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***Entocybe* is proposed as a new genus in the Entolomataceae (Agaricomycetes, Basidiomycota) based on morphological and molecular evidence**

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Abstract: Morphological and molecular characteristics support the recognition of a well-defined taxonomic group within the Entolomataceae. The distinctive basidiospore form and a three locus DNA analysis separate the species that share these characteristics from other species of *Entoloma s. l.* We propose here a new genus, *Entocybe*, to accommodate these taxa.

Key words: *Entoloma*, Section *Turfosa*, new combinations, nlsu, RPB2 and mitSSU sequences, *Rhodocybe*.

Introduction: The Entolomataceae is a species-rich family of Agaricales with over 1500 taxa described worldwide (Indexfungorum.org). Of the clades recognized so far (Moncalvo et al., 2002), *Entoloma s. l.* is by far the largest genus in this family with approximately 1000 taxa (Kirk et al., 2008). Several authors recognize segregate genera within *Entoloma s. l.* (Aime et al., 2010; Baroni & Halling, 2000; Baroni & Lodge, 1998; Largent & Baroni, 1988; Largent, 1994; Orton, 1991a, b; Pegler, 1977, 1983, 1986, 1997; Pegler & Young, 1978; Rutter & Watling, 1997), while others recognize a single genus *Entoloma*, either with subgeneric classifications (Noordeloos, 1981, 1992, 2004; Romagnesi, 1941, 1974; Romagnesi & Gilles, 1979) or without such a framework (Hesler, 1967). Horak, (1976, 1978, 1980, 2008) recognizes a few selected genera in *Entoloma s. l.* as distinct (i.e. *Claudopus*, *Pouzarella*, *Richoniella* and *Rhodogaster*), but, like Hesler (1967), does not employ a subgeneric classification system within *Entoloma s. l.* The recently published opinions in the *Dictionary of Fungi* (Kirk et al., 2008) suggest that only four genera be considered as members of the family Entolomataceae; however these comments do not seem to be supported by published evidence.

Based on macroscopic and microscopic morphological characteristics, at least 16 groups can be defined within *Entoloma s. l.* (Horak, 2008; Largent & Baroni, 1988; Largent, 1994; Noordeloos, 1981, 1992, 2004). The presence/absence or concentration of the urea also has been used to support the recognition of some genera (Largent & Benedict, 1970).

Molecular analyses suggested that species in the Entolomataceae form a monophyletic group within the Agaricales (Moncalvo et al., 2002; Matheny et al., 2006). However, these studies do not clearly show the Entolomataceae as monophyletic due to a lack of phylogenetic support (Moncalvo et al. 2002; single locus phylogeny [nucLSU] with 40 taxa) or because of

the low number of taxa sampled (Matheny et al., 2006; 6-loci used but with only eight taxa of Entolomataceae). More recently, Co-David et al (2009) published a 3-locus phylogeny for a broader sampling of Entolomataceae using outgroups sampled in the Lyophyllaceae and in the Tricholomataceae. The analyses presented by Co-David et al. (2009) suggested that the Entolomataceae is significantly supported as monophyletic group. However, the phylogeny of Matheny et al. (2006) recovered significant support for the monophyly of a clade including the Tricholomataceae-Lyophyllaceae-Entolomataceae based solely on maximum parsimony (MP) bootstrap analyses, and thus not confirming a clearly monophyletic Entolomataceae. We consequently readdressed the question of the monophyly of the Entolomataceae in the present study by sampling more basal outgroup taxa ('Catathelasma' clade; Matheny et al. 2006).

The two phylogenetic studies that used a representative sampling of the Entolomataceae (Moncalvo et al., 2002; Co-David et al., 2009) both recognized an *Entoloma s. l.* clade distinct from the rest of the Entolomataceae. Using three loci in combination (nucLSU, mitSSU and RPB2) the phylogeny depicted by Co-David et al. (2009) provided a limited amount of support for internal relationships within *Entoloma s. l.* except for the following subclades: a 'Prunulooides' clade (PP = 100%; maximum likelihood bootstrap support [MLBS] = 80%), a 'Rhodocyboid' clade (PP = 100%; MLBS = 100%), and a 'Nolanea-Claudopus' clade (PP = 100%; MLBS = 70%). In the 'Prunulooides' clade, two subgroups were identified: one including species centered around *Entoloma prunulooides* (Fr.) Quél., e.g. *E. bloxamii* (Berk. & Broome) Sacc., *E. gelatinosum* E. Horak, etc. and the other including some species of *Entoloma* previously placed in the genus *Rhodocybe*, Section *Rhodophana* based upon basidiospore morphology by Baroni & Largent (1989), e.g. *Rhodocybe trachyospora*

(Largent) T. J. Baroni & Largent and its varieties and related species. We propose here to formally recognize this last group of species as a new genus, *Entocybe*. Additional taxa that belong in *Entocybe* were previously recognized as a cohesive unit and placed in *Entoloma*, Subgenus *Entoloma*, Section *Turfosa* (Romagn.) Noordel. (Noordeloos, 1992). The unique basidiospore morphology and molecular data support the recognition of *Entocybe* in the *Entoloma s. l.* clade.

Materials and Methods

Taxon sampling and molecular phylogenetic analyses. —

Fifty-one collections were sampled in the Tricholomatoid clade *sensu* Matheny et al. (2006) – see Table 1. The Entolomataceae is represented by 34 collections (32 species): two *Alboleptonia* spp., three *Clitopilus* spp., *Clitopilopsis hirneola* (Fr.) Kühner ex Konrad & Maubl., seven *Entoloma* spp., five *Inocephalus* spp., two *Leptonia* spp., *Nolanea strictior* (Peck) Pomerl., nine *Rhodocybe* spp., *Paraeccillia sericeonitida* (P.D. Orton) Largent and *Trichopilus porphyrophaeus* (Fr.) P.D. Orton. The outgroup for this analysis, *Catathelasma ventricosum* (Peck) Singer, was identified as part of the ‘Catathelasma’ clade by Matheny et al. [2006]. We also sampled other representatives of the Tricholomatoid clade (Matheny et al. 2006): six species of the Lyophyllaceae (identified as the sister group of the Entolomataceae), nine species in the family Tricholomataceae and *Dendrocollybia racemosa* (Pers.) R. H. Petersen & Redhead. DNA was isolated from fresh material fixed in the field in a 2X cetyl-trimethyl-ammonium-bromide buffer (2x CTAB) or from warm air-dried basidiomata as described in Hofstetter et al. (2002). The latter paper also describes amplification and sequencing protocols. Three loci from three different parts of the genome were sequenced: *RPB2*, *LSU*, and *mtSSU*. For *RPB2*, the primers bRPB2-6F and

bRPB2-6F and BRPB2-7R were used (Hofstetter et al, 2002, Matheny et al, 2002)). For *nucLSU*, the primers LROR, LR16, LR3R, LR5 and LR7 were used (for more information refer to <http://www.biology.duke.edu/fungi/mycolab/primers.htm>). The primers used for *mtSSU* were MS1 and MS2 (White et al. 1990). Recovery of part of the *RPB2* gene (region 5[6]-7) followed Matheny et al. (2002). Because existing *RPB2* amplification primers were not well adapted for sequencing Entolomataceae and Lyophyllaceae, PCR products were cloned using pSTBlue-1 AccepTor Vector™ Kit (Novagen) and the sequencing used primers of the vector. Sequencing was performed using reagents and conditions of the *BigDye® Terminator v3.1 Cycle sequencing Kit* and an automated capillary sequencer ABI 3700 DNA analyzer (Perkin Elmer, Applied Biosystems, Foster City, CA, USA). Sequences were assembled and edited using the software package Sequencher 3.0 (Gene Codes Corp., USA).

