cryptogamie
Mycologie
2023 • 44 • 3

Three new species of genus *Russula* Pers. from Sal dominated forests of tropical India based on morphotaxonomy and multigene phylogenetic analysis

Aniket GHOSH, Bart BUYCK, Dyutiparna CHAKRABORTY, Manoj Emanuel HEMBROM, Ishika BERA & Kanad DAS

art. 44 (3) — Published on 21 March 2023
www.cryptogamie.com/mycologie

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Directeur de la publication / *Publication director*: Bruno DAVID
Président du Muséum national d'Histoire naturelle

Rédacteur en chef / *Editor-in-chief*: Philippe SILAR

Assistant de rédaction / *Assistant editor*: Chris LE COQUET-LE ROUX (myco@cryptogamie.com)

Mise en page / *Page layout*: Chris LE COQUET-LE ROUX

Rédacteurs associés / *Associate Editors*

Slavomír ADAMČÍK
Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523, Bratislava (Slovakia)

André APTROOT
Laboratório de Botânica / Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul,
Avenida Costa e Silva s/n, Bairro Universitário, CEP 79070-900, Campo Grande, Mato Grosso do Sul (Brazil)

Cony DECOCK
Mycothèque de l'Université catholique de Louvain, Earth and Life Institute, Microbiology, Université catholique de Louvain,
Croix du Sud 3, B-1348 Louvain-la-Neuve (Belgium)

André FRAITURE
Botanic Garden Meise, Domein van Bouchout, B-1860 Meise (Belgium)

Kevin D. HYDE
School of Science, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Valérie HOFSTETTER
Station de recherche Agroscope Changins-Wädenswil, Dépt. Protection des plantes, Mycologie, CH-1260 Nyon 1 (Switzerland)

Sinang HONGSANAN
College of Life Science and Oceanography, Shenzhen University, 1068, Nanhai Avenue, Nanshan, ShenZhen 518055 (China)

Egon HORAK
Schlossfeld 17, A-6020 Innsbruck (Austria)

Jing LUO
Department of Plant Biology & Pathology, Rutgers University New Brunswick, NJ 08901 (United States)

Ruvishika S. JAYAWARDENA
Center of Excellence in Fungal Research, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Chen JIE
Instituto de Ecología, Xalapa 91070, Veracruz (México)

Sajeewa S.N. MAHARCHCHIKUMBURA
Department of Crop Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University (Oman)

Pierre-Arthur MOREAU
UE 7144. Faculté des Sciences pharmaceutiques et biologiques. Université Lille Nord de France. F-59006 Lille (France)

Tian QING
Center of Excellence in Fungal Research, Mae Fah Luang University 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Sylvie RAPIOR
Laboratoire de Botanique, Phytochimie et Mycologie / UMR -CNRS 5175 CEFE, Faculté de Pharmacie, 15, avenue Charles-Flahault,
Université Montpellier I, BP 14491, 34093 Montpellier Cedex 5 (France)

Franck RICHARD
Université de Montpellier II, CEFE/CNRS Campus du CNRS, 1919, route de Mende, 34293 Montpellier Cedex 5 (France)

Naritsada THONGKLANG
Center of Excellence in Fungal Research, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Xiang-Hua WANG
CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany,
Chinese Academy of Sciences, Lanhei Road 132, Kunming 650201, P. R. (China)

Couverture / *Cover*:
Extraits d'éléments de la Figure 8 / Extracts of the Figure 8

Cryptogamie, Mycologie est indexé dans / Cryptogamie, Mycologie *is indexed in*:
- Biological Abstracts
- Current Contents
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal)

Cryptogamie, Mycologie est distribué en version électronique par / Cryptogamie, Mycologie *is distributed electronically by*:
- BioOne® (http://www.bioone.org/loi/crym)

Cryptogamie, Mycologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Mycologie *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publishes*: ***Adansonia***, ***Geodiversitas***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Comptes Rendus Palevol***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr
© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2023
ISSN (imprimé / *print*) : 0181-1584 / ISSN (électronique / *electronic*) : 1776-100

Three new species of genus *Russula* Pers. from Sal dominated forests of tropical India based on morphotaxonomy and multigene phylogenetic analysis

Aniket GHOSH
Central National Herbarium, Botanical Survey of India,
3rd MSO Building, DF block, sector 1, Salt Lake City, Kolkata 700064 (India)
ghosh.aniket87@gmail.com

Bart BUYCK
Institut de Systématique, Évolution, Biodiversité (ISYEB),
Muséum national d'histoire naturelle, Sorbonne Université, Université des Antilles,
CNRS, EPHE, case postale 39, 57 rue Cuvier, F-75231 Paris Cedex 05 (France)
bart.buyck@mnhn.fr

Dyutiparna CHAKRABORTY
Eastern Regional Centre, Botanical Survey of India,
Shillong 793003 (India)
dyuti.parna.mail@gmail.com

Manoj Emanuel HEMBROM
Acharya Jagadish Chandra Bose Indian Botanic Garden, Botanical Survey of India,
P. O. Botanic Garden, Howrah 711103 (India)
manojhembrom@yahoo.co.in

Ishika BERA
Kanad DAS
Central National Herbarium, Botanical Survey of India,
P. O. Botanic Garden, Howrah 711103 (India)
iamishika6@gmail.com
kanaddasbsi@gmail.com (corresponding author)

Submitted on 12 September 2022 | Accepted on 5 January 2023 | Published on 21 March 2023

Ghosh A., Buyck B., Chakraborty D., Hembrom M. E., Bera I. & Das K. 2023. — Three new species of genus *Russula* Pers. from Sal dominated forests of tropical India based on morphotaxonomy and multigene phylogenetic analysis. *Cryptogamie, Mycologie* 44 (3): 27-50. https://doi.org/10.5252/cryptogamie-mycologie2023v44a3. http://cryptogamie.com/mycologie/44/3

ABSTRACT
Since 2013, routine macrofungal explorations have been carried out in several *Shorea robusta*-dominated forest areas of tropical eastern India (Bihar, Jharkhand and West Bengal). Three novel species of *Russula* Pers. collected recently from these states of India, *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. in subg. *Compactae* (Fr.) Bon, emend. Buyck & V.Hofst., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. in subg. *Russula* emend. Buyck & V.Hofst., and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. in subg. *Heterophyllidiae* Romagnesi, emend. Buyck & V.Hofst., are described based on morphotaxonomy and molecular data. *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. is characterised by medium to large-sized (30-160 mm) pileus, a more intense blackening of the flesh after cutting or bruising, the unequal, polydymous lamellae with some forkings present at different distances from the stipe, the absence

of pileocystidia, the stronger reticulation of the spore ornamentation, the more-slender hyphal endings in the pileipellis and its occurrence under dipterocarps in Asia. *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. is unique in having very small to medium sized (10-45 mm) pileus, very long "primordial" hyphae usually with strong incrustations covering most of the surface, distinctly smaller spores and occurrence under *Shorea robusta* C.F.Gaertn. On the other hand, *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. is characterised by the absence of strong celery-like taste and odour, and is ectomycorrhizal with *Shorea robusta*. Detailed morphological descriptions, illustrations, phylogenetic analyses of ITS and three-locus (combined nrLSU-mtSSU-*rpb*2) phylogeny for these three species are presented in this communication. Comparisons with morphologically similar and genetically related species are also provided.

KEY WORDS
India,
Basidiomycota,
Compactae,
Heterophyllidiae,
Russula,
new species.

RÉSUMÉ

Trois nouvelles espèces du genre Russula *Pers. provenant de forêts dominées par le Sal en Inde tropicale, décrites d'après la morphotaxonomie et l'analyse phylogénétique multigénique.*

Depuis 2013, des expéditions macrofongiques de routine ont été menées dans plusieurs zones forestières dominées par *Shorea robusta* C.F.Gaertn. dans l'est tropical de l'Inde (Bihar, Jharkhand et Bengale occidental). Trois nouvelles espèces de *Russula* Pers. collectées récemment dans ces états de l'Inde, *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. dans le subg. *Compactae* (Fr.) Bon, emend. Buyck & V.Hofst., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. dans le subg. *Russula* emend. Buyck & V.Hofst., et *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. dans le subg. *Heterophyllidiae* Romagnesi, emend. Buyck & V.Hofst., sont décrites sur la base de la morphotaxonomie et des données moléculaires. *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. se caractérise par un pileus de taille moyenne à grande (30-160 mm), un noircissement plus intense de la chair après une coupe ou une blessure, des lames inégales en plusieurs séries et avec des bifurcations présentes à différentes distances du stipe, l'absence de pileocystidia, une réticulation plus forte de l'ornementation des spores, des terminaisons hyphales plus fines dans le pileipellis et sa présence sous des diptérocarpes en Asie. *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. est unique par son pileus de taille réduite (10-45 mm), ses « hyphes primordiales » très longues, généralement avec de fortes incrustations couvrant la plupart de la surface, ses spores nettement plus petites et sa présence sous *Shorea robusta*. D'autre part, *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. se caractérise par sa chair insipide et inodore, et est ectomycorhizien avec *Shorea robusta*. Des descriptions morphologiques détaillées et illustrées pour ces trois espèces sont fournies. Leurs positions systématiques précises sont déterminées sur les bases d'une analyse phylogénétique de l'ITS et une analyse combinée multigénique (nrLSU-mtSSU-*rpb*2).

MOTS CLÉS
Inde,
Basidiomycota,
Compactae,
Heterophyllidiae,
Russula,
espèces nouvelles.

INTRODUCTION

Russula Pers., one of the most taxonomically diverse genera of mushroom-forming fungi and second largest genus after *Cortinarius* (Pers.) Gray (Kalichman *et al*. 2020), occurs in disparate environments ranging from arctic tundra to tropical rainforests (Looney *et al*. 2018). *Russula* is also by far the most speciose genus in the ectomycorrhizal family Russulaceae (Russulales, Basidiomycota) with about 2000 species worldwide (Adamčík *et al*. 2019) of which, to date, more than 180 taxa have been reported from India (Ghosh *et al*. 2021). The genus is characterized by a colourful pileus, amyloid spore ornamentation, a brittle context due to the presence of abundant sphaerocytes and presence of gloeoplerous elements in part or all of its tissues. It lacks the branching lactiferous system ending in pseudocystidia at the basidiome surface which differentiates it from the genera *Lactarius* Pers. and *Lactifluus* (Pers.) Roussel (Buyck *et al*. 2018). Recently, Buyck *et al*. (2018, 2020) demonstrated that the anatomy of ectomycorrhiza added support to a new infrageneric classification system of *Russula* based on a new multi-locus analysis (nrLSU, mtSSU, *rpb*2, *rpb*1 and *tef*-1), which was followed in this study.

The family Dipterocarpaceae Blume is presumed to form ECM with various fungi (Alexander & Högberg 1986; Lee 1990) and represents a dominant component in the tropics of South Asia (India, Bangladesh, Nepal and Tibet). Family Dipterocarpaceae comprises 470 tree species including *Shorea robusta* C.F.Gaertn. that largely dominates tropical rain forests and represent a major source of commercial timber (Kumar & Atri 2016). In India, *S. robusta* (commonly known as "Sal") is an economically important and common dipterocarp hardwood. It is a major constituent of moist deciduous broad-leaved tropical forests in India. The species is predominantly distributed on the plains, lower foothills and valleys of the Himalayas (Kumar & Atri 2019). It spans central, eastern and north-western parts (Assam, West Bengal, Odisha, Madhya Pradesh, Chattishgarh, Haryana, Himachal Pradesh and Uttarakhand) of India (Singh & Singh 1992). Based on surveys of sporocarps in India, Sal trees have been

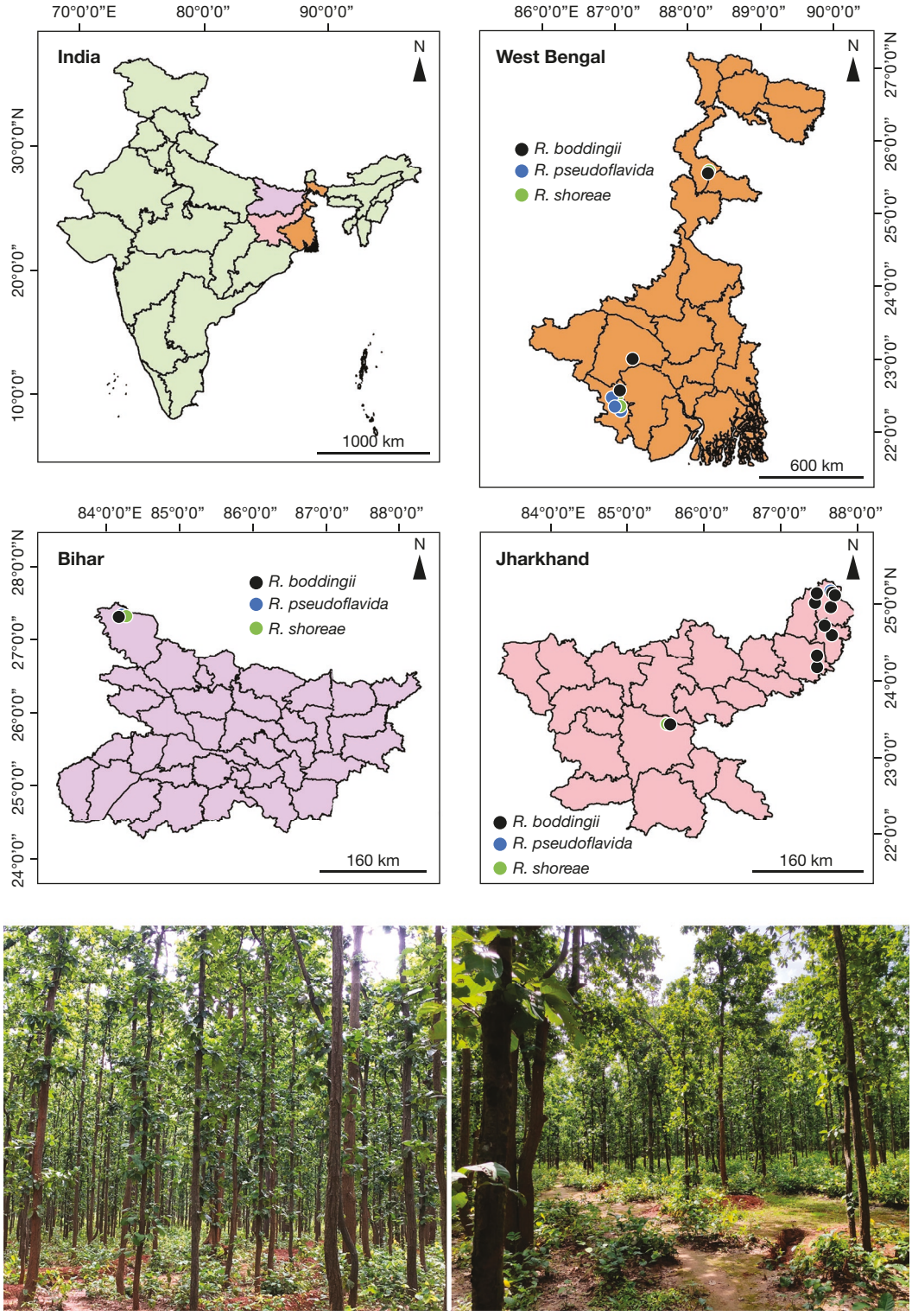

FIG. 1. — Distributional map and habitat of *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. in India.

reported to be putatively ectomycorrhizal and are associated with species of various fungal genera such as *Amanita* Pers., *Boletellus* Murrill, *Borofutus* Hosen & Zhu L. Yang, *Craterellus* Pers., *Indoporus* A. Parihar, K. Das, Hembrom & Vizzini, *Lactarius* Pers., *Pisolithus* Alb. & Schwein. and *Russula* (Natarajan *et al.* 2005; Kumar & Atri 2016; Buyck *et al.* 2017; Hembrom *et al.* 2017; Parihar *et al.* 2018a, b). *Russula* are among the commonest ectomycorrhizal mushrooms in tropical Sal dominated forest ecosystems in India (Dutta *et al.* 2015; Khatua *et al.* 2015, 2017, 2021; Kumar & Atri

2016, 2019, 2020; Verma *et al*. 2018, 2019; Yuan *et al*. 2020) but were very often identified based on overall similarity with their European and North American counterparts and without much critical comparative assessment of detailed macro- and, particularly, micromorphology (Pradhan *et al*. 2012, 2013; Ganguly *et al*. 2021). Unfortunately, in-depth taxonomic studies of these Sal-associated *Russula* species have not yet been undertaken in India, although a only five *Russula* species were reported from Sal forest (particularly from the state of West Bengal) combining morphological study and phylogenetic inferences (Dutta *et al*. 2015; Khatua *et al*. 2015, 2017, 2021; Yuan *et al*. 2020).

