Mycological Progress (2022) 21:93–145
https://doi.org/10.1007/s11557-021-01752-2

DGfM

ORIGINAL ARTICLE

Fungal diversity in the tropics: *Entoloma* spp. in Panama

Kai Reschke[1] · Machiel E. Noordeloos[2] · Cathrin Manz[1] · Tina A. Hofmann[3] · José Rodríguez-Cedeño[3] · Bálint Dima[4] · Meike Piepenbring[1]

Received: 30 August 2021 / Revised: 9 October 2021 / Accepted: 12 October 2021

Abstract
Entoloma (Agaricales, Basidiomycota) is a species-rich genus with approximately 2000 species known worldwide. In Central America, however, information about the species of this genus is sparse, despite the generally high biodiversity in this region. Recently, 124 specimens of *Entoloma* were collected in Panama, Chiriquí Province. In the present publication, the morphology of 20 species represented by more than one specimen is described and depicted with photographs, line drawings, and scanning electron micrographs. Molecular phylograms based on ITS or concatenated ITS and partial nc LSU rDNA sequences are provided. The taxonomic status of these species is evaluated and 17 species of *Entoloma* are described as new to science. Only one species could be assigned to an already known species, viz. *Entoloma belouvense*. *Nolanea albertinae*, described from Brazil, appeared similar and is combined in *E. belouvense* on varietal level. The identifications of two further species are uncertain. At least 30 other species, including potentially new species, cannot formally be described due to insufficient material. A preliminary key to the species of the genus *Entoloma* in Panama is provided. The spatial shape of the polyhedroid basidiospores of *Entoloma* spp. is discussed based on literature and the micrographs generated for the present study. Our re-evaluations indicate that the type of polyhedroid basidiospore and the structure of its base are not reliable as diagnostic characters for the delimitation of subgenera in *Entoloma*.

Keywords Neotropic · Entolomataceae · Taxonomy · Phylogeny · New species

Introduction

The genus Entoloma in Central America

The genus *Entoloma* (Agaricales, Basidiomycota) includes species with almost exclusively polyhedroid, faceted basidiospores, which are angled in outline and pinkish as seen with a light microscope. It comprises mainly species with agaricoid basidiocarps; few species develop secotioid or gasteroid basidiocarps (Co-David et al. 2009; Kinoshita et al. 2012; Vidal et al. 2016). Currently, approximately 2000 species of *Entoloma* are known to science (Noordeloos et al. 2018). Two monographic treatments of the genus exist for two regions of North America (Hesler 1967; Largent 1994). Such monographs are not available for South America, but some preliminary and regionally comprehensive treatments have been published (Horak 1978, 1982; Coimbra et al. 2013; Karstedt and Capelari 2013). Coimbra (2014) published a checklist including 271 species of Entolomataceae recorded for Central and South America. However, almost nothing is known about *Entoloma* species in Panama. Only one species, *Entoloma cylindrocapitatum* (T.J. Baroni & Ovrebo) Noordel. & Co-David, has been reported until now (Ovrebo and Baroni 2007; Hofmann and Piepenbring 2021). Few *Entoloma* species are reported from the other Central American countries, Belize, Costa Rica, El Salvador, Guatemala, Honduras, and Nicaragua: six species are reported

Section editor: Zhu-Liang Yang

✉ Kai Reschke
Reschke@em.uni-frankfurt.de

[1] Mycology Research Group, Faculty of Biological Sciences, Goethe University Frankfurt Am Main, Max-von-Laue Straße 13, 60438 Frankfurt am Main, Germany

[2] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

[3] Centro de Investigaciones Micológicas (CIMi), Herbario UCH, Universidad Autónoma de Chiriquí, 0427 David, Chiriquí Province, Panama

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

from Costa Rica (Baroni and Halling 2000; Halling and Mueller 2005), a single record exists for Belize (Largent et al. 2008a), and no species are known for El Salvador, Guatemala, Honduras, and Nicaragua (Coimbra 2014). From Colombia, the South American neighbouring country of Panama, six species of *Entoloma* spp. are reported (Franco-Molano and Uribe-Calle 2000; Vasco-Palacios and Franco-Molano 2013; Osorio and Osorio 2016).

Description of the study region

The province of Chiriquí is located between 8° and 9° north in the western part of Panama at the border to Costa Rica (Fig. 1). It forms part of the Mesoamerican biodiversity hotspot, one of the 25 biodiversity hotspots of the world recognised by Myers et al. (2000). There are several important protected areas in Chiriquí including the "Parque Nacional Volcán Barú" (PNVB) in the northern part of Chiriquí, which includes the highest mountain in Panama (Volcán Barú, 3475 m asl.), and the "Parque Internacional La Amistad" (PILA), which is listed as a UNESCO World Heritage Site and spans from Costa Rica to Panama. These two parks are mainly covered by montane mixed forests with *Quercus* spp. as the dominant trees, while at some locations *Alnus acuminata* Kunth is dominant. The "Reserva Forestal de Fortuna" is a mountainous forest reserve in the north-eastern part of Chiriquí. It includes forests dominated by *Oreomunnea mexicana* (Standl.) J.-F.Leroy in lower montane sites, while the higher montane forest is dominated by *Quercus* spp. South of David, the capital of Chiriquí, there are extensive mangroves and numerous small islands. The island of Parida is located about 10 km south of the coast and forms the centre of the "Parque Nacional Marino Golfo de Chiriquí". The lowlands of Chiriquí are mainly covered by cattle pastures and teak plantations. Chiriquí has a tropical climate, with a rainy season from April/May to December and a dry season from January to April. The annual rainfall in David (49 m asl.) is approximately 3900 mm and the average temperature 25.2 °C, in Boquete (1096 m asl.) 3810 mm and 18.4 °C, and in Volcán (1412 m asl.) 4400 mm and 16.9 °C, respectively (https://en.climate-data.org accessed 10-june-2021). The dry season is less pronounced in the mountains, with an average precipitation of approximately 60 and 70 mm in the driest month, February, in Volcán and Boquete, respectively, compared to 36 mm in David.

Material and methods

Fieldwork

Specimens of *Entoloma* spp. were collected by the authors and collaborators from 2014 to 2018, mainly in montane forests at 1600–2400 m asl. dominated by *Quercus* spp., sometimes by *Alnus acuminata*. Some collections were made in a forest dominated by *Oreomunnea mexicana* at 1200 m asl., a forest dominated by *Calophyllum longifolium* Willd. at 40 m asl. on Isla Parida, and close to a path in disturbed secondary vegetation at 120 m asl. in Los Algarrobos. Most of the specimens were photographed in the field. Further

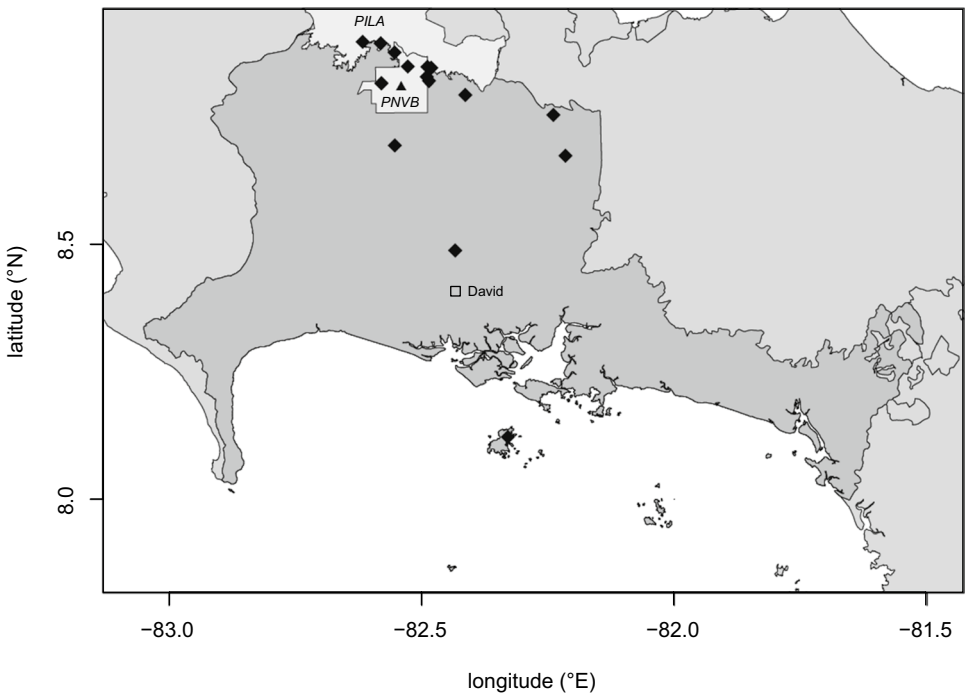

Fig. 1 Study locations in Chiriquí Province, Panama

photos were taken in the laboratory and ephemeral characters as colour, smell, and taste were registered. Colour terms and codes were determined using Kornerup and Wanscher (1967). Coordinates of the locations were recorded using a Garmin GPSmap 62 (Garmin Deutschland, Garching, Germany). The basidiocarps were dried at 40–45 °C on an electric food dehydrator and frozen for several days before storage in herbaria. Mainly specimens of species represented by at least two collections were studied in detail.

Light microscopy

Micromorphological characters of the basidiocarps were analysed by light microscopy on dried material. The size of the basidiospores, hymenial structures, and features of the pileipellis were investigated in hand-cut sections mounted in tap water or in 5–10% KOH. To measure the long cells of the hymenophoral trama and stipe surface, sections were soaked in KOH for 5 min, rinsed with deionised water, and stained with Congo Red. At least 20 basidiospores were measured from lamellae squash preparations for each collection. For some specimens, the presence or absence of clamp connections at the base of basidia was additionally examined using phase contrast. Spore sizes and *Q*-values are given in 5th percentile–mean–95th percentile. Spore sizes are rounded to the nearest 0.5 µm, *Q*-values to the nearest 0.05. Other values of measurements were less strictly rounded off to avoid pseudo-exact indication of sizes.

Scanning electron microscopy (SEM)

Fragments of basidiocarps were prepared for SEM following a protocol including the use of dioctyl sodium sulfosuccinate (DSS), based on Koch et al. (2021) and Erbar (1995) with several modifications. Small pieces of lamellae were soaked in a solution of 5% (w/v) DSS in 4:1 water:ethanol for 24 h. The samples were then rinsed three times in 4:1 water:ethanol and two times in 0.1 M sodium cacodylate buffer and thereafter fixed in 4% glutaraldehyde in 0.1 M sodium cacodylate buffer for 20–24 h. After fixation, the samples were rinsed two times in the cadodylate buffer and then dehydrated in a graded ethanol series of 30, 50, 70, 90, 100, and 100% for 10–20 min each. The dehydrated samples were stored in 100% ethanol until critical point drying using liquid CO_2. Dried samples were sputtered with gold and studied in a Hitachi (S 4500) scanning electron microscope. The description of basidiospore structures follows Pegler and Young (1979), except that polyhedron terminology is used instead of their spore types. The earlier term "dièdre basal" (Kühner and Boursier 1929) is used instead of "dihedral base" to avoid confusion with mathematical terms.

DNA extraction and PCR

Pieces of lamellae of 3–10 mm^2 were taken from dry basidiocarps and 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) or the innuPREP Plant DNA Kit (analytikjena, Jena, Germany) according to the instruction manuals. The ITS region was amplified by PCR in a peqSTAR gradient thermal cycler (PEQLAB, Erlangen, Germany) using the VWR Taq DNA polymerase (VWR, Darmstadt, Germany). To obtain the ITS sequences, the forward primer ITS1 or ITS1F and the reverse primer ITS4 or ITS4B (White et al. 1990; Gardes and Bruns 1993) were used. Further ITS sequences were obtained as described by Papp and Dima (2018). To obtain the D1/D2 region of the nc LSU rDNA, the primers LR0R together with LR5 (Vilgalys and Hester 1990) or NL1 together with NL4 (O'Donnell 1992) were used. Both rDNA regions were amplified using the same PCR protocol: 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. A partial sequence of the second largest subunit of RNA polymerase II (*RPB2*) was obtained using the primers rpb2-6F and rpb2-7.1R (Matheny 2005) 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. 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) for purification and Sanger sequencing.

Phylogenetic analyses

Sequences were edited with Geneious 2019.2.1 (Biomatters Ltd., Auckland, New Zealand) and aligned with Mafft (Katoh and Standley 2013) using the E-INS-i algorithm. The ends of the resulting alignments as well as unreliable terminal parts of sequences were manually pruned in AliView (Larsson 2014). For the phylogenetic analysis of sequences of subg. *Cyanula*, aligned ITS and LSU sequences were concatenated and a piece of 61 nucleotides at the 5′ end of the LSU, which was not available for many sequences, excluded from the final alignment. Maximum likelihood trees were built using RAxML 8.2.11 (Stamatakis 2014). The GTRGAMMA model was used for alignments of less than 50 sequences, the GTRCAT model with 45 per site rate categories for 50 sequences, and more, along with a bootstrap analysis (Felsenstein 1985) with 500 repetitions. Resultant phylogenetic trees were visualised using FigTree

(Rambaut 2014). All sequences generated are deposited in GenBank (Table 1).

Results

A total of 124 specimens of *Entoloma* spp. were collected. These specimens represent more than 50 species, with at least 22 species being represented by more than one specimen. Twenty of these species were studied in detail and are described below. Only one species could be assigned to an already described species and two species were identified with considerable uncertainty. Seventeen species are unknown to science and are described as new species below. The most frequently represented subclade was the subgenus *Cyanula*, with 35 specimens belonging to 18 species. Specimens of the subgenera *Alboleptonia*, *Cubospora Entoloma*, and *Nolanea* were frequently found as well (Table 2).

In 2017 and 2018, most specimens were collected in montane forests with abundant to dominating trees of *Quercus* spp. The highest number of *Entoloma* specimens for a single location, i.e. 22 specimens found during three visits, was collected in the PILA, in a montane forest dominated by *Alnus acuminata*, with some *Quercus* spp. and at least one individual of *Podocarpus* sp. On the contrary, only two specimens, both of subg. *Cyanula*, were collected in lowland habitats, one in a forest close to mangrove forest on Island Parida and the other one at a path in disturbed secondary vegetation (Table 3). This path in Los Algarrobos was the most often visited location in these years. The specimens collected in the years before 2017 were mainly collected during a local inventory project and are thus less informative for comparisons of diversity of habitats.

Shape of basidiospores

Polyhedroid basidiospores of 17 species of *Entoloma* from Panama were analysed by SEM. The basidiospores displayed a considerable degree of variability, increasing with the number of facets. Apart from the cuboid basidiospores, the number of angles of the respective facets was often variable and thus not determined. The adaxial facet is always a single facet and consistent in its position above the apiculus. The spatial formation of facets can abaxially be variable. The basal facet can either be next to the abaxial facet or separated from it by lateral facets (Fig. 2e). When two abaxial facets are formed, they can be next to each other or separated by lateral facets (Figs. 2i, 26d). Shape and a consistent base type of the basidiospores of two species of subg. *Entoloma* (*E. nubooccultatum* and *E. mediorobustum*, described below) could not be determined because of considerable variability of these characters. Five species have hendecahedroid spores, three of subg. *Cyanula* and two of subg. *Nolanea*. Two species each have heptahedroid, octahedroid, or decahedroid basidiospores, respectively, while one species each presents cuboid, enneahedroid, dodecahedroid, or tetrahedroid basidiospores. Reduced forms frequently occur, mainly concerning reduction or lack of the apical facet and/or reduction of the pair of adaxial facets to a single adaxial facet. Basidiospore shapes in subgenera are not consistent. The largest variability was observed in subg. *Alboleptonia*, including one species with mainly octahedroid, one species with enneahedroid, and another species with tetradecahedroid basidiospores. A simple base is formed in four species, two in subg. *Entoloma* and two in subg. *Nolanea*, while basidiospores with a dièdre basal are present in all subgenera, exclusively so in *Alboleptonia*, *Cubospora*, and *Cyanula*. A base built by three facets was found in the newly described species *E. mediorobustum* (Fig. 2l).

Taxonomy

The traditional infrageneric classification of *Entoloma* is based on morphological characters, viz., habit, lamellae attachment, pileipellis structure, and basidiospore shape (Romagnesi 1974; Romagnesi and Gilles 1979). This classification has been continuously revised and emended (Noordeloos 1981, 1992, 2004; Largent 1994). Co-David et al. (2009) demonstrated that a high number of subgroups in this classification were not monophyletic based on molecular phylogenetic results. With the incorporation of DNA sequence data, several subgenera have since been revised, viz., *Pouzarella* by He et al. (2013), *Leptonia* by Morozova et al. (2014a), *Entoloma* (as "*Rhodopolia*") by Kokkonen (2015), and *Claudopus* by He et al. (2019). The section *Cyanula* was elevated to the rank of subgenus by Noordeloos and Gates (2012) and two new subgenera, *Cubospora* and *Cuboeccilia*, were described by Karstedt et al. (2019). He et al. (2019) recognised 10 major clades, largely referring to the studies just cited. Baroni et al. (2011) described the genus *Entocybe* for a few aberrant species of the large, basal clade of *Entoloma*. This new genus, however, causes the basal clade to be paraphyletic and was, therefore, not recognised by He et al. (2019).

Subgenus Entoloma Fig. 3

As in most other subgenera, species of subgenus *Entoloma* are hard to identify on macroscopical characters in the field, as they are pretty uniform in colour and stature. Kühner and Romagnesi (1953, 1954) first considered the structure and pigmentation of the covering layer of the pileus as potential tools to distinguish species, besides size and shape of basidiospores. Noordeloos (1981, 1992, 2004) expanded the concept, resulting in an overview of sect. *Rhodopolia* in Europe

Table 1 Data corresponding to the sequences used for phylogenetic analyses, including GenBank accessions, if not stated otherwise

Species (annotation)	Specimen voucher	Origin	Accession		Reference
			ITS	LSU	
subgenus *Alboleptonia*					
Alboleptonia sericella	Lueck1	Germany	KP965765		Karich et al. 2015
Entoloma amistadosericellum	KaiR490	Panama	MZ611648		This study
Entoloma amistadosericellum	KaiR492	Panama	MZ611649		This study
Entoloma amistadosericellum	KaiR495	Panama	MZ611650		This study
Entoloma amistadosericellum	KaiR501	Panama	MZ611651		This study
Entoloma amistadosericellum	KaiR502	Panama	MZ611652		This study
Entoloma amistadosericellum	KaiR612, holotype	Panama	MZ611663		This study
Entoloma amistadosericellum	KaiR672	Panama	MZ611673		This study
Entoloma amistadosericellum	KaiR675	Panama	MZ611674		This study
Entoloma confusissimum	KaiR489	Panama	MZ611647		This study
Entoloma confusissimum	KaiR670	Panama	MZ611672		This study
Entoloma niveum	PDD104142	New Zealand	MZ611695		This study
Entoloma nubilosilvae	KaiR429	Panama	MZ611643		This study
Entoloma nubilosilvae	KaiR430	Panama	MZ611644		This study
Entoloma nubilosilvae	KaiR465, holotype	Panama	MZ611645		This study
Entoloma nubilosilvae	KaiR474	Panama	MZ611646		This study
Entoloma sericellum	KaiR1203	Sweden	MZ611636		This study
Entoloma sericellum	KaiR1214	Sweden	MZ611637		This study
Entoloma sericellum	LE254362	Russia	KC898453		Morozova et al. 2014a
Entoloma serrulatum	LE254361	Russia	KC898447		Morozova et al. 2014a
Subgenus *Cubospora*					
Entoloma aurantiovirescens	KaiR623, holotype	Panama	MZ611665		This study
Entoloma aurantiovirescens	PAN419	Panama	MZ611691		This study
Entoloma luteum	GDGM27698	China	JQ281486		He et al. 2012
Entoloma murrayi	MHHNU30602	China	MK250917		Zhang and Chen, unpublished
Entoloma murrayi	QI1001	China	KJ658967		He et al. 2015b
Entoloma murrayi	QI1002	China	KJ658968		He et al. 2015b
Entoloma murrayi	SDR NAMA 2017–160	USA, Wisconsin	MK575459		Russell, unpublished
Entoloma quadratum	LE254355	Russia	KC898452		Morozova et al. 2014a
Entoloma quadratum	MHHNU30632	China	MK250921		Zhang and Chen, unpublished
Entoloma quadratum	MHHNU82	China	KU518319		He and Chen, unpublished
Entoloma quadratum	PAN241	Panama	MZ611690		This study
Entoloma semilanceatum	NS2283	Cameroon	MN069544		Largent et al. 2019
Entoloma virescens	MHHNU30619	China	MK250919		Zhang and Chen, unpublished
Inocephalus murrayi	ECO-TA-HO 7874	Mexico	MF156254		Arias-Hernandez et al., unpublished
Subgenus *Cyanula*					
Entoloma aff. *griseocyaneum*	NL5097	USA	MZ869020	MK277993	This study/Varga et al. 2019
Entoloma aff. *griseocyaneum*	PO6	Canada, Ontario	KY706188		Hay et al. 2018
Entoloma aff. *necopinatum*	KaiR646	Panama	MZ611670	MZ678748	This study
Entoloma arcanum	KaiR614	Panama			This study
Entoloma arcanum	KaiR488, holotype	Panama		MZ678738	This study
			+ *RPB2*: MZ605445		

Table 1 (continued)

Entoloma caeruleomarginatum	CME3	Panama	MZ611627		This study
Entoloma caeruleomarginatum	KaiR535, holotype	Panama	MZ611658		This study
Entoloma caeruleomarginatum	CME11	Panama	MZ611622		This study
Entoloma cf. *catalaunicum*	E163	Estonia	Unite: UDB011680		Liiv, unpublished
Entoloma cf. *indutoides*	TU106924	Estonia	Unite: UDB015261		Liiv, unpublished
Entoloma cf. *largentii*	OSC144006	USA	KX574458		Gordon, unpublished
Entoloma cf. *pseudoturci*	Cro16	Croatia	MZ611633		This study
Entoloma cf. *unicolor*	PBM3995	USA	KY777373		Matheny et al., unpublished
Entoloma cf. *violaceobrunneum*	KaiR632	Panama	MZ678740		This study
Entoloma cf. *violaceobrunneum*	CME2	Panama			This study
Entoloma coracis	O-F-256850, holotype	Norway	MW934571	MW934251	Crous et al. 2021
Entoloma fuscosquamosum	KY744158	USA	KY744158		Matheny et al., unpublished
Entoloma glaucobasis	Roth 16–6-95/NL-2704	Germany/Sweden	MZ869021	MK277991	This study/Varga et al. 2019
Entoloma griseocaeruleum	CME8	Panama	MZ611631		This study
Entoloma griseocaeruleum	CME13	Panama	MZ611624		This study
Entoloma griseocaeruleum	KaiR536	Panama	MZ611659		This study
Entoloma griseocaeruleum	KaiR534, holotype	Panama	MZ611657		This study
Entoloma griseocyaneum	KaiR997	Germany	MZ611684		This study
Entoloma holmvassdalenense	O-F-304575	Norway	MZ869018	MZ678746	This study
Entoloma holmvassdalenense	O-F75311, holotype	Norway	KM610321		Weholt et al. 2014
Entoloma incanum	KaiR990	Germany	MZ611683		This study
Entoloma indutoides	WU19603	Austria	MZ869022		This study/Varga et al. 2019
Entoloma inocephalum	LE262922	Vietnam	KC898449	MH259311	Morozova et al. 2014a/Karstedt et al. 2019
Entoloma isborscianum	KaiR1004	Germany	MW934565		Crous et al. 2021/This study
Entoloma longistriatum	PBM4018	USA	KY744164		Matheny et al., unpublished
Entoloma mediterraneense	Cro26	Croatia	MZ611634		This study
Entoloma melleosquamulosum	KaiR638	Panama	MZ611669		This study
Entoloma melleosquamulosum	CME16, holotype	Panama	MZ611626		This study
Entoloma microserrulatum	KaiR413, holotype	Panama	MZ611642		This study
Entoloma microserrulatum	KaiR664	Panama	MZ611671		This study
Entoloma montanum	O-F-293389/N03-09–2010	Norway/Norway	MW340878	MZ678747	Noordeloos et al. 2021/This study
Entoloma montanum	GB191635, holotype	Sweden	MW340896		Noordeloos et al. 2021
Entoloma mougeotii	LE254352	Russia, Caucasus	KC898446		Morozova et al. 2014a
Entoloma nigrovelutinum	LE295077, holotype	Vietnam	MF898426	MF898427	Crous et al. 2017
Entoloma nipponicum	TNS-F70747	Japan	MK693223	MK696392	Crous et al. 2019
Entoloma norlandicum	O-F-76176, holotype	Norway	MW340899		Noordeloos et al. 2021
Entoloma ochromicaceum	TUF120040/DMS-9201008	Estonia/Denmark	Unite: UDB023715	MZ678743	Liiv, unpublished/ This study
Entoloma odoratum	DMS-166826	Denmark	MZ869017	MZ678745	This study
Entoloma querquedula	TUR	Finland	LN850627		Kokkonen 2015
Entoloma roseotinctum	JL-26–19	Norway	MZ869019		This study

Table 1 (continued)

Entoloma sarcitulum	K378, holotype	Great Britain	LN850561		Kokkonen 2015
Entoloma serrulatum	O-F-158208/DMS-730296	Norway/Denmark	MZ869016		This study
Entoloma sp.	PO2	Canada, Ontario	KY706185		Hay et al. 2018
Entoloma sp.	CM13_233	New Caledonia	KY774214		Carriconde et al., unpublished
Entoloma sp.	MES-534	Chile	KY462681		Truong et al. 2017
Entoloma sp.	KaiR511	Panama	MZ611655		This study
Entoloma sp.	OTA61944	New Zealand	KP191935		Lebel and Cooper, unpublished
Entoloma sp.	CY13_140_1	New Caledonia	KY774215		Carriconde et al., unpublished
Entoloma subcaesiocinctum	GDGM31059	China	KY972699		He et al. 2017
Entoloma subcoracis	LE312483, holotype	Russia	MW934593	MW934255	Crous et al. 2021
Entoloma subfarinaceum	SAT1518702	USA	KY777374		Matheny et al., unpublished
Entoloma subserrulatum	MGW1490	USA	KY744177		Matheny et al., unpublished
Entoloma subserrulatum	EL9	Canada	KY706167		Hay et al. 2018
Entoloma turci	WPR004	Germany	MZ611693		This study
Entoloma viiduense	G1602	Estonia	UDB015211	MK278008	Liiv, unpublished/ Varga et al. 2019
Entoloma violaceoserrulatum	TUR JV 8329F, isotype	Finland	MF476913	MF487803	Morozova et al. 2017
Entoloma yanacolor	QCAM6312, holotype	Ecuador	MG947210		Crous et al. 2018
Subgenus *Entoloma*					
Entoloma aff. *alpicola*	O:F7195	Norway	MZ868961		This study
Entoloma aff. *rhodopolium*	68–88	Finland	LN850500		Kokkonen 2015
Entoloma aff. *sinuatum*	TRTC156546	Canada	JN021019		Dentinger et al. 2011
Entoloma aff. *sordidulum*	PGL110817	Norway	MZ869007		This study
Entoloma alnobetulae	K53-59, G262083, holotype	France	LN850537		Kokkonen 2015
Entoloma alpicola	O:F-61507	Norway	MZ868967		This study
Entoloma atrosericeum	GG160811	Sweden	MZ868968		This study
Entoloma atrosericeum	K69-310, G262084, holotype	France	LN850607		Kokkonen 2015
Entoloma aurorae-borealis	O-F-254651, holotype	Norway	MH234486		Noordeloos et al. 2021
Entoloma baeosporum	holotype	France	MZ868973		This study
Entoloma bisporigerum	2047, K108895, holotype	United Kingdom	LN850536		Kokkonen 2015
Entoloma bisporigerum	OW-E20-14	Norway	MZ868976		This study
Entoloma boreale	106/09, TUR, holotype	Finland	LN850624		Kokkonen 2015
Entoloma borgenii	TB79.120, C5933	Greenland	LN850524		Kokkonen 2015
Entoloma brunneipes	TENN9029, holotype	USA	LN850621		Kokkonen 2015
Entoloma brunneocinereum	TENN12881, holotype	USA	LN850615		Kokkonen 2015
Entoloma brunneorugulosum	KaiR583	Panama	MZ611660		This study
Entoloma brunneorugulosum	KaiR691, holotype	Panama	MZ611676		This study
Entoloma brunneorugulosum	KaiR692	Panama	MZ611677		This study
Entoloma brunneorugulosum	KaiR695	Panama	MZ611679		This study
Entoloma brunneorugulosum	PAN532	Panama	MZ611692		This study
Entoloma bryorum	117/07	Finland	LN850539		Kokkonen 2015
Entoloma bryorum	O:F-303879	Norway	MZ868978		This study
Entoloma caccabus	"Podoba", G262081	France	LN850540		Kokkonen 2015
Entoloma caccabus	C157, 4226	The Netherlands	MZ868979		This study
Entoloma caccabus	C158, 4001	The Netherlands	MZ868981		This study

Table 1 (continued)

Entoloma carolinianum	TENN21855, holotype	USA	LN850617	Kokkonen 2015
Entoloma cf. *alpicola*	23, N1F31, 2	NA	HQ445607	Bjorbækmo et al. 2010
Entoloma cf. *alpicola*	O:F-260165	Norway	MZ869001	This study
Entoloma cf. *bryorum*	O:TEB 395–18	Norway	MZ868985	This study
Entoloma cf. *carolinianum*	IBUG:Montanez222	Mexico	MZ869010	This study
Entoloma cf. *rhodopolium*	DB03-06–2018-3	Hungary	MZ868960	This study
Entoloma cf. *spadiceum*	TENN070791	USA, Tennessee	MF686497	Matheny and Sanchez-Garcia, unpublished
Entoloma cf. *venosum*	WU19672		MZ868991	This study
Entoloma cistophilum	Trim2006, isotype	France	MZ868999	This study
Entoloma dulciodorans	IBUG:LGD7580	Mexico	MZ869011	This study
Entoloma dulciodorans	IBUG:Rodriguez322, paratype	Mexico	MZ869012	This study
Entoloma eminens	417/12, TUR, holotype	Finland	LN850584	Kokkonen 2015
Entoloma eminens	O:F-248409	Norway	MZ868982	This study
Entoloma eminens	TEB699-17	Norway	MZ868983	This study
Entoloma fasciculatum	TENN29376, holotype	USA	LN850614	Kokkonen 2015
Entoloma festivum	holotype	The Netherlands	MZ869009	This study
Entoloma gerriae	holotype	The Netherlands	MZ868980	This study
Entoloma gerriae	WU28035	Austria	MZ868990	This study
Entoloma griseopruinatum	JLC_030924-8, holotype	France	MZ868984	This study
Entoloma griseopruinatum	JLC030924-8, isotype	France	LN850556	Kokkonen 2015
Entoloma griseorugulosum	RFS-020921–01, isotype	Spain	LN850591	Kokkonen 2015
Entoloma indutoides	1617, K108968, holotype	United Kingdom	LN850608	Kokkonen 2015
Entoloma inusitatum	holotype	Germany	MZ868969	This study
Entoloma jubatum	PAM13-26	Sweden	MZ868975	This study
Entoloma lactarioides	Liiv217, holotype	Russia, Karelia	MZ869000	This study
Entoloma lacus	KUB110, holotype	Japan	LC088049	Kondo et al. 2017
Entoloma leucocarpum	MEN701, holotype	The Netherlands	MZ868970	This study
Entoloma *lividoalbum*	GE12-025	France	MZ868957	This study
Entoloma lividomurinum	TENN28208, holotype	USA	LN850616	Kokkonen 2015
Entoloma lupinum	13/14, TUR, holotype	Finland	LN850570	Kokkonen 2015
Entoloma majaloides	1168, K69959, holotype	United Kingdom	LN850489	Kokkonen 2015
Entoloma majaloides	GG160812	Sweden	MZ868966	This study
Entoloma mediorobustum	JR064, holotype	Panama	MZ611635	This study
Entoloma mediorobustum	PA728	Panama	MZ611688	This study
Entoloma melenosmum	JHP-338, C6229, holotype	Greenland	LN850508	Kokkonen 2015
Entoloma myriadophyllum	366VN10		MZ869004	This study
Entoloma myrmecophilum	IBUG:Quezada 1	Mexico	MZ869014	This study
Entoloma myrmecophilum	IBUG:SantosBarba 5	Mexico	MZ869013	This study
Entoloma myrmecophilum var. *coalescens*	holotype	Germany	MZ868958	This study
Entoloma nidorosum	GG160815	Sweden	MZ868997	This study
Entoloma nidorosum s. MEN	FR2016708	France	MZ868995	This study
Entoloma nidorosum s. MEN	MEN2012111	The Netherlands	MZ868996	This study
Entoloma nigrobrunneum	TENN9100, holotype	USA	LN850618	Kokkonen 2015
Entoloma noordeloosii	WU18780, holotype	Austria	MZ868962	This study
Entoloma noordeloosii	WU39739		MZ868963	This study
Entoloma nubooccultatatum	KaiR588	Panama	MZ611661	This study

