



# Phylogeny, taxonomy, and character evolution in *Entoloma* subgenus *Nolanea*

K. Reschke<sup>1</sup>, O.V. Morozova<sup>2</sup>, B. Dima<sup>3</sup>, J.A. Cooper<sup>4</sup>, G. Corriol<sup>5</sup>,  
A.Yu. Biketova<sup>6,7</sup>, M. Piepenbring<sup>1</sup>, M.E. Noordeloos<sup>8</sup>

## Key words

*Agaricales*  
biogeography  
concatenated alignment  
*Entolomataceae*  
polyphasic taxonomy  
ribosomal DNA  
species tree

**Abstract** *Nolanea* is a well-known and long-established subgenus of the genus *Entoloma* traditionally defined mainly by the mycenoid basidiocarps of the included species. Until now, revisions of this subgenus including molecular data exist only on a regional scale. In this study, the phylogeny of species of *Nolanea* is analysed based on multi-gene DNA sequences including data of specimens from all continents. New primers are designed for the mitochondrial small subunit and *RPB2*. The performance of the DNA loci in reconstructing the phylogeny in subg. *Nolanea* is evaluated. An ancestral state reconstruction is used to infer the character state evolution as well as the importance and reliability of morphological characters used to define subclades below subgeneric rank. Based on the results, seven sections are recognised in *Nolanea*: the sections *Holoconiota*, *Infularia*, *Mammosa*, *Nolanea*, *Papillata*, *Staurospora*, and the newly described sect. *Elegantissima*. A large phylogeny based on the fungal barcode rDNA ITS with numerous type sequences is used to evaluate current species concepts. Several names are revealed to be synonyms of older names. Four species new to science are described, namely *E. altaicum*, *E. argillaceum*, *E. cornicolor*, and *E. incognitum*. Lectotypes, epitypes or neotypes are designated for *E. cetratum*, *E. clandestinum*, *E. conferendum*, *E. cuspidiferum*, *E. hebes*, *E. minutum*, *E. nitens*, and *E. rhodocylix*. The re-evaluation of the limits of subg. *Nolanea* leads to an altered concept excluding species with distinct, lageniform cheilocystidia. The section *Ameides* is placed in subg. *Leptonia*. For several species formerly accommodated in *Nolanea*, but excluded now, viz., *E. lepiotoides*, *E. rhombisporum*, *E. subelegans*, and *E. velenovskyi* the taxonomic position remains unclear, because of the yet unresolved phylogeny of the whole genus *Entoloma*.

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## INTRODUCTION

### Morphological concept of *Nolanea*

*Entoloma* subg. *Nolanea* dates to Fries (1821) who described *Nolanea* as a tribus of his broad genus *Agaricus*. This misplaced term (Shenzhen Art. 37.6.) is valid due to an exception in the nomenclatural Code, Shenzhen Art. F.4.1. (Turland et al. 2018). The starting point of priority for this taxon over later described names is 1829, when Loudon (1829) treated it as *Agaricus* subg. *Nolanea*. Kummer (1871) raised *Nolanea* to generic rank. Since then, *Nolanea* has been treated at both of these ranks, viz., as a genus (Quélet 1872, Largent & Benedict 1971, Pegler

1977, Orton 1991, Largent 1994, Henkel et al. 2014, Karstedt et al. 2020) or subgenus (Quélet 1886, Romagnesi 1941, 1974a, Kühner & Romagnesi 1953, Romagnesi & Gilles 1979, Noordeloos 1980, 1987, 1992, 2004, Arnolds & Noordeloos 1981, Singer 1986, Noordeloos & Gates 2012, Vila et al. 2013) of the genus *Entoloma* (or *Rhodophyllus*). Initially mainly defined by basidiocarps with mycenoid habit, *Nolanea* was re-evaluated and emended in several treatments: Largent & Benedict (1971) emphasised the well differentiated pileipellis generally composed of repent hyphae (a cutis), often with a subpellis. They also detected a high urea content in species of *Nolanea* and *Claudopus* in opposite to those of *Alboleptonia*, *Entoloma*, and *Leptonia*, a feature never taken up by later authors. Romagnesi (1978) added the hygrophanous nature of the pileus as diagnostic for subg. *Nolanea*. Noordeloos (1980) used upon a suggestion by Kühner (1977) also the size and shape of trama elements, i.e., long, fusiform cells of 150–450 µm length or sometimes longer to delimit *Nolanea* from other subgenera.

### Sectional treatments

Largent & Thiers (1972) introduced the four sections *Holoconiota*, *Cosmeoexonema*, *Endochromonema*, and *Staurospori* in *Nolanea* at generic rank and accordingly established the autonymic section *Nolanea*. Romagnesi (1974a) proposed eight sections based on characteristics of the basidiospores, absence/presence of cystidia, basidiocarp colour, and the type

<sup>1</sup> Mycology Research Group, Faculty of Biological Sciences, Goethe University Frankfurt am Main, Max-von-Laue Straße 13, 60438, Frankfurt am Main, Germany;

corresponding author e-mail: [Reschke@em.uni-frankfurt.de](mailto:Reschke@em.uni-frankfurt.de).

<sup>2</sup> Komarov Botanical Institute of the Russian Academy of Sciences, 197376, 2 Prof. Popov Str., Saint Petersburg, Russia.

<sup>3</sup> Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, H-1117, Budapest, Hungary.

<sup>4</sup> Manaaki Whenua – Landcare Research, 54 Gerald Street, Lincoln 7608, New Zealand.

<sup>5</sup> National Botanical Conservatory of the Pyrenees and Midi-Pyrenees, Vallon de Salut, BP 70315, 65203 Bagnères-de-Bigorre, France.

<sup>6</sup> Institute of Biochemistry, Biological Research Centre of the Eötvös Loránd Research Network, Temesvári blvd. 62, H-6726 Szeged, Hungary.

<sup>7</sup> Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond TW9 3DS, UK.

<sup>8</sup> Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, The Netherlands.

of pigmentation, including those of Largent & Thiers (1972) and in addition the sections *Luctuari*, *Mammosi*, *Papillati*, and *Minuti*. Largent (1974) refined his earlier sections with subsections based on the absence/presence of clamp connections and cheilocystidia as well as basidiospore features and pileus and stipe colour. To accommodate species from tropical West Africa, Romagnesi (1978) described sect. *Paramammosi* and subsect. *Dryophilooides*. Based on a comprehensive study of species described from Europe, Noordeloos (1980) reworked the system of *Nolanea* using mainly basidiospore characters, absence/presence of cheilocystidia, lamellae colour, type of pigmentation, and absence/presence of clamp connections. This resulted in five sections, *Nolanea*, *Staurospora*, *Papillata*, *Fernandae*, and *Endochromonema*, which were further divided into nine subsections. Later, Noordeloos (1992) transferred sect. *Staurospora* to subg. *Inocephalus* due to the somewhat fibrillose pileus surface and the sometimes trichodermal aspect of the pileipellis of the species in this section. Largent (1994) introduced in his monograph of *Entolomataceae* from western North America the new section *Ameides* for the species with sweet odour around *E. ameides* and a new subsection for *E. juncinum* and similar species. Wölfel & Noordeloos (1997) re-evaluated *E. triste* and similar species and transferred them to a section of their own, viz., sect. *Tristia*, in subg. *Inocephalus*. Noordeloos & Gates (2012) described two new sections in *Nolanea*, *Astrofernandae* and *Lepiotoidei*, to accommodate some species from Tasmania which did not fit in the existing sections and transferred sect. *Staurospora* back to subg. *Nolanea*.

#### **Molecular assessments**

In the first larger molecular phylogeny of *Entoloma* spp. using three loci (Co-David et al. 2009), *Nolanea* appeared at a sister position of the clade of subgenera *Claudopus* and *Leptonia* s.str. Eight species were included in *Nolanea*, however, four of them were at this time not classified in this subgenus: *Entoloma pallideradicatum* and *E. valdeumbonatum*, at that time classified in subg. *Entoloma*, *E. conferendum*, at that time classified in subg. *Inocephalus*, and *E. cephalotrichum*, at that time classified in subg. *Alboleptonia*. Thus, subg. *Nolanea* was found to be paraphyletic and included in a larger ‘*Nolanea-Claudopus*-clade’. Vila et al. (2013) used ITS barcodes to re-evaluate species concepts and described new species in *Nolanea* with the main focus on species in South Europe. Further new *Nolanea* species were described alongside an ITS phylogeny by Raj & Manimohan (2016). Karstedt et al. (2020) presented a more elaborate phylogeny based on three loci, with a monophyletic clade that included mainly species which were also previously considered to belong to *Nolanea*. Therefore, they regarded *Nolanea* as sufficiently delimited at the rank of genus and described five new species in the genus, but without providing a revised generic circumscription. Reschke et al. (2022) described four species of subg. *Nolanea* from Panama, including a phylogram based on ITS with newly generated data of specimens from Panama and Europe. The holotype of *E. sublegans*, previously considered to belong to *Nolanea* (Noordeloos & Hausknecht 2016), fell out of the subgenus and took an isolated position at a long branch.

The aims of the present study are:

- i to determine the limits of *Entoloma* subg. *Nolanea*;
- ii to re-evaluate its taxonomic framework and the existing sections and subsections;
- iii to evaluate the DNA loci so far used for phylogenetic inference in *Entoloma*;
- iv to analyse correlations between morphological character states and molecular phylogeny;
- v to re-evaluate species concepts based on type studies and an ITS phylogeny.

Comprehensive morphological descriptions based on sequenced specimens of already known species are published in a revised monograph of *Entoloma* in Europe (Noordeloos et al. 2022b).

#### **MATERIAL AND METHODS**

##### **Morphology**

Nolaneoid specimens of *Entoloma* spp. were collected in Europe, New Zealand, Panama, and East to West Russia. Dried specimens, including types, were obtained of BBF, C, CMMF, H, K, KR, L, LE, MB, MICH, O, PDD, SLV, WU, ZT, and various private persons. Macromorphological features were studied based on fresh basidiocarps as well as their photos taken in the field. Microscopical characters were analysed by bright-field microscopy, using light microscopes. The size of basidiospores, hymenial structures and features of the pileipellis were investigated from hand slices mounted in tap water, 5–10 % KOH, or Congo red solutions. In a few cases, the presence/absence of clamp connections at the bases of the basidia was analysed within phase contrast. At least 20 basidiospores were measured for each specimen. Spore sizes and Q-values are given in 5th percentile—mean—95th percentile. Values of spore sizes were rounded to the nearest 0.5 µm, Q-values to the nearest 0.05. Other values of measurements were less strictly rounded to avoid pseudo-exact indication of sizes.

##### **DNA extraction and PCR**

Pieces of 1–10 mm<sup>2</sup> taken from dried basidiocarps were ground in a MM301 Mixer Mill (Retsch GmbH, Haan, Germany). DNA was extracted from the resulting powder using the peqGOLD fungal DNA mini kit (VWR, Darmstadt, Germany), the innuPREP Plant DNA Kit (analytikjena, Jena, Germany) according to the instruction manuals, or as described in Morozova et al. (2018). Sequences of five regions, complete nuc rDNA ITS1-5.8S-ITS2 (ITS), the D1/D2 region of the nc LSU rDNA (LSU), partial translation elongation factor 1-a (*EF-1α*), partial second largest subunit of RNA polymerase II (*RPB2*), and partial mitochondrial small subunit rDNA (mtSSU), were obtained via PCR in a peqSTAR 2× Gradient Thermal Cycler (PEQLAB, Erlangen, Germany) using the VWR Taq DNA Polymerase (VWR, Darmstadt, Germany). The forward primers ITS1 and ITS1F along with the reverse primers ITS4 and ITS4B (White et al. 1990, Gardes & Bruns 1993) were used to obtain ITS sequences with the following PCR conditions: denaturation at 98 °C for 4 min followed by 35 cycles of 95 °C for 45 s, 53 °C for 30 s and 72 °C for 60 s, with a final elongation step at 72 °C for 5 min. The primer pairs ITS1/ITS2 and ITS3/ITS4 or ITS4B (White et al. 1990) were used for difficult material, as old specimens, either with the aforementioned protocol or a touchdown protocol: denaturation at 95 °C for 4 min followed by 12 cycles of 94 °C for 45 s, 53 °C (−0.5 °C/cyc) for 60 s, and 72 °C for 60 s, thereafter 35 cycles of 94 °C for 30 s, 53 °C for 40 s, and 72 °C for 60 s, with a final elongation step at 72 °C for 10 min. DNA of further old specimens, including types, was extracted from a few milligrams of dried material with the NucleoSpin Plant II Mini Kit (Macherey-Nagel, Düren, Germany). The PCR amplifications were performed with the aforementioned primer combinations in a 10 µl reaction mix with 1 U Phusion High-Fidelity DNA polymerase and 5× HF buffer (ThermoScientific), 200 mM of each dNTP and 0.5 µM of each primer. The PCR reactions were run with the following settings: denaturation at 98 °C for 30 s, followed by 40 cycles of denaturation at 98 °C for 10 s, annealing at 55 °C for 30 s, and extension at 72 °C for 30 s. Further ITS sequences were obtained using the Phire Plant Direct PCR Kit (Thermo Scientific, USA) as described in Papp & Dima (2018). To obtain LSU sequences, the primers

**Table 1** New primers for *RPB2* and mtSSU designed in this study.

Primer name	Forward/Reverse	Sequence (5'→3')
RPB2-i6FB	forward	GAAGGYCAAGCMTGTTGGTCTYG
RPB2-iR	reverse	TGTTTACCCATKGAGAYTGR
MS0B	forward	TTATTTGTTAAAGGTAGTTGG
MS0F	forward	GTTAADGGTAGTTGGTRG
MF1.1	forward	TCYGATTGAACGTTTCAGTAG
MS1.2R	reverse	TTACCGAGTCTCTGGCACAG
MR1.1	reverse	GACAGCCATGCAACACCTG

LR0R (Cubeta et al. 1991) together with LR5 (Vilgalys & Hester 1990) or NL1 together with NL4 (O'Donnell 1992) were used along with the standard PCR protocol for ITS. *RPB2* sequences were obtained using the primers rpb2-6F and rpb2-7.1R (Matheny 2005), the newly designed internal primers RPB2-i6FB and RPB2-iR, or a combination of both, with a touchdown PCR protocol: denaturation at 95 °C for 4 min followed by 14 cycles of 94 °C for 45 s, 56 °C (−0.5 °C/cyc) for 60 s, and 72 °C for 60 s, thereafter 40 cycles of 94 °C for 30 s, 53 °C for 40 s, and 72 °C for 60 s, with a final elongation step at 72 °C for 10 min. The primers EF1-983F and EF1-2218R (Rehner & Buckley 2005) were used for *EF-1α* with a touchdown protocol: 95 °C for 4 min followed by 10 cycles of 94 °C for 45 s, 56 °C (−0.5 °C/cyc) for 60 s, and 72 °C for 75 s, thereafter 40 cycles of 94 °C for 30 s, 56 °C for 40 s, and 72 °C for 75 s, with a final elongation step at 72 °C for 10 min. Sequences of the mtSSU were obtained with the forward primers MF1.1, MS0F, and MS0B together with the reverse primers MS1.2R and MR1.1 (Table 1) in different pairings, mainly with the combination of MS0B and MR1.1, using a tripartite touchdown protocol: 95 °C for 4 min followed by 15 cycles of 94 °C for 45 s, 60 °C (−1 °C/cyc) for 60 s, and 72 °C for 60 s, then 10 cycles of 94 °C for 45 s, 45 °C (+1 °C/cyc) for 60 s, and 72 °C for 60 s, thereafter 25 cycles of 94 °C for 45 s, 53 °C for 60 s, and 72 °C for 60 s, with a final elongation step at 72 °C for 5 min. Success of amplification was checked by gel electrophoresis using a 1 % (w/v) agarose gel. Successfully amplified products were sent to Microsynth Seqlab (Göttingen, Germany) or LGC Genomics (Berlin, Germany) for purification and forward and reverse sequencing using the same primers as used for PCR. The sequences were submitted to GenBank and are accessioned under OL337991–OL338460 (ITS, often including LSU), OL338531–OL338545 (LSU), OL338461–

OL338530 (mtSSU), OL405190–OL405255 (*RPB2*), and OL405499–OL405553 (*EF-1α*).

### Primer design

Sequences of the mtSSU were extracted from mitochondrial genomes and whole genome shotgun (WGS) sequences obtained from GenBank and the Mycosom portal (Grigoriev et al. 2014) (Table 2). The sequences were aligned in MAFFT (Katoh & Standley 2013) using the E-INS-i model. The primers MS1 and MS2 (White et al. 1990) as well as U1 and CU6 (unpublished primers of Bruns lab, see online document of Binder & Hibbett 2003, [http://www2.clarku.edu/faculty/dhibbett/Protocols\\_Folder/Primers/Primers.pdf](http://www2.clarku.edu/faculty/dhibbett/Protocols_Folder/Primers/Primers.pdf), accessed 24 July 2021) were mapped on the alignment to delimit the target region. The new primer sequences MF1.1, MS0F, MS1.2R, and MR1.1 were manually inferred from the alignment and tested on DNA extracts of *Entoloma* spp. The matching of MS0F and MS1.2R was investigated on alignments of resultant sequences and the new primer MS0B was designed to replace MS0F, which had a mismatch at the third last position. The mtSSU sequences were aligned together with the complete mtSSU sequences of *Tricholoma matsutake* (JX985789: 15442–17595) and *Lentinula edodes* (AF481731). The positions of the variable domains V1–V6 were inferred from the detailed annotations of the sequence of *L. edodes* given by Barroso et al. (2003). The primers and variable domains were mapped on the mtSSU sequence of *T. matsutake* (Fig. 1).

Internal primers for *RPB2*, RPB2-i6FB and RPB2-iR, were manually designed by selecting suitable sequence stretches from alignments of own sequences of high quality. The internal forward primer RPB2-i6FB overlaps with RPB2-i6F (Co-David et al. 2009).

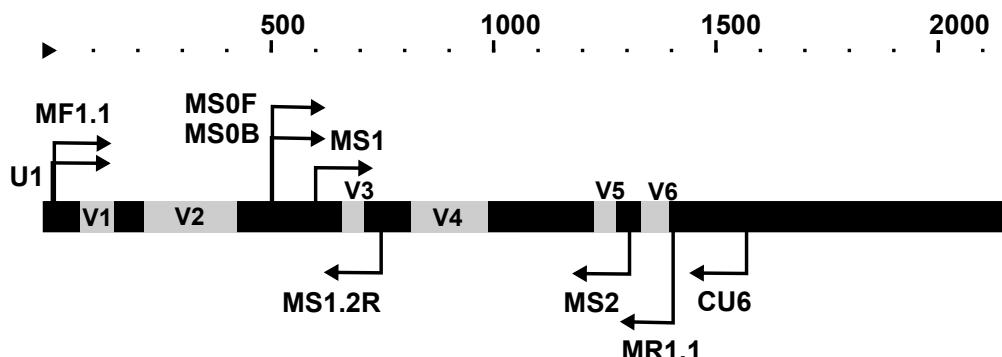
### Phylogenetic analyses

Sequences were edited and assembled using Geneious (Biomatters Ltd., Auckland, New Zealand) and aligned together with sequences obtained from GenBank (Table 3) with Mafft (Katoh & Standley 2013) using the E-INS-i algorithm. Unreliable terminal parts and parts of primer sequences as well as the ends of the resulting alignments were manually pruned in AliView (Larsson 2014). A Maximum Likelihood (ML) tree of the ITS sequences partitioned in spacers and 5.8S, was built using RAxML-HPC2 on XSEDE (v. 8.2.4) (Stamatakis 2014) via the Cipres Science Gateway (Miller et al. 2010) using the

**Table 2** Species of which mitochondrial genomes were used for primer design and mismatches of new and standard primers.

Species	Suborder	Accession/ JGI notation	Mismatching positions of the respective primer							Product size MS0B/MR1.1	
			U1	MF1.1	MS0B	MS1	MS1.2R	MS2	MR1.1		
<i>Agaricus bisporus</i>	Agaricineae	JX271275	3	0	1	0	0	2	0	5 <sup>1</sup>	944
<i>Coprinopsis cinerea</i>	Agaricineae	AACS02000068	2	0	1	1	0	4	0	3	910
<i>Crepidotus variabilis</i>	Agaricineae	Crevar1	2	0	1	1	0	4	0	1	974
<i>Cyathus striatus</i>	Agaricineae	Cyastr2	2	1	1	1	0	4	0	3	977
<i>Dendrothele bispora</i>	incertae sedis	Denbi1	2	0	2	0	0	4	0	0	839
<i>Auriculariopsis ampla</i>	Marasmiineae	Auramp1	2	0	1	3	1	1	0	0	1109
<i>Crinipellis perniciosa</i>	Marasmiineae	AY376688	2	0	3	0	0	1	0	2	916
<i>Lentinula edodes</i>	Marasmiineae	AB697988	2	1	3	0	0	4	0	1	944
<i>Moniliophthora roreri</i>	Marasmiineae	HQ259115	2	0	3	0	0	1	0	1	903
<i>Mycena galopus</i>	Marasmiineae	Mycgal1	3	2	2	0	0	1	0	2	950
<i>Amanita jacksonii</i>	Pluteineae	AYNK01002457	2	0	1	0	2	4	0	1	848
<i>Asterophora parasitica</i>	Tricholomataceae	MH725791	2	0	0	0	0	3	0	1	879
<i>Lepista nuda</i>	Tricholomataceae	Lepnud1	2	0	0	0	0	3	0	1	1032
<i>Lyophyllum decastes</i>	Tricholomataceae	MH447974	2	0	1	0	0	3	0	1	900
<i>Lyophyllum shimeji</i>	Tricholomataceae	MH447975	2	0	1	0	0	3	0	1	896
<i>Tricholoma matsutake</i>	Tricholomataceae	JX985789	2	0	1	1	0	4	0	0	955
<i>Tricholomella constricta</i>	Tricholomataceae	MH725800	2	0	0	0	0	3	0	1	904

<sup>1</sup> = including an indel.



**Fig. 1** Primer map of new and standard mtSSU primers, including the variable domains V1–V6 (V7–V9 not indicated). Nucleotide positions based on the mtSSU sequence of *Tricholoma matsutake* (JX985789).

GTRCAT model with 55 per site rate categories and 1000 rapid bootstrap repetitions (Felsenstein 1985). Transfer bootstrap expectations (TBE) (Lemoine et al. 2018) were calculated using the web interface (<http://booster.c3bi.pasteur.fr>). The resultant tree was visualised using FigTree (Rambaut 2014).

Preliminary ML trees were built for the five regions with RAxML v. 8.2.11 (Stamatakis 2014) using the GTRCAT model along with 100–500 rapid bootstrap repetitions (Felsenstein 1985). The statistical performance of the different loci was tested with Ktreedist. This program scales phylogenetic trees to a similar global divergence and then compares their relative branch lengths and topology and calculates a quantitative difference value, the K tree score (Soria-Carrasco et al. 2007). For this purpose, the data was reduced to sequences of the 57 specimens which were represented by all loci, ITS, LSU, RPB2, EF-1 $\alpha$ , and mtSSU. The sequences of each region were aligned and pruned as described above. The alignments were concatenated, and ML trees were calculated with RAxML v. 8.2.11 (Stamatakis 2014) for single regions, the concatenated alignments of all 5 regions, and the concatenated alignments of ITS, RPB2, EF-1 $\alpha$ , and mtSSU. The GTRCAT model was used with 25 per site rate categories and 250 rapid bootstraps. In total, eight partitions were used: ITS-spacers, 5.8S, EF-1 $\alpha$ -exons, EF-1 $\alpha$ -introns, RPB2-exons, RPB2-intron, mtSSU, and LSU. The resultant trees of the single regions and the 4-loci tree were then compared to the 5-loci tree using Ktreedist with the option to calculate Robinson-Foulds (RF) distances in addition to the K tree score. Due to poor performance in the preliminary trees and the statistical test, the LSU sequences were not used for further phylogenetic analyses.

Sequences of specimens which were represented by at least three of the four regions, ITS, RPB2, EF-1 $\alpha$ , and mtSSU, were used for a multi-loci phylogeny. The sequences were aligned and the alignments were pruned as described above for each region. Maximum likelihood trees were inferred for each alignment with RAxML v. 8.2.11 (Stamatakis 2014) using the GTRCAT model along with 200 rapid bootstraps. As no major inconsistencies were observed, the alignments were concatenated. The resultant alignment was used to infer a maximum likelihood tree using RAxML-HPC2 on XSEDE (v. 8.2.4) (Stamatakis 2014) via the Cipres Science Gateway (Miller et al. 2010) using the GTRCAT model with 25 per site rate categories for six distinct partitions, ITS, EF-1 $\alpha$ -exons, EF-1 $\alpha$ -introns, RPB2-exons, RPB2-intron, and mtSSU, along with 1000 rapid bootstrap repetitions (Felsenstein 1985). Transfer bootstrap expectations (TBE) (Lemoine et al. 2018) were calculated using the web interface (<http://booster.c3bi.pasteur.fr>).

A Bayesian MCMC analysis was conducted using MrBayes on XSEDE (v. 3.2.6) (Huelsenbeck & Ronquist 2001, Ronquist et al. 2012) via the Cipres Science Gateway (Miller et al. 2010).

Two runs of 2 million generations were set with four chains each, a sampling frequency of 200, and a burn-in of 250. The six partitions as above were used with the GTR model and a gamma distribution each, but with unlinked rates of reversible rate matrix, stationary state frequencies, and  $\alpha$ -shapes. A stop rule was set for the convergence of the average standard deviation of split frequencies  $< 0.01$ , which was reached after 1.28 million generations. The Bayesian tree was visualised, complemented with the support values of the other analyses, and edited using TreeGraph 2 (Stöver & Müller 2010).

The alignments are available on Figshare: <https://doi.org/10.6084/m9.figshare.19586503>.

#### Ancestral character state estimation

Ancestral character state estimations were calculated for clamp connections present/absent, basidiospore shape with average Q (Qav.)  $< 1.25$ /Qav.  $\geq 1.25$ /cruciform, and pigments intracellular/incrusting/both in R v. 3.4.4 (Ihaka & Gentleman 1996) using the packages ape (Paradis et al. 2004), phytools (Revell 2012), and ggtree (Yu et al. 2017). The concatenated alignment was reduced to include only sequences of one specimen per species, except sequences of two specimens for the variable *E. hirtipes*. A maximum likelihood tree was calculated with RAxML-HPC2 on XSEDE (v. 8.2.4) (Stamatakis 2014) via the Cipres Science Gateway (Miller et al. 2010) using the GTRCAT model with 25 per site rate categories, 8 partitions inferred using PartitionFinder (Lanfear et al. 2012), ITS, 3 triplet positions of RPB2 and EF-1 $\alpha$  each, and mtSSU, along with 1000 bootstrap repetitions (Felsenstein 1985). The tree was visualised and rooted in R. The character states were determined from sequenced specimens (Table S1). Species with dominant incrusting pigment and weak or only occasionally present intracellular pigment were treated as ‘incrusting’, and species with intracellular pigment which rarely have some additional incrusting pigment were treated as ‘intracellular’ for the analysis. Character states of species which were not analysed by the authors for this study were set to ‘unknown’, also were the character states of the non-randomly selected outgroup species set to ‘unknown’ to avoid bias. The likelihoods of the ancestral character states were analysed using an all-rates-different (ARD) model for presence/absence of clamp connections and equal rates (ER) for basidiospore shape and pigment type.

#### Nomenclature

Articles cited as ‘Art.x.y.’ refer to the current version of the International Code of Nomenclature for algae, fungi and plants (Shenzhen Code) (Turland et al. 2018).

**Table 3** Specimens used in the phylogenetic analyses based on multiple loci and the GenBank accession numbers of the respective sequences. Species names are used as annotated in GenBank for sequences obtained from this database.

Coll_no	Species (annotation)	origin	note	ITS	LSU	mtSSU	RPB2	TEF1
11CA014	<i>Nolanea cf. conferenda</i>	USA	–	KF738946	KF771351	MG702640		
aFP4	<i>Entoloma hirtipes</i>	Germany	–	OL338461	OL405499	–		
CME5	<i>Entoloma belouvense</i> var. <i>albertinae</i>	Panama	–	MZ611628	OL405500	–		
CME6	<i>Entoloma paraconferendum</i>	Panama	holotype	MZ611629	OL405201	OL405501	–	
CME9	<i>Entoloma transitionisporum</i>	Panama	–	MZ611632	OL405208	OL405502	–	
CME10	<i>Entoloma cremeostriatum</i>	Panama	–	OL338477	OL405199	OL405503	–	
CORT-5761TJB	<i>Entoloma alboumbonatum</i>	USA	–	MZ611621	MH190191	MH190124	MH190160	–
Cro17	<i>Entoloma hirtipes</i>	Croatia	–	OL338044	OL338463	OL405504	–	
DLL9531	<i>Nolanea cetrata</i>	USA	–	KF738942	KF771346	MG702639	MG702637	
DLL9640	<i>Leptonia umbrophila</i>	Australia	–	JQ756422	JQ756438	MG702619	HQ731518	
DLL9788	<i>Claudopus viscosus</i>	Australia	holotype	–	HQ731516	MG702619	–	
Eth14	<i>Entoloma</i> sp.	Ethiopia	–	OL338057	OL338473	OL405235	–	
FK0898	<i>Nolanea atropallidata</i>	Brazil	holotype	KF679354	KF738940	KF738929	MH190107	MH190137
FK0935	<i>Nolanea albertainae</i>	Brazil	holotype	KF679348	KF738936	KF738924	KF771344	–
FK1049	<i>Nolanea tricholomatoides</i>	Brazil	holotype	KF679352	KF738939	KF738928	KF771347	–
FK1140	<i>Nolanea parvispora</i>	Brazil	holotype	KF679353	KF738943	KF738931	KF771348	MH190143
FK11732	<i>Nolanea albertainae</i>	Brazil	holotype	KF679351	KF738938	KF738926	KF771345	–
FK2011	<i>Entoloma</i> sp.	Brazil	–	–	MG018327	MG018312	MG018335	MH190149
GC10041102	<i>Entoloma hirtipes</i>	France	–	OL338080	OL338462	OL405505	–	
GC13082801	<i>Entoloma sericeoalpinum</i>	France	–	OL338083	OL338545	OL405216	–	
GC13100602	<i>Entoloma hirtipes</i>	France	–	OL338088	OL338465	OL405192	OL405506	–
GDGM27564	<i>Entoloma caespitosum</i>	China	–	JQ281477	JQ320130	JQ983070	–	
GDGM43979	<i>Entoloma crepidoioides</i>	China	holotype	KJ958983	KJ958983	KJ958984	KJ958984	–
J.Wisman 2003-09-19	<i>Entoloma sinuatum</i>	–	‘50’	KC710109	GQ289193	GQ289264	–	
JM96110	<i>Entoloma strictius</i>	–	–	DQ494680	AF042620	EF421100	EF421017	EF421088
KA13_1522	<i>Entoloma hirtipes</i>	South Korea	–	MN088710	MN088715	MN088719	MN088719	–
KA15_373	<i>Entoloma chytrophilum</i>	South Korea	–	MN088709	MN088714	MN088718	MN088718	–
KaR213	<i>Entoloma hebes</i>	Germany	–	OL338117	OL338470	OL405197	–	
KaR237	<i>Entoloma sericeum</i>	Germany	–	OL338118	OL338542	OL405220	OL405220	
KaR299	<i>Entoloma leptopus</i>	Germany	–	OL338123	OL338471	OL405198	–	
KaR628	<i>Entoloma flavocornicum</i>	Panama	holotype	MZ611667	OL338511	OL405244	OL405507	–
KaR630	<i>Entoloma belouvense</i>	Panama	–	MZ611668	OL338476	OL405209	OL405508	–
KaR693	<i>Entoloma hebes</i>	Panama	–	OL338117	OL338524	OL405251	OL405509	–
KaR839	<i>Entoloma mithaleae</i>	Austria	–	OL338124	OL338478	OL405202	OL405510	–
KaR868	<i>Entoloma chlorinosum</i>	Austria	–	OL338129	OL338506	OL405232	OL405511	–
KaR875	<i>Entoloma fernandeae</i>	Austria	–	OL338130	OL338485	OL405212	OL405512	–
KaR932	<i>Entoloma cetratum</i>	Austria	–	OL338132	OL338481	OL405214	OL405513	–
KaR1005	<i>Entoloma hirtipes</i>	Germany	–	OL338139	OL338466	OL405194	OL405514	–
KaR1006	<i>Entoloma hirtipes</i>	Germany	–	OL338140	–	OL338467	OL405195	–
KaR1008	<i>Entoloma ortonii</i>	Germany	–	OL338141	OL338495	OL405221	OL405515	–
KaR1014	<i>Entoloma vindobonense</i>	Germany	–	OL338143	OL338504	OL405229	OL405516	–
KaR1175	<i>Entoloma infula</i>	Germany	–	OL338148	OL338505	OL405231	OL405517	–
KaR1121	<i>Entoloma minutisporum</i>	Croatia	–	OL338153	OL338491	OL405217	OL405518	–
KaR1143	<i>Entoloma assiduum</i>	Cyprus	–	OL338157	OL338499	OL405226	OL405519	–
KaR1144	<i>Entoloma olivaceohebes</i>	Cyprus	–	OL338158	OL338510	OL405236	OL405520	–
KaR1176	<i>Entoloma</i> sp.	Cyprus	–	OL338159	OL338500	OL405227	OL405521	–
KaR1182	<i>Entoloma hirtipes</i>	Cyprus	–	OL338162	OL338468	OL405193	–	
KaR1188	<i>Entoloma illinonae</i>	Cyprus	–	OL338166	OL338497	OL405224	–	
KaR1258	<i>Entoloma kristiansenii</i>	Sweden	–	OL338181	OL338469	OL405196	OL405523	–
KaR1259	<i>Entoloma seiceum</i>	Sweden	–	OL338182	OL338493	OL405219	OL405524	–
KaR1282	<i>Entoloma clandestinum</i>	Sweden	–	MZ611659	OL338523	OL405250	–	