During extensive macrofungal surveys to different Sal forests of three eastern Indian states Bihar, Jharkhand and West Bengal, a number of interesting species in the genus *Russula* were collected. Morphological examination and molecular phylogenetic analyses of these collections revealed three species new to science with affinities to different subgenera. These species are here described as *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. in subg. *Compactae* (Fr.) Bon, emend. Buyck & V. Hofst., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. in subg. *Russula* emend. Buyck & V. Hofst., and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. in subg. *Heterophyllidiae* Romagnesi, emend. Buyck & V. Hofst. Detailed macro- and micromorphological descriptions coupled with illustrations are given along with a phylogenetic analysis based on ITS and a three-locus (combined nrLSU-mtSSU-*rpb*2) phylogeny.

MATERIAL AND METHODS

Sampling

The studied survey sites were located in the eastern Indian subcontinents (Bihar, Jharkhand and West Bengal) (Fig. 1). Fruiting bodies were collected yearly from 2013 onwards between early August and late October. Geographic coordinates were recorded using a Garmin e-trax30 hand-held GPS receiver. The presence of all possible host trees was noted when collecting in the field. The collected specimens were dried with a field drier.

Morphology

Fresh specimens were macromorphologically fully described and images of the basidiomata were taken with Sony DSC-RX100 and Canon Power Shot SX 50 HS cameras. Colours were coded by using the Methuen Handbook of Colour (Kornerup & Wanscher 1978).

All micromorphological structures (basidia, hymenial cystidia and elements of pileipellis) were observed from free hand section of preserved dried tissues in 1% ammoniacal Congo red, after a short treatment in warm, aqueous 5% KOH solution to dissolve the gelatinous matrix and improve tissue dissociation. Tissues were mounted in Cresyl Blue (Buyck 1989), sulfovanillin (Caboň *et al*. 2017) and treated with carbolfuchsine (Romagnesi 1967) to observe the presence and colour changes of incrustations and cystidium contents. The terminology and scientific terms for morphological characterisation were according to Vellinga (1988). Drawings of micromorphological features were made with a drawing tube attached to Olympus CX 41 microscope at a magnification of 1000×. Microscopic photographs were taken with an Olympus BX 53 camera. Basidiospores were examined in Melzer's reagent and measured in side view, excluding ornamentations. These measurements are represented as: (MIN-)AV-SD-AV-AV+SD(-MAX) spore-length × (MIN-)AV-SD-AV-AV+SD(-MAX) spore-width and Q = (MIN-)AV-SD-AV-AV+SD(-MAX), in which MIN = the minimum value, MAX = the maximum value, AV = AVERAGE value of total measured collections, SD = standard deviation and Q = corresponds to basidiospore 'length/width ratio'. Statistics of other microscopic characters are expressed as the mean ± standard deviation with extreme values in parentheses. Basidium length excludes the length of sterigmata. Hyphal terminations and pileocystidia were observed both near the pileus margin and at the pileus centre. Scanning Electron Microscope (SEM) images of basidiospores (Fig. 2) were obtained from dry spores that were directly mounted on a double-sided adhesive tape pasted on a metallic specimen-stub and then scanned with silver coating to observe patterns of spore-ornamentation at different magnifications in high vacuum mode (20 KV). SEM work was carried out with a Zeiss Evo 18 special edition model imported from Germany and installed at USIC Dept., Hemvati Nandan Bahuguna Garhwal University (HNBGU) Srinagar (Garhwal) India. Specimens were deposited at the Central National Herbarium (CAL), Howrah. The subgeneric classification used in this study followed Buyck *et al*. (2018, 2020).

DNA extraction, Polymerase Chain Reaction (PCR) and sequencing

Genomic DNA was extracted from 100 mg of dried basidiome (for three species) with the InstaGeneTM Matrix Genomic DNA isolation kit (Biorad, United States) following the manufacturer's instructions. The primers ITS1-F and ITS4, LR0R and LR5, MS1 and MS2 and bRPB2-6F and fRPB2-7cR were used to amplify the ITS, part of the 28S, mtSSU and the region between conserved domains 6 and 7 of *rpb*2 respectively (White *et al*. 1990; Gardes & Bruns 1993; Liu *et al*. 1999; Matheny 2005). PCR amplification was carried out in a PCR thermal cycler (Gene Amp PCR System 9700, Applied Biosystems, United States) programmed for two minutes at 96°C, followed by 30 cycles of 30 seconds at 96°C, 40 seconds at 50°C, two minutes at 72°C, and a final seven minutes extension step at 72°C. The PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN, Germany). Both strands of the PCR fragment were sequenced on the ABI 3500 DNA Analyzer (Applied Biosystems) using the amplifying primers. The sequence quality was checked using Sequence Scanner Software v. 1 (Applied Biosystems). Sequence alignment and required editing of the obtained sequences were carried out using Geneious Pro v. 5.1 (Drummond *et al*. 2010). The newly generated sequences in this study were submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Accession numbers of species used in the multigene (nrLSU-mtSSU-*rpb*2) phylogenetic analysis (Fig. 3) are listed in the Table 1.

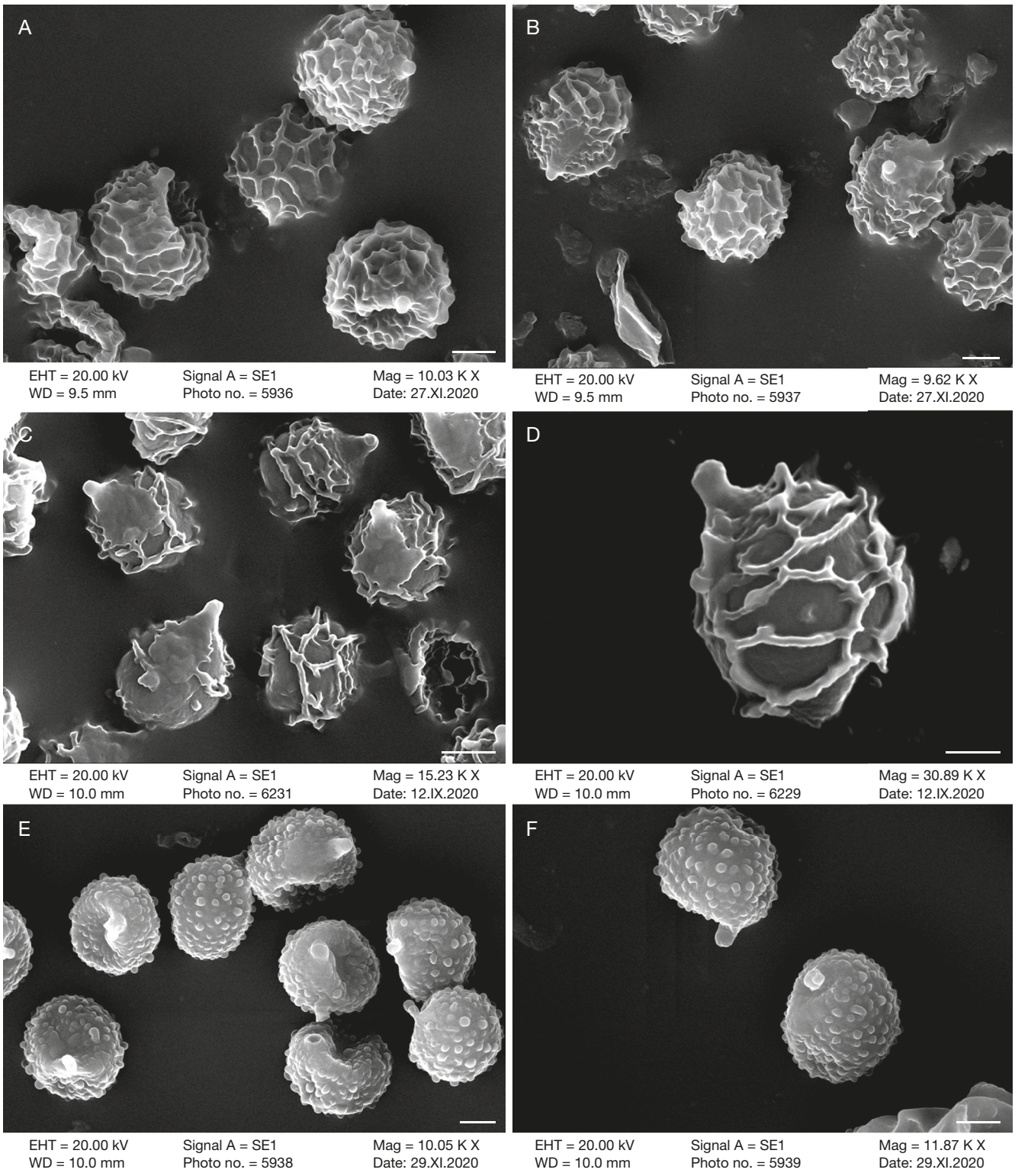

Fig. 2. — SEM micrographs of basidiospores: **A**, **B**, *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov.; **C**, **D**, *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov.; **E**, **F**, *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. Scale bars: A-C, E, F, 2 µm; D, 1 µm.

Phylogenetic analysis

The nrITS, nrLSU, mtSSU and *rpb2* sequences of the newly generated three *Russula* species (*Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov., and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov.) and their close relatives were retrieved from nBLAST search against GenBank (https://www.ncbi.nlm.nih.gov/genbank/),

TABLE 1. — List of specimens used in this study.

Species name	Voucher no.	GenBank accession no.		
		nrLSU	mtSSU	*rpb2*
Multifurca aurantiophylla	644/BB 09.119	KU237581	KU237429	KU237867
M. ochricompacta	580/BB 07.010	KU237565	KU237413	KU237851
Russula acrifolia	543/BB 08.662	KU237535	KU237381	KU237821
R. adusta	223/BB 06.562	KU237476	KU237320	KU237762
R. albonigra	SAV F-20197	MW182464	–	MW306673
R. albonigra	JK RUS 13090603	MW182461	–	MW306670
R. ambusta	SAV F-3358	MW182466	–	–
R. atramentosa	FH0170824-02	MW182483	–	MW306687
R. atramentosa	FH 2011-002R	MW182482	–	MW306685
R. aurantioflava	LAH35405	MN130122	MN161166	–
R. aurantioflava	LAH35408	MN130121	MN161165	–
R. aurantioflava	LAH35410	MN130120	MN161164	–
R. aurata	547/BB 07.211	KU237539	KU237385	KU237825
***R. boddingii* sp. nov.**	**MEH-16-32**	**ON365926**	**ON387510**	**ON418910**
***R. boddingii* sp. nov.**	**MEH-18-01**	**ON365924**	**ON387513**	**ON418909**
R. cf. *cyanoxantha*	BPL280	KT933837	–	KT933908
R. cf. *fuliginosa*	FH RUS 14091001	MW182487	–	MW306693
R. cf. *variata*	BPL241	KT933818	–	KT933889
R. cyanoxantha	GENT FH 12-201	KR364225	–	KR364341
R. cyanoxantha	UE29.09.2002-2	DQ422033	–	–
R. densifolia	439/BB 07.344	KU237502	KU237347	KU237788
R. densifolia	RDL 16-001/2	MW182484	–	MW306688
R. densifolia	RDL 17-024	MW182486	–	MW306690
R. densifolia	RDL 18-052	MW182485	–	MW306689
R. densissima	FH 2010 ST02	–	–	MW306692
R. densissima	FH 2014 ST04	–	–	MW306691
R. dissimulans	BPL285	KT933840	–	KT933911
R. fuliginosa	1178/M. Floriani	KU237597	KU237445	KU237882
R. fuliginosa	FH RUS 14091201	MW182488	–	MW306694
R. gracillima	441/BB 07.785	KU237504	KU237349	KU237790
R. inquinata	JAC9757	MW683608	–	–
R. inquinata	JAC11697	MW683635	–	–
R. inquinata	JAC13249	MW683667	–	–
R. lotus	LF321	MG214694	–	–
R. luteotacta	452/BB 07.188	KU237512	KU237358	KU237798
R. maguanensis	XHW4765	MH714537	–	MH939989
R. nigricans	429/BB 07.342	KU237495	KU237339	KU237781
R. nigricans	RDL 17-004	MW182489	–	MW306695
R. nigrifacta	RDL 16-044	MW182470	–	MW306677
R. peckii	BPL270	KT933830	–	KT933901
R. persicina	428/BB 07.271	KU237494	KU237338	KU237780
R. phloginea	CNX530524304	MK860703	MK860707	–
***R. pseudoflavida* sp. nov.**	**AG 20-058**	**ON365928**	**ON387512**	**ON398067**
***R. pseudoflavida* sp. nov.**	**AG 21-070**	**ON365929**	**ON387511**	**ON398068**
R. queletii	FH12237	KT933868	–	KT933939
R. redolens	BPL141	KT933808	–	KT933879
R. redolens	BPL260	KT933825	–	KT933897
R. sanguinea	FH12240	KT933869	–	KT933940
R. sardonia	FH12215	KT933860	–	KT933931
***R. shoreae* sp. nov.**	**AG 20-027**	**ON365931**	**ON387514**	**ON398070**
***R. shoreae* sp. nov.**	**NPDF917-10L**	**ON365930**	**ON387509**	**ON398069**
Russula sp.	GENT FH 12-064	–	MN161168	MN380517
R. substriata	XHW4785	MH714542	–	MH939994
R. subtilis	SAV F-3805	–	–	MN380524
R. velutipes	SAV F-3428	–	KY471604	KY616704
R. wielangtae	HO 593331	–	MN161196	–
R. wielangtae	HO 593332	–	MN161197	MN380531
R. zvarae	538/BB 08.639	KU237530	KU237376	KU237816

UNITE database (https://unite.ut.ee) and relevant published phylogenies (Looney *et al.* 2018; Adamčík *et al.* 2019; Das *et al.* 2020; Ghosh *et al.* 2020, 2021; Zhou *et al.* 2020; De Lange *et al.* 2021). Four datasets (nrITS, nrLSU, mtSSU and *rpb2*) were created separately. All the datasets were aligned separately using the online version of the multiple sequence alignment program MAFFT v. 7 (https://mafft.cbrc.jp/alignment/software/) with the L-INS-i strategy (Katoh *et al.* 2019). The alignment was checked and trimmed manually with MEGA v. 7 (Kumar *et al.* 2016). To eliminate ambiguous positions in the alignment as much objectively as possible, Gblocks 0.91b (Talavera & Castresana 2007) was used. The

