Two New Species of *Russula* Subsect. *Virescentinae* From Southern China

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Abstract

Two new species from southern China, *Russula subpunicea* and *R. albolutea*, were described and illustrated. *Russula subpunicea* is characterized by a pinkish to dark pink pileus with striations at the margin, white lamellae without lamellulae, subglobose to broadly ellipsoid to ellipsoid basidiospores with warts and spines sometimes joined to form a reticulum, hymenial cystidia that are mainly clavate, a suprapellis mainly composed of chains of short inflated cells with attenuated terminal cells and pileocystidia that are mainly clavate and turn reddish in sulfovanillin. *Russula albolutea* is recognized by a yellowish white pileus with long striations at the margin, a white stipe with a yellowish tinge, subglobose to broadly ellipsoid to ellipsoid basidiospores, hymenial cystidia that are mainly clavate and apically often obtuse and turn mauve in sulfovanillin, and a suprapellis mainly consisting of chains of short inflated cells with attenuated terminal cells. In this study, we performed phylogenetic analysis based on the ITS-nrLSU-*RPB2*-mtSSU dataset. By combining detailed morphological features with multigene phylogenetic evidence, we assigned the new taxa to *Russula* subsect. *Virescentinae*.

Introduction

Russula Pers. with eight subgenera is the largest genus of Russulaceae, which likely includes at least 2000 species (Buyck et al. 2018, 2020; Adamčík et al. 2019; Wijayawardene et al. 2020). This genus has a cosmopolitan distribution from Arctic tundra to tropical forests and forms ectomycorrhizae with a diverse range of plants in deciduous, evergreen, broadleaf and coniferous forests, scrubland and even meadows (Knudsen & Borgen 1982, Buyck et al. 1996, Looney et al. 2018). The genus is mainly characterized by conspicuous basidiomata, a colorful brittle pileus, amyloid warty basidiospores, abundant sphaerocytes in a heteromerous trama, an absence of latex and hyphae that lack clamp connections (Singer 1986, Romagnesi 1987, Sarnari 1998). Some members of *Russula* are well-known edible fungi and are also commercially traded worldwide (Wang et al. 2009; Looney et al. 2018; Wang 2020). According to recent statistics on the resource diversity of Chinese macrofungi, there are 78 edible species in China (Wu et al. 2019).

The main features of *Russula* subsect. *Virescentinae* Singer include typically cracked cuticles, a mild taste, white to cream spore prints and a pileipellis comprising mainly attenuated terminal cells with short inflated subterminal cells (Singer 1986, Sarnari 1998). Recently, many new species belonging to the subsect. *Virescentinae* have been reported in Asia (Das et al 2017, Song et al 2018, Hyde et al. 2019, Deng et al. 2020), indicating that Asia is a hot spot for the exploration of unknown *Russula* species. We also focused on this subsection and found a new member (*R. pallidula* B. Chen & J.F. Liang, Chen et al. 2019). During a survey on the habitat diversity and geographic distribution of Chinese *Russula* subsect. *Virescentinae*, some interesting specimens were found that were different from the known species. Here two taxa are proposed as new to science based on their morphological features and phylogenetic relations.

Materials And Methods

Morphological study

Fresh basidiomata were photographed under daylight in the field. Specimens were dried at 50–55°C and deposited in the herbarium of the Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITF). The macromorphological descriptions were based on detailed notes and photographs. The terminology for descriptive terms followed Vellinga (1988). The color designations were taken from Kernerup and Wanscher (1981). The description templates and terminology of the micromorphological features were taken from Adamčík et al. (2019). All experiments were performed on dried specimens using a ZEISS Imager M2 (Carl Zeiss AG; Germany). The basidiospores were observed in Melzer's reagent and measured from a lateral view excluding ornamentation. Other microscopic features were identified and measured with Congo red staining after pretreatment in 5% potassium hydroxide (KOH). The coloring of the cystidia contents was observed in a sulfovanillin (SV) solution. The pileipellis was examined with the brilliant cresyl blue test to verify the presence of ortho- or metachromatic reactions (Buyck 1989). The structure and ornamentation of the basidiospores were illustrated using scanning electron microscopy (SEM-JEOL JSM-6510). The statistics of the basidiospore measurements are presented as (Min–)AV-SD–AV+SD(–Max), where Min is the minimum value, Max is the maximum value, AV is the average value, SD is the standard deviation, and Q represents the length/width ratio of the basidiospores.

