Phytotaxa 267 (1): 040–050
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.267.1.4

A new species of *Inocybe* representing the Nothocybe lineage

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Abstract

Inocybe distincta sp. nov. is described from Kerala State, India. A comprehensive description, photographs, line drawings and comments are provided. The nuclear ribosomal internal transcribed spacer region (ITS), 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 nrLSU and RPB2 sequences and subsequent ML phylogenetic analysis of combined nrLSU and RPB2 sequences confirmed that *Inocybe distincta* is a representative of the Nothocybe lineage. As the Nothocybe lineage is assumed to have affinities to *I. cutifracta*, and as there are different interpretations of that species, we examined the holotype of *I. cutifracta* collected by T. Petch and another collection from Sri Lanka identified as *I. cutifracta* by D. N. Pegler, and we present here our observations on these collections.

Key words: Agaricales, Basidiomycota, Inocybaceae, tropical India, phylogeny, taxonomy

Introduction

Matheny *et al.* (2009), based on a multigene phylogenetic analysis, recognized seven major clades or lineages composed of *Inocybe* (Fries 1821: 254) Fries (1863: 346) and allies in the family Inocybaceae (Agaricales, Basidiomycota): Inocybe *sensu stricto*, Nothocybe, Pseudosperma, Mallocybe, Inosperma, Auritella and Mallocybella. Of these seven lineages, Auritella and Mallocybella are formally recognized as distinct genera, *Auritella* and *Tubariomyces*, respectively (Matheny & Bougher 2006a, 2006b; Alvarado *et al.* 2010). The remaining clades, other than Nothocybe, continue to be recognized as infrageneric categories of *Inocybe* as in Kuyper (1986), Larsson *et al.* (2009), and Cripps *et al.* (2010).

The Nothocybe lineage is known from a single unpublished collection (*Inocybe* sp. ZT9250) from Kerala State in southern India that showed affinities to *I. cutifracta* Petch (1917: 201) originally described from Sri Lanka (Matheny 2009). The Indian specimen is thought to be associated with *Casuarina*, and some of its basidiospores exhibit a slight angular outline (Matheny 2009). According to Matheny (2009), Nothocybe is an ancient, long isolated, and a relict lineage.

Remarkably, there are different interpretations of the microscopic features of *I. cutifracta*. While Pegler (1986) observed capitate cheilocystidia in *I. cutifracta* in agreement with the protologue of *I. cutifracta,* Horak (1980) observed clavate cheilocystidia in the type specimen of that species. Also, these authors did not observe angular basidiospores in *I. cutifracta.*

During the course of our studies on the genus *Inocybe* of Kerala (in southern tropical India), we came across a noteworthy species of *Inocybe* that showed 99% and 100% sequence similarities with RPB2 and nLSU regions respectively of *Inocybe* sp. ZT9250, the only representative of the Nothocybe lineage. Subsequent phylogenetic analysis proved the conspecificity of these different collections. The recent Kerala collection is described here as a new species of *Inocybe* and assigned phylogenetically to the Nothocybe lineage. Also, we present here our observations on the type specimen and an additional authentic collection of *I. cutifracta*.

Materials and Methods

Morphological studies

Microscopic observations were made on thin sections of dried material stained with 1 % aqueous solutions of Congo Red and mounted in 3 % aqueous KOH. For evaluation of the range of spore size, 20 basidiospores were measured each from one specimen of each collection cited. 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., 5D6) and the Online Auction Color Chart (Anonymous 2004) (e.g., OAC776) accompany color names in the description. The examined collections are deposited at Central National Herbarium (CAL), Kolkata, India and the CAL accession numbers (e.g., CAL 1310) are provided. The holotype collection and an additional authentic collection of *I. cutifracta* were obtained on loan from Kew (Mycology) herbarium for morphological comparisons.

For scanning electron microscopy, basidiospores from the lamellar surface were affixed to one side of a small piece of double-sided carbon tape attached to a standard aluminium stub. The captured basidiospores were directly coated with gold in a sputter coater to an approximate thickness of 200–300 Å. The gold coated basidiospores were examined in a scanning electron microscope (JEOL JSM-6490LA) at an accelerating voltage of 8 kV.

DNA extraction, PCR and sequencing

ITS, nrLSU and RPB2 gene regions were analyzed in this study. Genomic DNA was extracted from dried specimens (holotype: CAL 1310) of *Inocybe distincta* employing the procedure described by Izumitsu *et al.* (2012). PCR reactions were performed with the primer pairs ITS1/ITS4 for ITS (White *et al.* 1990), LROR/LR7 for nrLSU (Vilgalys & Hester 1990) and b6F/b7.1R for RPB2 (Matheny 2005). PCR thermal profiling and amplification reactions of ITS, nrLSU and RPB2 regions were performed following Latha & Manimohan (2015). The PCR products were examined on 1.0 % agarose gel, stained with ethidium bromide and viewed under a UV transilluminator. Amplified PCR products were purified using 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, CA, USA) using the same primers used for PCR. The generated sequences were edited manually using BioEdit sequence alignment editor v.7.0.9.0 (Tom Hall, Ibis Biosciences, Carlsbad, CA, USA). The edited sequences were then used for BLAST search in the GenBank database (www.ncbi.nlm.nih.gov). The newly generated sequences were deposited in GenBank (ITS: KX171343; nrLSU: KX171344; RPB2: KX171345).

