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ORIGINAL ARTICLE

New species and new records of *Crepidotus* (Crepidotaceae) from India

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Abstract
Five species of *Crepidotus* (Agaricales, Crepidotaceae) were documented during our ongoing efforts to characterize the fungi of Kerala State, India. Of these, three species are new to science, while *C. roseus* and *C. alabamensis* represent new Asian and Indian records, respectively. Herein, we fully describe and illustrate *Crepidotus exiguus*, *C. flavobrunneus*, and *C. tortus* and provide updated descriptions and distributional data for *C. alabamensis* and *C. roseus.* A phylogenetic reconstruction based on maximum likelihood analyses of nuclear ribosomal large subunit rDNA sequences is also included.

Keywords Diversity · Mycoflora · Phylogeny · Phytogeography · 3 new taxa

Introduction

The genus *Crepidotus* (Fr.) Staude was established as a "tribe" of *Agaricus* by Fries in 1821 and subsequently raised to the rank of genus by Staude (1857) with *Crepidotus mollis* (Schaeff.) Staude as the type species. It is a well-defined genus having cosmopolitan distribution with over 200 species described worldwide (Kirk et al. 2008). During our continuing study on the agaric family Crepidotaceae (Agaricales, Basidiomycota) of Kerala State, India, several noteworthy collections belonging to the genus *Crepidotus* were made. It appears that the genus *Crepidotus* is particularly rich in this region as evident from previous studies (Guzmán-Dávalos et al. 2017; Kumar et al. 2018a, b; Kumar et al. 2020).

Here, we describe five more species of *Crepidotus* of which three species are new to science and the other two species represents new Asian and new Indian records. Morphological, molecular, and phylogenetic details of these five species are discussed in detail in the present study.

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Materials and methods

Morphological studies

Kerala State is a narrow strip of land on the south-west corner of the Indian Peninsula. Most of the forested areas of the State are parts of the Western Ghats, which is one of the biodiversity hotspots of the world. The very high biological diversity of Kerala State is primarily due to the highly diversified ecological niches and the climate which is tropical, maritime, and monsoonal. Specimens examined were collected from different natural forests and other localities of the State. The macro-morphological descriptions were based on fresh collections made from Kerala State, India. Microscopic characters were studied on dried material using hand cut sections of basidiomata stained with 1% Congo red, mounted in 3% KOH, and examined under an Olympus CX43 optical microscope (Olympus, Japan). For evaluation of the range of spore size, 20 basidiospores of each collection were measured for length and width. Basidiospore measurements include both the mean and the standard deviation, together with the range of spore quotient (Q, length/width ratio) and its mean value (Qm). Basidiospore measurements exclude the hilar appendix. Color coding follows that of Kornerup and Wanscher (1978). Microphotographs

were made with a Magcam DC10 digital camera attached to the same microscope. Holotypes are deposited at Central National Herbarium (CAL), Kolkata, India. All additional materials examined are deposited at the Mycological Herbarium of Jawaharlal Nehru Tropical Botanic Garden and Research Institute, Thiruvananthapuram (TBGT).

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from fresh specimens following protocols of Izumitsu et al. (2012). The nuclear large subunit region (nrLSU) and the Internal Transcribed Spacer region (nrITS) of the ribosomal DNA were amplified and sequenced from the presented species. PCR reactions were performed with the primer pair ITS1 and ITS4 (White et al. 1990) for nrITS and LR0R and LR7 (Vilgalys and Hester 1990) for nrLSU. The protocols for PCR amplification and sequencing followed Kumar et al. (2018b). The newly generated sequences are deposited in GenBank.

Sequence alignment and phylogenetic analysis

The molecular phylogenetic analysis was performed using nrLSU sequences. The nrLSU sequences of the five species obtained and those retrieved from GenBank (based on BLAST similarities) were aligned using PRANK web tool (www.ebi.ac.uk/Tools/msa/prank/) with default settings. The final aligned data matrix have 73 taxa, including species of *Crepidotus* and related genera, viz., *Simocybe*, *Pleuroflammula*, *Neopaxillus*, and *Inocybe* (Table 1), then imported into BioEdit v7.2.6.1 (Hall 1999) for manual adjustment. *Inocybe phaeoleuca* Kühner and *I. subpaleacea* Kühner were selected as outgroup following Ge et al. (2017). Maximum likelihood (ML) analysis was performed in the web platform http://iqtree.cibiv.univie.ac.at (Trifinopoulos et al. 2016) with 1000 ultrafast bootstrap replicates. Transition model with equal frequency (TIM3e + I + G4) was selected automatically as the best fit substitution model as per BIC score in the same web platform. Bootstrap values (BS) ≥ 60% (Jeewon and Hyde 2016) were considered significant. The aligned sequence dataset has been deposited in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S28431). The phylogram inferred from ML analysis is displayed with MEGA 7.0.26 (Kumar et al. 2016).

Results

Molecular phylogeny

The phylogeny inferred from ML analysis of the data matrix of nrLSU sequences is provided in Fig. 1, where 12 clades were observed. *Crepidotus flavobrunneus* is placed near an undescribed species of *Crepidotus* from Japan (AF367954) with 100% ML bootstrap in clade 1. *Crepidotus tortus* was placed near *C. occidentalis* Hesler & A.H. Sm., from the USA (AF205678) in clade 3 with 100% ML bootstrap. *Crepidotus exiguus* nested in clade 6 close to *C. cinnabarinus* F.H. Møller & Westergaard (AF205686) from the USA with 100% ML bootstrap. Sequence of *C. roseus* Singer from India was placed close to *C. aureus* E. Horak from Puerto Rico (AF205685) with 100% ML bootstrap in clade 7, while the sequence of *C. alabamensis* Murrill from India generated in the present study nested close to *C. alabamensis* from the USA (AF367960) with 98% ML bootstrap. The nrLSU sequences of *C. exiguus*, *C. flavobrunneus*, and *C. tortus* from India are distinct from all sequences of *Crepidotus* species available in GenBank, as revealed by BLAST search and phylogenetic analyses.

Crepidotus tortus A.M. Kumar & C.K. Pradeep, sp. nov. (Fig. 2).

MycoBank: MB840204.

Diagnosis: Differs from *Crepidotus occidentalis* by its versiform contorted, flexuous branched cheilocystidia, pileipellis with distinct pileocystidia, and the different nrLSU sequence.

Typus: India. Kerala State, Thiruvananthapuram district, Palode, Plavara, 8.72° N, 77.02° E, elev. 150 m, on dead branch of rubber tree (*Hevea brasiliensis*) and on other dead angiosperm trees, 27 Oct. 2017, Manoj TBGT17194 (holotype CAL1740), nrITS (MK462161) nrLSU (MK462162).

Etymology: The specific epithet refers to the strangulated cheilocystidia.

Pileus 3–22 mm diam., laterally attached, convex, orbicular, flabelliform; surface chalky white when young, becoming champagne (4B4) in old ones; white woolly to appressed squamulose, nonstriate, nonhygrophanous, dry; margin incurved, undulating, entire, fringed (under stereomicroscope). Lamellae radiating from a lateral point, putty to brownish gray (4B2/5B2/5B4/6D4/7C2), up to 2 mm wide, close to subdistant with lamellulae of 2–3 lengths; edge whitish, entire. Stipe absent. Context thin, white. White mycelial mat present at the base. Odor mild, not characteristic.

