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Research article

Species of *Russula* subgenera *Archaeae*, *Compactae* and *Brevipedum* (Russulaceae, Basidiomycota) from Dinghushan Biosphere Reserve

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Abstract. Three novel species collected from Dinghushan Biosphere Reserve (DHSBR) in southern China, *Russula cylindrica* Y.Song sp. nov. and *R. lacteocarpa* Y.Song sp. nov. in subgenus *Archaeae* and *R. reticulofolia* Y.Song sp. nov. in subg. *Compactae*, are described based on morphological and molecular data. In addition, *Russula leucobrunnea* Y.Song nom. nov. is proposed in replacement of *R. leucocarpa* nom. illeg. in subg. *Brevipedum*, as *R. leucocarpa* (T.Lebel) T.Lebel had been described earlier. Differences between the three novel species and their closely related taxa were analyzed. Another two known species in subg. *Brevipedum*, *R. callainomarginis* J.F.Liang & J.Song and *R. japonica* Hongo were also identified among specimens from DHSBR and are described and illustrated. Phylogenetic analyses of ITS and a five-locus phylogeny (concatenated LSU, mtSSU, *rpb1*, *rpb2* and *tef1*) support the recognition of these taxa.

Keywords. New species, multi-locus phylogeny, taxonomy, morphology.

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Introduction

Russula Pers. is a hyper diverse ectomycorrhizal genus estimated including at least 2000 species with a worldwide distribution from temperate to tropical areas, playing important ecological roles in the maintenance of different ecosystems (Buyck *et al.* 2015, 2018; Adamčík *et al.* 2019). Due to its edibility, toxicity, ecological functions and diversity, *Russula* is among one of the most important lineages of macrofungi (Looney *et al.* 2016). At least 78 species of *Russula* are edible and consumed and 30 species are used as traditional medicine for at least 440 years in China (Wu *et al.* 2019). Taxonomic studies on *Russula* were also carried out in other Asian countries, such as India, Pakistan and Korea, with numbers of novel *Russula* species proposed (Das *et al.* 2017, 2018, 2020; Jabeen *et al.* 2017; Lee *et al.* 2017; Wisitrassameewong *et al.* 2020; Ghosh *et al.* 2021). Buyck *et al.* (2018, 2020) reorganized the infrageneric taxonomic system of *Russula* employing a 5-locus phylogenetic analysis and divided the genus into 8 subgenera, namely subgenera *Archaeae* Buyck & V.Hofst., *Brevipedum* Buyck & V.Hofst., *Compactae* (Fr.) Bon emend. Buyck & V.Hofst., *Crassotunicatae* Buyck & V.Hofst., *Heterophyllidiae* Romagnesi emend. Buyck & V.Hofst., *Malodorae* Buyck & V.Hofst., *Russula* Pers. emend. Buyck & V.Hofst. and *Glutinosae* Buyck & X.H.Wang. This infrageneric classification will be followed here.

This paper presents yet another report on the rich *Russula* diversity in Dinghushan Biosphere Reserve (DHSBR). For general geographical, ecological and climatic characteristics of this region in southern China we refer to Song *et al.* (2018b). During the past few years a total of 46 species of *Russula* have been documented from this subtropical Biosphere Reserve, including 20 species new to science (Das *et al.* 2017; Zhang *et al.* 2017; Song *et al.* 2018a, 2018b, 2021; Li *et al.* 2019; Yuan *et al.* 2019; Zhou *et al.* 2020; Song 2022). In this contribution, we will focus on additional species recorded for the subgenera *Archaeae*, *Brevipedum* and *Compactae*.

The common characters of subg. *Archaeae* mainly include small to moderately large fruiting bodies, dull coloured pileus, irregularly unequal lamellae, white spore print, very small spores with inamyloid suprahilar spot (Buyck *et al.* 2018). At present, most known species in subg. *Archaeae* were described from Europe and America (for a historical overview, see Das *et al.* 2018). With the exception of *R. butyroindica* K.Das & Buyck from India, no other species have been described from Asia. During our macrofungal survey in Dinghushan Biosphere Reserve (DHSBR) in southern China, two species of subg. *Archaeae* were collected. After detailed morphological and multi-locus phylogenetic analyses, they are described here as novel species, namely *Russula cylindrica* Y.Song sp. nov. (Figs 3–4) and *R. lacteocarpa* Y.Song sp. nov. (Figs 5–6). Our proposal of the two novel species in subg. *Archaeae* confirm the presence of the subgenus in China.

Members of subg. *Compactae* mostly have dull-coloured pileus, regularly unequal lamellae, obvious color change when bruised, white spore print, spores with inamyloid suprahilar spot (Buyck *et al.* 2018). Three species with widely spaced gills in this subgenus have previously been reported from DHSBR, namely *R. latolamellata* Y.Song & L.H.Qiu, *R. nigrocarpa* S.Y.Zhou, Y.Song & L.H.Qiu and *R. ochrobrunnea* S.Y.Zhou, Y.Song & L.H.Qiu (Zhou *et al.* 2020). A new species with crowded gills, *R. reticulofolia* Y.Song sp. nov., is now proposed in this study based on both morphological and phylogenetic analyses (Figs 7–8).

Species in subg. *Brevipedum* mostly have medium to very large fruiting bodies with thick flesh, whitish pileus often developing brownish stains with age, regularly unequal lamellae and whitish to yellow spore print (Buyck *et al.* 2018). Here, we report three species of subg. *Brevipedum* from DHSBR, namely *Russula callainomarginis* J.F.Liang & J.Song (Figs 9–10), *R. japonica* Hongo (Figs 11–13) and *R. leucobrunnea* Y.Song nom. nov. (Figs 14–15). The latter species is a new name to replace the illegitimate *R. leucocarpa* G.J.Li & C.Y.Deng (Li *et al.* 2020), as *R. leucocarpa* (T.Lebel) T.Lebel had been described earlier. Macro- and micromorphological characters are illustrated for these three species based on DHSBR specimens.

Material and methods

Sampling and morphological studies

Fruiting bodies of the specimens were all collected from Dinghushan Biosphere Reserve (DHSBR, 112°33′ E, 23°10′ N), Guangdong Province, China. Specimens were dried at about 40°C and deposited in the Herbarium of Guangdong Institute of Microbiology (GDGM). Macroscopic characteristics of the intact, fresh fruit bodies were studied in daylight in the field and were photographed using a Canon IXUS 220 hs digital camera. HTML Color Codes (https://htmlcolorcodes.com/color-names/) were used to describe the color terminology.

Tissue sections were immersed in 5% KOH and then stained with 1% aqueous Congo red solution to observe the microscopic characters. All tissues were also examined in Cresyl blue to verify presence of ortho- or metachromatic reactions as explained in Buyck (1989). Sulfovanillin (SV) was used to test for staining reactions of cystidia. Micromorphological features were observed and photographed using a NIKON E200 microscope. Basidiospores were observed in Melzer's reagent and measured in side view, excluding ornamentation and apiculus which was observed using scanning electron microscopy (SEM). The abbreviation [x/y/z] indicates that measurements were made on x basidiospores in y fruit bodies from z specimens. Basidiospore size was noted as "(a–)b–m–c(–d)", with b–c indicating the range including 95% of the measured values for length or width, with a and d corresponding to the extremes of all measurements, and "m" for mean value. Q indicates length/width ratio of basidiospores.

DNA extraction, PCR, sequencing and phylogenetic analyses

Protocols for DNA extraction followed the method described by (Zhou & Liang 2011). The internal transcribed spacer (ITS) region of nuclear ribosomal DNA were amplified with the primer pair ITS1F/ITS4 (White *et al.* 1990; Gardes & Bruns 1993). The protocol for PCR amplification is as follows: a 5 min activation at 94°C, followed by 32 cycles of 30 s at 94°C, 30 s at 52°C and 1 min at 72°C, and a final 12 min extension at 72°C. Primers and amplification protocols refer to Buyck *et al.* (2018). PCR products were purified using E.Z.N.A Gel Extraction Kit (OMEGA) and sequenced on an ABI3730xl DNA Analyzer (IGE, Guangzhou, China) using primers identical to PCR. The newly generated sequences were submitted to GenBank (www.ncbi.nlm.nih.gov).

Maximum Likelihood (ML) analyses based on ITS and concatenated 5-locus sequences (LSU, mtSSU, *rpb1*, *rpb2* and *tef1*) were conducted. Multi-locus dataset was concatenated in Sequence Matrix software. All the sequence dataset were automatically aligned by MAFFT ver. 7.427 (Katoh & Standley 2013), then manually adjusted and trimmed with BioEdit ver. 7.0.9 (Hall 1999). Incongruence length difference test (ILD test) was performed with PAUP* ver. 4.0b10 to check the homogeneity of different gene locus, the resulting P value is 0.04, indicating that the 5-locus alignment can be used for further phylogenetic analysis. Maximum Likelihood (ML) analysis was executed in RAxML ver. 7.2.6 (Stamatakis 2006), followed by a rapid bootstrapping (BS) algorithm of 1000 replicates and heuristic ML search for the best tree using the GTR+G+I model. The final ITS alignment was composed of 92 sequences with 840 bp including gaps, while the 5-locus alignment comprised 58 sequences with 4157 bp (nLSU 906 bp, mtSSU 546 bp, *tef1* 920 bp, *rpb2* 779 bp, *rpb1* 1006 bp). *Lactarius lignyotus* Fr. and *L. subdulcis* (Pers.) Gray were chosen as outgroups. All the sequences used in ITS and 5-locus phylogenetic analyses were listed in Table 1 and Table 2, respectively.

Results

Phylogenetic analyses

Subgenus *Archaeae*, *Brevipedum* and *Compactae* were all well resolved in the phylogenetic trees (Figs 1–2). *Russula cylindrica* sp. nov. and *R. lacteocarpa* sp. nov. were nested well in subg. *Archaeae*.

Table 1 (continued on next two pages)**.** ITS Sequences used in phylogenetic analysis. Sequences generated in this study are shown in bold.

Taxon	**Voucher specimen**	**Location**	**ITS accession number**
Subg. ***Archaeae***			
R. aff. *earlei*	Ex1186/BB 07.108 (PC)	USA	KY800363
R. archaea	BB2004-255 (PC)	USA	EU598165
R. archaeosuberis	1118/BB 12.085	Italy	KY800355
R. butyroindica	CAL1511 (holotype)	India	KY674859
R. camarophylla	PAM01081108 (PC)	France	DQ421982
R. camarophylla	Sarnari 8/8/94 (PC)	Europe	AY061662
R. cylindrica **sp. nov.**	**GDGM79551 (holotype)**	**China**	**MN275533**
R. cylindrica **sp. nov.**	**GDGM79552**	**China**	**MN275534**
R. cylindrica **sp. nov.**	**GDGM79553**	**China**	**MN275535**
R. cylindrica **sp. nov.**	**GDGM79554**	**China**	**MN275536**
R. earlei	WRW00-412 (PC)	USA	DQ422025
R. earlei	BPL245 (TENN)	USA	KT933961
R. gossypina	2/BB 06.002	Madagascar	KY800350
R. lacteocarpa **sp. nov.**	**GDGM79555 (holotype)**	**China**	**MN275537**
R. lacteocarpa **sp. nov.**	**GDGM79556**	**China**	**MN275538**
R. pseudoaurantiophylla	BB 09.223 (PC) (holotype)	New Caledonia	KY800354
Uncultured fungus	KI6	China	JX456818
Uncultured fungus	K159	China	JX456865
Subg. ***Brevipedum***			
R. aff. *chloroides*	FH12273 (GENT)	Belgium	KT934015
R. aucarum	Beenken1155 (PC)	South America	KY800351
R. australis	JAC10732	New Zealand	MW683746
R. brevipes	TENN:070667	USA	KY848511
R. byssina	HGAS-MF 009907 (holotype)	China	MN648951
R. callainomarginis	MH286463 (holotype)	China	MH286463
R. callainomarginis	**GDGM79715**	**China**	**MN275693**
R. callainomarginis	**GDGM79716**	**China**	**MN839555**
R. cf. *delica*	UE24.08.2004-20 (UPS)	Sweden	DQ422005
R. chloroides	Buyck 99.804 (PC)	Europe	AY061663
R. cremicolor	HGAS-MF 009901 (holotype)	China	MN648955
R. delica	Buyck 6085 (PC)	Europe	AY061671
R. japonica	MHHNU 31049	China	MK167414
R. japonica	HGAS-MF009915	China	MN648956
R. japonica	MHHNU 31484	China	OM760732
R. japonica	**GDGM79702**	**China**	**MN275680**
R. japonica	**GDGM79707**	**China**	**MN275685**
R. japonica	**GDGM79708**	**China**	**MN275686**
R. japonica	**GDGM79697**	**China**	**MN275688**

Table 1 (continued).

