

Deconstructing the Tricholomataceae (Agaricales) and introduction of the new genera *Albomagister*, *Corneriella*, *Pogonoloma* and *Pseudotricholoma*

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Abstract The family Tricholomataceae, contained within the Tricholomatoid clade, has traditionally been one of the largest families of the Agaricales. However, in this sense it is highly polyphyletic and requires emendation. Here, we present a phylogeny of the Tricholomatoid clade based on nucleotide sequence data from two nuclear ribosomal RNA genes (large subunit and small subunit) and the second-largest subunit of RNA polymerase II (*rpb2*). Our aim is to delimit the Tricholomataceae and identify monophyletic groups within the Tricholomatoid clade. We also infer a separate phylogeny, based on the three genes above, in addition to sequences of the nuclear ribosomal internal transcribed spacers (ITS), in order to evaluate generic-level boundaries within the Tricholomataceae s.str. Based on this analysis we recover seven monophyletic genera within the Tricholomataceae s.str. that correspond to *Leucopaxillus*, *Tricholoma*, *Pseudotricholoma* stat. nov., *Porpoloma* s.str., *Dennisiomyces*, *Corneriella* gen. nov., and *Albomagister* gen. nov. Of the 98 genera that have been traditionally assigned to the Tricholomataceae sensu Singer, only four can be placed within it (*Tricholoma*, *Porpoloma*, *Dennisiomyces*, *Leucopaxillus*). The genus *Porpoloma* is highly polyphyletic and divided into four genera: *Porpoloma* s.str., *Corneriella* gen. nov., *Pseudotricholoma* stat. nov., and *Pogonoloma* stat. nov. In all, four new genera are proposed. Taxonomic descriptions, and a key to genera of the Tricholomataceae as emended here are also presented.

Keywords Basidiomycota; classification; fungi; phylogeny; systematics

Supplementary Material The Electronic Supplement (Table S1) is available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>; alignments are available in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S16404>)

■ INTRODUCTION

Fungal classification has become more stable at the ordinal level and above (Hibbett & al., 2007) although novelties and relationships among higher-level taxa of Basidiomycota continue to be discovered (Zalar & al., 2005; Binder & al., 2010; Hodkinson & al., 2014). The order Agaricales is the largest order of mushroom-forming fungi (Agaricomycotina) with some 13,500 species (Kirk & al., 2008). Attempts have been made to recognize monophyletic groups within the Agaricales (Moncalvo & al., 2002) and major groupings within it (Matheny & al., 2006). These works, and others (Bodensteiner & al., 2004; Gulden & al., 2005; Garnica & al., 2007) have contributed to recognition of additional subclades and family-level groupings such as now found in regional Floras (Knudsen & Vesterholt, 2012).

One such grouping, the Tricholomatoid clade, which includes three families, the Tricholomataceae, Entolomataceae, and Lyophyllaceae (Matheny & al., 2006; Binder & al., 2010), has received considerable attention of late as the highly

polyphyletic genus *Clitocybe* (Fr.) Staude has undergone extensive revision (Harmaja, 2003; Ammirati & al., 2007; Vizzini & al., 2011b). The Entolomataceae (Co-David & al., 2009; Baroni & al., 2011; Morgado & al., 2013) and Lyophyllaceae (Hofstetter & al., 2002) have been revised as well. However, little attention has been given to the Tricholomataceae, which in a broad sense once included as many as 98 genera (Singer, 1986).

The Tricholomataceae was first referred to as the “Tricholomées” by Roze (1876), including *Tricholoma* (Fr.) Staude, *Entoloma* (Fr. ex Rabenh.) P.Kumm, and *Hebeloma* (Fr.) P.Kumm.; however, this name was not validly published since it contains a French termination instead of a Latin termination (McNeill, 2012: Art. 18.4). In 1927, Van Overeem (1927) published the name “Tricholomataceae” as a nomen nudum (Art. 38.1). Later Heim (1934) published the name “Tricholomaceae” also as a nomen nudum. Many authors continued using the name Tricholomataceae assuming it was validly published (e.g., Singer, 1975; Pegler, 1977). Pouzar (1983) provided a valid diagnosis and thus validly published the family name. To maintain the

traditionally accepted broad application of the name Tricholomataceae, despite the fact that numerous valid family names for it were published prior to 1983, the name Tricholomataceae is conserved against 24 other family names (McNeill & al., 2006).

Before the advent of molecular phylogenetics, others treated the Tricholomataceae in somewhat different ways. Bon (1974), for instance, split the family into six subfamilies: Tricholomatoideae (Sing.) Bon, Lepistoideae Bon, Leucopaxilloideae (Sing.) Bon, Lyophylloideae Kühner ex Bon, Collybioidae (Konr. & Maubl.) Bon, and Mycenoideae Bon. Jülich (1981) was the first to split the Tricholomataceae into separate families—Leucopaxillaceae Jülich (e.g., *Leucopaxillus* Boursier, *Porpoloma* Singer, *Cantharellula* Singer), Lyophyllaceae Jülich (e.g., *Lyophyllum* P.Karst and *Calocybe* Kühner), and Mycenaceae Overeem (e.g., *Mycena* (Pers.) Roussel, *Baeospora* Singer, *Dennisiomyces* Singer). Pouzar (1983) excluded some genera considered by Singer (1986) as part of the Tricholomataceae such as *Rhodotus* R.Maire, *Termitomyces* Heim, *Macrocystidia* Joss., and *Catathelasma* Lovejoy. Singer (1986) presented a broadly circumscribed Tricholomataceae encompassing 98 genera with a pale spore print (white, cream color, light creamy pink, pale violet, light greenish, or pale sordid grayish), lamellae variously attached to the stipe (sometimes free, adnexed, adnate, sinuate, or decurrent); lamellar trama interwoven, irregular, subregular or regular; spores amyloid or inamyloid; and occurring in a wide range of environments, e.g., on the ground in woods, on living hosts, or in prairies.

The polyphyly of the Tricholomataceae was demonstrated in several molecular systematic works (Hofstetter & al., 2002; Moncalvo & al., 2000, 2002; Matheny & al., 2006; Garnica & al., 2007). Some taxa previously included in Tricholomataceae have been placed in other families such as Lyophyllaceae (Hofstetter & al., 2002), Mycenaceae (Moncalvo & al., 2002), Physalacriaceae (Binder & al., 2006), and Hygrophoraceae (Lodge & al., 2014), vindicating some efforts of Jülich (1981) (see Electr. Suppl.: Table S1 for an overview of the currently known phylogenetic distribution of Singer's 98 genera of Tricholomataceae). Although there have been some efforts to delimit fungal families, the limits and constituents of the Tricholomataceae in its strict sense have not been redefined or identified based on molecular evidence.

The main focus of this research is to systematically re-evaluate the family Tricholomataceae. We present phylogenetic analyses of 160 taxa of the Tricholomatoid clade (Matheny & al., 2006), including ribosomal RNA (nLSU, nSSU, ITS), and *rpb2* sequences. The aims of this work are (1) to generate a multi-gene phylogeny on which to base a modern systematic revision of the Tricholomataceae s.str.; (2) to circumscribe genera belonging to this family based on a well-supported phylogeny; and (3) to provide a taxonomic key for their identification.

■ MATERIALS AND METHODS

Field collections and microscopy.— Notes of macroscopic features were taken from fresh collections in the field following protocols of Largent & al. (1977). Many were photographed

in situ or in a laboratory setting. Colors of fresh specimens were documented with the *Methuen Handbook of Colour* (Kornerup & Wanscher, 1984) or *Munsell Soil Color Charts* (Munsell, 1975). Specimens were then air-dried on a food dehydrator for later microscopic examination and DNA extraction. Dried materials collected by us, as well as, materials borrowed from herbaria were examined to obtain morphological information on spores, cystidia, pileipellis, and other microscopic characters.

Taxon sampling.— The selection of taxa for this study was based on previous works that included members of the Tricholomatoid clade (Moncalvo & al., 2000, 2002; Matheny & al., 2006; Binder & al., 2010; Vizzini & al., 2012). Sequences available in GenBank from previous studies were incorporated (Appendix 1). Additionally, new sequences were produced to extend taxon and gene sampling (Appendix 1). Nomenclatural types were specifically targeted for sequencing in order to correctly assign generic names to clades. Specimens were borrowed from the following herbaria: CONC, CORT, FH, FL, GB, IBUG, K, MICH, NYBG, TENN, XAL, and WTU. Type specimens of *Dennisiomyces griseus* (Dennis) Singer, *Hygrophorus subaustoralis* A.H.Sm. & Singer, *Leucopaxillus septentrionalis* Singer & A.H.Sm., *Porpoloma bambusarum* Desjardin & Hemmes, *Por. sejunctum* Singer, *Por. portentosum* Singer, *Por. terreum* Singer, and *Por. umbrosum* (A.H.Sm. & M.B.Walters) Singer were sampled for molecular annotation. Nomenclatural novelties have been registered in MycoBank (Crous & al., 2004).

DNA extraction, PCR, sequencing and cloning.— Genomic DNA was extracted using 10–30 mg of dried basidiome tissue. Samples were ground in liquid nitrogen with a mortar and pestle. DNA extractions were performed using the E.Z.N.A. Fungal DNA Kit (Omega Bio-Tek, Norcross, Georgia, U.S.A.), for specimens younger than 30 years old and the E.Z.N.A. HP Fungal DNA Kit (Omega Bio-Tek) for specimens older than 30 years.

Primer pairs used were as follows: for the internal transcribed spacer (ITS): ITS1F-ITS4, ITS1F-ITS2 and 5.8S-ITS4 (White & al., 1990; Gardes & Bruns, 1993); for the nuclear large subunit ribosomal DNA (nLSU): LR0R-LR7, LR0R-LR5 and LR0R-LR16 (Vilgalys & Hester, 1990, <http://www.biology.duke.edu/fungi/mycolab/primers/htm>); for the nuclear small subunit ribosomal DNA (nSSU): PNS1-NS8, PNS1-NS41 and NS51-NS8 (White & al., 1990; Hibbett, 1996) and for the second-largest subunit of RNA polymerase II (*rpb2*), b6f-b7.1R (Matheny, 2005). The same primers were used for sequencing with the addition of NS19b (<http://nature.berkeley.edu/brunslab/tour/primers.html>) for nSSU.

