



## *Inocybe gregaria*, a new species of the Inosperma clade from tropical India

K. P. DEEPNA LATHA & PATINJAREVEETIL MANIMOHAN\*

Department of Botany, University of Calicut, Kerala, 673 635, India

\*Corresponding author: [pmanimohan@gmail.com](mailto:pmanimohan@gmail.com)

### Abstract

*Inocybe gregaria* sp. nov. is described from Kerala State, India, based on morphological and molecular data. A comprehensive description, photographs, and comparisons with phenetically similar and phylogenetically related species are provided. The nuclear ribosomal internal transcribed spacer region (nrITS), a portion of the nuclear ribosomal large subunit (nrLSU) and a portion of the nuclear second-largest subunit of RNA polymerase II (*rpb2*) gene of this species were sequenced and analyzed. BLASTn searches using LSU and *rpb2* sequences and subsequent ML phylogram of combined LSU and *rpb2* sequences revealed that *I. gregaria* is conspecific with *Inocybe* sp. ZT8944, a collection assigned to the Inosperma clade that remains undescribed.

**Key words:** Agaricales, Basidiomycota, Inocybaceae, phylogeny, taxonomy

### Introduction

*Inocybe* (Fries 1821: 254) Fries (1863: 346) is one of the highly diverse genera in the Agaricales and comprises about 500 species known worldwide (Matheny *et al.* 2002; Kirk *et al.* 2008) and with more than 1800 names (including synonyms) listed by Species Fungorum ([www.speciesfungorum.org](http://www.speciesfungorum.org)). The ectomycorrhizal ecology and toxicity of most of its species are remarkable features of the genus (Matheny 2009; Kosentka *et al.* 2013). *Inocybe* species typically have brownish basidiomata with a squamulose and rimose texture to the pileus surface, brownish lamellae, a brown spore print, and occurrence on soil (Matheny *et al.* 2002). Based on multigene phylogenetic analyses, Matheny *et al.* (2009) proposed seven major clades consisting of *Inocybe* and its allies within the family Inocybaceae. The Inosperma clade, one of these clades, is generally characterized by smooth, mostly phaseoliform basidiospores, cheilocystidia, a hymenium devoid of pleurocystidia and metuloids, and occasional occurrence of necrobasidia (Kuyper 1986; Matheny & Watling 2004; Larsson *et al.* 2009). According to Matheny (2009), the clade Inosperma encompasses about 35 species worldwide. Recent molecular phylogenetic analyses using nuclear ribosomal and protein-coding genes recovered a monophyletic Inosperma clade, which consists of four distinct monophyletic groups: the Maculata clade (Larsson *et al.* 2009), the section *Cervicolores* and two Old World tropical clades (Old World tropical clade 1 and Old World tropical clade 2) (Kropp *et al.* 2013).

*Inocybe* sp. ZT8944 is a collection that was found to belong to the Old World tropical clade 2 (Kropp *et al.* 2013; Pradeep *et al.* 2016) of the Inosperma clade (Matheny *et al.* 2009). This collection from Kerala State, India has often been used in phylogenetic analyses of Inocybaceae (Matheny *et al.* 2009; Kropp *et al.* 2013; Horak *et al.* 2015; Pradeep *et al.* 2016; Latha & Manimohan 2015, 2016). However, that species has not been properly described and validly published so far. Only the DNA sequences (LSU: EU600903; *rpb2*: EU600902) of that collection deposited by Matheny *et al.* (2009), its association with *Casuarina*, and its collecting locality are known. Other details of that collection such as the macro- and microscopic descriptions, photographs and illustrations are not available.

During our studies on the Inocybes of Kerala State, India, we came across a hitherto undescribed species of *Inocybe*. The LSU and *rpb2* sequences of this interesting species of *Inocybe* were found to be identical with those of *Inocybe* sp. ZT8944 of Inosperma clade (99% sequence similarity). It is herein formally described as new and is assigned to the Old World tropical clade 2 of Inosperma clade.