A total of 76 nucleotide sequences were newly produced for this study (21 *nucLSU*; 28 *mitSSU*; 27 *RPB2*) while the others sequences were retrieved from Matheny et al. (2006) – Table 1.

Phylogenetic analyses. —

Alignments of nucleotide sequences were performed by eye using the editor of MacClade v.4.06 (Maddison and Maddison, 2003. Sinauer Associates, Inc., Sunderland, Massachusetts).

Topological incongruence was examined based on 500 bootstrap replicates conducted in RAxML-VI-HPC (RAxML-bs; Stamatakis et al. 2005) implementing a GTRMIX model with gamma distribution, approximated with four categories. RAxML bootstrap analyses were conducted on each locus separately (*mitSSU*; *nucLSU*; *RPB2*). To screen for putative conflict we used the program *compat.py* (available at www.lutzonilab.net), which compares ML-BS

values of the loci. Conflict between single gene BS analyses was considered significant when conflicting branches had bootstrap proportions \geq 70% (Mason-Gamer and Kellogg, 1996).

A maximum likelihood search for the most likely tree on our 3-locus 51 taxa data set was conducted in RAxML-VI-HPC, completing 50 replicates with the GTRMIX with the settings used for bootstrap analyses. Two different data set partitionings were used: 4 partitions (mitSSU; nuLSU; *RPB2* 1st + 2nd and *RPB2* 3rd) or 5 partitions (mitSSU; nuLSU; *RPB2* 1st; 2nd and 3rd). Bootstrap proportions were estimated for the two partitionings of the data based on 500 replicates of ML bootstrapping (MLbs) conducted in RAxML. Bootstrap proportions \geq 70% were considered significant (for a discussion on the interpretation of support values see: Alfaro et al., 2003; Lutzoni et al., 2004).

Results

Molecular results. —

The full alignment includes 4854 characters. After exclusion of ambiguous regions (2 spliceosomal introns in *RPB2* region, 1 intron ranging from 600-1200 bp found in mitSSU of *Inocephalus* "argenteus", *Clitopilus* "flaviphyllus" and *Rhodocybe pruinostipita* T.J. Baroni, Largent & Aime, 1 hyper variable region (50-300 bp) in mitSSU, the LR5-LR7 sequence region of nuLSU that was only obtained for half of the taxa, and respectively eight and four short ambiguous regions in nuLSU and mitSSU), the analyzed data set includes 2367 bp (nuLSU: 985 bp, mitSSU: 345 bp, *RPB2*: 1037 bp).

No incongruence was detected between individual data sets (mitSSU, nuLSU, and *RPB2*), therefore the three loci were used in combination. Data partitioning that maximized likelihood and BS support for our 3-locus 51-taxa dataset is the four partitions one (mitSSU;

nuLSU; *RPB2* 1st + 2nd and *RPB2* 3rd). The most likely tree ($\ln = -25298.0695$) based on 50 RAxML searches is depicted in Figure 1 with associated bootstrap values.

Using *Catathelasma ventricosum* as the outgroup, the most likely tree identifies three major clades (Figure 1): the family Entolomataceae is divided into two highly supported groups: Entolomataceae 1 (BS = 96%) and Entolomataceae 2 (BS = 95%). The Tricholomataceae-Lyophyllaceae clade (BS = 69%) is nested without significant support (sister with Entolomataceae 1, BS = 58%) within the family Entolomataceae. Basal relationships between these three clades remain consequently unresolved.

Internal relationships within the Entolomataceae 1 clade are poorly resolved except for a basal subgroup composed of *Rhodocybe trachyspora* (Largent) T.J. Baroni & Largent and three species of *Entoloma* (*E. nitidum* Quél., *E. turbidum* (Fr.) Quél. and *E. vinaceum* (Scop.) Arnolds & Noordel.). These four species are well supported as monophyletic (BS = 100%) and clearly separated from the rest of Entolomataceae 1 (BS = 100%). Some more terminal relationships within Entolomataceae 1 receive significant support: (1) the genus *Inocephalus* (BS = 100%) is sister with *Trichopilus porphyrophaeus* (BS = 82%); (2) *Alboleptonia* (BS = 74%) is sister with *Leptonia* "subdecurrentiba" (BS = 79%), and with *L. serrulata* (Fr.) P. Kumm. which occupies the most basal position within that subgroup; (3) *Entoloma abortivum* (Berk. & M.A. Curtis) Donk and *Paraeccilia sericeonitida* are monophyletic (BS = 100%) as well as (4) *Entoloma prunuloides*, *E. nidorosum* (Fr.) Quél. and *E. flavifolium* Peck (BS = 100%).

Internal relationships within the Tricholomataceae-Lyophyllaceae clade received low support except for (1) a monophyletic Lyophyllaceae (BS = 92%), (2) a monophyletic

Tricholoma (BS = 100%), (3) the monophyly of *Lepista nuda* (Bull.) Cooke, *Clitocybe dealbata* (Sowerby) Gillet and *Collybia tuberosa* (BS = 99%) and (4) the monophyly of *Clitocybe candicans* (Pers.) P. Kumm. and *C. subditipoda* Peck (BS = 80%). Basal relationships between these subclades remain unresolved as well as the position of *Dendrocollybia racemosa* and *Lepista nebularis* (Batsch) Harmaja within that clade.

The *Entolomataceae* 2 clade is well resolved and supported. It includes two subgroups of *Rhodocybe*. One of these subgroups includes *R. caelata* (Fr.) Maire, the type species of *Rhodocybe*, plus four other species (*R. pruinostipitata*, *R. aureicystidiata* Lennox ex T.J. Baroni, *R. gemina* (Paulet) Kuyper & Noordel. and *R. spongiosa* T.J. Baroni, Largent & Aime). The second *Rhodocybe* subgroup (BS = 99%) is monophyletic (BS = 97%) with *Clitopilus* (BS = 99%) and *Clitopilopsis* (BS = 100%) and nested between these two genera with a sister relationship with *Clitopilus* (BS = 86%) and with *Clitopilopsis* occupying a more basal position.

Morphological results. —

The species we place in *Entocybe gen. nov.* (Figure 1) were originally recognized as a unique and cohesive taxonomic unit by the following set of characteristics (Baroni and Largent, 1989): basidiospores small (less than 9 μm in the longest dimensions, excluding the hilar appendix), isodiametric with undulate-pustulate or rounded pustulate ornamentation (Fig. 2), with distinctly or obscurely rounded angles in polar view producing 6-10 facets (Fig. 3), obscurely angular or rounded angular in profile view or some species with scarcely angled spores, and spore walls evenly cyanophilic; the spore deposit color pinkish, flesh, vinaceous, vinaceous brown or rarely with grayish hues; the basidiomata small to medium sized (collybioid or tricholomatoid) and mostly fragile in construction, with lamellae attached (adnate or sinuate or emarginate or adnexed and in some cases almost free), the

pileus surface is typically hygrophanous and smooth, the stipe is frequently fragile and fibrillose-striate, clamp connections are obvious and present in all tissues.

Baroni and Largent (1989) recognized this core group of taxa and hypothesized their relationship to *Rhodocybe*, making several re-combinations of these formerly *Entoloma* species, e.g. *Entoloma trachyosporum* Largent, into *Rhodocybe*. Based on the molecular evidence presented here and previously by Co-David et al. (2009), we now realize these *Rhodocybe*-like taxa as a distinct group related to *Entoloma s. l.* and not belonging in *Rhodocybe*.