**Table 3** (cont.)

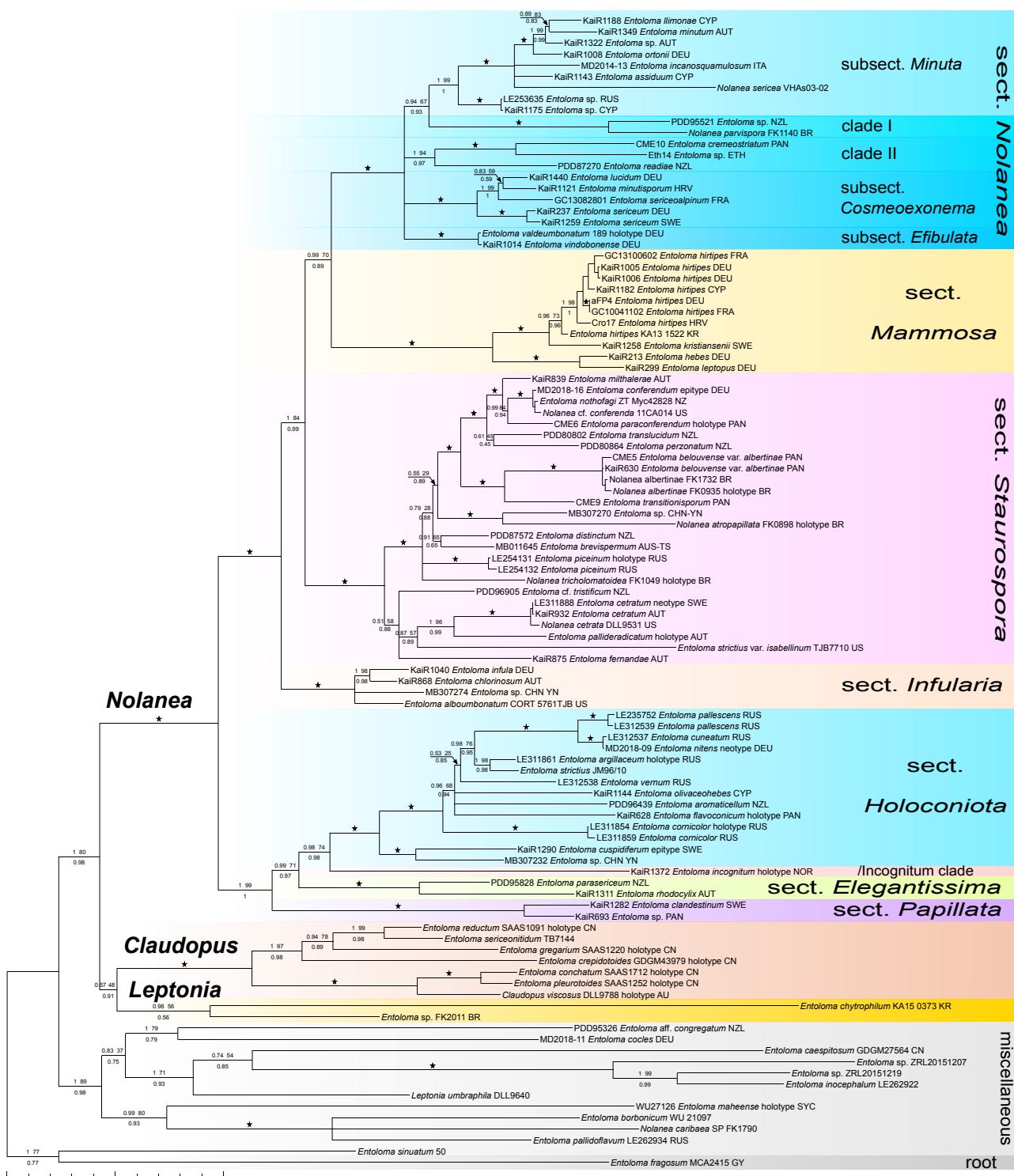
Coll_no	Species (annotation)	origin	note	ITS	LSU	mtSSU	RPB2	TEF1
KaiR1290	<i>Entoloma cuspidiferum</i>	Sweden	epitype	OL338190	OL338522	OL405247	OL405526	-
KaiR1311	<i>Entoloma rhodocylix</i>	Austria	-	OL338192	OL338525	OL405248	OL405527	-
KaiR1322	<i>Entoloma</i> sp.	Austria	-	OL338197	OL338498	OL405222	OL405528	-
KaiR1349	<i>Entoloma minutum</i>	Austria	-	OL338202	OL338496	OL405233	OL405529	-
KaiR1372	<i>Entoloma incognitum</i>	Norway	holotype	OL338204	OL338527	OL405252	OL405530	-
KaiR1440	<i>Entoloma lucidum</i>	Germany	-	OL338216	OL338541	OL338492	OL405218	OL405531
LE235752	<i>Entoloma pallescens</i>	Russia: Western Siberia	-	OL338242	OL338534	OL338512	OL405239	OL405532
LE253635	<i>Entoloma</i> sp.	Russia: European part	-	OL338246	OL338540	OL338501	OL405228	OL405533
LE254131	<i>Entoloma piceinum</i>	Russia: European part	holotypus	KM262035	OL338538	OL338483	OL405205	OL405534
LE254132	<i>Entoloma piceinum</i>	Russia: European part	-	KM262036	OL338539	OL338484	-	OL405535
LE262922	<i>Entoloma inocephalum</i>	Vietnam	-	KC898449	KC898449	MH90035	MH259313	MH190154
LE262934	<i>Entoloma pallidoflavum</i>	Vietnam	-	-	MH190183	MH190155	MH259314	MH190155
LE311854	<i>Entoloma cornicolar</i>	Russia: Far East	holotype	OL338257	OL338535	OL338519	OL405243	OL405536
LE311859	<i>Entoloma cornicolar</i>	Russia: Far East	-	OL338262	OL338536	OL338520	-	OL405540
LE311861	<i>Entoloma argillaceum</i>	Russia: Caucasus	holotype	OL338264	OL338531	OL338516	OL405237	OL405537
LE311888	<i>Entoloma inocephalum</i>	Sweden	neotype	OL338280	-	OL338482	OL405215	OL405538
LE312537	<i>Entoloma cetratum</i>	Russia: Caucasus	-	OL338281	-	OL338514	OL405241	-
LE312538	<i>Entoloma cuneatum</i>	Russia: European part	-	OL338282	OL338537	OL338518	OL405238	OL405539
LE312539	<i>Entoloma vernum</i>	Russia: European part	-	OL338283	OL338533	OL338513	OL405240	OL405541
MB011645	<i>Entoloma palesscens</i>	Russia: European part	-	OL338283	OL338533	OL338513	OL405240	OL405541
MB307232	<i>Entoloma brevispermum</i>	Australia: Tasmania	-	OL338305	-	OL338487	OL405207	OL405542
MB307270	<i>Entoloma</i> sp.	China: Yunnan	-	OL338306	OL338521	OL405245	-	-
MB307274	<i>Entoloma</i> sp.	China: Yunnan	-	OL338308	OL338509	OL405211	-	-
MCA2415	<i>Entoloma fragosum</i>	China: Yunnan	-	OL338309	OL338509	OL338507	OL405233	OL405543
MD2014-13	<i>Entoloma incanosquamulosum</i>	Guyana	holotype	-	KJ021700	KJ021690	KJ021694	MG702622
MD2018-09	<i>Entoloma nitens</i>	Italy	-	OL338320	OL338502	OL338502	OL405225	OL405544
MD2018-11	<i>Entoloma cocles</i>	Germany	neotype	OL338321	OL338515	OL405242	OL405545	-
MD2018-16	<i>Entoloma conferendum</i>	Germany	-	OL338323	OL338530	OL405253	OL405546	-
Meusers_E4565	<i>Entoloma valdeurnbonatum</i>	Germany	epitype	OL338324	OL338480	OL405253	OL405547	-
PDD80802	<i>Entoloma translucidum</i>	New Zealand	holotype	OL338333	GQ289203	GQ289343	GQ289271	-
PDD80864	<i>Entoloma perzonatum</i>	New Zealand	-	OL338377	OL338479	OL405204	OL405548	-
PDD87270	<i>Entoloma readiae</i>	New Zealand	-	OL338379	-	OL338488	OL405210	-
PDD87572	<i>Entoloma distinctum</i>	New Zealand	-	MZ611697	OL338503	OL405230	OL405549	-
PDD95326	<i>Entoloma aff. congregatum</i>	New Zealand	-	OL338386	OL338486	OL405206	-	-
PDD95521	<i>Entoloma</i> sp.	New Zealand	-	OL338391	OL338528	OL405254	OL405550	-
PDD95828	<i>Entoloma parasericeum</i>	New Zealand	-	OL338394	OL338508	OL405234	-	-
PDD96439	<i>Entoloma aromaticellum</i>	New Zealand	-	OL338396	OL338526	OL405249	OL405551	-
PDD96905	<i>Entoloma cf. tristifum</i>	New Zealand	-	OL338402	OL338517	OL405246	OL405552	-
SAAS1091	<i>Entoloma strictum</i>	China	holotype	OL338404	OL338489	OL405213	OL405553	-
SAAS1220	<i>Entoloma gregarium</i>	China	holotype	KU32123	KU32123	KU534232	KU534480	-
SAAS1252	<i>Entoloma pleurotooides</i>	China	holotype	KU32122	KU32122	KU534237	KU534474	-
SAAS1712	<i>Entoloma conchatum</i>	China	holotype	KU32113	KU32113	KU534227	KU534468	-
SP-FK1790	<i>Nolanea caribaea</i>	Brazil	-	KU32111	KU32111	KU534220	KU534459	-
TB7144	<i>Entoloma sericeonitidum</i>	-	-	-	MH190144	MH190144	MH190144	MH190144
TJB7710	<i>Entoloma strictius</i> var. <i>isabellinum</i>	USA	-	EF421108	AF261315	GU384594	EF421087	-
VHA903_2	<i>Nolanea sericea</i>	Austria	holotype	DQ367430	DQ367423	GU384618	GU384641	MG702625
WU189010	<i>Entoloma pallidopradicatum</i>	France: La Réunion	-	-	KU534423	KU534423	DQ367435	DQ367428
WU27126	<i>Entoloma borbonicum</i>	Seychelles	holotype	OL338444	OL338544	MH190098	MH190131	MH190166
ZRL20151207	<i>Entoloma maeneense</i>	China	holotype	LIT16038	KY418854	OL338529	OL405255	OL405563
ZRL20151219	<i>Entoloma</i> sp.	China	-	LIT16035	KY418850	-	KY419057	KY419054
ZT-Myc42828	<i>Entoloma nothofagi</i>	New Zealand	-	MH190203	MH190101	MH190134	MH190134	MH190169

## RESULTS

### PCR primers and sequencing

For this study 470 ITS sequences often including LSU (Table S1), 15 LSU sequences, 70 mtSSU sequences, 66 *RPB2* sequences, and 55 *EF-1 $\alpha$*  sequences were newly sequenced (Table 3). Sequencing of the ITS was most often successful, while the success rate was slightly lower for LSU and mtSSU. Sequencing of *RPB2* was often difficult and not successful for many specimens, while *EF-1 $\alpha$*  was the most difficult locus

to sequence. Sequencing was often successful also with old material. The oldest specimens of which ITS sequences were obtained were the lectotype of *E. minutum*, collected 1879, and the neotype of *E. palescens*, collected 1889. The oldest specimen of which an LSU sequence was obtained was the isotype of *E. vernum*, collected 1933. The oldest specimen of which a mtSSU sequence was obtained was a specimen of *E. hirtipes* (C-F-127082), collected 1977. The oldest specimen for both, *RPB2* and *EF-1 $\alpha$*  was the holotype of *E. maheense*, collected 2001.



**Fig. 2** Bayesian MCMC phylogram of species of *Entoloma* subg. *Nolanea* and outgroup based on concatenated alignments of ITS, mtSSU, *RPB2*, and *EF-1 $\alpha$* . Rooted to *E. sinuatum* and *E. fragosum*. Values above branches, left side = bayesian posterior probability, right side = maximum likelihood bootstrap, below branches = transfer bootstrap expectation. A star denotes maximum support in all calculations. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166. — Scale bar = estimated changes/nucleotide.

**Table 4** K tree score, scale factor, and symmetrical Robinson-Foulds distance of ML-phylogenies of the different molecular loci compared to the ML-phylogeny inferred from all loci.

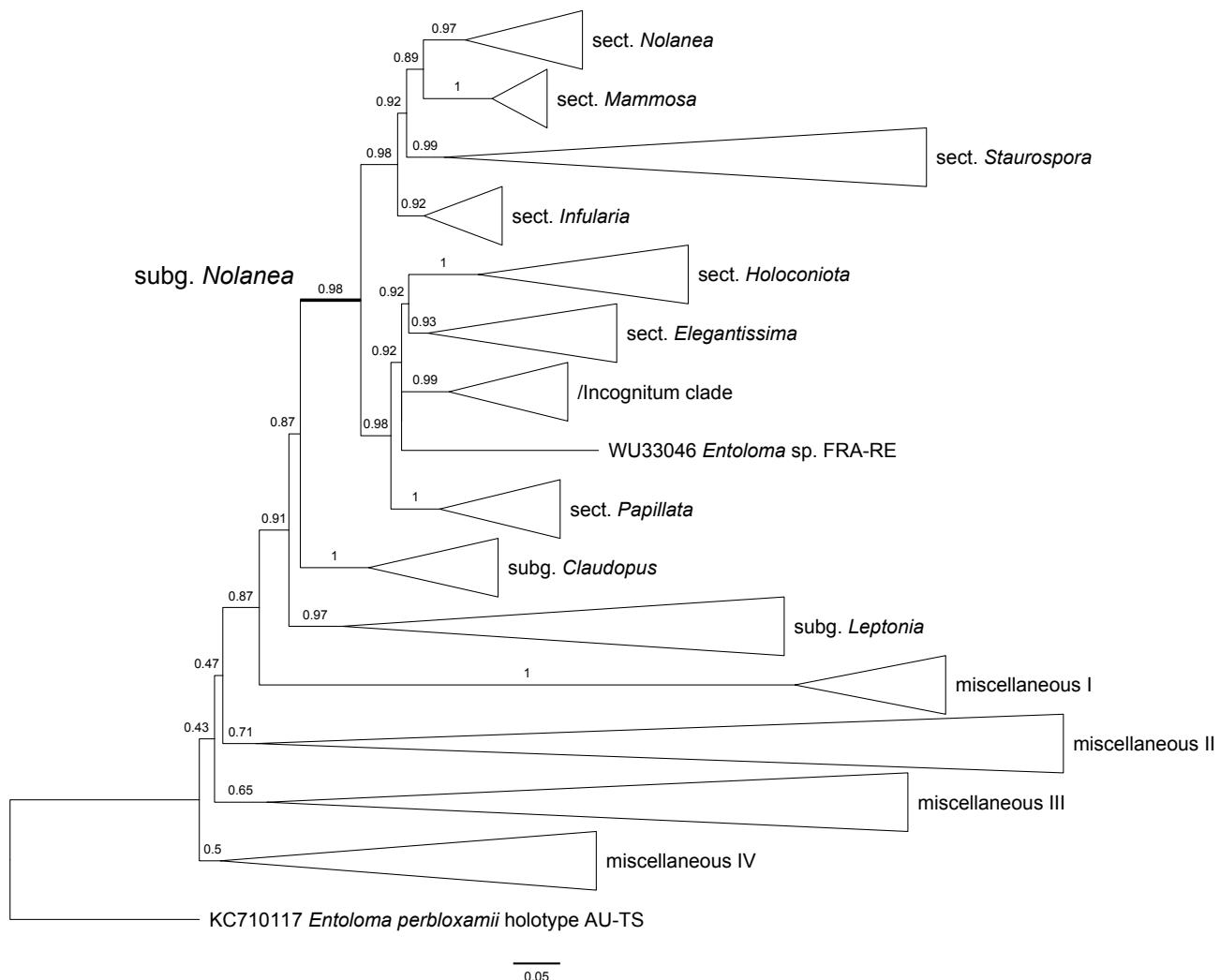
Region	K-score	Scale factor	RF distance
ITS	0.315	0.384	56
LSU	0.391	4.681	80
mtSSU	0.346	2.988	62
<i>RPB2</i>	0.223	1.230	24
<i>TEF1</i>	0.278	0.806	44
ITS+mtSSU+ <i>RPB2</i> + <i>TEF1</i>	0.050	1.026	4

The assembling of ITS and partial LSU sequences revealed often 1–3 mismatches in the target site of the primer ITS4B. Sequences of several specimens which failed with the standard *RPB2* primers could be obtained with the internal primers for *RPB2*, or with a combination of a standard and an internal primer. Virtual analyses revealed mismatches in the established mtSSU primers (Table 2) in the set of species of *Agaricales*, especially U1 with 2–3 mismatches and MS2 with 1–4 mismatches. The primer MS2 had mainly two mismatches, G instead of T at the 4th position and A instead of T at the 12th position, in the sequences of *Entoloma* spp. The assembled sequences obtained with the mainly used primer pair MS0B/MR1.1 were 780–840 nucleotides long. This range also covers the variable domain V6, in addition to the domains V3, V4, and

V5 covered by the standard primers MS1/MS2. The domains V3 and V5 have few differences among *Entoloma* spp., while the domains V4 and V6 are rich in indels.

#### Loci performance in phylogenetic inference

The ML 5-loci tree used as reference tree for the comparison of the regions had 57 tips, including five outgroup taxa, and 111 partitions (Fig. S1). Its topology was similar to that of the larger multi-loci tree (Fig. 2) and well-supported at almost all branches. The 4-loci tree, excluding LSU, was only slightly different. The best performing region was *RPB2* with a K tree score of 0.223 and a RF distance of 24 (Table 4), the scale factor was 1.23, meaning that the evolutionary rate of *RPB2* is somewhat lower than averaged from the five loci. All major clades were resolved and well-supported in the *RPB2* tree like in the reference tree. The next best performing region was *EF-1α*, with a K tree score of 0.278 and a RF distance of 44. However, the outgroup taxa fell in three different lineages in the *EF-1α* tree. The ITS had a medium performance in the comparison, with a K tree score of 0.315 and a RF distance of 56. The scale factor, 0.384, was the lowest of all regions, demonstrating a high evolutionary rate. One of the outgroup taxa was included within *Nolanea* in the ITS tree, apart from this all major clades were resolved, however, not with the same backbone topology like in the reference tree. The mtSSU had a K tree distance of 0.346 and a RF distance of 62. The sequence of *E. incognitum* nested in the outgroup, while apart from this the major clades



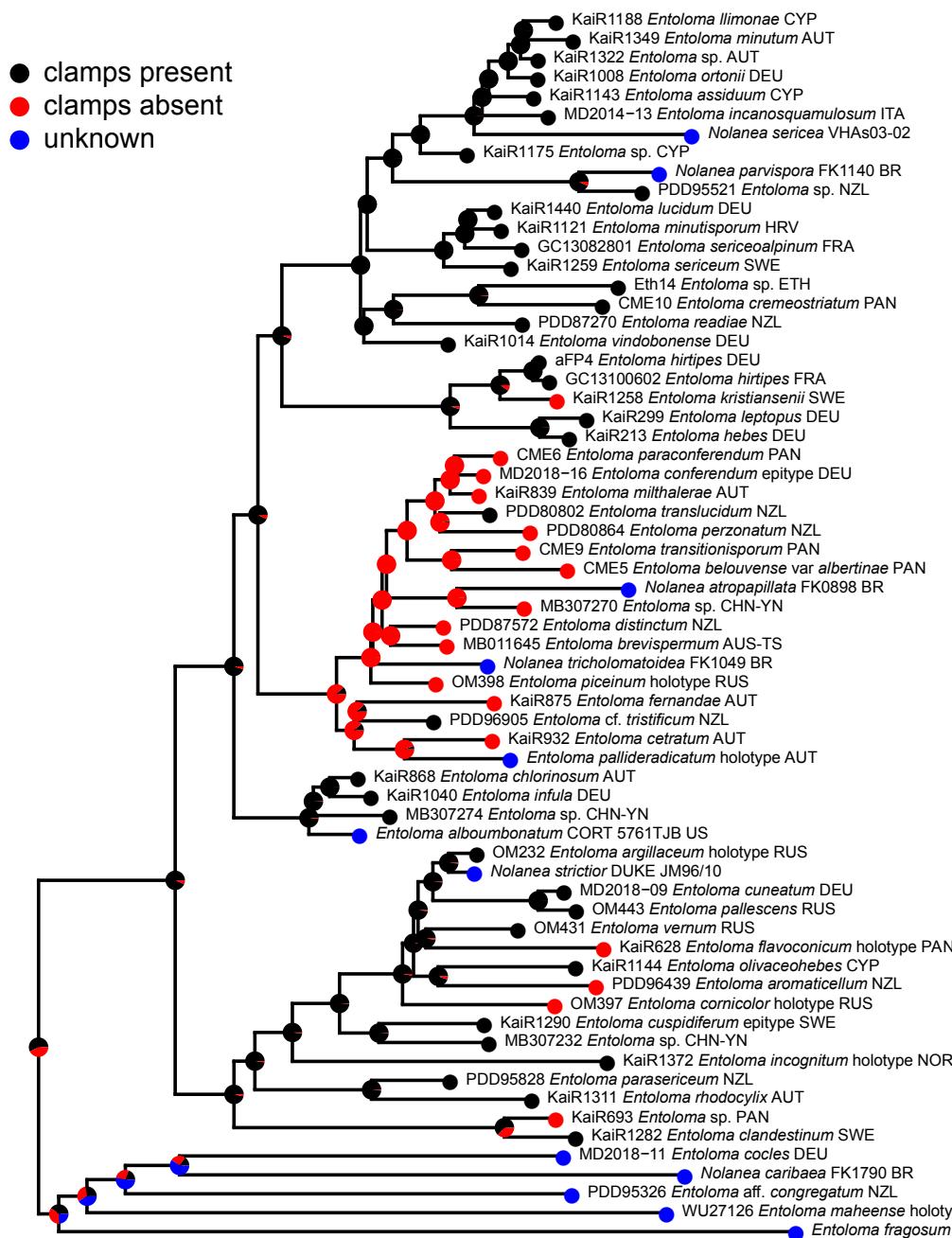
**Fig. 3** Overview of the ITS phylogram of species of *Entoloma* subg. *Nolanea*, including species of the subgenera *Claudopus* and *Leptonia*, as well as miscellaneous nolaneoid and outgroup taxa, rooted to *Entoloma perbioxamii*. Collapsed to the main clades, including the sections of subg. *Nolanea*. TBE values above or below branches. — Scale bar = estimated changes/nucleotide.

were resolved and well-supported in the mtSSU tree. The LSU had with a K tree score of 0.391 and a RF distance of 80 the worst performance. In addition, it had the highest scale factor, 4.681, demonstrating a low evolutionary rate. The outgroup was complete in the LSU tree, while the major clades were not resolved, the support values were generally low, and the sequences of several species were indifferent.

#### Phylogenetic limits of subgenus Nolanea

The subg. *Nolanea* forms a monophyletic clade with strong support in the multi-gene and the ITS phylogeny (Fig. 2, 3). It is sister to a clade of the subgenera *Claudopus* and *Leptonia*, in the multi-locus tree, while in the ITS tree it forms a clade together with subg. *Claudopus* which is sister to subg. *Leptonia*. The ITS phylogeny includes 150 lineages potentially at species level (Fig. S2). With certainty about the correct application of names, 87 species represented by DNA sequences are recognised within *Nolanea* (see synopsis). Most of them

were also previously considered to belong to the subgenus. In addition, some species previously placed in other subgenera are included, viz., *Entoloma albotomentosum* and *E. rhodocylix*, formerly placed in subg. *Claudopus*, *E. cephalotrichum*, formerly placed in subg. *Alboleptonia*, as well as *E. pallideradicatum* and *E. vindobonense* formerly placed in subg. *Entoloma*. *Entoloma conferendum*, which was sometimes treated within *Nolanea* (Largent & Thiers 1972, Noordeloos 1980) but later placed in subg. *Inocephalus* (Noordeloos 2004), is also included. On the contrary, several species and clades fall out of the subgenus: *Entoloma ameoides*, *E. calobrunneum*, *E. pleopodium*, and *E. sanvitalese* are included in subg. *Leptonia*. *Entoloma sericeonitens* belongs to subg. *Trichopilus* and is a synonym of *E. fuscotomentosum*. *Entoloma californicum*, *E. lepiotoides*, *E. rhombisporum*, and *E. sublegans* together with *E. velenovskyi* form long-branched lineages and cannot be assigned to an existing subgenus.



**Fig. 4** Ancestral character state reconstruction of absence/presence of clamp connections in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166.

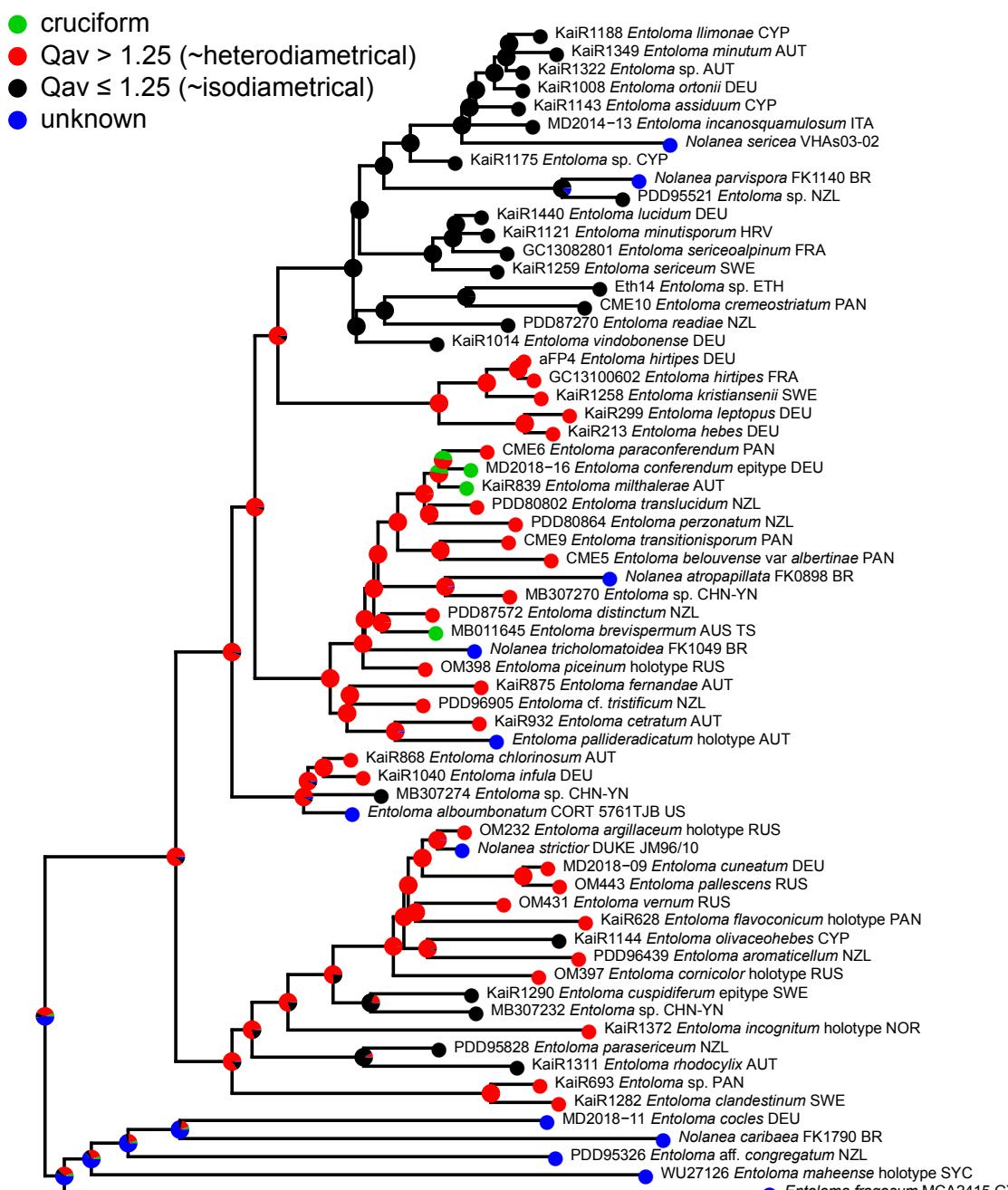
### Congruence of phylogeny and morphological characters

The ancestral character state estimations indicate that the common ancestor of species in *Nolanea* had clamp connections, heterodiametrical basidiospores, and incrusting pigment in the pileipellis with a likelihood of 93.7, 86.5, and 86.3 %, respectively. The presence/absence of clamp connections is relatively uniform within the major clades, however, some exceptions exist in both directions: clampless species in clades with in majority clamped species, and clamped species in clades with in majority clampless species (Fig. 4). Few exceptions also exist for the basidospore length/width quotient (Q) smaller or larger than 1.25. Several species of the sect. *Holoconiota* tend to have broadly heterodiametrical to subisodiametrical basidiospores, which have an average Q of 1.25 or slightly below, while in general the species in this section have heterodiametrical basidiospores. Cruciform basidiospores likely derived at least

two times from heterodiametrical spores in sect. *Staurosphaera* (Fig. 5). A pileipellis with mainly incrusting pigment is a still dominant plesiomorphic character state in subg. *Nolanea*. The sections *Nolanea* and *Elegantissima* have exclusively incrusting pigment as dominant pigment, while the pigment type varies in the other sections. With a likelihood of 57.5 % the ancestor of species of sect. *Staurosphaera* had both pigment types and species with exclusively intracellular or incrusting pigment derived from it (Fig. 6).

### Biogeographic aspects

Based on the phylogenetic analyses, species of subg. *Nolanea* occur in all continents. Most of the specimens corresponding to the sequences in the phylogeny were collected in Mediterranean, temperate to boreal habitats. Specimens from the tropics were mainly collected in montane habitats with Mediterranean to temperate floral elements, e.g., the specimens from Panama,



**Fig. 5** Ancestral character state reconstruction of basidiospore shape in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166.

which were collected in altitudes between 1500–2500 m a.s.l. in *Quercus* dominated forests (Reschke et al. 2022), and the specimens from Ethiopia, which were collected in the Kafa Biosphere Reserve between 1600–3200 m a.s.l. The species described by Karstedt et al. (2020) from Brazil were mainly collected south of the tropical belt, often in montane habitats. The specimens of *E. bisterigmatum* and *E. brunneoloaurantiacum*, described by Largent et al. (2019) from Cameroon, were collected at 650 m a.s.l. and represent the tropical collections at the lowest altitude known so far. Few specimens and sequences from Africa were available for this study. Unfortunately, no *Nolanea* species could be found during two three-week fieldtrips in Benin, West Africa by KR.

The species of the three subsections *Cosmeoexonema*, *Minuta*, and *Efibulata* in section *Nolanea* are restricted to the Northern Hemisphere, with the exemption of *E. sericeum*, which is also known from New Zealand, where it is possibly an introduced species (Horak 2008). Clade I in sect. *Nolanea* contains species

from the Southern Hemisphere, Southeast Asia, and France, whereas clade II contains species from Australasia, the tropics, and China. Species of the sect. *Mammosa* are only known from the Northern Hemisphere. The large and diverse sect. *Staurospora* contains species from all over the world, with a high and still incompletely investigated diversity in Australasia. Species of sect. *Infularia* are known from the Northern Hemisphere, the southernmost record is a potentially undescribed species from Panama. Section *Holoconiota* contains species from all over the world. Section *Elegantissima* (described below) contains one species known from Europe, *E. rhodoclylix*, while the other species are only known from Australasia. The / *Incognitum* clade contains only one known species, *E. incognitum* (described below), the other sequences in this clade were obtained from GenBank and are derived from material of North America. Species of sect. *Papillata* are only known from the Northern Hemisphere, the southernmost record is a potentially undescribed species from Panama.

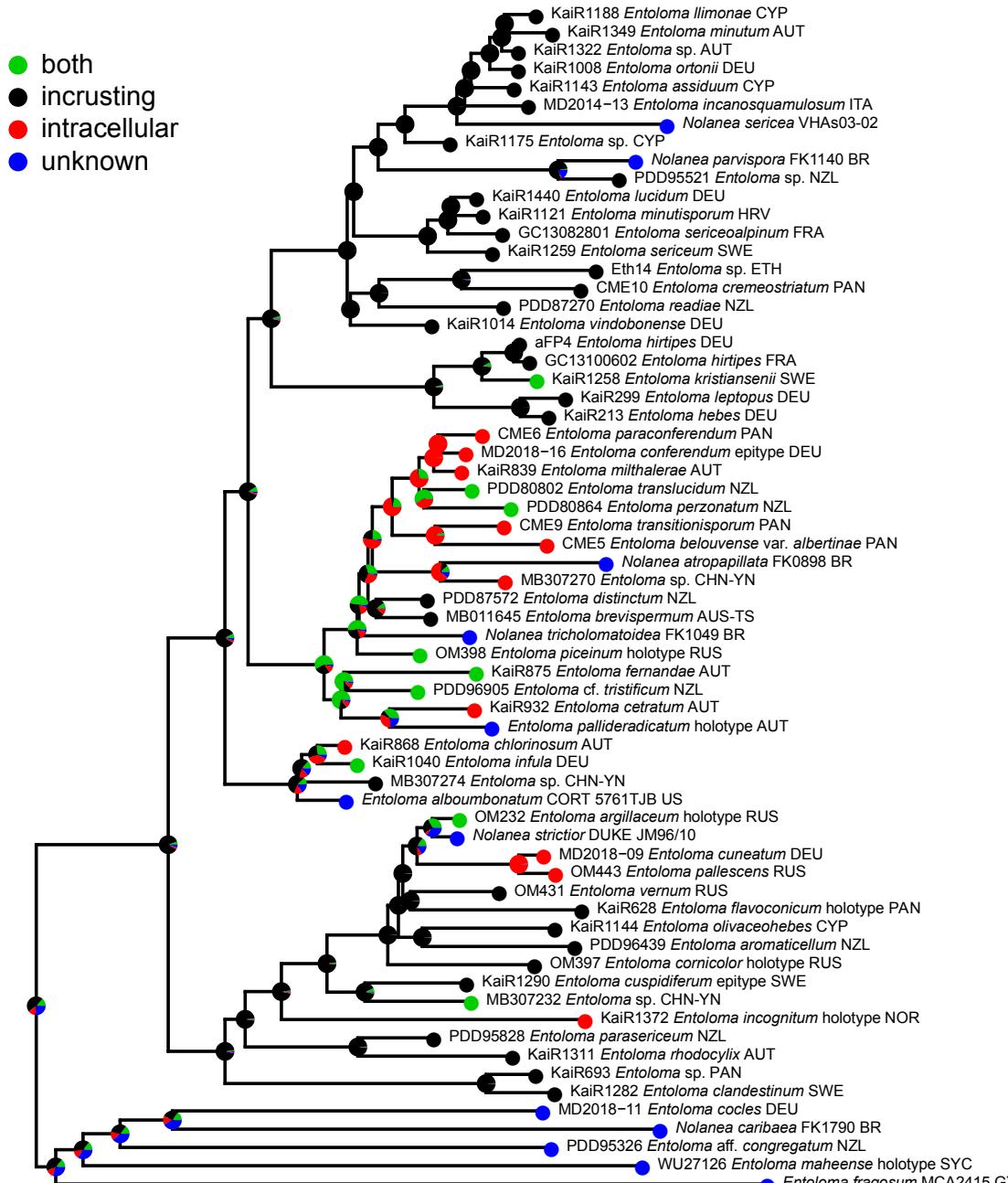


Fig. 6 Ancestral character state reconstruction of pigmentation type in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166.

**Table 5** Names of *Nolanea* species with priority and their synonyms.

Prior name	Synonym	Further synonym	Further synonym	Further synonym
<i>Entoloma belouvense</i> *	<i>Nolanea albertinae</i> * <sup>(1)</sup>			
<i>Entoloma cetratum</i> *	<i>Entoloma farinogustus</i>			
<i>Entoloma clandestinum</i> *	<i>Entoloma depressum</i> *	<i>Entoloma kerocarpus</i> *	<i>Entoloma papillatum</i>	
<i>Entoloma conicum</i>	<i>Entoloma alboumbonatum</i> *			
<i>Entoloma cuneatum</i> *	<i>Entoloma lanuginosipes</i>	<i>Entoloma nitens</i> *	<i>Entoloma testaceum</i> var. <i>bavaricum</i> *	
<i>Entoloma elegantissimum</i> *	<i>Entoloma orichalceum</i> *			
<i>Entoloma fernandae</i>	<i>Entoloma argentostriatum</i> *	<i>Entoloma defibulatum</i>	<i>Entoloma fractum</i> *	<i>Entoloma xanthocaulon</i> *
<i>Entoloma hirtipes</i>	<i>Entoloma kuehnerianum</i>	<i>Entoloma magnitudinis</i> *		
<i>Entoloma incanosquamulosum</i> *	<i>Entoloma brunneosericeum</i> *			
<i>Entoloma leptopus</i>	<i>Entoloma kitsii</i> *			
<i>Entoloma leuconitens</i> *	<i>Entoloma pseudofavrei</i> *			
<i>Entoloma lucidum</i> *	<i>Entoloma conicosericeum</i> *			
<i>Entoloma minutum</i> *	<i>Entoloma juncinum</i>			
<i>Entoloma ortonii</i> *	<i>Entoloma cinereopacum</i> *	<i>Entoloma terreum</i> *		
<i>Entoloma rhodocylix</i> *	<i>Entoloma reginae</i> *			
<i>Entoloma sericeum</i> *	<i>Entoloma cryptocystidiatum</i> *	<i>Entoloma fusciceps</i> *	<i>Entoloma occultipigmentatum</i> *	
<i>Entoloma translucidum</i> *	<i>Entoloma pluteimorphum</i> *			
<i>Entoloma ventricosum</i>	<i>Entoloma calthionis</i> *	<i>Entoloma langei</i> *		
<i>Entoloma vindobonense</i> *	<i>Entoloma valdeumbonatum</i> *			

\* type specimen sequenced.

