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RESEARCH ARTICLE

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Four new species of *Russula* from the Xizang Autonomous Region and other provinces of China

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ABSTRACT

Russula is the largest genus in the Russulales and is widespread throughout the world. Almost all *Russula* species are known to be ectomycorrhizal with high ecological and edible values, and some are lethal poisonous. In this study, four new species belonging to the subgenus *Russula* crown clade are identified based on morphological and phylogenetic evidence from the Xizang Autonomous Region and other provinces of China. Morphologically, *Russula paragraveolens* (sect. *Polychromae*, subsect. *Xerampelinae*) is mainly characterised by a cherry red to blood red pileus centre, a reddish orange pileus margin; *R. pseudograveolens* (sect. *Polychromae*, subsect. *Xerampelinae*) is characterised by a violet brown to brownish red pileus centre, a pale red to pastel red pileus margin and short basidia; *R. shigatseensis* (sect. *Flavisiccantes*, subsect. *Lepidinae*) is characterised by a brownish orange to madder red pileus centre, pinkish red pileus margin, and having lateral branches or branches of hyphal terminations in pileipellis; *R. yadongensis* (sect. *Tenellae*, subsect. *Laricinae*) is characterised by a dark purplish red pileus centre with brownish purple tints and having isolated to clustered spines of spore ornamentations. Their distinct taxonomic status is confirmed by the positions of the four new species in both the ITS and 4-locus (nucLSU, mtSSU, *rpb2*, *tef1*) phylogenetic trees.

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1. Introduction

Russula Pers. belongs to the Basidiomycota, Agaricomycetes, Russulales, Russulaceae, and is the type genus of Russulaceae (Kirk et al. 2008; He et al. 2019). *Russula* species are widespread throughout the world, from the tundra of Greenland in the north to the broad-leaved forest of New Zealand in the south (Looney et al. 2015). They form ectomycorrhizae with gymnosperms, such as *Abies*, *Larix,* *Picea*, *Pinus*, and *Pseudotsuga*, and angiosperms, such as Fabaceae, Fagales, Malpighiales, and Myrtaceae. They increase plant resistance, promote root growth and nutrient uptake, and closely correspond to the plant communities (Looney et al. 2018; Sarwar et al. 2020). Many species of *Russula* are important wild edible mushrooms, rich in nutritional elements, with anti-tumour, antioxidant, cholesterol-lowering, blood lipid-lowering, and blood sugar-lowering effects, such as *Russula cyanoxantha* (Schaeff.) Fr. and *R. griseocarnosa* X.H. Wang, Zhu L. Yang & Knudsen (Chen and Zhang 2010; Kaewnarin et al. 2016; Khatua et al. 2021; Liu et al. 2023). However, there are also toxic species such as *R. emetica* (Schaeff.) Pers. and *R. senecis* S. Imai, which often cause gastroenteritis-type poisoning when accidentally consumed. *Russula subnigricans* Hongo is a highly toxic species that has caused many deaths in food poisoning incidents (Chen et al. 2014; Cho and Han 2016; Matsuura et al. 2016).

In recent years, due to the rapid development of molecular biology techniques, the taxonomic research of *Russula* has been promoted. Phylogenetic relationships of infrageneric taxa have been more objectively elucidated. The latest

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classification system shows that the genus comprises eight subgenera, *Archaeae* Buyck & V. Hofst., *Brevipedum* Buyck & V. Hofst., *Compactae* (Fr.) Bon, *Crassotunicatae* Buyck & V. Hofst., *Glutinosae* Buyck & X.H. Wang, *Heterophyllidiae* Romagn., *Malodorae* Buyck & V. Hofst., *Russula* Buyck & V. Hofst (Looney et al. 2015; Buyck et al. 2018, 2020; Adamčík et al. 2019). Among them, subg. *Russula* consists of two major clades: The *Russula* core clade and the *Russula* crown clade. Since 2006, at least 68 new species have been published for the crown clade of subg. *Russula*, 48 of which are from Asia, and 23 new species have been described for this clade from China, demonstrating the extraordinary species richness of this clade of the *Russula* crown clade (Li et al. 2012, 2013a, 2013b, 2015, 2016; Jiang et al. 2018; Li et al. 2018a, 2018b, 2021; Caboň et al. 2019; Song et al. 2021; Li 2022; Zhou et al. 2022). Members of *Russula* crown clade mostly have unchanging, yellowing, browning, reddening, greying, or blackening of context when bruised, sometimes with distinct disagreeable to agreeable smell, mild to strongly acrid tasted context, white to yellow spore print (Buyck et al. 2018). Four new species of this clade were also identified in our macrofungal diversity survey, and these four new species were elucidated by morphological and phylogenetic analyses in this study.

2. Materials and methods

2.1. Morphological study

During collection, the macro-morphological characteristics of the specimens and the habitat were photographed with a camera (Canon EOS 80D), and fresh specimens were wrapped in tin foil in order to avoid mixing or crushing. After recording the macro-morphological characteristics in the field, the fresh specimens were dehydrated in a drying oven at 55 °C for 12 h in the laboratory. The dried specimens were deposited in the Mycological Herbarium, Institute of Microbiology, Chinese Academy of Sciences (HMAS). The description followed the criteria for *Russula* morphology observation (Adamčík et al. 2019). The colour designation refers to HTML Color Codes (https://htmlcolorcodes.com).

Specimens were rehydrated with 5% KOH solution. Observation of spores was made in Melzer's reagent. The morphology of hymenial cystidia and pileocystidia were stained with 1% aqueous Congo red solution (Heilmann-Clausen et al. 2000). Tissues of the pileus were also examined in Cresyl Blue solution to verify the presence of a metachromatic reaction (Buyck 1989). Carbolfuchsin was used to observe incrustations on primordial hyphae (Singer 1968). Sulfovanillin was used to observe the colouring of cystidia contents (Caboň et al. 2017).

2.2. DNA extraction, PCR and sequencing

DNA was extracted from 5 to 20 mg tissue of dried specimen with the Broad-spectrum Plant Rapid Genomic DNA Kit (Biomed, Beijing) following the manufacturer's instructions.

In this study, five loci were amplified and sequenced: ITS was amplified using primer pair ITS1-F/ITS4 (White et al. 1990); ribosomal nuclear large subunit (nucLSU) was amplified by LROR/LR5 (Moncalvo et al. 2000); ribosomal mitochondrial small subunit (mtSSU) was amplified by MS1/MS2 (White et al. 1990); second largest subunit of the RNA polymerase II (*rpb2*) was amplified by RPB2-6F/RPB2–7.1R (Matheny 2005); translation elongation factor 1-alpha (*tef1*) was amplified by EF1-983F/EF1-1567R (Rehner and Buckley 2005). The amplified PCR products were detected by electrophoresis and sent to BGI Genomics Co., Ltd. (Beijing) for purification and sequencing.

2.3. Molecular phylogenetic study

Newly generated and reference sequences obtained from GenBank are listed in Tables 1 and 2. The sequences were aligned in AliView v1.19 and manually adjusted to eliminate poorly aligned or ambiguous regions. The six partitions were assembled in PhyloSuite v1.2.2 (Zhang et al. 2020), in the order of six loci (nucLSU, mtSSU, *rpb2* exons, *rpb2* introns, *tef1* exons, *tef1* introns). The final alignments have been deposited in TreeBASE (study no. 30337, 30338).

The ITS-based phylogenetic analysis consisted of 152 sequences representing 109 species, with *R. emetica* as the outgroup. A total of 80 concatenated sequences representing 66 species were used for

Table 1. Sequences used in phylogenetic analysis based on ITS.

Taxon	Voucher specimen	Location	ITS accession number
Gymnomyces abietis	-	USA	AY239347
Gymnomyces abietis	-	USA	AY239348
Gymnomyces californicus	-	USA	AY239312
Gymnomyces californicus	-	USA	AY239308
Gymnomyces foetens	-	USA	AY239316
Gymnomyces monticola	-	USA	AY239313
Gymnomyces monticola	-	USA	AY239314
Gymnomyces setigerus	-	USA	AY239317
Gymnomyces subalpinus	-	USA	AY239309
Gymnomyces subalpinus	-	USA	AY239311
Macowanites vinaceodorus	-	Spain	AJ438034
Macowanites vinaceodorus	46374 (AH)	Spain	MK105695
Russula abbottabadensis	FH00304589 (holotype)	Pakistan	MG386704
Russula abietiphila	HCCN14799 (type)	South Korea	MN130060
Russula abietiphila	HCCN18498	South Korea	MN130061
Russula adwanitekae	AG 16-1430 (type)	India	MN263242
Russula adwanitekae	AG 16-1435	India	MN263243
Russula amethystina	LAH35058 (holotype)	Pakistan	KT953613
Russula amoenipes	309IS77	USA	AY061656
Russula aurantioflammans	r3245	Slovakia	KU928167
Russula brunneovinacea	RITF 2242 (holotype)	China	KY114148
Russula brunneoviolacea	MC01-507	Denmark	AM113956
Russula brunneoviolacea	PRM 922,557	Canada	MG687327
Russula buyckii	CUHAM277 (holotype)	India	KT962833
Russula cessans	CR19	Canada	KP406550
Russula changbaiensis	HMAS262369 (holotype)	China	KC412162
Russula claroflava	224IS76	USA	AY061665
Russula claroflava	FH12212	USA	KT933997
Russula clavatohyphata	CAL1756 (holotype)	India	MG934209
Russula clavipes	SAV:F-1327	Slovakia	KU205292
Russula coronaspora	GDGM79711 (holotype)	China	MN275689
Russula coronaspora	GDGM79712	China	MN275690
Russula cremeirosea	BPL289	USA	KT933983
Russula cremeoavellanea	SAV F-2125	Slovakia	KY582695
Russula cuprea	FH12250	USA	KT934010
Russula curtipes	1123IS77	USA	AY061668
Russula curtipes	FH12206	USA	KT933995
Russula decolorans	-	Germany	AF418637
Russula decolorans	FH12196	USA	KT933992
Russula dhakuriana	CUHAM343	India	MK414576
Russula emeticicolor	FH12253	USA	KT934011
Russula faginea	SAV F-1337	France	KU205289
Russula faginea	SAV F-997	Slovakia	KU205286
Russula favrei	SAV F-1333	Finland	KU205311
Russula favrei	UPS UE06.09.2003-9	Sweden	KU205272
Russula firmula	AT2004142	Sweden	DQ422017
Russula flavobrunnescens	TLXM (AK5024) (type)	Mexico	MN130082
Russula fontqueri	FH12223	USA	KT934003
Russula gnathangensis	CAL1733 (holotype)	India	MK253441
Russula graveolens	SAV F-1342	Slovakia	KU205302
Russula graveolens	SAV:F-1338	Belgium	KU205306
Russula griseocarnosa	KUN F51839 (holotype)	China	EF627042
Russula griseocarnosa	-	China	EF627043
Russula guangxiensis	HMAS267867 (holotype)	China	KT286852
Russula hakkae	HMAS267765 (holotype)	China	KT286848
Russula heilongjiangensis	HMAS255142 (holotype)	China	MG719932
Russula hookeri	CUHAM275 (holotype)	India	KP713777
Russula integra	FH12172	USA	KT933984
Russula jilinensis	HMAS194253 (holotype)	China	GU966632
Russula katarinae	BB03.159 (PC) (holotype)	USA	KP966377
Russula katarinae	BB03.159 (holotype)	USA	NR153255
Russula kewzingensis	CAL1636 (holotype)	India	MG674302
Russula khinganensis	HMAS278895 (holotype)	China	MG719928
Russula laeta	SAV F-3949	Slovakia	KY582708
Russula laricina	BB 08.681	Italy	JN944008
Russula laricina	E Watling 25556	Europe	AY061685
Russula lepida	-	Germany	AF418641
Russula madrensis	TLXM (AK3422) (type)	Mexico	MN130093
Russula magica	GENT (FH12-061) (type)	Thailand	MN130096
Russula messapica var. *messapica*	ALV1991	Spain	MK105669
Russula messapica var. *messapicoides*	JL1493	Spain	MK105674

(*Continued*)

Table 1. (Continued).

Taxon	Voucher specimen	Location	ITS accession number
Russula minor	GDGM79686 (holotype)	China	MN275666
Russula minor	GDGM79687	China	MN275665
Russula nauseosa	F30315	Canada	KJ748441
Russula nauseosa	F30317	Canada	KJ748443
Russula nuoljae	HMJAU37320	China	KY357333
Russula nuoljae	SAV:F-3092	Norway	KU205350
Russula nympharum	FH11121505 (holotype)	Spain	KU928157
Russula odorata	BB 07.186	Slovakia	JN944010
Russula olivaceohimalayensis	CAL 1659 (AG 17-1447) (type)	India	MN130097
Russula olivaceohimalayensis	CAL 1664 (AG 15-910)	India	MN130098
Russula paragraveolens	**HMAS281158 (holotype)**	**China**	**OQ871504**
Russula paragraveolens	**HMAS279574**	**China**	**OQ871506**
Russula paragraveolens	**HMAS279575**	**China**	**OQ871505**
Russula pascua	IB:1998/0124	Germany	KU205314
Russula peckii	BPL270	USA	KT933970
Russula pseudograveolens	**HMAS279577**	**China**	**OQ871507**
Russula pseudograveolens	**HMAS279579**	**China**	**OQ871508**
Russula pseudograveolens	**HMAS287385**	**China**	**OQ871497**
Russula pseudograveolens	**HMAS287384 (holotype)**	**China**	**OQ871496**
Russula pseudotsugarum	UBC:F33077	Canada	MF908478
Russula pseudotsugarum	UWBM:WTU-F-038562 (type)	USA	KX813578
Russula puellaris	nl1372 (TUB)	Germany	AF418628
Russula puellula	SAVF 3107	Slovakia	KY582704
Russula purpureoverrucosa	GDGM32902 (holotype)	China	MG214692
Russula purpureozonate	KD 18-003 (type)	India	MN267570
Russula purpureozonate	KD 18-15	India	MN269951
Russula pusilla	BPL267	USA	KT933968
Russula rosea	BB 07.780	France	JN944003
Russula rubra	SAV F-914	Slovakia	KY582723
Russula rugulosa	BPL654	USA	KY848516
Russula rutila	SAV F-1504	Slovakia	KY582687
Russula sancti-pauli	PC (BB 06.494) (type)	Mexico	MN130101
Russula sancti-pauli	PC (BB 06.499)	Mexico	MN130102
Russula sapinea	PA38	Latvia	KR019818
Russula seperina	GENT (Verbeken 2000-135)	Italy	MN130109
Russula seperina	SAV F-3156 (type)	Slovakia	MN130108
Russula shigatseensis	**HMAS287390**	**China**	**OQ871502**
Russula shigatseensis	**HMAS287389 (holotype)**	**China**	**OQ871501**
Russula shigatseensis	**HMAS287391**	**China**	**OQ871503**
Russula sichuanensis	HKAS 53885	China	JX391968
Russula sichuanensis	HKAS53792 (holotype)	China	JX391969
Russula sichuanensis	HMAS 255316	China	MG786566
Russula solaris	BB 07.282	Slovakia	JN944007
Russula sp.	FLAS-F-61146	USA	MH211767
Russula sp.	FLAS-F-61609	USA	MH211995
Russula sp.	HMAS:260700	China	KX441055
Russula sp.	JLF6993	USA	MN263039
Russula sp.	LM1553	UK	KM576511
Russula sp.	S.D. Russell 439	USA	MK397035
Russula sp.	SR48-10MX	Mexico	KT697966
Russula sp.	F30324	Canada	KJ748450
Russula sp.	S.D. Russell 7799	USA	MK532803
Russula subrutilans	RITF1874 (holotype)	China	KJ868237
Russula subsulphurea	F18743	Europe	KF810135
Russula subsulphurea	TENN:F18743	USA	NR153231
Russula subtilis	SAV F-3805 (type)	USA	KY509504
Russula subtilis	TENN-F-067624 (BPL666) (type)	USA	KY509511
Russula tengii	HMAS262728 (holotype)	China	MG386708
Russula tinctipes	SAVF-2494	Slovakia	KY582698
Russula uttarakhandia	CAL 1537 (holotype)	India	KY873997
Russula velenovskyi	526IS77	USA	AY061721
Russula versatilis	PRM 922558	Czech Republic	MG687329
Russula versicolor	BB 07.288	Slovakia	JN944009
Russula veternosa	SAV F-2588	Slovakia	KY582699
Russula vidalii	JC100508BT01, JMV800688 (BCN)	Spain	MK105693
Russula vidalii	JMV20160517-1 (BCN)	Spain	MK105694
Russula vinosa	nl1386	Germany	AF418638
Russula vinosa	SAV F-20024	Slovakia	KY582692
Russula vinosobrunneola	HMAS 278885	China	MG719925
Russula vinosobrunneola	HMAS281138 (holotype)	China	MG719927
Russula violaceoincarnata	O73136	Netherland	GU234047

(*Continued*)

Table 1. (Continued).

