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Molecular phylogeny and spore evolution of *Entolomataceae*

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Key words

Clitopilus
Entoloma
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Rhodocybe
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spore evolution

Abstract The phylogeny of the *Entolomataceae* was reconstructed using three loci (RPB2, LSU and mtSSU) and, in conjunction with spore morphology (using SEM and TEM), was used to address four main systematic issues: 1) the monophyly of the *Entolomataceae*; 2) inter-generic relationships within the *Entolomataceae*; 3) genus delimitation of *Entolomataceae*; and 4) spore evolution in the *Entolomataceae*. Results confirm that the *Entolomataceae* (*Entoloma*, *Rhodocybe*, *Clitopilus*, *Richoniella* and *Rhodogaster*) is monophyletic and that the combination of pinkish spore prints and spores having bumps and/or ridges formed by an epicorium is a synapomorphy for the family. The *Entolomataceae* is made up of two sister clades: one with *Clitopilus* nested within *Rhodocybe* and another with *Richoniella* and *Rhodogaster* nested within *Entoloma*. *Entoloma* is best retained as one genus. The smaller genera within *Entoloma* s.l. are either polyphyletic or make other genera paraphyletic. Spores of the clitopiloid type are derived from rhodocyboid spores. The ancestral spore type of the *Entolomataceae* was either rhodocyboid or entolomatoid. Taxonomic and nomenclatural changes are made including merging *Rhodocybe* into *Clitopilus* and transferring relevant species into *Clitopilus* and *Entoloma*.

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INTRODUCTION

The euagaric family *Entolomataceae* Kotl. & Pouzar is very species-rich. It is composed of more than 1 500 species and occurs worldwide, from arctic to tropical habitats (Horak 1980, 2008, Baroni 1981, Largent 1994, Noordeloos 2004, Gates & Noordeloos 2007, Noordeloos & Hausknecht 2007). The family is highly variable in terms of sporocarp morphology (tiny to large; pleurotoid, omphalioid, collybioid, mycenoid, and tricholomatoid, as well as sequestrate), and micromorphology (spore shape, pileipellis structures, pigmentation types, cystidia presence and shape, etc.; Noordeloos 2004; Fig. 1). Lifestyles are equally varied: Most species are saprotrophic on soil, wood or moss, but some are parasitic on other mushrooms (Noordeloos 2004), parasitic on plants or ectomycorrhizal (Antibus et al. 1981, Agerer & Waller 1993, Agerer 1997, Kobayashi & Hatano 2001, Montecchio et al. 2006). The family traditionally contains three main agaricoid genera: *Rhodocybe* Maire, *Clitopilus* (Fr. ex Rabenh.) P. Kumm. and *Entoloma* (Fr.) P. Kumm. s.l. The latter genus is sometimes split into more genera (e.g. 13 genera; Largent 1994). Additionally, three smaller non-agaricoid genera have been distinguished on the basis of habit, namely, the monotypic *Rhodocybella* T.J. Baroni & R.H. Petersen (with a cyphelloid habit), *Rhodogaster* E. Horak (secotioid) and *Richoniella* Costantin & L.M. Dufour (gasteroid).

It is no surprise that *Entolomataceae*, being such a large and highly variable family, raises questions that analysis of morphological characters alone cannot answer, either due to scarcity of characters and/or difficulty in interpreting the significance of the characters. Molecular phylogenetic methods are therefore used in our study to address four main systematic issues:

1. the monophyly of the *Entolomataceae*;
2. inter-generic relationships within the *Entolomataceae*;
3. genus delimitation of *Entolomataceae* and, with the addition of spore morphology;
4. spore evolution in the *Entolomataceae*.

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Monophyly of the Entolomataceae and intergeneric relationships

The members of *Entolomataceae* have been classified together because they all share the property of spore prints that are pink to brownish or greyish pink in combination with spores that are bumpy, ridged, or angular in polar or in all views. The spore wall ornamentations are unique, being formed by local thickenings in the spore wall, the epicorium (Clémençon et al. 2004). The presence of pink, angular spores has been considered so unique that *Entolomataceae*, in contrast to many other Agaricales families, has been widely regarded a natural group (Kühner 1980, Singer 1986).

Species from other genera had, in the past, been placed within *Entolomataceae.* However, recent studies have excluded them. *Macrocystidia* Joss. and *Rhodotus* Maire had been classified in the family on account of their pink spores, but molecular phylogenetic studies have placed them outside the family (Moncalvo et al. 2002). Comparison of the spore wall of *Rhodotus palmatus* (Bull.) Maire and members of *Entolomataceae* showed that their bumps are not homologous (Clémençon 1997). Also, the phylogenetic study by Moncalvo et al. (2002) suggested that *Catathelasma* Lovejoy and a strongly supported clade containing *Callistosporium* Singer, *Macrocybe* Pegler & Lodge and *Pleurocollybia* Singer were best included in *Entolomataceae*. The more recent phylogenetic study by Matheny et al. (2006) has excluded *Catathelasma* and *Callistosporium* from *Entolomataceae* with strong support.

Both phylogenetic studies (Moncalvo et al. 2002, Matheny et al. 2006) were based on relatively small samples of *Entoloma*, *Rhodocybe* and *Clitopilus* and none of *Rhodogaster*, *Richoniella* and *Rhodocybella*. Thus, phylogenetic relationships among these six genera had remained unresolved.

Spore evolution

Spore characters have been important both to characterize the family (having pink, angular spores) but also to separate its three main agaricoid genera, *Rhodocybe*, *Clitopilus* and *Entoloma*, from each other. *Rhodocybe* has spores with orna-

Fig. 1 *Entolomataceae* variation in basidiocarp morphology. a. *Entoloma prunuloides*; b. *E. sinuatum*; c. *E. catalaense*; d. *E. conferendum*; e. *E. camarophyllus*; f. *E. roseum*; g. *Clitopilus prunulus*; h. *Rhodocybe gemina*; i. *Entoloma rodwayi*; j. *Richoniella pumila*; k. *E. uranochroum*. — Photos by: a, b. Y. Deneyer; c. G. Consiglio; d. J. Vesterholt; e, g–i. M.E. Noordeloos; f. H. Huijser; j. M. Pilkington; k. M. Meusers.

mentations in the form of bumps and undulate ridges having various arrangements resulting in spores that are undulate to weakly angular in profile and face views, and angular in polar view (Baroni 1981). *Clitopilus* is characterized by spores with an ornamentation of longitudinal ridges. *Entoloma* has spores that are angular in all views due to its network of interconnected ridges that form facets and are highly varied in shape (Romagnesi 1974, Pegler & Young 1978, 1979).

There are two main theories on how spore shapes within *Entolomataceae* evolved. According to the first theory (Kühner 1980), rhodocyboid spores represent the plesiomorphic condition since they are the more similar to what he considered the closest relative of *Entolomataceae*, *Lepista* (Fr.) W.G. Sm. (*Tricholomataceae*). Species of that genus have pinkish, roughened spores. The spores of *Clitopilus* are the evolutionary intermediate between *Rhodocybe* and *Entoloma*. *Entoloma* spores are the most complex and represent the most evolved spore form. The second theory (Baroni 1981) is similar in that rhodocyboid spores are ancestral. However, Baroni based his argument that the rhodocyboid spore is the most primitive on

the assumption that since pink angular spores do not exist elsewhere in the Agaricales, the first *Entolomataceae* evolved from an unknown member of *Tricholomataceae* with slightly rounded-angular, pinkish spores. More pronounced angularity then derived from this. Furthermore, in contrast to Kühner's theory, clitopiloid and entolomatoid spores evolved independently from rhodocyboid spores. Note, however, that modern phylogenies support neither the sister relationship of *Lepista* nor any member of *Tricholomataceae* with a pink spore print. Rather, it is suggested that the *Lyophyllaceae* are the sister clade of *Entolomataceae* and that it is nested within other members of the Tricolomatoid clade (Hofstetter et al. 2002, Matheny et al. 2006).

These hypotheses can be evaluated through a phylogenetic reconstruction of *Entolomataceae* and its closest relatives and by subsequently mapping spore structure on the tree. In this framework, it is possible to reject hypotheses that are inconsistent with phylogeny. Hypotheses that are consistent with phylogeny can be further scrutinized and used as a basis for improved hypothesis formulation.

Genus delimitation of Entolomataceae

There are several problems with genus delimitation in *Entolomataceae* due to different interpretations of morphological evidence. Firstly, the genus *Rhodocybella* has rhodocyboid spores indicating a close relationship with *Rhodocybe* (Baroni & Petersen 1987). Secondly, *Rhodogaster* and *Richoniella* have entolomatoid spores and therefore these taxa are hypothesized to have been derived from or even to be members of *Entoloma* (Pegler & Young 1978, 1979, Kendrick 1994). Kuyper included *Rhodogaster* and *Richoniella* in *Entoloma* in the Dictionary of the Fungi (Kirk et al. 2008). Here we test this hypothesis and make the required nomenclatural changes.

Thirdly and most importantly, despite the generally agreed-upon distinction between the agaricoid genera due to spore shape, there are several taxa that are at the centre of dispute regarding the distinction between *Rhodocybe* and *Entoloma*. Baroni & Largent (1989) transferred *E. trachyosporum* Largent to *Rhodocybe*. They also proposed, although not formally, that *E. nitidum* Quél. be transferred to *Rhodocybe* (Baroni & Largent 1993, Castellano et al. 1999). Both proposals are based on their evaluation that the spores are rhodocyboid rather than entolomatoid. This evaluation implies that *Entoloma* species that are closely related to sect. *Trachyospora* and *E. nitidum* also belong to *Rhodocybe*, further blurring the distinction between the two genera. In contrast, Noordeloos (2004) retained *E. nitidum* in *Entoloma*, on the basis of his evaluation that the spores are entolomatoid rather than rhodocyboid.

Lastly, *Entoloma* is highly variable in terms of morphology. It is the second largest euagaric genus (after *Cortinarius*), with more than 1 500 species. Several mycologists therefore preferred to variously split this group into smaller genera (Orton 1960, 1991, Largent & Benedict 1971, Horak 1973, 1980, Largent 1977, 1994). These subdivisions do not show much consistency. Other mycologists have preferred to recognize one large genus (Romagnesi 1978, Noordeloos 1981, 1992, 2004). These authors noted problems with the delimitation of groups within *Entoloma* – particularly due to the existence of taxa with an intermediate position between subgenera. This study evaluates the existing proposals in a phylogenetic context. Proposals that are inconsistent with the phylogenetic relationships have to be rejected.

The present study uses molecular phylogenetic analyses of a 3-loci dataset together with spore characters scored from images captured using scanning electron microscopy (SEM) and transmission electron microscopy (TEM) to answer the following questions:

1. Is *Entolomataceae* monophyletic?;
2. Are the main genera *Rhodocybe*, *Clitopilus* and *Entoloma* monophyletic?;
3. What is the relationship of these three genera to each other?;
4. What theories on spore evolution in *Entolomataceae* are inconsistent with the phylogeny and should therefore be rejected, and what theories are consistent with it?;
5. How does the phylogeny inform the debate on the various taxonomic proposals for a possible generic delimitation within *Entoloma* s.l.?

MATERIALS AND METHODS

Taxon sampling

For outgroup, the analysis used 7 taxa from close relatives of *Entolomataceae* in the Tricholomatoid clade (sensu Matheny et al. 2006). *Tricholoma vaccinum*, *Lepista ovispora* and *Collybia tuberosa* were sequenced for this study. Sequences of *Calocybe*, *Lyophyllum*, *Clitocybe* and *Collybia* were downloaded from Genbank. For the ingroup, a total of 12 *Rhodocybe*, three *Clitopilus*, one *Rhodogaster*, one *Richoniella*, and 53 *Entoloma* accessions were sequenced. In addition, sequences of *R. aureicystidiata* and an AFTOL taxon identified as *E. prunuloides* were downloaded from Genbank. The AFTOL *E. prunuloides* turned out to be significantly different from the one sequenced for this study. Such discrepancies demonstrate the need for a system where sequences can be annotated (Bidartondo et al. 2008). It is here referred to as '*Entoloma sp*. 1'. The *Entoloma* species sampled represent 12 subgenera according to Noordeloos (2004). Subgenus *Entoloma* was more extensively sampled because preliminary analyses suggested that part of it is basal to the rest of the genus *Entoloma* and because it included *E. trachyosporum* and *E. nitidum*, taxa that have been at the centre of dispute regarding the distinction between *Rhodocybe* and *Entoloma*. We were not able to sequence *Rhodocybella* due to its insufficient collection. Table 1 summarizes taxonomic and collection information of the samples, as well as the DNA markers that were sequenced. The representatives of the *Entolomataceae* sequenced for this study were identified by the senior author, or are type-specimens.

DNA markers

Three loci from three different parts of the genome were sequenced: RPB2 (nuclear RNA polymerase second largest subunit gene), LSU (nuclear ribosomal large subunit gene) and mtSSU (mitochondrial ribosomal small subunit gene). For RPB2, the primers bRPB2-6F and bRPB2-7R were used (Matheny 2005). For some samples these primers failed to amplify any fragment either due to its high degeneracy or degradation of the template DNA. Internal primers were thus designed particularly for *Entolomataceae*: rpb2-i6f (5' GAA GGY CAA GCY TGY GGT CT 3') and rpb2-i7r (5' ATC ATR CTN GGA TGR ATY TC 3'). This new primer pair partially addressed the difficulty of amplification of RPB2 by being slightly less degenerate and by amplifying a shorter fragment. The large subunit of the nuclear ribosomal apparatus (LSU) was amplified and sequenced using LROR, LR16, LR3R and LR5 (more information from http://www.biology.duke.edu/fungi/mycolab/primers.htm). The primers used for mtSSU were MS1 and MS2 (White et al. 1990).

DNA extraction, amplification and sequencing

DNA was isolated from fresh lamellae preserved in a cetyl trimethylammonium bromide (CTAB) buffer and from dried herbarium material using a modified CTAB extraction method (Doyle & Doyle 1990). Varying amounts of fruitbody tissue were ground either by using a bleach-cleaned plastic pestle if the

Table 1 Species used in the phylogenetic analyses. All accessions were sequenced for this study except the last seven, which were downloaded from Genbank. The symbol * is placed before the names of species now transferred to *Clitopilus* and + for those transferred to *Entoloma*. Holotypes and isotypes are indicated with the collection number, as is the herbarium where the voucher specimen is deposited unless they are in L.