(1) *Nolanea albertinae* is included as variety: *Entoloma belouvense* var. *albertinae*.**TAXONOMIC PART****Synopsis of the sequenced species of subgenus Nolanea**

Taxa with superscript N<sup>(N)</sup> are newly described or combined below. An overview of synonyms based on ITS sequences is given in Table 5.

<i>Entoloma</i> subg. <i>Nolanea</i>	<i>Entoloma</i> sect. <i>Staurospora</i>	<i>Entoloma</i> conicum
<i>Entoloma</i> sect. <i>Nolanea</i> <sup>(N)</sup>	<i>Entoloma</i> acidophilum	<i>Entoloma</i> infula
<i>Entoloma</i> subsect. <i>Cosmeoexonema</i>	<i>Entoloma</i> atropapillatum	<i>Entoloma</i> sect. <i>Holoconiota</i> <sup>(N)</sup>
<i>Entoloma</i> lucidum	<i>Entoloma</i> belouvense	<i>Entoloma</i> albomentosum
<i>Entoloma</i> minutisporum	<i>Entoloma</i> bisterigatum	<i>Entoloma</i> argillaceum <sup>(N)</sup>
<i>Entoloma</i> sericeoalpinum	<i>Entoloma</i> brunneoloaurantiacum	<i>Entoloma</i> aromaticellum
<i>Entoloma</i> sericeum	<i>Entoloma</i> cephalotrichum	<i>Entoloma</i> aromaticum
<i>Entoloma</i> subsect. <i>Minuta</i>	<i>Entoloma</i> cetratum	<i>Entoloma</i> atlanticum
<i>Entoloma</i> altaicum <sup>(N)</sup>	<i>Entoloma</i> chrysopus	<i>Entoloma</i> cornicolor <sup>(N)</sup>
<i>Entoloma</i> anodinum	<i>Entoloma</i> conferendum	<i>Entoloma</i> cuneatum
<i>Entoloma</i> assiduum	<i>Entoloma</i> confusum	<i>Entoloma</i> cuspidiferum <sup>(N)</sup>
<i>Entoloma</i> fuligineocinereum	<i>Entoloma</i> cucurbita	<i>Entoloma</i> flavoconicum
<i>Entoloma</i> incanosquamulosum	<i>Entoloma</i> cuniculorum	<i>Entoloma</i> holoconiota
<i>Entoloma</i> llimonae	<i>Entoloma</i> distinctum	<i>Entoloma</i> olivaceohebes
<i>Entoloma</i> luteodiscum	<i>Entoloma</i> fernandae	<i>Entoloma</i> pallescens
<i>Entoloma</i> minutum	<i>Entoloma</i> fibrosopileatum	<i>Entoloma</i> subcapitatum
<i>Entoloma</i> ortonii	<i>Entoloma</i> globuliferum	<i>Entoloma</i> subviolaceovernum
<i>Entoloma</i> pygmaeopapillatum	<i>Entoloma</i> lushanense	<i>Entoloma</i> ventricosum
<i>Entoloma</i> subsect. <i>Efibulata</i> <sup>(N)</sup>	<i>Entoloma</i> luteofuscum	<i>Entoloma</i> vernum
<i>Entoloma</i> edulis	<i>Entoloma</i> maldea	<i>Entoloma</i> sect. <i>Elegantissima</i> <sup>(N)</sup>
<i>Entoloma</i> vindobonense	<i>Entoloma</i> melleum	<i>Entoloma</i> austrorhodocalyx
Incertae sedis (at subsection level)	<i>Entoloma</i> milthalerae	<i>Entoloma</i> elegantissimum
<i>Entoloma</i> cremeostriatum	<i>Entoloma</i> obscuratum	<i>Entoloma</i> grave
<i>Entoloma</i> karstedtii	<i>Entoloma</i> pallideradicatum	<i>Entoloma</i> parasericeum
<i>Entoloma</i> readiae	<i>Entoloma</i> pallidosalmoneum	<i>Entoloma</i> rhodocylix
<i>Entoloma</i> tortiliforme	<i>Entoloma</i> paraconferendum	<i>Entoloma</i> sulphureum
<i>Entoloma</i> sect. <i>Mammosa</i>	<i>Entoloma</i> perzonatum	<i>Entoloma</i> sect. <i>Papillata</i>
<i>Entoloma</i> fuscohebes	<i>Entoloma</i> piceinum	<i>Entoloma</i> brunneoplannatum
<i>Entoloma</i> hebes	<i>Entoloma</i> transitionisporum	<i>Entoloma</i> clandestinum
<i>Entoloma</i> hirtipes	<i>Entoloma</i> translucidum	<i>Entoloma</i> malenconii
<i>Entoloma</i> kristiansenii	<i>Entoloma</i> tricholomatoideum	Incertae sedis (at section level)
<i>Entoloma</i> leptopus	<i>Entoloma</i> sect. <i>Infularia</i> <sup>(N)</sup>	<i>Entoloma</i> incognitum <sup>(N)</sup>
<i>Entoloma</i> leuconitens	<i>Entoloma</i> calabrum	
<i>Entoloma</i> psammophilohebes	<i>Entoloma</i> chlorinosum	

**Entoloma subg. Nolanea** (Fr.) Noordel., Persoonia 10(4): 431. 1980

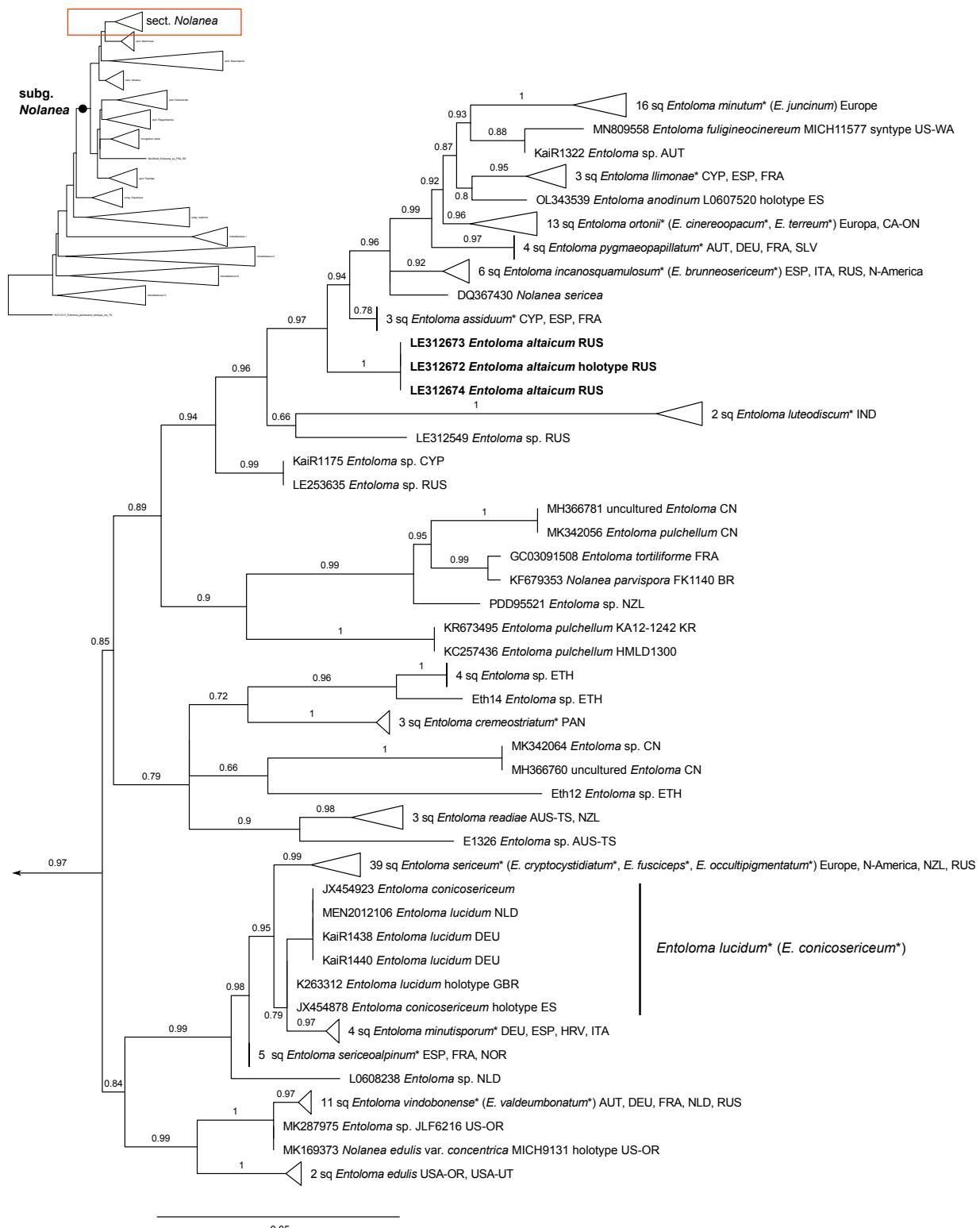
**Obligate synonyms.** *Agaricus* tribus *Nolanea* Fr., Syst. Mycol. 1: 10. 1821. — *Agaricus* subg. *Nolanea* (Fr.) Loudon, Encl. Pl.: 998. 1829. — *Nolanea* (Fr.) P. Kumm., Führer Pilzk.: 24. 1871. — Type species: *Entoloma pascuum* (Pers.) Donk (≡ *E. sericeum* Quél.).

**Basidiocarps** mainly mycenoid, rarely tricholomatoid or collybioid, exceptionally omphalinoid or pleurotoid. **Pileus** conical, convex to applanate with a papilla or umbo, rarely depressed or umbilicate, surface predominantly smooth, sometimes with some loose fibrils or minutely squamulose towards the centre, rarely with an ephemeral loosely pruinose cover in young basidio-

carps, yellowish orange, pale to dark brown, rarely with violet or olivaceous tones, rarely white, often translucently striate, at least at the margin, usually hygrophanous, except for the white species. Lamellae mainly adnexed, sometimes emarginate, rarely adnate to decurrent, predominantly ventricose, rarely segmentiform to subarcuate, initially whitish, greyish, or brown, becoming pink to greyish brown or rather dark brown. Stipe slender, mostly  $\leq 5$  mm broad, rarely broader, up to 10 mm, surface smooth, innately fibrillose to silvery-whitish fibrillose, or fibrillose striate. Odour often farinaceous or indis-

tinct, sometimes raphanoid, nitrous, sweetish aromatic, or like *Macrocystidia cucumis* when fresh and then becoming fishy. Taste farinaceous to rancid or rather indistinct.

*Basidiospores* iso-, subiso- to heterodiametrical, rarely cruciform, predominantly with 5–7 angles in outlines, rarely with 4 angles, but never truly cuboid. *Lamellar edge* predominantly fertile, sometimes sterile with abundant cheilocystidia, sometimes heterogeneous, then cheilocystidia scattered between the basidia, variably shaped, generally not well differentiated, cylindrical, subcapitate to somewhat tibiiform or sublageniform,



**Fig. 7** Partial maximum likelihood phylogram based on ITS of species of the section *Nolanea*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

and then often inconsistent within a species. *Hymenophoral trama* regular, composed of rather long subcylindrical to somewhat fusiform cells, often  $> 350 \mu\text{m}$  and in average  $> 150 \mu\text{m}$  long. *Pileipellis a cutis*, sometimes with loose and ascending hyphae or transitions to a trichoderm, composed of relatively narrow cells in the upper part, between 3–8  $\mu\text{m}$  broad, gradually passing into the pileitrama or with distinct subpellis of inflated cylindrical, fusiform to ellipsoid cells. *Pileitrama* similar to hymenophoral trama. *Pigment* dominantly present in the pileipellis, incrusting, intracellular, or a mix of both, in species with incrusting pigment frequently with some additional, but inconsistent intracellular pigment. *Clamp connections* present or absent, if present then predominantly at the base of basidia and sometimes in the subhymenium, rarely in other parts of the basidiocarp.

**Notes** — The type species of subg. *Nolanea* is *E. pascuum*, selected by Clements & Shear (1931). The subsequent selections of other type species, *E. hirtipes* by Largent (1974) and *Rhodophyllus mammosus* by Romagnesi (1974a), are nomenclaturally ineffective (Art. 10.5). *Entoloma pascuum* is here treated as a homotypic synonym of *E. sericeum* (see notes to *E. sericeum*). Detailed records of synonyms of subgenus and included species were published by Noordeloos (1980).

Species of *Nolanea* can be delimited from those of the /Rhomobisporum clade by the rhomboid basidiospores and distinct, lageniform cheilocystidia of the latter (Noordeloos et al. 2022a). Species of sect. *Cubospora* are different by their truly cuboid basidiospores (Karstedt et al. 2019). The species of the clade around *E. ameides* belong to subg. *Leptonia* (Vidal et al. 2016) and can be delimited by their sweetish odour in the Northern Hemisphere. Species of *Nolanea* s.str. with such odour exist in the Southern Hemisphere, however, no species of the /Ameides clade are known from there.

#### *Entoloma* sect. *Nolanea* (Largent & Thiers) Reschke & Noordel., comb. nov. — MycoBank MB 842252; Fig. 2, 7

**Basionym.** *Nolanea* sect. *Nolanea*, autonym in Largent & Thiers, Northw. Sci. 46: 34. 1972. — Type species: *Entoloma pascuum* (Pers.) Donk ( $\equiv E. sericeum$  Quél.).

**Obligate synonyms.** *Entoloma* sect. *Cosmeoexonema* (Largent & Thiers) Noordel., Persoonia 11(2): 141. 1981. — *Nolanea* sect. *Cosmeoexonema* Largent & Thiers, Northw. Sci. 46: 35. 1972. — Type species: *Entoloma sericeum* Quél.

**Heterotypic synonym.** *Rhodophyllus* sect. *Minuti* Romagn., Bull. Mens. Soc. Linn. Lyon 43(9): 331. 1974. — Type species: *Entoloma minutum* (P. Karst.) Noordel.

**Notes** — *Nolanea* sect. *Cosmeoexonema* and the unmentioned autonym *Nolanea* sect. *Nolanea* were simultaneously published by Largent & Thiers (1972). Combined into the genus *Entoloma* the autonym has priority over the homotypic synonym following Art. 11.6. Section *Nolanea* (Fig. 2, 7) is rather well defined, including almost exclusively species with clamp connections at basidia, mainly iso- to subisodiametrical basidiospores, but at least with an average  $Q < 1.25$ , and incrusting pigment at least in the pileipellis. A subpellis is rather weakly developed but sometimes distinct as a thin layer of relatively short, inflated cylindrical cells. Cheilocystidia are rarely present and then inconsistent and without taxonomic value. Many species in this section have a farinaceous odour and taste. Several species are morphologically similar, but different in their habitat preferences.

#### *Entoloma* subsect. *Cosmeoexonema* (Largent & Thiers) Noordel., Persoonia 10(4): 472. 1980

**Basionym.** *Nolanea* subsect. *Cosmeoexonema* Largent & Thiers, Northw. Sci. 46: 35. 1972. — Type species: *Entoloma sericeum* Quél.

**Notes** — This subsection is here restricted to the well supported clade of *E. sericeum* and the closely related *E. lucidum*, *E. minutisporum*, and *E. sericeoalpinum* (Fig. 7). These species have relatively robust basidiocarps, a rather broad, fibrillose stipe, basidiospores with rather pronounced angles, and a distinct farinaceous odour and taste.

#### *Entoloma* *sericeum* Quél., Mém. Soc. Émul. Montbéliard, Sér. 2, 5: 119. 1872

**Obligate synonyms.** *Entoloma* *pascuum* (Pers.) Donk, Bull. Bot. Gard. Buitenzorg, Ser. III, 18: 158. 1949. — *Agaricus* *pascuus* Pers., Comm. Schaeff. Icon. Pict.: 94. 1800, nom. sanct. Fr., Syst. Mycol. 1: 205. 1821.

**Heterotypic synonyms.** *Entoloma* *cryptocystidiatum* Arnolds & Noordel., Persoonia 10(2): 287. 1979. — *Entoloma* *fusciceps* (Kauffman) Noordel. & Co-David, in Co-David, Langeveld & Noordeloos, Persoonia 23: 168. 2009. — *Entoloma* *occultipigmentatum* Arnolds & Noordel. (as 'occultipigmentatum'), Persoonia 10(2): 292. 1979.

**Notes** — *Entoloma sericeum* is a well-known and widely distributed species. It also includes specimens with parietal pigment or cheilocystidia, described as *E. occultipigmentatum* and *E. cryptocystidiatum*. Another probable synonym is *E. tibiocystidiatum*, which is, however, not formally included here, as sequencing of authentical material failed. Such aberrant specimens are, however, rare. Tackling the identity of *E. pascuum*, it became clear that the only plausible candidate for a lectotype is the plate 413, f. 2 in Bulliard (1789) which serves also as lectotype of *E. sericeum*. Therefore, a proposal to conserve the name *E. sericeum* against the name *A. pascuus* was submitted to avoid an unfortunate name change (Reschke & Noordeloos 2022).

#### *Entoloma* *lucidum* (P.D. Orton) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 206. 1978

**Basionym.** *Nolanea* *lucida* P.D. Orton, Trans. Brit. Mycol. Soc. 43(2): 331. 1960.

**Heterotypic synonym.** *Entoloma* *conicosericum* Vila, F. Caball. & Eyssart., Fungi non Delineati 66: 21. 2013.

**Notes** — *Entoloma lucidum* was described from Britain as a species similar to *E. sericeum*, but with darker and initially conical pileus, which becomes strongly lustrous on drying (Orton 1960). The description of *E. conicosericum* fits well in this definition and is supported with similar ITS.

#### *Entoloma* subsect. *Minuta* (Romagn.) Noordel., Persoonia 10(4): 468. 1980

**Type species.** *Entoloma minutum* (P. Karst.) Noordel.

**Heterotypic synonym.** *Nolanea* subsect. *Bipigmentea* Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 248. 1994. — Type species: *Entoloma propinquum* Noordel. & Co-David ( $\equiv Nolanea$  *proxima* Largent).

**Misapp.** *Nolanea* subsect. *Fibulatae* Largent, Mycologia 66: 1008. 1974. — Type species: *Agaricus junceus* Fr.

**Notes** — Species of this subsection (Fig. 7) have generally less robust basidiocarps than those of subsect. *Cosmeoexonema*. Most species have a relatively narrow and often smooth or only moderately fibrillose stipe, however, the stipe surface can be variable or become fibrillose in old basidiocarps and species with a relatively fibrillose stipe surface exist. The basidiospores often have rather rounded angles. Several species frequently form basidiocarps with depressed pileus, for example *E. minutum*, *E. ortonii*, and *E. limonae*. Odour of the basidiocarps ranges from indistinct, raphanoid, spermatical, to farinaceous. The subsect. *Bipigmentea* is treated as a synonym here, as the type species, *E. propinquum*, is close or possibly identical to *E. minutum* considering its description.

***Entoloma minutum* (P. Karst.) Noordel., Persoonia 10(2): 248.**

1979

**Basionym.** *Nolanea minuta* P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 5: 24. 1879. — Lectotype (designated here): FINLAND, South Häme, Tammela, Mustiala, 22 Aug. 1878, P.A. Karsten 3755 (H6044678). — MycoBank MBT 10004732.

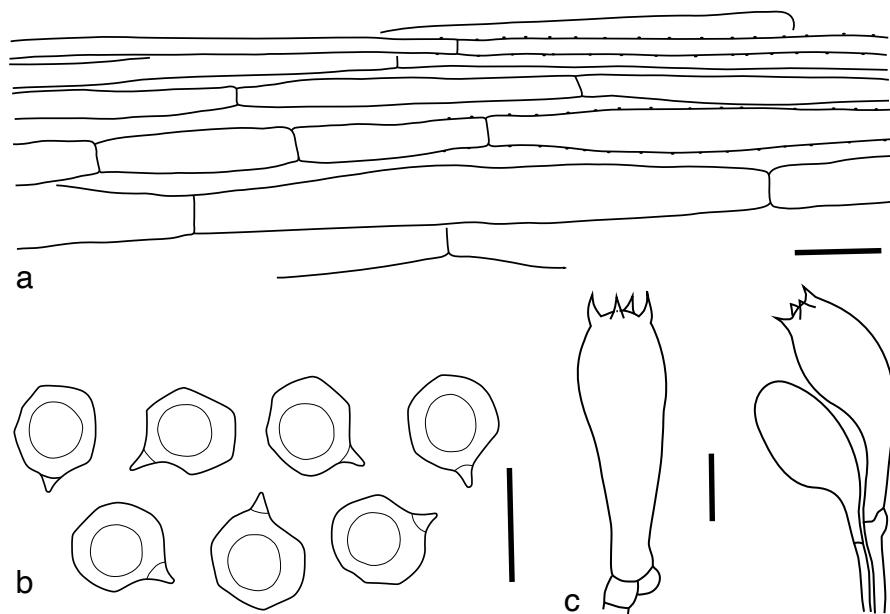
**Heterotypic synonyms.** *Entoloma juncinum* (Kühner & Romagn.) Noordel., Persoonia 10(2): 255. 1979. — *Rhodophyllus juncinus* Kühner & Romagn., Rev. Mycol. (Paris) 19(1): 5. 1954.

**Notes** — Karsten (1879) did not designate a type for *E. minutum* nor refer to a single specimen on which the description was based. However, a specimen of *E. minutum* marked ‘type’

was found in the material of Karsten and is selected here as lectotype. *Entoloma minutum* is a common species in North-western and Central Europe in moist deciduous forests (*Fagus*, *Quercus*, *Betula*, *Alnus*), often on black, nutrient-rich, humose soil. It is often known under the name *E. juncinum*, which is included as synonym here. The designation of an epitype for *E. juncinum* by Vila et al. (2013) was, however, ineffective (Art. 9.9). It was previously thought that this species occurs also in grassland, however, this is not confirmed here. The picture 99 in Noordeloos (2004) supposed to present such a specimen rather depicts *E. sericeum*.



**Fig. 8** Basidiocarps of *Entoloma* spp. a. *Entoloma altaicum* (LE312672, holotype), inset depicting the minutely wrinkled pileal surface; b. *Entoloma hebes* (GC96092300, epitype); c. original plate including *Agaricus conferendum* (26a, lectotype); d. *Entoloma conferendum* (MD2018-16, epitype); e. *Entoloma millicherae* (KaiR839). — c. Drawing by M. Britzelmayr. — Photos by: a. O. Morozova; b. G. Corriol; d. M. Dondl; e. K. Reschke.



**Fig. 9** Microscopic structures of *Entoloma altaicum* (LE312672, holotype) a. Pileipellis, incrusting pigment only partially indicated; b. basidiospores; c. basidia. — Scale bars: a = 20 µm; b–c = 10 µm.

***Entoloma altaicum* O.V. Morozova, Reschke, Noordel. & Ageev, sp. nov.** — MycoBank MB 842253; Fig. 8a, 9

**Etymology.** Refers to the Altay Mountain range in Asia, region of the type locality of the species.

**Holotype.** RUSSIA, Altay Republic, Altaiskiy Nature Reserve, cordon Chelyush, ± 500 m a.s.l., N51.411907° E87.796356°, on soil in grassland near farm, 28 Aug. 2018, O. Morozova (LE 312672).

**Basidiocarps** mycenoid to somewhat collybioid. **Pileus** 15–35 mm diam, broadly conical or hemispherical, becoming convex, then appanate to depressed with small papilla, with initially involute then straight margin, reddish brown, sepia or greyish brown, paler towards margin, with sharply delimited dark centre, pallescent on drying, pileal surface glabrous, minutely wrinkled with lustrous shine, when moist translucently striate almost up to the centre, hygrophanous. **Context** thin, concolorous with the surface or paler. **Lamellae** adnate to emarginate, with decurrent tooth, ventricose, moderately distant, initially whitish to beige, becoming pinkish, with entire concolorous edge and often somewhat transvenose sides. **Stipe** 40–80 × 1.5–3.0 mm, cylindrical or slightly broadened near the base, solid then fistulose, pale brown, grey-brown or yellowish brown, usually paler than pileus, pruinose at apex, downwards slightly to distinctly silvery fibrillose. **Basal mycelium** white, tomentose. **Odour** indistinct, taste not tested.

**Basidiospores** 7.5–8.1–8.5 × 6.5–7.1–8.0 µm, Q = 1.05–1.14–1.25 (–1.30) (n = 63 spores of 3 specimens), isodiametrical to subisodiametrical, with 5–7 angles in outlines. **Basidia** 30–46 × 11–13 µm, clavate, 4-spored, clamped. **Lamellar edge** fertile. **Hymenial cystidia** absent. **Pileipellis** a cutis of thin cylindrical or slightly fusiform hyphae, 2–5 µm wide, with sometimes ascending clavate terminal elements, subpellis weakly differentiated, sometimes with rather short, somewhat inflated cells. **Hyphae of pileitrama** cylindrical to fusiform, up to 10–15 µm wide. **Pigment** incrusting and in addition often weakly intracellular, yellowish in KOH. **Stipitipellis** a cutis of cylindrical hyphae, 5–7 µm wide, with pale intracellular pigment. **Caulocystidia** mostly present at the upper part of the stipe, 21–34 × 7–14 µm, clavate to cylindrical, caulobasidia sometimes also present. **Clamps** abundant in the hymenium, present but rather rare elsewhere.

**Habitat** — In small groups and solitary on soil in grasslands and a rocky river bank.

**Additional specimens examined.** RUSSIA, Altay Republic, Altaiskiy Nature Reserve, cordon Chelyush, ± 500 m a.s.l., N51.411907° E87.796356°, on soil in grassland near farm, 28 Aug. 2018, O. Morozova (LE 312673); Altay Republic, Chemalinskiy District, vicinities of Tolgojek Village, 440 m a.s.l., N51.229126° E86.085518°, on soil in the rocky bank of the Katun River, 03 Sept. 2019, D. Ageev (LE 312674).

**Notes** — *Entoloma altaicum* is characterised by its deeply translucently striate pileus with sharply delimited centre and a minutely wrinkled surface with lustrous shine, a slightly to distinctly silvery fibrillose stipe, isodiametrical to subisodiametrical basidiospores, clamped basidia, and incrusting pigment in the pileipellis. It has a rather basal position in subsect. *Minuta*. It is relatively close to *E. assiduum*, a strictly Mediterranean species with somewhat more robust basidiocarps and a darker, rather uniformly coloured pileus (Vila et al. 2021). Basidiocarps of *E. minutum* can be similar, but they are generally darker, have a pileus without a delimited centre and a polished stipe with at most few fibrils, and occur in forests.

***Entoloma ortonii* Arnolds & Noordel., Persoonia 10(2): 292. 1979**

**Replaced synonym.** *Nolanea farinolens* P.D. Orton, Trans. Brit. Mycol. Soc. 43(2): 330. 1960. — non *Entoloma farinolens* E. Horak, Beih. Nova Hedwigia 43: 11. 1973.

**Heterotypic synonyms.** *Entoloma terreum* Esteve-Rav. & Noordel., in Noordeloos, Entoloma s.l., Fungi Europaei vol. 5a: 1007. 2004. — *Entoloma cinereo-opacum* (Noordel.) Vila, Català & Noordel., Fungi non Delineati 66: 25. 2013. — *Entoloma sericeum* var. *cinereo-opacum* Noordel., Persoonia 10(4): 482. 1980.

**Notes** — *Entoloma ortonii* was initially described from *Alnus* forests (Orton 1960). Since then, however, it was mainly found in oligotrophic grasslands, mainly identified as *E. cinereo-opacum*, and a subalpine heath in the case of *E. terreum* (Noordeloos 2004).

***Entoloma incanosquamulosum* (Largent) Noordel. & Co-David, in Co-David, Langeveld & Noordeloos, Persoonia 23: 169. 2009**

**Basionym.** *Nolanea incanosquamulosa* Largent, Entolomataceae of the Western United States and Alaska: 266. 1994.

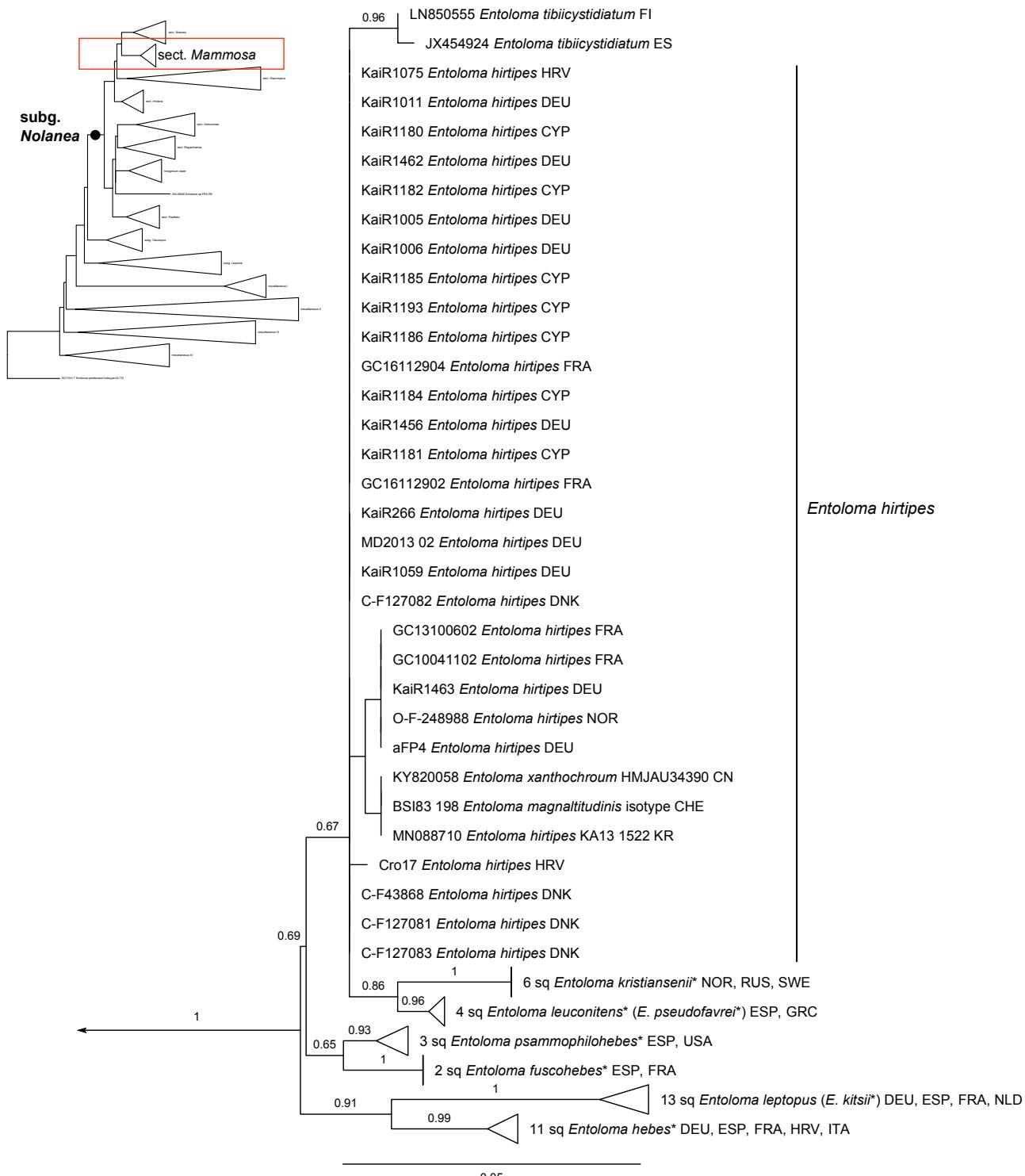
**Heterotypic synonym.** *Entoloma brunneosericeum* Noordel., Vila, F. Caball. & E. Suárez, Fungi non Delineati 66: 31. 2013.

Notes — The type sequence of *E. brunneosericum* nests within the sequences of *E. incanosquamulosum* in the ITS phylogeny (Fig. S2). Apart from specimens with smooth pileus described as *E. brunneosericum*, specimens with minutely squamulose pileus surface have also been depicted from Europe (Karich et al. 2021). The known occurrences in eastern Canada, Germany, Italy, Spain, Russia (European part, Siberia and Far East), and western USA indicate a Holarctic distribution of *E. incanosquamulosum*.

***Entoloma* subsect. *Efibulata*** (Largent) Reschke & Noordel., comb. nov. — MycoBank MB 842275

*Basionym.* *Nolanea* subsect. *Efibulatae* Largent, Mycologia 66: 1004. 1974.  
— Type species: *Entoloma edulis* (Peck) Noordel.  
non *Nolanea* subsect. *Efibulatae* Largent, Mycologia 66: 1008. 1974. — Type  
species: *Entoloma californicum* (Murrill) Blanco-Dios.

Notes — Largent (1974) described *Nolanea* subsect. *Efibulatae* simultaneously twice, with different types. We select here the subsection typified with *Entoloma edulis* (Peck) Noordel., according to Art. 11.5. This subsection currently includes *E. vindobonense* and *E. edulis* (Fig. 7). They share a rather car-



**Fig. 10** Partial maximum likelihood phylogram based on ITS of species of the section *Mammosa*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

tilaginous stipe, coarsely incrusting pigment and in addition intracellular pigment in granules.

***Entoloma vindobonense*** Noordel. & Hauskn., in Noordeloos, Entoloma s.l., Fungi Europaei vol. 5a: 907. 2004

*Heterotypic synonyms.* *Entoloma valdeumbonatum* Noordel. & Meusers, in Noordeloos, Entoloma s.l., Fungi Europaei vol. 5a: 909. 2004. — *Entoloma citerinii* Réaudin & Eyssart., Bull. Soc. Mycol. France 120(1-4): 357. 2005 '2004'.

**Notes** — *Entoloma vindobonense* and *E. valdeumbonatum* were simultaneously described, *E. vindobonense* is selected here, as its description fits better the re-evaluated concept of this species. An unpublished sequence of authentical material of *E. citerinii* revealed that this taxon was described from albino specimens of *E. vindobonense* (Réaudin and Henry, pers. comm.). No infraspecific taxon is created for such specimens here, as transitional specimens with pale brownish pileus exist. The ITS sequence of the holotype of *E. edulis* var. *concentrica* differs in two nucleotides from sequences of *E. vindobonense*. No taxonomic decision is taken here, as material of this taxon was not analysed for this study.

***Entoloma sect. Mammosa*** (Romagn.) Noordel., Entoloma s.l., Fungi Europaei vol. 5: 220. 1992

*Basionym.* *Rhodophyllus* sect. *Mammosi* Romagn., Bull. Mens. Soc. Linn. Lyon 43(9): 330. 1974. — Type species: *Entoloma mammosum* (L.) Hesler (= *E. hirtipes* (Schumach.) M.M. Moser). misappl. *Nolanea* sect. *Nolanea* s. Largent (1974).

**Notes** — This section (Fig. 10) is well defined, comprising species with a rather long and stiff stipe, a sterile or at least almost sterile lamellar edge, heterodiametrical basidiospores, and incrusting pigment in the pileipellis with or without additional intracellular pigment. A subpellis is not distinctly differentiated. All species but one, *E. kristiansenii*, have clamp connections at the base of basidia. A unique feature in sect. *Mammosa* is the peculiar odour of *Macrocystidia cucumis* in fresh basidiocarps of several species, becoming fishy in age.

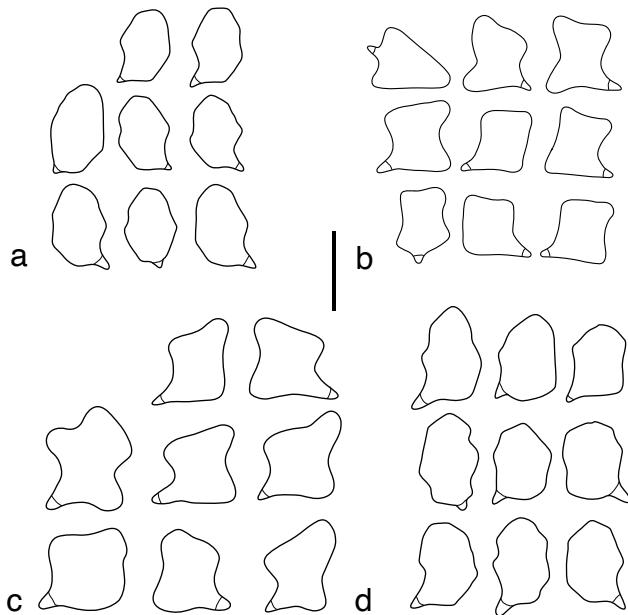
***Entoloma hirtipes*** (Schumach.) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 206. 1978

*Obligate synonyms.* *Agaricus hirtipes* Schumach., Enum. Pl. (Kjbenhavn) 2: 272. 1803, nom sanct., Fr., Syst. Mycol. 1: 206. 1821. — *Nolanea hirtipes* (Schumach.) P. Kumm., Führer Pilz. (Zerbst): 95. 1871.

