



Short communication

Russula rubrosquamosa (Russulaceae, Russulales), a new species from southwestern China

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ABSTRACT

Russula rubrosquamosa (Russulaceae, Russulales) is described as a novel species from Yunnan Province, southwestern China. It is morphologically recognised by a small basidiocarp with orange-yellow to orange-red scales on the pileus and stipe, white lamellae, orange-red to bright red basal mycelia, subglobose to broadly ellipsoid basidiospores with dense warts and short or long ridges. Phylogenetically analyses of DNA sequences from part of the 28S gene combined with the nuclear rDNA internal transcribed spacer (ITS) region also confirm that *R. rubrosquamosa* forms an independent lineage within *Russula* subgenus *Heterophyllidia* section *Ingratae*. A comprehensive description, color photographs of fresh basidiomata, line-drawings of microstructures and comparisons with morphologically similar species are provided in this paper.

Keywords: *Heterophyllidia*, molecular phylogeny, morphology, new taxon, taxonomy

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1. Introduction

Russula Pers. is one of the largest ectomycorrhizal genus in *Russulaceae*, speculated more than 2000 species worldwide (Adamčík et al., 2019; Buyck et al., 2018). Members of *Russula* are associated with multitudinous host plants, including broadleaved and conifer woods (Das et al., 2017; Dutta et al., 2015), playing an irreplaceable role in ecosystems as plant-root symbionts (Looney et al., 2018). Except for ecological values, *Russula* species attracted continuous attentions on account of their edible and pharmaceutical potentialities (Clericuzio et al., 2012; Panda et al., 2021; Wang et al., 2009). The latest molecular phylogenetic studies of multi-locus genes analyses demonstrating the genus *Russula* containing nine subgenera (Buyck et al., 2018, 2020, 2023) and *Russula* sect. *Ingratae* (Quél.) Maire was placed in subg. *Heterophyllidia*.

The section *Ingratae* is mainly characterised by a pileus with pale yellowish brown, yellowish brown, greyish brown to dark brown tints, a margin with tuberculate striation, lamellae equal or occasionally mixed with lamellulae or forked, taste mild to acrid, odour often fetid, spores print white to pale ochre, basidiospores inamyloid to partly amyloid in suprahilar spot, short-celled and branched hyphal terminations in the pileipellis (Singer, 1986; Romagnesi, 1987; Sarnari, 1998). As a nonnegligible member of sub-

gen. *Heterophyllidia*, species diversity of sect. *Ingratae* is high. So far, more than 60 species were accepted worldwide (Adamčík et al., 2019; Buyck et al., 2022; Das et al., 2010, 2013; Ghosh et al., 2020; Jabeen et al., 2017; Lee et al., 2017; Razaq et al., 2014; Razaq et al., 2023), of them 24 species distribute in China (Chen et al., 2021; Han et al., 2022, 2023; Li, 2014, 2015, 2021; Song et al., 2007, 2018, 2020; Wen & Ying, 2001; Yuan et al., 2019). With persistent field survey, more new species of the section will be found. During field investigation in Yunnan Province, a hot spot of biodiversity of southwestern China, some collections were found possessing characters distinct from those described species. These specimens were examined through morphological and molecular phylogenetic analyses, and proved to be a new species of *R.* subg. *Heterophyllidia* sect. *Ingratae* Quél. Therefore, a detailed description of the new taxon is presented here.

2. Materials and methods

2.1 Morphological studies

Fresh specimens were photographed in the field, a collection number was given for each specimen, and a detailed measurement and record of macroscopic characteristics of basidiocarp was also made. Specimens were dried at 50–60 °C and deposited in the Mycological Herbarium of Kunming Medical University (MHKMU), Kunming City, Yunnan Province, China. Color codes are from Kornerup & Wanscher (1981). The descriptive terminology and

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templates of micromorphological characters referred Adamčík et al. (2019). Sections of the pileipellis on the pileus were cut perpendicularly and taken between the center and margin of the pileus; sections of the stipitipellis on the stipe were taken from the middle part along the longitudinal axis of the stipe. Basidiospores were observed and measured in Melzer's reagent in side view, excluding apiculus and ornamentation; the structure and ornamentation of basidiospores were illustrated using a ZEISS Imager M2 (Carl Zeiss AG, Germany); estimates of basidiospore ornamentation density from scanning electron micrographs followed Adamčík & Marhold (2000). Hymenial cystidium density estimates followed Buyck (1991). The ortho- or metachromatic reactions of pileipellis were examined in Cresyl Blue as explained in Buyck (1989). Color changes of cystidia contents were tested in Sulfovanillin (SV) (Caboň et al., 2017). Microscopic observations and measurements were obtained from rehydrated materials, mounted in 5% KOH, and stained with 1% Congo Red solution with an optical light microscope (CX23, Olympus, Tokyo, Japan). All the microscopic structures were drawn free-hand. The number of measured basidiospores is expressed as n/m/p, where "n" represents the total number of basidiospores measured from "m" basidiomata of "p" collections. Dimensions of basidiospores are given as (a–)b–c(–d), where the range "b–c" represents a minimum of 90% of the measured values (5 to 95%), and extreme values (a and d), whenever present (a < 5%, d > 95%), are in parentheses, "e" refers to the average length/width of basidiospores. "Q" refers to the length/width ratio of basidiospores; "Qm" refers to the average "Q" of basidiospores and is given with standard deviation.

