

Genera of Inocybaceae: New skin for the old ceremony

P. Brandon Matheny, Alicia M. Hobbs & Fernando Esteve-Raventós

To cite this article: P. Brandon Matheny, Alicia M. Hobbs & Fernando Esteve-Raventós (2019): Genera of Inocybaceae: New skin for the old ceremony, *Mycologia*, DOI: [10.1080/00275514.2019.1668906](https://doi.org/10.1080/00275514.2019.1668906)

To link to this article: <https://doi.org/10.1080/00275514.2019.1668906>

 View supplementary material 

 Published online: 17 Dec 2019.

 Submit your article to this journal 

 Article views: 4

 View related articles 

 View Crossmark data 



Genera of Inocybaceae: New skin for the old ceremony

P. Brandon Matheny ^a, Alicia M. Hobbs^a, and Fernando Esteve-Raventós^b

^aDepartment of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; ^bDepartamento de Ciencias de la Vida (Area de Botánica), Universidad de Alcalá, 28805 Alcalá de Henares, Spain

ABSTRACT

A six-gene phylogeny of the Inocybaceae is presented to address classification of major clades within the family. Seven genera are recognized that establish a global overview of phylogenetic relationships in the Inocybaceae. Two genera—*Nothocybe* and *Pseudosperma*—are described as new. Two subgenera of *Inocybe*—subg. *Inosperma* and subg. *Mallochybe*—are elevated to generic rank. These four new genera, together with the previously described *Auritella*, *Tubariomyces*, and now *Inocybe* sensu stricto, constitute the Inocybaceae, an ectomycorrhizal lineage of Agaricales that associates with at least 23 plant families worldwide. *Pseudosperma*, *Nothocybe*, and *Inocybe* are recovered as a strongly supported inclusive clade within the family. The genus *Nothocybe*, represented by a single species from tropical India, is strongly supported as the sister lineage to *Inocybe*, a hyperdiverse genus containing hundreds of species and global distribution. Two additional inclusive clades, including *Inosperma*, *Tubariomyces*, *Auritella*, and *Mallochybe*, and a nested grouping of *Auritella*, *Mallochybe*, and *Tubariomyces*, are recovered but with marginal statistical support. Overall, the six-gene data set provides a more robust phylogenetic estimate of relationships within the family than do single-gene and single-gene-region estimates. In addition, Africa, India, and Australia are characterized by the most genera in the family, with South America containing the fewest number of genera. A total of 180 names are recombined or proposed as new in *Inosperma*, *Mallochybe*, and *Pseudosperma*. A key to genera of Inocybaceae is provided.

ARTICLE HISTORY

Received 29 March 2019
Accepted 13 September 2019

KEYWORDS

Agaricales; classification; fungi; nomenclature; phylogeny; systematics; 184 new taxa

INTRODUCTION

The Inocybaceae Jülich is a family of ectomycorrhizal mushroom-forming fungi in the Agaricales Underw. (Matheny et al. 2006). The family is monophyletic, occurs worldwide, associates with as many as 23 families of vascular plants in mycorrhizal symbiosis (TABLE 1), and is estimated to contain 1050 species (Matheny and Kudzma 2019). Members of the family are generally characterized by the production of basidiomes (FIG. 1) with a stipe, nonglutinous pileus, brownish mature lamellae, distinctive odors, pigmented basidiospores with a smooth exosporium and lack of a germ pore, presence of cheilocystidia and/or pleurocystidia, and occurrence on soil. A few exceptions to this combination of traits have been noted (Kuyper 1986; Matheny and Kropp 2001). Many species produce secondary metabolites such as muscarine, psilocybin, or other compounds (Kuyper 1986; Jensen et al. 2006; Zhao et al. 2009; Kosentka et al. 2013; Matheny et al. 2013). Specimens of Inocybaceae are notoriously difficult to culture whether from basidiome tissue or single spore isolates (Fries 1982; Boidin 1986). Consequently, this has resulted in heavy reliance upon morphological species

recognition (Taylor et al. 2006), which has underestimated the extent of taxonomic and genetic diversity in the family. However, many traditionally recognized morphological species are under revision, with a new emphasis on molecular phylogenetic underpinnings, epitypification of poorly understood species, and molecular annotation of type collections (e.g., Matheny and Kropp 2001; Kropp and Matheny 2004; Larsson et al. 2009, 2014, 2017; Cripps et al. 2010; Horak et al. 2015; Esteve-Raventós et al. 2016, 2018; Latha and Manimohan 2017; Matheny and Bougher 2017; Matheny and Swenie 2018; Bandini et al. 2019). Such work has now revealed that considerably more species of Inocybaceae exist worldwide, and new species continue to be described even in Europe despite more than 200 years of taxonomic effort there. Nevertheless, the genus *Inocybe* (Fr.) Fr. is presently paraphyletic according to a phylogenetic-based classification that recognizes the genera *Auritella* Matheny & Bougher and *Tubariomyces* Esteve-Rav. & Matheny (Matheny and Bougher 2006; Alvarado et al. 2010; Ryberg et al. 2010; Matheny et al. 2012). Decisions need to be made to reconcile such a classification within the family, one that purports to best taxonomic practices (Vellinga et al. 2015). This work does

CONTACT P. Brandon Matheny  pmatheny@utk.edu

 Supplemental data for this article can be accessed on the [publisher's Web site](#).

© 2019 The Mycological Society of America

Table 1. Mycorrhizal associations in the Inocybaceae by plant family, source of evidence, and study.

Plant family	Source of evidence	Selected references
Achatocarpaceae	Root molecular	Alvarez-Manjarrez et al. 2018
Betulaceae	Root molecular, field observations, anatomy	Ryberg et al. 2008; Cripps et al. 2010; Kennedy and Hill 2010; Kennedy et al. 2011; Ilyas et al. 2013
Casuarinaceae	Field observations	Matheny and Bougher 2017
Cistaceae	Field observations, anatomy	Malloch and Thorn 1985; Alvarado et al. 2010; Vizzini et al. 2013
Cyperaceae	Root molecular	Ryberg et al. 2008; Gao and Yang 2010
Dipterocarpaceae	Root molecular, field observations	Ryberg et al. 2008; Moyersoen 2012; Horak et al. 2015; Latha and Manimohan 2017; Pradeep et al. 2016
Ericaceae	Root molecular, field observations	Ryberg et al. 2008; Hynson and Bruns 2009; Kühndorf 2016
Fabaceae	Root molecular, field observations	Matheny et al. 2003; Matheny et al. 2012; Onguene and Kuyper 2012; Matheny and Bougher 2017; Matheny et al. 2017
Fagaceae	Root molecular, field observations	Kuyper 1986; Ryberg et al. 2008
Gnetaceae	Root molecular	Tedersoo and Pölme 2012
Juglandaceae	Root molecular	Rudawska et al. 2018
Malvaceae	Root molecular	Ryberg et al. 2008
Myrtaceae	Root molecular, field observations	Glen et al. 2001; Tedersoo et al. 2008; Matheny and Bougher 2017
Nothofagaceae	Root molecular, field observations	Horak 1977, 1979, 1980; Singer 1986; Tedersoo et al. 2008; Matheny and Bougher 2017
Noctaginaceae	Root molecular, field observation	Pegler 1983; Kropp and Albee-Scott 2010; Tedersoo et al. 2010; Alvarez-Manjarrez et al. 2018
Orchidaceae	Root molecular	Ryberg et al. 2008; Roy et al. 2009
Phyllanthaceae	Field observations	Matheny et al. 2009; Bougher et al. 2012; Onguene and Kuyper 2012; Pradeep et al. 2016
Pinaceae	Root molecular, field observations, in vitro synthesis	Chu-Chou and Grace 1981; Kuyper 1986; Repáč 1996; Ryberg et al. 2008; Walbert et al. 2010
Poaceae	Root molecular, field observations	Kuyper 1986; Ryberg et al. 2008
Polygonaceae	Root molecular, field observations	Pegler 1983; Gardes and Dahlberg 1996; Mühlmann et al. 2008; Tedersoo et al. 2010; Séné et al. 2015
Rhamnaceae	Root molecular, field observations	Tedersoo et al. 2008; Bougher et al. 2012
Rosaceae	Root molecular, field observations	Gardes and Dahlberg 1996; Ryberg et al. 2009; Cripps et al. 2010; Kropp et al. 2013
Salicaceae	Root molecular, field observations, in vitro synthesis	Cripps and Miller 1995; Gardes and Dahlberg 1996; Cripps 1997; Ryberg et al. 2009; Cripps et al. 2010

so based on broad global taxon sampling and phylogenetic analyses of six nuclear gene regions and represents the culmination of the dismemberment of *Inocybe* sensu lato begun more than 10 years ago into more meaningful taxonomic groups.

The Inocybaceae was first introduced including two genera—*Inocybe* and *Astrosporina* J. Schröt. (Jülich 1982), each separated by basidiospore morphology. Historically, however, *Inocybe* and *Astrosporina* (or *Astrosporina* as a taxonomic synonym of *Inocybe*) were treated by more modern authors in the family Cortinariaceae R. Heim ex Pouzar (Singer 1949, 1986; Malchol and Singer 1971; Horak 2005). This convention was later proved artificial by molecular phylogenetic analyses of D1–D2 domains of nuc 28S rDNA (28S) (Moncalvo et al. 2000, 2002) and multigene data (Matheny et al. 2002, 2006; Matheny 2005; Ryberg et al. 2010), thus reinforcing the conclusions of Jülich (1982), who commented on differences in basidiospore wall traits between Inocybaceae and Cortinariaceae as justification for their separation. In addition, functional mycorrhizal traits also differ between *Inocybe* (hydrophilic ectomycorrhizas) and *Cortinarius* (Pers.) Gray (hydrophobic ectomycorrhizas), which may reflect differential use of resources for metabolism (Chen et al. 2016). The molecular results led to recognition of the strongly supported lineage containing *Inocybe* and other newly but informally named major clades or lineages as the Inocybaceae

(Matheny 2005; Matheny et al. 2009). In addition, strong support was found for a sister-group relationship between the families Inocybaceae and Crepidotaceae Singer in broad multigene studies of the Agaricales (Matheny et al. 2006; Garnica et al. 2007). Both family names are eligible for use given that neither is subsumed within the conserved family Cortinariaceae (Pouzar 1985) based on multigene phylogenetic studies (Matheny et al. 2006; Garnica et al. 2007; Zhao et al. 2017).

Since these systematic treatments, however, recognition of Inocybaceae has not been uniform. Matheny (2009) discussed differences between the Inocybaceae and Crepidotaceae based on a combination of morphological feature (basidiome and anatomical traits), biochemical (secondary metabolites), and ecological (trophic mode and substrate) differences. Cannon and Kirk (2007), however, recognized a single family—Crepidotaceae, in which the Inocybaceae was subsumed. Knudsen and Vesterholt (2008, 2012) and Kirk et al. (2008) followed suit, although the latter regarded Crepidotaceae as a synonym of Inocybaceae. Here, we continue to recognize Inocybaceae as separate from the Crepidotaceae (Matheny 2009) pending outcomes from phylogenomic analyses and reevaluation of family-level boundaries within the suborder Agaricineae Fr. (Dentinger et al. 2016).

What we now recognize as the Inocybaceae has been recognized as a single genus since the onset of the 20th century by most workers (Masse 1904; Heim 1931;



Figure 1. Basidiome diversity of Inocybaceae. A. *Inocybe* clade (*Inocybe* sect. *Inocybe*): *I. tubarioides* (HRL2017; photo by Renée Lebeuf). B. *Nothocybe* lineage: *I. distincta* (CAL13010; photo by K. P. Deepna Latha). C. *Pseudosperma* clade: *I. notodyrina* (PBM3918; photo by P. Brandon Matheny). D. *Inosperma* clade: *I. calamistrata* (PBM2113; photo by P. Brandon Matheny). E. *Mallochybe* clade: *I. tomentosa* Ellis & Everh. (PBM4138; photo by P. Brandon Matheny). F. *Tubariomyces*: *T. inexpectatus* (AH25500; photo by Fernando Esteve-Raventós). G. *Auritella*: *A. hispida* (TH10463; photo by Noah Siegel). H. *Auritella brunnescens* (NLB963; photo by Neale L. Bougher). Bars = 1 cm.

Kühner and Romagnesi 1953; Kuyper 1986; Singer 1986; Horak 2005) or as two genera (Horak 1967, 1977, 1979). Few systematists have recognized more than two genera in the family. Earle (1909), however, unconventionally proposed four genera: *Inocybe*, *Astrosporina*, *Agmocybe* Earle, and *Inocibium* Earle. An additional genus typified by *I. calospora* Quél.—*Inocybella* Zerova—was also proposed (Zerova 1974), but this was not widely accepted (Singer 1986) and unsupported by morphological (Kuyper 1986) and molecular phylogenetic (Matheny et al. 2002; Matheny 2005) studies. All of Earle's genera were regarded as synonyms of *Inocybe* by Kuyper (1986) and Singer (1986) and never subsequently used. Furthermore, Kuyper (1986) noted that *Agmocybe* was illegitimate (International Code of Nomenclature for algae, fungi, and plants [ICN] Art. 52.1; Turland et al. 2018). Infrageneric classification systems, and agreement upon types, within *Inocybe* or *Astrosporina*, have varied widely (Heim 1931; Horak 1967; Kühner 1980; Kuyper 1986; Singer 1986; Kobayashi 2002). A summary of these classifications and predictions they make in a phylogenetic context is presented in Matheny (2009). With the advent of multigene molecular phylogenetic studies, however, combined with broad global sampling of taxa outside Europe, it became apparent that a phylogenetic classification system of European origin was inadequate to accommodate Inocybaceae globally. Thus, Matheny (2005) and Matheny et al. (2009) proposed a phylogenetic-based system using a mixture of available generic-level names and informal clade name designations, encouraging subsequent recognition of the informally recognized clades as genera in their own right (Matheny and Bougher 2006; Alvarado et al. 2010).

Multigene molecular phylogenetic analyses have now culminated in recognition of at least seven major lineages in the family: *Inocybe* sensu stricto, *Auritella* Matheny & Bougher, *Tubariomyces* Esteve-Rav. & Matheny (originally as the Mallocybella clade), the Inosperma clade, the Pseudosperma clade, the Nothocybe lineage (containing a single species), and the Mallocybe clade (Matheny 2005, 2009; Matheny et al. 2009, 2012; Alvarado et al. 2010; Latha et al. 2016). Other studies merged European-based classifications to a phylogenetic system but retained application of infrageneric names, some at different ranks, available in *Inocybe* (Larsson et al. 2009; Ryberg et al. 2010). Neither of these approaches is satisfying. The phylogenetic system of Matheny and colleagues has left *Inocybe* as a paraphyletic entity and maintains three of the major clades as genera, whereas the rest are labeled with informal clade names. The system by Larsson and colleagues is inadequate because *Inocybe* remains paraphyletic with respect to *Auritella* (Larsson et al. 2009; Ryberg et al. 2010), and major clades (some of which are

sister groups) are designated at different ranks (subgenera or sections), with informal names, or cumbersome numbering systems. Here, we propose to resolve these conflicts by proposing formal names of equal rank to each of the seven major lineages in the Inocybaceae.

Initial estimates of phylogenetic relationships in the genus in the broad sense, or across the family, used 28S data only (Moncalvo et al. 2000, 2002) and with very limited taxon sampling. Matheny and colleagues (e.g., Matheny 2005; Matheny et al. 2009; Matheny and Bougher 2017) used multigene sampling from a mixture of *rpb1*, *rpb2* (two genes that encode the largest and second largest subunits of RNA polymerase II), 28S, and/or nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (= ITS), with consideration of increasingly greater taxonomic depth on a global scale. Additional studies ramped up taxon sampling, with >400 taxa considering the 28S locus only (Ryberg and Matheny 2012; Kosentka et al. 2013) and with nearly 800 taxa using *rpb2* only (Matheny and Kudzma 2019). Larsson et al. (2009) and Ryberg et al. (2010) employed use of multiple ribosomal RNA gene regions—28S, ITS, and mt small subunit rDNA, with taxonomic emphasis on European species. Pradeep and colleagues and Latha and colleagues (e.g., Pradeep et al. 2016; Latha and Manimohan 2017) have used a combination of 28S, ITS, and *rpb2* data in their studies of poorly known palaeotropical taxa. Other taxonomic works generally focused on species-level relationships with reliance upon loci (e.g., ITS, 28S) that, in combination, have been useful to discriminate species (e.g., Larsson et al. 2014; Horak et al. 2015; Esteve-Raventós et al. 2018; Bandini et al. 2019). The generation of whole-genome data from samples of Inocybaceae is just beginning (Awan et al. 2018; Bahram et al. 2018). However, the accumulation of the taxon sampling necessary for a critical evaluation of major relationships in the family is insufficient. Only two genomes (*Inocybe terrigena* (Fr.) Kuyper and *I. corydalina* Quél.) have been produced to date. Here, we use a combination of portions of six nuclear loci—*rpb1*, *rpb2*, and *tef1* (the latter encoding translation elongation factor 1-alpha) and nuc 18S rDNA (18S), 28S, and nuc 5.8S rDNA (three ribosomal RNA loci)—to infer overall phylogenetic relationships among major clades of Inocybaceae. As a result, a reclassification of the family is proposed in light of robust hypothesized phylogenetic relationships.

MATERIALS AND METHODS

Taxon sampling.—Sixty-three taxa were included in a six-gene phylogenetic analysis (TABLE 2). Of these, nine were sampled from the Crepidotaceae, including

Table 2. DNA sequences from six nuclear loci used in this study.

Species	Specimen voucher	Geographic location	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	18S	28S	5.8S (ITS)
Crepidotaceae								
<i>Crepidotus applanatus</i>	PBM717	Washington	AY333303	AY333311	DQ028581	AY705951	AY380406	DQ202273
<i>Crepidotus prostratus</i>	PBM3463	Western Australia	MK415415	HQ728540	MK426172	HQ728539	HQ728538	HQ728537
<i>Crepidotus</i> sp.	PBM3237	Tasmania	MK415416	KT382280	MK426173	MK429929	KT382279	—
<i>Pleuroflammula flammea</i>	MCA339	Virginia	DQ447935	DQ474124	GU187741	DQ089021	AF367962	DQ494685
<i>Pleuroflammula praestans</i>	PBM3461	Western Australia	MK415417	HQ832441	MK426174	HQ832431	HQ832464	HQ832450
<i>Pleuroflammula tuberculosa</i>	PAM 02072903	France	MK415418	HQ832442	MK452789	KJ137265	HQ832465	HQ832452
<i>Simocybe phlebophora</i>	PBM3089	New Zealand	MK415419	MK415449	—	MK429930	MK421967	MK421963
<i>Simocybe serrulata</i>	PBM2536	Massachusetts	DQ447940	DQ484053	GU187755	DQ465343	AY745706	DQ494696
<i>Simocybe</i> sp.	PBM3031	Tennessee	KC669280	HQ832444	MK426175	KJ137267	GQ892979	GQ893023
Inocybaceae								
<i>Auritella</i>								
<i>Auritella brunnescens</i>	PBM3174	Queensland	MK415420	KJ702349	MK426176	MK429931	JQ313571	KJ702344
<i>A. dolichocystis</i>	T24844	New South Wales	AY351797	AY337371	—	—	AY380371	—
<i>A. foveata</i>	TBGT9631	India	MK415421	GU062738	MK426177	MK429932	GU062739	GU062740
<i>A. fulvella</i>	AQ669492 AQ669485	Queensland	MK415422	KJ702357	MK426178	MK429933	KJ702352	KJ702355
<i>A. hispida</i>	TH10009	Cameroon	MK415423	KT378215	MK426179	MK429934	KT378207	KT378203
<i>A. robusta</i>	I163	Tasmania	MK415424	KJ702360	MK426180	MK429935	KJ702358	KJ702359
<i>A. serpentinocystis</i>	PBM3188	New South Wales	MK415425	KJ756402	MK426181	MK429936	JQ313559	KJ729858
<i>A. spiculosa</i>	TH9866	Cameroon	MK415426	KT378214	MK426182	MK429937	KT378206	KT378204
<i>Inocybe</i> clade								
<i>Inocybe asterospora</i> aff.	PBM2453 PBM3309	New York Tennessee	DQ447914	KM245975	DQ435795	AY654889	AY702015	DQ404390
<i>I. cacaocolor</i>	PBM3790	Queensland	MK415427	KJ756422	—	MK429938	KJ756464	KJ778845
<i>I. corydalina</i>	TURA6488 Awan et al. 2018	Belgium France	AF389536	AY337370	Awan et al. 2018	Awan et al. 2018	AY038314	MH216083
<i>I. flavoalbida</i>	PBM3768	Queensland	MK415428	KJ729932	MK426183	MK429939	KJ729901	KJ729873
<i>I. fuscicothurnata</i>	PBM3980	North Carolina	MK415429	MF416408	MK426184	MK429940	KY990485	MF487844
<i>I. humidicola</i>	PBM3719	Queensland	MK415430	KJ811575	MK426185	MK429941	KJ801181	KP171126
<i>I. lanuginosa</i>	PBM956 PBM3023	Washington Pennsylvania	AF389541	KM245992	MK426186	MK429942	KP170923	HQ232480
<i>I. lasserooides</i>	PBM3749	Queensland	MK415431	KM245993	MK426187	MK429943	KP170924	KP171145
<i>I. luteifolia</i>	PBM2642 AHS6557	Tennessee Michigan	EU307815	EU307816	MK426188	MK429944	EU307814	FJ436331
<i>I. magnifolia</i>	MCA2441	Guyana	EU600898	EU600899	MK426189	MK429945	JN642244	JN642228
<i>I. melanopus</i>	PBM3975	Tennessee	MK415432	MH249807	MK426190	MK452791	MH220276	—
<i>I. pallidicremea</i>	PBM2039 PBM2744	Washington Maine	AF390020	AY337388	MK426191	AF287835	AY380385	KY990553
<i>I. persicinipes</i>	PBM2197 (E7044)	Western Australia	EU600835	EU600836	MK426192	MK429946	EU600837	KF977215
<i>I. pileosulcata</i>	TBGT10742	India	MK415433	KM406218	MK426193	MK429947	KP170979	KP308810
<i>I. pluvialis</i>	PBM3228 PBM3232	Tasmania	MK415434	KF891954	MK426194	MK429948	KF853401	KF871777
<i>I. relicina</i>	JV10258 IB19920112	Finland	AF389546	AY333778	—	—	AY038324	AF325664
<i>I. roseifolia</i>	CO5576	Oklahoma	MK452790	MH577441	MK426195	MK429949	MK421968	MH578026
<i>I. rufobadia</i>	NLB885	Western Australia	MK415435	KF991385	MK426196	MK429950	KF915290	KF977213
<i>I. serrata</i>	PBM3235 PBM3223	Tasmania	MK415436	KM555111	MK426197	MK429951	KP171012	KP636810
<i>I. spadicea</i>	PBM2203 (E7051)	Western Australia	EU600864	—	MK426198	MK429952	EU600865	KP636866
<i>I. subexilis</i>	PBM2620 ACAD11680	Tennessee Nova Scotia	EU307846	EU307847	MK426199	MK429953	EU307845	MH578001
<i>I. thailandica</i>	DED8049	Thailand	MK415437	KM656129	MK426200	MK429954	GQ892968	GQ893013
<i>I. torresiae</i>	PBM2157 (E6978)	Western Australia	EU600872	EU600873	—	MK429955	EU600874	KP641635
<i>I. tubarioides</i>	PBM2550 PBM2570	North Carolina N. Hampshire	EU307854	EU307855	MK426201	MK429956	AY732211	EU439453
<i>Inosperma</i> clade								
<i>I. adaequata</i>	JV16501F JV11290F	Finland	AY351791	AY333771	MK426202	MK429957	JQ815407	JQ801381
<i>I. calamistrata</i>	PBM1105	Washington	MK415438	JQ846466	MK426203	MK429958	JQ815409	JQ801386
<i>I. calamistrata</i> aff.	SAT9826004	Washington	MK415439	JQ846467	MK426204	MK429959	JQ815410	JQ801387
<i>I. carnosibulbosa</i>	TBGT12047	Thailand	MK415440	KT329443	MK426205	MK429960	KT329454	KT329448
<i>I. misakaensis</i>	PC96234	Zambia	EU569872	EU569873	MK426206	MK429961	EU569874	JQ801409
<i>I. mutata</i>	PBM2542 PBM2953 PBM4108	Massachusetts	DQ447917	DQ472729	MK426207	DQ457623	AY732212	MG773837
<i>I. rimosoides</i>	PBM2459	New York	DQ447915	DQ385884	DQ435790	AY752967	AY702014	DQ404391
<i>I. virosa</i>	TBGT753	India	MK415441	KT329446	MK426208	MK429962	KT329458	KT329452

(Continued)

Table 2. (Continued).

