



The genus *Entoloma* (*Basidiomycota*, *Agaricales*) in Europe: new taxa and amended species concepts in a phylogenetic context; neo-, lecto- and epitypifications of classical names

M.E. Noordeloos¹, K. Reschke², O. Morozova³, J.B. Jordal⁴, G.M. Jansen¹, T.E. Brandrud⁵, E. Bendiksen⁵, E. Larsson⁶, A. Karich⁷, I. Krisai-Greilhuber⁸, A.M. Ainsworth⁹, J. Nuytink¹, J. Borovička¹⁰, M.J.C. van der Vegte¹¹, T.G. Frøslev¹², B. Dima^{13*}

¹Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, The Netherlands

²Mycology Research Group, Faculty of Biological Sciences, Goethe University Frankfurt am Main, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany

³Korolev Avenue 2, 197341, Saint Petersburg, Russia

⁴Miljøfaglig Utredning, Gunnars veg 10, NO-6630 Tingvoll, Norway

⁵Norwegian Institute for Nature Research, Sognsveien 68, NO-0855 Oslo, Norway

⁶Biological and Environmental Sciences, University of Gothenburg, Box 463, 40530 Göteborg, Sweden

⁷TU Dresden / Internationales Hochschulinstitut Zittau, Markt 23, D-02763 Zittau, Germany

⁸Department of Botany and Biodiversity Research, Universität Wien, Rennweg 14, 1030 Wien, Austria

⁹Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

¹⁰Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, CZ-16500 Prague, Czech Republic

¹¹De Hucht 25, 7041 JN, 's-Heerenberg, The Netherlands

¹²Natural History Museum of Denmark, Center for Geogenetics, University of Copenhagen, Øster Voldgade 5–7, 1350 København K, Denmark

¹³Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117, Budapest, Hungary

*Corresponding author: Bálint Dima, cortinarius1@gmail.com

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Abstract: The taxonomy and phylogeny of several clades of the genus *Entoloma* were revised using morphological and molecular genetic methods. Phylogenetic relationships among European species of the clades */Alboleptonia*, */Caeruleopolitum*, */Claudopus*, */Griseorubidum*, */Leptonia*, */Olivaceotinctum*, */Omphaliopsis*, */Pouzarella*, */Prunuloides*, */Sphagneti*, */Turfosa*, */Undulatosporum*, */Velenovskyi*, and */Vinaceum* were inferred using 694 newly generated sequences derived from the nrDNA ITS region including 80 sequences from type specimens. Anticipating the second volume of a completely revised monograph of the genus *Entoloma* in Europe, the following names are neotypified or epitypes are designated where, in case holotypes or lectotypes appeared unsuitable for molecular studies, viz. *E. araneosum*, *E. byssisedum*, *E. griseorubidum*, *E. hirtum*, *E. lanicum*, *E. neglectum*, *E. ollare*, *E. opacum*, *E. plebejum*, *E. resutum*, *E. rusticoides*, *E. sericellum*, *E. triste*, *E. undatum*, *E. velenovskyi*, and *E. versatile*. New type sequences for *E. alliodorum*, *E. asperum*, *E. brunneoflocculosum*, *E. caeruleopolitum*, *E. calaminare*, *E. canosericeum*, *E. cettoi*, *E. cuboidoalbum*, *E. indutoides*, *E. iodiolens*, *E. jahnii*, *E. milleri*, *E. moguntinum*, *E. olivaceotinctum*, *E. ostreatum*, *E. politoflavipes*, *E. polyangulatum*, *E. pseudoconferendum*, *E. pseudonigellum*, *E. pseudosericeoides*, *E. ritae*, *E. sericeoides*, *E. sordidolamellatum*, and *E. undulatosporum* have been generated and deposited in GenBank. Twenty-nine species new to science are described and illustrated, viz. *E. albostriatum*, *E. amabile*, *E. assimile*, *E. bresadolae*, *E. brunneostrigosum*, *E. chloridicolor*, *E. cassiopeia*, *E. chioneum*, *E. cognatum*, *E. cornatum*, *E. eborinum*, *E. ermineum*, *E. fraudans*, *E. fusconigrum*, *E. griseopulchrum*, *E. hirsutum*, *E. ludwigii*, *E. nanoalbum*, *E. nix*, *E. olivaceovirens*, *E. ostreatum*, *E. paraindutoides*, *E. peraraneosum*, *E. pilosum*, *E. pumilionis*, *E. skadiae*, *E. umbrinotinctum*, *E. vilae*, and *E. weiriorum*, and *Entoloma* sect. *Atricoloria* is described as new to science. The name *E. myochroum* is validated and the replacement name *E. cobaltichlorum* is proposed. Morphological and molecular studies made it necessary

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**Abstract:**

to provide new, amended descriptions for *E. alliodorum*, *E. anthracinum*, *E. araneosum*, *E. brunneoflocculosum*, *E. byssisedum*, *E. calaminare*, *E. canosericeum*, *E. dysthaloides*, *E. griseorubidum*, *E. flocculosum*, *E. indutoides*, *E. inopiliforme*, *E. hirtum*, *E. lanicum*, *E. lidbergii*, *E. milleri*, *E. myochroum*, *E. neglectum*, *E. olivaceotinctum*, *E. ollare*, *E. opacum*, *E. plebejum*, *E. polyangulatum*, *E. pseudonigellum*, *E. pseudoparasiticum*, *E. pseudosericeoides*, *E. pseudoturbidum*, *E. resutum*, *E. rusticoides*, *E. sericellum*, *E. sericeoides*, *E. sordidolamellatum*, *E. triste*, *E. undatum*, *E. undulatosporum*, *E. velenovskyi*, and *E. versatile*.

INTRODUCTION

This study is part of a large-scale molecular phylogenetic and morphological revision of the genus *Entoloma* in Europe, working towards a new, completely revised monograph of all European species in two volumes of *Fungi Europaei* 5. The first part was published in Noordeloos *et al.* (2022a), the second and final volume is planned to be finished in 2026. The material in the present study comes from various sources. In the Nordic countries, much work has been done on *Entoloma* in the framework of the Norwegian *Entoloma* project and studies of the subarctic Mycota in Sweden resulting in a constant flow of publications in recent years (Brandrud *et al.* 2018, 2019, Noordeloos *et al.* 2018, 2021, Haelewaters *et al.* 2020, Crous *et al.* 2021), and many collections have been studied from Central, Southern and Eastern Europe, including the European part of Russia. An attempt has been made to transform the traditional morphological approach as used in earlier monographs (Noordeloos 1992, 2004) into a more integrated species concept, including morphology, ecology, and molecular data. The present contribution deals with a series of clades within the well-supported and large /Cyanula–Inocephalus superclade of the multi-locus phylogenies presented by Co-David *et al.* (2009) and Baroni & Matheny (2011), viz. the /Alboleptonia, /Leptonia, /Undulatosporum, /Griseorubidum, /Olivaceotinctum, /Claudopus and /Velenovskyi clades, as well as the /Pouzarella, the so-called basal grade (including the /Caeruleopolitum, /Prunuloides, /Sphagneti, /Turfosa and /Vinaceum clades), and some lineages of uncertain affinities.

MATERIAL AND METHODS

Morphology

All studied collections were photographed in the field and attention was paid in observing the surrounding vegetation and putative ecology for each collection based on above-ground observations. The material was described after collecting to document the ephemeral macroscopic characters (especially colours) and dried and stored in the respective fungaria. Microscopic characters were studied with standard light microscopy methods. Basidiospores, basidia, cystidia, and tramal structures were observed in squash preparations of small parts of the lamellae in water (fresh specimens) or in 5 % KOH or 1 % Congo Red in concentrated NH_4OH (fungarium specimens). The pileipellis was examined on a radial section of the pileus in water (fresh specimens) or in a weak NH_4OH solution. For basidiospores, measurements are given as follows: minimum length–maximum length $\times$ minimum width–maximum width of at least 95 % of the spores. In some cases, extreme values are given in brackets.

Average spore size refers to the range of the average values of single collections. The factors Q (quotient of length and width) and Qav (mean of Q values) were calculated. The range $Q = 1.10\text{--}1.50$, $Q_{\text{av}} = 1.20\text{--}1.30$ means Q value of all measured spores ranges from 1.10 to 1.50, Q_{av} = the range of mean Q values for all collections. Normally 10–15 basidiospores have been measured per specimen, and usually 1–2 specimens per collection were microscopically studied. The number of microscopically studied specimens is given in brackets: (80/4) means 80 spores measured from 4 specimens. Cystidia and basidia dimensions are based on observing at least 10 structures per collection. Basidia were measured without the sterigmata. Pileipellis structures were observed on radial sections. All studied material is deposited in the fungaria of Oslo (O), Gothenburg (GB), Leiden (L), or St Petersburg (LE), unless otherwise indicated. For details on the characters used in the taxonomy of *Entoloma* the reader is referred to Noordeloos *et al.* (2022a).

DNA extraction and sequencing

Fungal DNA was extracted and the nrDNA ITS barcode region sequenced as described in Dima *et al.* (2016), Morozova *et al.* (2018), Papp & Dima (2018), Hahn *et al.* (2019) and Reschke *et al.* (2022a). At Naturalis Biodiversity Center, Illumina MiSeq sequencing was used for herbarium specimens. The ITS1 and ITS2 regions were amplified separately using primer combinations ITS1-F/ITS2 and ITS3/ITS4 with Nextera™ tails (Illumina). Library preparation, sequencing and processing of Illumina sequence reads were performed as described in Delgat *et al.* (2019). Sequencing of some material was performed in the Norwegian Barcode of Life (NorBOL) project or by Alvalab (Oviedo, Spain). Chromatograms were checked and edited with the CodonCode Aligner v. 9.0.2 package (CodonCode Corp., Centerville, Massachusetts, USA) or Geneious v. 2019.2.1 (Biomatters Ltd., Auckland, New Zealand). Sequence comparisons with public and our own databases followed Noordeloos *et al.* (2017). Additional sequences were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/>) and UNITE (<https://unite.ut.ee/>) databases. The sequences were aligned in MAFFT v. 7.4.90 (Katoh & Standley 2013) using the E-INS-i algorithm. The resulting alignments were examined and manually pruned in AliView v. 1.26 (Larsson 2014). Maximum likelihood trees were calculated in RAxML v. 8.2.12 (Stamatakis 2014) using the GTRCAT model with 25 per site rate categories, 1000 rapid bootstraps and a thorough ML search thereafter, both with the standard seed '12345'. The resulting phylograms were inspected in FigTree v. 1.4.4 (Rambaut 2014) and thereafter edited in MEGA v. 7 (Kumar *et al.* 2016) and Microsoft PowerPoint (Microsoft 365).

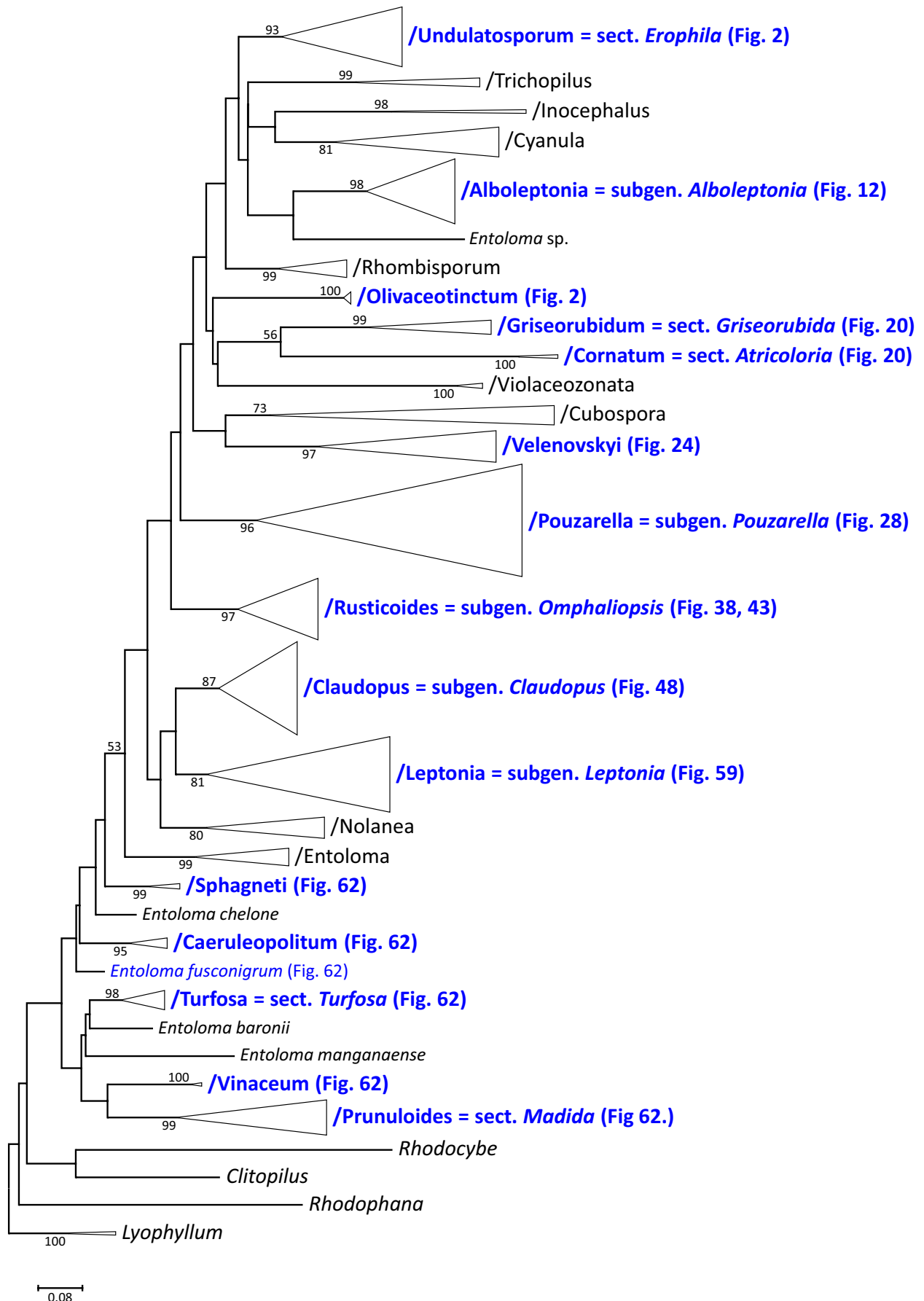


Fig. 1. Maximum Likelihood (RAxML) overview phylogenetic tree based on nrDNA ITS sequences of the genus *Entoloma* focusing on the studied lineages. ML bootstrap support values (> 50 %) are shown at the branches regardless of any value. Blue clades are treated in this paper. The scale bar indicates expected changes per site per branch.



RESULTS

Phylogeny

A total of 694 new ITS sequences were generated for this study, including 80 sequences of type specimens. The newly obtained sequences, together with 406 ITS sequences downloaded from GenBank and UNITE databases, were used as the basis for our phylogenetic analyses (Suppl. Table 1). For each of the main clades discussed in this study, separate trees were made. For */Undulatosporum* incl. */Olivaceotinctum*, 117 new and 27 database sequences were used; for */Griseorubidum* including */Cornatum*, 13 new and 14 database sequences; for */Velenovskyi*, 19 new and 21 database sequences; for */Claudopus*, 157 new and 94 database sequences; for */Alboleptonia*, 102 new and 38 database sequences; for */Leptonia*, 21 new and 51 database sequences; for */Pouzarella*, 100 new sequences and 68 database sequences; for */Rusticoides*, 74 new and 44 database sequences; and for the basal grade, 91 new and 54 database sequences. A reduced set of those alignments together with 35 additional GenBank sequences were used for the overview tree (Fig. 1). The resulting phylogenetic trees show differences in resolution between certain clades: the best resolved trees were obtained for subg. *Pouzarella* and sect. *Griseorubida*, which include several well-supported backbone branches and a comparatively high proportion of well-supported subclades. On the contrary, the trees of subg. *Omphaliopsis* and subg. *Claudopus* do not contain supported backbone branches and contain comparatively few supported subclades. The clades treated at species level were in general well-supported. Most of the species have rather uniform ITS sequences with only low or even no variability in the sequences analysed for this study. However, some species have a comparatively high variability, including distinct differences in several nucleotides and ambiguous nucleotides at certain sites. The resulting clades of such species are sometimes poorly supported, e.g., the clades of *E. sericellum* and *E. undatum*. Other species clades, such as *E. velenovskyi* and *E. ostreatum*, have distinct subclades, which potentially could represent different species. The backbone of the overview tree has generally low support values. However, the structure agrees with previous multi-gene studies where comparable relations are found, e.g. subg. *Cyanula* neighbouring subg. *Inocephalus* (Karstedt & Kapelari 2013), the positions of the basal grade and subg. *Entoloma* (Morgado *et al.* 2013), and the relation of the subgenera *Claudopus*, *Leptonia* and *Nolanea* (Reschke *et al.* 2022a).

Taxonomic part

Order of the clades/sections/subgenera treated here follow the topology of the phylogenetic tree in Fig. 1, while the species within each clade are presented in alphabetical order.

/Undulatosporum clade – *Entoloma* sect. *Erophila*

Entoloma* sect. *Erophila (Romagn.) Noordel., *Persoonia* 11: 86. 1980. **amend.** MB 860554.

Basionym: *Rhodophyllus* sect. *Erophili* Romagn., *Bull. Mens. Soc. linn. Lyon* 43: 332. 1974. MB 634423.

Synonym: *Entoloma* sect. *Tristia* (Noordel.) Noordel. & Wölfel., *Österr. Z. Pilzk.* 6: 26. 1997. MB 846106.

Type species: *Entoloma erophilum* (Fr.) P. Karst = *Entoloma plebejum* (Kalchbr.) Noordel.

Description (amended here): *Basidiomata* collybioid, tricholomatoid, mycenoid or omphalinoid. *Pileus* conical-convex or convex-umbilicate, sometimes deeply umbilicate; hygrophanous, or only weakly so, usually not translucently striate, often radially fibrous-micaceous to slightly to distinctly squamulose. *Lamellae* often tinged grey; stipe central. *Basidiospores* heterodiametrical to subisodiametrical with a 7–10 angular to subnodulose outline. *Lamella edge* fertile or heterogeneous with pronounced protruding cheilocystidia. *Pileipellis* usually consists of a transition between a cutis and trichoderm of cylindrical hyphae with clavate or subclavate terminal elements with intracellular pigment. *Clamp-connections* usually present.

Notes: In Europe the */Undulatosporum* clade comprises about 30 species with a collybioid, tricholomatoid, mycenoid or omphalinoid habit. The species in this group usually have a depressed to umbilicate pileus with a differentiated pileipellis, usually of a transition between a cutis and trichoderm of cylindrical hyphae with clavate or subclavate terminal elements with intracellular pigment, and clamped hyphae. Many species have irregular angular spores with a nodulose–angular outline, hence the name of this clade. Most of the species have relatively dark brown to almost black colours, and the majority occur in rather exposed habitats, such as subarctic or subalpine heaths and snowbed communities, pioneer vegetation such as coastal dunes and sandflats, as well as xerophytic grasslands on calcareous soils. Several of these taxa are exclusively vernal or appear in the colder months of the year. In the traditional morphology-based classifications, species belonging to this clade were placed in different subgenera: *E. undulatosporum* and *E. triste* in subgenus *Nolanea*, sect. *Tristia* (Noordeloos 1987, Wölfel & Noordeloos 1997a), and *E. opacum*, *E. plebeoides*, *E. plebejum*, and *E. resutum* in subgenus *Inocephalus*, sect. *Erophila* (Noordeloos 2004). Our phylogenetic studies, however, show that these species cluster together in a well-supported clade, together with several undescribed species (Fig. 2). Some of these species are described here as new, other phylogenetic species have insufficient data to be published formally now and have to remain unnamed for the time being. We propose to accommodate the species of this clade in the amended concept of sect. *Erophila*.

Entoloma amabile J.B. Jordal, E. Larss., Noordel., O.V. Morozova & Dima, **sp. nov.** MB 860384. Fig. 3.

Etymology: *amabilis* (Lat.) – lovely, referring to the lovely appearance of this species.

Typus: **Sweden**, Pite lappmark, Arjeplog, Skarim, 10 Aug. 2018, J.B. Jordal, E. Larsson & J. Vauras, EL6-18 (**holotype** GB-0207746); ITS sequence, GenBank PV018335.

Description: *Basidiomata* collybioid. *Pileus* 10–20 mm wide, conico-convex then convex with minute umbo, with straight margin, pale brown, almost white at margin, deeply translucently striate, probably hygrophanous, medium brown at centre, initially radially fibrillose, glabrescent with age,

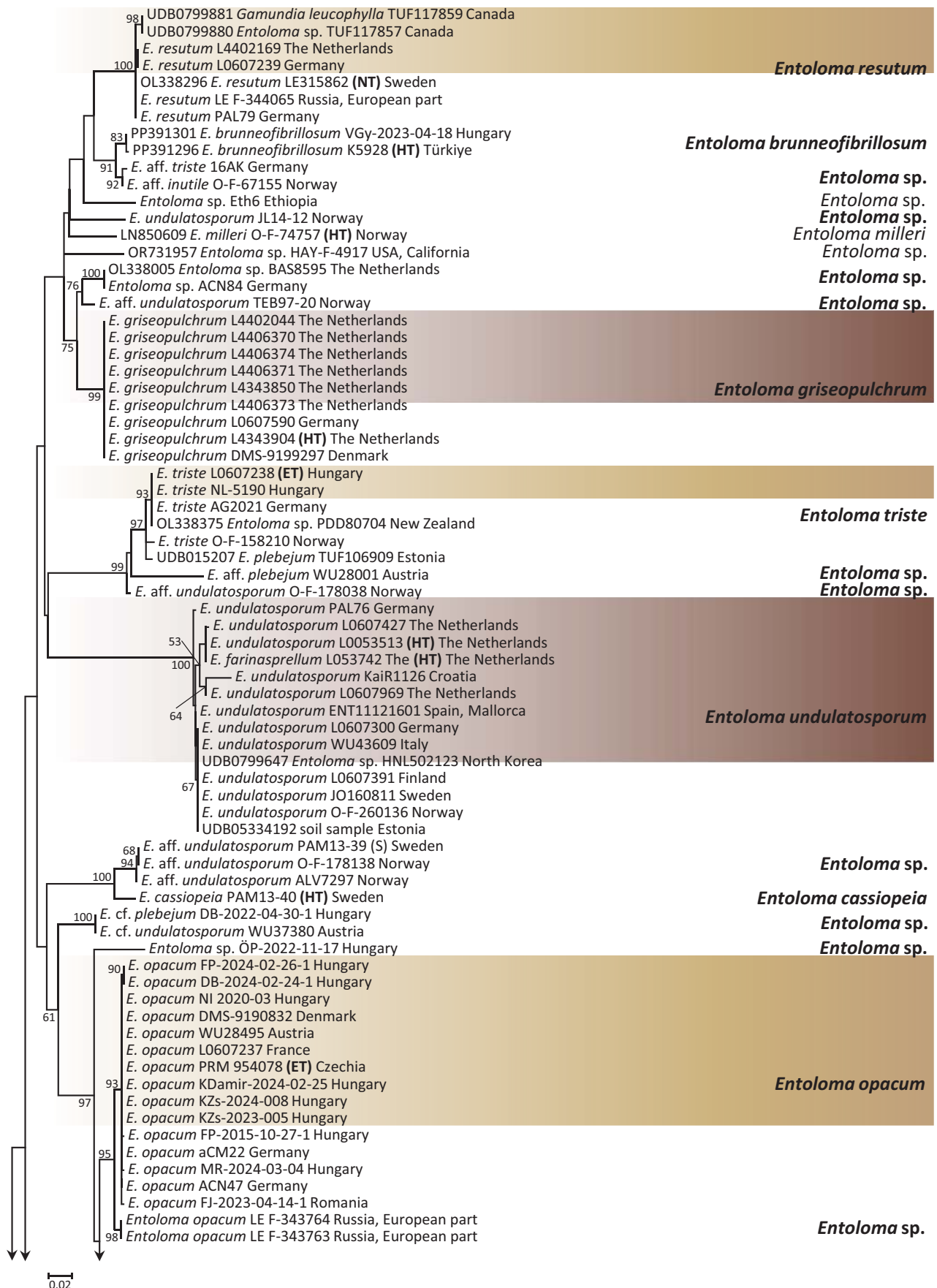


Fig. 2. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* sect. *Erophila* (= *Undulatosporum*). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



Basidiospores (50/3) 8.5–11.0 × 5.5–7.5 µm, on average 8.9–9.7 × 6.5–6.8 µm, Q = 1.30–1.70, Q_{av} = 1.45–1.50; nodulose-angular, thin-walled, heterodiametrical. *Basidia* 22–29 × 9–14 µm, clavate, 4-spored, clamped. Lamella edge heterogeneous, with scattered, subcylindrical to narrowly



clavate cheilocystidia, $30\text{--}44 \times 8\text{--}12 \mu\text{m}$. *Pileipellis* a cutis made up of cylindrical hyphae $4\text{--}9 \mu\text{m}$ wide, with brown granular and diffuse intracellular pigment. *Stipitipellis* a cutis of cylindrical hyphae, $5\text{--}14 \mu\text{m}$ wide; caulocystidia absent. *Clamp-connections* present in hymenium, rare in other tissues.

Habitat and distribution: The holotype collection originated from a rich alpine meadow, bordering a riverlet with *Bistorta vivipara*, *Thalictrum alpinum* and *Salix hastata*. This species has also been found on lakeside soil with *Salix* in subarctic Russia, and in a mixed broad-leaved alluvial forest (France). Known from Northern Sweden, Northern Russia, and France.

Additional material examined: **France**, Alsace, Haguenau, Schirrheimerweg Biological Reserve, Haguenau forest, plot 26, 1 Sep. 2023, J.-M. Trendel, JMT-23090113 (L0607184). **Russia**, Murmansk Oblast, vicinities of Apatity, bank of the Imandra Lake, on soil on roadside under *Salix* sp., 21 Aug. 2023, O. Morozova, 2AP23 (LE F-344066).

Notes: *Entoloma amabile* is distinguished by the pale, hardly fibrillose pileus, white, strongly fibrillose stipe, and presence of scattered cheilocystidia. *Entoloma milleri* from Svalbard is much darker, has different spores and a distant phylogenetic relationship within the sect. *Erophila*.

Entoloma anthracinum (J. Favre) Noordel., *Persoonia* **11**(2): 228. 1981. MB 112291. Fig. 4.

Basionym: *Rhodophyllus anthracinus* J. Favre, *Ergebn. wiss. Unters. Schweiz. Natn Parks* **5**(no. 33): 200. 1955. MB 305208.

Synonyms: *Entoloma subcollariatum* (Kühner) Bon, *Bull. trimest. Féd. Mycol. Dauphiné-Savoie* **31**(no. 122): 26. 1991. MB 128983

Entoloma phaeocarpoides Voto, *Mycological Observations* **4**: 33. 2022. MB 844177

Rhodophyllus atopellitus J. Favre, *Ergebn. wiss. Unters. schweiz. Natn Parks* **5**(no. 33): 200. 1955. MB 305212 (see notes, below).

Misapplied names: *Rhodophyllus anthracinus* sensu Kühner, *Bull. Soc. Mycol. France* **93**: 472–480 (1977), and *Entoloma anthracinum* sensu Noordeloos, *Persoonia* **12**: 289–290 (1984).

Typus: **Switzerland**, Graubünden, Val Nügli, Region of Fuorn, National Park, on bare ground, with *Saxifraga oppositifolia*, *Ranunculus alpestris*, *Festuca pumila*, 31 Aug. 1949, J. Favre, GK 13906 (**lectotype** designated in Kokkonen 2015, deposited at G); ITS sequence, GenBank LN850598.

Description (amended here): *Basidiomata* collybioid to omphalinoid. *Pileus* 20–30 mm wide, convex, with weak



Fig. 3. *Entoloma amabile* (A–D. GB-0207746, holotype; E. L0607184). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Pileipellis. Photos: A by J.-M. Trendel; B by J.B. Jordal; C by G.M. Jansen. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (spores, cheilocystidia), 40 μm (pileipellis).



umbo or slightly depressed at centre with thin, incurved margin, slightly hygrophanous, not translucently striate, blackish brown to umber brown when moist, with slightly paler margin, pallescent to grey brown when dry, with radially fibrillose-micaceous, at centre often somewhat granular surface. *Lamellae* moderately crowded ($L = 20\text{--}25$, $l = 1\text{--}3\text{--}7$), relatively broad, up to 4.5 mm, adnate-emarginate or adnate with short decurrent tooth, rather dark grey brown with pink tinge, often slightly veined on sides. *Stipe* 20–40 × 3–5 mm, usually attenuated towards base, but sometimes equal, solid then hollow, concolourous or distinctly paler than pileus, glabrous or slightly fibrillose. *Context* grey. *Smell* and *taste* indistinct. *Basidiospores* (150/10) $7.5\text{--}12.0 \times 5.5\text{--}10.0$ μm , on average $8.5\text{--}10.3 \times 6.5\text{--}7.5$ μm , $Q = (1.10\text{--})1.20\text{--}1.50$, $Q_{av} = 1.30\text{--}1.35$, heterodiametrical in outline with 5–8 nodulose angles in side view. *Basidia* 24–42 × 8.0–13.0 μm , 4- or 2-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Hymenophoral trama* made up of long, cylindrical to fusiform elements, 120–200 × 5–14 mm. *Pileipellis* a

differentiated cutis with narrow, cylindrical hyphae, 3–15 μm wide, with cylindrical to subclavate terminal elements, 10–20 μm wide; pigment brown, intracellular. *Stipitipellis* a cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in all tissues.

Habitat and distribution: Solitary or in small groups in rather exposed habitats with natural disturbances, in arctic and alpine zones in dwarf-shrub vegetation, as well in coastal sand dunes in association with *Ammophila*, also found in continental, steppe-like sites. Known from European Russia, Central Europe including the Alps, and from a few places along the Atlantic and Adriatic coast in West and southern Europe. The species has also been verified from Iran (ITS sequence, GenBank MH453494).

Additional material examined: **Austria**, Niederösterreich, Pottendorf: Landegg, Leitha-Au Südost, 4 Sep. 2008, M. Beisenherz (WU-Myc 28494); Niederösterreich, Lichtenwörth,



Fig. 4. *Entoloma anthracinum* (A, I. Voto fu14, holotype of *E. phaeocarpoides*; B. FP-2024-01-06-1; C–F. Favre (1960); G, H. BG-2019-11-23). A, B, G, H. Habit in situ. C. Lectotype of *E. anthracinum*. D. Lectotype of *E. atopellitum*. E. Line drawings of lectotype of *E. anthracinum*. F. Line drawings of lectotype of *E. atopellitum*. I. Basidiospores. Photos: A, I by P. Voto; B by P. Finy; G, H by G. Benkő. Scale bars: 1 cm (habit), 10 μm (spores).



Zillingsdorfer Wald Ost, G. Koller, Hausknecht 3403.0 (WU-Myc 24866); Wien, Donaustadt, Donauinsel, 19 Oct. 2007, T. Barta (WU-Myc 28003). **France**, Savoie, Vanoise National Park, Pralognan, at the foot of Col de Chavière, boundary of mineral soil, above the last *Salix herbacea*, alt. 2600 m, 12 Sep. 1969, R. Kühner, K 69–304 (G262078, **holotype** of *Rhodophyllus subcollariatus*). **Germany**, Hessen, Frankfurt am Main, Campus Riedberge, vor OSC, on soil in lawn, 25 Feb. 2018, K. Reschke, KaiR1473 (B 70 0105520); Hessen, Marburg-Biedenkopf, Amöneburg, wayside, on rather bare soil, 21 Jan. 2018, C. Manz & M. Theiss aCM10 (B 70 0105491). **Hungary**, Vas, Szombathely, in lawn in front of a shopping centre, 23 Nov. 2019, G. Benkő & K. Fábrics, BG-2019-11-23 (ELTE); Budapest, 18 Nov. 2022, Z. Bratek, BZ-2022-11-18 (ELTE); Bács-Kiskun, Fülöpháza, 6 Jan. 2024, P. Finy, FP-2024-01-06-1; Pest, Csévharaszt, 5 Mar. 2024, I. Ölvédi, ÖP-2024-03-05-1 (ELTE); *ibid.*, 5 Mar. 2024, I. Ölvédi, ÖP-2024-03-05-2 (ELTE). **Italy**, Veneto, Rovigo, Rosolina, Rosolina Mare, Porto Caleri, associated with *Pleurochaete squarrosa*, 14 Jan. 2007, P. Voto, fu14 (VER, **holotype** of *E. phaeocarpoides*). **Russia**, Volgograd Oblast, near Chapurniki Village, “Chapurnikovskaya Balka” protected area, sandy steppe, 18 Oct. 2013, T. Svetasheva (LE F-316081); *ibid.*, (LE F-316082); Astrakhan Oblast, Chernoyarsky District, on roadside soil, 22 Oct. 2019, Yu. Rebriev, BM1346 (LE F-316083). **The Netherlands**, prov. Noord-Holland, Amsterdamse Waterleiding Duinen, Van Limburg Stirum Vallei, in moist dune slack on bare, calcareous sand close to *Ammophila arenaria*, 14 Jan. 2018, L.M. Jalink, L4406372.

Notes: *Entoloma anthracinum* apparently is a widespread species with a preference for dynamic ecological conditions, such as high alpine snowbed communities and the sparsely vegetated, rather exposed coastal dune habitats in the Atlantic and Mediterranean regions, as well as dry, steppe vegetation and dunes in Central Europe. Kokkonen (2015) designated a lectotype and compared it with the lectotype of *E. subcollariatum* which is considered conspecific. Also, the recently described *E. phaeocarpoides* has an identical ITS barcode. Favre (1955) described and depicted rather regularly 5–7-angled spores with pronounced angles. However, Kokkonen (2015) indicated that the spores of the lectotypes of *E. anthracinum*, and *E. subcollariatum* (viz. 6–9, usually 6–8-angled) were deviating from their respective protologues, which place them in the *Undulatosporum* clade, and not in subgenus *Entoloma*, as suggested by Kühner (1977) and Noordeloos (1984). This is confirmed by our examination of the additional collections of this species. The sizes of the spores vary also considerably, which may be due to a varying number of 2- and 4-spored basidia. Kühner (1977) in his impressive study of subgenus *Entoloma* (= *Rhodopolia*) in the Alps gives three different descriptions of what he considered to be *E. anthracinum*. In the discussion he makes an interesting remark, viz. “The spores of *Rhodophyllus anthracinus* in the herbarium of Favre seem to us different from those depicted by the author (i.e., R. Kühner), and from those of the collections we just described above as *E. anthracinum*. In fact, they show an outline that is not so much different from *R. atropellitus* J. Favre, being nodulose-angled with 8–9(–10) angles. They also have the same dimensions as our *E. anthracinum*”. This observation confirms those mentioned above of Kokkonen

(2015), and supports our hypothesis, that the descriptions of *E. anthracinum* by Kühner (1977) and Noordeloos (1984) actually refer to another species, with spores being more or less regularly angular, and a pileipellis in form of a thin cutis or ixocutis of narrow, cylindrical, 3–7 µm wide hyphae, overlaying a subpellis of much wider hyphae, typical for species in subgen. *Entoloma* (/ *Rhodopolia*). Kühner (1977) also studied the original material (lectotype) of *E. atropellitum*, and concluded it might be considered a dwarfish form of *E. anthracinum*. He also compared the spore shape with those of *E. sphagnetii*, and wondered whether *E. atropellitum* might be a dwarfish alpine form of that species. As we know now, however, *E. sphagnetii* is a quite distinct and different species with a very distant phylogenetic position (Morgado *et al.* 2013). In summary, we believe now that *E. anthracinum* in its original sense, including *E. atropellitum*, belongs to sect. *Erophila*, characterised by relatively small, very dark basidiomata and heterodiametrical, nodulose-angled spores. As shown above, it is not a strictly alpine species.

Entoloma cassiopeia Noordel., P.-A. Moreau, Reschke & Dima, **sp. nov.** MB 860386. Fig. 5A, B.

Etymology: Κασσιόπεια (Greek) – referring to the association with *Cassiope* species.

Typus: **Sweden**, Torne Lappmark, Jukkasjärvi, Abisko, Latnja, among mosses on an alpine cliff with *Cassiope*, 18 Aug. 2013, P.-A. Moreau, E. Larsson & J. Vauras, PAM13-40 (**holotype** GB-0207742); ITS sequence, GenBank PV018337.

Description: *Basidiomata* mycenoid. *Pileus* about 15–20 mm wide, conical then conico-convex, indistinctly hygrophanous, sepia brown with darker centre, translucently striate up to centre, innately radially fibrillose, centre slightly rugulose. *Lamellae* moderately distant (L = 25–30, l = 3–5), adnate-emarginate, ventricose, pale cream then brownish pink with irregular, concolourous edge. *Stipe* 40–50 × 2–3 mm, pale brown, like pileus margin or paler, with scattered silvery longitudinal fibrils. *Context* concolourous with surface. *Smell* and *taste* not distinctive. *Basidiospores* (20/1) 9.0–12.5 × 5.5–8.5 µm, on average 9.5–10.7 × 6.5–7.2 µm, Q = 1.25–1.75, Q_{av} = 1.45–1.50, nodulose-angular in side view with pronounced angles and sharp apiculus. *Basidia* 20–34 × 7–12 µm, 4-spored. *Lamella edge* heterogeneous. *Cheilocystidia* absent or sparse, subcylindrical, slightly protruding from hymenium, 40–50 × 5–11 µm wide. *Pileipellis* a transition from a cutis to a trichoderm, made up of 5–12 µm wide hyphae with inflated terminal elements, 6–22 µm wide; pigment intracellular, brown. *Stipitipellis* a cutis of cylindrical hyphae, 5–11 µm wide. *Caulocystidia* absent. *Clamp-connections* present in hymenium, elsewhere not found.

Habitat and distribution: Among mosses on an alpine cliff with *Cassiope* sp. Only known from one locality in Northern Sweden.

Notes: *Entoloma cassiopeia* belongs to a small, but well-supported subclade within sect. *Erophila* which represents one (or more) subarctic/alpine species, morphologically similar to, but phylogenetically distant from the above-described *E. amabile* from a similar habitat. We were,



however, not able to establish consistent morphological differences between *E. cassiopeia* and *E. amabile* and they seem to have similar ecological requirements. However, the two are phylogenetically very distant, so they represent two well-separated barcode species. The subclade shows a considerable variation in ITS, so possibly more than one (barcode) species can be recognized within *E. cassiopeia* when more data are available.

Entoloma griseopulchrum M.v.d. Vegte, G.M. Jansen, Noordel. & Dima, **sp. nov.** MB 860383. Fig. 5C–F.

Etymology: *griseus* (Lat.) – grey; *pulcher* (Lat.) – beautiful.

Typus: **The Netherlands**, prov. Gelderland, Rheden, Heiderust, 26 Oct. 2022, M.J.C. van der Vegte & G.M. Jansen (**holotype** L4343904); ITS sequence, GenBank PX412037.

Description: *Basidiomata* mycenoid to collybioid. *Pileus* 10–20 mm wide, convex to plano convex usually with small umbo or slightly depressed centre, and involute then straight margin, pale grey to grey or dark brown grey sometimes almost black, but sometimes distinctly pale grey brown, indistinctly to distinctly hygrophanous, slightly to distinctly translucently striate when moist or not, slightly paler when dry, radially fibrillose to woolly-fibrillose, with silvery sheen (micaceous) and sometimes splitting when exposed, then showing the context of the pileus, resembling an *Inocybe*. *Lamellae* moderately distant ($L = 14\text{--}20$, $I = 3$), narrowly adnate, subventricose, up to 3.5 mm broad, pale to rather dark brown grey or olivaceous grey with pink tinge, with entire or eroded, concolourous or slightly paler edge, occasionally veined on the sides. *Stipe* 25–35 × 1–4 mm, cylindrical, narrowly hollow, at apex pale grey to pale greyish yellow, downwards grey brown or olivaceous grey, subpolished with scattered longitudinal fibrils, with white basal tomentum. *Context* very thin, pale brown. *Smell* faint or farinaceous; *taste* indistinct. *Basidiospores* (100/7) 7.5–11.5 × 5.0–7.0 µm, on average 8.5–9.7 × 6.0–6.2 µm, $Q = 1.30\text{--}1.80$, $Q_{av} = 1.45\text{--}1.6$, many-angled, sometimes almost nodulose. *Basidia* 20–40 × 5–11 µm, 4-spored, clamped. *Lamella edge* fertile, no cystidia present. *Hymenophoral trama* made up of cylindrical hyphae, 4.5–15 µm wide, somewhat constricted at septa, hyaline. *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical to slightly inflated hyphae, 7–22 µm wide, with brown, intracellular pigment. *Stipitipellis* a loose cutis of narrow, cylindrical hyphae, caulocystidia absent, *Clamp-connections* present, but scarce, often difficult to find.

Habitat and distribution: Terrestrial, among mosses in roadsides and in mixed forest on humus rich soil, with *Quercus*, *Acer*, sometimes also *Picea* and *Abies*. So far known from Denmark, Germany, and The Netherlands.

Additional material examined: **Denmark**, Jylland, Hjørring Kommunes Klitplantage, Rubjerg Knude, in *Abies* plantation on calcareous soil, 26 Jul. 2017, T. Læssøe, DMS-9199297 (C). **Germany**, Bayern, Landkreis Miesbach, Gemeinde Wargau, Taubenberg, Sulzgraben, in mixed mountain forest with *Abies*, *Picea* and *Fagus* on mineral rich soil, 27 Aug. 2020, M. Dondl, MD2020-02 (L0607590, as *E. winterhoffii*).

The Netherlands, prov. Drenthe, Mensingebos, along the road from Roden to Lieverden, 8 Sep. 1988, P.J. Keizer, 88318 (L4406371, as *E. undulatosporum*); *ibid.*, 29 Jun. 1987, P.J. Keizer, 87011 (L4406370, as *E. undulatosporum*); *ibid.*, 8 Sep. 1988, P.J. Keizer, (L4406373, as *E. undulatosporum*); prov. Zeeland, Axel, Axelse bos, 10 Aug. 1982, A. de Meyer, 349b (L4406374); prov. Gelderland, Heiderust, Rheden, 17 Oct. 2021, M.J.C. van der Vegte (L4343850); prov. Zuid-Holland, Voorschoten, Ter Horst, 28 Sep. 1977, M.E. Noordeloos s.n. (L4402044, as *E. plebeioides*).

Notes: *Entoloma griseopulchrum* differs from *E. undulatosporum* by the often umbonate, not umbilicate pileus and fibrillose stipe surface. *Entoloma triste* is macroscopically similar but has larger spores and more abundant clamp-connections. A collection made by M. Dondl (as *E. winterhoffii*) deviates a little in being pale grey, not as dark as the other collections, but otherwise it is very similar. The very rarely recorded *E. winterhoffii* differs by larger spores (Noordeloos 2004), but no ITS sequence is available of the holotype for comparison.

Entoloma milleri Noordel., *Mem. New York Bot. Gard.* **89**: 103. 2004. MB 367425. Figs 5G, H.

Etymology: Named in honour of the North American mycologist, Orson K. Miller (1930–2006).

Typus: **Norway**, Svalbard, Oscar II land, Stuphallet, (± 500 m), on soil in *Salix polaris* vegetation among *Racomitrium*, 6 Aug. 1986, G. Gulden & K.M. Jensen, GG 226/86 (**holotype**, O-F-74757).

Description: *Pileus* 10–25 mm broad, campanulate to conico-convex, expanding with age, with small umbo and inflexed margin, not hygrophanous or translucently striate, dark grey brown, squamulose at centre (umbo), radially fibrillose elsewhere, becoming fissurate with age. *Lamellae* moderately crowded ($L = 20\text{--}28$, $I = 1\text{--}3$), deeply emarginate or adnate, subventricose, to 2.5 mm broad, pale grey to brown grey, with concolourous, entire edge. *Stipe* 10–30 × 1.5–3 mm, cylindrical, concolourous with pileus, innately fibrillose, white tomentose at base, solid. *Context* dark grey to grey brown. *Smell* and *taste* indistinct. *Basidiospores* (15/1) 9.0–12.0(–13.0) × 6.5–8.0(–9.0) µm, on average 10–11 × 7–7.5 µm, $Q = 1.20\text{--}1.50$, $Q_{av} = 1.40$, heterodiametrical, many-angled almost nodulose in outline, rather thin walled. *Basidia* 20–50 × 10–18 µm, 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Hymenophoral trama* regular, consisting of long, inflated elements, ca. 300 × 15–35 µm. *Pileipellis* a cutis to 15 µm wide, inflated hyphae, at centre forming a transition to a trichoderm of inflated terminal elements. *Pileitrama* regular, consisting of long, inflated elements, 50–200 × 10–30 µm. Pigment brown, intracellular, often as dark clots in plasma, in pileipellis and upper pileitrama. *Stipitipellis* a loose cutis of narrow cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in hymenium and trama of pileus, lacking very scarce in other tissues.

Habitat and distribution: Terrestrial in polar *Dryas*/*Salix* heath, among *Racomitrium*. Only known from Svalbard (Norway).



Fig. 5. **A, B.** *Entoloma cassiopeia* (GB-0207742, holotype). **A.** Habit. **B.** Basidiospores. **C–F.** *Entoloma griseopulchrum* (L4343904, holotype). **C.** Habit in situ. **D.** Habit in studio. **E.** Basidiospores. **F.** Pileipellis. **G, H.** *Entoloma milleri* (O-F-74757, holotype). **G.** Habit. **H.** Basidiospores. Photos: A by P.-A. Moreau; C by M.J.C. van der Vegte; D–F by G.M. Jansen; G by G. Gulden. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores), 40 µm (pileipellis).



Notes: *Entoloma milleri* is distinctive on account of the grey colours, particularly of the lamellae, the squamulose pileus, and the relatively large, many-angled to nodulose, thin-walled spores. *Entoloma resutum* is somewhat similar, but has thicker-walled, regularly 6–7-angled spores, and has not been found in arctic(alpine) environments. *Entoloma hispidulum* has similar spores and a squamulose pileus, but it has slenderer basidiomata with minutely encrusted hyphae in the pileipellis, is not arctic and belongs to the distant subgen. *Leptonia*.

Entoloma opacum Noordel., *Beih. Nova Hedwigia* **91**: 135. 1987. MB 133098. Fig. 6.

Replaced synonym: *Clitocybe opaca* Velen., *České Houby* **2**: 268. 1920. MB 272953, nom. illegit., Madrid, Art. 53.1, non *Clitocybe opaca* Gillet, *Hyménomycètes* (Alençon): 164. 1874. MB 184587.

Typus: **Czechia**, Central Bohemia, Mnichovice, Aug. 1918, J. Velenovský, 186 (**holotype**, PRC, as *Clitocybe opaca* Velen., non *C. opaca* (With.) Gillet). **Czechia**, Praha, 12 Mar. 2020,



Fig. 6. *Entoloma opacum* (A, B, E. PRM 954078, epitype; C. MR-2024-03-04; D, F. L0607237). **A–D.** Habit. **E.** Basidiospores. **F.** Pileipellis. Photos: A, B, F by K. Tejkal; C by Re. Molnár; D, F by A. Grobelny. Scale bars: 1 cm (habit), 10 µm (spores), 20 µm (pileipellis).



K. Tejkal (**epitype** PRM 954078, designated here, deposited at PRM, MBT 10028194, **isoeptype** in L); ITS sequence, GenBank PX412053.

Description (amended here): *Basidiomata* tricholomatoid, rather sturdy, with relatively short stipes. *Pileus* 20–50 mm wide, convex to plano-convex, with a flattened to slightly depressed centre, sometimes with a small papilla, with deflexed sometimes undulating margin, not hygrophanous or translucently striate, very dark, almost black at centre, dark grey to dark grey brown towards margin, often more or less variegated-marbled or with darker spots, sometimes paler, more silvery grey, when old sometimes turning to grey beige with darker centre, finely radially wrinkled or fibrillose-subtomentose, when exposed sometimes breaking up in irregular patches showing the paler trama of the pileus, never really squamulose. *Lamellae* moderately crowded ($L = 40\text{--}60$, $I = 1\text{--}5$), adnate, deeply emarginate, sometimes with decurrent tooth, arcuate to ventricose, whitish greyish, then sordid grey pink, entire or eroded, concolourous edge. *Stipe* $30\text{--}35 \times 3\text{--}8$ mm, usually shorter than diameter of pileus, cylindrical or tapering towards base, light brown to cream, much paler than pileus, at apex finely pruinose-flocculose, downwards silvery fibrillose, solid then hollow. *Context* thin to thick, concolourous or distinctly paler than surface. *Smell* and *taste* indistinct to slightly farinaceous. *Basidiospores* (100/7) $8.0\text{--}10.5 \times 6.0\text{--}8.0$ μm , on average $9.0\text{--}9.5 \times 6.5\text{--}7.5$ μm , $Q = 1.25\text{--}1.40$, $Q_{\text{av}} = 1.30\text{--}1.35$, with 6–8 rounded angles in side view, not really nodulose, with relatively thick walls. *Basidia* $35\text{--}55 \times 12\text{--}14$ μm , 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Pileipellis* a cutis with transition to a trichoderm of cylindrical hyphae, with terminal elements up to 15(20) μm wide. *Pigment intracellular*, subpellis not differentiated. *Stipitipellis* a cutis with scattered caulocystidia in groups at apex of stipe, cylindrical to clavate or ampulliform, $20\text{--}50 \times 6\text{--}10$ μm . *Oleiferous hyphae* present in trama. *Clamp-connections* present in all tissues.

Habitat and distribution: In groups in open xerophytic vegetation, such as grasslands, orchards, parks, broad-leaved forest verges, etc., on calcareous soil. So far recorded and ITS confirmed from Austria, Czechia, Denmark, France, Germany, Hungary, and Romania, probably widespread in temperate Central Europe; almost exclusively recorded in late winter or spring.

Additional material examined: **Austria**, Niederösterreich, Schwechat, 22 Mar. 2008, *T. Barta*, WU-Myc 28495. **Denmark**, Møn, Jydelejet, Møns Klint, 23 Apr. 2017, *T. Kehlet* & *M. Vestergaard*, DMS-9190832 (C – material has been insect eaten). **France**, Dept. Moselle, Racrang, *A. Grobely* (L0607237). **Germany**, Hessen, Butzbach, Friedhof, 17 Mar. 2020, *C. Manz* & *F. Hampe*, aCM22 (B 70 0105493). **Hungary**, Veszprém, Öskü, in sandy pasture, 27 Oct. 2015, *P. Finy*, FP-2015-10-27-1; Békés, Gyula, under *Gleditsia*, *I. Nagy*, NI-2020-03; Békés, Hódmezővásárhely, Apr. 2023, *Zs. Kovács*, KZs-2003-05 (ELTE); Feb. 2024, *Zs. Kovács*, KZs-2024-008 (ELTE); Pest, Törökbálint, 4 Mar. 2024, *Re. Molnár*, MR-2024-03-04 (ELTE); Fejér, Velence, 26 Feb. 2024, *P. Finy*, FP-2024-02-26-1 (ELTE); Jász-Nagykun-Szolnok, Tószeg, on lawn, 24 Feb. 2024, *E. Gulyás*, DB-2024-02-24-1 (ELTE); Baranya, Pécs, 25 Febr 2024, *D. Kutváncsánin*,

Damir-1 (ELTE). **Romania**, Covasna, Sfântu-Gheorghe, on pasture, 14 Apr. 2023, *J. Farkas*, FJ-2023-04-14-1 (ELTE).

Notes: *Entoloma opacum*, like *E. plebejum*, often appears in winter and spring between February and May/June, but occasionally also in autumn, usually in rather exposed, thermophilic spots, like roadsides, orchards, grazed calcareous grassland, and the margins of broad-leaved forests (Battistin *et al.* 2013a). It clearly differs from *E. plebejum* by its rather stocky habit, with the stipe usually being shorter than the pileus diameter; the smaller, more isodiametrical spores, and the lack of cystidia. Macroscopically, it can be distinguished from vernal species within the *E. clypeatum* group by its dark, marbled pileus. Because the holotype is in bad condition it seemed sensible to designate an epitype with an ITS barcode. The epitype has been collected in the same geographical area as the type locality; for colour photos of the collection see Tejkal (2020).

Entoloma plebejum (Kalchbr.) Noordel., *Persoonia* 12: 462. 1985. MB 104249. Fig. 7A–D.

Basionym: *Agaricus plebejus* Kalchbr., *Icon. Sel. Hymenomomyc. Hung. (Budapest)* 2: 22. 1874. MB 372215. **Synonym:** *Entoloma erophilum* (Fr.) P. Karst., *Bidrag. Kännedom Finlands Natur. Folk* 32: 259. 1879. MB 202261.

Typus: Kalchbrenner (1874), *Icon. Sel. Hymenomomyc. Hung. (Budapest)* 2: pl. 12, fig. 1., **lectotype** (designated here, MBT 10028190). **Hungary**, Komárom–Esztergom, Gerecse Mts, Tatabánya, Turul monument, in *Quercus-Fraxinus* forest, 25 Apr. 2021, *A. Nagy* & *B. Dima*, DB-2021-04-25-1 (**epitype** L0607303, designated here, deposited at L, MBT 10028191); ITS sequence, GenBank PX412058.

Description (amended here): *Basidiomata* mycenoid to tricholomatoid. *Pileus* 30–60 mm wide, conical then expanding to conico-convex or convex with slight umbo, sometimes with slightly depressed centre, with involute then straight margin, not hygrophanous, not translucently striate, brown to grey brown, uniformly coloured or slightly paler towards margin, entirely radially fibrillose-tomentose, becoming more radially fibrillose to rimose with age, micaceous in patches, sometimes squamulose at centre. *Lamellae* moderately distant ($L = 25\text{--}40$, $I = 1\text{--}3$), adnexed, sometimes deeply emarginate to almost free, triangular at first then ventricose or arcuate then segmentiform, often veined on sides, white or grey then greyish pink with concolourous, entire edge. *Stipe* $60\text{--}90 \times 6\text{--}10$ mm, cylindrical or with broadened base, sometimes flattened with longitudinal groove, pallid, creamy white when fresh, turning yellowish brownish with age, floccose when young, then silvery fibrillose striate, white tomentose at base. *Context* thin. *Smell* slightly farinaceous, *taste* not recorded. *Basidiospores* (90/8) $(9.0\text{--})10.5\text{--}14.5\text{--}(17.0) \times 7.0\text{--}11.0$ μm , on average $12.0\text{--}12.8 \times 8.0\text{--}8.5$ μm , $Q = 1.10\text{--}1.70$, $Q_{\text{av}} = 1.45\text{--}1.55$, irregularly nodulose-angled in side view. *Basidia* $22\text{--}32 \times 6\text{--}10$ μm , 4- rarely also 2-spored, clamped. *Cheilocystidia*, if present then sparse or lacking, $35\text{--}100 \times 5\text{--}20 \times 2\text{--}9$ μm , fusiform to slenderly lageniform. *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical to inflated hyphae, 10–20 μm wide, with inflated terminal elements, $55\text{--}125 \times 15\text{--}25$ μm ; pigment abundant, brown, intracellular, diffuse or granular. *Stipitipellis* a loose cutis of



Fig. 7. A–D. *Entoloma plebejum* (A, C, D. L0607303, epitype; B. L0607278). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E–H.** *Entoloma resutum* (E, G, H. LE F-315862, neotype; F. L4402169). **E, F.** Habit. **G.** Basidiospores. **H.** Pileipellis. Photos: A, B by B. Dima; E by O. Morozova; F by M.E. Noordeloos; H by G.M. Jansen. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores), 40 μ m (pileipellis).



cylindrical hyphae, 4–11 µm, occasionally with clusters of cylindrical to subclavate caulocystidia. *Clamp-connections* present, but not at all septa.

Habitat and distribution: Solitary or in groups on various soil types (clay, sand) but usually more or less calcareous, also on humus rich soils, in broad-leaved or coniferous forests, and in open sand dunes, parks and gardens; spring and early summer, occasionally also in late autumn. Widespread in Europe, but not common. ITS sequence-verified collections were studied from France, Germany, Hungary, Norway, and The Netherlands.

Additional material examined: **France**, Calvados, Damblainville, Réserve naturelle nationale du coteau de Mesnil-soleil, 19 Nov. 2022, *J. Lagrandie* (herb. Boutard, L0607302). **Germany**, Sachsen, Hirschfelde, Neißetal, Restauration, alluvial area of the river bank, over slightly alkaline soil, with *Fraxinus* and *Quercus*, 15 Apr. 2017, *A. Karich* AK230817 (GLM-F139002). **Hungary**, Komárom–Esztergom, Vértes Mts, Várgesztes, in *Fraxinus-Quercus* forest, 13 Apr. 2019, *B. Dima*, DB15-19 (L0607278); Komárom–Esztergom, Vértes Mts, Szárliget, under *Fraxinus* and *Crataegus*, 21 Apr. 2023, *L. Vajda* & *G. Mokánszki*, VL-2023-04-21-2; Komárom–Esztergom, Gerecse Mts, Héreg, 20 May 2023, *Gy. Vrba*, VGy-2023-05-20 (Kaygusuz *et al.* 2024). **Norway**, Vestland, Hordaland, Tysnes, Kattenes, grassland in garden, 31 Oct. 2021, *P. Fadnes*, PF2140 (O-F-204290). **The Netherlands**, prov. Noord-Holland, Robbenoordbos, 5 Nov. 2013, *N. Dam*, MY958 (L0607255); prov. Flevoland, Lelystad, Jagersveld, 5 May 1984, *G. Tjallingii-Beukers* (L4402026); *ibid.*, 4 July 1987, *P.B. Jansen* (L4402036).

Notes: *Entoloma plebejum* is morphologically easily identified on account of the mycenoid to tricholomatoid habit with shiny-micaceous, radially fibrillose pileus, large spores and sometimes prominent cheilocystidia. It is normally a vernal species and can be found from February to June and in late autumn (November). *Entoloma triste* is very similar, differing among other things by the lack of cheilocystidia. The phylogenetically distant *E. brunneofibrillosum* known from Hungary and the Mediterranean region of Turkey is morphologically rather similar but has much smaller spores (Kaygusuz *et al.* 2024).

Entoloma resutum (Fr.) Quél., *Bull. Soc. Bot. France, Actual. Bot.* **23**: 326. 1877. MB 196455. Fig. 7E–H.

Basionym: *Agaricus resutus* Fr., *Epicrisis Systematis Mycologici*: 145. 1838. MB 461683.

Typus: **Sweden**, Jämtland, Krokom, Krokom Camping site near Östersund, 28 Aug. 2016, *O. Morozova*, *M.E. Noordeloos* & *B. Dima* (**neotype** LE F-315862, designated here, deposited at LE, MBT 10028192); ITS sequence, GenBank OL338296 (Reschke *et al.* 2022a).

Description (amended here): *Basidiomata* mycenoid to slenderly tricholomatoid. *Pileus* 10–30 mm wide, conical, then expanding to conico-convex or plano-convex, with or without small umbo, with inflexed then straight margin, not hygrophanous, not translucently striate, or rarely slightly

translucently striate at margin, dark grey brown or sepia brown, uniformly coloured, not or only slightly paler towards margin, micaceous–radially fibrillose, with aeriferous fibrils, subtomentose, initially even slightly squamulose at centre, then radially fibrillose, finally splitting up in radial rows of fibrillose squamules, showing paler trama between the fibrils. *Lamellae* distant ($L = 25\text{--}40$, $1 = 1\text{--}5$), thickish, narrowly adnate, ventricose, grey, then grey brown with pink tinge, paler towards the sub-entire to irregularly eroded edge. *Stipe* $20\text{--}45 \times 3\text{--}6$ mm, cylindrical to compressed with longitudinal groove, with slightly to distinctly broadened base, (grey) brown, paler than pileus, glabrous and polished or finely silvery fibrillose lengthwise, sometimes twisted, solid or fistulose. *Context* concolourous with surface in cortex, pale and fibrous in inner parts. *Smell* indistinct to distinctly farinaceous. *Taste* distinctly farinaceous-rancid. *Basidiospores* (45/3) $7.5\text{--}11.0\text{--}(12.0) \times 5.5\text{--}8.0$ µm, on average $9.5\text{--}10.2 \times 6.7\text{--}7.4$ µm, $Q = 1.25\text{--}1.70$, $Q_{av} = 1.35\text{--}1.45$, irregularly, mostly 7-angled in side view. *Basidia* $27\text{--}40 \times 8\text{--}11$ µm, 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Hymenophoral trama* regular made up of cylindrical hyphae. *Pileipellis* a trichoderm at centre, towards the margin a transition between a trichoderm and a cutis, made up of radially arranged, 10–23 µm wide, slightly inflated hyphae; pigment brown, intracellular. *Stipitipellis* a cutis of narrow cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in hymenium, elsewhere rare or absent.

Habitat and distribution: Terrestrial, among mosses in semi-natural grasslands and dune slacks in grey dunes, in calcareous grasslands in the lowlands, and in roadside verges in submontane, mixed *Picea/Fagus* forests. Widespread, but apparently rare everywhere. Sequence data available from Germany, Russia, Sweden and The Netherlands.

Additional material examined: **Germany**, Bayern, Erlangen, date unknown, *G. Wölfel*, MEN-14 (L0607239); Sachsen, Schöneck, road near Skislope, 24 Sep. 2022, *A. Karich* IHI-22Ent01 (GLM-F139798). **Russia**, Pskov Oblast, Pushkinogorsky District, vicinity of the Mikhailovskoye Village, roadside in a mixed forest, 11 Sep. 2018, *O. Morozova*, 6PG18 (LE F-344065). **The Netherlands**, prov. Friesland, Island of Terschelling, Dazenplak, 3 Nov. 1978, *M.E. Noordeloos* 842 (L4402169).

Notes: Since no original material exists, nor a plate to refer to as lectotype, we choose a neotype from Sweden to fix the current concept of *Entoloma resutum*. It is a relatively small, but compact, mycenoid to tricholomatoid species, with dark grey brown pileus and stipe, ventricose lamellae, fitting well with the protologue. Fries (1838, 1867) suggested that it is close to *Agaricus jubatus* and *A. griseocyaneus*, probably because of the robust mycenoid to tricholomatoid habit and fibrillose pileus. Due to the often nodulose spores, Noordeloos (1982) incorrectly assumed that *A. resutus* could be identical with *E. hispidulum*, a very different species in subgenus *Leptonia* (Morozova *et al.* 2014a). In contrast to some of its mainly vernal relatives, *E. resutum* is autumnal. The species was presented (including a photograph of the here selected neotype) under the provisional name *E. aff. triste* in Brandrud *et al.* (2018).



Entoloma sordidolamellatum Noordel. & Enderle, *Z. Mykol.* 61(2): 190. 1995. MB 413036. Fig. 8.

Typus: **Germany**, Bayern, Neu-Ulm/Pfuhl, Gymnasiums-gelände, in lawn, 4 Oct. 1992, *M. Enderle* (**holotype** L0064321); ITS sequence, GenBank PX412019.

Description (amended here): *Basidiomata* collybioid. *Pileus* 30–50 mm wide, convex then plano-convex with flattened to umbilicate centre, sometimes with a small, low umbo, with deflexed then straight margin, within the central depression, slightly hygrophanous, not translucently striate, grey brown to pale brown, uniformly coloured, pallescent along radial streaks, entirely finely to strongly radially fibrillose to squamulose? *Lamellae* moderately distant ($L = 30\text{--}40$, $I = 3\text{--}5$), adnate-emarginate with large decurrent tooth, ventricose, up to 10

mm broad, grey with entire, paler edge. *Stipe* 15–70 × 3–6 mm, cylindrical or compressed, greyish brown, more or less concolourous with pileus, pruinose at apex, strongly fibrillose striate-pruinose all over, white tomentose at base. *Context* brown. *Smell* and *taste* farinaceous to rancid. *Basidiospores* (60/4) $6.5\text{--}10.0 \times 5.5\text{--}7.5\text{--}(9.0) \mu\text{m}$, on average $7.3\text{--}8.0 \times 5.9\text{--}6.3 \mu\text{m}$, $Q = 1.00\text{--}1.30$, $Q_{av} = 1.20\text{--}1.25$, 6–7-angular, (sub)isodiametrical. *Basidia* 18–25(–35) × 8–11 μm , clavate, 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Pileipellis* a cutis with transitions to a trichoderm of inflated elements, $80\text{--}150 \times 20\text{--}40 \mu\text{m}$, with abundant brown, intracellular pigment. *Stipitipellis* a loose cutis of cylindrical hyphae, 4–11 μm wide, with scattered, cylindrical to clavate terminal elements (“caulocystidia”), $20\text{--}60 \times 4\text{--}11 \mu\text{m}$. *Clamp-connections* present in all tissues.

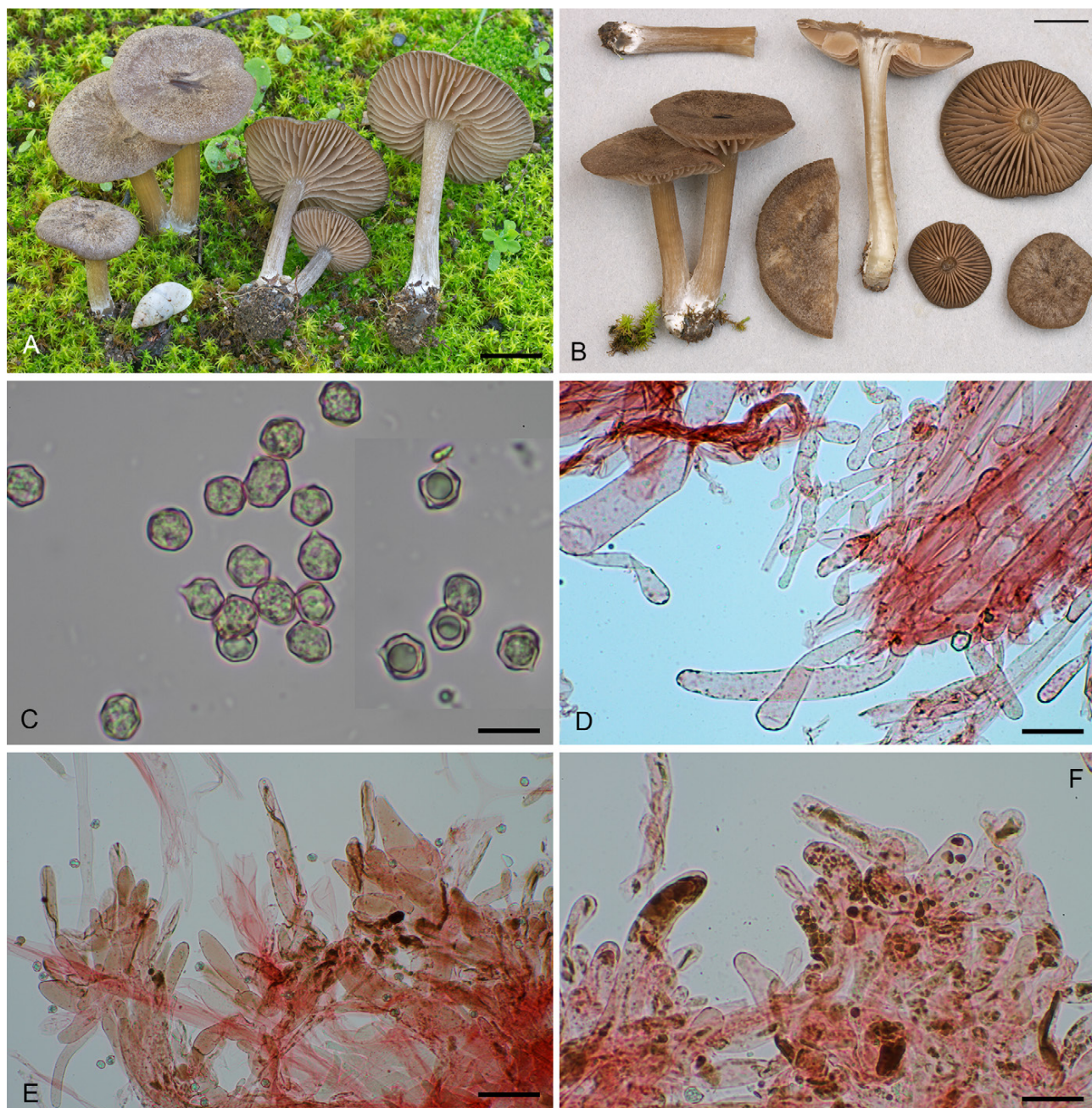


Fig. 8. *Entoloma sordidolamellatum* (L0607636). **A, B.** Habit. **C.** Basidiospores. **D.** Stipitipellis. **E, F.** Pileipellis. Photos: S. Saitta. Scale bars: 1 cm (habit), 10 μm (spores), 20 μm (pileipellis).



Habitat and distribution: Terrestrial in small groups in open lawn on calcareous soil (holotype), on sandy soil in parks (Austria, Hungary), and in coastal dunes among mosses accompanied by *Pistacia lentiscus*, *Eucalyptus globulus*, and *Pinus pinea* (South Italy). Known from Austria, Germany, Hungary and Italy.

Additional material examined: **Austria**, Niederösterreich, Wiener Neustadt: Ortsgebiet, Schottergruben, in xerophytic grassland, 8 Sep. 1984, R. Schütz (WU-Myc 6732); LSU sequence, GenBank MK278035 (Varga *et al.* 2019); Niederösterreich, Wien, Lobau, in xerophytic grassland, 14 Jun. 1986, A. Hausknecht (L0607631). **Hungary**, Csongrád–Csanád, Szeged, Erzsébet-liget, on sandy soil, in park, under *Quercus robur*, 25 May 2019, B. Dima, DB-2019-05-25-1 (ELTE). **Italy**, Sicily, Messina, Laghetti di Marinello, Oliveri, on soil amongst moss in dune environment, 10 Dec. 2020, S. Saitta (L0607636).

