

Article

A Contribution to Knowledge of *Russula* Section *Ingratae* (Russulales, Russulaceae) in China: Two New Taxa and Amended Descriptions of One Known Species

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Abstract: *Russula*, one of the main genera of Russulaceae (Russulales), is both ecologically and economically important. It is a large and complex genus including eight subgenera. Although many studies have focused on *Russula* in China, the diversity still remains incompletely understood. In the present study, several collections of *Russula* subgen. *Heterophyllidiae* sect. *Ingratae* from China were studied based on morphology and molecular phylogenetic analyses. Three species were recognized, two of them described as new, *R. fujianensis* and *R. oraria*, and one of them already a known taxon, *R. rufobasalis*. Detailed descriptions, color photos of fresh basidiomata, and line-drawings of microstructures of the three species are presented.

Keywords: molecular phylogeny; morphology; new taxon; taxonomy



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1. Introduction

Russula Pers. (Russulaceae, Russulales) is a highly diverse group with about 2000 species worldwide. Nearly all species of the genus are typical ectomycorrhizal fungi, which play an important role in maintaining biodiversity in forest ecosystems [1–3]. Due to the importance of ecological value, extensive studies about *Russula* have been performed. Recently, the genus has been divided into eight subgenera: *Archaeae* Buyck and V. Hofst., *Brevipedum* Buyck and V. Hofst., *Compactae* (Fr.) Bon, *Crassotunicatae* Buyck and V. Hofst., *Glutinosa* Buyck and X.H. Wang, *Heterophyllidiae* Romagn., *Malodorae* Buyck and V. Hofst., and *Russula* Pers [4,5]. Among them, subgen. *Heterophyllidiae*, especially sect. *Ingratae* (Quél.) has received much attention. The section is characterized by a pileus with yellow to brown tints, a margin with obvious radial tuberculate striate, a presence of distinctly fetid or acrid odour, and basidiospores inamyloid to partly amyloid in the suprahilar area [6–9]. In China, species diversity of sect. *Ingratae* is abundant, with 14 taxa confirmed to distribute across the country [9–16]. Moreover, the poisonousness of the section has attracted great interest in the country. For example, collections identified as *R. senecis* S. Imai were reported to be poisonous, which can cause gastroenteritis [17–19].

Although many species of sect. *Ingratae* have been described in China [9–16], with more field investigations, more novel species of the section will be uncovered. During field investigations in subtropical and tropical China, several *Russula* collections were made. These specimens were examined using morphology and molecular phylogenetic analyses, and were eventually confirmed to represent two novel species and one previously known species of sect. *Ingratae*. Thus, the three taxa were described/redescribed herein, aiming to contribute to new taxonomic knowledge of sect. *Ingratae*.

2. Materials and Methods

2.1. Morphological Studies

Fresh basidiomata were photographed in the field in daylight and their macroscopic characteristics were measured and recorded. Specimens were dried at 50–60 °C, then deposited in the Fungal Herbarium of Hainan Medical University (FHMU) (Index Herbariorum), Haikou City, Hainan Province, China. Color codes referred to Kornerup and Wanscher [20]. Templates of descriptions and terminologies of micromorphological characters were obtained from Adamčík et al. [21]. The pileipellis section taken from the pileus between the center and margin, and the stipitipellis from the middle part along the longitudinal axis of the stipe, were also observed [22]. Spore ornamentation density estimated from scanning electron microscopy pictures followed Adamčík and Marhold [23]. The hymenial cystidia density estimates referred to Buyck [24]. The pileipellis ortho- or metachromatic reactions were examined in Cresyl Blue after Buyck [25]. Sulfovanillin (SV) was used to observe color changes of cystidia contents [26]. Observations and measurements of microscopic features were made in 1% Congo Red, five percent potassium hydroxide (KOH), or Melzer's reagent. Basidiospore measurements exclude ornamentation and apiculus. The basidiospores were examined using a TM4000Plus scanning electron microscope (SEM). All the microscopic structures were drawn by free-hand. The number of measured basidiospores is given as n/m/p, where "n" represents the total number of basidiospores measured from "m" basidiomata of "p" specimens. Dimensions of basidiospores are presented as (a-)b-e-c(-d), where the "b-c" represents a minimum of 90% of the measured values (5th to 95th percentile), and extreme values (a and d), whenever present (a < 5th percentile, d > 95th percentile), are in parentheses, "e" refers to the average length/width of basidiospores. "Q" refers to the length/width ratio of basidiospores; "Qm" refers to the average "Q" of basidiospores and is given with standard deviation.

2.2. Molecular Procedures

Plant Genomic DNA Kit (CWBIO, Beijing, China) was used to extract total genomic DNA from silica gel-dried collections according to the manufacturer's instructions. Primer pairs used for amplification were: nuc 28S rDNA D1-D2 domains (28S) with LR0R/LR5 [27,28], nuc rDNA region including the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS) with ITS5/ITS4 [29]. PCR reactions were performed with 4 min initial denaturation at 95 °C, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at the appropriate temperature (50 °C for 28S and ITS) for 30 s, extension at 72 °C for 120 s and a final extension at 72 °C for 7 min. Amplified PCR products were purified using the DNA Purification Kit (TIANGEN, Beijing, China) according to the manufacturer's instructions, and then directly sequenced using a BigDye terminator v3.1 Kit and an ABI 3730xl DNA Analyzer (Guangzhou Branch of BGI, Guangzhou, China) with the same primers used for PCR amplification. DNA sequences were compiled with BioEdit v7.0.9 [30], and then deposited in GenBank (Table 1).

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

Taxon	Voucher	Locality	GenBank Accession Nos.		Reference
			ITS	28S	
<i>Russula</i> aff. <i>amoenolens</i>	HMJAU37318	Heilongjiang, NE China	KY357332	—	[31]
<i>R. ahmadii</i>	LAH 35004	Pakistan	KT834638	KX911834	[32]
<i>R. ahmadii</i>	LAH 18081013	Pakistan	KU535609	—	[32]
<i>R. amerorecondita</i>	F (PGA17-017)	USA	MN130066	—	[21]
<i>R. amerorecondita</i>	SH120828	USA	MN130067	—	[21]
<i>R. amoenolens</i>	46372 (AH)	Spain	MK105626	MK105707	[33]
<i>R. amoenolens</i>	TUB nl27.9.95.6	Germany	AF418615	AF325295	[34]

Table 1. Cont.

Taxon	Voucher	Locality	GenBank Accession Nos.		Reference
			ITS	28S	
<i>R. arunii</i>	CUH:AM270	India	KY450661	KY946733	[35]
<i>R. arunii</i>	CUH:AM261 (holotype)	India	KR872619	KY946732	[35]
<i>R. blennia</i>	569/BB08.066 (holotype)	Madagascar	MH545687	KU237556	[36]
<i>R. benghalensis</i>	CUH AM654 (holotype)	India	MK414583	MK496844	[37]
<i>R. catillus</i>	SFC20120725-52	Republic of Korea	KX574685	—	[38]
<i>R. catillus</i>	SFC20120827-01 (holotype)	Republic of Korea	KX574686	—	[38]
<i>R. catillus</i>	SFC20120919-35	Republic of Korea	KX574688	—	[38]
<i>R. catillus</i>	LHJ150915-19	Guangdong, southern China	MK860690	—	Unpublished
<i>R. cerolens</i>	F36	USA	JN681168	—	Unpublished
<i>R. cf. pseudolepida</i>	BPL247	USA	KT933962	KT933821	[39]
<i>R. clavulus</i>	RITF3300	Guizhou, SW China	MN317302	MN325079	[15]
<i>R. clavulus</i>	RITF3216	Guizhou, SW China	MN317303	MN325080	[15]
<i>R. clavulus</i>	RITF3204	Yunnan, SW China	MN317304	MN325081	[15]
<i>R. clavulus</i>	RITF3334 (holotype)	Yunnan, SW China	MN317301	MN325078	[15]
<i>R. compacta</i>	BPL242	USA	KT933960	KT933819	[39]
<i>R. compacta</i>	HFJAU0301	Jiangxi, SE China	MN258682	—	Unpublished
<i>R. echidna</i>	HO 593336	Australia	MN130079	—	[21]
<i>R. echidna</i>	HO 593337	Australia	MN130080	—	[21]
<i>R. elastica</i>	3/BB 06.009	Madagascar	—	KU237451	[40]
<i>R. ferruginea</i> subsp. <i>ferruginea</i>	HUA Corrales935	Colombia	MZ604289	MZ604284	[40]
<i>R. ferruginea</i> subsp. <i>ferruginea</i>	HUA Corrales1019	Colombia	MZ604291	MZ604286	[40]
<i>R. ferruginea</i> subsp. <i>ferruginea</i>	HUA Corrales944 (holotype)	Colombia	MZ604288	MZ604283	[40]
<i>R. ferruginea</i> subsp. <i>panamensis</i>	UCH A28 (holotype)	Panama	MZ604292	MZ604287	[40]
<i>R. flavobrunnea</i> var. <i>violaceotincta</i>	71//BB 06.050	Madagascar	—	KU237468	[40]
<i>R. fluvialis</i>	KUO (JR8666) (holotype)	Finland	MN130084	MN130125	[21]
<i>R. fluvialis</i>	KUO (JR8313)	Finland	MN130085	MN130126	[21]
<i>R. foetens</i>	HMJAU 32234	Heilongjiang, NE China	KX095018	—	Unpublished
<i>R. foetens</i>	TUB hue124	Germany	AF418613	AF325299	[34]
<i>R. foetens</i>	GENT FH-12-277	Germany	KT934016	KT933877	[39]
<i>R. foetentoides</i>	LAH 04081023	Pakistan	HE647707	—	[41]
<i>R. foetentoides</i>	LAH 13081034	Pakistan	HE647708	—	[41]
<i>R. foetentula</i>	156	USA	KJ834623	—	[42]
<i>R. fragrantissima</i>	98	Italy	KJ530751	—	[42]
<i>R. fujianensis</i>	N.K. Zeng1449 (FHMU993)	Fujian, SE China	ON332048	ON318391	This study
<i>R. fujianensis</i>	N.K. Zeng1431 (FHMU975) (holotype)	Fujian, SE China	ON332049	ON318392	This study
<i>R. garyensis</i>	F (PGA17-008)	USA	MN130088	—	[21]
<i>R. garyensis</i>	F (PGA1-910)	USA	MN130089	—	[21]
<i>R. gelatinosa</i>	K15052626 (holotype)	Guangdong, southern China	MH168575	—	[12]
<i>R. gelatinosa</i>	K16053119	Guangdong, southern China	MH168574	—	[12]

Table 1. Cont.