PCR conditions to amplify ITS, nLSU, and nSSU are outlined in White & al. (1990) and for *rpb2* in Matheny (2005). PCR products were visualized on a 1% agarose gel. Successfully amplified products were purified using the QIAquick PCR Purification Kit (Qiagen, Valencia, California, U.S.A.) following the manufacturer's protocol. Sequence reactions were prepared with BigDye Terminator 3.1 (Applied Biosystems, Foster City, California, U.S.A.), purified using Sephadex G-50 columns (General Electric Healthcare, Piscataway, New Jersey, U.S.A.), and sequenced on an automated DNA

sequencer (ABI 3730) at the Molecular Biology Resource Facility of the University of Tennessee. Raw sequences were edited and assembled using Sequencher v.4.9 (Gene Codes, Ann Arbor, Michigan, U.S.A.).

Some chromatograms showed sequences with several indels; therefore, the purified PCR products of those samples were inserted into a pCR 2.1-TOPO plasmid vector and cloned using the TOPO TA Cloning Kit (Invitrogen, Carlsbad, California, U.S.A.) following the manufacture's protocol. The analysis of the positive transformants was done screening colonies by PCR using the primer pairs M13F-M13R. When the presence of the expected product was observed in the electrophoresis gel, PCR products were purified and sequenced following the methods detailed above.

Phylogenetic analyses. — Two datasets were assembled, one containing members of the Tricholomatoid clade (Matheny & al., 2006; Binder & al., 2010) to show the placement and delimitation of the Tricholomataceae s.str. and the second containing only members of Tricholomataceae s.str. to delimit genera belonging to this family.

The Tricholomatoid dataset includes 123 taxa (120 nLSU, 62 nSSU, and 70 *rpb2* sequences). The Tricholomataceae dataset includes 110 taxa (65 nLSU, 26 nSSU, 38 *rpb2*, and 101 ITS sequences). For the latter dataset we included ITS sequences to increase resolution at the generic and infrageneric levels and to increase statistical support, as it has been shown in previous works (Lawrey & al., 2009; Lodge & al., 2014). One taxon that was not represented in the Tricholomatoid dataset, but included in the Tricholomataceae dataset, was *Porpoloma pes-caprae* (Fr.) Singer. This taxon could not be included in the larger and more inclusive analysis because it is represented by only an ITS sequence. However, the closest match in a BLASTn search was *Tricholoma myomyces* (Pers.) J.E.Lange (82%), which justifies its inclusion in the Tricholomataceae dataset.

Alignments were constructed separately for each rRNA region and *rpb2* using MAFFT v.6.717 (Kato & Toh, 2008), manually adjusted in MacClade v.4.08 (Maddison & Maddison, 2005), and concatenated in SeaView v.4.2.3 (Gouy & al., 2010). Regions of the ITS dataset with ambiguous alignments were excluded. Unsourced gene regions were coded as missing data. Simulation studies show that despite large amounts of missing data, adding taxa can improve phylogenetic resolution (Wiens, 2006; Wiens & Morrill, 2011). Partition strategies for each concatenated dataset and the best-fit models of molecular evolution were chosen using PartitionFinder v.1.0.1 (Lanfear & al., 2012). Alignments are available from TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:SI6404>).

Maximum likelihood (ML) was performed on both datasets using RAxML v.7.9.1 (Stamatakis, 2006), implementing the GTR+GAMMA+I model, and executing 1000 rapid ML bootstraps replicates. Bayesian inference (BI) analyses were performed using MrBayes 3.2.2, also implementing the GTR+GAMMA+I model (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Altekar & al., 2004) with two independent runs and four chains, sampling every 5000 generations. Output was evaluated using Tracer 1.5 (Rambaut & Drummond, 2007) and AWTY (Nylander & al., 2008) in

order to determine whether the chains reached the stationary phase and the appropriate number of generations to discard as burn-in. In addition, the standard deviation of split frequencies was considered for this purpose following the MrBayes manual. The BI analyses were run for 50 million generations with a burn-in of 12.5 million generations, leaving 7501 trees per run to summarize into a maximum clade credibility tree using TreeAnnotator v.1.7.5 distributed as part of the BEAST package (Drummond & al., 2012). We consider bootstrap values (BS) >70% and Bayesian posterior probabilities (PP) >0.95 as evidence for significant or strong support. *Infundibulicybe gibba* (Pers.) Harmaja was used to root the Tricholomatoid phylogeny following Matheny & al. (2006), Binder & al. (2010), and Lodge & al. (2014). The Tricholomataceae phylogeny was midpoint-rooted as the sister group of this family is not known with confidence. Rooting was done in FigTree v.1.4.0. Individual datasets (ITS, nLSU, nSSU, *rpb2*) were examined separately under the ML criterion to inspect for intergene conflict, in which different gene regions strongly support different topologies. After this assessment, the gene datasets were concatenated and analyzed using ML and BI as described above.

■ RESULTS

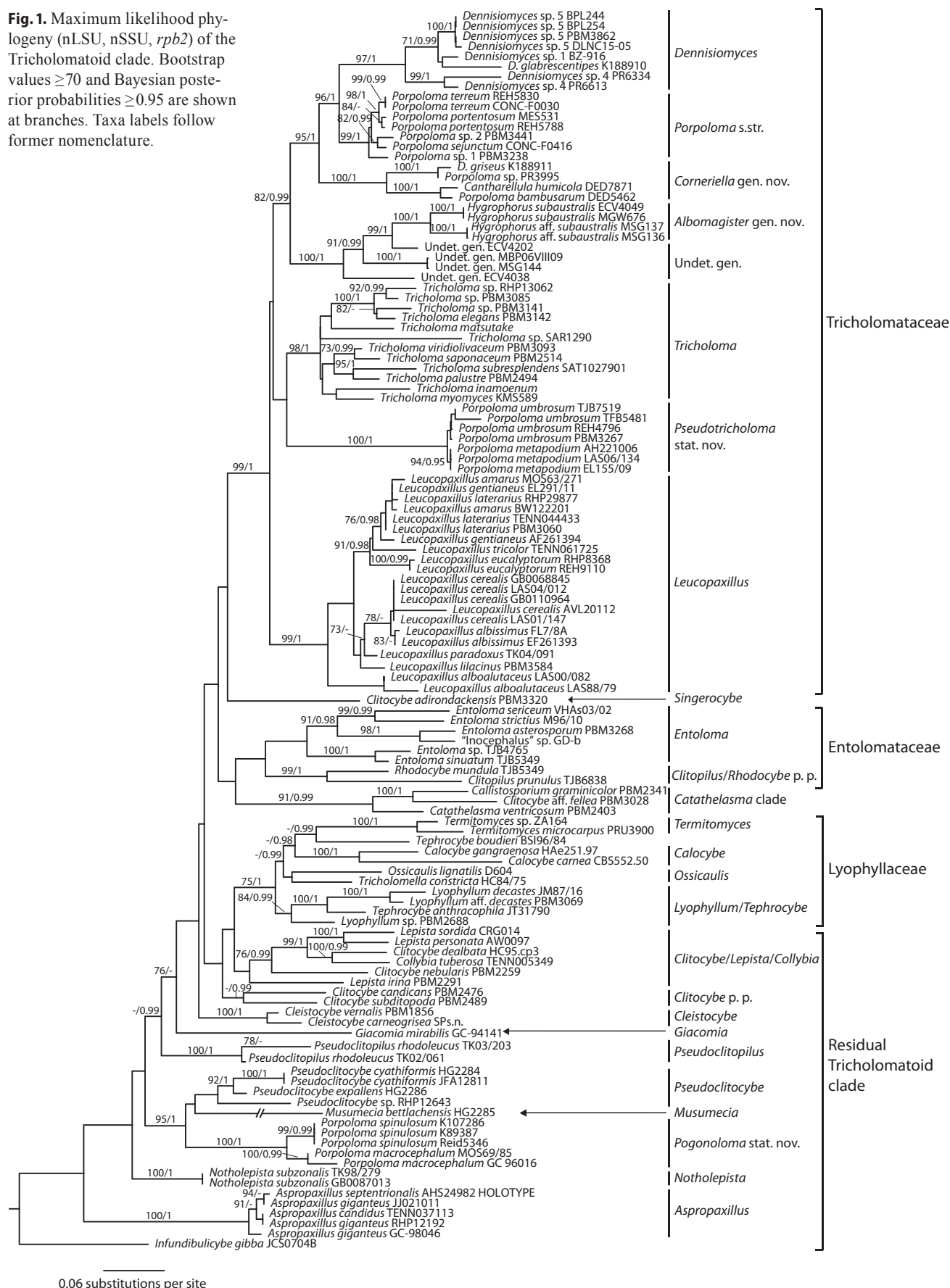
Delimitation of the family Tricholomataceae s.str. — The Tricholomatoid dataset contains 4372 included sites. The alignment was separated in five partitions: (1) nLSU; (2) nSSU; (3) *rpb2* first codon positions; (4) *rpb2* second codon positions; and (5) *rpb2* third codon positions. We did not detect cases of strongly supported intergene conflict.

The ML and Bayesian analyses of the concatenated datasets do not show major conflicts in any of the well-supported clades of the trees.

Phylogenetic analyses of the Tricholomatoid dataset (Fig. 1) recover a robust grouping (99% BS, 1.00 PP) composed of six major subgroups that share a most recent common ancestor with the genus *Tricholoma*. We recognize this group as the Tricholomataceae s.str. with the following genera: (1) *Dennisiomyces* (type: *D. glabrescentipes* Singer), (2) *Porpoloma* s.str. (type: *Por. sejunctum*), (3) *Corneriella* gen. nov. (type: *Co. bambusarum*), (4) *Albomagister* gen. nov. (type: *A. subaustralis*), (5) *Tricholoma* (type: *T. flavovirens* (Pers.: Fr.) S.Lundell), and (6) *Pseudotracheloma* stat. nov. (type: *Ps. umbrosum*) (7) *Leucopaxillus* (type: *L. paradoxus* (Costantin & L.M.Dufour) Boursier). The species *Clitocybe adirondackensis* (Peck) Sacc., is recovered as sister to the Tricholomataceae s.str. but with weak support (<50% BS and <0.95 PP).