## Materials and Methods

### Morphological studies

Light microscopic observations were made on material stained with 1% aqueous solutions of both phloxine and Congo Red and mounted in 3% aqueous KOH. For evaluation of the range of spore size, 30 basidiospores were measured from the collection cited. This collection consisted of ca. 100 fruitbodies. The hilar appendix is included in the basidiospore length. Basidiospore measurements include both the mean and the standard deviation for both the length and the width, together with the range of spore quotient (Q, the length/width ratio) and its mean value (Qm). Alphanumeric color codes from both Kornerup & Wanscher (1978) (e.g., 5E8) and the Online Auction Color Chart (Anonymous 2004) (e.g., OAC735) accompany color names in the description. The examined collection is deposited at the Central National Herbarium (CAL), Kolkata, India and the CAL accession number (CAL 1309) is provided.

### DNA extraction, PCR, and sequencing

The ITS, LSU and *rpb2* gene regions were analyzed in this study. The procedure described by Izumitsu *et al.* (2012) was followed for genomic DNA extraction of *I. gregaria*. PCR reactions were performed with the primer pairs ITS1 and ITS4 for ITS (White *et al.* 1990), LROR and LR7 for LSU (Vilgalys & Hester 1990) and b6F and b7.1R for *rpb2* (Matheny 2005). Protocols for PCR amplification and sequencing followed are those given in Latha & Manimohan (2015). The newly generated sequences were deposited in GenBank (ITS: KX852305; LSU: KX852306 and *rpb2*: KX852307).

### Sequence alignment, dataset assembly, and phylogenetic analysis

The phylogenetic analysis was performed using a combined data matrix of LSU and *rpb2* sequences. The newly generated LSU and *rpb2* sequences of *I. gregaria*, along with those retrieved from GenBank (54 sequences), were aligned using MAFFT web tool (<http://align.bmr.kyushu-u.ac.jp/mafft/online/server/>) with default settings. The final alignment including four outgroup taxa (Table 1) was then imported into AliView v.1.15 (Larsson 2014) for manual adjustment. The sequences of *Inocybe* species were selected based on their similarity indices and the sequences of representative species of Inosperma clade that were treated in previous phylogenetic studies (Kropp *et al.* 2013; Pradeep *et al.* 2016) were also added to the data matrix. Species of *Tubariomyces* Esteve-Rav. & Matheny (in Alvarado *et al.* 2010: 1390) were chosen as outgroup taxa for rooting purpose following Pradeep *et al.* (2016). Maximum likelihood (ML) analysis was performed with a partitioned dataset using RAxML-HPC2 (v.8.2.8) (Stamatakis 2014) on XSEDE platform implemented in the CIPRES Science Gateway web server (Miller *et al.* 2010). RAxML was run employing GTRGAMMA model with 1000 rapid ML bootstrap replicates and default settings for other options. Bootstrap values  $\geq 70\%$  were considered significant. The aligned sequence dataset has been deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19984>). The phylogram inferred from the ML analysis was displayed with FigTree 1.4.2 (Rambaut 2014).

**TABLE 1.** List of species, their geographic origin and the GenBank accession numbers of DNA sequences used in the molecular analysis.

Species	Geographic origin	GenBank accession no.	
		LSU	<i>rpb2</i>
<i>I. adaequata</i>	Finland	AY380364	AY333771
<i>I. aff. calamistrata</i> DED8134	Thailand	GQ892937	—
<i>I. aff. calamistrata</i> PBM2351	USA	AY380368	AY333764
<i>I. aff. calamistrata</i> REH8420	Costa Rica	JN975018	JQ846471
<i>I. aff. fastigiella</i>	USA	JQ815419	JQ846477
<i>I. aff. latericia</i>	Papua New Guinea	JN975023	JQ846487
<i>I. aff. maculata</i> PBM2446	USA	AY745700	EU569863
<i>I. aff. maculata</i> PBM3051	USA	JN975026	JQ846485

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TABLE 1. (Continued)

