

商品野生食用蘑菇“大红菌”物种多样性的重新评估

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摘要: “大红菌”是一类在我国南部广泛采食的具有红色菌盖的红菇。最初我国的大红菌被误定为欧洲的酒红菇。自2009年灰肉红菇 *Russula griseocarnosa* 被描述后, 这一名称成为大红菌唯一可用的名称。然而, 前人研究发现该种下存在多个系统发育分支, 而这些分支是否代表了真正的物种尚待研究。通过在我国南方大红菌的主产区进行广泛取样, 采用多基因片段进行系统发育物种识别, 我们鉴定出除灰肉红菇外的9个物种, 包括已知种达哈库尔红菇 *R. dhakuriana*、栎生红菇 *R. quercina*、紫环红菇 *R. purpureozonata* 和沿河红菇 *R. yanheensis*。研究发现了灰肉红菇的姊妹种隐匿红菇 *R. occulta* (新种) 以及4个尚待描述的种, 它们分别与鳞盖红菇 *R. lepida*、落叶松红菇 *R. laricina* 和紫环红菇近缘。基于5个DNA位点, 我们通过多基因谱系一致法进行系统发育物种识别, 在灰肉红菇内界定了6个系统发育分支。基因谱系间存在的冲突提示将灰肉红菇处理为一个系统发育种较为合适, 其下的6个分支可处理为种下分类单元。对灰肉红菇主模式标本进行的浅层基因组测序发现它的3个个体分属于3个不同的分支, 故使用其中的一个个体为其指定了后选模式。我们描述了一个主产区在云南哀牢山区的一个新变种: 灰肉红菇哀牢山变种 *R. griseocarnosa* var. *ailaoshanensis*, 它与原变种的区别在于其近白色的菌肉、较大的孢子和较膨大的盖表皮菌丝。本研究提供的形态和分子数据将有助于鉴定红菇亚属内的野生食用菌。

关键词: 中国; 后选模式; 新种; 系统发育物种识别; 红菇属; 野生食用菌

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Critical re-assessment of species diversity of marketed wild edible mushroom ‘dahongjun’

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Abstract: The informal term ‘dahongjun’ or ‘big red mushroom’ is a group of red-coloured russulas widely collected and consumed in southern China, originally mistakenly recognized as the European *Russula vinosa*. *Russula griseocarnosa* was described from China in 2009, and since then, it has become the only available scientific name for ‘dahongjun’. Nevertheless, several lineages exist within this complex, and whether these lineages represent real species is still an open question. Sampling in major producing areas of ‘dahongjun’ and phylogenetic species recognition using multi-locus data were conducted. Besides *R. griseocarnosa* nine additional species were identified under the commercial name ‘dahongjun’, including *R. dhakuriana*, *R. quercina*, *R. purpureozonata*, *R. yanheensis* and a new species sister to *R. griseocarnosa* here described as *R. occulta*. The others were undescribed species close to *R. laricina*, *R. lepida*, and *R. purpureozonata* respectively. Six evolutionary lineages within *R. griseocarnosa* were defined by genealogical concordance phylogenetic species recognition based on five-locus DNA data. Conflicts among different genealogies suggested that *R. griseocarnosa* is best considered as a single phylogenetic species, comprising several infraspecific taxa. Lower coverage whole genome sequencing of *R. griseocarnosa* holotype discovered that its three individuals belong to three different clades. Lectotypification was made using one of the three individuals. A new variety *R. griseocarnosa* var. *ailaoshanensis* is described to name one of the terminal clades that is mainly distributed in Ailao Mountains. This variety differs morphologically from the type variety in its nearly white context, bigger spores and more inflated hyphae in the pileipellis. The morphological and molecular data provided in this study are helpful to identify wild edible mushrooms of *Russula* subgen. *Russula*.

Keywords: China; lectotype; new species; phylogenetic species recognition; *Russula*; wild edible fungi

INTRODUCTION

In southern China, *Russula* (Russulaceae, Russulales) species are frequently sold in local markets (Wang *et al.* 2004; Wu *et al.* 2019; Deng *et al.* 2020; Wang *et al.* 2022; Huang *et al.* 2023). Among them ‘dahongjun’ (big red mushroom) is the most prized and sold at high price (RMB ¥70–100/kg or US \$17.00 when fresh). The price of dried products (RMB ¥700–1 500/kg or US \$100–200) is even higher than that of *Tricholoma matsutake* (S. Ito & S. Imai) Singer (matsutake mushroom). As an important non-timber forest product, ‘dahongjun’ represents the main source of income for people living in the mountains in eastern (Jiangxi), central (Hunan), southern (Guangdong, Guangxi), southeastern (Fujian) and southwestern (Yunnan) China.

In field and markets, ‘dahongjun’ can be recognized by a set of characteristics: basidiocarps robust, thick-fleshed; pileus vivid to dark red, dry or subgreasy, with a frequently much darker center and non-striate margin; context often graying; stipe surface often reddish; taste mostly mild (Wang *et al.* 2004; Chen 2010; Li & Hu 2010). Most of these characters are similar to those of European *R. vinosa* Lindblad, a name that was adopted for ‘dahongjun’ until about 15 years ago. Wang *et al.* (2009) compared the ITS sequences and morphology of Chinese samples with those of *R. vinosa* and found that ‘dahongjun’ was a different species, thus a distinct species *R. griseocarnosa* X.H. Wang *et al.* was described.

Soon after the publication of *R. griseocarnosa*, Li *et al.* (2010) sequenced a large number of samples of ‘dahongjun’ from southern China and identified three divergent lineages. Similar genetic variation was simultaneously presented by Chen (2010) based on eight samples from Fujian, Guangdong and Guangxi. Furthermore, Yu (2013) found that two ‘dahongjun’ samples from Fujian have ITS sequences only 91% similar to that of *R. griseocarnosa*. A large number of samples with such ITS type were recently discovered from central and southern Yunnan by Feng *et al.* (2020). These samples formed an additional major lineage to those discovered by Li *et al.* (2010). Yu *et al.* (2020) sequenced the genome of a sample of *R. griseocarnosa* collected from Guangxi. The ITS sequence of this sample is 97.7% similar to EF627042 (ITS of *R. griseocarnosa* holotype). In

GenBank there are more sequences (e.g. MT211446 and MT252594) similar to those of *R. griseocarnosa* but are not covered by the lineages of Li *et al.* (2010) and Feng *et al.* (2020). Whether the samples outside the core *R. griseocarnosa* lineage belong to different species is still an open question.

R. griseocarnosa previously was regarded as a species with dark red pileus and mainly distributed in the tropics (Wang *et al.* 2009). Das *et al.* (2010) reported a specimen of *R. griseocarnosa* with less reddish but more ochraceous pileus collected from mid-montane forest in Sikkim Himalaya, India. Specimens with such colour (HKAS 104790 and HKAS 104808, KUN) were also collected in Ailao Mountains (mid-south Yunnan) at altitude > 2 000 m. Moreover, we obtained some specimens with nearly white context in the pileus and the sequences of these specimens did not fall into the same lineage of typical *R. griseocarnosa*. It was suggested that there might hide multiple species under the local name ‘dahongjun’.

This study aims at re-evaluating the divergent lineages of *R. griseocarnosa* in former studies and detecting whether they represent species different from *R. griseocarnosa*; determining the identity of the specimens morphologically different from typical *R. griseocarnosa*; locating these species in the most up-to-date multi-gene phylogeny of *Russula* (Buyck *et al.* 2018). Broader sampling, phylogenetic species recognition (PSR) and morphological comparison were taken to achieve these aims.

1 MATERIALS AND METHODS

1.1 Sampling

Materials of ‘dahongjun’ were obtained from the main producing areas in southern China (Fujian, Guangdong, Guangxi, Hunan, Sichuan and Yunnan). Ailao Mountains National Nature Reserve in central-southern Yunnan, one of the most famous localities of ‘dahongjun’, was intensively visited. In total, 188 specimens were obtained: 82 from Fujian, 6 from Guangdong, 22 from Guangxi, 3 from Hunan and 75 from Yunnan. Among them, 63 specimens were collected in the field and 125 were purchased from markets or mushroom hunters. In addition, five specimens of four European edible species, *i.e.* *R. cremeoavellanea* Singer, *R. decolorans* (Fr.) Fr., *R. claroflava* Grove and *R. vinosa*, were used for comparison purpose.

Specimens are deposited in the Cryptogamic section (HKAS) of Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

1.2 Morphological analysis

Macroscopical descriptions are based on field notes of fresh materials and microscopical ones on dried specimens. Colour codes follow Kornerup and Wanscher (1961). Methods of morphological observation followed Wang *et al.* (2009). Microscopic photos were taken with a charge-coupled device SC 2000C connected to a Nikon ECLIPSE Ni-U compound microscope (Nikon Corporation).

1.3 DNA extraction and sequencing

DNA extractions and PCR amplification followed Wang *et al.* (2009). Five nuclear markers commonly used for PSR and phylogenetic inference in Russulaceae (*e.g.* Buyck *et al.* 2018; de Lange *et al.* 2021; Huang *et al.* 2023), *i.e.* ITS, nrLSU, *RPB1*, *RPB2* and *TEF1- α* , were amplified. Universal primers published by White *et al.* (1990), Moncalvo *et al.* (2000), Liu *et al.* (1999), Matheny *et al.* (2002) and Morehouse *et al.* (2003) and specific primers by Cao *et al.* (2023) were used. For sequences having INDELs among copies or ambiguous sites, PCR products were sequenced bidirectionally to make contigs of the amplified regions or verify the ambiguous sites. The method of Flot *et al.* (2006) was used to determine the INDEL heterozygosity and phase the sequences into two copies. Raw sequences generated with Sanger sequencing were edited and assembled in Sequencher v4.1.4 (Gene Codes Corporation). In rare cases where the amount of PCR products is not sufficient for sequencing or direct sequencing failed, they were cloned following the method of Wang *et al.* (2015). PCR of the holotype and one paratype (HKAS 51713) of *R. griseocarnosa* and several problematic samples failed. We thus conducted lower-coverage whole genome sequencing (“genome skimming”) by using the next generation sequencing on an Illumina NovoSeq-5500 platform to recover the target loci. Library preparation followed the protocol described by Zeng *et al.* (2018). The raw data were *de novo* assembled using GetOrganelle toolkit (Jin *et al.* 2020).

