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A phylogeny for North American *Mallocybe* (*Inocybaceae*) and taxonomic revision of eastern North American taxa

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Abstract: A multigene phylogenetic assessment of North American species of *Mallocybe* is presented based on analyses of *rpb1*, *rpb2*, ITS, and 28S rDNA nucleotide data. This framework enables a systematic revision of the genus for 16 eastern North American species and captures taxonomic and phylogenetic diversity in a global context. A grade of two unusual and poorly known North American species stems from the most recent common ancestor of the genus that gives rise to three core subgroups named here as clades Unicolores, Nothosperma, and Mallocybe. The grade of taxa includes the poorly known *Lepista praevillosa* from Florida and a new species from the southern Appalachians, *M. montana*, both of which appear to be narrow-range endemics. Clade Nothosperma is characterized by Australian and New Zealand species, whereas clade Unicolores is composed of six species from eastern North America and East Asia. Clade Mallocybe is dominated by numerous north temperate taxa and constitutes the sister group to clade Nothosperma. These major clades are distinguished by a combination of phylogeny, morphology, geographic distribution, and ecology. In addition, four North American species are described as new: *M. leucothrix, M. luteobasis, M. montana*, and *M. tomentella*. Several names originating in North America, long ignored or misunderstood in the literature, are revitalized and established by type comparisons and modern reference material collected from or near type localities. In addition, 11 species were subjected to mass spectrometry muscarine assays, none of which contained detectable amounts of muscarine except for two: *M. sabulosa* and *M. praevillosa*. This confirms a diffuse phylogenetic distribution of muscarine within the genus. Taxonomic descriptions are presented for 16 species, several synonymies proposed, and four new combinations made. A key to species of eastern North American *Mallocybe* is presented, along with illustrations of important diagnostic features.

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INTRODUCTION

The genus *Mallocybe*, one of seven genera of *Inocybaceae*, was recently elevated to generic rank by Matheny *et al*. (2020). Species of *Mallocybe* are distinguished from other genera of *Inocybaceae* by a combination of the presence of necropigmented basida (basidia that collapse and fill with ochraceus or brownish yellow pigment), smooth basidiospores, a typically dark reaction to alkali solutions on the pileus surface, non-reddening context; cheilocystidia arising as terminal elements of hymenophoral trama that are, in most species, less than 50 μm long; and the absence of pleurocystidia. Previous work has shown that the toxin muscarine is present in some species but not detectable in others (Kosentka *et al*. 2013).

In the field many species of *Mallocybe* typically feature adnate or subdecurrent lamellae, a squamulose or tomentose pileus surface, and a short stipe relative to the width of the pileus. Coloration of most species is typically some shade of brown, yellowish brown, or brownish yellow. However, several exceptions to this suite of features have been noted (*e.g.*, Cripps *et al*. 2010, Matheny & Bougher 2017). The genus is a strongly supported monophyletic group and is widely distributed across the globe occurring in Africa, Asia, Australia, Europe, New Guinea, New Zealand, and North America (Matheny *et al.* 2020). New species of *Mallocybe* continue to be described from Africa, Asia, and Europe (Crous *et al*. 2020, Saba & Khalid 2020, Aignon *et al.* 2021, Mao *et al*. 2022, Hu *et al*. 2023), and new combinations continue to be made into the genus (Saba *et al*. 2020) raising the number of species to about 65 worldwide. *Mallocybe* is most diverse at temperate latitudes forming ectomycorrhizal associations with a number of different plant families (*e.g*., Daskalopoulos *et al.* 2021), and some species are important constituents of alpine and arctic systems (Favre 1955, Kühner 1988, Cripps *et al*. 2010). A few species have been described or documented from the Old-World tropics (Horak 1980, Matheny *et al*. 2009, Horak *et al*. 2015, Matheny & Bougher 2017, Aignon *et al*. 2021), but none have yet been described from the Neotropics and southern South America.

European *Mallocybe* have generally been recognized as a small group containing anywhere from 5 to 25 species. An early attempt to classify species attributable to *Mallocybe* was done by Heim (1931), who proposed "Stirpe dulcamara" in *Inocybe* sect. *Dulcamarae*. The stirps contained five species. Singer (1986) placed European species of *Mallocybe* in *Inocybe* sect. *Depauperatae* typified by *Inocybe delecta* and recognized five species in the group. Alessio & Rebaudengo (1980) treated 12 taxa, including several infraspecific varieties and forms.

Kuyper (1986) established *Inocybe* subg. *Mallocybe* in the sense used here but did not include a taxonomic treatment for the ten estimated species he accepted at that time from the northern hemisphere. Kühner (1988) described ten new species in *Inocybe* sect. *Dulcamarae* from alpine zones in central Europe, which doubled the number of known species in the group. Stangl (1989) recognized eight species in *Inocybe* subg. *Mallocybe* from central Europe, and Kobayashi (2002) recognized five including consideration of samples from East Asia. Jacobbson & Larsson (2012) treated 14 species of *Inocybe* subg. *Mallocybe* in northern Europe. Bon (1997), however, referenced 31 taxa (among 23 species) in his keys, and Ludwig (2017) recognized 25. In North America no extensive revision has been made of species of *Mallocybe*, but Cripps *et al*. (2010) documented six intercontinental Euro-American species from arctic-alpine settings in western North America. Bessette & Fatto (1998) attributed a new species they described from New York, *I. angustispora* (see also Bessette *et al*. 2001), to an alliance with what would be recognized as *Mallocybe* today. However, Matheny & Ammirati (2003) showed that *I. angustispora* was a later synonym of *Cortinarius aureifolius*, an atypically smooth-spored species of *Cortinarius*. A few new taxa were documented or described from the Old-World tropics as cited above, and Matheny & Bougher (2017) added five new species to *Inocybe* subgenus *Mallocybe* from Australian temperate and tropical regions. Horak (2018) included a description of a new species, *I. callichroa*, from New Zealand, which superficially resembles other species of *Mallocybe*. Lastly, five new species were recently described from China (Mao *et al.* 2022, Hu *et al.* 2023). Globally, about 65 species of *Mallocybe* can now be recognized since Matheny (2009) initially estimated *ca*. 30 species worldwide in the group.

Mallocybe has long been recovered as a single clade based on molecular phylogenetic analyses. Matheny (2005) sampled 12 species-level lineages of *Inocybe* subg. *Mallocybe* based on phylogenetic analyses of three gene regions, and Matheny *et al.* (2009) followed up on that study by including 25 species of *Inocybe* subg. *Mallocybe* worldwide. Cripps *et al.* (2010) reconstructed an rDNA phylogeny that sampled 13 species-level lineages of *Inocybe* subg. *Mallocybe*, and Ryberg *et al.* (2010) included about a dozen lineages based on analyses of nuclear and mitochondrial rDNA. All these treatments recovered *Mallocybe* as a strongly supported monophyletic group. However, Bandini *et al.* (2018) recently excluded *Inocybe stenospora* from *Mallocybe*, where it had been previously proposed (Stangl 1986), based on molecular phylogenetic evidence. Unfortunately, phylogenetic studies have varied on identification of the sister group to *Mallocybe* and have lacked strong evidence in favor of any sister group arrangement (Matheny 2005, Matheny *et al.* 2009, 2012, 2020, Alvarado *et al.* 2010, Ryberg *et al.* 2010). *Auritella*, *Tubariomyces*, and *Inosperma*, or some configuration of these taxa, have all been recovered as potential sister groups to *Mallocybe* but without strong support. In addition, no prior works have proposed any infrageneric molecular systematic treatment, although Hu *et al*. (2023) recovered three major clades within the genus (identified as clades A, B, and C) with an infrageneric multigene phylogeny based on combined analysis of ITS, 28S, and *rpb2* sequences.

Our objectives here are to: (1) present a global molecular phylogenetic assessment of *Mallocybe* based on *rpb1*, *rpb2*, ITS, and 28S data; (2) focus on identification of major lineages within *Mallocybe* incorporating North American taxa; (3) assay relative abundance of muscarine in North American samples; and (4) revise and document species that occur in eastern North America relative to those elsewhere. In addition, we also highlight the uniqueness of several lineages documented from western North America. To stabilize application of names based on old or poorly preserved type collections, we collected fresh specimens at or near type localities of species attributable to *Mallocybe* described by Peck, Murrill, and others in New York and Florida. Taxonomic descriptions of 16 species of *Mallocybe* from eastern North America are presented, including description of four new species, clade designations within the genus, a taxonomic key, and illustrations of diagnostic microscopic features and photographs of basidiomes. The work also provides a framework to revise *Mallocybe* species from western North America and elsewhere in the future.

MATERIALS AND METHODS

Morphology

Notes on fresh samples from the field were aided by reference to the color guides Munsell Soil Color Chart (1954) [*e.g.*, 10YR 7/4), Ridgway (1912) [*e.g.*, Dresden Brown], and Kornerup & Wanscher (1967) [*e.g.*, 6E8]. "L" refers to the number of lamellae that reach the stipe. PDAB or *p*-dimethylaminobenzaldehyde (Matheny *et al.* 2013) and 5 % KOH (Kuyper 1986) were used to induce any microchemical reactions. After observation, fresh specimens were air-dried in a food dehydrator. Collections were accessioned at the Herbarium of the University of Tennessee (TENN) and the University of Washington Herbarium (WTU) or maintained in the private herbarium of L.V. Kudzma. Loans of specimens were obtained from the Royal Botanic Garden Edinburgh (E), the Fungarium of the Florida Museum of Natural

History (FLAS), the Herbarium of the University of Helsinki (H), the New York Botanical Garden (NY), and WTU. Herbarium codes follow Thiers [continuously updated]. Hand sections made with a razor and lamellar fragments were mounted in 5 % KOH to examine anatomical features such as the pileipellis, cheilocystidia, basidia, and basidiospore morphology and size (terminology following Kuyper 1986). Observations and measurements were made with a Nikon i80 Eclipse light microscope and Elements D software (Nikon Instruments Inc, Melville, New York). Outlier measurements constituting < 5 % of observations are indicated in parentheses, and mean values are italicized. Q-values are ratios of spore length to spore width and were calculated for each spore and then averaged. The total number of spores measured (x) and the number of specimens sampled (y) are indicated as x/y. Type collections were examined from FLAS, H, NY, TENN, and WTU.

DNA extractions and sequencing

Between 20 and 30 mg of dried pileal fragments were ground with liquid N and a pinch of sterile sand. In most cases, procedures for DNA extraction followed Judge *et al.* (2010) or Matheny *et al.* (2002). Recently collected samples underwent a rapid alkaline DNA extraction and PCR amplification as described by Matheny & Swenie (2018). ITS amplicons were amplified and sequenced using primers ITS1F and ITS4 (White *et al.* 1990). 28S amplicons were amplified using LR0R and LR7 and sequenced with these primers and LR5 (Vilgalys & Hesler 1990, Cubeta *et al.* 1991). The most variable region of *rpb1* was sequenced between conserved domains A and C using primers gAf (Stiller & Hall 1997) and fCr (Matheny *et al.* 2002). Both primers were used for sequencing along with internal primers int2F, int2.1F, and int2.1R (Frøslev *et al.* 2005). The most variable region of *rpb2* was amplified and sequenced between conserved domains 6 and 7 using primers b6F and b7.1R (Matheny 2005). For materials gathered in New Jersey, PCR procedures and sequencing followed Matheny & Kudzma (2019). For materials older than 30 years, the ITS spacers were amplified and sequenced separately following Sánchez-García *et al*. (2014). Chromatograms were constructed and edited in Sequencer v. 5.0.1 (Gene Codes Corp., Ann Arbor, Michigan). New sequences were submitted to GenBank and are shown in bold font in Table 1.

Taxon sampling

A list of taxa included in the phylogenetic analyses is presented in Table 1, including specimen-voucher number (where relevant), herbarium designation (if known), geographic origin, ecology (if known, including plant host information and edaphic factors), and GenBank accession numbers. DNA sequences of *rpb1*, *rpb2*, ITS, and 28S were used primarily from the following studies: Matheny *et al.* (2002, 2009), Matheny (2005), Ryberg *et al.* (2008), Larsson *et al.* (2009), Alvarado *et al.* (2010), Cripps *et al.* (2010), Ryberg *et al.* (2010), Vauras & Larsson (2011), Kosentka *et al.* (2013), Ariyawansa *et al.* (2015), Horak *et al.* (2015), Matheny & Bougher (2017), Crous *et al.* (2020), Aignon *et al.* (2021), Saba & Khalid (2020), Mao *et al.* (2022), and Hu *et al.* (2023). Blastn searches of sequences in GenBank that resulted in high similarity also led to inclusion of several *ad hoc* sequences (*e.g.*, Roy *et al.* 2009, Meza-Meneses *et al.* 2016), environmental sequences, and unpublished sequences. These are also included in Table 1.

Phylogenetic analyses

DNA sequences were aligned using ClustalX v. 2.0.9 (Larkin *et al.* 2007) and viewed and manually adjusted as nexus files in AliView v. 1.11 (Larson 2014). Outgroup sequences included *Auritella brunnescens*, *Crepidotus applanatus*, *Inosperma aff*. *mutatum*, *Inosperma rimosoides*, and *Tubariomyces* sp. following Matheny *et al.* (2020). Intron regions were identified following Matheny *et al.* (2002) and Matheny (2005). Data were partitioned by rDNA gene regions combined, 1st, 2nd, and 3rd codon positions separately, and RNA polymerase II intronic regions combined (Matheny *et al.* 2002, Matheny 2005). Because of their high divergence, sequences of ITS, intron-1 and intron-4 of *rpb1*, and intron-4 of *rpb2* were excluded from outgroups to facilitate alignments of the ingroup.

Three unlinked gene alignments were analyzed first. This included *rpb1* (conserved domains A to C), *rpb2* (conserved domains 6 to 7), and the ITS and 28S nuclear rDNA region combined. Maximum likelihood (ML) analyses were conducted in RAxML v. 8.2.9 (Stamatakis 2014) with 1 000 rapid bootstraps. Models of evolution used in ML analyses followed recommendations in the RAxML user manual (Stamatakis 2014), thus we applied a GTRCAT approximation to bootstrap trees, which was recommended for data sets with > 50 taxa. Any strongly intergenic conflicts (> 70 % bootstrap for incongruent groups) were noted before consideration of a final concatenated alignment.

We then assembled a 4-locus concatenated supermatrix partitioned into five-character sets (rDNA, the three codon positions separately, and RNA polymerase II introns combined) and conducted ML (see above) and Bayesian inference (BI) analyses in MrBayes v. 3.2.6 (Ronquist *et al.* 2012). Models used for each partition followed Matheny (2005). For all BI analyses, convergence diagnostics were examined to evaluate proper execution. These included examination of the standard deviation of split frequencies (reaching < 1.0 to ensure run convergence), potential scale reduction factors (PSRF) near 1.0, and effective samples size (ESS) > 100 for all parameters. Burn-in values of 25 % were applied, where tenable, or determined based on run convergence. We also performed a partitioned analysis of the 4-locus dataset in IQ-TREE v. 1.6.12 with 1 000 ultrafast (UF) bootstraps and the SH-aLRT test (SH) (Nguyen *et al.* 2015, Chernomor *et al.* 2016, Hoang *et al.* 2018). Any ML bootstrap proportions > 70 % were considered as evidence for strong support. Strong support was also noted if a clade received SH-aLRT > 80 % and UF bootstraps > 95 %.

The four alignments (*rpb1*, *rpb2*, nuc rDNA, 4-locus supermatrix), ML bipartition files including branch values and gene partitioning schemes, have been archived at FigShare (doi: 10.6084/m9.figshare.23604333).

Muscarine bioassays

Eleven samples of *Mallocybe* were subjected to mass spectrometry analysis for detection of muscarine, an alkaloid that stimulates the parasympathetic nervous system in animals (Kosentka *et al.* 2013). The samples included *M. heimii* (JV14932F), *M. isabellina* (NLB800/TENN-F-066800), *M. leucoblema* (PBM1539/WTU), *M. luteobasis sp. nov*. (PBM4437/TENN-F-075309), *M. montana sp. nov*. (PBM3872/TENN-F-067500/type), *M. myriadophylla* (JV5968F/WTU), *M. praevillosa comb. nov*. (FLAS-F-61523), *M. sabulosa* (NLB901/

TENN-F-066809), *M. squamosodisca comb. nov*. (PBM4621/TENN-F-075791), *M. subtomentosa comb. nov*. (PBM3910/TENN-F068440), and *Mallocybe* sp. 5 (PBM1922/WTU). These species were selected for this analysis because they are widely distributed across the *Mallocybe* phyogeny. The following samples were used as negative controls: *Psilocybe caerulipes* (DG21081110/TENN-F-076505, DG2108093/TENN-F-076504), *Inocybe picrosma* (RHM102910/TENN-F-066038), and *Inosperma mucidiolens* (PBM4323/TENN-F-074905) (Kosentka *et al.* 2013, Robbers *et al.* 1964, Strauss *et al.* 2022). Three positive controls were also used: *Inocybe occulta* (RAS920/TENN-F-76509), *I. aff. geophylla* (PBM4697/TENN-F-075834), and *Inosperma aff. maculatum* (PBM4522/TENN-F-075309). All three positive controls belong phylogenetically to inclusive groups known to contain muscarinic species (Kosentka *et al.* 2013).

The muscarine analyses were performed at the Biological Small Molecule Mass Spectrometry Core at the University of Tennessee Knoxville (RRID: SCR_021368). The analytical methodology was adapted from a previous study (Kosentka *et al*. 2013). Briefly, the ground samples ranging from 4–40 mg were placed into Eppendorf tubes, vortexed for 1 min, and extracted with 300 μL 4:1 Methanol:H_2O at -80 °C for 20 min. All solvents used were HPLC grade. The resulting suspension was centrifuged (16 100 rcf) for five min to remove particulates. The resulting supernatants were isolated, and an aliquot was diluted by a factor of 2 000. The diluted supernatant was stored at 4 °C until LCMS analysis in UltiMate 3 000 RS autosampler (Dionex, Sunnyvale, California).

An injection volume of 10 μL was used with reversed-phase chromatography utilizing a Phenomenex Gemini 5 μm C_{18} column (110 Å, 150 mm × 2 mm; Torrance, California). Ultra-high-performance liquid chromatography (UHPLC) was performed utilizing an UltiMate 3 000 pump. Separations were performed with a column temperature of 25 °C and a flow rate of 150 μL/min. The separation was carried out using water (solvent A) and acetonitrile (ACN) (solvent B) for 18 min creating a gradient elution profile as previously reported (Kosentka *et al*. 2013). The eluent was then introduced into a Thermo Scientific Q Exactive Orbitrap MS (Thermo Scientific, San Jose, California) for ion detection.

Electrospray ionization in positive ionization mode was used as described by Kosentka *et al*. (2013). Muscarine was detected using parallel reaction monitoring (PRM) for the unique product *m/z* 56.9857 ± 5 ppm at the collision energy *e*V 85. A 2.0 μM solution of muscarine was used as a standard (Fisher Scientific, Waltham, Massachusetts, USA). The muscarine standard was eluted from the column at a retention time of 1.9 min. Instrumental raw data files were converted to mzML format (Chambers *et al.* 2012). Peak areas were integrated from extracted ion chromatograms in the open-source software package El-MAVEN (Agrawal *et al*. 2019). Normalized peak areas refer to area count per mg or peak area per mg since the area after blank subtraction was sample mass normalized. Samples detected with abundance less than 2.5 times of the average abundance in the blank control were considered as below the limit of detection. Although the normalized peak area does not represent absolute concentration, it corresponds to the relative abundance in the samples.

RESULTS

DNA alignments

One hundred and ninety-seven new sequences (77 ITS, 53 28S, 33 *rpb1*, 34 *rpb2*) were produced. The *rpb1* dataset contained 55 taxa and 1 547 sites. The *rbp2* dataset contained 98 taxa and 774 sites. The rDNA dataset (ITS1-5.8S-ITS2+28S) included 304 taxa and 2 504 sites. The combined 4-gene region supermatrix included 304 taxa and 4 823 sites. Convergence diagnostics failed for the BI analysis of the 4-gene region supermatrix and resulted in spurious placements of several taxa represented by (partial) ITS data only. For this reason, we report phylogenetic results from the RAxML and IQ-TREE analyses only.

Murrill's *Inocybe* (*Lepista*) *praevillosa* is sister to *Mallocybe*

Both *rpb1* and *rpb2* gene trees (Supplementary Figs S1, S2, respectively) recovered *Mallocybe* as a strongly supported monophyletic group. Both trees indicated strong support for a grade of *Inocybe praevillosa*, originally described as *Lepista praevillosa* by W.A. Murrill, and the newly named *Mallocybe montana* giving rise to the remainder of *Mallocybe* described or documented from Asia, Australasia, Eurasia, and North America. Considerably denser taxon sampling of *Inocybaceae* and outgroups of *Crepidotaceae* and *Tubariaceae* reinforce these strongly supported results for both genes (unpubl. data). Both gene trees also recovered three main clades within the genus as previously shown by Hu *et al.* (2023). These three clades have yet to be named, but here we propose them informally as clades Unicolores, Nothosperma, and Mallocybe, and suggest they may be equivalent to potential subgenera depending on forthcoming revisions of European *Mallocybe.*

Both *rpb1* and *rpb2* recovered similar overarching topologies with respect to placement of *Inocybe* (*Lepista*) *praevillosa* and *M. montana* in position to the rest of *Mallocybe*. However, *rpb1* anchored clades Nothosperma and Unicolores as a monophyletic group with strong support, whereas *rpb2* recovered clades Nothosperma and Mallocybe as sister groups but with weak support. The rDNA-only tree did not recover *Mallocybe* as monophyletic due to the clustering of *I.* (*Lepista*) *praevillosa* among the outgroups, but this result was weakly supported. Clade Nothosperma was recovered as monophyletic with moderate support including a *Nothofagus*-associated sample from New Zealand sister to all other Australasian taxa. However, clade Mallocybe was found to be paraphyletic within which clade Unicolores and *M. montana* were placed.

A notable source of gene conflict was observed between the rDNA and *rpb2* gene trees. This concerned the placement of the recently described species *M. africana* (Aignon *et al.* 2021). Initial analyses of our rDNA and *rpb2* alignments (data not shown) placed it sister to *M. errata* with strong support (rDNA), or sister to the rest of *Mallocybe* with weak support (*rpb2*). Two *rpb2* sequences of *M. africana* from the same sample (MR00385) are available in GenBank, but these differ by 4.5 % percent identity. Because of concerns regarding gene duplication and paralogs, we excluded *M. africana* from further downstream analyses. A close relationship between *M. africana* (indicated as "*I. microdulcamara nom. prov.*") and *M. errata* and *M. heimii* was previously recovered by Matheny *et al.* (2009). Until new and additional *rpb1* and *rpb2* sequences can be produced, we regard *M. africana* as *incertae sedis* within the genus.

Table 1. Specimen data and DNA sequences analyzed for this study. New DNA sequences are in bold.