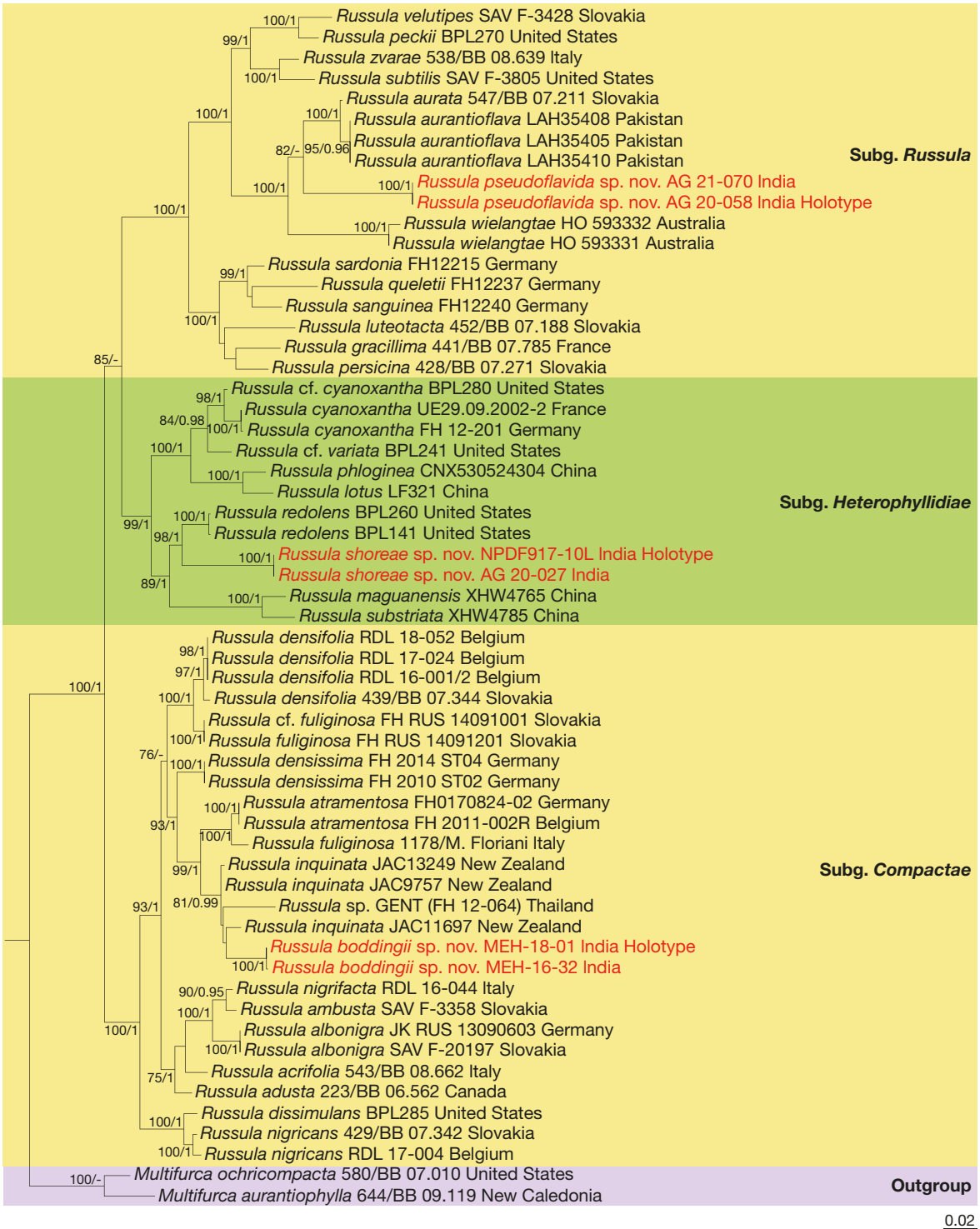

Fig. 3. — Phylogram generated by Maximum Likelihood analysis based on combined sequence data of nrLSU, mtSSU and *rpb2* for *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. and their allied species. Maximum Likelihood bootstrap support values (MLbs) ≥70% are shown on the left of "/" and Bayesian Posterior Probabilities (BPP) ≥0.95 are shown on the right above or below the branches at nodes. The new species are placed in **red font** to highlight their phylogenetic positions in the tree.

program was run with settings allowing for smaller blocks, gaps within these blocks and less strict flanking positions. Species delimitation was first examined using single locus phylogenies. When significant conflict was not observed among the single locus phylogenies, then we concatenated three single-locus datasets (nrLSU, mtSSU and *rpb2*) into one multi-locus dataset using BioEdit v. 7.0.9 (Hall 1999). The *rpb2* intron was excluded entirely in the phylogenetic analyses. The single-locus (nrITS) and three-loci (nrLSU-mtSSU-*rpb2*) datasets were phylogenetically analysed using both Maximum Likeli-

hood (ML) and Bayesian inference (BI) methods. ML was performed using raxmlGUI 2.0 (Edler *et al.* 2021) with the GTRGAMMA substitution model. ML analysis was executed applying the rapid bootstrap algorithm with 1000 replicates to obtain nodal support values. For BI, ITS alignments were divided into three partitions: ITS1, 5.8S and ITS2. In case of combined dataset (nrLSU-mtSSU-*rpb*2), five partitions (nrLSU, mtSSU, *rpb*2-pos1, *rpb*2-pos2 and *rpb*2-pos3) were assigned for BI analyses. PartitionFinder2 was used to find the best substitution models using the Akaike information criterion (AICc) with a greedy search over all models (Lanfear *et al.* 2017). BI was computed in MrBayes v. 3.2.6 (Ronquist *et al.* 2012) with four Markov chain Monte Carlo (MCMC) chains for 1 000 000 iterations until the standard deviation of split frequencies reached below the 0.01 threshold. Trees were sampled every 100th generation. The first 25% of trees were discarded as burn-in. Chain convergence was determined using Tracer 1.5 (Rambaut *et al.* 2014) to ensure sufficiently large effective sample size (ESS) values (> 200). Gaps in the alignment were treated as missing data in phylogenetic analyses. Maximum Likelihood bootstrap (MLbs) values ≥ 70% and Bayesian Posterior Probabilities (BPP) values ≥ 0.95 are shown in the phylogenetic tree (Figs 3; 4; 7; 10).

Phylogeny

The final nrITS datasets of three subgenera involving our three novel species (*R. boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov., *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. and *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov.) consisted of 75, 57 and 63 sequences with 590, 509 and 684 characters respectively including gaps. The final combined (nrLSU-mtSSU-*rpb*2) dataset consisted of 58 sequences including our consensus sequence and final alignment comprised 2191 characters including gaps (nrLSU 945 bp, mtSSU 605 bp, *rpb*2 641 bp). Both the ML and BI analyses resulted in essentially the same tree topologies and our three novel taxa are presented in the phylogenetic trees in bold red font (Figs 3; 4; 7; 10).

The nrITS phylogenetic analyses showed that *R. boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. (GenBank[OL469097, OL469118]) was placed in subg. *Compactae* sect. *Compactae*, where it was part of a fully supported *R. densifolia* lineage (MLbs = 100%, BPP = 1) that included also the European *R. densifolia* Secr. ex Gillet, *R. atramentosa* Sarnari, *R. densissima* Romagn., *R. fuliginosa* Sarnari, several Japanese lineages and the Australian *R. ingwa* Grgur. (Fig. 4). Within this lineage, our Indian sequences clustered together with sequence MN580113 obtained from a "*R. densifolia*" from dipterocarp forest in Thailand (Yuwa-Amornpitak & Yeunyaw 2020) which also represents our new species. Within the *R. densifolia* lineage, *R. boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. formed a significantly supported clade (MLbs = 79%, BPP = 0.99) together with another unnamed *Russula* sp. (GenBank[MN130076]) from Thailand and two *R. densifolia* lineages from Japan (subgroups A-5 and A-6; GenBank[AB291755, AB291758, AB291759, AB291763]). Our multigene phylogenetic estimations (Fig. 3) are showing that *R. boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. (voucher nos *MEH-16-32* and *MEH-18-01*) clustered with *R. inquinate* (voucher nos JAC11697, JAC13249 and JAC9757) collected from New Zealand and *Russula* sp. (voucher no. GENT[FH 12-064]) from Thailand with strong support (MLbs = 81%, BPP = 0.99) and is sister to European *R. fuliginosa* (voucher no. *1178/M. Floriani*) and *R. atramentosa* (voucher nos *FH2011-002R* and *FH0170824-02*) also with strong (MLbs = 99%, BPP = 1) support.

Phylogenetic analysis based on nrITS sequences revealed that the two collections of our second species, *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. (GenBank[OL471685, OL471686]) are clustered with an unidentified *Russula* sp. (GenBank[KP012681]) from Australia, being sister to the clade *R. flavida* Frost ex Peck originating from United States and Thailand with strong (MLbs = 100%, BPP = 1) support (Fig. 7). The phylogenetic analysis based on (combined nrLSU-mtSSU-*rpb*2) sequences exhibited that *R. pseudoflavaida* (voucher nos *AG 20-058* and *AG 21-070*) clustered with Pakistani *R. aurantioflava* Kiran & Khalid (voucher nos LAH35405, LAH35408 and LAH35410) and European *R. aurata* Fr. (voucher no. *547/BB07.211*) with strong (MLbs = 82%) support (Fig. 3).

Finally, the nrITS sequences (GenBank[OL461227, OL461230]) of both collections of our third new species, *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov., are clustered with Chinese *R. verrucospora* Y.Song & L.H.Qiu with significant support (MLbs = 74%, BPP = 1), both being sister to the North American *R. redolens* Burl. with strong (MLbs = 97%) support (Fig. 10). In our multigene phylogenetic analysis (Fig. 3) *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. (voucher nos *AG 20-027* and *NPDF917-10L*) is sister to North American *R. redolens* (voucher nos *BPL141* and *BPL260*) with strong (MLbs = 98%, BPP = 1) support.

RESULTS AND DISCUSSION

Order RUSSULALES Kreisel ex P.M.Kirk,
P.F.Cannon & J.C.David
Family Russulaceae Lotsy
Genus *Russula* Pers.

Russula boddingii

Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov.
(Figs 4-6)

Russula boddingii Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. is mainly separated from *R. densifolia* Secr. ex Gillet by a combination of medium to large-sized (30-160 mm) pileus, a more intense blackening of the flesh after cutting or bruising, the unequal, the absence of pileocystidia, the stronger reticulation of the spore ornamentation, the more slender hyphal endings (2-6 µm wide) in the pileipellis and its occurrence under dipterocarps in Asia.

Holotype. — **India**. West Bengal, Jhargram district, Lalgarh, Karamsol, 22°34'12.9"N, 87°05'25.2"E, alt. 73 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 1.VII.2018, M.E. Hembrom, *MEH-18-01* (holo-, CAL[CAL 1860]!).

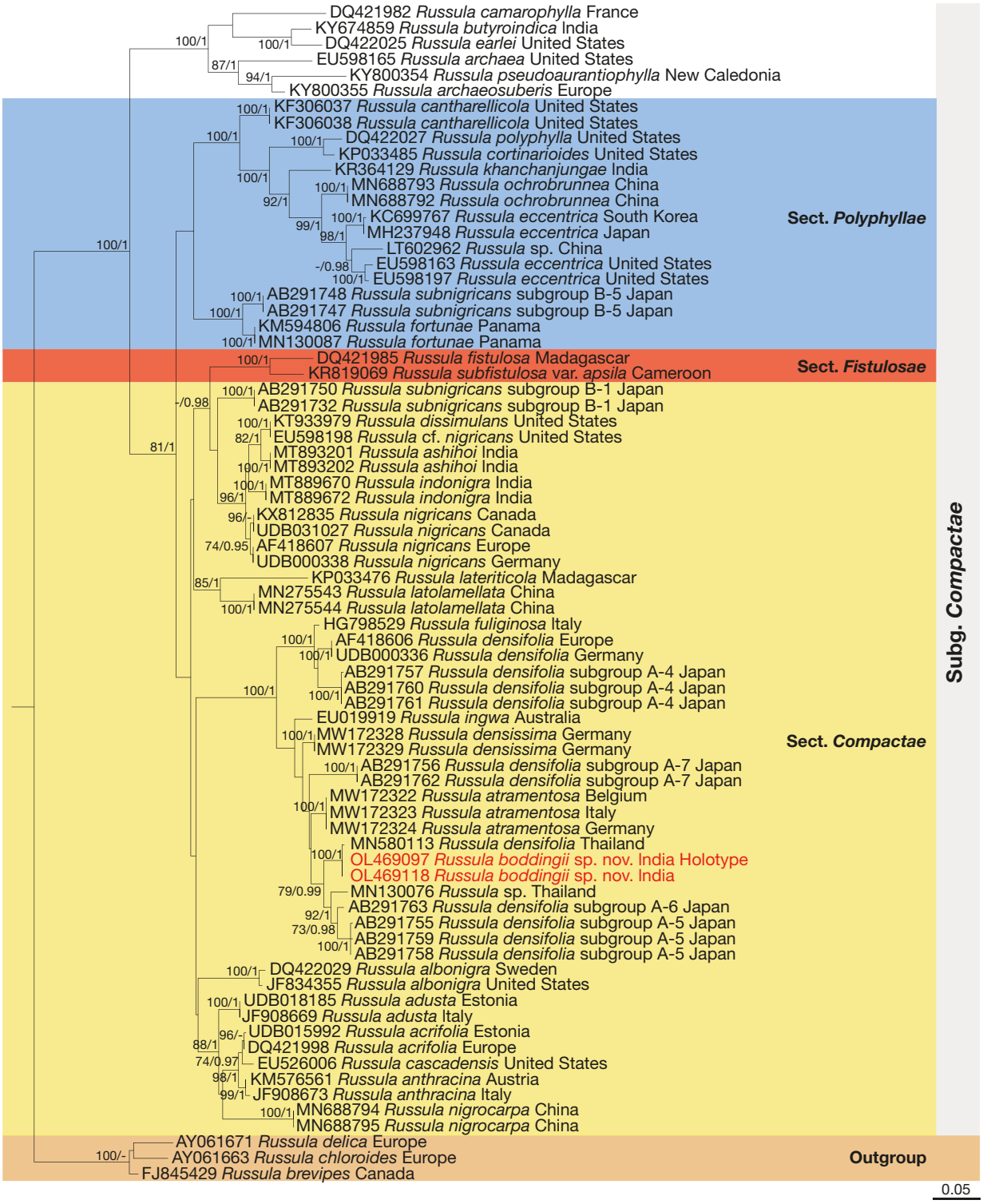

Fig. 4. — Phylogram generated by Maximum Likelihood analysis based on nrITS sequence data of *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. and allied species. Maximum Likelihood bootstrap support values (MLbs) ≥70% are shown on the left of "/" and Bayesian Posterior Probabilities (BPP) ≥0.95 are shown on the right above or below the branches at nodes. *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. is placed in **red font** to highlight its phylogenetic position in the tree.

Additional specimens examined. — **India**. Jharkhand, Rajmahal hills, Sahibganj district, Mandro block, near Mandro Fossil Park, 25°07'31.3"N, 87°31'22.3"E, alt. 142 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 20.VIII.2013, M.E. Hembrom, *MEH-13-03*; Sahibganj district, Borio block, Pir-Baba Kairasol forest area, 25°09'41.7"N, 87°40'31.9"E, alt. 126 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 24.VIII.2013, M.E. Hembrom, *MEH-13-27*; Rajmahal hills, Godda district, Boarijore block, Mangra Dahar-Langi and surroundings, 25°01'43.0"N, 87°28'13.8"E, alt. 136 m a.s.l., on ground, under *S. robusta* in tropi-

cal deciduous forests, 01.IX.2013, M.E. Hembrom, *MEH-13-31*; Rajmahal hills, Pakur district, Hiranpur block, Talpahari to Tugutola forest area, 24°37'02.6"N, 87°40'45.2"E, alt. 94 m. a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 22.VIII.2014, M.E. Hembrom, *MEH-14-28*; Pakur district, Litipara block, Sathiya to Sathiyapahar forest area, 24°44'44.3"N, 87°35'03.8"E, alt. 225 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 02.IX.2014, M.E. Hembrom, *MEH-14-33*; Rajmahal hills, Dumka district, Kathikund block, Kanhaidih reserve forest, 24°19'04.2"N, 87°29'14.3"E, alt. 132 m a.s.l., 18.IX.2015, on ground, under *Shorea robusta* in tropical deciduous forests, M.E. Hembrom, *MEH-15-09*; Dumka district, Sikaripara block, Karakata forest area, 24°13'19.0"N, 87°30'16.2"E, alt. 241 m a.s.l., on ground, under S. robusta in tropical deciduous forests, 23.X.2015, M.E. Hembrom, *MEH-15-17*; Sahibganj district, Taljhari block, Karanpurato village forest toward Gogi, 25°09'02.9"N, 87°43'02.3"E, alt. 61 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 06.XI.2016, M.E. Hembrom, *MEH-16-21*; Sahibganj district, Borio block, Dhogada-Paharia burial ground forest, 25°02'23.7"N, 87°39'35.8"E, alt. 110 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 08.XI.2016, M.E. Hembrom, *MEH-16-32* (CAL[CAL 1861]); Rajmahal hills, Sahibganj district, Borio block, Dhogada-Paharia burial ground forest, 25°02'23.7"N, 87°39'35.8"E, alt. 110 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 15.XI.2020, M.E. Hembrom, *MEH-20-10*; Rajmahal hills, Pakur district, Hiranpur block, Talpahari to Tugutola forest area 24°37'02.6"N, 87°40'45.2"E, alt. 94 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 26.VIII.2021, A. Ghosh, *AG 21-08* (JH); Ranchi district, Getalsud, 23°28'36.5"N, 85°33'23.8"E, alt. 570 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 09.X.2021, M.E. Hembrom, *MEH-21-25*; Bihar, West Champaran district, Valmiki national Park, Raghia range, Sitalbari enclosure, 27°20'14.4"N, 84°13'05.8"E, alt. 133 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 15.IX.2020, M.E. Hembrom, *MEH-20-104*; West Bengal, Bankura district, Joypur forest, 23°01'53.00"N, 87°15'15.73"E, alt. 73 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 08.VII.2020, A. Ghosh, *AG 20-004*; Paschim Medinipur district, Chandra, 22°21'01"N, 87°02'00"E, alt. 90 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 12.VIII.2020, D. Chakraborty, *NPDF917-17L*; Uttar Dinajpur, Kaliyaganj, Dhamja, 25°18'00"N, 88°20'35.9"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 07.IX.2020, D. Chakraborty, *RGJ-20-08*; Uttar Dinajpur, Kaliyaganj, Dhamja, 22°19'44"N, 87°02'39"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 13.VIII.2021, A. Ghosh, *AG 21-074*; Uttar Dinajpur, Kaliyaganj, Dhamja, 25°18'00"N, 88°20'35.09"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 10.X.2021, D. Chakraborty, *RGJ-21-05*.