1.4 Multi-gene phylogenetic constructions

Representative species were selected from the *Russula* phylogeny of Buyck *et al.* (2018, 2020, 2024). Two ITS-nrLSU-*RPB1*-*RPB2*-*TEF1- α*

combined datasets were used: dataset A to construct the phylogeny of *R.* subgen. *Russula* and B to resolve the phylogeny of *R. griseocarnosa* complex. In dataset A, ITS sequences were only included for the target species and their closely related species in the same section or subsection. We followed Buyck *et al.* (2018) to exclude the ambiguous sites of *RPB2* and introns and to set partitions. In dataset B, introns could be well aligned and were thus kept. The partitioning was the same as in dataset A, with introns treated as additional partitions. Alignments were made by MAFFT v7 (Katoh & Toh 2008) using the L-INS-I strategy and manually adjusted in BioEdit v.7.1.3.0 (Hall 1999). All best tree searches and bootstrap analyses of maximum likelihood (ML) were conducted in RAxML v. 7.7.7 (Stamatakis 2014) using the rapid bootstrap algorithm. Other settings of ML analysis followed Buyck *et al.* (2024). Trees were viewed and exported in FigTree v1.3.1 and further processed with Adobe Illustrator (Fig. 1).

1.5 Phylogenetic species recognition

We followed the genealogical concordance phylogenetic species recognition (GCPSR) method of Dettman *et al.* (2003) to determine species limits in the *R. griseocarnosa* complex. Five loci, *i.e.*, ITS, nrLSU, *RPB1*, *RPB2* and *TEF1- α* , were used. Duplicate sequences were filtered, leaving those covering genetic and morphological variation and geographical origins. Single genealogies were constructed in RAxML v. 7.7.7 (Stamatakis 2014). All introns were kept and partitioning was similar to that in the multi-gene phylogenetic analysis. To identify independent evolutionary lineages under the GCPSR, two criteria were adopted: (i) genealogical concordance, the clade was present in the majority (4/5) of the single-locus genealogies; (ii) genealogical non-discordance, the clade was well supported in at least one single-locus genealogy, as judged by ML bootstrap (ML-bs) $\geq 70\%$ and was not contradicted in any other single-locus genealogy at the same level of support. A conflict was assumed to be significant when two different relationships (one monophyletic and the other non-monophyletic) for the same set of taxa were both supported with ML-bs $\geq 70\%$. To decide which independent evolutionary lineages represented phylogenetic species, we conducted “exhaustive subdivision”, *i.e.*, all individuals had to be placed within a phylogenetic species in the combined phylogeny.

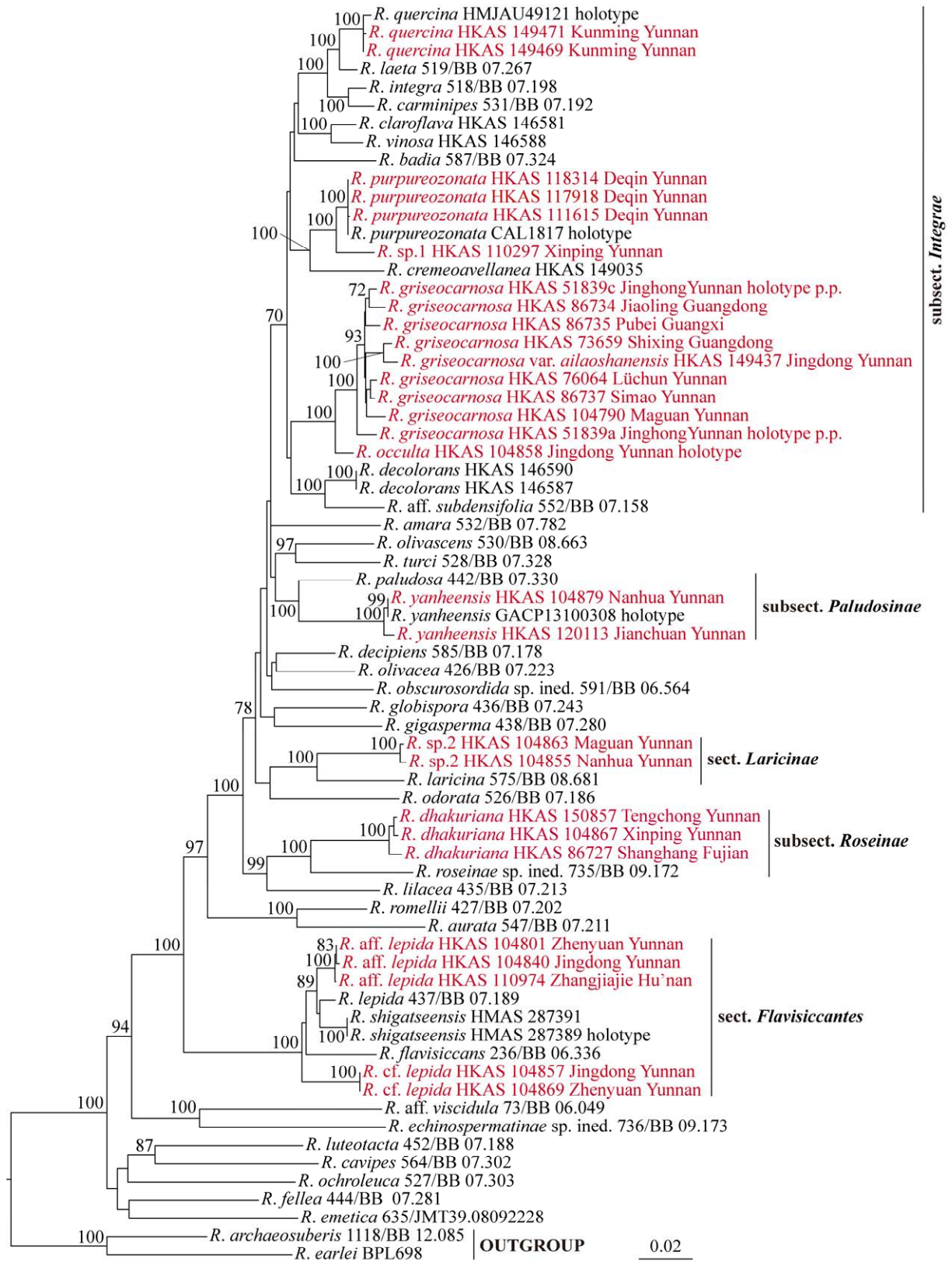


Fig. 1 Maximum likelihood phylogram generated from combined ITS-nrLSU-*RPB1-RPB2-TEF1-α* dataset of *Russula* subgen. *Russula*. Red-highlighted samples are those under the local name ‘dahongjun’. Names of these samples are given in the order of herbarium number, county name and province (autonomous region) name. The tree was rooted with two species of *R.* subgen. *Archaeae*.

2 RESULTS

2.1 Multi-gene phylogenetic inference

In total, 534 sequences were generated and deposited in GenBank (Table 1, plus PV974553–PV974750 and PX622224–PX622256 for ITS). Analysis of these sequences indicated that all the samples of ‘dahongjun’ collected from local markets belonged to the crown clade of clade VIII in the phylogeny of *Russula* (Buyck *et al.* 2018) representing the majority of *R.* subgen. *Russula*. Ten species were identified. Among them, *R. griseocarnosa*, *R. occulta* (HKAS 104858, holotype), *R. purpureozonata* K. Das *et al.*, *R. quercina* J.J. Zhou & R.Q. Ji and *R. sp.1* (HKAS 110297) were grouped with European *R. decolorans*, *R. cremeoavellanea*, *R. integra*, *R. vinosa* and *R. claroflava*, forming a clade with moderate support (ML-bs 70%). Taxonomically this clade corresponds to *R.* subsect. *Integrinae* Sarnari. The other five species are *R. yanheensis* T.C. Wen *et al.* of *R.* subsect. *Paludosinae* Jul. Schäff., *Russula sp.2* (HKAS 104863 and HKAS 104855) of *R.* sect. *Laricinae* (Romagn.) Bon., *R. dhakuriana* K. Das *et al.* of *R.* subsect. *Roseinae* Singer ex Sarnari and two species (*R. aff. lepida* and *R. cf. lepida*) of *Russula* sect. *Flavisiccantes* Buyck & V. Hofst. in Das *et al.* (2017).

2.2 Phylogenetic species recognition of the *Russula griseocarnosa* complex

Five loci of 57 representative samples were successfully sequenced. In the five-locus phylogeny, these specimens formed two major clades. Clade B (ML-bs 100%) consisted of nine specimens collected from Fujian (Sanming) and Yunnan (Nanhua, Jingdong and Xinping). This clade was present in all single genealogies with significant supports except for in *TEF1- α* , but the paraphyly in *TEF1- α* had no bootstrap support (Table 2). It met both genealogical concordance and genealogical non-discordance and was defined as an independent evolutionary lineage. Clade A (ML-bs 100%) was composed of 48 samples (Fig. 2) from Fujian, Guangdong, Guangxi, Hunan and Yunnan. These samples formed seven well-supported terminal clades (I–VI and VIII) and one clade with low support (VII, ML-bs 69%) (Fig. 2). All clades except for VI and VII met one or both criteria of evolutionary lineage (Table 2). Three of the four samples of clade VI (HKAS

51839c, 126726, 149452) formed a well-supported clade (ML-bs 75%) with HKAS 149364 of clade VII in the ITS genealogy (tree not shown). This contradicted the supported monophyly of clade VI in the *RPB1* genealogy (ML-bs 76%) and the monophyly of clade VII in the *RPB2* genealogy (ML-bs 96%). In the ITS genealogy, sample HKAS 86734 of clade VII and the two samples of clade IV (HKAS 86737 and HKAS 149482) formed a monophyly with significant support (ML-bs 81%, tree not shown). This also contradicted the monophyly of clade VII in the *RPB2* genealogy and invalidated the recognition of evolutionary lineages of the clade VI+VII, despite the significant support (ML-bs 98%) in the combined phylogeny. To achieve exhaustive subdivision, all the samples of clade A were lumped into one phylogenetic species. Only two phylogenetic species were recognized: *R. griseocarnosa* and *R. occulta*, a new species to be described below. Within clade II, seven specimens from Ailao Mts. formed a terminal clade with long branch.

