

***Entoloma* species of the rhodopolioid clade (subgenus *Entoloma*; Tricholomatinae, Basidiomycota) in Norway**

Tor Erik Brandrud¹, Egil Bendiksen¹, John Bjarne Jordal², Øyvind Weholt³, Siw Elin Eidissen³, Jostein Lorås³, Bálint Dima^{4,5}, Machiel E. Noordeloos⁶

¹Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway

²Biolog J.B. Jordal, Auragata 3, NO-6600 Sunndalsøra, Norway

³Nord University, Nesna, NO-8700 Nesna, Norway

⁴Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary

⁵Department of Biosciences, Plant Biology, Viikki Plant Science Centre, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

⁶Naturalis Biodiversity Center, section Botany, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands

Corresponding author: tor.brandrud@nina.no

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NØKKELOORD: DNA-sekvensering, økologi, utbredelse, *Salix-Alnus-Betula*-arter, *Tilia-Quercus*-arter

SAMMENDRAG

Gruppa omkring lutrødspore (*Rhodopolia*-gruppa) i slekta rødspore (*Entoloma*) i Norge presenteres. Gruppa består av musserongaktige og flathattaktige, sjelden traktsoppaktige, mykorrhiza(sopp)rot-dannende arter. I alt 24

arter innenfor *Rhodopolia*-gruppa er samlet og verifisert med DNA-sekvensering. Av disse er 10 nye for Norge og inkluderer også tre ubeskrevne arter. Fire forskjellige øko-geografiske elementer kan skilles ut: (i) det sørlige (boreonemorale) lind-eik-hassel-elementet, (ii) det boreal-arktisk-alpine seljevier-or-bjørk-elementet, (iii) det arktisk-alpine dvergvier(-reinrose)-elementet, og (iv) det boreale bjørk(-gran)-elementet. Alle 24 artene kommenteres i den taksonomiske delen, ordnet etter de fem slektskapsgruppene (klader) som framkommer i den fylogenetiske analysen.

ABSTRACT

The rhodopolioid species of *Entoloma* (subgen. *Entoloma*) in Norway are presented. The rhodopolioid clade consists of tricholomatoid or collybioid, rarely omphalinoïd, ectomycorrhizal species. Altogether 24 species of the rhodopolioid clade were recorded and verified by rDNA ITS sequence data, of which 10 are here reported as new to Norway, including three apparently undescribed species. Four different eco-geographical elements can be

distinguished from our material; (i) the southern (boreonemoral) *Tilia-Quercus-Coryluselement*, (ii) the boreal-arctic-alpine *Salix-Alnus-Betula* element, (iii) the arctic-alpine *Salix(-Dryas)* element, and (iv) the boreal *Betula(-Picea)* element. All 24 species are commented in the taxonomic part, arranged according to the five well-supported clades from phylogenetic analyses.

INTRODUCTION

Entoloma is one of the most species-rich genera within *Agaricales*, well characterized by many-angled spores that leave a pinkish brown spore print. Like *Cortinarius*, it is one of the few remaining “mammoth-genera” which (at least in Europe) is still kept as one single genus and not split into several smaller genera, despite the large morphological, genetic and ecological variation across the numerous lineages (cfr. monographs of subgenera such as Morgado et al. 2013, Morozova et al. 2014, and regional fungas such as Jeppesen et al. 2012, Krieglsteiner and Gminder 2003, Ludwig 2007). The reasons for this comprehensive approach are manifold, but are mainly based on the fact that variability in *Entoloma* is complex and still not fully understood, and more specifically, many clades in phylogenetic analyses show low support with the genetic markers applied so far (see e.g. Morgado et al. 2013). This fragile phylogenetic structure, combined with the manifest lack of data from *Entoloma* species from many parts of the world, makes it too preliminary to subdivide this mammoth into smaller genera.

Subgenus *Entoloma* is nevertheless one of the genetically, ecologically and morphologically better defined entities within the genus, especially since it apparently consists of (ecto)mycorrhizal species (Kobayashi and Hatano 2001, Sánchez-García and Matheny 2016, Tedersoo et al. 2010). According to phylogeny, the mycorrhizal species in *Entoloma* can be subdivided into two well-

supported clades, the rhodopolioid clade (including the type species of the genus *E. sinuatum*) and the Nolanidea clade (incl. *E. chypeatum* and allies). The latter group has apparently a special variant of mycorrhiza including parasitism, and is associated with wooden plants rarely forming (ecto)mycorrhiza, such as Rosaceae members like *Sorbus*, *Prunus* and *Malus*, as well as *Ulmus* (Kobayashi and Hatano 2001). The present paper will, however, only focus on the rhodopolioid species.

The rhodopolioid species can be distinguished from the *E. chypeatum* group (Nolanidea clade) at the section level (sect. *Entoloma*) or at the subgenus level (subgen. *Entoloma* = subgen. *Rhodopolia* s. Kokkonen 2015). The infrageneric taxonomy we do not consider further in this paper, and hence we preliminary apply the terms rhodopolioid clade and rhodopolioid species for our study group (cfr. also e.g. Sánchez-García and Matheny 2016).

The rhodopolioid clade has been extensively treated by Noordeloos (1981, introducing sect. *Rhodopolia*, 1992, 2004) and by Kokkonen (2015 as subgen. *Rhodopolia*). The former studies were based on morphological taxonomy, whereas the latter also included DNA sequence data, focusing on boreal(-alpine) species from Finland. The rhodopolioid species are distinguished from many other *Entoloma* taxa by their (i) often large and robust basidiomata (although also small, tiny representatives occur), (ii) rather uniform predominantly brown, yellow-brown or grey-brown colours due to simultaneously encrusted-intracellular-plasmatic pigments (contrasting the often vivid colours seen in other groups), and (iii) often pronounced farinaceous or nitrous smells (Noordeloos 1981, 1992, 2004, Kokkonen 2015). The pileipellis structures are fairly simple, mainly a cutis or ixocutis of narrow, cylindrical hyphae, with or without a distinguishable subpellis layer of inflated, short elements. A number of species (e.g. *E. serpens*,

E. sericatum) have fine hairs, particularly at the margin of young and fresh specimens, visible as pileocystidia, but these structures are ephemeral and disappear with age. Caulocystidia frequently occur at the apex of the stipe, variable in shape. Cheilocystidia are rarely differentiated, but seem to be characteristic and constant for some species. The spores show apparently little, taxonomic relevant variation, size variation mainly expressing size difference of two-spored versus four-spored basidia (Noordeloos 1981, 1992, 2004, Kokkonen 2015). Many species occur in moist forest-woodland-shrubland habitats, and a remarkable high percentage of the species seems to be associated mainly with *Salix*, *Populus*, *Betula* and *Alnus* hosts, including arctic-alpine habitats (Noordeloos 2004, Kokkonen 2015). Conifers such as *Picea abies* seem hardly to be involved in the mycorrhizae of the rhodopolioid species, although many boreal species occur in *Picea*-dominated forests (with presence of single trees of *Salix*, *Betula* and other frondose trees) (Kokkonen 2015, and this paper).

The present paper is part of the Norwegian *Entoloma* study 2015–2017, as part of The Norwegian Taxonomy Initiative and funded by The Norwegian Biodiversity Information Centre. It also includes data from a study on the *Entoloma* fungi of the Holmvassdalen nature reserve, Nordland (see e.g. Weholt et al. 2014, Noordeloos et al. in prep). The Norwegian *Entoloma* project has focused on *Entoloma* hotspot-habitats, such as calcareous (semi-)natural grasslands and calcareous forests, but due to moderately good fungal seasons in the grasslands, the collections from (calcareous) forests and semi-open woodlands contribute a considerably large amount of the data, including many samples from the rhodopolioid clade. Most of the study samples have been verified by rDNA ITS sequencing, mainly through NorBOL (Norwegian Barcode of Life Network; see

Ratnasingham and Hebert (2007, 2013).

The present study focus on the ecology and distribution of the taxa recorded, based on ITS-sequence- and morphology data, with an emphasis on new species to Norway. At present, we have not sufficient sequence- and morphology data to present a detailed taxonomy of the group. In particular, more studies are needed on the morphological variation of our phylogenetic taxa, and to what degree they are possible to distinguish morphologically.

MATERIAL AND METHODS

Approximately 250 samples of rhodopolioid species have been collected during the Norwegian 2015–2017 *Entoloma* study, and 176 samples were verified by ITS sequencing. The latter number includes some herbarium collections. In addition sequences of six type specimens and some important reference material, not collected by us, were studied in connection with the present project. Sampling focused on boreonemoral and southern/middle boreal regions of SE Norway, where also other mycological field projects were carried out during the period. Further, many samples were obtained from North Trøndelag, C Norway, during a project foray in 2016, and many from the study of Holmvassdalen nature reserve, Nordland, including some alpine sites. All sequenced material from Norway is listed under material examined. Collections labelled NOBAS or CAFUN were sequenced through NorBOL, those labelled ALV were sequenced by Pablo Alvarado (ALVALAB, Spain), and those with no sequence label are original (B. Dima, in Budapest, ELTE). All sequences were analyzed by us (see below). Collector's numbers (ID's) are included with the following initials: AKS=leg. A.K.Svendsen; EB=leg. E. Bendiksen; GG=leg. G. Gulden; ILF=leg. I.-L.Fonneland; JBJ=leg. J.B.Jordal; JL=leg. J. Lorås; KK=leg. K. Kokkonen; MEN=leg. M.E. Noordeloos; MP=leg. M. Pettersen; OW=leg. Ø. Weholt; TEB=leg.

T.E.Brandrud. All material is deposited or will be deposited in O (Botanical Museum, University of Oslo). For further data on each collection (habitat, coordinates), see herbarium database (http://www.nhm2.uio.no/botanisk/nxd/sopp/nsd_b.htm) and Artskart (<https://artskart.artsdatabanken.no/app/#map/>).

