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Five new species of Inocybe (Agaricales) from tropical India

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Five new species of *Inocybe* (Agaricales) from tropical India

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Abstract: Five new species of *Inocybe*, *I. iringolkavensis*, *I. keralensis*, *I. kuruvensis*, *I. muthangensis* and *I. wayanadensis*, are described from Kerala state, India, based on morphological and molecular data. All are associated with trees belonging to Dipterocarpaceae. *Inocybe iringolkavensis* is characterized by nodulose to somewhat stellate basidiospores, 1–4-spored basidia, and caulocystidia restricted to the stipe apex. *Inocybe keralensis* has a yellowish brown pileus, lamellae with whitish, serrate edges, smooth, ellipsoidal basidiospores and a duplex pileipellis with the superficial hyphae devoid of encrustations and encrusted hyphae beneath. The diagnostic features of *I. kuruvensis* include a dark brown pileus, stipe with a whitish base and grayish brown, floccose-fibrillose surface, nodulose basidiospores with saddle-shaped projections and faintly encrusted paracystidia with refractive contents. Violet basidiomata with a rimose, hygrophanous pileus, densely pruinose stipe with a marginate-bulbous base, and nodulose basidiospores are the major features of *I. muthangensis*. *Inocybe wayanadensis* is characterized by small, whitish basidiomata, a viscid pileus with a rimulose surface, a densely pruinose and fibrillose stipe with a marginate-bulbous base, nodulose basidiospores, thick-walled pleuro- cheilo- and caulocystidia and an ixotrichoderm-type pileipellis. The phylogenetic relationships of these new species are inferred from an analysis of nuc rDNA sequences of the internal transcribed spacers (ITS1-5.8S-ITS2) and the 28S gene. Except *I. keralensis,* which belongs to the Pseudosperma clade, all other species belong to the Inocybe clade. This study represents the second report of an *Inocybe* species (*I. muthangensis*) that combines violet basidiomata with nodulose basidiospores.

Key words: Basidiomycota, Inocybaceae, phylogeny, systematics, tropical agarics

Introduction

The genus *Inocybe* (Fr.) Fr. (Inocybaceae, Agaricales) is one of the most speciose genera of gilled mushrooms and is noteworthy for the ectomycorrhizal ecology and toxicity of most of its species (Matheny 2009). Species of *Inocybe* are characterized by brownish basidiomata, at times with a lilac or purplish tint, the coarsely fibrillose or squamulose texture of the pileus and the stipe, brownish lamellae, a brown spore-print and occurrence on soil. Several species have thick-walled cystidia with crystalline, apical encrustations and some species have a distinctive odor. While several species have smooth basidiospores, many species are characterized by gibbous or nodulose basidiospores. Although it originally was placed in the Cortinariaceae (Kuyper 1986, Singer 1986), recent phylogenetic analyses support Jülich's (1982) placement of *Inocybe* in its own family, the Inocybaceae (Matheny 2005, 2009). According to Kirk et al. (2008), about 500 species of the genus are described worldwide and new species are discovered on a regular basis. Although most species are known from temperate and arctic-alpine regions, some are known from the tropics (Matheny et al. 2009).

Although India encompasses some of the biologically richest and most endangered terrestrial ecoregions (Mittermeier et al. 2005), several areas remain unexplored or underexplored for many groups of fungi. Available literature on Indian agarics consists mostly of isolated and sporadic records. The situation in Kerala state, a narrow strip of land on the southwestern corner of India with a tropical, maritime and monsoonal climate, is somewhat different. The diversity of agarics of this region was explored intensively in the past three decades resulting in a recent checklist included 616 species in 112 genera (Farook et al. 2013). Monographic accounts of several agaric genera were published, for instance *Hymenagaricus* (Heinemann and Little Flower 1984), *Micropsalliota* (Heinemann and Leelavathy 1991), *Entoloma* (Manimohan et al. 1995, 2006), *Psilocybe* (Thomas et al. 2002), *Hygrocybe* (Leelavathy et al. 2006), *Lepiota* (Kumar and Manimohan 2009a), *Leucocoprinus* and *Leucoagaricus* (Kumar and Manimohan 2009b). Remarkably most of the forested areas of Kerala include parts of the western Ghats, one of the biodiversity hotspots of the world. To date 19 species of *Inocybe* were reported from Kerala (Farook et al. 2013). During our studies on the diversity of *Inocybe* in this region, we found five new species that are described here based on both morphology and molecular phylogenetic results.

Materials and methods

Morphology.—Specimens examined were collected from natural forests and other forested lands. Microscopic examinations were made on dried material stained with 1%

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aqueous solution of Congo red and mounted in 3% aqueous KOH. Color and pigment topography of cells and hyphae were observed on tissues mounted in water. For evaluation of the range of spore dimension, 20 basidiospores from one specimen of each collection cited were measured. Basidiospore measurements include both the hilar appendix and the nodules. In the description of the basidiospores, Q represents the range of ratio of basidiospore length/width calculated for each basidiospore and Qm is the average of the Q values. Alphanumeric color codes from both Kornerup and Wanscher (1978) (e.g. 5E7) and the Online Auction Color Chart (Anonymous 2004) (e.g. OAC768) accompany color names in the descriptions. All examined collections except one are deposited at Kew (Mycology) Herbarium, and the accession numbers (e.g. K(M) 191734) are indicated. One collection is presently maintained in the personal herbarium of the second author.

DNA extraction, PCR, and sequencing.—Genomic DNA was extracted from dried holotypes of the five new *Inocybe* species employing the procedure described by Izumitsu et al. (2012). The nuc rDNA sequences of the internal transcribed spacer (ITS = ITS1-5.8S-ITS2) and the 28S gene were analyzed. Primers LROR and LR7 (Vilgalys and Hester 1990) were used for amplifying the 28S. The ITS was amplified with the primer pair ITS1 and ITS4 (White et al. 1990). Amplification reactions were performed in a GeneAtlas™ thermal cycler (Astec, Fukuoka, Japan). Amplified PCR products were purified with column purification (GeneJet™ PCR purification kit, Thermo Fisher Scientific, Mumbai, India) as per manufacturer's guidelines and were subjected to automated DNA sequencing on an ABI3730xl DNA analyzer (Applied Biosystems, Foster City, California) using the same primers. The generated sequences were edited manually with BioEdit 7.0.9.0 (Hall 1999). The edited sequences were used for BLAST queries in the GenBank database (www.ncbi.nlm.nih.gov). Newly generated sequences were deposited in GenBank (accession numbers indicated in SUPPLEMENTARY TABLE I).

DNA sequence analysis.—Initial BLAST queries of the NCBI database were performed to identify related taxa for which sequences were available. The newly generated ITS and 28S sequences of the five newly discovered species and those retrieved from GenBank (66 sequences) were aligned with MUSCLE 3.8.31 (Edgar 2004). A final combined data matrix of ITS and 28S sequences of 67 taxa including one outgroup (SUPPLEMENTARY TABLE I) was manually adjusted in AliView 1.15 (Larsson 2014). The sequences of *Inocybe* species were selected based on BLASTn similarity indices with 0 e-value and >86% sequence identity for each species separately. Available sequences of phenetically similar species and those of representative species of the seven clades of Inocybaceae that are available in GenBank were employed in a phylogenetic analyses of the genus (Alvarado et al. 2010, Matheny et al. 2012) also were added to the data matrix. *Tubaria vinicolor* (Peck) Ammirati, Matheny & Vellinga was selected as outgroup taxon for rooting purpose following Matheny et al. (2012). Maximum likelihood (ML) analysis was conducted with RAxML 8.0.26 (Stamatakis 2014) employed in raxmlGUI 1.3.1 (Silvestro and Michalak 2012), implementing GTR+I+G model and executing 1000 rapid ML bootstrap replicates. Bayesian inference (BI) was performed with MrBayes 3.2.1 (Ronquist and Huelsenbeck 2003), also implementing the GTR+I+G model. A general time reversible model including a proportion of invariable sites and gamma distributed rate heterogeneity (GTR+I+G) model of molecular evolution was selected with TOPALi 2.5 (Milne et al. 2009). For BI four Markov chains were run 3 000 000 generations, sampling every 100th step, with two independent runs per analysis. The first 25% trees were burned before calculating posterior probability (PP) values. Bootstrap values above 70% and Bayesian posterior probability values above 0.95 were considered significant. The aligned sequence data matrix was deposited in TREEBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S16895). The phylogeny from BI and ML analyses were displayed with FigTree 1.4.2 (Rambaut 2014).

