Persoonia 49, 2022: 136–170
www.ingentaconnect.com/content/nhn/pimj

RESEARCH ARTICLE

ISSN (Online) 1878-9080
https://doi.org/10.3767/persoonia.2022.49.04

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

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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*.

Citation: Reschke K, Morozova OV, Dima B, et al. 2022. Phylogeny, taxonomy, and character evolution in Entoloma subgenus Nolanea. Persoonia 49: 136–170. https://doi.org/10.3767/persoonia.2022.49.04.
Effectively published online: 13 October 2022 [Received: 5 January 2022; Accepted: 5 May 2022].

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 tramal 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

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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. *Dryophiloides*. 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*, *Austrofernandae* 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. subelegans*, 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^2 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	GAAGGYCAAGCMTGTGGTCTYG
RPB2-iR	reverse	TGTTTACCCATKGCAGAYTGR
MS0B	forward	TTATTTTGTTTAAAGGTAGTTGG
MS0F	forward	GTTTAADGGTAGTTGGTRG
MF1.1	forward	TCYGATTGAACGTTTTTCAGTAG
MS1.2R	reverse	TTACCGAGTCTTCTGGCACCAG
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 mitochondrion genomes and whole genome shotgun (WGS) sequences obtained from GenBank and the Mycocosm 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, 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	CU6	
Agaricus bisporus	*Agaricineae*	JX271275	3	0	1	0	0	2	0	5[i]	944
Coprinopsis cinerea	*Agaricineae*	AACS02000068	2	0	1	1	0	4	0	3	910
Crepidotus variabilis	*Agaricineae*	Crevar1	2	0	1	1	0	4	0	1	974
Cyathus striatus	*Agaricineae*	Cyastr2	2	1	1	1	0	4	0	3	977
Dendrothele bispora	incertae sedis	Denbi1	2	0	2	0	0	4	0	0	839
Auriculariopsis ampla	*Marasmiineae*	Auramp1	2	0	1	3	1	1	0	0	1109
Crinipellis perniciosa	*Marasmiineae*	AY376688	2	0	3	0	0	1	0	2	916
Lentinula edodes	*Marasmiineae*	AB697988	2	1	3	0	0	4	0	1	944
Moniliophtora roreri	*Marasmiineae*	HQ259115	2	0	3	0	0	1	0	1	903
Mycena galopus	*Marasmiineae*	Mycgal1	3	2	2	0	0	1	0	2	950
Amanita jacksonii	*Pluteineae*	AYNK01002457	2	0	1	0	2	4	0	1	848
Asterophora parasitica	*Tricholomatineae*	MH725791	2	0	0	0	0	3	0	1	879
Lepista nuda	*Tricholomatineae*	Lepnud1	2	0	0	0	0	3	0	1	1032
Lyophyllum decastes	*Tricholomatineae*	MH447974	2	0	1	0	0	3	0	1	900
Lyophyllum shimeji	*Tricholomatineae*	MH447975	2	0	1	0	0	3	0	1	896
Tricholoma matsutake	*Tricholomatineae*	JX985789	2	0	1	1	0	4	0	0	955
Tricholomella constricta	*Tricholomatineae*	MH725800	2	0	0	0	0	3	0	1	904

[i] = including an indel.

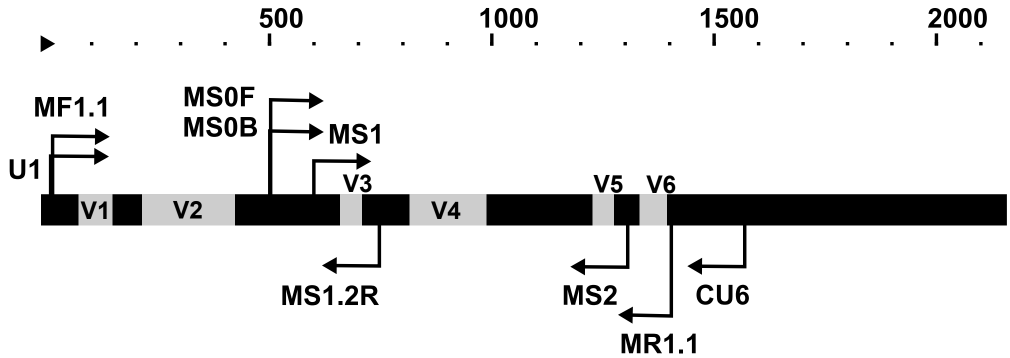

Fig. 1 Primer map of new and standard mtSSU primers, including the variable domains V1–V6 (V7–V9 not indicated). Nucleotide positions based on the mtSSU sequence of *Tricholoma matsutake* (JX985789).

GTRCAT model with 55 per site rate categories and 1 000 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-1α*, 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-1α*, 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-1α*-exons, *EF-1α*-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-1α*, 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-1α*-exons, *EF-1α*-introns, *RPB2*-exons, *RPB2*-intron, and mtSSU, along with 1 000 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 α-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. ≥ 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-1α* each, and mtSSU, along with 1 000 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	*Nolanea* cf. *conferenda*	USA	–	–	KF738946	KF738935	KF771351	MG702640
aFP4	*Entoloma hirtipes*	Germany	–	OL337994	OL338461	OL405190	OL405499	–
CME5	*Entoloma belouvense* var. *albertinae*	Panama	–	MZ611628	OL338474	OL405200	OL405500	–
CME6	*Entoloma paraconferendum*	Panama	holotype	MZ611629	OL338477	OL405201	OL405501	–
CME9	*Entoloma transitionisporum*	Panama	–	MZ611632	OL338475	OL405208	OL405502	–
CME10	*Entoloma cremeostriatum*	Panama	–	MZ611621	OL338472	OL405199	OL405503	–
CORT-5761TJB	*Entoloma alboumbonatum*	USA	–	–	MH190191	MH190091	MH190124	MH190160
Cro17	*Entoloma hirtipes*	Croatia	–	OL338044	OL338463	–	OL405504	–
DLL9531	*Nolanea cetrata*	USA	–	–	KF738942	KF738927	KF771346	MG702639
DLL9640	*Leptonia umbraphila*	Australia	–	–	JQ756422	JQ756407	JQ756438	MG702637
DLL9788	*Claudopus viscosus*	Australia	holotype	–	HQ731516	HQ731513	HQ731518	MG702619
Eth14	*Entoloma* sp.	Ethiopia	–	OL338057	OL338473	OL405235	–	–
FK0898	*Nolanea atropapillata*	Brazil	holotype	KF679354	KF738940	KF738929	MH190107	MH190137
FK0935	*Nolanea albertinae*	Brazil	holotype	KF679348	KF738936	KF738924	KF771344	–
FK1049	*Nolanea tricholomatoidea*	Brazil	holotype	KF679352	KF738939	KF738928	KF771347	–
FK1140	*Nolanea parvispora*	Brazil	–	KF679353	KF738943	KF738931	KF771348	MH190143
FK1732	*Nolanea albertinae*	Brazil	–	KF679351	KF738938	KF738926	KF771345	–
FK2011	*Entoloma* sp.	Brazil	–	–	MG018327	MG018312	MG018335	MH190149
GC10041102	*Entoloma hirtipes*	France	–	OL338080	OL338462	OL405191	OL405505	–
GC13082801	*Entoloma sericeoalpinum*	France	–	OL338083	OL338545	OL338490	OL405216	–
GC13100602	*Entoloma hirtipes*	France	–	OL338088	OL338465	OL405192	OL405506	–
GDGM27564	*Entoloma caespitosum*	China	–	JQ281477	JQ320130	JQ993070	JQ993078	–
GDGM43979	*Entoloma crepidotoides*	China	holotype	KJ958982	KJ958983	KJ958985	KJ958984	–
J.Wisman 2003-09-19	*Entoloma sinuatum*	–	'50'	KC710109	GQ289193	GQ289333	GQ289264	–
JM96/10	*Entoloma strictius*	–	–	DQ494680	AF042620	EF421100	EF421017	EF421088
KA13_1522	*Entoloma hirtipes*	South Korea	–	MN088710	MN088715	MN088719	MN095760	–
KA15_373	*Entoloma chytrophilum*	South Korea	–	MN088709	MN088714	MN088718	MN095759	–
KaiR213	*Entoloma hebes*	Germany	–	OL338117	OL338470	OL405197	–	–
KaiR237	*Entoloma sericeum*	Germany	–	OL338118	OL338542	OL338494	OL405220	–
KaiR299	*Entoloma leptopus*	Germany	–	OL338123	OL338471	OL405198	–	–
KaiR628	*Entoloma flavoconicum*	Panama	holotype	MZ611667	OL338511	OL405244	OL405507	–
KaiR630	*Entoloma belouvense*	Panama	–	MZ611668	OL338476	OL405209	OL405508	–
KaiR693	*Entoloma* sp.	Panama	–	MZ611678	OL338524	OL405251	OL405509	–
KaiR839	*Entoloma milthalerae*	Austria	–	OL338124	OL338478	OL405202	OL405510	–
KaiR868	*Entoloma chlorinosum*	Austria	–	OL338129	OL338506	OL405232	OL405511	–
KaiR875	*Entoloma fernandae*	Austria	–	OL338130	OL338485	OL405212	OL405512	–
KaiR932	*Entoloma cetratum*	Austria	–	OL338132	OL338481	OL405214	OL405513	–
KaiR1005	*Entoloma hirtipes*	Germany	–	OL338139	OL338466	OL405194	OL405514	–
KaiR1006	*Entoloma hirtipes*	Germany	–	OL338140	–	OL338467	OL405195	–
KaiR1008	*Entoloma ortonii*	Germany	–	OL338141	OL338495	OL405221	OL405515	–
KaiR1014	*Entoloma vindobonense*	Germany	–	OL338143	OL338504	OL405229	OL405516	–
KaiR1040	*Entoloma infula*	Germany	–	OL338148	OL338505	OL405231	OL405517	–
KaiR1121	*Entoloma minutisporum*	Croatia	–	OL338153	OL338491	OL405217	OL405518	–
KaiR1143	*Entoloma assiduum*	Cyprus	–	OL338157	OL338499	OL405226	OL405519	–
KaiR1144	*Entoloma olivaceohebes*	Cyprus	–	OL338158	OL338510	OL405236	OL405520	–
KaiR1175	*Entoloma* sp.	Cyprus	–	OL338159	OL338500	OL405227	OL405521	–
KaiR1182	*Entoloma hirtipes*	Cyprus	–	OL338162	OL338468	OL405193	–	–
KaiR1188	*Entoloma llimonae*	Cyprus	–	OL338166	OL338497	OL405224	OL405522	–
KaiR1258	*Entoloma kristiansenii*	Sweden	–	OL338181	OL338469	OL405196	OL405523	–
KaiR1259	*Entoloma sericeum*	Sweden	–	OL338182	OL338493	OL405219	OL405524	–
KaiR1282	*Entoloma clandestinum*	Sweden	–	MZ611639	OL338523	OL405250	OL405525	–

Table 3 (cont.)