Morphology

The macromorphological observations are based on field notes and photographs of the material studied. Microscopical observations were made using standard methods (see e.g. Morozova et al. 2014).

Molecular study

DNA extraction, PCR amplification and sequencing followed Weholt et al. (2014) and Noordeloos et al. (2017). Chromatograms were checked and edited with the CodonCode Aligner package (CodonCode Corp., Centerville, Massachusetts, USA).

Multiple sequence alignment was performed with MAFFT v. 7 using the E-INS-i algorithm (Katoh and Standley 2013). Manual adjustment was done in SeaView (Gouy et al. 2010). Maximum Likelihood (ML) analysis was carried out using RAxML (Stamatakis 2014) implemented in raxmlGUI (Silvestro and Michalak 2012). Rapid bootstrap analysis and 1,000 replicates under the GTRGAMMA substitution model were used for the partitioned alignment (ITS1, 5.8S, ITS2). The phylogenetic tree was edited in MEGA 7 (Kumar et al. 2016).

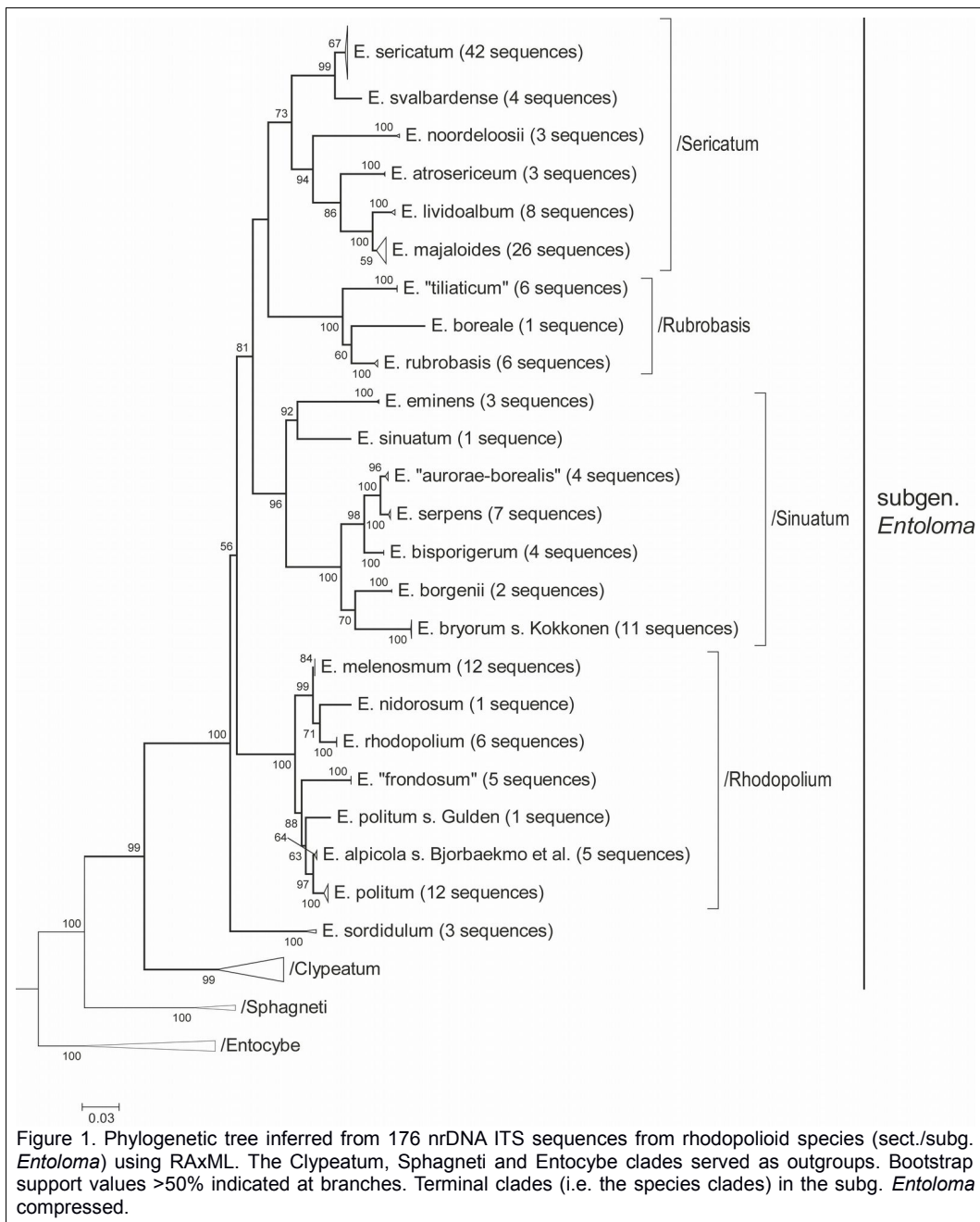
RESULTS AND DISCUSSION

Based on our phylogenetic analysis of the ITS sequences, 24 well-supported, rhodopolioid operational taxonomic units (OTUs) were recognized, of which 10 taxa are new to Norway (Figure 1, Table 1). Some of these OTUs show overlapping morphological characters, and should be regarded as cryptic or semi-cryptic species (see further comments under

taxonomic part). Among our 24 sequenced OTUs, 15 had a complete match with sequenced type materials (mainly sequenced by K. Kokkonen; six additional types originally sequenced), whereas six had a complete match with published reference materials (mainly from Morgado et al. 2013 and Kokkonen 2015), leaving three “nameless species” without a match with type or reference sequences.

An ITS phylogeny based on own sequences as well as sequences available from Kokkonen (2015) and other sources (GenBank, UNITE), distinguishes five well-supported (sub)clades within the rhodopolioid clade (Figure 1), the Sericatum clade, the Rubrobasis clade, the Sinuatum clade, the Rhodopolium clade, and finally the small Sordidulum clade, including only *E. sordidulum* s. Noordeloos in the Nordic countries. We present our rhodopolioid species according to these five clades. All 24 species are commented in the Taxonomic part, with focus on the 10 new ones. Our new/interesting species are found within all these five clades (Figure 1).

The material includes a remarkably high number of *Salix-Alnus* associates, and a remarkably low amount of coniferous forest associates, compared to other groups of ectomycorrhizal agarics (Table 1). Only one species (*E. boreale*) seems to be associated with *Picea* (or other conifers) in Norway, and since based only on one record, more data is needed to confirm this association. Altogether 11 species are mainly associated with *Salix* and *Alnus*, whereas five species seem to be associated (also) with *Betula* (Table 1). In other words, most of our Norwegian rhodopolioid taxa are associated with boreal deciduous trees, and many apparently with a wide range of hosts, but with preference for *Salix-Alnus*, and often in moist places. Altogether nine species are more or less exclusively associated with thermophilous deciduous trees (*Tilia*, *Corylus* and *Quercus*).



There is also a remarkably high amount of our species that have arctic-alpine populations, associated with dwarf shrubs of *Salix* and *Dryas* (10 species; Table 1). These populations

are often dwarfish, and often with so deviating features from the lowland populations, that they were described as own species. However, DNA sequencing with different molecular

markers has shown that some of these very likely are conspecific with lowland species, such as *E. subarcticum* (= *E. sericatum*) (Kokkonen 2015).

Based on their preferences for mycorrhizal hosts, and preferences for boreonemoral, boreal or arctic-alpine habitats, four major eco-geographical groups/elements can be distinguished in Norway (cf. Table 1);

- (i) the southern *Tilia-Quercus-Corylus* element
- (ii) the boreal-alpine-arctic *Salix-Alnus-Betula* element
- (iii) the arctic-alpine *Salix(-Dryas)* element
- (iv) the boreal *Betula (-Picea)* element

It should be noted that some of the species with a more or less wide habitat range might be difficult to place in one of these elements. This is further commented under the presentation of each element below.

The southern Tilia-Quercus-Corylus element

In Norway/Fennoscandia this is a fairly strict boreonemoral element, following the distribution of *Tilia cordata* and *Quercus* spp., but some northern outposts can be found in warm, southern boreal *Corylus* thickets, north to lake Randsfjorden-Mjøsa in southeastern Norway, and north to Møre and Romsdal along the western Norway coast. Altogether nine species belong to this southern element (Table 1), often occurring both in parks and forests, and often in richer clayey to calcareous soils. The majority of species are found only/mainly in calcareous *Tilia-Corylus(-Quercus)* forests (*E. eminens*, *E. lividoalbum*, *E. "tiliaticum"*, *E. noordeloosii*, *E. "frondosum"*) and a few only/mainly in rich *Quercus* forests (*E. sinuatum*, possibly also *E. sordidulum* s. Noordeloos). One species was found mainly in parks with *Tilia* (*E. bryorum* s. Kokkonen). Some of the other above mentioned species are also collected in grassy parks (*E. "tiliaticum"* and *E. lividoalbum* near *Tilia*; *E. sinuatum*, near *Quercus*).

Entoloma rhodopolium deviate from the above described pattern, since it is found both in boreonemoral forests with *Corylus(-Tilia)*, and southern boreal (coniferous) forests with *Betula*. Due to its mainly thermophilous distribution, it is placed here. *Entoloma nidorosum* s. Noordeloos is not possible to classify at the moment, but might belong here, based on the sole Norwegian collection from a thermophilous, mixed forest with *Corylus*, *Salix* and *Populus*.

Four of these species are new to Norway (Table 1) and two are new to Fennoscandia (see taxonomic part). Few of these southern taxa were reported in Kokkonen (2015) (only *E. bryorum* s. Kokkonen, *E. eminens*, and *E. lividoalbum*), who focused on the boreal element of rhodopolioid species in Finland. *Entoloma eminens* was reported by Kokkonen (2015) from boreal areas (near *Picea*, *Populus*, *Betula*), and with the present data it is not clear, whether this is a primarily boreal or a southern, boreonemoral species.

