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Morphology and molecular phylogeny of *Scleroderma yunnanense* and *Tricholoma olivaceum*, two edible mushrooms new to India

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Macrofungal explorations conducted in several forested areas of the East Khasi Hills and Ri Bhoi Districts of Meghalaya, India, unveiled two noteworthy members of *Scleroderma* and *Tricholoma*. After careful morphological characterisation, literature consultation, and molecular phylogenetic analysis, the species were identified as *Scleroderma yunnanense* and *Tricholoma olivaceum*, taxa recently described from China. The local tribal communities highly value these species as food. Here, we provide comprehensive morphological descriptions complemented with illustrations, comparisons with similar species, and nrITS-based phylogenetic analyses. *Scleroderma yunnanense* and *Tricholoma olivaceum* are reported for the first time from India.

Key words: *Basidiomycota*, Meghalaya, nrITS, taxonomy, edibility, ethnomycology.

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Tudu D., Chakraborty D., Ghosh A. (2024): *Scleroderma yunnanense* a *Tricholoma olivaceum*, dvě jedlé houby nové pro Indii, jejich morfologie a molekulární fylogeneze. – Czech Mycol. 76(2): 111–124.

Během výzkumu makromycetů v několika zalesněných územích okresů East Khasi Hills a Ri Bhoi ve státě Méghálaja v Indii byl zjištěn výskyt dvou pozoruhodných zástupců rodů *Scleroderma* a *Tricholoma*. Na základě morfologické charakteristiky, srovnání s literárními údaji a molekulárně fylogenetické analýzy byly určeny jako *Scleroderma yunnanense* a *Tricholoma olivaceum*, taxony nedávno popsané z Číny. Lidmi z místních kmenových společenství jsou tyto druhy vysoce ceněné jako jedlé houby. Článek přináší zevrubný popis morfologických struktur, doplněný ilustracemi, srovnáním s podobnými druhy a fylogenetickou analýzou založenou na nrITS. Pro oba druhy jde o první záznam o jejich výskytu na území Indie.

INTRODUCTION

Mushrooms are prised for their unique flavours, textures, and nutritional benefits, making them a cherished ingredient in various cuisines worldwide. In India, consumption of wild edible mushrooms is also common, specially in hilly forested areas.

The hilly state of Meghalaya lies between 24°02' and 26°07' N latitude and 89°48' and 92°51' E longitude, covering a geographical area of 22,429 km^2. Most of the area of Meghalaya is included in the 'Indo-Burma' global hotspot of biodiversity (Myers 2003). The diverse ecological conditions, for example broad variation in rainfall, temperature, altitude and soil types, and the inaccessible humid areas of the state, support luxuriant growth of tropical and subtropical vegetation, which is rich in angiosperms and mushrooms as well. The subtropical evergreen and semi-evergreen forests are primarily concentrated in large patches in remote areas of the state, which are characterised by rough, difficult terrain and have been less influenced by human activity. Pine forests are secondary in nature. These forests are mostly confined to the higher reaches of the Khasi and Jaintia Hills Districts and are highly fragmented (Tripathi et Tripathi 2011). East Khasi Hills occupies an area of 2,748 km^2 and lies between 25°07' and 25°41' N and 91°21' and 92°09' E. The maximum elevation is 1,957 m. Forests are mixed with dominance of *Pinus kesiya*, *Schima wallichii*, *Myrica esculenta*, and various members of the *Fagaceae*, including *Castanopsi*s, *Lithocarpus*, and *Quercus* species. The Meghalayan district of Ri Bhoi lies between 25°38' and 26°07' N and 91°21' and 92°16' E. Its elevations range from 41 m to 659 m. The major part is covered by Tropical moist deciduous forest with patches of Tropical semi-evergreen forest.

The tribal people of Meghalaya have built up practical knowledge about wild mushrooms which are edible and those that are inedible through generations. However, many wild edible mushrooms reported from Meghalaya are not properly identified (without any phylogenetic support) or identified only up to the genus level (Barua et al. 1998, Agrahar-Murugkar et Subbulakshmi 2005, Khaund et Joshi 2013, Das et al. 2014, Kalita et al. 2016). During a forest survey in East Khasi Hills, two interesting edible mushrooms were collected: *Scleroderma yunnanense* Y. Wang and *Tricholoma olivaceum* Reschke, Popa, Zhu L. Yang et G. Kost.

Tricholoma was first introduced as a tribus of the broad genus *Agaricus* (Fries 1821) and subsequently erected as a genus by Staude (1857). It seems to be most prominent in temperate to subtropical ecosystems (Ding et al. 2023). All known species are ectomycorrhizal (Ryberg et Matheny 2011) and grow mainly under *Pinaceae*, *Betulaceae*, and *Fagaceae*. Some species of *Tricholoma* are highly edible. Matsutake fungi are highly prised culinary mushrooms belonging to several species included in *Tricholoma* sect. *Caligata* Konrad et Moubl. ex Bon (Bon 1991).