Basidiospores 8–10.5 × 5.5–6.5 (6.8) µm ($L^m = 9.4 \pm 0.83$ µm, $W^m = 6.22 \pm 0.40$ µm); Q = (1.29)1.42–1.6 (1.78); Qm = 1.51, ellipsoid, yellowish brown in KOH, thick-walled, smooth. Basidia 22–29 × 6.5–7 µm, clavate, mostly 4-spored, occasionally with 1, 2-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia 20–48 × 6.5–13 µm, versiform, strangulated, cylindrical, contorted, branched, flexuous, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama subregular, hyphae 5–10 µm wide, thin-walled, hyaline. Subhymenium

Table 1 List of species, geographic origin, and GenBank accession numbers of nrLSU of sequences used in the molecular analysis. Species from the present study are indicated in bold. Sequences from type collections are indicated by "*"

Species	Geographic origin	GenBank no. (nrLSU)	Source	References
Crepidotus aff. *alabamensis*	USA	GQ892982	PBM2979	Horak et al. (2015)
Crepidotus alabamensis	USA	AF367960	MCA778	M. C. Aime (unpubl. data)
Crepidotus alabamensis	**India**	**MK459543**	**TBGT15610**	**This study**
Crepidotus amygdalosporus	USA	AF205675	MCA258	Aime (1999)
Crepidotus antillarum	Dominican Rep	AF205680	OKM26827	Aime (1999)
Crepidotus applanatus var. *applanatus*	USA	AF205694	MCA170	Aime (1999)
Crepidotus asiaticus	Thailand	MF077336	TJB9995LSU*	Guzmán-Dávalos et al. (2017)
Crepidotus aureus	Puerto Rico	AF205685	OKM27300	Aime (1999)
Crepidotus betulae	USA	AF205679	MCA384	Aime (1999)
Crepidotus brunnescens	USA	AF367936	MCA864	M. C. Aime (unpubl. data)
Crepidotus calolepis	USA	MF797668	TENN064170	P. B. Matheny, S. A. Trudell and M. G. Wood (unpubl. data)
Crepidotus cesatii	USA	AF205681	OKM26976	M. C. Aime (unpubl. data)
Crepidotus cf. *applanatus*	USA	AY380406	PBM717	Matheny (2005)
Crepidotus cf. *subaffinis*	Japan	AF205703	MCA604	Moncalvo et al. (2002)
Crepidotus cf. *subsphaerosporus*	Australia	AF367947	OKM24649	M. C. Aime (unpubl. data)
Crepidotus cinnabarinus	USA	AF205686	MCA387	Aime (1999)
Crepidotus croceitinctus	Russia	AF367937	IBNR1997/0947*	M. C. Aime (unpubl. data)
Crepidotus croceitinctus	Japan	AF367932	MCA580	Aime et al. (2005)
Crepidotus croceotinctus	India	MK878547	TBGT17271	Kumar et al. (2020)
Crepidotus crocophyllus	USA	GQ893025	PBM3047	Horak et al. (2015)
Crepidotus crocophyllus	USA	AY029707	OKM26173	Aime (2004)
Crepidotus distortus	USA	AF205671	MCA386	Aime (1999)
Crepidotus ellipsoideus	USA	MK277883	G1955	Varga et al. (2019)
Crepidotus epibryus	Russia	AF367934	IBNR1997/0948*	Aime et al. (2005)
Crepidotus exiguus	**India**	**MK567974**	**TBGT17176**	**This study**
Crepidotus exilis	India	MK878548	TBGT17157*	Kumar et al. (2020)
Crepidotus flavobrunneus	**India**	**MK567981**	**TBGT15841**	**This study**
Crepidotus fragilis	USA	AF367931	MCA904	Aime et al. (2005)
Crepidotus fraxinicola	USA	AF205699	OKM26739.5	Aime (1999)
Crepidotus fraxinicola	USA	AF205676	OKM26739	Aime (1999)
Crepidotus fraxinicola	USA	AF205701	OKM26748.2	Aime (1999)
Crepidotus globisporus	India	MK878540	TBGT17341*	Kumar et al. (2020)
Crepidotus indicus	India	MG735357	TBGT17161*	Kumar et al. (2018a)
Crepidotus inhonestus	Japan	AF205704	MCA638	Moncalvo et al. (2002)
Crepidotus kauffmanii	USA	MK277887	G1956	Varga et al. (2019)
Crepidotus lanuginosus	USA	AF367940	OKM27331	M. C. Aime (unpubl. data)
Crepidotus lundellii	Russia	AF367941	IBNR1997/0946*	M. C. Aime (unpubl. data)
Crepidotus malachioides	Slovakia	KF154018	SLO1250*	S. Jančovičová and M. Tomsovsky (unpubl. data)
Crepidotus malachius var. *malachius*	USA	AF205674	MCA343	M. C. Aime (unpubl. data)
Crepidotus martinii	Japan	AF367944	MCA640	M. C. Aime (unpubl. data)
Crepidotus melleus	Japan	AF205702	MCA672	Aime (1999)
Crepidotus mollis	USA	DQ071698	TUB011566*	Garnica et al. (2007)
Crepidotus mollis	USA	AF205677	OKM26279	Aime (1999)
Crepidotus mollis	USA	DQ986293	PBM1036 (WTU)	Matheny et al. (2007)
Crepidotus nyssicola	USA	AF205690	TJB8699*	Aime (1999)
Crepidotus occidentalis	USA	AF205678	OKM26740	Aime (1999)

Table 1 (continued)

Species	Geographic origin	GenBank no. (nrLSU)	Source	References
Crepidotus palodensis	India	MH310743	TBGT16716*	Kumar et al. (2018b)
Crepidotus podocarpi	Puerto Rico	AF205696	OKM27303	Aime (1999)
Crepidotus roseus	**India**	**MK567977**	**TBGT15507**	**This study**
Crepidotus sinuosus	USA	AF367945	OKM26290	M. C. Aime (unpubl. data)
Crepidotus sp.	Puerto Rico	AF367951	MCA499	M. C. Aime (unpubl. data)
Crepidotus sp.	Thailand	AF205684	OKM26899	Aime (1999)
Crepidotus sp.	Japan	AF367954	MCA 941	Aime (2004)
Crepidotus sp.	USA	AF367956	OKM27540	Aime (2004)
Crepidotus sp.	Australia	KP311341	MEL2363919	G. Bonito and T. W. May (unpubl. data)
Crepidotus sphaerosporus	USA	AF205682	OKM27013	Aime (1999)
Crepidotus stenocystis	Czech Rep	MF621024	PRM911279*	Jančovičová et al. (2017)
Crepidotus thermophilus	Puerto Rico	AF205669	OKM27270	Aime et al. (2002)
Crepidotus thermophilus	Puerto Rico	AF205691	TJB8496	Aime et al. (2002)
Crepidotus tobolensis	Russia	MK560762	LE287655*	Crous et al. (2019)
Crepidotus tortus	**India**	**MK462162**	**TBGT17194**	**This study**
Crepidotus uber	USA	AF367961	MCA1403	M. C. Aime (unpubl. data)
Crepidotus variabilis	Japan	AF367949	MCA633	M. C. Aime (unpubl. data)
Crepidotus versutus	Russia	AF367958	IBNR1997/0962	M. C. Aime (unpubl. data)
Crepidotus versutus	USA	AY820890	PBM 856 (WTU)*	Matheny and Bougher (2006)
Crepidotus volubilis	India	MH310742	TBGT15648*	Kumar et al. (2018b)
Inocybe phaeoleuca	Hungary	KJ399958	EL297–08	Larsson et al. (2014)
Inocybe subpaleacea	Finland	KJ849311	JV29282	Larsson et al. (2014)
Neopaxillus dominicanus	Dominican Rep	HQ452478	MCVE25727*	Vizzini et al. (2012)
Neopaxillus echinospermus	Brazil	JN033222	MPM2886	Vizzini et al. (2012)
Pleuroflammula praestans	Australia	HQ832464	PBM3461	Matheny et al. (2015)
Pleuroflammula sp.	Dominican Rep	AF367963	OKM27686	M. C. Aime (unpubl. data)
Simocybe amara	India	MG719983	TBGT16503	Kumar et al. (2018a)
Simocybe americana	USA	AF205709	VTMH3760	Moncalvo et al. (2002)

pseudoparenchymatous. Pileal trama composed of thin-walled, hyaline hyphae, 5.5–8 µm wide. Pileipellis a cutis, hyphae of 4–5.5 µm wide, interrupted at places with suberect to erect hyphae; terminal elements cylindric, flexuous with obtuse ends, 40–72 × 2–3 µm; pileus margin composed of tufts of slender highly flexuous coiled hyphae, rarely branched, with obtuse or bifid apices, 60–62 × 4–6.5 µm. Oleiferous hyphae abundant, yellowish. Clamp connections present.