Taxon	Voucher specimen	Location	ITS accession number
Russula xerampelina	DG05-28	UK	JQ888204
Russula xerampelina	UPS:UE14.09.2004-3	Sweden	KU205279
Russula yadongensis	**HMAS287387**	**China**	**OQ871499**
Russula yadongensis	**HMAS287386 (holotype)**	**China**	**OQ871498**
Russula yadongensis	**HMAS287388**	**China**	**OQ871500**
Russula zelleri	NYGB-761009 (type)	USA	KX812833
Russula zelleri	OSC 5610	USA	MK169364
Russula zvarae	BB 08.639	Italy	JN944004
Outgroup			
Russula emetica	lw81 (TUB)	Germany	AF418619
Russula emetica	UE05.10.2003-11	Sweden	DQ421997

Newly generated sequences are shown in bold.

multigene phylogenetic analyses, with *R. raoultii* Quél. and *R. viscida* Kudřna as the outgroups. The ITS and concatenated sequences were analysed using RAXMLGUI 1.3.1 (Silvestro and Michalak 2012) with the GTRGAMMAI model and 1,000 rapid bootstrap (BS) replicates. The best-fit model for ITS was selected using ModelFinder in PhyloSuite v1.2.2 (Kalyaanamoorthy et al. 2017). The best partitioning scheme and evolutionary models for six predefined partitions were selected using PartitionFinder2 in PhyloSuite v1.2.2 (Lanfear et al. 2017). Bayesian inference (BI) analyses was performed using MrBayes 3.2.6 (Ronquist et al. 2012) under the best model. Four Markov chains were run for 2 million generations, stopping when the average standard deviation of split frequencies fell below 0.01. Trees were sampled every 100th generation. The initial 25% of sampled data were discarded as burn-in.

The resulting file after tree construction was used to view the phylogenetic tree using FigTree 1.4.3 (Andrew 2016). Bootstrap Support (BS) ≥70% considered significantly supported. Bayesian Posterior Probability (PP) ≥95% was regarded as significant.

3. Results

3.1. Phylogeny

The best evolutionary model was selected using ModelFinder, with the BIC criterion: HKY+F+I+G4 for ITS. The best partitioning scheme and evolutionary models for six predefined partitions were selected using PartitionFinder2 (Lanfear et al. 2017), with greedy algorithm and AICc criterion: GTR+I+G for nucLSU, GTR+I+G for mtSSU, SYM+I+G for *rpb2* exons, HKY+G for *rpb2* introns, SYM+I+G for *tef1* exons, GTR+I+G for *tef1* introns.

Maximum likelihood and Bayesian analyses were performed on the ITS and 4-locus data sets, and both maximum likelihood and Bayesian analyses yielded the same topology. The four proposed new species, *R. paragraveolens*, *R. pseudograveolens*, *R. shigatseensis*, and *R. yadongensis*, are all nested in the *Russula* crown clade in both ITS and 4-locus (nucLSU-mtSSU-*rpb2*-*tef1*) trees, and are clearly separated from known species (Figures 1 and 2).

3.2. Taxonomy

Russula paragraveolens **S.H. Wang, G.J. Li, R.L. Zhao & B. Cao, sp. nov., Figures 3a, 4a, 4b, 5, 6, 13a**

Fungal Names: FN571273.

Typification CHINA. Jilin Province, Yanbian Korean Autonomous Prefecture, Wangqing County, Mantianxing National Forest Park, N 43°18′ E 129°45′, 381 m asl, 22 July 2016, *Ming-Zhe Zhang*, *Xu-Ming Bai*, *Rong-Chun Dai*, *Guo-Jie Li*, *ZRL20160546* (**holotype** HMAS281158). GenBank: OQ871504 (ITS), OQ875223 (nucLSU), OQ878262 (mtSSU), OQ933792 (*rpb2*), OQ948122 (*tef1*).

Etymology Named after its similarity to the species *R. graveolens* Romell.

Diagnosis Pileus medium-sized, with bright red tinge; lamellae dense, with yellowish white to pale yellow colour; stipe 25–40 × 10–17 mm, cylindrical and slightly thick near the base; spores (5.0–)5.5–5.9–6.3(–6.6) × (4.0–)4.6–5.0–5.4(–5.6) µm, broadly ellipsoid, large, with isolated or occasionally fused, prominent spines; basidia (31–)31–36–41(–50) × (10–)10–11–12(–14) µm, clavate; hymenial cystidia (42–)53–59–64(–71) × (8–)9–10(–11) µm, mainly clavate or fusiform, apically acute; hyphal terminations

Table 2. Sequences used in phylogenetic analysis based on 4-locus data.

Taxon	Voucher specimen	Location	nucLSU	mtSSU	*rpb2*	*tef1*
R. aff. *fucosa*	27/BB 06.596	Canada	KU237457	KU237301	KU237743	KU237892
R. aff. *subdensifolia*	552/BB 07.158	USA	KU237544	KU237390	KU237830	KU237974
R. aff. *turci*	433/BB 07.325	Slovakia	KU237497	KU237342	KU237783	KU237927
R. aff. *viscidula*	73/BB 06.049	Madagascar	KU237469	KU237313	KU237755	–
R. aff. *xerampelina*	592/DM fl07-14	USA	KU237576	KU237424	KU237862	KU238004
R. amara	532/BB 07.782	France	KU237524	KU237370	KU237810	KU237954
R. amethystina	529/BB 07.314	Slovakia	KU237521	KU237367	KU237807	KU237951
R. aurata	547/BB 07.211	Slovakia	KU237539	KU237385	KU237825	KU237969
R. azurea	537/BB 08.668	Italy	KU237529	KU237375	KU237815	KU237959
R. badia	587/BB 07.324	Slovakia	KU237571	KU237419	KU237857	KU237999
R. burlinghamiae	548/BB 05.108	USA	KU237540	KU237386	KU237826	KU237970
R. carminipes	531/BB 07.192	Slovakia	KU237523	KU237369	KU237809	KU237953
R. carpini	551/BB 07.262	Slovakia	KU237543	KU237389	KU237829	KU237973
R. cf. *aurantioflammans*	241/BB 06.603	Canada	KU237488	KU237332	KU237774	KU237917
R. cf. *brunneoviolacea*	524/BB 06.606	Canada	KU237516	KU237362	KU237802	KU237946
R. cf. *decipiens*	231/BB 06.521	Mexico	KU237482	KU237326	KU237768	KU237911
R. cf. *katarinae*	30/BB 06.617	Canada	KU237460	KU237304	KU237746	KU237895
R. cf. *odorata*	525/BB 07.219	Slovakia	KU237517	KU237363	KU237803	KU237947
R. cf. *olivobrunnea*	240/BB 06.505	Mexico	KU237487	KU237331	KU237773	KU237916
R. cf. *sejuncta*	557/BB 08.143	Madagascar	KU237547	KU237393	KU237833	–
R. cf. *sesenagula*	84/BB 06.129	Madagascar	KU237473	KU237317	KU237759	KU237904
R. cf. *vinosobrunea*	533/BB 07.231	Slovakia	KU237525	KU237371	KU237811	KU237955
R. citrinolutea sp. ined.	29/BB 06.611	Canada	KU237459	KU237303	KU237745	KU237894
R. corallina	229/BB 06.324	USA	KU237481	KU237325	KU237767	KU237910
R. cuprea	565/BB 07.233	Slovakia	KU237555	KU237401	KU237841	KU237984
R. decipiens	585/BB 07.178	Slovakia	KU237569	KU237417	KU237855	KU237997
R. decolorans	549/BB 07.322	Slovakia	KU237541	KU237387	KU237827	KU237971
R. discopus	48/BB 06.027	Madagascar	KU237467	KU237311	KU237753	KU237900
R. echinospermatinae sp. ined.	736/BB 09.173	New Caledonia	KU237589	KU237437	KU237874	KU238016
R. flavisiccans	236/BB 06.336	Mexico	KU237485	KU237329	KU237771	KU237914
R. gigasperma	438/BB 07.280	Slovakia	KU237501	KU237346	KU237787	KU237931
R. globispora	436/BB 07.243	Slovakia	KU237499	KU237344	KU237785	KU237929
R. heinemannianus	594/CS s.n.	Zimbabwe	KU237577	KU237425	KU237863	KU238005
R. integra	518/BB 07.198	Slovakia	KU237513	KU237359	KU237799	KU237943
R. laeta	519/BB 07.267	Slovakia	KU237514	KU237360	KU237800	KU237944
R. laricina	575/BB 08.681	Italy	KU237560	KU237408	KU237846	KU237991
R. lepida	437/BB 07.189	Slovakia	KU237500	KU237345	KU237786	KU237930
R. lilacea	435/BB 07.213	Slovakia	KU237498	KU237343	KU237784	KU237928
R. melliolens	554/BB 07.194	Slovakia	KU237545	KU237391	KU237831	KU237975
R. musaecolor sp. ined.	558/BB 08.063	Madagascar	KU237548	KU237394	KU237834	KU237977
R. nauseosa	588/BB 07.285	Slovakia	KU237572	KU237420	KU237858	KU238000
R. nothofagineae sp. ined.	723/BB 09.044	New Caledonia	KU237583	KU237431	–	KU238010
R. nothofagineae sp. ined.	725/BB 09.068	New Caledonia	KU237584	KU237432	KU237869	KU238011
R. nothofagineae sp. ined.	726/BB 09.069	New Caledonia	KU237585	KU237433	KU237870	KU238012
R. nothofagineae sp. ined.	732/BB 09.124	New Caledonia	KU237586	KU237434	KU237871	KU238013
R. nothofagineae sp. ined.	733/BB 09.125	New Caledonia	KU237587	KU237435	KU237872	KU238014
R. obscurosordida sp. ined.	591/BB 06.564	Canada	KU237575	KU237423	KU237861	KU238003
R. odorata	526/BB 07.186	Slovakia	KU237518	KU237364	KU237804	KU237948
R. olivacea	426/BB 07.223	Slovakia	KU237492	KU237336	KU237778	KU237921
R. olivascens	530/BB 08.663	Italia	KU237522	KU237368	KU237808	KU237952

(*Continued*)

Table 2. (Continued).

Taxon	Voucher specimen	Location	nucLSU	mtSSU	*rpb2*	*tef1*
R. paludosa	442/BB 07.330	Slovakia	KU237505	KU237350	KU237791	KU237935
R. paragraveolens	**HMAS281158**	**China**	**OQ875223**	**OQ878262**	**OQ933792**	**OQ948122**
R. paragraveolens	**HMAS279574**	**China**	**OQ875224**	**OQ878263**	**OQ933793**	**OQ948123**
R. pelargonia	586/BB 07.169	Slovakia	KU237570	KU237418	KU237856	KU237998
R. pseudograveolens	**HMAS279577**	**China**	**OQ875227**	**OQ878266**	**OQ933794**	**OQ948121**
R. pseudograveolens	**HMAS287385**	**China**	**OQ875226**	**OQ878265**	**OQ933796**	**OQ948120**
R. pseudograveolens	**HMAS287384**	**China**	**OQ875225**	**OQ878264**	**OQ933795**	**OQ948119**
R. puellaris	523/BB 07.311	Slovakia	KU237515	KU237361	KU237801	KU237945
R. romellii	427/BB 07.202	Slovakia	KU237493	KU237337	KU237779	KU237922
R. rosea	430/BB 07.780	France	KU237496	KU237340	KU237782	KU237925
R. roseinae sp. ined.	735/BB 09.172	New Caledonia	KU237588	KU237436	KU237873	KU238015
R. shigatseensis	**HMAS287390**	**China**	**OQ875231**	**OQ878270**	**OQ933788**	**OQ948115**
R. shigatseensis	**HMAS287389**	**China**	**OQ875230**	**OQ878269**	**OQ933787**	**OQ948114**
R. shigatseensis	**HMAS387391**	**China**	**OQ875232**	**OQ878271**	**OQ933789**	**OQ948116**
R. sichuanensis	HMAS255316	China	MG786572	MG792323	–	MG812160
R. sichuanensis	HMAS268888	China	KX441372	KX441619	–	MF893457
R. solaris	559/BB 07.282	Slovakia	KU237549	KU237395	KU237835	KU237978
R. subtilis	536/BB 05.107	USA	KU237528	KU237374	KU237814	KU237958
R. tlaxcalae	33/BB 06.542	Mexico	KU237463	KU237307	KU237749	KU237897
R. turci	528/BB 07.328	Slovakia	KU237520	KU237366	KU237806	KU237950
R. versicolor	589/BB 07.288	Slovakia	KU237573	KU237421	KU237859	KU238001
R. vinosobrunneola	HMAS278885	China	MG786570	MG792321	–	MG812158
R. vinosobrunneola	HMAS281138	China	MG786569	MG792320	–	MG812157
R. vinosobrunneola	HMAS278896	China	MG786567	MG792318	–	MG812155
R. vinosobrunneola	HMAS278960	China	MG786568	MG792319	–	MG812156
R. yadongensis	**HMAS287386**	**China**	**OQ875228**	**OQ878267**	**OQ933790**	**OQ948117**
R. yadongensis	**HMAS287388**	**China**	**OQ875229**	**OQ878268**	**OQ933791**	**OQ948118**
R. zvarae	538/BB 08.639	Italy	KU237530	KU237376	KU237816	KU237960
Outgroup						
R. raoultii	561/BB 08.674	Italy	KU237551	KU237397	KU237837	KU237980
R. viscida	425/BB 07.298	Slovakia	KU237491	KU237335	KU237777	KU237920

Newly generated sequences are shown in bold.

