Entoloma species of subgenus *Cyanula* (Tricholomatinae, Basidiomycota) in Norway, with emphasis on habitat preferences and distribution

Tor Erik Brandrud[1], Egil Bendiksen[1], John Bjarne Jordal[2], Øyvind Weholt[3], Jostein Lorås[3], Bálint Dima[4], Machiel E. Noordeloos[5]

[1]Norwegian Institute for Nature Research, Sognsveien 68, NO-0855 Oslo, Norway
[2]Miljøfaglig Utredning, Gunnars veg 10, NO-6630 Tingvoll, Norway
[3]Nord University, Nesna, NO-8700 Nesna, Norway
[4]Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117, Budapest, Hungary
[5]Naturalis Biodiversity Centre, P.O. Box 9517, 2300 RA, Leiden, The Netherlands

Corresponding author: tor.brandrud@nina.no

Norsk tittel: Rødsporer (*Entoloma*), underslekt *Cyanula* i Norge, med fokus på habitat og utbredelse

Brandrud TE, Bendiksen E, Jordal JB, Weholt Ø, Lorås J, Dima B, Noordeloos ME, 2023. *Entoloma* species of subgenus *Cyanula* (Tricholomatinae, Basidiomycota) in Norway, with emphasis on habitat preferences and distribution. Agarica 2023 vol. 43: 85-137.

KEYWORDS: barcoding, morphology, taxonomy, calcareous grasslands, calcareous forests

NØKKELORD: strekkoding, morfologi, DNA-ITS-sekvensering, taksonomi, kalkrik semi-naturlig eng, kalkskog

SAMMENDRAG
Dette er den tredje artikkelen med resultater fra det norske *Entoloma*-prosjektet 2015-2017. Her gir vi en oversikt over rødsporer i underslekt *Cyanula* i Norge. *Cyanula* utgjør en av de største gruppene av våre beitemarksopper. Dette er del av en større studie over de europeiske artene i underslekt *Cyanula*, som inkluderer en omfattende fylogenetisk undersøkelse som snart vil bli publisert, samt en nylig publisert bok med en oppdatert taksonomisk revisjon av gruppa. Det foreliggende arbeidet fokuserer på arter registrert i Norge ved hjelp av ITS strekkoding. Også en del nylige, sekvenserte innsamlinger gjort i nordsvenske fjellområder er inkludert her. Artene presenteres seksjonsvis, med vekt på data om habitat-preferanser og utbredelse. Til sammen 53 *Cyanula*-arter er presentert her, med oppdatert artsavgrensning og navnsetting. Mer enn halvparten av disse artene er rapportert nye for Norge siden starten av det norske *Entoloma*-prosjektet. Av disse er 18 beskrevet som nye for vitenskapen de siste tre årene, i stor grad basert på norsk materiale. To av disse er kun kjent fra Norge, og ytterligere to kun fra Skandinavia.

ABSTRACT
This is the third paper with results from the Norwegian *Entoloma* project 2015-2017. An overview is given of the species of *Entoloma* subgenus *Cyanula* in Norway. *Cyanula* includes, among other elements, many grassland fungi. This paper is part of a larger study concerning the European species of the subgenus *Cyanula*, including a multigene phylogeny that will be published in due course. Furthermore, a monograph with updated tax-

onomic revision is recently issued. This paper focuses mainly on the species recorded from Norway with help of ITS DNA barcoding, with reference to recent collections also from Northern Sweden, with extensive notes of their habitat requirements and distribution. Altogether 53 *Cyanula* species are presented here, with an updated circumscription and naming. More than half of these are reported new to Norway since the start of the Norwegian *Entoloma* project. Of these, 18 have been described as new during the last three years, largely based on Norwegian material. Four of these are known exclusively from Scandinavia.

INTRODUCTION

Entoloma is one of the most species-rich genera within Agaricales, well characterized by typically many-angled spores that leave a pinkish spore deposit. 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 many 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). The reasons for this comprehensive approach are manyfold, 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.

This is the third paper reporting major results from the Norwegian *Entoloma* project 2015-2017, including a series of workshops, publications of new species, etc. after that. In the first Agarica paper, results on the Rhodopolia clade (subgenus *Entoloma*) were reported (Brandrud et al. 2018a), and the second one treated some *Entoloma* species of smaller clades little known or new to Norway (Brandrud et al. 2020a). In the present paper subgenus *Cyanula* (Romagn.) Noordel. (Noordeloos & Gates 2012) is treated. Subgenus *Cyanula* is the species-richest among subgenera or major clades of *Entoloma* in Norway. In the past this group has often referred to as subgenus *Leptonia* (Noordeloos 2004). Recent phylogenetic results, however, show that *Leptonia* forms a distant clade, and is restricted to a small group of species mainly occurring in forests and often on litter or dead wood (Morozova et al. 2014, Noordeloos et al. 2022a). These species have clamped hyphae, whereas the species in subgenus *Cyanula* are clampless.

Subgenus *Cyanula* is one of the genetically, ecologically and morphologically better defined entities within *Entoloma*; the species are clampless, often with bright, highly variable colours (ranging from blue, violaceous to brown, yellow, green and pink) and an initially squamulose-fibrillose pileus (Noordeloos 2004, Noordeloos et al. 2022a). These are often connected to semi-natural grasslands on calcareous soils, but they are also frequently found in forest habitats on calcareous or mull soils. Potentially, they are powerful indicators for high species-diversity hotspots with endangered species and habitats, e.g. calcareous forests (Brandrud & Bendiksen 2018) and calcareous grasslands (Jordal et al. 2006, 2016). Many of the grassland species and the calcareous forest taxa are red-listed in Norway and elsewhere, and a good, updated status is needed to optimize management for this extremely diverse group.

Due to its high complexity, diversity and key role in threatened habitats, *Cyanula* is the subgenus/section that has been most deeply studied during the *Entoloma* project and post-project periods. The results of the Norwegian

project are also extended into a larger study, using data from all over Europe, including available type collections. This larger study has so far resulted in a book with an updated taxonomic revision of this and some other subgenera of *Entoloma* in Europe, and a phylogenetic paper dealing with extra-European taxa as well is under preparation. The book combines the new phylogenetic data with morphological evidence, provides an extensive key, and illustrates the morphological variation of the species in 224 pages with field/studio photos (Noordeloos et al. 2022a). The current paper can be seen as supplementary to this book, and it will primarily focus on a catalogue of the Norwegian species, with references to their habitat, ecology, and distribution in Norway. All species treated in the present paper, are described in detail and depicted in Noordeloos et al. (2022a).

MATERIAL AND METHODS

Sampling

Approximately 2000 samples of *Cyanula* have been collected within the project during and after the Norwegian *Entoloma* study (2015-2022), and 1093 samples were identified/verified by ITS sequencing. The latter number also includes many older fungarium collections, and a number of type specimens and some important reference material. Sampling focused on boreonemoral and southern/middle boreal regions of SE Norway and (coastal) W Norway, where also other mycological field projects were carried out during the period. Further, many samples were obtained from North Trøndelag, Central Norway, during a project foray in 2016, and many from the study of Holmvassdalen nature reserve, Nordland, including some alpine sites. During 2019-2022 many samples were obtained from coastal grasslands (e.g. Jordal et al. 2023). Collections were sequenced through NorBOL, or by Pablo Alvarado (ALVALAB, Spain), or by Bálint Dima, (Budapest, ELTE). All sequences were analysed by us (see below). All material is deposited or will be deposited in O (Natural History Museum, University of Oslo). For further data on each collection (habitat, coordinates), see fungarium database (https://nhm2.uio.no/lav/nld2/; select "fungi") and Artskart (https://artskart.artsdatabanken.no/app/#map/

Morphology

The macromorphological observations are based on descriptions of fresh material, field notes and photographs of the material studied. Photos are mainly by three of the authors and abbreviated in the figures: Bálint Dima; BD, John Bjarne Jordal; JBJ and Tor Erik Brandrud; TEB. Microscopic 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 4 (Gouy et al. 2010). Maximum Likelihood (ML) analysis was carried out using PhyML 3.1 (Guindon et al. 2010) with the following settings: GTR+I+G model of evolution, gamma distribution of 10 rate categories. The phylogenetic tree was edited in MEGA 7 (Kumar et al. 2016) and Microsoft PowerPoint.

RESULTS AND DISCUSSION

Based on our phylogenetic analysis of the 1093 obtained ITS sequences, 53 species of subgenus *Cyanula* are reported as verified from Norwegian material, including 29 which are reported as new to Norway in connection

with the present project (Figure 1, Table 1). Of these, no less than 18 species were new to science (Noordeloos et al. 2020, 2022b, Crous et al. 2021, Dima et al. 2021 and Vila et al. 2021). Via sequencing, eight more, undescribed species have been discovered from Norway, but not presented here, due to very scanty data. Some of the phylogenetically well-supported species apparently show overlapping morphological characters, and should with present knowledge be regarded as cryptic or semi-cryptic species; for further comments see the taxonomic part. More data and a closer study of their variation especially in young stages of basidiomata development, will probably show that several of these are possible to distinguish also morphologically.

Based on an ITS phylogeny from the obtained sequences as well as sequences available from other sources (GenBank, UNITE), a number of well-supported clades can be distinguished within *Cyanula* in Norway (Figure 1). According to Noordeloos et al. (2022a), these belong to the following 9 sections: *Cyanula*, *Griseocyanea*, *Atrocoerulea*, *Fuliginosa*, *Poliopodes*, *Caesiocincta*, *Carneogrisea*, *Asprella* and *Caesiocaules* (= *Chalybea*) (Figure 1). These 9 sections more or less reflect the variation in morphological characters, for instance the large sect. *Cyanula* includes comparatively large-sized species with initially deep blackish blue colours, tomentose-scaly pileus, fibrillose stipe and a well-developed sterile lamella edge. In the other end of the morphological variation, we find the large sect. *Poliopodes*, with tiny, small, usually violet-stiped species with rather smooth to glossy surfaces. Also, the section *Fuliginosa* is clearly defined morphologically, with grey brown to vividly golden-brown species usually without bluish tinges. However, some of the classic features used, such as presence/absence of a blue serrulate lamella edge, are not reflected in this classification, and appear to have little taxonomic relevance at the section level.

In the taxonomic part, we present our species according to the 9 sections shown in Figure 1. For further, detailed morphological descriptions of the species as well as many illustrations and an identification key, see Noordeloos et al. (2022a).

Habitat-preferences

Although most of our *Cyanula* species occurs both in grasslands and forests, the group stands out as one of the more important groups of macrofungi in the Norwegian semi-natural grasslands. It is still unclear if these are mainly to be regarded as saprotrophs or biotrophs. However, analysis of stable isotope ratios of carbon and nitrogen suggest that some species of the more habitat-specific grassland fungi (CHEGD fungi) feature a biotrophic mode of nutrition (Birkebak et al. 2013, Clavariaceae; Halbwachs et al. 2013, *Hygrocybe*). This has not yet been demonstrated for members of *Cyanula*, but seems rather likely.

Calcareous soils:

All species studied are occurring in richer mull soils, and very rarely in acid, organic raw humus soils with (only) ericoid plants. A number may occur in *Sphagnum*, but then in rich (margins of) mires/fens with a high calcium/electrolyte content. Almost half of the species were found exclusively in calcareous soils, and can be regarded as strictly calciphilous, whereas the others also occur in low-herb, medium calcium-rich soils, and can be regarded as moderately calciphilous/basiphilous (Table 1). However, when it comes to other habitat-parameters, most species have a wide range, occurring in dry as well as wet soils, and in open grasslands as well as in (semi-open) forests. A number of species prefer semi-natural grasslands versus forests, and vice versa, but hardly any species is found exclusively in one of those habitat categories.

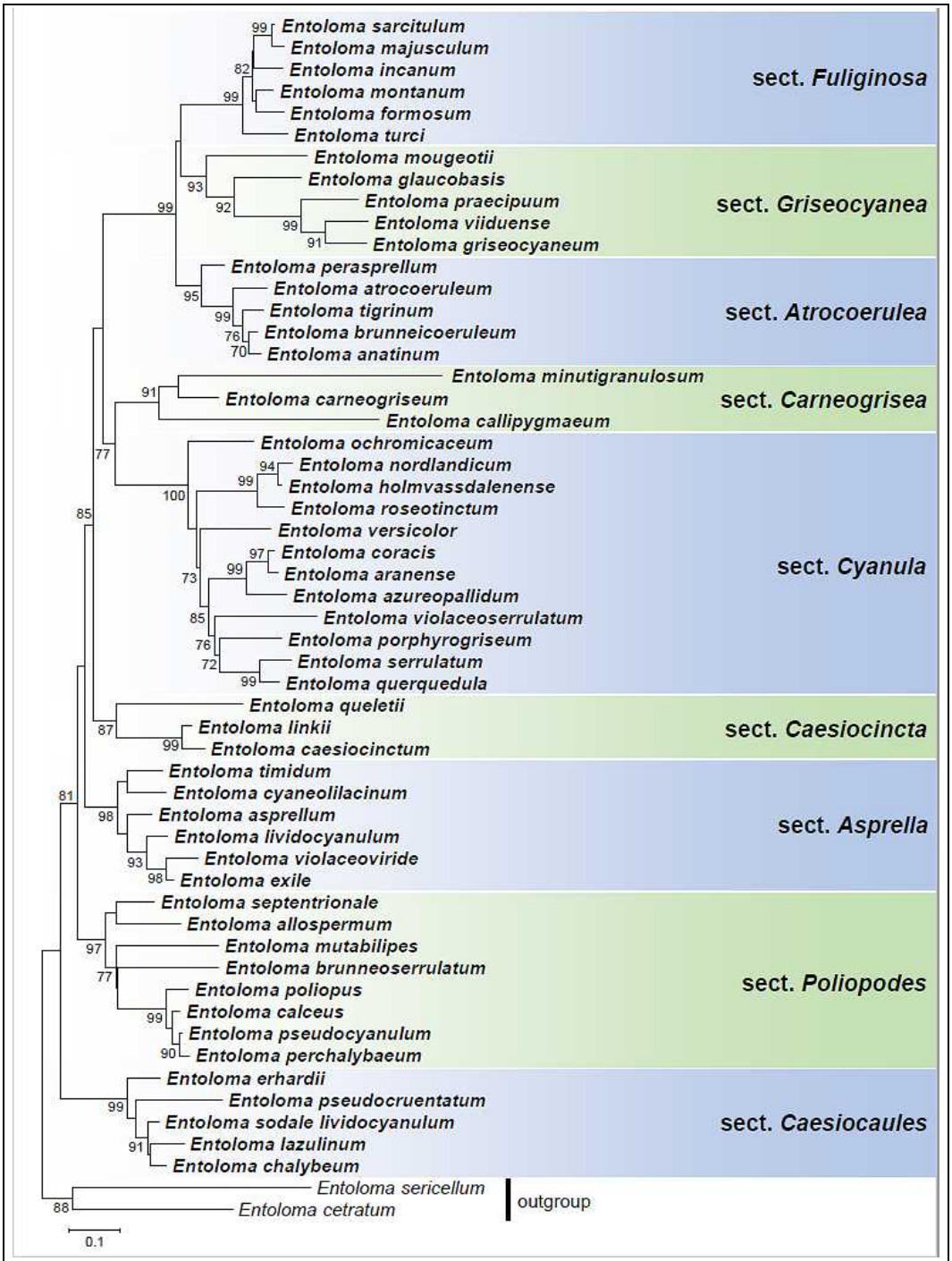

Figure 1. A phylogenetic tree of *Entoloma* subgen. *Cyanula* species documented from Norway, and the sections they belong to. Phylogeny based on nuDNA-ITS-sequences.

"New" habitats:
In our *Entoloma* project we have focused sampling in some calcareous regions and calcareous habitats formerly little documented for *Entoloma* species, such as rich, calcareous fens and fen margins, semi-open, calcareous *Picea* forests with tall-herb "meadows", semi-open calcareous *Pinus* forests and calcareous *Tilia-Corylus* forests. Furthermore, we have included some sites of naturally open grassland-shrubland on (coastal) shallow-soil limestone rocks. All these habitats appear to be rich in *Cyanula* species and can be regarded as hotspot habitats for *Cyanula* taxa. A number of *Cyanula* species new to Norway are apparently more or less restricted to these formerly little studied habitats. Many of these calcareous habitats are rare and declining, and house many threatened species. Especially in sect. *Cyanula* there are many new, strictly calciphilous and threatened species.