GenBank. — OL469097 (nrITS, holotype) and OL469118 (nrITS, specimen voucher no. *MEH-16-32*); ON365924 (nrLSU, holotype), ON365926 (nrLSU, specimen voucher no. *MEH-16-32*); ON387513 (mtSSU, holotype), ON387510 (mtSSU, specimen voucher no. *MEH-16-32*); ON418909 (*rpb2*, holotype), ON418910 (*rpb2*, specimen voucher no. *MEH-16-32*).

Etymology. — Commemorating Reverend Paul Olaf Bodding, a Norwegian missionary, linguist, folklorist and ethnobotanist who undertook pioneer work on the macrofungi of Rajmahal Hills.

MycoBank. — MB 844205.

Facesoffungi number. — FoF 11436.

Description

Pileus medium-sized to large, 30-160 mm in diam., convex when young, becoming planoconvex to applanate, centrally depressed to umbilicate at maturity; margin smooth, entire when young becoming decurved to plane, sometimes uplifted with age; cuticle smooth, viscid and shiny when wet, dull upon drying, peeling to ¼ of the radius, greyish white (1B2) to grey (2-5B2) with yellowish white (3A2) tinges. Pileus context firm and up to 9 mm thick at the disc centre, becoming narrower towards margin, chalky white (1-2A1), changing first orange red (8A8) or brownish red (8C6-7), then blackish when cut or bruised; turning dull green (27D3-4) with $FeSO_4$, and deep to dark turquoise (24E-F7-8) in guaiacol. Lamellae unequal, of different lengths, narrow, up to 5 mm deep, sub-decurrent to decurrent, crowded (15-22/cm at pileus margin), chalky white (1-2A1) to yellowish white (3A2), forked at different distances from the stipe; edges entire and concolorous. Stipe 25-57 × 9-23 mm, cylindrical, subclavate to clavate, central, firm and fleshy; surface dry, smooth, chalky white (1-2A1) to greyish white (1B2); turning dull green (27D3-4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol. Stipe context solid, chalky white (1-2A1), changing first orange red (8A8) or brownish red (8C6-7), then blackish when cut or bruised; turning dull green (27D3-4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol. Odour insignificant. Taste mild. Spore print not obtained.

Basidiospores globose, subglobose to broadly ellipsoid, (5.8-)6.2-6.7-7.2(-7.8) × (5.5-)5.6-6.0-6.5(-7) µm, Q = (1-)1.07-1.12-1.16(-1.20); ornamentation composed of relatively dense, obtuse-rounded, conical amyloid warts (up to 0.8 µm high), connected by thick ridges forming an almost complete network; suprahilar spot inamyloid; apiculi up to 1.2 µm long. Basidia (28-)34.5-40-45(-48) × 8-9-10(-11) µm, 4-spored, narrowly clavate to clavate, sterigmata up to 8 µm long; basidiola cylindrical to clavate. Hymenial gloeocystidia on the lamellae sides (22-)33.5-54.5-75.5(-112) × (4-)5-7.5-9.5(-10) µm, emergent up to 14 µm above the other elements of the hymenium, near the lamellae edges usually smaller and narrower, 31-43-55 (-65) × 3-5-6(-7) µm, cylindrical to clavate with capitate to moniliform apex; contents completely or partly filled with brown refractive bodies, not reacting in sulfovanillin. Marginal cells absent. Subhymenium layer up to 20 µm thick, pseudoparenchymatous. Hymenophoral trama mainly composed of large nests of sphaerocytes and intermixed with hyphal elements. Pileipellis orthochromatic in Cresyl Blue, sharply delimited from the underlying context, 300-380 µm thick, two-layered; suprapellis 140-200 µm thick, composed of narrow, ascending hyphal terminations; subpellis 160-180 µm deep, composed of more or less dense, horizontally oriented hyphae. Acid-resistant incrustations absent. Hyphal terminations near the pileus margin long, flexuous, densely septate, scarcely branched at the bases, sometimes with lateral branches, thin-walled, partly filled with irregular refractive bodies containing brown pigments; terminal cells (39-)44-58-72(-90) × (3-)4-4.5-5.5(-6) µm, narrowly cylindrical to subulate, apically obtuse-rounded or acute; subterminal cells and the cells below often gradually wider, usually shorter. Hyphal terminations near the pileus centre apically more attenuated; the terminal cells slightly shorter and less wide, measuring (26-)34.5-50-65(-85) × (2-)3-3.5-4.5(-5) µm. Pileocystidia absent. Clamp connections absent from all tissues.

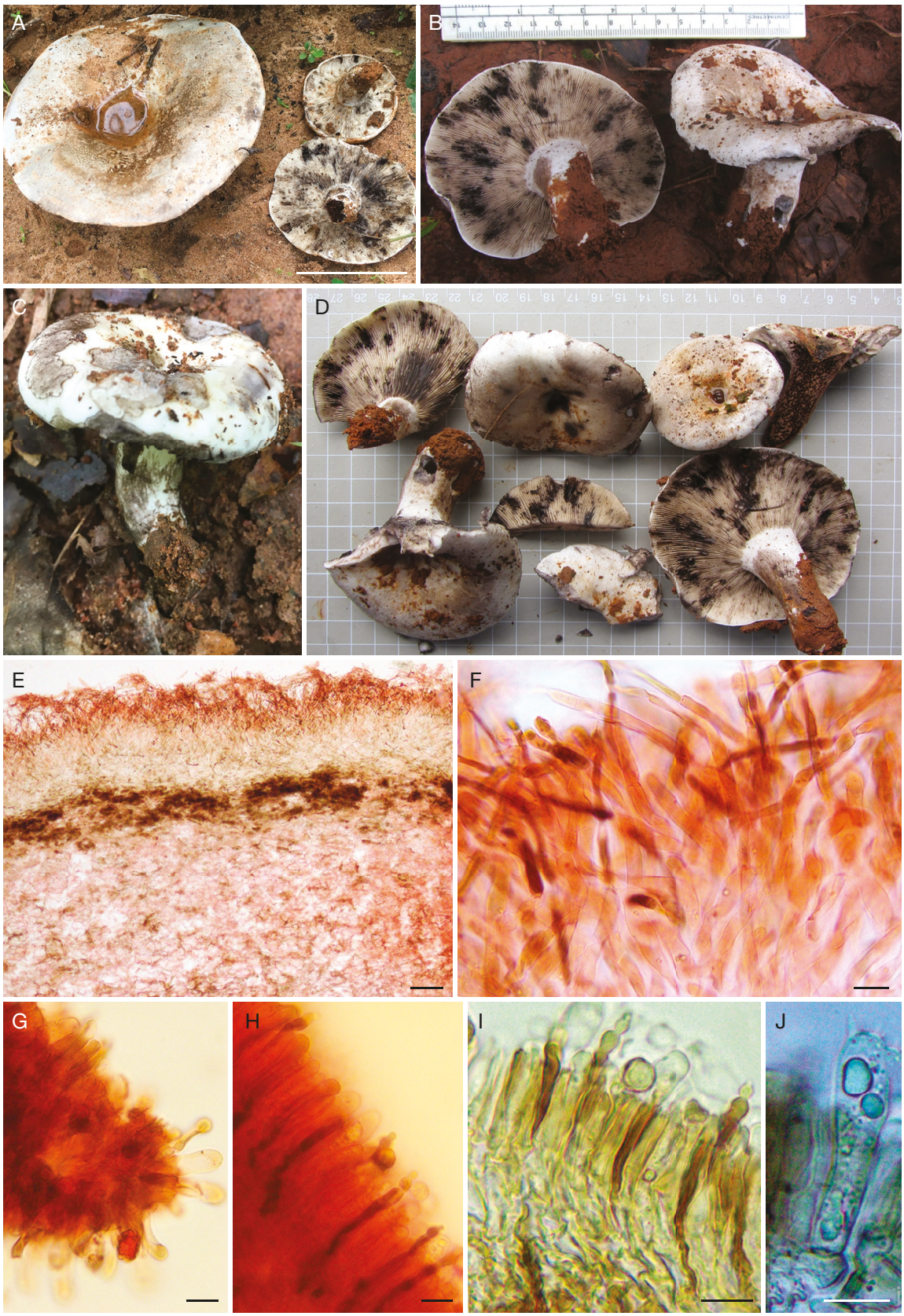

FIG. 5. — *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. (from holotype): **A**-**D**, fresh and dissected basidiomata in the field and basecamp; **E**, **F**, transverse section through pileipellis showing elements; **G**, transverse section through lamellae showing hymenial gloeocystidia near the lamellae edges; **H**, **I**, transverse section through lamellae showing hymenial gloeocystidia near the lamellae sides; **J**, transverse section through lamellae showing basidia. Scale bars: A, 40 mm; E, 100 µm; F-J, 10 µm.

Notes

In its most recent interpretation, *Russula* subg. *Compactae* (Fr.) Bon, emend. Buyck & V. Hofst. (Hongsanan *et al*. 2015) includes species that produce more or less thick-fleshed, very small to large basidiomata with dull to dingy white, brown, grey to black pileus, regularly unequal, polydymous lamellae, a mild to very acrid context that is reddening, greying, blackening, rarely browning and often with unpleasant smell, white spore print and spores with inamyloid suprahilar spot; gloeocystidia mostly capitate with one central knob or more frequently with two excentrical knobs. In a recent multilocus phylogeny (Buyck *et al*. 2018), this subgenus was shown to be composed of two highly supported lineages: sect. *Polyphyllae* Buyck & V. Hofst. and sect. *Nigricantinae* Bataille, which is the core group of this subgenus as it holds the European *R. nigricans*, the type species. With very few exceptions, species of sect. *Nigricantinae* have basidiomata that react most frequently by first reddening on bruising before turning to black. This feature, in combination with the unequal, polydymous gills, is still considered to constitute the easiest field character to recognize species of this section (Das *et al*. 2020).

A nBLAST of the obtained ITS sequences of our specimens undeniably placed our new species in sect. *Nigricantinae* with sequences MN075499 (99.51% similarity), MN580113 (99.05% similarity) and JN969389 (99.13% similarity), all three obtained from deciduous dipterocarp forests in Thailand (Phosri *et al*. 2012; Pachit *et al*. 2020; Yuwa-Amornpitak & Yeunyaw 2020), representing earlier reports of *R. boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. None of the other sequences resulting from nBLAST was more similar than 96% to our species, and all suggested a placement of our new species in the *R. densifolia* lineage.

In recent years, several new Asian species have been published in sect. *Nigricantinae* (Das *et al*. 2020; Zhou *et al*. 2020), but none of these had crowded gills as in the *R. densifolia* lineage. The latter lineage has been retrieved as a highly supported clade in recent multigene phylogenetic analyses (Buyck *et al*. 2018; De Lange *et al*. 2021). So far, only five described species have been shown to be part of this lineage, but molecularly quite distinct for our new species with very high support (Fig. 4): these species include the European *R. densifolia*, *R. densissima*, *R. atramentosa* and *R. fuliginosa*, the Australian *R. ingwa*, as well as at least five additional but undescribed Asian species in this lineage.

Russula pseudoflavida
A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov.
(Figs 7-9)

Russula pseudoflavida A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. differs from North American *R. flavida* Frost ex Peck in its very small to medium sized (10-45 mm) pileus, very long primordial hyphae usually with strong incrustations covering most of the surface, distinctly smaller spores and occurrence under *Shorea robusta*.

Holotype. — **India**. West Bengal, Jhargram district, Tuluha, 22°19'18"N, 87°05'34"E, alt. 80 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 13.VIII.2020, A. Ghosh, *AG 20-058* (holo-, CAL[CAL 1862]!).

Additional specimens examined. — **India**. West Bengal, Paschim Medinipur district, Chandra, 22°21'01"N, 87°02'00"E, alt. 90 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 12.VIII.2020, A. Ghosh, *AG 20-022*; Jhargram district, Lodhasuli, 22°19'50"N, 87°01'41"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 13.VIII.2020, A. Ghosh, *AG 20-036*; Jhargram district, Jhargram city, 22°25'01.1"N, 87°00'13.5"E, alt. 103 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 12.VIII.2021, A. Ghosh, *AG 21-070* (CAL[CAL 1863]); Bihar, West Champaran district, Valmiki national Park, Raghia range, Sitalbari enclosure, 27°20'14.4"N, 84°13'05.8"E, alt. 133 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 15.IX.2020, M.E. Hembrom, *MEH-20-110*; Jharkhand, Rajmahal hills, Sahibganj district, Borio block, Pir-Baba Kairasol forest area, 25°09'41.7"N, 87°40'31.9"E, alt. 126 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 24.VIII.2021, M.E. Hembrom, *MEH-21-06*; Rajmahal hills, Pakur district, Hiranpur block, Talpahari to Tugutola forest area, 24°37'02.6"N, 87°40'45.2"E, alt. 94 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 26.VIII.2021, A. Ghosh, *AG 21-11* (JH).

GenBank. — OL471685 (nrITS, holotype) and OL471686 (nrITS, specimen voucher no. *AG 21-070*); ON365928 (nrLSU, holotype), ON365929 (nrLSU, specimen voucher no. *AG 21-070*); ON387512 (mtSSU, holotype), ON387511 (mtSSU, specimen voucher no. *AG 21-070*); ON398067 (*rpb2*, holotype), ON398068 (*rpb2*, specimen voucher no. *AG 21-070*).

Etymology. — Referring to its being a look-alike and close relative of *R. flavida*, a North American species in the crown clade of *Russula* subg. *Russula*.

MycoBank. — MB 844206.

Facesoffungi number. — FoF 11437.

Description

Pileus very small to medium-sized, 10-45 mm in diam., convex when young, becoming planoconvex to applanate, uplifted with age, centrally depressed to umbilicate with maturity, margin tuberculate striate, decurved to plane with age; cuticle smooth, velvety, viscid and shiny when wet, dull upon drying, peeling to ½ of the radius, deep orange (6A-B7-8) or brownish orange (6-7C7-8) when young, then yellowish orange, orange yellow to deep yellow (4A7-8) or even orange to deep orange (5A7-8). Pileus context 5-10 mm thick at the disc, thinning towards the margin, brittle, chalky white (1-2A1), unchanging after bruising or cutting; turning salmon pink (6A4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol. Lamellae equal, 10-15 mm high, adnexed to narrowly adnate, normally spaced (10/cm) to crowded (up to 22/cm at pileus margin), rounded near pileus margin, chalky white (1-2A1), sometimes forked near stipe apex; edges even, marginate, deep orange or dark orange (5A8). Stipe 10-30 × 4-9 mm, cylindrical, central, firm, with dry, smooth, velvety surface that is concolorous to pileus, but chalky white (1-2A1) at the stipe apex, unchanging after bruising or cutting, turning salmon pink (6A4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol, stuffed and chalky white (1-2A1) inside, unchanging. Odour not distinctive. Taste mild. Spore print not obtained.