Table 1 (continued)

Entoloma nubooccultatatum	KaiR687, holotype	Panama	MZ611675	This study
Entoloma nubooccultatum	PA165	Panama	MZ611685	This study
Entoloma nubooccultatum	PA696	Panama	MZ611686	This study
Entoloma nubooccultatum	PA727	Panama	MZ611687	This study
Entoloma nubooccultatum	PA864	Panama	MZ611689	This study
Entoloma olorinum	G:00,126,192, holotype	France	MZ868998	This study
Entoloma paludicola	K178125, holotype	United Kingdom	LN850517	Kokkonen 2015
Entoloma palustre	101/14, TUR, holotype	Finland	LN850592	Kokkonen 2015
Entoloma paragaudatum	383/08, TUR, holotype	Finland	LN850530	Kokkonen 2015
Entoloma philocistus	WU18871, paratype	Portugal	LN850600	Kokkonen 2015
Entoloma platophylloides	MD2017-10	Italy	MZ868959	This study
Entoloma politum	289/09	Finland	LN850511	Kokkonen 2015
Entoloma politum	O:F61875	Norway	MZ869002	This study
Entoloma politum s. Gulden	O:F-73841	Norway	MZ869006	This study
Entoloma pruinosum	CME12	Panama	MZ611623	This study
Entoloma pruinosum	CME14	Panama	MZ611625	This study
Entoloma pruinosum	KaiR533, holotype	Panama	MZ611656	This study
Entoloma pseudorhodopolium	KUB102, holotype	Japan	LC088042	Kondo et al. 2017
Entoloma pusillulum	C-F-5917	Greenland	MZ611694	This study
Entoloma radicipes	42/14, TUR, holotype	Finland	LN850585	Kokkonen 2015
Entoloma rhodopolium	213/14, TUR, neotype	Sweden	LN850494	Kokkonen 2015
Entoloma rhodopolium	Montanez149-150	Mexico	MZ869015	This study
Entoloma rhodopolium	O:F-254019	Norway	MZ868993	This study
Entoloma rhodopolium	OF254444	Norway	MZ868992	This study
Entoloma rigidulum	PRM153709, holotype	Czech Republic	LN850629	Kokkonen 2015
Entoloma rivulare	703/12, TUR, holotype	Finland	LN850544	Kokkonen 2015
Entoloma roseoalbum	ARN6209, holotype	The Netherlands	MZ868972	This study
Entoloma rubrobasis	24,101, TURA	Finland	LN850580	Kokkonen 2015
Entoloma rubrobasis	O:F-304601	Norway	MZ868987	This study
Entoloma sarcopum	KUB205	Japan	LC088067	Kondo et al. 2017
Entoloma saussetiense	PC0085778, holotype	France	LN850594	Kokkonen 2015
Entoloma sericatum	237/11	Finland	LN850445	Kokkonen 2015
Entoloma sericatum	358/08	Finland	LN850444	Kokkonen 2015
Entoloma serpens	410/09, TUR, holotype	Finland	LN850526	Kokkonen 2015
Entoloma silvae-frondosae	L-DB6568	Hungary: Vas, Apatistvanfalva	MH790432	Crous et al. 2018
Entoloma sinuatum	J.Vauras 8181F	Finland	KC710116	Morgado et al. 2013
Entoloma sinuatum	J.Wisman, 2003–09-19	NA	KC710109	Morgado et al. 2013
Entoloma sordidulum	Co-David 2003	NA	KC710062	Morgado et al. 2013
Entoloma sordidulum s. MEN	ALV8406	Norway	MZ869008	This study
Entoloma sp.	46-18A		MZ868994	This study
Entoloma sp.	EL145-18	Sweden	MZ869005	This study
Entoloma sp.	JO160811	Sweden	MZ868971	This study
Entoloma sp.	KBEB83, 17	Norway	MZ868988	This study
Entoloma sp.	MEN2012125	The Netherlands	MZ868977	This study
Entoloma sp.	N128 Irmgard6540	USA	MZ868964	This study
Entoloma sp.	O:F304982	Norway	MZ869003	This study
Entoloma sp.	UBC, F-32218	Canada, BC	MF955123	Berbee et al., unpublished
Entoloma subarcticum	JHP-392, isotype	Greenland	MZ868974	This study

Table 1 (continued)

Entoloma subradiatum	"rhosse", G262076, lectotype	France	LN850596	Kokkonen 2015
Entoloma subrhodopolium	KUB1, holotype	Japan	LC088033	Kondo et al. 2017
Entoloma svalbardense	GG310/86, O74756, holotype	Svalbard	LN850610	Kokkonen 2015
Entoloma svalbardense	MENJG228	Norway, Svalbard	JF304386	Geml et al. 2012
Entoloma tiliae	LE254179	Russia, Saint Petersburg	MH790420	Crous et al. 2018
Entoloma tiliae	O:F-251963	Norway	MZ868986	This study
Entoloma transvenosum	MEN1215, holotype	Denmark	MZ868965	This study
Entoloma venosum	MD2012-15	Germany	MZ868989	This study
Rhodophyllus myrmecophilus	holotype	France	LN850462	Kokkonen 2015
uncultured *Entoloma*	NA	Mexico	KY574307	Garibay-Orijel and Garcia-Guzman, unpublished
uncultured fungus	NA	USA	EU807287	Hanson et al., unpublished
subgenus *Nolanea*				
Entoloma belouvense var. *belouvense*	WU27132, holotype	France, Reunion	MZ611698	This study
Entoloma belouvense var. *albertinae*	CME5	Panama	MZ611628	This study
Entoloma belouvense var. *albertinae*	KaiR630	Panama	MZ611668	This study
Entoloma cetratum	LE235480	Russia	KC898450	Morozova et al. 2014a
Entoloma clandestinum	KaiR1282	Sweden	MZ611639	This study
Entoloma conferendum	KaiR1342	Austria	MZ611640	This study
Entoloma conferendum	KaiR1358	Germany	MZ611641	This study
Entoloma conferendum	KaiR978	Germany	MZ611680	This study
Entoloma cremeostriatum	CME10	Panama	MZ611621	This study
Entoloma cremeostriatum	KaiR508	Panama	MZ611654	This study
Entoloma cremeostriatum	KaiR613, holotype	Panama	MZ611664	This study
Entoloma euchroum	KR-M-0032474	Germany	KC898421	Morozova et al. 2014a
Entoloma flavoconicum	KaiR609	Panama	MZ611662	This study
Entoloma flavoconicum	KaiR628, holotype	Panama	MZ611667	This study
Entoloma infula	KaiR988	Germany	MZ611681	This study
Entoloma infula	KaiR989	Germany	MZ611682	This study
Entoloma luteofuscum	K-M-188309, holotype	India	KF698730	Raj et al. 2014
Entoloma olivaceohebes	WU17841, holotype	Italy	JX454804	Vila et al. 2013
Entoloma olivaceohebes	WU20798	Italy	JX454803	Vila et al. 2013
Entoloma paraconferendum	CME6, holotype	Panama	MZ611629	This study
Entoloma paraconferendum	CME7	Panama	MZ611630	This study
Entoloma piceinum	LE254131, holotype	Russia	KM262035	Morozova et al. 2014b
Entoloma pulchellum	HMLD1300	China	KC257436	Wang and Bau, unpublished
Entoloma pulchellum	KA12-1242	South Korea	KR673495	Kim et al. 2015
Entoloma readiae	PDD71294	New Zealand	MZ611696	This study
Entoloma readiae	PDD87270	New Zealand	MZ611697	This study
Entoloma sericeum	KaiR1267	Sweden	MZ611638	This study
Entoloma sp.	KaiR626	Panama	MZ611666	This study
Entoloma sp.	KaiR693	Panama	MZ611678	This study
Entoloma subelegans	WU32902, holotype	Mauritius	MZ611699	This study
Entoloma transitionisporum	CME9	Panama	MZ611632	This study

Table 1 (continued)

Entoloma transitionisporum	KaiR503, holotype	Panama	MZ611653	This study
Entoloma vernum	LE312418	Russia	MF476911	Morozova et al. 2017
Nolanea albertinae	FK0912	Brazil	KF679349	Karstedt et al. 2020
Nolanea albertinae	FK0935, holotype	Brazil	KF679348	Karstedt et al. 2020
Nolanea albertinae	FK1731	Brazil	KF679350	Karstedt et al. 2020
Nolanea albertinae	FK1732	Brazil	KF679351	Karstedt et al. 2020
Nolanea atropapillata	FK0898, holotype	Brazil	KF679354	Karstedt et al. 2020
Nolanea pallidosalmonea	FK0891	Brazil	KF738923	Karstedt et al. 2020
Nolanea parvispora	FK1140	Brazil	KF679353	Karstedt et al. 2020
Nolanea sp.	FLAS-F-61537	USA	MH211959	Kaminsky et al., unpublished
Nolanea tricholomatoidea	FK1049, holotype	Brazil	KF679352	Karstedt et al. 2020

Table 2 Infrageneric positions of the specimens collected between 2014 and 2018

Subclade	Specimens	Number of species
Subg. *Cyanula*	35	18
Subg. *Entoloma*	23	5
Subg. *Alboleptonia*	17	3
Subg. *Nolanea*	15	7
Subg. *Cubospora*	11	6
Subg. *Pouzarella*	5	5
Subg. *Inocephalus*	3	3
Sect. *Calliderma*	3	1
Subg. *Claudopus*	1	1
Not determined	11	> 5

with species distinguished by a combination of macro- and microscopical characters. Since an ectomycorrhizal lifestyle was discovered for species of subg. *Entoloma* (Antibus et al. 1981; Loree et al. 1989; Agerer 1997), ecological characters are also considered to delimit species. Kokkonen (2015) used ITS sequence data as a new tool to tackle concepts of species in subg. *Entoloma* in Northern Europe. New species were defined based on a combination of morphological and ecological characteristics combined with an ITS phylogeny. As a result, nine species were described as new to science and many species were synonymised. Ongoing studies in Europe (Brandrud et al. 2018; Noordeloos et al. 2018) show that there are still many questions as how to interpret classical species, as well as how to deal with apparently cryptic speciation in this clade. Montañez et al. (2016) presented six species of subg. *Entoloma* collected in *Quercus-Pinus* forests in central Mexico. Also, Largent (1994) described species of subg. *Entoloma* from *Quercus*-dominated habitats. As *Quercus* spp. migrated from North America southwards and reached Central America approximately 10 million years ago (Kappelle et al. 1992; Hooghiemstra 2006), there should be links to species described from Mexico or southern USA. Unfortunately, hardly any molecular data of the species described from these regions are available for comparison and we must rely on morphological comparisons for several species.

Entoloma brunneorugulosum Reschke, Noordel. & Lotz-Winter, sp. nov., Figs. 4 and 5

Mycobank number: MB840935.

Typification: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, forest trail towards summit of volcano,

Table 3 Specimens per habitat in the years 2017 and 2018

Habitat	Specimens
Montane forest with abundant to dominant *Quercus* spp.	47
Montane forest dominated by *Alnus acuminata*	22
Montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*	9
Transition of submontane tropical forest dominated by *Oreomunnea mexicana* to montane *Quercus*-dominated forest	2
Montane tropical forest	1
Disturbed lower montane forest with *Quercus* spp. and *Alnus acuminata*	1
Lowland forest close to mangrove	1
Lowland, path in disturbed secondary vegetation	1
Total	84

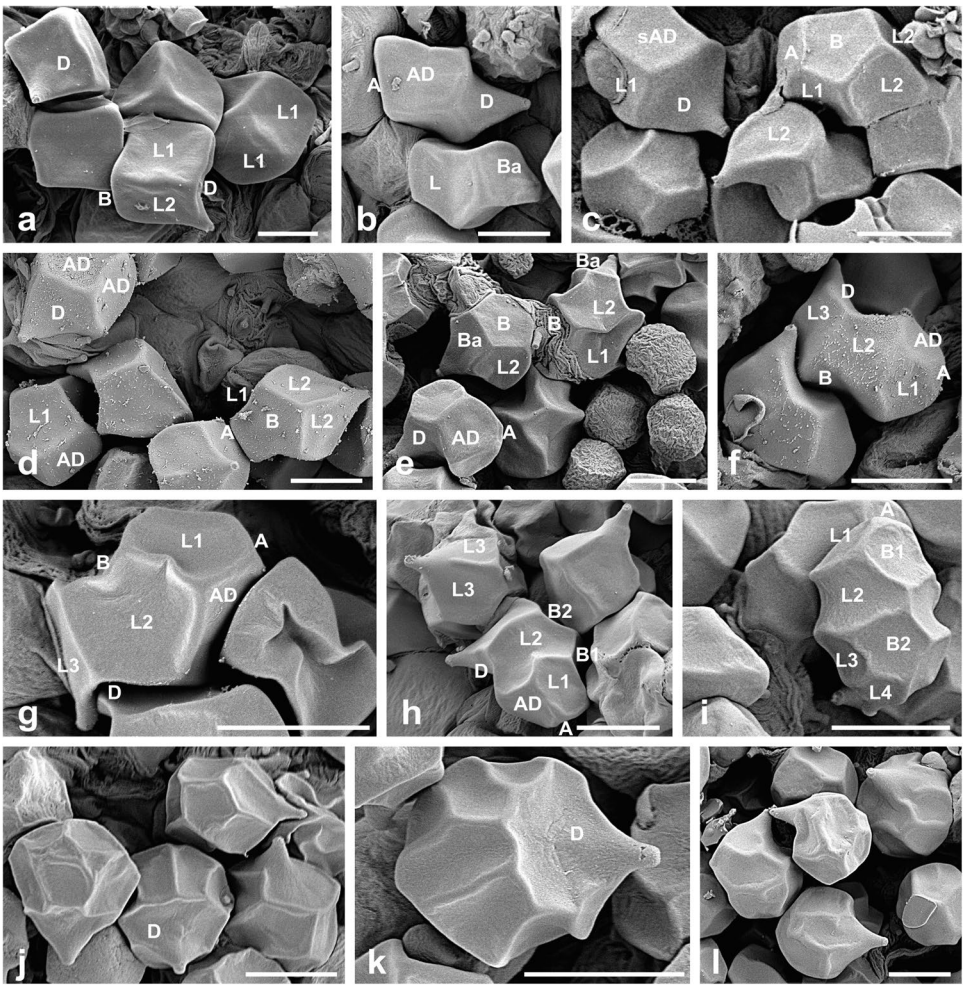

Fig. 2 Basidiospore shapes of *Entoloma* spp. as seen by SEM **a** cuboid with dièdre basal (KaiR623), **b** heptahedroid with simple base (CME6), **c** octahedroid with dièdre basal (KaiR465), **d** enneahedroid with dièdre basal (KaiR612), **e** decahedroid with simple base (KaiR691), **f** hendecahedroid with dièdre basal (KaiR628), **g** hendecahedroid with dièdre basal (KaiR534), **h** dodecahedroid with dièdre basal (CME16), **i** tetradecahedroid with dièdre basal (KaiR670), **j, k** indetermined shape with frequent small intercalary facets and more than two apico-adaxial facets (KaiR687), **l** indetermined shape with different base types, including a base formed by three facets, upper right (JR64); D: adaxial facet, AD: apico-adaxial facets, sAD: single apico-adaxial facet, A: apical facet, Ba: basal facet, B: abaxial facet, L: lateral facets; bars = 5 µm

approximately 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 28 June 2017, B. Wergen, KaiR691, holotype (M).

Etymology: brunneus (Latin) = brown, rugosus (Latin) = rugose; refers to colour and structure of the pileal surface.

Description: Basidiocarps tricholomatoid. Pileus 3.0–5.0 cm diameter, convex when young, becoming plane to depressed in old basidiocarps, usually with an obtuse umbo, margin initially deflexed, then straight, blackish brown to dark yellowish brown (5F8) in the centre, dark brown to light brown (6D7, 6E7, 6F7, 6F8), olive brown (4F8), yellowish brown (5E7, 5E8) to greyish yellow (4C6, 4C7) towards the margin, pileal surface glabrous, with a waxy appearance, rugulose, slightly translucently striate at the margin up to a quarter of the radius in fresh basidiocarps. Lamellae adnate to sinuate, segmentiform to ventricose, rather distant, relatively thick and broad, initially whitish with greyish to cream tinge, later greyish pink, with smooth, concolorous edges. Stipe 3.5–4.0 × 0.6–0.9 cm, cylindrical, solid in young basidiocarps, becoming hollow, basically yellowish brown (5E5, 5E6, 5E7) to olive brown (4E6, 4E7, 4E8, 4F6, 4F7), overlaid by whitish fibrils, paler, almost white, towards base, whitish fibrillose-flocculose at the apex when young. Basal mycelium white. Odour and taste farinaceous to farinaceous rancid.

Basidiospores 8.5–9.5–11.0 × 7.0–7.9–9.0 µm, $Q = 1.05–1.20–1.35$ ($n = 85$ spores of 4 specimens), decahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), two pairs of lateral facets (L1–L2), and a basal facet (Ba) forming a simple base, mainly subisodiametrical to broadly heterodiametrical, with 5–7, predominantly 6, pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 43–61 × 12–15 µm, clavate, hyaline, predominantly 4-spored, with up to 6 µm long sterigmata, rarely 2-spored. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by cylindrical to fusiform cells, 55–135 × 6–25 µm. Pileipellis a cutis formed by rather long, narrow, and cylindrical cells, 55–190 × 6.0–12.0 µm, with some cylindrical to clavate terminal cells, cells shorter and wider downwards, gradually passing into the pileitrama, composed of

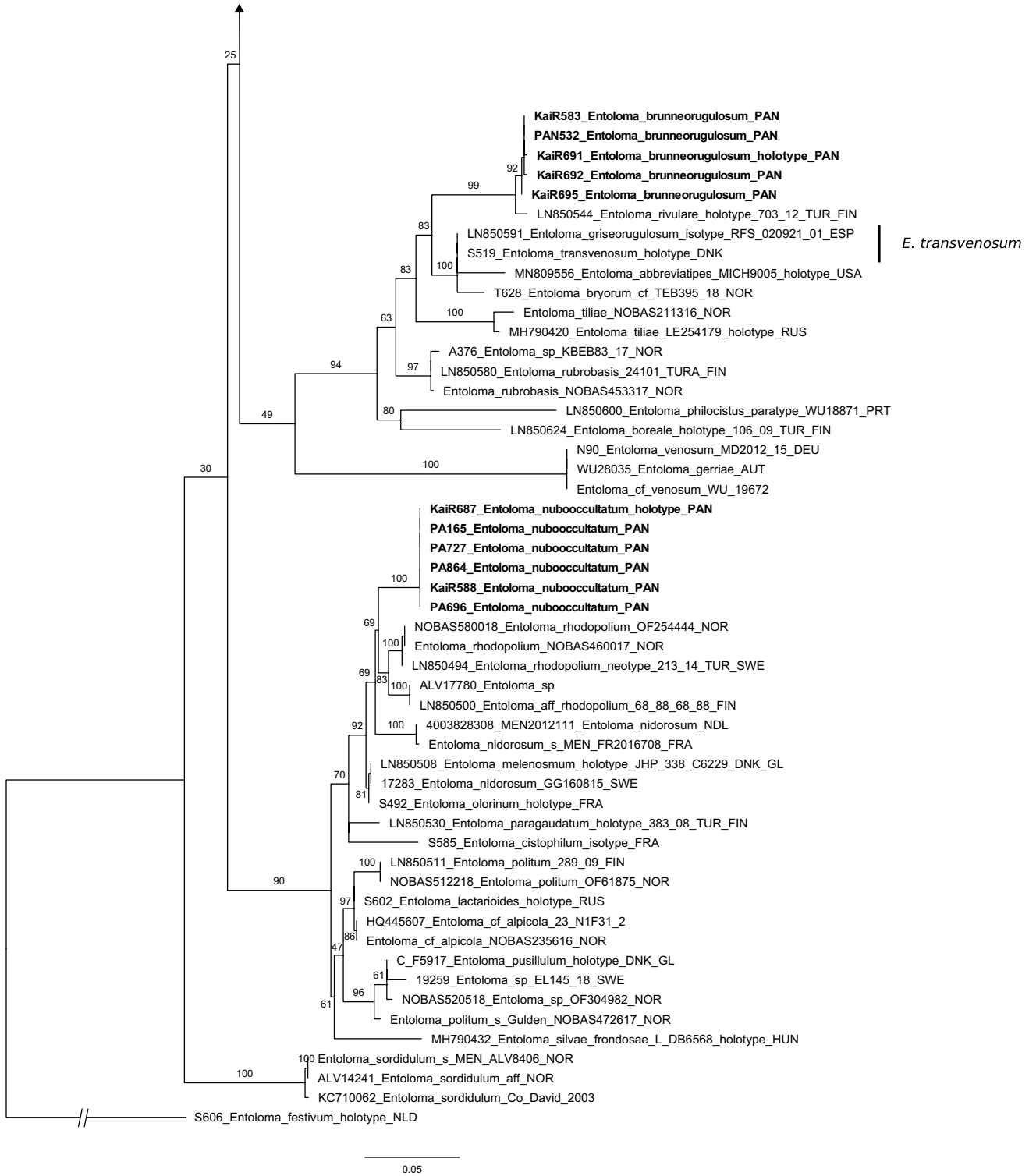

Fig. 3 Maximum Likelihood phylogram of species of subg. *Entoloma* based on ITS, rooted to *E. festivum*, bootstrap values above or below branches, bar = estimated changes/nucleotide

inflated to fusiform cells, up to 22 µm wide. Pigment intracellular, brown, mainly in dense clusters of brown granules in the upper pileipellis. Stipitipellis a cutis composed of cylindrical cells, 75–300 × 3.0–9.5 µm, with intracellular, brown, mainly granular pigment, like the pigment of the pileipellis. Caulocystidia absent. Oleiferous hyphae present in the trama. Clamp connections abundant in all parts of the basidiocarp.

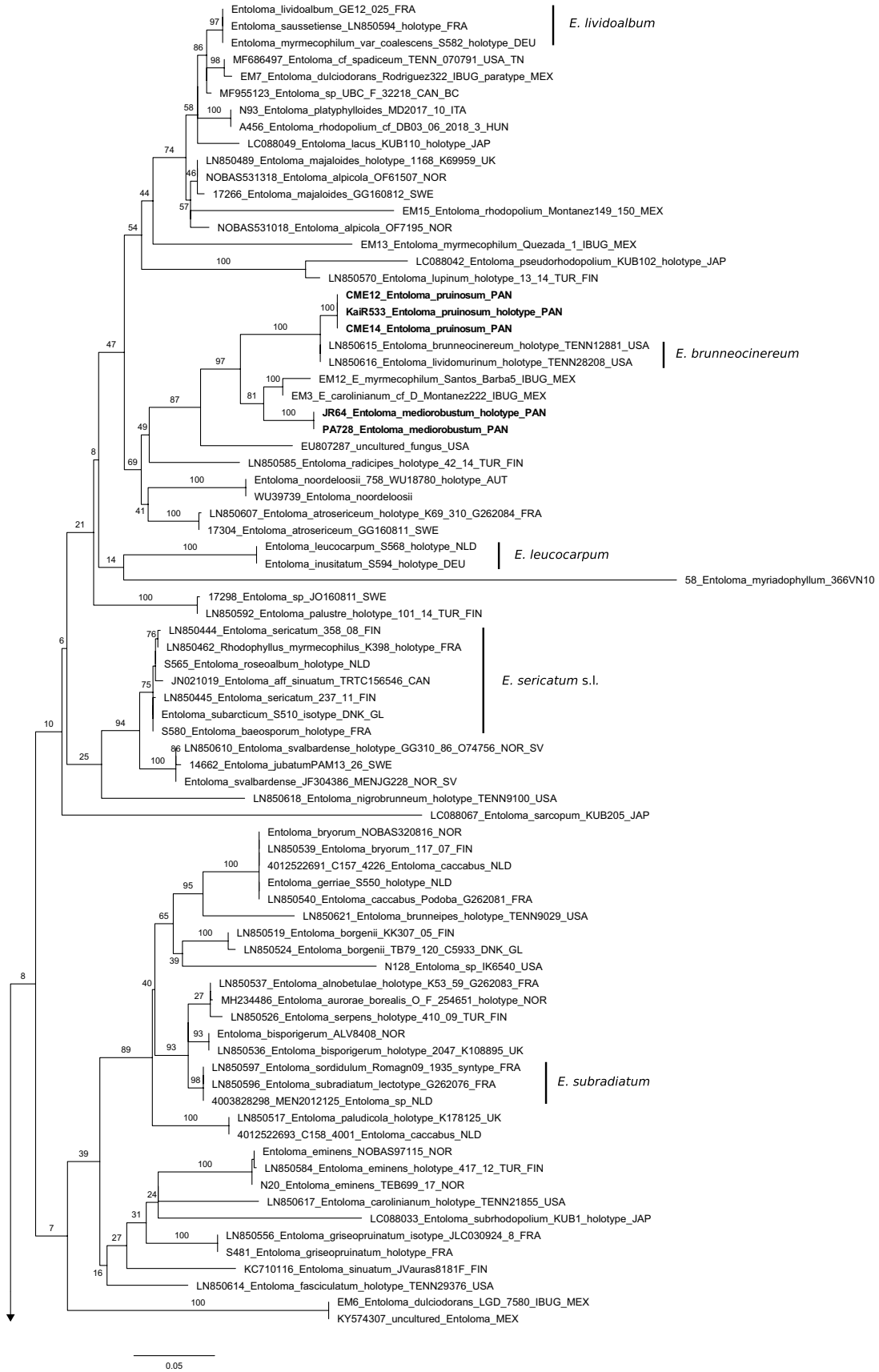

Fig. 3 (continued)

Fig. 4 Basidiocarps, and basidiospores as seen by SEM of *Entoloma brunneorugulosum* **a** (KaiR583) **b**, **c**, **d** (KaiR691, holotype) bars = 10 µm

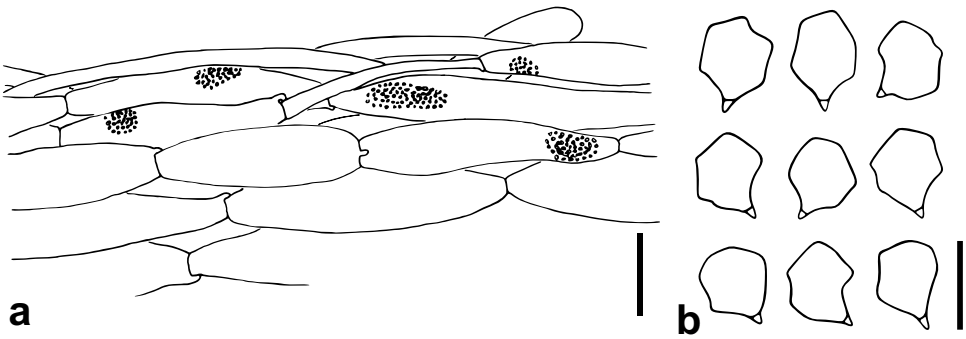

Fig. 5 Microscopic structures of *Entoloma brunneorugulosum* **a** pileipellis with intracellular pigment (KaiR691, holotype), bar = 20 µm **b** basidiospores (KaiR583), bar = 10 µm

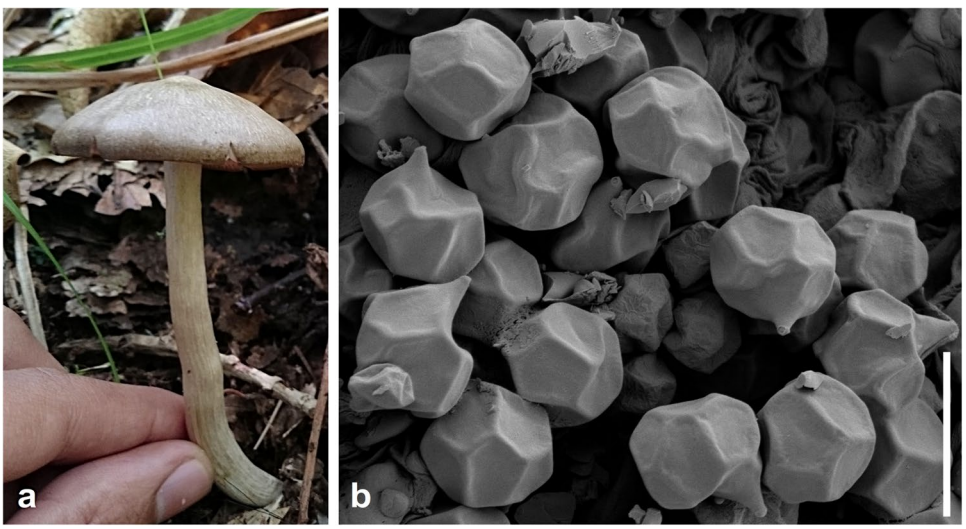

Fig. 6 Basidiocarp, and basidiospores as seen by SEM of *Entoloma mediorobustum* (JR64, holotype)

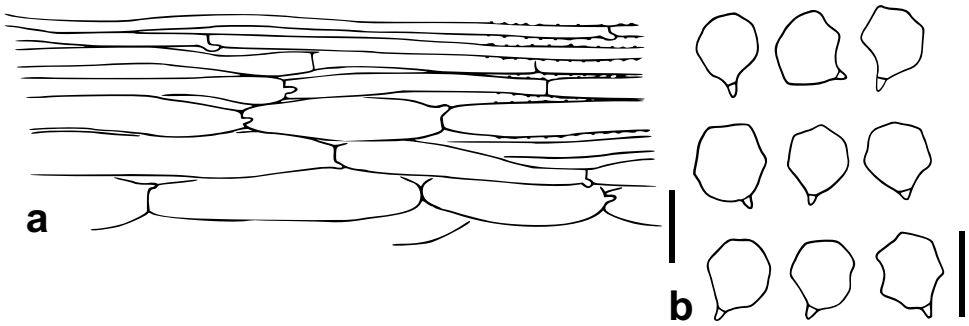

Fig. 7 Microscopic structures of *Entoloma mediorobustum* (JR64, holotype): **a** pileipellis with incrusting pigment indicated on the right hand side, bar = 20 µm; **b** basidiospores, bar = 10 µm

Habitat: Basidiocarps solitary to scattered in a group, in *Quercus*-dominated montane forest at around 2000 m asl. in Chiriquí, Panama. Probably ectomycorrhizal with *Quercus* spp. or *Comarostaphylis arbutoides*.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, approx. 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 10 July 2016, H. Lotz-Winter, PAN532 (M); ibid., 17 June 2017, E. Heinemann, KaiR583 (M); ibid., 28 June 2017, K. Reschke and T.A. Hofmann, KaiR692 (M); ibid., 28 June 2017, K. Reschke and T.A. Hofmann, KaiR695 (UCH9247, M).