Notes: *Entoloma sordidolamellatum* has long been known from the type-locality and one additional find in Austria only, but additional recent collections from Austria, Hungary and Italy helped us to position this species in sect. *Erophila* and made it possible to provide an amended description. It has been accommodated earlier in sect. *Griseorubida* subsect. *Parvispora* (Noordeloos 2004) on account of its collybioid habit, strongly radially fibrillose pileus, pileipellis with broad elements, intracellular pigment, presence of in all tissues, small spores and lack of cheilocystidia. Noordeloos (2004) pointed also to the similarity with *E. farinasprellum*, because

of the strong farinaceous smell and the general colour. As became apparent from the present phylogenetic study, both *E. sordidolamellatum* and *E. farinasprellum* (as synonym of *E. undulatosporum*, see above), belong to the sect. *Erophila*. The rather small, more or less isodiametrical, and regularly shaped spores are distinctive. It could therefore be confused with *E. sericeoides*, which has, however, a smoother pileus, more 5-angled spores, and encrusting pigments in the pileipellis, and belongs to subgen. *Claudopus* (see below).

Entoloma triste (Velen.) Noordel., *Persoonia* 10: 254. 1979. MB 450879. Fig. 9.

Basionym: *Nolanea tristis* Velen., *České Houby* 3: 630. 1921. MB 280730.

Typus: **Czechia**, Bohemia, Krč, May 1920, J. Velenovský (holotype, PRC). **Hungary**, Budapest, Széchenyi-hegy, in calcareous dry grassland, 13 Nov. 2014, L. Albert & B. Dima, DB5690 (epitype L0607238, designated here, deposited at L, MBT 10028193); ITS sequence, GenBank PX412069.

Description (amended here): *Basidiomata* mycenoid to tricholomatoid. *Pileus* 20–40 mm, convex to plano-convex with distinct umbo, not hygrophanous or translucently striate, dark reddish brown to grey brown, towards margin often somewhat paler, radially fibrillose with paler fibrils on dark background, sometimes very finely squamulose all over. *Lamellae* moderately distant (L = 24–40, l = 3–7), whitish to pale brown at first, contrasting with pileus, then with pink tinge, with an entire, concolourous edge. *Stipe* 30–50

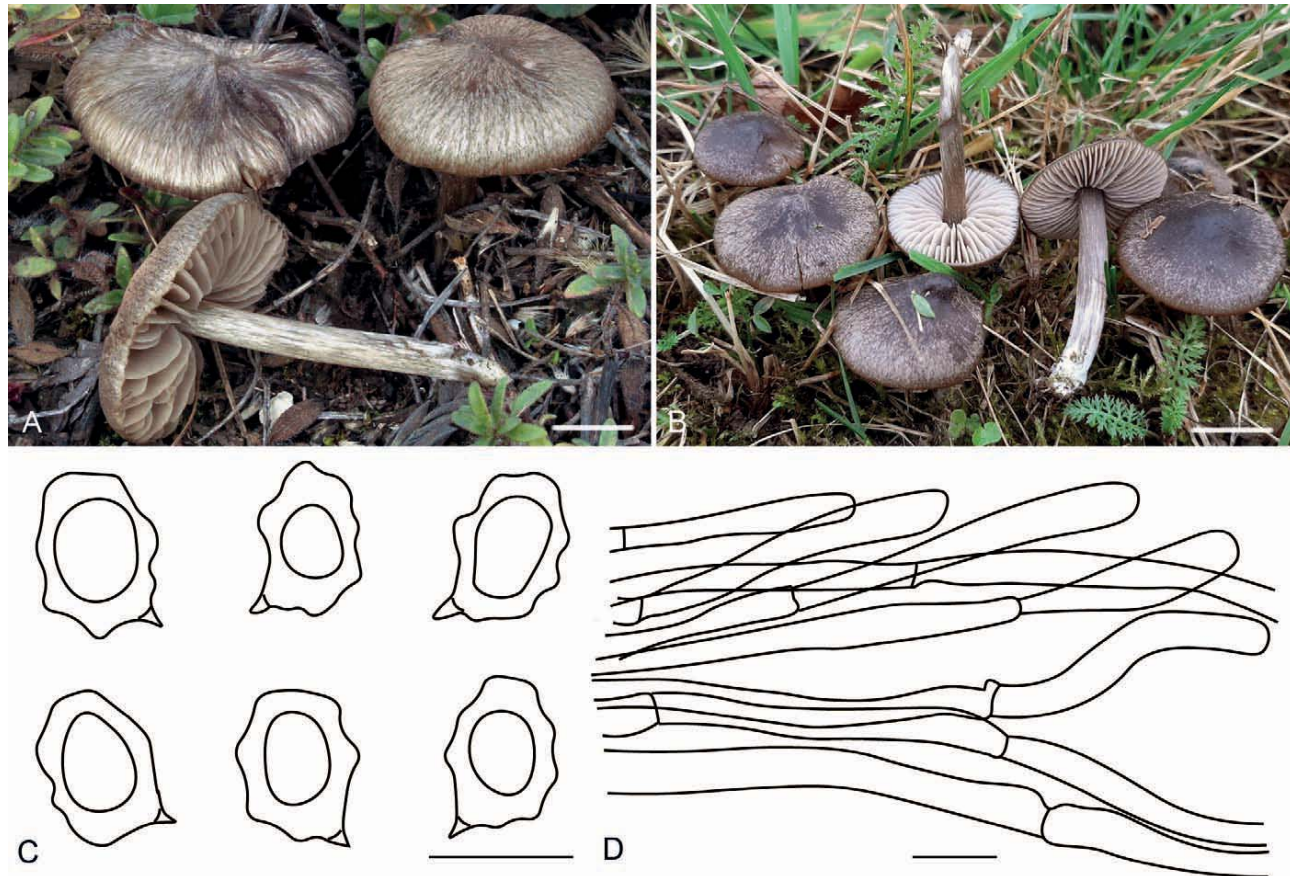


Fig. 9. *Entoloma triste* (A, C, D. L0607238, epitype; B. B 70 0105496). **A, B.** Habit. **C.** Basidiospores. **D.** Pileipellis. Photos: A by B. Dima; B by A. Gminder. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores), 20 µm (pileipellis).



× 2–5 mm, cylindrical, pale brown, often much paler than pileus, distinctly fibrillose with paler longitudinally fibrillose covering. *Context* thin, concolourous. *Smell* and *taste* not distinctive. *Basidiospores* (50/3) 9.5–11.5(–12.0) × 6.0–7.5 µm, on average 10.4–11.2 × 6.7–7.0 µm, Q = 1.20–1.60, Q_{av} = 1.25–1.35, nodulose-angular in side view. *Basidia* 29–48 × 7–11 µm, 4-spored, clamped. Lamella edge fertile. *Cheilocystidia* not observed. *Hymenophoral trama* regular, made up of medium-sized, cylindrical elements, 90–150 × 4–16 µm. *Pileipellis* a cutis with transitions to a trichoderm of 8–22 µm wide, cylindrical to subclavate elements; pigment intracellular, brown. *Stipitipellis* a loose cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present.

Habitat and distribution: In small groups in exposed, xerophytic semi-natural grasslands, apparently mainly in continental, more or less steppe-like sites. Probably widespread in Central Europe, with an outpost in Northern Europe. ITS sequence verified from Germany, Hungary, Norway, and surprisingly New Zealand.

Additional material examined: **Germany**, Baden-Württemberg, Aschaffenburg, 17 Nov. 2021, A. Gminder, AG2021 (B 70 0105496). **Hungary**, Bács-Kiskun, Kecskemét, Méntelek, in pasture, 21 Apr. 2006, L. Nagy, NL-5190 (SZMC), LSU sequence, GenBank MK278015 (Varga *et al.* 2019). **Norway**, Innlandet, Oppland, Vågå, Sandehorten,

calcareous dry meadow, near forest edge, 7 Sep. 2005, J.B. Jordal, JBJ-3030 (O-F-158210).

Notes: *Entoloma triste* is a small, robust mycenoid to tricholomatoid species, characterised by its umbonate pileus, and fibrillose stipe. Wölfel & Noordeloos (1997a) presented a wide concept of *E. triste*, including collections with the typical nodulose spores, and collections with angular spores. Now it appears that this concept is based on a mixture of different taxa. So, there is a need for an amended description. Since the holotype material is stored in liquid, and in a very poor state, it was decided to designate an epitype from Hungary, that fits the original diagnosis.

Entoloma umbrinotinctum Dima, Noordel., Benkő, E. Molnár & Vajda **sp. nov.** MB 860385. Fig. 10.

Etymology: *umbrinus* (Lat.) – umber brown, *tinctus* (Lat.) – coloured. Referring to the colour of the basidiomata.

Typus: **Hungary**, Veszprém, Bakony Mts, Bakonybél, on soil, under *Fagus* and *Fraxinus*, 2 May 2021, E. Molnár & Ru. Molnár, ME-2021-05-02 (**holotype**, L0607187); ITS sequence, GenBank PX412070.

Description: *Basidiomata* omphalinoid. *Pileus* 10–20 mm wide, convex-umbilicate with deflexed then straight margin, not hygrophanous, uniformly dark umber brown to



Fig. 10. *Entoloma umbrinotinctum* (A, C, D. ME-2021-05-02, holotype; B, E. VL-2021-04-22). **A, B, E.** Habit. **C, D.** Basidiospores. Photos: A by Ru. Molnár; B, E by L. Vajda; D by E. Molnár. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores).



blackish brown, covered with silvery radially arranged fibrils, translucently striate up to half the radius. Lamellae moderately distant ($L =$ about 25–30, $l = 1$ –3), adnate-emarginate with distinct decurrent tooth, initially greyish, then brownish-cream, later pinkish brown, with concolourous, eroded edge. Stipe 20–40 $\times$ 2–3, cylindrical, very dark brown like the pileus or slightly paler, pubescent when young, glabrescent with age and polished, at least in the upper part, basal part sometimes covered with white mycelium. *Context* concolourous with surface. *Smell* indistinct, *taste* not noted. *Basidiospores* (50/3) 7.5–12.0 $\times$ 4.0–9.5 μm , on average 10.0 $\times$ 6.7 μm , $Q = 1.10$ –1.90, $Q_{\text{av}} = 1.35$ –1.5, nodulose-angular in side view with rounded angles, very irregularly shaped. *Basidia* 22–40 $\times$ 7–11 μm , 4- rarely 2-spored, clamped. *Lamella edge* fertile; cystidia not observed. *Hymenophoral trama* regular, made up of cylindrical elements, 50–160 $\times$ 4–12 μm . *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical, 5–12 μm wide hyphae with cylindrical to inflated terminal elements, 40–110 $\times$ 5–18 μm ; pigment brown. *Stipitipellis* a thin cutis of cylindrical, 4–12 μm wide hyphae; caulocystidia absent. *Clamp-connections* seen in hymenium, but elsewhere seemingly lacking.

Habitat and distribution: Two collections were found in alluvial forests with *Fraxinus*, *Salix* and/or *Populus*. One collection originates from a warmer/drier site with *Quercus* and *Fraxinus*, another one from a cooler/moister habitat with *Fagus* and *Fraxinus*. So far only known from a few localities in springtime from West, South and Northwestern Hungary.

Additional material examined: **Hungary**, Komárom-Esztergom, Vértes Mts, Szárliget, on soil, near *Fraxinus*,

Quercus, 21 Apr. 2023, L. Vajda, VL-2023-04-21-3 (L0607188); Somogy, Belső-Somogy, Somogyudvarhely, on soil, in alluvial forest with *Salix*, *Populus* and *Fraxinus*, 22 Apr. 2021, L. Vajda, VL-2021-04-22 (ELTE); Vas, Sárvár, Szatmár-erdő, on soil, in alluvial forest, near *Cornus mas*, *Fraxinus excelsior*, *Quercus*, *Juglans nigra*, 7 May 2022, G. Benkő, K. Fábrics & R. Balka, BG-2022-05-07 (ELTE).

Notes: *Entoloma umbrinotinctum* is distinctive with its very dark and slender basidiomata (sometimes resembling *E. politum* from subgenus *Entoloma*), umbilicate pileus, relatively distant lamellae, and nodulose-angular, elongate spores.

***Entoloma undulatosporum* Arnolds & Noordel., Persoonia 10: 295. 1979. amend. MB 313841. Fig. 11.**

Synonym: *Entoloma farinasprellum* Arnolds, *Biblioth. Mycol.* 90: 329. 1982. MB 109414.

Etymology: The name refers to the undulate outline of the spores.

Typus: **The Netherlands**, prov. Drenthe, Beilen, along Linthorst-Homan Channel, in mossy short-grazed grassland on dry, acidic sandy soil, 11 Oct. 1976, E.J.M. Arnolds, Arnolds 3624 (**holotype** L0053513); ITS sequence, GenBank PX412020.

Description (amended here): *Basidiomata* collybioid. *Pileus* 5–30 mm wide, campanulate, conico-convex or convex then expanding, truncate with slightly to distinctly depressed centre, with incurved then deflexed margin, hygrophanous,

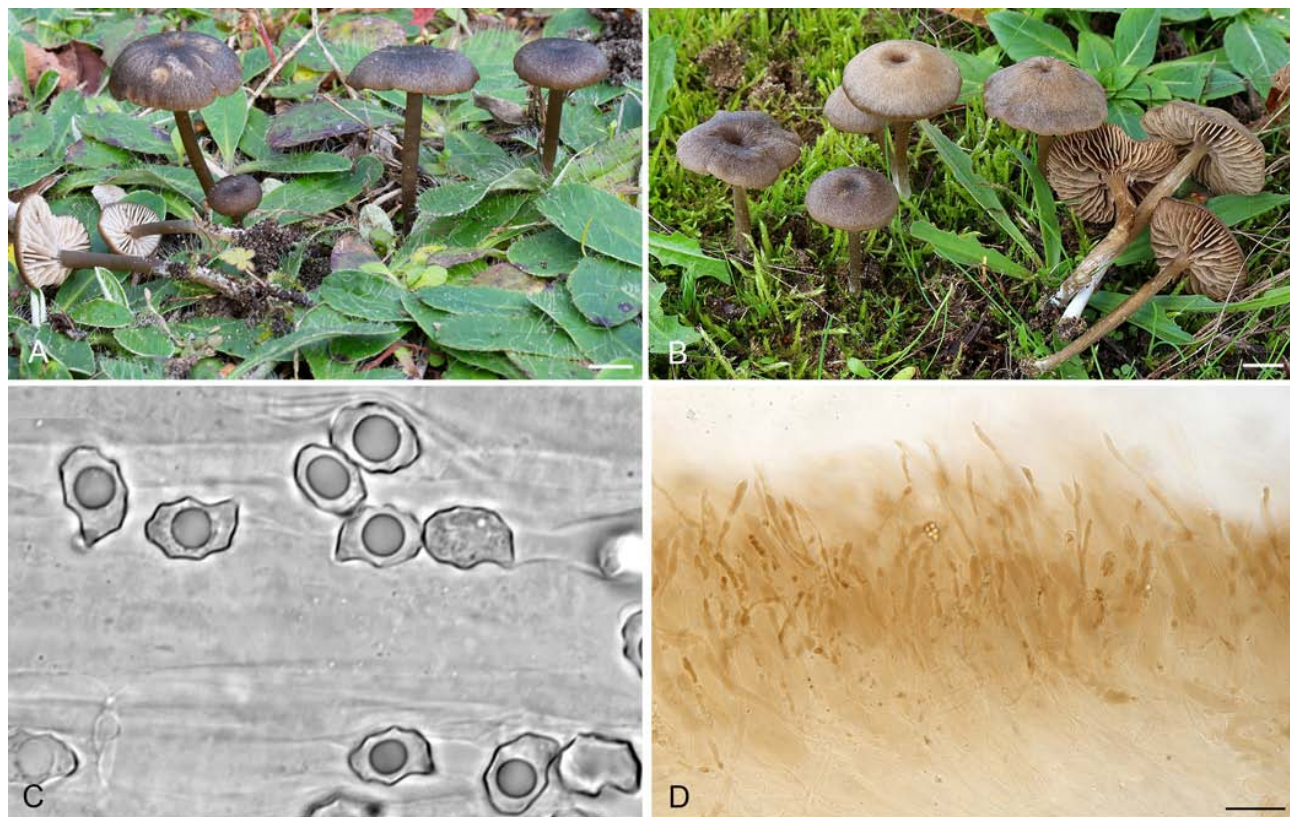


Fig. 11. *Entoloma undulatosporum* (A, C, D. L0607697; B. L0607427). **A, B.** Habit. **C.** Basidiospores. **D.** Pileipellis. Photos: A by H. Huijser; B by R. Enzlin; C, D by G.M. Jansen. Scale bars: 1 cm (habit), 10 μm (spores), 40 μm (pileipellis).



when moist dark grey brown, sepia, or blackish brown, sometimes with a slight olivaceous tinge, often slightly paler at the margin, translucently striate at margin only or up to centre, pallescent on drying to grey brown, shining, finely radially fibrillose, fibrillose to minutely squamulose at centre. *Lamellae* moderately distant ($L = 20\text{--}30$, $l = 1\text{--}3$), broadly adnate with decurrent tooth or adnate–emarginate to narrowly adnate, segmentiform to ventricose, pale grey brown then sordid pinkish brown or pinkish grey, with entire, slightly paler or concolourous edge. *Stipe* $20\text{--}35 \times 1\text{--}4$ mm, cylindrical or compressed, brown or olivaceous brown, usually somewhat paler than pileus, glabrous, polished, white tomentose at base. *Context* very thin, concolourous with surface. *Smell* and *taste* indistinctive or distinctly farinaceous. *Basidiospores* ($120/8$) $7.5\text{--}11.0 \times 5.5\text{--}7.0(-8.0)$ μm , on average $8\text{--}10 \times 6\text{--}7$ μm , $Q = 1.20\text{--}1.70$, $Q_{\text{av}} = 1.35\text{--}1.45$, heterodiametrical, irregularly 6–8 to many-angled or nodulose in side view, very thin-walled, slightly cyanophilous. *Basidia* $20\text{--}60 \times 6\text{--}11$ μm , clavate or constricted-clavate, 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Hymenophoral trama* regular, made up of more or less cylindrical elements, $50\text{--}120 \times 7\text{--}16$ μm . *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical to inflated hyphae, $8\text{--}15$ μm wide with inflated terminal elements, up to 25 μm wide; pigment brown, intracellular. *Stipitipellis* a cutis of cylindrical hyphae, $3.5\text{--}15$ μm wide with pale yellow brown intracellular pigment; caulocystidia absent. *Clamp-connections* usually abundant in hymenium, more scattered in all other tissues, exceptionally clampless (L0608395).

Habitat and distribution: Solitary or in small groups in semi-natural, xerophytic or moist grasslands and subalpine/subarctic heaths, from the lowland and Mediterranean up into the alpine zone, also in arctic sites (Norway, Svalbard), often in richer to calcareous soils (at least in northern regions). Widespread, from basidiomata data it is known from Denmark, Finland, Germany, Italy, Norway, Spain, Sweden, and The Netherlands, while based on environmental sequences *E. undulatosporum* occurs also in Estonia, Latvia, North Korea, Russia, and Pakistan.

Additional material examined: **Finland**, Outer Ostrobothnia, Rovaniemi, Muurola hospital area, grassland/lawn with *Pinus*, quite long continuity, 20 Sep. 2022, *T. Kekki*, Kekki3824 (L0607391). **Germany**, Mecklenburg-Vorpommern, Schlakendorf, Kiesgrube, 4 Nov. 2022, *A. Karich* (GLM-F139796). **Italy**, Tuscany, Castiglion Fiorentino, St. Stefano, 22 Oct. 2010, *M. Dondl*, MD5 (L0607300); Alto Adige, Roncegno, Cinque Valli, in mixed forest of *Castanea* and *Carpinus*, Sep. 1992, *A. Hausknecht* (WU-Myc 43609). **Norway**, Svalbard, Nordenskiöld Land, Hiorth hamn – Moskuslaguna, rich plain with moist places, grasses, *Salix* and *Bistorta*, 9 Aug. 2015, *A. Molia*, AM-35-2015 (O-F-260136). **Spain**, Mallorca, St. Elm, in Mediterranean shrub vegetation, 16 Dec. 2011, *J. Kleine*, *F. Hampe*, ENT11121601 (B 70 0105492). **Sweden**, Lule lappmark, Jokkmokk, Padjelanta NP, Arralåbuddå, 11 Aug. 2016, *J. Olsson*, JO160811 (GB-0207762). **The Netherlands**, prov. Drenthe, Beilen, Smalbroek, in dry grassy heathland on acid, nutrient poor soil, Nov. 1976, *J.M. Arnolds*, Arnolds3750 (L053742, **holotype** of *E. farinasprellum*; ITS sequence, GenBank PX412014); prov. Noord-Brabant, Nuenen, along cycling

path to Dierenrijk, 29 Oct. 2019, *H. Huijser* HU06 (L0607969); prov. Groningen, Wollinghuizen, Graveyard, 17 Oct. 2020 *R. Enzlin* ENZ200048 (L0607427).

Notes: The main characteristics of *E. undulatosporum* are the dark brown to almost black, often slightly to distinctly umbilicate pileus, the glabrous, polished stipe and the relatively small, thin-walled, many-angled spores with an undulate outline. Among the many collections labelled as *E. undulatosporum*, several other undescribed species appeared to be hiding after the molecular studies. Therefore, an amended description is made, based on sequence-verified material only. *Entoloma farinasprellum*, described from a similar habitat, appeared to be conspecific with the type of *E. undulatosporum* based on the analysis of the ITS sequences. This makes sense when comparing the original description. The epithet *farinasprellum* referred to the likeness with *E. asprellum*, a species in subgen. *Cyanula*, with a more or less similar habit and polished stipe, and the obvious farinaceous smell, which is unusual for *Cyanula* species (Noordeloos *et al.* 2022a). *Entoloma griseopulchrum*, described below, is rather similar, but differs by the umbonate pileus, fibrillose stipe, somewhat narrower spores and a distinct phylogenetic position.

/Alboleptonia clade – subgen. *Alboleptonia*

Entoloma* subgen. *Alboleptonia (Largent & R.G. Benedict) Noordel., *Persoonia* **10**: 246. 1979. MB 860360.

Basionym: *Alboleptonia* Largent & R.G. Benedict, *Mycologia* **62**(3): 439. 1970. MB 17036.

Synonym: *Rhodophyllus* subgen. *Alboleptonia* (Largent & R.G. Benedict) Romagn., *Beih. Nova Hedwigia* **59**: 59. 1979. MB 860361.

Type species: *Entoloma sericellum* (Fr.) P. Kumm.

The /Alboleptonia clade coincides with the current morphology-based concept of subgenus *Alboleptonia*. The basidiomata of this clade are usually white or pale coloured, or with ochre yellow or pale brown tinges, some are pink. It is a diverse group and is widespread all over the globe (Largent & Benedict 1970, Romagnesi & Gilles 1979, Horak 1980, Noordeloos 1987, 1992, 2004, Manimohan & Leelavathy 1988, Baroni & Lodge 1998, Henkel *et al.* 2011, Reschke *et al.* 2022a). In Europe, at least 11 phylogenetic species are currently distinguished, of which six are described as new below. *Entoloma sericellum* is neotypified, and an amended description is given. While morphological separation of these whitish species is not always easy, the ITS barcode differences are often large, and is helpful for identification. The phylogenetic tree (Fig. 12) includes several extralimital species. So far, we have not seen any European species being recorded from other continents, but on the contrary, the extralimital species included usually form well-supported clades of their own.

Entoloma albostriatum Brandrud, Noordel. & Dima, **sp. nov.** MB 860415. Fig. 13.

Etymology: *albus* (Lat.) – white, *striatus* (Lat.) – translucently striate, referring to the white, translucently striate pileus.

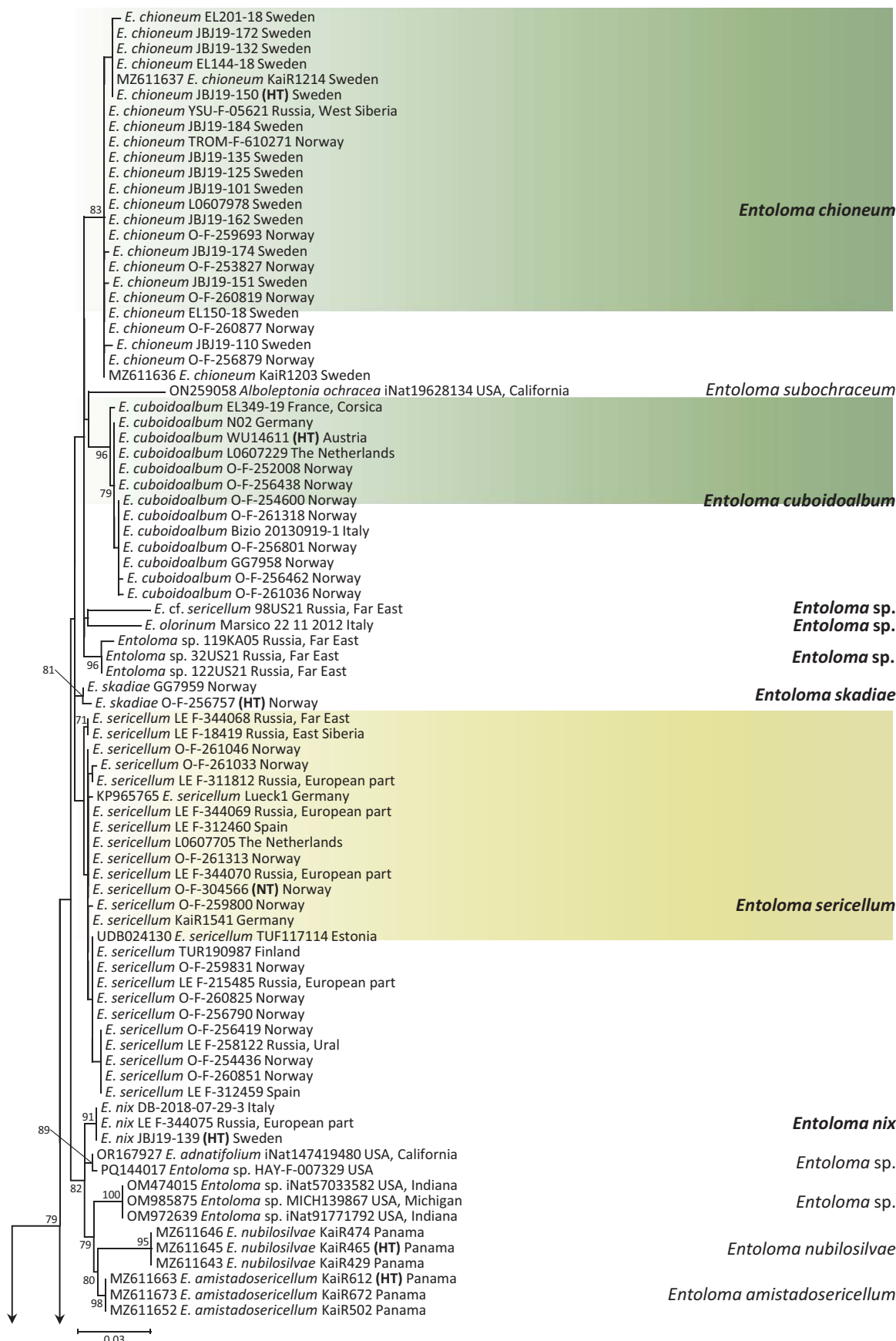


Fig. 12. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* subgen. *Alboleptonia* (= *Alboleptonia* clade). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.

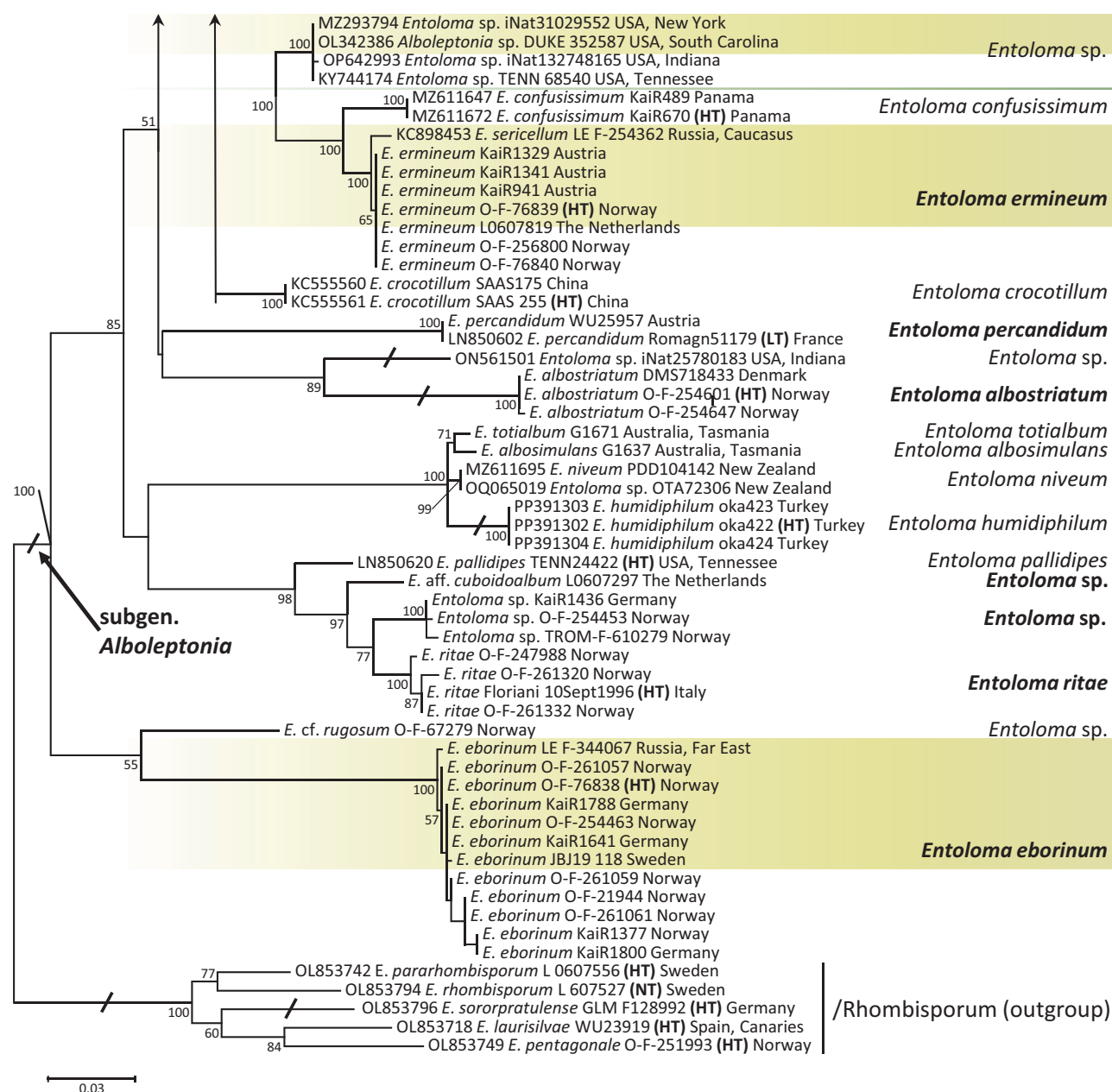


Fig. 12. (Continued).

Typus: **Norway**, Telemark, Porsgrunn, Kolbjørn-Frierflogene NW, on soil in calcareous *Corylus-Fraxinus* forest, 21 Sep. 2015, T.E. Brandrud & B. Dima, TEB 454-15 (**holotype** O-F-254601); ITS sequence, GenBank PX412021.

Description: *Basidiomata* minute, omphalinoid. *Pileus* 5–10 mm wide, convex then flattened, slightly to distinctly umbilicate, with deflexed margin, hygrophanous, white when moist or tinged pink, translucently striate to centre, becoming more or less opaque, dull-coloured upon drying, smooth, glabrous. *Lamellae* very distant ($L = 14\text{--}20$, $I = 1\text{--}3$), adnate-decurrent, white then pink with concolourous, entire edge. *Stipe* 20–25 × 1–2 mm, cylindrical, white, smooth, dull, not polished. *Context* very thin, brittle. *Smell* indistinct, *taste* not noted. *Basidiospores* (30/2) 9.5–15.0 × 7.0–9.0 µm, on average 12.40 × 7.80 µm, $Q = 1.35\text{--}1.85$, $Q_{av} = 1.50\text{--}1.60$, heterodiametrical, irregularly 7–9-angled with blunt angles.

Basidia 20–45 × 6–11 µm, 4- and 2-spored, clamped. *Lamella edge* heterogeneous with abundant, spread or clustered cheilocystidia, 40–80 × 4–10 µm, fusiform to lageniform, protruding from the hymenium. *Hymenophoral* and *pileitrama* regular, made up of short, inflated elements, 50–120 × 5–15 µm. *Pileipellis* a cutis of cylindrical, 5–15 µm wide hyphae, with scattered inflated terminal elements ("pileocystidia"), 40–70 × 7–17 µm. Pigment absent. *Stipitipellis* not observed. *Clamp-connections* rare, only seen in hymenium.

Habitat and distribution: So far known only from Denmark and Norway. The Norwegian collections were from margins of calcareous *Corylus-Fraxinus* and *Pinus* forests. The Danish collection grew on dead stems in an intensely studied coastal, scrubby plot (40 × 40 m) with more than 200 macro-fungal species recorded in three visits, hereof at least 19 species of *Entoloma* (T. Læssøe pers. comm.).



Additional material examined: **Denmark**, Sjælland, Eskebjerg Vesterlyng, Biowide 089, on rotten herbaceous stems in calcareous coastal scrub, 23 Sep. 2015, *T. Læssøe*, DMS-718433 (C). **Norway**, Telemark, Bamble, Røsskleiva NR north, grassy margin of calcareous *Pinus* forest, along small road (ski track), 14 Aug. 2016, *T.E. Brandrud* & *B. Dima*, TEB209-16 (O-F-254647).

Notes: *Entoloma albostriatum* is characterized by rather tiny, omphalinoid basidiomata, with hygrophanous, translucently striate pileus, large spores, and scattered large pileocystidia-like structures. It resembles *E. percandidum*, from which it differs by the much larger and almost nodulose-angular spores and presence of cheilocystidia. The lectotype of *E. percandidum* (Noordeloos 1987) has not successfully been

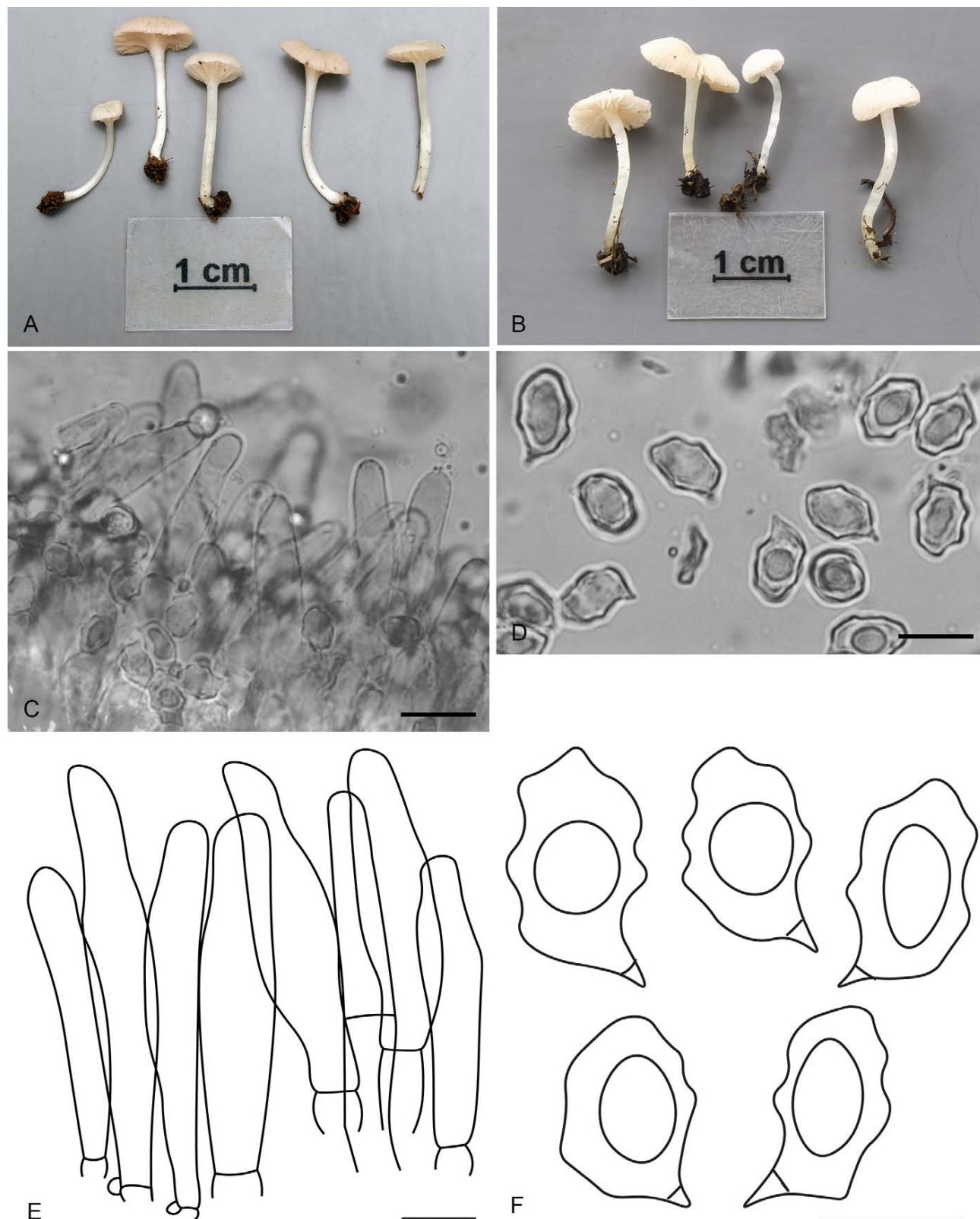


Fig. 13. *Entoloma albostriatum* (A, C–F. O-F-254601, holotype; B. TEB 209-16). **A, B.** Habit. **C, E.** Cheilocystidia. **D, F.** Basidiospores. Photos: A, B by B. Dima; C, D by M.E. Noordeloos. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores and cheilocystidia).



sequenced, but Kokkonen (2015) got an ITS barcode of a later collection, mentioned in the protologue. This sequence, GenBank LN850602, is definitely different from that of *E. albostriatum*. The current status of *E. percandidum*, however, is poorly known due to the lack of well-documented and sequenced material. *Entoloma olorum* sensu Noordeloos (1987) has some resemblance, but differs microscopically by the shorter, subisodiametrical spores and lack of cystidia. On the other hand, *E. olorum* in the original sense (based on *Rhodophyllus olorus*) was described as an *Alboleptonia* close to *E. sericellum*, but with a deeply translucently, striate pileus, slightly smaller, 5–6-angled spores and fertile lamella edge. A full description was given by Noordeloos (1987), based mainly on material from The Netherlands and Belgium. However, the lectotype of *E. olorum* turned out to be identical with that of *E. nidorosum* from subgen. *Entoloma*, and probably represents a dwarfish, white form of that species.

Since none of the collections cited by Noordeloos (l.c.) could be sequenced, it is hard to tell whether this concept of *E. olorum* is homogeneous or a mixture of species. Among the species described in this paper, *E. albostriatum* comes closest, but has much larger spores and well-developed cheilocystidia.

Entoloma chioneum J.B. Jordal, Reschke, Noordel., E. Larss., Dima & N. Filippova, *sp. nov.* MB 860398. Fig. 14.

Etymology: χιών (Greek) – “snow”, referring to the white basidiomata, and occurrence in snow-rich, alpine habitats.

Typus: Sweden, Åsele lappmark, Vilhelmina, Frimtsjåkke, on soil in calcareous alpine heath, 22 Aug. 2019, J.B. Jordal & E. Larsson, JBJ19-150 (**holotype** GB-0107743); ITS sequence, GenBank PV018320.



Fig. 14. *Entoloma chioneum* (A. JBJ19-150, holotype; B, D–F. EL75-18; C. JBJ19-151). A–C. Habit. D. Cheilocystidia. E, F. Basidiospores. Photos: A–C by J.B. Jordal; D, E by G.M. Jansen. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores).



Description: *Basidiomata* mycenoid to omphalinoid. *Pileus* 5–15 mm wide, conico-convex or hemispherical then convex, with blunt centre, white, not hygrophanous or translucently striate (when young), opaque, innately radially fibrillose, silky shining, becoming slightly pinkish yellow and translucently striate and glabrous with age. *Lamellae* very distant ($L = 10\text{--}16$, $I = 3\text{--}7$), adnate-decurrent, white then pink, with concolourous, subentire edge. *Stipe* 20–40 × 1–2(–3) mm, cylindrical, white, glabrous. *Context* thin, white, brittle. *Smell* and *taste* not noted. *Basidiospores* (200/18) 7.0–9.5(–10.0) × 5.5–8.0, on average 8.9–9.1 × 6.8–7.0 µm, $Q = 1.05\text{--}1.50$, $Q_{av} = 1.25\text{--}1.30$, 5–6-angled in side view with regular angles. *Basidia* 20–36 × 6–12 µm, 4-spored, clamped. *Lamella edge* sterile or heterogeneous, with abundant subcylindrical to lageniform cheilocystidia, 35–65 × 4–10 µm. *Hymenophoral trama* regular, elements sausage-shaped, 40–110 × 5–20 µm. *Pileipellis* a thin cutis of cylindrical hyphae with inflated terminal elements, 4–14 µm wide; pigment absent. *Stipitipellis* a cutis of cylindrical 4–9 µm wide hyphae. *Caulocystidia* absent. *Clamp-connections* rare to abundant.

Habitat and distribution: In groups in montane and subarctic heathlands, alpine meadows with dwarf *Salix* and *Betula nana*. Mainly alpine, some middle-northern boreal; so far verified from North Sweden, North and South Norway and West Siberia.

Additional material examined: **Norway**, Innlandet, Oppland, Vang, gamle kongevei, moist margin of old track road with grass and herbs (middle/northern boreal zone), 16 Aug. 2019, *E. Bendiksen*, KB&EB 69/19 (O-F-256879); Nordland, Alstahaug, Tjøtta, calcareous semi-natural grassland, 29 Aug. 2020, *J.B. Jordal*, JBJ20-E22 (O-F-260819); Troms, Karlsøy, Reinøya, Nordeidet, grazed mountain slope, 21 Aug. 1999, *V. Ravolainen*, VTR 88-99 (TROM-F-610271); Troms, Kåfjord, Manndalen, Lilledalen, low herb birch forest, 24 Jul. 2022, *G. Gaarder & J.O. Olsen*, GG8096 (O-F-259693); Trøndelag, Steinkjer, Kvamshaugen, Ryggadalen, margin of forest road, 20 Aug. 2016, *E. Bendiksen & B. Dima*, EB 82/16 (O-F-253827); Trøndelag, Sør-Trøndelag, Oppdal, Søndre Knutshø, calcareous alpine heath, 15 Aug. 2020, *G. Gaarder & P.G. Larsen*, GG7827 (O-F-260877). **Sweden**, Pite Lappmark, Arjeplog, west of Nuorta Krapesvarre, in rich alpine vegetation, 12 Aug. 2018, *J.B. Jordal & E. Larsson*, EL75-18 (GB-0207756) – ITS sequence, GenBank PV018334; Pite Lappmark, Arjeplog, NE side of Mt. Åkháris, alpine meadow on calcareous soil, 14 Aug. 2018, *J.B. Jordal & E. Larsson*, EL144-18 (GB-0207754); *ibid.*, *J.B. Jordal & E. Larsson*, EL150-18 (GB-0207753); Pite Lappmark, Arjeplog, Rijvatahkka, 15 Aug. 2018, *E. Larsson*, EL201-18 (GB-0207750); Åsele lappmark, Vilhelmina, Lasterfjället, Tjårnunjes, in alpine meadow on calcareous ground, 19 Aug. 2019, *J.B. Jordal*, JBJ19-101 (GB-0207757); *ibid.*, *J.B. Jordal*, JBJ19-110 (GB-0207755); Åsele lappmark, Vilhelmina, Murfjället, in alpine heath on calcareous ground, 20 Aug. 2019, *J.B. Jordal*, JBJ19-125 (GB-0207758); *ibid.*, *J.B. Jordal*, JBJ19-132 (GB-0207747); *ibid.*, *J.B. Jordal*, JBJ19-135 (GB-0207741); Åsele Lappmark, Vilhelmina, Frimtsjakke, in low alpine vegetation on calcareous soil, 22 Aug. 2019, *J.B. Jordal*, JBJ19-151 (GB-0207759); Jämtland, Frostviken, NW slope of Raavre, in low alpine calcareous heath 23 Aug. 2019, *J.B. Jordal*, JBJ19-162 (GB-0207748);

ibid., *J.B. Jordal*, JBJ19-172 (GB-0207751); *ibid.*, *J.B. Jordal*, JBJ19-174 (GB-0207749); *ibid.*, *J.B. Jordal*, JBJ19-184 (GB-0207752); Västernorrlands län, Kullen mountain, on soil in oligotrophic grassland grazed by sheep, 26 Aug. 2018, *K. Reschke*, KaiR1203 (M); *ibid.*, KaiR1214 (M). **Russia**, Khanty-Mansi Autonomous Okrug, Khanty-Mansiysk District, near Shapsha Village, on soil in mixed shrub vegetation and poorly developed undergrowth, 28 Jul. 2015, *N. Filippova*, YSU-F-05621 (dupl. LE F-343351).

Notes: *Entoloma chioneum* differs from *E. sericellum* particularly by the initially purely white, but later slightly yellowish-ochre tinged, innately fibrillose pileus, and somewhat smaller, 5–6-angled spores. It is the most common *Alboleptonia* in alpine regions of Northern Europe and seems to be a mainly (but not strictly) northern species, growing in alpine and mostly northern boreal localities in northern and central parts of Norway and Sweden. It has never been found in the rather well investigated areas of South Scandinavia. In addition, there is one sequence-verified record from the Siberian taiga.

Entoloma eborinum *J.B. Jordal, O.V. Morozova, Reschke, Noordel., Bendiksen & Dima, sp. nov.* MB 860410. Fig. 15.

Etymology: *eborinus* (Lat.) – referring to the ivory-coloured pileus.

Typus: **Norway**, Trøndelag, Sør-Trøndelag, Ørland, Tarva, Været, on soil in calcareous, semi-natural pasture, 25 Sep. 2020, *J.B. Jordal*, JBJ20-E83 (**holotype** O-F-76838); ITS sequence, GenBank PX412033.

Description: *Basidiomata* collybioid. *Pileus* 10–15 mm wide, convex to plano-convex, ivory to flesh coloured, somewhat hygrophanous, pallescent from the margin, bicoloured, centre may retain the original darker colour for a longer time, and there may also be a transitional phase with concentric paler and darker zones, never translucently striate, smooth, glabrous. *Lamellae* rather distant ($L = 20\text{--}25$, $I = 3\text{--}5$), adnate to adnate-decurrent, white then pink with a more or less serrulate, concolourous edge. *Stipe* 20–40 × 1–2.5 mm, cylindrical, glabrous, polished. *Context* brittle. *Smell* indistinct, *taste* not noted. *Basidiospores* (140/10) 7.5–11.0 × 6.0–7.5 µm, on average 9.0–9.6 × 6.9–7.1 µm, $Q = 1.20\text{--}1.60$, $Q_{av} = 1.30\text{--}1.40$ heterodiametrical, 5–6-angled in side view. *Basidia* 25–41 × 6–10 µm, 4-spored, clamped. *Lamella edge* sterile. *Cheilocystidia* subcylindrical to narrowly clavate or lageniform, 25–45 × 6–10(–15) µm, about as long as the basidia. *Hymenophoral- and pileitrama* regular, made up of cylindrical to slightly inflated (sausage-shaped) elements, 35–110 × 5–20 µm. *Pileipellis* a narrow cutis of cylindrical hyphae, 5–15 µm wide, without visible pigmentation. *Clamp-connections* present but sparse – in all tissues.

Habitat and distribution: In semi-natural pastures on calcareous soil, sometimes also in natural, calcareous, shallow soil grasslands, also recorded in alpine calcareous heath and along a riverbank. So far known from Norway, Sweden, Germany and the Russian Far East (Kamchatka). Apparently not rare in Scandinavia. The wide variation in recorded habitats indicates that this species probably has a



much wider geographical distribution and, in the past, it might have been recorded as *E. sericellum* coll.

Additional material examined: **Germany**, Hessen, Goldsteintal, near Wiesbaden, on soil in oligotrophic grassland, 12 Nov. 2022, *K. Reschke*, KaiR1641 (B 70 0105523); *ibid.*, 28 Oct. 2023, KaiR1788 (B 70 0105526); *ibid.*, 28 Oct. 2023, KaiR1800 (B 70 0105527). **Norway**, Oslo, Bygdøy, Rodeløkken, open calcareous meadow on shallow soil, 31 Aug. 2017, *E. Bendiksen*, 162/17 (O-F-254463); Telemark, Porsgrunn, Heistad, Lundebukta, open calcareous meadow on shallow soil, 11 Oct. 2013, *A. Molia & T. Læssøe*, AM-252f-2013 (O-F-21944); Vestland, Hordaland, Bømlo, Brandasund, semi-natural grassland, 29 Sep. 2021, *J.B. Jordal & P. Fadnes*, JBJ21-105 (O-F-261059); Vestland, Hordaland, Stord, Hovaneset, calcareous semi-natural grassland, 28 Sep. 2021, *J.B. Jordal & P. Fadnes*, JBJ21-101 (O-F-261057); Vestland, Hordaland, Stord, Nautøya,

on soil in coastal grassland, 6 Sep. 2019, *K. Reschke*, KaiR1377 (B 70 0105518); Vestland, Sogn og Fjordane, Luster, Hymavollen, semi-natural grassland, 9 Oct. 2021, *J.B. Jordal*, JBJ21-110 (O-F-261061). **Russia**, Kamchatka Krai, Bystrinsky District, near Esso Village, right bank of the Bystraya River, on grassland, 12 Aug. 2005, *O. Morozova*, 193KA05 (LE F-344067). **Sweden**, Åsele Lappmark, Vilhelmina, Lasterfjället, Tjårnunjes, calcareous alpine heath, 19 Aug. 2019, *Å. Kruys*, JBJ19-118 (GB-0207744).

Notes: *Entoloma eborinum* resembles *E. sericellum* and can be distinguished by the often rather smooth pileus that is ivory to pale flesh coloured when fresh, a polished stipe, small, 5–6-angled spores and a sterile lamella edge with rather inconspicuous cheilocystidia.

Entoloma ermineum J.B. Jordal, O.V. Morozova, Noordel. & Dima, *sp. nov.* MB 860419. Fig. 16A–C, E.



Fig. 15. *Entoloma eborinum* (A. JBJ21-101; B. JBJ22-230; C–E. O-F-76838, holotype). **A, B.** Habit. **C.** Basidiospores. **D, E.** Cheilocystidia. Photos: A, B by J.B. Jordal; E by M.E. Noordeloos. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores and cheilocystidia).



Etymology: *ermineus* (Lat.) – white with a touch of yellow, reminiscent of the cap-colour of *Lepiota erminea*.

Typus: **Norway**, Møre & Romsdal, Smøla, Jostøløya, on soil in semi-natural grassland, 30 Sep. 2020, J.B. Jordal, JBJ20-E92 (**holotype** O-F-76839); ITS sequence, GenBank PX412034.

Description: *Basidiomata* collybioid. *Pileus* 5–20 mm wide, conical, campanulate to hemispherical then convex with deflexed margin, with blunt centre, not hygrophanous or translucently striate, white, sometimes with a yellowish hue, particularly at centre, finely felt all over. *Lamellae* distant ($L = 16\text{--}20$, $I = 1\text{--}3$), adnate with decurrent tooth, white then pink with concolourous edge. *Stipe* 20–60 × 1–2 mm, cylindrical, white, dull, glabrous, apex somewhat pruinose

as seen in images. *Context* thin, brittle. *Smell* indistinct, *taste* not noted. *Basidiospores* (80/5) $8.5\text{--}11.0 \times 6.5\text{--}8.0$ μm , on average $10.0\text{--}10.7 \times 7.2\text{--}7.4$ μm , $Q = 1.20\text{--}1.55$, $Q_{av} = 1.35\text{--}1.40$, heterodiametrical, 6–7- angled in side view, with pronounced angles. *Basidia* 30–37 × 10–11.5 μm , clavate, 4-spored, clamped. *Lamella edge* heterogeneous. *Cheilocystidia* 25–65 × 5–18 μm , cylindrical, fusiform, scarce, in tufts. *Pileipellis* a cutis of cylindrical, 3–18 μm wide hyphae, with some subclavate, up to 20 μm wide terminal elements. *Stipitipellis* cutis of cylindrical, 4–10 μm wide, clamped hyphae. *Caulocystidia* in tufts at top of stipe, 60–90 × 8–17 μm , cylindrical, some with broadened apex, subclavate, clamped. *Clamp-connections* present in all tissues.

Habitat and distribution: On soil in semi-natural pastures, from coastal lowlands (West Europe) up into the subalpine



Fig. 16. A–C, E. *Entoloma ermineum* (A, C, E. O-F-76839, holotype; B. L0607819). A, B. Habit. C. Cheilocystidia. E. Basidiospores. D, F, G. *Entoloma nix* (JBJ 19-139, holotype). D. Cheilocystidia. F. Basidiospores. G. Habit. Photos: A, G by J.B. Jordal; B by M. Jagers; E, F by M.E. Noordeloos. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (spores and cheilocystidia).



zone (Central and Southeast Europe). Known from Austria, Norway, The Netherlands, and Russia (Caucasus).

Additional material examined: **Austria**, Vorarlberg, Kleinwalsertal, Walmendinger Horn, 17 Sep. 2018, K. Reschke, KaiR1341 (B 70 0105516); *ibid.*, Moosalpe, edge of a wet meadow, 16 Sep. 2018, S. Sarawi, KaiR1329 (B 70 0105515); Vorarlberg, Schwarzwasserbachthal, 23 Oct. 2017, K. Reschke, KaiR941 (B 70 0105506). **Norway**, Møre & Romsdal, Smøla, Jostøløya, semi-natural grassland, 30 Sep. 2020, J.B. Jordal, JBJ20-E101 (O-F-76840); Vestland, Sogn & Fjordane, Kinn, Refvika, medium calcareous, semi-natural grassland, 25 Sep. 2019, J.B. Jordal, JBJ19-064 (O-F-256800). **Russia**, Karachaevo-Cherkessia Republic (Caucasus), Teberda State Biosphere Reserve, Malaya Khatipara Mt, in grassland, 14 Aug. 2009, O. Morozova, 156TB09 (LE F-254362) (Morozova *et al.* 2014b, as *E. sericellum*). **The Netherlands**, prov. Overijssel, Weerselo, Lemselermaten, wet grassland on peaty soil, 16 Oct. 2019, M. Jagers, MJD19032 (L0607819).

Notes: *Entoloma ermineum* morphologically is very similar to *E. sericellum*, differing by the smoother cap surface. Both species appear to have approximately the same habitat-range. However, phylogenetically they are rather distant, and *E. ermineum* is more related to *E. confusissimum*, recently described from Panama (Reschke *et al.* 2022a) and an undescribed species from the USA (Fig. 12).

Entoloma nix Dima, J.B. Jordal, E. Larss., Noordel. & M. Palamarchuk, **sp. nov.** MB 860420. Fig. 16D, F, G.

Etymology: *nix* (Lat.) – snow, referring to the white basidiomata, and occurrence in alpine, snow-rich sites.

Typus: **Sweden**, Åsele lappmark, Vilhelmina, Fiehteres, on soil in calcareous, alpine heath, 21. Aug. 2019, J.B. Jordal & E. Larsson, JBJ19-139 (GB-0207745); ITS sequence, GenBank PV018336.

Description: *Basidiomata* collybioid. *Pileus* 10–15 mm wide, hemispherical then convex, not hygrophanous, or translucently striate, white with slight ochre yellow tinge at centre, minutely felted, subglabrous. *Lamellae* distant (L = about 20, l = 1–3), arcuate-decurrent, initially pallid whitish cream then pink, with an entire, concolourous edge. *Stipe* 20–30 × 1–2 mm, cylindrical, white, minutely pruinose at apex, downwards smooth. *Context* brittle, concolourous with surface. Smell indistinct, taste not noted. *Basidiospores* (30/2) (8.0–)8.5–11.0 × 6.5–8.0 µm, on average 8.9–10.0 × 7.0–7.2 µm, Q = 1.20–1.50(–1.65), Q_{av} = 1.15–1.45, 5–7-angled in side view with sharp angles. *Basidia* 23–40 × 6–11 µm, 4-spored, clamped. *Lamella edge* mostly sterile with dense clusters of cylindrical to lageniform or clavate cheilocystidia, 25–42 × 7–14 µm. *Pileipellis* a cutis of rather narrow, cylindrical, 6–15 µm wide hyphae, with scattered clavate terminal elements, 25–40 × 15–20 µm. *Stipitipellis* a cutis of narrow, cylindrical hyphae. *Caulocystidia* at apex of stipe only, cylindrical with rounded apex, 20–35 × 5–9 µm. *Pigment* absent. *Clamp-connections* present, but scarcely present, at least in hymenium, elsewhere not observed.

Habitat and distribution: In calcareous alpine grasslands, also found in pioneer vegetation along a riverbank. Known from North Italy, North Russia (Subpolar Ural Mountains), and North Sweden.

Additional material examined: **Italy**, South Tyrol, Solda, Madritsch, on soil in alpine environment, 29 Jul. 2018, B. Dima, DB-2018-07-29-3 (ELTE). **Russia**, Komi Republic, Intinsky District, Yugyd Va National Park, valley of the Khambaliyu River, river bank, on moss curtain, 20 Jul. 2012, M. Palamarchuk, SYKOf1707 (LE F-344075) (as *E. percandidum*, Palamarchuk 2016).

Notes: We have only very limited material of this species. The range of the spore size is the same as in *E. sericellum*, but the structure of the lamella edge differs by being (almost) entirely sterile with rather short cheilocystidia, similar to those found in the phylogenetically distant *E. eborinum*. In habitat preferences, *E. nix* resembles the mainly alpine *E. chioneum*, but this also possesses longer cheilocystidia and is also phylogenetically distant. Phylogenetically, *E. nix* belongs to a lineage with two species from Panama (*E. amistosericellum*, *E. nubilosilvae*; Reschke *et al.* 2022a) and two yet unnamed species from the USA (Fig. 12).

Entoloma percandidum Noordel., *Nordic J. Bot.* **2**(2): 161. 1982. MB 110654.

Replaced synonym: *Rhodophyllus omphaliiformis* Romagn. *Rev. Mycol. (Paris)* **19**(1): 7. 1954. MB 528890, non *Entoloma omphaliiforme* (Velen.) Noordel., *Persoonia* **10**(2): 262. 1979. MB 535080.

Typus: **France**, Seine & Oise, Chaumontel, La Charbonnière, in a marsh, 20 Aug. 1946, H. Romagnesi, Romagnesi 46.269 (**lectotype** in PC, designated in Noordeloos 1987, not sequenced).

Description (based on lectotype and Noordeloos 1987): *Basidiomata* omphalinoid. *Pileus* 4–10 mm wide, convex at first, often somewhat truncate, then expanding, but never entirely applanate, often with irregularly, undulating margin, hygrophanous, when moist deeply translucently striate, brilliantly white, opaque on drying, sometimes with slight yellow tinge with age, glabrous, finely satiny fibrillose when dry. *Lamellae* distant (L = 10–16, l = 1–3), often thick, adnate, sometimes emarginate or subdecurrent, triangular then segmentiform or subventricose, white then pink with entire, concolourous edge. *Stipe* (13–)24–45 × 0.5–2 mm, cylindrical, straight or somewhat flexuose, white, shiny, often hyaline and tinged yellow with age. *Context* very thin, brittle. *Smell* indistinct, taste not noted. *Basidiospores* (30/2) 7.0–11.5 × 5.5–8.0 µm, on average 9.5 × 7.0 µm, Q = 1.20–1.65, Q_{av} = 1.4, 6–10-angled in side view. *Basidia* 4-spored, clamped. *Lamella edge* fertile, cystidia absent. *Pileipellis* a cutis of narrow, cylindrical hyphae. *Clamp-connections* present in hymenium.

Habitat and distribution: On soil in damp places in forests, and in semi-natural grassland. In Europe, but distribution is unknown.



Additional material examined: **France**, Seine & Oise, Chaumontel, marshy wood, 18 Aug. 1951, *Robert & Causse*, herb. Romagnesi 51179 (PC); ITS sequence, GenBank LN850602 (Kokkonen 2015).

Notes: We have not seen recent material of this species, therefore we refer to Noordeloos (1987). Kokkonen (2015) studied original material of *R. omphaliiformis* in PC, and obtained an ITS sequence of a later collection from the type locality, but unfortunately not from the lectotype. *Entoloma percardidum* resembles *E. albostriatum* that differs in having pure white basidiomata, reminiscent of a *Hemimycena*, smaller spores and no cheilocystidia, and a distant phylogenetic position.

***Entoloma sericellum* (Fr.) P. Kumm., *Der Führer in die Pilzkunde*: 97. 1871. MB 225035. Fig. 17.**

Basionym: *Agaricus sericeus* β *sericellus* Fr., *Observ. Mycol. (Havniae)* 2: 145. 1818. MB 462569.

Typus: **Holotype** not existing. **Norway**, Innlandet, Hedmark, Alvdal, at roadside South of Alvdal, 20 Aug. 2016, *E.A. Thomsen* (**neotype** O-F-304566, designated here, deposited at O, MBT 10028204); ITS sequence, GenBank PX412066.

Description: *Basidiomata* mycenoid to collybioid. *Pileus* 5–20 mm wide, hemispherical then expanding, with inflexed to deflexed margin, not hygrophanous, not translucently striate, white with yellow ochre tinge at centre, very finely felted

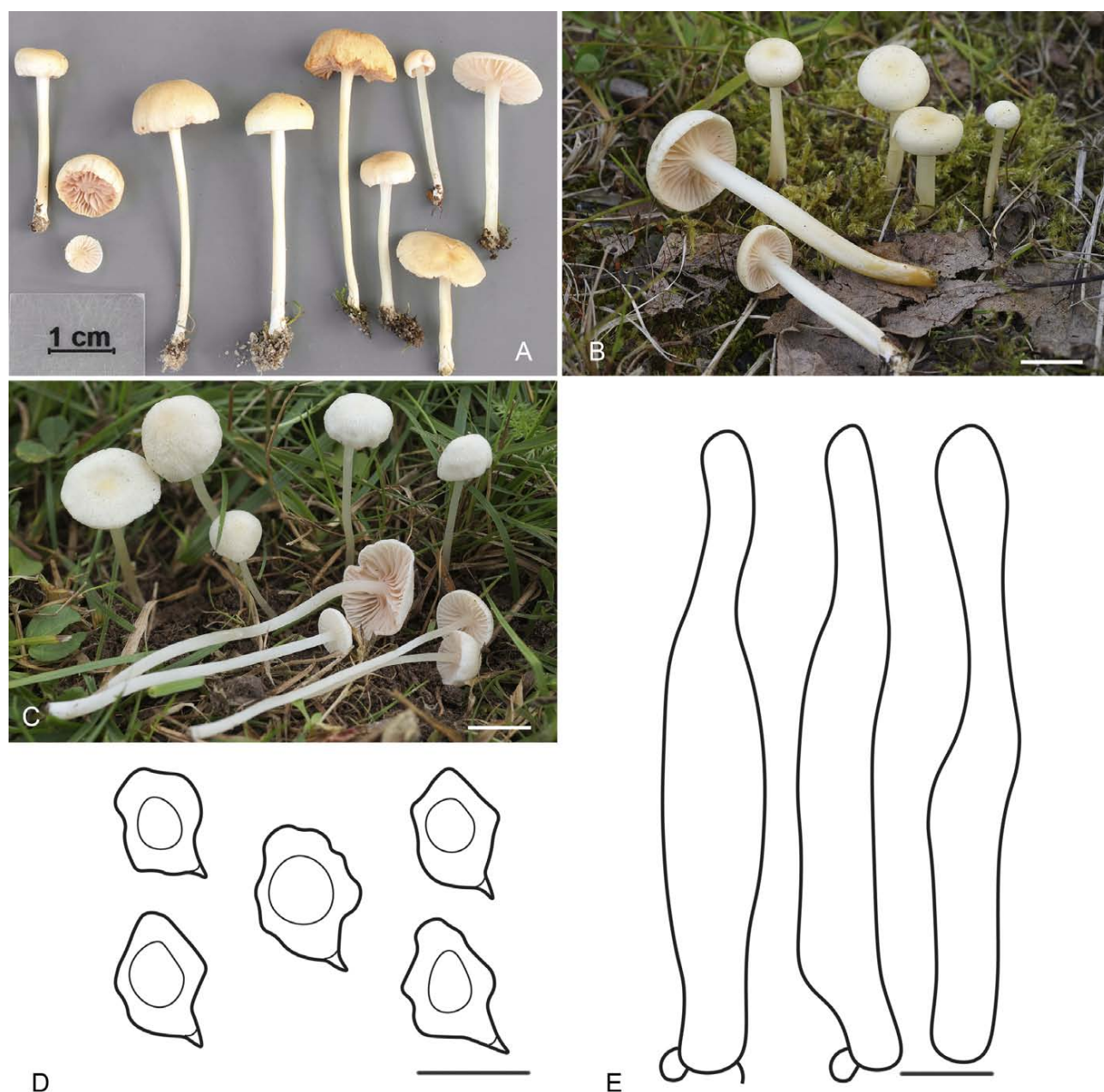


Fig. 17. *Entoloma sericellum* (A, D, E. O-F-304566, neotype; B. LE F-344070; C. LE F-311812). **A–C.** Habit. **D.** Basidiospores. **E.** Cheilocystidia. Photos: A by B. Dima; B, C by O. Morozova. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores).



to subsquamulose. *Lamellae* distant ($L = 30\text{--}40$, $L = 3\text{--}7$), adnate with decurrent tooth, purely pink with concolourous, entire edge. *Stipe* $20\text{--}40 \times 1\text{--}2$ mm, cylindrical, white to yellowish, pruinose at apex, more or less glabrous and polished below. *Context* thin, brittle, white. *Smell* and *taste* indistinct. *Basidiospores* ($200/15$) $9.5\text{--}14.0 \times 7.0\text{--}9.5$ μm , on average $10.6\text{--}11.7 \times 7.8\text{--}8.3$ μm ; $Q = 1.15\text{--}1.70$, $Q_{\text{av}} = 1.35\text{--}1.40$, heterodiametrical, 5–7-angled in side view with pronounced angles. *Basidia* $33\text{--}40 \times 9.5\text{--}12$ μm , 4-spored, clamped. *Lamella edge* heterogeneous. *Cheilocystidia* $35\text{--}50 \times 7\text{--}11.5$ μm , cylindrical, fusiform to lageniform, clamped. *Hymenophoral trama* and pileitrama regular, made up of sausage-shaped elements, $45\text{--}120 \times 5\text{--}20$ μm . *Pileipellis* is a transition between a cutis and a trichoderm, made up of cylindrical to slightly inflated hyphae, with cylindrical to clavate terminal elements, $25\text{--}90 \times 7\text{--}20$ μm ; pigment absent or very pale brown, intracellular. *Caulocystidia* $20\text{--}50 \times 5\text{--}12$ μm , subcylindrical to flexuous, mainly present at apex of stipe. *Clamp-connections* present in all tissues.

Habitat and distribution: In groups in calcareous and more oligotrophic, semi-natural grasslands, sometimes also in calcareous broad-leaved and pine forests, alpine heaths and road verges. Common and widespread in northern and temperate Eurasia.