Discussion: Using *Catathelasma ventricosum* as the outgroup, the monophyly of the *Entolomataceae* suggested by all previous phylogenetic studies (Moncalvo et al., 2002; Co-David et al., 2009; Matheny et al., 2006), remains questionable. Our 3-locus 51-taxa data set (Figure 1) suggests that members of the *Entolomataceae* are paraphyletic with the *Tricholomataceae*-*Lyophyllaceae* clade nested between the *Entoloma s. l.* clade and the *Rhodocybe*-*Clitopilus* clade sensu Co-David et al. (2009). However, the monophyly of *Entoloma s. l.* and the *Lyophyllaceae*-*Tricholomataceae* did not receive significant support (MLBS = 58%) in the present study. A phylogeny of the *Tricholomatoid* clade sensu Matheny et al. (2006), including a broader representative taxon sampling and more loci, is needed to help solve the internal relationships of this difficult white spored group of agarics. Co-David et al. (2009) show support for two distinct clades within the *Entolomataceae*, i. e., an *Entolomataceae* clade one (*Entoloma sensu lato*) and *Entolomataceae* clade two (*Rhodocybe/Clitopilus*). Using a slightly different set of taxa we also find this same result, even though we do not confirm monophyly for the *Entolomataceae*. In Co-David et al. (2009) they also concluded that in the *Entolomataceae* clade 1 there appears to be two distinct groupings, a

crown Entoloma clade and a basal Entoloma clade (labeled as a grade in their phylogenetic reconstruction). It is this basal clade that we address here and compare to our present data set (Fig. 1) drawing different conclusions from the phylogenetic evidence.

The new genus *Entocybe* is basal to the rest of *Entoloma s. l.* (Fig. 1) with significant support (BS 100%). Co-David et al. (2009) also show a core group of taxa, i. e. *Entoloma trachyospora*, *E. turbidum*, *E. nitidum*, etc., that appear as monophyletic (PP = 100%; MLBS = 83%) and the sister group of *E. prunuloides* and related species, similar to our conclusions. Thus the closest group of taxa to *Entocybe* is the *E. prunuloides* group. Morphologically *Entocybe* is easily distinguished from members of the *E. prunuloides* group and all other *Entoloma s. l.* by their basidiospore morphology.

The morphological taxonomy of the genera placed in the Entolomataceae is broadly based on analysis of basidiospore form and three distinct spore morphologies have traditionally been recognized (Singer, 1986; Baroni, 1981; Largent and Baroni, 1988): a rhodocybe type, a clitopilus type and an entoloma type (as rhodocybeoid, clitopiloid and entolomatoid in Co-David et al. 2009). The genus *Rhodocybe* is defined by the rhodocybeoid basidiospore that is multiple and minutely angular in polar view with typically 6-10 or more facets (Fig. 4), rarely angular in profile view, and with diagnostic undulate-pustulate ornamentations covering the surface of the basidiospores (Fig. 5). These ornamentations are visible under the compound light microscope but more clearly resolved with scanning electron microscope images (Figs. 4-5)(also see Baroni, 1981; Baroni and Horak, 1994). In contrast, members of the *Entoloma sensu lato* group produce entoloma type basidiospores clearly angular in all views, with the polar view displaying fewer, easily visualized angles with typically 4-6 facets (Fig. 6). The ornamentation of

short interconnected ridges, lacking discrete pustulate protrusions or bumps, is diagnostic (Fig. 7). The third basidiospore form, as represented by *Clitopilus*, displays multiple and for most species minutely angled basidiospores in polar view with (5-)6-12 facets (Fig. 8). The longitudinal ridges that ornament the surface and run the length of the basidiospore from apex to base (Fig. 9), make this clitopilus spore type highly distinctive (Singer, 1986; Baroni and Watling, 1999).

Baroni and Largent (1989) recognized that a group of supposedly entolomatoid taxa, *Entoloma trachyosporum* and its varieties, had rhodocybe-like basidiospores similar in form to basidiospores of *Rhodocybe priscua* T. J. Baroni and *Rhodocybe speciosa* Lennox ex T. J. Baroni in *Rhodocybe*, Section *Rhodophana* (Baroni, 1981). All of these taxa have nearly identical subglobose or globose basidiospores (= subisodiametric or isodiametric) that are obscurely angled in profile view, possess 6-10 minute facets in polar view, are endowed with a pustulate ornamented spore surface and show evenly cyanophilic spore walls. These basidiospores fit the rhodocybe-like profile. In addition, all of these taxa have clamp connections on their hyphae, a diagnostic character of *Rhodocybe*, section *Rhodophana* (Singer, 1973, Baroni, 1981). None of the 100+ species in the other sections of *Rhodocybe* possesses clamp connections on the hyphae of their basidiomata, supporting this as a significant morphological characteristic. Because of these similarities Baroni and Largent (1989) transferred *E. trachyosporum* and its varieties into *Rhodocybe*, section *Rhodophana*.

Based on the data of Co-David et al. (2009) and our results, it is now clear that these rhodocybe-like taxa are part of the *Entoloma s. l.* clade, not the *Rhodocybe/Clitopilus* clade, as Baroni and Largent (1989) had hypothesized based on morphological features alone. Our results from

the 3-locus 51 taxa analysis (Fig. 1) agree with the findings of Co-David et al. (2009) and clearly support the placement of *E. trachyosporum* and similar taxa in the *Entoloma s. l.* clade as a monophyletic group basal to but separate from other taxa in the *Entoloma s. l.* clade, supported by both molecular and morphological evidence.

Therefore, those taxa found in the *Entoloma trachyosporum* group, combined with *Rhodocybe speciosa*, *R. priscua* T.J. Baroni and a group of *Entoloma* taxa placed in section *Turfosa* (Noordeloos, 1992), e. g. *E. turbidum*, *E. vinaceum*, *E. pseudoturbidum* (Romagn.) M.M. Moser) form the core taxonomic unit we have identified with morphological and/or molecular characteristics as the genus *Entocybe*. This basal position of *Entocybe* in the *Entolomataceae* 1 clade (Fig. 1) supports an hypothesis proposed by Baroni (1981, p. 126) that this type of *Entocybe* spore form is ancestral to and was a precursor to the strongly angled basidiospores displayed by the rest of the members of *Entoloma s. l.*

A comparison of the main differences in basidiospore morphologies between *Entocybe* and *Entoloma s. l.* is provided in order to clarify the ease with which *Entocybe* can be recognized from a morphological perspective.

The derived basidiospore morphotype found in *Entoloma s. l.* of *Entolomataceae* clade 1, displays distinctively angled basidiospores in profile view (Fig. 6) that are produced by short interconnected ridges best seen under the scanning electron microscope (Fig. 7). Most importantly this spore type has only 4-5 (-6) angles in polar view, easily confirmed with a light microscope, and lacks pustule-like ornamentation (Figs. 6-7). By far, the majority of *Entoloma s. l.* species have basidiospores that are larger than 9 µm in length, with only a few exceptions found in *Entoloma*, subgenus *Entoloma*, e. g. *Entoloma prunuloides*, *E. bloxamii*, *E. rubellum* (Scop.) Gillet, *E. viridans* (Fr.) P. Karst. and *E. luteobasis* Ebert & E.

Ludwig (Noordeloos, 1992). These latter taxa comprising the *E. prunuloides* clade, with basidiospores less than 9 µm in length, have the typical entoloma-type basidiospore morphology with 4-6 angles in polar view and a surface ornamentation composed of short interconnected ridges (Figs. 6-7). Therefore the *E. prunuloides* clade is part of the *Entoloma s. l.* subgroup in the *Entolomataceae* 1 clade and is obviously different from its sister and basal group, *Entocybe*, based on the basidiospore morphology and the 3 gene analysis (Fig. 1; Co-David et al., 2009).