Species	Geographic origin	GenBank accession no.	
		LSU	<i>rpb2</i>
<i>I. apiosmota</i>	USA	AY038313	AY337365
<i>I. bicolorata</i>	Malayasia	GQ892938	JQ846464
<i>I. bongardii</i>	Finland	EU555448	—
<i>I. calamistrata</i> EL1904	Sweden	AM882938	—
<i>I. calamistrata</i> PBM1105	USA	JQ815409	JQ846466
<i>I. calamistratoides</i>	Australia	JQ815415	KJ729949
<i>I. carnosibulbosa</i>	India	KT329454	KT329443
<i>I. cervicolor</i>	Finland	JQ814417	JQ846474
<i>I. cf. reisneri</i>	Japan	EU555463	—
<i>I. curreyi</i>	USA	HQ201348	JQ846475
<i>I. erubescens</i>	Finland	EU569846	—
<i>I. geraniodora</i>	Sweden	FN550945	—
<b><i>I. gregaria</i></b>	<b>India</b>	<b>KX852306</b>	<b>KX852307</b>
<i>I. hirsuta</i> v. <i>maxima</i>	USA	EU569854	—
<i>I. jurana</i>	Finland	HQ201353	JQ846478
<i>I. latericia</i>	New Zealand	GU233413	—
<i>I. lanatodisca</i> PBM2451	USA	JQ319690	JQ846483
<i>I. lanatodisa</i> TURA1812	Finland	JQ319694	JQ846484
<i>I. maculata</i>	Sweden	AM882964	—
<i>I. misakaensis</i>	Zambia	EU569875	AY333767
<i>I. mucidiolens</i>	Canada	HQ201340	—
<i>I. mutata</i>	USA	AY732212	DQ472729
<i>I. neobrunnescens</i>	USA	EU569868	EU569867
<i>I. neobrunnescens</i> v. <i>leucothelota</i>	USA	JN975025	JQ846489
<i>I. proxima</i>	Thailand	EU600840	—
<i>I. quietiodor</i>	Sweden	AM882960	—
<i>I. rimosoides</i>	USA	AY702014	DQ385884
<i>I. rhodiola</i>	France	FJ904175	—
<i>Inocybe</i> sp. 137	Australia	JN975033	JQ846476
<i>Inocybe</i> sp. BB3233	Zambia	EU600885	—
<i>Inocybe</i> sp. L-GN3a	Papua New Guinea	JX316732	—
<i>Inocybe</i> sp. PBM3767	Australia	JO171094	KM656138
<i>Inocybe</i> sp. PBM3784	Australia	KP170990	KM406230
<i>Inocybe</i> sp. PC96013	Zambia	EU600883	EU600992
<i>Inocybe</i> sp. PC96073	Zambia	EU600870	EU600869
<i>Inocybe</i> sp. PC96082	Zambia	JN975027	—
<i>Inocybe</i> sp. TJB10045	Thailand	KT600659	KT600660

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TABLE 1. (Continued)

Species	Geographic origin	GenBank accession no.	
		LSU	<i>rpb2</i>
<i>Inocybe</i> sp. TR74-06	Papua New Guinea	JN975020	JQ846472
<i>Inocybe</i> sp. TR220-06	Papua New Guinea	JN975017	JQ846496
<i>Inocybe</i> sp. ZT8944	India	EU600903	EU600902
<i>I. subhirsuta</i>	Finland	EU555452	AY333763
<i>I. virosa</i>	India	KT329458	KT329446
<i>Tubariomyces hygrophoroides</i>	France	GU907094	GU907090
<i>T. inexpectatus</i>	Spain	GU907091	GU907088
<i>T. similis</i>	Spain	GU907092	GU907089
<i>Tubariomyces</i> species 2 BB6018	Zambia	EU600887	EU600886

## Results

### Taxonomy

*Inocybe gregaria* K. P. D. Latha & Manim., sp. nov. Figs. 1A–H  
Mycobank MB 818645