*Heterotypic synonyms.* *Entoloma mammosum* (L.) Hesler, Beih. Nova Hedwigia 23: 185. 1967. — *Agaricus mammosus* L., Sp. Pl.: 1174. 1753. — *Rhodophyllus mammosus* (L.) Quél., Enchir. Fung. (Paris): 64. 1886.

*Entoloma kuehnerianum* Noordel., Persoonia 12(4): 461. 1985. — *Rhodophyllus mammosus* var. *sericooides* Kühner, Rev. Mycol. (Paris) 19(1): 7. 1954. — *Entoloma hirtipes* var. *sericooides* (Kühner) Noordel., Persoonia 10(4): 442. 1980. — non *Entoloma sericeoides* (J.E. Lange) Noordel., Persoonia 10(4): 483. 1980.

**Notes** — *Entoloma hirtipes* was sometimes interpreted as a vernal species (Breitenbach & Kränzlin 1995, Vila et al. 2013), however, it was described and sanctioned from findings in autumn (Schumacher 1803, Fries 1821). Specimens from autumn were also mentioned later (Orton 1960, Noordeloos 1980, 1992). *Agaricus mammosus* is treated here as an earlier synonym of the sanctioned *E. hirtipes* following the species concept of Kühner & Romagnesi (1953, 1954). The scant description of Linné (1753) and the cited plate 21, f. 1 of Buxbaum (1733) do not allow for a certain interpretation and the possibility for a reasonable typification of this taxon. *Entoloma kuehnerianum* represents specimens from grassland found in autumn. No infraspecific rank is applied to such findings here. Generally, the ecology and phenology appear to be relatively variable and there is no correlation of specific differences in



**Fig. 11** Basidiospores of *Entoloma* spp. a. *Entoloma hebes* (GC96092300, epitype); b. *Entoloma conferendum* (MD2018-16, neotype); c. *Entoloma millicherae* (KaiR839); d. *Entoloma cetratum* (LE311888, neotype). — Scale bars: a-d = 10 µm.

ITS sequences to the latter. However, preliminary results of a multi-gene approach based on ITS, mtSSU, *RPB2*, and *EF-1α* indicate distinct lineages for vernal and autumnal specimens and potential incomplete lineage sorting for the ITS. More vernal specimens of this apparently widely distributed species must be studied to draw a sound taxonomic conclusion.

***Entoloma hebes*** (Romagn.) Trimbach, Doc. Mycol. 11(no. 44): 6. 1981 — Fig. 8b, 11a

*Basionym.* *Rhodophyllus hebes* Romagn., Rev. Mycol. (Paris) 19(1): 4. 1954. — Lectotype: FRANCE, Dept. Yvelines, St. Nom-la Bretèche, 8 Aug. 1942, H. Romagnesi (PC). — Epitype, designated here: FRANCE, Dept. Yvelines, Cernay-la-Ville, moist *Alnus glutinosa* forest, 23 Sept. 1996, G. Corriol GC96092300 (M). — MycoBank MBT 10004734.

**Notes** — *Entoloma hebes* is a species of moist deciduous, humous forests. The epitype was collected from close of the lectotype location and fits well in the concept of Romagnesi (Kühner & Romagnesi 1954). Due to morphological considerations *E. leptopus* was previously included in *E. hebes* (Noordeloos 1987). However, it is different from a molecular (Fig. 10) and ecological perspective (see below).

***Entoloma leptopus*** Noordel., Persoonia 10(4): 442. 1980

*Replaced synonym.* *Nolanea tenuipes* P.D. Orton, Trans. Brit. Mycol. Soc. 43(2): 334. 1960. — non *Entoloma tenuipes* Murrill, N. Amer. Fl. (New York) 10(2): 116. 1917.

*Heterotypic synonym.* *Entoloma kitsii* Noordel., Persoonia 12(1): 76. 1983.

**Notes** — *Entoloma leptopus* was described based on the rather small size of the basidiocarps and the *Macrocystidia cucumis* odour (Orton 1960). This odour was, however, reported to be inconsistent, which is confirmed here. Further differences to *E. hebes* are an in average darker pileus and the ecology. *Entoloma hebes* is mainly found in moist forests, often including tree species of *Fraxinus* or *Alnus*, *E. leptopus* on the contrary is mainly found in rather disturbed habitats like gardens and waysides with shrubs like *Prunus spinosa*, *Sambucus nigra*, and *Rubus* spp. *Entoloma kitsii* was apparently based on an aberrant specimen of *E. leptopus*. Several specimens from Spain were interpreted as *E. tenellum* (Vila et al. 2013), but

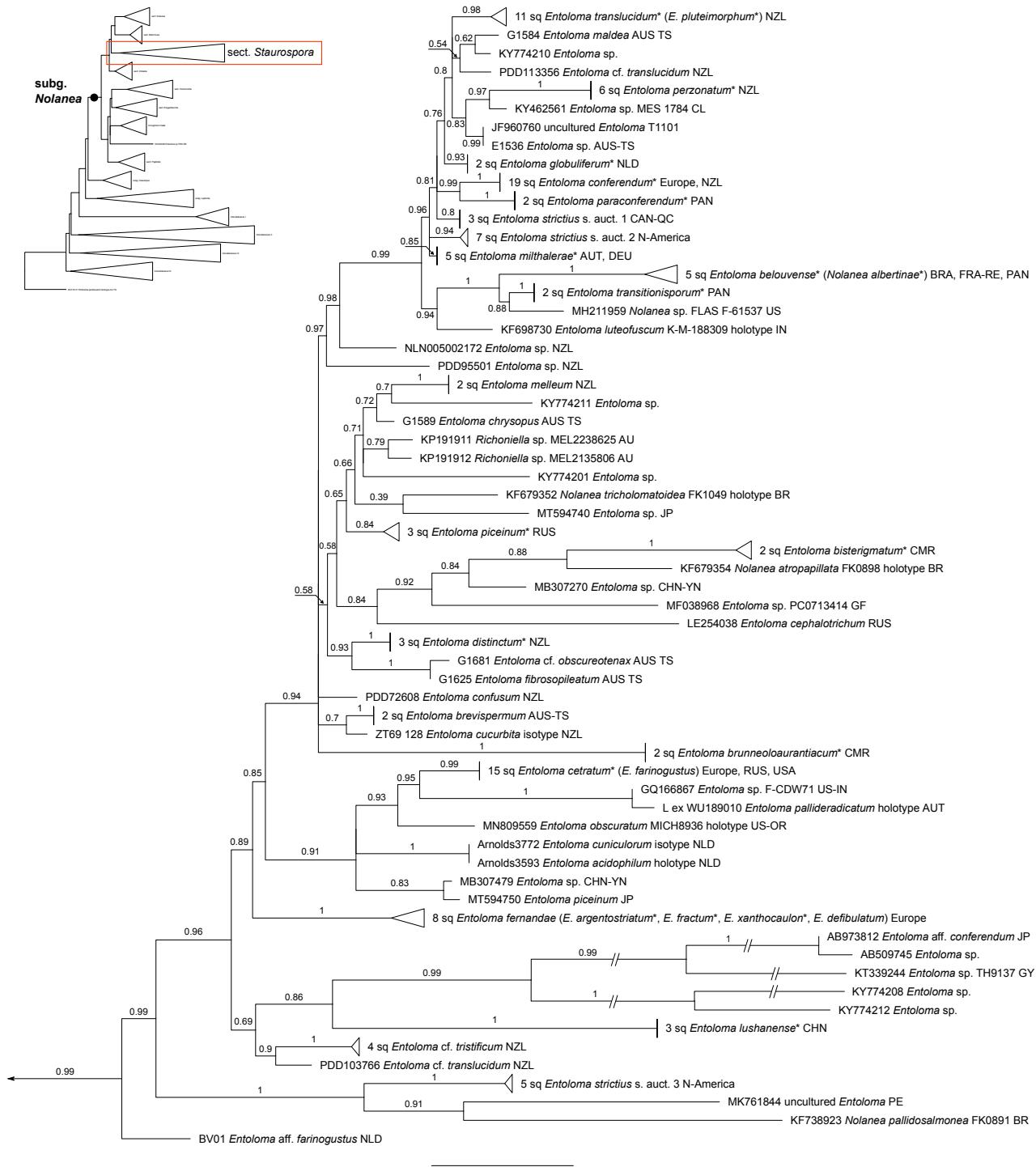
*E. tenellum* is in its original sense a species without clamps and described from alpine bogs (Favre 1948). It is apparently close to *E. kristiansenii*, however, the type specimen of *E. tenellum* is not suitable for sequencing.

**Entoloma leuconitens** Noordel. & Polemis, Mycotaxon 105: 302. 2008

Heterotypic synonym. *Entoloma pseudofavrei* Noordel. & Vila, Fungi non Delineati 66: 44. 2013.

Notes — *Entoloma leuconitens* was described from a pale specimen collected in Greece. The pigment was difficult to

observe and suggested to be intracellular (Noordeloos & Polemis 2008). Vila et al. (2013) described *E. pseudofavrei* from several specimens collected in Spain, including the Canaries, with cream to brown, translucently striate pileus, and incrusting as well as intracellular pigment. The ITS sequences of the types of these two taxa are similar and the slight morphological differences in the descriptions can be explained by the pale type specimen of *E. leuconitens*.



**Fig. 12** Partial maximum likelihood phylogram based on ITS of species of the section *Staurospora*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

***Entoloma sect. Staurospha*** (Largent & Thiers) Noordel.,  
*Persoonia* 10(4): 445. 1980

*Basionym.* *Nolanea* sect. *Staurospha* Largent & Thiers, Northw. Sci. 46: 37. 1972. — Type species: *Entoloma staurospermum* (Bres.) E. Horak (= *Entoloma conferendum* (Britzelm.) Noordel.).

*Heterotypic synonyms.* *Nolanea* sect. *Endochromonema* Largent & Thiers, Northw. Sci. 46: 36. 1972. — Type species: *Entoloma cetratum* (Fr.) M.M. Moser, nom. sanct. — *Entoloma* sect. *Fernandae* Noordel., *Persoonia* 10(4): 486. 1980. — Type species: *Entoloma fernandae* (Romagn.) Noordel. — *Entoloma* sect. *Cephalotricha* Noordel., *Persoonia* 12(4): 461. 1985. — Type species: *Entoloma cephalotrichum* (P.D. Orton) Noordel. — *Entoloma* sect. *Austrofernandae* Noordel., Entolomataceae of Tasmania (Hong Kong): 114. 2012. — Type species: *Entoloma chrysopus* Noordel. & G.M. Gates. — *Entoloma* sect. *Pallideradicata* Noordel. & Hauskn., Österr. Z. Pilzk. 8: 212. 1999. — Type species: *Entoloma pallideradicatum* Hauskn. & Noordel.

**Notes** — This is the most species rich section in subg. *Nolanea* with 57 OTUs likely referring to species in the ITS phylogeny (Fig. 12). The species in sect. *Staurospha* share a pileipellis with at least some loose upper hyphae to almost trichodermal parts and a distinct subpellis of broadly inflated, ellipsoid to ovoid cells, as well as heterodiametrical, in few species cruciform, basidiospores. Clamp connections are absent in most species, but a few exceptions exist. The pigment in the pileipellis is either intracellular or both, intracellular and incrusting, seldom incrusting without intracellular pigment. Cheilocystidia are rarely present, but they are apparently constant at least in the tropical species *E. belouvense* (Reschke et al. 2022).

***Entoloma conferendum*** (Britzelm.) Noordel., *Persoonia* 10(4): 446. 1980 — Fig. 8d, 11b

*Basionym.* *Agaricus conferendus* Britzelm., Ber. Naturhist. Vereins Augsburg 26: 140. 1881. — Lectotype (designated here): Britzelmayr, Hymenomyceten aus Südbayern, Abbildungen: f. 26a. [?1879–1881]. — MycoBank MBT 10004735; Fig. 8c. — Epitype, designated here: GERMANY, Bavaria, Landkreis Garmisch-Partenkirchen, Gemeinde Krün, Klais, meadows above Aschenmoos forest, between grasses in meadow, 1160 m a.s.l., 11 Sept. 2018, M. Dondl (M). — MycoBank MBT 10004736.

*Heterotypic synonyms.* *Entoloma staurospermum* (Bres.) E. Horak, Sydowia 28(1–6): 222. 1976 ‘1975–1976’. — *Nolanea staurospha* Bres., Fungi Trident. 1(2): 18. 1882. — *Entoloma kipukae* E. Horak & Desjardin, Mycologia 85(3): 485. 1993.

**Notes** — *Entoloma conferendum* is a common and widely distributed species, which was described several times. For a long time, it was known as *E. staurospermum*, until the plate of Britzelmayr was rediscovered. The plates of Britzelmayr were published in a book which was hand-coloured by himself. Accordingly, only few versions of this book exist and the exact date of publication, probably between 1879 and 1881, could not be found out. A copy of the original plate (in M), which is in the public domain, is therefore depicted here (Fig. 8c). For further synonyms of this taxon see Noordeloos (1980). *Entoloma kipukae* is included here as the mtSSU of the holotype (GenBank acc. MH190078) is identical to those of the specimens of *E. conferendum*, and there are no significant morphological differences according to the original description (Horak & Desjardin 1993). As several species with cruciform basidiospores exist, *E. botanicum* and *E. nothofagi* are not included here. Their identity must be resolved with reassessments of their original material, most beneficially including sequencing.

***Entoloma cetratum*** (Fr.) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 206. 1978 — Fig 11d, 13a

*Basionym.* *Agaricus cetratus* Fr., Observ. Mycol. (Havniae) 2: 218 (1818), nom. sanct. Fr., Syst. Mycol. 1: 207. 1821. — Neotype (designated here): SWEDEN, Stockholms län, Salem, N59.218034° E17.735541°, on soil in mixed forest, 1 Aug. 2015, O. Morozova (LE 311888) — MycoBank MBT 10004737.

*Heterotypic synonym.* *Entoloma farinogustus* Arnolds & Noordel., *Persoonia* 10(2): 292. 1979.

**Notes** — Fries (1818) described *Agaricus cetratus* originally with the habitat notes “inter folia faginea alibique” (= between *Fagus* litter and elsewhere) which highlights an untypical habitat for this species. The current concept for *E. cetratum* as a species mainly found in coniferous forest has been used for decades with international consensus and is not clearly excluded by the description of Fries, thus a typical specimen from mixed forest in Sweden is used here for a neotype to fix this concept. An ITS sequence of an authentical specimen of *E. farinogustus* is not significantly different from those of *E. cetratum*. As there are also no significant morphological differences, *E. farinogustus* is included in the latter species. Included is also *E. cetratum* f. *minimosporum*, a form with 4-spored basidia and smaller basidiospores. This form is apparently not rare in western North America.

***Entoloma melleum*** E. Horak, Beih. Nova Hedwigia 43: 34. 1973

**Notes** — Horak (1973) described *E. melleum* as a species on wood, with pale pileus, a cutis with intracellular pigment, and clamp connections in all parts of the basidiocarp. In the re-evaluation of the holotype, a cutis with incrusting pigment and a distinct subcutis composed of broad, inflated cells was observed, while clamp connections were not seen. The holotype consists of a single basidiocarp, therefore the concept of *E. melleum* is altered here. Allowance for sequencing was not granted for the holotype due to limited material, however, a sequenced specimen (PDD 80836) did morphologically agree and is therefore interpreted as *E. melleum*. According to this specimen and another sequenced record (PDD107364) the pileus of *E. melleum* can be coloured pale yellow but also brown.

***Entoloma milthalerae*** M. Kamke & Lüderitz (as ‘*milthalerae*’), in Lüderitz, Kamke, Specht, Ludwig, Lehmann, Schubert, Richter & Richter, Z. Mykol. 82(2): 407. 2016

**Notes** — *Entoloma milthalerae* is molecularly close to several species in the crown clade of sect. *Staurospha* based on ITS, viz., *E. conferendum*, *E. globuliferum*, *E. luteofuscum*, *E. maldea*, *E. strictius* s. auct. 1 & 2, and *E. translucidum*, with p-distances of 1.3–2.0 %. Despite its similarity to *E. conferendum*, *E. milthalerae* is not the sister species of the latter according to the phylogenies (Fig. 12). *Entoloma milthalerae* was originally described as a species with non-striate, not hygrophanous pileus with tomentose surface (Lüderitz et al. 2016). New findings revealed that the type specimen was apparently untypical and the basidiocarps of *E. milthalerae* are similar to small ones of *E. conferendum* (Fig. 8e). The basidiospore measurements resulted in 9.0–10.1–12.0 × 7.5–8.4–9.5 µm, Q = 1.05–1.21–1.45 (n = 142 spores of 5 specimens; Fig. 11c) which is somewhat smaller than originally given.

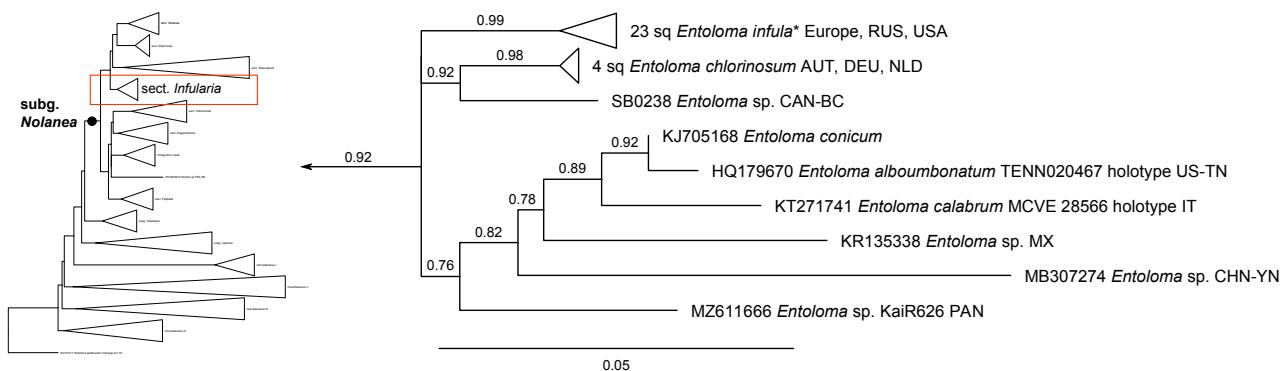
***Entoloma translucidum*** E. Horak, Beih. Nova Hedwigia 43: 51. 1973

*Heterotypic synonym.* *Entoloma pluteimorphum* E. Horak, Beih. Nova Hedwigia 65: 181. 1980.

**Notes** — *Entoloma translucidum* and *E. pluteimorphum* were both initially described without clamp connections (Horak 1973, 1980), however, inconsistent clamp connections were reported to exist later (Horak 1980, 2008). A re-evaluation of type specimens and recent material including sequencing of the ITS revealed consistent clamp connections, frequently present at the base of basidia. *Entoloma pluteimorphum* is a synonym



Fig. 13 Basidiocarps of *Entoloma* spp. a. *Entoloma cetratum* (LE311888, neotype); b–d. *Entoloma cornicolor*: b (LE311859), c (LE311854, holotype), d (LE311857); e, f. *Entoloma argillaceum*: e (LE311864), f (LE311861, holotype). — f. Photos by: a–e: O. Morozova; f. E. Zvyagina.



**Fig. 14** Partial maximum likelihood phylogram based on ITS of species of the section *Infularia*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

of *E. translucidum*, representing specimens on rotten wood. On the contrary, *E. perzonatum* is a distinct species without clamp connections. Both, *E. translucidum* and *E. perzonatum* have in addition to distinct intracellular pigment also some incrusting pigment in the pileipellis. Several specimens corresponding to distinct lineages in the ITS phylogeny were initially identified as *E. translucidum* (*Entoloma* cf. *translucidum* in Fig. 12).

***Entoloma fernandae* (Romagn.) Noordel., Persoonia 10(2): 250. 1979**

*Basionym.* *Rhodophyllus fernandae* Romagn., Rev. Mycol. (Paris) 1(3): 162. 1936.

*Heterotypic synonyms.* *Entoloma fractum* (Velen.) Noordel., Persoonia 10(2): 250. 1979. — *Nolanea fracta* Velen., Novit. Mycol.: 146. 1939. — *Entoloma argentostriatum* Arnolds & Noordel., Persoonia 10(2): 285. 1979. — *Entoloma defibulatum* Arnolds & Noordel., Persoonia 10(2): 290. 1979. — *Entoloma xanthocaulon* Arnolds & Noordel., Persoonia 10(2): 299. 1979.

**Notes** — *Entoloma fernandae* is morphologically more variable than previously thought and includes several other taxa. No sequences could be obtained from authentic specimens of *E. psilopus*, another probably close or identical taxon. The characteristic pigmentation of the pileipellis, with both, distinct incrusting and intracellular pigment is possibly a plesiomorphic character state of sect. *Staurospora* (Fig. 6).

***Entoloma acidophilum* Arnolds & Noordel., Persoonia 10(2): 285. 1979**

**Notes** — Partial ITS sequences obtained from types of *E. acidophilum* and *E. cuniculorum* do not have reliable differences. However, no synonymy is proposed here, as the sequences are short and of relatively low quality. The basidiospores of these two taxa were significantly different in the original descriptions, thus more material must be analysed to resolve their taxonomy.

***Entoloma* sect. *Infularia* (Romagn. ex Noordel.) Reschke & Noordel., comb. nov. — MycoBank MB 842280**

*Basionym.* *Entoloma* subsect. *Infularia* Romagn. ex Noordel., Persoonia 10(4): 503. 1980.

*Obligate synonyms.* *Nolanea* sect. *Infularia* (Romagn. ex Noordel.) Largent, Entolomatoïd fungi of the Western United States and Alaska (Eureka): 203. 1994. — *Rhodophyllus* sect. *Infularia* Romagn. (nom. nud.), Bull. Soc. Mycol. France 53: 332. 1937. — Type species: *Entoloma infula* (Fr.) Noordel.

**Notes** — Section *Infularia* (Fig. 14) is characterised by species forming typical mycenoid basidiocarps, with a conical to umboinate, never depressed pileus, a rather tough, cartilaginous stipe, and relatively pale lamellae. Several species have a

nitrous odour, which is, however, not always perceivable. The species included have generally small basidiospores, rarely reaching a length of 10 µm, with a rather simple shape with 4–6 angles, often including a fraction of tetragonal spores in outlines. The pileipellis is a cutis, which can be loose in some species resulting in a fibrillose pileal surface. The subpellis is weakly differentiated, sometimes with some short, inflated cells. The pigments are incrusting, intracellular, or of both types. Clamp connections are generally abundant in the hymenium of all species, some species have also frequently clamps in other parts of the basidiocarp.

***Entoloma chlorinosum* Arnolds & Noordel., Persoonia 10(2): 287. 1979**

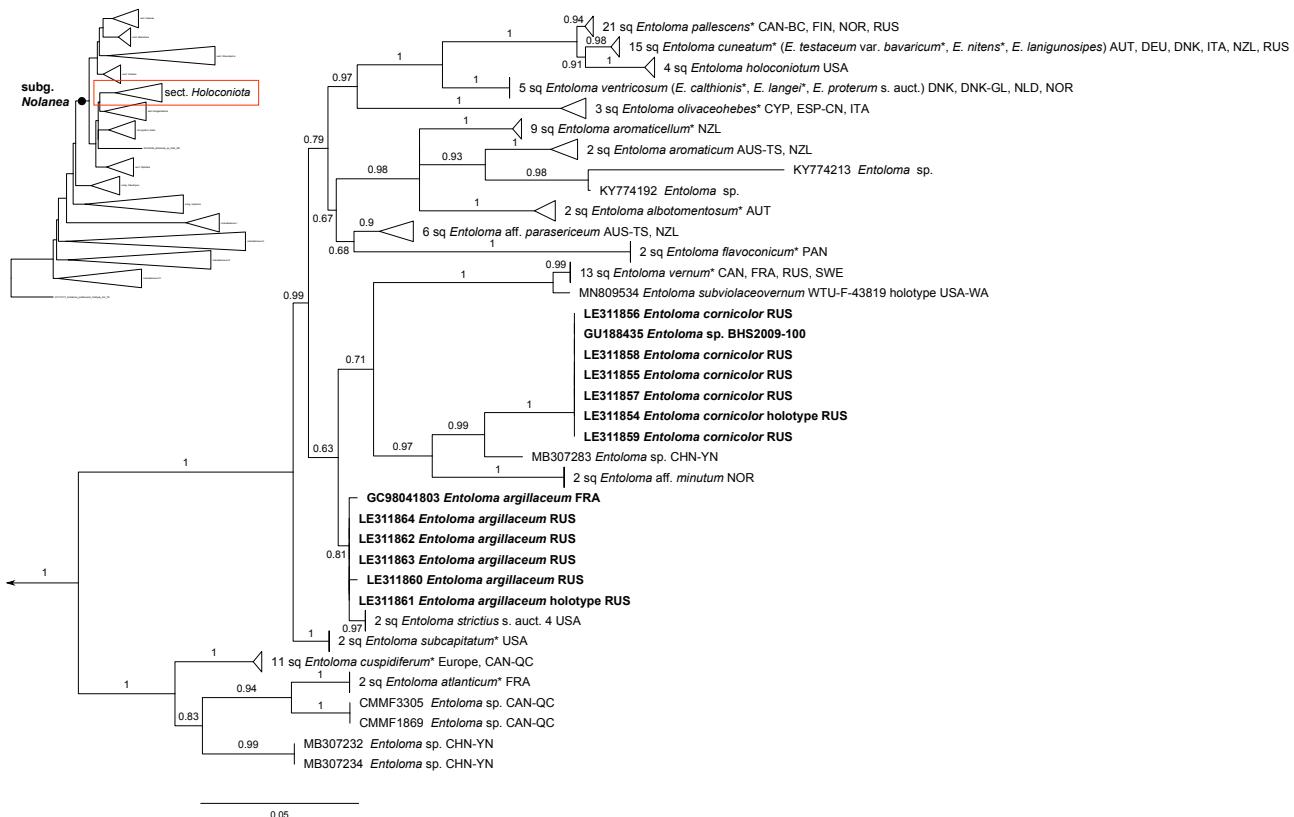
*Obligate synonym.* *Entoloma infula* var. *chlorinosum* (Arnolds & Noordel.) Noordel., Entoloma s.lat., Fungi Europaei vol. 5 (Saronno): 290. 1992.

**Notes** — *Entoloma chlorinosum* is molecularly close to *E. infula*, with a p-distance of 2.3 %, and an unnamed specimen from Canada (SB0238), with a p-distance of 2.8 %, based on ITS (Fig. 14). It was described as similar to *E. infula*, but with a strong nitrous (= chlorinose) odour and absent incrusting pigment (Arnolds & Noordeloos 1979, 1981). It was later treated as a variety of *E. infula* because of a weak correlation of these two characteristics (Noordeloos 1992). The re-evaluation of sequenced specimens revealed that like the initial concept incrusting pigment is scarcely present. However, *E. infula* specimens can also have a nitrous odour. Generally, the basidiocarps of *E. chlorinosum* are smaller than those of *E. infula* and the basidiospores are also slightly smaller (Arnolds & Noordeloos 1981).

***Entoloma* sect. *Holoconiota* (Largent & Thiers) Reschke & Noordel., comb. nov. — MycoBank MB 842276; Fig. 15**

*Basionym.* *Nolanea* sect. *Holoconiota* Largent & Thiers, Northw. Sci. 46: 34. 1972. — Type species: *Entoloma holoconiota* (Largent & Thiers) Noordel. & Co-David.

**Notes** — This section was described by Largent & Thiers (1972) for *E. holoconiota* because of its conspicuous capitate caulocystidia. Later, Largent (1974) indicated *E. cuneatum* as type species, probably considering *E. holoconiota* a synonym of this taxon. Section *Holoconiota* is defined by species with a conical pileus, an at least somewhat fibrillose stipe, and mainly heterodiametrical, sometimes subisodiametrical to broadly heterodiametrical, basidiospores. Clamp connections are abundant in the hymenium of most species, however, they are absent in a few species. A subpellis is not differentiated, or rather weakly so, with relatively long, inflated cells. Irregularly



**Fig. 15** Partial maximum likelihood phylogram based on ITS of species of the section *Holoconiota*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

shaped cylindrical cheilocystidia are sometimes present in a few species but are of low taxonomic value. Several species have long capitate caulocystidia, similar to those of *E. holocniontum*. Several species in sect. *Holoconiota* from the Northern Hemisphere fruit in spring as well as in autumn (Fig. 15).

#### *Entoloma cuneatum* (Bres.) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 205. 1978 — Fig. 16

Basionym. *Nolanea cuneata* Bres., Fungi Trident. 1(6-7): 77. 1887.

Heterotypic synonyms. *Entoloma lanuginosipes* Noordel., Persoonia 10(2): 248. 1979. — *Nolanea crassipes* Velen., České Houby 3: 627. 1921. — non *Entoloma crassipes* Petch, Ann. Roy. Bot. Gard. (Peradeniya) 9: 214. 1924.

Heterotypic synonyms. *Entoloma nitens* (Velen.) Noordel., Persoonia 10(2): 252. 1979. — *Nolanea nitens* Velen. České Houby 3: 627. 1921. — Neotype, designated here: GERMANY, Bavaria, Landkreis Miesbach, Gemeinde Bayerischzell, Geitau, Miesing, path to the summit Hochmiesing, in litter of *Pinus mugo*, 1870 m a.s.l., M. Dondl 1 July 2018 (M). MycoBank MBT 10004738. — Superseded neotype [as 'epitype']. Designated by Vila et al., Fungi non Delineati 66: 26. 2013. SPAIN, near Can Romegosa, Sant Fost de Campsentelles (Barcelona), alt. 140 m; under *Pinus pinea*, among mosses and lichens, in acid soil, 19 Nov. 2011, S. Català, J. Vila & F. Caballero, LIP JVG 1111119Q, 'isoepitypus' JVG 1111119-8. — excluded. *Entoloma nitens* sensu Vila et al., Fungi non Delineati 66: 26. 2013.

Heterotypic synonym. *Entoloma testaceum* (Bres.) Noordel. var. *bavaricum* Noordel. & Wölfel, in Noordel., Beih. Nova Hedwigia 91: 85. 1987.

Notes — Velenovský (1921) described *Nolanea nitens* as a species similar to *E. cetratum*, fruiting in spring to early summer in coniferous forests of Bohemia, Central Europe. Original material of *N. nitens* does not exist (Noordeloos 1979b). The concept of Romagnesi (1974b), followed by Noordeloos (1980), is interpreted here as referring to somewhat aberrant specimens of *E. minutum* with raphanoid odour. Vila et al. (2013) studied species of subg. *Nolanea* based on South European specimens and designated a neotype (as epitype) for *E. nitens*, which in fact is a thermophilic species fruiting in

autumn in Mediterranean habitats and was later described as the new species *E. assiduum* (Vila et al. 2021). This neotype is superseded here by a neotype which is closest to the original description of Velenovský. As a result, *E. nitens* turns out to be a synonym of *E. cuneatum*. *Entoloma testaceum* var. *bavaricum* represents specimens with cheilocystidia. Specimens with a pruinose stipe with abundant caulocystidia were previously named *E. lanuginosipes* (Noordeloos 1979b). Such forms have also been encountered in *E. pallescens*, and accordingly also identified as *E. lanuginosipes*. Since the holotype of *E. lanuginosipes* was collected in a forested park in Prague (Noordeloos 1979b), far south of the distribution range of the strictly boreal *E. pallescens*, we consider this species a synonym of *E. cuneatum*. The holotype of *E. lanuginosipes* is stored in ethanol and is not suitable for DNA extraction.

#### *Entoloma cornicolar* O.V. Morozova, Reschke & Noordel., sp. nov. — MycoBank MB 842254; Fig. 13b–d, 17a–c

Etymology. *cornu* (Latin) = deer antler; refers to the colour of the pileus, similar to that of deer antlers.

Holotype. RUSSIA, Primorsky Krai, Sikhote-Alin Nature Reserve, vicinities of Kunaleika cordon, path along the stream Khanova, N44.93288° E136.32425°, on litter and plant remnants in a coniferous-broadleaf valley forest (*Pinus koraiensis*, *Ulmus* sp., *Populus koreana*, *P. maximowiczii*), 29 Aug. 2013, O. Morozova (LE 311854).

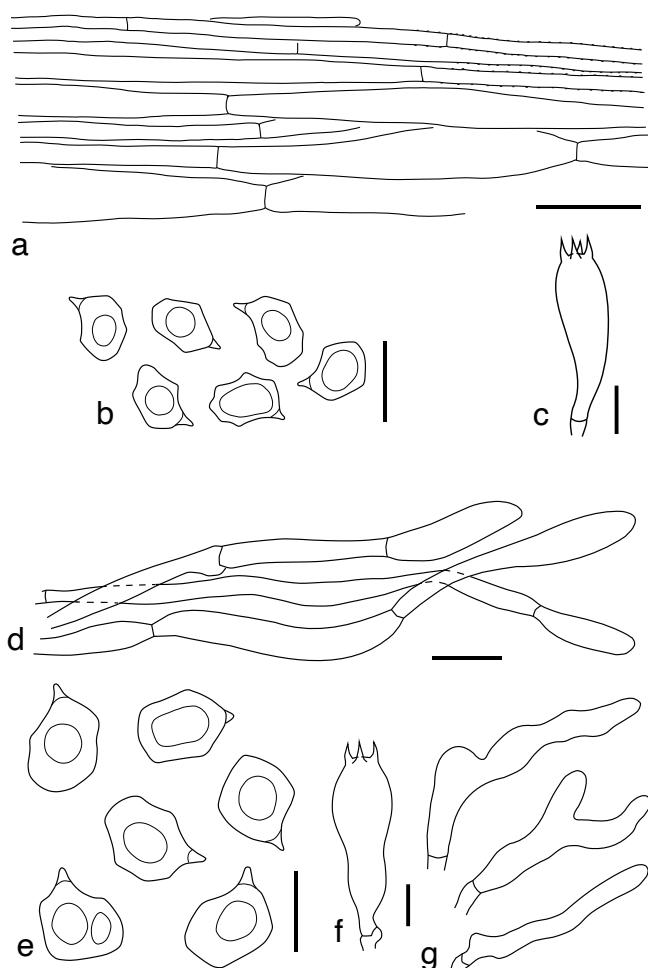
Basidiocarps mycenoid. Pileus 15–35 mm diam, conical, broadly conical to hemispherical with small umbo, becoming convex and depressed with small papilla, with firstly involute then straight margin, initially rather dark, sepia, yellowish brown or greyish brown, then pale ochraceous, beige, yellowish beige, with paler margin, darker towards the centre, often with contrasting dark umbo and radial stripes, pallescent on drying, smooth, glabrous, when moist translucently striate almost up



**Fig. 16** Basidiocarps of *Entoloma* spp. a. *Entoloma nitens* (MD2018-9, neotype); b. original plate of *Agaricus junceus* f. *cuspidatus* (lectotype), drawing by E.M. Fries; c. *Entoloma cuspidiferum* (KaiR1290, epitype); d. *Entoloma rhodocylix* (ACN40, neotype); e. *Entoloma incognitum* ex-situ (KaiR1372, holotype); f. *Entoloma clandestinum* (KaiR1273, neotype). — Photos by: a. M. Dondl; c–f: K. Reschke; d. V. Kummer.

to the centre, hygrophanous. Context thin, concolorous with the surface or paler. Lamellae adnate-emarginate with a small tooth to almost free, ventricose, moderately distant, whitish, becoming pinkish, with entire concolorous edge. Stipe cartilaginous, 40–80 × 1.5–3.0 mm, cylindrical, or slightly broadened towards the base, sometimes compressed with longitudinal groove, uniformly coloured yellowish brown, concolorous with dark parts of the pileus, contrasting with lamellae, fistulose, smooth, polished, somewhat waxy. Basal mycelium white, tomentose. Odour indistinct, taste not tested.