Sequence alignment and phylogenetic analysis

A combined nrLSU and RPB2-based phylogenetic analysis was performed. The newly generated nrLSU (691 bp) and RPB2 (645 bp) sequences of *Inocybe distincta* along with those retrieved from GenBank (40 sequences) were aligned using MUSCLE v.3.8.31 (Edgar 2004). A final dataset of combined nrLSU-RPB2 sequences of 42 taxa including two outgroups (Table 1) was manually edited in MEGA v.5.2 (Tamura *et al.* 2011). The combined nrLSU-RPB2-sequence dataset composed of sequences of representative species from seven clades of Inocybaceae that are available in GenBank were employed in previous phylogenetic analyses of the genus (Alvarado *et al.* 2010; Matheny *et al.* 2012; Latha & Manimohan 2015). *Tubaria confragosa* (Fries 1838: 169) Harmaja (1978: 55) and *T. vinicolor* (Peck 1909: 334) Ammirati, Matheny & Vellinga (in Matheny *et al.* 2007: 580) were chosen as outgroups for rooting purpose following Matheny *et al.* (2012). Maximum Likelihood (ML) analysis was conducted using RAxML v.8.0.26 (Stamatakis 2014) in raxmlGUI v.1.3.1 (Silvestro & Michalak 2012) implementing a GTR+I+G model with 1000 rapid ML bootstrap replicates. GTR+I+G model of molecular evolution was selected using a model selection tool of TOPALi v2.5 (Milne *et al.* 2009). Bootstrap values ≥70% were considered significant. The aligned sequence dataset has been deposited in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S19237). The phylogram inferred from the ML analysis was displayed with FigTree 1.4.2 (Rambaut 2014).

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

Species	Geographic origin	GenBank accession no.	
		nrLSU	RPB2
Auritella arenicolens	Australia	KJ729857	KJ729920
A. chamaecephala	Australia	AY635765	AY635781
A. dolichocystis	Australia	AY635764	AY337371
Inocybe adaequata	Finland	JQ815407	AY333771
I. aestiva	USA	EU600847	EU600846
I. calamistrata	USA	JQ815409	AY333764
I. calospora	Sweden	AY038313	AY337365
I. candidipes	USA	AY239019	AY337366
I. cercocarpi	USA	EU600890	EU600889
I. chelanensis	USA	AY239021	AY337368
I. corydalina	Belgium	AY038314	AY337370
I. distincta	**India**	**KX171344**	**KX171345**
I. dulcamara	USA/-	EU569836	AY388644
I. flocculosa	Norway	AY380375	AY337375
I. geophylla	Finland	AY380377	AY333777
I. godeyi	Italy	AY038316	AY337378
I. griseorubida	India	KT180327	KT180328
I. heimii	Italy	AY380379	AY337380
I. hystrix	Finland	AY380380	AY337381
I. lacera	USA	AY038318	KM245991
I. lanatodisca	USA	AY380382	JQ846480
I. lanuginosa	USA	AY038319	KM245992
I. leptocystis	Finland	AY380384	AY337386
I. leucoblema	Finland/-	EU569858	AY333310
I. maculata	-/USA	AY745700	EU569863
I. misakaensis	Zambia	EU569874	AY333767
I. napipes	USA/Norway	KP170955	AY337390
I. niveivelata	USA	JQ319695	AY333776
I. occidentalis	USA	EU600893	EU600892
I. praetervisa	USA	KP170982	AY337392
Inocybe species ZT8944	India	EU600903	EU600902
Inocybe species ZT9250	India	EU604546	EU600904
I. spuria	USA	EU600868	EU600867
I. stellatospora	Sweden	AY038328	AY337403
I. terrigena	Finland	AY380401	AY333309
I. umbrinella	-/USA	FJ904162	JQ846497
I. unicolor	USA	AY380403	AY337409

...Continued on next page

TABLE 1. (Continued)

Species	Geographic origin	GenBank accession no.	
		nrLSU	RPB2
Tubaria confragosa	USA	AY700190	DQ408113
T. vinicolor	USA	DQ536415	DQ536418
Tubariomyces hygrophoroides	Spain/France	GU907093	GU907090
T. inexpectatus	Spain	GU907091	GU907088
Tubariomyces species 2 BB6018	Zambia	EU600887	EU600886

Results

Taxonomy

Inocybe distincta K. P. D. Latha & Manim., *sp. nov*. Figs. 1A–G; Figs. 2A–E; Figs. 3A–C
MycoBank MB 816970

Etymology:—The specific epithet refers to the distinctive evolutionary lineage of this species.

Diagnosis:—*Inocybe distincta* has small basidiomata with a finely squamulose-rimulose pileus with mostly reflexed margin, a fibrillose-pruinose stipe with an abrupt base, smooth, phaseoliform to ovo-ellipsoid basidiospores occasionally showing a slight angular outline; copious, versiform, often septate cheilocystidia covered with a resinous substance towards the apex; a hymenium devoid of pleurocystidia and a cutis-type stipitipellis with plentiful caulocystidia formed of modified terminal cells of stipitipellis hyphae towards the apex.