Species of *Entocybe*, as noted previously, are easy to recognize because they produce obscurely angled basidiospores in profile view, have multiple minute angles in polar view (6-10 angles) (Fig. 3) and produce obscure to obvious pustulate ornamentation across the surface of the spores (Fig. 2) or in some cases display an incomplete interconnected ridge-like pattern with scattered pustulate ornamentation when examined under the scanning electron microscope (Fig. 10-12). The basidiospores of these species are always noticeably smaller (less than 9 µm in length), consistently isodiametric, and somewhat thinner walled than those of species in the *Entoloma*, subgenus *Entoloma* (Noordeloos, 1992). The distinctive basidiospore morphology of *Entocybe* spp. indicated they were out of place when compared with all other taxa in the *Entoloma s. l.* clade and the molecular analyses presented here (Fig. 1) and in the Co-David et al. (2009) paper confirm this hypothesis.

So far seven taxa have been identified in North America that belong in this new genus, four of these are varieties of *Entocybe trachyospora*. The remaining North American representatives are: *E. priscua*, *E. speciosa*, and *E. lignicola*. The other members of *Entocybe* that have been identified are European (Table 2), thus we know of only northern hemisphere temperate species of *Entocybe* so far. Most of these European species were previously classified in *Entoloma*, section

Turfosa (Noordeloos, 1992): i. e. *Entocybe turbida*, *E. pseudoturbida* and *E. vinacea* and its varieties. After studying collections of these species from Europe (Table 2), it was obvious from basidiospore morphology that these taxa belong in *Entocybe* and the molecular evidence presented here and in Co-David et al. (2009) support this conclusion.

At least one additional taxon, not originally recognized as a member of *Entoloma*, section *Turfosa* (Noordeloos, 1992), also belongs in *Entocybe*, viz. *E. nitida*. *Entocybe nitida* was previously placed in *Entoloma*, subgenus *Entoloma*, section *Entoloma* (Noordeloos, 1992). However, the isodiametric basidiospores that are less than 9 μm in length, possess 6-10 angles in polar view, and have low broad pustule-like ornamentations interspersed among the poorly developed or disrupted and not completely interconnected ridges (Fig. 10) place *E. nitida* in *Entocybe* using morphological characteristics. The molecular analysis (data presented here and Co-David et al., 2009) confirms this placement.

The papers by Co-David et al. (2009) and Gates and Noordeloos (2007) also indicate several other Southern Hemisphere temperate taxa from Tasmania that may be species of *Entocybe*. These taxa will be examined in the future to determine if they belong in *Entocybe*.

With the recognition of *Entocybe* as a distinct new taxonomic unit in the Entolomataceae, it is highly likely that more species will be discovered, especially for the southern hemisphere temperate regions. We fully expect the number of taxa placed in *Entocybe*, both newly discovered and re-evaluations of existing taxa, will rise quickly now that *Entocybe* can be recognized with the use of morphological and molecular datasets.

A few final comments about phylogenetic conclusions/hypotheses concerning clades within the Entolomataceae are discussed based on the

phylogenetic analysis presented here (Fig. 1). Co-David et al. (2009) transferred all existing species of *Rhodocybe* to the genus *Clitopilus* based on their molecular analysis. However, we would suggest that too little sampling has been done and too few species examined so far to make such large-scale taxonomic recombinations. Besides, the conclusions can be interpreted quite differently based on their and our results to warrant moving all taxa of *Rhodocybe* into *Clitopilus*. This question of whether all taxa in the Entolomataceae 2 clade should be considered in one large genus, *Clitopilus*, will be revisited at a later time after significantly more exemplars have been added to the analysis.

Conclusions

Based on phylogenetic and morphological evidence, the following taxonomic hypotheses are presented.

New taxon. —

Entocybe T. J. Baroni, Hofstetter & Largent, gen. nov.

A speciebus aliis Entolomatis sensu lato basidiosporis obscure angularibus, in visu polari angulis 6-10, exornatione superficiei ubique nunc isolatim undulato-pustulata vel rotundo-pustulata, nunc e cristis discontinuis interconjunctis pustulis isolatis interspersis praeditis composita differt; basidiosporis sub microscopio luce transmissa eis Rhodocybes similibus.

Differing from species of *Entoloma sensu lato* by obscurely angular basidiospores with 6-10 facets (angles) in polar view and undulate-pustulate or rounded pustulate surface ornamentation overall, similar to basidiospores of *Rhodocybe*, or ornamentation composed of broken interconnected ridges with isolated pustules

interspersed. Also differing from *Entoloma sensu lato* by RPB2, LSU, and mtSSU molecular sequences.

Etymology: partly from *Entoloma*, partly from *Rhodocybe* because of the morphological similarities, feminine as for other genera ending in -cybe.

TYPE SPECIES: *Entocybe trachyospora* (Largent) Largent, T. J. Baroni, & V. Hofstetter MB 519983

New Combinations. —

Entocybe turbida (Fr.) T. J. Baroni, V. Hofstetter & Largent, comb. nov.
MB 519996
= *Agaricus turbidus* Fr., Syst. Mycol. 1:205. 1821
= *Entoloma turbidum* (Fr.) Quél., Mém. Soc. Emul. Montbéliard. sér. II,5:119. 1872

Entocybe vinacea (Scop.) T. J. Baroni, V. Hofstetter & Largent, comb. nov.
MB 519993
= *Agaricus vinaceus* Scop., Fl. Carn. I:444. 1772.
= *Nolanea vinacea* (Scop.) Kummer, Fuhr. Pilzk. 95. 1871.
= *Entoloma vinaceum* (Scop.) Arnolds & Noordel. Persoonia 10:298. 1979.

Entocybe vinacea* var. *fumosipes (Arnold & Noordel.) T. J. Baroni, V. Hofstetter & Largent, comb. nov.
MB 519994
= *Entoloma vinaceum* var. *fumosipes* Arnold & Noordel., Persoonia 10(2):296. 1979.

Entocybe vinacea* var. *violeipes (Arnold & Noordel.) T. J. Baroni, V. Hofstetter & Largent, comb. nov.

MB 519995
= *Entoloma vinaceum* var. *violeipes* Arnold & Noordel., Persoonia 10(2):299. 1979.

Entocybe nitida (Quel.) T. J. Baroni, Largent & V. Hofstetter, comb. nov.
MB 519992
= *Entoloma nitidum* Quel., C. R. Ass. Franc. Av. Sci. (La Rochelle, 1882): 11:391. 1883.

Entocybe pseudoturbida (Romagn.) T. J. Baroni, V. Hofstetter & Largent, comb. nov.
MB 519991
= *Rhodophyllus pseudoturbidus* Romagn., Bull. Mens. Soc. Linn. Lyon (No. spec.):386. 1974.
= *Entoloma pseudoturbidum* (Romagn.) Moser, Beih. Sydowia 8:269. 1979.

Entocybe speciosa (Lennox ex T. J. Baroni) T. J. Baroni, Largent & V. Hofstetter, comb. nov.
MB 519990
= *Rhodocybe speciosa* Lennox ex T. J. Baroni, Beih. Nova Hedw. 67:59. 1981.

Entocybe priscua (T. J. Baroni) T. J. Baroni, V. Hofstetter & Largent, comb. nov.
MB 519989
= *Rhodocybe priscua* T. J. Baroni, Beih. Nova Hedw. 67:60. 1981.

Entocybe trachyospora (Largent) Largent, T. J. Baroni, & V. Hofstetter, comb. nov.
MB 519984
= *Entoloma trachyosporum* Largent, Madroño 22:369. 1974.
= *Rhodocybe trachyospora* (Largent) T. J. Baroni & Largent, Mycotaxon 34:48. 1989.
= *Rhodocybe carlottae* Redhead & T. J. Baroni, Can. J. Bot. 64:1451. 1986.

