RESEARCH ARTICLE



OPEN ACCESS Check for updates

A phylogeny of the *Inocybe alienospora* group (Agaricales) with emphasis on seven new species from China and emendation of sect. *Leptocybe*

Jia-Long Gao^a, Yu-Peng Ge^b, P. Brandon Matheny^c, Pan-Min He^a, Xiao-Peng Wu^d, Tolgor Bau^e, Wen-Jie Yu^a and Yu-Guang Fan^a

^aEngineering Research Center of Tropical Medicine Innovation and Transformation of Ministry of Education, International Joint Research Center of Human-machine Intelligent Collaborative for Tumor Precision Diagnosis and Treatment of Hainan Province, Hainan Provincial Key Laboratory of Research and Development on Tropical Herbs, School of Pharmacy, Hainan Medical University, Haikou, China; ^bShandong Key Laboratory of Edible Mushroom Technology, School of Agriculture, Ludong University, Yantai, China; ^cDepartment of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, USA; ^dAnalysis and Test Center, Chinese Academy of Tropical Agricultural Sciences, Haikou, China; ^eEngineering Research Centre of Chinese Ministry of Education for Edible and Medicinal Fungi, Jilin Agricultural University, Changchun, China

ABSTRACT

A multigene phylogeny of the *Inocybe alienospora* group is presented based on analyses of ITS, 28S, and *rpb2* nucleotide data. Four major subclades and three additional independent lineages were identified in the *I. alienospora* group. Two species with superficial similarities with the *I. alienospora* group, viz, *I. multicoronata* and *I. elata*, however, were not nested within the *I. alienospora* group. *Inocybe* sect. *Leptocybe* is proposed to accommodate the *I. alienospora* group in a more formal classification system. As such, sect. *Leptocybe* now includes 12 documented species and seven new species described in this work. The seven new species include *I. aprica* sp. nov., *I. casuarinoides* sp. nov., *I. haikouensis* sp. nov., three species associated with *Casuarina* from tropical China; also *I. heteromorpha*, a species associated with fagaceous trees from tropical China; and *I. acutata* are reported. The East Asian species *I. acutata* and the neotropical species *I. lasseri* were confirmed as members of sect. *Leptocybe*. A key to the 19 species in sect. *Leptocybe* is also provided.

ARTICLE HISTORY

Received 16 May 2024 Accepted 9 July 2024

KEYWORDS

Asia; Inocybaceae; new taxa; molecular phylogeny; taxonomy

1. Introduction

Fungi play vital roles in ecosystems as endophytes, pathogens and saprobes. The current estimate of fungal diversity is highly uncertain, ranging from 1.5 to 12 million, but only around 150,000 species have been named and classified to date (Bhunjun et al. 2022). In the past decades, a large number of macro-fungal resources have been recognised with the description of many new taxa (Wu et al. 2019), especially the pathogenic wood-rotting fungi (Liu et al. 2023; Yuan et al. 2023) in China. However, studies on many ectomycorrhizal groups, such as Inocybaceae, Cortinaceae, Russulaceae, ect., are still poorly reported.

The Inocybaceae Jülich (1982: 374) is an ectomycorrhizal family of fungi (Agaricales) commonly found in temperate and tropical forests, with over 1,050

described species in Africa, Asia, Europe, North America, Oceania, and South America (Matheny et al. 2020). The family has been revised based on the results of a recent phylogenetic study that divided the family into seven genera, with Inocybe (Fr.) Fr. (1863: 346) being the largest genus in the family (Matheny et al. 2020). In recent years, new species in the family have been continually discovered from all over the world (Matheny and Bougher 2017; Bandini et al. 2021, 2022a, 2022b, 2022c, 2023a, 2023b; Crous et al. 2021a, 2021b, 2023a, 2023b; Li et al. 2021; Mešić et al. 2021; Aïgnon et al. 2022; Bhunjun et al. 2022; Buyck et al. 2022; Esteve-Raventós et al. 2022a, 2022b; Muñoz et al. 2022; He et al. 2022; Kaufholtz-Couture and Moreau 2022; Kaygusuz et al. 2022a, 2022b; Khan et al. 2022; Marchetti et al. 2022; Matheny et al. 2022; Tan et al. 2022; Armada et al. 2023;

CONTACT Yu-Guang Fan mycena@qq.com; Wen-Jie Yu inocybe@qq.com Engineering Research Center of Tropical Medicine Innovation and Transformation of Ministry of Education, International Joint Research Center of Human-machine Intelligent Collaborative for Tumor Precision Diagnosis and Treatment of Hainan Province, Hainan Provincial Key Laboratory of rResearch and Development on Tropical Herbs, School of Pharmacy, Hainan Medical University, Haikou 571199, Hainan, China

This article was originally published with errors, which have now been corrected in the online version. Please see Correction (http://dx.doi.org/10.1080/21501203.2025.2481347).

^{© 2024} The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (http://creativecommons.org/licenses/by-nc/4.0/), which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

Dovana et al. 2023; Eberhardt et al. 2023; Lebeuf et al. 2023; Pošta et al. 2023; Razzaq et al. 2023; Senanayake et al. 2023; Fachada et al. 2024). In China, at least 120 species of Inocybaceae have been recorded (Fan and Bau 2010; Li et al. 2021; Bau 2022), but only seven species have been described from tropical China (Fan and Bau 2014; Deng et al. 2021b, 2022a, 2022b; He et al. 2022; Zhao et al. 2022; Hu et al. 2023; Zhou et al. 2023).

Members of *Inocybe* are often characterised by the presence of thick-walled hymenial cystidia and smooth, ellipsoid, nodulose, angular, or spinose basidiospores, typically with a distinct apiculus (Ryberg et al. 2010; Matheny et al. 2020). In tropical regions, some Inocybe species exhibit thinwalled hymenial cystidia, some the absence of pleurocystidia, but most possess basidiospores with nodules, and for some species, the nodules may be bifurcate or bear saddle-shaped projections (Horak 1979, 1980; Horak et al. 2015; Matheny and Bougher 2017; Deng et al. 2022b). Inocybe alienospora was originally described from Singapore in 1979 with nodulose basidiospores with saddleshaped projections, thick-walled pleurocystidia, and thin-walled cheilocystidia (Horak 1979). Initially, Horak et al. (2015) first recovered an unnamed clade including two broadly recognised species based on materials studied from Thailand: I. stellata and I. hydrocybiformis; the group was also found to contain a neotropical species I. lasseri. Indeed, I. lasseri from the neotropics and I. multicoronata from North America, and since confirmed in Europe, were considered close relatives in this group inferred by their similar basidiospores (Horak 1979). One year later, a study of Indian taxa by Pradeep et al. (2016) showcased several additional Australasian taxa centred around I. alienospora and I. lasseroides, together with newly recognised lineages from India (viz, I. papilliformis). Later, Matheny and Bougher (2017) documented the Northern Australian taxa and first referred to the clade as the Inocybe alienospora group; in addition, they found that further revision of the group was necessary owing to a large number of unnamed phylogenetic and morphologically recognisable taxa.

Work on tropical Indian taxa continued by Latha and Manimohan (2017) and revealed the Indian *I. babruka* and *I. kurvensis* also clustered in this group with full support, thereby increasing the species number to seven. In a recent three-gene phylogenetic analysis, the I. alienospora group received strong support in a subclade sister to another subclade unifying *Inocybe* epidendron, I. pulchella, and I. xerophytica from the neotropics (Aignon et al. 2022). Our recently described I. carpinicola, together with one phylogenetic lineage of I. stellata and two nodulose-spored species I. pseudoasterospora and I. perlucida from temperate Europe cluster within the *I. alienospora* group with full support (He et al. 2022). However, no prior works have been focused on species diversity and phylogeny of the I. alienospora group in tropical Asia. The present study proposes seven new species and new distributions for two previously recorded species within the *I. alienospora* group based on our collections from tropical, subtropical, and temperate China. For a better understanding of the phylogenetic inferences of this group of fungi, a summarised phylogenetic analysis of Inocybe as a genus was also performed.

2. Materials and methods

2.1. Field sampling and morphological studies

Specimens were collected from Hainan (tropical monsoon climate), Jilin (temperate monsoon climate), Shandong (temperate monsoon climate), Yunnan (subtropical Plateau Mountain Climate), and Zhejiang (subtropical monsoon climate) provinces of China with temperate continental mountain, subtropical and tropical climates. In the field, ecological images were taken using a digital camera. Basidiomata were documented when fresh with colour assignments given following Kornerup and Wanscher (1978). Specimens were then dried in a 45 °C electric oven overnight, sealed in plastic bags, and placed in an icebox for insecticide treatment (Yu et al. 2020; Deng et al. 2021a, 2021b, 2022a, 2022b; Zhao et al. 2022; Hu et al. 2023). After the study, the specimens were deposited at the Herbarium of Changbai Mountain National Natural Reserve (ANTU) with their FCAS numbers.

Macrofeatures were described based on field notes and digital images. Microscopic observations were conducted using a light microscope (Olympus CX23). Mushroom tissues from the pileus, lamellae, and stipes were cut into thin sections freehand with the aid of a stereoscope (AV100–240 V). Dried specimens were sliced and rehydrated in 5% KOH, and also 1% Congo red solution when necessary. Basidiospores, basidia, hymenophoral trama, pleurocystidia, cheilocystidia, cheiloparacystidia, pileipellis/ pileal trama, and stipitipellis/stipe trama, caulocystida, and oily hyphae were examined and measured. Side views of at least 100 mature basidiospores for each specimen were measured, excluding the apiculus, with the form [n/m/p], indicating the measurement of "n" basidiospores of "m" individuals from "p" collections. The measurement data were expressed in the form of (a) b-e-c (d), where "a" and "d" represent the minimum and maximum values in the measurement data, respectively, "b" and "c" represent the values when the species measurement data are arranged at 5% and 95% from small to large, and "e" represents the average value (Ge et al. 2021; Liu et al. 2021; Na et al. 2022). Additionally, the roundness of spores from a certain length (Q) conveniently distinguished different species, represented by the formula: Q = length/width ratio for individual basidiospore, Qm means the average of Q values, Qm ± SD represents Qm ± the sample standard deviation (Ge et al. 2021).

2.2. DNA extraction, PCR, and sequencing

Three loci were produced from samples in this study including the rDNA internal transcribed spacer region (ITS), 28S (LSU, large subunit of ribosomal DNA), and the second largest subunit of the DNA-directed RNA polymerase II (rpb2). Genomic DNA was extracted using the NuClean Plant Genomic DNA kit (ComWin Biotech, Beijing) and stored at -20 °C. Polymerase chain reaction (PCR) reactions were performed using the primer pairs ITS1-F/ITS4 for the ITS (Gardes and Bruns 1993), LROR/LR7 for the 28S (Vilgalys and Hester 1990), and rpb2-6F/rpb2-7.1R for rpb2 (Matheny 2005). The PCR setup was generally composed of 9.5 µL of water, 12.5 µL of 2× Tag Plus MasterMix (Dye), $1 \mu L$ of each primer, and $1 \mu L$ of template DNA. The PCR programme consisted of a 5 min heating step at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1.5 min at 50 °C, and 1 min at 72 °C. The final cycle was followed by a 10 min extension at 72 °C (Wang et al. 2021). After amplification, the PCR products were sent to BGI Biotech and Sangon Biotech (Guangdong) Ltd. for purification and sequencing. All sequencing results were read by BioEdit v7.0.9.0 software (Hall 1999) and assembled with SeqMan v. 7.1.0 under DNASTAR v7.1.0 (44.1) software (Burland 2000). Newly generated DNA sequences were submitted to GenBank.

2.3. Sequence alignment and phylogenetic analyses

In order to conduct phylogenetic analysis, several authentic sequences of the genus Inocybe were obtained from GenBank. Species from different groups, clades, and sections of Inocybe, such as I. praetervisa group, I. mixtilis group, I. napipes group, I. calida group, I. oblectabills group, I. asterospora group, I. xanthomelas group, I. lacera group, I. lanuginosa group, I. giacomi group, the smooth-spored temperate boreal clade, the smooth-spored temperate Austral clade and sect. Inocybe were selected on the basis of a literature survey (Matheny et al. 2002, 2009, 2013, 2020; Kropp and Matheny 2004; Matheny 2005; Yuwa-Amornpi et al. 2006; Tedersoo et al. 2007; Ryberg et al. 2008, 2010; Kokkonen and Vauras 2012; Ryberg and Matheny 2012; Osmundson et al. 2013; Kaewgrajang et al. 2014; Larsson et al. 2014, 2018; Marchetti et al. 2014; Esteve-Raventós et al. 2015; Horak et al. 2015; Vauras and Larsson 2015; Latha et al. 2016; Latha and Manimohan 2016, 2017; Bandini et al. 2017, 2020, 2022a; Matheny and Bougher 2017; Esteve-Raventós et al. 2018; Liu et al. 2018; Cripps et al. 2020; Cho et al. 2021; Aïgnon et al. 2022; He et al. 2022; Houlès et al. 2022; Raghoonundon et al. 2023). Nothocybe distincta (K.P.D. Latha & Manim.) Matheny & K.P.D. Latha was used for rooting purposes (Latha and Manimohan 2016; Matheny et al. 2020).

We first used the MAFFT online service (https:// mafft.cbrc.jp/alignment/server/.) with the E-INS-i iterative refinement strategy to align each of three partitions (Katoh et al. 2019). Then, we manually edited the sequence alignments using BioEdit v.7.0.9.0 (Hall 1999). Next, we concatenated the three individual partitions using MEGA v.5.02 (Tamura et al. 2011) to create a single multiplesequence alignment. The dataset was partitioned into three partitions (ITS, 28S, and rpb2). After that, we ran maximum likelihood (ML) analyses using the IQ-TREE web server with 1,000 bootstrap replicates of ultrafast bootstrap resamplings (Trifinopoulos et al. 2016). The best-fit models of each partitions for BI analyses were determined by MrModeltest v.2.3 (Nylander 2004). Finally, the Bayesian Inference (BI) analyses was performed using MrBayes v.3.2.7a (Ronguist et al. 2012) with the selected model for each partition. Four Markov chains were conducted with sampling for every 100th generation. The first 25% of trees were discarded after the average standard deviation of split frequencies under 0.01 (Ronquist et al. 2012). This analysis allowed to generate a posterior probability tree that reflected the most likely evolutionary history of the studied genes. The results were edited using the FigTree v.1.4.3 software. Support values (with an ML bootstrap proportion \geq 70% or BI posterior probability \geq 95%) were shown on each branch.

3. Results

3.1. Molecular phylogeny

This study generated 95 new sequences (31 of ITS, 32 of 28S, and 32 of rpb2) and submitted to GenBank (Table 1). Sequence alignment was deposited at TreeBase (submission ID TB2:S31402, www.treebase.org). In the dataset, the ITS partition included 138 taxa and 807 sites, the 28S partition included 147 taxa and 1,265 sites, and rpb2 included 112 taxa and 586 sites. The following DNA substitution models were automatically selected by IQTREE for the ML analyses: ITS (TVM+F+I+G4), 28S (GTR+F+I+G4), and rpb2 (TIM2e+I+G4). The ML phylogenetic analysis yielded a final log-likelihood value of -33333.751. The best-fit models selected by MrModeltest for each gene are GTR+I+G equally. For the Bayesian analysis, a total of 12,485,000 MCMC generations were run using four Metropolis Coupled Monte Carlo Markov chains to calculate posterior probabilities and the standard deviation of the split frequencies was terminated at 0.009985.

Our ML/BI tree shows *Inocybe lasseri*, *I. carpinocola*, and *I. acutata*, together with four well-supported major subclades (namely *alienospora* subclade, *hydrocybiformis* subclade, *stellata* subclade, and

pseudoasterospora subclade) clustered within the *I. alienospora* group. The *I. alienospora* group shows no clear relationship with respect to other lineages of the genus *Inocybe*. *Inocybe* multicoronata and *I. elata* cluster together but are distant from the *I. alienospora* group (Figure 1).

The seven potential new species formed separate lineages within the *I. alienospora* group with high support values. *Inocybe aprica*, *I. casuarinoides*, *I. haikouensis*, and *I. heteromorpha* nested in the *alienospora* subclade; *I. aprica* sister to *I. lasseroides*; *I. haikouensis* sister to *I. casuaroides*, *I. heteromorpha* clustered with *I.* aff. *alienospora* PBM3758 but with weak support. *Inocybe aurescens* and *I. juji* are nested in the *hydrocybiformis* subclade and are sister species to each other. *Inocybe peppa* nested in the *pseudoasterospora* subclade as a sister to *Inocybe* sp. FYG1146.

3.2. Taxonomy

Inocybe sect. *Leptocybe* Takah. Kobay., Nova Hedwigia 124: 28. 2002.

Type: *Inocybe acutata* Takah. Kobay. & Nagas. Mycotaxon 48: 461 (1993).

Diagnosis: Basidiomata small, brown or yellowish brown, *pileus* < 20 mm often appressed fibrillose to recurved-squamulose; lamellae moderately crowded, edge not distinctly fimbriate; stipe slender with an enlarged but non-bulbose base, brownish with a pronounced greyish white layer of veil remnants; basidiospores angular-nodulose to stellate or spinose with simple spiny or saddle-shaped projections; *pleurocystidia* absent in some species, when present slightly thick-walled with yellowish walls $<2 \,\mu m$ thick, or thin-walled with yellowish pigments; cheilocystidia mostly thin-walled, or slightly thick-walled; *caulocystidia* at stipe apex, if present. **Odor** often fungoid, spermatic, or aromatic. Forming a monophyletic group based on multi-gene phylogeny. Tropical to temperate Asia, Europe, North America, and northern South America; on soil forming plant associations with Betulaceae, Casuarinaceae, Dipterocarpaceae, Fagaceae, Pinaceae, Myrtaceae, and Salicaceae.

Included species: Inocybe acutata, I. alienospora, I. aprica sp. nov., I. aurescens sp. nov., I. babruka, I. casuarinoides sp. nov., I. carpinicola, I. haikouensis sp. nov., I. heteromorpha sp. nov., I. hydrocybiformis, I. juji sp. nov., I. kuruvensis, I. lasseri, I. lasseroides, I. papilliformis, I. perlucida, I. peppa sp. nov., I. pseudoasterospora, I. stellata.