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
M. africana	96012 (PC0088767)	Zambia	Miombo woodland	**MN178510**	**MN178542**	—	—
	96204 (PC0088756)	Zambia	Miombo woodland	**MN178511**	EU569871	—	—
M. agardhii	EL88-04 (GB)	Sweden	*Salix*, calcareous	FJ904123	FJ904123	—	—
	JV7485F (WTU)	Finland	*Betula*, *Quercus*, gravel	—	AY380365	AY351792	AY333772
	JV13740 (WTU)	Finland	*Salix*, *Betula*, wet depression	—	AY380366	AY337362	AY337362
	AB980912 (GB)	Denmark	*Salix*	HM209790	HM209790	—	—
M. arenaria	EL250-08 (GB)	France	—	FN550937	FN550937	—	—
M. arthrocystis	BJ900815 (GB)	Sweden	*Salix*	—	GU980655	—	—
	CLC1141 (MONT)	Colorado	*Salix*	GU980653	GU980653	—	—
	CLC1356 (MONT)	Colorado	*Salix*	GU980649	GU980649	—	—
	CLC1357 (MONT)	Colorado	*Salix*	—	GU980652	—	—
	CLC1688 (MONT)	Colorado	*Salix*	GU980651	GU980651	—	—
	CLC1752 (MONT)	Colorado	*Salix*	GU980650	GU980650	—	—
	EL62-07 (GB)	Sweden	*Salix*	FN550941	FN550941	—	—
	PBM2397 (WTU)	Norway	*Picea*, *Betula*, *Salix*, eutrophic spruce forest	—	AY380394	AY351817	AY337402
	SJ06-011	Sweden	*Salix*	GU980654	GU980654	—	—
M. aurantiidisca	2020ZD01 (MHKMU)	Zhejiang	Mixed broad-leaved	OM179937	—	—	—
	NJ3109 (MHKMU)	Zhejiang	*Fagaceae* dominant	OM179935	OM138834	—	OM835751
	NJ3396 (MHKMU, **holotype**)	Zhejiang	*Pinus* dominant	OM179936	OM138835	—	OM835752
M. crassivelata	AH29788	Spain	*Castanea* forest	MN536810	—	—	—
	AH46622	Spain	*Quercus*, *Pinus*	MN536811	—	—	—
	MCVE 21499	Italy	*Picea* forest	MN536813	—	—	—
	MCVE 29561 (**holotype**)	Slovenia	*Fagus*	MN536812	MN537138	—	—
M. delecta	JV21393	Finland	*Pinus*, *Betula*, *Salix*, *Quercus*	OQ448534	OQ448534	—	—
	P. Karsten 1636 (H, **holotype**)	Finland	—	OQ448533	—	—	—
M. depressa	FM1300 (BJTC)	Shanxi	*Pinus* dominant	OM801895	OM801900	—	OM780099
	FM1695 (BJTC, **holotype)**	Shanxi	*Pinus* dominant	OM801899	OM801904	—	OM780100
M. errata	DED8022 (SFSU; ZT13034)	Thailand	*Pinus*, *Dipterocarpus*	EU569844	EU569844	—	—
	ZT9238	Thailand	*Pinus*, *Dipterocarpus*	—	EU569845	—	—
	ZT10108 (**type**)	Thailand	*Pinus*	—	GQ892935	—	—
M. fibrillosa (=*I. dulcamara sensu* Cripps *et al*. 2010)	CLC1131 (MONT)	Montana	*Salix*	GU980639	GU980639	—	—
	CLC1160 (MONT)	Montana	*Salix*	GU980642	—	—	—
	CLC1241 (MONT)	Colorado	*Salix*	GU980637	GU980637	—	—
	CLC1295 (MONT)	Colorado	*Salix*	GU980636	GU980636	—	—
	CLC1333 (MONT)	Colorado	*Salix*	GU980635	GU980635	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	CLC1364 (MONT)	Colorado	*Salix*	GU980641	—	—	—
	CLC1408 (MONT)	Colorado	*Salix*	GU980647	GU980647	—	—
	CLC1421 (MONT)	Colorado	*Salix*	GU980646	GU980646	—	—
	CLC1458 (MONT)	Colorado	*Salix*?	GU980638	GU980638	—	—
	CLC1581 (MONT)	Wyoming	*Salix*	GU980634	GU980634	—	—
	CLC1664 (MONT)	Colorado	*Dryas*?	GU980640	GU980640	—	—
	CLC1841 (MONT)	Colorado	*Salix*	GU980644	GU980644	—	—
	EL33-05 (GB)	Norway	*Salix*	GU980645	GU980645	—	—
	EL59-05 (GB)	Norway	*Betula*	GU980643	GU980643	—	—
	LVK14371	Maine	Mixed woods	**MN178498**	**MN178526**	**MN203504**	**MN203517**
	LVK14390	Maine	—	**MN178499**	**MN178527**	—	**MN203518**
	LVK15242	Maine	*Picea*, *Betula*	**MN178500**	—	—	—
	LVK22085	Maine	Mixed woods	**OP917925**	**OP918013**	—	—
	PBM2350 (WTU)	Washington	Conifers	—	EU600834	EU600832	EU600833
	REH10168 (TENN-F-073177)	New York	*Abies*, *Picea*, *Betula*, *Thuja*, *Pinus*	MH024850	MH024886	MK415442	MH577503
	2030506-001 (UBC F19167 as *I. gymnocarpa*)	British Columbia	—	HQ604785	HQ604785	—	—
M. fulviceps	DPL13914 (TENN-F-076539)	Louisiana	*Quercus nigra*	**OQ707213**	—	—	—
	MES-3773 (FLAS-F-66615)	Florida	*Quercus*, karst	**MZ404927**	—	—	—
	MES-2993 (FLAS-F-66574)	Florida	*Quercus*, karst	**MT415969**	—	—	—
	PBM4533 (TENN-F-075556)	Florida	*Quercus*, *Pinus*, karst	**MZ404928**	**MZ375430**	—	—
	PBM4542 (TENN-F-75565)	Florida	*Pinus*, *Quercus*, karst	**MZ404929**	**MZ375431**	**MZ404598**	**MZ405010**
	PBM4715 (TENN-F-F077389)	Florida	*Pinus*, *Quercus*, karst	**OQ208757**	—	—	—
	PBM4718 (TENN-F-077392)	Florida	*Pinus*, *Quercus*, karst	**OQ208758**	—	—	—
	PBM4722 (TENN-F-077396)	Florida	*Pinus*, *Quercus*, karst	**OQ208759**	—	—	—
	PBM4726 (TENN-F-077450)	Florida	*Carpinus*, *Quercus*, karst	**OQ208760**	—	—	—
M. fulvipes (subclade B *sensu* Cripps *et al*. 2010)	CLC1490 (MONT)	Colorado	*Salix*	GU980612	—	—	—
	CLC1566 (MONT)	Wyoming	*Salix*	GU980606	GU980606	—	—
	CLC1580 (MONT)	Wyoming	*Salix*	GU980608	GU980608	—	—
	CLC1844 (MONT)	Colorado	*Salix*	GU980611	GU980611	—	—
	EL83-07 (GB)	Sweden	*Salix*	FN550935	FN550935	—	—
	SJ84030 (GB – same field no. as *I. granulosa*)	Sweden	*Salix*	GU980609	GU980609	—	—
M. fuscomarginata	BJ890718 (GB)	Sweden	*Salix*	GU980656	GU980656	—	—
	EL109-06 (GB)	Sweden	*Salix*	FN550940	FN550940	—	—
	EL77-07 (GB)	Sweden	*Dryas*	GU980657	GU980657	—	—
M. granulosa	EL138-09 (GB, **type**)	Sweden	*Salix*, likely calcareous ground	KR029727	KR029727	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	Kuhner70-147 (as *I. squarrosoannulata*)	—	—	GU980610	GU980610	—	—
	SJ11008	Sweden	*Salix*	KR029726	KR029726	—	—
	SJ12916	Norway	—	KR029728	KR029728	—	—
	SJ12017	Norway	*Salix*	KR029729	KR029729	—	—
	SJ84030 (as *I. squarrosoannulata*)	Sweden	*Salix*	KR029725	KR029725	—	—
M. gymnocarpa	SJ980707 (GB)	Sweden	—	AM882866	AM882866	—	—
	16413	Italy	—	JF908161	—	—	—
	EL78-04 (GB; as "dulcamara")	Sweden	—	AM882865	—	—	—
M. heimii	JV14932 (WTU)	Italy	*Pinus*, sandy soil	—	AY380379	AY351804	AY337380
	G0256 (NL-0874)	Hungary	—	—	MK278231	—	—
M. isabellina	NLB420 (PERTH 08072442)	Western Australia	*Eucalyptus*, lawn	KP171139	KP170917	**MN203505**	KJ811583
	NLB836 (PERTH 08318441)	Western Australia	*Agonis*, *Spyridium*, *Acacia*, *Melalecua*, heath-scrub	KP171141	KP170920	**MN203506**	KJ811586
	E8290 (PERTH 07699255, **type**)	Western Australia	*Eucalyptus*, lawn	KP171137	KP170915	—	KJ811581
	NLB405 (PERTH 08096635)	Western Australia	Grassy parkland	KP171138	KP170916	—	KJ811582
	PBM3610 (PERTH 08319766)	Western Australia	*Eucalyptus*, *Corymbia*, Jarrah-Marri forest	—	KP170919	—	KJ811585
	E3730 (PERTH 07712758)	Western Australia	Sand dunes	**MN178501**	**MN178528**	—	MH618212
	NLB836 (PERTH 08318441)	Western Australia	*Agonis*, *Spyridium*, *Acacia*, *Melaleuca*, heath-scrub	KP171141	KP170920	—	KJ811586
	NLB800 (PERTH 08318832)	Western Australia	*Eucalyptus*, *Corymbia*, burned Jarrah-Marri forest	KP171140	KP170918	—	KJ811584
M. isabellina aff.	NLB491 (PERTH 08073287)	Western Australia	*Eucalyptus*, parkland	KP171142	KP170921	—	KJ811587
	PBM2207 / E7056 (TENN-F-066822)	Western Australia	*Corymbia*, lawn	—	AY380381	AY351806	AY337382
	PBM3595 (TENN-F-066498)	Western Australia	*Eucalyptus*, *Corymbia*, burned Jarrah-Marri forest	KP171143	KP170922	—	KP170922
M. latifolia	Nr. 3908 (M-0216716), EL3 (**type** *M. acystidiata*)	Germany	*Picea*, calcareous	**OR139041**	—	—	—
	Isolate 136	Shaanxi	*Populus simonsii* ECM root	LC013759	—	—	—
	Isolate 1969	Shaanxi	*Populus simonsii* ECM root	LC013761	—	—	—
	LVK22088	Maine	Mixed woods	**OP918037**	**OP918067**	**OQ870543**	—
	LVK22089	Maine	Mixed woods	**OP918038**	—	**OQ870544**	**OP924514**
	MO364156	Arizona	*Populus*, Cypress	MN177633	—	—	—
	M-0216738 (**type** *M. latifolia*)	Germany	*Betula*, *Picea*, calcareous	OQ976965	—	—	—
	PBM4535 (TENN-F-075558)	Florida	*Pinus*, *Quercus*	**MZ404930**	**MZ375432**	**MZ404599**	—
	PBM4537 (TENN-F-075560)	Florida	*Quercus*, *Pinus*, *Carpinus*	**MZ404931**	**MZ375433**	**MZ404600**	**MZ405011**
M. latispora	EL212-06 (GB)	France	—	FN550938	FN550938	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	EL190-08 (GB)	Sweden	—	KR029724	KR029724	—	—
	EL3-04 (GB)	Sweden	—	AM882859	—	—	—
	JV19684 (TENN-F-074801)	Finland	*Populus*, *Salix*, *Pinus* seedlings, on calcareous mull	**MN178502**	—	—	**MN203519**
	JV19640F (TENN-F-063757)	Finland	*Salix*, *Betula*, *Pinus*, *Populus*, *Picea*, calcareous soil	**MN178503**	**MN178529**	—	**MN203520**
	JV19642F (TENN-F-063523)	Finland	*Salix*, *Betula*, *Pinus*, *Populus*, *Picea*, calcareous soil	**MN178504**	**MN178530**	—	**MN203521**
	JV19650F (TENN-F-063759)	Finland	*Pinus*, *Betula*, *Picea*, *Salix*, near limestone quarry	**MN178505**	**MN178531**	**MZ404601**	**MN203522**
	STU-F-0901665 (**type** *M. plebeia*)	Germany	*Salix*, *Pinus*, calcareous soil	ON003442	—	—	—
M. leucoblema	CLC1721 (MONT)	Colorado	*Dryas*	GU980632	GU980632	—	—
	EL66-08 (GB)	Sweden	—	FN550936	FN550936	—	—
	EM29	Russia	*Epipogium aphyllum* root	—	EU711227	—	—
	JV16437 (WTU)	Finland	*Pinus*, *Picea*, *Salix*, *Betula*, *Populus*, calcareous soil	—	EU569858	AH013036	AY333310
	JV2898	Finland	*Picea*, *Betula*	HM209789	HM209789	—	—
	Moser 71123 (TENN-F-037075)	France	—	FJ601811 & FJ601812	**MN178532**	—	—
	PBM1522 (WTU)	Wyoming	*Picea*, *Abies*, calcareous soil	—	**MN178533**	—	MH577511
	PBM2737 (TENN-F-062549)	Colorado	*Picea*	HQ232481	**MN178534**	**MN203507**	—
	SEB97-09 (GB)	Sweden	*Pinus*	GU980631	GU980631	—	—
	SM2324 (GB)	Sweden	*Picea*	GU980630	GU980630	—	—
	TAA128324 (GB)	Estonia	*Salix*	GU980633	GU980633	—	—
M. leucoloma	CLC1232 (MONT)	Colorado	*Salix*	GU980624	GU980624	—	—
	CLC1355 (MONT)	Colorado	*Salix*	GU980623	GU980623	—	—
	CLC1431 (MONT)	Colorado	*Salix*	GU980619	GU980619	—	—
	CLC1442 (MONT)	Colorado	*Salix*	GU980620	GU980620	—	—
	CLC1703 (MONT)	Colorado	*Salix*	GU980617	GU980617	—	—
	CLC1869 (MONT)	Colorado	*Salix*	GU980618	GU980618	—	—
	CLC1877 (MONT)	Colorado	*Salix*	GU980621	GU980621	—	—
	EL40-07 (GB)	Sweden	*Salix*	GU980615	GU980615	—	—
	EL41-07 (GB)	Sweden	*Salix*	GU980615	GU980615	—	—
	EL50-05 (GB)	Norway	*Dryas*, *Salix*	AM882855	AM882855	—	—
	EL106-07 (GB)	Sweden	*Salix*	GU980627	GU980627	—	—
	EL107-07 (GB)	Sweden	*Salix*	GU980625	GU980625	—	—
	EL1-06 (GB)	Norway	*Salix*	GU980626	GU980626	—	—
	EL69-05 (GB)	Norway	*Dryas*, *Salix*	GU980616	GU980616	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	Kühner 63-36 (G, **type**)	France	*Dryas*, *Salix*	GU980614	GU980614	—	—
	PBM1574 (WTU)	Wyoming	*Salix*	—	EU555458	—	—
	PBM2296 (WTU)	Washington	Conifers mixed with *Betula*, *Populus*	—	AY380372	AY351798	AY337373
M. leucothrix sp. nov.	iNat131154234 (sp-AZ01)	Arizona	*Pinus*, *Quercus*, *Juniperus*, calcareous soil	OP784362	—	—	—
	iNat131155272 (sp-AZ01)	Arizona	*Pinus*, *Quercus*, *Juniperus*, calcareous soil	OP784312	—	—	—
	iNat131844666 (sp-AZ01)	Arizona	*Pinus*, *Quercus*, *Juniperus*, calcareous soil	OP784364	—	—	—
	PBM4541 (TENN-F-075564, **type**)	Florida	*Quercus*, *Pinus*, karst topography	**MZ404932**	**MZ375434**	**MZ404602**	**MZ405012**
	PBM4531 (TENN-F-075554)	Florida	*Quercus*, *Pinus*, karst topography	**MZ404933**	**MZ375435**	**MZ404603**	**MZ405013**
M. longicystis	FYG6371 (MHKMU)	Hainan	Fagaceous trees	OM179926	OM135609	—	OM835746
	FYG6373 (MHKMU)	Hainan	Fagaceous trees	OM179927	OM135610	—	OM747850
	FYG6374 (MHKMU, **type**)	Hainan	Fagaceous trees	OM179928	OM135611	—	OM835747
	FYG6376	Hainan	Fagaceous trees	OM179929	OM135612	—	OM835745
M. luteobasis sp. nov.	MK06071503 (TENN-F-073751)	Illinois	*Carya*, *Juniperus*	**MN178506**	**MN178535**	**MN203508**	**MN203523**
	MK06211102 (TENN-F-073749)	Illinois	*Quercus*, *Carya*	**MT239045**	—	—	—
	MK07140307 (TENN-F-073752)	Indiana	Deciduous woods	**MN178507**	**MN178536**	**MZ404604**	**MN203524**
	MK07180705 (TENN-F-073750, **type**)	Illinois	*Quercus*	**MN165953**	**MN178537**	**MZ404605**	**MN203525**
	Sayers *s.n.* (TENN-F-063525)	Kansas	*Quercus*	—	JN975028	—	MH577502
M. malenconii	EL807	Spain	—	FN550939	FN550939	—	—
	HMAS 262707	China	—	KJ810603	—	—	—
	IK-00018	Poland	—	KX602259	—	—	—
	JV4470F (WTU)	Finland	*Pinus sylvestris*, sandy soil	—	GQ906704	—	**MN203526**
	JV5498A (WTU)	Finland	—	—	EU569870	—	EU569869
	JV5824F (WTU)	Finland	*Picea*, *Betula*, *Salix*, sandy soil	—	**MN178538**	—	—
	JV23101 (WTU)	Finland	*Betula*, *Salix*, *Picea*	HM209787	HM209787	—	—
	LVK21286	New York	Mixed conifers and hardwoods	**OP046391**	**OP046370**	—	**OP060362**
	LVK22039	Maine	*Quercus*, *Pinus*	**OP918252**	—	—	—
	LVK22045	Maine	*Quercus*, *Pinus*	**OP913409**	—	—	—
	PAM98941302	France	*Betula*, *Pinus*	HM209788	HM209788	—	—
	SJ030822 (GB)	Sweden	*Pinus*	AM882862	—	—	—
	2020521-001 (UBC F19123)	British Columbia	—	HQ604776	HQ604776	—	—
M. montana sp. nov.	PBM3872 (TENN-F-067500, **type**)	North Carolina	Riverine hardwood forest	**OP046392**	**OP046371**	**OQ866119**	**OP060363**
	PBM4190 (TENN-F-074532)	North Carolina	*Pinus*, *Betula*	**MN178512**	—	—	—
	PBM4614 (TENN-F-075781)	North Carolina	*Tsuga*, *Pinus*, *Quercus*, *Betula*	**OP046393**	**OP046372**	**OP060357 & OP060358**	**OP060364**
M. multispora	CO4248 (CSU)	Oklahoma	*Quercus*, *Carya*, *Ulmus*, *Fraxinus*, sand	**MN178509**	**MN178540**	**MZ404606**	—
	DPL13518 (TENN-F-077876)	Texas	Bottomland hardwood forest near *Pinus*	**OQ707215**	—	—	—
	iNat126273738	Florida	*Quercus*, *Pinus*, sandy soil, karst	OP101166	—	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	iNat131720866	Arizona	*Pinus*, *Quercus*, *Juniperus*, calcareous	OQ023952	—	—	—
	FLAS-F-66616	Florida	*Quercus*, karst	**MZ404934**	—	—	—
	FLAS-F-61779	Florida	*Pinus*, *Sabal*, sandy pine flatlands	MH281884	MH620328	—	—
	FLAS-F-70016	Florida	—	OP580228	—	—	—
	MycoMap 10129	Indiana	hardwoods	OM473595	—	—	—
	MycoMap 10246	Indiana	*Pinus*, *Quercus*	OM473596	—	—	—
	PBM4717 (TENN-F-077391)	Florida	*Pinus*, *Quercus*, karst	**OQ208761**	—	—	—
M. myriadophylla	IK-00039	Poland	—	KX602263	—	—	—
	JV19652F (TENN-F-063760 – AFTOL-ID 482)	Finland	*Pinus*, *Betula*, *Picea*, *Salix*, calcareous mull soil	DQ221106	AY700196	DQ447917	AY803751
	JV19678 (TENN-F-063761, **type**)	Finland	*Pinus*, *Picea*, *Salix*, *Betula*, *Populus*	HM209793	HM209793	—	—
	JV5968F (WTU)	Finland	*Betula*, *Picea*, *Pinus*, calcareous ground	HM209794	HM209794	—	—
	SZ01	Germany	—	MF807958	—	—	—
M. nuptialis	STU-F-0901660	Austria	*Salix*, *Juniperus*, *Dryas*, *Pinus*, *Alnus*	ON003443	—	—	—
	STU-F-0901661 (**type**)	Austria	*Salix*	ON003444	ON003444	—	—
	STU-F-0901662	Germany	*Salix*	ON003445	—	—	—
M. pallidipes	FYG3736 (MHKMU, **type**)	Jilin	*Populus*	OM179924	OM137052	—	OM835749
	FYG3727 (MHKMU)	Jilin	*Populus*	OM179925	—	—	OM835750
M. piceae	FM555 (BJTC, **type**)	Shanxi	*Picea*	OM801896	OM801901	—	OM780096
	FM569 (BJTC)	Shanxi	*Picea*	OM801897	OM801903	—	OM780097
	FM896 (BJTC)	Shanxi	*Picea*	OM802898	OM801902	—	OM780098
M. praevillosa comb. nov.	FLAS-F-61523	Florida	*Pinus*, *Quercus*	MH211949 & **OP046394**	MH620294 & **OP046373**	**OP060359**	**OP060365**
	PBM4724 (TENN-F-077398)	Florida	*Quercus*, *Pinus*, karst	**OQ208762**	—	—	—
M. pygmaea	EL48-05 (GB)	Norway	*Dryas*, *Salix*	GU980628	GU980628	—	—
	J. Favre (**type**)	Switzerland	*Salix*	GU980629	—	—	—
M. pyrrhopoda	MDB F292/10 (PERTH 08383278)	Western Australia	*Antidesma*, *Glochidion*, *Melaleuca*, *Eucalyptus*, tropical forest	KP308814	KP170984	—	KM406224
	MDB F18s/13 (PERTH 08557764)	Western Australia	*Melaleuca*, tropical	KP308815	KP170986	—	KM406226
	PBM3759 (TENN-F-066987, **type**)	Queensland	*Melaleuca*, *Lophostemon*, *Corymbia*, tropical swamp	KP308813	KP170983	**MN203509**	KM406223
	PBM3740 (TENN-F-066972)	Queensland	*Corymbia*, *Eucalyptus*, tropical woodland	—	KP170985	—	KM406225
	REH9670	Queensland	*Eucalyptus*, subtropical	KP641622	KP171077	—	—
M. sabulosa	NLB986 (PERTH 08383308)	Western Australia	*Corymbia*, *Acacia*, gray sand limestone	—	KP170998	**MN203510**	KM406238
	NLB901 (PERTH 08320292)	Western Australia	*Acacia*, *Templetonia*, *Eucalyptus*, shrubland	KP308825	KP170997	—	KM406237
	E8178 (PERTH 07680732)	Western Australia	*Eucalyptus*, *Corymbia*, woodland	KP308822	JN974916	—	KM406235
	E8182 (PERTH 07680775)	Western Australia	*Eucalyptus*, suburban bushland	KP308823	KP170995	—	KM406236
	NLB898 (PERTH 08320322, **type**)	Western Australia	*Eucalyptus* (planted)	KP308821	KP170994	—	KM406234

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	MDB F7/11 (PERTH 08383057)	Western Australia	*Corymbia*, *Albizzia*, tropical woodland	KP308824	KP170996	—	—
Mallocybe sp. 1	uncultured	Alaska	*Dryas*	JX630703	—	—	—
	—	Alaska	*Dryas*	JX630716	—	—	—
	—	Alaska	*Dryas*	JX630710	—	—	—
Mallocybe sp. 2 (=*I. marmoripes sensu* N. Am. *auct.*, *non* G.F. Atk.)	BK06069724 (WTU)	Oregon	Conifers	—	AY380400	AY351825	MH577505
	BK06069725 (WTU)	Oregon	Conifers	—	**MN178541**	—	—
	LLN93063018 (WTU)	Washington	*Pinus*, *Salix*, *Alnus*	**OQ734476**	—	—	—
	2070626 (UBC F19439 as *I. malenconii* var. *megalospora*)	British Columbia	—	HQ604786	HQ604786	—	—
Mallocybe sp. 3	PBM1615	Washington	*Picea*, *Pseudotsuga*	—	AY038327	AF389549	AY337374
Mallocybe sp. 4	PBM2290 (WTU)	Washington	Conifers	—	EU555446	—	EU555445
Mallocybe sp. 5	JFA13285 (WTU)	Washington	*Picea*, *Pinus*, *Abies*	**MN178514**	**MN178543**	**MZ404607**	**MN203527**
	PBM1922 (WTU)	Washington	*Picea*, *Pinus*, *Tsuga*, *Pseudotsuga*	—	EU600879	—	EU600878
	SDA470 (TENN-F-074895)	Washington	*Abies*, *Pseudotsuga*, *Pinus* spp.	—	**ON478242**	—	—
Mallocybe sp. 6	ADP060305 (TENN-F-063537)	Washington	*Pseudotsuga*	**MN178513**	EU600877	—	EU600876
	PBM1444 (WTU)	Washington	*Populus*, *Abies*, *Pseudotsuga*	**OQ707214**	—	—	—
Mallocybe sp. 7	NS2563 (PDD 107312)	New Zealand	*Nothofagus*	**MN047372**	—	—	—
Mallocybe sp. 8	CFSZ12101	China	—	OP204682	—	—	—
	CFSZ12091	China	—	OP204681	—	—	—
	CFSZ22975	China	—	OP204687	—	—	—
	P20 “type”	China	—	ON045553	—	—	—
	PBM4749 (TENN-F-077511)	West Virginia	*Picea*	**OQ208763**	**OQ225230**	**OQ866120**	**OQ866121**
Mallocybe sp. 9	UBC F19404 (as *terrigena*)	British Columbia	*Pseudotsuga*, *Arbutus*	HQ604783	HQ604783	—	—
	UBC F19332 (as *terrigena*)	British Columbia	*Pseudotsuga*, *Thuja*	HQ604779	HQ604779	—	—
	UBC F19432 (as *terrigena*)	British Columbia	—	HQ604780	HQ604780	—	—
	DAVFP 28178 (as *terrigena*)	British Columbia	*Pseudotsuga*	HQ650752	—	—	—
	BK0306992 (UTC)	Washington	*Pseudotsuga*, *Arbutus*	—	AY038315	—	—
M. siciliana	AMB18273	Italy	*Salix*	MG757416	MG757418	—	—
	AMB18274	Italy	*Salix*	MG757417	MG757419	—	—
	JV7987 (WTU)	Finland	*Pinus*, *Picea*, *Salix*, *Betula*, *Alnus* on calcareous ground	—	EU569834	—	—
M. squamosodisca comb. nov.	LVK20133 (TENN-F-077383)	Maine	—	**MZ404935**	**MZ375436**	—	**MZ405014**
	LVK22053	Maine	*Quercus*, *Pinus*	—	—	—	—
	PBM4307 (TENN-F-074869)	Tennessee	*Quercus*, *Pinus*	**MT196944**	—	—	**MZ405015**
	PBM4591 (TENN-F-075758)	North Carolina	*Pinus*, *Tsuga*, *Quercus*, *Betula*	**OP046395**	**OP046374**	—	**OP060366**
	PBM4621 (TENN-F-075791)	New York	*Pinus*, *Abies*, *Betula*, *Populus*	**OP046396**	**OP046375**	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	REH7036 (NY01034397)	Costa Rica	*Quercus*, *Comarostaphylis*	**OP048953**	—	—	—
M. squarroso-annulata	Kuhner 63-236 (G, **type**)	Switzerland	—	HM209795	—	—	—
M. subflavospora	E5880 (PERTH 07609256, **type**)	Western Australia	*Eucalyptus*, dry sclerophyll	—	AY380396	AY351820	AY351821
	NLB1078 (PERTH 08578931)	Western Australia	*Allocasuarina*, *Eucalyptus*, woodland	**MN178515**	**MN178544**	—	MH577504
	NLB915 (PERTH 08320861)	Western Australia	*Eucalyptus*	KP641619	KP171074	—	KM656118
	PBM3791 (TENN-F-067023)	Queensland	*Eucalyptus*, wet sclerophyll	KP641620	KP171075	—	KM656119
	PBM3677 (PERTH 08319081)	Western Australia	*Allocasuarina*, dry sclerophyll	KP641621	KP171076	—	KM656120
M. subflavospora aff.	PBM3763 (TENN-F-066995)	Queensland	*Eucalyptus*, dry sclerophyll	—	**MN178545**	**MN203511**	MH618248
M. subgranulosa	EL11-12	Sweden	*Pinus*, *Salix*	OQ448535	OQ448535	—	—
	P. Karsten 2499 (H, **type**)	Finland	—	OQ448532	—	—	—
M. substraminipes	CLC1375 (MONT)	Colorado	*Salix*	GU980605	GU980605	—	—
	CLC1649 (MONT)	Colorado	*Dryas*	GU980602	GU980602	—	—
	CLC1731 (MONT)	Colorado	*Dryas*, *Salix*	GU980603	GU980603	—	—
	CLC2292 (MONT)	Colorado	*Salix*	GU980604	GU980604	—	—
	EL30-07 (GB)	Sweden	*Dryas*, *Salix*	GU980599	GU980599	—	—
	EL83-07 (GB)	Sweden	*Salix*	FN550935	FN550935	—	—
	EL99-07 (GB)	Sweden	*Salix*	GU980600	GU980600	—	—
	Kühner70-148 (G, **type**)	France	*Dryas*	GU980601	GU980601	—	—
	PBM1529 (WTU)	Wyoming	*Picea*, *Abies*	—	EU569835	—	—
	T10763 (WTU)	Alaska	*Salix*, *Alnus*	—	EU569836	—	—
M. subtilior	E00116332 (E)	Sabah (Malaysia)	in flower pot	**MN178516**	**MN178546**	—	—
	E9112 (PERTH 08095388)	Western Australia	—	KP641628	KP171082	—	—
	E4810 (PERTH 07660634)	Western Australia	*Eucalyptus*	KP641628	KP171083	—	—
	MDB F75/11 (PERTH 08383081)	Western Australia	*Corymbia*, *Acacia*, *Triodia*, red sand woodland	KP641629	KP171084	—	KM656125
	OKM24631 (PERTH 08561745, **type**)	Western Australia	*Eucalyptus*, sand	—	AY380398	AY351823	AY337406
M. subtomentosa comb. nov.	DPL13020	Mexico	*Pinus*	**OP046397**	—	—	—
	DPL13025	Mexico	*Pinus*	**OQ208764**	—	—	—
	LVK14251	Maine	*Pinus strobus*	**MN178517**	—	—	—
	LVK16004 (TENN-F-077382)	New Jersey	*Pinus*, *Quercus*	**MN178518**	**MN178547**	—	**MN203528**
	LVK16006	New Jersey	*Pinus*, *Quercus*	**MN178519**	**MZ375437**	—	**MZ405016**
	LVK16235	New Jersey	*Pinus*, *Quercus*	—	**MN178548**	**MN203512**	**MN203529**
	LVK17005	New Jersey	*Pinus*, *Quercus*	**MN178520**	—	—	—
	ME12_A6	Alaska	Arctic	JX436908	—	—	—
	MO207009	Pennsylvania	Conifer grove, grass	—	—	—	**MN203530**
	PBM2460 (TENN-F-062321)	Massachusetts	Mixed woods including *Pinus*, *Quercus*	**MN178521**	**MN178549**	**MN203513**	**MN203531**
	PBM3910 (TENN-F-068440)	North Carolina	*Pinus*, *Quercus*, *Betula*	**OP046398**	—	—	—
	PBM4701 (TENN-F-75838)	New York	Mixed conifers and hardwoods	**ON503076**	—	—	—
	PBM4763 (TENN-F-077551)	West Virginia	*Tsuga*, *Betula*, *Pinus strobus*, acidic soil	**OQ707212**	—	—	—

Table 1. (Continued).

Species	Specimen-voucher (Herbarium)	Geographic origin	Ecology	GenBank Accession Numbers			
				ITS	28S	*rpb1*	*rpb2*
	SAT9923301 (WTU)	New Mexico	*Pinus*, *Quercus*, *Pseudotsuga*	—	AY380373	AY351799	AY388644
M. terrigena	EL22-99 (GB)	Estonia	*Picea*, calcareous	AY586680	AY586680	—	—
	EL24-08 (GB)	Wyoming	*Salix*	GU980648	GU980648	—	—
	EL117-04 (GB)	Sweden	*Picea*, calcareous	AM882864	AM882864	—	—
	JV16431	Finland	*Pinus*, *Picea*, *Salix*, *Betula*, *Populus*, calcareous soil	—	AY380401	AY333301	AY333309
	PBM1563 (WTU)	Wyoming	*Picea*, *Abies*	—	**MN178550**	**MN203514**	—
M. tomentella sp. nov.	SAT0622810 (WTU)	Alberta	—	**MN178508**	**MN178539**	**OQ872543**	—
	PBM4690 (TENN-F-075826, **type**)	New York	Mixed conifers and hardwoods	**OP046400**	**OP046376**	**OP060360**	**OP060367**
	PBM4694 (TENN-F-075831)	New York	Mixed conifers and hardwoods	—	**ON478244**	—	—
M. tomentosula	GF2321 (TLXM)	Mexico	*Pinus cembroides*	KR817255	—	—	—
	HRL0027 (TENN-F-071134)	Quebec	*Pinus strobus*	KX897446	—	—	—
	PBM4138 (TENN-F-071837)	Tennessee	*Quercus*, *Juniperus*, limestone quarry	MG773814	MK421969	MK415443	MH577506
	RAS123 (TENN-F-071659)	Tennessee	*Quercus*, *Juniperus*, limestone quarry	MF992166	MF797642	—	—
M. umbrinofusca	Kühner70-38 (G, **type**)	France	*Salix*	GU980613	—	—	—
M. unicolor	iNAT:53190985 (TENN-F-076529)	Iowa	Hardwood forest	**ON503067**	**OP046377**	**OP060361**	**OP060368**
	MK06181501 (TENN-F-073747)	Illinois	*Quercus*	MH578008	—	—	—
	MK06231101 (TENN-F-073748)	Illinois	Hardwoods	MH578010	—	—	—
	MK08281401 (TENN-F-074753)	Illinois	*Quercus*, *Carya*	MH578009	—	—	—
	PBM1481 (WTU)	Missouri	*Quercus*, *Carya*, karst	—	AY380403	AY351827	AY337409
	PBM2645 (TENN-F-062476)	North Carolina	*Quercus*, *Fagus*	**MN178522**	**MN178551**	—	—
	PBM2940 (TENN-F-062698)	Tennessee	*Carya*, *Fagus*, karst	**MN178523**	**MN178552**	—	—
	PBM2974 (TENN-F-062732)	Tennessee	*Quercus*, lawn, karst	**MN178524**	JQ313569	**MN203515**	**MN203532**
	REH5532 (WTU)	New York	*Quercus*, *Fagus*	—	**MN178553**	—	**MN203533**
	RV7/4 (DUKE)	North Carolina	—	DQ490637	AF042617	—	—
	SH082407-01 (TENN-F-063553)	New Jersey	*Quercus*, lawn	**MN178525**	**MN178554**	**MN203516**	**MN203534**
M. velutina	MSM0048 (LAH310057, **type**)	Pakistan	*Pinus*	**MK990129**	**MK999927**	—	—
	MSM0049	Pakistan	*Pinus*	**MK990130**	**MK999928**	—	—
	MSM00050	Pakistan	*Pinus*	**MK990131**	**MK999929**	—	—
OUTGROUPS							
Auritella brunnescens	PBM3173 (TENN-F-065354)	New South Wales	*Eucalyptus*, dry sclerophyll	KJ702343	JQ313558	MK415420	KJ702348
Crepidotus applanatus	PBM717 (WTU)	Washington	Hardwood log, mixed *Pseudotsuga* forest	DQ202273	AY380406	AY333303	AY333311
Inosperma mutatum	PBM2542 (TENN-F-062387)	Massachusetts	*Quercus*	—	AY732212	DQ447917	DQ472729
Inosperma rimosoides	PBM2459 (TENN-F-062320)	New York	*Quercus*, *Pinus*, *Carya*, *Juniperus*, calcareous	DQ404391	AY702014	DQ447915	DQ385884
Tubariomyces sp.	BB6018 (PC)	Zambia	Miombo woodland	MK421964	EU600887	MK415448	EU600886

The 4-locus supermatrix provides a robust phylogeny of *Mallocybe*

Figure 1 provides a single-page phylogenetic overview of major clades and some species-level lineages within *Mallocybe* and the species that reside within each. Outgroups were pruned from this figure. Figure 2 was split into three parts detailing the entire phylogram. Phylogenetic analyses of the 4-gene supermatrix recovered an overall topology most similar to the *rpb2* gene tree with strong support for the union of clades Nothosperma and Mallocybe as a monophyletic group, and sister to it clade Unicolores. Similar to the *rpb1* and *rpb2* gene trees, both *Inocybe* (*Lepista*) *praevillosa* and *M. montana* formed a paraphyletic assemblage from which clades Unicolores and Nothosperma + Mallocybe emerged. Every one of these major nodes received strong support (> 77 % ML bootstrap) despite differences in taxon sampling depth per gene region. Overall, at least 55 species-level lineages were detected.