The genera *Tricholoma*, *Dennisiomyces*, and *Leucopaxillus* were recovered as monophyletic. Each of these groups received high posterior probabilities and bootstrap values. We also recovered a monophyletic group containing *Hygrophorus subaustralis* and four undetermined specimens collected in the southern Appalachians that resemble small species of *Tricholoma*. However, their small inamyloid spores, prominent pleurocystidia and cheilocystidia, and presence of clamp connections exclude them from this and any other tricholomatoid

Fig. 1. Maximum likelihood phylogeny (nLSU, nSSU, *rpb2*) of the Tricholomatoid clade. Bootstrap values ≥ 70 and Bayesian posterior probabilities ≥ 0.95 are shown at branches. Taxa labels follow former nomenclature.



genera, thus *Albomagister* gen. nov. is proposed to accommodate *H. subaustralis*.

The genus *Porpoloma* is shown to be highly polyphyletic with species distributed in four different groups within the Tricholomatoid clade, three of which are found in the Tricholomataceae s.str.: (1) *Porpoloma* s.str., (2) *Corneriella* gen. nov., and (3) *Pseudotricholoma* stat. nov. The fourth clade, which is sister to *Pseudoclitocybe* (Singer) Singer and *Musumecia* Vizzini & Contu with strong support, contains *Porpoloma spinulosum* (Kühner & Romagn.) Singer and *Por. macrocephalum* (Schulzer) Bon. *Porpoloma* subg. *Pogonoloma* Singer is elevated to generic level to accommodate these two taxa.

Delimitation of seven genera in the Tricholomataceae s.str. — The Tricholomataceae dataset consists of 4729 characters after the exclusion of ambiguously aligned regions in the ITS (186–230, 244–273, 289–328, 808–823, 861–872). The alignment was separated into five partitions: (1) ITS; (2) nSSU and nLSU; (3) *rpb2* first codon positions; (4) *rpb2* second codon positions; and (5) *rpb2* third codon positions.

The ML and Bayesian analyses show consistent topologies recovering the same main clades with high support (>70% BS, >0.95 PP). The phylogeny produced from this dataset (Fig. 2) shows the same seven main clades as in Fig. 1, and a single branch representing *Porpoloma pes-caprae* referred to as the “*pes-caprae*” clade.

Leucopaxillus contains representatives from Europe, Australia, and North and South America, including samples from temperate and tropical regions. The genus is characterized by species with amyloid and verrucose spores and presence of clamp connections on basidiocarp tissues. The presence of clamp connections and absence of urticoid hymenial cystidia distinguish it from *Melanoleuca* Pat., species of which may outwardly resemble those of *Leucopaxillus*. *Melanoleuca*, however, is a member of the Pluteoid clade (Matheny & al., 2006; Garnica & al., 2007).

Sister to *Leucopaxillus* with strong support is *Pseudotricholoma* stat. nov., a clade that contains two temperate taxa from the Northern Hemisphere, *Ps. umbrosum* and *Ps. metapodium* (Fr.) Singer. The name *Pseudotricholoma* is elevated to genus level following the classification of Singer (1986) where he included *Porpoloma umbrosum* as the type of *Porpoloma* subg. *Pseudotricholoma* (Singer) Singer. The two species in this clade are united by their smooth amyloid spores and red bruising reaction to the context of the basidiocarps.

Tricholoma appears to be sister to *Pseudotricholoma* and *Leucopaxillus* but with weak support (Fig. 2). The circumscription and monophyly of *Tricholoma* has been well established (Bon, 1984; Riva, 2003). The “*pes-caprae*” clade (based on one sample and ITS data only) could also be the sister group to *Tricholoma*, but support for this relationship is not significant (<65% BS and <0.95 PP) (Fig. 2).

Porpoloma s.str. contains sequence data from three type specimens, *Por. sejunctum*, *Por. terreum*, and *Por. portentosum*. The first one, *Por. sejunctum*, is also the type of the genus, therefore, the generic name *Porpoloma* can readily be assigned to members of this clade. The other two species included in the group (*Porpoloma* sp. 1 and *Porpoloma* sp. 2) were collected

in Tasmania. In this clade there are also four environmental samples from South American *Nothofagus* forests (Nouhra & al., 2013), three of which correspond to *Por. terreum* and were isolated from *N. dombeyi* (Mirb.) Oerst. and *N. obliqua* (Mirb.) Oerst. roots. Another represents *Por. sejunctum* isolated from *N. dombeyi* roots. *Porpoloma* s.str. is restricted to the Southern Hemisphere forming ectomycorrhizal associations with *Nothofagus* (Trappe, 1962; Griffith, 2004) and probably with *Eucalyptus* L’Her and/or *Acacia* Mill.

The genus *Dennisiomyces* comprises mainly neotropical species. This clade contains the type of the genus name, *D. glabrescentipes*, the type of *D. griseus*, and five unidentified species, four from the Caribbean and one from the southeast United States (at least seven species in all).

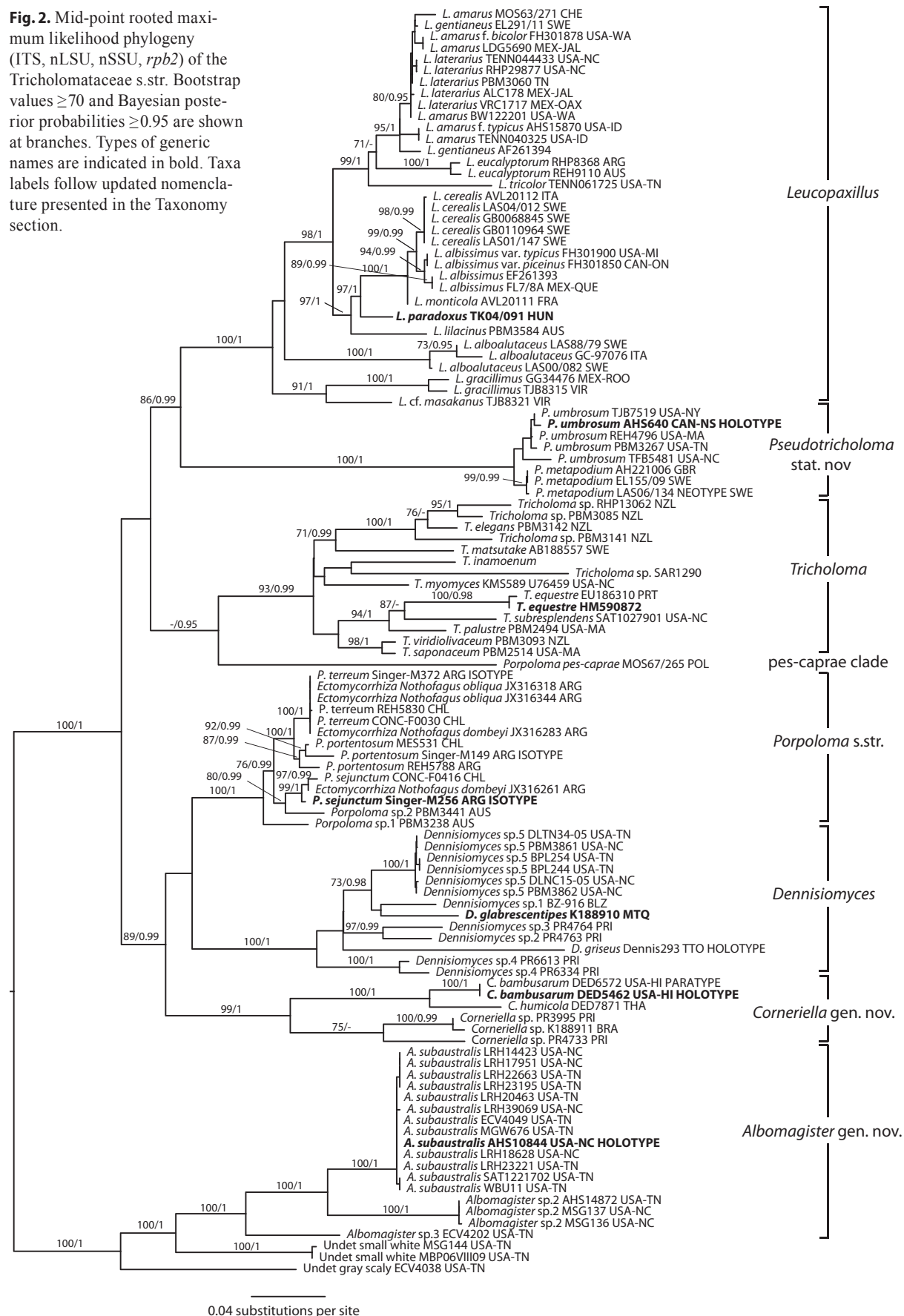
Sister to *Porpoloma* and *Dennisiomyces* is the new genus *Corneriella*. The grouping of these three genera receives significant support (89% BS, 0.99 PP). *Corneriella* includes four tropical species, *Porpoloma bambusarum* described from Hawaii, *Cantharellula humicola* Corner described from Malaysia, and two unidentified species from Puerto Rico and Brazil. The close relationship between *Porpoloma bambusarum* and *Cantharellula humicola* was previously suggested by Desjardin & Hemmes (2001). In the present work we confirm that these two taxa are closely related and belong to the new genus *Corneriella*. *Cantharellula* is not monophyletic as the type of the genus (*Ca. umbonata* J.F.Gmel.) is now placed in the Hygrophoraceae (Lodge & al., 2014). One of the unidentified species of *Corneriella* was previously labeled as *Porpoloma* sp. (PR3995). Sequences from this collection have been included in previous phylogenies (Moncalvo & al., 2002; Vizzini & al., 2012), where it has been treated as *Porpoloma*.

The last clade includes *Hygrophorus subaustralis* and three unidentified specimens collected from the southeast United States. *Hygrophorus subaustralis* superficially resembles some small white *Leucopaxillus* or *Tricholoma* species, however, its microscopic characters and phylogenetic placement suggest it belongs to a different genus. Therefore, the genus *Albomagister* gen. nov. is established to accommodate this and two other undescribed species. The latter two are morphologically similar to *H. subaustralis*, but they form separate phylogenetic lineages (Fig. 2). ITS sequences of these two are 82%–83% similar to those of *A. subaustralis*. The taxonomy of these is under investigation.