2.2 Molecular procedures

Total genomic DNA was extracted from 10–20 mg of dried basidioma tissue using a modified cetyltrimethylammonium bromide method (Doyle & Doyle, 1987). Primer pairs used for amplifying the nuclear ribosomal large subunit RNA (28S) were LROR/LR5 (James et al., 2006; Vilgalys & Hester, 1990), ITS5/ITS4 (White et al., 1990) for the nuclear rDNA region including the internal transcribed spacer1 and 2, along with the 5.8S rDNA (ITS). PCR reaction conditions followed the protocols of Tang et al. (2017). Amplified PCR products were checked in 1% (w/v) agarose gels, and positive reactions with a bright single band were purified and directly sequenced using an ABI 3730 DNA Analyzer (Sangon, Shanghai, China) with the same primers used for PCR amplification. Forward or reverse sequences were compiled with BioEdit v7.0.9 (Hall, 1999). Assembled sequences were deposited in GenBank (Table 1).

2.3 Dataset assembly

Seven DNA sequences (four of 28S and three of ITS) from four collections were newly generated with their GenBank accession numbers were deposited in GenBank (Table 1). For the concatenated dataset, the 28S and ITS sequences from new collections were aligned with selected sequences of *R. sect. Ingratae* from previous studies and GenBank (Table 1). *Russula dinghuensis* J.B. Zhang & L.H. Qiu (Zhang et al., 2017), *R. lotus* Fang Li (Li & Deng, 2018), and *R. subpallidirosea* J.B. Zhang & L.H. Qiu (Zhang et al., 2017) were chosen as outgroups based on the phylogeny in Chen et al. (2021). Sequences of 28S and ITS were aligned using MUSCLE (Edgar, 2004) respectively to test for phylogenetic conflict. Then sequences of the different genes were concatenated using Phyutility v2.2 for further analyses (Smith & Dunn, 2008).

2.4 Phylogenetic analyses

The combined nuclear data set (28S-ITS) was analyzed by using maximum likelihood (ML) and Bayesian inference (BI). ML tree generation and bootstrap analyses were performed with the program RAXML 7.2.6 (Stamatakis, 2006) running 1000 replicates combined with an ML search. Bayesian analysis with MrBayes 3.1 (Huelsenbeck & Ronquist, 2005) implementing the Markov Chain Monte Carlo (MCMC) technique and parameters predetermined with MrModeltest 2.3 (Nylander, 2004) was performed. For the two-gene combined data set of *Russula* subgenus *Heterophyllidia* section *Ingratae*, the best-fit likelihood models of 28S and ITS were GTR + I + G, HKY + I + G, respectively. Bayesian analysis was repeated for 7.2 million generations, and sampled every 100 generations. Trees sampled from the first 25% of the generations were discarded as burn-in; the average standard deviation of split frequencies was restricted to be below 0.01, and Bayesian posterior probabilities (PP) were then calculated for a majority consensus tree of the retained Bayesian trees.

3. Results

3.1 Molecular data

The two-locus data set (28S-ITS) consisted of 126 taxa and 1558 nucleotide sites. The alignment was submitted to TreeBASE (Accession 30469, <http://purl.org/phylo/treebase/phyloids/study/TB2:S30469>). The topologies of phylogenetic trees based on the combined data set generated from ML and BI analyses were identical, while statistical support for some branches showed slight differences. The phylogram with branch lengths generated from RAXML, including the support values, is shown in Fig. 1.

The molecular phylogenetic analyses showed that the collections numbered MHKMU M. Mu-532, MHKMU ZWH-810, MHKMU Jiang-433, MHKMU MJ-0009, respectively, grouped together with a high statistical support (BS = 100, PP = 1.00), forming an independent lineage within *R. sect. Ingratae* (Fig. 1).

3.2 Taxonomy

Russula rubrosquamosa L.P. Tang & S. Jiang, sp. nov. Figs. 2–4.
MycoBank no.: MB 849076.

Diagnosis: Basidiomata small-sized; differs from other species of *R. sect. Ingratae* in pileus and stipe covered with tiny, orange-yellow to orange-red squamules; pileus margin with tuberculate striation and orange-red to bright red basal mycelia; subglobose to broadly ellipsoid basidiospores with warts and ridges up to 0.9 µm high and thick pileipellis which is distinctively divided into two layers.

Holotype: CHINA, Yunnan Province, Qujing city, Shizong County, Junzi Shan, elev. 2913 m, 24 Jul 2020, MHKMU M. Mu-532.

Gene sequences ex-holotype: OR088574 (28S), OR088570 (ITS).

Etymology: Latin "*rubrosquamosa*" meaning orange-red, refer to the pileal and stipitate surface of the new species covered with orange-red squamules.

Description: Basidiomata small-sized. Pileus 3–4 cm diam, sub-hemispherical when young, then applanate, center slightly depressed when matured; cuticle slightly viscid when wet, peeling readily, sometimes cracked; margin slightly incurved; surface dry, white (2A1), covered with minute, orange-yellow (6A7) to orange-red (7A8) squamules; margin sulcate-striate when old; context 2–3 mm thick in the center of the pileus, white (1A2), un-

Table 1. Taxa, vouchers, locations, and GenBank accession numbers of DNA sequences used in this study. The new sequences are in bold.