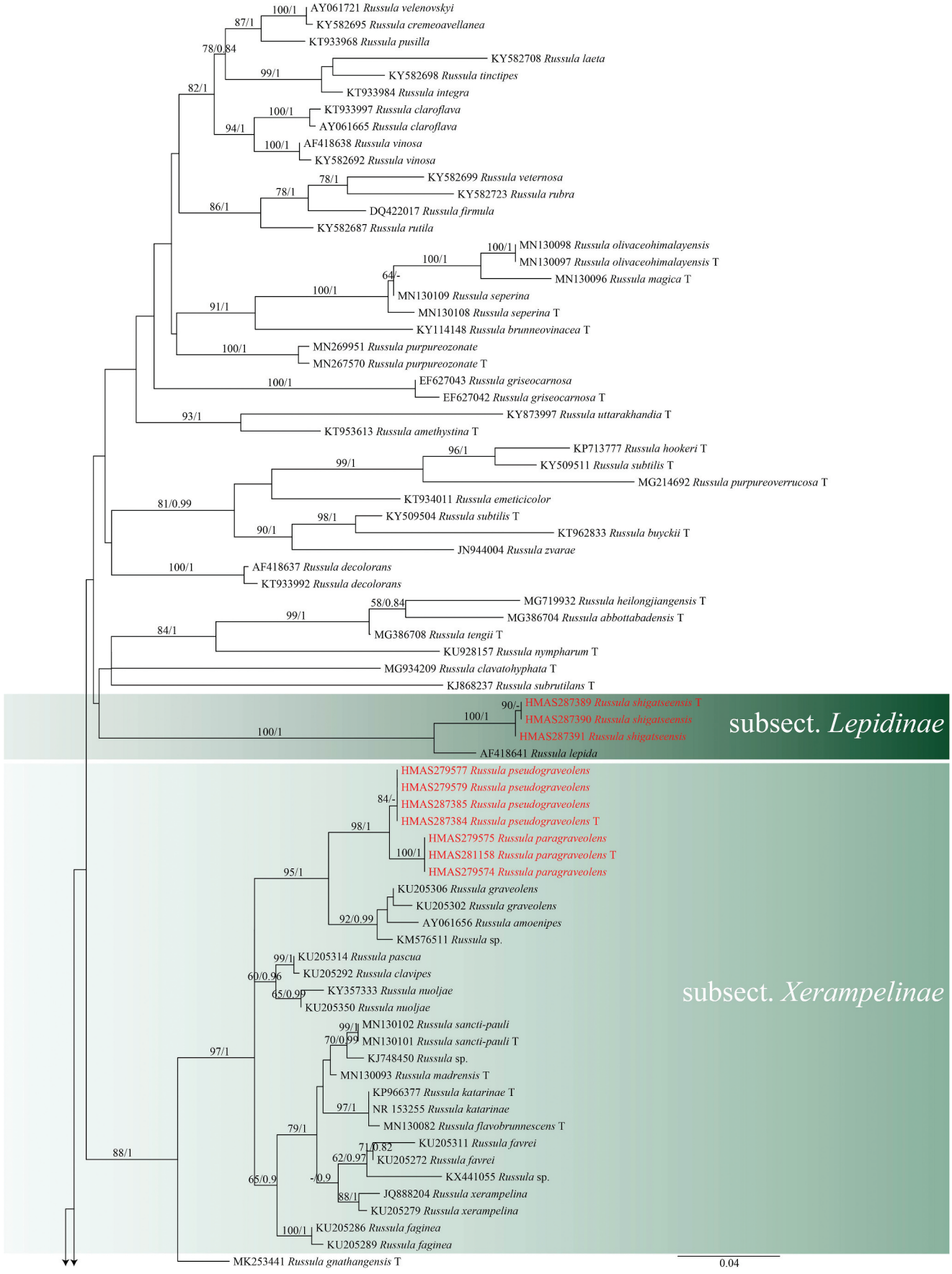

Figure 1. Maximum likelihood tree of subgen. *Russula* crown clade based on ITS sequences, bootstrap values higher than 70% were displayed around nodes. Accession numbers of the four species are shown in red. "T" refers to a type specimen.

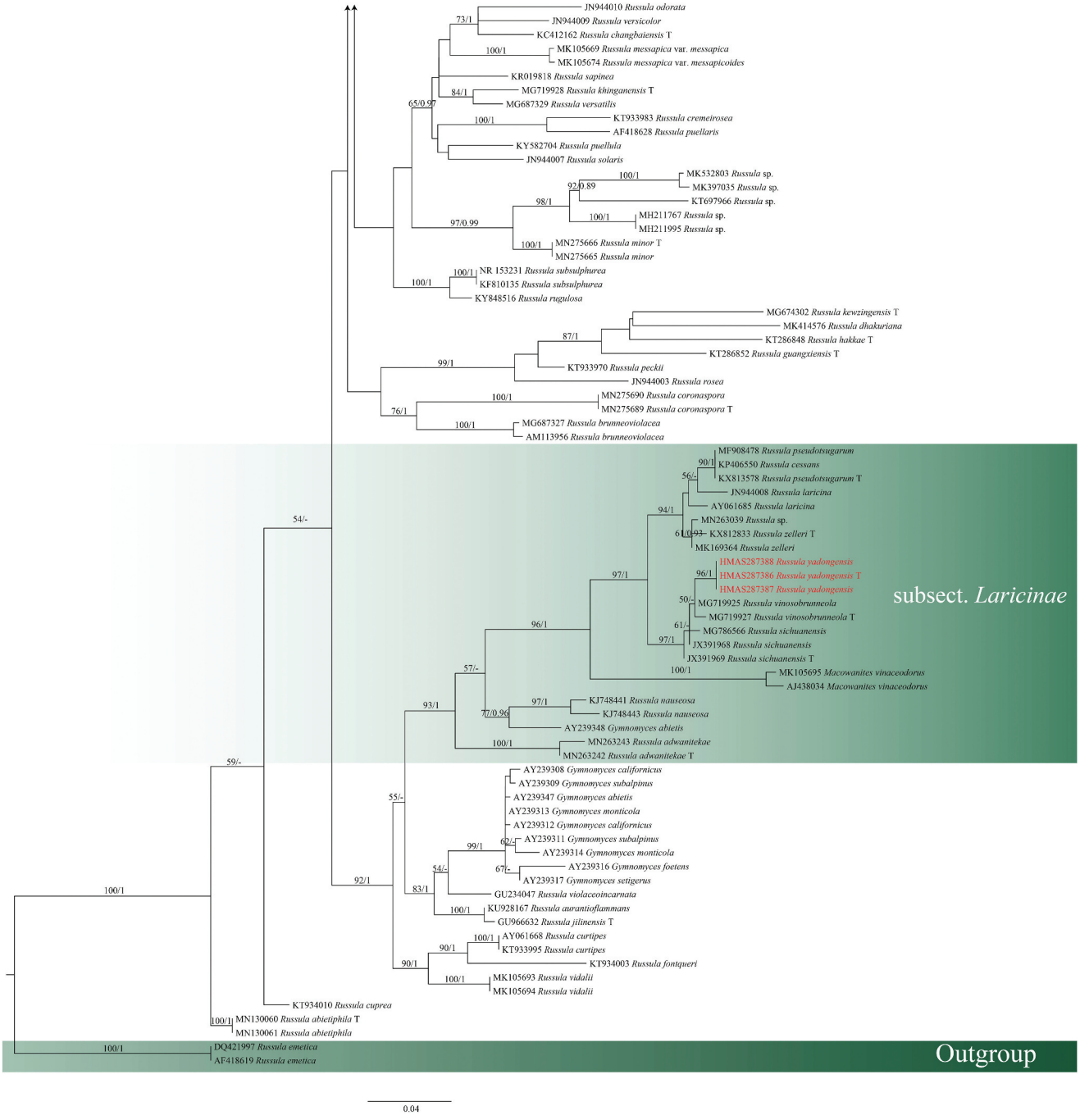

Figure 1. (Continued).

near the pileus margin occasionally narrow, thin-walled, terminal cells mainly cylindrical, apically obtuse or slightly constricted.

Pileus medium-sized, 40–70 mm diam., applanate with depressed centre; margin crenulate; cuticle smooth and shiny, peeling to 3/4 of the radius, bright red tinge (#AE1B0C), near the margin reddish orange (#CE4E24), towards the centre cherry red (#FE7C4D) to blood red (#6E1705), pale red (#FEB190) and pastel red (#F46733) when young, becoming cherry red (#FE7C4D) when mature. **Lamellae** 2–3 mm deep, adnate, dense, white (#F9F6E7) when young, becoming yellowish white (#F3F0CF) to pale yellow (#E4D39C) when mature; furcations absent, unequal with a few lamellulae of different lengths; edges concolorous

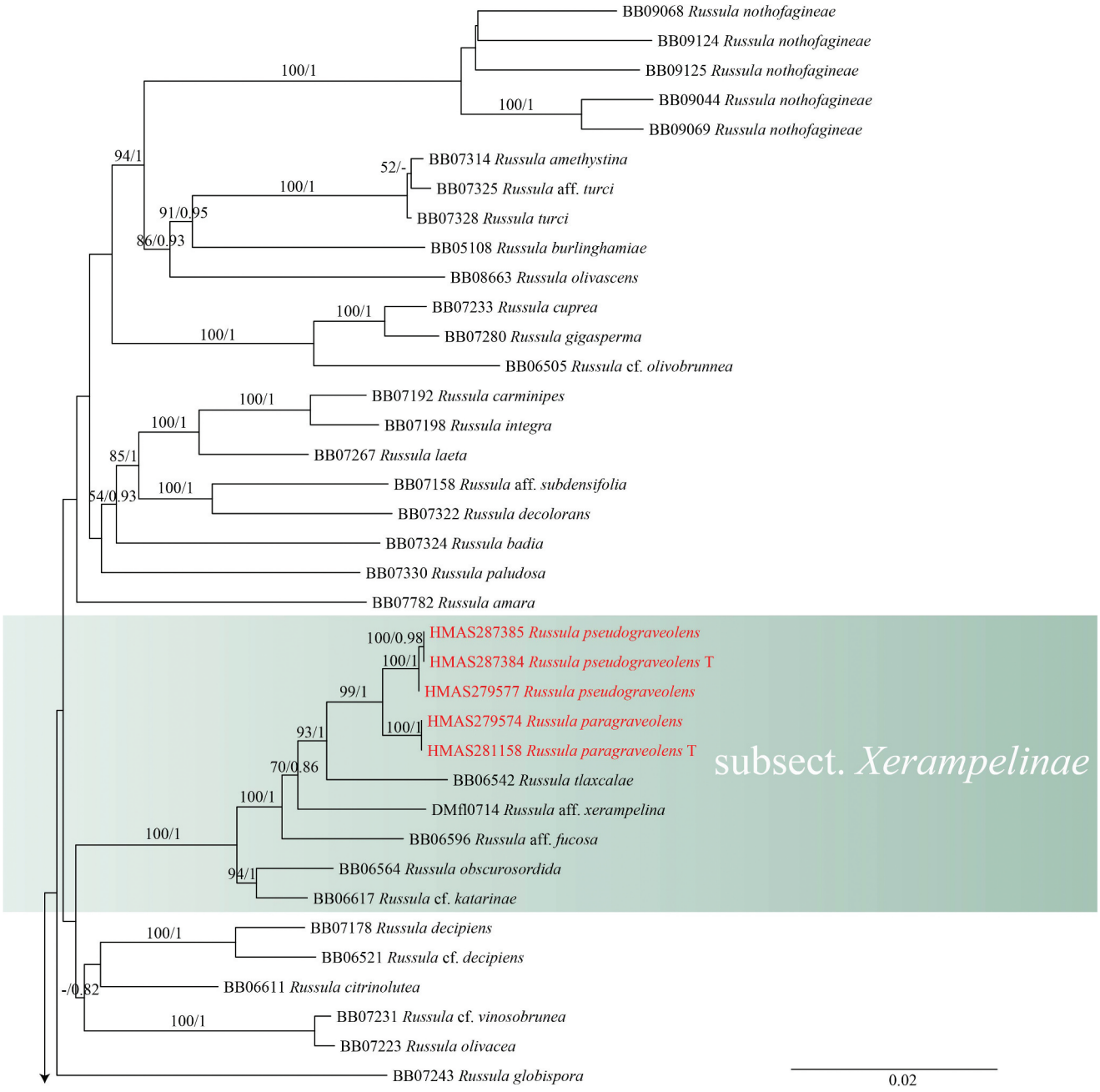

Figure 2. Maximum likelihood tree of subgen. *Russula* crown clade based on 4-locus (nucLSU-mtSSU-*rpb2*-*tef1*) combined sequences, bootstrap values higher than 70% were displayed around nodes. Collections of the two novel species are shown in red. "T" refers to a type specimen.

and even. **Stipe** 25–40 × 10–17 mm, cylindrical or slightly thicker near the base, white (#F9F6E7), staining yellowish brown (#F5DD93) when bruised; medulla stuffed and becoming hollow when mature. **Context** 2–3 mm thick in a half of the pileus radius, pale yellow (#E4D39C) to yellow (#F3E392), yellow (#F3E392) to yellowish brown (#F5DD93) when bruised; odour fishy; taste mild. **Spore print** ochre.