The boreal-arctic-alpine Salix-Alnus-Betula element

The six species belonging here occur both in boreal lowland areas and in arctic-alpine sites. Most collections of the boreal-arctic-alpine species are from the lowlands, but this could at least partly be due to a lowland sampling bias in our project. One of the species (*E. bisporigerum*) has not been found in arctic-alpine sites in Norway, but it has been recorded from an alpine site in Finland (Kokkonen 2015). The species we have included in this element, combines (i) a wide climatic range with an apparently often also (ii) a wide boreal deciduous tree host range, however, most with a preference for *Salix* and *Alnus*.

In the lowland sites, the species are found mainly in swampy-riparian forests or secondary habitats like road borders, parks, normally with *Salix* spp. and *Alnus* spp. Often *Betula* spp. and *Populus tremula* are also present on the

sites, and seem to be important co-associates for this element. Especially for the two most frequent species, *E. sericatum* and *E. majaloides*, our data strongly indicate that these have a broad range of deciduous tree hosts. They often occur in sites with a lot of *Picea abies*, but never in pure stands (e.g. pure plantations) without some deciduous trees in close vicinity. Therefore, we find it highly unlikely, that these are able to associate with *Picea abies* (or *Pinus sylvestris*). Also *E. serpens* seems to be associated with a wide range of boreal, deciduous tree hosts, but is not found in very moist habitats. *Entoloma bisporigerum* and *E. politum* seem to be associated only with *Alnus* and *Salix* in moist places in their Norwegian lowland sites, and the same is observed in Finland (Kokkonen 2015). *Entoloma politum* is according to present material the only species occurring in extreme, seasonally inundated, flooded forests along larger rivers and inland deltas in Norway.

Most species seem to prefer somewhat richer, often clayey soils. Some species, such as *E. serpens*, seem to be more or less calciphilous, and some species, such as *E. sericatum*, seem to tolerate rather high nitrogen levels, occurring sometimes with nitrophytes like *Urtica dioica*, which is a rare habitat for mycorrhizal agarics.

Our results, with a remarkable high amount of *Salix-Alnus(-Betula-Populus)* associates, are well in correspondence with those of Kokkonen (2015) from Finland. Kokkonen specifically focused swampy-wetland *Salix-Alnus*-dominated habitats, and found many species associated with these vegetation types, including some species hitherto not found in Norway, as well. Of these, at least *E. paludicola* very probably occurs also in our areas, since recorded both from Finland and England (as well as records from the Alps; Kokkonen 2015).

The arctic-alpine Salix(-Dryas) element

This is a group of four species solely recorded from arctic-alpine regions; *E. atrosericeum*, *E. svalbardense*, *E. borgenii*, and *E. alpicola* s. Bjorbækmo et al. These are totally or primarily associated with dwarf *Salix* species (*S. herbacea*, *S. polaris*, *S. reticulata*) or *Dryas* (see comments in the taxonomic part). Some of the boreal-alpine *Salix* associates of the last element discussed above, might co-occur with the present ones in arctic-alpine *Salix* snowbeds. However, the taxa of the above discussed element has a much wider habitat range than the present ones, and more often occur in alpine shrub vegetation of larger *Salix* species, such as *S. glauca* and *S. lapponum*, as well as lowland moist forests. So it seems reasonable to distinguish the wide habitat range species from the more specialized arctic-alpine ones in two elements. Also in other large ectomycorrhizal fungal genera such as *Cortinarius*, *Inocybe* and *Hebeloma*, one find in the arctic-alpine zones a mixture of lowland *Salix* species and more specialized arctic-alpine taxa (Beker et al. 2016).

It seems probable that many of the species from the two latter elements have a wide, circumpolar distribution. Finds in Greenland of some of these (cfr. Kokkonen 2015), support this hypothesis. *Entoloma majaloides* has also been verified by sequencing from British Columbia, Canada (S. Berch, pers. comm.).

The boreal Betula(-Picea) element

Some species do not fit in the above mentioned patterns, and seems to be mainly associated with *Betula* or possibly *Picea*. This includes taxa from the clades Rubrobasis and Rhodopolia. In Norway *Entoloma rubrobasis* is recorded mainly near *Betula*, including mixed *Betula-Picea* forest margins of summer farms, but also near *Salix caprea*. *Entoloma boreale* has so far only one documented find from Norway, in a *Picea* forest apparently devoid of *Betula*, and *Picea abies* is also

postulated as the major host for it in Finland (Kokkonen 2015). In Finland there is a couple of more species that seem *Picea-Betula* associated (*E. lupinum* and *E. radicipes* in the Sericatum clade). All these seem to be more or less northeastern “taiga-species” in Fennoscandia.

Within the clade Rhodopolium, *E. melanosum* (*E. nidorosum* s. Kokkonen), seems to be mainly associated with *Betula*, in moist, both richer and poorer habitats, including *Sphagnum*. It should be noted that the boreo-nemoral-southern boreal *E. rhodopolium* in Norway seems to be associated mainly with *Corylus*, but also often with *Betula* in southern boreal, calcareous *Picea* forests.

Continental versus oceanic boreal species in Fennoscandia

In our Norwegian *Entoloma* project presented here and in the Finnish Kokkonen (2015) study altogether almost 300 collections from Fennoscandia (including Svalbard) were sequenced. With this high number, it should be possible to see whether there are some geographical east-west patterns. And, indeed, there are some striking differences between Norway and Finland. Firstly, there is a fairly high amount of boreal species not yet found in Norway (7 species), and then, there are some species that are clearly more frequent in Norway, such as *E. serpens*. These differences indicate that there are considerable geographic patterns within Fennoscandia for this group, and especially, there seems to be a group of continental species, with an apparently north-eastern distribution in Europe. The arctic and alpine rhodopolioid species seem rather similar throughout Fennoscandia, and include some lowland species such as *E. majaloides*, *E. sericatum* and *E. politum*, which stand out as species with a very wide ecogeographical range. Finally, there is a group of southern, boreo-nemoral species in the Norwegian material not found in Finland, but this can be

explained by the focus on boreal habitats in the Kokkonen (2015) study.

Taxonomic part/comments

Clade /Sericatum

***Entoloma sericatum* (Britzelm.) Sacc. (= *E. myrmecophilum* Romagn.) Fig. 2 C, D, E**

According to our material, this is the most frequent rhodopolioid species in Norway, with 42 Norwegian collections verified by sequencing. It is also common in Finland (Kokkonen 2015). Usually it has medium-sized, slender basidiomata (Figure 2). However, it is remarkably variable morphologically and ecologically, including large and robust versus small and tiny specimens, with or without farina-ceous smell, dark to rather pallid, and with various degree of encrusted pigment in pileipellis hyphae, all these variants with identical ITS sequence. The ITS phylogeny thus shows that these features probably have a higher infraspecific character variation than formerly believed. Young basidiomata little exposed to rain and drought possess numerous fine whitish scales/hairs especially towards margin.

Although such fine hairs might be initially present in a number of rhodopolioid species, this feature is rarely as pronounced as here, and it could be a good differential feature towards resembling taxa. Kokkonen (2015) sequenced the type of *E. myrmecophilum*, which appeared to be conspecific with *E. sericatum*. Robust, dark variants of the present species with distinct encrusted pigment have apparently often been called *E. myrmecophilum*, whereas the more typical, slender, paler ones with no or little encrusted pigment have been assigned to *E. sericatum*.

Entoloma sericatum is apparently almost ubiquitous in Norway, found mainly in association with *Salix*, *Alnus* and often also *Betula* and *Populus*, from boreal(-boreo-nemoral) moist/swamp forest sites to arctic-alpine *Salix polaris*-*S. herbacea* snow beds (Figure 2). A

Table 1. The rhodopolioid *Entoloma* taxa in Norway, and their habitat and distribution.

New Norw = New to Norway ((x) = formerly reported, but probably misidentified (name use not in accordance with type). Boreonemoral = boreonemoral zone (southern coastal zone); boreal = boreal zone, incl. subalpine (x) = only found in southern boreal. Svalbard = records from arctic zone (no records from (sub)arctic parts of Finnmark).

The most frequent group of hosts (*Salix/Alnus*) is marked in **bold**. *Salix/Alnus* = *Salix* spp., *Alnus incana*; found predominantly with *Salix* spp. (and often *Alnus incana*) in moist habitat, also in parks/roadborders with *Salix caprea*. *Betula/Populus* = *Betula* spp., *Populus tremula*: found in moist *Betula* forests (or parks), or *Picea* forests with *Betula* and *Populus* (never pure *Picea* forests). *Tilia/Quercus*: found in calcareous *Tilia cordata-Corylus avellanea* forests, *Tilia* or *Quercus* forests/parks, or *Corylus* coppices. *Picea*: found in pure stands with *Picea abies*. KK = Kokkonen, MEN = M. E. Noordeloos.

rhodopolioid taxa in Norway	Total seq.	New Norw	boreonemoral	boreal	alpine	Svalbard (arctic)	Salix/Alnus	Betula/Populus	Tilia/Quercus	Picea
Clade Sericatum:										
<i>E. majaloides</i>	26	(x)	x	x	x		x	x		
<i>E. lividoalbum</i>	8		x	(x)					x	
<i>E. atrosericeum</i>	3				x	x	x			
<i>E. svalbardense</i>	3					x	x			
<i>E. sericatum</i>	42		x	x	x	x	x	x		
<i>E. noordeloosii</i>	3	x	x	(x)					x	
Clade Rubrobasis:										
<i>E. boreale</i>	1	x		x				?		x
<i>E. rubrobasis</i>	6	x		x			?	x		
<i>E. "tiliaticum"</i>	6	x	x						x	
Clade Sinuatum:										
<i>E. sinuatum</i>	1		x						x	
<i>E. eminens</i>	3	x	x						x	
<i>E. serpens</i>	7	x	x		x		x	x		
<i>E. "aurorae-borealis"</i>	4	x			x		x			
<i>E. bisporigerum</i>	4		x	x			x	?		
<i>E. borgenii</i>	2				x	x	x			
<i>E. bryorum</i> s. KK	11		x						x	
Clade Rhodopolium:										
<i>E. rhodopolium</i>	6		x	(x)				x	x	
<i>E. "frondosum"</i>	5	x	x						x	
<i>E. politum</i>	12		x	x	x		x			
<i>E. politum</i> s. Gulden	1				x		x			
<i>E. alpicola</i> s. Bjorbækmo et al.	5				?	x	x			
<i>E. melanosmum</i>	12		x	x			?	x		
<i>E. nidorosum</i> s. MEN	1	x	x						?	
Clade Sordidulum:										
<i>E. sordidulum</i> s. MEN	3		x						x	
24 species	176	10	16	10	7(8)	5	11	6	9	1

typical habitat is moist, richer mixed forests with *Alnus incana-Betula pubescens-Salix caprea* along brooks or tall-herb types including nitrophilous sites, and also parks and roadside verges. A few finds are boreonemoral from SW Norway, from mixed deciduous

forests with *Betula*, *Populus*, *Corylus* and *Quercus* (leg. A.K. Svendsen). Some collections are alpine, and the species is also verified from Svalbard (Spitsbergen) (leg. and det. A. Molia 43-2015; E. Larsson).