In the following, our hotspot habitats are commented in more detail:

Semi-natural grasslands:
The majority of species (34 taxa) were found in semi-natural grasslands, and many species (19 taxa) seem to have their major occurrence here (Table 1). Eight of the previously undescribed 18 taxa were found in such grasslands. Three groups of taxa can be distinguished, (i) those that are more or less restricted to grasslands within calcareous districts, mainly in SE Norway, Trøndelag and Nordland, (ii) those that have a wider distribution also in the many well-developed grasslands of Western Norway, and (iii) a few that are restricted to coastal Western Norway. Examples of the first group are *E. violaceoserrulatum*, *E. ochromicaceum* and *E. turci*, found mainly in some eastern and northern calcareous grassland sites characterized by demanding plants such as *Briza media* and *Gymnadenia conopsea*. Examples from the second group include *E. atrocoeruleum, E. poliopus* and *E. asprellum*, with a very wide grassland distribution. Also, some more demanding species were found in the west, especially in the calcareous Tysnes-Bømlo *Cyanula* hotspot region of S Hordaland. Species such as *E. griseocyaneum*, *E. incanum* and *E. mougeotii* were found along bands of (karstic) marble, in near-shore shell-beds or seasonal hydrophilous sites, e.g. with *Carex flacca*. Rare species such as *E. violaceoviride* and *E. cyaneolilacinum* were found exclusively in Western Norway. Most records from semi-natural sites are from grazed grasslands (pastures), but also from mown meadows, including some non-fertilized, herb-rich lawns (e.g. with *Bistorta vivipara*), parks and church yards on calcareous ground. It should be noted that a number of species also occur in grazed alpine habitats (Larsson et al. in prep., N Sweden).

Naturally open grasslands-shrublands on shallow-soil limestone rocks:
This "steppe-like" habitat with a special protection status in Norway ("selected nature type"), is nationally almost restricted to SE Norway, in coastal limestone sites. We have studied this habitat mainly in Bamble-Porsgrunn, Telemark, including sequencing of a number of collections made by A. Molia and T. Læssøe, from a study of open, calcareous grassland, as a Norwegian hotspot habitat (Bakkestuen et al. 2014). Altogether 13 species were found in this habitat, and many of the same were found in (margin of) calcareous pine forests in the same region, apparently representing a very similar habitat. Of typical species here can be mentioned *E. coracis* (= *E. corvinum* s. auct. p.p.), *E. mougeotii*, *E. glaucobasis* (= *E. coeruleoflocculosum*), *E. majusculum* and *E. incanum* (see Table 1).

Rich (calcareous) fen margins:
This habitat has in the present project been studied mainly in the Steinkjer-Snåsa-district

of Northern Trøndelag. Altogether 22 species were recorded from calcareous fens/mires, typically at fen borders and around springs, mainly in *Sphagnum*, and often in rather open, low herb vegetation with *Thalictrum alpinum and Bistorta vivipara*. Just a few had a major habitat here; *E. glaucobasis*, *E. mougeotii* (including marl deposits along calcareous lakes), *E. sarcitulum* (five out of six records) and *E. mutabilipes*. Also *E. queletii* and *E. carneogriseum*, seems to have some affinity to this habitat.

Alpine sites; calcareous meadows, Dryas-heaths and snow-beds (N Sweden):
Our project did not focus on alpine sites in Norway. However, we have included in Table 1 sequence data from a recent project from Lappland, N Sweden, in calcareous alpine areas belonging to the Scandinavian mountain chain, and not likely to differ from sites on the Norwegian side. Altogether, 15 Norwegian *Cyanula* taxa are so far verified by sequencing from northern Scandinavian mountains, including N Sweden sites (Larsson et al. in prep.; Table 1). Of these, *E. montanum* (= *E. alpigenes* s. auct.) and *E. perasprellum* are standing out, with almost exclusively alpine samples (Noordeloos et al. 2020, Dima et al. 2021). Furthermore, some widely distributed species are also present in the northern alpine region, such as *E. serrulatum*, *E. glaucobasis*, *E. griseocyaneum*, *E. majusculum*, *E. caesiocinctum* and *E. asprellum*. Also, the rare and northern *E. holmvassdalenense* was found in the Lappland study. It should be noted that very few *Cyanula* species have been found in truly arctic environments. Many *Entoloma* species have been collected from Svalbard, but so far none belonging to *Cyanula*!

Calcareous Tilia-Corylus-Fraxinus forests:
Thirty calcareous *Tilia-Corylus* forests were investigated in 2013-2015 and 2019-2021 due to a funded monitoring program of these sites (Brandrud et al. 2016, 2020b, 2022). As a result, 13 *Cyanula* species were recorded, but only in some sites. At the moment, we have no good explanation for this site-to-site variation, only that these *Cyanula* hotspots often coincided with hotspots for the genera *Lepiota*, *Cystolepiota* and *Echinoderma*, and that they are often found in very irregular/-rugged "limestone block terrain", including some small, canyon-like valleys. Three species had a major habitat in the *Tilia-Corylus-Fraxinus* sites; *E. coracis* (= *E. corvinum* s. auct. p.p.), *E. querquedula* and *E. roseotinctum*. Furthermore, *E. allospermum* (= *E. caeruleum* s. auct. p.p.) seems to have an optimum here and in calcareous pine forests. We have also recorded other rare or little known taxa such as *E. linkii*, *E. ochromicaceum*, and *E. brunneoserrulatum* in our monitoring *Tilia-Corylus* forests.

Rich (but not calcareous) thermophilous deciduous forests:
Altogether 12 species were found in other, rich, but not calcareous, deciduous forests with *Corylus, Quercus and Tilia*. Most of these records are from rich *Corylus* or *Corylus-Quercus* forests of scree type from Western Norway, including some more or less culturally influenced, partly grazed sites. This seem (after semi-natural grassland) to be the second most important habitat for *Cyanula* species in Western Norway, and is probably rather undersampled for these, especially the richest, grazed *Corylus* sites. Typical species include *E. queletii, E. lividocyanulum*, as well as rarities such as *E. linkii*, *E. violaceoviride*, *E. cyaneolilacinum*, *E. pseudocruentatum* and *E. erhardii*.

Calcareous pine forests:
A few of these have been studied within the project, especially Røsskleiva nature reserve, Bamble, Telemark, in connection with a

monitoring program (Brandrud & Dima 2017). Especially, semi-open grass/herb-rich calcareous pine forest can be very rich in *Cyanula* species. Many samples are from grassland-like paths or road borders and along exposed rock surfaces within these semi-open forests, and some are from cattle-grazed parts.

Altogether 24 species were verified from calcareous pine forests or forest borders, including a number of rare or little known and calciphilous ones, such as *E. anatinum, E. brunneoviolaceum*, *E. coracis*, *E. queletii*, *E. turci*, and *E. violaceoserrulatum*. This seems, together with calcareous tall-herb spruce forests, to be the richest forest type for *Cyanula* species in Norway.

Calcareous tall herb spruce forests:
Here is included both sites dominated by tall-herbs with stable moisture, but also seasonal hydrophilous, low-herb dominated patches. This habitat has been extensively studied in Grane, Nordland since ca. 2009, in connection with the Holmvassdalen project (see Noordeloos et al. 2018, 2020, Weholt et al. 2014). In this calcareous area, *Picea abies* forests are completely dominating, and *Cyanula* species appear mainly in meadow-like, naturally semi-open tall-herb stands, even with quite open patches, due to lack of spruce regeneration. Sometimes this element occurs also in more seasonal hydrophilous low-herb variants, in both cases strongly influenced by calcareous groundwater. In this semi-open, calcareous spruce forest habitat, no less than 35 of our 53 species have been recorded and verified by barcoding. Due to some degree of over-sampling of this habitat, it is difficult to assess how many species prefer this habitat, but the following seem to have this as a major habitat in Norway: *E. holmvassdalenense*, *E. lazulinum*, *E. nordlandicum*, *E. minutigranulosum*, *E. montanum* and *E. mutabilipes*. Except for *E. lazulinum*, these are more or less northern taxa in our material. Eight of the 18 species described as new in connection with the project were found in this habitat, in Nordland. *Entoloma holmvassdalenense*, *E. nordlandicum* and *E. septentrionale* are typified from Holmvassdalen (Weholt et al. 2014, Noordeloos et al. 2020).

Rich Alnus and Betula forests:
Some scattered observations indicate that also certain kinds of *Alnus incana* forests, especially slope forests with stony, mossy ground, and exposed river borders, can be good hotspots for *Cyanula* species. These occurrences seem to be associated with the combination of rich soils, with a kind of pioneer vegetation, with short-grown, pioneer mosses, around stones or on exposed sand. Also, riparian *Matteuccia struthiopteris* vegetation has been observed to be rich in *Cyanula* species, but little documented.

Northern, calcareous *Betula* forests of scree type are included in this category, but so far we know fairly little about the species diversity here. In Junkerdalen (Saltdal, Nordland) nine *Cyanula* species were verified from calcareous birch forest after only one day of sampling (Jordal et al. 2023). In such *Alnus* and *Betula* habitats, we have verified 21 species so far, including rare/little known ones such as *E. holmvassdalenense*, *E. carneogriseum*, *E. ochromicaceum, E. roseotinctum, E. timidum, E. viiduense* and *E. lazulinum*. Such rich *Alnus* and *Betula* forests, and maybe especially those with *Matteuccia,* should be investigated further.

A comparison with former habitat compilation
A number of our rare or little know *Cyanula* taxa seem to have a preference for forests. For instance, the species *E. roseotinctum* is according to our ca. 20 verified sequences so far only twice recorded from outside calcareous forests. In Jordal et al. (2016), the habitat preferences of groups of grassland species were compiled based on fungarium data and

Table 1. The taxa of subgen. *Cyanula* in Norway, and their habitat and distribution.
Species arranged according to sections. The order of sections follows that of Noordeloos et al. (2022a). For list of species in alphabetic order and a link to the sections they belong to, see Table 2 below.
OTU no = Operational Taxonomic Unit number(s) in our ITS-DNA phylogeny analyses. Tot seq = total number of serquences obtained in the project. New to Norw = New to Norway during *Entoloma* project (from 2015): **x**: reported new in present paper **(x)**: reported new in other, recent papers (see text). **X** = described as new to science in connection to the project (species name in **bold-faced** types). Habitat columns: xx= major habitat(s), x= other habitats in Norway. * records from N Sweden (Larsson et al., in prep). Nat. grassl shalls = natural grassland on shallow soil. Eight undescribed species are not included. For further explanation on habitat-types, see text.

Cyanula taxa in Norway	OTU no	Tot seq	**New to Norw**	Calci phil	Semi nat grassl	Nat grassl shalls	Rich fen marg	Alpine mead	Calc Tilia Coryl	therm decid	Calc Pinus	Calc tallh Picea	Alnus Betu
Sect. Cyanula:													
E. serrulatum	26/27/121	25		x	xx		x	x			x	x	
E. querquedula	25	25		x	x		x	x	xx		x	x	x
E. porphyrogriseum	21	39		xx	xx		x	x				x	x
E. coracis	22	19	**X**	xx	x	xx	x		xx		xx		
E. versicolor	24	8	**X**	xx	x				x			x	x
E. aranense	23	9	**x**	xx								xx	
E. azureopallidum	234	1	**x**	xx	xx								
E. violaceoserrulatum	20	27	**X**	xx	xx	x	x				x	x	x
E. ochromicaceum	16	18	**(x)**	xx	xx				x			x	x
E. holmvassdalenense	17	25		xx			x	x*				xx	x
E. nordlandicum	18	5	**X**	xx			x					xx	
E. roseotinctum	19/131	21	**(x)**	xx	x				xx	x		xx	x
sect Carneogrisea:													
E. carneogriseum	80	24	**(x)**	x	xx		x					x	x
E. minutigranulosum	9	12	**X**	xx	xx			x				xx	

E. callipygmaeum	227	2	**X**	xx	x							x	
sect Caesiocincta:													
E. caesiocinctum	165/166	18		x	xx		x	x			x		
E. linkii	5	10		x						x	x	x	x
E. queletii	6	11		xx	xx	x	x			x	x	x	
sect Poliopodes:													
E. poliopus	2	50		x	xx	x	x	x*	x		x	x	x
E. allospermum	4	59	**(x)**	x	xx	x			xx	x	xx	x	x
E. mutabilipes	1	45	**x**	x	x		xx	x			x	xx	
E. calceus	214	3	**X**				x						
E. pseudocyanulum	162	2	**x**		x		x						
E. perchalybeum	229	2	**X**	x				x*				x	
E. septentrionale	3	1	**X**	x								x	
E. brunneoserrulatum	117	13	**(x)**	xx	xx	x			x		xx		
sect. Asprella:													
E. asprellum	12	37		x	xx			x*			x	x	x
E. lividocyanulum	13	21		x	x		x			x	x	x	x
E. exile	15	31		x	xx				x		x	x	x
E. timidum	10	8	**X**	x	x					x		x	x
E. violaceoviride	14	16	**(x)**	x	xx					x			
E. cyaneolilacinum	11	13	**X**	x	xx					x			
sect. Caesiocaules:													
E. chalybeum	8	16		xx	xx				x		xx		
E. pseudocruentatum	125	1	**X**	x						x			

E. lazulinum	7	17		x	xx							xx	x
E. erhardii	233	1	**X**	xx						x			
E. sodale	222	1		x	x								
sect. Griseocyanea:													
E. mougeotii	31	31		xx	xx	x	xx	x*	x	x	x	x	
E. glaucobasis	30	25		xx	xx	x	xx	x			x	x	
E. griseocyaneum	28	31		xx	xx	x		x			x	x	x
E. viiduense	29	19	**x**	xx	xx							x	x
E. praecipuum	200	2	**X**	x	xx								
sect. Atrocoerulea:													
E. atrocoeruleum	33	125		x	xx	x							
E. brunneicoeruleum	82	3	**X**		x		x						x
E. anatinum	32	42		x	xx						x	x	x
E. perasprellum	207	1	**X**	x	x			x*					
E. tigrinum	169	1	**X**	x			x						
sect Fuliginosa:													
E. sarcitulum	36	9		x			xx					(x)	
E. majusculum	35/83/168	50		xx	xx	x	x	x*			x	x	x
E. turci	34	51		xx	xx	x		x*	x		xx	x	
E. montanum	39	17	**X**	x				xx*			x	xx	
E. formosum s.lat.	84	41		x	xx		x			x	x	x	
E. incanum	37	9		xx	x	x			x		x	x	
53 species		1093	**29/ 18**	50 (23)	38 (25)	13	22	15	13	12	24	35	21

Table 2. The 53 species of *Cyanula* in Norway sorted alphabetically, with link to the section they belong to. Number on section refers to the arrangement of the sections and their species in Noordeloos et al. (2022a), and in the Taxonomic part below and Table 1 above. The 18 species described as new 2020-2022 are marked in **bold-faced types**.

species	section		*species*	section
E.allospermum	4. Poliopodes		***E.montanum***	**9. Fuliginosa**
E.anatinum	8. Atrocoerulea		*E.mougeotii*	7. Griseocyanea
E.aranense	1. Cyanula		*E.mutabilipes*	4. Poliopodes
E.asprellum	5. Asprella		***E.nordlandicum***	**1. Cyanula**
E.atrocoeruleum	8. Atrocoerulea		*E.ochromicaceum*	1. Cyanula
E.azureopallidum	1. Cyanula		***E.perasprellum***	**8. Atrocoerulea**
E.brunneicoeruleum	**8. Atrocoerulea**		***E.perchalybeum***	**4. Poliopodes**
E.brunneoserrulatum	4. Poliopodes		*E.poliopus*	4. Poliopodes
E.caesiocinctum	3. Caesiocincta		*E.porphyrogriseum*	1. Cyanula
E.calceus	**4. Poliopodes**		***E.praecipuum***	**7. Griseocyanea**
E.callipygmaeum	**2. Carneogrisea**		***E.pseudocruentatum***	**6. Caesiocaules**
E.carneogriseum	2. Carneogrisea		*E.pseudocyanulum*	4. Poliopodes
E.chalybeum	6. Caesiocaules		*E.queletii*	3. Caesiocincta
E.coracis	**1. Cyanula**		*E.querquedula*	1. Cyanula
E.cyaneolilacinum	**5. Asprella**		*E.roseotinctum*	1. Cyanula
E.erhardii	**6. Caesiocaules**		*E.sarcitulum*	9. Fuliginosa
E.exile	5. Asprella		***E.septentrionale***	**4. Poliopodes**
E.formosum s.lat.	9. Fuliginosa		*E.serrulatum*	1. Cyanula
E.glaucobasis	7. Griseocyanea		*E.sodale*	6. Caesiocaules
E.griseocyaneum	7. Griseocyanea		***E.tigrinum***	**8. Atrocoerulea**
E.holmvassdalenense	1. Cyanula		***E.timidum***	**5. Asprella**
E.incanum	9. Fuliginosa		*E.turci*	9. Fuliginosa
E.lazulinum	6. Caesiocaules		***E.versicolor***	**1. Cyanula**
E.linkii	3. Caesiocincta		***E.violaceoserrulatum***	**1. Cyanula**
E.lividocyanulum	5. Asprella		*E.violaceoviride*	5. Asprella
E.majusculum	9. Fuliginosa		*E.viiduense*	7. Griseocyanea
E.minutigranulosum	**2. Carneogrisea**			

observations, including 29 *Cyanula* species (species with >10 Norwegian collections with habitat data). The percentage of records from forests varied from 0 to 44%, with an average forest record percentage of 15%. This compilation is based on non-sequenced data mainly, and since many of the *Cyanula* species has changed their circumscription considerably after sequencing, it is difficult to compare these numbers directly with our data. However, in some cases species identifications stand up to the sequencing, and these species can be compared. Two examples shall here be given:

E. turci: Jordal et al. (2016) compiled data from 180 collections of *E. turci*, with approx. 8% of the records from forests. In our data, almost 50% of the localities/sites are from forests. The many records from formerly little studied habitats such as semi-open, calcareous tall-herb *Picea* forests and calcareous *Pinus* forests, indicate that the percentage from Jordal et al (2016) based on fungarium data is probably too low. We thus estimate the true portion of *E. turci* populations in semi-open, calcareous forests to be >25%.