	Reference	Bandini et al. (2022c)	Bandini et al. (2017)	This study	This study	This study	Matheny and Bougher (2017)	Horak et al. (2015)	Matheny and Bougher (2017)		Matheny and Bougher (2017)	Matheny and Bougher (2017) Horak et al. (2015)	Matheny and Bougher (2017) Horak et al. (2015) This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study This study Larsson et al. (2018)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2010)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Marchetti et al. (2014)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Cripps et al. (2020)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Cripps et al. (2020) This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Byberg et al. (2018) Marchetti et al. (2014) Cripps et al. (2020) This study This study	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study This study Harsson et al. (2010) Marchetti et al. (2014) Cripps et al. (2020) This study Matheny et al. (2009)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study This study Hyberg et al. (2018) Marchetti et al. (2014) Cripps et al. (2020) This study This study Matheny et al. (2009) Latha and Manimohan (2017)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Marchetti et al. (2014) Cripps et al. (2020) This study This study This study Matheny et al. (2009) Latha and Manimohan (2017) Aignon et al. (2022)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Marchetti et al. (2014) Cripps et al. (2014) Cripps et al. (2020) This study This study This study Matheny et al. (2009) Latha and Manimohan (2017) Aignon et al. (2022)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Marchetti et al. (2014) Cripps et al. (2020) Marchetti et al. (2020) Matheny et al. (2009) Latha and Manimohan (2017) Aignon et al. (2022) Horak et al. (2015)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Ryberg et al. (2018) Ryberg et al. (2014) Marchetti et al. (2014) Cripps et al. (2020) Marchetti et al. (2020) Matheny et al. (2022) Aignon et al. (2022) Aignon et al. (2017) Matheny and Bougher (2017)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Ryberg et al. (2018) Ryberg et al. (2014) Gripps et al. (2014) Cripps et al. (2020) Marchetti et al. (2014) Gripps et al. (2020) This study Matheny et al. (2022) Aignon et al. (2022) Aignon et al. (2022) Matheny and Bougher (2017) Ryberg et al. (2008)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Ryberg et al. (2018) Ryberg et al. (2014) Cripps et al. (2014) Cripps et al. (2020) Marchetti et al. (2014) Cripps et al. (2020) Matheny et al. (2022) Afginon et al. (2022) Afginon et al. (2022) Matheny and Bougher (2017) Ryberg et al. (2008) Matheny et al. (2002)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Larsson et al. (2018) Ryberg et al. (2014) Cripps et al. (2014) Cripps et al. (2020) Marchetti et al. (2020) This study This study This study This study Matheny et al. (2022) Arginon et al. (2022) Horak et al. (2022) Matheny and Bougher (2017) Ryberg et al. (2002) He et al. (2002) He et al. (2002)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Byberg et al. (2018) Ryberg et al. (2014) Cripps et al. (2014) Cripps et al. (2020) Marchetti et al. (2020) This study Matheny et al. (2022) Afgnon et al. (2022) Afgnon et al. (2022) Horak et al. (2022) Matheny and Bougher (2017) Ryberg et al. (2002) He et al. (2022) He et al. (2022) He et al. (2022) He et al. (2022)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Byberg et al. (2018) Byberg et al. (2014) Gripps et al. (2014) Cripps et al. (2020) Marchetti et al. (2020) This study Matheny et al. (2022) Aignon et al. (2022) Aignon et al. (2022) Horak et al. (2022) Matheny and Bougher (2017) Byberg et al. (2002) He et al. (2022) He et al. (2022)	Matheny and Bougher (2017) Horak et al. (2015) This study This study This study Byberg et al. (2018) Byberg et al. (2014) Cripps et al. (2014) Cripps et al. (2020) Matheny et al. (2020) This study Matheny et al. (2022) Arginon et al. (2022) Arginon et al. (2022) Horak et al. (2022) Matheny and Bougher (2017) Byberg et al. (2002) He et al. (2022) He et al. (2022)				
b2 (a Bandini et al. (2) /a Bandini et al. (2) 5214 This study 6981 This study /a This study	 (a Bandini et al. (2) (a Bandini et al. (2) (5214 This study (6981 This study (a This study 	 A Bandini et al. (2 5214 This study 6981 This study /a This study 	5214 This study 6981 This study /a This study	6981 This study /a This study	/a This study	•	15973 Matheny and Bo	/a Horak et al. (20	15995 Matheny and Bo	15994 Matheny and Bo	15996 Matheny and Bo	15970 Matheny and Bo	15971 Matheny and Bo	15974 Matheny and Bo	(1) Horak et al (20)	1477 IINIAN CLAIN / TN	'5210 This study	5210 This study 5211 This study	 7422 Transmission of the study 5211 This study 6975 This study 	 7422 Trivian of an environment of the study 5211 This study 6975 This study 6976 This study 	 7422 This study 5210 This study 6976 This study 6976 This study 6376 Larsson et al. (2 	 7422 This study 5210 This study 6976 This study 	 7422 This study 5210 This study 5211 This study 6976 This st	 7422 This study 5210 This study 5211 This study 6976 This st	 7422 This study 5210 This study 5211 This study 6976 This study 7/a Cripps et al. (20 75213 This study 	 7422 Invitance on contract 5210 This study 5211 This study 6976 This study 7/a Ryberg et al. (20 7/a Cripps et al. (20 5213 This study 5212 This study 	 5210 This study 5211 This study 6975 This study 6976 This study 6976 This study 6976 This study 6976 This study 7 a Ryberg et al. (20 7 a Marchetti et al. (20 7 a This study 5213 This study 7364 Matheny et al. (20 	 7.2.2. This study 5.210 This study 6.975 This study 6.976 This study 6.976 This study 6.976 This study 7.4 Ryberg et al. (20 7.3 Ryberg et al. (20 7.3 Ryberg et al. (20 7.3 This study 7.3 This study 7.3 This study 7.3 This study 7.3 Antheny et al. (3237 Latha and Mani 	 7422 This study 5210 This study 6975 This study 6976 This study 7364 Ryberg et al. (20 7364 This study 7364 Matheny et al. (31 3237 Latha and Mani 73 7360 et al. (21 	 7422 This study 5210 This study 6975 This study 6976 This study 7364 Marchetti et al. 7364 This study 5213 This study 5213 This study 53237 Latha and Mani (a Aignon et al. (2) (a Aignon et al. (2) 	 7422 This study 5210 This study 6975 This study 6976 This study 7364 Marchetti et al. 7364 This study 5213 This study 5213 This study 5213 This study 63 Algnon et al. (20 73 Algnon et al. (20 	 7422 This study 5210 This study 6975 This study 6976 This study 6976 This study 6976 This study 6976 This study 7a Ryberg et al. (2) 7a Marchetti et al. 7364 Cripps et al. (20 5213 This study 5213 This study 5213 This study 5213 This study 6422 Matheny and B. 	 7322 This study 5210 This study 6975 This study 6976 This study 6976 This study 6976 This study 64 Ryberg et al. (2) 7a Marchetti et al. 7364 Cripps et al. (20 7364 This study 5213 This study 5213 This study 6422 Matheny et al. (2) 7a Nignon et al. (2) 7a Aignon et al. (2) 	 7322 This study 5210 This study 6975 This study 6976 This study 6976 This study 6976 This study 6976 This study 7a Ryberg et al. (20 7364 Marchetti et al. 7364 This study 7364 Matheny et al. (20 7364 Matheny and B 7365 Matheny and B 6422 Matheny and B 7365 Matheny et al. (20 	 7322 This study 5210 This study 6975 This study 6976 This study 6976 This study 6976 This study 6976 This study 7a Ryberg et al. (20 7a Marchetti et al. 7364 Marchetti et al. (21 7365 Marchetti et al. (22 7365 Marchetti et al. (222) 	 7.1 5.210 This study 5.211 This study 6.976 This study 6.976 This study 6.976 This study 7.10 Ryberg et al. (2) 7.11 Ryberg et al. (2) 7.12 A Marchetti et al. (2) 7.13 This study 7.364 Matheny et al. (2) 7.364 Matheny et al. (2) 7.364 Matheny et al. (2) 7.365 Matheny and B 7.365 Matheny and B 7.365 Matheny et al. (2022) 7.3087 He et al. (2022) 	 7.2.2. This study 5.210 This study 6.976 This study 6.976 This study 6.976 This study 6.976 This study 7.3.17 Ryberg et al. (20 7.3.13 This study 7.3.14 Matheny et al. (2) 7.3.17 Matheny et al. (2) 7.3.18 Matheny et al. (2) 7.3.19 Matheny et al. (2) 	 5210 This study 5211 This study 6975 This study 6976 This study 6976 This study 6976 This study 63 Ryberg et al. (20 7364 Marchetti et al. 7364 This study 7364 This study 7364 Matheny et al. (20 7364 Matheny et al. (20 7365 Matheny et al. (20 7365 Matheny and B 6422 Matheny et al. (20 7365 Matheny and C 7365 Matheny and A 7365 Matheny and A 7366 Matheny et al. (2022) 7085 He et al. (2022) 7085 He et al. (2022)
rpb2		n/a	n/a	OR77521	PP35698	n/a	KM24597	n/a	KM24599	KM24599	KM24599	KM24597	KM24597	KM24597		MH57742	MH57742 OR77521	MH57742 OR77521 OR77521	MH57742 OR77521 OR77521 PP35697	MH57742 OR77521 OR77521 PP35697	MH57742 OR77521 OR77521 PP35697 PP35697	MH57742 OR77521 OR77521 PP35697 n/a n/a	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a n/a n/a 0/a	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a n/a n/a OR77521	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a n/a OR77521 AY33736	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a n/a AY35721 AY33736 KY55323	MH57742 OR77521 OR77521 PP35697 n/a n/a n/a AY33736 KY55323 KY55323 N/a	MH57742 OR77521 OR77521 PP35697 n/a n/a AY33736 KY55323 N/a n/a	MH57742 OR77521 OR77521 PP35697 N/a n/a AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY33736 AY377521	MH57742 OR77521 OR77521 PP35697 N/a N/a N/a N/a AY33736 KY55323 N/a N/a N/a N/a N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a n/a n/a AY33736 KY55323 KY55323 N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a N/a N/a N/a N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a N/a N/a N/a N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a N/a N/a N/a N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a N/a N/a N/a N/a N/a N/a N/a	MH57742 MH57742 OR77521 PP35697 N/a N/a N/a N/a N/a N/a N/a N/a
	28S	OP164062	MG136997	OR760305	OR975609	n/a	KM197212	GQ892973	KP170927	KP170926	KP170928	KM197209	KM197210	KJ801158	60802047	74/70000	OR760197	OR760197 OR760266	OR760197 OR760266 OR975625	OR760197 OR760197 OR760266 OR975625 OR975626	OR760197 OR760166 OR975625 OR975626 KY033843	OR760197 OR760166 OR975625 OR975626 KY033843 FN550889	00015742 00075625 000975625 000975626 100033843 FN550889 n/a	00025242 000760197 0009756256 0009756256 0009756256 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756250 0009756255 00097555 0000000000	00025242 000760197 0009756256 0009756256 0009756250 0009756250 000760276 000760276	OCC 20197 OR760197 OR975626 OR975626 KY033843 FN550889 n/a MN296110 OR760276 n/a	OCTOR 100 CONTINUE CO	OR760197 OR760197 OR9756266 OR975626 KY033843 FN550889 n/a MN296110 OR760276 n/a AY239018 KY549116	OR760197 OR760197 OR9756256 OR9756256 KY033843 FN550889 n/a MN296110 OR760276 n/a AY239018 KY549116 MN097888	OR760197 OR760197 OR9756256 OR9756256 KY033843 FN550889 n/a MN296110 OR760276 n/a AY239018 KY549116 MN097888 n/a	OR760197 OR760197 OR9756256 OR9756266 KY033843 FN550889 n/a MN296110 OR760276 n/a AY239018 KY549116 MN097888 n/a GQ892974 GQ892974	OR760197 OR760197 OR975625 OR975626 OR975626 N/a MN296110 OR760276 n/a AY239018 KY549116 MN097888 MN097888 N/a GQ892974 KJ756464	OC72525 OR760197 OR760266 OR975626 OR975626 N/a MN296110 OR760276 n/a AY239018 KY549116 MN097888 KY549116 MN097888 KY549116 MN097888 KY549116 MN097888 KY549116 MN097888 AX882760	OC7560197 OR760197 OR975625 OR975626 OR975626 N/a N/a N/a N/a CQ892974 N/a GQ892974 N/3882760 AY038313	OC7560197 OR760197 OR756265 OR9756265 CN933843 FN550889 n/a MN296110 OR760276 n/a AV239018 KY549116 MN997888 n/a GQ892974 KY756464 AM882760 AY0338313 OP207866	OC20505 OR760197 OR760266 OR975626 OR975626 N/a MN296110 OR760276 n/a AV239018 KY549116 MN297888 n/a GQ892974 KY7549116 MN297888 AV239018 KY549116 MN297883 AV233018 CV756464 AM882760 AY033313 OP207866 OP2078669	OC7560197 OC760197 OC760197 OC760197 OC760266 N/a N/a N/a N/a AV239018 N/a AV239018 N/a GQ892974 K/549116 N/a GQ892974 K/549116 N/a GQ892974 K/549116 N/a S207869 OC756464 AM882760 AV038313 OC7207869 OP207868	OC205050 OR7560197 OR7560266 OR9756256 N/033843 FN550889 n/a MN296110 OR760276 n/a AY239018 KY549116 MN097888 N097888 N097888 AM882760 AM882760 AV038313 OP207866 OP2078667
len	ITS	NR_185439	MG136902	OR759137	OR975593	OR755906	KP171107	GQ893018	KP171148	KP171147	KP171149	KP171104	KP171105	KJ778848	GQ892988		OR755901	OR755901 OR755912	0R755901 0R755912 0R975607	0R755901 0R755912 0R975607 0R975608	OR755901 OR755912 OR975607 OR975608 KY033843	OR755901 OR755912 OR975607 OR975608 KY033843 FN550889	OR755901 OR755912 OR975607 OR975608 KY033843 FN550889 FN550889 KM873366	OR755901 OR755912 OR975607 OR975608 KY033843 FN550889 KM873366 MN296110	OR755901 OR755912 OR975607 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913	OR755901 OR755912 OR975608 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755902	OR755901 OR755912 OR975607 OR975608 KY033843 FN550889 KM873366 MN296110 OR755913 OR755913 OR755902	OR755901 OR755912 OR975607 OR975608 KY033843 FN550889 KM873366 MN296110 OR755913 OR755913 OR755902 N/a KY440086	OR755901 OR755912 OR975608 KY033843 FN550889 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755902 N/a KY440086 MN096196	OR755901 OR975607 OR975608 OR975608 KY033843 FN55089 KM873366 MN296110 OR755902 n/a KY440086 MN096196 MT994602	OR755901 OR975607 OR975608 OR975608 KY033843 FN55089 KW873366 MN296110 OR755902 N/a KY440086 MN096196 MN096196 MN096196 MN095123 NR_153123	OR755901 OR755912 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 MY296196 MN096196 MT994602 MR_153123 KJ778845	OR755901 OR755912 OR975607 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 N/a KY440086 MN096196 MT994602 MR_153123 KJ778845 AM882760	OR755901 OR755912 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 N/a KV440086 MN096196 MT994602 MT994602 NR_153123 KJ778845 AM882760 n/a	OR755901 OR755912 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 NN296196 MN096196 MT994602 NR_153123 KJ778845 AM882760 NR_153123 R1778845 OR207871	OR755901 OR755912 OR975608 KY033843 FN55089 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 NN296196 MN096196 MN096196 MN096196 MN096196 MN096196 MN096196 MN096196 MN096196 MN096196 MN096196 MN294602 NR_1778845 AM882760 OP207875 OP207875	OR755901 OR755912 OR975608 KY033843 FN550889 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 NN2961196 M1994602 MN096196 M1994602 NR_153123 KJ778845 MN096196 M1994602 NR_153123 KJ778845 OR207871 OP207875 OP207875	OR755901 OR755912 OR975608 KY033843 FN550889 KM873366 MN296110 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 OR755913 NN296196 MN996196 MN996196 MN996196 MN153123 KJ778845 MN2974602 NR_153123 KJ778845 MN297602 NR_153123 CO207877 OP207877 OP207877
	Locality	Germany	Finnland	China	China	China	Australia	Thailand	Australia	Australia	Australia	Australia	Australia	Australia	Thailand		China	China China	China China China	China China China China	China China China Norway	China China China Norway Sweden	China China China Norway Sweden	China China China Norway Sweden Sweden	China China China Norway Sweden Sweden China	China China China China Sweden Sweden China	China China China Norway Sweden Sweden China Guyana	China China China Norway Sweden Sweden Sweden China Guyana India	China China China Norway Sweden Sweden Sweden China Guyana India Benin	China China China Norway Sweden Sweden Sweden China Guyana Guyana Benin Benin	China China China China Sweden Sweden Sweden Sweden China Guyana Guyana Guyana Benin Benin Thailand	China China China China Sweden Sweden Sweden Sweden China Guyana Guyana India Benin Benin Australia	China China China China Sweden Sweden Sweden China Guyana India Benin Benin Australia Estonia	China China China China Sweden Sweden Guyana Guyana Guyana India Benin Benin Australia Estonia Sweden	China China China China Norway Sweden China Guyana Guyana Benin Benin Benin Benin Estonia Estonia China	China China China China Norway Sweden Sweden Benin Benin Benin Benin Estonia Estonia China	China China China China Norway Sweden Sweden Benin Benin Benin Estonia Sweden China China	China China China China Norway Sweden China Guyana Guyana India Benin Benin Benin Sweden China China China
	Voucher	STU SMNS STU F 0901691	DB24-8-15-7	NJ4747	NJ4119	FYG4322	PBM3758	DED8165	PBM3787	PBM3786	TJB10466	PBM3743	REH9667	TENN 067007 (PBM3775)	DED8139	EVG76AD		FYG7641	FYG7641 FYG9907	F1 G2 G41 FY G907 FY G908	F10,047 FYG9907 FYG9908 JV2238	F10/041 FYG9907 FYG908 JV2238 EL9906	F10,047 FYG9907 FYG9908 JV2238 EL9906 M 0020105	F10,047 FYG9907 FYG9908 JV2238 EL906 M 0020105 EL100-14	F10/041 FYG9907 FYG9908 JV2238 EL 906 M 0020105 EL 100-14 FYG2015387	F10,042 FYG7641 FYG9907 FYG908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387	F100,040 FYG7641 FYG9907 FYG908 JV2238 EL9006 M 0020105 EL100-14 FYG2015387 MCA 1232 MCA 1232	F100,044 FYG7641 FYG9907 FYG908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 FYG2871 MCA 1232 CAL 1344	F100,040 FYG7641 FYG9908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 MCA 1232 CAL 1344 HLA0390	F100,040 FYG9907 FYG9908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 MCA 1232 CAL 1344 HLA0390 HLA0390	F10,077 FYG9907 FYG9908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 FYG2015387 CAL 1344 HLA0390 HLA0390 HLA0467 ZT10102	F100,040 FYG5908 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2871 MCA 1232 CAL 1344 HLA0390 HLA0467 ZT10102 PBM3790	F100.047 FYG9908 JV2238 EL906 M 0020105 EL 100-14 FYG2015387 FYG2015387 FYG2015387 CAL 1344 HLA0390 HLA0390 HLA0467 ZT10102 PBM3790 TAA185175	F100,044 FYG5908 JV2238 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 FYG2015387 CAL 1344 HLA0390 HLA0390 HLA0467 ZT10102 PBM3790 TAA185175 JFA 12539	F100,047 FYG9908 JV2238 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 FYG2015387 CAL 1344 HLA0390 HLA0390 HLA0467 ZT10102 PBM3790 TAA185175 JFA 12539 FYG6297	F100.010 FYG9908 JV2238 JV2238 EL906 M 0020105 EL100-14 FYG2015387 FYG2015387 EL100-14 FYG2015387 FYG2015387 CAL 1344 HLA0467 TAA185175 JFA 12539 FYG6297 FYG6300	FYG7641 FYG9907 FYG9908 JV2238 EL906 M 0020105 EL 100-14 FYG2015387 FYG2015387 FYG2015387 FYG2015387 FYG2015387 FYG2015387 ALA0467 ALA0467 ALA0467 ALA0467 ALA0467 ALA0467 ALA0467 ALA0467 ATA0185175 JFA 12539 FYG6200 FYG6300 FYG6300	FYG7641 FYG9907 FYG9908 JV2238 EL906 M 0020105 EL 100-14 FYG2015387 FYG2015387 FYG2015387 FYG2015387 FYG2015387 FYG2015387 FYG2012 PBM3790 HLA0467 ZT10102 PBM3790 HLA0467 ZT10102 PBM3790 FYG6300 FYG6300 FYG6307 FYG6312
							ra	formis	S	Sa	es											ea	ва	Da	D2	Ø	8	8 _ 0	e ee	8	ea nilosa	e e	ee	ulosa	e e e	ee	a ae nulosa	a ae b b b b b b b b b b b b b b b b b b

(Continued)

