316	1179	47	18	1	6	0	6	1	0	2	85	1345	6.5
<i>Hygrocybe chlorophana</i>	LC		1281	1086	59	20	3	11	1	6	0	2	0	142	1330	11.1
<i>Hygrocybe citrinovirens</i>	EN	9	19	18	1	0	0	0	0	0	0	0	0	0	19	0.0
<i>Hygrocybe coccinea</i>	LC		1250	920	53	15	2	16	1	11	3	5	2	277	1305	22.2
<i>Hygrocybe colemanniana</i>	VU	139	238	215	12	5	0	0	0	4	0	0	1	13	250	5.5
<i>Hygrocybe conica</i>	LC		2516	1591	306	42	34	19	4	31	7	7	54	532	2627	21.1
<i>Hygrocybe flavipes</i>	NT	204	347	339	9	2	0	1	0	0	0	0	2	2	355	0.6
<i>Hygrocybe fornicata</i>	NT	206	317	286	17	1	0	0	0	3	0	0	2	24	333	7.6
<i>Hygrocybe glutinipes</i>	LC		237	204	18	2	0	1	0	1	0	0	0	21	247	8.9

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Hygrocybe helobia</i>	LC		405	374	10	2	0	11	0	1	0	8	1	10	417	2.5
<i>Hygrocybe ingrata</i>	VU	222	340	329	5	4	0	1	0	0	0	0	4	10	353	2.9
<i>Hygrocybe insipida</i>	LC		721	599	27	10	0	6	0	3	0	0	0	90	735	12.5
<i>Hygrocybe intermedia</i>	VU	73	126	115	8	1	0	0	0	0	0	0	0	7	131	5.6
<i>Hygrocybe irrigata</i>	LC		549	478	12	5	0	8	0	1	0	1	0	59	564	10.7
<i>Hygrocybe lacmus</i>	NT	163	218	184	8	3	1	3	1	1	1	0	0	43	245	19.7
<i>Hygrocybe laeta</i>	LC		1228	1075	32	8	2	23	1	7	0	3	3	122	1276	9.9
<i>Hygrocybe miniata</i>	LC		533	340	48	8	3	1	0	5	0	17	6	135	563	25.3
<i>Hygrocybe mucronella</i>	NT	136	210	146	12	3	0	1	1	2	3	2	1	53	224	25.2
<i>Hygrocybe nitrata</i>	NT	567	887	838	19	7	1	5	0	1	0	0	3	31	905	3.5
<i>Hygrocybe ovina</i>	VU	119	201	191	4	5	1	1	0	0	0	0	0	9	211	4.5
<i>Hygrocybe phaeococcinea</i>	LC	194	249	218	30	3	0	2	0	0	0	0	0	10	263	4.0
<i>Hygrocybe pratensis</i>	LC		1918	1593	74	19	1	10	0	8	2	2	6	266	1981	13.9
<i>Hygrocybe pratensis</i> var. <i>pallida</i>	LC		77	73	2	1	0	0	0	0	3	0	0	4	83	5.2
<i>Hygrocybe psittacina</i>	LC		1408	1231	42	17	7	15	0	8	2	1	2	130	1455	9.2
<i>Hygrocybe punicea</i>	LC		861	591	22	7	0	13	0	4	1	0	1	269	908	31.2
<i>Hygrocybe quieta</i>	NT	289	480	408	11	3	1	3	0	4	1	0	3	69	503	14.4
<i>Hygrocybe reidii</i>	LC		1240	1057	24	10	1	11	2	7	2	2	0	170	1286	13.7
<i>Hygrocybe russocoriacea</i>	NT	244	442	379	11	25	9	13	0	13	0	5	2	26	483	5.9
<i>Hygrocybe spadicea</i>	EN	19	23	18	3	0	0	0	0	2	0	0	0	1	24	4.3
<i>Hygrocybe splendidissima</i>	VU	247	438	423	6	3	0	6	0	1	0	0	0	23	462	5.3
<i>Hygrocybe subpapillata</i>	VU	29	41	37	5	0	0	0	0	0	0	0	0	1	43	2.4
<i>Hygrocybe turunda</i>	VU	114	151	138	4	2	0	0	0	2	0	1	1	5	153	3.3
<i>Hygrocybe virginea</i>	LC		1724	1299	163	29	13	13	1	21	2	5	15	238	1799	13.8
<i>Hygrocybe virginea</i> var. <i>fuscescens</i>	LC		59	45	2	1	2	0	0	4	0	1	1	6	62	10.2

Species	RL	Loc	N	Sem	Oth	Sea	Dun	Hea	Wat	Roc	Scr	Fen	Alp	For	TOT	% For
<i>Hygrocybe virginea</i> var. <i>ochraceopallida</i>	LC		18	13	0	1	3	0	0	2	0	0	0	1	20	5.6
<i>Hygrocybe vitellina</i>	VU	40	71	67	1	1	0	2	0	1	0	0	1	1	74	1.4
<i>Microglossum atropurpureum</i>	VU	110	235	195	14	4	3	1	0	0	0	0	0	24	241	10.2
<i>Microglossum fusciorubens</i>	VU	57	75	40	3	5	1	0	0	7	0	0	0	21	77	28.0
<i>Microglossum olivaceum</i>	VU	49	100	44	11	2	1	0	0	3	0	0	0	41	102	41.0
<i>Porpoloma metapodium</i>	EN	96	188	178	4	2	0	2	0	0	0	0	0	3	189	1.6
<i>Ramariopsis crocea</i>	VU	31	37	7	1	0	0	0	0	2	1	0	0	27	38	73.0
<i>Ramariopsis kunzei</i>	LC		144	59	8	0	0	1	0	5	2	0	0	76	151	52.8
<i>Ramariopsis subtilis</i>	NT	85	109	55	7	0	0	0	0	3	0	0	0	50	115	45.9
<i>Trichoglossum hirsutum</i>	LC		217	146	21	7	5	2	0	3	1	9	1	34	229	15.7
<i>Trichoglossum walteri</i>	VU	121	202	185	7	4	0	10	0	0	0	0	0	6	212	3.0
TOTAL			39818	32034	2147	561	188	351	24	487	64	188	240	5246	41530	13.2
Percent			100	80.45	5.39	1.41	0.47	0.88	0.06	1.22	0.16	0.47	0.60	13.17		
Number of species			132	132	113	88	52	68	14	98	35	52	68	121		

Table 3. Overview of species with frequency of occurrence in seminatural grasslands or forest habitats which significantly deviated from the average, sorted alphabetically within 5% intervals of occurrences in forest. Asterisks refer to Chi-square tests of observed frequency against expected frequency of 77.1% of occurrences in seminatural grasslands and 12.6% of occurrences in forest. The analyses are based on 41530 unique species-habitat records (sum of TOT in Table 2), and consequently the frequencies reported here deviate slightly from the frequencies in Table 2 (evaluated based on N). · p < 0.10, * p < 0.05, p < 0.01, *** p < 0.001.

Species	Red list status	No. of records	% seminatural grassland	% forest
0-5% of records in forest				
<i>Entoloma caeruleopolitum</i>	VU	78	96.2	1.3 **
<i>Entoloma griseocyaneum</i>	NT	575	90.1 *	1.7 ***
<i>Entoloma papillatum</i>	LC	528	87.1 ·	4.0 ***
<i>Entoloma velenovskyi</i>	VU	40	90.0	0.0 *
<i>Geoglossum cookeanum</i>	NT	106	57.5 ·	4.7 *
<i>Geoglossum difforme</i>	EN	88	84.1	0.0 **
<i>Geoglossum glutinosum</i>	LC	347	81.9	4.0 ***
<i>Hygrocybe flavipes</i>	NT	355	95.5 **	0.6 ***
<i>Hygrocybe helobia</i>	LC	417	89.7 *	2.4 ***
<i>Hygrocybe ingrata</i>	VU	353	93.2 *	2.8 ***
<i>Hygrocybe nitrata</i>	NT	905	92.6 ***	3.4 ***
<i>Hygrocybe ovina</i>	VU	211	90.5	4.3 **
<i>Hygrocybe phaeococcinea</i>	LC	263	82.9	3.8 ***
<i>Hygrocybe turunda</i>	VU	153	90.2	3.3 **
<i>Hygrocybe vitellina</i>	VU	74	90.5	1.4 *
<i>Porpoloma metapodium</i>	EN	189	94.2 ·	1.6 ***
<i>Trichoglossum walteri</i>	VU	212	87.3	2.8 ***
5-10% in forest				
<i>Camarophyllopsis schulzeri</i>	NT	280	90.4 ·	5.7 **
<i>Clavulinopsis helvola</i>	LC	878	86.2 *	7.3 ***
<i>Entoloma exile</i>	LC	279	84.9	7.5 *
<i>Entoloma infula</i>	LC	333	90.7 *	5.4 ***
<i>Entoloma pratulense</i>	VU	123	83.7	5.7 *
<i>Entoloma prunuloides</i>	NT	569	85.2	5.8 ***

Species	Red list status	No. of records	% seminatural grassland	% forest
<i>Entoloma sericeum</i>	LC	986	81.4	5.4 ***
<i>Geoglossum fallax</i>	LC	510	75.9	6.3 ***
<i>Hygrocybe acutoconica</i>	LC	604	61.3 ***	12.9
<i>Hygrocybe ceracea</i>	LC	1345	87.7 **	6.3 ***
<i>Hygrocybe colemanniana</i>	VU	250	86.0	5.2 **
<i>Hygrocybe fornicata</i>	NT	333	85.9	7.2 **
<i>Hygrocybe intermedia</i>	VU	131	87.8	5.3 *
<i>Hygrocybe laeta</i>	LC	1276	84.2 *	9.6 **
<i>Hygrocybe psittacina</i>	LC	1455	84.6 *	8.9 ***
<i>Hygrocybe russocoriacea</i>	NT	483	78.5	5.4 ***
<i>Hygrocybe splendidissima</i>	VU	462	91.6 *	5.0 ***
15-20% in forest				
<i>Clavaria falcata</i>	LC	264	63.3	17.8 *
<i>Clavulinopsis corniculata</i>	LC	647	71.4	17.6 **
<i>Entoloma asprellum</i>	LC	357	75.6	16.8 *
<i>Entoloma formosum</i>	LC	248	68.1	17.7 *
<i>Entoloma sericellum</i>	LC	933	73.7	15.5 *
<i>Entoloma serrulatum</i>	LC	572	69.8	17.5 **
20-30% in forest				
<i>Clavulinopsis umbrinella</i>	NT	88	70.5	22.7 *
<i>Dermoloma cuneifolium</i>	VU	69	59.4	23.2 *
<i>Entoloma bloxamii</i>	VU	133	57.9	23.3 **
<i>Entoloma caesiocinctum</i>	LC	394	61.7 **	27.9 ***
<i>Entoloma mougeotii</i>	NT	267	55.8 **	21.0 ***
<i>Entoloma undatum</i>	LC	167	58.7 *	24.6 ***
<i>Hygrocybe coccinea</i>	LC	1305	70.5 *	21.2 ***
<i>Hygrocybe conica</i>	LC	2627	60.6 ***	20.3 ***
<i>Hygrocybe miniata</i>	LC	563	60.4 ***	24.0 ***
<i>Hygrocybe mucronella</i>	NT	224	65.2	23.7 ***

Species	Red list status	No. of records	% seminatural grassland	% forest
<i>Hygrocybe punicea</i>	LC	908	65.1 **	29.6 ***
<i>Microglossum fuscobubens</i>	VU	77	51.9 ·	27.3 **
30-40% in forest				
<i>Entoloma coeruleoflocculosum</i>	VU	18	50.0	38.9 *
<i>Entoloma incanum</i>	NT	86	27.9 ***	38.4 ***
<i>Hygrocybe cantharellus</i>	LC	889	58.8 ***	31.0 ***
> 40% in forest				
<i>Camarophyllopsis micacea</i>	EN	16	18.8 *	62.5 ***
<i>Microglossum olivaceum</i>	VU	102	43.1 **	40.2 ***
<i>Ramariopsis crocea</i>	VU	38	18.4 ***	71.1 ***
<i>Ramariopsis kunzei</i>	LC	151	39.1 ***	50.3 ***
<i>Ramariopsis subtilis</i>	NT	115	47.8 **	43.5 ***

***Atractosporocybe polaris* – a new clitocyboid agaric described from arctic-alpine and northern boreal regions in Svalbard and Scandinavia**

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KEYWORDS

Arctic-alpine mycology, *Atractosporocybe*, *Clitocybe inornata*, molecular systematics, taxonomy

NØKKELOORD

Arktisk-alpin mykologi, *Atractosporocybe*, *Clitocybe inornata*, molekylærsystematikk, taksonomi

SAMMENDRAG

Arten *Atractosporocybe polaris* er beskrevet som ny for vitenskapen fra arktisk-alpine og nordboreale områder på Svalbard og i Skandinavia basert på fylogenetiske analyser av ITS og LSU data fra nukleært ribosomalt DNA. Av utseende ligner den ribbetraktopp (*A. inornata*), men har mørkere skiver, glattere hattkant og bare svak lukt; anatomiske forskjeller er ikke funnet. Arten vokser blant mose, lav, urter, lyng og dvergbusker (*Salix*

og *Dryas*) i arktiske og alpine områder og i vier- og orekratt (*Salix* og *Alnus*) i nordboreale områder, og er en typisk kalkgrunnsart.

ABSTRACT

The new species *Atractosporocybe polaris*, identified from the arctic archipelago of Svalbard and Scandinavia, is here described as new to science based on ITS and LSU sequence data from nuclear ribosomal DNA. In morphology it differs from *A. inornata* by darker gills, a smooth or faintly grooved cap margin, and a comparatively faint smell. It grows in arctic tundra and heathland among mosses, lichens, ericaceous plants, herbs, graminoids, and dwarf *Salix* and *Dryas* on calcareous ground. In Scandinavia it is found in the northern boreal zone growing among *Salix* scrubs and *Alnus*.

INTRODUCTION

Agarics with a clitocyboid habitus, originally described in the genus *Clitocybe* have been in focus of several recent molecular phylogenetic studies (Vizzini et al. 2010, Vizzini et al. 2011, Vizzini and Ercole 2012). The polyphyletic genus *Clitocybe* has been split up in several new genera to accommodate recovered clade relationships of monophyletic clades. *Atractosporocybe* was erected for species with greyish brown basidiomata, adnate to subdecurrent gills, and hyaline, long ellipsoid fusiform spores (Alvarado et al. 2015). The genus is currently monotypic, including the familiar

species that we until now have known as *Clitocybe inornata* (Sowerby) Gillet.

For many years and on several collecting trips to the arctic archipelago of Svalbard a fungus very similar to *Atractosporocybe inornata* (Sowerby) P. Alvarado, G. Moreno & Vizzini has been observed. The overall similarity with *A. inornata* is obvious but it differs by more or less lacking the grooves on the cap margin, having darker gills and a comparatively faint smell. The size and shape of the basidiospores are the characteristic and same as those of *A. inornata*. To find out if the fungus we find on Svalbard is identical to that found in the more southern parts of Scandinavia and Europe a molecular study was undertaken.

In the herbarium of the Natural History Museum in Oslo (O), several collections of the species from Svalbard have been deposited, often filed as *Clitocybe aggregata* (= *Lyophyllum decastes* coll.), all from dwarf willow sites. Also in the herbaria of Tromsø (TROM) and the University of Gothenburg (GB) there are some northern and alpine collections of *A. inornata* from *Salix* shrubs and northern boreal *Betula* and *Alnus* sites that could be suspected to represent the same taxon as on Svalbard.

In this study we describe the new species, *Atractosporocybe polaris*, a close relative to *A. inornata* but with a northern boreal to arctic-alpine geographic distribution range.

MATERIALS AND METHODS

The description of macro-morphology is based on fresh material and photographs. Colour designations follow Kornerup and Wanscher (1962), J.E. Lange's colour map published in Larsen (1932) and Cailleux (1981). Light microscopy study and measurements were done on squash preparations in KOH (5%), Cotton blue-lactic acid, and Melzer's reagent. The separate description and diagnose of the type material is followed by a more general

description of the new species based on all examined collections.

Molecular work

Fourteen specimens of *A. inornata* and *A. cf. inornata* from Svalbard, Sweden and Norway were selected for sequencing in this study. The sequenced specimens are indicated with asterisk in the lists of specimens examined and presented in Table 1. For comparison and putting our sequence data in a phylogenetic context additional ITS and LSU sequence data of *A. inornata*, *Leucocybe* and *Clitocybe subditopoda* were retrieved from GenBank, taken from a previous study on *Atractosporocybe* and *Leucocybe* (Alvarado et al. 2015). Based on results from earlier molecular phylogenetic studies of Agaricales and the Tricholomatoid clade, *Clitocybe nebularis*, *Collybia tuberosa* and *Lepista nuda* were selected as the outgroup for rooting of trees (Matheny et al. 2006, Alvarado et al. 2015).

Sequences from the complete ITS region and about 900 base pairs (bp) of the 5' end of the LSU nuclear ribosomal DNA were generated for the study. DNA extractions, PCR, and sequencing were performed as described in Larsson and Örstadius (2008). Primers used to amplify the complete ITS region and the 5' end of the LSU region were ITS1F (Gardes and Bruns 1993) and LR21, LR0R, and LR7 (Hopple and Vilgalys 1999). Primers used for sequencing were ITS1, ITS4 (White et al. 1990), Ctb6 (<http://plantbio.berkeley.edu/~bruns/>) and LR5 (Hopple and Vilgalys 1999). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan, U.S.A.). Sequences generated for this study have been deposited in GenBank under the accession numbers (KU709846–KU709860).

Alignment was performed using the L-INS-i strategy as implemented in MAFFT v. 7.017 (Katoh and Standley 2013). The alignment was adjusted manually using the data editor

Table 1. Data of sequenced specimens of *Atractosporocybe* included in the phylogenetic analyses, generated for this study or taken from GenBank.

Species	Coll. ID. / Origin	Ecology, substrate	GB no.
<i>A. inornata</i>	GG129/85 / Norway	Low herb conif. forest, calcareous	KU709846
<i>A. inornata</i>	GG708/67 / Norway	Spruce forest, calcareous	KU709847
<i>A. inornata</i>	LAS89/082-A / Sweden	Coniferous forest, calcareous	KU709848
<i>A. inornata</i>	GG85/10 / Norway	Mixed coniferous forest	KU709849
<i>A. inornata</i>	Skifte1193 / Norway	Birch forest	KU709850
<i>A. inornata</i>	TEB732-04 / Norway	Spruce-pine forest	KU709851
<i>A. inornata</i>	TEB379-00 / Norway	Rich pine (-spruce) forest	KU709852
<i>A. inornata</i>	PM141/92 / Norway	Pine forest	KU709853
<i>A. inornata</i>	WeholtO-56562/ Norway	Oak forest	KU709854
<i>A. inornata</i>	FR2014113 / France		KP192661
<i>A. inornata</i>	AH39144 / Spain		KJ680991
<i>A. inornata</i>	AH14204 / Spain		KJ680996
<i>A. inornata</i>	TO AV261012h / Italy		KJ680994
<i>A. polaris</i>	GG215/09 Holotype/ Svalbard	Arctic heath <i>Salix</i> , <i>Dryas</i>	KU709855
<i>A. polaris</i>	GG54/09 / Svalbard	Arctic heath <i>Salix</i> , <i>Dryas</i>	KU709856
<i>A. polaris</i>	SK10-06 / Sweden	<i>Salix</i> , border of rich mire	KU709857
<i>A. polaris</i>	LL000805 / Sweden	<i>Salix</i> bush, at forest road	KU709858
<i>A. polaris</i>	O-64025 / Sweden	<i>Salix</i> bush, at forest road	KU709859
<i>A. polaris</i>	SS920818 / Norway	<i>Salix</i> , bush, litter and naked soil	KU709860

in PAUP* 4.0b12 (Swofford 2003). For inferring phylogenetic relationships among species heuristic searches for the most parsimonious trees were performed using PAUP* (Swofford 2003). All transformations were considered unordered and equally weighted. Gaps were treated as missing data. Heuristic searches with 1,000 random-addition sequence replicates and TBR branch swapping were performed, saving at most 25 trees in each replicate. Relative robustness of clades was assessed by the bootstrap method using 1,000 heuristic search replicates with 100 random taxon addition sequence replicates and TBR branch swapping, the latter saving at most 25 trees in each replicate. In addition a Bayesian analysis was carried out in MrBayes 3.0 (Ronquist and Huelsenbeck 2003), with a best-fit model of nucleotide evolution supplied by MrModeltest 2.2 (Nylander 2004). Eight default-setting Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains

were run for 10 million generations with trees sampled every 5,000 generations and an initial burn-in of 1000 trees. After discarding the trees prior to the burn-in threshold a 50% majority-rule consensus phylogram was computed from the remaining 25.000 trees.

RESULTS

The aligned complete data set consisted of 28 sequences and 1601 characters. After exclusion of ambiguous regions mainly from the beginning and at the end of the data set 1539 characters remained for the analysis. Of these, 1374 were constant, 31 were variable but parsimony uninformative, and 134 were parsimony informative. The maximum parsimony analysis yielded 22.512 equally most parsimonious trees (length = 214 steps, CI = 0.8224, and RI = 0.8995). One of the trees is presented in Figure 1. The tree is presented as a phylogram to show character state changes on branches.

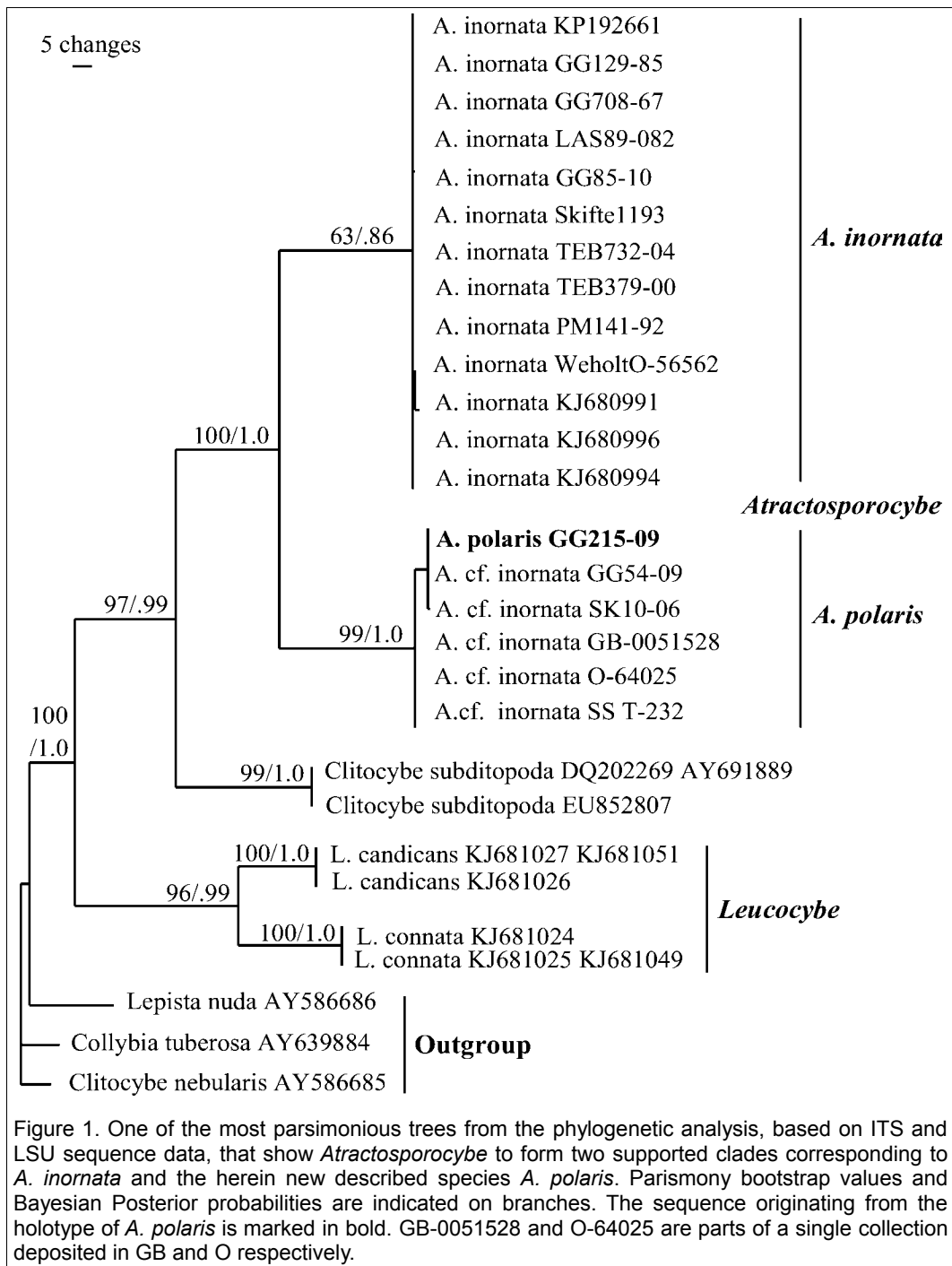




Figure 2. *Atractosporocybe polaris*, holotype, from Svalbard: Nordenskiöld Land, Revneset, GG 215/09 (O-76093). Photo: G. Gulden.