Habit, habitat, and phenology: Scattered on dead branch of rubber tree (*Hevea brasiliensis*) and on other dead angiosperm trees. May, Sep.–Nov.

Additional specimens examined: India. Kerala State, Thiruvananthapuram district, Palode, Plavara, on dead branch of rubber tree (*Hevea brasiliensis*) and on other dead angiosperm trees, 13 Sep. 2017, Manoj TBGT17095; 19 Oct. 2017, Manoj TBGT17159; 27 Oct. 2017, Manoj TBGT17194; 03 Nov. 2017, Manoj TBGT17233; 15 May 2018, Manoj TBGT17429; 16 Aug. 2018, Manoj TBGT17639; Thiruvananthapuram district, Palode, JNTBGRI campus, 12 May 2014, Manoj TBGT15043.

Notes: *Crepidotus tortus* is characterized by a distinctive combination of features such as small chalky white basidiomes, 1,2,4-spored basidia, ellipsoid, smooth basidiospores, versiform strangulated, cylindrical, contorted, branched, flexuous cheilocystidia and pileipellis with distinct cylindric, flexuous pileal elements. The pileus and basidiospores of *C. tortus* is similar to *C. occidentalis,* a species originally described from the USA (Hesler and Smith 1965). However, cheilocystidia in *C. occidentalis* are cylindric, subventricose and the pileipellis is a repent epicutis, whereas in *C. tortus*, cheilocystidia are versiform, strangulated, cylindrical, contorted, flexuous, and branched, besides pileipellis an interrupted cutis with cylindric flexuous elements.

Crepidotus tortus also resembles *C. podocarpi* Singer, *C. caspari* Velen., *C. albidus* Ellis & Everh., *C. acanthosyrinus* Singer, *C. autochthonus* J.E. Lange, *C. trichocraspedotus* T. Bau & Y.P. Ge, and *C.*

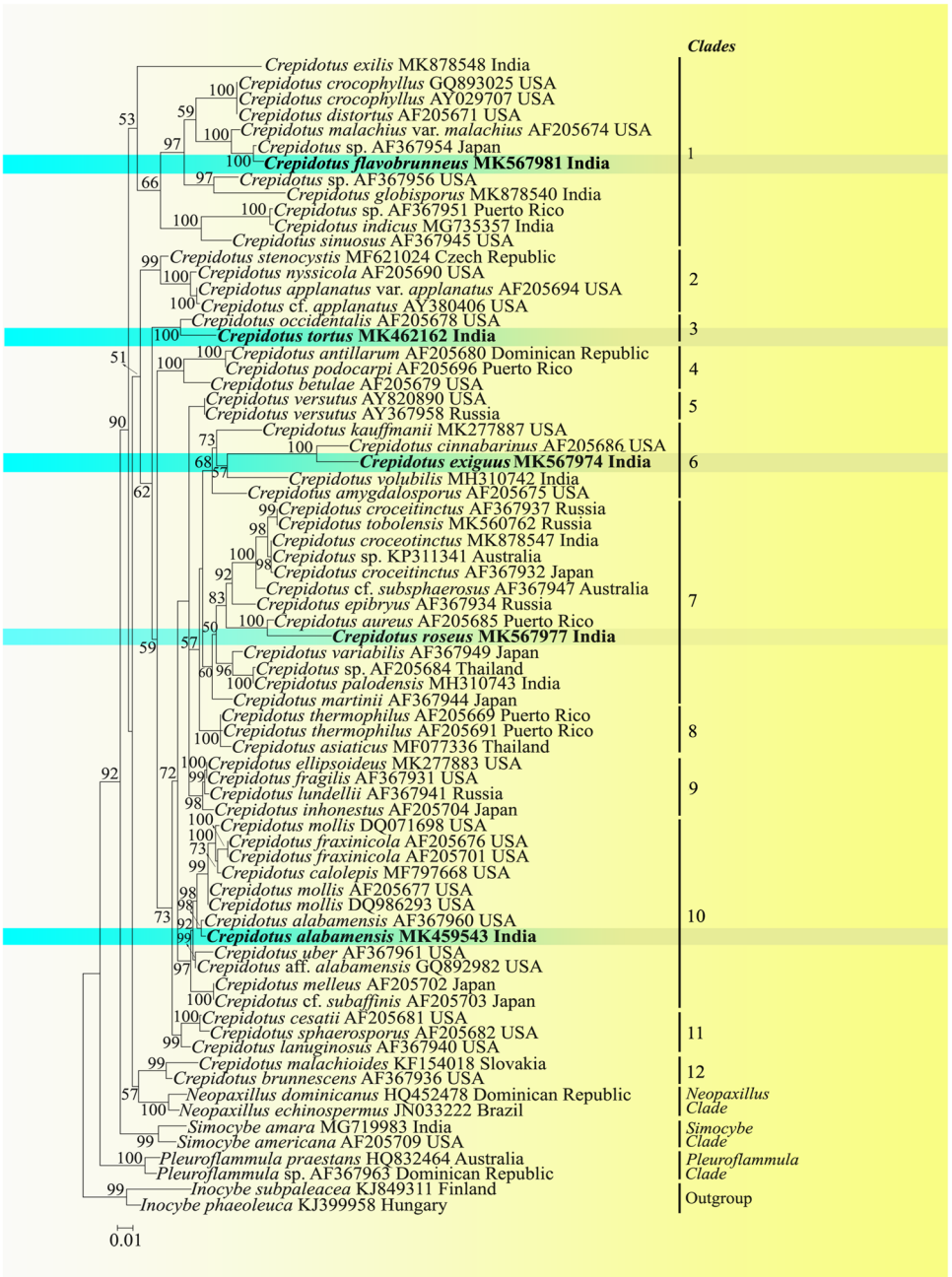

Fig. 1 Maximum likelihood phylogenetic tree illustrating the placement of *Crepidotus* species from the present study (in bold) with related species in Crepidotaceae based on nrLSU sequences. ML bootstrap values 50% and above are shown on branches

novae-zelandiae Pilát. *Crepidotus podocarpi* described from Argentina (Singer 1973) differs in having a slightly larger basidioma (9–33 mm), white hygrophanous pileus and smaller basidiospores (7.2–8 × 4.5–5 µm). The European *C. caspari* (Senn-Irlet 1995) is distinct from *C. tortus* by smaller, less broad (6–9.5 × 4–6 µm), marbled to faintly rugulose basidiospores, differently shaped cheilocystidia and pileipellis. *Crepidotus albidus* described from Bolivia and also reported from Argentina (Singer 1973) varies in having smaller, short ellipsoid to subglobose basidiospores (5–7.5 × 4.3–6 µm) and pileipellis with incrustations. *Crepidotus acanthosyrinus* originally described from Argentina (Singer and Digilio 1951) and also known from Brazil (Senn-Irlet and De Meijer 1998) differs by whitish to pale brown, smooth and glabrous pileus, slightly smaller basidiospores (7.5–9 × 5.0–6.5 µm), cylindrical to narrowly clavate cheilocystidia, and pileipellis an incrusted cutis. *Crepidotus autochthonus* differs in its smaller basidiospores (7.1–8.5 × 4.9–5.7 µm), unbranched, cylindrical, clavate cheilocystidia, gelatinized pileal trama, and terrestrial habitat (Consiglio and Setti 2008). *Crepidotus trichocraspedotus*, a recently described species from China (Ge and Bau 2020), is very closely related in