Table 1. (Continued).						
			GenBa	nk accession numb	er	
Таха	Voucher	Locality	ITS	28S	rpb2	Reference
I. carpinicola	HK 0987	China	n/a	PP346377	PP356978	This study
I. carpinicola	HK 0986	China	n/a	PP346378	PP356979	This study
I. casuarinoides	FYG8120	China	OR755908	OR759977	OR775205	This study
I. casuarinoides	FYG8122	China	OR755899	OR759975	OR775204	This study
I. casuarinoides	FYG8123	China	OR755909	OR759978	OR775206	This study
I. casuarinoides	FYG9871	China	OR975605	OR975623	PP356973	This study
I. casuarinoides	FY G9895	China	OR975606	OR975624	PP356974	This study
I. cerasphora	BSI 01/184	Chile	n/a	AY380370	AY337367	Matheny (2005)
I. chalcoceps	TENN:068946	Australia	n/a	NG_057228	n/a	Matheny and Bougher (2017)
I. chondroderma	PBM1776	USA	GU949579	JN974967	MH249789	Matheny et al. (2013)
I. conspicuospora	PC96042	Zambia	n/a	EU555471	EU555470	Matheny et al. (2009)
I. diabolica	EL9006	Sweden	FN550896	FN550896	n/a	Ryberg et al. (2010)
I. dunensis	EL 22906	France	FN550888	FN550888	n/a	Ryberg (Unpublished)
I. elata	HMJAU37797/HMJAU01	China	MG744559	KY773232	n/a	Liu et al (2018)
I. epidendron	TH9186	Guyana	JN168725	EU569840	n/a	Matheny et al. (2009)
I. ericetorum	TURA 177504	Finland	NR_119994	n/a	n/a	Kokkonen and Vauras (2012)
I. flavipes	MR00383	Togo	MN096197	MN097889	MW080915	Aïgnon et al. (2022)
I. flavipes	HLA0363	Benin	MT994601	n/a	n/a	Aïgnon et al. (2022)
I. flavoalbida	PBM3768	Australia	KJ729873	KJ729901	KJ729932	Matheny and Bougher (2017)
l. fuscicothurmata	PBM3980	North Carolina	MF487844	KY990485	MF416408	Larsson et al. (2014)
I. fuscobrunnea	MR00378	Burkina Faso	MN096201	MN097893	MW219733	Aïgnon et al. (2022)
I. fuscobrunnea	HLA0567	Ivory Coast	MT994603	n/a	n/a	Aïgnon et al. (2022)
I. giacomi	JV21543	Finland	MK153656	MK153656	n/a	Cripps et al. (2020)
I. glaucodisca	PC 96081	Zambia	n/a	EU569853	n/a	Matheny et al. (2009), Deng et al. (2022b)
I. haikouensis	FY G9866	China	OR975600	OR975618	PP356969	This study
I. haikouensis	FY G9867	China	OR975601	OR975619	PP356970	This study
I. haikouensis	FY G9868	China	OR975602	OR975620	PP356983	This study
I. haikouensis	FYG9870	China	OR975603	OR975621	PP356971	This study
I. haikouensis	FY G9893	China	OR975604	OR975622	PP356972	This study
I. heteromorpha	FY G5769	China	OR755900	OR759987	OR775207	This study
I. heteromorpha	FY G5769a	China	OR755910	OR760195	OR775208	This study
I. heteromorpha	FYG5769b	China	OR755911	OR760196	OR775209	This study
I. hopeae	OR1665	Thailand	n/a	ON831503	ON553692	Raghoonundon et al. (2023)
I. hydrocybiformis	CAL 1376	India	KY440090	KY549120	KY553240	Matheny and Bougher (2017)
I. hydrocybiformis	TBGT: 12318	India	KP171130	KP170911	KM245987	Matheny and Bougher (2017)
I. hydrocybiformis	ZT10077	Thailand	GQ893016	GQ892971	n/a	Matheny and Bougher (2017)
I. hydrocybiformis	CAL 1378	India	KY440091	KY549121	n/a	Matheny and Bougher (2017)
I. hydrocybiformis	ZT9879	Thailand	GQ893017	GQ892972	n/a	Horak et al. (2015)

⁽Continued)

			Genl	ank accession num	ber	
Таха	Voucher	Locality	ITS	28S	rpb2	Reference
I. juji	119	China	OR975594	OR975612	PP356965	This study
I. juji	147	China	OR975595	OR975613	PP356966	This study
I. juji	123	China	OR975596	OR975614	PP356982	This study
I. juji	653	China	OR975597	OR975615	PP356967	This study
I. juji	187	China	OR975598	OR975616	n/a	This study
I. juji	180	China	OR975599	OR975617	PP356968	This study
I. kapila	CAL 1346	India	KY 440093	KY549123	n/a	Latha and Manimohan (2017)
I. kurkuriya	CAL 1352	India	KY440095	KY549125	KY553245	Latha and Manimohan (2017)
I. kuruvensis	K(M) 191734	India	KM924522	KM924517	KY553246	Latha and Manimohan (2016)
I. lacera	PBM2541	USA	KP171144	JN974993	KM245991	Ryberg and Matheny (2012)
I. lacunarum	JV12244	Finland	KT958908	KT958908	n/a	Vauras and Larsson (2015)
I. lanuginosa	PBM3023	USA	HQ232480	KP170923	KM245992	Matheny et al. (2020)
I. lasseri	MCA 1971	Guyana	n/a	EU569857	EU569856	Matheny et al. (2009)
I. lasseroides	PBM3749	Australia	KP171145	KP170924	KM245993	Matheny and Bougher (2017)
I. lasseroides	PBM3750	Australia	KP171146	KP170925	n/a	Matheny and Bougher (2017)
I. leptophylla	BK 7-Sept-97-19 (UTC)		n/a	AY038320	n/a	Matheny et al. (2002)
I. lilacinosquamosa	MCA 1464	Guyana	n/a	AY380386	AY337389	Matheny et al. (2009)
I. lineata	DED8048	Thailand	n/a	GQ892958	KM245999	Horak et al. (2015)
I. melanopus	PBM3975	Tennessee	n/a	MH220276	MH249807	Matheny et al. (2020)
<i>I. mixtilis</i>	ARAN-Fungi 4711	Spain	MH500842	MH500842	MH496022	Esteve-Raventós et al. (2018)
I. multicoronata	DG1818A	Canada	MH578007	MH539763	n/a	Matheny and Hobbs (Unpublished)
l. napipes	PBM2376	Norway	n/a	AY239024	AY337390	Kropp and Matheny (2004)
I. nothomixtilis	AH 46558, MC0003	Spain, Italy	MT384015	n/a	MH496025	Esteve-Raventós et al. (2018)
I. oblectabilis	BJ920908	Sweden	AM882831	AM882831	n/a	Ryberg et al. (2008)
I. obtusiuscula	PAM02081710	France	HQ586869	HQ641112	n/a	Matheny and Bougher (2017)
I. occulta	AH 36443	Spain	NR_160564	n/a	MH496017	Esteve-Raventós et al. (2018)
I. pallidiangulata	MR00377	Burkina Faso	MN096202	MN097894	MW219732	Aïgnon et al. (2022)
I. pallidiangulata	MR00379	Burkina Faso	MZ605434	n/a	n/a	Aïgnon et al. (2022)
I. pallidicremea	PBM2448	USA	HQ201357	HQ201357	MF416425	Matheny and Swenie (2018), Matheny et al. (2020)
l. papilliformis	CAL 1372	India	KY440096	KY549126	n/a	Latha and Manimohan (2017)
l. papilliformis	CAL 1374	India	KY440097	KY549127	n/a	Latha and Manimohan (2017)
I. papilliformis	TBGT: 10480	India	KP171131	KP170912	KM245988	Latha and Manimohan (2017)
I. parvibulbosa	DED8021	Thailand	GQ892999	GQ892954	KM555134	Horak et al. (2015)
І. рерра	NJ4118	China	OR975591	OR975610	PP356984	This study
І. рерра	NJ4117	China	OR975592	OR975611	PP356980	This study
I. perlucida	DB20-8-16-33	Germany	MN803157	MN803157	n/a	Bandini et al. (2020)
I. perlucida	PBM4328	USA	MT228849	MT228849	n/a	Matheny and Lewis (Unpublished)
I. persicinipes	PBM2197	Australia	KF977215	EU600837	EU600836	Matheny et al. (2009), Matheny and Bougher (2017)
						(Continued)

Table 1. (Continued).

(Continued).	
1.	
e	
Tabl	

																																								-
	Reference	Latha and Manimohan (2017)	Bandini et al. (2020)	Esteve-Raventós et al. (2015)	Bandini et al. (2020)	Boutard (Unpublished)	Matheny et al. (2009)	Matheny et al. (2002)	Matheny and Bougher (2017)	Latha and Manimohan (2017)	Matheny and Bougher (2017)	Osmundson et al. (2013)	This study	Zhou (Unpublished)	Zhou (Unpublished)	Bonito et al. (Unpublished)	Bonito et al. (Unpublished)	Bonito et al. (Unpublished)	Matheny and Bougher (2017)	Horak et al. (2015)	Latha and Manimohan (2017)	Cho et al. (2021)	Zhou (Unpublished)	Kantharaja and Krishnappa (Unpublished)	Rockefeller (Unpublished)	Ryberg et al. (2008)	Matheny and Bougher (2017)	Matheny and Bougher (2017)	Matheny et al. (2009), Horak et al. (2015)	Matheny et al. (2009), Horak et al. (2015)	Matheny and Moreau (2009)	Esteve-Raventós et al. (2015)	Matheny et al. (2009)							
nber	rpb2	n/a	n/a	n/a	n/a	n/a	n/a	AY333778	KM555111	KY553250	KF830049	n/a	OR775215	n/a	n/a	n/a	n/a	n/a	KM656103	KM656106	KM656107	KM555135	KM656105	n/a	n/a	KM656104	KY553251	n/a	n/a	n/a	n/a	n/a	KM656115	KM656126	KM656129	EU600873	EU307855	n/a	n/a	
ıBank accession nur	28S	KY549128	MN512327	HQ604401	MN803152	MZ615409	EU600842	AY038324	KP171012	KY549135	KF808343	JF908197	OR760463	MW554023	MW554479	KP013044	KP013048	KP012875	KP171064	GQ892966	GQ892965	GQ892967	GQ892962	GQ892963	GQ892964	GQ892961	KY549136	n/a	MW554024	MW425863	MG871168	AM882754	KP171070	NG_057199	GQ892968	EU600874	AY732211	HQ641097	EU600880	
Ger	ITS	KY440098	MN512327	HQ604401	MN803152	MZ615409	n/a	AY038324	KP636810	KY440105	KF830031	JF908197	OR759138	MW554023	MW554479	KP013044	KP013048	KP012875	KP636868	GQ893011	GQ893010	GQ893012	GQ893007	GQ893008	GQ893009	GQ893006	KY440106	MW520962	MW554024	MW425862	MG871168	AM882754	KP636874	NR_153163	GQ893013	n/a	MK429956	HQ586856	n/a	
	Locality	India	Netherlands	Canada	Italy	No	Guyana	Finland	Australia	India	Australia	Italy	China	China	China	Australia	Australia	Australia	Australia	Thailand	India	Korea	China	India	Bangladesh	Finland	Australia	Australia	Thailand	Australia	USA	France	British Virgin Islands							
	Voucher	CAL 1362	STU:SMNS-STU-F-0901254	UBC:F19334	STU:SMNS-STU-F-0901288	a	MCA1122	JV 10258	PBM3235	CAL 1350	MR00219	TO-2011	FYG1146b	110114MFBPZH0771	130822MFBPL0312	MEL: 2382681	MEL: 2382684	MEL: 2382696	PBM3748	DED8015	DED8060	ECV3648	ECV3651	ZT10097	ZT10123	DED8162	CAL1369	KA18-0494	110114MFBPZH0761	KUBOT-KRMK-2020-34	Mushroom Observer.org/161869	EL 8905	PERTH:08074437	TENN:065735	DED8049	PBM2157/E6978	PBM2550	PAM08082901	GUA242	
	Таха	I. pileosulcata	I. pluppiana	I. praetervisa	I. pseudoasterospora	I. pseudoasterospora	I. pulchella	I. relicina	l. serrata	I. snigdha	<i>I.</i> sp.	<i>I.</i> sp.	l. sp.	<i>l.</i> sp.	<i>l.</i> sp.	<i>I.</i> sp.	<i>l.</i> sp.	<i>I.</i> sp.	I. spiniformis	I. stellata	l. stellata	I. stellata	I. stellata	I. stellata	I. stellata	I. stellata	I. stellata	l. subcarpta	l. subferruginea	I. sylvicola	I. thailandica	I. torresiae	I. tubarioides	I. xanthomelas	l. xerophytica					

MYCOLOGY 😸 819

<i>_</i> :	I
$\overline{\mathbf{n}}$	I
ă	I
¥	I
=	I
.⊑.	I
Ę	I
<u> </u>	I
0	I
Ú	I
9	
9	
1 .	
e 1. (C	
ole 1. (C	
ible 1. (C	
Table 1. (C	

			Gen	Bank accession num	ber		
Таха	Voucher	Locality	ITS	285	rpb2	Reference	
Nothocybe distincta	CAL 1310	India	KX171343	NG_057278	KX171345	Matheny et al. (2009), Latha et al. (2016)	
Nothocybe distincta	ZT 9250	India	n/a	EU604546	EU600904	Matheny et al. (2009), Latha et al. (2016)	
Uncultured ectomycorrhiza	L2360_In1	Seychelles	AM412271	AM412271	n/a	Tedersoo et al. (2007)	
Uncultured ectomycorrhiza	ECM9-PKDK	Thailand	DQ146372	DQ146372	n/a	Yuwa-Amornpi et al. (2006)	
Uncultured fungus	KT-32	New Caledonia	LC271312	LC271312	n/a	Houlès et al. (2022)	
Uncultured <i>Inocybe</i>	Ino6	Thailand	AB854674	AB854674	n/a	Kaewgrajang et al. (2014)	
Sequences updated in GenBank	and used in this study are shown in bold						1



Figure 1. Phylogram generated by ML and BI analysis based on a combined data set from nuclear genes (ITS, 28S, and *rpb2*). The tree is rooted with *Nothocybe distincta* (CAL1310 and ZT9250). Support values (ML-bp \geq 70% and BI-pp \geq 95% indicated by black circles; ML-bp \geq 70% and BI-pp \geq 95% indicated by grey circles centred in black; ML-bp < 70% and BI-pp \geq 95% indicated by black circles centred in grey) were shown in figure.

Species with uncertain position: Inocybe aurantiocystidiata, I. casuarinae, I. gemina, I. echinosimilis.

Remarks: Molecular phylogenetic analysis confirms the placement of 19 species in sect. Leptocybe, including its type, I. acutata. Inocybe subg. Leptocybe was established to accommodate species having angular, nodulose, echinulate, or stellate basidiospores, thinwalled cheilocystidia, and absence of metuloidal pleurocystidia with *I. acutata* as the type species (Kobayashi 1993), but this subgenus is polyphyletic as later Kobayashi (2002) established two sections within the subgenus: sect. Leptocybe, including I. acutata and I. hydrocibiformis and sect. Tylospora to accommodate I. cingulatipes and two varietal taxa within I. casimiri. The latter we equate with the I. lanuginosa group as I. casimiri has long been regarded as synonymous with I. leptophylla (Matheny and Kropp 2001). Inocybe sect. Inocybe is typified by *I. relicina* and includes species having fibrillose, woolly or scaly and brownish stipes and at times with yellowish, pinkish, or reddish pigments to the lamellae or context; the spores are nodulose, with some featuring a cruciate outline, but none have spores with bifurcate nodules; all species possess pleurocystidia (Matheny and Moreau 2009; Matheny and Kudzma 2019). Members of I. sect. Calosporae J.E. La-nge are characterised by spinose basidiospores and often with entirely pruinose stipes (Singer 1986); Inocybe lasseri was placed in I. sect. Calosporae by Singer (1986), but our results support placement in sect. Leptocybe. Inocybe petchii (Boed.) Horak was placed in I. sect. Calosporae by Singer (1986), but it has completely pruinose stipes and marginate stipe bases (Horak 1979). Furthermore, no sequence data were currently available, so it is not included in *I*. sect. *Leptocybe*.

Inocybe acutata Takah. Kobay. & Nagas., Mycotaxon 48: 461 (1993) Figures 2–3

Description: *Basidiomata* small, slender. *Pileus* 6–8 mm wide, campanulate or broadly conical with low umbo when young, when matured broadly campanulate or plano-convex with a pointed umbo; margin at first incurved, then recurved, excurved to straight when matured; surface dry, glabrous-fibrillose, silky-smooth with occasionally splited margin, veil remnants as appressed towards the umbo, striate outwards; uniformly yellowish-brown (4D6) when young, then darkly yellowish (5D8) or brownish

(5D6) to darkly brownish (5D8), brownish (5D5-5D6) with dirty whtite (1B2) umbo after matured, veil remnants whitish (4A1) to greyish white (4B2-4B3). Lamellae adnexed, close, up to 1.5 mm wide, alternately distributed with 3-4 tiers of lamellulae; colour whitish (4A1) or slightly yellowish (4B4-4B5), edge paler but not fimbriate. Stipe 27-30×0.9-1.2 mm, terete, equal with a slightly enlarged base; central, solid; surface dry, furfuraceous at apex, covered with a layer of appressed greyish white (4B2–4B3) fibrils made of veil remnants downwards; yellowish-brown (5C8-5D8) to brownish (5C6-5C7) when young, brown (5D6) to deeply brown (6D6) when matured. **Context** fleshy in Pileus, whitish (4A1) or slightly yellowish (4C4-4C5), 0.4-0.6 mm thick at mid-radius, up to 1.3 mm thick under the umbo; striate in stipe, whitish (4A1) or slightly yellowish (4C4-4C5). Odor indistinct.

Basidiospores [100/3/3], (8.0) 8.0-**8.9**-9.9 $(10.0) \times (6.0)$ 7.8–**8.2**–9.2 (10.0) µm, O = (1.00)1.00-1.06-1.14 (1.33), $Q_m \pm SD = 1.06 \pm 0.056$ excluding spines; (10.0) 10.9-12.3-13.7 (14.2) \times (9.5) 10.0-**11.4**-12.5 (13.0) μm, Q = (1.00) 1.00-**1.08**-1.16 (1.25), $Q_m \pm SD = 1.08 \pm 0.054$ including spines; spinose, globose or subglobose with numerous simple, nonbifurcate spines; slightly yellowish to yellowish in 5% KOH, some with yellowish ovoid inclusions. Basidia $30-36 \times 15-17 \,\mu$ m, clavate to broadly clavate, apex usually obtuse, bases obtuse or tapered, with 4- or 2sterigmata 2-6 µm length, colourless. Metuloidal Pleurocystidia absent, but instead of numerous paracystidia measured $19-32 \times 9-13 \mu m$, broadly clavate, sometimes cylindrical or utriform, apices rounded, base usually tapered into small pedicel, thin-walled, colourless. Cheilocystidia 35-52×12-18 µm, abundant, clavate or broadly clavate to utriform, at times with a median to apical constriction, thin-walled colorless. Hymenophoral trama 50-75 µm thick, sub-regular, consisting of inflated hyphae measured 7–15 μ m wide, colourless, smooth, thin-walled, walls colourless. Pileipellis 45-75 µm wide, regular to sub-regular, yellowish to goldish yellow in mass, consisting of cylindrical hyphae measured 5–10 µm, entrusted, walls yellowish. Pileal trama 130-200 µm wide, sub-regular, hyphae inflated, colourless, 10–16 µm wide. Stipitipellis sub-regular, composed of cylindrical hyphae 9–14 µm wide, encrusted, pale yellowish. Stipe trama regular, composed of colourless, thin-walled, smooth hyphae 3-10 µm wide. Caulocystida present at



Figure 2. Basidiomata of *Inocybe acutata*. (a) fan4322 (FCAS3814). (b–d) NJ4747 (FCAS3816). Scale bars: a = 10 mm; b-d = 1 mm. Photos: (a) by Y.-G. Fan; (b–d) by Y.-P. Ge.

the stipe apex or not observed in certain specimens. *Clamp* connections present in all tissues.