Taxon	Voucher	Locality	GenBank accession Nos.		Reference
			ITS	28S	
<i>Russula ahmadii</i>	LAH 35004	Pakistan	KT834638	KX911834	Jabeen et al. (2017)
<i>R. ahmadii</i>	LAH 18081013	Pakistan	KU535609	—	Jabeen et al. (2017)
<i>R. aff. amoenolens</i>	HMJAU37318	Heilongjiang, NE China	KY357332	—	Liu et al. (2017)
<i>R. amerorecondita</i>	F (PGA17-017)	USA	MN130066	—	Adamčík et al. (2019)
<i>R. amerorecondita</i>	SH120828	USA	MN130067	—	Adamčík et al. (2019)
<i>R. amoenolens</i>	46372 (AH)	Spain	MK105626	MK105707	Vidal et al. (2019)
<i>R. amoenolens</i>	TUB nl27.9.95.6	Germany	AF418615	AF325295	Eberhardt (2002)
<i>R. amoenolens</i>	MICH12838	France	KF245510	—	Unpublished
<i>R. amoenolens</i>	46371 (AH)	Spain	MK105625	—	Vidal et al. (2019)
<i>R. arunii</i>	CUH:AM270	India	KY450661	KY946733	Crous et al. (2017)
<i>R. arunii</i>	CUH:AM261	India	KR872619	KY946732	Crous et al. (2017)
<i>R. benghalensis</i>	CUH AM654	India	MK414583	—	Yuan et al. (2020)
<i>R. benghalensis</i>	CUH AM655	India	MK414584	—	Yuan et al. (2020)
<i>R. catillus</i>	SFC20120725-52	Korea	KX574685	—	Lee et al. (2017)
<i>R. catillus</i>	SFC20120827-01	Korea	KX574686	—	Lee et al. (2017)
<i>R. catillus</i>	SFC20120919-35	Korea	KX574688	—	Lee et al. (2017)
<i>R. catillus</i>	LHJ150915-19	Guangdong, S China	MK860690	—	Unpublished
<i>R. cerolens</i>	OSC76727	USA	KF245505	—	Unpublished
<i>R. cerolens</i>	F36	USA	JN681168	—	Unpublished
<i>R. cf. subfoetens</i>	JMV941022-7 (BCN)	Spain	MK105692	MK105737	Vidal et al. (2019)
<i>R. clavulus</i>	RITF3300	Guizhou, SW China	MN317302	MN325079	Chen et al. (2021)
<i>R. clavulus</i>	RITF3216	Guizhou, SW China	MN317303	MN325080	Chen et al. (2021)
<i>R. clavulus</i>	RITF3204	Yunnan, SW China	MN317304	MN325081	Chen et al. (2021)
<i>R. clavulus</i>	RITF3334	Yunnan, SW China	MN317301	MN325078	Chen et al. (2021)
<i>R. compacta</i>	HFJAU0301	Jiangxi, SE China	MN258682	—	Unpublished
<i>R. echidna</i>	HO 593336	Australia	MN130079	—	Adamčík et al. (2019)
<i>R. echidna</i>	HO 593337	Australia	MN130080	—	Adamčík et al. (2019)
<i>R. fluvialis</i>	KUO (JR8666)	Finland	MN130084	MN130125	Adamčík et al. (2019)
<i>R. fluvialis</i>	KUO (JR8313)	Finland	MN130085	MN130126	Adamčík et al. (2019)
<i>R. foetens</i>	HMJAU 32234	Heilongjiang, NE China	KX095018	—	Unpublished
<i>R. foetens</i>	TUB hue124	Germany	AF418613	AF325299	Eberhardt (2002)
<i>R. foetens</i>	GENT FH-12-277	Germany	KT934016	KT933877	Looney et al. (2016)
<i>R. foetentoides</i>	LAH 04081023	Pakistan	HE647707	—	Razaq et al. (2014)
<i>R. foetentoides</i>	LAH 13081034	Pakistan	HE647708	—	Razaq et al. (2014)
<i>R. foetentula</i>	156	USA	KJ834623	—	Melera et al. (2017)
<i>R. foetentula</i>	128	Switzerland	KJ834574	—	Melera et al. (2017)
<i>R. fragrantissima</i>	98	Italy	KJ530751	—	Melera et al. (2017)
<i>R. fragrantissima</i>	108	Italy	KJ834596	—	Melera et al. (2017)
<i>R. garyensis</i>	F (PGA17-008)	USA	MN130088	—	Adamčík et al. (2019)
<i>R. garyensis</i>	F (PGA15-910)	USA	MN130089	—	Adamčík et al. (2019)
<i>R. gelatinosa</i>	K15052626	Guangdong, S China	MH168575	—	Song et al. (2018)
<i>R. gelatinosa</i>	K16053119	Guangdong, S China	MH168574	—	Song et al. (2018)
<i>R. granulata</i>	PC BB2004-226	USA	EU598192	—	Unpublished
<i>R. granulata</i>	PC BB2004-225	USA	EU598190	—	Unpublished
<i>R. granulata</i>	HMAS252604	Jilin, NE China	KF850414	—	Li et al. (2021)
<i>R. granulata</i>	BPL272	USA	KT933971	KT933832	Looney et al. (2016)
<i>R. grata</i>	HMJAU38008	Heilongjiang, NE China	KY681444	—	Liu et al. (2017)
<i>R. hainanensis</i>	N.K. Zeng4888 (FHMU4860)	Hainan, S China	—	OM280996	Han et al. (2022)
<i>R. hainanensis</i>	N.K. Zeng4899 (FHMU4855)	Hainan, S China	OM280999	OM280997	Han et al. (2022)
<i>R. hortensis</i>	IB 1997/0787	Italy	HG798528	—	Unpublished
<i>R. illota</i>	MICH73719	France	KF245509	—	Unpublished
<i>R. illota</i>	UE26.07.2002-3	Sweden	DQ422024	—	Eberhardt (2002)
<i>R. inamoena</i>	107	Italy	KJ834597	—	Melera et al. (2017)
<i>R. inamoena</i>	109	Italy	KJ834595	—	Melera et al. (2017)
<i>R. indocatillus</i>	HGAS-MF009917	Guizhou, SW China	MN649191	—	Li et al. (2021)
<i>R. indocatillus</i>	HGAS-MF009903	Guizhou, SW China	MN649192	—	Li et al. (2021)
<i>R. indocatillus</i>	AG 17-1571	India	MN581483	—	Ghosh et al. (2020)
<i>R. indocatillus</i>	AG 18-1653	India	MN581165	—	Ghosh et al. (2020)
<i>R. insignis</i>	1223IS85	Europe	AY061700	—	Miller & Buyck (2002)
<i>R. insignis</i>	HMAS267740	Heilongjiang, NE China	KF850404	—	Li et al. (2021)
<i>R. laurocerasi</i>	FH12178	Germany	KT933988	KT933849	Looney et al. (2016)
<i>R. laurocerasi</i>	TUB nl1348	Germany	AF418614	—	Eberhardt (2002)
<i>R. laurocerasi</i>	E00290534	UK	KF245532	—	Unpublished
<i>R. livescens</i>	F0177	China	GU371295	—	Xie et al. (2010)
<i>R. lotus</i>	HKAS76139	Guangdong, S China	MG214687	MG214694	Li & Deng (2018)
<i>R. lotus</i>	HKAS79209	Guangdong, S China	MG214688	MG214695	Li & Deng (2018)
<i>R. mistiformis</i>	JC170305	Spain	MK105677	—	Vidal et al. (2019)