RESULTS

Results of BLAST query and phylogenetic analysis.—A comparison of ITS and 28S sequences of the five new species of *Inocybe* described here with nucleotide sequences of taxa available in GenBank suggests that they have distinct ITS and 28S sequences. The closest hits for the five new *Inocybe* species in the MegaBLAST queries of the GenBank nucleotide database using the ITS and 28S sequences are provided (TABLE I).

Molecular analyses yielded phylogenetic trees that showed the relative placement of the five new species. The phylogeny inferred from both maximum likelihood and Bayesian analyses of the combined data matrix of ITS and 28S sequence are provided (FIGS. 1, 2) and placed *I. iringolkavensis*, *I. kuruvensis*, *I. muthangensis* and *I. wayanadensis* in the Inocybe clade and *I. keralensis* in the Pseudosperma clade (Matheny 2009). In the Inocybe clade *I. iringolkavensis* was resolved with *Inocybe* sp. ZT10102 (from northern Thailand) with significant ML bootstrap support (100% BS) and BI posterior probability (1.0 PP). Similarly *I. kuruvensis* and *I. alienospora* (from Australia) formed a distinct clade with significant BI posterior probability (0.96 PP) and weak ML (67% BS) support. *Inocybe muthangensis* and *Inocybe* cf. *serrata* formed another clade but with weak support (56% BS, 0.91 PP). Within the Inocybe clade the position of *I. wayanadensis* was differentiated but was not well supported. In the Pseudosperma clade *Inocybe keralensis*, *I. rimosa* (USA) and *Inocybe* sp. PBM2321 (USA) formed a discrete clade. This group received significant support (100% BS, 1.00 PP), and within it *I. keralensis* represented a separate lineage with full ML bootstrap (100% BS) support and BI posterior probability (1.0 PP).

TABLE I. The BLAST query results of the five new *Inocybe* species, their closest hits and sequence identities for ITS and nLSU sequences

Species		Closest hits	Sequence identities
Inocybe iringolkavensis	ITS (669 bp)	*Inocybe* sp. ZT10102	95%
	nLSU (878 bp)	*Inocybe* sp. ZT10102	99%
I. keralensis	ITS (635 bp)	*Inocybe rimosa*	87%
	nLSU (902 bp)	*I. rimosa*	97%
		Inocybe sp. PBM2321	97%
I. kuruvensis	ITS (649 bp)	—	—
	nLSU (694 bp)	*Inocybe hydrocybiformis*	97%
		I. alienospora	97%
I. muthangensis	ITS (662 bp)	—	—
	nLSU (864 bp)	*Inocybe* sp. AU32	96%
		Inocybe cf. *serrata*	96%
I. wayanadensis	ITS (486 bp)	—	—
	nLSU (737 bp)	*Inocybe* cf. *scissa*	95%
		Inocybe sp. PBM3110	95%

TAXONOMY

Inocybe iringolkavensis K.P.D. Latha & Manim., sp. nov. FIGS. 3A, B; 4A–G

MycoBank MB810559

Typification: INDIA. KERALA STATE, Ernakulum District, Iringolkav, 4 Jun 2013, *K. P. Deepna Latha* (**holotype** K[M] 191731).

Etymology: Referring to Iringolkav, a sacred grove in Kerala state, India, where this species was first observed.

Diagnosis: Characterized by nodulose to somewhat stellate basidiospores, 1–4-spored basidia, caulocystidia restricted to the stipe apex, and association with dipterocarps in tropical India. Deviating from other species of Inocybe clade in the ITS by at least 15 nucleotide positions.

Description: Pileus 3–26 mm diam, somewhat paraboloid or conical-convex initially, becoming hemispherical to convex and finally applanate with a small umbo; surface initially yellowish brown (5E7–8)/(OAC768) on the disk and with golden brown (5D6–7)/(OAC748) squamules, becoming brown (6E8)/(OAC644) at the center and on squamules, gradually fading to grayish orange (5B3–4)/(OAC792) toward the margin with age, initially with appressed or slightly recurved squamules over all except at the center, becoming appressed to recurved squamulose or subsquarrose around the disk and becoming appressed-fibrillose toward the margin; margin initially incurved, becoming decurved to almost straight and finally reflexed, finely appendiculate initially, becoming crenate and slightly split. Lamellae adnate with a small decurrent tooth, close, initially orange gray (5B2)/(OAC808), becoming grayish orange (5B3)/(OAC792) or brownish orange (6C3)/(OAC653) with age, up to 2.5 mm deep, with lamellulae of 1–3 lengths; edges crenate, concolorous with the faces. Stipe 12–42 × 1.5–3 mm, central, terete, equal or slightly tapered toward the apex, flexuous toward the base, solid initially, fistulose with age; surface somewhat translucent or off white toward the apex, brownish orange (5C3)/(OAC800) toward the base initially, becoming grayish orange (5B3)/(OAC792) and finally brownish orange (5C5)/(OAC716) with age, sparsely to densely appressed-fibrillose all over, densely pruinose toward the apex; base swollen, not marginate, whitish, with basal mycelium. Context soft, up to 2 mm wide, brownish gray (5D2)/(OAC739). Odor and flavor not distinctive.

Basidiospores 10–12 × 8–11 (10.7 ± 0.6 × 9.5 ± 0.7) μm, Q = 1–1.4, Qm = 1.1, nodulose to somewhat stellate, with 7–8 nodules up to 3 μm long in profile, slightly thick-walled, pale brown or pale yellowish brown. Basidia 21–39 × 8–13 μm, two- or four-spored, rarely one-spored. Pleurocystidia metuloidal, 33–44 × 11–14 μm, infrequent, utriform or fusiform, wall up to 5 μm thick, hyaline; apices crystalliferous. Lamella edge heterogeneous with cheilocystidia mixed with clusters of paracystidia. Cheilocystidia metuloidal, 27–58 × 11–23 μm, fusiform, utriform, cylindrical, clavate, sublageniform or sublecythiform, rarely pedicellate, wall 2–5 μm thick toward the apex, hyaline; apices crystalliferous. Paracystidia 9–39 × 5–16 μm, clavate, inflated clavate, subglobose, ellipsoidal or rarely lageniform, walls up to 1 μm thick, hyaline. Pileipellis a disrupted cutis with ascending trichodermal patches; hyphae 4–21 μm diam, slightly thick-walled, with a yellowish brown, spirally encrusting pigment. Stipitipellis a cutis, often disrupted with ascending cystidioid