Species	Specimen voucher	Geographic location	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	18S	28S	5.8S (ITS)
<i>Mallcoyce</i> clade								
<i>I. myriadophylla</i>	JV19652F	Finland	DQ447916	AY803751	DQ435791	KX602262	AY700196	DQ221106
<i>I. subdecurrans</i>	REH10168	New York	MK415442	MH577503	MK426209	MK429963	MH024886	MH024850
<i>I. terrigena</i>	JV16431	Finland	AY333301	AY333309	SRP066410	SRP066410	AY380401	AM882864
	MR00339	Sweden						
	EL117/04							
<i>I. tomentosa</i>	PBM4138	Tennessee	MK415443	MH577506	MK426210	MK429964	MK421969	MG773814
<i>I. unicolor</i>	PBM1481	Missouri	AY351827	AY337409	MK426211	AF287836	AY380403	DQ490737
	PBM2589	North Carolina						
	RV7/4	Tennessee						
<i>Nothocybe</i> lineage								
<i>Inocybe distincta</i>	ZT9250	India	MK415444	EU600904	MK426212	MK429965	EU604546	KX171343
	CAL1310							
<i>Pseudosperma</i> clade								
<i>I. bulbosissima</i>	DBG19916	Colorado	MK415445	MH249788	MK426213	MK429966	MH024885	MH024849
<i>I. cercocarp</i>	BK2006986	Utah	EU600888	EU600889	MK426214	MK429967	EU600890	MK421964
<i>I. mimica</i> aff. (" <i>rimosa</i> ")	PBM2574	Massachusetts	EU307857	EU307858	MK426215	MK429968	EF561633	JQ408776
<i>I. notodryina</i>	CO4463	Oklahoma	MK415446	MH577509	MK426216	MK429969	MK421970	MH578028
<i>I. sororia</i>	PBM3901	North Carolina	MK415447	MH249810	MK426218	MK429971	MH220278	JQ408772
	MCA859	Virginia						
<i>I. spuria</i>	BK180809723	Utah	EU600866	EU600867	MK426219	MK429972	EU600868	JQ408794
<i>Tubariomyces</i>								
<i>Tubariomyces inexpectatus</i>	AH20390	Spain	—	GU907088	—	MK429973	EU569855	GU907095
	AH25500							
<i>Tubariomyces</i> sp.	BB6018	Zambia	MK415448	EU600886	MK426220	MK429974	EU600887	MK421965

Note. New sequences are in bold.

three species each from *Crepidotus* (Fr.) Staude, *Simocybe* P. Karst., and *Pleuroflammula* Singer for outgroup purposes. The remaining 54 taxa were sampled from the Inocybaceae and include representatives from all seven major lineages previously identified in the family (Matheny et al. 2009, 2012; Alvarado et al. 2010). Overall, 8 taxa were sampled from the Inosperma clade (including subg. *Inosperma* type *I. calamistrata* (Fr.) Gillet), 5 from the Mallocoyce clade (including subg. *Mallocoyce* type *I. terrigena*), 2 from *Tubariomyces* (including type *T. inexpectatus* (M. Villarreal, Esteve-Rav., Heykoop & E. Horak) Esteve-Rav. & Matheny), 8 from *Auritella* (including type *A. dolichocystis* Matheny, Trappe & Bougher), 6 from the Pseudosperma clade (including species from the *I. rimosa* (Bull.) P. Kumm. complex), the *Nothocybe* lineage (single species *I. distincta* K.P.D. Latha & Manim.), and 24 from *Inocybe* (including type *I. relicina* (Fr.) Quél.). Effort was made to sample taxa from diverse biomes, including 29 species from the north temperate zone, 9 from the south temperate zone, 1 from the neotropics, and 15 from the palaeotropics, including Africa, India, southern Asia, and northern Australia.

DNA processing and gene sampling.—DNA was extracted from dried basidiome tissues following procedures outlined in Judge et al. (2010) using a fungal DNA extraction kit manufactured by Omega Bio-Tek (Norcross, Georgia). For fresh basidiome tissues, DNA was extracted using an Extract-N-Amp

kit (Sigma-Aldrich, St. Louis, Missouri) (Matheny and Swenie 2018).

Portions of six nuclear gene regions were sequenced from three unlinked protein-coding genes and three linked ribosomal RNA gene regions—*rpb1*, *rpb2*, *tef1*, 28S, 18S, and 5.8S. Polymerase chain reaction (PCR) primers for *rpb1* (targeting conserved domains A to C) included gAf (Stiller and Hall 1997) and fCr (Matheny et al. 2002) or int2F (Frøslev et al. 2005) and fCr. Sequencing primers included those used for PCR and int2F, int2.1F, and int2.1R (Frøslev et al. 2005). To amplify and sequence the regions between domains 6 and 7 of *rpb2*, we used primers b6F and b7.1R (Matheny 2005). In addition, some taxa were sequenced between domains 5 and 7 using primers f5F and b7R (Liu et al. 1999) and b6F as an additional sequence primer. PCR primers for *tef1* included 983F and 2218R, using 1567R, EFcF, and 2212R as additional sequence primers (Rehner and Buckley 2005). For some taxa we amplified *tef1* using 526F and 1567R, with EFcF and 983F also used as sequencing primers (Rehner and Buckley 2005). A portion of the 28S (D1–D2 domains) was amplified and sequenced using primers LR0R and LR7 or LR5 (Vilgalys and Hester 1990; Moncalvo et al. 2000). The 18S was amplified in two parts, first using PNS1 and NS41 (Hibbett 1996; O'Donnell et al. 1998) (using NS19 and NS19b as additional sequencing primers) and secondly using NS51 and NS8 for PCR and NS51 and NS6 as sequencing primers (White et al. 1990). The 5.8S region was amplified and sequenced using ITS1F and ITS4

(White et al. 1990; Gardes and Bruns 1993). We also sequenced the two internal spacers but did not use these for phylogenetic analysis due to alignment concerns.

PCR protocols for *rpb1* were described in Matheny et al. (2002), *rpb2* in Matheny (2005) and Matheny et al. (2007), and *tefl* in Matheny et al. (2007). PCR protocols for 18S, 28S, and 5.8S (the ITS as a whole) were used as described in White et al. (1990). PCR amplicons were purified and sequenced at the University of Tennessee Genomics Core. Chromatograms were assembled in Sequencher 5.0.1 (Gene Codes, Ann Arbor, Michigan).

DNA alignments and phylogenetic analyses.—DNA sequences generated during this study have been deposited at GenBank (TABLE 1). Sequences were added to curated gene alignments by hand in MacClade 4.08 (Maddison and Maddison 2005) or edited in AliView 1.11 (Larsson 2014). Introns were identified using lowercase letters. Portions of the 3' end of *rpb1* intron 2 and *rpb1* introns 1, 3, and 4, in addition to *rpb2* introns 3 and 4 (see Matheny et al. 2002, 2007; Matheny 2005), were too variable to align and thus excluded before phylogenetic analyses. The same was done for *tefl* introns identified using Matheny et al. (2007). All regions of 18S, 28S, and 5.8S were included. Separate models of DNA substitution were applied to first, second, and third codon positions of the protein-coding genes. A single partition was applied to *rpb1* intron 2 and the rRNA gene regions separately. Thus, five different partitions were assigned to the concatenated alignment. Model choice was based on prior studies (Matheny et al. 2002, 2006, 2009; Matheny 2005) or recommendations in user manuals of the phylogenetic software packages.

Alignments of individual protein-coding genes and combined rRNA gene regions were analyzed by maximum likelihood (ML) including 1000 rapid bootstraps with GTRCAT approximation across different gene partitions using RAxML 8.2.9 (Stamatakis 2014). The resulting best-estimated ML trees were inspected for strongly supported conflict with more than 80% bootstrap support. After this procedure, the concatenated alignment was analyzed in RAxML with 1000 bootstrap replicates and in MrBayes 3.2.6 for a Bayesian inference (BI) analysis (Ronquist et al. 2012).

For BI analyses, GTR models with gamma distributed rate heterogeneity and a proportion of invariant sites parameter were assigned to each partition as indicated above. Two independent runs were executed for 10 million generations, sampling trees and other parameters every 10 000 generations. The default number of chains (four) and heating parameters were used. To

ensure convergence of the two independent runs, we examined the standard deviation of split frequencies and potential scale reduction factors (PSRFs) for all model parameters following recommendations in the MrBayes user manual. Posterior probabilities (BPP) were calculated after burning the first 25% of the posterior sample and ensuring that this threshold met the convergence factors described above.

Resulting tree files were viewed in FigTree 1.4.0 and rooted between the branch separating Inocybaceae from Crepidotaceae based on a strongly supported sister-group arrangement between these two families observed in previous studies (Matheny et al. 2006; Garnica et al. 2007; Zhao et al. 2017). Strongly supported nodes are those that receive >80% ML bootstrap support (BS) and >0.95 BPP. Moderately supported nodes are those that receive either strong ML BS or BPP but not both. Marginal support is used to describe nodes that receive 50–79% ML BS and nonsignificant BPP. The concatenated six-gene alignment and tree files are available as SUPPLEMENTARY FILE 1 and at http://mathenylab.ukt.edu/Site/Alignments_%26_Data_Sets.html.

An operational equivalency approach was used to gauge the amount of genetic similarity between samples of the seven major lineages of Inocybaceae on one hand and four of six genera of Crepidotaceae on the other. This approach was motivated by the question: Are molecular divergences among major lineages of Inocybaceae on par with those between recognized genera of Crepidotaceae? That is, are the divergences among genera in both families relatively similar? If no, then a decision to recognize one large encompassing genus *Inocybe* might be favored. If yes, this could support recognition of the major lineages within Inocybaceae at generic rank. Genetic data were not available for the monotypic genera *Episphaeria* Donk and *Nanstelocephala* Oberw. & R.H. Petersen for this comparison. ITS and 28S sequences were chosen representing each major lineage or genus (including generic types where possible), and intrafamilial comparisons made aligning all pairwise comparisons in the BLASTn suite at the National Center for Biotechnology Information (NCBI). Absolute genetic thresholds were not used. Comparisons were simply relative to each other.

RESULTS

A total of 140 new sequences were produced for this study (TABLE 1), and 360 sequences from six different gene regions were analyzed. A putative group I intron was detected in the 18S of several unrelated taxa: *Inocybe adaequata* (Britzelm.) Sacc., *I. sororia* Kauffman, *I. notodryina* Singer, I.J.A. Aguiar & Ivory,

I. melanopus D.E. Stuntz, *Simocybe serrulata* (Murrill) Singer, and *Simocybe* sp. PBM3031. This intron was removed before alignment of all gene regions, after which 7355 total sites remained across 63 taxa. Of the 63 taxa, 53 were represented by all six gene regions. *Inocybe relicina*, *Auritella dolichocystis*, and *Tubariomyces inexpectatus* were represented by four gene regions but included in the analysis because all are generic types. After exclusion of hypervariable spliceosomal introns and ambiguously aligned positions, the concatenated data set included 6339 aligned sites.

Phylogenetic reconstructions for individual gene regions (*rpb1*, *rpb2*, *tef1*, rRNA) are shown in SUPPLEMENTARY FIGS. 1–4. One instance of strongly supported conflict was observed. This entailed the monophyly of Australian samples of *Auritella* (95% BS in rRNA ML tree; SUPPLEMENTARY FIG. 4) but their paraphyly (94% BS) with respect to African taxa emanating from the *rpb1* gene tree (SUPPLEMENTARY FIG. 1). Australian species of *Auritella* were also recovered as paraphyletic in the *rpb2* gene tree (SUPPLEMENTARY FIG. 2) but with weaker support (60% BS). By contrast, the *tef1* gene tree—similar to the combined rRNA gene regions tree—recovered the monophyly of Australian *Auritella* but with moderate support (68%; SUPPLEMENTARY FIG. 3). The concatenated ML tree (FIG. 2) supported the monophyly of Australian *Auritella* with strong support (87% ML bootstrap, 0.99 BPP). No other strongly supported conflict was observed. Convergence diagnostics during the BI analysis were rapidly met, with the average standard deviation of split frequencies reaching <0.01 just after 400 000 generations. After the burn-in, 15 000 trees remained in the posterior distribution, from which PPs were calculated.

Phylogenetic analyses of the Inocybaceae reinforced the monophyly of the family with respect to Crepidotaceae (FIG. 2). All samples of Inocybaceae lacked *tef1* intron 11, in contrast to Crepidotaceae (and other Agaricomycete lineages). Depauperate clades of Inocybaceae, viz., those lacking pleurocystidia, formed a strongly supported grade giving rise to *Inocybe* sensu stricto, which is characterized, in part, by the presence of pleurocystidia, these most often of the metuloid type.

Overall, six of seven lineages of Inocybaceae characterized by >2 taxa were recovered with strong support (FIG. 2). The seventh lineage (Nothocybe containing *I. distincta*) is a single-stem line recovered with strong support as sister to *Inocybe* sensu stricto. Six of the seven lineages were recovered as monophyletic with various degrees of support in individual gene analyses, with the exception of the placement of *Auritella foveata* in the *rpb1* gene tree (SUPPLEMENTARY FIG. 1). Several other inclusive major monophyletic groupings were also observed: one of these included a strongly

supported nested hierarchical arrangement of the *Inocybe* sensu stricto and Nothocybe and Pseudosperma lineages; the second included a moderately supported (60% ML bootstrap, 0.99 BPP) arrangement of the Inosperma and Mallocybe clades together with the genera *Auritella* and *Tubariomyces*. The three lineages—Mallocybe clade and genera *Tubariomyces* and *Auritella*—were recovered as a monophyletic group with marginal support (68% ML bootstrap, 0.94 BPP).

Several notable relationships were also detected within several of the seven major lineages shown in FIG. 2. The Indian species *Auritella foveata* was strongly supported as sister to African and Australian species of *Auritella*. Within the Inosperma clade, species assigned to *Inocybe* sect. *Cervicolores* Kühner & Romagnesi ex Singer formed a monophyletic group and were sister with strong support to the African species *Inocybe misakaensis* Matheny & Watling. In addition, the Maculata clade was recovered as sister to *I.* sect. *Cervicolores* and *I. misakaensis*. This entire grouping was sister to an Old World and tropically distributed suite of species represented by *I. carnosibulbosa* C.K. Pradeep & Matheny and *I. virosa* K.B. Vrinda, A.V. Joseph & T.K. Abraham ex C.K. Pradeep et al. Within the Mallocybe clade, the species *I. unicolor* Peck was recovered with strong support as sister to the rest of the samples in the genus.

Twenty-four tips are shown in the *Inocybe* clade (= *I.* subg. *Inocybe*), but the backbone of this group was not resolved and was characterized by many short internodes, probably indicative of rapid diversification. However, some strongly supported clades were recovered, most of which do not correspond to named sections or any other taxonomic ranks. These include “STAC” (smooth-spored temperate austral clade), characterized by species with smooth basidiospores, metuloids, and a cool Southern Hemisphere distribution and “STBC” (smooth-spored temperate boreal clade), distinguished by species with smooth basidiospores, metuloids, and mainly cool Northern Hemisphere distribution (*I. flavoalbida*, of Australasian origin, was the sole exception but does feature smooth spores and metuloids). *Inocybe* sect. *Inocybe* formed a strongly supported monophyletic group represented by *I. relicina* (type of *Inocybe*) and *I. tubarioides* G.F. Atk.

Statistical support values for major clades of Inocybaceae are shown in TABLE 3 by gene region. The six-gene tree recovered the most robust phylogenetic estimate for the Inocybaceae overall compared with ML bootstrap analyses of the four individual gene regions (*rpb1*, *rpb2*, *tef1*, combined rRNA). Indeed, the following groupings received strong support from only the six-gene analysis: *Auritella*, *Tubariomyces*, and several groups within the *Inocybe* clade—STAC,

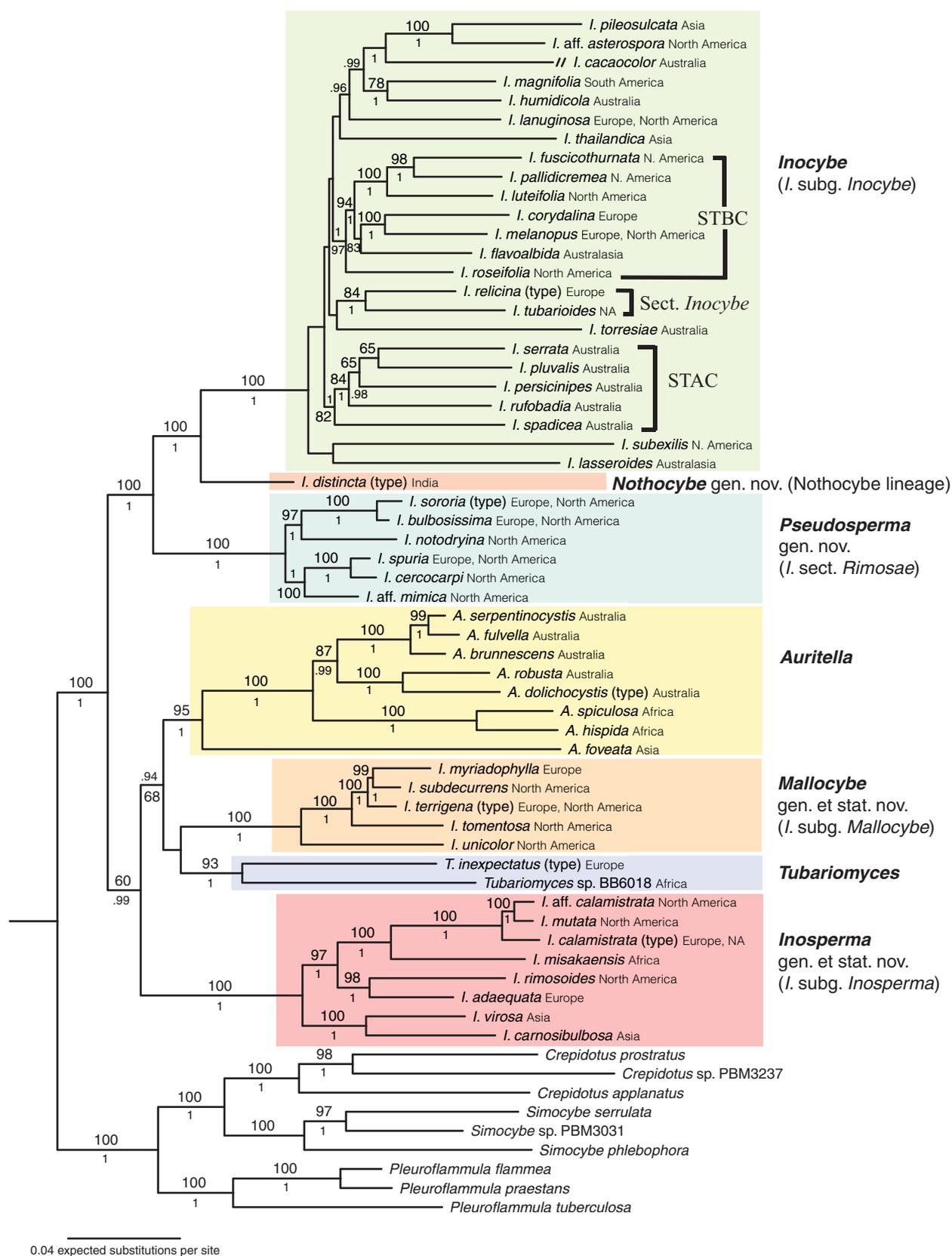


Figure 2. Best ML tree of the Inocybaceae based on phylogenetic analyses of the six-gene data set. Genera are highlighted in bold and include reference to the infrageneric classification of Kuyper (1986). The seven genera of Inocybaceae are highlighted by different colored boxes and labels. Generic types are indicated in parentheses. Whole numbers above or below branches represent bootstrap proportions, whereas asterisks below or above branches represent Bayesian posterior probabilities >0.95. Hashes indicate that a branch has been truncated for graphical presentation. Geographic origin is indicated by continent in tip labels (North America is spelled in full or abbreviated; Australasia includes the island of New Guinea). The tree is rooted between the families Crepidotaceae and Inocybaceae.