E. mougeotii: We found 50% of our sequence-verified collections of *E. mougeotii* from forests, whereas Jordal et al. (2016) found 23% of the records from forests. However, in this case, we assume that the most undersampled habitat for this one is calcareous fen margins. Based on the comparatively many records from fens in the fungaria (23 records), in spite of low sampling intensity, we assume this to be a major habitat for this species in Norway.

Taxonomic part/comments

Section *Cyanula*

This section is a large one and includes 12 species in Norway and so far 21 in Europe (Noordeloos et al. 2022a). The section is typified by *E. serrulatum*. Many species in sect. *Cyanula* are morphologically rather to very similar, but most should be possible to distinguish based on a combination of differentiation in morphology and ecogeographical patterns. Four of our Norwegian species have been described as new since the start of our *Entoloma* project, and three of these based on large populations from Norway; *E. coracis*, *E. nordlandicum* and *E. violaceoserrulatum*; the two former ones with Norwegian type specimens.

The section *Cyanula* is dominated by strictly calciphilous species (Table 1), with initially scaly-tomentose, blackish blue pilei and silky-fibrillose stipes. Cheilocystidia are abundant and well-developed, usually large, clavate-fusiform, sometimes also lageniform. The *E. serrulatum-E. querquedula* lineage includes species with a serrulate, black or blue lamella edge, whereas the other lineages lack this feature, or a coloured lamella edge (cystidia with dark contents) is only developed in patches, with age. The *E. nordlandicum-E. holmvassdalenense* lineage consists of species with usually rather pronounced, discrete squamulose pilei, rather than the more closed, velvety surface of the other taxa. Furthermore, the initially bluish stipes are less fibrillose.

Entoloma serrulatum (Fr.) Hesler
(OTU26/27/121; Fig. 2)

Entoloma serrulatum has for long time been regarded as a morphological intricate complex (Noordeloos 2004, Noordeloos et al. 2022a), and this is now also confirmed by phylogenetic data. As here circumscribed, it is genetically variable, and may include cryptic species. However, deeper, multigene studies are needed to unravel the genetic structure, and for the time being, we treat the complex as one species. Another close, but genetically well-supported species, *E. querquedula*, is morphologically very similar and hard to key out.

Entoloma serrulatum is characterized especially by the violaceous, bluish-black or black, serrulate lamella edge – the so-called

Figure 2. Serrulate sisters: *E. serrulatum* (above) and *E. querquedula*. Both with blue, serrulate lamella edge. The sisters are difficult to distinguish, but *E. querquedula* is usually paler, less bluish and often more greenish on stipe. From sect. *Cyanula*. (Photos: JBJ, BD)

serrulatum type, and also by the initially bluish grey to bluish black pilei, which remarkably soon fades to brown or with bluish tinges remaining just at the very margin. It also occurs in a striking pinkish-red form (*E. callirhodon* Hauskn. & Noordel.; see Noordeloos et al. 2022a).

It strongly resembles *E. querquedula*, but the latter apparently in most cases has a paler and less bluish pileus surface when young, and becomes still more pallid with age, sometimes almost whitish. The stipe of *E. querquedula* often goes from blue via a more glaucous-greenish blue stage before discolouring into pallid ochre grey, whereas *E. serrulatum* often keeps its bluish stipe colour rather persistently.

Ecologically, *E. querquedula* is mainly a forest species (but sometimes occurring in calcareous grasslands), whereas *E. serrulatum* appears to have a wide ecology, spanning from intermediate to rich grasslands to (open) forests, mires/fens and even road verges. Most of our 25 verified collections of *E. serrulatum* are, however, from pastures. Both species also occur in the alpine zone (N Sweden, Larsson et al. in prep.). The many non-sequenced collections labelled *E. serrulatum* in the Norwegian fungaria, should be regarded as *E. serrulatum* s.l, including *E. querquedula* and *E. caesiocinctum*. *Entoloma serrulatum* is widespread and possibly one of the most common *Cyanula* in Europe (Noordeloos et al. 2022a).

Entoloma querquedula (Romagn.) Noordel. (OTU25; Fig. 2))

Entoloma querquedula, often misidentified as *E. caesiocinctum*, is phylogenetically and morphologically very similar to *E. serrulatum*, and for comparison to *E. serrulatum*, see above.

So far, 25 Norwegian collections are verified as *E. querquedula*. Most of these are from calcareous forests, both from southern *Tilia* forests, *Fraxinus-Corylus* sites, *Pinus* sites and northern tall herb *Picea-Betula* sites. From Hungary, we have also sequenced material from a calcareous *Fagus* forest. One of our collections stems from a more or less calcareous fen, one from alpine Dryas heath and six collections from calcareous, semi-natural grasslands. *Entoloma caesiotinctum* is with difficulty distinguished by more brownish pileus colours (often with a bluish margin), and is genetically not closely related (see sect. *Caesiocinta*).

Entoloma porphyrogriseum Noordel. (OTU21; Fig. 3)

This, together with e.g. *E. coracis*, is part of what was formerly treated as *E. corvinum* (Kühner) Noordel. and *E. melanochroum* Noordel. in Norway and elsewhere. *Entoloma porphyrogriseum* is probably the most frequent taxon formerly included in the *E. corvinum* concept in Norway – especially in boreal regions – and in Scandinavia as a whole. For differences towards E. *coracis*, the other frequent taxon within this concept, see this species.

So far, we have sequence-verified 39 collections from Norway. Most collections are from calcareous, semi-natural grasslands and semi-open tall-herb *Picea* forests, but also from (margin of) calcareous fens, calcareous river banks and alpine sites. The species is verified only from the most calcareous districts of SE, C and N Norway, and so far, no collections from W Norway have been confirmed. Within a sequence screening of a large material collected by Virve Ravolainen from Reinøya north of Tromsø (Ravolainen 2000), this appeared to be one of the most frequent species, with 12 collections. The species occurs in subartic grasslands in Finnmark and was once recorded also from an alpine *Dryas* heath (Råtåsjøhø in Dovre mountains, Folldal, Hedmark). In North Sweden, the species was recorded in a number of alpine

Figure 3. Blackish blue brothers: *E. coracis* (above) and *E. porphyrogriseum*. *E. coracis* has larger spores and is typical for the dry calcareous forests around the Oslofjord, whereas *E. porphyrogriseum* is found mainly in pastures all over Norway. Both were formerly often called *E. corvinum*. (photos: BD, TEB)

sites (Larsson et al. in prep.). The species seems to have a somewhat more northern/-montane distribution in Scandinavia than the resembling species *E. coracis*, apparently occurring on less thermophilous sites. On the other hand, the species is also reported from

many localities in Denmark (type locality and with 89 records, https://svampe.databasen.org/taxon/13718, and with not confirmed records of *E. coracis*), and is apparently widespread in Central Europe (Noordeloos et al. 2022a).

Entoloma coracis Brandrud, Dima, Noordel., G.M. Jansen & Vila (OTU22; Fig. 3)
Entoloma coracis was introduced as a new species in Crous et al. (2021). It was formerly treated as part of *E. corvinum* s. auct. The true *E. corvinum* described by Kühner from E France, is a montane-alpine, very dark species, hitherto not found in Scandinavia, with a distant phylogenetic position (in section *Poliopodes*, Noordeloos et al. 2022a).

Entoloma coracis is after *E. porphyrogriseum* the most frequent taxon in the *E. corvinum* s. auct. complex in Norway. Both are characterized by an initially very dark, almost (bluish) black, velvety-scaly-fibrillose pileus, and a fibrillose stipe, with greyish-lilac-greyish-porphyrous-greyish colours, sometimes more distinctly bluish, initially rather dark at apex. With age, the pileus becomes smoother, and more (pale) brownish, and the stipe gradually might become polished. The lamellae are initially whitish, with concolorous edge, but sometimes the edges become in part bluish grey brown and serrulate with age. On average, *E. porphyrogriseum* seems to be somewhat paler than *E. coracis*, especially with age. Furthermore, *E. porphyrogriseum* sometimes develops a distinct pinkish grey tinge on the stipe. Microscopically, they are both characterized by a well-developed, sterile lamella edge, with numerous clavate(-fusiform) cheilocystidia. The spores are somewhat smaller in *E. porphyrogriseum*. *Entoloma coracis* can also recall *E. violaceoserrulatum* (see comments under that species).

Based on the 19 collections sequence-verified so far, *E. coracis* is in Norway associated mainly with calcareous (semi-open) forests, in calcareous *Pinus*- and calcareous *Tilia* forests, but in the Oslofjord area also in naturally open, steppe-like grassland/shrubland on shallow-soil limestone rocks, and once also recorded in a calcareous fen. The species is considerably more southeastern than *E. porphyrogriseum* in Norway, with most collections from the Oslofjord area, SE Norway, six collections from calcareous, dry pine-spruce forests at Steinkjer-Snåsa, Trøndelag, C Norway, while the two most northernmost finds are from near-shore shell-bed grassland in coastal Nordland (southern boreal). Elsewhere in Europe, the species is verified mainly from the Mediterranean region, indicating that this is generally a rather thermophilous species (Crous et al. 2021).

Entoloma versicolor P.-A. Moreau, Vila, Noordel. & Dima (OTU24)
Entoloma versicolor, a recently described species (Vila et al. 2021) is sequence-verified from 8 collections, representing 4 localities in Norway; two in calcareous spruce/pine forests (Holmvassdalen nature reserve, Nordland; Skrattåsen, Steinkjer, Trøndelag), one from calcareous *Corylus/Fraxinus/Tilia* forest at Skorpo, Tysnes, Hordaland, and one from calcareous grassland at Bømlo, Hordaland. The holotype population from France included a pure pink variant (Vila et al. 2021; see also Noordeloos et al. 2022a). This phenomenon is seen also in e.g. the related *E. porphyrogriseum*, and seems to have no taxonomic relevance except for identification purposes. The French material was collected in riparian *Corylus* copses. The morphological differentiation towards *E. porphyrogriseum* and *E. coracis* is small, but *E. versicolor* differs from both in having a serrulatum-type lamella edge with clusters of tramal hyphae protruding through the hymenium, whereas *E. porphyrogriseum* and *E. coracis* have the more regular poliopus-type lamella edge. *Entoloma porphyrogriseum* is mainly a grassland species,

whereas *E. coracis* occurs in more thermophilous types of habitats, often in forests. So far, *E. versicolor* is verified only from Norway and France. *Entoloma versicolor* has a close sister found in Eastern (Asian) Russia (O. Morozova, pers. comm.).

Entoloma aranense F. Caball. & Vila (OTU23)
This is a sister species of *E. coracis*, but appears to be somewhat paler, with a lilac-bluish tinged pileus when young, soon becoming brown fibrillose. The species seems widely distributed; it was described from subalpine meadows, on acid or basic soil at the margin of *Corylus* woodlands in Spain (Vila et al. 2013) and verified also from Russian Siberia (Altay) and Caucasus. In Norway, it seems to be a mainly northern taxon, and is so far only verified from nine collections from the Holmvassdalen nature reserve (Grane), and one from Mosjøen, both Nordland. The Nordland finds are mainly from calcareous tall-herb spruce forests.

Entoloma azureopallidum Corriol (OTU234)
This taxon was described by Corriol (2016) from the French Pyrenees, and it was found in Norway in 2020 in a calcareous, sandy, semi-natural grassland close to the sea at Molnes, Giske, Møre og Romsdal (Jordal et al. 2022). Phylogenetically, this species is closely related to *E. coracis* and *E. aranense*, but is according to the original description by Corriol (2016) much paler than *E. coracis* and with more smooth (not velvety-scaly) pileus and a rather pale stipe. However, the Norwegian specimens were darker blackish blue and with a more scaly pileus, and such darker specimens are also seen in material depicted in Noordeloos et al. (2022a). A bluish grey tinge on young lamellae, like in *E. chalybeum*, might be a good separating character towards *E. coracis* and *E. aranense*. The two latter have pure white lamellae when young, contrasting dark pileus and stipe apex. However, the typical features of *E. azureopallidum* must still be regarded as little known. The species is sequence-verified from Norway, Denmark, Estonia, France, Italy and Russian Caucasus.

Entoloma violaceoserrulatum Noordel., Brandrud, Morozova & Dima (OTU20; Fig. 4)
This is a beautiful, apparently mainly boreal species, characterized by its fibrillose-tomentose, lilac-violet grey to almost blackish blue pileus and paler lilac grey, persistently fibrillose stipe. The lilac-violet tinges, however, fade quickly, rendering the species more brownish grey. The lamellae are initially pure white. The edges are serrulate, usually concolorous, but they can also be dark bluish grey, at least in patches and with age. Microscopically, the species is characterized by very abundant intra-and extracellular, light dispersing granules, and also the large, abundant clavate-fusiform-lageniform cheilocystidia are filled with such granules. The latter distinguishes the species from e.g. *E. serrulatum* and *E. mougeotii*.

The phylogenetic position of the species is not quite resolved, but in most analyses, it occupies a basal position to the *E. coracis*-*E. aranense* lineage. The species is macromorphologically somewhat intermediate between *E. mougeotii* and *E. coracis*-*E. porphyrogriseum*. It is distinguished from *E. mougeotii* by an initially less lilac blue pileus and stipe (and never with an asymmetrical, undulate pileus), and from *E. corvinum*-*E. porphyrogriseum* by initially having somewhat more pronounced bluish tinges. Furthermore, the stipe is more pronounced and more persistently fibrillose and opaque than in *E. coracis*-*E. porphyrogriseum*, never becoming glossy.

Entoloma violaceoserrulatum appears to be a strictly calciphilous species. It is now recorded and verified from 27 localities in Norway, of which the majority (16) are from calcareous grasslands. Of these, 4 records are

Figure 4. Blue brother and a pale guy: *E. violaceoserrulatum* (above) and *E. ochromicaceum*. The former is beautifully dark violaceous blue when (very) young, the latter is pale grey. Both with gill edge densely set with cystidia, and both prefer calcareous grasslands. (photos: TEB)

from naturally open, coastal, steppe-like grasslands on shallow-soil limestone rocks in the Oslofjord region, the others are from semi-natural, partly mown grasslands, and partly

(sheep) grazed areas, often dominated by *Bistorta vivipara*. Furthermore, six collections are from rather open, calcareous forests including forest paths, mainly from calcareous tall herb *Picea-Betula* forests, but once also from boreonemoral calcareous *Pinus* forest (Ringerike). The species is also recorded from an old limestone quarry.

Entoloma violaceoserrulatum has a wide distribution in calcareous parts of Norway, ranging from southern Oslofjord (Bamble-Porsgrunn), via Ringerike-Hadeland, North-Trøndelag, Nordland (Holmvassdalen nature reserve) to Troms (Karlsøy) in Northern Norway. There is one western outpost recorded also at Fræna, Møre & Romsdal. Elsewhere, the species is reported from one locality in Jämtland, Sweden (Brandrud et al. 2018b), the type locality in Finland (Noordeloos 2004), three sites in Denmark (incl. in damp deciduous woodland on black mull soil) (Noordeloos et al. 2022a;
https://svampe.databasen.org/taxon/70205)
and from one site in The Netherlands (Crous at al. 2021). *Entoloma violaceoserrulatum* was initially invalidly published in Noordeloos (2004), since a holotype was indicated in both herb. L and herb. TUR. Subsequently, the species was validated in Dima et al. (2021), providing an updated description, based on the many additional collections since 2004 (see also Noordeloos et al. 2022a). Based on present data, this seems to be a truly Northern European species, with its major populations in Norway.

Entoloma ochromicaceum Noordel. & Liiv (OTU16; Fig. 4)
Entoloma ochromicaceum forms the most basal clade in sect. *Cyanula* (Figure 1), but with phylogenetic similarity to the E. nordlandicum-E. holmvassdalenense lineage (subsect. *Rhynchocystidiatae*). The species differs macroscopically considerably from the other members of the section, with its pale colours, almost completely devoid of bluish tinges. The pileus is pale grey, rather smooth-fibrillose, but not hygrophanous. The stipe is pale grey to faintly bluish grey; initially finely fibrillose, but soon glabrous and polished. Furthermore, it has well-developed, clavate-fusiform(-lageniform) cheilocystidia.