The bootstrap analysis recovered *Leucocybe* (96%), *Clitocybe subditopoda* (99%) and *Atractosporocybe* (100%) as monophyletic clades and with strong bootstrap support. *Atractosporocybe* splits up in two supported clades corresponding to *A. inornata* sensu stricto (63%), and *A. cf. inornata* (99%) with a northern boreal and arctic-alpine distribution. The sequence differences between the two clades are 4 substitutions and one 2 base pair (bp) insertion/deletion event in the ITS1 region, 6 substitutions and one 1 bp insertion/deletion event in the ITS2 region, and one substitution and one 1 pb insertion/deletion event in the first 900 bp of the 5' end of the LSU.

As suggested by MrModeltest, the nucleotide evolution model HKY+G was used for the ITS1 spacer; SYM+I was used for the

5.8S gene; HKY+G was used for the ITS2 spacer; and GTR+I+G was used for the LSU in the Bayesian analysis. The MCMC analysis converged well in advance of the burn-in threshold and chain mixing was found to be satisfactory, as assessed by using Tracer v1.5 (Drummond et al. 2012). In the Bayesian analysis the same clades as in the MP analysis were recovered and Bayesian posterior probability (BPP) is indicated on branches (Figur 1). The Bayesian tree topology was identical to the MP bootstrap tree.



Figure 3. *Atractosporocybe polaris*, holotype, showing watery grey gills and hollow stipe, GG 215/09 (O-76093). Photo: G. Gulden.

Taxonomy

Atractosporocybe polaris Gulden & E.

Larss. sp. nova – Figs. 2 - 5

Mycobank: MB 815967

Type collection: Cap 3.5-4 cm, moderately depressed in central part, margin incurved without or with very faint grooving, smooth, somewhat shiny, faintly innately radially fibrillose with a beige to pale grey brown over all colour, paler, almost ivory in central part, at margin with a cracking, white pruina that lasts for a long time. *Gills* slightly decurrent, moderately crowded, beige to grey brown, in places with darker edge. *Stipe* 3–3.5 × 0.3–0.5 cm, cylindrical, stuffed then somewhat hollow, grey brown like the ground colour of the cap, with longitudinal stripes of pruina, base white

tomentose, with white, branched rhizomorphs. *Flesh* white. *Smell* and taste not noted. Two specimens united at stem base. *Spores* 8–10(–10.5) × 4–4.5 μm, $Av_{40} = 9.0 \times 4.2 \mu\text{m}$, $Q = 2.1\text{--}2.2$, $Q_{av} = 2.1$, fusoid-rhomboid with applanation or shallow depression above apiculus, acyanophilic, inamyloid. *Basidia* 28–36 × 6.5–7 μm, 4-spored, hyaline, without siderophilous granulation. *Hymenophore* regular, of 3–5 μm wide pale brown hyphae. *Cystidia* absent. *Pileipellis* a cutis of radial, ± cylindrical hyphae, 3–12 μm wide, with medium long segments, evenly pale brown from wall pigment and ± brown zebra-incrusted, no pileocystidia. *Stipitipellis* of similar hyphae, caulocystidia absent. *Clamps* large, some as medaillons, abundant in all tissues.

Etymology: From the polar region.

Holotype: Norway: Svalbard: Nordenskiöld Land, Revneset, in *Dryas* and *Salix polaris* heath on calcareous ground, 16. August 2009, leg. G. Gulden and E. Larsson, GG215/09, (Herb. O-76093, GenBank No. KU709855).

General description: based on observations of fresh specimens and herbarium material from Svalbard and northern Scandinavia – Figs. 2 - 6.

Cap 2.5–10 cm, young convex-umbonate with inrolled margin that sometimes is slightly grooved, initially almost white and somewhat shiny from a white, sticky, fully covering pruina, becoming plane to slightly depressed, often with a remaining small central umbo, margin incurved and pubescent for a long time, slightly grooved or not, the pruina cracks and gradually disappears, most persistent at margin, surface often with ± dark spots mainly in central half, also faintly innately radially fibrillose, often appearing ± radially flamed, underneath pruina matt, dry, dark grey brown (T 70, T 51, R 70, N 70, P 70), becoming grey beige to ivory with age (M-L-K 92, 4B3-5B3), not hygrophorous. *Gills* emarginate-decurrent, close, with many lamellulae inserted from margin, thin, up to 7 mm high, easily removable from the flesh, beige to dark grey, dark grey brown, often appearing darker than the cap (M 50, N 70, P 51, R 70, 5C4, f 2, i 4), edge concolorous or in places darker than the sides. *Stipe* 2.5–10 × 0.3–1.1 cm, cylindrical, corticated, young stuffed, becoming hollow and sometimes laterally compressed, fibrillose, white tomentose at base, often with white, branched rhizomorphs, coloured ± like the cap. *Flesh* rather thin in pileus, firm-elastic, whitish, hyaline grey above lamellae and in cortex, pale greyish in cap centre. *Smell* weak, pleasant, slightly farinaceous; *taste* mild to somewhat unpleasant. *Spore deposit* white.

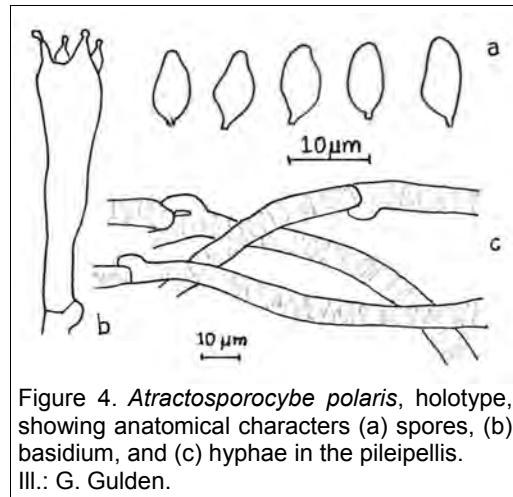


Figure 4. *Atractosporocybe polaris*, holotype, showing anatomical characters (a) spores, (b) basidium, and (c) hyphae in the pileipellis. Ill.: G. Gulden.

Spores 8–11(–12.5) × 3–4.5 µm, $Av_{210} = 9.3 \times 3.9 \mu\text{m}$, $Q = 2.0\text{--}2.9$, $Q_{av} = 2.4$, narrowly rhomboid or fusoid, with suprahilar appplanation-depression, hyaline, acyanophilic, inamyloid. *Basidia* 25–38 × 6–7 µm, 4-spored, hyaline, becoming brown-walled, not siderophilous. *Hymenophoral trama* regular, of 3–8.5 µm wide, almost hyaline to evenly brownish hyphae. *Pileipellis* a cutis of radially repent, cylindrical, 3.5–12 µm wide hyphae with brown zebra-incrustations. Hyphae of *stipitipellis* similar. *Clamps* present at all septa, rather large and sometimes as medallion clamps. *Pigment* membranous and incrusting.

Habit and habitats: More or less caespitose, often in aggregated groups, forming rings, arcs and rows (longest observed row ca. 100 m). On calcareous ground, often on unstable and periodically water soaked soils, almost naked or covered with mosses and lichens, dwarf *Salix*, and herbs and sedges such as *Saxifraga oppositifolia*, *Dryas octopetala*, *Bistorta vivipara*, *Cassiope tetragona*, *Carex misandra*; also found on solifluction lobes together with *Lepista multififormis* (Romell) Gulden.

Distribution: In arctic, subarctic, alpine and northern boreal regions of the northern



Figure 5. *Atractosporocybe polaris*, from Svalbard: Nordenskiöld Land, Revneset, GG 216/09 (O-76094). Photo: G. Gulden.

hemisphere; August. So far known from northern and central Scandinavia and from Svalbard, but is likely to have a broader, northern boreal and circumpolar distribution.

Published photos: Gulden and Jenssen (1988) p. 15 and back cover (as *C. inornata*), Carlsen et al. (2013), p. 44 (as *Clitocybe "polaris"*).

Specimens examined

Atractosporocybe polaris

Norway, Svalbard: Sabine Land: Sassendalen at Gjelhallet, 20. July 1981, G. Gulden, GG128/81 (O); Gjelrabbane, on beach terrace, in the *Dryas-Cassiope* zone, 25. July 1981, G. Gulden, GG198/81 (O). Nordenskiöld Land: Revneset, 16. Aug. 2009, G. Gulden

and E. Larsson, GG216/09 (O-76094) and GG215/09*, HOLOTYPUS (O-76093). Dickson Land: Kapp Wijk, near the cabin, in *Dryas* heath, 6. Aug. 1960, J. Stordal, JS11.686 (O-362406), as *Clitocybe aggregata*; on the plane E of the cabin, 6. Aug. 1960, J. Stordal, JS11.717 (O-362408) as *Clitocybe aggregata*; in *Dryas* and *Cassiope tetragona* tussock, 10. Aug. 1960, J. Stordal, JS11.774 (O-362401) and JS11.786 (O-362407) as *Clitocybe aggregata* (Figure 6); Ekmanfjorden, Coraholmen, 9. Aug. 1960, J. Stordal, JS11.764 (O-362419) as *Clitocybe aggregata*. Oscar II Land: Ny-Ålesund, the close vicinity, 30. July 1960, leg. B. Falkanger and P. Sunding, det. J. Stordal as *Clitocybe aggregata*, (O-362409); at the airfield, 14. Aug. 1988, leg. M. Lange, GG81/88 (O-362418); Lovén

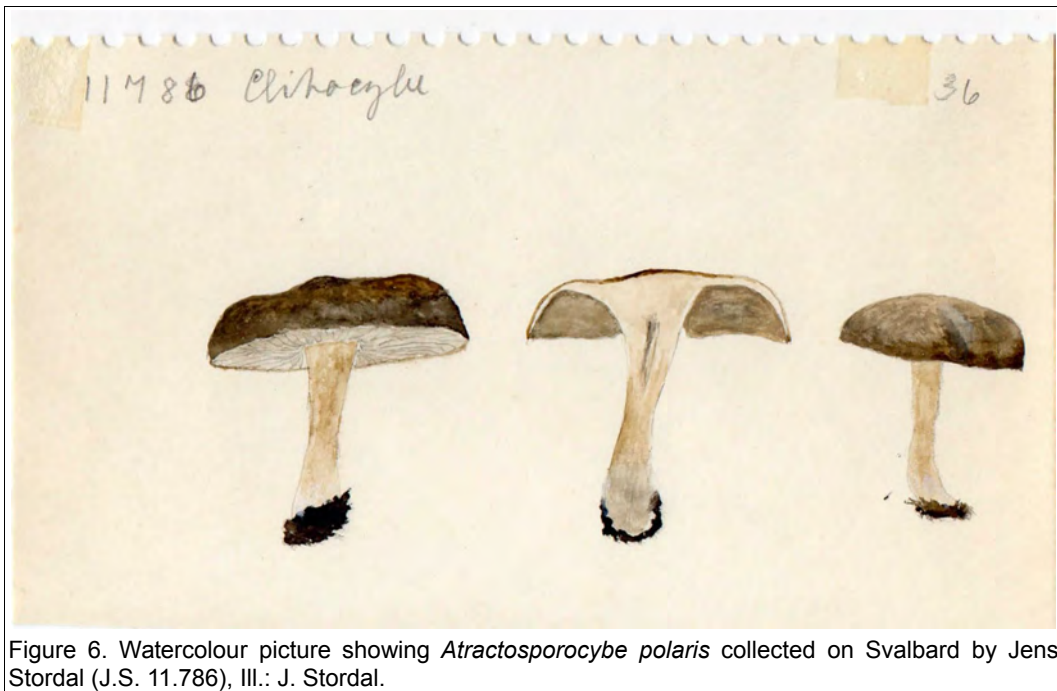


Figure 6. Watercolour picture showing *Atractosporocybe polaris* collected on Svalbard by Jens Stordal (J.S. 11.786), Ill.: J. Stordal.

glacier, at base of bird cliff, 12. Aug. 1988, leg. K.M. Jenssen, GG41/88 (O-195477); Gåsebu, 10–50 m a.s.l., 4. Aug. 2009, G. Gulden and R. Blaaid, GG54/09* (O-76095). Haakon VII Land: Blomstrandhalvøya, in a 10 m long row on solifluction soil among *Dryas* and *Saxifraga oppositifolia*, 5. Aug. 1986, G. Gulden, GG170/86 (O-76096).

Norway, mainland: Troms: Kåfjord, Kåfjorddalen, Oterholmen, 100 m a.s.l., *Alnetum*, 18. Aug. 1992, S. Sivertsen* (TROM F-232).

Sweden: Jämtland: Östersund, ÖSK-reservatet, under small *Salix* bush with litter and naked soil, 5. Aug. 2000, L. Lundberg*, (O-64025 and GB-005 1528, split collection). Lule Lappmark: Jokkmokk, Tuvori, *Salix*, border of rich mire, 24. July 2010, S. Kuoljok, SK10-06* (GB-008 7903).

Atractosporocybe inornata

Norway, mainland: Hedmark: Ringsaker, Stavsjø, pine forest, 5. Sept. 1992, P. Marstad and A. Hov, PM141/92* (O-165090). Oppland:

Lunner, Grindvold, Sløvikelva SE, near the road, spruce-pine forest on calcareous shallow soils, 19. Oct. 2004, T. E. Brandrud, TEB732-04* (O-167050); Østre Toten: S of Kapp, Kile, rich pine(-spruce)forest dominated by *Hylocomium splendens* on calcareous ground, 18. Oct. 2000, T. E. Brandrud, TEB379-00* (O-169038). Buskerud: Hole, Vik, spruce forest, 18. Aug. 1967, G. Gulden, GG708/67* (O-56554); Ringerike, Gullerud, mixed coniferous forest on calcareous ground, 3. Oct. 2010, G. Gulden, GG85/10* (O-294108). Telemark: Bamble, between Langesund and Stadthelle, oak forest on calcareous soil, 26. June 1980, Ø. Weholt* (O-56562); Porsgrunn, Frierflauene, herb rich coniferous forest on calcareous ground, 23. Sept. 1985, G. Gulden, GG129/85* (O-56557). Nordland: Narvik, Skjomen, Klubbvik, 29. Aug. 1981, A. Granmo (TROM F-1319). Tromsø, Tromsdalen, on mossy ground in the forest band (*Betula*), O. Skifte 1193* (TROM F-1318). Finnmark: Porsanger, Iggaldas, Stabbursnes, E-side of

road E6, among grass in deciduous forest, 17. Aug. 1981, G. Mathiassen and A. Granmo 226/81 (TROM F-1317).

Sweden: Västergötland: Götene, Medelplana, ONO Sjöskog, in coniferous forest on calcareous ground, 30. Sept. 1989, leg. L. and A. Stridvall, 89/082-A*, det. L. Stridvall (GB-006 0527).

Notes: The general aspect of *A. polaris* and *A. inornata* is rather much the same. However, the remarkably dark gills, the mostly even cap margin, and a faint smell distinguish *A. polaris*. Also habitat preferences and geographical range help to distinguish the two species. The dark colour, especially of the gills, easily awakes associations to *Lyophyllum*. In at least one collection (GG 280/86) a darkening of the flesh at cap margin and gill edges was observed; we believe the discolouring might be due to prolonged exposure to sunlight. *Atractosporocybe inornata* is generally described with a particular smell (fishy, spicy, or reminding of radish, mice urine, camembert, etc.) and inodorous material has been described as a separate taxon, subsp. *occidentalis* (Bigelow 1982). Smell is a notoriously difficult character to evaluate, especially in cold surroundings where it tends to be faint. In contrast to our observations and annotations with some collections, Lamoure (1972) describes material from *Dryas* habitats in Alpine Sweden and France, most probably of *A. polaris*, with a very characteristic, fishy smell. Rhizomorphs is a feature seen in both of the *Atractosporocybe* species, but the character is often left out in species' descriptions (e.g. Breitenbach and Kränzlin 1999, Bessette et al. 1995, Ludwig 2012) although Harmaja (1969) in his monograph of the genus *Clitocybe* states that they are almost always present. Also in the diagnosis of the new genus *Atractosporocybe* there is no mention of rhizomorphs, a character regarded as taxonomically important in the

genus *Rhizocybe* erected at the same time (Alvarado et al. 2015).

DISCUSSION

In this study we have shown that sequence data of specimens previously determined as *A. inornata* originating in northern regions (arctic-alpine to northern boreal) and southern regions (nemoral to boreal) of Europe form two supported clades. The northern clade is here recognised as *A. polaris* and the southern clade represents *A. inornata* s. str.. The *A. polaris* clade is strongly supported (BT99%, BPP 1.0) while *A. inornata* has got a rather low support value (BT63%, BPP .86) in the analyses. However, the relatively large and unambiguous sequence differences between the two clades, with 10 substitutions and 2 insertion/deletion events in the ITS region, and one substitution and one insertion/deletion event in the first 900 bp of the 5' end of the LSU, together with differences in morphology and distribution range, support the two clades as independent evolutionary lineages.

The arctic-alpine specimens of *A. polaris* occur in heathland and tundra vegetation among mosses and lichens, together with *Dryas*, dwarf *Salix*, *Bistorta*, *Carex* and graminoids, and the two more southern samples of this species from the Scandinavian mainland were collected among *Salix* shrubs and in *Alnus* vegetation. The specimens of *A. inornata* from the nemoral-southern boreal ecosystems in Scandinavia occurred in mixed coniferous forests and in oak (*Quercus*) forests while one specimen was from a birch (*Betula*) forest in North Norway. The four sequences retrieved from GenBank originate from Spain, Italy and France and show *A. inornata* to have a broad geographic distribution in Europe. Both species typically grow on calcareous ground. Interestingly, both *A. polaris* and *A. inornata* occur in the northern boreal region, but here *A. inornata* most probably is restricted to forests in locally warm sites.

In the literature there are some records from northern boreal and arctic-alpine regions of *A. inornata* that probably represent *A. polaris* suggesting *A. polaris* to have a fairly broad northern distribution. The first Scandinavian record of the species seems to be by Lamoure (1972) who reports *C. inornata* from the Abisko mountains in Swedish Lapland. Her material was found in *Dryas* heaths and characterised by dirty grey beige (gris-beige sale) gills, a distinct fish like smell, and spores measuring $8-9 \times 3-3.5 \mu\text{m}$. Lamoure (1972) and Kühner and Lamoure (1986) later on also report alpine material from Arc alpine in Vanoise, France. Schmid-Heckel (1985) describes one collection of *C. inornata* from the northern calcareous Alps in Bayern, Germany, that agrees well with *A. polaris*. He indicates a cap margin without any ribs, gills that are evenly watery grey, and spores measuring $(7-8-9(-10) \times 3-3.5(-4) \mu\text{m}$. Most interestingly, Hallgrímsson (2010) reports *C. inornata* from Iceland, from heathland with ericaceous plants and dwarf shrubs as well as from leaf or needle litter in woodlands. One of the four collections in the herbarium of Akureyri (AMNH) was collected among *Dryas* in a skiing area (Glerárdalur near Akureyri) and another originated from a relatively old larch plantation (Hallormsstaðir). Annotations with the alpine material tell about very small and relatively dark specimens, and that is very much like the Svalbard material in herb. O that was originally identified as *C. aggregata*; a photo of the larch forest material shows a mushroom with pale gills reminiscent of an ordinary *C. inornata*. Both of the *Atractosporocybe* species may thus be present in Iceland and *A. inornata* probably has been introduced with the *Larix*. Material recorded from the arctic zone in Greenland, from Qeqertarsuaq (Godhavn) just S of where the high arctic zone begins (Lamoure et al. 1982), most probably also belongs in *A. polaris* as do records by Karatygin et al. (1999) of *C. inornata* from in Arctic Siberia north of the

tree line (Polar Ural and the Taimyr peninsula). Occurrence of *A. polaris* in North America seems probable but further search is necessary in order to confirm this.

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Psathyrella jacobssonii Örstadius (Basidiomycetes, Agaricales) – new to Norway

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Norsk tittel: *Psathyrella jacobssonii* – ny for Norge

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KEY WORDS

Agaricales, distribution, Norway, *Psathyrella jacobssonii*, sequencing

NØKKLORD

Agaricales, Norge, *Psathyrella jacobssonii*, sekvensering, utbredelse

SAMMENDRAG

Psathyrella jacobssonii ble først publisert fra Sverige i 2001. I Norge ble arten funnet første gang i 2014 og den er så langt ikke kjent utenfor Fennoscandia. Den er her dokumentert fra fire lokaliteter i Norge. Artikkelen gir en beskrivelse av et funn fra Holmvassdalen i Nordland. En oversikt over andre funn i Fennoscandia er inkludert.

ABSTRACT

Psathyrella jacobssonii was first published from Sweden in 2001. In Norway the species was found for the first time in 2014, and it is so far not known outside Fennoscandia. We here record it from four localities in Norway. This paper provides a description of the material from Holmvassdalen in Nordland county, North Norway. A compilation of other finds in Fennoscandia is included.

INTRODUCTION

Very little is known about *Psathyrella* species in Norway; the main information is found in *Funga Nordica* (Knudsen and Vesterholt 2012), in an article by Leif Örstadius (Örstadius 2007) and a recent publication of new species by Örstadius et. al. (2015). In addition one of us (Ø. Weholt) has collected and studied *Psathyrella* species 30 years ago when he had close contact with the Dutch *Psathyrella* expert Kits van Waveren. Unfortunately, the results of the work were not published. However, this has also been a source of inspiration to resume the *Psathyrella* studies, initiated by the later works of Ellen Larsson and Leif Örstadius.