Taxon	Voucher	Locality	GenBank accession Nos.		Reference
			ITS	28S	
<i>R. mistiformis</i>	AMC H-69	Spain	MK105680	—	Vidal et al. (2019)
<i>R. multilamellula</i>	LHJ14092423	Guizhou, SW China	MT791347	MT793120	Chen et al. (2021)
<i>R. multilamellula</i>	wuxingliang03	Guizhou, SW China	MT791348	MT793121	Chen et al. (2021)
<i>R. mutabilis</i>	DPL10654	USA	KF810137	—	Looney (2014)
<i>R. mutabilis</i>	BHI-F384a	USA	MF161239	—	Haelewaters et al. (2018)
<i>R. obscuricolor</i>	KD 16-30	India	MF805816	—	Das et al. (2017)
<i>R. obscuricolor</i>	KD 16-22	India	MF805817	—	Das et al. (2017)
<i>R. ombrophila</i>	86	Spain	KF971694	—	Melera et al. (2017)
<i>R. pakistannica</i>	SB138	Pakistan	HG796943	—	Unpublished
<i>R. pectinata</i>	Buyck 2304	Europe	AY061706	—	Miller & Buyck (2002)
<i>R. pectinata</i>	2010BT02	Germany	KF318081	—	Melera et al. (2017)
<i>R. pectinata</i>	2010BT48	Germany	KF318082	—	Melera et al. (2017)
<i>R. pectinatoides</i>	MICH52692	USA	KF245518	—	Unpublished
<i>R. pectinatoides</i>	HMAS251202	Yunnan, SW China	JX425405	—	Li et al. (2021)
<i>R. pectinatoides</i>	NYS2303.1	USA	KU640189	—	Melera et al. (2017)
<i>R. pectinatoides</i>	BPL276	USA	KT933975	KT933836	Looney et al. (2016)
<i>R. pectinatoides</i>	UPS AT2001049	Sweden	DQ422026	—	Eberhardt (2002)
<i>R. pila</i>	JMV800654 (BCN)	Spain	MK105691	MK105736	Vidal et al. (2019)
<i>R. pila</i>	MA-Fungi 30667	Spain	AF230893	—	Calonge & Martin (2000)
<i>R. pilosella</i>	BRI-H5974	Australia	EU019941	—	Lebel & Tonkin (2007)
<i>R. pseudocatillus</i>	K16042406	Guangdong, S China	MK049974	—	Yuan et al. (2019)
<i>R. pseudocatillus</i>	K15060706	Guangdong, S China	MK049975	—	Yuan et al. (2019)
<i>R. pseudopectinatoides</i>	HMAS265020	Xizang, SW China	KM269079	—	Li et al. (2015)
<i>R. pseudopectinatoides</i>	HMAS251523	Xizang, SW China	KM269077	—	Li et al. (2015)
<i>R. pseudopectinatoides</i>	RITF1353	China	MK860689	—	Song et al. (2020)
<i>R. pulverulenta</i>	4-1144S79	USA	AY061736	—	Miller & Buyck (2002)
<i>R. pulverulenta</i>	PC BB2004-245	USA	EU598186	—	Unpublished
<i>R. punctipes</i>	K17052318	Guangdong, S China	MH168576	—	Song et al. (2018)
<i>R. punctipes</i>	K16051001	Guangdong, S China	MH168577	—	Song et al. (2018)
<i>R. putida</i>	IB 1997/0791	Italy	HG798527	HG798526	Unpublished
<i>R. recondita</i>	92	Switzerland	KJ530750	—	Melera et al. (2017)
<i>R. rubrosquamosa</i>	MHKMU M. Mu-532	Yunnan, SW China	OR088570	OR088574	This study
<i>R. rubrosquamosa</i>	MHKMU S. Jiang-433	Yunnan, SW China	OR088572	OR088576	This study
<i>R. rubrosquamosa</i>	MHKMU W.H. Zhang-810	Yunnan, SW China	OR088571	OR088575	This study
<i>R. rubrosquamosa</i>	MHKMU J. Ma-0009	Yunnan, SW China	—	OR088577	This study
<i>R. rufobasalis</i>	H17052204	Guangdong, S China	MH168570	—	Song et al. (2018)
<i>R. rufobasalis</i>	H15060622	Guangdong, S China	MH168567	—	Song et al. (2018)
<i>R. senecis</i>	CUH AM102	India	KP142981	—	Khatua et al. (2015)
<i>R. senecis</i>	SFC20110921-18	Korea	KX574698	—	Lee et al. (2017)
<i>Russula</i> sp.	LHJ170913-01	Guangdong, S China	MK860691	MK860694	Song et al. (2020)
<i>Russula</i> sp.	89-1A	Yunnan, SW China	JQ396513	—	Unpublished
<i>Russula</i> sp.	SC_ITS_113	Germany	GQ219916	—	Christ et al. (2011)
<i>Russula</i> sp. 7	FH12036	Thailand	MN130075	—	Adamčík et al. (2019)
<i>R. straminella</i>	HGAS-MF009920	Guizhou, SW China	MN649194	—	Li et al. (2021)
<i>R. straminella</i>	HGAS-MF009922	Guizhou, SW China	MN649195	—	Li et al. (2021)
<i>R. straminella</i>	HGAS-MF009925	Guizhou, SW China	MN649189	—	Li et al. (2021)
<i>R. subfoetens</i>	HMJAU 38006	Heilongjiang, NE China	KY681430	—	Liu et al. (2017)
<i>R. subpectinatoides</i>	HBAU15023	Jiangsu, E China	MW041163	—	Li et al. (2021)
<i>R. subpectinatoides</i>	HBAU15024	Jiangsu, E China	MW041164	—	Li et al. (2021)
<i>R. subpectinatoides</i>	HBAU15025	Jiangsu, E China	MW041165	—	Li et al. (2021)
<i>R. subpectinatoides</i>	HBAU15026	Jiangsu, E China	MW041166	—	Li et al. (2021)
<i>R. subpunctipes</i>	RITF2616	Guangdong, S China	MK860692	MK860695	Song et al. (2020)
<i>R. subpunctipes</i>	RITF2617	Guangdong, S China	MK860693	MK860696	Song et al. (2020)
<i>R. succinea</i>	HGAS-MF 009909	Guizhou, SW China	MN649196	—	Li et al. (2021)
<i>R. succinea</i>	HGAS-MF 009904	Guizhou, SW China	MN649188	—	Li et al. (2021)
<i>R. succinea</i>	HGAS-MF 009906	Guizhou, SW China	MN649198	—	Li et al. (2021)
<i>R. succinea</i>	HGAS-MF 009915	Guizhou, SW China	MN649190	—	Li et al. (2021)
<i>R. ventricosipes</i>	PC 0142480	USA	KY800364	—	Buyck et al. (2017)
<i>R. ventricosipes</i>	BHI-F397a	USA	MF161245	—	Haelewaters et al. (2018)
<i>R. vinaceocuticulata</i>	PDD 64246	New Zealand	GU222258	—	Unpublished