Coll_no	Species (annotation)	origin	note	ITS	LSU	mtSSU	RPB2	TEF1
KaiR1290	*Entoloma cuspidiferum*	Sweden	epitype	OL338190	OL338522	OL405247	OL405526	–
KaiR1311	*Entoloma rhodocylix*	Austria	–	OL338192	OL338525	OL405248	OL405527	–
KaiR1322	*Entoloma* sp.	Austria	–	OL338197	OL338498	OL405222	OL405528	–
KaiR1349	*Entoloma minutum*	Austria	–	OL338202	OL338496	OL405223	OL405529	–
KaiR1372	*Entoloma incognitum*	Norway	holotype	OL338204	OL338527	OL405252	OL405530	–
KaiR1440	*Entoloma lucidum*	Germany	–	OL338216	OL338541	OL338492	OL405218	OL405531
LE235752	*Entoloma pallescens*	Russia: Western Siberia	–	OL338242	OL338534	OL338512	OL405239	OL405532
LE253635	*Entoloma* sp.	Russia: European part	–	OL338246	OL338540	OL338501	OL405228	OL405533
LE254131	*Entoloma piceinum*	Russia: European part	holotypus	KM262035	OL338538	OL338483	OL405205	OL405534
LE254132	*Entoloma piceinum*	Russia: European part	–	KM262036	OL338539	OL338484	–	OL405535
LE262922	*Entoloma inocephalum*	Vietnam	–	KC898449	MH259311	MH190085	MH259313	MH190154
LE262934	*Entoloma pallidoflavum*	Vietnam	–	–	MH190183	MH190086	MH259314	MH190155
LE311854	*Entoloma cornicolor*	Russia: Far East	holotype	OL338257	OL338535	OL338519	OL405243	OL405536
LE311859	*Entoloma cornicolor*	Russia: Far East	–	OL338262	OL338536	OL338520	–	OL405540
LE311861	*Entoloma argillaceum*	Russia: Caucasus	holotype	OL338264	OL338531	OL338516	OL405237	OL405537
LE311888	*Entoloma cetratum*	Sweden	neotype	OL338280	–	OL338482	OL405215	OL405538
LE312537	*Entoloma cuneatum*	Russia: Caucasus	–	OL338281	–	OL338514	OL405241	–
LE312538	*Entoloma vernum*	Russia: European part	–	OL338282	OL338537	OL338518	OL405238	OL405539
LE312539	*Entoloma pallescens*	Russia: European part	–	OL338283	OL338533	OL338513	OL405240	OL405541
MB011645	*Entoloma brevispermum*	Australia: Tasmania	–	OL338305	–	OL338487	OL405207	OL405542
MB307232	*Entoloma* sp.	China: Yunnan	–	OL338306	OL338521	OL405245	–	–
MB307270	*Entoloma* sp.	China: Yunnan	–	OL338308	OL338509	OL405211	–	–
MB307274	*Entoloma* sp.	China: Yunnan	–	OL338309	OL338543	OL338507	OL405233	OL405543
MCA2415	*Entoloma fragosum*	Guyana	holotype	–	KJ021700	KJ021690	KJ021694	MG702622
MD2014-13	*Entoloma incanosquamulosum*	Italy	–	OL338320	OL338502	OL405225	OL405544	–
MD2018-09	*Entoloma nitens*	Germany	neotype	OL338321	OL338515	OL405242	OL405545	–
MD2018-11	*Entoloma cocles*	Germany	–	OL338323	OL338530	OL405253	OL405546	–
MD2018-16	*Entoloma conferendum*	Germany	epitype	OL338324	OL338480	OL405203	OL405547	–
Meusers_E4565	*Entoloma valdeumbonatum*	Germany	holotype	OL338333	GQ289203	GQ289343	GQ289271	–
PDD80802	*Entoloma translucidum*	New Zealand	–	OL338377	OL338479	OL405204	OL405548	–
PDD80864	*Entoloma perzonatum*	New Zealand	–	OL338379	–	OL338488	OL405210	–
PDD87270	*Entoloma readiae*	New Zealand	–	MZ611697	OL338503	OL405230	OL405549	–
PDD87572	*Entoloma distinctum*	New Zealand	–	OL338386	OL338486	OL405206	–	–
PDD95326	*Entoloma* aff. *congregatum*	New Zealand	–	OL338391	OL338528	OL405254	OL405550	–
PDD95521	*Entoloma* sp.	New Zealand	–	OL338394	OL338508	OL405234	–	–
PDD95828	*Entoloma parasericeum*	New Zealand	–	OL338396	OL338526	OL405249	OL405551	–
PDD96439	*Entoloma aromaticellum*	New Zealand	–	OL338402	OL338517	OL405246	OL405552	–
PDD96905	*Entoloma* cf. *tristificum*	New Zealand	–	OL338404	OL338489	OL405213	–	–
SAAS1091	*Entoloma reductum*	China	holotype	KU312123	KU534232	KU534419	KU534480	–
SAAS1220	*Entoloma gregarium*	China	holotype	KU312122	KU534237	KU534423	KU534474	–
SAAS1252	*Entoloma pleurotoides*	China	holotype	KU312113	KU534227	KU534424	KU534468	–
SAAS1712	*Entoloma conchatum*	China	holotype	KU312111	KU534220	KU534432	KU534459	–
SP-FK1790	*Nolanea caribaea*	Brazil	–	–	MH190214	MG018309	MH190114	MH190146
TB7144	*Entoloma sericeonitidum*	–	–	EF421108	AF261315	EF421098	EF421016	EF421087
TJB7710	*Entoloma strictius* var. *isabellinum*	USA	–	–	GU384618	GU384594	GU384641	MG702625
VHAs03_2	*Nolanea sericea*	–	–	DQ367430	DQ367423	EF421099	DQ367435	DQ367428
WU189010	*Entoloma pallideradicatum*	Austria	holotype/isotype	OL338230	GQ289176	GQ289316	GQ289247	–
WU21097	*Entoloma borbonicum*	France: La Reunion	holotype	–	MH190198	MH190098	MH190131	MH190166
WU27126	*Entoloma maheense*	Seychelles	holotype	OL338444	OL338544	OL338529	OL405255	OL405553
ZRL20151207	*Entoloma* sp.	China	–	LT716038	KY418854	–	KY419001	KY419057
ZRL20151219	*Entoloma* sp.	China	–	LT716035	KY418850	–	KY418998	KY419054
ZT-Myc42828	*Entoloma nothofagi*	New Zealand	–	–	MH190203	MH190101	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-1α* 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-1α* 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. pallescens*, 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-1α* was the holotype of *E. maheense*, collected 2001.

