

Taxonomic and phylogenetic evidence reveal two new *Russula* species (Russulaceae, Russulales) from northern Thailand

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Research Article

Keywords: Basidiomycota, Mushroom diversity, Phylogeny, Taxonomy, Tropical fungi

Posted Date: July 28th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-3114781/v1>

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Version of Record: A version of this preprint was published at Mycological Progress on September 26th, 2023. See the published version at <https://doi.org/10.1007/s11557-023-01921-5>.

Abstract

Russula is the most diverse genus within the family *Russulaceae* and has an ectomycorrhizal association with many host trees. During the monsoon season of 2022, five *Russula* specimens were collected in northern Thailand. After morphological and molecular analyses, the five specimens were determined to belong to *Russula* subgenus *Heterophyllidia*. A single specimen belonged to *R. bellissima*. Four other collected specimens were distinct from all other known species. We have identified these specimens as two new species, namely *R. pseudomodesta* and *R. sribuabanensis*. *Russula pseudomodesta* belongs to the subsection *Modestinae*, while *R. sribuabanensis* belongs to the subsection *Virescentinae*. The phylogenetic placement of two new species within *Russula* has been confirmed based on sequences of the nuclear internal transcribed spacer (nrITS) region and a large subunit (nrLSU) of the nuclear ribosomal RNA (nrRNA). Comprehensive morphological descriptions, field photographs, and comparisons of two new species with other morphologically and phylogenetically closely related species have been provided.

Introduction

The genus *Russula* Pers. was established by Persoon (1796). This is an important ectomycorrhizal mushroom genus that belongs to the family *Russulaceae*, order *Russulales*. This genus is distributed worldwide with more than 2,000 species that are associated with a wide range of host trees (broadleaf and coniferous plants) in different ecosystems (Paloi et al. 2018; Adamčík et al. 2019; Song et al. 2022). Several species of *Russula* have exhibited socioeconomic, industrial, ecological, and medicinal importance. In recent days, many *Russula* species have shown anticancer, anti-inflammatory, immunostimulatory, and beneficial antioxidant activities (Taengphan et al. 2019; Li et al. 2020; Khatua et al. 2021; Li et al. 2021; Zhang et al. 2021; Panda et al. 2022). Several taxonomic studies have concluded that *Russula* is a monophyletic genus (Buyck et al. 2008; 2018) that can be divided into eight subgenera, namely *Archaea* Buyck & V. Hofst., *Compactae* (Fr.) Bon, emend. Buyck & V. Hofst., *Crassotunicata* Buyck & V. Hofst., *Glutinosae* Buyck & X.H. Wang, *Heterophyllidia* Romagnesi, *Malodora* Buyck & V. Hofst., *Brevipedum* Buyck & V. Hofst., and *Russula*, emend. Buyck & V. Hofst. based on multigene phylogeny (Buyck et al. 2018; 2020). Among these eight subgenera, *Russula* subg. *Heterophyllidia* is characterized by the presence of medium to large basidiomata, equal lamellae, context unchanged or sometimes appearing yellowish to rusty brown, generally mild to strongly acrid taste, white or cream spore prints, suprahilar spots inamyloid or partly amyloid, as well as the presence of gloeocystidia and an absence of primordial hyphae (Buyck et al. 2018). Approximately, 163 species in the *Russula* subg. *Heterophyllidia* have been discovered all over the world (Han et al. 2023). *Russula* subg. *Heterophyllidia* is divided into four sections, namely *Aureotactae* Buyck & V. Hofst., *Heterophyllae* Fr., *Ingratae* Quel., and *Subvelatae* Sing (Buyck et al. 2018).

Northern Thailand covers an area of about 22,135 km² (18.7883° N, 98.9853° E), and its unique geographical location and vast climatic conditions make it an attractive habitat for the growth of macrofungi. According to Hyde et al. (2019), since 2005, most new macrofungal species (93%) have been reported to be from northern Thailand. Several new *Russula* species, namely viz. *R. bellissima* Manz & F. Hampe, *R. luteonana* M. Pobkwamsuk & K. Wisitrassameewong, *R. aurantiopectinata* F. Hampe & Manz, and *R. magica* Manz & F. Hampe., have been reported from Thailand (Hampe and Manz 2021; Wisitrassameewong et al. 2022). During a survey of macrofungi in Chiang Mai and Lamphun Provinces, northern Thailand of 2022, five specimens of *Russula* were collected. Based on morphological characteristics and multigene phylogenetic analyses, five specimens were identified as two distinct new species (introduced as *R. pseudomodesta* and *R. sribuabanensis*), as well as one previously known species (*R. bellissima*) that belongs to *Russula* subg. *Heterophyllidia*.

Materials and methods

Morphological study

Fresh basidiomata were collected from Chiang Mai and Lamphun Provinces, northern Thailand during the rainy seasons of 2022. Macro-morphological characteristics, ecological data, and certain chemical reactions to different chemicals (10% KOH and guaiacol) were noted in the field. Colour codes and terms were used according to Kornerup & Wanscher (1978). Specimens were dried at 45°C for 48 h. Microscopic characteristics were obtained from dried specimens using free hand sections by mounting them in 5% KOH, Congo red, and Melzer's reagent. They were then viewed through an Olympus CH30 microscope. The size of the basidiospores was documented based on 30 measurements recorded from each specimen. The Q value denotes the length/width ratio of the basidiospores. Basidiospore statistics have been presented as mean values (underlined). Scanned electron micrographs of basidiospores were obtained from spore prints coated with gold and viewed under a high vacuum mode to observe patterns of spore ornamentation. This work was carried out with the use of a JEOL JSM-IT800 scanning electron microscope (SEM) at Chiang Mai University. The holotype and other examined specimens were deposited at the Chiang Mai University Herbarium of the Department of Biology (CMUB) and the Sustainable Development of Biological Resources Laboratory (SDBR), Faculty of Science, Chiang Mai University, Thailand.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from fresh specimens using a DNA Extraction Mini Kit (FAVORGEN, Taiwan) according to the manufacturer's protocol. The nrITS, nrLSU, and *RPB2* regions were amplified by polymerase chain reaction (PCR) with ITS4/ITS5 (White et al. 1990), LROR/LR5 (Viilgalys and Hester 1990), and *RPB2*-6F/*RPB2*-7cR (Matheny et al. 2007) primer pairs, respectively. The amplification program for these three domains was performed in separate PCR reactions. PCR programs of nrITS and nrLSU were established by following the methods employed by Paloi et al. (2023). The amplification program for *RPB2* consisted of an initial denaturation step at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 s,

