

## **New species of *Inocybe* (Inocybaceae) from eastern North America<sup>1</sup>**

Authors: P. Brandon Matheny, and Linas V. Kudzma

Source: The Journal of the Torrey Botanical Society, 146(3) : 213-235

Published By: Torrey Botanical Society

URL: <https://doi.org/10.3159/TORREY-D-18-00060.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# New species of *Inocybe* (Inocybaceae) from eastern North America<sup>1</sup>

P. Brandon Matheny<sup>2</sup>

Department of Ecology and Evolutionary Biology, University of Tennessee  
1406 Circle Drive, Knoxville, TN 37996 USA

Linus V. Kudzma

37 Maple Ave., Annandale, NJ 08801

**Abstract.** Five species of *Inocybe* from eastern North America are described as new: *Inocybe carolinensis*, *Inocybe dulciolens*, *Inocybe friabilis*, *Inocybe glaucescens*, and *Inocybe vinaceobrunnea*. *Inocybe carolinensis* is a new species in *Inocybe* sect. *Inocybe*; *I. dulciolens* and *I. glaucescens* are two new species in *Inocybe* sect. *Lactiferae*; *I. friabilis* is described as new in the *Pseudosperma* clade (*Inocybe* sect. *Rimosae* sensu stricto); and *I. vinaceobrunnea* is newly described for *I. jurana* sensu Hesler in the *Inosperma* clade (*Inocybe* sect. *Rimosae* sensu lato). At least four of the five species are endemic to regions of eastern North America based on current distribution data. ITS, 28S rDNA, *rpb2*, and *rpb1* genes, in combination with morphological and ecological traits, are used to aid in species recognition. Phylogenetic trees, taxonomic descriptions, and illustrations are provided.

Key words: Agaricales, Basidiomycota, ectomycorrhizal fungi, systematics, taxonomy

The family Inocybaceae Jülich is a highly diverse taxonomic group of mushroom-forming fungi in the Agaricales with an estimated 700 species worldwide (Matheny *et al.* 2009). This figure as assessed is now an underestimate as nearly 450 species of *Inocybe* are said to occur in Europe with increasing aid of molecular data and refinement of species recognition methods (Bandini *et al.* 2017). In addition, nearly 150 species in the family have been recently recognized from

Australia (Matheny and Bougher 2017), including descriptions of 101 new species. Novel taxa continue to be described across the globe from South America (Matheny *et al.* 2012), Asia (Horak *et al.* 2015, Pradeep *et al.* 2016, Latha and Manimohan 2017), New Zealand (Horak 2018), and Africa (Matheny *et al.* 2017). Despite over two centuries of taxonomic work in Europe, new species of the genus *Inocybe* (Fr.) Fr. continue to be described there now using a combination of molecular, morphological, and ecological analyses of extant materials and type collections (*e.g.*, Kokkonen and Vauras 2012, Esteve-Raventos *et al.* 2016, Larsson, Vauras, and Cripps 2017, Ludwig 2017, Bandini *et al.* 2018). Indeed, Index Fungorum ([www.indexfungorum.org](http://www.indexfungorum.org)) now recognizes 1,050 accepted names of species in *Inocybe*.

Taxonomic studies of *Inocybe*, one of three genera in the Inocybaceae, culminated in North America with an early 20th century monograph by Kauffman (1924), who revised and centralized earlier taxonomic treatments by workers such as C.H. Peck, F.S. Earle, W.A. Murrill, G.F. Atkinson, and others. Kauffman's work recognized 105 North American species of *Inocybe*. Between 1947 and 1984, Stuntz and colleagues described an additional 40 new species from North America (*e.g.*, Stuntz 1947, Grund and Stuntz 1984), and Murrill contributed 30 new species described from Florida (*e.g.*, Murrill 1944, 1945). Many additional works ensued describing novel taxa and new reports of *Inocybe* from California (Nishida 1988, Kropp and Matheny 2004, Braaten *et al.* 2014), the Great Basin (Kropp, Matheny, and Hutchison

<sup>1</sup> The authors thank Allein Stanley, Glenda O'Neil, and Paul Super for fungal collecting permits at Mt. Mitchell State Park and the Great Smoky Mountains National Park. We thank Alain Belliveau, Vera Evenson, Roy Halling, Jay Justice, Any Methven, Christian Schwarz, Allison Walker, Andy Wilson, Denver Botanical Garden, E.C. Smith Herbarium at Acadia University, New York Botanical Garden, University of Central Oklahoma Herbarium, University of California Santa Cruz Fungal Herbarium, and the University of Washington Herbarium for providing materials during this study. Marisol Sánchez-García (Uppsala University) provided the Index fungorum species number estimate. Laboratory assistance was provided by Christine Braaten, Hailee Korotkin, Sarah Sprague, Rachel Swenie, and Aaron Wolfenbarger. Funding and other support for this work was provided by the Hesler Endowment Fund at the University of Tennessee, the Daniel E. Stuntz Memorial Foundation, and the North American Mycological Association.

<sup>2</sup> Author for correspondence: [pmatheny@utk.edu](mailto:pmatheny@utk.edu)  
doi: 10.3159/TORREY-D-18-00060.1

©Copyright 2019 by the Torrey Botanical Society

Received for publication December 5, 2018, and in revised form March 1, 2019; first published September 6, 2019.

2013), the Rocky Mountain alpine zone (Cripps, Larsson, and Horak 2011), the Pacific Northwest (Kropp, Matheny, and Nanagyulyan 2010, Matheny *et al.* 2013), Central America (Singer, Araujo, and Ivory 1983), and the Caribbean (Pegler 1983). While a small number of studies have documented rare or unusual taxa of *Inocybe* from eastern North America (Matheny and Moreau 2009, Kuo and Matheny 2015), little has been done to revise and describe new species from this large area in over 30 years.

Species of *Inocybe* are often characterized macroscopically by small, mundane-colored basidiomes with a dry scaly to fibrillose or rimose pileus, attached dull brown lamellae, a stipe, and distinctive odor. The basidiospores are generally dull brown pigmented, slightly thick-walled, smooth, angular, nodulose or spinose in outline, and typically lack a germ pore. In addition, most species of *Inocybe* are characterized by the presence of thick-walled hymenial cystidia, the apices of which typically bear crystals of calcium-oxalate (Kuyper 1986). The basidiomes of many species also contain the toxin muscarine, and a small number are hallucinogenic (Kosentka *et al.* 2013). Ecologically, *Inocybaceae* form ectomycorrhizal associations with *circa* 20 families of angiosperms and gymnosperms (Kuyper 1986, Matheny *et al.* 2009). Seven major clades have been recognized in the family, three of which are formally recognized as genera: *Auritella* Matheny & Bougher, *Inocybe*, and *Tubariomyces* Esteve-Rav. & Matheny (Matheny and Bougher 2017). The genus *Inocybe* comprises five major clades that have been informally named the *Inocybe*, *Pseudosperma*, *Inosperma*, *Mallocybe*, and *Nothocybe* clades (Matheny *et al.* 2009, Alvarado *et al.* 2010).

This study represents a contribution towards a revision of species of *Inocybaceae* from eastern North America. At present, about 200 species of *Inocybe* can be recognized from the region encompassing Greenland, eastern parts of Canada, west to Michigan and Minnesota, south to the Gulf Coast region, Mexico, Central America, and the Caribbean basin (Matheny 2017). For convenience, this number also includes species described from the Lesser Antilles, although Murrill (1914) considered this region as part of the South American flora. Here, we describe five new species of *Inocybe* from eastern North America using a combination of morphological, molecular, and

ecological data. Taxonomic descriptions, illustrations of key features, and molecular phylogenetic trees are presented in support of each new species.

**Materials and Methods.** Samples were collected in the field by the authors and air-dried on a food dehydrator for preservation. Macroscopic descriptions were made with color guides Munsell Soil Color Charts (1954) and Ridgway (1912). Colors from Munsell are in lower-case and indicated by plate, row, and hue (*e.g.*, 10YR 3/2). Colors from Ridgway (1912) are capitalized and in quotation marks. “L” refers to the number of lamellae that reach the stipe. Use of PDAB on basidiome tissue follows Matheny, Norvell, and Giles (2013).

Thin sections of the pileus, stipe surface, and lamellae were prepared and rehydrated in 5% KOH mixed with Congo red (Cléménçon 2009) and examined on a Nikon Eclipse 80i compound light microscope (Nikon Instruments, Tokyo, Japan). Cells were measured using using Nikon NIS-Elements D software, version 3.1. Description of microscopic features follows Kuyper (1986). Measurements of basidiospores include the mean (italicized). Outliers greater than two standard deviations from the mean are shown in parentheses. Q-values refer to basidiospore length divided by basidiospore width. The number (*n*) of total basidiospores (*x*) from (*y*) collections is indicated as *n* = *x*/*y*. Field collections, including types, are accessioned at TENN. Herbarium abbreviations follow Thiers (2019 [continuously updated]), except for those designated as “pers. herb.” of L. Kudzma (Annandale, New Jersey).

DNA extractions, PCR, and sequencing by P.B. Matheny follow protocols previously outlined in Judge *et al.* (2010). Four gene regions were sequenced but not for all samples: nuclear ITS1-5.8S-ITS2 rDNA (ITS), nuclear 28S rDNA (28S), and the most variable regions of *rpb1* and *rpb2*, the latter two encoding the largest and second largest subunit of RNA polymerase II, respectively. Primers ITS1F and ITS4 (White *et al.* 1990), LR0R and LR5 or LR7 (Vilgalys and Hester 1990), gRPB1-Af and fRPB1-Cr, and bRPB2-6F, and bRPB2-7.1R (Matheny 2005) were used for PCR and sequencing. Several internal sequencing primers were also used to obtain *rpb1* sequences: aRPB1-Br, Int2f, Int2.1f, and Int2.1r (Matheny *et al.* 2002; Froslev, Matheny, and Hibbett 2005). Resulting chromatograms were assembled in

Sequencher 5.0.1 (Gene Codes Corp., Ann Arbor, MI).

L.V. Kudzma extracted genomic DNA from dried basidiomes using the NucleoSpin Plant II Kit (Macherey-Nagel Inc., Bethlehem, PA). Products were amplified and sequenced as above except for the following modifications. The ITS region was amplified and sequenced using primers ITS1F and ITS6-R (Dentinger, Mararitescu, and Moncalvo 2010) or ITS4B (Gardes and Bruns 1993). A new primer, LSU0F, was designed upstream of the LR0R primer site for enhanced amplification and, where necessary, for nested PCR purposes (5'-GACCTCAAATCAGGTAGGA-3'). The most variable region of *rpb2* was amplified and sequenced using primers fRPB2-5F (Liu, Whelen, and Hall 1999) or bRPB2-6F and bRPB2-7.1R; in addition, bRPB2-7R (Matheny 2005) was used for sequencing. The highly variable region between conserved domains A and C of the *rpb1* gene was amplified and sequenced as above except that two newly designed internal primers specific to *Inocybe* were used for sequencing and/or nested PCR when initial amplification failed or gave weak results: iRPB1-intF1 (5'-CCTCTACTCGTTTCG-CACC-3') and iRPB1-midexF2 (5'-TGCGAACCTGATGATCC-3'). MyTaq HS Red Master Mix (Bioline USA, Taunton, MA) was used for PCR following protocols from the laboratory of D. Hibbett, Clark University. Sequencing was done by Genewiz Inc. (South Plainfield, New Jersey).

New sequences of 28S, *rpb2*, and *rpb1* were aligned manually in MacClade 4.08 (Maddison and Maddison 2005) with in-house alignments of these gene regions curated over the years (Matheny *et al.* 2009, Ryberg and Matheny 2012, Kosentka *et al.* 2013, Matheny and Bougher 2017). We inspected a global *rpb2* alignment of 782 taxa by phylogenetic analysis (described below) to focus placement of individual taxa in smaller multigene datasets. Alignments were then pruned to subjects of this study in four separate datasets and concatenated. Individual ITS datasets were assembled for two of these datasets (sect. *Lactiferae* R. Heim and clade *Adaequata*). ITS sequences of each were used as queries in BLAST searches on GenBank. ITS matches with > 90% sequence similarity were downloaded and aligned in ClustalX 2.0.9 (Larkin *et al.* 2007), manually adjusted by eye in MacClade, and aligned with new ITS sequences produced during this study. All separate

gene alignments were merged into a supermatrix for phylogenetic analysis after inspection for strongly supported intergene conflict. Conflict was observed if clade membership conflicted with > 70% bootstrap support when comparing gene trees.

Five datasets total were analyzed with Maximum Likelihood (ML) in RAxML v8 (Stamatakis 2014). The global *rpb2* alignment was partitioned by codon position and excluded the highly variable intron4 region (Matheny 2005). The ITS, 28S, and/or *rpb2*-intron4 portions of each alignment were partitioned under one model, whereas exon regions of *rpb2* were partitioned by each codon position following Matheny (2005). Sequences of *rpb1* were used for phylogenetic analyses of sect. *Inocybe* and clade *Adaequata*. A GTRGAMMA model was applied to each unlinked gene partition following recommendations in the RAxML user manual except for analysis of the *Adaequata* clade, which was characterized by few samples and a relatively high proportion of missing data. To assess support, 1,000 rapid bootstrap replicates were performed on all data sets, except 500 replicates for the global *rpb2* data set.

Bayesian inference (BI) phylogenetic analyses were also done using MrBayes v3.2 (Ronquist *et al.* 2012) using the same models and partitioning schemes in the ML analyses for all datasets except for the *rpb2* global dataset. One million generations were executed for each analysis, including two independent runs, sampling trees every 100 generations from the posterior distribution. A 25% burn-in was applied after checking convergence between runs using diagnostics explained in the MrBayes v3.2 user manual. Trees were rooted based on topologies presented in Larsson *et al.* (2009), Matheny *et al.* (2009), Ryberg, Larsson, and Jacobsson (2010), or along the longest internode in the tree (midpoint rooting). Bootstrap values > 70% and posterior probabilities > 0.95 were considered as evidence for strong support.