**Basidiospores** 7.5–8.5–9.5 × 5.5–6.2–7.0 µm, Q = 1.25–1.39–1.55 (n = 132 spores of 4 specimens), heterodiametrical, with 5–7 angles in outlines. Basidia 27.5–36.0 × 10.5–12.0 µm, 4-spored, clavate, clampless, sterigmata up to 4.0 µm long. **Lamellar edge** fertile. **Hymenial cystidia** absent. **Pileipellis** a cutis of thin cylindrical or slightly fusiform hyphae 1.5–5.0 µm wide, broader and fusiform towards pileitrama, without distinct subpellis, with abundant incrusting pigment, in addition also intracellular, yellowish in KOH. **Stipitipellis** a cutis of cylindrical hyphae 5–7 µm wide with pale intracellular pigment. **Caulocystidia** absent. **Clamp connections** absent.



**Fig. 17** Microscopic structures. a–c. *Entoloma cornicolor* (LE311854, holotype). a. Pileipellis, incrusting pigment only partially indicated; b. basidiospores; c. basidium. — d–g. *Entoloma argillaceum* (LE311861, holotype). d. Terminal parts of upper pileipellis hyphae; e. basidiospores; f. basidium; g. caulocystidia. — Scale bars: a, d = 20 µm; b–c, e–g = 10 µm.

**Habitat** — In small groups on litter and soil in *Quercus mongolica* forests, in mixed forest of *Quercus mongolica*, *Acer mono*, *Tilia amurensis*, *Pinus koreana* and in coniferous-broadleaf valley forests in eastern Russia, and among mosses in deciduous forest in the Netherlands.

**Additional specimens examined.** NETHERLANDS, Prov. Groningen, Glimmen, Appelbergen, among mosses in deciduous forest on damp, sandy soil, 238–573, 14 Sept. 2019, *Roeland Enzlin* 19-023 (L-0607054). — RUSSIA, Primorsky Krai, Sikhote-Alin Nature Reserve, vicinities of Blagodatnoye, N44.951517° E136.547233°, on litter and soil in mixed forest of *Quercus mongolica*, *Acer mono*, *Tilia amurensis*, *Pinus koreana*, 14 Aug. 2013, O. Morozova (LE 311857); ibid., N44.956033° E136.535133°, on litter in *Quercus mongolica* forest, 14 Aug. 2013, O. Morozova (LE 311858, LE 311859); ibid., vicinities of Maisa cordon, on litter in mixed forest of *Quercus mongolica*, *Acer mono*, *Tilia amurensis*, *Pinus koreana*, N45.238833° E136.511117°, 24 Aug. 2013, O. Morozova (LE 311855); ibid., N45.232056° E136.509528°, on litter and soil in coniferous-broadleaf valley forest (*Abies nephrolepis*, *Acer tegmentosum*, *Eleutherococcus senticosus*, *Matteuccia struthiopteris*), 27 Aug. 2013, O. Morozova, A. Fedosova (LE 311856).

**Notes** — *Entoloma cornicolor* is characterised by rather small mycenoid basidiocarps with a deeply translucently striate, beige to yellowish brown pileus with contrasting dark centre, a polished, almost waxy stipe, small, heterodiametrical basidiospores, incrusting pigment in the pileipellis, and the absence of clamp connections. Pale basidiocarps of *E. ventricosum* can be similar, however, *E. cornicolor* differs from this as well as most other species in sect. *Holoconiota* by the absence of clamp connections and small basidiospores. *Entoloma cornicolor* is

also somewhat similar to *E. cetratum*, and their habitats possibly overlap, however, microscopically *E. cetratum* is different by its 2-spored basidia, larger basidiospores, and intracellular pigment. In addition, it is phylogenetically quite distant. The ITS sequence of an unidentified *Entoloma* sp., BHS2009-100, (GenBank Accession GU188435), collected in USA, Massachusetts, is included in the clade of *E. cornicolor*, indicating a wide distribution of this species.

***Entoloma argillaceum* O.V. Morozova, Reschke, Corriol, Noordel., Zvyagina, E.F. Malysheva & Svetash., sp. nov.** — MycoBank MB 842255; Fig. 13e–f, 17d–g

**Etymology.** *argillaceus* (Latin) = clayey; refers to the colour of the pileus.

**Holotype.** RUSSIA, Karachaevo-Cherkessia Republic, Teberda Biosphere Reserve, Malaya Khatipara Mt, ± 2800 m a.s.l., N43.44042° E41.68399°, on soil in alpine grassland, 18 Aug. 2012, E. Zvyagina (LE 311861).

**Basidiocarps** mycenoid to somewhat tricholomatoid. **Pileus** 30–80 mm diam, conical, broadly conical to convex with acute umbo, with initially incurved, then straight margin, beige, iza-bella, pale yellowish beige to yellowish brown, usually rather uniformly coloured, paler on drying from the centre, pileal surface smooth, glabrous, somewhat translucently striate at the margin, hygrophanous. **Context** thin, concolorous with the surface or paler. **Lamellae** adnate-emarginate to almost free, ventricose, moderately distant, whitish, cream, becoming pink, with entire, concolorous edge. **Stipe** 40–120 × 3–8 mm, cylindrical, or broadened towards the base, fistulose, brittle, sometimes twisted, pale grey-brown, distinctly longitudinally striate with white fibrils on yellowish beige to brownish background. **Basal mycelium** white, tomentose. **Odour** and **taste** indistinct.

**Basidiospores** (9–)10.0–11.1–12.5(–13.5) × 7.5–8.5–9.5 µm, Q = 1.20–1.31–1.45 (n = 100 spores of 3 specimens), broadly heterodiametrical, sometimes subisodiametrical, with 4–7 angles in outlines. **Basidia** 32.5–44.0 × 10.5–13.0 µm, 4-spored, narrowly clavate to subcylindrical, clamped, with up to 4.0 µm long sterigmata. **Lamellar edge** fertile. **Hymenial cystidia** absent. **Pileipellis** a cutis of cylindrical cells, 3–10 µm wide and up to 150 µm long, with fusoid terminal cells 10–77 × 8–12 µm, broader, fusiform to inflated towards pileitrama, without distinct subpellis, pigment intracellular, yellowish in KOH, in addition sometimes minutely incrusting. **Pileitrama** regular, composed of cylindrical cells 6–12 µm wide, with abundant diverticulate oleiferous hyphae. **Stipitipellis** a cutis of cylindrical hyphae, 5–7 µm wide, with pale intracellular pigment. **Caulocystidia** narrowly clavate, cylindrical to lageniform, 15–75 × 4.5–7.0 µm. **Clamp connections** abundant in hymenium and subhymenium, rare to relatively frequent elsewhere.

**Habitat** — In spring and autumn on soil on alpine and subalpine grasslands in Russia and in deciduous forest in France.

**Additional specimens examined.** FRANCE, Essonne department, communal forest of Saint-Aubin, N48.715009° E2.126850°, 110 m a.s.l., on weakly acid soil in *Quercus-Castanea* forest at the bottom of a small valley, with *Peziza phyllogena* and *Morchella semilibera*, 18 Apr. 1998, G. Corriol & P.-A. Moreau (GC98041803). — RUSSIA, Karachaevo-Cherkessia Republic, Teberda Biosphere Reserve, Dombaj, Mussa-Achitara ridge, N43.292417° E41.64955°, alt. c. 2300 m, on soil on subalpine grassland with *Pulsatilla aurea*, 11 Aug. 2009, O. Morozova (LE 311863); ibid., Malaya Khatipara Mt, N43.4466° E41.71019°, alt. c. 2250 m, on soil on subalpine grassland, 16 Aug. 2009, O. Morozova (LE 311862); ibid., Arkhyz site, vicinities of the Sophiya waterfalls, N43.447958° E41.275535°, alt. c. 2200 m, on soil on subalpine grassland with *Pulsatilla aurea*, 23 Aug. 2009, E. Malysheva (LE 311860); ibid., Klukhor pass, N43.252741° E41.857758°, alt. c. 2700 m, among herbs and rocks on soil on alpine grassland, 23 Aug. 2012, T. Svetashova (LE 311864).

**Notes** — *Entoloma argillaceum* is characterised by the rather conical, uniformly coloured beige or yellowish beige, only

somewhat transluscently striate pileus, a fibrillose stipe, broadly heterodiametrical basidiospores with 4–7 angles in outlines, and the occurrence in alpine grasslands or deciduous forest in both, spring and autumn. Based on the phylogenetic analyses it is close to one of the four clades of sequences annotated as *E. strictius* or synonymous (Fig. 15). However, this species was demonstrated to belong to sect. *Mammosa*, and is possibly close to *E. hebes* (Noordeloos 2008a), so the specimens corresponding to these sequences are apparently misidentified. *Entoloma pallescens* is morphologically similar but differs by the distinctly translucently striate pileus and the occurrence in coniferous forests. *Entoloma ventricosum* has smaller basidiocarps as well as smaller basidiospores.

The specimen from France differs somewhat from those from Russia. Its pileus was distinctly darker, more brownish than yellowish, and it was collected in a deciduous forest in spring in contrast to the autumnal specimens from alpine to subalpine grasslands. The basidiocarps appeared to be rather immature, so the basidiospore measurements, resulting in smaller sizes, were not used for the description. Based on the available data it is not justified to treat it as a distinct taxon. Further findings are necessary to elucidate the somewhat obscure ecology and distribution of *E. argillaceum*.

***Entoloma ventricosum* Arnolds & Noordel., Persoonia 10(2): 298. 1979**

*Heterotypic synonyms.* *Entoloma calthionis* Arnolds & Noordel., Persoonia 10(2): 285. 1979. — *Entoloma langei* Noordel. & T. Borgen, in Noordel., Persoonia 12(3): 292. 1984.

*Notes* — *Entoloma ventricosum* and *E. calthionis* were simultaneously described by Arnolds & Noordeloos (1979). Based on morphological considerations, *E. calthionis* was later treated as a synonym of *E. ventricosum* (Noordeloos 2008b). No sequences could be obtained from the holotype specimen of *E. ventricosum*, however, there are no indications to question this decision. *Entoloma langei*, described from Greenland, represents specimens with cheilocystidia, thus *E. ventricosum* is another species with occasional presence of cheilocystidia. A specimen of this species was interpreted as *E. proterum* by Vila et al. (2013), however, that species is different by its incrusting pigment and the occurrence in coniferous forest and is most likely close to *E. vernum* (Noordeloos 1987). The type specimen of *E. proterum* could not be located, so it is unclear if it is a synonym of *E. vernum* or a distinct species.

***Entoloma albotomentosum* Noordel. & Hauskn., Z. Mykol. 55(1): 32. 1989**

*Notes* — This species was previously included in subg. *Cladopus* due to its small basidiocarps with eccentric stipe. Apart from this, it is also exceptional for subg. *Nolanea* by its growth on decaying grass remnants (Noordeloos & Hausknecht 1989, Jančovičová & Adamčík 2014). In the ITS phylogeny, it forms a clade together with *E. aromaticum* and *E. aromaticellum* described from New Zealand, as well as two further species possibly from New Caledonia (Fig. 15).

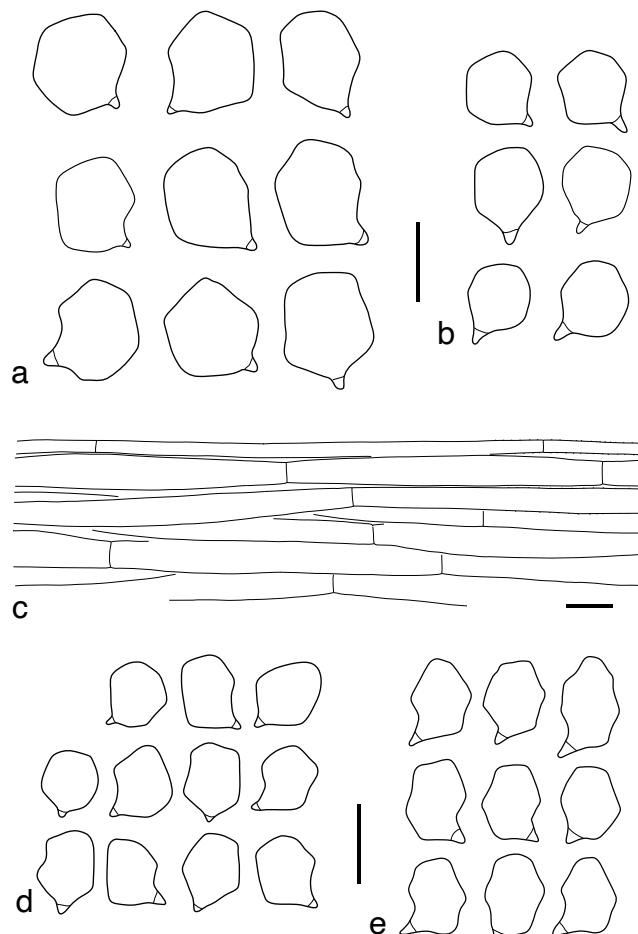
***Entoloma cuspidiferum* Reschke & Noordel., nom. nov. — MycoBank MB 843773; Fig 16c, 18a**

*Replaced synonym.* *Agaricus junceus* Fr., nom. sanct., var. *cuspidatus* Fr. (as 'v. *cuspidata*'), Icon. Sel. 1: t. 99: 2. 1875. — Lectotype (designated here): t. 99, f. 2 in Fr., Icon. Sel. 1. 1875. — MycoBank MBT 10004741; Fig. 16b. — Epitype (designated here): SWEDEN, Västernorrlands län, at lake Viggesjön, Högånge, N62°19'0.1" E16°41'14.1", 180 m a.s.l., sheep pasture, 30 Aug. 2018, K. Reschke, KaiR1290 (M). — MycoBank MBT 10004742. *Obligate synonym.* *Nolanea juncea* var. *cuspidata* (Fr.) Favre, Bull. Trimestriol Soc. Mycol. France 52: 137. 1936.

*Invalid synonyms.* *Rhodophyllus cuspidifer* Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 189. 1953 [inval., Shenzhen Art. 41.5]. — *Entoloma cuspidiferum* (Kühner & Romagn.) Noordel. (as 'cuspidifer'), Persoonia 10(4): 461. 1980.

*Illegitimate synonym.* *Rhodophyllus cuspidatus* (Fr.) J. Favre, Beitr. Kryptogamenfl. Schweiz 10 (no. 3): 44. 1948. — non *Rhodophyllus cuspidatus* Pat., Bull. Mus. Natl. Hist. Nat., Paris 30: 528. 1924.

*Notes* — *Entoloma cuspidiferum* was initially described by Fries (1867) as a distinct variety, var. *cuspidatus*, of *Agaricus junceus*. Favre (1936) provided a detailed description and combined the name to *Nolanea juncea* var. *cuspidata*. Kühner & Romagnesi (1953) recognised this variety on species level and gave it the new name *Rhodophyllus cuspidifer*, referring to the description of Favre. However, they failed to give a full and direct reference to the original description of the replaced synonym (Art. 41.5), so their new name and accordingly its combination to *Entoloma* by Noordeloos (1980) were invalid. Favre (1948) combined the species to *Rhodophyllus cuspidatus*, correctly citing the original description of Fries. However, *Rhodophyllus cuspidatus* was already used by Patouillard (1924), so the combination of Favre was a later homonym and thus illegitimate. This species is currently well-known in Europe as *E. cuspidiferum*, so this name is here used again for a valid new name to avoid further confusion. *Entoloma cuspidiferum* is one of the few species in subg. *Nolanea* with 2-spored basidia. Together with the incrusting pigment and the conspicuous caulocystidia, it is well defined and morphologically similar species are not known. As mentioned before (Noordeloos 1980), this species is not restricted to bogs, but can also occur in moist grassland.



**Fig. 18** Microscopic structures. a. Basidiospores of *E. cuspidiferum* (KaiR1290, epitype); b. basidiospores of *E. rhodocylix* (ACN40, neotype). — c-d. *Entoloma incognitum* (KaiR1372, holotype). c. Pileipellis, minutely incrusting pigment indicated on the right; d. basidiospores. — e. Basidiospores of *E. clandestinum* (KaiR1273, neotype). — Scale bars: a-b, d-e = 10 µm; c = 20 µm.

The pileus shape and colour of the epitype is relatively typical for this species, however, it can also be more robust and rather convex as well as distinctly darker brown to almost black, and then hardly translucently striate (P.-A. Moreau, pers. comm.).

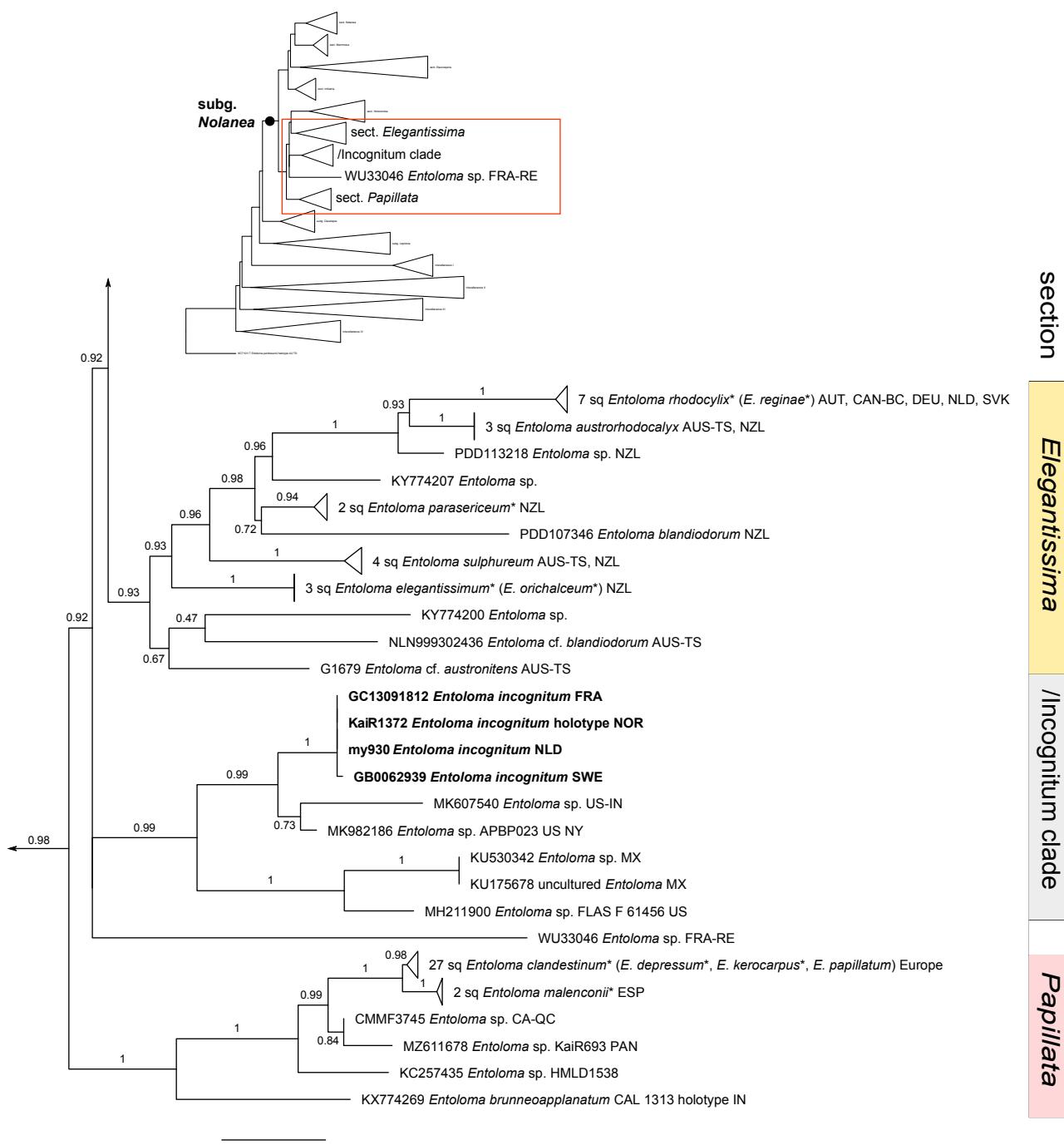
***Entoloma* sect. *Elegantissima* Reschke & Noordel., sect. nov.**  
— MycoBank MB 842256

Type species. *Entoloma elegantissimum* E. Horak. Fungi of New Zealand, Ngā Harore o Aotearoa 19: 220. 2008.

Species with mycenoid to omphalinoid basidiocarps. Pileus broadly conical, applanate to depressed, in various shades of brown, rather smooth, generally hygrophanous. Stipe thin, polished to fibrillose. Lamellae adnate to decurrent. Odour

indistinct, farinaceous, or sweetish aromatic. Basidiospores mainly isodiametrical to subisodiametrical, sometimes broadly heterodiametrical with average  $Q < 1.3$ , with 4–6 relatively rounded angles. Cheilocystidia rarely and inconsistently present. *Pileipellis* a cutis with indistinct to rather distinct subpellis of short, inflated cells, with minutely to distinctly incrusting pigment. Clamp connections abundant in all parts of the basidiocarp. On soil or rotten wood.

Notes — Species in this section (Fig. 19) are characterised by the combination of rather short, predominantly subisodiametrical basidiospores, incrusting pigment, and abundant clamp connections. Included are *E. austrorhodocalyx*, *E. elegantissimum*, *E. grave*, *E. parasericeum*, *E. rhodocylix* (see below), *E. sulphureum*, and possibly *E. blandiodorum*. A sequence



**Fig. 19** Partial maximum likelihood phylogram based on ITS of species of the sections *Elegantissima* and *Papillata*, and the */Incognitum* clade. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number after species name. Origin of corresponding specimens indicated by country codes after ISO 3166, combined to larger areas if appropriate. — Scale bar = estimated changes/nucleotide.

labelled *E. austronitens* is also included in the clade in the ITS phylogeny, however, it is not derived from type material and the specimen was not investigated for this study. Therefore, this species is not included here. Apart from *E. rhodoclylix* all known species in this section are distributed in the Southern Hemisphere.

***Entoloma elegantissimum*** E. Horak, Fungi of New Zealand, Ngā Harore o Aotearoa 19: 220. 2008

Heterotypic synonym. *Entoloma orichalceum* E. Horak, Fungi of New Zealand, Ngā Harore o Aotearoa 19: 130. 2008.

Notes — *Entoloma orichalceum* was simultaneously described with *E. elegantissimum*, the ITS sequences of the types of these two taxa are identical. *Entoloma orichalceum* was originally described with absent clamp connections, the examination of the holotype, however, revealed rather abundant clamp connections. Accordingly, the name *E. elegantissimum* is selected here, as the original description of this taxon fits better the current species concept.

***Entoloma rhodoclylix*** (Lasch) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 210. 1978 — Fig. 16d, 18b

Basionym. *Agaricus rhodoclylix* Lasch, Linnaea 4: 542. 1829, nom. sanct. Fr., Syst. Mycol. 3: 39. 1832. — Neotype (designated here): GERMANY, Brandenburg, Unterspreewald, Alt Schadow, c. N52°07'01" E13°56'32", approx. 45 m a.s.l., on rotten log of *Pinus* sp., 14 Oct. 2000, V. Kummer (M). — MycoBank MBT 10004743.

Heterotypic synonym. *Entoloma reginae* Noordel. & Chrispijn, in Noordeloos, Blumea 41(1): 7. 1996.

Notes — *Entoloma rhodoclylix* with its omphaloid habit with long decurrent lamellae is a rather untypical species in subg. *Nolanea*. A similar and relatively closely related species, *E. austrotrichocalyx*, occurs in the Southern Hemisphere. *Entoloma reginae* is here treated as a synonym described for reduced basidiocarps, as no significant differences are found in ITS and microscopical characters. Cheilocystidia were not observed in the neotype specimen as well as in several further specimens of *E. rhodoclylix*.

***Entoloma sect. Papillata*** (Romagn.) Noordel., Persoonia 10(2): 246. 1979

Basionym. *Rhodophyllus* sect. *Papillati* Romagn., Bull. Mens. Soc. Linn. Lyon 43: 330. 1974. — Type species: *Entoloma papillatum* (Bres.) Dennis (= *E. clandestinum* (Fr.) Noordel., nom. sanct.).

Notes — Based on monophyletic clades and the type species (Fig. 19), this section is quite different from the earlier concept (Noordeloos 1979b, 1980). Species of the sect. *Papillata* share a rather dark brown pileus, a smooth, rather polished stipe, relatively dark brown lamellae, heterodiametrical basidiospores, and incrusting pigment throughout the basidiocarp including the lamellae. The pileipellis is a cutis and a subpellis not differentiated. Clamp connections are present in the hymenium or absent. Cheilocystidia are occasionally present, but without taxonomic value.

***Entoloma clandestinum*** (Fr.) Noordel., Persoonia 10(4): 456. 1980 — Fig. 16f, 18e

Basionym. *Agaricus clandestinus* Fr., Observ. Mycol. (Havniae) 2: 166 (1818), nom. sanct. Fr., Syst. Mycol. 1: 206. 1821. — Neotype (designated here): SWEDEN, Jämtlands län, Östersund, Frösön, Summarhagen, N63°10'20.6" E14°31'14.8", 380 m a.s.l., horse pasture, 29 Aug. 2018, K. Reschke, KaiR1273 (M). — MycoBank MBT 10004744.

Heterotypic synonyms. *Entoloma papillatum* (Bres.) Dennis, Bull. Soc. Mycol. France 69: 162. 1953. — *Nolanea papillata* Bres., Fungi Trident. 1(6-7): 75. 1887. — *Entoloma kerocarpus* Hauskn. & Noordel., Österr. Z. Pilzk. 8: 207. 1999. — *Entoloma depresso* Noordel. & Vesterh., in Noordeloos, *Entoloma* s.l., Fungi Europaei vol. 5a: 1151. 2004.

Notes — *Entoloma clandestinum* is a common species in oligotrophic grasslands and was previously mainly known under the name *E. papillatum*. The possibility that these two taxa are conspecific was already indicated by Vila et al. (2013). Kokkonen (2015) included also *E. kerocarpus* based on the type study including sequencing. *Entoloma depresso* represents specimens with depressed pileus, which are generally rare in this species. *Entoloma clandestinum* was in Europe sometimes confused with *E. sanvitalese*, a nolaneoid species which belongs to sect. *Leptonia* (Vidal et al. 2016). This possibly accounts for the different descriptions regarding clamp connections (Noordeloos 1980, 1992, Kokkonen 2015). According to the specimens analysed for this study clamp connections are abundant in the hymenium, but rare elsewhere.

### /Incognitum clade

Notes — This distinct and well supported clade includes, apart from *E. incognitum* (see below), several species of unresolved identity, based on GenBank sequences of material from North America (Fig. 19).

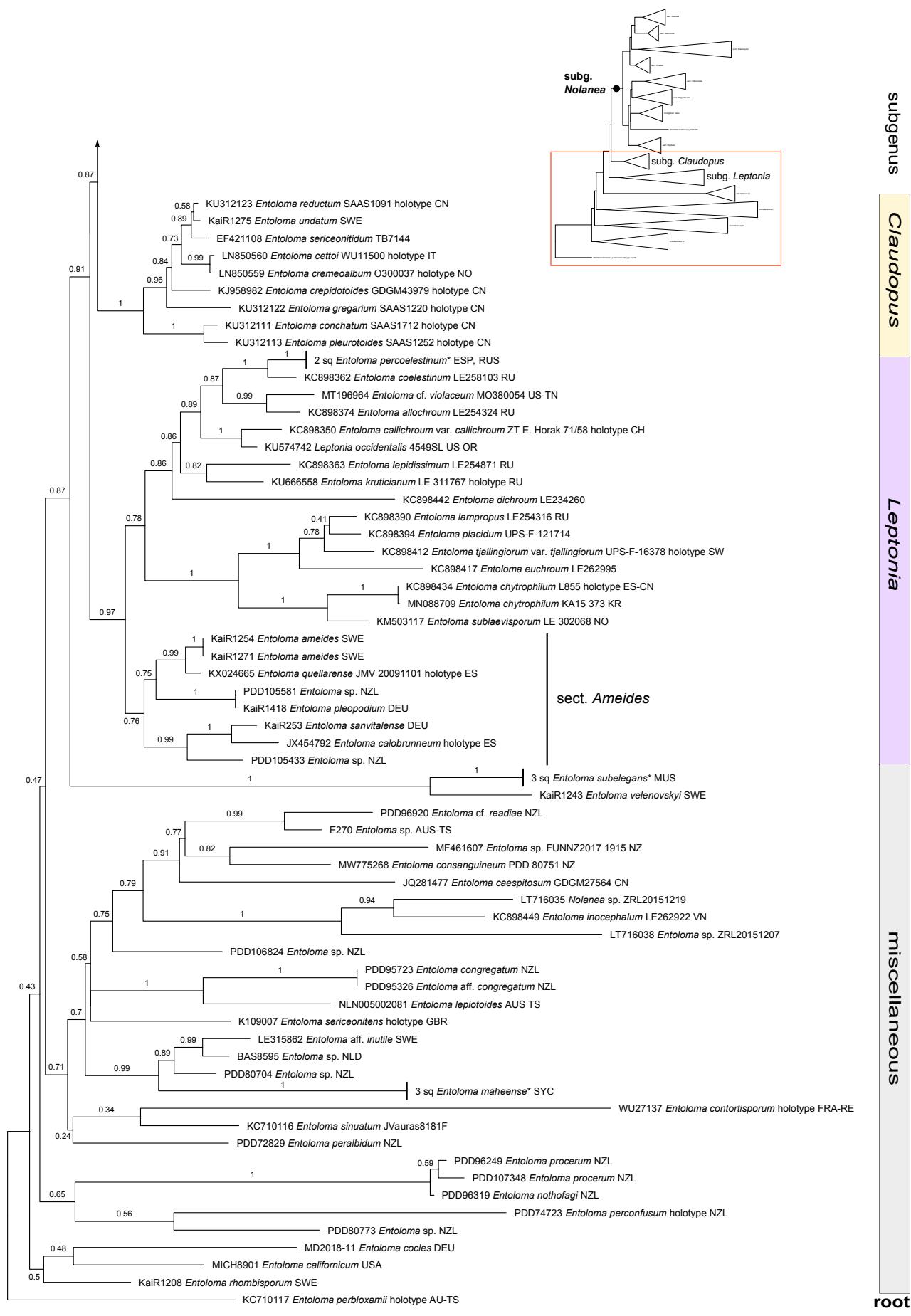
***Entoloma incognitum*** Reschke, Noordel., O.V. Morozova & Corriol, sp. nov. — MycoBank MB 842257; Fig. 16e, 18c, d misappl. *Entoloma solstitiale* (Fr.) Noordel., Persoonia 10(4): 505. 1980. — *Agaricus solstitialis* Fr., Epicr. Syst. Mycol. (Upsaliae): 152. 1838.

Etymology. *incognitus* (Latin) = undetected, incognito; refers to the rather anonymous history of this species, being known under a wrong name.

Holotype. NORWAY, near Stord, Hystadmarkjo, 10 m a.s.l., N59°47'21.2" E5°32'06.5", between bushes at the edge of a moist, *Alnus*-dominated forest, 4 Sept. 2019, T. Læssøe & J.H. Petersen, KaiR1372 (holotype M).

Basidiocarps mycenoid. Pileus 7–25 mm diam, conical, expanding to papillate convex, with deflexed to straight, sometimes crenate margin, brown at the centre, paler, yellowish brown with greyish tinge towards margin to almost white at the margin, pileal surface glabrous to minutely granulose, translucently striate almost to the centre, hygrophanous. Lamellae adnexed, almost free, ventricose, medium spaced to distant, initially white, pink upon maturity, with smooth and concolorous edge. Stipe rather cartilaginous, 15–50 × 0.6–2.5 mm, cylindrical, pale brownish grey, glabrous. Basal mycelium white, somewhat cottony. Odour indistinct to distinctly nitrous, taste not tested. Basidiospores 8.0–9.0–10.5 × 6.5–7.3–8.5 µm, Q = 1.05–1.24–1.40 (n = 83 spores of 3 specimens), mainly broadly heterodiametrical, sometimes subisodiametrical to rhomboid or almost quadrate in outlines, with predominantly 5, sometimes 4, or rarely 6 rather pronounced angles, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 26–35 × 11.0–12.5 µm, clavate, hyaline, 4-spored, sterigmata up to 4.5 µm long. Lamellar edge fertile. Hymenial cystidia absent. Hymenophoral trama regular, formed by long, cylindrical to subfusiform cells. Pileipellis predominantly a cutis, sometimes at parts loose and somewhat trichidermoid, composed of cylindrical upper hyphae, 6–12 µm wide, soon broader, cylindrical to fusiform towards pileitrama, without distinct subpellis. Pigment yellowish to pale brownish, intracellular and in addition minutely incrusting. Stipitipellis composed of long, cylindrical, 2.0–6.5 µm wide cells. Clamp connections abundant in hymenium and subhymenium, rare to absent elsewhere.

Habitat — With certainty known from brushy vegetation in coastal Norway, a montane *Ilex aquifolium* stand in the Pyrenees, and a coniferous forest in Sweden.



**Fig. 20** Partial maximum likelihood phylogram based on ITS of species of the subgenera *Claudopus* and *Leptonia*, as well as miscellaneous nolaneoid and outgroup taxa. Species clades collapsed, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166. — Scale bar = estimated changes/nucleotide.

*Additional specimens examined.* FRANCE, Département Hautes-Pyrénées, near Artigues, Le Garet, mountain *Ilex aquifolium* stand, 18 Sept. 2013, G. Corriol, GC13091812. — SWEDEN, Västra Götalands Län, Hällekis, near camping ground, between mosses in coniferous forest, 17 Aug. 1980, L. Stridvall (GB0062939, LE 302132).

Notes — *Entoloma incognitum* is characterised by basidiocarps with smooth, sometimes minutely granulose, deeply striate pileal surface, white lamellae, greyish, rather cartilaginous stipe, and a weakly differentiated pileipellis with rather minutely incrusting and distinct intracellular pigment. It was long treated under the name *E. solstitiale* (Noordeloos 1980). This species, however, was originally described with a dark, depressed pileus, emarginate lamellae, and fruiting in moist grassland in South Sweden (Scania) in mid of June (Fries 1838). The scanty description of Fries would allow to interpret *E. solstitiale* as a dark form of *E. vinaceum* or *E. sarcitum*, or a species of the complex around *E. sarcitulum/longistriatum*.

During the re-evaluations of species concepts in subg. *Nolanea*, it became clear that not only *E. chlorinosum* can have a nitrous odour, but also *E. infula* and *E. incognitum*. Thus, even though *E. incognitum* is only distantly related to species of sect. *Infularia*, it is morphologically strikingly similar to *E. infula* as well as *E. chlorinosum*. *Entoloma infula* has more regularly heterodiametrical basidiospores, distinctly incrusting pigment, and is seldom translucently striate more than halfway to the centre. *Entoloma chlorinosum* differs by smaller size of basidiocarps and basidiospores.

#### **Sections and subsections excluded from *Entoloma* subg. *Nolanea***

***Entoloma* sect. *Ameides*** (Largent) Reschke, O.V. Morozova, Noordel., comb. nov. — MycoBank MB 842258; Fig. 20

Basionym. *Nolanea* sect. *Ameides* Largent, Entolomatoid fungi of the Western United States and Alaska: 194. 1994. — Type species: *Entoloma ameides* (Berk. & Broome) Sacc.

Notes — *Entoloma ameides* is included in subg. *Leptonia* and forms a clade together with *E. calobrunneum*, *E. pleopodium*, *E. quellarens*, *E. sanvitale*, and an unidentified species (Fig. 20). These species share their nolanoid habit, have clamp connections at least at the base of basidia, and often have a sweet smell. *Entoloma quellarens* is as an exemptional species which develops gasteroid, hypogeous basidiocarps (Vidal et al. 2016). Section *Ameides* is a sister clade to the other species in *Leptonia* according to the ITS phylogeny (Fig. 20). However, a study focusing on *Leptonia* is necessary to re-evaluate the sectional system of this subgenus.