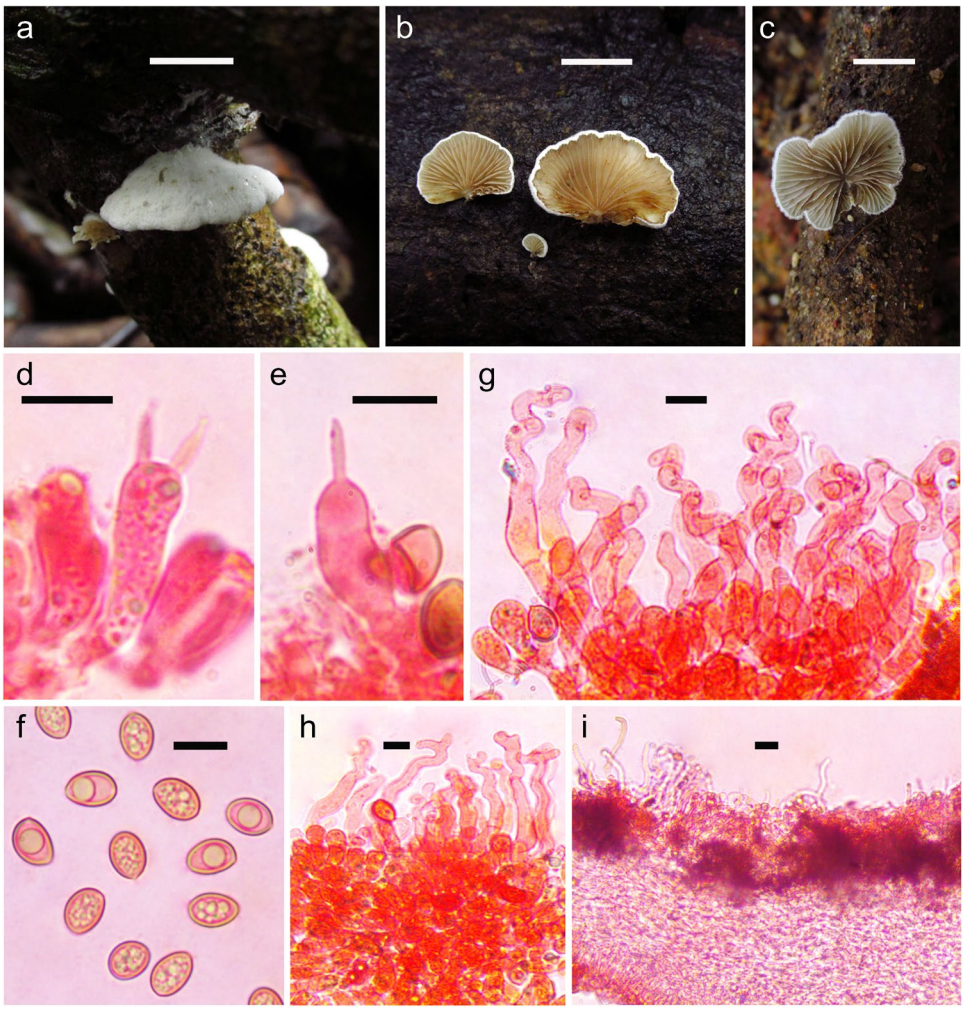

Fig. 2 *Crepidotus tortus* (CAL1740). **a–c** Habit in situ. **d–e** Basidia. **f** Basidiospores. **g**, **h** Cheilocystidia. **i** Pileipellis with pileal elements. Scale bars: **a–c** = 10 mm, **d–i** = 10 µm

its macro- and micromorphology to the present species, however differs in white to deep orange lamellae, slightly larger basidiospores [9.1–10.5 (–10.7) × 6.0–6.8 (–7.1) µm] and a trichodermal pileipellis with incrustations. *Crepidotus novae-zelandiae* originally described from New-Zealand (Pilát 1950) can be easily separated on account of its broadly ellipsoid larger basidiospores (11–12 × 8.3–8.6 µm). Smooth basidiospores and presence of clamp connections place *C. tortus* in subsect. *Fibulatini* of sect. *Crepidotus* (Singer 1986).

Crepidotus exiguus A.M. Kumar & C.K. Pradeep, sp. nov. (Fig. 3).

MycoBank: MB840206.

Diagnosis: Distinct from similar species by small, thin basidiomes, ellipsoid, warty basidiospores, characteristic versiform cheilocystidia, pileipellis an undifferentiated cutis and absence of clamp connections.

Typus: India. Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, 8.75° N, 77.02° E, elev. 150 m, on decaying log of an angiosperm tree, 23 Oct. 2017, Manoj TBGT17176 (holotype CAL1758), nrLSU: MK567974.

Etymology: The specific epithet refers to the small basidiomata.

Pileus 3–13 mm diam., convex, orbicular, flabelliform, conchate, surface white becoming yellowish white to pale orange (4A2/5A2/5A3), felted woolly with scattered white appressed squamules, dry, nonstriate, nonhygrophanous; margin incurved when young becoming straight, fringed with white hairs. Lamellae arising from a lateral rudimentary to reduced stipe, white becoming grayish orange to topaz (5B4/5C4/5C5), turning yellowish in aqueous KOH, up to 2 mm wide, close with lamellulae of 2 lengths; edge fimbriate, whitish (under stereomicroscope). Stipe rudimentary to reduced. Context thin, 1 mm, soft, golden blonde (5C4). Odor not characteristic. Taste mild. Spore print oak brown to clay (5D5/5D6).

Basidiospores 6.5–8 × 5–7 µm ($L^m = 7.3 \pm 0.55$ µm, $W^m = 5.8 \pm 0.46$ µm); Q = 1.17–1.3 (1.33); Qm = 1.25, mostly broadly ellipsoid, rarely ellipsoid, yellowish brown in aqueous KOH, moderately thick-walled,

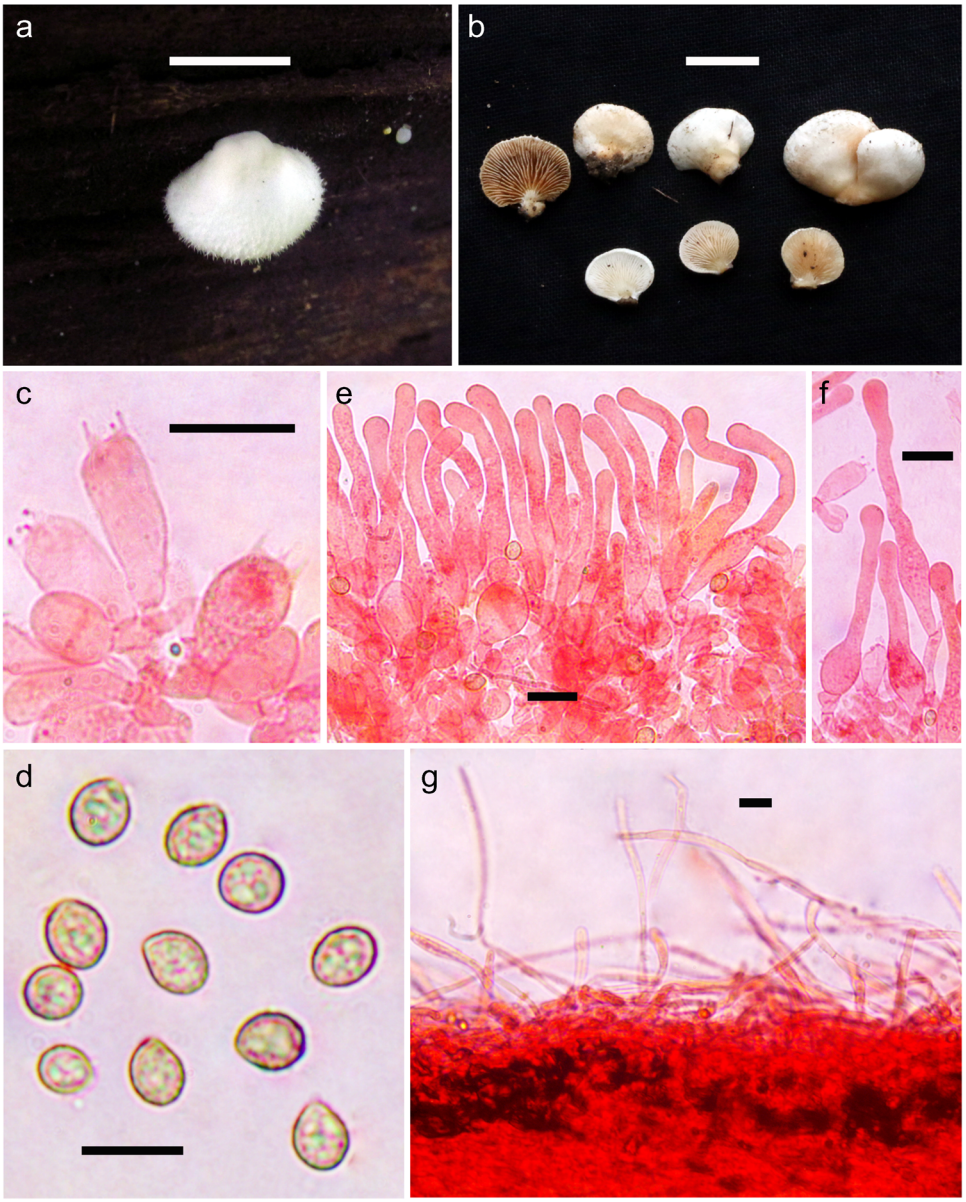

Fig. 3 *Crepidotus exiguus* (CAL1758). **a**–**b** Habit. **c** Basidia. **d** Basidiospores. **e**–**f** Cheilocystidia. **g** Pileipellis. Scale bars: **a**–**b** = 10 mm, **c**–**g** = 10 µm