**Results.** MOLECULAR ANALYSES SUPPORT RECOGNITION OF FIVE NEW SPECIES OF *INOCYBE* FROM EASTERN NORTH AMERICA. The *rpb2* global dataset is composed of 782 taxa and 774 included nucleotide sites. Analysis of this dataset (Supplementary Fig. 1; GenBank accessions are provided on this figure, 139 of which are newly released) suggests a close but poorly supported phylogenetic relationship between *I. carolinensis* sp. nov. and

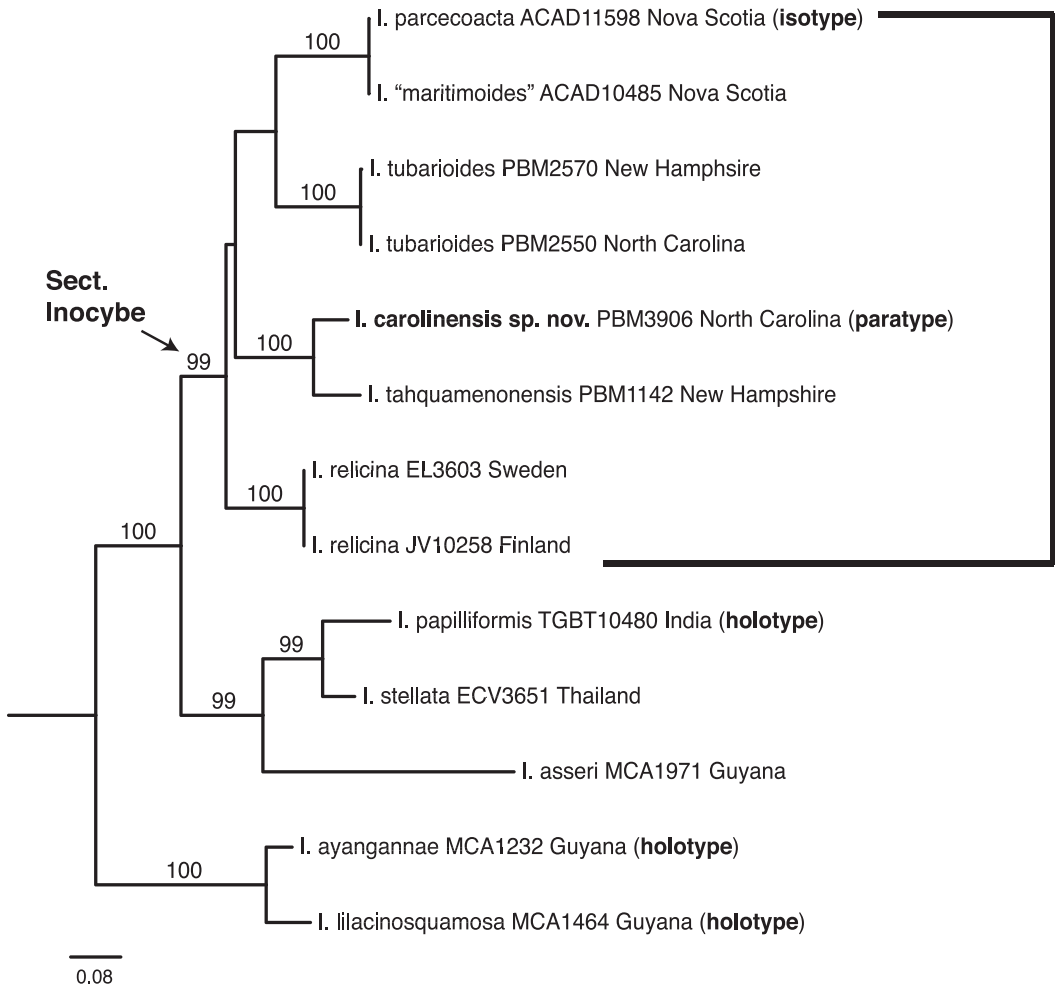


FIG. 1. ML tree of 28S, *rpb1*, and *rpb2* nucleotide sequences of *Inocybe* sect. *Inocybe*. Bootstrap values > 70% are indicated above branches and posterior probabilities > 0.95 below. The new species, *I. carolinensis*, is highlighted in bold. The tree is rooted along the branch leading to the clade of *I. ayangannae* and *I. lilacinosquamosa* based on Horak *et al.* (2015). The scale bar indicates the number of expected substitutions per site.

*Inocybe tahquamenonensis* D. E. Stuntz, *Inocybe tubarioides* G. F. Atk., and *Inocybe relicina* (Fr.) Quél., the latter the type of the genus *Inocybe*. This clade corresponds to *Inocybe* sect. *Inocybe* in Matheny and Moreau (2009), which was previously recovered as a strongly supported clade based on analysis of three loci: 28S, *rpb1*, and *rpb2*. This result guided taxon selection for a dataset based on 12 taxa and 3,383 total sites, all of which were included in the phylogenetic analysis. *Inocybe carolinensis* is most closely related to *I. tahquamenonensis* with 100% ML bootstrap support in sect. *Inocybe* (Fig. 1). *Inocybe carolinensis* is the fifth species now confirmed in sect.

*Inocybe*, four of which are endemic to eastern North America. This study also suggests the placement of the eastern Canadian species *I. parvecoacta* Grund & D.E. Stuntz in sect. *Inocybe*.

The *rpb2* global analysis also recovered a close phylogenetic relationship between members of sections *Lactiferae* and *Hysterices* Stangl & Veselský, consistent with previous phylogenetic analyses (Matheny 2005). This result guided taxon selection for a dataset based on 59 taxa and three loci—ITS, 28S and *rpb2*—and 3,049 total sites, of which 172 were excluded prior to phylogenetic analyses. DNA sequences (ITS, 28S, *rpb2*) from

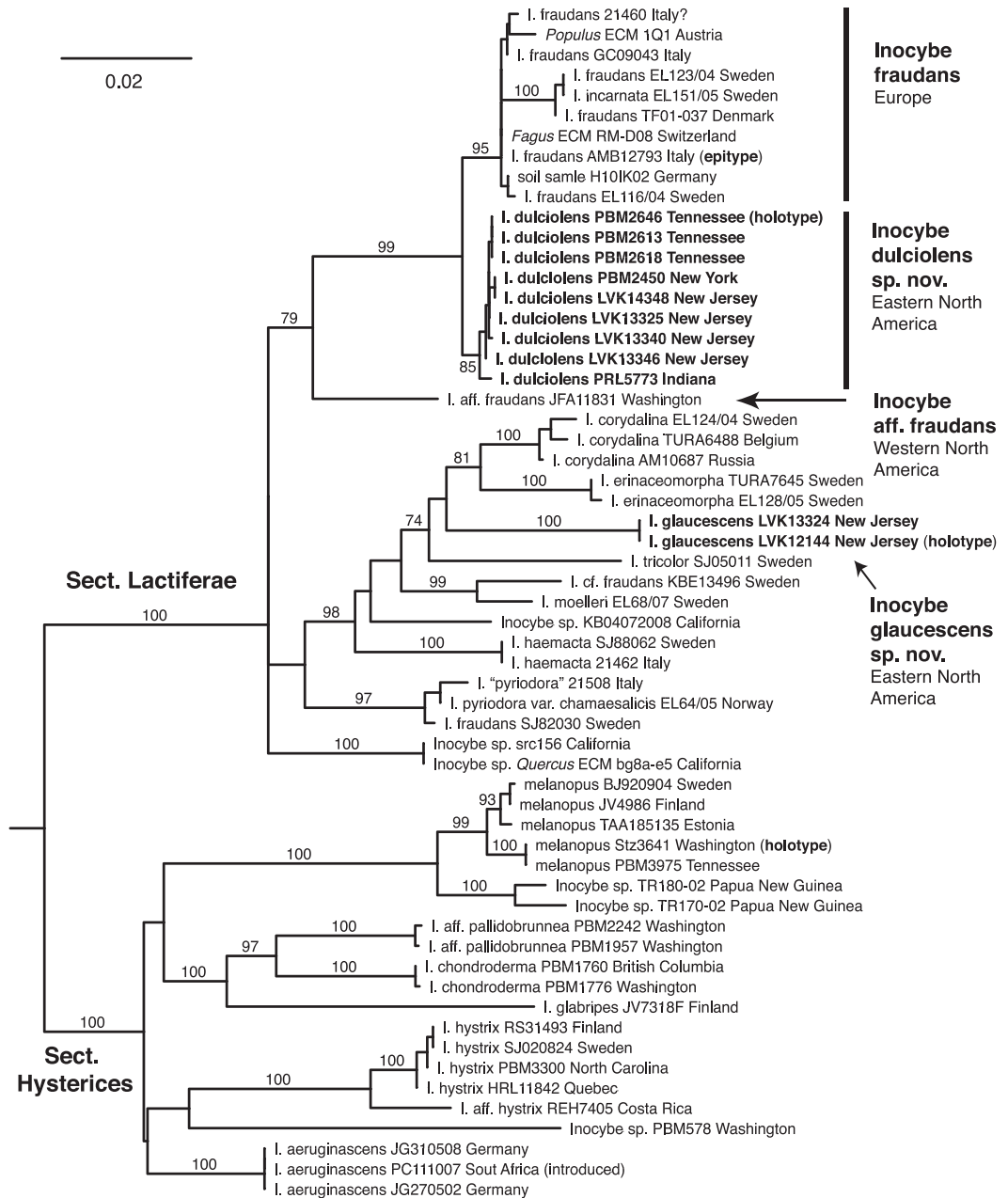


FIG. 2. ML tree of ITS, 28S, and *rpb2* nucleotide sequences of *Inocybe* sect. *Lactiferae* and sect. *Hysterices*, constituents of *Inocybe* clade I of Matheny (2005). Bootstrap values  $> 70\%$  are indicated above branches and posterior probabilities  $> 0.95$  below. Tips of the new species, *I. dulciolens* and *I. glaucescens*, are highlighted in bold. The tree is midpoint rooted. The scale bar indicates the number of expected substitutions per site.

nine samples of *I. dulciolens* sp. nov. (= *I. pyriodora* and *I. fraudans* sensu Am. auct.) form a monophyletic group and are the sister lineage to 10 samples of *I. fraudans* from Europe, including the epitype (Fig. 2). Both species-level clades are

recorded frequently from hardwood forests or in association with hardwood trees; however, pine associations cannot be ruled out for *I. dulciolens*. *Inocybe* aff. *fraudans* from Washington (JFA11831) likely represents a new species; it is

genetically and ecologically distinct (conifer association) from *I. fraudans* and *I. dulciolens*. All of these species are considered nonhallucinogenic taxa in sect. *Lactiferae*.

Sect. *Lactiferae* also includes several psilocybin-containing or hallucinogenic taxa described from Europe (Kuyper 1986), viz. *I. corydalina* QuéL., *I. haemacta* (Berk. & Cooke) Sacc., and *I. tricolor* Kühner. To this section we add the newly described species *I. glaucescens* sp. nov. from New Jersey and at least one undescribed species from California (KB04072008, TENN 063524; Fig. 2), both of which discolor blue-green or blue on the pileus surface and thus are putatively hallucinogenic. A third undescribed species from the west coast of North America has been recorded from central California in association with *Quercus* (*Inocybe* sp. src156).

Sect. *Hysterices* appears to be the sister clade to sect. *Lactiferae* and includes two North American described taxa: *I. melanopus* D. E. Stuntz and *I. chondroderma* D.E. Stuntz ex Matheny, Norvell & E.C. Giles, the European species *I. glabripes* Ricken and *I. aeruginascens* Babos (Fig. 2), and the widely distributed species *I. hystrix* (Fr.) P. Karst. Several undescribed or poorly documented species occur in the group as well from the Pacific Northwest and Papua New Guinea, the latter from *Castanopsis* (D. Don) Spach forests. Taxon sampling in this group is not exhaustive. However, the original concept of this section (Stangl and Veselský 1982) must be emended to include taxa with non-squarrose basidiomes.

The preliminary ML analysis of the global *rpb2* dataset also indicates that sequences of *I. friabilis* sp. nov. clusters with strong support with those of *Inocybe gracilissima* Matheny & Bougher (Matheny and Bougher 2017), *I. rimulosa* C.K. Pradeep & Matheny (Pradeep *et al.* 2016), *I. keralensis* K.P.D. Latha & Manim. (Latha and Manimohan 2016), and *I. griseorubida* K.P.D. Latha & Manim. (Latha and Manimohan 2015). Furthermore, this cluster of taxa was strongly supported as the sister group to clade A of *Inocybe* sect. *Rimosae* sensu stricto (Larsson *et al.* 2009) or the *I. rimosa* complex of the Pseudosperma clade (Kropp *et al.* 2013). These results guided composition of the *I. friabilis* dataset, which comprises 57 taxa and two loci—28S and *rpb2*—and 2,245 total sites, all of which were included in the phylogenetic analyses. Two major clades were recovered: the *Inocybe rimosae* complex or clade A of Larsson

*et al.* (2009) and clade *Gracilissima* composed of the new eastern North American species, *I. friabilis* sp. nov., *Inocybe* sp. PBM2601 from high-elevation forests in eastern Tennessee, and three Old World tropical species, *I. gracilissima*, *I. keralensis* (= *I. rimulosa*), and *I. griseorubida* (Fig. 3). Within *I. friabilis* two strongly supported cryptic subgroups were detected: one from New Jersey, New York, and Ohio, and the second from New Jersey, Virginia, and Tennessee.

