Mycol Progress (2016) 15: 24
DOI 10.1007/s11557-016-1174-z

ORIGINAL ARTICLE

New and noteworthy species of *Inocybe* (Agaricales) from tropical India

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Received: 2 September 2015 / Revised: 10 February 2016 / Accepted: 15 February 2016 / Published online: 24 February 2016

Abstract Eleven species of *Inocybe*, a highly diverse genus of ectomycorrhizal Agaricales, are documented from tropical India in Kerala State. Seven species are described as new. Furthermore, *I. pileosulcata* is reported from India for the first time. *I. virosa*, not previously validated, is validated here. Gross morphological and microscopic descriptions, illustrations, and phylogenetic affiliations are provided. Seven species feature nodulose or spinose basidiospores and belong to the *Inocybe* clade. The remaining four species are characterized by the combination of smooth spores and absence of pleurocystidia. Two of these share an alliance with the *Pseudosperma* clade, and the other two with the *Inosperma* clade. All 11 species likely share an ecological association with lowland tropical Dipterocarpaceae. The new combination *I. mucidiolens* is made (formerly *I. calamistrata* var. *mucidiolens*).

Keywords Ectomycorrhizal fungi · Inocybaceae · New species · Systematics · Taxonomy · Tropical fungi

Section Editor: Zhu-Liang Yang

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Introduction

The family Inocybaceae Jülich is a species-rich group of Agaricales (Basidiomycota) with some 700 species worldwide (Matheny et al. 2009). Species in the family can be recognized by their typically small but fleshy basidiomes, often with a dry, fibrillose, rimose or squamulose pileus, growth typically on soil, and yellowish brown basidiospores that lack a germ pore. The Inocybaceae occurs worldwide forming ectomycorrhizal (ECM) associations with numerous families of angiosperms and gymnosperms (Pinaceae, *Gnetum*) in tropical and temperate areas making it one of most diverse families of Agaricales (Kirk et al. 2008).

Species of *Inocybe* (Fr.) Fr. are poorly known in the tropics and elsewhere (Matheny et al. 2009, Bougher et al. 2012, Matheny et al. 2012a). Indeed, new taxa continue to be described from northern Europe, regions where the genus has been studied for some two hundred years (Kokkonen and Vauras 2012). In India, the genera *Inocybe* and *Auritella* Matheny & Bougher have thus far been recorded, but the family as a whole is poorly known in tropical regions of Asia. Despite this, India appears to be phylogenetically diverse in Inocybaceae containing lineages from six of seven major clades in the family (Matheny et al. 2009, 2012b). Only the genus *Tubariomyces* Esteve-Rav. & Matheny (Inocybaceae) has yet to be reported from India (Matheny et al. 2012b). Few Indian species, however, have been documented formally thus far (Horak 1981, Manjula 1983, Pradeep et al. 1996, Vrinda et al. 1997a, b, 1999, 2000, 2001, Natarajan et al. 2005, Matheny et al. 2012b, Farook et al. 2013, Latha and Manimohan 2015). The present study aims to clarify the taxonomic status of 11 species of *Inocybe* collected in a tropical region of India in the state of Kerala, all of which putatively form ECM associations with plant species of the family Dipterocarpaceae. Seven of these 11 taxa are described here as new, and one species is validated.

The state of Kerala lies along the southwest corner of peninsular India between 8°18′ and 12°48′ north latitudes and 74°52′ and 72°22′ east longitudes. It is situated between the Arabian Sea of the Indian Ocean to the west and the Western Ghats to the east, has an area of 38,864 sq km, which amounts to 1.2 % of the total geographic area of India. Situated along the west coast region of India, Kerala has a tropical climate with varied topographical features, high rainfall, and geographical conditions that favor the formation of highly diversified ecological niches. Most of the forested areas of the state are part of the Western Ghats, one of the mega diversity centers in India and a biodiversity hotspot. The forests of Kerala are considered very rich in species diversity and endemism. The state harbors 4694 taxa of flowering plants, of which 237 are endemic (Nayar et al. 2008), which is primarily due to the highly diversified ecological niches that occur from sea level to 2695 m above sea level. Champion and Seth (1968) recognize 26 forest types in Kerala, of which the major ones are west coast tropical evergreen, southern moist deciduous, dry mixed deciduous, subtropical hill forest, shola forest, southern mountain wet temperate grassland, mangroves, *Myristica* swamp forests, sub tropical hill savanna, and moist teak forests. The climate of Kerala is mainly wet and maritime tropical and heavily influenced by the seasonal monsoonal rains.

Materials and methods

Field collection and morphological analysis

Collections were studied using standard procedures for morphological examination of agarics. Gross morphological descriptions are based exclusively on fresh materials collected by the authors. Microscopic characters were studied on dried material using hand cut sections of basidiomes revived in a 3 % solution of KOH and examined under a Leica DME1000 compound microscope. Sections were stained with 1 % aqueous solution of Congo red and mounted in 3 % aqueous KOH. For evaluation of the range of spore size, 20 basidiospores were measured from each collection cited. Measurements of basidiospores include nodules, if present. Color notations refer to Kornerup and Wanscher (1978). Holotypes of newly described species are deposited at the University of Tennessee (TENN), and isotypes and paratypes examined are deposited at the Mycological Herbarium of Jawaharlal Nehru Tropical Botanic Garden and Research Institute, Trivandrum (TBGT). Herbarium designations follow Thiers [continuously updated].

DNA extraction, PCR, and sequencing

DNA was extracted from dried basidiomes following protocols in Baroni and Matheny (2011). Procedures for PCR, PCR purification, and sequencing preparation are provided in Judge et al. (2010). Gene regions examined during this study include the internal transcribed spacer 1, 5.8S ribosomal RNA gene, and internal transcribed spacer 2 (ITS) of the nuclear ribosomal RNA operon, the 25S rRNA gene that encodes the nuclear large subunit ribosomal RNA (nLSU), and the region between conserved domains 6 and 7 of the *rpb2* gene, which encodes the second largest subunit of RNA polymerase II. Primers used for PCR and direct sequencing are cited in these works (Matheny 2005, Judge et al. 2010, Baroni and Matheny 2011). DNA sequences were annotated using Sequencher 5.0.1 (Gene Codes Corporation, Ann Arbor, MI, USA).

Molecular analyses

Thirty-four DNA sequences (nLSU, ITS, *rpb2*) were generated for this study. BLASTn searches of all gene regions were performed on GenBank. Based on BLASTn results, sequences were manually aligned in five different matrices in MacClade (Maddison and Maddison 2005) and subjected to maximum likelihood (ML) phylogenetic analyses following procedures outlined in Baroni and Matheny (2011). RAxML v7.2.8 (Stamatakis 2006) was used to reconstruct phylogenetic trees bootstrapped with 1000 replicates. Data sets were partitioned by gene region. Outgroups for each matrix were designated based on more inclusive published phylogenetic results (Matheny et al. 2009, Matheny et al. 2012b, Horak et al. 2015). DNA alignments are available by request from the last author. Taxa used and GenBank accession numbers are provided in Table 1 (herbaria where specimens are deposited are indicated where known). In cases where specific subclade groupings were ambiguous (viz, *I. albonitens*, *I. parvisquamulosa*), we report the BLASTn results here, make assignment to a major clade per Matheny (2009), and predict any finer scale phylogenetic resolution.

Taxonomy

Inocybe papilliformis C.K. Pradeep & Matheny, **sp. nov**. Figs. 1 and 16a–b.

MycoBank: MB 813813

Diagnosis: Most similar to *Inocybe hydrocybiformis* and *I. petchii* but differs by the combination of very large basidiospores (15–19.5 × 14–18 μm), thin and small basidiomes, pileus with acute papillate umbo, and metuloid cheilocystidia and pleurocystidia. Phylogenetic placement: Inocybe clade.

Holotype: India, Kerala State, Wayanad District, Ponkuzhy, 15 Aug 2007, TENN070303 (GenBank accession no. KP171131-ITS, KP170912-nLSU, KM245988-*rpb2*); isotype TBGT10480.

Table 1 Taxon sampling and DNA sequences used for BLASTn and/or phylogenetic analyses

Species	Specimen-voucher	GenBank accession no.		
		ITS	LSU	*rpb2*
I. actinocephala ined.	PBM2863 (TENN)	JQ408789	JN975012	JQ846495
I. adaequata	JV16501F (WTU)	—	AY380364	AY333771
I. aestiva	BK18089706 (UTC)	EU600847	EU600847	EU600846
I. afromelliolens ined.	PC96013	JQ801383	EU600883	EU600992
I. alboflavella	TBGT11280 (type)	KP636859	KP171058	KM656097
I. alienospora	PBM3743 (TENN)	KP171104	KM197209	KM245970
	REH9667 (NY)	KP171105	KM197210	KM245971
I. alienospora aff.	PBM3728 (TENN)	KP171106	KM197211	KM245972
I. alienospora aff.	PBM3758 (TENN)	KP171107	KM197212	KM245973
I. apiosmota	PBM3020 (TENN)	JQ801385	JN975021	JQ846463
I. araneosa ined.	PBM3755 (TENN)	KJ729878	KJ729904	KJ729935
I. araneosa ined. aff.	PL58410 (BRI)	KJ729880	KJ729906	KJ729937
I. arenicola	RC-GB99-014	FJ904134	FJ904134	—
I. asterospora aff.	DJLTN06-58 (TENN)	—	JN974975	—
	PBM3309 (TENN)	—	KM197215	KM245976
	PBM2453 (TENN)	DQ404390	AY702015	—
I. asterspora cf.	MR00015	AM882897	AM882897	—
I. atrovirescens ined.	PBM1066 (WTU)	JQ801386	JQ815409	JQ846466
I. aurora	AU10245	HQ201337	HQ201338	—
I. bicolorata	ZT12187	GQ892984	GQ892938	JQ846464
I. bongardii	JV7450F (WTU)	—	EU555448	—
I. breviterincarnata	BK28080407 (UTC)	JQ408749	EU555451	EU555450
I. brunneicothurnata ined.	PBM1889 (WTU)	JQ408787	JQ319707	JQ846493
I. bulbosissima	EL6605	AM882765	AM882765	—
I. calamistrata	EL1904	AM882938	AM882938	—
	PBM1105 (WTU)	JQ801386	JQ815409	JQ846466
I. calamistrata aff.	DED8134 (SFSU)	GQ892983	GQ892937	—
I. calamistrata aff.	PBM2351 (WTU)	—	AY380368	AY333764
I. calamistrata aff.	REH8420 (NY)	JQ801390	JN975018	JQ846471
I. calamistratoides	PBM3384 (TENN)	JQ801393	JQ815415	KJ729949
I. carnosibulbosa	TBGT12047 (type)	KT329448	KT329454	KT329443
I. cercocarpi	BK20069806 (UTC)	—	EU600890	EU600889
I. cervicolor	TURA4761	JQ801395	JQ814417	JQ846474
I. conspicuospora	PC96042	—	EU555471	EU555470
I. curreyi sensu Hesler	PBM2871 (TENN)	HQ201348	HQ201348	JQ846475
I. cyanotrichia ined.	I37	JQ801396	JN975033	JQ846476
I. dulcamaroides	EL112-06	FJ904126	FJ904126	—
I. erubescens	JV9070F	—	EU569846	—
I. fastigiata	FO46800	—	DQ071697	—
I. fastigiella aff.	PBM3325 (TENN)	JQ801399	JQ815419	JQ846477
I. fissurata ined.	PBM2206 (PERTH)	JQ408770	QY732213	JQ421069
	PBM2195 (PERTH)	JQ408771	EU555466	EU555465
I. flavella	EL137-05	AM882776	AM882776	—
I. flavosquamulosa	TBGT10743 (type)	KT329450	KT329456	—
I. geraniodora	EL10606	FN550945	FN550945	—
I. gracillissima inded.	PBM3735 (TENN)	—	KJ729919	KJ729945
	PBM3738 (TENN)	KP171123	KJ801179	KJ729947

Table 1 (continued)

Species	Specimen-voucher	GenBank accession no.		
		ITS	LSU	*rpb2*
	JAC2809 (CANB)	JQ408755	JQ3196884	—
	NLB937 (PERTH)	KP171122	KJ801178	KJ729946
I. hirsuta v. *maxima*	PBM2222 (WTU)	—	EU569854	—
I. hydrocybiformis	TBGT12318	KP171130	KP170911	KM245987
	ZT10077	GQ893016	GQ892971	—
	ZT9879	GQ893017	GQ892972	—
I. hydrocybiformis aff.	DED8165 (SFSU)	GQ893018	GQ892973	—
I. hygrophorus	EL97-06	FJ904132	FJ904132	—
I. illudens ined. ("*renispora*")	I106 (HO)	JQ408769	JQ319699	JQ421068
I. insignis	MK07101101 (TENN)	—	KP170913	KM245989
I. isabellina ined.	NLB836 (PERTH)	KP171141	KP170920	KJ811586
I. jurana sensu Hesler	PBM2951 (TENN)	—	HQ201353	JQ846478
I. lanatodisca	PBM2451 (TENN)	JQ408759	JQ319690	JQ846483
	TURA1812	JQ408763	JQ319694	JQ846484
I. lasseri	MCA1971 (BRG)	—	EU569856	EU569857
I. lasseroides	PBM3749 (TENN)	KP171145	KP170924	KM245993
	PBM3750 (PERTH)	KP171146	KP170925	—
I. lasseroides aff.	PBM3786 (TENN)	KP171147	KP170926	KM245994
	PBM3787 (TENN)	KP171148	KP170927	KM245995
	TJB10466 (CORT)	KP171149	KP170928	KM245996
I. latericia	PDD92382	GU233367	GU233413	—
I. latericia aff.	TR109-02 (M)	JQ801405	JN975023	JQ846487
I. lepidotella	MCA1881 (BRG)	JN642233	JN642235	—
I. maculata	EL12604	AM882964	AM882964	—
I. maculata aff.	PBM3051 (TENN)	JQ801401	JN975026	JQ846485
	PBM2446 (TENN)	DQ241778	AY745700	EU569863
I. melliolens	PAM05052303	FJ904148	FJ904148	—
I. microfastigiata cf.	EL113-06	FJ904156	FJ904156	—
I. mimica	EBJ961997	FJ904124	FJ904124	—
I. misakaensis	Wat24830	JQ801409	EU569875	AY333767
I. mixtilis	HL2002 (CANB)	KP308781	KP170952	KM406195
	PAM05103003 (TENN)	HQ585870	HQ641113	KM406197
	PAM07110104 (LIP)	HQ586872	HQ641115	KM406196
	PBM1315 (WTU)	—	AY380387	AY337395
I. mucidiolens	DG1824 (WTU)	HQ201339	HQ201340	—
I. mutata	PBM2542	—	AY732212	DQ472729
I. neglecta	DED8063	EU600829	EU600829	—
I. neobrunnescens	PBM2452 (TENN)	—	EU569868	EU569867
I. neobrunnescens v. *leucothelota*	SAT0427406 (TENN)	JQ801411	JN975025	JQ846489
I. niveivelata	PBM2337 (WTU)	—	JQ313566	AY333776
I. nobilissima ined.	NLB972 (PERTH)	KP308790	KP170960	KM406203
	NLB974 (PERTH)	KP308791	KP170961	KM406204
	PBM3772 (TENN)	KP308789	KP170959	KM406202
I. obsoleta	EL17-04	AM882769	AM882769	—
I. occidentalis	BK27089703 (UTC)	EU600893	EU600893	EU600892
I. papilliformis	TBGT10480 (type)	KP171131	KP170912	KM245988
I. perlata	EL74-04	AM882771	AN882771	—