Holotype:—INDIA. Kerala State: Malappuram District, Calicut University Campus, 13 May 2015, *K. P. Deepna Latha*, *DKP336* (CAL 1310).

Description:—*Basidiomata* small. *Pileus* 6–17 mm diam., conico-convex when young, becoming broadly convex to somewhat applanate with a subumbonate center; surface initially grayish orange (5B4/OAC791) all over, becoming light brown (5D6/OAC776) at maturity, dull, finely squamulose around the center and rather rimulose towards the margin; margin decurved to straight, mostly becoming reflexed, crenate or somewhat wavy. *Lamellae* emarginate, subventricose, close, initially whitish, becoming orange gray (5B2/OAC815) or grayish orange (5B3/OAC814), up to 2.5 mm deep, with lamellulae of 2–3 lengths; edges fimbriate, whitish. *Stipe* 9–31 × 2–4 mm, central, terete, equal or slightly tapered towards the apex, solid; surface initially whitish, becoming grayish orange (5B3/OAC814) with age, appressed-fibrillose and finely pruinose all over, densely so towards the apex; base whitish, ending abruptly. *Context* soft, up to 1 mm wide, orange gray (5B2/OAC815). *Odor* and *taste* not distinctive.

Basidiospores 6–12 × 5–7 (9.3±1.7 × 5.8±0.6) µm, Q = 1.2–2.2, Qm = 1.6, phaseoliform in side view, ovo-ellipsoid in top view, smooth, occasionally with a slight angular outline, thick-walled. *Basidia* 23–34 × 8–12 µm, clavate or narrowly clavate, occasionally septate or short-pedicellate, thin-walled, hyaline, mostly guttulate, 4-spored or rarely 2-spored; sterigmata up to 5 µm long. *Pleurocystidia* absent. *Lamella-edge* sterile or occasionally heterogeneous with copious cheilocystidia. *Cheilocystidia* 17–70 × 7–10 µm, versiform: clavate, cylindrical, cylindrical with a truncate or capitate apex, flexuouso-cylindric, utriform, utriform with a median constriction, vesiculose or spathulate, mostly septate, rarely branched, slightly thick-walled, hyaline, often coated with a resinous substance especially towards the apex. *Lamellar trama* subregular; hyphae 3–20 µm wide, thin-walled, hyaline or pale yellow. Subhymenium pseudoparenchymatous. *Pileus trama* subregular composed of compactly arranged, inflated hyphae; hyphae 13–26 µm wide, thin-walled, hyaline. *Pileipellis* a cutis often disrupted by small patches of ascending hyphae towards the center; hyphae 6–20 µm wide, thin- to slightly thick-walled, with a pale yellow wall pigment and yellowish brown, spiral encrustations. *Stipitipellis* a cutis often disrupted with small bunches of caulocystidia especially towards the apex; hyphae 3–9 µm wide, thin-walled, hyaline. *Caulocystidia* formed of modified terminal cells of hyphae of the stipitipellis, 17–70 × 7–10 µm, clavate, cylindrical, flexuous, utriform with a capitate apex, occasionally coated with a resinous substance especially towards the apex, thin- to slightly thick-walled, hyaline. *Clamp connections* seen on all hyphae.