an annealing step at 54°C for 40 s, and an extension step at 72°C for 1 min on a peqSTAR thermal cycler (PEQLAB Ltd., UK). PCR products were checked on 1% agarose gels stained with ethidium bromide under UV light. PCR products were purified using a PCR clean-up Gel Extraction NucleoSpin® Gel and PCR Clean-up Kit (Macherey-Nagel, Germany) following the manufacturer's protocol. The purified PCR products were directly sequenced. Sequencing reactions were performed and the sequences were automatically determined by genetic analyzer at the 1st Base Company (Kembangan, Malaysia) with the PCR primers mentioned above.

Phylogenetic analyses

The sequences associated with a high degree of similarity to the newly generated sequences were retrieved from GenBank and from recent publications (Chen et al. 2019; Ullah et al. 2020; Chen et al., 2021; Khatua et al. 2021; Wisitrassameewong et al. 2022; Zhou et al. 2023), as is shown in Table 1. Three *Russula* species, *R. nigricans*, *R. dissimulans* and *R. camarophylla* were used for rooting purposes. Multiple sequence alignment was performed with MUSCLE (Edgar 2004) using default settings and improved where necessary using BioEdit v. 6.0.7 (Hall 2013). The final alignment was submitted to TreeBASE (30517). Phylogenetic analyses were carried out based on only the nrITS and nrLSU sequences because the amount of available sequence data of the *RPB2* gene sequences for the selected species were practically limited. A phylogenetic tree was constructed following maximum likelihood (ML) and Bayesian inference (BI) methods. Maximum likelihood analysis was carried out on RAxML-HPC2 version 8.2.10 (Stamatakis 2006) on the CIPRES web portal under the GTRCAT model with 25 categories and 1,000 bootstrap replications. Bayesian inference analysis was performed with MrBayes version 3.2.6 (Ronquist et al. 2012). The best substitution models for BI analyses were estimated by Akaike Information Criterion (AIC) in jModeltest 2.1.10 (Darriba et al. 2012). The best substitution models were determined to be GTR + I + G for nrITS and GTR according to nrLSU data. For BI analysis, six simultaneous Markov chains were run for one million generations with random initial trees, and every 1,000 generations were sampled. The burn-in was set to discard the first 2,000 trees, and the remaining trees were used to construct the 50% majority-rule consensus phylogram with calculated Bayesian posterior probabilities (PP). Branches with bootstrap support (BS) and PP values greater than or equal to 70% and 0.90, respectively, were considered significantly supported (Hillis and Bull 1993; Alfaro et al. 2003). Tree topologies were then visualized in FigTree version 1.4.0 (Rambaut 2009).

Table 1

Names, voucher numbers, countries, references and corresponding GenBank numbers of the taxa used in the phylogenetic analyses of this study.

Section/ Subsection	<i>Russula</i> species	Voucher	Country	GenBank accession number		Reference
				nrITS	nrLSU	
Subsect. <i>Virescentinae</i>	<i>R. pallidula</i>	JXM63	China	MH027958	MH027960	Chen et al. (2019)
	<i>R. pallidula</i>	LHJ14072505	China	MH027959	MH027961	Chen et al. (2019)
	<i>R. prasina</i>	HMAS 281232	China	MH454351	NA	Hyde et al. (2019)
	<i>R. xanthovirens</i>	H15060611	China	MG786056	NA	Zhou et al. (2020)
	<i>R. shanglaensis</i>	SUR433	Pakistan	MK579185	NA	Ullah et al. (2020)
	<i>R. shanglaensis</i>	SUR833	Pakistan	MK579184	NA	Ullah et al. (2020)
	<i>R. aureoviridis</i>	RITF4709	China	MW646980	MW646992	Chen et al. (2021)
	<i>R. mustelina</i>	FH12226	Germany	KT934005	KT933866	Looney et al. (2016)
	<i>R. mustelina</i>	503IS88	Europe	AY061693	NA	Miller and Buyck (2002)
	<i>R. cadaverolens</i>	TENN:067226	USA	KT933957	KT933816	Looney et al. (2016)
	<i>R. crustose</i>	BPL265	USA	KT933966	KT933826	Looney et al. (2016)
	<i>R. kanadii</i>	CUH AM086	India	KJ866936	KJ946376	Dutta et al. (2015)
	<i>R. luofuensis</i>	RITF4706	China	MW646973	MW646985	Chen et al. (2021)
	<i>R. alboareolata</i>	RMUKH23	Thailand	KX267648	NA	Unpublished
	<i>R. indoalba</i>	AG 15–628	India	KX234820	NA	Hyde et al. (2016)
	<i>R. pseudopunicea</i>	BJTC C335	China	MW554144	OP133202	Zhou et al. (2023)
	<i>R. pseudopunicea</i>	BJTC ZH1392	China	OP133164	OP133204	Zhou et al. (2023)
	<i>R. sribuabanensis</i>	CMUB40006	Thailand	OQ957188	OQ968132	This Study
	<i>R. sribuabanensis</i>	SDBR-CMUNK1760	Thailand	OQ957228	OQ968268	This Study
	Subsect. <i>Amoeninae</i>	<i>R. mariae</i>	SFC20120922-07	Korea	KF361777	KF361827
<i>R. mariae</i>		JMP0063	America	EU819426	NA	Palmer et al. (2008)
<i>R. amoenicolor</i>		311IX76	Europe	AY061655	NA	Miller and Buyck (2002)
<i>R. paravioleipes</i>		HBAU15001	China	MN658517	NA	Boonmee et al. (2021)
<i>R. violeipes</i>		208IS76	Europe	AY061726	NA	Miller and Buyck (2002)
<i>R. intervenosa</i>		CUH AM273	India	KT824241	KU928135	Crous et al. (2016)
<i>R. bellissima</i>		FH12-158	Thailand	MZ297951	NA	Wisitrasameewong et al. (2022)
<i>R. bellissima</i>		FH12-127	Thailand	MZ297950	NA	Wisitrasameewong et al. (2022)
<i>R. bellissima</i>		SDBR-CMUNK1785	Thailand	OQ957173	OQ957510	This study
<i>R. variispora</i>		H5855	Australia	EU019934	EU019934	Lebel and Tonkin (2007)
Subsect. <i>Modestinae</i>		<i>R. modesta</i>	BHI-F434a	USA	MF161265	NA
	<i>R. modesta</i>	BHI-F151a	USA	MF161182	NA	Haelewaters et al. (2018)
	<i>R. anatine</i>	13216	Italy	JF908698	NA	Osmundson et al. (2013)