Notes: *Entoloma brunneorugulosum* is characterised by small to medium basidiocarps with a rugulose, brown, umbonate pileus and a somewhat paler brown stipe, as well as intracellular, granular pigment, and possibly by an association to *Quercus* spp. Phylogenetically, it is a sister species to *Entoloma rivulare* Kokkonen with a *p*-distance of 1.7% in the ITS. *Entoloma rivulare* was described from a single collection in a moist *Alnus incana*/*Populus tremula* forest in Finland. Its basidiocarps are like those of *E. brunneorugulosum* in having a rather small, brown pileus, with a translucently striate margin and a farinaceous smell and taste. It differs, however, by the non-umbonate, darker pileus and smaller basidiospores with lower *Q*-values. Furthermore, these two species have different mycorrhizal hosts. *Entoloma griseorugulosum* Noordel. & Fernández Sas. is similar by its rugulose, dark grey-brown pilei, which are not translucently striate, and the size and shape of the basidiospores (Noordeloos 2004). Our molecular phylogenetic analysis (Fig. 5) suggests that *E. griseorugulosum* is a later synonym of *E. transvenosum* Noordel. *Entoloma transvenosum* was described with a translucently striate pileus and larger basidiospores (9.0–13.0 × 7.0–10 µm). Both descriptions note greyish, often transvenose lamellae, a stipe paler than pileus, intracellular pigment, and occurrence in rather open forest, often together with *Quercus* spp. in western Europe (Noordeloos 1982, 2004). Considering both concepts, *E. brunneorugulosum* differs by the warmer, lighter brown colour of the pileus, the often concolorous stipe, and the different habitat. Basidiocarps of *E. rugosostriatum* Largent & T.W. Henkel are like those of *E. brunneorugulosum* by rugulose, brown pilei with a striate margin; however, the basidiospores of *E. rugosostriatum* are isodiametrical, weakly angled and smaller (6.1–7.4 × 6.1–7.3 µm) (Largent et al. 2008b). None of the species described by Hesler (1967), Horak (1978, 1982), Largent (1994), and Montañez et al. (2016) combine a dark rugulose, non-hygrophanous pileus, and relatively paler stipe, and an association with *Quercus* spp.

Entoloma mediorobustum Reschke, J. Rodríguez-Cedeño & Noordel., sp. nov. Figs. 6 and 7

Mycobank number MB840629.

Typification: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, trail towards summit of volcano, N 8°48′57.1′″ W 82°24′35.2′″, 2,040 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 1 August 2015, J. Rodríguez, S. Cáceres, K. Barrera, R. Valdéz, JR64, holotype (UCH11749), isotype (M).

Etymology: medius (Latin) = medium, robustus (Latin) = robust; refers to the shape of the basidiocarps.

Description: Basidiocarps tricholomatoid. Pileus 4.2–4.8 cm diameter, convex, with initially incurved, later straight and undulating margin, yellowish brown (5E4, 5E5, 5D5, 5D6), pileal surface smooth, sometimes partly covered by a whitish pruina, not translucently striate, hygrophanous. Lamellae emarginate, medium-spaced to rather distant, greyish white when young, becoming dirty pink, with somewhat uneven to eroded, concolorous edges. Stipe 10.0 × 0.8–1.0 cm, cylindrical with radicating base, stuffed, whitish, fibrillose. Basal mycelium white, somewhat cottony. Odour and taste not tested.

Basidiospores 7.5–8.7–10.0 × 7.0–7.9–8.5 µm, $Q = 1.00–1.11–1.20$ ($n = 50$ spores of 2 specimens), spatial shape not determined, at least with 12 facets, base often built by 3 facets, isodiametrical to subisodiametriacal, with 5–7 rather blunt angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 30–43 × 9.0–11.0 µm, clavate to subclavate, hyaline, 4-spored, sterigmata up to 4.0 µm long. Lamellar edge fertile, hymenial cystidia

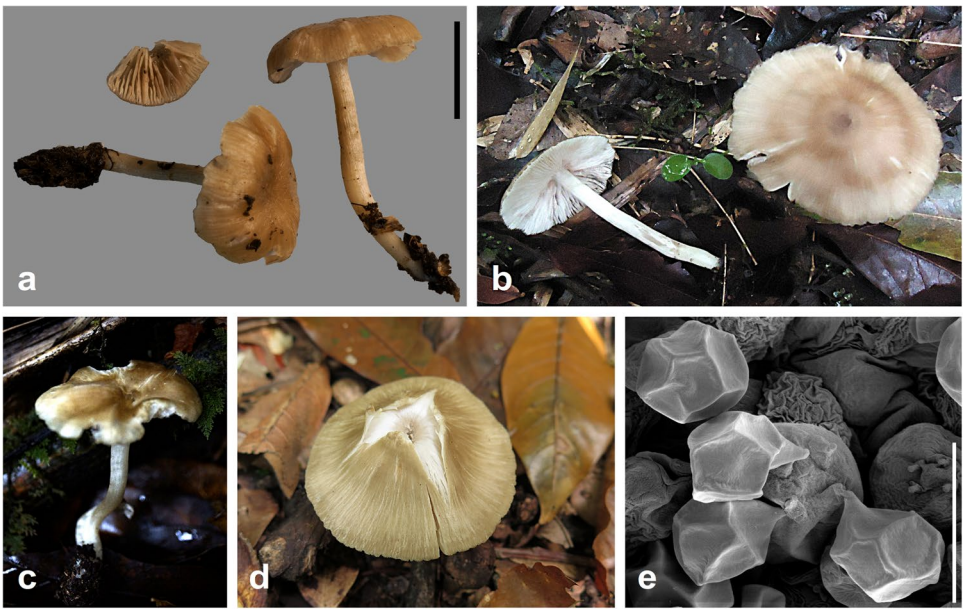

Fig. 8 Basidiocarps and basidiospores as seen by SEM of *Entoloma nubooccultatum*: **a, e** (KaiR687, holotype) bar = 10 µm; **b** (PA165) picture by S. Cáceres **c** (KaiR588); **d** (PA727)

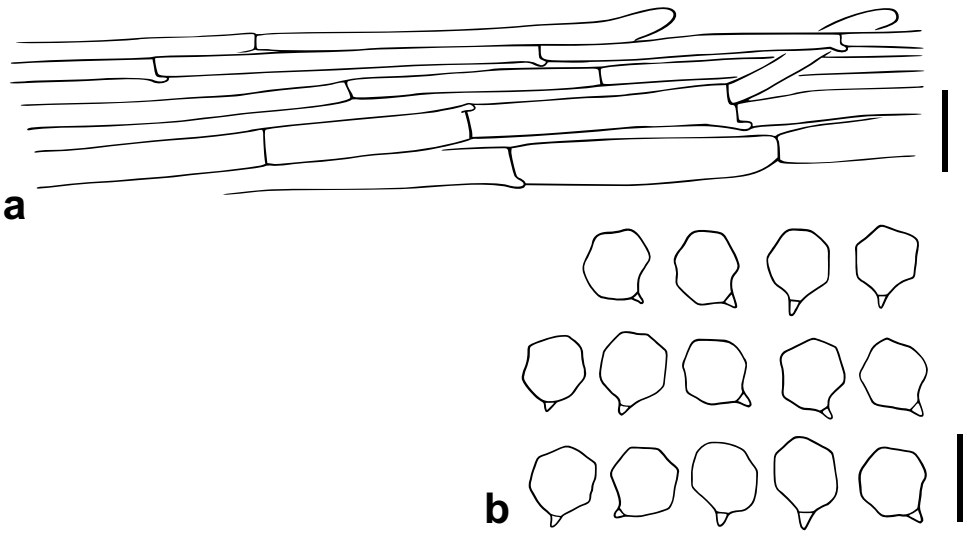

Fig. 9 Microscopic structures of *Entoloma nubooccultatum* (KaiR687, holotype): **a** pileipellis, intracellular pigment not indicated, bar = 20 µm; **b** basidiospores, bar = 10 µm

absent. Hymenophoral trama regular, formed by subcylindrical to fusiform cells, (40) 50–200 × 6.0–30 µm. Pileipellis a cutis composed of narrow, cylindrical cells, 70–250 × 3.5–9.0 µm, pigment incrusting, brownish in KOH. Stipitipellis a cutis composed of rather hyaline, cylindrical cells, 55–150 × 3.5–8.0 (9.5) µm. Caulocystidia absent. Clamp connections present in all parts of the basidiocarps.

Habitat: Basidiocarps solitary on soil in a montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, between 1950 and 2050 m asl. in Chiriquí, Panama. Probably ectomycorrhizal with *Quercus* spp. or *Comarostaphylis arbutoides*.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, N 8°48′55.4″ W 82°34′47.1″, 1,970 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 9 November 2015, T.A. Hofmann, J. Rodríguez, S. Cáceres, R. Villarreal, PA728 (M).

Notes: *Entoloma mediorobustum* is distinctive by the non-hygrophanous pileus with a distinct pruina, which is rather unusual in this subgenus. It clusters with two collections from Mexico, labelled as *E. myrmecophilum* and *E.* cf. *carolinianum*, respectively (Fig. 5), that differ by glabrous, relatively dark brown pilei (Montañez et al. 2016). These species have in common their possible association with *Quercus* spp. and the presence

of incrusting pigments in the pileipellis. *Entoloma pruinosum* is somewhat similar, but its basidiocarps are slightly darker, more robust, and have a more differentiated stipe surface. The two species share the relatively small, isodiametrical to subisodiametrical spores. Phylogenetically, however, they are quite distant (Fig. 5).

Entoloma nubooccultatum Reschke & Noordel., sp. nov., Figs. 8 and 9

Mycobank number: MB840632.

Typification: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, approximately 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 28 June 2017, K. Reschke and T.A. Hofmann KaiR687, holotype (UCH9243), isotype (M).

Etymology: nubes (Latin) = cloud, occultatum (Latin) = hidden; refers to the hidden life of this species in cloud forests.

Description: Basidiocarps collybioid. Pileus 1.5–6.5 cm diameter, convex umbilicate to depressed, with deflexed and uneven margin which is slightly incurved in young basidiocarps and straight in older basidiocarps, greyish yellow (4B4, 4B5, 4C5, 4C6), brownish orange (5C4, 5C5, 5C6), yellowish brown (5D5, 5D6, 5D7, 5E4, 5E5) to olive brown (4D5, 4D6), pileal surface glabrous, with a waxy appearance when wet, translucently striate at the margin about 1/3 to 2/3 the centre, hygrophanous, fading to yellowish grey (3B2). Lamellae broadly adnate to somewhat decurrent, segmentiform, close, whitish in young specimens, pinkish at maturity, with somewhat undulating and concolorous edges. Stipe 4.5–10×0.3–0.8 cm, cylindrical, often bent, stuffed to hollow, white, somewhat grooved, finely innately fibrillose, base often covered by adhering soil and litter. Basal mycelium white, with many small rhizomorphs. Odour indistinct or slightly sweetish, fruity, taste not tested.

Basidiospores 7.0–7.8–8.5 × 6.0–6.9–7.5 µm, Q = 1.05–1.13–1.25 (n = 146 spores of 6 specimens), spatial shape not determined, at least with 11–13 facets, mainly with a dièdre basal, sometimes incomplete, sometimes with a simple base, isodiametrical to broadly heterodiametrical, predominantly subisodiametrical, with 6–7 weak to pronounced, somewhat rounded angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia (30) 35–43 (48)×8.5–12.5 µm, subclavate, often almost urniform (formed like an urn), hyaline, 4-spored, with up to 6.0 µm long sterigmata, few 2-spored. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by cylindrical, somewhat fusiform to inflated cells, 45–150×6–20 (28) µm. Pileipellis a cutis of cylindrical cells, 35–185×(4.0) 6.0–12.5 µm, with intracellular pigment. Stipitipellis a cutis composed of short, cylindrical cells, 30–70×3.0–6.0 µm, not pigmented. Caulocystidia absent. Oleiferous hyphae present in the trama. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps solitary or in small groups in a montane *Quercus*-dominated forest with abundant *Comarostaphylis arbutoides* between 1900 and 2200 m asl. in Chiriquí, Panama. Probably ectomycorrhizal with *Quercus* spp. or *Comarostaphylis arbutoides*.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, approximately 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 17 June 2017, K. Reschke, KaiR588 (M); ibid., N 8°48′55.3′″ W82°34′43.5″, 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 28 September 2014, S. Cáceres, K. Barrera, T.A. Hofmann, R. Valdés, PA165 (M); ibid., N 8°48′53.4″ W82°34′48.0″, 1,960 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 9 November 2015, S. Cáceres, R. Valdés, J. Rodríguez, T.A. Hofmann, PA696 (M); ibid., N 8°48′55.4′″ W 82°34′47.1″, 1970 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 9 November 2015, T.A. Hofmann, J. Rodríguez, S. Cáceres, R. Valdés, PA727 (M); ibid., N 8°48′52.9″ W 82°34′47.7″, 1920 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 11 September 2016, T.A. Hofmann and M. Cuevas, PA864 (M).

Notes: *Entoloma nubooccultatum* is characterised by basidiocarps with collybioid habit, a brown, translucently striate, hygrophanous pileus, a white stipe, intracellular pigment in the pileipellis and rather small basidiospores. Phylogenetically, it forms part of a clade including *E. rhodopolium* (Fr.) P. Kumm. and several similar, closely related species, which have not yet been completely resolved (Kokkonen 2015; Brandrud et al. 2018). Its *p*-distance to these species ranges from 2.8 to 3.2% in the ITS. Habitually, it is not unlike *E. melenosmum* Noordel. However, *E. nubooccultatum* has basidiospores that are on average smaller than those of most species in the *E. rhodopolium* clade, and its distribution is probably restricted to tropical montane *Quercus* forests, while *E. rhodopolium* and related species are mainly distributed in northern temperate and boreal deciduous forests, predominantly associated with species of Betulaceae, sometimes *Fagus sylvatica* L., but rarely with *Quercus* spp. (Noordeloos 2004).

Entoloma pruinosum Reschke, Manz & Noordel., sp. nov., Figs. 10 and 11

Mycobank number: MB840622.

Typification: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, forest trail towards rock lookout, N 08°47′32.3″ W 82°24′50.3″, 1650 m asl., montane forest dominated by *Quercus* spp., 14 June 2017, K. Reschke, KaiR533, holotype (UCH009184), isotype (M).

Etymology: pruinosus (Latin) = pruinose; refers to the pruinose pileal surface.

Description: Basidiocarps tricholomatoid. Pileus 3.0–7.0 cm diameter, convex when young, becoming broadly convex to almost plane in old basidiocarps, with or without

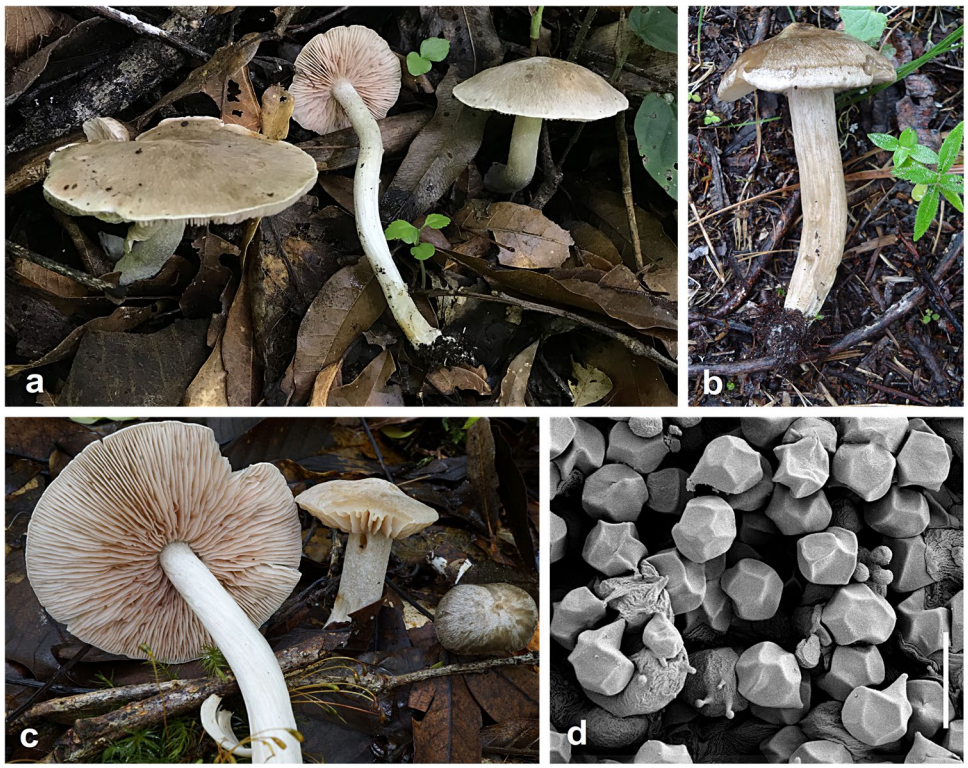

Fig. 10 Basidiocarps and basidiospores as seen by SEM of *Entoloma pruinosum*: **a** (CME14); **b** (PA167); **c, d** (KaiR533, holotype) bar = 10 µm

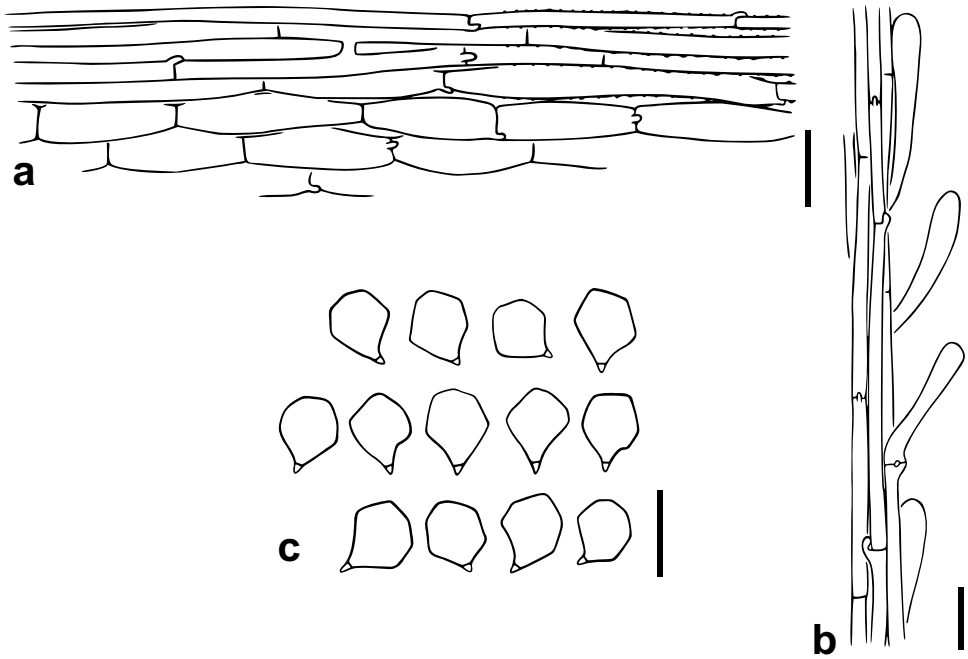

Fig. 11 Microscopic structures of *Entoloma pruinosum* (KaiR533, holotype): **a** pileipellis with incrusting pigment indicated at the right hand side, bar = 20 µm; **b** stipitipellis with caulocystidia, bar = 20 µm; **c** basidiospores, bar = 10 µm

an obtuse umbo, margin initially deflexed and still slightly deflexed in old basidiocarps, greyish yellow, pale olive brown, greyish brown, brownish grey to grey (4B4, 4D5, 4D6, 5B1, 5C2, 5D2, 5D3), uniformly coloured, pileal surface glabrous, with a waxy appearance, covered by a whitish, slightly fibrillose pruina, not translucently striate, not hygrophanous. Lamellae sinuate, segmentiform to ventricose, crowded, initially almost white to pale greyish, later pink, with slightly blunt serrate, concolorous edges and moderately to strongly transvenose sides. Stipe 8.0–12.0 × 0.8–1.0 cm, cylindrical to somewhat tapering towards base, solid, greyish yellow (4B4, 4B5, 4C3, 4C4, 4C5, 4C6, 4C7) under a whitish fibrillose to

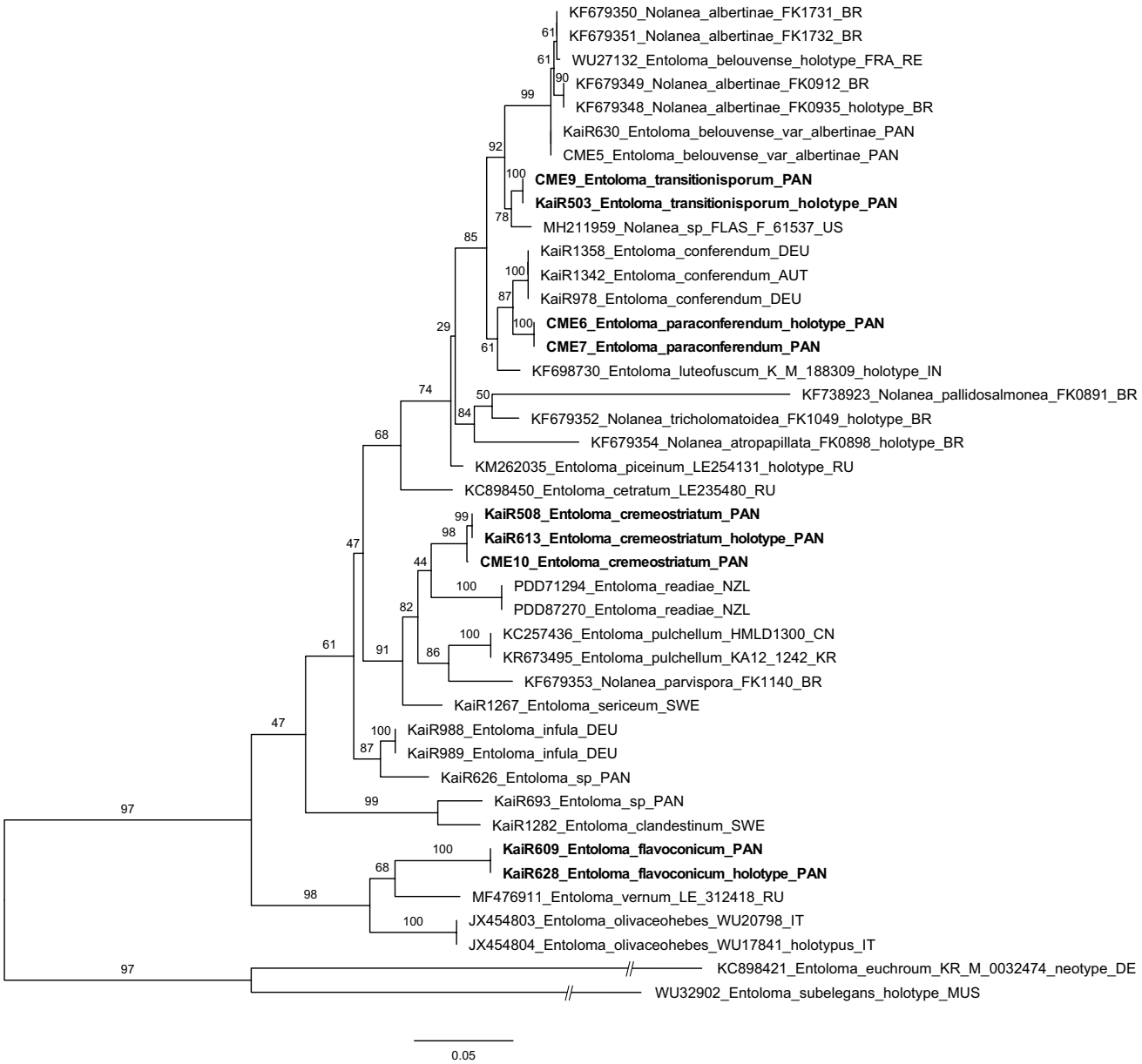

Fig. 12 Maximum Likelihood phylogram of species of subg. *Nolanea* based on ITS, rooted to *E. subelegans* and *E. euchroum*, bootstrap values above or below branches, bar = estimated changes/nucleotide

fibrillose-flocculose layer, staining brownish yellow (5C7, 5C8) after damage. Basal mycelium cottony, white. Odour not distinctive to weakly farinaceous when undamaged, farinaceous when cut, taste farinaceous.

Basidiospores 7.0–7.9–9.0 × 6.0–7.0–8.0 µm, $Q = 1.05–1.13–1.25$ ($n = 94$ spores of 4 specimens), decahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), two pairs of lateral facets (L1–L2), and a basal facet (Ba) forming a simple base, isodiametrical to subisodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 44–60 × 7.5–11.0 µm, clavate, hyaline, 4-spored, sterigmata up to 4.0 µm long. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, composed of somewhat fusiform to inflated cells in the centre, 50–120 × 6.0–14.0 µm, longer, up to 240 µm and narrower, narrowest 4.0 µm, towards the subhymenium. Pileipellis a cutis formed by cylindrical cells, 65–130 × 3.0–6.0 µm, with finely incrusting pigment, without distinct subpellis. Pileitrama composed of rather short and wide, subcylindrical to inflated cells, 40–65 × 9.0–11.5 µm. Stipitipellis a cutis composed of cylindrical cells, 40–200 × 3.5–7.0 µm, with incrusting pigment

Fig. 13 Basidiocarp of *Entoloma belouvense* var. *albertinae* (KaiR630)

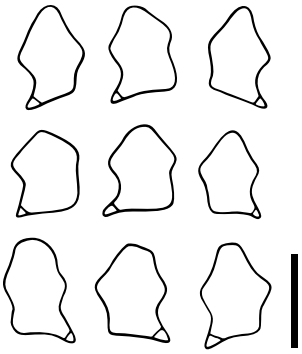

Fig. 14 Basidiospores of *Entoloma belouvense* var. *albertinae* (KaiR630), bar = 10 µm

at some hyphae. Caulocystidia clavate to subcylindrical, 35–65 × 6.5–10.0 µm. Oleiferous hyphae present in the trama. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps solitary or gregarious, in *Quercus*-dominated montane forests between 1650 and 1900 m asl. in Chiriquí, Panama. Probably ectomycorrhizal with *Quercus* spp.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Volcán, Paso Ancho, PNVB, N 08°48′55″ W82°34′46.8″, 1,900 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 28 September 2014, S. Cáceres, K. Barrera, T.A. Hofmann, R. Villarreal, PA167 (M); near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′26.9″ W 82°24′34.4″, 1,670 m asl., montane forest dominated by *Quercus* spp., 24 June 2018, T.A. Hofmann, CME12 (M); Bajo Boquete, Finca Lérida, forest trail, N 08°49′10.3″ W 82°29′09.2″, 1820 m asl., montane forest with *Quercus seemannii* and other *Quercus* spp., 28 June 2018, C. Manz and F. Hampe, CME14 (M).

Notes: Basidiocarps of *E. pruinosum* are characterised by a tricholomatoid habit, a brown surface of the pileus with a distinct pruina and relatively small basidiospores. This combination of characters is rather unique. No other known species in subg. *Entoloma* has such a strongly developed pruina on the pileus. The small, isodiametrical spores are more or less like those found in the /prunuloides clade, and the European *E. prunuloides* may have a slight, but not so strong pruina on the pileus. *Entoloma prunuloides*, however, like some other similar species, is phylogenetically very distant from subg. *Entoloma* (Morgado et al. 2013). *Entoloma pruinosum* belongs to a clade of species known from Central and North America. In the ITS phylogeny (Fig. 5), it is close to *E. brunneocinereum* Hesler, with a *p*-distance of 2.7% in the ITS1. This species has, however, somewhat smaller basidiospores (7.0–8.0 × 6.0–7.0 µm) and intracellular pigment (Noordeloos 1988). Based on type studies, Kokkonen (2015) demonstrated that *E. lividomurinum* Hesler is conspecific with *E. brunneocinereum*. *Entoloma griseopruinatum* Cheype & Noordel., a European species with a pruinose pileus, has larger basidiospores (9.0–11.0 × 7.0–8.0 µm), more greyish colours in stipe and pileus, intracellular pigment in the pileipellis, and is phylogenetically distant (Fig. 5).

Subgenus Nolanea *(Fr.)* Noordel (Fig. 12)

Traditionally, species of the subg. *Nolanea* are characterised by basidiocarps with a mycenoid habit, a rather smooth pileus surface, and relatively long cells in the hymenophoral trama (Noordeloos 1980). A preliminary study on this subgenus in Europe was published by Vila et al. (2013). Karstedt et al. (2020) described five new species from Brazil, using *Nolanea* at generic rank. Their molecular phylogeny based on three loci supports *Nolanea* as a monophyletic clade. The results of a large, worldwide study on this subgenus are currently being prepared for publication (Reschke et al., in prep.).

Entoloma belouvense Noordel. & Hauskn., Fungal Divers. 27: 112 (2007) **var.** *belouvense.*

Holotype WU27132: Several basidiocarps in good condition. Basidiospores heterodiametrical, 10.5–11.3–12.0 × 6.5–7.1–7.5 µm, $Q = 1.45–1.60–1.85$ ($n = 26$). Basidia 4-spored, rather broadly clavate. Hymenophoral trama with abundant oily content. Stipe surface composed of long and narrow cells. Clamp connections absent.

Specimen examined: LA RÉUNION, Saint-Benoît, Forêt de Belouve, on decaying, mossy wood of broadleaf tree in tropical highland rainforest, 28 March 2005, A. Hausknecht, holotype (WU 27,132).

Notes: *Entoloma belouvense* is a member of the clade around *E. conferendum* (Britzelm.) Noordel. In contrast to the original description (Noordeloos and Hausknecht 2007), no clamp connections were observed at the base of basidia.