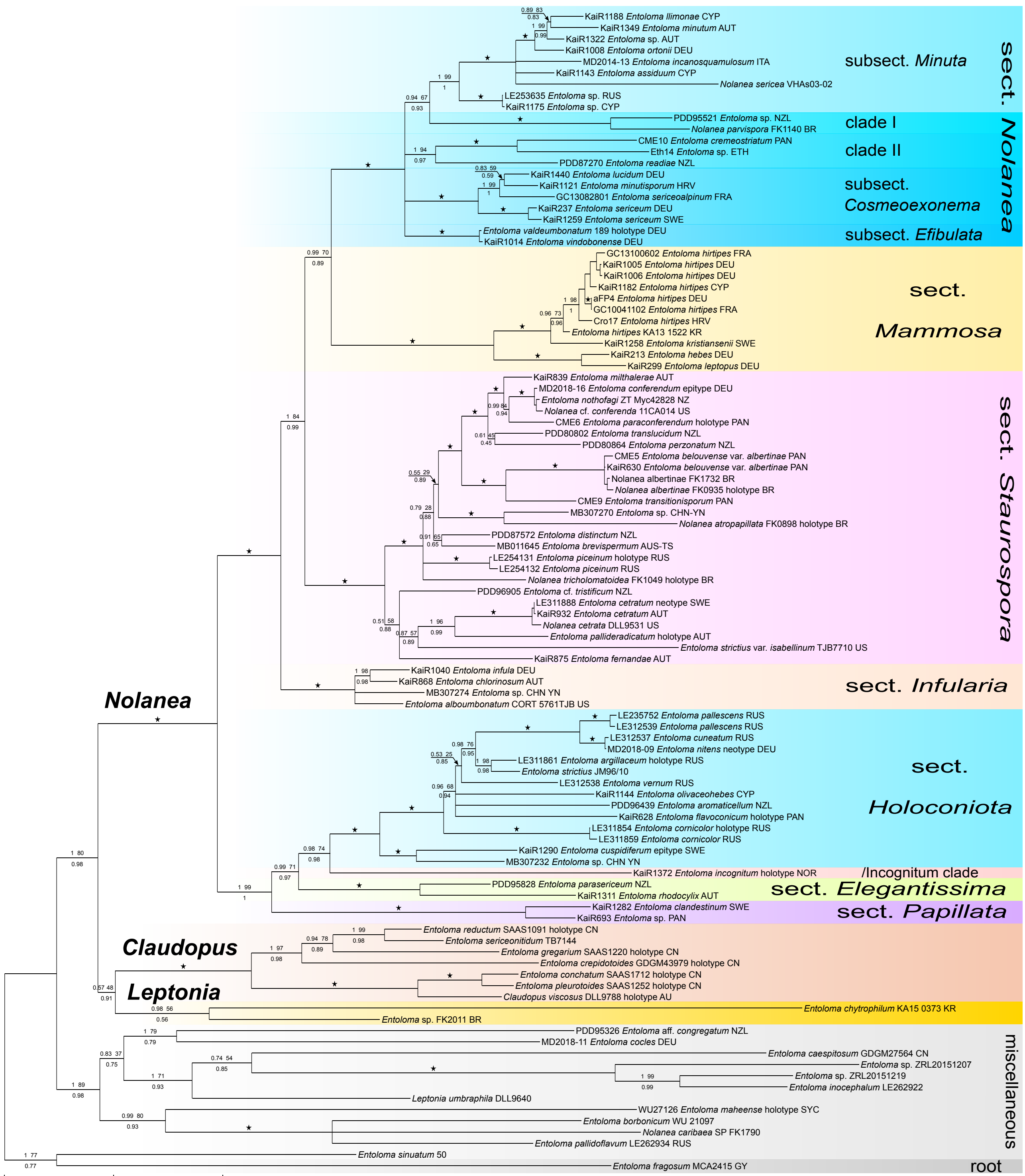

Fig. 2 Bayesian MCMC phylogram of species of *Entoloma* subg. *Nolanea* and outgroup based on concatenated alignments of ITS, mtSSU, *RPB2*, and *EF-1α*. Rooted to *E. sinuatum* and *E. fragosum*. Values above branches, left side = bayesian posterior probability, right side = maximum likelihood bootstrap, 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
RPB2	0.223	1.230	24
TEF1	0.278	0.806	44
ITS+mtSSU+*RPB2*+*TEF1*	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

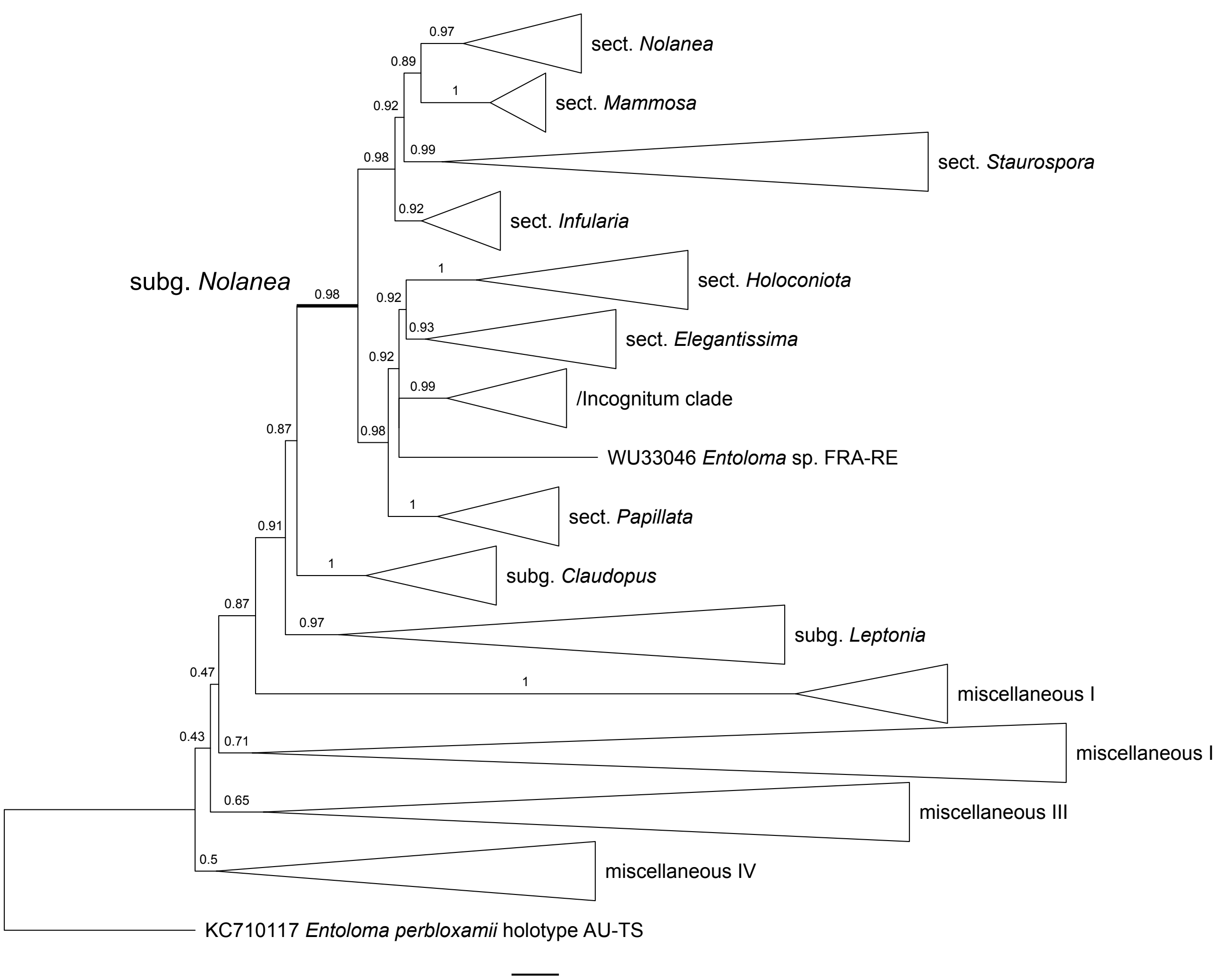

Fig. 3 Overview of the ITS phylogram of species of *Entoloma* subg. *Nolanea*, including species of the subgenera *Claudopus* and *Leptonia*, as well as miscellaneous nolaneoid and outgroup taxa, rooted to *Entoloma perbloxamii*. Collapsed to the main clades, including the sections of subg. *Nolanea*. 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 ameides*, *E. calobrunneum*, *E. pleopodium*, and *E. sanvitalense* 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. subelegans* together with *E. velenovskyi* form long-branched lineages and cannot be assigned to an existing subgenus.

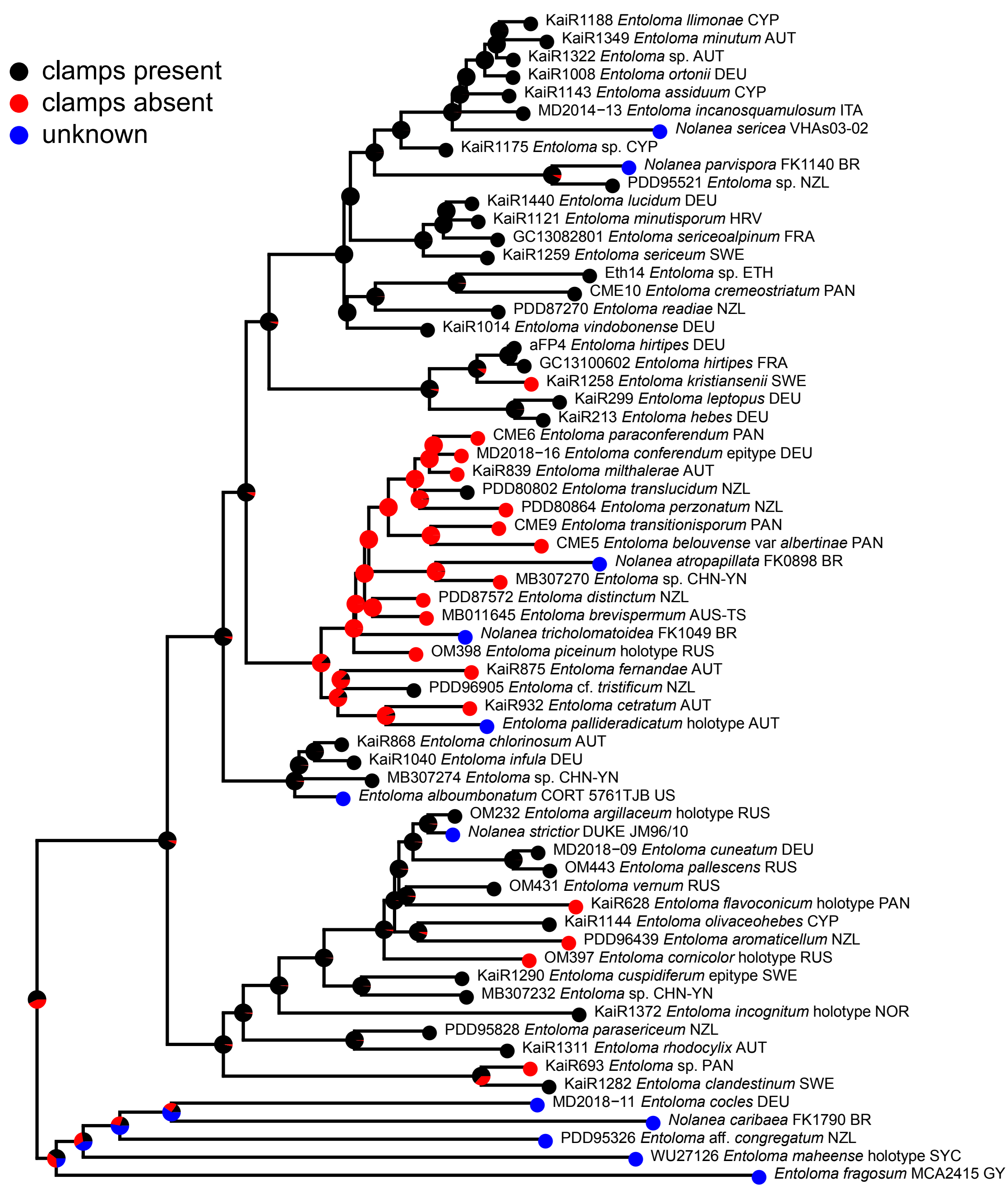

Fig. 4 Ancestral character state reconstruction of absence/presence of clamp connections in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO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