Maximum likelihood analyses of the global *rpb2* dataset also indicate a robust phylogenetic relationship between *I. vinaceobrunnea* sp. nov., *I. adaequata* (Britzelm.) Sacc., and an undescribed species from California; however, the placement of this group, here referred to as clade *Adaequata*, within the *Inosperma* clade was not resolved. Based on Larsson *et al.* (2009), *I. rhodiola* Bres. is closely related to *I. adaequata*. These two results thus guided our taxon and gene selection for the *Adaequata* dataset, which comprised 15 taxa and four loci—ITS, 28S, *rpb2*, *rpb1*—and 3,773 total sites, all of which were included in the phylogenetic analyses. Four samples of *I. vinaceobrunnea* from southern parts of the U.S., viz. Tennessee and Oklahoma, form a strongly supported monophyletic group (Fig. 4). It is not clear, however, whether *I. vinaceobrunnea* is most closely related to the European species *I. rhodiola* or an undescribed west coast species from North America. In attempt to examine the potential affect of missing data, phylogenetic analysis of ITS and 28S data only were similarly equivocal (not shown). *Inocybe vinaceobrunnea* is said to occur in central Europe as well (D. Bandini, pers. comm.), however, data extending the distribution of this species are not available for comparison.

### Taxonomic Treatment

*Inocybe carolinensis* Matheny & Kudzma, sp. nov. Type: U.S.A. North Carolina, Mt. Mitchell State Park, Balsam Nature Trail, scattered singly in conifer duff under *Abies fraseri* (Pursh) Poir., 35.7689°N, 82.2657°W, 1900 m, August 19, 2016, P.B. Matheny & S.R. Warwick PBM4065 (holotype: TENN 071091; Figs. 5A–B, 6). MycoBank MB 824546. ITS GenBank Accession No. MG663294.

*Diagnosis.* Most similar to *Inocybe tahquamenonensis* but differs from this species by the reddish brown basidiomes and overall furfura-

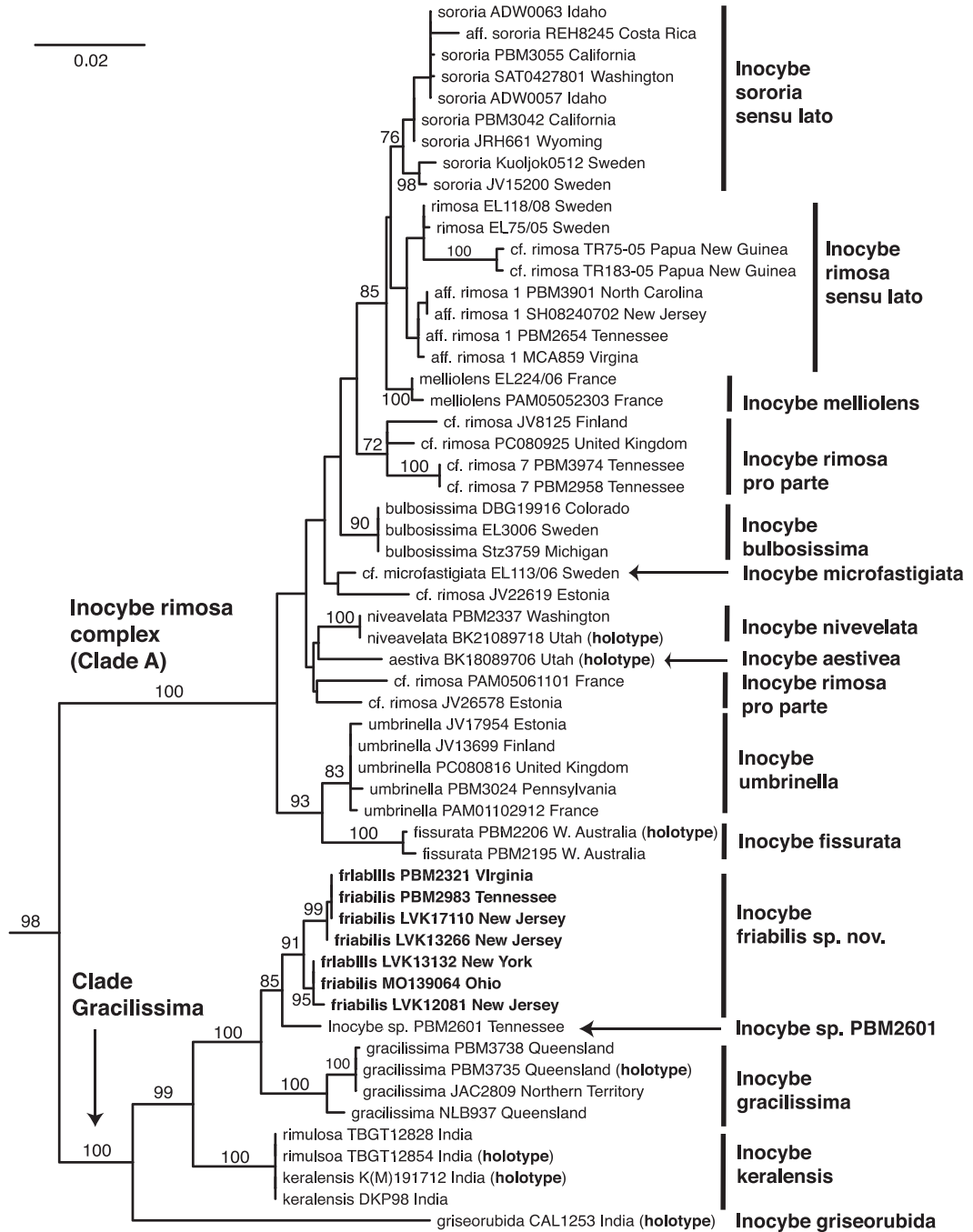


FIG. 3. ML tree of 28S and *rpb2* nucleotide sequences of the *Inocybe rimosa* complex (clade A of Larsson *et al.* (2009) and its sister group, clade Gracilissima, in the Pseudosperma clade. Bootstrap values are indicated above or below branches; posterior probabilities are indicated if > 0.95. Tips of the new species, *I. friabilis*, are highlighted in bold. The tree is midpoint rooted. The scale bar indicates the number of expected substitutions per site.



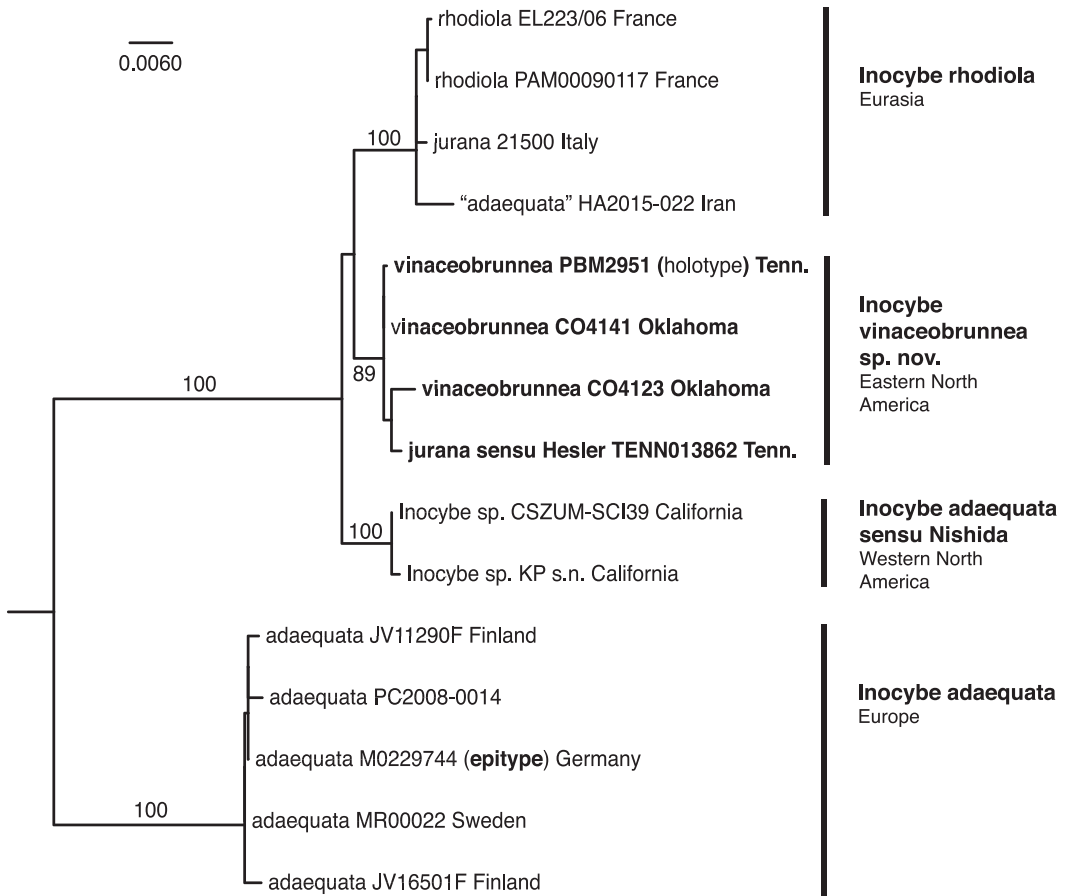


FIG. 4. ML tree of ITS, 28S, *rpb1*, and *rpb2* nucleotide sequences of clade Adaequata in the Inosperma clade. Bootstrap values > 70% are indicated above or below branches; posterior probabilities are indicated if > 0.95. Tips of the new species, *I. vinaceobrunnea*, are highlighted in bold. The tree is midpoint rooted. The scale bar indicates the number of expected substitutions per site.

ceous-fibrillose to furfureous-scaly pileus and stipe surface. Known only under high-elevation conifers (*Abies* Mill.) in the spruce-fir zone of the Southern Appalachians. In contrast *I. tahquamenonensis* is dark purplish-fuscous with a distinctly squarrose or squamose pileus and stipe surface and is a lower-elevation species widely distributed throughout deciduous forests of eastern North America.

Pileus 12–35 mm wide, pulvinate to convex in youth, later conical to broadly so, becoming plano-convex to plane with age, at times with a central depression, generally not umbonate; margin incurved in youth, otherwise decurved, uplifted in age; velipellis absent, surface dry, smooth in appearance when wet but otherwise with fine furfureous fibrils or small scales, not at all rimose, cracking at the disc or at the margin;

reddish brown to dark reddish brown (5YR 5/4, 5/6 to 4/4 or "hazel") to dark red (2.5YR 2/4) or castaneous; context colored like the surface just below the cuticle or throughout, otherwise reddish brown mixed with whitish streaks, not changing color where cut or bruised, up to 4 mm thick beneath the disc; odor and taste absent. Lamellae ascending-adnate to adnexed or sinuate, subdistant to moderately close, 28–36 L, with several tiers of lamellulae, up to 5 mm deep; pinkish-gray or light reddish-brown in youth (5.YR 6/3–4), becoming brown (7.5YR 5/4), eventually dark red (2.5YR 3/6) at maturity, with pallid-fimbriate edges. Stipe 35–65 × 3–7 mm, even or tapered toward the base, at times slightly swollen at the base but never bulbous; overall texture often tough, not at all fragile; cortina fugacious; surface generally with scattered furfureous fibrils or small fibrillose



FIG. 5. Basidiomes of five new species of *Inocybe*. (A) *Inocybe carolinensis* (PBM3906, paratype). (B) *Inocybe carolinensis* (PBM4965, holotype). (C) *Inocybe dulciolens* (PBM3949, paratype). (D) *Inocybe glaucescens* (LVK12144, holotype). (E) *Inocybe friabilis* (PBM3914, holotype). (F) *Inocybe vinaceobrunnea* (PBM2951, holotype). Scale bars = 1 cm.

scales; pinkish-brown to reddish-brown; the furfuroseous fibrils and scales distinctly reddish- to pinkish-brown contrasting at times with the background color (like that of the pileus), which is lighter; context solid with a pallid interior, not changing color where cut or bruised.

Basidiospores  $6\text{--}6.8\text{--}7.5 \times 4\text{--}4.9\text{--}5.5\text{--}(6) \mu\text{m}$ ,  $Q = 1.18\text{--}1.43\text{--}1.88$  ( $n = 33/2$ ), angular, trapeziform, cruciform, or triangular in outline typically with 4–6 moderate or low obtuse nodules, apiculus small but distinct, pale brown to pale yellowish

brown. Basidia  $28\text{--}36 \times 8\text{--}9 \mu\text{m}$ , 4-sterigmate, clavate, hyaline, many collapsed. Pleurocystidia  $65\text{--}90 \times 13\text{--}18 \mu\text{m}$ , fusiform, subcylindric, or digitiform, thin-walled to slightly thick-walled (walls ca.  $0.5\text{--}1.0 \mu\text{m}$  thick), hyaline; apices obtuse, bare or on occasion crystalliferous. Cheilocystidia similar to pleurocystidia, scattered singly on the lamellar edge, mixed with numerous paracystidia—these often clavate to pyriform, thin-walled, hyaline. Caulocystidia not observed. Pileipellis a cutis of cylindrical hyphae, these mostly 5–

15  $\mu\text{m}$  wide, thin-walled, weakly to moderately incrusting, ochraceous-tawny in mass. Lamellar trama regular, hyphae cylindrical to inflated, mostly 5–20  $\mu\text{m}$  wide, thin-walled, smooth, not appreciably pigmented. Clamp connections present, common in all tissues.

ADDITIONAL SPECIMENS EXAMINED. U.S.A. North Carolina: Mt. Mitchell State Park, on ground under conifers, 35.7689°N, 82.2657°W, 1,900 m, September 22, 2012, *D. Viess PBM3906* (TENN 067756). Mt. Mitchell State Park, on ground under conifers, 35.7689°N, 82.2657°W, 1,900 m, September 13, 2013, *E. Harrower PBM3979* (TENN 068427). Mt. Mitchell State Park, Old Mitchell Trail, near state park restaurant, on soil under *Abies fraseri*, 35.76296°N, 82.27199°W, 1,829 m, September 20, 2015, *P.B. Matheny PBM4057* (TENN 071274).