Species name	Genbank Accession numbers			Collection number	Country of collection
	mtssu	rpb2	lsu		
**Rhodocybe caelata*	GQ289348		GQ289208	"Exkursionsteilnehmer" 2005-08-28	Germany
**Rhodocybe fallax* [1]	GQ289350	GQ289276	GQ289210	ME Noordeloos 200367	Slovakia
**Rhodocybe fallax* [2]	GQ289349	GQ289275	GQ289209	ME Noordeloos 1997173	Italy
**Rhodocybe gemina*	GQ289351	GQ289277		G. van Zanen 2003-09-14	Belgium
**Rhodocybe hirneola*	GQ289352	GQ289278	GQ289211	ME Noordeloos 199956	Italy
**Rhodocybe mundula*		GQ289280	GQ289213	ME Noordeloos 9867	Austria
**Rhodocybe nitellina* [1]	GQ289355	GQ289282	GQ289215	ME Noordeloos 200435	Austria
**Rhodocybe nitellina* [2]	GQ289354	GQ289281	GQ289214	ME Noordeloos 2002021	Austria
**Rhodocybe pallidogrisea*	GQ289356	GQ289283	GQ289216	ME Noordeloos 2004032	Tasmania, Australia
**Rhodocybe pseudopiperita*	GQ289357	GQ289284	GQ289217	ME Noordeloos 2004068	Tasmania, Australia
**Rhodocybe* sp.	GQ289353	GQ289279	GQ289212	A. Gminder 2004-04-27	Germany
**Rhodocybe stangliana*		GQ289285	GQ289218	N. Dam 05094	Switzerland
+Rhodocybe zuccherellii	GQ289346		GQ289206	A. Zuccherelli 1996-01-25 [holotype]	Italy
+Rhodogaster calongei	GQ289298		GQ289158	PM Pasabán [holotype, MA]	Spain
+Richoniella pumila	GQ289304	GQ289235	GQ289164	G.Gates E2031	Tasmania, Australia
Clitopilus cystidiatus	GQ289287	GQ289220	GQ289147	ME Noordeloos 200350	Slovakia
Clitopilus pinsitus	GQ289288		GQ289148	G. Immerzeel 1990-11	Netherlands
Clitopilus prunulus	GQ289289	GQ289221	GQ289149	ME Noordeloos 2003-09-14	Belgium
Entoloma abortivum	GQ289290	GQ289222	GQ289150	H den Bakker 92	Canada
Entoloma albidoquadratum	GQ289291	GQ289223	GQ289151	P. Manimohan 667 [holotype]	Kerala, India
Entoloma alcedicolor	GQ289292	GQ289224	GQ289152	E. Arnolds 0276 [holotype]	Netherlands
Entoloma araneosum	GQ289293	GQ289225	GQ289153	ME Noordeloos 200314	Belgium
Entoloma bloxamii	GQ289294	GQ289226	GQ289154	ME Noordeloos 200442	Austria
Entoloma caccabus	GQ289295	GQ289227	GQ289155	ME Noordeloos 200324	Belgium
Entoloma cephalotrichum	GQ289297	GQ289229	GQ289157	C. Ulje 1997-08-01	Netherlands
Entoloma cocles	GQ289299	GQ289230	GQ289159	J. Vauras 9770F	Finland
Entoloma coeruleogracilis [1]	GQ289309	GQ289240	GQ289169	G. Gates E1220	Tasmania, Australia
Entoloma coeruleogracilis [2]	GQ289308	GQ289239	GQ289168	G. Gates E1777	Tasmania, Australia
Entoloma haastii	GQ289307	GQ289238	GQ289167	ME Noordeloos 2004055	Tasmania, Australia
Entoloma conferendum	GQ289300	GQ289231	GQ289160	ME Noordeloos 200313	Belgium
Entoloma costatum	GQ289301	GQ289232	GQ289161	G. Immerzeel 2000-10-10	Netherlands
Entoloma cretaceum	GQ289302	GQ289233	GQ289162	G. Gates E1181 [holotype]	Tasmania, Australia
Entoloma excentricum	GQ289303	GQ289234	GQ289163	M. Meusers E 1705	Germany
Entoloma gelatinosum	GQ289305	GQ289236	GQ289165	G. Gates E792	Tasmania, Australia
Entoloma griseolazulinum	GQ289306	GQ289237	GQ289166	P. Manimohan 738 [holotype]	Kerala, India
Entoloma hebes	GQ289310	GQ289241	GQ289170	C. Hartman 1992-10-28	Netherlands
Entoloma indigoticoumbrinum	GQ289311	GQ289242	GQ289171	ME Noordeloos 200406 3 [holotype]	Tasmania, Australia
Entoloma indoviolaceum	GQ289312	GQ289243	GQ289172	P. Manimohan 700 [holotype]	Kerala, India
Entoloma kermandii	GQ289313	GQ289244	GQ289173	G. Gates E227 [holotype]	Tasmania, Australia
Entoloma myrmecophilum	GQ289314	GQ289245	GQ289174	G. Tjallingii-Beukers 1981-10-30	Netherlands
Entoloma nitidum	GQ289315	GQ289246	GQ289175	ME Noordeloos 200426	Slovakia
Entoloma pallideradicatum	GQ289316	GQ289247	GQ289176	A. Hausknecht [isotype ex WU 189010]	Austria
Entoloma parasiticum	GQ289317	GQ289248	GQ289177	ME Noordeloos 200330	Belgium
Entoloma perbloxamii	GQ289318	GQ289249	GQ289178	ME Noordeloos 2004071 [holotype]	Tasmania, Australia
Entoloma phaeomarginatum	GQ289319	GQ289250	GQ289179	ME Noordeloos 2004127	Tasmania, Australia
Entoloma pluteisimilis	GQ289320	GQ289251	GQ289180	C. Hermosilla 2001-12-08 [holotype]	Spain
Entoloma politum	GQ289321	GQ289252	GQ289181	ME Noordeloos 200325	Belgium
Entoloma porphyrescens	GQ289322	GQ289253	GQ289182	ME Noordeloos 2004113	Tasmania, Australia
Entoloma procerum	GQ289323	GQ289254	GQ289183	ME Noordeloos 2004070	Tasmania, Australia
Entoloma prunuloides	GQ289324	GQ289255	GQ289184	ME Noordeloos 200340	Slovakia
Entoloma pygmaeopapillatum	GQ289325	GQ289256	GQ289185	ME Noordeloos 200364	Slovakia
Entoloma readiae	GQ289326	GQ289257	GQ289186	ME Noordeloos 2004050	Tasmania, Australia
Entoloma rhodopolium var. *nidorosum*	GQ289327	GQ289258	GQ289187	ME Noordeloos 2003-09-16	Belgium
Entoloma sarcitum	GQ289328	GQ289259	GQ289188	A. Hausknecht 1994-04-20	Austria
Entoloma sericatum	GQ289329	GQ289260	GQ289189	ME Noordeloos 200328	Slovakia
Entoloma sericellum	GQ289330	GQ289261	GQ289190	ME Noordeloos 200315	Belgium
Entoloma sericeum	GQ289331	GQ289262	GQ289191	ME Noordeloos 200329	Slovakia
Entoloma serrulatum	GQ289332	GQ289263	GQ289192	ME Noordeloos 2004062	Tasmania, Australia
Entoloma sinuatum	GQ289333	GQ289264	GQ289193	J. Wisman 2003-09-19	Netherlands
Entoloma sordidulum	GQ289334	GQ289265	GQ289194	Co-David 2003	Belgium
Entoloma sp. [2]	GQ289296	GQ289228	GQ289156	TJ Baroni 9895 [CORT]	Belize
Entoloma sphagnetii	GQ289335		GQ289195	C. Bas 6.86	Netherlands
Entoloma tectonicola	GQ289336	GQ289266	GQ289196	P. Manimohan 741 [holotype]	Kerala, India
Entoloma tjallingiorum	GQ289337	GQ289267	GQ289197	J. Vauras 14318F	Finland
Entoloma trachyosporum [1]	GQ289338		GQ289198	H. den Bakker 1153	Canada
Entoloma trachyosporum [2]	GQ289339		GQ289199	H. den Bakker 1901	Canada
Entoloma transmutans	GQ289340	GQ289268	GQ289200	ME Noordeloos 2004155	Tasmania, Australia
Entoloma turbidum	GQ289341	GQ289269	GQ289201	ME Noordeloos 200351	Slovakia
Entoloma undatum	GQ289342	GQ289270	GQ289202	ME Noordeloos 200327	Belgium
Entoloma valdeumbonatum	GQ289343	GQ289271	GQ289203	M. Meusers E4565 [holotype]	Germany
Entoloma vezzenaense	GQ289344	GQ289272	GQ289204	A. Hausknecht [isotype, ex WU 14588]	Italy
Entoloma violaceovillosum	GQ289345	GQ289273	GQ289205	P. Manomohan 645 [holotype]	Kerala, India
Lepista ovispora	GQ289347	GQ289274	GQ289207	E. Arnolds 05-183	Netherlands
Tricholoma vaccinum	GQ289358	GQ289286	GQ289219	H. v.d. Burg 2004-11-03	Netherlands
Calocybe carnea [CBS552.50]	AF357097	DQ825423	AF223178		
Clitocybe dealbata	AF357138	DQ825407	AF223175		
Collybia tuberosa [AFTOL-ID 557]		AY787219	AY639884		
Entoloma sp. [1; AFTOL-ID 523; identified as *E. prunuloides*]		DQ385883	AY700180		
Lyophyllum leucophaeatum	AF357101	DQ367434	AF223202		
**Rhodocybe aureicystidiata*		AY337412	AY380407		
Tephrocybe boudieri	AF357122	DQ825411	DQ825430		

sample was CTAB-preserved, or by agitating the dried tissue with a 7 mm diam glass ball in a 2 mL microcentrifuge tube in a mixer mill (MM 200, Retch GmbH & Co, Germany) and adding a total of 500 µL 2XCTAB buffer afterwards. Proteinase K (2 µL of 20 mg/ml, 20 U/mg) and RNAase (1 µL of 10 mg/ml) were added and the tubes were incubated at 60–70 °C for 40 min. The material was twice mixed and centrifuged at 18 000 rpm for 15 min with an equal volume of chloroform-isoamyl alcohol (24 : 1), keeping the aqueous phase and placing it in a new tube each time. DNA was precipitated using an equal volume of isopropanol to the aqueous extract, an incubation time varying from 0 min to overnight in -20 °C, and centrifugation at 10 000 rpm for 15 min. The resulting pellet was washed with 70 % ethanol and air-dried, then re-suspended in 0.1X TE buffer. In the occasion that a thick brown liquid precipitated upon the addition of isopropanol, or the resulting DNA extract failed to work, the extract was either diluted up to 100 times or was further cleaned. The first two buffers (AP1 and AP2) of DNeasy Plant Mini Kit (QIAGEN, Germany) were added to remove further impurities. The resulting precipitate was separated from the solution by centrifugation, and the DNA once more precipitated, washed, dried and re-suspended.

Polymerase chain reaction amplifications (PCR) were generally performed in 25–50 µL reaction volumes. The recipe for a 25 µL volume is: 10 pmol for each primer for LSU or mtSSU or 30 pmol for RPB2, 1× PCR Buffer (QIAGEN, Germany), 1 µL DNTPs, 2 µL $MgCl_2$, 0.5–1 µL BSA, 0.02 Taq polymerase. Products from multiple reactions were pooled if the products were low in concentration. The touch-down protocol used was: 5 min initial incubation at 94 °C, followed by cycles of 94 °C for 1 min, 67 °C annealing temperature for 1 min and 72 °C extension period of 1.5 min, with the annealing temperature decreasing by 1 °C every cycle until it reached 55–57 °C. A second round of 36 cycles was then used: 94 °C for 30–45 s, 55–57 °C for 1 min, and 73 °C for 1.5 min. The PCR protocol concluded with a 7-min final extension period. PCR products were visualized using agarose gel electrophoresis and ethidium bromide staining, and subsequently cleaned with the kit Nucleospin (Macherey-Nagel, Germany). When multiple bands were present, the bands of interest were cut out and cleaned according to kit instructions. When the resulting chromatograms were unreadable due to multiple signals and no better alternative specimen was available, cloning was performed to separate the strands of interest (using pGEM-T Easy Vector System and sequenced using the M13 primers with 35 cycles of 30 s at 95 °C, 30 s at 50 °C and 1 min at 72 °C).

Sequencing was performed either by cleaning with Sephadex G50 AutoSeq columns (GE Healthcare, Belgium) and run on an ABI 377 automated sequencer using the ABI BigDye Terminator chemistry for cycle sequencing (Applied Biosystems, USA), or by external services (using ABI 3730xl; Applied Biosystems, USA). The sequence chromatograms were processed using Sequencher v4.1.4 (Gene Codes Co., USA). The sequences generated for this study have been submitted to Genbank.

Multiple sequence alignments

Sequences were manually aligned in MacClade 4.06 (DR Maddison & WP Maddison, Sinauer Associates Inc., USA). In a few, small (< 12 bp), parts of the LSU and mtSSU alignment, it was difficult to unambiguously align the sequences across all taxa. If, in a section of the alignment, there was only a small fraction of taxa that could not be aligned with the remaining part, the unalignable portions (no more than 15 bp lengths) of these taxa were excluded from the analyses and were treated as missing. This procedure retained as much data as possible by preserving the information for the majority of the taxa where the alignment was unambiguous.

Conflict testing

Conflict between the RPB2, LSU and mtSSU datasets were evaluated in two ways: 1) using the ILD test (Farris et al. 1994) as implemented in PAUP* 4.b10 (Swofford 2002); and 2) by comparing phylogenetic analyses of single-locus datasets. In the second test, the results were compared to find conflicting branches in the tree that had > 70 % bootstrap support (both using maximum parsimony and maximum likelihood criteria) or that had 95 % posterior probability (p.p.) in Bayesian analyses. Some conflicts were found among the topologies of individual gene trees regarding the position of 6 species (see Results, Conflict testing). A second set of analyses that excluded these taxa was carried out for comparison to test if their inclusion had any effect on the phylogenetic reconstruction.

Phylogeny reconstruction

Maximum parsimony (MP) heuristic searches were performed using Parsimony Ratchet Analyses with PAUP* (PRAP) v1.21 using 200 ratchet replicates, 80 random addition cycles with 25 % of the characters weighted double (Müller 2004). Maximum parsimony bootstrap analyses were made with PAUP* 4.b10 (Swofford 2002) using 1 000 bootstrap replicates, each with 10 addition-sequence replicates using TBR branch swapping with a maximum of 10 trees saved per addition-sequence replicate. A bootstrap value of 70 % was considered significant.

Best-fit evolutionary models for the maximum likelihood and Bayesian analyses were selected for each single-locus dataset using MrModeltest 2.2 (Nylander 2004). The model GTR+I+G was indicated to be the best model to implement for all three loci.

Maximum likelihood (ML) analyses were performed using PHYML v3.0 (Guindon & Gascuel 2003). The following were implemented: GTR+G+I model of evolution, and four categories of the gamma distribution of the heterogeneity of the rates of evolution. SPR tree topology search was used and 1 000 bootstrap samples were used to calculate the maximum likelihood bootstrap support. A bootstrap value of 70 % was considered significant.

Bayesian analyses were performed using MrBayes v3.1.2p (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). In the 2- or 3-loci analyses, 2 or 3 partitions were set, respectively, each with a GTR+I+G model implemented. The prior on the gamma shape parameter was set to uniform ranging from 0.1 to 50. The following were implemented under the unlink command: revmat (substitution rates), pinvar (proportion of invariable sites), statefreq (character state frequencies) and shape (gamma shape parameter). Two runs, each with 11 chains were run with a temperature of 0.002 or 0.005, and three attempts at swapping every one or five generations. The topological convergence diagnostic (standard deviation of partition frequencies) was calculated every 10 000 generations but the stoprule was not implemented. The analyses were allowed to run up to 10 000 000 generations, sampling every 200 generations. More generations were added as necessary to reach convergence (as estimated by the topological convergence diagnostic equal to 0.01) between the two runs. In the case of the analysis of the LSU dataset, it reached an average standard deviation of split frequencies of only 0.014523 after 40 000 000 generations using 20 chains per run. Each LSU run was analysed separately and because the results were nearly identical in topology and support, one run was randomly chosen for the discussion and figures.

Scanning Electron Microscopy (SEM)

SEM pictures were taken to compare the taxa disputed to be either *Rhodocybe* or *Entoloma* (*E. nitidum*, *E. trachyosporum*)

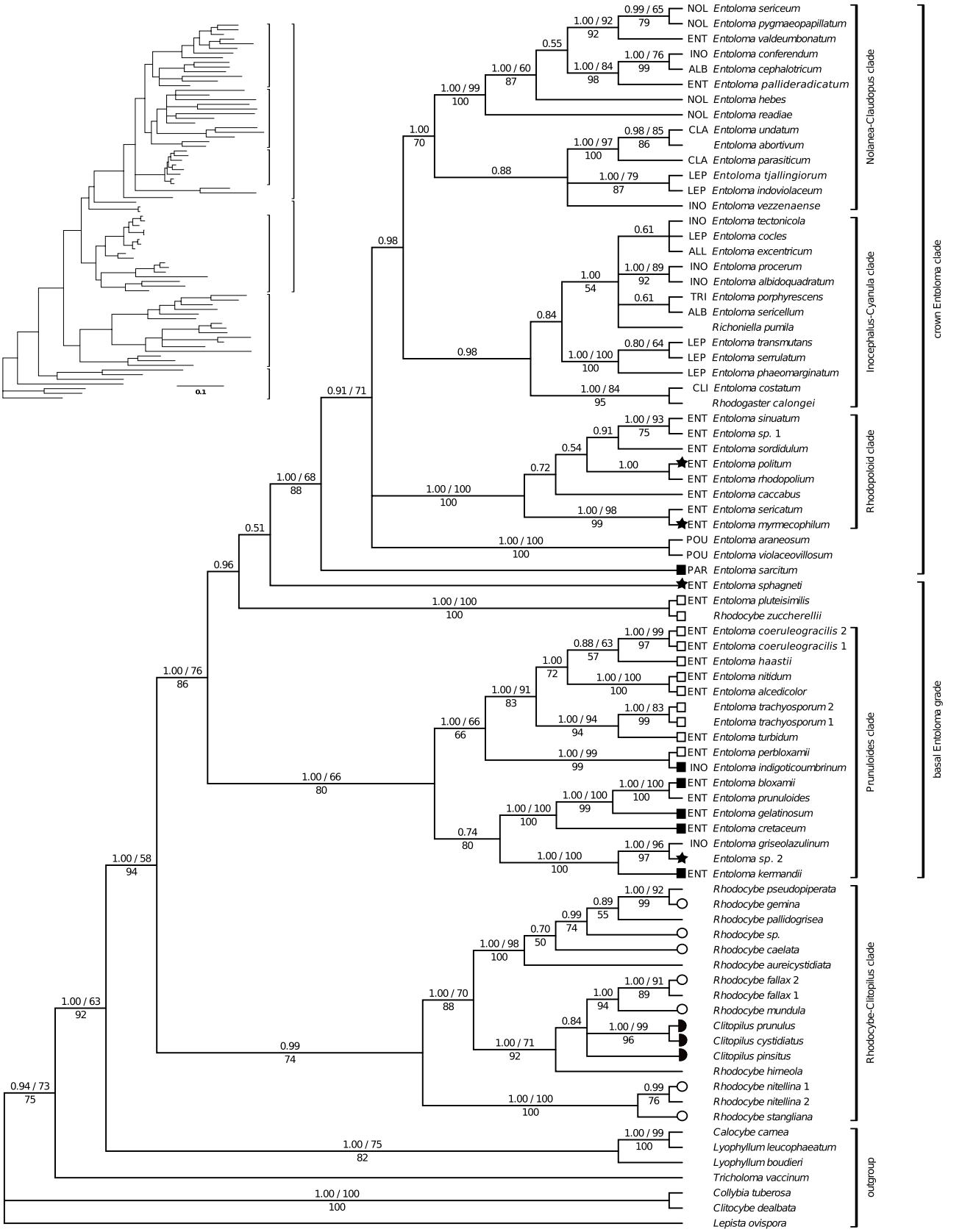

Fig. 2 Cladogram of Bayesian phylogenetic reconstruction using RPB2, LSU and mtSSU; phylogram of the same inset. Support is indicated with Bayesian p.p. / MP bootstrap percentage above the branches and ML bootstrap percentage below. Shapes at the ends of branches indicate spore type as determined using SEM except for *Clitopilus* spores which were determined through light microscopy: ★ regular entolomatoid spore, ■ irregular entolomatoid spore, no bumps; □ very irregular entolomatoid spore with bumps; ◯ rhodocyboid spore, ◗ clitopiloid spore. Subgenera of *Entoloma* species (according to Noordeloos 2004, Manimohan et al. 2006, Gates & Noordeloos 2007) is indicated as follows: ALB = *Alboleptonia*, ALL = *Allocybe*, CLA = *Claudopus*, CLI = *Clitopiloides*, ENT = *Entoloma*, INO = *Inocephalus*, LEP = *Leptonia*, NOL = *Nolanea*, PAR = *Paraleptonia*, POU = *Pouzarella*, TRI = *Trichopilus*.