Habitat and ecology: Solitary or scattered on clay soils in subtropical mixed broad-leaved and coniferous forests, under *Quercus*.

Distribution: China (Anhui, Jiangsu, Zhejiang), South Korea, Japan (type) and Thailand.

Specimen examined: CHINA. Zhejiang Province: Hangzhou City, Linan District, Tianmu Mountain Nature Reserve, 30°18′54″N, 119°26′38″E, 347 m asl., in forests dominated by *Quercus*, 8 September 2015. leg. Y.-G. Fan & W.-J. Yu, FYGfan4322 (FCAS3814); Lishui City, Hedi Town, at 27°33′44″N, 119°16′43″E, 1,014 m asl., 21 August 2022, leg. Y.-P. Ge & Q. Na, NJ4747 (FCAS 3816); Lishui City, Songyang county, at 28°16′59″N, 119°32′6″E, 573 m asl., 1 July 2022, leg. Y.-P. Ge & Q. Na, NJ4119 (FCAS3952). Anhui Province: Feidong County, Hefei City, Siding Mountain National Forest Park 31°37′35″N, 117°28′17″E, 37 m asl., 6 July 2020, leg. L.-Y. Zhu, HMJAU56857; Jiangsu Province: Nanjing City, Xuanwu



Figure 3. Microscopic features of *Inocybe acutata* (FCAS3816). (a–b) Basidiospores. (c–j) Basidia. (k–p) Cheilocystidia. (q–u) Paracystidia at lamellae side. (v) Pileipellis. (w) Hymenophoral trama. (x) Pileipellis hyphae. (y) Stipitipellis hyphae. (z) Stipitipellis. Scale bars: $a-y = 10 \mu m$; $z = 100 \mu m$. Photos by J.-L. Gao.

District, Linggu Temple Scenic Area 32°03'48"N, 118°50'22"E, 35 m asl., 6 July 2020, leg. L.-Y. Zhu, HMJAU56858.

Remarks: *Inocybe acutata* Takah. Kobay. & Nagas. was originally described from Tottori, subtropical Japan where it occurs in *Quercus* forests (Kobayashi 1993).

Inocybe acutata is characterised by the slender and snuff brown or umbrinous basidiomata, plano-convex pileus with a buffish pointed-acute umbo, spiny but non-bifurcate basidiospores, the absence of metuloidal pleurocystidia, and presence of thin-walled cheilocystidia (Kobayashi 1993). This species was first reported in China in 2022 based on collections from Anhui Province (Bau 2022). Recently, we obtained more specimens from Zhejiang Province in subtropical China. We failed to find caulocystidia at the stipe apex in the Zhejiang collections. However, the Chinese materials match well in the gross morphology with the original description of the species (Kobayashi 1993).

Interestingly, two specimens, ECV3648 from northern Thailand and KA18-0494 from South Korea, both treated as I. stellata E. Horak, Matheny & Desjardin clustered with I. acutata in a monophyletic lineage with 100% support. In the original description of I. stellata, two phylogenetic clades were recovered and clade I received weak support; ECV3648 is one of three specimens in clade I but showed distinct genetic differentiation compared to the other two samples (Horak et al. 2015). However, Horak and colleagues treated all these samples as *I. stellata* in a conservative approach. In our three-gene phylogeny, the morphological I. stellata can be seen split into four independent lineages. Of these, the *I. acutata* lineage is distinct from the core I. stellata clade. Indeed, I. acutata differs from *I. stellata* by the buff and pointed but non-acute umbonate pileus, simple and spinose basidiospores without saddle-shaped projections, the absence of metuloids, and thin-walled cheilocystidia.

Inocybe alienospora (Corner & E. Horak) Garrido, Biblthca Mycol. 120: 176 (1988).

≡ Astrosporina alienospora Corner & E. Horak, Persoonia 10(2): 173 (1979).

Remarks: *Inocybe alienospora* is a striking species originally described from Singapore in 1979 and reported in Australia in 2017 (Horak 1979; Matheny and Bougher 2017). This species is characterised by small basidiomata, nodulose basidiospores with saddle-shaped projections, metuloidal pleurocystidia, and thin-walled cheilocystidia. Recently, this species was reported in southern China but based on a single specimen (Bau 2022). The Chinese material was

collected from Guangdong Province in southern China. Unfortunately, we failed to obtain any sequence data from our material. Descriptions of this species can be found in Horak (1979), Matheny and Bougher (2017), and Bau (2022).

Habitat and ecology: On bare soil (Singapore); in sclerophyll vegetation (Australia); and in broad-leaved forests (China).

Distribution: Singapore (type), China (Guangdong), Australia (Queensland).

Inocybe aprica W.J. Yu, Y.G. Fan & L.J. Gao, sp. nov. Figures 4–5

MycoBank: MB853904.

Etymology: *aprica* (L.), in reference to occurrences in a sunward place near its host tree.

Diagnosis: *Inocybe aprica* has slender basidiomata, nearly glabrous pileus, nodulose basidiospores with saddle-shaped projections, metuloidal pleurocystidia; and thin-walled, yellowish pigmented cheilocystidia. It is mostly similar to *I. lasseroides*, but differs in the nearly glabrous umber pileus, smaller basidiospores, and thin-walled, yellowish pigmented cheilocystidia.

Holotype: CHINA. Hainan Province: Wenchang City, Wenjiao Town, Wusi Village, at 19°40′02"N, 110° 53′41″E, 16 m asl., Under forest dominated by *Casuarina equisetifolia* L., 25 November 2022, leg. Y.-G. Fan, W.-J. Yu, FYG7640 (FCAS3817). GenBank accession numbers: ITS (OR755901); LSU (OR760197) and *rpb2* (OR775210).

Description: Basidiomata small, slender. Pileus 3.5-12 mm wide, conico-campanulate when young, obtusely umbonate-convex to umbonate-applanate when matured; margin inflexed when young, then decurved for a long time, when old expended; surface dry, smooth to appressed fibrillose towards the disc, radially fibrillose to rimulose outwards, veil remnants present as appressedscattered patches, fugacious; initially uniformly dark brownish (5D7-5E7), brownish (5C5-5C6), and darkly brownish (5E5-5E6) umbonate after matured, paler outwards, margin pale brownish (5B5-5C5) to brownish (5D5-5E5); patches whitish (4A1). Lamellae adnexed, subdistant, up to 1 mm wide, alternately distributed with 3-4 tiers of length lamellulae; colour pale brownish (5B3-5B4), edge not fimbricate; margin uneven. Stipe $16-40 \times 0.5-1.3$ mm, terete, equal with a slightly enlarged base, central, solid; surface dry, fibrillose, brownish (5C5) to darkly brownish (5E6), but covered



Figure 4. Basidiomata of Inocybe aprica. (a-e) FYG7640 (FCAS3817, holotype). Scale bars: a-e = 10 mm. Photos by W.-J. Yu.

with a layer of veil remnants made up with whitish (4A1) subtomentose patches, densely so towards the base, fugacious upon maturity. **Context** fleshy, cream whitish (4A2) with pale brownish (5C3), 0.1–0.5 mm thick at mid-radius, up to 1 mm thick under the umbo; fibrillose, slightly brownish (5C4–5C5) to brownish (5C6), striate in Stipe. **Odor** slightly spermatic.

polyangular to star-shaped or slightly flange-like warts, apiculus small but distinct, yellowish to darkly yellowish in 5% KOH, thick-walled, with yellowish ellipsoid or ovoid contents. **Basidia** 27–45 × 10–14 µm, clavate, colourless or slightly yellowish, mostly 4-sterigmata, sometimes 2-sterigmata, sterigmata 3–7 µm in length, with yellowish ovoid contents, bases usually tapered. **Pleurocystidia** 48–72 × 12–21 µm, mostly clavate, sometimes cylindrical or utriform, colourless, apices crystalliferous, base usually tapered into small pedicel, walls thickened towards apices,



Figure 5. Microscopic features of *Inocybe aprica* (FCAS3817, holotype). (a–b) Basidiospores. (c–d) Basidia. (e) Pleurocystidia. (f–h) Cheilocystidia. (i) Pileipellis. (j) Pileipellis hyphae. (k) Hymenophoral trama. (l) Stipitipellis hyphae. (m) Stipitipellis. Scale bars: $a-m = 10 \mu m$. Photos by P.-M. He.

up to 2 μ m thick, thinner downwards, walls pale yellowish. **Cheilocystidia** 34–60 × 7–19 μ m, slenderly clavate, cylindrical or broadly clavate, pale yellowish, mostly thin-walled, at times walls somewhat thickened; mostly with yellow brownish to yellowish pigments; *Hymenophoral trama* 50–87 µm wide, sub-regular, consisting of inflated hyphae with thick measured 12–27 μ m wide, pale yellowish to colourless, smooth, thin-walled. *Pileipellis* 112–137 μ m wide, regular to sub-regular, pale yellowish to brownish in mass, consisting of cylindrical hyphae and inflated hyphae with thick measured 2–8 μ m and 11–20 μ m, respectively, thin-walled, pale yellowish, encrusted. *Stipitipellis* regular, cylindrical hyphae with thick measured 3–10 μ m, brownish, encrusted, or smooth. *Caulocystida* not observed. *Oily hyphae* 3–10 μ m wide, cylindrical, dark yellowish, smooth, in stipe and hymenophoral trama. *Clamp connections* present in all tissues.

Habitat and ecology: Scattered on sandy soil under artificial plantation of *Casuarina equisetifolia*.

Distribution: Known from the type locality in Hainan Province of China.

Additional specimens examined: CHINA. Hainan Province: Wenchang City, Wenjiao Town, Wusi Village, on sandy soil in *C. equisetifolia* forests, at 19°40′02"N, 110°53′41″E, 16 m asl., 25 November 2022, leg. Y.-G. Fan, W.-J. Yu, FYG7641 (FCAS3818); Wenchang City, Wenjiao Town, Wusi Village, on Sandy soil under *C. equisetifolia* forests, at 20° 1′37"N, 110°30′5″E, 6 m asl., 15 November 2023, leg. Y.-G. Fan, W.-J. Yu, FYG9907 (FCAS3939), FYG9908 (FCAS3940).

Remarks: Inocybe aprica was found in an open artificial plantation of C. equisetifolia in Wenchang City, Hainan Province. Morphologically, the new species is characterised by the slender basidiomata, nearly glabrous umber pileus, nodulose basidiospores with saddle-shaped projections, metuloid pleurocystidia; and thin-walled, yellowish pigmented cheilocystidia. At least two species should be compared with the new species. Inocybe alienospora shares high similarity with the new species in the shapes and sizes of basidiospores, cheilocystidia, and pleurocystidia. However, it has a dingy fawn to pale fuscous and scaly pileus with recurved scales towards the centre, fimbriate lamellae edges, and slightly smaller basidiospore sizes measured $8-10.5 \times 7-8.5 \,\mu m$ (Horak 1979; Matheny and Bougher 2017). Inocybe lasseroides (E. Horak) Garrido is another species having saddle-shaped projections on the basidiospores and has been documented from Singapore and Malaysia. However, it has a scaly pileus, subglobose to ovoid basidiospores measured 10.5-13 µm, thickwalled cheilo- and pleurocystidia, and the presence of thin-walled yellow pigmented caulocystidia (Horak 1979); this species was also reported to occur under *Allocasuarina* and *Eucalyptus* in sclerophyll forest in Australia (Matheny and Bougher 2017). Phylogenetically, *I. aprica* clusters with *I. lasseroides, I. alienospora, I. kuruvensis*, and a suite of undescribed taxa in a fully supported subclade.

Inocybe aurescens Y.G. Fan, J.L. Gao & W.J. Yu, sp. nov. Figures 6–7

MycoBank: MB853905.

Etymology: *aurescens* (L), refers to the golden yellowpigmented, thin-walled hymenial cystidia.

Diagnosis: *Inocybe aurescens* has small-sized basidiomata, subdistant lamellae, spinose basidiospores with saddle-shaped projections, and a fragrant smell. It is mostly similar to *I. juji*, but can be distinguished by the absence of a fuliginous tint towards the umbo, larger basidiospores, shorter cheilocytidia, and the fragrant smell.

Holotype: CHINA. Yunnan Province: Puer City, Zhenyuan Country, Mengda Town, on soil in subtropical evergreen broad-leaved forests, at 24°02′27″N, 100°49′6″E, 1,193 m asl., 22 November 2015, leg. Y.-G. Fan & W.-J. Yu, FYG2015387 (FCAS 3813). GenBank accession number: ITS (OR755913); LSU (OR760276); *rpb2* (OR775213).

Description: Basidiomata small, slender. Pileus 10-25 mm wide, conical to hemispheric when young, then convex with low umbo, when matured plano-convex to plane with a small umbo; margin at first inrolled, then depressed to straight, uneven; surface dry, felty or subtomentose when young, then striated-fibrillose to fibrillose, rimulose towards margin; uniformly brownish (5C6-5C7) when young, yellowish (4B8-4C8) or brownish yellow (5B7-5C7), brown (5C6–5C7) with fuliginosus tinge (5D8–5E8) towards the centre when matured; veil remnants slightly yellowish (4A2-4A3). Lamellae adnexed, subdistant, up to 3.5-4 mm wide, alternately distributed with 3 tiers lamellulae; colour yellowish (4B5-4B6) or pale brownish (5C6-5C7) to brownish (5C7), edge even, not fimbricate. Stipe 25-32 × 2-3 mm, terete, equal with a slightly enlarged base; central, solid; surface dry, covered with a layer of veil remnants, appressed-fibrillose to silky smooth; yellowish (4B6) to



Figure 6. Basidiomata of Inocybe aurescens. (a-g) FYG2015387 (FCAS3813, holotype). Scale bars: a-g = 1 mm. Photos by Y.-G. Fan.

brownish (5B6) when young, brownish (5D6) when matured. **Context** fleshy in pileus, white (4A1) with brownish (5D6) tinge near the cuticle, 0.2 mm thick at mid-radius, up to 2.5 mm thick under the umbo; fibrillose and striate in stipe, whitish (4A1) or slightly brownish (5B4). **Odor** fragrant.

Basidiospores [100/2/2], (7.0) 7.2–**8.5**–9.7 (10.0) × (5.5) 6.1–**7.5**–8.9 (9.5) μ m, Q = (1.00)1.02–**1.15**–1.32 (1.43), Q_m ± SD = 1.15 ± 0.1 without spines; sub-stellate or spinose with simple and bifurcate spinies, apiculus distinct, yellowish to darkly yellowish in 5% KOH, thick-walled, with yellowish ovoid contents. **Basidia** $30-35 \times 9-14 \mu$ m, clavate to broadly clavate, apex usually obtuse, bases tapered, with 4- or 2-sterigmata $2-6 \mu$ m length, slightly yellowish to yellowish. **Pleurocystidia** 25-46 × 9-23 µm, abundant, clavate or utriform, sometimes slenderly clavate, apices rounded or obtuse, base usually tapered into small pedicel, thin-walled, yellowish to goldish yellow, walls lightly yellowish. **Cheilocystidia** 29-52 × 9-20 µm,



Figure 7. Microscopic features of *Inocybe aurescens* (FCAS3813, holotype). (a–b) Basidiospores. (c^1-c^3) Basidia. (d^1-d^{16}) Pleurocystidia. (e–m) Cheilocystidia. (n) Pileipellis. (o) Hymenophoral trama. (p–q) Pileipellis hyphae. (r) Hymenophoral trama hyphae. (s) Stipitipellis. Scale bars: a–m, p–s = 10 µm; n–o = 100 µm. Photos by J.-L Gao.

resemble pleurocystidia, clavate or utriform, thin-walled, pale yellowish to yellowish. *Hymenophoral trama* 63–90 µm thick, sub-regular, consisting of inflated

hyphae measured 11–22 μ m wide, yellowish to colourless, smooth, thin- to thick-walled, up to 0.2 μ m, wall slightly yellowish. *Pileipellis* 50–100 μ m wide, sub-regular, yellowish to darkly brownish in mass, consisting of cylindrical hyphae measured 6–10 μ m, yellowish, walls lightly yellowish, with yellowish oily contents. *Pileal trama* 120–220 μ m wide, sub-regular, hyphae inflated, pale yellowish to yellowish, 14–27 μ m wide. *Stipitipellis* regular, hyphae cylindrical, 4–10 μ m wide, encrusted, yellowish. *Stipe trama* regularly arranged, composed of colourless, thin-walled, cylindrical hyphae 8–12 μ m wide. *Caulocystida* not observed. *Oily hyphae* 5–10 μ m wide, cylindrical, yellowish, smooth, diverticulate, in stipe. *Clamp connections* present in all tissues.

Habitat and ecology: Scattered on clay soil in subtropical evergreen broad-leaved forest.

Distribution: Known from two localities in Yunnan Province of China.

Additional specimens examined: CHINA. Yunnan Province: Baoshan City, Longling Country, at 24° 38'46"N, 98°46'20"E, 1,767 m asl., under forests dominated by fagaceous trees, 10 July 2018, leg. Y.-G. Fan & W.-J. Yu, FYG2871 (FCAS3815).

Remarks: *Inocybe aurescens* was discovered under fagaceous trees in Yunnan Province. It is characterised by small-sized basidiomata, subdistant lamellae, spinose basidiospores with saddle-shaped projections, and a fragrant smell. More impressively, the new species is distinguished by the golden yellow-pigmented hymenial cystidia and that lacks crystals at the apices. This kind of cystidium is rarely encountered in *Inocybe. Inocybe aurantiocystidiata* Turnbull and Watling, shares similarities in basidiospore and hymenial cystidia morphology, but it has a clay buff stipe with a vinaceous tinge, hazel to vinaceous context, and an ecology with *Shorea* trees (Dipterocarpaceae).

Phylogenetically, *I. aurescens* is a sister to another newly described species, *I. juji* (see below), and shares high similarity in morphology. However, the latter has a non-fuliginous tinged pileus centre, smaller basidiospores, and longer cheilocystidia without subcapitate apices. Other close relatives include *I. hydrocybiformis*, *I. babruka*, and *I. papilliformis*. These three tropical Asian species share spinose basidiospores usually with a distinct apiculus. *Inocybe papilliformis*, originally described from Kerala State, India has very slender basidiomata, an acute-papillate and conical-convex pileus, larger basidiospores measuring 15–19.5 × 14–18 µm, and thick-walled cheilocystidia (Predeep et al. 2016). Inocybe babruka, a species also described from Kerala, India has a bulbous-based stipe, flexuous-cylindric or strangulated cheilocystidia, and broadly clavate basidia with up to 16 µm long sterigmata (Latha and Manimohan 2017). Inocybe hydrocybiformis was originally described from tropical forests in Singapore and Malaysia (Horak 1979) but was subsequently found in India (Vrinda et al. 1999; Predeep et al. 2016; Latha and Manimohan 2017) and Thailand (Horak et al. 2015); it can be distinguished from *I. aurescens* by the often longer cheilocystidia usually with blunt, forked or irregular finger-like projections at the apices. Horak and colleagues noted that the Thai material has scattered pleurocystidia (Horak et al. 2015). In our present study, The Thai collection (DED8165) identified by Horak nested in a different phylogenetic lineage sister to I. babruka (Figure 1). We speculate that there are still cryptic taxa in this group waiting for recognition in tropical Asia.

Inocybe carpinicola Y.G. Fan, W.J. Yu & P.M. He, Phytotaxa 575(1): 83 (2022).

Remarks: *Inocybe carpinicola* is a recently described species from tropical China. Here, we obtained three additional specimens from Shandong Province in 2023. *Inocybe carpinicola* is characterised by the rather small and slender basidiomata, small pointed-umbo in pileus, angular-nodulose to substellate basidiospores, and slightly thick-walled hymenial cystidia. A detailed description and colour-plates of *I. carpinicola* can be found in He et al. (2022).

Habitat and ecology: Scattered or gregarious in *Carpinus* (Betulaceae) forests.

Distribution: Hainan and Shandong provinces in China.