Table 1 (continued)

Species	Specimen-voucher	GenBank accession no.		
		ITS	LSU	*rpb2*
I. rimulosa	TBGT12854 (type)	KP636860	KP171059	KM656098
	TBGT12828	KP636861	KP171060	KM656099
I. squamata	PAM05052301	FJ904132	FJ904132	—
I. stellata	DED8162 (SFSU)	GQ893006	GQ892961	KM656104
	ECV3651 (SFSU)	GQ893007	GQ892962	KM656105
	ZT10097 (type)	GQ893008	GQ892963	—
I. pileosulcata	DED8058 (SFSU)	EU600838	EU600838	KM406219
	DED8164 (SFSU)	GQ892996	GQ892951	—
	TBGT10742	KP308810	KP170979	KM406218
I. pileosulcata aff.	DED8163 (SFSU)	GQ892997	GQ892952	KM406219
I. pluviorum ined.	PL23408 (BRI)	—	KP170980	KM406221
I. proxima	DED8007 (SFSU)	EU600839	EU600840	—
I. purpureoflavida	TBGT3388 (type)	KT329451	KT329457	KT329445
I. quietiodor	EL11504	AM882960	AM882960	—
I. regisii ined.	PC96082	JQ801412	JN975027	—
I. reisneri cf.	MCA646 (WTU)	—	EU555463	—
I. rhodiola	EL223-06	FJ904175	FJ904175	—
I. rimosa	EL7505	AM882762	AM882762	—
I. rimosa aff.	MCA859 (TENN)	JQ408772	JQ319700	—
I. rimosa cf.	PBM3974 (TENN)	—	KP170989	KM406229
I. rimosa cf.	PBM1938 (WTU)	JQ408775	JQ319701	JQ846491
I. rimosoides ("*cookei*")	PBM2459 (TENN)	DQ404391	AY702014	DQ385884
I. rubriocosa ined.	PBM3784 (TENN)	KP308817	KP170990	KM406230
I. sabulosa ined.	E8178 (PERTH)	KP308822	JN974916	KM406235
I. sororia	Kuoljok0512	FJ904212	FJ904150	—
	JRH661 (WTU)	—	EU600863	—
I. spuria	SJ92017	AM882784	AM882784	—
I. "*stellata*"	DED8015 (SFSU)	GQ893011	GQ892966	KM656106
	DED8060 (SFSU)	GQ893010	GQ892965	KM656107
	ZT10123	GQ893009	GQ892964	—
I. subflavospora ined.	E5880 (PERTH)	—	AY380396	AY337404
I. subhirsuta (as "*calamistrata*")	JV11950 (WTU)	—	EU555452	AY333763
I. submaculata ined.	PC96073	JQ801417	EU600870	EU600869
I. torresiae	PBM2157 (TENN)	JQ085937	EU600874	EU600873
	PBM3722 (PERTH)	KP641634	KP171087	KM656131
	PBM3779 (PERTH)	KP641635	KP171088	KM656132
I. umbrinella	JV13699	FJ904165	FJ904165	—
I. vagata ined.	PBM3187 (CANB)	KP641639	KP171091	KM656135
	PDD72861	HM060326	HM060325	—
I. viridipes ined.	I153 (HO)	KP641646	KP171095	KM656139
	PBM3767 (TENN)	KP641645	JO171094	KM656138
I. virosa	TBGT753	KT329452	KT329458	KT329446
I. viscata	PDD27109	GU233318	—	—
	I102 (TENN)	KP641647	KP171096	—
	PBM3213 (TENN)	KP641648	KP171097	—
	PBM3445 (TENN)	KP641649	JQ313570	—
I. xanthocephala	PAM00100606	FJ904130	FJ904130	—

Table 1 (continued)

Species	Specimen-voucher	GenBank accession no.		
		ITS	LSU	*rpb2*
Inocybe sp.	BB3233 (PC)	JQ801415	EU600885	
Inocybe sp.	DED8044 (SFSU)	GQ892995	GQ892950	KM656121
Inocybe sp.	DJL-SJ14 (TENN)	JQ408784	EU600851	—
Inocybe sp.	DV04132011 (TENN)	KP636835	KP171040	—
Inocybe sp.	ECV3648 (SFSU)	GQ893012	GQ892967	KM555135
Inocybe sp.	I116	FJ904142	FJ904142	—
Inocybe sp.	L-GN3a	JX316732	JX316732	—
Inocybe sp.	MCA562 (WTU)	JQ408785	JN975016	JQ421077
Inocybe sp.	MTS2494 (UC)	JQ408786	JN975008	MTS2494
Inocybe sp.	PC96039	—	EU555474	EU555473
Inocybe sp.	PBM2321 (TENN)	JQ408788	JQ319708	JQ846494
Inocybe sp.	PBM3751 (TENN)	KP636851	KP171053	KM555145
Inocybe sp.	PBM3766 (TENN)	KP636852	KP171054	KM555146
	PL42609 (BRI)	KJ729879	KJ729905	KJ729936
Inocybe sp.	REH7418 (NY)	KP636854	JN974931	KM555149
	REH7965 (NY)	KP636855	JN974932	KM555150
Inocybe sp.	TJB10045 (CORT)	KT600658	KT600659	KT600660
Inocybe sp.	TM02-130	—	EU522733	—
Inocybe sp.	TR74-06 (M)	JQ801391	JN975020	JQ846472
Inocybe sp.	TR132-05 (M)	KP636863	KP171061	KM656101
	TR88-06 (M)	KP636862	JN974992	KM656100
Inocybe sp.	TR183-05 (M)	JQ408773	JN975005	JQ421070
	TR75-05 (M)	JQ408774	JQ815425	—
Inocybe sp.	TR104-05 (M)	KP636864	JN975011	—
	TR133-05 (M)	JQ408791	JQ319709	—
Inocybe sp.	TR138-05 (M)	JQ408792	JN975009	—
Inocybe sp.	TR49-05 (M)	JQ408790	JN975014	JQ421079
Inocybe sp.	TR194-02 (M)	JQ408793	JN975032	JQ421080
Inocybe sp.	TR198-03 (M)	KP636865	KP171062	—
Inocybe sp.	TR220-06 (M)	JQ801416	JN975017	JQ846496
Inocybe sp.	ZT8944	—	EU600903	EU600902
Inocybe sp.	ZT10106	GQ892987	GQ892941	—
Tubariomyces hygrophoroides	P05112008	GU907097	GU907094	GU907090
T. inexpectatus	AH25500	GU907095	GU907091	GU907088
T. similis	RFS0805	GU907096	GU907092	GU907089
Tubariomyces sp.	BB6018 (PC)	EU600887	EU600887	EU600886

Etymology: *papilliformis*, in reference to the acute or papillate umbo on the pileus

Pileus 4–20 mm wide, conic, convex, campanulate (in some specimens) with acute papillate umbo; surface uniformly brown (5F8) or with some shade of brown (5C4–5, 5D5, 6B3, 6C3, 7E4), appressed squamulose especially near the disc, smooth when young, striate up to the disc, hygrophanous, dry; margin straight, entire to incised. Lamellae adnexed, raw umber (5F8, 5C3, 5D4, 6D3), up to 2 mm deep, close with lamellulae of different lengths; edges concolourous with the sides or whitish, entire to naked eye. Stipe 18–110 × 0.5–3 mm, central, cylindric, narrowly tapering up from a slightly broad base (not marginate), narrowly hollow, brittle; brown (5F8, 5C4, 6E7); surface floccose squamulose becoming smooth. Context brown or pale, thin, soft. Odor mildly acidic.

Basidiospores 15–19.5 × 14–18 μm, avL = 17.5, avW = 15.8, Q = 1–1.14, avQ = 1.10, globose to subglobose,

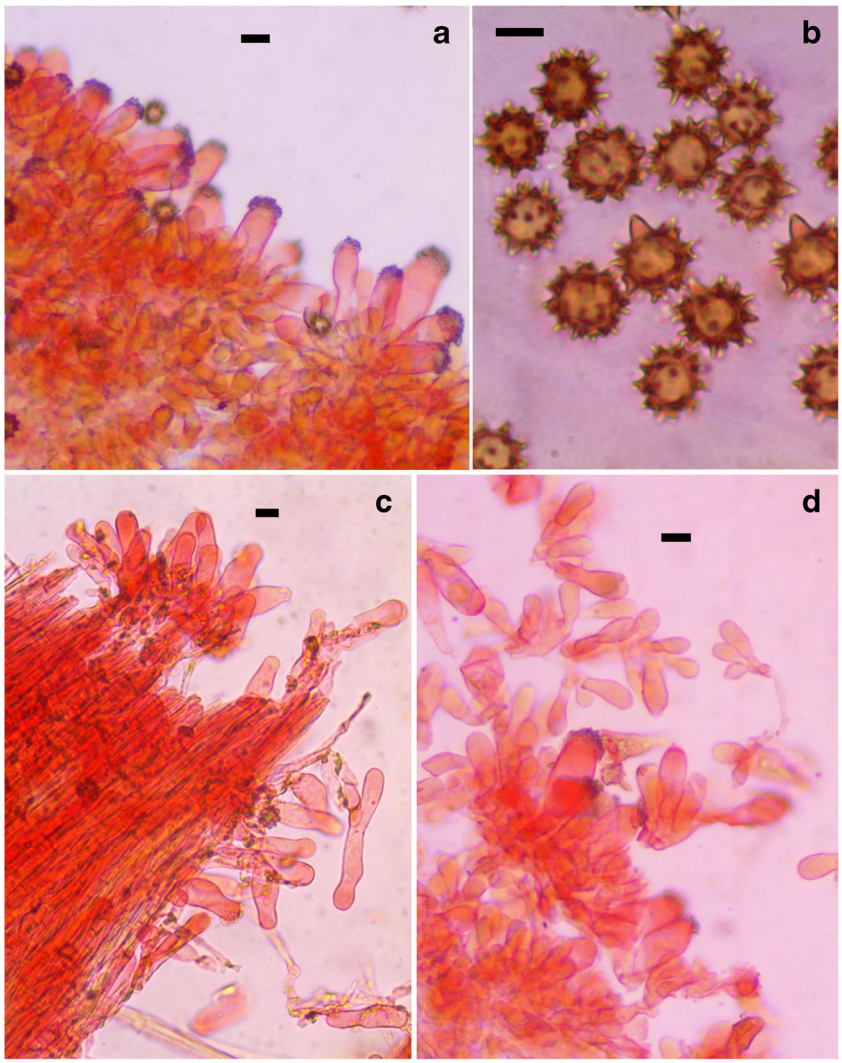

Fig. 1 *Inocybe papilliformis* (TENN070303). **a** hymenial cystidia. **b** spores. **c** caulocystidia. **d** cauloparacystidia. Scale bars = 10 μm

spinose with conic nodules, these often bifid or saddle shaped, yellowish brown, apiculus prominent and distinct. Basidia 22–35 × 10–13 μm, clavate, 4-spored, rarely 2-spored. Lamella edge crowded with cystidia. Cheilo- and pleurocystidia 25–46 × 10–23 μm, fusoid to lageniform, thick-walled, with small crystals at the apex, hyaline. Hymenophoral trama regular, hyphae 5–10 μm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous, 2–3 cells thick. Pileal trama composed of hyphae 7–15 μm wide, inflated, thin-walled, with yellowish brown contents. Pileipellis a cutis, rarely disrupted at the disc, hyphae 3–8 μm wide, incrusted with yellowish brown contents. Stipitipellis a cutis of parallel hyphae, incrusted 2.5–6.5 μm wide, with pale yellowish brown contents. Caulocystidia 32–55 × 10–17 μm, similar to hymenial cystidia, abundant, present on the upper part, absent elsewhere, intermixed with thin-walled cauloparacystidia. Cauloparacystidia 16–30 × 8–16 μm, clavate, cylindro-clavate, thin-walled, hyaline, crowded at the base of caulocystidia. Clamp connections present in all parts.

Habit and habitat: Solitary, scattered, or in groups or in pairs on riverine sandy soil under *Hopea parviflora and Vateria indica* (Dipterocarpaceae) trees.