Note: E = East, NE = Northeast, S = South, SE = Southeast, SW = Southwest.

changing in color when injured. Lamellae 3–4 mm in width, adnate, edge even, relatively dense, about 100–120 pieces per fruit-body, white (1A1), unchanging in color when injured; lamellulae

occasional to absent. Stipe 2.5–3.6 cm long, 0.6–1 cm diam, central, subcylindrical to cylindrical, usually slightly enlarged at base when mature, annulus absent; surface dry, white (1A1), densely covered



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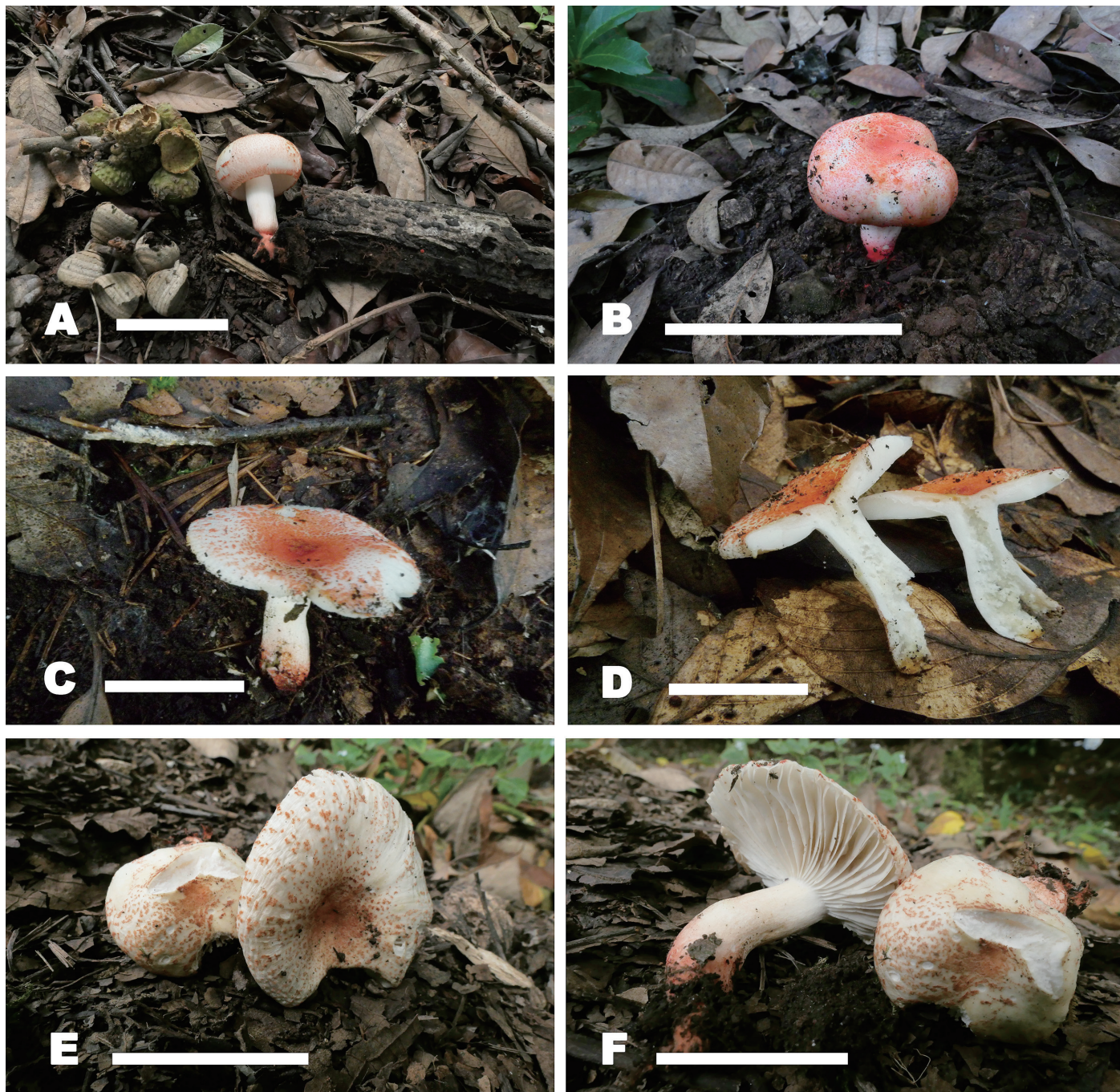