Taxon	Voucher	Locality	GenBank Accession Nos.		Reference
			ITS	28S	
<i>R. granulata</i>	PC BB2004-226	USA	EU598192	—	Unpublished
<i>R. granulata</i>	PC BB2004-225	USA	EU598190	—	Unpublished
<i>R. granulata</i>	HMAS252604	Jilin, NE China	KF850414	—	[43]
<i>R. granulata</i>	BPL272	USA	KT933971	KT933832	[39]
<i>R. grata</i>	HMJAU 38008	Heilongjiang, NE China	KY681444	—	[31]
<i>R. griseobrunnea</i>	JAC13201	New Zealand	MW683824	MW683661	Unpublished
<i>R. hainanensis</i>	N.K. Zeng4888 (FHMU4860)	Hainan, southern China	—	OM280996	[16]
<i>R. hainanensis</i>	N.K. Zeng4899 (FHMU4855) (holotype)	Hainan, southern China	OM280999	OM280997	[16]
<i>R. heterophylla</i>	UE20.08.2004-2	Sweden	DQ422006	—	[44]
<i>R. hortensis</i>	IB 1997/0787 (holotype)	Italy	HG798528	—	Unpublished
<i>R. illota</i>	MICH73719	France	KF245509	—	Unpublished
<i>R. illota</i>	UE26.07.2002-3	Sweden	DQ422024	—	[34]
<i>R. inamoena</i>	107	Italy	KJ834597	—	[42]
<i>R. inamoena</i>	109	Italy	KJ834595	—	[42]
<i>R. indocatillus</i>	HGAS-MF009917	Guizhou, SW China	MN649191	—	[9]
<i>R. indocatillus</i>	HGAS-MF009903	Guizhou, SW China	MN649192	—	[9]
<i>R. indocatillus</i>	AG 17-1571 (holotype)	India	MN581483	—	[45]
<i>R. indocatillus</i>	AG 18-1653	India	MN581165	—	[45]
<i>R. indosenecis</i>	AG-21-04A	India	OL701254	—	[46]
<i>R. indosenecis</i>	AG-21-06A (holotype)	India	OL701269	—	[46]
<i>R. insignis</i>	HMAS267740	Heilongjiang, NE China	KF850404	—	[9]
<i>R. laurocerasi</i>	FH12178	Germany	KT933988	KT933849	[39]
<i>R. laurocerasi</i>	TUB nl1348	Germany	AF418614	—	[34]
<i>R. laurocerasi</i>	E00290534	UK	KF245532	—	Unpublished
<i>R. livescens</i>	F0177	China	GU371295	—	[47]
<i>R. maguanensis</i>	XHW4765	Yunnan, SW China	MH724918	MH714537	[48]
<i>R. mistiformis</i>	JC170305NR	Spain	MK105677	—	[33]
<i>R. mistiformis</i>	AMC H-69	Spain	MK105680	—	[33]
<i>R. multilamellula</i>	LHJ14092423 (holotype)	Guizhou, SW China	MT791347	MT793120	[15]
<i>R. multilamellula</i>	wuxingliang03	Guizhou, SW China	MT791348	MT793121	[15]
<i>R. mustelina</i>	1176/S. Adamcik 09.88	Slovakia	—	KU237596	[40]
<i>R. mutabilis</i>	DPL10654	USA	KF810137	—	[49]
<i>R. mutabilis</i>	BHI-F384a	USA	MF161239	—	[50]
<i>R. obscuricolor</i>	KD 16-30 (holotype)	India	MF805816	—	[51]
<i>R. obscuricolor</i>	KD 16-22	India	MF805817	—	[51]
<i>R. oleifera</i>	254/BB 98.024	Burundi	—	KU237490	[40]
<i>R. ombrophila</i>	86	Spain	KF971694	—	[42]
<i>R. oraria</i>	N.K. Zeng4829 (FHMU5374)	Hainan, southern China	ON332052	OQ380695	This study
<i>R. oraria</i>	N.K. Zeng4823 (FHMU5355) (holotype)	Hainan, southern China	ON332053	OQ380696	This study
<i>R. pectinata</i>	2010BT02	Germany	KF318081	—	[42]
<i>R. pectinata</i>	2010BT48	Germany	KF318082	—	[42]
<i>R. pectinatoides</i>	HMAS251202	Yunnan, SW China	JX425405	—	[43]
<i>R. pectinatoides</i>	NYS2303.1	USA	KU640189	—	[42]
<i>R. pila</i>	JMV800654 (BCN)	Spain	MK105691	MK105736	[33]

Table 1. Cont.

Taxon	Voucher	Locality	GenBank Accession Nos.		Reference
			ITS	28S	
<i>R. pilosella</i>	BRI-H5974	Australia	EU019941	—	[52]
<i>R. pseudocatillus</i>	K16042406 (holotype)	Guangdong, southern China	MK049974	—	[14]
<i>R. pseudocatillus</i>	K15060706	Guangdong, southern China	MK049975	—	[14]
<i>R. pseudociliata</i>	545/BB 08.061	Madagascar	MH545688	KU237537	[40]
<i>R. pseudopectinatoides</i>	HMAS265020	Xizang, SW China	KM269079	—	[11]
<i>R. pseudopectinatoides</i>	HMAS251523 (holotype)	Xizang, SW China	KM269077	—	[11]
<i>R. pseudopectinatoides</i>	RITF1353	China	MK860689	—	[13]
<i>R. pseudosenecis</i>	AG 20-062 (holotype)	India	OL461233	—	[46]
<i>R. pseudosenecis</i>	AG 21-073	India	OL461234	—	[46]
<i>R. pulverulenta</i>	4-1144IS79	USA	AY061736	—	[53]
<i>R. pulverulenta</i>	PC BB2004-245	USA	EU598186	—	Unpublished
<i>R. punctipes</i>	K17052318	Guangdong, southern China	MH168576	—	[12]
<i>R. punctipes</i>	K16051001	Guangdong, southern China	MH168577	—	[12]
<i>R. recondita</i>	92	Switzerland	KJ530750	—	[42]
<i>R. rufobasalis</i>	H17052204 (holotype)	Guangdong, southern China	MH168570	—	[12]
<i>R. rufobasalis</i>	H15060622	Guangdong, southern China	MH168567	—	[12]
<i>R. rufobasalis</i>	N.K. Zeng1416 (FHMU961)	Fujian, SE China	ON332050	ON318393	This study
<i>R. rufobasalis</i>	N.K. Zeng1270 (FHMU827)	Fujian, SE China	ON332051	ON318394	This study
<i>R. senecis</i>	CUH AM102	India	KP142981	—	[54]
<i>R. senecis</i>	SFC20110921-18	Republic of Korea	KX574698	—	[38]
<i>R. siamensis</i>	Watling 28784	Thailand	AB206535	—	[55]
<i>R. straminella</i>	HGAS-MF009920	Guizhou, SW China	MN649194	—	[9]
<i>R. straminella</i>	HGAS-MF009922 (holotype)	Guizhou, SW China	MN649195	—	[9]
<i>R. straminella</i>	HGAS-MF009925	Guizhou, SW China	MN649189	—	[9]
<i>R. subfoetens</i>	HMJAU 38006	Heilongjiang, NE China	KY681430	—	[31]
<i>R. subpectinatoides</i>	HBAU15023 (holotype)	Jiangsu, eastern China	MW041163	—	[9]
<i>R. subpectinatoides</i>	HBAU15024	Jiangsu, eastern China	MW041164	—	[9]
<i>R. subpectinatoides</i>	HBAU15025	Jiangsu, eastern China	MW041165	—	[9]
<i>R. subpectinatoides</i>	HBAU15026	Jiangsu, eastern China	MW041166	—	[9]
<i>R. subpunctipes</i>	RITF2616 (holotype)	Hubei, central China	MK860692	MK860695	[13]
<i>R. subpunctipes</i>	RITF2617	Hubei, central China	MK860693	MK860696	[13]
<i>R. substriata</i>	WJ292	Yunnan, SW China	MH724919	MH714538	[48]
<i>R. substriata</i>	XHW4749	Yunnan, SW China	MH724920	MH714539	[48]
<i>R. substriata</i>	XHW4766 (holotype)	Yunnan, SW China	MH724921	MH714540	[48]
<i>R. substriata</i>	XHW4767	Yunnan, SW China	MH724922	MH714541	[48]
<i>R. substriata</i>	XHW4785	Yunnan, SW China	MH724923	MH714542	[48]
<i>R. succinea</i>	HGAS-MF 009909	Guizhou, SW China	MN649196	—	[9]
<i>R. succinea</i>	HGAS-MF 009904 (holotype)	Guizhou, SW China	MN649188	—	[9]
<i>R. succinea</i>	HGAS-MF 009906	Guizhou, SW China	MN649198	—	[9]
<i>R. succinea</i>	HGAS-MF 009915	Guizhou, SW China	MN649190	—	[9]
<i>R. variata</i>	BPL241	USA	KT933959	KT933818	[39]
<i>R. ventricosipes</i>	PC 0142480	USA	KY800364	—	[56]
<i>R. vinaceocuticulata</i>	PDD 64246	New Zealand	GU222258	—	Unpublished
<i>Russula</i> sp.	LHJ170913-01	Guangdong, southern China	MK860691	MK860694	[13]

SW = Southwestern, SE = Southeastern, NE = Northeastern.

2.3. Dataset Assembly

Twelve DNA sequences (6 of 28S, and 6 of ITS) from 6 collections were newly generated. Edited sequences were submitted to GenBank; the GenBank accession numbers of 28S and ITS are provided in Table 1, which are identified in boldface. For the concatenated dataset, newly generated 28S and ITS sequences were aligned with sequences of sect. *Ingratae* with greater representativeness as well as availability from previous studies and GenBank (Table 1). *Russula blennia* Buyck, *R. compacta* Frost and *R. griseobrunnea* McNabb were chosen as outgroup. MUSCLE was used to align the 28S and ITS sequences individually to test for phylogenetic conflict [57]. Then, the sequences of the different genes were concatenated using Phyutility v2.2 for further analyses [58].

2.4. Phylogenetic Analyses

Both Maximum Likelihood (ML) and Bayesian Inference (BI) were employed for phylogenetic analysis. Maximum Likelihood of the phylogenetic relationships was conducted with the program RAxML 7.2.6 running 1000 replicates combined with an ML search [59]. Bayesian analysis with MrBayes 3.1 implementing the Markov Chain Monte Carlo (MCMC) technique and parameters predetermined with MrModeltest 2.3 was performed [60,61]. The best-fit likelihood models for 28S and ITS were SYM + I + G and HKY + I + G, respectively. Bayesian analysis was repeated for 17 million generations, and sampled every 100. Trees sampled from the first 25% of the generations were discarded as burn-in, and Bayesian posterior probabilities (PP) were then calculated for a majority consensus tree of the retained Bayesian trees. Runs were terminated once the average standard deviation of split frequencies decreased below 0.01.