3 Nomenclature and taxonomy

3.1 Lectotypification of *Russula griseocarnosa*

The holotype of *R. griseocarnosa* is composed of three fruiting bodies. By next-generation sequencing, we obtained multi-genes from all of them. These individuals fell into three different clades of *R. griseocarnosa* by GCPSR: HKAS 51839a in VIII, HKAS 51839b in I and HKAS 51839c in VI (Fig. 2). The ITS sequence of HKAS 51839c is identical with the published holotype sequence EF627042. The spore measurements of the holotype in the original description are from HKAS 51839a and HKAS 51839b and the line drawings are from HKAS 51839a.

To avoid potential confusion of the identity of *R. griseocarnosa*, we need to select a fruiting body (specimen) to determine the application of this species name. HKAS 51839b does not have any priority, since neither the published ITS sequence (EF627042) nor the line drawings was from it. In GCPSR, clade VIII, where HKAS 51839a was nested, met both genealogical concordance and non-discordance, whereas clade VI, where HKAS 51839c was clustered, met neither.

Table 1 Samples sequenced in this study and used for investigating the species diversity of ‘dahongjun’ and phylogenetic species recognition of the *Russula griseocarnosa* complex

Species	Voucher specimen	Geographical origin	GenBank accession number				
			ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>
<i>R. badia</i>	587/BB 07.324 (PC0124709)	Slovakia	PX726806	KU237571	KU237715	KU237857	KU237999
<i>R. carminipes</i>	531/BB 07.192 (PC0124681)	Slovakia	PX726805	KU237523	KU237673	KU237809	KU237953
<i>R. claroflava</i>	WXH10952 (HKAS 146581)	Sweden	PV974715	PV973112	PV999097	PV999168	PV999017
<i>R. cremeoavellanea</i>	WXH10943 (HKAS 149035)	Sweden	PV974716	PV973113	PV999098	PV999169	PV999018
<i>R. decolorans</i>	WXH11050 (HKAS 146587)	Sweden	PV974717	PV973114	PV999099	PV999170	PV999019
<i>R. decolorans</i>	WXH11069 (HKAS 146590)	Sweden	PV974718	PV973115	PV999100	PV999171	PV999020
<i>R. dhakuriana</i>	CXH02 (HKAS 86727)	Shanghang, Fujian	PX622224 PX622225	PX558766	PX753901	PX580453 PX580454	PX694204
<i>R. dhakuriana</i>	WXH4518 (HKAS 104867)	Xinping, Yunnan	PX622226 PX622227	PX558767	PX580446 PX580447	–	PX580449
<i>R. dhakuriana</i>	YZL7713 (HKAS 150857)	Tengchong, Yunnan	PX622230	PX558768	PX694206	PX580455 PX580456	PX580450
<i>R. griseocarnosa</i> clade I	CXH03 (HKAS 86728)	Dapu, Guangdong	PV974585	PV973066	PV999049	PV999126	PV998967
<i>R. griseocarnosa</i> clade I	CXH04 (HKAS 86729)	Tengxian, Guangxi	PV974586	PV973067	PV999050	PV999127	PV998968
<i>R. griseocarnosa</i> clade I	CXH06 (HKAS 86731)	Pubei, Guangxi	PV974587	PV973068	PV999051	PV999128	PV998969
<i>R. griseocarnosa</i> clade I	CXH07 (HKAS 86732)	Yanling, Hunan	PV974588	PV973069	PV999052	PV999129	PV998970
<i>R. griseocarnosa</i> clade I	CXH10 (HKAS 86735)	Pubei, Guangxi	PV974589	PV973070	PV999053	PV999130	PV998971
<i>R. griseocarnosa</i> clade I	RTJ05 (HKAS 149431)	Sanming, Fujian	PV974578 PV974579	PV973065	PV999048	PV999125	PV998966
<i>R. griseocarnosa</i> clade I	WXH2125b (HKAS 51839b)	Jinghong, Yunnan	PV974584*	PV973140*	PV999118*	PV999191*	PV999040*
<i>R. griseocarnosa</i> clade II	CXH01 (HKAS 86726)	Shanghang, Fujian	PV974639	PV973077	PV999060	PV999137	PV998980
<i>R. griseocarnosa</i> clade II	CXH05 (HKAS 86730)	Rongxian, Guangxi	PV974640	PV973078	PV999061	PV999138	PV998981
<i>R. griseocarnosa</i> clade II	HJW02 (HKAS 149378)	Changting, Fujian	PV974605	PV973073	PV999056	PV999133	PV998975
<i>R. griseocarnosa</i> clade II	HJW07 (HKAS 149383)	Changting, Fujian	PV974610	PV973074	PV999057	PV999134	PV998976
<i>R. griseocarnosa</i> clade II	LJM12 (HKAS 149404)	Pucheng, Fujian	PV974599	PV973072	PV999055	PV999132	PV998973 PV998974
<i>R. griseocarnosa</i> clade II	RTJ02 (HKAS 149428)	Nanping, Fujian	PV974625 PV974626	PV973075	PV999058	PV999135	PV998977 PV998978
<i>R. griseocarnosa</i> clade II	WXH3163 (HKAS 73659)	Shixing, Guangdong	PV974630	PV973076	PV999059	PV999136	PV998979
<i>R. griseocarnosa</i> clade II	YYB04 (HKAS 149449)	Gutian, Fujian	PV974641	PV973079	PV999062 PV999063	PV999139	PV998982
<i>R. griseocarnosa</i> clade II	YYB10 (HKAS 149455)	Gutian, Fujian	PV974642 PV974643	PV973080	PV999064	PV999140	PV998983
<i>R. griseocarnosa</i> clade II	ZGY02 (HKAS 149353)	Rongxian, Guangxi	PV974591	PV973071	PV999054	PV999131	PV998972
<i>R. griseocarnosa</i> clade III	WXH4426 (HKAS 104790)	Maguan, Yunnan	PV974644	PV973089	PV999072	PV999148	PV998991
<i>R. griseocarnosa</i> clade III	WXH4506 (HKAS 104808)	Xinping, Yunnan	PV974645	PV973090	PV999073	PV999149	PV998992

(To be continued)

(Table 1 continued)

Species	Voucher specimen	Geographical origin	GenBank accession number				
			ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>
<i>R. griseocarnosa</i> clade IV	CXH12 (HKAS 86737)	Pu'er, Yunnan	PV974647	PV973091	PV999075	PV999150	PV998993
<i>R. griseocarnosa</i> clade IV	LSH28 (HKAS 149482)	Jingdong, Yunnan	PV974646	PV973141*	PV999074	PV999192*	PV999041
<i>R. griseocarnosa</i> clade V	WXH3527 (HKAS 76064)	Lüchun, Yunnan	PV974649	PV973092	PV999076	PV999151	PV998994
<i>R. griseocarnosa</i> clade V	ZP-2152 (MHHNU 8652)	Sangzhi, Hunan	PV974648*	PV973142*	PV999120*	PV999193*	PV999043*
<i>R. griseocarnosa</i> clade VI	LYC4252 (HKAS 149392)	Pingbian, Yunnan	PV974652	PV973094	PV999078	PV999153	PV998996
<i>R. griseocarnosa</i> clade VI	WXH2125c (HKAS 51839c) holotype p.p.	Jinghong, Yunnan	PV974650*	PV973143*	PV999119*	PV999194*	PV999042*
<i>R. griseocarnosa</i> clade VI	YYB07 (HKAS 149452)	Gutian, Fujian	PV974651	PV973093	PV999077	PV999152	PV998995
<i>R. griseocarnosa</i> clade VI	YZL6649 (HKAS 126726)	Ruili, Yunnan	PV974653	PV973095	PV999079	PV999154	PV998997
<i>R. griseocarnosa</i> clade VII	CXH09 (HKAS 86734)	Jiaoling, Guangdong	PV974657	PV973100	PV999085	PV999158	PV999003
<i>R. griseocarnosa</i> clade VII	ZGY08 (HKAS 149357)	Maoming, Guangdong	PV974654	PV973096 PV973097	PV999080	PV999155	PV998998 PV998999
<i>R. griseocarnosa</i> clade VII	ZGY09 (HKAS 149358)	Maoming, Guangdong	PV974655	PV973098	PV999081 PV999082	PV999156	PV999000 PV999001
<i>R. griseocarnosa</i> clade VII	ZGY19 (HKAS 149364)	Bobai, Guangxi	PV974656	PV973099	PV999083 PV999084	PV999157	PV999002
<i>R. griseocarnosa</i> clade VIII	MJM01 (HKAS 149417)	Nanping, Fujian	PV974677 PV974678	PV973101 PV973102	PV999086	PV999159	PV999004
<i>R. griseocarnosa</i> clade VIII	MJM08 (HKAS 149423)	Nanping, Fujian	PV974682	PV973103	PV999087	PV999160	PV999005 PV999006
<i>R. griseocarnosa</i> clade VIII	RTJ04 (HKAS 149430)	Nanping, Fujian	PV974687 PV974688	PV973104	PV999088	PV999161	PV999007
<i>R. griseocarnosa</i> clade VIII	WXH1989a (HKAS 51713)	Jinghong, Yunnan	PV974692*	PV973144*	PV999121*	PV999195*	PV999044*
<i>R. griseocarnosa</i> clade VIII	paratype WXH1989b (HKAS 51713)	Jinghong, Yunnan	PV974693*	PV973145*	PV999122*	PV999196*	PV999045*
<i>R. griseocarnosa</i> clade VIII	paratype WXH2125a (HKAS 51839a)	Jinghong, Yunnan	PV974694*	PV973146*	PV999123*	PV999197*	PV999046*
<i>R. griseocarnosa</i> clade VIII	WXH3509 (HKAS 76051)	Pu'er, Yunnan	PV974695	OP794377	OP805334	OP804711	PV999008
<i>R. griseocarnosa</i> clade VIII	YYB02 (HKAS 149447)	Gutian, Fujian	PV974698 PV974699	PV973105	PV999089	PV999162	PV999009 PV999010
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	LSH43 (HKAS 149483)	Jingdong, Yunnan	PV974624	PV973086	PV999069	PV999145	PV998988
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	SKM2 (HKAS 149437) holotype	Jingdong, Yunnan	PV974615	PV973081	PV999065	PV999141	PV998984
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	SKM5 (HKAS 149439)	Jingdong, Yunnan	PV974618	PV973082	PV999066	PV999142	PV998985
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	SKM6 (HKAS 149440)	Jingdong, Yunnan	PV974619	PV973083	PV999067	PV999143	PV998986
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	SKM7 (HKAS 149441)	Jingdong, Yunnan	PV974620	PV973084	PV999068	PV999144	PV998987
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	WXH4646 (HKAS 109819)	Nanhua, Yunnan	PV974636	PV973087	PV999070	PV999146	PV998989
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	WXH4649 (HKAS 104735)	Nanhua, Yunnan	PV974638	PV973088	PV999071	PV999147	PV998990
<i>R. griseocarnosa</i> var. <i>ailaoshanensis</i>	YZL7597 (HKAS 150851)	Baoshan, Yunnan	PX622248	PX558769	PX580448	PX580457	PX580451