Additional material examined (selection): **Finland**, Ostrobothnia kajanensis, Suomussalmi, ca. 7 km NW of Kiannaniemi, NW of Petäjävaara, N of the roadcross, on peaty soil, 27 Aug. 2011, J. Vauras, FIPUT323-14 (TUR190987). **Germany**, Thüringen, Arlesberg, Geratal, Schuchardswiese, on soil in nitrogen-poor grassland with abundant *Meum athamanticum* and *Plantago lanceolata*, 3 Nov. 2021, K. Reschke, KaiR1541 (B 70 0105522). **Norway**, Møre og Romsdal, Giske, Vigra: Molnes, semi-natural pasture, calcareous, 14 Sep. 2020, J.B. Jordal, JBJ20-E70 (O-F-261313); Møre og Romsdal, Sunndal, Jordalsøra, semi-natural grassland, mown, 20 Sep. 2019, J.B. Jordal, JBJ19-047 (O-F-256790); *ibid.*, Mogstad, Stortrøa, semi-natural grassland, 1 Oct. 2022, J.B. Jordal, JB22-165 (O-F-259800); *ibid.*, Tingvoll, Åkerfallet, semi-natural grassland, 13 Sep. 2021, J.B. Jordal, JB21-48 (O-F-261033); Nord-Trøndelag, Frosta, Tautra, Kuøra, semi-natural pasture, 31 Aug. 2020, J.B. Jordal, JBJ20-E64 (O-F-260851); Nordland, Alstahaug, Alstahaug: Tjøtta, semi-natural pasture, 29 Aug. 2020, J.B. Jordal, JBJ20-E32 (O-F-260825); Rogaland, Suldal, Suldal, Tveit, semi-natural pasture, 15 Sep. 2017, J.B. Jordal, JBJ17-2547 (O-F-254436); Trøndelag, Trøndelag, Sør-Trøndelag, Rennebu, Aunan, Lønshaugen, semi-natural pasture, 16 Sep. 2021, J.B. Jordal & S. Vatne, JB21-71 (O-F-261046); Vestland, Hordaland, Stord, Nautøya, calcareous, grazed near-shore grassland with shell-bed, 6 Sep. 2019, S. Weseth & T.E. Brandrud, NMC2019-124 (O-F-256419); Vestland, Hordaland, Bømlo, Lykling, Blyttarstemma, calcareous semi-natural pasture, 7 Oct. 2022, J.B. Jordal, P. Fadnes & A.H. Abaz, JB22-214 (O-F-259831). **Russia**, Altai Republic, near Gorno-Altaysk, on soil on ski slope, 1 Sep. 2018, O. Morozova, 115AL18 (LE F-344072); Altai Republic, Altaisky Nature Reserve, Teletskoye Lake shore, cordon Kokshi, on soil in grassland, 31 Aug. 2018, T.E. Brandrud, 111AL18 (LE F-344073); Komi Republic, Troitsko-Pechorsky District, Pechoro-Ilychsky Nature Reserve, Yaksha Village, on soil

on grassland, 31 Aug. 2011, M. Palamarchuk, SYKOf1706 (LE F-344074); Primorsky Krai, Sikhote-Alin' Nature Reserve, near Maisa forest station, on soil in mixed forest, 27 Aug. 2013, O. Morozova, 224CA13 (LE F-344068); Irkutsk Oblast, Bratsky District, near Kob' Village, on sandy soil in grassland, 20 Aug. 1983, A.N. Petrov, 83-8-117 (LE F-18419); Leningrad Oblast, Tosnensky District, near stop platform 104 km of the St Petersburg–Veliky Novgorod railway line, on soil in grassland, 21 Aug. 1999, O. Morozova, 59TO99 (LE F-215485); Murmansk Oblast, Khibiny Mountains, valley of the Vudayr Lake, south bank, on soil in the dwarf birch-heather tundra, 10 Aug. 1974, L.V. Mikhailovsky (LE F-9170); *ibid.*, valley of the Imandra Lake, on soil on the roadside, 25 Aug. 2023, Yu. Rebriev, 76AP23 (LE F-344070); Sverdlovsk Oblast, Prigorodny District, Visimsky Nature Reserve, near Big Galashki Village, on clay soil in the young pine forest, 3 Sep. 2002, L.V. Marina, LE F-258122; Tver Oblast, Zubtsov District, 2 km SE of Mozgovo Village, open place in calcareous pine forest, right bank of the Derzha River, 11 Sep. 2015, O. Morozova, 42TV15 (LE F-311812); Vologda Oblast, Kirillovsky District, Russian North National Park, *Calamagrostis* meadow with sparse pine undergrowth, 8 Sep. 2005, O. Shiryayeva (LE F-235260); St Petersburg, near Komarovo Village, bank of the Shchuchye Lake, open place in the pine forest, 19 Sep. 2020, O. Morozova, 12LO20 (LE F-344069). **Spain**, Catalunya, Comarca Ripollès, Núria, vora Santuari, Parc Natural de les Capçaleres del Ter I del Freser, 27 Aug. 2014, J. Vila, O. Morozova, JVG 1140827-4 (LE F-312460); Catalunya, Comarca Pallars Sobirà, Espot, Parc Nacional d'Aigüestortes i Estany de Sant Maurici, Port de la Bonaigua, 24 Aug. 2014, J. Vila, X. Llimona & O. Morozova, JVG 1140824-22 (LE F-312459). **The Netherlands**, prov. Gelderland, Staverden, Leemputten, on soil in moist, *Molinia*-rich grassland on loamy, calcareous soil, 22 Oct. 2019, F. Salzmänn & R. Salzmänn (L0607705).

Notes: The concept of *E. sericellum* is now fixed with a neotype and a derived ITS. This was necessary considering the extensive diversity revealed in our studies, with a dozen of similar looking, but morphologically and phylogenetically different species. Those that have sufficient data are described here as new species. *Entoloma sericellum* is a species with a white pileus, which is soon tinged yellow and often turns entirely yellowish ochre with age. Its surface is entirely fibrillose to minutely squamulose but not translucently striate. It has pure white lamellae turning pink from spores and a glabrous, whitish to yellowish ochre stipe (see description above). Microscopically, it is characterised by the relatively large, heterodiametrical spores and scattered, subcylindrical to lageniform cheilocystidia, which are much longer than the basidia. In Norway, *E. sericellum* is distributed up to the northern boreal zone and is mainly found in semi-natural grasslands. It is probably the most common species in the group in semi-natural grasslands also in temperate and central Europe, but this needs to be verified with more well-documented material, considering the morphological diversity in this group. In particular, the distributional, morphological and ecological differences between it and the very similar, but phylogenetically very distant *E. ermineum* need to be evaluated. Geographical and ecological factors might also have been of importance for speciation in this clade. *Entoloma chioneum* seems to be the most common *Alboleptonia* in the



northern, subarctic/alpine parts of Scandinavia, whereas other taxa have a more southern distribution. But conclusions can only be drawn when much more data is assembled. *Entoloma sericellum* generally is considered a species easy to identify in the field. Nothing could be further from the truth. Hopefully this study stimulates more critical collecting and sequencing of small, whitish *Entoloma* species.

Entoloma skadiae J.B. Jordal, Noordel., Reschke & Dima, *sp. nov.* MB 860399. Fig. 18.

Etymology: Named after “Skadi”, or “Skade” (old Norse *Skaði*), the goddess of winter, hunting and skiing; referring to the currently known distribution in Norway and the snow-white basidiomata.

Typus: **Norway**, Møre & Romsdal, Sunndal, Jordalssjøen, on soil in mown, semi-natural meadow, 15 Oct. 2018, J.B. Jordal, JBJ18-120 (**holotype** O-F-256757); ITS sequence, GenBank PX412068.

Description: *Basidiomata* collybioid; rather compact and sturdy with a relatively thick stipe. *Pileus* 15–20 mm wide, campanulate with irregular wavy-lobed margin, not hygrophanous or translucently striate, white, matt, finely tomentose all over. *Lamellae* moderately distant (L = about 30, l = 1–5), deeply emarginate, almost free, thickish, sometimes anastomosing, white then pale pink with thickish, concolourous edge. *Stipe* 25–70 × 3–5 mm, white, absolutely glabrous, matt, not polished. *Context* thin, brittle, white. *Smell* indistinct, *taste* not noted. *Basidiospores* (30/2) 9.0–13.5 ×

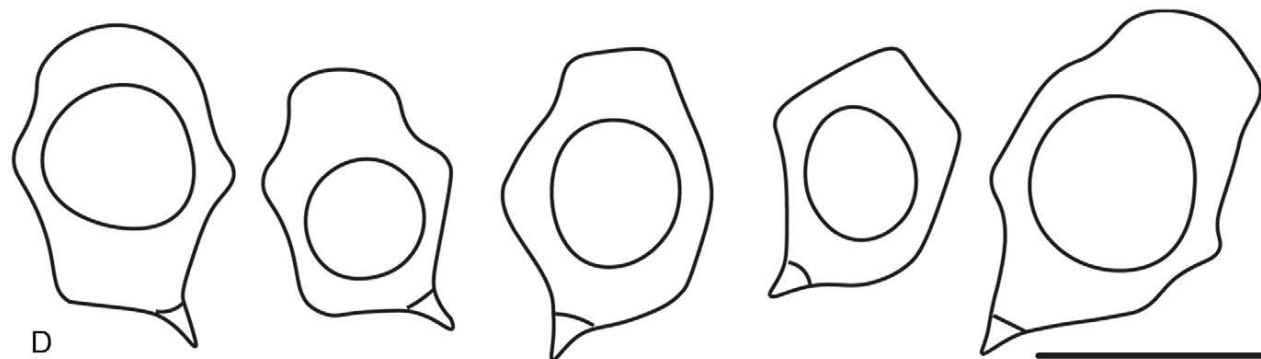
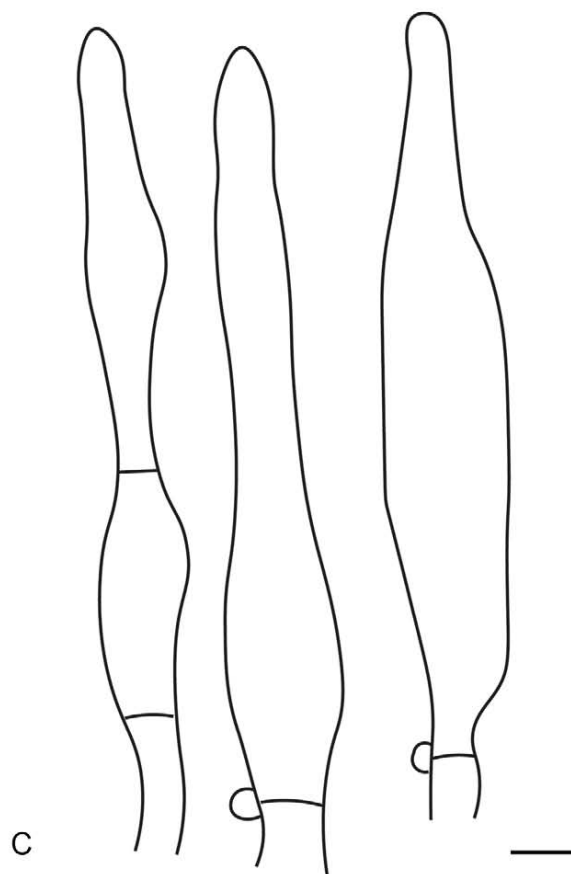


Fig. 18. *Entoloma skadiae* (O-F-256757, holotype). **A, B.** Habit. **C.** Cheilocystidia. **D.** Basidiospores. Photos: J.B. Jordal. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores and cheilocystidia).



6.0–10.0 μm , on average $11.2\text{--}11.4 \times 8.1\text{--}8.3 \mu\text{m}$, $Q = 1.20\text{--}1.65$, $Q_{av} = 1.35\text{--}1.40$, 6–7-angled in side view, with pronounced angles. *Basidia* $21\text{--}40 \times 7\text{--}14 \mu\text{m}$, 4-spored. *Lamella edge* heterogeneous. *Cheilocystidia* $50\text{--}100 \times 7\text{--}15 \mu\text{m}$, long, filiform-cylindrical to narrowly lageniform. *Pileipellis* a thin, loose cutis with transitions to a trichoderm of narrow hyphae, about $5 \mu\text{m}$ wide; no pigment detected. *Pileitrama* made up of short elements. *Stipitipellis* a cutis of narrow, cylindrical hyphae, $5\text{--}9 \mu\text{m}$ wide. *Clamp-connections* present.

Habitat and distribution: In semi-natural grassland. So far only known from two localities in Northwestern Norway.

Additional material examined: **Norway**, Trøndelag, Sør-Trøndelag, Hitra, Hifjellet south, on soil in weakly calcareous, moist forest meadow, 13 Sep. 2021, G. Gaarder & K. Svingen, GG7959 (O).

Notes: *Entoloma skadiae* is distinctive because of the sturdy stature for the group, white basidiomata, thin pileipellis, large spores and scattered, long cheilocystidia. The relatively large spores and long protruding cheilocystidia are similar to those of *E. sericellum*, which has, however, a tomentose to minutely squamulose pileus, that usually turns yellow ochre with age.

/Ritae subclade

The well-supported subclade /Ritae contains at least four species, one of them is *Entoloma ritae*, a well delimited species in subgen. *Alboleptonia* with pinkish brown basidiomata (Wölfel & Noordeloos 1997b), and the rather similar, pink-coloured *E. pallidipes* from North America (Noordeloos 1988). There are two more species in this clade, possibly undescribed, viz. *Entoloma* aff. *ritae* known from Norway and Germany, and *Entoloma* aff. *cuboidalbum* from The Netherlands (Fig. 12, both as *Entoloma* sp.). For both taxa, however, the material is too limited to describe them formally.

/Olivaceotinctum clade

This clade partly coincides with *Entoloma* sect. *Griseorubida*, subsect. *Parvisporigera* sensu Noordeloos (1987). It accommodates species with small spores and less pronounced cheilocystidia as compared to subsect. *Griseorubida*. In Noordeloos (2004), this subsection comprised seven species. From five of these, holotypes could be sequenced, while the types of *E. weholtii*, and *E. riofriense* unfortunately failed. As a result, *E. farinasprellum*, and *E. sordidolamellatum* were found to belong to sect. *Erophila*, and the remaining three species (*E. politoflavipes*, *E. moguntinum*, *E. olivaceotinctum*) appeared to be conspecific. Since the name *E. olivaceotinctum* has priority, the remaining two names were added to the synonymy of that species. Considering the remarkable morphological variation, an amended description is given that covers the clade and the currently only recognized species (Fig. 2).

Entoloma olivaceotinctum Noordel., *Persoonia* **12**(4): 461. 1985. MB 104246. Fig. 19.

Synonyms: *Entoloma politoflavipes* Noordel. & Liiv, *Persoonia* **15**(1): 29. 1992. MB 358182.

Entoloma moguntinum Noordel. & Prüfert, in Noordeloos, *Entoloma s.l., Fungi Europaei* vol. 5 (Saronno) **5a**: 1111. 2004. MB 491782.

?*Entoloma weholtii* Noordel., *Beih. Nova Hedwigia* **91**: 200. 1987. MB 133107.

Typus: **Finland**, Savonia Borealis, Kuopio, Puijo, Antikkala, 9 Aug. 1983, J. Vauras, 1552F (**holotype** L0608339, **isotype** TUR177404); ITS sequence, GenBank PX412050.

Description (amended here): *Basidiomata* collybioid. *Pileus* (5–)10–40 mm wide, campanulate or convex with slightly depressed to umbilicate centre and involute then deflexed margin, hygrophanous, when moist translucently striate at margin or up to centre, yellow brown, moderately dark brown, or grey brown sometimes with olivaceous green tinge, radially fibrillose at margin, rugulose to minutely squamulose at centre. *Lamellae* distant ($L = 10\text{--}30$, $I = 3\text{--}7$), broadly adnate often slightly emarginate or with small decurrent tooth, arcuate to segmentiform or ventricose, white or pale grey then pink with concolourous, entire edge. *Stipe* $10\text{--}50 \times 1\text{--}3 \text{ mm}$, cylindrical, sometimes slightly broadened towards base, whitish to pale brown, yellow brown or grey brown sometimes with distinct olivaceous tinge at least when young, polished or substriate with innate fibrils (lens), rarely silvery striate. *Context* concolourous with surface in cortex, pallid in inner parts. *Smell* and *taste* indistinct. *Basidiospores* (200/16) (5.5–)6.0–9.0 $\times$ 5.5–7.5 μm , on average $7.0\text{--}8.5 \times 6.2\text{--}6.8 \mu\text{m}$, $Q = 1.20\text{--}1.50$, $Q_{av} = 1.35\text{--}1.42$, 5–7-angled in side view. *Basidia* $20\text{--}30 \times 8\text{--}12 \mu\text{m}$, 4-spored, clamped. *Lamella edge* sterile or heterogeneous. *Cheilocystidia* $15\text{--}70 \times 6\text{--}20 \mu\text{m}$, very variable in shape from irregularly subcylindrical–subcoralloid to clavate or vesiculose, clamped. *Pileipellis* a cutis with transitions to a trichoderm, made up of strongly inflated, clavate to sphaeropedunculate, $12\text{--}25 \mu\text{m}$ wide elements; pigment brown to olivaceous–brown, intracellular. *Stipitipellis* a cutis of narrow, cylindrical, $3.0\text{--}12 \mu\text{m}$ wide hyphae; caulocystidia absent. *Brilliant granules* sparse in pileitrama. *Clamp-connections* abundant in hymenium, elsewhere rare.

Habitat and distribution: In small groups in xerophytic grasslands on calcareous soil or in semi-natural, grazed pastures, also found in forests on humus rich soil under *Carpinus* and *Quercus* on calcareous loam, and in mixed, often grazed forests, with *Alnus incana*, *Betula*, *Salix*, *Picea*, from July to October. Widespread in Europe.

Additional material examined: **Estonia**, Saaremaa, Viidu, 11 Aug. 1985, V. Liiv, Liiv 171 (L0054033, **holotype** of *E. politoflavipes*; ITS sequence, GenBank PX401858). **Denmark**, Sjælland, Fårevejle Kirkeby, Kårup Skov, Lerbjerg, semi-natural grassland, 31 Jul. 2011, R. Ejrnæs, DMS-159525. **Germany**, Rheinland-Pfalz, Mainz-Lerchenberg, Ober-Olmer Wald, 20 Jul. 2001, W. Prüfert (L0820376, **holotype** of *E. moguntinum*; ITS sequence, GenBank PX401857). **Hungary**, Veszprém, Bakony Mts, Eplény, 8 Sep. 2018, B. Dima, DB-2018-09-08-2 (ELTE). **Norway**, Møre og Romsdal, Rauma, Gjerde, semi-natural grassland, 1 Sep. 2000, J.B. Jordal (O-F-178061); Trøndelag, Sør-Trøndelag, Oppdal, Ørstad, by Egga, calcareous semi-natural grassland, 20 Aug. 2009, J.B. Jordal (O-F-291389); Akershus, Oppland,



Lunner, Amundrud nordre, rather dry, calcareous lawn, 6 Aug. 2014, T.E. Brandrud, TEB 61-14 (O-F-247975); Innlandet, Oppland, Sør-Fron, Ommundgardshågån (Hundorp), dry calcareous semi-natural grassland, 8 Sep. 2005, J.B. Jordal, JBJ-3080 (O-F-158260). **Russia**, Tver Oblast, Zubtsov District, 2 km to SE from Mozgovo Village, right bank of the Derzha River, on soil in calcareous grassland, 11 Sep. 2015, O. Morozova, 46TV15 (LE F-311802, as *E. moguntinum*); *ibid.*, 45TV15 (LE F-311803, as *E. moguntinum*; Morozova *et al.* 2016); Pskov Oblast, Pechory District, vicinity of Stary Izborsk Village, near the Truvor hillfort, on soil in calcareous grassland, 20 Aug. 2011, O. Morozova, 4IZ11 (LE F-311836); Karachaevo-Cherkessia Republic, Teberda Nature Reserve, near Teberda town, on soil in grassland, 6 Aug. 2009, O. Morozova, 17TB09 (LE F-343749); Altai Republic, Altaiskiy Nature Reserve, cordon Chelyush, on soil in grassland near farm, 28 Aug. 2018, O. Morozova, 13AL18 (LE F-343762). **The Netherlands**, prov. Zuid Holland, Voornes Duin, 7 Aug. 2023, E. Vis (L0607501); prov. Limburg, Nijswiller Noord, 16 Oct. 2019, F. & R. Salzmänn, PSLhg 00277 (L0607720).

Notes: *Entoloma olivaceotinctum* appears to be a very variable species. Despite the specific name, olivaceous tinges are not as often seen in this species as the name

suggests, and the microscopy with regard to size and shape of the cheilocystidia is very variable. It resembles species of subgen. *Cyanula*, with which it often co-occurs in calcareous grassland hotspots, but is different because of the presence of clamp-connections. It is usually also easily distinguished from *Cyanula* species by the structure of the pileipellis. Now it takes a rather isolated position in the ITS tree outside subgen. *Cyanula* (Fig. 1). In addition to the listed additional material, we have seen many more sequenced collections of this species (e.g. 16 collections from Denmark), which does not seem to be rare in Europe. We examined and sequenced several collections labelled *E. weholtii*, with broad clavate to vesiculose cheilocystidia, and these appeared to be conspecific with *E. olivaceotinctum*. However, the holotype of *E. weholtii* failed so far in our attempts to have it sequenced. So, the synonymy is not yet confirmed with a barcode sequence of the type.

/Griseorubidum clade – sect. *Griseorubida*

Entoloma sect. *Griseorubida* (Romagn.) Noordel., *Persoonia* 11(2): 147. 1981. MB 860553.

Basionym: *Rhodophyllus* sect. *Griseorubidi* Romagn., *Bull. Mens. Soc. Linn. Lyon* 43: 320. 1974. MB 634402.

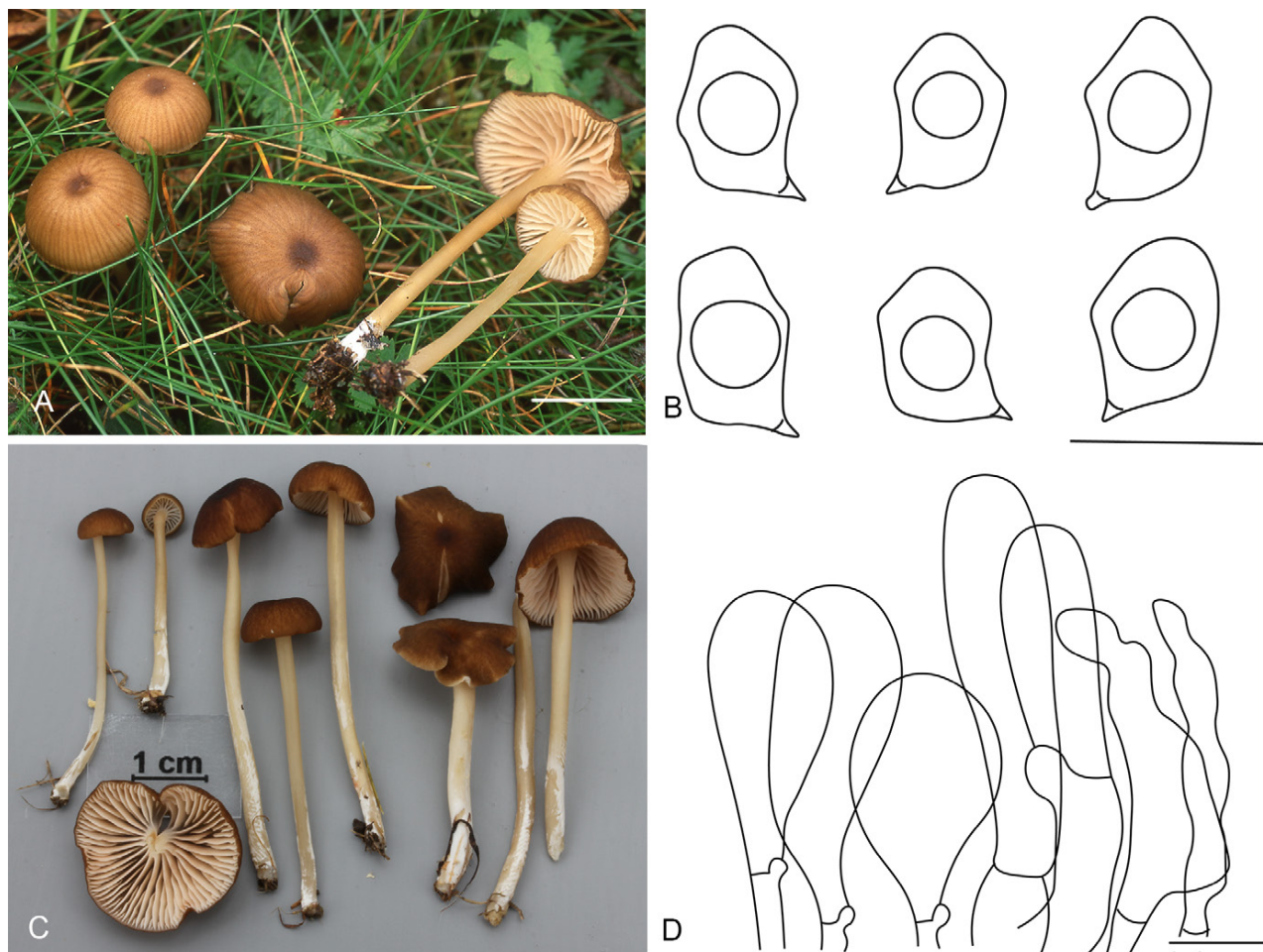


Fig. 19. *Entoloma olivaceotinctum* (A. TUR177404, isotype of *E. olivaceotinctum*; B. L0608339, holotype of *E. olivaceotinctum*; C. O-F-247975; D. Compiled from the isotypes of *E. politoflavipes*, holotypes of *E. olivaceotinctum* and *E. moguntinum*). **A, C.** Habit. **B.** Basidiospores. **D.** Cheilocystidia variability. Photos: A by J. Vauras; C by T.E. Brandrud. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores and cheilocystidia), 20 µm (pileipellis).



Type species: Entoloma griseorubidum Kühner ex Noordel.

This clade coincides with *Entoloma* sect. *Griseorubida* (Romagnesi 1974, Noordeloos 1987). The main morphological characters are the collybioid habit, usually with a distinctly umbilicate, fibrillose to minutely squamulose pileus; a polished stipe; large fusiform to lageniform cheilocystidia, sometimes in addition similarly shaped pleurocystidia, and presence of clamp-connections. Noordeloos (1987) distinguished two species, viz. *E. griseorubidum*, and *E. indutoides*, based on differences in colour and spore size. Noordeloos *et al.* (1995) concluded on the basis of some rich, additional collections that these differences did not stand and considered *E. griseorubidum* a synonym of *E. indutoides*. In the same paper, a new variety, *E. indutoides* var. *pleurocystidiatum* was introduced for a collection with distinct pleurocystidia. Noordeloos (1987) published *E. insolitum* as a new species in subgenus *Paraleptonia*, with an omphalinoid habit, and well differentiated cheilo- and pleurocystidia. The results of our molecular studies, however, show that we need to have a fresh look at species limits in this clade. *Entoloma griseorubidum* forms a distinct clade, and includes the holotypes of *E. indutoides* var. *pleurocystidiatum*, as well as that of *E. insolitum*. A sister-clade, differing by 7.5–8.5 % in the ITS, is described here as *E. paraindutoides*, based on one collection from Italy, and two from Estonia (UNITE). The holotype of *E. indutoides*, however, groups together with a few Norwegian collections as a distinct separate clade and must be considered a species in its own right. Despite the barcode gaps, the three species are morphologically hardly distinguishable. In the /Griseorubida clade (Fig. 20) we find, furthermore, the recently described *E. ochraceodiscum*, that can be distinguished by the colour of the basidiomata (Kaygusuz *et al.* 2024), and the extralimital *E. contortisporum* from the island of Réunion, with rather an aberrant spore shape (Noordeloos & Hausknecht 2007).

Entoloma griseorubidum Kühner ex Noordel., *Persoonia* 12(3): 196. 1984, **amend.** MB 106088. Fig. 21.

Synonyms: *Entoloma insolitum* Noordel., *Beih. Nova Hedwigia* 91: 348. 1987. MB 133092.

Entoloma indutoides var. *pleurocystidiatum* Noordel. *et al.*, *Öst. Z. Pilzk.* 4: 127. 1995. MB 413016.

Misapplied name: *Entoloma indutoides* (P.D. Orton) Noordel., *Persoonia* 12(3): 198. 1984, sensu Noordel. *et al.*, *Öst. Z. Pilzk.* 4: 126–127. 1995.

Typus: **Switzerland**, Neuchâtel, Marin, 10 Jul. 1965, H.S.C. Huijsman (**holotype** L, in poor condition, not sequenced).

Germany, Bayern, Bad Endorf, Antwort, Antwörter Berg, gregarious, on a moraine heap from the Würm glaciation, in a damp, herbaceous spot at the edge of a path, 24 Aug. 2013, M. Dondl (**epitype** L0607635, designated here, deposited at L, MBT 10028195; ITS sequence, GenBank PX412038).

Description (amended here): *Basidiomata* collybioid to omphalinoid. *Pileus* 15–30 mm, hemispherical to convex then expanding to applanate, with slightly depressed to umbilicate centre, with involute margin, slightly hygrophanous, not translucently striate, when moist very dark brown almost black to sepia, chocolate brown or dark grey brown, slightly pallescent on drying to brown, more or less coarsely radially fibrillose or tomentose, at centre sometimes breaking up in small squamules, opaque. *Lamellae* distant to somewhat crowded (L = 15–25, I = 1–5), very broad, up to 5 mm broad, thickish, adnate with indistinct decurrent tooth to distinctly decurrent, pale grey to grey brown with slight pink tinges, with an entire, slightly paler edge. *Stipe* 20–52 × 1.5–6 mm, cylindrical, equal, or with broadened base, young rather pale, almost white, then darkening to brown or grey brown, fibrillose, particularly in upper half or subglabrous; white pruinose to flocculose at apex, at base with white tomentum. *Context*

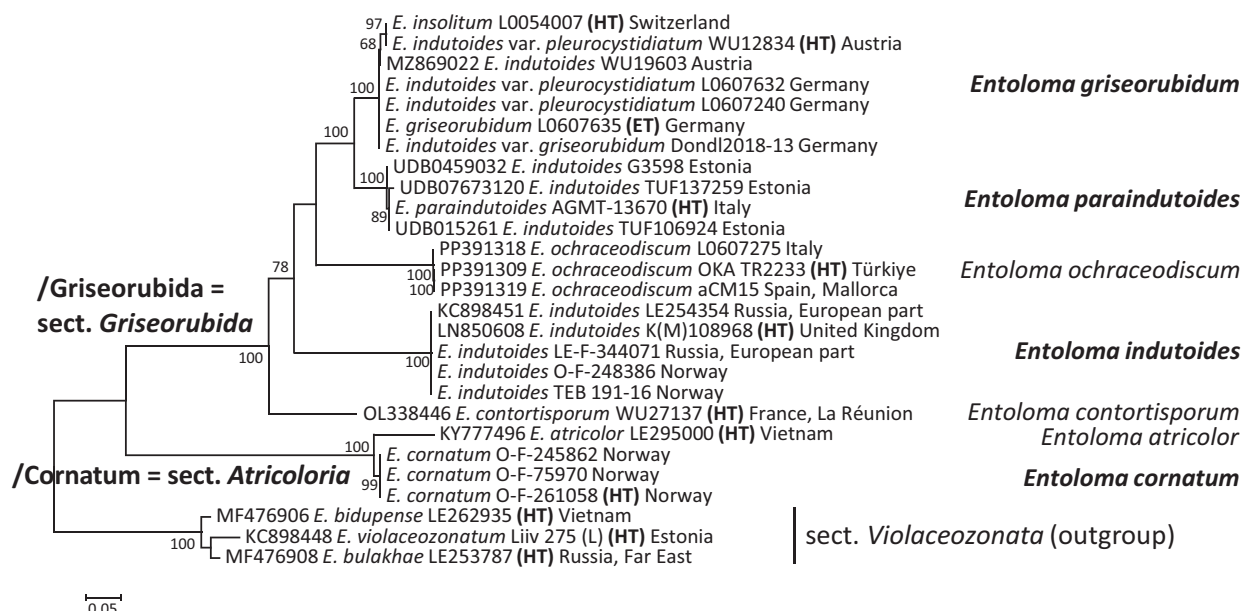


Fig. 20. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* sect. *Griseorubida* and sect. *Atricoloria*. ML bootstrap support values ≥ 50 % are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



white on drying, brown in cortex of pileus and stipe. *Smell* and *taste* not distinctive. *Basidiospores* (100/7) $10.5\text{--}14.0 \times 7.0\text{--}10.5\ \mu\text{m}$, on average $11.5\text{--}12.5 \times 8.5\text{--}9.0\ \mu\text{m}$, $Q = 1.30\text{--}1.70$, $Q_{av} = 1.40\text{--}1.45$, irregularly 6–10-angled in sideview. *Basidia* $25\text{--}45 \times 10\text{--}14\ \mu\text{m}$, 4-spored, clamped. *Lamella edge* heterogeneous. *Cheilocystidia* $40\text{--}145 \times 5\text{--}17\ \mu\text{m}$, variable in shape from cylindrical, often capitate, to lageniform with a long, tapering neck, abundant to sparse, often in clusters or solitary among basidia. *Pleurocystidia* $25\text{--}130 \times 5\text{--}20 \times 3\text{--}7\ \mu\text{m}$, cylindrical, often capitate, to lageniform, more or less similar to cheilocystidia, abundant to sparse, easily collapsing and often hard to find in dried material, possible sometimes

virtually absent. *Pileipellis* a cutis of radially arranged, cylindrical to inflated hyphae, up to $20\ \mu\text{m}$ wide, with cylindrical to inflated, terminal elements, $40\text{--}90 \times 6\text{--}10\ \mu\text{m}$. *Stipitipellis* a cutis of cylindrical hyphae, $4\text{--}15\ \mu\text{m}$ wide with scattered or clustered cylindrical to lageniform caulocystidia, at apex only, $20\text{--}55(80) \times 5\text{--}20\ \mu\text{m}$. *Pigment* brown, intracellular in pileipellis and stipitipellis. *Clamp-connections* abundant.

Habitat and distribution: On soil in grasslands, preferring calcareous soil, including rich/calcareous moraines, often in montane to subalpine habitats, also among grasses at roadsides in mixed parkland. Apparently rare.

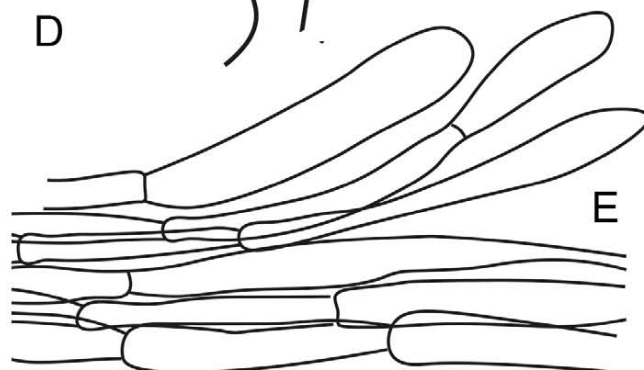
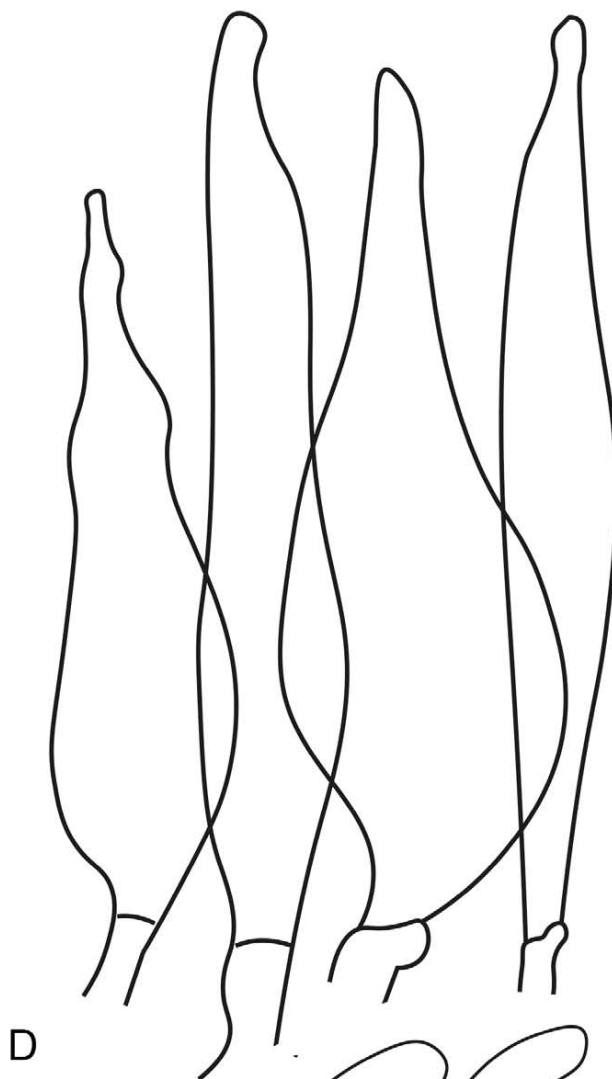
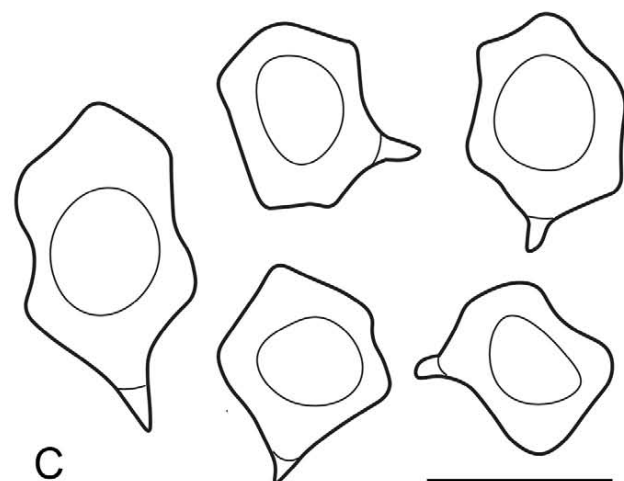


Fig. 21. *Entoloma griseorubidum* (A. L0607633; B. L0607632; C–E. Huijsman 10-Jul-1965, holotype). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Pileipellis. Photos: M. Dondl. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), $10\ \mu\text{m}$ (basidiospores and cheilocystidia), $20\ \mu\text{m}$ (pileipellis).



Additional material examined: **Austria**, Oberösterreich, Sankt Lorenz, Drachenwand Nord, 11 Sep. 1998, A. Hausknecht (WU-Myc 19603); Steiermark, Bad Gleichenberg, Kurpark 25 Jun. 1994, W. Klofac (WU12834, **holotype** of *E. indutoides* var. *pleurocystidium*; ITS sequence, GenBank PX412041). **Germany**, Bayern, Landkreis München, Baiersbrunn, western bank of the Isar, in alluvial forest on sandy fluvisol, 24 Jun. 2018, M. Dondl (L0607633); München, Fröttmaninger Heide, in a semi-natural grassland with *Salix* on calcareous soil, grazed by cattle, 27 Jun. 2009, M. Dondl (L0607632); *ibid.*, 18 Aug. 2010, M. Dondl (L0607240). **Switzerland**, Canton of Vaud, Pont de Nant sur Bex, 8 Sep. 1984, Th.W. Kuyper, 2528, (L0054007, **holotype** of *E. insolitum*; ITS sequence, GenBank PX412043).

Notes: The holotype being in bad condition, unsuitable for molecular studies, made it necessary to designate an epitype with an ITS barcode. Morphologically, *E. griseorubidum* is very similar to *E. indutoides* (see below). Both occur almost exclusively in calcareous, dry grasslands, but *E. griseorubidum* seems to be more montane-subalpine, mainly (only?) in Central Europe.

Entoloma indutoides (P.D. Orton) Noordel., *Persoonia* 12(3): 198. 1984, **amend.** MB 106091. Fig. 22A–D. **Basionym:** *Leptonia indutoides* P.D. Orton, *Trans. Brit. Mycol. Soc.* 43(2): 295. 1960. MB 333200.

Typus: **UK**, England, Yorkshire, Ingleton, in limestone pasture, 28 Aug. 1958, P.D. Orton [**holotype**, K(M)108968]; ITS sequence, GenBank LN850608.

Description (amended here): *Basidiomata* omphalinoid, rather compact and firm. *Pileus* 15–30 mm wide, convex, then plano-convex, umbilicate or slightly depressed, with deflexed then straight margin, not distinctly hygrophanous or translucently striate, sepia brown to dark grey brown, almost black or sepia brown, often with olivaceous hue, or entirely dark olivaceous brown, entirely covered in very fine, glistening fibrillose-patches or minute squamules, becoming micaceous and streaked with darker fibrils upon drying. *Lamellae* somewhat thickened ($L = 20\text{--}24$, $l = 1\text{--}3$), and veined at the base, adnate-subdecurrent or emarginate, segmentiform to subventricose, pale yellow brown then brown pink, with pale coloured or white, entire or minutely flocculose-denticulate edge. *Stipe* 15–40 × 2–4 mm, equal or tapering downwards or thickened at the apex, sometimes slightly eccentric, solid then hollow, concolourous with pileus or paler dull brown to dirty yellowish brown, sometimes slightly tinged olive brown, entirely covered in fine fibrillose patches or subfibrillose, contrasting with the darker background. *Context* concolourous with the surface in the cortex, pale in inner parts. *Smell* indistinct, *taste* not noted. *Basidiospores* (120/7) 11.0–15.0 × 7.0–10.5 µm, on average 12.0–12.5 × 8.5–9.5 µm, $Q = 1.25\text{--}1.70$, $Q_{av} = 1.40\text{--}1.50$, irregularly 6–8(–10)-angled in side view. *Basidia*

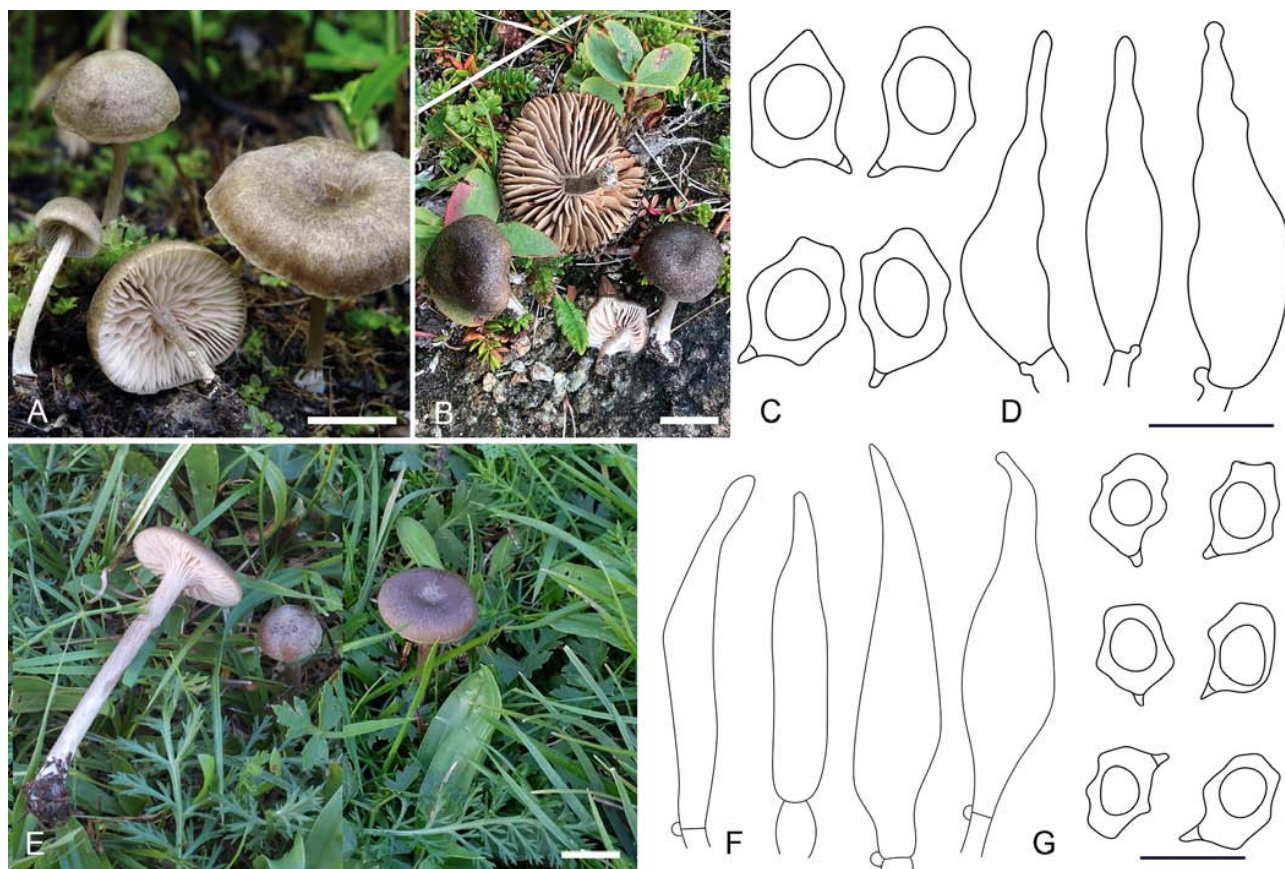


Fig. 22. A–D. *Entoloma indutoides* (A. LE F-254354; B. O-F-260876; C, D. Holotype). A, B. Habit. C. Basidiospores. D. Cheilocystidia. E–G. *Entoloma paraindutoides* (AGMT-13670, holotype). E. Habit. F. Cheilocystidia. G. Basidiospores. Photos: A by O. Morozova; B by G. Gaarder; E by S. Toninelli. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores and cheilocystidia), 20 µm (pileipellis).



4-spored, $44\text{--}50 \times 11\text{--}13\ \mu\text{m}$. *Cheilocystidia* $50\text{--}120 \times 10\text{--}22\ \mu\text{m}$, scattered along edge, and sometimes also found on sides close to the edge and then often called pleurocystidia, lageniform or irregularly cylindrical to flexuous, $4\text{--}10\ \mu\text{m}$ wide at the apex. *Pileipellis* a cutis of cylindrical, $4\text{--}22\ \mu\text{m}$ wide hyphae, with brown intracellular pigment. *Stipitipellis* a cutis of cylindrical hyphae, $5\text{--}15\ \mu\text{m}$ wide. *Caulocystidia* absent.

Habitat and distribution: In calcareous, dry, sometimes grazed grasslands, often in sites with many *Entoloma* subgen. *Cyanula* species. So far known from Norway, Russia, and the United Kingdom.

Additional material examined: **Norway**, Telemark, Bamble, Steinvika, in natural, dry grassland on limestone, 12 Aug. 2016, T.E. Brandrud & B. Dima, TEB 191-16 (O-F-254635); Telemark, Kragerø, Jomfruland, in semi-natural, grazed grassland on calcareous sand (shell-bed), Aug. 2011, T.E. Brandrud, TEB 55-11 (O-F-248386); Nordland, Bodø, Ausvika, calcareous meadow near the shore, 12 Aug. 2020, G. Gaarder & P. Alvereng, GG7826 (O-F-260876). **Russia**, Leningrad Oblast, Gatchina District, Pudost Village, on soil in calcareous grassland, 15 Jul. 2008, O. Morozova & E. Popov, LE F-254354; *ibid.*, Paritsy Village, on soil in calcareous grassland, 4 Sep. 2023, O. Morozova & E. Popov, 2LO23 (LE F-344071).

Notes: *Entoloma griseorubidum* and *E. indutoides* are very similar morphologically, but differ slightly in colour, *E. indutoides* may be sometimes somewhat darker and with olivaceous tinges. *Entoloma indutoides* also seems on average more omphalinoid. Microscopically, the occurrence of pleurocystidia seems to be of minor taxonomic importance, as they may be present or absent in both species. The

recently described *E. ochraceodiscum* differs from both *E. griseorubidum*, and *E. indutoides* by the combination of funnel-shaped basidiomata with deeply depressed, yellowish brown pilei, pale greyish to yellowish stipes with a dark yellow tinge, 5–8-angled basidiospores, and the presence of pleurocystidia and caulocystidia (Kaygusuz *et al.* 2024).

Entoloma paraindutoides Toninelli, Noordel. & Dima, *sp. nov.* MB 860387. Fig. 22E–G.

Etymology: παρά (para, Greek) – besides, along, referring to the close similarity to *Entoloma indutoides*.

Typus: **Italy**, Trentino, Castello-Molina di Fiemme (TN), Riserva Naturale Locale Brozin, on soil in open grassland, 29 Aug. 2014, S. Toninelli, ST77 (**holotype**, AGMT-13670); ITS sequence, GenBank PX412055.

Description: *Pileus* 20–30 mm wide, convex, umbilicate, with deflexed margin, not hygrophanous or translucently striate, sordid grey brown, sepia brown, more or less uniformly coloured or with slightly darker centre, innately fibrillose. *Lamellae* fairly distant ($L = 36\text{--}52$, $I = 3\text{--}7$), more or less segmentiform, adnate-subdecurrent, pallid then pink with entire, concolourous edge. *Stipe* $20\text{--}45 \times 2\text{--}4\ \text{mm}$, cylindrical, equal or thickened at the apex, pale grey brown, subconcolourous with the pileus, when young entirely covered in fine fibrillose patches contrasting with the darker background. *Basidiospores* (20/1) $10.0\text{--}13.5 \times 7.0\text{--}9.5\ \mu\text{m}$, on average $11.0\text{--}12.5 \times 8.0\text{--}9.0\ \mu\text{m}$, $Q = 1.20\text{--}1.60$, $Q_{av} = 1.30\text{--}1.50$, irregularly 6–8(–10)-angled in side view. *Basidia* 4-spored, clamped. *Cheilocystidia* $50\text{--}120 \times 10\text{--}22\ \mu\text{m}$, scattered along edge, and sometimes also found on sides (“pleurocystidia”), lageniform or irregularly cylindrical

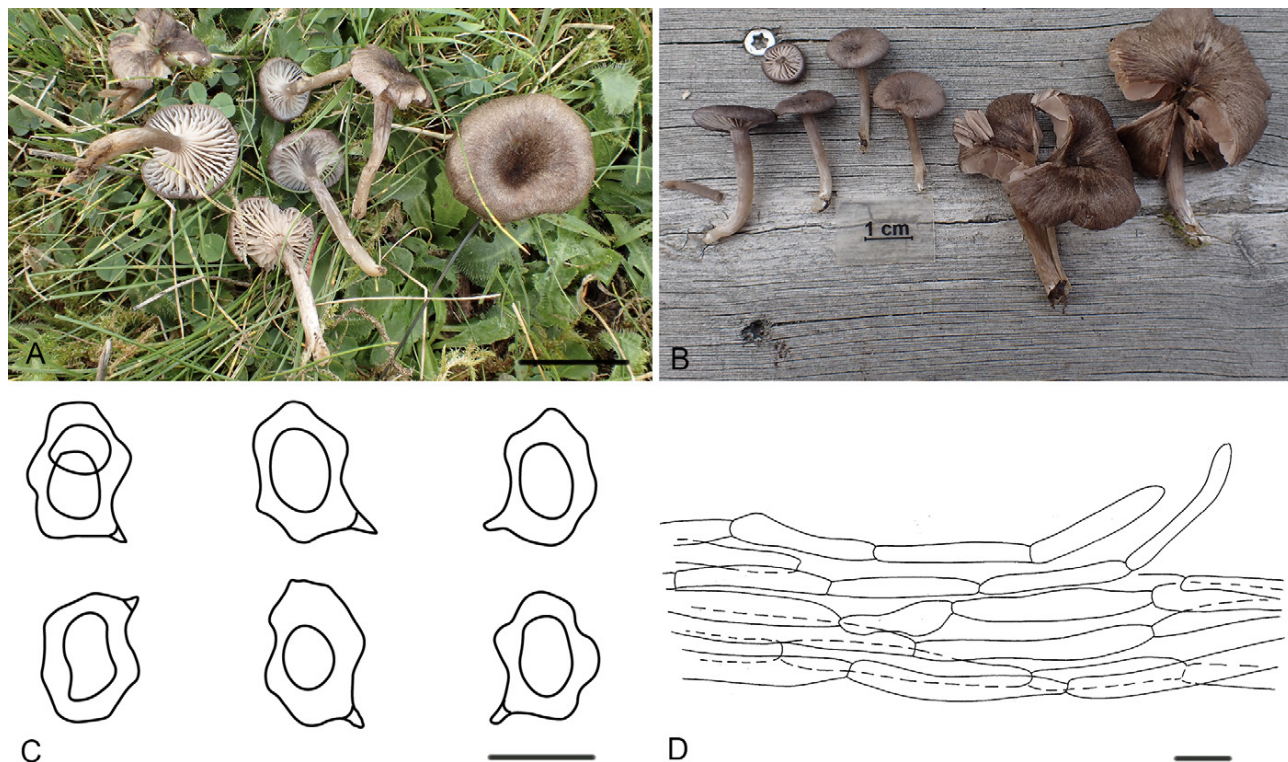


Fig. 23. *Entoloma cornutum* (A, C, D. O-F-261058, holotype; B. TEB 121-23). **A, B.** Habit. **C.** Basidiospores. **D.** Pileipellis. Photos: A by P. Fadnes & J.B. Jordal; B by T.E. Brandrud, Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (spores and cheilocystidia), 20 μm (pileipellis).



to flexuous 4–10 µm wide at the apex. *Pileipellis* a cutis of cylindrical, 4–20 µm wide hyphae, with brown intracellular pigment. *Stipitipellis* an undifferentiated cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in hymenium.

Habitat and distribution: So far known from the type locality in calcareous subalpine grassland of N Italy, and two collections with sequences from Estonia (UNITE), one of them from the Saaremaa Island (from calcareous grassland, alvar).

Additional material examined: **Estonia**, Lääne Makand, Lääne Nigula, Rannaküla, Haapsalu Inn, 28 July. 2023, *T. Ploompeu* (TUF137259); Saaremaa, Saaremaakond, Lümada val, Kihelkonna, Mäebe, 15 Aug. 2010, *V. Liiv* (TUF204343).

Notes: *Entoloma paraindutoides* is phylogenetically and morphologically close to *E. griseorubidum* and *E. indutoides* but is well-supported in the phylogenetic analysis having ITS sequences differing by 7.5–8.5 % from those of its closest sister *E. griseorubidum*. A good photograph of one of the Estonian collections can be found on the UNITE website (UDB015261). Because of the limited material that has been studied, assessment of variability of the individual species within sect. *Griseorubida* is not without problems. This could

explain the inability to morphologically separate several barcode species despite their distinct phylogenetic position.

/Cornatum clade – *Entoloma* sect. *Atricoloria*

Entoloma* sect. *Atricoloria Dima, Noordel., O.V. Morozova & Reschke, **sect. nov.** MB 860448. Fig. 20.

Description: *Basidiomata* collybioid to omphalinoïd with umbilicate to deeply umbilicate, dark coloured pileus, adnate to decurrent lamellae; *stipe* with fibrillose covering; *lamella* edge fertile or heterogeneous with subcylindrical to clavate cheilocystidia; *clamp-connections* present in all tissues.

Type species: *Entoloma atricolor* O.V. Morozova, Noordel., E.S. Popov & A.V. Alexandrova

Etymology: Named after the type species, *Entoloma atricolor*, and referring to the dark colour of its basidiomata.

Entoloma cornatum Fadnes, J.B. Jordal, Brandrud, Noordel. & Dima, **sp. nov.** MB 860388. Fig. 23.

Etymology: *cornu* (Lat.) – small horn, referring to the trumpet-like musical instrument.

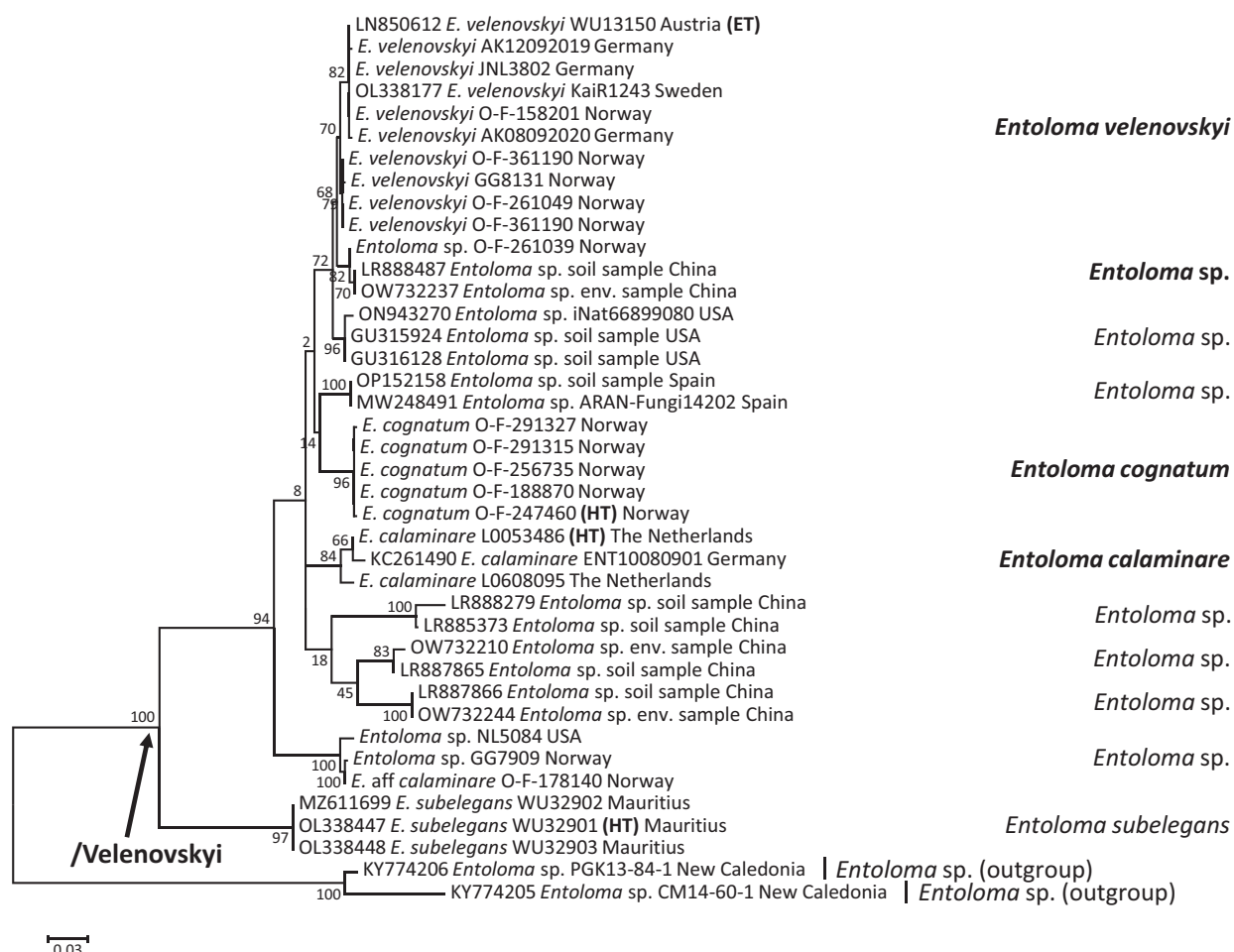


Fig. 24. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* clade /Velenovskyi. ML bootstrap support values ≥ 50 % are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



Typus: **Norway**, Vestland, Hordaland, Stord, Hovaneset, 4–5 m.a.s.l., semi-natural grassland, grazed by sheep, on shallow, calcareous soil near the sea, 28 Sep. 2021, *P. Fadnes & J.B. Jordal*, JB21-102 (**holotype** O-F-261058); ITS sequence, GenBank PX412031.

Description: *Basidiomata* collybioid to omphalinoid. *Pileus* 14–30 mm wide, weakly to deeply umbilicate, with involute, finally deflexed margin, not distinctly hygrophanous or translucently striate (or very weakly radially striate), medium to dark grey, sometimes greyish brown, but appearing paler because of the dense, fibrillose-aeriferous covering, greyish upon drying, with a dark grey brown “spot” at centre, surface radially fibrillose with silvery to dark fibrils, sometimes minutely squamulose, at centre sometimes weakly squamulose or granulose, shiny. *Lamellae* distant to moderately crowded ($L = 20\text{--}27$, $l = 1\text{--}3$), sometimes forked near the margin, arcuate-deeply decurrent, thickish, whitish, turning sordid pale grey pink with age; with entire, thick, concolourous edge, sometimes anastomosing basally. *Stipe* 20–40 × 2–3.5 mm, central or slightly eccentric, cylindrical, straight or slightly curved towards base, medium grey to greyish brown, entirely white felted-fibrillose. *Context* thin, concolourous with surface. *Smell* indistinct, *taste* not noted. *Basidiospores* (60/4) $8.4\text{--}11.2 \times 5.9\text{--}8.2 \mu\text{m}$, on average $9.6 \times 7.0 \mu\text{m}$, $Q = 1.20\text{--}1.55$ (–1.70), $Q_{av} = 1.30\text{--}1.35$, heterodiametrical with 6–8 angles in side view. *Basidia* 16–28 × 8–18 μm , narrowly clavate, 4-spored, clamp-connections absent. *Lamella edge* fertile. *Cheilocystidia* absent. *Hymenophoral trama* regular, made up of cylindrical elements, 60–110 × 5–9 μm . *Pileipellis* a cutis of narrow, cylindrical hyphae, 8–12 μm wide, with intracellular pigmentation; subpellis regular, made up of long hyphal elements, 6–25 μm wide. *Stipitipellis* a cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* not seen in any tissue.

Habitat and distribution: In groups in sheep-grazed, semi-natural grassland near the sea, on shallow soil influenced by calcareous, marine deposits (shell-beds). Autumn. Hitherto only three collections are known, two from places near the type locality, and one from another locality, all in coastal S Norway.

Additional material examined: **Norway**, Vestland, Hordaland, Stord, Hovaneset, semi-natural grassland grazed by sheep, 21 Aug. 2013, *P. Fadnes*, PF322 (O-F-245862); *ibid.*, 8 Sep. 2014, *P. Fadnes* (O-F-75970); Telemark, Kragerø, Østre Gumøy, semi-natural sheep-grazed grassland, on rich (more or less calcareous) shallow, seasonally moist soil, 27 Jul. 2023, *T.E. Brandrud*, TEB 121-23 (O-F-297402).

Notes: *Entoloma cornutum* is macroscopically reminiscent of *E. fridolfingense*, but that species is stouter, has somewhat different colours (the pileus is more brownish), the lamellae have a sterile to heterogeneous edge and are never forked or venose, and it is phylogenetically very distant. The species may also resemble *E. indutoides*, but this is more fibrillose-opaque and is not so markedly omphalinoid. *Entoloma cornutum* groups together with *E. atricolor* from Vietnam (Morozova *et al.* 2016) and is more distantly related to European species, like *E. violaceozonatum*.

/Velenovskyi clade

This well-supported clade (Fig. 1) contains several OTU's with a wide geographical distribution in Europe, North America, and Asia (China, Mascarenes). Morphologically, they are characterised by a more or less mycenoid habit, with conical to convex pileus, often with a truncate to subumbilicate apex, ascending, ventricose lamellae, and a slender, often more or less polished stipe. Microscopically, all exhibit voluminous, fusiform to lageniform cystidia along the lamella edge (cheilocystidia), and sometimes also on the sides in the proximity of the edge (pleurocystidia). As in sect. *Griseorubida*, the presence or absence of pleurocystidia appears to be not taxonomically informative. Basidiospores are usually large, but their sizes vary greatly, sometimes within one species. For that reason, it is hard to differentiate these species morphologically. Five clades are recognized as good species (Fig. 24), viz. the clades containing the holotype of respectively *E. calaminare* from Europe (Noordeloos 1984), and *E. subelegans* from the Mascarenes (Noordeloos & Hausknecht 2016). The latter has a basal position within the /Velenovskyi clade. The holotype of *E. velenovskyi* at PRC (as *Leptonia conica*), is preserved in ethanol, and for that reason unsuitable for DNA sequencing. An epitype has therefore been designated herein to fix the name *E. velenovskyi* with a representative specimen and ITS barcode. *Entoloma cognatum* is described here as new to science.

Entoloma calaminare Noordel., *Persoonia* 12(3): 198. 1984. MB 106081. Fig. 25.

Typus: **The Netherlands**, prov. Limburg, Cottessen, riverbank of de Geul, in xerophytic grassland with a high content of zinc, 21 Sep. 1978, *M.E. Noordeloos*, MEN729 (**holotype** L0053486); ITS sequence, GenBank PX401860.

Description: *Basidiomata* collybioid. *Pileus* 15–20 mm wide, hemispherical to conico-convex, often truncate, with umbilicate centre or with small papilla, with deflexed or straight margin, not or weakly hygrophanous, when moist variable in colour from very pale grey or ochraceous brown to warm reddish brown, with darker brown centre and striae, translucently striate at margin up to 2/3 of radius, pallescent to pale brown or almost white on drying, radially fibrillose, when exposed to weathering reminiscent of a species of *Inocybe*, shiny. *Lamellae* moderately distant ($L = 15\text{--}20$, $l = 1\text{--}3$), adnate-emarginate, sometimes with decurrent tooth, triangular to segmentiform or subventricose, white to pale grey or brown then greyish pink, with entire or fimbriate, concolourous edge. *Stipe* 25–50 × 1–3 mm, cylindrical, sometimes tapering towards base, pale cream or brownish grey, often with distinct ochre tinge near base, glabrous, polished or with scattered fibrils under lens, at base white tomentose. *Context* concolourous with surface, very brittle. *Smell* and *taste* indistinct. *Basidiospores* (50/3) $9.0\text{--}14.0 \times (6.7\text{--})7.0\text{--}9.0 \mu\text{m}$, on average $10.0\text{--}10.9 \times 7.0\text{--}7.2 \mu\text{m}$, $Q = 1.20\text{--}1.60$, $Q_{av} = 1.30\text{--}1.40$, irregularly nodulose-angled with 5–7 angles in side view, with basal facet. *Basidia* 27–45 × 10.5–14 μm , 4-spored, clamped. *Lamella edge* heterogeneous. *Cheilocystidia* abundant, 27–100 × 5–20 μm , irregular in shape, cylindrical to clavate, lageniform or



lecythiform, with rounded or capitate apex. *Hymenophoral trama* regular, made up of narrow, cylindrical hyphae 6–18 μ m wide. *Pileipellis* a cutis with scattered trichodermal tufts of clavate, up to 15 μ m wide terminal elements; pigment pale brown, intracellular. *Stipitipellis* a cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Brilliant* granules present in pileitrama. *Clamp-connections* present in hymenium, rare in other tissues.

Habitat and distribution: Terrestrial in semi-natural grasslands or on bare soil in broad-leaved forests, also in mossy, marshy places, including riverbanks, from August to November. Rare, only known from a few localities in Germany and The Netherlands. The type is Dutch, from Limburg, collected by a river influenced by the Calamine zinc mine in Belgium.



Fig. 25. *Entoloma calaminare* (A. ENT10080901; B. L0053486, holotype; C–F. L0608095). **A, D.** Habit. **B, G.** Basidiospores. **C, F.** Cheilocystidia. **E.** Pileipellis. Photos: A by J. Kleine; C by M.J.C. van der Vegte; D–G by G.M. Jansen. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores), 20 μ m (cheilocystidia and pileipellis).

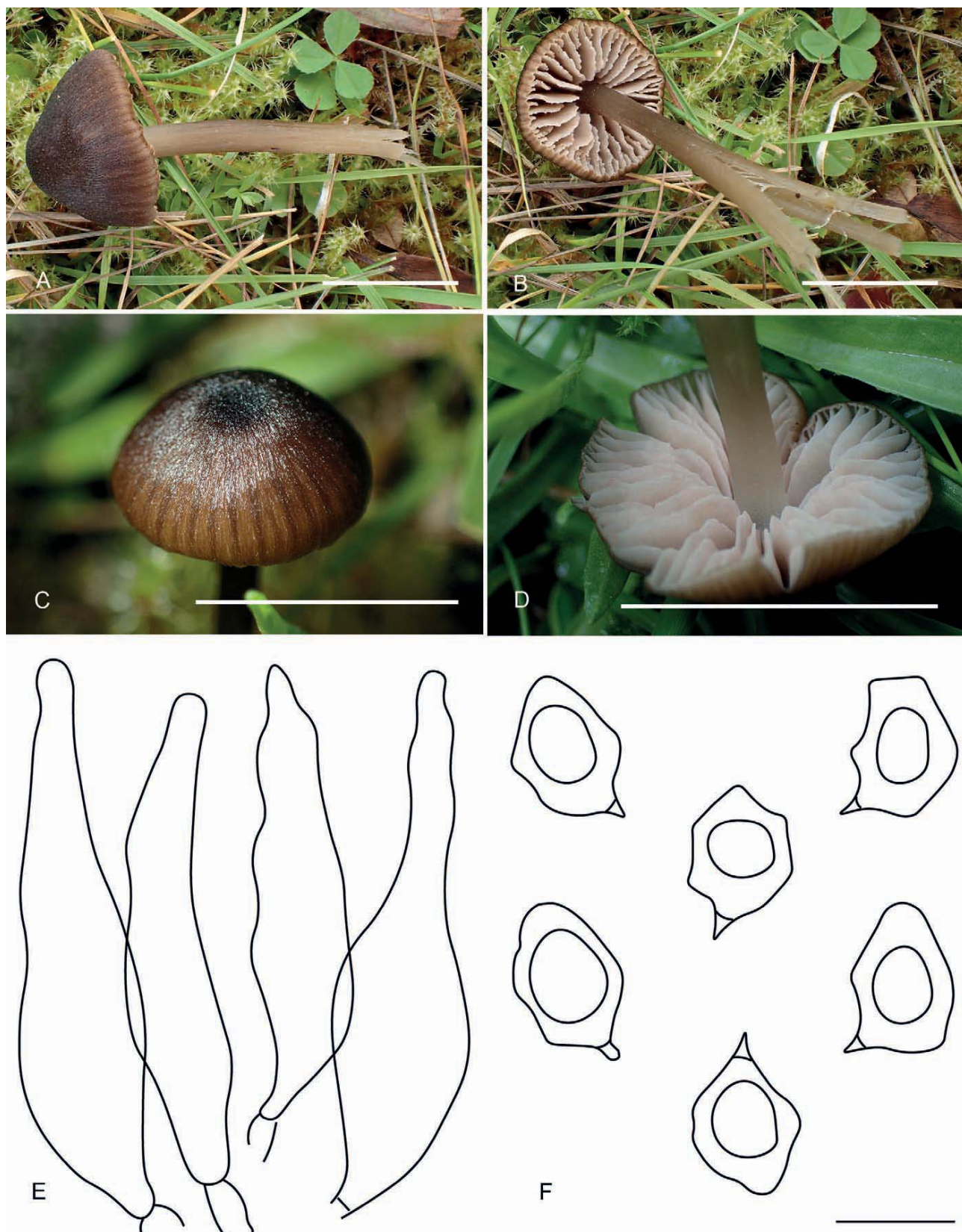


Fig. 26. *Entoloma cognatum* (A, B. JB18-007; C–F. O-F-247460, holotype). **A–D.** Habit. **E.** Cheilocystidia. **F.** Basidiospores. Photos: J.B. Jordal. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores and cheilocystidia).



Additional material examined: **Germany**, Sachsen, Leipzig, Nature Reserve Lehmliche Lauer, on bare loamy soil with broad-leaved trees, 9 Aug. 2010, *J. Kleine*, ENT10080901. **The Netherlands**, prov. Gelderland, Groesbeek, de Bruuk, in wet grassland, 2 Sep. 2018, *M.J.C. van der Vegte & G.M. Jansen* (L0608095).