"NA" = Not available in GenBank database. Specimens obtained from this study are in bold.

Section/ Subsection	<i>Russula</i> species	Voucher	Country	GenBank accession number		Reference
				nrITS	nrLSU	
	<i>R. parazurea</i>	MF01.10.2003	Europe	DQ422007	DQ422007	Unpublished
	<i>R. ochrospora</i>	Donelli20.07.2004	Europe	DQ422012	DQ422012	Unpublished
	<i>R. pseudomodesta</i>	CMUB40005	Thailand	OQ957419	OQ968300	This study
	<i>R. pseudomodesta</i>	SDBR-CMUSOU33	Thailand	OQ957482	OQ968301	This study
Subsect. <i>Heterophyllinae</i>	<i>R. vesca</i>	fo46762, TUB	Europe	AY606965	AF325320	Eberhardt and Verbeke (2004)
	<i>R. vesca</i>	TUB hue122	Germany	AF418610	NA	Unpublished
	<i>R. heterophylla</i>	UE20.08.2004-2, UPS	Europe	DQ422006	DQ422006	Unpublished
	<i>R. heterophylla</i>	TUB hue103	Germany	AF418609	AF325309	Eberhardt (2002)
	<i>R. brunneola</i>	r-03034	USA	JF834341	JF834489	Unpublished
Subsect. <i>Griseinae</i>	<i>R. ionochlora</i>	BB72_403_Bv_210507_R34	Europe	HM189875	NA	Unpublished
	<i>R. ionochlora</i>	978 ITS1F ITS4 TUBE220708_ed	Germany	GQ924690	NA	Unpublished
	<i>R. grisea</i>	UE2005.08.16-01, UPS	Europe	DQ422030	DQ422030	Unpublished
	<i>R. aeruginea</i>	TUB nl1292	Germany	AF418612	NA	Eberhardt (2002)
	<i>R. aeruginea</i>	AT2003017, UPS	Europe	DQ421999	DQ421999	Unpublished
	<i>R. wlingshanensis</i>	BJTC C335	China	MW554431	OP133207	Zhou et al. (2023)
Subsect. <i>Ilicinae</i>	<i>R. ilicis</i>	563IC52	Europe	AY061682	NA	Miller and Buyck (2002)
	<i>R. wernerii</i>	IB1997/0786, IB	Europe	DQ422021	DQ422021	Unpublished
Subsect. <i>Cyanoxanthinaceae</i>	<i>R. cyanoxantha</i>	FH 12-201	Germany	KR364093	KR364225	De Crop et al. (2016)
	<i>R. cyanoxantha</i>	TUB ue92	Germany	AF418608	NA	Eberhardt (2002)
	<i>R. variata</i>	JMP0078	America	EU819436	NA	Palmer et al. (2008)
	<i>R. nigrovirens</i>	HKAS 55222	China	KP171173	NA	Zhao et al. (2015)
	<i>R. subpallidirosea</i>	RITF 4083	China	MK860697	MK860702	Unpublished
	<i>R. pallidirosea</i>	UTC00274382	American Samoa	KR831283	NA	Kropp et al. (2016)
	<i>R. pseudocyanoxantha</i>	CUH AM177	India	MK414586	NA	Khatua et al. (2021)
Sect. <i>Ingratae</i>	<i>R. illota</i>	UE26.07.2002-3	Europe	DQ422024	DQ422024	Unpublished
	<i>R. granulate</i>	BPL272	USA	KT933971	KT933832	Looney et al. (2016)
	<i>R. pectinatoides</i>	AT2001049, UPS	Europe	DQ422026	DQ422026	Unpublished
Outgroup	<i>R. nigricans</i>	UE20.09.2004-07, UPS	Europe	DQ422010	DQ422010	Unpublished
	<i>R. dissimulans</i>	BPL285	America	KT933979	KT933840	Looney et al. (2016)
	<i>R. camarophylla</i>	PAM01081108, PC	Europe	DQ421982	DQ421982	Unpublished

"NA" = Not available in GenBank database. Specimens obtained from this study are in bold.

Results

Phylogenetic analysis

The newly generated nrITS and nrLSU sequences were deposited in the NCBI database and their accession numbers are indicated in Table 1. The combined nrITS and nrLSU sequence dataset consisted of a total number of 62 taxa and the aligned dataset was comprised of 1,751 characters including gaps (nrITS: 1–818 and nrLSU: 819–1751). The best scoring RAxML tree was established with a final ML optimization likelihood value of –

11706.494. The final average standard deviation value of the split frequencies at the end of the total MCMC generations was calculated as 0.00874 through BI analysis. Notably, the phylograms of the ML and BI analyses were similar in topology. Therefore, the phylogenetic tree obtained from ML analysis was selected and is presented in this study (Fig. 1). The final phylogenetic tree is divided into eight clades (clades a to h) that represent the subsect. *Virescentinae*, *Amoeninae*, *Griseinae*, *Heterophyllinae*, *Modestinae*, *Ilicinae*, and *Cyanoxanthinae*, and sect. *Ingratae*, respectively. Our specimens CMUB40006 and SDBR-CMUNK1760, introduced as *R. sribuabanensis* were placed in the subsect. *Virescentinae* (clade a). Both specimens formed a separate subclade from other members of the subsect. *Virescentinae* with higher support values (BS = 100% and PP = 1.00). Another collection of CMUNK1785 clumped together with *R. bellissima* (FH12-185 and FH12-127) was previously reported from Thailand (clade c). Additionally, two specimens, CMUB40005 and SDBR-CMUSOU33, introduced as *R. pseudomodesta* were monophyletic and formed a distinct subclade under the subsect. *Modestinae* (clade e) with high support values (BS = 100% and PP = 1.00).