Material examined (including sequencing):

Akershus, Asker, TEB 390-15 (NOBAS2115-16); Akershus, Asker, TEB 573b-17; Hordaland, Ulvik, EB297/80 (NOBAS4077-17); Møre og Romsdal, Rindal, O-F-249623, GB59-14 (NOBAS1500-15); Nordland, Grane (Dunfjellet), JL22-13 (ALV5328); Nordland, Grane (Dunfjellet), JL65-16 (ALV11362); Nordland, Grane (Holmvassdalen), JL83-14 (ALV4965); Nordland, Grane, JL20-13 (ALV5003); Nordland, Grane, JL52-16 (ALV11356); Nordland, Grane, MEN2010307; Nord-Trøndelag, Levanger, TEB 273-16 (NOBAS4347-17); Nord-Trøndelag, Steinkjer, TEB 273-16 (NOBAS4337-17); Nord-Trøndelag, Steinkjer, ODFL7029, TEB 306-16 (NOBAS4517-17); Nord-Trøndelag, Steinkjer, KK324/16 (NOBAS4536-17); Nord-Trøndelag, Steinkjer, TEB 304-16 (NOBAS4538-17); Nord-Trøndelag, Steinkjer, TEB 305-16 (NOBAS4540-17); Nord-Trøndelag, Steinkjer, KBEB105-16 (NOBAS4578-17); Oslo, Oslo, EB232/15 (NOBAS2243-16); Oslo, Oslo, EB773/11 (NOBAS4681-17); Rogaland, Strand, AKS-13-16 (ALV11027); Rogaland, Strand, AKS-43-16 (ALV11026); Rogaland, Strand, AKS-E1-14 (ALV4400); Rogaland, Strand, AKS-E4-14 (ALV4935); Svalbard, AM43-2015 (NOBAS2346-16); Svalbard, E. Larsson (NOBAS2171-16); Sør-Trøndelag, Rissa (Gurulia), OW-E6-13 (ALV6782); Østfold, Fredrikstad (Gansrød), OW-E27-17 (ALV-14246); Østfold, Fredrikstad (Hunnfeltet), MP-5-161015 (ALV6340); Østfold, Fredrikstad (Torpelund), MP-4-280915 (ALV6338); Østfold, Fredrikstad, Hunnfeltet, MP-10-110914 (ALV6774); Østfold, Fredrikstad, MP-1-031013 (ALV5661); MP-1-050914 (ALV5140); MP-1-220915 (ALV6335); MP-1-230914 (ALV5145); MP-17-070914 (ALV5141); MP-2-250816 (ALV10936); MP-3-170915 (ALV6771); MP-4-041014 (ALV5143); MP-6-170916 (ALV10935); MP-7-081114 (ALV4996); MP-8-060914 (ALV4995); MP-9-041014 (ALV5147).

***Entoloma svalbardense* Noordel.**

This sister species to *E. sericatum* seems to be mainly arctic, collected in *Dryas* heaths. In Norway the species has so far been found only at Svalbard, but one collection is verified from alpine region of N Sweden (E. Larsson, pers. comm.). Four records from Svalbard have been verified by sequencing, namely the type (Kokkonen 2015), another collection sequenced in NORBOL (leg. A. Aronsen), and two soil samples sequenced in Geml et al. (2012). Although close to *E. sericatum* (with 8 nucleotide differences in ITS1; Kokkonen 2015), the *E. svalbardense* cluster is almost 100% supported in the phylogeny (Figure 2). When dwarfish variants of *E. sericatum* occur in the same habitat (Svalbard), the morphological variation of the two species is apparently considerably overlapping, but *E. svalbardense* is distinguished on the presence of cheilocystidia (Noordeloos 2004). Furthermore, *E. svalbardense* is noted mainly from *Dryas* heaths, whereas *E. sericatum* in alpine-arctic habitats seems to be more associated with dwarfish *Salix* in snow-beds. These differences need further documentation.

Material examined (including sequencing):

Svalbard, leg. A. Aronsen (NOBAS2311-16). [Svalbard, GG310/86 (O-74756; holotype, sequenced by Kokkonen 2011)]

***Entoloma majaloides* P.D. Orton** Fig. 2 A, B
Entoloma majaloides is, after *E. sericatum*, the second most frequent rhodopolioid species in Norway, with 26 verified collections within the *Entoloma* project. Most collections are from moist (coniferous) forests with *Betula*, *Salix* or *Alnus*, sometimes also *Populus*; often along paths, roadside verges, but some collections are also from alpine *Salix herbacea* snow-beds. *Entoloma majaloides* has been notoriously misidentified in Scandinavia, and has formerly never been verified in Norway nor in Sweden (cfr. Brandrud et al. 2017).



Figure 2. Illustrations of the *Entoloma* species in clade *Sericatum*. A, B) *E. majaloides*, A) 92TB09, B) JBJ6457; C, D, E) *E. sericatum*, C) JL65-16, D) MP10.11.09, E) TEB 390-15/DB5790; F, G) *E. lividoalbum*, F) TEB 610-15, G) ØW21-17; H, I) *E. noordeloosii*, H) TEB 62a-16, I) TEB 315-17. Photos: A) O. Morozova; B) J.B. Jordal; C) J. Lorås; D) M. Pettersen; E, F, I) B. Dima; G) Ø. Weholt; H) K.H. Brandrud.

One reason for misinterpretation is the name, indicating that this is an early species fruiting in May. However, according to our material so far, it has a season very similar to other *Salix-Betula* species (such as *E. sericatum*) of the rhodopolioid clade in Scandinavia, fruiting from July.

Entoloma majaloides usually has firm and robust basidiomata, which can be distinguished from the robust variant of the often co-occurring *E. sericatum* on the slight olivaceous-yellow-ochre tinge on the pileus (Figure 2 B), especially in the first phases of drying out. This tinge might resemble that of some *Tricholoma* species like *T. saponaceum* agg. or *T. arvernense*. Furthermore, young specimens of *E. majaloides* lack the fine white hairy-flocculose pileus margin seen on young, undisturbed *E. sericatum*. *Entoloma majaloides* differs from the large *E. eminens* basidiomata by absence of a tomentose-hirsute stipe base and presence of an olivaceous-yellow-ochre tinge on the pileus. Finally, it differs from the large *E. lividoalbum* basidiomata by a different habitat (see below).

Material examined (including sequencing): Akershus, Bærum, TEB 878-04 (NOBAS4078-17); Hordaland, Ulvik, GG13-04 (NOBAS4121-17); Nordland, Grane (Holmvassdalen), JL77-16 (ALV11365); Nordland, Grane, MEN2010306 (N42); MEN2010301 (N44); Nord-Trøndelag, Namdalseid, KK (NOBAS4342-17); Nord-Trøndelag, Steinkjer, HH140/16 (ALV11318); Nord-Trøndelag, Steinkjer, TEB 296-16 (NOBAS4355-17); Nord-Trøndelag, Steinkjer, H. Schwencke (NOBAS4537-17); Nord-Trøndelag, Stjørdal, JB Jordal (NOBAS2208-16); Nord-Trøndelag, Verdal, EB173/09 (NOBAS2592-16); O-F-248391, TEB 63-11 (NOBAS968-15); Oppland, Lesja, O-F-249083, TEB 153-13 (NOBAS1016-15); Oppland, Lesja, O-F-249385, TEB 589-13 (NOBAS1069-15); Oppland, Lunner, EB143/06 (NOBAS2579-16); Oppland, Lunner, EB45-

16 (NOBAS4229-17); Oppland, Lunner, EB30-16 (NOBAS4238-17); Oppland, Øystre Slidre, O-F-249261, TEB 412-13 (NOBAS1036-15); Oslo, Oslo, EB18/16 (NOBAS4460-17); Rogaland, Strand, AKS-E2-15 (ALV7175); Sør-Trøndelag, Oppdal, JBJ3077 (NOBAS2197-16); Sør-Trøndelag, Oppdal, JB16531 (NOBAS4566-17); Telemark, Porsgrunn, O-F-249313, TEB 481-13 (NOBAS1053-15); Østfold, Fredrikstad (Gansrød), OW-E5-9 (ALV10651); Østfold, Fredrikstad (Regimentsmyra), MP-3-260915 (ALV6342); Østfold, Fredrikstad, MP-18-130914 (ALV6772).

***Entoloma lividoalbum* (Kühner & Romagn.) Kubička** Fig. 2 F, G; Fig. 5 A

Entoloma lividoalbum is characterized by fairly large and often robust and firm basidiomata with grey-brown to more yellow-brown pilei, white, clavate to radicate stipes, farinaceous smell and taste, and occurrence in Norway mainly in calcareous *Tilia* forests or parks.