Murrill's *Inocybe* (*Lepista*) *praevillosa*, recombined below as *Mallocybe praevillosa*, was recovered as sister to all other species of *Mallocybe*. Murrill's taxon is distinguished by the relatively robust but brittle basidiomes, rooting stipe, the rather pale [originally described as pale pinkish by Murrill (1942)] allantoid to cylindric basidiospores, the presence of a low relative concentration of muscarine (Fig. 3), absence of necropigmented basidia, and elongated cheilocystidia. Cystidioid elements were found on the stipe, but these were not arranged in any way similar to those that characterize species of the genus *Tubariomyces* (Alvarado *et al.* 2010). Furthermore, the pileipellis was found to be a cutis giving rise to upright and interwoven hyphae, also unlike *Tubariomyces*, which forms a trichodermial palisade. The species was collected by us under *Quercus laurifolia* near the type locality on karst topography but also on sandhills with *Quercus* and *Pinus*.

Mallocybe montana (described below) was observed as sister to the remainder of *Mallocybe* with strong support. This species is characterized by elongated cheilocystidia, elongated cylindric basidiospores, necropigmented basidia, lack of a detectable amount of muscarine (Fig. 3), and occurrences on sandy acidic soils in mountainous regions of the Southern Appalachians.

Clade Unicolores (= Clade C in Hu *et al.* 2023) appeared sister to the other two major clades within *Mallocybe*. Here we documented that two additional species described by Murrill from Florida, *M. fulviceps* and *M. multispora*, belong to this clade. The American species in clade Unicolores are characterized often by elongated cheilocystidia, elongated cylindric spores, stipe length longer than the pileus width, and putative ectomycorrhizal relationships with *Quercus* and/or *Pinus* on limestone soils. *Mallocybe unicolor*, the third eastern North American species in clade Unicolores, seems to have a wide ecological amplitude, occurring abundantly in areas characterized by *Quercus* and *Tilia* on karst topography; however, the species has also been recorded, but with low basidiome abundance, on acidic soils in montane regions of the Southern Appalachians. Three East Asian species were also recovered in clade Unicolores, all of which are also characterized by elongated cheilocystidia (Hu *et al.* 2023). Their plant associations include *Fagaceae* (*e.g.*, *Castanopsis*) and Salicaceae (*Populus*).

The second major grouping, clade Nothosperma (= Clade B in Hu *et al.* 2023) contained five named species from Australia and/or Malaysia and one unidentified species from New Zealand. Two species – *M. subflavospora* and *M. pyrrhopoda* – were non-monophyletic. Within clade Nothosperma, the New Zealand sample (*Mallocybe* sp. 7) is sister to the Australian lineages with strong support. The unpublished *Mallocybe* sp. 7 is characterized by elongated cheilocystidia and an association with *Nothofagus*, unlike the Australian species in this clade, all of which have short cheilocystidia and associations with *Myrtaceae*, *Casuarinaceae*, and *Fabaceae* (Matheny & Bougher 2017). *Mallocybe callichroa* (recombined into *Mallocybe* below), another *Nothofagus* associate from New Zealand with clavate and elongated cheilocystidia, may belong to this clade as well, but molecular confirmation is lacking. *Mallocybe sabulosa* was found to contain relatively high amounts of muscarine (Fig. 3), whereas *M. isabellina* lacked any detectable amount of the toxin.

The third major group is referred to as clade Mallocybe (= Clade A in Hu *et al.* 2023) and includes the generic type *M. terrigena* and 40 other species-level lineages primarily from temperate regions of the northern hemisphere (and three from or extending into tropical latitudes). Several mostly strongly supported inclusive groupings were also observed in clade Mallocybe. The first of these was the Arthrocystis clade containing four species, only two of which are presently described – the European species *M. arthrocystis* and the East Asian *M. piceae*, and two undescribed species from the Pacific Northwest in western North America; all analyses recovered the Arthrocystis clade as monophyletic but only with moderate support (*e.g.*, 61 % ML bootstrap).The Fuscomarginata clade likewise included four species, two of which are known in Europe – *M. fuscomarginata* and *M. gymnocarpa*; two additional unclarified species were identified from the Pacific Northwest.

The core Mallocybe clade was recovered with strong support and was characterized by the inclusion of the Heimii clade, the Terrigena grade, and the highly diverse Delecta clade. The Heimii clade was strongly supported as sister to rest of the core Mallocybe clade with five species from the northern hemisphere including South Asia, whereas the Terrigena grade was recovered as a paraphyletic assemblage of *M. luteobasis* (described as new below), *M. terrigena*, *M. fibrillosa* (= *I. dulcamara sensu auct. p.p., non* Persoon), and *M. leucoblema.* The Delecta clade contains 24 species from north temperate regions, including high elevations in Central America. Within clade Mallocybe, six samples were assayed for the presence of muscarine, but the toxin was undetected in all of them (Fig. 3; see also further results below).

In total, 16 species of *Mallocybe* were recovered from eastern North America (four described as new below, but also one additional species that cannot be described here due to insufficient data). Of these 16 species, 11 were recovered in clade Mallocybe, three in clade Unicolores, and two corresponded to the Montana and Praevillosa lineages. Several additional and probably undescribed species were also recovered from western North America. These will be addressed and treated in a forthcoming study.

Overall, many species of *Mallocybe* have been characterized by broad intercontinental biogeographic distributions (Cripps *et al.* 2010). However, some local endemism by continent or regions of continents was suggested by our results. Species known currently only from eastern North America included several species described as new or recombined into *Mallocybe* below – *M. leucothrix*, *M. montana, M. praevillosa*, *M. squamosodisca* (including Costa Rica), *M. luteobasis*, and *M. tomentosula* (including Mexico), *M. unicolor*, and *M. fulviceps*.

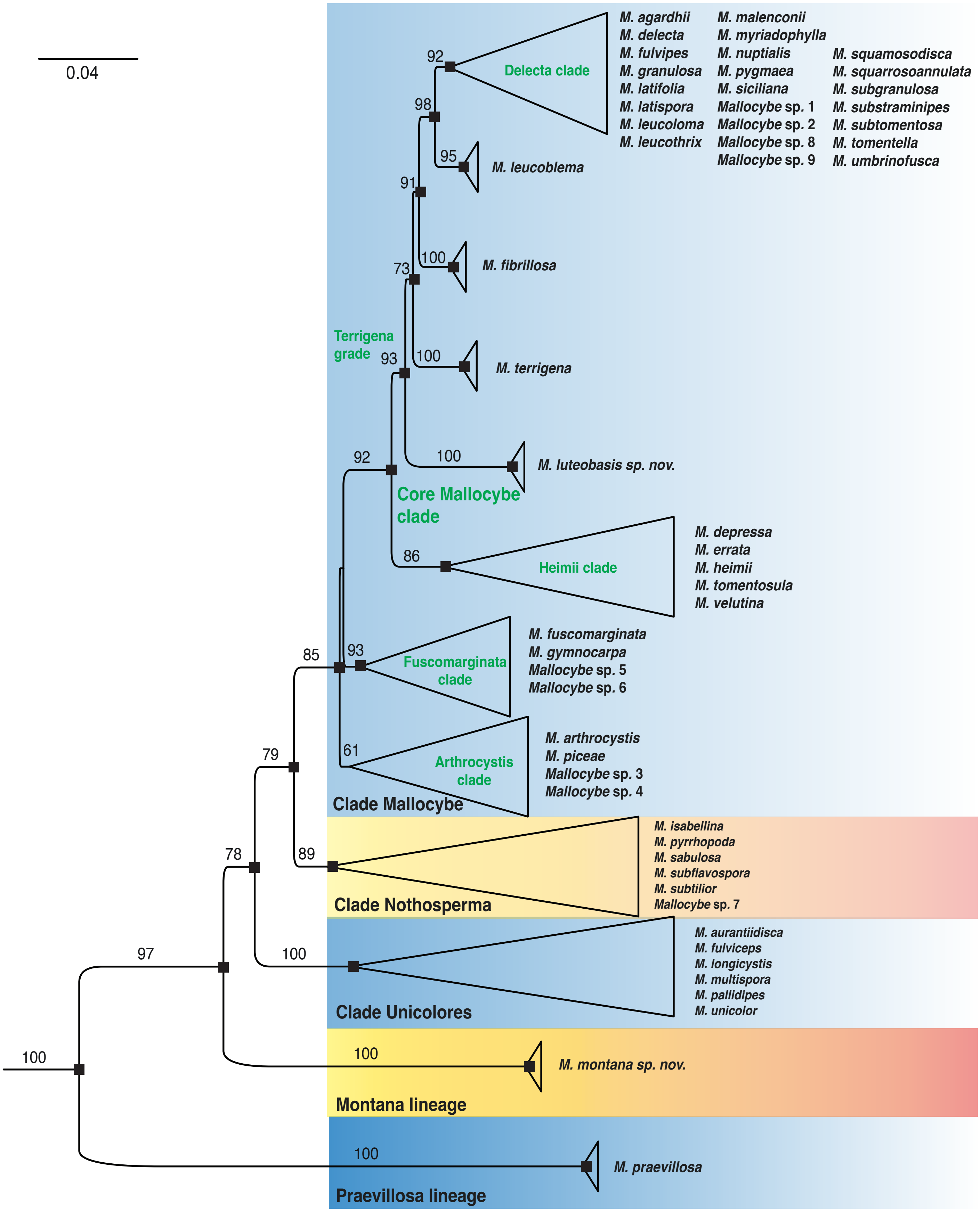

Fig. 1. Summary ML phylogram of *Mallocybe* based on a supermatrix of combined *rpb1, rpb2*, ITS, and 28S sequence data. Inclusive terminal groupings are cartooned to compress the figure for easier graphic presentation. Three major clades and two unresolved species-level lineages within *Mallocybe* are indicated: clades Mallocybe, Nothosperma, and Unicolores and the Montana and Praevillosa lineages. Within clade Mallocybe, several strongly supported nested groups were recovered: the Arthrocystis, Fuscomarginata, Heimii, core Mallocybe, and Delecta clades, in addition to a strongly supported paraphyletic group referred to as the Terrigena grade. Numbers above or below branches represent bootstrap proportions > 70 % except for the Arthrocystis clade. Black-filled squares indicate support values for internodes with SH-aLRT > 80 % and UF bootstraps > 95 %. The scale bar indicates the number of expected substitutions per site. Outgroups have been pruned.

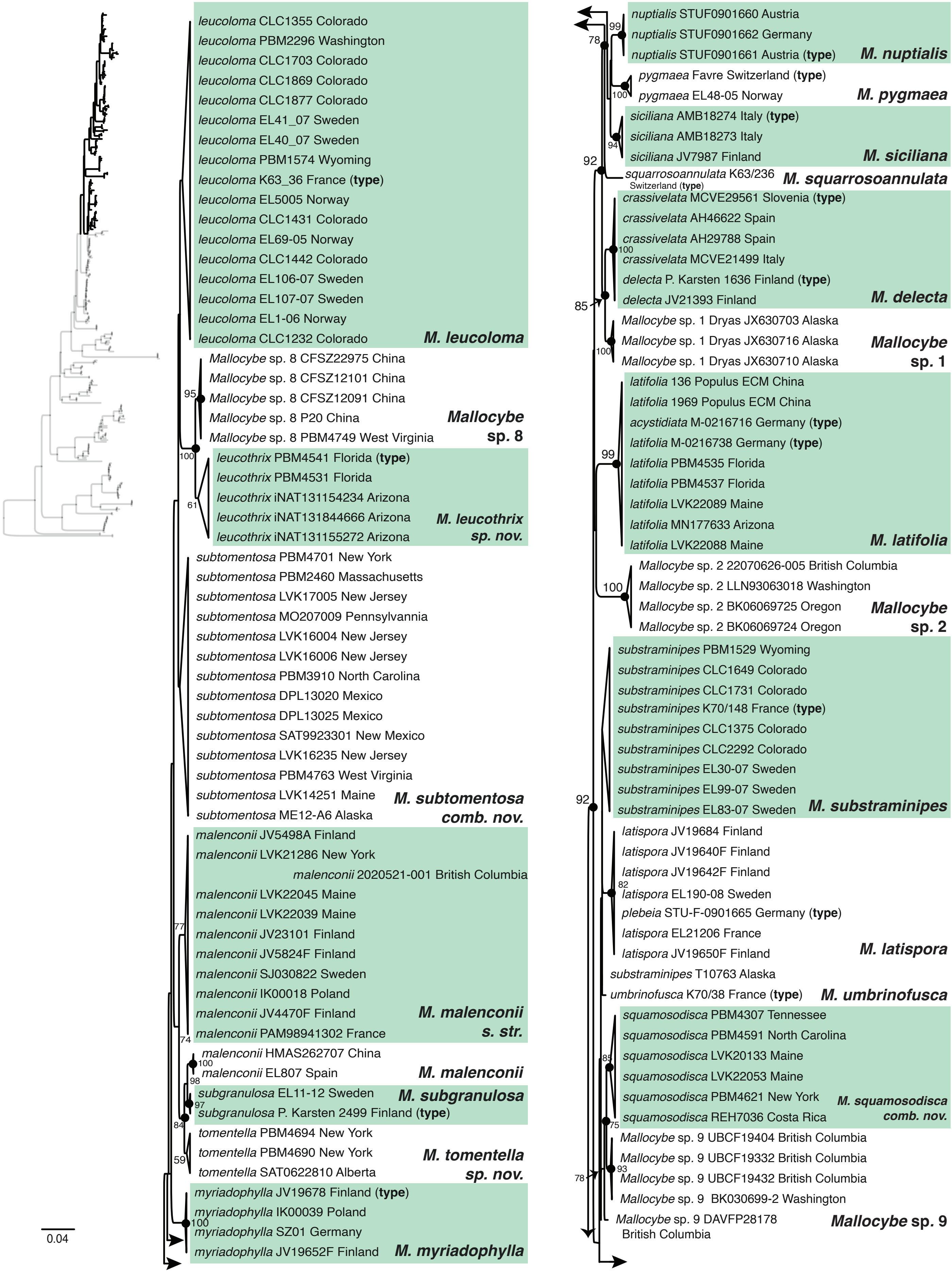

Fig. 2. The ML phylogeny of *Mallocybe* based on a supermatrix of combined *rpb1, rpb2*, ITS, and 28S sequence data. Numbers above or below branches indicate bootstrap proportions > 50 %. Black-filled circles indicate support values for internodes with SH-aLRT > 80 % and UF bootstraps > 95 %. The figure is divided into three parts (A, B, C). The scale bar equals the number of expected number of substitutions per site.

Fig. 2. (Continued).

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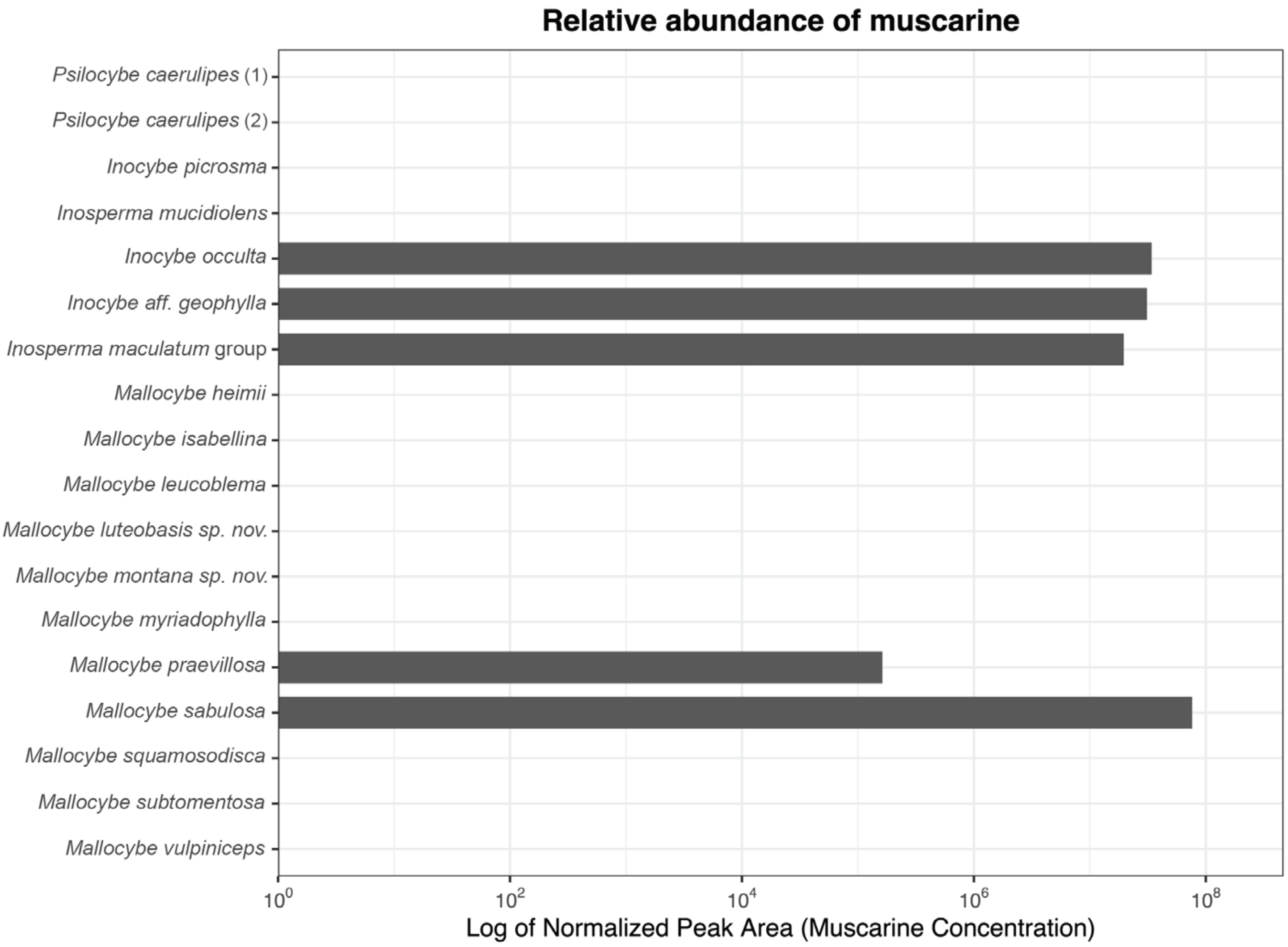

Fig. 3. Histogram showing the relative abundance of muscarine in select species of *Mallocybe* presented as a log normalized peak area, which refers to area count per mg or peak per mg since the aera after blank subtraction was sample mass normalized. Samples detected with abundance less than 2.5 times of the average abundance in the blank control were considered as below limit of detection. *Psilocybe caerulipes*, *Inocybe picrosma*, and *Inosperma mucidiolens* were used as negative controls, and *I. occulta*, *I. aff. geophylla*, and a species in the *Inosperma maculatum* group were used as positive controls. *Mallocybe unicolor* was also shown to lack muscarine by Kosentka *et al.* (2013). Of eastern North American species sampled, only *M. praevillosa* proved to contain a relative amount of muscarine but considerably lower than detected among the positive controls and the Australian species *M. sabulosa*. Stijve *et al.* (1985) also indicated the absence of muscarine from *M. terrigena*, the type of *Mallocybe*.

Two eastern North American species were also recorded from western regions and represent continental endemics to date: *M. tomentella* and *M. multispora*. All five described species from Australia appeared endemic to that continent, and the one species sampled from New Zealand is known thus far only from New Zealand.

Most species of *Mallocybe* lack detectable amounts of muscarine

Mass spectrometry revealed no detectable muscarine in samples of the following species: *Mallocybe heimii*, *M. isabellina*, *M. leucoblema*, *M. luteobasis*, *M. montana*, *M. myriadophylla*, *Mallocybe* sp. 5, *M. squamosodisca*, and *M. subtomentosa* (Fig. 3). A relatively high concentration of muscarine was detected in *M. sabulosa* and a relatively lower amount in *M. praevillosa*. As expected, none was detected in the negative controls *Psilocybe caerulipes*, *Inocybe picrosma*, and *Inosperma mucidiolens*. The three positive controls possessed relatively high concentrations of the toxin (Fig. 3).

TAXONOMY

Mallocybe (Kuyper) Matheny *et al.*, *Mycologia* **112**: 94. 2020 [2019].
Synonym: *Inocybe* subg. *Mallocybe* Kuyper, *Persoonia* **3** (Suppl.): 22. 1986.

Typification: *Agaricus terrigenus* Fr., *Öfvers. K. Svensk. Vetensk.-Akad. Förhandl.* **8**(2): 46. 1851.

Description: Cheilocystidia often present and arising as terminal elements of the hyphae of hymenophoral trama, typically < 50 µm, rarely as short incrusted chains (if cheilocystidia > 50 µm long, this is generally a shared ancestral trait); pleurocystidia absent, basidia often necropigmented; lamellae usually broadly attached (adnate, uncinate, or subdecurrent), pileus typically woolly-squamulose or tomentose-fibrillose, surface often darkening with application of alkali solutions, context not reddening. Ectomycorrhizal with a wide range of plant families.

Notes: About 65 species are known in the genus and occur in Africa, Asia, Australia, Europe, New Zealand, and North America.

Mallocybe clade Mallocybe

Description: Includes *Mallocybe* species from the northern hemisphere, most of which are characterized by short clavate, pyriform, or cylindric cheilocystidia (often < 50 µm long). Common in north temperate zones, but also present in tropical areas of South Asia and high elevations in Central America. Muscarine not detected from most species assayed, including the type, but reported from other species: *M. agardhii*, *I. caesariata*, *I. dulcamara*, and *M. malenconii*. Putative plant family associates include *Betulaceae, Cistaceae, Dipterocarpaceae, Fagaceae, Pinaceae, Rosaceae*, and *Salicaceae*.

Currently included species (51 accepted): *M. abruptibulbosa*, *M. agardhii*, *M. arthrocystis*, *M. attenuatipes*, *M. cotoneovelata*, *M. delecta* (= *M. crassivelata*), *M. depressa*, *M. errata*, *M. fibrillosa* (= *I. dulcamara sensu auct. p.p., non* Persoon), *M. errata*, *M. fulvipes*, *M. fulvoumbonata*, *M. fuscomarginata*, *M. granulosa*, *M. gymnocarpa*, *M. hebelomoides*, *M. heimii* (=*M. arenaria*), *M. homomorpha*, *M. lagenicystidiata*, *M. latifolia* (= *M. acystidiata*), *M. latispora* (=*M. plebeia*), *M. leucoblema*, *M. leucoloma*, *M. leucothrix sp. nov.*, *M. luteobasis sp. nov.*, *M. malenconii*, *M. megalospora*, *M. myriadophylla*, *M. nuptialis*, *M. pallidotomentosa*, *M. paludosa*, *M. parcesquamulosa*, *M. pelargoniodora*, *M. perbrevis*, *M. piceae*, *M. pseudodulcamara*, *M. pygmaea*, *M. siciliana*, *M. solidipes*, *M. squamosoannulata*, *M. squamosodisca comb. nov.*, *M. squarrosoannulata*, *M. subannulata*, *M. substraminipes*, *M. subtomentosa comb. nov.*, *M. terrigena*, *M. tomentella sp. nov.*, *M. tomentosula*, *M. umbrinofusca*, *M. velicoronata*, and *M. velutina*. *Inocybe favrei* Nespiak and *I. nespiaki* M. Bon are invalid names, but both species belong here. Note that *Inocybe stenospora* (contra Stangl 1989, Ludwig 2017), despite lacking pleurocystidia, belongs to the *Inocybe lanuginosa* group (Bandini *et al.* 2018) and not in *Mallocybe* as previously considered.

Notes: Most species of *Mallocybe* occur in clade Mallocybe upon consideration of their geographic distribution (non-Australasian), often short cheilocystidia (when present), and in most species average Q values for basidiospores < 2.0. In some species the stipe length is equal to or less than the pileus diameter. The clade includes all known arctic and alpine species. Daskalopoulos *et al*. (2021) noted some unique features to the ectomycorrhizal anatomy of *M. heimii* compared to other *Inocybaceae*: an open or variant anastomosis-type and presence of clamp connections on mantle hyphae.

Mallocybe clade Nothosperma

Etymology: *Nothosperma* (Gk.), southern seed, in reference to occurrence in the southern hemisphere.

Description: Includes *Mallocybe* species from the southern hemisphere (temperate and tropical regions) and tropical regions of southeast Asia (Malaysia) that associate with *Myrtaceae*, *Casuarinaceae*, and *Nothofagaceae*. Most species characterized by presence of short cheilocystidia (< 50 µm long); stipe often longer than the pileus diameter; pileipellis hyphae coarsely incrusted. Muscarine detected at relatively high concentration in *M. sabulosa*. No species have yet been recorded from South America.

Currently included species (seven accepted): *M. isabellina*, *M. pyrrhopoda*, *M. sabulosa*, *M. subflavospora*, and *M. subtilior* from Australia, *M. althofiae* from New Guinea, one unclarified species from Malaysia in association with *Allocasuarina*, and one unclarified species from New Zealand found with *Nothofagus*. *Inocybe callichroa* (Horak 2018) described from New Zealand, is placed here as well (see Taxonomy below). The occurrence of *M. cf*. *subtilior* in Sabah, Malaysia, was confirmed after sequencing a specimen from a flowerpot on bare earth (*leg*. *E.J.H. Corner*, 13 May 1964, E00116332). This species is likely introduced. However, another collection (E00116333) made by Corner from Johor, Malaysia, was made from bare sand in front of "*Casuarina*". This is an undescribed *Mallocybe* species characterized microscopically by large "laceroid" basidiospores (similar to *Inocybe lacera* in outline), 11.5–*12.4*–14(–14.5) × (5.5–)6-*6.2*–6.5(–7) µm, Q 1.85–*2.02*–2.33, short articulated cheilocystidia (28–45 × 12–25 µm), and presence of necrobasidia (Matheny 2003). No field notes accompanied the duplicate collection at Herbarium E. However, the combination of habit (stipe longer than the pileus diameter), small size, and coarsely incrusted pileipellis hyphae point to a relationship with Australian species of *Mallocybe*.

Mallocybe clade Unicolores

Etymology: *Unicolores* (L.), named after the oldest binomial in the clade, *Mallocybe unicolor.*

Description: A monophyletic group of *Mallocybe* species from East Asia and North America with distinct or elongated (> 50 µm long) cheilocystidia, stipe length generally longer than the pileus width, and association with angiosperms (*Fagales*, *Malvales*) and *Pinus*. Basidiospores with mean Q values > 1.90.

Currently included species (six accepted): *M. aurantiidisca*, *M. fulviceps*, *M. longicystis*, *M. pallidipes*, *M. multispora*, and *M. unicolor*. Known from eastern North America and East Asia.

Montana lineage

Description: A single stem lineage sister to clades Unicolores, Nothosperma, and Mallocybe. Characterized by elongated cheilocystidia, oblong-cylindric basidiospores, and narrow-range endemism in the Southern Appalachian Mountains in association with *Betulaceae*, *Fagaceae*, and/or *Pinaceae*. KOH dark on the pileus surface; necrobasidia present.

Currently included species (one accepted): *M. montana* (described as new below). Known only from the southeastern U.S.

Praevillosa lineage

Description: A single stem lineage sister to clades Unicolores, Nothosperma, and Mallocybe and the Montana lineage. Characterized by elongated cheilocystidia, oblong-cylindric to allantoid pale basidiospores, and narrow-range endemism in northern Florida in association with Fagaceae. KOH negative on pileus surface; necrobasidia not observed.

Currently included species (one accepted): *M. praevillosa* (recombined as new below). Known only from the southeastern U.S.

Mallocybe incertae sedis

Mallocybe africana Aïgnon, Yorou & Ryberg, *Phytotaxa* **478**: 53. 2021.

Species taxonomy

Mallocybe fibrillosa (Peck) Matheny & Esteve-Rav., *Mycologia* **112**: 106. 2019 [2020]. Figs 4A–C, 9A–C.
Basionym: *Inocybe fibrillosa* Peck, 1888, *non* (Cleland) Grgur., *Larger Fungi of South Australia*: 190. 1997.
Synonyms: *Inocybe dulcamara* Sacc., *Syll Fung* **5**:764. 1887 (*nom. illegit*., Art. 53.1), *non Inocybe dulcamara* (Pers.) P. Kumm., *Führ. Pilzk*.: 79. 1871.
Agaricus dulcamarus Alb. & Schwein., *Schr. Naturf. Ges, Leipzig*: no. 489. 1822 (*nom. illegit.* Art. 53.1), *non Agaricus dulcamarus* Pers., *Syn. Meth. Fung*. **2**: 324. 1801.
Inocybe subdecurrens Ellis & Everh., *J. Mycol*. **5**: 26. 1889.
Mallocybe subdecurrens (Ellis & Everh.) Matheny & Esteve-Rav., *Mycologia* **112**: 108. 2019 [2020].
Inocybe caesariata sensu Kauffman, *N. Am. Fl*. **10**(4): 255. 1924.

Pileus 15–40 mm wide, convex to plano-convex and eventually plane, margin incurved or inrolled at first and remaining so after expansion or becoming decurved, rarely subumbonate; surface dry, velipellis absent, heavily matted fibrillose to matted radially lanose or tomentose-fibrillose, disc at time with fibrillose scales, with white veil remnants when young; light brown (6C6–D6 or 6D5), brownish yellow, or fulvous throughout (10YR 5/6; Buckthorn Brown) brown with 3 % KOH, with cobwebby veil remnants at margin; context off-white, very pale brown, to yellowish white, unchanging where bruised, solid becoming hollow, *odor* mild or subtly sweet, *taste* mild. PDAB negative, guaiac dark olive green. *Lamellae* uncinate or subdecurrent to adnate, adnexed, close (up to 40 L) and with several tiers of lamellulae, light olive brown to olive brown (2.5Y 5/4–4/4), edges even or pallid and indistinctly fimbriate. *Stipe* 10–35 × 5–10 mm, equal, strict or curved; surface dry, heavily lanose to matted sublanose to squamulose, nowhere pruinose and not at all scaly, rarely peronate, with obvious partial veil remnants as a cortinate veil; light brown (lighter in color than the pileus surface) or with pale yellow ground color (2.5Y 2/4), white at the base; context solid becoming hollow, pale dingy yellow to olive yellow but nowhere bright yellow.