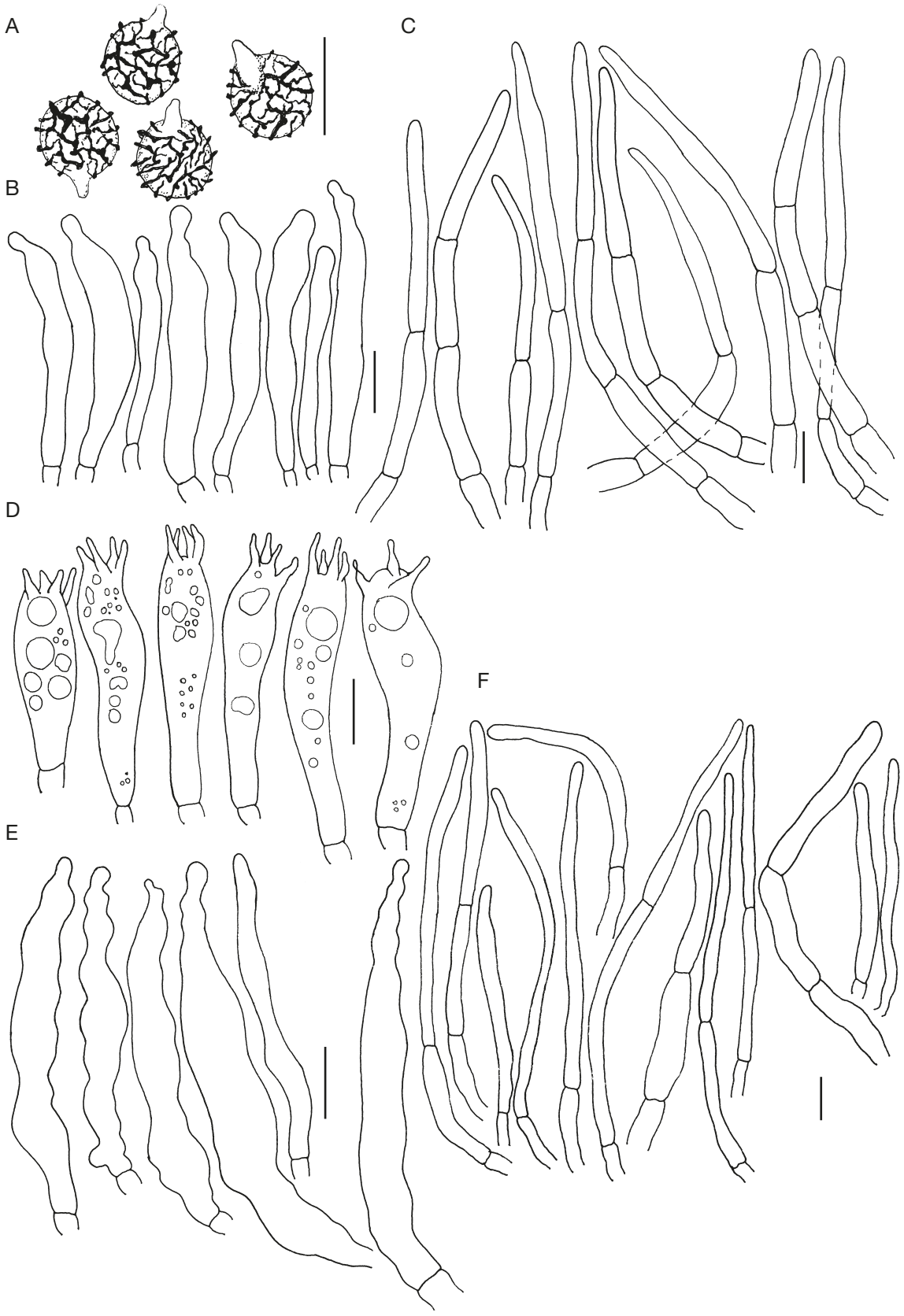

Fig. 6. — *Russula boddingii* Hembrom, D.Chakr., A.Ghosh & K.Das, sp. nov. (from holotype): **A**, basidiospore; **B**, hymenial gloeocystidia near the lamellae edges; **C**, elements of the pileipellis near the pileus centre: hyphal terminations; **D**, basidia; **E**, hymenial gloeocystidia near the lamellae sides; **F**, elements of the pileipellis near the pileus margin: hyphal terminations. Scale bars: 10 µm.

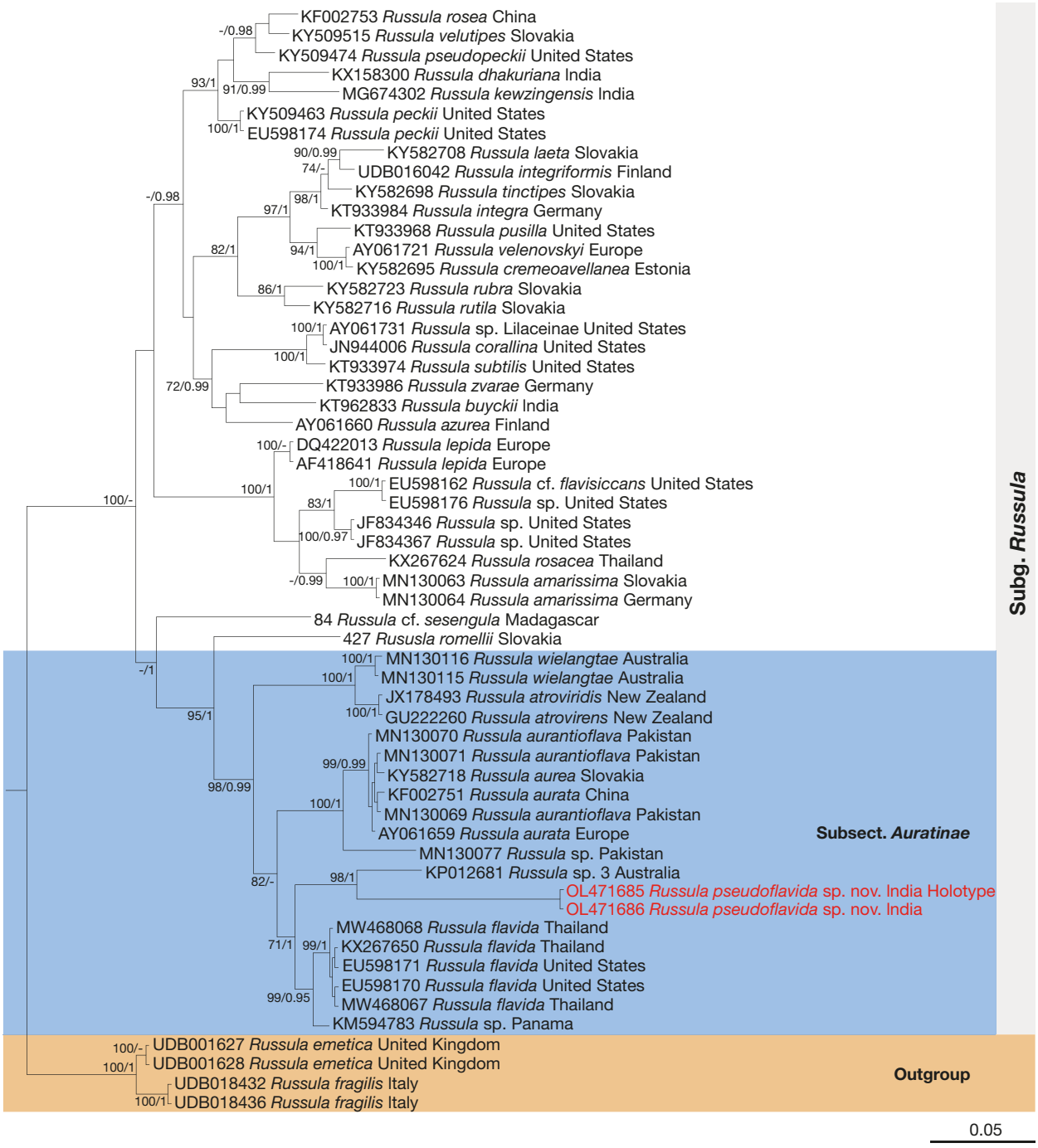

Fig. 7. — Phylogram generated by Maximum Likelihood analysis based on nrITS sequence data of *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. and allied species. Maximum Likelihood bootstrap support values (MLbs) ≥70% are shown on the left of "/" and Bayesian Posterior Probabilities (BPP) ≥0.95 are shown on the right above or below the branches at nodes. *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. is placed in **red font** to highlight its phylogenetic position in the tree.

Basidiospores globose, broadly ellipsoid to ellipsoid, (5.5-)5.7-6.05-6.5(-7.0) × (4.4-)4.8-5.2-5.5(-6.2) µm, Q = (1-)1.11-1.17-1.22(-1.25); ornamentation amyloid, composed of obtuse and relatively densely spaced warts, up to 0.6 µm high, merged in short ridges which are interconnected by numerous fine line connections; suprahilar spot amyloid, relatively large and conspicuous; apiculi up to 0.9 µm high. Basidia (18-)21-27-32(-39) × (9-)9-10-10.5(-11) µm, 4-spored, subclavate to clavate, sterigmata up to 5 µm long. Hymenial gloeocystidia on lamellae sides (39-)41.5-49-56(-60) × (7-)8-9.5-11(-12) µm, rare, clavate to subclavate and mostly rostrate at the tip (up to 13 µm long), others with narrowing or obtuse-rounded apex, emergent up to 15 µm above the other elements of the hymenium, few deeply embedded; near the lamellae edges usually smaller and narrower, measuring (27-)30-38.5-46.5(-52) × (6-)6.5-8.5-10(-11) µm; all hymenial cystidia with

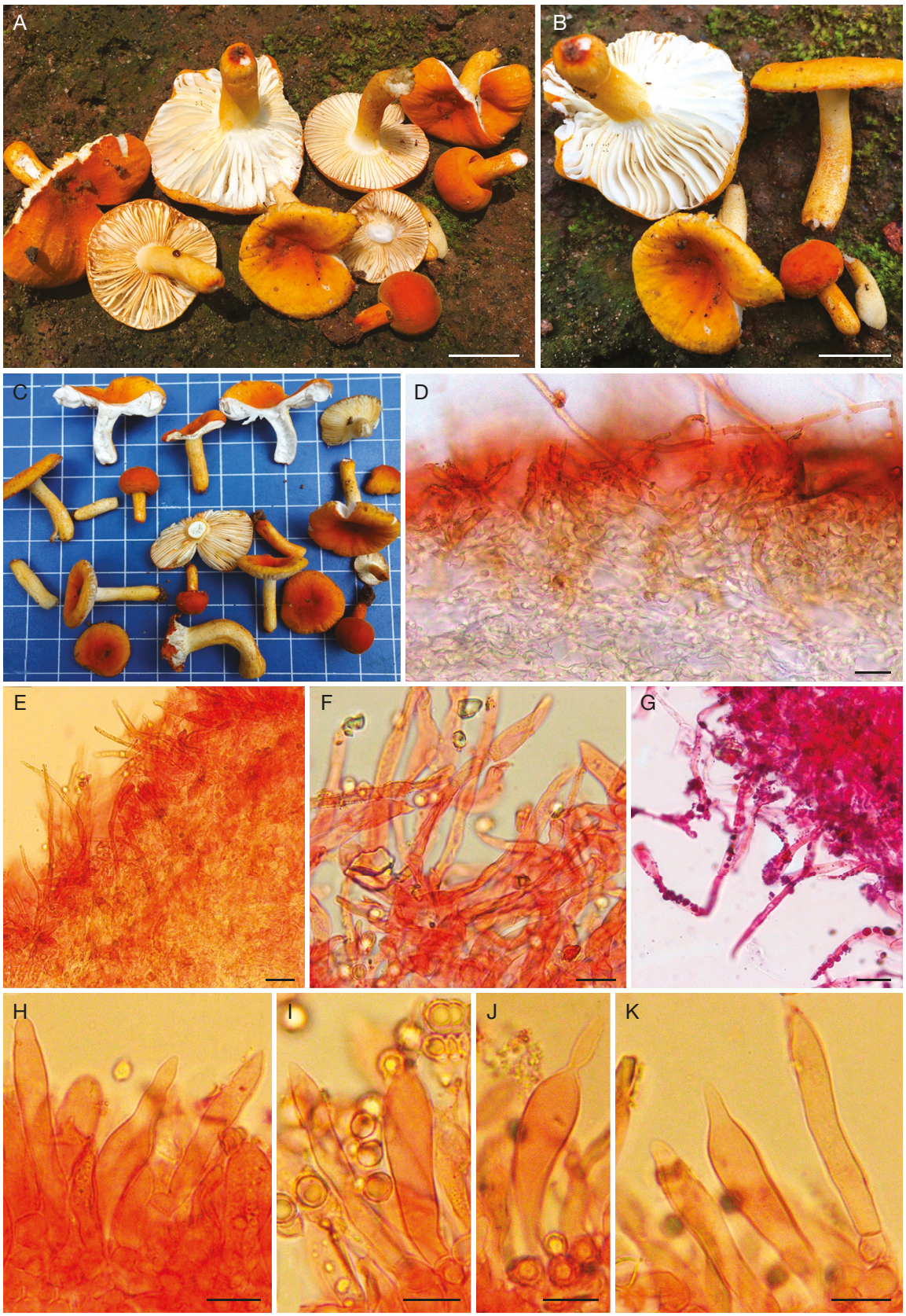

FIG. 8. — *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. (from holotype): **A**-**C**, fresh and dissected basidiomata in the field and basecamp; **D**-**F**, transverse section through pileipellis showing elements; **G**, primordial hyphae in carbolfuchsine; **H**-**J**, transverse section through lamellae showing hymenial gloeocystidia near the lamellae sides; **K**, transverse section through lamellae showing hymenial gloeocystidia near the lamellae edges. Scale bars: A, B, 20 mm; D, E, G, 20 µm; F, H-K, 10 µm.

scarce, granulose contents that do not react in sulfovanillin. Subhymenium layer up to 25 µm thick, pseudoparenchymatous. Marginal cells similar to hyphal terminations in pileipellis, mainly cylindrical, measuring (12-)15-22.5-29.5(-35) × (3.5-)4-5-6(-6) µm, apically obtuse-rounded; mixed with occasional basidia or basidioles. Hymenophoral trama mainly composed of large nests of sphaerocytes and intermixed with hyphal elements. Pileipellis orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, 100-200 µm deep, two-layered; vaguely divided in a 70-150 µm deep suprapellis a trichoderm composed of relatively dense, erect or ascending hyphal terminations; subpellis 30-50 µm deep, composed of more horizontally oriented, densely arranged hyphae. Acidoresistant incrustations uncertain. Hyphal terminations near the pileus margin flexuous, thin-walled, two- to three-celled, branched at the subterminal cells or the cells just below, pigment incrustations abundant; terminal cells measuring (16-)21.5-35-48.5(-66) × (4-)5-6.5-8(-9.5) µm, cylindrical or slightly narrowed towards apex or ventricose or narrowly uniform, apically obtuse-rounded or acute; subterminal cells usually equally long but sometimes wider (up to 11 µm), often with lateral projections. Hyphal terminations near the pileus centre of similar structure; terminal cells slightly shorter and less wide, measuring (14-)19-28-37(-45) × (3-)3.5-5-6.5(-9) µm, cylindrical or slightly narrowed towards apex or ventricose or narrowly uniform, apically obtuse-rounded or acute; subterminal cells usually equally long but sometimes wider (up to 13 µm). Potential primordial hyphae near the pileus margin typically 2- to 3-celled, flexuous, very long, thick-walled (up to 1 µm); terminal cells (58-)65.5-111-157(-225) × (2-)2.8-3.8-4.8(-6) µm, mainly attenuate, apically mostly acute, subterminal cells long, cylindrical; usually with strong incrustations covering most of its surface. Potential primordial hyphae near the pileus centre 2- to 3-celled, flexuous, very long, thick-walled (up to 1 µm), slightly shorter, terminal cells (45-)46-80.6-115(-165) × (2-)3.5-4.5-5.5(-6) µm, cylindrical to attenuate, apically mostly acute; usually with strong incrustations covering most of its surface. Pileocystidia not observed. Clamp connections absent in all parts.

Notes

In the field, our new species is a look-alike of the American *R. flavida* Frost. It differs microscopically from this American species in the smaller size of its basidiospores, as basidiospores of *R. flavida* holotype measure (7.1-)7.6-7.9-8.3(-8.6) × (5.8-)6-6.4-6.7(-7) µm (Adamčík *et al*. 2018), while their size was reported as 5.5-8.5(9.6) × 5-7 µm in Bills & Miller (1984) based on different collections.