Scleroderma Pers. (*Sclerodermataceae*, *Boletales*) is an easily recognisable genus of gasteroid fungi, characterised by subglobose, pyriform, or subturbinate basidiomata, a firm peridium which dehisces at maturity, and globose, coloured, and strongly ornamented basidiospores (Guzman 1970). *Scleroderma* is found globally in both temperate and tropical regions, forming ectomycorrhiza with a wide variety of woody plants of families such as *Caesalpiniaceae* (currently included in *Fabaceae*), *Dipterocarpaceae*, *Fagaceae*, *Myrtaceae*, *Phyllanthaceae*, and *Pinaceae* (Kumla et al. 2013, Wu et al. 2023).

The aim of this study is to broaden the knowledge of the two above-mentioned rare species, *Scleroderma yunnanense* and *Tricholoma olivaceum*, providing detailed descriptions of the recent collections with remarks on their distinguishing features and culinary value for local people.

MATERIAL AND METHODS

Morphological studies. Fresh young and mature specimens were collected from mixed forest dominated by *Pinus* sp. and *Quercus* sp. during the monsoon season from the East Khasi Hills and Ri Bhoi Districts. Macromorphological characters were recorded from fresh basidiomata in the field. Micromorphological characters were recorded and studied from basidiomata at the mycology laboratory of the Botanical Survey of India, Eastern Regional Centre, Shillong. Images of the fresh basidiomata were captured with PowerShot SX510 HS and OnePlus Nord CE. The colour codes of the Methuen Handbook of Colour (Kornerup et Wanscher 1978) were used to define colours. Micromorphological characters were established with an Olympus CX-43 (Olympus, Tokyo, Japan) compound microscope. Freehand sections from dried specimens were mounted in a mixture of 3% potassium hydroxide (KOH), 1% Phloxine and 1% Congo red. Microphotography was conducted using the Magcam DC Plus 10 camera attached to the microscope. All measurements were taken using standard MagVision software, specifically designed for the Olympus CX-43. The basidium length excludes sterigmata. Measurements of 30 basidiospores were recorded. Spore measurements and length/width ratios (Q) are recorded here as: minimum–mean–maximum. The Scanning Electron Microscope (SEM) image of the *Scleroderma* basidiospore was obtained from dry spores directly mounted on a double-sided adhesive tape pasted on a metallic specimen-stub and then scanned with gold coating to observe patterns of spore ornamentation at different magnifications in high vacuum mode (20 KV). The SEM work was carried out with a Zeiss Evo 18 special edition model imported from Germany and installed at Eastern Regional Centre, Botanical Survey of India, Shillong, Meghalaya, India. Specimens were deposited at the ASSAM herbarium, Shillong.

DNA extraction, polymerase chain reaction (PCR) and sequencing. The protocols for DNA extraction and sequencing of the ITS region of the nuclear ribosomal DNA (nrDNA) marker followed Ghosh et al. (2024). The forward and reverse reads of newly generated sequences were assembled using Geneious Pro v. 5.1 (Drummond et al. 2010) and submitted to GenBank (Tabs 1, 2).

Sequence alignment and phylogenetic analysis. To investigate the relationships of the nrITS sequences of the newly identified *Scleroderma yunnanense* and *Tricholoma olivaceum*, reference taxa sequences showing the closest matches were retrieved from GenBank, along with sequences from relevant published phylogenies (Tabs 1, 2). Two raw datasets of nrITS sequences were created separately for both species. All the datasets were aligned separately using the online version of the multiple sequence alignment programme MAFFT v. 7 (https://mafft.cbrc.jp/alignment/software/)

Tab. 1. List of species, GenBank accession numbers, origin and references of *Scleroderma* spp. and *Phlebopus* used in the phylogenetic analysis.