**Etymology:**—The specific epithet refers to the gregarious habit of this species.

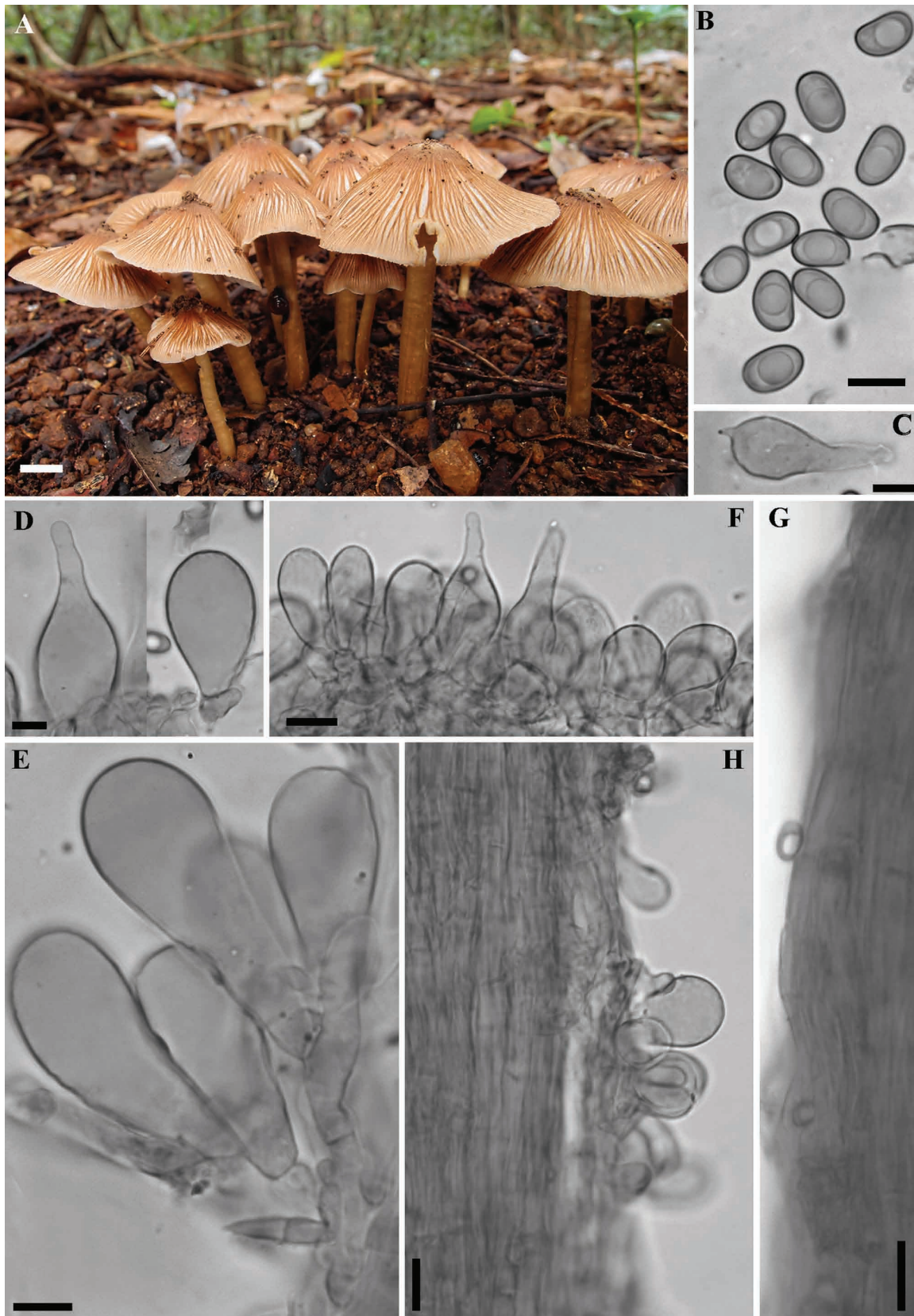
**Diagnosis:**—*Inocybe gregaria* has medium-sized basidiomata with a brown, fibrillose-rimose pileus; emarginate, occasionally bifurcate lamellae with a fimbriate edge; a fibrillose stipe often with a pruinose apex and a slightly enlarged, whitish base; smooth, ovo-ellipsoid to subphaseoliform, basidiospores; crowded, versiform, hyaline cheilocystidia; a cutis-type pileipellis, caulocystidia restricted to the extreme apex of the stipe, and distinctive ITS, LSU and *rpb2* sequences.

**Holotype:**—INDIA. Kerala State: Ernakulum District, Perumbavoor, Iringolkav sacred grove, 31 July 2012, K. P. Deepna Latha, DKP5 (CAL 1309).