The American *R. flavida* has not yet been placed in a multilocus phylogeny as essentially ITS sequences are available for this species. Our new *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. is here placed for the first time on the basis of three genes (Fig. 3). This placement supports the assumption made on the basis of an ITS phylogeny (Adamčík *et al*. 2019) that *R. flavida*, and now by extension also *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov., might be considered members of subsect. *Auratinae* Bon. This small subsection was until now limited to merely three species: the European *R. aurea* and its morphologically and genetically (4 bp difference in the ITS) very similar Asian counterpart, *R. aurantioflava*, recently reported from Pakistan (Adamčík *et al*. 2019), as well as the equally very similar, but rare American *R. xantho* Shaffer which has not yet been sequenced. Compared to *R. flavida* and *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov., these species are less uniform in colour with a pileus that varies from purplish to wine red, over brick red and orange to yellow, and a stipe that is frequently tinged with yellow but which can also be entirely white. Additionally, *R. xantho* is particular in the greying-blackening reaction of the context (Buyck 2005). The high support obtained in our multigene phylogenetic analyses (Fig. 3; MLbs = 100%, BPP = 1) and ITS (Fig. 7; MLbs = 98%, BPP = 1) also suggests that the / wielangtae-lineage should be considered part of *Auratinae*. This Oceanian lineage, comprising again very few species, the orange-red *R. wielangtae* from Australia and purplish-greenish *R. atroviridis* Buyck from New Zealand, offers a very similar microscopy as *R. aurea* and allies.

When blasting the ITS sequence (which is of perfect quality) of *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. against GenBank deposits, including environmental sequences, it is immediately evident that this sequence is very different from any other deposited sequence. For nearly complete coverage (100-93%), the closest match is a single Australian sequence at 85.85% similarity, and then similarity drops to less than 83% with first sequences for *R. flavida* and *Auratinae* arriving only at 81% similarity; coverage then drops very quickly to 70-60%. This is probably the reason why some of the closer species in multigene phylogenies (Buyck *et al*. 2018; Adamčík *et al*. 2019), such as the European *R. romellii* or the *R. wielangtae* lineage don't show up in these nBLAST results. When doing nBLAST of the ITS of *R. romellii*, neither *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. nor *Auratinae* are showing up in the first 100 results, but *R. flavida* is at 86% similarity for full coverage.

Host specificity seems not very high for species in *Auratinae*. The well-documented *R. aurea* has a distribution that extends from Mediterranean climates all the way into the colder parts of Europe. It occurs under various deciduous trees and conifers, and on various types of soil (Sarnari 2005). On the other side of the Atlantic Ocean, *R. flavida* is found in mixed forests with various *Quercus*, *Betula*, but also conifers (Bills & Miller 1984). *Russula aurantioflava* was originally reported as ectomycorrhizal with conifers (Adamčík *et al*. 2019). However, based on 100% similarity top scores in nBLAST for ITS sequence deposits MN704814 and MN704815 in GenBank, it occurs also in the very north-eastern part of China (Xing *et al*. 2020) in forests dominated (98%) by *Quercus mongolica* with intrusion (2%) of *Betula platyphylla* Sukaczev, resulting finally in a very similar host range as for both other species. *Russula xantho* is for the moment the only species of the subsection that seems to have a distinct preference for beech (Buyck 2005). Our new *R. pseudoflavida* A.Ghosh, Hembrom,

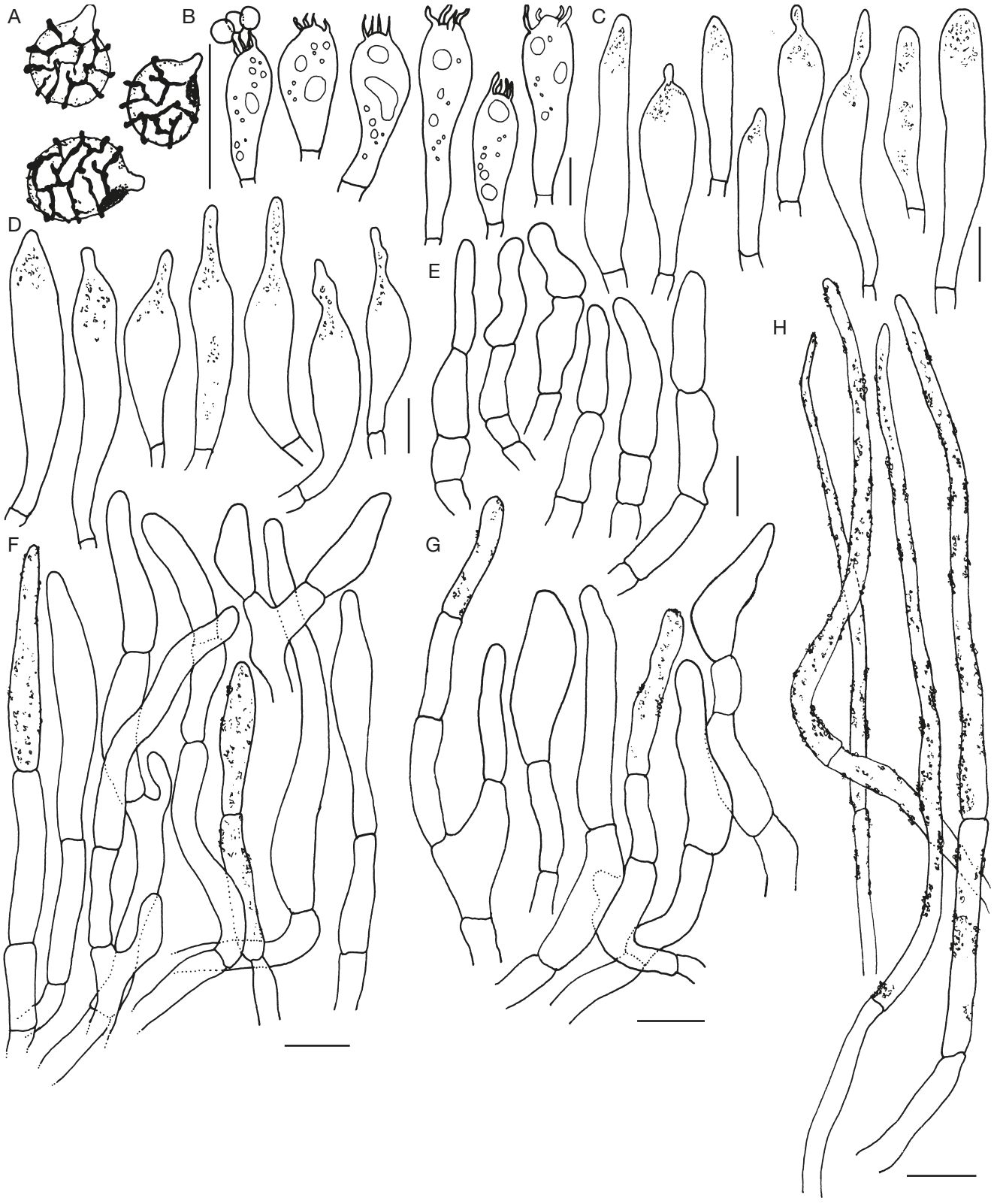

FIG. 9. — *Russula pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov. (from holotype): **A**, basidiospore; **B**, basidia; **C**, hymenial gloeocystidia near the lamellae edges; **D**, hymenial gloeocystidia near the lamellae sides; **E**, marginal cells; **F**, elements of the pileipellis near the pileus margin: hyphal terminations; **G**, elements of the pileipellis near the pileus centre: hyphal terminations; **H**, doubtfull primordial hyphae. Scale bars: 10 µm.

I.Bera & Buyck, sp. nov. is the first species in this lineage that associates with tropical dipterocarps.

The pileipellis of *Auratinae* has always been interpreted as devoid of any well-defined pileocystidia or primordial hyphae, but they have well-differentiated caulocystidia. However, for *R. flavida* and *R. pseudoflavida* A.Ghosh, Hembrom, I.Bera & Buyck, sp. nov., the question of absence/presence of primordial hyphae is more difficult to answer as the entire pileipellis is covered in yellow incrustations and many cells also present deposits inside hyphal terminations. Adamčík *et al.* (2019) mentioned presence of pileocystidia in the pileipellis of the *R. flavida* holotype, but absence of primordial hyphae. In our opinion, both primordial hyphae and dermatocystidia are absent in the pileipellis and on the stipe surface, although we admit that the reaction in carbolfuchsine (Fig. 8H) is open for interpretation as most of the colouration is situated inside the hyphae but with some guttules nevertheless sitting on top of the hyphal surface. All of the abovementioned species have also very poor contents in hymenial cystidia.

Russula shoreae
D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov.
(Figs 10-12)

Russula shoreae D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. is separated from North American *R. redolens* by the absence of a strong celery-like taste and odour and because of its ectomycorrhizal association with *Shorea robusta*.

Holotype. — **India**. West Bengal, Jhargram district, Lodhasuli, 22°19'57"N, 87°02'47"E, alt. 80 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 27.VIII.2021, D. Chakraborty, *NPDF917-10L* (holo-, CAL[CAL 1864]!).

Additional specimens examined. — **India**. West Bengal, West Bengal, Jhargram district, Lodhasuli, 22°19'59"N, 87°02'47"E, alt. 80 m a.s.l., on ground, under *Shorea robusta* in tropical deciduous forests, 13.VIII.2020, A. Ghosh, *AG 20-027* (CAL[CAL 1865]); Jhargram district, Jhargram city, 22°25'01.1"N, 87°00'13.5"E, alt. 103 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 12.VIII.2021, A. Ghosh, *AG 21-068*; Uttar Dinajpur, Kaliyaganj, Dhamja, 25°18'00"N, 88°20'35.9"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 07.IX.2020, D. Chakraborty, *RGJ-20-05*; Uttar Dinajpur, Kaliyaganj, Dhamja, 25°18'00"N, 88°20'35.9"E, alt. 80 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 10.X.2021, D. Chakraborty, *RGJ-21-03*; Bihar, West Champaran district, Valmiki national Park, Raghia range, Sitalbari enclosure, 27°20'14.4"N, 84°13'05.8"E, alt. 133 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 15.IX.2020, M.E. Hembrom, *MEH-20-114*; Jharkhand, Rajmahal hills, Sahibganj district, Borio block, Pir-Baba Kairasol forest area, 25°09'41.7"N, 87°40'31.9"E, alt. 126 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 24.VIII.2021, A. Ghosh, *AG 21-02* (JH); Ranchi district, Getalsud, 23°28'36.5"N, 85°33'23.8"E, alt. 570 m a.s.l., on ground, under *S. robusta* in tropical deciduous forests, 09.X.2021, M.E. Hembrom, *MEH-21-32*.

GenBank. — OL461227 (nrITS, holotype) and OL461230 (nrITS, specimen voucher no. *AG 20-027*); ON365930 (nrLSU, holotype), ON365931 (nrLSU, specimen voucher no. *AG 20-027*); ON387509 (mtSSU, holotype), ON387514 (mtSSU, specimen voucher no. *AG 20-027*); ON398069 (*rpb2*, holotype), ON398070 (*rpb2*, specimen voucher no. *AG 20-027*)

Etymology. — '*shoreae*' refers to *Shorea robusta* (Dipterocarpaceae), the host tree.

MycoBank. — MB 844207.

Facesoffungi number. — FoF 11435.

Description
Pileus small to medium-sized, 12-70 mm in diam., convex when young, becoming plano-convex to applanate, uplifted with age, centrally depressed to umbilicate at maturity; margin decurved to plane with age, entire; cuticle viscid and shiny when moist, dull upon drying, peeling to ½ of the radius, when young dark green (27F5-6) to dull green (26C-D3-4) with paler margin (26D4), at maturity with dark green (27F5-6) centre with alternating dark green and greyish green concentric rings (26D3-4, 25-26F7-8). Pileus context up to 6 mm thick at the disc, thinning towards the margin, compact, brittle, chalky white (1-2A1), unchanging after bruising or cutting; turning salmon pink (6A4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol. Lamellae up to 4 mm high, narrowly adnate to adnexed, subdistant to close (9-13/cm at pileus margin), chalky white (1-2A1), forked near the stipe apex, midway to the margin, or near the margin; lamellulae present in different lengths; edges entire and concolorous. Stipe 10-67 × 5-22 mm, cylindrical to clavate, central, firm and brittle; surface dry, smooth, chalky white (1-2A1) with dull green (26D4) tinges. Stipe context solid when young, becoming stuffed to hollow with maturity, surface chalky white (1-2A1), unchanging after bruising or cutting, becoming salmon pink (6A4) with $FeSO_4$ and deep to dark turquoise (24E-F7-8) in guaiacol. Odour not distinctive. Taste mild. Spore print not obtained.

Basidiospores subglobose, broadly ellipsoid to ellipsoid, rarely globose, (5.5-)6.3-7.0-7.7(-8.4) × (4.8-)5.4-6.0-6.6(-7.8) µm, Q = (1.02-)1.09-1.17-1.25(-1.41); ornamentation composed of amyloid isolated warts ; warts up to 0.5 µm high, pustulose or rounded, sometimes fused with each other; suprahilar spot distinct, large but inamyloid, apiculi up to 1.5 µm long. Basidia (46-)51-57-62(-65) × (9-)10-11-12(-13) µm, 4-spored, subclavate, tapering towards base, sterigmata up to 6 µm long. Hymenial cystidia rare on the lamellae sides, (50-)53.5-61-68(-76) × (7-)10-11.5-13.5(-15) µm, cylindrical, subclavate, clavate to fusiform with rostrate to moniliform apex, emergent up to 22 µm above the other elements of the hymenium; contents finely crystalline, near the lamellae edges usually smaller and narrower, measuring 46-51-55 × 9-11-12 µm; all hymenial cystidia not reacting in sulfovanillin. Lamellae edges fertile with basidia and cystidia. Subhymenium layer 35-40 µm thick, pseudoparenchymatous. Hymenophoral trama mainly composed of large nests of sphaerocytes and intermixed with hyphal elements. Pileipellis orthochromatic in Cresyl blue, sharply delimited from the underlying sphaerocytes of the context, 276-307 µm deep, two-layered and vaguely divided in a relatively dense suprapellis, 96-91 µm deep, composed of erect or ascending hyphal terminations forming a trichoderm, and a subpellis 180-216 µm deep, composed of more densely and more horizontally oriented hyphae. Acidoresistant incrustations

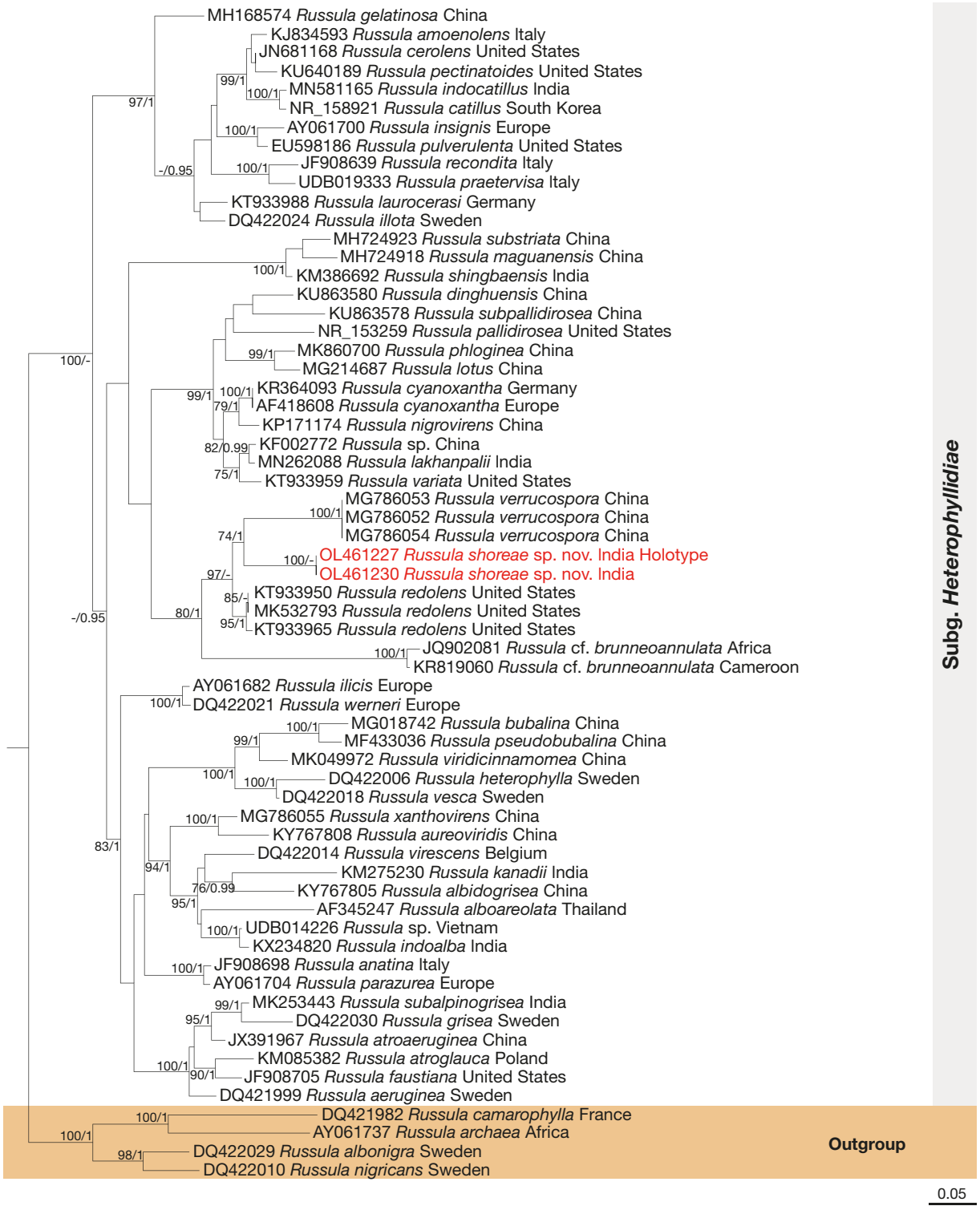

FIG. 10. — Phylogram generated by Maximum Likelihood analysis based on nrITS sequence data of *Russula shorae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. and their allied species. Maximum Likelihood bootstrap support values (MLbs) ≥ 70% are shown on the left of "/" and Bayesian Posterior Probabilities (BPP) ≥ 0.95 are shown on the right above or below the branches at nodes. *Russula shorae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. is placed in **red font** to highlight their phylogenetic positions in the tree.