Two additional lineages, ECV4038 and MBP06VIII09, form a grade with respect to *Albomagister*. Presently, each is known only from a single collection and they are insufficiently known.

Taxa outside the Tricholomataceae s.str. in the Tricholomatoid clade. — Two families, the Entolomataceae and Lyophyllaceae, cluster outside the Tricholomataceae s.str. (Fig. 1) as expected from prior works (Hofstetter & al., 2002; Moncalvo & al., 2002; Matheny & al., 2006). *Singerocybe*, as mentioned above, is recovered as sister to the Tricholomataceae s.str., but this result is weakly supported. An ensemble of additional clades was recovered in the Tricholomatoid clade consistent with several prior studies (Matheny & al., 2006; Ammirati & al., 2007; Vizzini & al., 2011a, 2012), but their

Fig. 2. Mid-point rooted maximum likelihood phylogeny (ITS, nLSU, nSSU, *rpb2*) of the Tricholomataceae s.str. Bootstrap values ≥ 70 and Bayesian posterior probabilities ≥ 0.95 are shown at branches. Types of generic names are indicated in bold. Taxa labels follow updated nomenclature presented in the Taxonomy section.



positions within the Tricholomatoid clade tend to be poorly supported and thus not well resolved: (1) a strongly supported group containing *Clitocybe* s.str., *Lepista* (Fr.) W.G.Sm., and *Collybia* (Fr.) Staude; (2) *Clitocybe* p.p.; (3) samples of the *Catathelasma* clade; (4) *Pseudoclitopilus* Vizzini & Contu; (5) *Giacomia* Vizzini & Contu; (6) a robust monophyletic grouping of *Pseudoclitocybe*, *Musumecia*, and *Pogonoloma* stat. nov.; (7) *Notholepista* Vizzini & Contu; (8) *Aspropaxillus*; and (9) *Infundibulicybe* Harmaja.

■ TAXONOMY

Tricholomataceae R.Heim ex Pouzar in *Česká Mykol.* 37: 175. 1983 – Type: *Tricholoma* (Fr.) Staude, *Schwämme Mitteldeutschl.*: xxviii, 125. 1857.

Habit tricholomatoid, rarely tricholomatoid-collybioid. Pileus conical, convex, plano-convex to applanate, smooth, tomentose, or scaly, dry or viscid, rarely hygrophanous. Lamellae adnate, adnexed, sinuate-emarginate to decurrent. Spore



Fig. 3. Genera of the Tricholomataceae s.str. **A**, *Hygrophorus subaustralis*, type of *Albomagister* gen. nov. (photo: Mike Wood); **B**, *Dennisiomyces* sp. 5; **C**, *Leucopaxillus laterarius*; **D**, *Tricholoma myomyces*; **E**, *Porpoloma bambusarum*, type of *Corneriella* gen. nov. (photo: Dennis Desjardin); **F**, *Porpoloma umbrosum*, now transferred to *Pseudotricholoma* (photo: Renée Lebeuf); **G**, *Porpoloma* s.str. sp. 1 from Australia. — Scale bars = 1 cm.

deposit pure white, rarely pale cream. Spores subglobose, ellipsoid or ellipsoid-oblong, hyaline, thin-walled, without a germ pore, smooth or verrucose, amyloid or inamyloid, not dextrinoid. Species with inamyloid spores never with decurrent lamellae. Basidia without siderophyllous granulation. Cystidia present or absent as cheilocystidia, pleurocystidia present in some groups. Hymenophoral trama regular. Pileipellis a cutis, ixocutis or trichoderm. Clamps present or absent. Mycorrhizal or saprotrophic on soil, humus and debris in forests and grasslands. Primarily north and south temperate in distribution, some tropical.

Genera included. – *Albomagister* gen. nov., *Corneriella* gen. nov., *Dennisiomyces*, *Leucopaxillus*, *Porpoloma*, *Pseudotricholoma* stat. nov., *Tricholoma* (Fig. 3A–G).

Albomagister Sánchez-García, Birkebak & Matheny, **gen. nov.**
– Type: *Albomagister subaustralis* (A.H.Sm. & Hesler) Sánchez-García, Birkebak & Matheny.
Mycobank MB807772

Habit tricholomatoid. Lamellae sinuate to adnexed, white, edges concolorous. Spores inamyloid, smooth, thin-walled. Cheilocystidia and pleurocystidia present and conspicuous, thin-walled and hyaline. Pileipellis with ascending interwoven cylindrical elements. Clamp connections present. On soil, in forests beneath woody vascular angiosperms and coniferous plants. Probably ectomycorrhizal (Birkebak & al., 2013).

Etymology. – From the Latin *albus* = white; *magister* = mister, referring to the field name applied to this fungus “Mr. white”.

Albomagister subaustralis (A.H.Sm. & Hesler) Sánchez-García, Birkebak & Matheny, **comb. nov.** ≡ *Hygrophorus subaustralis* A.H.Sm. & Hesler in Lloydia 5(1): 46. 1942 – Holotype: U.S.A. North Carolina, Great Smoky Mountains National Park, Martin’s gap, along the trail to Bryson Place, 2 Sep 1938, *A.H. Smith 10844* (MICH!). (Fig. 3A)
Mycobank MB807777

Corneriella Sánchez-García, **gen. nov.** – Type: *Corneriella bambusarum* (Desjardin & Hemmes) Sánchez-García.
Mycobank MB808480

Habit tricholomatoid. Lamellae adnexed to sinuate or decurrent, sometimes forked, white when young, becoming darker. Spores amyloid, smooth, thin-walled. Cheilocystidia present, conspicuous, of various shapes, cylindric to flexuous, lageniform or fusoid, thin-walled. Pleurocystidia absent. Pileipellis a cutis with suberect to erect terminal cells. Clamp connections present. On soil and humus. Putatively saprotrophic.

Eponymy. – Named after Edred John Henry Corner, a British botanist and mycologist who described *Cantharellula humicola*, a species now transferred to this genus.

Corneriella bambusarum (Desjardin & Hemmes) Sánchez-García, **comb. nov.** ≡ *Porpoloma bambusarum* Desjardin & Hemmes in Harvard Pap. Bot. 6: 97. 2001 – Holotype: U.S.A. Hawaii, O’ahu, Manoa Valley, Manoa Falls Trail,

8 Jan 1992, *D.E. Desjardin 5462* (SFSU n.v.; isotypes: BISH n.v., NYBG!). (Fig. 3E)
Mycobank MB808481

Corneriella humicola (Corner) Sánchez-García, **comb. nov.** ≡ *Cantharellula humicola* Corner in Nova Hedwigia Beih. 109: 13. 1994 – Holotype: MALAYSIA. Peninsular Malaysia, Pahang, Pasoh forest, 30 Sep 1966, *E.J.H. Corner* (E n.v.).
Mycobank MB808482

Dennisiomyces Singer in Anais Soc. Biol. Pernambuco 13: 225. 1955 – Type: *Dennisiomyces glabrescentipes* Singer in Anais Soc. Biol. Pernambuco 13: 225. 1955. (Fig. 3B)

Leucopaxillus Boursier in Bull. Trimestriel Soc. Mycol. France 41: 393. 1925 – Type: *Leucopaxillus paradoxus* (Costantin & L.M.Dufour) Boursier in Bull. Trimestriel Soc. Mycol. France 41: 393. 1925 ≡ *Clitocybe paradoxa* Costantin & L.M.Dufour, Nouv. Fl. Champ., ed. 2: 262. 1896 ≡ *Lepista paradoxa* (Costantin & L.M.Dufour) Maire in Bull. Trimestriel Soc. Mycol. France 40: 307. 1926 ≡ *Leucopaxillus albissimus* var. *paradoxus* (Costantin & L.M.Dufour) Singer & A.H.Sm. in Pap. Michigan Acad. Sci. 28: 112. 1943. (Fig. 3C)

Notes. – The current definition of *Leucopaxillus* excludes species with smooth spores characterized by a weak amyloid reaction. These species are now placed within *Aspropaxillus* Kühner & Maire (type: *A. giganteus* (Sowerby) Kühner & Maire) (Vizzini & al., 2012).

Porpoloma Singer in Sydowia 6: 198. 1952 – Type: *Porpoloma sejunctum* Singer in Sydowia 6: 198. 1952. (Fig. 3G)

Pseudotricholoma (Singer) Sánchez-García & Matheny, **stat. nov.** ≡ *Cantharellula* subg. *Pseudotricholoma* Singer in Sydowia 2: 30. 1948 ≡ *Porpoloma* sect. *Pseudotricholoma* (Singer) Bon in Doc. Mycol. 9(33): 25. 1978 – Type: *Pseudotricholoma umbrosum* (A.H.Sm. & M.B.Walters) Sánchez-García & Matheny.
Mycobank MB807899

Habit tricholomatoid, pileus dry, fibrillose. Lamellae adnate to emarginate, pale to brownish, edges concolorous, when bruised reddening then blackening. Spores amyloid, smooth, ellipsoid to ellipsoid-oblong, thin-walled. Cheilocystidia absent or rare. Pleurocystidia absent. Pileipellis a cutis of cylindrical hyphae. Clamp connections present. On soil, in woods and grasslands of the Northern Hemisphere. Probably biotrophic, possibly ectomycorrhizal.

Pseudotricholoma umbrosum (A.H.Sm. & M.B.Walters) Sánchez-García & Matheny, **comb. nov.** ≡ *Tricholoma umbrosum* A.H.Sm. & M.B.Walters in Mycologia 35: 477. 1943 ≡ *Cantharellula umbrosa* (A.H.Sm. & M.B.Walters) Singer in Lilloa 22: 238. 1951 ≡ *Porpoloma umbrosum* (A.H.Sm. & M.B.Walters) Singer in Sydowia 15: 53. 1962 (“1961”) ≡ *Porpoloma elytroides* var. *umbrosum* (A.H.Sm.

