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Article

Morphological Studies and Phylogenetic Analyses Unveil Two Notable New Species of *Russula* Subg. *Heterophyllinae* from China

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Abstract: *Russula*, a prominent genus of ectomycorrhizal fungi, is notably abundant and diverse in China. We present here the findings from studies on various Chinese *Russula* collections. Two notable species within subg. *Heterophyllinae*, namely *Russula leucoviridis* and *R. subswatica*, were described and illustrated based on comprehensive morphological characteristics and molecular evidence. Morphologically, *Russula leucoviridis* is characterized by its small to medium-sized basidiomata with a cuticle that cracks and breaks into small green patches near the center after mature, a pastel green to green pileus center with light yellow spots, and a white to greenish white pileus margin; whereas *R. subswatica* is distinguished by an infundibuliform pileus with a deeply depressed center after mature, a light orange to grayish orange pileus center, and a yellowish white to light orange margin with a purplish to purplish-black hue, and a white to yellowish white stipe that exhibits a purplish hue at the junction with the pileus. The phylogenetic analyses were constructed using a combined dataset of ITS, nrLSU, *RPB2* and *mtSSU*. Relying on both morphological characteristics and multigene phylogeny, the former species is classified within subsect. *Virescentinae*, while the latter is affiliated with subsect. *Griseinae*. In this study, we contribute new data on infrageneric phylogenetic relations and enrich the species diversity of Subg. *Heterophyllinae* in China.

Keywords: Basidiomycota; ectomycorrhizal fungi; Russulaceae; new species; China

1. Introduction

The genus *Russula* Pers., a type genus of the family Russulaceae, is recognized as the largest genus within the phylum Basidiomycota [1,2]. It comprises approximately 1,100 described species, with estimates suggesting the existence of at least 3,000 species [3,4]. Species of this genus typically form ectomycorrhizal symbiotic associations with a wide range of host trees primarily including *Pinus* spp., *Castanopsis* spp., *Picea* spp., *Larix* spp., *Fagus* spp. and *Castanea* spp., as well as with various herbs, sedges, and shrubs [5–7]. These fungi inhabit a diverse array of ecosystems, ranging from Arctic tundra to tropical forests, and play a crucial role in forest development and maintaining ecological balance [8,9]. Numerous species of *Russula* are renowned as wild edible mushrooms in various regions around the world and are commonly traded commercially [9–11]. Investigations and statistics on the resource diversity of Chinese macrofungi indicate that approximately 78 species of *Russula* are edible in China, with the *Russula griseocarnosa* complex and the *R. virescens* complex being particularly popular [10,12,13]. However, the genus *Russula* also includes several toxic species, making precise identification essential for the safe utilization of these fungi. The rapid advancements in molecular biology techniques have greatly advanced the study of the systematics and phylogeny of *Russula*. Recent molecular phylogenetic studies have indicated that the taxa within the genus *Russula* are divided into nine subgenera, namely: *R.* subg. *Glutinosae* Buyck & X.H. Wang, *R.* subg.

Archaeae Buyck & V. Hofst., *R.* subg. *Compactae* (Fr.) Bon, *R.* subg. *Brevipedum* Buyck & V. Hofst., *R.* subg. *Crassotunicatae* Buyck & V. Hofst., *R.* subg. *Heterophyllidia* Romagnesi, *R.* subg. *Cremeoohraceae* Buyck & X.H. Wang, *R.* subg. *Malodora* Buyck & V. Hofst., and *R.* subg. *Russula* Per. [14–16]. The infrageneric classification system in this study followed Buyck et al. [14–16].

Subgenus *Heterophyllidia* is one of the most complex and diverse groups within the genus *Russula*. The subgenus is mainly characterized by the mostly medium to large basidiomata, rarely very small basidiomata, almost all possible pileus colors, equal lamellae, mild to strongly acrid taste, mostly white or cream basidiospore print, basidiospores with inamyloid or partly amyloid suprahilar spot, mostly abundant gloeocystidia that are typically mucronate to obtuse-rounded, and pileipellis without primordial hyphae [14]. In China, numerous new species of subg. *Heterophyllidia* have been continuously described and reported in recent studies [17–22], underscoring the region as a hotspot for the discovery of previously unknown species. During surveys on the species diversity and geographic distribution of the subgenus *Heterophyllidia*, the first author of this paper discovered that many species, including the *R. virescens* complex, *R. cyanoxantha* complex, *R. heterophylla* complex, and several undescribed species, were being consumed and sold. Therefore, it is essential to clarify the species diversity within this subgenus to ensure the safe and sustainable consumption of these wild fungi. In this study, several new collections of subg. *Heterophyllidia* from China were examined using morphological characteristics and phylogenetic analyses, resulting in detailed descriptions and illustrations of two notable new species, along with an updated phylogenetic tree to confirm their distinct placements. This study significantly enhances our understanding of species diversity within the subg. *Heterophyllidia* in China.

2. Materials and Methods

2.1. Morphological Studies

Fresh basidiomata were collected and photographed in their natural forest habitat. All specimens were dried at temperatures ranging from 45 to 55 °C and subsequently deposited in the herbarium of the Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITF). The terminology used to describe the morphological characteristics follows the guidelines established by Adamčík et al. [3]. Macroscopic characteristics were documented through meticulous notes and high-resolution photographs. Color codes primarily adhere to the standards set by Kornerup and Wanscher [23]. Microscopic examination of the specimen sections was carried out using a ZEISS Imager M2 microscope. Estimates of spore ornamentation density were conducted in accordance with the methodology described by Adamčík and Marhold [24]. The estimates of hymenial cystidia density were performed referring to Buyck [25]. The basidiospores were observed and measured in Melzer's reagent from a lateral perspective, with ornamentation excluded. Following pretreatment of dried specimens with 5% potassium hydroxide (KOH), additional micromorphological characteristics were identified and measured in Congo red. The coloration of the cystidia contents was observed in a sulfovanillin (SV) solution [26]. The pileipellis were examined using cresyl blue to verify the presence of ortho- or metachromatic reactions [27]. The structure and ornamentation of the basidiospores were illustrated using a JEOL JSM-6510 scanning electron microscope (SEM). Basidiospore measurements are presented in the format (Min–)AV–SD–AV–AV+SD(–Max), where Min denotes the minimum value, Max denotes the maximum value, AV represents the average value, SD stands for the standard deviation, and Q indicates the length-to-width ratio of the basidiospores.

2.2. Molecular Study

Total genomic DNA was extracted from dry specimens using an optimized CTAB protocol [28]. The following four regions were amplified and sequenced using standard primer sets for enhanced accuracy and fluency: 600 base pairs of the ITS region of rDNA with the primers ITS1 and ITS4 [29]; 900 base pairs of the nuclear ribosome large subunit (nrLSU) with the primers LR0R and LR5 [30]; 700 base pairs of the second largest subunit of RNA polymerase II (*RPB2*) using the primers bRPB2-6f and fRPB2-7cr [31,32]; 600 base pairs of the ribosomal mitochondrial small subunit (mtSSU) using

primers MS1 and MS2 [29]. The successful PCR products were sequenced using an ABI 3730 DNA analyzer with the ABI BigDye 3.1 terminator cycle sequencing kit (Shanghai Sangon Biological Engineering Technology and Services Co., Ltd, Shanghai, China). The newly generated sequences have been submitted to the GenBank database.