Spores (5.0–)5.5–5.9–6.3(–6.6) × (4.0–)4.6–5.0–5.4(–5.6) µm, broadly ellipsoid, Q = (1.1–)1.13–1.18–1.23(–1.3); ornamentation of large, moderately distant [5–6(–6) in a 3 µm diam. circle] amyloid spines or warts, which are (0.7–)0.9–1.3 (–1.4) µm high, isolated or fused in pairs or short chains [0–1(–2) fusions in the circle]; line connections absent or dispersed; suprahilar spot large, amyloid. **Basidia** (31–)31–36–41(–50) ×

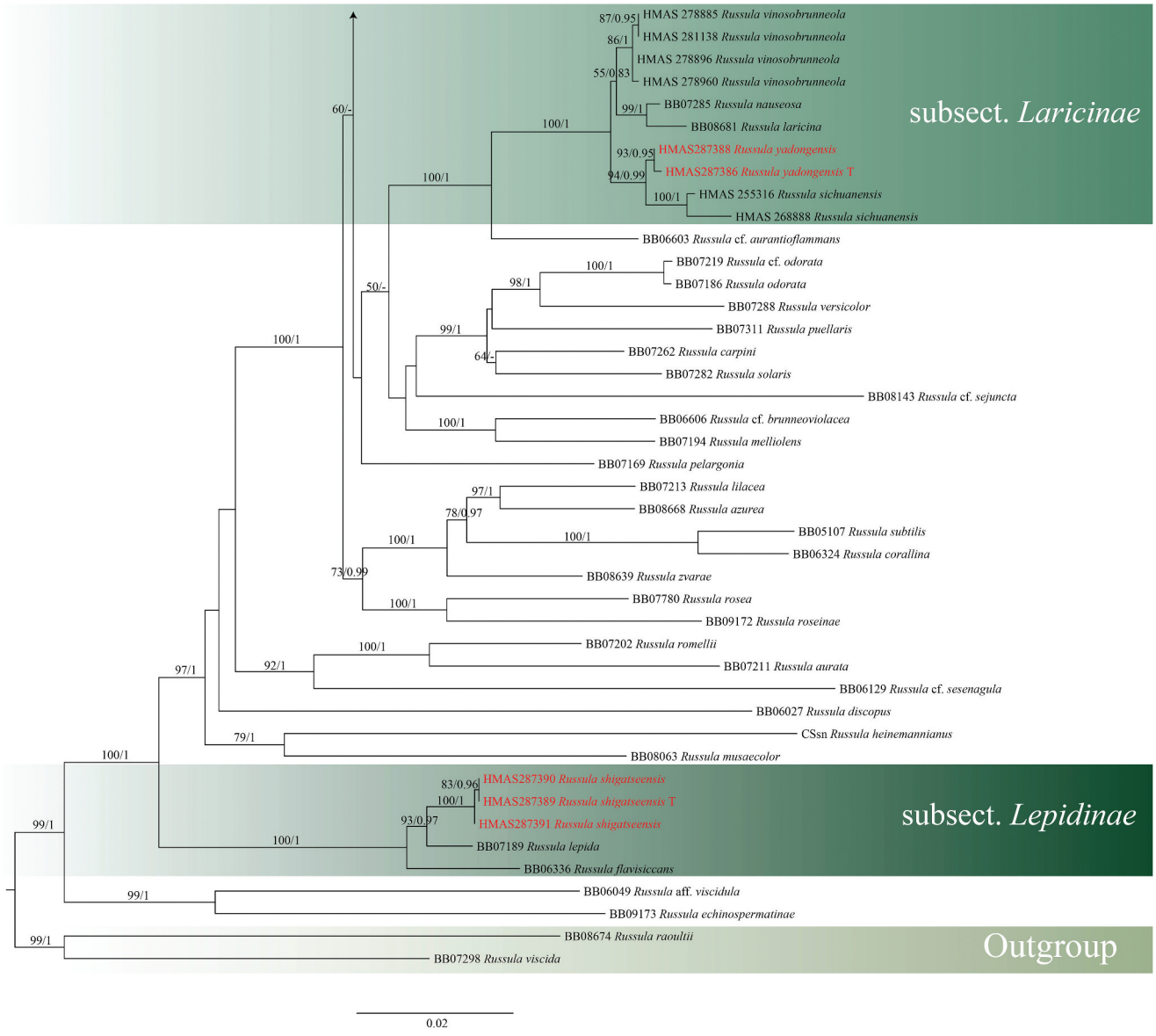

Figure 2. (Continued).

(10–)10–11–12(–14) µm, clavate, 4-spored; basidiola first cylindrical, then clavate, 8.5–10.5 µm wide. **Hymenial cystidia** dispersed to moderately numerous, 300–1,100/mm^2, (42–)53–59–64(–71) × (8–)9–10(–11) µm, mainly clavate or fusiform, apically acute, mucronate with a 1–9 µm long appendage, originating in subhymenium, thin-walled; contents completely heteromorphous crystalline, turning pale yellow-brown in sulfovanillin; abundant near the lamellae edges, (55–)58–62–65(–66) × (8–)9–10–11(–11) µm, similar to those on the sides. **marginal cells** (17–)20–23–26(–33) × (7–)8–9–10(–11) µm, undifferentiated. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying context, 220–450 µm deep, with a well-defined, strongly gelatinised, 70–120 µm deep suprapellis composed of ascending to erect hyphal terminations; subpellis 130–360 µm deep, composed of horizontally oriented, dense, intricate and narrow hyphae. **Acid-resistant incrustations** absent. Hyphal terminations near the pileus margin occasionally narrow, thin-walled; terminal cells (25–)33–47–60(–67) × (3–)3–4–5(–5) µm, cylindrical, apically obtuse or slightly constricted; subterminal cells usually equally long and wide, but often also shorter and wider, 1–2 µm wide. Hyphal terminations near the pileus centre similar, terminal cells even narrower, (38–)40–46–51(–58) × (3–)3–4(–4) µm;

subterminal cells unbranched and embedded in intricate hyphae of the subpellis. **Pileocystidia** near the pileus margin very abundant, typically 1-celled, sometimes 2-celled, usually clavate, occasionally slightly flexuous, thin-walled, terminal cells variable in length, (59–)61–64–68(−72) × (5–)6–7–9(−10) µm, mostly subcylindrical or narrowly clavate, apically mainly obtuse, occasionally subacute, contents heteromorphous, usually dense and crystalline-granulose, turning grey-brown to black in sulfovanillin. Pileocystidia near the pileus centre slightly smaller; terminal cells (46–)50–60–70(−77) × (5–)5–6–8(−8) µm, mostly subclavate, cylindrical or fusiform, apically obtuse but occasionally also subacute to constricted. **Cystidioid hyphae** in subpellis and context dispersed, with heteromorphous granulose contents, oleiferous hyphae frequent in the lower part of subpellis and context.

Habit and habitat Solitary on soil in secondary broad-leaved forest (dominated by *Quercus mongolica*) at 300–500 m.

Other specimens examined CHINA. Jilin Province, Yanbian Korean Autonomous Prefecture, Wangqing County, Mantianxing National Forest Park, N 43°18′ E 129°45′, 381 m asl, 22 July 2016, *Ming-Zhe Zhang, Xu-Ming Bai, Rong-Chun Dai, Guo-Jie Li, ZRL20162647* (HMAS279575); Jilin Province, Yanbian Korean Autonomous Prefecture, Wangqing County, Mantianxing National Forest Park, N 43°18′ E 129°45′, 381 m asl, 21 July 2016, *Ming-Zhe Zhang*, *Xu-Ming Bai*, *Rong-Chun Dai*, *Guo-Jie Li*, *ZRL20162503* (HMAS279574).

Notes: According to the ITS phylogenetic tree (Figure 1), *R. paragraveolens* is phylogenetically related to *R. amoenipes* and *R. graveolens*. However, there are clear morphological differences, with *R. paragraveolens* having smaller spores and a brighter red pileus colour (Romagnesi 1967, 1985; Sarnari 1998; Sarnari and Redeuilh 2005). The new species *R. paragraveolens* is sister to *R. pseudograveolens*, both species belong to subsect. *Xerampelinae* of sect. *Polychromae*, but is morphologically distinct. *Russula pseudograveolens* is clearly distinguished from *R. paragraveolens* by having shorter and slender basidia [basidia of *R. pseudograveolens* (27.0–)28.5–30.4–32.3 (−35.1) × (8.5–)9.1–9.7–10.2(−10.7) µm], longer projections of hymenial cystidia on lamellae sides [hymenial cystidia of *R. pseudograveolens* (41.3–)43.4–49.6–55.8(−64.1) × (5.4–)7.8–9.2–10.6(−10.3) µm], more lateral branches of hyphal terminations in pileipellis.

Russula pseudograveolens S.H. Wang, G.J. Li, R.L. Zhao & B. Cao, sp. nov., Figures 3b–f, 4 c–d, 7, 8, 13b

Fungal Names: FN571275.

Typification CHINA. Chongqing City, Chengkou County, Daba Mountain, Beiping Mountain, N 32°0′ E 108°44′, 1,570 m asl, 14 September 2021, *Xin-Yu Zhu*, *Ming-Zhe Zhang*, *Yang Liu*, *Chen-Hao Li, ZRL20211703* (**holotype** HMAS287384). GenBank: OQ871496 (ITS), OQ875225 (nucLSU), OQ878264 (mtSSU), OQ933795 (*rpb2*), OQ948119 (*tef1*).

Etymology Named after its similarity to the species *R. graveolens*.

Diagnosis Pileus medium-sized, with violet brown to brownish red colour; lamellae with yellowish white to pale cream colour; stipe 22–24 × 8–10 mm, cylindrical, mainly pale brown; spores (5.5–)6.0–6.3–6.6 (−6.9) × (4.7–)5.0–5.2–5.5(−5.7) µm, broadly ellipsoid, large; basidia (27–)28–30–32(−35) × (8.5–)9–10 (−11) µm, clavate; hymenial cystidia (41–)43–50–56 (−64) × (5–)8–9–11(−11) µm, mainly clavate or fusiform, apically acute; hyphal terminations near the pileus margin occasionally narrow, thin-walled, terminal cells mainly cylindrical, apically obtuse or slightly constricted. subterminal cells branched and embedded in intricate hyphae of the subpellis.

Pileus medium-sized, 40–47 mm diam., hemispherical when young, becoming applanate when mature, margin undulate, typically cracking when mature; near the centre darker and more brown (#56464F), violet brown (#6B5D6E) to brownish red (#623C47), near the margin pale red (#BD8791) to pastel red (#905361), cuticle dry, matt, minutely pruinose or encrusted with granulose tufts over entire surface which are darker than the background. **Lamellae** 2 mm deep, pale yellow (#C9CEC8), yellowish white (#F6FCFF) when young, yellowish white (#F6FCFF) to pale cream (#D0D3C8), adnate, dense, lamellulae and furcations absent; edges concolorous and even. **Stipe** 22–24 × 8–10 mm, cylindrical, mainly pale brown (#777671), near the lamellae yellowish white (#F6FCFF) to white (#C1CEED), medulla stuffed and becoming hollow when mature. **Context** 1 mm thick in a half of the pileus radius, yellowish white (#F6FCFF) to cream (#CDCDC3), yellow (#D2D5CA) to

Figure 3. Basidiomata in the field. (a) *Russula paragraveolens* (HMAS281158, holotype). (b) *R. pseudograveolens* (HMAS287384, holotype). (c–d) *R. pseudograveolens* (HMAS279577). (e–f) *R. pseudograveolens* (HMAS279579). (g–h) *R. yadongensis* (HMAS287387). (i) *R. yadongensis* (HMAS287386, holotype). (j) *R. yadongensis* (HMAS287388). (k–l) *R. shigatseensis* (HMAS287390). (m) *R. shigatseensis* (HMAS287389, holotype). (n–o) *R. shigatseensis* (HMAS287391).

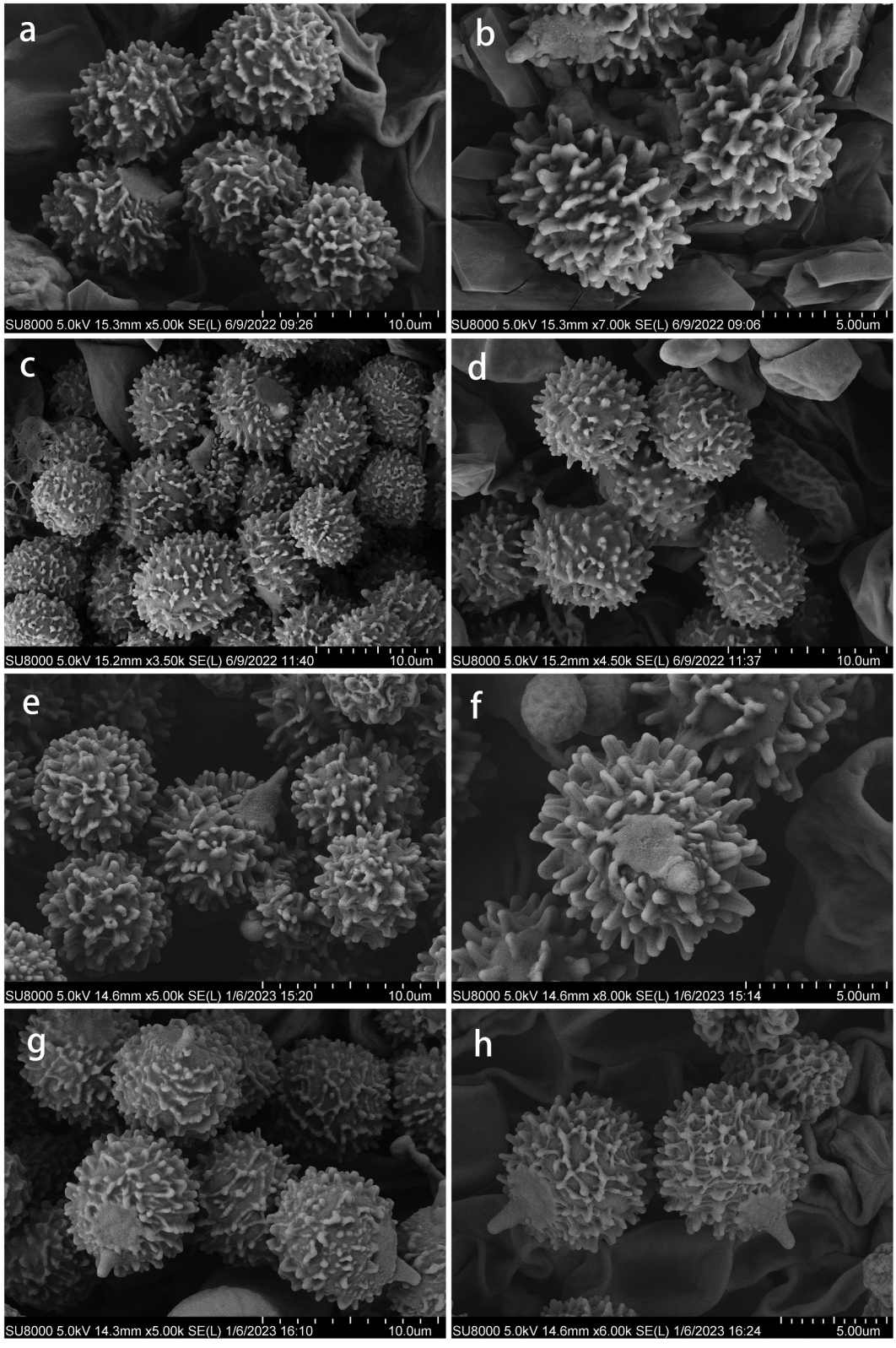

Figure 4. Basidiospores under scanning electron microscope. (a–b) *Russula paragraveolens* (HMAS281158, holotype). (c–d) *R. pseudograveolens* (HMAS287384, holotype). (e–f) *R. yadongensis* (HMAS287386, holotype). (g–h) *R. shigatseensis* (HMAS287389, holotype).

yellowish brown (#A29D83) when bruised; no distinct odour first, somewhat fishy when dry; taste mild. **Spore print** not observed.