Additional specimens examined: India, Kerala State, Trivandrum District, JNTBGRI campus: 4 Aug 1994, TBGT1300; 5 Aug 1994, TBGT1315; 5 Dec 1996, TBGT3712; 18 Jul 1997, TBGT1101; 7 Aug 2003, TBGT6448; 13 Jul 2004, TBGT7489; 10 Jun 2008, TBGT11044; 31 May 2011, TBGT13609; 2 Jun 2011, TBGT13617; 15 Jul 2011, TBGT13686; 8 Aug 2013, TBGT14771; Trivandrum District, Kallar, 7 Aug 2008, TBGT11651; 29 Oct 2008, TBGT12145; Ernakulam District, Iringole, 6 Jul 2004, TBGT7413; Wayanad District, 8 Nov 2007, TBGT10749; 16 Jul 2008, TBGT11413; 24 Sep 2008, TBGT11988; 23 Jul 2013, TBGT14746.

Discussion: *Inocybe papilliformis* is superficially related to a number of species in some macro- and micro-morphological features. These include *Inocybe petchii* Boedijn (Pegler 1986; Horak et al. 2015), *I. calospora* Quél. (Vauras 1989), *I. echinosimilis* (E. Horak) Garrido, *I. gemina* (E. Horak)

Garrido, *I. hydrocybiformis* (Corner & E. Horak) Garrido (Horak 1979; Horak et al. 2015), and *I. stellata* E. Horak, Desjardin & Matheny (Horak et al. 2015). However, *I. papilliformis* is distinguished by one or other characters and also molecularly. The distinctive features of the Indian taxon include: the small, thin, conico-convex, brown but hygrophanous pileus (which never becomes plane), presence of an acute papillate umbo; slender, long fragile stipe without a marginate basal bulb; mild acidic odor; and very large globose to subglobose spinose basidiospores with conic nodules that are often bifid or saddle-shaped.

Inocybe petchii (originally described as *Inocybe umbonata* Petch, non Quél.) was first recorded from Sri Lanka and appears most similar to *I. papilliformis*. Both species share the similarly sized and very large basidiospores, but basidiomes of *I. petchii* are more robust, the stipe is red brown and entirely pruinose and features a bulbous submarginate base (Horak et al. 2015). Though thought to be widespread in southeast Asia, molecular data for *I. petchii* are lacking for a more thorough comparison. *Inocybe acutata* Takahito Kobayashi & Eiji Nagasawa (Kobayashi 1993) originally described from Japan is also closely related to the present species. However, differs mainly by its smaller subglobose spiny spores (8.2–10.4 × 7.6–10.2 μm), lack of pleurocystidia and presence of rather abundant paracystidia. *Inocybe papilliformis* is phylogenetically most closely related to Thai and Indian specimens of *I. hydrocybiformis* (Fig. 3), documented below, which is characterized by its smaller spores, the thin-walled, yellow-pigmented (non-metuloid) cheilocystidia and absence of pleurocystidia.

Inocybe hydrocybiformis (Corner & E. Horak) Garrido, *Biblioth. Mycol*. 120: 176, 1988 Figs. 2 and 16c–d

Astrosporina hydrocybiformis Corner & E. Horak, *Persoonia* 10: 170 1979.

Pileus 4–15 mm wide, conic when young becoming convex to plane, with or without a small obtuse, acute to subacute umbo; pastel yellow to light yellow (3A4–5, 4A4), uniformly so when young, becoming pale brown, oak brown, to brown (5D5–6, 6E4), remaining yellowish towards margin when mature, appressed fibrillose-squamulose throughout when young, squamules wearing away during heavy rain, and then becoming brown without the shade of yellow; margin straight, striate, or incised. Lamellae adnexed, brown (6E4, 6D4) up to 2 mm deep, close to subcrowded with lamellulae of different lengths; edges yellowish, entire. Stipe 25–35 × 0.5–3 mm, central, cylindric, equal or narrowly tapering up from a slightly enlarged base (not marginate); pastel yellow (3A4), appressed-squamulose entirely, squamules vanishing during rain or on handling and then becoming brown (5D6, 6E4). Context dull white to brown, soft. Odor mild, agreeable.

Basidiospores 9.5–13.5 × 7.5–13 μm, avL = 12.1, avW = 10.8, Q = 1–1.26, avQ = 1.12, stellate with many (10–16) conic to saddle shaped spines around a subglobose to globose outline, yellowish brown with a prominent hilar appendix. Basidia 28–46 × 12–14 μm, clavate, 4-spored, rarely 2-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia 33–65 × 9–14 μm, cylindro-clavate, curved, often strangulated in the upper part, at times bifurcated at the apex, with dense yellowish refractive contents, thin-walled. Pleurocystidia absent. Hymenophoral trama regular, hyphae 7–13 μm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama composed of hyphae 8–16(–21) μm wide, some inflated, thin-walled, hyaline. Pileipellis a cutis, rarely disrupted, hyphae 4–12 μm wide, incrusted with yellowish brown contents. Stipitipellis composed of parallel hyphae, 4–7 μm wide, incrusted, with pale yellowish brown contents. Caulocystidia 46–82 × 4–10 μm, occurring in clusters on the upper part of the stipe, absent from lower part, similar to cheilocystidia. Clamp connections and oleiferous hyphae present.

Habit and habitat: Scattered on forest floor or in riverine sandy soil under *Hopea parviflora* (Dipterocarpaceae), *Garcinia gummigutta* (Clusiaceae) and *Holigarna arnottiana* (Anacardiaceae) trees.

Specimens examined: India, Kerala State, Wayanad District, Muthanga, Ponkuzhy: 16 Jul 2008, TBGT11402; 24 Sep 2008, TBGT 11989; Trivandrum District, JNTBGRI campus, 5 Nov 2008, TBGT12204; 6 Nov 2008, TBGT12211; 11 Nov 2008, TBGT12238; 28 Nov 2008, TBGT12318 (TENN070304) (KP171130-ITS, KP17091-nLSU, KM245987-*rpb2*).

Discussion: The above description matches with the type description of *Astrosporina hydrocybiformis* from Singapore (Horak 1979) except for the presence of occasional 2-spored basidia and more strangulated, bifid or branched cheilocystidia present in the Indian collections. DNA sequence data from TBGT12318 support the designation of *I. hydrocybiformis* to our material due to the very high ITS similarity (99 % similarity) and phylogenetic affinity to a collection under this name from Thailand (Horak et al. 2015; Fig. 3). Indian collections feature the characteristic spinose basidiospores, thin-walled yellow-pigmented cheilocystidia, and absence of pleurocystida. Despite this latter feature, the species is a confirmed member of the Inocybe clade (Horak et al. 2015). This species was previously reported from Kerala by Vrinda et al. (1999).

Inocybe parvisquamulosa C.K. Pradeep & Matheny, **sp.nov**. Figs. 4 and 16e

MycoBank: MB 813814

Diagnosis: Similar to *Inocybe brevisquamulosa* described from Thailand in dipterocarp forests, but differs by larger basidiomes, larger basidiospores, and ITS divergence (5 %). Phylogenetic placement: Inocybe clade.

Holotype: India, Kerala State, Trivandrum District, JNTBGRI campus, 26 Nov 2008, TENN070305 (GenBank accession no. KT329447-ITS, KT329453-nLSU, KT329442-*rpb2*); isotype TBGT12303

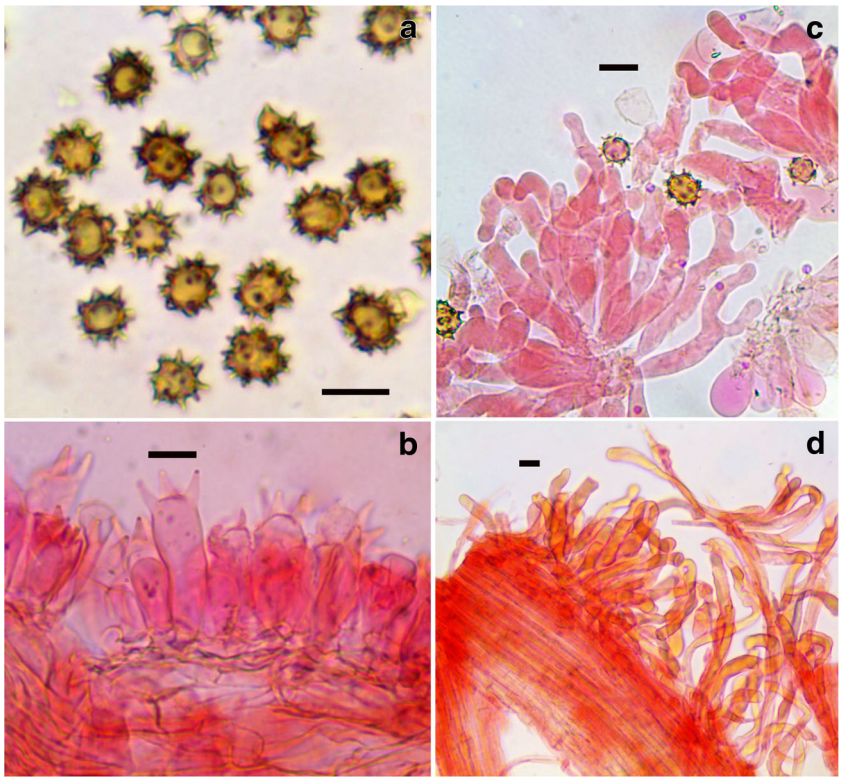

Fig. 2 *Inocybe hydrocybiformis* (TENN070304). **a** spores. **b** basidia. **c** cheilocystidia. **d** caulocystidia. Scale bars = 10 μm

Etymology: *parvus* (little), *squamulosus* (minutely scaly)

Pileus 7–35 mm wide, convex, plano-convex to applanate or becoming slightly uplifted in age, at times with a broad obtuse umbo; brown or with some shade of brown (6F4, 6E4–6, 6D4–6, 5D4–7) or slightly paler; surface fibrillose striate becoming squamulose towards the disc, rimose towards margin; margin straight, entire to incised. Lamellae adnexed, brown (6E4–5, 6D4) up to 4 mm deep, crowded with lamellulae of different lengths; edges concolourous with the sides, entire. Stipe 20–50 × 2–5 mm, central, cylindric, curved, equal or narrowly tapering up from a slightly broad base (not marginate), stuffed becoming hollow; dull white when young becoming brownish (5D4/5D5/6E5), fibrillose-striate, dry. Context dull white, thin, soft. Odor none. Basidiomes small to medium.

Basidiospores(8–)9–12(–13) × (6.5–)7.5–10.5(–11) μm, avL = 10.4, avW = 8.7, Q = 1.06–1.27, avQ = 1.19, distinctly nodulose or almost stellate, subglobose to broadly ellipsoid or ellipsoid in outline, with many (8–14) conic or obtuse nodules, yellowish brown. Basidia 28–34 × 11–12 μm, clavate, 4-spored, thin-walled, hyaline. Cheilo- and pleurocystidia 39–50 × 10–19 μm, fusoid, lageniform, thick-walled, metuloidal with crystals at the apex, yellowish brown. Hymenophoral trama regular, hyphae 6–12 (–14) μm wide, cylindric to inflated, thin-walled, hyaline. Subhymenium pseudoparenchymatous, 3–4 cells thick. Pileal tramal hyphae 7.5–17.5(–30) μm wide, at times inflated, thin-walled, hyaline. Pileipellis a cutis, rarely disrupted at the disc, hyphae 8–16 μm wide, incrusted with yellowish brown contents. Stipitipellis a cutis of parallel hyphae, incrusted, 2.5–5.5 μm wide, with pale yellowish brown contents. Caulocystidia none. Clamp-connections present in all tissues.

Habit and habitat: Solitary, scattered, in pairs or in groups on forest floor under *Hopea parviflora*, *Vateria indica* (Dipterocarpaceae), *Garcinia* sp. (Clusiaceae) or *Diospyrus montana* (Ebenaceae) trees in India. Recorded under *Dipterocarpus alatus* in Thailand.

Additional specimens examined: India, Kerala State, Trivandrum District, JNTBGRI campus, 5 Nov 2008, TBGT12198; 6 Nov 2008, TBGT12212; 25 Nov 2008, TBGT12296; 27 Nov 2008, TBGT12313; 28 Nov 2008, TBGT12326.