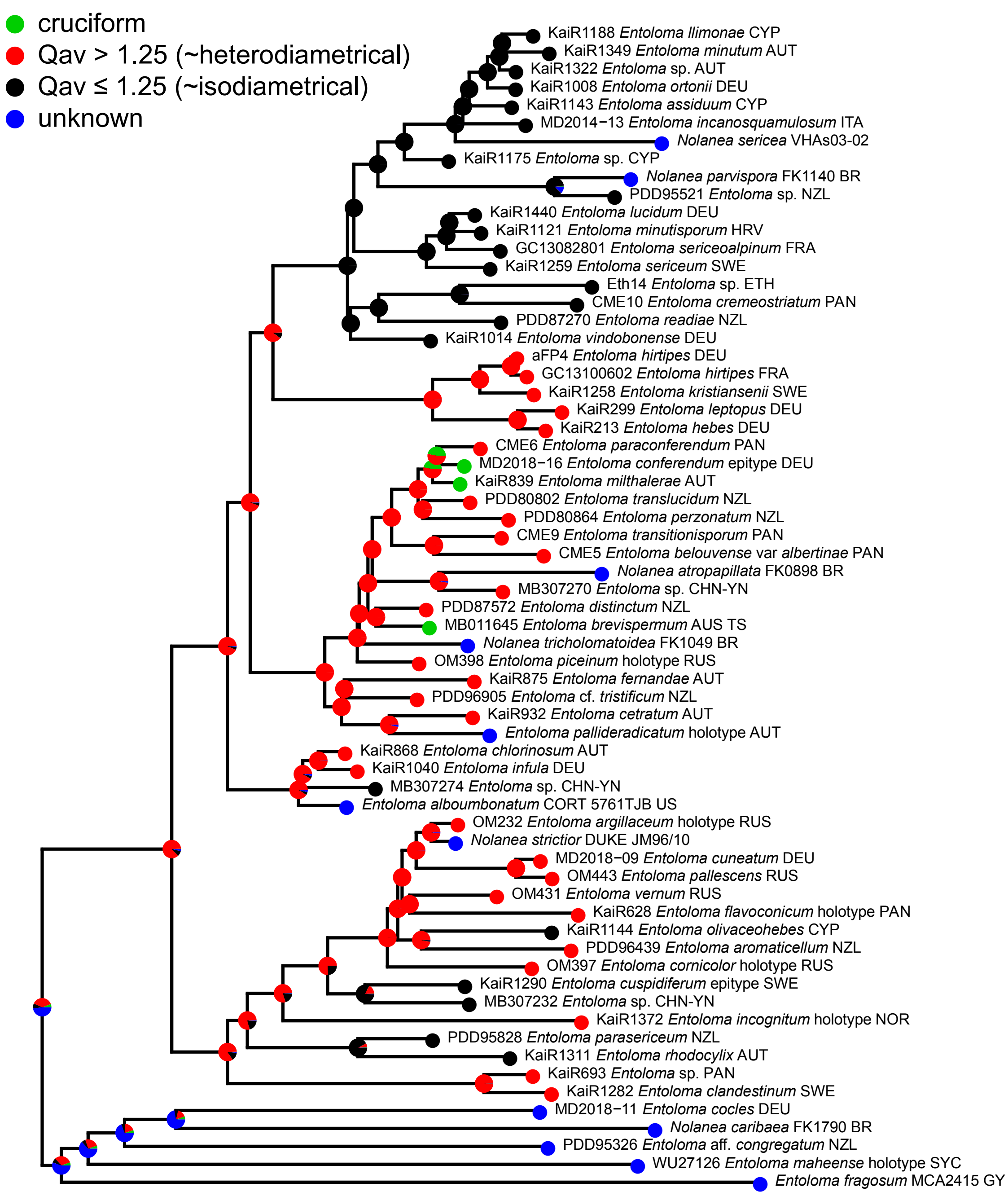

Fig. 5 Ancestral character state reconstruction of basidiospore shape in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166.

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. rhodocylix*, 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.

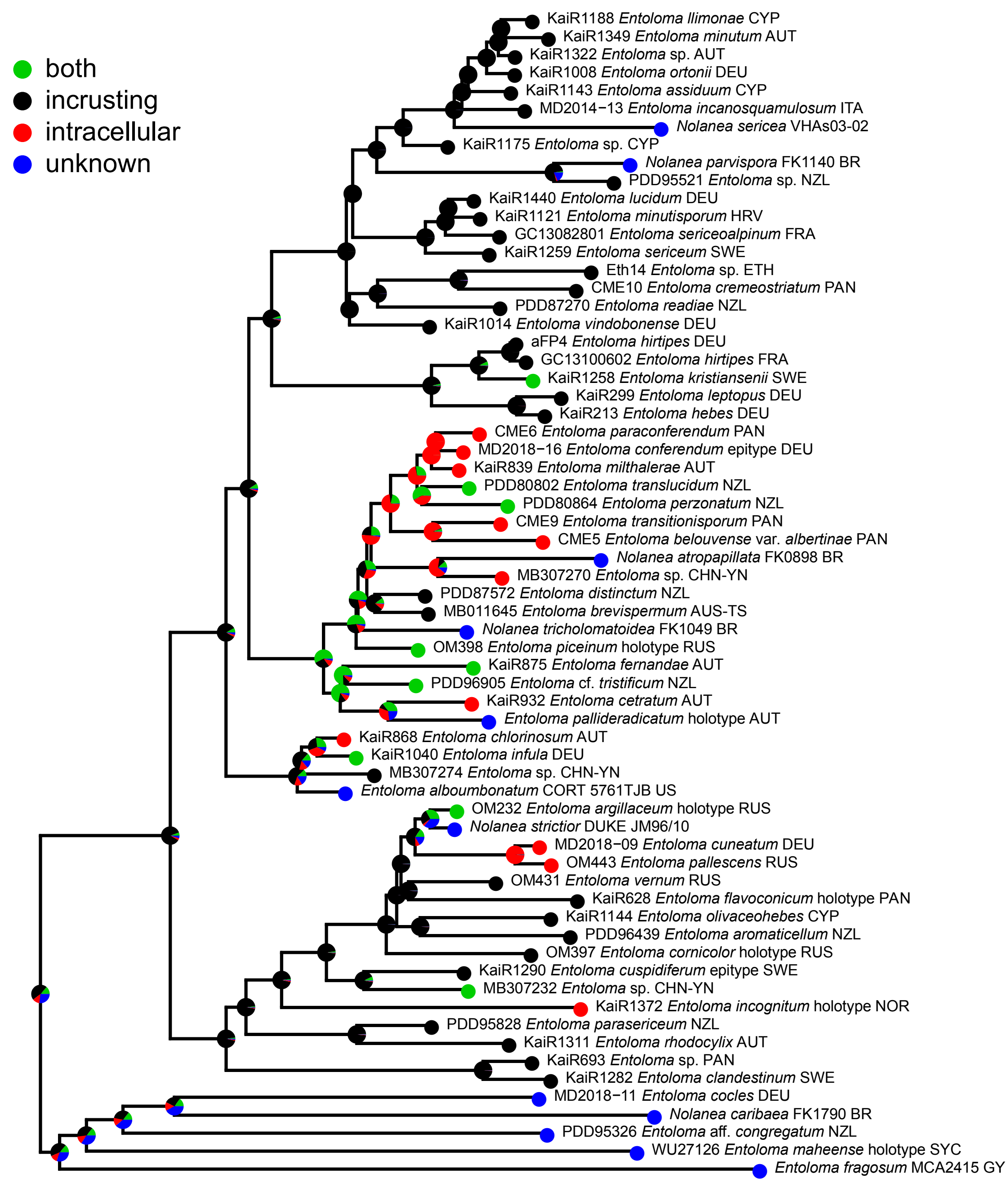

Fig. 6 Ancestral character state reconstruction of pigmentation type in subg. *Nolanea*. Newly sequenced specimens with specimen voucher before species name, GenBank data with specimen voucher after species name. Origin of corresponding specimens indicated by country codes after ISO 3166.

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

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

* 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 (N) are newly described or combined below. An overview of synonyms based on ITS sequences is given in Table 5.