Spores (5.5–)6.0–6.3–6.6(–6.9) × (4.7–)5.0–5.2–5.5(–5.7) µm, broadly ellipsoid, Q = (1.1–)1.18–1.20–1.23(–1.3); ornamentation of large, dense [7–8(–8) in a 3 µm diam. circle] amyloid spines or warts, which are (0.6–)0.7–0.9(–1.0) µm high, isolated or fused in pairs or short chains [0–1(–2) fusions in the circle]; line connections absent or dispersed; suprahilar spot large, amyloid. **Basidia** (27–)28–30–32(–35) × (8.5–)9–10(–11) µm, clavate, 4-spored; basidiola first cylindrical, then clavate, 6.8–8.6 µm wide. **Hymenial cystidia** dispersed to moderately numerous, 300–1,100/mm^2, (41–)43–50–56(–64) × (5–)8–9–11(–11) µm, mainly clavate or fusiform, apically acute, mucronate with a 6–10 µm long appendage, originating in subhymenium, thin-walled; contents completely heteromorphous crystalline, turning pale yellow-brown or pale greyish brown in sulfovanillin; abundant near the lamellae edges, (42–)42–48–54(–63) × (6–)6–7(–8) µm, similar to those on the sides but usually smaller. **Marginal cells** (13–)13–15–18(–19) × (5–)5–6–7(–8) µm, undifferentiated. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying context, 200–320 µm deep, with a well-defined, strongly gelatinised, 80–120 µm deep suprapellis composed of ascending to erect hyphal terminations; subpellis 110–200 µm deep, composed of horizontally oriented, dense, intricate and narrow hyphae. **Acid-resistant incrustations** absent. Hyphal terminations near the pileus margin occasionally narrow, thin-walled; terminal cells (36–)37–53–69(–83) × (1.6–)2.0–2.4–2.9(–3.0) µm, cylindrical, apically obtuse or slightly constricted; subterminal cells usually equally long and wide, but often also shorter and wider, 1–2 µm wide, branched or not. Hyphal terminations near the pileus centre similar, terminal cells even narrower, (28–)32–37–42(–43) × (1.5–)1.9–2.7–3.4(–3.7) µm; subterminal cells branched and embedded in intricate hyphae of the subpellis. **Pileocystidia** near the pileus margin very abundant, typically 1-celled, sometimes 2-celled, usually clavate, occasionally slightly flexuous, thin-walled, terminal cells variable in length, (48–)49–54–59(–60) × (4.2–)4.7–5.3–5.9(–5.9) µm, mostly subcylindrical or narrowly clavate, apically mainly obtuse, occasionally subacute, contents heteromorphous, usually dense and crystalline-granulose, turning grey-brown to black in sulfovanillin. Pileocystidia near the pileus centre slightly smaller; terminal cells (43–)47–51–55(–58) × (3.4–)4.0–4.8–5.6(–5.7) µm, mostly subclavate, cylindrical or fusiform, apically obtuse but occasionally also subacute to constricted. **Cystidioid hyphae** in subpellis and context dispersed, with heteromorphous granulose contents, oleiferous hyphae frequent in the lower part of subpellis and context.

Habit and habitat Solitary on soil in mixed coniferous and broad-leaved forest (dominated by Fagaceae spp. of *Castanopsis*, *Lithocarpus*, and *Quercus*, intermixed with *Pinus yunnanensis* var. *tenuifolia*) at 500–2,200 m.

Other specimens examined CHINA. Chongqing City, Chengkou County, Daba Mountain, Beiping Mountain, N 32°0′ E 108°44′, 1,570 m asl, 14 September 2021, *Xin-Yu Zhu*, *Ming-Zhe Zhang*, *Yang Liu*, *Chen-Hao Li*, *ZRL20211685* (HMAS287385); Guangxi Zhuang Autonomous Region, Baise City, Leye County, Yachang Orchid National Nature Reserve, N 24°44′ E 106°19′, 1,211 m asl, 6 August 2017, *Rui-Lin Zhao*, *GX20170438* (HMAS279577); Guangxi Zhuang Autonomous Region, Baise City, Leye County, Yachang Orchid National Nature Reserve, N 24°44′ E 106°19′, 1,211 m asl, 6 August 2017, *Hui-Jun Wang*, *GX20170498* (HMAS279579).

Notes: According to the ITS phylogenetic tree (Figure 1), *R. pseudograveolens* is phylogenetically related to *R. graveolens*. However, there are clear morphological differences, with *R. pseudograveolens* having smaller spores, shorter basidia, and a brighter red pileus colour (Romagnesi 1967, 1985; Sarnari 1998; Sarnari and Redeuilh 2005). The new species *R. pseudograveolens* is sister to *R. paragraveolens*. However, differences not only in morphology, but also in host plants and geographical distribution. *Russula paragraveolens* grows solitarily on the ground in secondary broadleaved forest (dominated by *Quercus mongolica*) at 300–500 m, while *R. pseudograveolens* grows at higher altitudes and has more complex host plants at 500–2,200 m. Furthermore, *R. paragraveolens* and *R. pseudograveolens* belong to different temperature zones, the former being a temperate species and the latter a subtropical species.

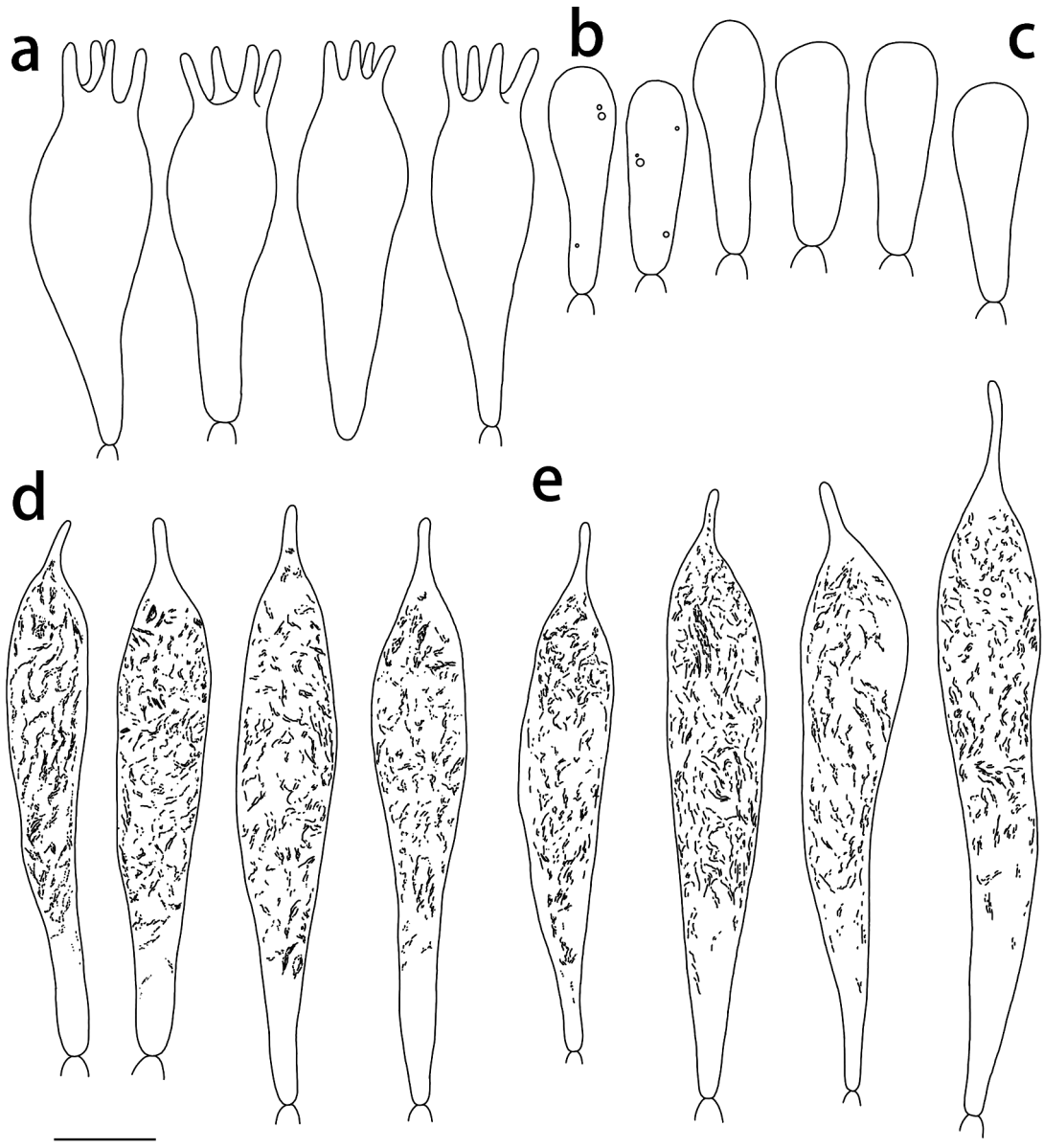

Figure 5. *Russula paragraveolens* (HMAS281158, holotype), hymenium. (a) Basidia. (b) Basidiola. (c) Marginal cells on the lamella edges. (d) Hymenial cystidia near the lamella sides. (e) Hymenial cystidia on the lamella edges. Cystidia with contents as observed in Congo red. Scale bar = 10 µm.

Russula shigatseensis S.H. Wang, R.L. Zhao & B. Cao, sp. nov., Figures 3k–o, 4g–h, 9, 10, 13c

Fungal Names: FN571577.

Typification CHINA. Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, N 27°25′ E 88°56′, 3,024 m asl, 26 July 2022, *Rui-Lin Zhao*, *Xin-Yu Zhu*, *Jia-Xin Li*, *ZRL20220194* (**holotype** HMAS287389). GenBank: OQ871501 (ITS), OQ875230 (nucLSU), OQ878269 (mtSSU), OQ933787 (*rpb2*), OQ948114 (*tef1*).

Etymology Refers to Shigatse Municipality, the locality of the type specimen.

Diagnosis Pileus medium-sized, with brownish orange to madder red colour; lamellae with yellowish white to pale cream colour; stipe 45–104 × 12–18 mm, cylindrical and slightly thick near the base; spores (5.6–)6.0–6.4–6.9(–7.5) × (4.8–)5.2–5.7–6.2(–6.7) µm, subglobose, medium-sized; basidia (24–)31–35–39(–39) × (8–)10–12–13(–13) µm, clavate; hymenial cystidia (64–)69–78–87(–97) × (5–)6–7–8(–8) µm, mainly clavate or fusiform, apically acute; hyphal terminations near the

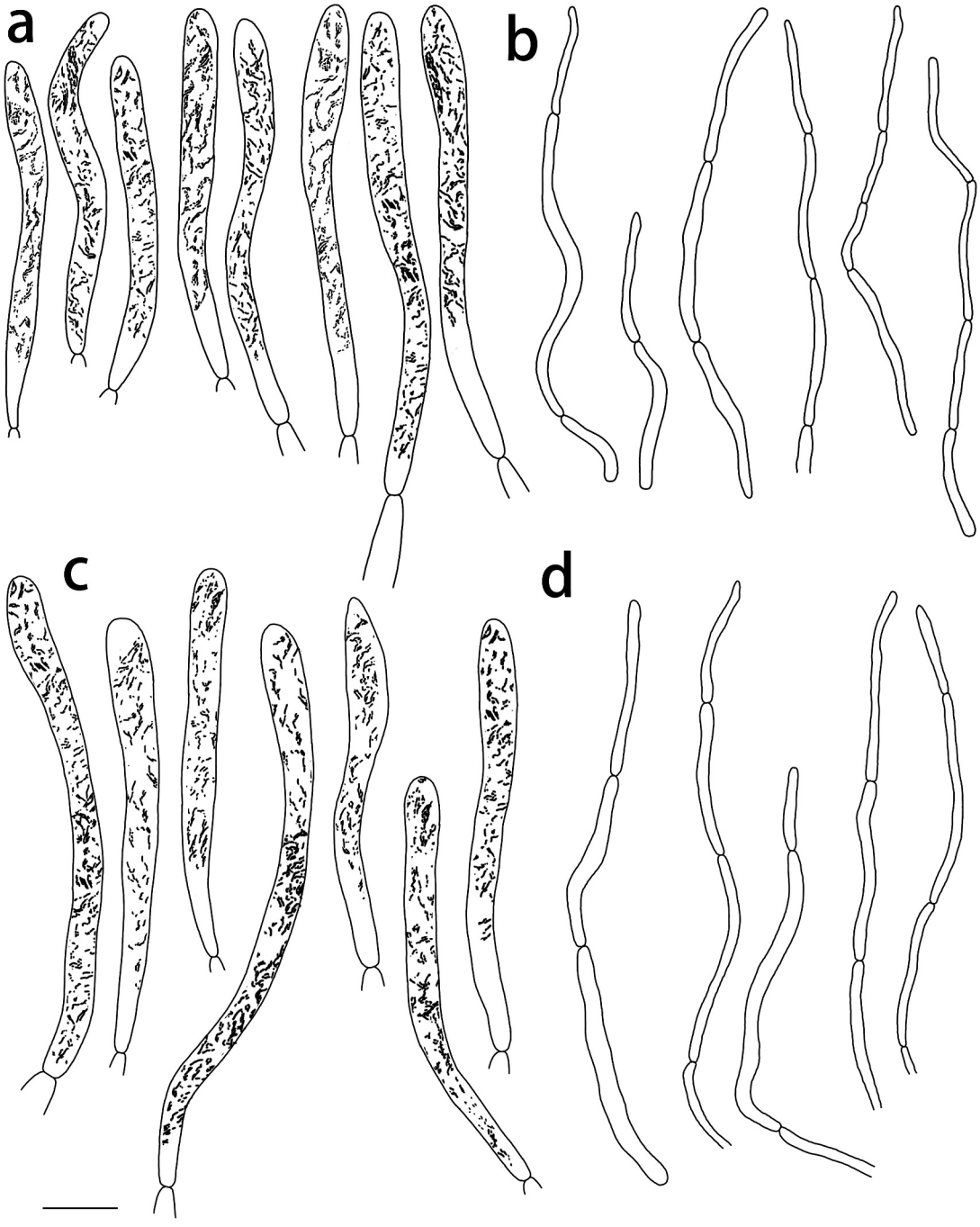

Figure 6. *Russula paragraveolens* (HMAS281158, holotype), pileipellis. (a) Pileocystidia near the pileus centre. (b) Hyphal terminations near the pileus centre. (c) Pileocystidia near the pileus margin. (d) Hyphal terminations near the pileus margin. Cystidial contents as observed in Congo red. Scale bar = 10 μm.

pileus margin occasionally narrow, thin-walled, terminal cells mainly cylindrical, apically obtuse or slightly constricted. subterminal cells branched and embedded in intricate hyphae of the subpellis.