absent. Hyphal terminations near the pileus margin often slightly flexuous, thin-walled, composed of chains of 1-3 cells, branched at the subterminal cells or the cells just below; terminal cells measuring (11-)13-21-29(-44.5) × (3-)4-4.5-5.5(-7) µm, mainly subulate or cylindrical, apically acute and distinctly attenuated or obtuse-rounded; subterminal cells mainly cylindrical, but sometimes wider. Hyphal terminations near the pileus centre of similar structure, terminal cells slightly less wide, measur-

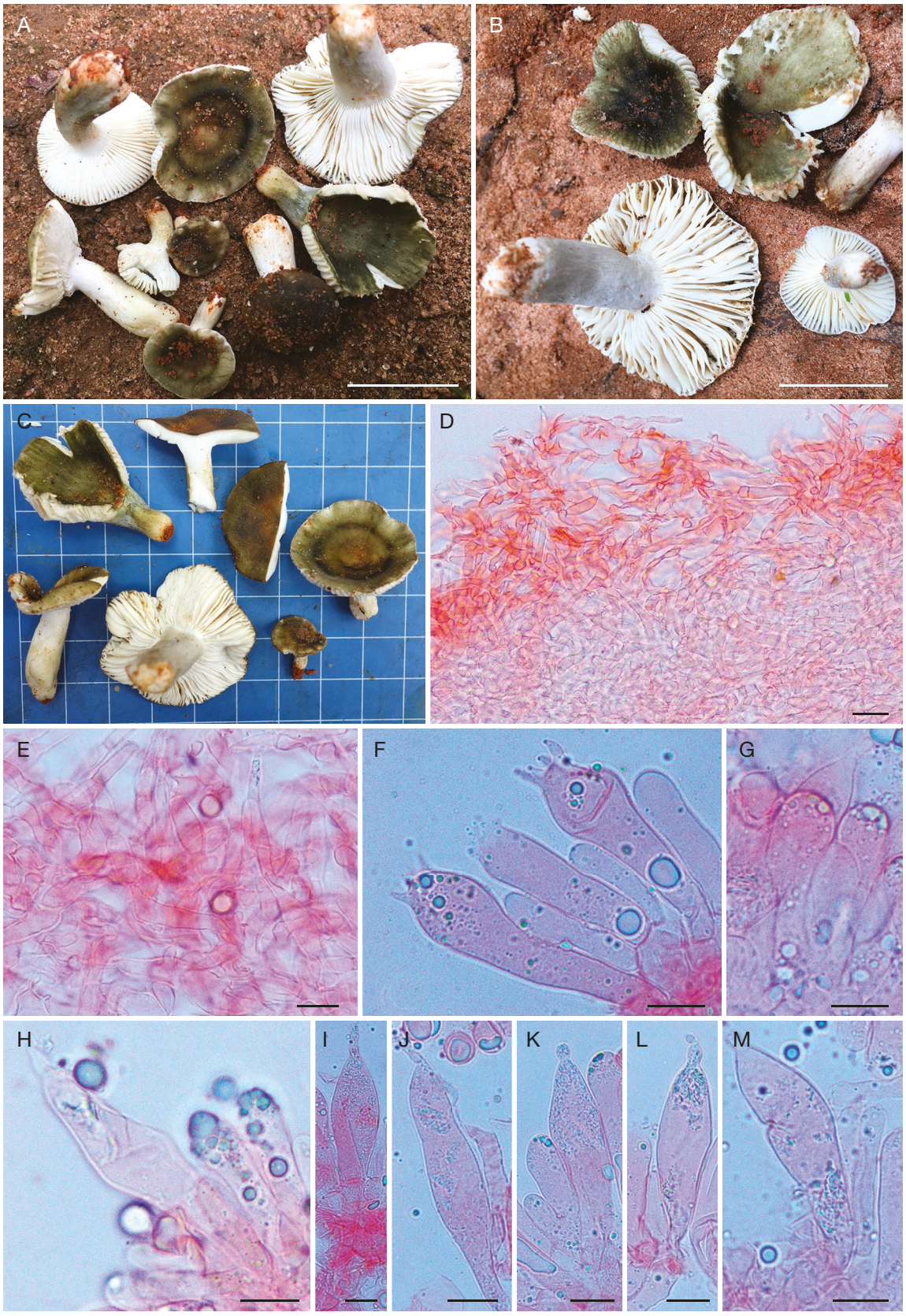

FIG. 11. — *Russula shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. (from holotype): **A**-**C**, fresh and dissected basidiomata in the field and basecamp; **D**, **E**, transverse section through pileipellis showing elements; **F**, transverse section through lamellae showing basidia; **G**, **H**, transverse section through lamellae showing hymenial cystidia near the lamellae edges; **I**-**M**, transverse section through lamellae showing hymenial cystidia near the lamellae sides. Scale bars: A, B, 20 mm; D, 20 µm; E-M, 10 µm.

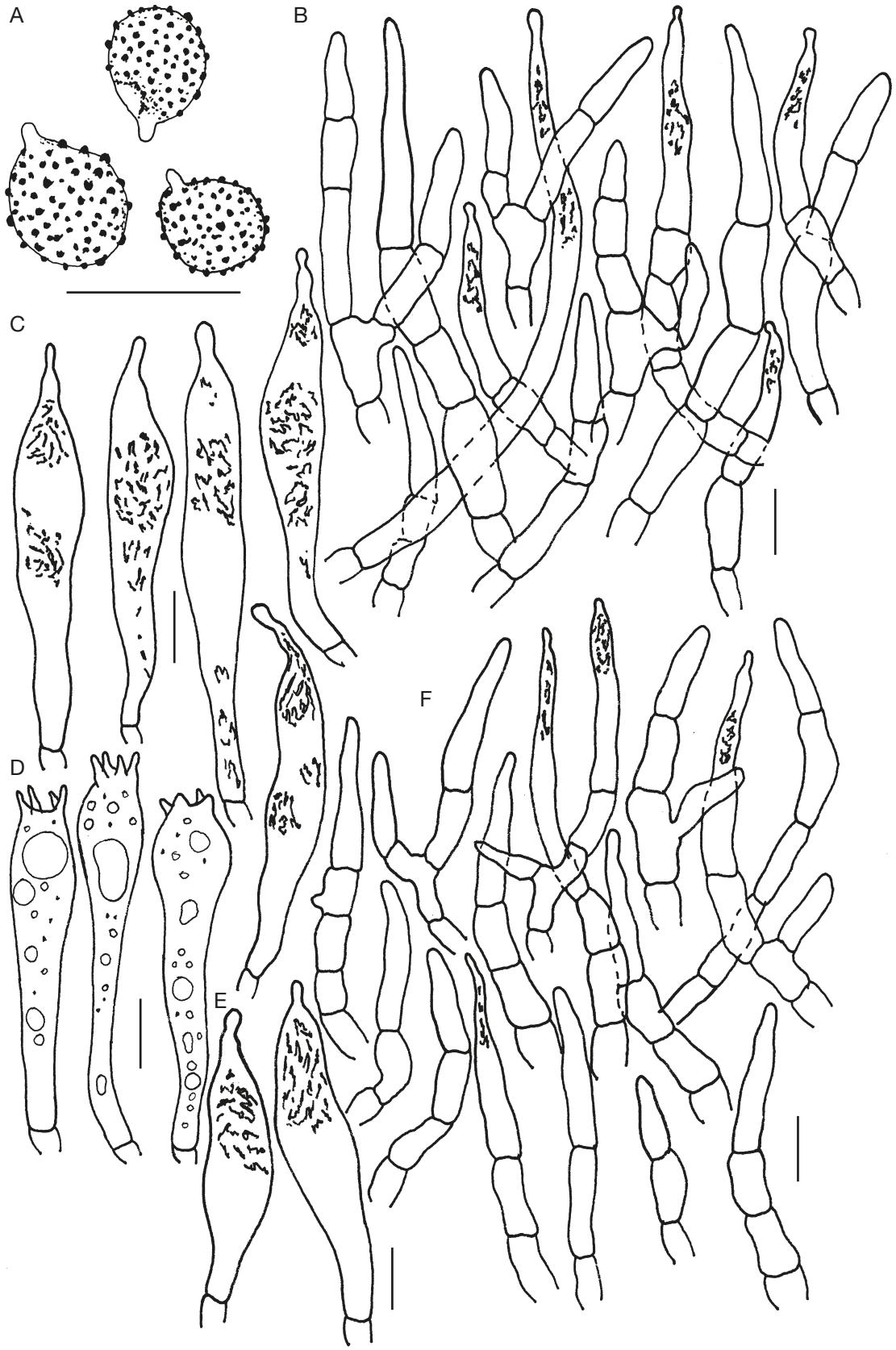

Fig. 12. — *Russula shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. (from holotype): **A**, basidiospore; **B**, elements of the pileipellis near the pileus margin: hyphal terminations and pileocystidia; **C**, hymenial cystidia near the lamellae sides; **D**, basidia; **E**, hymenial cystidia near the lamellae edges; **F**, elements of the pileipellis near the pileus centre: hyphal terminations and pileocystidia. Scale bars: 10 µm.

ing (9-)12.5-19.5-26.5(-30.5) × (2.5-)3-4-4.5(-5) µm, mainly subulate or cylindrical, apically acute and distinctly attenuated or obtuse-rounded; subterminal cells mainly cylindrical, but sometimes wider or with lateral appendages. Pileocystidia near the pileus margin typically one-celled, flexuous, thin-walled, (14-)17.5-40-62(-96) × (2.5-)3.5-4.5-5.5(-6) µm, mainly subulate, apically mostly mucronate or with short appendages; those near the pileus centre slightly shorter, (22-)24-31.5-39(-46) × (3.5-)4-4.5-5 µm; all with contents finely crystalline and without reaction in sulfovanillin. Clamp connections absent in all parts.

Notes

The nBLAST of the obtained ITS sequence places *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. in subg. *Heterophyllidiae*, which was also clearly suggested by its morphological characters, including the inamyloid suprahilar spot, the typical ramifying hyphal extremities at the pileus surface composed of chains of more or less inflated, short cells that become gradually narrower toward the terminal cell and one-celled, narrow and mucronate pileocystidia.

In our ITS phylogenetic analysis, the here newly described *R. shoreae* D.Chakr., A.Ghosh, K.Das & Buyck, sp. nov. is placed sister to the Chinese *R. verrucospora*, a subtropical species that has smaller spores and a more variable pileus colour with grey and vinaceous tints. Both are again placed sister to the North American and equally green *R. redolens* which has a unique and strong smell of parsley. These three species form a strongly supported clade, which is placed sister, again with strong statistical support, to the annulate *R. brunneoannulata* Buyck of the African subsect. Aureotactinae Heim ex Buyck (Buyck 1994). All these species have very similar microscopic features of pileipellis and share the same type of spore ornamentation consisting of isolated blunt warts. All of these species differ from subsect. *Cyanoxanthinae* Sing. in the absence of strong metachromatic reactions in Cresyl blue. Some of the above-mentioned species were also grouped with strong support in recent multilocus phylogenies. Indeed, a representative sampling of species belonging to subg. *Heterophyllidiae* was distributed over four significantly supported clades in the combined multilocus phylogeny, based on 28S, *rpb2* and *tef*-1 loci, that was published by Wang *et al.* (2019). In that phylogeny, subsect. Substriatinae was introduced as a new subsection that grouped with Aureotactinae as one of the four strongly supported clades in the subgenus. This topology was never recovered in ITS-based phylogenies, nor in the combined multilocus (based on the same loci) published by Vera *et al.* (2021) where *Aureotactinae*, impacted by the introduction of *R. redolens*, no longer grouped with *Substriatinae*.

Acknowledgements

The authors are grateful to the Director of the Botanical Survey of India, Kolkata for providing facilities. Aniket Ghosh and Dyutiparna Chakraborty are thankful to Science and Engineering Research Board (SERB) for providing the National Post-Doctoral Research Fellowship (files nos PDF/2021/000183 and PDF/2019/000917, respectively).

References

Adamčík S., Looney B., Caboň M., Jančovičová S., Adamčíková K., Avis P. G., Barajas M., Bhatt R. P., Corrales A., Das K., Hampe F., Ghosh A., Gates G., Kälviäinen V., Khalid A. K., Kiran M., De Lange R., Lee H., Lim Y. W., Luz A. K., Manz C., Ovrebo C., Park J. Y., Saba M., Taipale T., Verbeken A., Wisitrassameewong K. & Buyck B. 2019. — The quest for a globally comprehensible *Russula* language. *Fungal Diversity* 99 (1): 369-449. https://doi.org/10.1007/s13225-019-00437-2

Adamčík S., Jančovičová S. & Buyck B. 2018. — The Russulas described by Charles Horton Peck. *Cryptogamie, Mycologie* 39 (1): 3-108. https://doi.org/10.7872/crym/v39.iss1.2018.3

Alexander I. J. & Högberg P. 1986. — Ectomycorrhizas of tropical angiospermous trees. *New Phytologist* 102 (4): 541-549. https://doi.org/10.1111/j.1469-8137.1986.tb00830.x

Altschul S. F., Madden T. L., Schäffer A. A., Zhang J., Zhang Z., Miller W. & Lipman D. J. 1997. — Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucleic Acids Research* 25 (17): 3389-3402. https://doi.org/10.1093/nar/25.17.3389

Bills G. F. & Miller O. K. Jr. 1984. — Southern Applachian Russulas. I. *Mycologia* 76 (6): 975-1002. https://doi.org/10.1080/00275514.1984.12023944

Burlingham G. S. 1921. — Some new species of *Russula*. *Mycologia* 13 (3): 129-134. https://doi.org/10.1080/00275514.1921.12016869

Buyck B. 1989. — Valeur taxonomique du bleu de crésyl pour le genre *Russula*. *Bulletin de la Société mycologique de France* 105: 1-6.

Buyck B. 1994. — *Russula* II (Russulaceae), *in* Rammeloo J. & Heinemann P. (eds), *Flore illustrée des Champignons d'Afrique centrale*. Vol. 16. Ministère de l'agriculture, Jardin botanique national de Belgique, Bruxelles: 411-542.

Buyck B. 2005. — First record of the rare, northern *Russula xantho* from near Wildacres, North Carolina. *Cryptogamie, Mycologie* 26 (4): 283-291.