(To be continued)

(Table 1 continued)

Species	Voucher specimen	Geographical origin	GenBank accession number				
			ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>
<i>R. integra</i>	518/BB 07.198 (PC0124682)	Slovakia	PX726804	KU237513	KU237663	KU237799	KU237943
<i>R. laeta</i>	519/BB 07.267 (PC0124692)	Slovakia	PX726803	KU237514	KU237664	KU237800	KU237944
<i>R. laricina</i>	575/BB 08.681		JN944008	KU237560	KU237704	KU237846	KU237991
<i>R. lepida</i>	437/BB 07.189 (PC0124680)	Slovakia	PX726807 PX726808	KU237500	KU237649	KU237786	KU237930
<i>R. aff. lepida</i>	QWQ-R064 (HKAS 110974)	Zhangjiajie, Hunan	PV974708	PV973107	PV999091	PV999164	PV999012 PV999013
<i>R. aff. lepida</i>	WJ193 (HKAS 104840)	Jingdong, Yunnan	PV974707	PV973106	PV999090	PV999163	PV999011
<i>R. aff. lepida</i>	WXH4489 (HKAS 104801)	Zhenyuan, Yunnan	PV974710 PV974711	PV973108 PV973109	PV999092	PV999165	PV999014
<i>R. cf. lepida</i>	WJ211 (HKAS 104857)	Jingdong, Yunnan	PV974713	PV973110	PV999093 PV999094	PV999166	PV999015
<i>R. cf. lepida</i>	WXH4488 (HKAS 104869)	Zhenyuan, Yunnan	PV974714	PV973111	PV999095 PV999096	PV999167	PV999016
<i>R. occulta</i>	WJ192 (HKAS 104858) holotype	Jingdong, Yunnan	PV974729	PV973122 PV973123	PV999107	PV999178 PV999179	PV999027
<i>R. occulta</i>	CXH11 (HKAS 86736)	Pu'er, Yunnan	PV974728	PV973121	PV999106	PV999177	PV999026
<i>R. occulta</i>	WJ194 (HKAS 110373)	Jingdong, Yunnan	PV974730	PV973124	PV999108	PV999180	PV999028
<i>R. occulta</i>	WXH4492 (HKAS 104866)	Zhenyuan, Yunnan	PV974735	PV973126	PV999110	PV999183	PV999029
<i>R. occulta</i>	WXH4656 (HKAS 104854)	Nanhua, Yunnan	PV974737 PV974738	PV973127	PV999111	PV999184	PV999030
<i>R. occulta</i>	WXH4657 (HKAS 104853)	Nanhua, Yunnan	PV974739	PV973128	PV999112	PV999185	PV999031
<i>R. occulta</i>	WXH4662 (HKAS 104852)	Nanhua, Yunnan	PV974741	PV973130	PV999113	PV999186	PV999034
<i>R. occulta</i>	WXH4665 (HKAS 104851)	Nanhua, Yunnan	PV974742	PV973131	PV999114	PV999187	PV999035
<i>R. occulta</i>	ZP01 (HKAS 149414)	Sanming, Fujian	PV974743	PV973132	PV999115	PV999188	PV999036
<i>R. paludosa</i>	442/BB 07.330 (PC0142538)	Slovakia	PX754887	KU237505	KU237654	KU237791	KU237935
<i>R. purpureozonata</i>	WXH5155 (HKAS 111615)	Deqin, Yunnan	PV974723	PV973118	PV999103	PV999174	PV999023
<i>R. purpureozonata</i>	WXH8294 (HKAS 117918)	Deqin, Yunnan	PV974720	PV973116	PV999101	PV999172	PV999021
<i>R. purpureozonata</i>	WXH8707 (HKAS 118314)	Deqin, Yunnan	PV974722	PV973117	PV999102	PV999173	PV999022
<i>R. quercina</i>	WP-1 (HKAS 149469)	Kunming, Yunnan	PV974725	PV973119	PV999104	PV999175	PV999024
<i>R. quercina</i>	WP-3 (HKAS 149471)	Kunming, Yunnan	PV974727	PV973120	PV999105	PV999176	PV999025
<i>R. subdensifolia</i>	552/BB 05.158 (PC0124674)	USA	PX754886	KU237544	–	KU237830	KU237974
<i>R. vinosa</i>	WXH11053 (HKAS 146588)	Sweden	PV974746	PV973133	–	PV999189	PV999037
<i>R. yanheensis</i>	WXH4661 (HKAS 104879)	Nanhua, Yunnan	PV974748 PV974748	PV973136	PV999117	PV999190	PV999039
<i>R. yanheensis</i>	WXH7157 (HKAS 120113)	Jianchuan, Yunnan	PV974747	PV973134 PV973135	PV999116	–	PV999038
<i>Russula</i> sp.1	WXH4493 (HKAS 110297)	Zhenyuan, Yunnan	PV974736	PV973147*	PV999124*	PV999198*	PV999047*
<i>Russula</i> sp.2	WXH4658 (HKAS 104855)	Nanhua, Yunnan	PV974740	PV973129	PX694205	PV999182	PV999032
<i>Russula</i> sp.2	WJ50 (HKAS 104863)	Maguan, Yunnan	PV974731	PV973125	PV999109	PV999181	PV999033

Note: Sequences produced in this study are in bold and those marked with “*” are generated by next-generation sequencing.

Table 2 Maximum likelihood bootstrap value from the single-locus genealogies and five-locus combined phylogeny for each terminal clade of *Russula griseocarnosa* complex

Clade	ITS	LSU	<i>RPB2</i>	<i>TEF1-α</i>	<i>RPB1</i>	Five-locus combined	Criterion satisfied
I	98%	52%	–	55%	94%	100%	a & b
II	100%	74%	96%	81%	–	100%	a & b
III	96%	99%	100%	–	100%	100%	a & b
IV	84%	98%	–	–	–	90%	b
V	90%	90%	–	–	–	100%	b
VI	Supported paraphyly	–	63%	–	76%	84%	Neither
VII	Supported paraphyly	–	96%	–	–	69%	Neither
VI+VII	Supported paraphyly	–	86%	23%	93%	98%	Neither
VIII	–	56%	90%	51%	100%	100%	a & b
B	69%	80%	89%	–	100%	100%	a & b

Note: a: genealogical concordance; b: genealogical non-disconcordance. Missing values apply to non-monophyly lacking significant support.

Moreover, clade VIII includes the paratype HKAS 51713, and is the clade from which the morphological recognition of *R. griseocarnosa* is *de facto* made. Thus, HKAS 51839a has qualification to be a type and we here make a lectotypification for *R. griseocarnosa* using it: Lectotype (*hic designatus*): Yunnan Province, Jinghong, Xiaomengyang Township, Xishuangbanna National Nature Reserve, Guanping Station, 28 Jul. 2006, X.H. Wang 2125a (HKAS 51839a, KUN) (MycoBank registration number: MBT 10030945). The GenBank accession numbers of this lectotype are: PV974694-ITS, PV973146-nrLSU, PV999123-*RPB1*, PV999197-*RPB2* and PV999046-*TEF1- α* .

3.2 Taxonomy

Russula griseocarnosa var. *ailaoshanensis* K.M. Su, S.H. Li, Pei Zhang, Yu-Wu Li & X.H. Wang, var. nov. (灰肉红菇哀牢山变种) Fig. 3

MycoBank: MB 861588

Etymology: named after the type locality, Ailao Mts.

Holotype: China, Yunnan Province, Jingdong County, Taizhong Township, Ailao Mts. National Nature Reserve, 5 Aug. 2019, K.M. Su, no. SKM2 (HKAS 149437, KUN!).

Diagnosis: differing from *R. griseocarnosa* var. *griseocarnosa* by the white or less gray pileus context, bigger spores and more inflated hyphae in the subpellis of pileipellis.

Basidiocarps medium-sized to big, thick-fleshed, fragile. Pileus 70–90 mm diam., convex with a broadly depressed center; surface smooth, greasy when wet, soon dry, often with concentric wrinkles, cuticle cracked when mature, dark red to vivid red, locally paler or with orange tinge, cuticle peeling around 70% towards the center;

context white, rarely gray. Lamellae 3–6 mm broad, adnate, sub-crowded to crowded, brittle and fragile, nearly equal, whitish cream when young, then turning warm ochre, with rose red edge near the pileus margin; context 3–6 mm thick, white, rarely gray. Stipe 75–115 mm \times 15–20 mm, cylindrical or slightly expanding downwards; surface smooth, white or red when young, pale to dark rose red when mature; context pale gray. Taste mild, rarely acrid then hurting.