3. Results

3.1. Molecular Data

Sixty-three species of sect. *Ingratae*, four species of sect. *Heterophyllae*, two species of subsect. *Cyanoxanthinae*, and two species of subsect. *Substriatinae* were used for the construction of the phylogram of *Russula* sect. *Ingratae* (Figure 1). The topologies of the phylogenetic trees based on a single gene (28S and ITS) were identical, suggesting that the phylogenetic signals present in the different gene fragments (28S and ITS) were not in conflict. The two-locus data set (28S + ITS) consisted of 134 taxa and 1532 nucleotide sites. The topologies of phylogenetic trees generated from ML and BI analyses were identical, though statistical support for some branches showed slight differences. The phylogram with branch lengths inferred from the 28S and ITS dataset with RAxML is shown with the support values (Figure 1).

The current molecular data indicate that the Chinese specimens of sect. *Ingratae* were grouped into 24 independent lineages (1–24) (Figure 1). We were particularly interested in lineages 3, 20, and 21, which included our new collections. Lineage 3 had strong statistical support (BS = 100, PP = 1.0), and included two specimens (FHMU975 and FHMU993) from southeastern China; lineage 20 consisted of the holotype (H17052204) and one specimen (H15060622) of *R. rufobasalis* from southern China, and two collections (FHMU827 and FHMU961) from southeastern China, with high statistical support (BS = 100, PP = 1); lineage 21, which had strong statistical support (BS = 100, PP = 1) comprising two specimens (FHMU5355 and FHMU5374) from southern China (Figure 1).

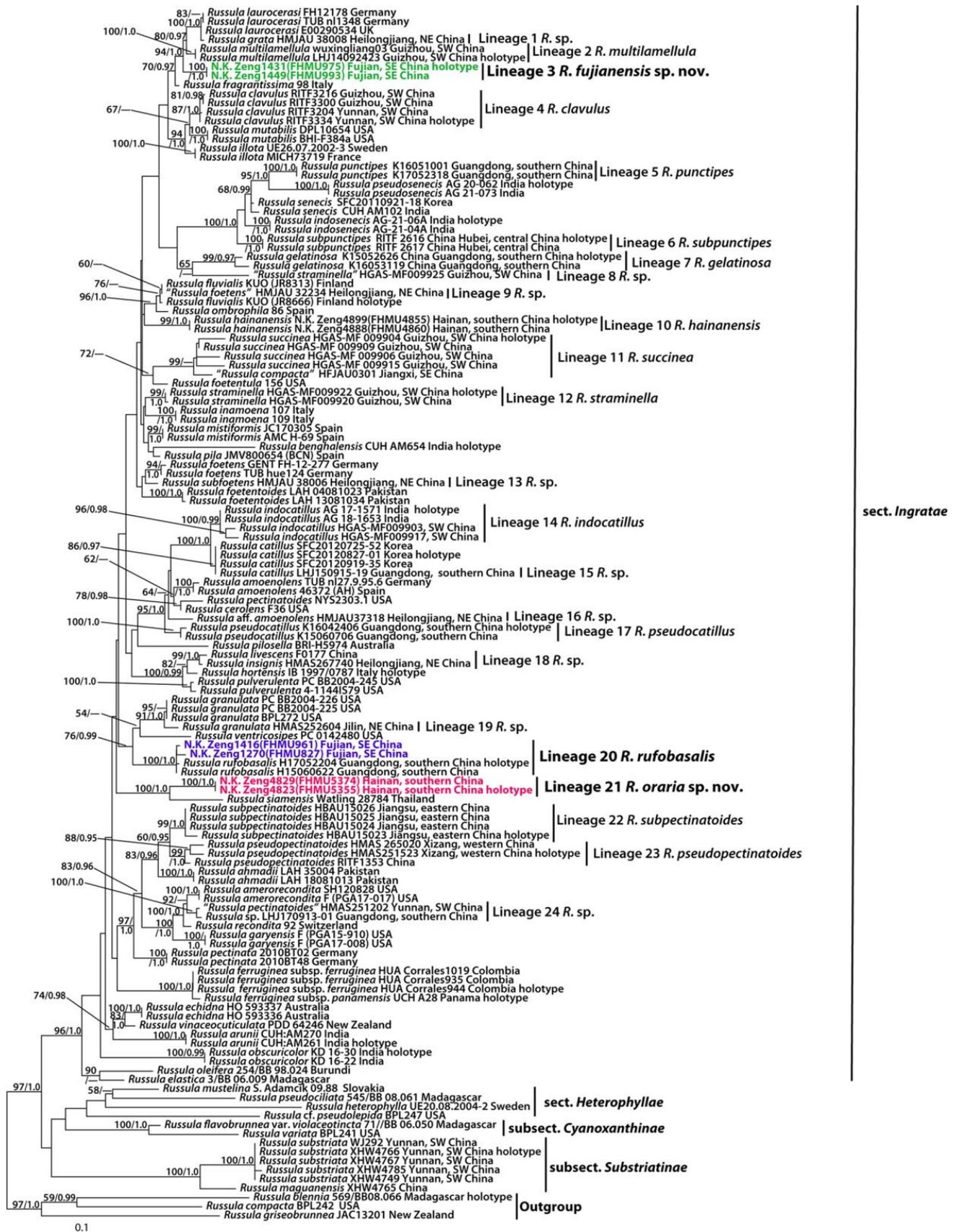


Figure 1. A phylogram of *Russula* sect. *Ingratae* inferred from a two-locus (rDNA 28S and ITS) dataset using RAxML. BS \geq 50% and PP \geq 0.95 are indicated above or below the branches as RAxML BS/PP. SW = Southwestern, SE = Southeastern, NE = Northeastern. Newly generated sequences are in color.

3.2. Taxonomy

Russula fujianensis N.K. Zeng, Y.X. Han & Zhi Q. Liang, sp. nov. (Figures 2a,b, 3a,b, 4 and 5).

Mycobank: MB 845634.

Etymology—Latin “*fujianensis*”, refers to Fujian Province, China, holotype locality.

Diagnosis—Differs from closest species of sect. *Ingratae* by a pale yellowish-brown pileus, a long, white stipe (ca. 6.5–12 cm), basidiospores usually with large wings (up to 2.0 μm), never forming a reticulum, a hymenophore with fewer pleurocystidia (less than 700/ mm^2), cystidia turning to yellowish brown in SV, and it is associated with trees of Fagaceae.



Figure 2. Basidiomata of *Russula* sect. *Ingratae* species. (a,b) *R. fujianensis* (a) from FHMU975, holotype; (b) from FHMU993); (c,d) *R. oraria* (c) from FHMU5355, holotype; (d) from FHMU5374); (e,f) *R. rufobasalis* (FHMU961). Bars: 1 cm. Photos: N.K. Zeng.

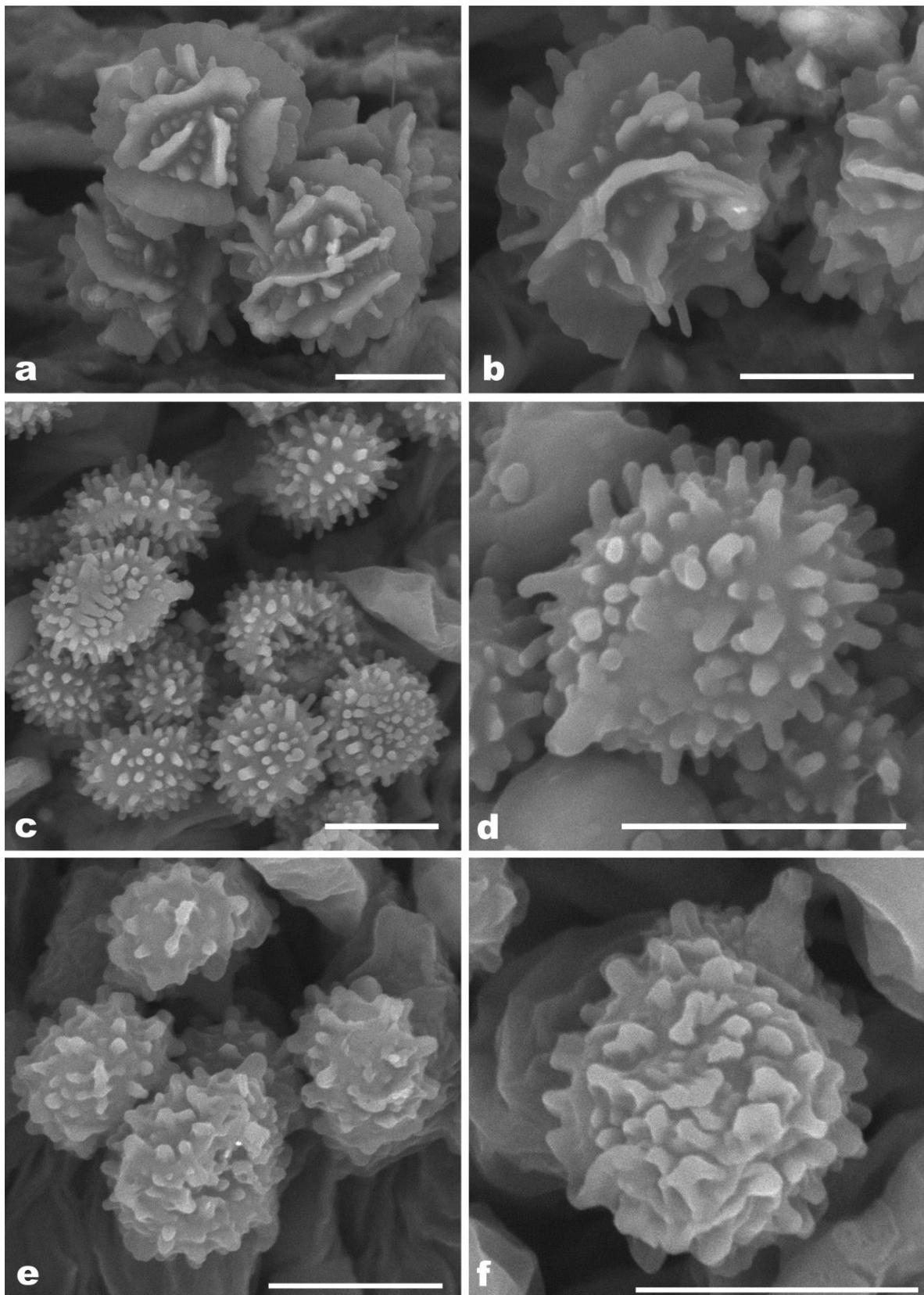


Figure 3. Basidiospores of *Russula* sect. *Ingratae* species from herbarium materials under SEM. (a,b) *R. fujianensis* (FHMU975, holotype); (c,d) *R. oraria* (FHMU5355, holotype); (e,f) *R. rufobasalis* (FHMU827). Bars: 5 μ m. Photos: Y.X. Han.