Entocybe trachyospora* var. *griseoviolacea

(Largent) Largent, T. J. Baroni, & V. Hofstetter, comb. nov.
 MB 519985
 ≡ *Entoloma trachyosporum* var. *griseoviolaceum* Largent, Madroño 22:370. 1974.
 ≡ *Rhodocybe trachyospora* var. *griseoviolacea* (Largent) T. J. Baroni & Largent, Mycotaxon 34:49. 1989.

Entocybe trachyospora* var. *purpureoviolacea

(Largent) Largent, T. J. Baroni, & V. Hofstetter, comb. nov.
 MB 519986
 ≡ *Entoloma trachyosporum* var. *purpureoviolaceum* Largent, Madroño 22:371. 1974.
 ≡ *Rhodocybe trachyospora* var. *purpureoviolacea* (Largent) T. J. Baroni & Largent, Mycotaxon 34:49. 1989.

Entocybe trachyospora* var. *vinacea

(Redhead & T. J. Baroni) Largent, T. J. Baroni, & V. Hofstetter, comb. nov.
 MB 519987
 ≡ *Rhodocybe trachyospora* var. *vinacea* (Redhead & T. J. Baroni) T. J. Baroni & Largent, Mycotaxon 34:49. 1989.
 ≡ *Rhodocybe carlottae* var. *vinacea* Redhead & T. J. Baroni, Can. J. Bot. 64:1451. 1986.

Entocybe lignicola (Largent) Largent, T. J. Baroni, & V. Hofstetter, comb. nov.
 MB 519988
 ≡ *Entoloma lignicola* Largent, Mycotaxon 34:129. 1989.

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PMid:18853362

Table 1: Taxon sampling and Genbank accession numbers. Collection sources : AFTOL = “Assembling the Tree Of Life” consortium; CBS = Centraalbureau voor Schimmelcultures, Netherlands; DUKE = Duke University NC, USA; IE-BSG = Institut d’Ecologie-Botanique Systématique et Geobotanique, University of Lausanne, Switzerland; MCA = M. Catherine Aime; PBM = P. Brandon Madthény WTU, Washington ; TB = Timothy J. Baroni; VHAs = Valérie Hofstetter.

Taxon ^a	Source	Genbank accession numbers		
		nucLSU ^b	mitSSU ^b	<i>RPB2</i> ^b
Family Entolomataceae				
<i>Alboleptonia</i> aff. <i>sericella</i>	MCA1978	GU384609	GU384583	GU384632
<i>Alboleptonia stylophora</i>	TB8475	GU384610	GU384584	GU384633
<i>Clitopilopsis hirneola</i>	CBS 577.87	AF223163	---	GU384645
<i>Clitopilopsis hirneola</i>	TB8490	GU384611	GU384587	GU384646
<i>Clitopilus</i> “ <i>cinerascens</i> ” ^c	TB8024	GU384613	GU384585	GU384647
<i>Clitopilus</i> “ <i>flaviphyllus</i> ” ^c	TB8067	GU384612	GU384606	GU384649
<i>Clitopilus prunulus</i>	TB8229	GU384615	---	GU384650
<i>Clitopilus prunulus</i>	TB9663	GU384614	GU384586	GU384648
<i>Entoloma abortivum</i>	TB6693	GU384616	GU384595	GU384642
<i>Entoloma flavifolium</i>	TB6215	AF261301	GU384597	GU384644
<i>Entoloma nidorosum</i>	TB9971	GU384617	GU384596	GU384643
<i>Entoloma nitidum</i>	TB7526	GU384626	GU384602	GU384655
<i>Entoloma prunuloides</i>	AFTOL523	AY700180	---	DQ385883
<i>Entoloma turbidum</i>	TB6949	GU384630	GU384603	GU384656
<i>Entoloma vinaceum</i>	TB8870	GU384631	GU384598	GU384651
<i>Inocephalus</i> “ <i>argenteus</i> ” ^c	MCA1475	GU384619	GU384607	GU384636
<i>Inocephalus</i> “ <i>fuscopunctatus</i> ” ^c	MCA1585	---	GU384592	GU384639
<i>Inocephalus</i> “ <i>squamulosus</i> ” ^c	MCA1867	GU384621	GU384591	GU384638
<i>Inocephalus</i> “ <i>virescens</i> ” ^c	MCA2479	GU384622	GU384593	GU384640
<i>Inocephalus murrayi</i>	VHAs02.02	GU384620	GU384590	GU384637
<i>Leptonia</i> “ <i>subdecurrentiba</i> ”	MCA1486	GU384623	GU384589	GU384635
<i>Leptonia serrulata</i>	VHAs01.02	GU384624	GU384588	GU384634
<i>Nolanea strictior</i>	TB7710	GU384618	GU384594	GU384641
<i>Paraecilia sericeonitida</i>	TB7144	AF261315	EF421098	EF421016
<i>Rhodocybe aureicystidiata</i>	PBM1902	AY380407	---	AY337412
<i>Rhodocybe caelata</i>	TB6995	GU384625	GU384600	GU384652
<i>Rhodocybe fallax</i>	CBS129.63	AF223166	AF357083	EF421018
<i>Rhodocybe gemina</i>	CBS 482.50	AF223167	GU384599	EF421019
<i>Rhodocybe mundula</i>	TB7599/ AFTOL521	AY700182	---	DQ474128
<i>Rhodocybe popinalis</i>	TB6378	AF261285	GU384601	GU384654
<i>Rhodocybe pruinostipitata</i>	MCA1492	GU384627	GU384608	GU384653
<i>Rhodocybe spongiosa</i>	MCA2129	GU384628	GU384604	GU384657
<i>Rhodocybe trachyspora</i>	TB5856	GU384629	GU384605	GU384658
<i>Trichopilus porphyrophaeus</i>	VHAs09.02/ TB6957	AF261290	EF421101	EF421020
Family Lyophyllaceae				
<i>Termitomyces</i> sp.	IE-BSGsp1	AF223174	AF357093	EF421010
<i>Tephrocycbe gibberosa</i>	CBS328.50	AF223197	AF357115	EF421005
<i>Asterophora lycoperdoides</i>	CBS170.86	AF223190	AF357109	DQ367431
<i>Calocybe carnea</i>	CBS552.50	AF223178	AF357097	DQ367432
<i>Lyophyllum decastes</i>	IE-BSG-JM87/16	AF042583	AF357136	EF421001
“ <i>Lyophyllum</i> ” <i>leucophaeatum</i> ^d	IE-BSG- HAe251.97	AF223202	AF357101	DQ367434
Family Tricholomataceae				
<i>Tricholoma myomyces</i>	DUKE-KMS589	U76459	EF421096	DQ367436
<i>Tricholoma portentosum</i>	DUKE-KMS591	U76464	AF357081	EF421014
<i>Tricholoma subaureum</i>	DUKE-KMS590	U76466	AF357082	EF421015
<i>Collybia tuberosa</i>	AFTOL557	AY639884	---	AY787219
<i>Clitocybe dealbata</i>	IE-BSG-HC95	AF223175	AF357138	DQ825407
<i>Lepista nebularis</i>	CBS36265	AF223217	AF357142	EF421011
<i>Lepista nuda</i>	DUKE-RW 84 1	AF042624	AF357141	EF421012
<i>Clitocybe candicans</i>	AFTOL541	AY645055	---	DQ385881
<i>Clitocybe subditopoda</i>	AFTOL533	AY691889	---	AY780942
‘ <i>Catathelasma</i> clade’				

<i>Catathelasma ventricosum</i>	AFTOL1488	DQ089012	---	DQ470830
<i>Incertae sedis</i>				
<i>Dendrocollybia racemosa</i>	DUKE-DEB5575	AF042598	GU384582	DQ825409