Taxonomy

Russula pseudomodesta Paloi, Suwannarach N. & Kumla J., sp. nov. (Figs. 2a, 2c and 3)

MycoBank: MB 848802

Holotype: THAILAND. Chiang Mai Province, Chiang Mai University, 18°48'0.8496" N; 98°57'21.2256" E, elevation 335 m, 20 August 2022, S. Paloi (Holotype, CMUB40005). GenBank numbers OQ957419 (nrITS), OQ968300 (nrLSU), and OQ973265 (*RPB2*).

Diagnosis: Differs from *R. modesta*, by the presence of a larger pileus, no interspace venose between lamellae, globose to subglobose basidiospores, and ornamentation upto 1.1 µm high.

Etymology: The name "*pseudomodesta*" refers to the similarity of the new species to *R. modesta*.

Basidiomata large to medium. *Pileus* 60–125 mm diam., convex or ovoid at early stage, become broadly convex to plano-convex with slightly depressed center; surface smooth to pruinose, moist to semi moist, greenish grey (1A2), yellowish grey (2B2–3B2), grayish yellow (3C3), orange grey (5B2–6B2), greyish orange (5B3–6B3), greyish green (25B2) to sometimes reddish grey (7B2) at center, becoming faded to ward margin greyish white (1A2), yellowish white (2A2), gray (3B1) to sometime white (1A1), no change after bruising, turned orange with KOH, light pinkish with guaiacol; margin wavy, cracked at maturity, striate; context up to 5 mm at the middle, white to off-white, no change after exposed with air. *Lamellae* adnate, up to 8 mm wide, regular, sometimes bi-forked near stipe, white (1A1), no change after bruising; edge smooth, concolorous; lamellulae zero to one in a row. *Stipe* 35–52 × 11–18 mm, central, more or less equal, cylindrical, sometimes slightly bulbous base; surface smooth to pruinose, semi-moist, white (1A1), no change after bruising, turned yellow with KOH, light pinkish with guaiacol; context firm, white (1A1), becoming light yellowish after exposed with air. Odor not recognized, not hard. *Taste* mild. *Spores print* white to off white.

Basidiospores 5.5–6.4–7.2 × 5.1–5.6–6.5 µm, Q = 1.0–1.1–1.1, globose to sub-globose, ornamentation amyloid, composed with 0.3–0.5 µm low to 0.7–1.1 µm high warts, few connected (1–3) together with fine line, 0.1 µm high, in between two wart very small wart present, never reticulate, suprahilar spot not amyloid. *Basidia* 35.5–53.6 × 9–11.3 µm, clavate to sub-clavate, sometimes cylindrical, thin-walled, hyaline, oil granules present when viewed with KOH, 4-spored; sterigmata 2.9–5.5 µm long, cylindrical. *Lamellae edge* composed of cystidia and basidia. *Subhymenium* pseudoparenchymatous. *Hymenial cystidia* 66–87 × 10.2–13 µm, cylindrical to sub-cylindrical or fusiform with short appendiculate to moniliform or sometimes obtuse apex, thin-walled, hyaline, heteromorphous contents present near gill edge; same as gill side. *Pileipellis* orthochromatic in cresyl blue, context composed with sphaerocytes; subpellis composed with densely arranged hyphae, 125–150 µm deep, gelatinized, hyphae 3.98–2.76 µm broad, thin-walled, hyaline, branched; suprapellis 95–150 µm deep, less gelatinized, composed with erect to sub-erect hyphal end, 30–65 × 2.2–7.1 µm, thin-walled, sometimes thick walled, septate, hyaline, hyphal end obtuse to sometimes pointed, subterminal cells 5.5–16.5 × 5–10.5 µm, globose, sub-globose to ellipsoid, thin-walled, hyaline, 3–5 cells in a row. *Pileocystidia* rare at margin, comparatively frequent toward center, different types, clavate to sub-clavate or sub cylindrical with obtuse to less pointed or moniliform to mucronate, 25.0–50.5 × 5.0–6.5 µm, sometimes very long 75–90 × 5.5–7.5 µm, cylindrical with obtuse to mucronate apex, one celled, thin-walled, hyaline, oil granule present with KOH. *Stipitipellis* composed with tightly arranged, interwoven hyphae, 3.0–4.5 µm broad, thin-walled, hyaline, branched, septate, hyphal end obtuse to clavate; context composed with sphaerocytes. *Caulocystidia* abundant, different shaped, 17.0–54.0 × 3.5–6 µm, few are very long, 4.0–6.0 µm wide, clavate to sub-clavate or sub-cylindrical with obtuse to round apex to moniliform or mucronate thin-walled, hyaline, oil granules present with KOH. *Clamp connection* absent in all tissue.

Ecology and distribution: Solitary to caespitose, growing under *Shorea* spp. (*Dipterocarpaceae*) tree. Known only from the type locality in northern Thailand.

Material examined: THAILAND. Chiang Mai Province, Chiang Mai University premises, 18°48'0.8496" N; 98°57'21.2256" E, elevation 335 m, 28 August 2022, S. Paloi and W. Phonrob, (SDBR-CMUSOU33). GenBank numbers OQ957482 (nrITS) and OQ968301 (nrLSU).