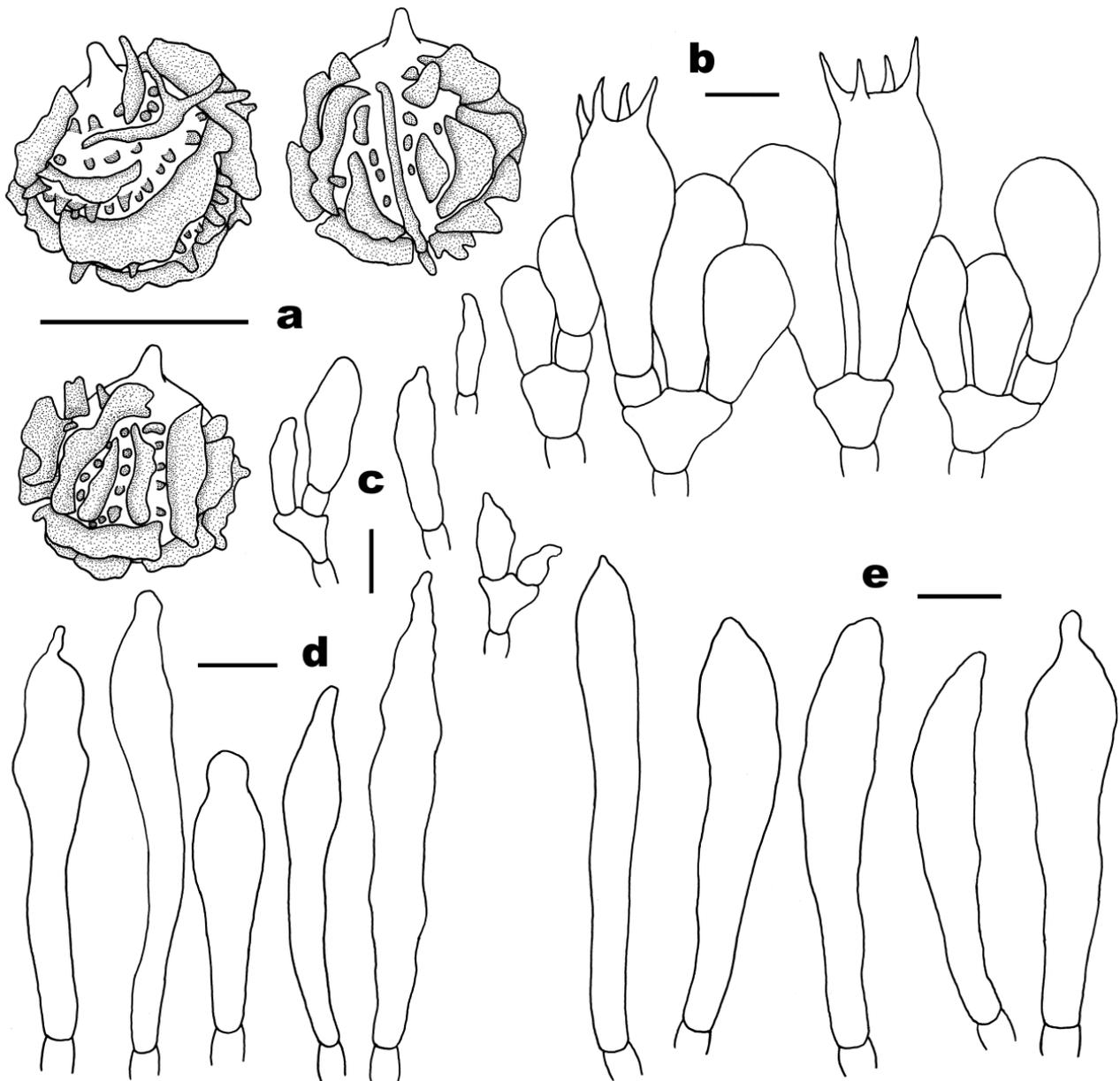


Figure 4. Microscopic features of *Russula fujianensis* (FHMU975, holotype). (a) Basidiospores. (b) Basidia and basidiola. (c) Marginal cells. (d) Pleurocystidia. (e) Cheilocystidia. Bars: 10 μ m. Drawings by Y.X. Han.

Holotype—CHINA. Fujian Province: Zhangping County, Xinqiao Town, Chengkou Village, elev. 350 m, 18 August 2013, N.K. Zeng1431 (FHMU975). GenBank accession numbers: 28S = ON318392, ITS = ON332049.

Description—*Basidiomata* medium-sized. *Pileus* 5–7 cm diameter, spherical at first, then subhemispherical, applanate, center slightly depressed; surface slightly sticky, pale yellowish-brown (1B3), pale brown (5D4) to dark brown (5E5), margin with obvious radial tuberculate-striate; context 4–5 mm thick at the center of the pileus, white (2A1), unchanging in color when injured. *Hymenophore* lamellate, adnate; lamellae about 5 mm in height, crowded, occasionally forked, white (2A1), unchanging in color when injured, edge even; lamellulae rare, concolorous with lamellae. *Stipe* 6.5–12 \times 1–1.8 cm, central, subcylindrical to cylindrical, hollow, annulus absent; surface white, sometimes tinted with peal brown (5B3) to peal yellowish-brown (1B4). *Taste* acid. *Odour* fetid. *Spore print* not obtained.

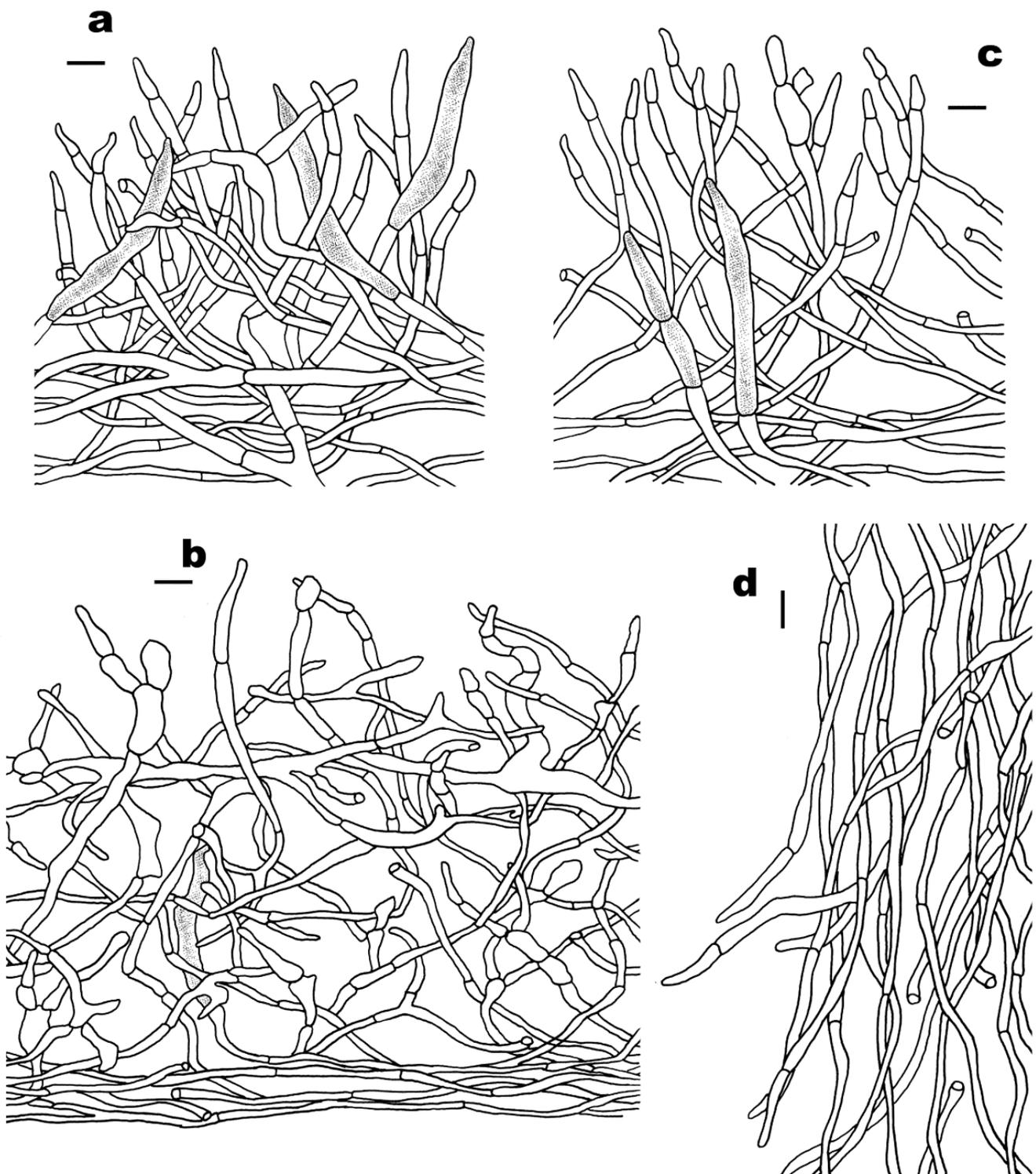


Figure 5. Microscopic features of *Russula fujianensis* (FHMU975, holotype). (a) Pileipellis at pileus margin. (b) Pileipellis at middle part between center and margin of pileus. (c) Pileipellis at pileus centre. (d) Stipitipellis. Bars: 10 μm . Drawings by Y.X. Han.

Basidiospores (excluding ornamentation) [40/6/2] 7–8.1–8.5 (–9) \times 6.5–7.6–8 (–8.5) μm , $Q = 1–1.14$ (–1.15), $Q_m = 1.07 \pm 0.04$, globose to subglobose, ornamentation composed of large, moderately distant to dense ((5–) 6–8 in a 3 μm diameter circle) amyloid warts or wings, 0.9–2.0 μm high, isolated or occasionally fused (0–3 fusions in the circle); wings nearly encircling the spores, mixed with numerous short, blunt, isolated warts, line connec-