Molecular study

Genomic DNA was extracted from dry specimens following an improved CTAB protocol (Zhou & Liang 2011). The following four loci were amplified: 600 base pairs of the ITS region of rDNA using the primers ITS1 and ITS4 (White et al. 1990); 900–1400 base pairs of the nuclear ribosome large subunit (nrLSU) using the primers LR0R and LR5 (Vilgalys & Hester 1990); 700 base pairs of the second largest subunit of RNA polymerase II (*RPB2*) using the primers bRPB2-6f and fRPB2-7cr (Liu et al. 2004; Matheny 2005); 600 base pairs of the

ribosomal mitochondrial small subunit (mtSSU) with primers MS1 and MS2 (White et al. 1990). The PCR products were subjected to automated DNA sequencing on an ABI 3730 DNA analyzer using an ABI BigDye 3.1 terminator cycle sequencing kit (Shanghai Sangon Biological Engineering Technology and Services CO., Ltd, Shanghai, China). The newly generated sequences were submitted to the GenBank database (Table 1).

Table 1. GenBank accession numbers of sequences used in the phylogenetic analysis. Newly generated sequences are in bold.

Taxon	Voucher	Location	ITS	nrLSU	<i>RPB2</i>	mtSSU	Reference
<i>R. aeruginea</i>	AT2003017	Sweden	DQ421999	DQ421999	DQ421946	–	Buyck et al. 2008
<i>R. albidogrisea</i>	K19061709	China	MN603051	–	–	–	Das et al. 2017
<i>R. albidogrisea</i>	RITF1871	China	MW397095	MW397128	–	MW403841	This work
<i>R. alboareolata</i>	SUT-1	Thailand	AF345247	–	–	–	Manassila et al. 2005
<i>R. albolutea</i>	RITF2653	China	MT672478	MW397120	MW411340	MW403833	This work
<i>R. albolutea</i>	RITF4460	China	MT672475	MW397121	MW411341	MW403834	This work
<i>R. albolutea</i>	RITF4461	China	MT672476	MW397122	MW411342	MW403835	This work
<i>R. albolutea</i>	RITF4462	China	MT672477	MW397123	MW411343	MW403836	This work
<i>R. aureoviridis</i>	H15060613	China	KY767808	–	–	–	Das et al. 2017
<i>R. aureoviridis</i>	RITF1868	China	MW397096	–	–	MW403842	This work
<i>R. bubalina</i>	K15052614	China	MG018742	–	–	–	Li et al. 2019
<i>R. bubalina</i>	RITF1863	China	MW397097	–	–	MW403843	This work
<i>R. crustosa</i>	BPL265	USA	KT933966	KT933826	KT933898	–	Looney et al. 2016
<i>R. cyanoxantha</i>	FH 12-201	Germany	KR364093	KR364225	KR364341	–	De Crop et al. 2017
<i>R. cyanoxantha</i>	UE29.09.2002-2	France	DQ422033	DQ422033	DQ421970	–	Buyck et al. 2008
<i>R. dinghuensis</i>	GDGM45244	China	KU863579	–	–	–	Zhang et al. 2017
<i>R. grisea</i>	FH12234	Germany	KT934006	KT933867	KT933938	–	Looney et al. 2016
<i>R. grisea</i>	UE2005.08.16-01	Sweden	DQ422030	DQ422030	DQ421968	–	Buyck et al. 2008
<i>R. heterophylla</i>	hue103 (TUB)	Europe	AF418609	AF325309	–	–	Eberhardt 2002
<i>R. heterophylla</i>	UE20.08.2004-2	Sweden	DQ422006	DQ422006	DQ421951	–	Buyck et al. 2008
<i>R. ilicis</i>	563IC52	Europe	AY061682	–	–	–	Miller & Buyck 2002
<i>R. indoalba</i>	AG 15-628	India	KX234820	–	–	–	Hyde et al. 2016
<i>R. kanadaii</i>	CUH AM086	India	KJ866936	–	–	–	Dutta et al. 2015
<i>R. lakhanpalii</i>	AG 17-1584	India	MN262088	–	–	–	Ghosh et al. 2020
<i>R. lotus</i>	RITF499	China	MK860699	MW397129	–	MK860706	Song et al. 2019, This work
<i>R. lotus</i>	LF1366	China	MG214688	–	–	–	Li et al. 2018
<i>R. maguanensis</i>	XHW4765	China	MH724918	MH714537	MH939989	–	Wang et al. 2019
<i>R. mariae</i>	HCCN19111	South Korea	KF361762	KF361812	KF361712	–	Park et al. 2013
<i>R. mustelina</i>	FH12226	Germany	KT934005	KT933866	KT933937	–	Looney et al. 2016
<i>R. orientipurpurea</i>	SFC20170819-08	South Korea	MT017550	–	MT199638	MT196926	Wisitrassameewong et al. 2020
<i>R. orientipurpurea</i>	SFC20170725-37	South Korea	MT017548	–	MT199639	MT196927	Wisitrassameewong et al. 2020
<i>R. pallidula</i>	RITF2613	China	MH027958	MH027960	MH091698	MW403845	Chen et al. 2019, This work
<i>R. pallidula</i>	RITF3331	China	MH027959	MH027961	MH091699	MW403846	Chen et al. 2020, This work