2.3. Phylogenetic Analyses

For phylogenetic analyses, species from the subgenus *Heterophyllidia* that exhibit high similarity to our new species were selected, along with representative species closely related to subsect. *Griseinae* Jul. Schäff. and subsect. *Virescentinae* Singer. *Russula maguanensis* J. Wang, X.H. Wang, Buyck & T. Bau and *R. substriata* J. Wang, X.H. Wang, Buyck & T. Bau were utilized as the outgroup. The NCBI accession numbers for the sequences employed in the phylogenetic tree are detailed in Table 1. Initial sequence alignment was conducted using the online version MAFFT 7.0 (<http://mafft.cbrc.jp/alignment/server/>). To ensure reliable and accurate results, manual evaluations and adjustments were made in BioEdit as necessary [33]. Maximum likelihood (ML) and Bayesian analysis (BA) methods were employed for conducting the phylogenetic analyses. Maximum likelihood (ML) analysis was performed using RAXML-HPC2 on XSEDE (8.2.12) via the CIPRES Science Gateway (www.phylo.org). The ML analysis utilized the rapid bootstrap algorithm with 1000 replicates to ensure the robustness of the results under the GAMMA model. Bootstrap support (BS) values of 70% or higher on the final tree were considered significant. Bayesian analysis (BA) was conducted using MrBayes 3.2.7a on XSEDE through the CIPRES Science Gateway (www.phylo.org) under the GTR model. A total of 50 million generations were executed across four independent Markov chains, with tree sampling occurring every 100 generations. For each analysis, the initial 25% of the trees were excluded as part of the burn-in phase. The 50% majority-rule consensus trees were used to obtain Bayesian posterior probability (PP) values, and nodes with PP values of 0.95 or higher were deemed to have significant support.

Table 1. GenBank accession numbers for the sequences used in the phylogenetic analysis are provided, with newly generated sequences highlighted in bold.

Taxon	Voucher	Location	ITS	LSU	<i>RPB2</i>	mtSSU
<i>R. aeruginea</i>	AT2003017	Sweden	DQ421999	DQ421999	DQ421946	–
<i>R. aeruginea</i>	MSCZ2017100110	China	MH422576	MK881944	–	MK882072
<i>R. albidogrisea</i>	TLH18053005	China	MN275581	MN839562	MT085637	MN839610
<i>R. albidogrisea</i>	RITF1871	China	MW397095	MW397128	–	MW403841
<i>R. albolutea</i>	RITF2653	China	MT672478	MW397120	MW411340	MW403833
<i>R. albolutea</i>	RITF4460	China	MT672475	MW397121	MW411341	MW403834
<i>R. atroglaucia</i>	SAV F-3019	Slovakia	MT738270	MT738248	MT732156	–
<i>R. aureoviridis</i>	H17071311	China	MN275564	MN839561	MT085636	MN839609
<i>R. aureoviridis</i>	H16082612	China	KY767809	MK881920	–	MK882048
<i>R. crustosa</i>	BPL265	USA	KT933966	KT933826	KT933898	–
<i>R. cyanoxantha</i>	FH 12-201	Germany	KR364093	KR364225	KR364341	–
<i>R. cyanoxantha</i>	UE29.09.2002-2	France	DQ422033	DQ422033	DQ421970	–
<i>R. faustiana</i>	FH 2011 BT314	Germany	MT738277	MT738253	MT732162	–
<i>R. grisea</i>	FH12234	Germany	KT934006	KT933867	KT933938	–
<i>R. grisea</i>	UE2005.08.16-01	Germany	DQ422030	DQ422030	DQ421968	–
<i>R. heterophylla</i>	hue103 (TUB)	Europe	AF418609	AF325309	–	–
<i>R. heterophylla</i>	UE20.08.2004-2	Sweden	DQ422006	DQ422006	DQ421951	–

<i>R. icterina</i>	RITF6686	China	PP700452	PP700462	PP707790	PP700443
<i>R. icterina</i>	RITF6773	China	PP700453	PP700463	PP707792	PP700445
<i>R. ilicis</i>	563IC52	Europe	AY061682	–	–	–
<i>R. indoilicis</i>	UZ-04-18	India	MW547505	–	–	–
<i>R. junzifengensis</i>	HMAS298101	China	OR826832	OR826833	OR915864	OR941507
<i>R. junzifengensis</i>	HMAS298102	China	OR880061	OR880054	OR915865	OR941508
<i>R. leucoviridis</i>	RITF3405	China	PQ373872	PQ373868	PQ381291	PQ373876
<i>R. leucoviridis</i>	RITF3406	China	PQ373873	PQ373869	PQ381292	PQ373877
<i>R. luofuensis</i>	RITF4708	China	MW646975	MW646987	–	MW646998
<i>R. luofuensis</i>	RITF4714	China	MW646977	MW646989	–	MW647000
<i>R. maguanensis</i>	XHW4765	China	MH724918	MH714537	MH939989	OQ586179
<i>R. mariae</i>	HCCN19111	South Korea	KF361762	KF361812	KF361712	–
<i>R. medullata</i>	FH 2011 BT001	Germany	MT738280	MT738256	MT732166	–
<i>R. mustelina</i>	FH12226	Germany	KT934005	KT933866	KT933937	–
<i>R. niveopicta</i>	FHMU958	China	OP837461	OP837453	–	–
<i>R. niveopicta</i>	FHMU941	China	OP837462	OP837454	–	–
<i>R. orientipurpurea</i>	SFC20170819-08	South Korea	MT017550	–	MT199638	MT196926
<i>R. orientipurpurea</i>	SFC20170725-37	South Korea	MT017548	–	MT199639	MT196927
<i>R. pallidula</i>	RITF2613	China	MH027958	MH027960	MH091698	MW403845
<i>R. pallidula</i>	RITF3331	China	MH027959	MH027961	MH091699	MW403846
<i>R. parvovirescens</i>	SDRM 6280	USA	MK532789	–	–	–
<i>R. perviridis</i>	RITF3131	China	OR907098	OR907072	OR914548	OR934523
<i>R. perviridis</i>	RITF2912	China	OR907100	OR907070	OR914547	OR934522
<i>R. phloginea</i>	RITF6905	China	OR907116	OR907051	OR914555	OR934516
<i>R. phloginea</i>	RITF6906	China	OR907117	OR907055	OR914558	OR934520
<i>R. prasina</i>	HMAS 281232	China	MH454351	–	–	–
<i>R. pseudocrustosa</i>	HBAU15015	China	MT337520	–	–	–
<i>R. pseudopunicea</i>	BJTC ZH1392	China	OP133164	OP133204	OP156853	OP143937
<i>R. pseudopunicea</i>	BJTC ZH1389	China	OP133163	OP133203	OP156852	OP143936
<i>R. shawarensis</i>	LAH36425	Pakistan	MT738293	MT738267	MT732176	–
<i>R. shawarensis</i>	LAH36426	Pakistan	MT738292	MT738268	MT732177	–
<i>R. subbubalina</i>	RITF4710	China	MW646978	MW646990	–	MW647001
<i>R. subbubalina</i>	RITF4715	China	MW646979	MW646991	–	MW647002
<i>R. subpunicea</i>	RITF3715	China	MN833635	MW397124	MW411344	MW403837
<i>R. subpunicea</i>	RITF2648	China	MN833638	MW397125	MW411345	MW403838
<i>R. substriata</i>	XHW4766	China	MH724921	MH714540	MH939992	OQ371394
<i>R. subswatica</i>	RITF2994	China	PQ373870	PQ373866	–	PQ373874
<i>R. subswatica</i>	RITF2995	China	PQ373871	PQ373867	–	PQ373875
<i>R. swatica</i>	MH142272016	Pakistan	MK389374	–	–	–
<i>R. variata</i>	BPL241	USA	KT933959	KT933818	KT933889	–