Pileus medium-sized, 59–80 mm diam., hemispherical when young, becoming applanate with depressed centre when mature, applanate with depressed centre; margin smooth; cuticle dry to viscid, smooth, peeling to 1/2 of the radius, brownish orange (#B66747) to madder red (#C43925) in the centre, pinkish red (#E68A99) towards the margin. **Lamellae** 1–7 mm deep, yellowish white (#A19D87) to white (#CED0CD) when young, yellowish white (#A19D87) to pale cream (#CAD0C9), adnate, dense,

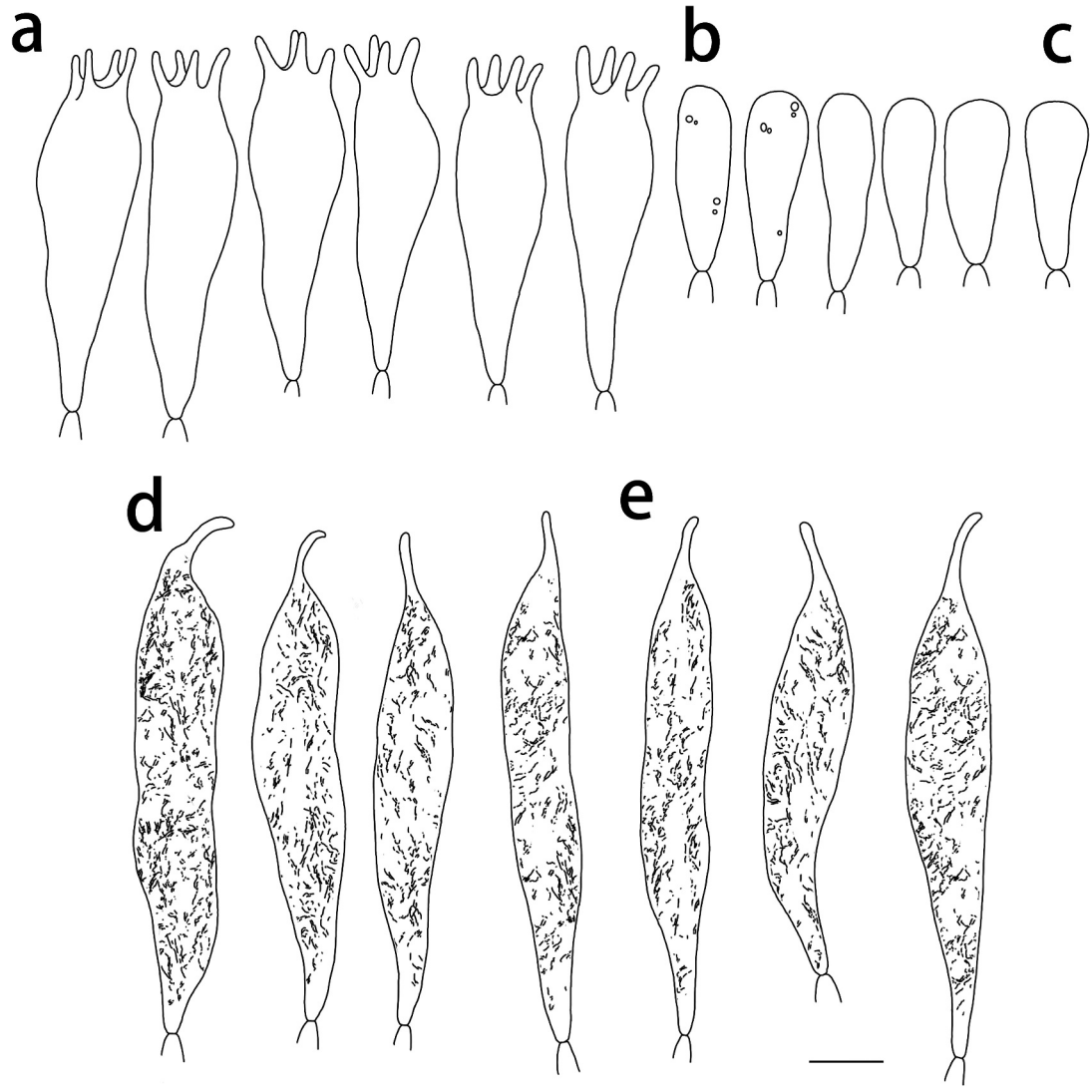

Figure 7. *Russula pseudograveolens* (HMAS287384, holotype), hymenium. (a) Basidia. (b) Basidiola. (c) Marginal cells on the lamella edges. (d) Hymenial cystidia near the lamella sides. (e) Hymenial cystidia on the lamella edges. Cystidia with contents as observed in Congo Red. Scale bar = 10 µm.

lamellulae and furcations absent; edges concolorous and even. **Stipe** 45–104 × 12–18 mm, cylindrical and slightly thick near the base, white (#CED0CD), often with pinkish flush or pink areas, medulla stuffed and becoming hollow when mature. **Context** 1–2 mm thick in a half of the pileus radius, yellowish white (#A19D87) to cream (#C1BDBA). **Spore print** not observed

Spores (5.6–)6.0–6.4–6.9(–7.5) × (4.8–)5.2–5.7–6.2 (–6.7) µm, subglobose, Q = (1.0–)1.0–1.13–1.18(–1.3); ornamentation of medium-sized, moderately distant to dense [6–8 (–12) in a 3 µm diam. circle] amyloid spines or warts, which are (0.5–)0.5–0.7(–0.8) µm high, isolated or fused in pairs or short chains [0–1(–2) fusions in the circle]; line connections absent or dispersed; suprahilar spot large, amyloid. **Basidia** (24–) 31–35–39(–39) × (8–)10–12–13(–13) µm, clavate, 4-spored; basidiola first cylindrical, then clavate, 7.0–10.7 µm wide. **Hymenial cystidia** dispersed to moderately numerous, 300–1,100/mm^2, (64–)69–78–87 (–97) × (5–)6–7–8(–8) µm, mainly clavate or fusiform, apically acute, mucronate with a 0–5 µm long appendage, originating in subhymenium, thin-walled; contents completely heteromorphous crystalline, turning grey-brown to black in sulfovanillin; abundant near the lamellae edges, (49–)50–58–65(–77) × (3–)5–6–7

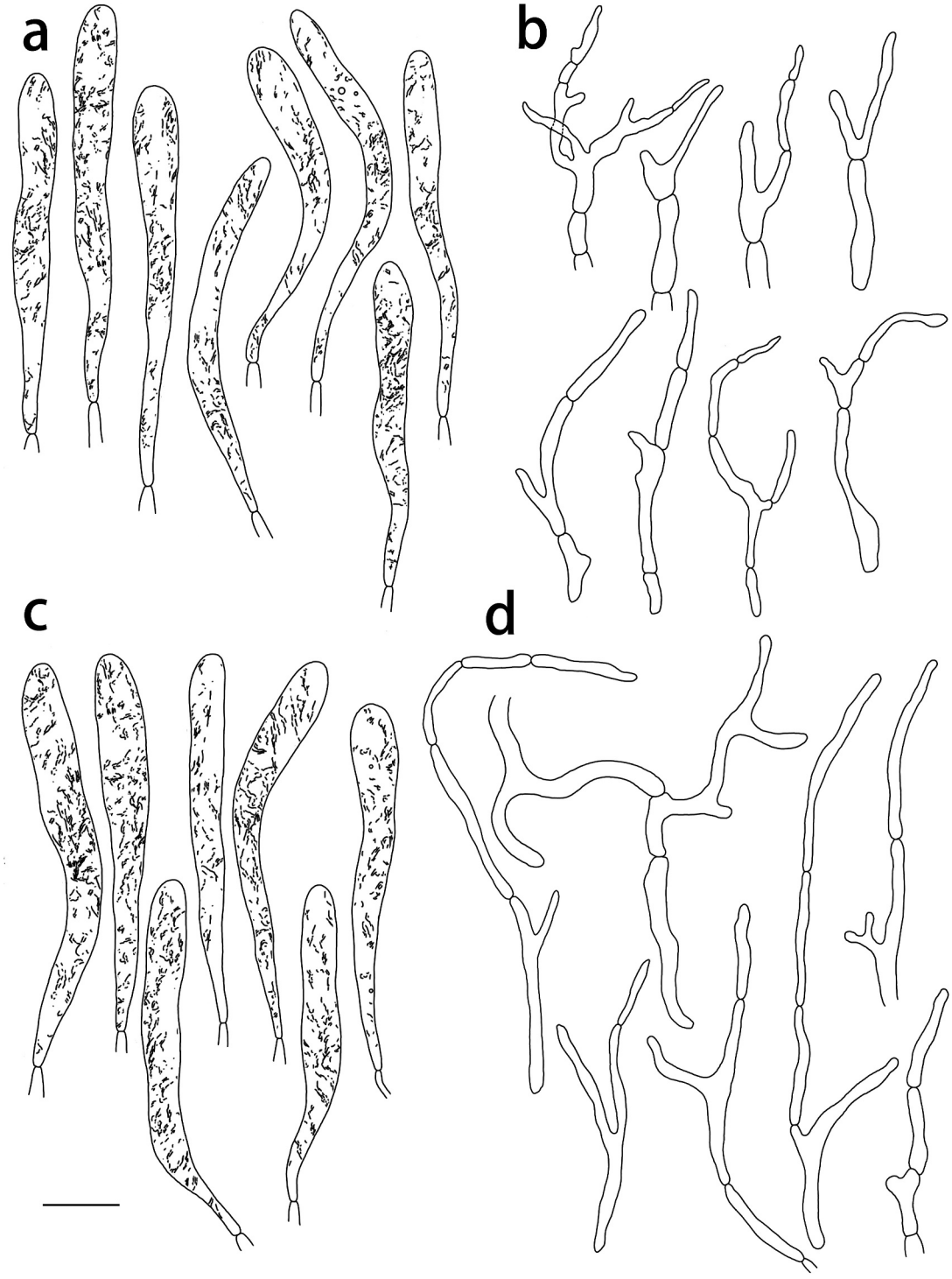

Figure 8. *Russula pseudograveolens* (HMAS287384, holotype), pileipellis. (a) Pileocystidia near the pileus centre. (b) Hyphal terminations near the pileus centre. (c) Pileocystidia near the pileus margin. (d) Hyphal terminations near the pileus margin. Cystidial contents as observed in Congo Red. Scale bar = 10 µm.

(–8) µm, similar to those on the sides but usually smaller. **Marginal cells** (9–)8–12–16(–21) × (4–)3–5–6(–9) µm, undifferentiated. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying context, 140–330 µm deep, with a well-defined, strongly gelatinised, 50–150 µm deep suprapellis composed of ascending to erect hyphal terminations; subpellis 90–180 µm deep, composed of horizontally oriented, dense, intricate and narrow hyphae. **Acid-resistant incrustations** absent. Hyphal terminations

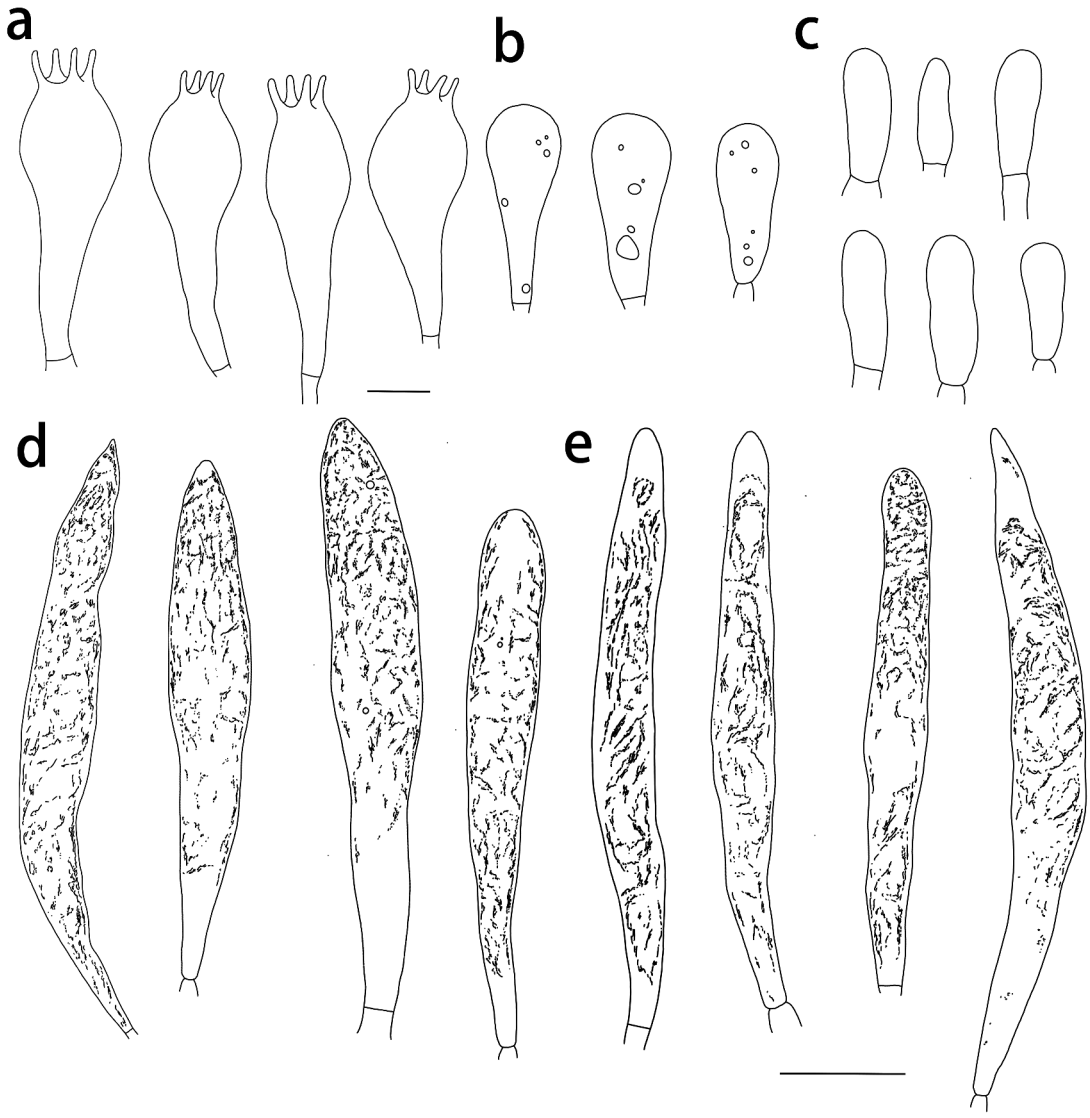

Figure 9. *Russula shigatseensis* (HMAS287389, holotype), hymenium. (a) Basidia. (b) Basidiola. (c) Marginal cells on the lamella edges. (d) Hymenial cystidia near the lamella sides. (e) Hymenial cystidia on the lamella edges. Cystidia with contents as observed in Congo Red. Scale bar = 10 µm.

near the pileus margin occasionally narrow, thin-walled; terminal cells (44–)57–86–116(−142) × (2.5–)3–4–5(−5) µm, cylindrical, apically obtuse or slightly constricted; subterminal cells usually equally long and wide, but often also shorter and wider, 1–2 µm wide, branched or not. Hyphal terminations near the pileus centre similar, terminal cells even narrower, (26–)29–38–46(−56) × (1.0–)1.3–1.9–2.5(−3.2) µm; subterminal cells branched and embedded in intricate hyphae of the subpellis. **Pileocystidia** near the pileus margin very abundant, typically 1–2-celled, seldom 3–4-celled, usually clavate, frequently slightly flexuous, thin-walled, terminal cells variable in length, (36–)40–46–52(−55) × (2.5–)2.9–3.4–4.0(−4.4) µm, mostly subcylindrical or narrowly clavate, apically mainly obtuse, occasionally subacute, contents heteromorphous, usually dense and crystalline-granulose, turning pale yellow-brown or pale greyish brown in sulfovanillin. Pileocystidia near the pileus centre slightly smaller; terminal cells (25–)28–35–41(−46) × (2.5–)2.7–3.2–3.7(−3.8) µm, mostly subclavate, cylindrical or fusiform, apically obtuse but occasionally also subacute to constricted. **Cystidioid hyphae** in subpellis and context dispersed, with heteromorphous granulose contents, oleiferous hyphae frequent in the lower part of subpellis and context.