finely warty. Basidia 19–24 × 8–9 µm, broadly clavate to clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia 48–76 × 8–14.5 µm, versiform, cylindrical, flexuous, narrowly lageniform to lageniform, often with a long flexuous narrow neck with a subcapitate apex, rarely clavate, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular, hyphae 4–12 µm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama hyphae 4–9.5 µm wide, thin-walled, hyaline. Pileipellis an interrupted epicutis with tufts of erect to semi-erect undifferentiated cylindrical hyphae, thin-walled, hyaline; scale cells form a thick tuft of thin cylindrical hyphae towards margin. Oleiferous hyphae present. Clamp connections absent in all tissues.

Habit, habitat, and phenology: Scattered on decaying log of an unidentified angiosperm tree. Oct. –Nov.

Additional specimens examined: India. Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, scattered on decaying log of an angiosperm tree, 13 Oct. 2017, Manoj TBGT17156; 03 Nov. 2017, Manoj TBGT17240.

Notes: *Crepidotus exiguus* is characterized by small, thin basidiomes, white becoming orange white, appressed squamulose pileus, broadly ellipsoid, warty basidiospores, characteristic versiform cheilocystidia, pileipellis an interrupted epicutis and absence of clamp connections.

Crepidotus effusus Pegler, *C. applanatus* (Pers.) P. Kumm., *C. versutus* Hesler & A.H. Sm., and *C. defibulatus* Singer are similar in their gross morphology and in

some microscopic characters. *Crepidotus effusus* described from Kenya (Pegler 1977) is distinct by its thin membranous basidiomata, imbricate habit, pale lamellae, slightly larger basidiospores (5.7–10 × 4.2–5.5 µm), and pileipellis an undifferentiated cutis. *Crepidotus applanatus* a widely distributed species (Hesler and Smith 1965; Senn-Irlet 1995; Consiglio and Setti 2008) differs by its distinct large cheilocystidia with capitate apex, smaller (4.5–7 µm) globose or subglobose punctate basidiospores, and with distinct pileocystidia. *Crepidotus versutus* (Hesler and Smith 1965) differs mainly by its long ellipsoid to cylindrical basidiospores (9–10.6 × 4.6–5.6 µm). *Crepidotus defibulatus* (Singer 1973) is similar in having a white pileus, clampless hyphae, and ornamented basidiospores but differs in its small, thin pileus (4–6 mm), smaller globose basidiospores (5.7–6.5 × 4.9–6 µm), and incrusted pileipellis hyphae.

Crepidotus exiguus is sister to *C. cinnabarinus* (AF205686) in our phylogenetic analyses (Fig. 1). *Crepidotus cinnabarinus* (Consiglio and Setti 2008) however is distinct by scarlet to cinnabar reddish pileus, subellipsoid larger basidiospores [7–9 (–10) × 5–6 µm], and fusoid ventricose cheilocystidia with reddish contents. *Crepidotus thermophilus* (Singer) Aime, T.J. Baroni, & O.K. Mill. originally described from the USA (as *Tubaria thermophile* Sing.) can easily be separated by its centrally stipitate basidiomata and hyphae with clamp connections.

Crepidotus flavobrunneus A.M. Kumar & C.K. Pradeep sp. nov. (Figs. 4, 5).

MycoBank: MB840207.

Diagnosis: Differing from *Crepidotus applanatus* by smaller, clavate to cylindro-clavate cheilocystidia, pileipellis a cutis lacking pileocystidia, incrusted pileal hyphae, and the different nrLSU sequence.

Typus: India. Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, 8.75° N, 77.02° E, elev. 150 m, scattered to gregarious on dead and decaying wood, stumps, dead branches, and roots of angiosperm trees and on moist soil in evergreen forests, 23 Sep. 2015, Manoj TBGT15841 (holotype CAL1759), nrLSU: MK567981.

Etymology: The specific epithet refers to the yellowish to brownish basidiomata.

Basidiomata small to large, fleshy, soft. Pileus 3–60 mm diam., plano-convex to applanate, flabelliform, semi-orbicular, spathulate; surface white to yellowish white (4A2) when young, becoming cream to brownish orange (4A3/4B4/5B3/5C3) when mature, becoming camel brown (6D4) in very old specimens, subtomentose to tomentose, villose, velvety, more towards the base (attachment), pellucid striate up to 2/3rd from the margin to the base, strongly hygrophanous; margin straight, wavy, entire to rarely incised, pellucid striate. Lamellae radiating from a lateral point, white to orange white (4A1/4A2/4A3/4B3/5A2) in fresh young basidiomes, becoming flesh (6B3) on keeping and finally attaining camel brown (6D4) in old ones, 4 mm wide, close to crowded with lamellulae of 3–5 lengths; edge concolorous to the sides, entire. Stipe rudimentary or reduced, present in young specimens, covered with cottony white hairs. Context thin, pale to off white, 1–2 mm wide. Odor indistinct to mild, not characteristic. Spore print brown (6E4/6E5).

Basidiospores 5.6–6.4 × 5.6–6.4 µm ($L^m = 5.8 \pm 0.36$ µm, $W^m = 5.8 \pm 0.36$ µm); Q = 1; Qm = 1, globose, pale yellow in KOH, thick-walled, minutely punctate, or warty. Basidia 25.6–32 × 8–8.8 µm, narrowly clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia (13.6) 20–36 × 8–28 µm, clavate to cylindro-clavate, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular to subregular, hyphae 4–5.6 µm wide, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama composed of thin-walled hyphae, 8–10 µm wide, hyaline. Pileipellis a cutis of parallel hyphae, 4–5 µm wide, thin-walled, incrusted, with pale brown contents. Clamp connections present in all tissues.

Habit, habitat, and phenology: Saprotrophic, scattered to gregarious on dead and decaying wood, stumps, dead branches, and roots of unidentified angiosperm trees and on moist soil in evergreen forests. Apr.–May; Sep. –Dec.

Additional specimens examined: India. Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, on dead and decaying wood, stumps, dead branches, and roots of unidentified angiosperm trees and on moist soil in evergreen forests, 11 May 2014, Manoj TBGT15032; 07 Oct. 2014, Manoj TBGT15369; 24 Oct. 2014, Manoj TBGT15416; 28 Apr. 2015, Manoj TBGT15575; 29 Apr. 2015, Manoj TBGT15587; 30 Apr. 2015, Manoj TBGT 15598, *ibid.* 15600, *ibid.* 15602; 01 May 2015, Manoj TBGT15611; 05 May 2015, Manoj TBGT 15615; 13 May 2015, Manoj TBGT15644; 19 Oct. 2015, Manoj TBGT15902; 19 Nov. 2015, Manoj TBGT15958; 21 Dec. 2015, Manoj TBGT16071; 26 May 2016, Manoj TBGT116193; 18 May 2017, Manoj TBGT16756; Palode, Plavara, 20 Oct. 2015, Manoj TBGT 15904; Bonacaud, 23 Sep. 2015, Manoj TBGT15838.