Discussion: *Inocybe parvisquamulosa* is a new species very similar to *I. brevisquamulosa* E. Horak, Matheny & Desjardin recently described from tropical dipterocarp forests in Thailand (Horak et al. 2015). The Indian species shares many features in common with *I. brevisquamulosa* including the squamulose pileus disc, fibrillose and non-pruinose stipe surface, lack of an odor, distinctly nodulose spores, absence of caulocystidia, and ectomycorrhizal association with dipterocarps. *Inocybe parvisquamulosa* differs from *I. brevisquamulosa* by its larger basidiomes (the pileus of the latter reaches only up to 10 mm wide and the stipe up to 1–1.5 mm thick), larger spores (8.5–10 × 5.5–6 μm in *I. brevisquamulosa*), and molecular sequence divergence (ITS 5 % dissimilar). Phylogenetically, *I. brevisquamulosa*

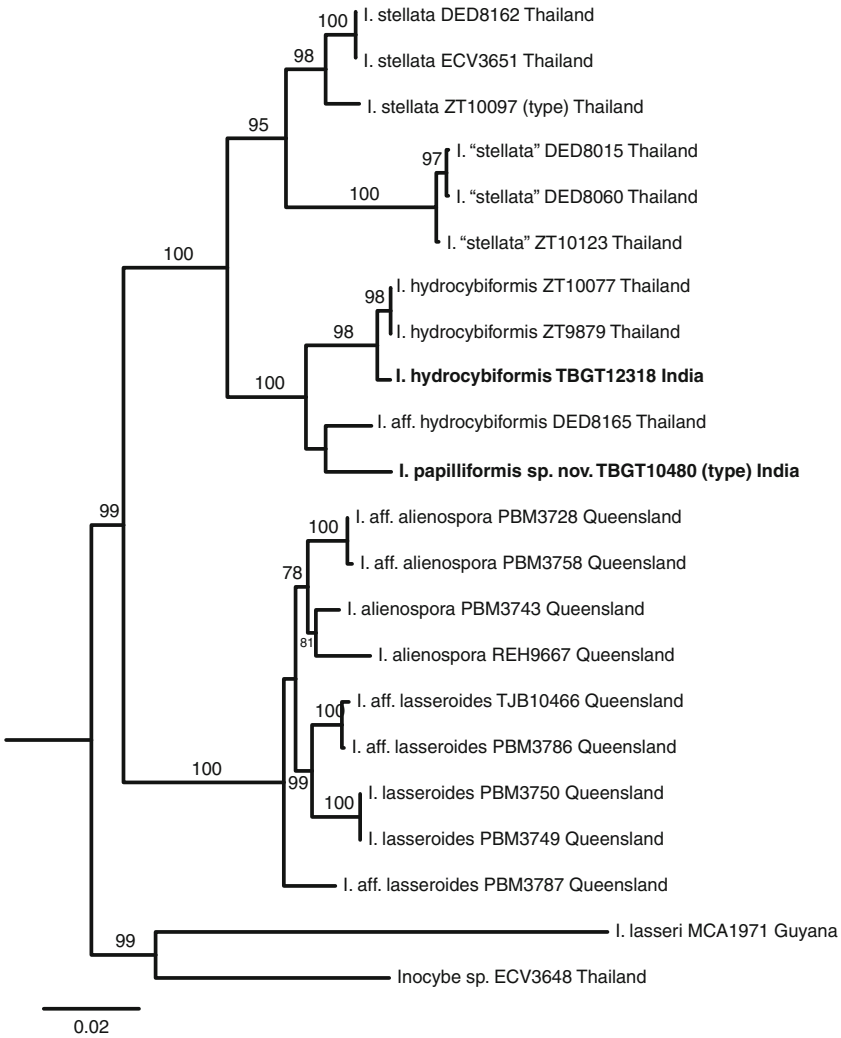

Fig. 3 ML tree showing phylogenetic placement of Indian *I. papilliformis* sp. nov. and *I. hydrocybiformis* (in *bold*). Numbers above and below branches indicate bootstrap support >70 %. The data set includes three gene regions (ITS, nLSU, *rpb2*) and 2828 nucleotide sites, of which 2808 were used in the phylogenetic analysis. *Inocybe lasseri* and *Inocybe* sp. ECV3648 were used for rooting purposes

appears to be sister to the *I. calospora* group, but this result is weakly supported (Horak et al. 2015). Thus, we consider the placement of *I. brevisquamulosa* and *I. parvisquamulosa* as incertae sedis within the *Inocybe* clade.

Inocybe parvisquamulosa has also been recorded from Thailand based on high (99 %) ITS similarity to a sequence (AB854670) produced from basidiomes sampled under *Dipterocarpus alatus* after a GenBank BLASTn search.

Inocybe pileosulcata E. Horak, Matheny & Desjardin, *Phytotaxa* 230: 227. 2015. Figs. 5 and 16f

Pileus 16–35 mm wide, convex, plano-convex to applanate, often uplifted in old ones, rarely with a broad obtuse umbo; surface dark brown to brownish grey (6F7–8) at centre and brown (6E4–5) elsewhere, smooth at centre, fibrillose-striate, rimose towards margin, splitting like the spokes of a wheel exposing the yellowish white (4A2) context below, dry; margin straight, entire to incised. Lamellae adnexed, yellowish white, reddish blonde, dark blonde or café-au-lait (4A2, 5C4, 5D4, 6D3), subdistant with lamellulae of different lengths; edges concolourous with the sides, entire. Stipe 23–44 × 2–4 mm, central, cylindric, solid, slightly curved, narrowly tapering up from a slightly broad marginate base; pale orange to orange white (5A2–3), becoming darker on handling; surface pruinose throughout; veil none. Context white, thin, up to 2 mm thick, soft. Odor none.

Basidiospores 9.5–11(12) × 8–9.5(10) μm, avL = 10.4, avW = 8.9, Q = 1.08–1.36, avQ = 1.16, subglobose, stellate, with more than 11 conspicuous obtuse knobs, yellowish brown. Basidia 25–41 × 9–12 μm, clavate, 4-spored. Lamella edge crowded with paracystidia intermingled with basidia and metuloids. Paracystidia 15–27 × 7–12 μm, clavate, thin-walled, hyaline. Metuloids abundant on both sides and edges of lamellae, 45–70 × 16–23 μm, ventricose fusoid, thick-walled, yellowish brown with crystals at apices. Hymenophoral trama regular, hyphae 3–13 μm wide, at times inflated to 24 μm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous, well developed 2–4 cells thick. Pileal tramal hyphae 18–34 μm wide, inflated, thin-walled, hyaline. Pileipellis a cutis of radially arranged hyphae 5–12 μm wide, incrusted with yellowish brown contents. Stipitipellis a cutis

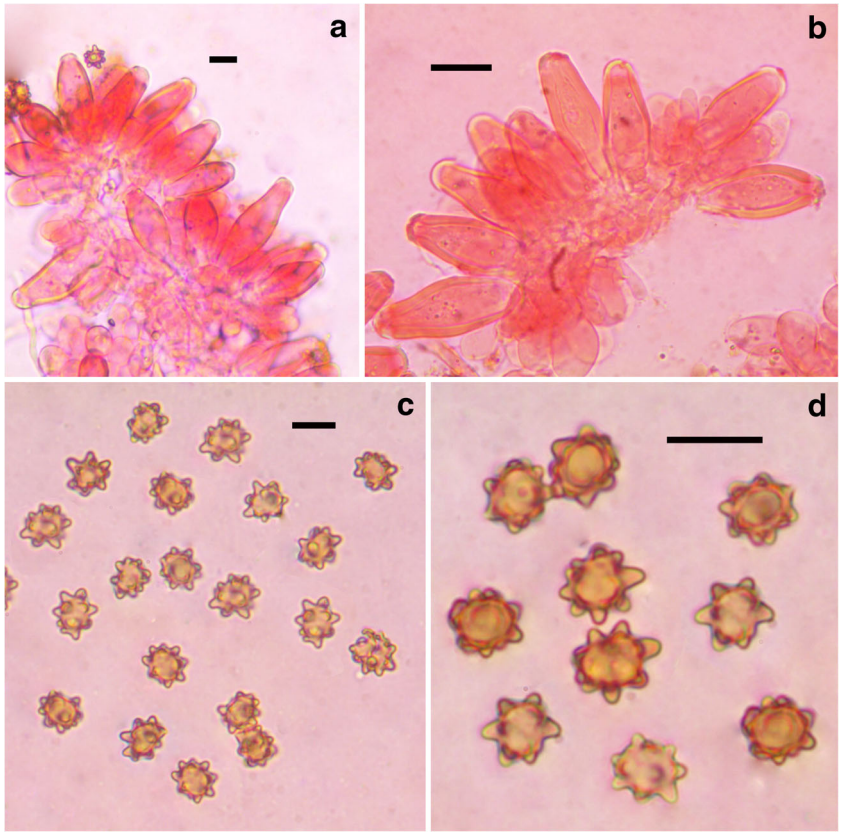

Fig. 4 *Inocybe parvisquamulosa* (TENN070305). **a**, **b**. hymenial cystidia. **c**, **d**. spores. Scale bars = 10 μm

of parallel hyphae, these incrusted 3–10 μm wide, with pale yellowish brown contents. Caulocystidia 54–63 × 17–26 μm, ventricose fusoid, thick-walled, yellowish with crystals at apices, abundant, present throughout the stipe, but more frequent on the upper part. Cauloparacystidia 15–22 × 9–14 μm, clavate, thin-walled, crowded at the base of the metuloid caulocystidia. Clamp connections and oleiferous hyphae present.

Habit and habitat: Scattered on riverine sandy soil under *Hopea parviflora* (Dipterocarpaceae).

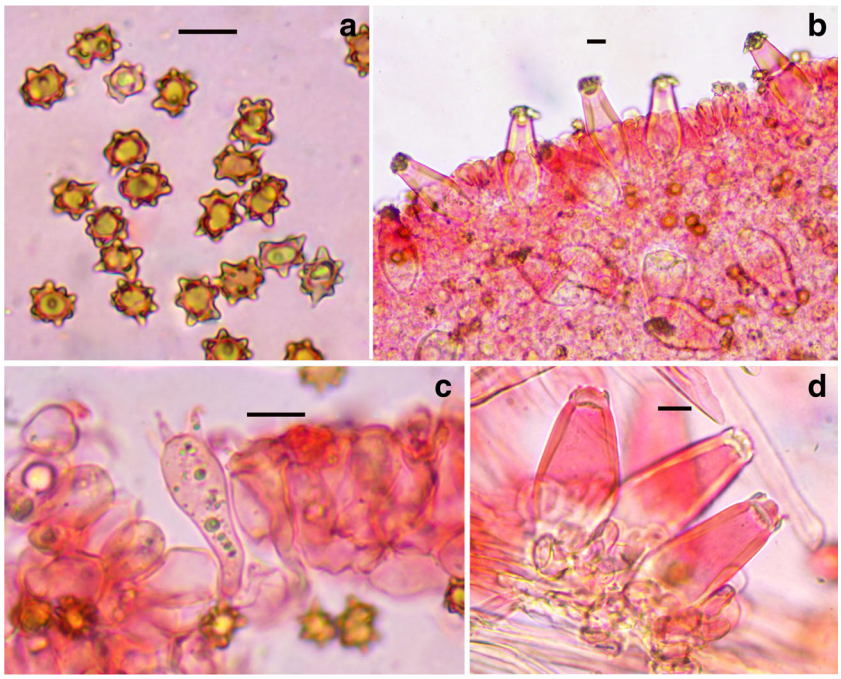

Fig. 5 *Inocybe pileosulcata* (TENN070306). **a** spores **b** hymenial cystidia. **c** basidium. **d** caulocystidia. Scale bars = 10 μm

Specimens examined: India, Kerala State, Wayanad District, Ponkuzhy, 7 Nov 2007, TBGT10742 (TENN070306) (GenBank accession no. KP308810-ITS, KP170979-nLSU, KM406218-*rpb2*); 8 Nov 2007, TBGT10754. Thailand. Chiang Mai Province, Highway 1095 at 22 km marker, 750 m elev., on soil in tropical submontane forest dominated by *Dipterocarpus*, 11 Jun 2006, DED8058 (holotype).

Discussion: *Inocybe pileosulcata* is best characterized by the combination of brown splitting fibrillose striate pileus, marginate stipe base, subglobose stellate spores, abundant caulocystidia, and association with Dipterocarpaceae in India and Thailand. DNA sequences (ITS, nLSU, *rpb2*; Data not shown) of Indian material are virtually identical to the type (DED8058, SFSU) and other collections of *I. pileosulcata* described from Thailand (Horak et al. 2015), where it occurs in lowland and montane tropical forests dominated by Dipterocarpaceae. *Inocybe miyiensis* T. Bau & Y.G. Fan (Fan and Bau 2014), a recently described species from subtropical China differs by its straw yellow pileus, 2- spored basidia and its apparent association with *Quercus*. The species is allied phylogenetically with *I. asterospora* Quél. group (Inocybe clade) and most closely related to two Australasian species, *I. vagata* Matheny & Bougher and *I. nobilissima* Matheny & Bougher, and *I. insignis* A.H. Sm. from North America (Matheny and Bougher 2015). *Inocybe pileosulcata* differs most readily from these and other species by geographic location (tropical Southeast Asia) and association with Dipterocarpaceae.

Inocybe rimulosa C.K. Pradeep & Matheny, **sp. nov**. Figs. 6 and 16g

MycoBank: MB 813815

Diagnosis: Pileus smooth, rimose, dark brown at the center, light brown towards the margin. Lamellae without olivaceous tones. Stipe white to cream, becoming brown on handling, not smooth, not scaly. Odor mild. Closely related to the tropical Australian species *Inocybe gracilissima* but differs by the absence of olivaceous tones on the pileus and non-conical pilei when young. Phylogenetic placement: Pseudosperma clade.

Holotype: India, Kerala State, Trivandrum District, JNTBGRI campus, 17 Aug 2009, TENN070307 (GenBank accession no. KP636860-ITS, KP171059-nLSU, KM656098-*rpb2*); isotype TBGT12854

Etymology: *rimulosus*, having small cracks

Pileus 10–35 mm wide, convex when young, becoming plano-convex to plane with a small obtuse umbo; brown or "titian red" (7D6), dark brown (7F8, 7F5, 8F6), or some shade of brown (6D4–5, 7E4–7, 7D5, 7E4) at centre, light brown (6C4–5, 7E5) towards the margin; surface dry, smooth at the center, fibrillose striate near the margin, rimose, often splitting radially to expose the underlying white context; margin incurved when young becoming straight, rarely uplifted, entire to incised. Lamellae adnexed, brownish orange, clay, dark blond, camel, greyish orange (5C3, 5D4–5, 6D4, 5B3), up to 3 mm deep, close with lamellulae of different lengths; edges whitish, entire. Stipe 18–50 × 1–4 mm, central, cylindric, equal, narrowly tapering up from a broad non-marginate base; white, cream, becoming brownish on handling (6C4, 6D4), pruinose throughout, denser at upper part. Context hollow, white, thin, soft. Odor mild, not diagnostic.

Basidiospores 9–13 × 5.5–6.5 μm, avL = 11.2, avW = 6, Q = 1.44–2.28, avQ = 1.84, smooth, ovoid-ellipsoid, elongate ellipsoid, phaseoliform, yellowish brown. Basidia 18–30 × 8.5–10 μm, clavate, 4-spored with contents. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia 18–58 × 10–15 μm, clavate, cylindro-clavate, lageniform, rarely bifid at apex, often with a pedicel, tramal in origin, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular, hyphae 2.5–15 μm(–23) wide, cylindric to inflated, thin-walled, hyaline. Subhymenium pseudoparenchymatous, 2–3 cells thick. Pileal tramal hyphae 4–29 μm wide, inflated, thin-walled, hyaline. Pileipellis a cutis, hyphae 3–11 μm wide, incrusted with brown contents. Stipitipellis a cutis of parallel hyphae, 5–10 μm wide, incrusted, thin-walled, hyaline. Stipitipellis hyphal ends project out as cystidioid elements on the upper part, 22–93 × 7.5–9 μm, cylindro-clavate, thin-walled, hyaline. Clamp-connections present in all tissues.