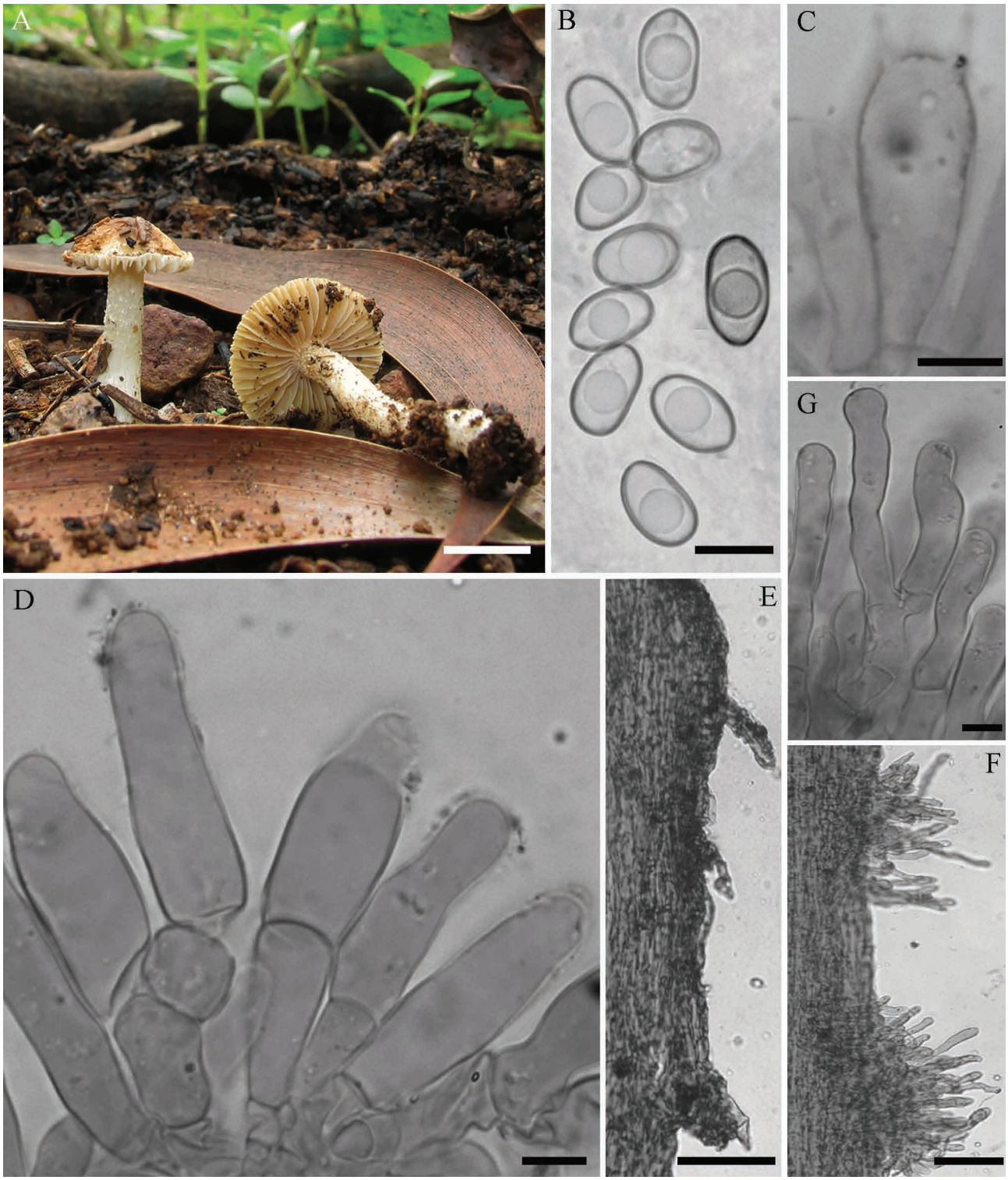

FIGURE 1. A–G: *Inocybe distincta* (CAL 1310, holotype). **A**. Basidiomata; **B**. Basidiospores; **C**. Basidium; **D**. Cheilocystidia; **E.** Pileipellis; **F**. Stipitipellis; **G.** Caulocystidia. Scale bars: **A**=10 mm; **B–D, G**=10 µm; **E–F**=100 µm. Photos by K.P. Deepna Latha.

Habitat:—scattered or in small groups, on soil, in *Acacia* groves.

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

Other material examined:—SRI LANKA. Central Province: Kandy District, Peradeniya, 15 October 1914, *T. Petch*, 4176 (K(M)203103, holotype of *I. cutifracta*); Western Province: Colombo District, Waga forest, amongst *Hevea* logs, 05 November 1974, *D. N. Pegler,* 2173 (K(M)203101, a collection labeled as *I. cutifracta*).

Comments:—The distinct status of the ITS (KX171343: 484 bp), nrLSU (KX171344: 691 bp) and RPB2 (KX171345: 645 bp) sequences of *I. distincta* was confirmed in BLASTn searches. No close hits with zero e-values

were obtained using the ITS sequence. *Inocybe* species ZT9250 was the closest hit with high sequence similarity (100% for nrLSU and 99% for RPB2) in BLASTn searches with both nrLSU (EU604546; Identities = 691/691 (100 %) and RPB2 (EU600904; Identities = 645/646 (99 %)) sequences.