Notes: *Crepidotus flavobrunneus* belongs to subsect. *Porpophorini* of sect. *Echinospori* owing to its minutely punctate to warty globose basidiospores and presence of clamp connections. The diagnostic features of this species invite comparison with a cluster of species such as *Crepidotus applanatus*, *C. crocophyllus* (Berk.) Sacc., *C. stenocystis* Pouzar, *C. malachioides* Consiglio, Prydiuk & Setti, *C. brunnescens* Hesler & A.H. Sm., *C. malachius* Sacc., and *C. ehrendorferi* Hauskn. & Krisai.

Crepidotus applanatus, a widely distributed species (Hesler and Smith 1965; Singer 1973; Watling and Gregory 1989; Nordstein 1990; Senn-Irlet 1995;

Fig. 4 *Crepidotus flavobrunneus* (CAL1759). **a**–**f** Habit in situ. Scale bars: **a**–**f** = 10 mm

Krisai-Greilhuber et al. 2002), is conspicuously distinct by its large clavate, flexuous cheilocystidia with a capitate apex, pileipellis with distinct pileocystidia, and hyaline pileipellis hyphae lacking incrustation. Many workers also proposed several varieties for this species based mainly on the size of basidiospores and nature of cheilocystidia. However, all these varieties are now considered conspecific. *Crepidotus malachius* described from the USA (Hesler and Smith 1965) differs in having slightly larger (5–8.5 µm), globose, at times subovoid, spores; longer less broad (24–52 × 5–12 µm) ventricose, bottle shaped, tenpin shaped cheilocystidia, and lack of incrustations in the pileipellis. Neotype and isotype studies of *C. applanatus* and *C. malachius* by Consiglio and Setti (2008) opined that it is quite difficult to separate these two species macroscopically, though there is a significant difference in basidiospore size. Bandala et al. (2008) on a detailed analysis considered *C. malachius* as a synonym of *C. applanatus.*

Crepidotus stenocystis and *C. brunnescens* are similar in most macro- and microscopic characters however differ

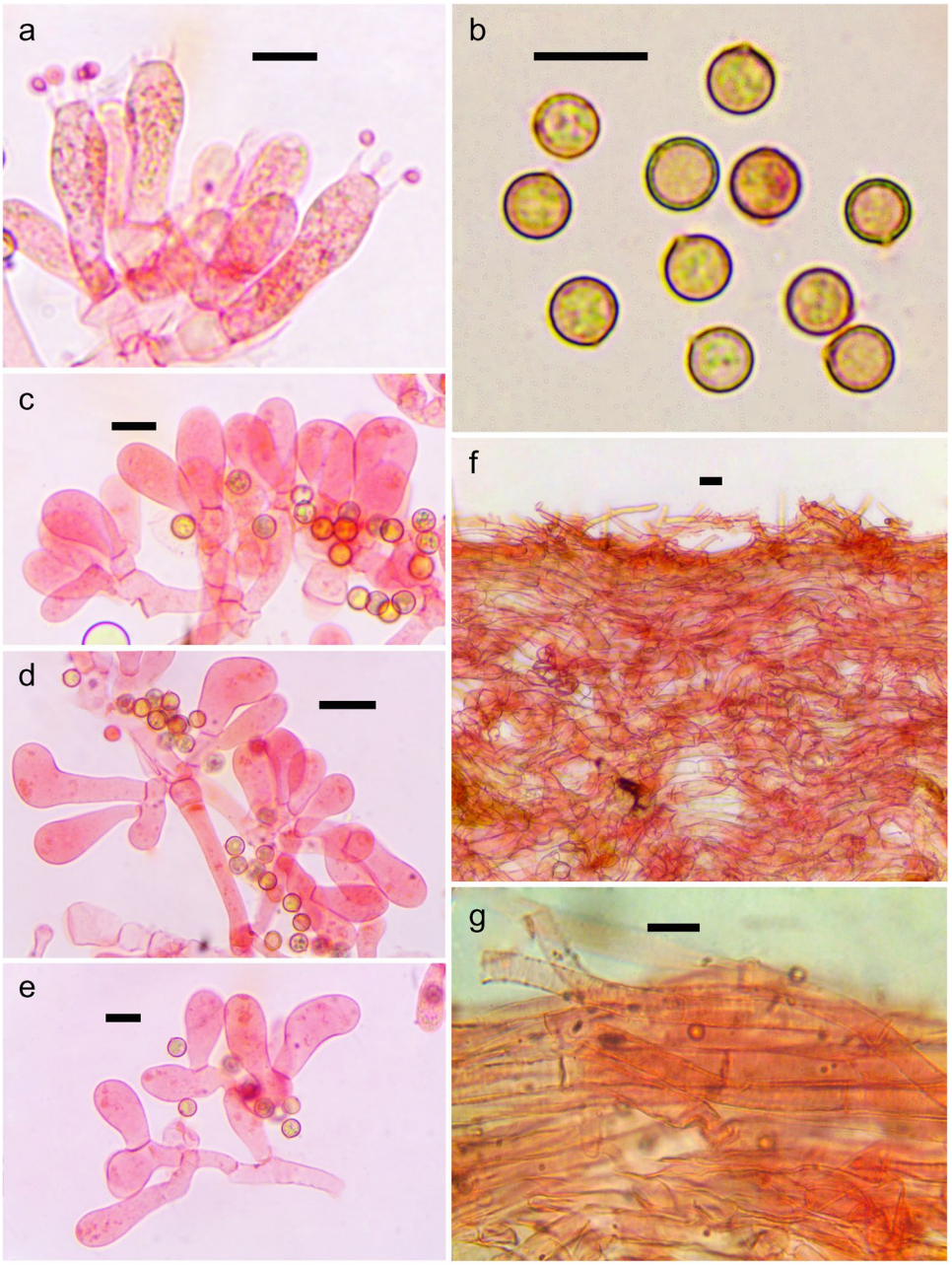

Fig. 5 *Crepidotus flavobrunneus* (CAL1759). **a** Basidia. **b** Basidiospores. **c**–**e** Cheilocystidia. **f** Pileipellis. **g** Pileal incrusted hyphae. Scale bars: **a**–**g** = 10 µm

among other things by their versiform cheilocystidia and pileipellis with distinct pileocystidia. Molecularly both species are having only 96% and 95% LSU sequence identity with our new species. *Crepidotus malachioides* can be distinguished by its strongly capitate, clavate cheilocystidia embedded in a thick brown mucus, and pileipellis a cutis with distinct pileocystidia similar to cheilocystidia. *Crepidotus ehrendorferi* differs by grayish orange to tinted yellow basidiomata with strigose fibrillose pileus, cylindrical, narrowly utriform flexuous branching cheilocystidia, and pileipellis a trichoderm with narrowly conical/cylindrical or mucronate elements. *Crepidotus flavobrunneus* is easily distinguished morphologically by its white to brownish orange tomentose pileus in contrast with the dull brown pileus of *C. crocophyllus* with brown to reddish brown fibrils that may aggregate in to small scales. The latter species also differs in having versiform cheilocystidia with subcapitate or branched apices and pileipellis a cutis with ascending hyphae.

Crepidotus alabamensis Murrill, N. Amer. Fl. 10(3): 150 (1917) (Figs. 6, 7).

Pileus 3–20 mm diam., convex, spathuliform, flabelliform or petaloid; surface pastel yellow to maize yellow (1A4–1A7/2A2–3A5/4A2–4A6), becoming apricot yellow (5B6) in old specimens, viscid to glutinous,

Fig. 6 *Crepidotus alabamensis*. **a**–**b** Habit in situ. Scale bars: **a**–**b** = 10 mm

hygrophanous, white tomentose-fibrillose to minutely villose near base, pellucid striate almost to the base; margin straight, pellucid striate, crenate. Lamellae radiating from a lateral point, sulfur yellow to grayish orange (1A5/1A6/2A2/3A3/5A3/4B4/6B5), up to 1 mm wide, close to subdistant with lamellulae of 2–4 lengths; edge concolorous to the sides, entire. Stipe rudimentary, present only in young basidiomata, lateral, absent in mature ones. Context thin, pale (2A2), up to 1 mm wide. White pubescent hairs present near base. Odor not characteristic. Spore print golden brown (5D7).