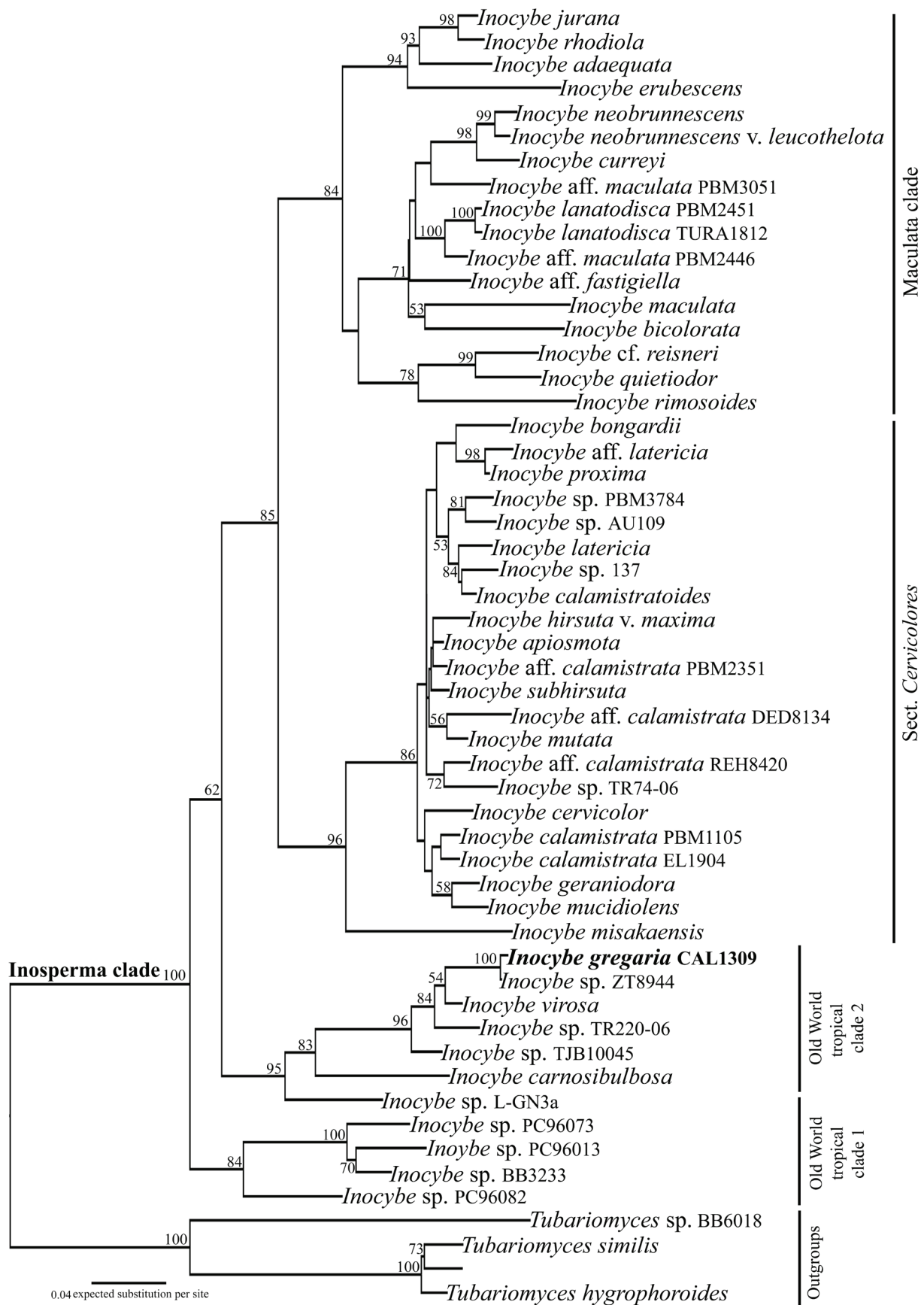
**Description:**—*Basidiomata* small to medium-sized. *Pileus* 10–72 mm diam., somewhat paraboloid when very young, becoming broadly conical to broadly convex with an umbo and finally plano-convex to almost appanate still with a broad umbo, often with a slight depression around the umbo; surface initially yellowish brown (5E8/OAC735) all over, becoming brown (6E8/OAC733) at the center and on the fibrils, brownish orange (6C4/OAC733) elsewhere, dry, appressed fibrillose and strongly rimose towards the margin; margin slightly incurved when young, becoming decurved to slightly reflexed with age, crenate or somewhat wavy, rather fissile. *Lamellae* emarginate, rarely bifurcate in the middle, crowded, initially creamy white or yellowish gray (4B2/OAC746), becoming brownish orange (6C3/OAC801), up to 2 mm wide, with lamellulae of 1–3 lengths; edge fimbriate, slightly paler. *Stipe* 35–87 × 3–7 mm, central, terete, almost equal, cartilaginous, solid; surface initially orange-white (5A2/OAC794), becoming grayish orange (5B3/OAC779) towards the apex and brownish orange (5C5/OAC718) towards the base, appressed-fibrillose all over, at times with some loose fibrils projecting out, finely pruinose towards the apex; base whitish, slightly enlarged, not marginate-bulbous. *Context* soft, up to 6 mm wide, off-white. *Odor* and *taste* not distinctive.