<i>R. vesca</i>	AT2002091	Sweden	DQ422018	DQ422018	DQ421959	–
<i>R. vesca</i>	BPL284	USA	KT933978	KT933839	KT933910	–
<i>R. violeipes</i>	SFC20121010-06	South Korea	KF361808	KF361858	KF361758	–
<i>R. violeipes</i>	SFC20121010-09	South Korea	KF361807	KF361857	KF361757	–
<i>R. virescens</i>	HJB9989	Belgium	DQ422014	DQ422014	DQ421955	–
<i>R. viridicinmamomea</i>	RITF3324	China	MW397098	MW397130	MW411348	MW403847
<i>R. viridicinmamomea</i>	K15091418	China	MK049972	MK881938	–	MK882066
<i>R. viridirubrolimbata</i>	HBAU15011	China	MT337526	–	–	–
<i>R. wernerii</i>	IB1997/0786	Sweden	DQ422021	–	–	–
<i>R. wulingshanensis</i>	BTJC C403	China	OP133166	OP133206	OP156855	OP143939
<i>R. wulingshanensis</i>	BTJC C399	China	OP133165	OP133205	OP156854	OP143938
<i>R. xanthovirens</i>	H15060611	China	MG786056	MN839560	T085635	MN839608
<i>R. xanthovirens</i>	B17091630	China	MG786055	MK881928	–	MK882056

3. Results

3.1. Phylogeny

Both the Maximum Likelihood (ML) and Bayesian Analysis (BA) of the combined ITS, nrLSU, *RPB2* and *mtSSU* sequence dataset produced consistent tree topologies, with only the ML tree depicted in Figure 1. Posterior probabilities from the Bayesian analysis (BA) are also indicated along the branches. The samples of our two new species each formed a strongly supported clade, nested within subsect. *Virescentinae* and *Griseinae*. They are distinctly separate from any known and sequenced species within subg. *Heterophyllidia*. Phylogenetic analyses also confirmed that both subsections *Virescentinae* and *Griseinae* are monophyletic groups, each with robust support indicated by bootstrap values (BS) of 100% and posterior probabilities (PP) of 1, while the monophyly of the remaining four subsections within subgenus *Heterophyllidia* was also significantly supported.

Russula leucoviridis is phylogenetically positioned as the sister taxon to a clade consisting of two Chinese species *R. prasina* G.J. Li & R.L. Zhao and *R. xanthovirens* Y. Song & L.H. Qiu, with 100% bootstrap support and 1.00 posterior probabilities. Our second species, *R. subswatica* clustered with Pakistani species *R. swatica* Sarwar & Hanif, demonstrating robust phylogenetic support with 100% bootstrap support and 1.00 posterior probabilities.

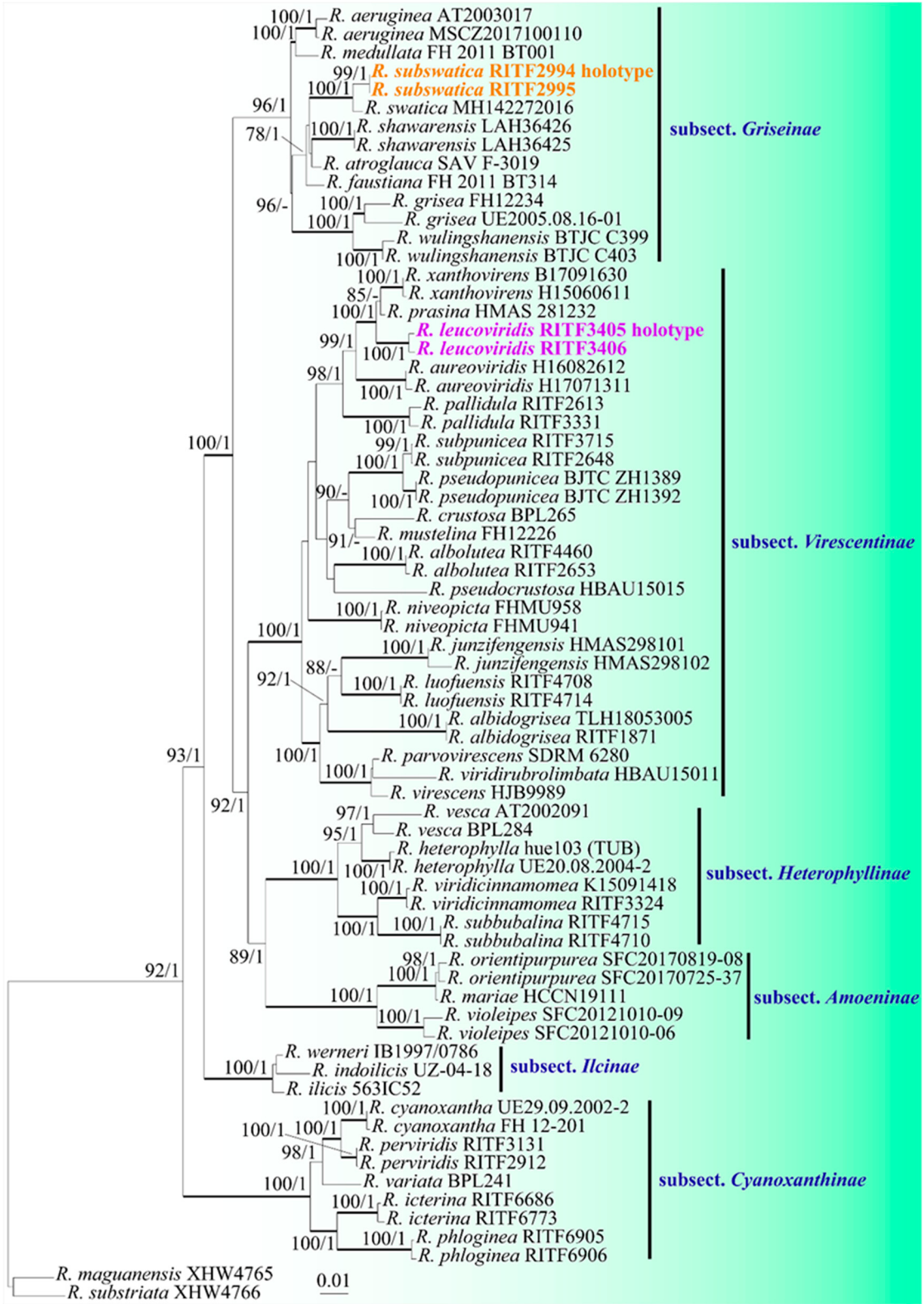


Figure 1. The phylogenetic tree based on the ITS-nrLSU-RPB2-mtSSU dataset. Species within the subgenus *Heterophyllidia* that exhibit high similarity to our new species, as well as representative species closely related to subsections *Griseinae* and *Virescentinae*, were selected. Support values are shown with Bootstrap support (BS) $\geq 70\%$ and Bayesian Posterior Probabilities (PP) ≥ 0.95 .