Russula sribuabanensis Paloi, Suwannarach N. & Kumla J., sp. nov. (Figs. 2b, 2d & 4)

MycoBank: MB 848803

Holotype: THAILAND. Lamphun Province, Mueang Lamphun District, Sribuaban Subdistrict, 18°32'11" N; 99°07'29" E, elevation 414 m, 19 August 2022, S. Paloi, N. Suwannarach and J. Kumla, (Holotype, CMUB40006). GenBank number OQ957188 (nrITS), OQ968132 (nrLSU), and OQ973264 (*RPB2*).

Diagnosis: Differs from *R. pallidula*, by the presence of larger pileus, long pileus terminal cells (up to 63 µm) and growing in association with *Shorea* sp. dominating mixed forest; from *R. shanglaensis*, by the presence of smaller caulocystidia and white coloured stipe.

Etymology: The Latin name "*sribuabanensis*" refers to Sribuaban Subdistrict, Lamphun Province where type species was collected.

Basidiomata medium to large. *Pileus* 25–105 mm diam., hemispherical to convex at early stage, becoming broadly convex, applanate to plano-concave with a central depression when mature, surface pruinose, moist, viscid when humid, greyish green (25C3–26C3), greenish grey (25B2–26B2), greenish white (25A2) at center, becoming faded toward margin grey (26B1), greenish white (25A2) to greenish grey (25B2), no change after bruising, turned light yellowish to yellowish brown with KOH; margin incurved, regular when young, becoming striate, cracked, sometime wavy at maturity. *Lamellae* adnate to narrowly adnate, up to 6 mm wide, regular, white (1A1) to cream; edge even, concolorous; lamellulae none, sometimes if present, one in a row. **Stipe** central, 45–70 × 7–19 mm, cylindrical, tapered towards the base, sometimes curved, smooth, white (1A1), turned light yellowish after bruising, light yellowish or yellowish-brown with KOH; context firm, white (1A1), becoming very light yellowish after exposed with air. Odor unknown. *Taste* mild. *Spores* print cream.

Basidiospores 6.2–7.4–8.2 × 5.6–6.2–7.2 µm, Q = 1.0–1.1–1.2, sub-globose to sub-ellipsoid, ornamentation amyloid, composed with 0.15–0.25 low to 0.3–0.4 µm high lines connected together, produced a complete reticulate ornamentation, suprahilar spot not amyloid to weak amyloid. *Basidia* 35.5–51.8 × 6.6–8.9 µm, sub-clavate to sub-cylindrical, thin-walled, hyaline, oil granules present with KOH, 4-spored, sterigmata up to 4 µm long. *Lamellae* edge composed with numerous cystidia, sterile. *Subhymenium* pseudoparenchymatous. *Hymenial cystidia* near gill edge, 61.2–108.8 × 7.9–13.7 µm, subclavate to sub-cylindrical with appendiculate to moniliform or pointed apex, thin-walled, hyaline, oil granules present with KOH, same as gill side, up to 53 µm long projection. *Pileipellis* orthochromatic in cresyl blue, context composed with sphaerocytes; subpellis 250–350 µm deep, composed with more or less loosely arranged hyphae, 2.5–4 µm broad, thin-walled, hyaline, sometimes oil granules present when viewed with KOH; suprapellis 49–90 µm deep, gelatinized, composed tightly arranged suberect to repent hyphal end, 21.5–63 × 3.5–5.6 µm, thin-walled, hyaline, sometimes fills with cytoplasmic contains, obtuse to pointed apex, subterminal cell 8.5–19.7 × 5.5–9.7 µm, globose, sub-globose to ellipsoid, thin-walled, hyaline. *Pileocystidia* absent or very rarely present in margin, frequently found in centre, 30.0–42.5 × 3.8–5.5 µm, clavate to cylindrical with mucronate, moniliform to obtuse apex, thin-walled, hyaline, fill with cytoplasmic contains, sometimes long cystidia observed 4.5–6.5 µm wide. *Stipitipellis* composed with tightly arranged, terminal hyphal, 2.5–4 µm broad, thin-walled, hyaline, pointed or obtuse apex; subterminal cell sub-globose to ellipsoid. *Caulocystidia* 20.5–41 × 3–5.5 µm, sub-clavate to obtuse apex, very rare appendiculate or mucronate apex, thin-walled, hyaline, fill with cytoplasmic contains, sometimes very long, 3.5–6.0 µm in diam. *Clamp connection* absent in all tissue.

Ecology and distribution: Solitary, growing in a forest dominated by *Shorea* spp. (*Dipterocarpaceae*). Known only from the type locality in northern Thailand.

Material examined: THAILAND. Lamphun Province, Mueang Lamphun District, Sribuaban Subdistrict, 18°32'11" N; 99°07'29" E, elevation 414 m, 25 August 2022, S.N. Suwannarach and J. Kumla (SDBR-CMUNK1760). GenBank: nrITS: OQ957228; nrLSU: OQ968132.