Notes: For the present study only three collections were available, that form a rather well-supported clade in the tree. GenBank KC261490 groups together with the holotype, and a collection from The Netherlands (specimen L0608095) is very similar morphologically and differs mainly in the longer, lageniform cheilocystidia. We succeeded in getting only the ITS2-part for the holotype of *E. calaminare* with some ambiguities included. This part has only one unambiguous difference to the other two sequences. The other two sequences differ by 2.5 % from each other, which may well mean that they are two different species. Unfortunately, the majority of the differences are in the ITS1 region, so that we cannot be sure that the collection from Germany is really as close to the type as the tree indicates. Clearly, more collections and possibly even an epitype are needed to solve this, so treating them as one species is the most suitable and pragmatic solution for now. Another distinct clade, with five collections from Norway, is described as a species new to science below:

Entoloma cognatum J.B. Jordal, Noordel. & Dima, *sp. nov.* MB 860389. Fig. 26.

Etymology: *cognatus* (Lat.) – related, similar, i.e., similar to *E. calaminare*.

Typus: **Norway**, Trøndelag, Nord-Trøndelag, Namdalseid, Heggdalisetran, on soil in semi-natural pasture, 11 Sep. 2013, *J.B. Jordal, H. Holien & H. Bratli* (**holotype** O-F-247460); ITS sequence, GenBank PX412030.

Description: *Basidiomata* mycenoid. *Pileus* 6–12 mm broad, dark sepia brown, somewhat hygrophanous, deeply radially translucently striate, innately radially fibrillose, silky shiny when dry. *Lamellae* moderately distant ($L = \text{about } 20, l = 3\text{--}5$), narrowly adnate with small tooth, ventricose, pale, cream with paler, irregularly eroded edge. *Stipe* 30–40 × 1–2 mm, cylindrical, pale brown, much paler than pileus, polished or with scattered fibrils. *Smell* and *taste* indistinct. *Basidiospores* (50/4) 10.0–14.0 × 7.0–9.0 µm, on average 8.3 × 6.7 µm, $Q = 1.05\text{--}1.40$, $Q_{av} = 1.20\text{--}1.30$, nodulose, 4–9-angular. *Basidia* 4-spored, clamped. *Lamella edge* heterogeneous. *Cheilocystidia* 55–95 × 10–25 × 2–4 µm, lageniform, often with a rather acute, narrow apex. *Pileipellis* a cutis of narrow, 2–7 µm wide hyphae; pigment brown, intracellular. *Stipitipellis* a cutis of narrow, cylindrical hyphae. *Caulocystidia* absent. *Brilliant granules* not observed. *Clamp-connections* present in all tissues.

Habitat and distribution: In small groups in semi-natural, calcareous grassland. So far only known from Norway (mainly from Central Norway).

Additional material examined: **Norway**, Innlandet, Oppland, Nord-Fron, Teige, semi-natural pasture, 20 Sep. 2004, *B.H.*

Larsen, BHL66 (O-F-188870); Trøndelag, Sør-Trøndelag, Oppdal, Slettvoll, calcareous, semi-natural pasture, 24 Aug. 2009, *J.B. Jordal* (O-F-291327); Oppdal, Nerskogen below Håkersetra, semi-natural pasture with scattered birch trees, 3 Aug. 2009, *J.B. Jordal* (O-F-291315); Rennebu, Jøldalen, Bortstugusetra, semi-natural pasture, 23 Aug. 2018, *J.B. Jordal*, JB18-007 (O-F-256735).

Notes: *Entoloma cognatum* is morphologically hardly differentiated from *E. calaminare* and *E. velenovskyi*, but phylogenetically distant. Therefore, it is considered a good phylogenetic species.

Entoloma velenovskyi Noordel., *Persoonia* **10**(2): 258. 1979. MB 313842. Fig. 27.

Replaced synonym: *Leptonia conica* Velen. *České Houby* **3**: 623. 1921. MB 486653, non *Leptonia conica* (Murrill) Sacc. & Trotter, *Syll. Fung.* **23**: 214. 1925. MB 173049.

Typus: **Czechia**, Central Bohemia, Mnichovice near Praha, Jul. 1919, *J. Velenovský* (**holotype** PRC 9972). **Austria**, Niederösterreich, Rohrbach, Rohrbachgraben, Buchberg, in calcareous grassland, 15 Sep. 1994, *A. Hausknecht & W. Klofac* (**epitype** WU-Myc 13150, designated here, deposited at WU, MBT 10028196); ITS sequence, GenBank LN850612.

Description: *Basidiomata* mycenoid-collybioid. *Pileus* 10–30 mm wide, acutely conical, campanulate or conico-convex, then expanding to convex, usually with prominent papilla, but also with a truncate centre, with margin slightly involute then straight and crenulate, weakly to distinctly hygrophanous, when moist translucently striate up to half the radius, rarely up to centre, moderately to dark grey brown, slightly paler at margin, slightly to strongly pallescent on drying to grey brown or ochraceous grey, glabrous to innately radially fibrillose, often slightly scurfy at centre. *Lamellae* moderately distant ($L = 20\text{--}30, l = 1\text{--}5$), adnexed, emarginate, often with decurrent tooth, or broadly adnate with decurrent tooth, arcuate to ventricose, fairly thick, white then pink with sordid grey or brown tinge, with concolourous, entire edge. *Stipe* 15–70 × 1–3 mm, cylindrical, straight or flexuose, pale grey brown or yellow brown, glabrous, polished, sometimes white tomentose at base. *Context* thin, membranaceous, concolourous with surface. *Smell* none, *taste* mild. *Basidiospores* (200/12) 10.0–14.0(–16.0) × 7.0–11.5 µm, on average 12.5 × 8.3 µm, $Q = 1.30\text{--}1.70$, $Q_{av} = 1.45\text{--}1.50$, rather variable in size and shape per collection, irregularly heterodiametrical, 5–9-angled in side view. *Basidia* 20–35 × 5–9 µm, 4-spored, clamped. *Lamella edge* sterile or heterogeneous. *Cheilocystidia* 50–150 × 6–20 × 2–5 µm, fusiform or lageniform, always distinct and abundant. *Pleurocystidia* (40–)60–100 × (8.5–)12.5–18 µm, similar to cheilocystidia, abundant or sparse, sometimes lacking. *Pileipellis* a thin cutis of narrow, cylindrical, up to 12 µm wide hyphae. *Pigment* brown, intracellular in pileipellis and upper pileitrama. *Stipitipellis* a cutis of cylindrical, 5–14 µm wide hyphae. *Caulocystidia* absent. *Clamp-connections* abundant.

Habitat and distribution: In small groups, terrestrial in semi-natural grasslands, mainly in more or less calcareous soils. Northern and Central Europe.

Additional material examined: **Germany**, Sachsen, Jonsdorf, Auf der Heide, Parkrasen, 8 Sep. 2020, *A. Karich & R. Ullrich*,



Fig. 27. *Entoloma velenovskyi* (A. WU-Myc 13150, epitype; B. O-F-158201; C–F. GLM-F139799). **A–C.** Habit. **D.** Basidiospores. **E.** Pleurocystidia. **F.** Cheilocystidia. Photos: A by W. Klofac; B by J.B. Jordal; C by A. Karich. Drawings by A. Karich. Scale bars: 1 cm (habit), 10 μ m (spores and cystidia).



IHI-20Ent07, AK08092020 (GLM-F139800); Lückendorf, Kurparkwiese, in poor grassland, 12 Sep. 2019, A. Karich & R. Ullrich, IHI-19Ent04, AK12092019 (GLM-F139799). **Norway**, Møre og Romsdal, Tingvoll, Eikrem, Skarahaugen, semi-natural grassland, 11 Sep. 2021, G. Gaarder, GG7956; *ibid.*, GG7957; Trøndelag, Sør-Trøndelag, Oppdal, Engan, in calcareous, semi-natural grassland, 22 Aug. 2005, J.B. Jordal, JBJ3129 (O-F-158201); Rennebu, Aunan, Lønshaugen, 16 Sep. 2021, J.B. Jordal & S. Vatne, JB21-74 (O-F-261049); Rogaland, Rennesøy, Brimse, calcareous pasture, 2 Oct. 2006, J.B. Jordal & J.I. Johnsen (O-F-361190); Vestland, Luster, Mørkridsdalen, Larsamoøy, semi-natural grassland, 23 Aug. 2022, G. Gaarder & A.H. Abaz, GG8131. **Sweden**, Jämtlands län, near Angsta, Storvålen, horse pasture, 27 Aug. 2018, K. Reschke, KaiR 1243 (B 70 0105512).

Notes: There is some molecular variation in *E. velenovskiy* as shown in the tree (Fig. 24), but so far, we regard this as intraspecific genetic variability and treat all the sequences as belonging to one variable species.

/Pouzarella clade – subgen. *Pouzarella*

Entoloma* subgen. *Pouzarella (Mazzer) Noordel., *Persoonia* **12**(3): 196. 1984. MB 840563.

Basionym: *Pouzarella* Mazzer, *Bibliotheca Mycol.* **46**: 69. 1976. MB 18357.

Type species: *Entoloma nodosporum* (G.F. Atk.) Noordel.

The /*Pouzarella* clade coincides with *Entoloma* subgen. *Pouzarella*, a well-supported and delimited clade within *Entoloma* (Fig. 1) characterised by a mycenoid (-inocyboid) habit, a non-hygrophanous pileus with metallic-shining, fibrillose-hairy or subsquamulose surface, encrusting pigments in all tissues and the absence of clamp-connections. Sometimes they look very similar to tiny *Inocybe* species. Most species are rarely recorded but considering their small brownish basidiomata and their preference for shady, damp places in forest undergrowth, they are most likely overlooked. *Pouzarella* species occur worldwide (Fig. 28), which is reflected in a number of publications. Detailed monographic studies in Europe (Noordeloos 1979), North America (Mazzer 1979) and SE Asia (Horak 1980) already showed a remarkable species diversity. Regional studies confirmed this diversity (He *et al.* 2018, 2018, China; Baroni *et al.* 2008, Dominican Republic and Jamaica; Baroni *et al.* 2012, Argentina; Raj & Manimohan 2017, India; Karstedt *et al.* 2007, Brazil; Largent *et al.* 2011b, Australia). Despite the rather limited material we had at hand, it appeared from our phylogenetic studies that the number of well delimited species in Europe is higher than known so far, and new species needed to be described, and neotypes to be designated.

/Versatilis subclade

This moderately supported subclade (ML 78 %) coincides with *Entoloma* sect. *Versatilia* containing its type species *E. versatile*. The frequent *E. araneosum* and the less common *E. canosericeum* also belong to this clade, as well as several unnamed lineages and a few that we describe as new to science.

Entoloma araneosum (Quél.) M.M. Moser, *Kl. Krypt.-Fl. (Stuttgart)* **2b/2**: 208. 1978. MB 313665.

Basionym: *Nolanea araneosa* Quél., *Bull. Soc. Bot. France* **23**: 327. 1877.

Synonym: *Entoloma araneosum* f. *robustum* Noordel., *Entoloma s.l., Fungi Europaei* vol. 5 (Saronno) **5a**: 971. 2004. MB 492423.

Typus: Quélet (1877), *Bull. Soc. bot. Fr.* **23**: pl II, fig. 3. (**lectotype**, designated here, MBT 10028206). **Belgium**, prov. Namur, Viroinval, Oignies-en-Thiérache, in rich deciduous forest on calcareous soil, 22 Sep. 2003, M.E. Noordeloos, MEN200314 (**epitype** L0607183, designated here, deposited at L, MBT 10028207); ITS sequence, GenBank KC710056 (Morozova *et al.* 2014a), LSU sequence, GenBank GQ289153, mtSSU sequence, GenBank GQ289293, *RPB2* sequence, GenBank GQ289225 (Co-David *et al.* 2009).

Additional material examined: **Finland**, Satakunta, Sastamala, Mouhijaervi, Salmi, Saviannokka, 18 Sep. 2011, L. Kosonen, FIPUT624-14 (TUR194139). **Germany**, Frankfurt am Main, Stadtwald, Jakobiweiher, in mixed deciduous forest on rich soil, wayside, on soil between leaf litter, 23 Oct. 2023, K. Reschke, KaiR1764 (B); Hessen, near Steinau an der Straße, Ulmbach, Naturreservat Weiherkopf, *Fagus* forest, 16 Oct. 2016, H. Böhning, C. Manz & A. Gminder, aCM02 (B); Sachsen, Lückendorf, Kurwiese, in calcareous grassland, 5 Nov. 2021, A. Karich, IHI-21Ent07 (GLM-F139004). **Norway**, Akershus, Bærum, Ostøya, calcareous mixed forest, 11 Sep. 2009, J. Markussen, T.E. Brandrud & E. Bendiksen, EB 202/06 (O-F-253938); Buskerud, Drammen, Strøtvat, by Boktrykker Köbkes bridge, edge of path in forest with *Acer*, *Fraxinus*, *Sorbus*, *Picea*, 22 Aug. 2014, G. Gulden, GG 4/14 (O-F-302288); Østfold, Moss, Reiertangen, wooded pasture with *Quercus* and *Salix caprea*, 8 Oct. 2012, R. Braathen & E.W. Hanssen (O-F-301579); Telemark, Kragerø, Kammerfossåsen, rich forest with *Tilia*, *Populus* and *Fraxinus* on amphibolite bedrock, 13 Jul. 2016, T.E. Brandrud, TEB 37a-16 (O-F-304846); Telemark, Bamble, Høgenheitunnelen V, calcareous *Tilia* forest, 20 Jul. 2016, T.E. Brandrud, TEB 66-16 (O-F-304862); *ibid.*, Bunestoppen, calcareous broad-leaved forest with *Corylus*, *Fraxinus*, *Quercus*, *Alnus incana*, *Betula* and *Equisetum hyemale*, 2 Oct. 2022, B. Rian, M.S. Olsen, E41 (O-F-204238); Oslo, Oslo, Vollebekk, Sep. 2022, E. Bendiksen, EB 287/22 (O). **Russia**, Moscow Oblast, Odintsovsky District, Zvenigorod Biological Station of Moscow State University, on soil in mixed forest, 12 Aug. 2013, E. Voronina (LE F-254043); Ulyanovsk Oblast, on chalk soil in *Tilia* forest, 9 Aug. 1990, A.I. Ivanov (LE F-18948, as *E. fulvostrigosum*); Samara Oblast, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana Village, Yagodnoye Pole, *Tilia cordata*-*Acer platanoides* forest, 5 Jul. 2005, E. Malysheva (LE F-234321); St Petersburg, Peter the Great Botanical Garden, on soil under *Tilia cordata* and *Acer platanoides*, 22 Sep. 2006, O. Morozova, Mycotheca Petropolitana, № 60 (LE F-262196); Pskov Oblast, Bezhanitsy District, Tzevlo Village, on soil in remnant of manor park with old-growth *Tilia*, 7 Sep. 2019, L. Kalinina (LE F-330284); Pskov Oblast, Pushkinogorsky District, between Bugrovo and Mikhailovskoye villages, on soil on roadside in a mixed forest, 11 Sep. 2018, O. Morozova, 3PG18 (LE F-315954); Karachay-Cherkess Republic, Teberda State Biosphere

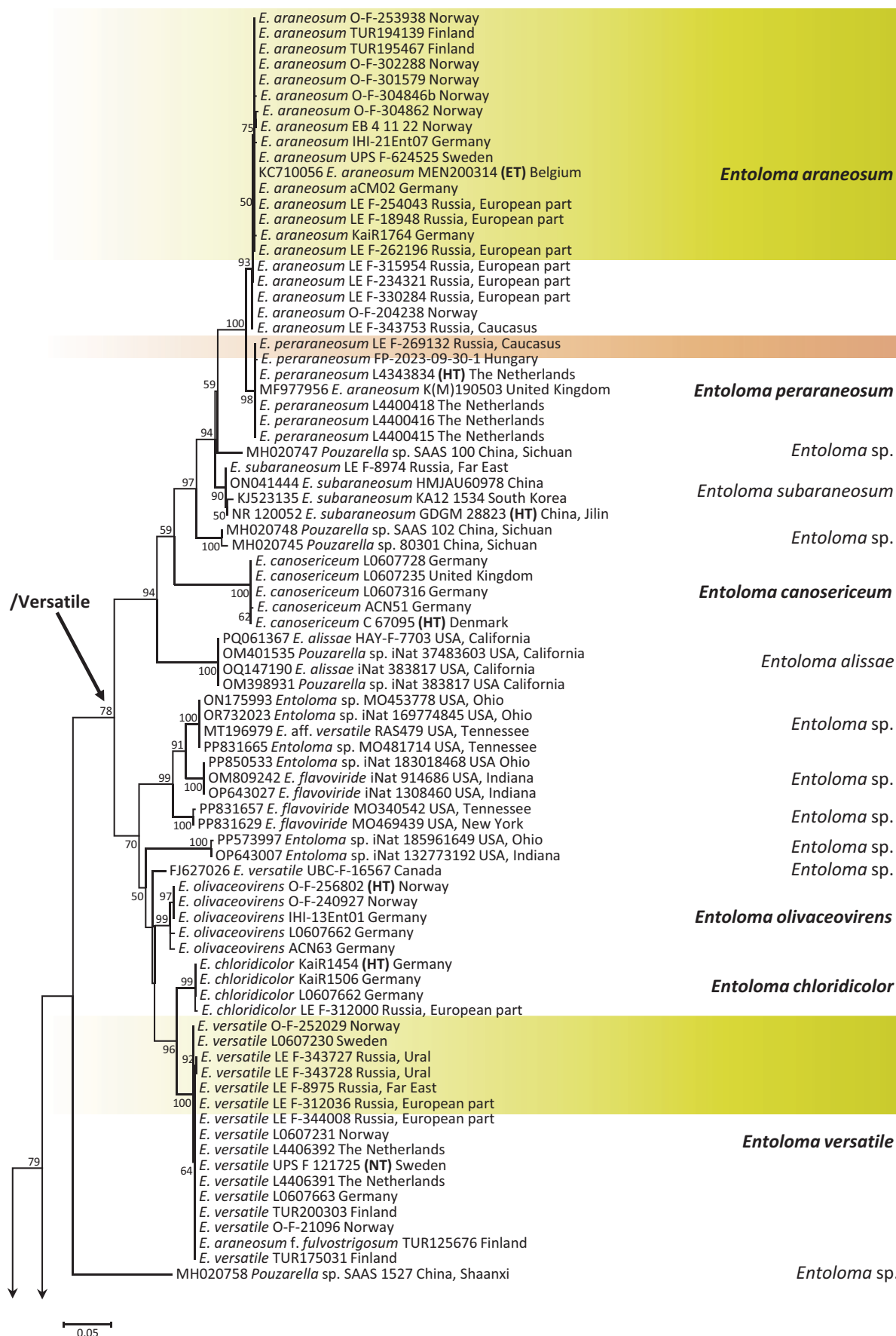


Fig. 28. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* subgen. *Pouzarella* (= /Pouzarella clade). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.

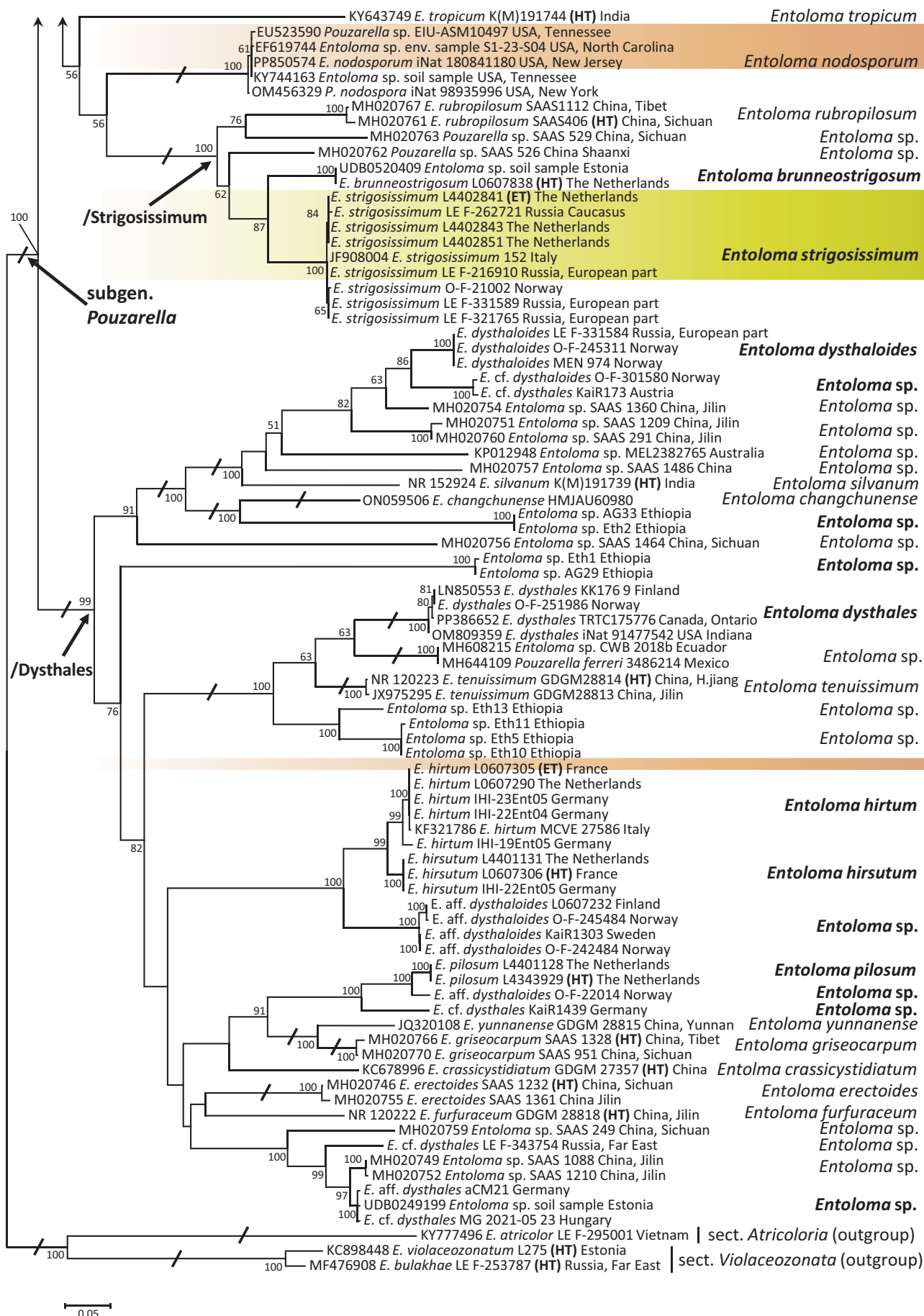


Fig. 28. (Continued).



Reserve, Arkhyz site, vicinity of the Bukovo Village, on soil in *Fagus orientalis*-*Carpinus betulus* forest, 22 Aug. 2009, O. Morozova, 228TB09 (LE F-343753). **Sweden**, Medelpad, Borgsjö, Granboda, 31 Aug. 1993, M.E. Noordeloos, MEN 93131 (L, **holotype** of *E. araneosum* f. *robustum*); Uppland, Uppsala, Kronåsen, under *Sambucus racemosa*, 12 Sep. 1980, S. Ryman, 5877 (UPS F-624525).

Notes: There is no original herbarium material of this species, but a description and plate are available. The latter is designated as lectotype (above). An epitype is designated to support the current concept with an ITS barcode. A full description and illustrations will be given in the forthcoming monograph (see introduction).

Entoloma canosericeum (J.E. Lange) Noordel., *Nordic J. Bot.* 2(2): 157. 1982. MB 110637. Fig. 29.

Basionym: *Rhodophyllus canosericeus* J.E. Lange, *Fl. Agaric. Danic.* 5(Taxon. Consp.): VIII, 98. 1940. MB 374415.

Typus: **Denmark**, Fyn, Kværndrup, on damp soil in old growth deciduous woodland, 14 Sep. 1938, J. Lange (**holotype** C-F-67095); ITS sequence, GenBank PX440385.

Description (amended here): *Basidiomata* mycenoid. *Pileus* 10–25 mm wide, conical, expanding with age to convex with broad umbo, slightly hygrophanous, deeply translucently striate when moist, fairly dark grey brown, sometimes with olivaceous hue, pallescent on drying, but later often turning blackish when very old, radially fibrillose to almost smooth, but in dry state somewhat felted-fibrillose. *Lamellae* moderately distant [$L = 20\text{--}36$, $I = 1\text{--}3(-5)$], adnate to almost free, ventricose, pale grey to dark grey, finally tinged pink, turning blackish when old, with an entire, concolourous edge. *Stipe* 20–60 × 1–3 mm, cylindrical, apex brown grey, downward grey to dark grey or almost black, over the whole length covered with silvery fibrils. *Context* thin, concolourous with surface. *Smell* indistinct, *taste* not noted. *Basidiospores* (110/5) 9.0–12.0 × 6.5–8.0(–8.5) µm, on average 10.4–11.0 × 7.2–7.6 µm, $Q = 1.20\text{--}1.40$, $Q_{av} = 1.25\text{--}1.30$, 5–6-angled in side view with rounded angles. *Basidia* 30–60 × 10.5–18 µm, 4-spored, necrobasidia frequent. *Cheilocystidia* 35–70(–80) × 10.5–18 × 2–4 µm, slender to broadly lageniform, often with long, protruding and slender neck, numerous. *Hymenophoral trama* regular, made up of cylindrical cells, 270–400 × 25–57 µm, often with minutely encrusted walls. *Pileipellis* a simple cutis of narrow, cylindrical, 4–11 µm wide



Fig. 29. *Entoloma canosericeum* (A. L0607728; B–D. L0607316). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. Photos: A by T. Glaser; B by G. Wölfel. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores), 20 µm (cheilocystidia).



hyphae, with minutely encrusted walls. *Stipitipellis* cutis of cylindrical hyphae 5–12 µm wide, with encrusted walls, and pale brown intracellular pigment. *Caulocystidia* absent. *Clamp-connections* absent (see notes).

Habitat and distribution: In damp places in broad-leaved forest on black soil. Known from Denmark, Germany and the United Kingdom.

Additional material examined: **Germany**, Bayern, Chiemsee, mixed broad-leaved forest on moist soil, 5 May 2019, T. Glaser (L0607728); Nordrhein-Westfalen, Sauerland, Rosengartenweg bei Geseke, in deciduous woodland, 1 Jun.

2013., G. Wölfel, E02/3 (L0607316); Nordrhein-Westfalen, Witten, Hohenstein, 30 Sep. 2020, T. Hülsewig, ACN51 (B 70 0105498). **UK**, England, Durham, Peterlee, mixed woodland, 18 Sep. 1970, C. Bas (L0607235).

Notes: Noordeloos (1982) published a redescription of Lange's species, based on a study of the holotype. A second collection made by E. Horak, of which only line-drawings and notes were available, was considered to be identical with the type. However, the material of Horak had abundant clamp-connections, in contrast to the holotype. Horak's collection has not been available for sequencing, unfortunately. Since neither the holotype nor the additional collections have clamp-

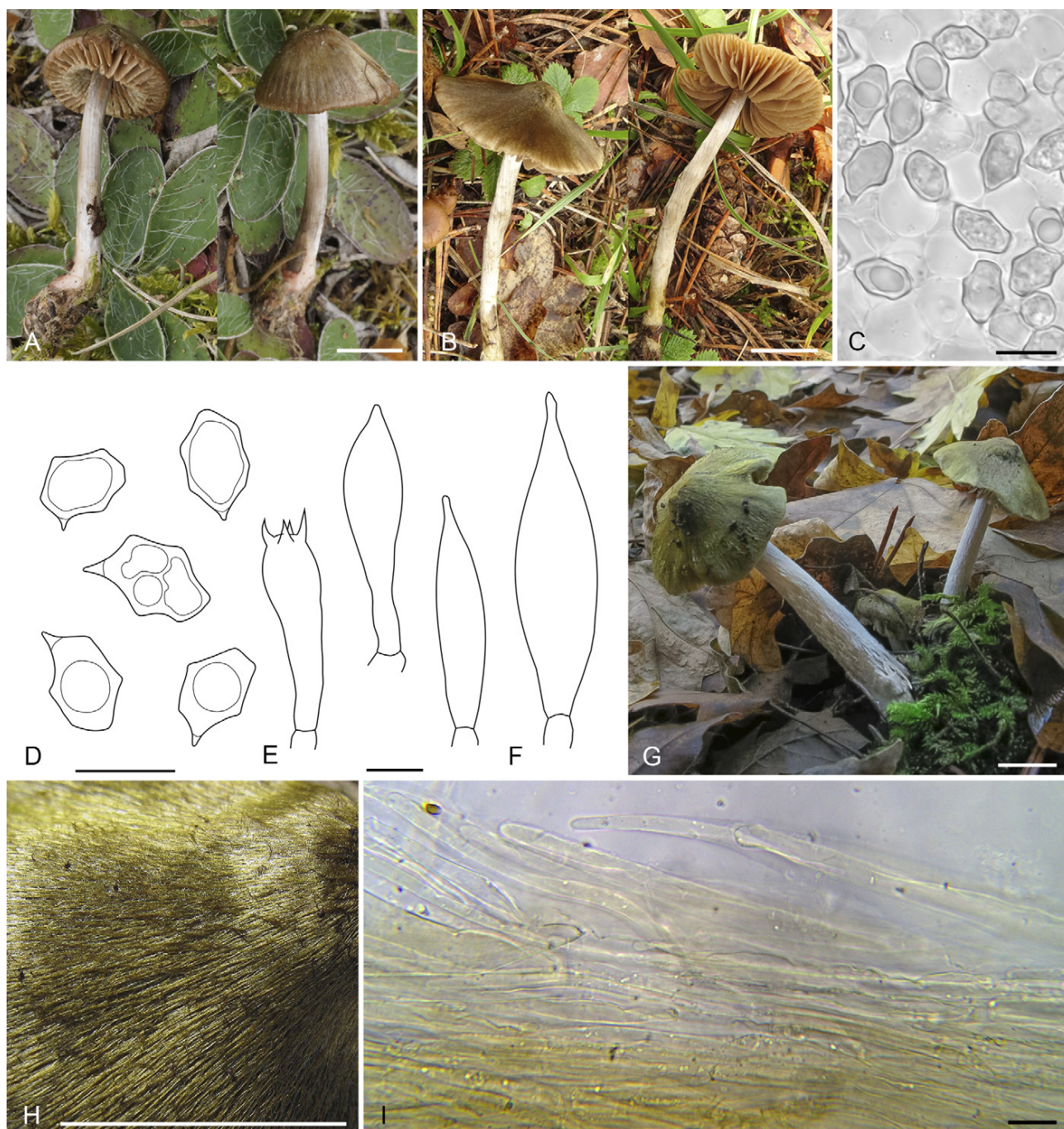


Fig. 30. *Entoloma chloridicolor* (A, B 70 0105521; B, C, I, B 70 0105519, holotype; D–H, LE F-0312000). **A, B, G.** Habit. **C, D.** Basidiospores. **E.** Basidium. **F.** Cheilocystidia. **H.** Pileal surface. **I.** Pileipellis. Photos: A–C, I by K. Reschke; G, H by I. Ukhanova. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores, cheilo- and caulocystidia), 20 µm (pileipellis).



connections, and the fact that the ITS sequences perfectly fit the subgen. *Pouzarella*, which is characterised by the lack of clamp-connections, it is now doubtful whether this second collection cited in Noordeloos (1982) really belongs to the same species. *Entoloma canosericeum* differs from the rest of the members of the */Araneosum* subclade particularly in the deeply translucently striate, fibrillose pileus, and smaller spores with a rounded 5–6 angular outline, and a less differentiated pileipellis of cylindrical hyphae.

Entoloma chloridicolor Reschke, O.V. Morozova, Ukhanova & Noordel., *sp. nov.* MB 860422. Fig. 30.

Etymology: Referring to the bird *Chloris chloris*, which has similar greenish and brownish grey colours.

Typus: **Germany**, Hessen, Wingertsberg, Bockenau, on soil between leaf litter at the edge of a calcareous grassland, 9 Nov. 2019, K. Reschke, KaiR1454 (**holotype** B 70 0105519); ITS sequence, GenBank PX412029.

Description: *Basidiomata* mycenoid. *Pileus* 20–50 mm wide, conical, expanding to conico-convex, slightly hygrophanous, not translucently striate or at margin only, variable in colour from dark brown to greyish brown to greenish-olivaceous, slightly pallescent from centre upon drying, minutely to rather pronouncedly silky fibrillose with micaceous sheen. *Lamellae* (L = 24–36, I = 3–7), distant, adnate-emarginate, ventricose, up to 10 mm broad, brown to greyish brown with pink tinge, with paler, fimbriate, slightly glistening edge. *Stipe* 35–85 × 1–6 mm, cylindrical, pale brown to pale grey brown, appearing paler by the dense whitish fibrillose covering, shiny. *Context* in pileus olivaceous brown to brown in pileus and stipe. *Smell* indistinct. *Taste* somewhat farinaceous. *Basidiospores* (60/4) 9.5–12.0(–13.5) × 6.5–8.0 µm, on average 10.6–11 × 7.0–7.5 µm, Q = 1.35–1.70(–1.90), Q_{av} = 1.40–1.50, 5–8 angular in side view. *Basidia* 36–46 × 9.5–11.5 µm, 4-spored, clavate, frequently with brown necropigment, clampless. *Lamella edge* heterogeneous with numerous lageniform to clavate-mucronate cheilocystidia, 65–150 × 15–31 × 3–5 µm. *Pleurocystidia* scattered, similar to cheilocystidia. *Hymenophoral trama* two-layered, with subcellular subhymenium with minutely encrusted walls, mediostratum regular, made up of cylindrical to subfusiform, 7–20 µm wide elements with membranal, and minutely encrusted walls. *Pileipellis* a loose cutis with transitions to a trichoderm of cylindrical hyphae with fusiform to subclavate terminal elements, 180–450 × 6–12 µm, gradually passing into pileitrama, subpellis not distinctly differentiated. *Pileitrama* regular, made up of cylindrical to inflated elements, up to 280 × 8–31 µm. *Pigment* in pileipellis mainly intracellular, diffuse and granular, in addition encrusted in pileipellis, hymenophoral, pilei- and stipititrama. *Stipitipellis* a cutis of cylindrical, 5–13 µm wide hyphae with brown encrusted walls, and light yellow brown, intracellular pigment. *Caulocystidia* absent, but outer stipitipellis hyphae with abundant cylindrical to slightly clavate, sometimes somewhat capitate outgrowths, up to 45 × 7.5 µm, mainly without septa, so continuous with stipitipellis hyphae, not encrusted. *Clamp-connections* absent.

Habitat and distribution: Terrestrial in grasslands, in litter in broad-leaved forest (*Quercus*, *Fagus*) and mixed forest (*Pinus*, *Acer*), on calcareous soils. Known from a few localities in Germany and Russia.

Additional material examined: **Germany**, Hessen, Wingertsberg, Bockenau, in calcareous grassland, 9 Nov. 2019, G. Wölfel (L0607662); Baden-Württemberg, Schwäbische Alp, Schelklingen, Justingen, Schachenheide, on soil in calcareous grassland, 3 Oct. 2023, S. Adamčík, KaiR1506, (as *E. canosericeum*; B 70 0105521). **Russia**, Stavropol Krai, Grachevsky District, near Krasnoye Village, on calcareous soil in *Pinus sylvestris* and *Acer* sp. planting, 26 Oct. 2011, I. Ukhanova (LE F-312000).

Notes: *Entoloma chloridicolor* is phylogenetically distinguishable from both *E. versatile*, and *E. olivaceovirens*. The holotype had a brown grey pileus, but additional material from Russia shows distinct green colours, like in *E. versatile*. So, they represent barcode species that cannot always be distinguished morphologically. *Entoloma canosericeum* differs among other features by having smaller basidiospores.

Entoloma olivaceovirens J.B. Jordal, Noordel. & Dima, *sp. nov.* MB 860423. Fig. 31.

Etymology: *olivaceus* (Lat.) – olivaceous, and *virens* (Lat.) – being green, referring to the colours of the basidiomata.

Typus: **Norway**, Møre & Romsdal, Ålesund, Fylling, on soil in *Corylus* forest, 25 Sep. 2019, P.R. Tingve, JBJ19-073 (**holotype** O-F-256802); ITS sequence, GenBank PX412051.

Description: *Basidiomata* inocyboid. *Pileus* 20–30 mm wide, conical to conico-convex with straight margin, not hygrophanous or translucently striate, olivaceous yellow, dark greyish with green shine of dark olivaceous, sometimes with paler, olivaceous yellow margin, entirely and coarsely radially fibrillose, reminiscent of an *Inocybe*. *Lamellae* moderately distant to fairly crowded [L = 36–50, I = 1–3(–5)], ascending, narrowly adnate, almost free, ventricose, dark grey, with pinkish tinge when mature, with slightly irregular, concolourous edge. *Stipe* 30–40 × 1–3, cylindrical, dark grey with green tinge, strongly silvery-fibrillose striate lengthwise, base with greyish mycelial tomentum. *Context* thin, concolourous with surface. *Smell* indistinct, *taste* not noted. *Basidiospores* (100/5) 7.5–11.0 × 6.5–8.0(–8.5) µm, on average 9.0–10 × 7.0–7.5 µm, Q = 1.20–1.60, Q_{av} = 1.35–1.40, rather regularly 5–7-angled in side view with pronounced angles. *Basidia* 45–60 × 7–15 µm, 4-spored, clamped, necrobasidia frequent. *Lamella edge* almost sterile. *Cheilocystidia* prominent, 60–120 × 9–25 µm, fusiform to lageniform, thin-walled. *Pleurocystidia* present close to edge, similar to cheilocystidia. *Hymenophoral trama* with distinct hymenopodium, two-layered, regular, made up of cylindrical, 4–12 µm wide hyphae, with subcellular subhymenium with minutely encrusted walls, mediostratum regular, comprising cylindrical, 20–30 µm wide elements with membranal, sometimes minutely encrusted walls. *Pileipellis* a cutis with transitions to a trichoderm of fusiform to subclavate terminal elements, 90–170(–200) × 12–21 µm. *Pileitrama* regular, of cylindrical to inflated elements, up to 280 × 8–31 µm. *Pigment* membranal to finely encrusting in the pileipellis and pileitrama, in addition granular-intracellular in pileipellis. *Clamp-connections* absent.

Habitat and distribution: In semi-natural grassland, also found on bare soil in mixed broad-leaved forest with *Fagus*



on calcareous loam. Known from a few places in Norway and Germany.

Additional material examined: **Germany**, Niedersachsen, Landkreis Holzminden, south of Holzminden, among leaf litter at a moist edge of the creek Holzminde, with *Corylus*, *Acer*, *Fagus*, *Alnus*, 5 Nov. 2023, R. Dost & F. Hampe, ACN63

(B 70 0105499); Nordrhein-Westfalen, Teutoburgerwald, Bad Meinsberg, among leaf litter in deciduous forest, 25 Aug. 1965, C. Bas, 4567 (L0607662); Sachsen, Oybin, Hausgrund, humose wet soil near calcareous spring, 5 Jul. 2017, A. Karich, IHI-13Ent01 (GLM-F139001). **Norway**, Møre & Romsdal, Ålesund, Litj-Kalvøya, Plassen, 5 m.a.s.l., 25 Sep. 1999, D. Holtan & J.B. Jordal (O-F-240927).

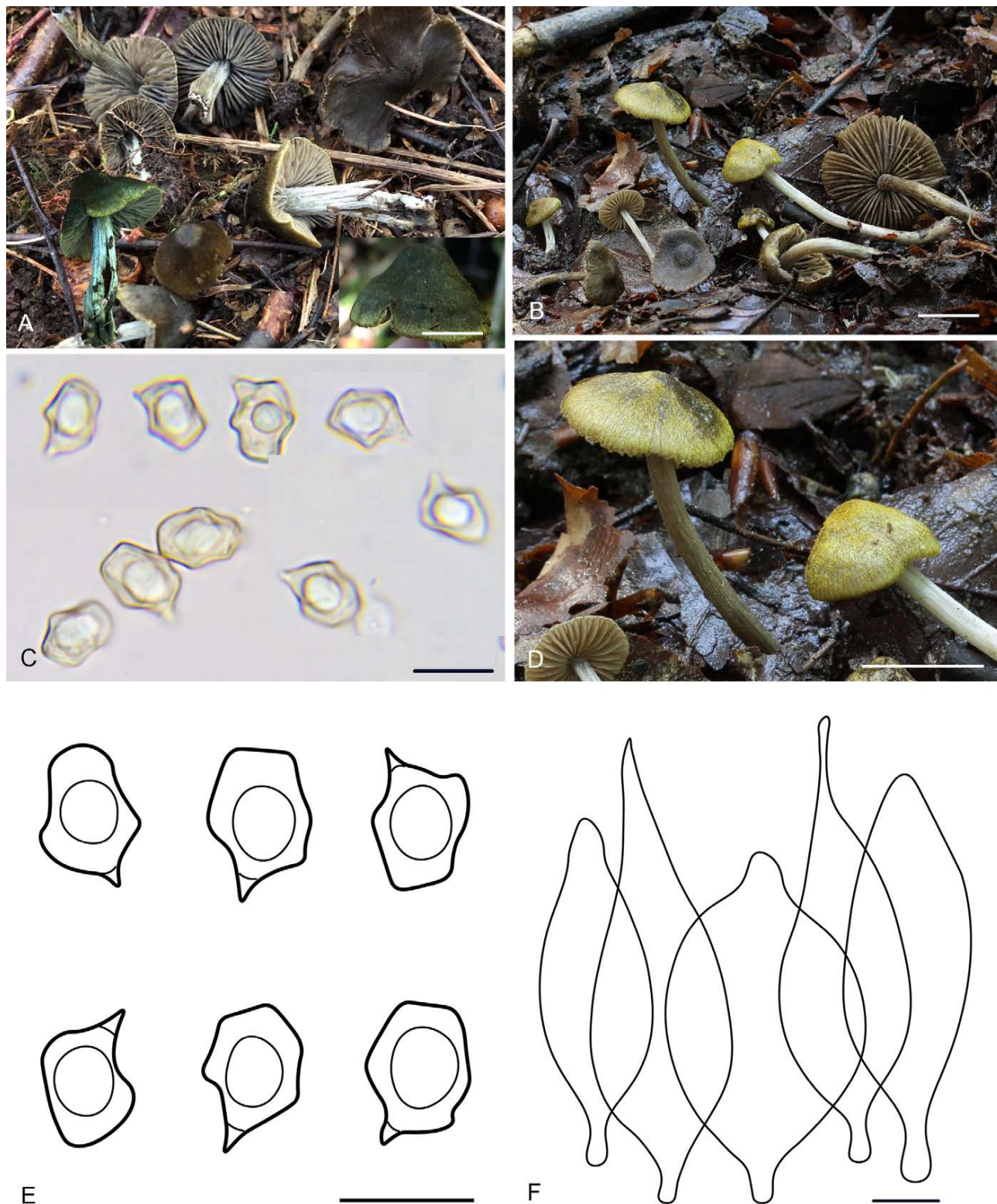


Fig. 31. *Entoloma olivaceovirens* (A. O-F-256802, holotype; B–D. IHI-13Ent01). **A, B, D.** Habit. **C, E.** Basidiospores. **F.** Cheilocystidia. Photos: A by P.R. Tingve; B–D by A. Karich. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (microstructures).



Notes: *Entoloma olivaceovirens* is a striking and beautiful species with its deep olivaceous grey colours, more intense than in the closely related *E. versatile*. In addition, the surface of the pileus is strongly fibrillose, reminiscent of an *Inocybe* species.

Entoloma peraraneosum G.M. Jansen, Noordel., Finy & Dima, **sp. nov.** MB 860424. Fig. 32.

Etymology: περ (Greek) – besides, along, referring to the close similarity with *E. araneosum*.

Typus: **The Netherlands**, prov. Utrecht, Breukelen, Nijenrode, in rich deciduous parkland on calcareous clay, 17 Oct. 2015, G.M. Jansen, C15-2707 (**holotype** L4343834); ITS sequence, GenBank PX412056.

Description: *Basidiomata* inocyboid. *Pileus* 10–20 mm wide, conico-convex, with straight margin, not hygrophanous or translucently striate, greyish brown, strongly radially fibrillose with paler, loose fibrils, sometimes appearing virgate. *Lamellae* distant (L = 20–26, l = 1–3), adnate-emarginate, ventricose, brown with slightly paler edge. *Stipe* 50–60 × 1–2 mm, cylindrical, slightly broadened at base, brown like the pileus, darker towards the base, minutely hairy with slightly paler fibrils on the entire length, with strigose hairs at base. *Context* thin, concolourous with surface. *Smell* and *taste* farinaceous. *Basidiospores* (60/4) 10.5–15.0 × 7.0–9.0 µm, on average 11.5–13.5 × 7.7–8.5 µm, Q = 1.35–1.80, Q_{av} = 1.60–1.70, 5–7-angled with rather pronounced angles. *Basidia* 4-spored, clampless. *Lamella edge* sterile. *Cheilocystidia* 70–115 × 20–40 × 2–5 µm, lageniform with long, tapering neck. *Pleurocystidia* sparse, similar to cheilocystidia. *Pileipellis* a cutis with transitions to a trichoderm, hyphae 4–9 µm wide, overlaying a darker layer of encrusted hyphae. Intracellular pigment not observed. *Stipitipellis* a cutis with transition to a trichoderm of narrow hyphal elements, with brown incrustations. *Clamp-connections* absent.

Habitat and distribution: Terrestrial on heavy clay soil in broad-leaved woodland and parkland. Known from three localities in The Netherlands, and one in Hungary, and one in Russia (Caucasus).

Additional material examined: **Hungary**, Vértess, Oroszlány, Gerencsérvár, in mixed deciduous forest, 30 Sep. 2023, P. Finy, FP-2023-09-30-1 (ELTE). **Russia**, Adygea Republic, Western Caucasus, Maykop District, vicinities of the Nikel Settlement, valley of the Syuk stream, overgrown sandbank, on soil in thickets of *Alnus*, 11 Sep. 2010, A.A. Kiyashko (LE F-269132). **The Netherlands**, prov. Zuid-Holland, Ridderkerk, Huijs ten Donk, deciduous parkland on heavy, calcareous clay, 12 Nov. 1977, T.W. Kuyper (L4400415); prov. Utrecht, Breukelen, Nijenrode, deciduous parkland on heavy, calcareous clay, 4 Nov. 1987, G. Immerzeel (L4400416); prov. Limburg, Valkenburg, Schaeltbergerbos, deciduous forest on calcareous loam, 20 Oct. 1991, E. Arnolds & P.J. Keizer (L4400418).

Notes: *Entoloma peraraneosum* is morphologically very similar to *E. araneosum*, however, it might be somewhat slenderer,

and its ITS sequence differs by 2 % (11–12 substitution and indel positions) from that of typical *E. araneosum*.

Entoloma versatile (Gillet) M.M. Moser, *Kl. Krypt.-Fl. (Stuttgart)* **2b/2**: 209. 1978. MB 313845.

Basionym: *Nolanea versatilis* Gillet, *Hyménomycètes (Alençon)*: 414. 1876. MB 178182.

Replaced synonym: *Agaricus versatilis* Fr., *Monogr. Hymenomyc. Suec. (Upsaliae)* **2(2)**: 297. 1863. MB 487577, nom. illegit., non *Agaricus versatilis* Bertero & Mont., in Montagne, *Annls Sci. Nat., Bot., sér. 2* **8**: 368. 1837. MB 102621.

Characteristics: *Basidiocarps* mycenoid. *Pileus* 15–30 mm broad, conical or campanulate then conico-convex, usually with small papilla, weakly hygrophanous, when moist not translucently striate or at margin only, usually rather dull-coloured olivaceous brown to olivaceous grey, occasionally more yellowish green, slightly paler when dry, glabrous or with innate fibrillose covering, sometimes minutely squamulose at centre, shining. *Lamellae*, distant, narrowly adnate to deeply emarginate, ventricose, grey then grey brown, finally with pink tinge, with floccose, concolourous edge. *Stipe* 25–50 × 2–3 mm, cylindrical, sometimes slightly broadened at base, pallid at apex, downwards grey to dark grey with distinct olivaceous tinge, at base often with reddish tinges, entirely striate to floccose with silvery fibrils, base strigose with white or reddish radiating hairs. *Context* thin, dark brown. *Smell* none or somewhat acidulous-spermatial. *Taste* not recorded. Terrestrial in humus of mixed or deciduous forest, along roadsides etc., preferably on rich, humus-rich soils. *Basidiospores* (9.0–)9.5–11.5(–12.5) × 7.0–8.0(–9.0) µm, Q = 1.20–1.50, Q_{av} = 1.30–1.40, heterodiametrical, 5–8-angled in side-view. *Basidia* 4-spored, clampless. *Lamella edge* heterogeneous. *Cheilocystidia* (40–)60–110 × 10–25 µm, narrowly to broadly lageniform with broad basal part and long, tapering neck with thin, colourless walls, numerous, but always mixed with basidia. *Pileipellis* a transition between a cutis and a trichoderm, made up of radially arranged, cylindrical to inflated hyphae with up to 20 µm wide terminal elements. *Pigment* pale olivaceous-brown, intracellular in pileipellis, in addition also minutely encrusting the hyphae of lower pileipellis and upper pileitrama. *Clamp-connections* absent.

Typus: **Holotype** not existing. **Sweden**, Uppland, Uppsala, Kronåsen terrestrial in forest under *Sambucus*, in company with *Entoloma araneosum* and *Melanophyllum echinatum*, 15 Sep. 1980, S. Ryman, 5876 (**neotype** UPS F-121725, designated here, deposited at UPS, MBT 10028205); ITS sequence, GenBank PX412071.

Notes: *Entoloma versatile* is one of the *Pouzarella* species with greenish-olivaceous tinges, which usually are rather pronounced, sometimes more yellow green when perfectly fresh. *Entoloma chloridicolor* tends to become more brown with age, and *E. olivaceovirens* is distinctly deeper green to almost blue green. There is no original material of this species which was first (illegitimately) described by Fries. A neotype from the Uppsala area is designated here to support the current concept with an ITS barcode. A full description will be given in the forthcoming monograph.



/Strigosissimum subclade

This well-supported (ML 100 %) subclade (Fig. 28) contains two European species, viz. *E. strigosissimum*, and the here newly described *E. brunneostrigosum* (see below), as well as three other species from China among which only *E. rubropilosum* has been described.

Entoloma brunneostrigosum Enzlin, Noordel. & Dima, *sp. nov.* MB 860538. Fig. 33A, C–F.

Etymology: *brunneus* (Lat.) – brown; *strigosus* (Lat.) – hairy, referring to the brown hairs on pileus and stipe.

Typus: **The Netherlands**, prov. Groningen, Island of Rottumerplaat, behind the shelter, 4 Nov. 2019, R. Enzlin, E24-081 (**holotype** L0607838); ITS sequence, GenBank PX412027.

Description: *Basidiomata* mycenoid. *Pileus* 8–25 mm wide, 4–6 mm high, broadly conical then semiglobose, later plano-

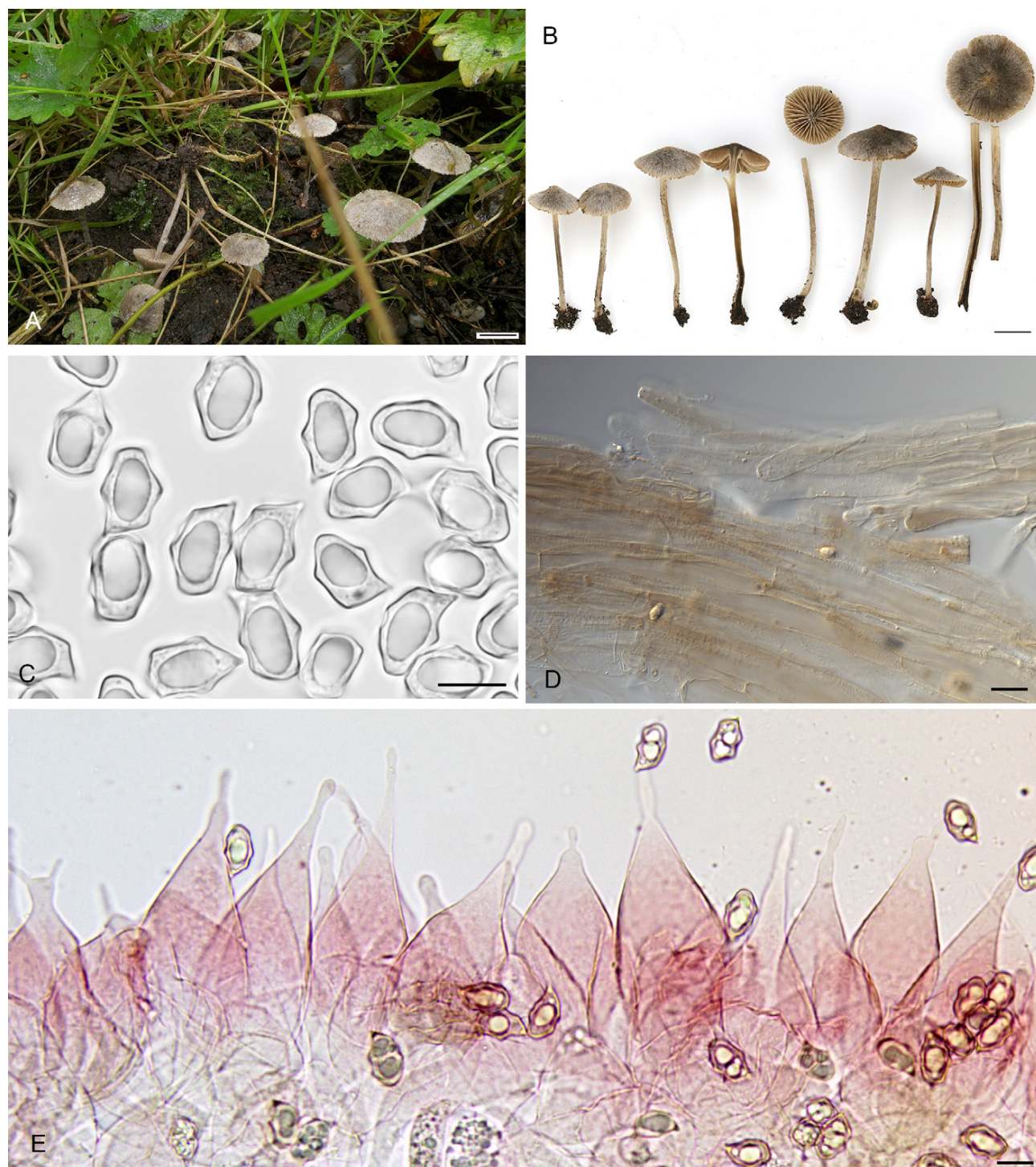


Fig. 32. *Entoloma peraraneosum* (L4343834, holotype). **A, B.** Habit. **C.** Basidiospores. **D.** Pileipellis. **E.** Lamella edge with cheilocystidia. Photos: G.M. Jansen. Scale bars: 1 cm (habit), 10 µm (spores), 20 µm (pileipellis and hymenial cystidia).



convex to applanate with slightly depressed centre with low umbo, with involute then straight margin, dark grey brown to brown at centre, not hygrophanous, not translucently striate, surface coarsely fibrous with uplifted squamules to squarrose. *Lamellae* moderately distant ($L = 20\text{--}30$, $I = 1\text{--}3$), subventricose to segmentiform, narrowly adnate, incarnate grey to dark grey brown with pink tinge, with slightly paler edge. *Stipe* $30\text{--}45 \times 1\text{--}2$ mm, cylindrical, base sometimes enlarged, grey brown, upper part fibrillose, hardly hairy, lower part with patent reddish hairs, basal mycelium of stiff, reddish hairs. *Context* thin, brown. *Smell* and *taste* indistinct. *Basidiospores* (20/1) $14.5\text{--}17.5 \times 7.5\text{--}10$ μm , on average 15.5×9.0 μm , $Q = 1.50\text{--}2.00$, $Q_{\text{av}} = 1.79$, nodulose-angular. *Basidia* 4-spored. *Cheilocystidia* $40\text{--}70 \times 5\text{--}18$ μm , cylindrical, lageniform or slender clavate. *Pileipellis* a cutis with transitions to a trichoderm of $7.5\text{--}15$ μm wide hyphae with thick, coarsely encrusted walls. *Stipitipellis* a cutis of

cylindrical, strongly encrusted hyphae, at base with very long, thick-walled setae with reddish walls and content. *Clamp-connections* absent.

Habitat and distribution: In coarse litter under *Ligustrum* bush on sandy, calcareous soil. So far only known from The Netherlands.

Notes: At first, we considered this collection to be *E. pulvereum* (Fig. 33B) in the sense of Orton and Noordeloos (Noordeloos 1979), but there are discrepancies, in particular in the size of the spores [$10.2\text{--}12.5(13.0) \times 7.0\text{--}8.1(8.7)$ μm , $Q = 1.30\text{--}1.40\text{--}1.60$], and lack of strigose hairs at the stipe base in *E. pulvereum*. It should be re-collected. *Entoloma strigosissimum* is similar but has long setae on the surface of the pileus, which are lacking in our species.

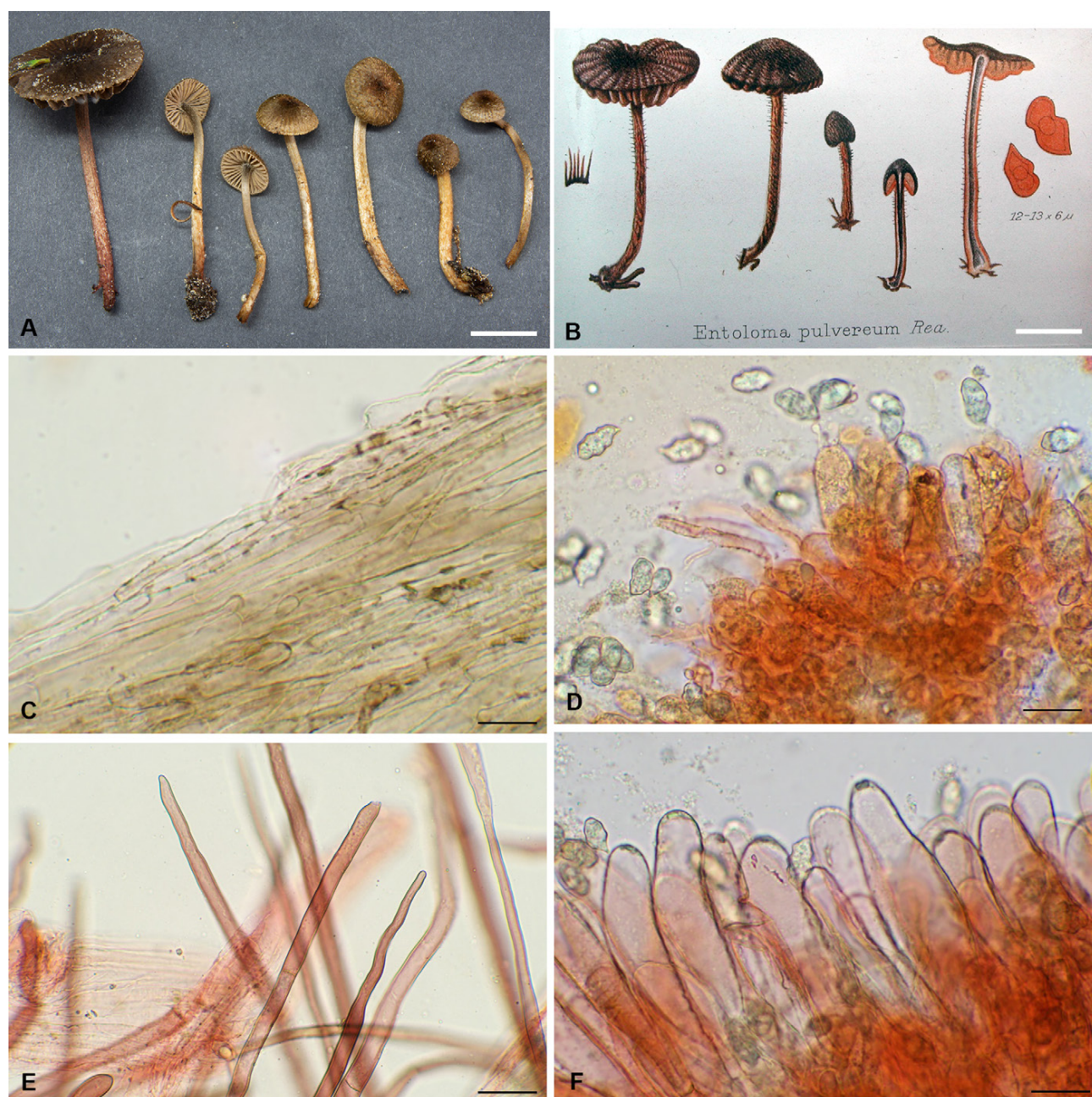


Fig. 33. A, C–F. *Entoloma brunneostrigosum* (L0607838, holotype). B. *Entoloma pulvereum* (Lectotype). A, B. Habit. C. Pileipellis details. D. Basidiospores. E. Setae on stipe. F. Cheilocystidia. Photos: R. Enzlin. Scale bars: 1 cm (habit), 10 μm (microstructures).



Entoloma strigosissimum (Rea) Noordel., *Persoonia* **10**(2): 211. 1979. MB 313822.

Basionym: *Nolanea strigosissima* Rea, *Trans. Brit. Mycol. Soc.* **6**(4): 325. 1920. MB 279003.

Typus: **UK**, England, Surrey, Weybridge, St. George's College, on rotten wood in pine forest, 9 Oct. 1919, Ph. J. Alexander (**holotype** in K, lost); Rea (1920), *Trans. Br. Mycol. Soc.* **6**: 325, pl. VII. (**lectotype**, designated here, MBT 10028209). **The Netherlands**, prov. Zuid Holland, Isl. Voorne, Parnassia Valley, 28 Jun. 1972, C. Bas, 5840 (**epitype** L4402841, designated here, deposited at L, MBT 10028210); ITS sequence, GenBank PX440389.

Notes: Noordeloos (1979) studied the type collection from Kew and depicted some of the microscopical details from this collection. However, a subsequent search for original material in the Fungarium of Kew was not successful, so we assume the type got lost. For that reason, the very informative type-plate of Rea is chosen here as lectotype. In addition, collection L4402841 is designated as epitype, since we were unable to locate recent material from England despite diligent search. This material was part of the description in Noordeloos (1979). For a full description refer to Noordeloos (1979).

/Dysthales subclade

This large basal subclade within subgen. *Pouzarella* (Fig. 28) is well-supported (ML 99 %) and contains *E. dysthales* and *E. dysthaloides* as well as several other, mainly unnamed lineages.

Entoloma dysthaloides Noordel., *Persoonia* **10**(2): 219. 1979. MB 313709. Fig. 34.

Typus: **Austria**, Bludenz, on soil in forest, 6 Jul. 1977, M. Moser, 77/44 (**holotype**, IB; **isotype** L0053995); ITS sequence, GenBank PX440386 (not included in the phylogenetic analysis).

Description: *Basidiomata* mycenoid. *Pileus* 4–12 mm wide, concavo-convex with involute then straight margin, not hygrophanous, dark grey brown or almost black, minutely radially fibrillose to subsquamulose with slightly paler fibrils. *Lamellae* distant (L = 20–25, I = 1–3), narrowly adnate to adnate-emarginate, thickish, very dark grey without distinct pink tinge, with entire, concolourous edge. *Stipe* 15–20 × 1–2.5 mm, cylindrical, concolourous with pileus, covered with silvery fibrils lengthwise, minutely hairy all over with paler, patent hairs, base pale brown, woolly-strigose. *Context* thin, brittle, dark brown. *Smell* and *taste* indistinct. *Basidiospores* (110/5) 9.0–15.5 × 6.5–9.0 µm, on average 12.0–12.5 × 7.6–7.9 µm, Q = 1.30–1.90, Q_{av} = 1.50–1.60, heterodiametrical, 6–9-angled, subnodulose in side view with thickened walls. *Basidia* 35–60 × 10–20 µm, 4-spored, clamped, with necropigment. *Lamella edge* sterile. *Cheilocystidia* 20–60 × 13–45 µm, septate, terminal elements narrowly to broadly clavate or vesiculose or more or less fusiform, with thickened, brown encrusted walls. *Pileipellis* a cutis of repent, 4–18 µm wide hyphae, with broader, up to 25 µm wide, clavate to fusiform terminal elements and coarsely encrusted walls.

Stipitipellis a cutis of 7–14 µm wide hyphae, with patent multiseptate hairs, gradually broadening towards apex, with clavate terminal elements up to 25 µm wide, with brown encrusted walls. *Clamp-connections* absent from all tissues.

Habitat and distribution: Among forest litter in broad-leaved forests, with trees such as *Betula*, *Corylus*, *Quercus*, and *Tilia*, partly dry calcareous sites, partly moist places. Probably widespread, but overlooked, and confused with similar species.

Additional material examined: **Norway**, Innlandet, Hedmark, Tynset, Nytrøya, along Gløta river, on muddy soil near *Betula*, 17 Jul. 1979, M.E. Noordeloos, 974 (L0607228); Telemark, Porsgrunn, Frierflogene, Frierstien, calcareous forest with much *Corylus*, 6 Sep. 2012, T. Læssøe & A. Molia, AM-238b-2012 (O-F-245311). **Russia**, Leningrad Oblast, Lomonosovsky District, Orzhytsy Village, on soil in abandoned park with broad-leaved trees (*Quercus robur*, *Ulmus* sp., *Acer platanoides*, *Tilia cordata*), 31 Jul. 2018, L. Kalinina, LE F-331584. **The Netherlands**, prov. Limburg, Gronsveld, Savelsbos, terrestrial in mixed broad-leaved forest on calcareous loam, 11 Sep. 1977, J. Schreurs & M.E. Noordeloos (L44013661).

Notes: In general, old collections of *Pouzarella* species are quite hard to sequence and thus we have not been able to sequence the isotype of *E. dysthaloides* with Sanger method, but within the frame of the FunDive project (<https://fun-diver.eu/>) using NGS method (Illumina), the ITS2 of the isotype was successfully sequenced and it corresponds well with our current concept of the species. Unfortunately, a good photograph of sequenced material is still lacking.

Entoloma hirsutum Noordel., Trendel, Karich & Dima *sp. nov.* MB 860433. Fig. 35.

Etymology: *hirsutus* (Lat.) – shaggy, roughly, bristly, referring to the aspect of the pileal surface.

Typus: **France**, Grand Est, Alsace, Offendorf, Reserve Naturelle Nationale de la Forêt d'Offendorf, in grassy roadside near *Quercus*, 19 Aug. 2019, J.-M. Trendel, JMT-19081915 (**holotype** L0607306); ITS sequence, GenBank PX412039.

Description: *Basidiomata* mycenoid. *Pileus* 10–15 mm wide, conio-convex, blackish brown to greyish brown, pallescent from centre to dark brown, slightly hygrophanous, translucently striate up to half the radius when fresh, then opaque, ribbed on the back of the lamellae, minutely felted-fibrillose with silvery fibrils, contrasting with the background. *Lamellae* distant (L = 20–24, I = 5–9), adnate-emarginate, segmentiform to ventricose, dark grey pink with fimbriate, concolourous or slightly paler edge. *Stipe* 20–60 × 1–3 mm, concolourous with pileus, minutely felted-fibrillose all over, at base with dark setose hairs. *Context* thin, brittle, concolourous with surface. *Smell* and *taste* indistinct. *Basidiospores* (60/3) 9.5–14 × 6.5–8.0 µm, on average 10–12.5 × 6.9–7.5 µm, Q = 1.45–2.00(–2.10), Q_{av} = 1.55–1.80, nodulose-angular. *Basidia* 25–45 × 8–12 µm, 4-spored, many sclerobasidia present. *Lamella edge* sterile with clavate to fusiform cheilocystidia with brown coloured, strongly brown encrusted



walls. *Pileipellis* a cutis with transitions to a trichoderm of long, septate, 8–15 μm hyphae, strongly brown encrusted, with tapering or subclavate thin-walled, usually non-encrusted terminal elements. *Stipitipellis* a cutis of 8–15 μm wide, more or less cylindrical, encrusted hyphae. *Caulocystidia* 30–100

$\times$ 8–25 μm , flexuose, subclavate or subcylindrical, non-encrusted. *Clamp-connections* absent.