Habit and habitat: Solitary, scattered, or in groups or in pairs on soil under *Hopea parviflora*, *Vateria indica* (Dipterocarpaceae), *Calophyllum* (Calophyllaceae), and *Myristica* (Myristicaceae) trees.

Additional specimens examined: India, Kerala State, Trivandrum District, JNTBGRI campus, 6 Aug 2009 TBGT12828 (TENN070308) (GenBank accession no. KP636861-ITS, KP171060-nLSU, KM656099-*rpb2*), 6 Aug 2009 TBGT12829; 7 Aug 2009, TBGT12832; 18 Aug 2009, TBGT12861; 19 Aug 2009, TBGT12870; 17 Sep 2009, TBGT12922; 22 Sep 2009, TBGT12931.

Discussion: *Inocybe rimulosa* is a member of the Pseudosperma clade and most closely related to a tropical Australian species, *I. gracilissima* Matheny & Bougher ined., and an undescribed species from eastern North America (Fig. 9). Aside from geographic location and differences in plant associates, *I. rimulosa* differs from these species by its convex to plane pileus (deeply conical when young in *I. gracilissima*) and absence of olivaceous tones.

Other tropical species with affinities to the Pseudosperma clade have yet to be placed phylogenetically and presently lack DNA sequences for comparison. These include *I. littoralis* Pegler and *I. ingae* Pegler (Pegler 1983) described from the neotropics and *I. cutifracta* Petch (Pegler 1986) described from Sri Lanka. *Inocybe littoralis* is characterized by its amber yellow pileus, subreniform basidiospores, clavate

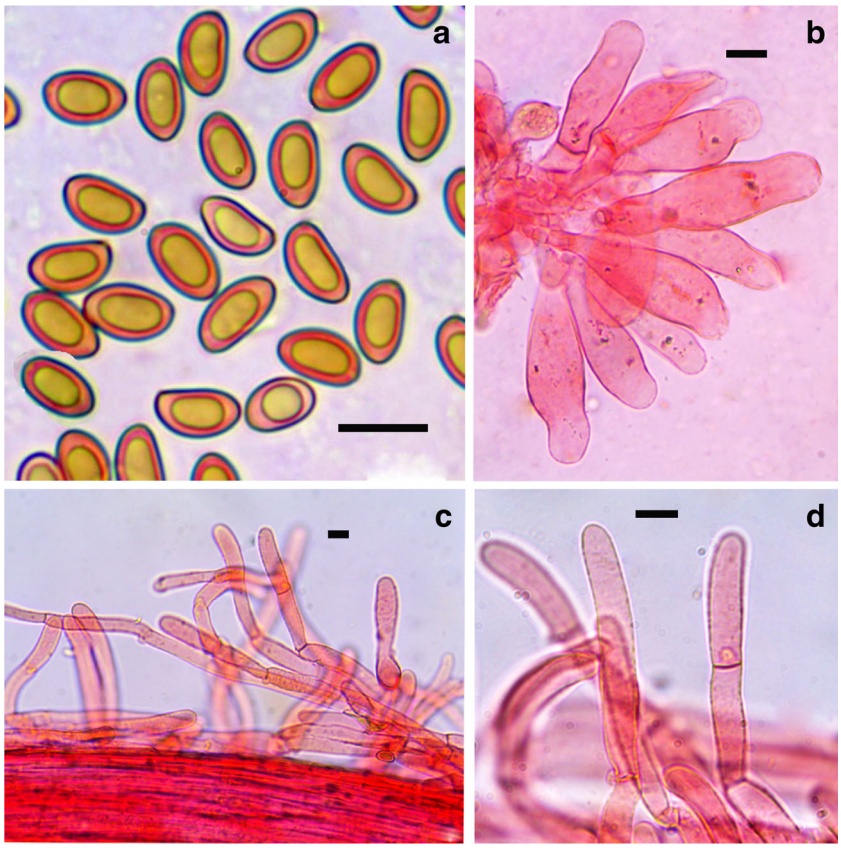

Fig. 6 *Inocybe rimulosa* (TENN070307). **a** spores. **b** cheilocystidia. **c**, **d** caulocystidioid elements. Scale bars = 10 μm

cheilocystidia, and absence of caulocystidia. *Inocybe ingae* is distinguished by its small thin basidiomes, cream silky fibrillose pileus with an acute umbo, white stipe, and inflated clavate cheilocystidia. *Inocybe cutifracta* differs from *I. rimulosa* by its smaller spores and distinct capitate cheilocystidia. None of the Indomalayan and Australasian species documented by Horak (1980) matches the present species. Both *I. littoralis* and *I. ingae* have been reported from India (Farook et al. 2013), but in our opinion the application of neotropical names to paleotropical taxa is highly doubtful. The recently described *Inocybe keralensis* K.P.D. Latha & Manim. (Latha and Manimohan 2015) differs by its yellowish brown, appressed fibrillose pileus, adnate to emarginate lamellae, brown fibrillose stipe, smaller spores, encrusted thick-walled cheilocystidia and a duplex pileipellis. Unfortunately the sequences are not available on GenBank for comparison.

Inocybe alboflavella C.K. Pradeep & Matheny, **sp. nov**. Figs. 7 and 17b, c

MycoBank: MB 813816

Diagnosis: Differs from similar tropical and neotropical species of the Pseudosperma clade by small yellowish white basidiomes, large variable spores, cylindro-clavate and septate cheilocystidia, lack of pleurocystidia and caulocystidia, and mycorrhizal host. Phylogenetic placement: Pseudosperma clade.

Holotype: India, Kerala State, TBGRI campus, 3 Jul 2008, TENN070309 (GenBank accession no. KP636859-ITS, KP171058-nLSU, KM656097-*rpb2*); isotype TBGT11280.

Etymology: *albus* (white), *flavellus* (pale yellow), in reference to the yellowish white pileus.

Pileus 7–20 mm wide, convex becoming plane with a small obtuse umbo, rarely without umbo; white, cream, yellowish white, putty (2A2, 4A2–3, 4B2, 5C4–5), becoming pale brown in old specimens; surface dry, not scaly, but covered with white silky fibrils over the center, elsewhere silky fibrillose striate, splitting radially to expose the underlying white context below, becoming rimose towards margin; margin straight, entire to incised, rarely appendiculate when young. Lamellae adnexed, cream becoming dark blonde (4A3, 5C4, 5D4), narrow, up to 2 mm deep, close to subcrowded with lamellulae of different lengths; edges whitish, fimbriate. Stipe 10–35 × 1–3 mm, central, cylindric, solid, equal, slightly tapering up from a slightly swollen base, non-marginate; cream, flocculose-fibrillose throughout, more so on the upper half, squamules vanishing on handling. Context white, thin, soft. Odor mild.

Basidiospores (7–)8–12(13) × 5–7 μm, avL = 10.2, avW = 5.9, Q = 1.35–2.06, avQ = 1.71, smooth, highly variable in shape and size, within a single specimen, ellipsoid to elongate, phaseoliform, thick-walled, pale yellowish (in KOH), rarely with an apical thinning. Basidia 23–40.1 × 9–

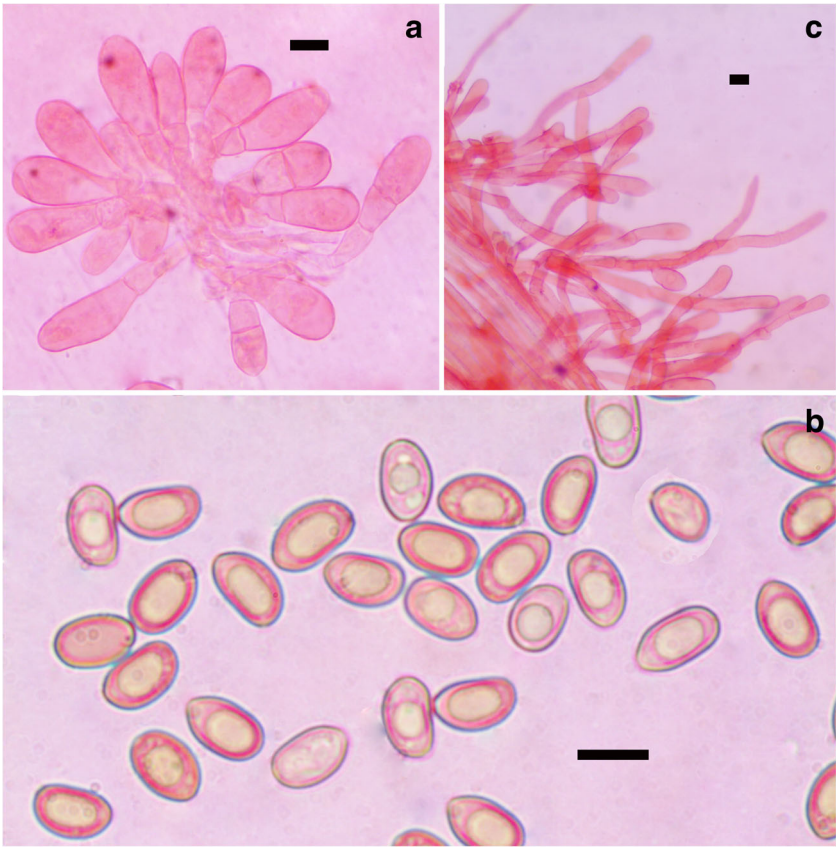

Fig. 7 *Inocybe alboflavella* (TENN070309). **a** cheilocystidia. **b** spores. **c** caulocystidia. Scale bars = 10 μm

13 μm, clavate, 4-spored, rarely 1, 2-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia 12–59 × 7–20 μm, clavate, cylindro-clavate, mostly septate (1, 2), thin-walled, hyaline, rarely with oleaginous contents, tramal in origin. Pleurocystidia absent. Hymenophoral trama regular, hyphae 3–33 μm wide, cylindric to inflated, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal tramal hyphae thin-walled, hyaline, 4.5–32 μm wide, inflated. Pileipellis an epicutis of radially arranged hyphae, these 4–14 μm wide, incrusted with yellowish contents. Stipitipellis a cutis of parallel hyphae 4–13 μm wide, incrusted, with pale yellowish contents. Caulocystidia 13–63 × 5–16 μm, cylindro-clavate to clavate, thin-walled, incrusted, hyaline, moderately abundant. Clamp connections and oleiferous hyphae present.

Habit and habitat: Solitary or scattered on soil under *Vitex altissima* (Lamiaceae) and nearby dipterocarps.

Additional specimens examined: India, Kerala State, TBGRI campus, 11 Nov 2007, TBGT12237; 24 Jun 2008, TBGT11225; 3 Jul 2008, TBGT11290; 4 Aug 2010, TBGT13412; 26 Oct 2010, TBGT13522; 28 Jun 2011, TBGT13671; 22 Sep 2011, TBGT13822; 7 Nov 2013, TBGT14864; 21 Nov 2013, TBGT14886.

Discussion: *Inocybe alboflavella* is placed phylogenetically in the Pseudosperma clade, where it occupies an isolated position, most closely related with strong support to an unidentified species from *Castanopsis* forest in Papua New Guinea (Fig. 8). Morphological data support placement in the Pseudosperma clade as *I. alboflavella* features traits typical of species in this group: the rimose pileus, coarsely fibrillose stipe covering, unchanging colors of the context, smooth spores, and absence of pleurocystidia. Some of the unique features of *I. alboflavella* include the white silky fibrils over the disc and yellowish pileal margin, absence of any odor, and potential association with trees of the Lamiaceae and/or Dipterocarpaceae.

Allied species from other tropical areas include *I. littoralis* Pegler and *I. ingae* Pegler (Pegler 1983). The former differs from *I. alboflavella* by its slightly larger basidiomes with an amber yellow pileus, ellipsoid to subreniform spores, absence of caulocystidia, and association with *Coccoloba* (Polygonaceae) in the neotropics. *Inocybe ingae* is another neotropical species characterized by its acutely umbonate

Fig. 8 ML tree showing phylogenetic placement of Indian *I. rimulosa* and *I. alboflavella* (in *bold*). Numbers above and below branches indicate bootstrap support >70 %. The data set includes two gene regions (nLSU, *rpb2*) and 2150 nucleotide sites, all of which were included in the phylogenetic analysis. The tree was rooted with Australian taxa of the *Inosperma* clade (*I. viridipes* ined.) and *Mallocybe* clade (*I. isabellina* ined., *I. sabulosa* ined., and *I. subflavospora* ined). The outgroups are pruned from the tree figure ▶


Inocybe sp. TR183-05 Papua New Guinea
Inocybe sp.TR75-05 Papua New Guinea
I. melliolens PAM05052303 France
I. rimosa EL7505 Sweden
I. sororia Kuoljok0512 Sweden?
I. sororia JRH661 Wyoming, USA
I. aff. rimosa MCA859 Virginia, USA
I. cf. rimosa PBM3974 Tennessee, USA
I. fastigiata FO46800 Germany
I. cf. microfastigiata EL113-06 Sweden
I. bulbosissima EL6605 Norway
Inocybe sp. MTS2494 California, USA
I. aestiva BK18089706 (type) Utah, USA
I. niveivelata PBM2337 Washington, USA
Inocybe sp. DV04132011 California, USA
Inocybe sp. TR104-05 Papua New Guinea
Inocybe sp. TR133-05 Papua New Guinea
Inocybe sp. PBM3766 Queensland
Inocybe sp. PL42609 Queensland
Inocybe sp. TR138-05 Papua New Guinea
I. "fissurata" PBM2206 Western Australia
I. "fissurata" PBM2195 Western Australia
I. umbrinella JV13699 Finland
I. "brunneicothurnata" PBM1889 Texas, USA
I. aurora AU10245 (type) Nova Scotia
I. obsoleta EL17-04 Sweden
I. perlata EL74-04 Sweden
Inocybe sp. TR49-05 Papua New Guinea
I. "gracilissima" PBM3735 Queensland
I. "gracilissima" PBM3738 Queensland
I. "gracilissima" JAC2809 Northern Territory
I. "gracilissima" NLB937 Queensland
Inocybe sp. PBM2321 Virginia, USA
I. rimulosa TBGT12854 (type) India
I. rimulosa TBGT12828 India
Inocybe sp. DJL-SJ14 U.S. Virgin Islands
I. flavella EL137-05 Sweden
I. xanthocephala PAM00100606 France
Inocybe sp. TM02-130 Ontario, Canada
I. squamata PAM05052301 France
I. hygrophorus EL97-06 Sweden
I. occidentalis BK27089703 (type) Utah, USA
I. cercocarpi BK2006986 Utah, USA
I. spuria SJ92017(type) Sweden
I. dulcamaroides EL112-06 Sweden
I. arenicola RC-GB99-014 France
I. mimica EBJ961997 Sweden
I. cf. rimosa PBM1938 Vermont, USA
I. breviterincarnata BK28080407 Utah, USA
Inocybe sp. MCA562 Japan
I. aff. "araneosa" PL58410 Queensland
I. "araneosa" PBM3755 Queensland
I. "illudens" I106 Tasmania
I. alboflavella TBGT11280 (type) India
Inocybe sp. TR194-02 Papua New Guinea
Inocybe sp. I116 Tasmania
Inocybe sp. PBM3751 Queensland
I. lepidotella MCA1881 (type) Guyana
I. neglecta DED8063 (type) Thailand
I. "actinocephala" PBM2863 Louisiana, USA
I. "pluviorum" PL23408 Queensland
0.03

and pale ochraceous pileus, smaller spores, absence of caulocystidia, and association with trees of the genus *Inga*.