Fig. 15 Basidiocarps and basidiospores as seen by SEM of *Entoloma cremeostriatum*: **a** (KaiR508); **b** (CME10) bar = 2 cm; **c, d** (KaiR613, holotype) bar = 10 µm

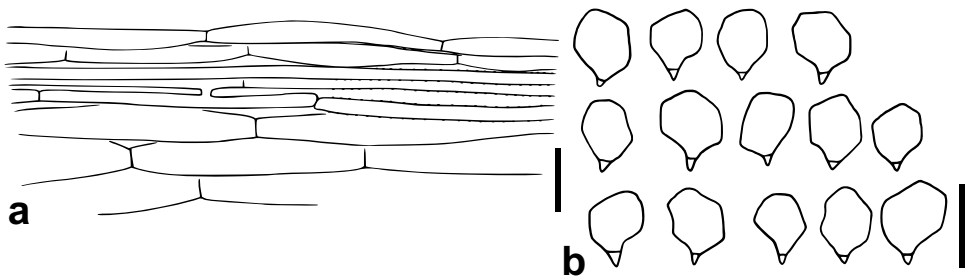

Fig. 16 Microscopic structures of *Entoloma cremeostriatum* (KaiR613, holotype): **a** pileipellis with incrusting pigment indicated on the right hand side, bar = 20 µm; **b** basidiospores, bar = 10 µm

Entoloma belouvense Noordel. & Hauskn. **var.** *albertinae* (Karstedt & Capelari) Reschke & Noordel. comb. & stat. nov., Figs.13 and 14

Basionym: *Nolanea albertinae* Karstedt & Capelari in Karstedt et al., Mycotaxon 135: 596 (2020).

Mycobank: MB840620.

Basidiocarps mycenoid. Pileus 1.5–2.0 cm diameter, broadly conical to expanded with pronounced papilla and straight to deflexed, somewhat uneven margin, greyish yellow–golden, brown to dark brown (4C6, 6E5, 6E6, 6F5, 6F6) with dark brown (6F6, 7F5) centre, pileal surface glabrous, somewhat innately fibrillose, translucently striate almost to the centre, hygrophanous and then with sericeous appearance. Lamellae adnexed to free, ventricose, medium-spaced to rather distant, greyish white when young, becoming brownish pink, with smooth and concolorous edges. Stipe 2.0–3.5 × 0.20–0.25 cm, cylindrical, getting slightly broader towards base, hollow, greyish yellow, greyish yellow–golden to yellowish brown (4C5, 4C6, 5D5), polished to somewhat innately fibrillose towards base, with silvery white fibrils when contorted. Basal mycelium white, with many short and fine rhizomorphs. Odour indistinct, taste not tested.

Basidiospores 9.0–9.9–11.0 × 6.0–7.1–7.5 µm, $Q = 1.25–1.40–1.60$ ($n = 53$ spores of 2 specimens), heterodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 26–34 × 9.5–11.0 µm, subclavate, hyaline, 4-spored, sterigmata up to 5.0 µm long. Lamellar edge heterogeneous, cheilocystidia scattered, solitary or in small groups between basidia, rather infrequent, approximately 25–50 × 5.0–8.5 µm, septate tibiiform to cylindrical capitate. Pileipellis a cutis of relatively long and narrow, 4.0 to 8.0

µm wide elements, pigment intracellular, brownish in KOH. Clamp connections absent from all parts of the basidiocarp.

Habitat: Basidiocarps found solitary or scattered in a small group in montane forests between 1600 and 2100 m asl. in Chiriquí, Panama.

Specimens examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, PNVB, Sendero Culebra, N 08°50′42.6″ W 82°28′52.5″, 1,670 m asl., montane forest dominated by *Quercus* spp., 22 June 2017, K. Reschke, J. Rodríguez, B. Wergen, KaiR630 (UCH11745, M); near Cerro Punta, Los Quetzales Lodge, N 08°52′30.4″ W 82°33′14.0″, 2030 m asl., montane tropical forest, 18 June 2018, C. Manz and F. Hampe, CME5 (M).

Notes: *Nolanea albertinae* was described from Brazil by Karstedt et al. (2020). Before, it had been treated as *E. belouvense* by Karstedt et al. (2019). In the phylogeny (Fig. 14), the ITS sequence of the holotype of *E. belouvense* var. *belouvense* is nested among the sequences of specimens of *E. belouvense* var. *albertinae*. However, the differences in spore size, resulting in higher *Q*-values in *E. belouvense* var. *belouvense*, are confirmed here. Apart from this, no differing characters were observed. *Nolanea albertinae* is treated here as a variety of *E. belouvense* because only one specimen of the type variety is available and ITS sequences may not be suitable to resolve such close relationships. More specimens from the type region, La Réunion, are needed to evaluate if this treatment is justified. Similar to the type variety, no clamp connections were observed in the specimens from Panama.

Entoloma cremeostriatum Reschke, Manz & Noordel., sp. nov., Figs. 15 and 16

Mycobank number: MB840936.

Typification: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, approx. 2300 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, J. Rodríguez, KaiR613, holotype (M).

Etymology: crème (French) = cream (here: colour), striatus (Latin) = striate; refers to the morphology of the pileus.

Description: Basidiocarps collybioid to omphalinoid. Pileus 2.5–3.9 cm diameter, convex umbilicate, margin deflexed to straight, slightly exceeding the lamellae, uniformly yellowish brown (5E7) in immature basidiocarps, soon paler, light yellow (4A4), greyish yellow (4B4), greyish orange (5B3, 5B4) to brownish orange (5C6), often darker, greyish yellow (4B6) to yellowish brown (5F7) in the centre, whitish at the very margin, pileal surface glabrous, with a waxy appearance when wet, innately fibrillose at the centre, with some fine, protruding fibrils all over, translucently striate almost to the centre, hygrophanous reaction not observed. Lamellae emarginate, segmentiform, medium-spaced to rather distant, greyish to cream when young, becoming pinkish, with slightly undulating and concolorous edges. Stipe 3.0–3.5 × 0.30–0.35 cm, cylindrical, hollow, similarly coloured as the pileus, greyish yellow (3B4, 4B5, 4C5), brownish orange (5C5, 5C6) to yellowish brown (5D6), innately fibrillose, partly overlaid by whitish fibrils, but not silvery fibrillose, slightly whitish fibrillose-flocculose at the tip. Basal mycelium white, with some short and fine rhizomorphs. Odour slightly nitrous or somewhat sweetish, taste not tested.

Basidiospores 6.5–7.6–8.5 × 5.5–6.2–6.5 µm, *Q* = 1.10–1.23–1.40 (*n* = 83 spores of 3 specimens), hendecahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, subisodiametrical to broadly heterodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, thick-walled. Basidia 21–29 × 8.5–10.0 µm, clavate, hyaline, 4-spored, sterigmata up to 4.0 µm long, with clamp connections. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by wide, somewhat fusiform cells in the mediostratum, and narrower, cylindrical cells towards the subhymenium, 100–360 × 3.5–25 µm, with slightly incrusting pigment at some hyphae. Pileipellis a cutis of narrow, cylindrical cells, 60–200 × 3.0–6.5 (10.0) µm, pigment finely incrusting, without a subpellis, gradually passing into pileitrama, composed of wider cells. Stipitipellis a cutis formed by long, cylindrical cells, 55–220 × 3.0–8.0 µm, with finely incrusting pigment. Caulocystidia absent. Oleiferous hyphae present in the trama. Clamp connections abundant in the hymenium, rarely present elsewhere.

Habitat: Basidiocarps solitarily to gregarious on soil, between mosses and litter, in *Alnus acuminata*-dominated montane forest and *Quercus*-dominated montane forest between 2300 and 2400 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA Sendero Cascada, N 08°53′51.6″ W 82°37′10.4″, 2380 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR508 (M); ibid., N 08°53′37.5″ W 82°36′54.4″, 2,030 m asl., montane forest dominated by *Alnus acuminata*, 22 June 2018, C. Manz and T.A. Hofmann, CME10 (M).

Notes: *Entoloma cremeostriatum* is characterised by a convex-umbilicate, pale, striate pileus, small, heterodiametrical basidiospores, and clamp connections at the base of basidia. With a *p*-distance of 5.5% between the ITS sequences, it is relatively close to *E. readiae* G. Stev., described from New Zealand (Stevenson 1962). This species has basidiocarps which are like those of *E. cremeostriatum* in shape. Moreover, the two species share finely incrusting pigments in the hyphae of the pileipellis and clamp connections at the base of the basidia. The basidiospores of *E.*

Fig. 17 Basidiocarps and basidiospores as seen by SEM of *Entoloma flavoconicum*: **a** (KaiR609); **b** (PA891); **c, d** (KaiR628, holotype), bar = 10 µm

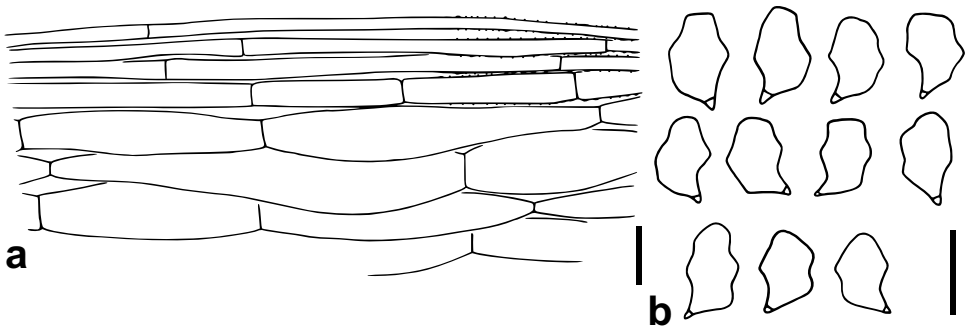

Fig. 18 Microscopic structures of *Entoloma flavoconicum* (KaiR628, holotype): **a** pileipellis with incrusting pigment indicated on the right hand side, bar = 20 µm; **b** basidiospores, bar = 10 µm

readiae are larger than those of *E. cremeostriatum* according to the original description (9–10 × 7–8 µm). Our measurements of two authentic specimens (Table 1) of *E. readiae*, however, resulted in somewhat smaller basidiospore sizes, 7.5–8.4–9.0 × 6.5–7.4–8.0 µm, $Q = 1.00–1.14–1.25$ ($n = 46$ of 2 specimens). However, these are still somewhat larger and have smaller Q-values than those of *E. cremeostriatum*. In addition, basidiocarps of *E. readiae* are brown and have a strongly farinaceous odour, while those of *E. cremeostriatum* are generally paler and have a slightly nitrous odour. Two sequences annotated as *E. pulchellum* (Hongo) Hongo are relatively close to those of *E. cremeostriatum* with *p*-distances of 5.2% between the ITS sequences. *Entoloma pulchellum* is described as having a convex-umbilicate, yellow to flesh-coloured pileus with brown tones, often a minutely squamulose pileus surface, especially in the centre, a striate pileus margin, heterodiametrical basidiospores of 10.0–12.5 × 7.0–9.0 µm, clavate to capitate cheilocystidia of 25–37 × 13.0–14.5 µm, and no clamp connections at the base of basidia (Hongo 1957). These characters, especially the squamulose pileus surface together with the absence of clamp connections and presence of distinct cheilocystidia, indicate a species of subg. *Cyanula*, probably close to *E. formosum* (Fr.) Noordel. Thus, the specimens corresponding to the ITS sequences (KR673495, KC257436) annotated as *E. pulchellum* in GenBank apparently are misidentified.

Entoloma flavoconicum Reschke & Noordel., sp. nov., Figs. 17 and 18

Mycobank number: MB840631.

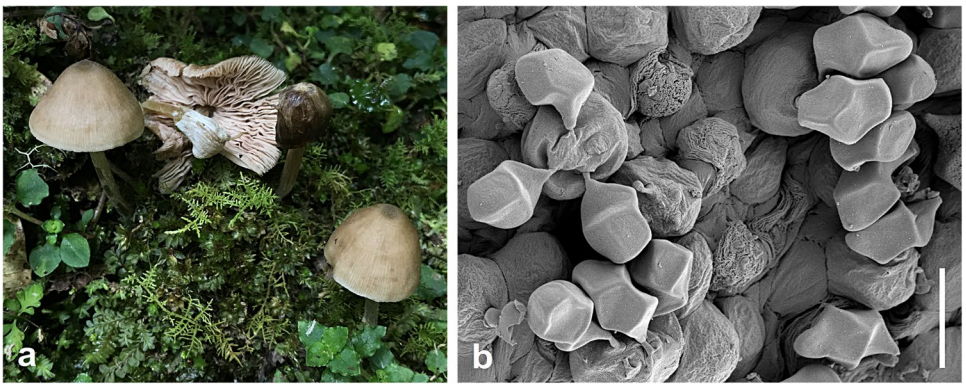

Fig. 19 Basidiocarps and basidiospores as seen by SEM of *Entoloma paraconferendum* (CME6, holotpye), bar = 10 µm

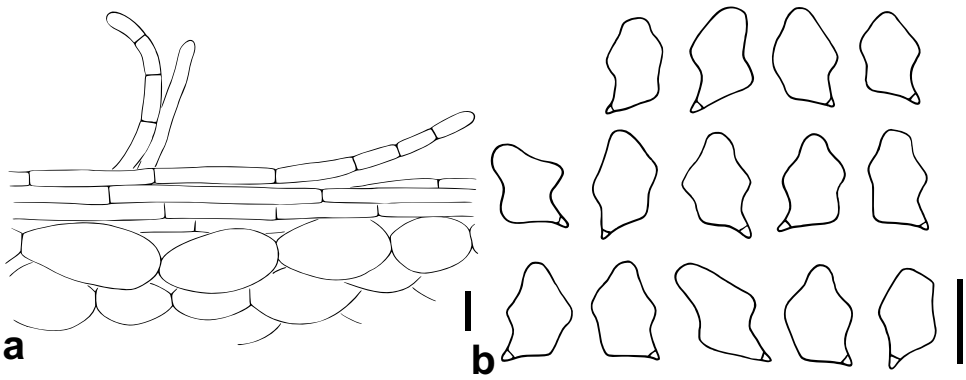

Fig. 20 Microscopic structures of *Entoloma paraconferendum* (CME6, holotype): **a** pileipellis with subpellis composed of inflated cells, intracellular pigment not indicated, bar = 20 µm; **b** basidiospores, bar = 10 µm

Typification: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′41″ W 82°35′01.5″, 2,340 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, K. Reschke, KaiR628, holotype (UCH9226), isotype (M).

Etymology: flavus (Latin) = yellow, konikos (Greek) = conical; refers to the colour and shape of the pileus.

Description: Basidiocarps mycenoid. Pileus 0.7–2.2 cm diameter, conical when young, remaining conical or becoming convex with a pronounced, acute umbo, either dark brown (6F7) to yellowish brown (5F6) or light yellow (4A5) to orange yellow (4A6) in the centre, towards the margin at first light brown (6D6, 6D7) to yellowish brown (5D7, 5D8, 5E8), then greyish yellow (4B6, 4C6, 4C7) to orange yellow (4B7) and eventually yellow (3A7) at the very margin, pileal surface glabrous, but overlaid by an ephemeral, fine, white pruina in young basidiocarps, translucently striate from the margin almost to the centre, hygrophanous reaction not observed. Pileal margin initially slightly incurved, later straight, slightly overlapping the lamellae. Lamellae emarginate to adnexed, ventricose, distant, relatively thick and broad, initially greyish, sometimes with yellow tinges, later greyish pink, with somewhat transvenose sides and smooth, concolorous edges. Stipe 1.0–3.5 × 0.14–0.25 cm, cylindrical to slightly clavate, hollow, brownish yellow (5C7, 5C8) sometimes darker, yellowish brown (5D7, 5D8) towards base, glabrous to innately fibrillose, finely whitish pruinose all over, especially towards the apex of the stipe. Basal mycelium white, often cottony. Odour indistinct, taste not tested.

Basidiospores 8.5–9.4–10.5 × 6.0–6.4–7.0 µm, Q = 1.30–1.46–1.65 (n = 70 spores of 3 specimens), hendecahedroid, composed of an adaxial facet (D), a pair of apicoadaxial facets (AD), an apical facet (A), an abaxial facet (B), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, heterodiametrical, with 5–6, predominantly 6, pronounced to nodulose angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 27–34 × 11.0–13.0 µm, clavate, hyaline, predominantly 4-spored, sterigmata up to 6.0 µm long. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by narrow, cylindrical and centrically broad fusiform cells, 125–520 × 3.5–27 µm, some hyphae with incrusting pigment, yellowish in KOH. Pileipellis a cutis formed by narrow, cylindrical cells, 40–260 × 3.5–9.5 µm, with incrusting and in addition scattered intracellular pigment, cells wider, somewhat inflated, towards pileitrama. Stipitipellis a cutis composed of cylindrical cells, 85–400 × 3.0–7.5 µm, with some incrusting pigment. Caulocystidia absent. Oleiferous hyphae present in the trama. Clamp connections absent from all parts of the basidiocarp.

Fig. 21 Basidiocarp and basidiospores as seen by SEM of *Entoloma transitionisporum* (KaiR503, holotype): **a** stipe **b** pileus from above; **c** basidiospores, including reduced forms, bar = 10 µm

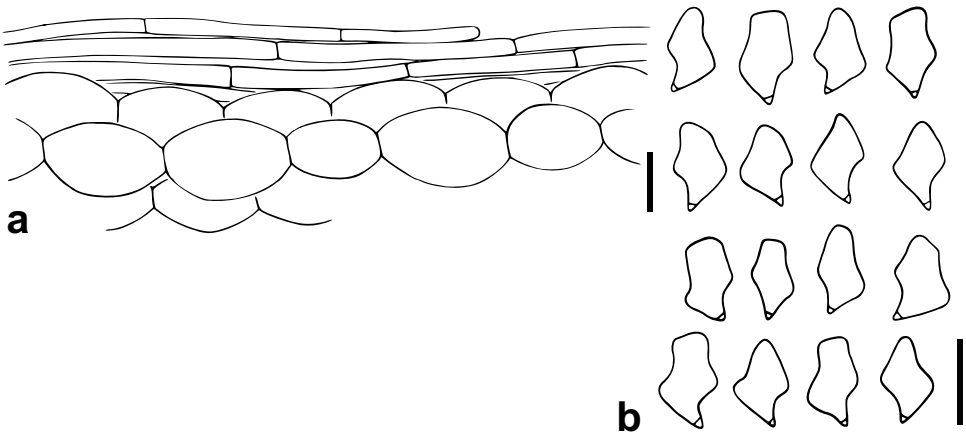

Fig. 22 Microscopic structures of *Entoloma transitionisporum* (CME6, holotype): **a** pileipellis with subpellis composed of inflated cells, intracellular pigment not indicated, bar = 20 µm; **b** basidiospores, bar = 10 µm

Habitat: Basidiocarps scattered in a group, in *Quercus*-dominated montane forests from 2000 to 2340 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′35.1″ W 82°34′53.2″, 2260 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, K. Reschke, T.A. Hofmann, J. Rodríguez, KaiR609 (M); near Volcán, Paso Ancho, PNVB, N 08°48′55.1″, W 82°34′42.6″, 2000 m asl., montane forest with abundant *Quercus* spp. and *Comarostaphylis arbutoides*, 26 October 2016, J. Rodríguez, T.A. Hofmann, K. Barrera, PA891 (M).

Notes: *Entoloma flavoconicum* is characterised by mycenoid, strongly yellowish basidiocarps, conical to acutely umbonate pilei, heterodiametrical basidiospores, incrusting pigment on the cells of the pileipellis, and absence of clamp connections. It forms a clade together with *E. olivaceohebes* Noordel. & Hauskn. and *E. vernum* S. Lundell (Fig. 14). However, these two species have basidiocarps with rather dark brown colours. In addition

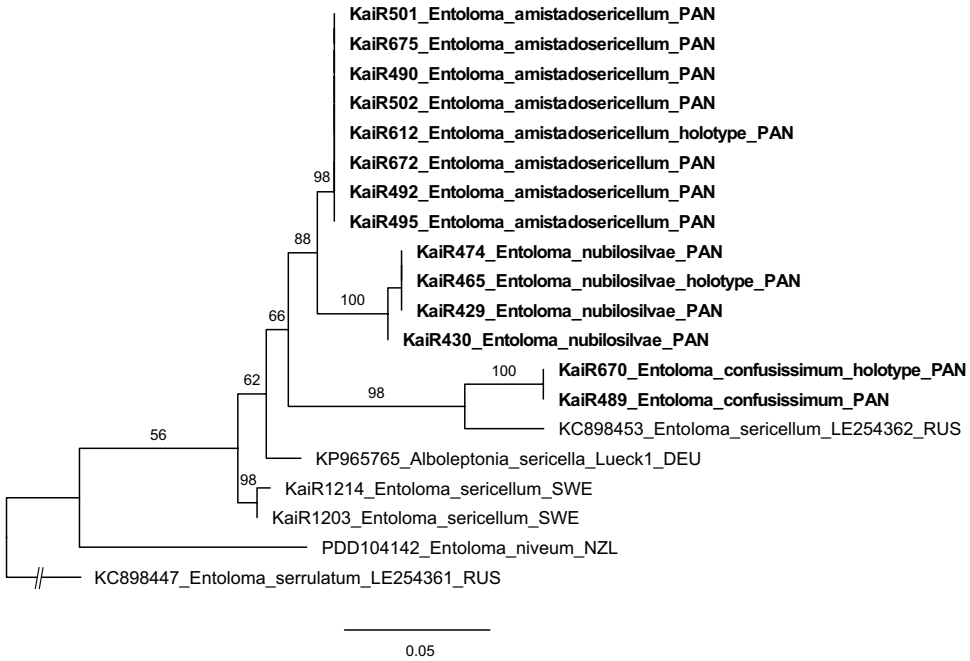

Fig. 23 Maximum likelihood phylogram of species of subg. *Alboleptonia* based on ITS, rooted to *E. serrulatum*, bootstrap values above branches, bar = estimated changes/nucleotide

to this, they can be distinguished from *E. flavoconicum* by micromorphological characters, like the presence of clamp connections in the hymenium (Noordeloos 1992, 2004; Horak 2008). *Entoloma subelegans* Noordel. & Hauskn., described from Mauritius (Noordeloos and Hausknecht 2016), is somewhat similar in colour and striation of the pileus. It differs, however, by depressed pilei, shape and size of the basidiospores, presence of cheilocystidia, and clamp connections in the hymenium. Phylogenetically, *E. subelegans* does not belong to *E.* subg. *Nolanea* (Fig. 14). *Entoloma aromaticum* E. Horak from Australia and New Zealand is another yellowish and clampless species, but the colour of the basidiocarps is somewhat more reddish yellow, and they have a strongly aromatic smell and taste (Horak 2008; Noordeloos and Gates 2012). No similar species is described in the monographs of Hesler (1967), Largent (1994), and Noordeloos (2004).

Entoloma paraconferendum Reschke, Manz, F. Hampe & Noordel., sp. nov., Figs. 19 and 20

Mycobank number: MB840628.

Typification: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′39.7″ W 82°34′55.0″, 2340 m asl., montane forest dominated by *Quercus* spp., 19 June 2018, C. Manz and F. Hampe CME6, holotype (UCH11747), isotype (M).

Etymology: para (Latin) = beside; refers to *Entoloma conferendum*, which is closely related and has morphologically similar basidiocarps.

Description: Basidiocarps mycenoid. Pileus 2.5–4.5 cm diameter, broadly conical to campanulate, slightly papillate, with straight, slightly uneven margin, greyish yellow (4B4, 4B5), with darker greyish yellow (4C5), delimited centre, whitish at the very margin, pileal surface glabrous, but finely scaly-pruinose if seen through a lens, translucently striate at about 1/3 the radius, hygrophanous. Lamellae adnexed to almost free, ventricose, close, initially whitish, later pink, with rather even and concolorous edges. Stipe 4.5–7.0 × 0.25–0.40 cm, cylindrical, hollow, greyish yellow (4B4, 4B5), fibrillose, overlaid by whitish, silky fibrils. Basal mycelium white, somewhat cottony. Odour somewhat musty, taste not tested.

Basidiospores 8.5–10.5–12.0 × 6.5–7.3–8.0 µm, $Q = 1.25–1.44–1.70$ ($n = 54$ spores of 2 specimens), heptahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), a pair of lateral facets (L), and a basal facet (Ba) forming a simple base, heterodiametrical, rarely irregularly cruciform, with 4–6, predominantly 5, pronounced, blunt angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 30–42 × 10.5–12.5 µm, clavate to subclavate, hyaline, 4-spored, sterigmata up to 4.0 µm long. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by long, cylindrical to somewhat inflated cells, rather wide centrally, narrower towards hymenium, 80–550 × 3.5–25 µm. Pileipellis a cutis composed of cylindrical cells, 45–145 × 5.0–12.0 µm, often disrupted by trichodermal sections formed by a few erect hyphal ends, composed

of cells of the same size or of relatively short cells, 15.0–40 × 6.5–12.0 µm, pigment intracellular, with a subpellis composed of inflated cells, 40–90 × 20–50 µm. Stipitipellis a cutis composed of long, cylindrical cells, 60–400 × 3.0–5.5 µm. Caulocystidia absent. Oleiferous hyphae frequently present in the trama. Clamp connections absent from all parts of the basidiocarp.

Habitat: Basidiocarps in small groups in *Quercus*-dominated montane forest at 2340 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′39.7″ W 82°34′55.0″, 2,340 m asl., montane forest dominated by *Quercus* spp., 19 June 2018, C. Manz and F. Hampe, CME7 (M).

Notes: *Entoloma paraconferendum* is characterised by mycenoid basidiocarps with a translucently striate pileus, a silky, fibrillose stipe, and heterodiametrical basidiospores. Its basidiocarps are macromorphologically like those of *E. conferendum*. These two species are also closely related based on ITS sequences (*p*-distance = 1.8%). However, they can easily be distinguished by the almost exclusively cruciform basidiospores of *E. conferendum* and predominantly heterodiametrical, only rarely subcruciform basidiospores of *E. paraconferendum*.

Entoloma transitionisporum Reschke, Manz & Noordel., sp. nov., Figs. 21 and 22

Mycobank number: MB840626.

Typification: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′48.0″ W 82°37′05.7″, 2320 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez KaiR503, holotype (UCH11743), isotype (M).

Etymology: transitio (Latin) = transition; refers to the transitional shape of the basidiospores, between heterodiametrical and cruciform.

Description: Basidiocarps mycenoid. Pileus 3.5–4.0 cm diameter, broadly conical to convex umbilicate, margin slightly incurved and uneven, brown to light brown (5E7, 5D6, 5D7) at centre, paler, brownish orange to greyish orange (5C4, 5C5 to 5B3), towards margin, pileal surface glabrous, translucently striate up to 2/3 of the centre, hygrophanous. Lamellae adnexed, almost free, medium-spaced to rather close, white to slightly greyish in immature basidiocarps, pink upon maturity, with slightly undulating and concolorous edges and transvenose sides. Stipe 7.0 × 0.4–0.5 cm, cylindrical to slightly broadening towards base, hollow, brownish orange (5C5, 5C6), overlaid by silvery whitish fibrils, innately fibrillose, sometimes contorted. Basal mycelium not recorded. Odour indistinct, taste not tested.

Basidiospores 7.5–9.2–10.5 × 6.0–6.6–7.5 µm, *Q* = 1.15–1.40–1.65 (*n* = 65 spores of 2 specimens), predominantly heptahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), a pair of lateral facets (L), and a basal facet (Ba) forming a simple base, reduced forms hexahedroid or more rarely pentahedroid (prismatic), with single AD-facet and/or reduced to absent A-facet, heterodiametrical to irregularly cruciform, with 4–5 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia

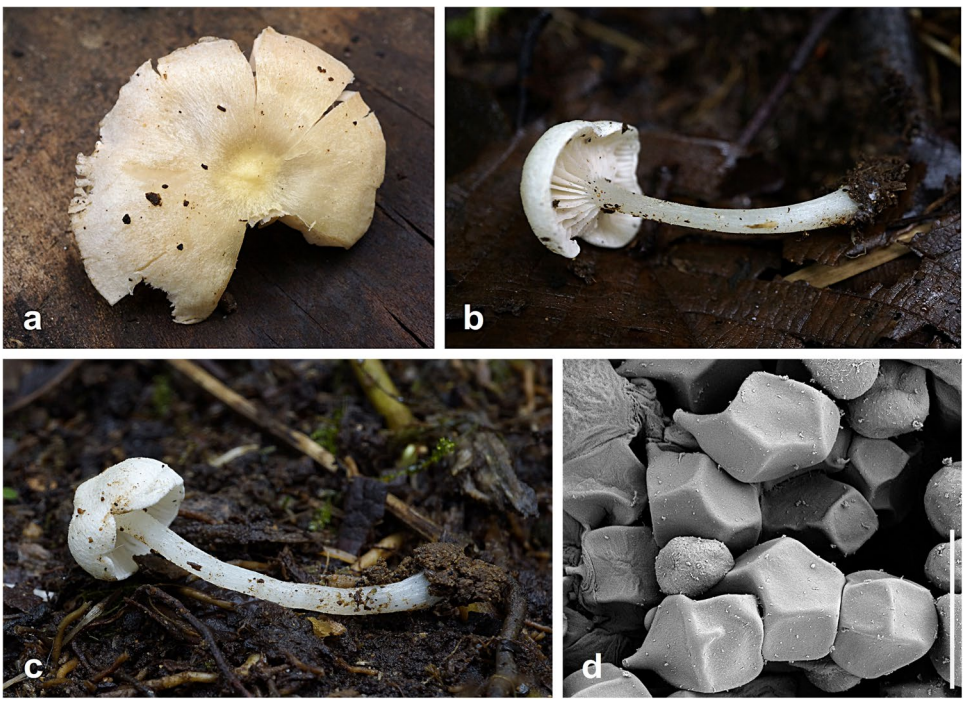

Fig. 24 Basidiocarps and basidiospores as seen by SEM of *Entoloma amistadosericellum*: **a** (KaiR612, holotype); **b** (KaiR502); **c** (KaiR672); **d** (KaiR612, holotype) bar = 10 µm

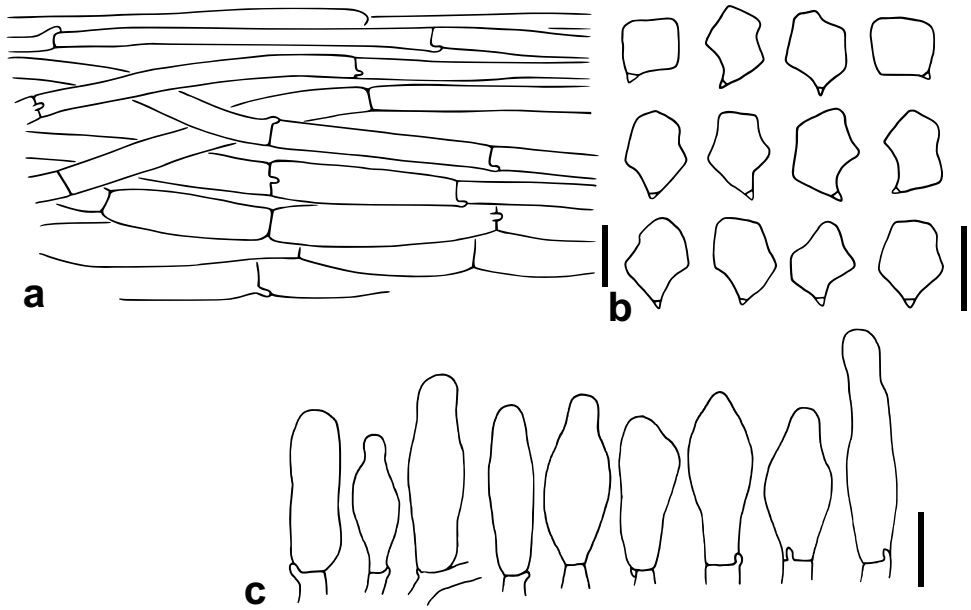

Fig. 25 Microscopic structures of *Entoloma amistadosericellum* (KaiR612, holotype): **a** pileipellis, bar = 20 µm; **b** basidiospores, bar = 10 µm; **c** cheilocystidia, bar = 20 µm

34–41 × 11.0–13.0 µm, subclavate, hyaline, 4-spored, sterigmata up to 5.0 µm long. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, formed by long, cylindrical to somewhat inflated cells, centrally 140–430 × 6.5–20 µm, narrower, 170–450 × 2.5–7.0 µm, towards hymenium. Pileipellis a cutis of relatively narrow cells, 70–110 × 3.0–9.0 µm, with yellowish to brownish, intracellular pigment and a distinct subpellis of inflated cells, 40–65 × 28–40 µm. Stipitipellis a cutis composed of long, cylindrical cells, 290–950 × 4.0–14.0 µm, with some intracellular, pale yellowish brown pigment, difficult to locate. Caulocystidia absent. Oleiferous hyphae present, abundant in hymenophoral trama. Clamp connections absent from all parts of the basidiocarp.