Discussion

A combination of certain morphological characteristics, such as grey to greyish green pileus, a mild taste, cream spore prints, erect to suberect terminal hyphae attached with globose to suglobose or ellipsoid subterminal cells, and the presence of caulocystidia, confirmed that *R. sribuabanensis* (CMUB40006 and SDBR-CMUNK1760) belongs to the subsect. *Virescentinae*. During the last few years, several members of this subsection were reported to be from different Asian countries. These are viz. *R. pallidula* (Chen et al. 2019), *R. prasina* (Hyde et al. 2019), *R. xanthovirens* (Zhou et al. 2020), *R. aureoviridis* (Chen et al. 2021), *R. luofuensis* (Chen et al. 2021), *R. albolutea* (Chen et al. 2021b), *R. subpunicea* (Chen et al. 2021b)d *pseudopunicea* (Zhou et al. 2023) from China; as well as *R. indoalba* (Hyde et al. 2016)d *kanadii* (Dutta et al. 2015) from India, and *R. shanglaensis* (Ullah et al. 2020) from Pakistan. However, our Thai collection of *R. sribuabanensis* (CMUB40006 and SDBR-CMUNK1760) has been found to be morphologically, as well as phylogenetically, closely related to *R. pallidula* and *R. shanglaensis*. *Russula pallidula* has comparatively smaller pileus (40–55 mm diam.), safrano-pink colour lamellae, short pileipellis terminal hyphae (22–37 µm long), and frequently grows in association with *Pinus* sp., *Picea* sp., and *Castanopsis* sp. (Chen et al. 2019). *Russula shanglaensis* has been reported to be from Pakistan in association with mixed coniferous forests at high altitudes (2,300–3,000 m). It has larger caulocystidia (40–130 µm long) and yellowish tints at the stipe base (Ullah et al. 2020). Other three Chinese species, viz. *R. albolutea* (Chen et al. 2021b), *R. subpunicea* (Chen et al. 2021b)d *pseudopunicea* (Zhou et al., 2023) were determined to belong to the same subsection, but *R. pseudopunicea* frequently grows in association with broadleaf forests dominated by *Betula costata* that are pileus reddish brown, light brown to brownish orange, possessing thick suprapellis (60–190 µm), and has comparatively longer pileocystidia (Zhou et al. 2023). *Russula albolutea*, which has been named according to the yellowish white pileus colour, is found in mixed hardwood forests dominated by *Fagus* sp. It has white spore prints, smaller basidia (28–43 µm long), and thicker suprapellis (120–160 µm deep); while *R. subpunicea* has yellowish white, pinkish, or greyish orange pileus, white spore prints, and grows in association with *Castanopsis hystrix* and *Betula alnoides* (Chen et al. 2021b).

Russula bellissima was previously reported from Thailand, while our collection is morphologically, as well as phylogenetically, similar to the type material in most cases. However, our samples were mostly small in size (12–25 mm diam) with a basidiospore size a little smaller than the type material. The suprapellis and subpellis are also thinner than the type material. However, the species can easily be recognized based on small to medium sized pileus with red colour, a smooth to purinose pileus surface, inamyloid suprahilar spots, basidiospore ornamentations that are composed of spines or warts connected by fine lines, and with hymenial cystidia and pileocystidia absent (Wisitrassameewong et al. 2022). *Russula bellissima* is morphologically and phylogenetically closely related to the *R. intervenosa* reported from India and frequently grows in association with *Shorea robusta* dominating forests. However, our collection differs from *R. intervenosa* by the presence of hymenial cystidia on the gill side, very thin suprapellis (47–64 µm deep), and a stipe surface that turned red to brownish red with guaiacol (Crous et al. 2016).

Another species of *R. pseudomodesta* (CMUB40005 and SDBR-CMUSOU33), that is frequently found on the premises of Chiang Mai University, is closely related to American *R. modesta*, as well as European *R. ochrospora*, *R. parazurea*, and *R. anatina*. *Russula modesta* differs from *R. pseudomodesta* by the presence of a small pileus (up to 64 mm diam.), interspace venose present between the lamellae, smaller broadly ellipsoid basidiospores (5–6.2 × 4.1–5.1 µm, Qm = 1.21) with a subreticulate ornamentation, and conical warts that are 0.3–0.5 µm high. However, both specimens contain long pileocystidia (Adamčík et al. 2013). *Russula anatina* has generally olivaceous to olive grey or vetiver green pileus, interviose lamellae, very fast reactions with guacol on the stipe, and an association with oak plants (Romagnesi 1967). *Russula parazurea* possesses dark green grey, olive grey, or iron-grey pileus, lamellae attachment attenuated-adnexate, becoming pale cream to yellowish cream when mature, and is quite common in deciduous forests (Mycobank; accessed on 15 May 2023).

Morphologically and phylogenetically, *R. sribuabanensis* and *R. pseudomodesta* have been collected from *Shorea* spp. that dominate the forests of northern Thailand. These belong to *Russula* subg. *Heterophyllidia*. Another *Russula* species, *R. bellissima*, is common and widely distributed throughout Lamphun Province. This species is also known to be consumed by local people during the monsoon season. Documentation of these two new species has contributed to the acknowledged diversity of Thai macrofungi. Finally, this finding may help to understand the distribution of *Russula* in Asia and around the world.

Declarations

Acknowledgements

We thank the National Research Council of Thailand (NRCT) for allowing Soumitra Paloi to conduct research in Thailand. The authors are grateful to Russell Kirk Hollis for the English correction of this manuscript.

Author contribution

N.S.: conceptualization. S.P., N.S., J.K.: formal analysis, writing original draft, review, and editing. S.P., J.K., S.C.K., N.S.: investigation, data curation. J.K., S.C.K., S.L., N.S.: review, and editing. N.S.: supervision, project administration, funding acquisition. All authors read and approved the final manuscript.

Funding

This study was supported by Chiang Mai University and National Research Council of Thailand (Grant number: N42A650198). Samantha C. Karunaratna thanks National Natural Science Foundation of China for the support (Grant number: 32260004).

Data availability

Sequence data generated for the present study have been deposited in GenBank with the accession numbers nrITS: OQ957188, OQ957228, OQ957173, OQ957419, and OQ957482; nrLSU: OQ968132, OQ968268, OQ957510, OQ968300, and OQ968301; *RPB2*: OQ973265 and OQ973264. The alignment file for conducting phylogenetic analyses is available in TreeBASE number 30517.

Ethics approval. No ethics approval is needed for the present study.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest. The authors declare no competing interests.