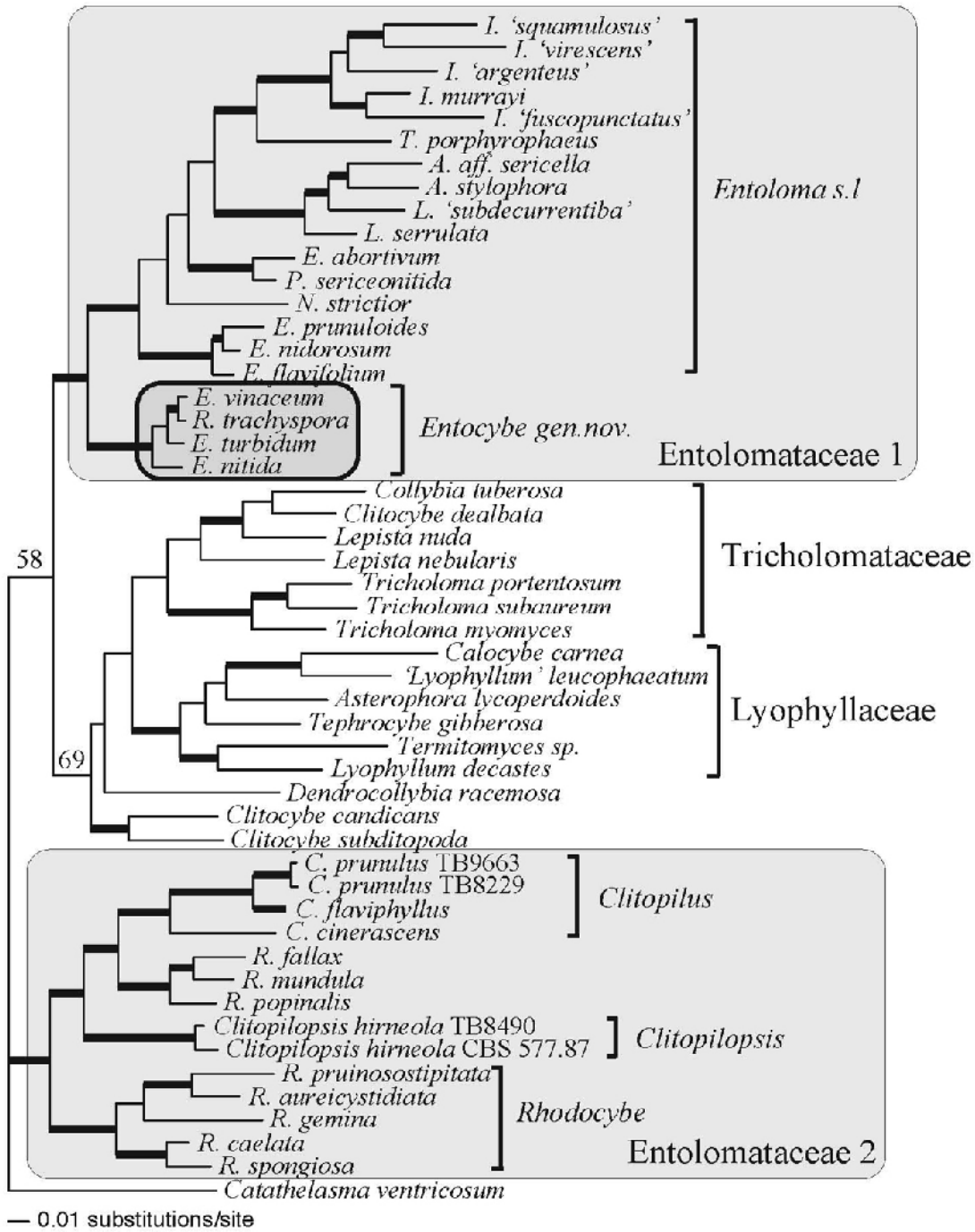
^a Regions sequenced : nuclLSU = nuclear ribosomal large subunit; mitSSU = mitochondrial ribosomal small subunit; *RPB2* = subunit B150 of the RNA polymerase II, region 5-7. ^b Classification follow Matheny et al (2006). Genera delimitations within the Lyophyllaceae follow Moser (1978). Genera delimitations within the Entolomataceae follow Largent (1994) ^c Species names indicated in brackets are herbarium names for undescribed taxa. ^d Conservation proposal (Redhead et al., 2008) to conserve a new type species, *Lyophyllum semitale* to replace *L. leucophaeatum*.

TABLE 2: *Entoloma* and *Entocybe* collections, collectors, locales and repositories of specimens used for morphological data and for illustrations (*) presented in this paper

<i>Entoloma bloxamii</i>	6117 T. J. Baroni*	California, North America ¹
<i>Entoloma</i> sp. aff. <i>prunuloides</i>	4765 T. J. Baroni*	New York, North America ¹
<i>Entocybe lignicola</i>	8747 D. L. Largent (Type)	California, North America ²
<i>Entocybe nitida</i>	2762 C. Bas*	Germany, Europe ³
“ “	2715 C. Bas	Europe ³
“ “	202 M. E. Noordeloos	Germany, Europe ³
“ “	1036 M. E. Noordeloos	Germany, Europe ³
“ “	7526 T. J. Baroni	New York, North America ¹
“ “	7749 T. J. Baroni	New York, North America ¹
<i>Entocybe priscua</i>	2695 S. A. Redhead (Type)*	New Brunswick, North America ^{2,4}
<i>Entocybe speciosa</i>	1533 J. W. Lennox (Type)*	Washington, North America ⁵
“ “	6298 T. J. Baroni	New York State, North America ¹
<i>Entocybe trachyospora</i>	2169 D. L. Largent (Type)	Washington, North America ²
var. <i>trachyospora</i>		
“ “ “	5794 T. J. Baroni	California, North America ¹
“ “ “	5801 T. J. Baroni*	California, North America ¹
“ “ “	5802 T. J. Baroni	California, North America ¹
<i>E. trachyospora</i>	1659 D. L. Largent (Type)	Washington, North America ²
var. <i>griseoviolacea</i>		
“ “ “	5803 T. J. Baroni	California, North America ¹
<i>E. trachyospora</i>	2197 D. L. Largent (Type)	Washington, North America ²
var. <i>purpureoviolacea</i>		
<i>Entocybe turbida</i>	809 M. E. Noordeloos	Netherlands, Europe ³
“ “	175 M. E. Noordeloos*	Netherlands, Europe ³
“ “	6949 T. J. Baroni	South Carolina, North America ¹
<i>Entocybe vinacea</i>	5510 C. Bas	Netherlands, Europe ³
“ “	5975 C. Bas	Netherlands, Europe ³
<i>Entocybe vinacea</i>	8870 T. J. Baroni	New York, North America ¹
var. <i>fumosipes</i>		
<i>Entocybe vinacea</i>	5511 C. Bas	Netherlands, Europe ³
var. <i>violeipes</i>		
“ “ “	3322 E. Arnolds	Netherlands, Europe ³

1 (CORT), 2 (NY), 3 (L), 4 (DAOM), 5 (WTU): acronyms from Index Herbariorum (<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>)

Fig. 1: Most likely phylogram obtained by ML analysis of 3-loci (RPB2, LSU, and mtSSU) used in combination for 51 taxa representative of the Entolomataceae and its closest relatives. Branches that received significant ML bootstrap support ($\geq 70\%$) are in bold. Bs values $\geq 50\%$ and $<70\%$ are reported above branches. Abbreviations used: A. = *Alboleptonia*, C. = *Clitopilus*, E. = *Entoloma*, I. = *Inocephalus*, . = *Leptonia*, N. = *Nolanea*, P. = *Paraeccillia*, R. = *Rhodocybe*, T. = *Trichopilus*.