Siw Elin Eidissen and Jostein Lorås have for some years mapped fungi in selected areas in Holmvassdalen nature reserve in Grane municipality in Nordland county, North Norway. The area consists partly of old spruce forest on calcareous soils, with moist shady grooves, springs and rich fens and was protected as a Nature Reserve in 2008. During one of our visits, a species of *Psathyrella* was collected, which after morphological and genetic examinations was identified as *P. jacobssonii*. This species was first described from Sweden in 2001 (Örstadius 2001).

Psathyrella jacobssonii has previously been recorded several times from Finland and Sweden, but not from Norway. In addition to the collection in Holmvassdalen, Weholt has examined collections from four other locations in Norway. The first material was found in Fredrikstad municipality in Østfold county in South Norway in 2014.

In the present work we report *P. jacobssonii* as new to Norway mainly based on examined and sequenced material from Holmvassdalen. A brief overview of its Fennoscandian distribution follows.

MATERIALS AND METHODS

Dried material from Holmvassdalen was observed in 10% NH₄OH using an Olympus CX31 light microscope with phase contrast equipment. The line drawings were made by hand. The material is deposited in the Natural History Museum in Oslo (O).

DNA extraction, PCR amplification and sequencing was performed at Alvalab in Spain. Details about the procedures employed are given in Weholt et al. (2015).

Description

Original description: Örstadius, 2001, Windahlia 24: 15-18:

”*Cap 15-30 mm broad, conico-convex or campanulate, then expanded convex with umbo, at first dark reddish brown, then fading to brown, faintly striate on the marginal area, hygrophorous, drying to pale brown without pink; veil flocculose almost to centre, evanescent. Gills adnate, medium spaced, pale brown in young specimens, dark brown at maturity with white edge. Stem 50-100 x 1-3 mm, with an up to 10 mm long pseudorrhiza, stiff, pale brown, pulverulent at apex, flocculose-fibrillose downwards. Smell indistinctive to unpleasant. Taste mild.*”

”*Spores 10.5-13 x 6-7 μm, av. 11.1-12.4 x 6.1-6.6 μm, Qav. = 1.8-1.9, oblong, narrowly ovoid, subcylindrical, in profile flattened on adaxial side, sometimes narrowly amygdaliform, in water dark red (Mu. 10R 3/6, 2.5YR 4/8); germ pore distinct. Basidia 4-spored, 18-38 x 10-11 μm. Pleurocystidia 35-70 x 11-22 μm, rather numerous, lageniform, fusiform, upper part sometimes rostrate or*

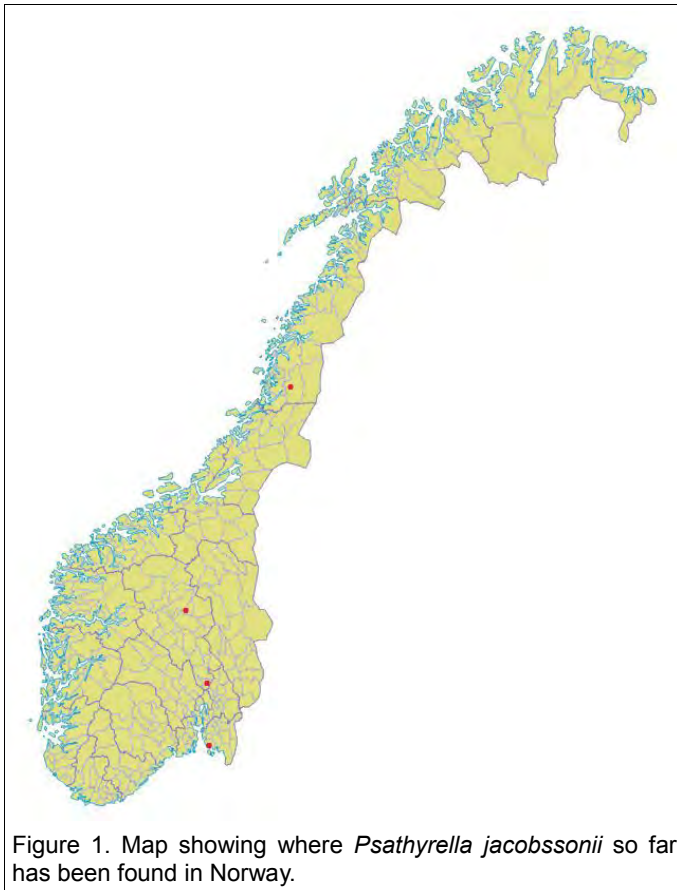
forked; walls pale or sometimes yellow. Cheilocystidia of two types: A: 25-70 x 7-17 μm, lageniform, fusiform, rarely capitate, abundant, B: clavate, not dominating; gill edge and cystidia in fresh specimens covered with drops staining green in a solution of ammonia. Caulocystidia seen at upper part of stem. Pileipellis a hymeniderm of 20-50 μm wide cells, pale; pileitrama of coarsely incrustated hyphae. Veil cells 20-130 x 4-20 μm, cylindrical-inflated, hyaline to yellow. Clamps present.”

”*Habitat and distribution: Solitary to caespitose in moist herb-rich forest, on soil, in leaves, in Sphagnum or among other mosses, “margin of eutrophic fen and forest near Picea abies, Betula and Salix” (Jukka Vauras pers. comm.). August – September*”

Norwegian material examined

Specimens examined: Norway, Østfold: Fredrikstad, Zinkvalseverket, among grass in old orchard, 21. Sept. 2014, leg. M. Pettersen, (O); Torp bruk, boggy, with *Salix, Alnus*, 30. Sept. 2014, leg. M. Pettersen (O); Oppland: Lunner, Myrabakken NE, north of Brovollveien, boggy, not in *Sphagnum*, 15. Aug. 2015, leg. Ø. Weholt 20 -15 (O); Sør-Fron, Gålå, Håkåsæterdalen, in *Sphagnum* in eutrophic fen, 16. Aug. 2015, leg. Ø. Weholt 21-15 (O). Nordland: Grane, Holmvassdalen Nature Reserve, in moss near a small pond in a moist shady groove, surrounded by old spruce-dominated, calcareous forests 19. Sept. 2015, leg. J. Lorås and S. E. Eidissen JL4-15 (O).

The following information is based on the specimens from Holmvassdalen – Figs. 1-4. The material from Holmvassdalen was found in moss near a small pond in a moist shady groove, surrounded by old spruce-dominated, calcareous forests. Several specimens (about 12-15) grew close together (caespitose) in a



tussock. A stream has gradually dug out the groove and produces a relatively constant humid microclimate. In September 2015 the pH value obtained from a soil sample taken beneath the moss layer was around 7. A few meters away, the very rare species *Entoloma graphitipes*, was found as new to northern Europe (Weholt et al. 2015).

Macroscopy

Two specimens were collected and examined. Pileus is 25-30 mm broad, with conical shape and umbo, reddish brown, striate margin, veil white flocculose. Lamellae rather crowded, adnate, dark brown with white edge. Stipe up to 110 x 3 mm, white, flocculose, with pseudorhiza.

Microscopy (dried material)

Spores 9.8-12.2 x 5.5-7.1 μm , average 11.0 x 6.2 μm (n = 50), germ pore central, distinct, Qav = 1.75, basidia 17-25 x 10-14 μm , pleurocystidia numerous, with acute apex, some few rostrate-forked, 40-60 x 12-15 μm , cheilocystidia 38-55 x 11-17 μm , gill edge homogenous, with acute apex, with pale green deposits in ammonia, clavate cheilocystidia scarce, clamps present.

Molecular identification

Results showed a 99% similarity in the ITS region with the holotype of *P. jacobssonii* (GenBank accession no. KC992855).

DISCUSSION

The species can be recognized by the copious veil, stem with more or less pronounced pseudorrhiza, green staining gill edge, abundant cheilocystidia, large spores, and moist habitat. Morphologically, it comes close to *P. microrhiza* from which it differs in the green staining gill edge and the more copious veil covering almost the whole cap when young. Moreover, the cheilocystidia are slightly longer. In the system of Kits van Waveren (1985) the species is placed in subgenus *Psathyrella* section *Psathyrella*. Phylogenetically *P. jacobssonii* is closely related to *P. sublatispora* that differs in having smaller spores, a scanty veil, and a dry habitat.

In the Nordic countries the five species *P. jacobssonii*, *P. lutensis*, *P. multipedata*, *P. supernula*, and *P. silvestris* (now *Cystoagaricus silvestris* (Gillet) Örstadius & E. Larss.) have gill edge and cystidia staining green drops in a 10 % solution of ammonia. The reaction



Figure 2. Habitat of *Psathyrella jacobssonii* in Holmvassdalen. Photo: J. Lorås.

varies from distinct to faint. The drops and reaction disappear gradually when the basidiomata are dried and fail to come by old herbarium material. The newly described *Psathyrella conferta* Eyssart. & Chiaffi from France also belongs to the group (Eyssartier 2004) and from America and Japan further six species are known (Hoashi 2008). The gill edge of *P. fusca* is covered with drops, but these drops are remaining colourless in a solution of ammonia.

The *Psathyrella* material from Holmvassdalen, as well as that of the two collections from Lunner and Sør-Fron, turned out to be *P. jacobssonii*, confirmed from genetic analyses in the ITS region. The material of the two collections from Fredrikstad was originally identified as *P. corrugis*/*P. microrrhiza*, but since, on re-examination, we found that the

cheilocystidia exhibited distinct greenish mucoid deposits in NH_4OH and all other characters agreed well with the newly described *P. jacobssonii*, we are convinced they represent this species.

Macroscopically all the Norwegian collections agree well with the original description of *P. jacobssonii*: pileus with dark red brown colour, the copious pileus velum, especially by young basidiomata, and the stem with pseudorrhiza. Microscopically, the cystidia with green deposits were evident in the material from Holmvassdalen and one of the collections from Sør-Fron (ØW 21-15). A positive reaction was not observed in the collection from Lunner (ØW 20-15), despite that this time fresh material was studied. Except from this, they were not possible to distinguish from each other. The genetic analy-

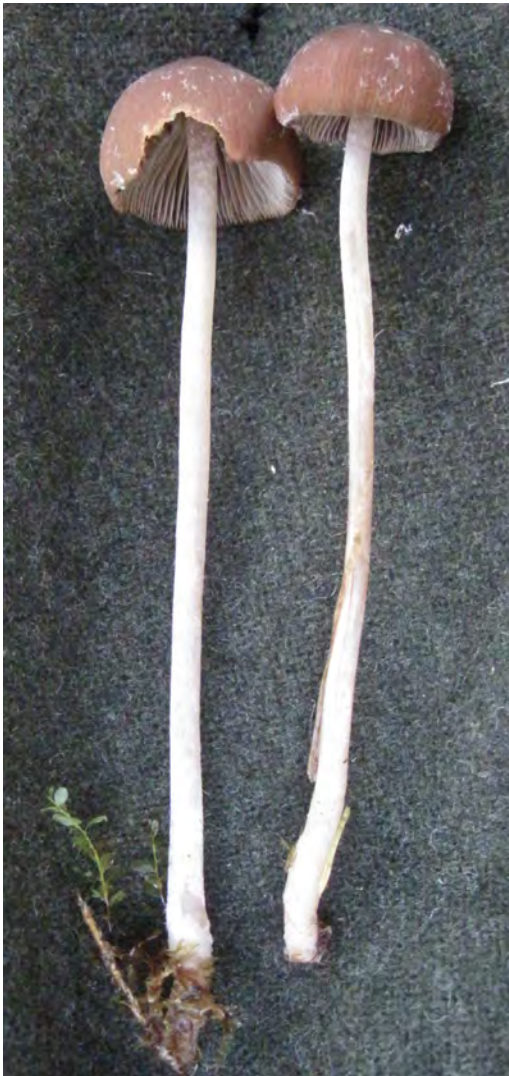


Figure 3. Two specimens of *Psathyrella jacobssonii* from Holmvassdalen. Photo: J. Lorås.

sis, however, demonstrated they had identical sequences in the ITS region. This shows that it sometimes can be difficult with certainty to identify *P. jacobssonii* morphologically, and that molecular assistance is necessary for a safe identification.

The compiled spore measurements of the Norwegian finds were in the range 9.8-13.0 x 5.5-7.2 μm , average (n = 50) 11.0-12.0 x 6.0-

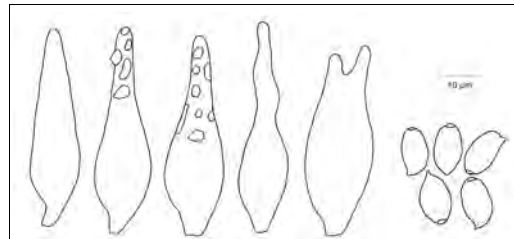


Figure 4. Cystidia and spores of *Psathyrella jacobssonii* from Holmvassdalen. III. Ø. Weholt and S. E. Eidissen.

6.6 μm , $Q_{av} = 1.75-1.9$. The collection from Holmvassdalen was in the lower range, with spores somewhat shorter than in the other collections and the type material.

All collections were found in distinctly moist sites, except one of the Fredrikstad collections that was found among grass in an orchard.

DISTRIBUTION

Until 2014, *P. jacobssonii* was only reported from Finland and Sweden. One of us (L. Örstadius) who has studied more than 100 *Psathyrella* collections from Iceland recalls that material of some of the collections reminded of *P. jacobssonii*. However, a safe reference of these collections to *P. jacobssonii* is not possible without sequencing. Hence, for the present the known distribution of *P. jacobssonii* is restricted to Fennoscandia.

More than 100 psathyrelloid species occur in Europe, some of them with a restricted distribution. *Psathyrella jacobssonii*, *P. boreifasciculata*, and *P. squamosa* are so far only known from the Nordic countries.

Collections examined by Leif Örstadius: Finland: Keski-Pohjanmaa. Raahe, Saloinen, SE. of Ryttilampi, 30.VIII.1995, S. Jakobsson (herb. Jakobsson 1321), 4.IX.1995, Jakobsson & Särkkä (herb. Jakobsson 1406), 20.IX.1996, Jakobsson & Risunen (herb. Jakobsson 2114); Koillismaa. Kuusamo, Juuma, Jäkälävuoma, 25.VIII.1978, Sjöblom & Albrecht (TURA); Mountain ridge Valtavaara, 26.VIII.1978, G.

Gulden 174/78 (O, as *Psathyrella* sp.); Perä-Pohjanmaa. Rovaniemi, Meltaus, "Kenkäkorpi", 23.VIII.1999, J. Vauras 15337F (TURA 8634); Pohjois-Savo. Kuopio, Pitkälähti, E. side of Matkusjärvi, 3.IX.1989, J. Vauras 3772 (TURA); Varsinais-Suomi. Karkkila, Haavisto, 7.IX.1995, J. Vauras 10700F (TURA). Sweden: Medelpad. Borgsjö, Julåsen, 31.VIII.1989, C. Eriksson (herb. LÖ 256-89); Uppland. Vänge, Fiby urskog, 8.IX.1994, I. Kytövuori (herb. LÖ 45-94); Västergötland. Timmele, Blanke-red, 15.IX.1992, Toresson & Örstadius (GB holotype; S isotype); Västmanland. Ramnäs, Kolfallsudden, 5.IX.2013, L. Bsenko (dubl. in herb. LÖ-233-13).

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The genus *Boubovia* (Velen.) Svrček in Norway

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Norsk tittel: Slekten *Boubovia* (Velen.) Svrček i Norge

Kristiansen R, 2016. The genus *Boubovia* (Velen.) Svrček in Norway. *Agarica* 2016, vol. 37: 51-65.

KEYWORDS

Ascomycota, Pezizales, Pyronemataceae, *Boubovia*, *luteola*, *vermiphila*, *ovalispora*

NØKKELOD

Ascomycota, Pezizales, Pyronemataceae, *Boubovia*, *luteola*, *vermiphila*, *ovalispora*

SAMMENDRAG

Forfatteren beskriver tre arter i slekten *Boubovia* (Velen.) Svrček fra Norge, med spesiell vekt på deres opptreden og økologi. Dette er observasjoner og data innsamlet av forfatteren over en periode på 30 år. Andre potensielle *Boubovia*-arter er antydnet.

ABSTRACT

The author describes three species in the genus *Boubovia* (Velen.) Svrček from Norway with emphasis on their appearance and ecology. This is observations and collecting of data over a period of 30 years. Other potential *Boubovia* species are indicated.

INTRODUCTION

The genus *Boubovia* was erected by Svrček (1977) based on Velenovsky's *Humaria luteola* (Velenovsky 1934) from Bohemia in the Czech Republic. Less than 15 years ago the genus *Boubovia* was monotypic within Pyronemataceae (Pezizales). However, van Brummelen

and Kristiansen (1999) described a new species, *Boubovia vermiphila* from the Hvaler archipelago in Østfold County, SE Norway. About simultaneously Yao and Spooner (1998) transferred several species with ellipsoid spores, previously placed in *Pulvinula*, in to *Boubovia* including the two species *Pulvinula ascoboloides* (Korf and Zhuang 1984) from China and *Pulvinula subprolata* (Korf and Zhuang 1991) from Tenerife, Canary Islands. Another ellipsoid *Pulvinula* is *P. ovalispora* described by Boudier (1917), and examined by Pfister (1976) and Korf and Zhuang (1984) probably also belongs to *Boubovia*. Yao and Spooner (loc.cit.) suggested that *P.ovalispora* may be conspecific with their *Boubovia nicholsonii*, described by Masee (1901) as *Humaria nicholsonii*, being an older species epithet. The type of *P.ovalispora* need to be re-evaluated, but the type-material is very scanty according to Korf and Zhuang (1984). However, Perry et al. (2007) showed in their phylogenetic study of Pyronemataceae that *Boubovia luteola* and *Pulvinula ovalispora* are strongly supported sister taxa. Then Hansen et al. (2013) further confirmed by phylogenetic analyses that *Boubovia nicholsonii* (as *Pulvinula ovalispora*) belongs within *Boubovia*, which formed a strongly supported group with the type species *Boubovia luteola*. It also showed for the first time that *Boubovia* is closely related to *Coprotus* and Ascodesmidaceae.

Today *Boubovia* comprises six species, but if we consider *Pulvinula ovalispora* conspecific with *Boubovia nicholsonii* it is only five.

Boubovia luteola (Velen.) Svrček in Norway
B. vermiphila van Brummelen and Kristiansen in Norway (type)
B. ascoboloides (Korf & Zhuang) Yao & Spooner

B. subprolata (Korf & Zhuang) Yao & Spooner
B. nicholsonii (Masseé) Spooner & Yao
B. ovalispora (Boudier) anon ined. = *B. nicholsonii*? in Norway

Lindemann et al. (2015) recently erected the new genus *Pseudoboubovia*, for the species *Kotlabaea benkertii* (Peric 2012) previously placed in *Kotlabaea*. Their phylogenetic analyses show that *K. benkertii* is close to the *Boubovia* lineage, which cover *B. luteola*, *B. nicholsonii* and *B. ovalispora*. Based on their observations they proposed *Pseudoboubovia benkertii* (Peric) Lindemann U, Vega M, Peric B. & Tena R. comb. nov. To discuss the characters and relationship to *Boubovia* is outside the scope of this article due to lack of phylogenetic data.

Norwegian records of species of the *Boubovia* are described, with emphasizes on their ecology. All photographs and illustrations are provided by the author, except for the scanning electron micrographs.

MATERIALS AND METHODS

All samples were originally examined on living material in different reagents, as Cotton blue in lactic acid, methyl blue, 3% KOH, Melzer's reagent, water on squashed mounts, and slices cut by a razor blade. Some examinations were also done on dried material soaked in water over night.

History

As already pointed out *Boubovia luteola* was originally described as *Humaria luteola* by Velenovsky (1934), and the diagnosis read as follows:

"*H. luteola* sp.n. Ap. 3-4 mm, solitaria, tota citrina, basi angustata sessila, glabra, discina, integra, crasse carnosa. As. 100 x 12-16, basi modice attenuati, apice angustati et truncati, par; simpl. flif., apice nondilatatae, sed spiraliter contortae. Sp. 25-28, ellipticae, laeves, guttulis 3-5 donatae, monostichae."

Ad humum silvaticum subfoliis marcidis humidis in silva umbrosa prope Bubova (Kalstejn) maio 1924. – Species mirabilis, facie Helotium revocans. As. jodo lutei."

Figure 1. Velenovsky's table XXVI, 18.

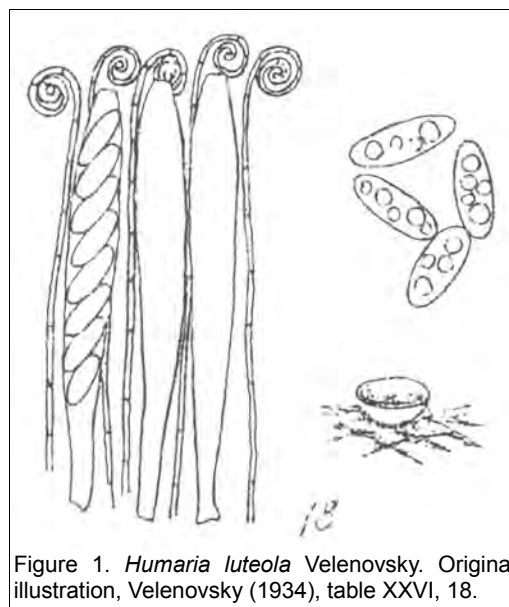


Figure 1. *Humaria luteola* Velenovsky. Original illustration, Velenovsky (1934), table XXVI, 18.

Then Svrček (1977, 1979) erected a new genus based on the specific characters, and the diagnosis read as follows:

"*Apothecia minuta vel mediocria, sessilia, concava, discina, crasse carnosa, margine integro, nuda, luteo-colorata. Excipulum ectale medullareque textura globulosa vel subglobulosa, cellulis ecoloratis, parietibus haud incrassatis. Asci cylindranei, non amyloidei, octospori. Paraphyses tenuiter filiformes, apice non dilatatae, conspecte curvatae et spiraliter contortae. Ascospores ellipsoideae, verrucosae, hyalinae.*"

Hab. ad terram.

Etymol. Boubová = hospitium ad marginem silvae prope pagum Bubovice, non procul Karlštejn (Bohemiae centralis), ubi J. Velenovský specimen suam. *Humaria luteola* Velen. legit.

Species typica generis (adhuc unica nota): *Boubovia luteola* (Velen) Svrček, comb.nov.

– Basionymum: *Humaria luteola* Velenovský. Mon. Disc. Boh. p. 227, tab. 26, fig.18, 1934 (PRM 149745, holotypus).

Figure 2. Svrček 1979, Table V.

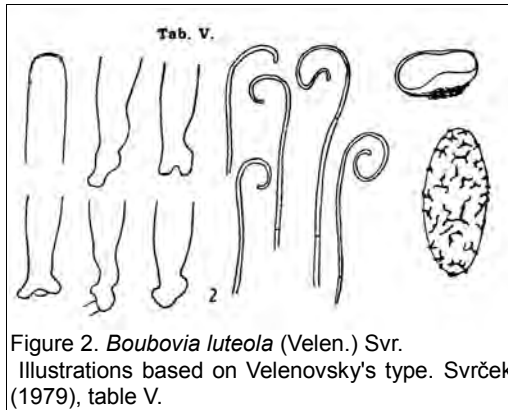


Figure 2. *Boubovia luteola* (Velen.) Svr. Illustrations based on Velenovsky's type. Svrček (1979), table V.