Basidia (26–)29–41 × 6–9 µm, 4-sterigmate, slenderly clavate, hyaline to ochraceous, necropigmented. *Basidiospores* (7.5–)8–*9.0*–9.5(–10) × 4.5–*5.0*–5.5(–6) µm, Q (1.50–)1.55–*1.76*–1.90(–2.24), smooth, elliptic, subphaseoliform, to (sub)amygdaliform with obtuse to bluntly pointed apices, with thickened walls, apiculus small and indistinct, ocher-buff to ochraceous-tawny (n = 53/3). *Pleurocystidia* absent. *Cheilocystidia* 16–45 × 9–14 µm, cylindric to clavate, occasionally flexuous, utriform, or short fusiform, apices obtuse or swollen, thin-walled, hyaline, edges of lamellae sterile. *Caulocystidia* not observed in the type but present as short clavate cells (at times elliptic or cylindric) at the extreme apex in *PBM2350*, usually hyaline, thin-walled; vesture hyphae brownish yellow in mass, incrusted, cylindric and up to 16 µm wide; stipe hyphae subhyaline in mass, refractive hyphae present. *Pileipellis* a cutis of parallel to subparallel hyphae, at times scattered upwards or tangled, tawny to brownish yellow in mass, hyphae cylindric, incrusted, 7–15 µm wide; tramal hyphae pale yellowish in mass, at times inflated, refractive hyphae present. *Lamellar trama* parallel, compact, pale yellowish or light yellowish brown in mass, hyphae cylindric and 7–15 µm wide. *Clamp connections* present.

Distribution: Widely distributed in the northeastern USA (Maine, New Jersey, New York), southeastern Canada (Quebec), the Pacific Northwest (British Columbia, Washington) and in the Rocky Mountains (Colorado, Wyoming), also northern Europe.

Habitat: On soil (at least some sites acidic) in mixed forests but with *Pinus* or other *Pinaceae* often present, also with *Salix*, and possibly *Dryas* in alpine areas of the USA, and with *Populus* in western subalpine areas, occurring with *Salix* or *Betula* in Europe. August–October in eastern North America, July–August in western North America.

Specimens examined: **USA**, Maine, Somerset Co., West Forks, Main Huts Trail (east end along Dead River), on ground in mixed woods, 19 Sep. 2014, *L.V. Kudzma*, LVK14371 (pers. herb.); Maine, Somerset Co., the Forks, Moxie Falls Trail, 20 Sep. 2014, *L.V. Kudzma*, LVK14390 (pers. herb.); *ibid.*, 22 Sep. 2015, *L.V. Kudzma*, LVK15242 (pers. herb.); Main, Limestone, Aroostook Co., Aroostook National Wildlife Refuge, on soil in mixed woods under *Picea*, *Abies*, *Betula*, *Larix*, *Populus*, 10 Sep. 2022, *L.V. Kudzma*, LVK22085 (pers. herb.); New Jersey, Gloucester Co., Newfield, under overhanging limbs of Norway spruce (*Picea*), Oct. 1887, *Ellis & Everhart* (**holotype** of *Inocybe subdecurrens*, NY 00775657, 00775658, 007775659, 00775660); Somerset Co., Woods Road School, under pine, 7 Oct. 1995, *R.M. Fatto*, RMF908 (NY 673247); *ibid.*, under conifers, 12 Oct. 1996, *R.M. Fatto*, RMF1009 (NY 673246); New York, Albany Co., Bethlehem, Corning Farm, on damp mossy banks in woods, Aug. (no day and year), *C.H. Peck s.n.* (**isotype** WTU part of NYSf1175); Essex Co., Peck Foray at the State University of New York (SUNY) College of Environmental Forestry (EFS) Newcomb Campus, Huntington Forest Preserve, 43.96929 -74.22022, 507 m elev., gregarious on soil under *Abies*, *Picea*, *Betula*, *Thuja*, *Pinus*, no date, *R.E. Halling*, REH10168 (NY 2861422, TENN-F-073177); Washington, King Co., exit 47 off Interstate 90, Pratt Lake Trail, scattered along moist bank along trail in second growth conifer forest dominated by *Pseudotsuga* and *Tsuga*, 25 Aug. 2002, *P.B. Matheny*, PBM2350 (WTU).

Other specimens examined (*Mallocybe delecta*): **Finland**, Tavastia australis, Tammela, Syrjä, no date, *P.A. Karsten*, 1636 (**holotype** of *Agaricus delectus*, H); *ibid.*, *P.A. Karsten*, 1637 (**isotype** of *Agaricus delectus*, H).

Notes: The name *Mallocybe fibrillosa* (syn. *I. fibrillosa* Peck) has not been widely used since synonymized with *I. caesariata* by Kauffman (1924) but in our judgement conforms to application of the name *Inocybe dulcamara* used by Cripps *et al*. (2010;

Fig. 4. Basidiomes of *Mallocybe* from eastern North America. **A.** *M. fibrillosa* (LVK14371, photo L. Kudzma). **B.** *M. fibrillosa* (REH10168, photo R. Halling). **C.** *M. fibrillosa* (PBM2350, photo B. Matheny). **D.** *M. fulviceps* (DPL13914, photo D. Lewis). **E.** *M. fulviceps* (PBM4533, photo B. Matheny). **F.** *M. fulviceps* (PBM4726, photo B. Matheny). **G.** *M. latifolia* (LVK22088, photo L. Kudzma). **H.** *M. latifolia* (PBM3731, photo B. Matheny). **I.** *M. latifolia* (MES3796, photo M. Smith). **J.** *M. leucothrix* (PBM4541, holotype, photo B. Matheny). **K.** *M. leucothrix* (PBM4531, photo B. Matheny). Scale bars = 1 cm.

see further discussion below about conflicting concepts for this species). We suggest that modern extant material studied from New York (NY 2861422) and elsewhere in northeastern states serves as adequate reference material for Peck's *Inocybe fibrillosa* originally described from the greater Albany area in New York. The species is characterized generally by the tomentose-fibrillose pileus, olivaceous hues to the moderately spaced lamellae, the tomentose to lacerate-fibrillose stipe with a white base, and, according to Cripps *et al.* (2010, as *I. dulcamara*), an odor of honey or burnt sugar. Washington material of *M. fibrillosa* exhibited a sweet earthy smell. The spores are not oblong and have a mean Q value less than 2.0. The cheilocystidia are short and generally cylindric. Cripps *et al.* (2010) reported the presence of 2-sterigmate basidia in some alpine collections and thus larger spores. Ecologically, the species is widespread, occurring in northern Europe and eastern and western North America at high latitudes or high elevation, including alpine areas (as confirmed by molecular data). The species may have a circumboreal distribution. The plant host range overall is somewhat broad and includes *Pinaceae*, particularly *Pinus* but also other genera, *Salicaceae* (*Salix*, *Populus*), *Betulaceae* (*Betula*), and *Rosaceae* (*Dryas*). Among other species that occur in eastern North America, *M. subtomentosa* differs from *M. fibrillosa* by the stipe length that is longer than the pileus width and the nearly smooth pileus. *Malllocybe squamosodisca* can be distinguished from *M. fibrillosa* by the cracked-areolate pileus surface that develops with age, longer spores on average, and the lack of any odor as well.

Our concept of *M. fibrillosa* is the same as that documented from western North America and Europe as *I. dulcamara* by Cripps (1997, in the sense of Albertini and Schweinitz) without molecular data and by Cripps *et al.* (2010, as *I. dulcamara* (Alb. & Schwein.) P. Kumm.) with molecular data. However, *Agaricus dulcamarus* Alb. & Schwein. 1822 is a later homonym of *Agaricus dulcamarus* Pers. 1801 and thus an illegitimate name per ICN Art. 53.1. Neither name was included in any sanctioning works of Fries. *Inocybe dulcamara* Sacc. 1887 is a homotypic synonym of *Agaricus dulcamarus* Alb. & Schwein. and is illegitimate because it is a later homonym of *Inocybe dulcamara* (Pers.) P. Kumm. 1871.

Agaricus dulcamarus Pers. represents a different species than interpreted by many modern authors including Ricken (1915), Heim (1931), Kühner & Romagnesi (1953), Favre (1955), Malloch (1973), Cripps *et al.* (2010), and that documented by Favre (1955), per Cripps and colleagues, as *I. dulcamara* 'forma typique'. The description in Persoon's protologue (Persoon 1801), and later an icon (Persoon 1803–1806) of *Agaricus dulcamarus* Pers. conflicts with the later interpretation of *I. dulcamara sensu auct. p.p.* (Matheny 2003). Persoon's fungus may actually represent *Inosperma cervicolor* (T.W. Kuyper, pers. comm.). Fries (1828) interpreted *A. dulcamarus* as his *A. lucifugus*, a name treated by Kuyper (1986) as a *nomen dubium.* Singer (1986) preferred to use the name *Inocybe delecta* in lieu of *I. dulcamara* (Alb. & Schwein.) P. Kumm. We examined the type collections of *Agaricus delectus* [H, No. 1636 (holotype) and 1637 (isotype)] and found the spores to be somewhat narrower and more oblong (8–*9.0*–10 × 4–*4.6*–5 µm, Q 1.80–*1.95*–2.13(–2.38)) than in *M. fibrillosa*. Since our examination of the types, Ellen Larsson (University of Gothenburg) was able to produce a molecular annotation (ITS) from the type of *Mallocybe delecta* (H, No. 1636; OQ448533) and modern reference material (JV21393; OQ448534 – ITS and 28S). Sequences from both samples cluster with strong support in a species-level lineage with *M. crassivelata*. Thus, we can safely eliminate the possibility of any conspecificity between *M. fibrillosa* and *M. delecta*.

The application of the name *I. dulcamara* (Fr.) Quél. by Stuntz (1947; Stz. 805), collected under high-elevation conifers in Washington, likely represents a different species, possibly *M. gymnocarpa* or a closely related species, based on the large size of the basidiomes, spore morphology, and absence of a veil.

Stuntz (1947) considered *I. subdecurrens* and *I. tomentosa* Ellis & Everh. (*non* Quél.) as synonymous, as others did before him (Kauffman 1924, Smith 1939), and applied the name *I. subdecurrens* to a single lowland collection under *Alnus* from lowland Washington state. From this single collection Stuntz noted a white ample cortina, the stipe longer than the pileus width, relatively narrow spores (8–10 × 4.5–5.5 µm), and pyriform to short-clavate articulated cheilocystidia. Stuntz' collection may fit *M. leucoloma* (see discussion under *M. subtomentosa*). Peck published *Inocybe fibrillosa* in 1888, which precedes by one year the publication of *I. subdecurrens*, hence, when considering the two as synonymous, *I. fibrillosa* has priority.

In the study by Matheny *et al.* (2020), *M. fibrillosa* was referred to as *I. subdecurrens*. The holotype of *I. subdecurrens* comprises three packets and four elements, all from the same original gathering and fixed to a single sheet at NY. Attempts to sequence two elements of the holotype (775657 and 775658) failed due to poor quality reads and sequence heterogeneity. We did not attempt to sequence the type of *I. fibrillosa*. Because we cannot distinguish the two species morphologically and ecologically, we regard them as the same with *M. fibrillosa* holding nomenclatural priority by a single year.

Phylogenetic analyses (Fig. 2A) support multiple samples from North America and Europe, including alpine and non-alpine populations, as a strongly supported clade. The geographic and ecological extent of *M. fibrillosa* in Europe awaits further revision.

Mallocybe fulviceps (Murrill) Matheny & Esteve-Rav., *Mycologia* **112**: 106. 2019 [2020]. Figs 4D–F, 9D–I.
Basionym: *Inocybe fulviceps* Murrill, *Quart. J. Florida Acad. Sci*. **8**: 187. 1945.
Synonyms: *Inocybe pertomentosa* Murrill, *Quart. J. Florida Acad. Sci*. **8**: 189. 1945.
Inocybe vialis Murrill, *Quart. J. Florida Acad. Sci*. **8**: 191. 1945.

Pileus 10–28 mm wide, obtusely conical to convex or subexpanded with a small pointed or low broad umbo; margin incurved, becoming decurved with age; surface dry, appressed tomentose-fibrillose to fibrillose-scaly, velipellis absent; fulvous or yellowish brown (10YR 5/6; near Buckthorn Brown or a shade lighter), at times paler over the disc, dark brown with 5 % KOH; context very thin, pallid with a pale yellow tone, *odor* spermatic, at least when first cut, or somewhat acidulous. *Lamellae* sinuate to uncinate, subdistant to moderately close with *ca*. 20–24 L and several tiers of lamellulae, ventricose, broad; pallid to yellowish brown becoming dark yellowish brown with age; edges pallid, indistinctly fimbriate. *Stipe* 10–33 × 2–3 mm, equal, not bulbous; surface dry, cortina fugacious and composed of fulvous fibrils, tattered fibrillose entire length, not scaly but on occasion with scattered bands of fibrils; pale yellow (2.5Y 7/4); context solid, pale yellow throughout including in the base.

Basidia 27–35 × 9–10 µm, 4-sterigmate, clavate, hyaline or necropigmented. *Basidiospores* (9.5–)10–*11.0*–13(–14) × (4.5–)5–*5.1*–5.5(–6) µm, Q 1.90–*2.15*–2.56 (n = 85/5), smooth, oblong-elliptic, oblong-phaseoliform, less often subamygdaliform, with obtuse apices; thick-walled, ochraceous-buff, apiculus small and indistinct. *Pleurocystidia* absent. *Cheilocystidia* 28–48 × 11–16(–22) µm, clavate to utriform but saccate and obovate cells also observed; thin-walled, hyaline; edges sterile. *Caulocystidia* in clusters, similar to cheilocystidia; stipe hyphae yellowish in mass, cylindric, 4–9 µm wide, weakly incrusted, refractive hyphae not observed. *Pileipellis* a cutis of parallel hyphae, yellowish brown to ochraceous in mass, hyphae cylindric, up to 15 µm wide, incrusted. *Lamellar trama* parallel, pale yellowish brown to subhyaline in mass, hyphae cylindric, up to 15 µm wide. *Clamp connections* present.

Distribution: Southeastern USA (Florida, Louisiana).

Habitat: Scattered to gregarious, singly or in small clusters on sandy soil on karst topography in mixed forests of *Quercus* and *Pinus* or under hardwoods such as *Carpinus* and *Quercus*, including *Q. nigra*, also in disturbed areas such as roadsides. July–December.

Specimens examined: **USA**, Florida, Alachua Co., Gainesville, 11 Aug. 1944, *W.A. Murrill*, F18506 (**isotype** of *Inocybe fulviceps* WTU, **isotype** TENN-F-021186); Alachua Co., Gainesville, gregarious in a path shaded by frondose trees, 20 Sep. 1944, *W.A. Murrill*, F20017 (**isotype** of *Inocybe vialis* WTU, **holotype** FLAS-F-20017); Alachua Co., Gainesville, gregarious to caespitose in moist shaded soil, no date, *W.A. Murrill*, F19657 (**isotype** of *Inocybe pertomentosa* WTU, **isotype** TENN-F-021192); Alachua Co., Gainesville, University of Florida, Natural Area Teaching Lab, 29.63389 -92.368728, 25 Aug. 2017, Florida Mycological Foray (FLAS-F-61501); Alachua Co., Wood Creek neighborhood, Gainesville, under *Quercus virginiana*, *Q. nigra*, 19 Sep. 2020, *M.E. Smith*, MES-3773 (FLAS-F-66615); Alachua Co., Alachua, Mill Creek Preserve, West Trail, on sandy soil under *Pinus palustris*, other *Pinus*, and *Quercus*, 6 Jul. 2022, *R.A. Swenie*, PBM4715 (TENN-F-077389); *ibid. P.B. Matheny*, PBM4718 (TENN-F-077392); *ibid.*, *P.B. Matheny*, PBM4722 (TENN-F-077396); Alachua Co., Gainesville, on sandy soil under *Carpinus*, *Quercus*, Blues Creek Ravine Preserve, 7 Jul. 2022, *P.B. Matheny*, PBM4726 (TENN-F-077450); Polk Co., Circle B Bar Reserve, Lakeland, on soil near a trail, 22 Oct. 2016, *S.-Y Wu*, MES2993 (FLAS-F-66574); Putnam Co., Ordway-Swisher Biological Station (UF), near west entrance, 45 m elev., gregarious to scattered singly or in small clusters on sandy soil on side of road under *Quercus* spp., *Pinus elliottii*, 12 Dec. 2020, *M.E. Smith & P.B. Matheny*, PBM4533 (TENN-F-075556); *ibid*., near Goose Lake, 12 Dec. 2020, *P.B. Matheny*, PBM4542 (TENN-F-075565); Louisiana, St. Landry Parish, Thistlethwaite Wildlife Management Area, Peckham Road, gregarious on soil under *Quercus nigra*, 17 Jul. 2021, *D.P. Lewis*, DPL13914 (TENN-F-076539).

Notes: This is the first documentation of *Mallocybe fulviceps* since it was described from northern Florida by Murrill in 1945. The species is characterized by the small basidiomes (pileus < 30 mm wide, stipe up to 3 mm thick), the often umbonate fulvous pileus, the pale stipe, oblong basidiospores with a mean Q > 2.0, and occurrence under *Quercus* and *Pinus* on sandy calcareous soil. A comparison of the types of *M. fulviceps*, *I. pertomentosa*, and *I. vialis* indicate all share the same brown color (7.5YR 4/4 or umber brown with a slight reddish tinge), similar small basidiome size, similar pileus surface, stipe texture, and basidiospore morphology. *Inocybe pertomentosa* shows a somewhat clustered habit that we also observed in freshly collected material near the type localities. We regard all three as synonymous taxa, yet all have equal priority as they were published in the same study by Murrill (1945). We choose *I. fulviceps* for priorable purposes because this epithet most accurately describes the species morphologically.

Phylogenetically, *M. fulviceps* is nested within clade Unicolores with strong support, and nine samples of the species from Florida and Louisiana form a strongly supported clade (Figs 1, 2C). The species is sister to the remainder of the Unicolores clade also with strong support. *Mallocybe multispora* (documented below) differs from *M. fulviceps* mainly by the slenderly clavate to subcylindric cheilocystidia. *Mallocybe unicolor* differs from *M. fulviceps* by the granulose-scaly pileus surface, presence of dark colored bands of fibrils and scales on the lighter colored stipe, and elongated cheilocystidia.

Descriptions of *M. perbrevis* by Heim (1931) and Stangl (1989) (both as *Inocybe perbrevis*) seem most similar to *M. fulviceps* including the small umbo, small stature, gregarious habit, and association with hardwoods like *Populus*, *Carpinus*, and *Fagus* in Europe. The basidiospores of *M. fulviceps* (including *I. vialis* and *I. pertomentosa*) are narrower than depicted by Heim (1931) but similar to those described by Stangl (1989). Modern molecular comparisons are needed between *bona fide* collections of *M. perbrevis* and *M. fulviceps*.

Mallocybe fulvoumbonata (Murrill) Matheny & Esteve-Rav., *Mycologia* **112**: 106. 2019 [2020].
Fig. 9J, K.
Basionym: *Inocybe fulvi-umbonata* Murrill, *Quart. J. Florida Acad. Sci*. **8**: 187. 1945.

Pileus up to 15 mm wide, convex to nearly expanded and with a small but prominent umbo; margin even, entire; surface dry, tomentose, isabelline with a fulvous umbo; context very thin, pallid. *Lamellae* plane, adnate, medium distant, inserted, pallid [dried specimens dark yellowish brown], fimbriate, broad. *Stipe* 30 × 2–3 mm, longer than the pileus width, equal, dry, fibrillose, isabelline.

Basidia 26–45 × 7–10 µm, clavate, hyaline or necropigmented, 4-sterigmate. *Basidiospores* 8–*8.7*–9(–10.5) × 4.5–*5.1*–5.5(–6) µm, smooth, Q (1.50–)1.55–*1.76*–1.91(–2.00) (n = 52/2), smooth, many phaseoliform or subamygdaliform, at times elliptic, pale brown, with thickened wall, apiculus small and indistinct. *Pleurocystidia* absent. *Cheilocystidia* 22–26 × 13–15 µm, reviving poorly, broadly clavate, thin-walled, hyaline (gill edges fimbriate per Murrill), in some sections none observed. *Stipitipellis* composed of a vesture of loose interwoven hyphae, these cylindric, weakly incrusted, thin-walled, mostly 5–10 µm wide, caulocystidia not observed. *Pileipellis* a cutis of cylindric hyphae, these cylindric, weakly incrusted, thin-walled, mostly 5–12 µm wide, yellowish brown in mass. *Lamellar trama* parallel, subhyaline or very pale brown in mass, hyphae cylindric. *Clamp connections* present.

Distribution: Southeastern USA (Florida).

Habitat: Under *Quercus laurifolia*. July.

Specimens examined: **USA**, Florida, Alachua Co., Gainesville, 8 Jul. 1944, *W.A. Murrill* (**holotype** FLAS-F-24503, **isotype** TENN-F-021187).

Notes: Initially, we mistook *M. latifolia* (documented below) as *M. fulvoumbonata*, but upon examination of the holotype and isotype, we believe it is more appropriate to maintain them as separate taxa. Thus, despite our efforts to re-collect Murrill species from Gainesville in July, none of our specimens matched *M. fulvoumbonata*. Therefore, *M. fulvoumbonata*, known only from the type collection, appears to be best characterized by the lack of any substantial veil remnants over the pileus, the small but prominent umbo, the stipe length longer than the pileus width, the relatively short clavate cheilocystidia, and the noticeably pale brown to light yellow spores that are mostly 8–9 × 5 µm in size.

The other small mallocyboid species described by Murril (*viz.*, *M. fulviceps*, *M. multispora*) differ principally by their elongated, darker, narrow spores and/or cheilocystidia with a different morphology. *Mallocybe latifolia* produces larger basidiomes without a distinct umbo and larger basidiospores (mostly 9–11 × 5.5–6.5 µm) that are more darkly pigmented (yellowish brown). *Mallocybe leucothrix* also produces larger basidiomes without a distinct umbo, and both the pileus and stipe are overlain with superficial whitish fibrils.

Mallocybe latifolia (E. Ludw.) Matheny & Esteve-Rav., *Mycologia* **3**: 107. 2020 [2019]. Figs 4G–I, 9L, M.
Basionym: *Inocybe latifolia* E. Ludw., *Pilzkompendium* (Eching) **4**: 153. 2017.
Synonyms: *Inocybe acystidiata* E. Ludw., *Pilzkompendium* (Eching) **4**: 152. 2017.
Mallocybe acystidiata (E. Ludw.) Matheny & Esteve-Rav., *Mycologia* **3**: 105. 2020 [2019].

Pileus 15–42 mm wide, convex to obtusely conical, expanding to plane in age with an obtuse umbo or depressed at the center; margin inrolled to incurved in youth, later decurved and with the edge remaining inrolled at times; surface dry, tomentose-fibrillose due to superficial thin white covering throughout, the covering wearing away with age, occasionally breaking up into appressed scales or becoming cracked-areolate, never rimose; ground color fulvous or brownish yellow to yellowish brown; context firm, whitish, unchanging where bruised, odor not remarkable. *Lamellae* adnate to uncinate, close to subcrowded with about 34–40 L and several tiers of lamellulae, medium to somewhat broad; light yellowish brown to light olive brown when young, becoming brown with age; edges whitish-fimbriate. *Stipe* 30–40 × 2–6 mm, equal, generally not longer than the pileus diameter after pileus expansion; surface dry, usually without a well-developed superior ring-zone (at times a weak ring-zone may be present); cortina white, fugacious; surface white when young due to the presence of superficial silky fibrils throughout, these wearing away, surface becoming coarsely fibrillose or tattered-fibrillose and revealing an isabelline or light yellowish brown ground color with age, base white, not yellow; context solid to hollow, pale brown.

Basidia 28–47 × 7–10 µm, slenderly clavate to subclavate, hyaline or necropigmented, 4-sterigmate. *Basidiospores* (8–)9–*10*–11(–12) × 5.5–*5.9*–6.5(–7) µm, Q (1.34–)1.50–*1.68*–1.88(–2.08) elliptic, subamygdaliform, or subphaseoliform, yellowish brown, with thickened wall, apices often obtuse, apiculus small and indistinct (n = 119/4). *Pleurocystidia* absent. *Cheilocystidia* 19–34 × 12–22 µm, clavate to saccate or pyriform, subtending cells often hyphal (not densely articulated), hyaline but many ocher-brown and/or incrusted or appearing with wrinkled walls, thin-walled or with slightly thickened walls, often collapsed in revived dried mounts. *Caulocystidia* 27–46 × 12–18 µm, pyriform to clavate or subcylindric, in scattered but dense clusters, often brownish incrusted, thin-walled or with slightly thickened walls. *Pileipellis* a cutis, ochraceous-tawny in mass, hyphae with thin to slightly thickened walls, incrusted, mostly 6–15 µm wide. *Lamellar trama* parallel, pale buff in mass, hyphae cylindric, smooth, mostly 5–15 µm wide. *Clamp connections* present.

Distribution: Eastern and western USA (Arizona, Florida, Maine), southeastern Canada (Quebec), north-central China (Shaanxi), and central Europe (Germany, type), broad and intercontinental.

Habitat: On calcareous soils in mixed forest of *Quercus*, *Pinus*, under planted *Quercus*, *Pinus*, or in mixed conifer forests including *Populus*, also under *Populus* at high elevation (Arizona) and with *Populus simonsii* (ectomycorrhizal roots) in Shaanxi Province, China; in Europe on calcareous soil under *Picea*. July–December in eastern USA.

Specimens examined: **USA**, Florida, Alachua Co., Gainesville, gregarious singly on soil under *Pinus*, *Quercus*, in suburban neighborhood, B'nai Israel Synagogue, 3830 NW 16th Blvd, ca. 29.645, -82.327, 9 Dec. 2020, *M.E. Smith*, MES-3796 (=PBM4535) (TENN-F-075558; FLAS-F-67923); Putnam Co., Melrose, Ordway-Swisher Biological Station, gregarious, often singly, on disturbed soil along roadside under *Quercus* and *Pinus*, 12 Dec. 2020, *M.E. Smith*, PBM4537 (TENN-F-075560); *ibid.,* by west gate entrance, 19 Oct. 2017, *M.E. Smith* (FLAS-F-61869); Maine, Aroostook Co., Limestone, Aroostook National Wildlife Refuge, Durepo Look Trail, in mixed forest under *Picea*, *Abies*, *Larix*, *Betula*, and *Populus*, 10 Sep. 2022, *L.V. Kudzma*, LVK22088 (pers. herb.); *ibid*., LVK22089 (pers. herb.).

Notes: Phylogenetic analysis of ITS data obtained from two German type collections (*Mallocybe acystidiata* and *M. latifolia*) form a strongly supported monophyletic group with sequences from basidiomes collected under *Populus* in Arizona and a mixed conifer forest including *Populus* in Maine, and from ectomycorrhizal root tip sequences of *Populus* from north-central China (Fig. 2A). In addition, the species has been recently confirmed from Quebec (J. Landry, pers. comm.). No American or Asian names are available for this species-level clade, but there are two equally competing names from Europe (*M. acystidiata* and *M. latifolia*) published in the same work (Ludwig 2017) that can be applied to it. We choose *M. latifolia* over *M. acystidiata* because cheilocystidia were actually observed in several samples, including a re-examination of the type of *M. acystidiata* (Bandini, unpubl. data). Overall, the species has a broad intercontinental distribution with a wide range of plant associates. Phylogenetically, *M. latifolia* is nested within the greater core Mallocybe clade.

Mallocybe latifolia can be distinguished from other eastern North American *Mallocybe* by the presence of a thin white vesture, occurrence on calcareous soils probably in association with *Populus*, *Pinus*, and *Picea* (and possibly *Quercus*), the relatively large basidiospores (9–11 × 5.5–6.5 µm), and the cheilocystidia that are collapsed in revived mounts. The species closely resembles *M. fibrillosa* but lacks the odor (like burnt sugar or honey) of that species. *Mallocybe leucothrix* also possesses a distinct white vesture but differs from *M. latifolia* by the smaller basidiospores (8–10 × 4.5–5.5 µm) and phylogenetic affinities with *M. leucoloma*.

Mallocybe leucothrix Matheny & M.E. Sm., ***sp. nov.*** MycoBank MB 847416. Figs 4J, K, 10A, B.

Etymology: *leucothrix* (Gk.), white hairs, in reference to the whitish veil encompassing the basidiomata and close phylogenetic relationship to *M. leucoloma*.

Typus: **USA**, Florida, Putnam Co., Ordway-Swisher Biological Station, east of Ashley Prairie near Goose Lake, Melrose, on disturbed soil at side of road under *Quercus*, *Pinus elliottii*, 29.705, -81.967, 12 Dec. 2020, *M.E. Smith*, PBM4541 (**holotype** TENN-F-075564).

Diagnosis: Distinguished from closely related species by the combination of the whitish veil enclosing medium-sized basidiomata, basidiospores with mean Q values < 2.0, presence of short cylindric to clavate cheilocystidia, and occurrence on calcareous soils with *Quercus* and *Pinus* in Florida and Arizona. Forming a unique monophyletic group apart from closest relatives including *M. leucoloma*, *M. subtomentosa*, and the undescribed *Mallocybe* sp. 8.