Species	GenBank accession no.	Origin	References
Scleroderma areolatum	EU819438	USA	Zhang et al. 2013
Scleroderma areolatum	EU819518	USA	Zhang et al. 2013
Scleroderma areolatum	GQ166910	USA	Zhang et al. 2013
Scleroderma verrucosum	EU784415	England	Zhang et al. 2013
Scleroderma polyrhizum	HM237173	China	Zhang et al. 2013
Scleroderma aurantium	HM237174	China	Zhang et al. 2013
Scleroderma sinnamariense	FM213364	Thailand	Zhang et al. 2013
Scleroderma sinnamariense	FM213363	Thailand	Zhang et al. 2013
Scleroderma sinnamariense	FM213361	Thailand	Zhang et al. 2013
Scleroderma sinnamariense	FM213362	Thailand	Zhang et al. 2013
Scleroderma sinnamariense	FM213357	Thailand	Zhang et al. 2013
Scleroderma guzmanii, holotype	NR_176725	USA	Ortiz-Rivero et al. 2021
Scleroderma guzmanii	MT270646	Mexico	Ortiz-Rivero et al. 2021
Scleroderma yunnanense	**PP535391**	**India**	**this study**
Scleroderma yunnanense, holotype	JQ639040	China	Zhang et al. 2013
Scleroderma yunnanense, holotype	JQ639041	China	Zhang et al. 2013
Scleroderma yunnanense, holotype	JQ639042	China	Zhang et al. 2013
Scleroderma yunnanense, holotype	JQ639043	China	Zhang et al. 2013
Scleroderma yunnanense	JQ639044	China	Zhang et al. 2013
Scleroderma yunnanense	JQ639045	China	Zhang et al. 2013
Scleroderma yunnanense	JQ639046	China	Zhang et al. 2013
Scleroderma bovista	GQ267487	New Zealand	Zhang et al. 2013
Scleroderma bovista	EU784409	England	Zhang et al. 2013
Scleroderma bovista	EU819517	USA	Zhang et al. 2013
Scleroderma cepa	EU819439	USA	Zhang et al. 2013
Scleroderma citrinum	GQ166907	USA	Zhang et al. 2013
Scleroderma citrinum	EU784413	England	Zhang et al. 2013
Scleroderma citrinum	FM213344	USA	Zhang et al. 2013
Scleroderma citrinum	EU784414	England	Zhang et al. 2013
Scleroderma citrinum	FJ824090	USA	Zhang et al. 2013
Phlebopus portentosus	GQ253574	China	Zhang et al. 2013

with L-INS-i strategy and default settings, respectively. The alignment was checked and trimmed with the conserved motifs manually in MEGA v. 7 (Kumar et al. 2016). The datasets of both species were phylogenetically analysed using the maximum likelihood (ML) method, which was performed using raxmlGUI 2.0 (Edler et al. 2021) with the GTRGAMMA substitution model. ML analysis was executed using the rapid bootstrap algorithm with 1000 replicates to obtain nodal support values. Maximum likelihood bootstrap (MLbs) values ≥70% are shown in the phylogenetic tree (Figs 1, 2).

Tab. 2. List of species, GenBank accession numbers, origin and references of *Tricholoma* spp. used in the phylogenetic analysis.

Species	GenBank accession no.	Origin	References
Tricholoma olivaceoluteolum	MW724353	China	Reschke et al. 2018
Tricholoma olivaceoluteolum	MW724378	China	Reschke et al. 2018
Tricholoma flavovirens	AF458449	USA	GenBank
Tricholoma flavovirens	AF458452	USA	GenBank
Tricholoma ulvinenii	LT000068	Finland	Heilmann-Clausen et al. 2017
Tricholoma ulvinenii	LT000069	Finland	Heilmann-Clausen et al. 2017
Tricholoma frondosae	LT000023	Denmark	Heilmann-Clausen et al. 2017
Tricholoma frondosae	LT000140	Slovenia	Heilmann-Clausen et al. 2017
Tricholoma citrinum	MF034262	China	Reschke et al. 2018
Tricholoma citrinum, holotype	MW724356	China	Cui et al. 2022
Tricholoma equestre	LT000019	Denmark	Heilmann-Clausen et al. 2017
Tricholoma cf. *equestre*	MW627996	Canada	GenBank
Tricholoma rapipes	LT000037	Denmark	Heilmann-Clausen et al. 2017
Tricholoma rapipes, epitype	LT000085	France	Heilmann-Clausen et al. 2017
Tricholoma saponaceum	LT000123	Norway	Heilmann-Clausen et al. 2017
Tricholoma saponaceum	MW724335	China	Ding et al. 2023
Tricholoma saponaceum	MW724389	China	Ding et al. 2023
Tricholoma saponaceum	MW724412	China	Ding et al. 2023
Tricholoma boudieri, epitype	LT000136	Slovenia	Heilmann-Clausen et al. 2017
Tricholoma boudieri	MW724322	China	Ding et al. 2023
Tricholoma boudieri	MW724373	China	Ding et al. 2023
Tricholoma boudieri	MW724437	China	Ding et al. 2023
Tricholoma olivaceum, holotype	MF034209	China	Reschke et al. 2018
Tricholoma olivaceum	MW724338	China	Ding et al. 2023
Tricholoma olivaceum	MW724351	China	Ding et al. 2023
Tricholoma olivaceum	**PP535396**	**India**	**this study**
Tricholoma sp.	MW724337	China	Ding et al. 2023
Tricholoma sp.	MW724342	China	Ding et al. 2023
Tricholoma pallens	MW628013	Canada	Lebeuf et al. 2023
Tricholoma viridiolivaceum	JX178633	New Zealand	Teasdale et al. 2013
Tricholoma sudum	LT000050	Denmark	Heilmann-Clausen et al. 2017
Tricholoma sudum, neotype	LT000051	Denmark	Heilmann-Clausen et al. 2017
Tricholoma forteflavescens, holotype	MF034207	China	Reschke et al. 2018
Tricholoma forteflavescens	MF034246	China	Reschke et al. 2018
Tricholoma olivaceotinctum	MW724372	China	Ding et al. 2023
Tricholoma olivaceotinctum	MW724380	China	Ding et al. 2023
Tricholoma terreum	EU439330	China	GenBank
Tricholoma terreum	LT000098	Germany	Heilmann-Clausen et al. 2017