***Entoloma* subsect. *Icterina*** Noordel. Persoonia 10(4): 514. 1980

Type species. *Entoloma icterinum* (Fr.) M.M. Moser, nom. sanct. = *E. pleopodium* (Bull. ex DC.) Noordel., nom. sanct.

Notes — *Entoloma pleopodium* is placed in subg. *Leptonia* and is related to *E. ameides*, which has a similar odour. A study focusing on subg. *Leptonia* is necessary to assess if the use of subsect. *Icterina* should be maintained with an emended concept.

***Entoloma* sect. *Canosericei*** Noordel., Beih. Nova Hedwigia 91: 95. 1987

Type species. *Entoloma canosericeum* (J.E. Lange) Noordel.

Notes — This section was described for *E. canosericeum* and *E. amicorum*. These two species share heterodiametrical

basidiospores, conspicuous cheilocystidia, incrusting pigment, and absence of clamp connections. Especially the broadly lageniform cheilocystidia exclude the placement of sect. *Canosericei* from subg. *Nolanea*.

***Entoloma* sect. *Lepiotoidei*** G.M. Gates & Noordel., Fungal Diversity Res. Ser. 22: 141. 2012

Type species. *Entoloma lepiotoides* G.M. Gates & Noordel.

Notes — *Entoloma lepiotoides* is a rather unique species with its peculiar pileipellis structure, concentrically cracking like in *Lepiota* spp. It is molecularly distant from *Nolanea* (Fig. 20). Two further species, *E. sepiaceovelutinum* and *E. strigosum* were placed in sect. *Lepiotoidei* (Noordeloos & Gates 2012), however, they were not included in the present study.

***Rhodophyllus* sect. *Luctuari*** Romagn., Bull. Mens. Soc. Linn. Lyon 43(9): 330. 1974

Type species. *Entoloma babingtonii* (A. Bloxam) Hesler.

Notes — Romagnesi (1974a) placed this section in subg. *Nolanea* but indicated that it is an alternative treatment of *Pouzarella* myces which itself was later replaced by *Entoloma* subg. *Pouzarella* due to nomenclatural reasons (Mazzer 1976, Noordeloos 1984). The description of sect. *Luctuari* was valid, thus it may be used in subg. *Pouzarella* in case the identity of *Agaricus babingtonii* can be resolved. The attempts and difficulties in interpreting the type specimen of this species were summarised by Noordeloos (1979a).

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

Basionym. *Entoloma* subsect. *Tristia* Noordel., Persoonia 10(4): 508. 1980. — Type species: *Entoloma triste* (Velen.) Noordel.

Notes — The sect. *Tristia* was initially described as subsection to accommodate *E. triste*, which deviates from species in *Nolanea* by nodulose basidiospores. Later, it was raised to the rank of section, placed in subg. *Inocephalus*, and *E. inutile*, *E. undulatosporum*, and *E. winterhoffii* were included (Wölfel & Noordeloos 1997). *Entoloma inutile* is distant from subg. *Nolanea* and now considered to belong to subg. *Trichopilus* (Haelewaters et al. 2020). No sequences of authentic material are currently published of the other three species, however, preliminary data (Noordeloos et al., unpubl.) indicate that none of them is close to subg. *Nolanea*. The combination of intracellular pigment, clamp connections, and nodulose spores is suitable to delimit these species morphologically from those of subg. *Nolanea*.

***Entoloma* subsect. *Cheilocystidiata*** Noordel., Persoonia 10(4): 510. 1980

Type species. *Entoloma velenovskyi* Noordel.

Notes — This subsection was erected for species with intracellular pigment and cheilocystidia of variable shape. *Entoloma velenovskyi* is distant from subg. *Nolanea* (Fig. 20) but none of the other species formerly included in subsection *Cheilocystidiata* is close to the type species. The other species previously included in this subsection either belong to other sections of *Nolanea*, viz., *E. langei* (= *E. ventricosum* in sect. *Holoconiota*), *E. magnalitudinis* (= *E. hirtipes* in sect. *Mammosa*), *E. cryptocystidiatum* (= *E. sericeum* in sect. *Nolanea*), *E. globuliferum* (in sect. *Staurospora*), or in the distant /Rhombisporum clade (*E. pratulense*) (Noordeloos et al. 2022a).

**Nolanea subsect. Cystomarginata** Largent, Mycologia 66(6): 1005. 1974

Type species. *Entoloma cystomarginatum* (Largent) Noordel. & Co-David.

Notes — This subsection was described for the type species with a relative unique combination of features: a sterile, serrulate lamellar edge with cylindrical to clavate cheilocystidia, incrusting pigment, and clamp connections in all parts of the basidiocarp. Later, the subsection was placed into *Inocephalus* (Largent 1994). Sequences of original material are not available. An ITS sequence in GenBank (MW732475) generated from a specimen identified as *Inocephalus cystomarginatus* (<https://mushroomobserver.org/355724>, accessed 12 Nov. 2021) has no close matches in Blast searches and can thus not be placed in an existing subgenus.

**Rhodophyllus sect. Paramammosi** Romagn., Les fondements de la taxonomie des *Rhodophylles* et leur classification: 60. 1978

Type species. *Entoloma elegans* (Romagn. & Gilles) Noordel. & Co-David

Notes — This section was described for species of *Nolanea* with intracellular pigment, often with clamp connections, and often with cheilocystidia. The type species, *E. elegans*, was not examined for this study. It has some affinities to *E. cocles* and *E. velenovskyi* and does not fit in the present, emended concept of *Nolanea*.

#### Species excluded from *Entoloma* subg. *Nolanea* or of unclear identity

**Entoloma palmense** Wölfel, Noordel. & Dähncke, in Wölfel & Noordeloos, Österr. Z. Pilzk. 10: 196. 2001

Notes — *Entoloma palmense* was described from the Canaries and regarding its description (Wölfel & Noordeloos 2001) it likely belongs to sect. *Staurosphaera*. However, the type specimen of *E. palmense* is lost, so new findings are necessary to assess its position.

**Entoloma pseudoconferendum** Noordel. & Wölfel, in Noordeloos, *Entoloma* s.l., Fungi Europaei vol. 5 (Saronno) 5(a): 955. 2004

Notes — A description of sequenced *E. pseudoconferendum* specimens was published by Karich et al. (2017). This species forms an unresolved, rather basal clade in *Entoloma* together with *E. sphagneti*.

**Entoloma pusillum** Noordel., Persoonia 12(3): 294. 1984

Notes — An ITS sequence of the type of *E. pusillum* was published by Reschke et al. (2022). It is a species in the /Rhopalopodium clade of subg. *Entoloma*. Morphologically it has some affinity to *E. politum* which is also phylogenetically a relatively close related species.

**Entoloma sphaerocystis** Noordel., Persoonia 10(4): 485. 1980

Notes — Attempts to sequence the holotype of *E. sphaerocystis* were unsuccessful. It is likely that the conspicuous cheilocystidia were aberrant like in other *Nolanea* species which have only on occasion cheilocystidia. Because of this, *E. sphaerocystis* can currently not unambiguously be interpreted.

**Entoloma violaceovernum** Noordel. & Wölfel, in Noordeloos, Beih. Nova Hedwigia 91: 81. 1987

Notes — This species was described as similar to *E. vernum* but with a violet tinge in the pileus, a rancid odour, and smaller basidiospores. The type of *E. violaceovernum* is lost and accordingly new findings are necessary to re-evaluate this species.

## DISCUSSION

### Performance of primers and DNA loci

The observed high success rates in sequencing of ITS and LSU, and lower success rates for *RPB2* and *EF-1 $\alpha$*  are similar to results of an extensive comparison of loci and primers by Stielow et al. (2015). Comparisons of sequencing success of the mtSSU and other loci are not known to us. The success rate was slightly below that of ITS and LSU. The higher success in mtSSU sequencing compared to that of the single copy genes can be explained by a higher number of copies per cell and relatively conserved primer sites which require no or only low degenerate primers.

Alignments of mtSSU sequences obtained with MS1/MS2 and MS0B/MR1.1 differ generally in the two mismatching nucleotides as long as the primer site of MS2 is included. Conversely, the use of ITS sequences obtained with the reverse primer ITS4B together with assembled ITS-LSU sequences masks differences in the variable target site of the primer ITS4B. So, in alignments of sequences obtained with different primers, at least the primer sites of the shorter sequences should be excluded.

The comparison of performance of the molecular markers in phylogenetic inference demonstrated the best performance of *RPB2*, followed in decreasing order by *EF-1 $\alpha$* , ITS, mtSSU, and LSU. Similar well performance of *RPB2* and poor performance of LSU were also demonstrated by Co-David et al. (2009) using a data set of *Entolomataceae*. Similar patterns were observed by visual comparison of preliminary ML-phylogenies with a larger number, but different composition of sequences. According to these preliminary trees, the performance of ITS improves more than that of *EF-1 $\alpha$*  when more sequences are used. The ITS has the highest evolutionary rate of the five regions (Table 4) and the molecular evolution of the ITS includes length variation. Thus, the accuracy of alignments of ITS sequences decreases with distantly related taxa but improves by dense sampling (Simmons & Freudenstein 2003), which is demonstrated here by the well-supported large ITS phylogeny (Fig. 3, 7, 10, 12, 14, 15, 19, 20). However, *EF-1 $\alpha$*  sequences were often difficult to obtain and are currently scarcely present in GenBank. Thus, a thorough comparison is not possible due to the limited data and *EF-1 $\alpha$*  may be similarly more accurate with a larger number of sequences. Matheny et al. (2007) reported a lower resolution performance of *EF-1 $\alpha$*  compared to *RPB2*, however, their *RPB2* sequences were in average twice as long as those of *EF-1 $\alpha$* . The *EF-1 $\alpha$*  sequences in the present study were generally somewhat longer than those of *RPB2* but the performance of *EF-1 $\alpha$*  was still lower. The mtSSU was the second last performing marker and had the second highest scale factor. The mtSSU evolves mainly in its variable domains, including large insertions and deletions which are sometimes difficult to align accurately (Barroso et al. 2003, Hong & Jung 2004). The evolutionary rate can thus be underestimated when unique sequence fragments are excluded from the analysis due to the lack of alignable counterparts (Bruns & Szaro 1992). A denser sampling will also improve alignments of mtSSU sequences and thus increase its performance in phylogenetic inference. The LSU performed poorly and the 4-loci tree excluding the LSU was

rather insignificantly different from the 5-loci tree. With its low evolutionary rate, the LSU is probably not divergent enough to provide sufficient informative sites for phylogenetic inferences in subg. *Nolanea*. This result is contradictory to the supposed value of the LSU as a supplementary barcode (Schoch et al. 2012), however, comparably few *Agaricales* were included in that study and the sampling may not have been dense enough to reveal identical sequences of different species.

Regarding the three factors: performance in phylogenetic inferences, difficulty of sequencing, and abundance of sequences in the databases, the use of the three regions ITS, RPB2, and mtSSU is suggested as a suitable set for updates of the phylogeny of subg. *Nolanea*. The publication of taxonomic studies of *Entoloma* spp. without including ITS sequences is therefore discouraged.

### **Phylogeny and treatment of *Nolanea***

Subgenus *Nolanea* is monophyletic as has been demonstrated before (Karstedt et al. 2020). However, several species previously considered in *Nolanea* form unique lineages. The position of these species, viz., *E. californicum*, *E. lepiotoides*, *E. rhombisporum*, *E. subelegans*, and *E. velenovskyi* remains unresolved. Several authors preferred to treat *Nolanea* at generic rank (Pegler 1977, Orton 1991, Largent 1994), recently Karstedt et al. (2020). However, the use of *Nolanea* at generic rank would leave the aforementioned species without assignment to a genus and therefore at least three new genera would have to be described. More such lineages might be found if material of more species, e.g., the specimens of Romagnesi & Gilles (1979), were studied. For these reasons, and also with regard to the coherent concept of *Entoloma* as a large genus, the use of *Nolanea* at subgeneric rank should be maintained.

### **Characters in subgenus *Nolanea***

Several taxa of *Nolanea* were described due to their relatively conspicuous cheilocystidia, e.g., *E. cryptocystidiatum* and *E. testaceum* var. *bavaricum*, which are now shown to be synonyms of species normally without cheilocystidia. Thus, the presence/absence of scattered cheilocystidia does not seem to have taxonomic importance. The species of sect. *Mammosa*, however, form an exception and share a lamellar edge which is sterile or at least almost sterile due to abundant cheilocystidia.

The pileipellis of species of *Nolanea* generally consists of a suprapellis of relatively narrow hyphae. As it is a character that is often hard to study on dried material, preferably fresh species should be observed. A well-differentiated subpellis of ellipsoid cells is characteristic for species of sect. *Staurospora*, while the subpellis is less or not distinctly differentiated in the species of the other sections. A differentiated subpellis was already noted for species of *Nolanea* by Largent & Benedict (1971) and Noordeloos (1980). However, this character has so far not been used to delimit infrageneric taxa. Apart from the obvious subpellis structure in sect. *Staurospora*, it is often rather indistinct in other sections, and hard to differentiate from the underlying trama. Species of sect. *Nolanea* have sometimes a subpellis of short, inflated cylindrical cells while *E. cuspidiferum* has a subpellis of relatively long inflated cells.

The presence/absence of clamp connections in *Entoloma* spp. was considered of large taxonomic importance by Kühner & Romagnesi (1953). Since then, it has been used in different extent: Orton (1960) completely neglected clamp connections. Hesler (1967) explained that he did not attach much value to this character and many of his species described without clamp connections are actually clamped (Noordeloos 1987). Horak (1973, 1980, 2008), Largent (Largent & Thiers 1972, Largent 1974, 1994), and Noordeloos (1980, 1992, 2004, Noordeloos

& Gates 2012) generally analysed and described the presence/absence of clamp connections, including the information if clamps occurred only in the hymenium or in all parts of the basidiocarp. However, the diagnosis of sect. *Efibulatae* (Largent 1974) for supposedly non-clamped species which were later revealed to be clamped demonstrates the difficulty of assessing this character. The presence/absence of clamp connections, including presence in all parts of the basidiocarp or only in the hymenium, is a consistent character in species of subg. *Nolanea* and indispensable for species identification. While the presence/absence of clamp connections is rather uniform in most sections, there are exceptions of the rule in almost all of them (Fig. 4). In general, as is demonstrated in recent attempts to reconstruct a phylogeny of the whole genus *Entoloma* (Co-David et al. 2009, Baroni & Matheny 2011, Noordeloos & Gates 2012, He et al. 2013), there seems to be a trend within the genus to lose clamp connections. The species of basal clades (e.g., sections *Calliderma* and *Turfosa*, /*Prunuloides* clade) have abundant clamp connections in the whole basidiocarp, whereas those of derived clades (e.g., subgenera *Cyanula* and *Pouzarella*) are often clampless. The ability to proliferate and reproduce without the necessity of clamp formation may be an evolutionary advantage. Apart from the general loss of clamp connections in *Nolanea* in parts other than the hymenium, the absence of clamps is strongest in the sect. *Staurospora*. However, it is not clear if the common ancestor of the species of this section had no clamp connections and a few species have regained these, or if the common ancestor had clamp connections and these were lost several times and only retained by few species.

The polyhedroid basidiospores of *Entoloma* spp. are the most peculiar feature in this genus. Noordeloos (1992) established that the use of isodiametrical, subisodiametrical, and heterodiametrical is used for spores with Q values of 1.0–1.1, 1.1–1.2, and > 1.2, respectively. A strong phylogenetic signal of spore shapes is demonstrated in the ancestral character state estimation (Fig. 5) using a simplified threshold of  $Q_{av.} = 1.25$  for 'isodiametrical' vs 'heterodiametrical' spores. Cruciform basidiospores evolved at least two times in sect. *Staurospora* from heterodiametrical basidiospores. According to small molecular distances between species with heterodiametrical and cruciform spores, and the existence of a species with transitional forms, *E. transitionisporum*, the evolution of cruciform basidiospores was supposed to happen relatively fast (Reschke et al. 2022). A few species with a fraction of in outline rhomboid to quadrate basidiospores were placed in *Nolanea*, especially *E. conicum*, and *E. alboumbonatum* which is here treated as a synonym of the latter. However, Karstedt et al. (2019) demonstrated that these spores are not cuboid. Regarding their three-dimensional form, basidiospores of *Entoloma* spp. have further characters and especially the structure of the spore base was considered to be a taxonomic informative character (Kühner & Boursier 1929, Romagnesi 1941, Pegler & Young 1979, Karstedt et al. 2019). Reschke et al. (2022) demonstrated that both types of the spore base, the simple base and the dièdre basal exist in subg. *Nolanea*. Few information is available about consistency of the basidiospore base in the sections of *Nolanea*. However, currently only species with simple base, *E. conferendum*, *E. paraconferendum*, *E. transitionisporum*, are known of the sect. *Staurospora*. Therefore, the base type of more species should be analysed to test the hypothesis that this character is useful for infrageneric classification at ranks below subgenus.

The type of pigmentation has been used to delimit taxa in subg. *Nolanea* since Kühner & Romagnesi (1953). Since then, this character has been regarded as phylogenetically informative and was used as one of the key characters to define sections in *Nolanea* (Largent & Thiers 1972, Romagnesi 1974a,

Noordeloos 1980). As demonstrated by the ancestral character state estimation (Fig. 6), this character is less reliable for infra-generic considerations than previously thought, only the sections *Nolanea* and *Elegantissima* have an exclusive, dominant pigment type. Species with dominantly incrusting pigment can, however, have some intracellular pigment in addition, which is often observed at species of sect. *Nolanea*. Such weak, additional intracellular pigment is apparently inconstant and is especially difficult to determine in old, dried specimens. Species with exclusively intracellular pigment, like *E. conferendum* and *E. milthalerae*, have only rarely some additional incrusting pigment in their pileipellis.

### Distribution patterns

Species of the subg. *Nolanea* occur all over the world, while they have their largest diversity apparently in north and south temperate regions. They seem hardly to be present in tropical lowland habitats while species of other subgenera, e.g., *Cyanula*, are known from such habitats (Reschke et al. 2022). However, the data used in this study were not equally distributed geographically. While Australasia and temperate to boreal Eurasia were relatively well represented, few data were available for Africa, South America, and South Asia, and the data were incomplete for North America. In addition, *Entoloma* is especially species-rich in habitats with high conservation value (Horak 1978, Noordeloos & Hausknecht 1989, Noordeloos & Morozova 2010, Griffith et al. 2013, Noordeloos et al. 2017), while pristine habitats in tropical lowlands are often either destroyed or difficult to access.

Four different main distribution patterns can be inferred: a worldwide distribution as in sections *Staurospora* and *Holoconiota*, a mainly north hemispherical distribution as in sect. *Infularia*, *Mammosa*, and subsections *Cosemeoexonema* and *Minuta*, a mainly south hemispherical distribution in sect. *Elegantissima*, and a (sub-)tropical to south hemispherical distribution as in clades I and II in sect. *Nolanea*. Possibly these patterns reflect to some extent the phylogeographic history of these clades. However, the proportion of further, not included species is likely to be high in some of the clades.

A sound estimation about the geographic area of origin of subg. *Nolanea* is not possible. The most basal clade, sect. *Papillata*, includes species from the Northern Hemisphere, i.e., North America and Eurasia, with the southernmost sequenced records from India and Panama. No species of this section were detected in the material studied from Australasia. Dennis (1953) reported *E. papillatum* from Trinidad. Based on this specimen and a further specimen from Chile, Horak (1978) concluded that the corresponding species is not conspecific with *E. papillatum* s.str. Thus, it remains unclear if species of sect. *Papillata* are distributed in South America. The clade around *E. incognitum* is also a relatively basal clade in subg. *Nolanea*. It consists of data representing material from the Northern Hemisphere, esp. North America. However, a long-branched singleton neighbouring the /*Incognitum* clade was derived from material from La Réunion. A denser sampling may reveal further basal lineages and is necessary to draw biogeographic conclusions.

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#### Supplementary material

**Fig. S1** Phylogenetic trees compared with Ktreedist, rooted to the (majority of) outgroup species (comparisons executed with unrooted trees). a. Reference tree of concatenated alignments of ITS, LSU, mtSSU, *RPB2*, and *EF-1 $\alpha$* ; b. ITS-tree; c. LSU-tree; d. mtSSU-tree; e. *RPB2*-tree; f. *EF-1 $\alpha$* -tree; g. 4-loci tree of concatenated alignments of ITS, mtSSU, *RPB2*, and *EF-1 $\alpha$* . — Scale bars = estimated changes/nucleotide.

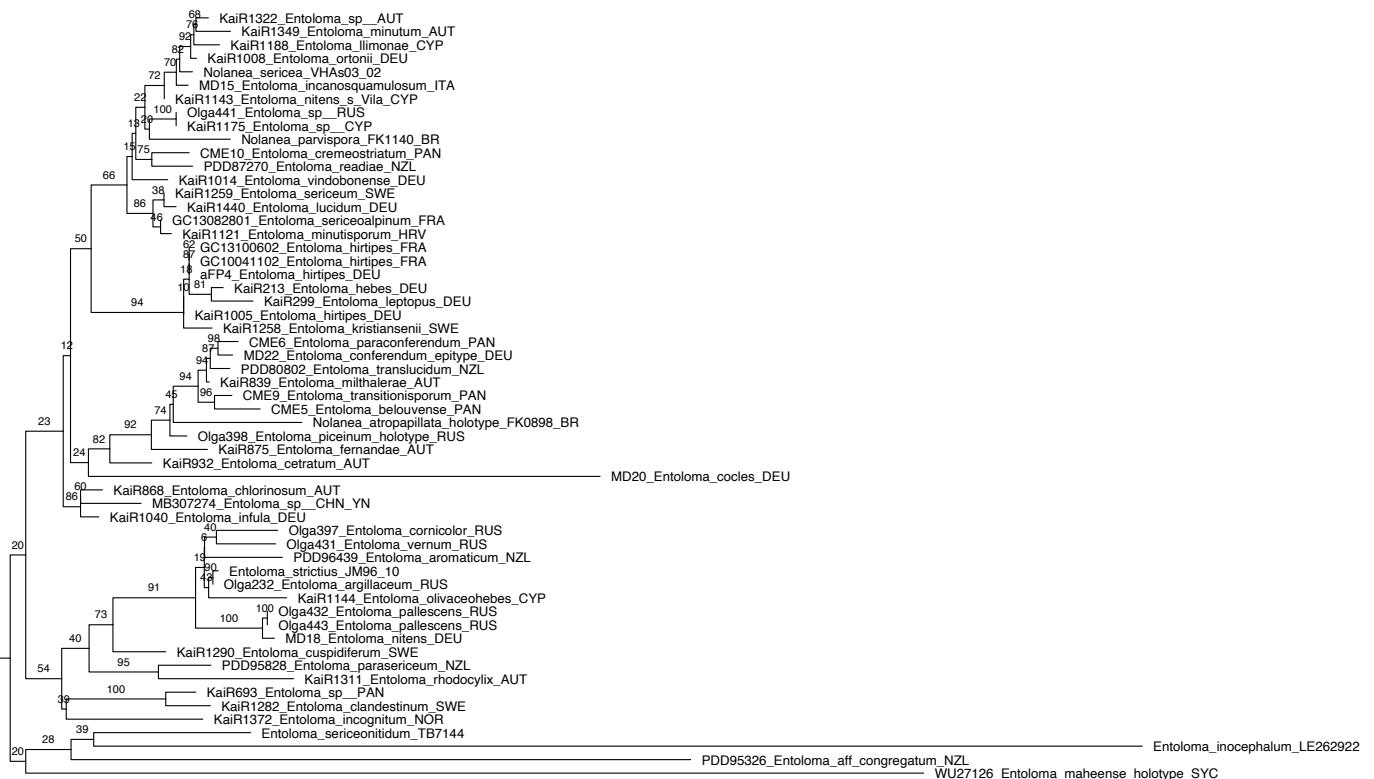
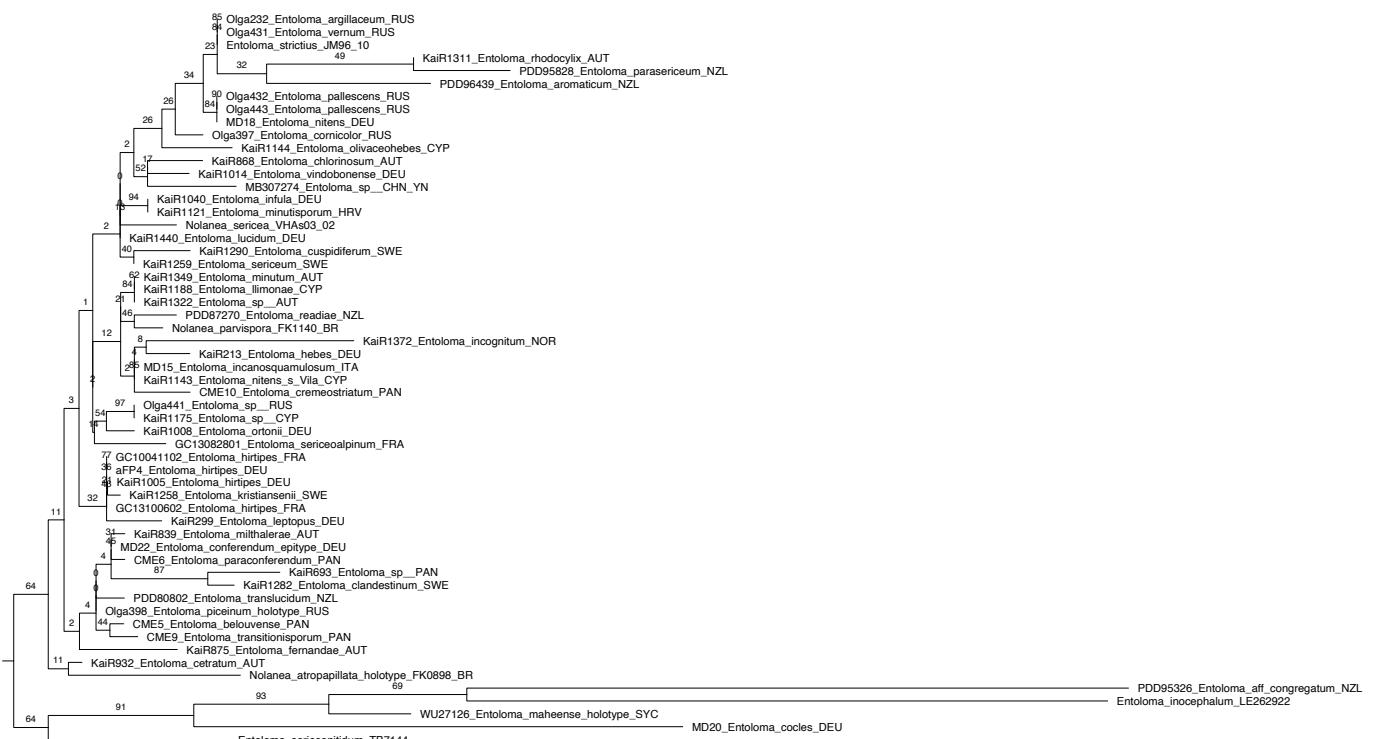
**Fig. S2** Maximum likelihood phylogram based on ITS of species of subg. *Nolanea*, including species of subgenera *Claudopus* and *Leptonia*, and species previously thought to belong to subg. *Nolanea*. Rooted to *Entoloma perbloxamii*. Values at branches = transfer bootstrap expectations. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166. — Scale bar = estimated changes/nucleotide.

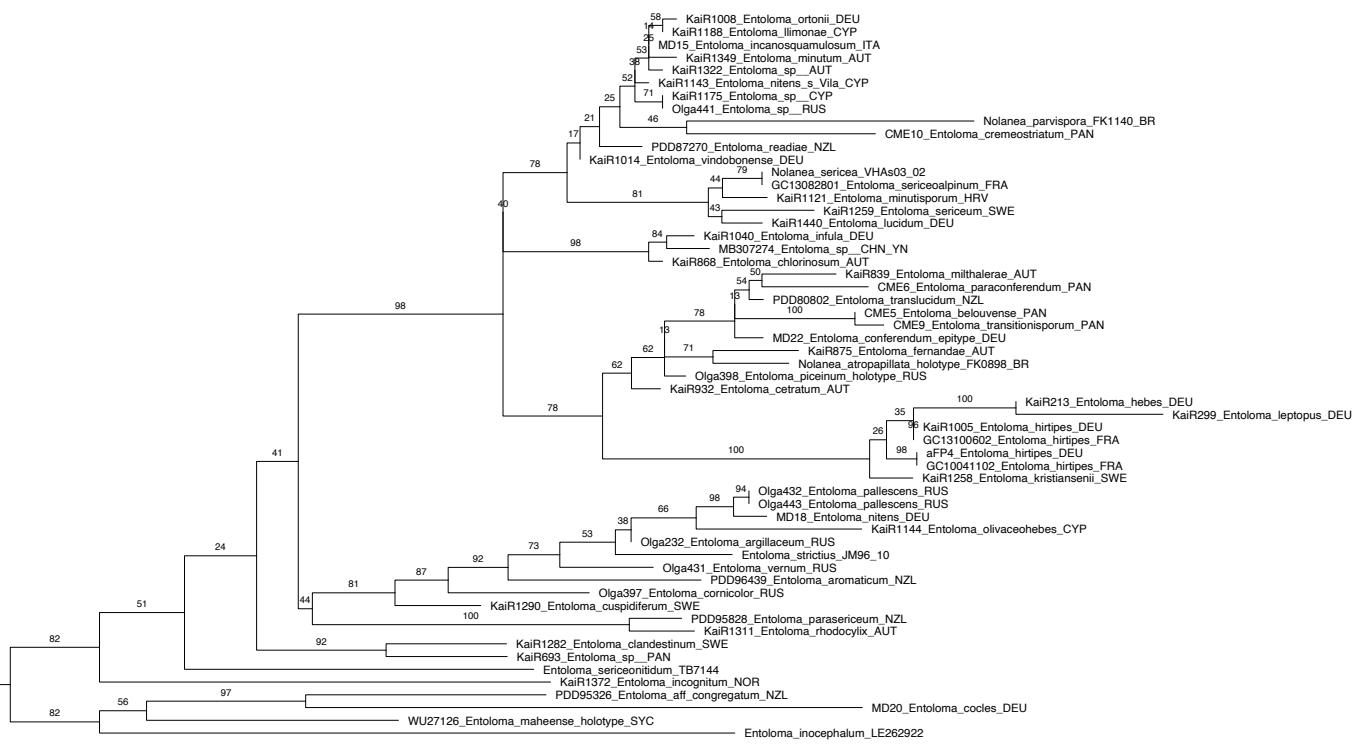
**Table S1** Accession numbers of DNA sequences and data of the corresponding specimens.

**a**

0.06

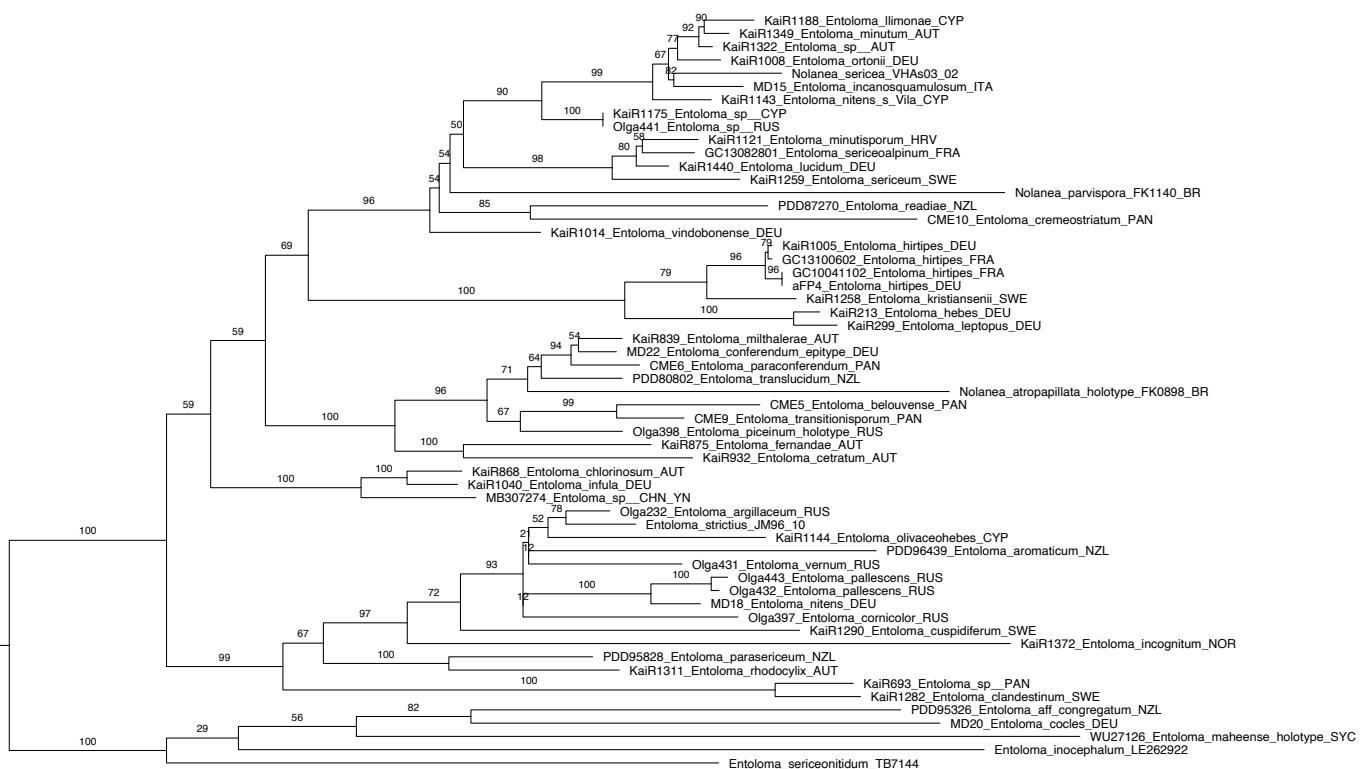
**Fig. S1** Phylogenetic trees compared with Ktreedist, rooted to the (majority of) outgroup species (comparisons executed with unrooted trees). a. Reference tree of concatenated alignments of ITS, LSU, mtSSU, *RPB2*, and *EF-1α*; b. ITS-tree; c. LSU-tree; d. mtSSU-tree; e. *RPB2*-tree; f. *EF-1α*-tree; g. 4-loci tree of concatenated alignments of ITS, mtSSU, *RPB2*, and *EF-1α*. — Scale bars = estimated changes/nucleotide.