Taxon	**Voucher specimen**	**Location**	**ITS accession number**
R. laevis	KUO (JR4016) (holotype)	Finland	MN130091
R. leucobrunnea nom. nov.	HGAS-MF 009910 (holotype)	China	MN648948
***R. leucobrunnea* nom. nov.**	**GDGM79692**	**China**	**MN275671**
***R. leucobrunnea* nom. nov.**	**GDGM79693**	**China**	**MN275672**
R. marangania	MEL2293694	Australia	EU019930
R. pallidospora	Walleyn 1901 (PC)	Europe	AY061701
R. pallidospora	JV02-218 (C)	Sweden	DQ422032
R. pumicoidea	Trappe14771	Australia	EU019931
R. sinuata	H4755	Australia	EU019943
R. vesicatoria	Ex573/BB 07.009 (PC)	USA	KY800359
R. sp.	FLAS-F-61515	Florida	MH211943
R. sp.	FLAS-F-61039	Florida	MH211706
R. subbrevipes	RITF3136 (holotype)	China	MH286460
Subg. *Compactae*			
R. acrifolia	UE12.09.2003-3 (UPS)	Sweden	DQ421998
R. adusta	Buyck 6020 (PC)	Europe	AY061652
R. albonigra	AT2002064 (UPS)	Sweden	DQ422029
R. anthracina	LAH-EM2-2013	Pakistan	KR011881
R. ashihoi	CAL1813 (holotype)	India	MT893202
R. atramentosa	FH 2011-002R	Belgium	MW172322
R. cantharellicola	UC1999420 (isotype)	USA	KF306036
R. cantharellicola	RG1	USA	KF306037
R. cascadensis	clone 90	USA	KT800120
R. cascadensis	OSC 1064009	USA	EU526006
R. cf. *eccentrica*	431/BB 07.132	USA	KP033478
R. cortinarioides	BB 07.133 (holotype)	USA	KP033485
R. cortinarioides	567/BB 07.103	USA	KP033480
R. densifolia	ue116 (TUB)	Germany	AF418606
R. densifolia	OSA-MY-4277	Japan	AB291754
R. densifolia	RDEN	Thailand	MN580113
R. densifolia subgroup A-4	OSA-MY-4282	Japan	AB291760
R. densifolia subgroup A-5	OSA-MY-1715	Japan	AB291755
R. densifolia subgroup A-6	OSA-MY-4285	Japan	AB291763
R. densifolia subgroup A-7	OSA-MY-4284	Japan	AB291762
R. densissima	FH 2014 ST04	Germany	MW172328
R. dissimulans	BPL285 (TENN)	USA	KT933979
R. eccentrica	BB2004-248 (PC)	USA	EU598197
R. fistulosa	BB99.529 (PC)	Sweden	DQ421985
R. fortunae	TUC (Corrales 180) (holotype)	Panama	KM594806
R. fuliginosa	IB 1992/0454 (holotype)	Italy	HG798529

Table 1 (continued)**.**

Taxon	Voucher specimen	Location	ITS accession number
R. indonigra	CAL1815 (holotype)	India	MT889672
R. ingwa	MEL2101936	Australia	EU019919
R. khanchanjungae	AV-KD-KVP09-106 (GENT)	India	KR364129
R. lateriticola	7/BB 06.031	Madagascar	KP033476
R. latolamellata	GDGM79561 (holotype)	China	MN275543
R. nigricans	UE20.09.2004-07 (UPS)	Sweden	DQ422010
R. nigrocarpa	GDGM79720 (holotype)	China	MN688794
R. ochrobrunnea	GDGM79718 (holotype)	China	MN688792
R. polyphylla	568/BB 07.023	USA	KP033481
R. polyphylla	1194/BB 07.134	USA	KP033486
***R. reticulofolia* sp. nov.**	**GDGM79559 (holotype)**	**China**	**MN275541**
***R. reticulofolia* sp. nov.**	**GDGM79560**	**China**	**MN275542**
R. sp.	MEH-18-01	India	OL469097
R. subfistulosa var. *apsila*	S16	Cameroon	KR819069
R. subnigricans	OSA-MY-4267	Japan	AB291750
Subg. *Glutinosae*			
R. fattoensis	Buyck 02.227 (PC) (holotype)	USA	MN315545
R. glutinosa	Roody WRWV 04.1154 (holotype)	USA	MN315541
R. glutinosoides	HKAS106678 (holotype)	China	MN434187
Outgroup			
Lactarius lignyotus	PBM2424(CUW)	USA	DQ221107
L. subdulcis	ED2008-27	Belgium	KR025572

The clade of *R. cylindrica* consisted of six ITS sequences all collected from DHSBR, four representing our specimens and two (JX456865 and JX456818) isolated from soil, with sequence similarity higher than 99% between each other. *Russula cylindrica* sp. nov. was relatively close to *R. camarophylla* Romagn., *R. butyroindica* K.Das & Buyck, *R. earlei* Peck (aff.). *Russula lacteocarpa* formed a distinct clade with significant support both in ITS and 5-locus phylogenetic analyses (BS = 85% and 100%, respectively).

Russula reticulofolia sp. nov. of subg. *Compactae* was highly supported in both phylogenetic trees (BS = 99% and 100%, respectively). In the multi-locus phylogram, *R. reticulofolia* sp. nov. clustered with *R. densifolia* Secr. ex Gillet, but showed apparent genetic distance between them. In the ITS phylogram, *R. reticulofolia* sp. nov. showed close relationship to *R. densifolia* subgroup A-4, with sequence similarity ca 97.6%.

Russula leucobrunnea nom. nov., *R. callainomarginis* and *R. japonica* of subg. *Brevipedum* were all well resolved in the 5-locus tree. Their sequences of DHSBR specimens were clustered with corresponding reference sequences downloaded from GenBank.

Morphological analyses

A total of six species of *Russula* were identified based on specimens collected from Dinghushan Biosphere Reserve, namely *Russula cylindrica* sp. nov. (Figs 3–4) and *R. lacteocarpa* sp. nov. (Figs 5–6) of subg.

Table 2 (continued on next two pages)**.** Sequences used in phylogenetic analysis based on 5-locus data. Sequences generated in this study are shown in bold.

Taxon	Voucher specimen	Location	Accession number				
			nLSU	mtSSU	*rpb1*	*rpb2*	*tef1*
Subg. ***Archaeae***							
R. aff. *earlei*	1181/MT s.n.	Costa Rica	KU237598	KU237446	–	KU237883	–
R. archaeosuberis	1118/BB 12.085	Italy	KU237593	KU237441	KU237732	KU237878	KU238019
R. camarophylla	PAM01081108 (PC)	France	DQ421982	–	–	DQ421938	–
R. cf. *camarophylla*	639/MPG11–7–09	Spain	KU237579	KU237427	KU237722	KU237865	KU238006
R. cylindrica **sp. nov.**	**GDGM79551 (holotype)**	**China**	**MK881930**	**MK882058**	**MT085523**	**MK880657**	**MT085571**
R. cylindrica **sp. nov.**	**GDGM79553**	**China**	**MN839556**	**MN839604**	**MT085516**	**MT085631**	**MT085603**
R. earlei	BPL245 (TENN)	USA	KT933820	–	KT957331	KT933891	–
R. gossypina	2/BB 06.002	Madagascar	KU237450	KU237293	–	KU237736	KU237886
R. lacteocarpa **sp. nov.**	**GDGM79555 (holotype)**	**China**	**MK881963**	**MK882090**	**MT085528**	**MK880690**	**MT085598**
R. pseudoaurantiophylla	740/BB 09.219	New Caledonia	KU237591	KU237439	KU237730	KU237876	KU238017
Subg. ***Brevipedum***							
R. aff. *chloroides*	FH12273	Belgium	KT933876	–	KT957386	KT933947	–
R. aff. *delica*	1119/BB 12.086	Italy	KU237594	KU237442	–	KU237879	KU238020
R. aff. *pallidospora*	640/MPG13–6–08	Spain	KU237580	KU237428	–	KU237866	KU238007
R. brevipes	226/BB 06.508	Mexico	KU237479	KU237323	KU237628	KU237765	–
R. callainomarginis	RITF2639 (holotype)	China	MH286468	MH911616	–	MH911624	–
R. callainomarginis	**GDGM79715**	**China**	**MN839582**	**MN839632**	**MT085535**	**MT085659**	**MT085602**
R. cf. *brevipes*	232/BB 06.441	Mexico	KU237483	KU237327	KU237632	KU237769	KU237912
R. cf. *delica*	1195/SA07.210	Slovakia	KU237600	KU237449	–	KU237885	–
R. chloroides	572/BB 07.209	Slovakia	KU237559	KU237407	KU237703	KU237845	KU237990
R. delica	233/BB 06.476	Mexico	KU237484	KU237328	KU237633	KU237770	KU237913
R. herrerae	239/BB 06.532	Mexico	KU237486	KU237330	KU237635	KU237772	KU237915
R. japonica	OSA–MY–1709	Japan	AB154697	–	–	–	–
R. japonica	**GDGM79697**	**China**	**MK881959**	**MK882086**	**MT085495**	**MK880686**	**MT085596**
R. japonica	**GDGM79710**	**China**	**MN839579**	**MN839629**	**MT085497**	**MT085656**	**MT085627**
R. laevis	KUO (JR4016) (holotype)	Finland	MN130128	MN161180	–	MN380529	–

Table 2 (continued).

Taxon	Voucher specimen	Location	Accession number				
			nLSU	mtSSU	*rpb1*	*rpb2*	*tef1*
***R. leucobrunnea* nom. nov.**	**GDGM79692**	**China**	**MK881934**	**MK882062**	**MT364342**	**MK880661**	**MT085575**
R. subbrevipes	RITF3136 (holotype)	China	MH286465	MH911617	–	MH911625	–
R. vesicatoria	1187/BB 07.034	USA	KU237599	KU237447	–	KU237884	–
Subg. *Compactae*							
R. acrifolia	543/BB 08.662	Italy	KU237535	KU237381	KU237684	KU237821	KU237965
R. adusta	223/BB 06.562	Canada	KU237476	KU237320	KU237625	KU237762	KU237907
R. aff. *areolata*	79/BB 06.090	Madagascar	KU237471	KU237315	–	KU237757	KU237903
R. albonigra	544/BB 07.291	Slovakia	KU237536	KU237382	KU237685	KU237822	KU237966
R. albonigra	AT2002064	Sweden	DQ422029	–	–	DQ421966	–
R. cf. *eccentrica*	431/BB 07.132	USA	KP033489	KU237341	KU237645	KP033500	KU237926
R. cf. *subfistulosa*	550/BB 08.176	Madagascar	KU237542	KU237388	KU237690	KU237828	KU237972
R. cortinarioides	567/BB 07.103	USA	KP033491	KU237402	–	KP033502	KU237985
R. densifolia	439/BB 07.344	Slovakia	KU237502	KU237347	KU237651	KU237788	KU237932
R. dissimulans	BPL285 (TENN)	USA	KT933840	–	–	KT933911	–
R. eccentrica	447/BB 07.044	USA	KP033490	KU237353	KU237657	KP033501	KU237937
R. fistulosa	535/BB 08.105	Madagascar	KU237527	KU237373	KU237677	KU237813	KU237957
R. fuliginosa	1178/MF s.n.	Italy	KU237597	KU237445	–	KU237882	–
R. inornata	571/BB 08.194	Madagascar	KU237558	KU237406	–	KU237844	KU237989
R. khanchanjungae	AV–KD–KVP09–106 (GENT)	India	JN389004	–	JN389201	JN375607	–
R. lateriticola	7/BB 06.031	Madagascar	KP033487	KU237297	KU237604	KP033498	KU237888
R. latolamellata	GDGM79561 (holotype)	China	MK881933	MK882061	MT085500	MK880660	MT085574
R. latolamellata	GDGM79563	China	MN839557	MN839605	MT085525	MT085632	MT085604
R. nigricans	429/BB 07.342	Slovakia	KU237495	KU237339	KU237643	KU237781	KU237924
R. nigricans	UE20.09.2004–07	Sweden	DQ422010	–	–	DQ421952	–
R. nigrocarpa	GDGM79720 (holotype)	China	MN839585	MN839635	MT085531	MT085662	MT085630
R. ochrobrunnea	GDGM79718 (holotype)	China	MN839584	MN839634	–	MT085661	MT085629

Table 2 (continued)**.**

Taxon	Voucher specimen	Location	Accession number				
			nLSU	mtSSU	*rpb1*	*rpb2*	*tef1*
R. polyphylla	568/BB 07.023	USA	KP033492	KU237403	KU237700	KP033503	KU237986
R. polyphylla	737/BB 09.215	New Caledonia	KU237590	KU237438	–	KU237875	–
***R. reticulofolia* sp. nov.**	**GDGM79559 (holotype)**	**China**	**MK881932**	**MK882060**	**MT085503**	**MK880659**	**MT085573**
Subg. *Glutinosae*							
R. fattoensis	Buyck 02.227 (holotype)	USA	MN315514	MN315537	–	MN326797	MN326800
R. glutinosa	Roody WRWV 04.1154 (holotype)	USA	MN315511	MN315532	–	MN326798	MN326799
R. glutinosoides	HKAS106678 (holotype)	China	MN428827	MN460313	–	–	–
Outgroup							
Lactarius lignyotus	PBM2424 (CUW)	USA	AY631898	–	–	DQ408128	–
L. subdulcis	ED2008–27	Belgium	JN389009	–	JN389206	JN375611	–

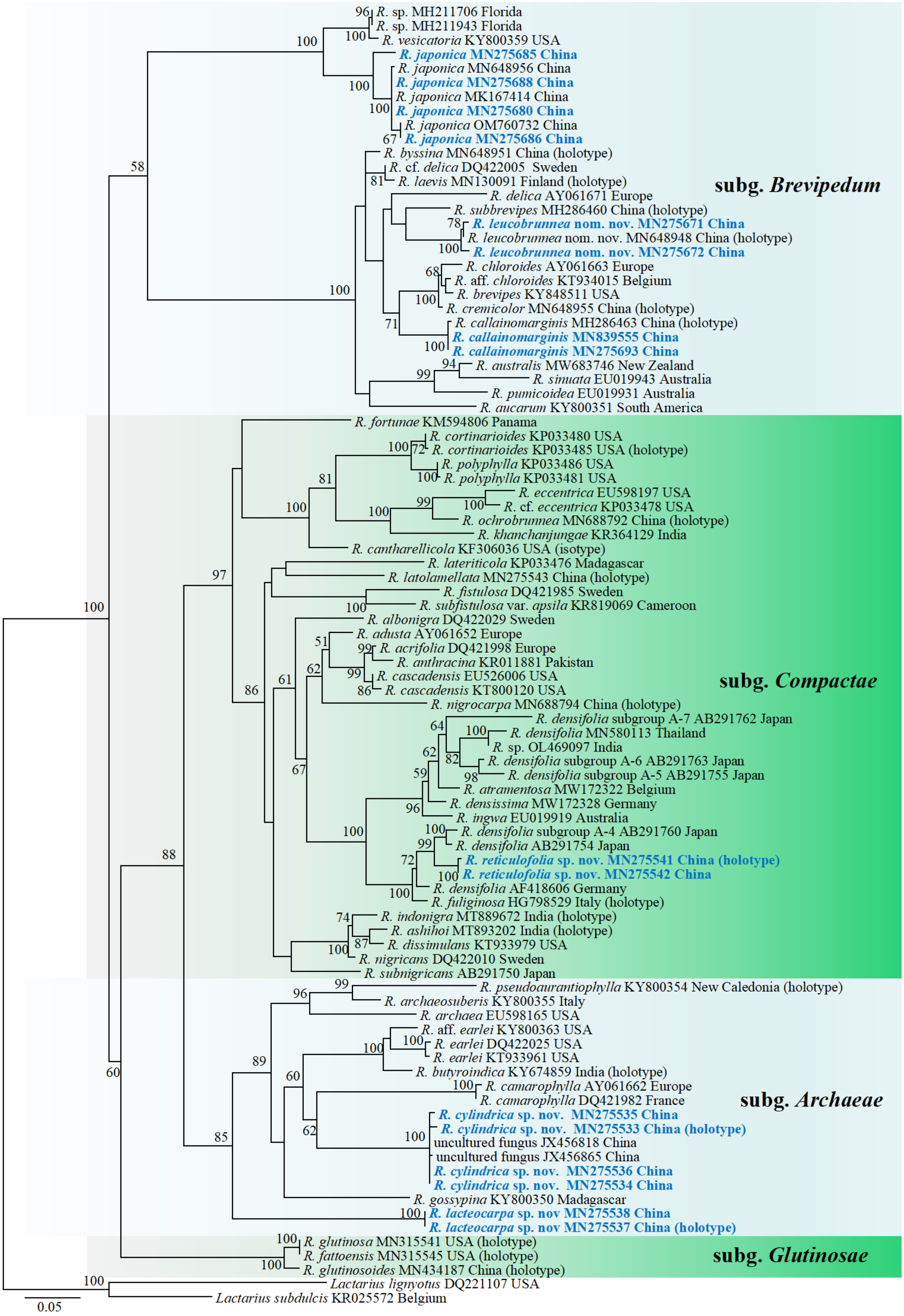

Fig. 1. Maximum Likelihood tree of *Russula* Pers. based on ITS sequences, bootstrap values higher than 50% were shown around the nodes. Sequences generated in this study are shown in bold blue.