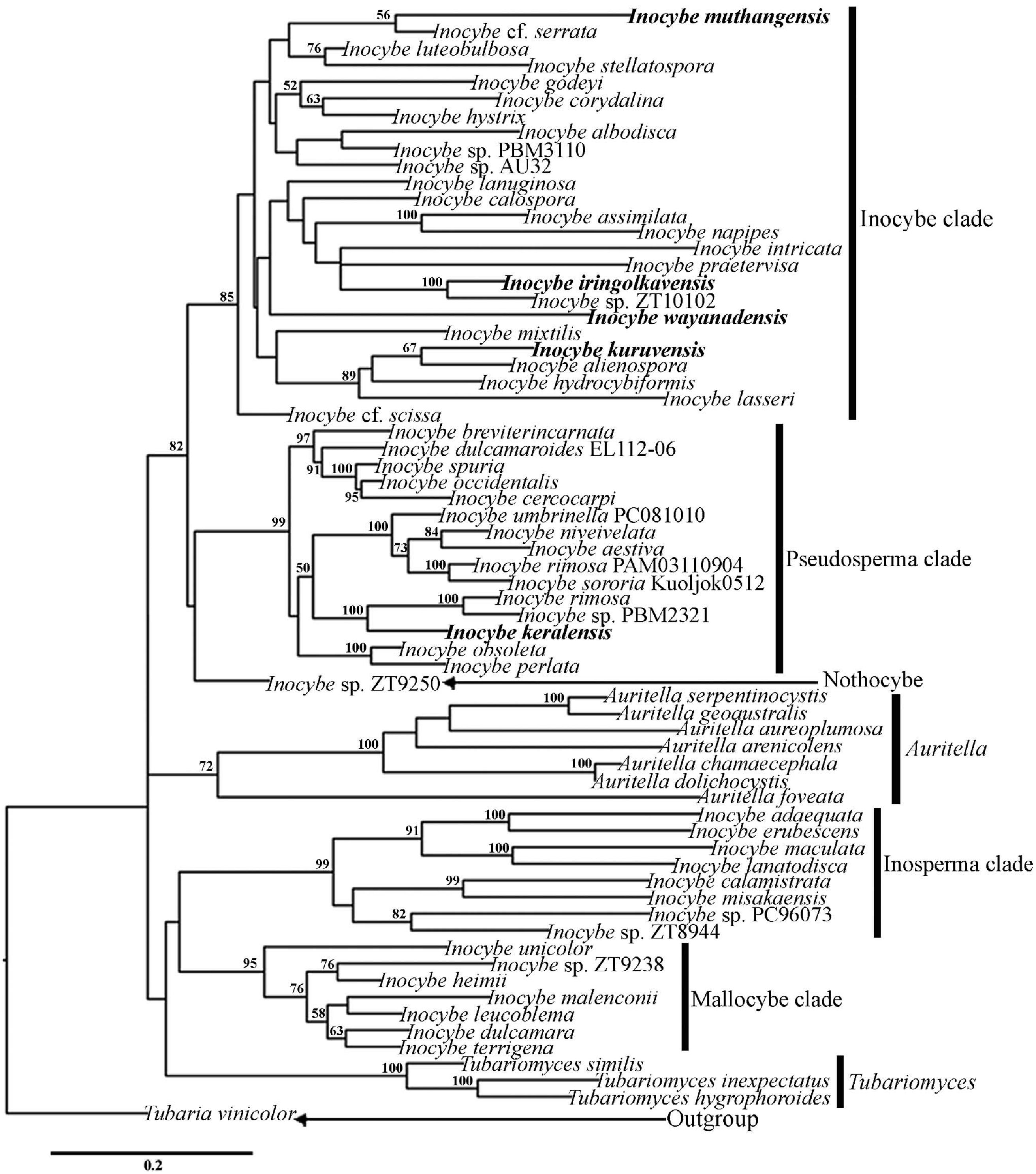

FIG. 1. Maximum likelihood phylogeny based on combined data matrix of ITS and 28S sequences showing the placement of the five new *Inocybe* species. Bootstrap values ≥50% are shown. Except the Mallocybella clade, which was proposed as the genus *Tubariomyces* by Alvarado et al. (2010), all other clade nomenclature follows Matheny et al. (2009). The names of the five new species are in boldface to highlight their phylogenetic positions.

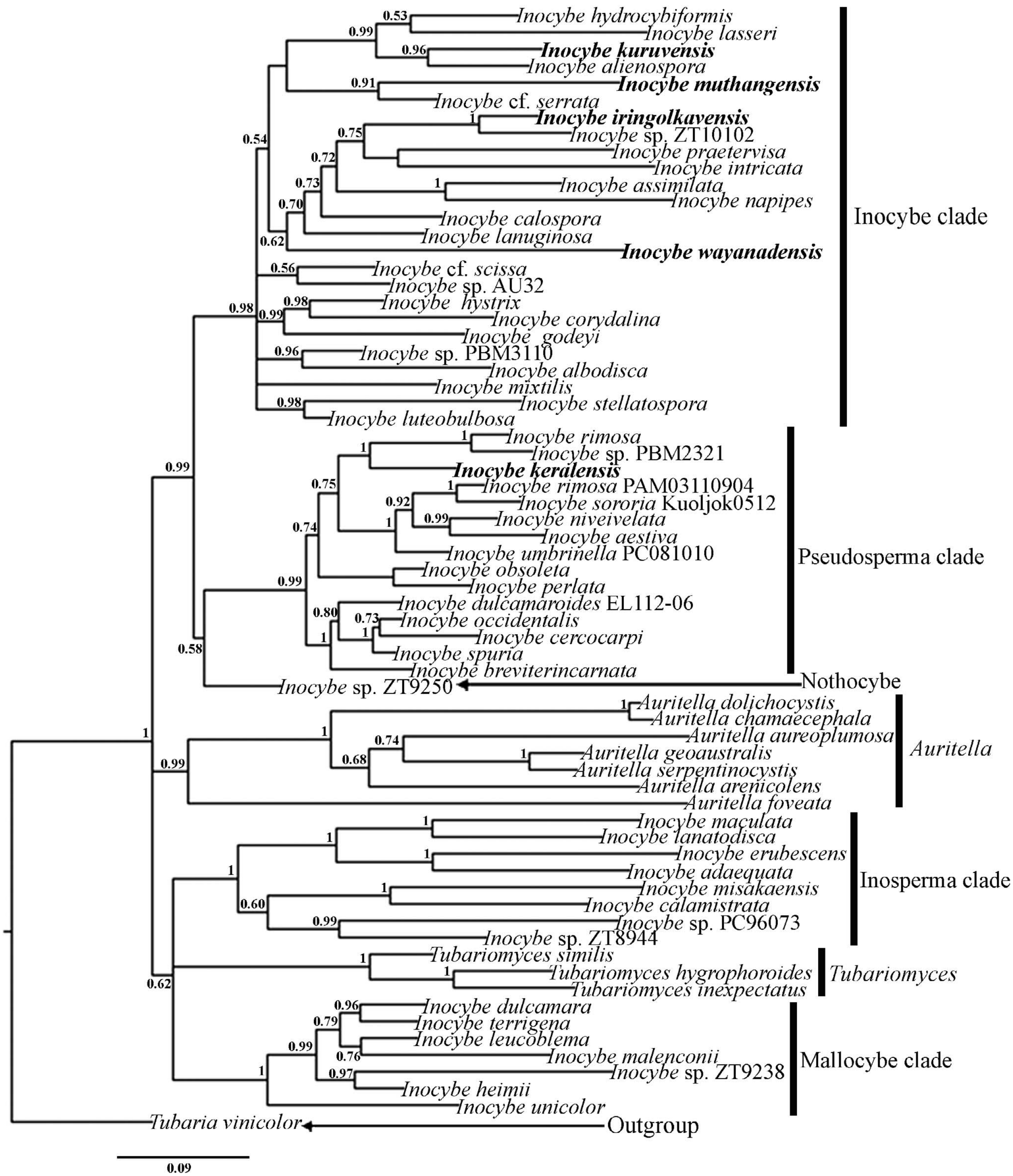

FIG. 2. The 50% majority-rule consensus tree obtained from Bayesian analysis using combined data matrix of ITS and 28S sequences. Values in the branches indicate the posterior probability (PP) support of the clades. PP values greater than 0.5 are shown. Except the Mallocybella clade, which was proposed as the genus *Tubariomyces* by Alvarado et al. (2010), all other clade nomenclature follows Matheny et al. (2009). The names of the five new species are in boldface to highlight their phylogenetic positions.