3.2. Taxonomy

Russula leucoviridis B. Chen & J. F. Liang, sp. nov. (Figures 2–4)

MycoBank: MB855842

Diagnosis: Pileus small to medium-sized; cuticle adhering many small frosty particles near the center when young, cracking and broken into small green patches near the center after mature, patches crowded towards the center; pastel green to green towards the center with light yellow spots, white to greenish white near the margin.

Holotype: China, Hainan Province, Wuzhishan City, Shuiman Town, Wuzhi Mountain National Reserve; 18°51'59.50" N, 109°40'30.59" E, 800m asl., in evergreen broad-leaved forest; 23 June 2016, leg. JXM105 (RITF3405).

Etymology: Leuco (Latin) = white; viridis (Latin) = green; the species name refers to white pileus margin and green center.

Description: Pileus small to medium-sized, 30–55 mm in diameter; initially hemispheric when young, expanding to planeconvex with a depressed center after mature; margin incurved, not cracked, striation up to the 1/3 of the radius; cuticle dry, glabrous, peeling to 1/4 of the radius, many small adhering frosty particles near the center when young, cracking and broken into small green patches near the center after mature, patches crowded towards the center; pastel green (27A4) to green (27A7) towards the center with light yellow (3A5) spots, white (1A1) to greenish white (28A2) near the margin. Lamellae adnate to almost free, 3–5 mm deep, 8–10 at 1 cm near the pileus margin, white (1A1) to cream; lamellulae sometimes present and irregular in length; furcations occasional near the stipe; edge entire and concolor. Stipe 20–55 × 7–16 mm, cylindrical, slightly inflated towards the base, white (1A1) to almond, medulla initially stuffed when young, becoming hollow after mature. Context 2–3 mm thick in half of the pileus radius, white (1A1), unchanging when bruised, taste mild, odor inconspicuous. Spore print white (1A1) to cream.

Basidiospores (5.7–)6.0–6.9–7.8(–8.8) × (4.8–)5.3–5.9–6.5(–7.0) μm, Q = 1.03–1.15–1.27(–1.36), subglobose to broadly ellipsoid; ornamentation of medium-sized, moderately distant [5–6(–8) in a 3 μm diameter circle] amyloid warts or spines, 0.3–0.5 μm high, locally reticulate, occasionally fused in short chains [0–2(–3) in the circle], occasionally to frequently connected by line connections [2–3(–4) in the circle]; suprahilar spot small, amyloid. Basidia (35.0–)39.0–46.0–53.0(–56.2) × (8.4–)9.3–10.3–11.4 μm, mostly 4-spored, sometimes 2- and 3-spored, clavate; basidiola subcylindrical or clavate, ca. 5.5–9.5 μm wide. Hymenial gloeocystidia on lamellae sides dispersed to moderately numerous, (46.0)48.6–57.7–66.8(76.0) × (7.4–)8.4–10.1–11.9(12.7) μm, typically fusiform, occasionally clavate, apically mainly obtuse, occasionally acute, sometimes with 4–8 μm long appendage, thin-walled; contents granulose or heteromorphous, turning reddish black in SV. Hymenial gloeocystidia on lamellae edges often narrower, (38.7–)44.8–55.7–66.5(–75.2) × (5.6–)6.3–7.8–9.2(–9.8) μm, typically clavate, sometimes fusiform, apically mainly obtuse, rarely mucronate, sometimes with 4–8 μm long appendage, thin-walled; contents heteromorphous, turning reddish black in SV. Marginal cells (16.7–)18.4–22.8–27.2(–30.6) × (3.2–)3.8–4.5–5.1 μm, clavate or lageniform, sometimes flexuous. Pileipellis orthochromatic in cresyl blue, not sharply delimited from the underlying context, 240–320 μm deep, two-layered; suprapellis 180–200 μm deep, composed of loose, ascending or erect hyphal terminations; subpellis 80–140 μm deep, composed of intricate, dense, 3–6 μm wide hyphae. Hyphal terminations near the pileus margin occasionally unbranched, sometimes flexuous, thin-walled; terminal cells (10.8–)13.2–22.3–31.4(–37.4) × (4.0–)4.5–5.0–5.7(–6.2) μm, mainly narrowly lageniform, occasionally cylindrical, apically attenuated or constricted, sometimes obtuse; subterminal cells often shorter and wider, ca. 5–8 μm wide, rarely branched. Hyphal terminations near the pileus center similar; terminal cells (8.0–)10.0–14.1–18.2(–25.0) × (2.6–)3.1–3.7–4.3(–4.7) μm, mainly lageniform or subcylindrical, apically attenuated or constricted; subterminal cells often shorter and wider, rarely branched, ca. 4–6 μm wide. Pileocystidia near the pileus margin always one-celled, (30.9–)32.3–37.5–42.8(–47.5) × (2.8–)3.8–5.0–6.2(–6.8) μm, mainly clavate, occasionally fusiform or lanceolate, apically typically obtuse, occasionally acute, sometimes with 2–5 μm long, round or ellipsoid appendage, thin-walled; contents granulose or heteromorphous, turning reddish black in SV. Pileocystidia near the pileus center similar, always one-celled, (29.6–)31.4–36.5–41.6(–44.6) × (3.3–)3.7–4.4–5.2(–5.4) μm,

thin-walled, mainly clavate or cylindrical, apically obtuse, contents granulose or heteromorphous, turning reddish black in SV.

Additional specimens examined: China, Hainan Province, Wuzhishan City, Shuiman Town, Wuzhi Mountain National Reserve; 18°51'59.50" N, 109°40'30.59" E, 800m asl., in evergreen broad-leaved forest; 23 June 2016, leg. JXM106 (RITF3406).

Notes: *Russula leucoviridis* is positioned within the subsection *Virescentinae* based on a combination of its morphological characteristics and phylogenetic analysis. In phylogenetic analysis, *R. leucoviridis* is the sister taxon to a clade consisting of *R. prasina* and *R. xanthovirens*, both originating from China, with strong support evidenced by 100% bootstrap values and 1.00 posterior probability. However, *R. prasina* often has the larger basidiomata (43–130 mm), a grass green pileus center and pale yellowish green margin, pale ocher lamellae and ochraceous yellow stipe base [34]; *R. xanthovirens* differs from *R. leucoviridis* in having the larger basidiomata (50–75 mm), a yellowish green to deep green pileus center with cracked yellowish margin when age, whitish lamellae with reddish hue, white stipe with green tinge, often shorter and wider basidia [(29–)30–51.5(–60) × (9.5–)10–9.5–14.5(–15) μm] and often longer pileocystidia (40–69.5 × 4–9 μm) [35].

Given cracking pileus surface, *R. virescens* (Schaeff.) Fr., *R. parvovirescens* Buyck, D. Mitch. & Parrent and *R. viridirubrolimbata* J. Z. Ying and *R. crustosa* Peck of subsect. *Virescentinae* resemble *R. leucoviridis*. However, *R. virescens*, originally described from Europe, can be distinguished by usually larger basidiomata [40–90(125) mm], a green to yellowish green pileus and shorter basidia (40–52 × 6–9.2 μm) [36]. The American species *R. parvovirescens* has a greenish brown to metallic bluish green pileus with green patches, often larger basidiospores (6.7–9.1 × 5.7–7.2 μm) and smaller Basidia (38–45 × 8–9 mm) [37]. *R. viridirubrolimbata*, (originally reported from China) is distinct in a light yellowish olive to yellowish olive pileus center with a pinkish red to light jasper red margin, smaller basidia (31–43 × 7–10 μm), larger hymenial gloeocystidia on lamellae sides (78–107 × 8–10 μm) and absence of hymenial gloeocystidia on lamellae edges [13,38]. *Russula crustosa*, initially described in North America, possesses a brownish-yellow, greenish or subolivaceous pileus, shorter basidia [(29–)30–32–33.5(–35) × (7.5–)8–9.5–10.5(–11) μm], longer hymenial gloeocystidia on lamellae sides [(59–)63–69–75(–80) × (7–)8–9.5–11(–13) μm] and absence of hymenial gloeocystidia on the lamellar edges [39].