In Svrček (1979) the type material consists of only two apothecia, and there are no additional records in the Czech Republic.

Yao & Spooner (loc. cit.) proposed that the ellipsoid species of *Pulvinula* would better fit in to *Boubovia* based on their microscopical characters, like forked ascus base and apically curved to spirally curled paraphyses, ascus wall thickened in the early stages of development contrary to other species with globose spores, and asci, which remain thin walled throughout development.

DESCRIPTIONS

Boubovia luteola (Velen.) Svrček

Figs. 3, 4, 5a, 5b, 6, 7.

Basionym

Humaria luteola Vel. Mon. Disc. Bohm. 1934.

The first finding was, as noted before done by Velenovsky in the Czech Republic 1924, but first described by him ten years later (Velenovsky 1934). However, Svrček (1979) revised Velenovsky's collection of discomycetes in the herbarium of the National museum in Prague, and erected the new genus *Boubovia* based on the specific characters.

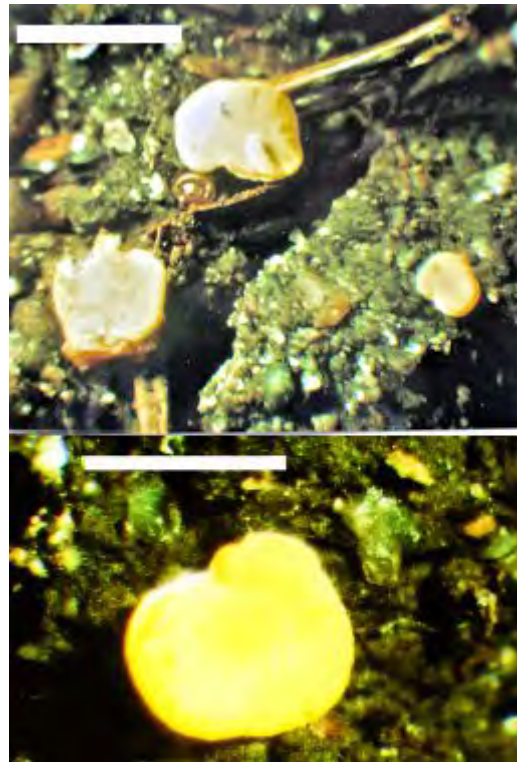


Figure 3. *Boudiera luteola* (Velen.) Svr. Torp, Fredrikstad. Scale bar 2 mm.

Apothecia shallowly cupulate, turbinate to plane discoid, sessile, 1-3 mm diameter, lemon yellow to pale yellow. Outside slightly pruinose. Outer and medium excipulum indistinct, consisting of globose to ellipsoid cells 10-20 μm in diameter, thin-celled, hyaline. Protruding asci at maturity.

Asci 8-spored, subcylindric, 140-180 x 12-18 μm , with a short bifurcate base.

Ascospores, one or two seriate, oblong ellipsoid, 19-22 x 8-9 μm without ornamentation, with 3-5 oil drops (fresh material), deBary-bubbles frequently seen; ornamented with irregular elongated veins and warts, 1.5-3.0 μm long and 0.6-0.8 μm broad and high. Ornamentation soluble in 3% KOH.

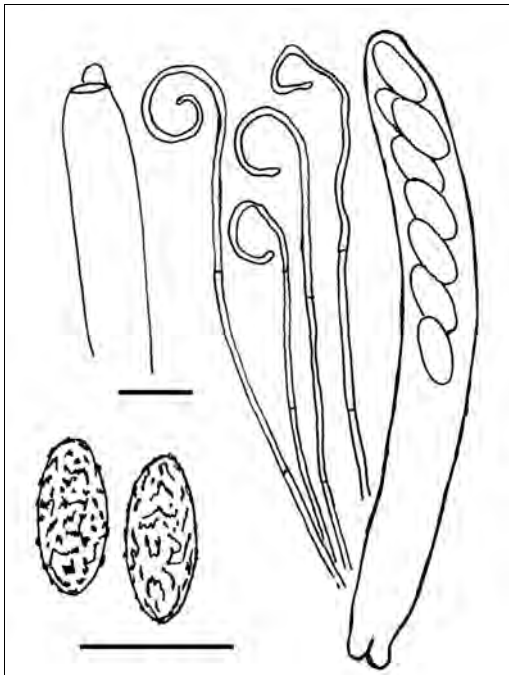


Figure 4. *Boubovia luteola*, Torp, Fredrikstad. Asci, paraphyses, spores in asci, and ascospores. Scale bar a. 15 μ m b. 20 μ m.

Paraphyses filiforme, 1.5-2.0 μ m thick, septated, unbranched, distinctly spirally curled apically.

The first finding in Norway was by Sigmund Sivertsen (Vitenskapsmuseet, NTNU, Trondheim) in Rana, Nordland county 4. September 1975. This find was included in the work by Kristiansen & Schumacher (1993), where also the first finding in Østfold county was described, done 5. July 1982 on pollutant ground introduced by man, at the village Torp, between Fredrikstad and Sarpsborg, at the eastern side of the Glomma river.

Material examined

Østfold, Fredrikstad, Borge, Torp, just south of the closed paper mill where large deposits of lime (pH 7.5) are stored, which have created a habitat for a large number of discomycetes over the years. 59° 14' 27.01" N, 11° 0'30.17" E.

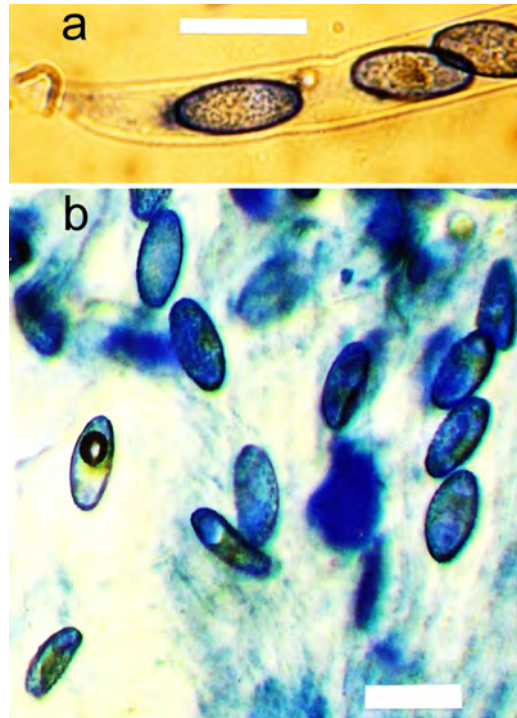


Figure 5. *Boubovia luteola*, Torp, Fredrikstad. a. spores in asci in Cotton blue. Scale bar 20 μ m. b. spores in Cotton blue. To the left with deBary-bubbles. Scale bar 20 μ m.

5., 10., 16. and 31. July 1982 (RK 82.156) (O); ibid.11. June 1983 (O); ibid. 4. July 1983 (RK 83.136) O; duplicates in C, TRH, CUP, PRM and LPS; ibid. 3. July 1983 (RK 83.172).

Østfold, Hvaler, Kirkøy, Ørdal, close to main road 501, in a ditch among tussocks and mosses, *Equisetum* sp., with sticks and branches from the surrounding *Alnus incana*, *Populus tremula*,



Figure 6. *Boubovia luteola*, Torp Fredrikstad. Thin section of apothecium. Field of view 2 mm.

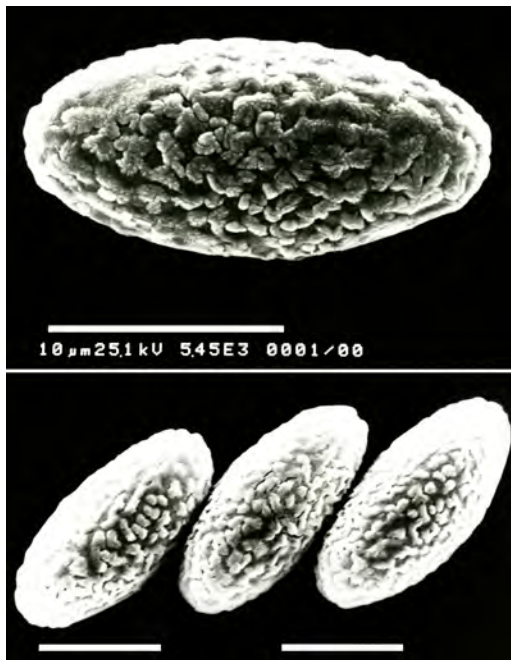


Figure 7. *Boubovia luteola*, Torp, Fredrikstad. Scanning electron micrography. Scale bar 10 μ m.

Corylus avellana and *Ulmus glabra*, close to a planted field of young spruces. On humid argillaceous soil (pH 7.1) 59° 3' 4.03" N 11° 0' 58.70" E. , 3. July 1983 (RK 83.172) (O); Østfold, Hvaler, Kirkøy, Botne, Hyttekasabakken, close to a track to Botneveten (73 m a.s.l.) on black mold soil (pH 7.6) in spruce wood. 59° 3' 32.49" N, 11° 3' 24.60" E. 4. and 10. October 1992 (RK 92.57) (O); *ibid.* 22. August 1993 (RK 93.26); *ibid.* 6. September 1994 (RK 94.05); *ibid.* 1. October 1995; (RK 95.74); *ibid.* 8. August 1998 (RK 98.98); *ibid.* 20. September 1998 (RK 98.154).

Comments

Unfortunately, the two pristine locations for *Boubovia luteola* at Kirkøy in the Hvaler archipelago is now completely damaged, even the locality in calcareous spruce forest (*Picea alba*), a rather rare nature type in the county of Østfold, where the bedrock mostly consists of granites and gneisses, and calciphile areas

are only found on old marine sediments, shell beds or materials introduced by man.

Ecological notes

The locality at Torp, where I first found *Boubovia luteola* is an area of ca. 2 hektar (ha), with introduced materials, a mixture of calcium carbonate, muddy lime-stone, gypsum and sodium salts. Thousands of tons of this waste product from a nearby closed (1972) papermill were dumped here over a period of more than 50 years. Today the area has the shape of a crater with a small lake in the bottom (Figure 8).

This place has been a "goldmine" for operculate discomycetes with over 70 different species. The vegetation is rather sparse and the ground floor consists mainly of mosses and tussocks intermixed with *Tussilago farfara*, shaded by *Salix-Alnus* vegetation, and *Betula pubescens*.

The numbers of other discomycetes are extensive, like *Marcellina pseudoanthracina*



Figure 8. Overview of the deposit of muddy limestone at Torp (grey area). Locality for *Boubovia luteola* and *Boubovia ovalispora*. Scale bar 50 m.

and *M. personii* (Moravec 1989, Hansen et al. 2005), large populations of *Chalazium helveticum* (Kristiansen 1991), *Tricharina ascophanoides* and its anamorph (Kristiansen 2014, Yang and Kristiansen 1989), *Octospora wrightii* (Kristiansen 1985), *Helvella pezizoides*, *Peziza ampelina* (Kristiansen (1982), *Peziza subisabellina* (Hansen 2001, Wergeland Krog 1997) and others, including a few hypogeous fungi. Agaricales are less common in this environment.

In 2016 the owner started looking at opportunities to use the area for residential purposes, implying that this nationally important location is threatened. However, a dialogue with the owner and authorities is initiated with the aim to secure the location for the future.

***Boubovia vermiphila* v. Brumm. & R. Krist.**

Figs. 9, 10, 11, 12, 13, 14, 15, 16a, 16b.

This species was first recognized July 1983, and was later collected in 1989, 1990, 1992, 1993, and 1998. Even though the spot is located in a very shaded area this tiny fungus dry out easily, and it was not found in the intervening years. The small size (< 1 mm) and the hyaline colour make it difficult to distinguish the fruitbodies from tiny quartz grains or shell pieces, and in the field it is hard to separate it from the associated *Chalazium sociabile*. It is not collected, so far, in the 21. century, but the locality is less visited in the last 15 years. As a type locality (Figure 16), and the only known locality for the species worldwide, I have pointed out the necessity to protect the place against all kinds of intervention (Kristiansen 2000), like cutting of trees, expansion of the road etc.

Because of the unique characters this minute fungi was a puzzle in the beginning and difficult to place, although somewhat reminiscent of *Boubovia luteola*, like the special curled paraphyses, the less developed excipulum and ascospores. These types of

paraphyses also appears in *Pulvinula*, and I had almost at the same time found *Pulvinula ovalispora*, which have many characters like a *Boubovia*, but – with the exception of *P. ovalispora* – have spherical ascospores.

At an early stage a collection was sent to Professor Richard P. Korf at the Cornell University, Ithaca, who became very interested and replied with a number of comments, like, quote: “Your “*Boubovia* sp. 2” with the spores heavily marked and many with polar caps of cyanophilic material has us somewhat puzzled. In

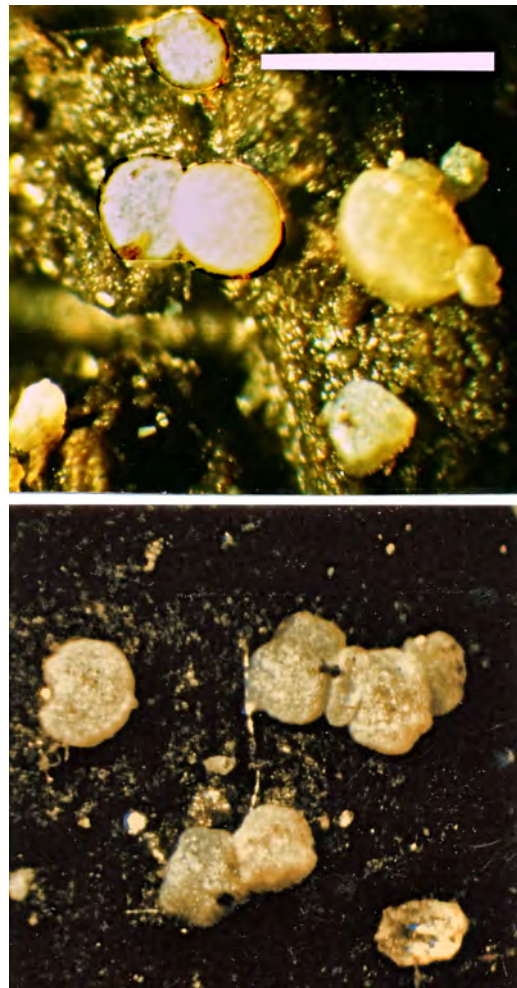


Figure 9. Apothecia of *Boubovia vermiphila*, Kirkøy, Hvaler. Scale bar 1 mm.

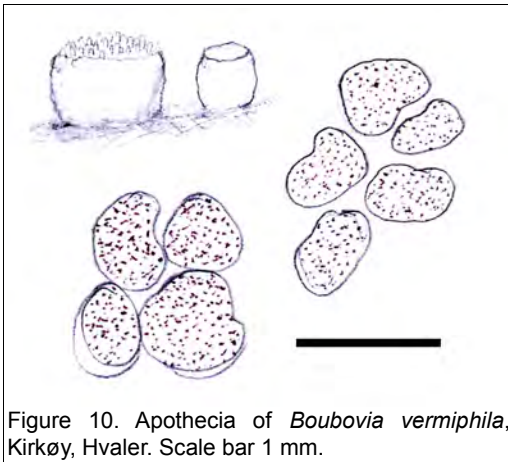


Figure 10. Apothecia of *Boubovia vermiphila*, Kirkøy, Hvaler. Scale bar 1 mm.

some ways the markings look rather like those of *P. (ulvinula) ascoboloides*, but you never has the spore sheath loosening as ours does, and we lack the obvious isolated warts that are so prominent in your species ... I have never seen anything else like it before! ... could well be a species of *Pulvinula*, related to *P. ascoboloides*. ... then possibly your species and *Pascoboloides* deserve a genus of their own?" (pers. comm. 9. August 1984).

Meanwhile, curator Sigmund Sivertsen at Vitenskapsmuseet (NTNU) had examined the fungus as well (1988), and his conclusion was that it is very close and related to *Pulvinula*

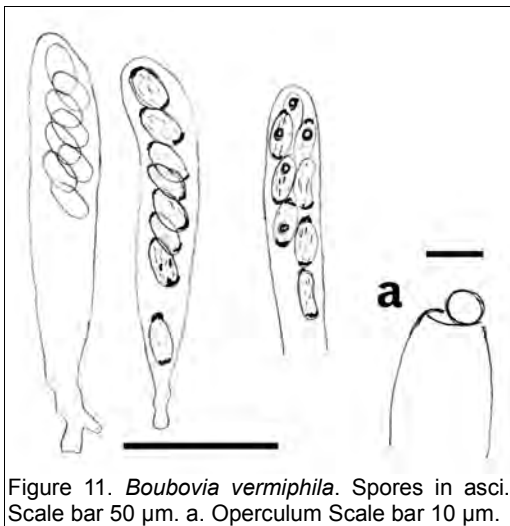


Figure 11. *Boubovia vermiphila*. Spores in asci. Scale bar 50 µm. a. Operculum Scale bar 10 µm.

ascoboloides as described by Korf and Zhuang (1984), – an opinion independent of Korf's statement 1984.

Several years later with still unsolved problems I consulted Dr. J. van Brummelen at the Rijksherbarium in Leiden, which was the start of a close correspondence on this unique discomycete. Quote: "I was astonished by the combination of characters. Although there are characters suggesting a relation with *Pulvinula*, e.g. the very thin, curved paraphysis, there are others, not fitting well with such a position, e.g. the large, clavate, mature asci, the ornamented ascospores, and the probably coprophilous habitat. I have never seen anything like this and would not hesitate to publish it as a new species and probably also a new genus." (pers. comm. 24. July 1990).

Years passed by, but in 1999 the first concept was ready, and van Brummelen wrote, quote:

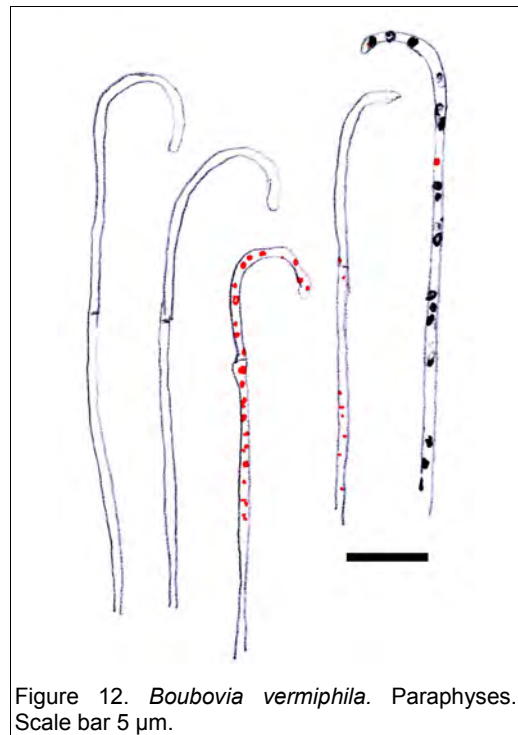


Figure 12. *Boubovia vermiphila*. Paraphyses. Scale bar 5 µm.

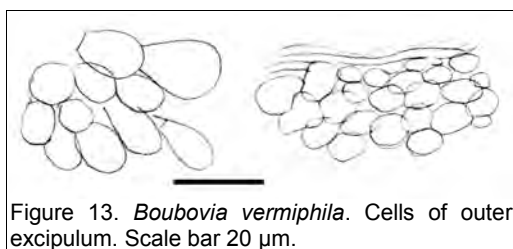


Figure 13. *Boubovia vermiphila*. Cells of outer excipulum. Scale bar 20 μ m.

“Rather long I felt somewhat uncertain about the taxonomic position of this species. The material was very delicate and rather brittle. So it was good you made so many drawings and photographs. ... Now I am convinced that the best place is in *Boubovia*. There are too few good differential characters to create a new genus for this species.”

The final description was published in 1999 (van Brummelen and Kristiansen 1999).

Apothecia solitary or in small groups, or caespitose, sessile, 0.2-0.5 (1.0) mm diam., up to 0.5 mm high. Receptacle first subglobular, cylindric to barrel-shaped, becoming pulvinate, smooth, whitish-hyaline; yellowish on drying. Rather fragile, margin not differentiated. Disc flat to convex, roughening by protruding asci, hyaline. Not with carotenes.

Hymenium 150 – 160 μ m thick. Outer cells of globular and subglobular thin-walled cells 10-25 x 6-20 μ m, without hairs or hyphae.

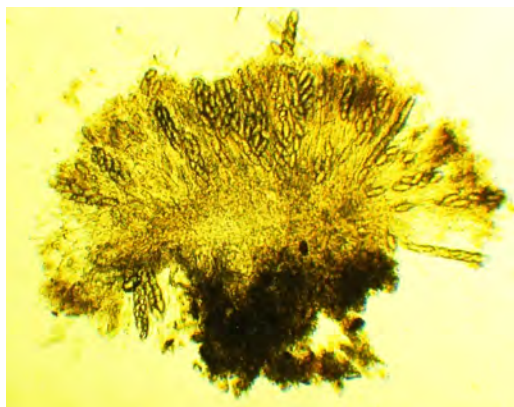


Figure 14. *Boubovia vermiphila*. Thin section of apothecium. Field of view, 1 mm.



Figure 15. *Boubovia vermiphila*. Scanning electron micrography. Scale bar 10 μ m.

Asci broadly clavate, attenuated at base, rounded above, with a large operculum, 8 μ m across. 130-160 x 20-26 μ m, 8-spored, but sometimes with only some spores developed.

Ascospores, uni- or biseriata, ellipsoid, 18-20 (22) x 9-11 μ m (without ornamentation) with one or two oil globules, ornamented with large small irregularly shaped warts staining with methyl blue, and usually with large apical caps. The ornamentation is soluble in 3% KOH, first the warts then the caps.

Paraphyses frequent, septate, filiform, rarely branched, hyaline 2.0-2.5 μ m thick with strongly spirally curved, not enlarged ends, containing small colourless vacuoles and granules staining red in Meltzer reagent.

Material examined

Østfold, Hvaler community, Kirkøy, close to Putten farm, roadside at mainroad 501 (Figure 16 A & B) sheltered by dense vegetation of deciduous wood, on black calcareous soil mixed with excrements of earthworms, and associated with *Chalazion sociabile* and *Ascobolous denudatus*, 18. and 22. July 1983 (RK 83.145 & RK 83.155) (L); *ibid.* 12. and 17. July 1989 (RK 89.18), holotype (L), isotype (O) (TRH); *ibid.* 19. and 24. June 1990 (RK 90.15) (L); *ibid.* 27. August 1992 (RK 92.10); *ibid.* 22. June 1993 (RK 93.12);



Figure 16. Type locality of *Boubovia vermiphila*, Putten, Kirkøy, Hvaler archipelago. A. early spring, B. summer.

ibid. 13.June 1998 (RK 98.30) (L); ibid. 6. July 1998 (RK 98.45).

Ecological notes

The ground floor consists of damp black soil, pH 8.0-8.3, mixed with tiny crushed fragments of seashells, and the fungi was found growing on the rounded surface and in the crevices of worm casts often covered by fallen leaves of *Populus tremula*. The area is densely shaded by *Populus tremula*, *Ulmus glabra*, *Quercus glabra*, *Prunus spinosa*, *Berberis vulgaris*, *Malus silvestris*, *Fraxinus excelsior*, and less abundant with *Juniperus communis* and *Sorbus aucuparia*. The vegetation was dominated by a dense cover of *Viola collina*, besides less frequent of *Mercurialis perennis*, *Primula veris*, *Melica nutans*, *Fragaria vesca*, *Veronica chamaedrys*, *Geranium sanguineum*, *Lathyrus pratensis*, *Ranunculus acris*, besides some ferns (Kristiansen 1990).