& M.B.Walters) Bon in Doc. Mycol. 20(78): 38. 1990 – Holotype: CANADA. Nova Scotia, prope Truro, 16 Jul 1931, *Wehmeyer 640*, leg. A.H. Smith (MICH!). (Fig. 3F) MycoBank MB807901

Pseudotricholoma metapodium (Fr.) Sánchez-García & Matheny, **comb. nov.** $\equiv$ *Agaricus metapodius* Fr., Observ. Mycol. 2: 110. 1818 $\equiv$ *Hygrophorus metapodius* (Fr.) Fr., Epicr. Syst. Mycol.: 328. 1838 (“1836–1838”) $\equiv$ *Camarophyllus metapodius* (Fr.) Wünsche, Pilze: 115. 1877 $\equiv$ *Neohygrocybe metapodia* (Fr.) Herink in Sborn. Severočesk. Mus., Přír. Vědy 1: 71. 1958 $\equiv$ *Hygrocybe metapodia* (Fr.) M.M.Moser in Gams, Kl. Krypt.-Fl., ed. 3, 2b/2: 63. 1967 $\equiv$ *Porpoloma metapodium* (Fr.) Singer in Beih. Sydowia 7: 19. 1973 $\equiv$ *Tricholoma metapodium* (Fr.) Papetti in Boll. Circ. Mic. “Giovanni Carini” 37: 48. 1999 – **Neotype (designated here)**: SWEDEN. Västergötland, Vänersborg, Vänersborg, Rudet SV, Gundlebosjön N, 8 Aug 2006, *Leif & Anita Stridvall 06/134* (GB!). MycoBank MB807902

Notes. – When Fries originally described this taxon, he did not indicate a type for the name. No later authors, including those of the subsequent combinations, designated a type. Despite an exhaustive search, we were unable to find any original material. Therefore, we select *Leif & Anita Stridvall 06/134* as the neotype. The specimen is from Sweden and it was collected relatively close from Femsjö, where Fries collected the original material.

Tricholoma (Fr.) Staude, Schwämme Mitteldeutschl.: xxviii, 125. 1857 – Type: *Tricholoma flavovirens* (Pers.:Fr.) S.Lundell. (Fig. 3D)

Tricholoma flavovirens (Pers.:Fr.) S.Lundell in Lundell & Nannfeldt, Fung. Exs. Suec. 23–24: no. 1102. 1942 $\equiv$ *Agaricus flavovirens* Pers. in Hoffmann, Abbild. Schwämme 3: t. 24. 1793 $\equiv$ *Agaricus aureus* Schaeff., Fung. Bavar. Palat. Nasc. 4: 19, t. 41. 1774 $\equiv$ *Agaricus luteus* Batsch, Elench. Fung.: 45. 1783 $\equiv$ *Amanita punctata* var. *aurea* (Schaeff.) Lam., Encycl. 1: 106. 1783.

$\equiv$ *Agaricus equestris* L., Sp. Pl.: 1173. 1753 $\equiv$ *Tricholoma equestre* (L.) P.Kumm., Führer Pilzk.: 130. 1871.

$\equiv$ *Agaricus auratus* Paulet, Traité Champ. 2: 137. 1793 $\equiv$ *Agaricus sinuatus* var. *arenarius* Laterrade, Fl. Bordel., ed. 4: 534. 1846.

Notes. – *Agaricus flavovirens* was sanctioned by Fries (1821) therefore, it has priority over its earlier synonyms *A. luteus* and *A. aureus* (Art. 13.1). For a detailed discussion about the synonymy of *T. flavovirens* and *T. equestre* see Deng & Yao (2005) and Moukha & al. (2013).

Pogonoloma (Singer) Sánchez-García, **stat. nov.** $\equiv$ *Porpoloma* subg. *Pogonoloma* Singer in Sydowia 15: 53. 1962 (“1961”) $\equiv$ *Porpoloma* sect. *Pogonoloma* (Singer) Bon in Doc. Mycol. 9(33): 25. 1978 – Type: *Pogonoloma spinulosum* (Kühner & Romagn.) Sánchez-García. MycoBank MB807897

Habit tricholomatoid, pileus with a pilose margin. Lamellae adnate to emarginate, white to cream sometimes turning pinkish or yellowish. Spores amyloid, smooth, ellipsoid, thin-walled. Cheilocystidia poorly differentiated or absent. Pleurocystidia absent. Pileipellis a cutis of cylindrical hyphae with intracellular pigments. Clamp connections present. On soil. Presumably saprotrophic.

Pogonoloma spinulosum (Kühner & Romagn.) Sánchez-García, **comb. nov.** $\equiv$ *Tricholoma spinulosum* Kühner & Romagn. in Bull. Mens. Soc. Linn. Lyon 16: 134. 1947 $\equiv$ *Porpoloma spinulosum* (Kühner & Romagn.) Singer in Sydowia 15: 53. 1962 (“1961”) – **Lectotype (designated here)**: FRANCE. Seine et Marne, Ozoir la Ferrière, near the intersection of Ferrandière, 7 Oct 1932, *R. Kühner* (G barcode G00126725 n.v.). MycoBank MB807900

Notes. – We studied a photograph of a specimen named *T. spinulosum* that was collected and annotated by Kühner as “typus”. Since this taxon has not been typified we designate this specimen as a lectotype.

Pogonoloma macrocephalum (Schulzer) Sánchez-García, **comb. nov.** $\equiv$ *Agaricus macrocephalus* Schulzer, Icon. Select. Hymenomyc. Hung.: 11, t. III. 1873 $\equiv$ *Coolia macrocephala* (Schulzer) Huijsman in Meded. Ned. Mycol. Ver. 28: 60. 1943 $\equiv$ *Leucopaxillus macrocephalus* (Schulzer) Bohus in Fragm. Bot. Mus. Hist.-Nat. Hung. 4(1–4): 37. 1966 $\equiv$ *Porpoloma macrocephalum* (Schulzer) Bon in Doc. Mycol. 9(3): 26. 1978 – **Lectotype (designated here)**: [illustration] “AGARICUS (TRICHOLOMA) MACROCEPHALUS SCHULZER” in Kalchbrenner & Schulzer, Icon. Select. Hymenomyc. Hung.: t. III, fig. 1. 1873. MycoBank MB807903

Singerocybe adirondackensis (Peck) Sánchez-García & Matheny, **comb. nov.** $\equiv$ *Agaricus adirondackensis* Peck in Rep. (Annual) New York State Mus. Nat. Hist. 23: 77. 1872 $\equiv$ *Clitocybe adirondackensis* (Peck) Sacc., Syll. Fung. 5: 180. 1887 – Holotype: U.S.A. New York, Essex Co., North Elba, Adirondack Mountains, Aug & Sep, watercolor by Peck (NYS n.v.). MycoBank MB807764

Notes. – We transfer this species to *Singerocybe* Harmaja on account of the inflated bladder-like intercalary cells in the pileipellis and a close ITS BLASTn match with European samples of *S. phaeophthalma* (Pers.) Harmaja (~97%).

Key to genera in Tricholomataceae s.str.

1. Spores inamyloid 2
1. Spores amyloid 3
2. Cheilocystidia and pleurocystidia conspicuous and long pedicelate arising below the hymenium; clamp connections present ***Albomagister***
2. Cheilocystidia present or absent; pleurocystidia rare, if

- present arising from the hymenium; clamp connections rarely present *Tricholoma*
3. Spores verrucose *Leucopaxillus*
3. Spores smooth 4
4. Cheilocystidia and pleurocystidia present *Dennisiomyces*
4. Pleurocystidia absent; cheilocystidia present or absent . 5
5. Cheilocystidia present, edges of lamellae sterile; distributed in the Southern Hemisphere *Porpoloma*
5. Cheilocystidia present or absent; distributed in temperate forests and grasslands of the Northern Hemisphere or in the tropics 6
6. Basidiocarps not changing color where cut or bruised; lamellae sometimes forked; cheilocystidia present and well differentiated; distributed in the tropics *Corneriella*
6. Basidiocarps changing red where cut or bruised; lamellae not forked; cheilocystidia absent or poorly differentiated; distributed in temperate forests and grasslands of the Northern Hemisphere *Pseudotricholoma*

DISCUSSION

Several attempts have been made to delimit the Tricholomataceae based on morphological features ranging from a broad and inclusive group (e.g., Singer, 1986) to a more reduced entity (Jülich, 1981). Floristic treatments (such as *Funga Nordica*) now take into consideration a much-reduced Tricholomataceae based on input from molecular phylogenetic studies (Moncalvo & al., 2002; Matheny & al., 2006; Garnica & al., 2007; Binder & al., 2010).

Some genera now recognized as Tricholomataceae s.str. have also been placed in other families. For example, *Dennisiomyces* was placed by Jülich (1981) in the Marasmiaceae, and *Porpoloma* and *Leucopaxillus* in the Leucopaxillaceae. Part of the taxonomic confusion stems from the fact that groups like *Porpoloma* and *Leucopaxillus* are not monophyletic.

The genus *Tricholoma* is one of the two genera of the family with inamyloid spores, and the only one that contains some species without clamp connections (Ovrebø & Tylutki, 1975; Bigelow, 1979; Riva, 2003; Bessette & al., 2013; Christensen & Heilmann-Clausen, 2013).

The genus *Porpoloma* was divided by Singer (1975) into three subgenera: subg. *Porpoloma*, subg. *Pseudotricholoma*, and subg. *Pogonoloma*. Here, we confirm that *Porpoloma* subg. *Porpoloma* contains species known to date only from temperate regions of the Southern Hemisphere and that form ectomycorrhizal associations. Members of this genus have smooth, amyloid, and ellipsoid spores, cheilocystidia, and a pileipellis with intracellular brown pigments. This excludes *Porpoloma bambusarum* and several other species not sampled here (e.g., *Por. boninense* (S. Ito & Imai) Hongo, and *Por. aranzadai* Laskibar & al.). *Porpoloma bambusarum* now serves as the type of the new genus *Corneriella*, but additional species of *Porpoloma* s.l. are in need of revision to determine their clade placement. For instance, the presence of cheilocystidia in *Por. boninense* and *Por. aranzadai* (Hongo, 1980; Laskibar & al., 2001) suggests

that these taxa could belong to *Porpoloma* s.str., however, there is no evidence that they form ectomycorrhizal associations as it occurs in *Porpoloma* s.str.