Habitat: Basidiocarps found solitary among mosses in *Alnus acuminata*-dominated montane forests between 2000 and 2400 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′37.5″ W 82°36′54.4″, 2,030 m asl., montane forest dominated by *Alnus acuminata*, 22 June 2018, C. Manz and T.A. Hofmann, CME9 (M).

Notes: *Entoloma transitionisporum* belongs to the clade of *E. conferendum* and its allies. It is characterised by a conical to convex umbilicate, brown, translucently striate pileus, a silvery fibrillose stipe, absence of clamps, and the shape of the basidiospores, which can be interpreted as a transitional state between heterodiametrical and cruciform. *Entoloma belouvense* is closely related based on ITS sequence data (Fig. 14). Its basidiocarps are on average smaller and paler than those of *E. transitionisporum* and their pilei have a contrasting darker centre, which was not observed in pilei of the latter species. In addition, the basidiospores of *E. belouvense* are somewhat longer and without transitional states to a cruciform shape. Basidiocarps of *E. conferendum* can have a similar habit, but *E. conferendum* is easily distinguished from *E. transitionisporum* by exclusively cruciform basidiospores. *Entoloma luteifuscum* K.N.A. Raj & Manim., described from India, differs by yellowish tones of the basidiocarps and slightly larger basidiospores, which are exclusively heterodiametrical (Raj et al. 2014). *Entoloma dissimile* (Singer) Horak, described from *Nothofagus*-forest in Argentinia, may be similar to *E. transitionisporum*. However, the pilei of *E. dissimile* are darker, basidiospores are slightly broader, and pigment is incrusting in the pileipellis (Horak 1978). No similar species were found in Largent (1994), Horak (1982), and Hesler (1967).

Subgenus *Alboleptonia* (Largent & R.G. Benedict) Noordel

The subgenus *Alboleptonia* in the traditional sense (Largent and Benedict 1970; Noordeloos 1987, 2004) is an assemblage of white or whitish species, often with a differentiated pileipellis. It appears to be polyphyletic, considering recent phylogenies (He et al. 2015c; Largent et al. 2016). Here, we focus on the core group of *Alboleptonia*, i.e., species around the type species *E. sericellum* (Fr.) P. Kumm. This species is widespread in Europe and appears to be a complex of several species, both in and outside of Europe. *Entoloma cuboidoalbum* Noordel. & Hauskn. was described from Austria (Noordeloos and Hausknecht 2009), but there are more species waiting to be described in this group, as evident by the results of the phylogenetic analysis (Fig. 23). In the present study, three new species from Panama are

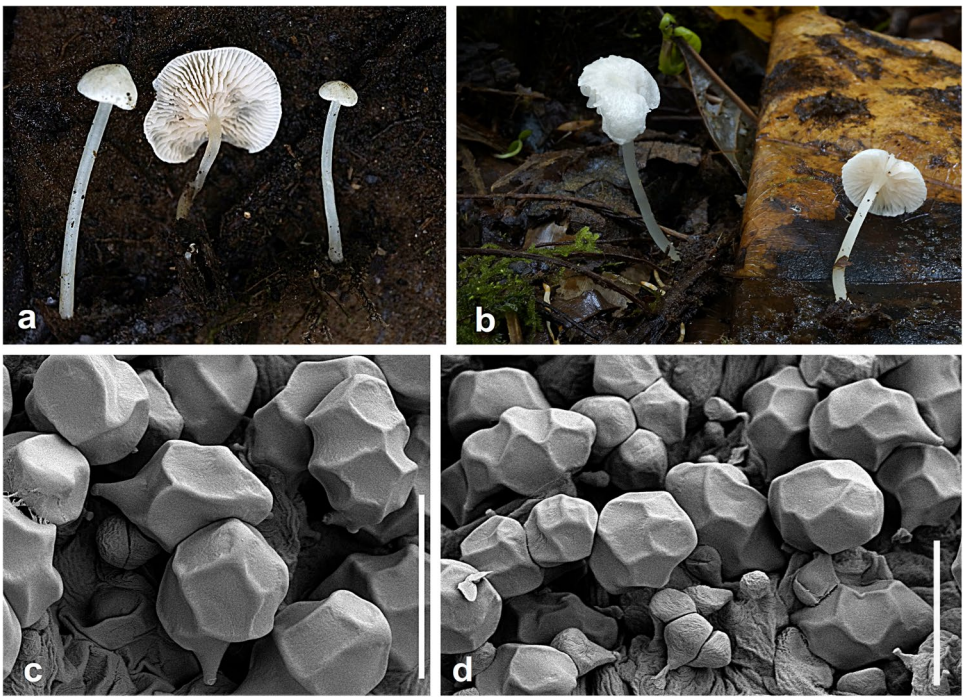

Fig. 26 Basidiocarps and basidiospores as seen by SEM of *Entoloma confusissimum*: **a** (KaiR489); **b**, **c**, **d** (KaiR670, holotype) bars = 10 µm

described in the clade of *E. sericellum* that can be well differentiated by their basidiospore characters.

Entoloma amistadosericellum Reschke & Noordel., sp. nov., Figs. 24 and 25

Mycobank number: MB840937.

Typification: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, around 2300 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, J. Rodríguez, KaiR612, holotype (M).

Etymology: named after its similarity to *Entoloma sericellum* and its occurrence in the Parque Internacional La Amistad, honouring the principle of friendship in nature conservation.

Description: Basidiocarps collybioid. Pileus 1.0–5.5 cm diameter, convex and often with an obtuse umbo when

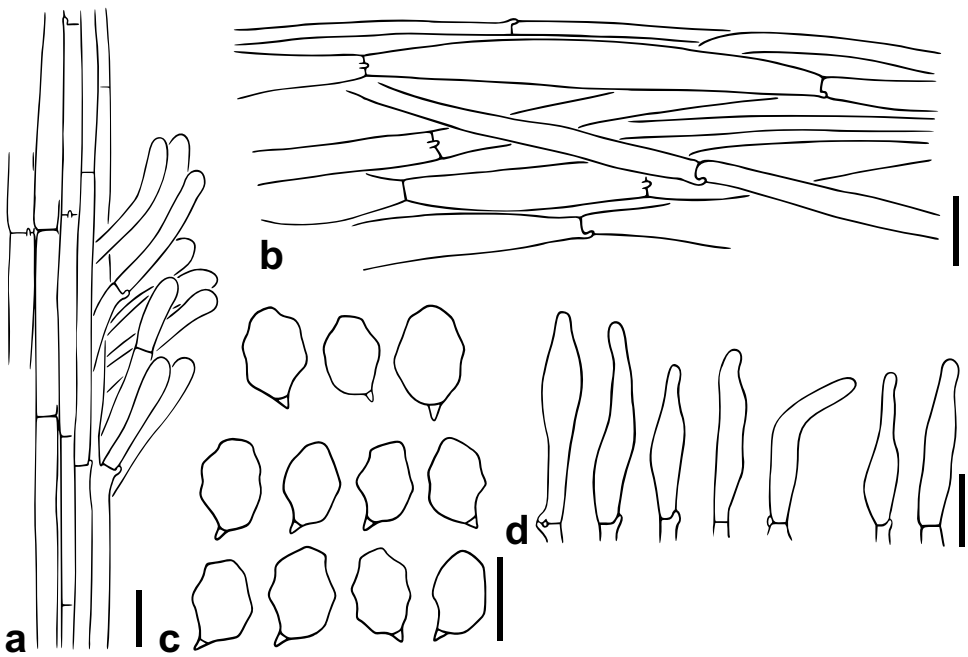

Fig. 27 Microscopic structures of *Entoloma confusissimum* (KaiR670, holotype): **a** stipitipellis with caulocystidia, bar = 20 µm; **b** pileipellis bar = 20 µm; **c** basidiospores, bar = 10 µm; **d** cheilocystidia, bar = 20 µm

young, becoming depressed, often remaining a small papilla, margin initially incurved, later straight, white in young and fresh basidiocarps, older basidiocarps with yellowish to pale brownish patches, pileal surface radially fibrillose, not translucently striate. Lamellae sinuate, adnate to decurrent, medium-spaced to rather distant, initially white, later pink, with smooth to slightly uneven, concolorous edges. Stipe 1.0–4.7 × 0.20–0.60 cm, cylindrical to slightly clavate towards base, rather fragile and hollow, translucently whitish, inconspicuously fibrillose and slightly pruinose all over. Basal mycelium white. Odour not distinctive, taste not tested.

Basidiospores 8.5–9.4–10.5 × 6.5–7.6–8.5 µm, $Q = 1.10–1.25–1.40$ ($n = 111$ spores of 5 specimens), enneahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), and two pairs of lateral facets (L1–L2), of which the basal pair (L2) forms a dièdre basal, reduced forms octa- or heptahedroid, often with single AD-facet and/or reduced to absent A-facet, mainly broadly heterodiametrical, some subisodiametrical, rhomboid, cruciform or almost quadratic, with 4–6, predominantly 5, pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 36–55 × 10.0–12.5 µm, clavate, hyaline, 4-spored, sterigmata up to 5.5 µm long. Lamellar edge almost sterile, cheilocystidia cylindrical, clavate to broadly lageniform, sometimes capitate, 37–73 × 10–19 µm. Hymenophoral trama composed of rather broadly cylindrical cells, 30–175 × 5–22 µm. Pileipellis a cutis formed by cylindrical cells, 70–175 × 3.5–11.5 µm, pigment absent; subpellis absent, gradually passing into pileitrama, composed of somewhat wider cells. Stipitipellis a cutis composed of cylindrical cells, 50–200 × 4.0–8.5 µm. Caulocystidia absent. Oleiferous hyphae present in the trama but rather infrequent. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps solitary to scattered, in *Alnus acuminata*-dominated montane forest and *Quercus*-dominated montane forest at around 2300 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′46.0″ W 82°37′01.″ 2270 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR490 (UCH11736, M); ibid., N 08°53′46.8″ W 82°37′01.4″, 2280 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR492 (UCH11737, M); ibid., N 08°53′46.8″ W 82°37′01.4″, 2280 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR495 (UCH11738, M); ibid., N 08°53′48.0″ W 82°37′05.7″, 2320 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR501 (M); ibid., N 08°53′48.0″ W 82°37′05.7″, 2320 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR502 (M); ibid., N 08°53′46.2″ W 82°37′01.4″, 2280 m asl., montane forest dominated by *Alnus acuminata*, 27 June 2017, K. Reschke, KaiR672 (M).

Notes: *Entoloma amistadosericellum* is characterised by whitish basidiocarps with convex to depressed pilei, a radially fibrillose pileal surface, abundant clamp connections, relatively broad cheilocystidia, and the presence of rhomboid to cruciform basidiospores. It is closely related to *E. nubilosilvae*, described below. Most species of subg. *Alboleptonia* s.l. are macromorphologically similar, however, they differ in micromorphological characters. *Entoloma cylindrocapitatum* (T.J. Baroni & Ovrebo) Noordel. & Co-David, also described from Panama, has rather small basidiospores as well as long, narrow, and capitate cheilocystidia (Ovrebo and Baroni 2007). *Entoloma cuboidoalbum* has larger basidiospores (9.0–11.5 × 7.5–10.5 µm) and lower *Q*-values (1.0–1.3) (Noordeloos and Hausknecht 2009) than *E. amistadosericellum* (8.5–10.5 × 6.5–8.5 µm, $Q = 1.10–1.40$). *Entoloma crocotillum* Xiao L. He has large, exclusively heterodiametrical basidiospores (He et al. 2015c). *Entoloma davidii* Noordel. & Co-David (syn. *Alboleptonia largentii* T.J. Baroni & Lodge), *E. laccarioides* T.H. Li et al. and *E. subroseum* (T.J. Baroni & Lodge) Noordel. & Co-David have cuboid basidiospores (Baroni and Lodge 1998; He et al. 2015a). *Entoloma sericellum* s. auct. has a temperate and boreal distribution, and heterodiametrical, 5–8 angled basidiospores. *Entoloma shwethum* Manim et al. has rather large basidiocarps (pileus 3–5 cm diameter), sterile lamellar edges, and large basidiospores (9–12 × 6–9 µm) (Manimohan et al. 1995). *Entoloma subochraceum* Blanco-Dios (syn. *Alboleptonia ochracea* Largent & R.G. Benedict) has basidiospores with an average length of 10.5 µm and only scattered clamp connections (Largent and Benedict 1970). Basidiocarps of *Entoloma theekshnagandhum* Manim. et al. can be differentiated from those of *E. amistadosericellum* by their odour of fermented rice soup and cuboid to isodiametrical basidiospores (Manimohan and Leelavathy 1988; Manimohan et al. 1995).

Entoloma confusissimum Reschke & Noordel., sp. nov., Figs. 26 and 27

Mycobank number: MB840938.

Typification: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′46.2″ W 82°37′01.4″, 2280 m asl., montane forest dominated by *Alnus acuminata*, 27 June 2017, K. Reschke, KaiR670, holotype (M).

Etymology: confusus (Latin) = confused; refers to the fact, that basidiocarps of this species can easily be

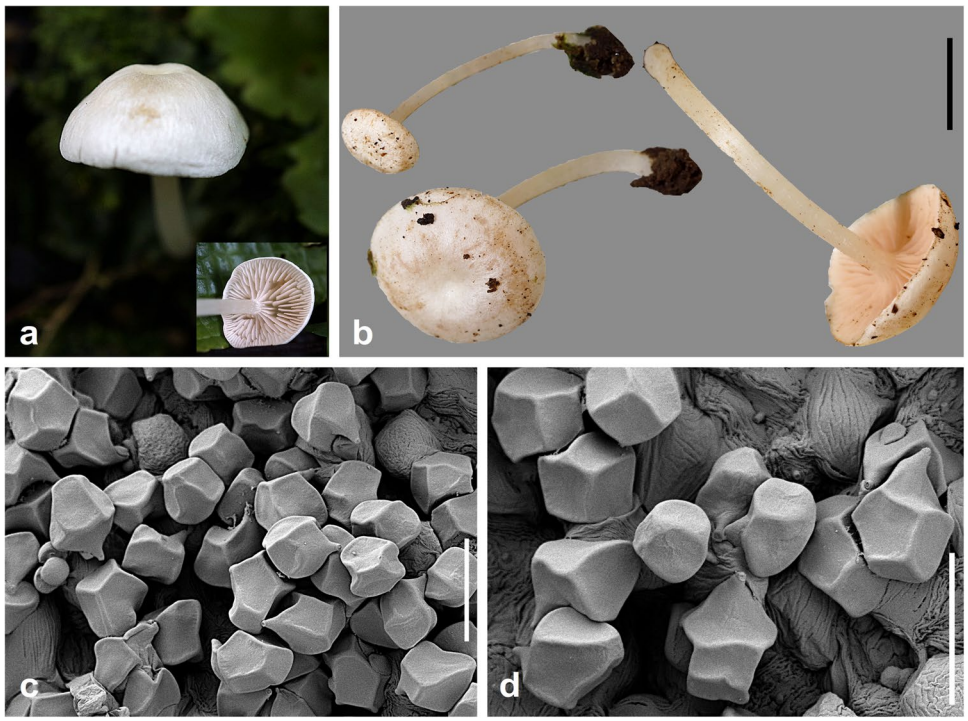

Fig. 28 Basidiocarps and basidiospores as seen by SEM of *Entoloma nubilosilvae*: **a** (KaiR429); **b** (KaiR465, holotype) bar = 1 cm; **c, d** (KaiR465, holotype) bars = 10 µm

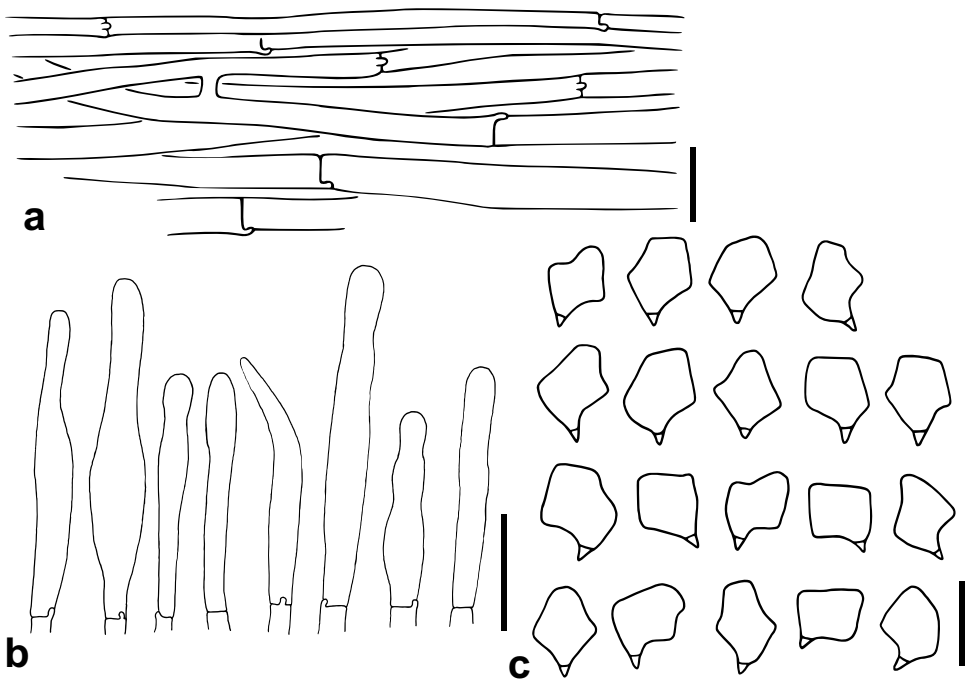

Fig. 29 Microscopic structures of *Entoloma nubilosilvae* (KaiR465, holotype): **a** pileipellis, bar = 20 µm; **b** cheilocystidia, bar = 20 µm; **c** basidiospores, bar = 10 µm

confused with those of several other species of *E.* subg. *Alboleptonia*.

Description: Basidiocarps mycenoid to collybioid. Pileus 0.5–5.0 cm diameter, broadly conical to convex, becoming depressed in old basidiocarps, margin initially somewhat incurved, later straight, white in young and fresh basidiocarps, older basidiocarps with slightly yellowish patches, pileal surface finely fibrillose squamulose, not translucently striate, not hygrophanous. Lamellae emarginate with decurrent tooth to decurrent, segmentiform, medium-spaced to distant, sometimes distinctly transvenose, initially white, later pink, with even to slightly undulating, concolorous edges. Stipe 2.0–5.0 × 0.15–0.25 cm, cylindrical, translucently whitish, polished to slightly fibrillose and pruinose, especially towards the apex, staining slightly yellowish after damage. Odour indistinct, taste not tested.

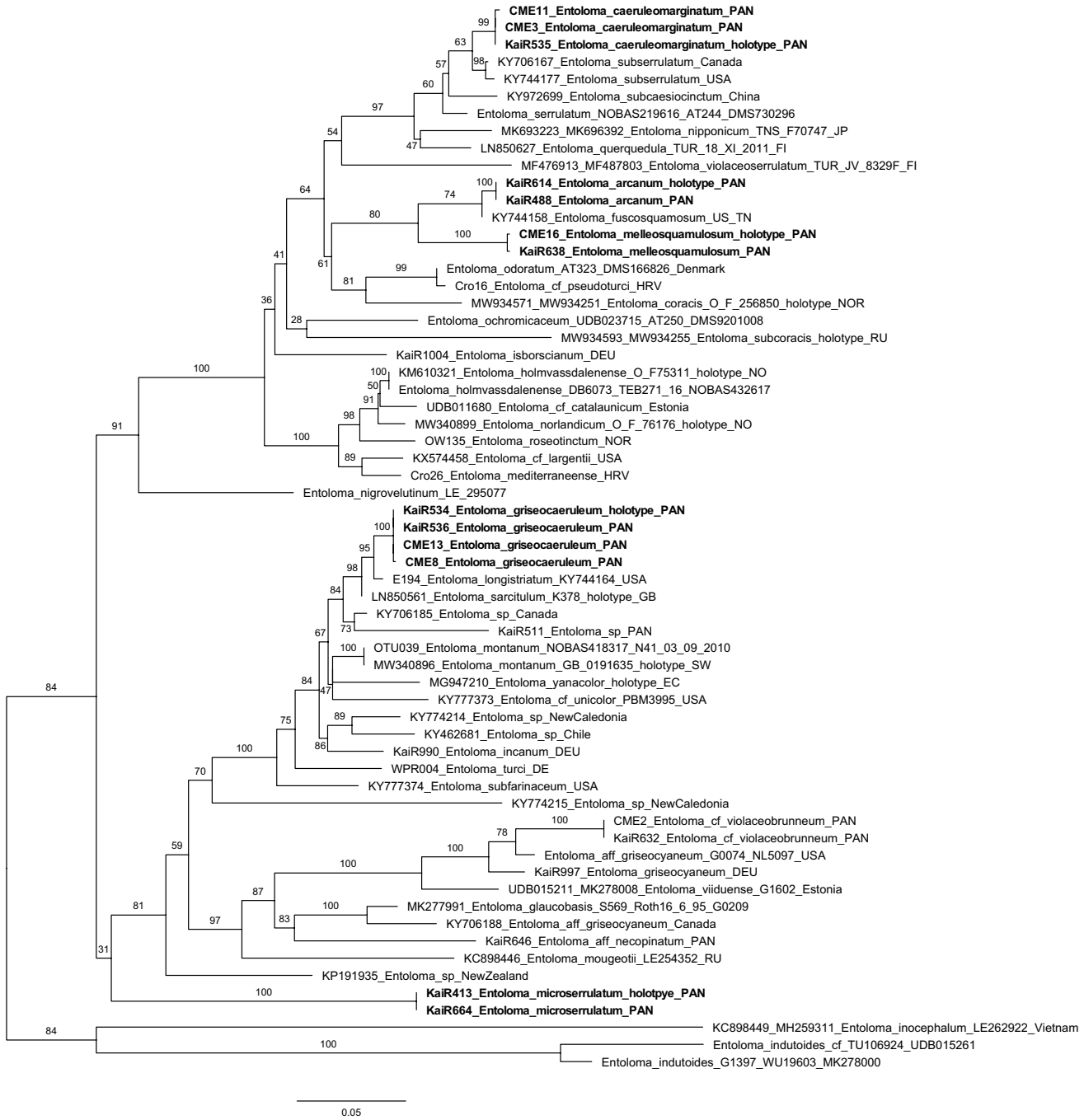

Fig. 30 Maximum likelihood phylogram of species of subg. *Cyanula* based on concatenated ITS and LSU sequences, rooted to *E. inocephalum*, *E. indutoides*, and *E.* cf. *indutoides*, bootstrap values above or below branches, bar = estimated changes/nucleotide

Basidiospores 9.0–10.3–12.0 × 6.5–7.2–8.0 µm, $Q = 1.35–1.44–1.60$ ($n = 44$ spores of 2 specimens), tetradecahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), two abaxial facets (B1, B2), and four pairs of lateral facets (L1–L4), of which the basal pair (L4) forms a sometimes incomplete dièdre basal, heterodiametrical, with 6–9 nodulose angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 30–40 × 10.0–13.0 µm, clavate to subclavate, hyaline, predominantly 4-spored, with up to 4.0 µm long sterigmata, few 2-spored. Lamellar edge heterogeneous, at some parts almost sterile, cheilocystidia 35–60 × 7.0–11.0 µm, subcylindrical to lageniform, often in clusters. Hymenophoral trama regular, mainly composed of rather short, broadly cylindrical to somewhat inflated cells, 70–200 × 7–25 µm, longer and narrower cells towards

the subhymenium, approximately 150–300 × 4.0–5.0 µm. Pileipellis a cutis formed by cylindrical to somewhat fusiform or locally inflated cells, 70–250 × 3.0–16.0 µm, without pigment, subpellis not developed, pileipellis gradually passing into pileitrama, composed of similar to somewhat wider cells. Stipitipellis a cutis composed of cylindrical cells, 60–180 × 4.5–8.0 µm. Caulocystidia present in dense bundles, cylindrical, often subcapitate, 30–65 (85) × (5.0) 6.5–10.0 (12.5) µm. Oleiferous hyphae present in the trama. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps scattered in small groups in *Alnus acuminata*-dominated montane forest between 2200 and 2300 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′46.0″ W 82°37′01.5″, 2270 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR489 (UCH11735, M).

Notes: *Entoloma confussisimum* is characterised by its *E. sericellum*-like habit and rather large and complex basidiospores with 6–9 angles in outline. Its ITS sequences have a *p*-distance of 5% to that of a specimen identified as *E. sericellum* from Caucasus, Russia (Fig. 23). *Entoloma sericellum* differs by smaller basidiospores with lower *Q*-values (1.1–1.5) and 5–8, predominantly 6 angles (Noordeloos 1992). *Entoloma subsericellum* Murrill, described from a coniferous forest of North America, has basidiospores of similar size, however, with only 5–6 angles (Murrill 1917; Largent and Benedict 1970). The absence of cheilocystidia, rare clamp connections, and a farinaceous odour indicates that *E. subsericellum* does not belong to the core clade of subg. *Alboleptonia*. *Entoloma aripoanum* Dennis, described from Trinidad, is similar in macromorphology and spore size, but differs by its very narrow lamellae, large, cylindrical cheilocystidia (70–160 × 10–16 µm), and occurrence on rotten wood (Dennis 1953).

Entoloma nubilosilvae Reschke & Noordel., sp. nov., Figs. 28 and 29

Mycobank number: MB840623.

Typification: PANAMA. CHIRIQUÍ: near Boquete, PNVB, Sendero Culebra, N 08°51′12.5″ W 82°29′01″, 1,830 m asl., montane forest with abundant *Quercus* spp., 9 June 2017, K. Reschke, KaiR465, holotype (UCH11733), isotype (M).

Etymology: nubilus (Latin) = cloudy, silva (Latin) = forest; refers to the occurrence in cloud forest.

Description: Basidiocarps collybioid. Pileus 0.8–2.7 cm diameter, convex, becoming depressed in old basidiocarps, margin initially incurved, later straight, white in young and fresh basidiocarps, older basidiocarps with yellowish to pale brownish patches, pileal surface radially fibrillose, not translucently striate. Lamellae slightly to distinctly decurrent, rather distant, initially white, later pink, with slightly uneven and finely pruinose, concolorous edges. Stipe 1.8–3.5 × 0.15–0.50 cm, cylindrical, rather fragile and hollow, translucently whitish, inconspicuously fibrillose and slightly pruinose all over, staining yellowish after damage. Odour sometimes perfume-like, taste not tested.

Basidiospores 7.0–8.8–10.0 × 6.0–7.1–8.0 µm, *Q* = 1.05–1.24–1.40 (*n* = 137 spores of 4 specimens), octahedroid, composed of a adaxial facet (D), predominantly a single apico-adaxial facet (sAD), an apical facet (A), an abaxial facet (B), and two pairs of lateral facets (L1–L2), of which the basal pair (L2) forms a dièdre basal, subisodiametrical to broadly heterodiametrical, often rhomboid to almost quadratic or cruciform, with 4–5 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 36–45 × 9.0–10.5 µm, clavate, hyaline, mainly 4-spored with up to 5.0 µm long sterigmata, some 2-spored. Lamellar edge heterogeneous, cheilocystidia 40–60 × 5.0–13.0 µm, subcylindrical, lageniform to capitate, often in clusters, with variable abundance. Hymenophoral trama regular, composed of rather short, broadly cylindrical cells, 40–100 × 5.0–18.0 µm. Pileipellis a cutis formed by

Fig. 31 Basidiocarps of *Entoloma arcanum*: **a** (KaiR488); **b** (KaiR614)

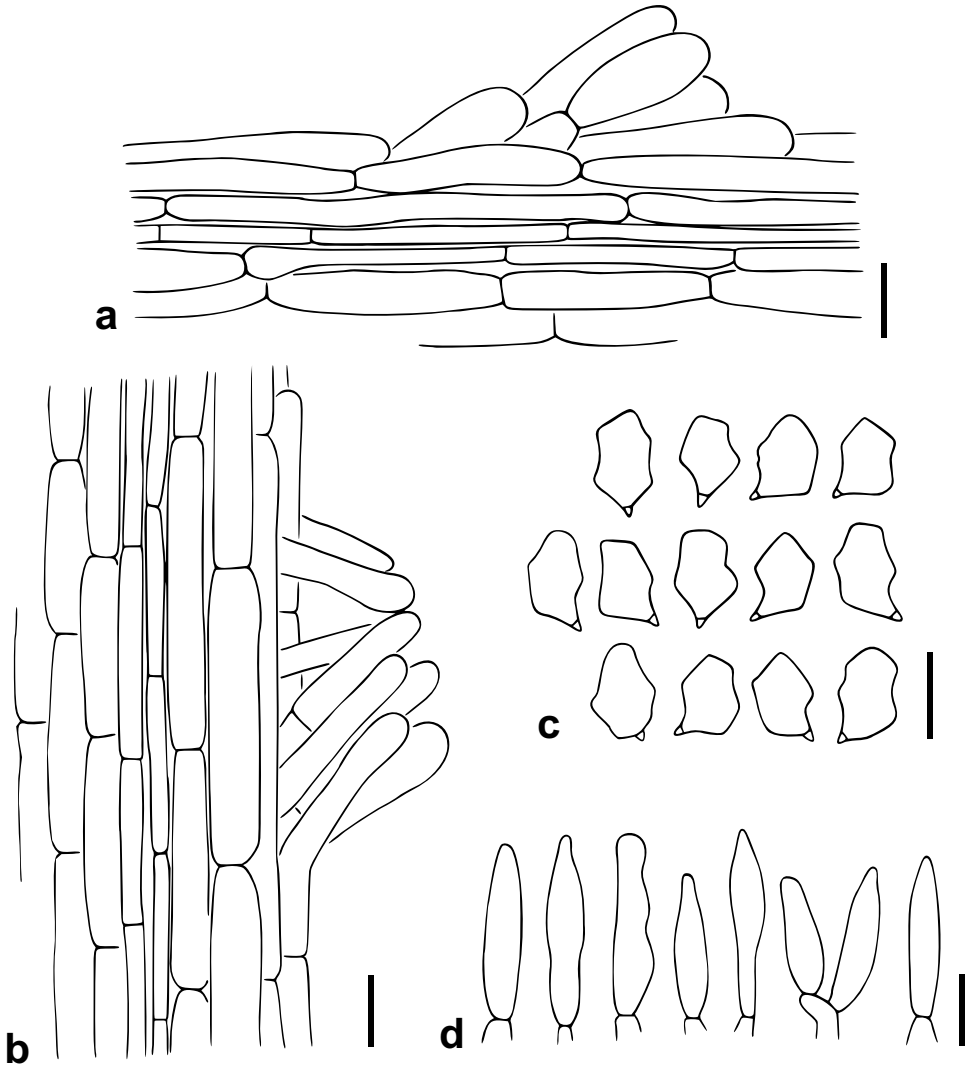

Fig. 32 Microscopic structures of *Entoloma arcanum*: **a–c** (KaiR488); **a** pileipellis, bar = 20 µm; **b** stipitipellis with caulocystidia, bar = 20 µm; **c** basidiospores, bar = 10 µm; **d** (KaiR614) cheilocystidia, bar = 20 µm

cylindrical to subcylindrical cells, 65–250 × 4.5–12.0 µm, pigment absent, without subpellis, gradually passing into pileitrama, composed of somewhat wider cells. Stipitipellis a cutis composed of narrow cylindrical cells, 60–210 × 3.0–6.0 µm. Caulocystidia absent. Oleiferous hyphae rare, but present at least in the pileitrama. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps found solitary to scattered in *Quercus*-dominated montane forest between 1750 and 1900 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Boquete, PNVB, Sendero Culebra, N 08°51′00.7″ W 82°28′55.2″, 1,760 m asl., montane forest with abundant *Quercus* spp., 6 June 2017, K. Reschke, KaiR429 (M); ibid., N 08°51′00.7″ W 82°28′55.2″, 1,760 m asl., montane forest with abundant *Quercus* spp., 6 June 2017, K. Reschke, KaiR430 (M); ibid., N 08°51′21.1″ W 82°29′02.5″, 1880 m asl., montane forest with abundant *Quercus* spp., 9 June 2017, K. Reschke, KaiR474 (M).