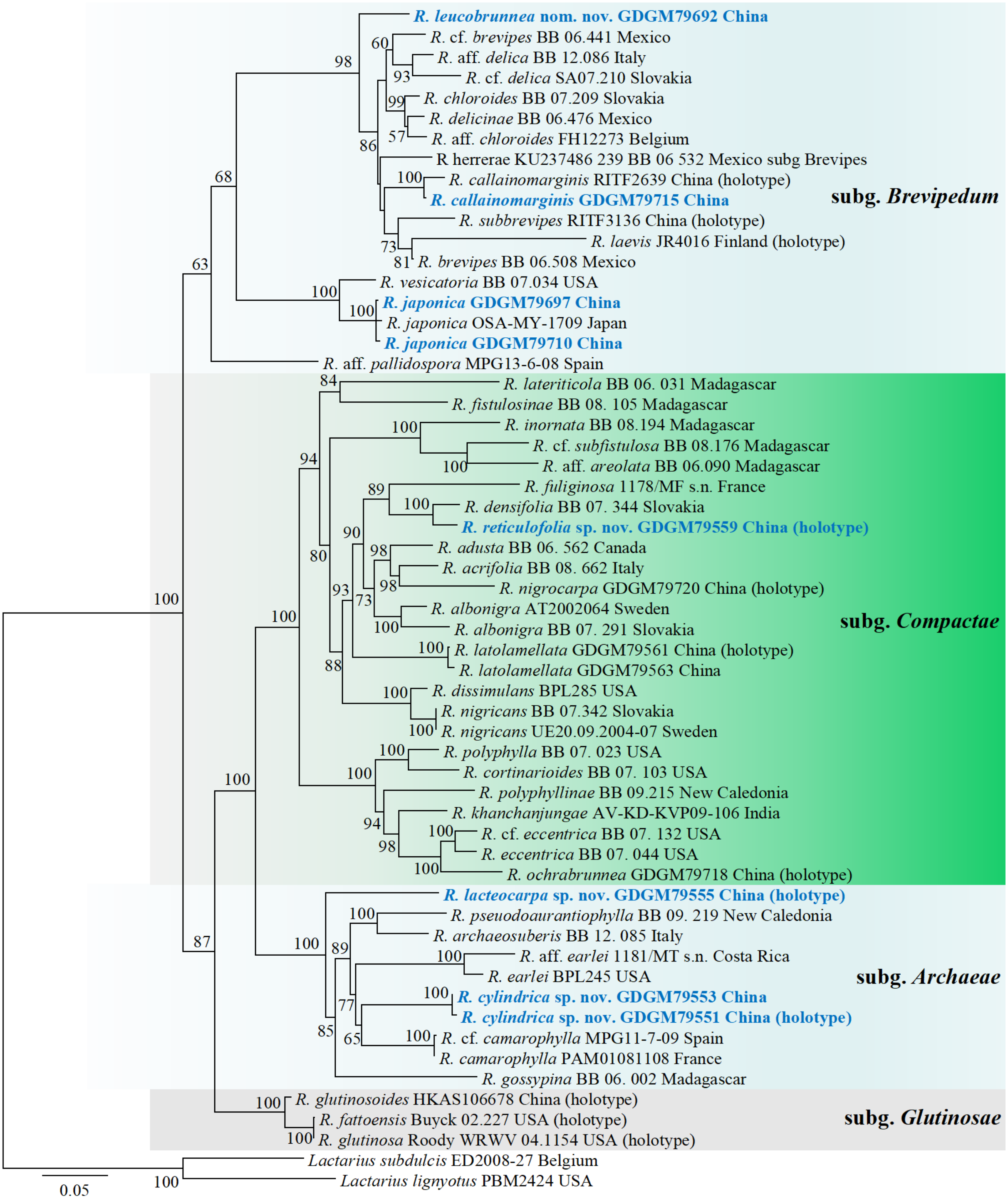

Fig. 2. Maximum Likelihood tree of *Russula* Pers. based on concatenated 5-locus (LSU, mtSSU, *rpb1*, *rpb2* and *tef1*) sequences. Bootstrap values higher than 50% were shown around the nodes. Sequences generated in this study are shown in bold blue.

Archaeae, *R. reticulofolia* sp. nov. of subg. *Compactae* (Figs 7–8), *R. callainomarginis* (Figs 9–10), *R. japonica* (Figs 11–13) and *R. leucobrunnea* nom. nov. (Figs 14–15). All these species are described and illustrated.

Taxonomy

Order Russulales Kreisel ex P.M.Kirk, P.F.Cannon & J.C.David
Family Russulaceae Lotsy
Genus *Russula* Pers.
Subgenus *Archaeae* Buyck & V.Hofst.

Russula cylindrica Y.Song sp. nov.
MycoBank: MB837414
Figs 3–4

Diagnosis

Russula cylindrica sp. nov. is mainly characterized by its cream buff to reddish brown pileus with obviously striate and undulate margin, white to cream lamellae becoming rusty brown when old, irregular presence of lamellulae, small spores ornamented with isolated warts and crests, cylindrical basidia and hymenial cystidia, and one-layered, gelatinized pileipellis with subcylindrical pileocystidia.

Etymology

Named after its cylindrical basidia and hymenial cystidia.

Type material

Holotype

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 12 Sep. 2016; *Y. Song K16091239*; GenBank nos: MN275533 (ITS), MK881930 (nLSU), MK882058 (mtSSU), MT085523 (*rpb1*), MK880657 (*rpb2*), MT085571 (*tef1*); GDGM79551.

Additional material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 8 Aug. 2016; *Y. Song K16080807*; GenBank no: MN275534 (ITS); GDGM79552 • same data as for preceding; *Y. Song K16080808*; GenBank nos: MN275535 (ITS), MN839556 (nLSU), MN839604 (mtSSU), MT085516 (*rpb1*), MT085631 (*rpb2*), MT085603 (*tef1*); GDGM79553 • same data as for preceding; *Y. Song K16080830*; GenBank no: MN275536 (ITS); GDGM79554.

Description

Basidiomata small to medium sized, agaricoid. *Pileus* 4–7 cm in diam., hemispherical to convex when young, turning applanate with maturity; surface glabrous, gelatinized or waxy, viscid when wet, not easy to peel, white to cream (#FAFAD2) with reddish brown tint (#F4A460, #F1B461), dark rust brown (#DF8E3D, #EA9540) at center when old; margin entire when young, turning irregularly undulate and slightly upward with maturity, obviously striate to sulcate when mature, sometimes cracked. *Lamellae* adnate, thick, unequal, slightly narrowed near stipe, rarely forked, interveined, white (#FDFEFE) at first, turning cream and then rust brown (#E68320, #D4700D) with maturity; edge entire, concolorous, often with white powder; lamellulae present. *Stipe* 2.5–4×1.5–2 cm, central, cylindrical, solid at first, turning spongy with age, white (#FFFAFA), often stained with reddish brown (#FAAA5A), longitudinally

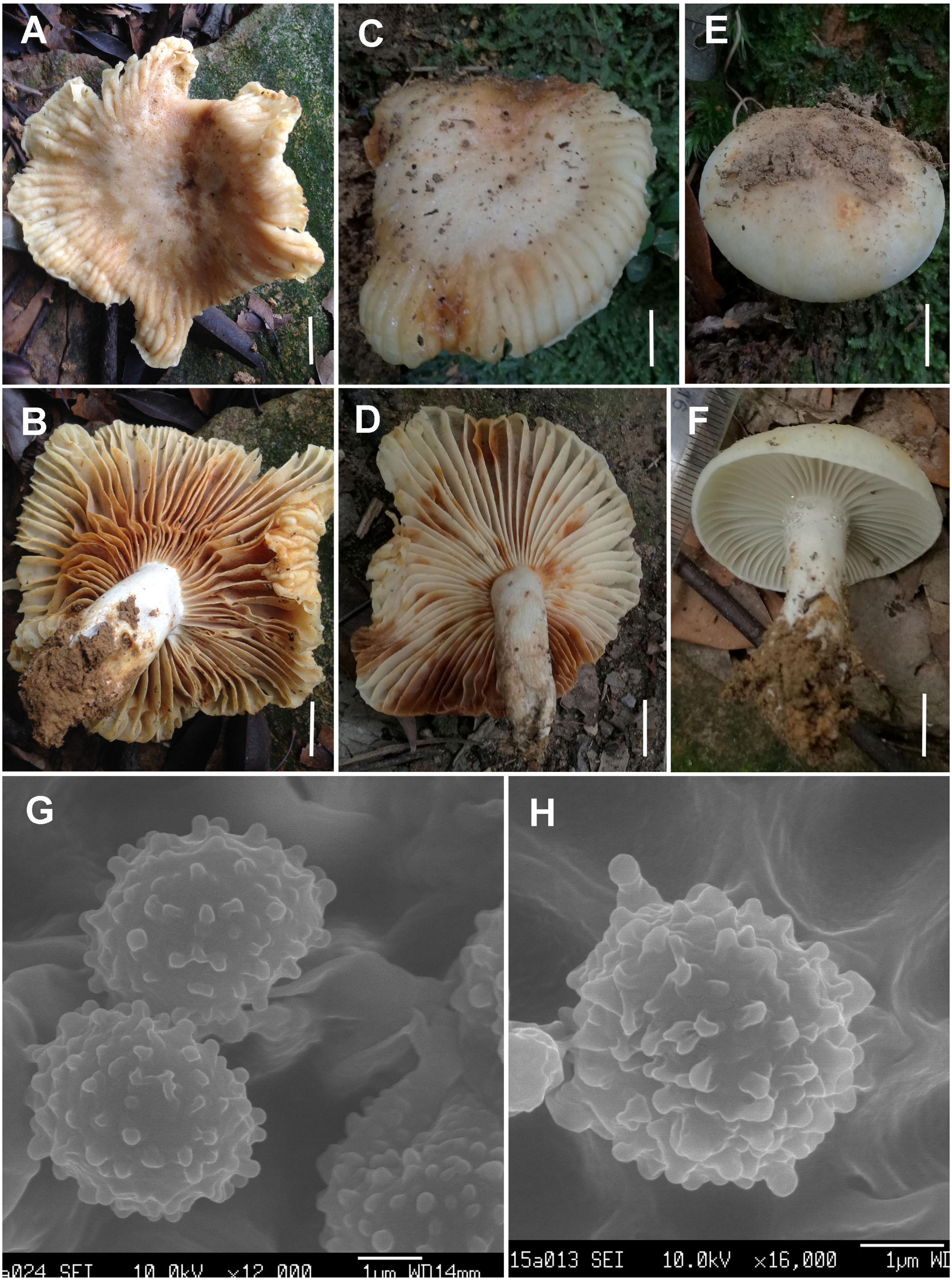

Fig. 3. *Russula cylindrica* Y.Song sp. nov., holotype GDGM79551(A–B, G–H), specimen GDGM79553 (C–D), specimen GDGM79552 (E–F). **A**–**F**. Fruiting bodies. **G**–**H**. Basidiospores under scanning electron microscope. Scale bars: A–F = 1 cm; G–H = 1 µm.

rugulose. *Context* whitish to chalky white (#F8F8FF). *Taste* mild. *Odor* indistinct. *Spore print* white (#FBFCFC).

Basidiospores subglobose to ellipsoid, rarely globose, small, (80/4/2) (4.4–)4.9–5.4–5.9(–6.5) × (4.1–) 4.6–4.8–5.2(–6.1) µm, [Q = (1.03–)1.07–1.23–1.39(–1.54)], hyaline in 5% KOH; ornamentation amyloid, composed of verrucous to subcylindircal warts less than 0.8 µm in height, mostly isolated, rarely fused into short crest or linked by lines, but not reticulate; suprahilar spot inamyloid. *Basidia* (17–)22–32–40 × 4.5–6–8 µm, subcylindrical to cylindrical, 2- or 4-spored; sterigmata 3.2–4.9 × 1.2–1.7 µm. *Pleurocystidia* (17–)25–37–65(–73) × 3–4–6 µm, cylindrical, with obtuse apices, thin-walled, with granular or irregular refractive contents, weakly positive in SV or negative in SV. *Cheilocystidia* not frequent, similar to pleurocystidia. *Lamellar trama* composed of numerous sphaerocytes surrounded by