tions absent; suprahilar spot inamyloid and indistinct. *Basidia* (35–) 39.5–45–51.5 (–54) × (10–) 14.5–15.5–16 (–17) μm, hyaline in KOH, thin-walled (up to 0.4 μm), clavate, 4-spored; sterigmata 4–7 μm, slightly tortuous, sometimes straight; basidiola clavate, ca. 7.5–15 μm wide. *Pleurocystidia* dispersed, less than 700/mm², (35–) 46–52–60 × (6.5–) 7.5–8.5–10 μm, narrowly clavate to clavate, apically often obtuse or acute, sometimes fusiform, occasionally with 2.5–4 μm long appendage, thin-walled (up to 0.4 μm); contents abundant granulose, yellowish in Congo Red, turning to yellowish brown in SV. *Cheilocystida* (45–) 49.5–52–62 × (6–) 7.5–9.5–11.5 μm, narrowly clavate to subcylindrical, apex obtuse or mucronate, sometimes with 1.5–4 μm long appendage, thin-walled (up to 0.3 μm); contents granulose, yellowish in Congo Red, turning to yellowish brown in SV. *Lamellae edges* fertile. *Marginal cells* (6–) 10.5–16.5–20.5 × 3.5–4–5 (–6.5) μm, clavate or subcylindrical, usually shorter than basidiola, thin-walled (up to 0.4 μm). *Lamellar trama* mainly composed of sphaerocytes measuring up to 49 μm in diameter, hyaline in KOH, thick-walled (1–1.5 μm). *Pileipellis* orthochromatic in Cresyl Blue, not sharply delimited from the underlying context, a trichoderm 120–200 μm thick, two-layered, weakly gelatinized; composed of suprapellis (50–100 μm thick) and subpellis (70–100 μm thick). *Suprapellis* composed of erect to suberect hyphae 3–7 μm in diameter, thin-walled (up to 0.3 μm). *Subpellis* composed of horizontally oriented, dense, 2.5–7 μm wide intricate hyphae. *Acid-resistant incrustations* absent. *Hyphal terminations near the pileus margin* composed of 1–3 unbranched cells, not flexuous, thin-walled (up to 0.3 μm); terminal cells (9–) 12–18–23 × 4–4.5–5 μm, mainly clavate, occasionally subcylindrical, apex obtuse, rarely mucronate; subterminal cells often wider and longer, rarely branched. *Hyphal terminations on the middle part between center and margin of pileus* 1–3 cells, less flexuous and unbranched, terminal cells (13–) 18–21.5–24 × (4–) 4.5–5–7 μm, mainly clavate, occasionally subcylindrical, apex obtuse, rarely mucronate; subterminal cells often wider and longer, occasionally branched. *Hyphal terminations near the pileus centre* 1–3 cells, not flexuous; shorter terminal cells 8–14–20 × 3–4–4.5 (–5) μm, subcylindrical, apically obtuse; subterminal cells often wider and longer, rarely branched. *Pileal trama* made up of hyphae up to 41 μm in diameter, thick-walled (up to 1 μm), hyaline to pale yellowish in KOH. *Pileocystidia near the pileus margin* always long, one-celled, (55–) 63–70–89 × 7–8–8.5 μm, cylindrical to clavate, apex occasionally obtuse or usually mucronate, contents yellow in Congo Red, turning to yellowish brown in SV. *Pileocystidia near the pileus centre* narrower cylindrical to clavate, 1–2 celled, (26–) 45–57–65 × 5–5.5–6 μm, contents granulose, yellow in Congo Red, turning to yellowish brown in SV. *Cystidioid hyphae* in subpellis and context, contents granulose. *Stipitipellis* a cutis composed of hyphae slightly thick-walled (up to 0.7 μm), 2–6 μm wide, hyaline in KOH; terminal cells 12–28 × 4–5.5 μm, subcylindrical or subclavate. *Stipe trama* mainly composed of sphaerocytes measuring up to 43 μm in diameter, hyaline to pale yellowish in KOH, thick-walled (1.5–2 μm). *Clamp connections* absent in all tissues.

Habitat—Gregarious or fascicled on the ground in forests dominated by *Castanopsis kawakamii* Hayata.

Known distribution—Eastern China (Fujian Province).

Additional specimen examined—China. Fujian Province: Zhangping County, Xinqiao Town, Chengkou Village, elev. 350 m, 20 August 2013, N.K. Zeng1449 (FHMU993).

Notes—Morphologically, some Asian members of section *Ingratae*, viz., *R. gelatinosa* Y. Song and L.H. Qiu, *R. punctipes* Singer, and *R. subpunctipes* J. Song share similar winged basidiospores with our new species. However, *R. gelatinosa*, originally described from Guangdong Province of southern China, has higher wings (up to 3.5 μm high) on basidiospores, short, blunt ridges and warts forming an incomplete network between basidiospores wings, and suprapellis composed of short, inflated to globular subterminal and terminal elements [12]; *R. punctipes*, originally described from Hunan Province of central China, has a smaller basidioma, a shorter stipe (3.5–5.5 cm long), higher wings (up to 3 μm high) on basidiospores, short, blunt ridges and warts forming an incomplete network between basidiospores wings, suprapellis mainly composed of inflated subterminal cells [12]; *R. subpunctipes*, originally described from Hubei Province of central China, has

a pileus cracking into patches towards the margin, higher wings (up to 2.5 μm high) on basidiospores, and suprapellis mainly composed of inflated subterminal cell [13].

Phylogenetically, *R. fujianensis* is closely related to *R. multilamellula* B. Chen and J. F. Liang (Figure 1). However, *R. multilamellula*, originally described from southwestern China, has a stipe with brownish spot at the base, smaller basidiospores measuring (5.6–) 6.3–6.9–7.4 (–8) \times (5–) 5.8–6.4–7 (–7.3) μm , a hymenophore with more abundant pleurocystidia (ca. 1000/ mm^2), and it is associated with trees of Pinaceae [15].

Russula oraria N.K. Zeng, Y.X. Han and Zhi Q. Liang, sp. nov. (Figures 2c,d, 3c,d, 6 and 7).

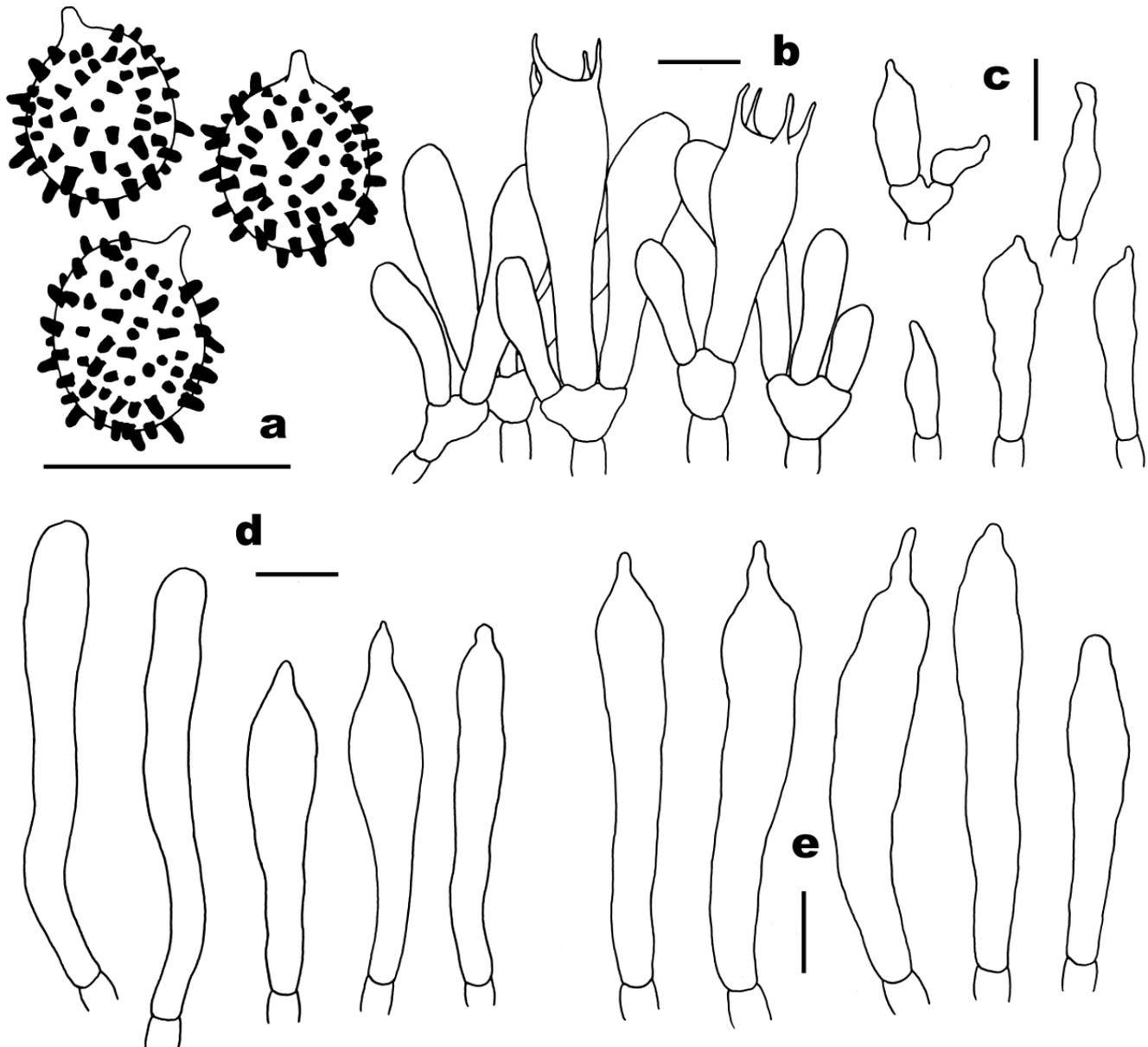


Figure 6. Microscopic features of *Russula oraria* (FHMU5355, holotype). (a) Basidiospores. (b) Basidia and basidiola. (c) Marginal cells. (d) Pleurocystidia. (e) Cheilocystidia. Bars: 10 μm . Drawings by Y.X. Han.

Mycobank: MB 845636.

Etymology—Latin “*oraria*”, refers to the new species growing near the coast.

Diagnosis—Differs from closest species of *R.* sect. *Ingratae* by a white pileus with pale yellow to pale yellowish brown at center, basidiospores with small, dense, cylindrical

to subcylindrical warts (0.5–1 μm high), never forming a reticulum, cystidia turning to yellowish brown in SV, and it is associated with trees of Dipterocarpaceae.

Holotype—China. Hainan Province: Wanning County, Shimei Bay, elev. 5 m, 28 August 2020, N.K. Zeng4823 (FHMU5355). GenBank accession numbers: ITS = ON332053.