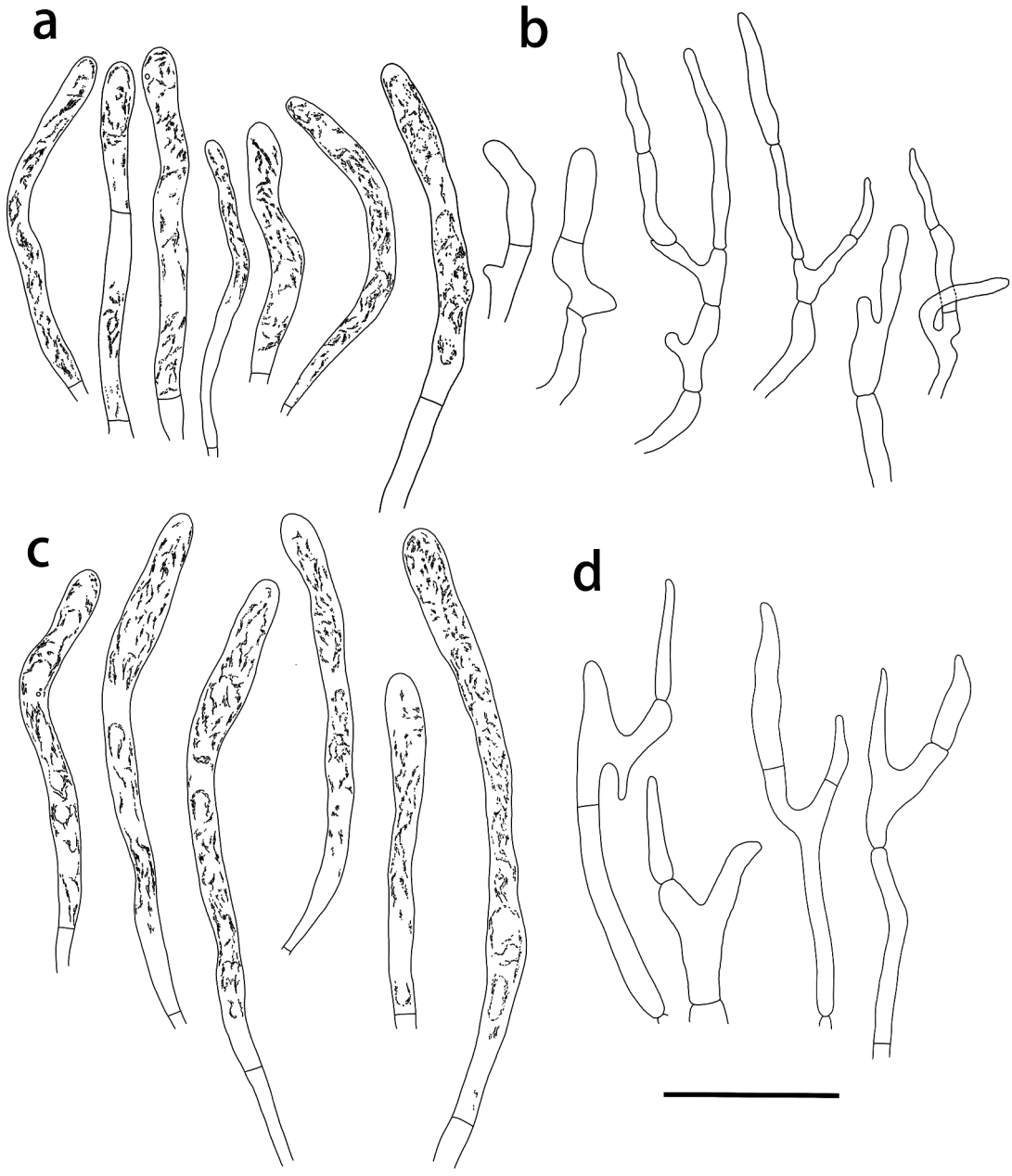

Figure 10. *Russula shigatseensis* (HMAS287389, holotype), pileipellis. (a) Pileocystidia near the pileus centre. (b) Hyphal terminations near the pileus centre. (c) Pileocystidia near the pileus margin. (d) Hyphal terminations near the pileus margin. Cystidial contents as observed in Congo Red. Scale bar = 10 µm.

Habit and habitat: Scattered in coniferous forests.

Other specimens examined CHINA. Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, N 27°25′ E 88°56′, 3,024 m asl, 26 July 2022, *Mao-Qiang He*, *Bin Cao*, *ZRL20220072* (HMAS287390); Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, N 27°25′ E 88°56′, 3,024 m asl, 26 July 2022, *Mao-Qiang He*, *Bin Cao*, *ZRL20220207* (HMAS287391).

Notes: According to the ITS and multigene phylogeny, *R. shigatseensis* belonging to sect. *Flavisiccantes*, subsect. *Lepidinae*, is represented in a well-supported clade (BS = 100%) by three specimens from the Shigatse region of Xizang, China. The species is closely related to *R. lepida* Fr., but *R. shigatseensis* has smaller spores [(5.6–)6.0–6.4–6.9(–7.5) × (4.8–)5.2–5.7–6.2(–6.7) µm]. Compared to *R. lepida* [2–9 × 4–7 µm], the spores of *R. shigatseensis* have spore ornamentations of more or less isolated spines (Sarnari and Redeuilh 2005). *R. flavisiccans* Bills also

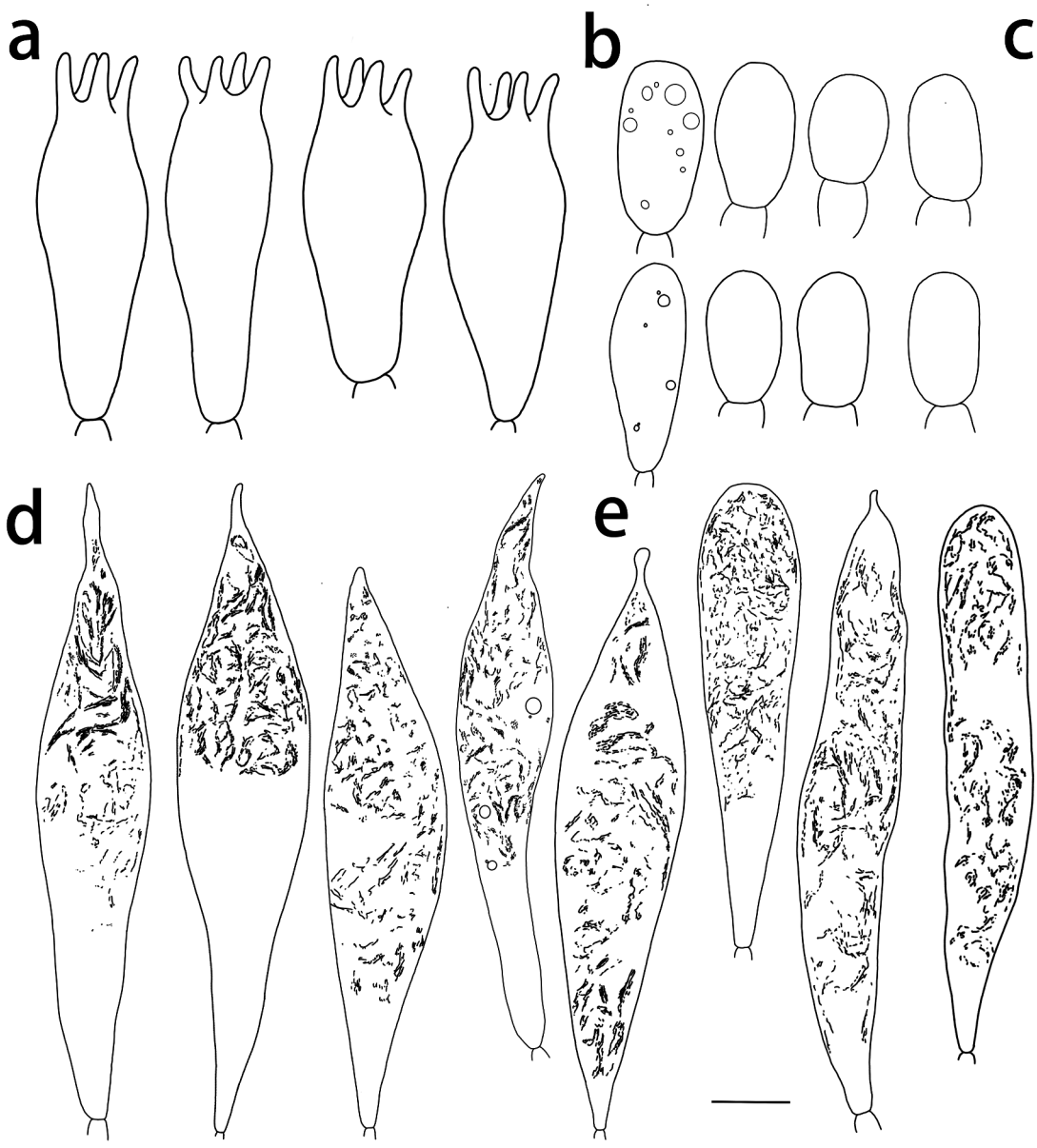

Figure 11. *Russula yadongensis* (HMAS287386, holotype), hymenium. (a) Basidia. (b) Basidiola. (c) Marginal cells on the lamella edges. (d) Hymenial cystidia near the lamella sides. (e) Hymenial cystidia on the lamella edges. Cystidia with contents as observed in Congo Red. Scale bar = 10 µm.

appeared close to the present species in multigene phylogeny but the former differs from newly proposed species in having adnate to notched, forked, or anastomosing lamellae with scattered lamellulae, larger spores [7–8.5(–9) × 6.5–8(–8.5) µm] (Bills 1989).

Russula yadongensis S.H. Wang, R.L. Zhao & B. Cao, sp. nov., Figures 3g–j, 4e–f, 11, 12, 13d

Fungal Names: FN571578.

Typification CHINA. Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, N 27°25′ E 88°56′, 26 July 2022, 3,024 m asl, *Mao-Qiang He*, *Bin Cao*, *ZRL20220204* (**holotype** HMAS287386). GenBank: OQ871498 (ITS), OQ875228 (nucLSU), OQ878267 (mtSSU), OQ933790 (*rpb2*), OQ948117 (*tef1*).

Etymology Refers to Yadong County, the locality of the type specimen.

Diagnosis Pileus medium-sized, light purple to purple, dark purplish red with brownish purple tints in the centre; lamellae with yellowish white to pale yellow colour; stipe 37–66 × 5–15 mm, cylindrical and slightly thick near the base; spores (6.0–)6.3–6.6–7.0(–7.2) ×

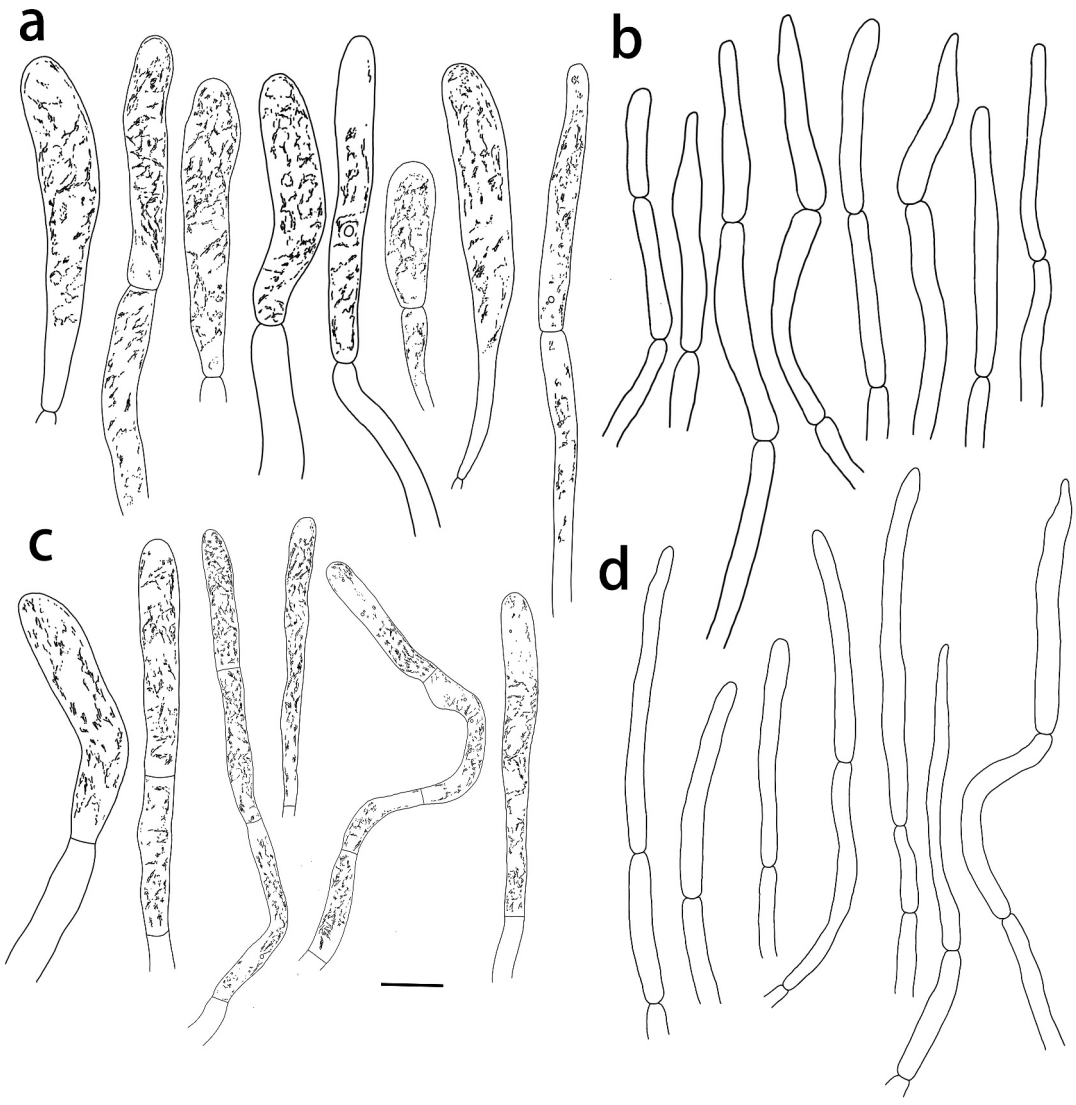

Figure 12. *Russula yadongensis* (HMAS287386, holotype), pileipellis. (a) Pileocystidia near the pileus centre. (b) Hyphal terminations near the pileus centre. (c) Pileocystidia near the pileus margin. (d) Hyphal terminations near the pileus margin. Cystidial contents as observed in Congo Red. Scale bar = 10 µm.