DISTRIBUTION AND HABITAT. Known to date only from Mt. Mitchell State Park at high elevations (1,900 m) under *Abies fraseri* (Pursh) Poir. in the spruce-fir zone of the Southern Appalachians.

PHENOLOGY. August and September.

CONSERVATION STATUS. *Inocybe carolinensis* has been recorded during four different years between 2012–2016 on at least two different trails, Balsam Nature Trail and Old Mitchell Trail, in Mt. Mitchell State Park during the North American Mycological Association regional foray near Little Switzerland, North Carolina. To date, it is not known from anywhere else and thus can be ascribed high conservation status.

ETYMOLOGY. (L.) The specific epithet “*carolinensis*” refers to the region (North Carolina) where this species occurs.

REMARKS. *Inocybe carolinensis* is now one of five species that can be placed, based on molecular phylogenetic data, in sect. *Inocybe* of subgenus *Inocybe* (Matheny and Moreau 2009). All five species possess nodulose basidiospores, at least some of which are cruciform in outline in four of the species, and a cortina. The section includes *I. relicina* (Moser 1978, type species of *Inocybe*), *I. tahquamenonensis* (Stuntz 1954, Matheny and Kropp 2001), *I. tubarioides* (Atkinson 1918, Matheny and Moreau 2009), and *I. parvecoacta* Grund & D.E. Stuntz (Grund and Stuntz 1977). *Inocybe relicina* is an endemic in Fennoscandia, where it occurs in *Picea abies* (L.) H. Karst. mixed

coniferous forests on acid soil typically with *Sphagnum*. It is the only European species in sect. *Inocybe* confirmed by molecular phylogenetic results. Morphologically, it is characterized by yellow lamellae when young and the dark umbrinous scaly basidiomes. *Inocybe tahquamenonensis* is an endemic in eastern North American deciduous forests and widespread between Michigan and eastern Canada, ranging south to northern Georgia (Matheny and Kropp 2001). Basidiomes of *I. tahquamenonensis* are scaly throughout and dark fuscous-purple with vinaceous lamellae. *Inocybe tubarioides* is likewise known only from eastern North American deciduous forests but has an unusual habit for *Inocybe*, occurring on logs and woody debris. Basidiomes of this species are not scaly and are otherwise drab brown, however, the pileus is hygrophanous, features that serve to distinguish the species readily from others in sect. *Inocybe*. *Inocybe parvecoacta* is a poorly known species described originally from Nova Scotia. It is characterized in part by dark brown fibrillose basidiomes, presence of thin-walled hymenial cystidia, nodulose basidiospores, presence of a cortina, aromatic odor, and association with *Picea*. One collection (ACAD 10485) attributed to *I. maritimoides* (Peck) Sacc. by Grund and Stuntz (1977) is molecularly identical to the type of *I. parvecoacta*, originally described from a single collection. Thus, we are now aware of *I. parvecoacta* from two collections. *Inocybe magnifica* (E. Horak) Garrido, described from Papua New Guinea under Nothofagaceae but with red context and cruciform-like basidiospores (Horak 1979), probably belongs to sect. *Inocybe* as well (Matheny and Moreau 2009).

Kobyashi (2002) established sect. *Parvecoactae* Takah. Kobay. in his subgenus *Pertenuis* Takah. Kobay. based on the presence of thin-walled pleurocystidia and cheilocystidia, yellowish brown angular to nodulose basidiospores, nonreddening context where cut, and a trichodermial pileipellis. The section includes two species: *I. parvecoacta* (type) and *I. leptophylla* G.F. Atk. The section and subgenus are polyphyletic. Moreover, *I. parvecoacta* belongs to the clade delimited here as sect. *Inocybe*. As a consequence we treat sect. *Parvecoactae* as a synonym of sect. *Inocybe*. *Inocybe leptophylla* is a member of the *I. languinosa* group, a strongly supported clade of nine described taxa from northern and southern temperate regions (Matheny and Bougher 2017).

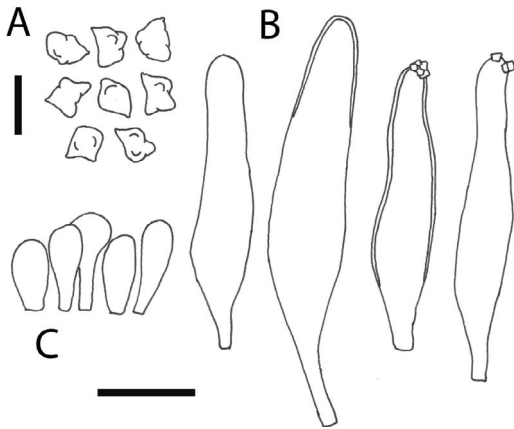


FIG. 6. Microscopic features of *Inocybe carolinensis* (PBM4965, holotype). (A) Basidiospores. (B) Pleurocystidia and cheilocystidia. (C) Paracystidia. Scale bar for A = 10  $\mu$ m. Scale bar for B–C = 25  $\mu$ m.

*Inocybe dulciolens* Matheny & Kudzma, *sp. nov.*

Type: U.S.A. Tennessee: Great Smoky Mountains National Park, Cades Cove, at Primitive Baptist Church, on soil in mixed forest under *Quercus* spp., *Tsuga canadensis*, *Carya* sp., *Pinus* spp., 35.60194°N, 83.81361°W, September 13, 2004, P.B. Matheny PBM2646 (holotype: TENN 062477). (Figs. 5C, 7). MycoBank MB 824547. ITS GenBank Accession No. MH216088.

ILLUSTRATIONS. Smith, Smith, and Weber (1979), Phillips (1991), Phillips (2005).

DIAGNOSIS. Basidiospores of *I. dulciolens* are somewhat smaller than those for *I. fraudans* and lack the apical papilla described and illustrated for this European species. *Inocybe dulciolens* has been detected only from eastern North America.

Pileus 20–100 mm wide, conical at first with deeply incurved margin that later becomes decurved or at times almost straight after expansion, expanding with age to conico-campanulate to plano-convex and often developing a low obtuse umbo, this becoming broad by maturity; center with prominent white velipellis, outward coarsely fibrillose or developing small appressed scales, at times almost entirely covered by velipellis when young, with extreme age developing large appressed scales, margin torn at times, not rimose; white where covered by velipellis, otherwise light gray to very pale brown (10YR 7/2 to 7/3) or pale yellow to yellow (2.5Y 7/4 to 7/6; “warm buff”,

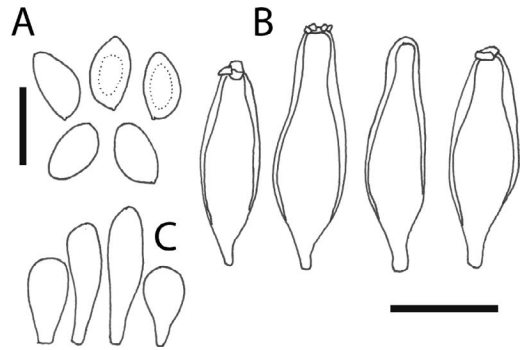


FIG. 7. Microscopic features of *Inocybe dulciolens* (PBM2646, holotype). (A) Basidiospores. (B) Pleurocystidia and cheilocystidia. (C) Paracystidia. Scale bar for A = 10  $\mu$ m. Scale bar for B–C = 25  $\mu$ m.

“honey yellow”, to “chamois”) toward the margin when young, becoming yellowish-brown (10YR 5/4), in extreme age with dark yellowish-brown (10YR 4/4) appressed scales against a very pale brown ground color; context 4–11 mm thick, firm, white but slowly reddening or staining pinkish red or at times weakly so, in age with some blackish-brown areas; odor at first a mixture of methyl-cinnamate and spermatic, becoming strongly of methyl-cinnamate. Lamellae adnexed, ascending adnate, or adnate, close to crowded; cream colored (10YR 8/3) or nearly white when very young, becoming light gray or pale brown (10YR 6/3 to 5/3) to brown or yellowish brown (10YR 4/4; “Dresden brown”), not obviously rubescent, at times reddening or with pinkish-brown to brown spots on older specimens, narrow to medium (3–5 mm deep), edges pallid-fimbriate, subventricose. Stipe 30–65 (–100)  $\times$  3–10 (–16) mm, terete or somewhat compressed, even but often with a widened base, this up to 16 mm wide; partial veil present as a cortina, this evanescent; surface at most pruinose at the extreme apex or upper 1/6, otherwise finely fibrillose; white becoming sordid buff in age, with reddish-brown or brown areas above the base; context solid, white, firm.

Basidiospores (8–)8.5–8.8–9.5  $\times$  5–5.4–6  $\mu$ m,  $Q = 1.45$ – $1.63$ – $1.80$  ( $n = 32/3$ ), smooth, (sub-)amygdaliform, yellowish-brown; apices conical, rarely papillate; apiculus small but distinct. Basidia 26–31  $\times$  7–10  $\mu$ m, 4-sterigmate, clavate, hyaline. Pleurocystida 50–65  $\times$  15–19  $\mu$ m, broadly fusiform, fusiform, utriform, or ventricose; apices obtuse, at times crystalliferous; thick-walled, walls

up to 2.0–2.5  $\mu\text{m}$  thick apically, hyaline. Cheilocystidia similar to pleurocystidia, often shorter and many utriform, mixed with hyaline paracystidia. Caulocystidia absent, extreme apex of stipe with few clusters of short clavate to short cylindrical cells similar to paracystidia, metuloid cystidia not observed or at most rare. Pileipellis a compact interwoven layer of cylindrical hyphae, these mostly 4–10  $\mu\text{m}$  wide, smooth, pale brown in mass, located above a distinct yellowish-brown pigmented layer of repent hyphae, these mostly 10–15  $\mu\text{m}$  wide, thin-walled, smooth. Clamp connects present.

ADDITIONAL SPECIMENS EXAMINED. U.S.A. New Jersey: Lebanon Township, Ken Lockwood Gorge Wildlife Management Area, in mixed woods, 40.6962°N, 74.8707°W, September 5, 2013, *L.V. Kudzma* LVK13325 (pers. herb.). *Ibidem.*, September 24, 2013, *L.V. Kudzma* LVK13340 (pers. herb.). *Ibidem.*, September 29, 2013, *L.V. Kudzma* LVK13346 (pers. herb.). *Ibidem.*, August 3, 2014, *L.V. Kudzma* LVK14348 (pers. herb.). New York: Albany, South Bethlehem, Joralemon Memorial Park, on calcareous ground in mixed forest under *Pinus strobus*, *Quercus* sp., *Carya* sp., *Populus* sp., 42.53167°N, 73.84722°W, September 20, 2003, *C. Baird* PBM2450 (TENN 062759). Tennessee: Great Smoky Mountains National Park, Cades Cove Picnic Area, 35.59833°N, on soil in mixed forest, 83.79167°W, September 9, 2004, *P.B. Matheny*, *E. Lickey*, & *M.C. Aime* PBM2618 (TENN 062454). Great Smoky Mountains National Park, Cades Cove, on way to Primitive Baptist Church, on soil in mixed forest, 35.60810°N, 83.82611°W, September 9, 2004, *M.C. Aime* PBM2622 (TENN 062458). Great Smoky Mountains, National Park, Schoolhouse Gap Trail, singly on soil under mixed hardwoods, 580 m, 35.6275°N, 83.73083°W, August 31, 2013, *P.B. Matheny* PBM3949 (TENN 068529). *Ibidem.*, on soil in mixed *Tsuga canadensis* forest, 35.6275°N, 83.73083°W, August 31, 2013, *J. Justice* PBM3951 (TENN 068528). Anderson County, Norris Dam State Park, Clear Creek Trail, on calcareous ground in deciduous forest under *Quercus* spp., *Fagus grandifolia*, and *Carya* sp., 36.24028°N, 84.10778°W, September 29, 2012, *P.B. Matheny* PBM3912 (TENN 068291). Knox County, Knoxville, Ijams Nature Center, on calcareous ground, 35.9560°N, 83.8679°W, September 21, 2009, *J.M. Birkebak* JMB092109-02a (TENN 068288). White County, Burgess Falls

State Park, 36.0441°N, 85.5947°W, September 25, 2018, *N.J. Justice* NJJ18-362 (TENN 074664).

DISTRIBUTION AND HABITAT. Widespread in eastern North American deciduous or mixed forests, typically on calcareous ground. Large numbers of basidiomes occasionally observed.

PHENOLOGY. August and September.

CONSERVATION STATUS. None. Widespread geographically throughout eastern North America, ranging from Michigan to Quebec, and southwards to Tennessee and North Carolina. Common.

ETYMOLOGY. (L.) The specific epithet “*dulciolens*” means sweet smelling, in reference to the sweet and spicy (Matsutake-like) odor.

REMARKS. In eastern North America *I. dulciolens* has previously been referred to as *I. pyriodora* (Pers.: Fr.) P. Kumm. (Earle 1903, Kauffman 1918, Kauffman 1924, Smith *et al.* 1979, Phillips 1991, Phillips 2005), lectotype of sect. *Lactiferae* (Singer 1986, Kobayashi 2002). The latter is now recognized as *I. fraudans* (Kuyper 1986), which was recently epitypified by Marchetti, Franchi, and Consiglio (2014) despite neotypification by Kuyper (1986). Unfortunately, the epitype designation by Marchetti *et al.* (2014) has no standing (ICN Art. 19.19). As Fig. 2 demonstrates, ITS, 28S, and *rpb2* sequences of samples of eastern North American materials of *I. dulciolens* form a strongly supported monophyletic group that is sister to the European species *I. fraudans*. The name *I. fraudans* has been misapplied to western North American material from Washington (JFA11831), which differs ecologically by its occurrence in conifer forests, probably on acidic soil. One such sample from Washington (JFA11831) is genetically and ecologically distinct from *I. dulciolens* and *I. fraudans*.