Comments

The associated *Chalazium sociabile* is difficult to distinguish in the field from *B. vermiphila*, but is very different microscopically. The fungus shows great similarity and structure with species of *Pulvinula* and *Boudiera luteola*.

We (van Brummelen & Kristiansen 1999) discussed the relationship between the genera *Boudiera* (s. str.) and *Pulvinula*, and were reluctant to accept *Pulvinulas* as conspecific as both *B. luteola* and *B. vermiphila* have complex and very distinct ascospore ornamentation as the development of the secondary wall undergoes a complex process. *Pulvinulas* are devoid of a secondary wall, while *Boubovia* should accommodate species with only ornamented spores (cfr. van Brummelen and Kristiansen 1999).

But as stated before Perry et al. (2007) shows that *Boubovia luteola* and *Pulvinula ovalispora* are strongly supported sister taxa, and Yao and Spooner (1998) emphasize the asci with thickened in the early stage.

Less than 100 meters east of the *B. vermiphila* spot I also found *Boubovia luteola* about the same time at Ørdal, see above.

Boubovia ovalispora (Boud.) anon. ined.

Figs. 17, 18, 19, 20.



Figure 17. Apothecia. Torp, Fredrikstad. Scale bar 5 mm.

Icones: Boudier 1917, plate V, figure III
Beyer et al. 1985, Pilzfarbtafeln nr. 44, 160

Basionym

Pulvinula ovalispora Boud.

This species was originally described by me as *Pulvinula ovalispora* (Kristiansen 1985), which at that time was still placed in the genus *Pulvinula*. So the following description is partly based on the old observations from 1982-1984.

Apothecia solitary 1-2 mm in diameter, 1 mm high, distinct plane-discoïd, rarely turbinate, or somewhat irregular caused by mutual pressure, sessile, distinct margin. Greyish orange, pale reddish yellow to pinkish yellow; outside paler.

Asci 8-spored, clavate, attenuated to a smaller base, often bifurcate, 130-160 x 12-13 μm , with protruding asci at maturity.

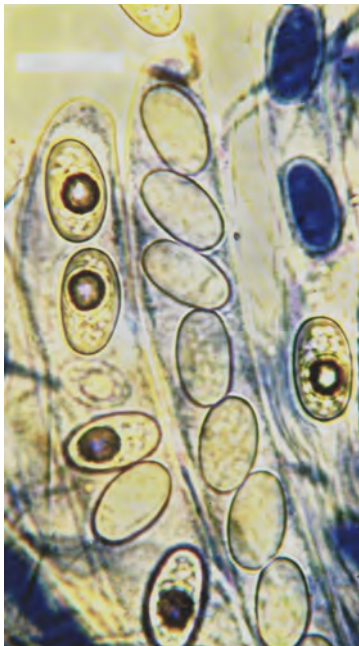


Figure 18. *Boubovia ovalispora*. Torp, Fredrikstad. Spores in asci with deBary-bubbles in Cotton blue. Immature spores to the right. Scale bar 15 μm .

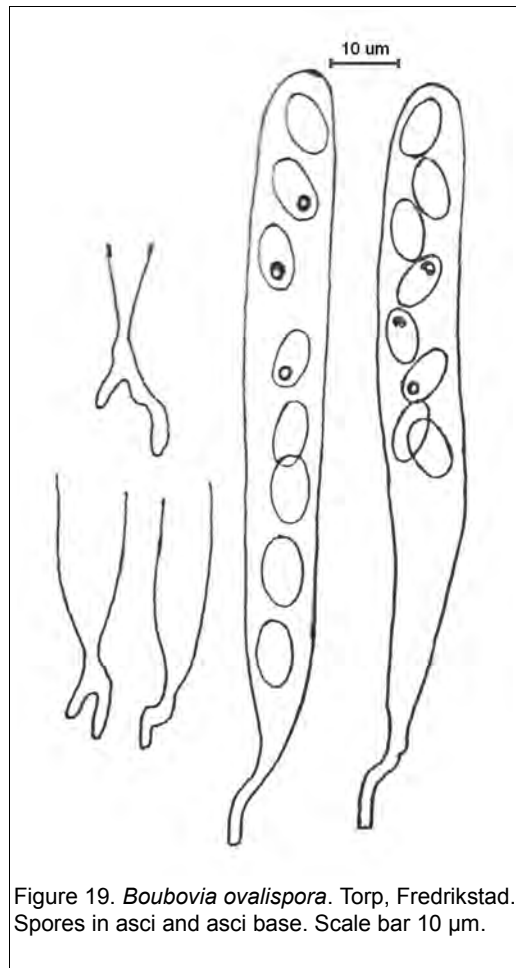


Figure 19. *Boubovia ovalispora*. Torp, Fredrikstad. Spores in asci and asci base. Scale bar 10 μm .

Ascospores, uni-seriate, ellipsoid, smooth, somewhat inequilateral in shape, with small oildrops near the poles, often with irregular deBary-bubbles (2-3) confluent, 12.6-14.4 x 7.4-8.8 μm .

Paraphyses filiform, strongly spirally curled apically, equally thick 1.0-1.5 μm .

Outer excipulum consists of globular-subglobular (textura globosa-angularis), 7 x 8 to 12 x 14 μm in diameter

Material examined

Østfold, Fredrikstad, Borge, Torp, near Kreuz-gate just south of the closed papermill, where

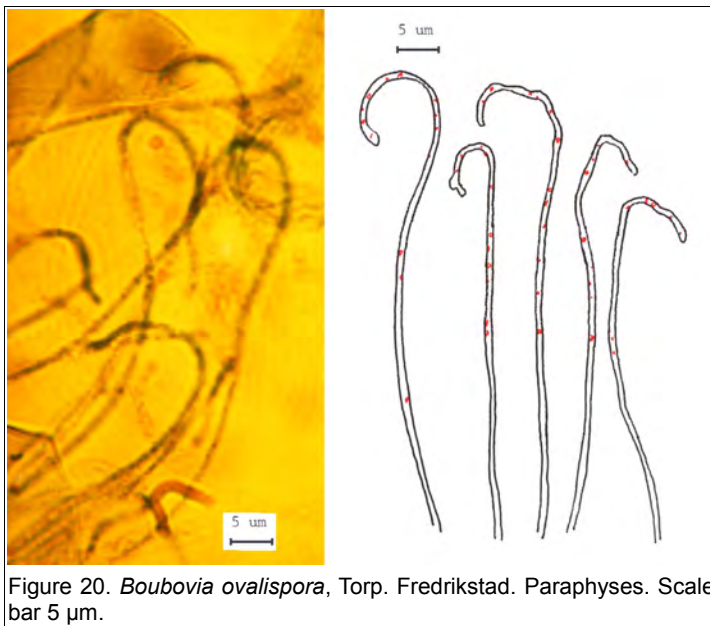


Figure 20. *Boubovia ovalispora*, Torp, Fredrikstad. Paraphyses. Scale bar 5 µm.

Comments

It seems that *B.ovalispora* is an almost cosmopolitan species, which is now found at the Canary Islands, Algerie (type locality), Madeira, Mallorca, USA, Jamaica, and several places in Europe, like Denmark, Germany and United Kingdom.

Korf and Zhuang (1984) stated that there are large variations of the ascospore size from one locality to the other of the specimens they had examined, so it is still an open question whether *B. ovalispora* is one species only or two different ones. More work is needed to

large deposits of muddy calcareous clay (pH 7.5) are stored, which have created a habitat for a large number of discomycetes over the years. The spot is ca.100 meter south of the *Boubovia luteola* locality.

The apothecia were found among dense populations of *Melilotus officinalis*, *Tussilago farfara*, and *Vicia sp.*, associated with *Lamprospora miniata* and *Ascobolus behnitziensis* (Kristiansen 2013). 7. July 1984 (RK 84.40); ibid. 11. August 1984 (RK 84.99); ibid. 31. July 1996 (RK 96.48) Herb. CUP, TRH, J.Mor. ; ibid. 27.July 1997 (RK 97.12). 59° 14' 23.56" N, 11° 0' 23.22"

Portugal, Madeira, close to Restaurante Estrele, Nuns valley, close to Eucalyptus trees, on solid brownish soil, 20. November 1994 (MA-18-RK).

clarify this question.

Simultaneously with the finding of *Boubovia ovalispora* at Torp in 1984, I found, a similar species, but with more red-orange pigment, close by (ca. 50 m). A subsequent microscopical examination, however, showed 4-spored asci, but still ellipsoid spores as for *B. ovalispora*, same anatomy, but with less curled paraphyses.

***Boubovia ovalispora* 4-spored**

Figs. 21a, 21b, 21c, 21F, 22, 23 Table1.

Description

Apothecia up to 1.5 mm in diameter, plane-discoid, rarely turbinate; reddish orange, outside paler, distinct margin.

Table1. Comparison of ascospore- and ascus size of 8- and 4-spored <i>Boubovia ovalispora</i>			
Samples	ascus µm	ascospores µm	average ascospores
8-spored RK 84.40	130-160 x 12.0-12.5	12.6-14.4 x 7.4-8.8	13.7 x 8.1
4-spored RK 84.100	143-157 x 12.0-13.7	12.6-13.7 x 7.6-8.4	13.5 x 8.1

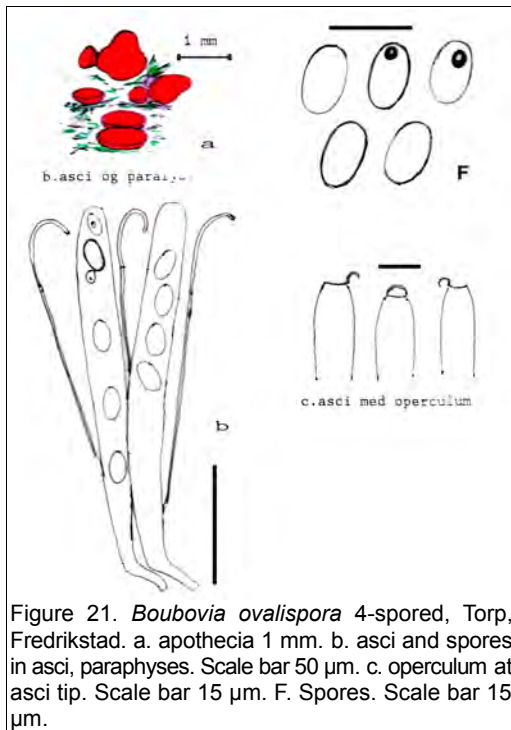


Figure 21. *Boubovia ovalispora* 4-spored, Torp, Fredrikstad. a. apothecia 1 mm. b. asci and spores in asci, paraphyses. Scale bar 50 µm. c. operculum at asci tip. Scale bar 15 µm. F. Spores. Scale bar 15 µm.

Asci 4-spored, some with two aborted spores in addition, clavate, attenuated against base, rarely bifurcate, 142.5-157.5 x 12.0-13.7 (15.0) µm, protruding 25-30 µm above the hymenium.

Ascospores uni-seriate, broad ellipsoid, smooth, rarely with deBary bubbles, 12.6-13.7 x 7.6-8.4 µm.

Paraphyses filiforme, more or less curved or bent apically less than *B. ovalispora*, 1.0-1.5 µm.

Outer excipulum consists of subglobular to angular cells 5 x 7 to 10 x 15 µm.

Material examined

Østfold, Fredrikstad, Borge, Torp, close to Kreutzgate, on naken muddy calcareous ground beneath a population of *Tussilago farfara*, 11. August 1984, (RK 84.100).

Comments

Often 4-spored asci develop larger spores than 8-spored, within the same taxon, and will not be considered as a separate species, but as a 4-spored forma.

However, in the present 4-spored species both asci and spores seem to be of the same magnitude as 8-spored. Besides, the colour is more intensified, and the paraphyses are less curved apically. A new collection is necessary if we are to find out if we are speaking of a new species or not.

Distribution, edaphic factors and discussions

All my *Boubovia* samples from Norway are collected in the low temperate zone less than 50 meters above sea level. The map shows locations in the county of Østfold (Figure 24). All are taken on calcareous ground, which means either marine sediments, shell beds, or locations created by man, and in both deciduous forest and spruce wood. Measurements of pH of soil samples from Torp, which is an artificial location, show small variations, 7.5/7.6. The locations at Hvaler varies more, from 7.1 to 7.6 (*B. luteola*), and 8.3 to 8.6 for the *B. vermiphila* locality. These are natural

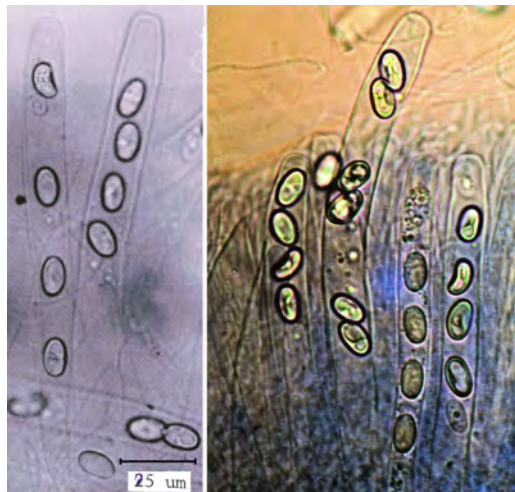


Figure 22. *Boubovia ovalispora* 4-spored. Four spores in asci. Scale bar 25 µm.

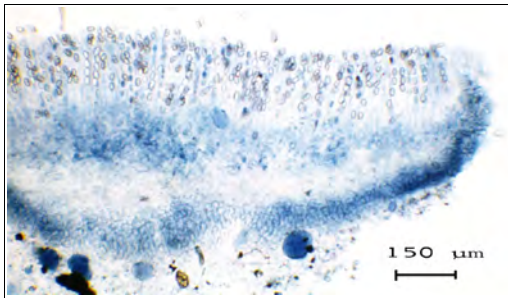


Figure 23. *Boubovia ovalispora* 4-spored. Thin section of apothecium. Scale bar 150 μm .

habitats. The populations of these fungi vary in number from year to year. The number of *Boubovia luteola* accounts to several hundreds, but varies from 5-6 species and up to approx. 100 in each finding. They appeared from 1982 to 1998. *B. vermiphila* was found in 1983, 1989, 1990, 1992, 1993 and 1998, and several hundreds were collected these years, although some were richer than others. *B. ovalispora* is less abundant than the others, and appeared only in 1984, 1996 and 1997, and few in numbers. The collection of *Boubovia luteola* from Rana in Nordland County was collected in the boreal zone about 100 meters asl, but not included here.

These fungi are not easy to find because of their small sizes, but the genus *Boubovia* itself are rarely collected, and the aim of the present paper is to focus on the different species and their characters and habitats. There are few mycologists who have found or collected these tiny fungi, but if we look at unusual habitats, like old industrial areas, overgrown heaps of trash, ditches, etc. there are chances for surprises as many of the smaller discomycetes are weak competitors in relation to Agaricales.

There is no existence of phylogenetic data for *B. vermiphila*, *B. ascoboloides* and *B. subprolata*, to confirm the combinations made by Yao and Spooner (1998). These species need to be re-examined to verify their taxonomic position.

Other potential *Boubovia*-candidates

There are at least 2 or 3 potential candidates from Japan and India. Geographically it may sound controversial to consider species from Japan and India in this connection, but quite many operculate discomycetes turn out to have a cosmopolitan distribution; consult *Boubovia ovalispora* herein, and according to Sigmund Sivertsen (pers. comm.) 60% of all discomycetes at Tierra del Fuego (Southern Hemisphere) occurs in Norway!

Japan: From Prof. Richard P. Korf (Cornell University, Ithaca, NY) sent me a slide with six mounted thin sections (20 μm) of a discomycete, which was found during the IMC3 workshop in Japan 1983.

R.P.K. wrote: "...Henry Dissing thought that one of the collections we took in Japan on the 1983 IMC3 foray was a *Boubovia*, but it was a very much larger fungus than the one you have."

The following note accompanied the slide: ex-CUP-JA 3557 *Aleuria* (field det. R.P.K.) *Boubovia* cfr. *luteola* (field det. H. Dissing). On bare sandy soil orange to orange-"luteus" (Rayner).

Spores grossly warted, non-guttulate. fide Dissing not an *Aleuria*, not an *Octospora*, not a *Melastiza*, not a *Cheilymenia*. What is it?

Photographed by M. Izawa.

Woods around Marunuma-ko, gumma Pref., Honshu, Japan. 20. VIII. 1983

Leg. IMC workshop workers. Sectioned by W. Y-Zhuang. Date 10.VIII 1984

Comments

Unfortunately I know nothing about the macroscopical features, like size or color of the apothecia. An microscopical examination by me shows oblong ellipsoid ascospores, 19-21 x 10-12 μm , ornamented by isolated warts about 1 μm , but I cannot observe curved paraphyses, but the excipulum is less



Figure 24. Distribution map of *Boubovia* species in the Østfold county. 1. Torp, Fredrikstad, 2. Ørdal, Hvaler, 3. Putten, Hvaler og 4. Botneveten, Hvaler.

developed as in *Boubovia*. The ornamentation on the spores is different from the known *Boubovia* species described herein. The sample should be traced and re-examined (by someone in Japan, who joined the IMC3).

India: In 1975 Khare published the description of four new species in the bryophilous genus *Octospora*, from locations in India (Khare 1975), although I cannot imagine that these samples belongs to *Octospora*, since none of them are connected to mosses, viz. not bryophilous, based on their habitats, which are described as decaying woods, on leaves, rotten leaves, and on soil.

There are especially two species that could be potential *Boubovia* species, viz. *Octospora spaniosa* and *O. decalvata*. They have both curved or hooked paraphyses, the spores are ornamented and they are hardly bryophilous. Especially the former have thick-walled asci in youth.

Richard P. Korf agreed to that in a letter 9. August 1984, quote:

“I must admit that we did not consider the two species described by Khare in *NJB*, *Octospora spaniosa* and *O. decalvata*. You are quite right that they are suspicious. The thick-walled young spores of the former make us suspect it is in the same alliance, but the latter I'm not sure about at all.”

ACKNOWLEDGEMENT

I am indebted to the late Henry Dissing, University of Copenhagen, and Trond Schumacher, University of Oslo for supplying scanning electron micrographies of *Boubovia luteola* and *Boubovia vermiphila*, respectively. The manuscript benefited from constructive comments by the referees.

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A comparison of aboveground sporocarps and belowground ectomycorrhizal structures of Agaricales, Boletales and Russulales in a sand dune ecosystem on Lista, South-western Norway

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Norsk tittel: En sammenlikning av sporokarper over bakken og ektomykorrhizastrukturer under bakken for Agaricales, Boletales og Russulales i et sanddyneøkosystem på Lista, Sørvest-Norge

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KEY WORDS

Ectomycorrhiza, molecular identification, sand dunes, sporocarps

NØKKELOD

Ektomykorrhiza, identifikasjon, molekylær, sanddyner, sporokarper

SAMMENDRAG

I dette arbeidet fokuserer vi på ektomykorrhizasopper i Agaricales, Boletales og Russulales, som alle har iøynefallende sporokarper. Dette gir oss en mulighet til å sammenlikne diversitet av ektomykorrhiza med diversitet av sporokarper av ektomykorrhizasopper. I sanddyneområdene på Lista, i Sørvest-Norge, ble det lagt ut ni plot med diameter 3 m i vegetasjon dominert av *Salix repens* (krypvier). Tre plot på dynetrau, tre plot på kuppeldyner og tre plot på eroderte dyner. I 2009 ble

ektomykorrhizarøtter av *Salix repens* samlet i hvert av plottene. Taksa av ektomykorrhizasopper ble identifisert ved hjelp av pyrosekvensering. I perioden 2008 til 2014 ble sporokarper samlet og identifisert i de samme plottene. Tretti taksa av de ektomykorrhizasoppene vi fokuserte på ble identifisert på røttene, 10 av dem ble også funnet sammen med sporokarper (i det minste i ett av plottene). I tillegg ble 11 taksa bare registrert som sporokarper. Det vanligste takson var *Hebeloma* spp. (reddiksopper), funnet i alle ni plottene. Det vanligste takson på artsnivå var *Cortinarius saniosus* (branngul slørsopp), som imidlertid bare ble registrert som ektomykorrhiza på røttene, mens sporokarper ble funnet utafør plottene. De vanligste ektomykorrhizaartene med sporokarper i det minste i ett plot var *Cortinarius casimiri* (storspore-slørsopp) og *Russula laccata* (skarp vierkremle). Av taksa typiske for sanddyner med *Salix repens* fant vi *Lactarius controversus* (rosaskiveriske), *Russula persicina* (aprikoskremle), *Tricholoma cingulatum* (grå ringmusserong), *Inocybe impexa* (strandtrevlesopp), *I. dunensis* (dynetrevesopp) og *Laccaria maritima* (dynelakssopp). De to siste taksa var bare representert ved sporokarper. Vi konkluderer med at en kombinert registrering av ektomykorrhiza på røtter og sporokarper er en optimal tilnærming hvis vi ønsker å dekke diversiteten av de ektomykorrhizasoppene vi har fokusert på.

ABSTRACT

In the present work we put focus on ectomycorrhizal Agaricales, Boletales and Russulales, all with conspicuous sporocarps, giving us an opportunity to compare the below ground ectomycorrhiza diversity with the aboveground sporocarp diversity. In the sand dune area on Lista, South-west Norway, nine plots of 3 m diameter were established in *Salix repens* (creeping willow) dominated vegetation; i.e. three plots on dune slacks, three plots on hummock dunes, and three plots on eroded dunes. In 2009 ectomycorrhizal *Salix repens* roots were sampled in each plot. Ectomycorrhizal taxa were identified by pyrosequencing. From 2008 to 2014 fungal sporocarps were collected and identified in the same plots. Of the 30 actual ectomycorrhizal taxa identified on the roots, 10 of them were also accompanied by aboveground sporocarps. In addition, 11 taxa were only recorded as sporocarps. The most frequent ectomycorrhizal taxon was *Hebeloma* spp, recorded in all nine plots. The most frequent taxon on species level was *Cortinarius saniosus*, however, only recorded on ectomycorrhizal roots while sporocarps were found outside the plots. The most frequent ectomycorrhizal species with at least one plot housing accompanied sporocarps were *Cortinarius casimiri* and *Russula laccata*. Some of the ectomycorrhizal taxa belong to the typical inventory of *Salix repens* dominated dune vegetation: *Lactarius controversus*, *Russula persicina*, *Tricholoma cingulatum*, *Inocybe impexa*, *I. dunensis* and *Laccaria maritima*; the two last taxa only represented by sporocarps. We conclude that a combination of sampling below ground ECM and monitoring aboveground sporocarps seems to be an optimal approach if we want to cover the diversity of conspicuous ECM fungi in an area.