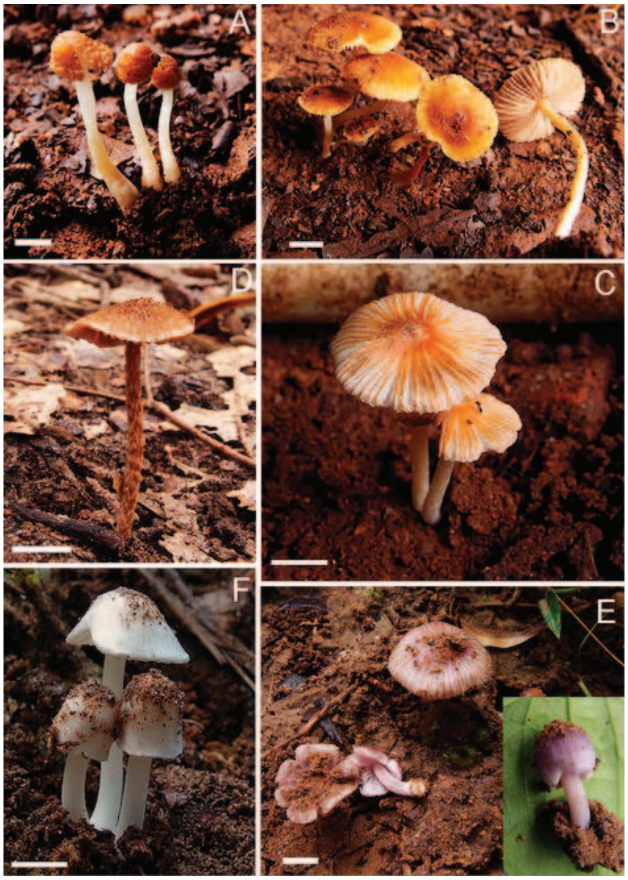

FIG. 3. A–F. Basidiomata of the five new species of *Inocybe*. A, B. *I. iringolkavensis*. C. *I. keralensis*. D. *I. kuruvensis*. E. *I. muthangensis*. F. *I. wayanadensis*. Bars = 10 mm.

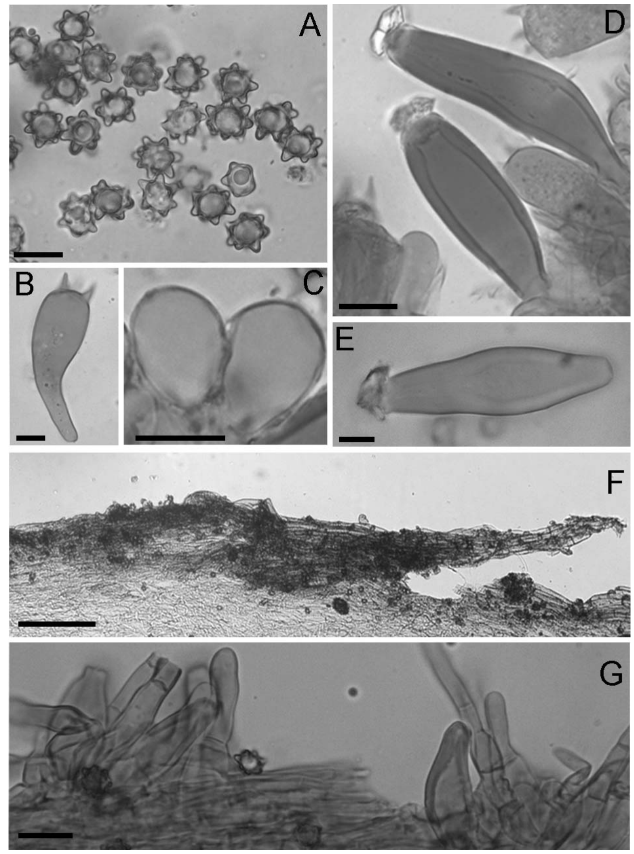

FIG. 4. A–G. *Inocybe iringolkavensis* (K[M] 191731, **holotype**). A. Basidiospores. B. Basidium. C. Paracystidia. D. Cheilocystidia. E. Pleurocystidium. F. Pileipellis. G. Stipitipellis. Bars = 10 μm.

terminal cells and also with scarce caulocystidia confined to the stipe apex, lacking cauloparacystidia; hyphae 2–10 μm diam, thin- to slightly thick-walled, with a pale yellow spirally encrusting pigment, rarely with brownish or yellowish brown amorphous contents. Caulocystidia metuloidal, 32–57 × 9–19 μm, fusiform, utriform, lageniform or conical, wall up to 2 μm thick toward the apex, hyaline; apices crystalliferous. Cystidioid terminal cells 21–67 × 5–13 μm, cylindrical-septate, flexuoso-cylindrical, sublageniform or submoniliform, wall up to 1.5 μm thick, hyaline, devoid of encrustations. Clamp connections present.

Habit, habitat and distribution: In small groups, on the ground, near *Vateria indica* and *Hopea ponga* (Dipterocarpaceae) trees, India.

Other specimens examined: INDIA. KERALA STATE, Wayanad District, Muthanga Wildlife Sanctuary, 4 Jul 2013, *K.P. Deepna Latha K(M) 191732*; 25 Sep 2013, *K.P. Deepna Latha K(M) 191733*.

Notes: Inocybe iringolkavensis is similar to *I. calospora* Quel., recorded from India (Horak 1981), in having a pileus with somewhat similar size, shape and surface features and in the presence of pleuro-, cheilo-, caulo- and paracystidia. *Inocybe calospora* is distinguished by its crowded lamellae, larger (65 mm), vinaceous brown stipe with an entirely pruinose surface, larger basidiospores with dense, long, conical projections, presence of cauloparacystidia in the stipitipellis and herbaceous odor. In addition, in *I. calospora* the frequency of the crystals at the apex of the cystidia varies, at times with small crystals, with resinous incrustations or sometimes lacking crystals. *Inocybe iringolkavensis* is somewhat similar to *I. hydrocybiformis* (Corner & E. Horak) Garrido, described from Singapore and Malaysia (Horak 1979) and Kerala (Vrinda et al. 1999), because of the comparable sizes of both the pileus and the basidiospores (10–12.5 × 8.5–11 μm). However, *I. hydrocybiformis* differs in having an acutely umbonate pileus with different surface features, veil remnants on the stipe, thin-walled and larger cheilocystidia and a stipitipellis with caulocystidia. *Inocybe iringolkavensis* is also similar to *I. asterospora* Quél. in having somewhat smaller basidiospores (10–14 × 8–12 μm) and morphology and pleuro-, cheilo- and caulocystidia, but *I. asterospora* has larger basidiomata, a pileus with an acute or conic umbo, a stipe with an entirely pruinose surface and

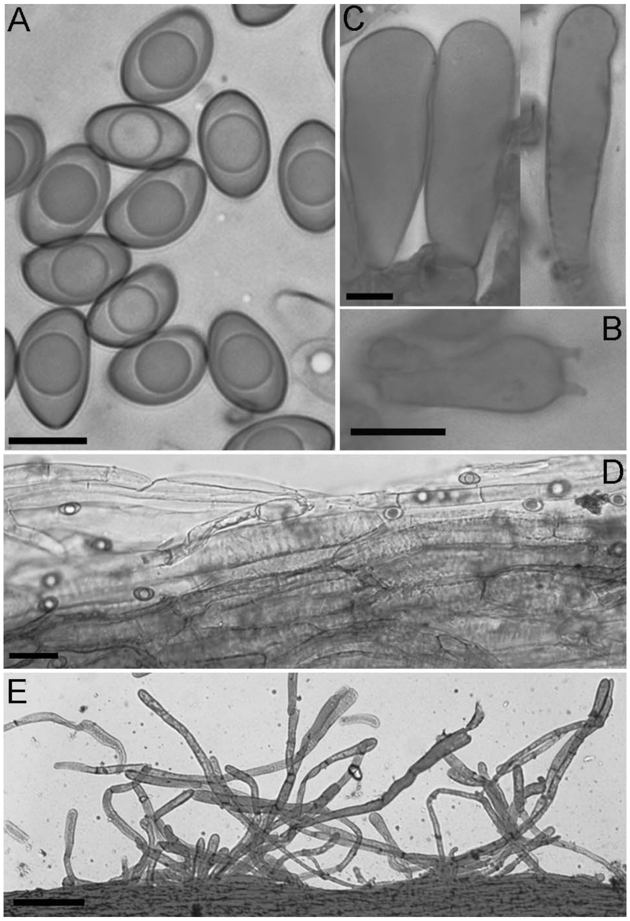

FIG. 5. A–E. *Inocybe keralensis* [K[M] 191712, **holotype**). A. Basidiospores. B. Basidium. C. Cheilocystidia. D. Pileipellis mounted in water. E. Stipitipellis. Bars = 10 μm.

subdiscoid to marginate-bulbous base and a cutis-type pileipellis (Horak 1979). Morphological characters of *Inocybe* sp. ZT10102, which was the closest hit in BLASTn query and from Thailand, are unavailable for comparison.