Specimens examined: CHINA. Hainan Province: Wuzhishan City, Nansheng Town, Wuzhishan substation of Hainan Tropical Rain Forest National Park, on clay soil under Carpinus forests, at 109° 40'43"E, 18°51'53"N, 690 m asl., 29 July 2021, leg. Y.-G. Fan, L.-S. Deng, L.-N. Zhao, J.-H. Hu, FYG6297 (FCAS3617), FYG6300 (FCAS3618), FYG6307 (FCAS3513: holotype); 30 August 2021, leg. W.-J. Yu, P.-M. He, Y.-G. Fan, FYG6312 (FCAS3620), FYG6315 (FCAS3621), W.-J. Yu & Y.-G. Fan, FYG6381 (FCAS3622); Shandong Province, Tai'an City, Dazinkou Town, Mount Tai, YuQuan Temple, at 117°05'12"E, 36°18'15"N, 554 m asl., 20 July 2023, leg. Y.-P. Ge & Q. Na, HK0985 (FCAS3941), HK0986 (FCAS3943), HK0987 (FCAS3942).

Inocybe casuarinoides Y.G. Fan, J.L. Gao & W.J. Yu, sp. nov. Figures 8–9

MycoBank: MB853906.

Etymology: Referring to its similar basidiospore shape with *Inocybe casuarina*, a tropical Asian species described originally from Malaysia.

Diagnosis: *Inocybe casuarinoides* has small, slender basidiomata, greyish umber pileus, weakly-angular basidiospores, cylindrical metuloid pleurocystidia, and thin-walled cheilocystidia. It is mostly similar to *I. casuarinoides*, but differs in smaller basidiomata, larger basidiospores, and cylindrical cheilo- and pleurocystidia.

Holotype: China. Hainan Province, Wenchang City, Wenjiao Town, Wusi Village, 19°40′02″N, 110°53′11″E, 16 m asl., in *C. equisetifolia* forest, 17 May 2023. Y.-G. Fan & W.-J. Yu, FYG8122 (FCAS3820), GenBank accession numbers: ITS (OR755899); LSU (OR759975) and *rpb2* (OR775204).

Description: Basidiomata small-sized, slender. Pileus 6-16 mm wide, at first hemispherical, later conico-convex to campanulate, applanate with a umbo when matured, margin depressed to straight; surface dry, fibrillose-tomentose from submembranous remnants of veil when young, becoming appressed-fibrillose to fibrillose or fibrillose-glabrous, occasionally splited at margin; red brownish (6E5) when young, tobacco (5D6-5E6), brownish (5D6) to dark brownish (5E7) at the centre, paler outwards; fibrillose-tomentose whitish (4A1) or greyish brown (4C3-4C2). Lamellae up to 1 mm broad, adnexed, moderately crowded, unequal in length, alternately distributed with 3-4 tiers of lamellulae, whitish (4A1) to pale brown (4A4), edge paler, indistinctly fimbricate. *Stipe* $14-31 \times 1-3$ mm, cylindrical; central or eccentric, solid, covered with a layer of appressed to protruding greyish white fibrils; partly pallid (4A1) in the upper part and yellowish tobacco (4C5) towards the base when young, uniformly tobacco brownish (4E4-4E5) when mature, at times slightly brownish (5B6-5C6) to darkly brownish (5E5). Context fleshy, whitish (4A1) in Pileus, 0.5 mm thick at mid-radius, up to 2 mm thick under the umbo; whitish (4A1) or slightly brownish (5B3) in Stipe. *Odor* spermatic.

Basidiospores [100/3/5], (6.0) 8.6-10.0-11.0 $(12.0) \times (4.5)$ 5.1–**6.19**–7.3 (8.0) µm, Q = (1.30) 1.39–**1.63**–1.86 (2.00), $Q_m \pm SD = 1.63 \pm 0.13$; elliptic with weak angular outlines, oblong, pale yellowish to yellowish in 5% KOH, apiculus indistinct, in some collections with circular oily contents. **Basidia** $24-34 \times 8-12 \mu m$, clavate with obtuse-rounded apex, tapered downwards, colourless, generally 4-spored, sometimes 2-spored, sterigmata 2-4 µm in length, with irregular oily contents. *Pleurocystidia* 45–83 × 10–18 µm, abundant, mostly cylindrical-clavate, less often subfusiform, occasionally utriform, colourless, apices usually encrusted with crystals, base usually tapered, rounded or less often subtruncate, thick-walled, walls up to 1.5 µm thick, -slightly yellowish. Cheilocystidia 31-62 × 11-18 μm, slenderly clavate, cylindrical to elongate-cylindrical, mostly thin-walled, at times walls somewhat thickened, up to 1 µm thick; slightly yellowish. Hymenophoral trama 38-108 µm thick, sub-regular, consisting of sub-inflated hyphae measured 9-15 µm wide, smooth. *Pileipellis* 75-175 µm wide, sub-regular, slightly yellowish to yellowish in mass, consisting of cylindrical hyphae with thick measured $7-12 \,\mu\text{m}$, thin-walled, walls yellowish, encrusted. Pileal trama 200-470 µm wide, colourless, regular, consisting of sub-inflated hyphae, 9-16 µm wide, thin-walled, smooth. Stipitipellis regular to sub-regular, hyphae thin-walled, cylindrical, 5–9 µm, yellowish, encrusted. Oily hyphae 4–13 µm wide, abundant, cylindrical, pale yellowish to yellowish, smooth, in stipitipellis and pileal trama. *Caulocystidia* $21-65 \times 10-14 \mu m$, clavate, cylindrical, thin-walled; colourless or slightly yellowish. Clamp connections present in all tissues. Habitat and ecology: Scattered on sandy soil under

Distribution: Known from the two localities in Hainan Province of China.

artificial plantations of Casuarina equisetifolia.

Additional specimens examined: CHINA. Hainan Province: Wenchang City, Wenjiao Town, Wusi Village, on sandy soil in *C. equisetifolia* forests, at 19°40'02"N, 110°53'11"E, 16 m asl., 17 May 2023, leg. Y.-G. Fan & W.-J. Yu, FYG8120 (FCAS3819), FYG8123 (FCAS3821); Haikou City, on sandy soil in *C. equisetifolia* forests, at 20°1'37"N, 110°30'5"E, 6 m asl., 12 November 2023, leg.



Figure 8. Basidiomata of *Inocybe casuarinoides*. (a, c, e) FYG8122 (FCAS3820, holotype). (b) FYG8123 (FCAS3821). (d) FYG8120 (FCAS3819). Scale bars: a = 10 mm; b-e = 1 mm. Photos by Y.-G. Fan.

Y.-G. Fan, W.-J. Yu, FYG9871 (FCAS3936), FYG9895 (FCAS3938).

Remarks: *Inocybe casuarinoides* was found in two localities in Hainan Province. It occurred under *Casuarina equisetifolia* in sandy soil, including a coastal sandy forest. This new species is characterised by small basidiomata, greyish umber pileus, weakly-angular basidiospores, cylindrical metuloid pleurocystidia, and thin-walled cheilocystidia. The subangular outline of basidiospores makes this new species very impressive. Inocybe casuarina Corner & E. Horak, a species originally described from Malaysia, resembles the new species in having subangular basidiospore outline and an ecology also under *C. equisetifolia*. However, it has larger basidiomata, smaller basidiospores measured $6.5-9 \times 4-5 \mu m$, and fusoid cheilo- and pleurocystidia (Horak 1980). Inocybe niigatensis Hongo (= Inocybe ammophila Hongo & Matsuda) described



Figure 9. Microscopic features of *Inocybe casuarinoides* (FCAS3820, holotype). (a–b) Basidiospores. (c^1-c^7) Basidia. (d^1-d^{18}) Pleurocystidia. (e–n) Cheilocystidia. (o) Pileipellis. (p) Hymenophoral trama. (q) Pileipellis hyphae. (r) Stipitipellis hyphae. (s) Oily hyphae. (t) Caulocystidia at stipe apex. Scale bars: a–n, q–t = 10 µm; o–p = 100 µm. Photos by J.-L Gao.

from temperate Japan is another species with greyish brown pileus and subangular basidiospores, but it has a marginate stipe base, subfusoid pleurocystidia, thick-walled cheilocystidia, a grassy smell, and ecology with *Pinus thunbergia* (Kobayashi 2002). Phylogenetically, *I. casuarinoides* is nested in the alienospora subclade and is sister to *I. alienospora* and allied taxa.

Inocybe haikouensis W.J. Yu, J.L. Gao & Y.G. Fan, sp. nov. Figures 10–11 MycoBank: MB853909.

Etymology: *haikouensis* (L.), Haikou City is the Capital of Hainan Province, and *haikouensis* refers to the type locality of this new species.

Diagnosis: *Inocybe haikouensis* is a small slender species having angular-nodulose basidiospores without distinct saddle-shaped projections, slightly thick-walled pleurocystidia, and thinwalled cheilocystidia with reflective inclusions. It is mostly similar to *I. casuarinoides* but differs in more nodulose basidiospores, slightly thick-walled pleurocystidia, and shorter cheilocystidia with reflective inclusions.



Figure 10. Basidiomata of Inocybe haikouensis. (a–h) FYG9868 (FCAS3934, holotype). Scale bars: a = 10 mm; b–h = 1 mm. Photos by Y.-G. Fan.



Figure 11. Microscopic features of *Inocybe haikouensis* (FCAS3934, holotype). (a–b) Basidiospores. (c–e) Basidia. (f^1-f^{20}) Pleurocystidia. (g–j) Cheilocystidia. (k) Pileipellis. (l) Hymenophoral trama. (m) Pileipellis hyphae. (n) Oily hyphae. (o) Hymenophoral trama hyphae. (p) Caulocystidia at stipe apex. Scale bars: a–j, m–p = 10 µm; k–l = 100 µm. Photos by J.-L Gao.

Holotype: CHINA. Hainan Province: Haikou City, at 20°01'15"N, 110°29'35"E, 2 m asl., in *Casuarina equisetifolia* forest, 12 November 2023, leg. Y.-G. Fan,

W.-J. Yu, FYG9868 (FCAS3934). GenBank accession numbers: ITS (OR975602); LSU (OR975620) and *rpb2* (PP366983).

Description: Basidiomata small to medium-sized, slender. Pileus 7-21 mm wide, at first hemispherical or sub-conical, later convex to plano-convex, applanate with a low umbo at maturity, margin rolled when young, then depressed to straight; surface dry, fibrillose-tomentose from whitish (4A1) or grey yellowish (4A2-4B2) submembranous remnants of veil when young, becoming appressed-fibrillose to fibrillose; greyish brown (5C3) to brownish (5E3) when young, brownish (5C5-5D5) to deep brown (5F6) when matured, paler outwards. Lamellae up to 3 mm broad, moderately crowded, adnexed, unequal in length, alternately distributed with 4-5 tiers of lamellulae, greyish white (5A2) to slightly brownish (5B3) or brownish (5E3), edge paler, indistinctly fimbricate. **Stipe** $29-48 \times 1-3$ mm, equal, cylindrical; central, solid; surface dry, furfuraceous at upper part, covered with greyish fibril downwards; brownish (5A3-5B3) when young, brown (5D3) to deep brown (5E3) when mature. **Context** fleshy in pileus, white (5A1) with pale yellowish tinge (4A2-4B2), 0.5-1 mm thick at mid-radius, up to 4 mm thick under the umbo; fibrillose in stipe, brownish (5B3) to yellowish brown (5D3) in Stipe. Odor funaoid.

Basidiospores [100/4/5], (8.0) 8.0-10.1-11.0 $(12.0) \times (6.0)$ 6.8–**7.8**–9.1 (10.0) µm, Q = (1.07) 1.14-**1.31**-1.41 (1.47), $Q_m \pm SD = 1.31 \pm 0.087$; nodulose to polygonal with 10-13 small nodules, occasionally with flange-like projections, apiculus small and indistinct; yellowish to yellowish brown, thick-walled, with yellowish intracellular ovoid contents. **Basidia** 22-36×9-14 µm, clavate to broadly clavate, apex obtuse, bases tapered, with 4-spored or 2-spored, sterigmata 3-7 µm length, colourless when young, yellowish when matured. Pleurocystidia 40-68×14-25 µm, abundant, fusiform, subfusiform or utriform, sometimes clavate, apices obtuse with crystals, base tapered into small pedicel, thin-walled, at times thick-walled towards the apices, colourless to with bright yellow pigments. *Cheilocystidia* 23–51×6–20 μm, resemble pleurocystidia or clavate to slenderly clavate, thin-walled, occasionally thicked-walled in the apices, colourless to yellowish, often with reflective inclusions. Hymenophoral trama 98-190 µm thick, sub-regular, consisting of inflated hyphae measured 18-27 µm wide, colourless, smooth, thin-walled. Pileipellis 138-228 µm wide, regular to sub-regular, slightly yellowish to yellowish in mass, consisting of cylindrical and encrusted hyphae measured 7–20 μ m, yellowish. *Pileal trama* 210–300 μ m wide, colourless, sub-regular, hyphae inflated, colourless, 15–25 μ m wide, thin-walled, smooth. *Stipitipellis* regular, composed of cylindrical hyphae 12–20 μ m wide, pale yellowish. *Stipe trama* regularly arranged, composed of colourless, thin-walled, hyphae 12–20 μ m wide, smooth. *Caulocystida* 23–65 × 7–14 μ m, abundant, fusiform or utriform, sometimes clavate, colourless, apices obtuse with crystals, base tapered. *Oily hyphae* 4–7 μ m wide, cylindrical, yellowish to darkly yellowish, smooth, in stipe. *Clamp connections* present in all tissues.

Habitat and ecology: Scattered on sandy soil in *Casuarina equisetifolia* forests.

Distribution: Known from the type locality in Hainan Province of China.

Additional specimens examined: CHINA. Hainan Province: Haikou City, on sandy soil under *C. equisetifolia* forests, at 20°01'15"N, 110°29'35"E, 6 m asl., 12 November 2023, leg. Y.-G. Fan, W.-J. Yu, FYG9866 (FCAS3932), FYG9867 (FCAS3933), FYG9870 (FCAS3935); 15 November 2023, leg. Y.-G. Fan, W.-J. Yu, FYG9893 (FCAS3937).

Remarks: Inocybe haikouensis occurred in a seashore forest dominated by Casuarina equisetifolia. It occurred scattered in small groups at the edge of a seashore forest. The new species is characterised by small basidiomata, slender stipe, angular-nodulose basidiospores, and thin-walled cheilocystidia with reflective inclusions. Inocybe haikouensis is phylogenetically placed in the subclade unifying *I. alienospora* and allied taxa and is sister to I. casuarinoides. The new species share high similarities in outwards appearance with I. casuarinoides, but the latter species has weak angular basidiospores and subcylindrical cheilocystidia with more thickened walls. Inocybe alienospora and I. heteromorpha both have nodulose basidiospores with distinct saddle-shaped projections, which distinguish them from *I. haikouensis*.

Inocybe heteromorpha Y.G. Fan, W.J. Yu & J.L. Gao, sp. nov. Figures 12–13

MycoBank: MB853910.

Etymology: *hetero*- (L), in reference to the hymenial cystidia as two types, thin-walled cheilocystidia, and metuloid pleurocystidia.

Diagnosis: *Inocybe heteromorpha* has small basidiomata, a non-umbonate pileus, nodulose basidiospores with saddle-shaped projections, metuloidal pleurocystidia, and thin-walled digitate cheilocystidia. It is mostly similar to *l. aprica*, but can be distinguished by the nonumbonate pileus and non-pedicellate pleurocystidia and ecological association with fagaceous trees.

Holotype: CHINA. Hainan Province, Baoting City, Miao Autonomous country, 18°42′03″N, 109°41′31″E, 269 m asl. under tropical forests dominated by fagaceous trees, 27 June 2020. Y.-G. Fan & W.-J. Y, FYG5769 (FCAS 3810), GenBank accession numbers: ITS (OR755900); LSU (OR759987) and *rpb2* (OR775207).

Description: Basidiomata small, slender. Pileus 2.5-9 mm wide, hemispheric when young, convex to plano-convex when matured; margin inflexed when young, becoming straight upon maturity, with indistinct small umbo; surface dry, glabrous-fibrillose when young, then radially fibrillose to appressed scaly with indistinct stripes; uniformly brown (5D8) when young, brownish (5C6) to dark brownish (5E5) when matured, dark brown (6E8) towards the centre, finely paler outwards. Cortina present in young specimens; Lamellae 1-1.5 mm wide, adnexed, moderately crowded, alternately distributed with 3-4 tiers of unequal length lamellulae; pale greyish (5B3) to brownish (5D5); edges paler, not fimbriate. Stipe $14-30 \times 0.6-1.3$ mm, cylindrical, terete, solid, equal with a sub-bulbous base, base up to 2 mm wide; covered with a layer of whitish fibrils made up of veil remnants; background whitish (4A1) or pale brownish (5C5) at upper part, brownish (5B6) to yellowish brown (5B4) downwards. Context fleshy in pileus, whitish (5A1) to off-white (5A1-5B1) with pale brownish (5C4) tinge, 0.1-0.3 mm thick at mid-radius, up to 1 mm thick under the umbo; fibrillose in stipe, slightly brownish (5C4) to brownish (5D4), striate. Odor not recorded.

Basidiospores [100/3/3] (7.8) 8.0–**8.9**–10.0 (11.0) × (6.2) 6.8–**7.7**–8.5 (9.0) µm. Q = (1.00) 1.02–**1.16**–1.29 (1.38), Qm ± SD = 1.16 ± 0.0083, nodulose with numerous saddle-shaped projections, apiculus small and inconspicuous, with ovoid or irregular oily contents, yellowish, thick-walled. **Basidia** 23–33 × 9–14 µm, clavate to broadly clavate, tapered downwards, apiculus indistinct, mostly 4-spored, sometimes 2-spored, sterigmata 3–6 mm in length, mostly colourless with yellowish inclusions. **Pleurocystidia** 48–66 × 12–20 µm, clavate to subfusiform, thick-walled, walls colourless, up to 2 µm thick towards the apex, thinner downwards, apices obtuse to rounded, usually encrusted with crystals, base obtuse or less often subtruncate, mostly with irregular contents.

Cheilocystidia $33-66 \times 5-10 \mu m$, narrowly clavate to clavate, thin-walled, partly with yellowish pigments. Cheiloparacystidia 17–29×6–11 µm, abundant, clavate, cylindrical-clavate, obovate, thin-walled, colourless or with yellowish pigments. Hymenophoral trama 60-75 µm wide, regular to subregular, consisting of inflated hyphae measured 12-25 µm, smooth, thin-walled, colourless. Pileipellis 50–75 µm wide, subregularly arranged, brownish to deep brown in mass, consisting of cylindrical hyphae measured 4–12 µm, slightly yellowish, thin-walled, encrusted. **Pileal trama** regular to subregular, pale yellowish, consisting of cylindrical and inflated hyphae measured 3-10 µm and 13-25 µm wide, colourless to slightly yellow, thin-walled, smooth. Stipitipellis regular, consisting of cylindrical hyphae measured 3-7 µm wide, pale yellowish to yellowish, smooth or encrusted, thin-walled, sometimes with slightly yellowish contents. Oily hyphae present in the stipe trama, cylindrical, 3-7 µm wide, often bent, smooth; yellowish, in stipe. Caulocystida not observed. Clamp connections present in all tissues.

Habitat: Scattered in small groups on bare soil in broad-leaved forest dominated by fagaceous trees.

Distribution: Known from the type locality in Hainan Province of China.

Additional specimens examined: CHINA. Hainan Province, Baoting City, Miao Autonomous Country, under fagaceous forests, at 18°42′03″N, 109°41′31″E, 269 m asl., 27 June 2020. Y.-G. Fan & W.-J. Y, FYG5769a (FCAS3811), FYG5769b (FCAS3812).

