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Peperomia accentus (Piperaceae), a new geophytic species endemic to the Sierra Madre Occidental, Mexico

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Molecular phylogeny and morphology reveal a new wood-inhabiting fungal species, *Vararia tuberculata* (Peniophoraceae, Russulales) from China

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Abstract

Vararia is a species-rich genus in the family Peniophoraceae and is polyphyletic. In this study, a new species, *Vararia tuberculata*, is proposed based on a combination of morphological features and molecular evidence. It is characterized by membranous, adnate basidiomata with tuberculate, white to cream, isabelline to slightly brown hymenial surface, a dimitic hyphal system with generative hyphae bearing simple septa, cylindrical, subulate, and cylindrical to bottle-shaped cystidia, cylindrical basidia with 4-sterigmata, and fusiform basidiospores measuring $13.5\text{--}15.1 \times 4.0\text{--}5.0\ \mu\text{m}$. The phylogenetic tree inferred from ITS+nLSU sequences reveals that *Vararia tuberculata* is nested within the family Peniophoraceae (Russulales), where it forms a sister species to *V. cremea* and *V. gillesii*. A full description, illustrations, and phylogenetic analysis results of the new species are provided.

Key words: Biodiversity, phylogenetic analyses, taxonomy, wood-inhabiting fungi, Yunnan Province

Introduction

Fungi represent one of the most diverse groups of organisms on the earth, with an indispensable role in the processes and functioning of forest ecosystems (Zhao *et al.* 2023, He *et al.* 2024, Hyde *et al.* 2024, Manawasinghe *et al.* 2025). The genus *Vararia* P. Karst. (1898: 32) belongs to the family Peniophoraceae of the order Russulales (Larsson & Larsson 2003, Miller *et al.* 2006, Larsson 2007, Chen *et al.* 2015, Liu 2019, Deng *et al.* 2024, Zhou *et al.* 2025). The Russulales is a well-known order that contains morphologically diverse mushrooms (Miller *et al.* 2006). Species from this order comprise many representative wood-inhabiting fungal taxa, including hydroid, corticioid, and polyporoid basidiomata with diverse hymenophoral and cystidial morphology (Yurchenko & Wu 2016, Riebesehl & Langer 2017, Yurchenko *et al.* 2017, Cui *et al.* 2019, Riebesehl *et al.* 2019, Jiang *et al.* 2021, Wu *et al.* 2022, Liu 2019, Deng *et al.* 2024).

The genus *Vararia* is a corticioid wood-inhabiting genus with a wide distribution, typified by *V. investiens* (Schwein.) P. Karst. (1898: 32). It was first described by Karsten as a subgenus of *Xerocarpus* P. Karst. (1881: 22) for *Xerocarpus alutarius* (Berk. & M. A. Curtis) P. Karst. (1889: 418), which was later found to be a synonym of *Radulum investiens* Schwein. Karsten (1834: 345) raised *Xerocarpus* subgen. *Vararia* to the generic rank (Karasinski 2010). The genus is characterized by the resupinate basidiomata, a dimitic hyphal system with simple-septa or clamped generative hyphae and often dextrinoid dichohyphae in Melzer's reagent, the presence of gloecystidia, and variously shaped smooth basidiospores with or without an amyloid reaction (Karsten 1898, Boidin & Lanquetin 1975, Boidin

et al. 1980; Bernicchia & Gorjón 2010, Zou *et al.* 2022, Deng & Zhao *et al.* 2023, Deng *et al.* 2024). The species of *Vararia* are found on fallen angiosperm branches, dead woody or herbaceous stems, or occasionally on gymnosperm wood (Yurchenko *et al.* 2017). Based on the MycoBank database (<http://www.mycobank.org>, accessed on 14 January 2026) and the Index Fungorum (<http://www.indexfungorum.org>, accessed on 14 January 2026), *Vararia* has registered 107 specific and infraspecific names, and the actual number of the species has reached up to 83, currently known, and they occur mainly in the tropical and subtropical areas of the world (Cunningham 1955, Gilbertson 1965, Boidin 1967, Pouzar 1982, Boidin & Lanquetin 1987, Stalpers 1996, Boidin & Gilles 1999, Larsson & Larsson 2003, Bernicchia & Gorjón 2010, Duhem & Buyck 2012, Sanyal *et al.* 2012, Nakasone 2015, Liu & He 2016; Zou *et al.* 2022, Deng & Zhao 2023, Deng *et al.* 2024, Manawasinghe *et al.* 2025). However, *Vararia* is still poorly studied in China (Dai 2010), from whence eighteen species, namely, *V. amphithallica* Boidin, Lanq. & Gilles (1980: 288), *V. bispora* S.L. Liu & S.H. He (2016: 553), *V. breviphysa* Boidin & Lanq. (1976: 462), *V. cinnamomea* Boidin, Lanq. & Gilles (1984: 250), *V. daweshanensis* L. Zou & C.L. Zhao (2022: 14), *V. fissurata* Y.L. Deng & C.L. Zhao (2024: 106), *V. fragilis* L. Zou & C.L. Zhao (2022: 16), *V. investiens* (Schwein.) P. Karst. (1898: 32), *V. isabellina* Y.L. Deng & C.L. Zhao (2024: 107), *V. lincangensis* Y.L. Deng & C.L. Zhao (2024: 111), *V. montana* S.L. Liu & S.H. He (2016: 554), *V. punctata* Y.L. Deng & C.L. Zhao (2024: 113), *V. racemosa* (Burt.) D.P. Rogers & H.S. Jacks. (1943: 299), *V. sinensis* Y.L. Deng & C.L. Zhao (2024: 116), *V. sphaericospora* Gilb. (1965: 176), *V. yaoshanensis* Y.L. Deng & C.L. Zhao (2024: 118), *V. yingjiangensis* Y.L. Deng & C.L. Zhao (2024: 22), and *V. yunnanensis* Y.L. Deng & C.L. Zhao (2023: 24) were reported in this country (Dai 2011, Liu 2019, Dai *et al.* 2021, Deng & Zhao 2023, Deng *et al.* 2024, Manawasinghe *et al.* 2025).