The name *E. lividoalbum* has probably been applied in a broad sense by many authors, but frequently it seems to have been applied to the present species. The present interpretation is also in accordance with that of Kokkonen (2015; = *E. sausetiense*).

Entoloma lividoalbum is a thermophilous, deciduous forest species in Norway, with eight verified collections; half of them from calcareous *Tilia-Corylus* forests in inner Oslofjord-Tyrixfjord (Akershus: Bærum, Asker; Oslo: Oslo; Buskerud: Hole), two from grassy *Tilia* parks in Østfold (Fredrikstad), one from rich, low-herb *Quercus-Corylus* forest in southernmost Norway (Aust-Agder; Grimstad), and, finally, one record from a southern boreal outpost of calcareous *Corylus* forest in Oppland, Lunner. According to Noordeloos (1992), the species in W/C Europe often occurs in open *Quercus-Fagus-Castanea* forests/parks.

There is a lot of collections labelled *E. lividoalbum* in Norwegian herbaria (see Artskart,

the Norwegian species database), but most of them are probably misidentifications, including many boreal finds, which could represent *E. majaloides* or stout variants of *E. sericatum*. To do a proper revision of these, the material will need sequencing, and such a herbarium revision is beyond the scope and time of our project. The species was verified by sequencing only once from Finland, collected near *Tilia* (Kokkonen 2015, based on a partial sequence).

Material examined (including sequencing): Akershus, Asker, TEB 531-15 (CAFUN066-17); Akershus, Bærum, TEB 610-15 (CAFUN077-17); Aust-Agder, Grimstad, ILF6804 (NOBAS4076-17); Buskerud, Hole, TEB 314-17 (N14); Oppland, Lunner, TEB 115-04 (NOBAS4736-17); Oslo, Oslo, EB184/04 (NOBAS4721-17); Østfold, Fredrikstad, OW-E21-17 (ALV13238); Østfold, Rygge, OW-E22-17 (ALV13746).

***Entoloma noordeloosii* Hauskn.** Fig. 2 H,I; Fig. 5 B

This thermophilous species was first verified for the Nordic countries in 2017, with three records from deciduous forests sites. Two records were from south-faced, rich *Tilia-Quercus*-forests; one calcareous site at Buskerud, Hole (Brandrud et al. 2017) and one moderately calcareous at Telemark, Kragerø. Finally, one record from a rich *Corylus* coppice outpost at Møre & Romsdal, Aure (leg. F. Oldervik) was verified as *E. noordeloosii*. It is otherwise known only from a few *Quercus-Carpinus-Corylus* localities in Austria (Noordeloos 2004), and a few colline *Quercus-Carpinus* sites of NW Caucasus (O. Morozova, pers. comm.). This seems to be a true rarity, confined to thermophilous deciduous forests, and so far not found in secondary habitats such as parks.

Entoloma noordeloosii is characterized by a slender habit, often caespitose growth, pale grey-brown, strongly hygrophane pileus, becoming whitish when dry, and a white stem

with a (sub)radicate base (Figure 2 H,I), often discolouring slightly yellowish at base (or where damaged by insects), almost lack of encrusted pigments in pileipellis and presence of cheilocystidia. In one collection we also observed considerably darker brownish grey colours when young, little exposed and water-soaked (Figure 2 I). We noticed a faint, sweetish smell, a nut-like smell was noted from Russian material (O. Morozova, pers. comm.), whereas a faint farinaceous smell was noted in the original description (see Noordeloos 2004). The species might resemble pale taxa in the *E. rhodopolium* complex, but these have a more or less nitrous smell, usually a tomentose-hirsute stipe base and no cystidia. *Entoloma lividoalbum* occurs in similar habitats, but is more robust, darker (never whitish when dry), usually has a stronger farinaceous smell and no cystidia. Another potentially co-occurring species, *E. "tiliaticum"*, has a much darker pileus and a stronger farinaceous smell.

Material examined (including sequencing):

Buskerud, Hole, TEB 315-17; Møre & Romsdal, Aure, O-F-188842, F. Oldervik 536.04 (NOBAS4720-17); Telemark, Kragerø, TEB 62a-16 (NOBAS4157-17).

***Entoloma atrosericeum* (Kühner) Noordel.**

According to our phylogeny, *E. atrosericeum* is related to *E. noordeloosii* (Fig. 1), but these differ in most respects as to morphology and habitat; *E. atrosericeum* being a dark, almost blackish, mealy-smelling, dwarfish alpine species, associated with dwarf-*Salix* species (and *Dryas*). We confirmed its identity by sequencing two Svalbard-collections and one S Norwegian alpine collection. There are more alpine collections from Northern Sweden (E. Larsson, pers. comm.).

Material examined (including sequencing):

Hordaland, Ulvik (Hardangervidda), G. Flatabø (NOBAS4116-17); Svalbard, A. Molia 2015

(NOBAS2342-16); Svalbard, A. Molia 2015 (NOBAS2372-16).

Clade /Sinuatum

Entoloma bryorum Romagn. s. Kokkonen

Fig. 3 F

Entoloma bryorum s. Kokkonen (2015) seems to be a very little known species. It was verified by sequencing from 11 collections quite locally in Østfold, Fredrikstad-Sarpsborg district, and one from Oslo. It was recorded mainly from a couple of parks, but also from grassland-margins. The parks with large populations were dominated by *Tilia*, but also with some park trees of *Quercus* and *Carpinus*. The lack of finds from other parts of Norway indicates that *E. bryorum* is a southern species in our regions. This is in accordance with Kokkonen (2015), who reports only two southern, boreo-nemoral finds; one from Sweden (*Tilia* park) and one from Finland (moist forest with *Tilia cordata* and *Alnus glutinosa*).

The species is characterized by rather small basidiomata, with depressed-papillate pilei with a pale greyish brownish to dark (brownish) grey colour (Fig. 3 F) (often dark papillae contrasting to paler outer part), and a weak farinaceous smell and taste. With its small, depressed-papillate basidiomata, it might resemble *E. politum*, but the latter is distinguished, e.g., by the habitat (moist *Alnus-Salix* forests/copses/wetlands) and the differently shaped and sized spores. It might also resemble another southern species in Norway, *E. sordidulum*, but the latter has a strong farinaceous smell and hardly depressed pileus.

Material examined (including sequencing):

Oslo, Oslo, leg. T. Jacobsen (NOBAS3208-16); Østfold, Sarpsborg (Hafslundparken), MP-E3-14 (ALV4396), MP-10-010914 (ALV4685), leg. M. Pettersen (NOBAS3140-16), leg. M. Pettersen (NOBAS3160-16), OW-E20-15 (ALV6051), OW-E6-15 (ALV6791), OW-E9-15 (ALV5697); Østfold, Sarpsborg

(Borregårdsparken), MP-8-010914 (ALV4991); Østfold, Fredrikstad, MP-9-090815 (ALV6057), OW-E4-10 (ALV11035).

Entoloma borgenii Noordel. Fig. 6 B

This species is closely related to *E. bryorum* as here circumscribed, but differs in darker pileus, habitat and distribution. The Norwegian sequenced collections were characterized by dark, glossy, umbonate-papillate to depressed-umbilicate pileus, and slightly decurrent lamellae. It is mainly an arctic-alpine taxon associated with *Salix* (dwarf) shrubs, but is also collected in lowland *Salix* copses in eastern and northern Finland (Kokkonen 2015). In our project, *E. borgenii* was confirmed twice by sequencing; from alpine and subalpine/northern boreal habitats in Nordland, Holmvassdalen nature reserve. The species is formerly reported also from Svalbard (Noordeloos 2012).

Material examined (including sequencing):

Nordland, Grane (Holmvassdalen NR), JL51-16 (ALV11355); JL63-16 (ALV11360).

Entoloma bisporigerum (P.D. Orton)

Noordel. s. lat. (= *E. alnobetulae* (Kühner)

Noordel.) Fig. 3 E

This species often has the omphaloid habit of *E. bryorum* and *E. politum*, with a depressed pileus with translucently striate margin (Noordeloos 1981, 1992). However, in the Norwegian material, the pileus has been more flattened than depressed and with little or no striate margin (Figure 3). Furthermore, it differs from *E. bryorum* and *E. politum* in the normally large spores from 2-spored basidia (Noordeloos 1981, 1992). However, according to Kokkonen (2015), the species might occur with 4-spored basidia and smaller spores, as well. *Entoloma politum* differs in often having a slightly nitrous smell.

Entoloma bisporigerum was within our project verified with sequences from four



Figure 3. Illustrations of the *Entoloma* species in clades Rubrobasis and Sinuatum. A, B) *E. tiliaticum* ined., A) TEB 211-14, B) EB169-15; C) *E. boreale* EB28.08.2014; D) *E. rubrobasis* JBJ-HH6619; E) *E. bisporigerum* ØW E20-14a; F) *E. bryorum* ØW E4-10. Photos: A) K.H. Brandrud; B, C) E. Bendiksen; D) J.B. Jordal; E, F) Ø. Weholt.

collections; three of them from Østfold, Fredrikstad region (leg. M. Pettersen, det. Ø. Weholt), and one from Møre & Romsdal, Rindal (leg. G. Bureid). Formerly it was reported (not confirmed by sequencing) also from northern Norway (Tromsø; Noordeoos 2012). The Norwegian collections are from

moist forests with *Salix* and *Alnus* mainly on clay soils. According to Kokkonen (2015) in Finland “it occurs rather commonly in old *Salix* thickets or moist forests on shores of lakes and rivers, often together with *E. politum* and *E. borgenii*.” Kokkonen (2015) mentions also one alpine collection near

Salix glauca, *S. herbacea* and *Betula nana*. According to Noordeloos (1981, 1992) the species is not uncommon in western Europe, in moist forests mainly with *Alnus glutinosa* and *Salix* spp., and often together with *E. politum*.