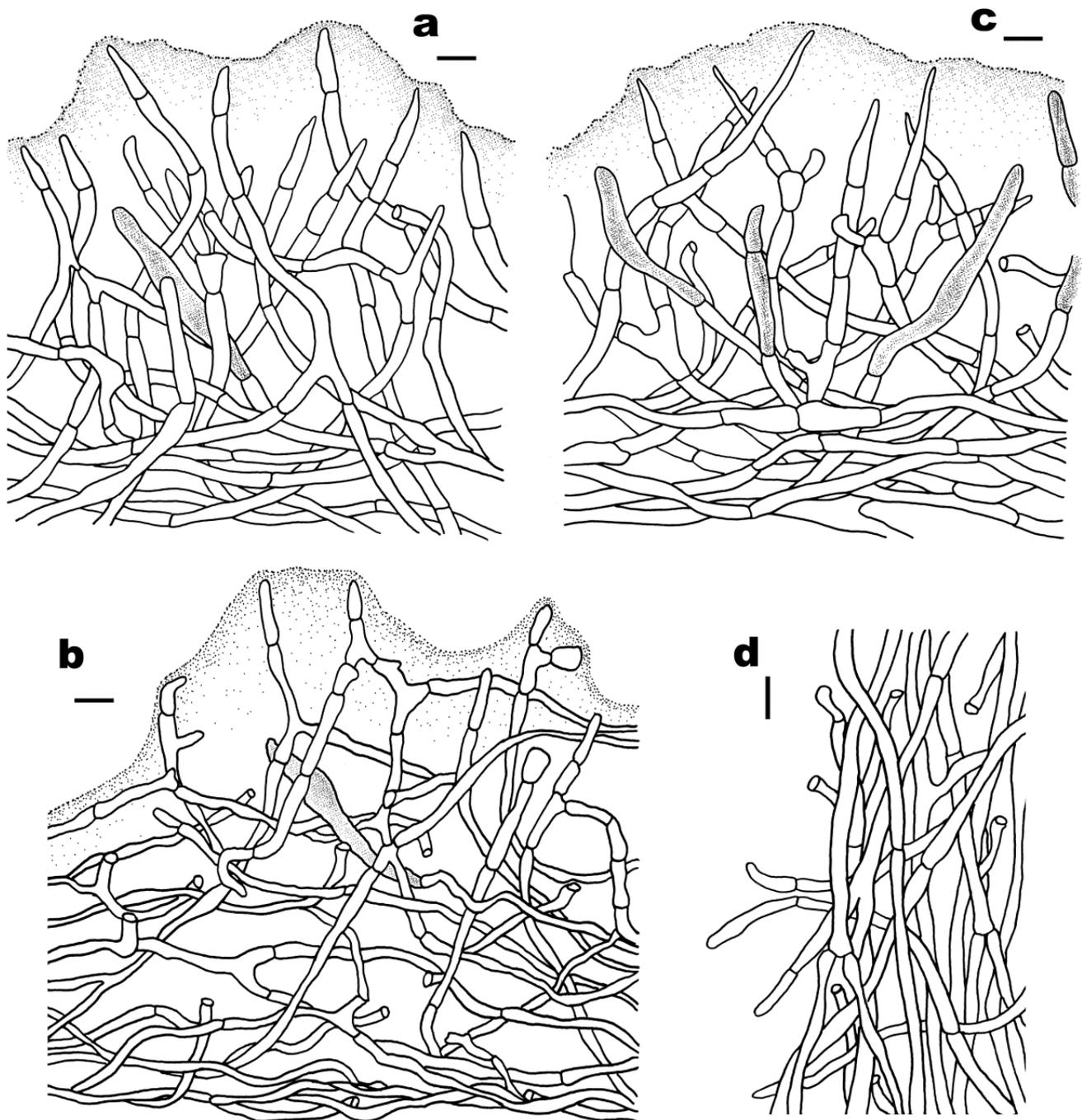


Figure 7. Microscopic features of *Russula oraria* (FHMU5355, holotype). (a) Pileipellis at pileus margin. (b) Pileipellis at middle part between center and margin of pileus. (c) Pileipellis at pileus centre. (d) Stipitipellis. Bars: 10 μm . Drawings by Y.X. Han.

Description—*Basidiomata* small-sized. *Pileus* 3.5–4 cm diameter, broadly convex to applanate, center slightly depressed, margin occasionally cracked; surface dry, white (2A1), pale yellow (3B2) to pale yellowish-brown (1B4) at center, margin with obvious radial tuberculate-striate; context about 2 mm thick at the center of the pileus, white (3A1),

unchanging in color when injured. *Hymenophore* lamellate, adnate; lamellae 4–5 mm in height, occasionally forked, white (3A1), unchanging in color when injured; lamellulae common, concolor with lamellae. *Stipe* 40–45 × 6–8 mm, central, subcylindric to cylindric, hollow, annulus absent; surface dry, white (3A1). *Taste* acrid. *Odour* fetid. *Spore print* not obtained.

Basidiospores (excluding ornamentation) [40/4/2] 6–6.6–7 (–7.5) × 5–5.4–6 μm, Q = 1.08–1.3 (–1.4), Qm = 1.24 ± 0.11, subglobose to broadly ellipsoid, ornamentation of relatively small, dense to very dense (9–14 in a 3 μm diameter circle) amyloid cylindric to subcylindrical warts, 0.5–1 μm high, isolated or rarely fused (0–2 fusions in the circle), line connections absent, never forming a reticulum; suprahilar spot inamyloid and indistinct. *Basidia* (28–) 29.5–32–36 × 7–9–10 (–11.5) μm, hyaline in KOH, thin- to slightly thick-walled (0.4–0.5 μm), clavate, 4-spored; sterigmata 4–6 μm, slightly tortuous, sometimes straight; basidiola cylindric, then narrowly clavate, ca. 4.5–9.5 μm wide. *Pleurocystidia* moderately numerous, ca. 1000/mm², (40.5–) 45–52–60.5 × 6–7–8 (–8.5) μm, narrowly clavate to subcylindrical, apex often obtuse or acute, sometimes moniliform, occasionally with 1–5 μm long appendage, slightly thick-walled (up to 0.5 μm); contents abundant granulose, yellowish in Congo Red, turning to yellowish-brown in SV. *Cheilocystidia* 40.5–52–55.5 (–61) × 7–8.5–9 μm, clavate to subcylindrical, apex obtuse or mucronate, sometimes with 3–7 μm long appendage, thin-walled (up to 0.4 μm); contents abundant granulose, yellowish in Congo Red, turning to yellowish-brown in SV. *Lamellae edges* fertile. *Marginal cells* (13–) 14.5–19–25 × (4–) 4.5–6–8 μm, clavate or subcylindrical, usually shorter than basidioles, thin-walled (up to 0.4 μm). *Lamellar trama* mainly composed of sphaerocytes measuring up to 39 μm in diameter, hyaline in KOH, thick-walled (1–1.5 μm). *Pileipellis* orthochromatic in Cresyl Blue, not sharply delimited from the underlying context, an ixotrichoderm 75–150 μm thick, two-layered, gelatinized; composed of suprapellis (50–100 μm thick) and subpellis (35–70 μm thick). *Suprapellis* composed of erect to suberect hyphae 1.5–7.5 μm in diameter, thin-walled (up to 0.4 μm). *Subpellis* composed of horizontally oriented, dense, 3–9 μm wide intricate hyphae. *Acid-resistant incrustations* absent. *Hyphal terminations near the pileus margin* composed of 1–3 unbranched cells, not flexuous, thin-walled (up to 0.4 μm); terminal cells (14–) 15–20–24.5 × 3.5–4–5 (–5.5) μm, narrowly subcylindrical or tapering upward; subterminal cells often wider, occasionally branched. *Hyphal terminations on the middle part between center and margin of pileus* 1–3 cells, unbranched and not flexuous; terminal cells 10–13–17.5 (–19) × (3–) 3.5–4–5 μm, subcylindrical, apex obtuse; subterminal cells often wider, occasionally branched. *Hyphal terminations near the pileus center* 1–3 cells, unbranched and not flexuous; terminal cells (10–) 14.5–17–38 (–40) × 3–4–5 (–5.5) μm, mainly clavate, occasionally subcylindrical; subterminal cells often shorter, unbranched. *Pileal trama* composed of hyphae up to 50 μm in diameter, thick-walled (1–2 μm), hyaline in KOH. *Pileocystidia near the pileus margin* one-celled, (40.5–) 48–56–70 × 5.5–7.5–8 (–8.5) μm, cylindrical to clavate, apex usually obtuse, contents granulose, yellow in Congo Red turning to yellowish-brown in SV. *Pileocystidia near the pileus centre* cylindrical to clavate, 1–2 celled, (12.5–) 20–47–67.5 × 4.5–5–6 (–7) μm, contents granulose, yellow in Congo Red turning to yellowish-brown in SV. *Cystidioid hyphae* in subpellis and context, contents granulose. *Stipitipellis* a cutis, composed of hyphae thin-walled (up to 0.4 μm), 3–8 μm wide, pale yellowish in KOH; terminal cells 10–30 × 3.5–5 μm, subcylindrical or subclavate. *Stipe trama* mainly composed of sphaerocytes measuring up to 46 μm in diameter, hyaline in KOH, thick-walled (1–1.5 μm). *Clamp connections* absent in all tissues.

Habitat—Gregarious on the ground in forests dominated by *Vatica mangachapoi* Blanco.

Known distribution—Southern China (Hainan Province).

Additional specimen examined—China. Hainan Province: Wanning County, Shimei Bay, elev. 5 m, 28 August 2020, N.K. Zeng4829 (FHMU5374).

Notes—Morphologically, some Asian members of section *Ingratae*, viz., *R. ahmadii* Jabeen, Razaq, Niazi, I. Ahmad and Khalid, *R. catillus* H. Lee, M.S. Park and Y.W. Lim, *R. clavulus* B. Chen and J.F. Liang, *R. natarajanii* K. Das, J.R. Sharma and Atri, *R. obscuricolor* K. Das, A. Ghosh and Buyck, *R. pseudocatillus* F. Yuan and Y. Song, *R. pseudopectinatoides*

G.J. Li and H.A. Wen, *R. straminella* G.J. Li and C.Y. Deng, *R. subpectinatoides* G.J. Li and Q.B. Sun, and *R. succinea* G.J. Li and C.Y. Deng are similar to *R. oraria*. However, *R. ahmadii* has a darker pileus, and larger basidiospores (5.6–) 6.1–9.2 (–9.4) × (5.4–) 5.7–6.6 (–7.5) μm with ornamentations composed of lower, irregular warts (up to 0.3 μm high), sometimes forming a partial reticulum, and it is associated with trees of Pinaceae [32]; *R. catillus* has basidiospores with lower ornamentations composed of mostly conical warts (up to 0.8 μm high), sometimes forming a partial reticulum, and it is associated with trees of Fagaceae [38]; *R. clavulus* has a larger basidioma (pileus 7–9 cm in diameter), larger basidiospores measuring (5.6–) 7.0–7.8–8.6 (–9.0) × (5.4–) 6.5–7.2–8.0 (–8.3) μm with ornamentations composed of larger, cylindrical warts (up to 1.6 μm high), often forming short or long ridges, and it is associated with trees of Fagaceae [15]; *R. natarajanii* has a larger basidioma (pileus 6–10.5 cm in diameter), larger basidiospores measuring 6.5–8.8 × 5.8–7.1 μm with ornamentations composed of minute warts and ridges (up to 0.4 μm high), forming an incomplete reticulum, and it is associated with trees of Fagaceae [62]; *R. obscuricolor* has a stipe with blood red coloration at stipe base, basidiospores with ornamentations composed of conical warts and ridges (up to 0.9 μm high), forming a partial to incomplete reticulum, and it is associated with trees of Fagaceae [51]; *R. pseudocatillus* has larger basidiospores measuring 7–7.9–8.6 (–9.2) × (5.1–) 5.5–6.1–6.6 (–6.7) μm with ornamentations composed of higher, conical to cylindrical warts (up to 1.2 μm high), cystidia negative in SV [14]; *R. pseudopectinatoides* has basidiospores with ornamentations composed of lower, conical warts (0.2–0.5 μm high), forming a partial reticulum, and it is associated with trees of Pinaceae [11]; *R. straminella* has a darker brown pileus, a stipe turning brownish-yellow when injured, basidiospores with ornamentations composed of conical warts (0.7–1 μm high), forming a partial reticulum, a hymenophore with fewer pleurocystidia (less than 500/mm²), and it is associated with trees of Pinaceae; *R. subpectinatoides* has a darker brown pileus, a context slowly turning pale ochre when injured, basidiospores with ornamentations composed of lower, long ridges (0.3–0.5 μm high), forming an incomplete to complete reticulum, a hymenophore with fewer pleurocystidia (less than 200/mm²), and it is associated with trees of Pinaceae; *R. succinea* has a stipe turning cream to pale ochre when injured, basidiospores with ornamentations composed of subcylindrical warts, forming an incomplete reticulum, and it is associated with trees of Pinaceae [9].