INTRODUCTION

The sand dune area on the Lista peninsula (Farsund municipality, Vest-Agder County,

SW Norway) consists of an approximately 10 km long beach-line from SE to NW, interrupted by short stretches of boulders or rocks (Figure 1) (Høiland 1978a). It houses a very interesting funga, encompassing many specialised species (Høiland 1974, 1975, 1977, 1978b, 2006). These registrations have been performed by monitoring visible sporocarps, where basidiomycetes belonging to Agaricales and Russulales are the most conspicuous and frequent, together with some few from Boletales. Of these the following genera are ectomycorrhizal (ECM): *Amanita*, *Tricholoma*, *Laccaria*, *Entoloma* (at least some), *Cortinarius*, *Inocybe*, *Hebeloma*, *Naucoria*, *Boletus*, *Leccinum*, *Paxillus*, *Russula* and *Lactarius*.

In the actual sand dune area, creeping willow *Salix repens* L. is the only ECM plant, as also documented from similar sand dune areas in the UK and The Netherlands (Watling and Rotheroe 1989, Rotheroe 1993, Arnolds and Kuyper 1995, van der Heijden and Vosatka 1999, van der Heijden et al. 1999). In *Salix repens* both ECM and arbuscular mycorrhiza coexist (Heijden and Vosatka 1999). A survey of ECM fungi on roots of *S. repens* in the sand dune area on Lista has newly been published by Botnen et al. (2015). The results, obtained by 454 pyrosequencing, identified ECM from many of the above-mentioned genera, but also from genera with no or inconspicuous sporocarps, like Thelephorales, Sebaciniales and Cantharellales. Approximately one quarter was Agaricales, Boletales and Russulales; the other quarter Thelephorales; the third quarter Sebaciniales and Cantharellales; and the fourth quarter Glomeromycota (arbuscular mycorrhiza) and Ascomycota.

Monitoring of sporocarps is a straightforward method if we want a survey of ECM species in an area, although we realise that the visible sporocarps represent roughly one quarter of the total ECM diversity below ground. The aim of the present work is to compare records of ECM taxa of Agaricales,



Figure 1. Sketch map of the Lista peninsula, Vest-Agder County, Farsund municipality. DS1, DS2, and DS3 are study plots from dune slacks; SRD1, SRD2, and SRD3 are study plots from hummock dunes; SRDE1, SRDE2, and SRDE3 are study plots from eroded dunes. The sand dune investigation area is marked with yellow.

Boletales and Russulales from aboveground sporocarps with records of ECM from the same group based on below ground *Salix repens* root samples. Moreover, the ecology of the actual species or genera will be commented.

MATERIALS AND METHODS

Collection of root samples and metagenomics of mycorrhizal fungi

Field work was carried out on the Lista peninsula in SW Norway (Figure 1, Table 1). In

October 2008, nine circular study plots of 3 m diameter including *S. repens* were established in the sand dune areas on the S and SE parts of the Lista peninsula; encompassing (1) dune slacks: DS1, DS2, DS3, (2) hummock dunes: SRD1, SDR2, SRD3, and (3) eroded dunes: SRDE1, SRDE2, SRDE3 (see Botnen et al. 2015). In 2009 two independent samples of approximately 10 cm continuous *S. repens* root were collected in each plot by excavating the individual roots. These samples were

Table 1. Description of the study plots, 3 m diameter, all positioned on Lista peninsula, Vest Agder County, SW Norway (see Figure 1).

Locality	Plot	Degrees N	Degrees E	Vegetation
Einarsneset-Husebysanden	DS1	58.06612	6.78315	Dune slack, relatively dry and rich
Einarsneset-Husebysanden	SRD1	58.06580	6.78369	Hummock dune in E end of DS1
Einarsneshalsen	DS2	58.06372	6.78761	Dune slack, wet
Lomsesanden	SRD2	58.06559	6.79160	Hummock dune 200 m W of a camping toilet
Lomsesanden	SRDE1	58.06562	6.79136	Eroded dune 220 m of the same toilet
Einarsneset	SRDE2	58.06488	6.78339	Eroded dune, blow out in <i>Ammophila</i> dune ridge
Havik	DS3	58.06754	6.73032	Dune slack, wet, E of parking place
Havik	SRD3	58.06717	6.73048	Hummock dune in SE end of DS3
Havik	SRDE3	58.06749	6.73075	Eroded dune in E end of DS3, N of SRD3

collected in April, July and October, altogether 54. Metagenomics with fungal specific ITS primers were performed by 454 pyrosequencing. For details about sampling, pyrosequencing and biostatistics, see Botnen et al. (2015). Fungi were considered ECM if they were listed by Tedersoo et al. (2010).

A list of all mycorrhizal OTUs from the 454 pyrosequencing is given by Botnen et al. (2015), Online Resource 2.

Monitoring of ECM sporocarps, DNA-methods, data mining and taxonomy

The fungal study group was ECM Basidiomycota belonging to Agaricales, Boletales and Russulales. From 2008 to 2014, each of the nine study plots was visited for monitoring sporocarps twice a year, July and October. Sporocarps outside the study plots were also collected. They were dried in a 20 °C air current from a standard air to air heat pump.

DNA was extracted from dried, crushed sporocarps following the 2% CTAB miniprep method (Murray and Thompson 1980). Primer pairs used in the PCR reactions included ITS5/ITS4 for the complete ITS1-5.8S-ITS2 region (White et al. 1990). PCR products were purified using ExoSAP-IT (Amersham Biosciences) prior to sequencing. Sequences

were generated with an ABI 3730 high-throughput capillary electrophoresis sequencer using the PCR primers as sequencing primers.

The taxonomic identification was based on sporocarp morphology using standard keys (Vesterholt 2005, Knudsen and Vesterholt 2008), combined with searches on the ITS sequences done in the NCBI nt/nr using BLAST_N.

Information about occurrence, ecology and distribution of all actual species recorded in the Lista sand dune area was obtained from Høiland (1974, 1975, 1977, 1978b, 2006, 2012), Høiland and Elven (1980), and The Norwegian Mycological Database, NMD (2010), as of April 2015.

In the present work all fungi are considered at species level, except *Hebeloma* and *Entoloma*, which are treated at genus level. The reason is difficulties to relate species identifications based on the morphology of sporocarps with species suggestions from BLAST_N on ITS sequences from the same sporocarps. The term taxon is therefore used to include either species or genera.

The nomenclature follows Index Fungorum (<http://www.indexfungorum.org/Names/Names.asp>, as of April 2015).

RESULTS AND DISCUSSION

Altogether 30 taxa of ECM Agaricales, Boletales and Russulales were recorded from root samples of *Salix repens* in the nine study plots (Table 2; see also Botnen et al. 2015, Online Resource 2). Of these, 20 taxa have been reported previously from the Lista sand dune area, based on sporocarp recordings. Ten taxa were represented by ECM sequences from root samples accompanied by aboveground sporocarps in at least one of the plots. Ten of the 30 ECM taxa have not been recorded from the area before. Two of them, *Inocybe chelaniensis* D.E. Stuntz and *I. straminipes* Romagn., are new to Norway. In addition, sporocarps, but no belowground ECM, of 11 taxa were found in at least one of the plots (Table 2).

The most frequent ECM taxon was *Hebeloma* spp., recorded in all nine plots, even in the plots from eroded dunes, which were scarce in other ECM taxa (Botnen et al. 2015). Sporocarps were found in three plots, one from dune slack, two from hummock dunes. *Hebeloma* species are regarded as generalist ECM builders on *Salix* (van der Heijden 1999, Aanen et al. 2000); some having a short life span adapted to pioneer situations, such as nutrient-poor, unstable sand dunes (Gryta et al. 1997). In the dune areas of Lista, sporocarps of various *Hebeloma* species have been reported by Høiland (1974, 1978b, Høiland and Elven 1980), mostly from dune slacks.

On species level, the most common ECM taxon was *Cortinarius saniosus* (Fr.) Fr. (Figure 2A) found in seven plots. However, no sporocarps were recorded in any plot, and the species fructified rather seldom in the investigation area (Høiland 1980). *Salix* is reported a common host for *C. saniosus* (Høiland 1980, Høiland and Elven 1980, van der Heijden et al. 1989, Niskanen et al. 2008). ECM of *C. casimiri* (Velen.) Huijsman was also frequent, recorded in six plots, with sporocarp in one, a hummock dune. This is a very common species, both under deciduous and coniferous

trees, but also under *Salix* (Brandrud et al. 1990-2013, Niskanen et al. 2008), and may be regarded as a generalist. *Cortinarius illuminus* Fr. was also frequent as ECM, in 6 plots, including two in eroded dunes. However, the species was not found with sporocarps, not even outside the plots, and it belongs to the most frequent of the “hidden” Agaricales in our area. According to Brandrud et al. (1990-2013) and Niskanen et al. (2008), it is common in mesic and acidic *Picea* forests, but is not mentioned under *Salix*. *Cortinarius parvannulatus* Kühner found as ECM in two plots, both hummock dunes, had a similar “hidden” appearance. This species is reported from *Salix*, preferably in alpine environments Brandrud et al. (1990-2013). *Cortinarius croceus* (Schaeff.) Gray, having a broad ecology, but preferring open environments (Høiland 1984), was found in 5 plots with sporocarps in one of them, here together with sporocarps of the closely related *C. cinnamomeus* (L.) Fr. ECM of *Cortinarius trivialis* J.E. Lange was found in two plots, both dune slacks, with sporocarps in one of them. This species has *Salix* as important host (Brandrud et al. 1990-2013, Niskanen et al. 2008), and has been reported from *Salix repens* by Watling and Rotheroe (1989), van der Heijden et al. (1999), van der Heijden and Kuyper (2003). It is rather common in dune slacks on the Lista peninsula (Høiland 1974, 1978b, Høiland and Elven 1980). Six species of *Cortinarius* were not recorded from the root samples, only as sporocarps. Sporocarps of *C. saturninus* (Fr.) Fr. was found in one plot, a hummock dune, but the species is common in all *Salix repens* dominated dune vegetation on Lista (Høiland 1974, 1978b, Høiland and Elven 1980). *Cortinarius uliginosus* Berk. found in plot DS3 was locally common also outside the wet dune slacks surrounding this plot.

Species of *Inocybe* are frequent in dune areas, especially on less acidic sand with none

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Table 2. Records of both ectomycorrhiza (ECM) and sporocarps of the same species *# green; only ECM * yellow; or only sporocarps # blue in the study plots (Table 1). Fungi in concern are Agaricales, Boletales and Russulales. ECM was sampled in 2009, sporocarps from 2008 to 2014. ECM and sporocarps sampled together in 2009 are marked with ! For further explanation of plot codes, see Table 1.

Plot	DS1	DS2	DS3	SRD1	SRD2	SRD3	SRDE1	SRDE2	SRDE3
Vegetation type	Dune slacks			Hummock dunes			Eroded dunes		
<i>Amanita muscaria</i>	-	-	-	-	-	#	-	-	-
<i>Cortinarius albovariegatus</i>	-	-	-	-	-	-	-	-	#
<i>Cortinarius anomalus</i>	-	-	-	-	-	#	-	-	-
<i>Cortinarius casimiri</i>	-	*	*	-	*	*#	*	-	*
<i>Cortinarius cinnamomeus</i>	-	-	-	-	#	-	-	-	-
<i>Cortinarius croceus</i>	-	*	*	*	*#	*	-	-	-
<i>Cortinarius illuminus</i> ²	-	*	*	-	*	*	*	-	*
<i>Cortinarius obtusus</i>	-	-	-	-	-	#	-	-	-
<i>Cortinarius parvannulatus</i> ²	-	-	-	*	-	*	-	-	-
<i>Cortinarius saniosus</i>	*	*	*	*	*	-	-	*	*
<i>Cortinarius saturninus</i>	-	-	-	#	-	-	-	-	-
<i>Cortinarius trivialis</i>	-	*	*#	-	-	-	-	-	-
<i>Cortinarius uliginosus</i>	-	-	#	-	-	-	-	-	-
<i>Entoloma</i> spp.	-	-	-	-	-	*	*	-	-
<i>Hebeloma</i> spp.	*#	*	*	*#	*	*#	*	*	*
<i>Inocybe acuta</i>	-	*	-	#	-	-	-	-	-
<i>Inocybe chelanensis</i> ¹	-	-	-	-	-	-	-	-	*
<i>Inocybe dulcamara</i>	*	-	-	-	-	-	-	-	-
<i>Inocybe dunensis</i>	#	-	-	-	-	-	-	-	#
<i>Inocybe impexa</i>	-	-	*	-	-	-	*	-	-
<i>Inocybe jacobi</i>	-	-	-	-	*	-	-	-	-
<i>Inocybe lacera</i>	#	*	*	-	-	-	-	-	-
<i>Inocybe napipes</i> ²	-	-	-	*	-	-	-	-	-
<i>Inocybe obscurobadia</i> ²	*	-	-	*	-	*	-	-	-
<i>Inocybe ochroalba</i> ²	*	-	-	-	-	*	-	-	*
<i>Inocybe paludinella</i>	-	*#	-	*	-	-	-	-	-
<i>Inocybe straminipes</i> ¹	-	-	*	-	-	-	-	-	-
<i>Inocybe subcarpta</i>	-	-	*	-	-	-	-	-	-
<i>Inocybe whitei</i> ²	-	-	-	-	-	*	-	-	-
<i>Laccaria laccata</i>	-	*	-	*	*	*#	-	-	*
<i>Laccaria maritima</i>	-	-	-	-	-	-	#	-	-
<i>Laccaria proxima</i>	-	*	-	-	*	*	-	-	*
<i>Lactarius controversus</i>	-	-	*	-	-	#	-	-	!*#
<i>Leccinum scabrum</i>	-	-	-	#	-	-	-	-	-
<i>Naucoria</i> aff. <i>bohemica</i> ²	-	-	*	-	-	-	-	-	-
<i>Naucoria tantilla</i> ²	-	-	-	-	-	*	-	-	-
<i>Paxillus involutus</i>	-	-	-	-	-	-	-	-	*
<i>Russula laccata</i>	-	*	*#	*	*	*	*	-	#
<i>Russula pascua</i>	-	-	#	-	-	-	-	-	#
<i>Russula persicina</i>	-	-	*#	-	*	#	-	-	*#
<i>Tricholoma cingulatum</i>	-	-	-	*#	-	*#	-	-	*

¹Not recorded from Norway before. ²Not previously recorded from the investigation area.



Figure 2. Common or typical ECM fungi on sand dunes with *Salix repens* on Lista peninsula, Vest-Agder county, Farsund municipality. A. *Cortinarius saniosus* found in seven of the nine study plots; all as ectomycorrhiza (ECM) on roots. B. *Lactarius controversus* found in three of the nine study plots; one as ECM accompanied by sporocarps, one as ECM, and one as sporocarp. C. *Russula persicina* found in four of the nine study plots; two as ECM accompanied by sporocarps, one as ECM, and one as sporocarp. D. *Tricholoma cingulatum* found in three of the nine study plots; two as ECM accompanied by sporocarps, one as ECM. (See Table 2.). Photo: K. Høiland.

or scarce amounts of organic matter (Andersson 1950, Høiland 1974, 1975, 1978b, 2006, Watling and Rotheroe 1989, van der Heijden et al. 1999). Typical sand dune species were *I. impexa* (Lasch) Kuyper (ECM on hummock dune and eroded dune) and *I. dunensis* P.D. Orton (sporocarps on dune slack and eroded dune). The other *Inocybe* species (Table 2) are not exclusively sand dune species, but many of them, e.g. *I. lacera* (Fr.) P. Kumm. and *I. dulcamara* (Pers.) P. Kumm., prefer sand or open soils and are therefore frequent in sand dune vegetation (Høiland 1974, 1978b, Jacobsson 2008). *Inocybe dulcamara* prefers calcareous soils (van der Heijden et al. 1999, van der Heijden and Kuyper 2003) and may be favoured by shell fragments in the sand. *Inocybe paludinella* (Peck) Sacc. is typical

for wet soils (Jacobsson 2008). Plot DS2, in which both ECM and sporocarps were found, is situated on a very moist dune slack, which is flooded from autumn to spring, and even in rainy summers. *Inocybe obscurobadia* (J. Favre) Grund & D.E. Stuntz and *I. ochroalba* Bruyl. have not been recorded from Lista before. ECM of both was detected in three plots. According to Jacobsson (2008) the two species prefer calcareous soils under conifers. They may be favoured by shell fragments in the sand, especially in the nutrient rich plots DS1 and SRD1 (Botnen et al. 2015, Online Resource 1). The rest of the *Inocybe* species will not be commented on since they were too infrequent, but, as mentioned, two of them are new for Norway.

Sporocarps of the variable *Laccaria laccata* (Scop.) Cooke are frequent in dune slacks on Lista (Høiland 1974, 1978b, Høiland and Elven 1980). ECM was recorded in five plots, with sporocarps in one of them (a hummock dune). *Laccaria maritima* (Theodor.) Singer ex Huhtinen, one of the most noticeable sand dune species (Andersson 1950, Høiland 1974, 1975, 1976), was found as sporocarps in one plot from an eroded dune, SRDE1. Eroded dunes are the most important habitat for this rare and threatened species (Høiland and Elven 1980, Høiland 2006). However, no ECM was detected.

Tricholoma cingulatum (Almfelt ex Fr.) Jacobshch (Figure 2D) is a well-known associate with *Salix* (Gulden 1969, Watling and Rotheroe 1989, Watling 1992, Rotheroe 1993, van der Heijden et al. 1999). Sporocarps are rather frequent on *Salix repens* hummock dunes on Lista (Høiland 1974, 1978b, 2006, Høiland and Elven 1980). ECM and sporocarps were recorded in two plots, SRD1 and SRD3, from hummock dunes, and one ECM in SRDE3, an eroded dune in vicinity of SRD3.

Russula laccata Huijsman, which is most frequent under *Salix* in arctic and alpine environments (Gulden et al. 1985, Knudsen et al. 2008), is also common in dunes with *Salix repens* (Watling 1992). ECM was recorded in root samples from six plots, spanning from dune slacks to eroded dunes, one of them with sporocarps. In addition sporocarps, but no ECM, were found in one plot, an eroded dune. Sporocarps of *R. laccata* are common in the dune areas on Lista (Høiland 1974, 1978b, Høiland and Elven 2008). ECM of *Russula persicina* Krombh. (Figure 2C) was found in three plots, two of them with sporocarps, from dune slack, hummock dune and eroded dune, respectively. Additional sporocarps, but no ECM, were found in one plot, a hummock dune. The

species is associated with deciduous trees (Knudsen et al. 2008) including *Salix repens* (Rotheroe 1993, van der Heijden et al. 1999, Taylor 2001). On Lista sporocarps were reported from various *Salix repens* vegetations, but preferably on hummock dunes (Høiland 1974, 1978b, 2006, Høiland and Elven 2006). The last species, *R. pascua* (F.H. Møller & Jul. Schäff.) Kühner, was only found as sporocarps in two nearby plots, DS3 and SRDE3, dune slack and eroded dune, respectively. This species is also reported under *Salix* in the UK (Watling and Rotheroe 1989).

The peculiar, nearly subterranean *Lactarius controversus* Pers. (Figure 2B) is typical under *Salix* or *Populus* (Heilmann-Clausen et al. 1998, Kalamees 2011), and sporocarps are recurrently found beneath *Salix repens* in sand dunes (Høiland 1974, 1978b, 2006, Høiland and Elven 1980, Watling and Rotheroe 1989, Rotheroe 1993, Heilmann-Clausen et al. 1998, van der Heijden et al. 1999, van der Heijden and Kuyper 2003). ECM and/or sporocarps were recorded from three nearby plots, DS3, SRDE3 and SRD3, dune slack, eroded dune and hummock dune, respectively. *Lactarius controversus* was the only species recorded both as ECM and sporocarps in the same year (2009) in the same plot (SRDE3) (Table 2). (However, 2009 was a bad year for sporocarps in the investigation area.)

The rest of the fungal taxa were found too seldom to be commented on.

Taxonomic remarks

Hebeloma is for reasons mentioned above only treated at genus level. Sequences from sporocarps gave by BLAST_N: *Hebeloma cavipes* Huijsman (syn. *H. lutense* Romagn.), *H. crustuliniforme* (Bull.) Quél. (syn. *H. longicaudum* (Pers.) P. Kumm.) and *H. leucosarx* P.D. Orton (syn. *H. velutipes* Bruchet) together with an undetermined species. ECM sequences from root samples gave by BLAST_N the

following species (Botnen et al. 2014, Online Resource 2): *Hebeloma alpinum* (J. Favre) Bruchet, *H. cavipes* and *H. kuehneri* Bruchet together with an undetermined species.

The name *Cortinarius trivialis* J.E. Lange is used in this investigation, although the BLAST_N results turned up with *C. alpinus* Boud. for both ECM and sporocarps (except one sporocarp identified as *C. trivialis*). However, Peintner (2008) showed that ITS sequences gave very little (or no) resolution between species determined *C. trivialis* or *C. alpinus*. Moreover, the material from Lista is morphologically closer to *C. trivialis* than to *C. alpinus* (Brandrud et al. 1990-2013, Niskanen et al. 2008). Therefore we prefer to consider it *C. trivialis*.

Inocybe impexa (Lasch) Kuyper is the correct name (Kuyper 1986) for *I. maritima* P. Karst. (Høiland 1975, Høiland and Elven 1980).

Inocybe dulcamara (Pers.) P. Kumm. was shown to be the correct determination for specimens previously named *I. caesariata* (Fr.) P. Karst. sensu Heim (now *I. heimii* Bon) (Høiland 1974, 1978b, 2006, 2012, Høiland and Elven 1980).

Russula laccata Huijsman was misinterpreted as *R. fragilis* Fr. by Høiland (1974, 1978b) and Høiland and Elven (1980).

Russula persicina Krombh. (Figure 2C) was repeatedly named *R. exalbicans* (Pers.) Melzer & Zvára (syn. *R. depallens* Cooke sensu auct.) by Høiland (1974, 1978b, 2006, 2012) and Høiland and Elven (1980). However, sequences of both ECM and sporocarps gave evidence by BLAST_N for *R. persicina*, a species which in Norway previously was found in Sør-Trøndelag, Trondheim (NMD 2010). Also, the morphology of the material from Lista

matches this species better than that of *R. exalbicans* (Knudsen et al. 2008).

CONCLUSION

Our investigation of ECM Agaricales, Boletales and Russulales in nine plots showed that 24% of the taxa were represented by below ground ECM accompanied by aboveground sporocarps (in at least one of the plots); 49% of the taxa were represented by below ground ECM not accompanied by aboveground sporocarps (but sporocarps may be found without below ground ECM in some other plots); and 27% of the taxa were represented only by aboveground sporocarps. To cover the total diversity of conspicuous ECM fungi, a combination of sampling belowground ECM and monitoring aboveground sporocarps seems to be an optimal approach.

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Sopper assosiert med *Pityogenes chalcographus*, *Polygraphus poligraphus* og *Tomicus piniperda*

(Fungi associated with *Pityogenes chalcographus*, *Polygraphus poligraphus* and *Tomicus piniperda*)

Ruben A. Lindseth¹ (student) og Halvor Solheim^{1,2} (veileder)

Masteroppgave (30 studiepoeng) ved NMBU 2015.