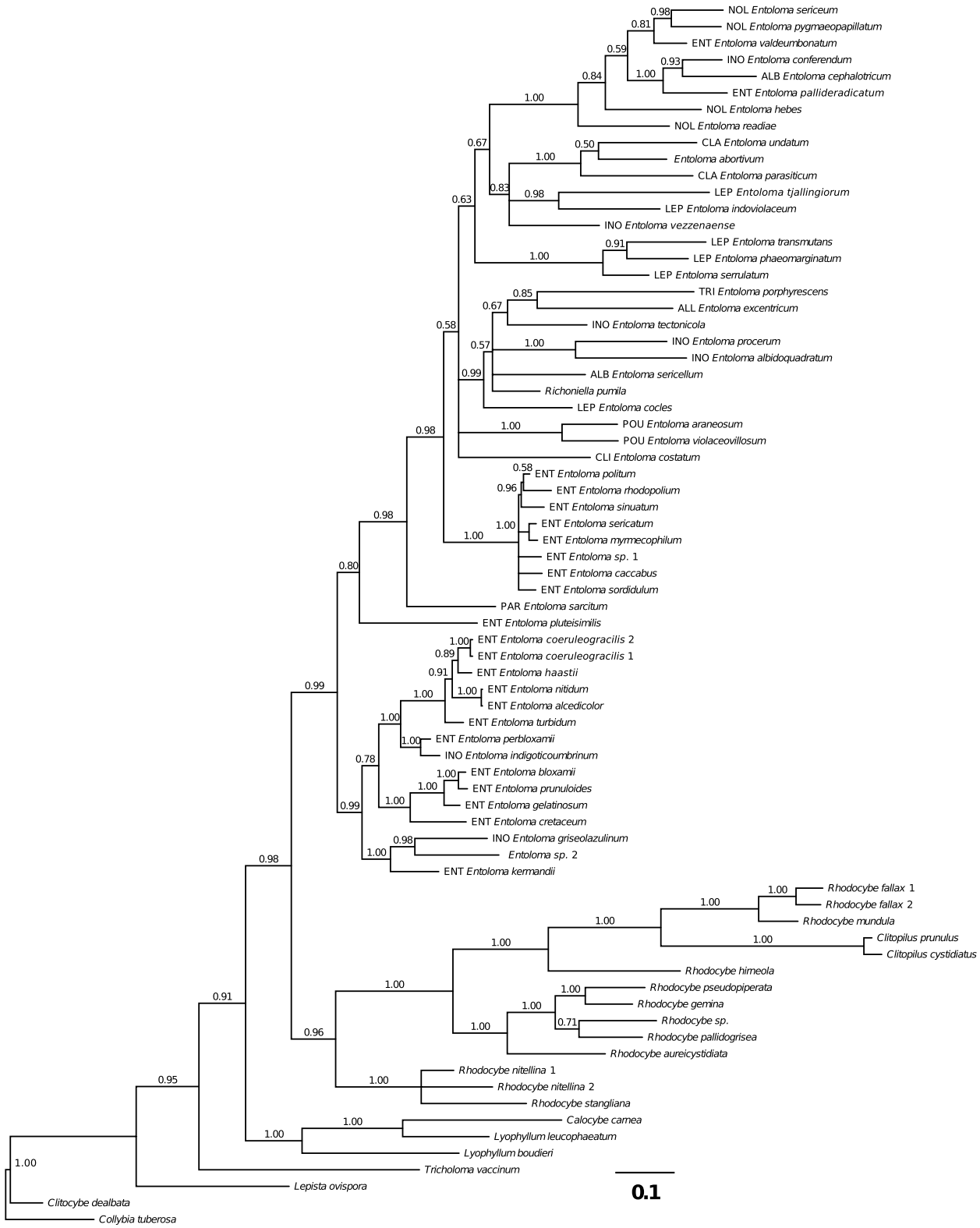

Fig. 3 Phylogram of Bayesian analysis of RPB2. Bayesian p.p. indicated above the branch. Subgenera of *Entoloma* species (according to Noordeloos 2004, Manimohan et al. 2006, Gates & Noordeloos 2007) is indicated as follows: ALB *Alboleptonia*, ALL *Allocybe*, CLA *Claudopus*, CLI *Clitopiloides*, ENT *Entoloma*, INO *Inocephalus*, LEP *Leptonia*, NOL *Nolanea*, PAR *Paraleptonia*, POU *Pouzarella*, TRI *Trichopilus*.

and compared with their supposed close relatives from *Rhodocybe* and *Entoloma* (see Table 1 where species samples for DNA and spores are noted). The spores were examined and scored for characters that define the difference between the classical entolomatoid and rhodocyboid spores:

1. the presence of isolated bumps and ridges (characteristic of rhodocyboid spores);
2. the presence of facets (characteristic of entolomatoid spores). If facets were present, then it was noted;
3. whether the facets were defined by a network of either incompletely or completely interconnected ridges. Ridges with an end that did not interconnect with another ridge were disregarded and not counted as irregular if the ridges ended towards the apiculus (and thus had no ridge to connect with) or if they symmetrically bisected a facet (with the argument that such bisections are regular).

Preparation of spores was from Baroni (1981), with the following modifications: preparations were washed twice in distilled

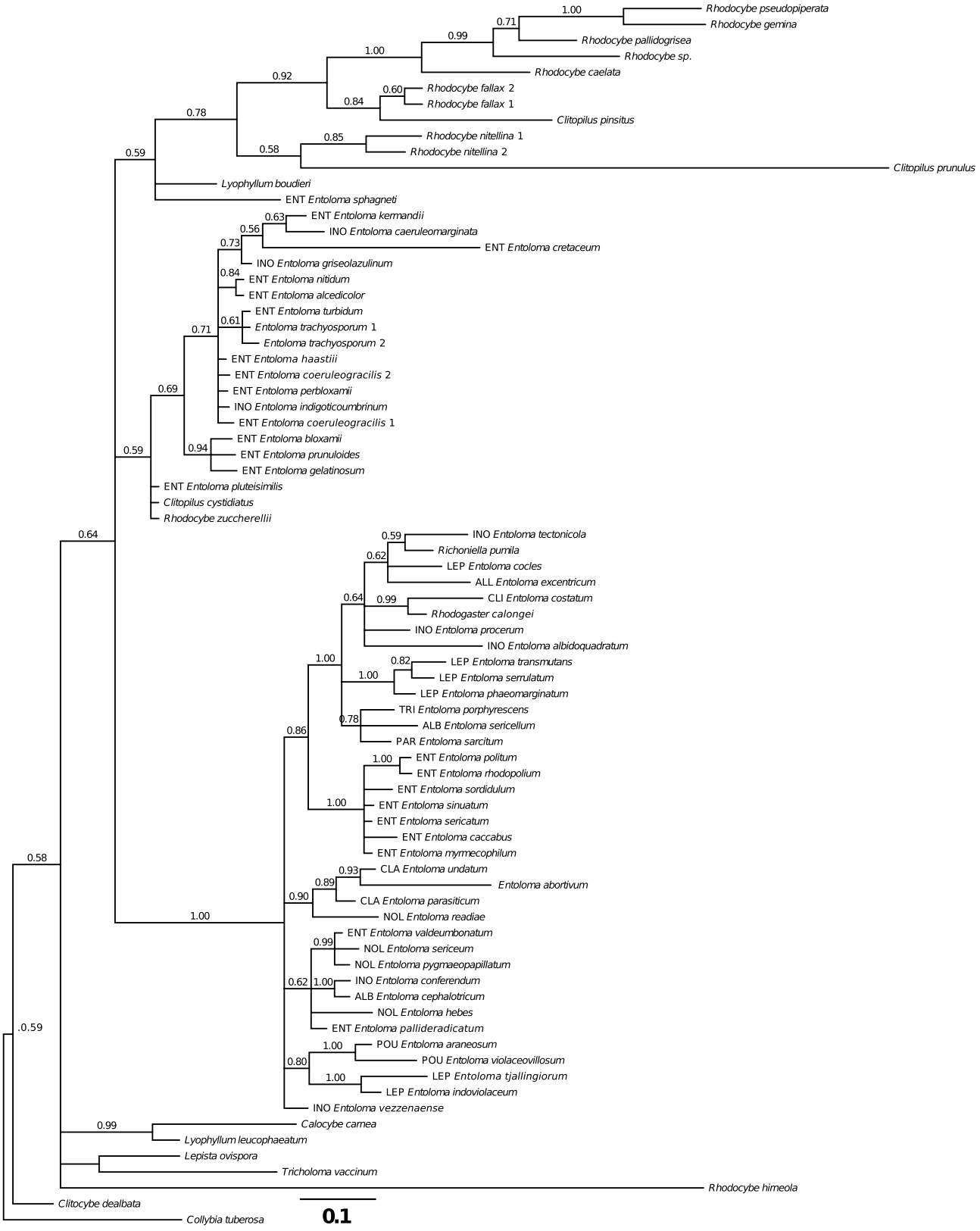

Fig.4 Phylogram of Bayesian analysis of mtSSU. Bayesian p.p. indicated above the branch. Subgenera of *Entoloma* species (according to Noordeloos 2004, Manimohan et al. 2006, Gates & Noordeloos 2007) is indicated as follows: ALB *Alboleptonia*, ALL *Allocybe*, CLA *Claudopus*, CLI *Clitopiloides*, ENT *Entoloma*, INO *Inocephalus*, LEP *Leptonia*, NOL *Nolanea*, PAR *Paraleptonia*, POU *Pouzarella*, TRI *Trichopilus*.

water before dehydration for 20 min in 50 % acetone, followed by 20 min in 100 % acetone, then critical-point dried in a Balzers CPD 030 Critical Point Dryer (BAL-TEC, Liechtenstein) and sputter-coated in a SCD 005 Sputter Coater (BAL-TEC, Liechtenstein). Finally, SEM pictures were taken using JSM-530 Scanning Microscope (Jeol Ltd., Japan).

Transmission Electron Microscopy (TEM)

TEM photos were taken of some *Entolomataceae* as well as some of its close relatives in the Tricholomatoid clade sensu Matheny et al. (2006) within which *Entolomataceae* is nested (Hofstetter et al. 2002, Moncalvo et al. 2002, Matheny et al. 2006). These relatives sampled have bumpy or roughened

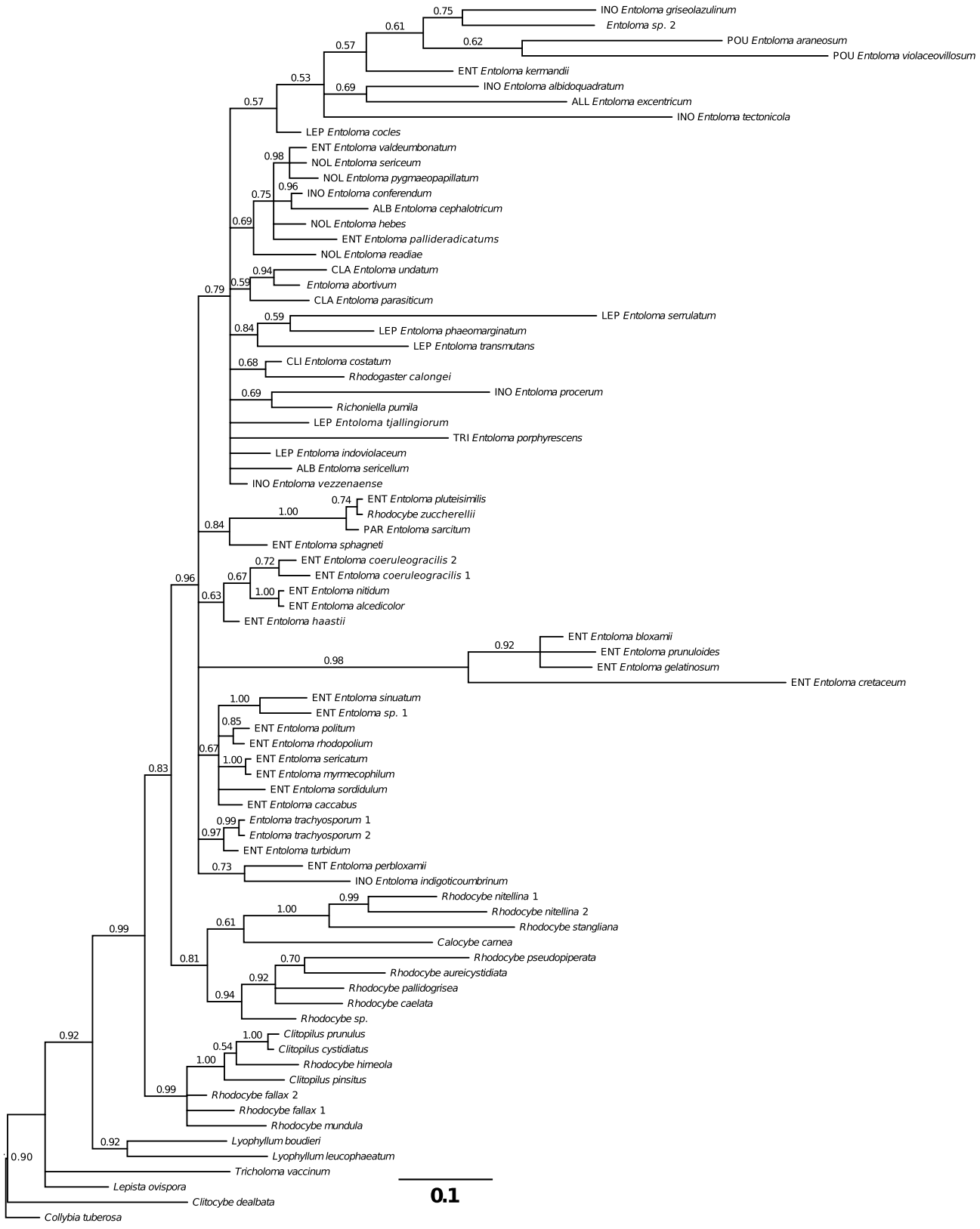

Fig. 5 Phylogram of Bayesian analysis of LSU. Bayesian p.p. indicated above the branch. Subgenera of *Entoloma* species (according to Noordeloos 2004, Manimohan et al. 2006, Gates & Noordeloos 2007) is indicated as follows: ALB *Alboleptonia*, ALL *Allocybe*, CLA *Claudopus*, CLI *Clitopiloides*, ENT *Entoloma*, INO *Inocephalus*, LEP *Leptonia*, NOL *Nolanea*, PAR *Paraleptonia*, POU *Pouzarella*, TRI *Trichopilus*.

spores: *Tephrocybe tylicolor* (Fr.) M.M. Moser, *Tephrocybe ambusta* (Fr.) Donk, *Lepista irina* (Fr.) H.E. Bigelow, *Lepista nuda* (Bull.) Cooke, and *Omphaliaster asterosporus* (J.E. Lange) Lamoure. It was noted what part of the spore wall formed the ornamentations to assess probably homologous structures.

Procedure follows Van der Ham (1990) with the following modifications: rehydration with glutaraldehyde was 3 w, fixing in OsO_4 was for 1.5 h, pre-staining was with 1 % uranylacetate and soaking in lead citrate (Reynolds 1963) was for 10 min. The thickness of the cuts was 800 microns. The TEM machine was JEOL JEM-1010 Electron Microscope, JEOL Ltd. (Korea).

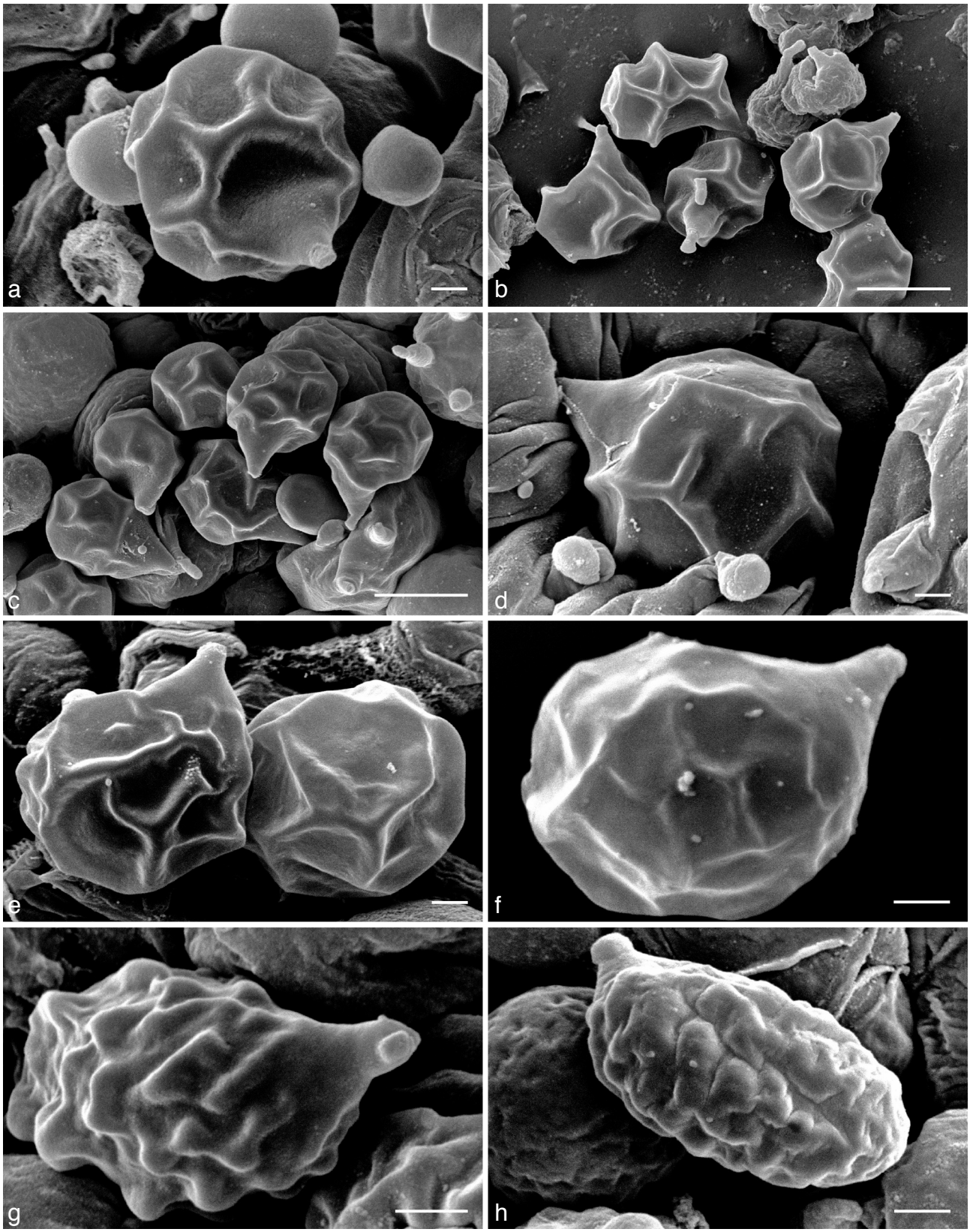

Fig. 6 SEM pictures of *Entolomataceae* spores. a, b. Regular entolomatoid spores. a. *Entoloma indigoticoumbrinum*; b. *E. sp.* — c, d. Slightly irregular entolomatoid spores. c. *E. kermandii*; d. *E. bloxamii.* — e, f. Very irregular entolomatoid spores with bumps. e. *E. nitidum*; f. *E. trachyosporum.* — g, h. Rhodocyboid spores. g. *Rhodocybe nitellina*; h. *R. caelata*.