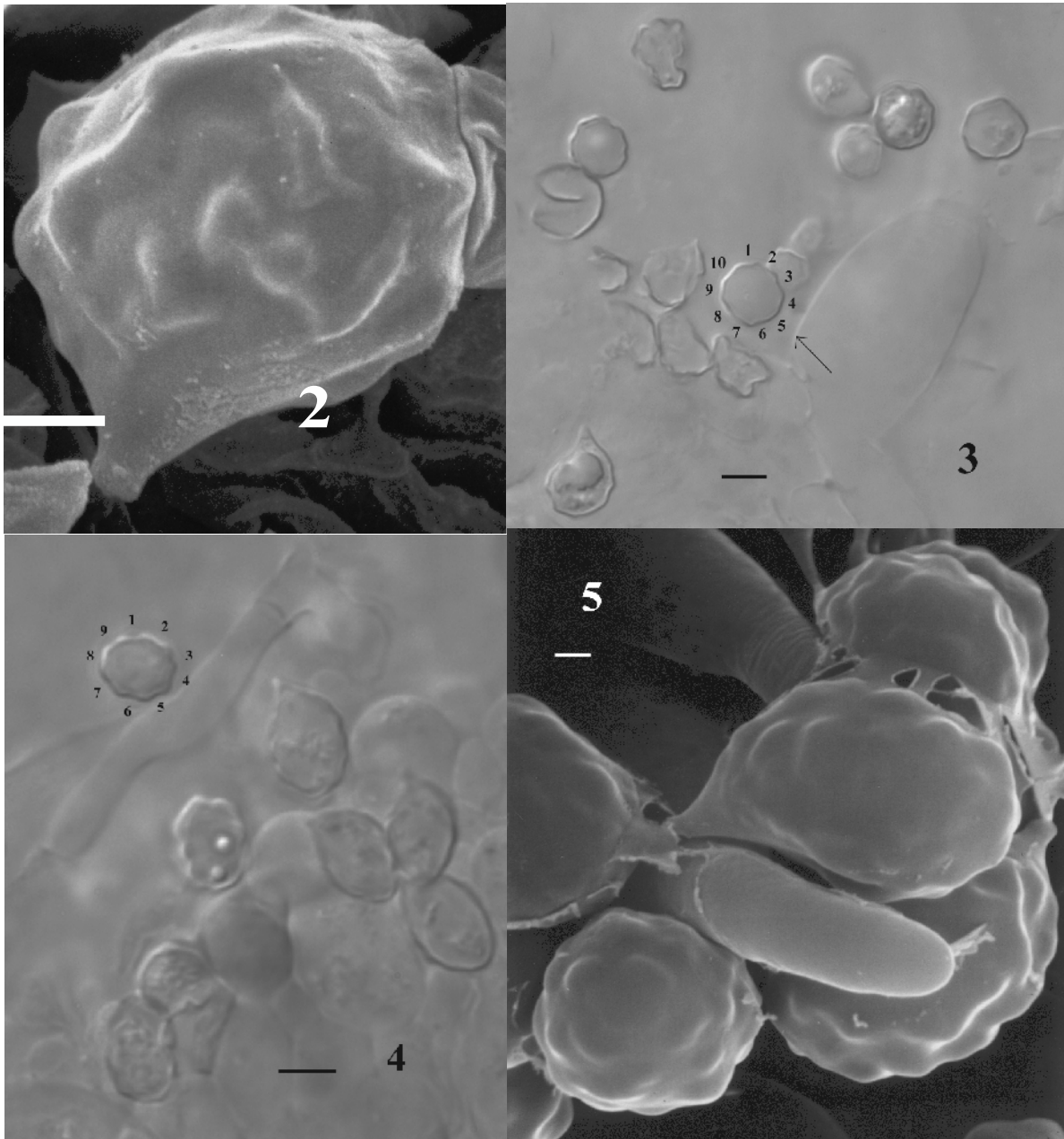


Fig. 2: *Entocybe turbida*: Scanning electron micrograph of a basidiospore in profile view. Note the pustulate ornamentation and few broken interconnecting ridges. 175 M. E. Noordeloos. Scale bar = 1 μ m. **Fig. 3:** *Entocybe trachyospora* var. *trachyospora*. Transmitted light image of basidiospores in profile and polar views. Basidiospore indicated by the arrow showing 10 facets in polar view. Note basidiospore in lower left hand corner in profile view showing obscure angles and rounded pustulate ornamentation. 5801 T. J. Baroni. Scale bar = 5 μ m. **Fig. 4:** *Rhodocybe stipitata*. Transmitted light image of basidiospores in profile and polar views. Basidiospore in polar view with 10 facets labeled. Note basidiospores in profile views with rounded pustulate ornamentation. 5523 T. J. Baroni. Scale bar = 5 μ m. **Fig. 5:** *Rhodocybe caelata*. Scanning electron micrograph of basidiospores. Note the pustulate ornamentation, the tapered cells are pseudocystidia. 3217 T. J. Baroni. Scale bar = 1 μ m