(4.5–)5.0–5.4–5.8(–6.2) µm, broadly ellipsoid, large; basidia (21–)22–24–26(–28) × (10–)10–11(–11) µm, clavate; hymenial cystidia (40–)35–41–46(–58) × (7–)7–8–9(–11) µm, mainly clavate or fusiform, apically acute; Hyphal terminations near the pileus margin occasionally narrow, thin-walled; terminal cells cylindrical, apically obtuse or slightly constricted; subterminal cells unbranched.

Pileus medium-sized, 32–46 mm diam., applanate with depressed centre; margin smooth or slightly striate; cuticle smooth and shiny, peeling to 1/3 of the radius, light purple (#CAB5B1) when young, purple (#996F7F) when mature, dark purplish red (#7B5E6A) with brownish purple tints in the centre. **Lamellae** 2–4 mm deep, adnate to free, dense, white (#D0D6E7) when young, becoming yellowish white (#D1DCD8) to pale yellow (#EBF6FA) when mature; lamellulae and furcations absent; edges concolorous and even. **Stipe** 37–66 × 5–15 mm, cylindrical and slightly thick near the base, white (#D0D6E7); medulla stuffed and becoming hollow when mature. **Context** 1–2 mm thick in a half of the pileus radius, white (#D0D6E7), yellowish white (#D1DCD8) to cream (#D7E0DF) when mature. **Spore print** not observed. **Spores** (6.0–)6.3–6.6–7.0(–7.2) × (4.5–)5.0–5.4–5.8(–6.2) µm, broadly ellipsoid, Q = (1.1–)1.15–1.23–1.3(–1.4); ornamentation of large, moderately distant [5–6(–7) in a 3 µm diam. circle] amyloid spines or

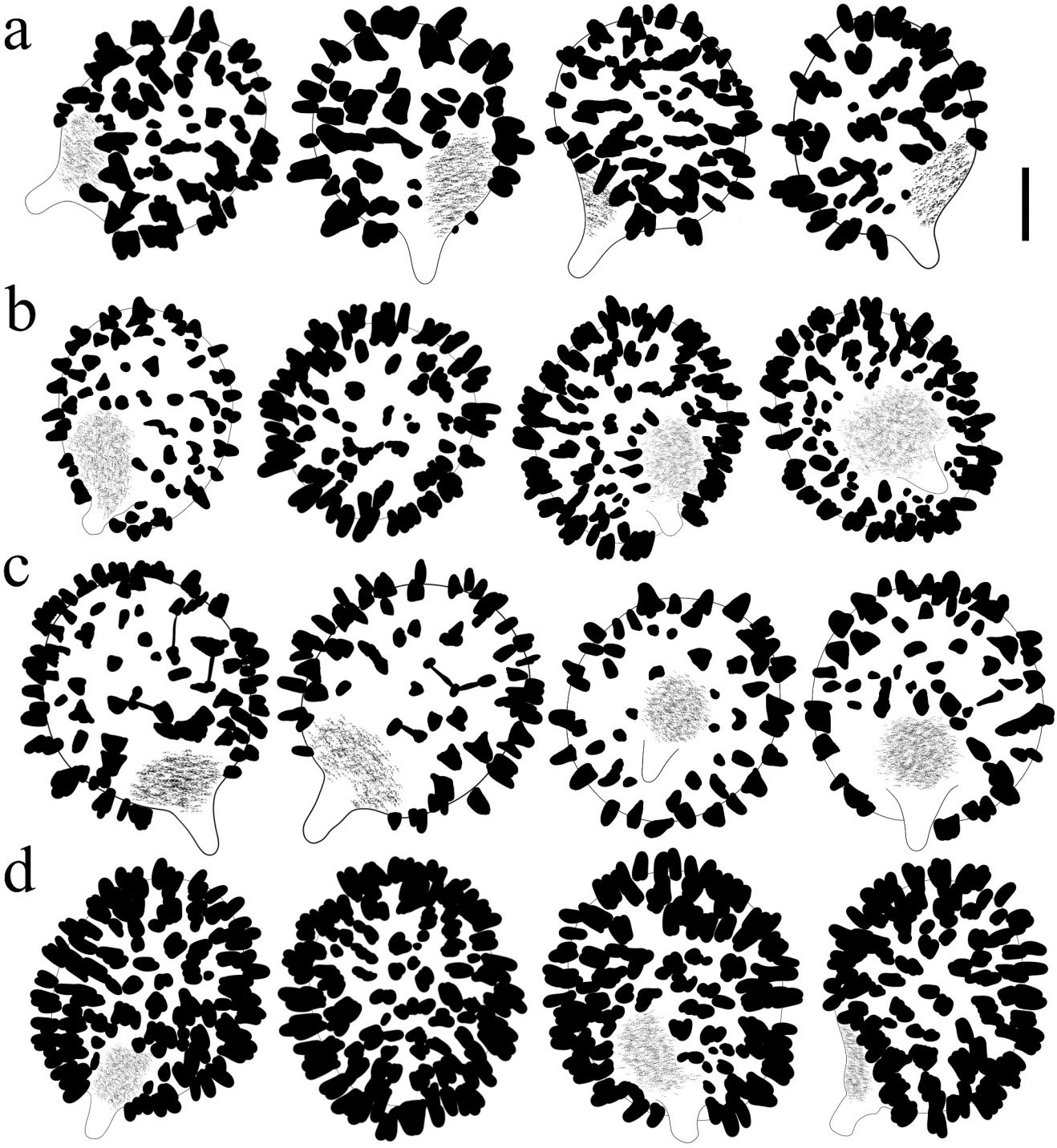

Figure 13. Spore drawings showing ornamentation in Melzer reagent. (a) *Russula paragraveolens* (HMAS281158, holotype). (b) *R. pseudograveolens* (HMAS287384, holotype). (c) *R. shigatseensis* (HMAS287389, holotype). (d) *R. yadongensis* (HMAS287386, holotype). Scale bar = 2 µm.

warts, which are (0.7–)0.9–1.2(–1.3) µm high, isolated or fused in pairs or short chains [0–1(–2) fusions in the circle]; line connections absent or dispersed; suprahilar spot large, amyloid. **Basidia** (21–)22–24–26(–28) × (10–)10–11(–11) µm, clavate, 4-spored; basidiola first cylindrical, then clavate, 7.2–9.1 µm wide. **Hymenial cystidia** dispersed to moderately numerous, 300–1,100/mm^2, (40–)35–41–46(–58) × (7–)7–8–9(–11) µm,

mainly clavate or fusiform, apically acute, mucronate with a 0–6 µm long appendage, originating in subhymenium, thin-walled; contents completely heteromorphous crystalline, turning pale yellow-brown or pale greyish brown in sulfovanillin; abundant near the lamellae edges, (30–)44–53–61(–58) × (5–)7–9–10 (–11) µm, similar to those on the sides. **Marginal cells** (9–)12–15–17(–18) × (6–)6–8–9(–10) µm, undifferentiated. **Pileipellis** orthochromatic in Cresyl blue, sharply delimited from the underlying context, 160–360 µm deep, with a well-defined, strongly gelatinised, 60–140 µm deep suprapellis composed of ascending to erect hyphal terminations; subpellis 100–220 µm deep, composed of horizontally oriented, dense, intricate and narrow hyphae. **Acid-resistant incrustations** absent. Hyphal terminations near the pileus margin occasionally narrow, thin-walled; terminal cells (26–)25–41–56 (–81) × (2–)2–3(–3) µm, cylindrical, apically obtuse or slightly constricted; subterminal cells usually equally long and wide, but often also shorter and wider, 1–2 µm wide. Hyphal terminations near the pileus centre similar, terminal cells even narrower, (25–)27–34–40(–45) × (1.2–)1.5–2.0–2.4(–2.6) µm; subterminal cells unbranched and embedded in intricate hyphae of the subpellis. **Pileocystidia** near the pileus margin very abundant, typically 1–2-celled, sometimes 2–3-celled, usually clavate, occasionally slightly flexuous, thin-walled, terminal cells variable in length, (31–)33–56–78(–103) × (3.5–)3.7–4.9–6.2(–7.8) µm, mostly subcylindrical or narrowly clavate, apically mainly obtuse, occasionally subacute, contents heteromorphous, usually dense and crystalline-granulose, turning grey-brown to black in sulfovanillin. Pileocystidia near the pileus centre slightly smaller; terminal cells (30–)33–44–55(–63) × (2.6–)3.7–4.6–5.6(–6.5) µm, mostly subclavate, cylindrical or fusiform, apically obtuse but occasionally also subacute to constricted. **Cystidioid hyphae** in subpellis and context dispersed, with heteromorphous granulose contents, oleiferous hyphae frequent in the lower part of subpellis and context.

Habit and habitat: Scattered in coniferous forests.

Other specimens examined CHINA. Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, N 27°22′ E 88°58′, 2,872 m asl, 26 July 2022, *Rui-Lin Zhao*, *Xin-Yu Zhu*, *Jia-Xin Li*, *ZRL20220152* (HMAS287387); Xizang Autonomous Region, Shigatse Municipality, Yadong County, Lower Yadong Township, Yanqinggang Village, N 27°25′ E 88°55′, 3,254 m asl, 27 July 2022, *Mao-Qiang He*, *Bin Cao*, *ZRL20220377* (HMAS287388).

Notes: Russula yadongensis belonging to subsect. *Laricinae* of sect. *Tenellae*, is represented by three specimens from the Shigatse region of Xizang, China in a well-supported clade (BS = 97%), and is phylogenetically related to *R. sichuanensis* G.J. Li & H.A. Wen and *R. vinosobrunneola* G.J. Li & R.L. Zhao (Figure 1). However, there are clear morphological differences, with *R. yadongensis* having smaller spores [(6.0–)6.3–6.6–7.0(–7.2) × (4.5–)5.0–5.4–5.8 (–6.2) µm], a deeper purple pileus colour. Compared with *R. vinosobrunneola and R. sichuanensis*, the spores of *R. yadongensis* have spore ornamentations of more or less isolated spines (Li et al. 2018a). *Russula yadongensis* is also closely related to *R. nauseosa* (Pers.) Fr. and *R. laricina* Fr. in the multigene phylogeny (Figure 2). Compared to the closely related species *R. nauseosa*, the spores of *R. yadongensis* are smaller [spores of *R. nauseosa* 7,8–10 × 6,6–7,8 µm] and the hymenial cystidia are slightly smaller [hymenial cystidia of *R. nauseosa* 45–80 × 9–13 µm] (Sarnari and Redeuilh 2005). Compared to the closely related species *R. laricina*, the spores of *R. yadongensis* are smaller [spores of *R. laricina* 6,5–9,5 × 6–8 µm] and have a deeper purple pileus colour (Sarnari and Redeuilh 2005).

4. Discussion

The ITS phylogenetic analyses are most commonly used for the practical identification of *Russula* species (Li et al. 2019). However, it is often difficult to distinguish between closely related species based on ITS phylogenetic analysis alone. Multi-locus phylogenetic analyses have become the preferred technique for revealing relationships within the *Russula* genus in recent years (Li et al. 2019; Buyck et al. 2020). In this study, the topological structure of the ITS and multi-locus phylogenetic analyses are basically similar, but the Bayesian posterior probability values and maximum likelihood bootstrap were higher in the multi-locus phylogenetic analyses.

In this study, four new species belong to three different subsections within the crown clade, namely subsect. *Laricinae* (*R. yadongensis*), subsect. *Lepidinae* (*R. shigatseensis*), subsect.

Xerampelinae (*R. paragraveolens* and *R. pseudograveolens*). In China, some new species of these three subsections have previously been reported, such as *R. cessans*, *R. faginea*, *R. laricina*, *R. lepida*, *R. nauseosa*, *R. nuoljae*, *R. pascua*, *R. sichuanensis*, *R. vinosobrunneola*, *R. xerampelina* (Li 2014; Li et al. 2018b; Cao et al. 2019).

Species of subsect. *Laricinae* generally have a purple pileus, white stipe, and a yellow spore print, and mainly grow in coniferous forests (Romagnesi 1967). Many species of this subsection have previously been reported, namely *R. adwanitekae* A. Ghosh, K. Das & Buyck, *R. cessans* A. Pearson, *R. curtipes* F.H. Møller & Jul. Schäff., *R. laricina*, *R. nauseosa*, *R. obscurozelleri* Bazzic., D. Mill. & Buyck, *R. pseudotsugarum* Bazzic., D. Mill. & Buyck, *R. sichuanensis*, *R. vidalii* Trappe & T.F. Elliott, *R. vinaceodora* (Calonge & J.M. Vidal) Trappe & T.F. Elliott, *R. vinosobrunneola*, *R. zelleri* Burl (Ghosh et al. 2021). In this study, ITS phylogenetic analyses showed significant support (BS = 93%) for *R. yadongensis* with other species in this subsection, while morphological and phylogenetic results could distinguish this species well from other known species within this subsection.

Subsection *Lepidinae* is characterised by a velvety pileus surface, hard context, the cystidia of the pileus, and hymenium not reacting to sulfovanillin, mild taste (Sarnari and Redeuilh 2005). Many species of subsect. *Lepidinae* have previously been reported, namely *R. amarissima* Romagn. & E.-J. Gilbert, *R. Baniyakundensis* A. Ghosh, K. Das & D. Chakr., *R. flavisiccans*, *R. indoarmeniaca* A. Ghosh, K. Das & R.P. Bhatt, *R. lepida*, *R. ochroleucoides* Kauffman (Kauffman 1917; Bills 1989; Sarnari and Redeuilh 2005; Ghosh et al. 2016, 2021). In this study, ITS phylogenetic analyses showed significant support (BS = 100%) for *R. shigatseensis* with other species in this subsection, while morphological and phylogenetic results could distinguish this species well from other known species within this subsection.

Species of the subsect. *Xerampelinae* can be easily recognised in field by following characters: tardily fishy context smell, mild taste, context slowly turning brownish when bruised or old, lamellae turning red in aniline, absence of acid-resistant incrustation on pileocystidia which turn grey in sulphovanillin (Adamczík and Marhold 2000; Adamcik 2002, 2003; Adamčík 2004; Adamčik and Knudsen 2004; Sarnari and Redeuilh 2005; Buyck and Adamcík 2013; Adamčík et al. 2016). Many species in this subsection have previously been reported, such as *R. faginea* Romagn., *R. favrei* M.M. Moser, *R. clavipes* Velen., *R. graveolens*, *R. nuoljae* Kühner, *R. pascua* (F.H. Møller & Jul. Schäff.) Kühner, *R. subrubens* (J.E. Lange) Bon, and *R. xerampelina* (Schaeff.) Fr (Adamčík et al. 2016). In this study, ITS phylogenetic analyses showed significant support (BS = 97%) for *R. paragraveolens* and *R. pseudograveolens* with other species in this subsection, while morphological and phylogenetic results could distinguish this species well from other known species within this subsection.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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