Remarks: Inocybe heteromorpha was found in late June in a broad-leaved forest dominated by fagaceous trees in Hainan Province. It can be recognised by its small basidiomata, non-umbonate pileus, nodulose basidiospores with saddle-shaped projections, metuloidal pleurocystidia, and thin-walled digitate cheilocystidia. This new species shares high similarities with I. alienospora, I. lasseroides, and I. aprica in macro- and micromorphology. However, I. alienospora has a scaly pileus and subclavate to lageniform pleurocystidia (Horak 1979; Matheny and Bougher 2017), I. lasseroides has larger basidiospores and metuloidal cheilocystidia (Horak 1979; Matheny and Bougher 2017), and *I. aprica* has an umbonate pileus, evenedged lamellae, and pedicellate pleurocystidia. Inocybe kuruvensis described from tropical India also shares saddle-like projections on the



Figure 12. Basidiomata of Inocybe heteromorpha. (a-g) FYG5769 (FCAS3810, holotype). Scale bars: a-g = 5 mm. Photos by Y.-G. Fan.

basidiospores, but it has a scaly pileus, larger basidiospores (9–11 \times 8–9.5 µm), and metuloidal cheilocystidia (Latha and Manimohan 2017).

Inocybe juji Y.G. Fan, Y.P. Ge & J.L. Gao, sp. nov. Figures 14–15 MycoBank: MB853911 **Etymology**: *juji* (L.), in reference to the spinose basidiospores like a hedgehog, which in anglicised Chinese is "juji".

Diagnosis: *Inocybe juji* has a dirty yellow to brownish yellow pileus, spinose basidiospores with saddle-shaped projections, and thin-walled and yellowish-reflective cheilo- and pleurocystidia. It is mostly similar to



Figure 13. Microscopic features of *Inocybe heteromorpha* (FCAS3810, holotype). (a–b) Basidiospores. (c–d) Basidia. (e) Pleurocystidia. (f–g) Cheilocystidia. (h) Pileipellis. (i) Pileipellis hyphae. (j) Hymenophoral trama. (k–l) Stipitipellis hyphae. (m) Oily hyphae. (n) Stipitipellis. Scale bars: $a-n = 10 \mu m$. Photos by P.-M. He.

l. aurescens, but differs in the subtomentose pileus without any bluish tint, smaller basidiospores, and larger cheilocystidia without subcapitate apices.

Holotype: CHINA. Anhui Province: Chizhou City, Shitai Country, at 30°04′54″N, 117°29′22″E, 246 m asl., Under forest dominated by evergreen broad-leaved forests, 9 October 2019, leg. Y.-P. Ge & Q. Na, 123 (FCAS3946). GenBank accession numbers: ITS (OR975596); LSU (OR975614) and *rpb2* (PP356982). **Description:** *Basidiomata* small to medium-sized, slender. *Pileus* 18–40 mm wide, at first sub-conical with umbo, later convex to plano-convex or conical with sharp umbo, margin depressed to straight, faintly striate-sulcate towards the subrimose margin; surface dry, fibrillose-tomentose from remnants of veil towards the centre, appressed fibrillose-rimulose outwards, at times rimose at the margin; yellowish brown (4C5–4E6) and paler outwards or uniformly dirty yellow (4B6); veil remnants yellowish (4C3) or darkly yellowish (4E5).



Figure 14. Basidiomata of *Inocybe juji*. (a–b) 123 (FCAS3946, holotype). (c) 187 (FCAS3948). (d–e) 119 (FCAS3944). (f–g) 653 (FCAS3947). Scale bars: a-g = 10 mm. Photos by Y.-G. Fan. And Y.-P. Ge.



Figure 15. Microscopic features of *Inocybe juji* (FCAS3946, holotype). (a–b) Basidiospores. (c–f) Basidia. (g_1-g_{18}) Pleurocystidia. (h–l) Cheilocystidia. (m) Pileipellis. (n) Hymenophoral trama. (o) Pileipellis hyphae. (p) Hymenophoral trama hyphae. (q) Caulocystidia at stipe apex. Scale bars: a–l, o–q = 10 µm; m–n = 100 µm. Photos by J.-L Gao.

Lamellae up to 3 mm broad, moderately crowded, adnexed, unequal in length, alternately distributed with 3–4 tiers of lamellulae, yellowish (4C3) or slightly brownish (5D4) to brownish (5D5) with pallid edge, not

fimbriate. **Stipe** $46-50 \times 2.5-3$ mm, cylindrical, slightly swollen at the base; central, solid; surface dry, covered with a layer of yellowish white (4A3) fibrils at the entire length of stipe; background brownish (4B4) when

young, yellowish brown (5B5) when mature; base with tomentose white (1A1) hyphae. *Context* fleshy in pileus, whitish (4A1) with pale yellowish (4B3) tinge, 0.5–3 mm thick; fibrillose in stipe, whitish (4A1). *Odor* not recorded.

Basidiospores [100/4/5] (5.0) 5.8-6.8-7.8 (9.0) × (4.5) 5.0-**5.6**-6.8 (8.8) μ m, Q = (1.00)1.03-**1.23**-1.41 (1.60), $Q_m \pm SD = 1.23 \pm 0.14$; spinose with numerous saddleshaped projections, apiculus distinct, yellowish to goldish yellow, with yellowish ovoid contents. **Basidia** $26-42 \times 10-15 \,\mu\text{m}$, clavate to broadly clavate, apex obtuse, bases tapered, with 4-spored or 2-spored, sterigmata 3-7 µm length, colourless or yellowish. *Pleurocystidia* 40-70×9-18 µm, abunclavate, thin-walled, elongate-clavate, dant, cylindrical, often flexuous, occasionally utriform, apices obtuse, usually tapered downwards, yellowish to goldish yellowish. Cheilocystidia 35-63×6-15 µm, resemble pleurocystidia, elongate-clavate to clavate, thinwalled, yellowish or full of goldish yellow inclusions. Hymenophoral trama 75-138 µm thick, sub-regular to regular, consisting of inflated hyphae measured 11-20 µm wide, colourless, smooth, thin-walled to finely thick-walled, walls up to 1 µm thick, encrusted with yellowish pigments. Pileipellis 25-75 µm wide, sub-regular, brownish in mass, consisting of cylindrical hyphae measured 5–10 µm wide, thin-walled with goldish yellow intracellular pigments. Pileal trama 120-240 µm wide, regular, colourless, hyphae inflated, colourless with pale yellowish walls, 6-18 µm wide. Stipitipellis sub-regular, hyphae cylindrical 6-15 µm wide, pale yellowish. Stipe trama regularly arranged, composed of yellowish hyphae 7–19 μ m wide, slightly thick-walled, walls up to 1 μ m, rough. Caulocystida 27-50×6-9 µm, rare, clavate or utriform, thin-walled, colourless to yellowish. Oily hyphae 4-6 µm wide, cylindrical, yellowish, smooth, present in stipe trama. Clamp connections present in all tissues.

Habitat and ecology: Scattered on soil, under subtropical evergreen broad-leaved forests dominated by fagaceous trees.

Distribution: Known only from the type locality in Anhui Province of China.

Additional specimens examined: CHINA. Anhui Province: Chizhou City, Shitai Country, under evergreen broad-leaved forests, at 30°04'54"N, 117°29'22"E, 284 m asl., 9 October 2019, leg. Y.-P. Ge & Q. Na, 119 (FCAS3944), 147 (FCAS3945); at 30°04'52"N, 117°29'20"E, 224 m asl., 15 October 2019, leg. Y.-P. Gai & Q. Na, 653 (FCAS3947); at 30°04'51"N, 117°29'18"E, 324 m asl., 25 July 2019, leg. Y.-P. Gai & Q. Na, 187 (FCAS3948), 180 (FCAS3949).

Remarks: Inocybe juji was found in subtropical broad-leaved forests dominated by fagaceous trees in Anhui Province. The new species is characterised by the dirty yellow to brownish yellow pileus, spinose basidiospores with saddle-shaped projections, thin-walled and yellowish-reflective cheilo- and pleurocystidia. Among the specimens we examined, FCAS3948 (187) has fewer pleurocystidia and dark yellow basidia, but FCAS3944 (119) has more abundant and pale yellow pleurocystidia. Phylogenetically, this new species is sister to I. aurescens. These two species share several similarities in macro- and micro-morphology, however, I. aurescens differs from I. juji by a conspicuous fuliginosus tinge towards the pileus umbo, larger basidiospores, and shorter cheilocystidia often with subcapitate apices. The ITS sequence from I. juji differs from I. aurescens at 16 positions (97.5% similarity), including 7 base pairs and 9 indels. LSU and rpb2 analysis reveal that there are 0.25% and 0.3% differences between the two species.

Inocybe peppa Y.G. Fan, Y.P. Ge, J.L. Gao & W.J. Yu, sp. nov. Figures 16–17

MycoBank: MB853913.

Etymology: *peppa* (L.), referring to the broadly fusiform hymenial cystidia shaped like the fat Peppa the Pig, a cartoon British character.

Diagnosis: *Inocybe peppa* is characterised by smallsized basidiomata, campanulate pileus, stellate basidiospores, and fusoid to broadly fusoid cheilo- and pleurocystidia. Most similar to *I. perlucida*, but differs by the campanulate pileus, stellate basidiospores with prominent conical noduloses, and fusoid to broadly fusoid cheilo- and pleurocystidia, and a habit under fagaceous trees.

Holotype: CHINA. Zhejiang Province: Lishui City, Songyang Country, at 28°16′59"N, 119°32′06″E, 573 m asl., Under forests dominated by subtropical evergreen broad-leaved forests, 1 July 2022, leg. Y.-P. Ge & Q. Na, NJ4118 (FCAS3951). GenBank accession numbers: ITS (OR975591); LSU (OR975610) and *rpb2* (PP356984).



Figure 16. Basidiomata of Inocybe peppa. (a–d) NJ4118 (FCAS3951, holotype). Scale bars: a = 10 mm, b–d = 1 mm. Photos by Y.-P. Ge.

Description: *Basidiomata* small, slender. *Pileus* 12–20 mm diam., at first hemispheric or sub-conical with umbo, when matured convex or conical to plano-convex, margin inrolled when young, becoming depressed to straight; surface dry, striated, fibrillose-tomentose from brownish (5D6) submembranous remnants of veil, becoming appressed-fibrillose to fibrillose; dark brownish with red-dish tinge (5E6) when young, becoming uniformly brown

(5D6). Lamellae up to 2 mm broad, adnexed, moderately crowded, unequal in length, alternately distributed with 3 tiers of lamellulae, slightly yellowish (4B3) to yellowish (4C5) or brownish (5D6), edge paler, indistinctly fimbricate. **Stipe** $15-23 \times 1-1.5$ mm, terete, equal with a slightly enlarged base; central, solid; surface dry, covered with a layer of greyish white fibrils made up of veil remnants; background brownish (5D5) to dark brown (6C8). **Context**



Figure 17. Microscopic features of *Inocybe peppa* (FCAS3951, holotype). (a–b) Basidiospores. (c–f) Basidia. (g_1-g_{12}) Pleurocystidia. (h–k) Cheilocystidia. (l) Pileipellis. (m) Hymenophoral trama. (n–o) Pileipellis hyphae. (p) Hymenophoral trama hyphae. (q) Caulocystidia at stipe apex. Scale bars: a–k, n–q = 10 µm; l–m = 100 µm. Photos by J.-L. Gao.

fleshy in pileus, white (1A1) to pale brownish (5b6), 0.3–0.5 mm thick; fibrillose in stipe, slightly brownish (5B5–5C6), striate. **Odor** not recorded.

nodulose, angular-stellate with 7-9 prominent conical projections, apiculus small and distinct, yellowish to brassy yellow in 5% KOH, thick-walled, at times with one or more spherical oily droplets. Basidia $27-37 \times 11-16 \,\mu$ m, clavate to broadly clavate, apices rounded or obtuse, bases tapered, 4-spored, sterigmata 3-8 µm length, colourless or yellowish. Pleurocystidia $42-70 \times 20-32 \,\mu m$, abundant, broadly fusiform, fusiform, broadly utriform, colourless, apices obtuse and encrusted with crystals, base usually tapered, thick-walled, walls up to 2 µm, pale yellowish. Cheilocystidia 29-60×13-24 µm, abundant, resemble pleurocystidia, utriform or fusiform, colourless, apices obtuse with crystals, base usually tapered, nearly thin-walled when young, thickwalled then matured, walls up to 2 µm, pale yellowish. Hymenophoral trama 75-100 µm thick, sub-regular to regular, consisting of inflated hyphae measured 9-16 µm wide, colourless, smooth, thinto slightly thick-walled, walls up to 1 µm, pale yellowish. Pileipellis a cutis, 100-120 µm wide, regular, goldish yellowish in mass, consisting of sub-inflated and inflated hyphae measured 8-30 µm, coarsely encrusted with yellowish pigments. Pileal trama 210–300 µm wide, regular, hyphae inflated, colourless, thin-walled, 12-20 µm wide. Stipitipellis a cutis, regular, hyphae cylindrical, 6–12 µm wide, encrusted, thin-walled, walls yellowish. Stipe trama regularly arranged, composed of colourless, thincylindrical hyphae 10–21 µm wide. walled, Caulocystida 37-62×14-26 µm, present at stipe apex, resemble pleurocystidia, fusiform to utriform, colourless, thick-walled, walls up to 2 µm. Oily hyphae 3–10 µm wide, cylindrical, yellowish, smooth, in stipe. Clamp connections present in all tissues.

Habitat and ecology: Scattered on clay soil in subtropical evergreen broad-leaved forest.

Distribution: Known from the type locality in Zhejiang Province of China.

Additional specimens examined: CHINA. Zhejiang Province: Lishui City, Songyang County, at 28°16'59"N, 119°32'06"E, 573 m asl., 1 July 2022, leg. Y.-P. Ge & Q. Na, NJ4117 (FCAS3950).

Remarks: *Inocybe peppa* is currently known only from the type locality in subtropical China. It is characterised by the small-sized basidiomata, campanulate pileus, stellate basidiospores, and fusoid to broadly fusiform cheilo- and pleurocystidia.

Phylogenetically, I. peppa nests in a subclade comprising two temperate European species I. perlucida and I. pseudoasterospora and two undescribed phylogenetic lineages. Inocybe pseudoasterspora [= I. deborae E. Ferrari (2003: 37)], however, has smaller and subtriangular, subguadrangular to cruciform basidiospores and larger sub-lageniform pleurocystidia measured $60-90 \times 13-17 \,\mu m$ (Kühner and Boursier 1932; Ferrari 2006; Bandini et al. 2020). Inocybe perlucida [= Inocybe pseudoasterospora var. mycenoides Bon & E. Ferrari (2006: 238)] is very similar to *I. peppa* in outward appearance, but it has substellate basidiospores with less prominent projections, nearly thin-walled cheilo-, caulo- and pleurocystidia, and an association with Larix Mill. (1754: 2) (Ferrari 2006; Bandini et al. 2020). According to our phylogeny, FYG1146 represents an undocumented sister species to *I. peppa*, but we obtained only one specimen under Populus davidiana in northeast China. However, FYG1146 has weakly angular to polyhedral basidiospores and sublageniform hymenial cystidia usually with a pedicel.

Inocybe sp. FYG1146 Figures 18–19

Description: Basidiomata small, slender. Pileus up to 12 mm diam., at first conico-convex with a low umbo, when matured plano-convex, margin slightly inflexed when young, then depressed to straight, excurveded when matured; surface dry, appressed fibrillosetomentose from greyish white (4A1-4A2) submembranous remnants of veil, becoming appressed-fibrillose to fibrillose; brownish (5D6) to darkly brown (5E8) with reddish pigments when young, uniformly brownish (5E8). Lamellae up to 1 mm broad, distant, adnexed, unequal in length, alternately distributed with 2-3 tiers of lamellulae, yellowish (4B4) to yellowish brown (4D5), edge even, concolorous with gill side, not fimbricate. Stipe 18-22 × 2-3 mm, cylindrical, terete, equal with a slightly enlarged base; central, solid; surface dry, covered with a thin layer of greyish white fibrils made up of veil remnants; background yellowish (4B3-4B4) to brownish (5D5). Context fleshy in pileus, whitish (4A1) with pale brownish (5B3), 0.2 mm thick; fibrillose in stipe, brownish (5B3), striate. Odor not recorded.



Figure 18. Basidiomata of Inocybe sp. (FYG1146). (a–b) FYG1146 (FCAS3809). Scale bars: a–b = 10 mm. Photos by Y.-G. Fan.

angular to irregular with several obtuse nodules, apiculus small and indistinct, yellow in 5% KOH, thick-walled. **Basidia** $31-38 \times 13-16 \mu m$, clavate to broadly clavate, apices rounded or obtuse, bases tapered, with 4- or 2-sterigmata 4-6 µm length, colourless. *Pleurocystidia* 37-83 × 14-29 µm, rare, lageniform to sublageniform sometimes fusiform or utiform, apices obtuse and encrusted with crystals, base usually tapered into small pedicel, slightly thick-walled, walls up to 1 µm, yellowish; colourless to slightly yellowish. Cheilocystidia rare, resemble cheilocystidia. Hymenophoral trama 47–118 µm thick, sub-regular to regular, consisting of inflated hyphae measured 15-25 µm wide, colourless, smooth, thin-walled, walls pale yellowish. Pileipellis a cutis, 110-163 µm wide, sub-regular to regular, goldish yellow in mass, consisting of inflated hyphae measured $10-19 \mu m$, wall pale yellowish, encrusted. **Pileal trama** $110-220 \mu m$, sub-regular to regular, hyphae inflated, colourless, $15-31 \mu m$ wide. **Stipitipellis** a cutis, regular, composed of cylindrical hyphae $4-10 \mu m$ wide, encrusted, pale yellowish, thin-wall, walls yellowish. **Stipe trama** regularly arranged, composed of colourless, thin-walled, hyphae $10-20 \mu m$ wide. **Caulocystida** $31-56 \times 13-27 \mu m$, resemble pleurocystidia, fusiform to utriform, at times irregular, colourless to pale yellowish. **Oily hyphae** $4-5 \mu m$ wide, cylindrical, yellowish, smooth, in stipe. **Clamp connections** present in all tissues.

Habitat: Singly on soils in *Populus ussuriensis* Kom. forests.



Figure 19. Microscopic features of *Inocybe* sp. (FYG1146). (a–b) Basidiospores. (c^1-c^6) Basidia. (d^1-d^{20}) Pleurocystidia. (e) Pileipellis. (f) Hymenophoral trama. (g, i) Pileipellis hyphae. (h) Hymenophoral trama hyphae. (j) Stipitipellis hyphae. (k) Caulocystidia. Scale bars: $a-d^{20}$, $g-k = 10 \ \mu\text{m}$; $e-f = 100 \ \mu\text{m}$. Photo by J.-L. Gao.

Distribution: Known from one locality in Jilin Province, China.

Specimen examined: China. Jilin Province, Antu County, Erdaobaihe Town, 42°12′15″N, 128°10′16″E,

1,080 m asl., 29 July 2017. Y.-G. Fan & W.-J. Yu, FYG1146b (FCAS3809).

Remarks: This is a very small species found under *Populus ussuriensis* trees. Phylogenetically, FYG1146

is sister to *l. peppa*, but the former has weak-angular basidiospores and lageniform hymenial cystida with slightly thickened walls. FYG1146 undoubtably represents a new species, unfortunately, we have obtained only one collection for this species. More collections are needed for a formal description of this taxa.