Figure 2. Basidiomata and microscopic structures of *Russula leucoviridis*. (A–D) Basidiomata. (E,F) Basidiospores in SEM (JSM-6510LV). Scale bars: 10mm (A–D), 2 µm (E), 1µm (F).

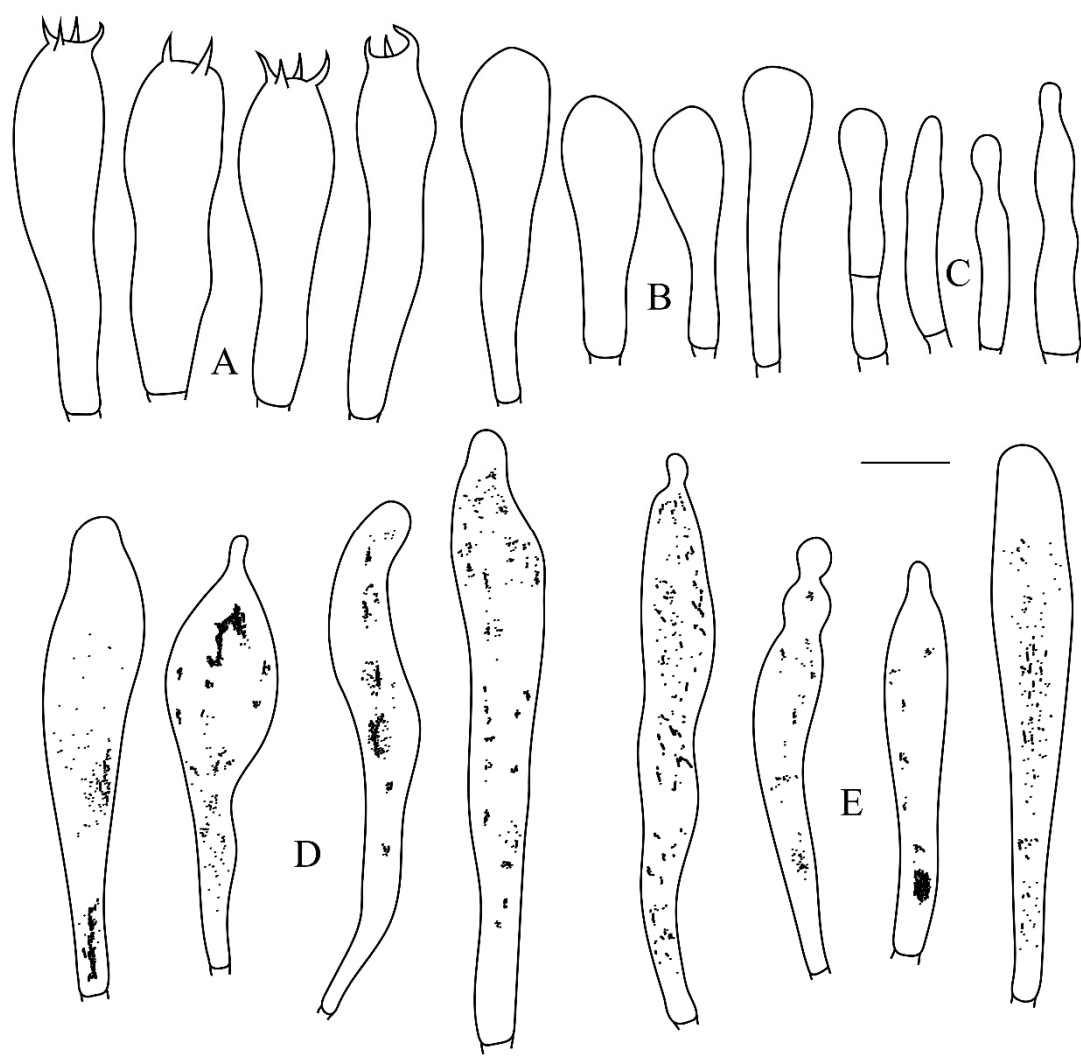


Figure 3. Microscopic structures of *Russula leucoviridis*. (A) Basidia. (B) Basidiola. (C) Marginal cells. (D) Hymenial gloeocystidia on lamellae sides. (E) Hymenial gloeocystidia on lamellae edges. Scale bar: 10 μ m.