Spores (180/8/8)(8–)8.5–9.3–10(–10.5) \times (7–)7.5–7.9–8.5(–9) μm , Q= (1.04–)1.11–1.17–1.25(–1.29), subglobose to broadly ellipsoid; ornamentation 1–1.8(–2) μm , composed of conical warts, warts mostly isolated, rarely fused; suprahilar spot totally amyloid. Basidia 40–65 \times 11–15 μm , clavate, 4-spored. Hymenophoral gloeocystidia common to abundant, emergent, 85–130 \times 12–18 μm , projecting 20–50(–85) μm beyond the basidia layer, base originating deeply from subhymenium or trama, fusiform, with flocculent, granular or crystalline contents, middle part often thick-walled (wall to 1 μm thick), apex rarely moniliform or mamillate. Lamellar edge fertile or sterile; cystidia rare to abundant, 67–126 \times 8–16 μm , fusiform, some cylindrical-clavate, with flocculent or granular contents. Pileipellis orthochromatic in cresyl blue, an (ixo) trichoderm, 120–220 μm thick, hyphae compactly ascending, branching, locally with long repent hyphae, with disperse rose pink pigmentation; hyphae in subpellis mostly 3–7 μm wide, some inflated to 13–15 μm wide; hyphae in suprapellis 3–7 μm wide, terminal cells 19–80 \times 4–8 (–10) μm , cylindrical, fusiform, with scattered zebroid ornamentation; pileocystidia absent. Stipitipellis a

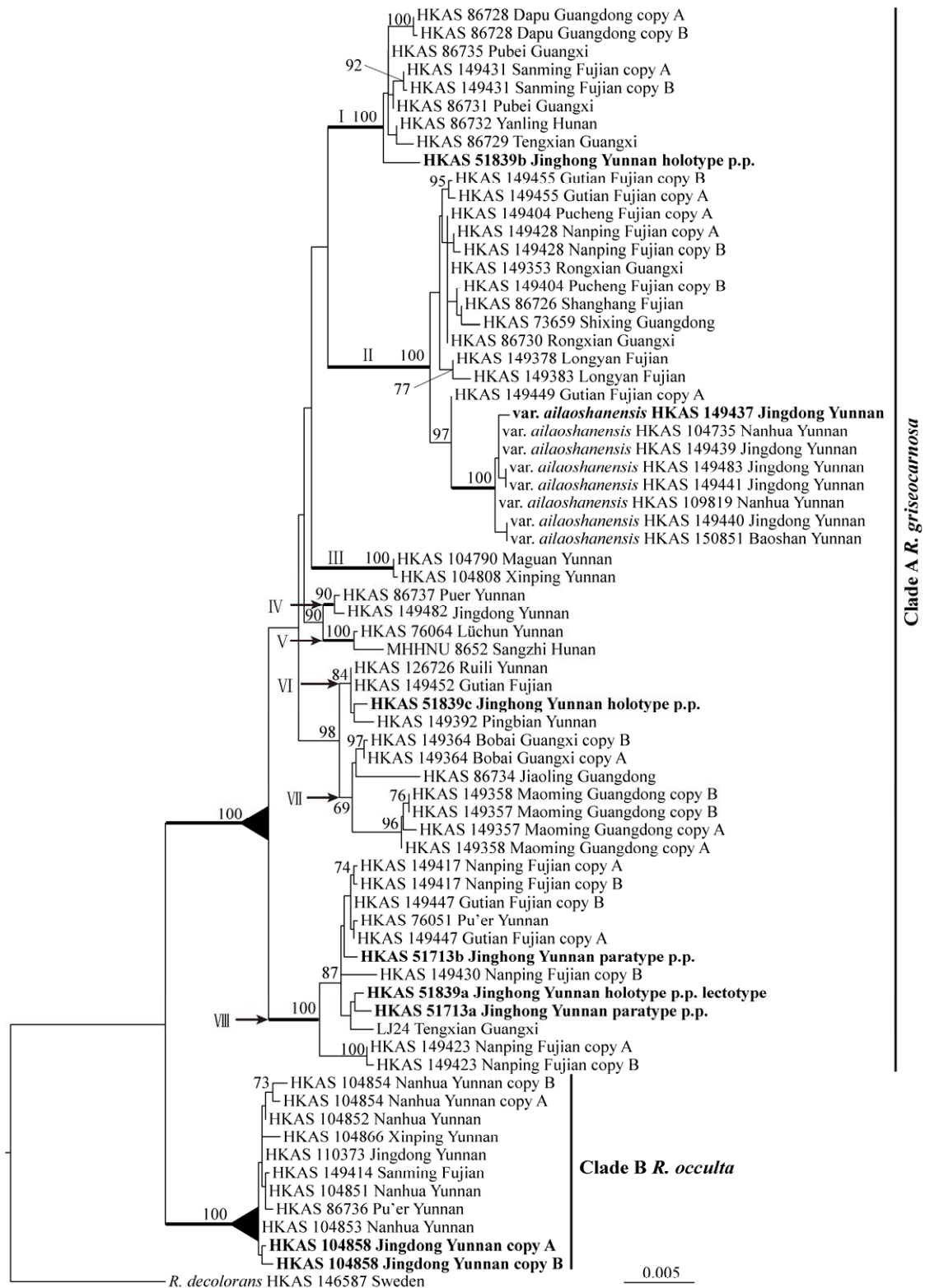


Fig. 2 Maximum likelihood phylogram generated from combined ITS-nrLSU-RPBI-RPB2-TEF1- α dataset of *Russula griseocarnosa* complex. The thick branches indicate independent evolutionary lineages and the triangles at the nodes two species recognized by genealogical concordance phylogenetic recognition. Note that clades VI and VII are not evolutionary lineages. Sample names are given in the order of herbarium number, county name and province (autonomous region) name. Copy A and B refer to the different copies of ITS or other loci when ITS has only one copy. Samples in bold are types. The tree was rooted with *R. decolorans*.

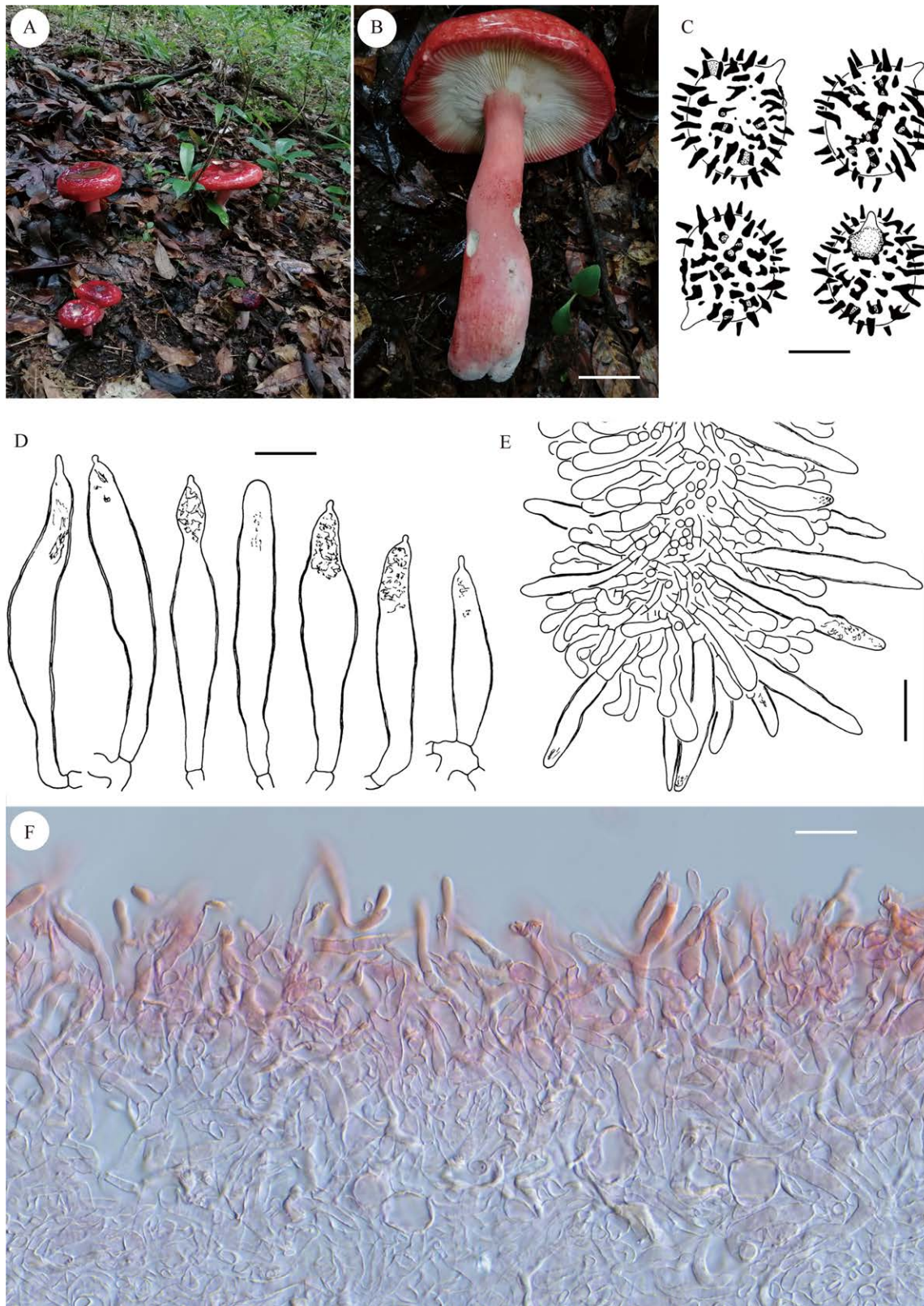


Fig. 3 *Russula griseocarnosa* var. *ailaoshanensis* (holotype). A: Basidiocarps in the habitat, B: Basidiocarp, C: Spores, D: Pleurocystidia, E: Lamellar edge, F: Pileipellis. Scale bars: B=2 cm, C=5 μ m, D=20 μ m, E, F= 25 μ m.

cutis, 50–150 μm ; hyphae 2–5 μm wide, hyaline; cystidia absent. Rosettes abundant in gill, pileus and stipe trama. Clamp connections absent.

Ecology: in group, in fagaceous forests, subtropical, mid-montane.

Distribution: Yunnan (Baoshan City, Dali City, Jingdong, Jinggu, Lincang, Nanhua).