Table 3. ML bootstrap support values for clades of Inocybaceae by gene region.

Clade	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	rRNA	Combined
<i>Auritella</i>	— ^a	31	74	77	95
<i>Auritella</i> —Australia ^b	Paraphyletic	Paraphyletic	68	95	87
	94	60			
<i>Inocybe</i>	100	100	99	99	100
STAC	14	74	—	—	82
<i>I.</i> sect. <i>Inocybe</i>	63	—	—	—	84
STBC	14	—	28	27	97
Inosperma clade	100	100	67	100	100
Maculata clade	Paraphyletic	39	Paraphyletic	99	98
	73		59		
<i>I.</i> sect. <i>Cervicolores</i> + <i>I. misakaensis</i>	97	70	67	98	100
Inosperma + Pseudosperma + Nothocybe + <i>Inocybe</i>	56	—	—	—	—
Mallocybe clade	100	100	90	99	100
Nothocybe + <i>Inocybe</i>	100	91	82	74	100
Pseudosperma clade	100	100	93	100	100
Pseudosperma + Nothocybe + <i>Inocybe</i>	99	NM	31	100	100
<i>Tubariomyces</i>	—	57	—	65	93
<i>Tubariomyces</i> + Mallocybe + <i>Auritella</i>	—	—	—	—	68

^aEm dash equates to nonmonophyletic.

^bStrongly supported monophyly of Australian *Auritella* (rRNA) conflicts with strongly supported paraphyly (*rpb1*).

STBC, and *Inocybe* sect. *Inocybe*. In addition, the six-gene tree is the only one to suggest the inclusive monophyly of *Auritella*, *Tubariomyces*, and the Mallocybe clade.

The seven major lineages of Inocybaceae are proposed below as seven genera after consideration of recommended best practices concerning guidelines for introduction of new genera of fungi (Vellinga et al. 2015). See Discussion for how these guidelines were met.

Geographic areas were ranked according to the number of major lineages present in the area. TABLE 4 summarizes the geographic distribution of the seven major lineages of Inocybaceae. The most diverse regions of the globe for Inocybaceae at this level included Africa, India, and Australia. Europe (southern and northern), North America, East Asia, and New Zealand were comparable in representation but slightly less so compared with Africa, India, and Australia. The least diverse region of Inocybaceae was South America (both southern and northern regions).

TABLE 5 presents criteria by which alternative classification systems within the Inocybaceae were assessed. Using an operational equivalency approach, the major lineages of Inocybaceae were similar to each other at the ITS locus with 82–88% nucleotide site identities (SUPPLEMENTARY TABLE 1). However, pairwise similarity scores were not produced between at least two pairwise comparisons with the Mallocybe clade and all comparisons involving *Tubariomyces* and *Auritella*. Only the 5.8S regions were alignable in these latter comparisons. At the 28S locus, the major lineages were similar with 87–97% identities. In comparison, genera of Crepidotaceae were similar to each other with 81–85% ITS identities and 94–96% 28S identities.

TAXONOMY

Inocybaceae Jülich, Bibliotheca Mycologica 85:374. 1982.

Type: Inocybe (Fr.) Fr.

Diagnosis (emend.): Basidiomes agaricoid or sequestrate, typically on soil, forming ectomycorrhizal and orchid symbioses, mycorrhizas hydrophilic (where known); pileipellis a cutis, trichoderm, or subhymeniform; cystidia often present as cheilocystidia and/or metuloid pleurocystidia or caulocystidia; basidia hyaline or necropigmented; basidiospores typically melanized, with thickened wall, germ pore usually absent, nondextrinoid, multinucleate, exosporium smooth, although the wall may protrude into nodules or spinal columns; clamp connections common on most tissues; many species producing secondary metabolites such as muscarine or psilocybin. Absence of *tef1* intron 11.

Distribution: About 1050 species worldwide, occurring in most terrestrial biomes, and on all continents except Antarctica.

Inocybeae Singer, Beihefte zur Nova Hedwigia 77:175. 1983.

Diagnosis: Same as that of the family.

Inocybe (Fr.) Fr., Monographia Hymenomycetum Sueciae 2:346. 1863.

Type: Agaricus relicinus Fr.

≡ *Agaricus* tribus *Inocybe* Fr., Systema mycologicum 1:11, 254. 1821.

= *Agaricus* tribus *Clypeus* Britzelm., Berichte des Naturhistorischen Vereins Augsburg 26:137. 1881.—*Clypeus* (Britzelm.) Fayod, Annales des Sciences Naturelles Botanique 9:362. 1889.

= *Astrosporina* J. Schröt., Kryptogamen-Flora von Schlesien 3-1(5):576. 1889.

Table 4. Geographic distribution of major lineages of Inocybaceae by major geographical regions (excluding exotic introductions).

Area	<i>Inocybe</i> s. str.	<i>Nothocybe</i> lineage	<i>Pseudosperma</i> clade	<i>Inosperma</i> clade	<i>Mallocybe</i> clade	<i>Tubariomyces</i>	<i>Auritella</i>
Africa (sub-Saharan)	+		+	+	+	+	+
India	+	+	+	+	+		+
Australia	+		+	+	+	+	+
Europe (southern)	+		+	+	+	+	
Europe (northern)	+		+	+	+		
East Asia	+		+	+	+		
North America	+		+	+	+		
New Zealand	+		+	+	+		
South America (northern)	+		+				
South America (southern)	+						

Note. Data drawn from Matheny et al. (2009), Alvarado et al. (2010), Matheny et al. (2012), Latha and Manimohan (2017), Matheny et al. (2017), and Matheny and Bougher (2017). Molecular confirmation of *Mallocybe* in New Zealand was provided by J. Cooper and N. Siegel (unpublished data but a GenBank record is released). Areas are ranked by frequency of representation of the seven major lineages.

Table 5. Alternative phylogenetic classifications of the Inocybaceae.

Criterion	7 genera: Proposed here	1 genus: 7 subgenera	3 genera: Status quo
Major lineages at equal rank	Yes	Yes	No
Evolutionarily based	Yes	Yes	No
Maximize phylogenetic information	Yes	Yes	No
Minimize redundancy	Yes	No	Yes
Evolutionary equivalence with Crepidotaceae	Yes	No	No
Operational equivalence (ITS, 28S) with Crepidotaceae	Yes	No	No
Predictive power	High	Moderate but cumbersome	Low
Applicability for comparative studies	High	Moderate but cumbersome	Low (<i>Inocybe</i> not monophyletic)
Applicability for conservation	High	Moderate but cumbersome	Low (<i>Inocybe</i> not monophyletic)
Nomenclatural stability	Low (ca. 184 new names)	Moderate (ca. 25 new names)	High (0 new names)
Percentage new names	Ca. 17%	Ca. 2%	0%
Long-term stability	High	High	Low
Utility	Moderate	High	Moderate

= *Agmocybe* Earle, Bulletin of the New York Botanical Garden 5:439. 1909. Nom. illegit. (ICN Art. 52.1).

= *Inocibium* Earle, Bulletin of the New York Botanical Garden 5:439. 1909.

= *Astrosporina* S. Imai, Journal of the Faculty of Agriculture of the Hokkaido Imperial University 43:222. 1938. Nom. illegit. (ICN Art. 53.1).

= *Inocybella* Zerova, Novosti Sistematiki Nizshikh Rastenii 11:163. 1974.

Diagnosis (emend.): Pleurocystidia present often as thick-walled crystalliferous metuloids (or rarely secondarily lost, and then spores nodulose or projectile-shaped), basidia hyaline and not necropigmented; basidiospores typically amygdaliform (less often elliptic or globose), angular, nodulose, or spinose, hilar appendix distinct in many species; includes few sequestrate forms. Ectomycorrhizal with wide range of plant families.

Etymology: *Inocybe* (Greek), fiber head, in reference to the pileus that is often fibrillose.

Distribution: About 850 species in Africa, Australasia, Asia, Europe, North America, Oceania, and northern and southern South America.

Nothocybe Matheny & K.P.D. Latha, gen. nov.
Mycobank MB830337

Type: *Inocybe distincta* K.P.D. Latha & Manim.

Diagnosis: Pileus finely squamulose-rimulose, stipe fibrillose-pruinose; basidiospores phaseoliform to ovate-elliptic with occasional weak angular outline, cheilocystidia often septate and covered apically with a resinous substance, caulocystidia present (at stipe apex) as modified terminal cells of stipitipellis hyphae, pleurocystidia absent. Probable ectomycorrhizal association with *Acacia*.

Etymology: *Nothocybe* (Greek), false head, in reference to the unique sister-group relationship to *Inocybe* sensu stricto.

Distribution: 1 species, India.

Nothocybe distincta (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha, comb. nov.

Mycobank MB830342

≡ *Inocybe distincta* K.P.D. Latha & Manim., in Latha, Manimohan & Matheny, Phytotaxa 267:43. 2016. Basionym.

Pseudosperma Matheny & Esteve-Rav., gen. nov.
Mycobank MB830338

Type: *Inocybe sororia* Kauffman.

= *Inocybe* sect. *Rimosae* (Fr.) Quél., Flore Mycologique de la France et des pays limitrophes:98. 1888.

Diagnosis: Cheilocystidia arising from modified basidia, pleurocystidia absent, basidia hyaline or not necropigmented; lamellae adnexed to sinuate; pileus fibrillose

or rarely squamulose, often rimose; stipe apex often distinctly pruinose, furfuraceous, or somewhat flocculose, stipe base usually even, stipe context not changing color where bruised; odor often spermatic, like green corn, or honey, occasionally nil; basidiospores usually elliptic to indistinctly phaseoliform. Ectomycorrhizal with wide range of plant families.

Etymology: *Pseudosperma* (Greek, neuter), in reference to superficial similarities with rimose species of *Inosperma*.

Distribution: About 70 species in Africa, Asia, Australasia, Europe, North America, and northern South America.

Pseudosperma sororium (Kauffman) Matheny & Esteve-Rav., comb. nov.
Mycobank MB830343

≡ *Inocybe sororia* Kauffman, North American Flora 10(4):259. 1924. Basionym.

Inosperma (Kühner) Matheny & Esteve-Rav., gen. et stat. nov.

Mycobank MB830339

Type: *Agaricus calamistratus* Fr.

≡ *Inocybe* subg. *Inosperma* Kühner, Bull mens Soc Linn Lyon 49:898. 1980. Basionym.

Diagnosis: Basidiospores often phaseoliform, basidia hyaline or necropigmented, cheilocystidia with cyanophilous contents in some species, pleurocystidia absent; stipe base even or bulbous in some species, context often reddening where bruised; odor often distinctive. Ectomycorrhizal with wide range of plant families.

Etymology: *Inosperma* (Greek, neuter), in reference to smooth spores.

Distribution: About 55 species in Africa, Australasia, Asia, Europe, and North America.

Inosperma calamistratum (Fr.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830345

≡ *Agaricus calamistratus* Fr., Systema mycologicum I:256. 1821. Basionym.

≡ *Inocybe calamistrata* (Fr.) Gillet, Hyménomycètes: 513. 1876.

Auritella Matheny & Bougher, Mycotaxon 97:232. 2006.

Type: *Auritella dolichocystis* Matheny, Trappe & Bougher ex Matheny & Bougher.

≡ *Auritella* Matheny & Bougher, Mycological Progress 5:5. 2006. Nom. inval. (ICN Art. 40.1).

Diagnosis: Cheilocystidia arising as terminal elements of the hyphae of hymenophoral trama, usually >50 µm, or as elongated, hyphal, pyramidal, chains that become thick-walled and incrustated with age, pleurocystidia absent, basidia necropigmented; lamellae free to

adnate, pileus tomentose, squarrose, or pitted; context brunnescent in some species, never reddening; basidiospores brownish to very pale brown; pileipellis a cutis, trichoderm, or subhymeniform layer; includes one known sequestrate species. Ectomycorrhizal with Casuarinaceae, Dipterocarpaceae, Fabaceae, and Myrtaceae.

Etymology: *Auritella* (Latin), golden tissue or golden web, in reference to the ochraceous hymenium.

Distribution: 15 species in Africa, Australia, and India.

Mallocybe (Kuyper) Matheny, Vizzini & Esteve-Rav., gen. et stat. nov.

Mycobank MB830340

Type: *Agaricus terrigenus* Fr.

≡ *Inocybe* subg. *Mallocybe* Kuyper, Persoonia 3 (Suppl):22. 1986. Basionym.

Diagnosis: Cheilocystidia often present and arising as terminal elements of the hyphae of hymenophoral trama, usually <50 µm, rarely as short incrustated chains, pleurocystidia absent, basidia necropigmented; lamellae adnate or subdecurrent, pileus often woolly-squamulose and becoming noticeably dark upon application of ammonium hydroxide, context not reddening. Ectomycorrhizal with a wide range of plant families.

Etymology: *Mallocybe* (Greek), woolly head, in reference to the texture of the pileus.

Distribution: About 55 species in Africa, Asia, Australia, Europe, New Zealand, and North America.

Mallocybe terrigena (Fr.) Matheny, Vizzini & Esteve-Rav., comb. nov.

Mycobank MB830346

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

≡ *Pholiota terrigena* (Fr.) P. Karst., Bidrag till Kännedom av Finlands Natur och Folk 32:292. 1879.

≡ *Togaria terrigena* (Fr.) W.G. Sm., Synopsis of the British Basidiomycetes:122. 1908.

≡ *Inocybe terrigena* (Fr.) Kühner, Flore Analytique des Champignons Supérieurs:218. 1953. Nom. inval. (ICN Art. 41.5).

≡ *Inocybe terrigena* (Fr.) Kuyper, Persoonia 12:482. 1985.

Tubariomyces Esteve-Rav. & Matheny, Mycologia 102:1390. 2010.

Type: *Tubariomyces inexpectatus* (M. Villarreal, Esteve-Rav., Heykoop & E. Horak) Esteve-Rav. & Matheny.

Description: Basidiomes often small and tubarioid or omphalinoid with decurrent or adnate lamellae; pileus velutinous, furfuraceous, tomentose to squamulose, context not reddening; stipe pruinose throughout and

never bulbous, basidia necropigmented; basidiospores pale yellowish brown or ochraceous, apiculus indistinct or small; pleurocystidia absent; cheilocystidia present, thin- or thick-walled, occasionally with pigmented mucoid deposits or rarely crystalliferous; caulocystidia present entire length of the stipe and similar to cheilocystidia; pileipellis a trichoderm or a subhymeniform-like covering of clavate, subcylindric, or irregular (pileocystidiate) terminal hyphae. Presumably ectomycorrhizal with Cistaceae, Fagaceae, Myrtaceae, and Phyllanthaceae.

Etymology: *Tubariomyces* (Latin), due to similarity in habit to *Tubaria* (W.G. Sm.) Gillet.

Distribution: 6 species in sub-Saharan Africa, northern Australia, and southern Europe.

TAXONOMIC KEY TO GENERA OF INOCYBACEAE

1. Pleurocystidia present, or, if absent, then basidiospores nodulose or long projectile-shaped *Inocybe*
- 1'. Pleurocystidia absent and basidiospores smooth and globose, elliptic, (sub)amgydaliform, (sub)phaseoliform, or weakly angular in outline 2
2. Stipe apex pruinose, fibrillose, furfuraceous, or flocculose; basidiomes not changing color, basidia hyaline (not necropigmented) 3
- 2'. Stipe apex smooth or basidiomes rubescent or brunnescent or basidia necropigmented 4
3. Spores elliptic or indistinctly phaseoliform; widespread and associating with numerous diverse plant genera but not *Acacia*; cheilocystidia without resinous substance *Pseudosperma*
- 3'. Spores phaseoliform to ovate-elliptic, at times with weak angular outline; known only from tropical India in association with *Acacia*; cheilocystidia with resinous substance *Nothocybe*
4. Pileus rimose and stipe smooth; basidia hyaline and not slender ($Q < 4.0$) *Inosperma* (including *Maculata* clade)
- 4'. Pileus tomentose, woolly, squarrose, or pitted and stipe not smooth; basidia necropigmented and slender ($Q > 4.0$) 5
5. Basidiomes small and with distant decurrent or adnate lamellae (habit tubarioid, omphalinoid), pileipellis a palisade of subhymeniform hyphae, stipe with caulocystidia entire length *Tubariomyces*
- 5'. Basidiomes not small (habit tricholomatoid) and lamellae close, pileipellis various in structure but stipe lacking caulocystidia the entire length ... 6
6. Basidiomes rubescent and usually with distinct odor like fish, old wine caskets, bruised geranium

leaves, or earthy *Inosperma* (including *Inocybe* sect. *Cervicolores*)

- 6'. Basidiomes brunnescent or not staining where bruised; odor, if present, like honey, unpleasant, or not as above 7
7. Cheilocystidia $>50 \mu\text{m}$ (or absent if sequestrate) and thin-walled and hyaline in Australian taxa or as pyramidal, pigmented, thick-walled chains in Afro-Indian taxa; occurring in African rainforests, Indian wet evergreen forests, and in seasonally dry tropical sclerophyll and temperate areas of Australia *Auritella*
- 7'. Cheilocystidia often $<50 \mu\text{m}$, thin-walled, and hyaline, but in few species articulated as short chains or brown-incrusted but never arising as pyramidal chains; if cheilocystidia $>50 \mu\text{m}$ long, then from temperate regions; predominant in temperate regions of the Northern and Southern Hemispheres (Australia, New Zealand), less diverse in seasonally dry tropics of Africa and Australia and tropical forests of south Asia *Mallocybe*

DISCUSSION

Meeting guidelines for introduction of new fungal genera.—Vellinga et al. (2015) recommended six guidelines by which to introduce new genera of fungi. The first of these—the reciprocal monophyly criterion—is established here by recognizing the seven major lineages of Inocybaceae, each a monophyletic group or well-placed single-stem lineage, at generic rank. As a result, *Inocybe* is no longer paraphyletic. The second guideline recommends broad taxonomic sampling by the number of species, including all necessary types, and their geographic distribution in a molecular phylogenetic context. We have satisfied this approach by reconstructing a data set that includes multiple representatives from each newly recognized genus, and their respective types, with broad geographic coverage including taxa that originate from Africa, Asia, Australasia, Europe, North America, and South America. The third guideline recommends that sufficient measures of statistical support should be present in the phylogenetic tree. We have met this guideline, as six of the seven genera of Inocybaceae receive strong measures of statistical support by ML and BI methods. The seventh genus, *Nothocybe*, is a single-stem lineage; however, its placement as the sister lineage to *Inocybe* (but not including diagnostic characters of the latter) is strongly supported. The fourth guideline—consideration of alternative classification scenarios—is elaborated upon below.

The fifth guideline strongly encourages generation of phylogenetic evidence from multiple loci. We have satisfied this criterion by production and analysis of a six-gene-region data set. The sixth guideline strongly encourages the publication of both the supporting evidence and new taxonomy in peer-reviewed publications. This criterion is met here.

Alternate classification schemes of the *Inocybaceae*.—

A seemingly logical alternative to the system proposed here would instead equate all of the seven major lineages at subgeneric rank, rather than at genus level, and the node containing all seven subgenera as genus *Inocybe*. The relative costs and benefits of a subgeneric system, and those of the system we propose here, and the status quo, are evaluated in TABLE 5. Several of the criteria listed were drawn from Heenan and Smitsen (2013).

Recognition of a broad and inclusive *Inocybe* would render *Auritella* and *Tubariomyces* as synonyms of *Inocybe* but with potential to maintain these taxa at subgeneric ranks in *Inocybe*. This alternative would require no new genera or tribes but would require five new subgeneric names and about 20 new combinations (or nom. nov.) of species of *Auritella* and *Tubariomyces* into *Inocybe*, far fewer than the 180 new combinations in our proposal. *Inocybe* could be recognized in the monotypic *Inocybaceae* or subsumed as the tribe *Inocybeae*, but either would be redundant to *Inocybe* in this approach. Alternatively, a broad inclusive *Inocybe* could be recognized in a more inclusive monophyletic family *Crepidotaceae* to eliminate taxonomic redundancy.

Maintenance of the status quo is the least preferred option, as it generally underperforms across most criteria in TABLE 5 and as discussed in Introduction. However, a generic system and subgeneric systems would be equal in regard to recognition of major lineages at equal rank (genus versus subgenus), both would be evolutionarily based, and both could provide long-term nomenclatural stability. We concede that a subgeneric system and maintenance of a single “super-genus” *Inocybe* could be interpreted as more utilitarian or user-friendly (Kuyper 1994), if a user-defined taxonomy is based on ease of morphological recognition as for clinical purposes (viz., muscarine poisoning). We suggest that the generic system proposed here is independent of user-defined goals of taxonomy (Vilgalys et al. 1994) and that recognition of species in the varying genera of *Inocybaceae* will be accomplished with improved taxonomic resources (morphological, anatomical, biochemical, molecular) and subsequent revisions and species discovery.