Basidiospores 5.6–7 × 4.8–5 (5.5) µm ($L^m = 6.38 \pm 0.46$ µm, $W^m = 5.0 \pm 0.20$ µm); Q = 1.17–1.33; Qm = 1.27, broadly ellipsoid to ellipsoid, yellowish brown in KOH, thick-walled, smooth. Basidia 19–22 × 6.5 µm, clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia tramal in origin, 17.5–40 × 5–10.5 µm, versiform, often septate, flexuous, strangulated, lageniform, ampullaceous, ventricose, often with long coiled beaks, bifurcated or with irregular excrescences, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular, hyphae 2.5–4 µm wide, gelatinized, thin-walled, hyaline. Subhymenium pseudoparenchymatous. Pileal trama composed of thin-walled, gelatinized hyphae, 5.5–9.5 µm wide, hyaline. Pileipellis an ixocutis, hyphae 2.5–6.5 µm in diam., incrusted, transforming to a trichoderm towards the center. Trichodermial elements 25.5–33.5 × 3–5.5 µm, versiform, cylindric to narrowly lageniform, strangulated, curved, or with short beaks. Pileal hyphae, incrusted with light brown pigment. Oleiferous hyphae abundant, yellowish. Clamp connections absent in all tissues.

Habit, habitat, and phenology: Scattered to gregarious on dead and decaying bark and wood of unidentified angiosperm trees in evergreen forests. May–Aug.; Oct. –Nov.

Specimens examined: India. Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, on dead and decaying bark and wood of unidentified angiosperm trees

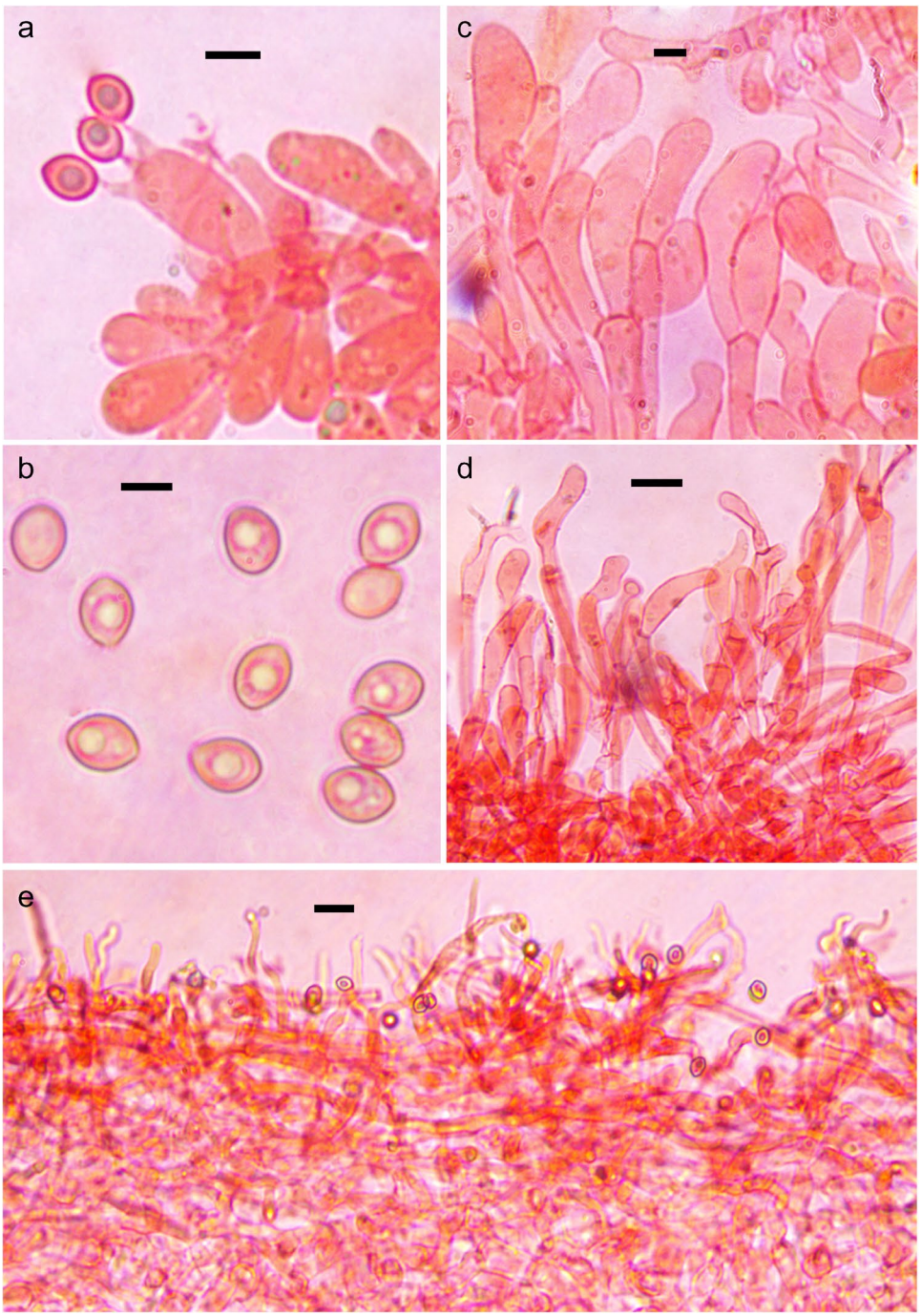

Fig. 7 *Crepidotus alabamensis.* **a** Basidium. **b** Basidiospores. **c**–**d** Cheilocystidia. **e** Pileipellis with pileocystidia. Scale bars: **a**–**c** = 5 µm. **d**–**e** = 10 µm

in evergreen forests, 1 May 2015, Manoj TBGT15609, *ibid.* Manoj TBGT15610; 20 Oct. 2015, Manoj TBGT15903; 17 Nov. 2015, Manoj TBGT15949; 17 May 2018, Manoj TBGT17454; 12 Jun. 2018, Manoj TBGT17531; 13 Jun. 2018, Manoj TBGT17532; 14 Jun. 2018, Manoj TBGT17539; 23 Jul. 2018, Manoj TBGT17595; Kollam district, Cheenikala, 23 Aug. 2016, Manoj TBGT16552.

GenBank LSU: MK459543; ITS: MK459545.

Notes: The Kerala collections agree with *Crepidotus alabamensis* morphologically and molecularly which is originally described from the USA (Murrill 1917; Hesler and Smith 1965). In a BLAST search in NCBI using nrLSU sequence (957 bp), the closest hit was *C. alabamensis* (AF367960,) with 99.37% sequence identity with zero e-value. In the ML phylogram, the Indian collection of *C. alabamensis* (MK459543) is placed close to *C. alabamensis* from the USA (AF367960) with 98% ML Bootstrap. However, slightly smaller basidiomata and presence of incrusted pileipellis hyphae are the additional/minor differences observed in the Indian collections.

Crepidotus alabamensis was so far not known from India and therefore phytogeographically significant. It belongs to sect. *Crepidotus* subsect. *Crepidotus*.

Crepidotus roseus Singer, Lilloa 13: 87 (1947) (Figs. 8, 9).

Pileus up to 12 mm diam., laterally attached, convex, orbicular to flabelliform; surface peach to pastel pink (7A4/8A4/9A4/10A3/11A4), white cottony, woolly to villose when young and sparse towards margin in mature ones, nonhygrophanous, nonstriate, dry; margin straight, variously lobed, whitish. Lamellae radiating from a lateral point, concolorous to pileus (7A4–11A4), up to 1 mm wide, close to subdistant with lamellulae of 2–4 lengths; edge concolorous to the sides or whitish. Stipe rudimentary or absent. Context thin, venetian pink (10A3). Odor not distinctive.