This is another, apparently strictly calciphilous species, mainly associated with semi-natural, grazed or mown grassland, but also found in calcareous *Tilia-Corylus* forests and in calcareous *Betula* scree forests, and with a distribution manly in the Oslofjord-Hadeland-Mjøsa region and Nordland (Grane-Saltdal-Bodø). It is also verified from a calcareous *Corylus-Pinus* woodland in Sunnhordland, W Norway. At present, the species is DNA-verified from 18 localities. It seems to be rare but widespread in Europe; from France to Russia, with the type locality on the Saarenmaa limestone alvar of Estonia (Noordeloos 1992).

Entoloma holmvassdalenense Eidissen, Lorås & Weholt (OTU17; Fig. 5)
Entoloma holmvassdalenense is distinguished from its close relatives *E. nordlandicum* and *E. roseotinctum* and *E. coracis* and *E. porphyrogriseum,* by the two-spored basidia and large spores, as well as the usually broadly clavate-mucronate to lageniform cheilocystidia. The *E. holmvassdalen-E. nordlandicum* lineage differs from the other clades in sect. *Cyanula* by a different type of lamella edge and by the shape of cheilocystidia - designated the rhynchocystidiatae type (after *E. rhynchocystidiatum*), a species mainly known from alvar grasslands in Estonia and so far not found in Norway (see e.g. Noordeloos et al. 2022a).

Entoloma holmvassdalenense is so far known mainly from Holmvassdalen and adjacent districts in Grane, Nordland (Weholt et al. 2014), but it has also been found on Kvamsfjellet, Steinkjer, Nord-Trøndelag, at Vang in Valdres (Oppland) and Romsås, Oslo.

Figure 5a. The northern blue brothers: *E. holmvassdalenense* (5a) and *E. nordlandicum* (see Fig. 5b next page). Both in Norway found mainly in Holmvassdalen NR, Nordland. The former is distinguished on the two-spored basidia and larger spores than the latter. (photo TEB)

Recently, it has also been confirmed from an alpine site in N Sweden (Larsson et al. in prep.) and from C Finland (Kokkonen 2021). So far, it is only known from Fennoscandia. North Norway seems to be its core area, being sequence-verified from more than 20 localities.

Entoloma holmvassdalenense is according to data at hand, a typical species of middle/-northern boreal calcareous forests and forest margins, where it is found in semi-open calcareous tall herb spruce forests and margin of rich mires with *Salix* and *Picea*, sometimes in *Sphagnum*, rarely in alpine, calcareous habitats (Table 1).

Entoloma nordlandicum Noordel., Lorås, Eidissen & Dima (OTU18; Fig. 5)
This species is macroscopically very similar to *E. holmvassdalenesis*, but it has 4-spored basidia and medium large spores. The pileus is velvety-scaly and bluish black when young, and the stipe is initially finely fibrillose and bright blue.

Entoloma nordlandicum was described in Noordeloos et al. (2020), based mainly on material from four localities in the Holmvassdalen and Geitklauvmyra nature reserves in Grane, Nordland. Here it was found in calcareous spruce forests, in moist sites, both moist tall-herb types as well as more seasonal hydrophilous ones; also in *Sphagnum*. It is also found in a moist, apparently somewhat calcium/base-rich peat bog in the Netherlands (Noordeloos et al. 2020). Since that, the species has been sequence-verified also from a damp forest site in Denmark (Sjælland; Helvigstrup Skov; a hotspot for *Cyanula*, see Noordeloos et al. 2022a; https://svampe.databasen.org/taxon/70206).

Figure 5b. *Entoloma nordlandicum*. This differs from the often co-occurring blue brother *E. holmvassdalenense* in smaller spores. (aquarelle: Hermod Karlsen)

Entoloma roseotinctum Noordel. & Liiv (OTU19/131)

Entoloma roseotinctum, as here circumscribed, is a phylogenetic complex not yet completely resolved. Our material has a match with the type from Estonia. *Entoloma glaucodubium* Corriol is phylogenetically very close, and should probably be regarded as conspecific (Noordeloos et al. 2022a).

Entoloma roseotinctum is characterized by the umbilicate pileus being initially finely scaly, then pronounced radially fibrillose, and grey-brown but apparently with a faint bluish tinge when young. The stipe is blue-grey and polished. It may strongly resemble *E. allospermum* (in sect. *Poliopodes*), which can co-occur in calcareous *Tilia-Corylus* forests. However, *E. roseotinctum* is distinguished by the well-developed cheilocystidia. As in some other *Cyanula* species, pinkish coloured variants are encountered Noordeloos et al. 2022a), hence the name *E. roseotinctum*, which is not a very descriptive name for the most common morphotype.

The species is sequence-verified from 21 collections. So far it has been found almost exclusively in calcareous forests, both in *Tilia-Corylus-Fraxinus* forests as well as in semi-open *Picea* forests, both with low-herbs and with tall herbs. The species is found mainly in calcareous districts of SE, C and N Norway (north to Reinøya, Troms). Three collections are from calcareous *Tilia-Corylus-Fraxinus* forests in the Oslofjord region, and two collections are from a south-faced *Corylus* forest along the Sunndal- and Trondheimsfjord. These broad-leaved forest sites indicate that this a more thermophilous species than its close relatives, *E. holmvassdalenense* and *E. nordlandicum*. In N Norway, the species is found mainly in calcareous spruce forests, but also in calcareous *Betula* woodlands of scree type, once also in a calcareous pasture (Troms) and once in a sand dune meadow (Lofoten). Outside Norway, this species is verified from Finland, Austria, France and Spain.

Section *Carneogrisea*

This is a small section, in our phylogenetic tree placed as sister group to sect. *Cyanula* (Fig. 1). However, this sister position is not well supported. The section *Carneogrisea* is represented by three, rather morphologically different species in Norway. These three are so far the only known members in Europe of this section. Two of the three species were described in Dima et al. (2021).

Entoloma carneogriseum (Berk. & Broome) Noordel. (OTU80)

This is a widespread but little-known species with a (blackish-)brownish, serrulate lamella edge, and it has often been misidentified as *E. serrulatum* or *E. caesiocinctum*, and more

rarely as *E. poliopus* or *E. brunneoserrulatum*. It can probably be distinguised from *E. serrulatum*, *E. querquedula*, *E. caesiocinctum* and *E. brunneoserrulatum* by the more slender habit, with striate, hardly ever bluish tinged pileus, which rarely is depressed. The lamella edge is usually blackish-brownish (rarely bluish when young), and sometimes only coloured in patches.

Altogether 24 collections are verified from Norway. Most of them are from grazed grasslands, but also from rich fens, rich *Alnus* forests, and from calcareous *Picea* forests. It seems to occur in intermediate to more strongly calcareous soils. The species is widely distributed in E, W and C Norway, but so far only recorded twice in N Norway (Tromsø region). On a European scale, the species seems to be a northern one, outside Norway so far only sequence-verified from Estonia (four collections). The type of *E. carneogriseum* was collected "amongst fir needles" in Aberdeenshire, Scotland.

Entoloma minutigranulosum O.V. Morozova, Noordel., Brandrud & Dima (OTU09)
This species, published in Dima et al. (2021), is characterized by brownish, finely granulate pilei and initially pale bluish grey, soon grey, more or less polished stipes. The stipe is apparently always bluish tinged when very young, but this soon fades, leaving the stipe more metallic grey and finally brownish tinged. In these stages, the species resembles *E. ochromicaceum*. A blue tinge may persist for some time at stipe base, resembling that of *E. glaucobasis*. The lamella edge is concolorous, or sometimes brown spotted, with clavate cystidia.

So far 12 samples are verified from Norway, mainly from N Norway, north to Porsanger, Finnmark, and only one sample from S Norway (Valdres). Many collections stem from the Holmvassdalen Nature Reserve (Grane, Nordland). The species occurs both in calcareous grasslands including coastal shell-beds and in calcareous *Picea* forests, both in low-herb and tall-herb vegetation. There is also one record from alpine, calcareous *Dryas* heath at Dovre mountains, South Trøndelag, and also one from alpine, calcareous habitat in N Sweden (Larsson et al. in prep.). The species is widely distributed in Europe, including adjacent parts of Asia, east to Altai.

Entoloma callipygmaeum O.V. Morozova, Noordel. & Dima (OTU227)
Entoloma callipygmaeum is a very tiny, somewhat umbilicate-scaly, blue species typified from Far East Russia (Dima et al. 2021, and it represents *E. gomerense* sensu Noordeloos and Morozova (2010). A few western European collections (from Norway, Denmark, France) deviate slightly in ITS sequences from this, but preliminary we regard these to belong to the same species. The first Norwegian collection was made in Reinøya (Karlsøy, Troms) 26 Aug 1999 by Virve Ravolainen, in calcareous semi-natural grassland (grazed by sheep and goat; Ravolainen 2000). The other sequence-verified collection was made by Jostein Lorås in Holmvassdalen 5 Sept 2011 (this collection deviates slightly in ITS), and was included as *E. gomerense* in Weholt et al. (2014). It should be noted that another collection cited in this paper under the name *E. gomerense* represent another, still undescribed species, based on ITS sequence results (OTU163). None of the here mentioned interpretations of *E. gomerense* apparently corresponds with the original concept of *E. gomerense*, described from La Gomera on the Canary Islands. In Northern Sweden there are three collections of *E. callipygmaeum* from three different areas, in calcareous alpine vegetation (Larsson et al. in prep.).

Section *Caesiocincta*
This is a small clade, including the sister species *E. caesiocinctum* and *E. linkii*, as well as the more distant and morphologically quite deviating *E. queletii*. The *E. caesiocinctum-E. linkii* clade is a remarkable parallel to the *E. serrulatum-E. querquedula* clade. These clades are genetically distant, but with a quite similar morphology, characterized e.g. by a bluish-black(-brown), serrulate lamella edge (serrulatum-type). Altogether 6 species of sect. *Caesiocincta* are known from Europe (Noordeloos et al. 2022a).

Entoloma caesiocinctum (Kühner) Noordel. (OTU165, 166)
Entoloma caesiocintum resembles *E. serrulatum* and *E. querquedula*, and these taxa have often been mistaken for each other. *Entoloma caesiocinctum* has, however, an initially less fibrillose-tomentose pileus, which typically has bluish tinges only at the pileus margin when young. Soon the pileus becomes entirely brownish, contrasting the blue stipe. And finally, the fruitbody becomes uniformly brown, with a brown to blue brown, serrulate lamella edge. The pileus is not discolouring to very pale, as seen especially in *E. querquedula*. The pileus margin is also more translucently striate than in *E. serrulatum*. Our material of *E. caesiocinctum* is phylogenetically slightly heterogeneous.

Entoloma caesiocinctum apparently has a rather wide habitat-preference, based on the 18 sequence-verified samples studied. It was found several times during our *Entoloma* foray at Steinkjer 2016, mainly in more or less calcareous, rich fens at Kvamsfjellet, but also in calcareous, grazed alpine grassland-heathland at Hårskallen, Levanger. Further records are from Bømlo in Hordaland, Sunndal in Møre og Romsdal, Tjøtta in Nordland and Lunner in Oppland from grazed or mown grasslands, and from Porsgrunn, Telemark in richer pine forests. The species does not seem to be strictly calcareous. Our data so far indicate a habitat differentiation between the close *E. caesiocintum* (mainly grasslands, fens) and *E. linkii* (mainly forests), but more material will be needed to confirm this. There is a lot of non-sequenced collections of *E. caesiocinctum* in the Norwegian fungaria. Most collections with blue, serrulatum-like lamella edge, and with no or little bluish tinges on the pileus have been named *E. caesiocinctum*. Some of them may belong here, but others more likely with *E. querquedula*.

Entoloma linkii (Fr.) Noordel. (OTU05)
The Friesian *E. linkii*, as interpreted in Noordeloos (1982, 2004, Noordeloos et al. 2022a), is a species that morphologically resembles *E. serrulatum* and *E. querquedula* with an initially dark (bluish-) greybrown pileus soon fading to pale brownish, and with a gill edge of the serrulatum-type. The pileus has a tendency to become depressed early on, and the lamellae then become decurrent, and these features can with caution separate *E. linkii* from the *E. serrulatum-E. querquedula* group. Bluish colours on the pileus are hardly present in *E. linkii*, and if present, only at the very margin. The Norwegian material also seems to be rather thin-fleshed, soon developing a translucently striate pileus margin. For differences towards the related *E. caesiocintum*, see this one.

One of our collections represents a remarkable distinct pinkish variant, with pinkish lamella edge, earlier published as *E. callirhodon* (Jordal 2005). However, the ITS DNA is completely identical to that of the bluish-brown collections of *E. linkii*. The type of *E. callirhodon* (see Noordeloos 2004) is, instead, a striking colour variant of *E. serrulatum*.

So far, ten collections have been verified; from Nordland (3 collections from Holmvassdalen nature reserve), from W Norway (Storsøy, Stord, Hordaland; Eikesdalen, Nesset,

Møre & Romsdal) and from the Oslofjord-Randsfjord region (Frierflaugene, Porsgrunn, Telemark; Lunner, Oppland). Most of the collections are from calcareous forests, ranging from moist to very dry; the Holmvassdalen collections were found in riparian, regularly flooded *Alnus incana* forest with *Matteuccia struthiopteris*, and semi-open, calcareous, tall-herb *Picea abies* forest; the Lunner collections from low-herb spruce forests, the others from calcareous *Pinus*-*Corylus* forests and a steep, rich, *Corylus*-*Ulmus* forest. Elsewhere, the species is often reported from moist forests including *Fagus* forests, and partly on rotten wood of *Fagus* and *Alnus* (Noordeloos 2004). The species is widespread, and probably somewhat overlooked. It might well be that a number of fungarium collections identified as *E. serrulatum* and *E. caesiocinctum* belong here.

Entoloma queletii (Boud.) Noordel. (OTU06)
Entoloma queletii is in a European context a well-characterized and rather isolated species. It is easily recognized when young by the pinkish, scaly pileus. However, the pileus soon discolours and sometimes fruitbodies are apparently without pinkish tinges from the start. Such variants have been named *E. kervernii*. However, these variants are identically phylogenetically, and we believe that the species always possess some reddish colours when very young, but in open habitats, this colour might fade very early.

The 11 sequenced collections are mainly from rich/calcareous, grazed grasslands, but also from a calcareous *Corylus*-*Pinus* forest (Sunnhordaland). There are approx. 50 non-sequenced collections (including collections labelled *E. kervernii*) in the Norwegian fungaria, all reliable identified, since this one hardly can be mistaken. Most of the collections are from semi-natural grasslands, including shell-bed pastures and calcareous rock outcrops near the sea. However, some are recorded from other habitats, such as rich (*Quercus*-) *Corylus* forests of scree type, calcareous, tall-herb *Picea* forests, calcareous *Pinus* forests, and from calcareous rich fens/mires. According to Jordal et al. (2016), approx. 40% of the Norwegian collections are from forests.

Section *Poliopodes*
This large section comprises eight rather tiny species in Norway. Many of these are little known, and are also difficult to distinguish. Three species were recently described based mainly or even exclusively on Scandinavian material (Noordeloos et al. 2020, 2022b). Most sect. *Poliopodes* species have a brownish pileus contrasting a bluish, glossy stipe, but a few are initially entirely deep violet blue. Some species soon develop a bicoloured pileus, with a pale margin and a "drop" of dark greyish brown at centre. The pileus soon becomes (strongly) translucently striate. The lamella edge is completely fertile, or more or less sterile with inconspicuous, basidiole-like cells. Some species, such as *E. calceus* and *E. pseudocyanulum*, are (very) small and tiny, and they have in part very pronounced violaceous colours. These are also characterized by large spores, some of them up to 11-15 um long. Based on our phylogenetic analyses, there are four more, small, violaceous species close to *E. calceus* and *E. pseudocyanulum* in Norway, but these are not yet formally described due to limited data, and are not included here. Altogether 12 species are included in Noordeloos et al. (2022a), and when the four undescribed are considered as well, there are at present 16 species known from Europe of this section.

Entoloma poliopus (Romagn.) Noordel. (OTU02; Fig. 6)
Prior to sequencing, the Norwegian material of OTU02 had been identified to no less than 16 different species, indicating the big varia-

bility of this species resulting in identification problems. Our molecular study showed, that the traditional concept of *E. poliopus*, based on the works of Noordeloos (1992, 2004), needed to be amended drastically. Particularly, the colours of the pileus appeared to show a whole range of variation, from dark blue via sepia brown to greyish brown. The lamella edge normally is sterile and brown, but also collections with concolorous lamella edge and (partly) fertile edge belong here. The stipe is normally polished and usually vividly violaceous blue when young, often fading with age. It should be added, however, that much of the difficulties in identification apparently have to do with the collection of older, non-optimal material. Furthermore, the variability of sterility of lamella edge has also led to much confusion. Besides blue-brown forms also pinkish variants exist (Noordeloos et al. 2022a), but none in the Norwegian material.