Inocybe keralensis K.P.D. Latha & Manim., sp. nov. FIGS. 3C, 5A–E

MycoBank MB810560

Typification: INDIA. KERALA STATE, Ernakulum District, Iringolkav, 1 Sep 2013, *K.P. Deepna Latha* (**holotype** K[M] 191712).

Etymology: Referring to Kerala state, India, the region where this species first was observed.

Diagnosis: Characterized by a yellowish brown pileus; lamellae with whitish, serrate edges; smooth, ellipsoidal basidiospores; a duplex pileipellis with superficial hyphae devoid of encrustations and encrusted hyphae beneath; and association with dipterocarps in tropical India. Deviating from other species of the Pseudosperma clade in the ITS region by at least 45 nucleotide positions.

Description: Pileus 11–35 mm diam, convex initially, becoming plano-convex to almost applanate and finally somewhat concave or almost infundibuliform with a small umbo on the disk, often with a slight depression around the umbo; surface yellowish brown (5D7)/(OAC755) on the disk and on the fibrils and orange gray (5B2, 6B2)/(OAC760, OAC808) elsewhere initially, becoming light brown (6D5–6)/(OAC728) at the center and on the fibrils with age, appressed-fibrillose all over, radially rimose exposing paler tissue beneath; margin slightly incurved initially, becoming decurved to almost straight and finally reflexed, crenate or somewhat wavy, slightly split. Lamellae adnate or emarginate with a small decurrent tooth, slightly wavy, close, initially orange-gray (6B2)/(OAC794) or paler, finally brown (6E7)/(OAC748), up to 3 mm deep, with lamellulae of one length; edges serrate, whitish. Stipe 15–50 × 1.5–3 mm, central, equal or slightly tapering toward the apex, cartilaginous, fistulose or becoming hollow; surface orange-gray (6B2)/(OAC794) initially, finally light brown (6D4–5)/(OAC659, OAC666) toward the apex and brownish orange (6C3)/(OAC653) toward the base, appressed-fibrillose all over, finely pruinose at the apex; base slightly enlarged, not marginate, whitish. Context soft, up to 2.5 mm wide, orange-gray (5B2)/(OAC816). Odor and flavor not distinctive.

Basidiospores 8–12 × 5–7 (10.1 ± 0.9 × 6.1 ± 0.4) μm, Q = 1.4–2.0, Qm = 1.7, smooth, ellipsoidal to subphaseoliform, slightly thick-walled, pale yellowish brown. Basidia 19–33 × 7–15 μm, four-spored. Lamella edge sterile. Cheilocystidia abundant, 30–77 × 10–22 μm, oblong, clavate, fusiform, utriform, flexuose-cylindrical, cylindrical with a median and apical constriction, or rarely clavate with apical protrusions, thin- to slightly thick-walled, hyaline, rarely with hyaline or pale yellow encrustations. Pleurocystidia absent. Pileipellis a duplex with a superficial disrupted cutis of 3–17 μm diam, thin- to slightly thick-walled, nearly hyaline, smooth hyphae and a distinct hypodermal band composed of 5–20 μm diam, thin- to slightly thick-walled hyphae with yellowish brown spiral encrustations. Stipitipellis a cutis, frequently disrupted by loose hyphal projections often with cystidioid terminal cells at the stipe apex; hyphae 3–12 μm diam, thin- to slightly thick-walled, with pale yellow or pale brownish yellow wall pigment, occasionally encrusted, rarely with yellowish brown amorphous contents; terminal cells 36–66 × 7–12 μm, clavate or cylindrical with an obtuse apex, nearly hyaline with faint spiral encrustations, thin- to slightly thick-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat and distribution: In small groups, on the ground, near *Vateria indica* and *Hopea ponga* (Dipterocarpaceae) trees, India.

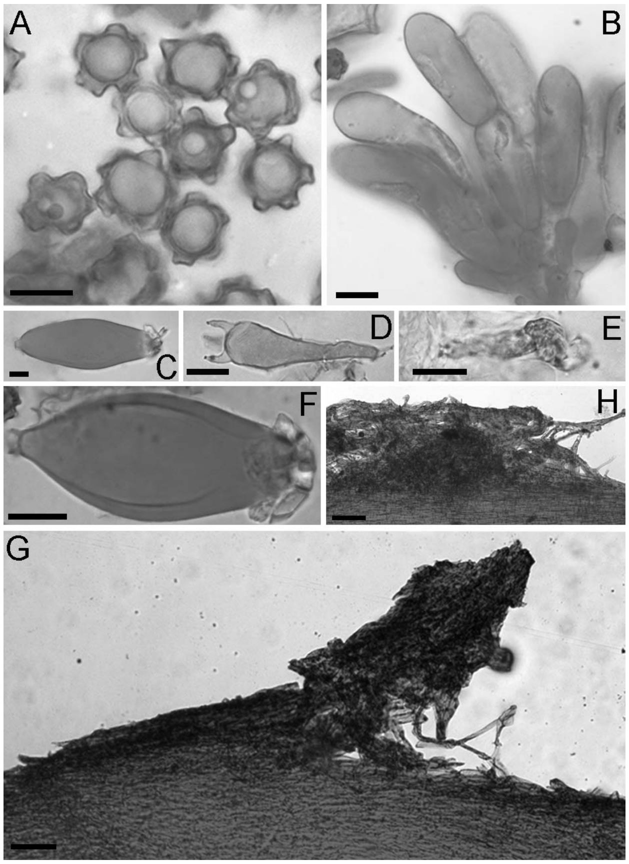

FIG. 6. A–H. *Inocybe kuruvensis* (K[M] 191734, **holotype**). A. Basidiospores. B. Paracystidia. C. Pleurocystidium. D. Basidium. E. Necrobasidium. F. Metuloidal Cheilocystidia. G. Pileipellis. H. Stipitipellis. Bars = 10 μm.

Other specimens examined: INDIA. KERALA STATE, Ernakulum District, Iringolkav, 23 Sep 2012, *K.P. Deepna Latha K(M) 191729*; Wayanad District, Muthanga Wildlife Sanctuary, 21 Aug 2013, *K.P. Deepna Latha K(M) 191730.*

Notes: The combination of a radially appressed-fibrillose to rimose pileus, smooth, ellipsoidal to subphaseoliform basidiospores, clavate or cylindrical cheilocystidia and absence of pleurocystidia are indicative of the clade Pseudosperma. Several macro- and microscopic features of *I. keralensis* are similar to those of *I. littoralis* Pegler, a species recorded from the Lesser Antilles (Pegler 1983) and also reported from Kerala (Pradeep et al. 1996). These two species have basidiomata of similar size with similar pileus and stipe surfaces, a sterile, whitish and serrated lamella edge, somewhat similarly sized basidiospores (9–11 × 5.2–7 μm), and a hymenium devoid of pleurocystidia. However, according to Pegler (1983), *I. littoralis* has a conical pileus, non-fibrillose stipe surface and smaller cheilocystidia that lack encrustations. *Inocybe palaeotropica* E. Turnbull & Watling (synonym: *I. umbrina* Massee) from Singapore (Horak 1980), also reported from Kerala (Vrinda et al. 1997a), has somewhat similar basidiomata with an appressed-fibrillose and rimose pileus, fibrillose stipe, sterile lamella edge, pseudoparenchymatous subhymenium and smooth basidiospores. However, this species differs from *I. keralensis* in having a larger pileus, crowded lamellae with a fimbriate edge, a longer and solid stipe, smaller, ovoid to ellipsoidal basidiospores (6–9 × 4–6 μm), vesiculose cheilocystidia, pileipellis hyphae with brown encrusting pigment and a stipitipellis with caulocystidia.