<i>R. parvovirescens</i>	SDRM 6280	USA	MK532789	–	–	–	Unpublished
<i>R. phloginea</i>	CNX530524068	China	MK860701	MK860704	–	MK860708	Song et al. 2019
<i>R. phloginea</i>	CNX530524304	China	MK860700	MK860703	–	MK860707	Song et al. 2019
<i>R. prasina</i>	HMAS 281232	China	MH454351	–	–	–	Hyde et al. 2019
<i>R. pseudocrustosa</i>	HBAU15015	China	MT337520	–	–	–	Deng et al. 2020
<i>R. sp.</i>	y207	Japan	LC367872	–	–	–	Miyamoto et al. 2018
<i>R. subpallidirosea</i>	RITF4083	China	MK860697	MK860702	–	MK860705	Song et al. 2019
<i>R. subpunicea</i>	RITF3715	China	MN833635	MW397124	MW411344	MW403837	This work
<i>R. subpunicea</i>	RITF2648	China	MN833638	MW397125	MW411345	MW403838	This work
<i>R. subpunicea</i>	RITF1435	China	MN833637	MW397126	MW411346	MW403839	This work
<i>R. subpunicea</i>	RITF2615	China	MN833636	MW397127	MW411347	MW403840	This work
<i>R. substriata</i>	XHW4766	China	MH724921	MH714540	MH939992	–	Wang et al. 2019
<i>R. variata</i>	BPL241	USA	KT933959	KT933818	KT933889	–	Looney et al. 2016
<i>R. vesca</i>	AT2002091	Sweden	DQ422018	DQ422018	DQ421959	–	Buyck et al. 2008
<i>R. vesca</i>	BPL284	USA	KT933978	KT933839	KT933910	–	Looney et al. 2016
<i>R. violeipes</i>	SFC20121010-06	South Korea	KF361808	KF361858	KF361758	–	Park et al. 2013
<i>R. virescens</i>	HJB9989	Belgium	DQ422014	DQ422014	DQ421955	–	Buyck et al. 2008
<i>R. viridicinnamomea</i>	K15091418	China	MK049972	–	–	–	Yuan et al. 2019
<i>R. viridicinnamomea</i>	RITF3324	China	MW397098	MW397130	MW411348	MW403847	This work
<i>R. viridirubrolimbata</i>	HBAU 15011	China	MT337526	–	–	–	Deng et al. 2020
<i>R. weneri</i>	IB1997/0786	Sweden	DQ422021	–	–	–	Unpublished
<i>R. xanthovirens</i>	GDGM 71145	China	MG786056	–	–	–	Song et al. 2018