Moreover, a generic-level system is utilitarian in its own right from a molecular operational approach (SUPPLEMENTARY TABLE 1).

The generic system proposed here contains several other advantages over a subgeneric one. First, redundancy of ranks is less, as the family *Inocybaceae* contains seven genera but currently one tribe. In the future, it may be possible to recognize more than one tribe as well, for instance, one that includes *Auritella*, *Tubariomyces*, *Mallochybe*, and *Inosperma*, if this grouping is maintained pending the addition of new genetic loci and taxa. Second, a multiple generic system in *Inocybaceae* shares evolutionary equivalency with *Crepidotaceae*, which currently contains six genera. Third, both families are at similar levels of operational equivalency as well because genera within each family share similar percent identities at the ITS and 28S loci (SUPPLEMENTARY TABLE 1). Indeed, some genera of *Inocybaceae* appear less similar to each other than those in the *Crepidotaceae*, and spacer regions of the ITS locus across *Inocybaceae* cannot be reliably aligned. A recent study in *Agaricus* has suggested use of divergence times to provide taxonomic scales to ranks (Zhao et al. 2016), but we do not apply such a criterion here, as estimated dates of divergence within the *Inocybaceae* vary and/or confidence intervals range widely across node heights (Matheny et al. 2009; Ryberg and Matheny 2012; Kosentka et al. 2013; Varga et al. 2019) depending on taxonomic sampling, gene regions, and calibrations used. If the *Inocybaceae* has an early Cenozoic origin (Ryberg and Matheny 2012; Kosentka et al. 2013; Varga et al. 2019), then the family may have unusually elevated substitution rates at nuclear loci. This topic remains to be explored.

We also suggest that a generic system has more predictive power and resolution, and thus more communicative ability, is more applicable to studies using comparative methods, and has higher applicability to conservation and identification of hot spots of phylogenetic and biological diversity. Because it is evolutionarily based, a subgeneric system could suffice in these areas but, we argue, would be more cumbersome to use and entail a loss of precision. Biological information is reduced, for example, in discussion of *Inocybe inexpectatus* in contrast to *Tubariomyces inexpectatus*, and biological information is gained in discussion of *Nothocybe distincta*, the only known species in the genus (as opposed to *Inocybe distincta*) from an important hot spot of biological diversity (Kerala, India). Our new generic system can now drive interest by nontaxonomists in comparative evolutionary studies and conservation by highlighting and emphasizing the new lineages at generic rank. Overall, we conclude that

a system that most readily distinguishes diversity of inocyboid taxa at the genus level, based on a combination of morphological and molecular features and plant host and geographic diversity, would be most easily communicated and conveyed using a system of generic ranks. As such, future studies would be couched in a more predictive and precise system to accommodate new taxa and revision.

***Auritella*.**—*Auritella* (type *A. dolichocystis*) is a strongly supported monophyletic group that includes about 15 species in Africa, Australia, and India (TABLE 4; Matheny and Bougher 2006, 2017; Matheny et al. 2012, 2017). ITS data are quite divergent and difficult to align reliably for all taxa, notably that of the Indian species *A. foveata* (Matheny et al. 2017). Diversification within the genus has occurred on a continental scale, with species from three different former Gondwanan areas forming distinct monophyletic groups or lineages. Single-gene treatments weakly support (*rpb2*; SUPPLEMENTARY FIG. 2) or do not support (*rpb1*; SUPPLEMENTARY FIG. 1) the monophyly of *Auritella* due to the rogue position of *A. foveata* (see also Matheny and Kudzma 2019; 782-taxon *rpb2* supplemental tree figure). Here, however, multigene data recovered a strongly supported clade of Australian lineages on one hand and African lineages on the other, reinforcing the study by Matheny et al. (2017). *Auritella foveata* is recovered as the sister group to the clade containing Australian and African species with strong support based on analyses of the six-gene data set (FIG. 2). However, *A. foveata* is unusual because of the combination of globose basidiospores, the pitted pileus surface attributed to a trichoderm or almost hymeniderm-like pileipellis, and isolated location in tropical India (Matheny et al. 2012). The sister group to *Auritella* is still not clear, but this is the first study to suggest a close relationship between *Auritella*, *Mallochybe*, and *Tubariomyces* with marginal support.

The gross morphology of Australian species of *Auritella* (Matheny and Bougher 2006, 2017) is strikingly different that of from African and Indian species (Matheny et al. 2012, 2017; FIG. 1), and the genus overall displays considerable anatomical variation considering the pileipellis (cutis, trichoderm, subhymeniform), stipe texture (scaly, fibrillose), spore shape (globose to cylindrical), and cheilocystidial morphology (long thick-walled chains of terminal hyphae, thin-walled elongated cells). There are no obvious gross morphological synapomorphies for the union of Afro-Indian taxa with those from Australia, but molecular data strongly support these lineages as a monophyletic group (FIG. 2).

Muscarine is absent from two Australian species sampled to date (Kosentka et al. 2013).

Evidence for the ectomycorrhizal (ECM) status of *Auritella* stems largely from field observations of species underknown ECM plants such as *Eucalyptus* (Myrtaceae), *Gilbertiodendron* and *Acacia* (Fabaceae), and possibly *Allocasuarina* (Casuarinaceae). Molecular confirmation of the ECM status of *A. aureoplumosa* has been confirmed from a caesalpinoid plant root in Africa (Matheny et al. 2017).

***Inocybe*.**—We now estimate about 850 species of *Inocybe* in its strict sense worldwide. This number will increase as continued revisions of morphological species are conducted and undersampled areas are explored. Almost all species of *Inocybe* can be distinguished from other genera of Inocybaceae by the presence of pleurocystidia and the basidiospores that are amygdaliform, elliptic, subcylindrical, angular, nodulose, or spinose, typically with a distinct apiculus. Development of basidiomes is highly varied in this genus, but separation of supersections “Marginatae” and “Cortinatae” (Kuyper 1986), based on absence or presence of a veil and distribution of caulocystidia on the stipe, does not correspond to monophyletic groupings (Matheny et al. 2002; Ryberg et al. 2010). References to these supersections should be abandoned (Kropp and Matheny 2004; Kropp et al. 2010). Pleurocystidia have been evolutionarily lost in a few species—*I. leptophylla*, *I. nigricans*, and *I. stenospora* (Matheny and Kropp 2001; Matheny and Bougher 2017; Bandini et al. 2019), all three of which are concentrated in the *I. lanuginosa* group.

We are not convinced that molecular phylogenetic efforts will resolve the backbone or earliest branching events in *Inocybe*. Rather, we suggest that the genus evolved by relatively simultaneous explosive diversification in different hemispheres after evolution of metuloid cystidia and muscarine and modification of basidiospore structure in combination with novel ecological opportunities. There appears to be a bias in favor of diversification of smooth-spored taxa in certain habitats on different continents. That is, Mediterranean habitats of North America and Australia are preponderantly rich in smooth-spored species (Nishida 1989; Matheny and Bougher 2017). By contrast, tropical regions are dominated by nodulose-spored species (Matheny et al. 2003, 2012; Horak et al. 2015; Latha and Manimohan 2017).

Consideration for a revised classification in *Inocybe* is within sights given the efforts to document and describe new species in Europe and elsewhere. We would not be

surprised, for instance, if numerous new taxonomic units were recognized in the genus worldwide. However, we strongly urge investigators to use multiple molecular loci (not only 28S and ITS) for phylogenetic purposes and clade or infrageneric designation.

Inocybe, now in its restricted sense, is confirmed as ectomycorrhizal by the strength of anatomical studies (Agerer 1987–2006), stable isotope analysis (Mayor et al. 2009), synthesis experiments (Chu-Chou and Grace 1981; Cripps and Miller 1995), and molecular evaluation of plants roots (Ryberg et al. 2009; Tedersoo and Smith 2013). A few species in the genus also form orchid mycorrhizas (Ryberg et al. 2008; Roy et al. 2009). This is the most widespread genus of Inocybaceae, as it is currently distributed on all continents except Antarctica (TABLE 4). *Inocybe sensu stricto* is the only genus of Inocybaceae found in southern South America.

***Inosperma*.**—*Inosperma* is composed of about 55 species formerly classified in *Inocybe* sect. *Cervicolores*, the Maculata clade, and at least two Old World tropically distributed lineages of *Inocybe* (Matheny and Watling 2004; Larsson et al. 2009; Matheny et al. 2009; Pradeep et al. 2016). Some species of *Inosperma* are generally recognizable by a rimose pileus, smooth stipe, and the tendency for the stipe to have a bulbous base and/or bruising reaction. These species from typically north temperate areas correspond to the Maculata clade of Larsson et al. (2009). The other well-known species are often scaly or feature necropigmented basidia similar to *I. calamistrata* and allies in *I. sect. Cervicolores* (Matheny and Bougher 2017). Overall, many *Inosperma* species exhibit reddening context and distinctive odors. In addition, all species of *I. sect. Cervicolores*, and almost all species of the Maculata clade, are characterized by a unique GC-splice site for intron 4 of *rpb2* (data not shown; but consult GenBank reference data in Matheny and Kudzma 2019). More will be learned about *Inosperma* once the earliest diverging lineages are documented and described in detail from regions such as south Asia, New Guinea, and Africa (Matheny et al. 2009; Pradeep et al. 2016). At this time, we are not aware of any morphological synapomorphies for *Inosperma* in its entirety, hence two separate entries in the key.

The genus is considered ectomycorrhizal based on stable isotope analysis of one species (Mayor et al. 2009; *Inocybe hirsuta* var. *maxima* A.H. Sm.) and molecular evidence of plant root fungal ITS sequences (Ryberg et al. 2008). Species of *Inosperma* are widespread globally but absent from natural habitats in South America. Only species similar to *I. calamistrata* are known from

the neotropics at this time (Ryberg et al. 2008), but many occur in the Old World tropics of Africa, Australia, New Guinea, and south Asia.

***Mallocybe*.**—Species of *Mallocybe* are common in temperate areas of the Northern Hemisphere (Stangl 1989; Cripps et al. 2010; Ludwig 2017) and temperate and tropical regions of Australia. Several species also occur in arctic-alpine habitats (Favre 1955; Kühner 1988; Cripps et al. 2010). Additional species are known from Africa, Australia, New Guinea, New Zealand, and south Asia (Matheny et al. 2009; Horak et al. 2015; Matheny and Bougher 2017; Horak 2018). Morphologically, almost all species of *Mallocybe* are characterized by the presence of short cheilocystidia, if present, in contrast to species of *Auritella*. The pilei of European species darken with the application of weak ammonia solution (Kuyper 1986), but this trait has yet to be thoroughly evaluated for taxa outside Europe.

The genus is considered ectomycorrhizal based on anatomical observations (Agerer 1987–2006) and molecular evidence from ECM plant root tips (Ryberg et al. 2009). *Mallocybe terrigena* and *Inocybe dulcamara* associate with the mycoheterotrophic orchid *Epipogium aphyllum* as well (Roy et al. 2009). *Mallocybe* is fairly widespread across the globe but has yet to be recorded from southern South America and the neotropics.

Vizzini et al. (2013) referred to the combinations *Mallocybe dulcamara*, *Mallocybe terrigena*, and *Mallocybe leucoblema*, but these were invalid per ICN Art. 38.1(a).

***Nothocybe*.**—This genus is intriguing for several reasons, as only one species has been identified to date (Matheny et al. 2009; Latha et al. 2016) and it forms the sister group to genus *Inocybe* in the strict sense, which is unusually hyperdiverse taxonomically. *Nothocybe distincta* is known only from south India (Kerala) but overall shares morphological affinities with species of *Pseudosperma* (furfuraceous stipe surface, absence of metuloids, hyaline basidia, smooth spores) but differs from these principally by the somewhat angular outline to the spores, a resinous substance on the cheilocystidia, ecological association with *Acacia*, and phylogenetic placement as the sister lineage to *Inocybe*. This result was first reported by Matheny et al. (2009) and replicated and reinforced in a detailed study by Latha et al. (2016). Recognition of *Nothocybe* apart from *Inocybe* in the strict sense here is maintained because diagnostic morphological features

of *Inocybe* (presence of pleurocystidia or nodulose spores and spores often with a distinct apiculus) are lacking for *N. distincta*.

Nothocybe distincta is likely an ECM associate of *Acacia* (Fabaceae) (Latha et al. 2016) and not *Casuarina* as earlier reported (Matheny 2009). Evidence for the ECM status is weak, but given the occurrence of basidiomes on soil under *Acacia* (tropical species of which are ECM; Duponnois et al. 2005; Diagne et al. 2013) and phylogenetic affinities with other ECM genera (viz, *Inocybe* and *Pseudosperma*), it is reasonable to conclude that *Nothocybe* is also ECM pending evidence from other sources such as root anatomy, stable isotopes, and molecular root tip confirmation.

***Pseudosperma*.**—*Pseudosperma* is a strongly supported monophyletic genus (FIG. 2). The clade has been also referred to as *Inocybe* sect. *Rimosae* sensu stricto by Larsson et al. (2009). Originally, *I. sect. Rimosae* included a wide diversity of species of *Inocybe*, including many that are now recognized here in *Inocybe* sensu stricto. Heim (1931) narrowed the scope of the section to include three stirpes: “fastigiata,” “cookie,” and “maculate.” The latter two stirpes are now treated in *Inosperma* (or in the *Maculata* clade of Larsson et al. [2009]).

Aside from *Nothocybe*, species of *Pseudosperma* are generally recognizable in the field given the combination of the rimose pileus, conspicuously fimbriate edges of the lamellae, and fibrillose, furfuraceous, or almost flocculose stipe apex. The spores are generally elliptic or at most indistinctly phaseoliform, and the basidia are never slender. However, in some species such as *I. flavella*, *I. xanthocephala*, *I. renispora*, and *I. hygrophorus*, the spores are clearly phaseoliform (or reniform). Unlike some rimose species of *Inosperma*, the stipe is often even and never smooth throughout and the context does not change color where bruised. However, a few species of *Pseudosperma* may feature a bulbous stipe base, such as *I. bulbosissima* and *I. pseudocookei*. *Inocybe* differs from *Pseudosperma* by the presence of pleurocystidia (often as metuloids) or nodulose spores. At least one molecular marker serves to distinguish most species of *Inosperma* from *Pseudosperma*—the possession of a GC-splice site at intron 4 of the *rpb2* gene.

Earle (1909) proposed the new genus *Agmocybe*, typified by *Agaricus rimosus* Bull.: Fr., and equated it with *Clypeus* (Britzelm.) Fayod, non *Clypea* Blume, typified by *Inocybe asterospora*, a species with distinct nodulose or stellate spores. Per Kuyper (1986) *Agmocybe* is illegitimate

and thus rejected at the time under ICBN Art. 63.1 (Voss et al. 1983). According to Donk (1962), *Clypea* Blume is not an earlier homonym for *Clypeus* (Britzelm.) Fayod; thus, Earle’s introduction of *Agmocybe* in lieu of *Clypeus* was superfluous. It is clear from Earle’s description that *Agmocybe* was intended as a genus characterized by species with nodulose or angular spores and a rimose pileus (as in *I. asterospora*), and that Earle’s interpretation of *Agaricus rimosus* differs from that of Kuyper (1986).

Agaricus rimosus is the holotype of *Inocybe* sect. *Rimosae* (Kuyper 1986), which equates with the *Pseudosperma* clade. We propose the new genus name *Pseudosperma* typified by *Inocybe sororia* Kauffman. A revision of *I. sororia* and allies is necessary to resolve the taxonomic status of lineages reported from Europe under *Salix* (Larsson et al. 2009) and from western North America under conifers and eastern North America under hardwoods. Nonetheless, based on rules governing autonyms, *I. sect. Rimosae* becomes equated with *Pseudosperma* sect. *Pseudosperma*. The advantages to select *I. sororia* as type are as follows: the species appears to be common, widespread, has been reported from Europe and North America (Moëgne-Loccoz et al. 1990; Bon 1997; Larsson et al. 2009; Matheny and Kudzma 2019) and is backed by a holotype collection of specimens. By contrast, the concept of *I. rimosus* has been variously interpreted, the holotype consists of an illustration only, the species is highly polyphyletic, and it has not been epitypified (Larsson et al. 2009; Kropp et al. 2013). Indeed, arguments against epitypification of *I. rimosus* and other taxa were presented by Larsson et al. (2009). Moreover, our six-gene region phylogenetic analysis includes a sample of what we currently interpret as *I. sororia* from eastern North American hardwood forests. Other possible candidates for type of *Pseudosperma* include species in the *I. rimosus* complex of Larsson et al. (2009). Of these, *I. umbrinella* Bres. might seem a reasonable choice, but it has not been epitypified and is more distantly related to the clade containing *I. rimosus* in Larsson et al. (2009) compared with *I. sororia*.

Pseudosperma is ectomycorrhizal given the strength of stable isotope analysis of multiple samples (Mayor et al. 2009) and molecular evidence from ECM root tips (Ryberg et al. 2008, 2009). Aside from *Inocybe*, the genus *Pseudosperma* is widespread worldwide, including in the neotropics and palaeotropics, but has yet to be discovered under native vegetation in southern South America.

***Tubariomyces*.**—The genus *Tubariomyces* (type *T. inexpectatus*) has been previously recovered as a monophyletic group (FIG. 2; Alvarado et al. 2010;

Matheny et al. 2012; Vizzini et al. 2013) with varying amounts of support. Our results corroborate these earlier studies and strongly support the monophyly of an undescribed Zambian lineage and the type, *T. inexpectatus* (originally described in *Inocybe*; Villarreal et al. 1998). Four species of *Tubariomyces* form a moderately supported monophyletic group based on phylogenetic analysis of *rpb2* data only (Matheny and Kudzma 2019). Species of *Tubariomyces* can be recognized by the combination of their small omphalinoid or tubarioid basidiomes, entirely pruinose stipe, necropigmented basidia, and trichodermial or subhymeniform-like pileipellis. The presence of a partial veil has only been reported in *T. inexpectatus* (Villarreal et al. 1998). Muscarine is absent from the type species of the genus (Kosentka et al. 2013).

Basidiomes of *Tubariomyces* have been observed in association with Cistaceae and/or *Quercus* in Europe, with Phyllanthaceae and Fabaceae in Zambia, and with Myrtaceae in northern Australia (Matheny et al. 2009; Alvarado et al. 2010; Matheny and Bougher 2017), but molecular confirmation from mycorrhizal roots is lacking (Tedersoo and Smith 2013). *Tubariomyces* is currently known only from southern Europe, sub-Saharan Africa, and northern Australia.

Inclusive taxonomic groups of clades within Inocybaceae.

—The union of *Inocybe*, *Nothocybe*, and *Pseudosperma* as a strongly supported inclusive clade has been observed in several studies (Matheny et al. 2009; Alvarado et al. 2010; Matheny et al. 2012; Latha et al. 2016). Support values for this clade and for the union of *Inocybe* and *Nothocybe* have been generally high, but analyses of our six-gene data set resolve these relationships with 100% ML bootstrap support and 1.0 BPP. Although species of *Inocybe* are easily characterized typically by possession of pleurocystidia and/or nodulose basidiospores, all three genera in this inclusive clade lack species that produce necropigmented basidia. Moreover, the basidia are simple clavate (typically with Q value < 4.0) and thus not slender. In addition, the presence of muscarine, although highly plastic in the Inocybaceae and Agaricales, was found as a shared derived trait in this cluster of three genera (Kosentka et al. 2013).

The union of the remaining four genera—*Auritella*, *Inosperma*, *Mallocybe*, and *Tubariomyces*—was recovered by earlier studies using *rpb1*, *rpb2*, and 28S data with strong (92% ML bootstrap in Alvarado et al. 2010) or at best marginal (58% ML bootstrap in Matheny et al. 2012) support, as was done here despite the addition of three more gene regions (18S, 5.8S, and *tef1*). The varying degree of support for this node may

be due to decisions made regarding exclusion of highly variable nucleotide positions such as the spliceosomal intron regions of *rpb1* and *rpb2*. When these regions are more aggressively included, we have observed higher bootstrap support for the node including *Auritella*, *Inosperma*, *Mallocybe*, and *Tubariomyces* (data not shown). Effects of taxon sampling on the strength of this node have not been explored. Nonetheless, unlike species of *Nothocybe* and *Pseudosperma*, species in this particular clade are characterized mostly by possession of slender necropigmented basidia, with the exception of species of the Maculata clade in *Inosperma*.

Previous studies have not been able to resolve with confidence the relationships among *Auritella*, *Inosperma*, *Mallocybe*, and *Tubariomyces*. Three studies (Alvarado et al. 2010; Matheny et al. 2012; Latha et al. 2016) resolve *Inosperma* as sister to *Auritella* but with weak (<50%) or moderate (65%) ML bootstrap support. Here, for the first time, we recover a grouping of *Auritella*, *Mallocybe*, and *Tubariomyces* with marginal support (68% ML bootstrap, 0.94 BPP) as sister to *Inosperma*. This grouping makes some intuitive sense, as all species of *Auritella*, *Mallocybe*, and *Tubariomyces* are characterized by necropigmented basidia. In any event, it is premature at this time to impose a series of tribes across the Inocybaceae, uniting the various genera, until more robust phylogenetic estimates are obtained.

Family recognition.

—Although progress has been made with respect to designation of suborders within the Agaricales (Dentinger et al. 2016), much work remains to revise families in the order (Vizzini et al. 2019). We have recognized Inocybaceae as a family in its own right for a variety of reasons, including historical precedence (Jülich 1982) and arguments in favor of its unique biology (e.g., ectomycorrhizal ecology, production of unique secondary metabolites) apart from its strongly supported sister group, the Crepidotaceae (Matheny 2005, 2009; Matheny et al. 2006). In addition to these prior works, we found here that all *tef1* sequences of Inocybaceae are characterized by presence of introns 2, 5, and 19 and the absence (loss) of intron 11 (Matheny et al. 2007). The presence of *tef1* intron 11 characterizes numerous lineages of Agaricomycetes but is notably absent from some taxa of Agaricaceae, Bolbitiaceae, Psathyrellaceae, and all Inocybaceae examined to date. As such, the loss of this intron serves as a molecular synapomorphy for the Inocybaceae.