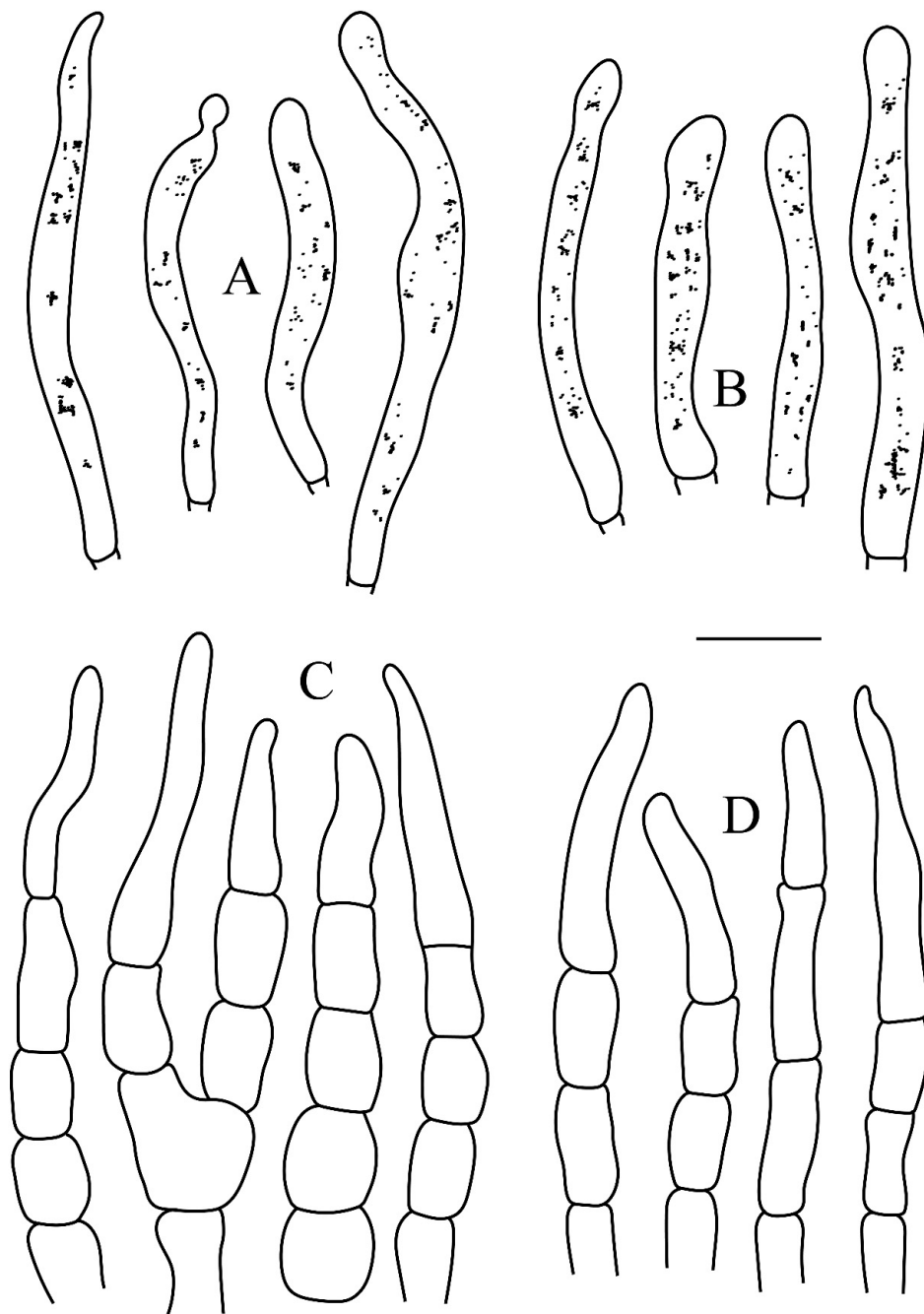


Figure 4. Microscopic structures of *Russula leucoviridis*. (A) Pileocystidia near the pileus margin. (B) Pileocystidia near the pileus center. (C) Hyphal terminations near the pileus margin. (D) Hyphal terminations near the pileus center. Scale bar: 10 μ m.

Russula subswatica B. Chen & J. F. Liang, sp. nov. (Figures 5–7)

MycoBank: MB855843

Diagnosis: Pileus medium-sized to large; initially flat hemispheric when young, expanding and infundibuliform with a deeply depressed center after mature; light orange to grayish orange near the center, yellowish white to light orange towards the margin, partially with a purplish to purplish-black hue. Stipe white to yellowish white, exhibiting a purplish hue at the junction with the pileus.

Holotype: China. Xizang Autonomous Region, Nyingchi City, Motuo County; 29°22'13.43" N, 95°26'58.75" E, 900m asl., in mixed forest dominated by *Quercus aquifolioides* Rehder & E. H. Wilson; 15 July 2014, leg. T25530 (RITF2994).

Etymology: The species name refers to its morphological resemblance to *Russula swatica*.

Discription: Pileus medium-sized to large, 55–70 mm in diameter; initially flat hemispheric when young, soon expanding and infundibuliform with a deeply depressed center after mature; margin incurved, sometimes cracked after mature, striation short and inconspicuous; cuticle smooth, dry, glabrous, peeling to 1/3 of the radius; light orange (5A4) to grayish orange (6B5) near the center, yellowish white (2A2) to light orange (5A4) towards the margin, partially with a purplish to purplish-black hue. Lamellae deccurent, 2–4 mm deep, 8–11 at 1 cm near the pileus margin, white (1A1) to cream; lamellulae present and irregular in length; furcations occasional near the stipe; edge entire and concolor. Stipe 60–70 × 12–15 mm, cylindrical, slightly inflated towards the base, white (1A1) to yellowish white (2A2), exhibiting a purplish hue at the junction with the pileus, medulla initially stuffed when young, becoming hollow after mature. Context 3–5 mm thick in half of the pileus radius, white (1A1), unchanging when bruised, taste mild, odor inconspicuous. Spore print white (1A1) to yellowish white (2A2).

Basidiospores (5.7–)6.0–7.0–8.0(–8.5) × (4.7–)5.1–6.2–7.2(–8.3) μm , $Q = 1.03\text{--}1.15\text{--}1.27\text{--}(1.36)$, subglobose to broadly ellipsoid; ornamentation of medium-sized, dense [9–11(–12) in a 3 μm diameter circle] amyloid warts, 0.2–0.8 μm high, occasionally to frequently fused in short or long chains [2–3(–4) in the circle], occasionally connected by line connections [0–1(–2) in the circle]; suprahilar spot medium-sized, amyloid. Basidia (36.6–)39.8–44.0–48.0(–54.0) × (6.4–)8.5–9.6–10.7(–11.0) μm , mostly 4-spored, sometimes 2- and 3-spored, clavate; basidiola clavate or subcylindrical, ca. 6–9.5 μm wide. Hymenial gloeocystidia on lamellae sides dispersed to moderately numerous, (55.3)60.5–72.4–84.3(97.0) × (10.2)7.7–8.8–9.9(10.5) μm , typically clavate or fusiform, occasionally lanceolate, apically mainly mucronate, occasionally obtuse, often with 4–10 μm long appendage, thin-walled; contents heteromorphous or granulose, turning yellowish brown in SV. Hymenial gloeocystidia on lamellae edges often shorter, (44.8–)52.4–68.3–84.2(–95.8) × (5.5–)7.8–9.6–11.4 μm , typically clavate or subcylindrical, occasionally fusiform, apically mainly obtuse, occasionally mucronate, usually with 3–6 μm long appendage thin-walled; contents heteromorphous, turning reddish black in SV. Marginal cells (15.8–)19.6–24.2–28.8(–35.5) × (3.6–)3.8–5.3–6.7(–9.0) μm , subcylindrical or clavate, sometimes flexuous. **Pileipellis** orthochromatic in cresyl blue, not sharply delimited from the underlying context, 200–260 μm deep, two-layered; suprapellis 140–180 μm deep, composed of loose, ascending or erect hyphal terminations; subpellis 80–100 μm deep, composed of relatively dense, intricate, 3–5 μm wide hyphae. Hyphal terminations near the pileus margin rarely unbranched, occasionally flexuous, thin-walled; terminal cells (9.2–)12.4–19.3–26.3(–35.2) × (4.3–)4.9–5.6–6.3(–7.0) μm , typically lageniform, occasionally clavate or subcylindrical, apically attenuated or constricted, sometimes obtuse; subterminal cells frequently shorter and wider, ca. 5–7 μm wide, typically unbranched. Hyphal terminations near the pileus center similar; terminal cells (13.7–)16.8–20.7–25.3(–27.7) × (3.7–)4–4.5–5(–6.7) μm , mainly lageniform or subcylindrical, apically attenuated or constricted; subterminal cells often shorter and wider, unbranched, ca. 4–6.5 μm wide. Pileocystidia near the pileus margin always one-celled, (45.5–)49.4–59.5–69.6(–77.4) × (5.8–)6.0–6.8–7.6(–10.0) μm , mainly clavate, occasionally subcylindrical, apically obtuse, occasionally mucronate, sometimes with 3–5 μm long, round or ellipsoid appendage, thin-walled; contents heteromorphous, turning yellowish brown in SV. Pileocystidia near the pileus center often shorter and narrower, always one-celled, (38.3–)42.6–52.6–62.5(–70.8) × (4.8–)5.5–6.3–7.0 μm , thin-walled, mainly clavate or fusiform, apically obtuse or mucronate, sometimes with 3–6 μm long appendage, contents heteromorphous or granulose, turning r yellowish brown in SV.

Additional specimens examined: China, Xizang Autonomous Region, Nyingchi City, Motuo County; 29°22'13.43" N, 95°26'58.75" E, 900m asl., in mixed forest dominated by *Quercus aquifolioides* Rehder & E. H. Wilson; 15 July, 2014, leg. T25531 (RITF2995).