RESULTS

After sequencing and aligning, mtSSU yieled an alignment length of 360 bp and 95 parsimony-informative sites. RPB2 yielded an alignment length of 576 bp and 266 parsimony-informative sites. LSU yielded an alignment length of 707 bp and 169 parsimony-informative sites.

Of the three DNA loci sequenced, RPB2 yielded the best-resolved and best-supported phylogenetic reconstruction and LSU the least resolved and supported. The results of the 3-loci analyses are summarized in Fig. 2, while Fig. 3–5 show the Bayesian analyses of the single-gene datasets. The alignments of taxa with particularly long branch lengths (*R. hirneola*, *C. prunulus*) were examined. Both species were not misaligned and each had a large number of autapomorphies.

Conflict testing

Evaluation of conflicts by comparing the different trees from the single-gene analyses led to the conclusion that gene trees were mostly compatible and had no significantly supported conflicts (> 70 % MP or ML bootstrap or 0.95 Bayesian posterior probability) among the resulting reconstructions with the exception of two taxa: *C. cystidiatus* and *E. sarcitum.*

In the phylogenetic reconstructions with RPB2 and LSU, *C. cystidiatus* was strongly supported as sister group to *C. prunulus* in the Rhodocybe-Clitopilus clade. On the other hand, in the mtSSU reconstruction, *C. cystidiatus* was sister to *E. prunuloides* with 75 % MP bootstrap and 91 % ML bootstrap. These two taxa were placed within the insignificantly supported Entoloma clade.

The placement of *E. sarcitum* was different in the phylogenetic reconstructions of all three loci. It was placed in the Inocephalus-Cyanula clade in the ML and Bayesian analyses of mtSSU (57 % ML bootstrap and 0.99 Bayesian posterior probability; MP analyses were unresolved). Using LSU, *E. sarcitum* was strongly supported in a clade with *E. pluteisimilis* and *R. zuccherellii* (100 % MP bootstrap, 100 % ML bootstrap, and 1.00 Bayesian posterior probability), but with its relationship to others in the Entoloma clade was unresolved. In contrast, ML and Bayesian analyses of RPB2 placed it as sister to most of the genus *Entoloma* excluding the Prunuloides clade (that is, the rest of the crown Entoloma clade; 0.98 Bayesian posterior probability and 64 % ML bootstrap), while it was unresolved in the MP analysis.

Four other taxa had different positions in the single-gene analyses, but these placements did not receive significant support. Their strongly supported placements in the 3-loci analyses are more consistent with morphological studies. The first, *E. kermandii*, is in the Prunuloides clade in the Bayesian and ML analyses of RPB2 and mtSSU, while the same analyses of LSU place it among members of the Inocephalus-Cyanula clade. Second, *Calocybe carnea* (selected as outgroup) was in the Bayesian and ML analyses in one clade with *Rhodocybe*. Third and fourth, Bayesian and ML analyses of mtSSU had *Lyophyllum boudieri* in the Rhodocybe-Clitopilus clade while *R. hirneola* (Fr.) P.D. Orton was with the rest of the outgroup. The consensus tree of the most parsimonious trees of these analyses did not show the same unexpected placement, but it had poor resolution.

Analyses of single-gene and 3-loci datasets after the exclusion of these 6 taxa produced trees that were very similar with respect to topology and the level of support of the recognized clades, with some exceptions in the 3-locus dataset. The Bayesian posterior probability values for the monophyly of *E. pluteisimilis*, *R. zuccherellii*, *E. sphagneti*, and the rest of *Entoloma* excluding the Prunuloides clade changed from 0.96 to 0.84. Similarly, in the ML analyses, bootstrap support for the Nolanea-Claudopus clade decreased from 70 % to 60 %. On the other hand, support for the monophyly of a clade composed of Nolanea-Claudopus, Inocephalus-Cyanula, Pouzarella and the Rhodopolioid clades increased from 88 % to 100 %. Nonetheless, the phylogenetic reconstructions and conclusions drawn were not affected by these changes.

The ILD test indicated that while RPB2 and mtSSU were not significantly incongruent (P = 0.133), LSU was incongruent with both RPB2 and mtSSU (both P = 0.001). In order to test whether the taxa mentioned above caused the incongruence, the ILD test was once again performed without these taxa. The new analysis yielded the same conclusions.

Entolomataceae spore types from SEM photos — Fig. 6

Three main spore types could be recognized:

1. clitopiloid spores with longitudinal grooves and ridges;
2. rhodocyboid spores with irregular bumps and ridges;
3. entolomatoid spores with facets.

Entolomatoid spores are subdivided into three subtypes:

1. regular entolomatoid spores with ridges that completely interconnect to form facets and that have no isolated bumps;
2. irregular entolomatoid spores with at least one ridge end not connecting with another ridge to delineate a facet, giving a slightly to very irregular look, but without bumps and;
3. very irregular entolomatoid spores with bumps.

Irregular entolomatoid spores have not been reported before and bumps have previously not been known to occur in *Entoloma* (Baroni & Largent 1989). The degree of irregularity is highly variable among species. The regular and irregular entolomatoid spores grade into each other. Some very irregular spores with bumps are similar at first glance to some rhodocyboid spores with many ridges. However, regular and irregular entolomatoid spores are united by the presence of facets, and these are never present in rhodocyboid spores.

The spore wall of species with irregular entolomatoid spores is usually thinner than that of regular entolomatoid spores when viewed under a light microscope. We cannot exclude the possibility that the spores are truly regular, and that the apparent irregularity of the spore ridges is an artifact of spore preparation for SEM due to the thin spore walls. If this is the case, it is a phylogenetically informative artifact.

The spore types are mapped on the 3-loci phylogenetic reconstruction in Fig. 2. The Prunuloides clade is characterized by mostly irregular entolomatoid spores, with one subclade predominantly having very irregular spores with bumps and the other subclade having irregular spores without bumps. The Crown Entoloma clade, having regular entolomatoid spores (based on observations under the light microscope and SEM pictures by Pegler & Young 1978, 1979), contrasts with the rest of *Entoloma* (Prunuloides clade, the clade of *E. pluteisimilis* and *R. zuccherellii*, and *E. sarcitum*), as the latter set of species have mostly irregular entolomatoid spores (with or without bumps).

Ultrastructure of the spore-wall in relation to the ornamentation using TEM — Fig. 7

Comparison of the spore wall structures in *Entolomataceae* and five representatives of the Tricholomatoid clade sensu Matheny et al. (2006) with ornamented spores showed that the structures forming the angularity or bumps in the *Entolomataceae* are different from those of the ornamentation of its closest relatives; none of the latter are formed with an epicorium and tunica.

DISCUSSION

Conflict testing

The two tests for conflict yielded two kinds of apparent conflict. In the first instance, taxa had different positions according to different single-locus analyses. In the second instance, the ILD test indicated that analyses based on both mtSSU and RPB2 were incongruent with LSU. In the first case, phylogenetic analyses performed after the removal of the relevant taxa resulted in no significant changes to the phylogeny. In the case of the ILD test, the 2-loci phylogenetic analyses with just the supposedly congruent RPB2 and mtSSU yield phylogenetic reconstructions similar to the results of 3-loci analyses, supporting the conclusions of this study. We conclude that RPB2 and LSU informed the analyses more than LSU. Furthermore, there are cases

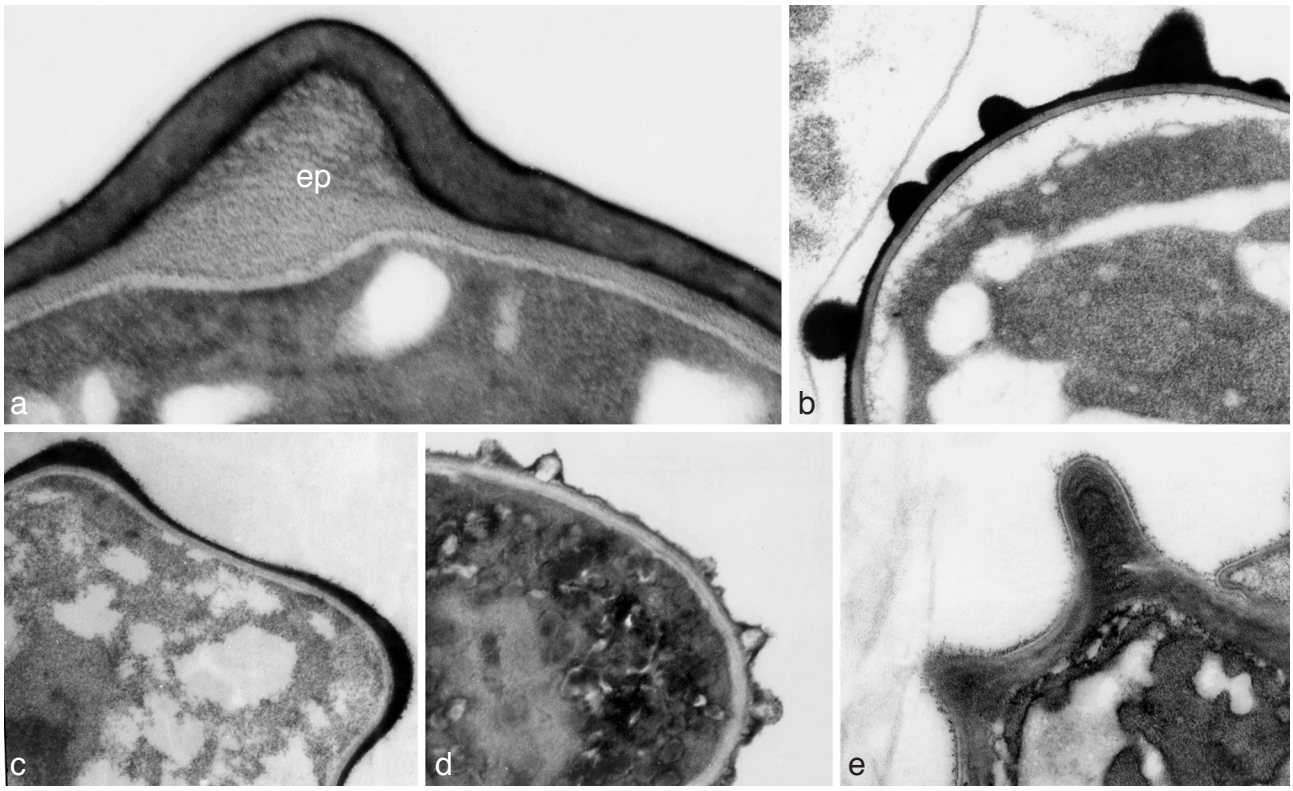

Fig. 7 TEM of spore walls of members of the Tricholomatoid clade sensu Matheny et al. (2006) that have some bumpy or roughened spores. a. *Entoloma gelatinosum* is an example of a typical *Entolomataceae* spore wall with a distinct grainy lower layer, the coriotunica and an evenly electron-dense upper layer, the tunica. The ornamentation is formed by the epicorium (ep), which appears continuous with the eusporium (G.Gates E792, L). b. *Tephrocybe tylicolor* and c. *Tephrocybe ambusta* both have a coriotunica and tunica. The ornamentation is formed by the thickening of the tunica (rather than by an epicorium) (E.Arnolds 5151, L). This is also how *Lepista irina* (not shown) forms its roughened spores. d. *Lepista nuda* has a coriotunica and a myxosporium, a layer that corresponds to the other species' tunica, though here it is not as thick and evenly electron-opaque. Bumps are formed by 'bubbles' in the myxosporium with a hollow or electron-transparent interior (E.Arnolds 6866, L). e. *Omphaliaster asterosporus*. The spore walls have three layers: from the outside, a thin, grainy electron-dense layer, a thin, electron-transparent layer and a thick, electron-dense layer, thickenings of which form the bumps (ECVellinga 1110, L).

where the ILD test fails (Dolphin et al. 2000, Darlu & Lecointre 2002) and this may have been the case here.

Monophyly of the Entolomataceae

The results of this molecular phylogenetic study are consistent with recent studies, based on both morphology and molecular phylogenetics data, that the family *Entolomataceae* is a natural group (Singer 1986, Noordeloos 1981, 1992, 2005) and is monophyletic (Matheny et al. 2006). *Entolomataceae* comprises the genera *Entoloma*, *Rhodocybe*, *Clitopilus*, *Richoniella* and *Rhodogaster*, and probably *Rhodocybella* as well. This study confirms that the presence of pink, angular or bumpy spores with a well-developed epicorium in the spore wall, which forms the facets, ridges or bumps and which was traditionally used to define the family *Entolomataceae*, has evolved only once among the euagarics. The ornamentations found among relatives, the members of the Tricholomatoid clade, are different and not homologous with those of *Entolomataceae*, as noted already before by Kühner (1980) and Clemençon et al. (2004).

Generic delimitation of Entolomataceae

Entolomataceae is divided into two monophyletic clades: one containing *Rhodocybe* and *Clitopilus*, and the other containing *Entoloma*, *Richoniella* and *Rhodogaster*.

In the Rhodocybe-Clitopilus clade, *Rhodocybe* is paraphyletic and *Clitopilus* is, with significant support, well-nested within *Rhodocybe*. Previous studies had already suggested this relationship (Moncalvo et al. 2002, Matheny et al. 2006). Some *Rhodocybe* spores have bumps and ridges arranged linearly along the spore length (Baroni 1981), presenting a spore shape that approaches clitopiloid spores. Kühner (1980) had already united *Clitopilus* with *Rhodocybe* in one genus on account of the characters these groups share: predominantly clitocyboid habit, decurrent lamellae, and resemblance in basal structure of the ornamentation of the spores. We formally merge *Rhodocybe* into *Clitopilus* (the oldest valid name) and make the necessary new combinations (see Appendix).

We consider it highly likely that future molecular phylogenetic studies will show that the cyphelloid *Rhodocybella* is nested within the Rhodocybe-Clitopilus clade. If so, its generic status will be untenable. This likelihood is indicated by the genus' rhodocyboid spores and the existence of somewhat similar, reduced forms (pleurotoid rather than cyphelloid) in the clade.

Delimitation of the genus Entoloma

Phylogenetic analyses demonstrate that the sequestrate genera *Richoniella* and *Rhodogaster* arose from within *Entoloma*. Therefore, *Entoloma* is monophyletic only if these genera are included. Placement of these sequestrate genera within *Entoloma* had been suggested before (Kuyper in Kirk et al. 2008).

Richoniella and *Rhodogaster* do not form a monophyletic group. The sequestrate habit arose at least twice from agaricoid ancestors within *Entoloma*. Only one species of each genus was included in these studies and so the monophyly of each genus could not be tested. Future studies can address this possibility of parallel evolution. It is generally accepted that sequestrate taxa were derived many times from agaricoid forms and that this character was much overemphasized in the past (Peintner et al. 2001). We emend the description of *Entoloma* to include these sequestrate taxa (see Appendix).

The independent evolution of *Rhodogaster* and *Richoniella* shows that *Rhodogaster* (secotioid, and intermediate in form between agaricoid and gasteroid sporocarps) is not an evolutionary intermediate or the missing link between *Entoloma* and *Richoniella.*

Should *Entoloma* be maintained as one genus or should it be split, based on the results of our phylogenetic analyses? While a phylogeny per se allows different answers to that question, we propose it is best to retain *Entoloma* as a very large and morphologically variable genus in order to have a stable classification that is consistent with phylogeny. Our proposal to retain one large genus *Entoloma* conforms to the taxonomic tradition (Romagnesi 1974, 1978, Noordeloos 2004). Relevant nomenclatural changes are made (see Appendix).

The inclusion of *Rhodogaster* and *Richoniella* in a monophyletic *Entoloma* strengthens our argument. If *Entoloma* had not been monophyletic, alternative proposals of smaller genera would have been strengthened.

The currently proposed smaller subgenera are polyphyletic or paraphyletic, leaving one large genus indeed as the only viable option. Horak's (1973, 1980) division of *Entoloma* s.l. into three genera is inconsistent with phylogeny. Horak separated the strikingly morphologically distinct *Pouzarella* and *Claudopus* (pleurotoid species only) from the rest of *Entoloma* and treated them on a generic level. However, this classification would result in a paraphyletic *Entoloma* s.s. and a polyphyletic *Claudopus*. Among the 13 proposed genera of Largent (1994), this study shows that at least five genera, viz. *Entoloma*, *Leptonia*, *Nolanea*, *Alboleptonia*, and *Calliderma* are not monophyletic. Of these, the first four are the largest genera containing most of the known species and the only major genus not demonstrably polyphyletic is *Inocephalus*. The monophyly of the other seven genera can also neither be disproven nor supported with the current phylogenetic reconstruction due to lack of sampling. Most species of *Entoloma* s.s. are in two different strongly supported clades, one of which, the Rhodopolioid clade, is more closely related to members of *Nolanea* or *Leptonia* than to the other, the Prunuloides clade. *Leptonia* species are in three different clades and *Alboleptonia* in two. Species, which show morphological characters of *Calliderma*, viz., *E. indigoticoumbrinum* and *E. griseolazulinum*, are nested and not monophyletic within the Prunuloides clade. Furthermore, *Nolanea* is paraphyletic since the well-supported clade containing *Nolanea* also contains members of *Entoloma* s.s. and *Alboleptonia* (Fig. 2).