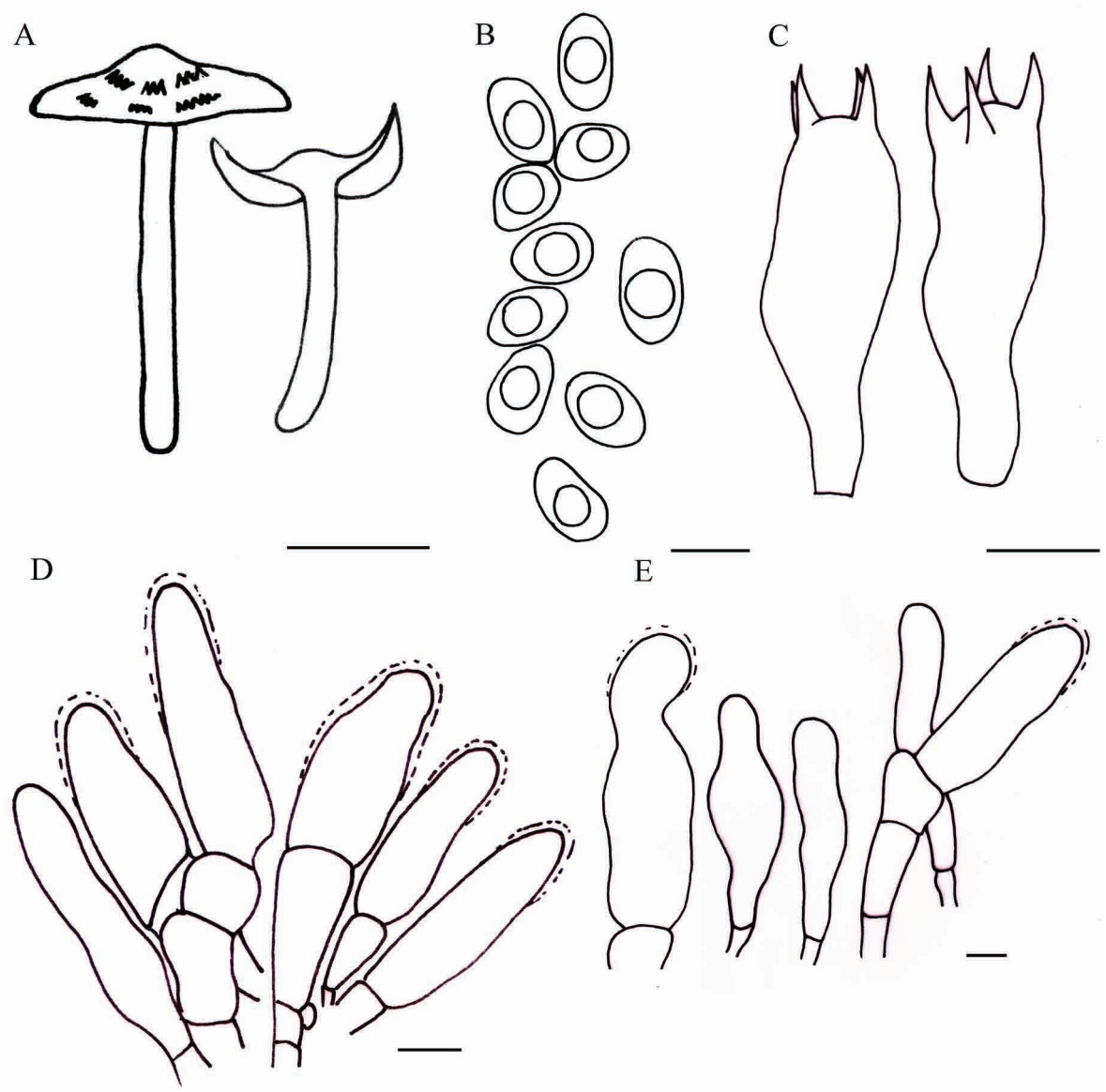

FIGURE 2. A–E: *Inocybe distincta* (CAL 1310, holotype). **A**. Basidiomata; **B**. Basidiospores; **C**. Basidia; **D**. Cheilocystidia; **E.** Caulocystidia. Scale bars: **A**=10 mm; **B**–**E**=10 µm. Drawings by K.P. Deepna Latha.

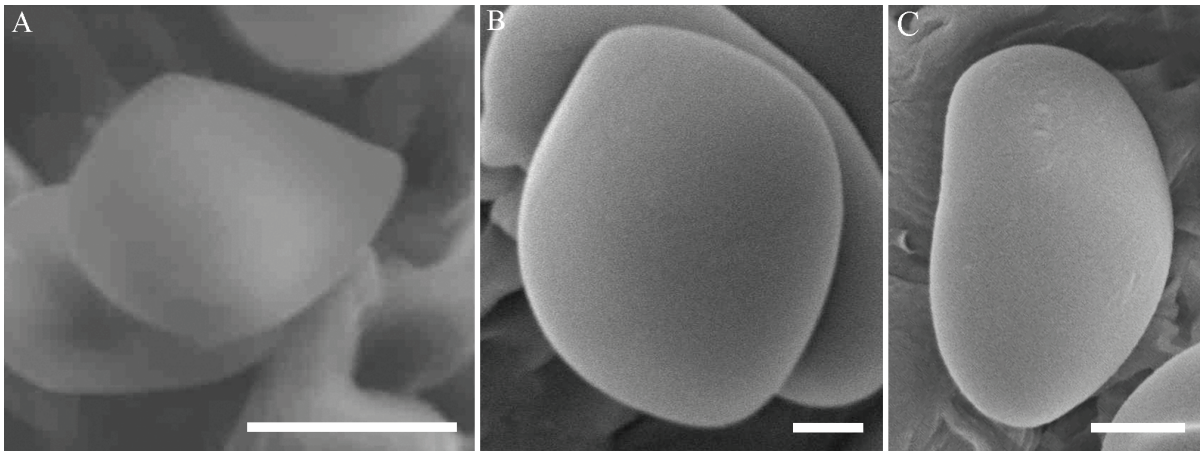

FIGURE 3. A–C: SEM images of basidiospores of *I. distincta* (CAL 1310, holotype). Scale bars: **A** = 5 µm; **B**–**C** = 1 µm. Photos by K.P. Deepna Latha.