Buyck B., Duhem B., Das K., Jayawardena R. S., Niveiro N., Pereira O. L., Prasher I. B., Adhikari S., Albertó E. O., Bulgakov T. S., Castañeda-Ruiz R. F., Hembrom M. E., Hyde K. D., Lewis D. P., Michlig A., Nuytinck J., Parihar A., Popoff O. F., Ramirez N. A., Da Silva M., Verma R. K. & Valerie H. 2017. — Fungal Biodiversity Profiles 21-30. *Cryptogamie, Mycologie* 38 (1): 101-146. https://doi.org/10.7872/crym/v38.iss1.2017.101

Buyck B., Zoller S. & Hofstetter V. 2018. — Walking the thin line… ten years later: the dilemma of above- versus below-ground features to support phylogenies in the Russulaceae (Basidiomycota). *Fungal Diversity* 89 (1): 267-292. https://doi.org/10.1007/s13225-018-0397-5

Buyck B., Wang X. H., Adamčíková K., Caboň M., Jančovičová S., Hofstetter V. & Adamčík S. 2020. — One step closer to unravelling the origin of *Russula*: subgenus *Glutinosae* subg. nov. *Mycosphere* 11 (1): 285-304. https://doi.org/10.5943/mycosphere/11/1/6

Caboň M., Eberhardt U., Looney B., Hampe F., Kolarik M., Jančovičová S., Verbeken A. & Adamčík S. 2017. — New insights in *Russula* subsect. *Rubrinae*: phylogeny and the quest for synapomorphic characters. *Mycological Progress* 16: 877-892. https://doi.org/10.1007/s11557-017-1322-0

Das K., Ghosh A., Buyck B. & Hembrom M. E. 2020. — Two new species of *Russula* subgenus *Compactae* from Indian Himalaya based on morphology and molecular phylogenetic inference. *Nordic Journal of Botany*: e02962. https://doi.org/10.1111/njb.02962

Das K., Dowie N. J., Li G. J. & Miller S. L. 2014. — Two new species of *Russula* (Russulales) from India. *Mycosphere* 5 (5): 612-622. https://doi.org/10.5943/mycosphere/5/5/2

De Lange R., Adamčík S., Adamčíková K., Asselman P., Borovička J., Delgat L., Hampe F. & Verbeken A. 2021. — Enlightening the black and white: species delimitation and UNITE species hypothesis testing in the *Russula albonigra* species complex. *IMA Fungus* 12: 20. https://doi.org/10.1186/s43008-021-00064-0

Drummond A. J., Ashton B., Buxton S., Cheung M., Cooper A., Heled J., Kearse M., Moir R., Stones-Havas S., Sturrock S., Thierer T. & Wilson A. 2010. — Geneious v. 5.1. Available from https://www.geneious.com/.

Dutta A. K., Paloi S., Pradhan P. & Acharya K. 2015. — A new species of *Russula* (Russulaceae) from India based on morphological and molecular (ITS sequence) data. *Turkish Journal of Botany* 39 (5): 850-856. https://doi.org/10.3906/bot-1407-1

Edler D., Klein J., Antonelli A. & Silvestro D. 2021. — raxmlGUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* 12 (2): 373-377. https://doi.org/10.1111/2041-210X.13512

Ganguly A., Nad S., Singha K., Pathak R., Hazra P., Singha P., Dhua P., Mohapatra P. K. D. & Mandal A. 2021. — Diversity and distribution of wild mushrooms in different forest areas of Bankura district, WB, India. *Acta Biologica Szegediensis* 65 (2): 185-198. https://doi.org/10.14232/abs.2021.2.185-198

Gardes M. & Bruns T. D. 1993. — ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2 (2): 113-118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Ghosh A., Das K. & Chakraborty D. 2021. — Morphology and molecular approach reveal a new species of the genus *Russula* subsect. Lepidinae (Russulaceae). *Phytotaxa* 483 (3): 244-254. https://doi.org/10.11646/phytotaxa.483.3.4

Ghosh A., Das K., Bhatt R. P. & Hembrom M. E. 2020. — Two new species of the genus *Russula* from western Himalaya with morphological details and phylogenetic estimations. *Nova Hedwigia* 111 (1-2): 115-130. https://doi.org/10.1127/nova_hedwigia/2020/0588

Hall T. A. 1999. — BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.

Hembrom M. E., Das K., Adhikari S., Parihar A. & Buyck B. 2017. — First report of *Pterygellus* from Rajmahal hills of Jharkhand (India) and its relation to *Craterellus* (Hydnaceae, Cantharellales). *Phytotaxa* 306 (3): 201-210. https://doi.org/10.11646/phytotaxa.306.3.2

Hongsanan S., Hyde K. D., Bahkali A. H., Camporesi E., Chomnunti P., Ekanayaka H., Gomes A. A. M., Hofstetter V., Jones E. B. G., Pinho D. B., Pereira O. L., Tian Q., Wanasinghe D. N., Xu J.-C. & Buyck B. 2015. — Fungal Biodiversity Profiles 11-20. *Cryptogamie, Mycologie* 36 (3): 355-380. https://doi.org/10.7872/crym/v36.iss3.2015.355

Kalichman J., Kirk P. M. & Matheny P. B. 2020. — A compendium of generic names of agarics and Agaricales. *Taxon* 69 (3): 425-447. https://doi.org/10.1002/tax.12240

Katoh K., Rozewicki J. & Yamada K. D. 2019. — MAFFT: online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20 (4): 1160-1166. https://doi.org/10.1093/bib/bbx108

Khatua S., Dutta A. K. & Acharya K. 2015. — Prospecting *Russula senecis*: a delicacy among the tribes of West Bengal. *PeerJ* 3: e810. https://doi.org/10.7717/peerj.810

Khatua S., Dutta A. K., Chandra S., Paloi S., Das K. & Acharya K. 2017. — Introducing a novel mushroom from mycophagy community with emphasis on biomedical potency. *PLoS One* 12 (5): e0178050. https://doi.org/10.1371/journal.pone.0178050

Khatua S., Paloi S., Das K. & Acharya K. 2021. — An untold story of a novel mushroom from tribal cuisine: an ethno-medicinal, taxonomic and pharmacological approach. *Food & Function* 12: 4679. https://doi.org/10.1039/D1FO00533B

Knudsen H., Ruotsalainen J. & Vauras J. 2012. — *Russula* Pers., *in* Knudsen H. & Vesterholt J. (eds), *Funga Nordica*. Nordsvamp, Copenhagen: 144-186.

Kornerup A. & Wanscher J. H. 1978. — *Methuen Handbook of Colour*. Third Edition. Methuen, London, 252 p.

Kumar J. & Atri N. S. 2016. — Characterisation of ectomycorrhiza of *Russula* and *Lactifluus* (Russulaceae) associated with *Shorea robusta* from Indian Shiwalik. *Nova Hedwigia* 103 (3-4): 501-513. https://doi.org/10.1127/nova_hedwigia/2016/0368

Kumar J. & Atri N. S. 2019. — Characterisation and identification of ectomycorrhizae of *Russula* (Russulaceae: Basidiomycota) associated with *Shorea robusta*. *Journal of Tropical Forest Science* 31 (1): 114-124. https://doi.org/10.26525/jtfs2019.31.1.114124

Kumar J. & Atri N. S. 2020. — New records of lamellate mushrooms associated with Sal from Shiwaliks, India. *Kavaka* 54: 30-37. https://doi.org/10.36460/Kavaka/54/2020/30-37

Kumar S., Stecher G. & Tamura K. 2016. — MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33 (7): 1870-1874. https://doi.org/10.1093/molbev/msw054

Lanfear R., Frandsen P. B., Wright A. M., Senfeld T. & Calcott B. 2017. — PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34 (3): 772-773. https://doi.org/10.1093/molbev/msw260

Lee S. S. 1990. — The mycorrhizal association of the Dipterocarpaceae in the tropical rain forests of Malaysia. *Ambio* 19: 383-385.

Liu Y. L., Whelen S. & Hall B. D. 1999. — Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16 (12): 1799-1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Looney B. P., Meidl P., Piatek M. J., Miettinen O., Martin F. M., Matheny P. B. & Labbé J. L. 2018. — Russulaceae: a new genomic dataset to study ecosystem function and evolutionary diversification of ectomycorrhizal fungi with their tree associates. *New Phytologist* 218 (1): 54-65. https://doi.org/10.1111/nph.15001

Matheny P. B. 2005. — Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution* 35 (1): 1-20. https://doi.org/10.1016/j.ympev.2004.11.014

Natarajan K., Kumaresan V. & Narayanan K. 2005. — A checklist of Indian agarics and boletes (1984-2002). *Kavaka* 33: 92.

Pachit P., Disyatat N. R. & Piapukiew J. 2020. — Temporal changes in enzyme activities associated with ectomycorrhizas and soil from secondary deciduous dipterocarp forest fragments. *Pedobiologia* 81-82: 150661. https://doi.org/10.1016/j.pedobi.2020.150661

Parihar A., Hembrom M. E., Vizzini A. & Das K. 2018a. — *Indoporus shoreae* gen. et sp. nov. (Boletaceae) from tropical India. *Cryptogamie, Mycologie* 39 (4): 447-466. https://doi.org/10.7872/crym/v39.iss4.2018.447

Parihar A., Hembrom M. E., Vizzini A. & Das K. 2018b. — A new species of *Boletellus* (Boletaceae, Basidiomycota) from tropical India. *Nordic Journal of Botany* 36 (12): e02089. https://doi.org/10.1111/njb.02089

Phosri C., Põlme S., Taylor A. F. S., Kõljalg U., Suwannasai N. & Tedersoo L. 2012. — Diversity and community composition of ectomycorrhizal fungi in a dry deciduous dipterocarp forest in Thailand. *Biodiversity and Conservation* 21 (9): 2287-2298. https://doi.org/10.1007/s10531-012-0250-1

Pradhan P., Dutta A. K., Roy A., Basu S. K. & Acharya K. 2012. — Inventory and spatial ecology of macrofungi in the *Shorea robusta* forest ecosystem of lateritic region of West Bengal. *Biodiversity* 13 (2): 88-99. https://doi.org/10.1080/14888386.2012.690560

Pradhan P., Dutta A. K., Roy A., Basu S. K. & Acharya K. 2013. — Macrofungal diversity and habitat specificity: a case

study. *Biodiversity* 14 (3): 147-161. https://doi.org/10.1080/14888386.2013.805660

Rambaut A., Suchard M. A., Xie D. & Drummond A. J. 2014. — Tracer version 1.6. Available from https://beast.bio.ed.ac.uk/tracer.

Romagnesi H. 1967. — *Les Russules d'Europe et d'Afrique du Nord*. Bordas, Paris, 998 p.

Ronquist F., Teslenko M., van der Mark P., Ayres D. L., Darling A., Höhna S., Larget B., Liu L., Suchard M. A. & Huelsenbeck J. P. 2012. — MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61 (3): 539-542. https://doi.org/10.1093/sysbio/sys029

Sarnari M. 2005. — *Monografia illustrate del Genere Russula in Europa*. Tomo Secondo. Centro Studi Micologici, Trento, 768 p.

Shaffer R. L. 1962. — The subsection *Compactae* of *Russula*. *Brittonia* 14: 254-284. https://doi.org/10.2307/2805261

Singh J. S. & Singh S. P. 1992. — *Forests of Himalaya*. Gyanodaya Prakashan, Naini Tal, 257 p.

Song Y. U., Li J., Buyck B., Zheng J. & Qiu L. 2018. — *Russula verrucospora* sp. nov. and *R. xanthovirens* sp. nov., two novel species of *Russula* (Russulaceae) from southern China. *Cryptogamie, Mycologie* 39 (1): 129-142. https://doi.org/10.7872/crym/v39.iss1.2018.129

Talavera G. & Castresana J. 2007. — Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56 (4): 564-577. https://doi.org/10.1080/10635150701472164

Vellinga E. C. 1988. — Glossary, *in* Bas C., Kuyper Th. W., Noordeloos M. E. & Vellinga E. C. (eds), *Flora Agaricina Neerlandica* 1. Balkema A. A., Rotterdam: 54-64.

Vera M., Adamčík S., Adamčíková K., Hampe F., Caboň M., Manz C., Ovrebo C., Piepenbring M. & Corrales A. 2021. — Morphological and genetic diversification of *Russula floriformis*, sp. nov., along the Isthmus of Panama. *Mycologia* 113 (4): 807-827. https://doi.org/10.1080/00275514.2021.1897377

Verma R. K., Pandro V. & Pyasi A. 2018. — Diversity and distribution of *Russula* in India with reference to central Indian species. *International Journal of Current Microbiology and Applied Science* 7 (10): 3078-3103. https://doi.org/10.20546/ijcmas.2018.710.359

Verma R. K., Pandro V. & Rao G. R. 2019. — Three Records of *Russula* Mushrooms from Sal Forest of Central India. *International Journal of Current Microbiology and Applied Science* 8 (2): 445-455. https://doi.org/10.20546/ijcmas.2019.802.050

Wang J., Buyck B., Wang X. H. & Bau T. 2019. — Visiting *Russula* (Russulaceae, Russulales) with samples from southwestern China finds one new subsection of *Heterophyllidia* with two new species. *Mycological Progress* 18: 771-784. https://doi.org/10.1007/s11557-019-01487-1

White T. J., Bruns T., Lee S. & Taylor J. 1990. — Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, *in* Innis M. A., Gelfand D. H., Sninsky J. J. & White T. J. (eds), *PCR Protocols: A Guide to Methods and Applications*. Academic Press Inc., San Diego: 315-322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Xing P., Xu Y., Gao T., Li G., Zhou J., Xie M. & Ji R. 2020. — The community composition variation of Russulaceae associated with the *Quercus mongolica* forest during the growing season at Wudalianchi City, China. *PeerJ* 8: e8527. https://doi.org/10.7717/peerj.8527

Yuan H. S., Lu X., Dai Y. C., Hyde K. D., Kan Y. H., Kušan I., He S. H., Liu N. G., Sarma V. V., Zhao C. L., Cui B. K., Yousaf N., Sun G. Y., Liu S. Y., Wu F., Lin C. G., Dayarathne M. C., Gibertoni T. B., Conceição L. B., Garibay-Orijel R., Villegas-Ríos M., Salas-Lizana R., Wei T. Z., Qiu J. Z., Yu Z. F., Phookamsak R., Zeng M., Paloi S., Bao D. F., Abeywickrama P. D., Wei D. P., Yang J., Manawasinghe I. S., Harishchandra D., Brahmanage R. S., De Silva N. I., Tennakoon D. S., Karunarathna A., Gafforov Y., Pem D., Zhang S. N., De Azevedo Santiago A. L. C. M., Bezerra J. D. P., Dima B., Acharya K., Alvarez-Manjarrez J., Bahkali A. H., Bhatt V. K., Brandrud T. E., Bulgakov T. S., Camporesi E., Cao T., Chen Y. X., Chen Y. Y., Devadatha B., Elgorban A. M., Fan L. F., Du X., Gao L., Gonçalves C. M., Gusmão L. F. P., Huanraluek N., Jadan M., Jayawardena R. S., Khalid A. N., Langer E., Lima D. X., De Lima-Júnior N. C., De Lira C. R. S., Liu J. K., Liu S., Lumyong S., Luo Z. L., Matočec N., Niranjan M., Oliveira-Filho J. R. C., Papp V., Pérez-Pazos E., Phillips A. J. L., Qiu P. L., Ren Y. H., Castañeda-Ruiz R. F., Semwal K. C., Soop K., De Souza C. A. F., Souza-Motta C. M., Sun L. H., Xie M. L., Yao Y. J., Zhao Q. & Zhou L. W. 2020. — Fungal diversity notes 1277-1386: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 104: 1-266. https://doi.org/10.1007/s13225-020-00461-7

Yuwa-Amornpitak T. & Yeunyaw P.-N. 2020. — Diversity of Wild Mushrooms in the Community Forest of Na Si Nuan Sub-District, Thailand. *Journal of Biochemical Technology* 11 (3): 28-36.

Zhou S., Song Y., Chen K., Li J., Buyck B. & Qiu L. 2020. — Three novel species of *Russula* Pers. subg. *Compactae* (Fr.) Bon from Dinghushan Biosphere Reserve in southern China. *Cryptogamie, Mycologie* 41 (14): 219-234. https://doi.org/10.5252/cryptogamie-mycologie2020v41a14

Submitted on 12 September 2022;
accepted on 5 January 2023;
published on 21 March 2023.