Basidiospores 5.5–8 × 5–7 µm, ($L^m = 6.68 \pm 0.87$ µm, $W^m = 6.12 \pm 0.68$ µm); Q = 1–1.14; Qm = 1.09, globose to subglobose, light brown in KOH, moderately thick-walled, coarsely verrucose. Basidia 22.5–24 (26.5) × 8–9 µm, clavate, 4-spored, thin-walled, hyaline. Lamella edge sterile with crowded cheilocystidia. Cheilocystidia versiform, 20–44 × 8–13 µm cylindro-clavate to broadly clavate, rarely with bifid apices, slightly strangulated, often with a narrow stalk, thin-walled, hyaline. Pleurocystidia absent. Hymenophoral trama regular, hyphae 2.4–3 µm wide, thin-walled. Subhymenium pseudoparenchymatous. Pileal trama composed of thin-walled, hyaline hyphae, 8–12 µm wide. Pileipellis a cutis of 4–5 µm wide hyphae, often projecting to form a turf of hyphae, thin-walled, hyaline. Oleiferous hyphae absent. Clamp connections present in all tissues.

Habit, habitat, and phenology: Scattered on dead and decaying bark of dicot trees in evergreen forest. Rarely

Fig. 8 *Crepidotus roseus*. **a–d** Habit in situ. Scale bars: **a–d** = 10 mm

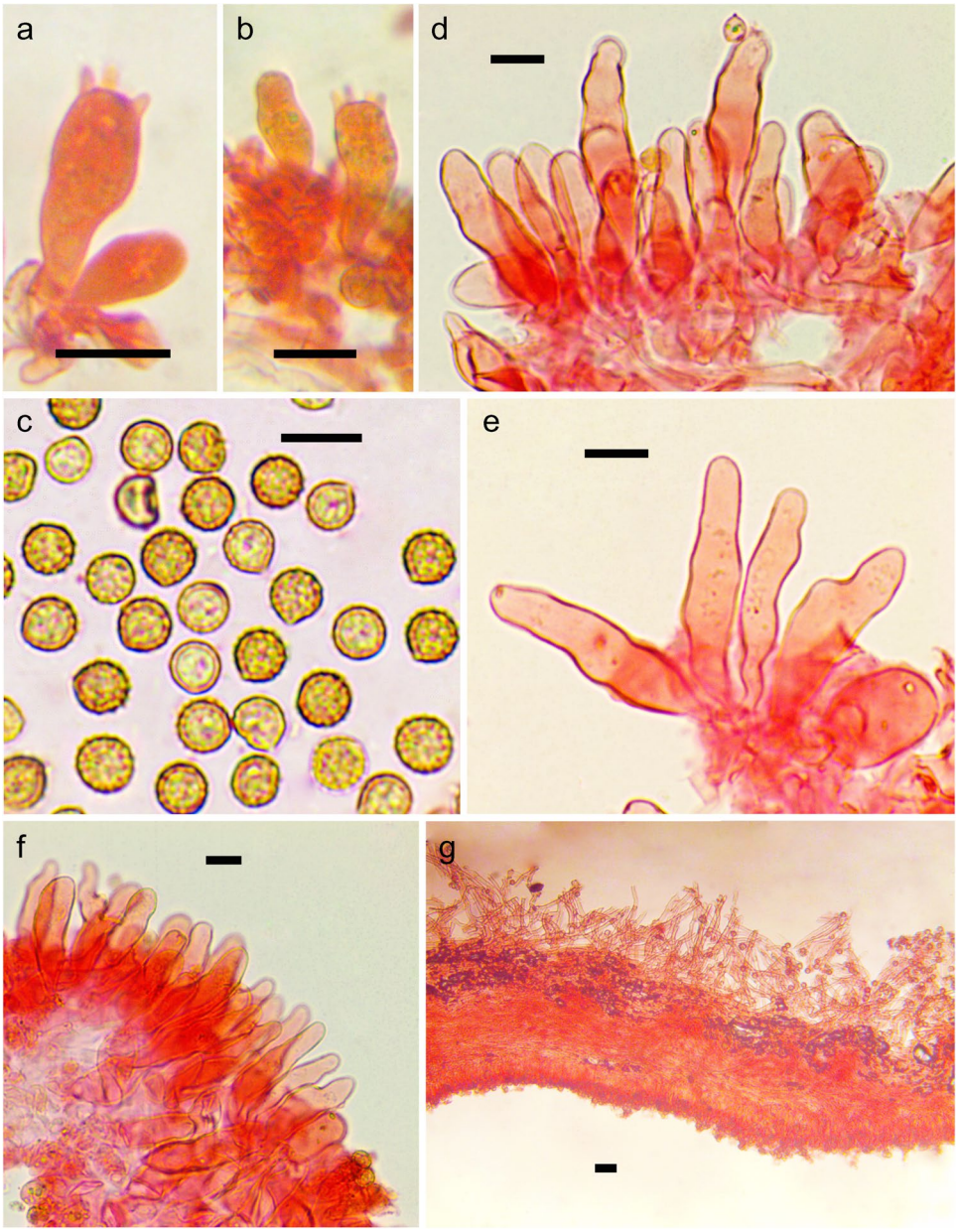

Fig. 9 *Crepidotus roseus*. **a**–**b** Basidia. **c** Basidiospores. **d**–**f** Cheilocystidia. **g** Pileipellis. Scale bars: **a**–**g** = 10 µm

found to cohabit with *Crepidotus citrinus* Petch. Sep. –Nov.

Specimens examined: India. Kerala State, Palakkad district, Dhoni, on dead and decaying bark of dicot trees in evergreen forest, 31 Oct. 2014, Manoj TBGT15512; Chittur, 10 Oct. 2014, Manoj TBGT15505; 17 Sep. 2015, Manoj TBGT15842; Thiruvananthapuram district, Palode, 15 Nov. 2014, Manoj TBGT15507; Ernakulam district, Thripunithura, 02 Sep. 2016, Manoj TBGT16584.

GenBank nrLSU: MK567977; nrITS: MK567976.

Notes: *Crepidotus roseus* is distinct and characterized by the small peach to pinkish basidiomes, globose to subglobose, coarsely verrucose basidiospores, versiform cheilocystidia, and presence of clamp connections. In the literature, one can find only a few species of *Crepidotus* having pinkish basidiomata, viz., *C. roseolus* Sing., *C. roseoornatus* Pöder & Ferrari, and *C. reversus* (Berk. & Broome) Sacc. Among these species, Indian collection is similar to *C. roseus* (Singer 1973; Hesler and Smith 1965) in most macro- and micromorphological characters. However, Singer (1973) and Hesler and Smith (1965) noted some cystidia slightly away from the edges of lamellae, which they considered pleurocystidia which is not observed in the Indian collections.

Crepidotus roseolus described from Argentina (Singer 1973) is similar in gross morphology, however differs in its smaller globose basidiospores (5–6.2×5.5 µm) and characteristic ventricose cheilocystidia with finger like and claviculate appendages. *Crepidotus roseoornatus* originally described from Italy, though similar to the present collection, may probably represent *C. roseolus* (Senn-Irlet 1995). *Crepidotus reversus* originally described from Sri Lanka (Pegler 1986) is distinct in having squamulose reddish pileus, differently shaped cheilocystidia, and pileipellis with a strongly differentiated cutis with numerous diverticulate to branching outgrowths.

In a BLAST search with nrLSU sequence (967 bp), the closest hit was *C. aureus* from Puerto Rico (AF205685) with 96.20% sequence identity and with 100% ML Bootstrap. *Crepidotus aureus* however is characterized by golden yellow to deep yellow pileus, fusoid to lageniform cheilocystidia which are incrusted with a resinous material or with distinct crystals. *Crepidotus roseus* was so far not reported from any Asian countries, and thus, the present Indian report is significant as it extends its distribution to the tropical Asian regions.

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Author contributions All authors (AMK, CKP, MCA) contributed to the study conception and design. AMK and CKP conducted field work in the state of Kerala, India. AMK and CKP conducted the microscopical and molecular study of the collections. AMK generated the molecular data and conducted the phylogenetic analysis. CKP wrote the first draft of the manuscript, and all authors commented on previous versions of the manuscript. MCA reviewed all aspects of the manuscript before submission. All authors read and approved the final manuscript.

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Data availability All voucher collections are deposited in registered herbaria. All relevant molecular data has been deposited in GenBank and TreeBase. (This has been already indicated in the main text.)

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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