Fig. 2 – Basidiomata of *Russula rubrosquamosa*. (A: MHKMU W.H. Zhang-810; B: MHKMU S. Jiang-433; C, D: MHKMU J. Ma-0009; E, F: M. Mu-532, holotype). Bars: 1 cm. Photos by M. Mu, J. Ma, S. Jiang and W.H. Zhang.

with tiny, orange-yellow (6A6), orange-red (7A8) to bright red (11A7) squamules; context soft to hollow, white, unchanging in color when injured. Basal mycelium orange-red (7A5) to bright red (11A7). Odor not distinctive. Spore print not obtained.

Basidiospores [60/3/2] 7–8–9 × (5–)5.5–6.2–7 μm, $Q = 1.14$ –1.28–1.41(–1.5), $Q_m = 1.28 \pm 0.08$, subglobose to broadly ellipsoid; ornamentation of relatively small, dense to very dense [(8–)10–12 (–15) in a 3 μm diam. circle] amyloid warts measuring 0.3–0.7 μm in height, isolated or frequently fused in short to long chains or ridges (0–4 fusions in the circle), connected by occasional, fine line connections (0–3 in the circle), ridges up to 0.9 μm high, not forming a reticulum; suprahilar spot inamyloid and indistinct. Basidia

(29–)33–44–58(–60) × (9–)10–12.5–15(–16) μm, subclavate to clavate, hyaline in KOH, thin- to slightly thick-walled (up to 0.5 μm), 4-spored; sterigmata 3–8 μm long, straight to slightly flexuous. Pleurocystidia moderately numerous, ca. 900/mm², (20–)43–55.5–66 (–74) × (6–)8.5–10–12(–14) μm, subclavate to subfusiform, apically often acute, sometimes mucronate or moniliform, occasionally with 2–4 μm long appendage, thin-walled; contents abundant granulose, yellowish in Congo Red, turning to brownish black in SV. Cheilocystidia are similar to but narrower than pleurocystidia, moderately numerous, ca. 800/mm², (22–)34–53–70(–75) × (4–)6–9–12(–14.5) μm, narrow clavate to subfusiform, apex obtuse or mucronate, sometimes moniliform, usually with 2–13 μm long