Additional specimens examined: China, Yunnan Province, Chuxiong City, Xishelu Township, Ailao Mts. National Nature Reserve, Gamo Village, collected from local mushroom hunters, 7 Sept. 2024, X.H. Wang & P. Zhang, no. XHW12556 (HKAS 149442), XHW12557 (HKAS 149443), XHW12558 (HKAS 149444), XHW12559 (HKAS 149445); Jingdong County, Taizhong Township, Ailao Mts. National Natural Reserve, Xujiaba, 5 Aug. 2019, K.M. Su, no. SKM1-1 (HKAS 149435), SKM1-2 (HKAS 149436), SKM2 (HKAS 149437), SKM4 (HKAS 149438), SKM4-2 (HKAS 149468), SKM5 (HKAS 149439), SKM6 (HKAS 149440), SKM7 (HKAS 149441), SKM8 (HKAS 149464), SKM9 (HKAS 149465), SKM10 (HKAS 149466), SKM11 (HKAS 149467); Jingdong County, Ailao Mts. National Nature Reserve, 10 Aug. 2019, J. He, no. LSH03 (HKAS 149481), LSH43 (HKAS 149483); Nanhua County, Majie Township, Ailao Mts. National Nature Reserve, Dazhongshan, 16 Aug. 2017, X.H. Wang, B. Buyck & J. Wang, no. XHW4646 (HKAS 109819), XHW4648 (HKAS 111683), XHW4649 (HKAS 104735); Nanhua County, Majie Township, Ailao Mts. National Nature Reserve, Dazhongshan, Boluoshan, in fagaceous forest, 24°48'11.10"N 100°51'34.59"E, alt. 2 551 m, 14 Aug. 2024, X.H. Wang & P. Zhang, no. XHW11935 (HKAS 145185).

Note: This variety corresponds to lineage 1-1 in Li *et al.* (2010) and part of clade I in Feng *et al.* (2020). All the specimens of this variety in Li *et al.* (2010) and in the present study are from Ailao Mt, except for HKAS 150851 from Gaoligong Mts. Some specimens of Feng *et al.* (2020) are from Jinggu, Lincang and Dali, surrounding areas of Ailao Mts.

Different from *R. griseocarnosa* var. *griseocarnosa* as represented by HKAS 51839a and HKAS 51713a and 51713b (clade VIII in Fig. 2), this variety has white or less gray context in the pileus. Among the lineages of *R. griseocarnosa*, this variety and the other samples in clade II, clades VI and VII have bigger spores. The taste of context is often mild, but we did find specimen

with acrid taste (HKAS 104735). Hyphae in the subpellis are often more inflated than those of *R. occulta* and *R. griseocarnosa* var. *griseocarnosa*.

Russula occulta X.H. Wang, Pei Zhang & J. Wang, **sp. nov.** (隐匿红菇) Fig. 4

MycoBank: MB 861589

Holotype: China. Yunnan Province, Jingdong County, Yinsheng market, 15 Aug. 2017, Jing Wang 192 (HKAS 104858).

Etymology: *occulta* = hidden, naming a species that has been hidden in its sibling species *R. griseocarnosa*.

Diagnosis: A species characterized by thick-fleshed basidiocarps, smooth dark red pileus hardly with striates, white context in the pileus, relatively small spores (6.5–8 \times 5.5–7 μm) with blunt warts and short ridges partly connected and pileipellis an (ixo)trichoderm. Differing from *R. griseocarnosa* in the whitish context in pileus and smaller spores with more coalescent ornamentation.

Basidiocarps medium-sized to big, thick-fleshed, fragile. Pileus 40–120 mm diam., broadly depressed in the center, margin applanate, not or with very short striates; surface slightly greasy when wet, soon dry, smooth, locally cracked when mature, particularly so closer to the margin, margin sometimes rugose, cuticle peeling 10% to 50% towards the center, greyish red (10B4), red (10B5), brownish red (10D7) to violet brown (11F7) in the center, sometimes with cream-ochre spots, paler (11B7) towards margin; context 3–7 mm thick, white. Lamellae 3–9 mm broad, equal, adnate, sub-crowded to crowded, 6–11 L/cm, brittle, not or exceptionally forking away from stipe, cream-coloured, warm ochre when mature. Stipe 60–80 mm \times 20–25 mm, cylindrical or slightly narrowing downwards, neither extremely fragile nor very hard, white (10A1) or pink (11A3, 11A4), sometimes with grayish tinge, spongy inside, white or pale gray (paler than 10B1). Taste mild or slightly acrid, rarely strongly acrid.

Spores (260/13/7)(6–)6.5–7.2–8(–8.5) \times (5–)5.5–6.2–7(–7.5) μm , $Q = (1.03–)1.11–1.16–1.20(–1.23)$, subglobose, broadly ellipsoid, rarely globose; ornamentation 0.3–0.7(–1) μm high, composed of blunt warts and short ridges fused or connected by fine lines, rarely forming a broken reticulum, suprahilar spot totally amyloid. Basidia (27–)30–55 \times 8–13(–16) μm , clavate, 4-spored. Hymenophoral gloecystidia scattered to common,

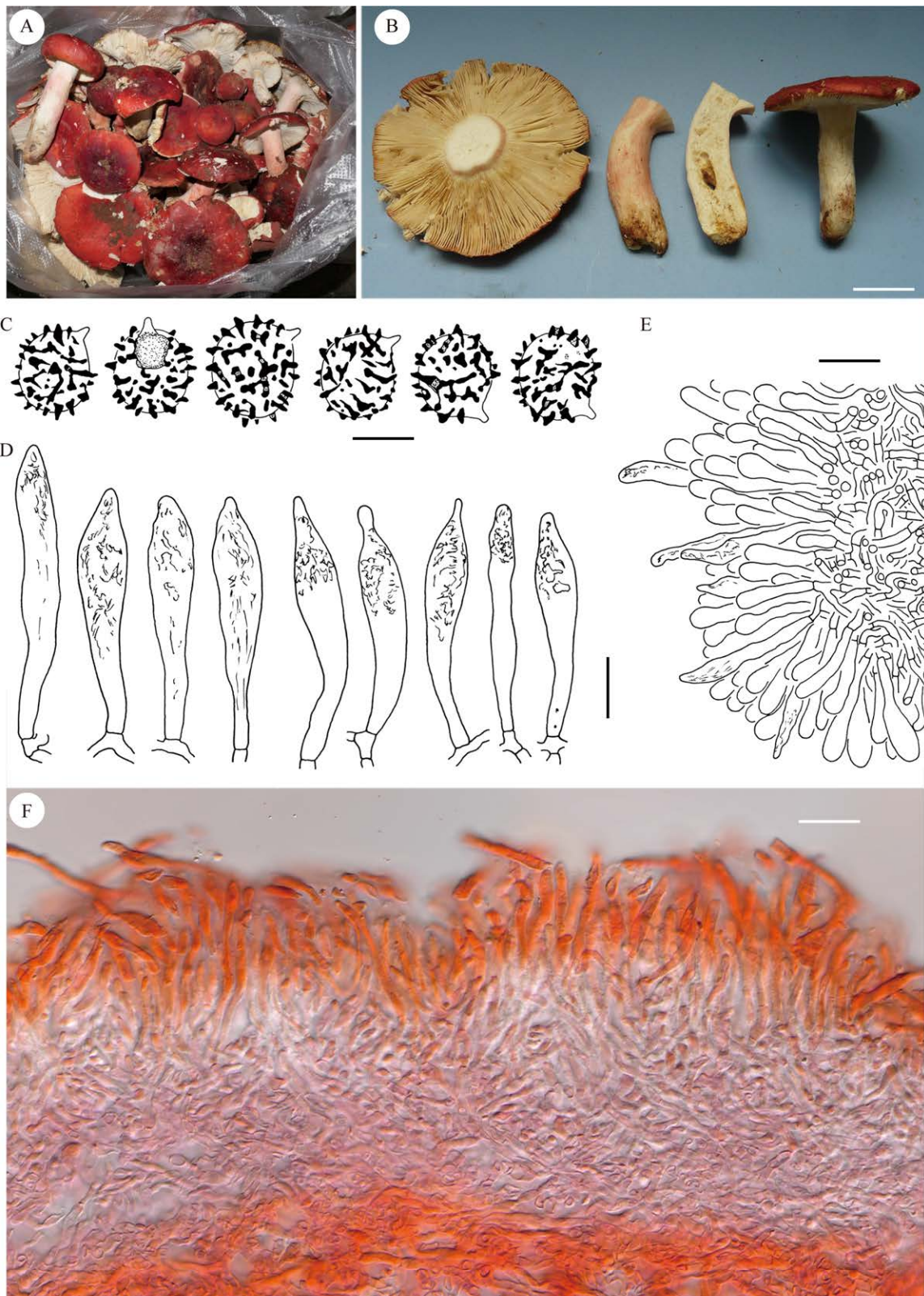


Fig. 4 *Russula occulta* (holotype). A: Basidiocarps sold in market, B: Basidiocarps, C: Spores, D: Pleurocystidia, E: Lamellar edge, F: Pileipellis. Bars: B=1 cm, C=5 μ m, D=20 μ m, E, F=25 μ m.

56–112 × 7–17 μm, originating deeply from the subhymenium or trama, emergent, projecting 10–35(–74) μm beyond the basidia layer, fusiform, cylindrical-clavate, rarely thick-walled (wall 0.5–1 μm thick), with dense pale yellow granular, crystalline or flocculent contents in the middle and upper parts. Lamellar edge fertile or sterile; cheilocystidia rare to common, 23–97 × 8–13 μm, subfusiform, cylindrical, rarely thick-walled (wall up to 1 μm thick), with flocculent or granular contents. Pileipellis orthochromatic in cresyl blue, an (ixo)trichoderm, 100–180 μm thick, sometimes with a mucous layer 30–50 μm thick, hyphae compactly ascending, locally with long repent hyphae, with disperse rose pink pigmentation; hyphae in subpellis 3–5 μm wide, in suprapellis 3–7 μm wide, terminal cells 30–45 × 3–7 μm, cylindrical, subfusiform, surface rarely with zebroid ornamentation; pileocystidia absent. Stipitipellis a cutis, 65–165 μm, hyphae 2–5 μm wide; cystidia absent. *Rosettes* abundant in gill, pileus and stipe trama. Clamp connections absent.