Pileus 15–55 mm wide, obtusely conical or pulvinate in youth, expanding to broadly convex and plano-convex, at last plane to depressed at the center with age, umbo absent; margin incurved and usually remaining so or decurved when plane; surface dry, appressed tomentose-fibrillose, not at all scaly; color a mixture of various shades of very pale brown, pale brown, or light yellowish brown due to variable coating of a white velipellis, at times with a dull olive tone in areas (10YR 7/3–6/3–6/4; overall near clay color to isabella color where velipellis is exposed); surface dark brown with KOH, fleetingly brown with ammonia; context firm and with a pale yellow tone, confluent with the stipe, unchanging where bruised, *odor* absent or indistinct. *Lamellae* adnate to subdecurrent, close; pale olive (5YR 6/3) to grayish olive, becoming yellowish brown (10YR 5/4; clay color), edges indistinctly pallid-fimbriate. *Stipe* 20–35 × 3–6 mm, equal, often longer than the pileus width (but not always); cortina white and fugacious, not leaving a distinct annular zone; dry, surface overlain with a white vesture of superficial fibrils part of the overall veil, these wearing away revealing a pale brown to yellowish brown ground color, white at the base (not yellow); solid, becoming hollow, pallid with a pale yellow tone like the pileus context.

Basidia 30–35 × 6–15 µm, 4-sterigmate, slenderly clavate, hyaline or necropigmented. *Basidiospores* (7.5–)8–*9.1*–10(–11) × 4.5–*5.1*–5.5 µm, Q (1.50–)1.55–*1.78*–2.04(–2.08) (n = 41/2), smooth, mostly amygdaliform to somewhat phaseoliform due to a ventral depression, occasionally ovate, apices bluntly pointed, yellowish brown to brownish yellow in KOH, apiculus small and indistinct, wall slightly thickened. *Pleurocystidia* absent. *Cheilocystidia* 18–32 × 6–10 µm, cylindric to clavate or short-cylindric to short-clavate, arising from short hyphal segments or articulated hyphae, thin-walled, hyaline, edges of lamellae sterile or nearly so. *Caulocystidia* present at the extreme apex of the stipe, similar to cheilocystidia. *Pileipellis* an interwoven cutis, rusty brown to tawny in mass; hyphae cylindric, noticeably incrusted, thin-walled or slightly thick-walled, mostly 5–14 µm wide. *Lamellar trama* parallel, hyphae mostly 3–19 µm wide, cylindric to inflated, light yellowish brown in mass, thin-walled, smooth. *Clamp connections* present.

Distribution: Southeastern (Florida) and southwestern USA (Arizona).

Habitat: Scattered to gregarious on karst topography under *Quercus virginiana*, other *Quercus* spp., and *Pinus elliottii* in Florida, also on calcareous soils under *Pinus engelmannii* and *Quercus hypoleucoides* in Arizona. August (Arizona) and December (Florida).

Other specimen examined: **USA**, Florida, Putnam Co., Ordway-Swisher Biological Station, east of Ashley Prairie near Goose Lake, Melrose, 29.705, -81.967, 12 Dec. 2020, *C.R. Noffsinger & P.B. Matheny*, PBM4531 (TENN-F-075554).

Notes: *Mallocybe leucothrix* forms a monophyletic group with moderate support based on five samples collected under *Quercus* and *Pinus* on calcareous soils in Florida and Arizona. The species is most closely related to an undescribed species that differs ecologically by association with *Picea* on acidic soils in West Virginia, Quebec, and China. Because of the phylogenetic and ecological differences, we recognize both clades as separate species even though both are united as a strongly supported monophyletic group. Both species are closely related to the intercontinental species *M. leucoloma*, which to date has been observed in western North America in alpine settings with shrub and dwarf *Salix* and in conifer forests mixed with *Betula* and *Populus*. Several similarities with *M. leucoloma* include the relatively distinct white veil covering of the basidiomata, white cortina, white stipe base, and the stipe length at times longer than the pileus width. *Mallocybe leucoblema* can be distinguished from *M. leucothrix* generally by the more robust size, occurrence on calcareous soils in alpine and montane regions of western North America and Europe, and unique phylogenetic position sister to the Delecta clade.

Mallocybe subtomentosa differs from *M. leucothrix* by the subsmooth pileus, occurrence on acidic soils with *Quercus* and/or *Pinus*, and by phylogenetic position. *Mallocybe tomentella* (described as new below) differs from *M. leucothrix* by the bicolorous pileus, presence of a cortinate ring-zone on the stipe, occurrence on acidic soils, and phylogenetic association with members of the *M. malenconii* group.

Mallocybe luteobasis Matheny & M. Kuo, ***sp. nov.*** MycoBank MB 847417. Figs 5A–C, 10C, D.

Etymology: *luteobasis* (L.), yellow base, in reference to the yellow base of the stipe.

Typus: **USA**, Illinois, Coles Co., Charleston, Fox Ridge State Park, on soil under *Quercus*, 18 Jul. 2007, *M. Kuo*, MK07180705 (**holotype** TENN-F-073750).

Diagnosis: Distinguished from closely related species by the combination of the medium-sized basidiomata often with large appressed scales, yellow stipe base or yellow basal mycelium, the broad basidiospores with a mean Q value < 2.0, elongate digitiform cheilocystidia, and occurrence on calcareous soils under fagaceous trees. Forming a monophyletic group within the Terrigena grade.

Pileus 20–55 mm wide, convex becoming plano-convex to plane, margin inrolled; surface dry, appressed-squamose to appressed-fibrillose; scales reddish brown, strong brown, or fulvous against a lighter background color, center at times reddish brown; gray or dark brown with KOH; context up to 3 mm thick under the disc, pale yellow, unchanging where bruised, *odor* none or not distinctive. *Lamellae* broadly adnate to uncinate, moderately close, lamellulae frequent; pale yellow when young or whitish to brownish yellow or with olivaceous tone, becoming olive-brown (Dresden Brown) with age; edges noticeably fimbriate, white to yellowish. *Stipe* 25–60 × 3–9 mm, more or less equal or tapered to the base; apex with decurrent lamellar lines; veil cortinate and thick and fibrillose covering the lamellae entirely when young, this becoming a cortinate ring-zone at times but not always; surface dry, fibrillose-scaly or shaggy-fibrillose below the veil, at times fibrils forming bands; fibrils and scales brownish

Fig. 5. Basidiomes of *Mallocybe* from eastern North America. **A.** *M. luteobasis* (MK0611102, photo M. Kuo). **B.** *M. luteobasis* (MK07180705, holotype, photo M. Kuo). **C.** *M. luteobasis* (G. Sayers *s.n.*, photo G. Sayers). **D.** *M. malenconii* (LVK21286, photo L. Kudzma). **E.** *M. montana* (PBM4585, photo B. Matheny). **F.** *M. montana* (PBM3872, holotype, photo B. Matheny). **G.** *M. montana* (PBM4190, photo B. Matheny). **H.** *M. multispora* (PBM4717, photo B. Matheny). **I.** *M. multispora* (FLAS66616, photo M. Smith). Scale bars = 1 cm.

to reddish brown against a dull yellowish ground color; basal mycelium sulphur yellow, especially beneath the soil; context pale yellow, unchanging where bruised, typically yellow at the base when fresh.

Basidia 36–41 × 7–8 µm, 4-sterigmate, slenderly clavate, soon collapsed, becoming necropigmented. *Basidiospores* (8.5–)9–*9.6*–10(–12) × (5–)5.5–*5.6*–6(–7) µm, Q (1.50–)1.64–*1.71*–1.90(–2.18) (n = 45/3), smooth; elliptic, subphaseoliform, or nearly amygdaliform, at times with a ventral depression; thick-walled, brownish in KOH, apiculus indistinct. *Pleurocystidia* absent. *Cheilocystidia* 18–60(–65) × 4–10 µm, many digitiform or irregularly cylindric with a flexuous outline and tapered apices, at times mixed with shorter cylindric cells or apices obtuse or rarely swollen, thin-walled (rarely slightly thickened), hyaline or infrequently ochraceous. *Stipitipellis* a vesture of superficial hyphae, these dark russet or dark tawny in mass, 5–12 µm wide, weakly incrusted or smooth, thin-walled, *caulocystidia* not observed; tramal hyphae hyaline, smooth, thin-walled, cylindric. *Pileipellis* a turf or interwoven cutis of dark russet or dark rusty colored hyphae in mass, these cylindric and mostly 5–12 µm wide, weakly incrusted or smooth, thin-walled. *Lamellar trama* parallel, pale yellow to subhyaline in mass, hyphae cylindric, many 4–10 µm wide, smooth, thin-walled. Lamellar trama parallel. *Clamp connections* present.

Distribution: Midwestern (Illinois, Indiana, Kansas) and southeastern states (Tennessee), USA.

Habitat: On calcareous ground under hardwoods including *Quercus*, *Fagus*, *Carpinus*, and/or *Carya*. June–September.

Other specimens examined: **USA**, Illinois, Coles Co., Charleston, Lakeview Park, on ground under *Quercus* mixed with *Carya* and *Juniperus*, 21 Jun. 2011, *M. Kuo*, MK06211102 (TENN-F-073749); *ibid*., 29 Jul. 2020, *M. Kuo*, MK07292005 (herb. Kuo); Marion Co., gregarious under *Carya glabra*, *Ulmus rubra*, *Juniperus virginina*, 7 Jun. 2015, *M. Kuo*, MK06071503 (TENN-F-074751); Indiana, Parke Co., on soil in deciduous woods, 14 Jul. 2003, *M. Kuo*, MK07140307 (TENN-F-074752); Kansas, locality unknown, in mixed hardwood forest under *Quercus*, 7 Aug. 2008, *G. Sayers s.n.* (TENN-F-063525); Tennessee, Anderson Co., Norris Dam State Park, Clear Creek Trail, on soil in hardwood forest under *Quercus*, *Fagus*, *Carpinus*, *Carya*, 21 Sep. 2018, *P.B. Matheny*, PBM4194 (TENN-F-074601); *ibid.* 8 Aug. 2019, *P.B. Matheny & R.A. Swenie*, PBM4312 (TENN-F-074884); *ibid*. 16 Aug. 2020, *P.B. Matheny*, PBM4437 (TENN-F-075309); *ibid*. 3 Sep. 2020, *P.B. Matheny*, PBM4479 (TENN-F-075351); Knox County, William Hastie Natural Area, on soil on karst topography under *Quercus*, *Carya*, *Pinus virginiana*, 5 Jul. 2023, *R.A. Swenie*, RAS1119 (TENN-F-078399).

Notes: *Mallocybe luteobasis* is described here as new to accommodate a species recognized by the conspicuous reddish brown to fulvous appressed scales against a lighter background pileus color, dark colored fibrils and scales on the stipe, the yellow stipe base, pale yellow context, and occurrence under hardwoods (*Fagales*) on calcareous soils in midwestern and southeastern states of the USA. The spores are somewhat wider than all other eastern North American *Mallocybe* and have an average Q value less than 2.0. An additional distinctive feature of *M. luteobasis* is the digitiform or subcylindric cheilocystidia that may be elongated. The species could be confused with *M. unicolor*, but the latter differs from *M. luteobasis* by the granulose-scaly pileus surface, whitish stipe base, the typically oblong spores, and the differently shaped cheilocystidia (irregularly cylindric to fusiform at times with subcapitate apices). The two species are sympatric and co-occur at the same localities but are distantly related. *Mallocybe fulvipes* (Cripps *et al.* 2010) is somewhat similar given the squamulose-fibrillose reddish brown pileus and yellow stipe base, but this species can be distinguished from *M. luteobasis* by its occurrence in alpine regions with *Salix* in western North America and Europe and phylogenetic position within the Delecta clade.

Phylogenetically, *M. luteobasis* represents the first split in the Terrigena grade (Fig. 1) where it is strongly supported as sister to the rest of the core Mallocybe clade. Four specimens sequenced from Illinois (type), Indiana, and Kansas form a strongly supported group. Samples from Tennessee have also been observed.

Smith & Hesler (1968) drew some similarities between *Pholiota sola* and *Inocybe*. *Pholiota sola* is similar to *M. luteobasis* in outward appearance other than the notably elongated stipe in relation to the pileus width in *P. sola*. This species was described based on a single collection with the type from Michigan, not Washington D.C. as stated in the protologue. The spores are somewhat narrower compared to *M. luteobasis*, and chrysocystidia and pleurocystidia were described as present, which would support placement in *Pholiota*. Smith & Hesler (1968) also noted the dry pileus and the absences of gelatinous tissues and of a germ pore in *P. sola*, similarly to *Mallocybe*.

Mallocybe malenconii (R. Heim) Matheny & Esteve-Rav., *Mycologia* **112**: 107. 2019 [2020]. Figs 5D, 10E, F.
Basionym: *Inocybe malenconii* R. Heim, *Encyclopédie Mycol*. **1**: 163. 1931.
Synonym: *Inocybe marmoripes sensu N. Am. auct. p.p.*

Pileus 10–25 mm wide, convex to plano-convex or almost plane, never depressed at the center, margin incurved for long durations but not inrolled; surface dry, center decorated with prominent, short, woolly tufts of fibrils that are concolorous with or slightly darker than the rest of the surface, at first simply fibrillose; center dark reddish brown to yellowish red (Argus Brown to Amber Brown (5YR 3/4–4/6), shading to Buckthorn Brown (10YR 5/6–5/8) towards the margin (Sienna color per Heim); context fleshy, firm, pale ocher-pink; *odor* and *taste* indistinct. *Lamellae* adnate or mostly uncinate, moderately close, ventricose but somewhat narrow; cinnamon but becoming much darker with age, edges pallid. *Stipe* 15–40 × 3–5 mm, irregularly cylindric, usually flexuous, often curved or twisted, equal towards the base; surface dry, in age with darker brown scattered fibrillose tufts; light brownish or paler at the apex and at the base; context fibrous, tough, not putrescent, more or less hollow.

Basidia 20–32 × 6–9 µm, 4-sterigmate, slenderly clavate to subcylindric, hyaline but becoming necropigmented. *Basidiospores* (9–)9.5–*10.7*–12 × 4–*4.5*–5 µm, Q (2.11–)2.20–*2.39*–2.75(–2.88) (n = 50/3), smooth; oblong-cylindric, oblong-subphaseoliform, or oblong-amygdaliform (“laceroid”), often with a ventral depression and obtuse to bluntly pointed apices; brownish yellow to pale brown, wall slightly thickened, apiculus small and indistinct. *Pleurocystidia* absent. *Cheilocystidia* 17–26 × 10–16(–20) µm, short clavate or short cylindric to sphaeropedunculate or obclavate, thin-walled, hyaline to ochraceous, rarely brownish incrusted; lamellar edges sterile. *Caulocystidia* similar to cheilocystidia, restricted to the extreme apex of the stipe (possibly just an extension of the hymenium at the extreme stipe apex); superficial hyphae sparse, yellowish brown to ochraceous in mass, cylindric, 6–13 µm wide, weakly incrusted. *Pileipellis* composed of tufts of trichodermial hyphae, these Tawny to Ochraceous-Tawny in mass, cylindric to inflated and mostly 10–18 µm wide, incrusted to coarsely so, with slightly thickened walls. *Lamellar trama* parallel; hyphae light yellowish in mass, 10–18 µm wide, smooth, thin-walled. *Clamp connections* present.

Distribution: Northern regions of eastern and western North America (British Columbia, Maine, New York, Quebec, Washington). Also, northern and central Europe (type), eastern Russia, Korea.

Habitat: On sandy acidic soils under mixture of conifers (*Pinus*, *Picea*) and/or *Salix* and *Betula*. April–May in the Pacific Northwest, August–September in the northeast USA and southeastern Canada.

Specimens examined: **Canada**, British Columbia, Cranbrook, on trail to Lloyds Meadows off Crowsnest Highway, 1 100 m elev., 21 May 2002, *O. Ceska*, 2020521-001 (UBC F19123; image only). **Finland**, Pohjois-Häme, Saarijärvi, Linnankylä, along margin of road 13, in sandy soil on bank of road near *Pinus sylvestris* and young *Betula pubescens*, *Salix caprea*, and *Salix phylicifolia*, 18 Aug. 1989, *J. Vauras*, JV3590F (TURA, WTU); Satakunta, Kankaanpää, Niinisalo, the spring Yskänlähde, on sandy soil near *Pinus sylvestris*, 24 Jul. 1990, *J. Vauras*, JV4470F (TURA, WTU); Perä-Pohjanmaa, Rovaniemi rurual commune, Jaatila, Jaatilanvaara, near Savioja, edge of the main road near young *Picea abies*, *Betula*, and *Salix* on sandy soil, 24 Aug. 1991, *J. Vauras*, JV5824F (TURA, WTU). **USA**, Maine, Medway, Penobscot Co., Route 11 south of Grindstone Falls Rest Area, on soil along roadside under *Quercus*, *Pinus*, 9 Sep. 2022, *L.V. Kudzma*, LVK22039 (pers. herb.); *ibid.*, LVK22045 (pers. herb.); New York, Essex Co., Bloomingdale, in sandy soil under mixed conifers and hardwoods, 13 Aug. 2021, *L.V. Kudzma*, LVK21286 (pers. herb.); Washington, Snohomish Co., Point Wells, near Richmond Beach, 2 Apr. 1941, *D.E. Stuntz*, 948 (WTU).

Other specimen examined (Inocybe subgranulosa): **Finland**, Tavastia australis, Tamella, Barrskog., på brända sandmarker (Mustiala på Syrjä), 2 Oct. 1892, *P. Karsten* (**holotype** H 2499).

Notes: The gross morphological description of *M. malenconii* is taken mainly from Heim (1931, as *Inocybe malenconii*) but modified to fit the formatting here and supplemented with observations from material collected in the USA. No other previously described North American taxon appears to match this species though it is very closely related to what we now interpret here as *M. tomentella* described as new below. Several studied European specimens agree morphologically and genetically with North American samples from the Pacific Northwest, New York, and Maine and thus, for the first time, confirm the presence of *M. malenconii* from North America. It has also been recently confirmed in Quebec (J. Landry, pers. comm.). Where the ecology is known, the species appears to occur on sandy acidic soils.

Mallocybe malenconii resembles forms of *Inocybe lacera* in outward appearance, and microscopically has similar oblong “laceroid” basidiospores with an average Q value > 2.00. However, the absence of pleurocystidia and presence of necrobasidia easily distinguish the species from *I. lacera*. The species in a restricted sense is monophyletic with strong support, but references to collections of *M. malenconii* from China and Spain are very closely related to those of *M. subgranulosa* (including its type) from Sweden and Finland (Fig. 2A). *Mallocybe malenconii* differs from *M. tomentella* morphologically by the narrower “laceroid” shaped spores, however, both were observed to co-occur in the same sandy acidic soil habitats in New York.

Mallocybe malenconii has been reported from Kamchatka in Russia (Peintner & Horak 2002) and Korea (Cho *et al*. 2021) and thus would have a broad circumboreal distribution, however, Asian samples have yet to be confirmed in the *M. malenconii* clade in the strict sense. Kauffman (1924) and Stuntz (1940) recognized the species from the Pacific Northwest but under the broadly misapplied name of *Inocybe marmoripes*. The latter, as interpreted by Kauffman (1924) and Stuntz (1940), actually included two species (*M. malenconii* and *Mallocybe* sp. 2 in Fig. 2A). Upon inspection of these materials, *Mallocybe* sp. 2 was found to differ from *M. malenconii* genetically and by the longer basidiospores. Note that *Inocybe marmoripes* is considered a later synonym of *M. unicolor* (see below).

Mallocybe megalospora differs from *M. malenconii* by the wider spores and association with *Salix* and *Alnus* in Europe (Stangl & Bresinsky 1983). This taxon has not been confirmed from North America. An unpublished sequence (GenBank HQ604786) under this name has been reported from British Columbia, but that sequence represents *Mallocybe* sp. 2, which appears to be endemic to the Pacific Northwest.

Mallocybe montana Matheny, ***sp. nov*.** MycoBank MB 847419. Figs 5E–G, 10G, H.

Etymology: *montana* (L.), mountain, in reference to occurrence in the southern Appalachian Mountains.

Typus: **USA**, North Carolina, Haywood Co., Great Smoky Mountains National Park, Big Creek, Baxter Creek Trail, scattered to gregarious on sandy acidic soil in riverbed under hardwoods in a riparian hardwood forest, 518 m elev., 9 Aug. 2012, *P.B. Matheny*, PBM3872 (**holotype** TENN-F-067500).

Diagnosis: Characterized by the small to medium-sized basidiomata, finely velutinous pileus, lighter colored stipe, cylindric basidiospores with a mean Q value > 2.0, presence of elongated cheilocystidia that are pale brown in mass in KOH, and occurrence on poor, sandy, acidic soils in Appalachian montane mixed forests. Distinguished phylogenetically as the sister lineage to clades Unicolores, Nothosperma, and Mallocybe.

Pileus 8–35 mm wide, convex at first, occasionally obtusely conical, expanding to broadly convex or nearly plane with age, umbo absent, center slightly depressed with age; margin incurved to decurved, entire; surface dry, velipellis and veil remnants absent, finely tomentose to finely velutinous or matted woolly tomentose under a hand lens, appearing subsmooth to the naked eye; strong brown (7.5YR 4/4) to yellowish brown or dark yellowish brown (10YR 5/6–5/8–6/6–4/4; Prout’s Brown to Dresden Brown), brownish with 5 % KOH; context watery pale brown to olive-yellow when moist, up to several mms thick under the disc, not changing color where bruised; *odor* noticeable when first cut, nearly acidulous but with an unpleasant component, at times not remarkable; PDAB negative. *Lamellae* adnate to uncinate, seceding, subdistant with 18–22 L and several tiers of lamellulae; brown to yellowish brown (10YR 5/3–5/4) or dark yellowish brown with age; medium, up to 4 mm deep; edges crenate or nearly so, not white but colored pale brown like the faces. *Stipe* 14–40 × 2–5 mm at the apex, equal, not bulbous, cortina not observed; surface dry, with scattered fine brown fibrils against a pale brown or pale yellow (buff) to light yellowish brown ground color (2.5Y 7/4, 10YR 6/3–6/4), overall paler than the pileus; context not confluent, pale brown throughout, base encased in sand, basal mycelium white, solid.

Basidia 42–60 × 7–10 µm, 4-sterigmate, slenderly clavate to subcylindric, necropigmented. *Basidiospores* (10–)11–*12.2*–13.5(–14) × (4.5–)5–*5.4*–6 µm, Q (1.82–)1.92–*2.27*–2.55(–2.80) (n = 60/4), smooth, oblong-amygdaliform or cylindric, yellowish brown with thickened walls, apiculus not distinctive. *Cheilocystidia* 26–74 × 8–16 µm, slenderly clavate or elongate-clavate to somewhat cylindric, arising from short articulated cells, apices often swollen or subcapitate, thin-walled or weakly thickened in places, pale brown in mass, on occasion with fine apical incrustations, necropigmented with age. *Pleurocystidia* absent. *Stipitipellis* with clusters of dense short clavate to subcylindric caulocystidia, 27–40 × 8–12 µm, these thin-walled and hyaline; or without caulocystidia, composed of scattered interwoven brownish to ocher-tawny tufts of terminal hyphae similar to pileipellis hyphae; terminal cells cylindric, not particularly cystidioid, pigmented and smooth to incrusted, mostly 8–20 µm wide; with numerous refractive hyphae present in stipe trama. *Pileipellis* a tangled interwoven trichoderm or short turf, composed of loose chains of hyphae, ocher-tawny in mass in KOH; hyphae cylindric, mostly 8–20 µm wide, walls thin or slightly thickened and often with pale brownish to ocher-tawny pigment, at times incrusted or coarsely so, terminal cells occasionally cystidioid or differentiated in appearance. *Lamellar trama* parallel; hyphae pale yellowish in mass, 4–15 µm wide, smooth or weakly incrusted. *Clamp connections* present.

Distribution: Southeastern USA (North Carolina).

Habitat: Scattered singly or in pairs, often on very sandy acid soil in mixed forests of *Quercus*, *Pinus*, *Betula*, and *Tsuga* or under hardwoods in sandy riparian areas. July–September.

Other specimens examined: **USA**, North Carolina, Macon Co., Highlands, Wahalla Road, Blue Valley Road, scattered singly on sandy acid soil on side of dirt road under *Pinus strobus*, *Betula alleghaniensis*, *Quercus*, 760 m elev., 8 Sep. 2018, *P.B. Matheny*, PBM4190 (TENN-F-074532); *ibid.*, on sandy acid soil on side of dirt road under *Quercus, Pinus*, 760 m elev., 26 Jul. 2021, *R.A. Swenie & P.B. Matheny*, PBM4585 (TENN-F-075751); North Carolina, Macon Co., Nantahala National Forest, Rock Gap, Appalachian Trail near Standing Indian Campground, scattered singly on acid soil in mixed forest under *Tsuga*, *Pinus strobus*, *Quercus*, *Betula*, 885 m elev., 30 Jul. 2021, *P.B. Matheny*, PBM4614 (TENN-F-075781).

Notes: *Mallocybe montana* is an unusual species of *Mallocybe* characterized by the elongated, clavate, pale brown pigmented cheilocystidia, long basidia, and narrow oblong spores. The species is currently only known from the southern Appalachian Mountains at several different localities in western North Carolina where it occurs on acidic and often sandy soils. To the eye, the pileus may seem almost smooth but is velutinous to woolly-tomentose under a hand lens, and no veil remnants have yet been observed. It matches none of the prior descriptions of species made by North American workers, thus the species is described here as new.

Mallocybe montana represents a significant discovery because, together with *M. praevillosa* (see below), it forms a strongly supported grade (paraphyletic group) from which the remainder of *Mallocybe* is derived (Figs 1, 2C). Three samples of *M. montana* collected in different regions of western North Carolina form a strongly supported monophyletic group. *Mallocybe multispora* is somewhat similar but differs from *M. montana* by the hyaline or rarely ochraceous cheilocystidia, convex to conical pileus with a small conical or subacute umbo, the more tomentose to scaly pileus covering, occurrence at lower elevations in mixed pine-oak or hardwood forests, and phylogenetic placement in clade Unicolores sister to *M. unicolor*.

Mallocybe multispora (Murrill) Matheny & Esteve-Rav., *Mycologia* **112**: 107. 2019 [2020]. Figs 5H, I, 10I, J.
Basionym: *Inocybe multispora* Murrill, *Proc. Florida Acad. Sci*. **7**:122. 1944.

Pileus 7–20 mm wide, convex to conical and often with a distinct (sub)conical or subacute umbo, margin incurved in youth, soon decurved or nearly straight; surface dry, umbo covered with a grayish velipellis, with appressed fibrillose scales at the center, coarsely fibrillose or tomentose towards the margin, not rimose but margin occasionally split; pale isabelline to fulvous or ochraceous tan (yellowish brown or fulvous when dried 10YR 5/6–5/8 or 7.5YR 5/6); context thin, *odor* sweet [in protologue], "fishy" when cut, or mild. *Lamellae* adnexed to adnate, moderately close, broad, edges white and fimbriate, yellowish brown to brown. *Stipe* 15–35 × 1.5–3 mm, subequal above a small bulb or swollen to enlarged, dry, ochraceous-buff, roughened with longitudinal fibrils; context concolorous, not hollow.

Basidia 30–40 × 7–10 µm, 4-sterigmate, slenderly clavate, hyaline or necropigmented. *Basidiospores* 10–*11.3*–13(–14) × 4.5–*5.3*–6(–6.5) µm, Q 1.82–*2.14*–2.47(–2.55) (n = 43/2), smooth, yellowish-brown, oblong-elliptic, oblong-subphaseoliform, or oblong-amygdaliform, often with a ventral depression, apices obtuse to bluntly pointed, germ pore absent, thick-walled, apiculus small and indistinct. *Pleurocystidia* absent. *Cheilocystidia* 27–55 × 8–15(–20) µm, subcylindric or slenderly clavate with obtuse to subcapitate apices, thin-walled, hyaline (rarely ochraceous), edges of lamellae sterile. *Caulocystidia* absent, numerous opaque refractive hyphae present among stipe hyphae. *Pileipellis* a cutis forming trichodermial fascicles, hyphae cylindric to inflated, many 7–12(–20) µm wide and coarsely incrusted and with thickened walls, bright tawny or bright fulvous in KOH. *Lamellar trama* parallel, yellowish brown in mass, hyphae cylindric and up to 11 µm wide. *Clamp connections* present.

Distribution: Southern USA (Florida, Oklahoma, Texas).

Habitat: Gregarious on sandy soil, at times pure sand, on calcareous soils (where known) under *Quercus*, *Pinus*, palms, or in hardwood forests including *Quercus* and *Carya*. June–November.

Other specimens examined: **USA**, Florida, Alachua Co., Gainesville, gregarious under a palm, 8 Jun. 1938, *W.A. Murrill*, F17380 (**isotype** TENN-F-021190, **isotype** WTU); *ibid.*, Green Acres Park, under *Quercus* *virginiana* and *Q. nigra*, 14 Jun. 2020, *M.E. Smith & O. Smith*, MES3732 (FLAS-F-66616); Alachua Co., Alachua, Mill Creek Preserve, West Trail, on sandy soil under *Pinus palustris*, other *Pinus*, and *Quercus*, 6 Jul. 2022, *P.B. Matheny*, PBM *4717* (TENN-F-77391); Martin Co., Jonathan Dickson State Park, on sandy moist pine flatlands with abundant *Sabal etonia* (Scrub Palmetto) and forbs, 22 Nov. 2017, *L. Kaminsky* (FLAS-F-61779); Oklahoma, Pontotoc Co., Pontotoc Ridge Nature Preserve, 15.5 miles south of Ada, gregarious on soil in mixed hardwoods under *Quercus*, *Carya*, *Ulmus*, *Fraxinus*, 21 Sep. 2002, *C.L. Ovrebo*, CO4248 (CSU); Texas, Newton County, Bleakwood, Lewis properties front lot by state highway 87, on soil in bottomland hardwood forest near *Pinus*, 36 m elev., 3 Jun. 2020, *D.P. Lewis*, DPL13581 (TENN-F-0778786).