Habitat and distribution: On soil amongst litter or in grass in roadside verges near *Quercus*, on loamy soils, the German

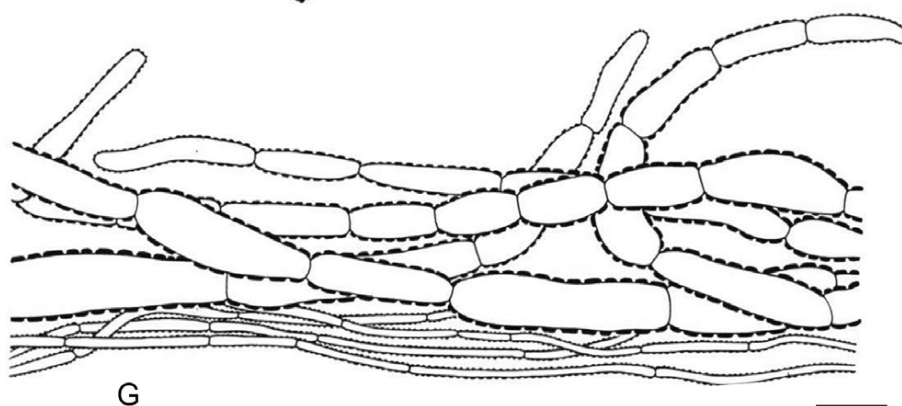
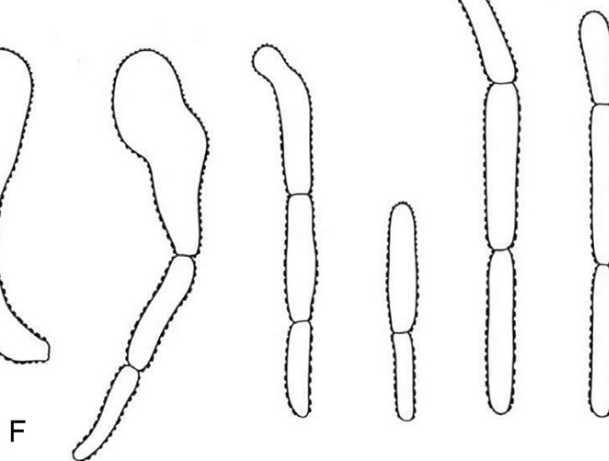
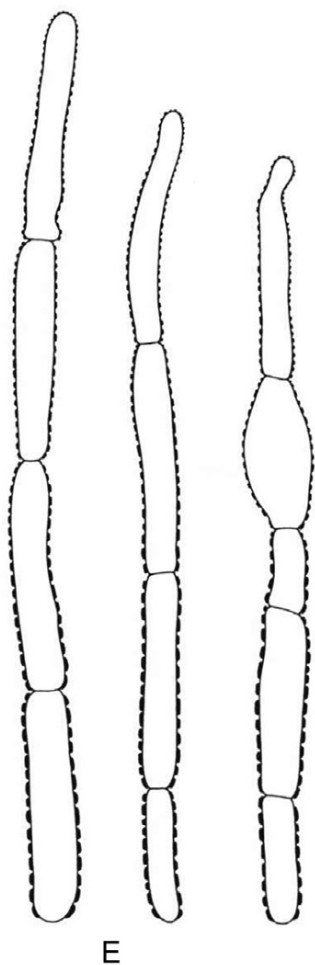
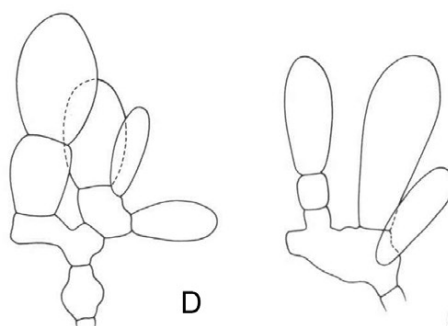
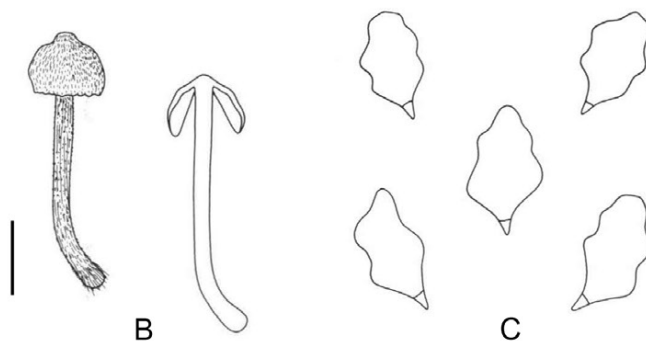
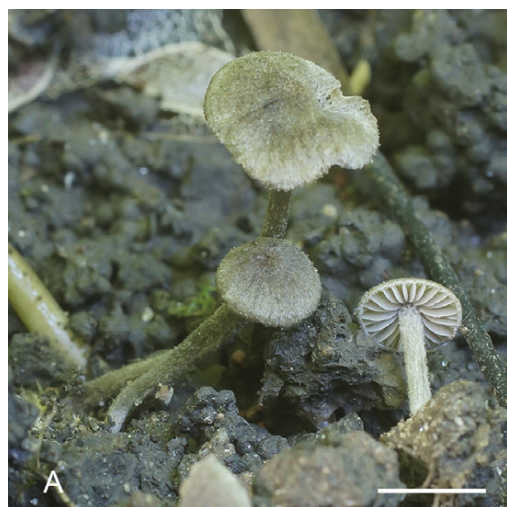


Fig. 34. *Entoloma dysthaloides* (A. LE F-331584; B–G. L0053995, isotype). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Hairs on pileus. **F.** Hairs on stipe. **G.** Pileipellis. Photo: L. Kalinina. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (microstructures).



collection in an old limestone quarry with *Populus tremula*, *Acer platanoides*, some *Betula pendula* and *Corylus avellana*, and with only *Corylus*. Known from France, Germany, and The Netherlands.

Additional material examined: **Germany**, Sachsen, Schöpstal, Kalkbruch, in an old limestone quarry with *Populus tremula*, *Acer platanoides*, some *Betula pendula* and *Corylus avellana*, and with only *Corylus*, 5 Oct. 2022, A. Karich & R. Ullrich, IHI-

22Ent05 (GLM-F139006). **The Netherlands**, prov. Limburg, Venlo, terrestrial among grasses and humus near *Quercus*, 12 Jul. 1986, G.M. Gatzert (L4401131).

Notes: *Entoloma hirsutum* can be distinguished by the narrow spores, strongly membranous encrusted cheilocystidia, and non-encrusted caulocystidia. *Entoloma hirtum* is close, with similar caulocystidia, different cheilocystidia and somewhat broader spores.



Fig. 35. *Entoloma hirsutum* (A. L0607306, holotype; B–F. GLM-F139006). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Caulocystidia. **F.** Pileipellis. Photos: A by J.F.M. Trendel; B–F by A. Karich. Scale bars: 1 cm (habit), 10 µm (all other figs).



Entoloma hirtum (Velen.) Noordel., *Persoonia* 10(2): 223. 1979. MB 313733. Fig. 36.

Basionym: *Nolanea hirta* Velen., *Mykologia* 6(2–3): 25. 1929. MB 267208.

Typus: **Czechia**, Central Bohemia, Radotín, calcareous grassland, Jun. 1926, J. Velenovský (**holotype**, PRM). **France**, Grand Est, Alsace, Dalgrunden, in litter in broad-leaved forest, 15 Oct. 2017, J.-M. Trendel, JMT17101507 (**epitype** L0607305, designated here, deposited at L, MBT 10028208); ITS sequence, GenBank PX412040.



Fig. 36. *Entoloma hirtum* (A. L0607305, epitype; B. GLM-F139003; C–F. Holotype). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Hairs of stipe. **F.** Hairs of pileipellis. Photos: A by J.F.M. Trendel; B by A. Karich. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (all other figs).



Description: *Basidiomata* mycenoid. *Pileus* 10–30 mm wide, 10–15 mm high, conical, conico-campanulate, expanding to conico-convex, surface very dark grey to grey brown, entirely finely fibrillose-subsquamous with adpressed or slightly uplifted, silvery shiny, fibrillose patches, contrasting with the background, slightly hygrophanous, obscurely translucently striate up to about half or two thirds of the pileal radius, sometimes striate from the margin to the centre. *Lamellae* distant ($L = 20\text{--}25$, $I = 3\text{--}7$), adnate-deeply emarginate, ventricose, grey brown with concolourous or slightly paler edge. *Stipe* 20–80 × 2–3 mm, cylindrical, concolourous or slightly paler than pileus, strongly fibrillose-striate, sometimes twisted, and finely pruinose to hairy with silvery patent hairs; with a yellowish brown or reddish brown strigose base. *Context* thin, concolourous with surface, brittle. *Smell* indistinct, *taste* not noted. *Basidiospores* (120/5) (10.0–)10.5–13.0(–14.5) × (6.0–)6.5–8.0 µm, on average 11–12 × 7.0–7.7 µm, $Q = 1.40\text{--}1.90$, $Q_{av} = 1.50\text{--}1.60$, heterodiametrical, 6–9-angled-nodulose in side view. *Basidia* 2- and 4-spored, clampless. *Lamella edge* sterile. *Cheilocystidia* 30–60 × 15–25 µm, ellipsoid to clavate or subfusiform, rather thin-walled. *Pleurocystidia* absent. *Hymenopodium* indistinct, not much differentiated from trama, not encrusted. *Pileipellis* a transition between a cutis and a trichoderm made up of septate hyphae, with subcylindrical to fusiform terminal elements, with yellowish brown, sparsely encrusted walls. *Stipitipellis* a cutis with numerous caulocystidia, usually 2–3 septate, with irregularly clavate, utriform or lageniform terminal elements, and brown, non-encrusted walls. *Clamp-connections* absent.

Habitat and distribution: In thermophilous, semi-natural grasslands on calcareous soil, in litter in *Crataegus* copse in coastal dunes, or in litter in broad-leaved forest. Sequence based records known from France, Germany, Italy (ITS sequence, GenBank KF321786), and The Netherlands.

Additional material examined: **Germany**, Sachsen, Hainewalde, Gampenstein, 19 Sep. 2022, A. Karich, IHI-22Ent04 (GLM-F139005); Thüringen, Krölpa, Buchberg; calcareous thermophilic grassland, 10 Oct. 2019, A. Karich, IHI-19Ent05 (GLM-F139003). **The Netherlands**, prov. Noord Holland, Wijk aan Zee, 2 Nov. 2023, E. Brouwer (L0607290).

Notes: The concept of *E. hirtum* coincides with that of Noordeloos (1979) and Battistin *et al.* (2013b). It is distinguished from the closely related *E. hirsutum* mainly by the slightly broader spores, less strongly encrusted hyphae, and non-encrusted caulocystidia. It also occurs in rather dry grassland habitat besides forests. *Entoloma hirsutum* is very similar, and has slightly narrower spores, and somewhat more pronouncedly encrusted cheilocystidia. Whether these morphological differences stand when more material is studied, needs to be seen. Probably one should consider these two taxa as barcode (“cryptic”) species. Records in literature must therefore be treated with care. Both *E. hirtum* and *E. hirsutum* differ from other species in sect. *Dysthales* by the non-encrusted caulocystidia.

Entoloma pilosum G.M. Jansen, M.v.d. Vegte & Noordel., *sp. nov.* MB 860434. Fig. 37.

Etymology: *pilosus* (Lat.) hairy, referring to the surface of the pileus and stipe.

Typus: **The Netherlands**, prov. Gelderland, Rheden, Heiderust, in moss rich grassy spot on a graveyard, 5 Aug. 2023, M.J.C. van der Vegte & G.M. Jansen (**holotype** L4343929); ITS sequence, GenBank PX412057.

Description: *Basidiomata* mycenoid. *Pileus* 7–16 mm wide, conico-convex to convex, not hygrophanous, not translucently striate, grey brown, sometimes grooved on sides of lamellae, densely hairy fibrillose. *Lamellae* distant, ($L = \text{about } 20$, $I = 1\text{--}3$), narrowly adnate-emarginate, ventricose, grey brown with white, fimbriate edge. *Stipe* 25–60 × 1–3 mm, grey brown, felted-hairy all over like pileus, with pale ochre basal mycelium. *Context* thin, brittle, brown. *Smell* and *taste* indistinct. *Basidiospores* (40/2) 10.0–18.0 × 8.0–10.0 µm, on average 12.5–15.0 × 8.0–8.3 µm, $Q = 1.30\text{--}2.10$, $Q_{av} = 1.45\text{--}1.80$, heterodiametrical, irregularly 8–10-angled, almost nodulose, relatively thick-walled, brown in water. *Basidia* 45–60 × 9–15 µm, 2- and 4-spored. *Lamella edge* sterile. *Cheilocystidia* 46–70 × 15–32 µm, elliptical to clavate, thick-walled, encrusted with brown pigment. *Hymenophoral trama* with well-developed mediostratum of narrow hyphae. *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical, septate, 5–20 µm wide hyphae, with fusiform to clavate terminal elements, 25–90 × 5–20 µm. *Stipitipellis* a cutis with transitions to a trichoderm, of 6–22 µm wide, septate hyphae, with fusiform terminal elements, 30–65 × 5–20 µm. All hyphae of pileipellis, pileitrama and stipitipellis strongly brown encrusted. *Clamp-connections* absent.

Habitat and distribution: Terrestrial, on unpaved roadside in a cemetery, and amongst litter in *Populus* plantation on clay or with *Crataegus*. So far only known from The Netherlands.

Additional material examined: **The Netherlands**, prov. Zeeland, Oostburg, de Plaote, amongst litter in *Populus* plantation, 31 Jul. 1980, A. de Meyer, 124 (L4401128).

Notes: Despite the large barcode gap between *E. dysthaloides* and *E. pilosum*, they are morphologically very similar. The spore size of *E. pilosum* is, however, somewhat larger, more or less intermediate between *E. dysthales* and *E. dysthaloides*, but more material is needed to evaluate these differences.

/Rusticoides clade – subgenus *Omphaliopsis*

Entoloma* subgenus *Omphaliopsis Noordel., *Persoonia* **11**: 148. 1981. MB 90830, **amend.**

Synonym: *Rhodophyllus* sect. *Clitopiloides* Romagn., *Beih. Nova Hedwigia* **59**: 71. 1978. MB 562984.

Entoloma sect. *Clitopiloida* (Romagn.) Noordel., *Persoonia* **11**: 139. 1981. MB 543690.

Clitopiloides (Romagn.) Largent, *Entolomatoid fungi of the Western United States and Alaska* (Eureka): 30. 1994. MB 543690.

Omphaliopsis (Noordel.) P.D. Orton, *Mycologist* **5**(4): 173. 1991. MB 25334.



Type species: Rhodophyllus leptonipes Kühner & Romagn. = *Entoloma incarnatofuscescens* (Britzelm.) Noordel.

The /Rusticoides clade coincides with *Entoloma* subgenus *Omphaliopsis* (Fig. 38). This clade contains species with a predominantly omphalinoid to clitopiloid basidiomata, often isodiametrical spores, encrusting pigment and clampless

hyphae. It is amended here by including *E. sericeoides*, formerly included in subgen. *Clitopiloida*, which now is considered synonymous with *Omphaliopsis*. Ecologically the species in this clade are also rather specialised, as most prefer rather exposed habitats, on bare (mineral) soil or in places with scanty vegetation, such as roadsides, gardens, coastal dunes, (sub-) alpine moraine and other exposed



Fig. 37. *Entoloma pilosum* (L4343929, holotype). **A, B.** Habit. **C.** Basidiospores. **D.** Cheilocystidia and basidium. **E.** Surface of stipe. **F.** Pileipellis. Photos: A, C–F by G.M. Jansen; B by M.J.C. van der Vegte. Scale bars: 1 cm (habit), 10 μ m (microstructures).

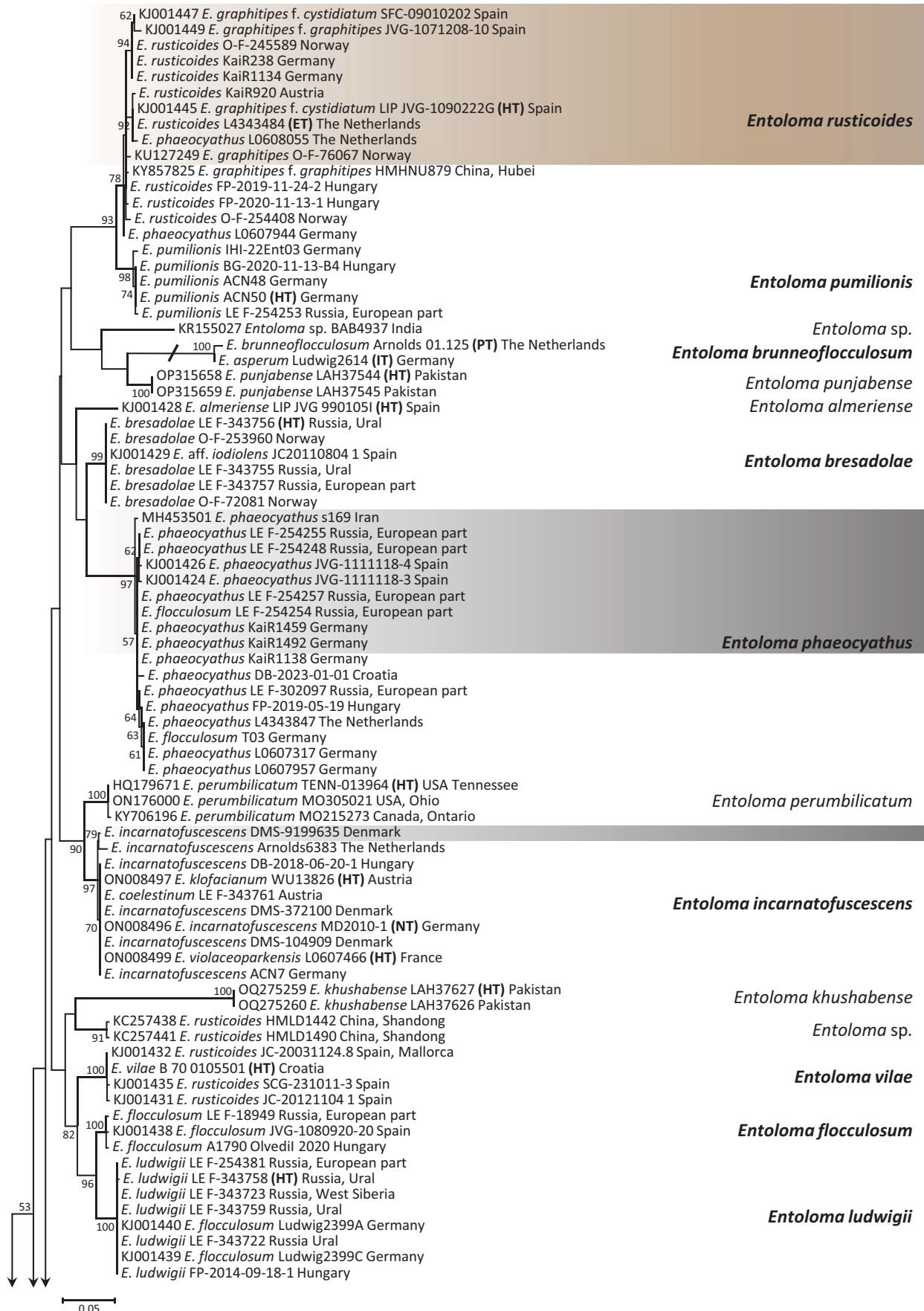


Fig. 38. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* subgen. *Omphaliopsis* (= *Rusticoides* clade). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.

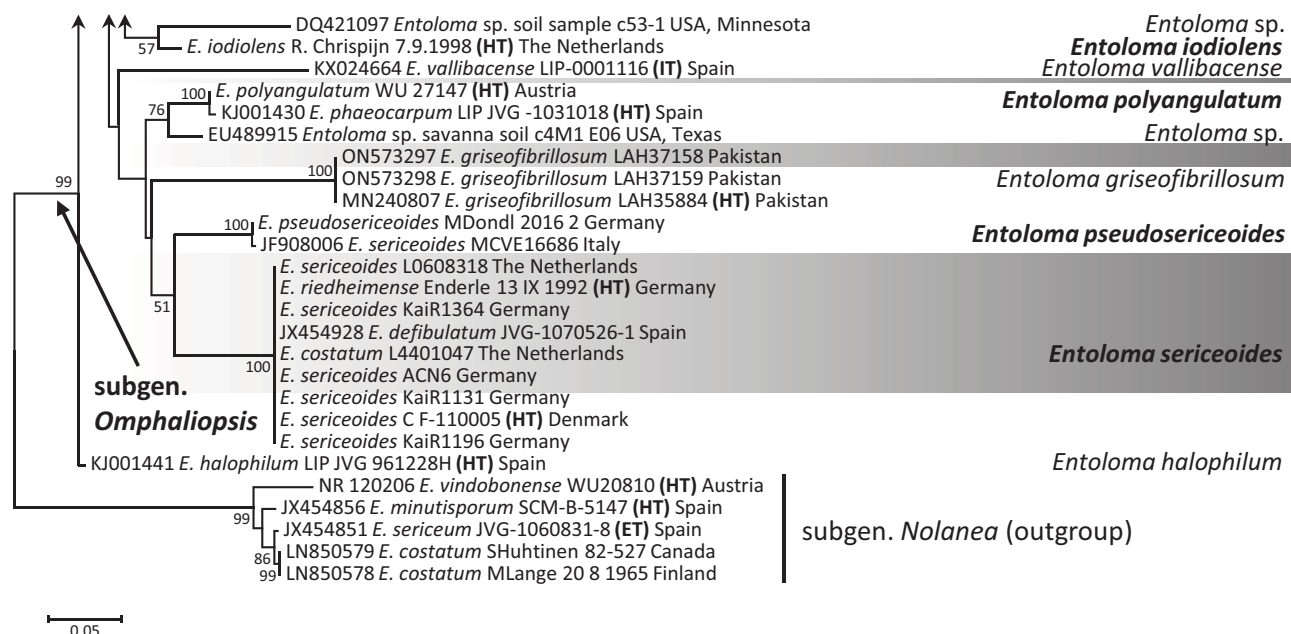


Fig. 38. (Continued).

habitats, xerophytic grassland, and Mediterranean shrub vegetation. An extensive study has been published by Vila *et al.* (2014), which we reflect upon, with some updates and amendments, including typifications. The typification of *E. incarnatofuscescens* was discussed in Noordeloos *et al.* (2022a, b). Subgenus *Omphaliopsis* also includes the gasteroid *E. vallibacense* (Vidal *et al.* 2016).

Entoloma bresadolae O.V. Morozova, Noordel., Reschke, Bendiksen, K. Potapov & A. Filippova, **sp. nov.** MB 860438. Fig. 39.

Etymology: Named in honour of Giacomo Bresadola (1847–1929), an eminent Italian mycologist, author of 1017 species of fungi including some representatives of *Entoloma* subgenus *Omphaliopsis*.

Typus: **Russia**, Sverdlovsk Oblast, Nizhneserginsky District, Arakaev Village, “Deer Creeks” Nature Park, left bank of the Serga River, on soil in steppe meadow, 23 Aug. 2024, A. Filippova & O. Morozova, 128SV24 (**holotype** LE F-343756); ITS sequence, GenBank PX412026.

Description: *Basidiomata* omphalinoid. *Pileus* 7–15 mm wide, depressed in centre, with slightly involute then straight, sometimes crenate margin, hygrophanous, more or less translucently striate, distinctly squamulose, more densely so in the centre, when moist dark yellow brown, or sepia with darker centre, pallescent on drying. *Lamellae* moderately distant ($L = 12\text{--}18$, $I = 1\text{--}4$), broadly adnate-decurrent, arcuate to segmentiform, pale brown, beige then pinkish brown with entire concolourous edge. *Stipe* 10–20 × 1.5–2 mm, cylindrical or slightly broader towards the base, yellow brown with greyish tinge towards the base, smooth, glabrous, solid then fistulose. *Context* concolourous with surface. *Smell* indistinct. *Taste* not reported. *Basidiospores* (100/6) 7.2–8.6 × 6.4–7.5 µm, on average 8.1–8.3 × 7.0–7.3 µm, $Q = 1.0\text{--}1.30$, $Q_{av} = 1.15\text{--}1.20$, subsisdiametrical, with 5–7 weak angles in side view. *Basidia* 32–35 × 11–12 µm, 2–4-spored, clampless.

Lamella edge sterile or heterogeneous. *Cheilocystidia* 24–35 × 7.5–20 µm, clavate, broadly clavate, sphaeropedunculate or lageniform. *Pileipellis* a cutis of radially arranged, 5–8 µm wide hyphae, with transition to a trichoderm with ascending inflated, 15–25 µm wide hyphae with clavate or sphaeropedunculate (54–77 × 29–25 µm) or also fusiform (60–95 × 18–37 µm) terminal elements; subpellis made up of long, inflated, 5–20 µm wide elements. *Hymenophoral* and *pileitrama* regular, made up of long, cylindrical 5–10 µm wide hyphae. *Pigment* abundant in pileipellis and pileitrama, mostly brown and intracellular, sometimes agglutinate, additionally distinctly encrusted. *Stipitipellis* consisting of cylindrical, 6–8 µm wide hyphae, sometimes encrusted. *Caulocystidia* present in upper part of the stipe, similar to cheilocystidia, clavate or sphaeropedunculate. *Clamp-connections* absent.

Habitat and distribution: In xerophytic grasslands or in steppes on sandy, clayey or calcareous soil (one site with semi-natural, mown/grazed grassland). Reported from European Russia including the Ural Mountains, Norway and Spain.

Additional material examined: **Norway**, Akershus, Nesodden: Steilene, on soil in open, calcareous, near-shore grassland with shallow soil, 14 Oct. 2006, *E. Bendiksen*, EB 232/06 (O-F-253960); Buskerud, Drammen, Ryghsetra, on soil in calcareous semi-natural, mown meadow, 11 Aug. 1998, *G. Gulden*, 121/98 (O-F-72081); Innlandet, Oppland, Dovre, Dombås, Hjelldalså, on sand dunes by the river Gudbrandsdalslågen, 11 Aug. 2017, *P.G. Larsen & D. Holtan*, PGL110817 (O). **Russia**, Tatarstan Republic, 23 Sep. 2013, *K. Potapov*, PK11731 (LE F-343757); Kurgan Oblast, Petukhovskiy District, shore of the Medvezhiye lake, salted burnt steppe, on soil, 19 Jul. 2016, *O. Shiryayeva*, 107-07-16 (LE F-343755).

Notes: *Entoloma bresadolae* phylogenetically is sister to *E. phaeocyathus*, which, however, usually has larger and darker basidiomata and significantly larger spores. The name

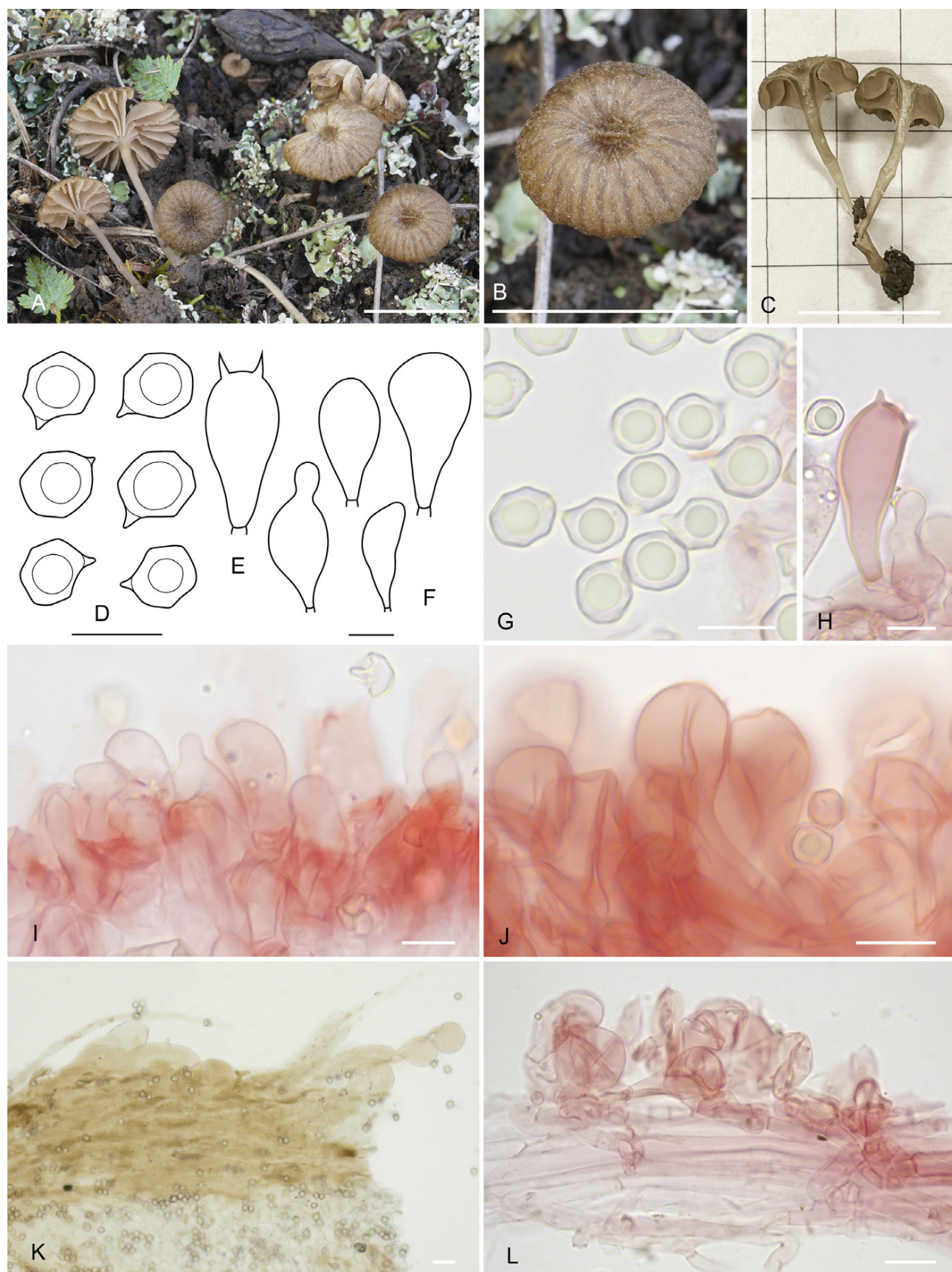


Fig. 39. *Entoloma bresadolae* (A–I, K, L. LE F-343756, holotype; J. LE F-343755). A–C. Habit. D, G. Basidiospores. E, H. Basidia. F, I, J. Cheilocystidia. K. Pileipellis. L. Caulocystidia. Photos: O. Morozova. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (microstructures).



E. phaeocyathus has historically been misapplied to this species in Norway, in red data lists, management documents and species databases. The new species differs from *E. ludwigii*, which occurs in the same habitats and is very similar in appearance, by its hygrophanous, not completely fibrillose pileus, longer stipe, and also by less pronounced incrustations in the pileipellis hyphae.

Entoloma flocculosum Bres. ex Pacioni, *Micol. Veg. Medit.* 2(2): 148. 1988. MB 133932. Fig. 40.

Replaced synonym: *Leptonia flocculosa* Bres., *Iconogr. Mycol.* 12: tab. 577(1). 1929. MB 373505, nom. illegit., Madrid, Art. 52.1.

Typus: Bresadola (1929), *Iconogr. Mycol.* 12: tab. 577(1) (**lectotype**, designated here, MBT 10028213).

Description: *Basidiomata* omphalinoid to collybioid. *Pileus* 8–15 mm wide, hemispherical then convex, with distinctly depressed centre, with deflexed, or straight margin, not hygrophanous or translucently striate, when moist very dark reddish brown to grey or blackish brown, entirely finely floccose to squamulose with pointed squamules. *Lamellae* moderately distant ($L = 12\text{--}15$, $I = 1\text{--}3$), broadly adnate, usually with small decurrent tooth, dark brown concolourous pileus then with pink tinge, with entire, concolourous edge. *Stipe* 6–15 × 0.5–2 mm, cylindrical or with attenuate base, concolourous with pileus or slightly paler, smooth, almost glabrous or with scattered whitish fibrils. *Context* thin, brittle, brown. *Smell* and *taste* unknown. *Basidiospores* (60/3) 7.5–9.5 × 6.6–8.7 µm, on average 8.2–9.0 × 7.8–8.5 µm, $Q = 1.00\text{--}1.20$, $Q_{av} = 1.10$, subisodiametrical to isodiametrical, with 6–8 weak angles in side view, almost rounded in outline. *Basidia* 4-, rarely also 2-spored, clampless. *Lamella* edge fertile or heterogeneous. *Cheilocystidia* mostly absent but some weakly differentiated septate cells can be present on lamellar edge. *Pileipellis* a cutis with transitions to a trichoderm, made up of repent to ascending, cylindrical, up to 20 µm wide hyphae with more or less clavate terminal elements, 30–70 × 15–25 µm. *Pigment* dark brown, strongly encrusting the hyphae of pileipellis and upper pileitrama, often zebra striped, and in addition intracellular. *Clamp-connections* absent.

Habitat and distribution: On soil in short-grazed grassland and in xerophytic grassy vegetation (steppe), preferably on calcareous soils. Widespread but rare, known so far from Italy, Hungary, Russia and Spain.

Additional material examined: **Hungary**, Pest, Csévharaszt, on sandy soil with *Pinus* and *Populus*, 25 Jun. 2020, *I. Ölvedi*, DB-2020-06-25-1 (ELTE). **Russia**, Penza Oblast, Neverkinsky District, “Privolzhskaya Lesostep” Nature Reserve, Kuncharovskaya steppe, on soil, 3 Aug. 1990, *A.I. Ivanov* (LE F-18949). **Spain**, Catalunya, Serrat de l’Artigot, la Quar (Barcelona), 780 m.a.s.l., on basic soil among lichens and mosses, under *Satureja montana*, near *Buxus sempervirens*, 20 Sep. 2008, *J. Vila* & *F. Caballero*, JVG 1080920-20 (LIP) (*Vila et al.* 2014).

Notes: *Leptonia flocculosa* is an illegitimate name as it included the type of the older name *Eccilia watsonii* (Peck)

Sacc. Pacioni ‘combined’ this illegitimate name to *Entoloma*, which is not admissible, because the basionym of a legitimate new must be legitimate. However, according to the Madrid Code Art. 6.12 (a) and 6.14 the stated ‘comb. nov.’ is to be treated as a correctable error and, thus, the name *Entoloma flocculosum* was introduced by Pacioni as a *nomen novum* for the illegitimate name *L. flocculosa*. As the description by Bresadola is referred to, the requirements for valid description are fulfilled. Among other xerophytic species with small, more or less omphalinoid basidiomata, *E. flocculosum* is recognized by almost non-decurrent lamellae, non-hygrophanous pileus and by spores with rounded outlines with weak angles.

Entoloma incarnatofuscescens (Britzelm.) Noordel., *Persoonia* 12(4): 461. 1985. MB 104243.

Basionym: *Agaricus incarnatofuscescens* Britzelm., *Hymenomyceten aus Südbayern* 10(VII): 6. 1894. MB 372150.

Synonyms: *Entoloma klofacianum* Noordel., Wölfel & Hauskn., *Öst. Z. Pilzk.* 4: 128. 1995. MB 413018.

Entoloma violaceoparkensis Noordel. & Trichies, in Noordeloos, *Entoloma* s.l., *Fungi Europaei* vol. 5a: 1120. 2004. MB 491870.

Rhodophyllus leptonipes Kühner & Romagn., *Rev. Mycol.* 19(1): 6. 1954. MB 305239.

Material examined: **France**, Seine et Oise, Yerres, Sep. 1932, *H. Romagnesi*, 32.12 (**holotype** of *Rhodophyllus leptonipes*, PC); ITS sequence, GenBank PX444434.

Notes: *Entoloma incarnatofuscescens* has been neotypified in Noordeloos *et al.* (2022b), with a full description given. *Rhodophyllus leptonipes* was listed as a synonym with question mark, because we did not have molecular proof by that time. Recently, we successfully obtained ITS from the holotype, which was shown to be identical with the neotype of *E. incarnatofuscescens*, which now confirms the synonymy.

Entoloma ludwigii O.V. Morozova, Noordel., Reschke, Dima, O. Shiryayeva & I. Gorbunova, **sp. nov.** MB 860437 Fig. 41.

Misapplied name: *Entoloma flocculosum* sensu Ludwig (2007).

Etymology: Named in honour of Erhard Ludwig (1938–2019), German mycologist and master painter, remembered for his monumental Pilzkompedium with beautiful drawings, in particular, of *Entoloma*.

Typus: **Russia**, Sverdlovsk Oblast, Nizhneserginsky District, near Arakaevo Village, “Deer Creeks” Nature Park, left bank of the Serga River, on soil in steppe meadow, 23 Aug. 2024, *A. Filippova* & *O. Morozova*, 131SV24 (**holotype** LE F-343758); ITS sequence, GenBank PX412046.

Description: *Basidiomata* omphalinoid. *Pileus* 10–20 mm wide, depressed to umbilicate, with initially involute then rather straight margin, not hygrophanous, not translucently striate or striate at the pileus margin only, radially fibrillose to subsquamose, when moist dark grey brown, sepia, yellow brown, pallescent on drying. *Lamellae* moderately distant



($L = 12\text{--}20$, $I = 1\text{--}5$), broadly adnate-decurrent, arcuate to segmentiform, pale brown then dark pinkish brown with entire concolourous edge. *Stipe* $10\text{--}15 \times 2\text{--}3$ mm, cylindrical or slightly broader towards the base, grey brown or yellow brown, concolourous with the pileus, smooth, almost glabrous or slightly fibrillose-striate lengthwise, solid then fistulose. *Context* concolourous with surface. *Smell* indistinct. *Taste* not reported. *Basidiospores* ($140/6$) $7.5\text{--}9.4 \times 6.0\text{--}8.0$ ($\text{--}8.5$) μm , on average $8.1\text{--}8.5 \times 7.1\text{--}7.6$ μm , $Q = 1.0\text{--}1.30$, $Q_{av} = 1.15\text{--}1.20$, subisodiametrical, with 5–7 weak angles in side view. *Basidia* $30\text{--}35 \times 10\text{--}11$ μm , 4-spored, clampless. *Lamella edge* sterile, heterogeneous or fertile. *Cheilocystidia* $22\text{--}32 \times 11.5\text{--}17$ μm , clavate, broadly clavate, sphaeropedunculate or lageniform, sometimes absent. *Pileipellis* a cutis of radially arranged, $2.5\text{--}8$ μm wide hyphae, with transition to a

trichoderm with ascending clavate terminal elements, $48\text{--}96 \times 15\text{--}25$ μm , subpellis made up of long, inflated, $5\text{--}20$ μm wide elements. *Hymenophoral* and *pileitrama* regular, made up of long, cylindrical $5\text{--}10$ μm wide hyphae. *Pigment* abundant in pileipellis and pileitrama, distinctly encrusting, sometimes arranged spirally or resembling zebra stripes, but also brown and intracellular. *Stipitipellis* of cylindrical, $6\text{--}8$ μm wide hyphae $6\text{--}8$ μm broad, sometimes encrusted. *Caulocystidia* similar to the cheilocystidia, clavate or lageniform, septate, composed of inflated cells up to 15 μm broad with lageniform terminal elements. *Clamp-connections* absent.

Habitat and distribution: In poor xerophytic grasslands or in steppes on sandy, clayey or calcareous soil. Reported from Germany and both European and Asian Russia.

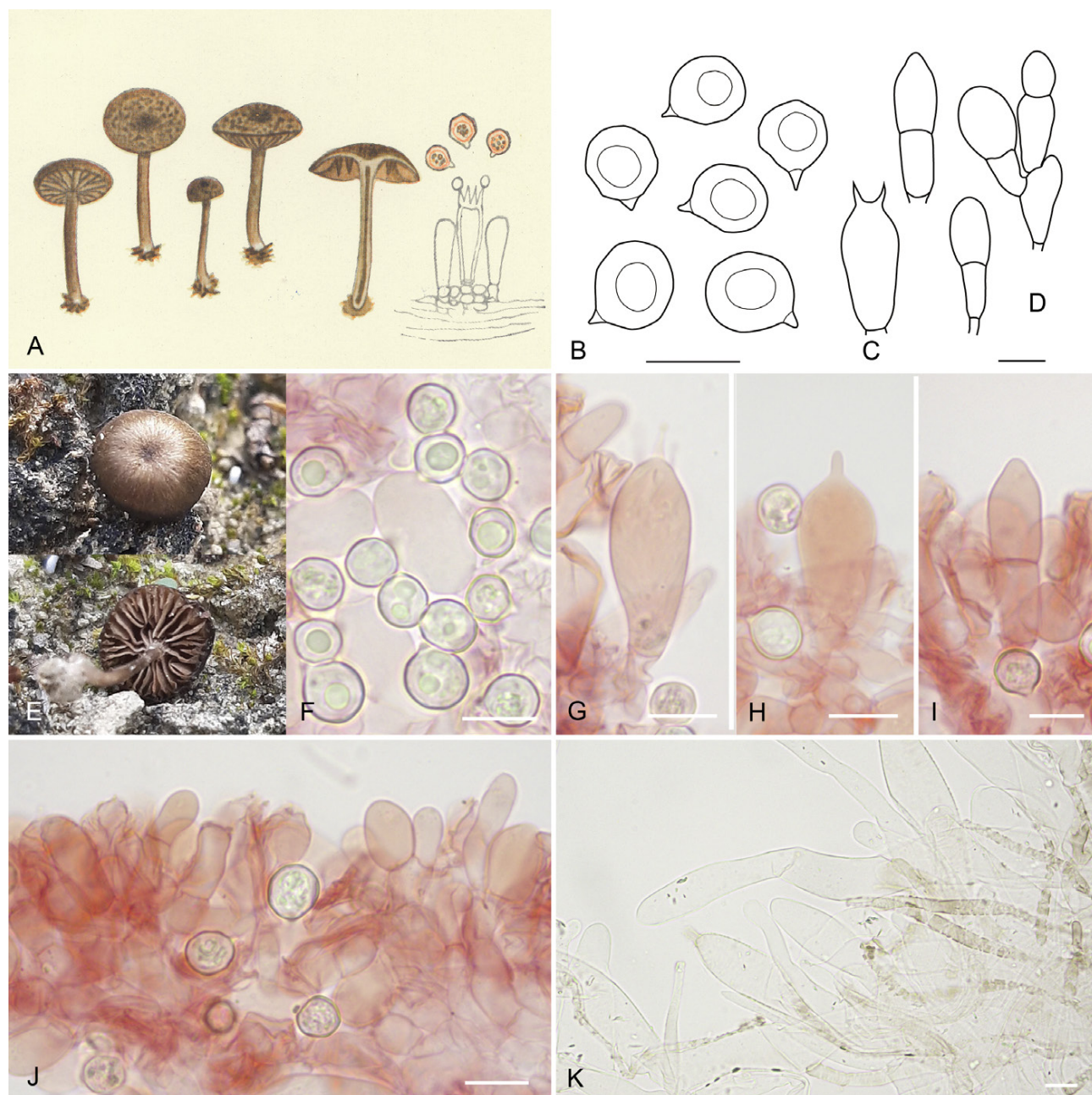


Fig. 40. *Entoloma flocculosum* [A. Lectotype (Bresadola 1929); B–D, F–K. LE F-18949; E. DB-2020-06-25-1). **A, E.** Habit. **B, F.** Basidiospores. **C, G, H.** Basidia. **I.** Cheilocystidia. **J.** Lamellae edge. **K.** Pileipellis. Photos: E by I. Ölvedi; F–K by O. Morozova. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (microstructures).

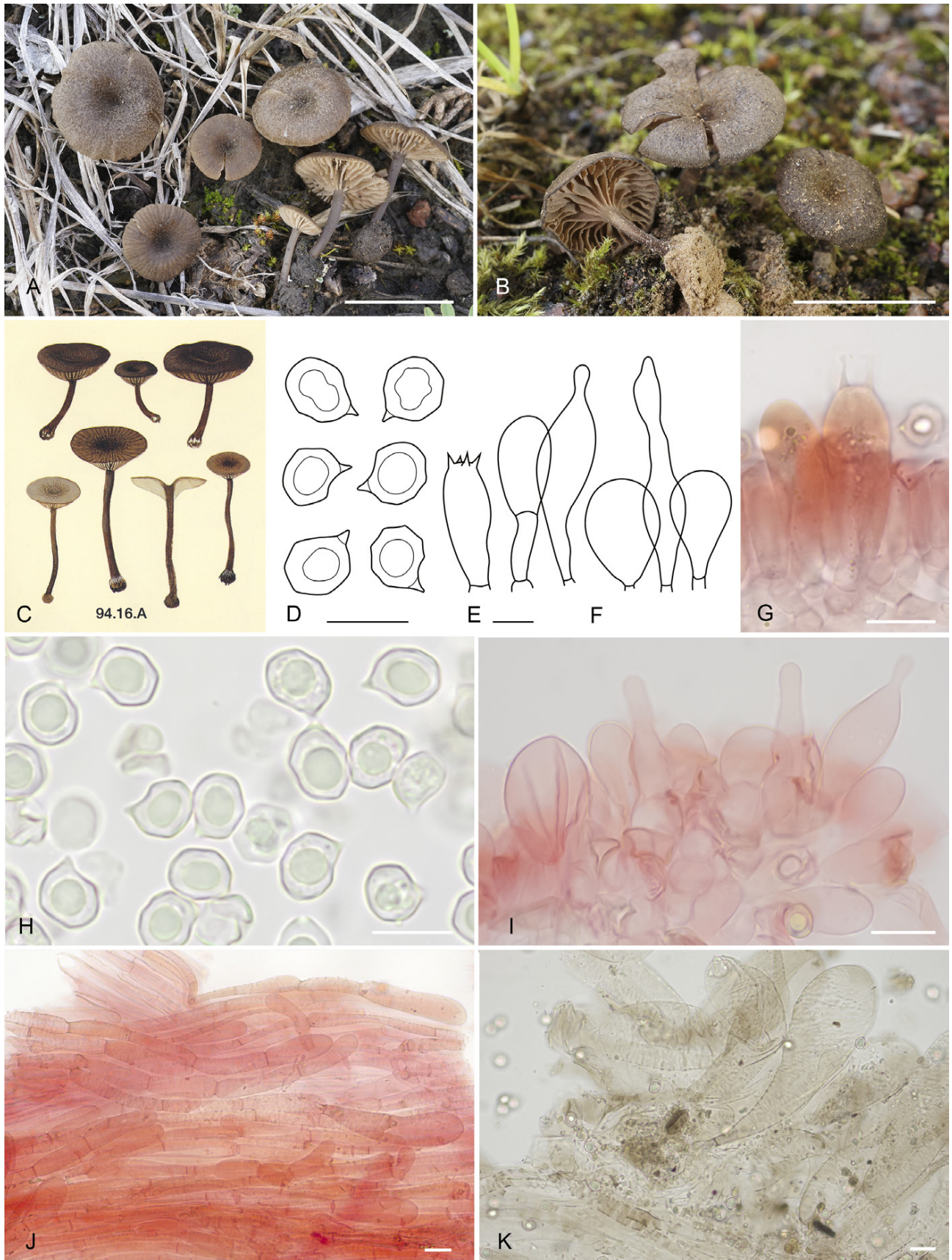


Fig. 41. *Entoloma ludwigii* [A, D–I, K. Holotype; B. LE F-254381; C. Ludwig 2399A (Ludwig 2007); J. LE F-343759]. **A–C.** Habit. **D, H.** Basidiopores. **E, G.** Basidia. **F.** Cheilocystidia. **I.** Lamellae edge. **J.** Stipitipellis. **K.** Pileipellis. Photos: O. Morozova. Drawings: C by E. Ludwig; D–F by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (microstructures).



Additional material examined: **Germany**, Brandenburg, Lebus, Nature reserve, in road-side on sandy soil among *Deschamptia*, 2 Sep. 1994, W. Dieckow, Ludwig Herb. Nr. 2399A (M) (Vila et al. 2014). **Hungary**, Fejér County, Vértes Mts, Csákerény, 18 Sep. 2014, P. Finy, FP-2014-09-18-1 (ELTE). **Russia**, Novgorod Oblast, Batetsky District, near Ivnya Village, river bank, on sandy soil, 19 Sep. 2012, O. Morozova (LE F-254381, as *E. flocculosum*); Sverdlovsk Oblast, Nizhneserginsky District, Arakaev Village, “Deer Creeks” Nature Park, left bank of Serga River, on soil in steppe meadow, 23 Aug. 2024, A. Filippova & O. Morozova, 129SV24 (LE F-343759); Kurgan Oblast, Petukhovskiy District, shore of the Medvezhiye lake, salted burnt steppe, on soil, 19 Jul. 2016, O. Shiryayeva, 106-07-16 (LE F-343722); Altai Republic, Kosh-Agach District, near Kurai Village, right bank of the River Chuya, steppe, on soil, 26 Jun. 2014, I. Gorbunova, 06260062-63 (LE F-343723).

Notes: This species differs from the closely related *E. flocculosum* by more decurrent lamellae, smaller spores and often also by the presence of cheilocystidia. *Entoloma ludwigii* was considered by Ludwig (2007) as *E. flocculosum* and has been included in the wide concept of *E. flocculosum* in Vila et al. (2014).

Entoloma polyangulatum Noordel. & Hauskn., *Österr. Z. Pilzk.* **18**: 169. 2009. MB 515311. Fig. 42.

Synonym: *Entoloma phaeocarpum* F. Caball. et al., *Revista Catal. Micol.* **35**: 90. 2014. MB 807471.

Typus: **Austria**, Niederösterreich, Wolkersdorf im Weinviertel: Münichsthal, 29 Jul. 2001, T. Barta, Herbarium A. Hausknecht 2421.0 (**holotype** WU-Myc 27147); ITS sequence, GenBank PX412059.

Description (amended here): *Basidiomata*: omphalinoid. *Pileus* 5–15 mm wide, up to 7 mm high, hemispherical to plano-convex, sometimes with shallow depression at centre,

with involute to deflexed margin, grey brown to dark brown, sometimes with blackish brown centre, micaceous-fibrillose to tomentose, with age becoming translucently striate at margin, and slightly hygrophanous, pallescent on drying. *Lamellae* moderately distant ($L = 20\text{--}30$, $I = 1\text{--}3$), broadly adnate or decurrent with tooth, very broadly ventricose, occasionally veined on sides, brown to greyish brown, then with lilac-pink tinges, with entire, concolourous lamellar edge. *Stipe* $15\text{--}22 \times 1\text{--}3$ mm, cylindrical, ochre grey, to greyish brown, finely pruinose at apex, downwards glabrous, polished. *Context* brown. *Smell* indistinct, sometimes slightly fruity, *taste* not recorded. *Basidiospores* $7.0\text{--}10.0 \times 6.5\text{--}10.0$ μm , on average $8.5\text{--}9.5 \times 8.2\text{--}9.2$ μm , $Q = 1.00\text{--}1.20$, $Q_{av} = 1.05\text{--}1.10$, isodiametrical to subisodiametrical, rounded-polyangular with 5–9 weak angles, thin-walled. *Basidia* $20\text{--}60 \times 7\text{--}16$ μm , 4-spored, clampless. *Lamellar edge* fertile or heterogeneous. *Cheilocystidia*, if present, $20\text{--}42 \times 5\text{--}11$ μm , clavate, fusiform or lageniform, with refringent walls. *Pileipellis* a differentiated cutis of septate, cylindrical, $4\text{--}20$ μm wide hyphae. *Pigment* brown, strongly encrusting the hyphae of pileipellis and pileitrama. *Pileitrama* regular, made up of medium-sized, up to 25 μm wide hyphal elements. *Clamp-connections* absent.

Habitat and distribution: On soil in thermophilous broad-leaved forest (in terms of *E. polyangulatum*) and in Mediterranean *Pinus halepensis* forest on sandy soil (*E. phaeocarpum*). Known from Austria and Spain.

Additional material examined: **Spain**, La Rioja, Calahorra, 18 Oct. 2003, A. Caballero (LIP JVG 1031018, **holotype** of *E. phaeocarpum*).

Notes: Type studies and ITS barcodes confirmed the synonymy of *E. phaeocarpum* with *E. polyangulatum*. This might be another more or less thermophilous southern(-eastern) “Rusticoides” species in Europe, but more material is needed to confirm ecological-chorological patterns.

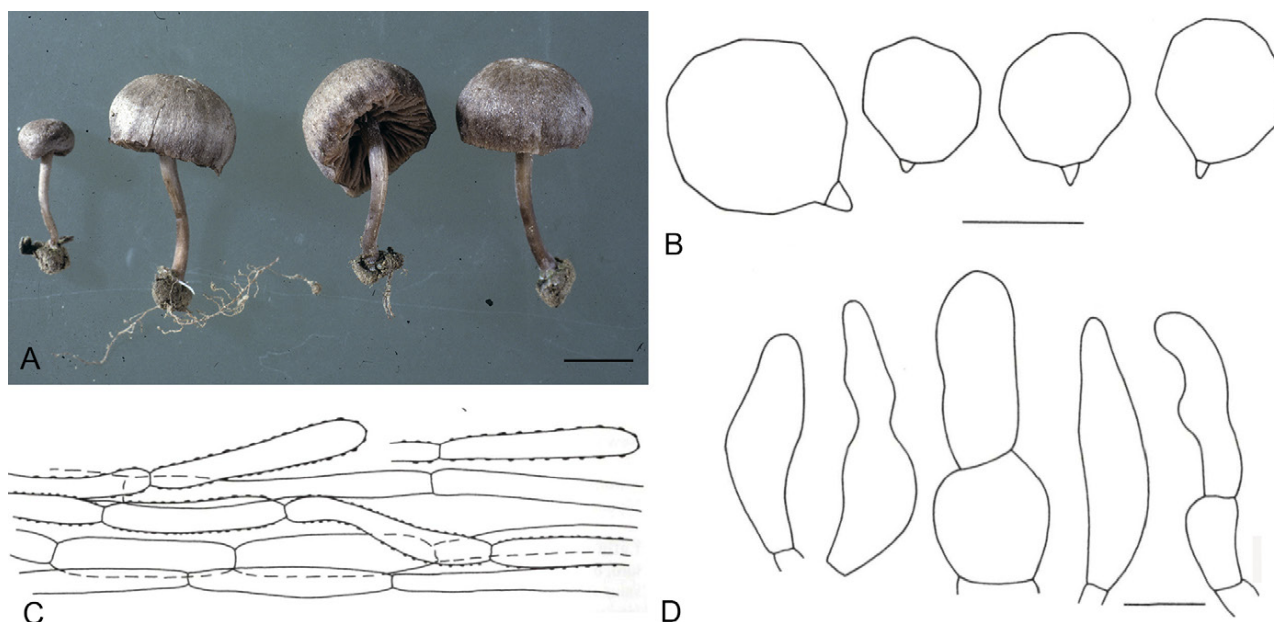


Fig. 42. *Entoloma polyangulatum* (WU-Myc 27147, holotype). **A.** Habit. **B.** Basidiospores. **C.** Pileipellis. **D.** Cheilocystidia. Photo: A. Hausknecht. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (microstructures).



Entoloma pseudosericeoides Hauskn. & Noordel., Österr. Z. Pilzk. 7: 244. 1998. MB 450561. Figs 43, 44.

Typus: **Austria**, Niederösterreich, Maissau, in garden with *Thuja*, *Chamaecyparis* and *Pinus mugo*, 19 Jun. 1993, A. Hausknecht (**holotype** WU 18082, **isotype** in L); ITS sequence, GenBank PX440388.

Description: *Basidiomata* omphalinoid to clitocyboid. *Pileus* 10–35 mm broad, already when young deeply infundibuliform with inrolled margin, slightly hygrophanous, translucently striate in marginal zone only, uniformly dark brown, olivaceous brown to blackish brown; pallescent in radial streaks on drying to brown beige or grey brown, glabrous, at centre scurfy-subsquamous. *Lamellae* crowded, slightly to deeply decurrent, narrow, pale grey brown then pink, with concolourous edge, which sometimes turns brown with age. *Stipe* 30–70 × 3–7 mm, cylindrical or compressed with or without slightly enlarged base, beige brown to greyish, sometimes with weak olivaceous tinge, finely longitudinally fibrillose striate to adpressed woolly-tomentose. *Context* thin, pale brown to olivaceous grey. *Smell* and taste spermatic, then farinaceous. *Basidiospores* (120/5) 7.2–8.7 × 6.0–6.8 µm, on average 7.5–7.6 × 6.5–6.7 µm, Q = 1.10–1.40, Q_{av} = 1.15–1.25, subisodiametrical, 4–6 angled. *Basidia* 4-spored, clampless. *Lamella edge* heterogeneous. *Cheilocystidia* absent, sparse to abundant, mixed with basidia, 30–62 × 6–13 µm, cylindrical, clavate or lageniform. *Pileipellis* a cutis of cylindrical hyphae, 10–14 µm wide, with transitions to a trichoderm at centre, made up of inflated, 10–18(–22) µm wide, terminal elements. *Pigment* intracellular and also finely encrusting. *Clamp-connections* absent in all tissues.

Habitat and distribution: In woody places, along forest tracks, in gardens, in dry grasslands, and in alluvial mixed forests on

calcareous and sandy soil. So far known from a few localities in Austria, Germany, and Italy (GenBank JF908006, as *E. sericeoides*) and from several places in Hungary.

Additional material examined: **Austria**, Steiermark, Landkreis Hartberg-Fürstenfeld, Hartberg, Ringwarte, along a brook with *Acer*, *Fraxinus* and *Picea*, 19 May 2019, B. Dima, A. Nagy & M. Fodor, DB-106-19 (ELTE). **Germany**, Landkreis Bad Tölz-Wolfratshausen, Icking, Isaruferweg, in alluvial forest (*Fraxinus*, *Salix*, *Crataegus*, *Picea*, *Alnus*, *Acer*) on sandy, gravelly soil, 28 May 2016, M. Dondl (L0607182). **Hungary**, Heves County, Heves-Borsodi Hills, Bükkészék, Csoma Mt, in *Pinus sylvestris* plantation, 14 May 2017, E. Szabó, SzEr-2017-05-14 (ELTE); Komárom-Esztergom County, Gerecse Mts, in grassland, 11 May 2019, Gy. Vrba, VGy-2019-05-11-1; Vértes Mts, in grassland, near Várgesztes, 18 May 2019, Gy. Vrba, VGy-2019-05-18-1; Veszprém County, Bakony Mts, Balatonfüred, in alluvial forest near *Acer* and *Fraxinus*, 16 Apr. 2019, M.K. Frits, DB-24-19 (ELTE); Várpalota, in park among grasses, 21 May 2019, Gy. Vidra, VidraGy-2019-05-21-1 (ELTE); *ibid.*, in park among grasses, under *Pinus nigra*, 25 May 2019, Gy. Vidra, VidraGy-2019-05-25-1 (ELTE); *ibid.*, in park among grasses, under *Betula pendula*, 25 May 2019, Gy. Vidra, VidraGy-2019-05-25-2 (ELTE).

Notes: *Entoloma pseudosericeoides* morphologically comes very close to *E. sericeoides*. Based on the material studied, it seems that *E. pseudosericeoides* has in average more infundibuliform, a slightly paler brown, and often distinctly translucently striate pileus, sometimes up to the half. *Entoloma sericeoides* has a glabrous pileus, and lacks cheilocystidia, which are, however, present and abundant in the holotype of *E. pseudosericeoides*, but apparently absent in the German collection. According to our data, the species fruits from spring (April, May) to early summer (June) and

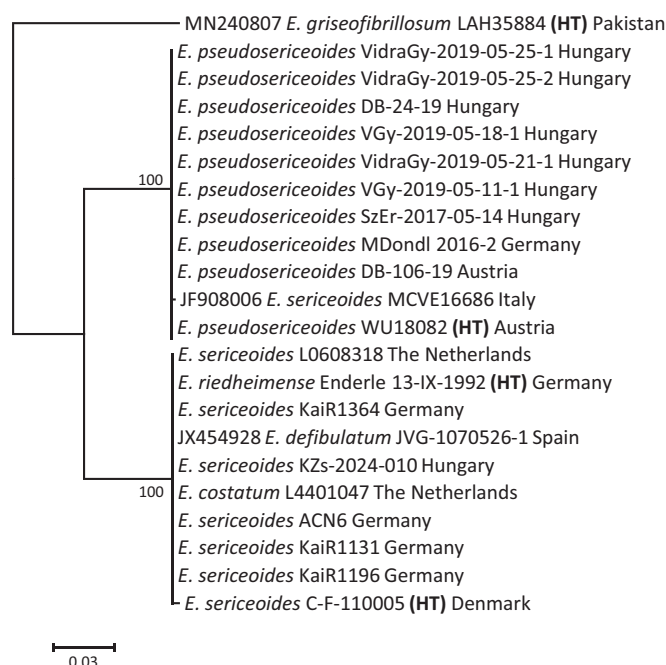


Fig. 43. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences depicting the relationship of *Entoloma sericeoides* and *E. pseudosericeoides* within subgen. *Omphaliopsis* (= *Rusticoides* clade) using additional sequences not included in Fig. 38. ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



Fig. 44. *Entoloma pseudosericeoides* (A, D, G. L0607182; B. VidraGy-2019-05-21-1; C. DB106-19; E. VidraGy-2019-05-25-1; F. SzEr-2017-05-14; H. Holotype). **A–F.** Habit. **G.** Basidiospores. **H.** Cheilocystidia. Photos: A, D, G by M. Dondl; B, E by Gy. Vidra; C by B. Dima; F by Er. Szabó. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (microstructures).



may have on average more southern distribution than that of *E. sericeoides*.

Entoloma pumilionis Reschke, O.V. Morozova, Noordel., Dima, Hülsewig & E.S. Popov, *sp. nov.* MB 860436. Fig. 45.

Etymology: *pumilio* (Lat.) – dwarf, referring to the size of the basidiomata.

Typus: **Germany**, Nordrhein-Westfalen, Witten, Hohenstein, roadside, on rich soil, 5 Nov. 2022, T. Hülsewig, 1027, ACN50 (**holotype** B 70 0105497); ITS sequence, GenBank PX412063.

Description: *Basidiomata* collybioid to omphalinoid. *Pileus* 1–3 mm wide, initially convex, soon becoming umbilicate, with involute, slightly to deeply undulating margin, pale greyish brown to medium brown, darker, brown to dark brown towards the centre, not translucently striate in young basidiomata, sometimes soon becoming translucently striate, especially in paler basidiomata, covered with fine, whitish, fibrillose scales, often less fibrillose-scaly towards the margin. *Lamellae* moderately distant ($L = 6\text{--}12$, $I = 1\text{--}5$), moderately to deeply decurrent, with concolourous, entire edge. *Stipe* 1–5 × 0.2–0.4 mm, cylindrical, pale to moderately dark greyish brown, partly covered by white fibrillose-flocculose tufts, with white, cottony base. *Context* very brittle, brown. *Smell* not perceptible, *taste* not noted. *Basidiospores* (120/5) 8.0–10.0(–11.5) × 7.5–9.5 µm, on average 8.7–9.2 × 8.1–8.9, $Q = 1.00\text{--}1.20$ (–1.40), $Q_{av} = 1.10\text{--}1.15$, isodiametrical to subisodiametrical, rounded-angular, with 6–9 rather indistinct angles. *Basidia* (22–)26–40 × 9.5–12(–18.5), mainly 4-spored, some 2-spored, clampless. *Lamella edge* fertile, cystidia absent. *Pileipellis* a cutis at the margin, often with transitions to a trichoderm towards centre, composed of cylindrical to inflated, 5–30 µm wide hyphae with repent to somewhat erect or ascending terminal elements, 55–170 × 15–30 µm. *Subpellis* not distinctly developed. *Hymenophoral* and *pileitrama* regular, made up of narrow, cylindrical to broad, inflated elements, 4–32 µm wide. *Stipitipellis* a thin cutis of narrow, cylindrical hyphae. *Caulocystidia* not observed. *Pigment* brown, encrusting in pileipellis as well as in pileal and hymenophoral trama. *Clamp-connections* absent in all tissues.

Habitat and distribution: On soil in dry steppe communities or in anthropogenic habitats (road verges, gardens). Known from Germany, Hungary and Russia.

Additional material examined: **Germany**, Mecklenburg-Vorpommern, Malchin, Ferienanlage Salem, parking area, on soil, 4 Nov. 2022, V. Kummer, IHI-22Ent03 (GLM-F139802); Nordrhein-Westfalen, Witten, Hohenstein, wayside, on soil, 31 Oct. 2020, T. Hülsewig, 617, ACN48 (B 70 0105495). **Hungary**, Vas, Döröske, in garden, on soil among grass and mosses, G. Benkő & K. Fábrics, BG-2020-11-13-B4 (ELTE). **Russia**, Volgograd Oblast, Sredneakhtubinsky District, near Chapaevets Village, Volga-Akhtuba Floodplain Nature Park, on soil on slope with sparse grasses, *Artemisia* spp., and *Populus* shoots, 17 Oct. 2013, E.S. Popov, ESP-000311 (LE F-254253).

Notes: *Entoloma pumilionis* is characterised by its tiny size and the not, or only somewhat translucently striate pileus. It has some resemblance to *E. iodolens*, which has, however, larger basidiomata and an iodoform smell.

Entoloma rusticoides (Gillet) Noordel., *Persoonia* 11: 150. 1981. MB 112303. Fig. 46A–I.

Basionym: *Eccilia rusticoides* Gillet, *Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France*: 425. 1876. MB 185876.

Synonyms: *Entoloma graphitipes* E. Ludw., *Pilzkompendium* (Eching) 2(2): 290. 2007. MB 548552.

Entoloma graphitipes f. *cystidiatum* Ferr. Caball., Vila & Català, *Revta Catal. Micol.* 35: 78. 2014. MB 807473.

Typus: Gillet, *Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France*: pl. 276 (1874–1898) (**lectotype**, designated here, MBT 10028211). **The Netherlands**, prov. Gelderland, Rheden, Heiderust, among mosses in an old graveyard on sandy soil, 28 Dec. 2019, M. Plekkenpol, M.J.C van der Vegte & G.M. Jansen (**epitype** L4343484, designated here, deposited at L, MBT 10028212); ITS sequence, GenBank PX412065.

Description: *Basidiomata* omphalinoid. *Pileus* 8–20 mm wide, convex with depressed centre, with straight margin, hygrophanous, deeply translucently striate up to ½ the radius when moist, brown with slightly darker centre, pallescent on drying, with fibrillose covering. *Lamellae* distant ($L = 14\text{--}20$, $I = 4\text{--}6$), shortly decurrent, with furcations, pale brown when young then brown pink with concolourous, entire edge. *Stipe* 15–45 × 1–2 mm, cylindrical, glabrous, pale brown to dark brown, slightly darker towards base, base covered with white mycelium. *Context* thin, brown. *Smell* insignificant, *taste* not noted. *Basidiospores* (210/9) 7.5–10.0 × 6.0–8.0 µm, on average 8.4–8.7 × 6.8–7.1 µm, $Q = 1.10\text{--}1.40$ (–1.45), $Q_{av} = 1.18\text{--}1.25$, isodiametrical to shortly heterodiametrical, 5–6-angled in side view. *Basidia* 33–45 × 10.5–13.5 µm, clavate, 4-spored, clampless. *Lamella edge* sterile, heterogeneous or fertile. *Cheilocystidia* 20–60 × 4–10 µm, septate, hyaline, terminal element conical, lageniform or acutely conical. *Pileipellis* a cutis of cylindrical, 6–14 µm wide hyphae, with up to 15 µm wide, subclavate terminal elements with brown, finely encrusted walls. *Pileitrama* regular, made up of inflated hyphae, elements 100–350 × 5 × 40 µm with finely encrusted brown pigment. *Stipitipellis* a cutis of cylindrical hyphae, 4–15 µm, finely brown encrusted with irregularly shaped, subclavate terminal elements (“caulocystidia”). *Clamp-connections* absent.

Habitat and distribution: Terrestrial, in various grasslands, rarely in forests, mainly in dry places, among mosses, often on sandy soil. Widely distributed and not uncommon in Europe.

Description of the holotype of E. graphitipes: The holotype consists of 7 intact to somewhat fragmented basidiomata, with brown, convex to rather applanate pileus with distinct umbilicus, strongly decurrent, brown lamellae, and dark grey stipe. Microscopically the *basidiomata* are heavily infected by an *Aspergillus* sp. with largely collapsed vesicles,

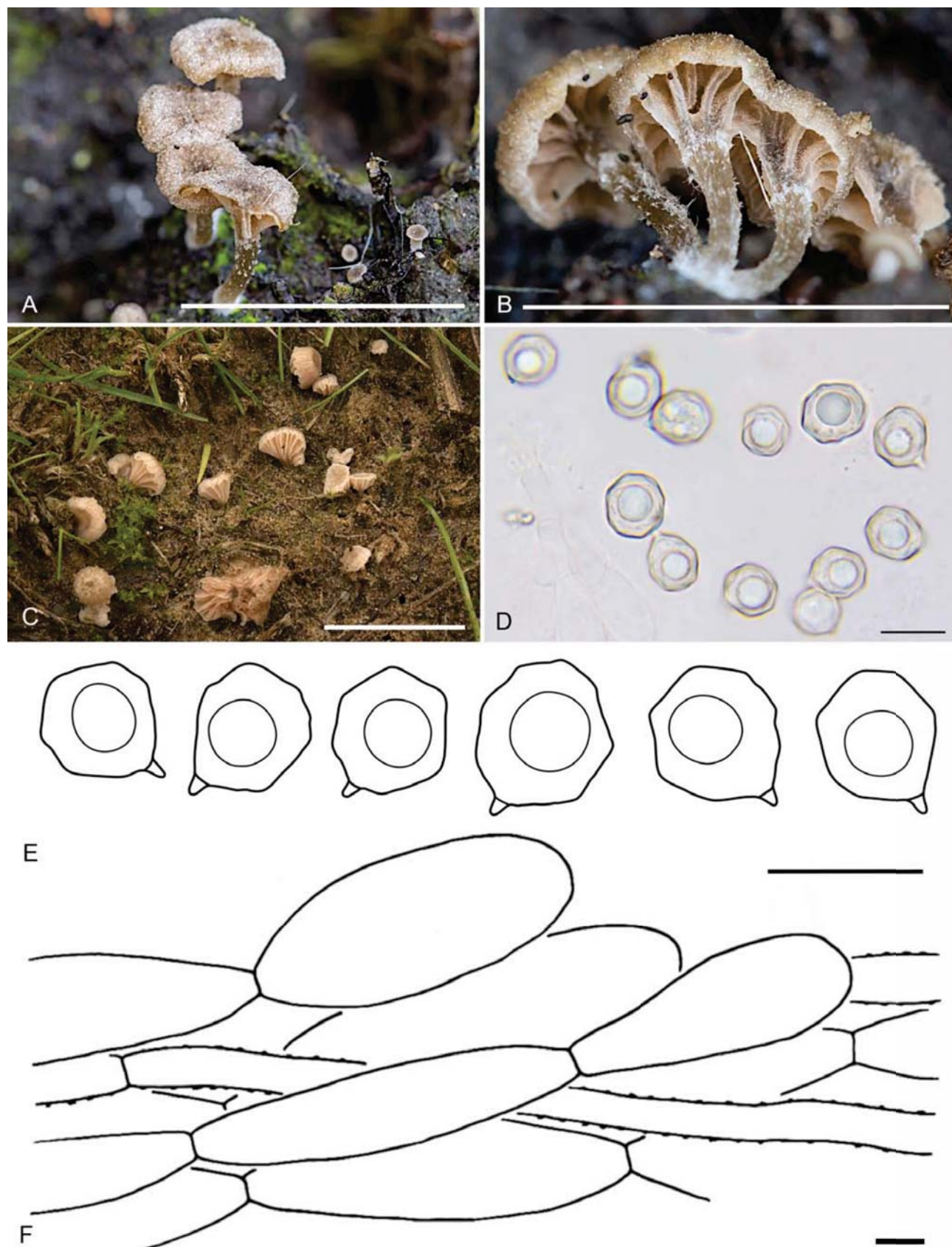


Fig. 45. *Entoloma pumilionis* (A, B, D–F. B 70 0105497, holotype; C. LE F-254253). **A–C.** Habit. **D, E.** Basidiospores. **F.** Pileipellis. Photos: A, B by T. Hülsewig; C by E. Popov; D–F by K. Reschke. Scale bars: 1 cm (habit), 10 μ m (microstructures).



and dematiaceous hyphomycetes with didymospores and dictyospores. *Basidiospores* (20/1) 8.5–11.0(–12.0) × (6.5–)7.0–9.5(–10.0) µm, on average 9.6 × 8.2 µm, Q = (1.00–)1.10–1.35(–1.60), Q_{av} = 1.18, subisodiametrical to broadly heterodiametrical, rarely completely isodiametrical, rarely relatively long heterodiametrical, 5–7-angled in side view, with rather weak, rounded angles. *Basidia* 4-spored as far as evaluable, clavate to broadly clavate, without clamp connection, generally few mature, intact basidia present. Absence or presence of *hymenial cystidia* not successfully evaluated. *Pileipellis* a cutis as far as evaluable, pigment difficult to locate, possibly parietal in some parts, some encrusting pigment present, but mainly at damaged and collapsed hyphae. *Clamp-connections* absent.