*Inocybe dulciolens* is very similar in outward appearance to *I. fraudans* (Kuyper 1986), however, the basidiospores of *I. dulciolens* are somewhat smaller than described for *I. fraudans* by Kuyper and lack the apical papilla described and illustrated for the European species. Both seem to share similar ecological niches in association with hardwoods such as *Fagus* and *Quercus* and conifers like *Pinus* on nutrient-rich calcareous soil.

*Inocybe rubellipes* is a poorly known rubescent species described by Atkinson (1918) that has smooth basidiospores and pleurocystidia. We have not studied the type but are confident this species differs from *I. dulciolens* by a number of features:

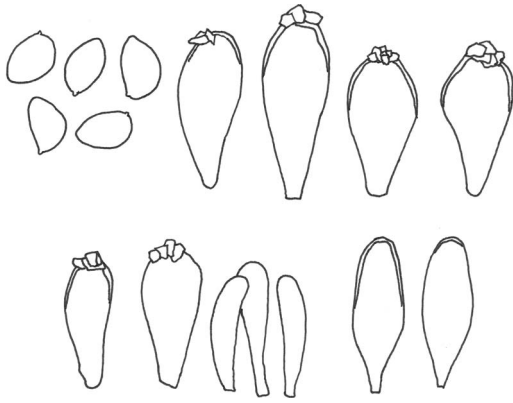


FIG. 8. Microscopic features of *Inocybe glaucescens* (LVK12144, holotype). (A) Basidiospores. (B) Pleurocystidia. (C) Cheilocystidia and paracystidia. (D) Caulocystidia. Scale bar for A = 10  $\mu\text{m}$ . Scale bar for B–D = 25  $\mu\text{m}$ .

the much smaller pileus (10–15 mm wide) and per Kauffman (1924) the pruinose stipe and strong odor reminiscent of meal or cornsilks. The pileus of *I. dulciolens* is large for *Inocybe* reaching up to 100 mm wide, and the stipe is nowhere pruinose. The odor of *I. dulciolens* is quite distinctive smelling exactly like that of North American matsutake—*Tricholoma magnivelare* (Peck) Redhead and *T. murrillianum* Singer (Trudell *et al.* 2017). Kauffman (1918) described the odor as “sweet, spicy or like bumble-bee honey, becoming disagreeable” or “like that of ripe pears or clove pinks” (p 451).

*Inocybe scabra* (O.F. Müll.) Quél. *sensu* Grund and Stuntz (1970) was noted with a sweet-aromatic or pungent-aromatic odor but differs from *I. dulciolens* by the smaller size of the basidiomes, uniformly dark or bister pileus, non-reddening tissues, and occurrence under *Picea* in Nova Scotia.

***Inocybe glaucescens* Matheny & Kudzma, *sp. nov.***

Type: U.S.A. New Jersey: Hunterdon County, Lebanon Township, Ken Lockwood Gorge Wildlife Management, scattered on ground in mixed woods under primarily deciduous trees, 40.6931°N, 74.8750°W, 125 m, August 18, 2012, *L.V. Kudzma LVK12144* (holotype: TENN 073754). (Figs. 5D, 8). MycoBank MB 824843. ITS GenBank Accession No. MH216097.

**Diagnosis.** Phenotypically similar to *Inocybe coelestium* Kuyp., and molecularly similar to *I. corydalina* and *I. erinaceomorpha* Stangl & J.

Veselský, but differs from these all by the distinctly reddening stipe, short clavate pleurocystidia, and/or phylogenetic placement. Differs from *I. tricolor* by the ochraceous pileus with blue-green tinges and short clavate pleurocystidia.

Pileus 10–30 mm wide, obtusely conical when young, expanding with age, becoming campanulate, umbo broad and obtuse; margin incurved when young, becoming decurved; surface dry, coarsely fibrillose with appressed scales or exco-riate scaly around the center, disc often with blue-green tinged velipellis, ochraceous-tawny to ochre yellow elsewhere, edge of margin yellowish, with age center becoming brown or dark brown; odor distinctive and unusual, not spermatic and unlike that of *I. dulciolens* (described above). Lamellae adnexed to uncinata, close to almost crowded, pale pinkish in youth becoming “Fawn Color” to pinkish-brown or “avellaneous,” eventually pale brown to yellowish-brown with age, edges pallid and fimbriate, reddening where damaged. Stipe 30–35  $\times$  4–6 mm at the apex mm; base swollen or enlarged up to 9 mm wide, rounded bulbous; surface dry, apex finely furfuraceous fibrillose, finely fibrillose below, cortina evanescent; ground color at first yellowish but with white furfuraceous fibrils above and white fibrils below, becoming ochraceous or reddish to pink above the base and upwards or cinnamon brown with age, reddening faintly where cut or bruised.

Basidiospores 7.5–8.8–9.5  $\times$  5.0–5.7–6.5  $\mu\text{m}$ , Q = 1.36–1.55–1.70 ( $n = 30/2$ ), smooth, almost citroniform or broadly amygdaliform with pointed to bluntly pointed apices, with thickened wall, yellowish brown, apiculus distinct. Basidia 28–34  $\times$  7–10  $\mu\text{m}$ , 4-sterigmate, clavate, hyaline. Pleurocystidia 26–38  $\times$  12–17  $\mu\text{m}$ , short and obese or short clavate to short utriform, generally not projecting much beyond the hymenium, apically thick-walled (walls 2.5  $\mu\text{m}$  thick) but thin elsewhere or thin-walled, apices broadly rounded and often crystalliferous. Cheilocystidia similar to pleurocystidia, infrequent, mixed with abundant, slenderly clavate, thin-walled, hyaline paracystidia. Caulocystidia similar to cheilocystidia, infrequent at the extreme stipe apex but mixed with abundant cauloparacystidia like those on the lamellae edges. Pileipellis a cutis of compact interwoven hyphae, these cylindrical, mostly smooth, thin-walled, pale brownish in mass and mostly 4–10  $\mu\text{m}$  wide; this layer subtended by a zone of ochraceous-tawny pigmented hyphae,

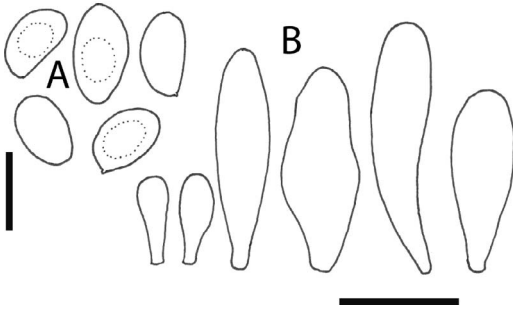


FIG. 9. Microscopic features of *Inocybe friabilis* (PBM3914, holotype). (A) Basidiospores. (B) Cheilocystidia and paracystidia-like cells. Scale bar for A = 10  $\mu$ m. Scale bar for B = 25  $\mu$ m.

these often weakly incrustated, cylindric, about 4–10  $\mu$ m wide. Clamp connections present.

ADDITIONAL SPECIMEN EXAMINED. U.S.A. New Jersey: Hunterdon County, Lebanon Township, same location as the type, September 12, 2013, *L.V. Kudzma LVK13324* (TENN 073755).

DISTRIBUTION AND HABITAT. Known from one site, under deciduous trees in a mixed eastern deciduous forest in New Jersey.

PHENOLOGY. August and September.

CONSERVED STATUS. Probably rare. The species is known to date only from the type location.

ETYMOLOGY. (L.) The specific epithet “*glaucescens*” refers to the blue-green tinges that develop at the center of the pileus.

REMARKS. *Inocybe glaucescens* is a new species in sect. *Lactiferae* characterized by a suite of unique features including the ochraceous to ochre-yellow pileus and stipe when young, blue-green tinged pileal disc, reddening stipe surface, pinkish-brown young lamellae, unusual odor, smooth basidiospores, and abundant slenderly clavate paracystidia. The species is most closely related to *I. corydalina*, *I. erinaceomorpha*, and *I. tricolor* from Europe (Fig. 2), all three of which are psilocybin-producing species. Given the blue-green discoloration on the basidiomes of *I. glaucescens* and its phylogenetic affinities with three other psilocybin-producing taxa, it is reasonable to conclude that *I. glaucescens* also contains psilocybin and thus represents the first hallucinogenic *Inocybe* described from North America. *Inocybe coelestium* Kuyp., rare in central Europe,

shares the overall stature, greenish tinges to the pileus surface, and the abundant slenderly clavate paracystidia (Kuyper 1986, Stangl 1989) but lacks the distinctive reddening stipe and has longer pleurocystidia. No representative DNA sequences exist yet for this species.

*Inocybe friabilis* Matheny & Kudzma, *sp. nov.*

Type: U.S.A. Tennessee, Knoxville, West Hills, scattered singly on soil in lawn under planted *Quercus phellos*, 35.9172°N, 84.0397°W, 275 m, June 12, 2013, *P.B. Matheny PBM3914* (holotype: TENN 068384) (Figs. 5E, 9). MycoBank MB 824548. ITS GenBank Accession No. MH216095.

*Diagnosis.* Most closely related phylogenetically to (sub)tropical Australian and tropical Indian species *I. gracilissima*, *I. keralensis*, and *I. griseorubida*. Differs from these by the small brittle basidiomes, association with ectomycorrhizal plant associates *Quercus* and *Carya*, geographical distribution in the eastern United States, and phylogenetic placement.

Pileus 15–30 mm wide when expanded, smaller in buttons, campanulate to deeply conical when very young, expanding to broadly conical and eventually plane in age, disc often with a small conical umbo; margin long decurved in youth, becoming straight upon expansion, eventually upturned when plane, at times torn; surface dry, velipellis absent, smooth and unbroken over the disc, long-rimose toward the margin; bicolorous—disc fulvous or strong brown to yellowish-brown (10YR 5/6–5/8, “buckthorn brown”), margin pale brown (10YR 6/3), light yellowish-brown (2.5Y 6/4 or nearly “isabella color”), or olive yellow (2.5Y 6/4–6/6), olive-buff between the spreading fibrils, buttons also have a lighter colored margin than the disc; edge of margin weak or slight whitish remnants of partial veil when very young, odor at first not remarkable or after collection becoming similar to green corn but not strong; context pallid, thin under the disc, no reactions to PDAB. Lamellae sinuate to adnexed, moderately close with 26–30 L and several tiers of lamellulae, narrow, pale brown in youth and remaining so even when expanded, eventually light olive-brown or isabelline with age, edges distinctly pallid-fimbriate. Stipe 12–55  $\times$  2–4 mm, terete, even or slightly enlarged below, not bulbous, fragile or brittle, base easily breaking when collected; surface scurfy-furfuraceous at the apex, elsewhere

densely to finely white silky fibrillose imparting a whitish color overall, cortina not observed but neither confirmed absent; ground color buff, dull ochraceous, or dull yellow.

Basidiospores (7.5–) 8–10.2–12 (–12.5)  $\times$  5–6.1–7 (–8)  $\mu\text{m}$ ,  $Q = 1.36\text{--}1.67\text{--}2.00$  ( $n = 36/3$ ), smooth, elliptic to subamygdaliform, apices often rounded or occasionally somewhat bluntly pointed, yellowish brown, apiculus small and indistinct. Basidia 26–32  $\times$  10–12  $\mu\text{m}$ , clavate, hyaline, 4-sterigmate. Pleurocystidia absent. Cheilocystidia 40–60  $\times$  11–15  $\mu\text{m}$ , mostly clavate or less often utriform or subcylindric, thin-walled, hyaline, mixed with shorter cells similar to paracystidia. Caulocystidia not observed, refractive hyphae relatively frequent in stipe trama. Pileipellis a cutis of thin repent hyphae, these cylindric, thin-walled, smooth, subhyaline, mostly 3–6  $\mu\text{m}$  wide; beneath this a broad distinctly pigmented zone of tawny to dark ochraceous-tawny hyphae, these a mixture of cylindric to inflated or subsodiametric hyphae, thin-walled, coarsely or distinctly incrustated, up to 25  $\mu\text{m}$  wide. Clamp connections present.

ADDITIONAL SPECIMENS EXAMINED. U.S.A. New Jersey: Flemington, South Branch Reservation, Stanton Station Section, in scattered groups along trailside in moss under mixed hardwood trees, 40.5690°N, 74.8676°W, August 11, 2012, *L. Kudzma* LVK12081 (pers. herb.). *Ibidem.*, August 30, 2013, *L. Kudzma* LVK13266 (pers. herb.). Ken Lockwood Gorge Wildlife Management Area, Lebanon Township, in mixed hardwoods, 40.6962°N, 74.8707°W, July 22, 2017, *L. Kudzma* LVK17110 (pers. herb.). New York: Bedford, I-684 rest area, scattered in grass and moss under *Quercus* sp., 41.2299°N, 73.6821°W, July 12, 2013, *L. Kudzma* LVK13122 (pers. herb.). Ohio: Salem, Grandview Cemetery, July 7, 2013, *W. Sturgeon* MO139064 (pers. herb.). Tennessee: Knox County, Knoxville, West Hills, scattered singly on soil in lawn under planted *Quercus phellos*, 35.9172°N, 84.0397°W, 275 m, August 1, 2008, *P.B. Matheny* PBM2983 (TENN 062741). *Ibidem.*, July 22, 2012, *P.B. Matheny* PBM3799 (TENN 067064); on limestone soil in oak-hickory forest under *Fagus grandifolia*, *Quercus* sp., and *Carya* sp. 36.2123°N, 84.0738°W, 253 m, September 21, 2018, *P.B. Matheny* PBM4201 (TENN 074608). Virginia: Shenandoah National Park, Dickey Ridge, scattered singly on clay soil in oak-hickory forest, 600 m, coordinates not known,

June 22, 2002, *P.B. Matheny & E.C. Durman* PBM2321 (WTU).

DISTRIBUTION AND HABITAT. On lawns under planted red oaks and in eastern deciduous forests in Tennessee, Virginia, Ohio, New Jersey, and New York.

PHENOLOGY. June to September.

CONSERVED STATUS. None. The species is geographically widespread in the eastern United States.