Notes: This is the first report of *Mallocybe multispora* since the species was described from northern Florida in the 1940s (Murrill 1944). We confirm, based on morphological comparisons, extant collections from Florida, Oklahoma, and Texas. Of the available names in *Mallocybe* (under the genus *Inocybe*) originally described by Murrill, *M. multispora* matches the modern samples best by virtue of the gregarious habit, small basidiome size, pileus with a conical umbo, pallid stipe, and subcylindric to slenderly clavate cheilocystidia. Murrill also described (from a single collection) the presence of a bulbous stipe base for *M. multispora*, a feature, however, we did not observe in fresh material. *Mallocybe fulviceps* is very similar to *M. multispora*, and closely related to it but differs by the shorter clavate, utriform, or saccate cheilocystidia and phylogenetic position. *Mallocybe montana* is similar microscopically to *M. multispora*, but the pileus is not umbonate, the cheilocystidia are often pale brown pigmented, and it occurs on acidic soils in mountainous areas of the Southern Appalachians.

Of European species, *M. multispora* seems most similar to *M. perbrevis* reported in association with hardwoods (Heim 1931, Stangl 1989). This species, like *M. multispora* and *M. fulviceps*, is also depicted with a small pointed umbo, small stature, and gregarious habit similar to *M. multispora*. Until direct molecular comparisons can be made with *bona fide* reference material of *M. perbrevis*, we prefer to point to the superficial similarities but maintain the autonomy of the two American species. *Mallocybe arthrocystis*, a pan-north temperate species with oblong or cylindric-shaped spores, associates with *Salix* in western North America in alpine settings (Cripps *et al.* 2010). It differs from *M. multispora* by the short articulated cheilocystidia, bell-shaped pileus, and white lamellae in youth.

Phylogenetically, *M. multispora* is confirmed with strong support as a closely related sister species to *M. unicolor* (Figs 1, 2C) in clade Unicolores. *Mallocybe unicolor* differs from *M. multispora* and *M. fulviceps* by the larger basidiomes, pileus without a conical umbo, distinctly granulose-squamulose pileus surface, bands of dark colored fibrils on the stipe, and elongated cheilocystidia.

The ecology of *M. multispora* is still coming into focus. The subtropical Florida sample was collected in pure sand among pines and palms, whereas our more recent material was collected under oaks. Murrill's protologue states the type was collected under a palm, a non-ectomycorrhizal plant; however, the Oklahoma material was found in mixed hardwoods under *Quercus*, *Carya*, *Ulmus*, and *Fraxinus* on sandy soil. The evidence from recent collections suggest that this taxon is likely an ectomycorrhizal associate of *Fagales*, but we cannot rule out associations with *Pinaceae* as well.

Mallocybe praevillosa (Murrill) Matheny, ***comb. nov.*** MycoBank MB 84723. Figs 6A, 10K–N.
Basionym: *Lepista praevillosa* Murrill, *Lloydia* **5**: 155. 1942.
Synonym: *Inocybe praevillosa* Murrill (Murrill), *Mycologia* **36**: 122. 1944.

Pileus 15–47 mm wide, habit tricholomatoid, convex, broadly convex to conico-convex, expanding to plano-convex with age, not umbonate, margin incurved to decurved; surface dry, villous to fine suede-like smooth over the disc and towards the margin, not rimose, margin entire and at times finely fibrillose, velipellis absent, matt, dull; very pale brown (10YR 7/4) to yellow (2.5Y 7.6) or light yellowish brown (2.5Y 6/4) or Cream-Buff to Chamois or Honey Yellow with Isabella Color tones (2.5Y 5/4–5/6) in places with age, surface negative with 5 % KOH; context thick, white, not changing color where bruised, firm, tough, confluent with the stipe, *odor* and *taste* somewhat unpleasant, remaining unpleasant after dried. *Lamellae* sinuate to uncinate, close to nearly crowded with few tiers of lamellulae, narrow to somewhat broad, brittle, very pale brown to pale brown or light yellowish brown (10YR 7/4–6/3–6/4), edges pallid but indistinctly fimbriate. *Stipe* 40–80 × 8–11 mm, equal, terete, at times slightly curved, much of the lower part buried in sand; surface dry, rough, scurfy-fibrillose, no veil observed even in a young button; whitish to white throughout, KOH negative on surface; context white, confluent with pileus. *Spore print* "pale-purplish in mass" per the protologue.

Basidia 31–36 × 7–9 µm, slenderly clavate, 4-spored, hyaline, at times collapsed but none necropigmented. *Basidiospores* (8–)8.5–*9.7*–11(–12) × 3.5–*4.2*–4.5(–5) µm, 1.89–*2.30*–2.67(–2.75) (n = 62/3), allantoid to oblong-cylindric or oblong-phaseoliform in profile, oblong-cylindric to minimally angular in face view, apices obtusely conical, very pale brown in KOH (noticeably pale), no reaction in Melzer's, apiculus not distinctive. *Pleurocystidia* absent. *Cheilocystidia* 25–61 × 12–22 µm, broadly clavate to broadly fusiform or utriform, at times fusiform, occasionally long-pedicellate, apices often smooth and obtuse but on occasion developing a filiform appendage, thin-walled, hyaline, edges of lamellae sterile. *Stipitipellis* with protruding cylindric, fusiform, and irregularly cylindric terminal cells 37–66 × 6–8 µm but not appearing in tufts or in a gregarious hymenial formation, these hyaline, more or less thin-walled. *Pileipellis* a cutis giving rise to trichodermial tufts or interwoven upturned hyphae, thin-walled or slightly thick-walled, 5–12 µm wide, lacking any noticeable incrustations, light yellowish brown or brownish yellow to ocher-tawny in mass (not darkening appreciably in KOH mounts and no exudation of pigment), terminal cells mostly cylindric to slightly clavate. *Lamellar trama* parallel, dull yellow in mass, hyphae smooth in appearance, thin-walled, up to 10 µm wide. *Clamp connections* present.

Distribution: Southeastern USA (Florida).

Habitat: Solitary to scattered or gregarious in calcareous sand or sandy soil in high oak-pine forests and sandhill habitat under *Pinus palustris* and *Quercus* or under *Quercus laurifolia*. July–August.

Specimens examined: **USA**, Florida, Alachua Co., Gainesville, solitary in high *Pinus-Quercus* woods, 12 Jul. 1939, *W.A. Murrill* (**holotype** FLAS-F-19723); *ibid*., same habitat as above, 6 Jul. 1939, *W.A. Murrill* (FLAS-F-19703); Alachua Co., Alachua, Mill Creek Preserve, West Trail,

Fig. 6. Basidiomes of *Mallocybe* from eastern North America. **A.** *M. praevillosa* (PBM4724, photo B. Matheny). **B.** *Mallocybe* sp. 8 (PBM4749, photo B. Matheny). **C.** *M. squamosodisca* (PBM4307, photo B. Matheny). **D.** *M. squamosodisca* (LVK20133, photo L. Kudzma). **E.** *M. subtomentosa* (SAT-99-233-01, photo S. Trudell). **F.** *M. subtomentosa* (LVK16004, photo L. Kudzma). Scale bars = 1 cm.

on sandy soil under *Quercus laurifolia* with *Pinus palustris* in the general vicinity, 6 Jul. 2022, *C.R. Noffsinger*, PBM4724 (TENN-F-077398); Putnam Co., Ordway-Swisher Biological Station, by Blue Pond, 29.71008 -81.992526, in sandhill habitat under *Quercus*, *Pinus palustris*, 28 Aug. 2017, *L. Kaminsky & D. Borland* (FLAS-F-61523).

Notes: Comparisons of two recent collections from northern Florida with the holotype of *Lepista praevillosa* indicates they are conspecific with the holotype based on the similar basidiome morphology, ecology, and microscopic features. Blast searches using ITS (GenBank MH211949) and 28S (GenBank MH620294) sequences produced from the modern reference materials were inconclusive and did not provide confident generic placement for this unusual species. Indeed, our rDNA phylogeny placed samples of this species outside *Mallocybe* among outgroups but with poor support (Supplementary Fig. S3). However, we re-extracted DNA from FLAS-F-61523 and PBM4724 and produced longer 28S reads than GenBank MH620294, as well as and partial *rpb1* and *rpb2* sequences. In Figs 1 and 2C, one can now see that *Lepista praevillosa* forms the sister species to the remainder of *Mallocybe*. Classification of *Lepista praevillosa* in *Mallocybe* appears warranted by the rather robust tricholomatoid basidiomes, smooth basidiospores, absence of pleurocystidia, and presence of distinct cheilocystidia. However, the species exhibits some features that deviate from most other species of *Mallocybe*: (i) the basidia are not necropigmented; (ii) the pileus surface does not darken with application of 5 % KOH; and (iii) the basidiospores are lighter pigmented. One might consider placing *L. praevillosa* in a separate genus, but this would require description of a new genus to accommodate a single species, so at this time we prefer to classify it in *Mallocybe*, which is supported by our phylogenetic analyses.

The species shares a few features in common with *Tubariomyces*, including the allantoid to oblong-cylindric spores and occurrence in sandy soils and sand in oak-pine habitats subject to disturbance by fire (Villarreal *et al.* 1998, Alvarado *et al.* 2010, Vizzini *et al.* 2012, Matheny & Bougher 2017). Species of *Cistaceae* (genera *Lechea* and *Crocanthemum*) do occur in sandhill habitats in northern Florida where one reference specimen was made, so we cannot rule out the possibility of an ectomycorrhizal association with *Cistaceae*, a feature of some Mediterranean *Tubariomyces*. However, other key features of *Tubariomyces* are not found in *M. praevillosa*, namely, the omphalinoid habit, the broadly attached to decurrent lamellae, and the presence of caulocystidia on the entire length of the stipe.

Index Fungorum mistakenly indicates *Inocybe praefarinacea* (Murrill) Singer as the current name for *I. praevillosa*. However, the former is a smooth-spored metuloid-bearing species similar to *Inocybe serotina* but is phylogenetically allied with the *I. metrodii* group (Eberhardt *et al.* 2023).

Our muscarine assay detected its presence in *M. praevillosa* but at a low relative concentration compared to the only other species of *Mallocybe* in which we detected the compound, *M. sabulosa*. The relative muscarine concentration in *M. sabulosa* was 760 times greater than that found in *M. praevillosa.*

Mallocybe sp. 8. Figs 6B, 11A, B.

Pileus 11–47 mm wide, hemispherical in youth, becoming convex and expanding to nearly plane with age, umbo absent, margin incurved to decurved; surface dry, covered with white, superficial, floccose-tomentose fibrils when young, these relegated to the margin after expansion, not scaly, becoming smooth over the disc; generally fulvous to brown; odor slightly acidulous. *Lamellae* sinuate-uncinate, close to subcrowded, light olive brown to yellowish brown, edges white-fimbriate. *Stipe* 25–40 × 3–6 mm, often longer than or equal to the pileus width, equal, terete; surface dry, cortina whitish (not yellow), coarsely fibrillose to lacerate-fibrillose, colored like the pileus, base white mycelioid; context solid, becoming hollow, light yellowish brown.

Basidia 25–34 × 7–9 µm, 4-sterigmate, slenderly clavate, hyaline, necropigmented with age. *Basidiospores* (8–)8.5–*8.9*–9.5(–10.5) × 4.5–*5.0*–5.5 µm, Q (1.60–)1.70–*1.79*–1.93(–2.00) (n = 31/1), smooth, subphaseoliform, subamygdaliform, or elliptic, rarely compressed or subangular, apices often bluntly pointed, wall slightly thickened, apiculus small and not very distinct, yellowish brown. *Pleurocystidia* absent. *Cheilocystidia* 20–33 × 10–16 µm, mostly clavate, at times utriform or pyriform, hyaline, thin-walled. *Pileipellis* a cutis of cylindric incrusted hyphae with slightly thickened walls, mostly 6–11 µm wide, russet brown to tawny in mass. *Lamellar trama* regular; hyphae cylindric, smooth, thin-walled, 4–14 µm wide. *Clamp connections* present. *Distribution*: Central Appalachian Mountains of the eastern USA (West Virginia), also China.

Habitat: On acidic soil under *Picea rubens* in conifer forest, *ca*. 1 500 m elev. August.

Specimen examined: **USA**, West Virginia, Pendleton County, Spruce Knob, Whispering Spruce Trail, gregarious to scattered singly on acidic soil under *Picea rubens*, *ca*. 1 500 m elev., 8 Aug. 2022, *P.B. Matheny*, PBM4749 (TENN-F-077511).

Notes: We initially took this single collection as representative of *M. subtomentosa* in the field but noted the relatively conspicuous white fibrils especially towards the margin of the pilei. Blast searches of sequence data and phylogenetic analyses, however, revealed our West Virginia sample as conspecific with several unidentified samples from China forming a monophyletic group with strong support. The species is very closely related and sister to *M. leucothrix* (Fig. 2A). Both species, as well as *M. leucoloma*, which is also closely related, share the relatively distinct white veil covering of the basidiomata, white cortina, white stipe base, and the stipe length often longer than the pileus is wide. *Mallocybe leucoloma* differs from these by the longer spores and occurrence primarily with *Salix* and/or *Dryas* in alpine and montane regions of western North America and Europe. *Mallocybe leucothrix* associates with *Quercus* and/or *Pinus* in Florida and Arizona and occurs in areas with karst topography. By contrast, *Mallocybe* sp. PBM4947 was observed on acidic soils under *Picea* but does share a similar spore size and shape with that of *M. leucothrix. Mallocybe subtomentosa* has a less pronounced initial whitish covering, a subsmooth pileus, and principally occurs with *Quercus* and *Pinus*.

As we know the species from only a single sample, we defer to our Asian colleagues to provide a more thorough account and description of this species.

Mallocybe squamosodisca (Peck) Matheny & Kudzma, ***comb. nov***. MycoBank MB 847424. Figs 6C, D, 11C, D.
Basionym: *Inocybe squamosodisca* Peck, *Bull. N.Y. St. Mus*. **75**: 18. 1904.

Pileus 10–50 mm wide, convex to broadly so, umbo absent, margin incurved and inrolled throughout all stages at least when young, becoming decurved; surface dry, velipellis absent, tomentose-fibrillose, at times breaking into areolate or cracked scales; yellowish brown to ochraceous buff (10YR 5/6–5/8; Buckthorn Brown to Dresden Brown, 6E8–4B4), dark brown with KOH; context whitish with a pale yellow tone (Colonial Buff, 4B4), not confluent with the stipe, rather firm, unchanging where bruised, *odor* mild or not remarkable. *Lamellae* adnate to ascending adnexed or sinuate, close with ca. 38–42 L and several tiers of lamellulae, pale yellow (5Y 8/4–7/4, Colonial Buff to Deep Colonial Buff, 5C3) to yellowish brown (10YR 5/6, 6E5); edges even, not fimbriate, more or less concolorous with the faces, medium to broad. *Stipe* 10–50 × 3–12 mm, short or typically not longer than the pileus width, equal or tapered towards the base, not bulbous, terete; cortina yellowish brown, fugacious; surface dry, nowhere pruinose, heavily silky fibrillose to coarsely fibrillose or villose with scattered tufts of fibrils, becoming lacerate; cortina and/or annular zone buff (5A4–B4); overall brownish yellow (10YR 6/6), somewhat lighter than or nearly concolorous with the pileus but with yellowish brown fibrils; context solid becoming hollow, pale yellow or whitish overall mixed with a pale yellow tone, with a whitish to yellow interior at the base.

Basidia 26–39 × 6–9 µm, (2–)4-spored, slenderly clavate, hyaline to ochraceous. *Basidiospores* (8–)8.5–*9.6*–10.5(–12.5) × (4.5–)5–*5.3*–5.5(–6) µm, Q (1.60–)1.67–*1.82*–2.00(–2.27) (n = 69/5), smooth, phaseoliform to elliptic or subamygdaliform, at times subcylindric and weakly angular, apiculus indistinct, slightly thick-walled, ochraceous buff to brownish yellow, the occasional long and cylindric spore presumably from 2-spored basidia. *Pleurocystidia* absent. *Cheilocystidia* 12–38 × 7–14 µm, short-cylindric, clavate, to obovate, fusiform, or filiform, at times subtended by articulated hyphal cells, thin-walled, hyaline to ochraceous. *Pileipellis* an irregular or interwoven cutis including tufts of uplifted hyphae, these tawny in mass, cylindric to somewhat inflated, 5–18 µm wide, incrusted and at times coarsely so, thin-walled to slightly thickened. *Caulocystidia* not observed; superficial hyphae similar to pileipellis hyphae, often coarsely incrusted. *Lamellar trama* parallel; hyphae ochraceous to pale yellow in mass, cylindric to inflated, 4–19 µm wide. *Clamp connections* present.

Distribution: Eastern USA (Maine, New York, North Carolina, Tennessee), extending southwards into high elevation oak forests in Costa Rica.

Habitat: On acidic soils under *Quercus*, *Pinus*. June–September.

Other specimens examined: **Costa Rica**, Cartago, Prusia, Parque Prusia, west slope of Volcan Irazu, on acidic soil under *Quercus costaricensis*, *Comarostaphylis*, *Vaccinium*, 20 Jul. 1993, *R.E. Halling*, REH7036 (NY). **USA**, Maine, Somerset Co., Appalachian Trail near Pleasant Pond, Caratunk, on soil, 1 Sep. 2020, *L.V. Kudzma*, LVK20133 (TENN-F-077383); Maine, Penobscot Co., Route 11 south of Grindstone Falls Rest Area, on soil along roadside under *Quercus*, *Pinus*, 9 Sep. 2022, *L.V. Kudzma*, LVK22053 (pers. herb.); North Carolina, Macon Co., Highlands, Cliffside Lake Recreation Area, on acidic soil in mixed woods under *Pinus strobus*, *Tsuga*, *Quercus*, 27 Jul. 2021, *P.B. Matheny*, PBM4591 (TENN-F-074869); Tennessee, Cumberland County I-40 Rest Area, near Crab Orchard, on soil among bryophytes under *Quercus* and near planted *Pinus*, 3 Aug. 2019, *P.B. Matheny*, PBM4307 (TENN-F-074869); New York, Franklin Co., Paul Smith's Visitor Interpretive Center, Barnum Brook Trail, 9 Aug. 2021, *S. Hopkins*, PBM4621 (TENN-F-075791); New York, Adirondack Park, Sacandaga Lake, gregarious under pine trees on lakeshore, 17 Aug. *ca*. 1903, *C.H. Peck* (**isotype** WTU, **isotype** MICH 11088; image only).

Notes: *Inocybe squamosodisca* is broadly distributed in the eastern USA and Central America and occurs typically with *Quercus* and/or *Pinus*. ITS data from our materials are 98 % similar to sequences of *M. substraminipes* (*fulvipes* group A; Cripps *et al.* 2010) and sequences mislabeled "*M. terrigena*" (here labeled as *Mallocybe* sp. 9) from the Pacific Northwest based on blast searches. Phylogenetically, our samples clustered independently in the Delecta clade (Fig. 1) apart from *M. substraminipes*, *M. latispora*, and their close relatives (Fig. 2A). Morphologically, our specimens feature stipe context with a pale yellow tone and with white (when very young) or yellow in the stipe base similar to *M. substraminipes* and allies in *fulvipes* group A of Cripps *et al.* (2010). Peck's protologue made no mention of the color of the stipe context but did describe the pileus context as whitish or yellowish white, consistent with our observation of fresh specimens. In addition, these collections are consistent microscopically with the type, and some of the specimens show a cracked-areolate pileus surface with age. These features, in combination with the longer spores on average and lack of any noticeable odor, serve to distinguish the species from *M. fibrillosa*.

Smith (1939) considered *Inocybe squamosodisca* as a possible synonym of *I. caesariata sensu* Kauffman. This latter name has been applied in various ways by North American authors (Kauffman 1924, Lincoff 1981), but the stipe has generally been recognized as scaly, a feature at odds with *I. squamosodisca*. Application of the name *I. caesariata* in Europe is not clear (Stangl 1989). However, the protologue describes the stipe as fibrillose, not scaly. Given the range of materials observed and similarities with the type, including the cracked-areolate pileus surface that develops with age and microscopic similarities, we prefer to recognize this unique phylogenetic entity as Peck's *I. squamosodisca*, hence, the recombination in *Mallocybe*. Specimens from New York and Maine studied by us and sequenced here serve credibly as reference material for this species.

Mallocybe subtomentosa (Peck) Matheny & Kudzma, ***comb. nov*.** MycoBank MB 847425. Figs 6E, F, 7A, B, 11E–H.
Basionym: *Inocybe subtomentosa* Peck, *Ann. Rep. NY St. Mus*. **48**: 109. 1897 [1895].

Pileus 8–35 mm wide, conical to obtusely conical, margin incurved, umbo absent or rarely low and obtuse; surface dry, not hygrophanous, finely fibrillose, not at all scaly, almost smooth with age, velipellis usually absent; yellowish brown (10YR 5/4–5/6–5/8 or Buckthorn Brown), mixed with some light olive brown tones (2.5Y 5/4 or Isabella Color) or dark yellowish brown (10YR 4/4) at the center, surface brown with 3 % KOH; context pallid with pale yellowish tinge, not changing color where bruised, *odor* faintly acidulous or not remarkable. *Lamellae* adnate with slight decurrent tooth, moderately close with several tiers of lamellulae (up to 40 L), light olive buff to pale brown, becoming yellowish brown to dark yellowish brown with age (10YR 5/4–4/4), edges pallid but at most indistinctly fimbriate. *Stipe* 20–40 × 3–5 mm at apex, longer than pileus width, tapered below or equal, terete; cortina forming thin, silky, cobwebby, white fibrils, fugacious; surface dry, scurfy at extreme apex, elsewhere fibrillose, at times with fine silky white vesture, mostly light yellowish brown (2.5Y 6/4) mixed with light olivaceous tones (Isabella Color) or whitish with dull yellow tones (2.5Y 8/4; Cream-Buff), extreme base with whitish appressed mycelium; context solid becoming hollow, whitish throughout, *not* yellow at the base.

Basidia 24–33 × 6–9 µm, 4-sterigmate, slenderly clavate, ochraceous or hyaline. *Basidiospores* 7.5–*8.9*–9.5(–11) × 4.5–*5.0*–5.5 µm, Q 1.55–*1.77*–1.90(–2.00) (n = 52/5) smooth, subphaseoliform, subamygdaliform, or elliptic, apices often obtuse, yellowish brown, with slightly thickened wall, apiculus not distinct. *Cheilocystidia* 13–40 × 7–17 µm, short clavate or pyriform (*Opuntia*-like), arising from articulated hyphae, occasionally utriform. *Pleurocystidia* absent. *Caulocystidia* not observed; stipitipellis composed of a vesture of tangled, sparse, cylindric hyphae, similar to hyphae of the pileipellis, refractive hyphae not observed. *Pileipellis* a cutis of repent to tangled hyphae, these cylindric and up to 13 µm wide, faintly incrusted with thin or slightly thickened walls, ochraceous-tawny to tawny in mass, refractive hyphae frequent. *Lamellar trama* parallel, yellowish in mass, hyphae cylindric to inflated and mostly 5–12 µm wide, thin-walled, smooth. *Clamp connections* present.

Distribution: Northern regions of North America (Alaska, Maine, Massachusetts, New York, New Jersey, Pennsylvania, Quebec), and at higher elevations in the central and southern Appalachian Mountains (North Carolina, West Virginia), and in montane regions of New Mexico and Mexico (Michoacán).

Habitat: On soil (probably acidic) often under *Pinus* or *Pinus* mixed with *Quercus*. June–September.

Other specimens examined: **Mexico**, Michoacán, Tlalpujahua, Municipio San Felipe del Progresso, Centro Ceremonial Mazahua, on soil in pine forest, 2 889 m elev., 8 Aug. 2018, *D.P. Lewis*, DPL13020 (TENN-F-074582); *ibid*., *D.P. Lewis*, DPL13025 (TENN-F-074575). **USA**, Maine, Ogunquit Museum of Art, on soil under *Pinus strobus*, 4 Aug. 2014, *L.V. Kudzma*, LVK14251 (pers. herb.); Massachusetts, Northbridge, scattered singly on soil among woodchips along roadside in mixed woods including *Pinus* and *Quercus*, 26 Sep. 2003, *J.C. Slot*, PBM2460 (TENN-F-062321); New Jersey, Brendan T. Byrne State Forest near Pakim Pond parking area, on soil under *Pinus* and *Quercus*, 15 May 2017, *L.V. Kudzma*, LVK17005 (pers. herb.); *ibid.*, 17 May 2017, *L.V. Kudzma*, LVK16004 (TENN-F-077382); *ibid.*, *L.V. Kudzma*, LVK16006 (pers. herb.); New Mexico, Santa Fe National Forest, Jemez Mountains, Camp Shaver (YMCA), near Battleship Rock, 5 km south of La Cueva, in mixed forest of *Pinus ponderosa*, *Pseudotsuga*, *Quercus gambelii*, *Juniperus*, 2 060 m elev., 21 Aug. 1999, *S.A. Trudell*, SAT-99-233-01 (WTU); New York, Rouses Point (near the Canadian border), gregarious or subcaespitose in gravelly soil among fallen leaves, Sep. (day and year not known), *C.H. Peck* (**isotype** WTU 018341); Franklin County, Paul Smith's Visitor Interpretive Center, Barnum Brook Trail, on acid soil in mixed woods under conifers, including *Pinus strobus*, *Betula*, *Fagus*, *Populus*, 14 Aug. 2021, *P.B. Matheny & S. Hopkins*, PBM4701 (TENN-F-075838); Franklin County, Hayes Brook Truck Trail, near Paul Smith's VIC, scattered singly to clustered on acidic sandy soil under conifers including *Pinus sylvestris*, *Abies*, 14 Aug. 2021, *S. Hopkins* & *L. Kudzma*, PBM4703 (TENN-F-075840); North Carolina, Little Switzerland, Blue Ridge Parkway, on acid soil in mixed forest under *Quercus*, *Pinus*, *Betula, ca*. 1 000 m elev., 22 Sep. 2012, *B.P. Looney & M. Sánchez-García*, PBM3910 (TENN-F-068440); Tucker Co., Blackwater Falls State Park, Davis, Lindy Point Overlook Trail, on acid soil in hemlock forest under *Tsuga*, *Pinus strobus*, *Betula*, 11 Aug. 2022, *R.A. Swenie*, PBM4763 (TENN-F-077551).

Notes: Numerous samples of *M. subtomentosa* from the eastern USA and western regions of North America form a weakly supported monophyletic group sister to *M. leucoloma* and *M. leucothrix*, all of which are placed in the Delecta clade within the core Mallocybe clade (Fig. 2A). The species has also been recorded in central Mexico at high elevation, as well as in Quebec (J. Landry, pers. comm.). Of Peck's available names, this species best fits the protologue of *Inocybe subtomentosa*. Based on composite data, *M. subtomentosa* is characterized by the small basidiome size, almost smooth pileus surface, the stipe length longer than the pileus width, the merely fibrillose to scurfy stipe surface, white fugacious cortina, white stipe base, and relatively narrow spores with Q-values less than 2.0. Compared to *M. fibrillosa*, the pileus of *M. subtomentosa* is almost smooth, a seemingly distinctive feature. Both *M. fibrillosa* and *M. squamosodisca* also have short stipes in relation to the width of the pileus, unlike *M. subtomentosa*. *Mallocybe squamosodisca* can be further distinguished from *M. subtomentosa* by the pale yellow tone to the stipe context and usually yellowish stipe base. *Mallocybe subtomentosa* was described with a white mycelioid base, which we observe here consistently among the collections examined.

Mallocybe leucoloma and *M. leucothrix* can be distinguished from *M. subtomentosa* by the presence of a superficial covering of white tissue when young that remains on the pileus margin or stipe with age (Cripps *et al.* 2010; see also under *M. leucothrix*). As in *M. subtomentosa*, the cortina is white and often copious and the odor faint or not noticeable. In North America, *M. leucoloma* is distributed in western states better known from alpine areas of the Rockies, but the species also occurs in montane conifer forests of Wyoming and Washington.

Stuntz's application of the name *Inocybe subdecurrens* (Stuntz 1947) could fit our concept of *M. subtomentosa* given the ample white cortina, stipe length longer than the pileus width, similar spore size, and the short articulated cheilocystidia. A single collection (Stz. 604) was cited under *Alnus* and *Acer* in lowland Washington state. Stuntz described the pileus as campanulate to plane with a small obtuse umbo and densely appressed lanuginose forming squamules toward the margin. This last feature deviates from all the material we have observed and is more consistent with *M. fibrillosa*, of which we consider *I. subdecurrens* a synonym, or Stz. 604 could represent a non-alpine *M. leucoloma*.

We observed many single nucleotide polymorphic sites (SNPs) across samples of *M. subtomentosa* in our concatenated alignment at ITS (5), 28S (4), *rpb1* (8), and *rpb2* (30) loci. Taxon sampling was uneven across the four loci sequenced, but the relatively consistent occurrence of SNPs at all four loci may suggest some degree of hybridization among divergent populations within *M. subtomentosa* or with closely related species.

Mallocybe tomentella Matheny & Kudzma, ***sp. nov***. MycoBank MB 847421. Figs 7C, D, 11I, J.

Etymology: *tomentella* (L.), somewhat hairy, in reference to the fibrillose-tomentose pileus.

Typus: **USA**, New York, Franklin Co., Bloomingdale, Bloomingdale Bog, scattered to gregarious, singly or in pairs, on very sandy acidic soil along roadside under mixture of trees including *Picea*, *Abies*, *Pinus strobus*, *Larix*, *Populus*, *Betula*, *Alnus*, 490 m elev., 13 Aug. 2021, *S. Hopkins & P.B. Matheny*, PBM4690 (**holotype** TENN-F-075826).

Diagnosis: Pileus generally tomentose-fibrillose, at times bicolorous due to accumulation of cobwebby whitish fibrils at the margin; *odor* absent; stipe often with a distinct apical cortinate ring-zone, context light yellowish brown to isabelline; differing from *Mallocybe malenconii* by the shorter, wider, and differently shaped basidiospores, these mostly 8–10.5 × 4.5–5.5 µm (Q value < 2.00); cheilocystidia < 40 µm long, hyaline; on poor acidic sandy soils under *Picea*, *Populus*.