**b****Fig. S1** (cont.) b. ITS-tree.**c****Fig. S1** (cont.) c. LSU-tree.



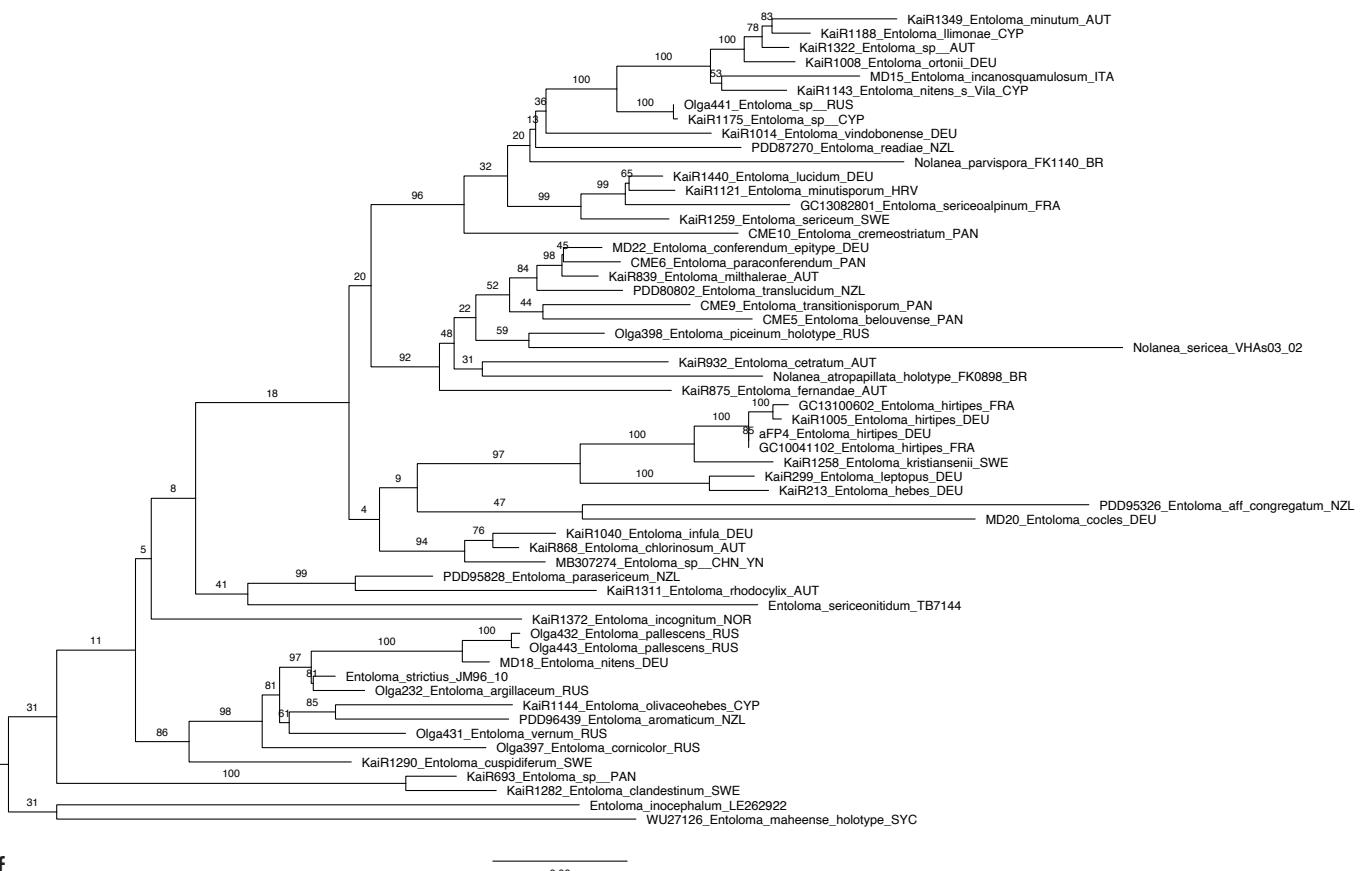
d

**Fig. S1** (cont.) d. mtSSU-tree.

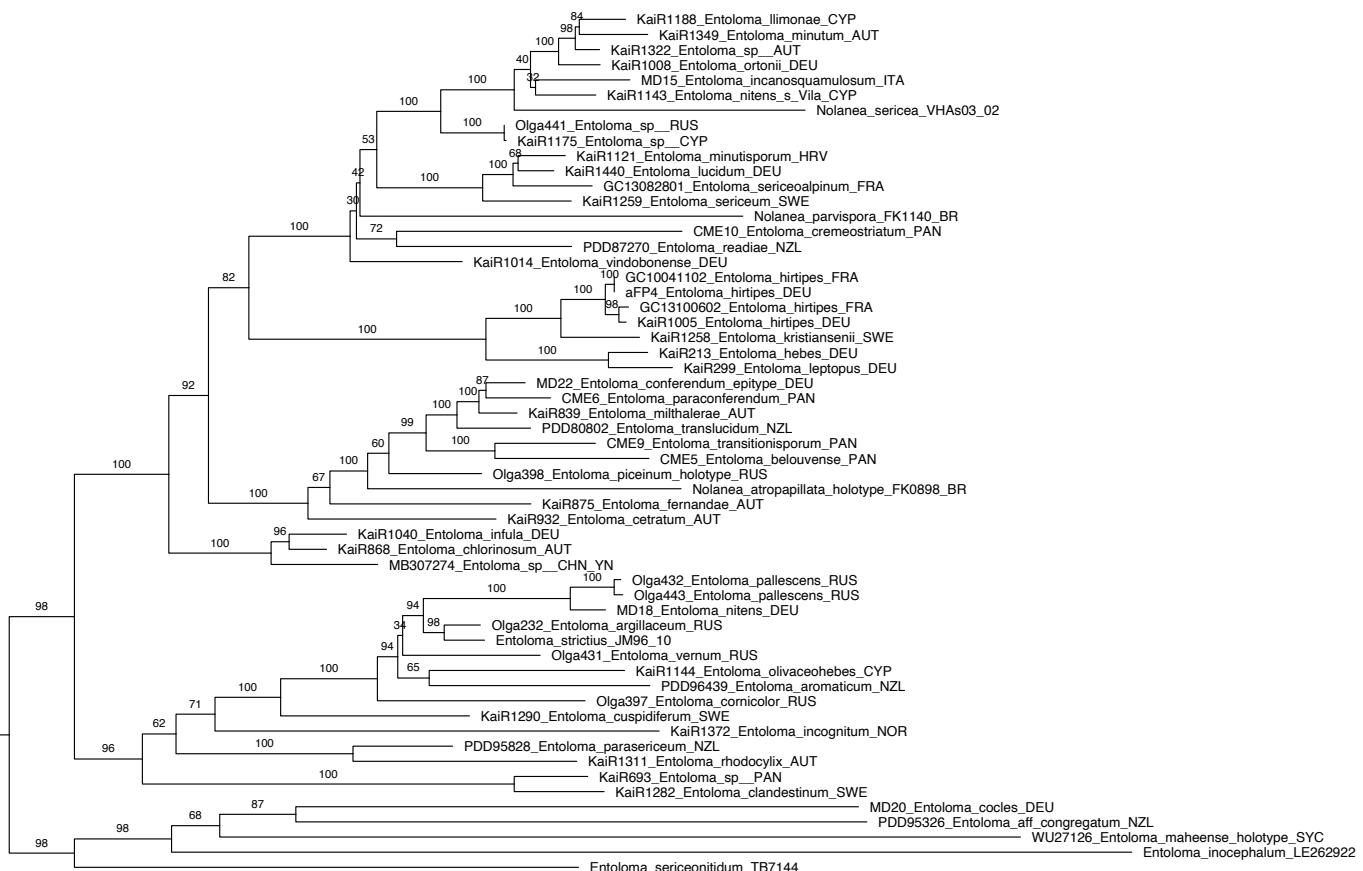


e

**Fig. S1** (cont.) e. *RPB2*-tree.

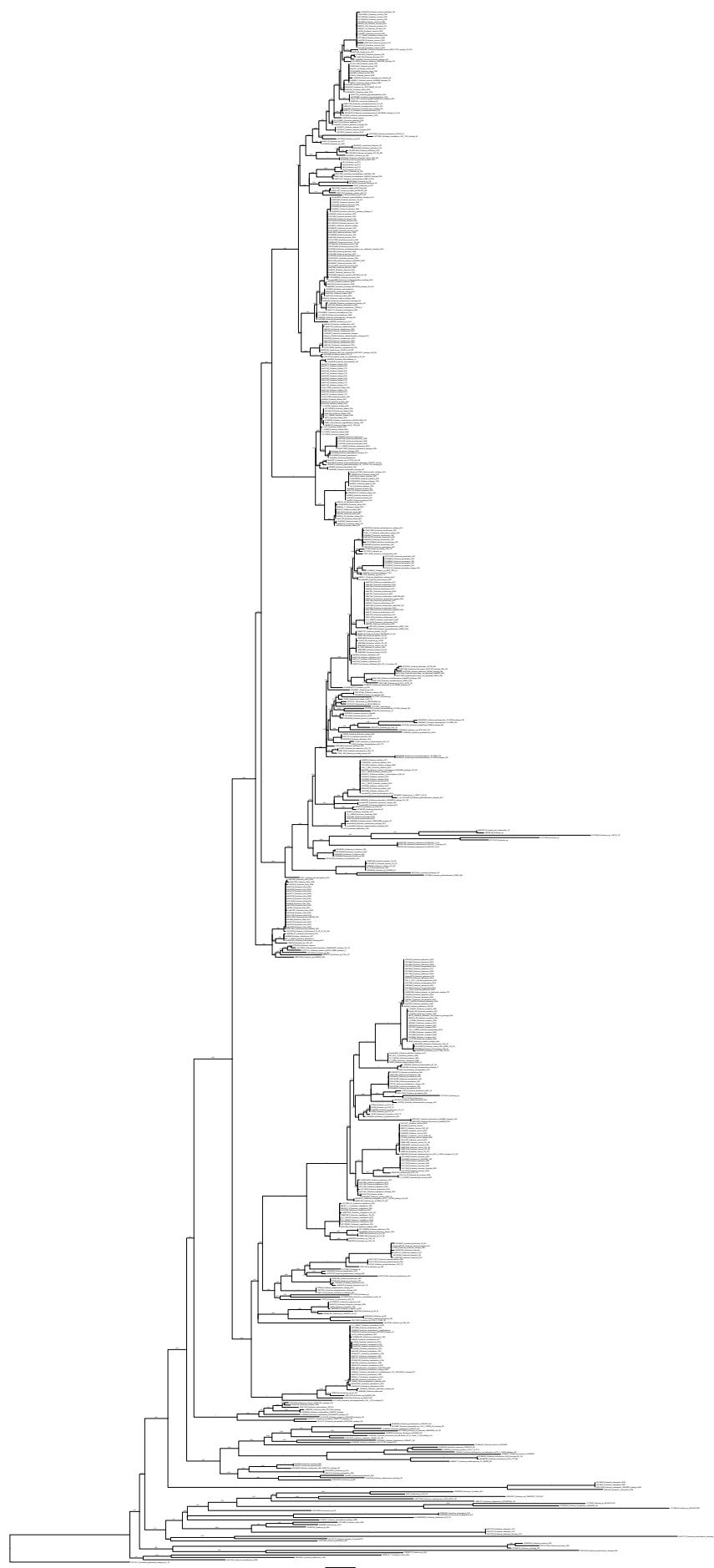


f

Fig. S1 (cont.) f. EF-1 $\alpha$ -tree.

g

Fig. S1 (cont.) g. 4-loci tree of concatenated alignments of ITS, mtSSU, RPB2, and EF-1 $\alpha$ .



**Fig. S2** Maximum likelihood phylogram based on ITS of species of subg. *Nolanea*, including species of subgenera *Claudopus* and *Leptonia*, and species previously thought to belong to subg. *Nolanea*. Rooted to *Entoloma perbioxamii*. Values at branches = transfer bootstrap expectations. Novel sequences with specimen voucher before species name, GenBank sequences with accession number before, and specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166. — Scale bar = estimated changes/nucleotide.

**Table S1** Accession numbers of DNA sequences and data of the corresponding specimens.

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
LE254327	<i>Entoloma</i>	<i>perplexum</i>	<i>Perplexum</i>	-	AU-TS	Australia: Tasmania	-	-	-	KC710117	
LE258103	<i>Entoloma</i>	<i>gallinaceum</i> var. <i>callochroum</i>	<i>gallinaceum</i> var. <i>callochroum</i>	CH	Switzerland	-	-	holotype	KC898359		
LE254871	<i>Entoloma</i>	<i>percolestinum</i>	<i>coelestinum</i>	RU	Russia	-	-	holotype	KC898359		
LE254324	<i>Entoloma</i>	<i>lepidissimum</i>	<i>coelestinum</i>	RU	Russia	-	-	holotype	KC898362		
UPS-F-121714	<i>Entoloma</i>	<i>allochroum</i>	<i>allochroum</i>	RU	Russia	-	-	holotype	KC898363		
UPS-F-163788	<i>Entoloma</i>	<i>lampropus</i>	<i>lampropus</i>	RU	Russia	-	-	holotype	KC898374		
LE2629956	<i>Entoloma</i>	<i>placidum</i>	<i>placidum</i>	SW	Sweden	-	-	holotype	KC898390		
L855	<i>Entoloma</i>	<i>tjallingiorum</i> var. <i>tjallingiorum</i>	<i>tjallingiorum</i> var. <i>tjallingiorum</i>	SW	Sweden	-	-	holotype	KC898394		
LE234260	<i>Entoloma</i>	<i>euchroum</i>	<i>euchroum</i>	-	Spain: Canaries	-	-	holotype	KC898412		
LE262922	<i>Entoloma</i>	<i>chytrophilum</i>	<i>chytrophilum</i>	-	-	-	-	holotype	KC898417		
FK0935	<i>Entoloma</i>	<i>dichroum</i>	<i>dichroum</i>	-	-	-	-	holotype	KC898442		
FK1732	<i>Entoloma</i>	<i>inocephalum</i>	<i>inocephalum</i>	VN	Vietnam	-	-	holotype	KC898449		
FK1049	<i>Nolanea</i>	<i>alberinae</i>	<i>alberinae</i>	BR	Brazil	-	-	holotype	KF679348		
FK1140	<i>Nolanea</i>	<i>tricholomatoides</i>	<i>tricholomatoides</i>	BR	Brazil	-	-	holotype	KF679351		
FK0898	<i>Nolanea</i>	<i>parvispora</i>	<i>parvispora</i>	BR	Brazil	-	-	holotype	KF679353		
K-N-188309	<i>Entoloma</i>	<i>atropapillata</i>	<i>atropapillata</i>	BR	Brazil	-	-	holotype	KF679354		
FK0891	<i>Entoloma</i>	<i>luteofuscum</i>	<i>luteofuscum</i>	IN	India	-	-	holotype	KF698730		
GDGM43979	<i>Nolanea</i>	<i>pallidosalmonea</i>	<i>pallidosalmonea</i>	BR	Brazil	-	-	holotype	KF738923		
Olga429	<i>Entoloma</i>	<i>percolestinum</i>	<i>percolestinum</i>	ES	Spain	-	-	holotype	KF745927		
MEL2238625	<i>Entoloma</i>	<i>conicum</i>	<i>conicum</i>	CN	China	-	-	holotype	KJ705168		
MEL2135806	<i>Entoloma</i>	<i>crepidotooides</i>	<i>crepidotooides</i>	RU	Russia	-	-	holotype	KJ968982		
KA12-1242	<i>Entoloma</i>	<i>piceinum</i>	<i>piceinum</i>	CA-BC	Canada: British Columbia	-	-	OM429	KM262035		
MCVE-28566	<i>Entoloma</i>	<i>sublaevigatum</i>	<i>sublaevigatum</i>	NO	Norway	-	-	holotype	KM503117		
TH9137	<i>Richonella</i>	sp.	sp.	AU	Australia	-	-	holotype	KP191911		
SAAS1712	<i>Richonella</i>	sp.	sp.	AU	Australia	-	-	holotype	KP191912		
SAAS1252	<i>Entoloma</i>	uncultured	<i>Entoloma</i>	CA-BC	Canada: British Columbia	-	-	holotype	KP403072		
SAAS1220	<i>Entoloma</i>	sp.	sp.	MX	Mexico	-	-	holotype	KR135338		
SAAS1091	<i>Entoloma</i>	sp.	sp.	KR	South Korea	-	-	holotype	KR673495		
F12-JS-73	<i>Entoloma</i>	<i>pulchellum</i>	<i>pulchellum</i>	IT	Italy	-	-	holotype	KT271741		
LE311767	<i>Entoloma</i>	<i>calabrum</i>	<i>calabrum</i>	GY	Guyana	-	-	holotype	KT339244		
LE311767	<i>Entoloma</i>	sp.	sp.	MX	Mexico	-	-	holotype	KU175678		
LE311767	<i>Entoloma</i>	uncultured	<i>Entoloma</i>	CN	China	-	-	holotype	KU312111		
LE311767	<i>Entoloma</i>	<i>conchatum</i>	<i>conchatum</i>	CN	China	-	-	holotype	KU312113		
LE311767	<i>Entoloma</i>	<i>pleurotooides</i>	<i>pleurotooides</i>	CN	China	-	-	holotype	KU312122		
LE311767	<i>Entoloma</i>	<i>gregarium</i>	<i>gregarium</i>	CN	China	-	-	holotype	KU312123		
LE311767	<i>Entoloma</i>	<i>reductum</i>	<i>reductum</i>	CN	China	-	-	holotype	KU530342		
LE311767	<i>Entoloma</i>	sp.	sp.	MX	Mexico	-	-	holotype	KU574737		
LE311767	<i>Nolanea</i>	sp.	sp.	US-OR	USA: Oregon	-	-	holotype	KU574738		
LE311767	<i>Entoloma</i>	<i>verna</i> var. <i>isodiametrica</i>	<i>verna</i> var. <i>isodiametrica</i>	US-OR	USA: Oregon	-	-	holotype	KU574742		
LE311767	<i>Leptonia</i>	cf. <i>bicoloripes</i>	cf. <i>bicoloripes</i>	US-OR	USA: Oregon	-	-	holotype	KU666558		
LE311767	<i>Entoloma</i>	<i>occidentalis</i>	<i>occidentalis</i>	RU	Russia	-	-	holotype	KX024665		
LE311767	<i>Entoloma</i>	<i>krutikanum</i>	<i>krutikanum</i>	ES	Spain	-	-	holotype	KX523174		
LE311767	<i>Entoloma</i>	<i>quellarensis</i>	<i>quellarensis</i>	DE	Germany	-	-	holotype	KX574752		
LE311767	<i>Entoloma</i>	<i>mittalae</i>	<i>mittalae</i>	IN	India	-	-	holotype	KX774267		
LE311767	<i>Entoloma</i>	<i>luteodiscum</i>	<i>luteodiscum</i>	IN	India	-	-	holotype	KX774268		
LE311767	<i>Entoloma</i>	<i>brunneoplumatum</i>	<i>brunneoplumatum</i>	CL	Chile	-	-	holotype	KY462561		
LE311767	<i>Entoloma</i>	<i>vernatum</i>	<i>vernatum</i>	US-CA	USA: California	-	-	holotype	KY510810		
LE311767	<i>Entoloma</i>	sp.	sp.	-	-	-	-	holotype	KY774200		

**Table S1** (cont.)

Table S1 (cont.)

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
C-F127081	<i>Entoloma</i>	<i>hirtipes</i>			Denmark		18-Nov-1979	T. Brandt-Petersen			
C-F127082	<i>Entoloma</i>	<i>hirtipes</i>			Denmark		16-Oct-1977	H. Knudsen			
C-F127083	<i>Entoloma</i>	<i>hirtipes</i>			Denmark		21-Oct-1976	H. Knudsen			
C-F18094	<i>Entoloma</i>	<i>ventricosum</i>			Denmark		12-Apr-1992	M. Christensen			
C-F27786	<i>Entoloma</i>	<i>cuneatum</i>			Denmark		19-Apr-1998	E. & P.E. Brandt			
C-F29704	<i>Entoloma</i>	<i>cuneatum</i>			Denmark		14-Jun-1986	J. Vesterholt			
C-F38494	<i>Entoloma</i>	<i>cuneatum</i>			Denmark		13-Apr-1998	M. Sasa			
C-F43868	<i>Entoloma</i>	<i>hirtipes</i>			Denmark		27-Oct-2004	J. Vesterholt			
C-F90612	<i>Entoloma</i>	<i>cuneatum</i>			Denmark		02-Jun-1988	J. Vesterholt			
C4-3959	<i>Entoloma</i>	<i>depressum</i>			Denmark		29-Sep-2003	J. Vesterholt			
C5929	<i>Entoloma</i>	<i>langei</i>			Denmark		09-Aug-1979	T. Borgen			
CH15111605	<i>Entoloma</i>	<i>ortionii</i>			Denmark		16-Nov-2015	C. Hannoire			
Chrispijn090784	<i>Entoloma</i>	<i>reginae</i>			Netherlands		09-Jul-1984	R. Chrispijn			
CMMF1286	<i>Entoloma</i>	<i>vernun</i>			Canada: Quebec		04-May-1991	Y. Lamoureux			
CMMF1445	<i>Entoloma</i>	sp.			Canada: Quebec		25-Aug-1991	Y. Lamoureux			
CMMF1737	<i>Entoloma</i>	sp.			Canada: Quebec		09-Aug-1992	Y. Lamoureux			
CMMF1798	<i>Entoloma</i>	<i>incanosquamulosum</i>			Canada: Quebec		05-Sep-1992	Y. Lamoureux			
CMMF1869	<i>Entoloma</i>	sp.			Canada: Quebec		22-Jun-1993	Y. Lamoureux			
CMMF3305	<i>Entoloma</i>	sp.			Canada: Quebec		28-May-1999	Y. Lamoureux			
CMMF3307	<i>Entoloma</i>	<i>cuspidiferum</i>			Canada: Quebec		30-Jun-1999	Y. Lamoureux			
CMMF3357	<i>Entoloma</i>	<i>cuspidiferum</i>			Canada: Quebec		18-Aug-1999	Y. Lamoureux			
CMMF3358	<i>Entoloma</i>	sp.			Canada: Quebec		18-Aug-1999	Y. Lamoureux			
CMMF3741	<i>Entoloma</i>	<i>incanosquamulosum</i>			Canada: Quebec		23-Jul-2003	Y. Lamoureux			
CMMF3745	<i>Entoloma</i>	sp.			Canada: Quebec		24-Jul-2003	Y. Lamoureux			
CMMF3956	<i>Entoloma</i>	<i>sericeum</i>			Canada: Quebec		24-Sep-2005	Y. Lamoureux			
CMMF432	<i>Entoloma</i>	<i>vernum</i>			Canada: Quebec		13-May-1989	Y. Lamoureux			
CMMF4787	<i>Entoloma</i>	<i>sericeum</i>			Canada: Quebec		15-Aug-1999	R. Boyer			
CMMF693	<i>Entoloma</i>	sp.			Canada: Quebec		27-Aug-1989	Y. Lamoureux			
CMMF7094	<i>Entoloma</i>	<i>vernum</i>			Canada: Quebec		12-May-1984	R. McNeil			
CMMF7540	<i>Entoloma</i>	<i>vernum</i>			Canada: Quebec		12-May-1984	R. McNeil			
CMMF8550	<i>Entoloma</i>	sp.			Canada: Quebec		20-May-2006	J. Labrecque			
CMMF8583	<i>Entoloma</i>	sp.			Canada: Quebec		24-May-2006	J. Labrecque			
CMMF8584	<i>Entoloma</i>	sp.			Canada: Quebec		25-May-2006	J. Labrecque			
CMMF8593	<i>Entoloma</i>	sp.			Canada: Quebec		28-May-2006	J. Labrecque			
CMMF9486	<i>Entoloma</i>	sp.			Canada: Quebec		07-Jul-2007	J. Labrecque			
Cro15	<i>Entoloma</i>	<i>leptopus</i>			Germany		2016	C. Manz			
Cro17	<i>Entoloma</i>	<i>hirtipes</i>			Croatia		Oct-2016	K. Göttl			
E1326	<i>Entoloma</i>	sp.			Australia: Tasmania		22-Nov-2001	G. Gates			
E1536	<i>Entoloma</i>	sp.			Australia: Tasmania		25-May-2002	G. Gates			
E1620	<i>Entoloma</i>	sp.			Australia: Tasmania		01-Aug-2001	G. Gates			
E1889	<i>Entoloma</i>	sp.			Australia: Tasmania		20-Jun-2003	G. Gates			
E1894	<i>Entoloma</i>	sp.			Australia: Tasmania		01-Jul-2003	G. Gates			
E270	<i>Entoloma</i>	sp.			Australia: Tasmania		20-Mar-1999	G. Gates			
EF02-A472	<i>Entoloma</i>	<i>leuconitens</i>			Greece		29-Oct-2002	E. Polemis			
Eth12	<i>Entoloma</i>	sp.			Ethiopia		11-Dec-2014	A. Gminder			
Eth14	<i>Entoloma</i>	sp.			Ethiopia		05-Dec-2014	A. Gminder			
Eth3	<i>Entoloma</i>	sp.			Ethiopia		2014	A. Gminder			
Eth4	<i>Entoloma</i>	sp.			Ethiopia		2014	A. Gminder			
Eth7	<i>Entoloma</i>	sp.			Ethiopia		2014	A. Gminder			
Eth8	<i>Entoloma</i>	sp.			Ethiopia		2014	A. Gminder			
G1584	<i>Entoloma</i>	<i>maidea</i>			Australia: Tasmania		2011				

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
G1589	Entoloma	chrysopus			Australia: Tasmania	-	2011	-	OL338059		
G1592	Entoloma	sp.			Australia: Tasmania	-	2009	-	OL338060		
G1603	Entoloma	brevispermum			Australia: Tasmania	-	1999	-	OL338061		
G1625	Entoloma	fibrospileatum			Australia: Tasmania	-	2011	-	OL338062		
G1655	Entoloma	austrotrichocalyx			Australia: Tasmania	-	2003	-	OL338063		
G1672	Entoloma	aromaticum			Australia: Tasmania	-	2011	-	OL338064		
G1679	Entoloma	sp.			Australia: Tasmania	-	2011	-	OL338065		
G1681	Entoloma	sp.			Australia: Tasmania	-	2011	-	OL338066		
GB0062939	Entoloma	incognitum			Sweden	-	17-Aug-1980	L. & A. Stridvall	OM486		
GB0074419	Entoloma	clandestinum			Sweden	-	14-Sep-1978	S. Jacobsson	OM487		
GC00092201	Entoloma	ortionii			France	-	22-Sep-2000	G. Corriol			
GC01102507	Entoloma	sericeum			France	-	25-Oct-2001	G. Corriol			
GC02100401	Entoloma	ortionii			France	-	04-Oct-2002	G. Corriol			
GC02102301	Entoloma	clandestinum			France	-	23-Oct-2002	G. Corriol			
GC02102306	Entoloma	leptopus			France	-	23-Oct-2002	G. Corriol			
GC02102308	Entoloma	sericeum			France	-	23-Oct-2002	G. Corriol			
GC03091508	Entoloma	tortiliforme			France	-	15-Sep-2003	G. Corriol			
GC04102601	Entoloma	minutum			France	-	26-Oct-2004	G. Corriol			
GC05043001	Entoloma	vernus			France	-	30-Apr-2005	G. Corriol			
GC05091403	Entoloma	clandestinum			France	-	14-Sep-2005	G. Corriol			
GC07092601	Entoloma	pygmaeopapillatum			France	-	26-Sep-2007	G. Corriol			
GC10041102	Entoloma	hirtipes			France	-	11-Apr-2010	G. Corriol			
GC11092508	Entoloma	atlanticum			France	-	25-Sep-2011	G. Corriol			
GC12091101	Entoloma	cuspidiiferum			France	-	11-Sep-2012	G. Corriol			
GC13082801	Entoloma	sericeoalpinum			France	-	28-Aug-2013	G. Corriol			
GC13091803	Entoloma	minutum			France	-	18-Sep-2013	G. Corriol			
GC13091804	Entoloma	minutum			France	-	18-Sep-2013	G. Corriol			
GC13091812	Entoloma	incognitum			France	-	18-Sep-2013	G. Corriol			
GC13091816	Entoloma	sericeum			France	-	18-Sep-2013	G. Corriol			
GC13100602	Entoloma	hirtipes			France	-	06-Oct-2013	G. Corriol			
GC13102801	Entoloma	assiduum			France	-	28-Oct-2013	G. Corriol			
GC14112812	Entoloma	sericeum			France	-	28-Nov-2014	G. Corriol			
GC14112815	Entoloma	sericeum			France	-	28-Nov-2014	G. Corriol			
GC15081913	Entoloma	hirtipes			France	-	19-Aug-2015	G. Corriol			
GC16112902	Entoloma	hirtipes			France	-	29-Nov-2016	G. Corriol			
GC16112904	Entoloma	hebes			France	-	29-Nov-2016	G. Corriol			
GC17090301	Entoloma	cuspidiiferum			France	-	03-Sep-2017	G. Corriol			
GC17090302	Entoloma	vindobonense			France	-	03-Sep-2017	G. Corriol			
GC18010303	Entoloma	lilimoneae			France	-	03-Jan-2018	G. Corriol			
GC19102406	Entoloma	ortionii			France	-	24-Oct-2019	G. Corriol			
GC36092300	Entoloma	hebes			France	-	23-Sep-1996	G. Corriol			
GC37090302	Entoloma	sericeum			France	-	03-Sep-1997	G. Corriol			
GC97122208	Entoloma	cuspidiiferum			France	-	22-Dec-1997	G. Corriol			
GC38041803	Entoloma	argillaceum			France	-	03-Jan-2018	G. Corriol			
GC38070301	Entoloma	caeruleum			France	-	18-Apr-1998	G. Corriol			
GC38091203	Entoloma	clandestinum			France	-	03-Jul-1998	G. Corriol			
GC39100110	Entoloma	sericeum			France	-	12-Sep-1998	G. Corriol			
GC39100111	Entoloma	clandestinum			France	-	01-Oct-1999	G. Corriol			
GC39101014	Entoloma	clandestinum			France	-	01-Oct-1999	G. Corriol			
GC39102302	Entoloma	leptopus			France	-	10-Oct-1999	G. Corriol			
He016849	Entoloma	pallescens			Finland	-	23-Oct-1999	G. Corriol			
						-	03-Jun-2010	U. & P. Salo			

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
H6044678	Entoloma	<i>minutum</i>			Finland		22-Aug-1878	P.A. Karsten	S771	lectotype	OL338110
JNL0804	Entoloma	<i>infula</i>			Netherlands		13-Oct-2017	P.-J. Keizer, J. Nuytinck & L. Kam		-	OL338111
K109007	Entoloma	<i>sericeonitens</i>			UK		12-Dec-1956	P.D. Orton		holotype	OL338113
K263312	Entoloma	<i>lucidum</i>			UK		01-Nov-1957	P.D. Orton		holotype	OL338114
K69721	Entoloma	<i>ortoni</i>			UK		22-Aug-1955	P.D. Orton		holotype	OL338112
KaIR1001	Entoloma	<i>sericeum</i>			Germany		27-Oct-2017	K. Reschke		-	OL338138
KaIR1005	Entoloma	<i>hirtipes</i>			Germany		27-Oct-2017	K. Reschke		-	OL338139
KaIR1006	Entoloma	<i>hirtipes</i>			Germany		27-Oct-2017	J. Schieber		-	OL338140
KaIR1008	Entoloma	<i>ortoni</i>			Germany		27-Oct-2017	J. Griese		-	OL338141
KaIR1011	Entoloma	<i>hirtipes</i>			Germany		27-Oct-2017	K. Reschke		-	OL338142
KaIR1014	Entoloma	<i>vindobonense</i>			Germany		27-Oct-2017	K. Reschke		-	OL338143
KaIR1015	Entoloma	<i>vindobonense</i>			Germany		27-Oct-2017	K. Reschke		-	OL338144
KaIR1019	Entoloma	<i>infula</i>			Germany		27-Oct-2017	K. Reschke		-	OL338145
KaIR1020	Entoloma	<i>hirtipes</i>			Germany		27-Oct-2017	K. Reschke		-	OL338146
KaIR1027	Entoloma	<i>conferendum</i>			Germany		28-Oct-2017	K. Reschke		-	OL338147
KaIR1040	Entoloma	<i>infula</i>			Germany		28-Oct-2017	K. Reschke		-	OL338148
KaIR1052	Entoloma	<i>clandestinum</i>			Germany		28-Oct-2017	K. Reschke		-	OL338149
KaIR1059	Entoloma	<i>hirtipes</i>			Germany		31-Oct-2017	K. Reschke		-	OL338150
KaIR1075	Entoloma	<i>hirtipes</i>			Croatia		12-Nov-2017	K. Reschke		-	OL338151
KaIR1104	Entoloma	<i>hebes</i>			Croatia		15-Nov-2017	K. Reschke		-	OL338152
KaIR1121	Entoloma	<i>minutisporum</i>			Croatia		17-Nov-2017	K. Reschke		-	OL338153
KaIR1125	Entoloma	<i>hebes</i>			Croatia		17-Nov-2017	K. Reschke		-	OL338154
KaIR1130	Entoloma	<i>leptopus</i>			Germany		21-Nov-2017	K. Reschke		-	OL338155
KaIR1132	Entoloma	<i>vindobonense</i>			Cyprus		24-Nov-2017	K. Reschke & W. Prüter		-	OL338156
KaIR1143	Entoloma	<i>assiduum</i>			Cyprus		14-Dec-2017	K. Reschke		-	OL338157
KaIR1144	Entoloma	<i>olivaceohebes</i>			Cyprus		14-Dec-2017	K. Reschke		-	OL338158
KaIR1175	Entoloma	sp.			Cyprus		20-Dec-2017	K. Reschke		-	OL338159
KaIR1180	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338160
KaIR1181	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338161
KaIR1182	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338162
KaIR1184	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338163
KaIR1185	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338164
KaIR1186	Entoloma	<i>hirtipes</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338165
KaIR1188	Entoloma	<i>limonae</i>			Cyprus		21-Dec-2017	K. Reschke		-	OL338166
KaIR1193	Entoloma	<i>hirtipes</i>			Cyprus		24-Dec-2017	K. Reschke		-	OL338167
KaIR1205	Entoloma	<i>infula</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338168
KaIR1208	Entoloma	<i>rhombisporum</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338169
KaIR1211	Entoloma	<i>infula</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338170
KaIR1215	Entoloma	<i>infula</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338175
KaIR1218	Entoloma	<i>infula</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338176
KaIR1220	Entoloma	<i>infula</i>			Sweden	320 m asl	26-Aug-2018	K. Reschke		-	OL338177
KaIR1222	Entoloma	<i>infula</i>			Sweden	360 m asl	27-Aug-2018	K. Reschke		-	OL338178
KaIR1225	Entoloma	<i>confundens</i>			Sweden	+ 350 m asl	28-Aug-2018	J. Ginwirt		-	OL338179
KaIR1227	Entoloma	<i>ameoides</i>			Sweden	150 m asl	28-Aug-2018	K. Reschke		-	OL338180
KaIR1243	Entoloma	<i>kristiansenii</i>			Sweden	150 m asl	28-Aug-2018	K. Reschke		-	OL338181
KaIR1259	Entoloma	<i>sericeum</i>			Sweden	150 m asl	28-Aug-2018	K. Reschke		-	OL338182
KaIR1260	Entoloma	<i>sericeum</i>			Sweden	150 m asl	28-Aug-2018	K. Reschke		-	OL338183

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
KaiR1262	Entoloma	<i>sericeum</i>			Sweden	150 m asl	28-Aug-2018	K. Reschke			OL338184
KaiR1271	Entoloma	<i>ameoides</i>			Sweden	360 m asl	29-Aug-2018	K. Reschke			OL338185
KaiR1273	Entoloma	<i>cladostinum</i>			Sweden	380 m asl	29-Aug-2018	K. Reschke			OL338186
KaiR1275	Entoloma	<i>undatum</i>			Sweden	380 m asl	29-Aug-2018	K. Reschke			OL338187
KaiR1278	Entoloma	<i>cladostinum</i>			Sweden	380 m asl	29-Aug-2018	K. Reschke			OL338188
KaiR1286	Entoloma	<i>sericeum</i>			Sweden	180 m asl	30-Aug-2018	K. Reschke			OL338189
KaiR1290	Entoloma	<i>cuspiferum</i>			Sweden	180 m asl	30-Aug-2018	K. Reschke			OL338190
KaiR1292	Entoloma	<i>cladostinum</i>			Sweden	210 m asl	30-Aug-2018	K. Reschke			OL338191
KaiR1311	Entoloma	<i>rhodocylix</i>			Austria		13-Sep-2018	K. Reschke			OL338192
KaiR1314	Entoloma	<i>millihalerae</i>			Austria		14-Sep-2018	K. Reschke			OL338193
KaiR1316	Entoloma	<i>conferendum</i>			Austria		14-Sep-2018	K. Reschke			OL338194
KaiR1317	Entoloma	<i>millihalerae</i>			Austria		14-Sep-2018	K. Reschke			OL338195
KaiR1318	Entoloma	<i>conferendum</i>			Austria		14-Sep-2018	K. Reschke			OL338196
KaiR1322	Entoloma	sp.			Austria		14-Sep-2018	M. Theiss			OL338197
KaiR1334	Entoloma	<i>millihalerae</i>			Austria		16-Sep-2018	K. Reschke			OL338198
KaiR1340	Entoloma	<i>cuneatum</i>			Austria		16-Sep-2018	K. Reschke			OL338199
KaiR1346	Entoloma	<i>conferendum</i>			Austria		17-Sep-2018	K. Reschke			OL338200
KaiR1348	Entoloma	<i>conferendum</i>			Austria		17-Sep-2018	K. Reschke			OL338201
KaiR1349	Entoloma	<i>minutum</i>			Austria		17-Sep-2018	K. Reschke			OL338202
KaiR1359	Entoloma	<i>minutum</i>			Germany		08-Oct-2018	K. Reschke			OL338203
KaiR1372	Entoloma	<i>incognitum</i>			Norway		04-Sep-2019	T. Lassoe & J.H. Petersen			
KaiR1399	Entoloma	<i>sericeum</i>			Germany		11-Oct-2019	K. Reschke & W. Prüfert			
KaiR1403	Entoloma	<i>cladostinum</i>			Germany		11-Oct-2019	K. Reschke & W. Prüfert			
KaiR1406	Entoloma	<i>cladostinum</i>			Germany		11-Oct-2019	K. Reschke & W. Prüfert			
KaiR1410	Entoloma	<i>infula</i>			Germany		11-Oct-2019	K. Reschke & W. Prüfert			
KaiR1411	Entoloma	<i>ortonii</i>			Germany		11-Oct-2019	K. Reschke & W. Prüfert			
KaiR1412	Entoloma	<i>minutum</i>			Germany		13-Oct-2019	K. Reschke			
KaiR1418	Entoloma	<i>plesiopodium</i>			Germany		21-Oct-2019	K. Reschke			
KaiR1426	Entoloma	<i>leptopus</i>			Germany		25-Oct-2019	K. Reschke			
KaiR1435	Entoloma	<i>infula</i>			Germany		08-Nov-2019	C. Manz			
KaiR1437	Entoloma	<i>infula</i>			Germany		08-Nov-2019	C. Manz			
KaiR1438	Entoloma	<i>lucidum</i>			Germany		08-Nov-2019	C. Manz			
KaiR1440	Entoloma	<i>lucidum</i>			Germany		08-Nov-2019	C. Manz			
KaiR1441	Entoloma	<i>cladostinum</i>			Germany		08-Nov-2019	C. Manz			
KaiR1446	Entoloma	<i>minutisporum</i>			Germany		08-Nov-2019	C. Manz			
KaiR1451	Entoloma	<i>vindobonense</i>			Germany		09-Nov-2019	K. Reschke, G. Wölfel & W. Prüfert			
KaiR1452	Entoloma	<i>hirtipes</i>			Germany		09-Nov-2019	K. Reschke, G. Wölfel & W. Prüfert			
KaiR1456	Entoloma	<i>ortonii</i>			Germany		09-Nov-2019	S. Jancovicova			
KaiR1457	Entoloma	<i>hirtipes</i>			Germany		09-Nov-2019	K. Reschke & W. Prüfert			
KaiR1462	Entoloma	<i>hirtipes</i>			Austria		09-Nov-2019	C. Manz			
KaiR1463	Entoloma	<i>vindobonense</i>			Germany		09-Nov-2019	C. Manz			
KaiR1466	Entoloma	<i>hirtipes</i>			Germany		10-Nov-2019	K. Reschke			
KaiR213	Entoloma	<i>vindobonense</i>			Germany		10-Nov-2019	K. Reschke			
KaiR1470	Entoloma	<i>cladostinum</i>			Germany		10-Nov-2019	W. Prüfert			
KaiR1471	Entoloma	<i>confertum</i>			Austria		29-Sep-2016	K. Reschke			
KaiR181	Entoloma	<i>confertum</i>			Germany		15-Oct-2016	K. Reschke			
KaiR206	Entoloma	<i>confertum</i>			Germany		16-Oct-2016	K. Reschke			
KaiR211	Entoloma	<i>hebes</i>			Germany		26-Oct-2016	K. Reschke			
KaiR237	Entoloma	<i>sericeum</i>			Germany		28-Oct-2016	K. Reschke			
KaiR253	Entoloma	<i>sanvitalese</i>			Germany		30-Oct-2016	K. Reschke			
KaiR257	Entoloma	<i>leptopus</i>			Germany		04-Nov-2016	K. Reschke			
KaiR266	Entoloma	<i>hirtipes</i>			Germany		10-Nov-2016	K. Reschke			
KaiR273	Entoloma	<i>leptopus</i>			Germany						OL338122

Table S1 (cont.)