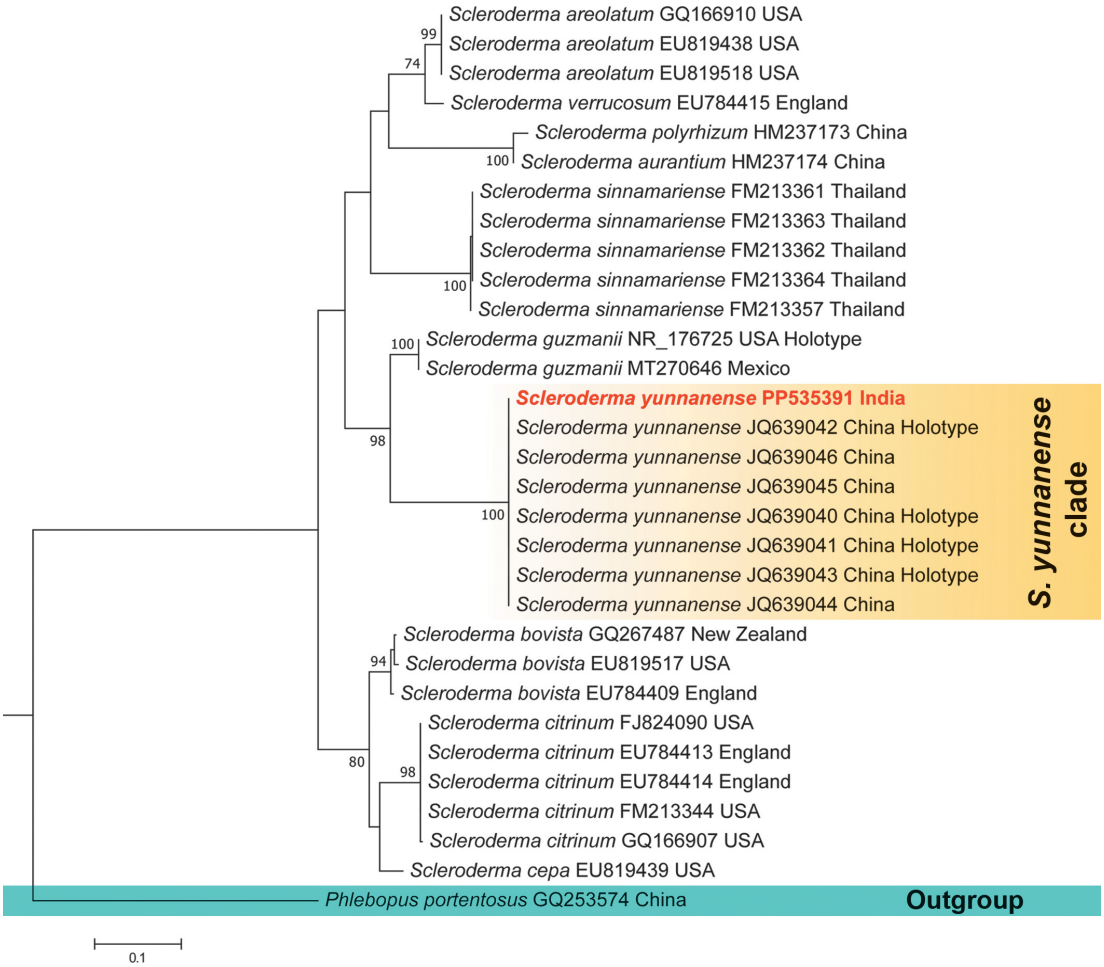

Fig. 1. Phylogram generated by means of maximum likelihood analysis based on nrITS sequence data of *Scleroderma* spp. Maximum likelihood bootstrap support ≥70% shown above or below the branches at nodes.