Ecology: habitat not fully known, growing in *Quercus* forests in subtropical mid-montane areas.

Distribution: southeast and southwest China (Fujian and Yunnan).

Additional materials examined: China. Fujian Province, Sanming, Dec. 2024, collected from local markets by Y.J. Ma, no. ZP01 (HKAS 149414), ZP02 (HKAS 149415), ZP03 (HKAS 149416); Nanping City, Wuyi Mt., collected from local market by J.M. Miao, no. MJM04 (HKAS 149419); Yunnan Province, Dali City, Cangshan, west slope, Xueshanhe reserve, 12 Aug. 2020, J. He, Z.Q. Zhang & J. Gao, no. sj136 (HKAS 128490); Jingdong County, Yinsheng market, 15 Aug. 2017, J. Wang 194 (HKAS 110373); Nanhua County, wild mushroom market, 17 Aug. 2017, X.H. Wang, B. Buyck & J. Wang, no. XHW4656 (HKAS 104854), XHW4657 (HKAS 104853), XHW4662 (HKAS 104852), XHW4665 (HKAS 104851); Simao, Nanping Township, Manxie Village, 7 Sept. 2013, Bo Xiao, no. CXH11 (HKAS 86736); Yunlong County, Caojian Township, market, X.H. Wang 7887 (HKAS 117515); Zhenyuan County, Heping Township, market, X.H. Wang, B. Buyck & J. Wang, no. XHW4492 (HKAS 104866).

Note: This is the real sibling of *R. griseocarnosa*. It is not as common as *R.*

griseocarnosa and seems to prefer less tropical areas. In the field and markets, it can be separated from typical *R. griseocarnosa* by the white pileus context. Microscopically it can be easily separated from *R. griseocarnosa* by the much smaller spores with more coalescent ornamentation. Taste of flesh varies among individuals, being mild (HKAS 104852 and HKAS 104854), weakly acrid (HKAS 105851), acrid but not very strong (HKAS 104853), to strongly acrid (HKAS 104858). The acrid taste and the white context suggest *R. chichuensis* W.F. Chiu, described by Chiu (1945) from central Yunnan. *Russula chichuensis* has paler pileus and bigger spores. *Russula griseocarnosa* var. *ailaoshanensis* has nearly white pileus context, but it has much bigger spores and more inflated hyphae in the pileipellis.

Russula purpureozonata K. Das, A. Ghosh & Buyck, *European Journal of Taxonomy* 782: 164 (2021) (紫环红菇, 新拟) Fig. 5F

Basidiocarps big, stout, thick-fleshed, compact. Pileus 65–135 mm diam., convex with a broadly depressed center; surface smooth, subgreasy to greasy, first nearly black, cuticle cracked into patchy scales, these forming concentric zones, center reddish gray (12C2), pale yellowish brown or olivaceous brown with purplish tinge towards margin, locally paler or with orange tinge, cuticle peeling around 1/5–2/3 towards the center, margin not striate; context 5–7 mm thick, smoky gray to grayish black, then ±discoloring reddish brown (similar to the discoloration in *Russula* sect. *Nigricantinae* Bataille). Lamellae 5–11 mm broad, adnate, sub-crowded (5–7 L/cm), equal, ±brittle, slightly buttery when touched, edge even or toothed, anastomosing towards context, forking near the stipe apex, yellowish white (2A2, 3A2) to pale yellow (2A3, 3A3), sometimes with grayish tinge, then turning pale brownish, with rose red edge near the pileus margin. Stipe 50–90 mm × 16–25 mm, expanding downwards, hard, spongy inside; surface smooth, yellowish white with pinkish flush or nearly purplish red; context smoky gray. Taste mild.

Spores (40/2/2) (7.5–)8–8.4–9(–9.5) × 6.5–7.3–8 μm, Q= 1.09–1.14–1.20(–1.23), broadly ellipsoid; ornamentation 0.1–0.5 μm high, composed of blunt warts and short irregular ridges, those mostly isolated, rarely fused; suprahilar spot totally amyloid. Basidia 45–60 × 11–14 μm, clavate, 4-spored, some with dark brownish



Fig. 5 Species similar in appearance to ‘dahongjun’. A: *Russula griseocarnosa* clade VIII (HKAS 76051); B: *R. griseocarnosa* clade III (HKAS 104808); C: *R. dhakuriana* (HKAS 104867); D: *R. aff. lepida* (HKAS 104840); E: *R. cf. lepida* (HKAS 104869); F: *R. purpureozonata* (HKAS 118314); G: *Russula* sp1 (HKAS 110297); H: *R. quercina* (HKAS 149469); I: *Russula* sp.2 (HKAS 104855); J: *R. yanheensis* (HKAS 104879).

contents. Hymenophoral gloeocystidia abundant, emergent, $68\text{--}100 \times 9\text{--}13 \mu\text{m}$, projecting $10\text{--}30 \mu\text{m}$ beyond the basidia, base originating deeply from subhymenium or trama, slightly thick-walled, fusiform with a long narrow base and wide and blunt upper part, tips rarely constricted, with needle-like contents. Lamellar edge sterile, marginal cells $20\text{--}35 \times 4\text{--}7 \mu\text{m}$; cheilocystidia common, $55\text{--}70 \times 8\text{--}16 \mu\text{m}$, cylindrical, subfusiform, with granular or crystalline contents. Pileipellis orthochromatic in cresyl blue, a thick subtrichoderm, $170\text{--}260 \mu\text{m}$ thick, hyphae compactly packed and interwoven, those in suprapellis mostly ascending, in subpellis more horizontally oriented, branching, $3\text{--}5 \mu\text{m}$ wide; pileocystidia common, distributed at different depths, cylindrical, $60\text{--}140 \times 5\text{--}8 \mu\text{m}$, $2\text{--}3$ celled, with pale yellowish brown granular or crystalline contents. Stipitipellis a cutis, $70\text{--}100 \mu\text{m}$; hyphae compactly packed, $2.5\text{--}4 \mu\text{m}$ wide, hyaline, hyphal ends projecting, clavate, $4\text{--}7 \mu\text{m}$ wide; caulocystidia common, long, $4\text{--}7 \mu\text{m}$ wide. Rosettes abundant in gill, pileus and stipe trama, locally with dark brown contents. Clamp connections absent.

Ecology: scattered in *Abies* forests, subalpine.

Distribution: China (northwestern Yunnan) and India (Sikkim).

Specimens examined: China, Yunnan Province, Deqin County, Benzilan Township, Baima Snow Mts., road from Benzilan to Deqin, $28^{\circ}18'40''\text{N}$ $99^{\circ}07'40''\text{E}$, alt. 3 600 m, 11 Aug. 2018, X.H Wang 5155 (HKAS 111615); Deqin County, Yanmen Township, Yugong Village, west slope of Baima Snow Mts., $28^{\circ}30'13.83''\text{N}$ $98^{\circ}54'47.41''\text{E}$, alt. 3 406 m, 23 Aug. 2020, X.H. Wang & Z. Wang, no. XHW8294 (HKAS 117918); Yunling Township, road from Deqin to Gongshan, Kongqushan mountain pass, 26 Aug. 2018, X.H. Wang 5846 (HKAS 116519); Deqin County, Yunling Township, road from Nanzhong mountain pass to Xidang Village, $28^{\circ}23'39.49''\text{N}$ $98^{\circ}49'15.17''\text{E}$, alt. 3 712 m, 26 Aug. 2020, X.H. Wang & Z. Wang, no. XHW8634 (HKAS 118247); *ibid.*, 27 Aug. 2020, X.H. Wang & Z. Wang, no. XHW8707 (HKAS 118314).

Note: The morphology of the Chinese specimens cited above meets the original description of this species given by Das *et al.* (2021), except that the flesh of the Chinese species is initially smoky gray (*i.e.* not changing to gray) and the spore ornamentation is much lower ($0.3\text{--}1.2 \mu\text{m}$ in Indian specimens). This is a typical

subalpine species, specifically growing with *Abies* trees. In the field, it looks like a “dingy olivaceous-purple” *R. griseocarnosa*. Microscopically the spores with blunt ornamentation and presence of pileocystidia are good characters separating it from *R. griseocarnosa*.

4 DISCUSSION AND CONCLUSION

4.1 *Russula griseocarnosa*: a phylogenetic species with high genetic and morphological variations

Although Li *et al.* (2010) and Feng *et al.* (2020) defined several lineages in *R. griseocarnosa*, they did not answer whether these lineages represent real phylogenetic species. By broader sampling, adding two loci (*RPB1* and *TEF1- α*) and conducting GCPSR, the present study concludes that these lineages are not real phylogenetic species. There exists discordance among the ITS, *RPB1* and *RPB2* genealogies. On the context of current sampling, if we take each of the evolutionary lineages as different species, the samples of clade VI and VII will be left as unclassified, since these clades do not meet the criterion of being an evolutionary lineage and thus independent species. We recognized only two phylogenetic species: *R. griseocarnosa* and *R. occulta*.

The lineages of *R. griseocarnosa* vary considerably in size and geographical range. By combining all the ITS sequences of Li *et al.* (2010), Feng *et al.* (2020), Yu *et al.* (2020) with our own data, we could compare the genetic variations among the lineages based on ITS sequences. Clade I has the biggest within-group genetic distance. It was found from 11 counties of five province-level administrative regions (Fujian, Guangdong, Guangxi, Hunan, Yunnan). Clade VII is the most common lineage, with 205 documented samples from 15 counties of four province-level administrative regions (Fujian, Guangdong, Guangxi, Yunnan). In this clade, 150 specimens belong to *R. griseocarnosa* var. *ailaoshanensis* and they are only found in subtropical Yunnan, mainly from Ailao Mts. The three exclusive lineages discovered in this study (III, IV and V) have smallest population size and genetic variation. The lowest within-species ITS similarity is 92% after all these clades were lumped in *R. griseocarnosa*.

We have to admit that such cutoff is too tolerant and even much lower than the popularly acknowledged cutoff of OTU in environmental studies. *Russula griseocarnosa* may eventually fall into several species if broader sampling and/or more DNA loci, e.g. genome data are used. For the time being, this taxonomic treatment does not seem to be unacceptable, as at least the trade of ‘dahongjun’ will benefit more from recognizing only one species than splitting into many small species.