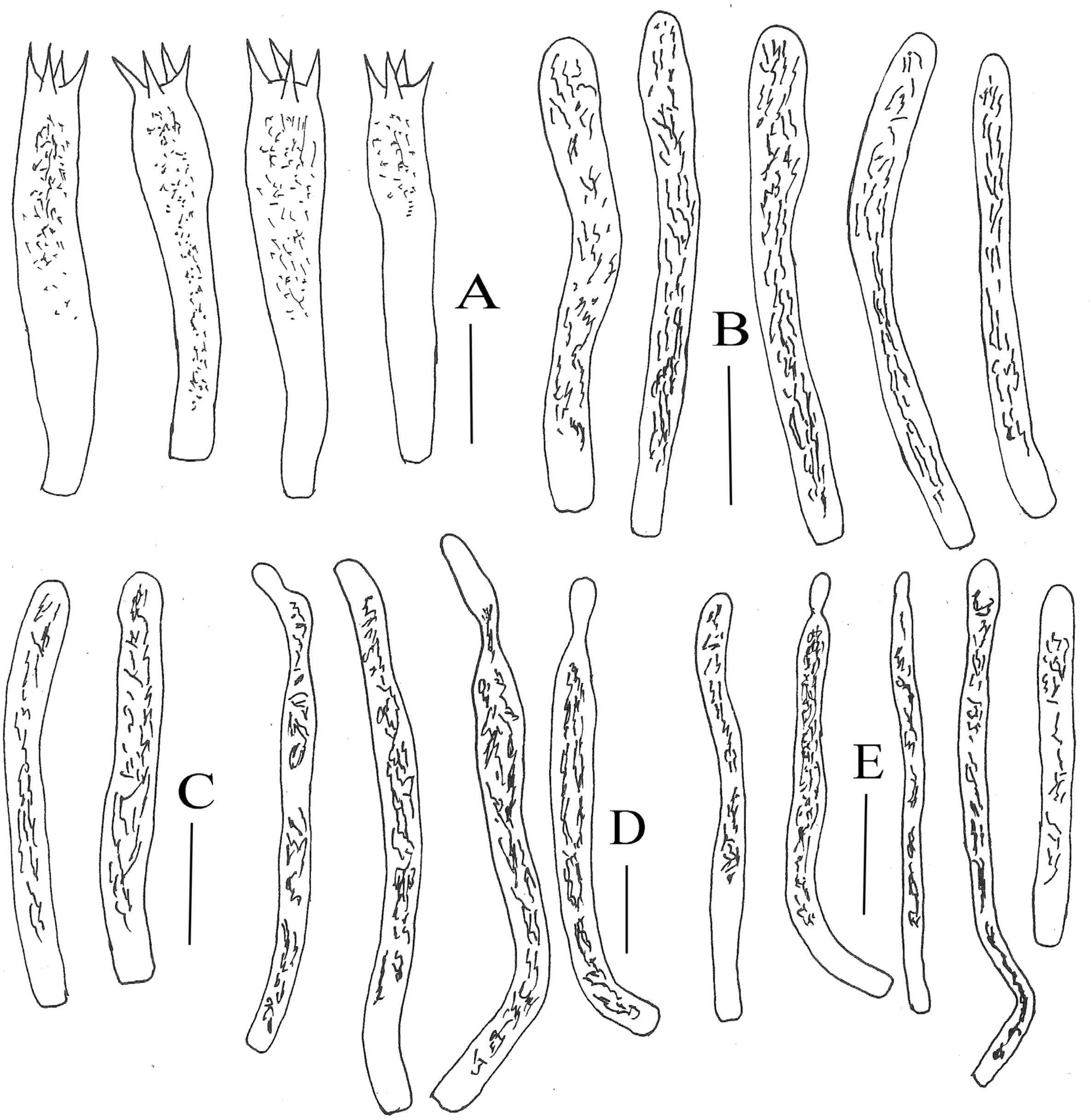

Fig. 4. *Russula cylindrica* Y.Song sp. nov., holotype (GDGM79551). **A**. Basidia. **B**. Pleurocystidia. **C**. Cheilocystidia. **D**. Pileocystidia. **E**. Caulocystidia. Scale bars = 10 µm.

connective hyphae, sphaerocytes measuring 10–26 × 7–22 µm. *Subhymenium* pseudoparenchymatous. *Pileipellis* an ixo-cutis, 33–120 µm thick, composed of cylindrical, septate and hyaline hyphae 2–5.5 µm wide; cystidioid hyphae present in the trama, 4–6 µm wide; terminal cells (7–)14–25–72 × 1.5–3–5.5 µm, cylindrical, rarely lageniform, with obtuse or tapering apices, thin-walled, hyaline. *Pileocystidia* (73–)82–95.5–114 × 3.5–4.5–6 µm, cylindrical, often constricted at upper part, with obtuse apices, with refractive contents, negative in SV. *Stipitipellis* a cutis, composed of hyphae measuring 1.5–4.5 µm wide, rarely septate, incrusted hyphae frequent; terminal cells 9.5–19–30(–34) × 1.5–2–2.5 µm, cylindrical with obtuse apices, hyaline. *Caulocystidia* (17–)26–43–70(–81) × 2–3–5 µm, cylindrical, obtuse or papillate, with refractive contents. *Clamp connections* absent in all tissues.

Comments

The newly described *R. cylindrica* sp. nov. has all the typical features of the subgenus *Archaeae* (see introduction). It belongs to sect. *Archaeinae* R.Heim ex Buyck & Sarnari and differs from all other known species so far especially in its very pale overall color which lacks the dominant yellowish or brownish tones in young stages for the other species. The brownish discoloration (Fig. 3) sets in only at later stages when fruiting bodies start to suffer from age. As in other *Archaeinae* collected from (sub)tropical climates (*R. pseudoaurantiophylla* Buyck & V.Hofst., *R. archaea* Heim, *R. earlei* Peck, *R. gossypina* Buyck), it possesses a very thin-fleshed pileus.

The only other Asian species in the subgenus, *R. butyroindica*, still only known from India, is easily distinguished in the field from *R. cylindrica* sp. nov. by its yellowish and often cracked pileus, detailed micromorphological characters refer to Das *et al.* (2018).

Russula lacteocarpa Y.Song sp. nov.

MycoBank: MB837415
Figs 5–6

Diagnosis

Russula lacteocarpa sp. nov. is mainly characterized by its milky to ivory white, dull pileus with striate margin, milky to ivory white gills, white stipe often irregularly fissured, very small spores with predominantly isolated, obtuse warts, slender cylindrical basidia and hymenial cystidia, and the one-layer pileipellis composed of gelatinized, incrusted hyphal terminations intermixed with often mucronate to rostrate pileocystidia.

Etymology

Named after its ivory-white pileus.

Type material

Holotype

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 24 Sep. 2017; *Y. Song K17092401*; GenBank nos: MN275537 (ITS), MK881963 (nLSU), MK882090 (mtSSU), MT085528 (*rpb1*), MK880690 (*rpb2*), MT085598 (*tef1*); GDGM79555.

Additional material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 16 Sep. 2016; *Y. Song K16091606*; GenBank no: MN275538 (ITS); GDGM79556.

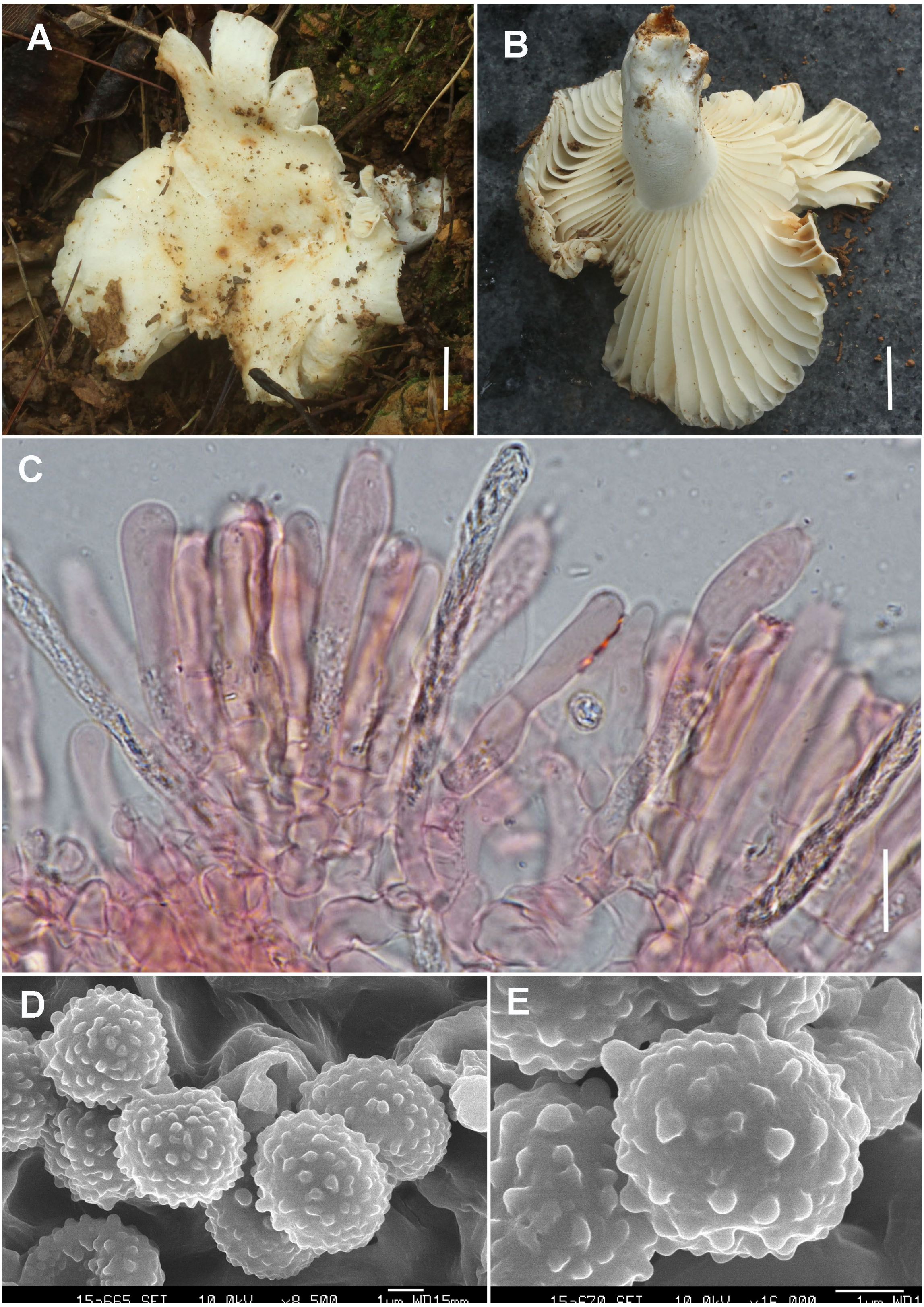

Fig. 5. *Russula lacteocarpa* Y.Song sp. nov., holotype (GDGM79555). **A**–**B**. Fruiting bodies. **C**. Basidia and pleurocystidia in hymenium. **D**–**E**. Basidiospores under scanning electron microscope. Scale bars: A–B = 1 cm; C = 10 µm; D–E = 1 µm.

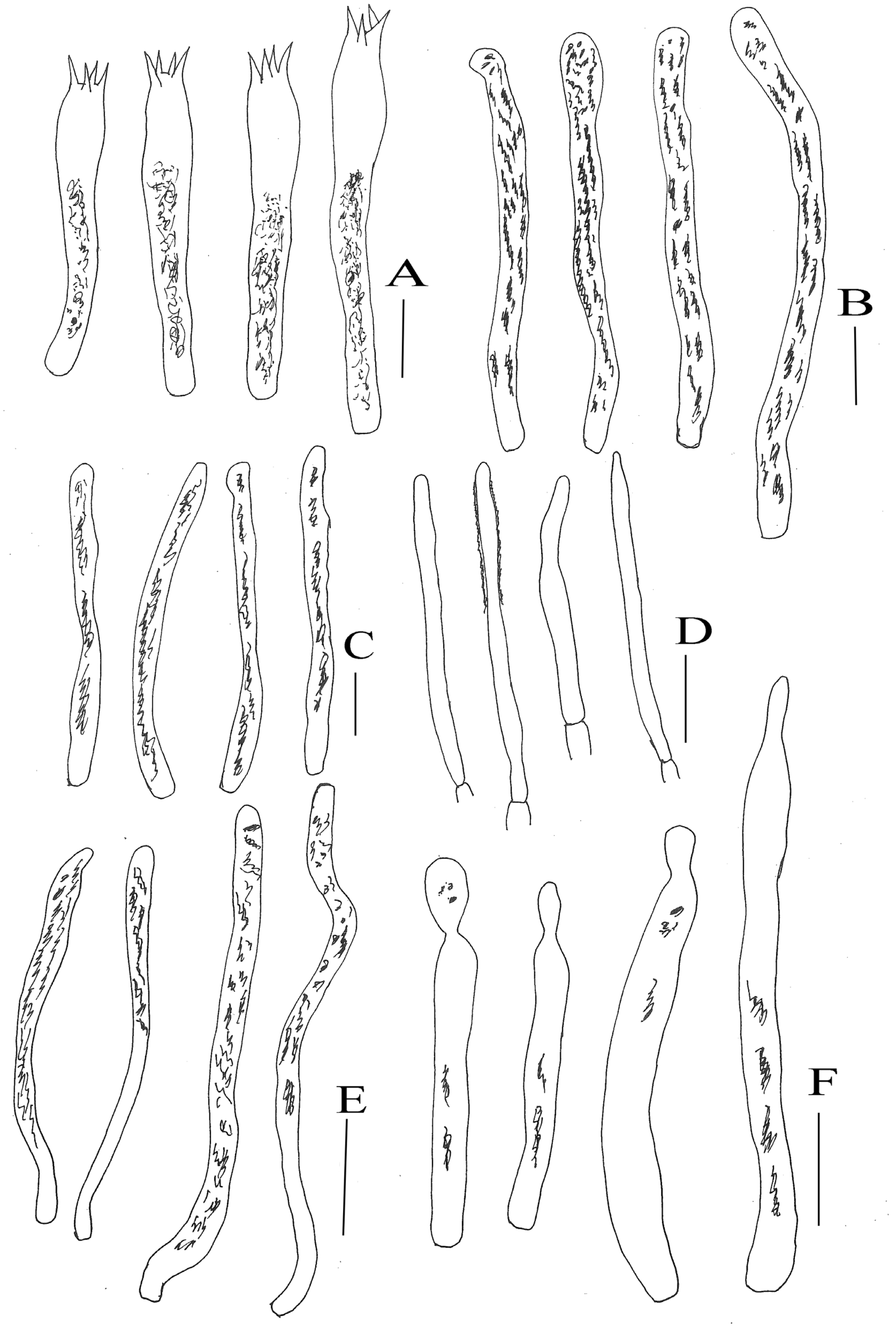

Fig. 6. *Russula lacteocarpa* Y.Song sp. nov., holotype (GDGM79555). **A**. Basidia. **B**. Pleurocystidia. **C**. Cheilocystidia. **D**. Terminal cells and incrustations. **E**. Caulocystidia. **F**. Pileocystidia. Scale bars = 10 µm.

Description

Basidiomata small to medium sized. *Pileus* 4–8 cm in diam., hemispherical to convex when young, applanate with maturity; surface glabrous, dry, milky to ivory white (#FDFEFE, #FFFFF0), often slightly stained with reddish brown (#F4C270, #F3BD5D); margin entire when young, turning undulate with age, often cracked, not striate. *Lamellae* adnate, widely spaced, unequal with mostly one lamellula per lamella, usually very short but of unequal length, slightly narrowed and not anastomosing near stipe, strongly attenuated toward pileus margin, milky white to cream (#FDFEFE, #FFFFF0); edge entire, concolorous. *Stipe* central, 3–5 cm long, cylindrical, white (#FFFFFF, #FFFFF0), often stained with rust brown (#A0522D, #8B4513) at base, irregularly fissured, solid at first, turning spongy to hollow with age. *Context* white, becoming pink to light brown (#FFDEAD, #FFEBCD) when reacting with 5% $FeSO_4$. *Taste* mild. *Odor* indistinct. *Spore print* white (#FBFCFC).