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

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 basidiocarps, 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 ≤ 5 mm broad, rarely broader, up to 10 mm, surface smooth, innately fibrillose to silvery-whitish fibrillose, or fibrillose striate. *Odour* often farinaceous or indistinct, 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,

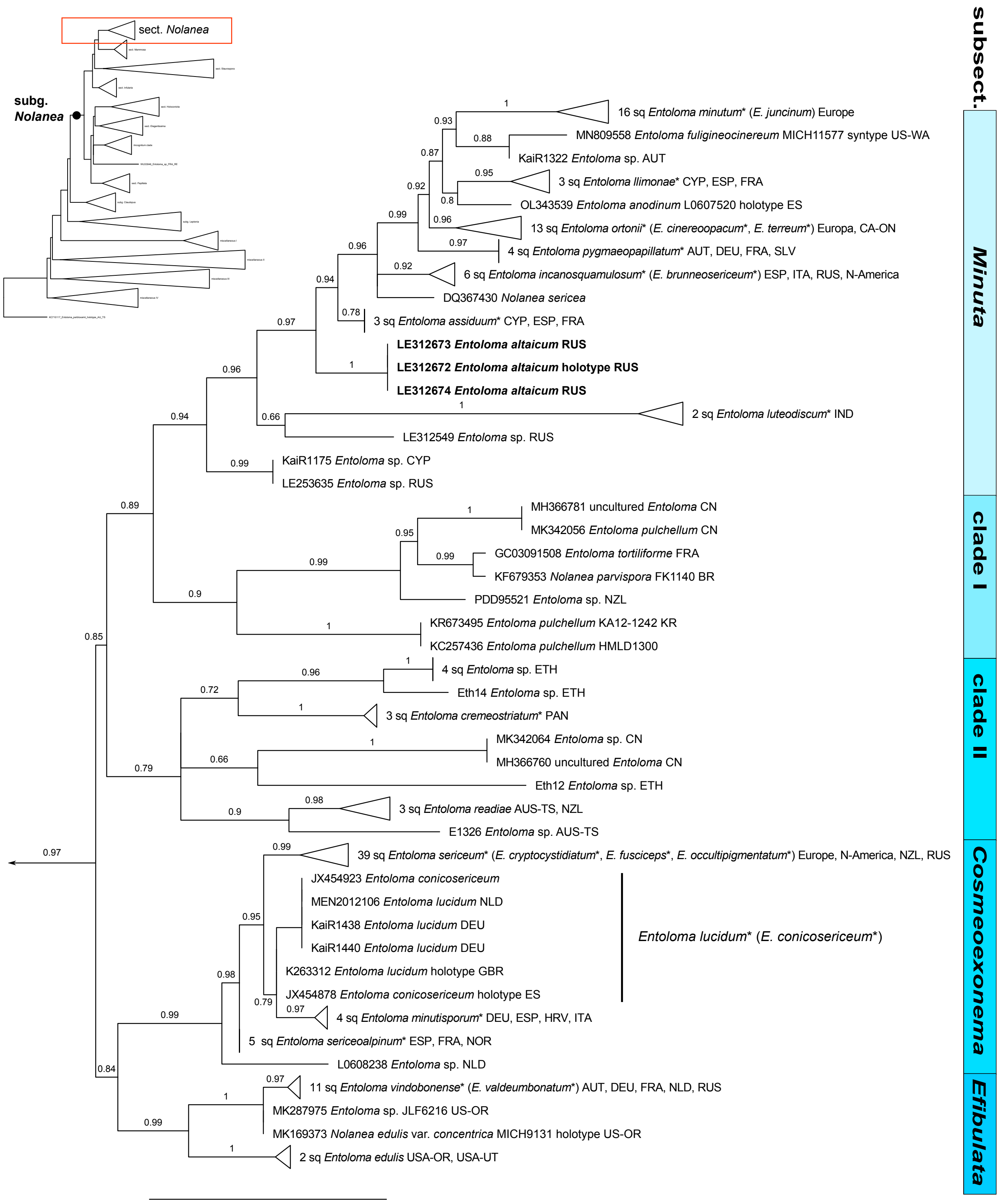

Fig. 7 Partial maximum likelihood phylogram based on ITS of species of the section *Nolanea*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. Novel 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 µm and in average > 150 µm 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 µm 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 /Rhombisporum 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 (≡ *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 '*occultopigmentatum*'), 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. tibiicystidiatum*, 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 conicosericeum* 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. conicosericeum* 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 (≡ *Nolanea proxima* Largent).

misappl. *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. llimonae*. 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 Northwestern 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 conferendus* (26a, lectotype); d. *Entoloma conferendum* (MD2018-16, epitype); e. *Entoloma milhalerae* (KaiR839). — c. Drawing by M. Britzelmayr. — Photos by: a. O. Morozova; b. G. Corriol; d. M. Dondl; e. K. Reschke.

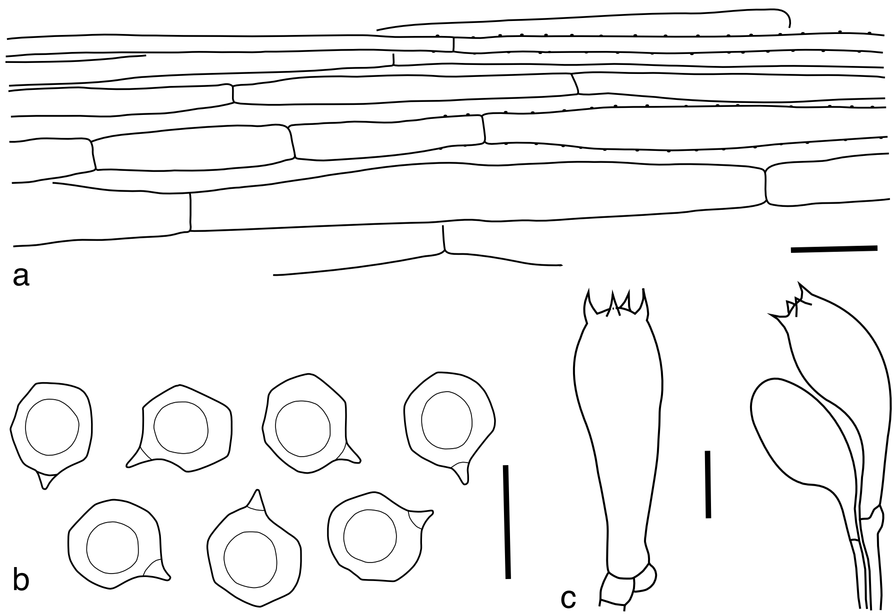

Fig. 9 Microscopic structures of *Entoloma altaicum* (LE312672, holotype) a. Pileipellis, incrusting pigment only partially indicated; b. basidiospores; c. basidia. — Scale bars: a = 20 µm; b–c = 10 µm.

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 hemisphaerical, becoming convex, then applanate 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 Tolgoyek 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, Entolomatoid fungi 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. brunneosericeum* nests within the sequences of *E. incanosquamulosum* in the ITS phylogeny (Fig. S2). Apart from specimens with smooth pileus described as *E. brunneosericeum*, 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-

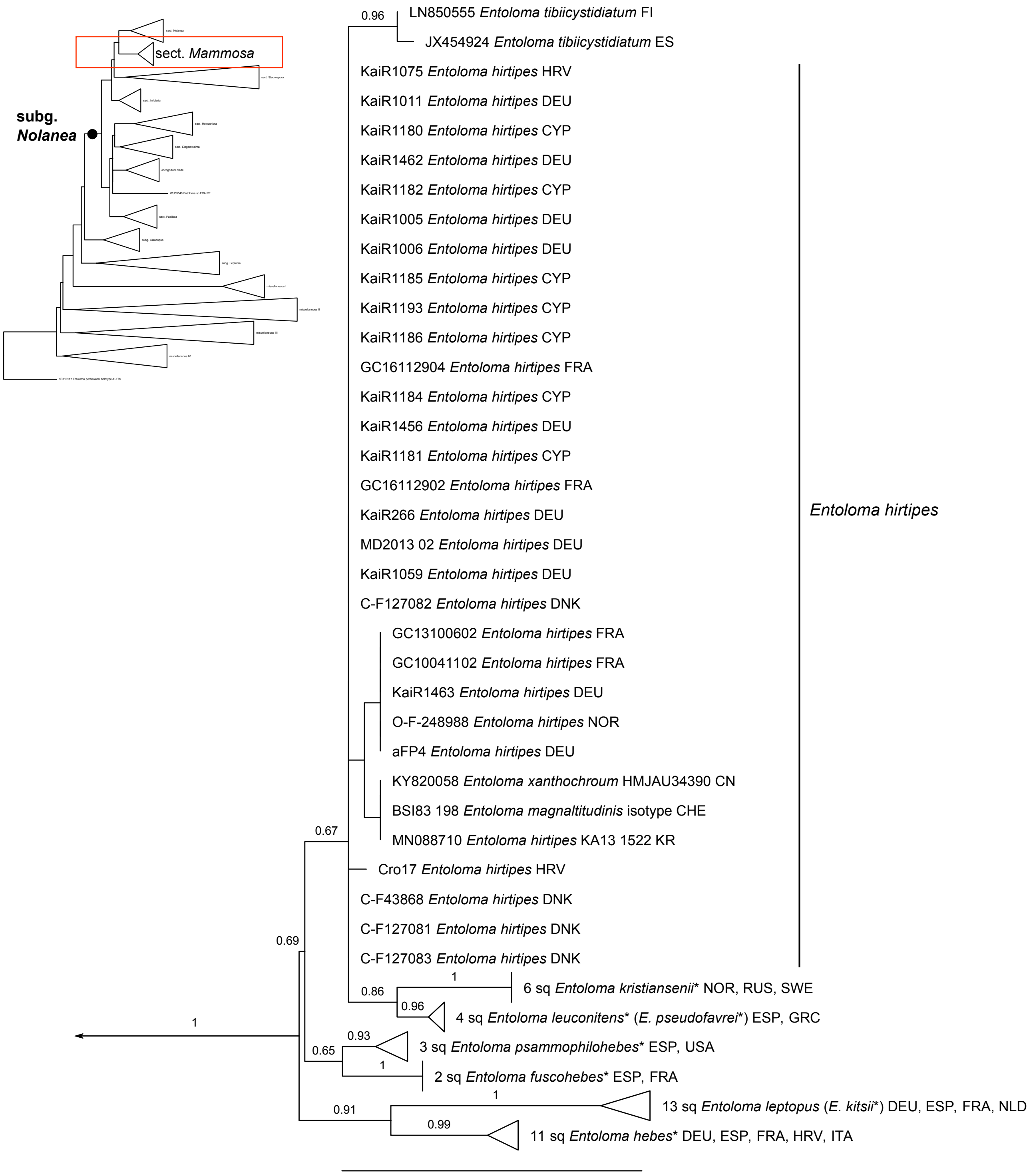

Fig. 10 Partial maximum likelihood phylogram based on ITS of species of the section *Mammosa*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, 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