Phylogenetic analysis

Preliminary multiple sequence alignment was performed using the online version MAFFT 7.0 (<http://mafft.cbrc.jp/alignment/server/>) with manual evaluations and adjustments in BioEdit when necessary to obtain reliable and reasonable results (Hall 1999). The final alignment was submitted to TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S27504>). Species in the subg. *Heterophyllidia* with high similarity to our new species were selected for phylogenetic analyses using maximum likelihood (ML) and Bayesian analysis (BA). The ML was determined using RAxML-HPC2 on XSEDE (8.2.12) through the CIPRES Science Gateway (www.phylo.org). The ML analysis was executed by applying the rapid bootstrap algorithm with 1000 replicates to affirm the consistency of the results under the GAMMA model. Bootstrap support (BS) $\geq 70\%$ was regarded as significant. The BA was performed using XSEDE (3.2.7a) through the CIPRES Science Gateway (www.phylo.org) under the GTR model. The BA was run with 4 chains for a total of 50000000 generations, trees were sampled every 100 generations, and the first 25% of the trees were discarded as the burn-in phase of each analysis. The Bayesian posterior probability (PP) values were obtained from the 50% majority-rule consensus trees, and nodes with $PP \geq 95\%$ were considered significantly supported.

Results

Phylogenetic analysis

The final ITS-nrLSU-*RPB2*-mtSSU sequence dataset was analyzed using ML and BA. Both the ML analysis and BA resulted in similar tree topologies, and only the ML tree is shown in Fig. 1. The posterior probabilities for the BA are also shown along the branches. The phylogenetic analyses showed that subsect. *Virescentinae* was a monophyletic group; this was strongly supported by BS (100%) and PP (1). Additionally, the remaining 5 subsections of sect. *Heterophyllidia* were significantly supported as a monophyly.

The samples of the two new species, *R. subpunicea* and *R. albolutea*, formed a strongly supported clade (BS 100%, PP 1.00) and were clearly distinct from known and sequenced species of the subsect. *Virescentinae*. *R. subpunicea* clustered together with unidentified environmental samples of *R. sp.* from Japan, which is the sister taxon to a clade comprising *R. crustosa* Peck and *R. mustelina* Fr. with 85% bootstrap support and 1.00 posterior probabilities. *R. albolutea* is the sister taxon, without support, for a clade of all of the abovementioned species.

Taxonomy

Russula subpunicea B. Chen & J. F. Liang, sp. nov., Figs. 2a–g, 3 and 4

Mycobank: MB836124

Diagnosis: Basidiomata small to medium-sized; yellowish white to pinkish to dark pink pileus; adnate to subfree lamellae; spore print white; subglobose to broadly ellipsoid to ellipsoid basidiospores with relatively small amyloid warts or spines; hymenial cystidia mainly clavate; subcylindrical, lageniform or clavate marginal cells; terminal cells of hyphal terminations in pileipellis lageniform or clavate; suprapellis mainly composed of chains of short inflated cells with attenuated terminal cells; and pileocystidia mainly clavate.

Holotype: China, Guangxi Zhuang Autonomous Region, Pingxiang City, Fubo Forest Farm, 22°01'42.11" N, 106°50'1.07" E; 641 m asl., in mixed forests of *Castanopsis hystrix* and *Betula alnoides*, 19 August 2016, JXM189 (RITF3715).

Etymology: The Latin word “subpunicea” refers to the pinkish pileus.