Inocybe rimosa (Bull.: Fr.) Kumm. was the closest hit in BLASTn query for both ITS and 28S. *Inocybe rimosa* sensu lato is polyphyletic, comprising several phylogenetic species (Larsson et al. 2009, Kropp et al. 2013). Therefore a morphological comparison of *I. keralensis* with the taxa of the *I. rimosa* complex might not be informative.

Inocybe kuruvensis K.P.D. Latha & Manim., sp. nov. FIGS. 3D, 6A–H

MycoBank MB810561

Typification: INDIA. KERALA STATE, Wayanad District, Kuruva Islets in River Kabani, 27 Sep 2013, *K. P. Deepna Latha* (**holotype** K[M] 191734).

Etymology: Referring to Kuruva islets in River Kabani of Kerala state, India, where this species was first observed.

Diagnosis: Characterized by a dark brown pileus, stipe with a whitish base and a grayish brown, floccose-fibrillose surface, nodulose basidiospores with saddle-shaped projections, faintly encrusted paracystidia with refractive contents, and association with dipterocarps in tropical India. Phylogenetically well resolved from other species of the Inocybe clade.

Description: Pileus 5–21 mm diam, obtusely conical or conical-convex with a small umbo initially, becoming convex to plano-convex with a small umbo; surface brown (6F6)/(OAC636) initially, becoming dark brown (6F6–7)/(OAC637) on the squamules and fibrils and brownish orange (6C4)/(OAC653) elsewhere, appressed- to slightly recurved-squamulose toward the center, appressed-fibrillose and rimose toward the margin; margin initially incurved, becoming decurved to straight or slightly reflexed with age, finely fissile. Lamellae emarginate, subventricose to ventricose, close, initially off white, becoming brownish orange (6C3–4)/(OAC653) or light brown (6D4)/(OAC647) or brown (6D7)/(OAC644) with age, up to 4.5 mm deep, with lamellulae of three lengths; edges crenulate, slightly paler. Stipe 9–53 × 2–3 mm, central, terete, equal, solid; surface brownish orange (6C4)/(OAC652) initially, becoming brown (6E6–7)/(OAC644), covered with grayish brown floccose-fibrils all over, densely so toward the base, somewhat woolly at the apex; base slightly swollen, whitish, not marginate, with basal mycelium. Cortina present initially,

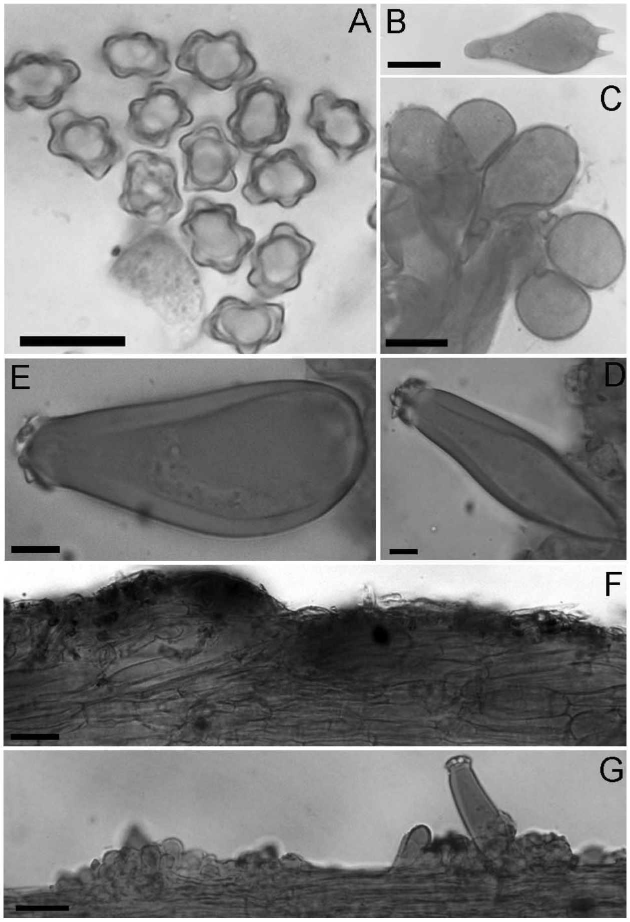

FIG. 7. A–G. *Inocybe muthangensis* (K[M] 191735, **holotype**). A. Basidiospores. B. Basidium. C. Paracystidium. D. Pleurocystidium. E. Cheilocystidium. F. Pileipellis mounted in water. G. Stipitipellis. Bars = 10 μm.

fugacious. Context soft, up to 2.5 mm wide, grayish orange (6B3)/(OAC654). Odor and flavor not distinctive.

Basidiospores 9–11 × 8–9.5 (9.7 ± 0.6 × 8.5 ± 0.5) μm, Q = 1.0–1.3, Qm = 1.1, nodulose, with 6–7 or rarely nine saddle-shaped, up to 2 μm long projections in profile, slightly thick-walled, pale yellowish brown. Basidia 28–37 × 8–14 μm, four-spored, occasionally filled with pigmented contents and collapsed (necrobasidia). Pleurocystidia metuloidal, 53–66 × 19–24 μm, utriform or fusiform with a short stalk, wall up to 4 μm thick, hyaline; apices crystalliferous. Lamella edge sterile, with clusters of paracystidia mixed with scattered metuloidal cheilocystidia. Metuloidal cheilocystidia 39–71 × 18–27 μm, versiform, fusiform, ampulliform, ovoid, utriform, clavate, pyriform or obclavate, wall 2–4 μm thick toward the apex, hyaline; apices often muricate with crystalloid deposits. Paracystidia 11–79 × 8–39 μm, versiform: globose, ellipsoid, flexuose, clavate, spheropedunculate, obpyriform, fusiform, ovoid, cylindrical or cylindrical with a median constriction, wall up to 1 μm thick, hyaline, with some refractive contents, occasionally faintly encrusted. Pileipellis a disrupted cutis with ascending trichodermal patches; hyphae 5–25 μm diam, with dense, yellowish brown, spiral encrustations, slightly thick-walled. Stipitipellis a disrupted cutis with loose, ascending trichodermal patches; hyphae 5–20 μm diam, with dense, pale yellowish brown, spiral encrustations, thin- to slightly thick-walled. Caulocystidia absent. Clamp connections present.

Habit, habitat and distribution: In small groups, on soil, near *Hopea ponga* (Dipterocarpaceae) trees, India.

Other specimens examined: INDIA. KERALA STATE, Wayanad District, Kuruva Islets in River Kabani, 6 Sep 2013, *K.P. Deepna Latha DKP196*.

Notes: Inocybe kuruvensis is strikingly similar to *I. lasseroides* (E. Horak) Garrido, a species described from Papua New Guinea (Horak 1979) with similar basidiomata and similarly shaped basidiospores with saddle-shaped projections. However, the latter species has lamellae with even, concolorous edges, slightly larger basidiospores (10.5–13 μm), smaller pleuro- and metuloidal cheilocystidia, absence of paracystidia, and stipitipellis with caulocystidia. *Inocybe alienospora* (Corner & E. Horak) Garrido, a species described from Singapore (Horak 1979), has a pileus with similar surface features, basidiospores of similar morphology and the presence of pleuro- and cheilocystidia. However, *I. alienospora* differs from *I. kuruvensis* in having a plane to slightly concave pileus, subdistant lamellae, stipe with a fibrillose-villous surface, smaller and thin-walled paracystidia devoid of encrustations and refractive contents, pleurocystidia with resin-incrusted apices, cutis-type pileipellis and lack of both a cortina and metuloidal cheilocystidia.