Heterotpic 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 albinotic 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 Pilzk. (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. *sericoides* Kühner, Rev. Mycol. (Paris) 19(1): 7. 1954. — *Entoloma hirtipes* var. *sericoides* (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

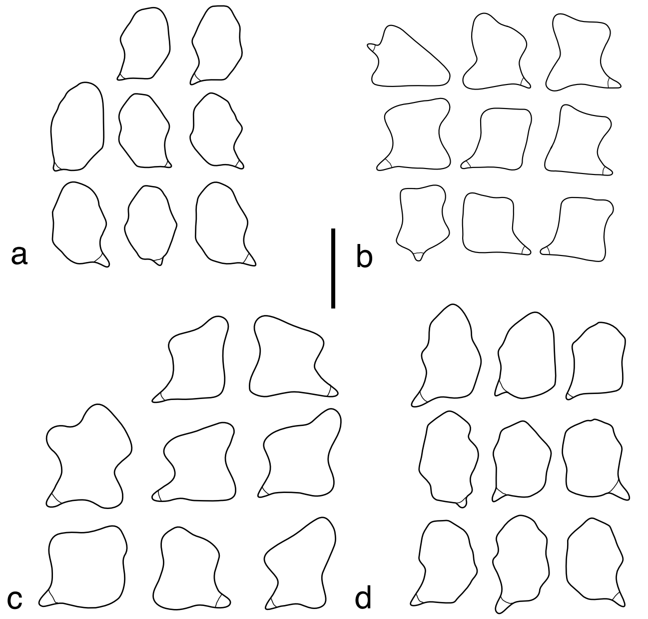

Fig. 11 Basidiospores of *Entoloma* spp. a. *Entoloma hebes* (GC96092300, epitype); b. *Entoloma conferendum* (MD2018-16, neotype); c. *Entoloma milthalerae* (KaiR839); d. *Entoloma cetratum* (LE311888, neotype). — Scale bars: a–d = 10 µm.

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*.

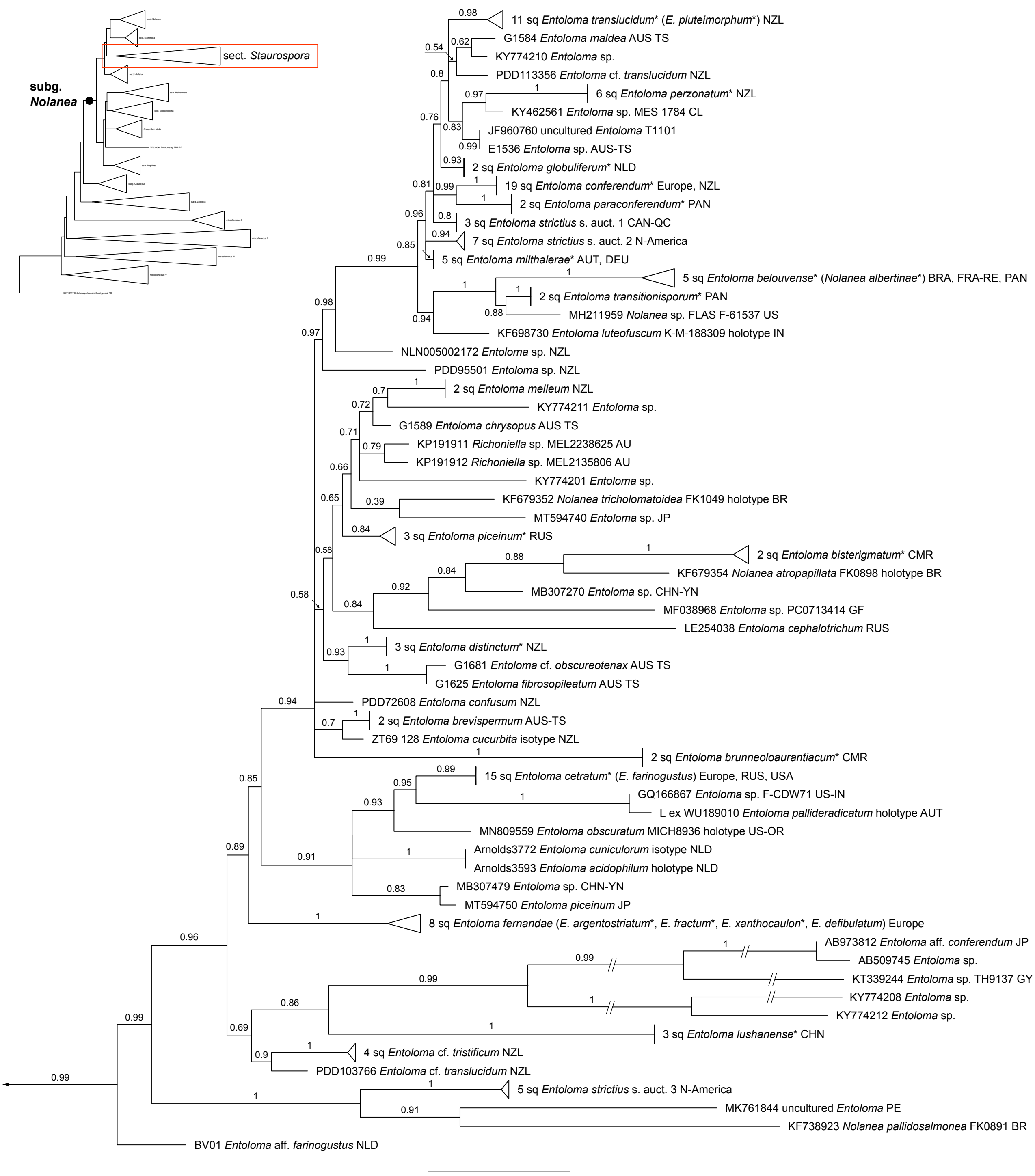

Fig. 12 Partial maximum likelihood phylogram based on ITS of species of the section *Staurospora*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species 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. *Staurospora (Largent & Thiers) Noordel., Persoonia 10(4): 445. 1980

Basionym. Nolanea sect. *Staurospori* Largent & Thiers, Northw. Sci. 46: 37. 1972. — Type species: *Entoloma staurosporum* (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. *Staurospora* 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 staurosporum (Bres.) E. Horak, Sydowia 28(1-6): 222. 1976 ‘1975–1976’. — *Nolanea staurospora* 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. staurosporum*, 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 ‘*milthaleri*’), 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. *Staurospora* 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.

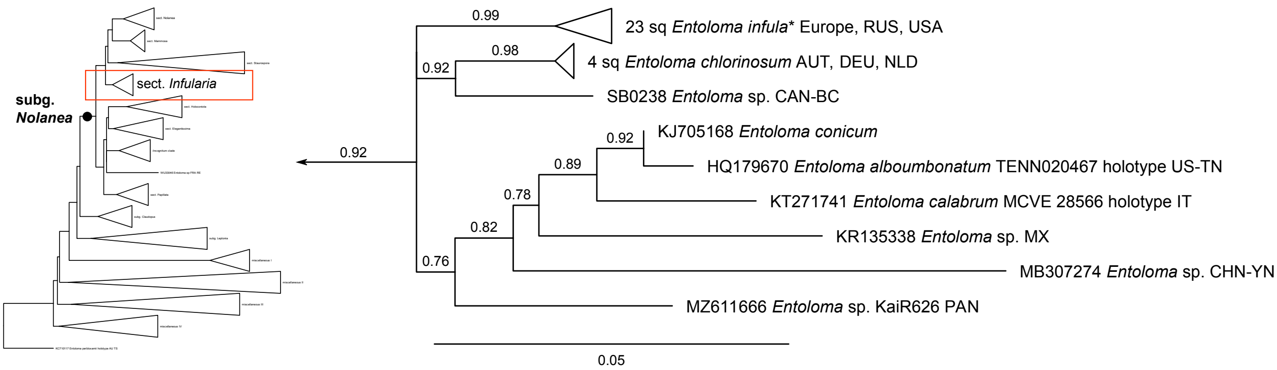

Fig. 14 Partial maximum likelihood phylogram based on ITS of species of the section *Infularia*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences with specimen voucher before species name, 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, Entolomatoid fungi of the Western United States and Alaska (Eureka): 203. 1994. — *Rhodophyllus* sect. *Infularii* 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 umbonate, 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. holoconiotum* because of its conspicuous capitate caulocystidia. Later, Largent (1974) indicated *E. cuneatum* as type species, probably considering *E. holoconiotum* 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