Of the 35 Norwegian collections sequenced in the beginning of our *Entoloma* project, 9 was initially identified as *E. poliopus*, 5 as *E. chalybeum*, 3 as *E. pseuocoelestinum*, 3 as *E. corvinum*, 2 as *E. violaceoserrulatum*, and the rest identified as 12 different taxa! Unfortunately, the lectotype of *E. poliopus* appeared to be unsuitable for DNA extraction, so it was decided to designate an epitype to fix the concept (see Noordeloos et al. 2022a). *Entoloma poliopus* is widely distributed, and appears to have a rather broad habitat-preference. Most of our material are, however, from calcareous soils, both from semi-natural grasslands, *Tilia-Corylus* forests, *Pinus* forests and from mires/fens.

Entoloma allospermum Noordel. (OTU04; Fig. 6)

Along with *E. poliopus* and *E. mutabilipes*, this is one of the most frequent species found within our *Entoloma* project. It had at the end of 2021 no less than 59 verified records, mainly from calcareous forests and intermediate to calcareous semi-natural grasslands. However, it has been a struggle to find a suitable name. For long, we used the working name *E.* aff. *caeruleum*, but our species does not correspond well with the protologue of *E. caeruleum* (Orton 1960) and we have not been able to produce a sequence from the type, nor to re-find a suitable epitype from Great Britain. Now, we have a match with the type of *E. allospermum* and have decided to apply this name for our species. The species is characterized by a comparatively glabrous (somewhat radially fibrillose) and comparatively depressed-omphaloid pileus. The pileus is initially greyish brown with or without a faint bluish tinge, but soon fades to a rather pale brownish. The species has initially a distinctly bluish, glossy stipe. When mature it is rather pale and without much bluish, and can then easily be misidentified with *E. lividocyanulum*. However, it is distinguished from the latter by the presence of inconspicuous cheilocystidia. Tiny, omphaloid specimens have sometimes been identified as *E. incarnatofuscescens* (Britzelm.) Noordel. that belongs to the *E. rusticoides* group outside *Cyanula* (Noordeloos et al. 2022b).

The species seems rather strictly associated with calcareous soils but has otherwise wide habitat preferences. Our sequenced material is mainly from calcareous *Tilia-Corylus* forests (15 samples) in Norway, some also from rich (not strictly calcareous) *Tilia-Corylus* forest. The species is also found in calcareous, dry *Pinus* forests (including clear-cuts), and dry (semi)natural grasslands. The species is rather southern (mainly boreo-nemoral), with just a couple of finds in northern Norway, and never found in the well-investigated Holmvassdalen area in Nordland, and never recorded in the alpine zone.

Figure 6. The frequent chameleons: *E. allospermum* (= *E. caeruleum* s. auct.). (above) and *E. poliopus. Entoloma allospermum* is often anonymous bluish grey, but often recognized on the clitocyboid-omphaloid habit with depressed pileus centre. Although very variable, *E. poliopus* can normally be recognized by tiny, striate, brown pileus contrasting polished, blue stipe. Often the lamella edge is partly dark coloured from cystidia. Photo from epitype population in S. Oppdalen, Lunner (photos: TEB)

Entoloma mutabilis Noordel. & Liiv (OTU01; Fig. 7)
Entoloma mutabilipes is a widespread, frequent and previously remarkably overlooked species. It was published as new to the Nordic countries in connection with the present project (Brandrud et al. (2018b; as *E. caesiellum*). The species is normally characterized by its pronounced bicoloured pileus, usually being pale pinkish brown with a dark blackish brown "eye" at centre, - and a glossy, rather strongly bluish stipe. Initially, the entire pileus might be rather dark greyish brown with a bluish tinge, but soon fades to pinkish brown in the outer part. The centre is initially finely diffracted-scaly to granulose. Variants with a more bluish tinged pileus have been called *E. caesiellum*. The lamella edge is normally sterile with small, inconspicuous, clavate cystidia, but sometimes the edge is partly or entirely fertile.

The species has often been misidentified as *E. lividocyanulum* but differs in the usually more or less sterile lamella edge, and the often distinctly bicoloured pileus, with more or less pinkish brown tinge, and a dark spot at centre. *Entoloma mutabilipes* is one of the *Cyanula* species with most sequenced samples in our material (45). These are mainly from calcareous fens and calcareous tall-herb spruce forests but also from semi-natural grasslands (Table 1).

Entoloma calceus Noordel., Bendiksen, Brandrud, P.-A. Moreau & Vila (OTU214; Fig. 7)
Entoloma calceus was recently described, mainly based on material from Norway, including the type (Noordeloos et al. 2022b). The tiny species resembles *E. cyanulum* (Lasch) Noordel. (not yet recorded in Norway) and *E. pseudocyanulum*. The pileus is initially dark violet blue to blackish blue and radially fibrillose, with age becoming strongly translucently striate almost to centre. The stipe is violaceous blue and polished. The spores are large, sometimes up to 15 um long.

The species is now known from three localities in Norway; Skotjernsfjellet, Lunner, Oppland (the type locality), Dalasjøbekken, Lunner and Røsvassholmen, Hattfjelldal, Nordland. In the two first cases, it was growing in *Sphagnum*, at the margin of a slightly rich (intermediate) fen and along a brook, and in the last case it was growing in the inundation (regulation) zone of a lake (adjacent to a spruce forest). The species has, furthermore, been recorded in an ombrotrophic bog in France. A single Danish record is also from a *Sphagnum/Molinia* dominated bog in association with other *Cyanula* species (T. Læssøe, pers. comm.; https://svampe.databasen.org/observations/675773). It seems that *E. calceus* is one of very few *Cyanula* species that can occur in truly oligotrophic *Sphagnum* bogs (although not seen in Norway).

Entoloma pseudocyanulum Wölfel (OTU162)
This is a little known species that belongs to a morphological complex of apparently very rare taxa. These are small and slender species, with radially translucent striate pilei, with striae almost to centre (due to very thin context). *Entoloma pseudocyanulum* is characterized by initially a dark (bluish) grey brown pileus that soon change to pale grey brown, with darker striae, and almost blackish at centre. This grey brown pileus is contrasting the dark bluish, polished stipe. The lamellae are white with a patch wise brown-tinged lamella edge. The spores are large (up to 15 um long), and the lamella edge is set with clusters of well-differentiated cystidia.

In Norway this was found in the Fredrikstad region (Morten Pettersen 05-180818) in *Sphagnum* in a moist mixed spruce/deciduous forest, and in Hustadvika (Skutholmen, Møre og Romsdal) in oligotrophic mown grassland in moss (J.B.Jordal 24.09.2004). The species is also sequence-verified from Denmark

Figure 7a. The deep violet small guy: *E. calceus*. When young the recently described *Sphagnum*-dwelling *E. calceus* seems unmistakable, with tiny habit, deep violet colours and large spores. (photo: TEB)

from deciduous forest adjacent to a lake (not particularly small basidocarps; https://svampe.databasen.org/observations/9326529), Germany (deciduous forest) and Russian Altai (moist alder floodplain forest) (Noordeloos et al. 2022a). We have a couple of more sequences (OTU161, 163) in this complex, which for the time being have no match with other samples. These are not further commented here.

Entoloma septentrionale Noordel., Lorås, Eidissen & Dima (OTU03)
Entoloma septentrionale produces tiny, bluish basidocarps (Noordeloos et al. 2020). The pilei are porphyrous/bluish brown, translucently striate, finely fibrillose-glabrous; the lamella edge is brownish and the stipe glossy and distinctly bluish. The broadly clavate cheilocystidia are abundant. *Entoloma septentrionale* resembles the *E. cyanulum* morpho-complex. However, *E. septentrionalis* occupies a basal position in the sect. *Poliopodes* (sister species to *E. allospermum*) and is only distantly related to the lineages with *E. calceus*, *E. pseudocyanulum* and relatives (Figure 1). It has smaller spores and not so developed cystidia as in the latter species.

The species has so far only been recorded from the type collection at Holmvassdalen nature reserve, Grane, Nordland, where it was growing in moist patch with *Sphagnum*, adjacent to a calcareous *Picea abies* forest (Noordeloos et al. 2020).

Entoloma perchalybeum Noordel., J.B. Jordal & Dima (OTU229)
Entoloma perchalybeum is together with *E. calceus* in the present section, and *E. praecipuum* in sect. *Griseocyanea*, the most recently described *Cyanula* species (Noordeloos et al. 2022b). This striking species is distinguished when young by the combination of deep violet blue colours on all surfaces, including bluish tinged lamellae, and a tomentose-squamulose pileus. The bluish tinge on young lamellae is othervise not seen in sect. *Poliopodes* species, and recalls the distantly related *E. chalybeum*, hence the name. It can be separated from *E. chalybeum* by the colourless lamella edge and the pileus that soon becomes smooth and translucently striate. *Entoloma perchalybeum* is so far sequence-documented from the two most intensively *Entoloma*-studied sites in Northern Norway; Holmvassdalen nature reserve, Grane, Nordland (calcareous *Picea* forest), and Reinøya north of Tromsø (calcareous pasture). The species is also sequence-documented from a calcareous alpine site in Northern Sweden (type locality), as well as from a site in NE Finland (Noordeloos et al. 2022b), and may well be a truly northern taxon in Europe.

Figure 7b. The pale pink guy: *E. mutabilipes* (= *E. caesiellum* s. auct.) when mature has a pinkish tinged pileus with a brown "eye" at centre. (photo: BD)

Entoloma brunneoserrulatum Eyssart. & Noordel. (OTU117)
This species seems according to the studied material to be rather variable, but it often develops a brownish, serrulate lamella edge, and our material corresponds to the type of *E. brunneoserrulatum*. It also corresponds with the type of *E. variabilisporum* E. Ludw., which was described as having mainly 2-spored basidia and corresponding large spores (Ludwig 2007). It seems initially to be characterized by a rather dark brownish grey-(brownish black) pileus, a violaceous tinged stipe, and may resemble *E. atrocoeruleum* or *E. poliopus*. With its often rather glabrous and depressed pileus, it may also resemble the closely related *E. allospermum*. The species is verified from 10 collections in Norway, of which 6 are from Bamble-Porsgrunn in Telemark, one from inner Oslofjord, one from Bodø area, one from Lofoten, Nordland and one from Reinøya north of Tromsø. So far it has been recorded from calcareous pine forests, calcareous lime forests, naturally open grassland/shallow-soil limestone rocks and once from a near-shore shell-bed grassland.

Section *Asprella*
Sect. *Asprella* species are morphologically very similar to those of sect. *Poliopodes;* typically with brownish, translucently striate pilei and glossy, bluish stipes. Six species are recorded from Norway (Table 1), and 10 from entire Europe (including some southern taxa; Noordeloos et al. 2022a). Some of our species, such as *E. asprellum* and *E. lividocyanulum*, have fertile lamella edges, and others, e.g. *E. exile*, has sterile edges. At least two species seem to be more or less northwestern in Europe, with major populations in (Western) Norway; *E. cyaneolilacinum* and *E. violaceoviride*.

Entoloma asprellum (Fr.) Fayod (OTU12)
Entoloma asprellum is one of our more frequent and widely distributed *Cyanula* taxa. It is (poorly) characterized by a combination of

a brown pileus, glossy, blue stipe and fertile lamella edge. Initially, the pileus is finely scaly to concentrically diffracted, and then it becomes more smooth and translucently striate with age. The species differs from the close *E. lividocyanulum* by darker colours and a more intensively bluish stipe (when young). It differs from the similar *E. poliopus* by the fertile lamella edge (and never dark bluish tinges on pileus), and from *E. glaucobasis* by a distinctly bluish and glossy (not fibrillose) stipe surface.

Entoloma asprellum has been verified from 37 collections, mainly from semi-natural grasslands, with some finds also from more or less calcareous coniferous forests. Furthermore, the species is recorded also from the alpine zone in N Sweden (Larsson et al. in prep.). The species is widespread in Europe (Noordeloos et al. 2022a).

Entoloma lividocyanulum (Kühner) Noordel. (OTU13)
Entoloma lividocyanulum recalls a pale *E. asprellum*, with a a pileus that only is granulose at centre. It is, furthermore, characterized by an initially bluish grey brown pileus that soon discolours to (pinkish) grey with a dark brown "eye" at centre, and small spores. The stipe is polished and blue-greyish but soon discolouring to pale ochre grey. As in *E. asprellum* the lamella edge is more or less completely fertile. The species is often correctly identified, but may be mistaken for other frequent species with a pale pileus with a dark centre, such as *E. allospermum* (with larger spores) and *E. mutabilipes* (with a more or less sterile lamella edge).

Entoloma lividocyanulum is one of the *Cyanula* species with the widest ecological amplitude in Norway; based on the 20 samples sequenced, it can be found in grasslands, forests, mires and road verges, on calcareous to intermediate rich soils. The species seems to have a very wide distribution in Norway and in Europe as a whole (Noordeloos et al. 2022a).

Entoloma exile (Fr.) Hesler (OTU15; Fig. 8)
Entoloma exile is a fairly characteristic species that is rarely misidentified. It is mainly characterized by the saffron yellow tints that often develop when mature. This feature is usually seen as saffron spots at the stipe base, but entire basidiomes may become yellowish with age. The species is furthermore small and gracile, with an often distinctly radially fibrillose (and striate) pileus. The pileus colours are variable, initially rather dark brownish grey with a bluish tinge but soon discolouring to pale greyish, with a dark greyish brown "eye" at centre. The combination of a bluish tinge and a slight yellow discolouration, often gives a greenish reflex on the stipe in certain stages. The lamella edge is sterile, with well-developed, abundant, clavate cystidia. *Entoloma exile* has a sister species with fertile lamella edge (*E. chloropolium* M. M. Moser), but this has not yet been recorded in Norway.

Entoloma exile is one of the *Cyanula* taxa that apparently is rather frequent both in forest and grassland sites. According to Jordal et al. (2016) 85% of 279 records were in semi-natural grasslands, and 7,5% in forests. On the other hand, many of our 31 sequence-verified finds are from calcareous *Pinus* and *Tilia* forests, low-herb *Betula* forests, as well as tall herb *Picea* (and *Alnus*) sites. The species prefer rich soils, but is not restricted to calcareous sites. *Entoloma exile* has a slightly southern distribution, being widespread in S and C Norway north to Nordland. Outside Norway, it is distributed mainly in Western and Northern Europe where it may be locally fairly common (Noordeloos et al. 2023).

Entoloma timidum O.V. Morozova, Noordel., Brandrud, J.B. Jordal & Dima (OTU10; Fig. 8)
Entoloma timidum is a tiny, pale and anonymous species, with a rather smooth, trans-

Figure 8. The saffron-tinged and the modest: *E. exile* (above) and *E. timidum*. *E. exile* is characterized by its saffron yellow tinge basally at least with age, whereas the newly described *E. timidum* is modest and anonymous in all characters; small size, pale colours, and apparently no particular habitat requirements. (photos: BD, TEB)

lucently striate pale greyish brown, beige to almost greyish white pileus, and a glossy, (bluish) grey stipe. The name refers to its "modesty" in all features (Dima et al. 2021). It resembles pale and non-blue species such as *E. ochromicaceum*, but *E. timidum* is smaller, with initially paler and more translucently striate pilei. Especially, the initially almost whitish pileus margin seems to be a distinguishing feature towards look-a-likes. Eight collections are verified from Norway. The majority stems from calcareous forests (tall/low herb *Picea* forest, and rich *Tilia-Fraxinus-Corylus* forests), but also from calcareous mown or grazed grasslands, ranging from the Oslofjord to Senja, N Norway. The species is probably somewhat overlooked nationally as well as internationally. Outside Norway, this is so far verified by sequencing from Russia (European part) including Caucasus and from Denmark (https://svampe.databasen.org/observations/10008313), indicating a wide distribution in Europe (Dima et al. 2021, Noordeloos et al. 2022a).

Entoloma violaceoviride Arnolds & Noordel. (OTU14; Fig. 9)
Entoloma violaceoviride is characterized by an initially rather dark blackish blue, sometimes papillate pileus, greyish or even grey bluish tinged lamellae and a polished, bluish stipe. The stipe is turning somewhat greenish with age, probably due to bluish combining with a slight yellowish discolouring, reminiscent of the reaction in *E. exile*. The lamella edge is fertile to sterile. Based on the sequence-verified collections, this is a western species in Norway, found mainly in calcareous, grazed grasslands in Sunnhordland (Bømlo, Stord, Tysnes), one collection from a *Corylus* forest at Midsund, Møre og Romsdal, and four collections from Tingvoll, Møre og Romsdal, which are so far the northernmost sites. According to the protologue, the species was found in a moist *Fraxinus-Alnus* forests and in grasslands in the Netherlands (Noordeloos 2004). This seems to be a rare species everywhere, with a coastal Western-Northwestern European distribution, occurring in W Norway, Scotland, The Netherlands, Belgium and France (Noordeloos et al. 2022a).