Notes: *Entoloma nubilosilvae* is characterised by whitish basidiocarps with a convex to depressed pileus, a radially fibrillose pileal surface, abundant clamp connections, rather narrow cheilocystidia, and the presence of rhomboid to cruciform basidiospores. It is closely related to *E. amistadosericellum*, described above, which has broader cheilocystidia and slightly larger basidiospores. As basidiocarps of *E. nubilosilvae* are quite similar to those of *E. amistadosericellum* micro- and macromorphologically, it differs from all the species mentioned in the notes of the latter in the same way. *Entoloma adnatifolium* (Murrill) Blanco-Dios has basidiospores and cheilocystidia of similar size as *E. nubilosilvae*; however, rhomboid basidiospores were not mentioned in the description of *E. adnatifolium* and clamp connections are rare to scattered on the hyphae of the pileipellis and the stipe surface (Largent and Benedict 1970).

Fig. 33 Basidiocarp and cellular structures as seen by SEM of *Entoloma caeruleomarginatum* (KaiR535, holotype): **a** view from below, depicting lamellae with serrulatum structure; **b** view from above **c** basidiospore, bar = 10 µm; **d** cheilocystidia, bar = 10 µm

Subgenus Cyanula *(Romagn.) Noordel*

Species of the subgenus *Cyanula* form a well-supported clade in the ITS/LSU phylogeny (Fig. 30). They develop basidiocarps with often bright colours, a differentiated pileipellis with a trichodermal structure, intracellular pigment, and clampless hyphae. The lamellar edge of many species is formed by tramal hyphae that grow through the hymenium forming a sterile band along the edge, with dense clusters of more or less clavate or fusiform terminal cells. These terminal cells often contain blue or brown intracellular pigment, causing a coloured border along the edge, the "serrulatum-type" lamellar edge (Noordeloos 2004). Species of this clade occur worldwide, from the arctic tundra to the tropical rainforest. In Europe, they are characteristic of oligotrophic grasslands, habitats which are generally threatened in Europe (Janssen et al. 2016). The subgenus *Cyanula* is the most species-rich subgenus within *Entoloma*, with approximately 500–600 species already described (Hesler 1967; Horak 1980, 2008; Largent 1994; Noordeloos 2004; Noordeloos and Gates 2012; Crous et al. 2021; Noordeloos et al. 2021; Dima et al. 2021). Species delimitation is often rather difficult. Morphological look-alikes occurring on several continents are often phylogenetically distant and must therefore be considered as semi-cryptic.

Entoloma arcanum Reschke & Noordel., sp. nov., Figs. 31 and 32

Mycobank number: MB840624.

Typification: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′46.0″ W 82°37′01.5″, 2,270 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR488, holotype (UCH11734), isotype (M).

Etymology: arcanus (Latin) = arcane; refers to the dark appearance of the basidiocarps and its isolated position in the phylogenetic tree.

Description: Basidiocarps collybioid. Pileus 3.0–4.5 cm diameter, hemispherical to convex with umbilicate centre, margin initially incurved, remaining somewhat incurved in old basidiocarps, blackish blue (19F5, 19F6, 19F7), blue tones becoming brownish while ageing, pileal surface squamulose-velutinous in the centre, squamulose to squamulose-fibrillose towards margin, not translucently striate, not hygrophanous. Lamellae broadly adnate to slightly decurrent, segmentiform, close, white with creamish tinge, becoming pink at maturity, with somewhat crenate and concolorous edges. Stipe 2.0–4.0×0.5 cm, cylindrical, sometimes compressed, hollow, initially concolorous to the pileus, blue tones soon becoming brownish, finely squamulose. Basal mycelium white, cottony, sometimes with obvious, thick rhizomorphs. Odour unpleasant, similar to old basdidiocarps of *Tricholoma* spp. or burnt potatoes, taste not tested.

Basidiospores 9.5–10.3–11.0 × 6.5–7.0–7.5 µm, Q = 1.30–1.48–1.65 (n = 53 spores of 2 specimens), heterodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 30–38 (40) × 8.5–11.0 µm, clavate to subclavate, hyaline,

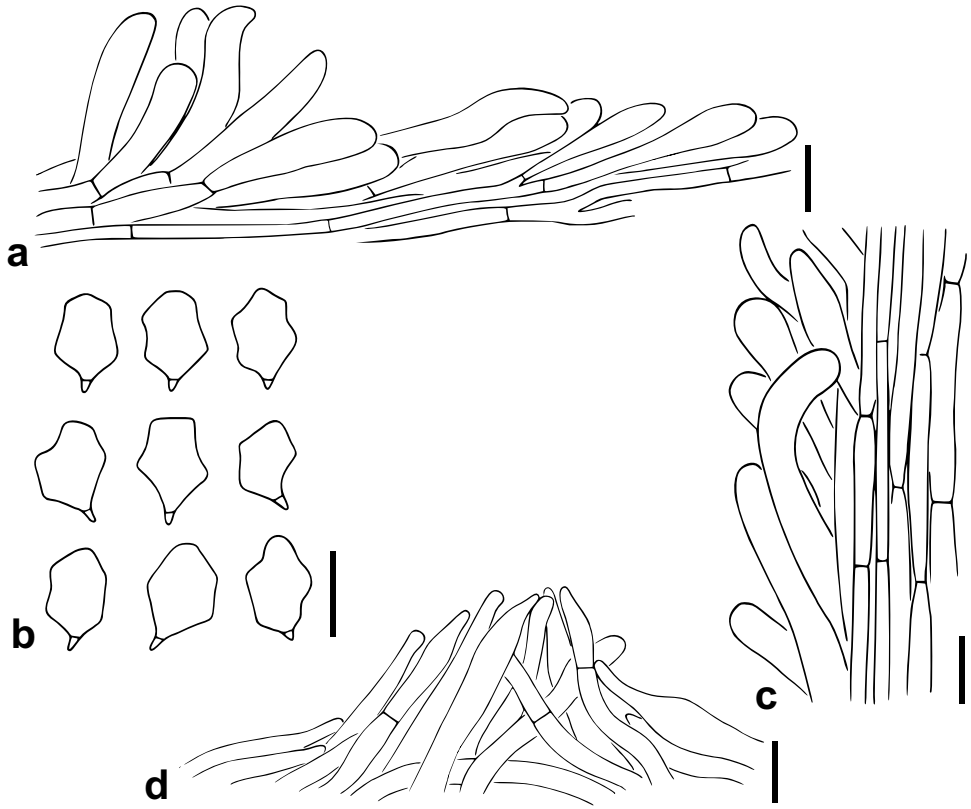

Fig. 34 Microscopic structures of *Entoloma caeruleomarginatum* (KaiR535, holotype): **a** pileipellis, bar = 20 µm; **b** basidiospores, bar = 10 µm; **c** stipitipellis, bar = 20 µm; **d** cheilocystidia, bar = 20 µm

4-spored, with up to 5.5 µm long sterigmata. Lamellar edge sterile, cheilocystidia predominantly broadly fusiform, sometimes lageniform, more rarely irregularly cylindrical to moniliform, 25–55 × 8.0–14.0 µm. Hymenophoral trama regular, formed by subcylindrical cells, somewhat constricted at septae, 55–275 × 3–20 µm. Pileipellis a cutis with transitions to a trichoderm, composed of broadly cylindrical to inflated end cells, 40–140 × 10.5–19.0 µm, upper pileipellis cells 43–110 × 5.0–15.0 µm, and a subpellis of narrower cells, 4.0–7.0 µm wide, pigment intracellular as clumps, violet in water, soluble and then brownish in KOH. Stipitipellis similar to pileipellis, composed of subcylindrical to somewhat inflated cells, 50–180 × 7.5–15.0 µm, with emerging end cells in bundles and below a layer of narrower hyphae, 4.0–7.5 µm wide. Caulocystidia absent. Oleiferous hyphae present in the trama. Brilliant granules abundant. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps solitary to scattered in a small group in *Quercus*- and *Alnus*-dominated montane forests between 2250 and 2300 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, approximately 2300 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, E. Heinemann, KaiR614 (M).

Notes: *Entoloma arcanum* is characterised by dark, blackish blue basidiocarps and a sterile lamellar edge with mainly fusiform cheilocystidia. It is phylogenetically relatively close to a specimen identified as *E. fuscosquamosum* Hesler (Fig. 30). This species has basidiocarps with more greyish colours, larger basidiospores (9–13 × 6–7.5 µm), and cylindric-capitate cheilocystidia (Hesler 1967) or no cheilocystidia at all (Noordeloos 1988). The *RPB2* sequence of *E. arcanum* is close to a sequence (KR233903) labelled *E. trichomatum* (Largent) Noordel. & Co-David with a *p*-distance of 3%. This species is morphologically similar to *E. arcanum* but differs by clavate to cylindrical cheilocystidia. *Entoloma trichomatum* is known from coniferous forests in western North America (Largent 1994), while *E. arcanum* was found in tropical montane forests with broadleaved trees.

Entoloma caeruleomarginatum Reschke, Manz, & Noordel., sp. nov., Figs. 33 and 34

Mycobank number: MB840627.

Typification: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′27.3″ W 82°24′34.3″, 1660 m asl., montane forest dominated by *Quercus* spp., 14 June 2017, K. Reschke and M. Cuevas, KaiR535, holotype (UCH11744), isotype (M).

Etymology: caeruleus (Latin) = dark blue, margo (Latin) = edge; refers to the dark blue lamellar edge.

Description: Basidiocarps collybioid to somewhat omphalinoid. Pileus 1.5–2.0 cm diameter, convex

Fig. 35 Basidiocarps and cellular structures as seen by SEM of *Entoloma griseocaeruleum*: **a, b** (KaiR534, holotype) bar = 10 µm; **c** (KaiR536); **d** (KaiR534, holotype) cheilocystidia, bar = 10 µm

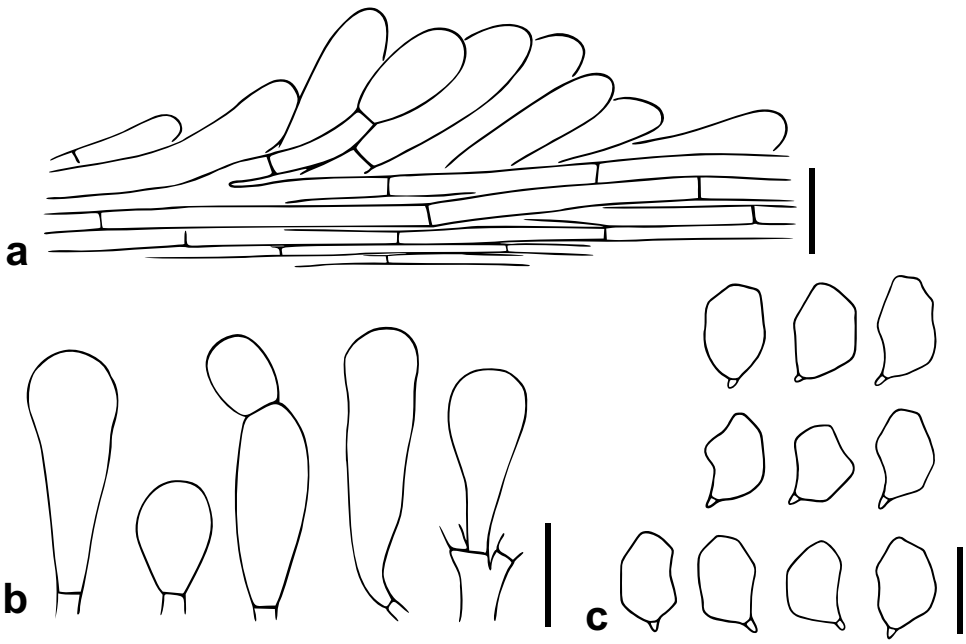

Fig. 36 Microscopic structures of *Entoloma griseocaeruleum* (KaiR534, holotype): **a** pileipellis, bar = 20 µm; **b** cheilocystidia, bar = 20 µm; **c** basidiospores, bar = 10 µm

umbilicate with incurved margin in young basidiocarps, expanded umbilicate with straight margin in older basidiocarps, bluish grey to greyish blue (20C2, 20D6), centre and squamules dark blue (20E4) to blackish blue (20F8), pileal surface squamulose, not translucently striate in young and fresh basidiocarps, but somewhat translucently striate at the margin of old and soaked basidiocarps. Lamellae broadly adnate, slightly emarginate to decurrent, segmentiform to arcuate, medium-spaced to rather distant, pale blue in young basidiocarps, later pinkish, edges blackish blue (20F6) serrulate. Stipe 4.0–5.0 × 0.30–0.35 cm, cylindrical, hollow, bluish grey to greyish blue (20D3, 21C6, 21C7, 21D7) with dark blue (20E5) fine, fibrillose squamules. Bluish tones discolouring to brown in old basidiocarps. Basal mycelium white, cottony. Odour indistinct, taste not tested.

Basidiospores 9.0–9.8–11.0 × 6.0–7.0–8.0 µm, $Q = 1.20–1.41–1.60$ ($n = 69$ spores of 3 specimens),

hendecahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, heterodiametrical, with 5–6 (7) pronounced, sometimes rather nodulose angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 34–48 × 8.0–11.0 µm, subclavate, hyaline, 4-spored, with up to 4.0 µm long sterigmata. Lamellar edge sterile, of the serrulatum-type, cheilocystidia 40–85 (135) × (5.5) 7.5–12.0 (17.0) µm, lageniform, subfusiform to cylindrical, sometimes subcapitate, with dark violet, intracellular pigment in clumps, soluble, and then becoming brown in KOH. Hymenophoral trama regular, formed by long, cylindrical to slightly fusiform cells, 55–175 × 6.0–16.0 µm. Pileipellis a cutis with transitions to a trichoderm, especially towards centre, composed of clavate, sometimes fusiform end cells, 70–210 × 13–26 µm, with violet, intracellular pigment, cells narrower, 6.0–12.0 µm wide, towards pileitrama, cylindrical to slightly fusiform. Stipitipellis similar to pileipellis, composed of cylindrical cells, 60–210 × 4.0–7.5 (9.5) µm, with subcylindrical to somewhat fusiform terminal cells, 75–150 × 10.5–16.0 µm. Oleiferous hyphae absent or not distinctive. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps found solitary in a *Quercus*-dominated montane forest between 1650 and 1700 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′26.9″ W 82°24′34.4″, 1670 m asl., montane forest dominated by *Quercus* spp., 15 June 2018, C. Manz and F. Hampe, CME3 (M); ibid., 24 June 2018, C. Manz and F. Hampe, CME11 (M).

Notes: *Entoloma caeruleomarginatum* belongs to the clade of *E. serrulatum* and closely related species. It is characterised by basidiocarps with a dark blue pileus, blue serrulate lamellar edges, a fibrillose-squamulose stipe surface, and heterodiametrical basidiospores with an average length of approximately 10 µm. The European *E. serrulatum* is morphologically very similar and hard to distinguish. The latter, however, is widely distributed and common in northern hemisphere temperate to boreal grasslands. It is phylogenetically rather distant with a *p*-distance of 10.5% in the ITS sequences. For this reason, we consider them semi-cryptic species, separated by ecological and geographical characters as well as molecular sequence data. Both, *E. subserrulatum* (Peck) Hesler and *E. subcaesiocinctum* Xiao-Lan He & W.H. Peng are phylogenetically closer to *E. caeruleomarginatum* based on ITS/LSU-data than *E. serrulatum* (Fig. 30). *Entoloma subserrulatum* differs by basidiocarps with a pale and translucently striate pileus (Hesler 1967). *Entoloma subcaesiocinctum* differs from *E. caeruleomarginatum* by basidiocarps with a pale pileus and by smaller basidiospores (He et al. 2017). *Entoloma proximum* Horak, described from Argentina, differs by basidiocarps with an appressed fibrillose to subsquamulose pileal surface, slightly larger basidiospores, and relatively short, cylindrical to subclavate cheilocystidia (Horak 1978).

Entoloma griseocaeruleum Reschke, Manz & Noordel., sp. nov., Figs. 35 and 36

Mycobank number: MB840630.

Typification: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′26.1″ W 82°24′29.9″, 1,650 m asl., montane forest dominated by *Quercus* spp., 14 June 2017, K. Reschke, KaiR534, holotype (UCH9185), isotype (M).

Etymology: griseus (Latin) = grey, caeruleus (Latin) = dark blue; refers to the colour of the basidiocarps.

Description: Basidiocarps collybioid to somewhat omphalinoid. Pileus 1.5–3.5 cm diameter, hemispherical to convex with depressed to umbilicate centre, margin initially incurved, later straight, initially greyish blue to bluish grey (20B3, 20B4, 20B5, 20B6) with dark blue to blackish blue (20E6, 20F6) squamules, blue tones becoming brownish while ageing, pileal surface squamulose, squamulose-velutinous in the centre, slightly sulcate-rimose to distinctly sulcate almost to the centre, not hygrophanous. Lamellae broadly adnate, sometimes with decurrent tooth, segmentiform, rather distant, white with greyish tinge, becoming pink at maturity, edges even and concolorous. Stipe 3.0–4.5 × 0.15–0.30 cm, cylindrical, hollow, greyish blue to bluish grey (20D5, 20D4, 20D3), blue tones becoming brownish, innately fibrillose to polished, rarely finely flocculose. Basal mycelium white, cottony, with some short and fine rhizomorphs, often staining red when touched and then remaining reddish also in dried specimens. Odour indistinct, taste not tested.

Basidiospores 9.0–10.1–11.5 × 6.0–6.8–7.5 µm, *Q* = 1.35–1.49–1.65 (*n* = 96 spores of 4 specimens), hendecahedroid, composed of an adaxial facet (D), a pair of apico-adaxial facets (AD), an apical facet (A), an abaxial facet (B), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, heterodiametrical, with 5–6 blunt angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 25–31 (40) × 8.5–10.0 µm, clavate, hyaline, predominantly 4-spored, with up to 6.0 µm long sterigmata, few 2-spored. Lamellar edge heterogeneous, cheilocystidia scattered between basidia, rather inconspicuous, broadly clavate to cylindrical, often subcapitate, (19) 25–63 (75) × 12.0–15.0 µm. Hymenophoral trama regular, formed by cylindrical to fusiform cells, 60–310 × 5–25 (33) µm. Pileipellis a cutis with transitions to a trichoderm, a trichoderm at the very centre, composed of relatively short and wide end-cells, 55–140 × 15–30 (33) µm, upper

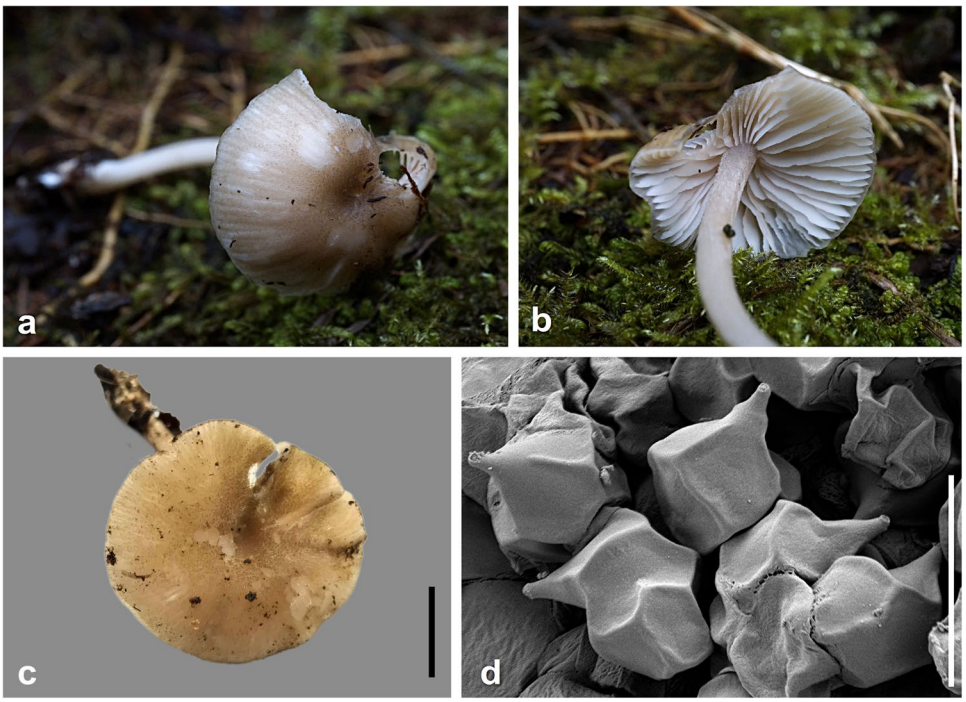

Fig. 37 Basidiocarps and cellular structures as seen by SEM of *Entoloma melleosquamulosum*: **a, b** (KaiR638); **c** (CME16, holotype) bar = 1 cm; **d** (CME16, holotype) bar = 10 µm

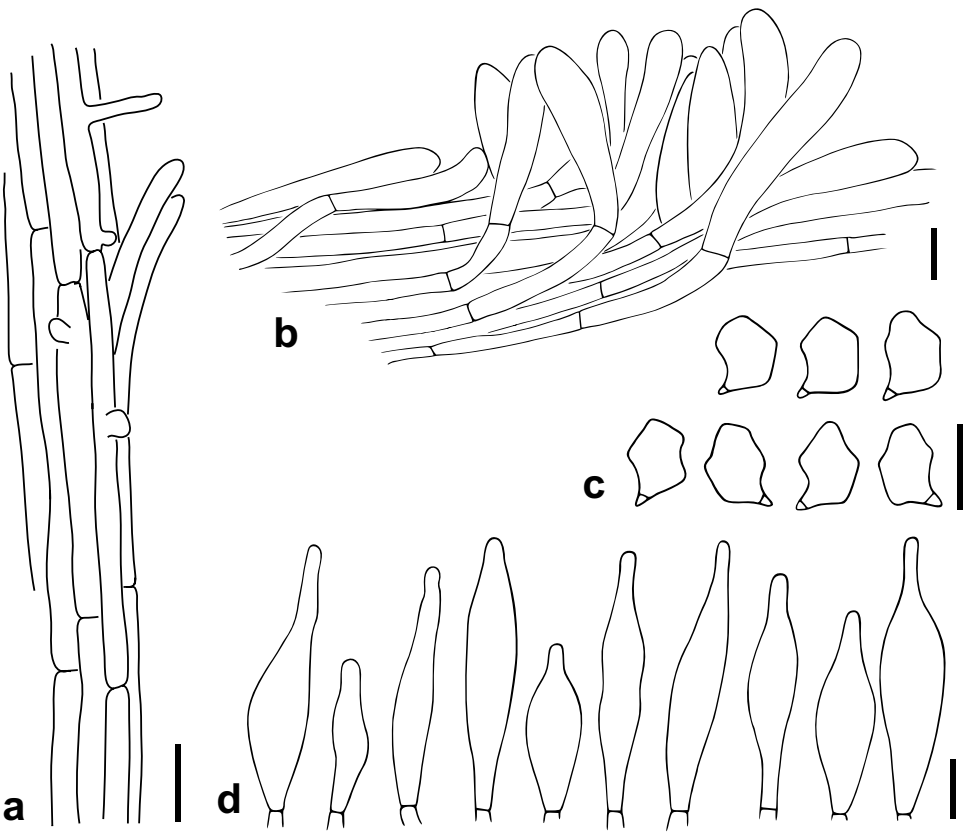

Fig. 38 Microscopic structures of *Entoloma melleosquamulosum* (KaiR413, holotype): **a** stipitipellis with outgrowths, bar = 10 µm; **b** pileipellis, bar = 20 µm; **c** basidiospores, bar = 10 µm; **d** cheilocystidia, bar = 10 µm

Fig. 39 Basidiocarps and basidiospore as seen by SEM of *Entoloma microserrulatum*: **a, b** (KaiR413, holotype); **c** (KaiR664); **d** (KaiR413, holotype) bar = 10 µm

pileipellis cells 43–110 × 5.0–10.0 µm, and a subpellis of narrower cells, 3.0–7.0 µm wide, pigment intracellular as clumps, violet in water, soluble and then brownish in KOH. Stipitipellis a cutis composed of narrow, cylindrical cells, 105–210 (330) × 3.0–6.0 µm. Caulocystidia absent. Oleiferous hyphae present in the trama, but rare. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps solitary to scattered in a small group in *Quercus*-dominated montane forests between 1650 and 2350 m asl. in Chiriquí, Panama.

Additional specimens examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′32.3″ W 82°24′50.3″, 1650 m asl., montane forest dominated by *Quercus* spp., 14 June 2017, K. Reschke, KaiR536 (M); near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′39.7″ W 82°34′55.0″, 2340 m asl., montane forest dominated by *Quercus* spp., 19 June 2018, C. Manz and F. Hampe, CME8 (M); Bajo Boquete, Finca Lerida, N 08°49′10.3″ W 82°29′09.2″, 1820 m asl., montane forest with *Quercus seemannii* and other *Quercus* spp., 28 June 2018, C. Manz and F. Hampe, CME13 (M).

Notes: *Entoloma griseocaeruleum* is a typical representative of subg. *Cyanula* by its blue colours, deeply striate, minutely squamulose pileus, and white lamellae. It forms a well-supported clade together with *E. longistriatum* (Peck) Noordel. and *E. sarcitulum* (P.D. Orton) Arnolds (Fig. 30). These species have brown basidiocarps, which do not look like those of *E. griseocaeruleum*. *Entoloma yanacolor* A. Barili et al., described from Ecuador, has basidiocarps with blue tones according to the picture of the holotype specimen (Crous et al. 2018). This was, however, described as black, resembling *E. corvinum* (Kühner) Noordel., and with a smooth, waxy pileus surface. No species similar to *E. griseocaeruleum* were found in Hesler (1967), Horak (1978, 1982), Largent (1994), and Noordeloos (1992, 2004).

Entoloma melleosquamulosum Reschke, Manz & Noordel., sp. nov., Figs. 37 and 38

Mycobank number: MB840939.

Typification: PANAMA, CHIRIQUÍ: near Hornito, N 08°45′11.1″ W 82°14′22.6″, 1210 m asl., submontane tropical forest dominated by *Oreomunnea mexicana* in transition to montane *Quercus*-dominated forest, 29 June 2018, C. Manz and F. Hampe, CME16, holotype (M).

Etymology: melleus (Latin) = honey, squamulosus (Latin) = minutely scaly; refers to the colour of the pileus and the structure of its surface.

Description: Basidiocarps collybioid. Pileus 2.3–2.7 cm diam., convex umbilicate in young basidiocarps, expanding to plane umbilicate, with straight, slightly uneven to undulating margin, beige to brownish orange (4C3, 5C4, 5C5), darker, yellowish brown towards the centre (5D5, 5E5), pileal surface finely scaly all over, but most distinct in the centre, indistinctly translucently striate at the very margin to distinctly translucently striate at about half the centre. Lamellae sinuate to adnate, segmentiform to ventricose, medium-spaced to rather distant, initially greyish white, later pink, with uneven, slightly serrate to irregularly undulating, concolorous to somewhat paler edges. Stipe 4.0–5.0 × 0.3 cm, cylindrical, slightly broader towards base, hollow, pale yellow to yellowish white (4A3, 4A2),

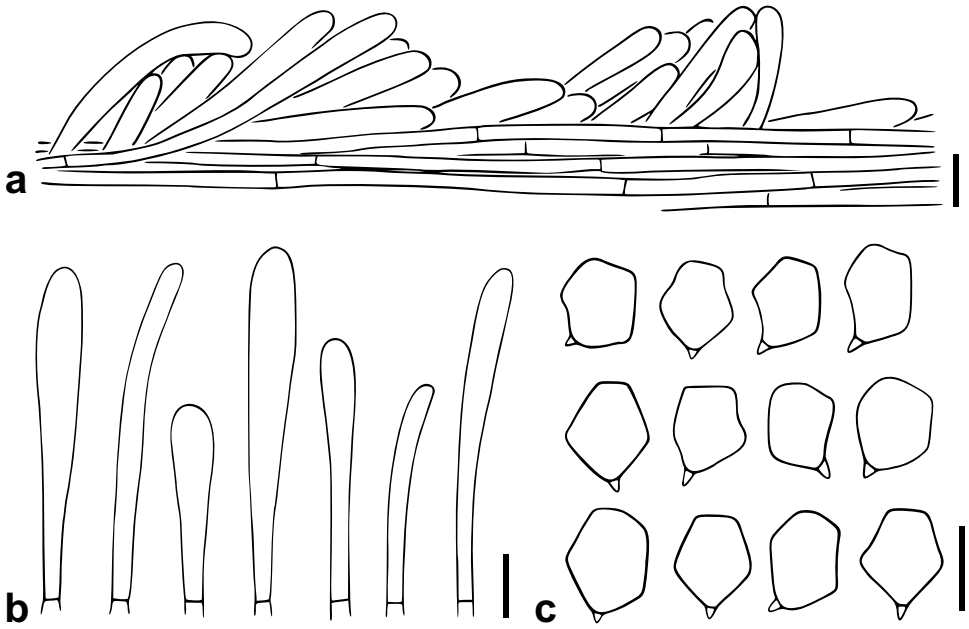

Fig. 40 Microscopic structures of *Entoloma microserrulatum* (KaiR413, holotype): **a** pileipellis, bar = 20 µm; **b** cheilocystidia, bar = 20 µm; **c** basidiospores, bar = 10 µm

fibrillose, apical pruinose to finely scaly. Basal mycelium white, cottony, with some short and fine rhizomorphs. Odour indistinct to slightly fruity, taste not tested.