Basidiospores subglobose to ellipsoid, rarely globose, small, (40/2/2) (4.1–)4.8–5.2–5.6(–5.9) × (4.1–) 4.6–5.0–5.4(–5.7) µm, [Q = (1.08–)1.12–1.26–1.38(–1.52)], hyaline in 5% KOH; ornamentation amyloid, composed of obtuse, isolated warts, up to 1 µm high, rarely fused into short crest; suprahilar spot inamyloid. *Basidia* (33.5–)36–44–50 × (5.0–)6.5–7.0–8.5 µm, subcylindrical to cylindrical, slender, thin-walled, 2- or 4-spored; sterigmata 4.3–5.3 × 1.2–2.1 µm. *Pleurocystidia* (43–)46–56–69(–72) × 3.5–5–6 µm, cylindrical, with obtuse apices, thin-walled, one-celled, with irregular refractive contents, weakly positive in SV to negative in SV. *Cheilocystidia* 45–50–57.5 × 3.5–4.5–6 µm, similar to pleurocystidia, but smaller, negative in SV. *Marginal cells* not differentiated. *Subhymenium* pseudoparenchymatous. *Lamellar trama* composed of numerous sphaerocytes surrounded by connective hyphae. *Pileipellis* an ixo-cutis, 150–240 µm thick, composed of cylindrical, septate and hyaline hyphal terminations 1.5–5.0 µm wide; terminal cells (7–)11–23–35 × 1.5–2–3.0 µm, slender, cylindrical, with obtuse apices, often incrusted. *Pileocystidia* (16.5–)20–42.5–60(–96) × 2–3–5 µm, cylindrical, mucronate to rostrate or constricted at upper part, thin-walled, with few refractive contents, unchanging in SV. *Stipitipellis* 50–80 µm, composed of uprising to erect hyphae measuring 1–3 µm wide, septate, thin-walled, hyaline; terminal cells cylindrical, with obtuse hyaline apices. *Caulocystidia* (15.5–)20–37–52(–60) × 1.5–3–5.5 µm, cylindrical, apices obtuse or tapering, with refractive contents. *Clamp connections* absent in all tissues.

Comments

Russula lacteocarpa sp. nov. has a unique morphology in subgenus *Archaeae*. Its uniqueness is also reflected in its systematic position as both our ITS phylogeny (Fig. 1) and the combined 5-locus analysis (Fig. 2) place it in a basal position and sister to the rest of the subgenus with high support (BS = 85% and 100%, respectively). In the field, it is more reminiscent of species in subg. *Brevipedum* sect. *Pallidosporinae* or even some white capped *Lactifluus*. It is easily distinguished from these in the typically very small spores and the hymenophore that is not polydymous, but having a more or less equivalent number of lamellae and lamellulae. Together with *R. cylindrica* sp. nov. described above, it is also unique in the subgenus because of the very pale, creamy-whitish pileus.

Order Russulales Kreisel ex P.M.Kirk, P.F.Cannon & J.C.David
Family Russulaceae Lotsy
Genus *Russula* Pers.
Subgenus *Compactae* (Fr.) Bon emend. Buyck & V.Hofst.

Russula reticulofolia Y.Song sp. nov.
MycoBank: MB837416
Figs 7–8

Diagnosis

Russula reticulofolia sp. nov. is mainly characterized by its grey to black brown pileus with a surface that becomes minutely cracked toward the margin, abundantly and irregularly forked lamellae that sometimes even form a partial reticulate pattern, the remarkably small and reticulate spores, brown pigmented hyphae in pileipellis and stipitipellis, and pileocystidia with typical two-knobbed apices.

Etymology

Named after its frequently forked and reticulum-like lamellae.

Type material

Holotype

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in coniferous and broad-leaf mixed forest; 13 Sep. 2016; *Y. Song H16091306*; GenBank nos: MN275541 (ITS), MK881932 (nLSU), MK882060 (mtSSU), MT085503 (*rpb1*), MK880659 (*rpb2*), MT085573 (*tef1*); GDGM79559.

Additional material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in coniferous and broad-leaf mixed forest; 12 Sep. 2016; *Y. Song H16091234*; GenBank no: MN275542 (ITS); GDGM79560.

Description

Basidiomata medium sized to large. *Pileus* 5–11 cm in diam., hemispherical to convex when young, turning applanate with depressed center to infundibuliform; surface dry, with villose squama, not easy to peel, off-white to grey (#F5F5DC, #DCDCDC) with dark brown (#6D614C, #988970) center, turning black brown (#403524, #5B5539) with age; margin entire, involute. *Lamellae* adnate to subdecurrent, narrow, unequal from irregularly dispersed lamellulae that often fuse with lamellae near the pileus margin, crowded, frequently and irregularly forked, especially near stipe but also near pileus margin, often partially reticulate, off-white to cream (#FFF5EE, #FFFAF0), sometimes tinged reddish brown (#D2B48C, #F5DEB3); edge entire, concolorous. *Stipe* central, cylindrical, solid at first, turning spongy with age, 5–8 cm long, off-white (#FFFFFF, #F8F8FF), with brown (#F5DEB3, #FAE5B4) powdery or villose pubescence on the surface. *Context* white. *Odor* pungent. *Spore print* white to cream (#FCF3CF).

Basidiospores subglobose to ellipsoid, rarely globose, small, (80/4/2) (5.4–)5.8–6.5–8.3(–8.7) × (5.1–)5.4–5.9–7.5(–7.9) µm, [Q = (1.03–)1.04–1.15–1.27(–1.40)], hyaline in 5% KOH; ornamentation amyloid, composed of low ridges forming a complete or nearly complete reticulum; suprahilar spot inamyloid. *Basidia* 24.5–28–31(–33) × 5–7–8 µm, subcylindrical to clavate, thin-walled, 2-, 3- or 4-spored; sterigmata 1.8–4 × 1.1–1.6 µm. *Pleurocystidia* (35.5–)46–56.5–67(–69) × 3.5–5–6(–8) µm, projecting up to 25 µm, cylindrical, with mucronate to lanceolate or moniliform apices, non-septate, thin-walled, with few granular refractive contents, unchanging in SV. *Cheilocystidia* similar to pleurocystidia, 46–53–57.5 × 3.5–5–6 µm. Subhymenium pseudoparenchymatous. *Lamellar trama* composed of numerous sphaerocytes surrounded by connective hyphae. *Pileipellis* 130–180 µm thick, orthochromatic in cresyl blue, divided into two layers: suprapeillis composed of ascending to erect hyphae, while subpellis a cutis, 120–150 µm thick; hyphae cylindrical, thin-walled, septate, often with brown pigment, 2–5 µm wide; terminal cells 13–32–43(–47) × 2.5–4–7.5 µm, subcylindrical to ampuliform, often tapering upwards, frequently with brown pigment. *Pileocystidia* (19.5–)21–26.5–37(–39) × 3.5–5.5–7 µm, not frequent, subcylindrical to fusoid, apices mucronate, frequently with two lateral knobs (referred to as the 'Mickey Mouse' type in Buyck *et al.* 2018), thin-walled, with refractive contents, unchanging in SV. *Stipitipellis* a cutis, composed of hyphae measuring 1–4 µm wide, cylindrical, septate, often with

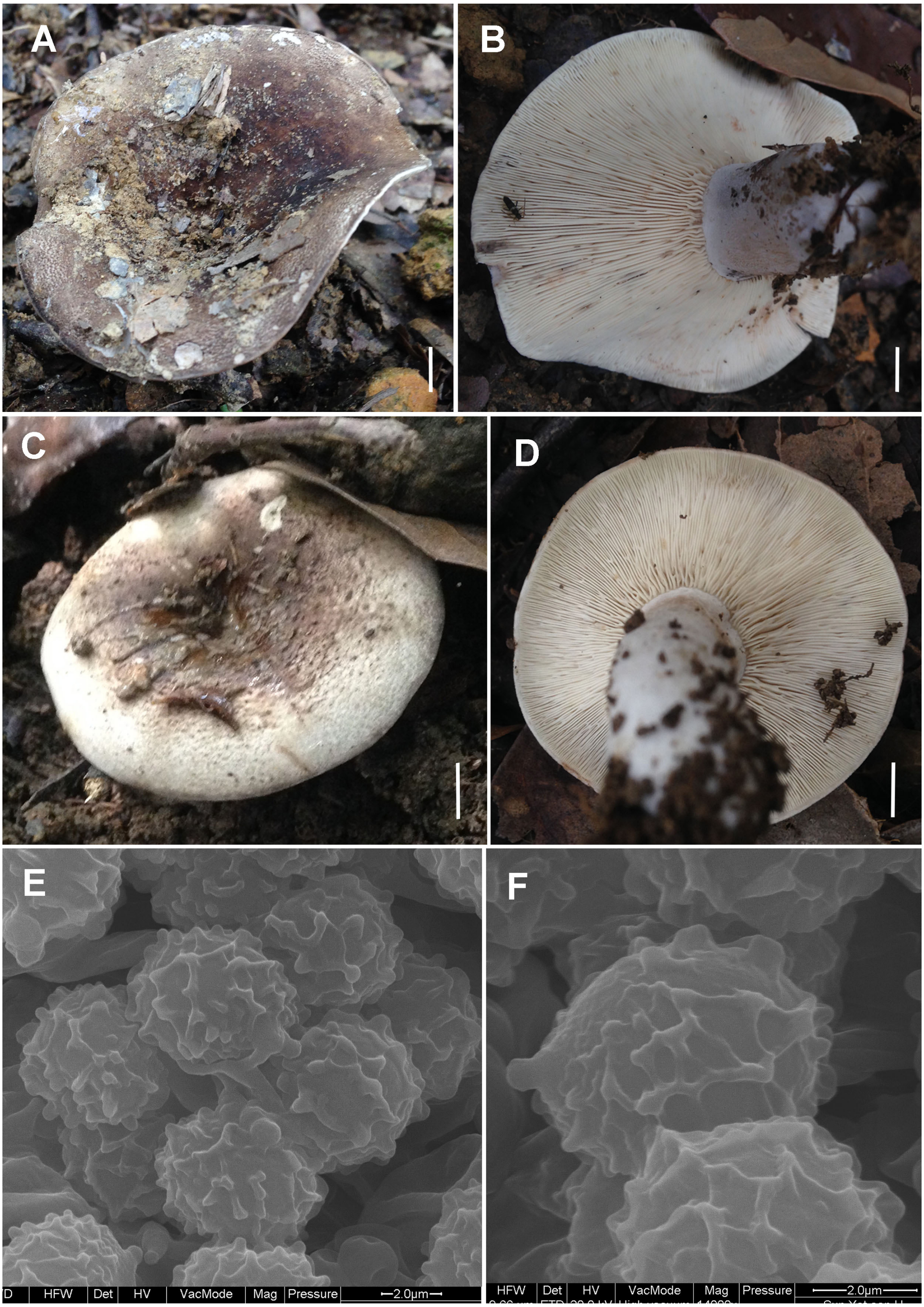

Fig. 7. *Russula reticulofolia* Y.Song sp. nov., holotype (GDGM79559) (A–B, E–F), GDGM79560 (C–D). **A**–**D**. Fruiting bodies. **E**–**F**. Basidiospores under scanning electron microscope. Scale bars: A–D = 1 cm; E–F = 2 µm.

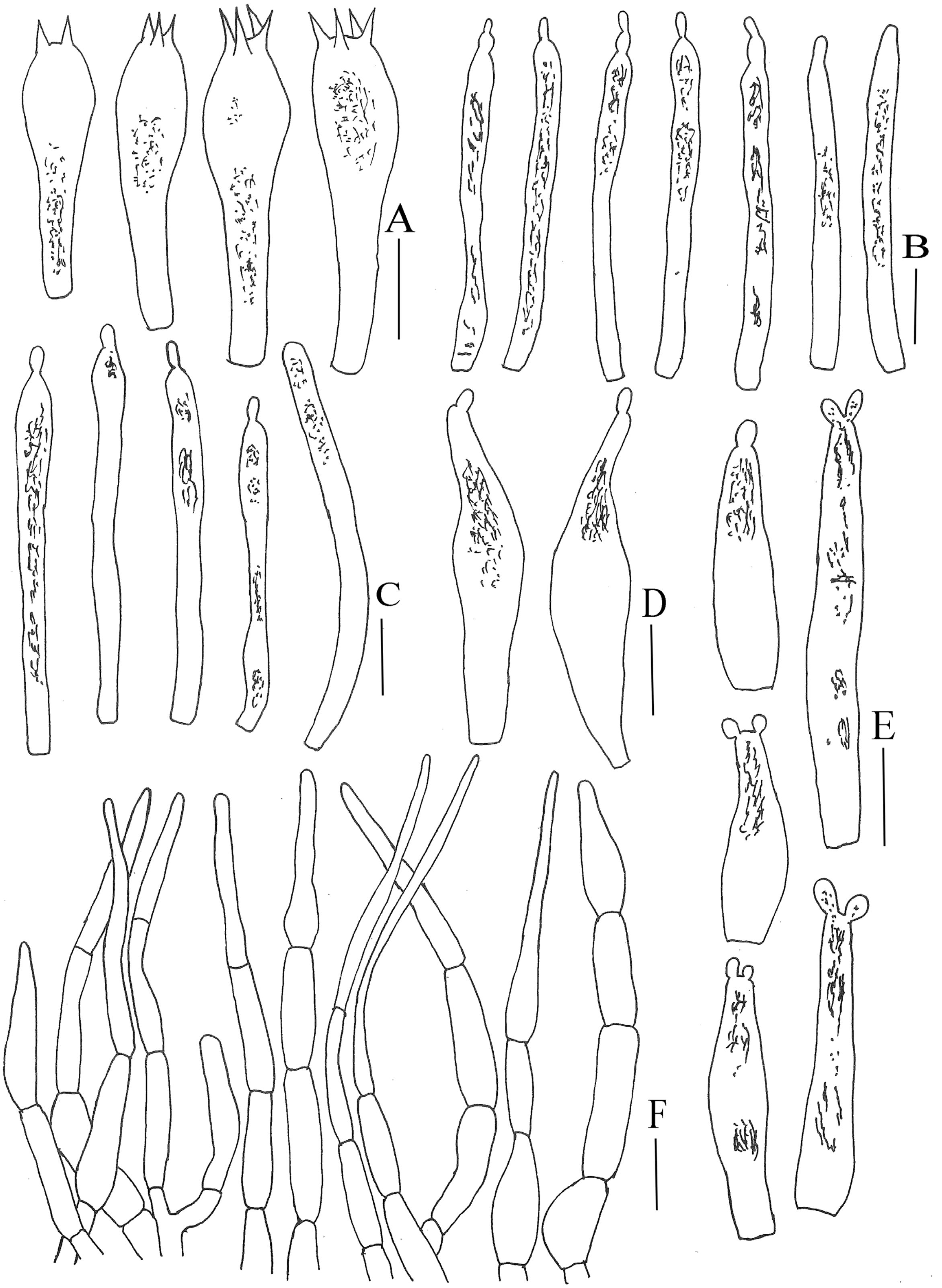

Fig. 8. *Russula reticulofolia* Y.Song sp. nov., holotype (GDGM79559). **A**. Basidia. **B**. Pleurocystidia. **C**. Cheilocystidia. **D**. Caulocystidia. **E**. Pileocystidia. **F**. Terminal elements in pileipellis. Scale bars = 10 µm.

brown pigment; terminal cells (10–)12–20–27 × 2–3.5–6 µm cylindrical to lageniform, with obtuse apices, mostly slender, thin-walled. *Caulocystidia* 4.5–10.5 µm wide, not frequent, fusoid, mucronate to papillate, thin-walled, with few refractive contents. *Clamp connections* absent in all tissues.