Russula griseocarnosa as defined in this study holds high morphological variations. The two specimens of clade III (HKAS 104790 and HKAS 104808) have pileus with mixed dingy ochraceous and dull reddish color (Fig. 5B). Spores of this clade are smallest among all the lineages (av. $7.8 \times 6.8 \mu\text{m}$). This lineage merits an infraspecific taxon if the variations are confirmed by more specimens. The Indian “*Russula griseocarnosa*” with a less reddish and more ochraceous pileus documented by Das *et al.* (2010) might belong here, except that their spores are slightly bigger (av. $8.5 \times 7.3 \mu\text{m}$). Spore of clades II, VI, and VII are much bigger (av. $9.3\text{--}9.7 \times 8\text{--}8.2 \mu\text{m}$), whereas those of clades I, IV, V, and VIII are intermediate (av. $8.3\text{--}8.7 \times 7.2\text{--}7.5 \mu\text{m}$). All the clades have greyish context, except that the populations of Ailao and Gaoligong Mts. of clade II have white or nearly white context. Microscopically they all have spores ornamented with isolated warts and lack pileocystidia in the pileipellis. If *R. griseocarnosa* is split into more species, some of them would be cryptic. Given that the geographical ranges of these lineages strongly overlap, we speculated a prevalent sympatric speciation scenario.

4.2 ‘dahongjun’: an assemblage of lookalikes consisting of several phylogenetically distinct species

After *R. griseocarnosa* was described to replace the name *R. vinosa* for Chinese specimens (Wang *et al.* 2009), for a long time it was nearly the only available scientific name for marketed ‘dahongjun’ in China. This study discovered a high species diversity under ‘dahongjun’. These species are placed in five sections/subsections (Fig. 1). The most acknowledged and prized species is still *R. griseocarnosa*. It is widely distributed in subtropical-tropical areas, including Fujian, Guangdong, Hunan, Guangxi, Yunnan and Sichuan

(voucher specimen SAAS 3706). The less common species is *R. occulta*, living in untypically tropical places (Ailao Mts. and northwards and Fujian). This species has whitish context and much smaller spores (Fig. 3). In the subalpine coniferous forests of Yunnan, *R. purpureozonata*, a species originally described from subalpine Himalayan India (Ghosh *et al.* 2021), is firstly discovered. This thick-fleshed species has dulled purple pileus and typically greyish context (Fig. 5F). In the field it is strongly reminiscent of *R. griseocarnosa*. However, multi-gene phylogenetic analysis showed that it was not sister to *R. griseocarnosa*, but to an undescribed species (HKAS 110297) which was also sold in Ailao Mts. under ‘dahongjun’. These two species formed a clade sister to European *R. cremeoavellanea*. We have not seen *R. purpureozonata* in local market, but it has potential commercial value. In a very small local market near Kunming, fresh fruiting bodies of *R. quercina*, a species originally described from Heilongjiang, northeast China (Zhou *et al.* 2022), were occasionally seen (Fig. 5H). Apparently, they were collected from the forest nearby and taken as edible mushrooms by the local people. It has less dark pileus, white flesh, yellower lamellae and less stout basidiocarps. The five species above all belong to *R.* subsect. *Integrae* or to the “Decolorantes” group.

The other four species regarded as ‘dahongjun’ in Yunnan markets are dispersed in three section/subsections. In sect. *Flavisiccantes*, *R.* aff. *lepida* (Figs. 1 and 5D) formed a sister of European *R. lepida*. This species is very common in subtropical-tropical markets in Yunnan. In Yunnan market, there is another less common species of this section (*R.* cf. *lepida* in Figs. 1 and 5E, represented by HKAS 104857 and HKAS 104869). In GenBank an ITS sequence from China (PP930946) and two from India (OQ653085 and PP582965), which are misidentified as *R. shigatseensis* S.Hui Wang *et al.* belong to this species. We did not find reliable difference among this species, *R.* aff. *lepida* and European *R. lepida* and here left it as a cryptic species. *Russula shigatseensis* has much smaller spores (Wang *et al.* 2024). Microscopically the more or less reticulate spores and the presence of pilocystidia of the species above can help to separate them from *R. griseocarnosa* and *R. occulta*.

Russula yanheensis, a species originally described from Guizhou (Tibpromma *et al.* 2017),

was seen in the markets of Nanhua and Jianchuan, Yunnan. It was placed in *R.* subsect. *Paludosinae* in our phylogeny. This species has white context and quite stout basidiocarps, hardly separated from *R. occulta* based simply on macromorphology. In the original description, the spores of *R. yanheensis* were described as having “moderately large and distant amyloid warts”. The spore photos were not taken in Melzer’s reagent, therefore it is not possible to see the details of ornamentation. Our two specimens have spores with very fine and low ornamentation (0.1–0.3 μm high), composed of ridges and warts partly connected into a broken reticulum. Wang *et al.* (2022) reported “*Russula vinosa*” from Pu’er market in tropical Yunnan. Their voucher specimen (HKAS 122380) is actually *R. yanheensis*. “*Russula paludosa*” reported by Zhang *et al.* (2021, ITS GenBank no. MW874552) from Yunnan is also *R. yanheensis*. Further analysis of ITS sequences shows that *R. yanheensis* has wide geographical distribution. We collected this species in *Quercus* forest from Bomi, Xizang (HKAS 116446; ITS GenBank no. PV974750). The Japanese sample OMS-113 (ITS

GenBank no. LC667117) reported by Shirakawa *et al.* (2022) and UDB0777983 from Laos and UDB013215 from Papua New Guinea in the UNITE database also belong to this species.

The last known species, *R. dhakuriana*, was originally described from India (Das *et al.* 2006). It belongs to *R.* subsect. *Roseinae*. We did not see it in markets, but local people in Gaoligong Mts. picked and ate it. When fresh, the white flesh, vivid red pileus and the relatively slender fruiting bodies are helpful to recognition (Fig. 5C). Microscopically the subpellis of pileus with regular layers of globose cells and the short erect hyphae in the suprapellis, together with the medium-sized spores ornamented with isolated warts are characteristic. *Russula dhakuriana* reported by Zhao & Ji (2021) does not fit this species. The photos represent a species of *R.* subgen. *Archaeae*, most likely *R. butyroindica* K. Das & Buyck. Their spores (5.2–6.8 \times 3.2–4.8 μm) are too small for *R. dhakuriana*. This species is common in Ailao Mts. and also detected from environmental samples in central Japan (GenBank accessions LC096755 and LC096756, Uesugi *et al.* 2016).

To separate the species of ‘dahongjun’, a key is provided here:

1. Context of pileus grayish or grayish black 2
1. Context of pileus white to cream-colored, at most pale gray 6
2. Pileus predominantly red to dark red 3
2. Pileus dark purple or dingy ochraceous or olivaceous with reddish tinge 5
3. Pileocystidia present; spores av. 8.1 \times 7.1 μm , ornamentation 0.2–0.5 μm high, of low and blunt warts partly connected; subtropical Yunnan *Russula* sp.1 (HKAS 110297)
3. Pileocystidia absent; ornamentation 1–1.5(2) μm high, composed of high and conical isolated warts 4
4. Spores av. 9.3–9.5 \times 8–8.1 μm ; Fujian, Guangdong, Guangxi, Sichuan, Yunnan *R. griseocarnosa* clades II, VI and VII
4. Spores av. 8.3–8.7 \times 7.2–7.5 μm ; Fujian, Guangdong, Guangxi, Hunan, Yunnan *R. griseocarnosa* clades I, IV, V and VIII
5. Pileus dingy ochraceous with dull reddish tinge at centre; spores 7–8 \times 6–7 μm (av. 7.8 \times 6.8 μm); pileocystidia absent; in subtropical mid-montane broad-leaved forest in Yunnan *R. griseocarnosa* clade III
5. Pileus dingy olivaceous brown, often with purplish or ochraceous; spores 8–9 \times 6.5–8 μm (av. 8.3 \times 7.3 μm); pileocystidia present; in subalpine coniferous forest in Yunnan *R. purpureozonata*
6. Pileocystidia present 7
6. Pileocystidia absent 10
7. Lamellae pale yellow; spore ornamentation composed of isolated warts rarely fused; in northeast and mid-montane southwest China *R. quercina*
7. Lamellae white; spore ornamentation more or less reticulate 8
8. Stipe with a hard cortex, not fragile; pileus rose-red, pruinose; pileipellis an (ixo)trichoderm; spore ornamentation composed of low warts and short ridges, partly connected by fine lines, forming a broken or nearly complete reticulum; Hunan and Yunnan *R. cf. lepida* (HKAS 104869), *R. aff. lepida* (HKAS 104869, HKAS 105857)
8. Stipe soft, fragile; pileus not pruinose, often subgreasy 9
9. Spores ornamentation up to 0.3 μm high, of blunt warts and ridges partly connected forming a very broken reticulum;

- pleurocystidia 74–120(150) × 10–16 µm, strongly emergent; Guizhou, Xizang and Yunnan *R. yanheensis*
9. Spores ornamentation up to 0.7 µm high, of acute warts and ridges connected and forming a more complete reticulum; pleurocystidia smaller, 53–93 × 8–11 µm, not strongly emergent; Yunnan *Russula* sp.2 (HKAS 104855, HKAS 104863)
10. Pileus vivid red, margin with short striates; pileipellis of a typical “virescens-type” structure; spore ornamentation of fine and dense conical warts; subtropical Yunnan *R. dhakuriana*
10. Pileus dark red, margin without striates; pileipellis a trichoderm, hyphae of subpellis at most inflated 11
11. Spores 6.5–8 × 5.5–7 µm (av. 7.2 × 6.2 µm), ornamentation 0.3–0.8(1) µm high, composed of blunt warts connected by fine lines; pileus dry to subgreasy; subtropical Yunnan *R. occulta*
11. Spores 8.5–10 × 7.5–8.5 µm (av. 9.3 × 7.9 µm), ornamentation 1–1.5(2) µm, composed of isolated conical warts rarely fused; pileus often greasy; subtropical Yunnan *R. griseocarnosa* var. *ailaoshanensis*

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Author contributions

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Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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