A phylogenetic study of the genus *Entoloma* using a larger dataset is currently in progress (Co-David & Noordeloos, unpubl. data). This study will use both molecular and morphological data to distinguish well-supported monophyletic clades, with implications for infrageneric taxonomy and character evolution.

The distinction between Rhodocybe and Entoloma

We reject the proposed transfer of *E. nitidum* and *E. trachyosporum* to *Rhodocybe* (Baroni & Largent 1993, Castellano et al. 1999). These taxa belong, with significant support, to the Prunuloides clade of *Entoloma*. *Rhodocybe zuccherellii* also belongs to *Entoloma* and we make the transfer.

SEM pictures revealed that their spores have facets, which rhodocyboid spores do not (*E. nitidum* and *E. trachyosporum* on Fig. 6). The confusion regarding their generic placement likely arose because the pattern of their spores, and those of many of their close relatives, is irregular. The ridges that define the facets do not always interconnect, and sometimes there are bumps. This irregularity as well as the difficulty in seeing facets under the light microscope may be because the ridges themselves are thinner and not as distinct as those in spores with regular facets.

The placement of these taxa in *Entoloma* also makes sense in the light of morphology. The presence of clamps distinguishes them from most of the taxa of *Rhodocybe* except for section *Rhodophana*, which does have abundant clamp-connections. A morphological character that distinguishes the relevant *Entoloma* species from *Rhodophana* is pileipellis structure: Species in *Rhodophana* have a compact, uni-layered cutis gradually passing into the trama without a well-developed subpellis, while these *Entoloma* species have a bi-layered pileipellis with a thin suprapellis of narrow hyphae, and a well-developed subpellis of inflated elements (Baroni 1981, Noordeloos 2004).

Spore evolution

The monophyly of *Entolomataceae* shows that pink, angular spores arose once. Given that the family is nested in the Tricholomatoid clade (sensu Matheny et al. 2006), its ancestral spore likely arose from white, smooth spores that are common in the clade.

The ancestral spore of *Entolomataceae* is yet unknown. However, it was either rhodocyboid or entolomatoid. Both reconstructions are consistent with the phylogeny. Clitopiloid spores are definitely not the ancestral spores of *Entolomataceae*. Rather, clitopiloid spores arose from rhodocyboid spores. This conclusion is further supported by observations that some rhodocyboid spores are more elongate and have their ridges and bumps aligned in rows along the length of the spore, similar to clitopiloid spores (Baroni 1981). Consequently, we reject Kühner's (1980) theory that the spores of *Clitopilus* are intermediate between *Rhodocybe* and *Entoloma* because it is inconsistent with the phylogenetic reconstruction, where *Clitopilus*, is well-nested within *Rhodocybe*. *Clitopilus* is also too distant from *Entoloma* to have shared an ancestor with clitopiloid spores. Baroni's (1981) theory that clitopiloid and entolomatoid spores were both independently derived from rhodocyboid spores is consistent with the phylogenetic reconstruction.

Another hypothesis must be taken into account, because it is equally consistent with the phylogeny, namely that the entolomatoid rather than rhodocyboid spore type is ancestral. In this theory, entolomatoid spores (regular or irregular) gave rise to rhodocyboid spores that, in turn, gave rise to clitopiloid spores. We suggest two major reasons why this hypothesis (the entomolatoid spore as ancestral character state) has never been proposed before.

First is the assumption that *Entolomataceae* evolved from *Tricholomataceae* combined with the assumed homology between bumps on *Rhodocybe* spores and the bumps on the spores of the putative *Tricholomataceae* ancestral taxa (Kühner 1980, Baroni 1981). These bumpy-spored relatives of the Tricholomatoid clade are nested among their smooth-spored relatives, as is *Entolomataceae* (Moncalvo et al. 2002, Matheny et al. 2006), making it likely that these taxa all evolved spore wall ornamentations independently. Furthermore, the putative homology between species with bumpy spores itself is incorrect. Our study confirms that the spore walls of species in the Tricholomatoid clade with bumpy spores are not homologous to those found in *Entolomataceae* (as earlier implied by Clémençon 1997, Clémençon et al. 2004). This lack of homology refutes the possible argument for rhodocyboid ancestral spores that members of the Tricholomatoid clade have a spore feature that allows it to frequently, independently evolve rhodocyboid spores.

The second reason for the predominance of the hypothesis that rhodocyboid spores are ancestral is the implicit assumption on the direction of spore character evolution. The assumption is that, in evolution, complex structures are more derived (or advanced) than simple structures. This assumption is not always

the case, the derivation of more simple sequestrate forms from more complex agaricoid ones being an example (Peintner et al. 2001, this study). Also, the assumption that if there is a morphological gradation (smooth spores to bumpy spores to faceted spores), then evolution must have occurred along the direction of the gradation is not necessarily true either. Therefore, we must consider both the rhodocyboid and entolomatoid spore type as possible ancestral states for *Entolomataceae* spores until further studies disprove either possibility.

APPENDIX
TAXONOMIC AND NOMENCLATURAL CHANGES

Entolomataceae Kotl. & Pouzar, Česká Mykol. 26: 218. 1972 emend. Co-David & Noordel.

Rhodogoniosporaceae Heim, Treb. Mus. Ci. Nat. Barcelona 15: 86. 1934 (invalid). — *Jugasporaceae* Singer, Ann. Mycol. 34: 327. 1936 (invalid). — *Clitopilaceae* P.D. Orton, Trans. Brit. Mycol. Soc., Suppl.: 6. 1960 (invalid). — *Rhodophyllaceae* Singer, Lilloa 22: 601. 1949 (1951) (invalid).

Type genus. *Entoloma* (Fr.) P. Kumm. emend. Co-David & Noordel.

Genera. *Entoloma* (Fr.) P. Kumm., *Clitopilus* (Fr.) P. Kumm. *Rhodocybella* T.J. Baroni & R.H. Petersen.

Basidiomata agaricoid, cyphelloid, secotioid or gasteroid; spore print pink; spores provided with either bumps or undulate ridges, or longitudinal ridges, and then angular in polar view, or faceted and angular in all views; spore wall in TEM with a distinct epicorium forming the bumps and ridges. Saprotrophic, mycorrhizal or parasitic. Cosmopolitan.

Notes — The family *Entolomataceae* is emended here to include the gasteroid *Richoniella* and the secotioid *Rhodogaster.*

Entoloma (Fr.) P. Kumm.

Agaricus tribus *Entoloma* Fr., Epicrisis: 143. 1838; *Agaricus* subgenus *Entoloma* (Fr.) Rabenh., Deutschl. Krypt.-Fl. 1: 508. 1844; *Entoloma* (Fr.) P. Kumm., Führer Pilzk.: 23. 1871. — *Nolanea* (Fr.) P. Kumm., Führer Pilzk.: 23. 1871. — *Leptonia* (Fr.) P. Kumm., Führer Pilzk.: 23. 1871. — *Eccilia* (Fr.) P. Kumm., Führer Pilzk.: 23. 1871. — *Claudopus* Gillet, Hymenom. Fr.: 426. 1876. — *Rhodophyllus* Quél., Enchiridion: 56. 1886. — *Latzinia* Kuntze, Revis. Gen. Pl. 2: 857. 1891. — *Leptoniella* Earle, Bull. New York Bot. Gard. 5: 424. 1909. — *Lanolea* Nieuwl., Amer. Midl. Naturalist 4: 381. 1916. — *Richoniella* Costantin & L.M. Dufour, Nouv. Fl. Champ. ed. 5. 203. 1916. — *Pouzaromyces* Pilát, Acta Mus. Nat. Prag. (B) 9, 2: 60. 1953. — *Rhodogaster* E. Horak, Sydowia 17: 190. 18 June 1964 ('1963'). — *Alboleptonia* Largent & R.G. Benedict, Mycologia 63: 439. 1970. — *Pouzarella* Mazzer, Biblthca Mycol. 46: 69. 1978. — *Trichopilus* (Romagn.) P. D. Orton, Mycologist 5, 4: 175. 1991. — *Paraleptonia* (Romagn. ex Noordel.) P.D. Orton, Mycologist 5, 4: 174. 1991. — *Clitopiloidea* (Romagn.) Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 31. 1994. — *Calliderma* (Romagn.) Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 31. 1994. — *Fibropilus* (Noordel.) Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 32. 1994.— *Paraeccilia* Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 368. 1994. — Lectotype (Donk, Beih. Nova Hedwigia 5: 95. 1962): *Entoloma prunuloides* (Fr.) Quél.

Basidiomata agaricoid, secotioid or gasteroid; spore print pink; spores angular in all views. Facets formed by completely or incompletely interconnecting ridges, rarely with isolated bumps.

Notes — The generic concept of *Entoloma* is emended here to include *Rhodogaster* and *Richoniella.* Kirk et al. (2008) listed *Rhodocybe* and *Rhodocybella* as synonyms of *Entoloma*, but this is evidently an error. This has now been corrected (see http://www.indexfungorum.org/Names/fundic.asp).

Clitopilus (Fr. ex Rabenh.) P. Kumm., Führer Pilzk.: 23. 1871 emend. Co-David & Noordel.

Agaricus tribus *Clitopilus* Fr., Epicrisis: 148. 1838. — *Hexajuga* Fayod, Ann. Soc. Bot. VII.9: 389. 1889. — *Octojuga* Fayod, Ann. Soc. Bot. VII.9: 390. 1889. — *Orcella* Earle, Bull. New York Bot. Gard. 5: 430. 1909. — *Rhodocybe* Maire, Bull. Soc. Mycol. France 40: 298. 1925. — *Clitopilopsis* Maire, Publ. Inst. Bot. 3, 4: 82. 1937. — *Hirneola* Velen., Nov. Myc.: 73. 1939. — *Pluteispora* Maire, Bull. Soc. Mycol. France 50: xxvii. 1935 (1934). — *Rhodophana* Kühner ex Métrod, Rev. Mycol. 17: 69. 1952 (invalid).

Type species. *Clitopilus prunulus* (Scop.) P. Kumm.

Basidiomata agaricoid. Spore print pink. Spores either provided with longitudinal ribs, appearing angular in polar view, or with bumps, which may be more or less evenly distributed or arranged in lines, never with true facets.

Notes — *Clitopilus* is emended here to include *Rhodocybe* Maire. Its phylogenetic relationship with the cyphelloid genus *Rhodocybella* T.J. Baroni & R.H. Petersen has not yet been established.

NEW COMBINATIONS AND NEW NAMES

Clitopilus acerbus Noordel. & Co-David, *nom. nov.* — MycoBank MB509853

Basionym. Rhodocybe amara T.J. Baroni & G.M. Gates, Austral. Syst. Bot. 19: 352. 2006. Non *Clitopilus amarus* A. de Haan. 1998.

Clitopilus albovelutinus (G. Stev.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509854

Basionym. Lentinus albovelutinus G. Stev., Kew Bull. 19, 1: 32. 1964.

Clitopilus alutaceus (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509855

Basionym. Rhodocybe alutacea Singer, Mycologia 38: 688. 1946.

Clitopilus alutaceus var. ***carpogenus*** (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509856

Basionym. Rhodocybe alutacea var. *carpogena* T.J. Baroni, Beih. Nova Hedwigia 67: 86. 1981.

Clitopilus amarellus (Cons., D. Antonini, M. Antonini & Contu) Noordel. & Co-David, *comb. nov.* — MycoBank MB509817

Basionym. Rhodocybe amarella Cons., D. Antonini, M. Antonini & Contu, Riv. Micol. 47: 319. 2004.

Clitopilus angustisporus (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509858

Basionym. Rhodocybe angustispora Singer, Fieldiana, Bot. 21: 122. 1989.

Clitopilus ardosiacus (E. Horak & Griesser) Noordel. & Co-David, *comb. nov.* — MycoBank MB509859

Basionym. Rhodocybe ardosiaca E. Horak & Griesser, Beitr. Kenntn. Pilze Mitteleur. 3: 268. 1987.

Clitopilus aureicystidiatus (Lennox ex T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509860

Basionym. Rhodocybe aureicystidiata Lennox ex T.J. Baroni, Beih. Nova Hedwigia 67: 49. 1981.

Clitopilus australis (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509861

Basionym. Rhodocybe australis Singer, Beih. Nova Hedwigia 29: 335. 1969.

Clitopilus azalearum (Murrill) Noordel. & Co-David, *comb. nov.* — MycoBank MB509862

Basionym. Clitocybe azalearum Murrill, Lloydia 5: 137 (1942).

Clitopilus balearicus (Courtec. & Siquier) Noordel. & Co-David, *comb. nov.* — MycoBank MB509863

Basionym. Rhodocybe balearica Courtec. & Siquier, Boll. Gruppo Micol. 'G. Bresadola' (Trento) 40, 2–3: 182. 1998 (1997).

Clitopilus brunneus (Contu) Noordel. & Co-David, *comb. nov.* — MycoBank MB509864

Basionym. Rhodocybe brunnea Contu, Micol. Veget. Mediterr. 21: 88. 2007.

Clitopilus brunnescens (T.J. Baroni & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509865

Basionym. Rhodocybe brunnescens T.J. Baroni & E. Horak, Mycologia 86, 1: 140. 1994.

Clitopilus caelatoideus (Dennis) Noordel. & Co-David, *comb. nov.* — MycoBank MB509866

Basionym. Rhodocybe caelatoidea Dennis, Kew Bull. 15, 1: 154. 1961.

Clitopilus carlottae (Redhead & T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509868

Basionym. Rhodocybe carlottae Redhead & T.J. Baroni, Canad. J. Bot. 64, 7: 1451. 1986.

Clitopilus carlottae var. ***vinaceus*** (Redhead & T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509869

Basionym. Rhodocybe carlottae var. *vinacea* Redhead & T.J. Baroni, Canad. J. Bot. 64, 7: 1451. 1986.

Clitopilus cedretorum (Bidaud & Cavet) Noordel. & Co-David, *comb. nov.* — MycoBank MB509870

Basionym. Rhodocybe cedretorum Bidaud & Cavet, Bull. Mycol. Bot. Dauphiné-Savoie 31 (no. 124): 25. 1992.

Clitopilus claudopus (Singer ex T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509871

Basionym. Rhodocybe claudopus Singer ex T.J. Baroni, Beih. Nova Hedwigia 67: 68. 1981.

Clitopilus collybioides (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509872

Basionym. Rhodocybe collybioides Singer, Lilloa 25: 425. 1952 (1951).

Clitopilus conchatus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509873

Basionym. Rhodocybe conchata E. Horak, New Zealand J. Bot. 17, 3: 275. 1979.

Clitopilus conicus (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509874

Basionym. Rhodocybe conica Singer, Fieldiana, Bot. 21: 122. 1989.

Clitopilus crepidotoides (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509875

Basionym. Rhodocybe crepidotoides Singer, Beih. Sydowia 7: 95. 1973.

Clitopilus crystallinus (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509876

Basionym. Rhodocybe crystallina T.J. Baroni, Mycologia 84, 3: 411. 1992.

Clitopilus cupressicola (Carassai, Papa & Contu) Noordel. & Co-David, *comb. nov.* — MycoBank MB509877

Basionym. Rhodocybe cupressicola Carassai, Papa & Contu, Micol. Veget. Mediterr. 15, 1: 64. 2000.

Clitopilus cyathiformis (Corner & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509878

Basionym. Rhodocybe cyathiformis Corner & E. Horak, Sydowia 31, 1–6: 69. 1979 (1978).

Clitopilus densifolius (T.J. Baroni & Ovrebo) Noordel. & Co-David, *comb. nov.* — MycoBank MB509879

Basionym. Rhodocybe densifolia T.J. Baroni & Ovrebo, Mycologia 80, 4: 511. 1988.

Clitopilus dingleyae (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509880

Basionym. Rhodocybe dingleyae E. Horak, New Zealand J. Bot. 17, 3: 280. 1979.

Clitopilus eccentricus (T.J. Baroni & Ovrebo) Noordel. & Co-David, *comb. nov.* — MycoBank MB509881

Basionym. Rhodocybe eccentrica T.J. Baroni & Ovrebo, Mycologia 80, 4: 508. 1988.

Clitopilus fibulata (Pegler) Noordel. & Co-David, *comb. nov.* — MycoBank MB509882

Basionym. Rhodocybe fibulata Pegler, Kew Bull., Addit. Ser. 6: 526. 1977.

Clitopilus finnmarchiae (Noordel.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509883

Basionym. Rhodocybe finnmarchiae Noordel., Norweg. J. Bot. 26, 4: 277. 1979.

Clitopilus fuligineus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509884

Basionym. Rhodocybe fuliginea E. Horak, New Zealand J. Bot. 17: 280. 1979.

Clitopilus fuscofarinaceus (Kosonen & Noordel.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509885

Basionym. Rhodocybe fuscofarinacea Kosonen & Noordel., Karstenia 34, 2: 43. 1994.

Clitopilus galerinoides (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509886

Basionym. Rhodocybe galerinoides Singer, Sydowia 15: 81. 1962 (1961).

Clitopilus geminus (Fr.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509887

Basionym. Agaricus geminus Fr., Epicrisis: 38. 1838. See Persoonia 13: 379. 1987.

Clitopilus geminus var. ***mauretanicus*** (Maire) Noordel. & Co-David, *comb. nov.* — MycoBank MB509888

Basionym. Rhodopaxillus truncatus var. *mauretanicus* Maire, Bull. Soc. Mycol. France 40: 298. 1924.