Basidiomata: Small to medium-sized; pileus 12–87 mm in diameter; initially hemispheric when young, applanate to convex, convex with a depressed center after mature; margin incurved, cracked, and striations up to 1/4 of the radius; surface smooth, glabrous, slightly viscous when humid, peeling to 1/4 of the radius; yellowish white (2A2) with pinkish tinge when young, pinkish or dark pink after maturation, shallower at the margin. **Lamellae:** Adnate to subfree, 2–4 mm deep, dense, white (1A1) to cream, lamellulae absent, edge entire and concolor. **Stipe:** 25–40 × 7–15 mm, cylindrical, slightly attenuated at the base, white (1A1) to dirty white, and medulla initially stuffed becoming hollow. **Context:** 2–3 mm thick in half of the pileus radius, white (1A1), unchanging when bruised, taste slightly bitter or spicy, odor unpleasant. **Spore print:** White.

Basidiospores: (4.9)5.3–6.3–7.4 × (4.3)4.6–5.3–6.0(7.1) μm , $Q = 1.00\text{--}1.14\text{--}1.35$, subglobose to broadly ellipsoid to ellipsoid; ornamentation of relatively small, moderately distant to dense [3–5(–6) in a 3 μm diameter circle] amyloid warts or spines, 0.4–0.8 μm high, occasionally reticulate, fused in short or long branched chains [1–2(–3) in the circle], frequently connected by line connections [0–1(–2) in the circle]; suprahilar spot large, amyloid. **Basidia:** 30–34.3–39(40) × (5)6.5–8.8–10.7(12.8) μm , mostly 4-spored, some 2- and 3-spored, clavate; basidiola clavate or subcylindrical, ca. 5–9 μm wide. **Hymenial cystidia on lamellae sides:** Moderately numerous, ca. 1200–1500/mm², 44–75.5–105(114) × (5.8)6.2–8.4–10 (10.4) μm , clavate or subcylindrical, apically mainly obtuse, often with 2–6 μm long appendage, thin-walled; contents heteromorphous or granulose, mainly in the middle and upper part, turning tawny in SV. **Hymenial cystidia on lamellae edges:** Sometimes shorter, (51.5)52.4–70.6–93(95) × 6–8–9.6(10.9) μm , clavate or cylindrical, apically mainly obtuse, sometimes with 2–5 μm long appendage thin-walled; contents heteromorphous-crystalline, almost without color change in SV. **Marginal cells:** (9.5–)12.5–16.8–23.5(25.3) × (3.7)4.4–5.8–7.2(7.5) μm , subcylindrical, lageniform or clavate, sometimes flexuous. **Pileipellis:** Orthochromatic in cresyl blue, sharply delimited from the underlying context, 120–180 μm deep, two-layered; suprapellis 50–70 μm deep, composed of chains of short inflated cells with attenuated terminal cells; subpellis 80–120 μm deep, composed of horizontally oriented, relatively dense, intricate, 2–6 μm wide hyphae. Hyphal terminations near the pileus margin typically branched, occasionally flexuous, thin-walled; terminal cells (10)11–19.5–34(42) × (2.3)2.6–4.6–7.2(8) μm , mainly attenuated or narrowly lageniform, occasionally clavate or cylindrical, apically constricted or obtuse; subterminal cells frequently shorter, ca. 3–8 μm wide, typically unbranched. Hyphal terminations near the pileus center similar to those near the pileus margin; terminal cells (9.2)9.5–16.6–20.5(23.8) × 2.8–4.6–6 μm , cylindrical, clavate, lageniform, apically obtuse or occasionally constricted; subterminal cells often shorter, rarely branched, ca. 4–9 μm wide. Pileocystidia near the pileus margin always one-celled, (30)35–45–55 × 4.2–5.4–6.5(–7) μm , mainly clavate, occasionally fusiform, apically typically obtuse, sometimes with ellipsoid 2–5 μm long appendage, thin-walled; contents granulose or crystalline, turning reddish in SV. Pileocystidia near the pileus center similar in size, always one-celled, (26)26.7–36.7–

56.7(61.5) × (4)4.5–6–7.3(9) µm, thin-walled, mainly clavate, occasionally fusiform, apically often obtuse or occasionally mucronate, occasionally with 2–5 µm long appendage, contents granulose, turning reddish in SV. **Cystidioid hyphae:** In subpellis and context with granulose contents, oleiferous hyphae in context with granulose or crystalline contents.