Notes: The integration of morphological characteristics and phylogenetic analysis positions *R. subswatica* within the subsection *Griseinae*. In the phylogenetic tree, *R. subswatica* is clustered with Pakistani species *R. swatica*, exhibiting strong phylogenetic support with 100% bootstrap support and 1.00 posterior probabilities. However, *R. swatica* is distinguished from *R. subswatica* by its light brown to gray pileus, narrower basidiospores (6–8 × 4–6 μm), and often shorter and wider hymenial gloeocystidia (59–70 × 10–15 μm) [40].

Morphologically, *R. subswatica* exhibits certain similarities with *R. medullata* Romagn., and *R. shawarensis* Kiran & Khalid, both of which belong to subsect. *Griseinae*. However, *R. medullata*, originally report from Europe, can be distinguished by a lilac, flesh-pink, pinkish brown, and pinkish grey pileus, ochraceous lamellae after mature and ochre spore print [36,41]. The Pakistani species *R. shawarensis* has a light pinkish brown to grey buff pileus, very rare to absent lamellulae, shorter basidia [(31.5–)34–39.5(–41) × (7–)9–10.5(–11) μm], often larger hymenial gloecystidia on lamellae sides [(66–)72–92.5(–105) × (9.5–)10–13(–14) μm], longer the terminal cells of the hyphae near both the pileus margin (av. 48.2 × 3.8 μm) and the pileus center (av. 41.5 × 4.2 μm), and longer pileocystidia near the pileus center (av. 58 × 7 μm) [42].

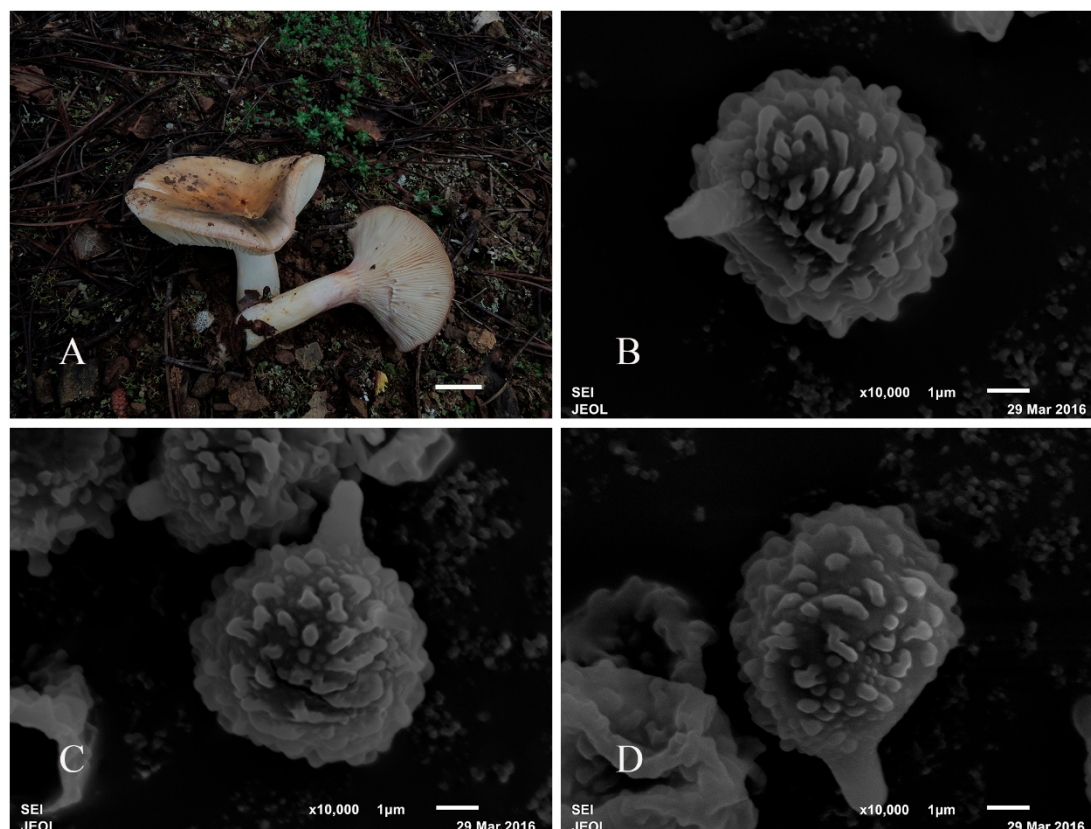


Figure 5. Basidiomata and microscopic structures of *Russula subswatica*. (A) Basidiomata. (B–D) Basidiospores in SEM (JSM-6510LV). Scale bars: 15mm (A), 1μm (B–D).