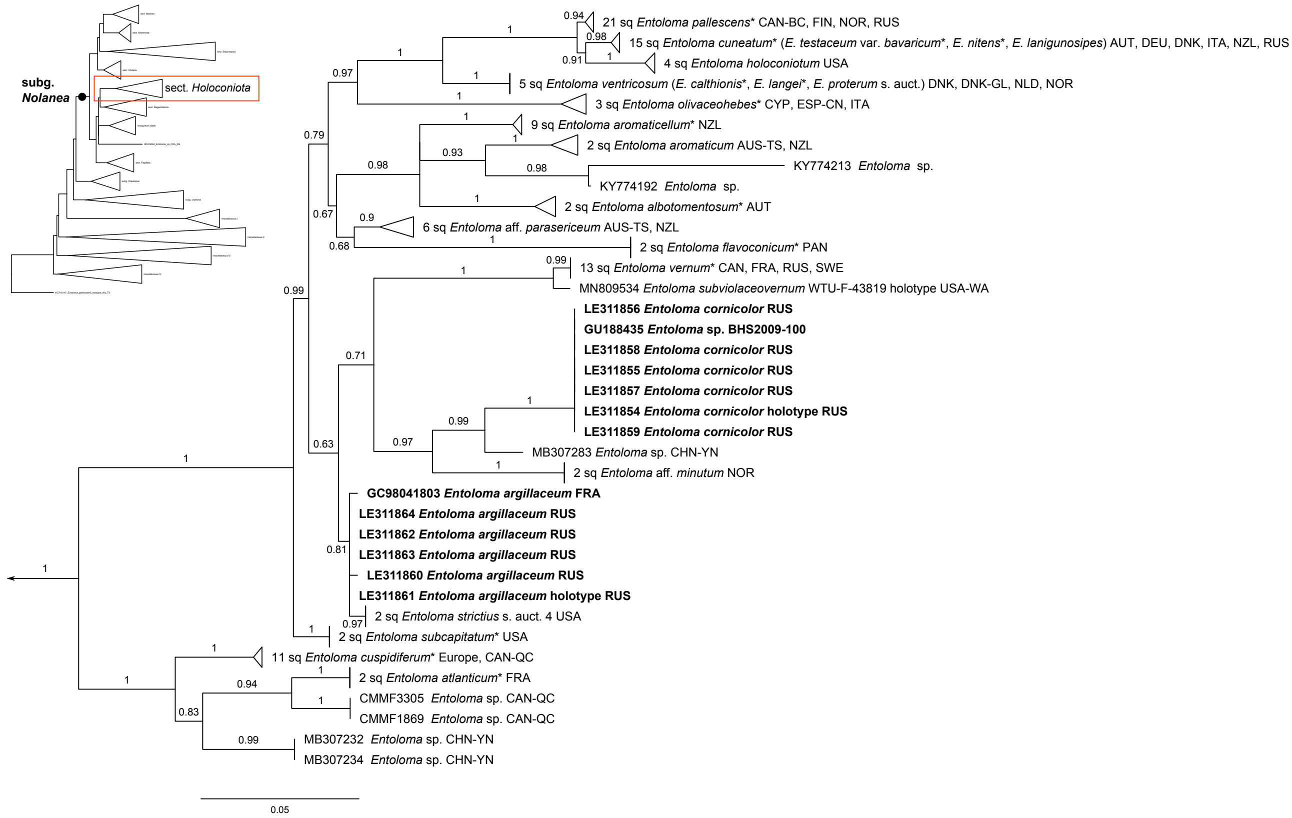

Fig. 15 Partial maximum likelihood phylogram based on ITS of species of the section *Holoconiota*. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. 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. holoconiotum*. 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. Catala, 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 — Velenovskỳ (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 Velenovskỳ. 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 cornicolor 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, N44.932889° 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, e–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.

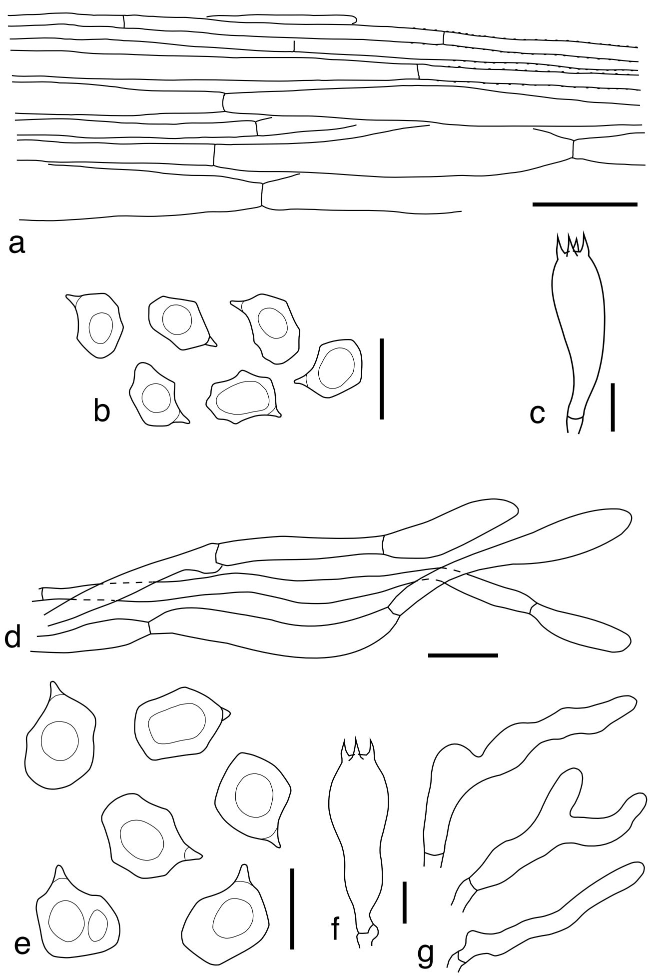

Fig. 17 Microscopic structures. a–c. *Entoloma cornicolor* (LE311854, holotype). a. Pileipellis, incrusting pigment only partially indicated; b. basidiospores; c. basidium. — d–g. *Entoloma argillaceum* (LE311861, holotype). d. Terminal parts of upper pileipellis hyphae; e. basidiospores; f. basidium; 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-Cherkesia 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, izabella, pale yellowish beige to yellowish brown, usually rather uniformly coloured, pallescent 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-Cherkesia 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. Svetasheva* (LE 311864).

Notes — *Entoloma argillaceum* is characterised by the rather conical, uniformly coloured beige or yellowish beige, only somewhat translucently 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 snyonym 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. *Claudopus* 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, Högänge, 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.) J. Favre, Bull. Trimestriel 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.

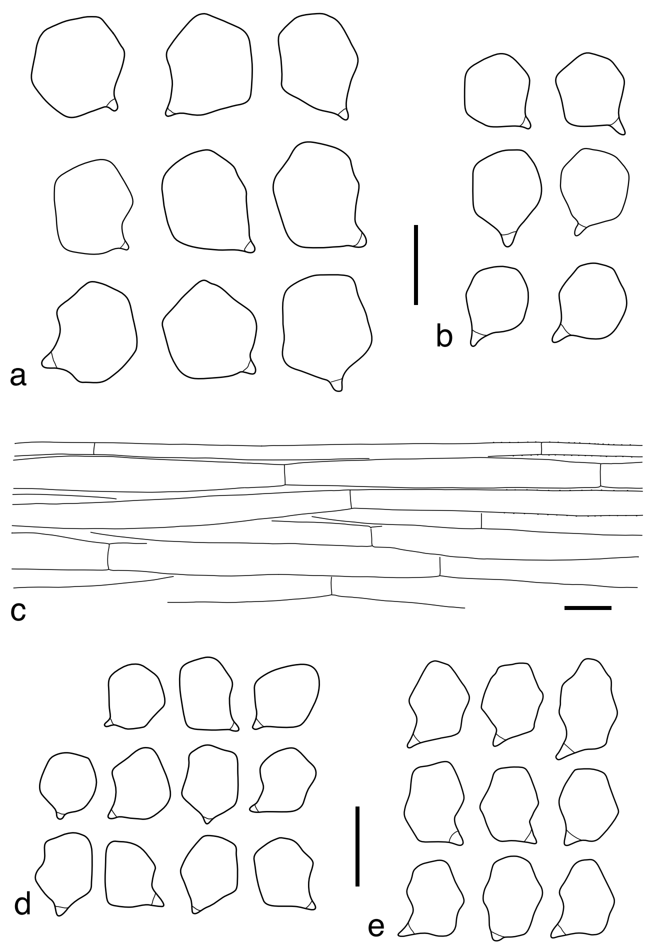

Fig. 18 Microscopic structures. a. Basidiospores of *E. cuspidiferum* (KaiR1290, epitype); b. basidiospores of *E. rhodocylix* (ACN40, neotype). — c–d. *Entoloma incognitum* (KaiR1372, holotype). c. Pileipellis, minutely incrusting pigment indicated on the right; d. basidiospores. — e. Basidiospores 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