RESULTS AND DISCUSSION

Phylogenetic inferences

The Indian collection of *Scleroderma yunnanense* (voucher no. ASSAM F-008, GenBank accession no. PP535391) yielded a fungal nrITS sequence 100% identical to the holotype of *S. yunnanense* (accession nos. JQ639040–JQ639043) from China, revealing the presence of this species in India. The nrITS data matrix of *S. yunnanense* contained a total of 31 sequences including the outgroup. The final

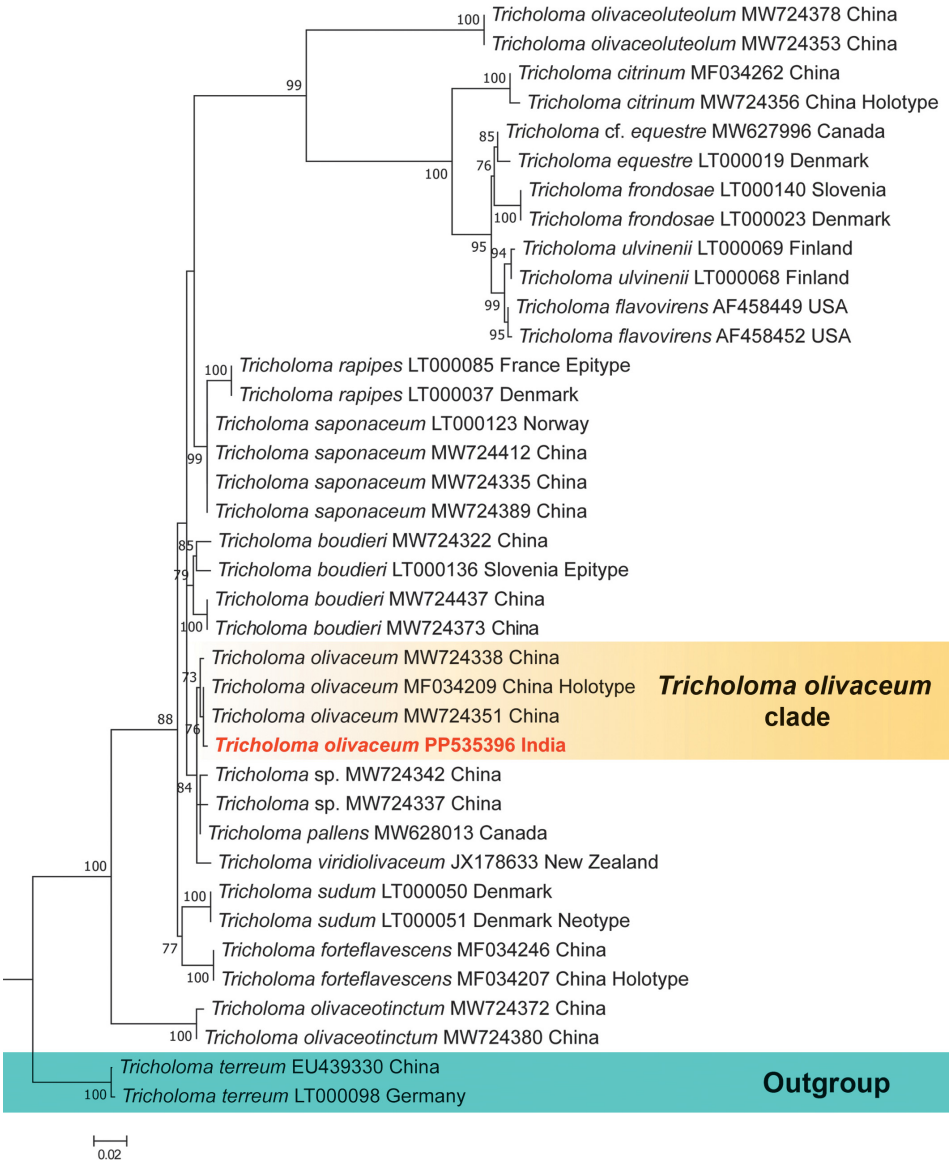

Fig. 2. Phylogram generated by means of maximum likelihood analysis based on nrITS sequence data of *Tricholoma* spp. Maximum likelihood bootstrap support ≥70% shown above or below the branches at nodes.

aligned dataset comprised a total of 499 positions, out of which 197 were distinct patterns, 182 parsimony-informative, 54 singleton sites, and 263 constant sites. The phylogenetic analysis based on the ITS region revealed that the sequence of

the Indian collection is clustered with the sequences of *S. yunnanense* collected from China, suggesting its strong similarity or conspecificity with a strong (MLbs = 100%) support (Fig. 1).

On the other hand, the Indian collection of *Tricholoma olivaceum* (voucher no. ASSAM F-010, GenBank accession no. PP535396) yielded a fungal nrITS sequence 99.34% identical to the holotype of *T. olivaceum* (accession no. MF034209) from China, revealing the presence of this species in India. The nrITS data matrix of *T. olivaceum* contained a total of 38 sequences including the outgroup. The final aligned dataset comprised a total of 690 positions, out of which 251 were distinct patterns, 176 parsimony-informative, 13 singleton sites, and 501 constant sites. Similarly, the phylogenetic analysis using nrITS data revealed that the sequence of Indian collection clustered within the *T. olivaceum* clade consisting of samples from China, suggesting strong similarity or conspecificity with robust (MLbs = 73%) support (Fig. 2).