3.3. Morphological key to species of Inocybe sect. Leptocybe

1	Basidiospores spinose2
1	Basidiospores nodulose to angular-nodu-
	lose8
2	Basidiospores spinose with simple spinies,
	pleurocystidia absentl. acutata
2	Basidiospores spinose with bifurcate spinies, pleur-
	ocystidia as metuloids or thin-
	walled3
3	Pleurocystidia thick-walled, crystalliferous4
3	Pleurocystidia absent, or thin-walled with yellowish
	reflective pigments5
4	Pileus centre with small recurved, concolorous squa-
	mules or small scales, basidiospores (10-) 12-16 µm,
	under Fagaceae treesl. stellata
4	Pileus appressed-fibrillose, basidiospores
	$15-19.5 \times 14-18 \mu m$, under Dipterocarpaceae
	treesI. papilliforimis
5	Pleuro- and cheilocystidia thin-walled, with gold-
	ish yellow reflective pigments
5	Pleurocystidia absent, cheilocystidia thin-walled
	with goldish yellow reflective pigments7
6	Pileus ochraceous, yellow-brown or fuscous,
	smooth or sprinkled with minute concolorous
	or pinkish fibrils (from the veil), basidia
	$25-30 \times 5-6 \ \mu m$ l. hydrocybiformis
6	Pileus dark brown to brown, appressed-fibrillose all
	over, basidia 33–41 × 8–13 μm <i>I. babruka</i>
7	Pileus brownish yellow, appressed-fibrillose
	with fuliginosus umbo, basidiospores
	7.2–9.7 × 6.1–8.9 μ m <i>I. aurescens</i>
7	Pileus dirty yellow, appressed-fibrillose with con-
	colourous or brownish umbo, basidiospores
	5.8–7.8 × 5.0–6.8 μm <i>l. juji</i>
8	Occurring in north temperate/to north tropics,
	associated Betulaceae, Fagaceae, or Pinaceae
	tree

8	Occurring in tropical Asia to tropical Australia, or
	in neotropics, associated with Casuarinaceae or
~	Fagaceae or Fabaceae trees
9	Occurring in Europe
9	Occurring in East Asia
10	Under <i>Larix</i> , pleurocystidia $50-70 \times 13-20 \mu\text{m}$
	l. perlucida
10	Under Quercus-Ligustrum, pleurocystidia
	60–90 × 13–17(–20) μm <i>I. pseudoasterospora</i>
11	Under Carpinus, in temperate to north tropic of
	China, basidiospores nodulose to substel-
	late I. carpinicola
11	Under Fagaceae trees, in subtropical China, basi-
	diospores stellate with prominent conical
	nodulesI. peppa
12	Basidiospores weakly angular to elongate poly-
	gonal with indistinct few
	nodules I. casuarinoides
12	Basidiospores nodulose with flange-like to saddle-
	shaped projections
13	Cheilocystidia as metuloid, walls up to 3 µm
	thick
13	Cheilocystidia thin- to slightly thick-walled or
10	sparsely mixed with metuloids
14	Occurring in tropical India under Hopea ponga
	(Dipterocarpaceae) trees basidiospores
	$0.11 \times 8.05 \text{ µm}$
1/	$\rho = 11 \times 6^{-9.5} \mu m$
14	Australia Under Castanonsis Lithogarous
	Australia, Onder Castanopsis-Lithocarpus
	(Fagaceae) Torests of Anocasaanna-Lacayptas Tor-
	ests, basiciospores 9.5–13 μm m
4 -	diam <i>I. lasseroides</i>
15	Basidiospores nodulose with small nodules and
	flange-like projections, chellocystidia thin-walled
	with colourless reflective inclu-
	sionsI. haikouensis
15	Basidiospores nodulose with saddle-shaped projec-
	tions, cheilocystidia with yellowish pig-
	ments16
16	Pleurocystidia thick-walled with obtuse or
	subtruncate bases, Under Fagaceae
	trees I. heteromorpha
16	Pleurocystidia thick-walled with tapered and ped-
	icellate bases, under Casuarinaceae or Fabaceae
	trees
17	Stipe glabrous at apex, with lavender

- 18 Pileus reddish brown to dark brown, appressedfibrillose at disc, basidiospores 8.8–11.0 × 7.5–9.8 μm

4. Discussion

This study enriches what is known about the I. alienospora group (Matheny and Bougher 2017) by describing seven new species from tropical and temperate China. New geographic distribution records are added for I. carpinicola (Shandong Province in warm temperate China) and I. acutata (Zhejiang Province in subtropical China). The former was known previously from tropical China (He et al. 2022), whereas the latter was known only from Japan and Anhui Province of China (Kobayashi 1993; Bau 2022). The *I. alienospora* group, here referred to within a formal classification as I. sect. Leptocybe, is a strongly supported clade in the genus Inocybe but shows ambiguous relationships with other groups in the genus. Inocybe multicoronata, a poorly known species described from Nova Scotia and since reported in Europe (Vauras 1989), shares similar nodulose basidiospores with saddle-shaped projections and was considered to be closely related to I. alienospora (Horak 1979). However, this species, as well as the southwest Chinese I. elata, appear distantly related to the *I. alienospora* group.

Kobayashi (2002) originally described I. sect. Leptocybe as an autonym in his I. subg. Leptocybe (typified by *I. acutata*), and included a second section, *I.* sect. Tylospora, typified by I. casamiri in his new subgenus. Prior works concluded that I. casimiri is a later synonym of I. leptophylla (Kuyper 1985; Matheny and Kropp 2001). Accepting this, I. subg. Leptocybe is polyphyletic but referable to *I. acutata* and the group in which it resides. It is far easier and more convenient to recognise Kobayashi's section name and attribute the I. alienospora group to it for several reasons: (1) a section-level classification within *lnocybe* is preferable at this time (e.g. Heim 1931; Singer 1986; Jacobsson 2008) since many more names of sections and subsections exist compared to available subgeneric names; (2) Inocybe is composed of many different groups. Applying subgeneric names to each would require an unnecessary inflation of new names. *Inocybe acutata*, originally described from Japan (Kobayashi 1993) and since reported in China (Bau 2022) has been confirmed as a member of the *I. alienospora* group. Thus, the easiest solution at this point is to apply *I.* sect. *Leptocybe* to the name of this clade in a formal classification system. Other species we find in sect. *Leptocybe* include *I. lasseri*, originally described from Rio Chacaito, Venezuela by Dennis (1953) and recorded in Guyana. *Inocybe lasseri* has nodulose basidiospores with one or more bifid nodules, thick-walled pleurocystidia, and slightly thick-walled cheilocystidia (Dennis 1953; Horak 1979; Matheny et al. 2012). Phylogenetically, *I. lasseri*, *I. acutata*, and *I. carpinicola* form three independent lineages within sect. *Leptocybe*.

In addition, four major subclades were retrieved from the three-gene phylogeny, viz. the *alienospora* subclade, *hydrocybiformis* subclade, *stellata* subclade, and the *pseudoasterospora* subclade. Globally, *l.* sect. *Leptocybe* now comprises 19 documented species and still a suite of undescribed phylogenetically recognisable taxa. We provide a tentative key to described species of this group. Morphologically, species in sect. *Leptocybe* typically have brownish smallsized baisidiomata, nodulose, spinose to weak-angular basidiospores, thin- to slightly thick-walled pleurocystidia, and mostly thin-walled cheilocystidia.

The seven new species were phylogenetically placed into different subclades. The core subclade of sect. Leptocybe we called the alienospora subclade now includes I. alienospora, I. lasseroides, four new species from tropical China, and a suite of undescribed species from Australia. Species in this subclade share angular, angular-nodulose to coarsely nodulose basidiospores often with crested or saddle-shaped projections, metuloid pleurocystidia, and thin-walled cheilocystidia with yellow inclusions. The weakly angular and angular-nodulose basidiospores without conspicuous saddle-shaped projections occur in our new species I. casuarinoides and I. haikouensis, respectively. Ecologically, I. heteromorpha grows under broad-leaved native trees in tropical lowland rainforests in China; whereas I. haikouensis, I, casuarinoides, and I. aprica were only found in sandy C. equisetifolia forests. Native C. equisetifolia is distributed in Australia and southeast Asia. but it was introduced to southern China over 100 years ago (Zhong et al. 2005). Accordingly, these

three species found under *C. equisetifolia* were probably introduced into southern China together with their exotic host trees. However, *Casuarina equisetifolia* has been found to be arbuscular mycorrhizal and questionably ectomycorrhizal by Brundrett and Tedersoo (2018). We do not think collectors missed other potential ECM vegetation in the *Casuarina plantations*. Resolving the mycorrhizal status of *Inocybe* vis-à-vis *Casuarina* will have to be a topic of future research.

Inocybe aurescens and I. juji are sister to each other, and they cluster with I. hydrocybiformis, I. papilliformis, I. babruka in the hydrocybiformis subclade. These species are united by the presence of spinose basidiospores with saddle-shaped projections and mostly thin-walled cheilocystidia with yellow pigmentations. According to the original descriptions, pleurocystidia are absent in both I. hydrocybiformis and I. babruka (Horak 1979; Latha and Manimohan 2017). However, we found numerous thinwalled, non-metuloidal, yellow-pigmented cells developed from subhymenial hyphae though hardly higher than hymenium layer in the two new species from China. We treated these pigmented elements as thin-walled pleurocystidia since their high similarities with cheilocystidia and distinctions from basidia and basidioles. Debates on microcharacters in a certain species are not rare. For example, described cheilo- and pleurocystidia as metuloids in I. papilliformis (Predeep et al. 2016), but Latha and Manimohan (2017) found no pleurocystidia in this species. Horak (1979) reported pleurocystidia as absent in I. hydrocybiformis from material collected in Singapore and Malaysia, but present though scattered in Thai material (Horak et al. 2015). Further studies are required to determine whether pleurocystidia are present in aforementioned species.

Inocybe stellata, a species having spinose basidiospores and metuloidal hymenial cystidia was originally described from Thailand (type) and Bangladesh (Horak et al. 2015). This species was frequently encountered in tropical lowland and tropical montane forests dominated by *Dipterocarpus* and fagalean trees (Horak et al. 2015). However, the specimens assigned in the morphological species concept of *I. stellata* were classified into four terminal phylogenetic lineages. The *stellata* subclade contains three of these phylogenetic lineages. We labelled the lineage containing the holotype specimen (ZT10097) as *I. stellata* sensu stricto. There are still two phylogenetic species in the *stellata* subclade in need of further study.

Inocybe peppa was found in fagaceous forests from subtropical China. This species clusters with FYG1146 from northeastern China, and *I. pseudoasterospora* and *I. perlucida* from Europe and/or North America in the pseudoasterospora subclade. Currently, this subclade comprises non-tropical elements. Taxa in this subclade occur in north temperate regions only. Species in this subclade usually have stellate, substellate, weakly angular basidiospores, and slightly thickwalled hymenial cystidia.

Acknowledgments

We would like to thank Mrs. Li-Yang Zhu (Jilin Agricultural University) for providing specimens of *l. acutata*, Dr. Yong Zhang (Chinese Academy of Forestry) and Dr. David Bush (Australian Tree Seed Centre) for identifying the host tree species, to Dr. Brendan Lepschi (Australian National Herbarium), Dr. Ian Dickie (University of Canterbury), Dr. Mark Brundrett (University of Western Australia), and Dr. Leho Tedersoo (University of Tartu) for kind discussions of the ectomycorrhizal status of *Casuarina*. We thank anonymous reviewers for their meticulous reviews.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the National Science Foundation of China [32260005], the Hainan Province Science and Technology Special Fund [ZDYF2024SHFZ129], the Hainan Provincial Natural Science Foundation [323MS044], and the Scientific Research Project of Hainan Higher Education Institutions [Hnky2023ZD-8] (Y.G. Fan and W.J. Yu); the U.S. National Science Foundation [DEB-2030779], and the University of Tennessee Hesler Endowment Fund (P.B. Matheny); the Postgraduate Innovation Fund Project of the Hainan Medical University [HYYS2022B09] (J.L. Gao).

References

- Aïgnon HL, Jabeen S, Verbeken A, Matheny PB, Yorou NS, Ryberg M. 2022. Four new nodulose-spored species of *Inocybe* (Agaricales) from West Africa. Fungal Syst And Evol. 10(1):1–18. doi: 10.3114/fuse.2022.10.01.
- Armada F, Esteve-Raventós F, Garrido-Benavent I. 2023. *Inocybe* ochrogaleata sp. nov, un nouvel *Inocybe* récolté dans la péninsule lbérique [*Inocybe ochrogaleata* sp. nov., a new *Inocybe* from the Iberian Peninsula]. Bull mycol bot Dauphiné-Savoie-n. 250:5–24. French.

- Bandini D, Bandini G, Bensch K, Rodríguez Campo FJ, Oertel B, Valade F, Eberhardt U. 2023a. Three new smooth-spored species of *Inocybe*, two new epitypes, and updates on earlier epitypifications. Integr Syst. 6(2):1–37. doi: 10.18476/2023. 787646.
- Bandini D, Brandrud TE, Dima B, Dondl M, Fachada V, Hussong A, Mifsud S, Oertel B, Rodríguez-Campo FJ, Thüs H, et al. 2022a. Fibre caps across Europe: type studies and 11 new species of *Inocybe* (Agaricales, Basidiomycota). Integr Syst. 5:1–85. doi: 10.18476/2022.901982.
- Bandini D, Christan J, Eberhardt U, Ploch S, Ali T, Oertel B, Thines M. 2017. Inocybe sphagnophila sp. nov., eine neue art der höckersporigen untersektion napipedinae der Gattung Inocybe (Agaricales) [Inocybe sphagnophila sp. nov., a new species of the bump-spored subsection napipedinae of the genus Inocybe (Agaricales)]. Mycol Bavar. 18:11–34. French.
- Bandini D, Oertel B, Eberhardt U. 2021. A fresh outlook on the smooth-spored species of *Inocybe*: type studies and 18 new species. Mycol Prog. 20(9):1019–1114. doi: 10.1007/s11557-021-01712-w.
- Bandini D, Oertel B, Eberhardt U. 2022b. Mycol Bavar. 22 (22):31–138. German.
- Bandini D, Oertel B, Eberhardt U. 2022c. More smooth-spored species of *Inocybe* (Agaricales, Basidiomycota): type studies and 12 new species from Europe. Persoonia. 48(1):91–149. doi: 10.3767/persoonia.2022.48.03.
- Bandini D, Oertel B, Eberhardt U. 2023b. Noch mehr risspilze (4): vierzehn neue arten der familie Inocybaceae [Even more crack fungi (4): fourteen new species of the Inocybaceae family]. Mycol Bavar. (23):1–50. German.
- Bandini D, Oertel B, Schüssler C, Eberhardt U. 2020. Noch mehr risspilze: fünfzehn neue und zwei wenig bekannte arten der gattung *Inocybe* [Even more crack fungi: fifteen new and two little-known species of the genus Inocybe. Mycol Bavar. (20):13–101. German.
- Bau T. 2022. Sinica Fungarum China vol. 53: Inocybaceae. Beijing: Science Press; p. 1–250.
- Bhunjun CS, Niskanen T, Suwannarach N, Wannathes N, Chen YJ, McKenzie EHC, Maharachchikumbura SSN, Buyck B, Zhao CL, Fan YG, et al. 2022. The numbers of fungi: are the most speciose genera truly diverse? Fung Divers. 114(1):387–462. doi: 10.1007/s13225-022-0050.
- Brundrett MC, Tedersoo L. 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. 220:1108–1115. doi: 10.1111/nph.14976.
- Burland TG. 2000. DNASTAR's lasergene sequence analysis software. Methods Mol Biol. 132:71–91. doi: 10.1385/1-59259-192-2:71.
- Buyck B, Eyssartier G, Armada F, Corrales A, Hembrom ME, Rossi W, Bellanger JM, Das K, Dima B, Ghosh A, et al. 2022. Fungal biodiversity profiles 111–120. Cryptogam Mycol. 43(2):23–61. doi: 10.5252/cryptogamie-mycologie2022v43a2.
- Cho S, Kwag Y, Han S, Kim CS. 2021. Seven newly recorded macrofungi of Inocybaceae (Agaricales, Basidiomycota) in Korea. Kor J Mycol. 49(2):139–153. doi: 10.4489/KJM.20210015.
- Cripps CL, Larsson E, Vauras J. 2020. Nodulose-spored *Inocybe* from the Rocky Mountain alpine zone molecularly linked to

European and type specimens. Mycologia. 112(1):133–153. doi: 10.1080/00275514.2019.1677419.

- Crous PW, Costa MM, Kandemir H, Vermaas M, Vu D, Zhao L, Arumugam E, Flakus A, Jurjević Ž, Kaliyaperumal M, et al. 2023a. Fungal planet description sheets: 1550–1613. Persoonia. 51(1):280–417. doi: 10.3767/persoonia.2023.51.08.
- Crous PW, Cowan DA, Maggs-Kölling G, Yilmaz N, Thangavel R, Wingfield MJ, Noordeloos ME, Dima B, Brandrud TE, Jansen GM, et al. 2021a. Fungal planet description sheets: 1182–1283. Persoonia. 46:313–528. doi: 10.3767/ persoonia.2021.46.11.
- Crous PW, Osieck ER, Jurjevi Ž, Boers J, Van-Iperen AL, Starink-Willemse M, Dima B, Balashov S, Bulgakov TS, Johnston PR, et al. 2021b. Fungal planet description sheets: 1284–1382. Persoonia. 47(1):178–374. doi: 10. 3767/persoonia.2021.47.06.
- Crous PW, Osieck ER, Shivas RG, Tan YP, Bishop-Hurley SL, Esteve-Raventós F, Larsson E, Luangsa-Ard JJ, Pancorbo F, Balashov S, et al. 2023b. Fungal planet description sheets: 1478–1549. Persoonia. 50(1):158–310. doi: 10.3767/persoonia.2023.50.05.
- Deng LS, Kang R, Zeng NK, Yu WJ, Chang C, Xu F, Deng WQ, Qi LL, Zhou YL, Fan YG. 2021a. Two new *Inosperma* (Inocybaceae) species with unexpected muscarine contents from tropical China. MycoKeys. 85:87–108. doi: 10.3897/ mycokeys.85.71957.
- Deng LS, Yu WJ, Zeng NK, Liu LJ, Liu LY, Fan YG. 2021b. *Inosperma subsphaerosporum* (Inocybaceae), a new species from Hainan, tropical China. Phytotaxa. 502(2):169–178. doi: 10.11646/phytotaxa.502.2.5.
- Deng LS, Yu WJ, Zeng NK, Zhang YZ, Wu XP, Li HJ, Xu F, Fan YG. 2022a. A new muscarine-containing *Inosperma* (Inocybaceae, Agaricales) species discovered from one poisoning incident occurring in tropical China. Front Microbiol. 13:923435. doi: 10.3389/fmicb.2022.923435.
- Deng LS, Zhao LN, Yu WJ, Fan YG. 2022b. Phylogenetic analyses reveal high species diversity and distribution pattern of an ectomycorrhizal mushroom genus. Proceedings of The 11 th International Conference on Mycorrhiza and the 5 th InternationalMolecular Mycorrhiza Meeting; August 1 to 5; Beijing. Okanagan: International Mycorrhiza Society; August 1 to 5. p. 143.
- Dennis RWG. 1953. Les Agaricales de l'ile de la Trinité: rhodosporae-ochrosporae [The Agaricales of Trinidad: rhodosporae-ochrosporae]. Bull Trimest Soc Mycol Fr. 69(2):145– 198. French.
- Dovana F, Bandini D, Eberhardt U, Olariaga I, Bizio E, Ferisin G, Esteve-Raventós F. 2023. Re-evaluation of the taxonomic status of species within the *Inocybe similis* complex. J Fungi. 9(6):679. doi: 10.3390/jof9060679.
- Eberhardt U, Grilli E, Schütz N, Bartlett P, Beker HJ. 2023. Old but not obsolete: a new life for some of Murrill's (*Hebeloma*) names. Mycologia. 115(3):375–426. doi: 10.1080/00275514. 2023.2188387.
- 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(1):213–236. doi: 10.3767/persoonia.2018.41.11.