Given the evolutionary plasticity of the ectomycorrhizal symbiosis in the Agaricales (Matheny et al. 2006;

Wolfe et al. 2012; Tedersoo and Smith 2013; Sánchez-García et al. 2016), it is reasonable to reevaluate the degree of weight assigned to an ectomycorrhizal ecological status at the family level. Such a view might then support the merge of Inocybaceae (ECM) and Crepidotaceae (saprotrophs) into a single family. If so, the name Crepidotaceae would have priority (both family names are legitimate names as long as neither competes with Cortinariaceae [Pouzar 1985]). However, we believe that such an evaluation would best be made in a phylogenomic context. For now, we continue to separate and recognize these two families.

ADDITIONAL NEW COMBINATIONS AND NEW NAMES

In many cases below, the newly proposed combinations are based on published phylogenetic evidence or, in some cases, on unpublished or publically released GenBank sequences from type collections. For taxa lacking phylogenetic placement and molecular annotation, we considered morphological attributes from the literature and collection data, including type studies, many of these unpublished, to predict their generic assignment.

Inosperma adaequatum (Britzelm.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830347

Basionym: *Agaricus adaequatus* Britzelm., *Berichte des Naturhistorischen Vereins Augsburg* 27:154. 1883.

Evidence: Phylogenetic (Matheny 2005; Larsson et al. 2009; Matheny et al. 2009; Ryberg et al. 2010; Matheny and Kudzma 2019; epitype sequenced).

Inosperma akirnum (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830348

Basionym: *Inocybe akirna* K.P.D. Latha & Manim., *Inocybes of Kerala* 1:125. 2017.

Evidence: Phylogenetic (Latha and Manimohan 2017; holotype sequenced).

Inosperma apiosmotum (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830349

Basionym: *Inocybe apiosmota* Grund & D.E. Stuntz, *Mycologia* 67:21. 1975.

Evidence: Phylogenetic (Kropp et al. 2013; Pradeep et al. 2016; isotype sequenced).

Inosperma armoricanum (R. Heim) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830350

Basionym: *Inocybe armoricana* R. Heim, *Encyclopédie Mycologique* 1:295. 1931.

Evidence: Morphological (Heim 1931; Bon 1997; Kropp et al. 2013; non sensu Smith and Stuntz 1950). Similar to *Inosperma cookei* but with an even stipe (Kuyper 1986).

Inosperma aureostipes (Kobayasi) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830351

Basionym: *Inocybe aureostipes* Kobayasi, *Nagaoa* 2:95. 1952.

Evidence: Morphological (Kobayasi 1952; Kobayashi 2002). The small narrow spores and almost smooth stipe with bright orange brown coloration support placement in *Inosperma* rather than *Pseudosperma*. Kobayasi also noted a resemblance to *Inocybe jurana*.

Inosperma bicoloratum (E. Horak, Matheny & Desjardin) Matheny & Esteve-Rav., comb. nov.

Mycobank MB831767

Basionym: *Inocybe bicolorata* E. Horak, Matheny & Desjardin, *Phytotaxa* 230:206. 2015.

Evidence: Phylogenetic (Kropp et al. 2013; Horak et al. 2015; Pradeep et al. 2016; holotype sequenced).

Inosperma bongardii (Weinm.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830352

Basionym: *Agaricus bongardii* Weinm., *Hymeno- et Gastero-Mycetes hucusque in imperio Rossico observatos*:190. 1836.

Evidence: Phylogenetic (Larsson et al. 2009; Matheny et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma calamistratoides (E. Horak) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830353

Basionym: *Inocybe calamistratoides* E. Horak, *New Zealand Journal of Botany* 15:716. 1977.

Evidence: Phylogenetic (Matheny 2005; Matheny et al. 2009; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Inosperma carnosibulbosum (C.K. Pradeep & Matheny) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830354

Basionym: *Inocybe carnosibulbosa* C.K. Pradeep & Matheny, *Mycological Progress* 15 (no. 24):16. 2016.

Evidence: Phylogenetic (Pradeep et al. 2016; Latha and Manimohan 2017; isotype sequenced).

Inosperma cervicolor (Pers.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830355

Basionym: *Agaricus cervicolor* Pers., Synopsis methodica fungorum:325. 1801.

Evidence: Phylogenetic (Larsson et al. 2009; Matheny et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma changbaiense (T. Bau & Y.G. Fan) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830356

Basionym: *Inocybe changbaiensis* T. Bau & Y.G. Fan, Mycosystema 37:696. 2018.

Evidence: Phylogenetic (Bau and Fan 2018; holotype sequenced).

Inosperma chlorochroum (Corriol & Guinberteau) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830357

Basionym: *Inocybe chlorochroa* Corriol & Guinberteau, Errotari 10:46. 2013.

Evidence: Morphological (Corriol and Guinberteau 2013; Cervini 2015). Similar to *Inosperma maculatum*.

Inosperma cookei (Bres.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830358

Basionym: *Inocybe cookei* Bres., Fungi Tridentini 2 (8-10):17. 1892.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013).

Inosperma cyanotrichium (Matheny, Bougher & G.M. Gates) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830360

Basionym: *Inocybe cyanotrichia* Matheny, Bougher & G.M. Gates, Fungi of Australia:457. 2017.

Evidence: Phylogenetic (Kropp et al. 2013 as *Inocybe "cyanotincta"*; Matheny and Bougher 2017; isotype sequenced).

Inosperma erubescens (A. Blytt) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830361

Basionym: *Inocybe erubescens* A. Blytt, Skrifter udgivne af Videnskabs-Selskabet i Christiania. Matematisk-Naturvidenskabelig Klasse 6:54. 1905.

Evidence: Phylogenetic (Larsson et al. 2009; Matheny et al. 2009; Ryberg et al. 2010; Kropp et al. 2013).

Inosperma fastigiellum (G.F. Atk.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830362

Basionym: *Inocybe fastigiella* G.F. Atk., American Journal of Botany 5:211. 1918.

Evidence: Phylogenetic (Matheny 2005; Kropp et al. 2013).

Inosperma fulvum (Bon) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830363

Basionym: *Inocybe maculata* f. *fulva* Bon, Documents Mycologiques 21(81):47. 1991.

Evidence: Phylogenetic (Larsson et al. 2009; Kropp et al. 2013 as *Inocybe lanatodisca*).

Inosperma fulvoumbrinum (Bres.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830364

Basionym: *Inocybe fulvoumbrina* Bres. in Sacc., Flora Italica cryptogama 1(14):728. 1916.

Evidence: Morphological (Saccardo 1916; unpublished type study).

Inosperma fuscospinulosum (Corner & E. Horak) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830365

Basionym: *Inocybe fuscospinulosa* Corner & E. Horak, Persoonia 11:11. 1980.

Evidence: Morphological (Horak 1980). Related to *Inosperma cervicolor*.

Inosperma geraniodorum (J. Favre) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830366

Basionym: *Inocybe geraniodora* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:200. 1955.

Evidence: Phylogenetic (Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma geraniodorum* var. *depauperatum (J. Favre) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830367

Basionym: *Inocybe geraniodora* var. *depauperata* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:200. 1955.

Evidence: Morphological (Favre 1955).

Inosperma gregarium (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830368

Basionym: *Inocybe gregaria* K.P.D. Latha & Manim., Phytotaxa 286:110. 2016.

Evidence: Phylogenetic (Matheny et al. 2009, Kropp et al. 2013, Pradeep et al. 2016 as *Inocybe* sp. ZT8944; Latha and Manimohan 2016b, 2017; holotype sequenced).

Inosperma griseolum (Takah. Kobay.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830369

Basionym: *Inocybe griseola* Takah. Kobay., Beihefte zur Nova Hedwigia 124:25. 2002.

Evidence: Morphological (Kobayashi 2002). Allied to *Inosperma cervicolor* and allies.

Inosperma hirsutum (Lasch: Fr.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB831768

Basionym: *Agaricus hirsutus* Lasch: Fr., Index Alphabeticus Generum, Specierum et Synonymorum in Eliae Fries Systemate Mycologico ejusque Supplemento 'Elencho Fungorum' Enumeratorium:23. 1832, non Schaeff. 1774.

Evidence: Phylogenetic (unpublished). *Agaricus hirsutus* Schaeff. is not sanctioned.

Inosperma insignissimum (Romagn.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830370

Basionym: *Inocybe insignissima* Romagn., Beihefte zur Sydowia 8:350. 1979.

Evidence: Morphological (unpublished type study); Ludwig (2017) separates *I. insignissima* from *I. reisneri*.

Inosperma ionides (Corner & E. Horak) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830371

Basionym: *Inocybe ionides* Corner & E. Horak, Persoonia 11:8. 1980.

Evidence: Morphological (Horak 1980). The small phaseoliform spores, smooth stipe with an enlarged base, and the lilac pileus that ages dark brown suggest an alliance with *Inosperma*.

Inosperma kuthanii (Stangl & J. Veselský) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830372

Basionym: *Inocybe kuthanii* Stangl & J. Veselský, Česká Mykologie 33:134. 1979.

Evidence: Morphological (Stangl and J. Veselský 1979; Outen and Cullington 2015; holotype studied).

Inosperma lanatodiscum (Kauffman) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830373

Basionym: *Inocybe lanatodisca* Kauffman, The Agaricaceae of Michigan:459. 1918.

Evidence: Phylogenetic (Matheny 2005; Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma latericum (E. Horak) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830374

Basionym: *Inocybe latericia* E. Horak, New Zealand Journal of Botany 15:716. 1977.

Evidence: Phylogenetic (Ryberg and Matheny 2012; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Inosperma lilofastigiatum (Stangl & J. Veselský) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830375

Basionym: *Inocybe fastigiata* subsp. *lilofastigiata* Stangl & J. Veselský, Česká Mykologie 31:190. 1977.

Evidence: Morphological (Dermek and Veselský 1977; Outen and Cullington 2015; unpublished type study).

Inosperma maculatum (Boud.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830376

Basionym: *Inocybe maculata* Boud., Bulletin de la Société Botanique de France 32:283. 1885.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma maximum (A.H. Sm.) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830378

Basionym: *Inocybe hirsuta* var. *maxima* A.H. Sm., Papers of the Michigan Academy of Sciences, Arts & Letters 24:96. 1938.

Evidence: Phylogenetic (Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma misakaense (Matheny & Watling) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830381

Basionym: *Inocybe misakaensis* Matheny & Watling, Mycotaxon 89:498. 2004.

Evidence: Phylogenetic (Matheny and Watling 2004; Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; holotype sequenced).

Inosperma mucidiolens (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830382

Basionym: *Inocybe calamistrata* var. *mucidiolens* Grund & D.E. Stuntz, Mycologia 62:929. 1970.

Evidence: Phylogenetic (Pradeep et al. 2016; isotype sequenced).

Inosperma mutatum (Peck) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830383

Basionym: *Agaricus mutatus* Peck, Annual Report on the New York State Museum of Natural History 24:69. 1872.

Evidence: Phylogenetic (Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma neobrunnescens (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830384

Basionym: *Inocybe neobrunnescens* Grund & D.E. Stuntz, *Mycologia* 62:934. 1970.

Evidence: Phylogenetic (Kropp et al. 2013; Pradeep et al. 2016).

Inosperma neobrunnescens* var. *leucothelotum (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830385

Basionym: *Inocybe neobrunnescens* var. *leucothelota* Grund & D.E. Stuntz, *Mycologia* 69:395. 1977.

Evidence: Phylogenetic (Matheny et al. 2009 as *Inocybe fastigiella* p.p.; isotype sequenced).

Inosperma pallidifolium (Murrill) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830386

Basionym: *Hebeloma pallidifolium* Murrill, *Quarterly Journal of the Florida Academy of Science* 8:185. 1945.

Evidence: Morphological (unpublished type study).

Inosperma pisciodorum (Donadini & Rioussset) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830387

Basionym: *Inocybe pisciodora* Donadini & Rioussset, *Documents Mycologiques* 5(20):5. 1975.

Evidence: Phylogenetic (Ryberg et al. 2010).

Inosperma proximum (E. Horak, Matheny & Desjardin) Matheny & Esteve-Rav., comb. nov.

Mycobank MB831769

Basionym: *Inocybe proxima* E. Horak, Matheny & Desjardin, *Phytotaxa* 230:212. 2015.

Evidence: Phylogenetic (Matheny et al. 2009; Kropp et al. 2013; Horak et al. 2015; Pradeep et al. 2016; holotype sequenced).

Inosperma quercinum (Hongo) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830388

Basionym: *Inocybe quercina* Hongo, *Transactions of the Mycological Society of Japan* 23:195. 1982.

Evidence: Morphological (Kobayashi 2002). Similar to *Inosperma cervicolor*.

Inosperma quietiodor (Bon) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830389

Basionym: *Inocybe quietiodor* Bon, *Documents Mycologiques* 6(24):46. 1976.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma rhodiolum (Bres.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830390

Basionym: *Inocybe rhodiola* Bres., *Fungi Tridentini* 1 (6–7):80. 1887.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Kudzma 2019).

Inosperma reisneri (Velen.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830391

Basionym: *Inocybe reisneri* Velen., *Ceske Houby* 2:384. 1920.

Evidence: Phylogenetic (Ryberg et al. 2008; Matheny et al. 2009; Kropp et al. 2013; all as *Inocybe* cf. *reisneri*). Treated as an earlier heterotypic synonym of *Inocybe insignissima* (Kuyper 1986) but separated by Ludwig (2017).

Inosperma rimosoides (Peck) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830392

Basionym: *Inocybe rimosoides* Peck, *Bulletin of the New York State Museum* 150:32. 1911.

Evidence: Phylogenetic (Matheny et al. 2009 as *I. aff. cookei*); morphological (unpublished type study).

Inosperma rosellicaulare (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830692

Basionym: *Inocybe rosellicaularis* Grund & D.E. Stuntz, *Mycologia* 75:265. 1983.

Evidence: Morphological (Grund and Stuntz 1983; unpublished type study). Given the smooth appearance overall to the stipe, the preponderance of small phaseoliform spores, and overall similarity with *In. fastigillum*, placement in *Inosperma* is reasonable.

Inosperma rubricosum (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830400

Basionym: *Inocybe rubricosa* Matheny & Bougher, *Fungi of Australia: Inocybaceae*:460. 2017.

Evidence: Phylogenetic (Pradeep et al. 2016; Matheny and Bougher 2017; isotype sequenced).

Inosperma saragum (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830401

Basionym: *Inocybe saraga* K.P.D. Latha & Manim., *Inocybes of Kerala* 1:133. 2017.

Evidence: Phylogenetic (Latha and Manimohan 2017; holotype sequenced).

Inosperma subhirsutum (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830402

Basionym: *Inocybe subhirsuta* Kühner, Documents Mycologiques 19(74):25.

Evidence: Phylogenetic (Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016).

Inosperma subrubescens (G.F. Atk.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830403

Basionym: *Inocybe subrubescens* G.F. Atk., American Journal of Botany 5:216. 1918.

Evidence: Phylogenetic (Kropp et al. 2013).

Inosperma sulcatum (Moënné-Locc., Poirier & Reumaux) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830404

Basionym: *Inocybe sulcata* Moënné-Locc., Poirier & Reumaux, Fungorum Rariorum Icones Coloratae 19:13. 1990.

Evidence: Morphological (Moënné-Loccoz et al. 1990). Similar to *Inosperma pisciodorum*.

Inosperma tenerrimum (G.F. Atk.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830405

Basionym: *Inocybe tenerrima* G.F. Atk., American Journal of Botany 5:216. 1918.

Evidence: Morphological (Atkinson 1918; unpublished type study).

Inosperma umbrinovirens (E. Horak) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830406

Basionym: *Inocybe umbrinovirens* E. Horak, Persoonia 11:9. 1980.

Evidence: Morphological (Horak 1980). Allied with *Inosperma calamistratoides* and *In. calamistratum*.

Inosperma veliferum (Kühner) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830407

Basionym: *Inocybe geraniadora* var. *velifera* Kühner, Documents Mycologiques 19(74):19. 1988.

Evidence: Morphological (Kühner 1988).

Inosperma viridipes (Matheny, Bougher & G.M. Gates) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830408

Basionym: *Inocybe viridipes* Matheny, Bougher & G.M. Gates, Fungi of Australia: Inocybaceae:463. 2017.

Evidence: Phylogenetic (Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; isotype sequenced).

Inosperma virosum (C.K. Pradeep, K.B. Vrinda & Matheny) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830409

Basionym: *Inocybe virosa* C.K. Pradeep, K.B. Vrinda & Matheny, Mycological Progress 15:22. 2016.

Evidence: Phylogenetic (Pradeep et al. 2016; paratype sequenced).

Mallocybe abruptibulbosa (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830410

Basionym: *Inocybe abruptibulbosa* E. Ludw., Pilzkompendium 4:162. 2017.

Evidence: Morphological (Ludwig 2017).

Mallocybe acystidiata (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830411

Basionym: *Inocybe acystidiata* E. Ludw., Pilzkompendium 4:151. 2017.

Evidence: Morphological (Ludwig 2017). Treated in *I.* subg. *Mallocybe*.

Mallocybe agardhii (N. Lund) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830412

Basionym: *Agaricus agardhii* N. Lund, Conspectus Hymenomycetum circa Holmian crescentium:40. 1846.

Evidence: Phylogenetic (Matheny 2005; Larsson et al. 2009; Matheny et al. 2009; Ryberg et al. 2010; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe althoffiae (E. Horak) Matheny & Esteve-Rav., comb. nov.

MycoBank MB831770

Basionym: *Inocybe althoffiae* E. Horak, Persoonia 11:5. 1980.

Evidence: Morphological (Horak 1980). Attempts to sequence the type resulted in contamination (Matheny et al. 2009 = *Pseudosperma sororium*) and a likely chimeric sequence (unpublished but released sequence data). Horak allied the species to *Inocybe* sect. *Dulcamarae*.

Mallocybe arenaria (Bon) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830413

Basionym: *Inocybe agardhii* var. *arenaria* Bon, Documents Mycologiques 13(50):28. 1983.

Evidence: Phylogenetic (Ryberg et al. 2010 as *Inocybe agardhii* var. *arenaria*).

Mallocybe arthrocytis (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830414

Basionym: *Inocybe arthrocytis* Kühner, Documents Mycologiques 19(74):17. 1988.

Evidence: Phylogenetic (Matheny 2005 as *Inocybe* sp. PBM 2397; Cripps et al. 2010; Ryberg et al. 2010; Vauras and Larsson 2012).

Mallocybe attenuatipes (E. Ludw.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830415

Basionym: *Inocybe attenuatipes* E. Ludw., Pilzkompendium 4:169. 2017.

Evidence: Morphological (Ludwig 2017). Treated in *I.* subg. *Mallocybe*.

Mallocybe coloradoensis (Tracy & Earle) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830416

Basionym: *Naucoria coloradoensis* Tracy & Earle, Plantae Bakerianae 1:25. 1901.

Evidence: Morphological (Kaufmann 1924). Similar to *Mallocybe unicolor*.

Mallocybe cotoneovelata (E. Ludgw.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830417

Basionym: *Inocybe cotoneovelata* E. Ludw., Pilzkompendium 4:143. 2017.

Evidence: Morphological (Ludwig 2017). Treated in *I.* subg. *Mallocybe*.

Mallocybe delecta (P. Karst.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830418

Basionym: *Inocybe delecta* P. Karst., Bidrag till Kännedom av Finlans Natur och Folk 32:460. 1879.

Evidence: Morphological (Karsten 1879; Singer 1986; unpublished type study).

Mallocybe fibrillosa (Peck) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830790

Basionym: *Inocybe fibrillosa* Peck, Annual Report of the New York State Museum of Natural History 41:65. 1888.

Evidence: Phylogenetic (Matheny et al. 2009 as *Inocybe "osmodes"*; Cripps et al. 2010 as *Inocybe dulcamara* (Alb. & Schwein.) P. Kummer.

Mallocybe fulviceps (Murrill) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830421

Basionym: *Inocybe fulviceps* Murrill, Quarterly Journal of the Florida Academy of Science 8:187. 1945.

Evidence: Morphological (unpublished type study).

Mallocybe fulvipes (Kühner) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830422

Basionym: *Inocybe fulvipes* Kühner, Documents Mycologiques 19(74):18. 1988.

Evidence: Phylogenetic (Larsson et al. 2009; Cripps et al. 2010; Ryberg et al. 2010; Ariyawansa et al. 2015).

Mallocybe fulvoumbonata (Murrill) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830423

Basionym: *Inocybe fulvombonata* Murrill [as "*fulvi-umbonata*"], Quarterly Journal of the Florida Academy of Science 8:187. 1945.

Evidence: Morphological (unpublished type study).

Mallocybe fuscomarginata (Kühner) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830435

Basionym: *Inocybe fuscomarginata* Kühner, Bulletin de la Société Mycologique de France 71:169. 1956 [1955].

Evidence: Phylogenetic (Cripps et al. 2010; Ryberg et al. 2010; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe granulosa (Jacobsson & E. Larss.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830436

Basionym: *Inocybe granulosa* Jacobsson & E. Larss., Fungal Diversity 75:201. 2015.

Evidence: Phylogenetic (Ariyawansa et al. 2015; holotype sequenced).

Mallocybe gymnocarpa (Kühner) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830437

Basionym: *Inocybe gymnocarpa* Kühner, Bulletin de la Société Mycologique de France 71:169. 1956 [1955].

Evidence: Phylogenetic (Ryberg et al. 2010; Vauras and Larsson 2012).

Mallocybe hebelomoides Matheny & Esteve-Rav., nom. nov.
MycoBank MB830438

Basionym: *Inocybe hebelomoides* Kühner, Documents Mycologiques 19(74):20. 1988 (Nom. illegit., ICN Art. 53.1).

Evidence: Morphological (Kühner 1988; unpublished type study).