Inocybe carnosibulbosa C.K. Pradeep & Matheny **sp. nov**. Figs. 9 and 17d, f

MycoBank: MB 813817

Diagnosis: Distinct from all species in the Inosperma clade by large, fleshy, tricholomatoid basidiomes, bicolorous pileus when mature, stipe with a large pronounced basal bulb, subglobose or broadly ellipsoid basidiospores, absence of pleurocystidia, and septate cheilocystidia with long narrow neck reaching lengths >100 μm. Phylogenetic placement: Inosperma clade, "Old World Tropical clade 2".

Holotype: India, Kerala State, Trivandrum District, JNTBGRI campus, 25 Sep 2008, TENN070310 (GenBank accession no. KT329448-ITS, KT329454-nLSU, KT329443-*rpb2*); isotype TBGT12047

Etymology: *carnosus* (fleshy), *bulbosus* (bulbous), in reference to the large fleshy basidiomes with a pronounced bulbous stipe base

Pileus 45–105 mm wide, convex when young, becoming plano-convex to applanate with a broad obtuse umbo or slightly depressed at centre become slightly uplifted with age; uniformly yellowish white to cream (3A2, 4A3) when young, becoming more brownish over the disc (6C3–4, 6D4, 6E5–6) and cream to yellowish white (4A2–3) elsewhere, thus becoming bicolorous; surface dry, appressed fibrillose striate except at the disc that is smooth and unbroken, becoming squamulose when dry or rimose, often splitting radially exposing the underlying white context; margin incurved when young becoming straight, entire to incised. Lamellae adnexed, white to yellowish white when young, becoming brownish orange (5C3–4) with age, up to 14 mm deep, crowded, lamellulae of different lengths; edges paler, entire. Stipe 50–120 × 7–17 mm, central, cylindric, with or without a marginate bulbous base tapering abruptly below; white to yellowish white (5A2–3), become brownish on handling (6C4, 6D4, 6F4), fibrillose striate. Context solid, white, soft. Odor mild. Basidiomes thick, fleshy, tricholomatoid.

Basidiospores (5.5–)6–8 × 5–6.5 μm, avL = 7.1, avW = 5.6, Q = 1.07–1.42 avQ = 1.26, smooth, subglobose to broadly ellipsoid, rarely phaseoliform, yellowish brown, thick-walled. Basidia 27–31 × 7–8 μm, clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with tufts of cheilocystidia. Cheilocystidia 29–140 × 6–13 μm, clavate, vesiculose, lageniform with a long narrow neck, multi-septate, tramal in origin, thin-walled, hyaline. Hymenophoral trama regular composed of short to medium, thin-walled, hyaline hyphae, 5.5–14 μm wide. Subhymenium pseudoparenchymatous, 2–3 cells thick. Pileal trama composed of loosely arranged hyphae 2.5–12.5(–22) μm wide, inflated, thin-walled, hyaline. Pileipellis a cutis, interrupted at places, composed of parallel hyphae 3–5 μm wide, incrusted, with yellowish brown contents. Stipitipellis a cutis of parallel hyphae, these 2.5–5 μm wide, incrusted, thin-walled, hyaline. Caulocystidia absent. Clamp connections present in all tissues.

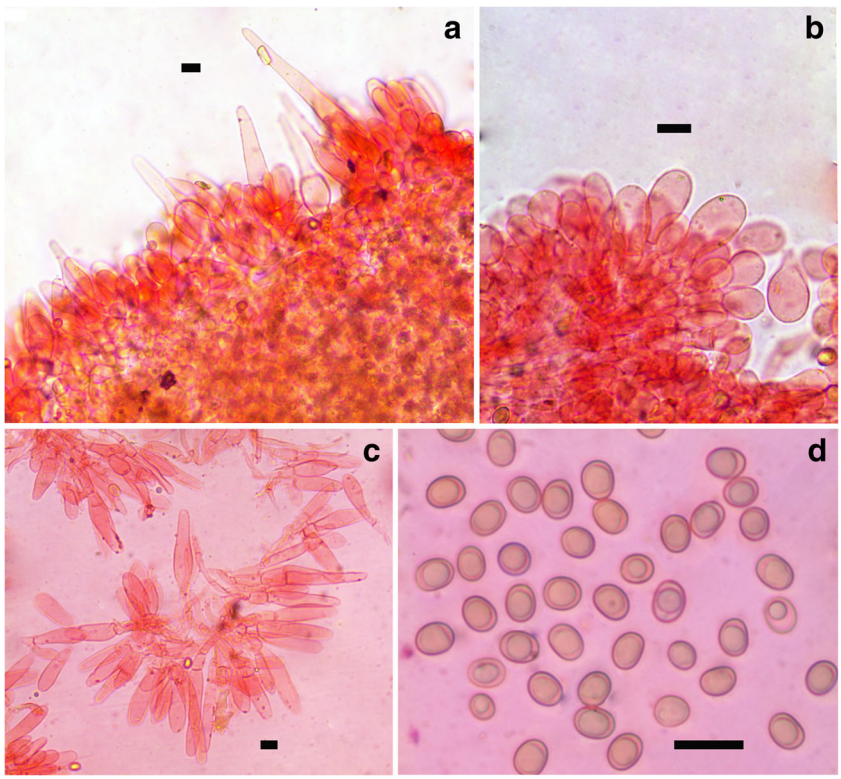

Fig. 9 *Inocybe carnosibulbosa* (TENN070310). **a**–**c** cheilocystidia. **d** spores. Scale bars = 10 μm

Habit and habitat: Scattered, in groups or in pairs on forest soil under *Hopea parviflora* (Dipterocarpaceae) and *Xanthophyllum* (Polygalaceae) trees.

Additional specimens examined: India, Kerala State, Trivandrum District, TBGRI campus, 20 Nov 2008, TBGT12276; 14 Oct 2009, TBGT12976; 23 Oct 2009, TBGT13011; 16 Nov 2011, TBGT13898; 17 Nov 2011, TBGT13906; 18 Nov 2011, TBGT13909; Trivandrum District, Ex-Service Colony, 20 Jul 2015, TBGT15769.

Discussion: *Inocybe carnosibulbosa* is distinguished by its large fleshy tricholomatoid basidiomes, cream to yellowish white pileus with a brownish disc, the stipe often with a marginate bulbous base, small subglobose to broadly ellipsoid smooth spores, presence of clavate to vesiculose septate cheilocystidia often with a long narrow neck, absence of pleurocystidia and caulocystidia, and association with *Xanthophyllum* and *Hopea* trees.

In gross morphology this can be compared to *Inocybe perlata* (Cooke) Sacc. (Vauras and Huhtinen 1986), *I. umbrina* Massee (Horak 1980) and *I. rimosa* (Bull.: Fr.) Kumm. (Kuyper 1986). All these species can be separated among other things by their larger spores, shorter clavate cheilocystidia, and different plant associates.

BLASTn results of nLSU and *rpb2* sequences from TBGT12047 suggest this species is most closely related to but distinct from other species in the Inosperma clade. Indeed, *I. carnosibulbosa* shares its nearest phylogenetic affinities with several unclarified species from India, Thailand, and Papua New Guinea in "Old World tropical clade 2" recovered by Kropp et al. (2013) and shown in Fig. 15.

Specimens of *I. carnosibulbosa* (TBGT15769) were made at a local site after reports of human poisoning and the deaths of a cat and chicken after consumption of this species. The affected people were admitted to hospital and fully recovered.

Inocybe albonitens C.K. Pradeep & Matheny, **sp. nov**. Figs. 10 and 17e, g

MycoBank: MB 813818

Diagnosis: Most similar to but distinct from *Inocybe alboviscida* by the larger broadly ellipsoid to ellipsoid nodulose basidiospores, dipterocarp association, and occurrence in lowland tropical habitats.

Holotype: India, Kerala State, Wayanad District, Muthanga, 24 Sep 2008, TENN070311 (GenBank accession no. KT329449-ITS, KT329455-nLSU); isotype TBGT11987.

Etymology: *albus* (white), *nitens* (shining, greasy), in reference to the sticky white pileus

Pileus 8–30 mm wide, convex, plano-convex to uplifted with a small obtuse umbo; chalky white when young, which is smooth and glabrous, not striate, later becoming dull white to brownish orange (5C3) to slightly darker in old specimens; surface sticky when wet, sulcate-striate to plicate in dry weather; margin straight, entire, becoming rimose with age. Lamellae adnexed, off-white to birch gray (5C2) to brownish orange (6C3), up to 2 mm deep, crowded with lamellulae of different lengths; edges concolourous with the sides, entire in appearance. Stipe 15–46 × 1–4 mm, central, cylindric, tapering narrowly from a broad base; often with a rim at the base; surface white, smooth and glabrous but pruinose under lens. Context white, thin. Odor mildly spermatic.

Basidiospores 7.5–11 × 6–9.5 μm, avL = 9.3, avW = 7.4, Q = 1.05–1.62, avQ = 1.26, nodulose with 9–11 moderate-sized conical nodules about a broadly ellipsoid to ellipsoid (subglobose) outline, yellowish brown. Basidia 26–33 × 10–12 μm, clavate, 4-sterigmate, hyaline. Lamella edge heteromorphous. Cystidia present on both sides and edges of lamellae. Cystidia 47–82 × 19–28 μm, lageniform to subfusoid, mostly without a pedicel or rarely with a short pedicel, thick-walled, walls mostly 4–7 μm thick, hyaline with crystalline apex. Hymenophoral trama regular, hyphae 2–21 μm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama of interwoven hyphae, these 2.5–21 μm wide, often inflated, thin-walled, hyaline. Pileipellis an interrupted ixocutis of gelatinized hyphae, 2–4 μm wide, thin-walled, hyaline. Stipe trama composed of parallel hyphae, these 4–18 μm wide, inflated, thin-walled, hyaline. Stipitipellis composed of parallel hyphae 2.5–7 μm wide, thin-walled with pale yellowish contents. Caulocystidia 52–88 × 20–34 μm, similar to hymenial cystidia, present throughout the stipe, thick-walled; intermingled with thin-walled paracystidia, these 12–32 × 5–10 μm, in groups at the base of caulocystidia, hyaline. Clamp connections present in all tissues.

Habit and habitat: Scattered on riverbanks in sandy soil under *Hopea parviflora*.

Additional specimens examined: India, Kerala state, Wayanad District, Muthanga, 15 Aug 2007, TBGT10472; 8 Nov 2007, TBGT10745; 16 Jul 2008, TBGT11405.