Additional specimens examined: China, Zhejiang Province, Lishui City, Baiyunshan Ecology Forest Farm, 28°28'50.14" N, 119°55'0.46" E, 141 m asl., 20 August 2015, JXM33 (RITF2648); Hunan Province, Yongzhou City, Dongan County, Shunhuang Mountain National Forest Park, 26°23'54.40" N, 111°02'54.97" E, 457 m asl., 5 July 2012, yy37 (RITF1435); *ibid.*, 13 July 2015, LYK49 (RITF2615).

Notes: The combination of morphological features and phylogenetic analysis place *R. subpunicea* in subsect. *Virescentinae*.

Phylogenetically, our new species *R. subpunicea* is clustered with an unidentified environmental sample of "*R. sp.*" from Japan, which share 97% query coverage and 99.82% identity with the new species. Unfortunately, there are no details available except the sequence information in GenBank. *Russula subpunicea* is sister to a clade comprising the North American species *R. crustosa* and the European species *R. mustelina* with good support. However, *R. crustosa* differs from *R. subpunicea* in having a brownish yellow, greenish or subolivaceous pileus with a cuticle that is cracked and forms small spot-like areolae or pseudoverrucous papules and often has short hymenial cystidia on the lamellae sides [(59)63–69–75(80) × (7)8–9.5–11(13) µm] (Peck 1886, Adamcik et al. 2018); *R. mustelina* is distinct in having a honey brown or tawny brown to dark brown pileus and often larger basidiospores (7–9.7 × 5.8–7.8 µm) and basidia (50–70 × 6–10 µm, Sarnari 1998).

Morphologically, *R. subpunicea* may be confused in the field with two recently reported new species: *R. maguanensis* J. Wang, X.H. Wang, Buyck & T. Bau and *R. substriata* J. Wang, X.H. Wang, Buyck & T. Bau from China. However, *R. maguanensis* has a sticky tuberculate-striate pileus, a finely to coarsely cracked pileus cuticle, larger basidiospores [(7.5) 8.0–8.5–9.5 × (6.5) 7.0–7.4–8.0(8.5) µm] with isolated warts, shorter hymenial cystidia on the lamellae edges (32–52 × 7–12) and a thicker pileipellis (500–800 µm, Wang et al. 2019), whereas *R. substriata* possesses a sticky tuberculate-striate pileus, a finely to coarsely cracked pileus cuticle, larger basidiospores [8.0–9.0–10.0 (11.0) × (6.5) 7.0–7.5–8.0 (9.0) µm] with isolated warts, shorter hymenial cystidia on the lamellae edges (23–45 × 6–11 µm), and typically one-layered and locally two-layered pileipellis (220–400 µm, Wang et al. 2019).

Russula albolutea B. Chen & J. F. Liang, sp. nov., Figs. 2 h–k, 5 and 6

Mycobank: MB836126

Diagnosis: Basidiomata small to medium-sized, yellowish white pileus, white stipe with yellowish tinge, subglobose to broadly ellipsoid to ellipsoid basidiospores with relatively small ornamentation, hymenial cystidia mainly clavate, apically often obtuse, contents granulose or crystalline, turning mauve in SV, suprapellis mainly composed of chains of short inflated cells with attenuated terminal cells, pileocystidia clavate, apically typically obtuse.

Holotype: China, Hubei Province, Shennongjia Forestry District, Hongping Town, 31°40'17.86" N, 110°26'40.53" E; 2560 m asl., in mixed hardwood forests dominated by *Fagus*; 10 August 2016, LYK89 (RITF2653).

Etymology: The Latin word "*albolutea*" refers to the yellowish white pileus.