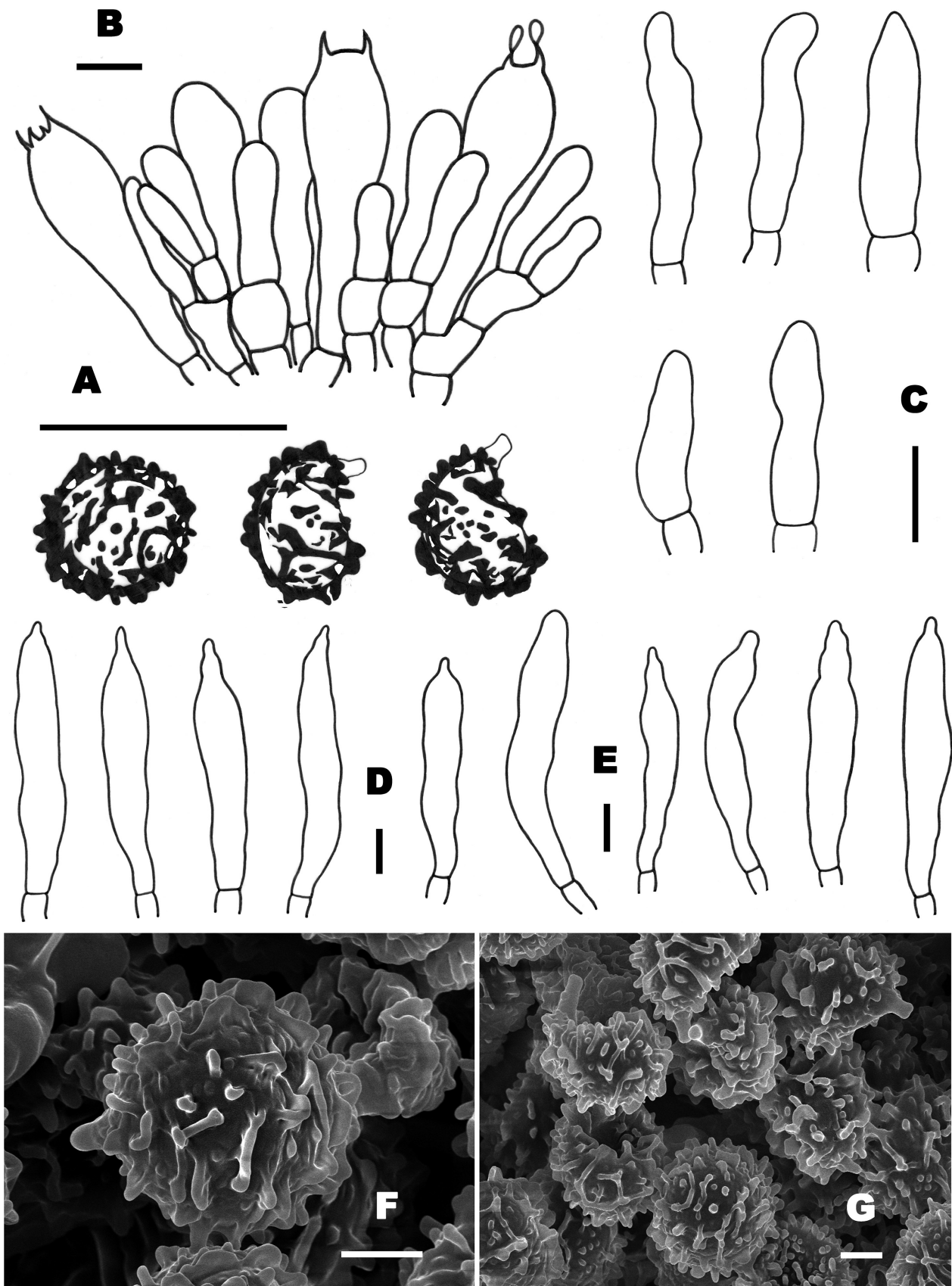


Fig. 3 – Microscopic features of *Russula rubrosquamosa* (MHKMU M. Mu-532, holotype). A: Basidiospores. B: Basidia and basidioles. C: Marginal cells. D: Pleurocystidia. E: Cheilocystidia. F, G: Scanning electron microscopy (SEM) photographs of basidiospores. Bars: A–E 2 μ m ; F, G 10 μ m. Drawings by S. Jiang.

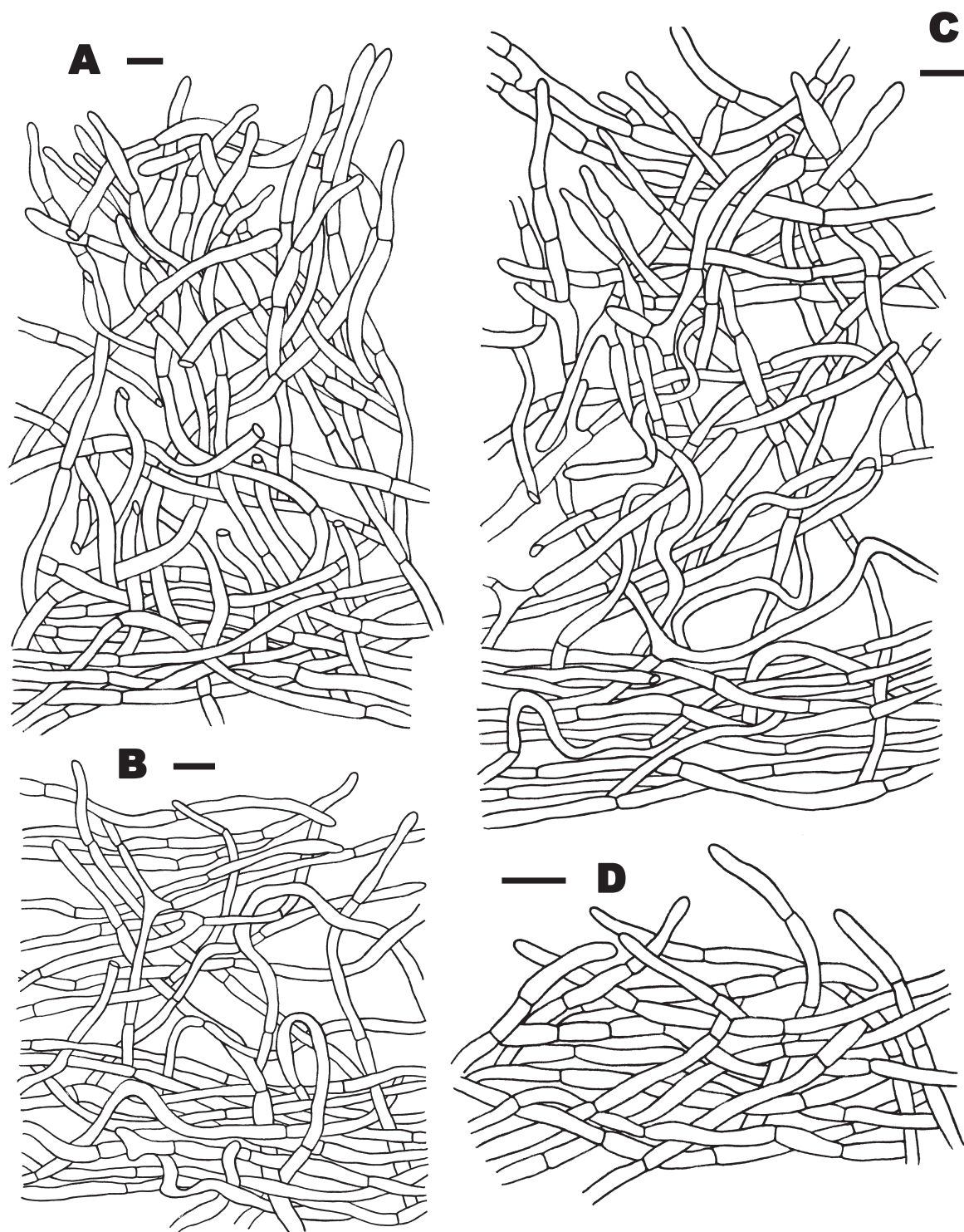


Fig. 4 – Microscopic features of *Russula rubrosquamosa* (MHKMU M. Mu-532, holotype). A: Pileipellis at pileus center. B: Pileipellis at middle part between center and margin of pileus. C: Pileipellis at pileus margin. D: Stipitipellis. Bars: 10 μ m. Drawings by S. Jiang.