Comments

Russula reticulofolia sp. nov. is similar to *R. densifolia* Secr. ex Gillet in its blackish brown pileus, very dense lamellae, reticulate spore ornamentations, but it differs from the latter species in its frequently and irregularly forked lamellae, sometimes even forming a partial reticulate pattern, and in the more slender hyphal extremities in the pileipellis. In addition, spores (7–11.2 × 6–8.6 µm) and basidia (39–67 × 7.2–12 µm) of *R. densifolia* (Shaffer 1962) are obviously larger than in *R. reticulofolia* sp. nov., so are those of other species in this same complex. The similarities in ITS sequences between *R. reticulofolia* sp. nov. and its phylogenetically closest match (*R. densifolia* subgroup A-4 from Japan) are about 97.5%, and these two species showed obvious genetic distance in the five-locus phylogenetic analysis. The combination of the unique morphological features and genetic distance support *R. reticulofolia* sp. nov. as a novel species.

Russula fuliginosa Sarnari also has blackish pileus, but it has fusiform hymenial cystidia, much bigger spores (7.2–8.8 × 5.6–7 µm) and basidia (39–52 × 8–11 µm) than *R. reticulofolia* sp. nov. (Sarnari 1993).

Order Russulales Kreisel ex P.M.Kirk, P.F.Cannon & J.C.David
Family Russulaceae Lotsy
Genus *Russula* Pers.
Subgenus *Brevipedum* Buyck & V.Hofst.

Russula callainomarginis J.F.Liang & J.Song

Figs 9–10

Material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 10 Jun. 2018; *Y. Song K18061013*; GenBank nos: MN275693 (ITS), MN839582 (nLSU), MN839632 (mtSSU), MT085535 (*rpb1*), MT085659 (*rpb2*), MT085602 (*tef1*); GDGM79715 • same data as for preceding; 22 Apr. 2019; *Y. Song K19042220*; GenBank no: MN839555 (ITS); GDGM79716.

Description

Basidiomata medium to large sized. *Pileus* 6–10 cm in diam., hemispherical to convex when young, turning applanate with depressed center to infundibuliform; surface glabrous, dry, viscid when wet, white to cream (#FFFAFA, #FFFFF0) with reddish brown (#F5DEB3, #F2E0B7) tint; margin slightly undulate and upward. *Lamellae* adnate to decurrent, unequal with multidymous lamellulae, often forked near stipe and pileus margin, interveined, white at first, turning cream with brown tint (#FEEABA, #FAEDB3) with maturity; edge entire, concolorous. *Stipe* central, subcylindrical, solid at first, turning hollow with age, 4–6 cm long, white, stained with reddish brown (#F9E197, #F2D782) when old, longitudinally rugulose. *Context* white. *Odor* distinct. *Spore print* whitish.

Basidiospores subglobose to ellipsoid, rarely globose, (40/2/2) (5.4–)5.7–6.3–7.1(–7.4) × (4.9–)5.2–5.6–6.1(–6.5) µm, [Q = (1.03–)1.04–1.16–1.24(–1.36)], hyaline in 5% KOH; ornamentation amyloid, composed of verrucous to cylindrical warts less than 1 µm in height, some fused into short crests, mostly connected by fine lines forming partial reticulum; suprahilar spot amyloid. *Basidia* (25–)27–29.5–32(–34) × 8–9.5–11(–12) µm, clavate, 2- or 4-spored, thin-walled; sterigmata 4–10.5 × 0.8–

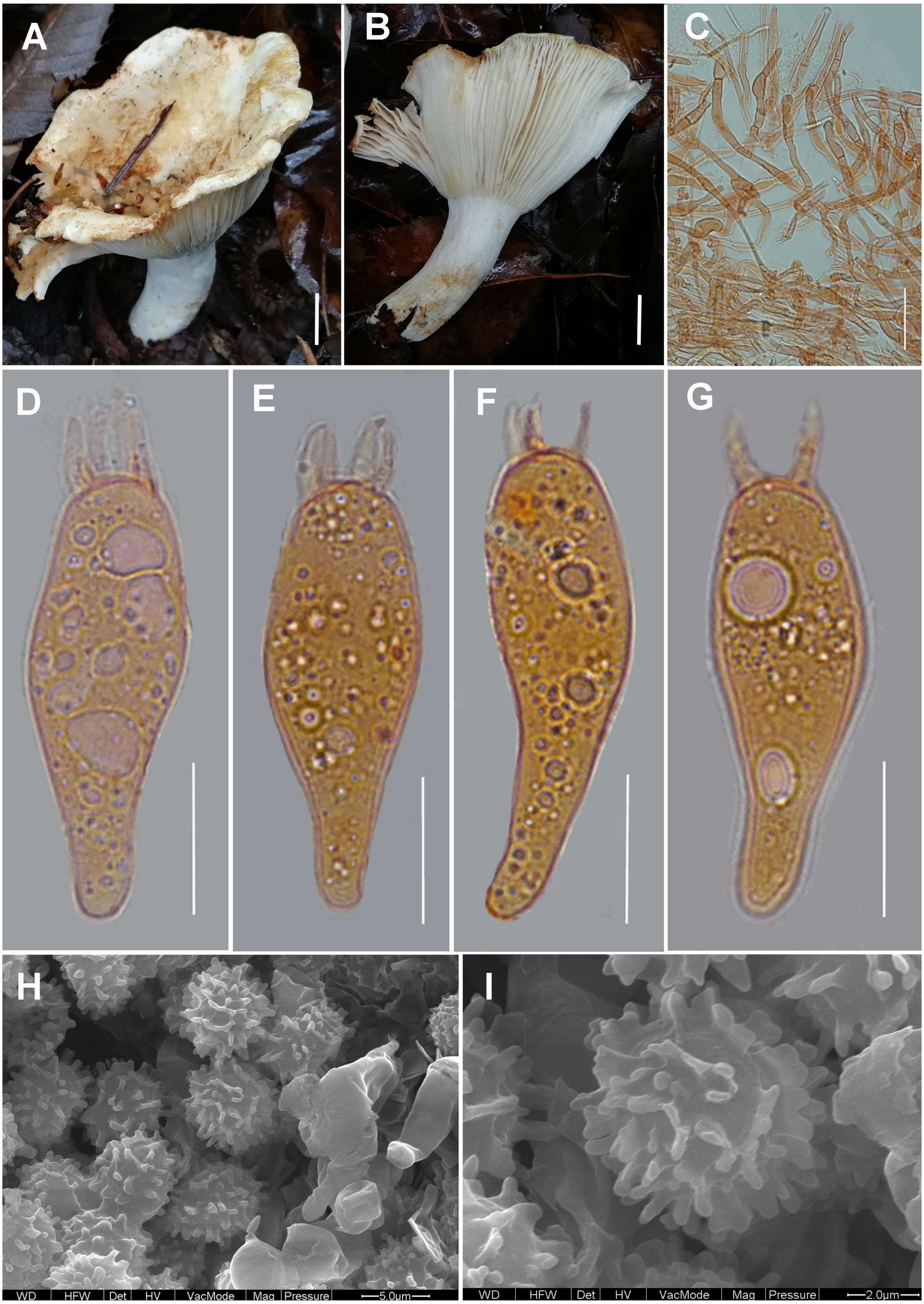

Fig. 9. *Russula callainomarginis* J.F.Liang & J.Song (GDGM79715). **A**–**B**. Fruiting bodies. **C**. Terminal elements in pileipellis. **D**–**G**. Basidia. **H**–**I**. Basidiospores under scanning electron microscope. Scale bars: A–B = 1 cm; C = 25 μm; D–G = 10 μm; H–I = 1 μm.

1.6 µm. *Pleurocystidia* (23–)27–43–81(–101) × 5–7.5–10.5 µm, mostly typical fusiform, with obtuse, mucronate or papillate apices, thin-walled, with refractive contents mostly distributed in middle to upper parts, some subcylindrical, arising from deep in subhymenium, weakly positive in SV. *Cheilocystidia* (23.5–)26–33–39(–41.5) × (5.5–)6.5–7.5–10 µm, fusiform, with obtuse or mucronate apices, thin-walled, with refractive contents mostly at medium parts. *Subhymenium* pseudoparenchymatous. *Lamellar trama* composed of numerous sphaerocytes surrounded by connective hyphae, sphaerocytes measuring 10–28 × 7.5–23 µm. *Pileipellis* composed of ascending to erect hyphae, 100–140 µm thick;

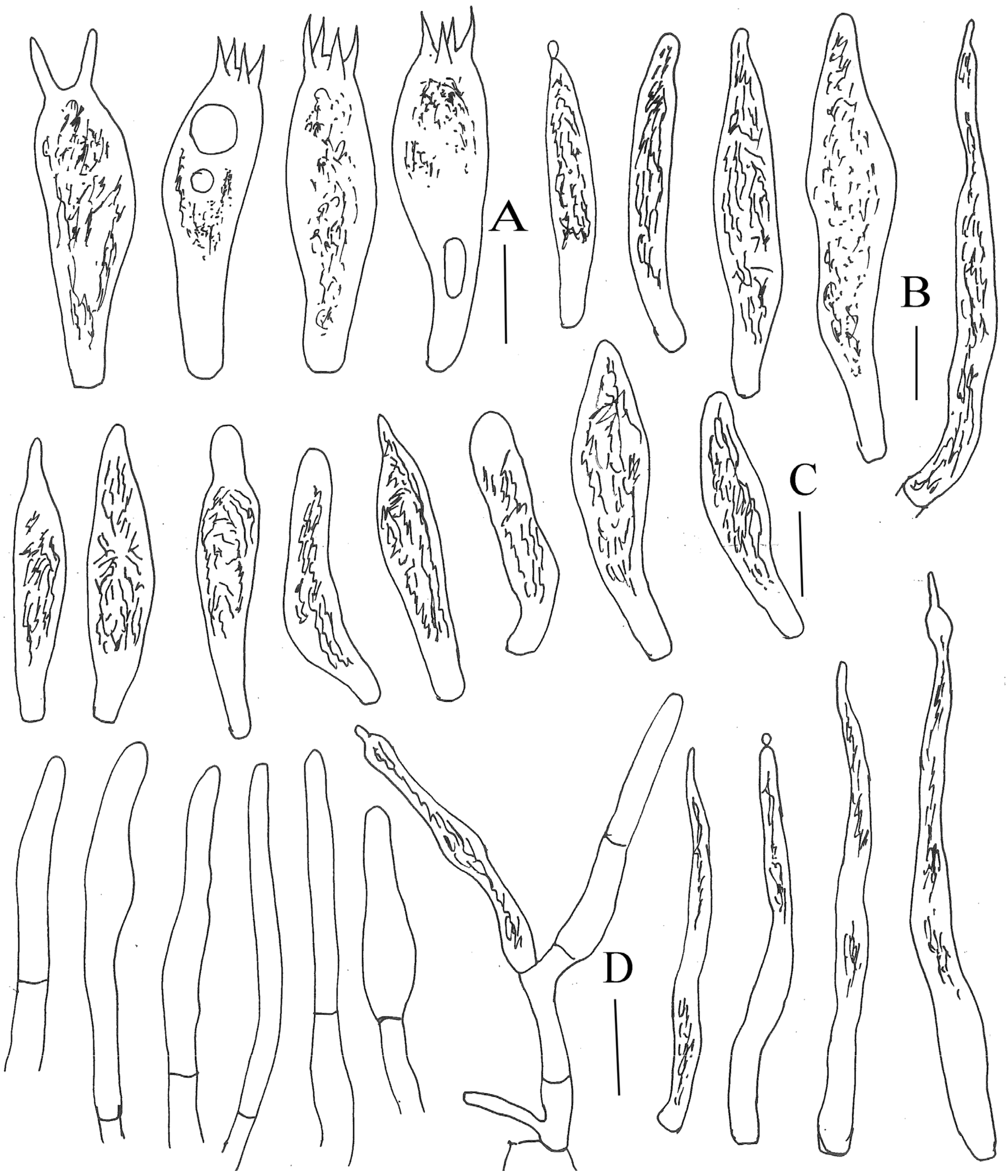

Fig. 10. *Russula callainomarginis* J.F.Liang & J.Song (GDGM79715). **A**. Basidia. **B**. Pleurocystidia. **C**. Cheilocystidia. **D**. Terminal elements in pileipellis. Scale bars = 10 µm.

hyphae cylindrical, septate, hyaline, thin-walled, 1.5–5 µm wide; terminal cells (8–)10.5–19–35 × 2.5–3.5–5.5 µm, cylindrical, rarely lageniform, with obtuse apices, hyaline, some incrusted. *Pileocystidia* (11–)26–55.5–80(–84) × 2–4–6(–7) µm, cylindrical to fusiform, with obtuse, mucronate to papillate apices, with granular refractive contents, unchanging in SV. *Stipitipellis* composed of cylindrical, septate hyphae measuring 1.5–4 µm wide; terminal cells cylindrical with obtuse apices, hyaline. *Caulocystidia* (16.5–)30–54–68(–74) × 1.5–4–6.5 µm, cylindrical, obtuse or papillate, with refractive contents. *Clamp connections* absent in all tissues.

Comments

Russula callainomarginis was recently described from China (Song *et al.* 2022). Collections of this species from DHSBR are mostly in accordance with the original morphological descriptions, except that DHSBR specimens have obviously smaller basidia [(25–)27–29.5–32(–34) × 8–9.5–11(–12) µm] and pileocystidia unchanging in SV (turning dark grey to blackish when first described).