Basidiomata: Small to medium-sized, pileus 50–75 mm in diameter, hemispheric when young, convex with a depressed center when mature; margin incurved, not cracked, striations up to 1/3 of the radius; surface smooth, glabrous, slightly viscous when humid, peeling to 1/3 of the radius; yellowish white (2A2) at the center; margin white (1A1). **Lamellae:** Adnate, 3–4 mm deep, moderately distant, white (1A1), lamellulae absent or rare, edge entire and concolor. **Stipe:** 30–40 × 8–15 mm, cylindrical or clavate, curved and slightly inflated at the base, rugulose longitudinally, white with yellowish tinge (2A2), medulla hollow. **Context:** 2–3 mm thick in half of the pileus radius, white (1A1), without color change when bruised, taste mild to slightly bitter, odor indistinct. **Spore print:** White.

Basidiospores: 5.8–6.6–8.2 × 5–6–6.8(–7.2) µm, Q = 1.00–1.11–1.32(1.38), subglobose to broadly ellipsoid to ellipsoid; ornamentation of relatively small, moderately distant [4–6(–8) in a 3 µm diameter circle] amyloid warts, 0.3–0.5 µm high, subreticulate, rarely isolated, fused in long branched chains [1–2(–3) in the circle], occasionally connected by line connections [0–1(–2) in the circle]; suprahilar spot large, imamyloid. **Basidia:** 28(28.5)–32.8–39(43) × (7)8.3–10–11.6(14) µm, mostly 4-spored, some 2- and 3-spored, clavate or fusiform; basidiola clavate or subcylindrical, ca. 5–11 µm wide. **Hymenial cystidia on lamellae sides:** Dispersed to moderately numerous, ca. 600–800/mm², (38)41–50.6–63(68) × 5–8.1–12 µm, clavate, fusiform or subcylindrical, apically always obtuse, occasionally mucronate, thin-walled; contents abundant granulose or crystalline, turning mauve in SV. **Hymenial cystidia on lamellae edges:** Dispersed, often smaller in

size, 27(27.5)–40–63(66) × (6)6.5–8.1–9.8 µm, clavate or cylindrical, apically often obtuse or mucronate, sometimes with 2–4 µm long appendage, thin-walled; contents granulose or crystalline, mainly in the middle and upper part, turning mauve in SV. **Marginal cells:** (14)14.7–20–26.2(26.7) × (4.4)5.3–7.2–9.8 µm, clavate or subcylindrical, sometimes flexuous. **Pileipellis:** Orthochromatic in cresyl blue, sharply delimited from the underlying context, 160–220 µm deep, two-layered; suprapellis 120–160 µm deep, mainly composed of chains of short inflated cells with attenuated terminal cells; subpellis 50–70 µm deep, composed of horizontally oriented, relatively dense, intricate, 2–6 µm wide hyphae. Hyphal terminations near the pileus margin occasionally branched, sometimes flexuous, thin-walled; terminal cells (10.4)10.8–18.8–34(42) × (3.6)4–5.2–6.8(7.1) µm, mainly subcylindrical or clavate, apically obtuse; subterminal cells often wider, ca. 5–8 µm wide, always unbranched. Hyphal terminations near the pileus center similar to those near the pileus margin; terminal cells (11.4)12.5–21.7–28(40) × 3.7–4.8–6.4(7.3) µm, mainly subcylindrical, occasionally ellipsoid, apically obtuse; subterminal cells often wider, ca. 5–7 µm wide, always unbranched. Pileocystidia near the pileus margin always one-celled, (35)39–49–60(85) × (3.6)4–5.4–8.1(9.6) µm, cylindrical, clavate or fusiform, occasionally curved at the middle part, apically usually obtuse, sometimes constricted; contents abundant, granulose or crystalline, turning reddish in SV. Pileocystidia near the pileus center often smaller, always one-celled, (28)32–43–54(58) × 4.2–5.1–6.1(6.3) µm, thin-walled, clavate or cylindrical, apically typically obtuse or occasionally mucronate, contents granulose or occasionally crystalline, turning reddish in SV. **Cystidioid hyphae:** In subpellis and context with heteromorphous-granulose contents, oleiferous hyphae in context with granulose or crystalline contents.