Mallocybe heimii (Bon) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830439

Basionym: *Inocybe heimii* Bon, Documents Mycologiques 14(56):11. 1984.

Evidence: Phylogenetic (Matheny 2005; Matheny et al. 2009).

Mallocybe homomorpha (Kühner) Matheny & Esteve-Rav., stat. et comb. nov.

MycoBank MB830420

Basionym: *Inocybe dulcamara* var. *homomorpha* Kühner, Bulletin de la Société Mycologique de France 71:169. 1956 [1955].

Evidence: Morphological (Kühner 1955).

Mallocybe isabellina (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830440

Basionym: *Inocybe isabellina* Matheny & Bougher, Fungi of Australia: Inocybaceae:467. 2017.

Evidence: Phylogenetic (Matheny 2005 and Matheny et al. 2009 as *Inocybe "jarrahae"*; Matheny and Bougher 2017; holotype sequenced).

Mallocybe lagenicystidiata (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830441

Basionym: *Inocybe lagenicystidiata* E. Ludw., Pilzkompodium 4:158. 2017.

Evidence: Morphological (Ludwig 2017). Treated in *I.* subg. *Mallocybe*.

Mallocybe latifolia (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830442

Basionym: *Inocybe latifolia* E. Ludw., Pilzkompodium 4:153. 2017.

Evidence: Morphological (Ludwig 2017).

Mallocybe latispora (Bon) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830443

Basionym: *Inocybe dulcamara* var. *latispora* Bon, Beihefte zur Sydowia 8:76. 1979.

Evidence: Phylogenetic (Ryberg et al. 2010; Ariyawansa et al. 2015).

Mallocybe leucoblema (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830444

Basionym: *Inocybe leucoblema* Kühner, Bulletin de la Société Mycologique de France 71:169. 1956 [1955].

Evidence: Phylogenetic (Matheny et al. 2009; Cripps et al. 2010; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe leucoloma (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830445

Basionym: *Inocybe leucoloma* Kühner, Documents Mycologiques 19(74):22. 1988.

Evidence: Phylogenetic (Cripps et al. 2010; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe malenconii (R. Heim) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830446

Basionym: *Inocybe malenconii* R. Heim, Encyclopédie Mycologique 1:163. 1931.

Evidence: Phylogenetic (Matheny et al. 2009; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe megalospora (Stangl & Bresinsky) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830447

Basionym: *Inocybe malenconii* var. *megalospora* Stangl & Bresinsky, Hoppea Denkschrift der Regensburgischen Naturforschenden Gesellschaft 41:411. 1983.

Evidence: Morphological (Stangl & Bresinsky 1983; unpublished type study).

Mallocybe multispora (Murrill) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830448

Basionym: *Inocybe multispora* Murrill, Proceedings of the Florida Academy of Sciences 7:122. 1945.

Evidence: Morphological (unpublished type study).

Mallocybe myriadophylla (Vauras & E. Larss.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830449

Basionym: *Inocybe myriadophylla* Vauras & E. Larss., Karstenia 51:32. 2012.

Evidence: Phylogenetic (Matheny et al. 2009; Vauras and Larsson 2012; Ariyawansa et al. 2015).

Mallocybe pallidotomentosa (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830455

Basionym: *Inocybe pallidotomentosa* E. Ludw., Pilzkompodium 4:154. 2017.

Evidence: Morphological (Ludwig 2017).

Mallocybe paludosa (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830456

Basionym: *Inocybe paludosa* Kühner, Documents Mycologiques 19(74):23. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Mallocybe parcesquamulosa (J. Favre) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830457

Basionym: *Inocybe dulcamara* f. *parcesquamulosa* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:75. 1955.

Evidence: Morphological (Favre 1955).

Mallocybe pelargoniodora (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830458

Basionym: *Inocybe pelargoniodora* Kühner, Documents Mycologiques 19(74):23. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Mallocybe perbrevis (Weinm.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830459

Basionym: *Agaricus perbrevis* Weinm., Gallicum:185. 1836.

Evidence: Morphological (Heim 1931; Stangl 1989). Weinmann's original description is inconclusive, but Heim and Stangl refer clearly to *Mallocybe*.

Mallocybe peronata (J. Favre) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830460

Basionym: *Inocybe dulcamara* f. *peronata* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:200. 1955.

Evidence: Morphological (Favre 1955).

Mallocybe pseudodulcamara (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830462

Basionym: *Inocybe pseudodulcamara* E. Ludw., Pilzkompendium 4:159. 2017.

Evidence: Morphological (Ludwig 2017). Treated in *I.* subg. *Mallocybe*.

Mallocybe pygmaea (J. Favre) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830463

Basionym: *Inocybe dulcamara* f. *pygmaea* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:200. 1955.

Evidence: Phylogenetic (Cripps et al. 2010; Ariyawansa et al. 2015; holotype sequenced).

Mallocybe pyrrhopoda (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830464

Basionym: *Inocybe pyrrhopoda* Matheny & Bougher, Fungi of Australia: Inocybaceae:471. 2017.

Evidence: Phylogenetic (Matheny and Bougher 2017; holotype sequenced).

Mallocybe sabulosa (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830465

Basionym: *Inocybe sabulosa* Matheny & Bougher, Fungi of Australia: Inocybaceae:474. 2017.

Evidence: Phylogenetic (Matheny and Bougher 2017; holotype sequenced).

Mallocybe solidipes (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830466

Basionym: *Inocybe solidipes* Kühner, Documents Mycologiques 19(74):24. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Mallocybe squamosoannulata (J. Favre) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830467

Basionym: *Inocybe dulcamara* f. *squamosoannulata* J. Favre, Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 5:200. 1955.

Evidence: Morphological (Favre 1955).

Mallocybe squarrosoannulata (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830468

Basionym: *Inocybe squarrosoannulata* Kühner, Documents Mycologiques 19(74):24. 1988.

Evidence: Phylogenetic (Cripps et al. 2010; Ariyawansa et al. 2015; holotype sequenced).

Mallocybe subannulata (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830469

Basionym: *Inocybe subannulata* Kühner, Documents Mycologiques 19(74):25. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Mallocybe subdecurrens (Ellis & Everh.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830470

Basionym: *Inocybe subdecurrens* Ellis & Everh., Journal of Mycology 5:26. 1889.

Evidence: Morphological (unpublished type study).

Mallocybe subflavospora (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830472

Basionym: *Inocybe subflavospora* Matheny & Bougher, Fungi of Australia: Inocybaceae:477. 2017.

Evidence: Phylogenetic (Matheny et al. 2009; Matheny and Bougher 2017; isotype sequenced).

Mallocybe substraminipes (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830473

Basionym: *Inocybe substraminipes* Kühner, Documents Mycologiques 19(74):26. 1988.

Evidence: Phylogenetic (Cripps et al. 2010; Ariyawansa et al. 2015; holotype sequenced).

Mallocybe subtilior (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830474

Basionym: *Inocybe subtilior* Matheny & Bougher, Fungi of Australia: Inocybaceae:481. 2017.

Evidence: Phylogenetic (Matheny et al. 2009 as *Inocybe "subtilisior"*; Matheny and Bougher 2017; isotype sequenced).

Mallocybe tomentosula Matheny & Esteve-Rav., nom. nov.
MycoBank MB830475

Basionym: *Inocybe tomentosa* Ellis & Everh., Journal of Mycology 5:26. 1889 (non *Inocybe tomentosa* Quél. 1888).

Evidence: Morphological (unpublished type study).

Mallocybe umbrinofusca (Kühner) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830476

Basionym: *Inocybe umbrinofusca* Kühner, Documents Mycologiques 19(74):26. 1988.

Evidence: Phylogenetic (Cripps et al. 2010; holotype sequenced).

Mallocybe unicolor (Peck) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830477

Basionym: *Inocybe unicolor* Peck, Annual Report on the New York State Museum of Natural History 50:104. 1897.

Evidence: Phylogenetic (Matheny 2005; Matheny et al. 2009).

Mallocybe velicoronata (E. Ludw. & M. Huth) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830478

Basionym: *Inocybe velicoronata* E. Ludw. & M. Huth, Pilzkompendium 4:143. 2017.

Evidence: Morphological (Ludwig 2017).

Pseudosperma aestivum (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830479

Basionym: *Inocybe aestiva* Kropp, Matheny & Hutchison, Mycologia 105:732. 2013.

Evidence: Phylogenetic (Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma araneosum (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830479

Basionym: *Inocybe araneosa* Matheny & Bougher, Fungi of Australia: Inocybaceae:481. 2017.

Evidence: Phylogenetic (Pradeep et al. 2016; Matheny and Bougher 2017; isotype sequenced).

Pseudosperma arenicola (R. Heim) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830481

Basionym: *Inocybe fastigiata* f. *arenicola* R. Heim, Encyclopédie Mycologique 1:178. 1931.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma arenicola* var. *mediterraneum (Kuyper) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830482

Basionym: *Inocybe arenicola* var. *mediterranea* Kuyper, Persoonia 3(Suppl.):57. 1986.

Evidence: Phylogenetic (Kropp et al. 2013).

Pseudosperma aureocitrinum (Esteve-Rav.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830483

Basionym: *Inocybe aureocitrina* Esteve-Rav., Plant Biosystems 148(1-2):378. 2014.

Evidence: Phylogenetic (unpublished type sequence); morphological (Esteve-Raventós 2014).

Pseudosperma aurora (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830484

Basionym: *Inocybe aurora* Grund & D.E. Stuntz, Mycologia 67:24. 1975.

Evidence: Phylogenetic (Kropp et al. 2013 as *Inocybe obsoleta*; Pradeep et al. 2016; Matheny and Bougher 2017; isotype sequenced).

Pseudosperma aurora* var. *inodoratum (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830485

Basionym: *Inocybe aurora* var. *inodorata* Grund & D.E. Stuntz, Mycologia 75:257. 1983.

Evidence: Phylogenetic (unpublished but released sequence data).

Pseudosperma avellaneum (Kobayasi) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830486

Basionym: *Inocybe avellanea* Kobayasi, Nagaoa 2:94. 1952.

Evidence: Morphological (Koybayashi 2002). The elliptic to broadly elliptic spores and more or less even stipe support placement in *Pseudosperma*.

Pseudosperma bisporum (Hongo) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830487

Basionym: *Inocybe bispora* Hongo, Journal of Japanese Botany 33:349. 1958.

Evidence: Morphological (Kobayashi 2002). The elliptic to broadly elliptic spores, broad basida, and even fibrillose stipe support placement in *Pseudosperma*.

Pseudosperma brevierincarnatum (D.E. Stuntz ex Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830488

Basionym: *Inocybe brevierincarnata* D.E. Stuntz ex Kropp, Matheny & Hutchison, Mycologia 105:734. 2013.

Evidence: Phylogenetic (Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma brunneosquamulosum (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830489

Basionym: *Inocybe brunneosquamulosa* K.P.D. Latha. & Manim., Fungal Diversity 83:167. 2017.

Evidence: Phylogenetic (Tibpromma et al. 2016; Latha and Manimohan 2017; holotype sequenced).

Pseudosperma bulbosissimum (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830490

Basionym: *Inocybe rimosa* var. *bulbosissima* Kühner, Documents Mycologiques 19(74):24. 1988.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; Matheny and Kudzma 2019).

Pseudosperma cerinum (Malençon) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830496

Basionym: *Inocybe fastigiata* var. *cerina* Malençon, Flore des champignons supérieurs du Maroc 1:359. 1970.

Evidence: Morphological (Malençon and Bertault 1970; Bon 1997; unpublished type study).

Pseudosperma cercocarpi (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830497

Basionym: *Inocybe cercocarpi* Kropp, Matheny & Hutchison, Mycologia 105:736. 2013.

Evidence: Phylogenetic (Matheny et al. 2009 as *Inocybe* sp. BK20069806; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma copriniforme (Reumaux) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830498

Basionym: *Inocybe copriniformis* Reumaux, Bulletin de la Société Mycologique de France 120(1–4):111. 2005 [2004].

Evidence: Morphological (Reumaux 2004).

Pseudosperma curreyi (Berk.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830499

Basionym: *Agaricus curreyi* Berk., Outlines of British Fungology:155. 1860.

Evidence: Morphological (Heim 1931; non sensu Helsen in Kropp et al. 2013 and Pradeep et al. 2016).

Pseudosperma dulcamaroides (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830501

Basionym: *Inocybe dulcamaroides* Kühner, Documents Mycologiques 19(74):18. 1988.

Evidence: Phylogenetic (Larsson et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma fissuratum (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830502

Basionym: *Inocybe fissurata* Matheny & Bougher, Fungi of Australia: Inocybaceae:440. 2017.

Evidence: Phylogenetic (Matheny et al. 2009 as *Inocybe* cf. *renispora*; Kropp et al. 2013 as *Inocybe* aff. *renispora*; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma flavellum (P. Karst.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830503

Basionym: *Inocybe flavella* P. Karst., Meddelanden af Societas pro Fauna et Flora Fennica 16:100. 1890.

Evidence: Phylogenetic (Jacobsson and Larsson 2009; Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma flavellum* var. *roseipes (Bon) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830504

Basionym: *Inocybe xanthophylla* f. *roseipes* Bon, Documents Mycologiques 12(48):44. 1983.

Evidence: Morphological (Bon 1983, 1997).

Pseudosperma fusipes (Bizio, Franchi & M. Marchetti) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830505

Basionym: *Inocybe fusipes* Bizio, Franchi & M. Marchetti, Rivista de Micologia 49:13. 2006.

Evidence: Morphological (Bizio et al. 2006; unpublished type study).

Pseudosperma godfrinioides (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830506

Basionym: *Inocybe godfrinioides* Kühner, Documents Mycologiques 19(74):19. 1988.

Evidence: Phylogenetic (Osmundson et al. 2013); morphological (Kühner 1988; Jamoni 2008; unpublished type study).

Pseudosperma gracilissimum (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830507

Basionym: *Inocybe gracilissima* Matheny & Bougher, Fungi of Australia: Inocybaceae:445. 2017.

Evidence: Phylogenetic (Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma griseorubidum (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830508

Basionym: *Inocybe griseorubida* K.P.D. Latha & Manim., Phytotaxa 221:169. 2015.

Evidence: Latha and Manimohan (2015, 2017).

Pseudosperma guttuliferum (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830509

Basionym: *Inocybe guttulifera* (as “*guttulifer*”) Kühner, Documents Mycologiques 19(74):19. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Pseudosperma himalayense (Razaq, Khalid & Kobayashi) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830510

Basionym: *Inocybe himalayensis* Razaq, Khalid & Kobayashi, Sydowia 70:238. 2018.

Evidence: Phylogenetic (Liu et al. 2018); holotype sequenced.

Pseudosperma holoxanthum (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830511

Basionym: *Inocybe holoxantha* Grund & D.E. Stuntz, Mycologia 73:667. 1981.

Evidence: Phylogenetic (unpublished but released sequence data; paratype sequenced).

Pseudosperma hygrophorus (Kühner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830512

Basionym: *Inocybe hygrophorus* Kühner, Bulletin de la Société Mycologique de France 71:169. 1956 [1955].

Evidence: Phylogenetic (Jacobsson and Larsson 2009; Larsson et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma illudens (Matheny, Bougher & G.M. Gates) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830513

Basionym: *Inocybe illudens* Matheny, Bougher & G. M. Gates, Fungi of Australia: Inocybaceae:449. 2017.

Evidence: Phylogenetic (Kropp et al. 2013 as *Inocybe renispora*; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma ingae (Pegler) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830514

Basionym: *Inocybe ingae* Pegler, Kew Bulletin Additional Series 9:531. 1983.

Evidence: Morphological (Pegler 1983). The fragile context with no odor, rimose pileus, and slender even stipe with a pruinose apex support placement in *Pseudosperma*. However, the spores are narrow and phaseoliform to elongate-elliptic, a feature similar to some species of *Inosperma*.

Pseudosperma keralense (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830515

Basionym: *Inocybe keralensis* K.P.D. Latha & Manim., Mycologia 108:116. 2016.

Evidence: Phylogenetic (Latha and Manimohan 2016a, 2017; Pradeep et al. 2016 and Matheny and Bougher as *Inocybe rimulosa*; both holotypes sequenced).

Pseudosperma lepidotellum (Matheny & Aime) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830516

Basionym: *Inocybe lepidotella* Matheny & Aime, Kurtziana 37:31. 2012.

Evidence: Phylogenetic (Matheny et al. 2012; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma littorale (Pegler) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830517

Basionym: *Inocybe littoralis* Pegler, Kew Bulletin Additional Series 9:531. 1983.

Evidence: Morphological (Pegler 1983). The even stipe with a pruinose apex, somewhat broad elliptic to subreniform spores, and absence of an odor support an affiliation with *Pseudosperma*.

Pseudosperma lobatum (R. Heim) Matheny & Esteve-Rav., comb. et stat. nov.

MycoBank MB830518

Basionym: *Inocybe fastigiata* var. *lobata* R. Heim, Encyclopédie Mycologique 1:189. 1931.

Evidence: Morphological (Heim 1931).

Pseudosperma luteobrunneum (K.P.D. Latha & Manim.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830519

Basionym: *Inocybe luteobrunnea* K.P.D. Latha & Manim., Fungal Diversity 83:172. 2017.

Evidence: Phylogenetic (Latha and Manimohan 2017; Tibpromma et al. 2017; holotype sequenced).

Pseudosperma macrospermum (Hongo) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830520

Basionym: *Inocybe macrosperma* Hongo, Journal of Japanese Botany 34:243. 1959.

Evidence: Morphological (Kobayashi 2002). The pruinose stipe apex, indistinct odor, and large oblong spores point best to an alliance with *Pseudosperma*. However, the stipe base is described as abruptly bulbous, and the species is allied with those of *Inosperma* by Kobayashi because of this latter feature.

Pseudosperma maleolens (Carteret & Reumaux) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830521

Basionym: *Inocybe maleolens* Carteret & Reumaux, Bulletin de la Societ  Mycologique de France 131(1–2):32. 2017.

Evidence: Morphological (Carteret and Reumaux 2017).

Pseudosperma melliolens (K hner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830522

Basionym: *Inocybe melliolens* K hner, Documents Mycologiques 19(74):22. 1988.

Evidence: Morphological (K hner 1988; unpublished type study).

Pseudosperma microfastigiatum (K hner) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830523

Basionym: *Inocybe microfastigiata* K hner, Documents Mycologiques 19(74):22. 1988.

Evidence: Morphological (K hner 1988; unpublished type study).

Pseudosperma mimicum (Massee) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830524

Basionym: *Inocybe mimica* Massee, Annals of Botany 18:492. 1904.

Evidence: Phylogenetic (Larsson et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma nanum (F.H. M ll.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830525

Basionym: *Inocybe nana* F.H. M ll., Fungi of the Faeroes 1:224. 1945.

Evidence: Morphological (M ller 1945; Kuyper 1986).

Pseudosperma neoumbrinellum (T. Bau & Y.G. Fan) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830526

Basionym: *Inocybe neoumbrinella* T. Bau & Y.G. Fan, Mycosystema 37:697. 2018.

Evidence: Phylogenetic (Bau and Fan 2018; holotype sequenced).

Pseudosperma niveivelatum (D.E. Stuntz ex Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830527

Basionym: *Inocybe niveivelata* D.E. Stuntz ex Kropp, Matheny & Hutchison, Mycologia 105:739. 2013.

Evidence: Phylogenetic (Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma notodryinum (Singer, I.J. Araujo & Ivory) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830528

Basionym: *Inocybe notodryina* Singer, I.J. Araujo & Ivory, Beihefte zur Nova Hedwigia 77:175. 1983.

Evidence: Phylogenetic (Kropp et al. 2013 as *Inocybe* aff. *perlata*; unpublished but released sequence data; holotype sequenced).

Pseudosperma obsoletum (Romagn.) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830555

Basionym: *Inocybe obsoleta* Romagn., Bulletin trimestriel Societ  mycologique de France:145. 1958.

Evidence: Phylogenetic (Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma occidentale (Kropp, Matheny & Hutchison) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830556

Basionym: *Inocybe occidentalis* Kropp, Matheny & Hutchison, Mycologia 105:742. 2013.

Evidence: Phylogenetic (Matheny et al. 2002 as *Inocybe* “*maculata*”; Matheny 2005 and Matheny et al. 2009 as *Inocybe* sp. PBM525; Jacobson and Larsson 2009 as *Inocybe* sp.; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma orbatum (Malen on) Matheny & Esteve-Rav., comb. nov.

MycoBank MB830557

Basionym: *Inocybe orbata* Malençon, Flore des champignons supérieurs du Maroc 1:386. 1970.

Evidence: Morphological (Malençon and Bertault 1970; unpublished type study).

Pseudosperma palaeotropicum (E. Turnbull & Watling) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830558

Basionym: *Inocybe palaeotropica* E. Turnbull & Watling, Edinburgh Journal of Botany 52:357. 1995.

Evidence: Morphological (Horak 1980; Turnbull 1995). The scurfy-fibrillose even stipe without a bulbous base and the ovate to subelliptic spores support an alliance with *Pseudosperma*.

Pseudosperma perlatum (Cooke) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830559

Basionym: *Agaricus perlatus* Cooke, Grevillea 15:40. 1886.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma pakistanense (Z. Ullah, S. Jabeen, H. Ahmad & A.N. Khalid) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830560

Basionym: *Inocybe pakistanensis* Z. Ullah, S. Jabeen, H. Ahmad & A.N. Khalid, Phytotaxa 348:282. 2018.

Evidence: Phylogenetic (Ullah et al. 2018; holotype sequenced).

Pseudosperma permelliolens (Carteret & Reumaux) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830674

Basionym: *Inocybe permelliolens* Carteret & Reumaux, Bulletin de la Société Mycologique de France 131(1–2):20. 2017.

Evidence: Morphological (Carteret and Reumaux 2017).