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Figures

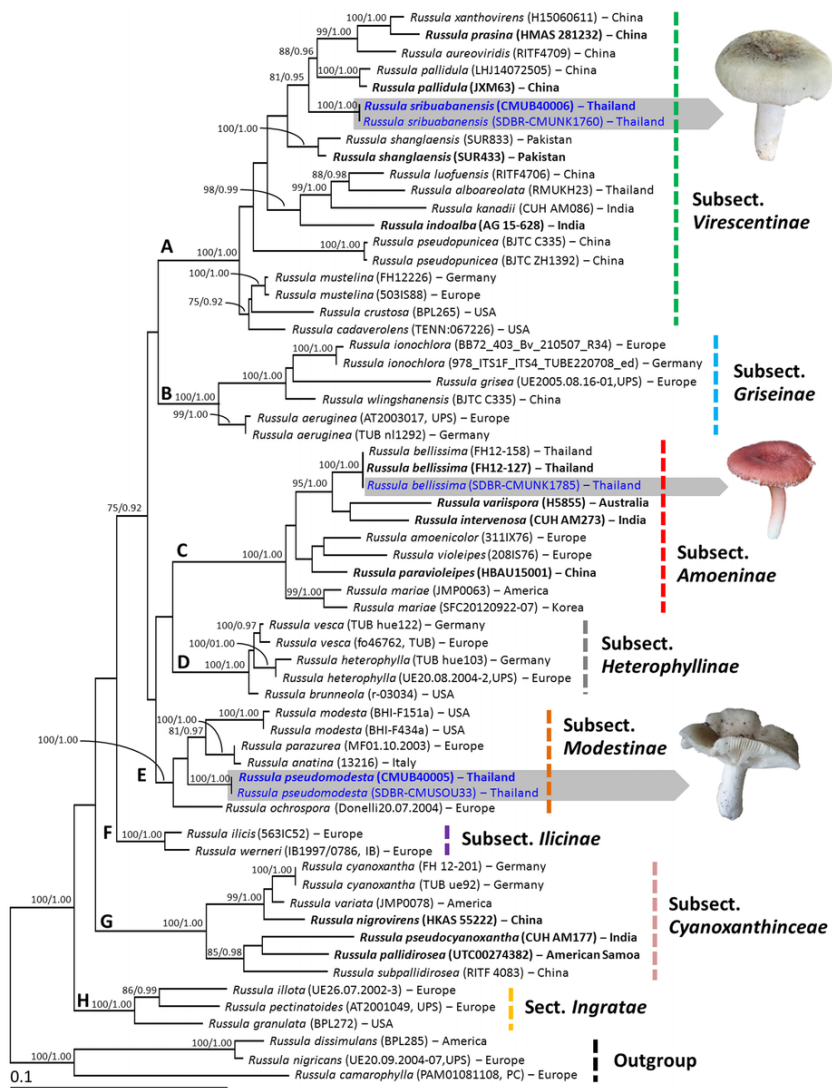


Figure 1

A combined (nrITS+nrLSU) phylogram derived from maximum likelihood analysis of 62 taxa. Three *Russula* species, *R. nigricans*, *R. dissimulans*, and *R. camarophylla* were used for rooting purposes. The numbers above branches represent maximum likelihood bootstrap percentages (right) and Bayesian posterior probabilities (left). Bootstrap values $\geq 75\%$ and Bayesian posterior probabilities ≥ 0.90 are shown above the branches. The scale bar represents the expected number of nucleotide substitutions per site. Type sequences highlighted in bold front. Newly reported species in this study are highlighted (blue front) and corresponding species pictures are provided.

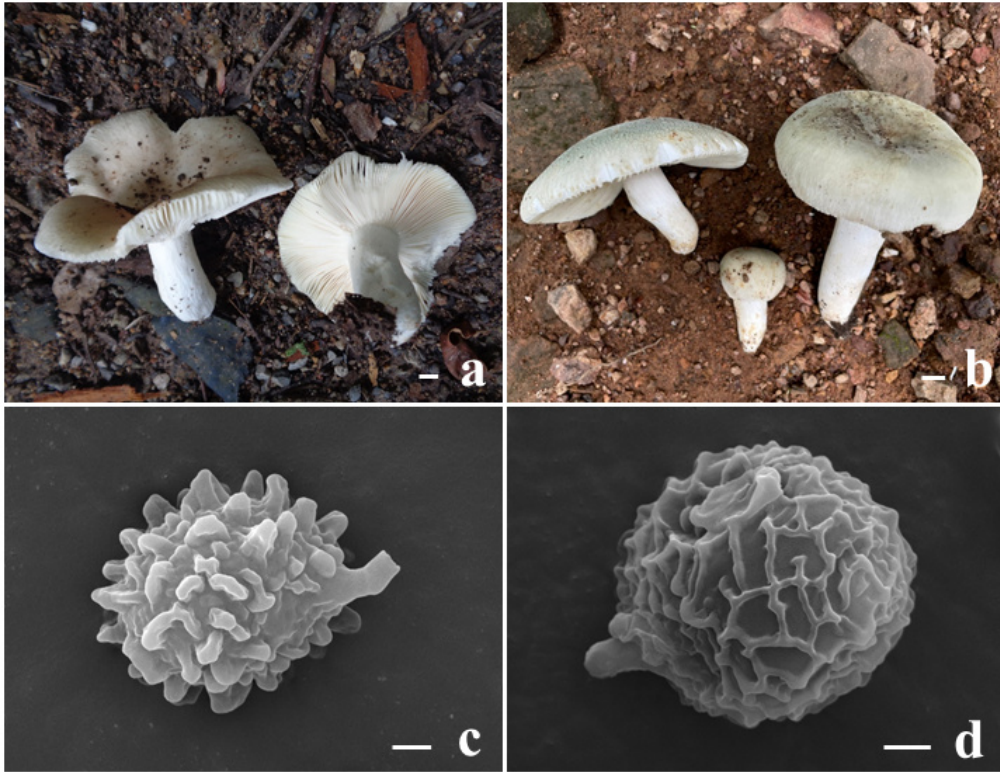


Figure 2

Filed photograph of genus *Russula*. **a** *Russula pseudomodesta*(CMUB40005, Holotype). **b** *R. sribuabanensis* (CMUB40006, Holotype). Scanning electron microscope photographs of basidiospores. **c** *R. pseudomodesta*. **d** *R. sribuabanensis*. Scales bar: **a-b** = 10 mm and **c-d** = 1 μ m.