BLASTn queries with 28S sequences lead to *Inocybe hydrocybiformis,* followed by *I. alienospora. Inocybe hydrocybiformis*, a species known from Singapore and Malaysia (Horak 1979) and also from Kerala (Vrinda et al. 1999), has similarly sized basidiomata and similarly shaped basidiospores, pileipellis with a similar type of encrusting pigment, and cheilocystidia. However, *I. hydrocybiformis* differs from *I. kuruvensis* in lacking metuloidal pleuro- and cheilocystidia and in having a yellowish brown, hygrophanous, sulcate-striate pileus with an acute umbo, apically pruinose stipe, larger basidiospores (10–12.5 × 8.5–11 μm), smaller basidia, and smaller, strangulated cheilocystidia with yellowish brown plasmatic pigment.

Inocybe muthangensis K.P.D. Latha & Manim., sp. nov.
FIGS. 3E, 7A–G

MycoBank MB810562

Typification: INDIA. KERALA STATE, Wayanad District, Muthanga Wildlife Sanctuary, 21 Aug 2013, *K. P. Deepna Latha* (**holotype** K[M] 191735).

Etymology: Referring to Muthanga, a wildlife sanctuary in Kerala state, India, where this species was first observed.

Diagnosis: Characterized by violet basidiomata with a rimose and hygrophanous pileus, densely pruinose stipe with a marginate-bulbous base, nodulose basidiospores, and association with dipterocarps in tropical India. Phylogenetically well resolved from other species of the Inocybe clade.

Description: Pileus 5–29 mm diam, somewhat paraboloid initially, becoming convex to plano-convex with a small umbo and finally applanate with a slight depression around the umbo; surface initially lavender (18B3–4)/(OAC421) on the disk and gradually fading to violet-white (17A2, 18A2)/(OAC424) toward the margin, with age becoming dull lilac (15C3) or grayish violet (15C5)/(OAC429–430) on the disk and on the fibrils, finally hygrophanous and becoming violet-gray (17B2)/(OAC410), slightly tacky, radially fibrillose-rimose; margin incurved initially, finally becoming straight or slightly reflexed, crenate or somewhat wavy, finely fissile. Lamellae emarginate with a small decurrent tooth, close, initially pale violet (17A3)/(OAC422), finally reddish lilac (14C3)/(OAC492), up to 2.5 mm deep, with lamellulae of one length; edges fimbriate, concolorous with the faces. Stipe 7–28 × 2–3 mm, central, terete, equal, slightly flexuous toward the base, which has a distinct marginate bulb, solid; surface light violet (17A4–5)/(OAC415, OAC422) initially, finally reddish lilac (14B3, 14C3)/(OAC492–493), appressed-fibrillose as well as densely pruinose (easily removed on handling) over entire length; base with basal mycelium. Context soft, up to 2.5 mm wide, dull lilac (16C3)/(OAC430). Odor and flavor not distinctive.

Basidiospores 8–11 × 6–8 (9.1 ± 0.6 × 6.8 ± 0.6) µm, Q = 1.1–1.5, Qm = 1.4, nodulose with 5–6 nodules, up to 2 µm long in profile, slightly thick-walled, yellowish brown. Basidia 20–30 × 7.5–14 µm, mostly four-spored, rarely two-spored. Pleurocystidia metuloidal, 41–72 × 14–24 µm, narrowly utriform, utriform, or fusiform, hyaline, wall up to 4 µm thick toward the apex; apices crystalliferous. Lamella edge sterile or rarely heterogeneous with cheilocystidia mixed with clusters of paracystidia. Cheilocystidia metuloidal, scarce, 33–72 × 16–32 µm, obclavate, fusiform, utriform, ovoid, broadly ellipsoid, conical or obovoid, hyaline, wall 4–5 µm thick towards the apex; apices crystalliferous. Paracystidia 12–22 × 8–14 µm, clavate, inflated clavate, subglobose, or obovoid, wall up to 1 µm thick, hyaline. Pileipellis a cutis, composed of somewhat loose, slightly entangled hyphae; hyphae 2–16 µm diam, slightly thick-walled, with yellowish brown wall pigment, often with a violet tint, occasionally with pale yellowish brown spiral encrustations. Stipitipellis a cutis often disrupted with scattered caulocystidia mixed with bunches of cauloparacystidia over entire length of the stipe; hyphae 2–12 µm diam, thin- to slightly thick-walled, with a pale yellow wall pigment, often with a pale violet tint, occasionally with pale brownish yellow spiral encrustations. Caulocystidia metuloidal, 28–72 × 11–37 µm, fusiform, utriform, sublageniform, conical, pyriform, obclavate, or ellipsoid, rarely with a median constriction, wall up to 4 µm thick toward the apex, hyaline, with crystalliferous apices. Cauloparacystidia 12–24 × 7–14 µm, clavate, inflated clavate, or obovoid, wall up to 1 µm thick, hyaline. Oleiferous hyphae observed in all trama. Clamp connections present.

Habit, habitat and distribution: Scattered or in small groups, on the ground, near *Hopea ponga* (Dipterocarpaceae) trees, India.

Other specimens examined: INDIA. KERALA STATE, Wayanad District, Muthanga Wildlife Sanctuary, 7 Sep 2013, *K.P. Deepna Latha K(M) 191736.*

Notes: Extensive searches in the literature reveal no violet species of *Inocybe* with nodulose basidiospores. *Inocybe corneri* (E. Horak) Garrido, a species reported from Sabah (Horak 1979), somewhat resembles *I. muthangensis* in having a pileus and stipe that initially are violaceous, somewhat similar-shaped basidiospores, presence of both pleuro- and cheilocystidia and a cutis-type pileipellis. However, *I. corneri* differs from *I. muthangensis* in having larger basidiomata with an acutely umbonate pileus, pileus and stipe becoming pale brown with age, pale yellow to ochraceous lamellae, an apically pruinose stipe, smaller basidiospores (7–8 × 5.5–6 µm), thin-walled pleuro- and cheilocystidia with resinous incrustations, thin-walled, subfusoid or cylindrical non-metuloidal caulocystidia and lack of metuloidal caulocystidia and cauloparacystidia and violet tint in the hyphae of pileipellis. The closest hit in BLASTn query with 28S sequence was *Inocybe* sp. AU32 followed by a collection labeled as *Inocybe* cf. *serrata*. *Inocybe* sp. AU32 is an unpublished species described from Australia. *Inocybe serrata* Cleland is a species originally reported from southern Australia (Matheny and Bougher 2010). The Australian species strongly differs from *I. muthangensis* in having smaller basidiomata with a pallid brown pileus and smooth basidiospores.

Inocybe wayanadensis K.P.D. Latha & Manim., sp. nov. FIGS. 3F, 8A–H

MycoBank MB810563

Typification: INDIA. KERALA STATE, Wayanad District, Kuruva Islets in River Kabani, 5 Sep 2013, *K.P. Deepna Latha* (**holotype** K[M] 191737).

Etymology: Referring to Wayanad, a district in Kerala state, India, where this species was first observed.

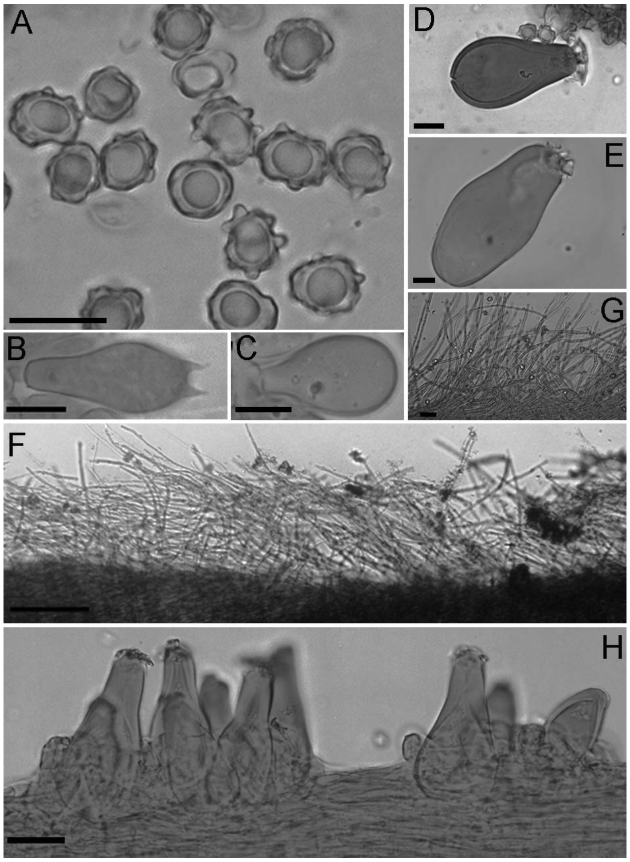

FIG. 8. A–H. *Inocybe wayanadensis* (K[M] 191737, **holotype**). A. Basidiospores. B. Basidium. C. Paracystidium. D. Cheilocystidium. E. Pleurocystidium. F. Pileipellis (300×). G. Pileipellis (600×). H. Stipitipellis. Bars = 10 μm.