Russula japonica Hongo

Figs 11–13

Material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 1 Oct. 2017; *F. Yuan & Y. Song K17100106*; GenBank nos: MN275688 (ITS), MK881959 (nLSU), MK882086 (mtSSU), MT085495 (*rpb1*), MK880686 (*rpb2*), MT085596 (*tef1*); GDGM79697 • same data as for preceding; *Y. Song K17100104*; GDGM79709 • same data as for preceding; 26 May 2015; *Y. Song K15052631*; GDGM79700 • same data as for preceding; 13 Sep. 2015; *J.B. Zhang & Y. Song K15091301*; GenBank no: MN275680 (ITS); GDGM79702 • same data as for preceding; 14 Sep. 2015; *J.B. Zhang & Y. Song K15091419*; GDGM79703 • same data as for preceding; 31 May 2016; *Y. Song K16053108*; GDGM79704 • same data as for preceding; 8 Aug. 2016; *Y. Song K16080813*; GDGM79705 • same data as for preceding; *Y. Song K16080825*; GDGM79706 • same data as for preceding; 12 Sep. 2016; *Y. Song K16091228*; GenBank no: MN275685 (ITS); GDGM79707 • same data as for preceding; 5 May 2018; *Y. Song K18050528*; GenBank nos: MN839579 (nLSU), MN839629 (mtSSU), MT085497 (*rpb1*), MT085656 (*rpb2*), MT085627 (*tef1*); GDGM79710 • On the ground in coniferous forest; 2 Sep. 2014; *Y. Song Z14090205*; GDGM79698 • On the ground in broad-leaf and coniferous mixed forest; 8 May 2015; *Y. Song H15050805*; GDGM79699 • same data as for preceding; 6 Jun. 2015; *Y. Song H15060608*; GDGM79701 • same data as for preceding; 12 Jul. 2017; *Y. Song H17071211*; GenBank no: MN275686 (ITS); GDGM79708.

Description

Basidiomata medium sized to large. *Pileus* 7–14 cm in diam., hemispherical to convex when young, turning applanate with depressed center to infundibuliform; surface glabrous, dry, jet white to chalk white (#FFFFFF, #FAF9F9), often tinged or stained with reddish brown (#FD863D; #F7BE81) when mature; margin undulate and slightly inrolled, rarely cracked. *Lamellae* adnate to slightly decurrent, crowded, unequal with multidymous lamellulae, sometimes forked near stipe, interveined, white at first, turning brownish, reddish brown or yellowish brown (#FDBC78; #F5DA81) with maturity, often rust brown (#FAAC58) stained when old; lamellulae frequent. *Stipe* 2.5–7 × 2.5–4 cm, central, subcylindrical, often slightly tapering towards base, solid at first, turning spongy with age, white, longitudinally rugulose, turning reddish brown (#FDB262) when bruised. *Context* white, becoming reddish brown (#FDB262) when bruised and brownish in 5% $FeSO_4$. *Odor* distinct. *Spore print* cream (#FCF3CF).

Fig. 11. Fruiting bodies of *Russula japonica* Hongo. **A**–**B**. GDGM79699. **C**–**D**. GDGM79710. **E**. GDGM79706. **F**. GDGM79704. Scale bars = 1 cm.

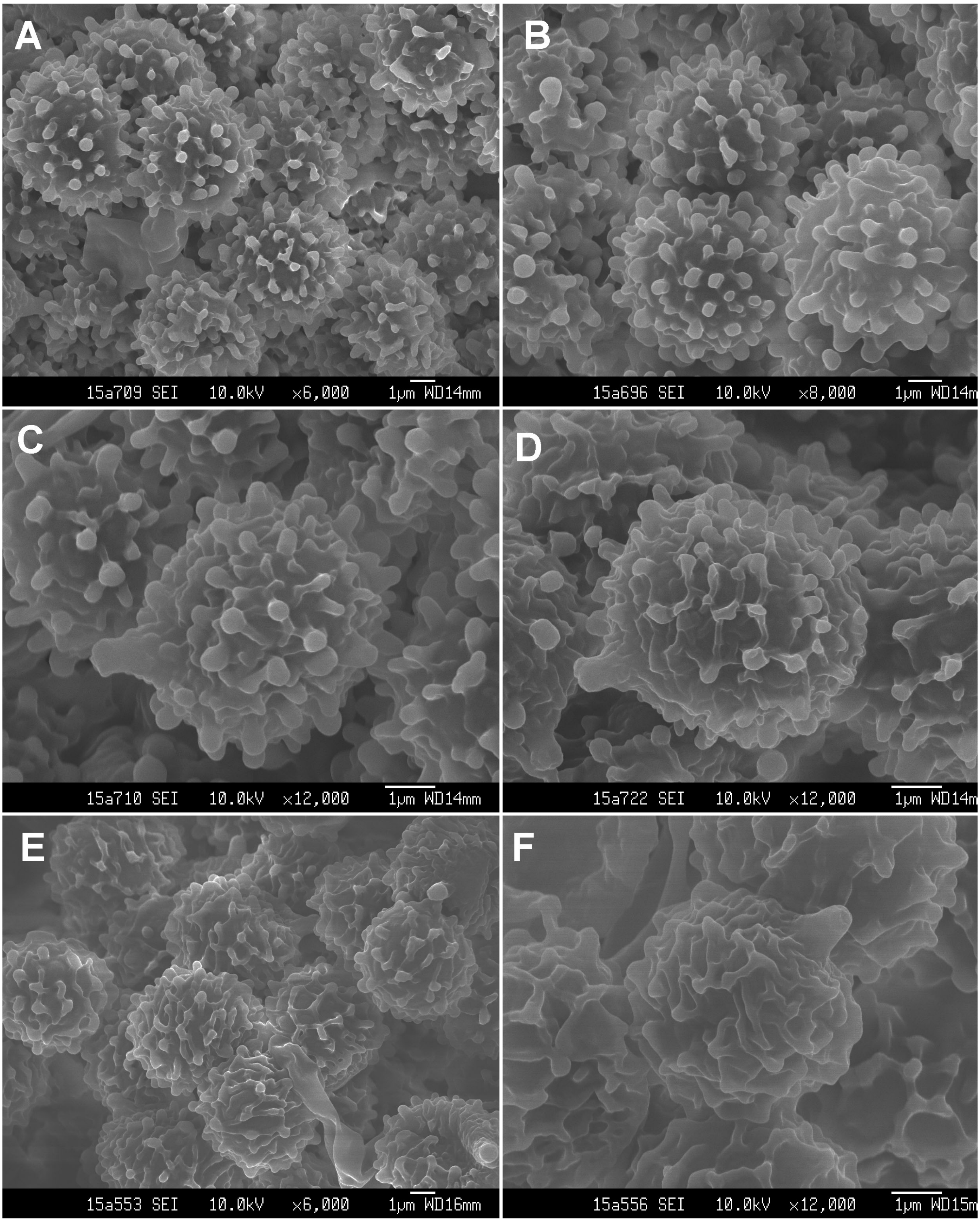

Fig. 12. Basidiospores under scanning electron microscope of *Russula japonica* Hongo. **A**–**C**. GDGM79699. **D**. GDGM79704. **E**–**F**. GDGM79706. Scale bars = 1 µm.

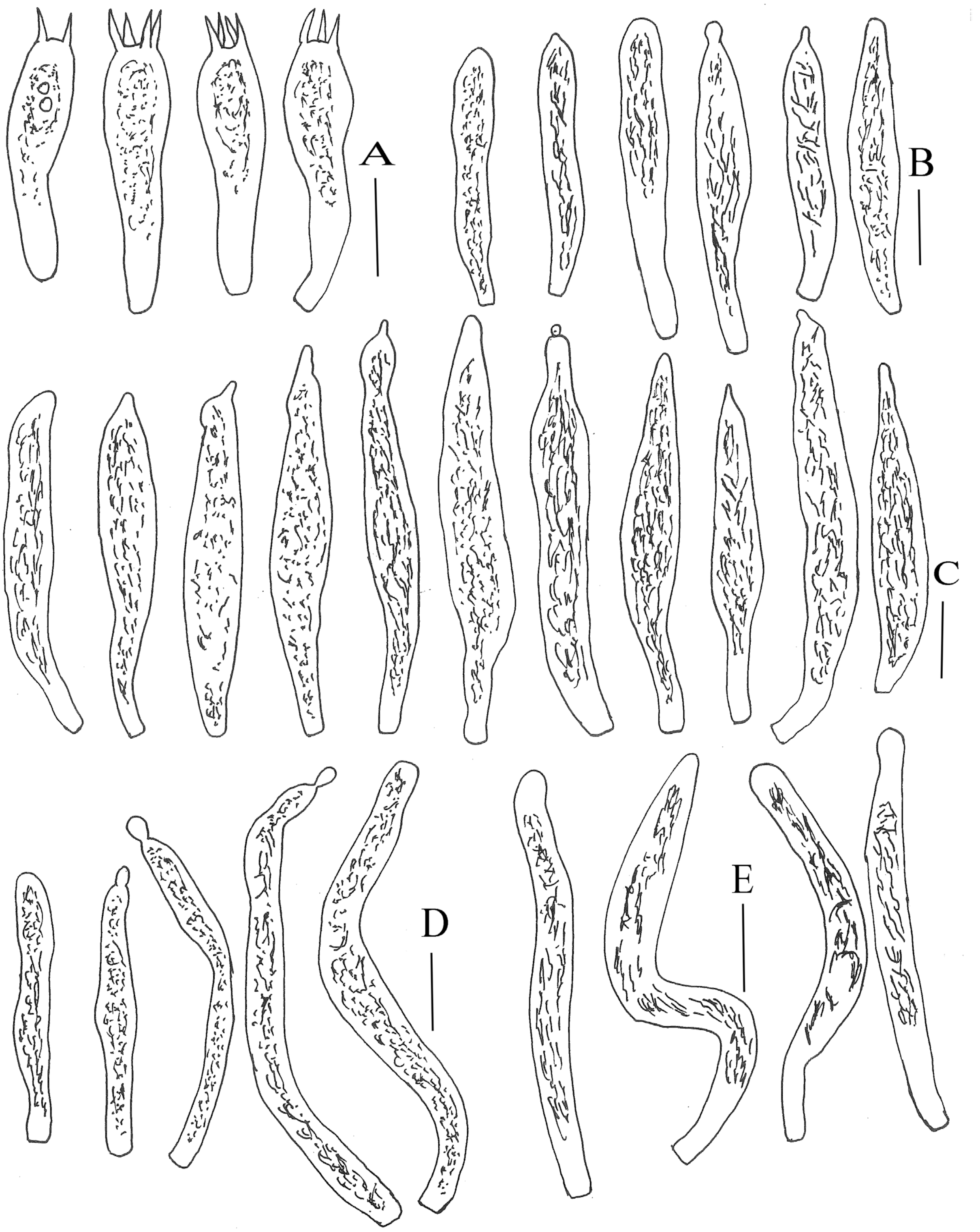

Fig. 13. *Russula japonica* Hongo (GDGM79697). **A**. Basidia. **B**. Cheilocystidia. **C**. Pleurocystidia. **D**. Pileocystidia. **E**. Caulocystidia. Scale bars = 10 µm.

Basidiospores subglobose to broad ellipsoid, (100/5/5) (5.1–)5.8–6.2–6.6(–6.9) × (4.9–)5.3–5.7–6.1(–6.5) µm, [Q = (1.02–)1.04–1.12–1.20(–1.23)], hyaline in 5% KOH; ornamentation amyloid, composed of verrucous to cylindrical warts less than 1 µm in height, some fused into crest, mostly connected by fine lines forming partial reticulum; suprahilar spot inamyloid. *Basidia* 23–30–33(–38) × 5–7–9(–12) µm, clavate, 2- or 4-spored, thin-walled; sterigmata 3.5–5.5 × 1–1.5 µm. *Pleurocystidia* (34–)38–52–64(–72) × 4.5–8–10 µm, subcylindrical to fusiform, with mucronate or papillate apices, thin-walled, with refractive contents, negative in SV. *Cheilocystidia* similar to pleurocystidia in shape, but smaller, 35.5–40–45.5 × 5.5–7.0–8 µm, thin-walled, with refractive contents, negative in SV. *Subhymenium* pseudoparenchymatous. *Lamellar trama* composed of numerous sphaerocytes surrounded by connective hyphae, sphaerocytes measuring 6.5–21 × 5–17 µm. *Pileipellis* divided into two layers, 80–130 µm thick suprapellis composed of ascending to erect hyphae, and 160–240 µm thick subpellis composed of reptant hyphae; hyphae cylindrical, septate, hyaline, thin-walled, 1.5–5 µm wide; terminal cells (8.5–)19–26–35(–44) × 1.5–2–3.5 µm, cylindrical, with obtuse apices. *Pileocystidia* (26.5–)32–58–103(–120) × 3–4.5–6.5(–8) µm, frequent, distributed both in suprapellis and subpellis, cylindrical, with obtuse or papillate apices, with granular refractive contents, unchanging in SV. *Stipitipellis* 100–190 µm thick, composed of cylindrical, septate hyphae measuring 1.5–3.5 µm wide; terminal cells 11.5–17–24.5×1.3–2–3 µm, cylindrical with obtuse apices, hyaline, thin-walled. *Caulocystidia* 33–86 × 4–8 µm, cylindrical, obtuse or papillate, with refractive contents. *Clamp connections* absent in all tissues.

Comments

Russula japonica has been collected 14 times during our survey and it is a frequent species in DHSBR. Our identification is based on detailed macromorphological comparison and a deposited LSU sequence for a Japanese specimen (AB154697). It is characterized in the field by the nearly smooth pileus and crowded polydymous gills and the appearance of brownish tinges with age. The same characters are also found in *R. polyphylla* Peck of subg. *Compactae* with which it can easily be confused in the field, but the latter has different microscopic features (see Buyck *et al.* 2003).

Russula japonica was described (Hongo 1954) from Japan as a mild endemic species close to *R. delica* Fr., which is the type species of subsect. *Lactarioideae* Maire, now placed in subg. *Brevipedum*. Both in the field and under the microscope, it is a morphological twin of *R. vesicatoria* Murrill, notwithstanding several errors in Hongo's original description that suggest the opposite. Spores of Japanese specimens of *R. japonica* have ornaments that are minutely interconnected, just as in *R. vesicatoria* (see Buyck & Adamčík 2013), and do not have isolated warts as mentioned in the original description (Buyck unpubl. data) and both possess nearly identical dermatocystidia and hymenial cystidia.