Additional specimens examined China, Chungking City, Shizhu County, Huangshui Town, Dafengbao Nature Reserve Communities, 30°14'33.12" N, 108°23'31.10" E, 1557 m asl., 28 July 2016, LHJ160728-04 (RITF4460); Yunnan Province, Yuxi City, Huaning County, 24°12'48.36" N, 102°56'44.72" E, 1600 m asl., August 2016, LHJ-3735 (RITF4461); Yunnan Province, Menghai County, Mengzhe Town, Mannong Village, 21°54'17.80" N, 100°17'23.32" E, 1242 m asl., 10 August 2016, MH2016-83 (RITF4462).

Notes: Both morphology and phylogeny place *R. albolutea* clearly in subsect. *Virescentinae*. In our phylogenetic tree, *R. subpunicea* is the sister taxon to *R. albolutea* but differs from it by the yellowish white to pinkish to dark pink pileus, often with smaller hymenial cystidia on the lamellar sides and larger hymenial cystidia on the lamellar edges.

Given the pileus coloration, the present species resembles four taxa (*Russula pseudocrustosa* G.J. Li & Chun Y. Deng, *R. pallidula* and *R. indoalba* A. Ghosh et al., and *R. albidogrisea* J.W. Li & L.H. Qiu) of this subsection. However, *R. pseudocrustosa*, originally described from China, possesses a cracked pileus with a radically disrupted cuticle and typically larger hymenial cystidia (67–88 × 8–12 µm, Deng et al. 2020). The Chinese species *R. pallidula* can be distinguished by the typically smaller basidiomata (40–55 µm) and pale turtle green to pale olive-buff pileus with minute white to cream scales at the margin (Chen et al. 2019). *Russula indoalba* (originally reported from India) is distinct in its wavy to interrupted pileus margin, adnexed to almost free lamellae, yellowish-cream spore print, larger basidia (45–60 × 9–13 µm) and hymenial cystidia on the lamellae sides (47–90 × 8–16 µm, Hyde et al. 2016). *Russula albidogrisea*, originally reported from China, has larger basidia (41–48 × 9–11 µm) and smaller hymenial cystidia on the lamellar sides (35–50 × 5–11 µm, Das et al. 2017).

Declarations

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Data availability Sequence data have been deposited in GenBank.

Compliance with ethical standards

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interest The authors declare that they have no competing interests.

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Figures

Figure 1

Phylogenetic tree based on the ITS-nrLSU-RPB2-mtSSU sequence dataset. Bootstrap support (BS, when $\geq 70\%$) and Bayesian posterior probabilities (PP, when ≥ 0.95) were shown. Infrageneric classification of *Russula* follows Buyck et al. (2018).

Figure 2

Fruiting bodies (a–d) and basidiospores (e–g) of *Russula subpunicea* (RITF 2653). Fruiting bodies (h–i) and basidiospores (j–k) of *R. albolutea* (RITF 3715). Scale bars a–d = 10mm, h–i = 15mm.

Figure 3

Russula subpunicea (Holotype, RITF 3715). a Basidia. b Basidiola. c Marginal cells. d Hymenial cystidia on lamellae sides. e Hymenial cystidia on lamellae edges. Scale bars = 10 μ m.

Figure 4

Russula subpunicea (Holotype, RITF 3715). a Pileipellis and pileocystidia near the pileus margin. b Pileipellis and pileocystidia near the pileus centre. Scale bar = 10 μ m.

Figure 5

R. albolutea (Holotype, RITF 2653). a Basidia. b Basidiola. c Marginal cells. d Hymenial cystidia on lamellae sides. e Hymenial cystidia on lamellae edges; Scale bars = 10 μ m.

Figure 6

Russula albolutea (Holotype, RITF 2653). a Pileipellis and pileocystidia near the pileus margin. b Pileipellis and pileocystidia near the pileus centre. Scale bar = 10 μ m.