**Basidiospores** 7–8.5(9) × 5–5.5(6) (8.1±0.5 × 5.1±0.2) µm, Q = 1.3–1.8, Qm = 1.6, smooth, ovo-ellipsoid to subphaseoliform, slightly thick-walled. **Basidia** 20–26 × 8–11 µm, clavate, thin-walled, hyaline or pale yellow, 4-spored; sterigmata up to 5 µm long. **Pleurocystidia** none. **Lamella edge** sterile. **Cheilocystidia** 24–60 × 16–24 µm, crowded, versiform: mostly obovoid, clavate, broadly clavate or balloon-shaped, rarely lageniform, thin- to slightly thick-walled, hyaline. **Lamellar trama** subregular, composed of both narrow and inflated hyphae; hyphae 3–22 µm wide, thin-walled, hyaline or very pale yellow. **Subhymenium** pseudoparenchymatous. **Pileus trama** subregular; hyphae 5–10 µm wide, inflated up to 31 µm, thin-walled, nearly hyaline or pale yellow with a tint of brown. **Pileipellis** a cutis of radially arranged hyphae; hyphae 4–15 µm wide, thin- to slightly thick-walled, with a pale yellow wall pigment and faint, hyaline, spiral encrustations. **Stipitipellis** a cutis often disrupted with isolated or small clusters of caulocystidia

at the extreme stipe apex; hyphae 2.5–13  $\mu\text{m}$  wide, thin- to slightly thick-walled, with a pale yellow wall pigment, rarely with a brownish tint and hyaline spiral encrustations, occasionally with amorphous, yellowish brown contents. *Caulocystidia* 15–55  $\times$  10–22  $\mu\text{m}$ , clavate, broadly clavate or vesiculose, hyaline, thin- to slightly thick-walled. *Oleiferous hyphae* scattered in all tramal tissues. *Clamp-connections* observed on all hyphae.



**FIGURE 1.** A–H: *Inocybe gregaria* (CAL 1309, holotype). A. Basidiomata; B. Basidiospores; C. Basidium; D. Cheilocystidia; E. Caulocystidia; F. Lamella-edge; G. Pileipellis. H. Stipitipellis. Scale bars: A=10 mm; B–E=10  $\mu\text{m}$ ; F–H= 20  $\mu\text{m}$ . Photos by K. P. Deepna Latha.



**FIGURE 2.** ML phylogram based on a combined LSU and *rpb2* data matrix depicting the placement of *Inocybe gregaria* within the Old World tropical clade 2 of Inosperma clade. Values at nodes indicate bootstrap support. BS values  $\geq 50\%$  are shown.

Habitat:—gregarious, often as large, discrete clusters, on soil, near *Vateria indica* (Dipterocarpaceae) trees.

Geographical distribution range:—known only from the type locality in Kerala State, India.