Clitopilus geminus var. ***subvermicularis*** (Maire) Noordel. & Co-David, *comb. nov.* — MycoBank MB509889

Basionym. Rhodopaxillus truncatus var. *subvermicularis* Maire, Bull. Soc. Mycol. France 40: 298. 1924.

Clitopilus gibbosus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509890

Basionym. Rhodocybe gibbosa E. Horak, Sydowia 31, 1–6: 64. 1979 (1978).

Clitopilus griseolus (T.J. Baroni & Halling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509892

Basionym. Rhodocybe griseola T.J. Baroni & Halling, Mycologia 84, 3: 413. 1992.

Clitopilus griseosporus (A. Pearson) Noordel. & Co-David, *comb. nov.* — MycoBank MB509893

Basionym. Collybia griseospora A. Pearson, Trans. Brit. Mycol. Soc. 35, 2: 102. 1952.

Clitopilus hawaiiensis (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509894

Basionym. Rhodocybe hawaiiensis Singer, Fieldiana, Bot. 21: 123. 1989.

Clitopilus heterosporus (Murrill) Noordel. & Co-David, *comb. nov.* — MycoBank MB509895

Basionym. Eccilia heterospora Murrill, Lloydia 9: 324. 1946.

Clitopilus himantiigenus (Speg.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509896

Basionym. Clitocybe himantiigena Speg., Bol. Acad. Nac. Ci. 23, 3–4: 373 [no. 16, reprint page 11]. 1919.

Clitopilus hispanicus (Esteve-Rav. & G. Moreno) Noordel. & Co-David, *comb. nov.* — MycoBank MB509897

Basionym. Rhodocybe hispanica Esteve-Rav. & G. Moreno, Beitr. Kenntn. Pilze Mitteleur. 3: 159. 1987.

Clitopilus hondensis (Murrill) Noordel. & Co-David, *comb. nov.* — MycoBank MB509898

Basionym. Clitocybe hondensis Murrill, Mycologia 5: 209. 1913.

Clitopilus horakii (Pacioni & Lalli) Noordel. & Co-David, *comb. nov.* — MycoBank MB509899

Basionym. Rhodocybe horakii Pacioni & Lalli, Micol. Ital. 13, 1: 78. 1984.

Clitopilus hygrophoroides (T.J. Baroni & Halling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509900

Basionym. Rhodocybe hygrophoroides T.J. Baroni & Halling, Mycologia 84, 3: 414. 1992.

Clitopilus ilicicola (Lonati) Noordel. & Co-David, *comb. nov.* — MycoBank MB509901

Basionym. Rhodocybe ilicicola Lonati, Micol. Veget. Mediterr. 13, 1: 9. 1998.

Clitopilus incarnatus (T.J. Baroni & Halling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509902

Basionym. Rhodocybe incarnata T.J. Baroni & Halling, Mycologia 84, 3: 416. 1992.

Clitopilus iti (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509903

Basionym. Rhodocybe iti E. Horak, New Zealand J. Bot. 17, 3: 277. 1979.

Clitopilus lactariiformis (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509904

Basionym. Rhodocybe lactariiformis Singer, Sydowia 15: 81. 1962 (1961).

Clitopilus laetus (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509905

Basionym. Rhodocybe laeta Singer, Sydowia 15: 80. 1962 (1961).

Clitopilus lateralipes (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509906

Basionym. Rhodocybe lateralipes E. Horak, Sydowia 31, 1–6: 62. 1979 (1978).

Clitopilus lateritius (T.J. Baroni & G.M. Gates) Noordel. & Co-David, *comb. nov.* — MycoBank MB509907

Basionym. Rhodocybe lateritia T.J. Baroni & Gates, Austral. Syst. Bot. 19: 346. 2006.

Clitopilus luteocinnamomeus (T.J. Baroni & Ovrebo) Noordel. & Co-David, *comb. nov.* — MycoBank MB509908

Basionym. Rhodocybe luteocinnamomea T.J. Baroni & Ovrebo, Fung. Diversity 27, 1: 164. 2007.

Clitopilus lutetianus (E.-J. Gilbert) Noordel. & Co-David, *comb. nov.* — MycoBank MB509909

Basionym. Rhodopaxillus lutetianus E.-J. Gilbert, Bull. Soc. Mycol. France 42: 66. 1926.

Clitopilus mairei (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509910

Basionym. Rhodocybe mairei T.J. Baroni, Beih. Nova Hedwigia 67: 108. 1981.

Clitopilus maleolens (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509911

Basionym. Rhodocybe maleolens E. Horak, New Zealand J. Bot. 17, 3: 278. 1979.

Clitopilus marasmioides (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509912

Basionym. Rhodocybe marasmioides Singer, Lilloa 25: 424. 1952 (1951).

Clitopilus melleus (T.J. Baroni & Ovrebo) Noordel. & Co-David, *comb. nov.* — MycoBank MB509913

Basionym. Rhodocybe mellea T.J. Baroni & Ovrebo, Mycologia 80, 4: 513. 1988.

Clitopilus melleopallens (P.D. Orton) Noordel. & Co-David, *comb. nov.* — MycoBank MB509914

Basionym. Rhodocybe melleopallens P.D. Orton, Trans. Brit. Mycol. Soc. 43: 380. 1960.

Clitopilus mordax (G.F. Atk.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509915

Basionym. Eccilia mordax G.F. Atk., J. Mycol. 8: 113. 1902.

Clitopilus multilamellatus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509916

Basionym. Rhodocybe multilamellata E. Horak, Fungi of New Zealand, Ngā Harore o Aotearoa 5: 86. 2008.

Clitopilus muritai (G. Stev.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509917

Basionym. Lepista muritai G. Stev., Kew Bull. 19: 7. 1964.

Clitopilus mustellinus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509918

Basionym. Rhodocybe mustellina E. Horak, Norsk Polarinst. Skr. 31, 1–6: 66. 1979 (1978).

Clitopilus mycenoides (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509919

Basionym. Rhodocybe mycenoides Singer, Lilloa 25: 423. 1952 (1951).

Clitopilus naucoria (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509920

Basionym. Rhodocybe naucoria Singer, Lilloa 25: 425. 1952 (1951).

Clitopilus nitellinus (Fr.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509921

Basionym. Agaricus nitellinus Fr., Epicrisis: 80. 1838.

Clitopilus nitellinoides (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509922

Basionym. Rhodocybe nitellinoides E. Horak, Sydowia 31, 1–6: 63. 1979 (1978).

Clitopilus nuciolens (Murrill) Noordel. & Co-David, *comb. nov.* — MycoBank MB509923

Basionym. Melanoleuca nuciolens Murrill, Mycologia 5: 218. 1913.

Clitopilus obscurus (Pilát) Noordel. & Co-David, *comb. nov.* — MycoBank MB509924

Basionym. Rhodopaxillus obscurus Pilát, Sborn. Nár. Muz. Praze 913, 2: 67. 1953.

Clitopilus obtusatulus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509925

Basionym. Rhodocybe obtusatula E. Horak, Sydowia 31, 1–6: 74. 1979 (1978).

Clitopilus ochraceopallidus (Ballero & Contu) Noordel. & Co-David, *comb. nov.* — MycoBank MB509926

Basionym. Rhodocybe ochraceopallida Ballero & Contu, Mycotaxon 48: 1. 1993.

Clitopilus pallens (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509927

Basionym. Rhodocybe pallens E. Horak, Sydowia 31, 1–6: 66. 1979 (1978).

Clitopilus pallidogriseus (T.J. Baroni & G.M. Gates) Noordel. & Co-David, *comb. nov.* — MycoBank MB509928

Basionym. Rhodocybe pallidogrisea T.J. Baroni & Gates, Austral. Syst. Bot. 19: 348. 2006.

Clitopilus parilis var. ***wagramensis*** (Hauskn. & Noordel.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509929

Basionym. Rhodocybe parilis var. *wagramensis* Hauskn. & Noordel., Öst. Z. Pilzk. 8: 218. 1999.

Clitopilus paurii (T.J. Baroni, Moncalvo, R.P. Bhatt & S.L. Stephenson) Noordel. & Co-David, *comb. nov.* — MycoBank MB509930

Basionym. Rhodocybe paurii T.J. Baroni, Moncalvo, R.P. Bhatt & S.L. Stephenson, Mycologia 96: 860. 2004.

Clitopilus peculiaris (Contu & Bon) Noordel. & Co-David, *comb. nov.* — MycoBank MB509931

Basionym. Rhodocybe peculiaris Contu & Bon, Doc. Mycol. 21, 81: 44. 1991.

Clitopilus pegleri (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509932

Basionym. Rhodocybe pegleri T.J. Baroni, Kew Bull. 54, 3: 778. 1999.

Clitopilus perplexus (T.J. Baroni & Watling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509933

Basionym. Rhodocybe perplexa T.J. Baroni & Watling, Mycotaxon 72: 61. 1999.

Clitopilus perstriatus (Corner & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509934

Basionym. Rhodocybe perstriata Corner & E. Horak, Sydowia 31, 1–6: 70. 1979 (1978).

Clitopilus piperatus (G. Stev.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509935

Basionym. Lepista piperata G. Stev., Kew Bull. 19, 1: 6. 1964.

Clitopilus pleurogenus (Pegler) Noordel. & Co-David, *comb. nov.* — MycoBank MB509936

Basionym. Rhodocybe pleurogena Pegler, Kew Bull., Addit. Ser. 6: 527. 1977.

Clitopilus porcelanicus (Dennis) Noordel. & Co-David, *comb. nov.* — MycoBank MB509937

Basionym. Eccilia porcelanica Dennis, Kew Bull. 15: 145. 1961.

Clitopilus praesidentialis (Cons., Contu, M. Roy, Selosse & Vizzini) Noordel. & Co-David, *comb. nov.* — MycoBank MB509938

Basionym. Rhodocybe praesidentialis Cons., Contu, M. Roy, Selosse & Vizzini, Riv. Micol. 50: 26. 2007.

Clitopilus priscuus (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509939

Basionym. Rhodocybe priscua T.J. Baroni, Beih. Nova Hedwigia 67: 60. 1981.

Clitopilus pseudonitellinus (Dennis) Noordel. & Co-David, *comb. nov.* — MycoBank MB509940

Basionym. Rhodocybe pseudonitellina Dennis, Bull. Soc. Mycol. France 69: 197. 1953.

Clitopilus pseudopiperitus (T.J. Baroni & G.M. Gates) Noordel. & Co-David, *comb. nov.* — MycoBank MB509941

Basionym. Rhodocybe pseudopiperita T.J. Baroni & G.M. Gates, Austral. Syst. Bot. 19, 4: 345. 2006.

Clitopilus pulchrispermus (T.J. Baroni & Halling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509942

Basionym. Rhodocybe pulchrisperma T.J. Baroni & Halling, Brittonia 37, 3: 182 (1985).

Clitopilus radicatus (Cleland) Noordel. & Co-David, *comb. nov.* — MycoBank MB509943

Basionym. Leptonia radicata Cleland, Trans. & Proc. Roy. Soc. South Australia 57: 189. 1933.

Clitopilus reticulatus (Cleland) Noordel. & Co-David, *comb. nov.* — MycoBank MB509944

Basionym. Entoloma reticulatum Cleland (publ. as "*reticulata*"), Trans. & Proc. Roy. Soc. South Australia 57: 189. 1933.

Clitopilus rhizogenus (T.J. Baroni & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509945

Basionym. Rhodocybe rhizogena T.J. Baroni & E. Horak, Mycologia 86, 1: 138. 1994.

Clitopilus russularia (Singer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509946

Basionym. Rhodocybe russularia Singer, Sydowia 15: 80. 1962 (1961).

Clitopilus semiarboricola (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB509947

Basionym. Rhodocybe semiarboricola T.J. Baroni, Beih. Nova Hedwigia 67: 104. 1981.

Clitopilus stanglianus (Bresinsky & Pfaff) Noordel. & Co-David, *comb. nov.* — MycoBank MB509948

Basionym. Squamanita stangliana Bresinsky & Pfaff, Z. Pilzk. 34: 169. 1968.

Clitopilus stipitatus (A.H. Sm. & Hesler) Noordel. & Co-David, *comb. nov.* — MycoBank MB509949

Basionym. Claudopus stipitatus A.H. Sm. & Hesler, J. Elisha Mitchell Sci. Soc. 56: 303. 1940.

Clitopilus subcaespitosus (Esteve-Rav.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509950

Basionym. Rhodocybe subcaespitosa Esteve-Rav., Micologia 2000 (Trento): 178. 2000.

Clitopilus tasmanicus (T.J. Baroni & G.M. Gates) Noordel. & Co-David, *comb. nov.* — MycoBank MB509951

Basionym. Rhodocybe tasmanica T.J. Baroni & G.M. Gates, Austral. Syst. Bot. 19: 350. 2006.

Clitopilus tergipes (Corner & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509952

Basionym. Rhodocybe tergipes Corner & E. Horak, Sydowia 31, 1–6: 68. 1979 (1978).

Clitopilus testaceus (Dennis) Noordel. & Co-David, *comb. nov.* — MycoBank MB509953

Basionym. Rhodocybe testacea Dennis, Kew Bull. 15: 155. 1961.

Clitopilus tillii (Krisai & Noordel.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509954

Basionym. Rhodocybe tillii Krisai & Noordel., Öst. Z. Pilzk. 7: 264. 1998.

Clitopilus umbrosus (T.J. Baroni & Halling) Noordel. & Co-David, *comb. nov.* — MycoBank MB509955

Basionym. Rhodocybe umbrosa T.J. Baroni & Halling, Brittonia 52, 2: 128. 2000.

Clitopilus variisporus (Voto) Noordel. & Co-David, *comb. nov.* — MycoBank MB509956

Basionym. Rhodocybe variispora Voto, Bull. Amer. 73–74: 40. 2008.

Clitopilus verrucosus (Thiers) Noordel. & Co-David, *comb. nov.* — MycoBank MB509957

Basionym. Rhodophyllus verrucosus Thiers, Mycologia 50, 4: 522. 1958.

Clitopilus villosus (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509958

Basionym. Rhodocybe villosa E. Horak, Sydowia 33: 105. 1980.

Entoloma abbreviatipes (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509959

Basionym. Nolanea abbreviatipes Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 224. 1994.

Entoloma aciculocystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509960

Basionym. Rhodophyllus aciculocystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 410. 1979.

Entoloma acuferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509962

Basionym. Rhodophyllus acufer Romagn. & Gilles, Beih. Nova Hedwigia 59: 507. 1979.

Entoloma acutoumbonatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509963

Basionym. Leptonia acutoumbonata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 142. 1994.

Entoloma acutum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509964

Basionym. Rhodophyllus acutus Romagn. & Gilles, Beih. Nova Hedwigia 59: 542. 1979.

Entoloma afrum (Pegler) Noordel. & Co-David, *comb. nov.* — MycoBank MB509965

Basionym. Richoniella afra Pegler, Kew Bull., Addit. Ser. 32, 1: 12. 1977.

Entoloma albivellum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509966

Basionym. Rhodophyllus albivellus Romagn. & Gilles, Beih. Nova Hedwigia 59: 169. 1979.

Entoloma albomurinum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509967

Basionym. Rhodophyllus albomurinus Romagn. & Gilles, Beih. Nova Hedwigia 59: 355. 1979.

Entoloma alboroseum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509968

Basionym. Rhodophyllus alboroseus Romagn. & Gilles, Beih. Nova Hedwigia 59: 171. 1979.

Entoloma ambiguum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509969

Basionym. Rhodophyllus ambiguus Romagn. & Gilles, Beih. Nova Hedwigia 59: 357. 1979.

Entoloma andersonii (Mazzer) Noordel. & Co-David, *comb. nov.* — MycoBank MB509970

Basionym. Pouzarella andersonii Mazzer, Biblthca Mycol. 46: 110. 1976.

Entoloma angustisporum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509971

Basionym. Rhodophyllus angustisporus Romagn. & Gilles, Beih. Nova Hedwigia 59: 111. 1979.

Entoloma anisothrix (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509972

Basionym. Rhodophyllus anisothrix Romagn. & Gilles, Beih. Nova Hedwigia 59: 184. 1979.

Entoloma applanatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509973

Basionym. Rhodophyllus applanatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 536. 1979.

Entoloma approximatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509975

Basionym. Leptonia approximata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 52. 1994.

Entoloma arcuatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509976

Basionym. Rhodophyllus arcuatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 358. 1979.

Entoloma argenteolanatum (T.J. Baroni, Perd.-Sánch. & S.A. Cantrell) Noordel. & Co-David, *comb. nov.* — MycoBank MB509977

Basionym. Pouzarella argenteolanata T.J. Baroni, Perd.-Sánch. & S.A. Cantrell, N. Amer. Fungi 3: 247. 2008.

Entoloma asterospermum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509978

Basionym. Rhodophyllus asterospermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 510. 1979.

Entoloma asterosporum (Coker & Couch) Noordel. & Co-David, *comb. nov.* — MycoBank MB509979

Basionym. Nigropogon asterosporus Coker & Couch, Gasteromycetes East. U.S. 1928.

Entoloma atrifucatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509980

Basionym. Leptonia atrifucata Largent, Biblthca Mycol. 55: 152. 1977.

Entoloma atrovelutinum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509981

Basionym. Rhodophyllus atrovelutinus Romagn. & Gilles, Beih. Nova Hedwigia 59: 450. 1979.

Entoloma atrovelutinum var. ***leiopus*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509982

Basionym. Rhodophyllus atrovelutinus var. *leiopus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 452. 1979.

Entoloma atroviolaceum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB509983

Basionym. Rhodophyllus atroviolaceus Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma atypicum (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB509984

Basionym. Pouzaromyces atypicus E. Horak, Beih. Nova Hedwigia 65: 40. 1980.

Entoloma avellanicolor (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509985

Basionym. Rhodophyllus avellanicolor Romagn. & Gilles, Beih. Nova Hedwigia 59: 582. 1979.