Phylogenetically, *R. oraria* is closely related to *R. siamensis* Yomyart, Piap., Watling, Whalley and Sihan. (Figure 1), originally described from Thailand. However, the latter has a smaller basidioma (pileus 2.8 cm in diameter), a dark brownish beige to pale ochraceous grey pileus with flakes or squamules, and larger basidiospores measuring 8–9 × 6–7 μm [55].

Russula rufobasalis Y. Song and L.H. Qiu, Cryptog. Mycol. 39 (3): 352, 2018 (Figures 2e,f, 3e,f, 8 and 9).

Mycobank: MB 824892.

Description—*Basidiomata* small-sized. *Pileus* 3–3.7 cm diameter, subhemispherical at first, then appanate, center slightly depressed; margin occasionally cracked; surface barely sticky, pale yellowish-brown (1B5), brown (5C5) to dark brown (5C8), margin with obvious radial tuberculate-striate; context about 2 mm thick at the center of the pileus, white (1A1), unchanging in color when injured. *Hymenophore* lamellate, adnate; lamellae 2 mm in height, distant, not forked, edge sparsely serrate, white (2A1), unchanging in color when injured; lamellulae rare. *Stipe* 30–35 × 5–6 mm, central, subcylindrical to cylindrical, hollow, annulus absent; surface white (3A1), sometimes tinted with pale yellowish-brown (1B5), base reddish. *Taste* mild. *Odour* indistinct. *Spore print* not obtained.

Basidiospores (excluding ornamentation) [40/2/2] 5–6–6.5 (–7) × 4.5–5.2–6 μm, Q = 1–1.3, Q_m = 1.15 ± 0.09, globose to broadly ellipsoid, ornamentation of relatively small, moderately distant to dense ((6–) 7–8 (–10) in a 3 μm diameter circle) amyloid warts, 0.4–0.8 μm high, isolated or occasionally fused (0–3 fusions in the circle), small crests and ridges forming an incomplete reticulum, connected by occasional line connections ((0–) 1–3 in the circle); suprahilar spot inamyloid, distinct. *Basidia* (20.5–) 25–35–41 × 5–6–7.5(–8) μm, hyaline in

KOH, thin-walled (up to 0.4 μm), narrowly clavate to subcylindrical, 4-spored; sterigmata 3–5 μm , slightly tortuous, sometimes straight; basidiola cylindrical, then narrowly clavate, ca. 4.5–8 μm wide. *Pleurocystidia* abundant, ca. 3200/mm², (40–) 45–51.5–57 (–60) \times (6–) 6.5–7–8.5 μm , narrowly clavate to clavate, apically often obtuse, sometimes with mucronate apices, appendage 2.5–4 μm long, slightly thick-walled (up to 0.6 μm); contents abundant granulose, yellowish in Congo Red, turning to brownish in SV. *Cheilocystida* (32–) 46–50–58.5 (–70) \times (7–) 7.5–8–8.5 μm , narrowly clavate to subcylindrical, apically obtuse or mucronate, sometimes with 3–5 μm long appendage, thin-walled (up to 0.4 μm); contents granulose, yellowish in Congo Red, turning brownish in SV. *Lamellae edges* fertile. *Marginal cells* (10–) 13–16.5–20 \times 4.5–5–6 (–6.5) μm , clavate or subcylindrical, usually shorter than basidioles thin-walled (up to 0.4 μm). *Lamellar trama* mainly composed of sphaerocytes measuring up to 30 μm in diameter, hyaline in KOH, thick-walled (1–1.5 μm). *Pileipellis* orthochromatic in Cresyl Blue, not sharply delimited from the underlying context, a trichoderm 200–400 μm thick, two-layered, weakly gelatinized; composed of suprapellis (80–130 μm thick) and subpellis (150–300 μm thick). *Suprapellis* composed of erect to suberect hyphae 2.5–7 μm in diameter, slightly thick-walled (0.4–0.5 μm). *Subpellis* composed of frequently undulate-sinuous intricate hyphae (2.5–7 μm in diameter). *Acid-resistant incrustations* absent. *Hyphal terminations near the pileus margin* composed of 1–3 unbranched cells, not flexuous, slightly thick-walled (0.4–0.5 μm); terminal cells (7–) 12–18–26 \times 3–4.5–5 μm , narrowly subcylindrical or tapering upward; subterminal cells often wider, occasionally branched. *Hyphal terminations on the middle part between center and margin of pileus* 1–3 cells, unbranched and not flexuous; terminal cells (14–) 18–20–25 \times 2.5–3–3.5 μm , subcylindrical; subterminal cells often wider and longer, rarely branched. *Hyphal terminations near the pileus centre* 1–3 cells, sometimes branched and not flexuous; terminal cells 12–18–24.5 (–27) \times 3–4–5 (–5.5) μm , subcylindrical or tapering; subterminal cells often wider and longer, occasionally branched. *Pileal trama* composed of hyphae up to 35 μm in diameter, thick-walled (up to 1 μm), hyaline in KOH. *Pileocystidia near the pileus margin* one-celled, (30–) 45–54–61.5 \times 4–5–6 μm , cylindrical to clavate, apex usually obtuse or occasionally mucronate, contents granulose, yellow in Congo Red, turning to yellowish-brown in SV. *Pileocystidia near the pileus centre* cylindrical to clavate, one-celled, (49–) 53.5–61–80 \times 3.5–4–5.5 μm , contents yellow in Congo Red, turning to yellowish-brown in SV. *Cystidioid hyphae* in subpellis and context, contents granulose. *Stipitipellis* a cutis composed of hyphae slightly thick-walled (up to 0.5 μm), 2.5–8 μm wide, hyaline to pale yellowish in KOH; terminal cells 15–40 \times 4–5.5 μm , subcylindrical or subclavate. *Stipe trama* mainly composed of sphaerocytes measuring up to 40 μm in diameter, hyaline in KOH, thick-walled (up to 1 μm). *Clamp connections* absent in all tissues.

Habitat—Solitary on the ground in forests dominated by *Pinus massoniana* Lamb or *Castanopsis kawakamii* Hayata.

Known distribution—Southern China (Guangdong Province) and eastern China (Fujian Province) [12].

Specimens examined—China. Fujian Province: Zhangping County, Xinqiao Town, Chengkou Village, elev. 80 m, 17 August 2013, N.K. Zeng1416 (FHMU961); Zhangping County, Fuzhige Park, elev. 80 m, 24 July 2013, N.K. Zeng1270 (FHMU827).

Notes—*Russula rufobasalis* was originally described from Guangdong Province of southern China [12]. In the present study, it was also found to be distributed in Fujian Province, southeastern China. The species was redescribed according to our new specimens; it is characterized by a pale yellowish-brown, brown to dark brown pileus, lamellate edges sparsely serrate, a stipe with reddish base, basidiospores with small crests and ridges (0.4–0.8 μm high), forming an incomplete reticulum, and it is associated with both trees of Pinaceae and Fagaceae. The previous description indicated the basidioma of *R. rufobasalis* is larger (3–6 cm), and the lamellulae are frequent [12], whereas the newly collected specimens have smaller basidiomata (3–3.7 cm) and rare lamellulae.

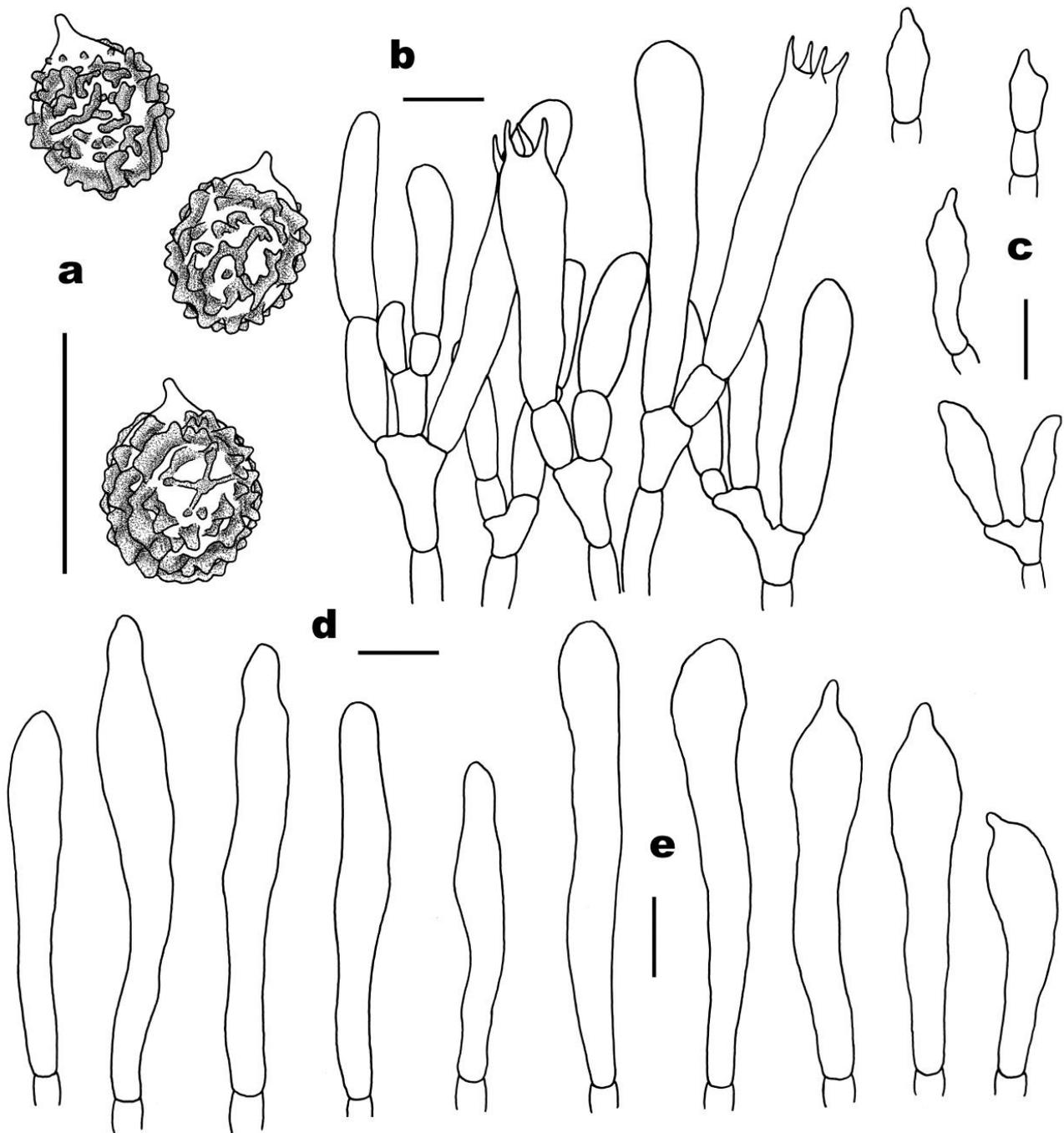


Figure 8. Microscopic features of *Russula rufobasalis* (FHMU827). (a) Basidiospores. (b) Basidia and basidiola. (c) Marginal cells. (d) Pleurocystidia. (e) Cheilocystidia. Bars: 10 μm . Drawings by Y.X. Han.