Entoloma cyaneolilacinum Noordel., J.B. Jordal, Brandrud & Dima (OTU11; Fig. 9)
This is a beautiful, pale lilac blue to deep violet species, with a rather smooth pileus with translucently striate margin and lamellae that initially are whitish with a bluish reflex. The stipe is polished and rather persistently pale bluish (Crous et al. 2021). In one collection a yellow basal mycelium was observed. The lamella edge is fertile. The species may have a spermatic or *Lepiota cristata*-like smell when young, but no smell was noted in the Norwegian material.

This was apparently treated as *E. lepiotosmum* in Noordeloos (2004). However, there are considerable discrepancies with the protologue of *Rhodophyllus lepiotosmus* Romagn. (Romagnesi 1954). It was described as having a blackish brown, virgate pileus, reminiscent of an *Inocybe*, a fibrillose stipe surface, a strong smell like that of *Lepiota cristata*, and larger spores. Furthermore, the lectotype did not yield useful sequences. Considering the conflict with the protologue and the lack of molecular data, it was decided to describe the present taxon as new, and with a type from Norway (Liabygda, Stranda, Møre og Romsdal) (Crous et al. 2021).

The species is so far known with certainty from 13 localities in oceanic Western Norway north to Trøndelag; Vindafjord, Rogaland (W-faced, rich thermophilous deciduous forest with *Fraxinus*, *Ulmus* and *Corylus*) and then Rennesøy, Rogaland; Tysnes in Sunnhordland, Stranda (the type), Sunndal, Surnadal and Tingvoll in Møre & Romsdal (semi-natural grasslands) as well as Rennebu and Indre Fosen, Trøndelag (also semi-natural grass-

Figure 9. The western cowboys: *E. violaceoviride* (above) and *E. cyaneolilacinum*. These rare and beautiful bluish guys seem to be restricted to coastal Western Europe, preferentially in grazed grasslands. *E. violaceoviride* seems often to show a bluish green tinge on stipe with age, whereas *E. cyaneolilacinum* seems to be characterized by its rather smooth pileus with a translucently striate margin. (photos: Per Fadnes, JBJ)

lands). The species is elsewhere sequence-verified only from Denmark (https://svampe.databasen.org/taxon/70779, where it initially was named *E. microchalybeum* nom.prov.) and The Netherlands (Noordeloos et al. 2022a), and seems to be a Western European taxon, with possibly internationally important (major) populations in Norway.

Section *Caesiocaules* (= sect. *Chalybea* s. Noordeloos et al. 2022a)

This section is characterized by initially deeply bluish black species, such as *E. chalybeum* (Pers.) Noordel., with bluish grey lamellae. Common features of the species are the bluish tinges in pileus and stipe, a colourless or brown, lamella edge, and a polished or at most weakly innately fibrillose stipe surface. This section comes out basally in the *Cyanula* tree (Figure 1). The deep blue species may resemble those of sect. *Cyanula*, although without tomentose-fibrillose pileus surfaces, but othervise the morphology resembles mostly that of sect. *Asprella* species. The section comprises five species in Norway, of which only *E. chalybeum* is well-known. On a European scale, eight species are sequence-verified (Noordeloos et al. 2022a).

Entoloma chalybeum (Pers.) Noordel. (OTU08; Fig. 10)

Entoloma chalybeum, sometimes spelled *E. chalybaeum*, is one of the more easily identifiable taxa among the bluish black ones in *Cyanula*, at least when it is young and well-developed, with its deep violet-bluish black colours, including bluish grey lamellae and a rather polished stipe. The closely related *E. lazulinum* and *E. pseudocruentatum,* as well as *E. violaceoviride* from sect. *Asprella*, may also have bluish grey tinged lamellae, but *E. lazulinum* has tiny basidocarps with translucently striate pilei; *E. pseudocruentatum* is not so dark and may have a yellowing stipe base, and *E. violaceoviride* has a stipe that usually turns greenish. The yellow discolouration seen in *E. pseudocruentatum* has also been observed once in *E. chalybeum* (JB. Jordal 08.09.2010, Stranda, Møre & Romsdal). Also, the very rare *E. perchalybeum* and *E. azureopallidum* have bluish lamellae.

Most of the 16 sequence-verified collections are from calcareous, grazed grassland, including rather small, open patches in grazed forests. Some collections are from calcareous pine forests, but then mainly from old road borders with "grassland character", or from cattle-grazed forests.

The species is within our project verified mainly from calcareous districts around the Oslofjord-Tyrifjord-Mjøsa (SE Norway), including a few fjord districts in W-NW Norway (Sogndal, Stranda). However, there are in the Norwegian fungaria a number of apparently fairly reliable identifications of *E. chalybeum* also from W, C and N Norway, mainly from calcareous grasslands, in a couple of cases also from calcareous pine forests (see habitat compilation in Jordal et al. 2016). According to Jordal et al. (2016) 11% of the Norwegian fungarium collections (mainly non-sequenced) are from forests, the rest mainly from grasslands.

Entoloma pseudocruentatum Noordel., Brandrud, G.M. Jansen, Dima & Læssøe (OTU125; Fig. 10)

Entoloma pseudocruentatum was described as new in Fungal Planet description sheets in 2021 (in Crous et al. 2021) as a replacement name for *E. cruentatum* Quélet sensu Noordeloos (1984).

The species is so far only verified from a single Norwegian collection; from Drangedal, Telemark, SE Norway. This was characterized by dark bluish to grey brown pileus, bluish grey lamellae, and base of stipe turning yellowish, almost saffron yellow. However, the yellow discolouration of the stipe base does

not seem to be a constant character. A few Norwegian specimens identified as *E. cruentatum*, turned out upon sequencing to represent *E. violaceoviride* of sect. *Asprella*. There are other specimens labelled *E. cruentatum* in the fungarium (herb. O), that may belong to the present species, but these should be verified by sequencing. The Drangedal collection was growing in herb-grass-dominated *Fraxinus-Quercus* forests (rich with *Anemone hepatica*, but not calcareous). The species is verified from only a few other localities in Northwestern Europe; one from the Netherlands (the type, from grassland in airfield) and several from Denmark (grasslands; https://svampe.databasen.org/taxon/70776) (Noordeloos et al. 2022a).

Entoloma lazulinum (Fr.) Noordel. (OTU07)
Entoloma lazulinum, often recorded as *E. chalybeum* var. *lazulinum*, is distinguished from *E. chalybeum* by the smaller, more slender basidicarps, by early developing a translucently striate pileus, and often also possess whitish lamellae when young (bluish grey tinged in *E. chalybeum*). The species may also resemble *E. poliopus*, but it is usually darker, more bluish and with a brown lamella edge. Altogether 17 collections are verified by sequencing, of which 5 are from Holmvassdalen nature reserve, Nordland. The majority of the Holmvassdalen collections are from calcareous *Picea* forests, in meadow-like, rather open tall-herb type. One collection is from a riparian, flooded, *Alnus incana* forest with *Matteuccia struthiopteris*. The remaining collections from N, W and SE Norway are from calcareous grasslands, including subalpine summer-farm region. This has a stronger affinity to calcareous tall-herb spruce forests than the related *E. chalybeum*.

Entoloma erhardii Noordel., Dima, Svetash., Læssøe & Kehlet (OUT 233)
Entoloma erhardii was when described in Crous et al. (2019) not known from Norway. Since then it has been sequence-verified by one collection (Geir Gaarder at Tingvoll, Møre & Romsdal), in rich *Corylus* forest (Jordal et al. 2023). The species is when young magnificent, metallic violaceous blue, both on pileus and stipe, resembling taxa in subgenus *Leptonia*. Leptonias, however, never become glossy on the stipe, and they have clamped hyphae. *Entoloma erhardii* is elsewhere recorded from Denmark (https://svampe.databasen.org/taxon/69430) and Caucasus, Russia, from both forests and grasslands (Noordeloos et al. 2022a).

Entoloma sodale Kühner & Romagn. ex Noordel. (OTU222)
Entoloma sodale is not easy to recognize, with its brown pileus and blue, polished stipe, it looks like a quite a few other *Cyanula* species. It was formerly regarded as a rather widespread species in Norway, with more than a dozen collections in Norwegian fungaria. However, these collections seem all or mostly to be misidentifications. Many seem to belong to *E. glaucobasis*, which have rather similar microcharacters, e.g. broadly clavate-balloon shaped cheilocystidia. At the moment, only one Norwegian collection has been verified as *E. sodale* in the concept of Noordeloos et al. (2022a). It is nested in sect. *Caesiocaules* close to *E. chalybeum* (Fig. 1). The Norwegian collection stems from a semi-natural grassland in Sunndal region (Jordalssjøen; Jordal et al. 2023). All material labelled *E. sodale* in Norwegian fungaria should be revised by sequencing.

Section *Griseocyanea*
The section consists in Norway of five rather well-defined and relatively easily recognizable taxa. Only one species (E. praecipuum)

Figure 10. The blue gilled guys: *E. chalybeum* (above) and *E. pseudocruentatum*. Among the deep (blackish) blue taxa, the widespread and fairly well-known *E. chalybeum* can be distinguished on the normally greyish lamellae with a bluish tinge when young. The newly described *E. pseudocruentatum* is so far only known from Drangedal in Norway, and it appears to be paler. The Norwegian material also showed a yellow discolouration at base. *E. pseudocruentatum* seems to be another western cowboy in Europe. (photos: BD, TEB)

can be considered as rare and has been described since the start of our project. The section is somewhat heterogeneous, with three morphologically rather different lineages; the *E. griseocyaneum-E. viiduense* lineage, the *E. glaucobasis* lineage and the *E. mougeotii* lineage. These differ much e.g. in colouration and presence/absence of cystidia, and are distinguished as subsections in Noordeloos et al. (2022a). They normally possess a pronounced scaly-tomentose, non-hygrophanous pileus, and a silky fibrillose stipe surface. No additional species are known from other parts of Europe (Noordeloos et al. 2022a).

Entoloma mougeotii (Fr.) Hesler (OTU31)
When young, this is a striking species, with its velvety-tomentose, bright lilac blue pileus, fibrillose lilac stipe, and contrasting pure white lamellae that may have a dark brown edge. The pileus is often depressed, and often slightly excentric. The lamella edge is sterile, with numerous large, clavate to fusiform cystidia, which sometimes are filled with brown contents. Such variants, previously named *E. mougeotii* var. *fuscomarginatum* Noordel., are however, identical in ITS, and form part of the morphological variation.

In Norwegian fungaria, there are approx. 200 collections labelled *E. mougeotii*, and most of these are believed to be correctly identified. Of 31 samples sequenced, only five samples, mainly with older/suboptimal specimens without bluish colours were misidentified prior to sequencing. The species is one of our more strict, calciphilous *Cyanula* species, but occurs in a wide range of wet to dry calcareous habitats, from natural- and semi-natural grasslands, (semi-open) forests to rich fens, even in *Sphagnum*, including marl beds along calcareous lakes. According to the compilation by Jordal et al (2016), 23% of the Norwegian fungarium collections of *E. mougeotii* are from forests. In Sweden, it is also verified from calcareous vegetation in the alpine zone (Larsson et al. in prep.). The species is widely distributed in most districts of Norway, however, with only very few records from the generally non-calcareous regions in south and west (Agder-Rogaland-Hordaland-Sogn & Fjordane).

Entoloma glaucobasis Huijsman ex Noordel. (OTU30; Fig. 11)
Entoloma glaucobasis is characterized by a brownish, granulate-diffracted-scaly pileus, contrasting a sometimes bicoloured, fibrillose stipe, brown above and blue below. Variants with uniform bluish stipes have often been identified as *E. coeruleoflocculosum*. Both variants, however, have the same ITS and occur mixed in the clade, so the names are treated as synonyms. Microscopically, it is well-characterized by abundant, broadly clavate-balloon shaped, often brown coloured cheilocystidia, and relatively broad, 5-9-angled, sometimes almost nodulose spores.

Entoloma glaucobasis is, like its relatives in sect. *Griseocyanea*, one of the apparently strictly calcareous *Cyanula* species. In Norway it has a very wide nemoral-alpine distribution, occurring in wet to very dry sites, but almost exclusively restricted to open grasslands, heathlands and fens. According to sequenced material (25 samples), it occurs preferentially in grazed, semi-natural grasslands and rich fens/mires (including *Sphagnum* mats) in SE-C Norway, but also in some natural, near-shore grasslands (dry meadow-shrubland) and shell bed pastures along the coast, and in richer to calcareous grasslands in inner fjord districts. It is one of few calciphilous *Cyanula* species that is found regularly in rich pastures/grasslands in fjord districts such as the inner Sognefjord (see e.g Brandrud & Breistøl 2020). It is furthermore recorded in calcareous, alpine snow-beds (Aure, Møre & Romsdal), and according to a new study, it seems to be rather frequent in calcareous

Figure 11. With fibrillose, pale grey-blue stipe: *E. glaucobasis* (above) and *E. griseocyaneum*. Widespread in calcareous grasslands; *E. glaucobasis* with brown, broadly clavate cheilocystidia, *E. griseocyaneum* with fertile lamella edge. (photos: TEB, BD)

alpine vegetation in N Sweden (Larsson et al. in prep.). It is recorded north to Reinøya (Karlsøy, Troms). Only a few, verified records are from semi-open forests (calcareous *Pinus* and *Picea* forests, Grane-Holmvassdalen, Nordland). According to compilation of all samples identified to *E. coeruleoflocculosum* in the Norwegian fungaria, the proportion of collections from forests are much higher, but some of these could be misidentifications (Jordal et al. 2016). *Entoloma glaucobasis* has a wide distribution in Europe, occurring in calcareous grasslands, mires and also in dune grasslands along the Atlantic coast (Noordeloos et al. 2022a). Pink variants have also been reported, but not verified from Norway.

Entoloma griseocyaneum (Fr.) P. Kumm. (OTU28; Fig. 11)
Entoloma griseocyaneum is a rather large, characteristic species, with a mouse grey tomentose-scaly pileus, and an initially silvery, blue-grey, fibrillose stipe. Sometimes the stipe is completely grey, and then it has been called *E. scabropellis*, which appear to be a synonym. Furthermore, the lamella edge is fertile (in contrast to e.g the related *E. glaucobasis*). When well-developed, this is an unmistakable *Cyanula*.

Only two out of 31 collections verified by sequencing was misidentified prior to sequencing. Therefore, we regard the fungarium material of this as quite reliable. According to a compilation of 549 fungarium collections and observations (from 390 localities), Jordal et al. (2016) found only 1.8% of the samples to be from forests, and the rest from grasslands, including a number from coastal shell-bed pastures, a few from naturally open, shallow-soil limestone rock sites and a few from alpine zone. In N Sweden it has also been found a few times in calcareous alpine vegetation (Larsson et al. in prep.). The species clearly prefers calcareous conditions, and most sites are influenced by limestone, shell-beds or lime-rich ground-water. The species is distributed in almost all parts of Norway, except non-calcareous districts in W-SW Norway (in W-SW Norway mainly found in Sunnhordland and around the Boknafjord). *Entoloma griseocyaneum* is a good indicator species for more or less calcareous grasslands, rich in *Cyanula* species and other habitat-specific taxa.

Entoloma viiduense Noordel. & Liiv (OTU29)
Entoloma viiduense is the sister species of *E. griseocyaneum*, and the two have many similar characters including fairly robust and tall basidiocarps, with silvery fibrillose grey-blue stipes. However, *E. viiduense* is distinguished from *E. griseocyaneum* by the initially dark bluish-violaceous tinges on the pileus, later often with a porphyrous brown tinge. Normally the lamella edge is fertile, but occasionally it is heterogeneous, with cystidia in groups among the basidia. It has often been misidentified as *E. atrocoeruleum*, but it should normally be easy to distinguish based on the more robust basidiocarps, and the distinctly fibrillose stipe.

So far 19 collections are verified by DNA-ITS sequencing. Most of them are from Møre og Romsdal, Trøndelag and N Norway, being distributed from Nord-Aurdal (Oppland) and Austevoll (Hordaland) to the Tromsø region of N Norway. Most localities are calcareous grasslands, including coastal shell-beds, and two sites are in calcareous spruce and birch forests, respectively.

Entoloma praecipuum J. B. Jordal, Noordel. & Dima (OTU200; Fig. 12)
This species belongs to the subsect. *Griseocyanea* (Noordeloos et al. 2022a), but is morphologically fairly deviating from *E. griseocyaneum* and *E. viiduense* by the almost smooth, translucently striate pileus, and by the complete lack of bluish-lilac tinges. The pileus is uniformly brown, also in young

stages, contrasting the whitish lamellae and stipe. The lamella edge is sterile, and the stipe is very pale to whitish with innate fibrils. This is a quite recently described species, and it is so far known only from Norway (Noordeloos et al. 2022b). In spite of its characteristic habitus, *E. praecipuum* is so far recorded only from two adjacent semi-natural grasslands (mown meadows) at Jordalsgrend, Sunndal, Møre & Romsdal.