## Supplementary material

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
KaR299	Entoloma	leptopus			Germany		04-Nov-2016	H. Sandau			OL338123
KaR839	Entoloma	mithalerae			Austria		17-Sep-2017	K. Reschke			OL338124
KaR843	Entoloma	clandestinum			Czech Republic						OL338125
KaR849	Entoloma	infula			Czech Republic		17-Sep-2017	C. Manz			OL338126
KaR850	Entoloma	clandestinum			Czech Republic		17-Sep-2017	C. Manz			OL338127
KaR851	Entoloma	sericeum			Czech Republic		17-Sep-2017	C. Manz			OL338128
KaR868	Entoloma	chlorinatum			Austria		18-Sep-2017	K. Reschke			OL338129
KaR875	Entoloma	fernandeae			Austria		18-Sep-2017	K. Reschke			OL338130
KaR901	Entoloma	conferendum			Austria		20-Sep-2017	K. Reschke			OL338131
KaR932	Entoloma	cetratum			Austria		23-Sep-2017	K. Reschke			OL338132
KaR942	Entoloma	conferendum			Austria		23-Sep-2017	K. Reschke			OL338133
KaR943	Entoloma	clandestinum			Austria		23-Sep-2017	K. Reschke			OL338134
KaR962	Entoloma	hebes			Germany		21-Oct-2017	K. Reschke			OL338135
KaR986	Entoloma	ortonii			Germany		26-Oct-2017	K. Reschke			OL338136
KaR987	Entoloma	infula			Germany		26-Oct-2017	K. Reschke			OL338137
KR-M-5012	Entoloma	pygmaeopapillatum			Germany		21-Oct-1984	W. Winterhoff			OL338228
L_ex_WU189010	Entoloma	pallideradicatum			Austria		15-Oct-1988	A. Hausknecht			OL338230
L0608238	Entoloma	sp.			Netherlands		28-Sep-2019	M. van der Vegte & G.M. Jansen			OL338229
LE17626	Entoloma	vernun			Sweden		19-May-1933	S. Lundell			OL338231
LE217908	Entoloma	clandestinum			Russia: European part		21-Aug-2003	O. Morozova			OL338232
LE217931	Entoloma	palescens			Russia: European part		26-Jun-2002	O. Morozova			OL338233
LE226542	Entoloma	vindobonense			Russia: European part		18-Dec-2006	Yu. Rebriv			OL338234
LE234678	Entoloma	cetratum			Russia: European part		09-Oct-2003	T. Svetashova			OL338235
LE234744	Entoloma	albotomentosum			Russia: European part		28-Jul-2004	O. Morozova			OL338236
LE234754	Entoloma	palescens			Russia: European part		03-Jul-2004	O. Morozova			OL338237
LE235264	Entoloma	palescens			Russia: European part		10-Jun-2004	O. Kirillova			OL338238
LE235381	Entoloma	sericeum			Russia: European part		12-Sep-2004	O. Morozova			OL338239
LE235431	Entoloma	cuneatum			Russia: European part		03-Jul-2004	O. Morozova			OL338240
LE235480	Entoloma	cetratum			Russia: European part		02-Oct-2005	O. Morozova			OL338241
LE235752	Entoloma	palescens			Russia: West Siberia		04-Jul-2010	E. Zuyagina			OL338242
LE235753	Entoloma	palescens			Russia: West Siberia		05-Jul-2010	E. Zuyagina			OL338243
LE256222	Entoloma	palescens			Russia: European part		22-May-2008	V. Kotkova			OL338244
LE256334	Entoloma	sericeum			Russia: European part		01-Sep-2008	E. Popov			OL338245
LE256363	Entoloma	sp.			Russia: European part		04-Dec-2006	Yu. Rebriv			OL338246
LE256368	Entoloma	sericeum			Russia: European part		01-Sep-2006	E. Popov			OL338247
LE256369	Entoloma	vernun			Russia: European part		01-May-2007	E. Popov			OL338248
LE253704	Entoloma	fernandeae			Russia: European part		05-Sep-2008	O. Morozova			OL338249
LE253796	Entoloma	rhodocylix			Russia: European part		17-Sep-2006	O. Morozova			OL338250
LE253817	Entoloma	palescens			Russia: European part		17-Sep-2008	O. Morozova			OL338251
LE254038	Entoloma	cephalotrichum			Russia: European part		31-Jul-2013	E. Voronina			OL338252
LE258112	Entoloma	palescens			Russia: Ural		09-Jun-2000	L. Marina			OL338253
LE302051	Entoloma	sericeum			Russia: European part		09-Sep-2011	O. Morozova			OL338254
LE311795	Entoloma	infula			Russia: European part		11-Sep-2015	O. Morozova			OL338255
LE311813	Entoloma	sericeum			Russia: European part		11-Sep-2015	O. Morozova			OL338256
LE311854	Entoloma	cornicolar			Russia: Far East		29-Aug-2013	O. Morozova			OL338257
LE311855	Entoloma	cornicolar			Russia: Far East		24-Aug-2013	O. Morozova			OL338258
LE311856	Entoloma	cornicolar			Russia: Far East		27-Aug-2013	O. Morozova & A. Fedosova			OL338259
LE311857	Entoloma	cornicolar			Russia: Far East		14-Aug-2013	O. Morozova			OL338260
LE311858	Entoloma	cornicolar			Russia: Far East		14-Aug-2013	O. Morozova			OL338261
LE311859	Entoloma	cornicolar			Russia: Far East		14-Aug-2013	O. Morozova			OL338262
LE311860	Entoloma	argillaceum			Russia: Caucasus		23-Aug-2009	E. Malysheva			OL338263
LE311861	Entoloma	argillaceum			Russia: Caucasus		28-Aug-2012	E. Zuyagina			OL338264

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
LE311862	<i>Entoloma</i>	<i>argillaceum</i>			Russia: Caucasus	2250 m asl	16-Aug-2009	O. Morozova	OM899		
LE311863	<i>Entoloma</i>	<i>argillaceum</i>			Russia: Caucasus	2300 m asl	11-Aug-2009	O. Morozova	OL338266		
LE311864	<i>Entoloma</i>	<i>argillaceum</i>			Russia: Caucasus	2700 m asl	23-Aug-2012	T. Svetashova	OL338302		
LE311865	<i>Entoloma</i>	<i>pallescens</i>			Russia: East Siberia	-	17-Aug-2015	E. Malysheva	OM932		
LE311866	<i>Entoloma</i>	<i>infila</i>			Russia: European part	1880 m asl	16-May-2010	S. Arslanov	OL338268		
LE311869	<i>Entoloma</i>	<i>vernum</i>			Russia: Caucasus	-	13-Aug-2009	O. Morozova	OL338269		
LE311870	<i>Entoloma</i>	<i>vernum</i>			Russia: European part	-	13-May-2009	O. Morozova	OL338270		
LE311871	<i>Entoloma</i>	<i>minutum</i>			Russia: European part	-	04-May-2005	T. Svetashova	OL338271		
LE311874	<i>Entoloma</i>	<i>kristiansenii</i>			Russia: European part	-	24-Sep-2011	O. Morozova	OL338272		
LE311875	<i>Entoloma</i>	<i>cetratum</i>			Russia: European part	-	03-Jul-2009	O. Morozova	OL338273		
LE311880	<i>Entoloma</i>	<i>sericeum</i>			Russia: European part	-	26-May-2010	S. Arslanov	OL338274		
LE311882	<i>Entoloma</i>	<i>sericeum</i>			Russia: European part	-	30-Sep-2013	O. Morozova	OL338275		
LE311883	<i>Entoloma</i>	<i>minutum</i>			Russia: West Siberia	-	20-Aug-2010	O. Morozova	OL338276		
LE311884	<i>Entoloma</i>	<i>fernandeae</i>			Russia: European part	-	22-Sep-2011	O. Morozova	OL338277		
LE311885	<i>Entoloma</i>	<i>piceinum</i>			Russia: West Siberia	-	-	N. Filippova	OL338278		
LE311886	<i>Entoloma</i>	<i>cetratum</i>			Russia: European part	-	-	S. Arslanov	OL338279		
LE311888	<i>Entoloma</i>	<i>cuneatum</i>			Russia: European part	-	-	O. Morozova	OL338280		
LE312537	<i>Entoloma</i>	<i>vernuum</i>			Russia: European part	-	27-Jul-2015	S. Arslanov	OM931	neotype	
LE312538	<i>Entoloma</i>	<i>pallescens</i>			Russia: European part	-	01-Aug-2015	O. Morozova	OM894		
LE312539	<i>Entoloma</i>	<i>minutum</i>			Russia: European part	-	11-Oct-2016	O. Morozova	OM931		
LE312540	<i>Entoloma</i>	<i>conferendum</i>			Russia: European part	-	04-Jun-2013	S. Arslanov	OM431		
LE312546	<i>Entoloma</i>	<i>sericeum</i>			Russia: European part	-	29-May-2013	S. Arslanov	OM432		
LE312547	<i>Entoloma</i>	<i>cuspitiferum</i>			Russia: European part	-	18-Jul-2015	S. Arslanov	OM942		
LE312548	<i>Entoloma</i>	<i>sp.</i>			Russia: European part	-	17-Sep-2008	O. Morozova	OM430		
LE312549	<i>Entoloma</i>	<i>kristiansenii</i>			Russia: European part	-	23-Aug-2009	O. Morozova	OM736		
LE312550	<i>Entoloma</i>	<i>altaicum</i>			Russia: European part	-	14-Aug-2006	O. Morozova	OM752		
LE312672	<i>Entoloma</i>	<i>altaicum</i>			Russia: European part	-	-	Rebr_1211	OL338287		
LE312673	<i>Entoloma</i>	<i>altaicum</i>			Russia: European part	-	-	OM795	OL338288		
LE312674	<i>Entoloma</i>	<i>cetratum</i>			Russia: West Siberia	-	20-Aug-2010	O. Morozova	OL338289		
LE312699	<i>Entoloma</i>	<i>cetratum</i>			Russia: West Siberia	500 m asl	28-Aug-2018	O. Morozova	OL338290		
LE315859	<i>Entoloma</i>	<i>pallescens</i>			Russia: Far East	-	03-Sep-2019	D. Ageev	OL338291		
LE315860	<i>Entoloma</i>	<i>pallescens</i>			Russia: Far East	-	-	E. Bulakh	OL338292		
LE315862	<i>Entoloma</i>	<i>aff. intitile</i>			Russia: West Siberia	500 m asl	09-Aug-2005	O. Morozova	OL338293		
LE315863	<i>Entoloma</i>	<i>pallescens</i>			Russia: Far East	-	28-May-2019	I. Krom	OL338294		
LE315864	<i>Entoloma</i>	<i>cuneatum</i>			Russia: West Siberia	-	28-Aug-2016	O. Morozova	OL1236		
LE315865	<i>Entoloma</i>	<i>pallescens</i>			Sweden	-	13-Sep-2009	E. Bendiksen	OM1254		
LE315866	<i>Entoloma</i>	<i>cuneatum</i>			Norway	-	29-Sep-2016	E. Bendiksen	OM1355		
LE315867	<i>Entoloma</i>	<i>incanosquamulosum</i>			Norway	-	-	M. Theiss	OM1179		
LS103	<i>Entoloma</i>	<i>fernandeae</i>			Norway	-	-	M. Theiss	OM1178		
MB011577	<i>Entoloma</i>	<i>readiae</i>			Norway	-	30-Sep-2016	E. Bendiksen	OM1177		
MB011645	<i>Entoloma</i>	<i>brevispernum</i>			Australia: Tasmania	-	19-Jul-2016	N. Kudashova	OL338300		
MB307232	<i>Entoloma</i>	<i>sp.</i>			Australia: Tasmania	-	16-Aug-1984	L. Spoomahers	OL338301		
MB307234	<i>Entoloma</i>	<i>sp.</i>			China: Yunnan	-	25-Apr-2019	G. Kost	OL338303		
MB307270	<i>Entoloma</i>	<i>sp.</i>			China: Yunnan	-	09-May-2019	F. Popa, Z.-L. Yang, K.-H. Rexer & G. Kost	OL338304		
MB307274	<i>Entoloma</i>	<i>sp.</i>			China: Yunnan	-	26-Jul-2015	F. Popa, Z.-L. Yang, K.-H. Rexer & G. Kost	OL338305		
MB307283	<i>Entoloma</i>	<i>sp.</i>			China: Yunnan	-	26-Jul-2015	F. Popa, Z.-L. Yang, K.-H. Rexer & G. Kost	OL338306		
							-	-	OL338307		

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
MB307479	Entoloma	sp.	-	-	China: Yunnan	-	28-Jul-2015	F. Popa, Z.-L. Yang, K.-H. Rexer & G. Kost	-	-	OL338311
MD2006-11	Entoloma	hebes	-	-	Germany	-	23-Nov-2006	M. Dondl	MD1	-	OL338312
MD2009-07	Entoloma	chlorinovum	-	-	Germany	-	07-Sep-2009	M. Dondl	MD3	-	OL338313
MD2011-17	Entoloma	cuspidiferum	-	-	Germany	-	22-Sep-2011	M. Dondl	MD8	-	OL338314
MD2012-09	Entoloma	minutum	-	-	Germany	-	22-Jul-2012	M. Dondl	MD9	-	OL338315
MD2012-10	Entoloma	minutum	-	-	Italy	-	15-Oct-2012	M. Dondl	MD10	-	OL338316
MD2012-10b	Entoloma	minutum	-	-	Italy	-	16-Oct-2012	M. Dondl	MD11	-	OL338317
MD2013-02	Entoloma	hirtipes	-	-	Germany	-	14-Oct-2013	M. Dondl	MD13	-	OL338318
MD2014-12	Entoloma	clandestinum	-	-	Germany	-	30-Aug-2014	M. Dondl	MD16	-	OL338319
MD2014-13	Entoloma	incanosquamulosum	-	-	Italy	-	22-Oct-2014	M. Dondl	MD15	-	OL338320
MD2018-09	Entoloma	nitens	-	-	Germany	-	01-Jul-2018	M. Dondl	MD18	neotype	OL338321
MD2018-10	Entoloma	cuspidiferum	-	-	Germany	-	08-Sep-2018	M. Dondl	MD19	-	OL338322
MD2018-11	Entoloma	cocles	-	-	Germany	-	13-Sep-2018	M. Dondl	MD20	-	OL338323
MD2018-16	Entoloma	conferendum	-	-	Germany	-	11-Sep-2018	M. Dondl	MD22	-	OL338324
MD2018-20	Entoloma	hebes	-	-	Germany	-	12-Sep-2010	M. Dondl	MD26	-	OL338325
MD2018-21	Entoloma	hebes	-	-	Italy	-	19-Oct-2010	M. Dondl	MD27	-	OL338326
MD2018-22	Entoloma	hebes	-	-	Netherlands	100 m asl	19-Oct-2010	M. Dondl	MD28	-	OL338327
ME2012104	Entoloma	leptopus	-	-	Netherlands	100 m asl	24-Oct-2012	M.E. Noordeloos	4003828260	-	OL338329
ME2012106	Entoloma	lucidum	-	-	Netherlands	100 m asl	24-Oct-2012	M.E. Noordeloos	4003828284	-	OL338330
ME2012127	Entoloma	leptopus	-	-	Netherlands	100 m asl	24-Oct-2012	M.E. Noordeloos	4003828227	-	OL338331
ME2012159	Entoloma	cetratum	-	-	Netherlands	100 m asl	24-Oct-2012	M.E. Noordeloos	4003828339	-	OL338332
ME811	Entoloma	globuliferum	-	-	Netherlands	-	18-Oct-1978	M.E. Noordeloos	-	holotype	OL338333
Meusers_E4565	Entoloma	valdeumbonatum	-	-	Germany	-	09-Oct-2001	N. Meusers & K. Wehr	-	-	OL338334
MICH8854	Entoloma	edulis	-	-	USA: Utah	-	07-Jun-1986	K.H. McKnight	-	-	OL338335
MICH8901	Entoloma	sp.	-	-	USA: Idaho	-	29-Sep-1954	A.H. Smith, H.E. Bigelow	-	-	OL338336
MICH9298	Entoloma	holoconiatum	-	-	USA: Idaho	-	08-Aug-1964	A.H. Smith	-	-	OL338337
MICH9383	Entoloma	holoconiatum	-	-	USA: Idaho	-	22-Sep-1964	A.H. Smith	-	-	OL338338
MICH9417	Entoloma	cetratum f. minimosporum	-	-	Norway	-	13-Oct-1984	A.H. Smith	-	-	OL338340
MP-3-140915	Entoloma	chlorinovum	-	-	France	-	14-Sep-2015	M. Petersen	-	-	OL338341
MP-E32-17	Entoloma	ventricosum	-	-	Italy	-	04-Jan-2020	M. Piepenbring	-	-	OL338339
MF5460	Entoloma	fuscohebes	-	-	Italy	-	06-Aug-1924	G. Bresadola	-	-	OL338342
MU88	Entoloma	cuneatum	-	-	0 m asl	-	26-Aug-2013	M.E. Noordeloos	4007594406	-	OL338343
my172	Entoloma	clandestinum	-	-	0 m asl	-	13-Oct-2013	M.E. Noordeloos	4007598390	-	OL338344
my930	Entoloma	incognitum	-	-	USA	-	20112	L. Nagy	G0066	-	OL338345
NL-5126	Entoloma	sp.	-	-	USA	-	20112	L. Nagy	G0032	-	OL338346
NL-5155	Entoloma	sp.	-	-	Australia: Tasmania	-	2006	-	G1633	-	OL338347
NLN005002081	Entoloma	leptooides	-	-	New Zealand	-	2006	-	G1604	-	OL338348
NLN00502172	Entoloma	sp.	-	-	Australia: Tasmania	-	2004	-	G1667	-	OL338349
NLN99302436	Entoloma	sp.	-	-	Norway	-	30-Aug-2005	J.B. Jordal	NOBAS3257	-	OL338350
O-F-158253	Entoloma	clandestinum	-	-	Norway	-	13-Oct-2012	T. Laesoe, A. Molia	NOBAS473117	-	OL338351
O-F-245651	Entoloma	hirtipes	-	-	Norway	-	09-May-2013	T.E. Brandrud	NOBAS1352	-	OL338352
O-F-248988	Entoloma	kristiansenii	-	-	Norway	-	26-Sep-2013	T.E. Brandrud, B. Dima	NOBAS110015	-	OL338353
O-F-249492	Entoloma	cuspidiferum	-	-	Norway	-	31-Aug-2011	J.B. Jordal	NOBAS326216	-	OL338356
O-F-252357	Entoloma	sp.	-	-	Norway	-	31-Aug-2011	J.B. Jordal	NOBAS3257	-	OL338357
O-F-252363	Entoloma	confertum	-	-	Norway	-	24-Jun-2014	E. Bendiksen	NOBAS466917	-	OL338358
O-F-253979	Entoloma	cuspidiferum	-	-	Norway	-	28-Aug-1994	G. Gaarder, J.B. Jordal	NOBAS5715	-	OL338359
O-F-254410	Entoloma	ventricosum	-	-	Norway	-	11-Aug-2015	A. Molia	NOBAS2345	-	OL338360
O-F-260150	Entoloma	sericealpinum	-	-	Norway	-	12-Aug-2015	A. Molia	NOBAS2366	-	OL338361
O-F-260179	Entoloma	fernandeae	-	-	Norway	-	12-Jul-2011	G. Guiden	NOBAS520018	-	OL338362
O-F-302922	Entoloma	confertum	-	-	Norway	-	02-Aug-1979	E. Bendiksen	NOBAS512018	-	OL338363
O-F-61670	Entoloma	-	-	-	-	-	-	-	-	-	-

Table S1 (cont.)

## Supplementary material

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
O-F-61851	<i>Entoloma</i>	<i>pallidescens</i>			Norway		28-Jun-1980	E. Bendiksen	NOBAS472917		OL338351
OW-E3-18	<i>Entoloma</i>	sp.			Norway		-	O. Weholt	ALV18356		OL338363
PAK061089	<i>Nolanea</i>	<i>pascua</i> var. <i>pallidescens</i>			Finland		06-Oct-1889	P.A. Karsten	S770	neotype	OL338364
PAM13	<i>Entoloma</i>	<i>ortonii</i>			Sweden		-	P.-A. Moreau			OL338365
DDD103766	<i>Entoloma</i>	sp.			New Zealand		14-May-2013	M. Padamsee			OL338408
DDD105433	<i>Entoloma</i>	sp.			New Zealand		06-Jan-2014	J.A. Cooper			OL338409
DDD105581	<i>Entoloma</i>	sp.			New Zealand		09-Mar-2014	J.A. Cooper			OL338410
DDD105618	<i>Entoloma</i>	<i>sericeum</i>			New Zealand		25-Apr-2014	J.A. Cooper			OL338411
DDD106030	<i>Entoloma</i>	sp.			New Zealand		16-May-2015	J.A. Cooper			OL338412
DDD106183	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		03-Dec-2015	J.A. Cooper			OL338413
DDD106648	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		02-Feb-2017	J.A. Cooper			OL338414
DDD106824	<i>Entoloma</i>	sp.			New Zealand		27-Dec-2016	J.A. Cooper			OL338415
DDD107035	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		19-Apr-2017	J.A. Cooper			OL338416
DDD107042	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		22-Apr-2017	J.A. Cooper			OL338417
DDD107346	<i>Entoloma</i>	sp.			New Zealand		10-May-2018	G. Gates			OL338418
DDD107348	<i>Entoloma</i>	sp.			New Zealand		08-May-2018	T. Davies			OL338419
DDD107364	<i>Entoloma</i>	<i>melleum</i>			New Zealand		29-Jun-2018	G. Smith			OL338420
DDD107365	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		15-Jul-2018	G. Smith			OL338421
DDD107369	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		11-Jun-2018	G. Smith			OL338422
DDD113003	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		06-Apr-2019	N. Siegel			OL338423
DDD113119	<i>Entoloma</i>	<i>distinctum</i>			New Zealand		18-Apr-2019	N. Siegel			OL338424
DDD113218	<i>Entoloma</i>	sp.			New Zealand		23-Apr-2019	N. Siegel			OL338425
DDD113222	<i>Entoloma</i>	<i>aromaticum</i>			New Zealand		23-Apr-2019	N. Siegel			OL338426
DDD113253	<i>Entoloma</i>	<i>austrothodocalyx</i>			New Zealand		25-Apr-2019	N. Siegel			OL338427
DDD113277	<i>Entoloma</i>	<i>austrothodocalyx</i>			New Zealand		26-Apr-2019	N. Siegel			OL338428
DDD113343	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		03-May-2019	N. Siegel			OL338429
DDD113344	<i>Entoloma</i>	<i>conferendum</i>			New Zealand		03-May-2019	N. Siegel			OL338430
DDD113356	<i>Entoloma</i>	sp.			New Zealand		03-May-2019	N. Siegel			OL338431
DDD27024	<i>Entoloma</i>	<i>pluteinotropum</i>			New Zealand		05-Dec-1967	E. Horak			OL338366
DDD71135	<i>Entoloma</i>	<i>orichalcium</i>			New Zealand		19-Mar-2000	E. & A. Horak			OL338367
DDD71238	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		26-Apr-2000	E. & A. Horak			OL338368
DDD72608	<i>Entoloma</i>	<i>confusum</i>			New Zealand		26-Apr-2001	E. & A. Horak			OL338369
DDD72829	<i>Entoloma</i>	<i>peralbidum</i>			New Zealand		22-May-2001	E. & A. Horak			OL338370
DDD72841	<i>Entoloma</i>	<i>elegantissimum</i>			New Zealand		23-May-2001	E. & A. Horak			OL338371
DDD74723	<i>Entoloma</i>	<i>perconfusum</i>			New Zealand		06-May-1981	E. Horak			OL338372
DDD74730	<i>Entoloma</i>	<i>paraserricium</i>			New Zealand		08-May-2000	E. & A. Horak			OL338373
DDD80163	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		22-Oct-2001	J.A. Cooper			OL338374
DDD80704	<i>Entoloma</i>	sp.			New Zealand		27-Mar-2005	J.A. Cooper			OL338375
DDD80773	<i>Entoloma</i>	sp.			New Zealand		04-Apr-2005	J.A. Cooper			OL338376
DDD80802	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		05-Apr-2004	J.A. Cooper			OL338377
DDD80836	<i>Entoloma</i>	<i>melleum</i>			New Zealand		06-Apr-2005	J.A. Cooper			OL338378
DDD80864	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		08-Apr-2005	J.A. Cooper			OL338379
DDD86824	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		18-Dec-2005	J.A. Cooper			OL338380
DDD86959	<i>Entoloma</i>	<i>sericeum</i>			New Zealand		01-Apr-2006	J.A. Cooper			OL338381
DDD86974	<i>Entoloma</i>	<i>sericeum</i>			New Zealand		01-Apr-2006	J.A. Cooper			OL338382
DDD87428	<i>Entoloma</i>	<i>sulphureum</i>			New Zealand		10-May-2007	J.A. Cooper			OL338383
DDD87430	<i>Entoloma</i>	<i>sulphureum</i>			New Zealand		11-May-2007	J.A. Cooper			OL338384
DDD87461	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		13-May-2007	J.A. Cooper			OL338385
DDD87572	<i>Entoloma</i>	<i>distinctum</i>			New Zealand		16-May-2008	J.A. Cooper			OL338386
DDD87573	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		15-May-2008	S. Kerr			OL338387
DDD87704	<i>Entoloma</i>	<i>sericeum</i>			New Zealand		09-Apr-2008	J.A. Cooper			OL338388

Table S1 (cont.)

Coll_no/voucher	Genus	epitheton	as	Country code	Country	Altitude	Collection date	Collected by	temporary numbers	Note	Accession
PDD92673	<i>Entoloma</i>	sp.			New Zealand		10-May-2007	G. Gates, D. Ratkowsky			
PDD92805	<i>Entoloma</i>	sp.			New Zealand		10-May-2007	G. Gates, D. Ratkowsky			
PDD95326	<i>Entoloma</i>	sp.			New Zealand		02-Mar-2009	J.A. Cooper			
PDD95333	<i>Entoloma</i>	<i>sulphureum</i>			New Zealand		02-Mar-2009	J.A. Cooper			
PDD95501	<i>Entoloma</i>	sp.			New Zealand		29-May-2009	J.A. Cooper			
PDD95521	<i>Entoloma</i>	sp.			New Zealand		15-May-2009	J.A. Cooper			
PDD95723	<i>Entoloma</i>	sp.			New Zealand		15-Feb-2010	J.A. Cooper			
PDD95828	<i>Entoloma</i>	<i>paraserriceum</i>			New Zealand		03-May-2010	J.A. Cooper			
PDD96146	<i>Entoloma</i>	<i>cuneatum</i>			New Zealand		13-Mar-2011	J.A. Cooper			
PDD96203	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		24-Apr-2011	J.A. Cooper			
PDD96249	<i>Entoloma</i>	<i>procernum</i>			New Zealand		06-Aug-2012	J.A. Cooper			
PDD96272	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		18-May-2011	J.A. Cooper			
PDD96319	<i>Entoloma</i>	sp.			New Zealand		15-May-2011	S.R. Pennycook			
PDD96439	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		24-May-2011	J.A. Cooper			
PDD96760	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		21-Oct-2012	J.A. Cooper			
PDD96905	<i>Entoloma</i>	sp.			New Zealand		19-May-2013	J.A. Cooper			
PDD96920	<i>Entoloma</i>	sp.			New Zealand		19-May-2013	J.A. Cooper			
PDD96940	<i>Entoloma</i>	sp.			New Zealand		26-May-2013	J.A. Cooper			
PDD96941	<i>Entoloma</i>	<i>sericeum</i>			New Zealand		26-May-2013	J.A. Cooper			
R6183	<i>Entoloma</i>	<i>testaceum</i> var. <i>bavaricum</i>			Germany		Apr-1983	G. Wölfi			
RKris10782	<i>Entoloma</i>	<i>kristiansenii</i>			Norway		11-Jul-1982	R. Kristiansen			
SAVF1192	<i>Entoloma</i>	<i>pigmaeopapillatum</i>			Slovakia		09-Oct-2005	S. Adamčík			
SB0238	<i>Entoloma</i>	sp.			Canada: British Columbia		23-Jul-2016	S. Berch			
SB0290	<i>Entoloma</i>	<i>pallescens</i>			Canada: British Columbia		27-Jul-2016	S. Berch			
SB0373	<i>Entoloma</i>	<i>vernun</i>			Canada: British Columbia		1-Jul-2017	S. Berch			
Tassi02026	<i>Entoloma</i>	<i>atlanticum</i>			France		22-Oct-2002	G. Tassi			
TUR194029	<i>Entoloma</i>	<i>rhodocylix</i>			Finland		13-Sep-2011	S. Huhtinen			
UPS-F-645763	<i>Entoloma</i>	<i>pallescens</i>			Sweden		-	K. Jaederfeldt			
Vauras1270	<i>Entoloma</i>	<i>pallescens</i>			Finland		27-Jun-1982	J. Yauras			
Waveren211083	<i>Entoloma</i>	<i>kitsii</i>			Netherlands		21-Oct-1980	E.K. van Waveren			
WU20829	<i>Entoloma</i>	<i>occultopigmentatum</i> var. <i>cystidiatum</i>			Austria		20-Aug-2000	H. Voglmayr			
WU22009	<i>Entoloma</i>	<i>cuneatum</i>			Austria		09-May-2002	W. Till			
WU27125	<i>Entoloma</i>	<i>maeheense</i>			Austria		10-Feb-2001	A. Hausknecht			
WU27126	<i>Entoloma</i>	<i>maeheense</i>			Seychelles		13-Feb-2001	A. Hausknecht			
WU27127	<i>Entoloma</i>	<i>maeheense</i>			Seychelles		17-Feb-2001	A. Hausknecht			
WU27137	<i>Entoloma</i>	<i>contortisporum</i>			France: La Reunion		02-Apr-2005	A. Hausknecht			
WU32901	<i>Entoloma</i>	<i>subdelegans</i>			Mauritius		20-Jan-2008	A. Hausknecht			
WU32903	<i>Entoloma</i>	<i>subdelegans</i>			Austria		23-Jan-2008	A. Hausknecht			
WU33046	<i>Entoloma</i>	sp.			France: La Reunion		06-Mar-2011	A. Hausknecht			
WU7052	<i>Entoloma</i>	<i>albotomentosum</i>			Austria		08-Oct-1987	A. Hausknecht			
YSU-F-05111	<i>Entoloma</i>	<i>pallescens</i>			Russia: West Siberia		24-Jun-2015	N. Filippova			
YSU-F-06209	<i>Entoloma</i>	<i>cuneatum</i>			Russia: West Siberia		23-Aug-2015	N. Filippova			
YSU-F-06347	<i>Entoloma</i>	<i>cetratum</i>			Russia: West Siberia		31-Aug-2015	N. Filippova			
YSU-F-06384	<i>Entoloma</i>	<i>cetratum</i>			Russia: West Siberia		10-Sep-2014	T. Bulyonkova			
YSU-F-4691	<i>Entoloma</i>	<i>cetratum</i>			Russia: West Siberia		09-Mar-1968	E. Horak			
Z168-117	<i>Entoloma</i>	<i>translucidum</i>			New Zealand		13-Mar-1969	E. Horak			
Z176-128	<i>Entoloma</i>	<i>cucurbita</i>			New Zealand		03-Apr-1969	E. Horak			
Z179-215	<i>Entoloma</i>	<i>perzonatum</i>			New Zealand		31-Aug-2015	E. Horak			
Z18562	<i>Entoloma</i>	<i>distinctum</i>			New Zealand		26-Apr-2000	E. Horak			
Z18747	<i>Entoloma</i>	<i>aromaticellum</i>			New Zealand		25-Mar-2000	E. Horak			
Z19392	<i>Entoloma</i>	<i>elegantissimum</i>			New Zealand		23-May-2001	E. Horak			