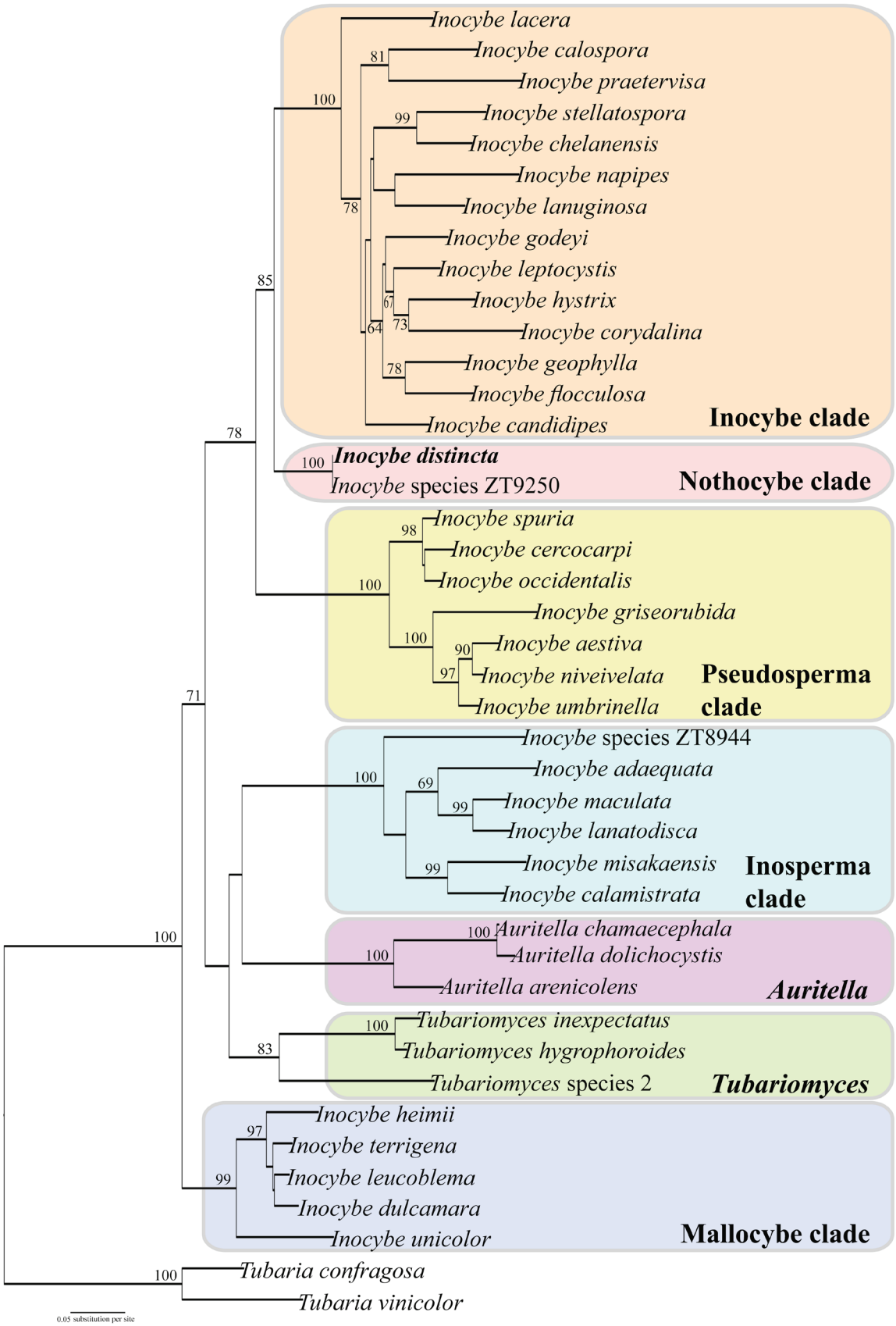

FIGURE 4. A combined nrLSU and RPB2-sequence based phylogram generated from ML analysis showing the placement of *Inocybe distincta* within the Nothocybe clade. Except the Mallocybella clade, which was proposed as the genus *Tubariomyces* by Alvarado *et al.* (2010), all other clade nomenclature follows Matheny *et al.* (2009). Values at nodes indicate bootstrap support. BS values ≥50% are shown.

The phylogram inferred from a ML analysis of the combined nrLSU and RPB2-sequence dataset (Fig. 4) shows the relative placement of *I. distincta.* The phylogenetic tree revealed seven distinct clades with maximum (100% ML BS) support where *I. distincta* was nested in the Nothocybe lineage. *Inocybe distincta* was found to be paired with *Inocybe* sp. ZT9250 with full (100% ML BS) support. Additionally, a pairwise alignment of RPB2 and nLSU sequences of *I. distincta* and *Inocybe* sp. ZT9250 showed 99% and 100% sequence similarities respectively.