Discussion: *Inocybe alboviscida* Horak (Horak 1979), originally described from Papua New Guinea with *Anisoptera* (Dipterocarpaceae) and *Intsia* (Fabaceae) plant associates, most closely matches the Indian materials described here in many macro- and microscopic features. However, the Indian species is distinguished from *I. alboviscida* by its larger spores with a broadly ellipsoid to ellipsoid outline and different plant associates in low-elevation tropical habitats. *Inocybe conicoalba* E. Horak (Horak 1980) is similar to *I. albonitens* as well but differs markedly by its conic to obtuse papillate pileus, presence of persistent veil remnants on the stipe, and smooth amygdaliform to sublimoniform spores. *Inocybe olivaceonigra* f. *volvata* (E. Horak) Garrido appears similar to *I. albonitens* but differs principally by the dry pileus with an olive-black disc, smaller spores(8.0–9.5 × 5.5–6.5 μm), and association with *Castanopsis* in Papua New Guinea. The non-volvate form of *I. olivaceonigra* has recently been reported from *Castanopsis* forests in Yunnan Province, China (Fan

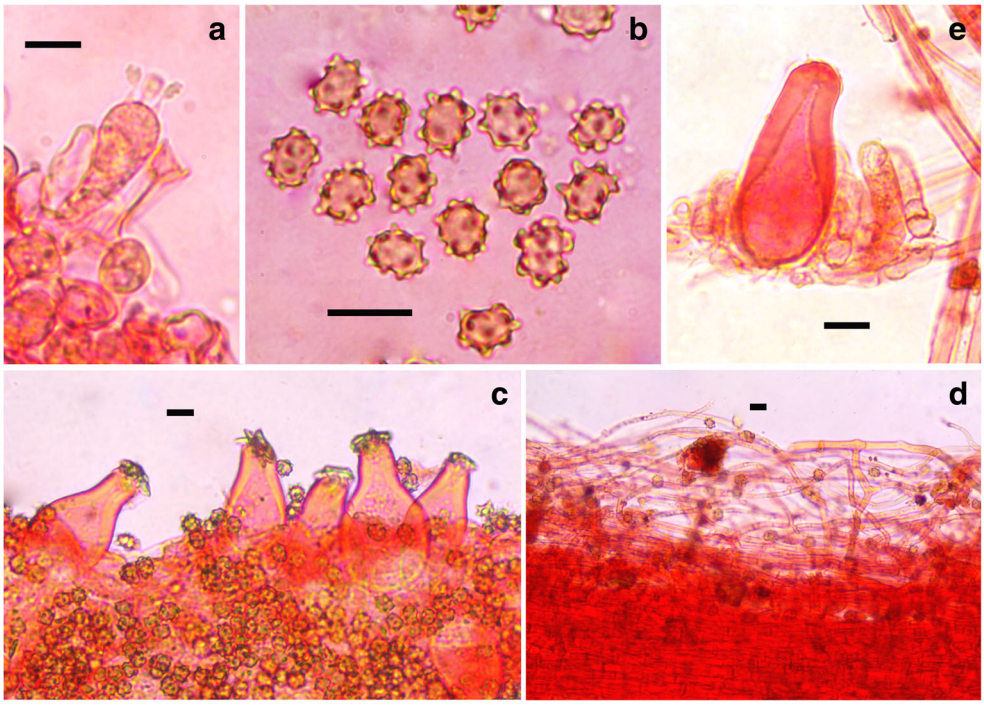

Fig. 10 *Inocybe albonitens* (TENN070311). **a** basidia. **b** spores. **c** hymenial cystidia. **d** pileipellis. **e** caulocystidia. Scale bars = 10 μm

and Bau 2013). Other than an obvious alliance with the Inocybe clade, LSU and ITS BLASTn results are equivocal with respect to phylogenetic affinities and reveal no close matches >98 % and >90 %, respectively (the latter with low query coverage). *Inocybe wayanadensis* K.P.D. Latha & Manim. (Latha and Manimohan 2015) though closely related, differs by its small basidiomata with rimulose pileus, marginate, bulbous stipe and pileipellis an ixotrichoderm. GenBank details are unavailable for this species for molecular comparison.

Inocybe flavosquamulosa C.K. Pradeep & Matheny, **sp. nov**. Figs. 11 and 17a

MycoBank: MB 813819

Diagnosis: Differs from the *Inocybe viscata* by its smaller basidiomes, dry pileus with yellowish scales around the umbo, smaller spores, and epicutis of non-gelatinized hyphae. Phylogenetic placement: Inocybe clade (*Inocybe viscata* group).

Holotype: India, Kerala State, Wayanad District, Ponkuzhy, 8 Nov 2007, TENN070312 (GenBank accession no. KT329450-ITS, KT329456-nLSU); isotype TBGT10743.

Etymology: *flavus* (yellow), *squamulosus* (minutely scaly)

Pileus 17–30 mm wide, convex to plano-convex with a broad obtuse umbo; brown to light brown (6E5, 6D4) and pompeian yellow (5C6, 5B4, 5C4, 5D4–5,) elsewhere; surface dry, smooth at the disc, with concolorous (pompeian yellow) appressed to recurved squamules around the umbo, fibrillose-rimose elsewhere; margin straight, entire. Lamellae adnexed, snuff brown (5D5, 6B2, 6C3, 6F4), up to 4 mm deep, crowded with lamellulae of different lengths; edges concolourous with the faces, entire. Stipe 20–45 × 3–5 mm, central, cylindric, curved, narrowly tapering up from a broad base or marginate bulb (this sometimes absent); clay to light brown (5C3, 5D4–5, 6D4); surface fibrillose-striate, entirely pruinose, veil absent. Context stuffed, white, soft. Odor mild to spermatic.

Basidiospores 6.5–8(–9.6) × 4.5–5.5 um, avL = 6.9, avW = 5, Q = 1.14–1.66, avQ. = 1.39, yellowish brown with brown wall (in KOH) with low nodules (knobs not prominent). Basidia 24–29 × 7–8 um, clavate, 4-spored, hyaline or with yellowish brown contents. Lamella edge heteromorphous with metuloidal cystidia and thin-walled paracystidia. Paracystidia difficult to revive in dried specimens, 13–29 × 7–11 μm, clavate, thin-walled, hyaline. Pleurocystidia 31–69 × 13–21 μm, fusoid-ventricose, thick-walled, with apical crystals, abundant. Hymenophoral trama regular, hyphae 8–19 μm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama of interwoven hyphae, these 8–17 μm wide, inflated, thin-walled, hyaline. Pileipellis an epicutis of radially arranged hyphae, these 6–10 μm wide, incrusted with yellowish brown contents. Stipitipellis a cutis of parallel incrusted hyphae 3–6 μm wide, hyaline. Caulocystidia 39–89 × 9–17 μm, narrowly lageniform, cylindrical with a broad base, yellowish brown, with apical crystalline deposits, in tufts, more frequent in the upper part; cauloparacystidia 9–26 × 4–13 μm, clavate, cylindro-clavate, thin walled, hyaline. Clamp connections abundant.

Habit and habitat: Solitary, scattered or in groups on riverine sandy soil under *Hopea parviflora* (Dipterocarpaceae).

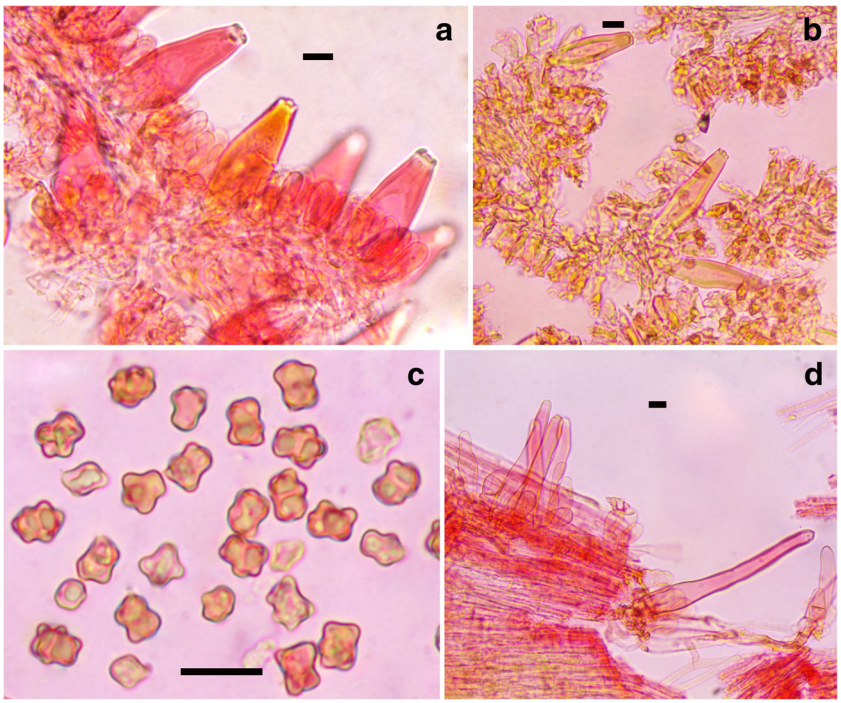

Fig. 11 *Inocybe flavosquamulosa* (TENN070312). **a** cheilocystidia with paracystidia. **b** pleurocystidia. **c** spores. **d** caulocystidia with paracystidia. Scale bars = 10 μm

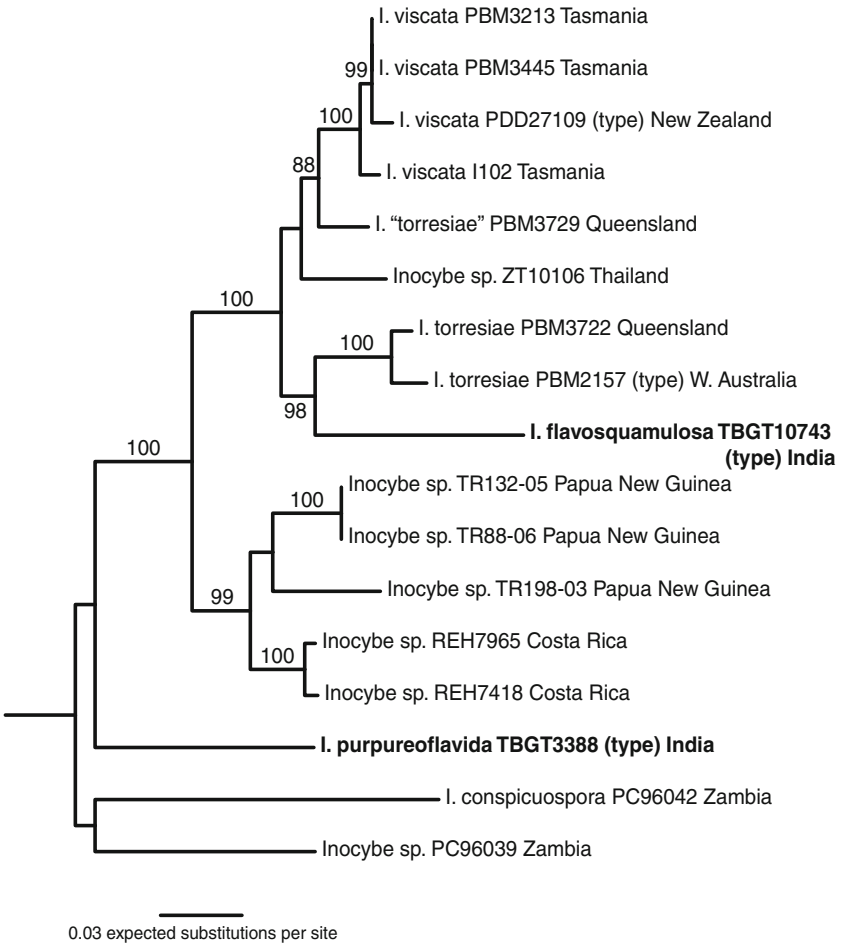

Fig. 12 ML tree showing phylogenetic placement of Indian *I. flavosquamulosa* and *I. purpureoflavida* (in *bold*). Numbers above and below branches indicate bootstrap support >70 %. The data set includes three gene regions (ITS, nLSU, *rpb2*) and 2737 included nucleotide sites. The tree was rooted with *I. conspicuospora* and *Inocybe* sp. PC96039 based on Matheny et al. (2009)

Additional Specimens examined: India, Kerala State, Wayanad District, Ponkuzhy, 15 Aug 2007, TBGT10469; 12 Aug 2008, TBGT11686; 16 Aug 2008, TBGT 11404; 24 Sep 2008, TBGT12000.

Discussion: *Inocybe flavosquamulosa* is a new species in the *Inocybe viscata* (E. Horak) Garrido group (Matheny and Bougher 2015). Based on BLASTn searches of ITS and nLSU sequences, the new Indian species is most closely related to *I. viscata* (E. Horak) Garrido (Horak 1977, Matheny and Bougher 2015) and *I. torresiae* Matheny, Bougher & M.D. Barrett (Bougher et al. 2012). Indeed, our phylogenetic analysis (Fig. 12) supports a close evolutionary relationship between *I. flavosquamulosa* and *I. torresiae* from Queensland and northern Western Australia. *Inocybe viscata* is distinguished by its moderately large basidiomes with a lubricous pileus, large spores, and strongly gelatinized pileipellis. *Inocybe torresiae* is characterized by its gibbous pentagonal to subtrapeziform spores with 7–10 small obtusely and sharply conical nodules and strong sweet citrine-like odor. This latter species is common at tropical and warm temperate latitudes in northern Australia (Matheny and Bougher 2015). Several other species in the *I. viscata* group are undescribed or undetermined (Matheny and Bougher 2015), but, aside from *I. viscata*, all occur in tropical regions (Costa Rica, Papua New Guinea, southeast Asia).

Inocybe purpureoflavida K.B. Vrinda & C.K. Pradeep, *Mycotaxon* 64: 3 (1997). Figures 13 and 17i

Habit and habitat: Solitary, scattered on riverine sandy soil under *Hopea parviflora* (Dipterocarpaceae).