ETYMOLOGY. (L.) The specific epithet “*friabilis*” refers to the fragile or brittle basidiomes, the base of which may be broken upon collection and the strongly split pileus surface.

REMARKS. *Inocybe friabilis* is most closely related to the northern Australian species *I. gracilissima* Matheny & Bougher, which occurs in tropical sclerophyll habitats in association with ectomycorrhizal plants of Myrtaceae, Casuarinaceae, and/or Fabaceae (Matheny and Bougher 2017). Both species produce a deeply conical pileus when young, similar pileus colors and texture, narrow lamellae, no distinctive odors, and similar sized basidiospores. *Inocybe keralensis* K.P.D. Latha & Manim. (= *I. rimulosa* C.K. Pradeep & Matheny) forms the sister group to the lineage containing *I. friabilis* and *I. gracilissima*. This species occurs in tropical India in association with Dipterocarpaceae, Calophyllaceae, and Myristicaceae, lacks the olivaceous tones on the pileus, and young pilei are convex, not deeply conical (Latha and Manimohan 2016, Pradeep *et al.* 2016 as *I. rimulosa*).

The basidiomes of *I. friabilis* are characterized by their small size, fragile and brittle nature, and conspicuously rimose pileus surface. The species appears to have a preference for calcareous soil.

*Inocybe vinaceobrunnea* Matheny, Ovrebo & Kudzma, *sp. nov.* Type: U.S.A. Tennessee: Great Smoky Mountains National Park, Cades Cove, road to the Primitive Baptist Church, scattered singly on soil along roadside in mixed forest under hardwoods and conifers, 35.6086°N, 83.8261°W, 525 m, July 24, 2008, *P.B. Matheny, D.J. Lodge, & A.D. Wolfenbarger* PBM2951 (holotype: TENN 062709). (Figs. 5F, 10). MycoBank MB 824549. ITS GenBank Accession No. FJ601813.



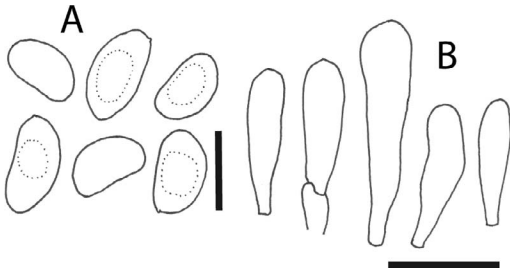


FIG. 10. Microscopic features of *Inocybe vinaceobrunnea* (PBM2951, holotype). (A) Basidiospores. (B) Cheilocystidia. Scale bar for A = 10  $\mu$ m. Scale bar for B = 25  $\mu$ m.

*Illustrations.* Kauffman (1924).

*Diagnosis.* The combination of relatively large basidiomes that are more or less vinaceous brown, the acutely umbonate pileus, the red spotting lamellae, sickly sweet complex odor, and eastern North American distribution serve to distinguish *I. vinaceobrunnea* from other vinaceous species in subg. *Inosperma*. *Inocybe adaequata* (Britzelm.) Sacc. is a similar species with the pileus at times breaking up into scales, the stipe slowly staining somewhat vinaceous, and a strong odor of beetroot or disagreeable ranging from spermatic, rotting acorns, green corn, or sickly-sweetish. It is best distinguished from *I. vinaceobrunnea* by molecular phylogenetic data and European distribution. *Inocybe rhodiola* Bres. has a more slender habit, a fibrillose pileus with appressed scales, the stipe becoming distinctly vinaceous red towards the base, a weak odor, and European distribution. A similar species, *I. adaequata sensu* Nishida, is known under *Quercus* spp. in California but is distinguished molecularly and is presently undescribed.

Pileus 30–80 mm wide, conical, convex-conic, to conico-campanulate, expanding with age, center often acute with a prominent umbo; margin often incurved at first, becoming decurved or straight, uplifting or upturned with age; disc generally smooth and unbroken, nowhere scaly, radially fibrillose towards the margin, rimulose when young but becoming rimose and conspicuously so with age, margin at times torn; velipellis absent, surface dry; disc quite dark or “dark livid brown” and almost black at times but especially so with age or when weathered, otherwise dusky red (2.5YR 3/2) mixed with weak red (2.5YR 5/2) or “vinaceous brown,” “army brown,” “vinaceous fawn,” or “sorghum brown”; context pinkish or reddish vinaceous beneath the cuticle, thick below the disc,

odor complex—a mixture of sickly sweet but at times aromatic, possibly with a green-corn element. *Lamellae* adnexed to sinuate, close; light gray when young (2.5Y 7/2), becoming brownish gray (2.5Y 6/2), and eventually light olive brown (2.5Y 5/4) or yellowish brown with age, becoming reddish spotted; edges whitish and fimbriate; narrow to medium, up to 5 mm deep. *Stipe* 40–110  $\times$  4–11 mm at the apex, terete or slightly compressed with age, even or base subbulbous, partial veil remnants not observed even on young specimens; extreme apex white or whitish furfuraceous or pruinose, surface otherwise finely fibrillose streaked below; extreme apex whitish, elsewhere vinaceous brown or pinkish red or dark red brown streaked mixed with whitish streaks, becoming vinaceous brown where handled; context solid, whitish with vinaceous brown streaks, base with reddish areas.

Basidiospores 9–10.7–13  $\times$  5.5–6.3–7.5  $\mu$ m,  $Q = 1.36$ – $1.69$ – $2.00$  ( $n = 55/4$ ), smooth, phaseoliform to elliptic, brownish-yellow or near “ochraceous-tawny,” apiculus not distinctive, wall slightly thickened. Basidia 35–38  $\times$  10–11  $\mu$ m, 4-sterigmate, clavate, hyaline. Pleurocystidia absent. Cheilocystidia 30–53  $\times$  7–13  $\mu$ m, mostly subclavate or slenderly clavate to subutriform, cylindrical, or slightly fusiform, thin-walled, hyaline but exceptionally ochraceous to vinaceous ochre, edges of lamellae sterile. Caulocystidia similar to cheilocystidia, mostly clavate, at apex of stipe. Pileipellis a cutis of cylindrical hyphae, mostly 3–8  $\mu$ m wide, vinaceous to pink in mass, thin-walled, pigment cytoplasmic but walls weakly incrustated, refractive hyphae frequent, vinaceous pigments exude from samples mounted in 3% KOH. Clamp connections present.

ADDITIONAL SPECIMENS EXAMINED. U.S.A. North Carolina: Highlands, Mt. Satulah, 35.03638°N, 83.19222°W, August 16, 1936, *L. R. Hesler* (TENN 009244). Oklahoma: Lincoln County, off E0930 Road 1.7 mi E of N3390 Road, scattered on ground under *Populus deltoides*, *Acer negundo*, and *Morus* sp., September 21, 2001, *C. Ovrebo* CO4123 (CSU). Pontotoc County, Pontotoc Ridge Nature Preserve, 15.5 mi S of Ada, long, September 22, 2001, *D. Miller* CO4141 (CSU). Tennessee: Knox County, Ball Camp Pike, on soil in oak woods, 35.97638°N, 84.05583°W, July 26, 1941, *L.R. Hesler* (TENN 013862) (HQ201351-ITS1, HQ201352-ITS2); Great Smoky Mountains National Park, Cades Cove, same locality as the holotype, July 24, 2008, *P.B. Matheny*, *D.J. Lodge*, and *A.D.*

Table 1. Taxon sampling and DNA sequences used in this study. Sequences in bold are new. Unless otherwise noted, specimen vouchers of L.V. Kudzma (LVK) reside in his personal herbarium.

Species	Specimen voucher (Herbarium Accession No.)	Locality	GenBank Accession No.			
			ITS	28S	<i>rpb2</i>	<i>rpb1</i>
<i>Inocybe adaequata</i>	JV11290F (TURA 5924)	Finland	JQ801381	JQ815407	—	—
	JV16501F (WTU)	Finland	—	AY380364	AY333771	AY351791
	M0229744 ( <b>epitype</b> )	Germany	KM873367	—	—	—
	MR00022	Sweden	AM882706	AM882706	—	—
<i>Inocybe aeruginascens</i>	PC2008-0014 (GB)	Unknown	FJ904177	FJ904177	—	—
	JG270502 (TENN 063863)	Germany	GU949590	JN974970	—	—
	JG310508 (TENN 063936)	Germany	GU949591	<b>MH220256</b>	<b>MH249787</b>	—
<i>Inocybe aestiva</i>	PC111007 (TENN 063908)	South Africa	GU949592	<b>MH220257</b>	—	—
	BK18089706 ( <b>holotype</b> UTC 255656)	Utah	EU600847	EU600847	EU600846	EU600845
<i>Inocybe bulbosissima</i>	DBG19916	Colorado	MH024849	MH024885	<b>MH249788</b>	—
	EL30/06	Sweden	FJ904158	FJ904158	—	—
<i>Inocybe carolinensis</i> sp. nov.	Stz3759 (WTU)	Michigan	MF461595	MF423724	—	—
	PBM3906 (TENN 067756)	North Carolina	KP636853	KP171055	KM555147	—
	PBM4065 ( <b>holotype</b> TENN 071091)	North Carolina	MG663294	—	—	—
<i>Inocybe chondroderma</i>	PBM1760 (WTU)	British Columbia	GU949586	<b>MH220258</b>	—	—
	PBM1776 (WTU)	Washington	GU949579	JN974967	<b>MH249789</b>	—
<i>Inocybe corydalina</i>	AM10687	Russia	<b>MH216083</b>	<b>MH220259</b>	<b>MH249790</b>	—
	EL124/04	Sweden	AM882736	AM882736	—	—
<i>Inocybe dulciolens</i>	TURA 6488 (WTU)	Belgium	—	AY038314	AY337370	AF389536
	LVK13325	New Jersey	—	<b>MH220260</b>	<b>MH249791</b>	—
	LVK13340	New Jersey	<b>MH216084</b>	<b>MH220261</b>	<b>MH249792</b>	—
	LVK13346	New Jersey	<b>MH216085</b>	<b>MH220262</b>	<b>MH249793</b>	—
	LVK14348	New Jersey	<b>MH216086</b>	<b>MH220263</b>	<b>MH249794</b>	—
	PBM2450 (TENN 062759)	New York	<b>MH216087</b>	<b>MH220264</b>	<b>MH249795</b>	—
	PBM2613 (TENN 062449)	Tennessee	EU523566	—	—	—
	PBM2618 (TENN 062454)	Tennessee	EU524570	—	—	—
	PBM2646 ( <b>holotype</b> TENN 062477)	Tennessee	<b>MH216088</b>	<b>MH220265</b>	<b>MH249796</b>	—
	PRL5773 (F)	Indiana	GQ166903	—	—	—
<i>Inocybe erinaceomorpha</i>	EL128/05	Sweden	AM882735	AM882735	—	—
	JV14756F (TURA 7645)	Sweden	<b>MH216089</b>	<b>MH220266</b>	<b>MH249797</b>	—
<i>Inocybe fissurata</i>	PBM2195	Western Australia	JQ408771	EU555466	EU555465	EU555464
	PBM2206	Western Australia	JQ408770	AY732213	JQ421069	—

Table 1. Continued.

Species	Specimen voucher (Herbarium Accession No.)	Locality	GenBank Accession No.			
			ITS	28S	<i>rpb2</i>	<i>rpb1</i>
<i>Inocybe fraudans</i>	AMB 12793	Italy	KM873363	—	—	—
	( <b>epitype</b> )					
	AMB 21460	Italy?	JF908178	—	—	—
	EL116/04	Sweden	AM882731	AM882731	—	—
	EL123/04	Sweden	AM882729	—	—	—
	EL151/05 as	Sweden	AM882730	AM882730	—	—
	<i>Inocybe incarnata</i>					
	GC 09043 (AMB)	Italy	KM873362	—	—	—
	<i>Fagus</i> ECM-RM-D08	Switzerland	KX886032	—	—	—
	<i>Populus</i> ECM-1Q1	Austria	EF644133	—	—	—
	soil H10IK02	Germany	HF675551	—	—	—
	TF01-037	Denmark	AJ889953	—	—	—
<i>Inocybe</i> cf. <i>fraudans</i>	KBE13496	Sweden	FN550914	FN550914	—	—
<i>Inocybe</i> aff. <i>fraudans</i>	JFA11831 (WTU)	Washington	—	EU433887	EU433889	EU433888
<i>Inocybe friabilis</i>	LVK12081	New Jersey	<b>MH216090</b>	<b>MH220267</b>	<b>MH249798</b>	<b>MH523618</b>
	LVK13132	New York	<b>MH216091</b>	<b>MH220268</b>	<b>MH249799</b>	<b>MH523619</b>
	LVK13266	New Jersey	<b>MH216092</b>	<b>MH220269</b>	<b>MH249800</b>	—
	LVK17110	New Jersey	—	<b>MH220270</b>	<b>MH249801</b>	<b>MH523620</b>
	MO139064 (pers. herb.)	Ohio	<b>MH216093</b>	<b>MH220271</b>	<b>MH249802</b>	<b>MH523621</b>
	PBM2321 (WTU)	Virginia	JQ408788	JQ319708	JQ84649	—
	PBM2983 (TENN 062741)	Tennessee	—	JN975015	JQ421078	<b>MH523622</b>
	PBM3799 (TENN 067064)	Tennessee	<b>MH216094</b>	—	—	—
	PBM3914 ( <b>holotype</b> TENN 068384)	Tennessee	<b>MH216095</b>	<b>MH220272</b>	—	—
<i>Inocybe glabripes</i>	JV7318F (TURA 3804)	Finland	<b>MH216096</b>	—	<b>MH249803</b>	—
<i>Inocybe glaucescens</i> sp. nov.	LVK12144 ( <b>holotype</b> TENN 073754)	New Jersey	<b>MH216097</b>	<b>MH220273</b>	<b>MH249804</b>	—
	LVK13324 (TENN 073755)	New Jersey	—	<b>MH220274</b>	<b>MH249805</b>	—
<i>Inocybe gracilissima</i>	JAC2809 (CBG 816878)	Northern Territory	JQ408755	JQ319684	—	—
	NLB937 (PERTH 8373116)	Queensland	KP171122	KJ801178	KJ729946	—
	PBM3735 ( <b>holotype</b> PERTH 8362912)	Queensland	—	KJ729919	KJ729945	—
	PBM3738 (TENN 066946)	Queensland	KP171123	KJ801179	KJ729947	—
<i>Inocybe griseorubida</i>	CAL1253 ( <b>holotype</b> )	India	KT180326	KT180327	KT180328	—
<i>Inocybe haemacta</i>	SJ88062	Sweden	AM882737	AM882737	—	—
	AMB 21462	Italy	JF908180	—	—	—
<i>Inocybe hystrix</i>	HRL11842	Quebec	KX897428	—	—	—
	SJ020824	Sweden	AM882810	AM882810	—	—
	PBM3300 (TENN 064304)	North Carolina	GU949588	<b>MH220275</b>	—	—
	RS31493 (WTU)	Finland	—	AY380380	AY337381	AY351805
<i>Inocybe</i> aff. <i>hystrix</i>	REH7405 (NY)	Costa Rica	GU949589	JN974969	<b>MH249806</b>	—

Table 1. Continued.