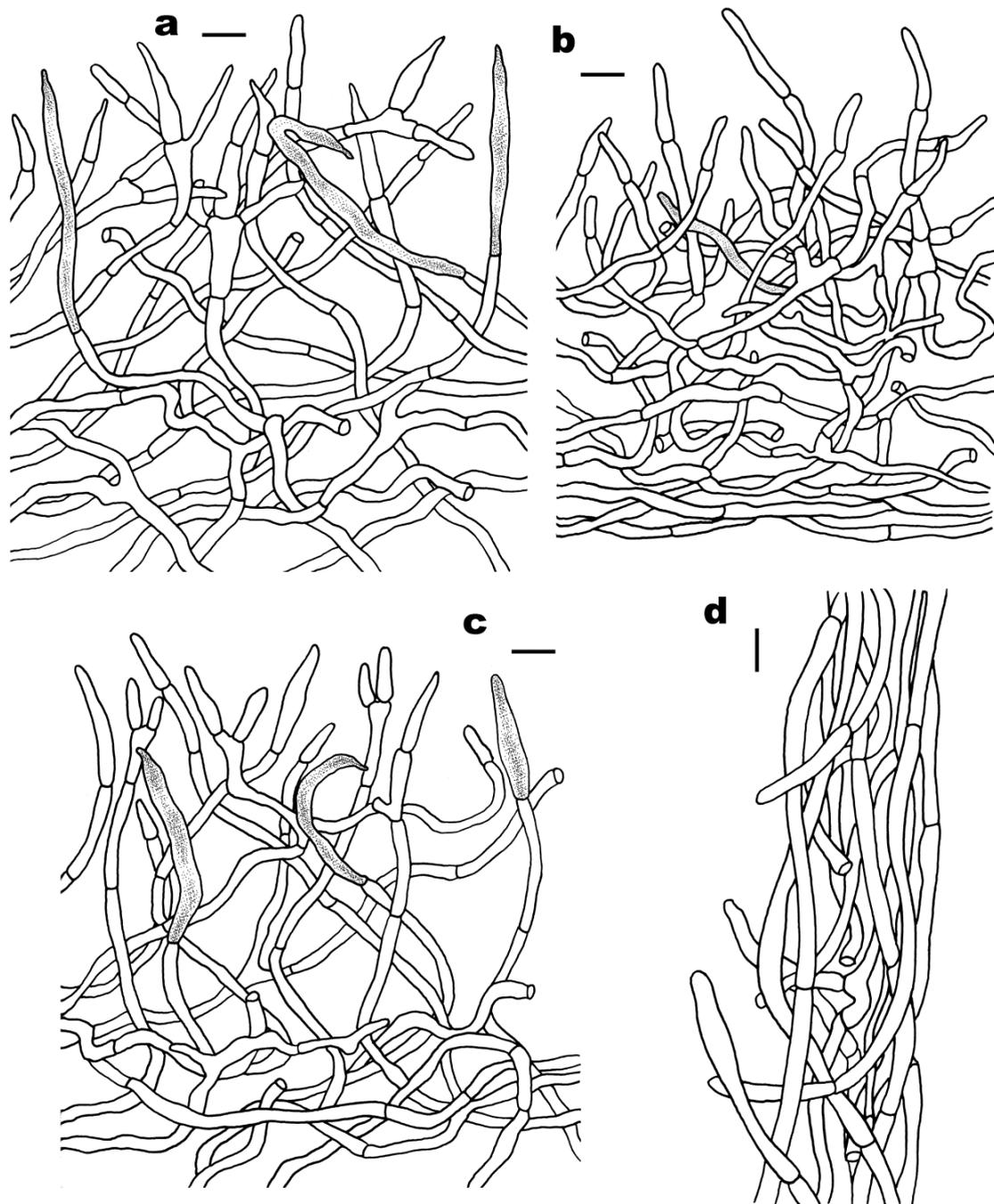


Figure 9. Microscopic features of *Russula rufobasalis* (FHMU827). (a) Pileipellis at pileus centre. (b) Pileipellis at middle part between center and margin of pileus. (c) Pileipellis at pileus margin. (d) Stipitipellis. Bars: 10 µm. Drawings by Y.X. Han.

4. Discussion

4.1. Species Diversity of Sect. *Ingratae* in China

High species diversity of sect. *Ingratae* in China was revealed in this study, and 24 lineages of the section were identified (Figure 1). Two lineages (lineages 3 and 21) were described as new species: *R. fujianensis* and *R. oraria*; thirteen lineages (lineages 2, 4, 5, 6, 7, 10, 11, 12, 14, 17, 20, 22 and 23) represent known species: *R. multilamellula*, *R. clavulus*, *R. punctipes* Singer, *R. subpunctipes* J. Song, *R. gelatinosa* Y. Song and L. H. Qiu, *R. hainanensis* N.K. Zeng, Y.X. Han and Zhi Q. Liang, *R. succinea*, *R. straminella*, *R. indocatillus* A. Ghosh, K. Das and R.P. Bhatt, *R. pseudocatillus* F. Yuan and Y. Song, *R. rufobasalis*, *R. subpectinatoides*, and

R. pseudopectinatoides [9,11–16]; other lineages (1, 8, 9, 13, 15, 16, 18, 19, and 24) also included Chinese specimens wait to be further identified, combing with morphological evidence. Aside from the aforementioned species/lineages, four additional taxa, viz., *R. foetens* Pers., *R. guangdongensis* Z.S. Bi and T.H. Li, *R. laurocerasi* Melzera, and *R. senecis* have also been described/reported from China [10,63,64]. *Russula guangdongensis*, originally described from southern China, should be examined with DNA sequences and more collections, while the collections identified as *R. foetens*, *R. laurocerasi*, and *R. senecis* in China should be re-evaluated.

4.2. Species Delimitation of Sect. *Ingratae* in China

Although the diagnosis of sect. *Ingratae* is relatively straightforward, species within the section are difficult to distinguish. This is explained by the lack of molecular phylogenetic studies as well as morphological convergence documented in this group in previous studies [65]. With the wide application of molecular phylogenetic analyses, the diversity of species in sect. *Ingratae* was revealed in China (Figure 1). In order to delimit the phylogenetic species, we should pay much attention to the ornamentations of basidiospores, which are more reliable characters for species of sect. *Ingratae*. For example, basidiospores of *R. clavulus*, *R. indocatillus*, *R. multilamellula*, *R. pseudocatillus*, and *R. subpunctipes* are absent of reticula [9,12,14,15]; those of *R. gelatinosa*, *R. hainanensis*, *R. pseudopectinatoides*, *R. punctipes*, *R. rufobasalis*, *R. straminella*, and *R. succinea* often form incomplete reticulums; *R. subpectinatoides* has basidiospores with incomplete to complete reticula [9,11,12,16]. Moreover, five ornamentation types, viz., cone, cylinder, crest, ridge, and wing were observed; for example, basidiospores ornamentations of *R. indocatillus* and *R. straminella* mostly composed of conical warts [9], *R. subpectinatoides* mostly composed of long ridges [9], *R. clavulus* and *R. multilamellula* composed of cylindrical warts and ridges [15], *R. subpunctipes* composed of cylindrical warts and wings [13], *R. hainanensis* composed of crests and ridges [16], *R. pseudocatillus* composed of conical to cylindrical warts [14], *R. pseudopectinatoides* composed of conical warts and ridges [11], *R. succinea* composed of crests and ridges [9], *R. gelatinosa* and *R. punctipes* composed of cylindrical warts, ridges and wings [12], *R. rufobasalis* composed of subcylindrical warts, crests and ridges [12]. In addition, the height of ornamentations is also a useful character: *R. gelatinosa*, *R. punctipes*, and *R. subpunctipes* have basidiospores with high ornamentations (>2 μm) [12,13]; that of *R. clavulus*, *R. fujianensis*, *R. multilamellula*, *R. pseudocatillus*, and *R. succinea* is moderately high (1–2 μm) [9,14,15]; while that of *R. hainanensis*, *R. indocatillus*, *R. oraria*, *R. pseudopectinatoides*, *R. rufobasalis*, *R. straminella*, and *R. subpectinatoides* is low (<1 μm) [9,11,12,16]. As to our new species, viz., *R. fujianensis* and *R. oraria* are absent of reticula; *R. oraria* is mostly composed of cylindrical warts, while *R. fujianensis* is composed of cylindrical warts and wings.

Besides ornamentations of basidiospores, the ecological preferences should also be noted; for example, *R. clavulus* and *R. subpunctipes* are associated with Fagaceae [13,15], while *R. multilamellula*, *R. pseudopectinatoides*, *R. straminella*, *R. subpectinatoides*, and *R. succinea* are associated with Pinaceae [9,11,15]. Some species, e.g., *R. indocatillus* and *R. rufobasalis* can be associated with both Pinaceae and Fagaceae [9,45]. More particularly, *R. hainanensis* is associated with Dipterocarpaceae [16]. As to our new species, *R. fujianensis* and *R. oraria* are associated with Fagaceae and Dipterocarpaceae, respectively.

4.3. Phylogenetic Relationships and Geographic Divergence of Chinese Sect. *Ingratae*

Recent phylogenetic studies have provided new perspectives into the phylogeny and geography of sect. *Ingratae* [9,15,16]. Besides revealing two new species of sect. *Ingratae*, our molecular data have also contributed to other knowledge of this group (Figure 1). The molecular data indicated that the affinities of sect. *Ingratae* species between northeastern China and Europe are obvious, two species-level lineages (1 and 9) occurring in the two regions (Figure 1). Similar patterns have been documented in other fungi [66–70]. Moreover, we also noted that some Chinese species are closely related to the North America taxa; for example, one collection identified as *R. granulata* (lineage 19) from northeastern China

is affiliated with one taxon labelled as *R. granulata* from USA; lineage 24 from China is closely related to one species identified as *R. amerorecondita* also from USA (Figure 1). Our study did not identify disjunct populations of the same purported taxon in the two regions (Figure 1). In addition, we also noted that *R. indocattillus* occurs both in China and India (Figure 1).

5. Conclusions

In this study, three species of *Russula* sect. *Ingratae* are recognized in China; two of them are described as new: *R. fujianensis* and *R. oraria*, and one of them is an already known taxon: *R. rufobasalis*.

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