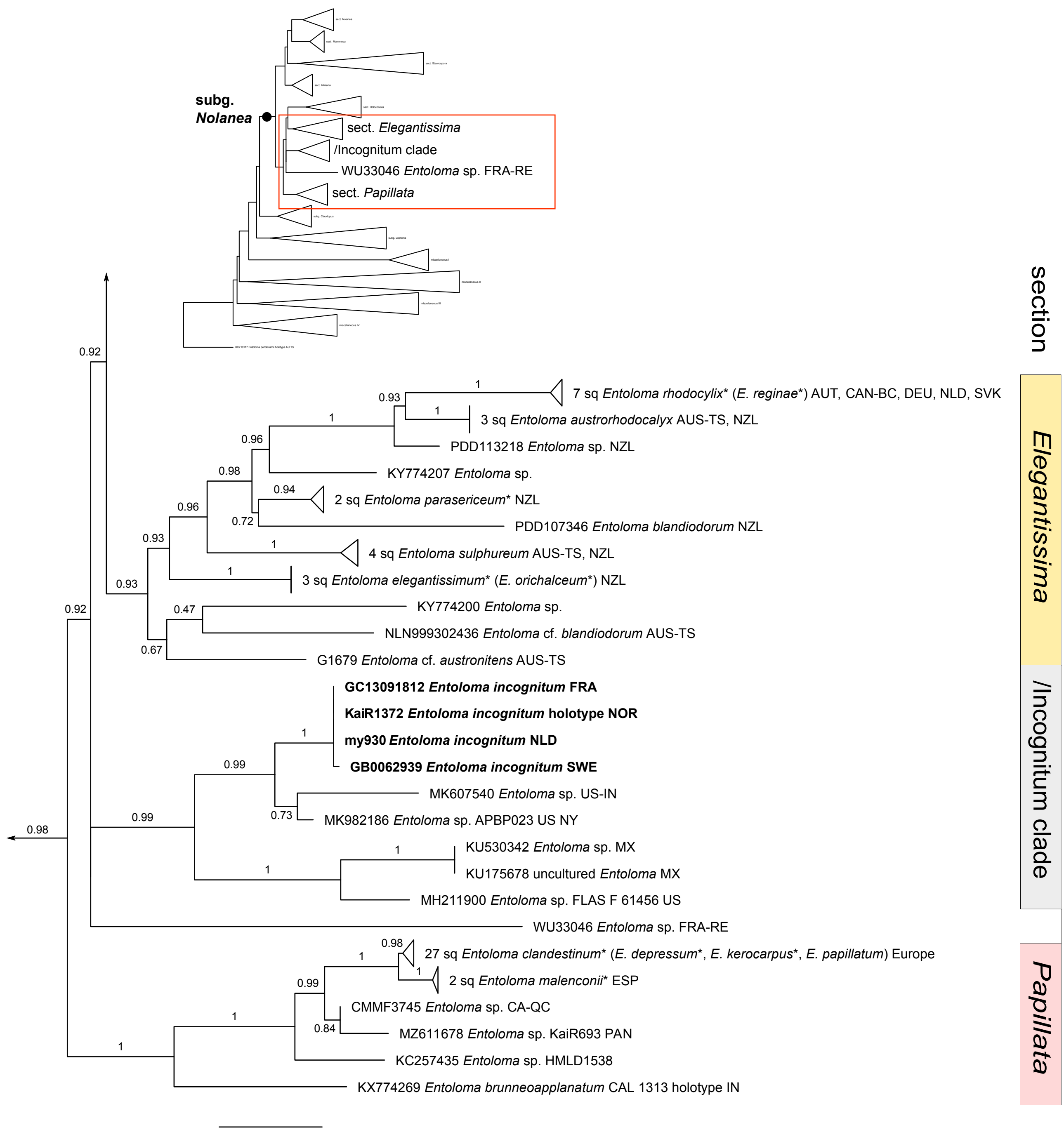

Fig. 19 Partial maximum likelihood phylogram based on ITS of species of the sections *Elegantissima* and *Papillata*, and the /Incognitum clade. Species clades collapsed with synonyms in brackets, sq = sequences, an asterisk denotes included type sequences. The newly described species **bold** and not collapsed. TBE values above or below branches. Novel sequences with specimen voucher before species name, GenBank sequences with accession number 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.

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. rhodocylix* 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 rhodocylix (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 rhodocylix 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 rhodocylix* with its omphalinoid habit with long decurrent lamellae is a rather untypical species in subg. *Nolanea*. A similar and relatively closely related species, *E. austrorhodocalyx*, 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. rhodocylix*.

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 depressum* 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 depressum* represents specimens with depressed pileus, which are generally rare in this species. *Entoloma clandestinum* was in Europe sometimes confused with *E. sanvitalense*, 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 brushes 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 trichodermoid, 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.

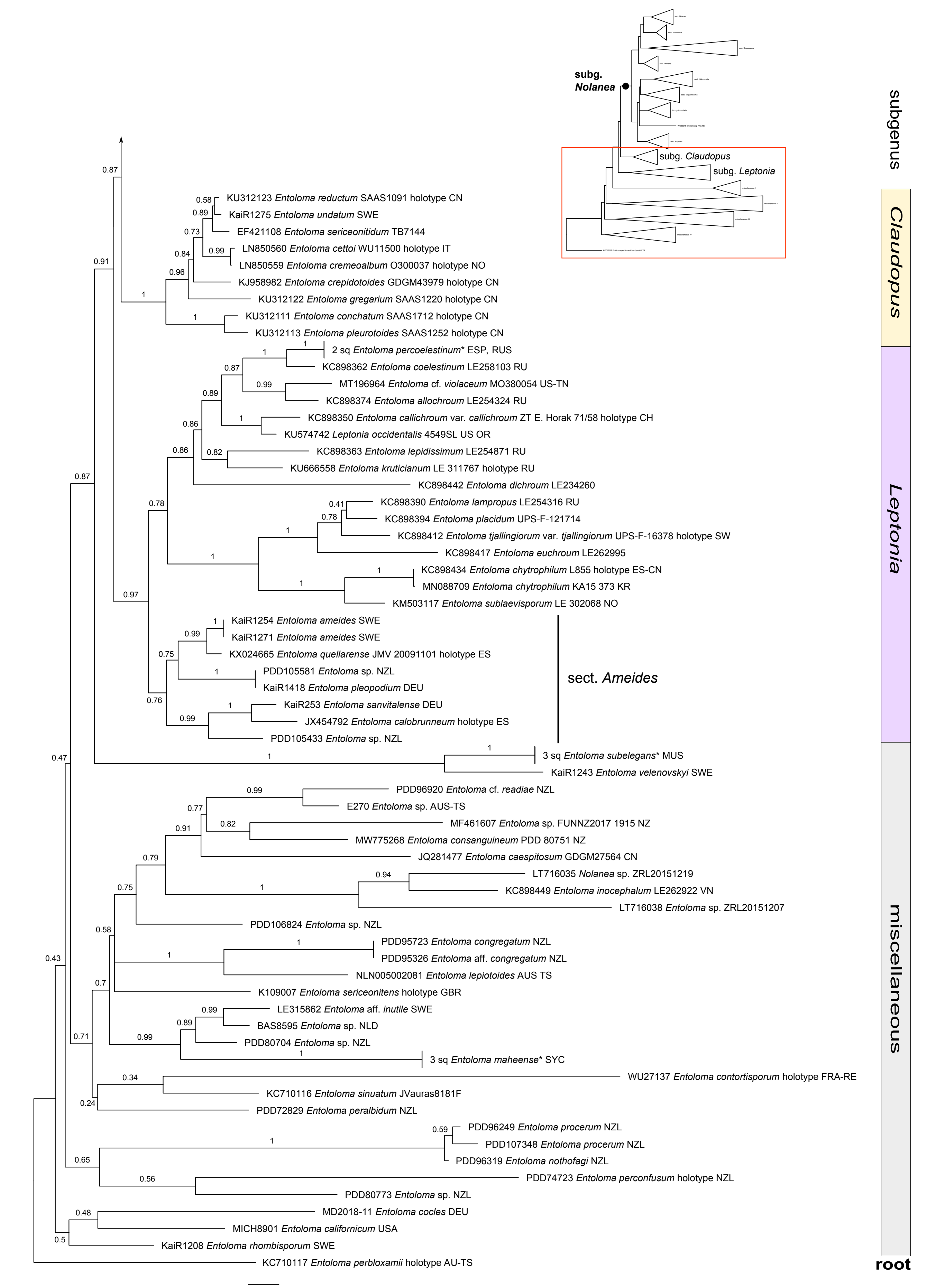

Fig. 20 Partial maximum likelihood phylogram based on ITS of species of the subgenera *Claudopus* and *Leptonia*, as well as miscellaneous nolaneoid and outgroup taxa. Species clades collapsed, sq = sequences, an asterisk denotes included type sequences. TBE values above or below branches. Novel sequences 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, montain *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. quellarense*, *E. sanvitalense*, 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 quellarense* 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 *Pouzaromyces* 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 subsect. *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. magnaltitudinis* (= *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. *Staurospora*. 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 pusillulum Noordel., Persoonia 12(3): 294. 1984

Notes — An ITS sequence of the type of *E. pusillulum* was published by Reschke et al. (2022). It is a species in the /Rhodopolium 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-1α* 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-1α*, 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-1α* 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-1α* 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-1α* may be similarly more accurate with a larger number of sequences. Matheny et al. (2007) reported a lower resolution performance of *EF-1α* compared to *RPB2*, however, their *RPB2* sequences were in average twice as long as those of *EF-1α*. The *EF-1α* sequences in the present study were generally somewhat longer than those of *RPB2* but the performance of *EF-1α* 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 underlaying 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 Qav. = 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 infrageneric 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 exlusively 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.

Acknowledgements The curators and staff of BBF, C, CMMF, K, KR, H, L, LE, MB, MICH, O, PDD, SLV, WU, and ZT are thanked for organizing loans. Christian Lange (C) is in addition thanked for checking unpublished material of C.F. Schuhmacher. We thank Timothy Barony and an anonymous reviewer for many valuable comments. Staff of M is thanked for the plate of Britzelmayr. Jose Maciá-Vicente is thanked for scripts and help in python and R. Gunnhild Marthinsen and Katriina Bendiksen are thanked for several sequences of the Norwegian Barcode of Life project. We thank Vassiliki Fryssouli, Georgios Zervakis, and Elias Polemis for the holotype sequence of *E. leuconitens*. Shannon Berch, Irmgard Krisai-Greilhuber, Ellen Larsson, and Lászó Nagy are thanked for the allowance to use their sequences. Matthias Dondl is thanked for extensively documented specimens and the allowance to use his pictures. We are grateful for valuable specimens of Genevieve Gates, Andreas Gminder, Cathrin Manz, Matthias Theiss, Dmitry Ageev, Anna Fedosova, Ekaterina Malysheva, László Nagy, Yury Rebriev, Tatiana Svetasheva, Elena Zvyagina, Wolfgang Prüfert, Thomas Læssøe, Jens H. Petersen, Carole Hannoire, and numerous further collectors. Felix Hampe is thanked for information about *E. tortiliforme* and specimens. Maren Kamke is thanked for a piece of the type of *E. milthalerae*. Volker Kummer is thanked for providing specimens and pictures for possible typifications. Konstanze Bensch and Shaun Pennycook are thanked for nomenclatural advice. Jordi Vila is thanked for valuable information about species with South European distribution. Participants of the Russulales Congress 2018 in Borgsjö and the Nordic Mycological Congress 2019 in Stord are acknowledged for providing KR with their *Entoloma* collections. KR is grateful for significant help of Jan-Olof Tedebrand in collecting *Entoloma* spp. in Sweden. The Willkomm-Stiftung, Frankfurt, provided travelling grants for Kai Reschke to congresses in Sweden and Norway. The work of Bálint Dima was supported by the ELTE Thematic Excellence Programme 2020 (TKP2020-IKA-05), financed by the National Research, Development and Innovation Office. Jerry Cooper is funded through the Strategic Science Investment Fund of the New Zealand Ministry of Business, Innovation and Employment.

Declaration on conflict of interest The authors declare that there is no conflict of interest.

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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-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.

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.