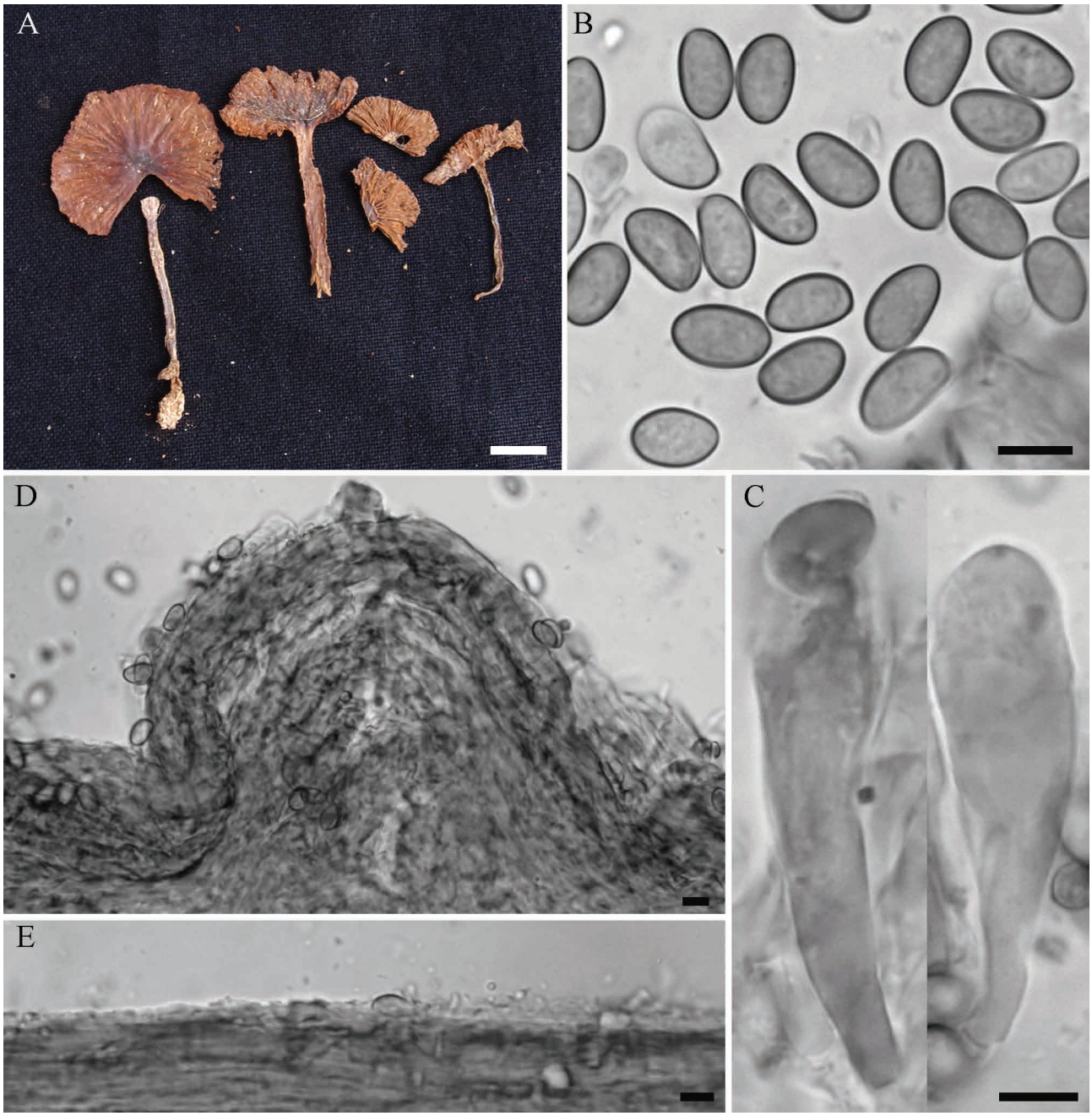

FIGURE 5. A–E: *Inocybe cutifracta* (K(M)203103, holotype). **A**. Basidiomata; **B**. Basidiospores; **C**. Cheilocystidia; **D**. Pileipellis. **E.** Stipitipellis. Scale bars: **A** = 10 mm; **B**–**E** = 10 µm. Photos by K.P. Deepna Latha

As the Nothocybe lineage is assumed to have affinities to *I. cutifracta* (Matheny 2009), and as there are different interpretations of that species, we examined the holotype of *I. cutifracta* collected by Petch and another collection from Sri Lanka identified as *I. cutifracta* by D. N. Pegler. Our observations are as follows: microscopic observation of the holotype specimen of *I. cutifracta* (K(M)203103) (Fig. 5) reveal that it has ellipsoid or subphaseoliform and smaller basidiospores (8–10 × 5–6 µm) lacking any angularity, a sterile lamella-edge, typically clavate cheilocystidia that are hyaline or occasionally with a pale yellowish brown plasmatic-pigmented and devoid of resinous substances, a disrupted cutis-type pileipellis and a stipitipellis devoid of caulocystidia. The collection of *I. cutifracta* (K(M)203101) made by Pegler (Fig. 6) show features that considerably differ from the type specimen of *I. cutifracta* as well as from

I. distincta. *Inocybe distincta* differs from *I. cutifracta* in having slightly shorter (7–9(10) × 5–6 µm), ovo-ellipsoid to subamygdaliform basidiospores devoid of any angularity and with somewhat smaller Qm (1.5) value, the presence of both clavate and utriform cheilocystidia (sometimes with a median constriction) apart from the capitate forms and a stipitipellis devoid of caulocystidia. Pegler's collection (K(M)203101) has slightly shorter (7–9(10) × 5–6 µm), ovo-ellipsoid to subamygdaliform basidiospores with somewhat smaller Qm (1.5) value, typically capitate cheilocystidia with refractive contents and secretions, a disrupted cutis-type pileipellis with scattered tufts of semi-erect hyphae and a stipitipellis devoid of caulocystidia. Unfortunately, no DNA was extracted from the type and additional specimen of *I. cutifracta* following the strict restrictions placed on the loan from Kew (M) Herbarium.