Species	Specimen voucher (Herbarium Accession No.)	Locality	GenBank Accession No.			
			ITS	28S	<i>rpb2</i>	<i>rpb1</i>
<i>Inocybe keralensis</i>	DKP98	India	KY440094	KY549124	KY553244	—
	K(M)191712	India	KM924523	KM924518	KY553243	—
	(holotype)					
	TBGT12828 as <i>Inocybe rimulosa</i>	India	KP636861	KP171060	KM656099	—
	TBGT12854	India	KP636860	KP171059	KM656098	—
	(holotype <i>Inocybe rimulosa</i> )					
<i>Inocybe melanopus</i> (originally as “ <i>melanopoda</i> ”)	BJ920904	Sweden	AM882725	AM882725	—	—
	JV4986	Finland	AM882727	AM882727	—	—
	PBM3975 (TENN 068973)	Tennessee	—	<b>MH220276</b>	<b>MH249807</b>	—
	Stz3641 (holotype WTU)	Washington	—	HQ201359	—	—
	TAA185135	Estonia	AM882726	—	—	—
<i>Inocybe melliolens</i>	EL224/06	France	FJ904149	FJ904149	—	—
	PAM05052303	France	FJ904148	FJ904148	—	—
<i>Inocybe</i> cf. <i>microfastigiata</i>	EL113/06	Sweden	FJ904156	FJ904156	—	—
<i>Inocybe moelleri</i>	EL68/07	Sweden	FN550913	FN550913	—	—
<i>Inocybe niveivelata</i>	BK21089718	Utah	EU600831	EU600831	—	EU600830
	(holotype UTC 255662)					
	PBM2337 (WTU)	Washington	—	JQ313566	AY333776	—
<i>Inocybe</i> aff. <i>pallidobrunnea</i>	PBM1957 (WTU)	Washington	<b>MH216098</b>	<b>MH220277</b>	<b>MH249808</b>	—
	PBM2242 (WTU)	Washington	<b>MH216099</b>	JN974968	<b>MH249809</b>	—
<i>Inocybe pyriodora</i> var. <i>chamaesalicis</i>	EL64/05	Norway	AM882733	AM882733	—	—
	SJ82030 as <i>Inocybe fraudans</i>	Sweden	AM882732	—	—	—
	AMB 21508 as <i>Inocybe pyriodora</i>	Italy	JF908206	—	—	—
<i>Inocybe rhodiola</i>	EL223/06	France	FJ904175	FJ904175	—	—
	HA2015-22 as <i>I. adaequata</i>	Iran	KX263009	—	—	—
	PAM00090117	France	FJ904176	FJ904176	—	—
	21500 as <i>I. jurana</i>	Italy	JF908202	—	—	—
<i>Inocybe rimosa</i> pro parte	JV8125	Finland	FJ904152	FJ904152	—	—
	JV22619	Estonia	FJ904157	FJ904157	—	—
	JV26578	Estonia	FJ904154	FJ904154	—	—
	PAM05061101	France	FJ904155	FJ904155	—	—
	PC080925	United Kingdom	FJ904153	FJ904153	—	—
	PBM2958 (TENN 062716)	Tennessee	JQ408777	JN975006	JQ421071	—
	PBM3974	Tennessee	—	KP170989	KM406229	—

Table 1. Continued.

Species	Specimen voucher (Herbarium Accession No.)	Locality	GenBank Accession No.			
			ITS	28S	<i>rpb2</i>	<i>rpb1</i>
<i>Inocybe rimosa</i> sensu lato	EL118/08	Sweden	FJ904146	FJ904146	—	—
	EL75/05	Sweden	AM882762	AM882762	—	—
	MCA859	Virginia	JQ408772	JQ319700	—	—
	PBM2654 (TENN 062484)	Tennessee	EU123474	EU600853	—	—
	PBM3901 (TENN 067764)	North Carolina	—	<b>MH220278</b>	<b>MH249810</b>	—
	SH08240702 (TENN 066039)	New Jersey	<b>MH216100</b>	<b>MH220279</b>	—	—
	TR75-05 (M)	Papua New Guinea	JQ408774	JQ815425	—	—
	TR183-05 (M)	Papua New Guinea	JQ408773	JN975005	JQ421070	—
<i>Inocybe sororia</i> sensu lato	ADW0057 (TENN 063512)	Idaho	JQ408778	JQ319702	JQ421072	—
	ADW0063 (TENN 063514)	Idaho	JQ408779	JQ319703	JQ421073	—
	JRH661 (WTU)	Wyoming	—	EU600863	—	EU600862
	JV15200	Sweden	FJ904151	FJ904151	—	—
	Kuoljok0512	Sweden	FJ904150	FJ904150	—	—
	PBM3042 (TENN 062793)	California	JQ408780	JQ319704	JQ421074	—
	PBM3055 (TENN 063504)	California	JQ408781	JQ319705	JQ421075	—
	REH8245 (NY)	Costa Rica	JQ408783	JN975004	JQ421076	—
	SAT0427801 (TENN 071585)	Washington	JQ408782	JQ319706	JQ846492	—
	<i>Inocybe</i> sp.	CZSUM SCI39	California	<b>MH216101</b>	<b>MH220280</b>	<b>MH249811</b>
KP s.n. (UC 1859623)		California	<b>MH216102</b>	—	—	—
<i>Inocybe</i> sp.	KB04072008 (TENN 063524)	California	<b>MH216103</b>	JN974963	<b>MH249812</b>	<b>MH523624</b>
<i>Inocybe</i> sp.	PBM578 (WTU)	Washington	<b>MH216104</b>	JN974961	<b>MH249813</b>	—
<i>Inocybe</i> sp.	PBM2601 (TENN 062439)		EU523562	EU600852	—	—
<i>Inocybe</i> sp.	<i>Quercus</i> ECM bg8a- e5	California	EF559275	—	—	—
<i>Inocybe</i> sp.	src156	California	DQ974804	—	—	—
	TR170-02 (M)	Papua New Guinea	—	JN974964	<b>MH249814</b>	—
	TR180-02 (M)	Papua New Guinea	—	JN974965	—	—
<i>Inocybe tricolor</i>	SJ05011	Sweden	AM882738	AM882738	—	—
<i>Inocybe umbrinella</i>	JV13699	Finland	FJ904165	FJ904165	—	—
	JV17954	Estonia	FJ904166	FJ904166	—	—
	PAM01102912	France	—	FJ904162	—	—
	PBM3024 (TENN 062781)	Pennsylvania	<b>MH216105</b>	JN975010	JQ846497	—
	PC080816	United Kingdom				
		Tennessee				
<i>Inocybe</i> <i>vinaceobrunnea</i>	PBM2951 ( <b>holotype</b> TENN 062709)	Tennessee	FJ601813	HQ201353	JQ846478	<b>MH523625</b>
	TENN 013862 as <i>I.</i> <i>jurana</i> sensu Hesler	Tennessee	HQ201351 HQ201352	—	—	—
	CO4123 (CSU)	Oklahoma	<b>MH216106</b>	<b>MH220281</b>	—	—
	CO4141 (CSU)	Oklahoma	<b>MH216107</b>	<b>MH220282</b>	—	—

*Wolfenbarger PBM2966* (TENN 062724). Virginia: Giles County, Mountain Lake Biological Station, near Pembroke, under *Quercus* sp. along side of trail (near first pond) not far from the main building, coordinates unknown, 1,310 m, August 13, 1999, *J. Herr JRH295* (WTU). Texas: Polk County, Big Thicket, in mixed woods in the Menard Creek Corridor, June 8, 2013, *R. Pastorino MO140452*.

OTHER SPECIMENS EXAMINED. FINLAND. Varsinais-Suomi: Lohja commune, Kyrkstad, park south of the former limestone processing factory, gregarious on lawn and on bare soil at *Tilia* sp. alley, July 25, 1996, *J. Vauras 112990F* (WTU ex TURA 5924 *I. adaequata*); *Ibidem.*, July 8, 2000, *J. Vauras 16501F* (WTU ex TURA *I. adaequata*).

DISTRIBUTION AND HABITAT. Known from eastern deciduous or mixed forests including conifers in North Carolina, Tennessee, Virginia, Ohio, and Michigan. Under *Populus deltoides* in Oklahoma and in mixed woods in riparian habitat of east Texas.

PHENOLOGY. June to August.

CONSERVED STATUS. None. The species, although conspicuous and infrequently reported, is geographically widespread in eastern North America.

ETYMOLOGY. (L.) The specific epithet “*vinaceobrunnea*” refers to the overall vinaceous brown basidiome colors.

REMARKS. *Inocybe vinaceobrunnea* was likely first reported from North America in Michigan as *I. frumentacea* Bres. by Kauffman (1918). However, Kuyper (1986) indicates that Bresadola misapplied the name *I. frumentacea* to what is *I. jurana* (Pat.) Sacc., the correct name of which is *I. adaequata* (Britz.) Sacc. The latter was epitypified in a study by Marchetti *et al.* (2014) despite a neotype designation by Stangl (1985). Unfortunately, the epitype designation by Marchetti *et al.* (2014) has no standing (ICN Art. 19.19). Kauffman (1924) later reported *I. jurana* from Ohio, and Hesler (1937, 1941) documented the same from western North Carolina and eastern Tennessee. Since 1947, however, it has not been reported from eastern North America. Nishida (1989) applied the name *I. adaequata* to collections made under *Quercus* in northern and southern California. Two samples from northern California cluster in a unique monophyletic group.

At least four species can now be recognized in the *Adaequata* clade: European *I. adaequata*,

Eurasian *I. rhodiola*, eastern North American *I. vinaceobrunnea* (formerly *I. jurana* sensu Hesler), and what likely represents an undescribed western North American species previously misinterpreted by Nishida (1989) as *I. adaequata* (Fig. 4). Of these, *I. vinaceobrunnea* appears most similar to *I. rhodiola* based on the slender aspect of the basidiomes, however, the odor of *I. vinaceobrunnea* is characteristically strong—sickly-sweet or unpleasant, and the pileus center becomes almost black with age. Two collections of *I. rhodiola* in Larsson *et al.* (2009) are both *Salix* associates. One of the Oklahoma collections (CO4123) of *I. vinaceobrunnea* was recorded under *Populus*.

Muscarine is absent from from European *I. adaequata* (Stijve, Klan, and Kuyper 1985) and of no clinical significance in *I. vinaceobrunnea* (Kosentka *et al.* 2013).

#### Literature Cited

- ALVARADO, P., J. L. MANJON, P. B. MATHENY, AND F. ESTEVE-RAVENTÓS. 2010. *Tubariomyces*, a new genus of Inocybaceae from the Mediterranean region. *Mycologia* 102: 1389–1397.
- ATKINSON, G. F. 1918. Some new species of *Inocybe*. *Am. J. Bot.* 5: 210–218.
- BANDINI, D., J. CHRISTIAN, U. EBERHARDT, S. PLOCH, A. TAHIR, B. OERTEL, AND M. THINES. 2017. *Inocybe sphagnophila* sp. nov., eine neue Art der höckersporigen Untersektion *Napipedinae* der Gattung *Inocybe* (Agaricales). *Mycol. Bav.* 18: 11–34.
- BANDINI, D., B. OERTEL, S. PLOCH, T. ALI, J. VAURUS, A. SCHNEIDER, M. SCHOLLER, U. EBERHARDT, AND M. THINES. 2018. Revision of some central European species of *Inocybe* (Fr.: Fr.) Fr. subgenus *Inocybe*, with the description of five new species. *Mycological Progress* 18: 247–294.
- BRAATEN, C. C., P. B. MATHENY, D. L. VIESS, M. G. WOOD, J. H. WILLIAMS, AND N. L. BOUGHER. 2014. Two new species of *Inocybe* from Australia and North America that include novel secotioid forms. *Botany* 92: 9–22.
- CLÉMENÇON, H. 2009. Methods for Working with Macrofungi: Laboratory Cultivation and Preparation of Larger Fungi for Light Microscopy. IHW-Verlag., Eching, Germany. 88 pp.
- CRIPPS, C. L., E. LARSSON, AND E. HORAK. 2011. Subgenus *Mallocybe* (*Inocybe*) in the Rocky Mountain alpine zone with molecular reference to European arctic-alpine material. *N. Am. Fungi* 5: 97–126.
- DENTINGER, B.T.M., S. MARARITESCU, AND J.-M. MONCALVO. 2010. Rapid and reliable high-throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. *Mol. Ecol. Resources* 10: 628–633.
- EARLE, F. S. 1903. A key to the North American Species of *Inocybe*—I. *Torreya* 3: 168–170.
- ESTEVE-RAVENTÓS, F., G. MORENO, P. ALVARADO, AND I. OLARIAGA. 2016. Unraveling the *Inocybe praetervisa*