Pseudosperma pluviorum (Matheny & Bougher) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830675

Basionym: *Inocybe pluviorum* Matheny & Bougher, Fungi of Australia: Inocybaceae:451. 2017.

Evidence: Phylogenetic (Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma pseudocookei (Métrod ex Bon) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830676

Basionym: *Inocybe pseudocookei* Métrod ex Bon, Documents Mycologiques 26(102):20. 1996.

Evidence: Morphological (Métrod 1953).

Pseudosperma pseudo-orbatum (Esteve-Rav. & García Blanco) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830677

Basionym: *Inocybe pseudo-orbata* Esteve-Rav. & García Blanco, Österreichische Zeitschrift für Pilzkunde 12:94. 2003.

Evidence: Phylogenetic (unpublished type sequence); morphological (Esteve-Raventós et al. 2003).

Pseudosperma pseudoumbrinellum (E. Ludw.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830678

Basionym: *Inocybe pseudoumbrinella* E. Ludw., Pilzkompodium 4:208. 2017.

Evidence: Morphological (Ludwig 2017; unpublished type study).

Pseudosperma pusillum Matheny & Esteve-Rav., nom. nov.

Mycobank MB830679

Basionym: *Inocybe pusilla* F.H. Möller, Fungi of the Faeroes 1:225. 1945.

Evidence: Morphological (Möller 1945; Kuyper 1986). Not to be confused with *Inocybe putilla* Bres., a nodulose-spored species.

Pseudosperma renisporum (E. Horak) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830691

Basionym: *Inocybe renispora* E. Horak, New Zealand Journal of Botany 15:715. 1977.

Evidence: Morphological (Horak 1977, 2018). The pruinose to fibrillose stipe and absence of an odor suggest an affiliation with *Pseudosperma*. Horak (1977) also noted an alliance with *I. fastigiata*. The spores, however, are described as reniform, a feature often characteristic of *Inosperma*.

Pseudosperma rimosum (Bull.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830693

Basionym: *Agaricus rimosus* Bull., Herbar de la France 9:t.388. 1789.

Evidence: Phylogenetic (Larsson et al. 2009; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; Matheny and Kudzma 2019).

Pseudosperma spurium (Jacobsson & E. Larss.) Matheny & Esteve-Rav., comb. nov.

Mycobank MB830694

Basionym: *Inocybe spuria* Jacobsson & E. Larss., Mycotaxon 109:204. 2009.

Evidence: Phylogenetic (Jacobsson and Larsson 2009; Larsson et al. 2009 as *Inocybe* sp.; Matheny et al. 2009

as *Inocybe squamata*; Ryberg et al. 2010; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017; holotype sequenced).

Pseudosperma squamatum (J.E. Lange.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830695

Basionym: *Inocybe squamata* J.E. Lange, Dansk botanisk Arkiv 2:39. 1917.

Evidence: Phylogenetic (Jacobsson and Larsson 2009; Larsson et al. 2009; non Matheny et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma subfuscum (Kühner) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830696

Basionym: *Inocybe subfusca* Kühner, Documents Mycologiques 19(74):25. 1988.

Evidence: Morphological (Kühner 1988; unpublished type study).

Pseudosperma transiens (Takah. Kobay.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830698

Basionym: *Inocybe transiens* Takah. Kobay., Beihefte zur Nova Hedwigia 124:20. 2002.

Evidence: Morphological (Kobayashi 2002). Similar to *Inocybe fastigiata* and *Pseudosperma flavellum*.

Pseudosperma tropicale (Guzmán) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830699

Basionym: *Inocybe tropicalis* Guzmán, Mycotaxon 16:258. 1982.

Evidence: Morphological (Guzmán 1982). The rimose pileus, even stipe, absence of an odor, non-reddening flesh, and elliptic spores best support an alliance with *Pseudosperma*. The stipe is described as whitish to yellowish and finally brownish red, a feature more in common with some species of *Inosperma*.

Pseudosperma umbrinellum (Bres.) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830700

Basionym: *Inocybe umbrinella* Bres. Annales Mycologici 3:161. 1905.

Evidence: Phylogenetic (Larsson et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma validius (Alessio) Matheny & Esteve-Rav., comb. et stat. nov.
MycoBank MB830701

Basionym: *Inocybe fastigiata* var. *validior* Alessio, Bolletino Gruppo Micologico G. Bresadola 27(1–2):31. 1984.

Evidence: Morphological (Alessio 1984; unpublished type study).

Pseudosperma vinosistipitatum (Grund & D.E. Stuntz) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830705

Basionym: *Inocybe vinosistipitata* Grund & D.E. Stuntz, Mycologia 75:269. 1983.

Evidence: Phylogenetic (unpublished but released sequence data; holotype sequenced).

Pseudosperma xanthocephalum (P.D. Orton) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830706

Basionym: *Inocybe xanthocephala* P.D. Orton, Transactions of the British Mycological Society 43:277. 1960.

Evidence: Phylogenetic (Jacobsson and Larsson 2009; Larsson et al. 2009; Kropp et al. 2013; Pradeep et al. 2016; Matheny and Bougher 2017).

Pseudosperma yunnanense (T. Bau & Y.G. Fan) Matheny & Esteve-Rav., comb. nov.
MycoBank MB830708

Basionym: *Inocybe yunnanensis* T. Bau & Y.G. Fan, Mycosystema 37:699. 2018.

Evidence: Phylogenetic (Bau and Fan 2018; holotype sequenced).

TAXA AWAITING VALIDATION

Inocybe nespiaki Bon, Documents Mycologiques 26-(102):20. 1996 (Nom. inval., ICN Art. 40.6).

Bon (1996) published this replacement name for *Inocybe favrei* Nespiak (1990), non *I. favrei* Bon (Bon 1985). Nespiak (1990) cites “*Inocybe dulcamara* fo. aff. *malenconii* Favre” as the basionym, but this designation in Favre (1955) lacks a Latin diagnosis and type. Thus, *Inocybe favrei* Nespiak is not only illegitimate but also invalid. *Inocybe nespiaki* can be validated if provided with a diagnosis or description, registration number, and a type designation. Placement should be in *Mallochybe*.

Inocybe laeta Alessio, Economia Trentina Supplement 1:98. 1979 (Nom. inval., ICN Art. 40.1).

A type was never indicated. The name can be validated if provided with a diagnosis or description, registration number, and type designation. Placement should be in *Pseudosperma*.

TAXA OF UNCERTAIN POSITION

Inocybe cutifracta Petch, Annals of the Royal Botanic Gardens Peradeniya 6:201. 1917.

Evidence: An examination of the holotype by Horak (1980) suggested an alliance with *Pseudosperma* and an

early misinterpretation of the name. Pegler (1986) later misapplied the name per Latha et al. (2016). Buyck and Eyssartier (1999) reported *I. cutifracta* as consumed for food in tropical parts of Asia but cited no specimen vouchers. Because the type is in such poor condition, an epitype backed by molecular annotation is needed to stabilize application of the name.

Inocybe dulcamara (Pers.) P. Kumm. Der Führer in die Pilzkunde:79. 1871.

Basionym: *Agaricus dulcamarus* Pers., Synopsis methodica fungorum:324. 1801, non *Agaricus dulcamarus* Alb. & Schwein. 1822.

Evidence: The concept of this species needs to be reconciled with the original description and name by Persoon, non Alb. & Schwein, the latter illegitimate. As such, Persoon's species is questionably a *Mallocybe* as widely interpreted but not in the sense of the original author.

Inocybe praevillosa (Murrill) Murrill, Mycologia 36:122. 1944.

Evidence: We have not studied the type, but unpublished notes of this species by D. E. Stuntz and L. R. Hesler differ somewhat in their documentation of the cheilocystidia. Neither documented the presence of necropigmented basidia.

ACKNOWLEDGMENTS

We thank Rachel Swenie and En-Jing Tian for laboratory assistance, and Joe May for his assistance with sequencing at the University of Tennessee (UT) Genomics Core. We acknowledge Marisol Sánchez-García for providing species number estimates from Index Fungorum. We thank Cathie Aime, Matt Barrett, Neale Bougher, Bart Buyck, Dennis Desjardin, Genevieve Gates, Roy Halling, Terry Henkel, Egon Horak, Brad Kropp, Ellen Larsson, Pierre-Arthur Moreau, Clark Ovrebo, C.K. Pradeep, David Ratkowsky, Martin Ryberg, Steve Trudell, and Jukka Vauras for sharing specimen information or specimens sequenced for this study. Renée Lebeuf, K. P. Deepna Latha, Neale Bougher, Terry Henkel, and Noah Siegel provided photographs. Jerry Cooper and Noah Siegel kindly shared unpublished molecular results confirming the presence of *Mallocybe* in New Zealand. The authors also appreciate assistance from Konstanze Bensch, Luis Alberto Parra, Shaun Pennycook, Scott Redhead, and Keith Seifert for guidance and suggestions regarding rules of nomenclature and registration of new taxa. Thomas Kuyper, Martin Ryberg, and Ricardo García-Sandoval provided reviews of an earlier version, the comments of which greatly improved this study.

FUNDING

The Daniel E. Stuntz Memorial Foundation provided support for revisionary work of North American Inocybaceae, which contributed to this study. Support was also provided by National Science Foundation (NSF) grant DEB-1733750 to Karen Hughes, Brandon Matheny, and Ron Petersen at the

University of Tennessee. Esteve-Raventós wishes to acknowledge the Ministerio de Educación, Cultura y Deporte (Spain) for granting the Project CGL2017-86540-P concerning the taxonomic study of European species of *Inocybe*.

ORCID

P. Brandon Matheny  <http://orcid.org/0000-0003-3857-2189>

LITERATURE CITED

- Agerer R. 1987–2006. Colour atlas of ectomycorrhizae. 1–13th delivery. Schwäbisch Gmünd, Germany: Einhorn-Verlag Edward Dientenrur. 214 Pl.
- Alessio CL. 1984. Complemento allo studio del genere *Inocybe*: 4° contributo. Bolletino Gruppo Micologico G. Bresadola 27:21–34.
- Alvarado P, Manjón JL, Matheny PB, Esteve-Raventós F. 2010. *Tubariomyces*, a new genus of Inocybaceae. Mycologia 102:1389–1397.
- Alvarez-Manjarrez J, Garibay-Orijel R, Smith ME. 2018. Caryophyllae are the main hosts of a unique set of ectomycorrhizal fungi in a Neotropical dry forest. Mycorrhiza 28:103–115.
- Ariyawansa H, Hyde K, Jayasiri S, Buyck B, Kandawatte T, Dai D-Q, Dai Y-C, Daranagama D, Jayawardena R, Lücking R, Ghobad-Nejhad M, Niskanen T, Thambugala K, Voigt K, Zhao R-L, Li G-J, Doilom M, Boonmee S, Yang Z-L, Chen X-H. 2015. Fungal diversity notes 111–252—taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 75:27–274.
- Awan AR, Winter JM, Turner D, Shaw WM, Suz LM, Bradshaw AJ, Ellis T, Dentinger B. 2018. Convergent evolution of psilocybin biosynthesis by psychedelic mushrooms. *BioRxiv*, doi:10.1101/374199
- Bahram M, Vanderpool D, Pent M, Hiltunen M, Ryberg M. 2018. The genome and microbiome of a dikaryotic fungus (*Inocybe terrigena*, Inocybaceae) revealed by metagenomics. Environmental Microbiology Reports 10:155–166.
- Bandini D, Oertel B, Ploch S, Ali T, Vauras J, Schneider A, Scholler M, Eberhardt U, Thines M. 2019. 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.
- Bau T, Fan Y-G. 2018. Three new species of *Inocybe* sect. *Rimosae* from China. Mycosystema 37:693–702.
- Bizio E, Franchi P, Marchetti M. 2006. *Inocybe fusipes* una nuova specie dell'areale mediterraneo. Rivista di Micologia 49:13–19.
- Boidin J. 1986. Intercompatibility and the species concept in the saprobic Basidiomycotina. Mycotaxon 26:319–336.
- Bon M. 1983. Novitates. Validations de taxons. Documents Mycologiques 12 (48):44.
- Bon M. 1985. Quelques nouveaux taxons de la flore mycologique alpine. Bulletin trimestriel de la Fédération Mycologique Dauphiné-Savoie 97:23–30.
- Bon M. 1996. Novitates (suite). Documents Mycologiques 26 (102):17–20.

- Bon M. 1997. Clé monographique du genre *Inocybe* (Fr.) Fr. (1ère partie: généralités et espèces acystidiées = Ss.-g. *Inosperma* Kuhner). Documents Mycologiques 27(105):1–51.
- Bougher NL, Matheny PB, Gates GM. 2012. Five new species and records of *Inocybe* (Agaricales) from temperate and tropical Australia. *Nuytsia* 22:57–74.
- Buyck B, Eyssartier G. 1999. Two new species of *Inocybe* (Cortinariaceae) from African woodland. *Kew Bulletin* 54:675–681.
- Cannon PF, Kirk PM. 2007. Fungal families of the world. Wallingford, UK: CAB International. 456 p.
- Carteret X, Reumaux P. 2017. Miettes sur les *Inocybes* (8 série). *Inocybes jaunes ou jaunâtres*, 1ère partie. *Bulletin de la Société Mycologique de France* 131:1–96.
- Cervini M. 2015. *Inocybe chlorochroa*, una bella specie di recente creazione. *Revista di Micologia* 1:63–69.
- Chen J, Hofmockel KS, Hobbie EA. 2016. Isotopic analysis of sporocarp protein and structural material improves resolution of fungal carbon sources. *Frontiers in Microbiology* 7:1994.
- Chu-Chou M, Grace LJ. 1981. Mycorrhizal fungi of *Pseudotsuga menziesii* in the north island of New Zealand. *Soil Biology and Biochemistry* 13:247–249.
- Corriol G, Guinberteau J. 2013. Un nuevo *Inocybe* de los valles atlánticos del suroeste de Francia *Errotari* 10:45–51.
- Cripps CL. 1997. The genus *Inocybe* in Montana aspen stands. *Mycologia* 89:670–688.
- Cripps CL, Larsson E, Horak E. 2010. Subgenus *Mallocybe* (*Inocybe*) in the Rocky Mountain alpine zone with molecular reference to European arctic-alpine material. *North American Fungi* 5:97–126.
- Cripps CL, Miller OK Jr. 1995. Ectomycorrhizae formed in vitro by quaking aspen: including *Inocybe lacera* and *Amantia pantherina*. *Mycorrhiza* 5:357–370.
- Dentinger BTM, Gaya E, O'Brien H, Suz LM, Lachlan R, Díaz-Valderrama JR, Koch RA, Aime MC. 2016. Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. *Biological Journal of the Linnean Society* 117:11–32.
- Dermek A, Veselský J. 1977. *Inocybe fastigiata* (Schaeff. ex Fr.) Quél.—vláknica kuzelovitá a taxonómia jej poddruhov. *Ceská Mykologie* 31:189–192.
- Diagne N, Thioulouse J, Sanguin H, Prin Y, Krasova-Wade T, Sylla S, Galiana A, Baudoin E, Meyra M, Svistoonoff S, Lebrun M, Duponnois R. 2013. Ectomycorrhizal diversity enhances growth and nitrogen fixation of *Acacia mangium* seedlings. *Soil Biology and Biochemistry* 57:468–476.
- Donk MA. 1962. The generic names proposed for Agaricaceae. *Beihefte zur Nova Hedwigia* 5:1–320.
- Duponnois R, Founoune H, Masse D, Pontanier R. 2005. Inoculation of *Acacia holosericea* with ectomycorrhizal fungi in a semiarid site in Senegal: growth response and influences on the mycorrhizal soil infectivity after 2 years plantation. *Forest Ecology and Management* 207:351–362.
- Earle FS. 1909. The genera of the North American gill fungi. *Bulletin of the New York Botanical Garden* 5(18):373–462.
- Esteve-Raventós F. 2014. *Inocybe aureocitrina* (Inocybaceae), a new species of section *Rimosae* from Mediterranean evergreen oak forests. *Plant Biosystems* 148:377–383.
- Esteve-Raventós F, Bandini D, Oertel B, González V, Moreno G, Olariaga I. 2018. Advances in the knowledge of the *Inocybe mixtilis* group (Inocybaceae, Agaricomycetes), through molecular and morphological studies. *Persoonia* 41:213–236.
- Esteve-Raventós F, García Blanco A, Sanz Caraso M, Del Val JB. 2003. *Inocybe aurantiobrunnea* and *I. pseudoorbata*, two new Mediterranean species found in the Iberian peninsula. *Österreichische Zeitschrift für Pilzkunde* 12:89–99.
- Esteve-Raventós F, Moreno G, Alvarado P, Olariaga I. 2016. Unraveling the *Inocybe praetervisa* group through type studies and ITS data: *Inocybe praetervisoides* sp. nov. from the Mediterranean region. *Mycologia* 108:123–134.
- Favre J. 1955. Les champignons supérieurs de la zone alpine du Parc National Suisse. *Ergebnisse der Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks* 5:1–212.
- Fries N. 1982. Effects of plant roots and growing mycelia on basidiospore germination in mycorrhiza-forming fungi. In: Laursen GA, Ammirati JF, eds. *Arctic and alpine mycology*. Seattle, Washington: University of Washington Press. p. 493–508.
- Frøslev TG, Matheny PB, Hibbett DS. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2, and ITS phylogenies. *Molecular Phylogenetics and Evolution* 37:602–618.
- Gao Q, Yang ZL. 2010. Ectomycorrhizal fungi associated with two species of *Kobresia* in an alpine meadow in the eastern Himalaya. *Mycorrhiza* 20:281–287.
- Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for Basidiomycetes: application to identification of mycorrhizae and rusts. *Molecular Ecology* 2:113–118.
- Gardes M, Dahlberg A. 1996. Mycorrhizal diversity in arctic and alpine tundra: an open question. *New Phytologist* 133:147–157.
- Garnica S, Weiss M, Walther G, Oberwinkler F. 2007. Reconstructing the evolution of agarics from nuclear gene sequences and basidiospore ultrastructure. *Mycological Research* 111:1019–1029.
- Glen M, Tommerup IC, Bougher NL, O'Brien PA. 2001. Interspecific and intraspecific variation of ectomycorrhizal fungi associated with *Eucalyptus* ecosystems as revealed by ribosomal DNA PCR-RFLP. *Mycological Research* 105:843–858.
- Guzmán G. 1982. New species of fungi from the Yucatan Peninsula. *Mycotaxon* 16:249–261.
- Heenan PB, Smitsen RD. 2013. Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscospora*, *Lophozonia*, and *Trisyngyne* (Nothofagaceae). *Phytotaxa* 146:1–31.
- Heim R. 1931. Le genre *Inocybe*, encyclopédie mycologique 1. Paris: Paul Lechevalier & Fils. 429 p.
- Hibbett DS. 1996. Phylogenetic evidence for horizontal transmission of Group I introns in the nuclear ribosomal DNA of mushroom-forming fungi. *Molecular Biology and Evolution* 13:903–917.
- Horak E. 1967. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). *Beiträge zur Kryptogamenflora der Schweiz* 13:1–741.
- Horak E. 1977. Fungi Agaricini Novaezelandiae VI. *Inocybe* (Fr.) Fr. and *Astrosporina* Schroeter*. *New Zealand Journal of Botany* 15:713–747.
- Horak E. 1979. *Astrosporina* (Agaricales) in Indomalaya and Australia. *Persoonia* 10:157–2005.