Pileus 12–40 mm wide, pulvinate with an incurved margin at first, becoming convex, soon plane, at times depressed at the center and with somewhat raised margins, with or without a low obtuse umbo; surface dry, velipellis absent, generally

Fig. 7. Basidiomes of *Mallocybe* from North America. **A.** *M. subtomentosa* (PBM4703, photo B. Matheny). **B.** *M. subtomentosa* (LVK16006, photo L. Kudzma). **C.** *M. tomentella* (PBM4690, holotype, photo B. Matheny). **D.** *M. tomentella* (SAT-06-228-10, photo S. Trudell). **E.** *M. tomentosula* (PBM4138, photo B. Matheny). **F.** *M. tomentosula* (HRL0027, photo R. Lebeuf). Scale bars = 1 cm.

tomentose-fibrillose, exceptionally forming minute floccose scales; often bicolorous (at least when fresh) with the center yellowish brown (10YR 5/8; Buckthorn Brown) and the margin light yellowish brown (10YR 6/4) or noticeably pale due to the accumulation of radially, cobwebby, whitish fibrils; with age the center may be dark brown or umbrinous but also ranging to fulvous or almost so throughout; surface dark brown with 5 % KOH; context dull dingy pale brown, not yellow, unchanging color where bruised, PDAB negative, *odor* absent. *Lamellae* adnate to weakly subdecurrent, close with several tiers of lamellulae, narrow to medium, not broad; pale brown to brown (10YR 6/3–5/3), yellowish brown with age (10YR 5/4), at times with olivaceous tones. *Stipe* 25–45 × 2–6 mm, equal or at times with a slightly swollen base, cortina whitish and often forming a distinct apical or superior cortinate ring-zone, veil remnants appendiculate along the margin of the pileus at times; surface dry, nowhere pruinose, fibrillose to coarsely so or tattered fibrillose, the superficial fibrils silky and pallid against the light yellowish brown to isabelline ground color; context soon hollow, colored like the stipe ground color.

Basidia 24–30 × 7–9 µm µm, 4-sterigmate, slenderly clavate to subcylindric, hyaline or necropigmented.

Basidiospores 8–*9.0*–10.5(–11) × 4.5–*5.0*–5.5 µm, Q (1.48–)1.60–*1.81*–2.00(–2.09) (n = 76/3), elliptic to subphaseoliform or subamygdaliform, at times suboblong, not at all or rarely subangular, apices obtuse or bluntly pointed, brownish yellow to yellowish brown, with a slightly thickened wall. *Pleurocystidia* absent. *Cheilocystida* 20–34 × 11–16 µm, mostly clavate to broadly so (not short-clavate) to saccate or spheropedunculate, thin-walled, hyaline. *Caulocystidia* not observed. *Pileipellis* a cutis of cylindric hyphae, these often coarsely incrusted and with slightly thickened walls and 7–17 µm wide, russet brown in mass. *Lamellar trama* parallel; hyphae pale yellow in mass, cylindric, thin-walled, mostly 4–12 µm wide. *Clamp connections* present.

Distribution: Northern regions of eastern and western North America (New York, Quebec, Alberta).

Habitat: On poor, sandy, acidic soils under *Picea*, *Populus tremuloides*, or in mixed forests including these trees. August.

Other specimens examined: **Canada**, Alberta, Division No. 14, Bighorn Recreation Trail, Robb Road/Cold Creek Road, near Hinton, on soil in *Picea-Populus tremuloides* forest, 1 160 m elev., 16 Aug. 2010, *S.A. Trudell*, SAT0622810 (TENN-F-071587). **USA**, New York, Franklin Co., Bloomingdale, Bloomingdale Bog, scattered to gregarious, singly or in pairs, on very sandy acidic soil along roadside under mixture of trees including *Picea*, *Abies*, *Pinus strobus*, *Larix*, *Populus*, *Betula*, *Alnus*, 490 m elev., 13 Aug. 2021, *S. Hopkins & P.B. Matheny*, PBM4694 (TENN-F-075831).

Notes: *Mallocybe tomentella* is characterized namely by the white cobwebby fibrils covering the pileus margin and darker disc when fresh, depressed pileus center usually with a small umbo, long incurved pileus, presence of a cortinate ring-zone, basidiospores with Q value < 2.00 on average, and putative association with *Picea* and possibly *Populus* on acidic soils. Our phylogenetic analyses support a broad northerly distribution between Alberta on one hand and New York and Quebec on the other [the latter as *Inocybe* sp. RL8 (GenBank MN992187)].

Both *M. malenconii* and *M. subgranulosa* can be distinguished from *M. tomentella* by the fine scaly pilei and narrow laceroid or minimally angular basidiospores with higher Q values. Support values for the clade of *M. tomentella* are only moderate, but together the samples form a robustly supported monophyletic group with *M. subgranulosa* and two orphaned samples of *M. malenconii* from China and Spain (Fig. 2A). However, given the differences in morphology, including the pileus surface structure (not granulose) and basidiospore morphology (not subangular and "laceroid"), we prefer to recognize *M. tomentella* as a distinct taxon. Further samples from Asia, Europe, and North America, including more genetic data, will be needed to ascertain whether the group might be a complex of entities surrounding *M. subgranulosa*. This *M. subgranulosa* "complex" is sister to *M. malenconii s.str.* with strong support.

A similar species, *M. tomentosula*, is presented below. The two species share the presence of cortinate ring-zone and non-laceroid basidiospores with mean Q values < 2.00. However, *M. tomentosula* differs from *M. tomentella* by occurring on limestone soils with *Quercus* and/or *Pinus strobus*. It also differs from *M. tomentella* by the darker colored pileus, phenology, and phylogenetic position where it occurs in a well-supported group containing *M. heimii*, *M. velutina*, *M. depressa*, and *M. errata* (*viz.*, the Heimii clade; Fig. 1).

Mallocybe tomentosula Matheny & Esteve-Rav., *Mycologia* **112**: 109. 2019 [2020]. Figs 7E, F, 11K–M.
Basionym: *Inocybe tomentosa* Ellis & Everh., *J. Mycol*. **5**: 26. 1889, *nom. illegit*., Art. 53.1, *non Inocybe tomentosa* Quél. 1888.

Pileus 12–45 mm wide, convex or obtusely conical in youth, soon expanding to plano-convex or plane with age, umbo generally absent, center occasionally depressed, margin incurved at first and remaining slightly so when expanded or decurved with age; surface dry, velipellis absent, densely fibrillose-tomentose, at times with few scattered appressed scale-like aggregates of fibrils, not rimose; yellowish brown or fulvous (10YR 5/6–5/8) to strong brown or nearly rusty brown (7.5YR 4/4) with age, after drying specimens noticeably umbrinous; context whitish to olivaceous or with olivaceous streaks, *odor* none. *Lamellae* adnate or uncinate, close with 40–50 L and several tiers of lamellulae; light yellowish brown to light olive brown (2.5Y 6/4–5/4–5/6) to rusty brown with age, edges even and not appearing fimbriate, medium (2–4 mm deep). *Stipe* 10–35 × 3–5 mm, equal, cylindric, not bulbous; surface cortinate in youth, cortina composed of fine whitish silky fibrils, often leaving a superior annular zone; nowhere pruinose, dry, fibrillose to coarsely so, nowhere scaly, colored more or less like the pileus or with isabelline areas; base not yellow.

Basidia 24–36 × 7–8 µm, 4-sterigmate, slenderly clavate to cylindrico-clavate, hyaline or necropigmented. *Basidiospores* (8–)8.5–*9.4*–10.5(–11) × (4.5–)5–*5.4*–6(–6.5) µm, Q (1.50–)1.61–*1.74*–1.98(–2.04) (n = 71/3), smooth, subamygdaliform to elliptic, at times subphaseoliform due to a ventral depression, apices bluntly pointed or obtuse, yellowish brown, wall slightly thickened, apiculus small and not very distinct. *Pleurocystidia* absent. *Cheilocystidia* 14–34 × 8–13 µm, short-cylindric to short-clavate or pyriform, arising from articulated hyphal cells, hyaline or brownish incrusted, thin-walled, edges of lamellae becoming pigmented with age. *Pileipellis* a cutis of regularly to somewhat tangled and coarsely incrusted hyphae, russet or dark tawny in mass, hyphae cylindric and mostly 7–17 µm wide, more or less thin-walled; tramal hyphae light yellowish brown in mass, smooth, thin-walled. *Caulocystidia* not observed. *Lamellar trama* parallel, hyaline in mass, hyphae mostly 4–12 µm wide, smooth, thin-walled. *Clamp connections* present.

Distribution: Eastern North America (Quebec, New Jersey, Tennessee), including Mexico (Tlaxcala).

Habitat: On calcareous soils in Tennessee and Mexico, under *Quercus*, *Pinus strobus* or *P. cembroides* (plantation), and/or *Juniperus*; type recorded near *Picea abies* in New Jersey, soil conditions unknown. April and November (southern range), July–September (northern range).

Specimens examined: **Canada**, Quebec, Saint-Alban, under *Pinus strobus* sandy soil, 20 Sep. 2006, *R. Lebeuf*, HRL0027 (TENN-F-071134); **USA**, New Jersey, Gloucester, Newfield, in grass around Norway spruce, Sep. 1888 (no day and no collector cited) [**holotype** NY 00775649, 00775650, 0075656, 00775651 (**isotype** ex Barnard College)]; Tennessee, Knox County, Knoxville, Ijams Nature Center, on dry gravelly soil under *Quercus montana* and *Juniperus virginianus* at a limestone quarry, *ca*. 300 m elev., 17 Apr. 2016, *R.A. Swenie*, RAS123 (TENN-F-071659); *ibid.*, 11 Nov. 2017, *P.B. Matheny*, PBM4138 (TENN-F-071134).

Notes: *Mallocybe tomentosula* is most closely related to the European species *M. heimii*, the South Asian species *M. velutina* (Saba & Khalid 2020), and the East Asian *M. depressa* from China (Mao *et al.* 2022) (Fig. 2B). This strongly supported assemblage forms a sister group to *M. errata* from Thailand. *Mallocybe fuscomarginata* is superficially similar to *M. tomentosula* in that both may be characterized by the presence of brownish incrusted cheilocystidia, the cigar brown colored pileus, and the veil in *M. fuscomarginata* that at times forms a thin ring-zone (Jacobbson & Larsson 2012). However, both the spores and cystidia of *M. fuscomarginata* are larger than in *M. tomentosula*, and the gill edges of the latter are not noticeably dark brown. The two species are distantly related (Fig. 2B).

Mallocybe tomentosula has a wide geographic distribution ranging from Quebec to central Mexico (Meza-Meneses *et al.* 2016), where it associates with species of *Pinus* subg. *Strobus* and *Quercus* on limestone soils where known. The ecology, in combination with the medium sized basidiomes, the presence of a superior cortinate ring-zone, spores mostly 8.5–10.5 × 5–6 µm, and the short articulated cheilocystidia that become brownish with age, serve to distinguish it from other eastern North American *Mallocybe*. In addition, the phenology of *M. tomentosula* is unusual in that it has been recorded as early as April in Tennessee on multiple occasions, and again in November. In Quebec the species was recorded with *Quercus*, *Populus*, *Salix*, and/or *Picea* in city parks and forested areas between July and September (J. Landry, pers. comm.). The soil conditions of the Canadian samples are not known.

Matheny *et al*. (2020) introduced *Mallocybe tomentosula* Matheny & Esteve-Rav. as a *nom. nov*. for *I. tomentosa* Ellis & Everh., an illegitimate name due to the publication of the same binomial, *I. tomentosa* Quél. during the prior year. The ecology of the type is not clear with the mention only that the species occurred near planted Norway spruce in New Jersey.

The holotype of *I. tomentosa* comprises four parts on a single sheet, all from the same original gathering, one of which is an ex-isotype, since rejoined with the holotype, from Barnard College. Attempts to produce molecular annotations by Sanger sequencing (775651 and 775656) failed due to very poor quality and heterogeneous nature of the reads. All four elements resemble each other and are consistently light yellowish brown overall. We could not glean any data regarding the cheilocystidia morphology from the holotype, but the spore shape and size are consistent with our other observations of what we interpret as this species. Unpublished observations of the type of *I. tomentosa* by D.E. Stuntz in Feb. 1964 featured clavate to spheropedunculate cheilocystidia 28–36 × 12–14 µm in size. This feature is also consistent with our other studied specimens. Thus, the presence of a cortinate ring-zone, probable association with *Quercus* and *Pinus* (and possibly other plants), spore and cystidium morphology, and geography (New Jersey) are all consistent with sequenced samples studied by us from Quebec and Tennessee.

Kauffman (1924) and Smith (1939) considered *I. tomentosa* (our *M. tomentosula*) as synonymous with *I. subdecurrens*, however, we recognize the latter as a later synonym of *Mallocybe fibrillosa.* Our interpretation of *M. fibrillosa* differs from *M. tomentosula* in that *M. fibrillosa* lacks a cortinate ring-zone and tends to feature a (subtly) sweet odor. Phylogenetically, the two species are distantly related (see commentary below).

Mallocybe unicolor (Peck) Matheny & Esteve-Rav., *Mycologia* **112**: 109. 2019 [2020]. Figs 8A–D, 12A–F.
Basionym: *Inocybe unicolor* Peck, *Ann. Rep. NY St. Mus*. **50**: 104. 1897.
Synonyms: *Inocybe lorillardiana* Murrill, *Mycologia* **3**: 101. 1911.
Inocybe marmoripes G.F. Atk., *Am. J. Bot*. **5**: 213. 1918.
Inocybe caesariata sensu N. Am. auct. p.p., *non* Kauffman 1924.

Illustrations: Lincoff (1981, as *I. caesariata*); Phillips (2010, as *I. caesariata*).

Pileus 15–50 mm wide, deeply convex when young to obtusely conical or parabolic to conical, becoming subcampanulate and finally plane, an obtuse umbo sometimes present, margin incurved to decurved; surface dry, granulose due to very fine recurved or appressed squamules (resembling *Cystoderma*), at times velvety in appearance, margin entire (not rimose), dark brown with 3–5 % KOH (pale or light brown with 10 % NH_4OH); the scales dark yellowish brown or strong brown (Cinnamon Brown) at the center (10YR 4/4–7.5YR 4/4) against a yellowish brown or fulvous ground color (10YR 5/6–5/8; Buckthorn Brown), on occasion faded to light yellowish brown; context up to 3 mm thick beneath the disc, whitish, not confluent with stipe; *odor* and *taste* not remarkable. *Lamellae* narrowly adnate to uncinate, moderately close with 24–30 L and several tiers of lamellulae; cream colored or pale yellow when young (2.5 Y7/4), becoming light olive brown or isabelline (2.5Y 5/4) to dark yellowish brown (10YR 4/4) with an olive tinge or olive brown (2.5Y 4/4); equal to subventricose, up to 6 mm deep; edges white and fimbriate. *Stipe* 30–50 × 2–7 mm, often longer than the pileus diameter, terete or compressed, usually equal but occasionally slightly swollen or tapered at the base; cortina yellowish brown, fugacious; surface dry, densely fibrillose when very young but soon breaking up into yellowish brown or cinnamon brown squamules, these recurved at times, against a pale yellowish brown ground color (contrasting with the darker colored scales), dark brown with 5 % KOH; apex of stipe finely fibrillose, not pruinose; context solid becoming hollow but with a tough cortex, dingy whitish or with slight yellowish tinge, unchanging color where bruised or exposed. Context negative with guaiac and PDAB.

Basidia 28–38 × 7–10 µm, 4-sterigmate, clavate hyaline but becoming necropigmented. *Basidiospores* (8.5–)9.0–*9.9*–11.5(–12) × (4.0–)4.5–*5.0*–5.5(–6.0) µm, Q 1.64–*1.97*–2.33(–2.44) (n = 72/4), smooth, oblong-elliptic to oblong-subamygdaliform or oblong-subphaseoliform, at times with a ventral depression, apices obtuse or bluntly pointed, thick-walled to slightly thick-walled, brownish yellow (Ochraceous-Buff), apiculus small and indistinct. *Pleurocystidia* absent. *Cheilocystidia* 32–65 × 9–13 µm, irregularly cylindric, at times strangulated, or fusiform, narrowly utriform to lageniform, apices often swollen or indistinctly subcapitate, thin-walled, hyaline, edges of lamellae sterile. *Caulocystidia* not observed, superficial hyphae on stipe forming a trichoderm or interwoven layer of cylindric hyphae, these 4–10 µm wide, ocher-tawny in mass, end cells undifferentiated or at times flexuous or lageniform; subtending hyphae pale yellow brown to hyaline in mass, up to 14 µm wide, with walls that appear smooth. *Pileipellis* a cutis giving rise to fascicles of trichodermial elements that are ocher-tawny in mass; hyphae cylindric to inflated and up to 18 µm wide, incrusted, with slightly thickened walls; hyphae of subpellis up to 25 µm wide. *Lamellar trama* parallel, pale yellowish brown to hyaline in mass, hyphae

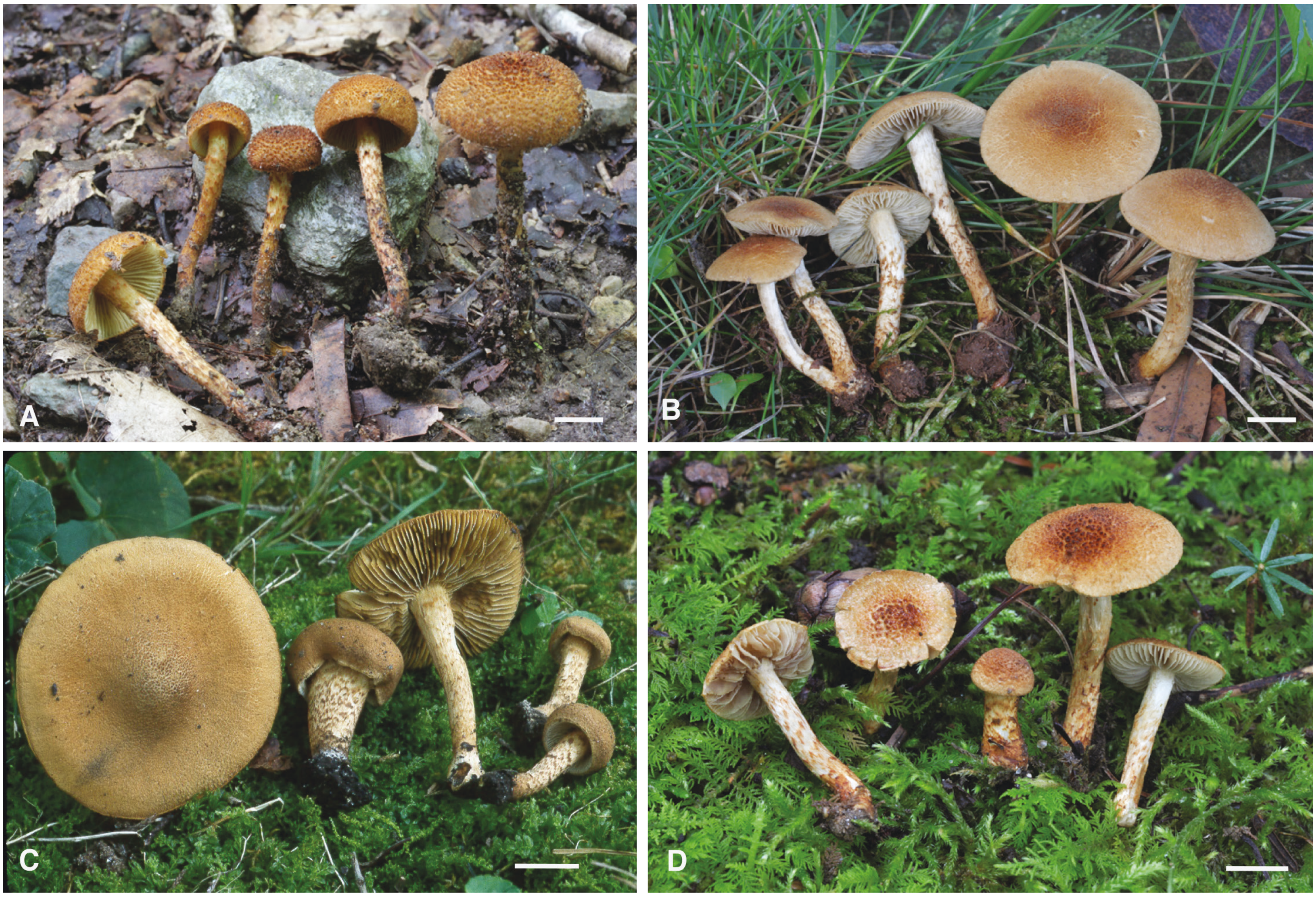

Fig. 8. Basidiomes of *Mallocybe unicolor* from eastern North America (all photos by B. Matheny). **A.** PBM4013. **B.** PBM3794. **C.** PBM1481. **D.** PBM4451. Scale bars = 1 cm.

cylindric and up to 12 µm wide, rusty colored refractive hyphae present. *Clamp connections* present.

Distribution: Throughout eastern North America. Common.

Habitat: Scattered to gregarious, at times forming troops, singly or in small groups on calcareous soil under *Quercus*, *Carya*, and *Carpinus*, or under planted *Quercus* or *Tilia*, at times on lawns in grass, generally in oak-hickory forests, or mixed mesic forests including *Quercus* and *Tsuga* on acidic soils. June–October.

Specimens examined: **USA**, Illinois, Coles Co., Charleston, First and Harrison, gregarious in grass under *Quercus*, 18 Jun. 2015, *M. Kuo*, MK06181501 (TENN-F-073747); Coles Co., Charleston, Fox Ridge State Park, picnic area, on gravelly soil under *Quercus*, *Carya*, 28 Aug. 2014, *M. Kuo*, MK08281401 (TENN-F-074753); *ibid.*, 28 Aug. 2014, *M. Kuo*, MK08281401 (TENN-F-074753); Iowa, Linn County, Mount Vernon, Palisades-Kepler State Park, on karst topography in hardwood forest, 15 Jul. 2020, *S. DeLong-Duhon*, iNAT53190985 (TENN-F-076529); Missouri, Taney Co., Mark Twain National Forest, Ozark Mountains, Coy Bald Trail at Hercules Glen, on soil in campground along creek in under *Quercus*, *Carya*, *Juglans*, 4 Jul. 1999, *P.B. Matheny*, PBM1481 (WTU); New York, Menands, on clay soil, July, *C.H. Peck s.n.* (**isotype** of *I. unicolor*, WTU); Bronx Co., New York Botanical Garden, on soil in lawn under *Quercus*, *Fagus*, *Acer*, 20 Sep. 1987, *R.E. Halling*, REH5532 (WTU); New York City, in front of museum building, caespitose in grass under *Carya*, 25 Jul. 1916, *W.A. Murrill s.n.* (WTU 63030); Tompkins Co., near Glenwood (suburb of Ithaca), west of Cayuga Lake, solitary to subcaespitose on ground in woods, July, *B. Walker*, Atk24275 (**isotype** of *I. marmoripes*, WTU); North Carolina, Haywood Co., Great Smoky Mountains National Park, Baxter Creek Trail, 11 Sep. 2004, *P.B. Matheny*, PBM2645 (TENN-F-062476); *ibid.*, 7 Jul. 2015, *P.B. Matheny*, PBM3997 (TENN-F-70346); Macon Co., Highlands Biological Research Station, under *Pinus Quercus*, and *Rhododendron* on acid soil, 29 Jul. 2021, *C.R. Noffsinger*, PBM4604 (TENN-F-075771); Yancey Co., Burnsville, Carolina Hemlocks campground, in hemlock dominant forest under *Quecus*, *Tsuga*, *Rhododendron* on acid soil, 20 Aug. 2020, *P.B. Matheny*, PBM4452 (TENN-F-075323); Tennessee, Anderson Co., Norris Dam State Park, Clear Creek Trail, under *Quercus*, *Carpinus*, *Fagus*, *Carya*, 11 Oct. 2009, *P.B. Matheny*, PBM3331 (TENN-F-063892); Blount Co., Great Smoky Mountains National Park, Schoolhouse Gap Trail, 8 Jun. 2012, *C.C. Braaten*, CCB48 (TENN-F-067079); *ibid.*, 17 Jul. 2019, *R.A. Swenie & S.R. Warwick*, PBM4301 (TENN-F-074863); Cocke Co., Great Smoky Mountains National Park, Low Gap Trail, 10 Oct. 2010, *M.G. Wood*, MGW869 (TENN-F-065333); Cumberland Co., Interstate 40 rest area between exits 324-325, on ground under *Quercus*, 23 Jul. 2018, *P.B. Matheny*, PBM4167 (TENN-F-074483); Knox Co., west Knoxville, residential area, on soil in grass under planted *Quercus phellos*, 29 Jul. 2008, *P.B. Matheny*, PBM2974 (TENN-F-062732 – muscarine assay); Knox Co., University of Tennessee campus, the Hill, in lawn on soil under planted *Tilia americana*, 7 Aug. 2009, *P.B. Matheny*, PBM3322 (TENN-F-063887); Knox Co., Sharp's Ridge Memorial Park, on soil under hardwoods, 2 Aug. 2022, *R.A. Swenie*, RAS1007 (TENN-F-077502); Sevier Co., Great Smoky Mountains National Park, Alum Cave Bluffs Trail, 11 Aug. 2005, *E.B. Lickey* (TENN-F-061152); Virginia, Shenandoah National

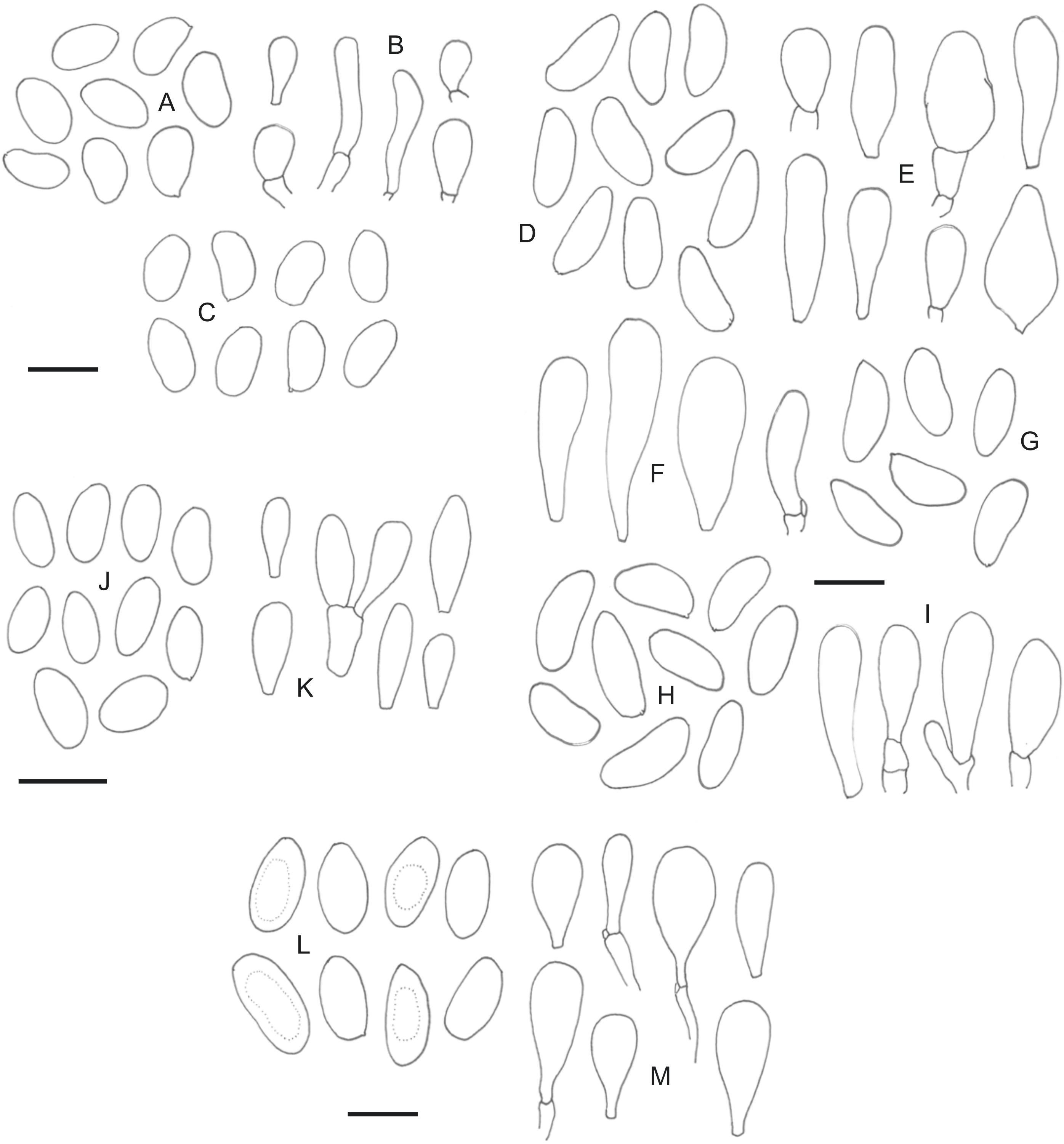

Fig. 9. Microscopic features of *Mallocybe*. **A.** Basidiospores of *M. fibrillosa* (isotype). **B.** Cheilocystidia of *M. fibrillosa* (isotype). **C.** Basidiospores of *M. fibrillosa* (isotype of *Inocybe subdecurrens*). **D.** Basidiospores of *M. fulviceps* (isotype). **E.** Cheilocystidia of *M. fulviceps* (isotype). **F.** Cheilocystidia of *M. fulviceps* (isotype of *I. pertomentosa*). **G.** Basidiospores of *M. fulviceps* (isotype of *I. pertomentosa*). **H.** Basidiospores of *M. fulviceps* (isotype of *I. vialis*). **I.** Cheilocystidia of *M. fulviceps* (isotype of *I. vialis*). **J.** Basidiospores of *M. fulviumbonata* (holotype). **K.** Cheilocystidia of *M. fulvioumbonata* (holotype). **L.** Basidiospores of *M. latifolia* (PBM4537). **M.** Cheilocystidia of *M. latifolia* (PBM4537). Scale bars = 10 µm for spores; 25 µm for cystidia.

Park, north park entrance, Dickey Ridge Trail, 600 m elev., on clay soil in Oak-Hickory forest (*Quercus*, *Carya*, *Juglans*, *Liriodendron*, *Robinia*), 22 Jun. 2002, *P.B. Matheny & E.C. Durman*, PBM2320 (WTU).