appendage, thin-walled; contents granulose, yellowish in Congo Red, turning to yellowish brown in SV. Lamellae edges fertile. Marginal cells (13–)18–22–29(–32) $\times$ (4–)5–7–9(–11) μ m, narrowly clavate to subcylindrical, usually flexuous, thin-walled. Lamellar trama mainly composed of sphaerocytes measuring up to 56 μ m in diam, hyaline in KOH, thin-walled. Pileipellis orthochromatic in Cresyl blue, not sharply delimited from the underlying context, a trichoderm 150–790 μ m thick, two-layered, composed of suprapel-

lis (100–150 μ m thick) and subpellis (200–750 μ m thick); Suprapellis composed of hyphae 3–6.5 μ m in diam, often branched and interwoven, hyaline to pale yellow in KOH, thin- to slightly thick-walled (up to 0.4 μ m); Subpellis composed of subparallel hyphae 3–6 μ m in diam, thin-walled, colorless in KOH. Acid-resistant incrustations absent. Hyphal terminations near the pileus margin composed of thin-walled cells; terminal cells (12–)14–24–35(–41) $\times$ 3–4–4.5(–5) μ m, mainly cystidioid, occasionally subcy-

lindrical, with obtuse apex; Hyphal terminations on the middle part between center and margin of pileus (19–)21–29–39(–58) × 3.5–3.7–4(–4.5) µm, subcylindrical, apex obtuse; Hyphal terminations near the pileus center occasionally flexuous; terminal cells 10–30–44(–65) × (3–)3.5–4–5 µm, subcylindrical or cystidioid, apex obtuse or occasionally attenuated. Pileal trama made up of sphaerocytes up to 58 µm in diam, thin-walled, colorless to pale yellow in KOH. Pileocystidia near the pileus margin always long, one-celled, (40–)45–58–67(–72) × 7–9.4–11(–12) µm, narrowly clavate to subcylindrical, apically often obtuse, sometimes with mucronate apices, appendage 3–6 µm long, thin- to slightly thick-walled (up to 0.5 µm); contents yellowish in Congo Red, turning to yellowish brown in SV. Pileocystidia near the pileus centre usually flexuous, one-celled, narrower subcylindrical to clavate, apex obtuse, (28–)32–47–63(–67) × 5–5.7–7 µm, thin- to slightly thick-walled (up to 0.4 µm); contents yellowish in Congo Red, turning to yellowish brown in SV. Stipitipellis a cutis 30–70 µm thick, composed of hyphae thin- to slightly thick-walled (up to 0.4 µm), 3–7 µm wide, yellowish brown in KOH; terminal cells 7–37 × 3–7 µm, subcylindrical, apex obtuse, sometimes attenuated. Stipe trama mainly composed of sphaerocytes measuring up to 55 µm in diam, hyaline to yellowish in KOH, thin-walled. Clamp connections absent in all tissues.

Habitat and distribution: Solitary or scattered on the ground in mixed forests of coniferous and broadleaf trees dominated by *Cyclobalanopsis* spp., *Quercus* spp., and *Pinus yunnanensis*. Currently known from southwestern China (Yunnan Province).

Additional materials examined: CHINA, Yunnan Province, Qujing City, Dadidishui Forestry Farm, elev. 2055 m, 3 Oct 2021, MH-KMU ZWH-810, MHKMU Jiang-433; Qujing City, Haizhai Forestry Farm, elev. 2133 m, 2 Oct 2021, MHKMU MJ-0009.

4. Discussion

The phylogenetic analyses indicated that *R. rubrosquamosa* is a member of *R. sect. Ingratae* (Fig. 1) based on a combined dataset (28S-ITS), and obviously the independent lineage formed by the new species is genetically distant from other related taxa in sect. *Ingratae*. In this study, no sister of the new taxon was found. Moreover, the morphological characters of *R. rubrosquamosa* also match the concept of *Ingratae* (Buyck et al., 2018; Li et al., 2021).

Morphologically, *R. rubrosquamosa* resembles two described Asian taxa, viz. *R. ryukokuensis* Shimono & T. Kasuya (Shimono et al., 2021) and *R. sp.7* (GENT FH12-036) (Adamčík et al., 2019). However, Japanese *R. ryukokuensis* was placed in subg. *Russula* sect. *Russula* subsect. *Emeticinae*, it differs from *R. rubrosquamosa* in its quite small basidiocarp (4–10 mm across), longitudinally striate stipe, white mycelia and shorter basidiospores measuring 6.7–7.4 × 5.4–6.7 µm. The unnamed taxon *R. sp.7* (GENT FH12-036) from Thailand is distinguished from *R. rubrosquamosa* in its yellowish stipe tapering towards the base, narrower basidiospores measuring (5.9–)6.3–6.6–6.8(–7.1) × (–5)5.4–5.7–6(–6.6) µm, pleurocystidia turning pale brown in SV and associated with *Dipterocarpus tuberculatus*. In addition, *R. rubrosquamosa* resembles several collections with similar color discovered from Africa, and all of the African species had small and mucronate pileocystidia (Adamčík et al., 2019; Buyck, 1993, 1994). However, pileocystidia in the pileus margin of *R. rubrosquamosa* is obviously larger, measuring (40–)45–58–67(–72) × 7–9.4–11(–12) µm.

As we all know *Russula* species are ectomycorrhizal mushroom, according to different host plants to distinguish *Russula* species seems reasonable. Species of *R. sect. Ingratae* usually associate with host plants of different families, such as *Dipterocarpaceae* (Dutta et

al. 2015; Han et al., 2022), *Fagaceae* (Das et al., 2006; Lee et al., 2017), *Pinaceae* (Ghosh et al., 2022; Jabeen et al., 2017), *Fagaceae* and *Pinaceae* (Ghosh et al., 2020; Li et al., 2021), and *Myrtaceae* (Adamčík et al., 2019). Besides, characters of basidiospore ornamentation is useful and reliable in species delimitation of sect. *Ingratae*, researchers could pay more attentions through microscopic inspection.

Disclosure

The authors declare no conflicts of interest. All the experiments undertaken in this study comply with the current laws of the country where they were performed.

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