Section *Atrocoerulea*

Section *Atrocoerulea* is close to sect. *Griseocyanea* (above) and sect. *Fuliginosa* treated below. Most species of *Atrocoerulea* possess a fertile lamella edge like in *E. griseocyaneum* and *E. viiduense* of the former section, however, some other species of this section have a completely sterile edge. The sect. *Atrocoerulea* species show some similarities with the sect. *Cyanula* species, but in general, the species of the former have more slender basidiocarps, with an initially faintly fibrillose, then more or less polished stipe, and different pileus colours. Popularly speaking, sect. *Atrocoerulea* is intermediate between the *Cyanula* and *Griseocyanea* sections with species having a typically opaque, fibrillose stipe surface, and on the other hand, the *Poliopodes* and *Asprella* sections, with most species showing more tiny stipes, being glossy-polished from early stages.

In the beginning of the Norwegian *Entoloma* project in 2015, there were only two species from this clade verified from our area; *E. atrocoeruleum*, and *E. anatinum*. Now

Figure 12. The Sunndal lonely rider: *E. praecipuum*. Brown pileus contrasting white lamella and stipe. So far only recorded from Sunndalen, NW Norway. (photo: JBJ)

this number has increased to five, including three species described as new to science since 2020, partly based on data from our project. Furthermore, there are two more undescribed Norwegian species not treated here. In addition to these taxa, *E. nigroflavescens* Armada, Bellanger, Noordel. & Dima (Buyck et al. 2022) has been sequence-verified from calcareous alpine habitats in Northern Sweden (Larsson et al. in prep.). This species most likely also occurs in Norway. No more species of this section is known from Europe (Noordeloos et al. 2022a).

Entoloma atrocoeruleum Noordel. (OTU33; Fig. 13)
Entoloma atrocoeruleum is a rather frequent, variable species that occurs in the Norwegian fungaria under a whole series of names (e.g. *E. asprellum*, *E. coeruleoflocculosum*, *E. corvinum*, and *E. poliopus*). It has initially a bluish, sometimes almost black-bluish velvety-fine scaly pileus and a dark bluish, finely fibrillose stipe. In these stages, the species resembles taxa in sect. *Cyanula*, such as *E. coracis* and *E. porphyrogriseum*. However, the pileus soon fades to paler (porphyrous-) brownish, becoming smoother, and the stipe soon becomes polished bluish(-grey). The young, bluish tinged stages are, however, easily distinguished from taxa in the *E. coracis* group, on the more or less fertile lamella edge. The edge might sometimes be partly sterile (heteromorphous), but never with a distinct, dense layer of large cheilocystidia as in *E. coracis*, *E. porphyrogriseum* and allies. The sometimes partly sterile lamella edge has, nevertheless, led to many misidentifications as *E. corvinum*. The closely related *E. anatinum*, which also possess a more or less fertile lamella edge, is distinguished on the initially uniformly (ochraceous) brown pileus.

A high number of fungarium collections labelled "*E. atrocoeruleum*" and "*E. corvinum*" have been sequenced to sort out misidentifications. Approximately 80 of these turned out to be *E. atrocoeruleum*; and totally 125 collections are sequence verified. Almost all verified *E. atrocoeruleum* collections are from herb-rich to calcareous grasslands, mostly from grazed pastures but also from natural near-shore, dry grasslands, e.g. in *Polygonatum odoratum* vegetation. Very few are recorded from forest (margins). This is a more or less coastal species in Norway, and it is one of the more frequent species in the rich "*Entoloma* grasslands" of Western Norway. It is recorded north to Finnmark. This is further one of very few species in our material that is verified almost only from grasslands, and the same apparently also applies to Sweden (Brandrud et al. 2018b).

Entoloma brunneicoeruleum O.V. Morozova, Noordel., Brandrud, J.B. Jordal & Dima (OTU82; Fig. 13)
This was described in Dima et al. (2021) and may be characterized as a somewhat more brown, tiny variant of *E. atrocoeruleum*, almost without violaceous tinges on young pilei, and with a violaceous blue, soon polished stipe. The species may also resemble the tiny *E. poliopus*, which, however, can be distinguished on more pronounced cheilocystidia, and by often developing a darker lamella edge. The species seems to be well distinguished from the other species of sect. *Atrocoerulea*, as well as *E. poliopus*, by the large, partly almost nodulose spores, 10-14(-15) um long.

Entoloma brunneicoeruleum has been sequence-verified from 3 localities in Norway; Strand, Rogaland (moist, low-herb, oceanic *Betula* forest, Figure 13), Valldal in Norddal, now Fjord municipality, Møre & Romsdal (cattle-grazed grassland, not calcareous), and Holmvassdalen NR, Grane, Nordland (*Sphagnum* mire, apparently mesotrophic, not calcareous). This species seems to have an oceanic/western preference in Norway and,

Figure 13. The atrocoeruleum sisters: *E. atrocoeruleum* (above) and *E. brunneicoeruleum*. The former with pileus darker and more (blackish) blue when young, and with smaller spores. The former is widespread, the latter newly described and apparently rare, mainly western in Norway. The photographed material of *E. brunneicoeruleum* collected by Andreas Svendsen from Strand, Rogaland is the so far only rich, well-developed material of this species documented and depicted. (photos: JBJ, Andreas Svendsen)

furthermore, it does not seem to have a preference for calcareous sites. *Entoloma brunneicoeruleum* is still poorly known and is so far only sequence-verified from Northern Europe, including European Russia and Estonia.

Entoloma anatinum (Lasch) Donk (OTU32)
Entoloma anatinum (= *E. fulvoviolaceum* Noordel. & Vauras) is characterized by a brown to sometimes vividly fulvous-ochraceous brown pileus contrasting a (grey-)bluish stipe. The pileus is usually distinctly diffracted-scaly, and the stipe is initially more or less fibrillose, becoming more polished with age. The lamella edge is fertile. The combination of a brown, scaly pileus, a blue, fibrillose stipe and lack of cystidia, makes this rather easy identifiable. Among other taxa with fertile lamella edges, it is sometimes misidentified as *E. asprellum*, but should be recognizable on the more scaly-diffracted pileus and initially fibrillose, non-polished stipe. The closely related *E. atrocoeruleum* is dark, almost bluish black on the pileus when young (never with ochraceous-fulvous tinges) and is strictly associated with grasslands (see above). Superficially, the species may resemble *E. glaucobasis*, but the latter is easily distinguished by the broadly clavate-balloon-shaped, brown cheilocystidia.

According to the 42 samples sequenced, this species has its major habitat in calcareous forests, mainly in semi-open, calcareous *Picea* and *Pinus* forests (low- and tall herb types), including grazed types. Most collections are from the calcareous regions of SE & C Norway and Nordland, and almost all of these are from forests. The more scattered, verified finds around the coast are mainly from grasslands. It is recorded north to calcareous grasslands at Reinøya (Karlsøy, Troms).

Entoloma tigrinum Noordel., O.V. Morozova, Brandrud, J.B. Jordal & Dima (OTU169)
This is a grey brownish, rather anonymous species without any bluish tinges. It was typified from Norway, Steinkjer, Kvamsfjellet (Dima et al. 2021). Macroscopically, it resembles *E. turci* and *E. sarcitulum*, but microscopically it differs from these by the larger spores. *Entoloma tigrinum*, furthermore, often develops a finely diffracted-scaly pileus surface, resembling that of *Lentinus tigrinus*. It is only known from the holotype in Norway. It was found in *Sphagnum* at the margin of a subalpine, rich fen. There are a few finds from alpine, calcareous vegetation in Northern Sweden (Larsson et al. in prep.), and the species could probably occur in similar habitats also in (North) Norway. The species is only known from Northern Scandinavia.

Entoloma perasprellum Corriol, Dima, O.V. Morozova, J.B. Jordal & Noordel. (OTU207)
This is an *E. asprellum* look-a-like with a brown pileus and initially a more or less bluish, polished stipe, which differs from *E. asprellum* by the often brown-coloured, sterile lamella edge and the almost nodulose spores. It was described in Dima et al. (2021), and is once verified from Norway (Trøndelag, Rennebu) from a summer farm pasture, with more finds from calcareous, alpine habitats in North Sweden (Larsson et al. in prep.). The species apparently has a wide Eurasian distribution, with verified records from subalpine-alpine grasslands in Russian Caucasus and Far East (Kamchatka) (Noordeloos et al. 2022a). It may well have a circumpolar distribution. It is, however, also found further south in the temperate region of W Europe, being verified from a xerothermous grassland in the Paris region of France (Corriol 2016, as *E. cyaneoturci* nom. prov.), indicating a wider habitat range than seen in Scandinavia-Russia.

Section *Fuliginosa*
This section consists mainly of grey brownish to more vivid yellow brown to golden brown species without any bluish tinges, but the striking green *E. incanum* also belongs here. Six species are sequence-verified from Norway, depending on the species circumscription; if *E. xanthochroum* is regarded as separate from *E. formosum*, there are seven. This is the second largest section (after sect. *Cyanula*) on a European scale, with 18 species distinguished, including some xerothermous ones (Noordeloos et al. 2022a).

Entoloma sarcitulum (P.D. Orton) Arnolds (OTU36; Fig. 14)
Entoloma sarcitulum is a very anonymous *Cyanula*, with grey brown to brown colours and a pileus which is usually translucently striate nearly to the centre. The complete lack of bluish tinges, even when young, is in fact a good, characterizing feature. The species is, however, very close to *E. majusculum*, and these can hardly be distinguished when mature (see *E. majusculum*). The *E. sarcitulum-E. majusculum* complex was formerly often named *E. longistriatum* (Peck) Noordel. However, *E. longistriatum* was described from North America, and since the type is not sequenced, we do not know if this is a separate North American species, or if it could be conspecific with *E. sarcitulum* or *E. majusculum* (Noordeloos et al. 2022a).

Entoloma sarcitulum is in Norway much rarer than *E. majusculum*, and the verified collections are so far mainly from calcareous/-rich fens/mires, in *Sphagnum*. Of the 9 verified samples, at least 6 are from *Sphagnum*; from Oppland; Lunner, Vang and Sel, and from Nord-Trøndelag; Steinkjer. Another sample was from the Holmvassdalen area of Nordland, and was found in a (moist?) calcareous *Picea* forest. In N Sweden, a few collections of *E. sarcitulum* have been verified from moist, calcareous alpine habitats, including mires with *Sphagnum* (Larsson et al. in prep.). *Entoloma caliginosum* (Romagn. & J. Favre) Bon & Courtec., described from *Sphagnum* habitats, could be a synonym, and the name will have to replace *E. sarcitulum* if this can be substantiated.

Entoloma majusculum (Kühner & Romagn.) Noordel., O.V. Morozova, Brandrud & Dima in print s.l. (OTU35/83/168; Fig. 14)
Based on ITS phylogeny, *Entoloma majusculum* as here circumscribed forms a cluster with some internal variation and is assigned to three OTUs. Both phylogenetically and morphologically *E. majusculum* is very similar to *E. sarcitulum*, both are anonymous (grey)brown species, but *E. majusculum* differs by often showing a faintly bluish grey tinge on the stipe when young, and a stipe base that usually turns reddish with age or in exsiccates. The latter feature it has in common with *E. turci*, which is a more robust, fleshy species with a more scaly-tomentose pileus. The lamella edge of *E. majusculum* varies from sterile to more or less fertile. Ecologically, *E. majusculum* and *E. sarcitulum* can be distinguished on the preference of the latter for *Sphagnum* mires.

This is one of the more frequent species (species complex) in *Cyanula* hotspots, especially in calcareous grasslands. Altogether, approx. 50 collections have been sequenced, and most of them stem from the calcareous districts of Oslofjord-Mjøsa, Nord-Trøndelag (Steinkjer) and Nordland (Holmvassdalen, Grane, coastal grasslands in Brønnøy and Alstadhaug; and calcareous birch forest in Saltdal). More than half of the verified samples are from calcareous, grazed, semi-natural grassland, some are from natural, coastal grasslands on shallow-soil limestone rocks, a few are from rich fens with *Sphagnum*, and a few from a calcareous pine forests. From Sweden, a few collections of *E. majusculum* s.l. have been sequenced also from calcareous

Figure 14. The anonymous brown brothers. *E. majusculum* (above) and *E. sarcitulum*. These close look-a-likes can be distinguished mainly on the habitat (*E. sarcitulum* mainly in *Sphagnum*). Furthermore, *E. majusculum* normally initially shows a faint bluish tinge on stipe and often a pink tinge at base when exposed or bruised. (photo: TEB)

alpine meadow habitats, including *Dryas* heaths (Larsson et al. in prep.).

Entoloma turci (Bres.) M.M. Moser (OTU34; Fig. 15)
This robust species with a mouse grey-brown, tomentose pileus and a reddish discolouring stipe base and is one of the more easily identifiable *Cyanula* species. It usually has well-developed, sterile lamella edges, but variants with fertile edges may occur. The species is widely distributed, but strictly calciphilous, and a good indicator of *Entoloma* hotspots. Our verified, sequenced material is mainly from the Oslofjord-Mjøsa region, Trøndelag, Nordland and Troms.

Of the approx. 51 sequenced collections the majority are from calcareous, grazed grasslands, the others from calcareous pine forests, calcareous tall herb spruce forests and calcareous lime forests. When the number of localities is considered, there are as many sequence-verified localities from calcareous forests as from grasslands. On a sequence screening of a large material from calcareous pastures at Reinøya north of Tromsø (Ravolainen 2000), this appeared to be the most frequent species, with 16 collections, indicating that this is an important indicator species for calcareous grasslands throughout Norway. In N Sweden this species has also been found two times in alpine habitats (Larsson et al. in prep.)

There are more than 100 non-sequenced collections in the Norwegian fungaria, and most of them are believed to be correctly identified (most of our studied collections were correctly pre-sequence identified). According to this, a very high majority of our fungarium samples are from calcareous grasslands, including naturally open shallow-soil limestone rock sites and alpine sites, and only a few from calcareous forests (8% from forests, according to compilation in Jordal et al. 2016). Our new data from the *Entoloma* project indicate that the calcareous forests is somewhat undersampled for this one in the fungarium data, and we estimate the true portion of *E. turci* populations in semi-open, calcareous forests to be >20%.

Entoloma montanum Noordel., J.B. Jordal, Lorås, Eidissen, E. Larss. & Dima (OTU39; Fig. 15)
Entoloma montanum was recently described (Noordeloos et al. 2020). It occupies a rather isolated position within European species of sect. *Fuliginosa*, and also morphologically, it is somewhat deviating. It lacks the vividly ochre-brown to grey brown colours of e.g. *E. formosum* and *E. sarcitulum*. Instead, it initially has a distinctly violaceous grey tinge, at least on the polished stipe. The often campanulate shape of the pileus seems also to be charactestic.

The species is in Norway found mainly in the north, with most verified finds from the Holmvassdalen NR-Auster-Vefsna district, Nordland, and a couple of finds also from North Trøndelag. It occurs in rich to calcareous *Picea abies* forests, in rather open low-herb, tall-herb to rather swampy sites, once also recorded in alpine *Dryas* heath (17 sequence-verified samples). From N Sweden, there are many finds from calcareous alpine sites (Larsson et al. in prep.), and the type is from the alpine Pite Lappmark (Noordeloos et al. 2020). Outside Scandinavia, it is also verified from montane W Caucasus, and subalpine sites in the Pyrenées and the Dolomites, so the species probably has a wide distribution in montane-alpine Europe. It has apparently been called *E. poliopus* var. *alpigenes* Favre by many, but the lectotype of this name belongs to a very distant clade, and therefore of no relevance here.

Figure 15. The ubiquitose and the alpine: *E. turci* (above) and *E. montanum*. *E. turci* in normally easy recognized by its initially tomentose greybrown pileus and pink tinged stipe base. It is not frequent, but widely distributed in calcareous soils. *E. montanum* is characterized by its bluish tinges, often campanulate pileus and habitat mainly in alpine regions. (photos: TEB, JBJ)

Entoloma formosum Noordel. s.l.
(OTU38/84/85)
Entoloma formosum is here treated collectively, including variants with yellow-ochraceous lamellae and brown lamella edge (*E. xanthochroum* (P. D. Orton) Noordel.), and variants with pale lamellae and concolorous lamella edge (*E. formosum* s. str.). The ITS-DNA sequences of these variants differ slightly, but to resolve the phylogenetic structure of this complex, an analysis of more genes is probably needed. Morphologically, the complex is characterized by vivid yellow ochre-golden brown colours on pileus and stipe.