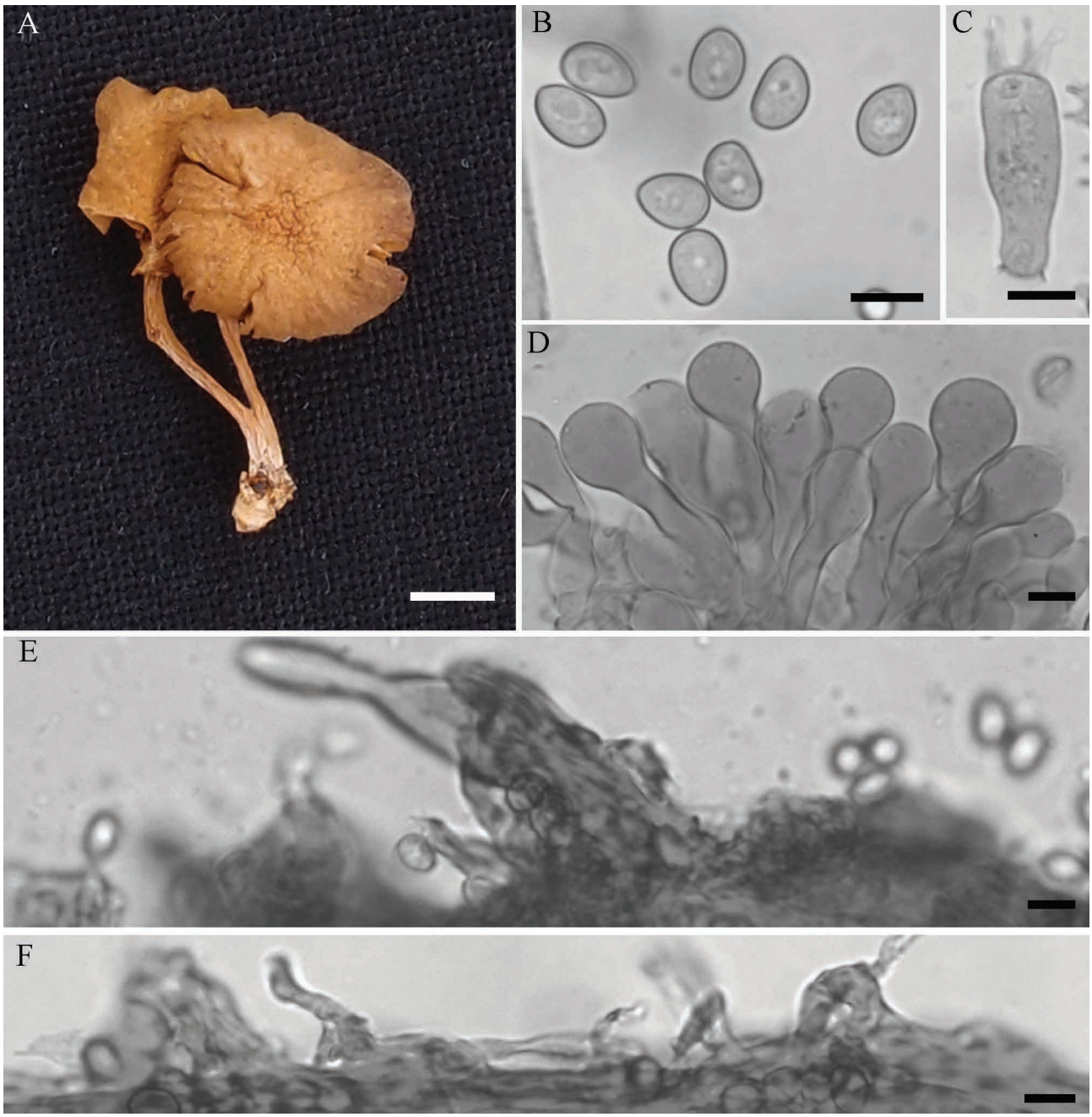

FIGURE 6. A–F: *Inocybe cutifracta* (K(M)203101). **A**. Basidiomata; **B**. Basidiospores; **C**. Basidium; **D.** Cheilocystidia; **E**. Pileipellis. **F.** Stipitipellis. Scale bars: **A** = 10 mm; **B**–**F** = 10 µm. Photos by K.P. Deepna Latha.

Inocybe sp. ZT9250 was assumed to have association with *Casuarina* trees (Matheny 2009). Remarkably, *I. distincta* was collected from an *Acacia* (Fabaceae) grove. This indicates that either it has no association with *Casuarina* as was previously assumed or it has a broad host range.

Acknowledgments

We are thankful to the staff of Kew (Mycology) Herbarium for arranging a loan of materials. KPDL acknowledges support from the Kerala State Council for Science, Technology and Environment (KSCSTE) in the form of a PhD fellowship (Grant No. 001/FSHP/2011/CSTE) and is thankful to the Principal Chief Conservator of forests, Kerala State, for granting permission (No. WL10-4937/2012, dated 03-10-2013) to collect agarics from the forests of Kerala.

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