Additional material examined: **Austria**, Hirscheegg, Kleinwalsertal, near Haus Marburg, forest edge of a *Picea abies*-dominated forest, on soil between moss and litter, 22 Sep. 2017, K. Reschke, KaiR920 (B 70 0105505). **Germany**, Bayern, Warngau, Taubenberg, Schwarzer Berg, on soil among *Petasites* and *Urtica* in mixed mountain forest of *Fagus*, *Picea*, and *Abies*, 6 Aug. 2016, M. Dondl (L0607944); Berlin, Berlin-Lichtenrade, children's playground at the John-Locke street, on bare sand, partly between grasses, partly on an old fire site, 22 May 1982, E. Ludwig, 3348 (**holotype** of *E. graphitipes*, M-0159113); Hessen, Frankfurt, Wissenschaftsgarten, mesotrophic grassland, 17 Oct. 2016, K. Reschke, KaiR238 (B 70 0105503); Rheinland-Pfalz, Mainz, near Gonsenheim, grassland on rather sandy soil, 24 Nov. 2017, K. Reschke & W. Prüfert, KaiR1134 (B 70 0105510). **Hungary**, Bács-Kiskun, Bugac, Nagylegélő, on sandy cattle pasture, 24 Nov. 2019, P. Finy, FP-2019-11-24-2 (ELTE); Bócsa, in open sand dune, 13 Nov. 2020, P. Finy, FP-2020-11-13 (ELTE). **Norway**, Møre og Romsdal, Sunndal, Grøvdalen, Gammelsetra, moist grassland, 16 Sep. 1997, J.B. Jordal, JB97-404 (O-F-254408); Telemark, Bamble, Langesundstangen, open grassy spot in calcareous pine woodland, 15 Oct. 2012, A. Molia & T. Læssøe, AM-347i-2012 (O-F-245589). **The Netherlands**, prov. Gelderland, Rheden, Heiderust, in mossy lawn of churchyard, 22 Nov. 2017, M.J.C. van der Vegte & G.M. Jansen (L0608055).

Notes: *Entoloma rusticoides* is widely distributed, and the most common and best known species of subgen. *Omphaliopsis* in Europe, thus this subgenus has also been called the *Rusticoides* clade. Vila *et al.* (2014) designated an "epitype" for *E. rusticoides* using a specimen from a coastal Mediterranean habitat south of Tarragona, Spain, however, without indication of a holo-, lecto-, or neotype, so that this epitypification is nomenclatural ineffective (Madrid, Art. 9.9). Gillet (1876) published an illustration of *Eccilia rusticoides*, however, the publication date is difficult to trace. The text of the "Hyménomycètes" was consecutively published in three parts: 1874, 1876, and 1877 or 1878 (see Stafleu & Cowan 1976–1988, pp. 944–946). The description of *Eccilia rusticoides* was included in the second part. These parts were later bound together without changing the title page. The volume of the "Hyménomycètes" consulted for this study includes a separately paginated part "Liste de tous les champignons continues dans l'ouvrage sur les Hyménomycètes et rangés par ordre alphabétique" which provides page and plate numbers for each species. The

plates were similarly published consecutively 1874–1898, while small parts of additional text, describing species for which so far only a plate had been published, were published 1884 and 1890 (Stafleu & Cowan, l.c.). The individual contents of the plate issues and their exact publication dates are not clear. It is possible that the plate of *Eccilia rusticoides* was published later than the text. However, the date of publication of the plate is nomenclaturally irrelevant (Madrid, Art. 9.4). The publication of the plates was announced in the text part and we have no reason to believe they were not existing at the time the text was published. There are understandable reasons that the plates were published at a comparably slow pace. The economy of the early French Third Republic was dominated by small family companies, with often fewer than five employees. Apparently, the publisher of the "Hyménomycètes", Ch. Thomas was such a small company. Printing illustrations at that time required the preparation of lithograph plates. In addition, the illustrations of the "Hyménomycètes" were hand-coloured after print. So, as Gillet's illustration of *Eccilia rusticoides* is the only known original material, it has to be selected as lectotype. It is also depicted here (Fig. 46A). To provide for a modern concept, based on a well-preserved specimen with colour photographs and an ITS-barcode sequence, a specimen is selected as an epitype that coincides well with the traditional concept of this species, as described among others in Kühner & Romagnesi (1953), and Noordeloos (1981, 1987, 1992, 2004), and as interpreted by the authors of this study. This concept matches the concept of *E. graphitipes* of Vila *et al.* (2014), which they treated as a distinct species based on an ITS sequence of the holotype. Regarding the original description of *E. graphitipes*, with nodulose heterodiametrical basidiospores, without encrusting pigment and the fruiting in spring, it appeared that this species might rather belong to sect. *Erophila* than to subgen. *Omphaliopsis*. This seemed to be supported by the fact that Ludwig compared his new species to *E. farinasprellum*, a species that we now know is a synonym of *E. undulatosporum*. The description of *E. graphitipes* by Vila *et al.* (2014) deviates in several characters from that of Ludwig and represents a typical member of the *Rusticoides* clade with rather iso- to subisodiametrical spores and encrusting pigment. The pictures provided by Vila *et al.* (2014) illustrate a remarkable variability of this species, but the differences between their concept of *E. graphitipes* in comparison with the original one were not explained or discussed. A cross-contamination in the sequencing process or in the extreme case a mixed collection was considered by the present authors. However, the re-examination of the holotype revealed that *E. graphitipes* fits rather well into the concept of *E. rusticoides*. Each of the basidiomes of the holotype specimen were studied and the possibility of a mixed collection has been rejected. The deviation of the holotype of *E. graphitipes* from typical specimens of *E. rusticoides*, especially the lack of distinct encrusting pigment, can well be explained by the bad state of the basidiomata. The fact that also the infecting *Aspergillus* sp. is in a bad state of preservation, indicates that the specimen was already infected prior to drying. Nodulose basidiospores as depicted by Ludwig (2007) were not found in a healthy state, however, abortive, rather thin-walled spores without cell content were abundant and had sometimes similar shapes as those nodulose spores of the original description. The distinct proportion of broadly



Fig. 46. A–I. *Entoloma rusticoides* (A. Gillet 1874–1898; B, C, G–I. L4343484, epitype; D. FP-2019-11-24-2; E, F. FP-2020-11-13-2). **A–E.** Habit (A. Lectotype). **F, G.** Basidiospores. **H.** Cheilocystidia. **I.** Pileipellis. **J.** *Entoloma vilae* (B 70 0105501, holotype). Habit. Photos: A by K. Reschke; B, C, G–I by G.M. Jansen; D–F by P. Finy; J by C. Manz & A. Gminder. Scale bars: 1 cm (habit), 10 µm (microstructures).



heterodiametrical spores is in general not contradicting the concept of *E. rusticoides*. Gillet included in his microscopical drawing isodiametrical to broadly heterodiametrical spores (Fig. 46A), Q-values of 1.0–1.5 were given for this species by Noordeloos (2004), and also the concept as revised here, based on sequenced specimens, includes a proportion of broadly heterodiametrical spores. Therefore, *E. graphitipes* has to be synonymised with *E. rusticoides*, and represents a specimen with an unusual fruiting date in spring of a species that is generally mainly found in late autumn. Like in many other species of *Entoloma*, cheilocystidia are present or absent in *E. rusticoides*, and must be considered of limited diagnostic value. The species treated as *E. rusticoides* by Vila *et al.* (2014) is a different species, which is only known from pronounced Mediterranean habitats. It is described as a new species, *E. vilae*, below.

Entoloma sericeoides (J.E. Lange) Noordel., *Persoonia* **10**(4): 483. 1980. MB 113479. Figs 43, 47A–D.

Basionym: *Rhodophyllus sericeoides* J.E. Lange, *Fl. Agaric. Danic.* **5**: VIII. 1940. MB 290538.

Synonym: *Entoloma riedheimense* Noordel. & Enderle, *Z. Mykol.* **61**(2): 189. 1995. MB 545621.

Misapplied names: *Entoloma costatum* s. J. Lange, Romagnesi, Noordeloos; *Entoloma defibulatum* s. Vila *et al.*

Typus: **Denmark**, Fyn, Kværndrup, in forest (*Fagus* and *Picea*), 12 Jul. 1938, J.E. Lange (**holotype** C-F-110005); ITS sequence, GenBank PX412067.

Description (amended here): *Basidiomata* clitocyboid, often relatively stout, more rarely omphalinoid or collybioid. *Pileus* (10–)20–80 mm broad, convex then expanding to applanate, slightly depressed to umbilicate, with involute margin, with undulating marginal zone when old, hygrophanous, when moist dark grey brown, sepia, red brown, or blackish brown, not or indistinctly translucently striate, pallescent on drying to yellow brown or grey brown, smooth, glabrous, but becoming strongly radially fibrillose on drying. *Lamellae* crowded (L = 30–60, l = 1–5), broadly adnate with decurrent tooth or emarginate, arcuate to segmentiform, rarely subventricose, sometimes transvenose, pale brown then dark brown pink with entire or more or less serrate, concolourous edge. *Stipe* 25–90 × 3–10 mm, cylindrical or compressed, often tapering at base, grey brown or red brown, usually paler than pileus, coarsely fibrillose-striate lengthwise, solid then fistulose. *Context* concolourous with surface in cortex, inner parts white, fairly brittle. *Smell* indistinct. *Taste* mild to rancid. *Basidiospores* (120/6) (6.5–)7.0–9.5(–10.5) × (6.0–)7.0–8.0(–9.0) µm, on average 8.3–9.0 × 7.4–7.7 µm, Q = 1.00–1.30, Q_{av} = 1.15–1.20, subisodiametrical, (4–)5–6-angled in side view. *Basidia* 20–36 × 8–14 µm, 4-, occasionally 2-spored, clamped. *Lamella edge* fertile or heterogeneous. *Cheilocystidia* usually absent, rarely scattered or abundant, then often in clusters, 60–75(–80) × 4–8(–9) µm, subcylindrical. *Pileipellis* a cutis of radially arranged, 2.5–8 µm wide hyphae, with numerous cylindrical to clavate, up to 15 µm wide terminal elements; subpellis made up of long, inflated elements, 90–180 × 4–20 µm. *Hymenophoral* and *pileitrama* regular, made up of long, cylindrical 5–25 µm wide hyphae. *Pigment* brown, intracellular, diffuse and granular, in pileipellis and upper pileitrama, in addition often distinctly

encrusting. *Clamp-connections* absent (but present in the holotype of *E. riedheimense*).

Habitat and distribution: In groups in grasslands, both in semi-natural grasslands and in lawns, on dikes, etc., on clayey soil. Widespread in Northwestern Europe, and Spain (Vila *et al.* 2013, as *E. defibulatum*).

Additional material examined: **Germany**, Hessen, Frankfurt am Main, Campus Riedberge, Wissenschaftsgarten, in lawn, 19 Apr. 2018, H. Lotz-Winter, KaiR1196 (B 70 0105511); *ibid.*, 4 Apr. 2019, H. Lotz-Winter, KaiR1364 (B 70 0105517); Baden-Württemberg, Schwäbische Alb, 18 Oct. 2019, F. Hampe, ACN6 (B 70 0105494); Bayern, Riedheim, in lawn, 13 Sep. 2002, M. Enderle (**holotype** of *E. riedheimense*, deposited in L; ITS sequence, GenBank PX412018); Frankfurt am Main, Niederursel, Kreuzerhohl, in semi-natural grassland, 22 Nov. 2017, K. Reschke, KaiR1131 (B 70 0105509). **The Netherlands**, prov. Gelderland, Hennisdijk, Buren, in grassland on heavy clay, 9 Oct. 2020, G.M. Jansen & M.J.C. van der Vegte (L0608318).

Notes: The amended description now also acknowledges the occasional presence of encrusting pigment in the pileipellis of several collections studied, as well as forms with cheilocystidia. Small, more omphalinoid specimens (type of *E. sericeoides*) can be encountered besides the more typical robust sized *E. costatum* s. auct. form. The present concept represents *Rhodophyllus costatus* as interpreted by Lange (1937: 13, pl. 76F), and Romagnesi (1974), whose interpretations formed the basis of the description in Noordeloos (1981). It is a fairly characteristic species, with usually relatively stout basidiomata with a dark brown, umbilicate pileus, grey brown lamellae, relatively short, concolourous, fibrous stipe, odourless context, growing in groups in grasslands, often in company of the common *E. sericeum*. The small, rounded-isodiametrical spores, and clampless hyphae furthermore characterise this species, which instigated Romagnesi (In Romagnesi & Gilles 1979) to place it in a new section *Clitopiloides*, which accordingly was elevated to the rank of subgenus by Noordeloos (1992), and raised to generic rank in Largent (1994) as *Clitopiloides*. In our ITS phylogeny, however, it fits well in subgen. *Omphaliopsis*. *Entoloma sericeoides* was described by Lange (1940) as a relatively small, dark brown, omphalinoid (eccilioid) species, with a relatively thin-fleshed, shortly translucently striate and umbilicate pileus, growing in a roadside in a forest with *Fagus* and *Picea*. As such, it appears to be a smaller, thin-fleshed version of *E. costatum* s. auct., which was confirmed by the ITS sequence of the holotype of *E. sericeoides*. Vila *et al.* (2014) erroneously identified *E. sericeoides* as *E. defibulatum* (GenBank JX454928.1). As a result, many records of *E. defibulatum* in recent publications, and in GenBank, actually refer to *E. sericeoides*. However, the true *E. defibulatum* is a synonym of *E. fernandae*, a very distant species in subgenus *Nolanea* (Reschke *et al.* 2022b, Noordeloos *et al.* 2022a).

Entoloma vilae Reschke, Noordel., O.V. Morozova, Manz & Dima, **sp. nov.** MB 860435. Fig. 46J.

Misapplied name: *Entoloma rusticoides* sensu Vila *et al.* (2014).



Etymology: The species is dedicated to the late Jordi Vila, a researcher of the mycobiota of Catalonia (Spain), who made an invaluable contribution to the study of *Entoloma*.

Typus: **Croatia**, Premantura, Kap Kamenjak, on soil in open thermophilous vegetation with *Rosmarinus* and *Cistus*, 1 Nov. 2016, C. Manz & A. Gminder (**holotype** B 70 0105501); ITS sequence, GenBank PX412072.

Description: *Basidiomata* omphalinoid. *Pileus* 10–12 mm wide, convex, deeply umbilicate, with involute margin, dark brown with blackish brown centre, distinctly translucently striate, soon opaque on drying, at centre somewhat felted-fibrillose, towards margin more or less virgate with darker and paler fibrils. *Lamellae* moderately distant ($L = 10\text{--}20$, $l = 1\text{--}3$), deeply decurrent, with concolourous, entire edge. *Stipe* 12–15 × 1–2 mm, cylindrical, pale to dark brown, sometimes darkening at apex, innately fibrillose, white felted at base. *Context* concolourous with sides. *Smell* indistinct, *taste* not noted. *Basidiospores* (20/1) $7.0\text{--}8.0 \times 6.5\text{--}7.5 \mu\text{m}$, on average $6.4 \times 7.1 \mu\text{m}$, $Q = 1.00\text{--}1.20$, $Q_{av} = 1.05$, very rounded-angular. *Basidia* 4-spored, $33\text{--}40 \times 9.5\text{--}11 \mu\text{m}$, clampless. *Lamella edge* fertile, cystidia absent. *Pileipellis* a cutis with transitions to a trichoderm of cylindrical, 4–15 μm wide hyphae, with fine incrustations and pale intracellular pigment. *Pileitrama* regular. *Stipitipellis* a thin cutis of narrow hyphae. *Caulocystida* absent. *Clamp-connections* absent in all tissues.

Habitat and distribution: In short grazed, semi-natural, thermophilous grassland and Mediterranean shrubland with *Olea*, *Pistacia* and *Thymus*, also with *Cistus* and *Rosmarinus*, on calcareous soil. Known from Croatia and Spain.

Notes: As pointed out above, the concept of *Entoloma rusticoides* has been amended, and consequently *E. rusticoides* sensu Vila *et al.* (2014) needs to be described as a new species. It resembles *E. rusticoides* in many respects, but the ecology and distribution are Mediterranean. Three GenBank accessions (KJ001431, KJ001432, KJ001435) from Spain (Vila *et al.* 2014) also refer to *E. vilae*.

/Brunneroflocculosum subclade

The monotypic /Brunneroflocculosum subclade takes a long-branched, isolated position in the ITS phylogeny within the subgen. *Omphaliopsis*, sister to *Entoloma punjabense* from Pakistan without statistical support (Fig. 38). So far it had only been known from the type locality, but during our studies it appeared that the ITS is very similar to the type of *E. asperum*, described a few years later from Germany. Both type specimens were found in a xerophytic grassland in a calcareous area. Macroscopically both collections are rather similar with a dark brown felted-floccose pileus and polished stipe, but microscopically there are slight differences in spore size and the occurrence of cheilocystidia in the holotype of *E. asperum*. Since they belong to one well-supported clade phylogenetically, we treat these two taxa as one species for the time being.

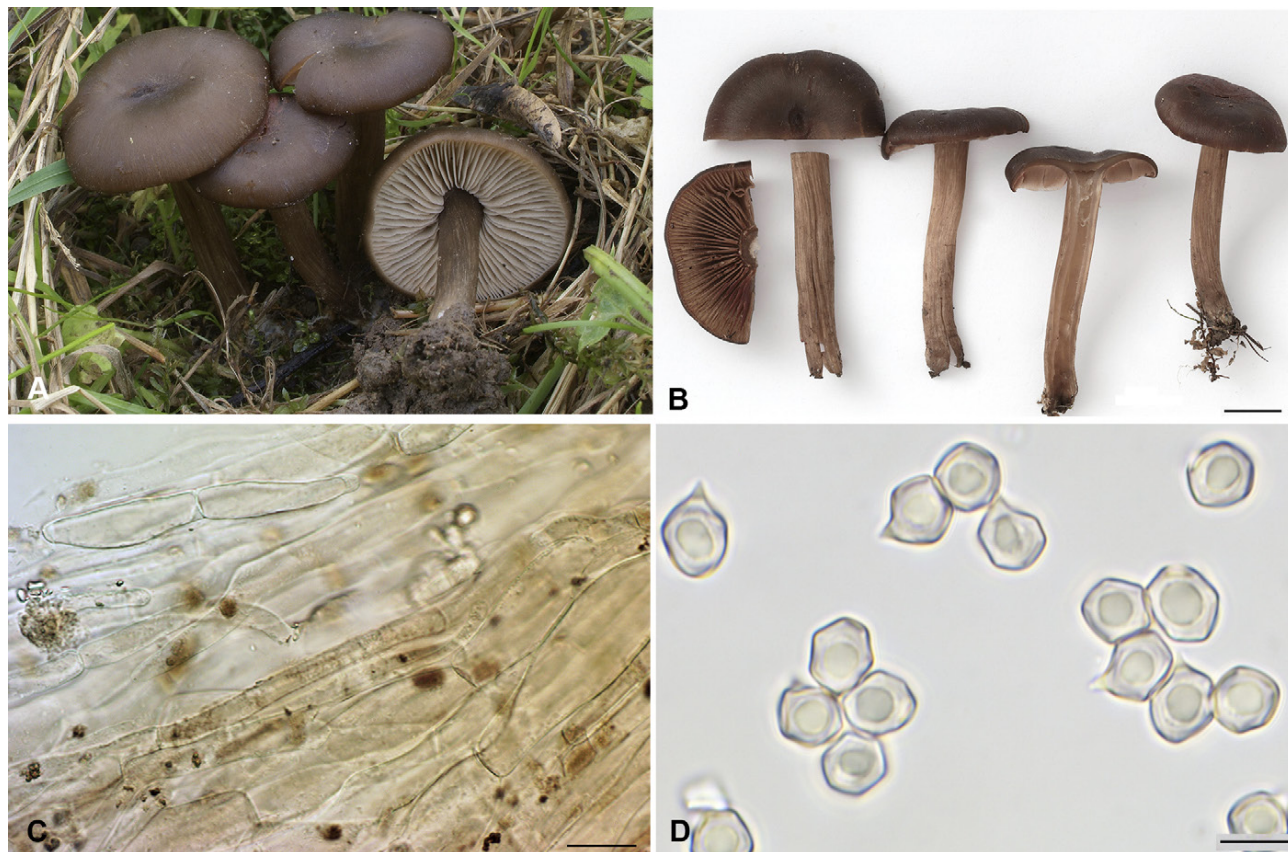


Fig. 47. A–D. *Entoloma sericeoides* (L0608318). **A, B.** Habit. **C.** Pileipellis. **D.** Basidiospores. **E–H.** *Entoloma polyangulatum* (WU-Myc 27147, holotype). **E.** Habit. **F.** Basidiospores. **G.** Pileipellis. **H.** Cheilocystidia. Photos: A by M.J.C. van der Vegte; B, C, D by G.M. Jansen; E by A. Hausknecht. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (microstructures).



Entoloma brunneoflocculosum Arnolds & Noordel., in Noordeloos, *Entoloma s.l., Fungi Europaei* vol. **5a**: 982. 2004. MB 491533.

Synonym: *Entoloma asperum* E. Ludw., Hensel & M. Huth, *Pilzkompendium* **2**(2): 484. 2007. MB 548578.

Typus: The Netherlands, prov. Limburg, Wittem, N.W. of Nijswiller, 30 Sep. 2001, *E. Arnolds*, Arnolds 01-116 (**holotype** L0607236, not sequenced), *ibid.*, Arnolds 01-125 (**paratype**, deposited in L); ITS sequence, GenBank PX401863.

Description (amended here): *Basidiomata* mycenoid: *Pileus* 13–29 mm wide, obtusely conical to conico-convex, expanding to almost applanate with umbo, with crenulate margin, not hygrophanous, not translucently striate, centre dark brown, entirely felted-minutely squamulose, then furfuraceous-flocculose at centre, towards margin fibrillose-virgate, grey brown to yellow brown, exposing the paler context of the pileus between the fibrils. *Lamellae* moderately crowded (L = 21–23, I = 1–3), adnexed to emarginate, ventricose, white then flesh-coloured pink with concolourous, entire or paler, fimbriate edge. *Stipe* 15–30 × 1.5–3 mm, cylindrical, grey brown, darker blackish brown at base, apex pruinose, downwards polished. *Context* thin, pale grey brown in pileus, whitish in stipe. *Smell* and *taste* weak, fungoid. *Basidiospores* (40/2) (6.5–)7.0–10.0 × 6.0–8.0 µm, on average 8.5–9.2 × 7.0–7.5 µm, Q = 1.05–1.35, Q_{av} = 1.20–1.25, subisodiametrical to heterodiametrical, 5–6-angled with pronounced angles. *Basidia* 23–30 × 10–12 µm, 4-, also sometimes 2-spored, in part thick-walled, clamped. *Lamella edge* fertile or heterogeneous with scattered, lageniform to utriform cheilocystidia, 30–55 × 4–12 µm. *Hymenophoral trama* regular, made up of relatively short, hyaline elements, 50–150(–165) × 3.5–30 µm. *Pileipellis* a cutis with trichodermal tufts of sub cylindrical to clavate, lageniform or fusiform terminal elements, 53–140 × 9–24 µm. Pigment pale to dark brown, diffusely intracellular. *Clamp-connections* present in hymenium and in trama, but infrequent.

Habitat and distribution: In poor, moss-rich xerophytic grasslands on loamy or calcareous soils. So far only known from The Netherlands and Germany.

Additional material examined: **Germany**, Sachsen-Anhalt, Thüringen, Müncheroda near Freyburg, Langer Berg, in xerophytic grassland on calcareous soil, 15 Aug. 2005, G. Hensel & M. Huth, Ludwig 2614 (**holotype** of *E. asperum*, M); ITS sequence, GenBank PX412013.

Notes: The type collections of *Entoloma brunneoflocculosum* and *E. asperum* were very similar in their ITS regions, so we consider them conspecific. This enabled us to get a better picture of the morphological variability within the species. The type of *E. asperum* has a larger percentage of 2-spored basidia, which explains the larger spore sizes observed. The presence of cystidia in *E. asperum* may indicate a degree of morphological differentiation, but in many *Entoloma* species presence or absence of cheilocystidia is a variable character and of limited diagnostic value. Illustrations of basidiomata and microscopic characters can be found in Noordeloos (2004) and Ludwig (2007).

/Claudopus clade – *Entoloma* subgen. *Claudopus*

Entoloma* subgen. *Claudopus (Gillet) Noordel., *Persoonia* **11**: 147. 1981. MB 860550.

Basionym: *Claudopus* Gillet, *Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France*: 426. 1876. MB 17311.

Synonyms: *Entoloma* subgen. *Paraleptonia* Romagn. ex Noordel. in *Persoonia* **11**: 149. 1981. MB 90850.

Paraleptonia (Romagn. ex Noordel.) P.D. Orton, *Mycologist* **5**(4): 174. 1991. MB 25374. – Type species: *Entoloma neglectum* (Lasch) Arnolds

Paraeccilia Largent, *Entolomatoid fungi of the Western United States and Alaska*: 368. 1994. MB 27619. – Type species: *Eccilia sericeonitida* P.D. Orton (= *E. undatum*).

Type species: *Agaricus byssisedus* Pers. = *Entoloma byssisedum* (Pers.) Donk

The /*Claudopus* clade coincides with subgen. *Claudopus* in the sense of He *et al.* (2019) and is an assemblage of small species with omphalinoid basidiomata or reduced, pleurotoid basidiomata, with an eccentric, lateral, or completely absent stipe. It contains species around the morphospecies *E. byssisedum* (pleurotoid) and *E. undatum* (omphalinoid). The species around *E. rusticoides*, i.e. the /*Rusticoides* clade included in the traditional concept of *Entoloma* subgen. *Claudopus* (Romagnesi 1974, Noordeloos 1981), form a distant clade (subgen. *Omphaliopsis*) and are excluded here from subgen. *Claudopus* (see also Vila *et al.* 2014, He *et al.* 2019). Since *E. neglectum* and related species are embedded within subgen. *Claudopus*, the (sub)genus *Paraleptonia* is considered a synonym of *Claudopus*. The same applies to *Paraeccilia* Largent, with its type *E. sericeonitida*, which is a synonym of *E. undatum*.

Species in subgen. *Claudopus* are often rather polymorphic and may vary from pleurotoid, with or without a strongly reduced lateral stipe (and then often identified as *E. byssisedum*), to omphalinoid with a well-developed, eccentric or central stipe (often identified as *E. undatum*). Considering this and the limited diagnostic value of micromorphological characters such as the size of basidiospores, presence or absence of cheilocystidia and pigmentation, it is often hard to distinguish morphological species within the subgenus. In addition, interpretation of classical names is not without problems, resulting in misapplications in literature. The ITS barcode differences may, however, support identification. Species of subgen. *Claudopus* have a world-wide distribution and, apart from our own sequences, additional data from various continents originating from recent publications (Largent *et al.* 2011a, Deng *et al.* 2015, He *et al.* 2015, 2019, Morozova *et al.* 2022), iNaturalist, and GenBank have been incorporated in our phylogenetic tree (Fig. 48). European names have often been applied to extra-European material, and therefore, in order to improve the taxonomy of subgen. *Claudopus*, we first attempt here to designate a lecto- an epitype for *E. byssisedum*, and a neotype for *E. undatum*. In addition, new sequences were obtained from recently described species, supplemented by many newly generated sequences from well-documented collections we could lay our hands on. As a result, we have a fairly large phylogenetic tree (Fig. 48) with numerous OTUs, and it is apparent that

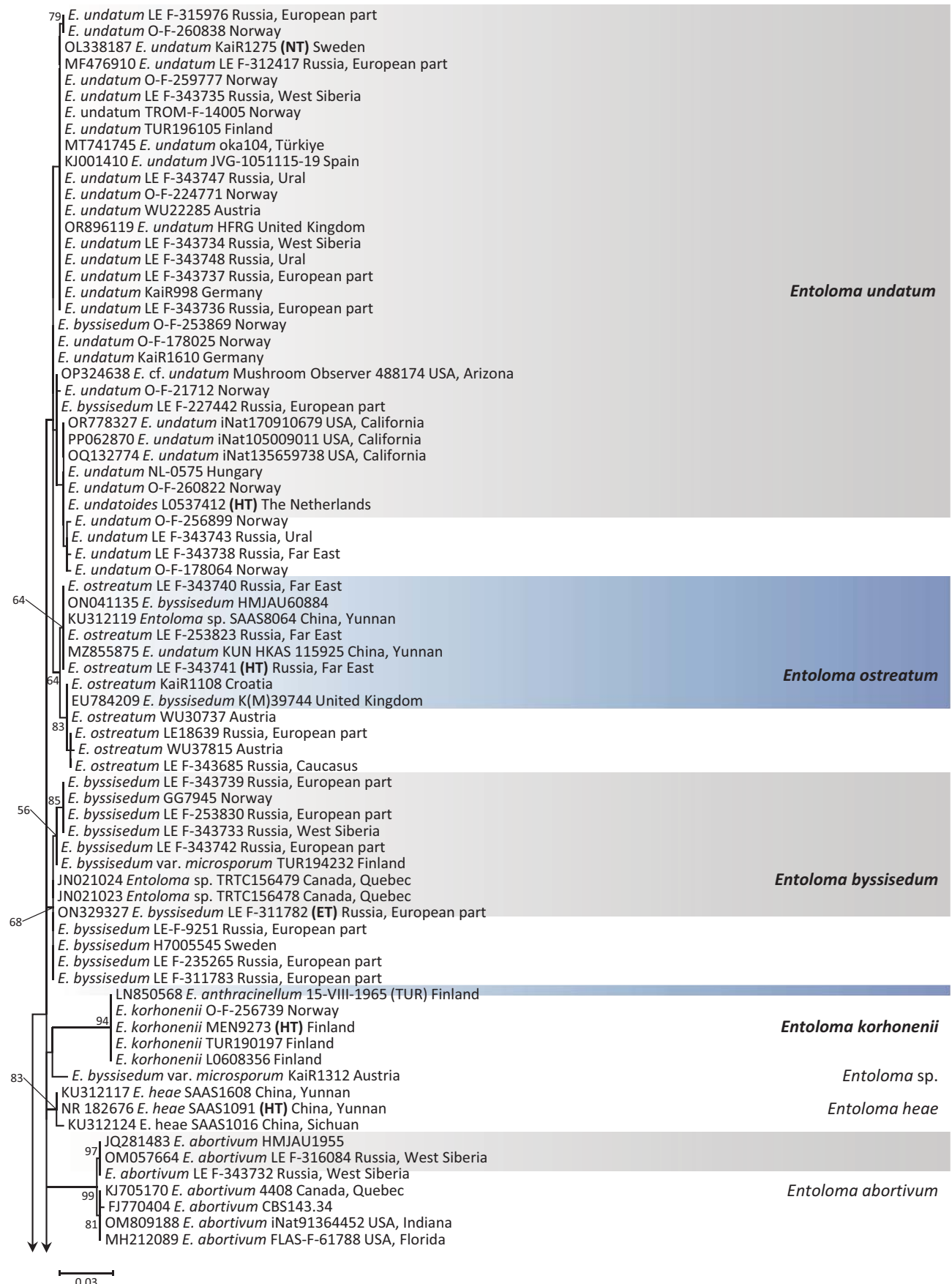


Fig. 48. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* subgen. *Claudopus* (= *Claudopus* clade). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.

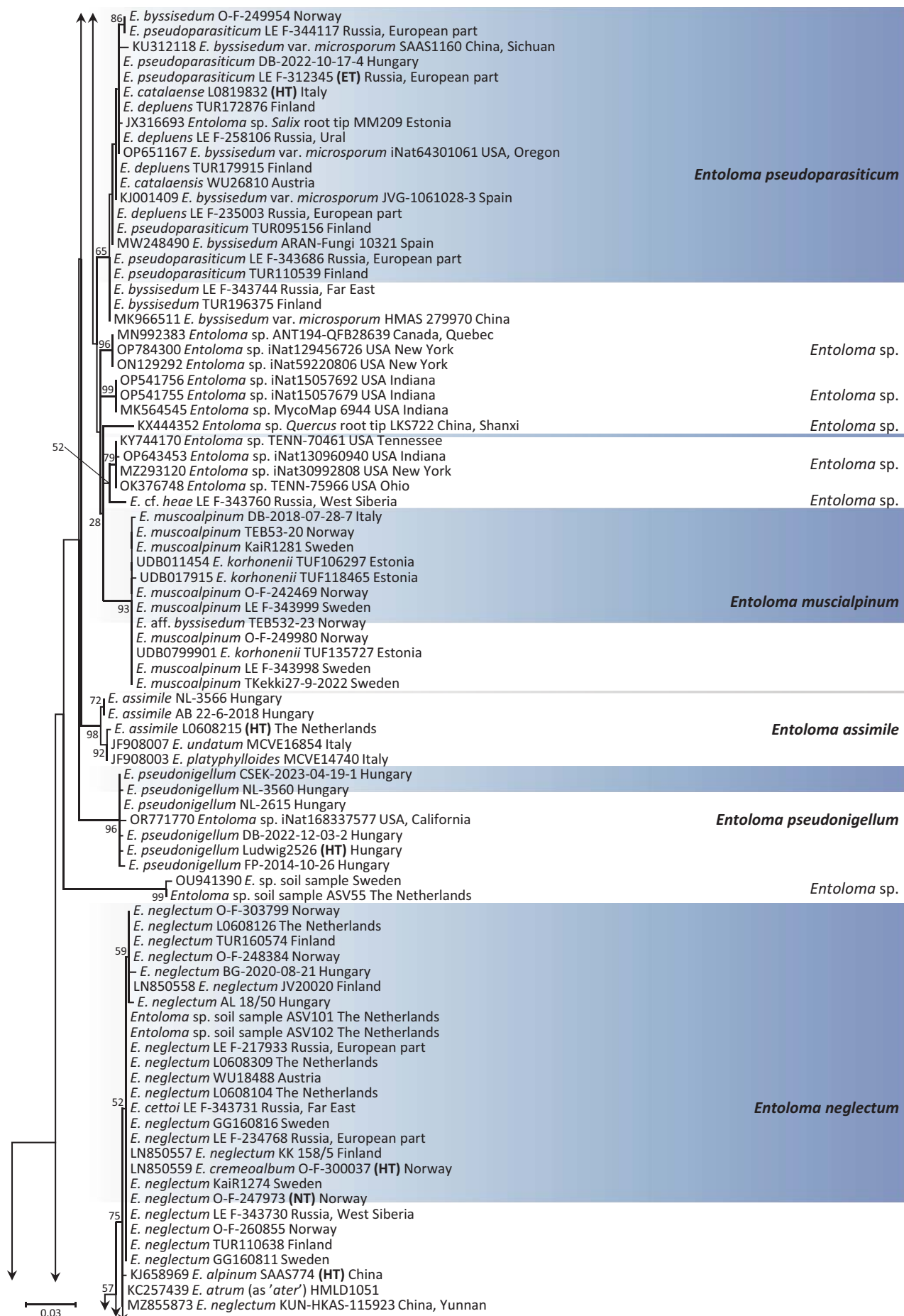


Fig. 48. (Continued).

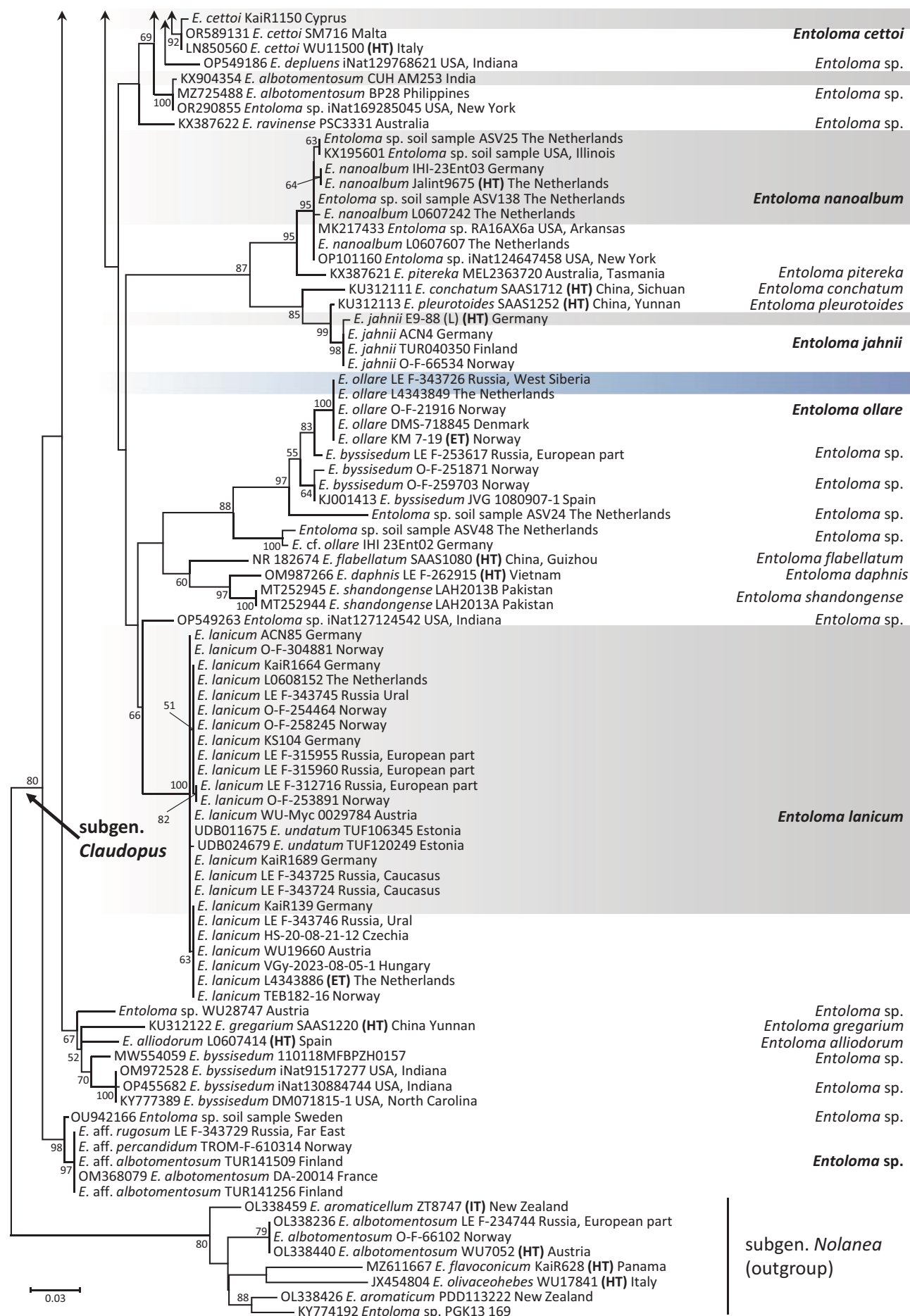


Fig. 48. (Continued).



most of the European names used outside Europe seem to have been misapplied. Several of the clades representing unknown species are described here as new to science.

Within subgen. *Claudopus*, traditionally a segregation was made between omphalinoid species (*E. undatum* type) and pleurotoid species (*E. byssisedum* type). In our study, we found that both of these morphotypes occur in several subclades of the tree. The top half of the present phylogenetic tree (the /Undatum clade (*E. undatum*–*E. pseudonigellum*)) contains a couple of clades that often differ only in a few nucleotides, and includes both morphotypes mentioned above. There is little internal variation. The *Entoloma undatum* clade includes the holotype of *E. undatoides*. This means that some morphological variability must be accepted with regard to basidiomata colour and degree of zonation of the pileus. The next two subclades of the /Undatum clade contain species with pleurotoid basidiomata, generally identified as *E. byssisedum* *sensu lato*. The lower clade includes the epitype of *E. byssisedum*, the one above is described as the new species *E. ostreatum*. Within this last clade there is a slight segregation into European and Asian subclades. *Entoloma korhonenii*, originally described as a variety of *E. undatum*, appears to be a well-supported clade and a species in its own right. Other omphalinoid species sometimes confused with *E. undatum*, like *E. lanicum*, *E. assimile*, *E. pseudonigellum* and *E. muscialpinum* form well-supported clades in the lower parts of the tree. A rather well separated clade is formed by three extralimital species, including *E. heae* from China, and *E. abortivum* from North America. *Entoloma pseudoparasiticum*, with a pleurotoid appearance, is distant from *E. byssisedum*, and fixed here with an epitype. It also includes *E. catalaense*, and several collections identified as *E. byssisedum* var. *microsporum*. A

number of small, pleurotoid species with pale basidiomata, often found hidden in vegetal debris or on rotten wood, is relatively poorly known. In the field they can be confused with *Clitopilus* or *Crepidotus* species. The subgenus includes *E. jahnii* and *E. ollare*, as well as a new species, *E. nanoalbum* which forms a well-supported clade with the rather similar *E. pitereka* from Australia. As is clear from the phylogeny, there are several (extralimital) lineages that represent potential new species, but they cannot be formally described because of the lack of sufficient morphological and ecological data.

Entoloma alliodorum Esteve-Rav., E. Horak & A. Ortega, *Mycotaxon* **86**: 228. 2003. MB 372435.

Typus: Spain, Malaga, Yunquera, Sierra de las Nieves, Tajo de la Caina, on organic debris, among mosses (*Homalothecium sericeum* and *Pleurochaete squarrosa*) and lichens (*Cladonia* sp.) and very rotten wood of *Abies pinsapo*, *Cistus albidus* and *Ulex baeticus*, 1 Nov. 1994, L. Alcoba, F. Esteve Raventós, E. Horak & A. Ortega (**holotype** AH 16907, **isotype** L0607414); ITS sequence, GenBank PX412022.

Notes: *Entoloma alliodorum* is a rather isolated species in the phylogeny, only known from the type locality, and characterised by the white basidiomata and strong garlic smell. A full description can be found in Noordeloos (2004).

Entoloma assimile G.M. Jansen, Noordel., Biketova, L. Nagy & Dima, **sp. nov.** MB 860392. Fig. 49.

Etymology: *assimile* (Lat.) – similar, referring to the likeness with *E. undatum*.



Fig. 49. *Entoloma assimile* (L0608215, holotype). **A–C.** Habit. **D.** Basidiospores. Photos: G.M. Jansen. Scale bars: 1 cm (habit), 10 µm (spores)



Typus: The Netherlands, prov. Zuid Holland, Oostvoorne, 25 Sep. 2015, G.M. Jansen, C149-2190 (**holotype** L0608215); ITS sequence, GenBank PX412024.

Description: *Basidiomata* omphalinoid, resembling *E. undatum*, but deeper umbilicate. *Pileus* about 10–25 mm wide, convex, deeply umbilicate to infundibuliform, warm reddish brown, deeply translucently striate, hygrophanous, subglabrous, with a few silvery, fibrillose patches, sometimes with concentric zones. *Lamellae* crowded (L = 30–46, l = 3–5), ascending and with decurrent tooth to deeply decurrent, pinkish brown then brown, almost like pileus, with concolourous, entire edge. *Stipe* 20–25 × 1–2 mm, cylindrical, flexuous, brown like pileus, glabrous, with basal mycelium. *Context* thin, brittle, brown. *Smell* and *taste* farinaceous. *Basidiospores* (40/2) 8.5–10.0 × 6.0–7.0 µm, on average

6.4 × 7.3 µm, Q = 1.30–1.60, Qav = 1.40–1.45, 6–7-angled with rather blunt angles. *Basidia* 23–40 × 8–11 µm, 4-spored, clamped. *Lamella edge* fertile, without cheilocystidia. *Pileipellis* a cutis of repent hyphae, 3–10 µm wide, with brown, intracellular and encrusting pigment. *Pileitrama* regular, made up of cylindrical to inflated hyphae, 5–20 µm wide, with brown, sometimes minutely incrustated walls. *Stipitipellis* a simple cutis of narrow, more or less encrusted, 5–15 µm wide hyphae; *caulocystidia* not observed. *Clamp-connections* present in all tissues.

Habitat and distribution: Gregarious in grassland on sandy soil in Atlantic coastal dunes (holotype) as well as continental steppe-like, semiarid grasslands and from an artificial island in the Venetian Lagoon. Known from The Netherlands, Italy and Hungary.

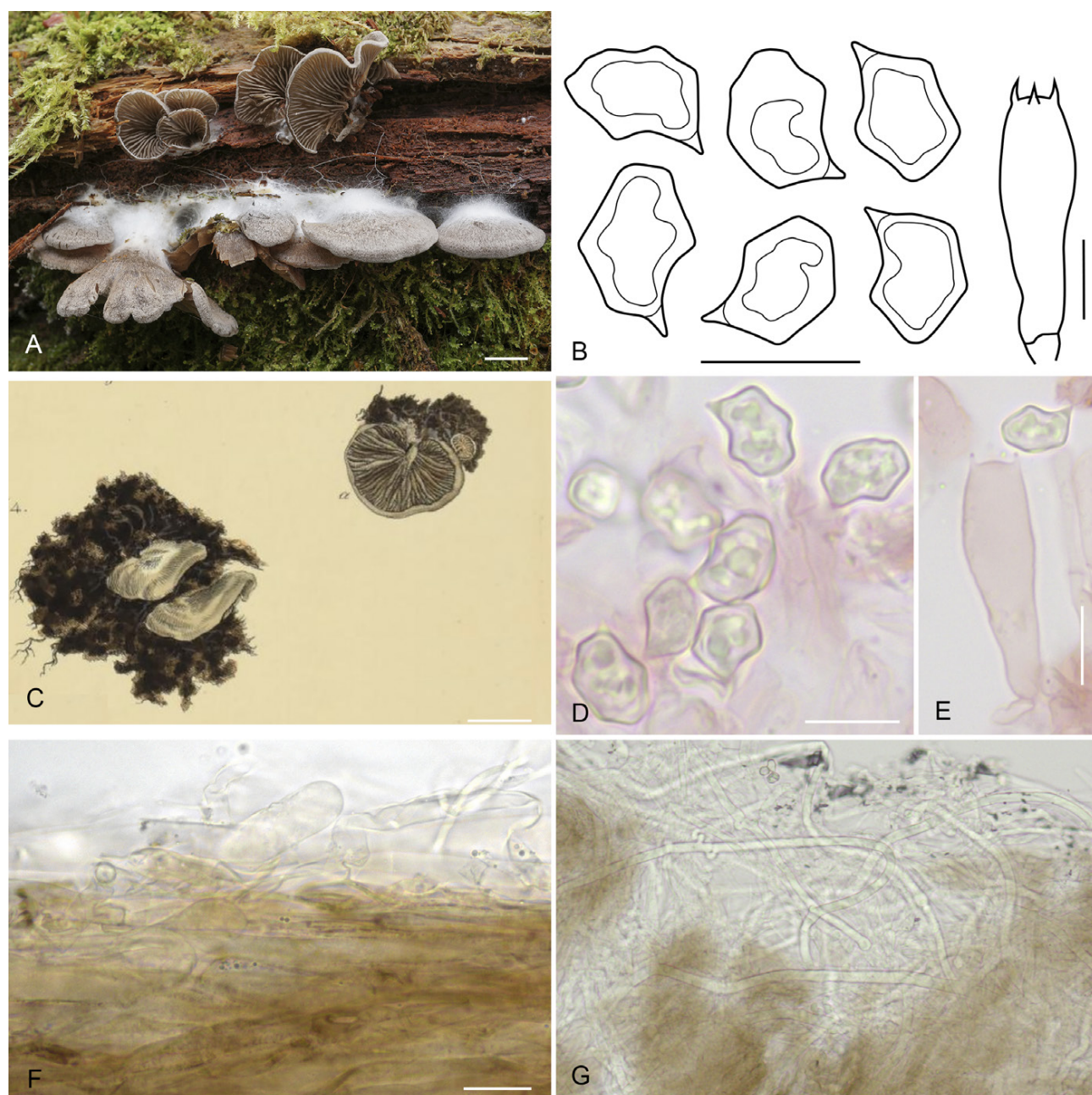


Fig. 50. *Entoloma byssisedum* (A–B, D–G. LE 311782, epitype; C. Lectotype). **A.** Habit. **B, D.** Basidiospores. **C.** Lectotype plate C.H. Persoon. **E.** Basidium. **F, G.** Pileipellis. Photos: O. Morozova. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (all other figs).



Additional material examined: **Hungary**, Bács-Kiskun, Kecskemét, L. Nagy, NL-3566 (SZMC); Bács-Kiskun, Tompa, on sandy soil, 22 Jun. 2018, A. Biketova, DB-2018-06-22-1 (ELTE). **Italy**, Veneto, Venezia, Cassa di Volnata, 30 Oct. 2004, E. Bizio & E. Campo (MCVE16854) (Osmundson et al. 2013).

Notes: *Entoloma assimile* is a phylogenetic species, morphologically rather similar to *E. undatum*, but phylogenetically distant, growing mainly in sandy pioneer vegetation, possibly with slightly smaller spores and more reddish tinges.

Entoloma byssisedum (Pers.) Donk, *Bull. Bot. Gdns Buitenz.* **18**: 158. 1949. MB 297238. Fig. 50.

Basionym: *Agaricus byssisedus* Pers., *Icon. Desc. Fung. Min. Cognit. (Leipzig)* **2**: 56. 1800. MB 494576.

Typus: Persoon, 1800, *Icones et descriptiones Fungorum minus cognitorum* 2, tab. XIV, fig. 4 (**lectotype**, designated here, MBT 10028198). **Russia**, Tver Oblast, Staritsky District, vicinity of the Krutitsy Village, in *Picea abies* forest, on rotten *Picea* log, 13 Sep. 2015, O. Morozova, 76TV15 (**epitype** LE 311782, designated here, deposited at LE, MBT 10028199); ITS sequence, GenBank ON329327.

Description of the epitype: *Basidiomata* pleurotoid. *Pileus* 5–35 mm wide, plano-convex to applanate with irregularly undulating or lobed margin, slightly involute when young, sometimes concave, ovoid to reniform or irregular when seen from above, not hygrophanous or translucently striate, pale grey or greyish brown, entirely radially fibrillose, sometimes zonate, often densely covered with white arachnoid mycelium around the place of attachment to the substrate, turning into white rhizomorphs in the substrate. *Lamellae* moderately distant ($L = 10\text{--}25$, $I = 1\text{--}5$), to fairly crowded, thin, adnate to subdecurrent, ventricose, pale grey, then pinkish brown, with entire or slightly eroded, concolourous edge. *Stipe* (1–)3–5 × 0.5–3 mm, strongly reduced to almost indistinct, lateral, pale grey brown, concolourous with pileus, pruinose to distinctly silky-striate, with white mycelial strands at base, solid. *Context* thin, concolourous with surface. *Smell* and *taste* indistinct to slightly farinaceous. *Basidiospores* (140/8) $8.0\text{--}10.0\text{--}(10.8) \times 5.5\text{--}7.0 \mu\text{m}$, on average $9.0 \times 6.3 \mu\text{m}$, $Q = 1.30\text{--}1.60$, $Q_{av} = 1.40\text{--}1.45$, heterodiametrical, 5–7-angled in side view. *Basidia* 4-spored, clamped. *Lamella edge* fertile or heterogeneous, cheilocystidia absent in epitype, but sometimes present in other collections studied. *Pileipellis* a cutis, sometimes with transitions to a trichoderm, made up of radially arranged, 2–9 μm wide, cylindrical or slightly inflated hyphae, with up to 12 μm wide, ascendant, inflated terminal elements; pigment membranous and additionally encrusting. Arachnoid covering consists of long, 5–8 μm broad, clamped hyphae. Oleiferous hyphae present in the pileitrama. *Clamp-connections* present, at least in hymenium.

Habitat and distribution: In groups on rotten wood, often on *Picea* logs, but also recorded on *Alnus*, *Fagus* and *Betula*. Widespread in boreal-temperate Europe, East to West Siberia.

Additional material examined: **Finland**, Savonia borealis, Kuopio, Puijo, Antikkalanrinne, herb-rich forest dominated by

Picea abies, on stump, 9 Sep. 2011, K. Kokkonen, KK299/11, FIPUT626-14 (TUR194232). **Norway**, Buskerud, Ringerike, Ringkollen, moss-rich blueberry spruce forest, on decayed wood of spruce, 6 Sep. 2013, W.E. Johansen, B. Sunde & H.K. Johnsen (O-F-301245); Trøndelag, Sør-Trøndelag, Orkland, Grytdalen NR, Nordslættbekken, on decayed wood of spruce in mountain forest, 4 Sep. 2021, G. Gaarder, GG7945. **Russia**, Murmansk Oblast, Khibiny Mountains, Polar-Alpine Botanical Garden, on *Alnus* stump in a mixed forest, 4 Sep. 1974, L. Mikhailovsky, 1947-M-119 (LE F-9251); Novgorod Oblast, Valday District, Valdaisky National Park, near Shuya Village, in *Pinus sylvestris*-*Picea abies* forest, on decayed wood, 22 Aug. 2003, R. Halling, LE F-253830; Tver Oblast, Staritsky District, near Krutitsy Village, in *Picea abies* forest, on fallen log, 10 Sep. 2011, E. Pravdolyubova, LE F-311783; Komi Republic, Koygorodsky District, near the “Gran” touristic camp, left bank of the Mytets River, mixed forest, on a decaying stump, 16 Aug. 2022, M. Palamarchuk, SYKO4200 (LE F-343742); Khanty-Mansiysk AO, Khanty-Mansiysk District, Shapsha Village, mixed predominantly coniferous forest, on soil among mixed litter, 3 Aug. 2015, N. Filippova, YSU-F-05690 (LE F-343733); Vologda Oblast, Kirillovsky District, Russian North National Park, Nylovitskoye forestry, 10 Sep. 2005, O. Shiryayeva, LE F-235265. **Sweden**, Jämtland, Skaerkan, rather old, selectively logged spruce birch forest, on a fallen *Betula pubescens*, 18 Aug. 2011, O. Miettinen, FIAPH196-12 (H7005545).

Notes: In the mycological tradition, *Entoloma byssisedum* has been interpreted as a small pleurotoid species with a pale grey brown, silky-fibrillose pileus, pinkish lamellae, and a reduced, whitish, pubescent stipe, growing on rotten wood, connected with white mycelial threads to the substrate (“byssisedus”). Our studies, however, have shown that there is more than one phylogenetic species answering these criteria, and therefore, we have chosen an epitype that fits well with the lectotype and original diagnosis. The photograph of the epitype shows several basidiomata connected to the rotten woody substrate with white mycelial threads that matches the original plate (lectotype). Noordeloos (1988) gave a description of *E. byssisedum*, based on very few collections, with rather large spores, $10\text{--}12 \times 6.5\text{--}8 \mu\text{m}$, apparently extending beyond the normal range for this species. As a consequence, a small-spored collection from Spain was described as *E. byssisedum* var. *microsporum* (Noordeloos 2004). Our current molecular study of numerous collections labelled *E. byssisedum* or *E. byssisedum* var. *microsporum* reveals that the epithets *byssisedum* and *byssisedum* var. *microsporum* appear in several non-related clades. In addition, we found that spore size may vary greatly in *E. byssisedum* but lies mostly within the range of $7.5\text{--}11 \times 5.5\text{--}7.5 \mu\text{m}$. We had to decide to choose one of these clades to represent the true *E. byssisedum*, in order to be able to clarify the nomenclature of the group. Accordingly, we have chosen a well-documented collection, nicely fitting the lectotype and protologue. Several collections labelled either *E. byssisedum* or *E. byssisedum* var. *microsporum* clustered in other clades, and belong to other species, including *E. pseudoparasiticum*, *E. ollare*, *E. undatum* and *E. lanicum*. Unfortunately, the holotype of *E. byssisedum* var. *microsporum* failed to yield a barcode sequence several times, so we cannot give a final opinion regarding the status of this variety. Some of the extralimital *E.*



byssisedum or *E. byssisedum* var. *microsporum* identifications appear to be of different species that need to be studied more closely (e.g. in He et al. 2019). *Entoloma byssisedum* var. *microsporum* identified from China (He et al. 2019) belongs to *E. pseudoparasiticum*.

Entoloma lanicum (Romagn.) Noordel., *Persoonia* 11: 149. 1981. MB 112299. Fig. 51.

Basionym: *Rhodophyllus lanicus* Romagn., *Revue Mycol.* 1(3): 158. 1936. MB 268941.

Typus: **France**, Dept. Seine & Oise, Villecresnes, Sep. 1932, *H. Romagnesi* (**lectotype** in PC, designated by Noordeloos 1981). **The Netherlands**, prov. Zuid Holland, Voornes Duin, 64 200/435 866, 28 Aug. 2015, *E. Vis* (**epitype** L4343886, designated here, deposited at L, MBT 10028201); ITS sequence, GenBank PX412045.

Description: *Basidiomata* omphalinoid. *Pileus* 5–30 mm wide, convex to plano-convex, slightly depressed to umbilicate, or funnel-shaped, with involute then deflexed margin, not or slightly hygrophanous, not translucently striate, pale pinkish brown to medium brown with incarnate reflex or grey brown, slightly pallescent on drying, finely felted with loose, radially oriented fibrils, indistinctly to distinctly zonated, slightly pallescent on drying. *Lamellae* moderately distant ($L = 20\text{--}26$, $l = 1\text{--}3$), adnate-decurrent, arcuate to subventricose, grey at first then pinkish brown to pinkish grey with concolourous, entire edge. *Stipe* 10–20 × 1–2 mm, central or slightly

eccentric, cylindrical or tapering towards base, concolourous with pileus, with a white fibrillose-pruinose covering, with dense white mycelium at the base. *Context* thin, brittle, brown. *Smell* and *taste* indistinct or slightly farinaceous. *Basidiospores* (180/16) $7.0\text{--}10.0 \times 5.5\text{--}7.0 \mu\text{m}$, on average $7.8\text{--}8.5 \times 5.5\text{--}6.7 \mu\text{m}$, $Q = 1.20\text{--}1.55$, $Q_{av} = 1.40\text{--}1.50$, heterodiametrical, (4–)5–9-angled in side view. *Basidia* 20–24 × 6–11 μm , 4-spored, clamped. *Lamella edge* fertile, cystidia absent. *Pileipellis* a cutis of radially arranged, cylindrical, 1.5–7 μm wide hyphae; pigment minutely encrusting *Stipitipellis* a cutis of cylindrical hyphae, 3–9 μm wide. *Caulocystidia* present, 20–40 × 5–12, subcylindrical, irregularly flexuous with rounded apex. *Clamp-connections* present in all tissues.

Habitat and distribution: Terrestrial or on woody litter (especially *Fagus*, *Picea*), also found on burnt wood, in calcareous forests, forest margins, etc., summer to autumn. Widespread in Europe, but not often recorded.

Additional material examined: **Austria**, Niederösterreich, Zwettl, Friedersbach, Schacher-Reuthofried, in mixed coniferous forest with scattered deciduous trees on mossy embankment, 11 Jul. 2009, *A. Hausknecht* (WU-Myc 0029784); Oberösterreich, Zell am Moos, Ruine Wildeneck, in forest margin, 5 Sep. 1999, *A. Hausknecht* (as *E. neglectum*, WU-Myc 19660). **Czechia**, Sidonie, Sidonie Nature Reserve, in *Fagus* forest, near the road together with *Echinoderma asperum*, 21. Aug. 2020, *H. Ševčíková*, HS-20-8-21-12 (BRM). **Germany**, Baden-Württemberg, Odenwald, near



Fig. 51. *Entoloma lanicum* (A, B, D. L4343886, epitype; C. LE F-343746). **A–C.** Habit. **D.** Basidiospores. Photos: A by E. Vis; B by G.M. Jansen; C by O. Morozova. Scale bars: 1 cm (habit), 10 μm (spores).



Ursenbach, L-trail, on soil between *Fagus*-litter, 13 Aug. 2023, K. Reschke, KaiR1689 (B 70 0105525); Bavaria, Paterzell, Paterzeller Eibenwald, moist *Fagus*-dominated forest with old *Taxus baccata* trees, on soil and attached to rotten wood pieces, 12 Sep. 2016, K. Reschke, KaiR139 (B 70 0105502); Steigerwald, near Ebrach, *Fagus*-dominated broad-leaved forest, on soil between leaf litter, 7 Aug. 2023, K. Reschke, KaiR1664 (B 70 0105524); Hessen, near Biedenkopf, Martinsbachtal, on rich soil under *Fraxinus excelsior*, 6 Aug. 2016, M. Theiss, ACN85 (B 70 0105500); Thüringen, Hasenthal, Pfmersbach, wayside beside brook, on probably calcareous soil, 15 Sep. 2023, A. Karich, IHI-23Ent04 (GLM-F139007). **Norway**, Akershus, Bærum, Dælivann, Godthåp, in calcareous *Corylus-Fraxinus* woodland, TEB 182-16 (O), DB6042 (ELTE); Akershus, Oppland, Lunner, Søndre Oppdalen, Mørkomdalen, Olstadskogen, timber track road in low herb *Picea* forest, 2 Sep. 2017, E. Bendiksen, EB 225/17 (O-F-254464), Mørkomdalen, Bredli SE, in track road (for timber) in low herb forest, 26 Aug. 2006, E. Bendiksen, EB 43/06 (O-F-253891); Telemark, Porsgrunn, Kolbjørn-Frierflogene NV, in calcareous *Corylus-Fraxinus* woodland, 9 Sep. 2015, T.E. Brandrud, TEB 216-15, RB-01 (O-F-254567); Telemark, Kragerø, Kammerfossåsen, rich *Tilia* forest margin, 4 Aug. 2016, T.E. Brandrud, TEB 98-16 (O-F-304881); Vestland, Sogn og Fjordane, Luster, Dalsdalen, Øygarden nord, on decaying *Ulmus glabra* log in broad-leaved forest, 6 Sep. 2018, G. Gaarder, GG7710/7726 (O-F-258245). **Russia**, Bryansk Oblast, Suzemsky District, “Bryansky forest” Nature Reserve, on rotten log in broad-leaved forest, 8 Aug. 2015, O. Morozova, 21BR15 (LE

F-312716); Pskov Oblast, Pushkinogorsky District, near Mikhailovskoye Village, on soil on roadside in a mixed forest, 11 Sep. 2018, O. Morozova, 4PG18 (LE F-315955); *ibid.*, 12PG18 (LE F-315960); Stavropolsky Krai, Pyatigorsk, Perkalsky Arboretum, on soil in mixed forest, 4 Aug. 2009, O. Morozova, 1TB09 (LE F-343724); Karachay-Cherkess Republic, Teberda State Biosphere Reserve, near Teberda, on *Fagus* log in *Fagus orientalis*-*Abies nordmanniana* forest, 6 Aug. 2009, O. Morozova, 23TB09 (LE F-343725); Sverdlovsk Oblast, vicinity of Krasnoufimsk, “Nizhneirginskaya oak grove” protected area, on soil in grassland, 27 Aug. 2024, O. Morozova, 178SV24 (LE F-343745); *ibid.*, 186SV24 (LE F-343746).

Notes: *Entoloma lanicum* is similar to *E. undatum*, differing mainly by tomentose, often opaque, sometimes zonated, loosely fibrillose pileus, silvery fibrillose stipe, and slightly smaller spores. It differs also very slightly in ecology and prefers richer to calcareous forest sites, including rotten wood and wood chips, whereas *E. undatum* prefers grasslands, roadsides, or open spots in sandy dunes. *Entoloma muscialpinum* has an even more overlapping habitat and can sometimes co-occur with *E. lanicum* in rich forest (margins). The lectotype of *E. lanicum*, studied by Noordeloos (1981) could not be located in PC and might be lost. Therefore, an epitype is selected to fix this species with a recent collection and ITS barcode.

Entoloma nanoalbum Jalink, Noordel. & Dima, *sp. nov.* MB 860391. Fig. 52.

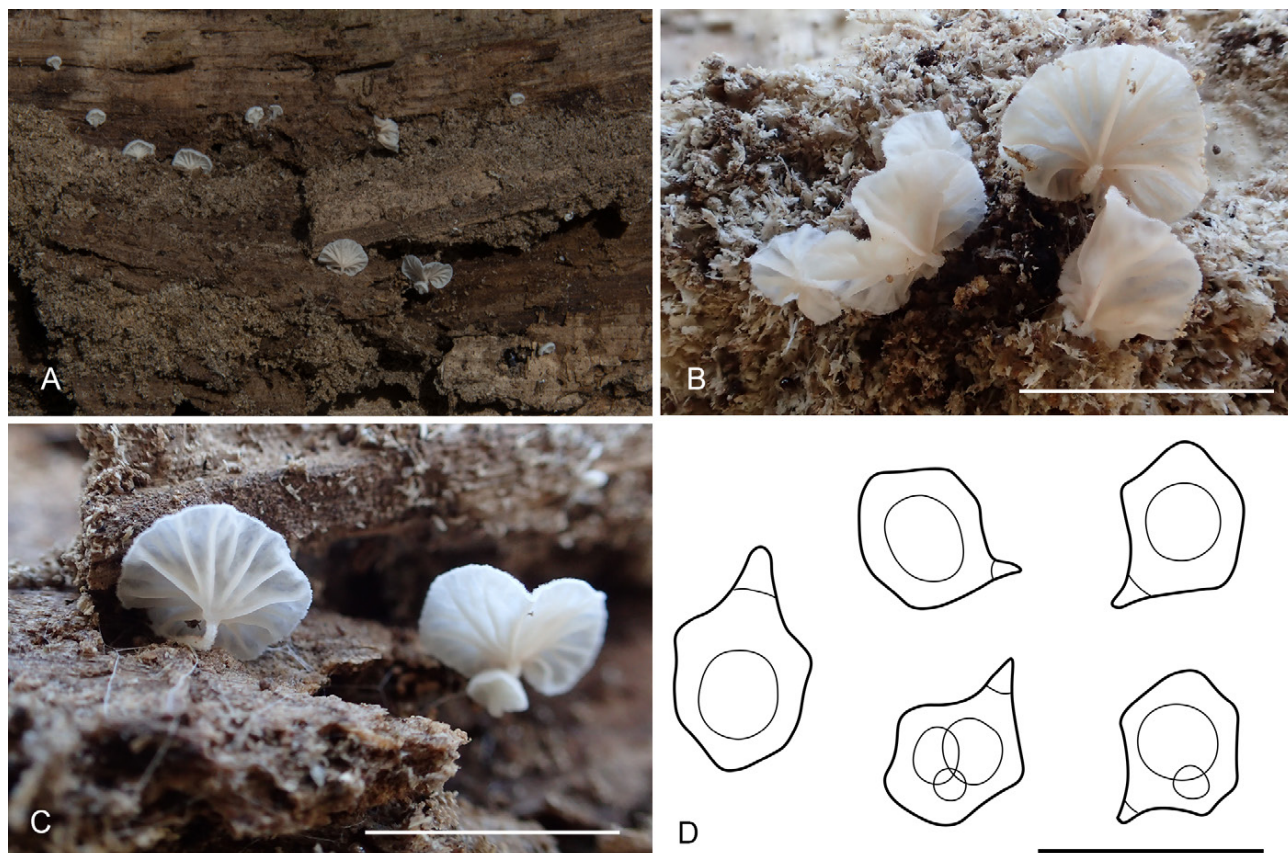


Fig. 52. *Entoloma nanoalbum* (Jalink 9675, holotype). **A–C.** Habit. **D.** Basidiospores. Photos: L. Jalink. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μ m (spores).



Etymology: *nanus* (Lat.) – dwarf, *albus* (Lat.) – white, referring to the tiny, white basidiomata.

Typus: **The Netherlands**, prov. Zuid Holland, Wassenaar, Meijndel, Kijfhoek East, on rotten wood of *Fagus sylvatica*, or on soil in broad-leaved forest, 22 Jul. 2019, L. Jalink, Jalink9675 (**holotype**, L); ITS sequence, GenBank PX412048.

Description: *Basidiomata* small collybioid to pleurotoid with reduced stipe. *Pileus* (1.5–)3–7 mm wide, applanate with deflexed margin, white, very thin (and opaque or slightly translucent), surface densely covered with woolly hairs. *Lamellae* very distant (L = 8–10, I = 0–1), sometimes forked and reduced, vein-like, white then pink from ripe spores. *Stipe* very short, central or lateral, white, slightly pubescent to felted. *Context* thin, brittle, white. *Smell* indistinct, *taste* not noted. *Basidiospores* (60/4) 7.5–10.0 × 5.8–7.9 µm, on average 9.1–9.3 × 6.8 µm, Q = 1.10–1.60, Q_{av} = 1.35–1.45, heterodiametrical, 5–6(–7)-angled in side view. *Basidia* 26–41 × 9–11 µm, 4-, rarely also 2-spored, clamped. *Lamella edge* fertile, cystidia absent. *Pileipellis* a loose cutis of cylindrical hyphae, 3–9 µm wide with abundant loose, semi-uplifted terminal elements, not pigmented. *Clamp-connections* present in all tissues.