Hongo's species was originally described as mild, but was later given as having slightly bitter or slowly acrid components, but was never reported to be sometimes burningly acrid as in *R. vesicatoria*. Also *R. vesicatoria* has been described as being very variable in taste, mostly exhibiting a acridity of variable intensity that develops slowly – at least in younger specimens – after an initial mild to bitter sensation. Kibby & Fatto (1990) describe the acridity of *R. vesicatoria* as "burningly hot, blistering the lips and long lasting", thus resuming the elaborate paragraph on taste from Burlingham's original description (1944). Bills (1986), on the other hand, gives the taste as bitter to disagreeable or mild for older specimens, with the acridity limited to younger specimens. Buyck's collections from New Jersey were completely mild.

Russula vesicatoria is one of the more common and sometimes very abundant associates of pine on deep sandy soil in the eastern United States. It was originally only known from Florida (Burlingham 1944). In later years, Bills (1986) reexamined this species in detail and extended its distribution with records from Mississippi, New Jersey, South Carolina and Virginia, describing the closely related *R. angustispora* Bills with very elongate spores and darker spore print. Shaffer (1964) designed a lectotype for *R. vesicatoria* and described *R. cascadensis* Shaffer. The latter species is equally assumed to be very closely related, differing principally by the absence of a clear odor and in being a west-coast species in America. Shaffer (1964) also introduced the new *R. inopina* Shaffer, differing conspicuously, according to Shaffer, by the absence of a strongly acrid-bitter taste and a different smell.

All the above species are conifer associates, principally associated with *Pinus*, and sometimes highly host-specific as in the case of *R. angustispora*, apparently a strictly associate of *Pinus virginiana* Mill. in its entire range of distribution (Bills 1986). *Russula vesicatoria* associates with various 2–3 needle pines (*Pinus taeda* L., *P. virginiana*, *P. palustris* Mill., etc…) always growing in pure sand or sandy soil (Bills 1986). However, whereas *R. japonica* was originally described as being associated with *Pinus densiflora* Siebold & Zucc. (Hongo 1954), it has since mostly been found under *Castanopsis* sp. and *Quercus* sp. in Japan. Interestingly, a morphologically identical collection to *R. vesicatoria* has more recently also been collected under *Quercus oleoideis* in the tropical lowlands of Costa Rica (Buyck unpubl. data), which seems to suggest that both species are not strict conifer associates.

Both *R. callainomarginis* and *R. leucobrunnea* nom. nov. (illustrations followed) can be distinguished from *R. japonica* because of their different spore ornamentation with much less differentiated warts.

Russula leucobrunnea Y.Song nom. nov.
MycoBank: MB847839
Figs 14–15

Basionym

Russula leucocarpa G.J.Li & C.Y.Deng, *Mycosystema* 39 (4): 5 (Li *et al.* 2020).

Material examined

CHINA • Guangdong Province, Zhaoqing City, Dinghushan Biosphere Reserve, on the ground in evergreen broad-leaf forest mainly with Fagaceae trees; 12 Sep. 2016; *Y. Song K16091221*; GenBank nos: MN275671 (ITS), MK881934 (nLSU), MK882062 (mtSSU), MT364342 (rpb1), MK880661 (rpb2), MT085575 (tef1); GDGM79692 • same data as for preceding; 17 Sep. 2018; *Y. Song K18091702*; GenBank no: MN275672 (ITS); GDGM79693.

Discussion

In combination of detailed morphological studies and phylogenetic analyses based on ITS and 5-locus (LSU, mtSSU, *rpb1*, *rpb2* and *tef1*) sequences, three species collected from the Dinghushan Biosphere Reserve (DHSBR) in southern China, namely *Russula cylindrica* sp. nov. and *R. lacteocarpa* sp. nov. in subg. *Archaeae*, and *R. reticulofolia* sp. nov. in subg. *Compactae*, are proved to be novel species (Figs 3–8). Proposal of the three novel species further indicates the high species richness of *Russula* in DHSBR, from where 22 new taxa of Russulaceae have been described since 2014 (Song *et al.* 2021, 2022). Especially, the descriptions of the two new species of subg. *Archaeae* fully confirms the distribution of the group in China.

There are three species of subg. *Brevipedum* identified from DHSBR, namely *R. leucobrunnea* nom. nov., *R. callainomarginis* and *R. japonica*. *Russula leucocarpa* G.J.Li & C.Y.Deng was first described from southwestern China in 2020, based on morphological studies and ITS sequence (Li *et al.* 2020). But the nomenclature of the species (*Russula leucocarpa* G.J.Li & C.Y.Deng) is illegitimate because *R. leucocarpa* (T.Lebel) T.Lebel has already been published in 2017. *Russula leucobrunnea* nom. nov. was proposed to replace *R. leucocarpa* G.J.Li & C.Y.Deng, with the epithet referring to the white pileus staining brownish when mature (Figs 7–8). Compared with original descriptions based on holotype, specimens from DHSBR have obvious reddish brown stains on pileus, much bigger spores

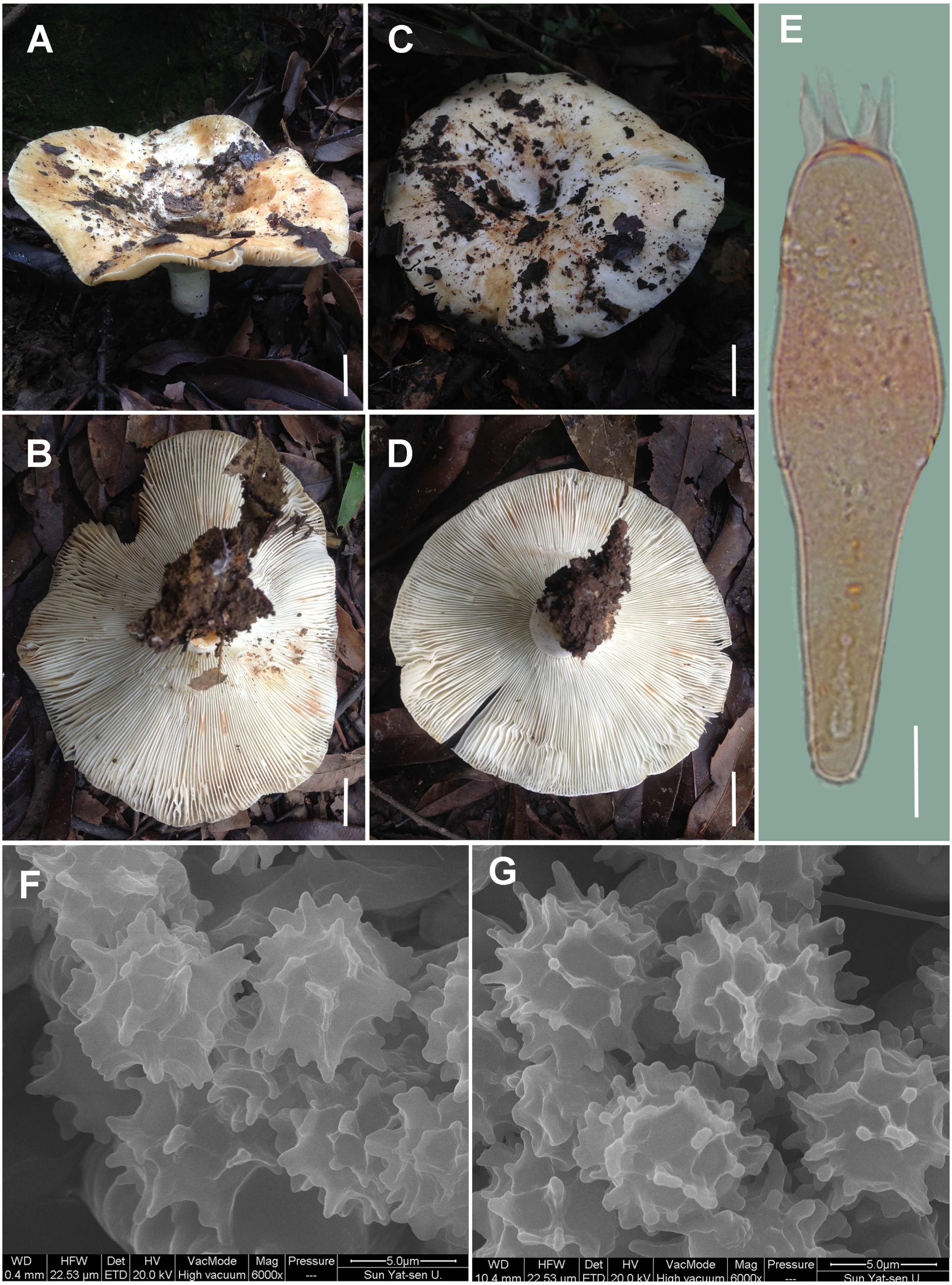

Fig. 14. *Russula leucobrunnea* Y.Song nom. nov., GDGM79693 (A–B), GDGM79692 (C–G). **A**–**D**. Fruiting bodies. **E**. Basidia. **F**–**G**. Basidiospores under scanning electron microscope. Scale bars: A–D = 1 cm; E = 10 µm; F–G = 5 µm.

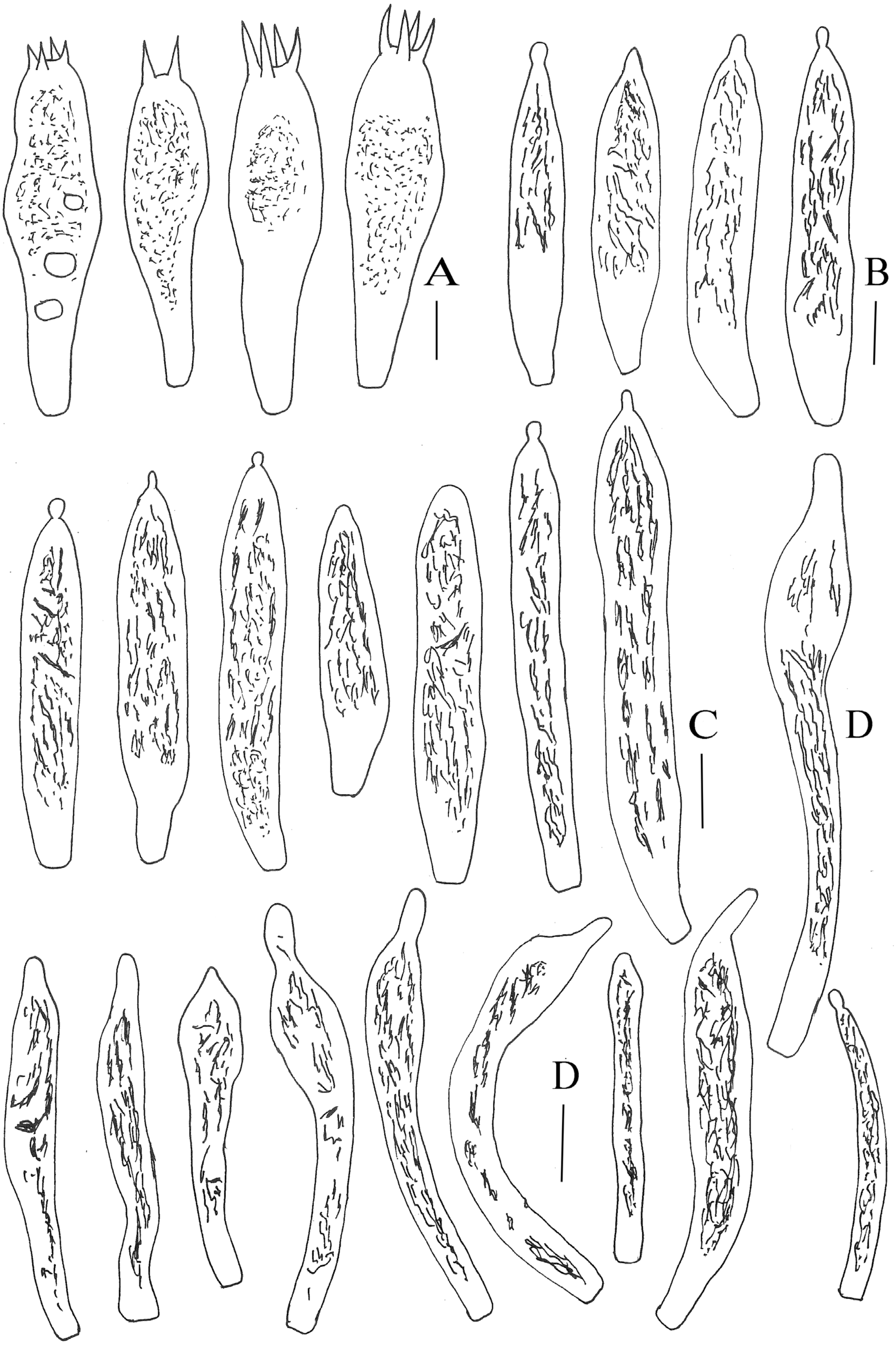

Fig. 15. *Russula leucobrunnea* Y.Song nom. nov. (GDGM79692). **A**. Basidia. **B**. Cheilocystidia. **C**. Pleurocystidia. **D**. Caulocystidia. Scale bars = 10 µm.

[(7.7–)8.3–9–10.1(–10.6) × (6.3–)7.4–8.4–9.2(–9.9) µm] with higher ornamentation (up to 2 µm), much bigger basidia (46–70 × 14.5–19.5 µm) and abundant rather than absent caulocystidia.

A total of 14 specimens of *R. japonica* (Figs 11–13) have been collected during our survey. It can therefore be considered to be a frequent species in DHSBR. This allowed us to better appreciate several of its features. For instance, spores of *R. japonica* from different mature fruiting bodies have been studied under scanning electron microscope and we found that spore ornamentation can be quite variable: warts can be either interconnected by thin lines or forming crests to constitute a partial or nearly complete reticulum. In addition, we could establish that both pileo- and caulocystidia are abundantly present (mentioned as absent in the original description), but that all of the cystidioid elements (including hymenial cystidia) react negatively to sulfovanillin.

During the revision process of our paper, Chen *et al.* (2023) published several new species in subgenus *Brevipedum*, but these authors unfortunately added a lot of confusion by publishing incongruent sequence data for ITS and LSU for their new species. Indeed, whereas ITS sequences for their new *R. brevispora* Y.L.Chen & J.F.Liang, are more than 99.8% similar to those of our specimens identified here as *R. japonica*, their LSU sequences are merely 98.7% similar to both the original Japanese and our own sequences for *R. japonica*. It is not clear at this moment whether *R. brevispora* is a later synonym of *R. japonica*, or not.

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