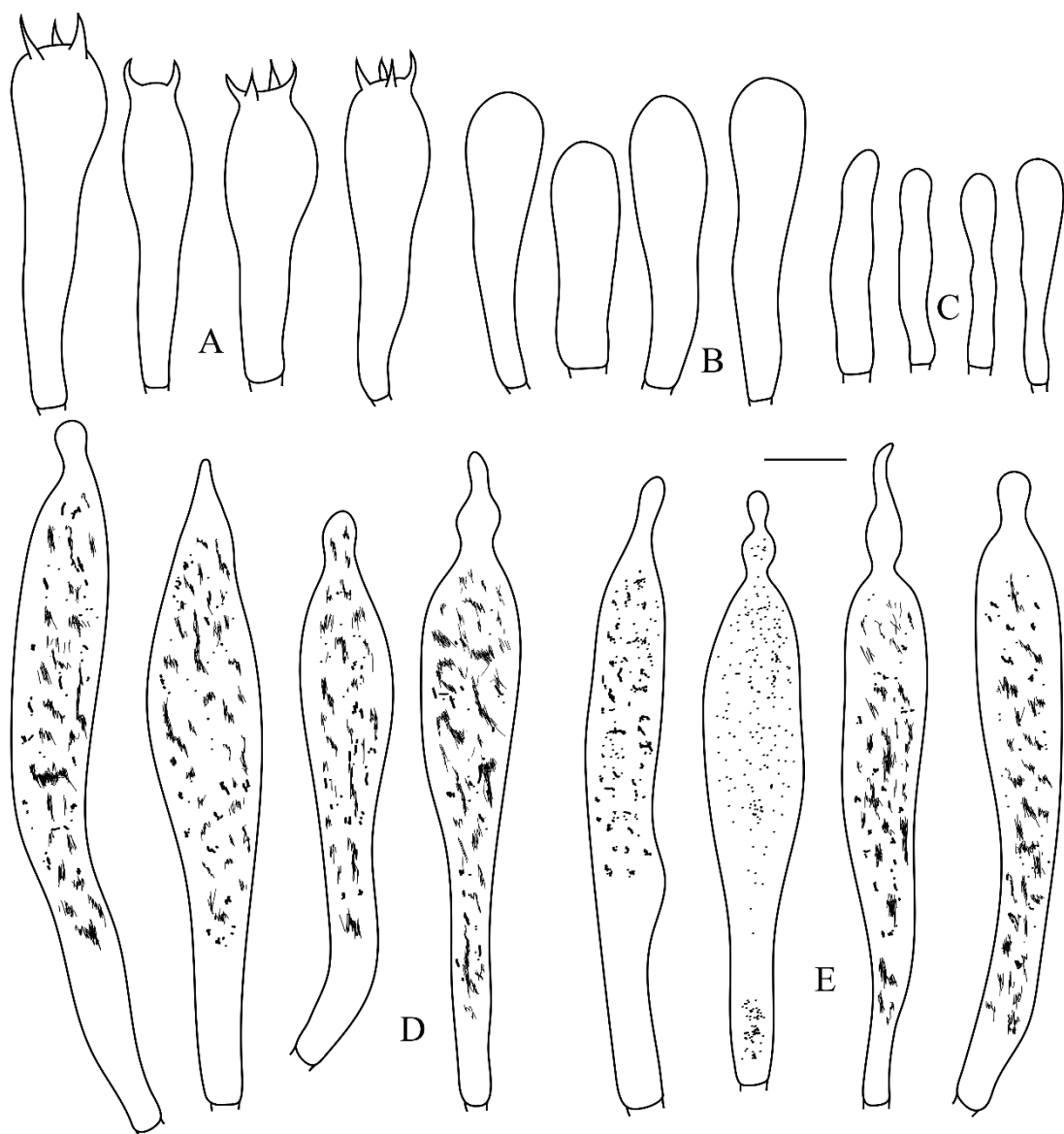


Figure 6. Microscopic structures of *Russula subswatica*. (A) Basidia. (B) Basidiola. (C) Marginal cells. (D) Hymenial gloeocystidia on lamellae sides. (E) Hymenial gloeocystidia on lamellae edges. Scale bar: 10 μm.

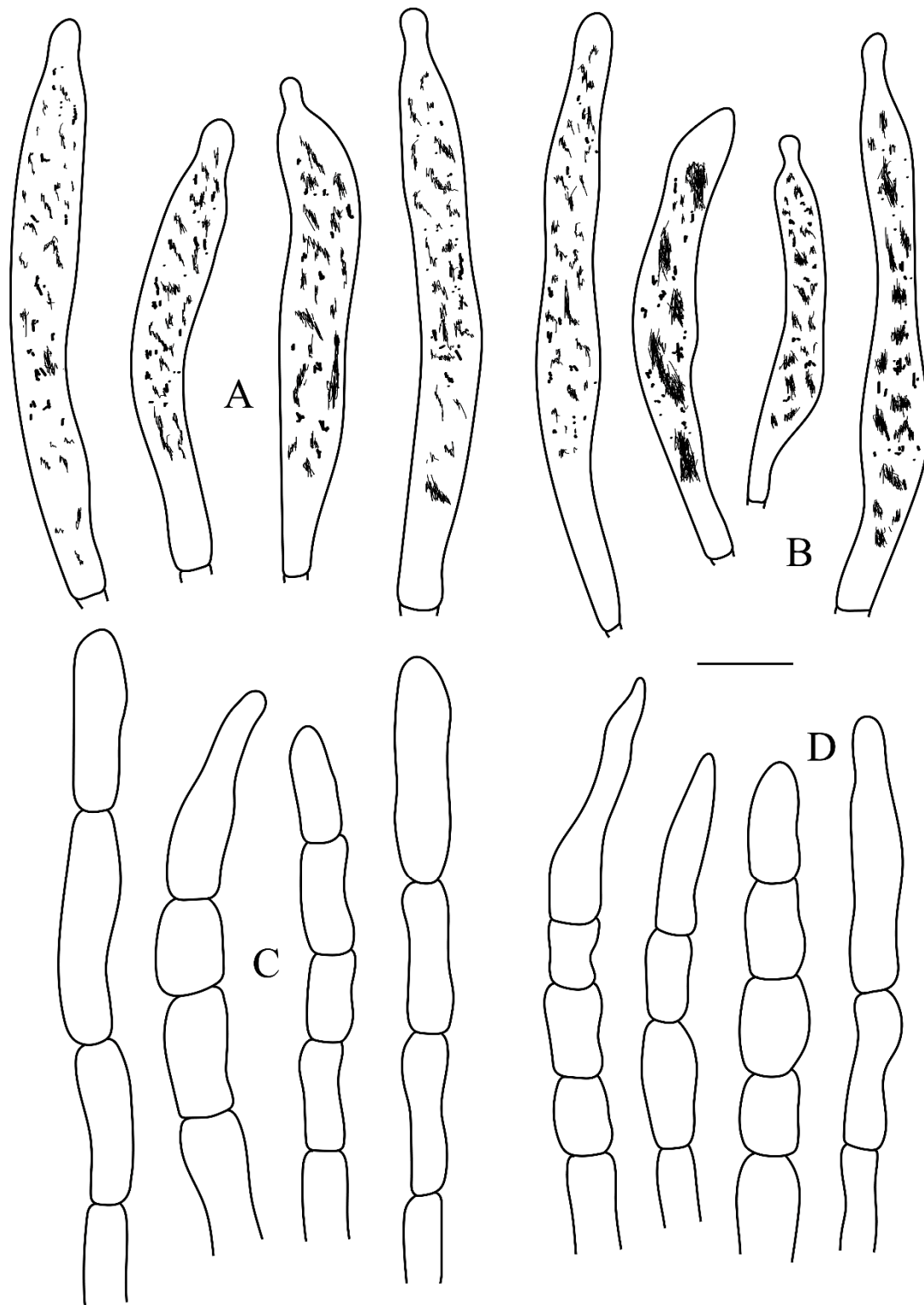


Figure 7. *Russula subswatica* of *Russula subswatica*. (A) Pileocystidia near the pileus margin. (B) Pileocystidia near the pileus center. (C) Hyphal terminations near the pileus margin. (D) Hyphal terminations near the pileus center. Scale bar: 10 μ m.

4. Discussion

In this study, we have described and named two new species of *Russula* subg. *Heterophyllinae*: *R. leucoviridis* and *R. subswatica*. The identification and characterization of these species enhance our understanding of the biodiversity and phylogenetic relationships within the subg. *Heterophyllinae* in China. These findings highlight the richness and diversity of ectomycorrhizal fungi in the region,

significantly contributing to both taxonomic and ecological studies. *Russula leucoviridis* is notable for its small to medium-sized basidiomata with a cuticle that cracks and breaks into small green patches near the center after mature, a pastel green to green pileus center with light yellow spots, and a white to greenish white pileus margin. In contrast, *R. subswatica* is characterized by its infundibuliform pileus, a light orange to grayish orange pileus center, and a yellowish white to light orange margin with a purplish to purplish-black hue, and a white to yellowish white stipe that exhibits a purplish hue at the junction with the pileus. These unique morphological characteristics are crucial for differentiating these new species from closely related ones, and their distinctiveness is further confirmed by multi-gene phylogenetic analysis. Phylogenetic studies based on ITS, nrLSU, *RPB2*, and *mtSSU* regions, offer robust support for the classification of these species. The assignment of *R. leucoviridis* to subsection *Virescentinae* and *R. subswatica* to subsection *Griseinae* suggests distinct evolutionary pathways and adaptation strategies within the subg. *Heterophyllinae*. In conclusion, the combination of molecular evidence and morphological characteristics provides strong support for the recognition and delineation of these new species. The addition of *R. leucoviridis* and *R. subswatica* not only enriches the taxonomic diversity of the subgenus but also highlights the ongoing need for meticulous taxonomic research to uncover the hidden diversity of fungi.

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Conflicts of Interest: The authors declare no conflict of interests.

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