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Barkbiller knyttet til bartrær har med seg sopper. Noen av disse gir en blåfarging av veden rett under barkbillenes gangsystemer og er tradisjonelt kalt blåvedsopper. Nå brukes betegnelsen ophiostomatoide sopper om disse. Barkbillene har imidlertid også med seg sopper fra andre soppgrupper, noen er velkjente i mange sammenhenger, andre er lite kjent. I denne studien er tre barkbiller undersøkt: *Pityogenes chalcographus* (sekstannet granbarkbille), *Polygraphus poligraphus* (dobbeløyet barkbille) og *Tomicus piniperda* (stor margborer). For de to førstnevnte artene, som begge angriper gran, ble innsamlede barkbiller lagt på maltagar og sopper dyrket fram, mens prøver i tilknytning til *T. piniperda*, som lever på furu, ble tatt i veden rett under gangsystemer. Materialet ble samlet inn i sju forskjellige kommuner; Alta, Engerdal, Flesberg, Nannestad, Rendalen, Trysil og Ås. Oppgava hadde tilknytning til artsprosjektet «Ophiostomatoid fungi in Norway» finansiert av Artsdatabanken.

Skåler med soppvekst ble fulgt over flere måneder, og sopper ble rensert ut til forskjellige tider. Rendyrkede sopper ble først gruppert etter morfologi basert på vekst, farge, tekstur, konidiebærende strukturer og konidier. Fra hver morfotype ble opptil fem isolater sekvensert med primerne ITS1F og ITS4. Sekvensene ble sammenlignet med sekvenser i Genbank.

Noen få isolater ble også sekvensert med primere i β -tubulin regionen.

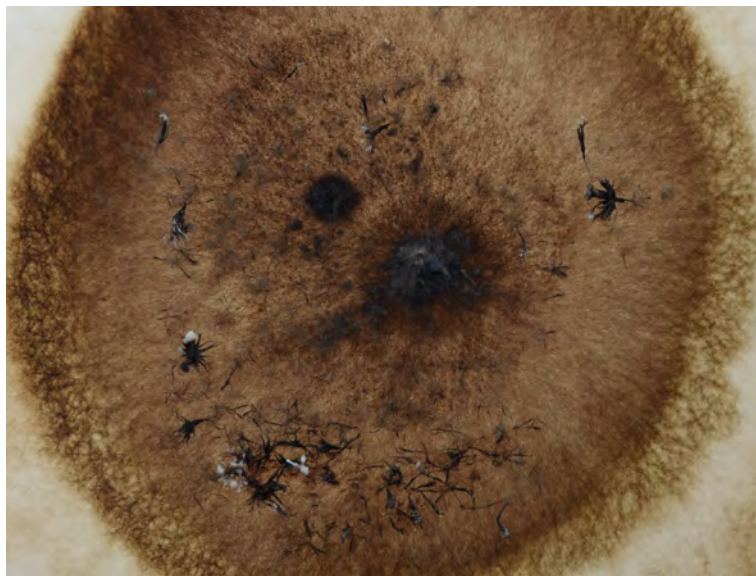
I alt ble det tatt 76 prøver (biller) fra *P. chalcographus* samlet i fire kommuner, 59 prøver (biller) fra *P. poligraphus* samlet i to kommuner og 50 vedprøver fra *T. piniperda* samlet i fire kommuner.

Det ble i alt funnet 14 arter/artskomplekser innen de ophiostomatoide soppene, åtte fra de to granbarkbilleartene, mens det ble isolert seks fra ved under gangsystemer til *T. piniperda*. Halvparten av artene var *Ophiostoma*-arter; *O. bicolor*, *O. brunneo-ciliatum*, *O. floccosum*, *O. fuscum*, *O. minus*, *O. piceae* og en ubeskrevet *Ophiostoma* art. Det ble funnet to *Graphilbum*-arter, begge ubeskrevne arter, tre *Grosmannia*-arter; *G. cucullata*, *G. penicillata* og en art i *G. piceiperda*-komplekset og *Leptographium chlamydatum*. Tre arter/artskomplekser ble funnet i tilknytningen til alle tre billeartene; *L. chlamydatum*, en art som er beskrevet fra Norge, *O. minus* som er en vanlig art knyttet til barkbiller på furu og en art i *G. piceiperda*-komplekset. Dette komplekset blir undersøkt i en japansk PhD-studie, men resultatene derfra er ennå ikke publisert. Når det gjelder slekten *Graphilbum* så er lite gjort, og begge artene som ble funnet er ubeskrevne arter. Også i denne gruppen er det en pågående PhD-studie, denne i Sør-Afrika.

Det ble funnet 19 andre arter i denne studien. De fleste av dem var andre sopper innen Ascomycota, men ingen av dem var særlig vanlige. Ingen ble funnet på mer enn 10% av billene. Mest interessant var isoleringen av råtesoppen *Heterobasidion parviproum* (granrotkjuke) fra *P. chalcographus*. Dette er gran-skogens verste skadegjører. Den ble imidlertid

isolert kun fra én barkbille, så transport med barkbiller er nok en sjeldenhet. Fra ved under gangsystemet til *T. piniperda* ble det isolert fire andre arter innen Basidiomycota; *Chondrostereum purpureum* (sølvglanssopp), *Cylindrobasidium laeve*, *Peniophora pini* (furutorneskinn) og *Sistotrema brinkmannii*. Disse kan ha etablert seg i veden uten hjelp av barkbiller.

I Norge var bare 22 arter av ophiostomatoide sopper publisert før denne masteroppgaven startet. Det ble funnet seks nye ophiostomatoide arter i denne oppgava. I tillegg til de to ubeskrevne *Graphilbum*-artene nevnt over, ble følgende nye arter funnet: *Ophiostoma brunneo-ciliatum*, *O. floccosum*, *O. fuscum*, *O. minus*. Denne oppgava gir et godt bidrag til økt kunnskap omkring biodiversitet av ophiostomatoide sopper i Norge.



Kultur på maltagar av *Graphilbum* sp., en ny art.
Culture on malt agar of a new Graphilbum sp. species. Photo: H. Solheim.

Mastergrad/Master thesis

Fungi associated with three common bark beetles species in Norwegian Scots pine forest

(Sopper assosiert med tre vanlige barkbiller i norske furuskoger)

Max E. Waalberg¹ (student) and Halvor Solheim^{1,2} (supervisor)

Master thesis (30 credits) at NMBU 2015:

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Fungi associated with bark beetles living on Scots pine have never been studied in Norway. In this study three bark beetles were chosen, all common bark beetles in Scots pine, *Ips acuminatus* (skarptannet barkbille), *Pityogenes bidentatus* (totannet barkbille) and *P. quadridens* (firtannet barkbille). Bark beetles were collected in various sites in South-Eastern Norway; in Engerdal, Flesberg, Frogn and Grue. The project was connected with the species project financed by the Norwegian Biodiversity Information Centre «Ophiostomatoid fungi in Norway».

Each bark beetle was cut up in three parts which was placed on separate Petri dishes with malt extract agar. The Petri dishes were inspected from day two and subcultures were taken from growing tips of mycelia or from sporulating structures for up to three months.

Each purified culture was used to group the fungi in morpho-types based on growth, colour, texture, conidiophores and conidia. From each morpho-type five cultures were grown on malt extract agar covered with a cellophane membrane filament. Pure mycelium was removed and used for DNA extraction and later on for ITS sequencing, using ITS1F and ITS4 primers. DNA from a few samples was also used for β -tubulin and elongation factor 1- α genes. Sequences were compared with sequences in GenBank.

A total number of 60 specimens of *P. bidentatus*, 66 of *P. quadridens* and 30 of *I. acumi-*

natus were dissected and placed in Petri dishes. All together 11 species of ophiostomatoid fungi were isolated from the three bark beetles; five species from *P. bidentatus*, six species from *P. quadridens* and four species from *I. acuminatus*. *Ophiostoma* species were most common with six different species isolated; *O. bicolor*, *O. ips*, *O. macrosporum*, *O. minus*, *O. saponiodorum* and an undescribed *Ophiostoma* species. The other species were an undescribed *Graphilbum* species, an undescribed *Graphium* species, *Grosmannia olivacea*, a species in the *Grosmannia piceiperda* complex, and *Leptographium chlamydatum*. Two of the species were isolated from all three bark beetles; *O. minus*, a species associated with several bark beetles in the northern boreal forests, and an undescribed *Graphilbum* species. The undescribed *Graphilbum* species was the most common species isolated from both of *P. bidentatus* and *I. acuminatus* while *O. minus* was most common with *P. quadridens*.

In addition to the ophiostomatoid fungi 34 other species were isolated, mostly at low frequencies. However, a few species were isolated from more than 20 % of the *P. quadridens* bark beetles. Those were *Allantophomopsis* sp., *Geosmithia* sp and *Phacidiopycnis* sp. Of these, *Geosmithia* is of great interest since some species has been reported from bark beetles in other studies and no species of this genus has been reported from Norway before. In this study three different undescribed *Geosmithia* species were detected. As a group *Penicillium* sp. was most common with five species isolated. Only 2-3 species within Basidiomycota were found in this study; *Fuscoporia* sp., having 97-98 % similarity with *F. gilva*, which is not a European species,

Phellinus sp., with sequences close to *Fuscosporia* sequences, but still different, and a species which could be an *Entomocorticium* species.

In Norway only 22 species of ophiostomatoide fungi had been published before this Master thesis started. In this thesis seven new ophiostomatoid species for Norway was found.

In addition to the three undescribed species mentions above the following species are new to Norway, *Ophiostoma ips*, *O. macrosporum*, *O. minus* and *O. saponiodorum*. This Master thesis gives a good contribution to learn more about the biodiversity of ophiostomatoid fungi in Norway.



Culture of *Ophiostoma ips* growing on malt agar. Photo: H. Solheim.

Popularisert sammendrag/bidrag

Peziza nordica, en ny art på vasstrukken ved, fra Hallingskarvet

Roy Kristiansen, Postboks 32, NO-1650 Sellebakk

Sammendrag

Dette er historien om oppdagelsen av den nye arten *Peziza nordica* Kristiansen, LoBuglio & Pfister. Arten karakteriseres av en lang stilk, sporer med glatte eller svakt utviklede transverse rynker og gule dråper i parafysene. Soppen ble funnet på død vasstrukken ved av fjellbjørk og vier i et bekkeleie i Buskerud, nær Hallingskarvet nasjonalpark ca. 1000 m.o.h. Den er beslektet med *P. oliviae*, *P. lohjaoensis* og *P. montirivicola*.

Abstract

This is the history of the discovery of the new species *Peziza nordica* Kristiansen, LoBuglio & Pfister. The species is characterized by a distinct stipe, ascospores with smooth or weakly developed transverse wrinkled surface

and yellow vacuolar inclusions in the paraphyses. It was found on dead water soaked wood of birch and willow scrubs in a small stream in Buskerud county, close to the Hallingskarvet national park, ca. 1000 m asl. It is genetically related to *P. oliviae*, *P. lohjaoensis* and *P. montirivicola*.

Innledning

I august 2014 ferierte jeg noen dager på Gurostølen ved Myrland i Hol kommune, tett opp til Hallingskarvet nasjonalpark. Her ligger det regulerte Strandavatn, ca. 950 m.o.h. (Figur 1). Flere steder langs strendene på østsiden av vannet ligger store mengder døde nakne greiner og stokker av fjellbjørk og vier, revet løs under snøsmelting eller avsatt som følge av høyt nivå i Strandavatn (Figur 2).



Figur 1. Hallingskarvet. Kart som viser lokaliteten for *Peziza nordica*.
Map showing the location of *Peziza nordica*. Photo: R. Kristiansen.



Figur 2. Typelokaliteten for *Peziza nordica*.
Type locality of *Peziza nordica*. Photo: R. Kristiansen.

Mye av dette ligger i større og mindre bekkeleier, og holdes kontinuerlig fuktige med tilsig av rennende smeltevann. Denne veden er sterkt vasstrucken, uten å være direkte råttan, og synes og holde på fuktigheten hele året, og er naturligvis snødekket hele vinteren. Fenologien varierer mye i fjellheimen og dette påvirker naturlig nok fremveksten av blomster og sopp.

I et fuktig bekkeleie med mye dødt vassstruktent vedavfall, på utkikk etter akvatiske begersopper (slektene *Adelphella*, *Pachyella*, *Vibrissea*, *Cudoniella* og *Scutellinia*), kom jeg tilfeldigvis over en stor oransjebrun beger-sopp med lang stilk, voksende på en vasstrucken død staur av fjellbjørk. Soppen var umiddelbart helt ukjent for meg. Den minnet overfladisk litt om en *Helvella* morfologisk, men farge, habitatet og konsistens passet dårlig.

Soppene var noe forkomne (Figur 3), flere hadde kollapset og tidspunktet, medio august, kunne indikere en forsommer-/vårart? En påfølgende mikroskopering med bl.a. Meltzer



Figur 3. *Peziza nordica*, første funn 2014.
Peziza nordica, first finding 2014. Photo: R. Kristiansen.



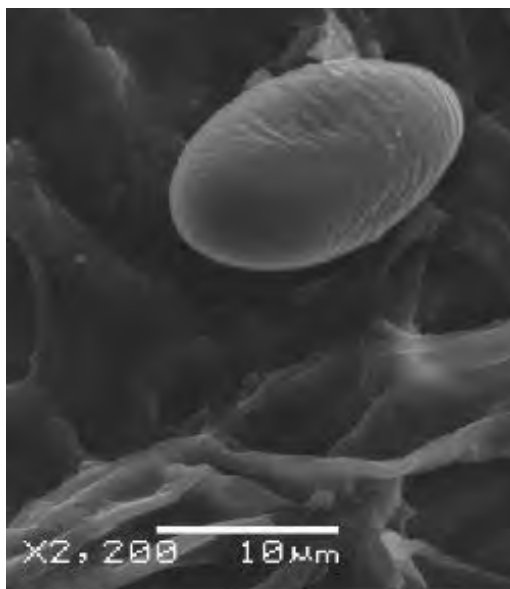
Figur 4. *Peziza nordica*, funn 2015.
Peziza nordica, *finding 2015*. Photo: R. Kristiansen.

reagens viste amyloid reaksjon og dermed en slekt i Pezizaceae. Også andre karakterer indikerte en art i *Peziza*-slekten, men med påfallende stilk, noe som er svært uvanlig for slekten.

Jeg tok umiddelbart kontakt med professor Don Pfister ved Farlow-herbariet ved Harvard universitetet i USA, en av de fremste eksperter på *Peziza*-slekten. Han ble straks veldig interessert og det beste av det tørkede materiale ble sendt ham, sammen med bilder og relevant informasjon om funnstedet og mine mikroskopiske observasjoner. Våre innledende morfologiske og fylogenetiske studier fikk



Figur 5. Asci med sporer og tydelig amyloid reaksjon i toppen.
Asci with spores showing operculum and amyloid reaction. Photo: R. Kristiansen.



Figur 6a. Scanning elektron mikrografi som viser tverrgående rynker.
SEM showing transverse wrinkles on ascospore.

Photo: D. Nishio-Hamane.

Figur 6b. Scanning elektron mikrografi som viser glatte sporer.
SEM showing apparently smooth ascospores.

Photo: D. Nishio-Hamane.

oss til å undersøke andre arter i den store og heterogene *Peziza*-slekten, og den nærmeste nærstående var en nybeskrevet art fra Oregon i USA, *Peziza oliviae* Frank (Frank 2013), som vokste under rennende vann, på tre- og planteavfall på bunnen, mer enn 1000 m.o.h. Påfølgende sekvenseringer ved Harvard viste, foruten *P. oliviae*, et slektskap med en art fra Finland, *P. lohjaensis* (Harmaja 1988) og den

nybeskrevne *P. montirivicola* fra Montenegro (Peric og Grebenc 2015). Disse artene synes å ha en boreal utbredelse og fruktifiserer tidlig i sesongen. De innledende undersøkelsene tydet på at vi sto ovenfor en ny art i *Peziza*-slekten og arten ble detaljert beskrevet av Pfister et al. (2016) og fikk navnet *Peziza nordica*.

Et nytt funn på samme lokaliteten tidlig i august 2015 viste langt friskere apothecier (Figur 4), men også mange små og umodne eksemplarer, noe som kunne skyldes den usedvanlige kalde sommeren (molta var fortsatt i blomst og blåbærene ennå bare som små rosa bjeller) og sen fremvekst. Dette var igjen indikasjon på en forsommerart. Ved en

befaring i midten av august 2016 ble det funnet nesten et dusin eksemplarer, dvs. tredje året på rad, men flere var litt medtatte.

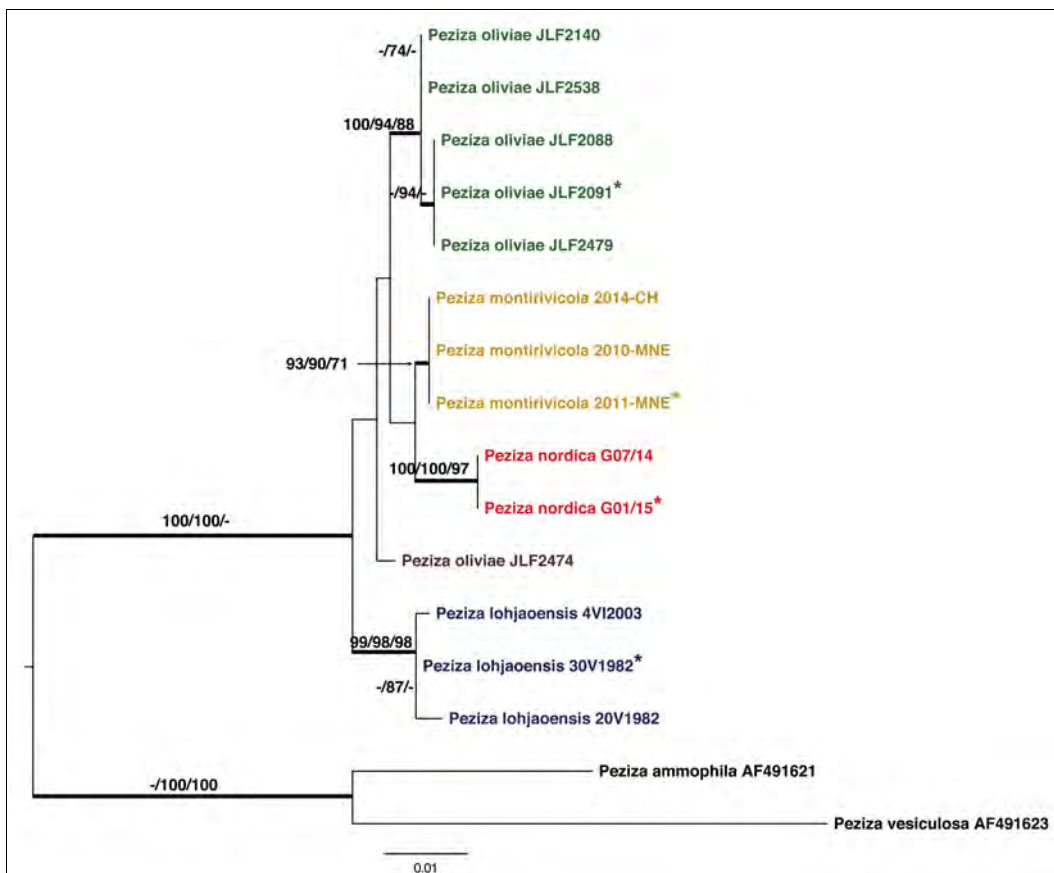
Beskrivelse

Mikroskopiske karakterer, observasjoner og fotografering er gjort på friskt materiale.

Det er gjort squash-preparater i vann, i Meltzer reagens og Cotton blue i melkesyre. Til undersøkelsen er det anvendt et Olympus stereomikroskop og et Kyowa lysmikroskop.

Figs. 3, 4, 5, 6a, 6b.

Apothecier 4-8 cm i diameter, dypt begerformet, ofte med lappet kant og delt i flere kammer. Hymenium lyst brunt til brunlig



Figur 7. Fylogram som viser slektskapet mellom *P. nordica* og nærstående arter. *Phylogenetic diagram showing P. nordica and related similar species.* Copy from Pfister et al. (2016).

oransje, utsiden glatt eller litt pruinøs og noe hygroman, og av samme farge eller mer gulaktig. Distinkt stilk, blek brun til gulig hvit, 2-5 cm høy, 0,5-1 cm tykk. Kjøttet er skjørt, men noe fleksibelt. Ingen melkesaft.

Asci (Figur 5): 8-sporet, men enkelte aborterte, J^+ , 300-350 x 15-18 μm , med en tydelig utviklet amyloid ring i toppen, avsmalnende mot basis, brunlige vegger.

Ascosporer: en-radet, smalt ellipsoide, 22-25 x 11-12 μm , hyaline, uten oljedråper, men med grynet innhold, spesielt på umodne sporer. de Bary bobler opptrer sjeldent; først helt glatte og tykkveggede. På enkelte sporer utvikles en svak transvers rynket overflate, som ikke farges i Cotton blue, men som sees godt i scanning elektron mikrografi (Figur 6 a og b).

Parafyser: rette eller svakt bøyde i toppen, 5-7 μm tykke, til 9-10 μm i toppen, med mange små gule dråper (vacuoler) i øvre septa. Disse inklusjonene løser seg i vann. Eksipulum består av tre indistinkte lag og de ytterste cellene er runde, opp til 80 μm , hvor det vokser korte vridde eller bøyde hyfer ca. 100 μm lange.

Undersøkt materiale: Buskerud, Hol kommune, i sydenden av Strandavatn nær Gurostølen i Myrland, på grensen til Hallingskarvet nasjonalpark, ca. 950-1000 m over havet, på død vasstrukken ved av fjellbjørk og vier, 60° 40' 14.08 " N, 7° 56' 26.37 " Ø.

11. august 2014 (# G 07/14) Herb. FH 00304780 og (O).

1. august 2015 (# G 01/15) Herb. FH 00304781, isotype (O).

16. august 2016 (# G 01/16) Herb. (O).

Kommentarer: Det er flere klare karakterer på denne soppen; den er bl.a. langstilket og dette er svært uvanlig for *Peziza s. str.*, men lik *P. oliviae* og *P. montirivicola*. I originalartikkelen

(Pfister et al. 2016) er det laget en tabell som sammenlikner morfologien og økologien for disse nærstående artene. *P. nordica* er f.eks. større enn *P. oliviae*. Dråpene/vacuolene i parafysene skiller den fra alle de andre artene i *Peziza s. str.* De fire nærstående artene synes å vokse på ved som er gjennomvåt av ferskvann og forekommer på våren eller tidlig i sesongen. Et utsnitt av fylogrammet fra Pfister et al. (2016) viser slektskapet (Figur 7).

De diffuse tverrgående rynkene på sporene på vår art kan være et modningsfenomen og er vanskelig å se i lysmikroskopet og farges ikke i Cotton blue. Denne karakteren er ikke helt ukjent, men er langt mer utpreget på f.eks. *Plectania rhytida* (Sarcosomataceae) uten sammenlikning forøvrig.

Allerede i 1983 fant vi en ny art fra samme område: *Lamprospora norvegica* Benkert, Aas & Kristiansen (Benkert et al. 1991) sammen med flere andre discomyceter. Ikke langt unna, på Geiteryggen, beskrev vi enda en ny bryofil art, *Octospora splachnophila* (Benkert og Kristiansen 2008), og nå *Peziza nordica* – og det er kanskje ikke den siste?

Den foreliggende presentasjon er ment å informere sopp-plukkere og mykologer utover i det ganske land med tanke på andre funnsteder i fjellheimen fordi voksestedet ikke er enestående. Men man må fokusere på større ansamlinger av død vasstrukken ved i bekke- og elveleier i rimelig høyde over havet, men neppe høyere enn tregrensen.