- group through type studies and ITS data: *Inocybe praetervisoides* sp. nov. from the Mediterranean region. *Mycologia* 108: 123–134.
- FROSLEV, T. G., P. B. MATHENY, AND D. S. HIBBETT. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): A comparison of RPB1, RPB2, and ITS phylogenies. *Mol. Phylogenet. Evol.* 37: 602–618.
- GARDES, M. AND T.D. BRUNS. 1993. ITS primers with enhanced specificity for basidiomycetes—Application to the identification of mycorrhizae and rusts. *Mol. Ecol.* 2: 113–118.
- GRUND, D. W. AND D. E. STUNTZ. 1970. Nova Scotian *Inocybes*. II. *Mycologia* 62: 925–939.
- GRUND, D. W. AND D. E. STUNTZ. 1977. Nova Scotian *Inocybes*. IV. *Mycologia* 69: 392–408.
- GRUND, D. W. AND D. E. STUNTZ. 1984. Nova Scotian *Inocybes*. VIII. *Mycologia* 76: 733–740.
- HESLER, L. R. 1937. Notes on Southern Appalachian fungi, II. *J. Tenn. Acad. Sci.* 12: 239–254.
- HESLER, L. R. 1941. Notes on Southern Appalachian fungi, IV. *J. Tenn. Acad. Sci.* 17: 242–249.
- HORAK, E. 1979. *Astrosporina* (Agaricales) in Indomalaya and Australasia. *Persoonia* 10: 157–205.
- HORAK, E. 2018. Agaricales (Basidiomycota) of New Zealand. 2. Brown spored genera p.p. *Crepidotus*, *Flammulaster*, *Inocybe*, *Phaeocollybia*, *Phaeomarasmius*, *Pleurostammula*, *Pyrrhoglossum*, *Simocybe*, *Tubaria* and *Tympanella*. *Fungi of New Zealand / Ngā Hekaheka o Aotearoa* 6: 1–205.
- HORAK, E., P. B. MATHENY, D. E. DESJARDIN, AND K. SOYTON. 2015. The genus *Inocybe* (Inocybaceae, Agaricales, Basidiomycota) in Thailand and Malaysia. *Phytotaxa* 230: 201–238.
- JUDGE, B. S., J. F. AMMIRATI, G. H. LINCOFF, J. H. TRESTRAIL, AND P. B. MATHENY. 2010. Ingestion of a newly described North American mushroom species from Michigan resulting in chronic renal failure: *Cortinarius orellanosus*. *Clin. Toxicol.* 48: 545–549.
- KAUFFMAN, C.H. 1918. The Agaricaceae of Michigan. Michigan Geological and Biological Survey, Publication 26, Biol. Series 5: 1–924.
- KAUFFMAN, C. H. 1924. *Inocybe*. *N. Am. Flora* 10: 227–260.
- KOBAYASHI, T. 2002. The taxonomic studies of the genus *Inocybe*. *Nova Hedwigia* 124: 1–246.
- KOKKONEN, K. AND J. VAURAS. 2012. Eleven new boreal species of *Inocybe* with nodulose spores. *Mycol. Prog.* 11: 299–341.
- KOSENTKA, P., S. L. SPRAGUE, M. RYBERG, J. GARTZ, A. L. MAY, S. R. CAMPAGNA, AND P. B. MATHENY. 2013. Evolution of the toxins muscarine and psilocybin in a family of mushroom-forming fungi. *PLoS ONE* 8(5): e64646.
- KROPP, B. R. AND P. B. MATHENY. 2004. Basidiospore homoplasy and variation in the *Inocybe chelanensis* group in North America. *Mycologia* 96: 295–309.
- KROPP, B. R., P. B. MATHENY, AND L. J. HUTCHISON. 2013. *Inocybe* section *Rimosae* in Utah: Phylogenetic affinities and new species. *Mycologia* 105: 728–747.
- KROPP, B. R., P. B. MATHENY, AND S. G. NANAGYULYAN. 2010. Phylogenetic taxonomy of the *Inocybe splendens* group and evolution of supersection “*Marginatae*”. *Mycologia* 102: 560–573.
- KUO, M. AND P. B. MATHENY. 2015. Contemporary documentation of the rare eastern North American species *Inocybe insignis* (Inocybaceae, Agaricales). *MycKeys* 11: 23–31.
- KUYPER, T. W. 1986. A revision of the genus *Inocybe* in Europe: I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia* 3(Suppl.): 1–247.
- LARKIN, M. A., G. BLACKSHIELDS, N. P. BROWN, R. CHENNA, P. A. MCGETTIGAN, H. MCWILLIAMS, F. VALENTIN, I. M. WALLACE, A. WILM, R. LOPEZ, J. D. THOMPSON, T. J. GIBSON, AND D. G. HIGGINS. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947–2948.
- LARSSON, E., M. RYBERG, P.-A. MOREAU, Å. D. MATHIESEN, AND S. JACOBSSON. 2009. Taxonomy and evolutionary relationships within species of section *Rimosae* (*Inocybe*) based on ITS, LSU, and mtSSU sequence data. *Persoonia* 23: 86–98.
- LARSSON, E., J. VAURAS, AND C. L. CRIPPS. 2017. *Inocybe lemmi*, a new species of section *Marginatae* from the alpine region of Sweden. *Karstenia* 57: 1–9.
- LATHA, K. P. D. AND P. MANIMOHAN. 2015. *Inocybe griseorubida*, a new species of Pseudosperma clade from tropical India. *Phytotaxa* 221: 166–174.
- LATHA, K. P. D. AND P. MANIMOHAN. 2016. Five new species of *Inocybe* (Agaricales) from tropical India. *Mycologia* 108: 110–122.
- LATHA, K. P. D. AND P. MANIMOHAN. 2017. *Inocybes* of Kerala. *SporePrint Books, Calicut, India*. 181 pp.
- LIU, Y. J., S. WHELEN, AND B. D. HALL. 1999. Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerase II subunit. *Mol. Biol. Evol.* 16: 1799–1808.
- LUDWIG, E. 2017. *Pilzkompedium*. Band 4. *Cortinariaceae (Galerina, Hebeloma, Inocybe, Phaeogalera, Cortinarius Teil I mit den Untergattungen Cortinarius, Dermocybe, Leprocybe, Phlegmacium)*. *Fungicon-Verlag, Berlin, Germany*.
- MADDISON, D. R. AND W. P. MADDISON. 2005. *MacClade 4* version 4.08 for OS X. Sinauer Associates. Sunderland, MA.
- MARCHETTI, M., P. FRANCHI, AND G. CONSIGLIO. 2014. Tipificazione de alcune *Inocybe* di Britzelmayr. *Riv. Micol.* 57: 127–178.
- MATHENY, P. B. 2005. Improving phylogenetic inference of mushrooms using RPB1 and RPB2 sequences (*Inocybe*, Agaricales). *Mol. Phylogenet. Evol.* 35: 1–20.
- MATHENY, P. B. 2017. *Key to Species of Inocybe From Eastern North America—v04*. University of Tennessee, Knoxville. 20 pp. [[http://mathenylab.utk.edu/Site/The\\_Inocybaceae\\_Post\\_files/Key\\_Inocybe\\_easternNA\\_v04.pdf](http://mathenylab.utk.edu/Site/The_Inocybaceae_Post_files/Key_Inocybe_easternNA_v04.pdf)]
- MATHENY, P. B. AND N. L. BOUGHER. 2017. *Fungi of Australia: Inocybaceae*. Australian Biological Resources Study, Canberra. CSIRO Publishing, Melbourne, Australia. 582 pp.
- MATHENY, P. B. AND B. R. KROPP. 2001. A revision of the *Inocybe lanuginosa* group and allied species in North America. *Sydowia* 53: 93–139.

- MATHENY, P. B. AND P.-A. MOREAU. 2009. A rare and unusual lignicolous species of *Inocybe* (Agaricales) from eastern North America. *Brittonia* 61: 163–171.
- MATHENY, P. B., L. L. NORVELL, AND E. C. GILES. 2013. A common new species of *Inocybe* in the Pacific Northwest with a diagnostic PDAB reaction. *Mycologia* 105: 436–446.
- MATHENY, P. B., M. C. AIME, M. E. SMITH, AND T. W. HENKEL. 2012. New species and reports of *Inocybe* (Agaricales) from Guyana. *Kurtziana* 37: 23–39.
- MATHENY, P. B., Y. LIU, J. F. AMMIRATI, AND B. D. HALL. 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *Am. J. Bot.* 89: 688–698.
- MATHENY, P. B., T. W. HENKEL, O. SENE, H. B. KOROTKIN, B. T. M. DENTINGER, AND M. C. AIME. 2017. Two new species of *Auritella* (Inocybaceae) from Cameroon, with a worldwide key to the known species. *IMA Fungus* 8: 287–298.
- MATHENY, P. B., M. C. AIME, N. L. BOUGHER, B. BUYCK, D. E. DESJARDIN, E. HORAK, B. R. KROPP, D. J. LODGE, J. M. TRAPPE, AND D. S. HIBBETT. 2009. Out of the palaeotropics? Historical biogeography and diversification of the cosmopolitan mushroom family Inocybaceae. *J. Biogeogr.* 36: 577–592.
- MOSER, M. M. 1978. *Fungorum Rariorum Icones Coloratae*. VII. J. Cramer, Vaduz, Liechtenstein. 48 pp.
- MUNSELL SOIL COLOR CHARTS. 1954. Munsell Color Company, Inc. Baltimore, MD.
- MURRILL, W. A. 1914. (Agaricales) Agaricaceae (pars). *N. Am. Fl.* 10(1): 1–76.
- MURRILL, W. A. 1944. New Florida fungi. *Proc. Fla. Acad. Sci.* 7: 107–128.
- MURRILL, W. A. 1945. New Florida fungi. *Quart. J. Fla. Acad. Sci.* 8: 175–198.
- NISHIDA, F. H. 1988. New species of *Inocybe* from southern California. *Mycotaxon* 33: 213–222.
- NISHIDA, F. H. 1989. Key to the species of *Inocybe* in California. *Mycotaxon* 34: 181–196.
- PEGLER, D. 1983. *Agaric flora of the Lesser Antilles*. Kew Bull. Ser. IX: 1–668.
- PHILLIPS, R. 1991. *Mushrooms of North America*. Little, Brown and Company, Boston, MA. 319 pp.
- PHILLIPS, R. 2005. *Mushrooms and Other Fungi of North America*. Firefly Books, Buffalo, NY. 319 pp.
- PRADEEP, C. K., VRINDA K. B., S. VARGHESE, AND P. B. MATHENY. 2016. New and noteworthy species of *Inocybe* (Agaricales) from tropical India. *Mycol. Prog.* 15: article 24.
- RIDGWAY, R. 1912. *Color Standards and Nomenclature*. Published by the author. Washington DC. 43 pp., 53 pl.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M. A. SUCHARD, AND J. P. HUELSENBECK. 2012. MrBayes 3.2.: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542.
- RYBERG, M., E. LARSSON, AND S. JACOBSSON. 2010. An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). *Mol. Phylogenet. Evol.* 55: 431–442.
- RYBERG, M. AND P. B. MATHENY. 2012. Asynchronous origins of ectomycorrhizal clades of Agaricales. *Proc. R. Soc. B Biol. Sci.* 279: 2003–2011.
- SINGER, R. 1986. *The Agaricales in Modern Taxonomy*. Koeltz Scientific Books, Koenigstein, Germany. 981 pp., 88 pl.
- SINGER, R., I. ARAUJO, AND M. H. IVORY. 1983. The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia. *Nova Hedwigia Beih.* 77: 1–339.
- SMITH, A. H., H. V. SMITH, AND N. S. WEBER. 1979. *How to Know the Gilled Mushrooms*. Wm. C. Brown Company Publishers, Dubuque, IA. 334 pp.
- STAMATAKIS, A. 2014. RAXML 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- STANGL, J. 1985. *Inocybe adaequata* (Britz. 1882) Sacc. 1887, gültiger Name für *Inocybe jurana* (Pat. 1886) Sacc. 1887. *Intern. J. Mycol. Lichenol.* 2: 21–30.
- STANGL, J. 1989. Die Gattung *Inocybe* in Bayern. *Hoppea, Denkschr. Regensb. Bot. Ges.* 46: 5–388.
- STANGL, J. AND J. VESELSKÝ. 1982. Risspilze der Section *Lilacinae* Heim. *Česká Mykol.* 36: 85–99.
- STUJVE, T., J. KLAN, AND T. W. KUYPER. 1985. Occurrence of psilocybin and baecystin in the genus *Inocybe* (Fr.) Fr. *Persoonia* 12: 469–473.
- STUNTZ, D. E. 1947. Studies in the genus *Inocybe*. I. New and noteworthy species from Washington. *Mycologia* 39: 21–55.
- STUNTZ, D. E. 1954. Studies on the genus *Inocybe* II. New and noteworthy species from Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* 39: 53–84.
- THIERS, B. 2019 [continuously updated]. *Index herbariorum: A Global Directory of Public Herbaria and Associated Staff*. New York Botanical Garden's Virtual Herbarium <<http://sweetgum.nybg.org/ih>>.
- TRUDELL, S. A., J. XU, I. SAAR, A. JUSTO, AND J. CIFUENTES. 2017. North American matsutake: Names clarified and a new species described. *Mycologia* 109: 379–390.
- VILGALYS, R. AND M. HESTER. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J. Bacteriol.* 173: 4238–4246.
- WHITE, T. J., T. BRUNS, S. LEE, AND J. W. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, pp. 315–322. *In* M. A. INNIS, D. H. GELFAND, J. J. SNINSKY, AND T. J. WHITE [eds.], *PCR protocols: A Guide to the Methods and Applications*. Academic Press, New York, NY. 482 pp.