Scleroderma yunnanense Y. Wang, Mycotaxon 125: 195, 2013 Fig. 3

Specimen examined

India. Meghalaya, Ri Bhoi District, village of Sumer, 25°41'41" N, 91°54'16" E, elev. 950 m, 13 June 2023, coll. D. Chakraborty and D. Tudu, DC ML-109 (ASSAM F-008). GenBank accession no. PP535391 (nrITS).

Description. Basidiomata globose to subglobose, 34–60 mm diam. and 40–60 mm in height, dirty yellow (2B–C4), areolate scales present on surface. Basal part narrow, covered with a white tuft of rhizomorphs. Rhizomorphs composed of hyaline hyphae, usually 2–3(5) µm in diam., with hyphae branched at right angles and numerous clamp-connections, some hyphae with crystalloid incrustations.

Peridium 2–3 mm thick, two-layered. Outer layer or exoperidium 0.5 mm thick, composed of thin, hyaline, yellowish hyphae with clamp connections. Endoperidium composed of thick, interwoven hyphae without any clamp connections. Gleba firm, yellowish white when young, purplish when mature, composed of hyaline hyphae, 1.5–2.0 µm in diam., with a few thick dark hyphae up to 3 µm in diam. Basidiospores globose to subglobose, 8.0–8.5–9.5 × 7.0–8.2–8.4 µm, Q = 1.10–1.14-1.17, ornamentation present, covered with dense narrow pyramidal warts, 1–1.2 µm long. Smell mushroomy. Taste sweet.

Habitat. Scattered, growing on soil in association with *Pinus kesiya* in tropical mixed forest.

Notes. Edibility in *Scleroderma* is a little controversial, as most mushroom books and scientific papers state that *Scleroderma* species are suspected to be undesirable, inedible, or poisonous. In contrast, *S. yunnanense* is found to be