We elevate *Porpoloma* subg. *Pseudotricholoma* to the generic level confirming within it two species: *Pseudotricholoma umbrosum* ($\equiv$ *Por. umbrosum*) and *Ps. metapodium* ($\equiv$ *Por. metapodium*). *Pseudotricholoma umbrosum* and *Ps. metapodium* are morphologically similar. It has been suggested they are different forms or geographic variants of the same species (Singer, 1986). Our phylogeny (Fig. 2) shows the separation of two clades, *Ps. umbrosum* representing specimens from North America and *Ps. metapodium* represented by collections from Europe, thus geographic separation is the main difference between these two species. Additionally, *Ps. metapodium* is usually found in meadows, while *Ps. umbrosum* is found in forests (Smith & Walters, 1943; Bon, 1978).

Porpoloma elytroides resembles *Pseudotricholoma* in having reddening flesh and a farinaceous odor, and could be placed in this genus following our taxonomic key. However, we have not studied collections of *Por. elytroides*.

Singer (1956) described *Porpoloma* subg. *Pes-caprae* Singer to accommodate *Por. pes-caprae*, which was later transferred to *Porpoloma* subg. *Pseudotricholoma* (Singer, 1962). Here, we find that *Por. pes-caprae* is an independent lineage apart from the rest of *Porpoloma* and may form a sister lineage to *Tricholoma* (Fig. 2). Multiple gene sequence data from additional collections are necessary to confirm the autonomous position of *Por. pes-caprae*.

Bon (1978) included two species in *Porpoloma* subg. *Pogonoloma*: *Por. macrocephalum* and *Por. macrorrhizum* (Sacc.) Bon. Our results (Fig. 1) suggest that *Por. macrocephalum* and *Por. spinulosum* form an independent clade sister to *Pseudoclitocybe* and *Musumecia*. Based on this evidence we have elevated subgenus *Pogonoloma* to generic level including *Por. spinulosum* ($\equiv$ *Tricholoma spinulosum*) and *Por. macrocephalum*.

Porpoloma bambusarum is the other species sampled that does not belong to *Porpoloma* s.str. This species is transferred to the new genus *Corneriella* together with *Cantharellula humicola*. The genus *Cantharellula* Singer was shown to be polyphyletic in a recent analysis by Lodge & al. (2014), where the type *Ca. umbonata* was recovered as a sister group to *Pseudoarmillariella ectypoides* (Peck) Singer, both now included in the Hygrophoraceae. In that analysis *Ca. humicola* was recovered within the Tricholomatoid clade and was excluded from *Cantharellula* s.str. based on the presence of cheilocystidia and regular rather than tridirectional lamellar trama. Members of *Corneriella* have smooth and amyloid spores and cheilocystidia, but lack pleurocystidia.

Dennisiomyces is a poorly known genus with only five species described to date: *D. glabrescentipes*, *D. fuscoalbus* Singer, *D. rionegrensis* Singer from Brazil, *D. griseus* from Trinidad, and *D. lanzonii* Robich from Italy (Dennis, 1951; Singer, 1955, 1989; Robich, 1989).

Dennisiomyces can be separated from other groups in the Tricholomataceae s.str. by the smooth and amyloid spores, the presence of cheilocystidia and pleurocystidia, presence of

clamp connections, and erect to suberect terminal cells of the pileipellis.

This genus is more diverse than previously thought as we have detected what are probably five undescribed species from the Neotropics and southeast U.S. Two additional species with affiliations to *Dennisiomyces* include *Gymnopus fulvidiscus* Murrill and *Pleurella ardesiaca* (Svenson & Taylor) E.Horak (Singer, 1986). The type of *G. fulvidiscus* fits the description of *Dennisiomyces* because of the amyloid and smooth spores, presence of cheilocystidia and pleurocystidia, and presence of clamp connections based on notes deposited with the specimen. Singer (1986) suggested the transfer of *G. fulvidiscus* to *Dennisiomyces*, and we predict it will indeed belong to the genus but have not studied the type.

Pleurella ardesiaca is a lignicolous species from New Zealand characterized by smooth, amyloid spores and presence of cheilocystidia and clamp connections, which suggest a close relationship with *Porpoloma* s.str. (Horak, 1971). However, the lignicolous habitat is not consistent with placement in *Dennisiomyces* or *Porpoloma*. An ITS sequence (JQ694106) is publically available from a collection (PDD 87446) referred to as *Pleurella ardesiaca* from New Zealand. BLASTn results suggest the nearest alliance of this specimen to *Baeospora* in the Marasmioid clade (Matheny & al., 2006) or to *Hypsizygus* (Gillet) Singer in the Lyophyllaceae. A thorough analysis of the type is required to confirm its taxonomic and phylogenetic position.

The genus *Albomagister* is macroscopically similar to *Leucopaxillus* or *Tricholoma*, however, its smooth inamyloid spores separate it from *Leucopaxillus*, while the presence of prominent pleuro- and cheilocystidia distinguish it from *Tricholoma*. The hyphae of the lamellar trama are parallel rather than divergent as in *Hygrophorus* Fr.

Albomagister subaustralis is a species now known from North Carolina and Tennessee. Dennis (1953) also reported it from Trinidad. However, this is doubtful since in his description he notes the presence of cheilocystidia and pleurocystidia with long tapering apices, a feature inconsistent with the type and other collections studied by us (Fig. 3A). We consider Dennis' material of *H. subaustralis* to represent another species possibly of *Albomagister*.

Within *Albomagister* we examined numerous collections of *A. subaustralis* studied by Hesler & Smith (1963), including the type specimen, and found one collection (AHS14872) identified as such that represents most likely an undescribed species of *Albomagister* (as *Albomagister* sp. 2 in Fig. 2). This specimen was collected in the same locality as *A. subaustralis* showing that these two species co-exist in similar environments. In addition, we found one more collection that resembles *A. subaustralis*, but it seems to be a different phylogenetic species of *Albomagister* (as *Albomagister* sp. 3 in Fig. 2). This species was also found co-existing with *A. subaustralis*.

The two undetermined specimens (ECV4038 and MBP-06VIII09) are insufficiently known, and we cannot derive any conclusion regarding its taxonomy. The former possesses cheilocystidia, pleurocystidia and inamyloid spores, whereas the latter lacks pleurocystidia.

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Appendix 1. Species sampled and GenBank accession numbers.

Species name in this study (previous name [if existent]), country, voucher number [asterisk indicates type specimen], ITS, nLSU, nSSU, *rpb2*. Collector's abbreviations are as follows: *ADW*, A.D. Wolfenbarger; *AH*, A. Henrici; *AHS*, A.H. Smith; *ALC*, A. Loeza; *BPL*, B.P. Looney; *DED*, D.E. Desjardin; *ECV*, E.C. Vellinga; *EL*, E. Larsson; *FL*, F. Landeros; *GC*, G. Consiglio; *GD*, G. Daniele; *GG*, G. Guzmán; *JCS*, J.C. Slot; *JFA*, J.F. Ammirati; *JPF*, J.P. Fiard; *JT*, J. Trappe; *LAS*, L. & A. Stridvall; *LGD*, L. Guzmán-Dávalos; *LRH*, L.R. Hesler; *MBP*, M.B. Pilkington; *MES*, M.E. Smith; *MGW*, M.G. Wood; *MOS*, M.M. Moser; *MSG*, M. Sánchez-García; *PBM*, P.B. Matheny; *REH*, R.E. Halling; *RHP*, R.H. Petersen; *SAR*, S.A. Rehner; *SAT*, S.A. Trudell; *TJB*, T.J. Baroni; *TK*, T. Knutsson; *VRC*, V. Ramírez-Cruz; *WBU*, W. Burnette).