Entoloma azureum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509986

Basionym. Leptonia azurea Largent, Biblthca Mycol. 55: 102. 1977.

Entoloma badissimum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509987

Basionym. Leptonia badissima Largent, Biblthca Mycol. 55: 247. 1977.

Entoloma bicoloripes (Largent & Thiers) Noordel. & Co-David, *comb. nov.* — MycoBank MB509990

Basionym. Nolanea bicoloripes Largent & Thiers, Northw. Sci. 46, 1: 35. 1972.

Entoloma bisporiferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509991

Basionym. Rhodophyllus bisporifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 266. 1979.

Entoloma bituminosum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509992

Basionym. Rhodophyllus bituminosus Romagn. & Gilles, Beih. Nova Hedwigia 59: 485. 1979.

Entoloma brunneolamellatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB509993

Basionym. Nolanea brunneolamellata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 249. 1994.

Entoloma brunneoloroseum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509994

Basionym. Rhodophyllus brunneoloroseus Romagn. & Gilles, Beih. Nova Hedwigia 59: 268. 1979.

Entoloma caeruleonigrum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509995

Basionym. Rhodophyllus caeruleoniger Romagn. & Gilles, Beih. Nova Hedwigia 59: 277. 1979.

Entoloma caesiolimbatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509996

Basionym. Rhodophyllus caesiolimbatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 279. 1979.

Entoloma caesiomurinum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509997

Basionym. Rhodophyllus caesiomurinus Romagn. & Gilles, Beih. Nova Hedwigia 59: 281. 1979.

Entoloma caesiopileum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509998

Basionym. Rhodophyllus caesiopileus Romagn. & Gilles, Beih. Nova Hedwigia 59: 282. 1979.

Entoloma callidermoides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB509999

Basionym. Rhodophyllus callidermoides Romagn. & Gilles, Beih. Nova Hedwigia 59: 284. 1979.

Entoloma callidermum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513565

Basionym. Rhodophyllus callidermus Romagn., Bull. Jard. Bot. État Bruxelles 26: 171. 1956.

Entoloma callithrix (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513566

Basionym. Rhodophyllus callithrix Romagn. & Gilles, Beih. Nova Hedwigia 59: 415. 1979.

Entoloma callithrix var. ***lasiopus*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513567

Basionym. Rhodophyllus callithrix var. *lasiopus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 418. 1979.

Entoloma calongei (E. Horak & G. Moreno) Noordel. & Co-David, *comb. nov.* — MycoBank MB513568

Basionym. Rhodogaster calongei E. Horak & G. Moreno, Sydowia 50, 2: 188. 1998.

Entoloma campanulatum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513569

Basionym. Rhodophyllus campanulatus Romagn., Les Rhodophylles de Madagascar: 152. 1941.

Entoloma candicans (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513570

Basionym. Rhodophyllus candicans Romagn. & Gilles, Beih. Nova Hedwigia 59: 151. 1979.

Entoloma capitatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513571

Basionym. Rhodophyllus capitatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 352. 1979.

Entoloma capnoides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513572

Basionym. Rhodophyllus capnoides Romagn. & Gilles, Beih. Nova Hedwigia 59: 360. 1979.

Entoloma celatum (Mazzer) Noordel. & Co-David, *comb. nov.* — MycoBank MB513573

Basionym. Pouzarella celata Mazzer, Biblthca Mycol. 46: 74. 1976.

Entoloma chilense (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB513574

Basionym. Rhodogaster chilensis E. Horak, Sydowia 17: 190. 1964 (1963).

Entoloma chloroconus (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513575

Basionym. Rhodophyllus chloroconus Romagn. & Gilles, Beih. Nova Hedwigia 59: 400. 1979.

Entoloma chloroides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513576

Basionym. Rhodophyllus chloroides Romagn. & Gilles, Beih. Nova Hedwigia 59: 476. 1979.

Entoloma chlorospilum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513577

Basionym. Rhodophyllus chlorospilus Romagn. & Gilles, Beih. Nova Hedwigia 59: 330. 1979.

Entoloma ciliferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513578

Basionym. Rhodophyllus cilifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 190. 1979.

Entoloma cinereovirens (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513579

Basionym. Rhodophyllus cinereovirens Romagn. & Gilles, Beih. Nova Hedwigia 59: 333. 1979.

Entoloma clavipilum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513580

Basionym. Rhodophyllus clavipilus Romagn. & Gilles, Beih. Nova Hedwigia 59: 167. 1979.

Entoloma coactum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513581

Basionym. Leptonia coacta Largent, Biblthca Mycol. 55: 99. 1977.

Entoloma coeleste (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513582

Basionym. Rhodophyllus coelestis Romagn. & Gilles, Beih. Nova Hedwigia 59: 93. 1979.

Entoloma coelopus (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513583

Basionym. Rhodophyllus coelopus Romagn. & Gilles, Beih. Nova Hedwigia 59: 516. 1979.

Entoloma concavum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513584

Basionym. Inocephalus concavus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 402. 1994.

Entoloma coprinoides (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513585

Basionym. Rhodophyllus coprinoides Romagn., Les Rhodophylles de Madagascar: 151. 1941.

Entoloma cremeoluteum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513586

Basionym. Inocephalus cremeoluteus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 387. 1994.

Entoloma crenulatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513587

Basionym. Leptonia crenulata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 140. 1994.

Entoloma cristalliferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513588

Basionym. Rhodophyllus cristallifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 288. 1979.

Entoloma cupressum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513589

Basionym. Leptonia cupressa Largent, Biblthca Mycol. 55: 150. 1977.

Entoloma curtissimum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513590

Basionym. Rhodophyllus curtissimus Romagn. & Gilles, Beih. Nova Hedwigia 59: 289. 1979.

Entoloma cyananthes (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513591

Basionym. Rhodophyllus cyananthes Romagn., Bull. Jard. Bot. État Bruxelles 26: 174. 1956.

Entoloma cyanocalix (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513592

Basionym. Rhodophyllus cyanocalix Romagn. & Gilles, Beih. Nova Hedwigia 59: 291. 1979.

Entoloma cyanoides (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513593

Basionym. Rhodophyllus cyanoides Romagn., Les Rhodophylles de Madagascar: 150. 1941.

Entoloma cyathus (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513594

Basionym. Rhodophyllus cyathus Romagn. & Gilles, Beih. Nova Hedwigia 59: 617. 1979.

Entoloma cylindrocapitatum (T.J. Baroni & Ovrebo) Noordel. & Co-David, *comb. nov.* — MycoBank MB513595

Basionym. Alboleptonia cylindrocapitata T.J. Baroni & Ovrebo, Fung. Diversity 27, 1: 165. 2007.

Entoloma cystidioliferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513596

Basionym. Rhodophyllus cystidiolifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 561. 1979.

Entoloma cystomarginatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513597

Basionym. Nolanea cystomarginata Largent, Mycologia 66, 6: 1005. 1974.

Entoloma davidii Noordel. & Co-David, *nom. nov.* — MycoBank MB513598

Basionym. Alboleptonia largentii T.J. Baroni & Lodge, Mycologia 90, 4: 682. 1998. Non *Entoloma largentii* Courtec. 1986.

Entoloma debile (Corner & E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB513599

Basionym. Pouzaromyces debilis Corner & E. Horak, Beih. Nova Hedwigia 65: 38. 1980.

Entoloma deconicoides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513600

Basionym. Rhodophyllus deconicoides Romagn. & Gilles, Beih. Nova Hedwigia 59: 94. 1979.

Entoloma decurrentius (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513601

Basionym. Rhodophyllus decurrentior Romagn. & Gilles, Beih. Nova Hedwigia 59: 96. 1979.

Entoloma deformisporum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513602

Basionym. Rhodophyllus deformisporus Romagn. & Gilles, Beih. Nova Hedwigia 59: 518. 1979.

Entoloma denticulatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513603

Basionym. Rhodophyllus denticulatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 341. 1979.

Entoloma dichrooides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513604

Basionym. Rhodophyllus dichrooides Romagn. & Gilles, Beih. Nova Hedwigia 59: 230. 1979.

Entoloma dicubospermum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513605

Basionym. Rhodophyllus dicubospermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 362. 1979.

Entoloma dimorphocystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513604

Basionym. Rhodophyllus dimorphocystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 419. 1979.

Entoloma diversum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513607

Basionym. Leptonia diversa Largent, Biblthca Mycol. 55: 171. 1977.

Entoloma dochmiopus (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513608

Basionym. Rhodophyllus dochmiopus Romagn. & Gilles, Beih. Nova Hedwigia 59: 156. 1979.

Entoloma dochmiopus var. ***obsoletum*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513609

Basionym. Rhodophyllus dochmiopus var. *obsoletus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 158. 1979.

Entoloma domingense (T.J. Baroni) Noordel. & Co-David, *comb. nov.* — MycoBank MB513610

Basionym. Pouzarella domingensis T.J. Baroni, N. Amer. Fungi 3: 251. 2008.

Entoloma dryophiloides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513611

Basionym. Rhodophyllus dryophiloides Romagn. & Gilles, Beih. Nova Hedwigia 59: 584. 1979.

Entoloma dubium (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513612

Basionym. Rhodophyllus dubius Romagn. & Gilles, Beih. Nova Hedwigia 59: 139. 1979.

Entoloma dulcisaporum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513613

Basionym. Claudopus dulcisaporus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 365. 1994.

Entoloma ealaense (Beeli) Noordel. & Co-David, *comb. nov.* — MycoBank MB513614

Basionym. Leptonia ealaensis Beeli, Bull. Soc. Roy. Bot. Belgique 61, 1: 82. 1928.

Entoloma eburneum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513615

Basionym. Rhodophyllus eburneus Romagn. & Gilles, Beih. Nova Hedwigia 59: 600. 1979.

Entoloma eburneum var. ***luteomaculatum*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513616

Basionym. Rhodophyllus eburneus var. *luteomaculatus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 604. 1979.

Entoloma effugiens (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513617

Basionym. Rhodophyllus effugiens Romagn. & Gilles, Beih. Nova Hedwigia 59: 365. 1979.

Entoloma elaeidis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513618

Basionym. Rhodophyllus elaeidis Romagn. & Gilles, Beih. Nova Hedwigia 59: 588. 1979.

Entoloma elegans (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513619

Basionym. Rhodophyllus elegans Romagn. & Gilles, Beih. Nova Hedwigia 59: 544. 1979.

Entoloma elongatum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513620

Basionym. Rhodophyllus elongatus Romagn., Les Rhodophylles de Madagascar: 150. 1941.

Entoloma euchloroides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513621

Basionym. Rhodophyllus euchloroides Romagn. & Gilles, Beih. Nova Hedwigia 59: 366. 1979.

Entoloma eudermum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513622

Basionym. Rhodophyllus eudermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 489. 1979.

Entoloma eudermum var. ***prionophyllum*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513623

Basionym. Rhodophyllus eudermus var. *prionophyllus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 489. 1979.

Entoloma euteles (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513624

Basionym. Rhodophyllus euteles Romagn. & Gilles, Beih. Nova Hedwigia 59: 564. 1979.

Entoloma exalbidum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513625

Basionym. Leptonia exalbida Largent, Biblthca Mycol. 55: 157. 1977.

Entoloma fabaceolum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513626

Basionym. Leptonia fabaceola Largent, Biblthca Mycol. 55: 73. 1977.

Entoloma fastigiatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513627

Basionym. Leptonia fastigiata Largent, Biblthca Mycol. 55: 150. 1977.

Entoloma ferreri (T.J. Baroni, Perd.-Sánch. & S.A. Cantrell) Noordel. & Co-David, *comb. nov.* — MycoBank MB513628

Basionym. Pouzarella ferreri T.J. Baroni, Perd.-Sánch. & S.A. Cantrell, N. Amer. Fungi 3: 243. 2008.

Entoloma ferreri var. ***pallidonigrescens*** (T.J. Baroni & S.A. Cantrell) Noordel. & Co-David, *comb. nov.* — MycoBank MB513629

Basionym. Pouzarella ferreri var. *pallidonigrescens* T.J. Baroni & S.A. Cantrell, N. Amer. Fungi 3: 245. 2008.

Entoloma fibrillosipes (Murrill) Noordel. & Co-David, *comb. nov.* — MycoBank MB513630

Basionym. Nolanea fibrillosipes Murrill, North Amer. Fl. 10: 100. 1917.

Entoloma fibulatum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513631

Basionym. Rhodophyllus fibulatus Romagn. Bull. Jard. Bot. État Bruxelles 26: 179. 1956.

Entoloma flexuosipes (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513632

Basionym. Rhodophyllus flexuosipes Romagn. & Gilles, Beih. Nova Hedwigia 59: 192. 1979.

Entoloma foliocontusum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513633

Basionym. Leptonia foliocontusa Largent, Biblthca Mycol. 55: 169. 1977.

Entoloma fructufragrans (Largent & Thiers) Noordel. & Co-David, *comb. nov.* — MycoBank MB513634

Basionym. Nolanea fructufragrans Largent & Thiers, Northw. Sci. 46, 1: 37. 1972.

Entoloma fulviceps (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513635

Basionym. Rhodophyllus fulviceps Romagn., Bull. Soc. Mycol. France 48, 3: 321. 1932.

Entoloma furfuraceidiscus (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513636

Basionym. Inocephalus furfuraceodiscus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 408. 1994.

Entoloma fuscatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513637

Basionym. Leptonia fuscata Largent, Biblthca Mycol. 55: 94. 1977.

Entoloma fusciceps (Kauffman) Noordel. & Co-David, *comb. nov.* — MycoBank MB513638

Basionym. Leptonia fusciceps Kauffman, Pap. Michigan Acad. Sci. 11: 197. 1930.

Entoloma fuscoocellatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513639

Basionym. Rhodophyllus fuscoocellatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 293. 1979.

Entoloma fuscoortonii (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513640

Basionym. Nolanea fuscoortonii Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 252. 1994.

Entoloma fusicystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513641

Basionym. Rhodophyllus fusicystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 366. 1979.

Entoloma fusiferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513642

Basionym. Rhodophyllus fusifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 240. 1979.

Entoloma gabonicum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513643

Basionym. Rhodophyllus gabonicus Romagn. & Gilles, Beih. Nova Hedwigia 59: 248. 1979.

Entoloma galeroides (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513644

Basionym. Rhodophyllus galeroides Romagn. & Gilles, Beih. Nova Hedwigia 59: 554. 1979.

Entoloma gasteromycetoides Co-David & Noordel., *nom. nov.* — MycoBank MB513645

Basionym. Richoniella pumila G. Cunn., New Zealand J. Sci. Technol., ser. B 22: 62B. 1940. Non *Entoloma pumilum* E. Horak (2008).

Entoloma geminum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513646

Basionym. Rhodophyllus geminus Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma gigaspermum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513647

Basionym. Rhodophyllus gigaspermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 597. 1979.

Entoloma gilvum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513648

Basionym. Rhodophyllus gilvus Romagn. & Gilles, Beih. Nova Hedwigia 59: 368. 1979.

Entoloma glaucogilvum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513649

Basionym. Rhodophyllus glaucogilvus Romagn. & Gilles, Beih. Nova Hedwigia 59: 370. 1979.

Entoloma glutiniceps (Hongo) Noordel. & Co-David, *comb. nov.* — MycoBank MB513650

Basionym. Rhodophyllus glutiniceps Hongo, Mem. Natl. Sci. Mus. (Tokyo) 10: 38. 1977.

Entoloma grammatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513651

Basionym. Rhodophyllus grammatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 98. 1979.

Entoloma granulatum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513652

Basionym. Rhodophyllus granulatus Romagn., Les Rhodophylles de Madagascar: 152. 1941.

Entoloma griseipes (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513653

Basionym. Rhodophyllus griseipes Romagn. & Gilles, Beih. Nova Hedwigia 59: 296. 1979.

Entoloma griseoroseum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513654

Basionym. Rhodophyllus griseoroseus Romagn. & Gilles, Beih. Nova Hedwigia 59: 372. 1979.

Entoloma griseovioleum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513655

Basionym. Rhodophyllus griseovioleus Romagn. & Gilles, Beih. Nova Hedwigia 59: 298. 1979.

Entoloma hirtellum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513656

Basionym. Rhodophyllus hirtellus Romagn., Les Rhodophylles de Madagascar: 151. 1941.

Entoloma holocyaneum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513657

Basionym. Rhodophyllus holocyaneus Romagn, Les Rhodophylles de Madagascar: 150. 1941.

Entoloma holoconiotum (Largent & Thiers) Noordel. & Co-David, *comb. nov.* — MycoBank MB513658

Basionym. Nolanea holoconiota Largent & Thiers, Northw. Sci. 46, 1: 34. 1972.

Entoloma horridum (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB513659

Basionym. Pouzaromyces horridus E. Horak, Beih. Nova Hedwigia 65: 38. 1980.

Entoloma humicola (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513660

Basionym. Rhodophyllus humicola Romagn. & Gilles, Beih. Nova Hedwigia 59: 553. 1979.

Entoloma hypochlorum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513661

Basionym. Rhodophyllus hypochlorus Romagn. & Gilles, Beih. Nova Hedwigia 59: 557. 1979.

Entoloma hypoglaucum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513662

Basionym. Rhodophyllus hypoglaucus Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma ianthomelas (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513663

Basionym. Rhodophyllus ianthomelas Romagn. & Gilles, Beih. Nova Hedwigia 59: 302. 1979.

Entoloma incanosquamulosum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513664

Basionym. Nolanea incanosquamulosa Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 266. 1994.

Entoloma incurvum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513665

Basionym. Rhodophyllus incurvus Romagn. & Gilles, Beih. Nova Hedwigia 59: 501. 1979.

Entoloma infundibulare (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513666

Basionym. Rhodophyllus infundibularis Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma inocybospermum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513667

Basionym. Rhodophyllus inocybospermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 376. 1979.

Entoloma inodes (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513668

Basionym. Rhodophyllus inodes Romagn. & Gilles, Beih. Nova Hedwigia 59: 238. 1979.