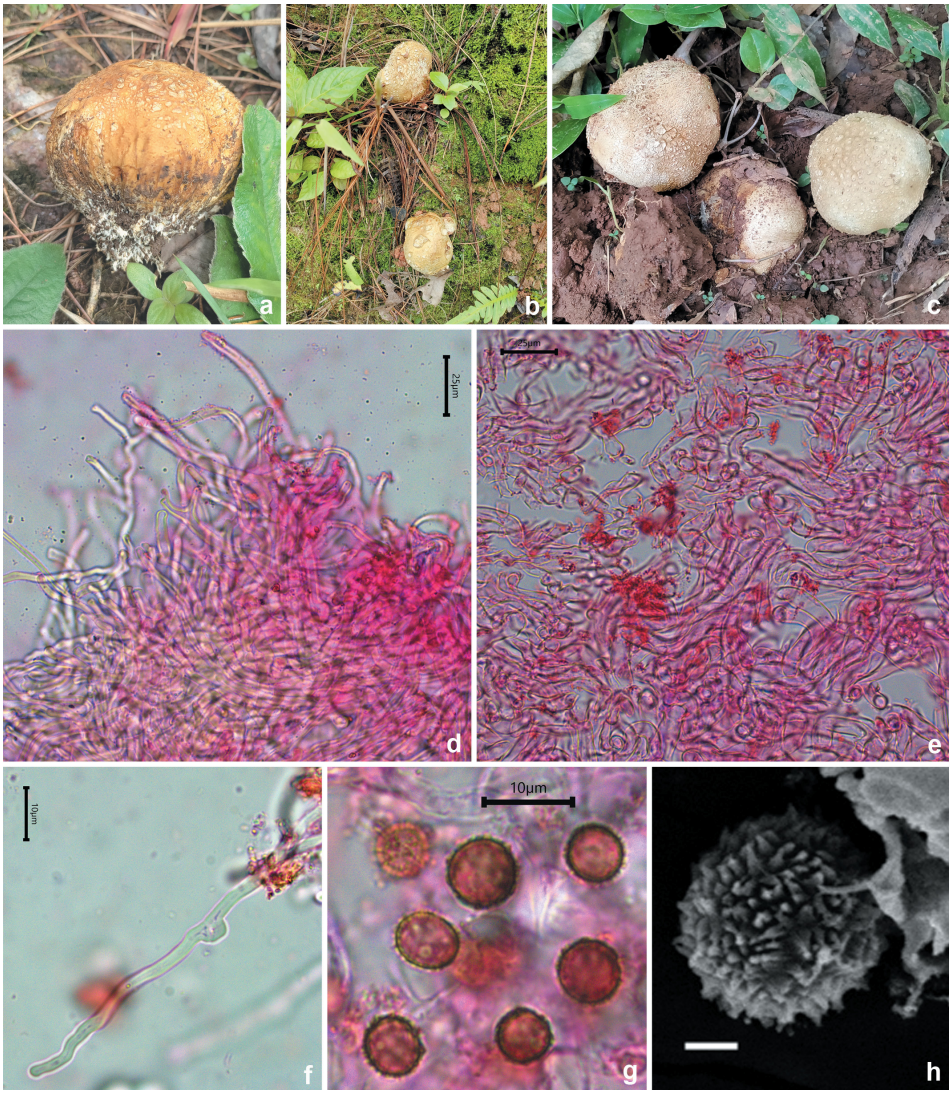

Fig. 3. *Scleroderma yunnanense* (ASSAM F-008): **a–c** – fresh basidiomata in situ, **d** – exoperidial hyphae, **e** – endoperidial hyphae, **f** – clamped hyphae of exoperidium, **g** – basidiospores, **h** – basidiospore showing ornamentation under SEM. Bars: d, e – 25 µm; f, g – 10 µm; h – 2 µm. Photos Dyutiparna Chakraborty.

highly valued and consumed in Yunnan Province and characterised by having clamp connections, a thicker peridium with a hyaline inner surface and a non-reticulate basidiospore ornamentation made up of dense narrow pyramidal warts (Zhang et al. 2013). In Meghalaya, these wild mushrooms were also eaten with

delicacy by the Khasi tribal people and sold at local markets as 'Tit-balls' during the rainy season.

The combination of characters like the pale yellow to dirty yellow basidiomata, areolate scales on the surface, a thick peridium, exoperidial hyphae with clamps, greyish brown to purplish gleba, basidiospores with dense pyramidal ornamentation, along with nrITS based phylogeny confirm our Indian collection to be *Scleroderma yunnanense*.

Morphologically, *Scleroderma citrinum* Pers. and *Scleroderma cepa* Pers. are very close to *S. yunnanense*, but *S. citrinum* has brighter yellow basidiomata with brownish scales at maturity and also larger basidiospores (9–13 µm diam.). In addition, *S. cepa* can be distinguished from *S. yunnanense* by the absence of clamped hyphae (Zhang et al. 2013, Zhang et al. 2020). *Scleroderma guzmanii* Ortiz-Rivero, Watling, Guzmán-Dávalos et M.P. Martín (originally reported from USA) is phylogenetically close to *S. yunnanense* (Fig. 1), but the former differs morphologically by having a tobacco brown to cocoa coloured gleba and basidiospores with subreticulate to reticulate ornamentation (Ortiz-Rivero et al. 2021).

Tricholoma olivaceum Reschke, Popa, Zhu L. Yang et G. Kost, Mycologia 110(6): 1101, 2018 Fig. 4

Specimen examined

India. Meghalaya, East Khasi Hills District, village of Thangsalai, 25°34'51" N, 92°03'27" E, elev. 1181 m, 21 August 2023, coll. D. Chakraborty and D. Tudu, DC ML-159 (ASSAM F-010). GenBank accession no. PP535396 (nrITS).

Description. Pileus 30–60 mm in diam., convex, with narrowly lobed umbo, margin incurved with a sterile flap of tissue; surface olivaceous grey (2E2–3F8), darker towards centre, glabrous with shiny, inconspicuously innate radial fibrils, particularly in centre. Context white. Lamellae cream white, sinuate, distant (8/cm), lamellulae in 4 series. Stipe 50–60 × 10–11 mm, central, cylindrical to clavate, solid, covered with grey brown (4E–F2) squamules, bulbous at base with rooting base, slightly reddening when bruised.

Basidiospores 5.1–5.6–6.0 × 3.5–4.1–4.8 µm, Q = 1.2–1.4–1.7, ellipsoidal, thin-walled, hyaline, smooth, inamyloid. Basidia 24–39 × 4–5 µm, clavate, hyaline, predominantly 4-spored. Gill edge fertile. Cystidia absent in hymenial layer. Pileipellis a cutis formed by cylindrical, 4–10 µm wide hyphae, with encrusting and intracellular pigments, yellowish in KOH. Clamps distinct and frequent.

Habitat. Scattered, growing in association with *Pinus* sp. in pine-dominated mixed forest.