Comments:—*Inocybe gregaria* is somewhat similar to *I. virosa* C.K. Pradeep, K.B. Vrinda & Matheny (in Pradeep *et al.* 2016), a species previously described from Kerala (Vrinda *et al.* 1996), in having basidiomata of similar size, color and surface texture of the pileus, crowded lamellae with a fimbriate edge, a fibrillose stipe, a sterile lamella-edge with crowded cheilocystidia, and a cutis-type pileipellis. However, *I. virosa* has adnexed lamellae, a longer stipe devoid of apical pruinosity and an abrupt base, ellipsoid and slightly smaller basidiospores ( $6.5\text{--}7.5 \times 4.5\text{--}5 \mu\text{m}$ ), smaller cheilocystidia of a different shape, and a stipitipellis devoid of caulocystidia. Beside these differences, the ITS sequences of these two species exhibited only 91% identity in a pairwise alignment. *Inocybe palaeotropica* Turnbull & Watling (in Turnbull 1995: 357), a widespread species (Horak 1980) also reported from Kerala by Vrinda *et al.* (1997, as *I. umbrina* Masee 1914: 74), shares with *I. gregaria* a few features such as an umbonate pileus with a fibrillose-rimose surface and similar color, crowded lamellae with a fimbriate edge, a fibrillose stipe which is apically pruinose, basidiospores of a comparable size ( $6\text{--}9 \times 4\text{--}6 \mu\text{m}$ ), similar cheilocystidia, a hymenium devoid of pleurocystidia, a cutis-type pileipellis and the presence of caulocystidia. *Inocybe palaeotropica*, however, is distinguished from *I. gregaria* in having a larger pileus (100 mm), adnexed to nearly free lamellae lacking bifurcations, a longer stipe (110 mm) occasionally with remnants of a veil and an abrupt base, ovoid to subelliptic basidiospores lacking a phaseoliform outline, slightly larger cheilocystidia rarely with a yellow-brown plasmonic or encrusting pigment, and a strong, unpleasant odor.

*Inocybe cutifracta* Petch (1917: 201), a species originally described from Sri Lanka (Petch 1917; Pegler 1986), also has a pileus with a broad umbo, lamellae with a fimbriate, slightly paler edge, a stipe with a slightly bulbous base, similar basidiospores, a sterile lamella-edge with crowded cheilocystidia, and a hymenium lacking pleurocystidia. However, *I. cutifracta* differs from *I. gregaria* in having smaller basidiomata with a yellowish brown, furfuraceous-squamulose to subrimose pileus, moderately crowded adnexed lamellae lacking bifurcations, larger basidiospores ( $7\text{--}11 \times 4.5\text{--}6 \mu\text{m}$ ), 4- and 2-spored basidia, distinct capitate cheilocystidia often with refractive secretions, an epicutis-type pileipellis with repent to semi-erect hyphae, and a stipitipellis lacking caulocystidia.

A comparison of the ITS (KX852305: 631 bp), LSU (KX852306: 762 bp) and *rpb2* (KX852307: 660 bp) sequences derived from the Kerala collection with the nucleotide sequences of taxa available in GenBank indicates that *I. gregaria* has distinct ITS, LSU, and *rpb2* sequences. BLASTn queries with ITS sequences led to *I. virosa* (KT329452) as the closest hit with 91% identity. With 99% identities, *Inocybe* sp. ZT8944 was the closest hit in BLASTn searches with both LSU (EU600903) and *rpb2* (EU600902) sequences.

The phylogeny was inferred from Maximum Likelihood (ML) analysis of the combined LSU and *rpb2* data matrix. The phylogram revealed four distinct monophyletic groups together representing a larger Inosperma clade with full (100% BS) bootstrap support. Within this Inosperma clade, *I. gregaria* was found to be nested in the Old World tropical clade 2 where it clustered with *Inocybe* sp. ZT8944 with maximum (100% BS) bootstrap support. In addition, a pairwise alignment of LSU and *rpb2* sequences of *I. gregaria* and *Inocybe* sp. ZT8944 showed 99% sequence similarity.

*Inocybe* sp. ZT8944 is assumed to be associated with *Casuarina* trees (Matheny *et al.* 2009). However, *I. gregaria* was collected from a grove containing several different tree species including *Vateria indica* (Dipterocarpaceae) trees but no *Casuarina* trees. This suggests that this species has either a broad host range or no association with *Casuarina*.

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