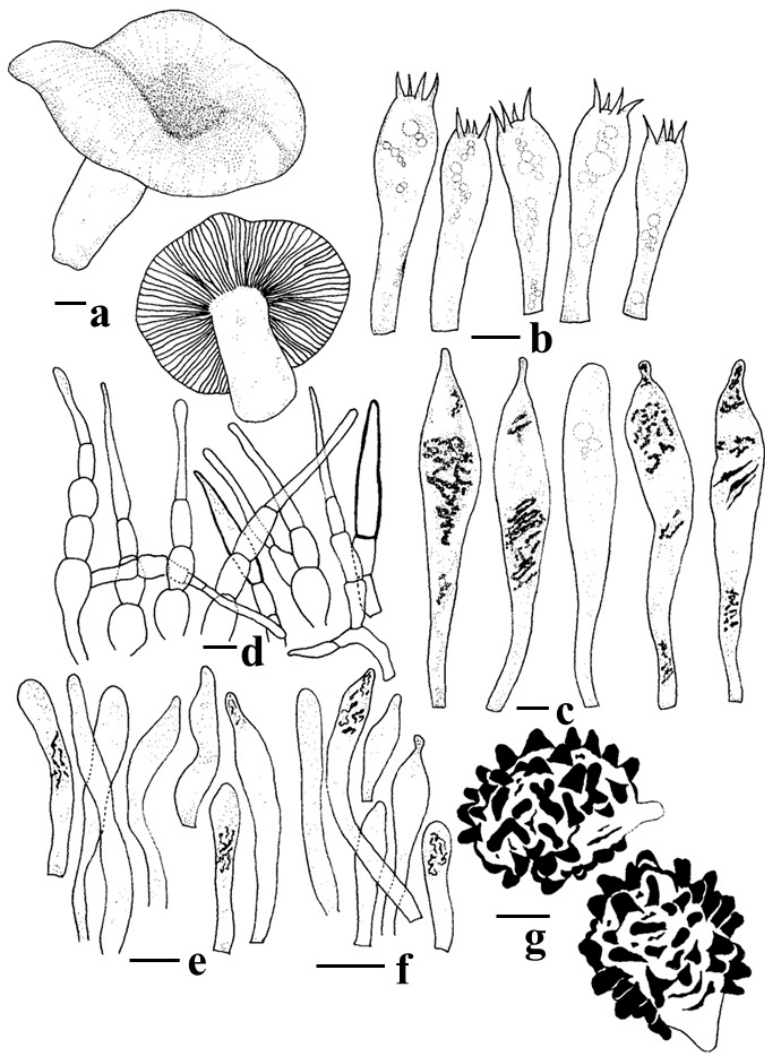


Figure 3

Russula pseudomodesta (Holotype). **a** fruitbodies. **b** basidia. **c** chymenial cystidia. **d** terminal elements of pileipellis. **e** epileocystidia. **f** caulocystidia. **g** basidiospores. Scales bar: **a** = 10 mm, **b-f** = 10 μ m and **g** = 2 μ m (Drawing by S. Paloi).

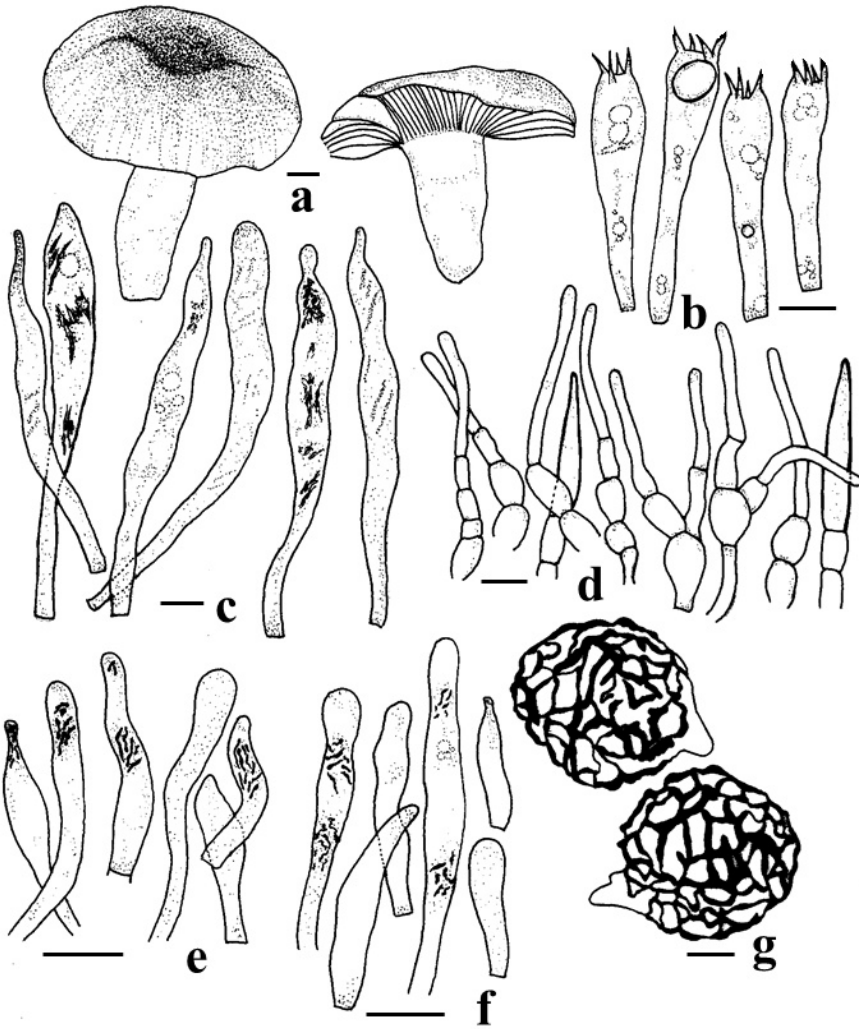


Figure 4

Russula sribuabanensis (Holotype). **a** fruitbodies. **b** basidia. **c** chymenial cystidia. **d** terminal elements of pileipellis. **e** epilecystidia. **f** caulocystidia. **g** basidiospores. Scales bar: **a**= 10 mm, **b-f** = 10 μ m and **g** = 2 μ m (Drawing by S. Paloi).