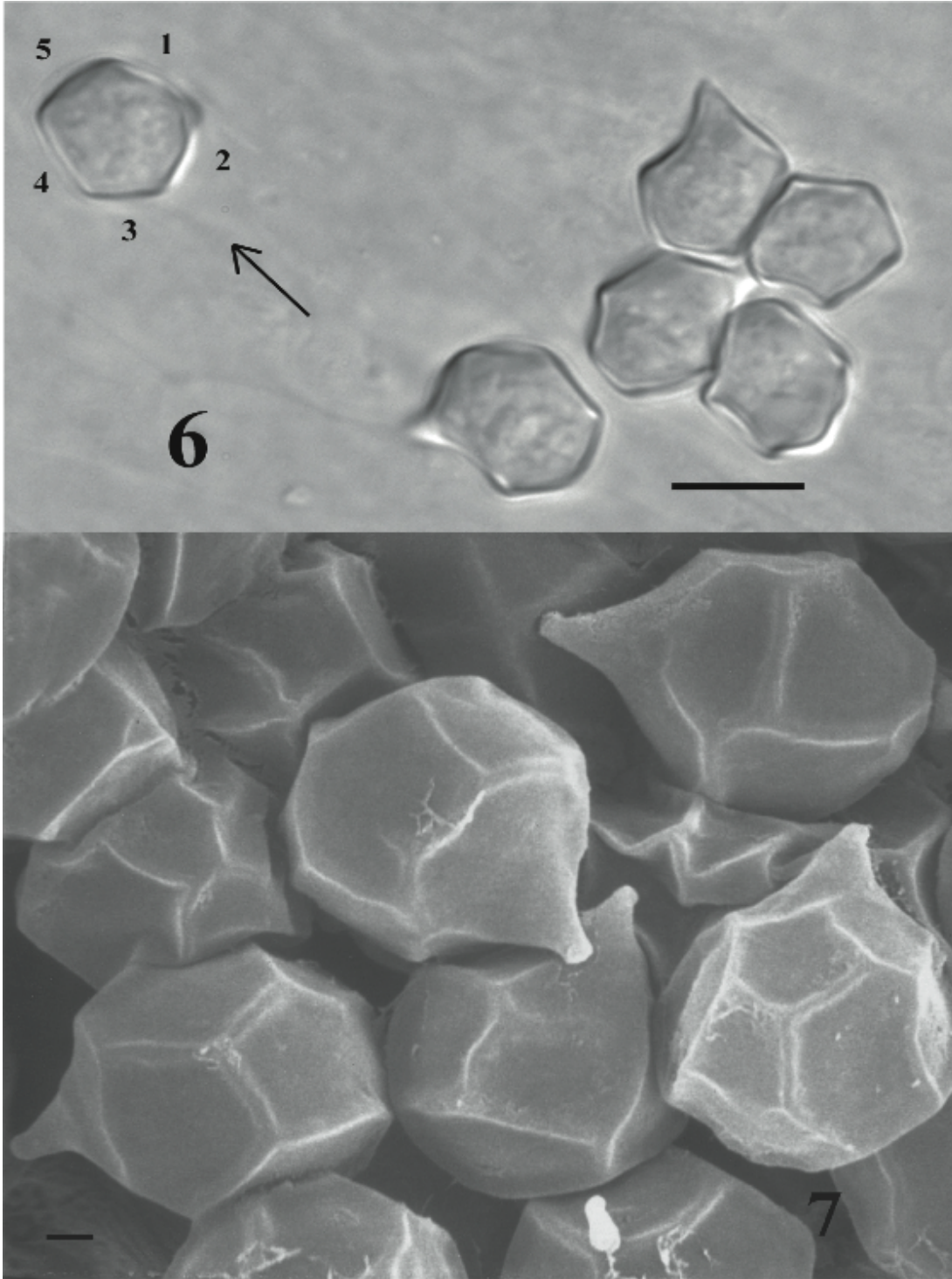


Fig. 6: *Entoloma* sp. aff. *prunuloides*. Transmitted light image of basidiospores in profile and polar view. Basidiospore indicated by the arrow showing 5 facets or angles in polar view. Note the basidiospores are distinctly faceted or angled in all views. 4765 T. J. Baroni. Scale bar = 5 μ m. **Fig. 7:** *Entoloma bloxamii*. Scanning electron micrograph image of basidiospores showing interconnected ridges producing the plate-like angular form characteristic of the spores of species of *Entoloma* sl. 6117 T. J. Baroni. Scale bar = 1 μ m.

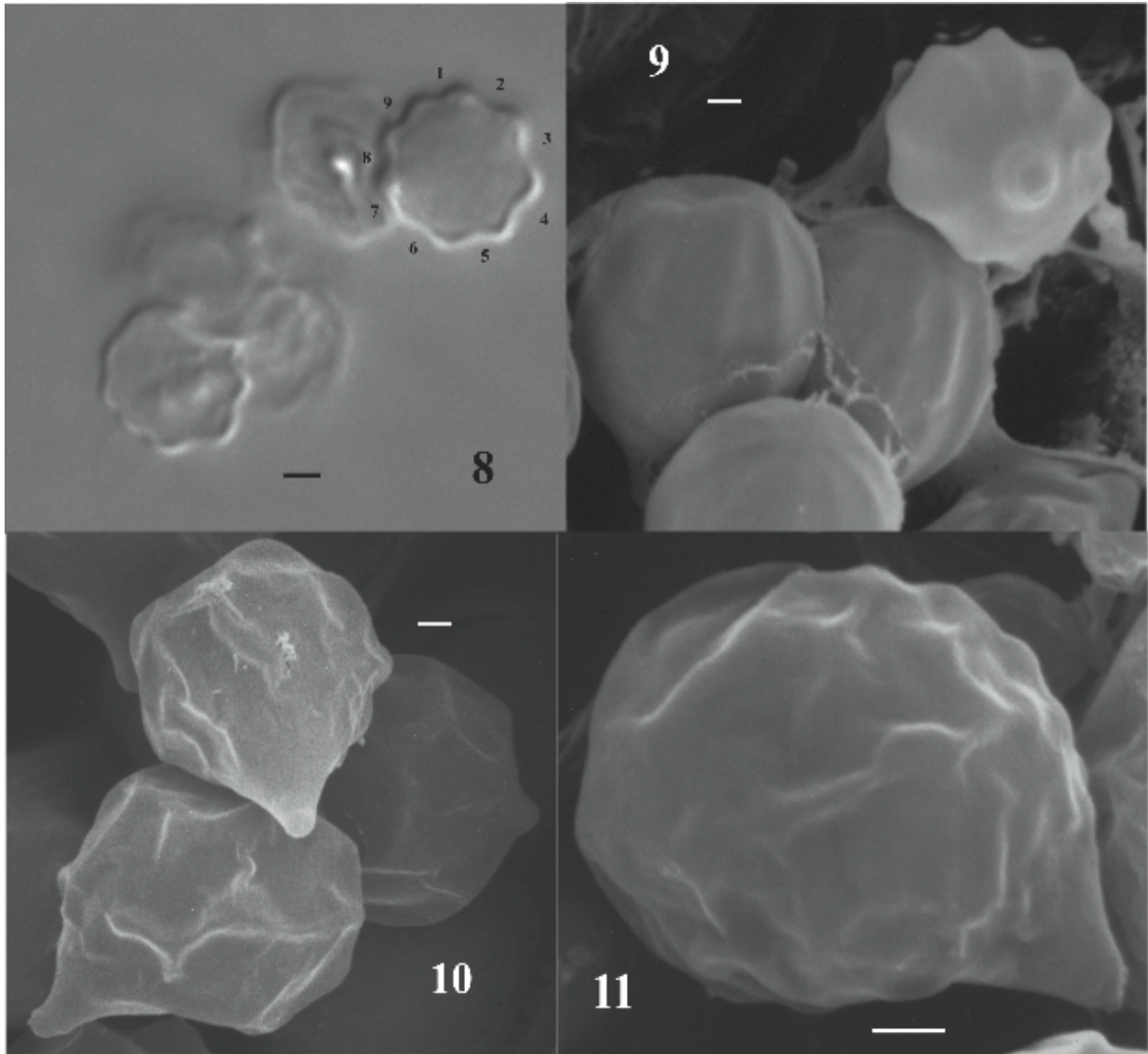


Fig. 8: *Clitopilus argentinus*. Transmitted light image of basidiospores in polar view with 9 facets labeled. 7058 T. J. Baroni. Scale bar = 1 μ m. **Fig. 9:** *Clitopilus chalybescens*. Scanning electron micrograph image of basidiospores showing longitudinal ridges running from pole to pole on the spores. 7019 D. E. Desjardin. Scale bar = 1 μ m. **Fig. 10:** *Entocybe nitida*. Scanning electron micrograph of three basidiospores. Note the broken interconnected ridge-like pattern with scattered pustulate ornamentation. 2762 C. Bas. Scale bar = 1 μ m. **Fig. 11:** *Entocybe priscua*: Scanning electron micrograph of a single basidiospore in profile view. Note the broken interconnected ridge-like pattern with scattered pustulate ornamentations. S. A. Redhead 2695 TYPE. Scale bar = 1 μ m.

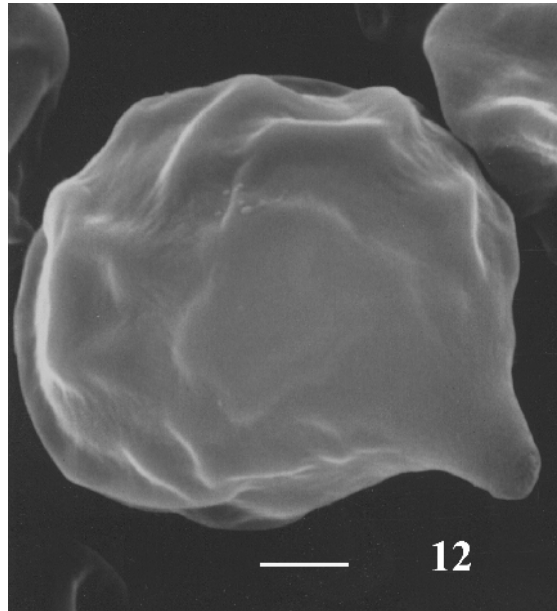


Fig. 12: *Entocybe speciosa*: Scanning electron micrograph of a single basidiospore taken obliquely from the hilar appendix end of the basidiospore. Note the broken interconnected ridge-like pattern with scattered pustulate ornamentations. J. Williams 1533 TYPE. Scale bar = 1 μ m