"Inocypha" sp., U.S.A., *GD-b* (CORD), DQ457683, DQ457622, DQ472728; **Albomagister sp. 2** (*Hygrophorus subaustralis* A.H.Sm. & Hesler), U.S.A., *MSG137* (TENN:068776), KJ417247, KJ417178, –, KJ424363; **Albomagister sp. 2** (*Hygrophorus subaustralis*), U.S.A., *MSG136* (TENN:068775), KJ417248, –, –, KJ424364; **Albomagister sp. 2** (*Hygrophorus subaustralis*), U.S.A., *AHS14872* (MICH:058090), KJ417249, –, –, **Albomagister sp. 3** (*Hygrophorus subaustralis*), U.S.A., *ECV4202* (TENN:065323), KJ417250, KJ417179, –, KJ424365; **Albomagister subaustralis** (A.H.Sm. & Hesler) Sánchez-García, Birkebæk & Matheny (*Hygrophorus subaustralis*), U.S.A., *ECV4049* (TENN:064621), KJ417251, KJ417180, –, KJ424366; **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *MGW676* (TENN:064620), KJ417252, KJ417181, KJ417255, KJ424367; **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *WBU11* (TENN:066902), KJ417253, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH14423* (TENN:014423), KJ417254, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH23221* (TENN:023221), KJ417255, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH39069* (TENN:039069), KJ417256, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH20463* (TENN:020463), KJ417257, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH18628* (TENN:8018628), KJ417258, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH22663* (TENN:022663), KJ417259, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH23195* (TENN:023195), KJ417260, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *LRH17951* (TENN:017951), KJ417261, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *AHS10844* (MICH:010951)*, KJ417262, –, –, **Albomagister subaustralis** (*Hygrophorus subaustralis*), U.S.A., *SAT1221702* (TENN:067343), KJ417263, –, –, **Aspropaxillus candidus** (Bres.) Raithelth., AUSTRIA, *MOS71116* (TENN:037113), –, KJ417182, –, –, **Aspropaxillus giganteus** (Quél.) Kühner & Maire, RUSSIA, *RHP12192* (TENN:060129), –, KJ417183, KJ417256, KJ424368; **Aspropaxillus giganteus**, U.S.A., *JJ021011* (GB), –, KJ417240, –, –, **Aspropaxillus giganteus**, ITALY, *GC-98046* (G. Consiglio, pers. hb.), –, JQ639152, –, –, **Aspropaxillus septentrionalis** (Singer & A.H.Sm.) Vizzini, U.S.A., *AHS24982* (MICH:005826)*, –, KJ417184, –, –, **Callistosporium graminicolor** Lennox, U.S.A., *PBM2341* (WTU), –, AY745702, AY752974, KJ424369; **Calocybe carnea** (Bull.) Donk, –, –, (CBS:552.50), –, AF223178, DQ367418, DQ367432; **Calocybe gangraenosa** (Fr.) Hofstetter, Moncalvo, Redhead & Vilgalys, –, *Hae251.97* (–), –, AF223202, DQ367420, DQ367434; **Catathelasma ventricosum** (Peck) Singer, U.S.A., *PBM2403* (WTU), –, DQ089012, DQ435811, DQ470830; **Cleistocybe carneogrisea** (Malençon) Vizzini, FRANCE, *S. Poumarat s.n.* (TENN:063842), –, HQ728527, HQ728528, –, **Cleistocybe vernalis** Ammirati, A.D.Parker & Matheny, U.S.A., *PBM1856* (WTU), –, AY647208, DQ092913, –, **Clitocybe aff. fellea** Peck, U.S.A., *PBM3028* (TENN:062782), –, HQ728534, HQ728535, HQ728536; **Clitocybe candicans** (Pers.) P.Kumm., U.S.A., *PBM2476* (CUW), –, AY645055, AY771609, DQ385881; **Clitocybe dealbata** (Sowerby) P.Kumm., –, *HC95.cp3* (–), –, AF223175, DQ825431, DQ825407; **Clitocybe nebularis** (Batsch) P.Kumm., U.S.A., *PBM2259* (WTU), –, DQ457658, DQ437681, DQ470833; **Clitocybe subditopoda** Peck, U.S.A., *PBM2489* (CUW), –, AY691889, AY771608, AY780942; **Clitopilus prunulus** (Scop.) P.Kumm., U.S.A., *TJB6838* (CORT), –, AY700181, AY771607, DQ825408; **Collybia tuberosa** (Bull.) P.Kumm., SWEDEN, *RHP7300* (TENN:053540), –, AY639884, AY771606, AY787219; **Corneriella bambusarum** (Desjardin & Hemmes) Sánchez-García (*Porpoloma bambusarum* Desjardin & Hemmes), U.S.A., *DED5462* (NYBG)*, KJ417264, KJ417185, –, KJ424370; **Corneriella bambusarum** (*Porpoloma bambusarum*), U.S.A., *DED6572* (NYBG:0775752), KJ417265, –, –, **Corneriella humicola** (Corner) Sánchez-García (*Cantharellula humicola* Corner), THAILAND, *DED7871* (SFSU), KF291051, KF291052, KF291053, –, **Corneriella sp.** (*Dennisiomyces* sp.), PUERTO RICO, *PR-4733* (CFMR), KF306336, KF306337, –, KF306338; **Corneriella sp.** (*Porpoloma* sp.), PUERTO RICO, *PR-3995* (CFMR), EF421106, AF261395, –, AF421013; **Corneriella sp.** (*Dennisiomyces griseus* (Dennis) Singer), MARTINIQUE, *JPF943A* (K:188911), KJ417324, KJ417234, –, –, **Dennisiomyces glabrescentipes** Singer, MARTINIQUE, *JPF1000A* (K:188910), KJ417326, KJ417235, –, –, **Dennisiomyces griseus**, TRINIDAD & TOBAGO, *Dennis-293* (K:160882)*, KJ417325, –, –, **Dennisiomyces sp. 1**, BELIZE, *BZ-916* (CFMR), KF291063, KF291064, –, KF291066; **Dennisiomyces sp. 2** (*Porpoloma* sp.), PUERTO RICO, *PR-4763* (CFMR), KJ417269, KJ417191, –, –, **Dennisiomyces sp. 3** (*Porpoloma* sp.), PUERTO RICO, *PR-4764* (CFMR), KJ417270, –, –, **Dennisiomyces sp. 4** (*Porpoloma* sp.), PUERTO RICO, *PR-6334* (CFMR), KJ417271, KJ417192, KJ417258, –, –, **Dennisiomyces sp. 4** (*Porpoloma* sp.), PUERTO RICO, *PR-6613* (CFMR), KJ417268, KJ417190, KJ417257, –, **Dennisiomyces sp. 5**, U.S.A., *BPL244* (TENN:067232), –, KJ417186, –, KJ424371; **Dennisiomyces sp. 5**, U.S.A., *PBM3862* (TENN:067469), –, KJ417187, –, KJ424372; **Dennisiomyces sp. 5**, U.S.A., *BPL254* (TENN:067388), KJ417266, KJ417188, –, KJ424373; **Dennisiomyces sp. 5**, U.S.A., *PBM3861* (TENN:067462), KJ417267, KJ417189, –, KJ424374; **Dennisiomyces sp. 5**, U.S.A., *DLNC15-05* (TENN:061833), KJ417327, KJ417239, –, –, **Dennisiomyces sp. 5**, U.S.A., *DLTN34-05* (TENN:061851), KJ417328, –, –, **Entoloma asterosporum** (Coker & Couch) T.J.Baroni & Matheny, U.S.A., *PBM3268* (TENN:064538), –, JF706310, JF706311, JF706312; **Entoloma sericeum** Quél., –, *VHA 03-02* (–), –, DQ367423, DQ367421, DQ367435; **Entoloma sinuatum** (Bull.) P.Kumm., U.S.A., *TJB5349*, –, AY691891, AY657007, KJ424375; **Entoloma sp.**, U.S.A., *TJB4765* (–), –, AY700180, AY665784, DQ385883; **Entoloma strictius** (Peck) Sacc., –, *M96/10* (–), –, AF042620, AF287832, AY218483; **Giacoma mirabilis** (Bres.) Vizzini & Contu, ITALY, *GC-94141* (G. Consiglio, pers. hb.), –, JQ639154, –, –, **Infundibulicibe gibba** (Pers.) Harmaja, U.S.A., *JCS0704B* (CUW), –, DQ457682, DQ115780, DQ472727; **Lepista irina** (Fr.) H.E.Bigelow, U.S.A., *PBM2291* (WTU), –, DQ234538, AY705948, DQ385885; **Lepista personata** (Fr.) Cooke, U.S.A., *ADW0097* (TENN:066100), –, KJ417193, KJ417259, KJ424376; **Lepista sordida** (Schumacher) Singer, U.S.A., *CRG014* (GLM:45949), –, AY207225, KJ417260, KJ137273; **Leucopaxillus albissimus** (Peck) Singer, MEXICO, *FL7/8A* (XAL), KJ417272, KJ417194, –, –, **Leucopaxillus albissimus**, –, –, (DAOM:182713), –, AF261393, –, –, **Leucopaxillus albissimus**, CANADA, *F9693* (FH:00301850), KJ417273, –, –, **Leucopaxillus albissimus**, U.S.A., *Singer-301900* (FH:00301900), KJ417274, –, –, **Leucopaxillus alboalutaceus** (F.H.Møller & Jul.Schäff.) F.H.Møller, SWEDEN, *LAS00/082* (GB:0065210), KJ417275, KJ417195, KJ417261, KJ424377; **Leucopaxillus alboalutaceus**, SWEDEN, *LAS88/79* (GB:0065215), KJ417245, –, –, **Leucopaxillus alboalutaceus**, ITALY, *GC-97076* (G. Consiglio, pers. hb.), JQ639147, –, –, **Leucopaxillus amarus** (Alb. & Schwein.) Kühner, U.S.A., *TFB54925* (TENN:040325), KJ417276, –, –, **Leucopaxillus amarus**, SWITZERLAND, *MOS63/271* (TENN:037007), –, KJ417196, –, –, **Leucopaxillus amarus**, MEXICO, *LGD5690* (IBUG), KJ417277, –, –, **Leucopaxillus amarus**, U.S.A., *BW122201* (WTU:F-8827), KJ417278, KJ417197, –, –, **Leucopaxillus amarus**, U.S.A., *AHS15870* (MICH:0073741), KJ417279, –, –, **Leucopaxillus amarus**, U.S.A., *Cooke 22708* (FH:00301878), KJ417280, –, –, **Leucopaxillus cerealis** (Lasch) Singer, SWEDEN, *LAS01/031* (GB:0110964), KJ417281, –, –, KJ424378; **Leucopaxillus cerealis**, SWEDEN, –, (GB:0068895), KJ417282, KJ417198, KJ417262, KJ424379; **Leucopaxillus cerealis**, SWEDEN, *LAS04/012* (GB:065211), KJ417283, –, –, KJ424380; **Leucopaxillus cerealis**, SWEDEN, *LAS01/147* (GB), KJ417246, KJ417241, –, –, **Leucopaxillus cerealis**, ITALY, *AVL20112* (TO), JQ639148, JQ639149, –, –, **Leucopaxillus cf. masakanus** Pegler, U.S. VIRGIN ISLANDS, *TJB8321* (CORT), KJ417284, –, –, **Leucopaxillus eucalyptorum** (Cleland) Grgur., AUSTRALIA, *REH9110* (NYBG:01115433), KJ417285, KJ417199, –, –, **Leucopaxillus eucalyptorum**, ARGENTINA, *RHP8368* (TENN:055040), KJ417286, KJ417200, –, –, **Leucopaxillus gentianeus** (Quél.) Kotl., SWEDEN, *EL291/11* (GB), KJ417287, KJ417201, –, KJ424381; **Leucopaxillus gentianeus**, U.S.A., –, (TENN:05616), –, AF261394, –, –, **Leucopaxillus gracillimus** Singer & A.H.Sm., MEXICO, *GG34476* (XAL), KJ417288, –, –, **Leucopaxillus gracillimus**, U.S. VIRGIN ISLANDS, *TJB8315* (CORT), KJ417289, –, –, **Leucopaxillus laterarius** (Peck) Singer & A.H.Sm., U.S.A., *PBM3060* (TENN:063507), KJ417290, KJ417202, KJ417263, –, –, **Leucopaxillus laterarius**, U.S.A., *TFB56010* (TENN:044433), KJ417291, KJ417203, –, –, **Leucopaxillus laterarius**, U.S.A., *RHP29877* (TENN:029877), KJ417292, KJ417204, –, –, **Leucopaxillus laterarius**, MEXICO, *ALCI78* (IBUG), KJ417293, –, –, **Leucopaxillus laterarius**, MEXICO, *VRC1717* (IBUG), KJ417294, –, –, **Leucopaxillus lilacinus** Bougher, AUSTRALIA, *PBM3584* (TENN:066653), KJ417295, KJ417205, KJ417264, KJ424382; **Leucopaxillus monticola** (Singer & A.H.Sm.) Bon, ITALY, *AVL20111* (TO), JQ639156, –, –, **Leucopaxillus paradoxus** (Costantin & L.M.Dufour) Boursier, HUNGARY, *TK04/091* (GB:0110968), KJ417296, KJ417206, KJ417265, KJ424383; **Leucopaxillus tricolor** (Peck) Kühner, U.S.A., *TFB13462* (TENN:061725), KJ417323, KJ417207, KJ417266,

Appendix 1. Continued.