Diagnosis: Characterized by small, whitish basidiomata; viscid pileus with a rimulose surface; densely pruinose and fibrillose stipe with a marginate-bulbous base; nodulose basidiospores; thick-walled pleuro- cheilo- and caulocystidia; an ixotrichoderm-type pileipellis and association with dipterocarps in tropical India. Phylogenetically well resolved from other species of the Inocybe clade.

Description: Pileus 6–18 mm diam, obtusely conical or somewhat paraboloid initially, becoming conico-campanulate or convex to plano-convex with a small umbo with age; surface white, not hygrophanous, not pellucid-striate, slightly viscid and often with adhering sand grains, appressed-fibrillose and rimulose; margin slightly incurved when young, becoming decurved to almost straight and finally somewhat reflexed, crenate, finely split. Lamellae adnate, subventricose, close, initially orange white (6A2)/(OAC655), finally brownish orange (6C4)/(OAC653), up to 2 mm deep, with lamellulae of one length; edges fimbriate, concolorous with the faces. Stipe 14–33 × 1–4 mm, central, terete, equal or tapering toward the apex, cartilaginous, fistulose; surface white, densely pruinose (easily removed on handling) as well as fibrillose all over; base with a marginate bulb and basal mycelium. Context soft, up to 1 mm wide, white. Odor and flavor not distinctive.

Basidiospores 7–10 × 6–8 (8.6 ± 0.6 × 6.5 ± 0.6) μm, Q = 1.0–1.6, Qm = 1.3, nodulose, with inconspicuous or rarely saddle-shaped nodules, slightly thick-walled, pale yellow. Basidia 16–31 × 9–13 μm, four-spored or rarely two-spored. Pleurocystidia metuloidal, 45–60 × 18–21 μm, utriform or broadly utriform or oblong, wall up to 5 μm thick toward the apex, hyaline, with crystalliferous apices. Lamella edge sterile or heterogeneous with cheilocystidia mixed with clusters of paracystidia. Cheilocystidia metuloidal, 43–75 × 14–31 μm, obclavate, lageniform, fusiform, utriform, subpyriform, ampulliform or rarely ellipsoid, wall 6–8 μm thick toward the apex, hyaline; with crystalliferous apices. Paracystidia 12–18 × 5–12 μm, clavate, inflated clavate, or subglobose, wall thin or up to 0.5 μm thick, hyaline. Pileipellis an ixotrichoderm, with supra- and subpellis regions; suprapellis composed of somewhat loose, gelatinized, hyaline hyphae devoid of encrustations, terminal elements 29–68 × 3–4 μm, narrowly cylindrical with an obtuse apex or flexuoso-cylindrical, thin-walled; subpellis composed of compactly arranged parallel, non-gelatinized, pale grayish yellow hyphae, at times with faint pale yellowish brown encrustations; hyphae 5–14 μm diam, thin- to slightly thick-walled. Stipitipellis a cutis frequently disrupted with clustered or scattered caulocystidia mixed with short bunches of cauloparacystidia over entire stipe length; hyphae 3–9 μm diam, thin- to very slightly thick-walled, hyaline or pale gray, sometimes faintly encrusted. Caulocystidia metuloidal, 42–85 × 18–40 μm, obclavate, broadly lageniform, fusiform, subutriform, or conical, wall up to 8 μm thick toward the apex, hyaline; apices crystalliferous. Cauloparacystidia 8–23 × 6–12 μm, clavate or inflated clavate, obovoid, wall up to 1 μm thick, hyaline. Clamp connections present.

Habit, habitat and distribution: Scattered or in small groups, on the ground, near *Hopea ponga* and *H. parviflora* (Dipterocarpaceae) trees, India.

Other specimens examined: INDIA. KERALA STATE, Wayanad District, Muthanga Wildlife Sanctuary, 29 Oct 2013, *K. P. Deepna Latha K(M) 191738.*

Notes: The Indian species is strikingly similar to *I. alboviscida* (E. Horak) Garrido, described from Papua New Guinea (Horak 1979) in the color of the basidiomata, the shape and surface features of both pileus and stipe and the presence of pleuro-, cheilo- and caulocystidia. *Inocybe alboviscida* is distinguished, however, by its larger basidiomata (25 mm diam), crowded lamellae, smaller basidiospores (6–7.5 × 5.5–6.5 μm), larger pleuro-, cheilo- and caulocystidia, absence of para- and cauloparacystidia, a cutis-type pileipellis composed of gelatinized hyphae and a spermatic odor. The closest hit in BLASTn query with 28S sequence was a collection labeled *Inocybe* cf. *scissa* followed by *Inocybe* sp. PBM3110. *Inocybe scissa* (E. Horak) Garrido, a species described by Horak (1977) from New Zealand has some characters of *I. wayanadensis* such as a pileus with a fibrillose-rimose surface, stipe with a pruinose surface and a marginate-bulbous base, somewhat similar-sized basidiospores (8–11 × 4.8–8.8 μm), and pleuro-, cheilo- and caulocystidia. However, *I. scissa* has larger basidiomata, pale yellow to straw yellow pileus with a dry surface, basidiospores with prominent nodules and a cutis-type pileipellis. The description of the *Inocybe* sp. PBM3110 from Australia is unavailable.

DISCUSSION

With the present study the number of species of *Inocybe* known from Kerala is 24. All grow on soil and are putatively associated with trees belonging to Dipterocarpaceae, Myristicaceae or Euphorbiaceae (Vrinda et al.1996, 1997b). The five new species of *Inocybe* reported here are assumed to be associated with *Hopea parviflora, H. ponga* and *Vateria indica* of Dipterocarpaceae. In Kerala we can find *Inocybe* species only in those forests or woodlands that have dipterocarps. The consistent association of *Inocybe* species with Dipterocarpaceae in this region is remarkable.

The presence of necrobasidia in *I. kuruvensis* is noteworthy. Necrobasidia are basidia that collapse and become ochraceous after sporulation (Kuyper 1986). In Inocybaceae necrobasidia are a characteristic feature of the clade Mallocybe and the genus *Auritella* (Matheny 2005, 2009) and also are observed in the clade Inosperma (Matheny and Watling 2004) and the genus *Tubariomyces* (Matheny 2009, Alvarado et al. 2010). According to Matheny and Watling (2004), necrobasidia have evolved more than once or have been repeatedly lost in Inocybaceae.

Although several *Inocybe* species have violet basidiomata (Horak 1980, Matheny and Bougher 2005), rarely do these also feature nodulose basidiospores. As far as we know, *I. muthangensis* described here is the second report, after *I. corneri,* of an *Inocyb*e species that has both entirely violet basidiomata and nodulose basidiospores.

Hitherto no Indian *Inocybe* species were treated in molecular phylogenetic analyses except for the collections labeled *Inocybe* sp. ZT9250, *Inocybe* sp. ZT8944 and *Inocybe* sp. ZT9238 (Matheny et al. 2009). *Inocybe* sp. ZT9250 belongs to the Nothocybe lineage, which is characterized by a single Indian collection (Matheny et al. 2009, Alvarado et. al 2010). *Inocybe* sp. ZT8944 was confined in Inosperma clade and *Inocybe* sp. ZT9238 provisionally was named *"I. errata"* and was placed in Mallocybe clade (Matheny et al. 2009). These three species collected from Kerala state, however, remain to be validly published.

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