Basidiospores 8.5–9.4–10.5 × 6.0–6.8–8.0 µm, Q = 1.20–1.38–1.55 (n = 58 spores of 2 specimens), dodecahedroid, composed of an adaxial facet (D), a pair of apicoadaxial facets (AD), an apical facet (A), two abaxial facets (B1, B2), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, heterodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 26–35 × 8.0–10.0 µm, clavate, hyaline, predominantly 4-spored, with small sterigmata, 1.0–2.0 µm, rarely up to 3.0 µm long, 2-spored and 1-spored basidia rather frequent. Lamellar edge sterile. Cheilocystidia 23–64 × 6.5–10.0 (15.0) µm, lageniform, hyaline. Hymenophoral trama regular, formed by cylindrical cells, 65–200 × 4.0–19.0 µm. Pileipellis a cutis with transitions to a trichoderm composed of rather broad, cylindrical cells, 50–130 × (11) 14–21 µm, pigment intracellular, soluble in KOH. Stipitipellis a cutis composed of long, cylindrical cells, 40–250 × 3.0–6.0 µm, rather loosely arranged marginally, with some clumped erect hyphae and scattered outgrowths at the apex of the stipe, pigment faint, intracellular. Caulocystidia absent. Oleiferous hyphae present in the trama. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps solitary in transitional state of submontane *Oreomunnea mexicana*-dominated to montane *Quercus*-dominated forest and *Quercus*-dominated montane forest between 1200 and 1750 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, PNVB, Sendero Culebra, N 08°50′56.7″ W 82°28′54.6″, 1,730 m asl., montane forest dominated by *Quercus* spp., 22 June 2017, K. Reschke, J. Rodríguez, B. Wergen, KaiR638 (UCH11746, M).

Notes: *Entoloma melleosqamulosum* is characterised by basidiocarps with a honey-coloured, squamulose pileus, basidia with small sterigmata, rather small basidiospores, and lageniform cheilocystidia. It has a relatively isolated position in the molecular phylogenetic analysis (Fig. 30). *Entoloma olivaceosquamosum* Hesler is a somewhat similar species; however, its basidiocarps differ from those of *E. melleosquamosum* by larger squamules, olivaceous to greenish tones of the pileus and larger cheilocystidia (Hesler 1967; Noordeloos 1988). Basidiocarps of *Entoloma mediterraneense* Noordel. & Hauskn. have a somewhat similar habit but show ephemeral blue tones, form smaller basidiospores and clavate cheilocystidia (Noordeloos and Hausknecht 2002). In addition, this species is phylogenetically distant from *E. melleosquamulosum* (Fig. 30). No similar species were found in Horak (1978, 1982) and Largent (1994).

Entoloma microserrulatum Reschke & Noordel., sp. nov., Figs. 39 and 40

Mycobank number: MB840625.

Typification: PANAMA. CHIRIQUÍ: near Bajo Boquete, PNVB, Sendero Culebra, N 08°50′56.3″ W 82°28′54.9″, 1730 m asl., montane forest with abundant *Quercus* spp., 6 June 2017, K. Reschke, KaiR413, holotype (UCH11742), isotype (M).

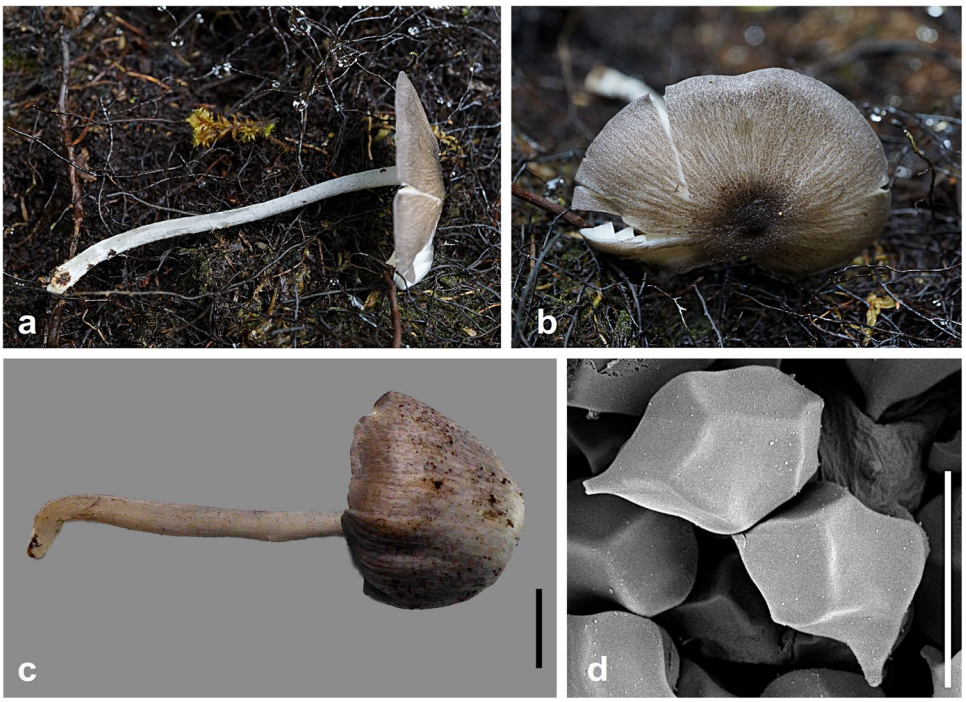

Fig. 41 Basidiocarps and basidiospores as seen by SEM of *Entoloma* cf. *violaceobrunneum*: **a, b** (KaiR632); **c** (CME2) bar = 1 cm; **d** (KaiR632) bar = 10 µm

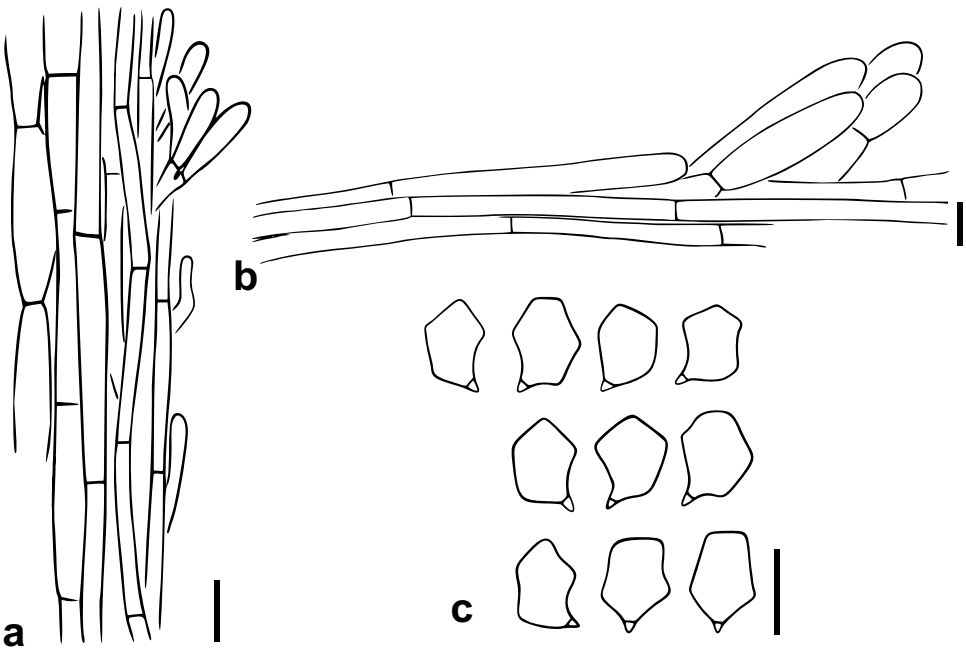

Fig. 42 Microscopic structures of *Entoloma* cf. *violaceobrunneum* (KaiR632): **a** stipitipellis with caulocystidia, bar = 20 µm; **b** pileipellis, bar = 25 µm; **c** basidiospores, bar = 10 µm

Etymology: mikros (Greek) = small; refers to the small basidiocarps and the serrulatum-type lamellar edge.

Description: Basidiocarps collybioid. Pileus 0.6–1.0 cm diameter, hemispherical to convex umbilicate, margin incurved in young basidiocarps and remaining so, violet-brown (10F5) in young basidiocarps, violet tinges soon discolouring to brown, pileal surface squamulose, not translucently striate. Lamellae broadly adnate to slightly decurrent, segmentiform, medium-spaced to rather distant, whitish in young basidiocarps, later pinkish, with dark violet-brown, serrulate edges. Stipe 1.2–1.5 × 0.10–0.15 cm, cylindrical, white, greyish yellow (3B5) to olive yellow (3C6), smooth to finely pruinose, shining. Basal mycelium white, with dense, short, hirsute rhizomorphs. Odour indistinct, taste not tested.

Basidiospores 8.5–10.4–12.5 × 7.0–8.5–10.0 µm, $Q = 1.10–1.23–1.35$ ($n = 53$ spores of 2 specimens), octahedroid, composed of an adaxial facet (D), a single apico-adaxial facet (sAD), an apical facet (A), an abaxial facet (B), and two

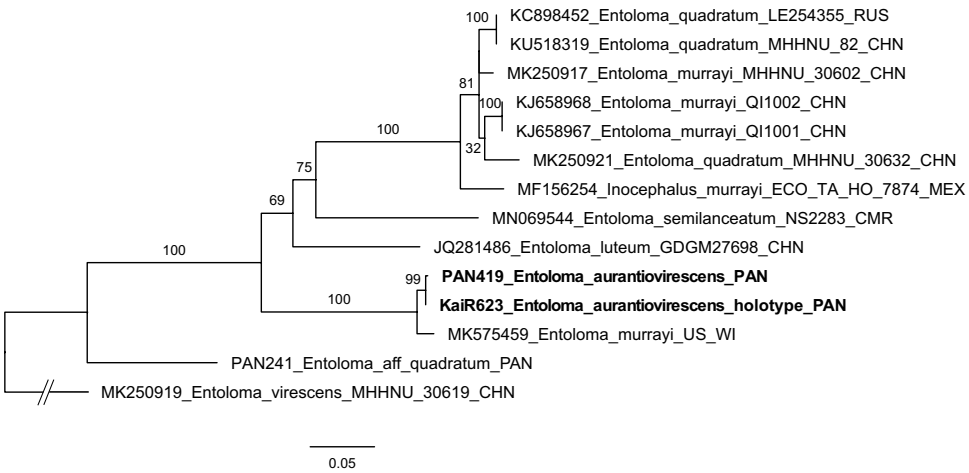

Fig. 43 Maximum Likelihood phylogram of species of subg. *Cubospora* based on ITS, rooted to *E. virescens*, bootstrap values above or below branches, bar = estimated changes/nucleotide

Fig. 44 Basidiocarps, and basidiospores as seen by SEM of *Entoloma aurantiovirescens* **a** (KaiR623, holotype) **b** (PAN419) picture by H. Lotz-Winter **c**, **d** (KaiR623, holotype) bar = 10 µm

pairs of lateral facets (L1–L2), of which the basal pair (L2) forms a dièdre basal, broadly heterodiametrical, with 5, rarely 4, pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 33–38 × 10.0–16.5 µm, clavate, hyaline, 2-spored, with up to 6.5 µm long sterigmata, rarely 1-spored. Lamellar edge sterile, of the serrulatum-type, cheilocystidia clavate, 55–120 × 6.0–15.0 µm, with purplish brown, intracellular pigment. Hymenophoral trama regular, formed by cylindrical to somewhat inflated cells, 35–180 × 4.0–15.0 µm. Pileipellis a cutis with transitions to a trichoderm, end cells 35–115 (200) × 8.0–14.0 µm, pigment intracellular, brown in KOH. Stipitipellis a cutis composed of narrow, cylindrical cells, 45–125 × 2.5–5.5 µm. Caulocystidia absent. Pigment not soluble in 5% KOH. Oleiferous hyphae present in the trama. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps solitary to scattered in a small group in *Alnus acuminata*-dominated montane forest between 1650 and 1750 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, Jaramillo Arriba, El Musgo, N 08°47′26.9″ W 82°24′32.9″, 1660 m asl., montane forest with abundant *Quercus* spp., 25 June 2017, K. Reschke, KaiR664 (M).

Notes: *Entoloma microserrulatum* occupies a basal position in the subgenus *Cyanula* and is very distant from all other species of *Cyanula* included in the analysis (Fig. 30). It is characterised by minute basidiocarps with purplish brown

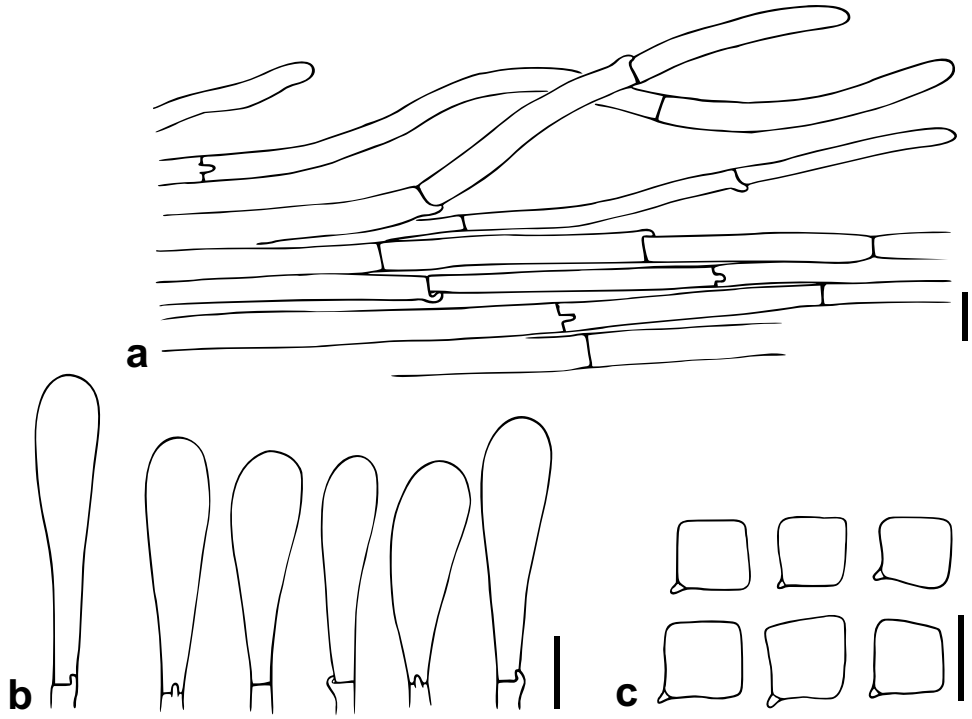

Fig. 45 Microscopic structures of *Entoloma aurantiovirescens* (KaiR623, holotype) **a** pileipellis, bar = 25 µm **b** cheilocystidia, bar = 20 µm **c** basidiospores, bar = 10 µm

colour, a dark violet-brown serrulatum-type lamellar edge and 2-spored basidia. This set of features is unique within the subgenus *Cyanula*. No similar species were found in literature.

Entoloma* cf. *violaceobrunneum Hesler, Beih. Nova Hedwigia 23: 51 (1967), Figs. 41 and 42

≡ *Leptoniella alachuana* Murrill, Proc. Fla. Acad. Sci. 7: 117 (1945).

non *Entoloma alachuanum* Murrill, Mycologia 33: 443 (1941).

Description: Basidiocarps collybioid. Pileus 2.8–3.7 cm diameter, broadly conical when young becoming low convex, somewhat depressed in centre with broad papilla, with straight and even to slightly uneven margin, initially bluish grey, violet-grey to grey (16E2, 23B1, 23B2, 23C1, 23C2) and darker bluish grey to violet-grey in the centre (16F2, 23D2, 23D3), bluish and violet tones fading to brownish tones while ageing, with squamulose surface, slightly radially sulcate almost to the centre. Lamellae broadly adnate to emarginate, medium-spaced to rather distant, segmentiform, white, with slightly undulating and concolorous edges. Stipe 5.0–6.0 × 0.25–0.30 cm, cylindrical, hollow, dull blue to grey (23A1, 23B1, 23C1), overlaid by whitish, fibrillose floccules. Basal mycelium white, sparse. Odour indistinct, taste not tested.

Basidiospores 9.5–10.2–11.5 × 7.0–7.7–8.5 µm, $Q = 1.20–1.33–1.45$ ($n = 43$ spores of 2 specimens), hendecahedroid, composed of an adaxial facet (D), a pair of apicoadaxial facets (AD), an apical facet (A), an abaxial facet (B), and three pairs of lateral facets (L1–L3), of which the basal pair (L3) forms a dièdre basal, often with reduced apical facet, heterodiametrical, with 5–6 pronounced angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 35–40 × 10.0–13.5 µm, clavate to subclavate, hyaline, predominantly 4-spored, with up to 4.5 µm long sterigmata, rarely 2-spored. Lamellar edge fertile, hymenial cystidia absent. Hymenophoral trama regular, mainly formed by long, cylindrical cells, 70–250 × 4.0–9.0 µm, with some larger cells, 300–350 × 12.0–18.0 µm. Pileipellis a cutis with transitions to a trichoderm, with rather wide end cells, 40–125 × 13.5–27 µm, pigment diffusely intracellular as well as in clustering granules and clumps. Stipitipellis a cutis of narrow, cylindrical cells, 30–125 × (3.0) 4.5–7.0 µm. Caulocystidia cylindrical to clavate, 20–55 × 6.0–8.0 µm. Oleiferous hyphae present in the trama. Clamp connections absent from any part of the basidiocarp.

Habitat: Basidiocarps found solitary in *Quercus*-dominated montane forest between 1650 and 1850 m asl. in Chiriquí, Panama.

Specimens examined: PANAMA. CHIRIQUÍ: near Bajo Boquete, PNVB, Sendero Culebra, N 08°50′44.5″ W 82°28′54.2″, 1680 m asl., montane forest dominated by *Quercus* spp., 22 June 2017, K. Reschke and J. Rodriguez, B. Wergen, KaiR632 (M); Bajo Boquete, Finca Lerida, N 08°49′10.3″ W 82°29′09.2″, 1820 m asl., montane forest with *Quercus seemannii* and other *Quercus* spp., 13 June 2018, T.A. Hofmann, CME2 (M).

Notes: *Entoloma* cf. *violaceobrunneum* is characterised by a bluish grey to violet-grey pileus that soon becomes

Fig. 46 Basidiocarps of *Entoloma* cf. *indigoferum*: **a** (KaiR509); **b** (KaiR678)

brownish, and the absence of cheilocystidia. It is phylogenetically relatively close to *E. griseocyanum* with a *p*-distance of 6% in the ITS2. This species is common in oligotrophic grasslands in Europe and forms basidiocarps with a greyish brown pileus and a blue stipe. *Entoloma violaceobrunneum* was described by Murrill (1944), as *Leptoniella alachuana*, from a *Quercus* forest in Florida. The pileus of this species was described as shining in fresh basidiocarps, which was not the case in the specimens from Panama. However, new collections and DNA sequence data are necessary to resolve the identity of *E. violaceobrunneum*.

Subgenus Cubospora *Karstedt* et al. (Fig. 43)

The subgenus *Cubospora* was recently erected by Karstedt et al. (2019) for species with a convex to conical pileus, cuboid basidiospores, abundant clamp connections, and often abundant oily contents. They were formerly placed in subgenus *Inocephalus* Noordel. Most species of the subgenus *Cubospora* have a tropical to subtropical distribution (Horak 1976, 1977; Romagnesi and Gilles 1979) and few occur in temperate/boreal habitats. Several species of the widely distributed complex of *E. quadratum* (Berk. & M.A. Curtis) E. Horak and *E. murrayi* (Berk. & M.A. Curtis) Sacc. & P. Syd. were found in Panama. One of these is described here.

Entoloma aurantiovirescens Reschke, Lotz-Winter, & Noordel., sp. nov., Figs. 44 and 45

Mykobank number: MB840940.

Typification: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, N 08°53′49″ W 82°35′03.2″, 2330 m asl., montane forest dominated by *Quercus* spp., 21 June 2017, K. Reschke, KaiR623, holotype (M).

Etymology: aurantium (Latin) = gold, virescent (Latin) = becoming green; refers to colour and staining of the basidiocarps.

Description: Basidiocarps mycenoid. Pileus 2.0–4.0 cm diameter, conical to broadly conical with distinct, rather acute papilla, with straight, undulating margin, yellowish orange (4A8, 4B8, 4B7), pileal surface appressed fibrillose, almost smooth when wet, not translucently striate when dry, but translucently striate at the margin up to 1/3 of the radius in wet specimens, not hygrophanous, staining greyish green (25C7, 25D7) while ageing or after being touched. Lamellae adnexed, segmentiform to ventricose, medium-spaced to rather distant, slightly transvenose, orange (5A8, 5B8), with uneven, finely fimbriate and somewhat paler edges. Stipe 6.5–10.0 × 0.25–0.50 cm, cylindrical, slightly broader towards base, solid to stuffed, basically coloured orange-yellow to greyish yellow (4A6, 4A7, 4B6, 4B7), covered by appressed whitish fibrils, which stain greyish green (25C7, 25D7) while ageing or touched. Basal mycelium white, with some short rhizomorphs. Odour indistinct, taste not tested.

Basidiospores 8.5–9.5–10.5 × 8.0–9.0–10.0 µm, Q = 1.01–1.05–1.13 (n = 41 spores of 2 specimens), cuboid with dièdre basal, with 4 angles in outline, weakly pigmented yellowish pink, somewhat thick-walled. Basidia 48–60 × 10.0–13.5 µm, subclavate, hyaline, 4-spored, sterigmata up to 6.0 µm long. Lamellar edge sterile, cheilocystidia clavate, 50–85 (110) × 11.0–18.0, thin walled. Hymenophoral trama regular, formed by rather long, cylindrical cells, 90–350 × 6.0–23 µm. Pileipellis a loose cutis composed of cylindrical cells, 115–250 × 5.0–17.0 µm, with intracellular, yellowish pigment. Stipitipellis a cutis composed of long, cylindrical

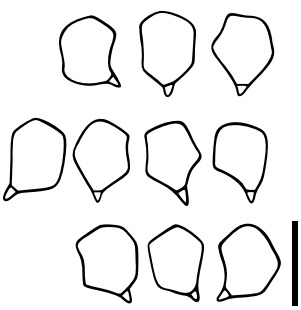

Fig. 47 Basidiospores of *Entoloma* cf. *indigoferum* (KaiR509), bar = 10 µm

cells, 160–300×5.0–11.0 µm, with intracellular, yellowish pigment. Caulocystidia absent. Oily contents abundant, especially in hyphae of the lamellae, with yellowish pigment. Clamp connections abundant in all parts of the basidiocarp.

Habitat: Basidiocarps solitary to gregarious in a small group in *Quercus*-dominated montane forest at about 2300 m asl. in Chiriquí, Panama.

Additional specimen examined: PANAMA. CHIRIQUÍ: near Cerro Punta, Entre Ríos, Montaña Azul, PILA, about 2300 m asl., montane forest dominated by *Quercus* spp., 28 July 2015, H. Lotz-Winter, PAN419 (UCH11748, M).

Notes: *Entoloma aurantiovirescens* belongs to the species complex of *E. quadratum* and *E. murrayi* s.l. Its basidiocarps are characterised by salmon colour, a conical, papillate pileus, cuboid spores, and a green staining reaction while ageing or after being touched. The typical habit of basidiocarps of *E. quadratum* is similar. However, green stains have not been reported for *E. quadratum* and are typical for *E. virescens* and its allies. These differ from *E. aurantiovirescens*, however, by a blue colour of pileus and stipe and are phylogenetically distant from the *E. quadratum* complex (Karstedt et al. 2019). A sequence annotated *E. murrayi* is phylogenetically close to those of *E. aurantiovirescens* (Fig. 45), with a *p*-distance of 4.7–5.0% in the ITS. However, *E. murrayi* forms straw yellow basidiocarps which do not stain greenish (Berkeley and Curtis 1859).

Section Calliderma *(Romagn.) Noordel*

The section *Calliderma* in its traditional sense includes species with a hymeniderm to a pallisadic trichoderm and rather robust basidiocarps of various colours (Romagnesi 1974; Romagnesi and Gilles 1979; Noordeloos 2004). Apparently, it is not monophyletic (He et al. 2012). We consider this section here with a narrow concept, only including species with tricholomatoid basidiocarps, blue colours, pileipellis a hymeniderm to trichoderm, iso- to subisodiametrical basidiospores, rather long and narrow basidia, intracellular pigment, and abundant clamp connections. Several species that fit into this concept have been described in recent years, often with a tropical to subtropical distribution (Manimohan et al. 2006; Gates and Noordeloos 2007; Karstedt and Capelari 2010; Aime et al. 2010; Eyssartier et al. 2012; Largent et al. 2014). It is, however, at the moment not possible to give a phylogenetic overview of this group because DNA sequence data of authentical specimens of *E. callidermum* (Romagn. ex Romagn.) Noordel., the type species of sect. *Calliderma*, as well as many other species which potentially belong into this section is lacking. The occurrence together with species of Sarcolaeonaceae and *Uapaca* (Phyllantaceae) in Madagascar (Eyssartier et al. 2012) as well as *Podocarpus* sp. (Podocarpaceae) in Panama suggests that the species of this clade are ectomycorrhizal.

Entoloma* cf. *indigoferum (Ellis) Sacc., Sylloge Fungorum 5: 688 (1887), Figs. 46 and 47

≡ *Agaricus indigoferus* Ellis, Bull. Torrey Bot. Club 6: 75 (1876).

Description: Basidiocarps tricholomatoid. Pileus 3.5–7.0 cm diameter, convex to plane, sometimes irregularly depressed in old basidiocarps, margin incurved in young basidiocarps, long remaining so, becoming straight in old basidiocarps, deep blue (19D8, 19E8), pileal surface velvety, not translucently striate, not hygrophanous. Lamellae emarginate, medium-spaced to rather distant, initially segmentiform, ventricose at expanded pilei, white to cream, becoming pink, with undulating and concolorous edges and transvenose sides. Stipe 3.0–6.0 × 1.0–1.8 cm, cylindrical to clavate or fusiform, solid to somewhat stuffed, deep blue (19D8, 19E8) with white longitudinal striations, appressed fibrillose. Basal mycelium white, cottony with some rhizomorphs in the upper part of the base, densely hirsute from numerous rhizomorphs downwards. Odour indistinct, taste not tested.

Basidiospores 7.0–7.7–8.5 × 5.5–6.4–7.0 µm, $Q = 1.05–1.20–1.35$ ($n = 51$ spores of 2 specimens), subisodiametrical to broadly heterodiametrical, with predominantly 5, sometimes 4, pronounced angles, weakly pigmented yellowish pink, somewhat thick-walled. Basidia (45) 50–60 (70)×10.0–11.5 µm, clavate, hyaline, 4-spored, sterigmata up to 6.0 µm long, with clamp connections. Hymenial cystidia absent. Hymenophoral trama regular, mainly formed by cylindrical cells, 30–100×4.0–7.0 µm, with some oleiferous hyphae composed of cells of 150–400×5.0–7.0 µm. Pileipellis a palisadic trichoderm, with blue, intracellular pigment, soluble in KOH. Stipitipellis a cutis composed of rather short, cylindrical cells, 30–60×2.5–6.5 µm, with subcylindrical, clavate to somewhat lageniform caulocystidia, 15–50×4.5–12.5 µm. Clamp connections abundant in all parts of the basidiocarp, sometimes degenerated at the base of basidia.

Habitat: Basidiocarps in small groups close to a large *Podocarpus* sp. in an *Alnus acuminata*-dominated montane forest at about 2400 m asl. in Chiriquí, Panama. Possibly ectomycorrhizal with *Podocarpus* sp.

Specimens examined: PANAMA. CHIRIQUÍ: Cerro Punta, Las Nubes, PILA, Sendero Cascada, N 08°53′58.5″ W 82°37′11.1″, 2390 m asl., montane forest dominated by *Alnus acuminata*, 11 June 2017, K. Reschke and J. Rodríguez, KaiR509 (UCH11739, M); ibid., 27 June 2017, K. Reschke, KaiR678 (M); ibid., 8 July 2015, J. Rodríguez, Y. Castillo, C. Rodríguez, JR59 (M).

Notes: All specimens of this species were collected at the same place and probably belong to the same individual. The basidiocarp of the specimen KaiR678 was immature. This species is characterised by tricholomatoid basidiocarps with a deep blue pileus, rather small basidiospores, and a palisadic

trichoderm as pileipellis. It is morphologically close or identical to *E. indigoferum*, which was described by Ellis (1876) from a swamp in New Jersey, USA. We have not studied authentical material of this species and molecular sequence data are not available for *E. indigoferum*. *Entoloma callidermum*, described by Romagnesi (1941, 1956) from Madagascar and Congo, is somewhat similar, but its basidiocarps are slenderer and were found in habitats very different from the one in Panama.

Discussion

The investigation of species of *Entoloma* from Panama revealed 17 species new to science; one species could be identified with certainty, and two further species are presented with uncertain identifications. Further specimens representing more than 30 additional species were not thoroughly studied due to limited material. Further fieldwork and investigation of specimens will increase the number of species known for Panama and will lead to many further species new to science.

Most species recorded for Panama belong to the subgenera *Cyanula*, *Entoloma*, *Alboleptonia*, and *Nolanea* and thereby show a pattern similar to *Entoloma* species diversity in temperate zones. Species of the section *Calliderma* as well as the subgenera *Cubospora* and *Inocephalus* are unknown from European temperate to boreal regions, but they are present in North America (Hesler 1967; Horak 1976; Largent 1994; Karstedt et al. 2019). This result is not surprising because most collections were made in montane locations around 2000 m asl. with temperatures similar to subtropical or temperate climate. However, such comparisons based on infrageneric groups of *Entoloma* are generally difficult to make at this moment, as the infrageneric classification of *Entoloma* is changing and the position of a large number of species needs to be reassessed. Two specimens representing two species of the subgenus *Cyanula* were found in lowland habitats at 40 and 120 m asl., respectively. Thereby, this subgenus is not only the most species rich but also the one with the most widely distributed species in the present study. Species of this subgenus have been reported northwards up to arctic habitats (Noordeloos 1984) and southwards to temperate regions in the southern hemisphere (Horak 2008; Noordeloos and Gates 2012).

The results of fieldwork in 2017 and 2018 show that primary forests in the mountains of Chiriquí harbour a higher diversity and abundance of species of *Entoloma* than disturbed lowland vegetation. This difference may be explained by different elevations or the degrees of disturbance. In Europe, the diversity and abundance of certain grassland fungi, like *Entoloma* spp., is used to evaluate the value of locations for nature conservation (McHugh et al. 2001; Newton et al. 2003; Griffith et al. 2013). Horak (1978) reported that in South American virgin forests, *Entoloma* can outnumber all other agaric genera in species richness at certain times of the year. Diversity of *Entoloma* spp. may be a promising marker for habitats and locations valuable for nature conservation; however, studies that would examine the possibility of a relationship between disturbance and diversity are needed.