- Horak E. 1980. *Inocybe* (Agaricales) in Indomalaya and Australasia. *Persoonia* 11:1–37.
- Horak E. 2005. Röhrlinge und Blätterpilze in Europa. Heidelberg, Germany: Spektrum Akademischer Verlag. 575 p.
- Horak E. 2018. Fungi of New Zealand/Ngā Hekaheka o Aotearoa. Vol. 6. Agaricales (Basidiomycota) of New Zealand. 2. Brown spored gener p.p. *Crepidotus*, *Flammulaster*, *Inocybe*, *Phaeocollybia*, *Phaeomarasmius*, *Pleuroflammula*, *Pyrrhoglossum*, *Simocybe*, *Tubaria* and *Tympanella*. Utrecht, The Netherlands: Westerdijk Fungal Biodiversity Institute. 205 p.
- Horak E, Matheny PB, Desjardin DE, Soytong K. 2015. The genus *Inocybe* (Inocybaceae, Agaricales, Basidiomycota) in Thailand and Malaysia. *Phytotaxa* 230:201–238.
- Hynson NA, Bruns TD. 2009. Evidence of a myco-heterotroph in the plant family Ericaceae that lacks mycorrhizal specificity. *Proceedings of the Royal Society B: Biological Sciences* 276:4053–4059.
- Ilyas S, Razaq A, Khalid AN. 2013. *Inocybe nitidiuscula* and its ectomycorrhizae associated with *Alnus nitida* from Galyat, Pakistan. *Mycotaxon* 124:247–254.
- Jacobsson S, Larsson E. 2009. *Inocybe spuria*, a new species in section *Rimosae* from boreal coniferous forests. *Mycotaxon* 109:201–207.
- Jamoni PG. 2008. Funghi alpini delle zone alpine superiori e inferiori. Trento, Italy: Associazione Micologica Bresadola. 544 p.
- Jensen N, Gartz J, Laatsch H. 2006. Aeruginascin, a trimethylammonium analogue of psilocybin from the hallucinogenic mushroom *Inocybe aeruginascens*. *Planta Medica* 72:665–666.
- Judge B, Ammirati JF, Lincoff G, Trestrail JH, Matheny PB. 2010. Ingestion of a newly described North American mushroom species from Michigan resulting in chronic renal failure: *Cortinarius orellanosus*. *Clinical Toxicology* 48:545–549.
- Jülich W. 1982. Higher taxa of Basidiomycetes. *Bibliotheca Mycologica* 85:1–485.
- Karsten PA. 1879. Rysslands, Finlands och den Skandinaviska halföns Hattsvampar. Förra Delen: Skifsvampar. *Bidrag till Kännedom av Finlands Natur och Folk* 32:1–571.
- Kauffman CH. 1924. *Inocybe*. *North American Flora* 10:227–260.
- Kennedy PG, Garibay-Orijel R, Higgins LM, Angeles-Arguiz R. 2011. Ectomycorrhizal fungi in Mexican *Alnus* forests support the host co-migration hypothesis and continental-scale patterns in phylogeography. *Mycorrhiza* 21:559–568.
- Kennedy PG, Hill LT. 2010. A molecular and phylogenetic analysis of the structure and specificity of *Alnus rubra* ectomycorrhizal assemblages. *Fungal Ecology* 3:195–204.
- Kirk P, Cannon PF, Minter DW, Stalpers JA. 2008. The dictionary of fungi. Wallingford, UK: CAB International. 771 p.
- Knudsen H, Vesterholt J, eds. 2008. *Funga nordica: agaricoid, boletoid and cyphelloid genera*. Copenhagen, Denmark: Nordsvamp. 965 p.
- Knudsen H, Vesterholt J, eds. 2012. *Funga nordica: agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera*. 2 Vols. Copenhagen, Denmark: Nordsvamp. 1083 p.
- Kobayashi T. 2002. The taxonomic studies of the genus *Inocybe*. *Beihefte zur Nova Hedwigia* 124:1–246.
- Kobayasi Y. 1952. On the genus *Inocybe* from Japan. *Nagaoa* 2:76–114.
- Kosentka P, Sprague SL, Ryberg M, Gartz J, May AL, Campagna SR, Matheny PB. 2013. Evolution of the toxins muscarine and psilocybin in a family of mushroom-forming fungi. *PLoS ONE* 8:e64646.
- Kropp BR, Albee-Scott S. 2010. *Inocybe tauensis*, a new species from the Samoan Archipelago with evidence for a Paleotropical origin. *Fungal Biology* 114:790–796.
- Kropp BR, Matheny PB. 2004. Basidiospore homoplasy and variation in the *Inocybe chelanensis* group in North America. *Mycologia* 96:295–309.
- Kropp BR, Matheny PB, Hutchison LJ. 2013. *Inocybe* section *Rimosae* in Utah: phylogenteic affinities and new species. *Mycologia* 105:728–747.
- Kropp BR, Matheny PB, Nanagyulan SG. 2010. Phylogenetic taxonomy of the *Inocybe splendens* group and evolution of supersection “Marginatae”. *Mycologia* 102:560–573.
- Kühndorf K. 2016. Diversity and identification of mycorrhizal fungi of the Ericaceae *Comarostaphylis arbutoides* from Costa Rica [PhD doctoral dissertation]. Cottbus, Germany: Brandenburgischen Technischen Universität Cottbus-Senftenberg.
- Kühner R. 1955. Compléments à la “Flore Analytique”. VI) *Inocybe* goniosporés et *Inocybe* acystidiés. Espèces nouvelles ou critiques. *Bulletin de la Société Mycologique de France* 71:169–201.
- Kühner R. 1980. Les Hyménomycètes agaricoides. *Bulletin Mensuel de la Société Linnéenne de Lyon* 49:1–1027.
- Kühner R. 1988. Diagnoses de quelques nouveaux *Inocybes* récoltés en zone alpine de la Vanoise (Alpes françaises). *Documents Mycologiques* 19(74):1–27.
- Kühner R, Romagnesi H. 1953. *Flore analytique des champignons supérieurs*. Paris: Masson et Cie. 556 p.
- Kuyper TW. 1986. A revision of the genus *Inocybe* in Europe 1. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia* 3(Suppl):1–247.
- Kuyper TW. 1994. Genera in the Agaricales: advances and retreats in search of a natural system. *Mycologia Helvetica* 6:141–159.
- Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30:3276–3278.
- Larsson E, Vauras J, Cripps CL. 2014. *Inocybe leiocephala*, a species with an intercontinental distribution range—disentangling the *I. leiocephala*–*subbrunnea*–*catalaunica* morphological species complex. *Karstenia* 54:15–39.
- Larsson E, Ryberg M, Moreau P-A, Mathiesen ÅD, Jacobsson S. 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, Vauras J, Cripps CL. 2017. *Inocybe praetervisa* group—a clade of four closely related species with partly different geographical distribution ranges in Europe. *Mycoscience* 59:277–287.
- Latha KPD, Manimohan P. 2015. *Inocybe griseorubida*, a new species of *Pseudosperma* clade from tropical India. *Phytotaxa* 221:166–174.
- Latha KPD, Manimohan P. 2016a. Five new species of *Inocybe* (Agaricales) from tropical India. *Mycologia* 108:110–122.

- Latha KPD, Manimohan P. 2016b. *Inocybe gregaria*, a new species of the Inosperma clade from tropical India. *Phytotaxa* 286:107–115.
- Latha KPD, Manimohan P. 2017. *Inocybes of Kerala*. Calicut, India: SporePrint Books. 181 p.
- Latha KPD, Manimohan P, Matheny PB. 2016. A new species of *Inocybe* representing the Nothocybe lineage. *Phytotaxa* 267:40–50.
- Liu L-N, Razaq A, Atri NS, et al. (including 49 additional co-authors). 2018. Fungal systematics and evolution: FUSE 4. *Sydowia* 70:211–286.
- Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among Ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16:1799–1808.
- Ludwig E. 2017. *Pilzkompedium*. Band 4 (two parts). Berlin, Germany: Fungicon Verlag. 793 p.
- Maddison DR, Maddison WP. 2005. *MacClade 4: analysis of phylogeny and character evolution*. Version 4.08a. Sunderland, Massachusetts: Sinauer Associations.
- Malchol RE, Singer R. 1971. Bayesian analysis of generic relations in Agaricales. *Nova Hedwigia* 21:753–787.
- Malençon G, Bertault R. 1970. *Flore des Champignons Supérieurs du Maroc*. Tome 1. Rabat, Morocco: Institut Scientifique Chérifien et Faculté des Sciences. 604 p.
- Malloch D, Thorn RG. 1985. The occurrence of ectomycorrhizae in some species of Cistaceae in North America. *Canadian Journal of Botany* 63:872–875.
- Massee G. 1904. A monograph of the genus *Inocybe*, Karsten. *Annals of Botany* 18:459–504.
- Matheny PB. 2005. Improving phylogenetic inference of mushrooms using RPB1 and RPB2 sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution* 35:1–20.
- Matheny PB. 2009. A phylogenetic classification of the Inocybaceae. *McIlvainea* 18:11–21.
- Matheny PB, Aime MC, Bougher NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DL, Soyton K, Trappe JM, Hibbett DS. 2009. Out of the palaeotropics? Historical biogeography and diversification of the cosmopolitan mushroom family Inocybaceae. *Journal of Biogeography* 36:577–592.
- Matheny PB, Aime MC, Henkel TW. 2003. New species of *Inocybe* from *Dicymbe* forests of Guyana. *Mycological Research* 107:495–505.
- Matheny PB, Bougher NL. 2006. The new genus *Auritella* from Africa and Australia (Inocybaceae, Agaricales): molecular systematics, taxonomy and historical biogeography. *Mycological Progress* 5:2–17.
- Matheny PB, Bougher NL. 2017. *Fungi of Australia: Inocybaceae*. Australian Biological Resources Study, Canberra, Melbourne, Australia: CSIRO Publishing. 582 p.
- Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W, Yang Z-L, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele G, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS. 2006. Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia* 98:982–995.
- Matheny PB, Henkel TW, Sene O, Korotkin HB, Dentinger BTM, Aime MC. 2017. New species of *Auritella* (Inocybaceae) from Cameroon, with a worldwide key to the known species. *IMA Fungus* 8:287–298.
- Matheny PB, Kropp BR. 2001. A revision of the *Inocybe lanuginosa* group and allied species in North America. *Sydowia* 53:93–139.
- Matheny PB, Kudzma LV. 2019. New species of *Inocybe* (Agaricales) from eastern North America. *Journal of the Torrey Botanical Society* 146:213–235.
- Matheny PB, Liu YJ, Ammirati JF, Hall BD. 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *American Journal of Botany* 89:688–698.
- Matheny PB, Norvell LL, Giles EC. 2013. A common new species of *Inocybe* in the Pacific Northwest with a diagnostic PDAB reaction. *Mycologia* 105:436–446.
- Matheny PB, Pradeep CK, Vrinda KB, Varghese SP. 2012. *Auritella foveata*, a new species of Inocybaceae (Agaricales) from tropical India. *Kew Bulletin* 67:119–125.
- Matheny PB, Swenie RA. 2018. The *Inocybe geophylla* group in North America: a revision of the lilac species surrounding *I. lilacina*. *Mycologia* 110:618–634.
- Matheny PB, Wang Z, Binder B, Curtis JM, Lim YW, Nilsson RH, Kughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughling DJ, Wilson AW, Frøslev T, Ge Z-W, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS. 2007. Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Molecular Phylogenetics and Evolution* 43:430–451.
- Matheny PB, Watling R. 2004. A new and unusual species of *Inocybe* (Inosperma clade) from tropical Africa. *Mycotaxon* 89:497–503.
- Mayor JR, Schuur EAG, Henkel TW. 2009. Elucidating the nutritional dynamics of fungi using stable isotopes. *Ecology Letters* 12:171–183.
- Métrod G. 1953. Espèces du genre *Inocybe*. *Schweizerische Zeitschrift für Pilzkunde* 31(9–10):151–159.
- Moëgne-Locoz P, Poirier J, Reumaux R. 1990. *Fungorum rariorum icones coloratae*. Berlin, Germany: J. Cramer. 55 p.
- Møller FH. 1945. *Fungi of the Farøes, Part I: Basidiomycetes*. Copenhagen, Denmark: Munksgaard. 295 p.
- Moncalvo J-M, Lutzoni F, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* 49:278–305.
- Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Cléménçon H, Miller OK Jr. 2002. One hundred and seventeen clades of euagarics. *Molecular Phylogenetics and Evolution* 23:357–400.
- Moyersoen B. 2012. Dispersion, an important radiation mechanism for ectomycorrhizal fungi in neotropical lowland forests? In: Sudarshana P, Nageswara-Rao M, Soniji JR, eds. *Tropical forests*. Rijeka, Croatia: InTech. p. 93–116.
- Mühlmann O, Bacher M, Peintner U. 2008. *Polygonum viviparum* mycobionts on an alpine primary successional glacier forefront. *Mycorrhiza* 18:87–95.
- Nespiak A. 1990. *Strzepek (Inocybe)*. *Flora Polska, Grzyby (Mycota)*, Tome XIX. Warsaw, Poland: Polska Akademia Nauk, Instytut Botaniki.

- Nishida F. 1989. Key to the species of *Inocybe* in California. *Mycotaxon* 34:181–196.
- O'Donnell KL, Cigelnik E, Benny GL. 1998. Phylogenetic relationships among the Harpellales and Kickxellales. *Mycologia* 90:624–639.
- Onguene NA, Kuyper TW. 2012. Habitat and diversity of ectomycorrhizal fungi in forests of South Cameroon. *Cameroon Journal of Experimental Biology* 8:26–34.
- Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM. 2013. Fillings gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* 8: e62419.
- Outen AR, Cullington P. 2015. Keys to British species of *Inocybe*. Edition 3:1, Apr 2015. 62 p.
- Pegler D. 1983. Agaric flora of the Lesser Antilles. *Kew Bulletin Series IX*:1–668.
- Pegler D. 1986. Agaric flora of Sri Lanka. *Kew Bulletin Additional Series XII*:1–519.
- Pouzar Z. 1985. Proposals for the conservation of five family names of fungi. *Taxon* 35:709–712.
- Pradeep CK, Vrinda KB, Varghese S, Matheny PB. 2016. New and noteworthy species of *Inocybe* (Agaricales) from tropical India. *Mycological Progress* 15:24.
- Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98.
- Repáč I. 1996. Inoculation of *Picea abies* (L.) Karst. seedlings with vegetative inocula of ectomycorrhizal fungi *Suillus bovinus* (L.: Fr.) O. Kuntze and *Inocybe lacera* (Fr.) Kumm. *New Forests* 12:41–54.
- Reumaux P. 2004. Fantômes à suivre. *Bulletin de la Société Mycologique de France* 120(1–4):105–117.
- Ronquist F, Teslenko M, van der Mark P, Ayers DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.
- Roy M, Yagame T, Yamato M, Iwase K, Heinz C, Faccio A, Bonfante P, Selosse M-A. 2009. Ectomycorrhizal *Inocybe* species associate with the mycoheterotrophic orchid *Epipogium aphyllum* but not its asexual propagules. *Annals of Botany* 104:595–610.
- Rudawska M, Leski T, Wilgan R, Karliński K, Jujawska M, Janowski D. 2018. Mycorrhizal associations of the exotic hickory trees, *Carya laciniosa* and *Carya cordiformis*, grown in Kórnik Arboretum in Poland. *Mycorrhiza* 28:549–560.
- Ryberg M, Larsson E, Jacobsson S. 2010. An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). *Molecular Phylogenetics and Evolution* 55:431–442.
- Ryberg M, Larsson E, Molau U. 2009. Ectomycorrhizal diversity on *Dryas octopetala* and *Salix reticulata* in an alpine cliff ecosystem. *Arctic, Antarctic, and Alpine Research* 41:506–515.
- Ryberg M, Matheny PB. 2012. Asynchronous origins of ectomycorrhizal clades of Agaricales. *Proceedings of the Royal Society B: Biological Sciences* 279:2003–2011.
- Ryberg M, Nilsson RH, Kristiansson E, Töpel M, Jacobsson S, Larsson E. 2008. Mining metadata from unidentified ITS sequences in GenBank: a case study in *Inocybe* (Basidiomycota). *BMC Evolutionary Biology* 8:50.
- Saccardo PA. 1916. *Flora Italica cryptogama. Pars I: Fungi. Hymeniales (Ceterae Agaricaceae, Polyporaceae, Hydnceae, Thelephoraceae, Tremellaceae).* Volume 1, Fascicolo 15. Rocca S. Casciano : Stabilimento tipografico L. Cappelli.
- Sánchez-García M, Aime MC, Smith ME, Matheny PB, Henkel TW. 2016. A new genus of ectomycorrhizal fungi (*Guyanagarika*, Agaricales) from the neotropics. *Fungal Biology* 120:1540–1553.
- Séne S, Avril R, Chaintreuil C, Geoffroy A, Ndiaye C, Diédhiou AG, Sadio O, Courtecuisse R, Sylla SN, Selosse M-A, Bâ A. 2015. Ectomycorrhizal fungal communities of *Coccoloba uvifera* (L.) L. mature trees and seedlings in the neotropical coastal forests of Guadeloupe (Lesser Antilles). *Mycorrhiza* 25:547–559.
- Singer R. 1949. The Agaricales (mushrooms) in modern taxonomy. *Lilloa Revista de Botánica* 22:5–832.
- Singer R. 1986. *The Agaricales in modern taxonomy.* 4th ed. Koenigstein, Germany: Koeltz Scientific Books. 981 p.
- Smith AH, Stunt DE. 1950. New or noteworthy fungi from Mount Rainier National Park. *Mycologia* 42:80–134.
- Stamatakis A. 2014. RAxML 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.
- Stangl J. 1989. Die Gattung *Inocybe* in Bayern. *Hoppea* 46:1–409.
- Stangl J, Bresinsky A. 1983. *Inocybe stenospora* spec. nov. und *Inocybe malençonii* Heim var. *megalospora* var. nov. *Hoppea* 41:409–421.
- Stangl J, Veselský J. 1979. *Inocybe kuthanii* sp. nov. Eine neue Art in Sektion *Rimosae*, Stirps *Cookei* Heim gehörend (Beiträge zur Kenntnis seltenerer Inocyben Nr. 15). *Ceská Mykologie* 33:134–137.
- Stiller JW, Hall BD. 1997. The origin of red algae: implications for plastid evolution. *Proceedings of the National Academy of Sciences of the United States of America* 94:4520–4525.
- Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.
- Taylor JW, Turner E, Townsend JP, Dettman JR, Jacobson D. 2006. Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philosophical Transactions of the Royal Society B* 361:1947–1963.
- Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, Saar I, Kõljalg U. 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytologist* 180:479–490.
- Tedersoo L, Pölme S. 2012. Infrageneric variation in partner specificity: multiple ectomycorrhizal symbionts associate with *Gnetum gnemon* (Gnetophyta) in Papua New Guinea. *Mycorrhiza* 22:663–668.
- Tedersoo L, Sadam A, Zambrano M, Valenica R, Bahram M. 2010. Low diversity and high host preference of ectomycorrhizal fungi in western Amazonia, a neotropical biodiversity hotspot. *ISME Journal* 4:465–471.

- Tedersoo L, Smith ME. 2013. Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* 27:83–99.
- Tibpromma S, Hyde KD, Jeewon R, et al. (123 other co-authors). Fungal diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 83:1–292.
- Turland NJ, Wiersma JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen P, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF, editors. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Glashütten: Koeltz Botanical Books. doi:10.12705/Code.2018
- Turnbull E. 1995. *Inocybe* in peninsular Malaysia. *Edinburgh Journal of Botany* 52:351–359.
- Ullah Z, Jabeen S, Ahmad H, Khalid AB. 2018. *Inocybe pakistanensis*, a new species in section *Rimosae* s.str. from Pakistan. *Phytotaxa* 348:279–288.
- Varga T, Krizsán K, Földi C, Dima B, Sánchez-García M, Sánchez-Ramírez S, Szöllösi GJ, Szarkándi JG, Papp V, Albert L, Andreopoulos W, Angelini C, Antonín V, Barry KW, Bougher NL, Buchanan P, Buyck B, Bense V, Catcheside P, Chovatia M, Cooper J, Dämon W, Desjardin D, Finy P, Geml J, Haridas S, Hughes K, Justo A, Karasinski D, Kautmanova K, Kiss B, Kocsubé S, Kotiranta H, LaButti KM, Lechner BE, Liimatainen K, Lipzen A, Lukács Z, Mihaltcheva S, Morgado LN, Niskanen T, Noordeloos ME, Ohm RA, Ortiz-Santana B, Ovrebo C, Rác N, Riley R, Savchenko A, Shiryayev A, Soop K, Spirin V, Czebenyi C, Tomsovsky M, Tullos RE, Uehling J, Grigoriev IV, Vágvölgyi C, Papp T, Martin FM, Miettinen O, Hibbett DS, Nagy LG. 2019. Megaphylogeny resolves global patterns of mushroom evolution. *Nature Ecology and Evolution* 3:668–678.
- Vauras J, Larsson E. 2012. *Inocybe myriadophylla*, a new species from Finland and Sweden. *Karstenia* 51:31–36.
- Vellinga EC, Kuyper TW, Ammirati J, Desjardin DE, Halling RE, Justo A, Læssøe T, Lebel T, Lodge DJ, Matheny PB, Methven AS, Moreau P-A, Mueller GM, Noordeloos ME, Nuytinck J, Ovrebo CL, Verbeken A. 2015. Six simple guidelines for introducing new genera of fungi. *IMA Fungus* 6:65–68.
- Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172:4238–4246.
- Vilgalys R, Hopple J, Hibbett DS. 1994. Phylogenetic implications of generic concepts in fungal taxonomy: the impact of molecular systematic studies. *Mycologia Helvetica* 6:73–91.
- Villarreal M, Esteve-Raventós F, Heykoop M, Horak E. 1998. *Inocybe inexpectata*, a new and unusual species of subgenus *Mallocybe*. *Mycological Research* 102:479–482.
- Vizzini A, Consiglio G, Marchetti M. 2019. *Mythicomycetaceae* fam. nov. (Agaricineae, Agaricales) for accommodating the genera *Mythicomyces* and *Stagnicola*, and *Simocybe parvispora* reconsidered. *Fungal Systematics and Evolution* 3:41–56.
- Vizzini A, Maggiora MC, Tolaini F, Ercole E. 2013. A new cryptic species in the genus *Tubariomyces* (Inocybaceae, Agaricales). *Mycological Progress* 12:375–381.
- Voss EG, Burdet HM, Chaloner WG, Demoulin V, Hiepko P, McNeil J, Meikle RD, Nicolson DH, Rollins RC, Silva PC, Greuter W. 1983. International code of nomenclature: adopted by the Thirteenth International Botanical Congress, Sydney, August 1981. Utrecht, The Netherlands: Bohn, Scheltema & Holkema. 472 p.
- Walbert K, Ramsfield TD, Ridgway HJ, Jones EE. 2010. Ectomycorrhizal species associated with *Pinus radiata* in New Zealand including novel associations determined by molecular analysis. *Mycorrhiza* 20:209–215.
- White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenies. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds. *PCR protocols: a guide to methods and applications*. San Diego, California: Academic Press. p. 315–322.
- Wolfe BE, Tulloss RE, Pringle A. 2012. The irreversible loss of a decomposition pathway marks the single origin of an ectomycorrhizal symbiosis. *PLoS ONE* 7:e39597.
- Zerova MY. 1974. *Atlas of Ukrainian mushrooms*. Kiev, Ukraine: Scientific Thought.
- Zhao JK, Wang HX, Ng TB. 2009. Purification and characterization of a novel lectin from the toxin wild mushroom *Inocybe umbrinella*. *Toxicon* 53:360–366.
- Zhao R-L, Li G-J, Sanchez-Ramirez A, Stata M, Yang Z-L, Wu G, Dai Y-C, He S-H, Cui B-K, Zhou J-L, Wu F, He M-Q, Moncalvo J-M, Hyde KD. 2017. A six-gene phylogenetic overview of Basidiomycota and allied phyla with estimated diverge times of higher taxa and a phyloproteomics perspective. *Fungal Diversity* 84:43–74.
- Zhao R-L, Zhou J-L, Chen J, Margaritescu S, Sanchez-Ramirez S, Hyde KD, Callac P, Parra LA, Li G-J, Moncalvo J-M. 2016. Towards standardizing taxonomic ranks using divergence times—a case study for reconstruction of the *Agaricus* taxonomic system. *Fungal Diversity* 78:239–292.