Entoloma insuetum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513669

Basionym. Leptonia insueta Largent, Biblthca Mycol. 55: 118. 1977.

Entoloma intervenosum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513670

Basionym. Rhodophyllus intervenosus Romagn. & Gilles, Beih. Nova Hedwigia 59: 306. 1979.

Entoloma invisibile (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513671

Basionym. Rhodophyllus invisibilis Romagn. & Gilles, Beih. Nova Hedwigia 59: 160. 1979.

Entoloma ionocyanum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513672

Basionym. Rhodophyllus ionocyanus Romagn. & Gilles, Beih. Nova Hedwigia 59: 308. 1979.

Entoloma ionocyanum var. ***parvipapillosum*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513673

Basionym. Rhodophyllus ionocyanus var. *parvipapillosus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 309. 1979.

Entoloma irinum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513674

Basionym. Rhodophyllus irinus Romagn. & Gilles, Beih. Nova Hedwigia 59: 503. 1979.

Entoloma kansaiense (Hongo) Noordel. & Co-David, *comb. nov.* — MycoBank MB513676

Basionym. Rhodophyllus kansaiensis Hongo, J. Jap. Bot. 49, 10: 299. 1974.

Entoloma lamellirugum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513678

Basionym. Rhodophyllus lamellirugus Romagn. & Gilles, Beih. Nova Hedwigia 59: 370. 1979.

Entoloma lasium (Berk. & Broome) Noordel. & Co-David, *comb. nov.* — MycoBank MB513679

Basionym. Agaricus lasius Berk. & Broome, J. Linn. Soc., Bot. 11: 539. 1871.

Entoloma lateripes (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513680

Basionym. Rhodophyllus lateripes Romagn. & Gilles, Beih. Nova Hedwigia 59: 611. 1979.

Entoloma lateritium (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513681

Basionym. Rhodophyllus lateritius Romagn. & Gilles, Beih. Nova Hedwigia 59: 346. 1979.

Entoloma latisporum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513682

Basionym. Rhodophyllus latisporus Romagn. & Gilles, Beih. Nova Hedwigia 59: 348. 1979.

Entoloma lecythiocystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513682

Basionym. Rhodophyllus lecythiocystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 118. 1979.

Entoloma lecythiophorum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513684

Basionym. Rhodophyllus lecythiophorus Romagn. & Gilles, Beih. Nova Hedwigia 59: 121. 1979.

Entoloma leptohyphes (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513685

Basionym. Rhodophyllus leptohyphes Romagn., Les Rhodophylles de Madagascar: 149. 1941.

Entoloma leptoniisporum (Costantin & L.M. Dufour) Noordel. & Co-David, *comb. nov.* — MycoBank MB513686

Basionym. Richoniella leptoniispora Costantin & L.M. Dufour [as '*leptoniaespora*'], Nouv. Fl. Champ., ed. 5: 203. 1916.

Entoloma leucocephalum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513687

Basionym. Rhodophyllus leucocephalus Romagn. & Gilles, Beih. Nova Hedwigia 59: 204. 1979.

Entoloma leucopus (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513688

Basionym. Rhodophyllus leucopus Romagn. & Gilles, Beih. Nova Hedwigia 59: 206. 1979.

Entoloma lisalense (Beeli) Noordel. & Co-David, *comb. nov.* — MycoBank MB513689

Basionym. Galera lisalensis Beeli, Bull. Soc. Roy. Bot. Belgique 61, 1: 89. 1928.

Entoloma longissimum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513690

Basionym. Rhodophyllus longissimus Romagn. & Gilles, Beih. Nova Hedwigia 59: 428. 1979.

Entoloma lutense (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513691

Basionym. Rhodophyllus lutensis Romagn. & Gilles, Beih. Nova Hedwigia 59: 570. 1979.

Entoloma lutulentum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513692

Basionym. Leptonia lutulenta Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 406. 1994.

Entoloma macrosporum (J.W. Cribb) Noordel. & Co-David, *comb. nov.* — MycoBank MB513693

Basionym. Richoniella macrospora J.W. Cribb, Pap. Dept. Univ. Queensland 3: 128. 1956.

Entoloma mammiferum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513694

Basionym. Rhodophyllus mammifer Romagn., Bull. Jard. Bot. État Bruxelles 26: 152. 1956.

Entoloma margaritiferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513695

Basionym. Rhodophyllus margaritifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 208. 1979.

Entoloma mediofuscum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513696

Basionym. Rhodophyllus mediofuscus Romagn. & Gilles, Beih. Nova Hedwigia 59: 311. 1979.

Entoloma megalothrix (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513697

Basionym. Rhodophyllus megalothrix Romagn. & Gilles, Beih. Nova Hedwigia 59: 570. 1979.

Entoloma membranaceum (Pegler) Noordel. & Co-David, *comb. nov.* — MycoBank MB513698

Basionym. Nolanea membranacea Pegler, Kew Bull., Addit. Ser. 6: 538. 1977.

Entoloma microcystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513699

Basionym. Rhodophyllus microcystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 457. 1979.

Entoloma minutopilum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513700

Basionym. Inocephalus minutopilus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 406. 1994.

Entoloma minutostriatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513701

Basionym. Nolanea minutostriata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 258. 1994.

Entoloma miraculosum (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB513702

Basionym. Claudopus miraculosus E. Horak, Beih. Nova Hedwigia 65: 33. 1980.

Entoloma modestissimum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB13703

Basionym. Rhodophyllus modestissimus Romagn. & Gilles, Beih. Nova Hedwigia 59: 315. 1979.

Entoloma modicum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513704

Basionym. Rhodophyllus modicus Romagn. & Gilles, Beih. Nova Hedwigia 59: 123. 1979.

Entoloma mondahense (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513705

Basionym. Rhodophyllus mondahensis Romagn. & Gilles, Beih. Nova Hedwigia 59: 570. 1979.

Entoloma nidorosiforme (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513706

Basionym. Rhodophyllus nidorosiformis Romagn., Bull. Jard. Bot. État Bruxelles 26: 160. 1956.

Entoloma nudipileum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513708

Basionym. Rhodophyllus nudipileus Romagn. & Gilles, Beih. Nova Hedwigia 59: 381. 1979.

Entoloma nudum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513709

Basionym. Rhodophyllus nudus Romagn. & Gilles, Beih. Nova Hedwigia 59: 210. 1979.

Entoloma obnubile (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513710

Basionym. Rhodophyllus obnubilis Romagn. & Gilles, Beih. Nova Hedwigia 59: 458. 1979.

Entoloma obscuratum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513711

Basionym. Nolanea obscurata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 228. 1994.

Entoloma obscuromarginatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513712

Basionym. Rhodophyllus obscuromarginatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 104. 1979.

Entoloma ocellatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513713

Basionym. Rhodophyllus ocellatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 524. 1979.

Entoloma oncocystis (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513714

Basionym. Rhodophyllus oncocystis Romagn. & Gilles, Beih. Nova Hedwigia 59: 572. 1979.

Entoloma oncocystis var. ***pseudococles*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513715

Basionym. Rhodophyllus oncocystis var. *pseudococles* Romagn. & Gilles, Beih. Nova Hedwigia 59: 574. 1979.

Entoloma ovatosporum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513716

Basionym. Leptonia ovatospora Largent, Biblthca Mycol. 55: 232. 1977.

Entoloma pallidius (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513717

Basionym. Rhodophyllus pallidior Romagn. & Gilles, Beih. Nova Hedwigia 59: 211. 1979.

Entoloma pallidissimum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513718

Basionym. Rhodophyllus pallidissimus Romagn. & Gilles, Beih. Nova Hedwigia 59: 248. 1979.

Entoloma pallidocarneum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513719

Basionym. Rhodophyllus pallidocarneus Romagn. & Gilles, Beih. Nova Hedwigia 59: 179. 1979.

Entoloma pallidocarneum var. ***lilliputianum*** (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513720

Basionym. Rhodophyllus pallidocarneum var. *lilliputianus* Romagn. & Gilles, Beih. Nova Hedwigia 59: 181. 1979.

Entoloma pallidosporum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513721

Basionym. Rhodophyllus pallidosporus Romagn. & Gilles, Nova Hedwigia 32, 4: 847. 1981.

Entoloma pandanicola (E. Horak) Noordel. & Co-David, *comb. nov.* — MycoBank MB513722

Basionym. Claudopus pandanicola E. Horak, Beih. Nova Hedwigia 65: 35. 1980.

Entoloma pardinum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513723

Basionym. Rhodophyllus pardinus Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma paucifolium (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513724

Basionym. Rhodophyllus paucifolius Romagn. & Gilles, Beih. Nova Hedwigia 59: 213. 1979.

Entoloma perflavifolium Noordel. & Co-David, *nom. nov.* — MycoBank: MB513726

Basionym. Alboleptonia flavifolia T.J. Baroni & Lodge, Mycologia 90, 4: 684. 1998. Non *Entoloma flavifolium* Peck (1905).

Entoloma perfuscum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513727

Basionym. Leptonia perfusca Largent, Biblthca Mycol. 55: 79. 1977.

Entoloma phaeoxanthum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513725

Basionym. Rhodophyllus phaeoxanthus Romagn. & Gilles, Beih. Nova Hedwigia 59: 251. 1979.

Entoloma phaeum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513728

Basionym. Rhodophyllus phaeus Romagn. & Gilles, Beih. Nova Hedwigia 59: 461. 1979.

Entoloma pigmentosipes (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513729

Basionym. Leptonia parva forma *pigmentosipes* Largent, Biblioth. Mycol. 55: 188. 1977.

Entoloma pilosellum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513730

Basionym. Rhodophyllus pilosellus Romagn. & Gilles, Beih. Nova Hedwigia 59: 215. 1979.

Entoloma planoconvexum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513731

Basionym. Rhodophyllus planoconvexus Romagn. & Gilles, Beih. Nova Hedwigia 59: 383. 1979.

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Basionym. Rhodophyllus platyspermus Romagn. & Gilles, Beih. Nova Hedwigia 59: 126. 1979.

Entoloma pluricolor (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513733

Basionym. Rhodophyllus pluricolor Romagn. & Gilles, Beih. Nova Hedwigia 59: 317. 1979.

Entoloma poliothrix (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513734

Basionym. Rhodophyllus poliothrix Romagn. & Gilles, Nova Hedwigia 32, 4: 844. 1981 (1980).

Entoloma polyphyllum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513735

Basionym. Rhodophyllus polyphyllus Romagn. & Gilles, Beih. Nova Hedwigia 59: 560. 1979.

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Entoloma pseudobulbipes (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513738

Basionym. Leptonia pseudobulbipes Largent, Biblthca Mycol. 55: 144. 1977.

Entoloma pseudocystidiatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513739

Basionym. Rhodophyllus pseudocystidiatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 526. 1979.

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Basionym. Rhodophyllus pseudodenticulatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 385. 1979.

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Basionym. Rhodophyllus pseudodochmiopus Romagn. & Gilles, Beih. Nova Hedwigia 59: 215. 1979.

Entoloma peudohirtipes (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513742

Basionym. Nolanea pseudohirtipes Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 188. 1994.

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Basionym. Rhodophyllus pseudorrhombosporus Romagn. & Gilles, Beih. Nova Hedwigia 59: 252. 1979.

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Basionym. Nolanea pseudostrictia Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 272. 1994.

Entoloma pseudotruncatum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513745

Basionym. Rhodophyllus pseudotruncatus Romagn. & Gilles, Beih. Nova Hedwigia 59: 215. 1979.

Entoloma pudicum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513746

Basionym. Rhodophyllus pudicus Romagn. & Gilles, Beih. Nova Hedwigia 59: 215. 1979.

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Basionym. Rhodophyllus pulcherrimus Romagn., Les Rhodophylles de Madagascar: 150. 1941.

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Basionym. Rhodophyllus pulveripes Romagn. & Gilles, Beih. Nova Hedwigia 59: 385. 1979.

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Basionym. Rhodophyllus punctipileus Romagn. & Gilles, Beih. Nova Hedwigia 59: 385. 1979.

Entoloma punctulatum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513751

Basionym. Rhodophyllus punctulatus Romagn., Les Rhodophylles de Madagascar: 152. 1941.

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Basionym. Nolanea quadrospora Largent & O.K. Mill., Mycologia 78, 1: 136. 1986.

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Basionym. Leptonia rectangula Largent, Biblthca Mycol. 55: 202. 1977.

Entoloma remotum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513756

Basionym. Rhodophyllus remotus Romagn. & Gilles, Beih. Nova Hedwigia 59: 574. 1979.

Entoloma rigidipus (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513757

Basionym. Inocephalus rigidipus Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 394. 1994.

Entoloma rhodanthes (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513758

Basionym. Rhodophyllus rhodanthes Romagn., Les Rhodophylles de Madagascar: 150. 1941.

Entoloma rhodellum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513759

Basionym. Rhodophyllus rhodellus Romagn., Les Rhodophylles de Madagascar: 150. 1941.

Entoloma rigens (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513760

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Entoloma rostratum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513763

Basionym. Leptonia rostrata Largent, Biblthca Mycol. 55: 145. 1977.

Entoloma rotula (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513764

Basionym. Rhodophyllus rotula Romagn., Les Rhodophylles de Madagascar: 150. 1941.

Entoloma rufum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513765

Basionym. Rhodophyllus rufus Romagn. & Gilles, Beih. Nova Hedwigia 59: 481. 1979.

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Basionym. Rhodophyllus rugifer Romagn. & Gilles, Beih. Nova Hedwigia 59: 466. 1979.

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Basionym. Paraleptonia scabrulosa Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 410. 1994.

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Basionym. Leptonia separata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 212. 1994.

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Basionym. Rhodophyllus simplex Romagn., Les Rhodophylles de Madagascar: 152. 1941.

Entoloma spermaticum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513772

Basionym. Rhodophyllus spermaticus Romagn. & Gilles, Beih. Nova Hedwigia 59: 387. 1979.

Entoloma spurium (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513773

Basionym. Rhodophyllus spurius Romagn. & Gilles, Nova Hedwigia 32, 4: 842. 1981 (1980).

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Basionym. Rhodophyllus stylobates Romagn. & Gilles, Beih. Nova Hedwigia 59: 225. 1979.

Entoloma subalbidulum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513775

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Basionym. Rhodophyllus subbulbosus Romagn. & Gilles, Beih. Nova Hedwigia 59: 444. 1979.

Entoloma subcapitatum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513777

Basionym. Nolanea subcapitata Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 212. 1994.

Entoloma subfusiferum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513778

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Entoloma subglabrum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513779

Basionym. Rhodophyllus subglaber Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma subgracile (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513780

Basionym. Leptonia subgracilis Largent, Biblthca Mycol. 55: 83. 1977.

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Entoloma subsericeoides (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513787

Basionym. Nolanea subsericeoides Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 246. 1994.

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Basionym. Nolanea subsolstitialis Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 208. 1994.

Entoloma subsquamosum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513786

Basionym. Rhodophyllus subsquamosus Romagn., Les Rhodophylles de Madagascar: 154. 1941.

Entoloma subviduense (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513789

Basionym. Nolanea subviduense Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 128. 1994.

Entoloma subviolaceovernum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513790

Basionym. Nolanea subviolaceoverna Largent, Entolomatoid fungi of the Western United States and Alaska (Eureka): 244. 1994.

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Basionym. Rhodophyllus tenebrosus Romagn. & Gilles, Beih. Nova Hedwigia 59: 128. 1979.

Entoloma tenuipileum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513793

Basionym. Rhodophyllus tenuipileus Romagn. & Gilles, Beih. Nova Hedwigia 59: 134. 1979.

Entoloma thiersii (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513794

Basionym. Leptonia thiersii Largent, Biblthca Mycol. 55: 104. 1977.

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Basionym. Rhodophyllus tigrinellus Romagn., Les Rhodophylles de Madagascar: 149. 1941.

Entoloma titthiophorum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513796

Basionym. Rhodophyllus titthiophorus Romagn. & Gilles, Beih. Nova Hedwigia 59: 349. 1979.

Entoloma tortile (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513797

Basionym. Rhodophyllus tortilis Romagn., Les Rhodophylles de Madagascar: 153. 1941.

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Basionym. Pouzaromyces transitus E. Horak, Beih. Nova Hedwigia 65: 40. 1980.

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Basionym. Leptonia trichomata Largent, Biblthca Mycol. 55: 198. 1977.

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Basionym. Rhodophyllus tristissimus Romagn. & Gilles, Beih. Nova Hedwigia 59: 394. 1979.

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Basionym. Rhodophyllus truncatus Romagn., Les Rhodophylles de Madagascar: 153. 1941.

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Basionym. Rhodophyllus variesporus Romagn. & Gilles, Beih. Nova Hedwigia 59: 256. 1979.

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Basionym. Rhodophyllus velutipileus Romagn. & Gilles, Beih. Nova Hedwigia 59: 471. 1979.

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Basionym. Rhodophyllus vestipes Romagn. & Gilles, Beih. Nova Hedwigia 59: 259. 1979.

Entoloma vetulum (Romagn.) Noordel. & Co-David, *comb. nov.* — MycoBank MB513810

Basionym. Rhodophyllus vetulus Romagn., Les Rhodophylles de Madagascar: 143. 1941.

Entoloma vinosulum (Romagn. & Gilles) Noordel. & Co-David, *comb. nov.* — MycoBank MB513811

Basionym. Rhodophyllus vinosulus Romagn. & Gilles, Beih. Nova Hedwigia 59: 351. 1979.

Entoloma violaceonigrum (Largent) Noordel. & Co-David, *comb. nov.* — MycoBank MB513812

Basionym. Leptonia violaceonigra Largent, Biblthca Mycol. 55: 63. 1977.

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Basionym. Rhodophyllus xanthophaeus Romagn. & Gilles, Beih. Nova Hedwigia 59: 446. 1979.

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Basionym. Leptonia zanthophylla Largent, Biblthca Mycol. 55: 109. 1977.

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

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