Shape of basidiospores

Polyhedroid basidiospores are a unique and striking feature of *Entoloma* spp. The usefulness of their shape and base type for infrageneric classification has been disputed. Pegler and Young (1979) reported a "precise arrangement and order of development" of the facets for a given species. Kühner and Boursier (1929), however, stated that the variability of basidiospore shape rises together with the complexity of the spores. The present study confirmed the latter because a certain variability of the arrangement at the abaxial side was observed as well as there being two species, for which a general basidiospore type could not be determined. In addition to that, Co-David et al. (2009) and Baroni et al. (2011) presented basidiospores with irregular and incomplete facets. Therefore, a fixed number of facets can most likely not be determined for the basidiospores of every species. A possibility to describe such spores may be the use of ranges of numbers of facets, like x-hedroid to $(x+a)$-hedroid.

Romagnesi (1941) as well as Pegler and Young (1979) suggested that "simple" basidiospore shapes, like prismatic and cuboid ones, are more primitive than those with many facets. This is contradicted by the fact that molecular phylogenies consistently demonstrate that species with prismatic and cuboid basidiospores are located in several clades, but not in the basal one (Co-David et al. 2009; Karstedt et al. 2019). Considering the relatively large fraction of species with irregular and bumpy basidiospores in the basal clade (Co-David et al. 2009; Baroni et al. 2011), it is more likely that the basidiospores of the ancestral species of *Entoloma* had a rather rhodocyboid morphology, as proposed by Mazzer (1976). Cuboid and prismatic basidiospores are most likely derived from "complex" basidiospores through reduction of the number of facets. *Entoloma conferendum* is nested between species with heterodiametrical hepta- to hendecahedroid basidiospores in subg. *Nolanea*. Thus, its prismatic basidiospores are most likely derived from these basidiospores, similar to the frequently reduced basidiospores in *E. transitionisporum*. Regarding the small difference in ITS sequences between *E. paraconferendum* and *E. conferendum*, such reduction-driven evolution can obviously happen relatively rapidly. The cuboid basidiospore with dièdre basal is shared by all members of the subgenera *Cubospora* and *Cuboeccilia* (Karstedt et al. 2019). It remains unknown if this shape evolved more than once. Both subgenera, *Cyanula* and

Nolanea, share species with hendecahedroid basidiospores with dièdre basal. Whether this spore type has evolved once or several times is unclear. Diverse basidiospore shapes in species of the subgenus *Alboleptonia* show that the shape of basidiospores in *Entoloma* spp. does not reliably reflect systematic relationships. The basidiospore type should thus only carefully be used for infrageneric classification.

In both the subgenera, *Entoloma* and *Nolanea*, basidiospores with different base types occur. This is in accordance with the observations of Pegler and Young (1979). Thus, the base type cannot be used as a major character to define subgenera in *Entoloma*. However, it is possible that this character is consistent in some subgenera or may be useful in subclades at lower rank. More species have to be analysed to assess the phylogenetic value of this character.

Preliminary key to *Entoloma* spp. in Panama

Species with comment "not covered" include the one species already reported for Panama and macromorphologically conspicuous species which were not studied in detail.

1 Basidiocarps mycenoid 2
1* Basidiocarps collybioid to omphalinoid or tricholomatoid 10
2 Basidiospores cuboid 3
2* Basidiospores not cuboid, predominantly with more than 4 angles in outline 5
3 Basidiocarps bright yellow, with pronounced papilla..... *E.* aff. *murrayi* (not covered)
3* Basidiocarps yellowish orange to red-orange, papillate or not 4
4 Basidiocarps yellowish orange, staining green with age or upon touch ..... *E. aurantiovirescens*
4* Basidiocarps orange to red-orange ..... *E.* aff. *quadratum* (not covered)
5 Basidiocarps initially white, often staining yellowish; pileal surface fibrillose 17
5* Basidiocarps coloured, at least the pileus 6
6 Stipe with superficial white or whitish fibrils 9
6* Stipe polished or finely pruinose, fibrillose only when contorted 7
7 Lamellae brownish, pileus rather uniformly brown ..... *E.* aff. *clandestinum* (not covered)
7* Lamellae greyish white, pileus paler, yellowish brown to yellow towards margin 8
8 Pileus translucently striate at about 1/2 the radius ..... *E. flavoconicum*
8* Pileus translucently striate almost to the centre ..... *E. belouvense*
9 Basidiospores 7.5–10.5 µm long, often subcruciform ..... *E. transitionisporum*
9* Basidiospores 8.5–12 µm long, rarely subcruciform ..... *E. paraconferendum*
10 Basidiocarps tricholomatoid; pileus deep blue, surface velvety ..... *E.* cf. *indigoferum*
10* Basidiocarps tricholomatoid without blue colour or collybioid to omphalinoid 11
11 Basidiocarps tricholomatoid to collybioid; pileal surface smooth, sometimes rugulose or with pruina 12
11* Basidiocarps collybioid to omphalinoid; pileal surface appressed fibrillose to squamulose 16
12 Basidiocarps collybioid/omphalinoid to tricholomatoid, rather thin-fleshed; pileus usually translucently striate 13
12* Basidiocarps tricholomatoid, robust; pileus not or only slightly translucently striate 14
13 Pileus translucently striate almost to the centre; stipe concolorous with pileus .....*E. cremeostriatum*
13* Pileus translucently striate up to half the radius; stipe white .....*E. nubooccultatum*
14 Pileus surface glabrous, somewhat rugulose; pigment intracellular ..... *E. brunneorugulosum*
14* Pileus surface not rugulose, often pruinose; pigment incrusting 15
15 Pileus surface pruinose, not hygrophanous; lamellae crowded ..... *E. pruinosum*
15* Pileus surface sometimes pruinose, hygrophanous; lamellae medium-spaced .....*E. mediorobustum*
16 Basidiocarps initially white, often staining yellowish; pileal surface fibrillose 17
16* Basidiocarps coloured 20
17 Basidiospores small, 6.5–9.0 × 5.5–7.5 µm; cheilocystidia long cylindrical-capitate; odour and taste farinaceous ..... *E. cylindrocapitatum* (not covered)
17* Basidiospores larger; cheilocystidia different; odour and taste not farinaceous 18
18 Basidiospores 9.0–12.0 µm long, with 6–9 angles in outline ..... *E. confusissimum*
18* Basidiospores 7.0–10.5 µm long, with 4–6 angles in outline 19
19 Basidiospores 7.0–10.0 × 6.0–8.0 µm, with 4–5 angles in outline, often rhomboid to subcruciform; cheilocystidia 5.0–13.0 µm wide ..... *E. nubilosilvae*
19* Basidiospores 8.5–10.5 × 6.5–8.5 µm, with 5–6 angles in outline, some rhomboid to cruciform; cheilocystidia 10.0–19.0 µm wide ..... *E. amistadosericellum*
20 Lamellar edge dark blue or dark violet-brown, with serrulatum-structure 21
20* Lamellar edge concolorous with faces, without serrulatum-structure 22
21 Pileus violet-brown, up to 1 cm diam.; lamellar edge violet-brown ..... *E. microserrulatum*
21* Pileus blue, up to 2 cm diam.; lamellar edge dark blue ..... *E. caeruleomarginatum*

22 Basidiocarps bright yellow-green .... *E.* aff. *necopinatum* (not covered)
22* Basidiocarps with yellow, brown, grey, blue or violet colours 23
23 Basidiocarps without blue or violet colour, pileus yellowish brown ..... *E. mellosquamulosum*
23* Basidiocarps with blue or violet colour on stipe and/or pileus 24
24 Both, stipe and pileus with blue or violet colour 25
24* Either stipe or pileus with blue or violet colour 27
25 Pileus bluish grey to violet-grey; stipe dull blue to grey, with white fibrillose floccules .... *E.* cf. *violaceobrunneum*
25* Pileus and stipe blue 26
26 Pileus blackish blue, fine squamulose; lamellar edge sterile, cheilocystidia +/- fusiform ..... *E. arcanum*
26* Pileus greyish blue, with rather coarse squamules; lamellar edge heterogeneous, with scattered, broadly clavate to cylindrical cheilocystidia ..... *E. griseocaeruleum*
27 Stipe bright blue; pileus pale yellow-brown .... *E.* aff. *sodale* (not covered)
27* Stipe white; pileus bluish grey to violet-grey .... *E.* cf. *violaceobrunneum*

Acknowledgements We thank Hermine Lotz-Winter and Felix Hampe for invaluable support. Kenneth Barrera, Christian Fischer, Eike Heinemann, Javier de León, Ruben Valdés, and Björn Wergen are thanked for support in the field and for contributing specimens. Sofia Cáceres is thanked for support in the field and the permission of the use of a picture. Gunnhild Marthinsen and Katriina Bendiksen are thanked for several sequences of the Norwegian Barcode of Life project. We thank Olga Morozova, Ellen Larsson, Irmgard Krisai-Greilhuber, and László Nagy for the permission to use their sequences. Laura Guzmán-Dávalos and Diégo Montañez, Øyvind Weholt, Jostein Lorås, Matthias Dondl, and Guillaume Eyssartier are thanked for the permission to use sequences of their specimens. Curators and staff of C, L, LE, G, IBUG, O, PC, PDD, and WU are acknowledged for organising loans. Karl-Heinz Rexer is thanked for a piece of DSS and information about SEM preparation. Manlio Cuevas is thanked for organisation and logistics of field trips as well as support in the field. Fernanda Karstedt is thanked for literature. Jesko Kleine is thanked for help with Latin names. Orlando Cáceres is thanked for his support during permit procedures with the Environmental Ministry of Panama (MiAmbiente, corresponding collection permits SE/APH-4-14, SE/APH-2-15, SE/APH-2-16, SE/AP-17-16, SE/P-13-17, SE/PH-4-18, and export permits SEX/H-4-15, SEX/H-4-17, SEX/H-5-17, SEX/H-2-18). An anonymous reviewer is thanked for valuable comments and suggestions.

Author contribution The study was initially designed by Kai Reschke and Meike Piepenbring. Tina Hofmann, Machiel Noordeloos, and Bálint Dima contributed to the conception. Kai Reschke, Cathrin Manz, José Rodríguez, and Tina Hofmann collected specimens. Kai Reschke did the morphological analyses. Sequencing and molecular phylogenetic analyses were done by Kai Reschke and Bálint Dima. The first draft of the manuscript was written by Kai Reschke and Machiel Noordeloos and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The work of Bálint Dima was supported by the ELTE Thematic Excellence Programme 2020 financed by the National Research, Development and Innovation Office (TKP2020-IKA-05).

Data availability Specimens are deposited in M and UCH. DNA sequences have been submitted to GenBank. Alignments can be obtained from the first author.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

References

Agerer R (1997) *Entoloma sinuatum* (Bull.: Fr.) Kummer + *Salix* spec. Descr Ectomyc 2:13–18
Aime MC, Largent DL, Henkel TW, Baroni TJ (2010) The Entolomataceae of the Pakaraima Mountains of Guyana IV: new species of *Calliderma*, *Paraeccilia* and *Trichopilus*. Mycologia 102:633–649. https://doi.org/10.3852/09-162
Antibus RK, Croxdale JG, Miller OK, Linkins AE (1981) Ectomycorrhizal fungi of *Salix rotundifolia* III. Resynthesized mycorrhizal complexes and their surface phosphatase activities. Can J Bot 59:2458–2465. https://doi.org/10.1139/b81-297
Baroni T, Hofstetter V, Largent DL, Vilgalys R (2011) *Entocybe* is proposed as a new genus in the Entolomataceae (Agaricomycetes, Basidiomycota) based on morphological and molecular evidence. N Am Fungi 6:1–19. https://doi.org/10.2509/naf2011.006.012
Baroni TJ, Halling RE (2000) Some Entolomataceae (Agaricales) from Costa Rica. Brittonia 52:121–135
Baroni TJ, Lodge DJ (1998) *Alboleptonia* from the Greater Antilles. Mycologia 90:680–696. https://doi.org/10.2307/3761227
Berkeley MJ, Curtis MA (1859) On new species of North American fungi. Ann Mag Nat Hist 3:284–296
Bjorbækmo MFM, Carlsen T, Brysting A et al (2010) High diversity of root associated fungi in both alpine and arctic Dryas octopetala. BMC Plant Biol 10:244. https://doi.org/10.1186/1471-2229-10-244
Brandrud TE, Bendiksen E, Jordal JB et al (2018) *Entoloma* species of the rhodopolioid clade (subgenus *Entoloma*; Tricholomatinae, Basidiomycota) in Norway. Agarica 38:21–46
Co-David D, Langeveld D, Noordeloos ME (2009) Molecular phylogeny and spore evolution of Entolomataceae. Persoonia 23:147–176. https://doi.org/10.3767/003158509X480944
Coimbra VRM (2014) Checklist of Central and South American Agaricales (Basidiomycota) I: Entolomataceae. Mycosphere 5:475–487

Coimbra VRM, Wartchow F, Gibertoni TB (2013) Studies on *Entoloma* (Agaricales, Basidiomycota) in the Atlantic Forest, Northeast Brazil. Nova Hedwigia 97:139–157. https://doi.org/10.1127/0029-5035/2013/0100

Crous PW, Carnegie AJ, Wingfield MJ et al (2019) Fungal Planet description sheets: 868–950. Persoonia 42:291–473

Crous PW, Cowan DA, Maggs-Kölling G et al (2021) Fungal Planet description sheets: 1182–1283. Persoonia 46:313–528

Crous PW, Wingfield MJ, Burgess TI et al (2018) Fungal planet description sheets: 716–784. Persoonia 40:240–393

Crous PW, Wingfield MJ, Burgess TI et al (2017) Fungal planet description sheets: 625–715. Persoonia 39:270–467. https://doi.org/10.3767/persoonia.2017.39.11

Dennis RWG (1953) Les Agaricales de l'Ile de la Trinité. Rhodosporae-Ochrosporae. Bull Soc Mycol Fr 69:145–198

Dentinger BTM, Didukh MY, Moncalvo J-M (2011) Comparing COI and ITS as DNA barcode markers for mushrooms and allies (Agaricomycotina). PLoS ONE 6:e25081. https://doi.org/10.1371/journal.pone.0025081

Dima B, Brandrud TE, Corriol G et al (2021) Fungal systematics and evolution: FUSE 7. Sydowia 73:271–340. https://doi.org/10.12905/0380.sydowia73-2021-0271

Ellis JB (1876) New fungi found at New Field, New Jersey (Continued). Bull Torrey Bot Club 6:75–77

Erbar C (1995) On the floral development of *Sphenoclea zeylanica* (Sphenocleaceae, Campanulales)—SEM-investigations on herbarium material. Bot Jahrb Syst 117:469–483

Eyssartier G, Randrianjohany É, Buyck B (2012) Trois Entolomes (Entolomatales, Basidiomycota) à épicutis Hyméniforme de la Réserve Spéciale d'Ambohitantely, Madagascar. Cryptogam, Mycol 33:157–166. https://doi.org/10.7872/crym.v33.iss2.2012.157

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791. https://doi.org/10.2307/2408678

Franco-Molano AE, Uribe-Calle E (2000) Hongos Agaricales y Boletales de Colombia. Biota Colombiana 1:25–43

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Gates GM, Noordeloos M (2007) Preliminary studies in the genus *Entoloma* in Tasmania - I. Persoonia 19:157–226

Geml J, Timling I, Robinson CH et al (2012) An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. J Biogeogr 39:74–88

Griffith GW, Camarra JGP, Holden EM et al (2013) The international conservation importance of Welsh "waxcap" grasslands. Mycosphere Online 4:969–984

Halling RE, Mueller GM (2005) Common mushrooms of the Talamanca Mountains, Costa Rica. New York Botanical Garden, New York

Hay CR, Thorn RG, Jacobs CR (2018) Taxonomic survey of Agaricomycetes (Fungi: Basidiomycota) in Ontario tallgrass prairies determined by fruiting body and soil rDNA sampling. Can Field Nat 132:407–424

He X-L, Horak E, Li T-H et al (2015a) Two new cuboid-spored species of *Entoloma* s. l. (Agaricales, Entolomataceae) from Southern China. Cryptogam, Mycol 36:237–249. https://doi.org/10.7872/crym/v36.iss2.2015.237

He X-L, Horak E, Wang D et al (2019) Descriptions of five new species in *Entoloma* subgenus *Claudopus* from China, with molecular phylogeny of *Entoloma* sl. MycoKeys 61:1

He X-L, Li T-H, Jiang Z-D, Shen Y-H (2012) Four new species of *Entoloma* s.l. (Agaricales) from southern China. Mycol Progr 11:915–925. https://doi.org/10.1007/s11557-012-0807-0

He X-L, Li T-H, Xi P-G et al (2013) Phylogeny of *Entoloma* s.l. subgenus *Pouzarella*, with descriptions of five new species from China. Fungal Divers 58:227–243. https://doi.org/10.1007/s13225-012-0212-7

He X-L, Peng W-H, Gan B-C (2015b) Morphological and molecular evidence for a new species in *Entoloma* subgenus *Claudopus* from Sichuan Province, southwest China. Mycoscience 56:326–331. https://doi.org/10.1016/j.myc.2014.10.001

He X-L, Wang D, Peng W-H, Gan B-C (2017) Two new *Entoloma* s.L. species with serrulatum-type lamellar edge from Changbai Mountains, Northeast China. Mycol Progr 16:761–768. https://doi.org/10.1007/s11557-017-1313-1

He X-L, Ye X-J, Li T-H et al (2015) New and noteworthy species of white *Entoloma* (Agaricales, Entolomataceae) in China. Phytotaxa 205:99–110. https://doi.org/10.11646/phytotaxa.205.2.3

Hesler LR (1967) *Entoloma* in southeastern North America. J. Cramer, Leutershausen

Hofmann TA, Piepenbring M (2021) Checklist of fungi in Panama 2020. Dataset. The Smithsonian Institution. https://doi.org/10.25573/data.13341605.v2

Hongo T (1957) Notes on Japanese larger fungi (11). J Jap Bot 32:208–214

Hooghiemstra H (2006) Immigration of oak into Northern South America: a paleo-ecological document. In: Kappelle M (ed) Ecology and conservation of neotropical montane oak forests. Springer, Berlin, Heidelberg, pp 17–28

Horak E (1978) *Entoloma* in South America. I. Sydowia 30:40–111

Horak E (1982) *Entoloma* in South America. II. Sydowia 35:75–99

Horak E (2008) Agaricales of New Zealand 1: Pluteaceae-Entolomataceae. Fungal Diversity Press, Hong Kong

Horak E (1980) *Entoloma* (Agaricales) in Indomalaya and Australasia. J. Cramer, Vaduz

Horak E (1976) On cuboid spored species of *Entoloma* (Agaricales). Sydowia 28:171–236

Horak E (1977) Additions to "On cuboid-spored species of *Entoloma*". Sydowia 29:289–299

Janssen JAM, Rodwell JS, García Criado M et al (2016) European red list of habitats part 2. Terrestrial and freshwater habitats. European Commission

Kappelle M, Cleef AM, Chaverri A (1992) Phytogeography of Talamanca montane *Quercus* forests, Costa Rica. J Biogeogr 19:299–315. https://doi.org/10.2307/2845453

Karich A, Kellner H, Schmidt M, Ullrich R (2015) Ein bemerkenswertes Mykotop im Zittauer Gebirge mit *Microglossum rufescens* als Erstnachweis für Deutschland. Boletus 36:151–163

Karstedt F, Bergemann SE, Capelari M (2020) Five *Nolanea* spp. nov. from Brazil. Mycotaxon 135:589–612

Karstedt F, Capelari M (2013) *Inocephalus* (Entolomataceae, Agaricales) from São Paulo State, Brazil. Nova Hedwigia 96:279–308

Karstedt F, Capelari M (2010) New species and new combinations of *Calliderma* (Entolomataceae, Agaricales). Mycologia 102:163–173. https://doi.org/10.3852/09-019

Karstedt F, Capelari M, Baroni TJ et al (2019) Phylogenetic and morphological analyses of species of the Entolomataceae (Agaricales, Basidiomycota) with cuboid basidiospores. Phytotaxa 391:1–27. https://doi.org/10.11646/phytotaxa.391.1.1

Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: improvements in performance and usability. Mol Biol Evol 30:772–780. https://doi.org/10.1093/molbev/mst010

Kim CS, Jo JW, Kwag Y-N et al (2015) Mushroom flora of Ulleunggun and a newly recorded *Bovista* species in the Republic of Korea. Mycobiology 43:239–257

Kinoshita A, Sasaki H, Nara K (2012) Multiple origins of sequestrate basidiomes within *Entoloma* inferred from molecular phylogenetic analyses. Fungal Biol 116:1250–1262. https://doi.org/10.1016/j.funbio.2012.09.006

Koch JA, Fischer A, Manz C, Rexer K-H (2021) Rehydration of dried mushroom specimens with Aerosol® OT for scanning electron microscopy. Mycol Progr 20:747–754. https://doi.org/10.1007/s11557-021-01697-6

Kokkonen K (2015) A survey of boreal *Entoloma* with emphasis on the subgenus *Rhodopolia*. Mycol Progr 14:116. https://doi.org/10.1007/s11557-015-1135-y

Kondo K, Nakamura K, Ishigaki T et al (2017) Molecular phylogenetic analysis of new *Entoloma rhodopolium* -related species in Japan and its identification method using PCR-RFLP. Sci Rep 7:14942. https://doi.org/10.1038/s41598-017-14466-x

Kornerup A, Wanscher JH (1967) Methuen handbook of colour, 2nd. Methuen & Co., Ltd., London

Kühner R, Boursier J (1929) La forme des spores chez les Agarics rhodo-goniosporés. Bull Soc Mycol Fr 45:264–277

Kühner R, Romagnesi H (1953) Flore analytique des champignons superieurs. Masson, Paris

Kühner R, Romagnesi H (1954) Espèces nouvelles ou critiques de *Rhodophyllus*. Revue De Mycologie 19:3–46

Largent DL (1994) Entolomatoid fungi of the western United States and Alaska. Mad River Press, Eureka, California

Largent DL, Aime MC, Henkel TW, Baroni TJ (2008) The Entolomataceae of the Pakaraima Mountains of Guyana 2: *Inocephalus dragonosporus* comb. nov. Mycotaxon 105:185

Largent DL, Benedict RG (1970) Studies in the rhodophylloid fungi II: *Alboleptonia*, a new genus. Mycologia 62:437–452. https://doi.org/10.2307/3757517

Largent DL, Bergemann SE, Abell-Davis SE (2014) *Entoloma* species from New South Wales and northeastern Queensland, Australia. Mycotaxon 129:329–359. https://doi.org/10.5248/129.329

Largent DL, Henkel TW, Aime MC, Baroni TJ (2008b) The Entolomataceae of the Pakaraima Mountains of Guyana I: four new species of *Entoloma* s. str. Mycologia 100:132–140. https://doi.org/10.3852/mycologia.100.1.132

Largent DL, Henkel TW, Siegel N et al (2019) New species of Entolomataceae from Cameroon. FUSE 5:151–167

Largent DL, Kluting KL, Anderson NM, Bergemann SE (2016) New leptonioid species from New South Wales and northeastern Queensland, Australia. Mycotaxon 131:153–176

Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30:3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Loree MAJ, Lumme I, Niemi M, Tormala T (1989) Inoculation of willows (*Salix* spp.) with ectomycorrhizal fungi on mined boreal peatland. Plant Soil 116:229–238

Manimohan P, Leelavathy KM (1988) Two new species of *Alboleptonia* (Agaricales, Entolomataceae) from southern India. Trans Br Mycol Soc 91:710–712

Manimohan P, Noordeloos ME, Dhanya AM (2006) Studies on the genus *Entoloma* (Basidiomycetes, Agaricales) in Kerala State, India. Persoonia 19:45–93

Manimohan P, Vijaya Joseph A, Leelavathy KM (1995) The genus *Entoloma* in Kerala state, India. Mycol Res 99:1083–1097. https://doi.org/10.1016/S0953-7562(09)80777-6

Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). Mol Phylogenet Evol 35:1–20. https://doi.org/10.1016/j.ympev.2004.11.014

Mazzer SJ (1976) A monographic study of the genus *Pouzarella*: a new genus in the Rhodophyllaceae, Agaricales, Basidiomycetes. J. Cramer, Vaduz

McHugh R, Mitchel D, Wright M, Anderson R (2001) The fungi of Irish grasslands and their value for nature conservation. Biol Environ 101B:225–243

Montañez D, Noordeloos ME, Rodríguez O et al (2016) Notes on the genus *Entoloma* (Basidiomycota, Agaricales) in two volcanic areas of Jalisco, Mexico. Phytotaxa 277:211–236. https://doi.org/10.11646/phytotaxa.277.3.1

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

Morozova OV, Noordeloos ME, Popov ES, Alexandrova AV (2017) Three new species within the genus *Entoloma* (Basidiomycota, Agaricales) with clamped basidia and a *serrulatum*-type lamellae edge, and their phylogenetic position. Mycol Progr 1–12.https://doi.org/10.1007/s11557-017-1364-3

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

Morozova OV, Voronina EY, Arslanov SN (2014b) *Entoloma piceinum*, a new lignicolous species of Entolomataceae (Agaricales) from the European Russia. Nov Sist Nizs Rast 48:181–187

Murrill WA (1944) New Florida fungi. Proc Fla Acad Sci 7:107–127

Murrill WA (1917) North American Flora. Vol. 10. Part 2. New York Botanical Garden

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Newton AC, Davy LM, Holden E et al (2003) Status, distribution and definition of mycologically important grasslands in Scotland. Biol Conservat 111:11–23. https://doi.org/10.1016/S0006-3207(02)00243-4

Noordeloos ME (1981) Introduction to the taxonomy of the genus *Entoloma* sensu lato (Agaricales). Persoonia 11:121–151

Noordeloos ME (1992) *Entoloma* s.l., Fungi Europaei 5. Libreria editrice Giovanna Biella, Saronno, Italy

Noordeloos ME (2004) *Entoloma* s.l., Fungi Europaei, 5A. Edizioni Candusso, Alassio, Italy

Noordeloos ME (1982) Notes on *Entoloma*. New and rare species of *Entoloma* from Scandinavia. New names and combinations. Nord J Bot 2:155–162. https://doi.org/10.1111/j.1756-1051.1982.tb01176.x

Noordeloos ME (1988) *Entoloma* in North America. Gustav Fischer Verlag, Stuttgart, New York

Noordeloos ME (1980) *Entoloma* subgenus *Nolanea* in the Netherlands and adjacent regions with a reconnaissance of its remaining taxa in Europe. Persoonia 10:427–534

Noordeloos ME (1984) Entolomataceae (Agaricales, Basidiumycetes) in Greenland—I. The Genus *Entoloma*. Persoonia 12:263–305

Noordeloos ME (1987) *Entoloma* (Agaricales) in Europe. J. Cramer, Berlin-Stuttgart

Noordeloos ME, Gates GM (2012) The Entolomataceae of Tasmania. Springer Science & Business Media

Noordeloos ME, Hausknecht A (2007) The genus *Entoloma* (Basidiomycetes, Agaricales) of the Mascarenes and Seychelles. Fungal Divers 27:111–144

Noordeloos ME, Hausknecht A (2016) Die Gattung *Entoloma* von den Maskarenen und Seychellen. Z Mykol 82:295–347

Noordeloos ME, Hausknecht A (2009) New and interesting *Entoloma* species from Central Europe. Österr Z Pilzk 18:169–182

Noordeloos ME, Hausknecht A (2002) Weitere neue *Entoloma*-Arten aus Südeuropa. Österr Z Pilzk 11:117–131

Noordeloos ME, Lorås JA, Eidissen SE et al (2021) Three new *Entoloma* species of the *Cyanula* clade from (sub)alpine habitats in Northern Norway and Sweden. Sydowia 73:185–196. https://doi.org/10.12905/0380.sydowia73-2020-0185

Noordeloos ME, Weholt Ø, Bendiksen E et al (2018) *Entoloma aurorae-borealis* sp. nov. and three rare *Entoloma* species in the Sinuatum clade (subg. *Entoloma*) from northern Europe. Sydowia 70:199–210

O'Donnell K (1992) Ribosomal DNA internal transcribed spacers are highly divergent in the phytopathogenic ascomycete *Fusarium sambucinum* (*Gibberella pulicaris*). Curr Genet 22:213–220

Osorio CAP, Osorio JP (2016) Primer reporte de *Entoloma hochstetteri* (Entolomataceae, Agaricales, Basidiomycota) para el departamento de Santander, Colombia. Revista Biodiversidad Neotropical 6:126–130. https://doi.org/10.18636/bioneotropical.v6i2.181

Ovrebo CL, Baroni TJ (2007) New taxa of Tricholomataceae and Entolomataceae (Agaricales) from Central America. Fungal Divers 27:157–170

Papp V, Dima B (2018) New systematic position of *Aurantiporus alborubescens* (Meruliaceae, Basidiomycota), a threatened old-growth forest polypore. Mycol Progress 17:319–332. https://doi.org/10.1007/s11557-017-1356-3

Pegler DN, Young TWK (1979) Spore form and phylogeny of Entolomataceae (Agaricales). Beih Sydowia 8:290–303

Raj KNA, Latha KPD, Kumar TKA, Manimohan P (2014) A new species of *Entoloma* from India. Mycoscience 55:400–404. https://doi.org/10.1016/j.myc.2014.01.003

Rambaut A (2014) FigTree v1. 4. University of Edinburgh, Edinburgh, UK. Version v1.4.2URL http://tree.bio.ed.ac.uk/software/figtree/

Romagnesi H (1974) Essai d'une classification des Rhodophylles. Bull Mens Soc Linn Lyon 43:325–332. https://doi.org/10.3406/linly.1974.10142

Romagnesi H (1941) Les Rhodophylles de Madagascar:(*Entoloma*, *Nolanea*, *Leptonia*, *Eccilia*, *Claudopus*). Laboratoire de cryptogamie du Museum national d'histoire naturelle, Paris

Romagnesi H (1956) Les Rhodophylles du Congo belge d'apres les recoltes de M^me Goossens-Fontana. Bull Jard Bot Brux 26:137–182

Romagnesi H, Gilles G (1979) Les Rhodophylles des forêts côtières du Gabon et de la Côte d'Ivoire: avec une introduction générale sur la taxinomie du genre. Cramer

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stevenson G (1962) The Agaricales of New Zealand: III. Kew Bull 16:227–237. https://doi.org/10.2307/4118823

Truong C, Mujic AB, Healy R et al (2017) How to know the fungi: combining field inventories and DNA-barcoding to document fungal diversity. New Phytol 214:913–919

Varga T, Krizsán K, Földi C et al (2019) Megaphylogeny resolves global patterns of mushroom evolution. Nat Ecol Evol 3:668. https://doi.org/10.1038/s41559-019-0834-1

Vasco-Palacios AM, Franco-Molano AE (2013) Diversity of Colombian macrofungi (Ascomycota-Basidiomycota). Mycotaxon 121:499

Vidal JM, Bellanger J-M, Moreau P-A (2016) Tres nuevas especies gasteroides del género *Entoloma* halladas en España. Boletín Micológico De FAMCAL 11:53–78

Vila J, Carbó J, Caballero F et al (2013) A first approach to the study of the genus *Entoloma* subgenus *Nolanea* sensu lato using molecular and morphological data. Fungi Non Delineati 66:3–62

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172:4238–4246

Weholt Ø, Lor\a as J, Eidissen SE (2014) One new and one rare species of *Entoloma* from the Norwegian nature reserve Holmvassdalen. Österr Z Pilzk 23:55–60

White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. pp 315–322