KJ424384; *Lyophyllum decastes* (Fr.) Singer, —, *JM 87/16* (—), —, AF042583, DQ367419, DQ367433; *Lyophyllum* aff. *decastes*, U.S.A., *PBM3069* (TENN:063624), —, HQ832459, HQ832426, HQ832437; *Lyophyllum* sp., U.S.A., *PBM 2688* (CUW), —, DQ094785, DQ457628, —; *Musumecia bettlachensis* Vizzini & Contu, ITALY, *HG2284* (TO), —, JF926521, —, —; *Notholepista subzonalis* (Peck) Vizzini & Contu, SWEDEN, *K. Kjellström s.n.* (GB:0087013), —, KJ417208, KJ417267, KJ424385; *Notholepista subzonalis*, SWEDEN, *TK98/279* (GB), —, KJ417242, —, —; *Ossicaulis lignatilis* (Pers.) Redhead & Ginns, —, — (DAOM:188196), —, AF261396, AF334923, DQ825410; *Pogonoloma macrocephalum* (Schulzer) Sánchez-García (*Porpoloma macrocephalum* (Schulzer) Bon), AUSTRIA, *MOS69/85* (TENN:037026), —, KJ417209, KJ417268, —; *Pogonoloma macrocephalum* (*Porpoloma macrocephalum*), ITALY, *GC-96016* (G. Consiglio, pers. hb.), —, JQ639163, —, —; *Pogonoloma spinulosum* (Kühner & Romagn.) Sánchez-García (*Porpoloma spinulosum* (Kühner & Romagn.) Singer), UNITED KINGDOM, *Reid S346* (K:005346), —, KJ417236, —, —; *Pogonoloma spinulosum* (*Porpoloma spinulosum*), UNITED KINGDOM, *D.A. Reid s.n.* (K:089387), —, KJ417237, —, —; *Pogonoloma spinulosum* (*Porpoloma spinulosum*), UNITED KINGDOM, *J. Pitt s.n.* (K:107286), —, KJ417238, —, KJ424401; *Porpoloma pes-caprae* (Fr.) Singer, POLAND, *MOS67/265* (TENN:037121), KJ417297, —, —, —; *Porpoloma portentosum* Singer, CHILE, *MES531* (FL), KJ417298, KJ417210, —, KJ424386; *Porpoloma portentosum*, ARGENTINA, *REH5788* (NYBG), KJ417299, KJ417211, —, KJ424387; *Porpoloma portentosum*, ARGENTINA, *Singer-M149* (MICH: 011834)*, KJ417300, —, —, —; *Porpoloma sejunctum* Singer, CHILE, *G. Palfner s.n.* (CONC:F0416), KJ417301, KJ417212, —, KJ424388; *Porpoloma sejunctum*, ARGENTINA, *Singer-M256* (MICH:01183)*, KJ417302, —, —, —; *Porpoloma sejunctum*, ARGENTINA, Root sample, JX316261, —, —, —; *Porpoloma sp. 2*, AUSTRALIA, *PBM3441* (TENN:065358), KJ417303, KJ417213, KJ417269, KJ424389; *Porpoloma sp. 1*, AUSTRALIA, *PBM3238* (TENN:065473), KJ417304, KJ417214, KJ417270, KJ424390; *Porpoloma terreum* Singer, CHILE, *REH5830* (NYBG), KJ417305, KJ417215, —, KJ424391; *Porpoloma terreum*, CHILE, *G. Palfner s.n.* (CONC:F0030), KJ417306, KJ417216, —, —; *Porpoloma terreum*, ARGENTINA, *Singer-M372* (MICH:011746)*, KJ417307, —, —, —; *Porpoloma terreum*, ARGENTINA, Root sample, JX316283, —, —, —; *Porpoloma terreum*, ARGENTINA, Root sample, JX316318, —, —, —; *Porpoloma terreum*, ARGENTINA, Root sample, JX316344, —, —, —; *Pseudoclitocybe cyathiformis* (Bull.) Singer, U.S.A., *JFA12811* (WTU), —, EF551313, GU187659, GU187515; *Pseudoclitocybe cyathiformis*, ITALY, *HG2284* (TO), —, JF926523, —, —; *Pseudoclitocybe expallens* (Pers.) M.Moser, ITALY, *HG2286* (TO), —, JF926525, —, —; *Pseudoclitocybe sp.*, U.S.A., *RHP12643* (TENN:061314), —, KJ417217, —, KJ424392; *Pseudoclitopilus rhodoleucus* (Sacc.) Vizzini & Contu, SWEDEN, *TK03/203* (GB:0110967), —, KJ417218, —, KJ424393; *Pseudoclitopilus rhodoleucus*, SWEDEN, *TK02/061* (GB), —, KJ417243, —, —; *Pseudotricholoma metapodium* (Fr.) Sánchez-García & Matheny (*Porpoloma metapodium* (Fr.) Singer), UNITED KINGDOM, *AH22102006* (K), KJ417308, KJ417219, KJ417271, KJ424394; *Pseudotricholoma metapodium* (*Porpoloma metapodium*), SWEDEN, *LAS06/134* (GB:066422)*, KJ417309, KJ417220, —, KJ424395; *Pseudotricholoma metapodium* (*Porpoloma metapodium*), NORWAY, *EL155/09* (GB), KJ417310, —, —, KJ424396; *Pseudotricholoma umbrosum* (A.H.Sm. & M.B.Walters) Sánchez-García & Matheny (*Porpoloma umbrosum* (A.H.Sm. & M.B.Walters) Singer), U.S.A., *TFB5481* (TENN:052643), KJ417311, KJ417221, —, —; *Pseudotricholoma umbrosum* (*Porpoloma umbrosum*), U.S.A., *REH4796* (NYBG:505218), KJ417312, KJ417222, —, KJ424397; *Pseudotricholoma umbrosum* (*Porpoloma umbrosum*), U.S.A., *TJB7179* (CORT), KJ417313, KJ417223, —, —; *Pseudotricholoma umbrosum* (*Porpoloma umbrosum*), CANADA, *Wehmeyer-640* (MICH:012331)*, KJ417314, —, —, —; *Pseudotricholoma umbrosum* (*Porpoloma umbrosum*), U.S.A., *PBM3267* (TENN:064489), KJ417315, KJ417224, —, KJ424398; *Rhodocybe mundula* (Lasch) Singer, U.S.A., *TJB7599* (CORT), —, AY700182, DQ089017, —; *Singerocybe adirondackensis* (Peck) Sánchez-García & Matheny (*Clitocybe adirondackensis* (Peck) Sacc.), U.S.A., *PBM3320* (TENN:064660), —, HQ728530, HQ728531, HQ728532; *Tephroclybe anthracophila* (Lasch) P.D.Orton, AUSTRALIA, *JT31970* (—), —, KJ417225, —, —; *Tephroclybe boudieri* (Kühner & Romagn.) Derbsch, —, *BS196/84* (—), —, DQ825430, DQ825433, DQ825411; *Termitomyces microcarpus* (Berk. & Broome) R.Heim, —, *PRU3900* (—), —, AF042587, DQ851581, —; *Termitomyces* sp., SOUTH AFRICA, *ZA164* (—), —, DQ110875, DQ092922, DQ437070; *Tricholoma elegans* G.Stev., NEW ZEALAND, *PBM3142* (TENN:063711), KJ417316, KJ417226, —, —; *Tricholoma equestre* (L.) P.Kumm, —, —, —, —, HM590872, —, —, —; *Tricholoma flavovirens* (Alb. & Schwein.) S.Lundell, PUERTO RICO, —, —, —, —, EU186310, —, —, —; *Tricholoma inamoenum* (Fr.) Gillet, —, —, —, —, AY293215, AY293161, —; *Tricholoma matsutake* (S.Ito & S.Imai) Singer, —, —, —, —, AB188557, U62964, U62538, —; *Tricholoma myomyces* (Pers.) J.E.Lange, —, *KMS589* (—), DQ825428, U76459, DQ367422, DQ367436; *Tricholoma palustre* A.H.Sm., U.S.A., *PBM2494* (CUW), AY700197, AY757267, DQ484055; *Tricholoma saponaceum* (Fr.) P.Kumm., U.S.A., *PBM2514* (CUW), DQ494700, AY647209, AY654883, —; *Tricholoma sp.*, NEW ZEALAND, *PBM3141* (TENN:063710), KJ417317, KJ417227, KJ417272, —; *Tricholoma sp.*, NEW ZEALAND, *PBM3085* (TENN:063664), KJ417318, KJ417228, KJ417273, —; *Tricholoma sp.*, NEW ZEALAND, *RHP13062* (TENN:061065), —, KJ417229, KJ417274, —; *Tricholoma sp.*, —, *SAR1290* (—), —, AF042592, AF287839, —; *Tricholoma subresplendens* (Murrill) Murrill, U.S.A., *SAT1027901* (TENN:065679), KJ417319, KJ417230, KJ417275, —; *Tricholoma viridiolivaceum* G.Stev., NEW ZEALAND, *PBM3093* (TENN:063670), JF706316, JF706317, JF706318, JF706319; *Tricholomella constricta* (Fr.) Zerova ex Kalamees, —, *HC84-75* (—), —, AF223188, DQ825434, DQ825412; *Undet. gray scaly*, U.S.A., *ECV4038* (TENN:064609), KJ417320, KJ417231, KJ417276, KJ424399; *Undet. small white*, U.S.A., *MBP06VII09* (TENN:064359), KJ417321, KJ417232, KJ417277, KJ424400; *Undet. small white*, U.S.A., *MSG144* (TENN:068777), KJ417322, KJ417233, —, KJ424402