Material examined (including sequencing): Møre og Romsdal, Rindal, GB69-14 (ALV4607); Østfold, Fredrikstad, MP-1-240816 (ALV10937); Østfold, Fredrikstad, OW-E23-14 (ALV8408); Østfold, Fredrikstad (Hunnfeltet), MP-E2-14 (ALV4192).

***Entoloma serpens* Kokkonen** Fig. 6 A

Entoloma serpens is, together with its sister species *E. "aurorae-borealis"* (see below), characterized by a (very) dark, umbonate pileus, being fine rimose-hairy-scaly at umbo and initially often at margin, sometimes also with a slightly rugulose-irregular pileus surface. Both species possess cheilocystidia. Both are associated mainly with *Salix*, but the former mainly in the lowlands, the latter so far only in alpine habitats.

Entoloma serpens is reported new to Norway within the present *Entoloma* project (Noordeloos et al. in prep.). It is now verified from seven Norwegian localities, mainly in the boreonemoral Oslofjord region (preferentially near *Salix caprea*, but probably also *Betula*, mainly on calcareous ground), with one northern outpost recorded in alpine zone in Nord-Trøndelag (Levanger, Øvre Forra nature reserve, the Hårskallen mountain). The species will be further described and commented in Noordeloos et al. (in prep.).

Material examined (including sequencing): Buskerud, Røyken (Bønipa), TEB 748-13; Nord-Trøndelag, Levanger (Øvre Forra NR), EB94-16 (NOBAS4433-17); Østfold, Fredrikstad (Hunnfeltet), MP-1-240915 (ALV6770), MP-7-130915 (ALV6339), MP-E1-14 (ALV4191); Østfold, Fredrikstad (Tofteberg),

MP-5-060815 (ALV6344); Østfold, Fredrikstad (Vesten), MP-2-120914 (ALV4992).

***Entoloma "aurorae-borealis"*, ined.**

This species is recorded from four alpine sites with *Salix herbacea* snow-beds within the Holmvassdalen nature reserve, Grane, Nordland, and will be described as new to science and further commented in Noordeloos et al. (in prep.). For differences towards the closely related *E. serpens*, see above.

Material examined (including sequencing):

Nordland, Grane (Holmvassdalen NR, Dunfjellet), JL67-16 (ALV11364), JL118-16 (ALV11374); Nordland, Grane (Holmvassdalen NR), JL85-14 (ALV4625), JL10-15 (ALV6511).

***Entoloma sinuatum* (Bull.) P. Kumm.**

The poisonous *E. sinuatum* has characteristic, large and robust basidiomata, being the only European rhodopolioid species with initially distinctly yellow lamellae (Noordeloos 1992). It is well-known and has for a long time been precisely identified in Norway due to its toxicity. Thus, it has not been given priority in our project (only one Norwegian collection was sequenced; see Figure 1).

According to the national species database (Artskart) and the Norwegian red-list fact-sheet (<https://www.artsdatabanken.no/Rodliste>) the species is known from approx. 30 localities in Norway, restricted to the Oslofjord region, and the southernmost coastal region (coast of Agder) with one outpost near *Quercus* in Møre og Romsdal. Only in the southern Agder coast region the species is more or less regularly recorded. Finds from the Oslofjord region are few and partly old (e.g. from Asker). In the Fredrikstad area, Østfold (outer Oslofjord), where the rhodopolioid species are well investigated, it is recorded only at a few sites at Kråkerøy (known from the 1960ies and re-found recently). Most collections are from

richer (but rarely calcareous) low-herb, rather open *Quercus* forests, sometimes mixed *Quercus-Corylus(-Tilia)* forests. Although intensively investigated, we have never recorded this one in our calcareous *Tilia(-Corylus)* forests. It seems thus to be a more or less strict associate of *Quercus* in Norway.

Material examined (including sequencing): Aust-Agder, Arendal (Vigeland/Bjellands-haugane NR), O-F-75429, IL Fonneland 09.09.2014 (NOBAS107-14).

***Entoloma eminens* Kokkonen**

Entoloma eminens is a striking species, being large and tall, with prominent hirsute-tomentose stipe base. It was described by Kokkonen (2015) from eastern and northern Finland, from rich *Picea abies* dominated forests, with presence of deciduous trees such as *Populus tremula* and *Betula*. From Norway, the species is verified from three collections from a boreo-nemoral calcareous *Tilia(-Corylus)* forest (Telemark, Bamble). These are the first finds outside Finland. Whereas most other species in Norway seem to have either a clear preference for thermophilous deciduous trees or boreal deciduous trees/shrubs, this seems to be a “crossover”, being associated with *Tilia-Corylus* in SE Norway, and apparently with *Populus* and *Betula* in Finland (see further details in Noordeloos et al. in prep.).

Material examined (including sequencing): Telemark, Bamble (Høgenheitunellen W), O-F-248409, TEB 97-11 (NOBAS971-15); TEB 226-16 (CAFUN098-17); TEB 699-17.

Clade /Rubrobasis

***Entoloma rubrobasis* Noordel.** Fig. 3 D;
Fig. 6 C

This species is characterized by often rather large, slender basidiomata with (dark) brownish grey convex-umbonate pileus, initially greyish lamellae and white to pale greyish stipe, with

a reddening base (Figure 3). The reddish spots at the stipe base are a good separating character (otherwise the species may look very much like e.g. *E. sericatum*), but it is not constant. However, on all our six sequence-verified collections at least a couple of specimens had reddish spots.

The verified collections are mainly from central-northern Norway (north part of Møre & Romsdal, Nord-Trøndelag, Nordland), including one from western Norway (Bergen district). The species is said to be rather common in Finland, at least in eastern Finland (Kokkonen 2015). So based on available data, it seems to be a mainly northeastern species in Fennoscandia, and probably in Europe as a whole.

The Norwegian finds seem to be mainly near *Betula* in secondary habitats along forest margins. It was found amongst tall-herbs in margins of semi-natural grasslands of summer farms (near *Betula* and some *Picea*), in grassy-mossy gardens/churchyards near *Betula*, and in one case also along a road near *Salix caprea*. Since *Picea* is a quite uncertain associate for rhodopolioid species in general (very few finds in pure *Picea*/conifer forests), *Betula* seems to be the major host of *E. rubrobasis*. According to Kokkonen (2015) the species occurs in a wide range of habitats in Finland, such as rich *Picea* forests, swamps, shore forests, and parks, but often growing near *Betula*. This characteristic species was first published for Norway by Holien et al. (2014) based on two finds from Nord-Trøndelag.

Material examined (including sequencing): Hordaland, Bergen, H. Kivistø (ALV13101); Møre & Romsdal, Rindal, GB55-10 (NOBAS4699-17); Nordland, Grane (Holmvassdalen NR), O-F-249973, JL55-09 (NOBAS1595-15); Nord-Trøndelag, Steinkjer (Ulvensetran), H.Holien and J.B. Jordal (NOBAS2621-16); Nord-Trøndelag, Steinkjer (Egge church), H. Schwencke, TEB 295-16

(NOBAS4356-17); Nord-Trøndelag, Steinkjer, KK328/16 (NOBAS4533-17).

***Entoloma boreale* Kokkonen** Fig. 3 C

This unspectacular, *E. sericatum*-like species seems to have few distinguishing features. According to Kokkonen (2015), a more pronounced farinaceous smell could be a differential character towards look-a-likes such as *E. sericatum*. On average, the pileipellis hyphae of *E. boreale* are less encrustated than those of *E. sericatum*. Ecologically, the species is interesting, since it is one of very few with a seemingly major association with *Picea abies*. According to Kokkonen (2015), many finds are from rich to calcareous *Picea* forests, and the Norwegian find (Oppland, Etnedal) was from a pure, mesotrophic *Picea abies* forests (although presence of *Betula* at the site cannot be completely excluded). The species is not rare in Finland (Kokkonen 2015), and there is also a number of finds from Sweden (K. Kokkonen, pers. comm.). Judging from the data available, it seems, as its relative *E. rubrobasis*, to be a northeastern species in Fennoscandia/Europe.

Material examined (including sequencing):

Oppland, Etnedal (Breie), EB 28.08.2014 (NOBAS2576-16)

Entoloma “tiliaticum”, ined. Fig. 3 A,B

This species belongs to the thermophilous deciduous forest element, with most Norwegian finds from calcareous *Tilia* forests, but it is also found near *Tilia* in rich/calcareous soils in parks (Table 1). All six verified records are from the Oslofjord region. Four verified collections come from calcareous *Tilia* forests. From this habitat we have more non-sequenced collections, which very probably belong to the present species. Two verified collections are from parks. The species is characterized by a dark brownish grey (initially even almost blackish), glossy to finely rimose pileus, a pale greyish (never whitish), fibrillose stipe

and a distinct farinaceous smell. The basidiomata are large to medium in size. On a few occasions, we have seen reddish spots at the base of stem, a feature otherwise seen only in the related *E. rubrobasis*.

The species has been found co-occurring with *E. lividoalbum*, but is distinguished by darker colours. The colour differences are even more pronounced against the pale *E. noordeloosii* and *E. rhodopolium* collections, which also occur in *Tilia-Corylus-Quercus* forests. However, discoloured mature/older specimens with paler pilei could be hard to distinguish, at least from *E. lividoalbum*.

The ITS sequence of the species gave no match with sequenced types or reference materials. Our species corresponds in many respects with the original description of *E. griseoluridum* (Kühner in Kühner & Romagnesi 1954). However, our species deviates in some important characters, for instance, in the protologue of *E. griseoluridum* Kühner mentioned a purplish tinge on pileus and stipe, never seen by us, so we regard these as two different species, and here treat the present one under the working name *E. “tiliaticum”*. It has not been possible to obtain an ITS sequence of the type material of *E. griseoluridum*. Due to its dark pileus *E. “tiliaticum”* has been identified also as *E. gerriae*, possibly also as *E. griseopruinatum*, but the types of *E. gerriae* and *E. griseopruinatum* fall into other clades, and are thus not applicable. A few authors such as Ludwig (2007) have regarded *E. griseopruinatum* and *E. griseoluridum* as synonymous.