- Esteve-Raventós F, Larsson E, Pancorbo F, Scholler M. 2022a. Typification of *Inocybe oblectabilis* f. *macrospora*, and additional data on the phylogeny of the *Tiliae* and *Pseudohiulca* groups in Europe. Bol Soc Micol Madrid. 46:49–63.
- Esteve-Raventós F, Moreno G, Bizio E, Alvarado P. 2015. *Inocybe flavobrunnescens*, a new species in section *Marginatae*. Mycol Prog. 14(4):1–12. doi: 10.1007/s11557-015-1036-0.
- Esteve-Raventós F, Pancorbo F, Larsson E, Turégano Y, Moreno G, Altés A. 2022b. *Inocybe vaurasii* (Agaricales, Inocybaceae), a new species of the *I. xanthomelas* group and similar European species with asteriform spores. Phytotaxa. 566 (2):171–188. doi: 10.11646/phytotaxa.566.2.2.
- Fachada V, Bandini D, Beja-Pereira A. 2024. Two new species of *Inocybe* from Mediterranean Cistaceae heathlands. Mycologia. 116(1):1–16. doi: 10.1080/00275514.2023.2284557.
- Fan YG, Bau T. 2010. A revised checklist of the genus *lnocybe* (Fr.) Fr. in China. J Fungal Res. 8:189–193. doi: 10.5555/20113032256.
- Fan YG, Bau T. 2014. *Inocybe hainanensis*, a new lilac-stiped species from tropical China. Mycosystema. 33(5):954–960. doi: 10.13346/j.mycosystema.140043.
- Ferrari E. 2006. *Inocybe* alpine e subalpine, fungi non delineati XXXIV-XXXV-XXXVI [Alpine and subalpine *Inocybe*: fungi not delineated XXXIV-XXXV-XXXVI]. Alassio: Edizioni Candusso. Italian.
- Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Mol Ecol. 2(2):113–118. doi: 10.1111/ j.1365-294X.1993.tb00005.x.
- Ge Y, Liu Z, Zeng H, Cheng X, Na Q. 2021. Updated description of *Atheniella* (Mycenaceae, Agaricales), including three new species with brightly coloured pilei from Yunnan Province, southwest China. MycoKeys. 81:139–164. doi: 10.3897/myco keys.81.67773.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. Nucleic Acids Symp Ser. 41(41):95–98.
- He PM, Fan YG, Deng LS, Yu WJ. 2022. *Inocybe carpinicola* (Inocybaceae, Agaricales), a new nodulose-spored species from Hainan Province, China. Phytotaxa. 575(1):79–88. doi: 10.11646/phytotaxa.575.1.5.
- Heim R. 1931. Le genre *Inocybe*, encyclopédie mycologique [The *Inocybe* genus: mycological encyclopedia]. Paris: Lechevalier; p. 1–431. French.
- Horak E. 1979. *Astrosporina* (Agaricales) in Indomalaya and Australasia. Persoonia. 10(2):157–205.
- Horak E. 1980. *Inocybe* (Agaricales) in Indomalaya and Australasia. Persoonia. 11(1):1–37.
- Horak E, Matheny PB, Desjardin DE, Soytong K. 2015. The genus *Inocybe* (Inocybaceae, Agaricales, Basidiomycota) in Thailand and Malaysia. Phytotaxa. 230(3):201–238. doi: 10. 11646/phytotaxa.230.3.1.
- Houlès A, Gotty K, Joussemet F, Vincent B, Hannibal L, Patrois M, Jourand P, Ducousso M. 2022. The nurse plant acacia spirorbis enriches ectomycorrhizal community composition

of a target species: *Tristaniopsis calobuxus*. Diversity. 14(2):1–13. doi: 10.3390/d14020107.

- Hu JH, Yu WJ, Deng LS, Fan YG, Bau T, Tang LP, Lin WF, Deng CY. 2023. The detection of major clades and new species of *Mallocybe* (Inocybaceae, Agaricales) from China with elon-gate cheilocystidia. Mycol Prog. 22(2):15. doi: 10.1007/s11557-022-01854-5.
- Jacobsson S. 2008. *Inocybe*. In: Knudsen H Vesterholt J, editors. Funga Nordica. Copenhagen: Nordsvamp; p. 868–906.
- Kaewgrajang T, Sangwanit U, Kodama M, Yamato M. 2014. Ectomycorrhizal fungal communities of *Dipterocarpus alatus* seedlings introduced by soil inocula from a natural forest and a plantation. J Fungal Res. 19(2):260–267. doi: 10.1007/ s10310-013-0408-z.
- Katoh K, Rozewicki J, Yamada KD. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Brief Bioinform. 20(4):1160–1166. doi: 10. 1093/bib/bbx108.
- Kaufholtz-Couture C, Moreau PA. 2022. Une nouvelle espèce de champignon proche de l'*Inocybe curvipes* découverte au Québec: *Inocybe squalida* sp. nov. (Inocybaceae, Agaricales)[A new species of fungus close to *Inocybe curvipes* discovered in Quebec: *Inocybe squalida* sp. nov. (Inocybaceae, Agaricales)]. Nat Can. 146(1):10–16. doi: 10.7202/1086644ar. Franch.
- Kaygusuz O, Bandini D, ÇeliK A. 2022a. *Inocybe kusadasiensis* (Inocybaceae: Agaricomycetes), a new species from Turkey. Phytotaxa. 570(1):1–15. doi: 10.11646/phytotaxa.570.1.1.
- Kaygusuz O, Knudsen H, Bandini D, Türkekul İb. 2022b. *Inocybe viscida* (Inocybaceae: Agaricomycetes), a new species from Mediterranean forests of Turkey. Turk J Bot. 46(5):517–527. doi: 10.55730/1300-008X.2727.
- Khan M, Naseer A, Aqdus F, Ishaq M, Fiaz M, Khalid AN. 2022. *Inocybe quercicola* sp. nov. (Agaricales, Inocybaceae), from Pakistan. Microb Biosyst. 6(2):22–29. 10.21608/mb.2022. 109930.1047.
- Kobayashi T. 1993. A new subgenus of *Inocybe Leptocybe* from Japan. Mycotaxon. 48:459–469.
- Kobayashi T. 2002. Notes on the genus *Inocybe* of Japan: I. Mycoscience. 43(3):207–211. doi: 10.1007/S102670200030.
- Kokkonen K, Vauras J. 2012. Eleven new boreal species of *Inocybe* with nodulose spores. Mycol Prog. 11:299–341.
- Kornerup A, Wanscher JH. 1978. Methuen handbook of colour. 3rd edn. London: Eyre Methuen; p. 1–256.
- Kropp BR, Matheny PB. 2004. Basidiospore homoplasy and variation in the *Inocybe chelanensis* group in North America. Mycologia. 96(2):295–309. doi: 10.1080/15572536. 2005.11832979.
- Kühner R, Boursier J. 1932. Notes sur le genre *Inocybe* 1) Les *Inocybes* goniosporés (Suite) [Notes on the genus *Inocybe* 1) goniosporous *Inocybes* (Continued)]. Bull. Soc Myc. 48:118–161. French.
- Kuyper TW. 1985. Studies in *Inocybe*-I: revision of the new taxa of *Inocybe* described by Velenovsky. Persoonia. 12(4):375–400.
- Larsson E, Vauras J, Cripps C. 2018. *Inocybe praetervisa* group–A clade of four closely related species with partly different geographical distribution ranges in Europe. Mycoscience. 59(4):277–287. doi: 10.1016/J.MYC.2017.11.002.

854 👄 J-L. GAO ET AL.

- 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. doi: 10. 29203/KA.2014.461.
- Latha KPD, Manimohan P. 2016. Five new species of *Inocybe* (Agaricales) from tropical India. Mycologia. 108(1):110–122. doi: 10.3852/14-358.
- Latha KPD, Manimohan P. 2017. Inocybes of Kerala. India Calicut: SporePrint Books; p. 1–181.
- Latha KPD, Manimohan P, Matheny PB. 2016. A new species of *Inocybe* representing the Nothocybe lineage. Phytotaxa. 267 (1):40–50. doi: 10.11646/phytotaxa.267.1.4.
- Lebeuf R, Landry J, Ammirati JF, Aronsen A, Cantillo T, Castillo R, Corazon-Guivin MA, da Silva GA, Dirks AC, Healy RA, et al. 2023. Fungal systematics and evolution. Sydowia. 75:313–377. doi: 10.12905/0380.sydowia75-2023-313.
- Li SN, Xu F, Jiang M, Liu F, Wu F, Zhang P, Fan YG, Chen ZH. 2021. Two new toxic yellow *Inocybe* species from China: morphological characteristics, phylogenetic analyses and toxin detection. MycoKeys. 81:185–204. doi: 10.3897/myco keys.81.68485.
- Liu L, Abdul R, Atri NS, Bau T, Belbahri L, Bouket AC, Kitaura MJ. 2018. Fungal systematics and evolution. Sydowia. 70:211– 286. doi: 10.12905/0380.sydowia70-2018-0211.
- Liu SL, Wei HW, Zhou LW. 2023. Xenasmatellales ord. nov. and Xenasmatellaceae fam. nov. for *Xenasmatella* (Agaricomycetes, Basidiomycota). Mycology. 14(3):175–189. doi: 10.1080/ 21501203.2023.2216213.
- Liu Z, Na Q, Cheng X, Wu X, Ge Y. 2021. *Mycena yuezhuoi* sp. nov. (Mycenaceae, Agaricales), a purple species from the peninsula areas of China. Phytotaxa. 511(2):148–162. doi: 10.11646/phytotaxa.511.2.3.
- Marchetti M, Consiglio G, Consiglio G. 2022. Inocybe mediterranea, una nuova specie trovata nella Pineta di Salinella (Sicilia) e osservazioni sui rapporti fra I. lapidicola e I. deianae [Inocybe mediterranea, a new species found in the Salinella Pinewood (Sicily) and observations on the relationships between I. lapidicola and I. deianae]. RdM. 64(3):195–220. Italian.
- Marchetti M, Franchi P, Consiglio G. 2014. Typification of some of Britzelmayr's *Inocybe* species. Riv Micol. 2014(2):127–178.
- Matheny PB. 2005. Improving phylogenetic inference of mushrooms with *RPB1* and *RPB2* nucleotide sequences (*Inocybe*; Agaricales). Mol Phylogenet Evol. 35(1):1–20. doi: 10.1016/j. ympev.2004.11.014.
- Matheny PB, Aime MC, Bougher NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DJ, Soytong K, Trappe JM, et al. 2009. Out of the palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. J Biogeogr. 36(4):577–592. doi: 10. 1111/j.1365-2699.2008.02055.x.
- Matheny PB, Bougher NL. 2017. Fungi of Australia: Inocybaceae. Canberra: ABRS & Melbourne: CSIRO Publishing; p. 1–592.
- Matheny PB, Corrales A, Graddy MG, Halling RE, Kalichman J, Kudzma LV, Ovrebo CL, Swenie RA, Walker NC. 2022. A revision of the *Inocybe grammata* group in North America

including four new taxa. Brittonia. 74(4):436–464. doi: 10. 1007/s12228-022-09720-0.

- Matheny PB, Hobbs AM, Esteve-Raventós F. 2020. Genera of Inocybaceae: new skin for the old ceremony. Mycologia. 112 (1):83–120. doi: 10.1080/00275514.2019.1668906.
- 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* (Inocybaceae) from eastern north America. J Torrey Bot Soc. 146(3):213–235. doi: 10.3159/TORREY-D-18-00060.1.
- Matheny PB, Liu YJ, Ammirati JF, Hall BD. 2002. Using *RPB1* sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). Am J Bot. 89(4):688–698. doi: 10. 3732/ajb.89.4.688.
- Matheny PB, Moreau P. 2009. A rare and unusual lignicolous species of *Inocybe* (Agaricales) from eastern North America. Brittonia. 61:163–171. doi: 10.1007/s12228-008-9066-4.
- Matheny PB, Norvell LL, Giles EC. 2013. A common new species of *Inocybe* in the Pacific Northwest with a diagnostic PDAB reaction. Mycologia. 105(2):436–446. doi: 10.3852/12-155.
- Matheny PB, Pradeep CK, Vrinda KB, Varghese SP. 2012. *Auritella foveata*, a new species of Inocybaceae (Agaricales) from tropical India. Kew Bull. 67:119–125. doi: 10.1007/s12225-012-9329-9.
- Matheny PB, Swenie RA. 2018. The *Inocybe geophylla* group in North America: a revision of the lilac species surrounding *I. lilacina*. Mycologia. 110(3):618–634. doi: 10.1080/00275514. 2018.1469880.
- Mešić A, Haelewaters D, Tkalčec Z, Liu J, Kušan I, Aime MC, Pošta A. 2021. *Inocybe brijunica* sp. nov., a new ectomycorrhizal fungus from Mediterranean Croatia revealed by morphology and multilocus phylogenetic analysis. J Fungi. 7 (3):199. doi: 10.3390/jof7030199.
- Muñoz G, Pancorbo F, Turégano-Carrasco Y, Esteve-Raventós F. 2022. New species and combinations of *Inocybe* with lilac or violet colours in Europe. Fungi Iberici. 2:7–26. doi: 10.51436/ funiber/02.001.
- Na Q, Hu Y, Zeng H, Song Z, Ding H, Cheng X, Ge Y. 2022. Updated taxonomy on *Gerronema* (Porotheleaceae, Agaricales) with three new taxa and one new record from China. MycoKeys. 89:87–120. doi: 10.3897/mycokeys.89.79864.
- Nylander J. 2004. MrModeltest V2. program distributed by the author. Bioinformatics. 24:581–583. doi: 10.1093/bioinfor matics/btm388.
- Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM. 2013. Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. PLoS One. 8(4):e62419. doi: 10.1371/ journal.pone.0062419.
- Pošta A, Bandini D, Mešić A, Pole L, Kušan I, Matočec N, Malev O, Tkalčec Z. 2023. *Inocybe istriaca* sp. nov. from Brijuni National Park (Croatia) and its position within Inocybaceae revealed by multigene phylogenetic analysis. Diversity. 15 (6):755. doi: 10.3390/d15060755.

- Pradeep CK, Vrinda KB, Varghese SP, Korotkin HB, Matheny PB. 2016. New and noteworthy species of *Inocybe* (Agaricales) from tropical India. Mycol Prog. 15(3):24. doi: 10.1007/s11557-016-1174-z.
- Raghoonundon B, Vadthanarat S, Hu Y, Raspé O. 2023. *Inocybe hopeae* sp. nov. and first record of *Pseudosperma keralense* (Inocybaceae) from Thailand. Eur J Taxon. 870:30–45. doi: 10. 5852/ejt.2023.870.2115.
- Razzaq A, Naseer A, Khalid AN. 2023. Inocybe subhimalayanensis (Agaricales, Inocybaceae), a new smooth spored Inocybe species from Pakistan. Eur J Taxon. 870:76–86. doi: 10.5852/ ejt.2023.870.2119.
- Ronquist F, Teslenko M, van der Mark P, Ayres 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. Syst Biol. 61:539– 542. doi: 10.1093/sysbio/sys029.
- Ryberg M, Larsson E, Jacobsson S. 2010. An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). Mol Phylogenet Evol. 55(2):431–442. doi: 10.1016/j.ympev. 2010.02.011.
- Ryberg M, Matheny PB. 2012. Asynchronous origins of ectomycorrhizal clades of Agaricales. P Roy Soc B-Biol Sci. 279 (1735):2003–2011. doi: 10.1098/rspb.2011.2428.
- 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 Evol Biol. 8(1):50. doi: 10.1186/1471-2148-8-50.
- Senanayake IC, Rossi W, Leonardi M, Weir A, McHugh M, Rajeshkumar KC, Verma RK, Karunarathna SC, Tibpromma S, Ashtekar N, et al. 2023. Taxonomic and phylogenetic contributions on fungal genera and species emphasis in south China. Fungal Divers. 122(1):161–403. doi: 10.1007/s13225-023-00523-6.
- Singer R. 1986. The Agaricales in modern taxonomy. 4th ed. Koenigsten: Koeltz Scientific Books; p. 1–981.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol. 28(10):2731–2739. doi: 10.1093/molbev/msr121.
- Tan YP, Bishop-Hurley SL, Shivas RG, Cowan DA, Maggs-Kölling G, Maharachchikumbura SSN, Pinruan U, Bransgrove KL, De La Peña-Lastra S, Larsson E, et al. 2022. Fungal planet description sheets: 1436–1477. Persoonia. 49(1):261–350. doi: 10.3767/persoonia.2022.49.08.
- Tedersoo L, Suvi T, Beaver K, Kõljalg U. 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native Vateriopsis seychellarum (Dipterocarpaceae) and Intsia bijuga (Caesalpiniaceae) to the introduced Eucalyptus robusta

(Myrtaceae), but not *Pinus caribea* (Pinaceae). New Phytol. 175 (2):321–333. doi: 10.1111/j.1469-8137.2007.02104.x.

- Trifinopoulos J, Nguyen LT, Von Haeseler A, Minh BQ. 2016. W-IQTREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Res. 44(W1):232–235. doi: 10. 1093/nar/gkw256.
- Vauras J. 1989. *Inocybe* section *Calosporae* in NW Europe. Karstenia. 28:79–86.
- Vauras J, Larsson E. 2015. *Inocybe caprimulgi* and *I. lacunarum*, two new nodulose-spored species from Fennoscandia. Karstenia. 55:1–18. doi: 10.29203/ka.2015.465.
- Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. J Bacteriol. 172(8):4238– 4246. doi: 10.1128/jb.172.8.4238-4246.1990.
- Vrinda KB, Pradeep CK, Mathew S, Abraham TK. 1999. Agaricales from Western ghats-6. Indian Phytopath. 52:198–200.
- Wang SN, Hu YP, Chen JL, Qi LL, Zeng H, Ding H, Huo GH, Zhang LP, Chen FS, Yan JQ. 2021. First record of the rare genus *Typhrasa* (Psathyrellaceae, Agaricales) from China with description of two new species. MycoKeys. 79:119– 128. doi: 10.3897/mycokeys.79.63700.
- Wu F, Zhou LW, Yang ZL, Bau T, Li TH, Dai YC. 2019. Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. Fungal Divers. 98:1–76. doi: 10.1007/s13225-019-00432-7.
- Yu WJ, Chang C, Qin LW, Zeng NK, Wang SX, Fan YG. 2020. Pseudosperma citrinostipes (Inocybaceae), a new species associated with Keteleeria from southwestern China. Phytotaxa. 450(1):8–16. doi: 10.11646/phytotaxa.450.1.2.
- Yuan Y, Bian LS, Wu YD, Chen JJ, Wu F, Liu HG, Zeng GY, Dai YC. 2023. Species diversity of pathogenic wood-rotting fungi (Agaricomycetes, Basidiomycota) in China. Mycology. 14 (3):204–226. doi: 10.1080/21501203.2023.2238779.
- Yuwa-Amornpi T, Vichitsoont T, Tanticharoen M, Cheevadhanar S, Ratchadawo S. 2006. Diversity of ectomycorrhizal fungi on dipterocarpaceae in Thailand. J Biol Sci. 6 (6):1059–1064. doi: 10.3923/jbs.2006.1059.1064.
- Zhao LN, Yu WJ, Deng LS, Hu JH, Ge YP, Zeng NK, Fan YG. 2022. Phylogenetic analyses, morphological studies, and muscarine detection reveal two new toxic *Pseudosperma* (Inocybaceae, Agaricales) species from tropical China. Mycol Prog. 21(9):75. doi: 10.1007/s11557-022-01822-z.
- Zhong CL, Bai JY, Zhang Y. 2005. Introduction and conservation of *Casuarina* trees in China. Scientia Silvae Sinicae. 3:345–350.
- Zhou YL, Deng LS, Yang SD, Liu CF, Fan YG, Yu WJ. 2023. Phylogenetic analysis, morphological studies, element profiling, and muscarine detection reveal a new toxic *Inosperma* (Inocybaceae, Agaricales) species from tropical China. Front Microbiol. 14:1326253. doi: 10.3389/fmicb. 2023.1326253.