Habitat and distribution: In groups on rotten wood of *Fagus sylvatica*, or on soil in broad-leaved forest. So far known in Europe from three localities in The Netherlands, and one in Germany (see note below).

Additional material examined: **Germany**, Chemnitz, Stärker Wald, on soil in a moist tyre track, 26 Aug. 2022, P. Welt, IHI-23Ent03 (GLM-F139801). **The Netherlands**, prov. Groningen, Trimunt, on soil in deciduous forest, 9 Aug. 2013, I. Somhorst, MY127 (L0607242); prov. Overijssel, Huize Dorth, Harfsen, NL 52.22358, 6.29453, on soil in deciduous forest, 11 Jul. 2020, M. Gotink (L0607607).

Notes: This species could well be mistaken for pleurotoid specimens of *E. albotomentosum*, but that species usually has much larger, 4–5-angled spores, no clamp-connections and is phylogenetically very distant belonging to subgenus *Nolanea* (Reschke *et al.* 2022b). *Entoloma parasiticum* differs by having isodiametrical spores. Interestingly, ITS sequences derived from soil samples (environmental DNA) from The Netherlands (ASV25 and ASV138) are identical to the holotype sequence, as well as to three sequences from the USA (GenBank KX195601, MK217433, OP101160). The matching soil-derived sequences indicate that this tiny and easily overlooked species apparently has a much wider geographic distribution.

Entoloma neglectum (Lasch) Arnolds, *Biblioth. Mycol.* **90**: 339. 1982. **amend.** MB 112299. Fig. 53A–D.

Basionym: *Agaricus neglectus* Lasch, *Linnaea* **3**: 401. 1828. MB 372191.

Synonym: *Entoloma cremeoalbum* J.B. Jordal & Noordel., Öst. Z. Pilzk. **19**: 127. 2010. MB 519096.

Typus: **Holotype** not existing. **Norway**, Akershus, Oppland, Lunner, Rønningsåsen NV, Bestemorsmyra, calcareous fen/

mire, 3 Aug. 2014, T.E. Brandrud, TEB 52-14 (**neotype** O-F-247973, designated here, deposited at O, MBT 10028202); ITS sequence, GenBank PX412049.

Description (amended here): *Basidiomata* omphalinoid. *Pileus* 5–40 mm wide, plano-convex with umbilicate centre to infundibuliform, with involute or inflexed margin, often with irregularly lobed margin when old, not hygrophanous nor translucently striate, opaque, whitish to beige or very pale cream, flesh-coloured or pale brownish-isabella, entirely finely fibrillose-tomentose, sometimes aeriferous zonated, dull. *Lamellae* moderately distant to distant (L = 15–36, I = 1–3–7), broadly adnate to decurrent, sometimes forked, arcuate to segmentiform, up to 4.5 mm broad, sometimes thickish, white then pink with an entire to minutely serrate, concolourous edge. *Stipe* 10–30 × 1.5–2.5(–3) mm, often distinctly shorter than the diameter of the pileus, cylindrical or compressed, sometimes with somewhat swollen to bulbous base, white or hyaline, sometimes with grey or yellow tinge, usually with white arachnoid, fibrillose covering or white tomentose. *Context* thin, hyaline. *Smell* strongly farinaceous. *Taste* rancid farinaceous. *Basidiospores* in 4-spored forms (90/6) 9.0–13.0 × 6.0–10 µm, on average 10.5–12.0 × 7.5–9.0 µm, Q = 1.20–1.50, Q_{av} = 1.30–1.35, heterodiametrical, 5–7-angled in side view; in 2-spored forms (40/3) 12.0–17.0(–18.5) × 7.5–10.0 µm on average 14.5–16.5 × 8.5–9.8 µm, Q = 1.40–2.20, Q_{av} = 1.60–1.70, heterodiametrical, nodulose-angular, 6–10-angled in side view. *Basidia* 19–35 × 8–12 µm, 2- or 4-spored, clamped. *Lamella edge* fertile or heterogeneous, rarely entirely sterile with cheilocystidia, 20–75 × 8–25 µm, cylindrical-capitate to tibiiform or lageniform, thin-walled. *Hymenophoral trama* regular, made up of cylindrical elements, 80–160 × 7–35 µm. *Pileipellis* a cutis with transitions to a trichoderm, made up of 4–17 µm wide, inflated terminal elements, pigment intracellular, often almost invisible, in addition sometimes minutely encrusting. *Pileitrampa* regular, made up of more than 200 × 5–30 µm wide, inflated elements, with abundant brilliant granules. *Caulocystidia* at apex scarce to abundant, 20–70 × 3–14 µm, cylindrical to capitate. *Clamp-connections* scattered to abundant.

Habitat and distribution: Gregarious in poorly managed, semi-natural grassland, meadows, roadsides, dune valleys, etc., preferably on (slightly) calcareous soil, also found in marshy vegetation with *Sphagnum*, including calcareous fens; up to the subalpine region in N Sweden; summer–autumn. Widespread all over Europe.

Additional material examined: **Czechia**, Český Šternberk, in artificial mossy grassplot (former meadow) on fluvial sediments, apparently distributed preferably on the interface between the lawn and the mineral soil dug up by moles, 4 Jun. 2016, J. Borovička (PRM 935993) – ITS sequence, GenBank PQ871413. **Norway**, Nordland, Bodø, Ausvika, calcareous, sandy, semi-natural grassland, 12 Aug. 2020, G. Gaarder & P. Alvereng, GG7805 (O-F-260855); Østfold, Fredrikstad, Sellebakk, among grass, sandy soil, 30 Jun. 2013, Ø. Weholt (O-F-303799); Telemark, Kragerø, Jomfruland landskapsvernområde, Saltstein, grazed, rich sandy dry meadow, shallow soil, 5 Jul. 2011, T.E. Brandrud, TEB 53-11 (O-F-248384); Trøndelag, Sør-Trøndelag,



Oppdal, Aunsetra, in weakly calcareous semi-natural grassland grazed by sheep, 30 Aug. 2010, *J.B. Jordal*, *P.G. Larsen* (O-F-300037, **holotype** of *E. cremeoalbum*). **Russia**, Kamchatka Krai, near Esso Village, left bank of Uksichan River, on grassland soil, 7 Aug. 2005, *O. Morozova*, LE F-343729; Leningrad Oblast, Vyborgsky District, Berezovye Islands, Bolshoy Beryozovy Island, on soil on *Calamagrostis epigejos* grassland, *O. Morozova*, LE F-235368; Novgorod Oblast, Valdaisky District, vicinities of the Bolshoye Nasakino Village, on soil on grass-forb meadow on calcareous moraine, 20 Aug. 2003, *O. Morozova*, LE F-217933; Tyumen Oblast, Tobolsk, Kirov Street, on soil on grass turf, 2 Sep. 2016, *B. Kapitonov*, P9026251 (LE F-343730). **Sweden**, Jämtlands län, Östersund, Frösön, Summarhagen, horse pasture, 29

Aug 2018, *K. Reschke*, KaiR1274 (B 70 0105513); Lule Lappmark, Jokkmokk Padjelanta NP, Arranoajvve, 11 Aug. 2016, *G. Gulden*, GG160811 (GB-0207763); Lule lappmark, Jokkmokk Padjelanta NP, Ajajaure, 16 Aug. 2016, *G. Gulden*, GG160816 (GB-0207764); Norrbotten, Arjeplog, Vuoggatjålme SV, 11 Aug. 2018, *J. Vauras*, *E. Larsson* & *J.B. Jordal*, EL48-18 (GB-0207760; ITS sequence, GenBank PV018338).

Notes: *Entoloma neglectum* is a rather widespread species which occurs in a wide range of habitats. It has pale, rather small, somewhat short-set, omphalinoid basidiomata. Kokkonen (2015) compared several Finnish sequences with the holotype sequences of the two-spored *E. cremeoalbum*,



Fig. 53. A–D. *Entoloma neglectum* (A. O-F-300037, holotype of *E. cremeoalbum*; B–D. O-F-247973, neotype). **A, B.** Habit. **C.** Basidiospores. **D.** Pileipellis. **E–G.** *Entoloma cettoi* (WU 11500, holotype). **E.** Habit. **F.** Basidiospores. **G.** Cheilocystidia. Photos: A by J.B. Jordal; B. by T.E. Brandrud; E from A. Hausknecht. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (all other figs).



and of *E. cettoi* and concluded that they probably can be considered synonymous. Our studies confirm the status of *E. cremealbum*, but the available accessions of *E. cettoi* (Fig. 53E–G) made us decide otherwise. Although there are only 3–4 differences in the ITS sequences compared to *E. neglectum*, the deviating morphology, and possibly also the thermophilous character of this southern species, made us decide to keep this species apart, also in view of the relatively small differences between many species in the whole *Claudopus* clade. *Entoloma heterocystis*, another morphologically close species, is probably very similar, differing mainly by the azonate pileus and lack of clamp-connections, but the holotype has not been successfully sequenced yet.

Entoloma ollare E. Ludw. & T. Rödiger ex E. Ludw. & T. Rödiger, *Fungi Europaei* 5a: 1139. 2004. MB 491792. Fig. 54.
Synonym: *Entoloma ollare* E. Ludw. & T. Rödiger, *Z. Mykol.* 58(2): 193. 1992. MB 358406, nom. inval., Madrid, Art. 40.3.

Typus: **Germany**, Berlin, Schöneberg, on compost in flower pot, 16 Dec. 1986, T. Rödiger (**holotype** L0607186 – in poor condition, **isotype** in M). **The Netherlands**, prov. Gelderland, Rheden, Heiderust, 17 Oct. 2021, unpaved, sandy path with mosses in a graveyard, M.J.C. van der Vegte (**epitype** L4343849, designated here, deposited at L, MBT 10028203); ITS sequence, GenBank PX412052.

Description: *Basidiomata* minute, pleurotoid. *Pileus* 2.5–10 mm wide, convex, expanding with depressed centre to infundibuliform, with slightly involute margin, indistinctly hygrophanous, when young only slightly translucently striate and covered with a white bloom or arachnoid layer of silvery fibrils, glabrescent with age and then more distinctly translucently striate, first pale grey then pale cream-coloured. *Lamellae* adnate to slightly decurrent ($L = 20\text{--}30$, $I = 1\text{--}3$), subdistant, thickish, white then pink. *Stipe* 1–4 × 1 mm, central to eccentric, attenuated towards base, curved, concolourous with pileus, finely tomentose. *Context* very thin. *Smell* and *taste* indistinct or farinaceous. *Basidiospores* (60/4) $8.5\text{--}13.5 \times 6.0\text{--}9.0 \mu\text{m}$, on average $10.5\text{--}11.7 \times 7.5\text{--}7.8 \mu\text{m}$, $Q = 1.20\text{--}1.90$, $Q_{av} = 1.40\text{--}1.60$, narrowly heterodiametrical with up to 7(–8), rather blunt angles. *Basidia* $20\text{--}40 \times 6\text{--}12 \mu\text{m}$, 4-, rarely also 2-spored, clampless. *Lamella edge* fertile. *Cystidia* absent. *Pileipellis* a trichoderm of septate, 3–15 μm wide hyphae with both minutely encrusting and pale brown, intracellular pigment. *Clamp-connections* absent.

Habitat and distribution: On compost in flowerpots indoors (holotype; Germany; epitype, Norway); terrestrial on bare soil with some liverworts, indoors, or on calcareous shallow-soil grassland or sandy soil in grasslands. Apparently widespread in Europe (but partly in glasshouses), and east to West Siberia.



Fig. 54. *Entoloma ollare* (A, B, C, E. L4343849, epitype; D. LE F-343726). **A, C, D.** Habit. **B.** Basidiospores. **E.** Pileipellis. Photos: A, C by M.J.C. van der Vegte; B, E by G.M. Jansen; D by O. Morozova. Scale bars: 1 cm (habit), 10 μm (spores and pileipellis).



Additional material examined: **Denmark**, Hejrede SØ (Biowide 120), on soil in fertilized grassland, 25 Sep. 2015, *T. Læssøe* & *T. Smidth*, DMS-718845 (C). **Germany**, Brandenburg, Hutelandschaft Altranft, base rich, semiarid grassland, 21 Oct. 2023, *A. Karich* & *R. Ullrich* (GLM-F139797). **Norway**, Telemark, Porsgrunn, Skjelsvika, in open calcareous, shallow soil grassland, 10 Oct. 2013, *T. Læssøe* & *A. Molia*, AM-248d-2013 (O-F-21916); Trøndelag, Sør-Trøndelag, Ørland, Tollefsvika, 16 Jun. 2019, in flower pot in glasshouse, *K. Mandal* & *Ø. Weholt*, KM-7-19. **Russia**, Khanty-Mansiyskiy autonomous okrug, 22.5 km E from Khanty-Mansiysk, in grassland, 20 Aug. 2010, *O. Morozova*, 46KH10 (LE F-343726).

Notes: Unfortunately, the holotype in Leiden as well as the isotype material deposited in Munich could not be sequenced, although attempts were made both with Sanger and NGS methods. Therefore, an epitype was selected (also from a flowerpot), and the description was amended. Despite the specific epithet, this species can be found both indoors and outdoors, in (often fertilized) grasslands. *Entoloma exiguum*, another pleurotoid species, differs from *E. ollare* by the slightly smaller spores, absence of incrustations in the pileipellis, and clamped hyphae. The holotype of *E. exiguum* has not been sequenced yet.

Entoloma ostreatum O.V. Morozova, Noordel., Reschke, Dima & E. Malysheva, **sp. nov.** MB 860390. Fig. 55.

Etymology: *ostrea* (Lat.) – oyster, referring to the pleurotoid habit of the basidiomata.

Typus: **Russia**, Primorsky Krai, Sikhote-Alin Nature Reserve, cordon Maisa, right bank of the Maisa River, mixed forest including *Pinus koraiensis*, *Abies nephrolepis*, *Tilia amurensis*, *Acer mono*, *Quercus mongolica*, on fallen log of a broad-leaved tree, 26 Aug. 2013, *O. Morozova* (**holotype** LE F-343741); ITS sequence, GenBank PX412054.

Description: Basidiomata pleurotoid. *Pileus* 5–35 mm wide, plano-convex to applanate, flat or uplifted, with at first incurved, then straight, sometimes crenulate margin, ovoid to reniform, shell-shaped or irregular in outline, not or only slightly hygrophanous, not translucently striate, pale grey or greyish brown, sometimes radially zonate, entirely radially fibrillose, with white arachnoid mycelium around the place of attachment to the substrate. *Lamellae* moderately crowded ($L = 10\text{--}20$, $I = 3\text{--}7$), thin, adnate to adnexed, ventricose, pale grey, then pinkish brown, with entire or slightly eroded, concolourous edge. *Stipe* (1–)3–10 × 0.5–3 mm, strongly reduced, eccentric or lateral, pale grey brown, concolourous with pileus, pruinose, sometimes with white, mycelial strands at base. *Context* concolourous with surface. *Smell* and *taste* farinaceous or not. *Basidiospores* (120/6) (7.8–)8.3–10.2(–11.0) × (5.5–)5.8–6.9(–7.2) µm, on average 9.2 × 6.5 µm, $Q = 1.30\text{--}1.60$ (–1.70), $Q_{av} = 1.40\text{--}1.45$, heterodiametrical, 4–7-angled in side view. *Basidia* 4-spored, clamped. *Lamella* edge fertile or heterogeneous, cheilocystidia cylindrical, flexuose, lageniform or irregular, if present. *Pileipellis* a cutis with transitions to a trichoderm, made up of radially arranged, 2–9 µm wide, cylindrical or slightly inflated hyphae, with 6–15 µm wide, ascendant, inflated or sometimes capitate, terminal

elements, pigment membranal and additionally encrusting in some hyphae. Arachnoid covering consisting of 5–8 µm broad, clamped hyphae. Oleiferous hyphae present in the pileitrama. *Clamp-connections* present.

Habitat and distribution: In groups on rotten wood of broad-leaved trees. In Mediterranean to subalpine Europe and North Asia/Russian Far East.

Additional material examined: **Austria**, Oberösterreich, Kirchdorf an der Krems, NP Nördliche Kalkalpen, Rosenau am Hengstpaß, Krumme Steyrling-Tal, Blöttenbach-Tal, Blumauer Alm, xerophytic grassland, 16 Sep. 2016, *I. Krisai-Greilhuber* (WU-Myc 37815); *ibid.*, 16 Sep. 2016, *I. Krisai-Greilhuber* (WU-Myc 30737). **Croatia**, Cap Kamenjak, near Premantura, 15 Nov. 2017, on bark of unidentified log, *A. Gminder*, KaiR1108 (B 70 0105508). **Russia**, Samara Oblast, Zhyguli Nature Reserve, in *Tilia cordata* forest, on dead wood, 21 Aug. 1990, *A.I. Ivanov* (LE F-18639); Karachaevo-Cherkessia Republic, Teberda Nature Reserve, near Teberda town, mixed forest, on dead wood, 15 Aug. 2009, *E. Malysheva*, LE F-343685; Primorsky Krai, Kedrovaya Pad Nature Reserve, near the Drovyanoi stream, mixed forest, on fallen log of a broad-leaved tree, 20 Aug. 2005, *O. Morozova*, LE F-253823; *ibid.*, Sikhote-Alin Nature Reserve, cordon Blagodatnoye, bank of the Sukhoy stream, mixed forest including *Pinus koraiensis*, *Quercus mongolica*, on fallen log of a broad-leaved tree, 16 Aug. 2013, *O. Morozova*, LE F-343740.

Notes: *Entoloma ostreatum* resembles *E. byssisedum* in many respects and can best be distinguished with the help of an ITS barcode. Both species grow on decayed wood, not on the ground. Because some of the collections studied had well developed cheilocystidia, it was suggested that this species could represent *E. depluens* in the sense of Orton (1960). For various reasons we are not inclined to apply the name *E. depluens* for the present clade. The epithet *depluens* goes back to Batsch (1786) and has been sanctioned by Fries (1821). It described a small, pleurotoid *Entoloma* with a thin, pale, hairy cap, reddish lamellae and a reduced white stipe, growing among mosses on soil. In literature, *E. depluens* has been variously interpreted. *Entoloma depluens* sensu Bresadola (1929) depicts a greyish form, growing on soil, that has been interpreted as *E. byssisedum*, e.g. in Kühner & Romagnesi (1953). Cooke (1884: pl. 371) depicts a small whitish, stipitate *Claudopus* on wood and saw dust that Orton (1960) considered *E. parasiticum*. Orton (1960) published a more detailed description of a pinkish grey *Claudopus*, growing on soil, as *E. depluens*, differing from his concept of *E. byssisedum* mainly in the slightly larger spores, and presence of cylindrical cheilocystidia. The colour of the basidiomata he considered of minor value, since Orton states that both species are grey. Noordeloos (1982) described *E. depluens* from Denmark, which fits quite well with the description of Orton, growing on rotten *Fagus* wood, however. Unfortunately, we do not have sequence data of both Orton's and Noordeloos's material. The spore size given by Orton and Noordeloos for *E. depluens* fits rather well in the range given here for *E. byssisedum*, and, furthermore, cheilocystidia are present or absent in both *E. byssisedum*, and *E. ostreatum*. And as for the ecology, *E. ostreatum*



and *E. byssisedum* grow on wood, whereas *E. depluens* is supposed to grow on the soil. So, in conclusion, we think *E. ostreatum* is not in agreement with the current concept of *E. depluens*. The question remains whether a true *E. depluens* exists. In our tree, the name *E. depluens* turns up also in the /pseudoparasiticum clade, a species with a different ecology, growing on decayed fungi, soil, and vegetal debris.

Entoloma pseudonigellum E. Ludw. & Noordel., *Pilzkompedium* 2: 299. 2007. MB 548553. Fig. 56.

Typus: Hungary, Bács-Kiskun, Kunbaracs, Ősborókás, on sandy soil near *Pinus* and *Quercus*, 10 Oct. 2004, E. Ludwig, 2526 (**holotype**, M); ITS sequence, GenBank PX412060.

Description (amended here): *Basidiomata* omphalinoid. *Pileus* 10–35 mm wide, hemispherical then convex, finally

infundibuliform, with umbilicate centre, margin slightly enrolled when young, then deflexed or straight, not hygrophanous or translucently striate, black to greyish black, blackish brown when young then dark sepia brown to horn brown, greyish brown when old, radially fibrillose to very finely adpressed squamulose when young, becoming smooth with age and when exposed. *Lamellae* relatively distant ($L = 20\text{--}30$, $I = 2\text{--}5$), variably inserted, from adnate to decurrent, arcuate, 1–3 mm broad, dark grey brown or horn brown like the pileus, then tinged pink, with concolourous, entire edge. *Stipe* 10–50 × 1–2.5 mm, cylindrical, concolourous or paler than pileus, glabrous, shiny, slightly innately fibrillose lengthwise, dull. *Context* thin, brittle, brown. *Smell* indistinct or somewhat farinaceous, like mown grass. *Basidiospores* (40/3) $7.0\text{--}12.5 \times 6.0\text{--}7.5 \mu\text{m}$, on average $9.5\text{--}11.0 \times 6.5\text{--}7.0 \mu\text{m}$, $Q = 1.20\text{--}1.90$, $Q_{av} = 1.40\text{--}1.45$, heterodiametrical, with 6–9 weak angles, a rather large number of deformed spores usually

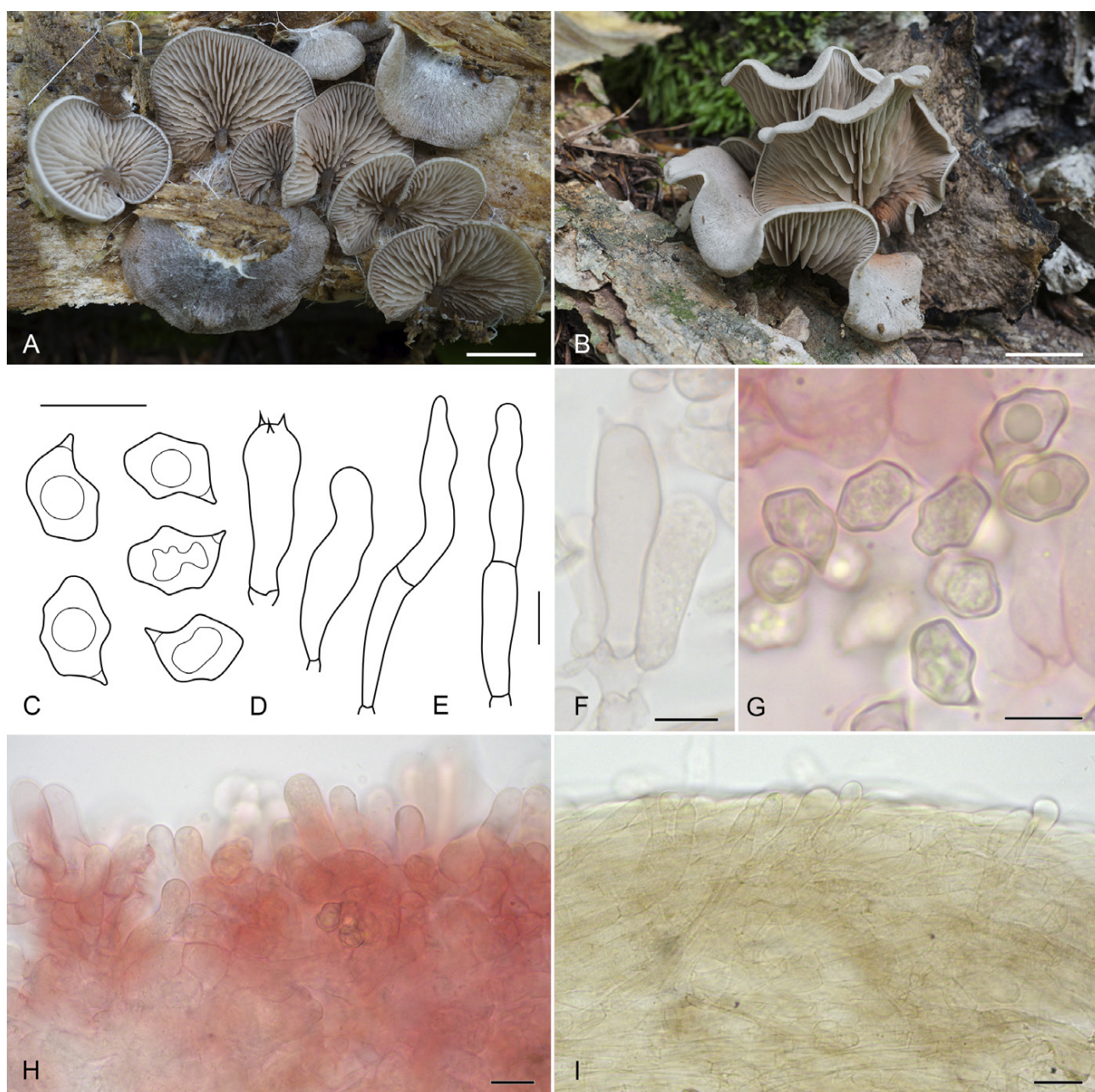


Fig. 55. *Entoloma ostreatum* (A, C–I. LE F-343741, holotype; B. LE F-343740). **A, B.** Habit. **C, G.** Basidiospores. **D, F.** Basidia. **E.** Cheilocystidia. **H.** Lamellae edge. **I.** Pileipellis. Photos: O. Morozova. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (all other figs).



present, up to $15 \times 7\text{--}8\ \mu\text{m}$. *Lamella edge* heterogeneous. *Cheilo-* and *pleurocystidia* usually present, scattered among the basidia, clavate to globose to sphaeropedunculate, $30\text{--}38 \times 15\text{--}22\ \mu\text{m}$, thin-walled and easily collapsing. *Hymenophoral* and *pileitrama* regular to irregular, made up of cylindrical hyphae, with elements $70\text{--}190 \times 5\text{--}13\ \mu\text{m}$. *Pileipellis* a cutis with transitions to a trichoderm, made up of cylindrical to inflated, $5\text{--}22\ \mu\text{m}$ wide hyphae; pigment coarsely encrusting and in addition intracellular, brown. *Stipitipellis* a cutis of narrow hyphae. *Caulocystidia* absent. *Clamp-connections* present.

Habitat and distribution: In sandy soils including dunes, often near *Populus*, *Juniperus* and *Crataegus*. According to our observation and the publication of Nagy & Gorliczai (2007) the species is rather frequent in the steppe areas of central Hungary. However, based on ITS sequence data in GenBank (OR771770, PV056348), this species also occurs in California, USA, where it was found in two different counties (El Dorado and Siskiyou, see <https://www.inaturalist.org/observations/168337577> and <https://www.inaturalist.org/observations/255804247>, respectively).

Additional material examined: **Hungary**, Bács-Kiskun, Kecskemét, on sandy steppe, L. Nagy, NL-2615 (SZMC), *ibid.*, L. Nagy, NL-3560 (SZMC); Bócsa, on sandy soil, near *Juniperus* and *Populus*, 3 Dec. 2022, Re. Molnár, DB-2022-12-03-2 (ELTE); Fülöpháza, on sandy steppe, among mosses, 19 Apr. 2023, K.E. Császárné, CSEK-2023-04-19-1

(ELTE); Pest, Alsónémedi, at margin of a sandy pasture, 26 Oct. 2014, P. Finy, FP-2014-10-26 (ELTE).

Notes: *Entoloma pseudonigellum* is a remarkable species close to *E. undatum* from which it differs by the very dark, finely squamulose pileus and presence of cheilo- and pleurocystidia. The notable disjunct distribution of the species between Central Hungary and California, USA is not yet fully understood.

Entoloma pseudoparasiticum Noordel., *Entoloma s.l.*, *Fungi Europaei* 5: 610. 1992. MB 361990. Fig. 57.

Synonym: *Entoloma catalaense* Noordel. & Contu in Noordeloos, *Entoloma s.l.*, *Fungi Europaei* vol. 5 (Saronno) 5a: 1146. 2004. MB 491544.

Typus: Sweden, Uppland, Börstil, Tusko, 29 Aug. 1953, E. Almkvist (**holotype** UPS F-738326, not sequenced). **Russia**, Tatarstan Republic, Zelenodolsky District, Ilyinskoye Village, Aiminskoye Forestry, *Picea abies*-*Pinus sylvestris* forest, on basidiomes of *Cantharellus cibarius*, 26 Aug. 2015, O. Safiullina & K. Potapov (**epitype** LE F-312345, designated here, deposited at LE, MBT 10028200); ITS sequence, GenBank PX412061.

Description: *Basidiomata* pleurotoid. *Pileus* 5–25 mm wide, plano-convex to applanate with irregularly undulating or lobed margin, slightly involute when young, round, ovoid to reniform, shell-shaped or irregular seen from above, not or

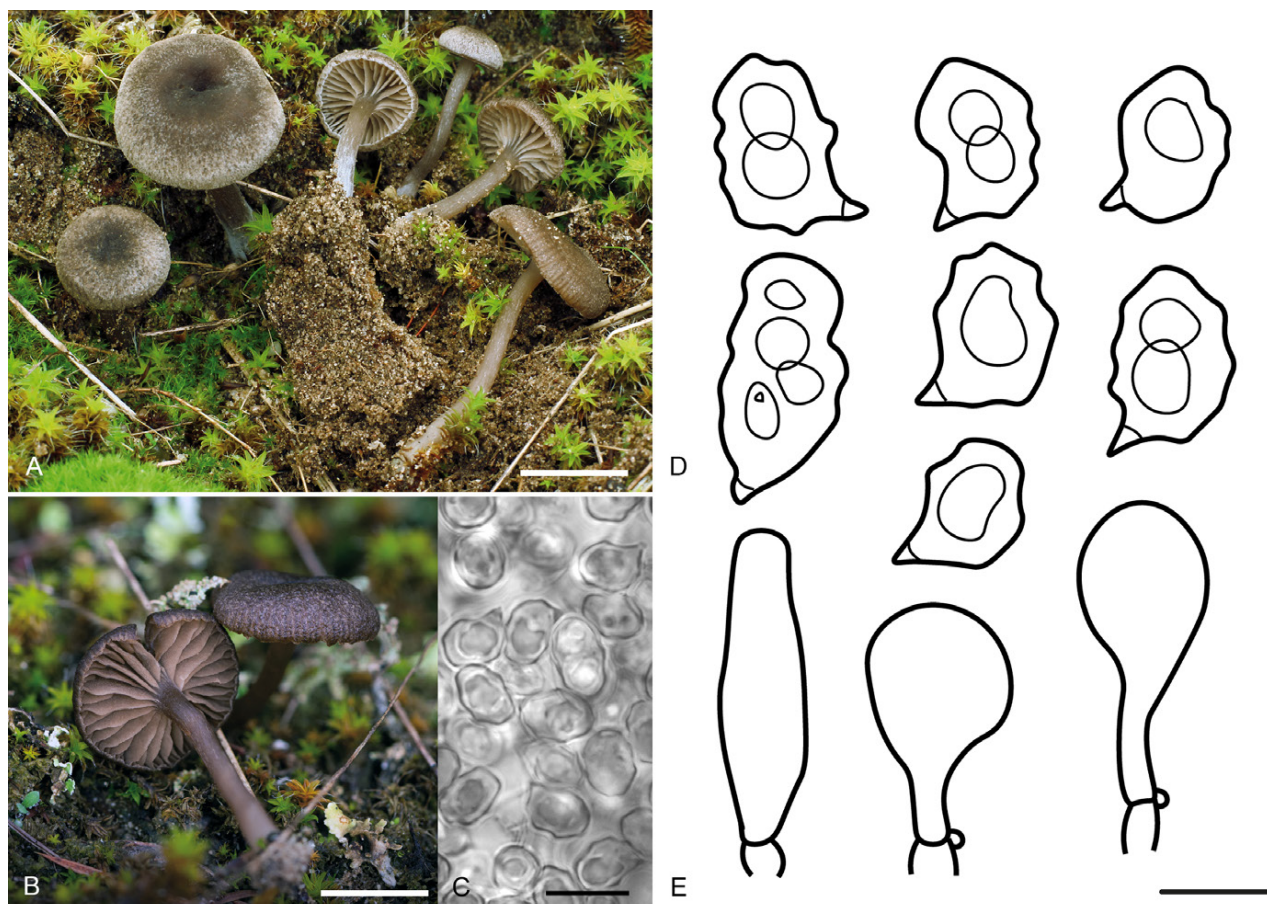


Fig. 56. *Entoloma pseudonigellum* (A. FP-2014-10-26; B. DB-2022-12-03-2; C–E. NL-2615). **A, B.** Habit. **C, D.** Basidiospores. **E.** Cheilocystidia. Photos: A by P. Finy; B by R. Molnár; C by L. Nagy. Drawings by L. Nagy. Scale bars: 1 cm (habit), 10 µm (all other figs).



only slightly hygrophanous, not translucently striate or, when moist, at margin only, pale grey or greyish brown, entirely radially fibrillose, often densely covered with white arachnoid tomentum. *Lamellae* moderately distant to fairly crowded ($L = 10\text{--}25$, $l = 1\text{--}5$), adnexed, adnate to decurrent, ventricose, pale grey, then pinkish brown, with entire or slightly eroded, concolourous edge. *Stipe* $3\text{--}15 \times 0.5\text{--}3$ mm, strongly reduced, eccentric or lateral, sometimes central, pale grey brown, concolourous with pileus, pruinose to distinctly silky-striate, with white mycelial covering at base, turning into white rhizomorphs at the substrate. *Context* concolourous with surface. *Smell* indistinct or fishy-rancid; *taste* not reported. *Basidiospores* (200/12) $8.0\text{--}10.4 \times 5.5\text{--}7.0$ μm , on average $9.3\text{--}9.5 \times 6.1\text{--}6.3$ μm , $Q = 1.20\text{--}1.60$, $Q_{\text{av}} = 1.30\text{--}1.40$, heterodiametrical, 5–7-angled in side view. *Basidia* $26\text{--}43 \times 9\text{--}12.5$ μm , 4-spored, clamped. *Lamella edge* fertile, cystidia

absent. *Pileipellis* a cutis with transitions to a trichoderm, made up of radially arranged, 2–6 μm wide, cylindrical or slightly inflated hyphae, with up to 10 μm wide, ascendant, inflated, terminal elements; pigment pale, intracellular and membranal. Oleiferous hyphae present in the pileitrama. *Clamp-connections* present at least in hymenium.

Habitat and distribution: In groups on basidiomata of *Cantharellus* and *Craterellus* spp., on rotten wood or on debris and soil. Rare, but widespread in Europe east to the Ural Mountains, recorded, and ITS verified also from the Russian Far East, China and North America.

Additional material examined: **Finland**, Regio aboensis, Koski, Hongisto, 18 Sep. 2004, M.-L. Heinonen & P. Heinonen, FIPUT514-14 (TUR172876); *ibid.*, 15 Oct.

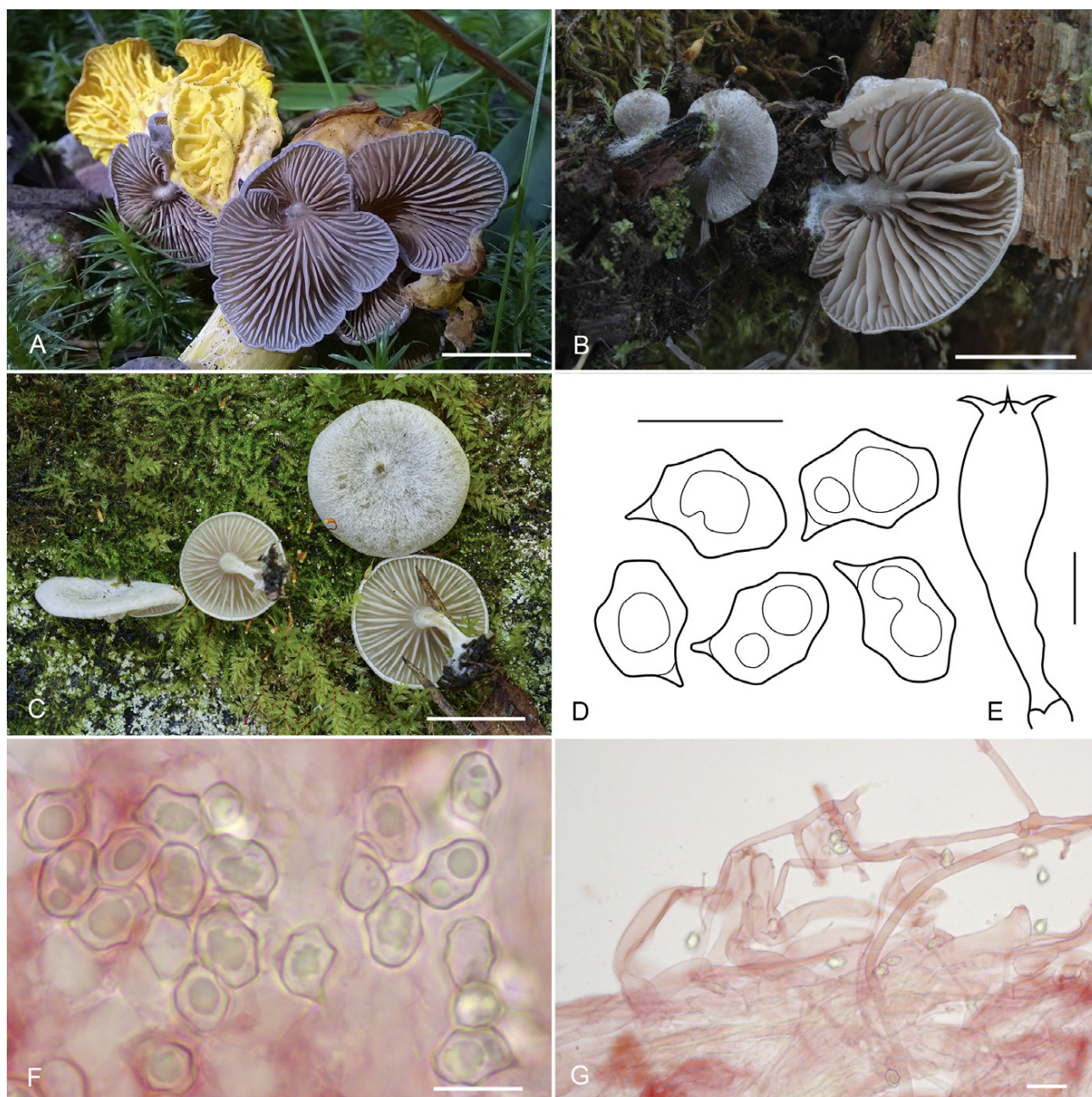


Fig. 57. *Entoloma pseudoparasiticum* (A, D–G. LE F-312345, epitype; B. LE F-343744; C. LE F-344117). **A–C.** Habit. **D, F.** Basidiospores. **E.** Basidium. **G.** Pileipellis. Photos: A by K. Potapov; B, C, F, G by O. Morozova. Drawing by M.E. Noordeloos. Scale bars: 1 cm (habit) 10 μm (all other figs).



2011, *M.-L. Heinonen & P. Heinonen*, FIPUT643-14 (TUR196375); Halikko, Vuorentaka, Vaisakko, on *Craterellus cornucopioides*, 7 Sep. 1988, *A. Puolasmaa*, FIPUT428-14 (TUR095156); Lemu, Nyynäainen, fairly rich forest dominated by *Quercus robur*, on *Cantharellus cibarius*, 6 Sep. 1993, *L. Lindgren*, FIPUT433-14 (TUR110539); Regio kuusamoensis, Kuusamo, Oulanka natural park, near Nurmisaarenrinne, lower course of the dried brook of Tulilammenpuro, 3 Sep. 2007, *J. Vauras & K. Kokkonen*, FIPUT575-14 (TUR179915). **Hungary**, Veszprém, Bakony Mts, Fenyőfő, in road boarder, on sandy calcareous *Pinus sylvestris* forest, on dead plant debris, 17 Oct. 2022, *B. Dima, V. Papp & B. Palla*, DB-2022-10-17-4 (ELTE). **Italy**, Sardinia, prov. Sassari, Calangianus, Catala, among lichens and mosses on roadside, 12 Sep. 2003, *M. Contu, G. Consiglio & L. Perrone* (L0819832, **holotype** of *E. catalaense*; ITS sequence, GenBank PX412028). **Norway**, Nordland, Grane, Holmvassdalen NR, calcareous tall herb spruce forest, on remains of tall herbs, 5 Aug. 2011, *S. Eidissen & J. Lorås*, JL 204-11 (O-F-249954); Troms, Storfjord, Helligskogen, on wood of *Betula*, 17 Aug. 1992, *E. Johannesen* (TROM-F-94). **Russia**, Murmansk Oblast, near Kandalaksha town, coast of the Kandalaksha Gulf, mixed *Pinus sylvestris*-*Picea obovata* forest, on soil, 24 Aug. 2023, *O. Morozova*, NVP1033 (LE F-344117); Moscow Oblast, border of the Stupino and Serpukhov Districts, in mixed forest, on *Cantharellus cibarius*, 13 Aug. 2019, *T. Bekker*, LE F-343686; Tula Oblast, Belyovsky District, near the former Village Khutora, on a rotten stump in *Picea* forest, 1 Oct. 2003, *T. Svetasheva*, LE F-235003; Sverdlovskaya Oblast, Prigorodny District, Visimsky Nature Reserve, on soil in *Betula* forest, 26 Aug. 1999, *L.V. Marina*, LE F-258106; Kamchatka Krai, Bystrinsky District, near Esso Village, right bank of the Bystraya River, on a rotten stump in *Populus-Salix* forest, 11 Aug. 2005, *O. Morozova*, 156KA05 (LE F-343744).

Notes: *Entoloma pseudoparasiticum* and *E. parasiticum* are found to grow on different species of *Cantharellaceae*. *Entoloma pseudoparasiticum* differs from *E. parasiticum* by the brown coloured pileus, and small, heterodiametrical spores. Furthermore, *E. pseudoparasiticum* is apparently not exclusively parasitic on fungi but also occurs on soil or very decayed wood or other plant debris. Our results show that the type specimen of *E. catalaense* belongs to the same clade and represents a later synonym. *Entoloma catalaense* was considered to be characterised by its very strong, fishy-rancid smell, like that of *Macrocyttidia cucumis*, but obviously this is not typical for the species, as this smell has not been noted for the majority of the known collections. *Entoloma alliodorum* differs by a differentiated pileipellis consisting of up to 15 µm broad elements, larger spores, and less frequent clamp-connections (Esteve-Raventós et al. 2003), and is phylogenetically distant. *Entoloma pseudoparasiticum* apparently has a very wide distribution, as it has also been recorded from China (He et al. 2019 and North America (e.g. iNat64301061), both as *Entoloma byssisedum* var. *microsporum*).

Entoloma undatum (Gillet) M.M. Moser, *Kl. Krypt.-Fl. (Stuttgart)* 2b/2: 211. 1978. MB 313840. Fig. 58.

Basionym: *Clitopilus undatus* Gillet, *Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France*: 407. 1876. MB 241395.

Replaced synonym: *Agaricus undatus* Fr., *Epicrisis Systematis Mycologici*: 149. 1838. MB 461571, nom. illegit., non *Agaricus undatus* Berk. MB 239409.

Synonyms: *Entoloma undatoides* Arnolds, *Ecol. Coenol. Macrofungi Grassl. Heathl. Drenthe, Netherlands* 3: 352. 1983. MB 108868

Entoloma sericeonitidum (P.D. Orton) Arnolds, *Ecol. Coenol. Macrofungi Grassl. Heathl. Drenthe, Netherlands* 3: 350. 1983. MB 108867.

Excluded: *Entoloma undatum* f. *longipes* Noordel. *Annls Univ. Turku., Ser. A II (Rep. Kevo subarct. Res. Stn 17)* 66: 39. 1981. MB 118022 (= *E. korhonenii*).

Typus: **Holotype** not existing. **Sweden**, Jämtlands län, Östersund, Frösön, Summarhagen, 29 Aug. 2018, *K. Reschke*, KaiR1275 (**neotype** B 70 0105514, designated here, deposited at B, MBT 10028197); ITS sequence, GenBank OL338187.

Description (amended here): *Basidiomata* omphalinoid. *Pileus* 8–40 mm wide, convex to concave, usually deeply umbilicate, with slightly to distinctly involute margin when young, then straight or reflexed in old specimens, not distinctly hygrophanous, not translucently striate, dark grey brown, sometimes paler with age, or appearing pale grey brown from the aeriferous covering, densely radially fibrillose with adpressed to loosely attached silvery-greyish fibrils, often with one or more concentric zones, shiny, especially when dry. *Lamellae* fairly crowded ($L = 20\text{--}35$, $I = 1\text{--}5$), decurrent arcuate, grey or brown, then tinged pink, with an entire, concolourous edge. *Stipe* 10–30 × 1–4(–6) mm, cylindrical or compressed, sometimes broadened at base, pale brown to yellow brown paler than pileus, smooth or finely white pruinose in upper part. *Context* thin, concolourous with surface. *Smell* none or distinctly farinaceous. *Taste* none or farinaceous to rancid. *Basidiospores* (200/20) (7.0–)7.5–10.0 × 6.0–7.0 µm, on average 8.4–9.5 × 6.5–6.8 µm, $Q = 1.20\text{--}1.65$, $Q_{av} = 1.35\text{--}1.50$, 6–8-angled in side view with weak, rounded angles. *Basidia* 20–32 × 9.5–14 µm, 4-spored, clamped. *Lamella edge* fertile. *Cheilocystidia* absent, rarely some scattered subcylindrical elements present, 25–60 × 3.5–8 µm. *Pileipellis* a cutis of radially arranged, cylindrical to clavate, terminal elements, up to 15 µm wide. Pigment yellow brown, membranous and encrusting the hyphae of pileipellis and pileitrama. *Stipitipellis* a cutis of cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in all tissues.

Habitat and distribution: Terrestrial, rarely on well decayed wood, in groups in grasslands, also on bare soil, often in pioneer vegetation on rather poor, sandy or gravelly soil, including tracks/road verges and inner sand-dunes or in rich, broad-leaved forests; summer to autumn. Widespread and common, Europe.

Additional material examined: **Austria**, Steiermark, Stainach-Pürgg, Wörschachwald, Spechtensee, 5 Sep. 2002, *A. Hausknecht et al.*, WU-MYC 22285. **Finland**, Ostrobothnia ultima, Keminmaa, Vanha kirkko, 18 Sep. 2011, *T. Kekki*, FIPUT637-14 (TUR196105). **Germany**, Hessen, Darmstadt, near Pfungstadt, in sandy *Pinus sylvestris* forest on humus



rich soil under shrubs, 4 Nov. 2022, *K. Reschke*, KaiR1610 (B); Rheinland-Pfalz, Bad Kreuznach, Schlossböckelheim, Heimberg, oligotroph grassland, 27 Oct. 2017, *K. Reschke*, KaiR998 (B 70 0105507). **Hungary**, Bács-Kiskun, Kecskemét, on sandy soil, *L. Nagy*, NL-0575 (SZMC). **Norway**, Nordland, Alstahaug, Tjøtta, semi-natural pasture, 30 Aug. 2020, *J.B. Jordal*, JBJ20-E47 (O-F-260838); *ibid.*, 29 Aug. 2020, *J.B. Jordal*, JBJ20-E28 (O-F-260822); Oslo, Nordmarka, Finnerud, pasture, forest farm, well grazed by cattle and sheep, 27 Sep. 2016, *E. Bendiksen*, EB 180/16, (O-F-253869); Nordland, Evenes, Botn, birch forest, 16 Aug. 2005, *Tromsø Soppforening* (TROM-F-14005); Agder, Vest-Agder, Farsund, Hamrestranda, semi-natural pasture on sand, 24 Sep. 2012, *J.B. Jordal* (O-F-224771); Møre og Romsdal, Giske, Vigra, Molnes, calcareous semi-natural grassland, 27 Sep. 2022, *J.B. Jordal*, JB22-131 (O-F-259777); *ibid.*, 30 Sep. 2020, *J.B. Jordal* (O-F-178025); Møre og Romsdal, Hustadvika, Farstadsanden, on sand in stable sand dune, 24 Sep. 2004, *J.B. Jordal* (O-F-178064); Akershus, Asker, Ormodden, calcareous *Tilia-Corylus* woodland, 12 Sep. 2019, *B. Dima & E. Bendiksen*, EB 105/19 (O-F-256899); Telemark, Porsgrunn, Skjelsvika, on open, calcareous, shallow soil, 20 Aug. 2013, *A. Molia & T. Læssøe*, AM-102p-2013 (O-F-21712). **Russia**, Komi Republic, Ust-Kulomsky District, Don Village, on soil on grassland, 26 Aug. 2008, *M. Palamarchuk*, SYKO622 (LE F-343737); Altai Krai, Krasnoshchokovsky District, near Tigirek Village, Chainaya Mt, on soil in the *Dasiphora fruticosa* thickets, 12 Aug. 2016, *I. Gorbunova*, LE F-343735; Kamchatka Krai, vicinities of the Esso Village, left bank of the Uksichan River, on soil on

roadside, 7 Aug. 2005, *O.V. Morozova*, LE F-343738; Perm Krai, Perm City, protected area “Chernyayevsky Forest”, on soil in secondary broad-leaved forest, 3 Sep. 2024, *O. Morozova, A. Alexandrova & T. Svetasheva*, 290SV24 (LE F-343748); Leningrad Oblast, Kirovski District, vicinity of the Turyshkino Village, on a piece of wood on the roadside, 2 Sep. 2004, *O. Morozova*, 6TU04 (LE F-343736); Novgorod Oblast, Valdaisky National Park, near Sokolovo Village, on soil on grassland, 24 Aug. 2003, *O. Morozova*, 03-08-252 (LE F-312417) (*Morozova et al.* 2018); Novosibirsk Oblast, Novosibirsk, Central Siberian Botanical Garden, 39 quarter, in oak and larch planting, 15 Aug. 2018, *D. Ageev*, Ageev272 (LE F-343734); Pskov Oblast, Pushkinogorsky District, between Mikhailovskoye and Savkino Villages, roadside in a mixed forest, 28 Aug. 2019, *O. Morozova*, 59aPG19 (LE F-315976); Samara Oblast, Stavropolsky District, Zhigulyovsky Biosphere Reserve, on rotten wood in *Populus tremula* forest, 12 Aug. 2003, *E.F. Malysheva*, LE F-227442; Sverdlovsk Oblast, Krasnoufimsk District, near the Emanzelga Village, “Emanzelga Mount” protected area, on soil in broad-leaved forest, 30 Aug. 2024, *O. Legoshchina*, 266SV24 (LE F-343747); *ibid.*, on soil in birch forest, 30 Aug. 2024, *O. Morozova*, 258SV24 (LE F-343743). **The Netherlands**, Drenthe, Rolde, Eexterveld, mossy meadow close-cropped by sheep, 28 Oct. 1976, *E. Arnolds*, Arnolds 3702 (L0537412, **holotype** of *E. undatoides*; ITS sequence, GenBank PX401859).

Notes: *Entoloma undatum* is taken here in a rather broad sense, including odourless forms and those with a farinaceous

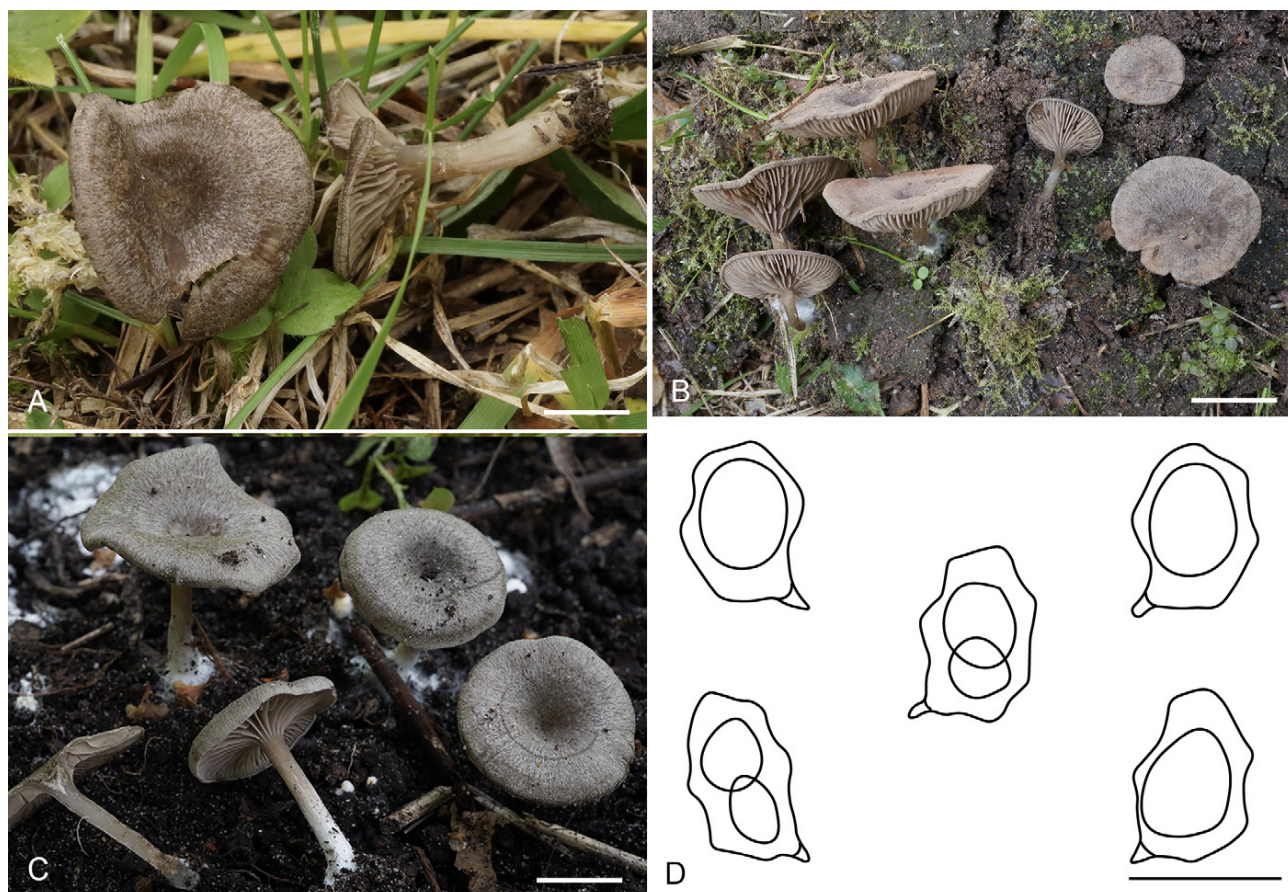


Fig. 58. *Entoloma undatum* (A. B 70 0105514, neotype; B. LE F-315976; C. LE F-343748; D. L0537412). **A–C.** Habit. **D.** Basidiospores. Photos: A by *K. Reschke*; B, C by *O. Morozova*. Drawing by *M.E. Noordeloos*. Scale bars: 1 cm (habit), 10 μ m (spores).



smell, and those with distinctly zonate pileus or not, including *E. undatoides*. In order to decide which of the clades/OTUs represents the true *E. undatum* we chose this OTU because the macro- and micromorphology coincides with the widely

accepted current concept as used for example in Kühner & Romagnesi (1953), Orton (1960), Noordeloos (1987, 1992). A specimen collected in Sweden is chosen as neotype owing to the fact that the species was first (illegitimately) described by Fries.

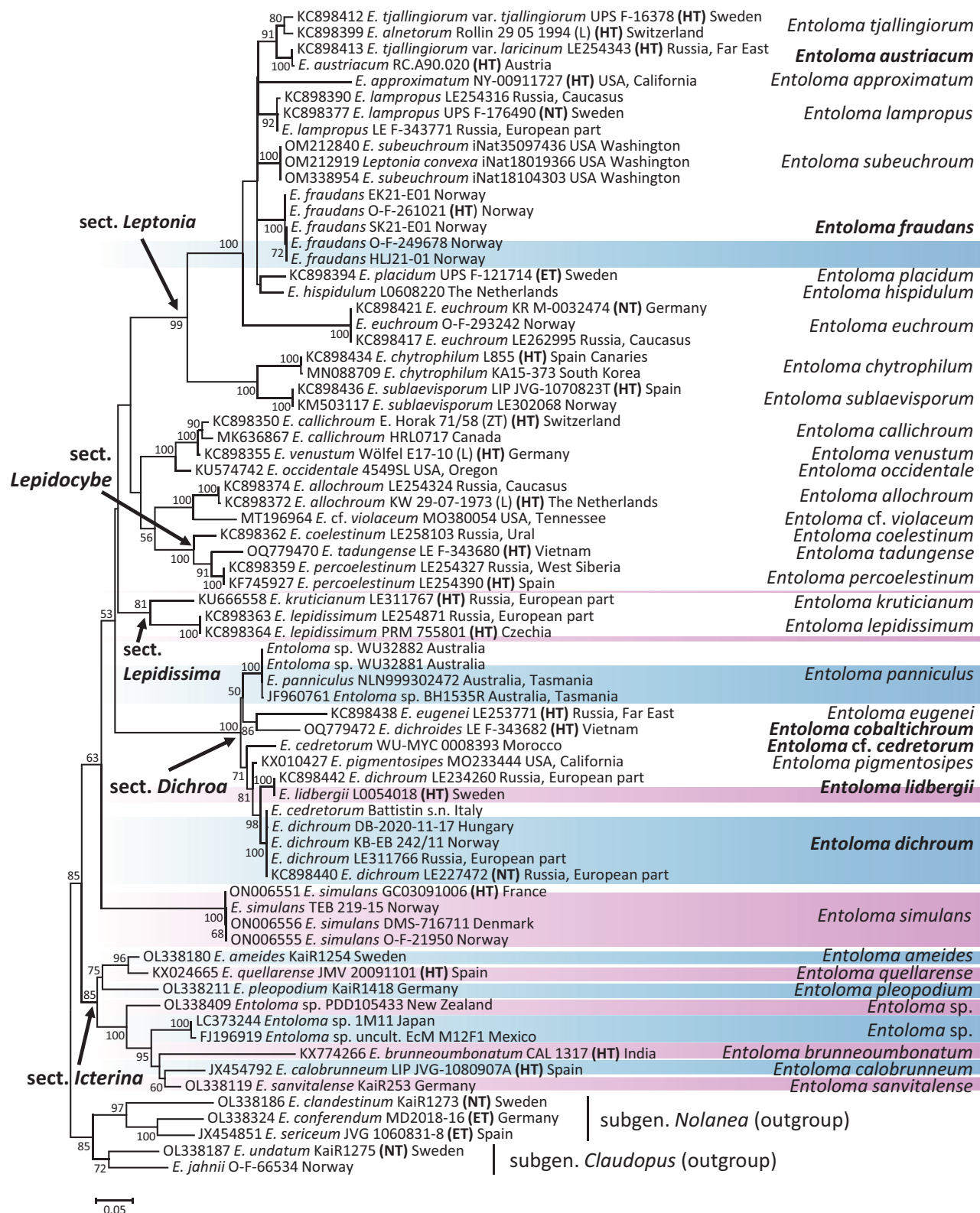


Fig. 59. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of *Entoloma* subgen. *Leptonia* (= /Leptonia clade). ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contain accession numbers, while for the newly generated sequences only voucher numbers are indicated. Countries of origin are indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



/Leptonia clade – subgen. *Leptonia*

Entoloma* subgen. *Leptonia (Fr.) Noordel. *Persoonia* **11**: 146. 1981. MB 842393.

Basionym: *Agaricus* trib. *Leptonia* Fr., *Syst. Mycol. (Lundae)* **1**: 10, 201. 1821. MB 700044.

Type species: *Entoloma euchroum* (Pers.) Donk

The /*Leptonia* clade coincides with subgenus *Leptonia* and has monographically been treated for Europe in Morozova *et al.* (2014a), and Noordeloos *et al.* (2022a). In Noordeloos *et al.* (2022a), section *Lepidissima* included a series of morphologically rather different species, viz. *E. allochroum*, *E. callichroum*, *E. coelestinum*, *E. kruticianum*, *E. lepidissimum*, *E. percoelestinum* and *E. venustum*. Ongoing research, however, demonstrated that these species actually belong to four different clades (Fig. 59). Section *Lepidissima* is now restricted to *E. lepidissimum* and *E. kruticianum*. *Entoloma coelestinum* and the related *E. percoelestinum* and the Asian *E. tadungense*, form a distinct clade of their own and can be accommodated in *Entoloma* sect. *Lepidocybe*. This necessitates the following new combination:

Entoloma* sect. *Lepidocybe (Largent) O.V. Morozova, Noordel., Reschke & Dima, **comb. nov.** MB 860450.

Basionym: *Leptonia* sect. *Lepidocybe* Largent, *Mycologia* **66**: 1017. 1974. MB 842274.

Type species: *Entoloma coelestinum* (Fr.) Hesler

The status of the remaining species (*E. allochroum*, *E. callichroum* and *E. venustum*) within sect. *Lepidissima* sensu lato remains uncertain for the time being.

Entoloma* sect. *Icterina (Konrad & Maubl.) Reschke, Noordel., O.V. Morozova & Dima, **comb. nov.** MB 860549

Basionym: *Nolanea* sect. *Icterinae* Konrad & Maubl., *Icon. sel. Fungorum* (fasc. 7): 210. 1932. MB 860547.

Synonym: *Nolanea* sect. *Ameides* Largent, *Entomatoid fungi of the Western United States and Alaska*: 194. 1994. MB 538893. – *Type species*: *Entoloma ameides* (Berk. & Broome) Sacc.

Type species: *Agaricus icterinus* Fr. = *Entoloma pleopodium* (Bull.) Noordel.

Reschke *et al.* (2022b) combined *Nolanea* sect. *Ameides* into *Entoloma* and placed it in subg. *Leptonia*. However, they did not recognise that *Nolanea* sect. *Icterinae* was an older, valid name for this section. The 'Icones selectae Fungorum' were first published in 10 fascicles from 1925–1936. The 'Entolomées' were included in the 7th fascicle, published in 1932, so a Latin description was not required. It should be noted that *Agaricus icterinus* is a synonym of *E. pleopodium*.

Entoloma cobaltichroum O.V. Morozova, T.H.G. Pham & Reschke, **nom. nov.** MB 860447.

Replaced synonym: *Entoloma dichroides* O.V. Morozova & T.H.G. Pham, *J. Fungi* **9** (6, no. 621): 17. 2023. MB 848531, nom. illegit., Madrid, Art. 53.1, non *Entoloma dichroides* (Romagn. & Gilles) Noordel. & Co-David, in Co-David *et al.*,

Persoonia **23**: 167. 2009. MB 513604.

Etymology: Referring to the cobalt blue dye – the colour of the basidiomata.

Typus: **Viet Nam**, Dak Nong Province, Dak Glong District, Ta Dung National Park, northwest of the Ta Dung Mt, TK 1781, N11.923056, E 108.00194, 1000 m.a.s.l., on soil in evergreen broad-leaved forest with *Parashorea chinensis*, *Rhodoleia championii*, *Fagaceae*, *Lauraceae*, and *Hypericaceae*, 1 Jun. 2022, T.H.G. Pham (**holotype** LE F-343682; **isotype** HG09 in VRTC); ITS sequence, GenBank OQ779472.

Description: For original description see Morozova & Pham (2023).

Entoloma fraudans J.B. Jordal, Noordel., O.V. Morozova & Dima, **sp. nov.** MB 860421. Fig. 60.

Etymology: *fraudans* (Lat.) – cheating, i.e., posing as *E. euchroum*.

Typus: **Norway**, Vestland, Sogn & Fjordane, Luster, Mørkridsdalen, Bratten-Dalen, 112 m.a.s.l., in old, mixed broad-leaved forest with big *Ulmus glabra*, low herb-tall herb vegetation, on dead wood of *Alnus incana*, 9 Oct. 2021, T.H. Hofton, THH21159 (**holotype** O-F-261021); ITS sequence, GenBank PX412035.

Description: *Basidiomata* collybioid. *Pileus* 20–30 mm wide, conico-convex then convex, with involute margin, not hygrophanous or translucently striate, very dark purple brown then medium dark reddish brown with purple-blue tinges, particularly near margin, entirely minutely squamulose with dark brown grey, fibrillose, adpressed squamules, in mature specimens showing the slightly paler background colour of the context. *Lamellae* moderately distant (L = around 30, l = 3–7), adnate-emarginate, with small decurrent tooth, subventricose, bright purple-lilaceous, then pink-dusted with spores, with more or less entire, concolourous edge. *Stipe* 20–40 × 3–6 mm, cylindrical, dark purple-lilaceous then darker grey, coarsely fibrillose lengthwise, with abundant whitish mycelium at base. *Context* concolourous with surface. *Smell* indistinct, *taste* not noted. *Basidiospores* (60/4) 8.8–10.5(–11.5) × 6.2–7.6 µm, on average 9.6–10.0 × 7.0–7.2 µm, Q = 1.40–1.70, Qav = 1.50–1.58, heterodiametrical with 6–9 rather blunt angles in side view. *Basidia* 40–36 × 10–9.5 µm, 4-spored, narrowly clavate, clamped. *Lamellae* edge fertile or heterogeneous. *Cheilocystidia* 24–60.8 × 5.6–8.9 µm, scattered among basidia, cylindrical, narrowly clavate or lageniform, sometimes septate, thin-walled, hyaline. *Pileipellis* a trichoderm at centre, plagiotrichoderm towards the pileus margin, made up of cylindrical, septate hyphae with clavate or ovoid, 11–30 µm wide terminal elements, with brown (in KOH) intracellular, sometimes agglutinated pigment. *Stipitipellis* of long, 5–10 µm wide, septate hyphae, with slightly thick-walled, up to 200 µm long hairs with brown intracellular and sometimes incrusting pigment. *Caulocystidia* absent. *Clamp-connections* present in all tissues.

Habitat and distribution: So far only found in the fjord districts of Western Norway; on trunks of *Ulmus glabra* and *Alnus*

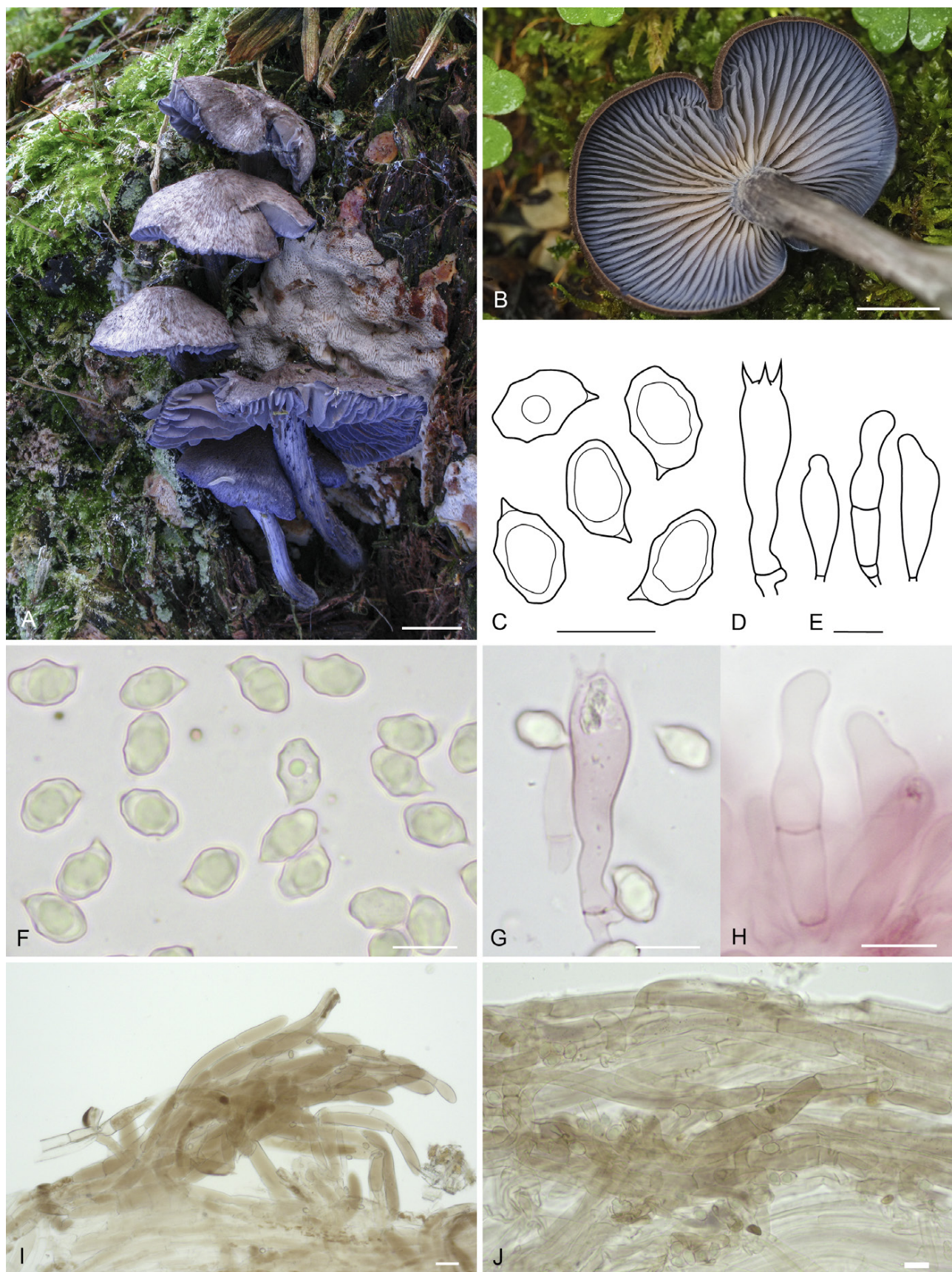


Fig. 60. *Entoloma fraudans* (O-F-261021, holotype). **A, B.** Habit. **C, F.** Basidiospores. **D, G.** Basidium. **H.** Cheilocystidia. **I, J.** Pileipellis. Photos: A, B by T.H. Hofton; F–H by G.M. Jansen. Drawings by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 µm (spores and cheilocystidia).



incana, partly on very coarse, moss-covered trunks of very old trees.