The species was not documented for Finland in the extensive study of Kokkonen (2015). However, it was found near *Tilia* in the Botanical Garden in St Petersburg (sequence-verified collections; O. Morozova, pers. comm.). Based on the rather many finds around the Oslofjord, and the Russian finds, the species probably has a wider boreonemoral-nemoral distribution in S. Sweden and in southernmost

Finland, probably showing a pattern very similar to that of *E. lividoalbum*.

Material examined (including sequencing): Buskerud, Røyken (Bøsnipa E), TEB 532-15 (NOBAS2120-16); EB169/15 (NOBAS2235-16); Oslo, Oslo, TEB 366-15 (NOBAS2113-16); TEB 367-15 (NOBAS2114-16); TEB 211-14 (T117); Østfold, Sarpsborg, Hafslundparken, OW-E21-15 (ALV6784).

Clade /Rhodopolium

Entoloma rhodopolium (Fr.) P. Kumm.

Fig. 4 A,B; Fig. 5 C

The *E. rhodopolium*-*E. nidorosum* complex in Norway includes a number of species that are morphologically and (partly) ecologically hard to distinguish. All these are slender, thin-fleshed, brittle, pale taxa with a convex to more depressed pileus, and with a more or less nitrous (chlorine-like) smell. The smell is rather variable and is perceived differently, sometimes compared to that of soap, and sometimes with a weak, sweetish, perfume- or apple-like component, but hardly farinaceous as in many other groups.

Entoloma rhodopolium is a classical, Friesian species, and was neotypified by Kokkonen (2015) on material from a beech forest in S Sweden. This is a southern, in Norway apparently mainly *Corylus*-*Betula*-(*Tilia*-*Quercus*) associated species, and mainly in calcareous forests, including calcareous *Pinus*-*Picea* forests with *Corylus*. It extends north to the southern boreal zone in SE Norway (Figure 5 C), where it occurs here and there in calcareous *Picea* forests near *Betula*. Since belonging to a critical complex, *E. rhodopolium* s. str. is difficult to identify without sequencing. So far we therefore have rather limited knowledge on the precise habitat preferences and distribution of this one. Altogether six collections have been sequenced, all from calcareous sites in the Oslofjord(-Randsfjord) area. At least three of them very probably

were associated with *Corylus* (boreonemoral), at least one very probably with *Betula* (southern boreal). The species is strictly southern in Finland (Kokkonen 2015).

Material examined (including sequencing): Akershus, Bærum, EB20215 (NOBAS2239-16); Oppland, Lunner, EB165-16 (NOBAS4201-17); Oslo, Oslo, EB234/15 (NOBAS4600-17); Telemark, Porsgrunn (Frierflogene N), TEB 461-15 (NOBAS2118-16); Telemark, Porsgrunn, ILF2015-29 (NOBAS4317-17); Vestfold, Andebu, O-F-361608, P. Marstad 150-06 (NOBAS4714-17).

Entoloma “frondosum” ined. Fig. 4 C

This taxon is genetically well-defined, and rather dissimilar to the *E. rhodopolium* s. str. in ITS sequences (see Figure 1). However, these two are morphologically quite similar, and with overlapping habitat preferences (Table 1). All sequenced samples of the *E. rhodopolium*-complex from calcareous *Tilia* forests appeared to be this one (5 collections), so *E. “frondosum”* is probably the most common one in the calcareous *Tilia* forests, where the *E. rhodopolium* complex as such is frequent. So far the known distribution of this one is restricted to the Oslofjord district, and it is not known in other parts of Fennoscandia (Kokkonen 2015), but it is by us also verified from a *Carpinus* forest in Hungary, and there is a match with the UNITE sequence UDB 015210 from Estonia (V. Liiv, sub nom. *E. speculum*). So this seems to be a fairly widespread, more or less calciphilous, thermophilous frondose forest species (hence the working name *E. “frondosum”*), apparently associated mainly with *Tilia*-*Corylus*-*Carpinus* forests.

Material examined (including sequencing): Akershus, Asker, (Håkavikvegen), O-F-249276, TEB 432-13 (NOBAS1035-15); Akershus, Asker (Tverråsen), TEB 389-15 (CAFUN010-17); Telemark, Bamble (Røsskleiva), TEB 338-13



Figure 4. Illustrations of the *Entoloma* species in clade Rhodopolium. A, B) *E. rhodopolium*, A) EB202-15, B) TEB 461-15; C) *E. frondosum* ined. TEB 389-15; D) *E. nidorosum* MEN201220129; E, F) *E. melanosmum* E) RK E6-14, F) TEB 275-16; G, H) *E. politum*, G) TEB 44-15, H) DB6076. Photos: A) E. Bendiksen; B, C, D, H) B. Dima; D) M.E. Noordeloos; E) R. Kristiansen; G) K.H. Brandrud.

(NOBAS4700-17); Telemark, Bamble (Høgenheitunellen W), TEB 225-16 (CAFUN097-17); TEB 302-15 (CAFUN006-17).

***Entoloma melenosmum* Noordel. (= *E. nidorosum* (Fr.) Quél. s. Kokkonen) Fig. 4 E, F**

Entoloma melenosmum (= *E. nidorosum* s. Kokkonen 2015) appears to be a quite northern boreal-subalpine(-subarctic) species, rather well-distinguished from the others in the *Rhodopolium* (sub)clade by habitat and distribution. Morphologically, the species is on average more slender and with initially darker and more often depressed pileus than the other taxa in the complex. The stipe surface reminds often of *E. politum*. It has a variable, more or less nitrous to aromatic smell.

Altogether 12 Norwegian collections have been verified by sequencing, most of them from Trøndelag-Nordland in Central-North Norway. Most of our collections are from moist forests, swamps, along brooks, near *Betula*, a number also in subalpine *Betula* forests including young secondary forests/forest rims towards grassland/lawns. The species is recorded in richer or poor soils, including *Sphagnum*. This is also in correspondence with habitats given in Kokkonen (2015). She interpreted this species as *Entoloma nidorosum* Fries (1838). However, Fries (1838) described it from rather open (park-like) deciduous forests around Uppsala (“in nemoribus frondos. circa Upsalium”), which probably refers to the rich, at that time rather open *Quercus-Corylus*(-*Betula*) woodland around Uppsala, a habitat corresponding better with other, more southern taxa in the group.

Furthermore it was described as having a definite alkaline (nitrous) smell. *Entoloma melenosmum* is a more northern boreal-subarctic species, mainly in different, more acidophilic habitats, and probably does not correspond with the current usage of the name *E. nidorosum*. *Entoloma nidorosum* has often been treated as a variety or a form of *E. rhodopolium*,

and should be morphologically very close to *E. rhodopolium* (Noordeloos 1992). For the moment, we name our northern species *E. melenosmum*, described from *Betula* forest on Greenland (Noordeloos 1984), and verified by sequencing of Kokkonen (2015), and the southern taxon is named here *E. nidorosum* sensu Noordeloos (1992).

Entoloma paragaudatum Kokkonen (2015), another boreal species in the complex, has so far not been recorded from Norway. It is similar to *E. melenosmum*, may be a bit darker, and is described from somewhat drier, calcareous forests with *Betula*, *Picea* and *Populus*.

Material examined (including sequencing):

Akershus, Fet (Øya, Fetsund), OW-E12-14 (ALV8405); Møre og Romsdal, Rindal (Aunesetra), GB54-14 (ALV3913); Møre og Romsdal, Nordal (Muldal), S.Vatne-E1-13 (ALV5493); Nordland, Grane (Holmvassdalen NR), JL62-16 (ALV11359); Nordland, Sørfold (Kobbelv), R. Kristiansen-E6-14 (ALV4692); Nord-Trøndelag, Levanger (Øvre Forrra NR, Hårskallen), TEB 274-16 (NOBAS4348-17); TEB 275-16 (NOBAS4349-17); Nord-Trøndelag, Steinkjer, O. Morozova (NOBAS4338-17); KK326/16 (NOBAS4534-17); KK325/16 (NOBAS4535-17); TEB 303-16 (NOBAS4539-17); Sør-Trøndelag, Rissa (Stadsbygd), EH-E1-17 (ALV14256).

***Entoloma nidorosum* Fr. s. Noordel. Fig. 4 D**

This is a more southern species than *E. melenosmum*, mainly of moist, mixed forests. It seems to represent the prevailing central-western European concept of *E. nidorosum* (see Noordeloos 1981, 1992), although some also treat *E. nidorosum* as a synonym of *E. rhodopolium* (Ludwig 2007). The present species is in the Nordic countries so far only confirmed from one, sequenced collection in Norway, from the Fredrikstad district (rich site near *Corylus*, *Populus*, *Salix*; leg. & det. Ø, Weholt). Morphologically, this seem indi-

stinguishable from *E. rhodopolium* in most stages, and it should probably be regarded as semi-cryptic species with the present knowledge.

Material examined (including sequencing): Østfold, Fredrikstad (Skremmelia), OW-E21-14 (ALV8407).

***Entoloma politum* (Pers.) Donk** Fig. 4 G, H

This species is widespread and rather common, mainly in moist forests, swamps and along rivers/lakes, near *Salix* spp. and *Alnus*, but occurs also in alpine *Salix* habitats (Fig. 4). *Entoloma politum* is characterized by small, omphaloid, often dark basidiomata, resembling *Entoloma bryorum* and *E. borgenii* from the clade Sinuatum, but differs e.g. by the often nitrous smell, which indicate its relationship with the *E. rhodopolium*-*E. nidorosum* complex. The species might also resemble the often co-occurring *E. bisporigerum*, but the latter normally has 2-spored basidia and larger spores. So far, the species has been verified from 12 collections from both southern and central Norway, including three alpine sites from Trøndelag-Nordland. However, we have visited only a few fairly typical *E. politum* habitats such as swamp forests and wetlands. Probably this is the most common rhodopolioid species in these habitats, and should be regarded as “undersampled”. The species is frequent also in Finland (Kokkonen 2015).