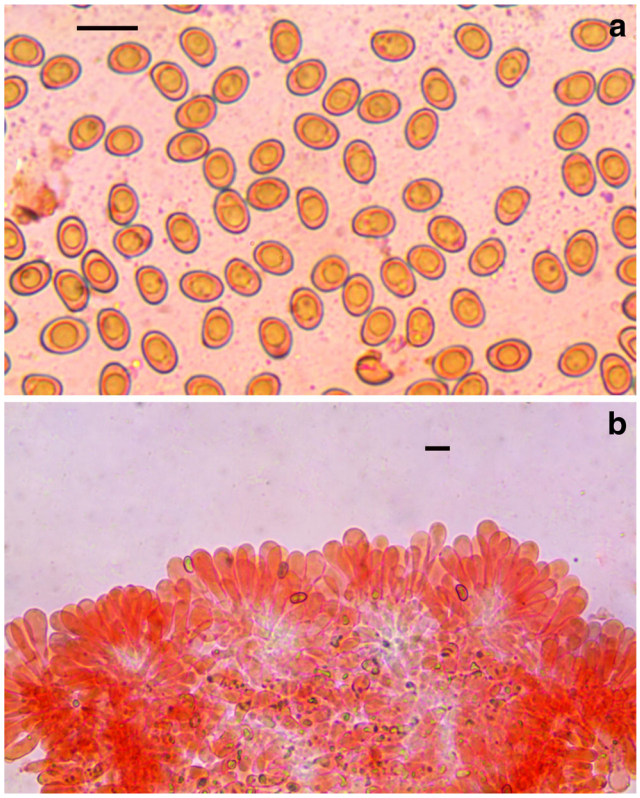

Fig. 14 *Inocybe virosa* (TENN070314). **a** spores. **b** cheilocystidia. Scale bars = 10 μm

Specimens examined: India, Kerala State, Trivandrum District, Palode, TBGRI campus, 15 Apr 1996, TBGT2851; ibid., 12 Jul 1996, TBGT3388 (holotype), TENN070313

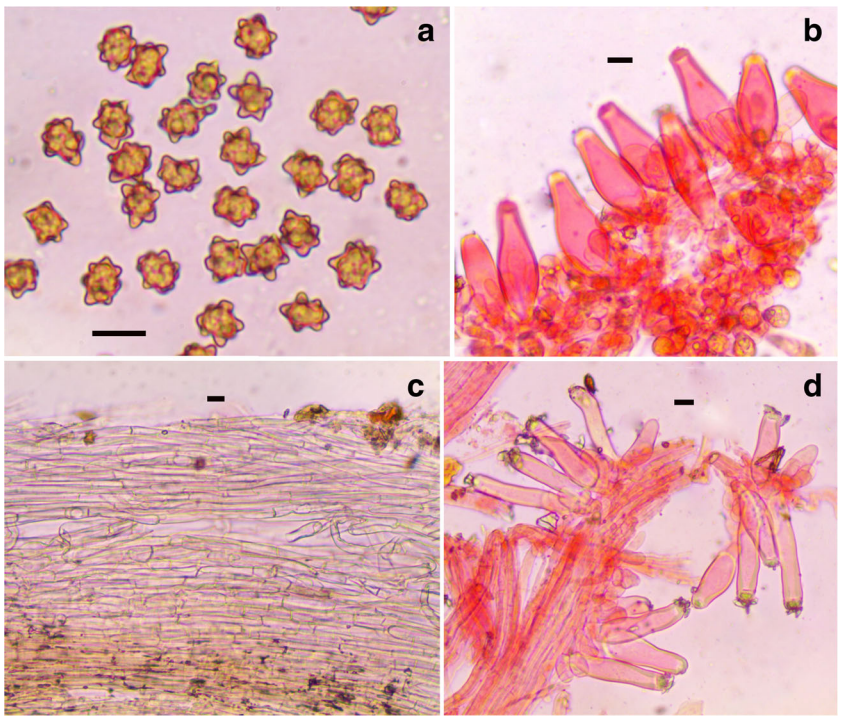

Fig. 13 *Inocybe purpureoflavida* (TENN070313). **a** spores. **b** hymenial cystidia. **c** pileipellis. **d** caulocystidia. Scale bars = 10 μm

(isotype) (GenBank accession no. KT329451-ITS, KT329457-nLSU, KT329445-*rpb2*).

Discussion: For a complete description of this species, see Vrinda et al. (1997a, b). *Inocybe purpureoflavida* is remarkable due to the dark purple glutinous pileus, yellowish white stipe with a purple marginate base, odor of radish, large subglobose to ellipsoid spores with 9–12 prominent nodules, presence of thick-walled metuloidal hymenial cystidia and

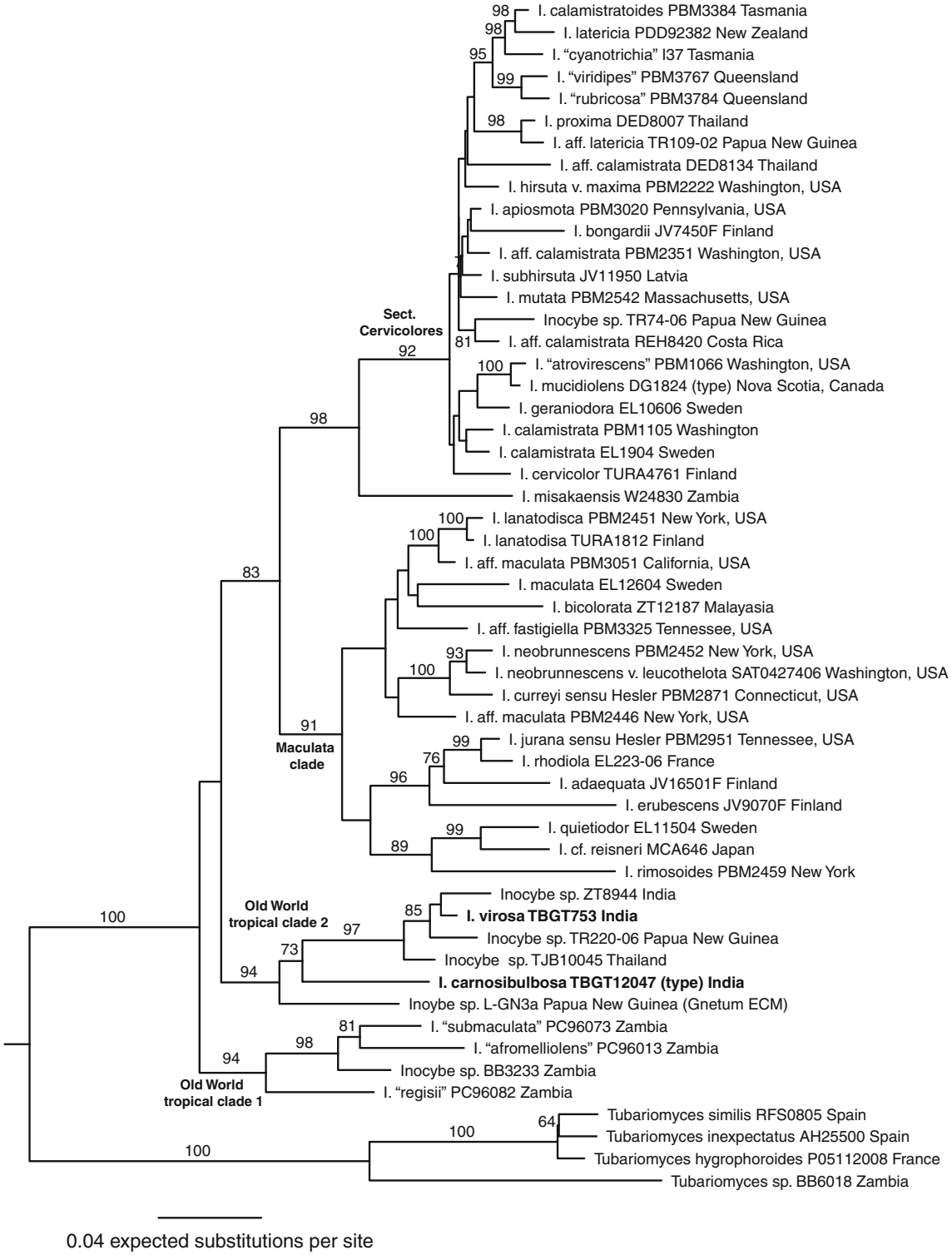

Fig. 15 ML tree showing phylogenetic placement of Indian *I. virosa* and *I. carnosibulbosa* (in *bold*). Numbers above and below branches indicate bootstrap support >70 %. The data set includes two gene regions (nLSU, *rpb2*) and 2167 nucleotide sites, all of which were included in the phylogenetic analysis. The tree was rooted with *Tubariomyces* based on Matheny et al. (2012b)

caulocystidia, and association with Dipterocarpaceae. BLASTn results of the ITS sequence suggest *I. purpureoflavida* may be distributed in Malaysia as well. The nearest ITS match to the type is a mislabeled "*Russula* sp." sampled from a basidiome in Malaysia (KP071103) with high (97 %) sequence similarity. BLASTn results of nLSU suggest an alliance with *Inocybe viscata* (E. Horak) Garriod and related species. Figure 12 illustrates their phylogenetic relationships. This group is characterized by the presence of numerous tropical lineages sampled from Costa Rica, Thailand, Australia, and Papua New Guinea, many of these undescribed or unclarified. BLASTn results of *rpb2* are inconclusive (90 % similar to many other nodulose-spored species of *Inocybe*), however, *rpb2* sequences of *I. viscata* are lacking. *Inocybe viscata* shares the presence of a glutinous pileus with *I. purpureoflavida*, nodulose basidiospores, and presence of caulocystidia at least to the center of the stipe.

Inocybe virosa K.B Vrinda, C.K. Pradeep, A.V. Joseph & T.K. Abraham ex C.K. Pradeep, KB Vrinda & Matheny, **sp. nov**. Figs. 14 and 17h

MycoBank: MB 813820

Inocybe virosa K.B. Vrinda, C.K. Pradeep, A.V. Joseph & T.K. Abraham, *Mycotaxon* 57: 171. 1996 (invald. Art. 40.7, Melbourne code).

Fig. 16 Habit in situ. **a**, **b** *Inocybe papilliformis* (TENN070303). **c**, **d**. *I. hydrocybiformis* (TENN070304). **e** *I. parvisquamulosa* (TENN070305). **f** *I. pileosulcata* (TENN070306). **g** *I. rimulosa* (TENN070307). Scale bars = 10 mm

Diagnosis: Differs from species in the Inosperma clade by the combination of the rimose pileus, fibrillose striate stipe, context that does not change color upon exposure, absence of any distinctive odor, small ellipsoid spores, Old World tropical distribution, and presence of muscarine. Differs from the Indian *Inocybe carnosibulbosa* (described above) by the smaller size of the basidiomes and the non-bulbous stipe base. Unique evolutionary lineage in the Inosperma clade: "Old World tropical clade 2" of Kropp et al. (2013).

Holotype: India, Kerala State, Trivandrum District, TBGRI campus, 18 Jul 1994, Vrinda1098 [28908K (M)].

Habit and habitat: Solitary, scattered or in groups on forest floor or on sandy riverine soil under *Myristica*, *Knema attenuata* (Myristicaceae), *Vateria indica*, *Hopea parviflora* (Dipterocarpaceae), and *Aporusa acuminata* (Phyllanthaceae) trees.

Specimens examined: India, Kerala State, Trivandrum District, Palode, TBGRI campus, 16 Oct 1993, TBGT18; 19 Oct1993, TBGT34; 21 Oct 1993 TBGT74; 24 Nov 1993, TBGT431; 26 Nov1993, TBGT441; 22 Apr 1994, TBGT642; 25 May 1994, TBGT753 (TENN070314) (GenBank accession no. KT329452-ITS, KT329458-nLSU, KT329446-*rpb2*); Palakkadu District, Silent Valley National

Fig. 17 Habit in situ. **a** *Inocybe flavosquamulosa* (TENN070312). **b**, **c**. *I. alboflavella* (TENN070309). **d**, **f**. *I. carnosibulbosa* (TENN070310). **e**, **g** *I. albonitens* (TENN070311). **h** *I. virosa* (TENN070314). **i** *I. purpureoflavida* (TENN070313). Scale bars = 10 mm

Park, 18 May1994, TBGT718; 14 Jun 1994, TBGT911; 28 Jul 1994 TBGT1994; Trivandrum District, Agasthyamala, 26 Jul 1994, TBGT1258; Trivandrum District, Kallar, 17 Jun 1994, TBGT884.

Discussion: For a complete description and illustrations, see Vrinda et al. (1996). *Inocybe virosa* is a now confirmed member of the Inosperma clade of Matheny (2009) where it shares its closest alliance with species in "Old World tropical clade 2" of Kropp et al. (2013) based on BLASTn results of ITS, nLSU, and *rpb2* gene sequences, as well as phylogenetic analysis (Fig. 15). The species does not share features in common with many species of the Maculata clade, a major subgrouping within the *Inosperma* clade, nor with sect. *Cervicolores*, the other major subgrouping in the *Inosperma* clade according to Larsson et al. (2009). Many species of the Maculata clade exhibit phaseoliform spores, thin-walled, often clavate to pyriform cheilocystidia, context that changes color upon exposure, a smooth stipe (some with a distinctly bulbous base), and distinctive non-spermatic odors (Larsson et al. 2009). Many of these traits are shared with species of sect. *Cervicolores*, although many of the European species of the latter tend to have a fibrillose to scaly stipe and/or scaly pileus and lack muscarine (Kuyper 1986). *Inocybe virosa* differs from these subgroupings by the combination of its longitudinally fibrillose striate stipe lacking a bulbous base, rimose pileus, non-changing context, apparent absence of any distinctive odor, and elliptic spores. The presence of what is likely muscarine (Vrinda et al. 1996) distinguishes this species from sect. *Cervicolores*, and some species of the Maculata clade as well, which lack muscarine. Thorough morphological notes are lacking for other taxa in "Old World tropical clade 2", thus documentation and validation of *I. virosa* are critical to understand species in this novel group. The species is fairly close related to *I. carnosibulbosa* described above, together with other species from India, Thailand, and Papua New Guinea. *Inocybe virosa* differs from *I. carnosibulbosa* by the smaller size of the basidiomes and the non-bulbous stipe base (Figs. 16 and 17).

The name *Inocybe virosa* was not validly published due to failure to cite the herbarium in which the holotype was deposited (see Art. 40.7, Melbourne code). The herbarium holding the holotype collection is cited here, together with a diagnosis, thus validating the name.

Notes on extralimital taxa

Inocybe mucidiolens (Grund & D.E. Stuntz) Matheny, **comb. nov. et stat.nov**.

MycoBank: MB 814358

Basionym: *Inocybe calamistrata* var. *mucidiolens* Grund & D.E. Stuntz, *Mycologia* 62(5): 929 (1970).

Discussion: As Fig. 15 demonstrates, this variety of *I. calamistrata* (Fr.: Fr.) Gillet (sequences analyzed and produced from the isotype) does not cluster with any Fennoscandian sequences of *I. calamistrata*. Thus, the new combination at the species rank is made. *Inocybe mucidiolens* is characterized by its green corn odor, dingy yellowish umber pileus, and occurrence under conifers in Washington and Nova Scotia (Grund and Stuntz 1970).

Acknowledgments PBM is supported by a research grant from the U.S. National Science Foundation (DEB-1354802) awarded to Matthew E. Smith and PBM.

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