Notes: *Mallocybe unicolor* is easy to recognize in the field due to the granulose-scaly pileus, the dark colored fibrillose scales on the stipe, the dull olivaceous to brownish lamellae, and habitat typically under oaks. The species is also characterized by the elongated cheilocystidia and oblong spores with mean Q-values ranging mostly between 1.90 and 2.25. *Mallocybe unicolor* is widespread in eastern North America and common in Oak-Hickory forests and urban habitats in lawns under planted *Quercus*, *Carya*, and *Tilia*, typically on karst topography. To a lesser extent it has been found in mixed mesic Hemlock

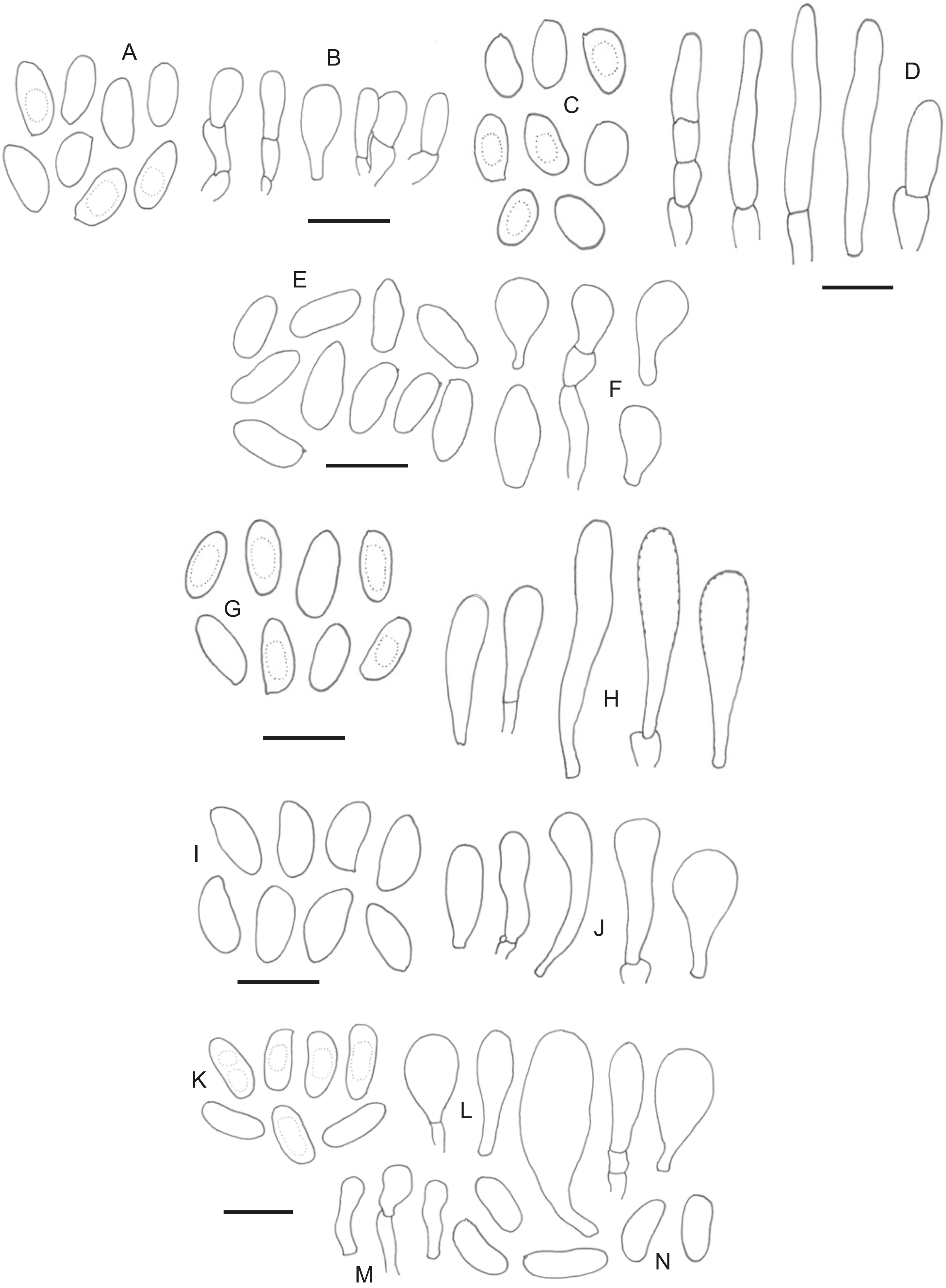

Fig. 10. Microscopic features of *Mallocybe*. **A.** Basidiospores of *M. leucothrix* (paratype – PBM4531). **B.** Cheilocystidia of *M. leucothrix* (paratype – PBM4531). **C.** Basidiospores of *M. luteobasis* (paratype – Sayers *s.n.*). **D.** Cheilocystidia of *M. luteobasis* (paratype – PBM4312). **E.** Basidiospores of *M. malenconii* (JV4470F). **F.** Cheilocystidia of *M. malenconii* (JV4470F). **G.** Basidiospores of *M. montana* (holotype). **H.** Cheilocystidia of *M. montana* (holotype). **I.** Basidiospores of *M. multispora* (isotype). **J.** Cheilocystidia of *M. multispora* (isotype). **K.** Basidiospores of *M. praevillosa* (FLAS-F-61523). **L.** Cheilocystidia of *M. praevillosa* (FLAS-F-61523). **M.** Caulocystidia of *M. praevillosa* (PBM4724). **N.** Basidiospores of *M. praevillosa* (holotype). Scale bars = 10 µm for spores; 25 µm for cystidia.

Fig. 11. Microscopic features of *Mallocybe*. **A.** Basidiospores of *Mallocybe* sp. 8 (PBM4749). **B.** Basidiospores of *Mallocybe* sp. (PBM4749). **C.** Basidiospores of *M. squamosodisca* (isotype). **D.** Cheilocystidia of *M. squamosodisca* (isotype). **E.** Basidiospores of *M. subtomentosa* (isotype). **F.** Cheilocystidia of *M. subtomentosa* (isotype). **G.** Cheilocystidia of *M. subtomentosa* (SAT-99-233-01. **H.** Basidiospores of *M. subtomentosa* (SAT-99-233-01). **I.** Basidiospores of *M. tomentella* (holotype). **J.** Cheilocystidia of *M. tomentella* (holotype). **K.** Basidiospores of *M. tomentosula* (RAS123). **L.** Cheilocystidia of *M. tomentosula* (RAS123). **M.** Basidiospores of *M. tomentosula* (holotype of *Inocybe tomentosa* - 00775651). Scale bars = 10 µm for spores; 25 µm for cystidia.

(*Tsuga*) forests including *Quercus* and *Betula* on acidic soils characterized by presence of *Rhododendron*. It is unknown at this time if these ecological differences correspond to divergent populations.

Because the species is so common throughout eastern North America, it is not surprising it has been described as new independently by several early 20th century taxonomists. Under incandescent light the scales of *M. unicolor* could be interpreted

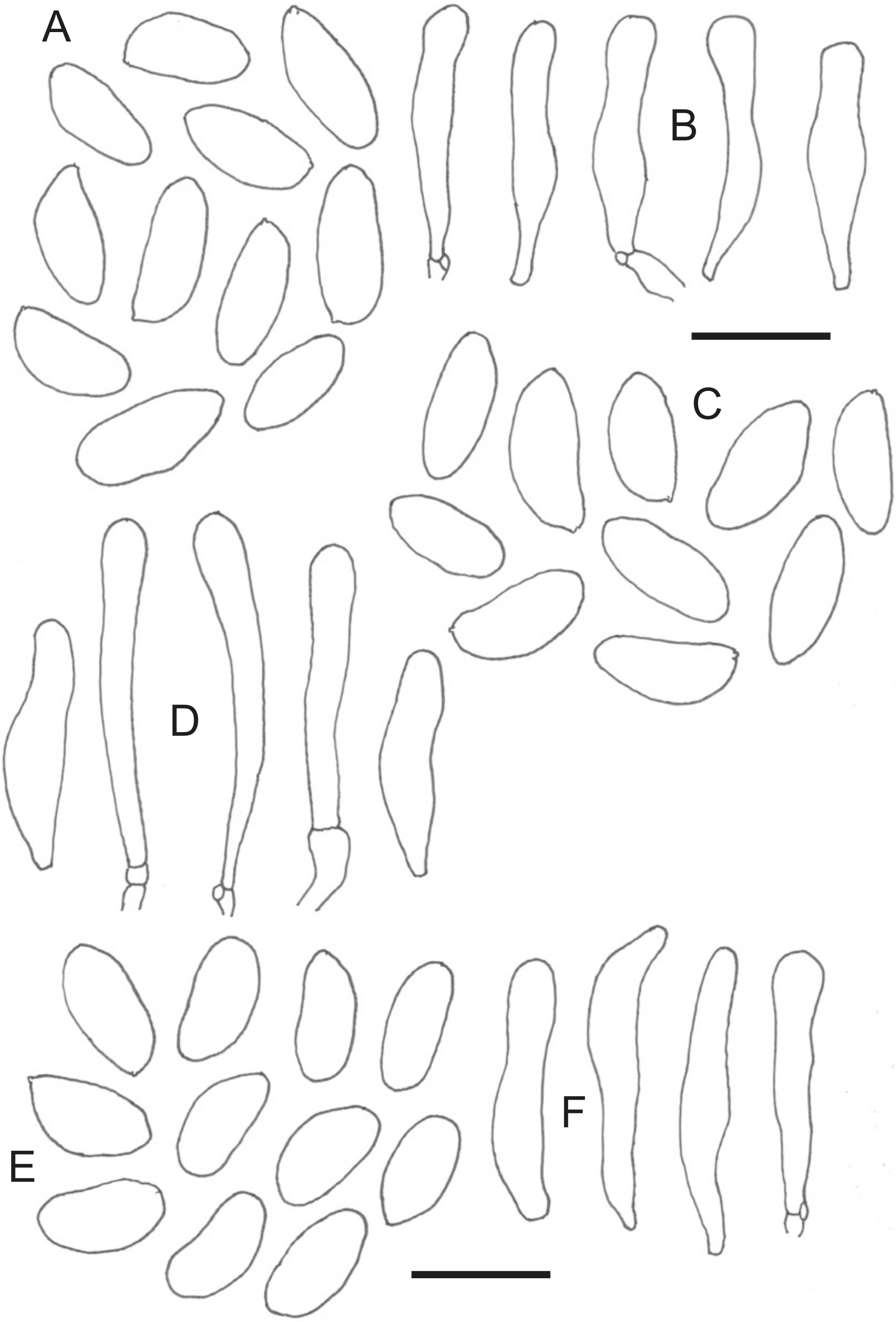

Fig. 12. Microscopic features of *Mallocybe unicolor*. **A.** Basidiospores (isotype). **B.** Cheilocystidia (isotype). **C.** Basidiospores (isotype of *Inocybe marmoripes*). **D.** Cheilocystidia (isotype of *I. marmoripes*). **E.** Basidiospores (isotype of *I. lorillardiana*). **F.** Cheilocystidia (isotype of *I. lorillardiana*). Scale bars = 10 µm for spores; 25 µm for cystidia.

as "ferrugineous" as described by Murrill for *Inocybe lorillardiana* based on examination of authentic material gathered by Murrill from the type locality. Bessette & Fatto (1998) presented a thorough study of the holotype of *I. marmoripes* consistent with our evaluation of the isotype at WTU. The basidiospore dimensions of *I. marmoripes* fall within range of the collections studied here, although the mean Q value (2.25) is longer than those of some other collections (1.86–1.89), but similar to the Virginia material (2.12) and the type of *M. unicolor* (2.09). At present, DNA sequences from numerous samples of *M. unicolor* form a cohesive strongly supported monophyletic group (Fig. 2C), but some separation was noted for two samples from New York and Missouri (REH5532 and PBM1481) characterized by the shorter Q values (1.86–1.89). Murrill's collection of *I. lorillardiana* also shares the shorter spores (mean Q 1.86). However, based on current sampling, we regard these differences as indicative of population-level variability based on current sampling. Additional collections, backed by further genetic data, are needed to determine if there is any taxonomic significance to the shorter-spored variants consistent with *I. lorillardiana*, and whether these might be correlated with edaphic factors.

Kauffman (1924) reported *I. marmoripes* from Maryland and Washington, however, his description of the cheilocystidia as clavate is not in concordance with the type. Kauffman's concept of *I. marmoripes* was a broad one including *M. malenconii* and the undescribed *Mallocybe* sp. 2 from Oregon and British Columbia (the latter reported as *M. malenconii* var. *megalospora* by its GenBank authors). Stuntz (1940) applied the name *I. marmoripes* to what we interpret as *M. malenconii*, which can be distinguished from *M. unicolor* by the smaller basidiomes (pileus up to 20 mm wide), short clavate cheilocystidia, and slightly narrower and somewhat angular basidiospores (9–12 × 4–5 µm) similar to those of *Inocybe lacera* in appearance.

The name *Inocybe caesariata* (Fr.) P. Karst. (*non* Kauffman) has been widely applied to *M. unicolor* by Hesler (1936), Lincoff (1981), Phillips (2010), and Roberts & Evans (2011). Use of the name *I. caesariata* by Kauffman (1924) in our opinion corresponds to *M. fibrillosa* Peck.

One MyCoPortal record (CMMF002038) from Quebec is misidentified as *I. unicolor*. The photograph of the specimens resembles those of *M. subtomentosa*.

A liquid chromatography-tandem mass spectrometry assay by Kosentka *et al.* (2013) did not detect muscarine in sample TENN-F-062732 (PBM2974).

Extralimital taxa

Mallocybe callichroa (E. Horak) Matheny, ***comb. nov***. MycoBank MB 847422.
Basionym: *Inocybe callichroa* E. Horak, *Westerdijk Biodiversity Series* **16**: 76. 2018.

Notes: *Inocybe callichroa* (Horak 2018) bears many features indicative of *Mallocybe*: the overall ocher-brown coloration of the basidiomes, the slenderly clavate basidia, the smooth slenderly phaseoliform basidiospores with an average Q value at or near 2.00, the absence of pleurocystidia, the presence of cheilocystidia and clamp connections, and a cutis to trichoderm type of pileipellis. Furthermore, the pileus was described as velutinous to minutely squamulose and the odor as indistinct. All of these features are consistent with *Mallocybe*. Horak, however, did note that KOH failed to darken the pileus surface, and no explicit statement of the presence of necrobasidia was made. Despite this, and given the overall combination of features above, placement in *Mallocybe* seems most warranted, hence the new combination above. The species is a *Nothofagus* associate, and the first species of *Mallocybe* described from New Zealand.

Key to Eastern North American species of *Mallocybe*

1a.	Pileus granulose-scaly and stipe with bands of dark colored fibrillose-scales against a lighter background	***M. unicolor***
1b.	Pileus and stipe not as above	**2**
2a.	Basidiospores oblong, mean Q > 2.0	**3**
2b.	Basidiospores not oblong, mean Q < 2.0	**6**
3a.	Basidiomes robust (mature stipe 8–10 mm wide), flesh tough, lamellae brittle, pileus surface not darkening with application of KOH solution, basidiospores pale brown in KOH	***M. praevillosa***
3b.	Basidiomes not robust (mature stipe < 8 mm wide), flesh soft and lamellae soft, pileus surface darkening with KOH, basidiospores yellowish brown in KOH	**4**
4a.	Pileus convex to plano-convex at first and not umbonate; cheilocystidia short-clavate, pyriform to short-cylindric (< 30 µm long); on acidic soil in northern forests	***M. malenconii***
4b.	Pileus convex to broadly convex and not umbonate; cheilocystidia elongated (> 30 µm long); on acidic soil in southern Appalachian montane forests	***M. montana***
4c.	Pileus conical at first and umbonate, cheilocystidia differently shaped than above (> 30 µm long); on calcareous soil, northern Florida in oak-pine forests	**5**
5a.	Cheilocystida subcylindric or slenderly clavate with obtuse to subcapitate apices	***M. multispora***
5b.	Cheilocystidia clavate (not slenderly so), utriform, saccate, and/or obovate	***M. fulviceps***
6a.	Stipe base yellow and/or stipe context with pale yellow tone	**7**
6b.	Stipe base white and stipe context without a yellow tone	**8**
7a.	Basidiospores 6–6.5 µm wide, on karst topography under oak-hickory	***M. luteobasis***
7b.	Basidiospores 5–5.5 µm wide, on acid soils under oaks, pine, ericaceous trees and/or shrubs, or other conifers (*Pseudotsuga*)	***M. squamosodisca***
8a.	Stipe with a distinct cortinate ring-zone	**9**
8b.	Stipe without a distinct cortinate ring-zone	**10**

9a. Pileus brown to dark brown, not bicolorous, in areas with limestone under *Quercus* or *Pinus* .... ***M. tomentosula***
9b. Pileus two-toned or bicolorous with a brown disc and whitish margin due to heavy accumulation of superficial fibrils, on acidic soils under *Picea* or in mixed forests including *Picea* .... ***M. tomentella***

10a. Pileus subsmooth in age and often without an umbo, on acidic soils **11**
10b. Pileus tomentose-fibrillose to squamulose, at times umbonate, soil type various **12**

11a. Under *Quercus* and/or *Pinus* .... ***M. subtomentosa***
11b. Under *Picea* .... ***Mallocybe* sp. PBM4749**

12a. On acidic soils in northern and alpine regions, odor often sweet .... ***M. fibrillosa***
12b. On calcareous soils in various regions (Maine, Florida, Arizona) but not alpine; odor not remarkable **13**

13a. Pileus not umbonate, with a distinct hairy white vesture; basidiospores 8–10 × 4.5–5.5 µm, yellowish brown in KOH; cheilocystidia < 12 µm wide .... ***M. leucothrix***
13b. Pileus at most weakly umbonate, with a distinct hairy white vesture; basidiospores 9–11 × 5.5–6.5 µm, yellowish brown in KOH; cheilocysatidia > 12 µm wide .... ***M. latifolia***
13c. Pileus with a small but prominent umbo, without a distinct hairy white vesture; basidiospores 8–9 × 4.5–5.5 µm, very pale brown to light yellow in KOH; cheilocystidia > 12 µm wide .... ***M. fulvoumbonata***

Unclarified species of *Mallocybe* from North America, Asia, and Australasia

Nine insufficiently known species, seven from western North America, one from eastern North America, and one from New Zealand, are recognized from one or few collections or are known only from environmental samples. These species will be documented taxonomically elsewhere pending evaluation of additional data.

Mallocybe sp. 1 was recovered from three environmental root system samples of *Dryas integrifolia* in the Alaskan arctic by Timling *et al.* (2012); the species is very closely related to *M. delecta* (syn. *M. crassivelata*), a European species found in hardwood and conifer forests (Crous *et al.* 2020). We are unaware of any collections associated with *Mallocybe* sp. 1 at this point. *Inocybe marmoripes sensu* D.E. Stuntz (Stuntz 1940) undoubtedly represents *Mallocybe* sp. 2, which we have documented from Oregon and confirmed from British Columbia (see discussion above under *M. unicolor*). Sufficient collections are on-hand eventually to describe this species. *Mallocybe* sp. 3 (PBM1615) is known from a single collection under montane conifers in Washington state and is the sister species to the northern European species *M. arthrocystis* (FIG. 2B) with strong support. *Mallocybe* sp. 4 (PBM2290) is yet another likely undescribed species from Washington state that is also in the Arthrocystis clade, but it is known only from one collection. *Mallocybe* sp. 5 (JFA13285, PBM1922, SDA470) is likewise an independent lineage collected under montane conifers from Washington state and is sister to *M. fuscomarginata* from Europe; we intend to present a formal description of this species at a later date. *Mallocybe* sp. 6 (ADP060305, PBM1444) is yet another montane conifer-associate found in Washington state; it is strongly supported in a sister position to all other species in the Fuscomarginata clade and will be formally described in forthcoming works. *Mallocybe* sp. 7 represents an unclarified species with an omphalinoid habit from New Zealand found in likely association with *Nothofagus.* It does not appear to match any of the previously described species attributed to *Mallocybe* from this region (Horak 2018); it is known from a single collection at this time. *Mallocybe* sp. 8 is represented by one known American collection studied by us from West Virginia and several samples from China and Quebec (the latter communicated by J. Landry); this species is probably undescribed. *Mallocybe* sp. 9 is known from several samples from the Pacific Northwest to which the name *Inocybe terrigena* has been misapplied; this entity forms a paraphyletic group in our analyses but deserves further scrutiny. Lastly, the status of some collections documented from Australia by Matheny & Bougher (2017) related to *M. isabellina*, *M. subflavospora*, and *M. pyrrhopoda* await further revision.

Excluded Eastern North American species attributed to *Mallocybe*

Inocybe angustispora Bessette & Fatto, *Mycotaxon* **66**: 123. 1998.
Synonym: *Inocybe taedophilia* Murrill, *Proc. Florida Acad. Sci*. **7**: 122. 1944.

Both *I. angustispora* and *I. taedophila* are later synonyms of *Cortinarius aureifolius* Peck (Matheny 2003, Matheny & Ammirati 2003). Gene sequences of 28S, *rpb1*, and *rpb2* have been produced from the holotype of *I. angustispora*.

Inocybe ferruginosa A.H. Sm., *Pap. Mich. Acad. Sci*. **24**: 93. 1939.

Ammirati (1972) synonymized *I. ferruginosa* and *Cortinarius uliginosus* var. *nauseosus* with *Cortinarius uliginosus*. However, Niskanen (2014) combined *I. ferruginosa* in *Cortinarius*. An ITS sequence has been produced from the holotype, which supports assignment of the species in *Cortinarius*.

Inocybe weberi Murrill, *Proc. Florida Acad. Sci*. **7**: 123. 1944.

The punctate elliptic to subamygdaliform basidiospores (8–9 × 5–5.5 µm), in combination with the yellowish lamellae and presence of anthraquinone interhyphal pigment deposits, suggest the type is synonymous with *Cortinarius croceus* (Matheny 2003).

DISCUSSION

This study is the first systematic revision of *Mallocybe* as it occurs in eastern North America. We used four different gene regions for phylogenetic analyses and considered taxon sampling across the globe. Our intent was to revise first those species that occur in eastern North America and generate a useful and predictive infrageneric systematic arrangement. To facilitate stable application of names, we have produced sequenced reference specimens for seven species described in historical works by Peck, Ellis & Everhart, and Murrill. Some authors have had success with molecular annotation of types and other historical collections of *Inocybe* (Cripps *et al.* 2010, Matheny & Swenie 2018, Matheny & Kudzma 2019). However, the process to do so must take steps to avoid contamination from non-target fungi (*e.g.*, *Aspergillus*) and laboratory aerosols and equipment. These problems can be mitigated with careful laboratory procedures and taxon-specific primers. Even with these approaches, the success rate is still low for collections made by Murrill from northern Florida in the 1930s and 1940s (Looney 2014). This is probably due to poor preservation technique by the original collector, the age of the specimens, or degradation of DNA over time. Moreover, some of Murrill's types are scanty or composed of single basidiomes. In addition, recent studies by Eberhardt *et al*. (2022, 2023) were only able to produce partial molecular annotations for one of six species of *Inocybaceae* described by Peck more than 100 years ago, and only a few *Inocybaceae* described by Murrill could be partially annotated. While epitypification is a useful tool to ultimately clarify and stabilize species recognition (Hyde & Zhang 2008), we avoided this procedure because interpretation of North American types attributable to *Mallocybe* could be accomplished based on morphology and ecology, most often in comparison to modern reference materials collected by us at or near type localities. As a consequence, several unused names attributable to *Mallocybe* have been resurrected in this study based on our interpretations of the types (*M. fibrillosa*, *M. subtomentosa*, *M. squamosodisca*, and *M. unicolor* of Peck; *M. fulvoumbonata*, *M. fulviceps,* and *M. multispora* of Murrill; and *M. tomentosula*, a replacement name based on the type of *Inocybe tomentosa* Ellis & Everh.). In addition, we were able to resuscitate the Murrill name *Lepista praevillosa* and recombine it in *Mallocybe*, which was discovered as the sister species to all other *Mallocybe*. Despite resurrecting several old names, we still detected undescribed lineages to which no prior names could be applied and described four of those as new – *M. leucothrix*, *M. luteobasis*, *M. montana*, and *M. tomentella*. We are also aware of additional species from eastern North America (*e.g.*, *Mallocybe* sp. 8) that remain unclarified or possibly undescribed but are not yet sufficiently documented.

Our study also recovered three strongly supported clades within *Mallocybe* that could correspond to subgenera (clades Mallocybe, Nothosperma, and Unicolores) but await formal description pending efforts at revision of additional taxa. Clade Mallocybe contains the bulk of known *Mallocybe* species, and these primarily originate from temperate regions of the northern hemisphere and are often characterized by presence of short cheilocystidia. Clade Nothosperma contains species known from Australasia (Australia, New Zealand, New Guinea) and Malaysia; most of these species too are primarily characterized by the presence of short cheilocystidia. Clade Unicolores contains six species, three of which are endemic to eastern North America and characterized by spores with mean Q values near or greater than 2.00 and often elongated cheilocystidia (> 50 µm in length) (Hu *et al.* 2023).

One challenge we encountered during this work was the phylogenetic placement of the recently described western and southern African tropical species *M. africana* (Aignon *et al.* 2021). We have been aware of this species for some time (see Matheny *et al.* 2009 where it was treated as "*I. microdulcamara nom. prov.*") based on nuclear ribosomal DNA sequences only and found the species to cluster with another Old World tropical lineage from south Asia, *M. errata*, with strong support (Matheny *et al.* 2009). Aignon *et al.* (2021) were able to generate *rpb2* data from recent materials, but our phylogenetic analysis of RNA polymerase II data only (not shown) placed *M. africana* in a sister position to all other species of *Mallocybe*. Unfortunately, gene sampling across *Mallocybe* is uneven (*e.g.*, *rpb2* data could not be generated for *M. errata*, and we could not independently obtain new *rpb2* and *rpb1* sequences from *M. africana* either), so we cannot exclude the possibility that uneven gene and taxon sampling could impact the placement of this unusual species, or that existing data provide conflicting phylogenetic signal. Thus, we treat *M. africana* as *incertae sedis* within *Mallocybe*. Additional specimens and loci (*e.g.*, *rpb1*) of *M. africana* will need to be produced and re-analyzed, and data produced from *M. althoffiae* by the senior author but analyzed by Aignon *et al.* (2021) should be discarded as artifacts (Matheny *et al.* 2020).

Our rDNA phylogeny (Supplementary Fig. S3) was ambiguous about the placement of *Mallocybe praevillosa*, where it clustered with weak support among outgroup taxa. However, individual analyses of *rpb1* and *rpb2* (Supplementary Figs S1, S2) and analyses of the combined data (Figs 1, 2), strongly supported *M. praevillosa* as sister to all other *Mallocybe* in this work. *Mallocybe praevillosa* possesses some character states unlike other *Mallocybe* in that (i) the pileus surface did not darken with KOH, (ii) the basidia were not necropigmented, and (iii) the flesh of the basidiomes was tough and the lamellae brittle. In addition to these features, the basidiospores were found to be noticeably pale, but this trait has been noted in other species (*e.g.*, *M. subflavospora*, *M. fulvoumbonata*). Furthermore, *M. praevillosa* was the only eastern North American sample for which we detected muscarine. One might consider accommodation of *M. praevillosa* in a separate (new) genus apart from *Mallocybe* due to the unique combination of traits highlighted above, but we decided against this decision owing to taxonomic redundancy (viz, establishing a monotypic genus), the few specimens studied, and the fact that the species forms a strongly supported clade with the rest of *Mallocybe*.

This work also recapitulates and highlights some significant evolutionary and ecological findings. Hu *et al.* (2023) demonstrated that the presence of elongated cheilocystidia was a shared ancestral state in *Mallocybe*. Our study reinforces this result even with the discoveries of *M. montana* and *M. praevillosa*. The shift to short-clavate or short-pyriform cystidia may have occurred in the most recent common ancestor of clades Mallocybe and Nothosperma or perhaps independently in these groups. We also find it notable that species of the Montana and Praevillosa lineages, as well as those in clade Unicolores, exhibit relative narrow ranges of endemism, and all either originate in eastern North America or east Asia. The Australasian species in clade Nothosperma likewise exhibit narrow-range endemism either restricted to Australia or New Zealand. By contrast, many species in the core Mallocybe clade exhibit broad intercontinental geographic distributions as noted previously by Cripps *et al.* (2010).

Our work also provides a multigene phylogenetic framework to continue studies and revision of additional taxa from other parts of the world. For example, we detected seven species-level lineages that occur in western North American conifer forests that are likely undescribed. In addition, further attention is necessary to clarify some Australasian species of *Mallocybe* (Matheny & Bougher 2017).

Detection of the secondary metabolite muscarine varies within *Mallocybe.* Here we report the non-detection of muscarine in nine of the 11 species sampled. Muscarine was detected at relatively high amounts in two distantly related species (*M. sabulosa* from Australia and *M. praevillosa* from Florida). Kosentka *et al.* (2013) and Stijve *et al.* (1985) also reported the lack of detectable amounts of muscarine from *M. unicolor* and *M. terrigena*, respectively. The evolutionary and ecological significance of the absence and sporadic presence of muscarine across the genus are poorly understood at this time. Future efforts are needed to assess the relative concentrations of the toxin among multiple samples within species and confirm the taxonomy and earlier reports of muscarine-containing *Inocybe* attributable to *Mallocybe* today (Stijve *et al.* 1985, Gurevich & Nezdoiminogo 1992), including species *M. agardhii*, *I. caesariata*, *I. dulcamara*, and *M. malenconii* (Kosentka *et al*. 2013).

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Supplementary information

Fig. S1. ML *rpb1* gene phylogeny of *Mallocybe*. Numbers above or below branches indicate bootstrap proportions > 50 %.

Fig. S2. ML *rpb2* gene phylogeny of *Mallocybe*. Numbers above or below branches indicate bootstrap proportions > 50 %.

Fig. S3. ML ITS+28S rDNA gene phylogeny of *Mallocybe*. Numbers above or below branches indicate bootstrap proportions > 50 %.