The *E. formosum* complex is widespread in Norway, and has a wide habitat spectrum. Our sequenced material (approx. 40 samples) has habitat preferences ranging from more or less calcareous forests, rich fens to calcareous grazed grasslands, confirming former habitat data treatment (Jordal et al. 2016). According to Jordal et al (2016) 19% of the total fungarium records (incl. non-sequenced) are from forests. The species is also found in pionér stages after clear-cutting of coniferous forests. The *E. formosum* complex is widespread in Europe, and this is one of very few *Cyanula* species that is verified both from Europe and from North America (Canada). *Entoloma formosum* "var. *xanthochroum"* is so far sequence-verified only from Norway and Denmark, but with type material from Great Britain.

Entoloma incanum (Fr.) Hesler (OTU37)
With its fairly persistent green to blue-green colours on pileus and stipe, this is a very striking species. Apart from the sister species *E. verae* (Crous et al. 2021, with larger spores, recorded from Russia, Germany and the Netherlands), there is no other species in Europe known with these features. According to the compilation in Jordal et al. (2016), there are 75 records (49 localities) of *E. incanum* s.l.in Norwegian fungaria. Of these 24 are from semi-natural grasslands, 15 from other kind of grasslands (lawns, parks and road verges), 8 from naturally open, shallow-soil limestone rock sites, and 33 from calcareous forests/forest borders; that is 44% of the finds from forests. This makes *E. incanum* the *Cyanula* species with the highest proportion of records from forests (versus grassland and other open sites), within the compilation of Jordal et al. (2016). In our project we have recorded this both in calcareous *Pinus, Picea* and *Tilia-Coylus* forests, but also typically along small road verges or along lime quarries in forest margins in calcareous districts. The species appears strictly calciphilous. It should be noted that only 9 of our collections of *E. incanum* are verified by sequencing (Table 1), and it cannot be ruled out that the morphologically very similar sister species *E. verae* also occurs in Norway.

Concluding remarks
As shown above it will be difficult to identify a high proportion of the known Norwegian *Cyanula* species without using sequence data, at least for the non-specialists. Especially for the 18 new species described during 2020-2022, we still do not know much of the range of morphological character variability. However, the availability of verified ITS barcodes make it possible to identify these species with certainty, which is a great advantage for those that do ecological studies and inventories, and have no time to specialize in this particular groups of fungi. When studied repeatedly over time we are furthermore convinced that most of these taxa are possible to distinguish morphologically when young and well-developed material is at hand, but with present, fragmented knowledge, many of these are to be regarded as semi-cryptic species.

With more than 1000 collections sequence-verified, it is tempting to think that we now have documented most of the *Cyanula* species truly occurring in Norway. However, we still

find new species to Norway and new to science almost every year, and we still find species in new regions and in new habitats, so it is too preliminary to draw firm conclusions about the true number of species and their ecology and distribution. Still many potentially rich habitats are undersampled, for instance our calcareous alpine habitats. At the moment, we have eight undescribed species with too few or too sparse collections to allow a formal description. Furthermore, there are 39 more sequence-verified *Cyanula* species known from Europe, and many of them occur in adjacent regions or areas with a climate comparable to ours (Noordeloos et al. 2022a). At the moment six of the species presented here have only been verified once from Norway (Table 1), and the number of species new to Norway has been rapidly and steadily increasing during the project. Based on this it seems fair to estimate that the true number of *Cyanula* in Norway must be > 80 species.

Acknowledgements
The Norwegian *Entoloma* project 2015-2017 was financed by the Norwegian Taxonomy Initiative, with funding from the Norwegian Biodiversity Information Centre (NBIC). The majority of our material was sequenced through NorBOL, and we thank G. Marthinsen and K. Bendiksen, NHM, University of Oslo, for performing most of the barcoding work. Furthermore, we thank Pablo Alvarado (ALVALAB, Oviedo, Spain), for sequencing another, substantial part of our material (collections labelled ALV). A number of samples were sequenced in Eötvös Loránd University, Budapest, Hungary, partly financed by the Norwegian Institute for Nature Research (NINA) and by Miljøfaglig Utredning. Some sequences, especially from Holmvassdalen nature reserve (Nordland), were financed by Nord University. The foundation Rijksherbariumfonds Dr. E. Kits van Waveren supported the sequencing of types and other valuable material for this study and enabled the necessary travelling for M. E. Noordeloos. We appreciate the permission to use photos provided by Per Fadnes, Stord and Andreas Svendsen, Strand (Rogaland) and an aquarelle by Hermod Karlsen, Fredrikstad. Others involved in the European *Entoloma* research group, especially Olga Morozova, Komarov Botanical Institute, St Petersburg and Jordi Vila, Olot, Spain are thanked for contributing data from other countries and for fruitful taxonomic discussions. Many taxonomists, ecologists, mappers and "citizen scientists" from Norway have contributed to our study with valuable material. Especially should be mentioned Per Fadnes, Stord, Geir Gaarder, Miljøfaglig Utredning, Tingvoll, Håkon Holien, Nord University, Steinkjer, Thomas Læssøe, University of Copenhagen, Anne Molia, NHM, University of Oslo, Morten Pettersen, Fredrikstad, Virve Ravolainen, Tromsø and Hans Schwencke, Otta who have provided much data. Ellen Larsson, University of Gothenburg, is thanked for the possibility to use data from the comprehensive *Entoloma* collection from Northern Sweden, stored in GB. The work of Bálint Dima was partly supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences, the National Research, Development and Innovation Office of Hungary (OTKA FK-143061) and the ELTE Thematic Excellence Programme 2020 (TKP2020-IKA-05).

REFERENCES

Bakkestuen V, Stabbetorp O, Molia A, Evju M, 2014. Hotspot åpen grunnlendt kalkmark i Oslofjordområdet. Beskrivelse av habitatet og forslag til overvåkingsopplegg fra ARK-Oprosjektet. – NINA Rapport 1102. 46 s.

Birkebak JM, Taylor JR, Martin-Rydberg K, Brandon-Matheny P. 2013. A systematic, morphological, and ecological overview of the Clavariaceae (Agaricales). *Mycologica* 105:4, 896-911, DOI: 10.3852/12-070

Brandrud TE, Bendiksen E, 2018. Faggrunnlag for kalkbarskog. NINA rapport 1513. Norsk institutt for naturforskning.

Brandrud TE, Bendiksen E, Bredin YK, Dima B, Eng S, Kauserud H, Thoen E, 2022. Nasjonal overvåking av kalklindeskog og kalklindeskogsopper. Aktiviteter i 2021, samt sammenstilling av basisdata fra 1. og 2. overvåkingsomløp 2013-2021. NINA Rapport 2164. Norsk institutt for naturforskning.

Brandrud TE, Bendiksen E, Jordal JB, Weholt Ø, Eidissen SE, Lorås J, Dima B, Noordeloos ME, 2018a. *Entoloma* species of the rhodopolioid clade (subgenus *Entoloma*; Tricholomatinae, Basidiomycota) in Norway. *Agarica 38: 21–46*.

Brandrud TE, Bendiksen E, Jordal JB, Weholt Ø, Dima B, Morozova O, Noordeloos ME 2020a. On some new or little known *Entoloma* species (Tricholomatinae, Basidiomycota) from Norway. *Agarica* 39: 31-52.

Brandrud TE, Bendiksen E, Noordeloos ME, Dima B, Morozova O 2018b. Entolomaarter funna i Jämtland och Medelpad 2016 - Entoloma species found in Jämtland and Medelpad (Sweden) in 2016. Svensk Mykologisk Tidskrift 38 (3): 25-35.

Brandrud TE, Brandrud MK, Dima B, 2020b. Nasjonal overvåking av kalklindeskog og kalklindeskogsopper. Resultater fra andre overvåkingsomløp, første år (2019). NINA rapport 1793. Norsk institutt for naturforskning.

Brandrud TE, Breistøl A, 2020. Rv. 5 Loftesnes-Kaupanger, Sogndal kommune. Kartlegging av naturtypar og artar. NINA Rapport 1864. Norsk institutt for naturforskning.

Brandrud TE, Dima B, 2017. Overvåking av jordboende sopp i Røsskleiva NR, Bamble 2016. NINA Kortrapport 80. Norsk institutt for naturforskning.

Brandrud TE, Evju M, Blaalid R, Skarpaas O, 2016. Nasjonal overvåking av kalklindeskog og kalklindeskogsopper. Resultat fra første overvåkingsomløp 2013−2015. - NINA Rapport 1297. 128 s.

Buyck B, Eyssartier G, Armada F, Corrales A, Hembrom ME, Rossi W, Bellanger J-M, Das K, Dima B, Ghosh A, Noordeloos ME, Parihar A, Krisai-Greilhuber I, Leonardi M, Manz C, Vera M, Vila J, Adamčíková K, Bizio E, Caboň M, Hampe F, Piepenbring M, Adamčík S, 2022. −Fungal Biodiversity Profiles 111-120. Cryptogamie, Mycologie 43 (2): 23-61. https://doi.org/10.5252/cryptogamie-mycologie2022v43a2 http://cryptogamie.com/mycologie/43/2

Corriol G, 2016. Algunos *Entoloma* inéditos del subgénero *Leptonia*. Errotari 13: 33-50.

Crous, P.W. et al. 2019. Fungal Planet description sheets: 785-867. Persoonia 42: 291-473, ISSN (Online) 1878-9080, https://doi.org/10.3767/persoonia.2019.42.11.

Crous PW, Cowan DA, Maggs-Kölling, et al., 2021. Fungal Planet description sheets: 1182–1283. Persoonia 46: 313 – 528. https://doi.org/10.3767/persoonia.2021.46.11

Dima B, Brandrud TE, Corriol G, Jansen GM, Jordal JB, Khalid AN, Larsson E, Lorås J, Morozova OV, Naseer A, Noordeloos ME, Rossi W, Santamaria S, Sarwar S, Sesli E, Usman M, Afshan NS, Ahmad I, Banerjee A, Banerjee K, Bendiksen E, Colombo DRS, De Kesel A, Dovana F, Ferisin G, Hussain S, Islam S, Jesus AL, Kaygusuz O, Krisai-Greilhuber I, Mahammad S, Mishra DK, Nath PS, da Paixão SCO, Panja B, Papp V, Pires-Zottarelli CLA, Radnóti Á, Rana D, Saha R, Türkekul I, Haelewaters D, 2021. Fungal Systematics and Evolution: FUSE 7. Sydowia 73: 271–339.

Gouy M, Guindon S, Gascuel O, 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27: 221–224.

Guindon S, Dufayard JF, Lefort V, *et al.* 2010. New algorithms and methods to estimate Maximum-Likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321.

Halbwachs H, Dentinger BTM, Detheridge AP, Karasch P, Griffith GW, 2013. Hyphae of Waxcap Fungi colonize plant roots. *Fungal Ecology* 6: 489-492.

Jordal JB, 2005. *Entoloma callirhodon* - en ny, rosa rødskivesopp. *Sopp og nyttevekster 1*: 20-21.

Jordal JB, Brandrud TE, Larsen BH, 2006. Kartlegging av rødlistearter av sopp i kalkrike kulturlandskap i Gudbrandsdalen, Oppdal og på Hadeland. *Rapport J.B. Jordal nr. 1-2006*, 44 s.

Jordal JB, Evju M, Gaarder G, 2016. Habitat specificity of selected grassland fungi in Norway. Agarica 37: 5-32.

Jordal JB, Gaarder G, Lorentzen MN, Larsen BH, 2022. Kartlegging av beitemarkssopper i 2021 [Investigations of grassland fungi in 2021]. Miljøfaglig Utredning Report 2022-4. 68 pp.

Jordal JB, Gaarder G, Lorentzen MN, Tellnes S, Larsen BH, 2023. Nasjonal kartlegging av beitemarkssopper i 2022 [National investigations of grassland fungi in 2022]. Miljøfaglig Utredning Report 2023-28. 101 pp.

Katoh K, Standley DM, 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kokkonen K, 2021. New northern records of Entoloma with three new species of subgenus Rhodopolia and typification of E. nidorosum. Karstenia 59: 55-69. https://doi:10.29203/ka.2021.510

Kumar S, Stecher G, Tamura K, 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. Molecular Biology and Evolution 33 (7): 1870–1874. https://doi.org/10.1093/molbev/msw054.

Larsson E, Jordal JB, Dima B, (in prep.) Rödlingar (*Entoloma* spp.) i nordsvenska fjäll baserat på DNA-sekvensering. Undersläktet *Cyanula* (noppingar). Svensk Mykologisk Tidskrift.

Ludwig E, 2007. Pilzkompendium. Band 2. Die größeren Gattungen der Agaricales mit farbigem Sporenpulver (ausgenommen Cortinariaceae). Beschreibungen + Abbildungen. Fungicon-Verlag. Berlin.

Morgado LN, Noordeloos ME, Lamoureux Y, Geml J, 2013. Multi-gene phylogenetic analyses reveal species limits, phylogeographic patterns, and evolutionary histories of key morphological traits in Entoloma (Agaricales, Basidiomycota). Persoonia 31: 159–178. https://doi.org/10.3767/003158513X673521

Morozova OV, Noordeloos ME, Vila J, 2014. *Entoloma* subgenus *Leptonia* in boreal-temperate Eurasia: towards a phylogenetic species concept. Persoonia 32: 141-169. https://doi.org/10.3767/003158514X681774

Noordeloos ME, 1982. Notes on *Entoloma*. New and rare species of *Entoloma* from Scandinavia. New names and combinations. Nordic Journal of Botany 2: 155–162.

Noordeloos ME, 1984. Studies in *Entoloma* 10-13. Persoonia 12: 193-223.

Noordeloos ME, 1992. *Entoloma* s.l. Fungi Europaei, vol. 5. Giovanna Biella, Saronno, Italy.

Noordeloos ME, 2004. *Entoloma* s.l. Fungi Europaei, vol. 5a. Edizione Candusso, Italy.

Noordeloos ME, Dima B, Weholt Ø, Eidissen SE, Lorås J, Brandrud TE, 2017. *Entoloma chamaemor*i (Entolomataceae, Basidiomycota) - a new boreal species, with isolated phylogenetic position. Phytotaxa 298(3): 289-295.

Noordeloos ME, Gates GM 2012. The Entolomataceae of Tasmania. Fungal Diversity Research Series. Vol. 22. Springer Dordrecht, Heidelberg, New York, London. https://doi.org/10.1007/978-94-007-4679-4

Noordeloos ME, Lorås J, Eidissen SE, Brandrud TE, Bendiksen E, Morozova O, Jordal JB, Weholt Ø, Jansen GM, Larsson E, Dima B, 2020. Three new *Entoloma* species of the Cyanula clade (Entolomataceae, Agaricales) from (sub)alpine habitats in Northern Norway and Sweden. Sydowia 73: 185–196.

Noordeloos ME, Morozova O, Dima B, Reschke K, Jansen G, Brandrud TE, Jordal JB, Bendiksen E, Vila J, 2022a. *Entoloma* s.l. Flora agaricina neerlandica, vol. 1, supplement. 968 pp. Fungi Europaei 5B. Candusso; Origgio.

Noordeloos ME, Vila J, Jordal JB, Kehlet T, Brandrud TE, Bendiksen E, Moreau P-A, Dondl M, Lorås J, Larsson E, Dima B 2022b. Contributions to the revision of the genus *Entoloma* (Basidiomycota, Agaricales) in Europe: six new species from subgenus *Cyanula* and typification of *E. incarnato-fuscescens*. Fungal Systematics and Evolution 9: 87–97. doi: 10.3114/fuse.2022.09.06

Noordeloos ME, Weholt Ø, Bendiksen E, Brandrud TE, Eidissen SE, Lorås J, Morozova O, Dima B, 2018. *Entoloma aurorae-borealis* sp. nov. and three rare *Entoloma* species in the Sinuatum clade (subg. *Entoloma*) from northern Europe. Sydowia 70: 199-210.

Orton PD, 1960. New check list of British agarics and boleti. Part 3. Notes on genera and species in the list. Trans. Brit. Mycol. Soc. 43:159-439.

Ravolainen VT, 2000: Diversity, synecology and chorology of macrofungi in seminatural grassland on Reinøya, Troms, North Norway. Cand. scient. thesis, Department of Biology, University of Tromsø. 80 pp.

Romagnesi E, 1954. Propositions au Comité special. Bulletin de la Société mhycologique de France 70 (suppl.): 36-37.

Vila J, Carbó J, Caballero F, Catà S, Llimona X, Noordeloos ME, 2013. A first approach to the study of the genus *Entoloma* subgenus *Nolanea* sensu lato using molecular and morphological data. Fungi non Delineati LXVI (Studies on Entoloma): 3-61, 93-135 (iconography). Edizione Candusso, Italy.

Vila J, Noordeloos ME, Reschke K, Moreau P-A, Battistin E, Ribes MA, Marulli U, Corriol G, Polemis E, Loizides M, Dima B, 2021. New species of the genus Entoloma (Basidiomycota, Agaricales) from Southern Europe. Österr. Z. Pilzk. 29: 123-153.

Weholt Ø, Lorås J, Eidissen SE, 2014. One new and one rare species of *Entoloma* from the Norwegian nature reserve Holmvassdalen. Österr. Z. Pilzk. 23:55-60.