Notes. The combination of macro- and micromorphological characters like the olivaceous pileus, involute margin, stipe with dark olive to dark brown fibrils

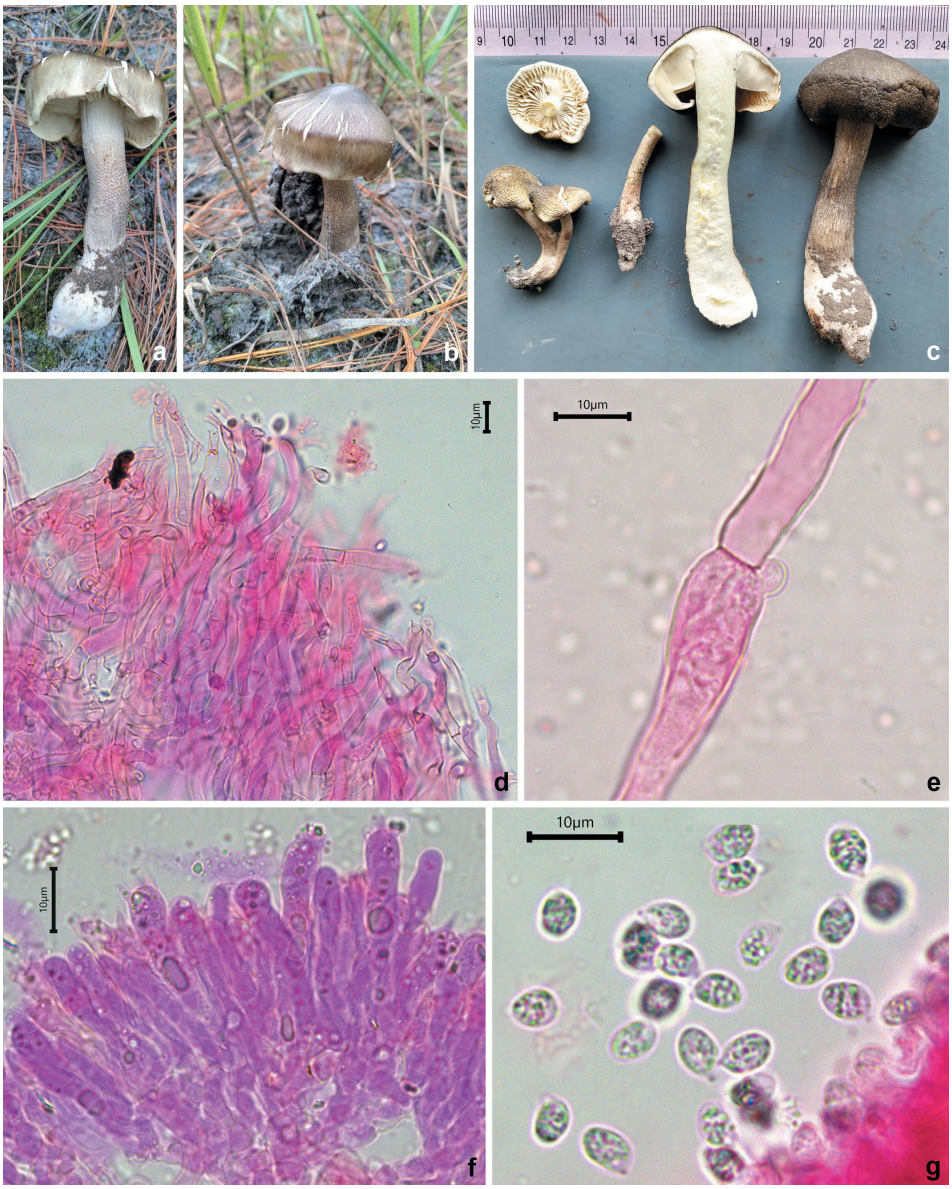

Fig. 4. *Tricholoma olivaceum* (ASSAM F-010): **a–c** – fresh basidiomata in situ and ex situ, **d** – pileipellis, **e** – clamped pilear hypha, **f** – basidia and basidioles, **g** – basidiospores. Bars: d–g – 10 µm. Photos Dyutiparna Chakraborty.

or squamules, sinuate gills, clamped hyphae in all tissues, association with *Pinus* sp., and nrITS based phylogenetic analysis confirm the Indian collection to be *Tricholoma olivaceum*. Morphologically, this species can be confused with *Tricholoma viridiolivaceum* G. Stev. in the field, but the latter has larger basidiospores (6–7 × 4–5 µm) and a different distribution: to date, it has only been found under *Nothofagus* sp. and *Leptospermum* sp. in New Zealand (Stevenson 1964).

Species in the genus *Tricholoma* are significant for their edibility, while others are poisonous (Yang et al. 2017, Li et al. 2021). *Tricholoma olivaceum*, like other species in *Tricholoma* sect. *Rigida*, has no well-documented information regarding its edibility, while *T. saponaceum* (a popular species of sect. *Rigida*) is treated as inedible or edible with caution due to saponaceous compounds (Li et al. 2021). However, *T. olivaceum* collected from India is consumed as a local delicacy by the Khasi tribe of Meghalaya and is sold at local markets as 'Tit-Kdats' during the rainy season. In this communication, we are reporting it as an edible mushroom for the first time from India.

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