Material examined (including sequencing): Akershus, Fet (Øya, Fetsund), OW-E13-14 (ALV6991); Akershus, Ullensaker, E.A. Thomsen (NOBAS4334-17); Nordland, Grane (Holmvassdalen NR, Dunfjellet), JL114-16 (ALV11372); Nordland, Grane (Holmvassdalen NR), JL88-16 (ALV11385); Nord-Trøndelag, Levanger (Øvre Forra NR, Hårskallen), E.A. Thomsen (NOBAS4343-17); B. Dima (NOBAS4345-17); Oppland, Sel (Otta, Nordre Veggem), TEB 115-15 (NOBAS2129-16);

Oppland, Sel (Gudbrandsdalslågen ved Otta), O-F-251991, H. Schwencke, JBJ15-E08 (NOBAS2137-16); Oslo, Oslo, EB231/15 (NOBAS2242-16); Telemark, Kragerø (Sjåtjenna S), TEB 44-15 (NOBAS2127-16); Østfold, Rygge, E.W. Hanssen, R. Braathen (NOBAS2492-16); OW-E19-10 (ALV11040).

***Entoloma alpicola* (J. Favre) Bon & Jamoni s. Bjorbækmo et al.**

This is the *E. alpicola* as sequenced in connection with the study of *Dryas mycorrhizae* by Bjorbækmo et al. (2010) from Svalbard. When a number of *Entoloma*-collections from Svalbard were sequenced through NorBOL in 2016, this was the most frequent one, with four collections (and a fifth collection sequenced earlier). Neither notes nor photos are available from these Svalbard collections, so we have little data on our sequenced collections. A number of alpine collections from mainland Norway have been identified as *E. alpicola*, but at the moment, none of these have been verified by sequencing, and thus could include some of the other, alpine rhodopolioid species. With the present data, *E. alpicola* s. Bjorbækmo et al. is a strict arctic species in North Europe. The type of *E. alpicola* was, however, described by J. Favre from the Swiss Alps, and is not sequenced yet. We thus cannot confirm that our apparently frequent arctic *E. alpicola* is the true *E. alpicola* sensu Favre.

Material examined (including sequencing): Svalbard, 23-N1F31-2 (HQ445607); E. Larsson (NOBAS2327-16); (NOBAS2356-16); A. Molia 45-2015 (NOBAS2357-16); A. Molia 48-2015 (NOBAS2380-16).

***Entoloma politum* s. G. Gulden**

One collection identified as *E. politum* from *Salix herbacea* snow-bed in middle alpine zone at Finse, Hardangervidda came out as a well-supported sister species to *E. alpicola* s. Bjorbækmo et al. and *E. politum*. This seems

to be a new, undescribed, alpine species, with at present very little data. Noordeloos and Gulden (1989) reported *E. politum* from the Hardangervidda, based on five collections (not including the current one). So far these have not been sequenced, but shall be done in the near future, to find out whether they fit with this unknown species, or represent the true *E. politum*.

Material examined including sequencing):

Hordaland, Ulvik (Nordre Kongsnuten, Hardangervidda), leg. E. Søyland, det. G. Gulden, GG35/04 (NOBAS4726-17).

Clade /Sordidulum

***Entoloma sordidulum* (Kühner & Romagn.)**

P.D. Orton s. Noordeloos Fig. 5 D

This species has an isolated position within the rhodopolioid clade (Fig 1). We have so far three sequenced collections of it from Norway, one from W Norway (Hordaland, Tysnes, leg. P. Fadnes; margin of calcareous grassland, with *Corylus* and *Quercus*) and two from SE Norway (Østfold, Fredrikstad region, leg. Ø. Weholt, one from moist *Quercus* forest, the other from rich, rather open woodland, near *Corylus*, but also few *Quercus*). Our interpretation follows the concept of Noordeloos (1992), not that of Kokkonen (2015) (see below). *Entoloma sordidulum*, as applied here, is a small, convex-umbonate, greyish brown species, with non-striate pileus, a subpolished stipe, strongly farinaceous smell and taste and encrusting pigments in the pileipellis, looking somewhat like a small *E. sericatum*. This species (possibly in a wide sense) is frequent in large parts of northwestern and central Europe in thermophilous deciduous forests and parks, apparently with a preference for *Quercus* (Noordeloos 1992, 2012).

Kokkonen (2015) examined a syntype of *E. sordidulum* from the herbarium of Romagnesi in Paris, but did not find the lectotype.

The syntype of *E. sordidulum* had the same sequence as the lectotype of *E. subradiatum*, and hence should be called *E. subradiatum*. *Entoloma subradiatum* (= syntype *E. sordidulum*) is quite distant from our species phylogenetically. It is a sister species to the *E. serpens*-*E. bisporigerum*-*E. "aurorae-borealis"* group in clade /Sinuatum (not shown), and presence of *E. subradiatum* is not yet confirmed from the Nordic countries.

Material examined (including sequencing):

Hordaland, Tysnes (Skorpeneset), O-F-75968, P. Fadnes (NOBAS928-15); Østfold, Fredrikstad (Skremmelia), OW-E25-17 (ALV14241); Østfold, Fredrikstad, OW-E18-14 (ALV8406).

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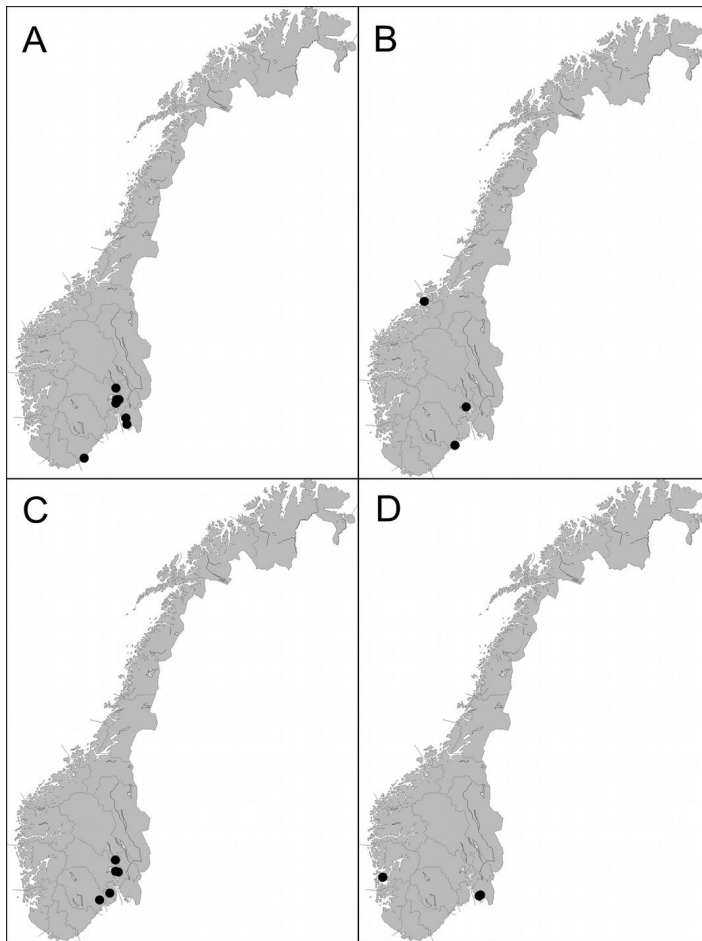


Fig. 5. Distribution maps of some of the rhodopolioid *Entoloma* species in Norway, belonging to the southern *Tilia-Quercus-Corylus* element. Only records verified by sequencing are included. A) *E. lividoalbum*; B) *E. noordeloosii*; C) *E. rhodopolium*; D) *E. sordidulum*.

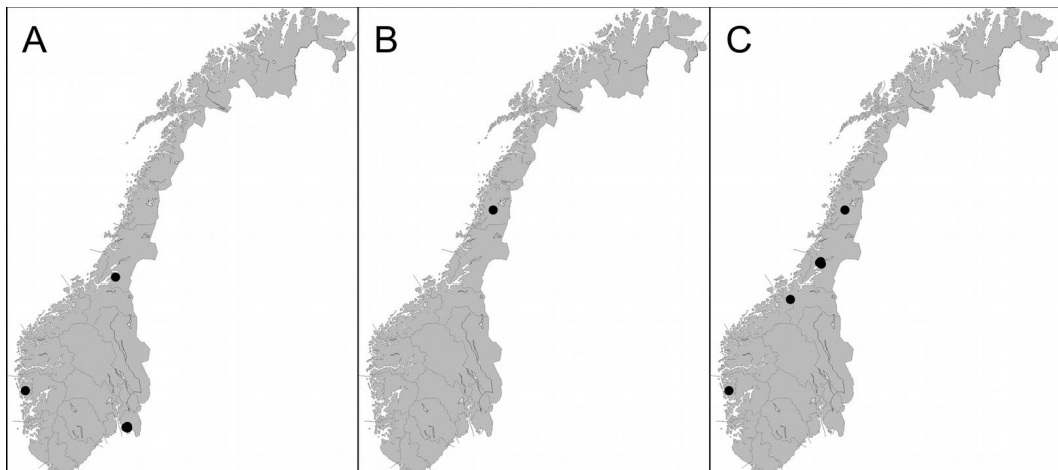


Fig. 6. Distribution maps of some of the boreal-arctic-alpine rhodopolioid *Entoloma* species in Norway. Only records verified by sequencing are included. A) *E. serpens* (the boreal-arctic-alpine *Salix-Alnus-Betula* element); B) *E. borgenii* (the arctic-alpine *Salix-Dryas* element); C) *E. rubrobasis* (the boreal *Betula* element).