Avslutningsvis kan det nevnes at soppen fikk bred omtale i lokalavisa Hallingdølen i august 2016 (Sandvik 2016).

Interesserte kan få oversendt en pdf-fil av originalartikkelen (Pfister et al. 2016) på forespørsel.

Takk

I am deeply indebted to Dr. Daisuke Nishio-Hamane, The Institute for Solid state Physics, University of Tokyo, for scanning electron micrography of the ascospores.

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Thor Dybhavn 80 år

En markant skikkelse i soppmiljøet i Norge, Thor Dybhavn, rundet 80 år 23. februar. Thor er en mann med stor kapasitet og mange interesser, med et imponerende omfang og spennvidde. Foruten sopp strekker interessene seg fra tegning og sportsfiske til paleontologi, historie, arkitektur, mytologi, parapsykologi, litteratur og viner. Og da har vi nok ikke fått med alt!



Når det gjelder Thor snakker vi ikke om overfladisk interesse, eller kunnskap. Han setter seg grundig inn i alt han interesserer seg for og har holdt foredrag og skrevet artikler om mange av disse emnene. Som et bevis på hans solide kunnskaper på mange områder kan nevnes at han gikk til topps i NRK's spørreprogram «Eldprøva» i 1980.

Interessene hans har også ført ham ut på mange reiser, flere som turleder. Og Thor klarer seg selvsagt godt hvor enn han er i verden da han behersker både engelsk, tysk, fransk, spansk, russisk og visstnok noe mandarin.

Thor har heller aldri vært redd for å engasjere seg og mange foreninger har nytt godt av hans solide innsats. Han har vært formann i Fredrikstad Forsvarsforening, styremedlem i reserveoffisersforeningen, medlem av Fredrikstad bystyre, 1. direktør i klubbsekskapet Phønix, styremedlem i Fredrikstad tegne- og maleklubb, president i Fredrikstad Lions, «Ridder av det tunge lodd» i Fredrikstad handelsstandsforening og deltagende i Norsk klassisk forbund.

Så er vi i soppmiljøet så heldig at en av Thors kanskje største lidenskaper har vært sopp. Han var med på å stifte Fredrikstad

Soppforening i 1973 og har vært med i styret hele tiden siden den gang, både som formann og med andre verv. Fortsatt er han styremedlem og selvsagt er han også blitt tildelt æresmedlemskap. Før Norges sopp- og nyttevekstforbund ble dannet satt han i styret i

Nyttevekstforeningen. I Agarica var han medlem av redaksjonen den tiden tidsskriftet ble drevet av FSF og han bidro selv også med flere artikler. Kunnskapene hans om sopp er store, blant annet har han jobbet mye med kremler, og vært en nasjonal kapasitet på det området. Og Thor har aldri vært lei på å dele sine kunnskaper med andre, hverken når det gjelder sopp eller annet. Vi er mange soppinteresserte som har vært så heldige å ha ham som mentor og fått nytte av hans raushet. Og på FSF's turer har Thors historiske foredrag, enten de har vært planlagte eller spontane, vært populære og imponerende innslag.

Thor har fylt 80 år, men har på ingen måte gitt seg. Han har stått i sin jobb som tannlege helt til nå, men det ryktes visstnok at han nå skal trappe ned. Men for soppens sake er han fortsatt aktiv og en stor bidragsyter for Fredrikstad Soppforening.

Vi gratulerer deg, Thor, på det hjerteligste med 80 fylte år og takker samtidig for alt du har vært, og alt du har gjort, for foreningen. Og håper vi i mange år fremover fortsatt får hygge oss i ditt gode selskap og øse av din kunnskap.

Varme hilsener
Styret i Fredrikstad Soppforening

Emanuele Campo: *Hygrophorus, Hygrocybe e Cuphophyllus del Friuli Venezia Giulia*

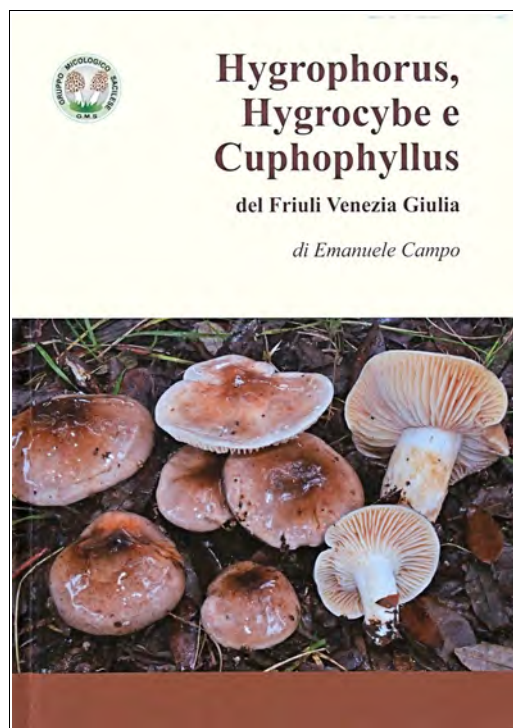
Gruppo Micologico Sacilese, Sacile (PN), Italia, 2015, 182 sider. På italiensk.

Pris € 20 + porto.

Kan bestilles fra:

gruppomicologicosacilese@gmail.com

eller direkte fra forfatteren: ecampo@alice.it



Helt i det nordøstre hjørnet av Italia finner vi regionen Friuli Venezia Giulia. Den er ikke stor, omtrent halvparten så stor som Buskerud fylke, men har variert topologi og klima idet den strekker seg fra den oseanisk Adriaterhavskysten til et kontinentalt klima i Alpene med høyeste topp 2700 m. Her fins en mykologisk forening som nylig har utgitt en bok om regionens vokssopper. Området har imponerende mange vokssopper. Boka behandler hele 83 arter/varieteter fordelt på

42 engvokssopper (slektene *Hygrocybe* og *Cuphophyllus*) og 41 skogvokssopper (*Hygrophorus*), og de aller fleste av dem fins også i Norge. Her kjenner vi 85 vokssopper hvorav 53 arter/varieteter er engvokssopper og 32 er skogvokssopper i følge Funga Nordica (2012).

Vokssoppboka minner i oppsett, format og størrelse om den nyeste boka om musseronger (Christensen og Heilmann-Clausen 2013, anmeldt i *Agarica* 35, 2014). Hver art har et oppslag på to sider og her er beskrivelser samt svært gode fotografier av både fruktlegemer og sporer. Boka inneholder dessuten vakre akvareller av nær alle artene laget av den nylig avdøde Ennio Cautero, tydeligvis en *primus motor* i regionens soppmiljø. For hver art er det i tillegg kart som viser utbredelse i regionen og/eller fotos av typiske voksesteder. Innledningsvis fins en bestemmelsesnøkkel til artene, men denne og beskrivelsene har man nok best nytte av hvis man skjønner italiensk. Boka holder seg til en relativt moderne oppfatning og navngiving av artene, og representerer ikke revolusjonerende ny forskning basert på molekylære studier. Men siden den omfatter de fleste av artene her i Norden, og dessuten presenterer en del sydlige arter i Europa, kan den være nyttig for oss.

I Norge og Norden er skogvokssoppene relativt dårlig undersøkt og det er lite tilgjengelig litteratur. Sveriges Mykologiske Forening har sett dette, og startet nylig et landsomfattende prosjekt for utforskning av skogvokssoppene med en tilhørende nyttig liten feltguide (Larsson m. fl. 2011). Allerede nå er arter nye for Norden og vitenskapen oppdaget gjennom prosjektet og feltguiden trenger oppdatering. Engvokssopper derimot har blitt samlet og studert nøye i senere år i forbindelse med deres signalverdi for verneverdig kulturlandskap og rødlistestatus

og vi har god bestemmelseslitteratur (Boertmann 2010).

Som det framgår vil jeg anbefale denne boka; den er både vakker og relevant, og koster ikke all verden heller!

Litteratur

- Boertman D, 2010. 2. ed. The genus *Hygrocybe*. Fungi of Northern Europe – 1.
 Christensen M, Heilmann-Clausen J, 2013. The genus *Tricholoma*. Fungi of Northern Europe – 4.

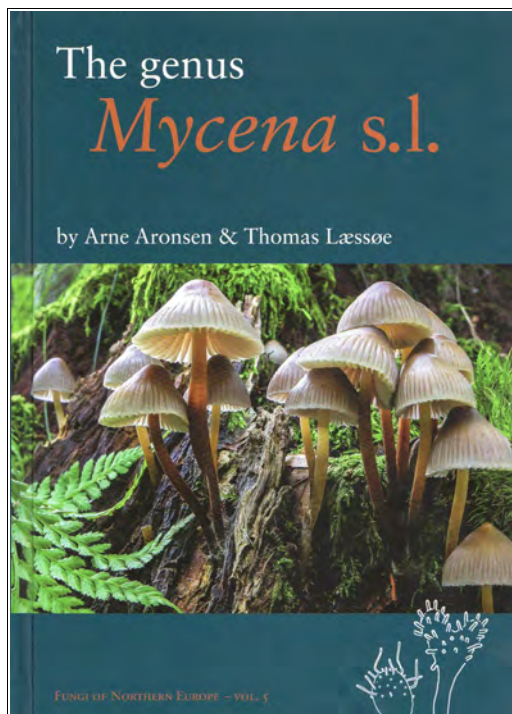
Larsson E, Jacobsson S, Stridvall A, 2011. Släktet *Hygrophorus*, skogsvaxskivlingar i Sverige. En fältguide till SMS's svampväxteri «Vaxvakt». Mykologiska publikationer 3.

Gro Gulden



Arne Aronsen og Thomas Læssøe: The genus *Mycena* s. l.

Fungi of Northern Europe, vol. 5,
København 2016. ISBN 978-87-983581-2-1.
Kan bestilles fra Svampetryk
www.svampe.dk, pris DKK 375,-/450,-
medlem/ikke medlem



Dette er en usedvanlig vakker bok. De fremragende fotografiene av alle de små hettesoppene og de nitide tegningene av alle viktige mikroskopiske karakterer kan knapt gjøres bedre. Nesten hvert bilde er et kunstverk. Artene er fotografert i naturen og Arne Aronsen har vært mester for de fleste av bildene, men en rekke andre fotografer har også bidratt. Både de avbildete soppene og fotografen kan identifiseres ut fra billedteksten som befinner seg litt diskret på siden av bildet. Tegningene er i sin helhet utført av Aronsen. Det er langt fra enkelt å mikroskopere og lage tegninger av slikt som hatt- og stilkhud med diverse

utvekster og cystider hos mange av de ørsmå soppene; det vitner om både stor nøyaktighet og tålmodighet. Bak de utførlige beskrivelsene av i alt 115 arter, med makro- og mikroskopiske karakterer, ligger nok adskillige arbeidstimer. Men hvem skulle trodd at vi har så mange hettesopper? De er jo nesten like tallrike som riskene og kremlene! De fleste er utsøkt elegante, riktignok ikke så utpreget fargesprakende med en fargeskala hovedsakelig i brunt, grått og svart, men enkelte er gule, rosa, og røde, og mange arter er nærmest hvite. Dessuten kan samtlige arter forekomme i helt hvite former (albinos) slås det fast på side 44.

Boka inngår som vol. 5 i serien «Fungi of Northern Europe» og dokumenterer på fremragende vis 115 arter av i alt ca 160 som skal være kjent i Nord-Europa. Det går ikke tydelig fram om alle de 115 er funnet her i Norden, eller om også enkelte andre nord-europeiske arter er med. En nesten 4-siders tabell, hvor artene er sortert etter substrat og habitat, og hele 12 fotografier som viser typiske habitater for hettesopper – fra havstrand til høyfjell – formidler viktige observasjoner om hettesoppenes økologi; mange av dem er spesialister på hvert sitt habitat eller substrat! Jeg savner noe mer informasjon om geografiske forhold selv om den kjente nord-europeiske utbredelsen i korte trekk er angitt i teksten. Utbredelseskart er kanskje lite hensiktsmessige tatt i betraktning at en god del av artene er sjeldne eller stort sett bare kjent av spesialister og derfor lite registrert. En bemerkning verd er at mange av artene også er kjent i Nord-Amerika og trolig bør klassifiseres som sirkumboreale.

Med to forskjellige bestemmelsesnøkler – den ene (17 sider) hovedsakelig basert på makroskopiske karakterer, den andre (11 sider) med utgangspunkt i mikroskopiske karakterer skal leseren være godt rustet for å identifisere hettesopper. Jeg har ikke prøvd nøklene, men

de følger ganske nøyaktig dem vi finner i *Funga Nordica* (2012) som begge forfatterne står som forfattere for – og disse fungerer erfaringsmessig veldig bra. Begrepene/termene som brukes i nøklene, både for makro- og mikroskopiske karakterer, er forklart og illustrert med ypperlige fotos og tegninger. Hvis man skulle finne en liten, tynnstilket, hvitsporet sopp som man ikke umiddelbart vet er en hettesopp kan oversikten over i alt 27 andre slekter som inneholder hettesopp-lignende arter være svært nyttig, kanskje spesielt den nesten fire siders lange nøkkelen til disse, som avslutter avsnittet. Den kan sikkert også være nyttig i mange andre sammenhenger!

Forfatterne framholder allerede i forordet at denne boka er mindre vitenskapelig enn det forrige volumet (om musseronger) i serien av nord-europeiske fungaer. Ikke desto mindre er boka en nøyaktig dokumentasjon, proppet med egne observasjoner, data og erfaringer om hettesopper. Nomenklatoriske problemer er i liten grad diskutert og antallet synonymer som er angitt er relativt lavt. Det mangler også noe informasjon om det studerte materialet. Det svært korte avsnittet med overskriften «Material and Methods» har overhode ingen opplysninger om materialet. Men av avsnittet med takk til medhjelperne, som er plassert aller først i boka, går det fram at herbariemateriale har vært innlånt fra både herbarier og privatpersoner. Jeg antar at forfatterne selv har gjort det meste av innsamlingene, men hvor disse så befinner seg er en gåte.

Det store dilemmaet for forfatterne har forståelig nok vært hvordan slekten *Mycena* i denne boka bør avgrensnes mot andre slekter og hva som bør settes ut til andre slekter. De fremholder at artene utvilsomt før eller siden vil bli fordelt på en rekke nye slekter, og det vises til at flere nye 'småslekter' basert på molekylære analyser allerede er formelt publisert. I boka har de valgt å framstille slekten i ganske så tradisjonell forstand, på linje med slik den er presentert i *Funga Nordica*

hvor bare de to morfologisk definerte slektene *Roridomyces* og *Recinomyцена* (hver med én art i området) er anerkjent. Siden mange biter enda mangler i dette puslespillet om slektskap, er dette etter mitt syn et fornuftig standpunkt. Vi støter også på et annet av dagens dilemmaer, nemlig oppløsningen av enkelte av de gamle «artene» i flere biologiske arter på grunnlag av DNA-analyser. Forfatterne stadfester at flere av artene i boka snart kommer til å oppløses i slike molekylært baserte arter — som muligens senere ved nøyaktige observasjoner vil kunne gjenkjennes på morfologi. De forespeiler oss dessuten at flere av de aksepterte artene i boka vil kunne bli slått sammen på grunnlag av molekylære studier.

Helt utenfor den nye molekylære æra har forfatterne dog ikke vært. I boka publiseres bl.a. to nye arter for vitenskapen: *Mycena mucoroides* Aronsen og *Mycena pasvikensis* Aronsen, begge analysert med hensyn på molekylære forskjeller men egentlig opprinnelig erkjent på basis av morfologiske karakterer. I boka finner vi ytterligere 10 arter som er blitt beskrevet som nye av Aronsen tidligere, enten alene eller med medforfattere, og 1 art som er beskrevet av Læssøe og Bugge Harder. Bare to av disse 11 for vitenskapen relativt nye artene har blitt studert molekylært.

Tatt i betraktning at slekten *Mycena* har vært gjenstand for en rekke omfattende monografier tidligere, noe som er behørig omtalt i bokas innledende kapittel, er det ganske påfallende at så mange nye hettesopper er blitt beskrevet i senere tid fra Norden. Jeg tror det kan være en ny påminnelse om at nordiske arter i stor grad har vært oversett og ofte dyttet inn i og fått navn etter mer tempererte arter. Dette er sikkert ikke uten grunn, men har foregått fordi nordiske mykologiske verker med beskrivelser av boreale arter i liten grad har foreligget. Vi begynner kanskje å se en endring i dette mønsteret bl.a. ved publiseringen av viktige monografier som «Fungi of Northern Europe».

Boka er skrevet på engelsk og i stor grad basert på forarbeider på Aronsens hjemmeside (<http://www.mycena.no/>). Læssøes innsats er vanskeligere å få øye på, men hans omfattende taksonomiske kunnskaper, brede felterfaring og nesten livslange interesse for hettesopper er sikkert nedfelt i både tekst og artsopppfatninger. Også «Art director» Jens H. Petersen skal

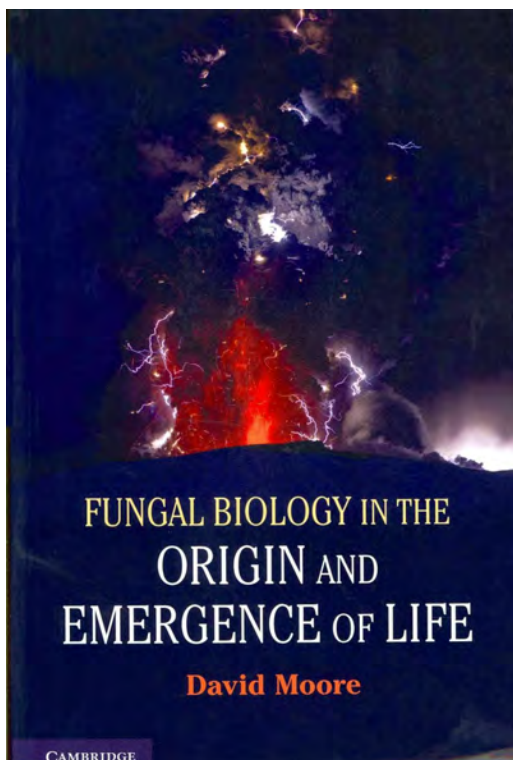
utvilsomt ha en del av æren for bokas tiltalende utseende. Den kommer til å bli et absolutt «must» for alle med interesse for slekten *Mycena* både hjemme og ute, også for dem som sverger til nettet vil jeg mene.

Gro Gulden



David Moore: Fungal Biology in the Origin and Emergence of Life

Cambridge University Press, Cambridge
2013, ISBN 978-1-107-65277-4. Paperback.
Pris € 27,99, US \$ 42,99.



Ei bok om sopp og livets opprinnelse virker, mildt sagt, spesielt. Førsteintrykket mitt var at dette her må være nok et forsøk på å mystifisere. Slike bøker er det skrevet nok av. Men forfatteren, David Moore, er ingen hvemsomhelst innen mykologien. Han har blant annet skrevet meget gode lærebøker om soppene og deres biologi. Med andre ord, han er ingen alternativforfatter som vil skape blest om sine tanker om sopp, verden og Universet, gjerne ispedd litt overtro og hallusinasjoner. Den som håper på slikt, blir skuffet!

Boka er derimot en fryd å lese for den som interesserer seg for soppenes generelle biologi, basal evolusjon, livets opprinnelse, paleontologi, fysiologi osv. Stoffet er vanskelig – det skal jeg ikke underslå – men Moore skriver knakende godt og inspirerende. Litt grunnkunnskaper i biokjemi vil nok likevel være en fordel.

Det første kapittelet starter med ideer om livets opprinnelse og evolusjon, men går raskt over til soppene, der vi får en kortfattet, men innholdsrik behandling av soppriket, med for mykologer velkjente aspekter som råte, mutualisme, parasittisme, øl og vin, cyklosporin osv.

Så følger et kapittel om soppenes grunnleggende biologi, med fine skjematisk illustrasjoner om oppbygging av cellevegg og indre strukturer i hyfetuppen (hvordan enzymer går ut og næring inn i hyfen). Biokjemiske ting som kolesterol og ergosterol, cellulose, kitin og glukose forklares med enkle strukturformler. Videre beskrives oppbygningen av de enkle algesoppene fram til mer kompliserte mycel hos stilksporesoppene.

De neste kapitlene går inn på hvordan det ble liv. Hvilke grunnleggende forhold må til? Jordas første milliard år. Hvilke basale kjemiske byggesteiner fantes? Kom livet fra andre steder i Universet (panspermia-hypotesen)? Hvor forfatteren konkluderer: “Whether it is or not; I think, we should put the fanciful notion of panspermia and life on a cosmic scale on the back burner and return to planet Earth.” Videre: Hvordan ble de organiske stoffene som er nødvendige for liv syntetisert før det ble liv? Hvorledes ble livet til? Lyn og UV, undersjøiske vulkanutblåsninger, eller fra kometer og asteroider? Hva er liv? Og hva skjedde og hvor? Her omtales mange interessante biokjemiske hypoteser. Deretter blir vi kjent med LUCA

(Last Universal Common Ancestor) og hvilke kandidater som er bidragsytere til LUCA. Moore ser for seg at de nødvendige reaksjonene kom i stand der regnvann eller sjøvann sildret på tak av vulkanske huler på ei vulkanøy hvor det akkumulerte seg en biofilm av ulike proteiner, nukleinsyrer, karbohydrater osv. Jeg liker forfatterens avslutning på kapittelet om LUCA: “You can forget all those theories in which the origin of life occurs in an oceanic primeval soup or in a deep, hot place somewhere, or even a warm little pond. Life originated as a biofilm, and the precursors and components of the first fully working biofilm were brought together by oscillations of drifting aerosol droplets from around the globe that acted as dynamic reaction vessels. You don’t need to stare dreamingly into the distant sky, or to the far horizon of the boundless ocean to find the field of play where life’s game on Earth was first played out. It’s in the rainwater and seawater trickling through the roofs of volcanic caves on the spindrift-washed shore of a volcanic island in the endless shallow sea. Step carefully; it’s in the slime on the volcanic sand at your feet.”

Deretter kommer kapitler om hvordan de eukaryote oppsto, fra LUCA til ELCA (Eukaryotes Last Common Ancestor), og derfra til soppenes opprinnelse. Kapitlet om sopp

inneholder mye viktig om soppenes tidlige evolusjon og fylogeni, deres relasjon til andre riker, og om diverse fossile sopp. Visste dere at for omtrent 400 millioner år siden fantes sopper som kunne bli opptil 10 meter høye og en meter breie? Det var *Protaxites*, som lenge ble trodd å være en stamme av et bartre.

Det siste kapittelet oppsummerer evolusjonen av de eukaroyte fra ELCA til dagens verden, og hvordan soppene på ulike måter har grepet inn i evolusjonen og økologien. Skikkelig fascinerende! La meg sitere det siste avsnittet, og dere må lese hvorfor: “That’s why I suggest it’s fair to say that fungi co-operate with humans, and it involves the oldest of the fungi, the chytrids. They waited nearly 1.5 billion years to give human evolution a show in the right direction. Thank fungus for that!”

Det avsluttes med en nyttig tabell over alle eoner, æraer og perioder fra midt-prekambrium (proterozoikum) til i dag, og hva som skjedde i de ulike tidene.

For alle som er interessert i mykologi litt utafor “boksen” og samtidig vil “strekke” seg litt mht mykologifaget. Dette er boka!

Klaus Høiland