Additional material examined: **Norway**, Møre & Romsdal, Molde, Eikesdalen, Under Rangåfjellet, in *Corylus* forest with *Alnus incana* and *Galium odoratum*, 25 Sep. 2009, W.E. Johansen (O-F-249678); Vestland, Luster, Mørkridsdalen, tall herb *Ulmus glabra* forest, 9 Oct. 2021, H.L. Jensen, HLJ21-01 (O); *ibid.*, on dead wood of *Ulmus glabra*, 9 Oct. 2021, S. Khalsa, SK21-E01 (O); *ibid.*, on dead lying *Ulmus glabra* trunk, 9 Oct. 2021, E. Kagne, EK21-E01 (O).

Notes: *Entoloma fraudans* is similar to *E. euchroum*, a species of subgen. *Leptonia* that is widespread in Europe on dead wood (mostly *Alnus*, but also *Fagus*, *Quercus*, *Sorbus*, *Corylus*, *Acer*, and *Prunus*) (Morozova *et al.* 2014a). The new species differs by the darker, pronounced squamulose pileus, coarsely fibrous stipe, and by having a concolourous lamella edge. Microscopically, it is distinguished by the hyaline, thin-walled and scattered cheilocystidia in contrast with the sterile edge in *E. euchroum*. In the phylogeny, its position is sister to *E. lampropus* which has similar cheilocystidia.

Entoloma lidbergii Noordel., *Österr. Z. Pilzk.* 3: 38. 1994. MB 362387. Fig. 61.

Typus: **Sweden**, Medelpad, Borgsjö, Julåsen, in a gravelly roadside, 25 Aug. 1986, M.E. Noordeloos, 86100 (**holotype** L0054018); ITS sequence, GenBank PX440387.

Description (amended here): *Basidiomata* collybioid. *Pileus* 4–10 mm wide, convex or conico-convex then applanate, with blunt centre or with small umbo, with straight or involute margin, hygrophanous, when moist translucently striate up to half of the radius, very pale pinkish brown or violaceous, paler towards margin, very finely squamulose all over, becoming paler, opaque, finely tomentose upon drying. *Lamellae* very distant ($L = 10\text{--}16$, $I = 0\text{--}1$), free to adnexed, ventricose, pink with an entire, concolourous edge. *Stipe* 12–30 × 0.5–1 mm, cylindrical, violaceous-pink, violaceous to dark bluish-violaceous, minutely striate with blue fibrils on the entire length, base white tomentose, but slowly turning yellow when bruised. *Context* very thin, concolourous with surface. *Smell* none. *Taste* not noted. *Basidiospores* (30/2) (8.2–)9.0–11.0 × (6.3–)7.0–8.0 µm, on average 9.5–9.7 × 7.1–7.3 µm, $Q = 1.20\text{--}1.60$, $Q_{av} = 1.30\text{--}1.35$, rather regularly to slightly irregularly (4–)5–7-angled in side view. *Basidia* 16–40 × (7.0–)9.0–15.0 µm, 4-spored, clamped. *Lamella* edge heterogeneous. *Cheilocystidia* single or in clusters, 30–90 × 5.0–10.0 µm, often septate, irregularly coralloid. *Hymenophoral trama* regular, made up of inflated elements, up to 150 × 420 µm. *Pileipellis* a cutis with transitions to a trichoderm, made up of clavate terminal elements, 40–70 × 8–17 µm, with intracellular pigmentation. *Stipitipellis* a loose cutis of cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in all tissues.

Habitat and distribution: Solitary, terrestrial, on gravelly, slightly calcareous soil at a roadside in a boreal *Picea* forest with scattered *Salix caprea* (type) and temperate, rich *Tilia* forest (SW Russia along Volga). So far only known from the type locality in Sweden and one in Russia.

Additional material examined: **Russia**, Samara Oblast, Zhigulevsky Nature Reserve, vicinities of Bakhilova Polyana, Maloye Kamennoye Pole, on soil in *Tilia cordata* forest, 3 Jul. 2005, E. Malysheva (LE234260, as *E. dichroum*; ITS sequence, GenBank KC898442; mtSSU sequence, GenBank KC898487; nrLSU sequence, GenBank KC898528; Morozova *et al.* 2014a).

Notes: *Entoloma lidbergii* clearly belongs to subgen. *Leptonia* on account of its violaceous-blue, striate stipe and clamped hyphae. Also, the heterogeneous lamella edge with scattered, coralloid cheilocystidia is very typical for this group. It differs from all taxa in subgenus *Leptonia* by its very small size, and pale pinkish brown to violaceous, more or less translucently striate pileus. Basidiospores with well-defined angles indicate that the species belongs to section *Dichroa* and this is also confirmed by the molecular data. Other representatives of the section have larger basidiomata with blue pilei and stipes. Therefore, macromorphologically the basidiomata of this species, due to the combination of a pinkish or lilac pileus and a violaceous blue stipe, are more similar to *E. callichroum*, that differs, however, by its larger basidiomata, larger, differently shaped spores, and fertile lamella edge.

The basal grade

The term basal grade refers here to the papers of Morgado *et al.* (2013), and Baroni & Matheny (2011), in which the position of several clades basal in the *Entoloma* phylogeny is discussed. These basal clades shown in Fig. 62 include */Caeruleopolitum*, */Prunuloides* (sect. *Madida*), */Sphagneti*, */Turfosa* and */Vinaceum*, as well as the singleton *E. fusconigrum*. The genus *Entocybe* (*/Turfosa* and */Vinaceum*) is not accepted here, for obvious reasons, as accepting it in our opinion would lead to excessive splitting of the genus *Entoloma* as has happened in *Rhodocybe* s.l.

Entoloma fusconigrum G.M. Jansen, Dima, A.M. Ainsw., M.A. Roberts & Biketova, **sp. nov.** MB 860439. Fig. 63.

Etymology: *fuscus* (Lat.) – brown, *niger* (Lat.) – black, referring to the colour of the basidiomata.

Typus: **The Netherlands**, prov. Flevoland, Dronten, Roggebotzand, near conifers on sandy soil, 7 Mar. 2014, M. Kroese & G.M. Jansen (**holotype** L0607801); ITS sequence, GenBank PX412036.

Description: *Basidiomata* collybioid. *Pileus* 20–45 mm wide, convex, flattening, sometimes with low or more prominent umbo, with involute margin often becoming wavy, indistinctly hygrophanous, not translucently striate, brown to very dark brown or almost black, uniformly coloured, glabrous or with fine, white crystals, particularly around centre. *Lamellae* distant to moderately distant ($L = 40\text{--}50$, $I = 1\text{--}4$), adnate to emarginate with decurrent tooth, subventricose, up to 2.0 mm broad, light brown, with entire, concolourous edge, slightly veined on the sides. *Stipe* 35–55 × 4–10 mm, slightly and gradually broader towards the base, fibrous, beige with darker brown, longitudinal fibrils; base with white tomentum. *Context* thin, brown in cortex, whitish inside. *Smell* farinaceous. *Taste* not known. *Basidiospores* (40/2) 6.0–8.0 × 5.0–7.0 µm, on



average $6.9\text{--}7.0 \times 6.0\text{--}6.2\ \mu\text{m}$, $Q = 1.00\text{--}1.30$, $Q_{\text{av}} = 1.10\text{--}1.15$, iso- to subisodiametrical, rounded angular, thin-walled. *Basidia* $30\text{--}40 \times 8\text{--}11\ \mu\text{m}$, 4-spored, clamped. *Lamellar edge* fertile, no cystidia present. *Hymenophoral trama* regular; tramal hyphae $3\text{--}20\ \mu\text{m}$ wide, inflated and appearing constricted at the septa. *Pileipellis* a cutis with transitions to a trichoderm, of cylindrical, $2\text{--}8\ \mu\text{m}$ wide hyphae; terminal elements of suprapellis subclavate to clavate with light brown, intracellular pigment. *Stipitipellis* consists of a cutis of loose, narrow, $6\text{--}9\ \mu\text{m}$ wide hyphae; *caulocystidia* not observed. *Clamp-connections* present in all tissues.

Habitat and distribution: Terrestrial; gregarious in coniferous debris or in litter in mixed woodland (*Quercus*, *Corylus*, *Pinaceae*). Currently only recorded at two sites (both in March): the holotype was collected near *Pinaceae* in The Netherlands and the paratype was found on a wooded embankment in North Wales, UK.

Additional material examined: **UK**, Wales, Denbighshire (VC50), Melin-y-Wig, in woodland, 14 Mar. 2022, M.A. Roberts [K(M)265247].

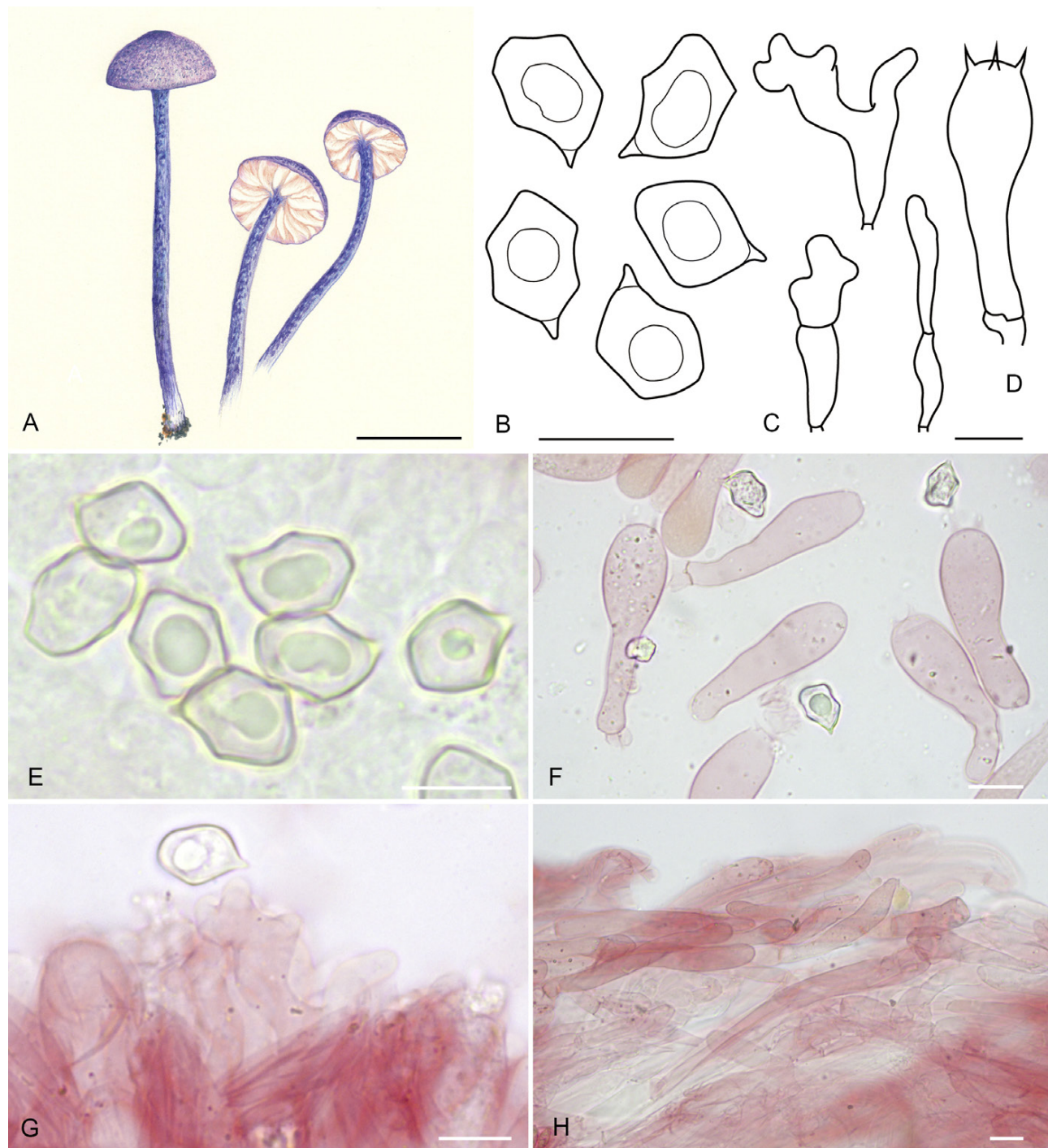


Fig. 61. *Entoloma lidbergii* (LE F-234260). **A.** Habit. **B, E.** Basidiospores. **C, G.** Cheilocystidia. **D, F.** Basidia. **H.** Pileipellis. Photos: G.M. Jansen. Drawings: A by V. Malysheva; B, C, D by M.E. Noordeloos. Scale bars: 1 cm (habit), 10 μm (microscopic structures).



Notes: This remarkable dark-coloured species was initially identified as *E. pseudoturbidum* on account of the small, rounded, thin-walled spores, typical for the sect. *Turfosa* (= sect. *Trachyospora*). However, the phylogeny shows that this species has an isolated position in the tree, sister to the / *Caeruleopolitum* clade, and very distant, also morphologically, from *E. pseudoturbidum* in sect. *Turfosa*. The Welsh collection was initially identified as *E. cf. chytrophilum* because of the macroscopical similarity, but that species belongs to the phylogenetically very distinct subgenus *Leptonia* and differs considerably in micromorphology (Noordeloos *et al.* 2022a).

/Turfosa clade – sect. *Turfosa*

Entoloma* sect. *Turfosa (Romagn.) Noordel., *Persoonia* 10: 529. 1980.

Basionym: *Rhodophyllus* sect. *Turfosi* Romagn., *Bull. Mens. Soc. Linn. Soc. Bot. Lyon* 43: 332. 1974. **Type species:** *Entoloma turbidum* (Fr.) Quél.

Synonym: *Entoloma* sect. *Trachyospora* Largent, *Mycologia* 66(6): 995. 1974.

Entocybe T.J. Baroni *et al.*, *N. Amer. Fungi* 6(12): 8. 2011. **Type species:** *Entoloma trachyosporum* Largent.

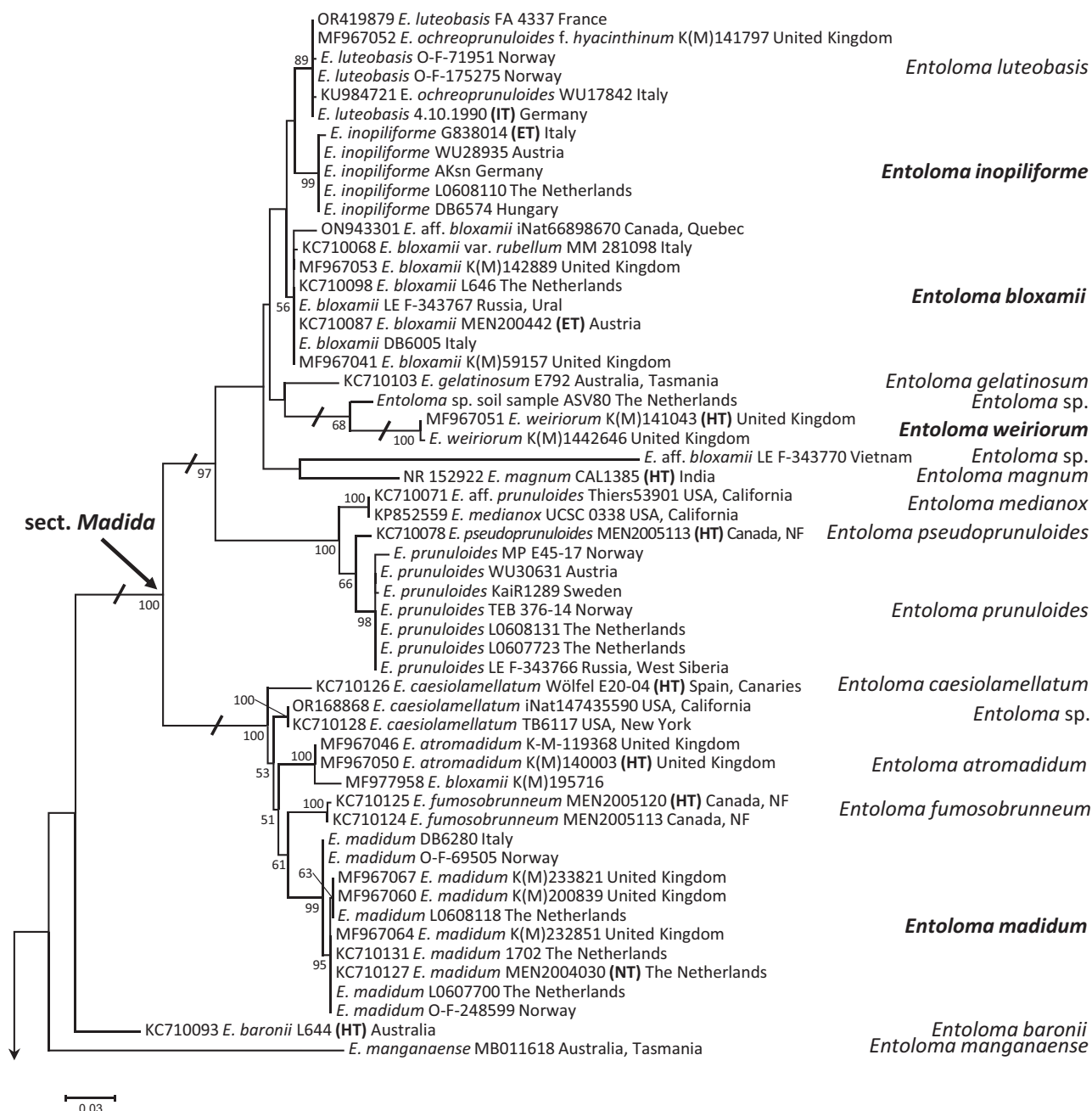


Fig. 62. Maximum Likelihood (RAxML) phylogenetic tree based on nrDNA ITS sequences of the basal grade (sect. *Madida*, /*Turfosa*, /*Vinaceum*, /*Caeruleopolitum* and /*Sphagnetii*) of the genus *Entoloma*. ML bootstrap support values $\geq 50\%$ are presented at the brackets. Sequences used from public databases (i.e. GenBank, UNITE) contains accession numbers, while for the newly generated sequences only voucher numbers are indicated. The country of origin is indicated in any case. Type specimens are shown as abbreviations: HT (holotype), NT (neotype), ET (epitype). The scale bar indicates expected changes per site per branch.



The /*Turfosa* clade partly coincides with the genus *Entocybe*, but we do not accept the latter on a generic level. We prefer treating this clade as a section within *Entoloma*, for which the name *Turfosa* is available. Romagnesi's revised classification was published in November 1974, while Largent's study was published on 31 December 1974, so *Turfosa* has priority over *Trachyospora*. The position of the /*Vinaceum* clade, originally included in the concept of *Entocybe*, is unclear (Fig. 62), and should therefore be excluded from sect. *Turfosa* in strict sense (see also below). This will eventually necessitate an amended concept of sect. *Turfosa*. Species in both clades have rather small, thin-walled spores, that are only weakly angled, a reason why they sometimes have been confused with *Rhodocybe* sensu stricto species. However, the ultrastructure of the spore wall is typically entolomatoid, as is demonstrated in Co-David *et al.* (2009), and the

phylogenies confirm the inclusion of this clade in *Entoloma*. The basidiomata are usually mycenoid or collybioid, often with a fusiform stipe with a tapering base, and the pileipellis is often (sub)viscid. The species of this section are widespread in the Northern and Southern Hemispheres (Noordeloos & Gates 2012).

Entoloma myochroum Noordel. & E. Ludw. ex Noordel. & E. Ludw., **sp. nov.** MB 860440. Fig. 64A, B.

Synonym: *Entoloma myochroum* Noordel. & E. Ludw., in Noordeloos, *Entoloma s.l., Fungi Europaei* vol. 5a: 839. 2004, MB 504388, nom. inval., Madrid, Art. 40.5; holotype designated in two herbaria.

Etymology: μῦς (Greek) – mouse, referring to the mouse-coloured pileus.

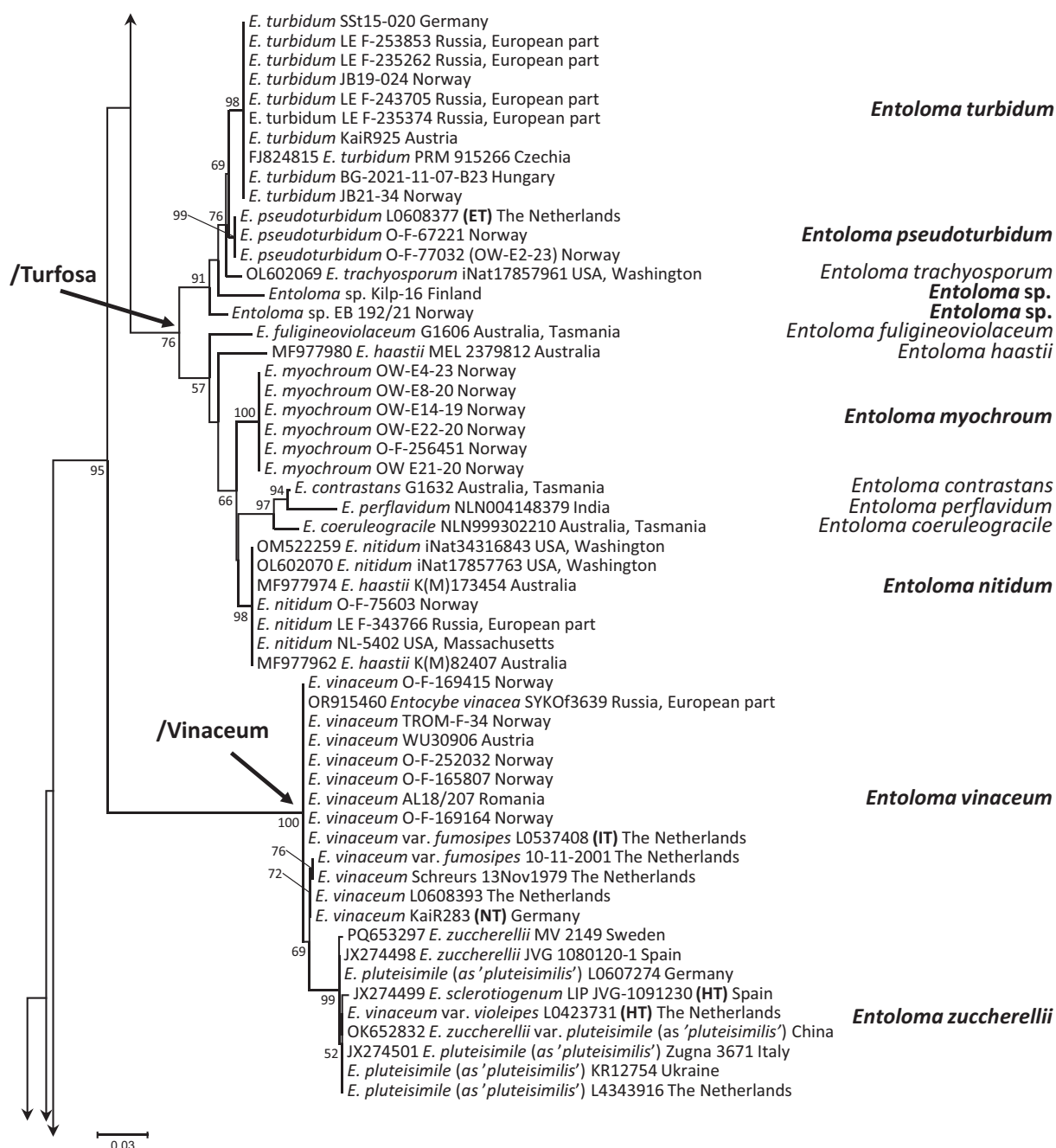


Fig. 62. (Continued).

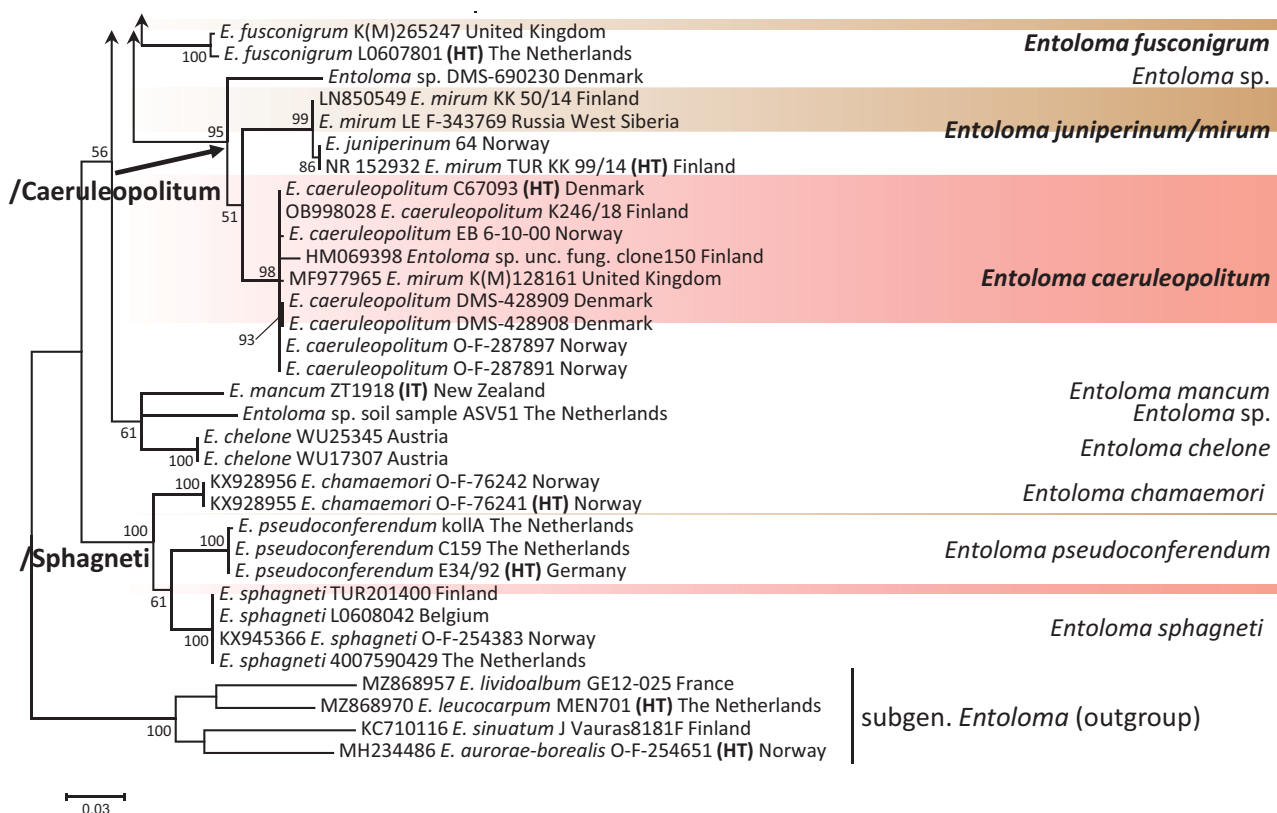


Fig. 62. (Continued).

Typus: Germany, Rheinland-Pfalz (Eifel), Strohn Schweiß, in *Fagus* wood on basalt, 6 Oct. 1990, H. Ebert (**holotype** L0608353, failed in sequencing both with Sanger and NGS methods).

Description (amended here): *Basidiomata* robust, tricholomatoid. *Pileus* 40–100 mm wide, convex then expanding to plano-convex with low umbo, finally concave with depressed centre, with involute margin, hygrophanous or not, not translucently striate, mousegrey with slight ochre tinge, subviscid, glabrous, shining. *Lamellae* crowded ($L = 40\text{--}60$, $I = 5\text{--}7$), adnate-emarginate with short decurrent tooth, narrow, subventricose, white then pink with irregular, concolourous edge. *Stipe* 80–95 × 10–18 mm, cylindrical-flexuous, irregularly shaped, whitish, longitudinally fibrillose. *Context* thin in pileus, thick and solid in stipe. *Smell* and *taste* slightly farinaceous. *Basidiospores* (60/3) 6.0–9.0(–10.0) × 6.0–8.5 μm, on average 6.9–8.5 × 7.0–7.7 μm, $Q = 1.00\text{--}1.35$, $Q_{av} = 1.10\text{--}1.15$, iso- to subisodiametrical, 4–6-angled in side view, often with rounded angles. *Basidia* 24–45 × 7–11 μm, 4-spored, clamped. *Lamella edge* fertile. *Cystidia* absent. *Pileipellis* a narrow cutis of cylindrical, 2–7 μm wide hyphae, gradually passing into pileitrama; pigment brown, intracellular. *Hymenophoral* and *pileitrama* regular, made up of short, inflated elements. *Stipitipellis* a cutis of cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* present in all tissues.

Habitat and distribution: Terrestrial in woodland, associated with *Fagus* or *Quercus*. Very rare, only known from Germany and Norway.

Additional material examined: Norway, Hordaland, Stord, Agdestein, on soil in low-herb oak forest, 6 Sep. 2019, T.E. Brandrud, NMC2019-156 (O-F-256451); Østfold, Fredrikstad, Torsnes, Nes, on soil under *Quercus*, 23 Aug. 2023, Ø. Weholt, E4-23 (O-F-77031); Østfold, Hvaler, Vesterøy, Bankerød, on soil under *Quercus* and *Populus*, 22 Aug. 2019, Ø. Weholt, OW-E14-19; *ibid.*, 6 Oct. 2020, Ø. Weholt, OW-E8-20; *ibid.*, 12 Oct. 2020, Ø. Weholt, OW-E21-20; *ibid.*, 12 Oct. 2020, Ø. Weholt, OW-E22-20.

Notes: *Entoloma myochroum* is a remarkable species with a tricholomatoid habit, reminiscent of *E. sinuatum*, *E. lividoalbum*, *E. noordeloosii* or other species from the /Rhodopolia clade (i.e., subgen. *Entoloma*), differing mainly by the small, often rounded, 4–6-angled spores. Phylogenetically, it is not related to subgen. *Entoloma*, but it is rather close to *E. nitidum* (16 substitution and indel differences in the ITS region) in the basal grade, which makes it a member of sect. *Turfosa* (i.e. *Entocybe* as circumscribed by Baroni *et al.* 2011). Most species in this clade have small, rounded-angular spores. Sequencing of the holotype of *E. myochroum* failed in sequencing both with Sanger and NGS methods. The concept used here is consistent with the original description and there are not any morphological discrepancies in the specimens from Norway, which would indicate a potential different species. Good material from the type-area is needed to designate an epitype for this species.

***Entoloma pseudoturbidum* (Romagn.) M.M. Moser, Beih. Sydowia 8: 269. 1979. MB 313798. Fig. 64C–G.**

Basionym: *Rhodophyllus pseudoturbidus* Romagn., Bull.



Mens. Soc. Linn. Soc. Bot. Lyon **43**: 386. 1974. MB 322736.
 Synonym: ?*Entoloma turbidum* var. *pachylamellatum*
 Noordel., *Persoonia* **11**: 222. 1981. MB 117682.

Typus: **France**, Dept. Oise, Forêt de Hez-Froidmont, 18 Nov. 1960, *J. Gasnier* (**holotype** Romagnesi 58.432 in PC, not sequenced); **The Netherlands**, prov. Drenthe, Norg, 8 Nov. 2013, *H. Pras* (**epitype** L0608377, designated here, deposited at L, MBT 10028214); ITS sequence, GenBank PX412062.

Description (amended here): *Basidiomata*: tricholomatoid. *Pileus* 20–85 mm wide, bluntly conical or hemispherical, expanding to plano-convex with broad umbo, often situated within a slight depression, with margin slightly rounded-incurved when young, becoming straight or even reflexed and translucent with age, hygrophanous, not translucently

striate or at outer margin only, dark umber brown or sepia with darker umbo, slightly pallescent to greyish brown on drying, subviscid when moist, becoming strongly radially fibrillose-virgate, subrugulose or minutely squamulose, and satiny shiny on drying. *Lamellae* distant ($L = 32\text{--}40$, $l = 1\text{--}3$), with numerous lamellulae, ascending and almost free with very small tooth on stipe, ventricose, 7–11 mm broad, greyish white then grey brown with pink tinge, finally reddish brown, with distinctly irregular, concolourous edge, sometimes transversally veined. *Stipe* 30–110 × 4–13 mm, cylindrical or distinctly broadened at base, greyish or greyish-brownish, grey, steel grey then umber brown, almost concolourous with pileus, distinctly fibrilliose striate lengthwise, sometimes twisted. *Context* thick, rather fragile, whitish but brownish when wet. *Smell* and *taste* strongly farinaceous. *Basidiospores* (60/4) $6.5\text{--}8.0 \times 5.5\text{--}7.5\text{--}(8.0)$ μm , on average $7.1\text{--}7.5 \times 6.0\text{--}7.0$ μm , $Q = 1.00\text{--}1.30$, $Q_{av} = 1.15\text{--}1.20$, thin-



Fig. 63. *Entoloma fusconigrum* (A, C, E. K(M)265247; B, D, F. L0607801, holotype). **A–C, E.** Habit. **D.** Basidiospores. **F.** Pileipellis. Photos: A, C, E by M.A. Roberts; B, D, F by G.M. Jansen. Scale bars: 1 cm (habit), 10 μm (microstructures).



walled, subglobose in outline with 5 to 9, rather weak angles in side view. *Basidia* 20–35 × 6–11 µm, 4-spored. *Lamella edge* fertile. *Cheilocystidia* absent. *Hymenophoral trama* regular, made up of inflated, up to 20 µm wide elements. *Pileipellis* two-layered, epicutis and ixocutis, made up of 2.5–6 µm wide, cylindrical hyphae, over a subpellis made up of short, inflated, up to 25 µm wide elements. Pigment brown, intracellular. *Stipitipellis* a cutis of cylindrical hyphae. *Caulocystidia* absent. *Clamp-connections* abundant in all tissues.

Habitat and distribution: Terrestrial in semi-natural grassland or on grassy roadside near *Picea*, *Fagus*, or *Quercus*. Known from France, Norway, and The Netherlands.

Additional material examined: **Norway**, Nordland, Alstahaug: Skålvær, Buøya, on soil in old pasture, 17 Sep. 2004, A.B. Stærnes, J.B. Jordal, A. Knutsen, P. Fadnes & D. Pettersen (O-F-67221); Østfold, Fredrikstad, near Borge Varde, open deciduous woodland, 6 Aug. 2023, Ø. Weholt, E2-23 (O-F-77032); Østfold, Hvaler, Bankerud, Vesterøy, open woodland with *Quercus*, 22 Aug. 2019, Ø. Weholt, E14-19 (O-F-77034) – not included in the phylogenetic analysis; 12 Oct. 2020, Ø. Weholt, E21-20 (O-F-77033) – not included in the phylogenetic analysis.

Notes: Despite the fact that unfortunately no molecular data are available from the holotype, we conclude, after a careful comparison with the original description and personal microscopic notes on the type material, that we should refer our specimens to *E. pseudoturbidum*. This species is very close to *E. turbidum*, with a very similar microscopy, characterised by small, rounded spores. The main differences are found in the dark pilei in *E. pseudoturbidum* that become radially fibrillose, rugulose or squamulose with age, the somewhat more distant lamellae, and dark stipe surface, in addition to its phylogenetic position. Furthermore, it seems to prefer more or less open grasslands or roadsides, whereas *E. turbidum* is most frequently found in heathlands and forests on acidic soils.

/Vinaceum clade

The /Vinaceum clade has an unstable position in our analyses. In the overview tree presented in Fig. 1 it clustered sister to the /Prunuloides clade (= sect. *Madida*) without support, while in the detailed analysis of the basal grade (Fig. 60), it formed a sister and basal clade of both /Prunuloides and /Turfosa (sect. *Turfosa*) with high support (ML BS = 95 %).



Fig. 64. A, B. *Entoloma myochroum* (A. Weholt E14-19; B. L0608353, holotype). A. Habit. B. Basidiospores. C–G. *Entoloma pseudoturbidum* (C, D, G. Weholt E2-23; E, F. L0608377, epitype). C–F. Habit. G. Basidiospores. Photos: A, C, D, by Ø. Weholt; B by M.E. Noordeloos; E, F by H. Pras; G by G.M. Jansen. Scale bars: 1 cm (habit), 10 µm (spores).



Entoloma vinaceum (Scop.) Arnolds & Noordel., *Persoonia* **10**(2): 298. 1979. MB 313847.

Basionym: *Agaricus vinaceus* Scop., *Fl. carniol.*, Edn 2 (Wien) **2**: 444. 1772. MB 451282.

Synonyms: *Entoloma vinaceum* var. *fumosipes* Arnolds & Noordel., *Persoonia* **10**(2): 298. 1979. MB 348093.

Entoloma fuliginarium P. Karst., *Hedwigia* **31**: 292. 1892. MB 194178.

Typus: **Holotype** not existing, described from Slovenia. **Germany**, Hessen, Burgwald, Rotes Wasser/ Franzosenwiesen, poor grassland, 25 Nov. 2016, K. Reschke, KaiR283 (**neotype** B 70 0105504, designated here, deposited at B, MBT 10028215); ITS sequence, GenBank PX412073.

Additional material examined: **Finland**, Kanta-Häme, Tavasta, Mustiala, among mosses, Sep. 1891, P. Karsten (H, **holotype** of *E. fuliginarium*; ITS sequence, GenBank PX444435).

Norway, Innlandet, Oppland, Lunner, Morstadhaugen, oligotrophic, on soil in xeric (lichens, *Calluna*) pine forest, 4 Oct. 2001, E. Bendiksen, EB 204/01 (O-F-169164); *ibid.*, 29 Sep. 2004, E. Bendiksen, 246/04 (O-F-165807); S. Korsvatnhaugen, on soil in old *Vaccinium myrtillus*-*Picea* forest, 9 Oct. 2015, E. Bendiksen, EB 279/15 (O-F-252032); Oslo, Grorud, Frankrig N, on soil in mixed forest, 26 Sep. 1984, E. Bendiksen, EB 362/84 (O-F-169415); Troms, Storfjord, Helligskogen, on soil in mixed birch-willow forest, terrestrial in very poor *Vaccinium-Empetrum* heath, 17 Aug. 1992, M.E. Noordeloos (TROM-F-34-1). **The Netherlands**, prov. Drenthe, Westerbork, Hullenland, 3 Nov. 1976, E.J.M. Arnolds, 3728 (L0537408, **isotype** of *Entoloma vinaceum* var. *fumosipes*; ITS sequence, GenBank PX401861).

Notes: *Entoloma vinaceum* is an inconspicuous species, not uncommonly found in semi-natural grasslands and heathlands, preferably late in the season (see e.g. Brandrud *et al.* 2019). It is also one of the few *Entoloma* species growing in moss-rich, oligotrophic spruce and mixed spruce/pine forests in Fennoscandia. Like in the closely related *E. zuccherellii*, and in the North American *E. trachysporum*, colour varies within the species, which includes populations with violaceous tinges in either pileus or stipe. These colour forms do not deserve a separate taxonomic rank.

Entoloma zuccherellii (Noordel. & Hauskn.) Noordel. & Co-David, *Persoonia* **23**: 175. 2009. MB 491771.

Basionym: *Rhodocybe zuccherellii* Noordel. & Hauskn., *Boll. Gruppo Micol. 'G. Bresadola' (Trento)* **43**(3): 29. 2000. MB 482854.

Synonym: ?*Entoloma pluteisimile* Noordel. & C.E. Hermos. [as '*pluteisimilis*'], in Noordeloos, *Entoloma s.l.*, *Fungi Europaei* vol. **5a**: 918. 2004. MB 491771.

Entoloma sclerotigenum Fern. Caball., Higuelmo, Català & Vila, *Errotari* **9**: 122. 2012. MB 800680.

Entoloma vinaceum var. *violeipes* Arnolds & Noordel., *Persoonia* **10**(2): 299. 1979. MB 348094.

Notes: Several collections under the name *E. pluteisimile*, *E. zuccherellii*, and the holotypes of *E. vinaceum* var. *violeipes*, and *E. sclerotigenum* cluster together as a sister species of *E. vinaceum*. Unfortunately, we do not have ITS sequences of the holotypes of *E. pluteisimile* and *E. zuccherellii* for

comparison. For the time being we assume that all names refer to the same species. *Entoloma zuccherellii* has priority.

Additional material examined: **The Netherlands**, prov. Drenthe, Westerbork, Mantinger Zand, in heathland on sandy soil, 13 Nov. 1974, E.J.M. Arnolds, 3322 (L0423731, **holotype** of *Entoloma vinaceum* var. *violeipes*; ITS sequence, GenBank PX401862); prov. Overijssel, Rijssen, Rijsserberg, on rotten stem of *Fagus*, 22 Feb. 2022, I. Wind (L0607274); prov. Noord Holland, de Bijvanck, on trunk of *Quercus*, 3 Jan 2023, G.M. Jansen & M.J.C. van der Vegte (L4343916). **Ukraine**, Uholka Shyrokyi Luh, old *Fagus sylvatica* forest, among litter, 8 Oct 2013, F. Popa & K.-H. Rexer, KR12754 (MB).

/Prunuloides clade – sect. *Madida*

Entoloma* sect. *Madida (Romagn.) N. Schwab, *Index Fungorum* **541**: 1. 2023. MB 559994.

Basionym: *Rhodophyllus* sect. *Madidi* Romagn. 1974, *Bull. Mens. Soc. Linn. Soc. Bot. Lyon* **43**(9): 332. 1974. MB 634425.

Type species: *Entoloma madidum* Gillet

Notes: The /Prunuloides clade coincides with *Entoloma* sect. *Madida* and contains species usually with a tricholomatoid, rarely mycenoid habit, a tapering stipe, frequently with yellow tinges at the base, some with bright lilac blue tinges, and relatively small, iso- or subisodiametrical spores with pronounced angles. It coincides with clade B2 in the phylogeny of Morgado *et al.* (2013), and it is clearly separated from the /Turfosa clade (*Entocybe*, clade B1 in Morgado *et al.* 2013). Species in this clade can be found in both the Northern and Southern Hemispheres. They are often rather indicative of high natural/ecological quality, in particular in grassland habitats, and most of the known species are on local and international red data lists (Fraitire & Otto 2015). The species complex around *E. bloxamii* is rather diverse, and several new species have been described in recent years. In this paper we add another new one, see *E. weirorum* below, so far only known from the United Kingdom. There is a great genetic diversity in this clade, which is not always reflected in clear cut morphological concepts. The ITS barcodes are useful for identification purposes. *Entoloma inopiliforme*, ranged in the synonymy of *E. prunuloides* in earlier works, is now reinstated, and fully described based upon a study of the holotype and several recent collections.

Entoloma inopiliforme Bon, *Doc. Mycol.* **12**(46): 32. 1982. MB 109748. Fig. 65A–D.

Replaced synonym: *Entoloma inocybiforme* Bon, *Doc. Mycol.* **10**(37–38): 90. 1980. MB 113834, nom. illegit., Madrid, Art. 53.1, non *Entoloma inocybiforme* Murrill, *N. Amer. Fl. (New York)* **10**(2): 120. 1917. MB 151697.

Typus: **France**, Dept. Somme, Abbeville, in calcareous grassland, date not given, M. Bon, Bon 79111804 (**holotype** in LIP, failed in sequencing both with Sanger and NGS methods). **Italy**, Piemonte, Alessandria, Borghetto di Borbera, 330 m.a.s.l., on soil in mixed forest with *Castanea sativa*, *Populus tremula* and *Quercus pubescens*, 13 Oct. 2012, M. Carbone & F. Calleda (**epitype** L0607181, designated here,



deposited at L, MBT 10028216); ITS sequence, GenBank PX412042.

Description (amended here): *Basidiomata* tricholomatoid, often rather robust. *Pileus* 20–70 mm wide, conical then expanding to conico-convex, often with a broad umbo, not distinctly hygrophanous or translucently striate, initially rather dark sepia brown, grey brown, or with a purple tinge, often paler toward margin and somewhat marbled-spotted with paler and darker lines and spots, when old and dry often more ochre brown, waxy to subviscid when moist, soon dry, distinctly and often strongly radially fibrillose. *Lamellae* moderately distant ($L = 30\text{--}40$, $l = 3\text{--}5$), adnate-emarginate, ventricose, whitish to pale grey then pink, finally sordid pink, with subentire, concolourous edge. *Stipe* 25–80 × 4–12 mm, often tapering

towards base, white, pale grey or, in older stages, sometimes tinged ochre, particularly in the middle, innately fibrillose, dry. *Context* white, firm. *Smell* somewhat aromatic, fruity, not very strong. *Taste* mild to slightly rancid. *Basidiospores* (80/5) 7.0–10.0 × 6.0–8.0 μm, on average 8.0–8.5 × 7.0–7.3 μm, $Q = 1.00\text{--}1.30$, $Q_{av} = 1.10\text{--}1.20$, iso- to subisodiametrical, 5–6-angled with very rounded outline. *Basidia* 35–60 × 9–14.5 μm, 4-spored, clamped. *Lamella edge* fertile, cystidia absent. *Pileipellis* a thin (ixo)cutis of cylindrical, 2.5–7 μm wide hyphae; subpellis made up of inflated-fusiform or sausage-shaped elements, 40–85 × 15–25 μm; pigment pale brownish, intracellular in supra- and subpellis, sometimes membranous, not encrusted, in subpellis. *Stipitipellis* a cutis of cylindrical, 2.0–6.0 wide hyphae. *Caulocystidia* not observed. *Clamp-connections* present in all tissues.



Fig. 65. A–D. *Entoloma inopilliforme* (A, C. Carbone 13-Oct-2012, epitype; B. DB6574; D. L0608110). A–C. Habit. D. Basidiospores. E, F. *Entoloma weirorum* (K-M000141043, holotype). E. Habit. F. Basidiospores. Photos: A, C by M. Carbone; B by B. Dima; D by P. Salzmann; E by T. Rogers; F by J. Weir. Scale bars: 1 cm (habit), 10 μm (spores).



Habitat and distribution: In calcareous grasslands and in mixed forest on calcareous soil. So far known from Austria, France, Germany, Hungary, Italy, and The Netherlands.

Additional material examined: **Austria**, Niederösterreich, Hinterbrühl, Sparbach, Naturpark, in calcareous forest, 6 Nov. 2008, *M. Beisenherz*, Herbarium Hausknecht 2773.1 (WU-Myc 28935). **Germany**, Sachsen, Geyer, Hermannsdorfer, Wiesen, calcareous grassland, 6. Oct. 2023, *A. Karich*, IHI-23Ent07 (GLM-F139803). **Hungary**, Vas, Őrség NP, Szalafő, on soil in the margin of a mixed forest with *Pinus*, *Quercus*, *Fagus*, *Carpinus* and *Picea*, 30 Sep. 2017, *B. Dima*, DB6574 (ELTE). **The Netherlands**, prov. Limburg, Stokhem, Dijkersweide, calcareous grassland, 23 Aug. 2017, *F. Salzmänn & R. Salzmänn*, PSLhg00135 (L0608110).

Notes: *Entoloma inopiliiforme* was described by Bon, initially as *E. inocybiforme*, which, however, was illegitimate being a later homonym of *E. inocybiforme* Murrill. Despite several attempts, including the FunDive project, we failed to sequence the holotype, kindly provided by R. Courtécuisse. However, in view of the original diagnosis giving way for the current interpretation, and striking similarly with the recent collections, it was decided to accept the name *E. inopiliiforme* for our species, and an epitype was designated. *Entoloma inopiliiforme* is distinguished by the often striking purple brown tinged pileus, that becomes medium brown with age, and the often very clearly radially fibrillose pileus, hence the name *E. inopiliiforme*. In the phylogeny, it forms a sister group to *E. luteobasis* in the /*Bloxamii* subclade, albeit without support.

Entoloma weiriorum A.M. Ainsw., B. Douglas, D.J. Harries, Speed, T. Rogers, Watt, Suz & Dima, **sp. nov.** MB 860441. Fig. 65E, F.

Etymology: Named for John & Sheila M. Weir, who collected the holotype.

Typus: **UK**, England, West Lancashire (VC60), Silverdale, Eaves Wood, in open, mixed woodland, 20 Sep. 2005, *J. Weir & S.M. Weir* (**holotype** K-M000141043); ITS sequence, GenBank MF967051.

Description: *Basidiomata* tricholomatoid. *Pileus* 30–55 mm wide, bluntly conical with involute margin, becoming conico-convex then flattening to convex with broad umbo and wavy margin that may remain slightly involute, dark violaceous blue grey becoming more brownish at maturity especially at the umbo, glabrous and tacky when damp, becoming innately, radially fibrillose and sometimes splitting around the margin. *Lamellae* crowded ($L = 60\text{--}80$, $I = 3$), narrowly adnate (emarginate), subventricose, up to 3.0 mm broad, creamy white when young, with entire, concolourous edge, occasionally veined on the sides. *Stipe* 35–55 × 7–12 mm, cylindrical with tapering base, white with dark violaceous blue grey longitudinal fibrils that become more grey brown when mature, base creamy white or tinged yellow and lacking fibrils. *Context* pale brown. *Smell* weakly farinaceous. *Taste* not recorded. *Basidiospores* (40/2) 7.0–9.0 × 6.5–8.5 µm, on average 7.9–8.0 × 7.6 µm, $Q = 1.00\text{--}1.10$, $Q_{av} = 1.03\text{--}1.05$, isodiametrical to subisodiametrical. *Basidia* 40–60 × 9–12 µm, 4-spored, clamped. *Lamellar edge* fertile, no cystidia present.

Hymenophoral trama hyphae 5–25 µm wide, inflated and constricted at the septa. *Pileipellis* an ixocutis of cylindrical to slightly torulose, 2–7 µm wide hyphae, with blue intracellular pigment. *Clamp-connections* present in all tissues.

Habitat and distribution: Terrestrial, in open, semi-natural, mixed woodland on thin calcareous soils overlying limestone. Currently only recorded at two sites, both of which are in Northwest England: the holotype was collected from a group of 15 basidiomata found in a grassy glade and the paratype was a singleton collected approximately 2 km away under *Taxus* near an open grassy area.

Additional material examined: **UK**, England, West Lancashire (VC60), Silverdale, Gait Barrows, Grid Ref. SD483775, woodland, 27 Sep. 2020, *H. Speed*, NWFG01 (K-M001442646).

Notes: If historical collections exist, they are likely to have been assigned to *E. bloxamii*. With currently available data, *E. weiriorum* seems morphologically and ecologically very close to the modern, epitypified concept of *E. bloxamii* and, unless further discriminatory characters are forthcoming, DNA barcode analysis is therefore recommended to assign material of *E. bloxamii* s.l. to the correct species. The ITS sequence of the holotype of *E. weiriorum* (as *Entoloma* sp.), as well as coloured photographs (Figs 2, 7D) were originally published in Ainsworth *et al.* (2018).

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REFERENCES

- Ainsworth AM, Douglas B, Suz LM (2018). Big blue pinkgills formerly known as *Entoloma bloxamii* in Britain: *E. bloxamii* s. str., *E. madidum*, *E. ochreoprunuloides* forma *hyacinthinum* and *E. atromadidum* sp. nov. *Field Mycology* **19**: 5–14. <https://doi.org/10.1016/j.fldmyc.2018.01.004>
- Baroni TJ, Lodge DJ (1998). *Alboleptonia* from Greater Antilles. *Mycologia* **90**: 680–696. <https://doi.org/10.1080/00275514.1998.12026957>
- Baroni TJ, Cantrell SA, Perdomo-Sanchez OP, *et al.* (2008). New species of *Pouzarella* (Entolomataceae, Agaricales) from the Dominican Republic and Jamaica. *North American Fungi* **3**(7): 241–260. <http://dx.doi.org/10.2509/naf2008.003.007161>
- Baroni TJ, Hofstetter V, Largent DL, *et al.* (2011). *Entocybe* is proposed as a new genus in the Entolomataceae (Agaricomycetes, Basidiomycota) based on morphological and molecular evidence. *North American Fungi* **6**: 1–19. doi: <http://dx.doi.org/10.2509/naf2011.006.012>
- Baroni TJ, Matheny PB (2011). A re-evaluation of gasteroid and cyphelloid species of Entolomataceae from Eastern North America. *Harvard Papers in Botany* **16**: 293–310. <https://doi.org/10.3100/0.25.016.0205>
- Baroni TJ, Albertó E, Niveiro N, *et al.* (2012). Nuevas especies y nuevas citas de *Pouzarella* (Agaricomycetes, Entolomataceae) del norte argentino. *Kurtziana* **37**: 41–63.
- Batsch AJG (1786). *Elenchi fungorum continuatio prima*. Halle.
- Battistin E, Chiarello O, Righetto N (2013a). Contributo alla conoscenza del raro *Entoloma opacum* Noordel. *Revista Catalana de Micologia* **35**: 43–48.
- Battistin E, Righetto N, Alvarado P (2013b). Nuove date morfologici e moleculare sull raro *Entoloma hirtum*. *Micologia e Vegetazione Mediterranea* **28**: 99–107.
- Brandrud TE, Bendiksen E, Noordeloos ME, *et al.* (2018). *Entoloma*-arter funna i Jämtland och Medelpad 2016 – *Entoloma* species found in Jämtland and Medelpad (Sweden) in 2016. *Svensk Mykologisk Tidskrift* **38**: 25–35.
- Brandrud TE, Bendiksen E, Jordal JB, *et al.* (2019). On some *Entoloma* species (*Tricholomatinae*, *Basidiomycota*) little known or new to Norway. *Agarica* **39**: 31–51.
- Bresadola J (1929). *Iconographia Mycologica*. Vol. 12. Mediolani.
- Co-David D, Langeveld D, Noordeloos ME (2009). Molecular phylogeny and spore evolution of Entolomataceae. *Persoonia* **23**: 147–176. <https://doi.org/10.3767/003158509X4809>
- Cooke MC (1884) [1886]. Illustrations of British Fungi (*Hymenomycetes*), to serve as an atlas to the “Handbook of British Fungi vol. 3”.
- Crous PW, Cowan DA, Maggs-Kölling G, *et al.* (2021). Fungal Planet description sheets: 1182–1283. *Persoonia* **46**: 313–528. <https://doi.org/10.3767/persoonia.2021.46.11>
- Delgat L, Dierickx G, De Wilde S, *et al.* (2019). Looks can be deceiving: the deceptive milkcaps (*Lactifluus*, *Russulaceae*) exhibit low morphological variance but harbour high genetic diversity. *IMA Fungus* **10**: 14. <https://doi.org/10.1186/s43008-019-0017-3>
- Deng WQ, Li TH, Wang CQ, *et al.* (2015). A new crepidotoid *Entoloma* species from Hainan Island (China). *Mycoscience* **56**: 340–344. <https://doi.org/10.1016/j.myc.2014.11.002>
- Dima B, Lindström H, Liimatainen K, *et al.* (2016). Typification of Friesian names in *Cortinari* sections *Anomali*, *Spilomei*, and *Bolares*, and description of two new species from northern Europe. *Mycological Progress* **15**: 903–919. <https://doi.org/10.1007/s11557-016-1217-5>
- Esteve-Raventós F, Horak E, Ortega A (2003). *Entoloma alliodorum*, a new species of subgenus *Claudopus* with garlic odour. *Mycotaxon* **86**: 227–232.
- Favre J (1955). Les Champignons Supérieurs de la Zone Alpine du Parc National Suisse. Liestal, Switzerland.
- Fraiture A, Otto P (2015). Distribution, ecology & status of 51 macromycetes in Europe. – Results of the ECCF Mapping Programme. *Scripta Botanica Belgica* vol 53; Meise Botanic Garden. ISBN 9789082352559.
- Fries EM (1821). *Systema mycologicum*. 1. Lundae.
- Fries EM (1838). *Epicrisis Systematis Mycologici*. Upsaliae
- Fries EM (1867). *Icones selectae Hymenomycetum nondum delineatorum*. I. Holmiae.
- Gillet CC (1876). *Hyménomycètes de France*. Paris.
- Haelewaters D, Dima B, Abdel-Hafiz BII *et al.* (2020). Fungal Systematics and Evolution 6. – *Sydowia* **72**: 231–356. <https://doi.org/10.12905/0380.sydowia72-2020-0231>
- Hahn C, Fries G, Krisai-Greilhuber I (2019). *Sarcodon fennicus*, a boreo-montane stipitate hydroid fungus with a remarkable smell. *Österreichische für Zeitschrift für Pilzkunde* **27**: 43–52.
- He X-L, Horak E, Wang D, *et al.* (2018). Three new species of *Entoloma* subgenus *Pouzarella* from China based on morphological and molecular data. *MycKeys* **44**: 1–18. <https://doi.org/10.3897/mycokeys.44.24998>
- He X-L, Horak E, Wang D, *et al.* (2019). Descriptions of five new species in *Entoloma* subgenus *Claudopus* from China, with molecular phylogeny of *Entoloma* s.l. *MycKeys* **61**: 1–26. <https://doi.org/10.3897/mycokeys.61.46446>



- He X-L, Peng WH, Gan BC (2015). Morphological and molecular evidence for a new species in *Entoloma* subgenus *Claudopus* from Sichuan Province, southwest China. *Mycoscience* **56**: 326–331. <https://doi.org/10.1016/j.myc.2014.10.001>
- Henkel TW, Aime MC, Largent DL, *et al.* (2011). The *Entolomataceae* of the Pakaraima Mountains of Guyana 5: new species of *Alboleptonia*. *Mycotaxon* **114**: 115–126. <http://dx.doi.org/10.5248/129.119>
- Horak E (1980). *Entoloma* (Agaricales) in Indomalaya and Australasia. J. Cramer, Vaduz.
- Karstedt F, Capelari M. (2013). *Inocephalus* (Entolomataceae, Agaricales) from São Paulo State, Brazil. *Nova Hedwigia* **96**: 279–308.
- Karstedt F, Capelari M, Stürmer SL (2007). A new combination and new records of *Pouzarella* (Agaricales, Entolomataceae) from Brazil. *Mycotaxon* **102**: 147–153.
- 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>
- Kaygusuz O, Reschke K, Kaya A, *et al.* (2024). Morphology and molecular phylogeny of four new species of *Entoloma* (Entolomataceae, Agaricales) from Europe and Western Eurasia. *Mycological Progress* **23**: 11. <https://doi.org/10.1007/s11557-024-01972-2>
- Kokkonen K (2015). A survey of boreal *Entoloma* with emphasis on the subgenus *Rhodopolia*. *Mycological Progress* **14**: 1–116. <https://doi.org/10.1007/s11557-015-1135-y>
- Kumar S, Stecher G, Tamura K (2016). MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Kühner R (1977). Agaricales de la zone alpine. Genre *Rhodophyllus* Quélet. *Bulletin Trimestriel de la Société Mycologique de France* **93**: 445–502.
- Kühner R, Romagnesi H (1953). Flore analytique des champignons supérieurs (Agarics, Bolets, Chanterelles). Paris.
- Lange JE (1937). *Flora agaricina Danica*. Vol. 2. Copenhagen.
- Lange JE (1940). *Flora agaricina Danica*. Vol. 5. Copenhagen.
- Largent DL (1994). *Entolomatoid fungi of the Pacific Northwest and Alaska*. Mad River Press, USA.
- Largent DL, Benedict RG (1970). Studies in the rhodophylloid fungi II: *Alboleptonia*, a new genus. *Mycologia* **62**: 437–452. <https://doi.org/10.1080/00275514.1970.12018985>
- Largent DL, Abell-Davis SE, Cummings GA, *et al.* (2011a). Saxicolous species of *Claudopus* (Agaricales, Entolomataceae) from Australia. *Mycotaxon* **116**: 253–264. <https://doi.org/10.5248/116.253>
- Largent DL, Bergemann SF, Cummings GA, *et al.* (2011b). *Pouzarella* (Agaricales, Entolomataceae) species from New South Wales (Barrington Tops National Park) and northeastern Queensland, Australia. *Mycotaxon* **117**: 435–483. <http://dx.doi.org/10.5248/117.435>
- Larsson A (2014). AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* **30**: 3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Ludwig E (2007). Pilzkompedium. Band 2. Die größeren Gattungen der Agaricales mit farbigem Sporenpulver (ausgenommen Cortinariaceae). Beschreibungen + Abbildungen. Fungicon-Verlag. Berlin.
- Manimohan P, Leelavathy KM (1988). Two new species of *Alboleptonia* (Agaricales, Entolomataceae) from southern India. *Transactions of the British Mycological Society* **91**: 710–712. [https://doi.org/10.1016/S0007-1536\(88\)80053-6](https://doi.org/10.1016/S0007-1536(88)80053-6)
- Mazzer SJ (1979). A monographic study of the genus *Pouzarella*. *Bibliotheca Mycologica* **46**: 1–134.
- Morgado LN, Noordeloos ME, Lamoureux Y, *et al.* (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, Pham THG (2023). New species of *Entoloma* subgenera *Cubospora* and *Leptonia* (Agaricales, Basidiomycota) from central Vietnam. *Journal of Fungi* **9**: 621. <https://doi.org/10.3390/jof9060621>
- Morozova OV, Alexandrova AV, Popov ES, *et al.* (2016). New data on the agaricoid basidiomycetes of the Tver Region. *Novosti Sistematiki Nizshikh Rastenii* **50**: 174–186. <https://doi.org/10.2478/pfs-2018-0003>
- Morozova OV, Noordeloos ME, Popov ES, *et al.* (2018). Three new species within the genus *Entoloma* (Basidiomycota, Agaricales) with clamped basidia and a serrulatum-type lamellae edge, and their phylogenetic position. *Mycological Progress* **17**: 381–392. <https://doi.org/10.1007/s11557-017-1364-3>
- Morozova OV, Noordeloos ME, Vila J (2014a). *Entoloma* subgenus *Leptonia* in boreal-temperate Eurasia: towards a phylogenetic species concept. *Persoonia* **32**: 141–169. <https://doi.org/10.3767/003158514X681774>
- Morozova O, Popov E, Alexandrova A, *et al.* (2022). Four new species of *Entoloma* (Entolomataceae, Agaricomycetes) subgenera *Cyanula* and *Claudopus* from Vietnam and their phylogenetic position. *Phytotaxa* **549**: 1–21. <https://doi.org/10.11646/phytotaxa.549.1.1>
- Morozova OV, Voronina EYu, Arslanov SN (2014b). *Entoloma piceinum*, a new lignicolous species of Entolomataceae (Agaricales) from the European Russia. *Novosti Sistematiki Nizshikh Rastenii* **48**: 181–187. <http://dx.doi.org/10.31111/nsnr/2014.48.181>
- Nagy L, Gorliczai Zs (2007). Further data to the knowledge of the fungi of the Great Hungarian Plain (in Hungarian). *Mikológiai Közlemények, Clusiana* **46**: 211–256.
- Noordeloos ME (1979). *Entoloma* subgenus *Pouzaromyces* emend. *Persoonia* **10**: 207–243.
- Noordeloos ME (1981). Introduction to the taxonomy of the genus *Entoloma* sensu lato (Agaricales). *Persoonia* **11**: 121–151.
- 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). Entolomataceae (Agaricales, Basidiomycetes) in Greenland. I. The genus *Entoloma*. *Persoonia* **12**: 263–305.
- Noordeloos ME (1987). *Entoloma* (Agaricales) in Europe. Synopsis and keys to all species and a monograph of the subgenera *Trichopilus*, *Inocephalus*, *Alboleptonia*, *Leptonia*, *Paraleptonia*, and *Omphaliopsis*. *Beihfte zur Nova Hedwigia* **91**: 1–419.
- Noordeloos ME (1988). *Entoloma* in North America. The species described by L.R. Hesler, A.H. Smith, and S.J. Mazzer, type-studies and comments. *Cryptogamic Studies* 2. Fischer Verlag, Stuttgart / New York.
- Noordeloos ME (1992). Fungi Europaei vol. 5, *Entoloma* sensu lato. Edizione Candusso, Alessio.
- Noordeloos ME (2004). *Entoloma* sensu lato, Fungi Europaei vol. 5a. Edizione Candusso, Alessio.
- Noordeloos ME (2008). *Entoloma* in North America 2: the species described by C.H. Peck – type studies and comments. *Österreichische Zeitschrift für Pilzkunde* **17**: 87–152.



- Noordeloos ME, Hausknecht A (2007). The genus *Entoloma* (Basidiomycetes, Agaricales) of the Mascarenes and Seychelles. *Fungal Diversity* **27**: 111–144.
- Noordeloos ME, Hausknecht A (2016). *Entoloma* (Basidiomycetes, Agaricales) of the Mascarenes and Seychelles 2. *Zeitschrift für Mykologie* **82**: 295–332.
- 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, Dima B, Weholt Ø, *et al.* (2017). *Entoloma chamaemori* (Entolomataceae, Basidiomycota) – a new boreal species, with isolated phylogenetic position. *Phytotaxa* **298**: 289–295. <https://doi.org/10.11646/phytotaxa.298.3.9>.
- Noordeloos ME, Hausknecht A, Wölfel G (1995). Über neue, kritische oder seltene Rötlinge aus dem östlichen Österreich. *Österreichische Zeitschrift für Pilzkunde* **4**: 119–136.
- Noordeloos ME, Lorås J, Eidissen SE, *et al.* (2021). Three new *Entoloma* species of the Cyanula clade (Entolomataceae, Agaricales) from (sub)alpine habitats in Northern Norway and Sweden. *Sydowia* **73**: 185–196. <https://doi.org/10.12905/0380.sydowia73-2020-0185>
- Noordeloos ME, Morozova O, Dima B, *et al.* (2022a). *Entoloma* s.l. In *Fungi Europei* vol. 5b. Candusso Editrice.
- Noordeloos ME, Vila J, Jordal JB, *et al.* (2022b). Contributions to the revision of the genus *Entoloma* (Basidiomycota, Agaricales) in Europe: six new species from subgenus *Cyanula* and typification of *E. incarnatofuscescens*. *Fungal Systematics and Evolution* **9**: 87–97. <https://doi.org/10.3114/fuse.2022.09.06>
- Noordeloos ME, Weholt Ø, Bendiksen E, *et al.* (2018). *Entoloma aurorae-borealis* sp. nov. and three rare *Entoloma* species in the Sinuatum clade (subg. *Entoloma*) from northern Europe. *Sydowia* **70**: 199–210. <https://doi.org/10.12905/0380.sydowia70-2018-0199>
- Orton PD (1960). New checklist of British Agarics and Boleti. III. Notes on genera and species in the list. *Transactions of the British Mycological Society* **43**: 159–439.
- Osmundson TW, Robert VA, Schoch CL, *et al.* (2013). Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* **8**: e62419. <https://doi.org/10.1371/journal.pone.0062419>
- Palamarchuk MA (2016). Agaricoid basidiomycetes of the northern part of the National Park «Yugyd Va» (Subpolar Ural). *Mikologiya i Fitopatologiya* **50**(1): 24–34. (In Russian) <https://doi.org/10.15468/2nvarx>
- Papp V, Dima B (2018). New systematic position of *Aurantiporus alborubescens* (Meruliaceae, Basidiomycota), a threatened old-growth forest polypore. *Mycological Progress* **17**: 319–332. <https://doi.org/10.1007/s11557-017-1356-3>.
- Raj KN Anil, Manimohan P (2017). Four new species of *Entoloma* subgenus *Pouzarella* from India. *Phytotaxa* **307**: 104. <https://doi.org/10.11646/phytotaxa.307.2>
- Rambaut A (2014). *FigTree v1. 4*. University of Edinburgh, Edinburgh, UK.
- Reschke K, Noordeloos ME, Manz C, *et al.* (2022a). Fungal diversity in the tropics: *Entoloma* spp. in Panama. *Mycological Progress* **21**: 93–145. <https://doi.org/10.1007/s11557-021-01752-2>.
- Reschke K, Morozova OV, Dima B, *et al.* (2022b). Phylogeny, taxonomy, and character evolution in *Entoloma* subgenus *Nolanea*. *Persoonia* **49**: 136–170. <https://doi.org/10.3767/persoonia.2022.49.04>
- Romagnesi H (1974). Étude de quelques Rhodophylles. Travaux mycol. dédiés à R. Kühner. *Numéro Spécial du Bulletin de la Société Linnéenne de Lyon* **43**: 365–387.
- Romagnesi H, Gilles G (1979). Les Rhodophylles des forêts côtières du Gabon et de la Côte d'Ivoire avec une introduction générale sur la taxonomie du genre. *Beihefte Nova Hedwigia* **59**: 1–649.
- Stafleu FA, Cowan RS (1976–1988). *Taxonomic literature*, 2nd ed. Bohn, Scheltema & Holkema, Utrecht.
- Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.
- Tejkal K (2020). The rare *Entoloma opacum* (Velen.) Noordel. was found in Prague [In Czech]. *Mykologický Sborník* **97**: 43–48.
- Varga T, Krizsán K, Földi C, *et al.* (2019). Megaphylogeny resolves global patterns of mushroom diversification. *Nature Ecology & Evolution* **3**: 668–678. <https://www.nature.com/articles/s41559-019-0834-1>
- Vidal JM, Bellanger JM, Moreau PA (2016). Three new gasteroid species of the genus *Entoloma* found in Spain. *Boletín Micológico de FAMCAL* **11**: 53–78.
- Vila J, Carbó J, Caballero F, *et al.* (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*): 3–62, 93–135 (iconography). Edizione Candusso, Italy.
- Vila J, Caballero F, Carbó J, *et al.* (2014). Preliminary morphologic and molecular study of the *Entoloma rusticoides* group (Agaricales-Basidiomycota). *Revista Catalana de Micologia* **35**: 65–99.
- Wölfel G, Noordeloos ME (1997a). *Entoloma triste* und nahe verwandte Arten. *Österreichische Zeitschrift für Pilzkunde* **6**: 23–33.
- Wölfel G, Noordeloos ME (1997b). *Entoloma ritae*, eine neue rosafarbige *Entoloma* aus dem Trentin. *Bollettino del Gruppo Micologico 'G. Bresadola'* **40**: 491–495.

SUPPLEMENTARY MATERIAL

Table S1. Sequences used in the phylogenetic analyses. Newly generated sequences for this study are marked in boldface. The taxonomic labels of the sequences taken from public databases (i.e. GenBank, UNITE) are indicated in brackets. Sequences not included in the phylogenetic analysis are marked with an asterisk (*).