Classification of the kingdom of fungi has been updated continuously, driven by the frequent inclusion of DNA sequence data in many phylogenetic studies (Yurchenko *et al.* 2020). These pioneering research studies into the family Peniophoraceae were just the prelude to the molecular systematics period (Zou *et al.* 2022). The phylogenetic diversity displayed by corticioid fungal species, based on ITS1-5.8S-ITS2-nrLSU nuclear rDNA, revealed that taxa of Peniophoraceae were nested within the russuloid clade, which holds a considerable share of the phylogenetic framework, and included the genera *Asterostroma* Massee (1925: 291) and *Baltazaria* Leal-Dutra, Dentinger & G.W. Griff. (2018: 47), *Dichostereum* Pilát, Gloiothele Bres. (1926: 223), *Lachnocladium* Lév. (1846: 108), *Michenera* Berk. & M.A. Curtis (1869: 333), *Peniophora* Cooke (1879: 20), *Scytinostroma* Donk (1956: 19), *Vesiculomyces* E. Hagstr. (1977: 53), and *Vararia* (Larsson & Larsson 2003, 2004, Larsson 2007, Leal-Dutra *et al.* 2018, Zou *et al.* 2022, Li *et al.* 2023). The previous phylogenetic analyses revealed that the genera *Dichostereum* and *Asterostroma* Massee (1889: 154) are monophyletic, whereas *Vararia* and *Scytinostroma* are polyphyletic (Liu *et al.* 2017). Morphologically, *Scytinostroma* was similar to *Vararia*, which usually differed in having the typical dichohyphae (Bernicchia & Gorjón 2010). The taxonomic distinction between *Scytinostroma* and *Vararia* has been questioned (Hallenberg 1985, Boidin & Lanquetin 1987, Stalpers 1996, Boidin *et al.* 1998). However, there has been general agreement that the two genera were closely related and that they together made up a natural group. Larsson and Larsson (2003) strongly suggested that neither skeletal hyphae nor their branching patterns have any predictive power in a phylogenetic context.

During investigations of wood-inhabiting fungi in Yunnan Province, China, 24 specimens of the genus *Vararia* were collected, and they represent an unknown species. To clarify the placement and relationships of the new species, we conducted a phylogenetic and taxonomic study of *Vararia* based on ITS and LSU sequences.

Materials and methods

Morphological studies

Fresh basidiomata of the fungus were collected in Dehong, Yunnan Province, China; collection details were recorded (Rathnayaka *et al.* 2025), and the specimens were transported to the laboratory in mushroom collection boxes. Specimens were dried in an electric food dehydrator at 40 °C (Hu *et al.* 2022), then sealed in an envelope bag and deposited in the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macromorphological descriptions are based on field notes and photos collected in the field and in the lab. Color terminology follows Petersen (1996). Micromorphological data were obtained from the dried specimens by light microscopy, following methods described in previous studies (Zhao *et al.* 2023, Dong *et al.* 2024). The following abbreviations are used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer's Reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore

width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied and n = a/b (number of spores (a) measured from given number (b) of specimens).

Molecular procedures and phylogenetic analyses

The EZNA HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming, China) was used to extract DNA from the dried specimens, with some modifications. The nuclear ribosomal ITS region was amplified with primers ITS5 and ITS4 (White *et al.* 1990). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s, and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The nuclear LSU region was amplified with primer pair LR0R and LR7 (Vilgalys & Hester 1990, Rehner & Samuels 1994). The PCR procedure for LSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min, and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR procedure for ITS and LSU followed a previous study (Dong *et al.* 2024). All of the newly generated sequences were deposited in NCBI GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) (Table 1).

TABLE 1. List of species, specimens, and GenBank accession numbers of sequences used in this study; — and * refers to the data unavailability and type material, respectively.

Speciesname	SpecimenNo.	GenBank accession No.		Country	References
		ITS	nLSU		
<i>Asterostroma bambusicola</i>	He4132	KY263865	KY263871	Thailand	Liu <i>et al.</i> 2017
<i>A. cervicolor</i>	He2314	KY263859	KY263869	China	Unpublished
<i>A. cervicolor</i>	He4020	KY263860	KY263868	Thailand	Unpublished
<i>A. muscicola</i>	He4397	MK625630	MK625563	China	Unpublished
<i>Confertobasidium olivaceoalbum</i>	FP90196	AF511648	AF511648	Sweden	Larsson & Larsson 2003
<i>Dichostereum boidinii</i>	He4410	MH538315	MH538331	China	Vu <i>et al.</i> 2019
<i>D. boidinii</i>	He5026	MH538324	MH538330	China	Liu <i>et al.</i> 2019
<i>D. pallescens</i>	CBS:718.81	MH861456	MH873198	USA	Vu <i>et al.</i> 2019
<i>Metulodontia nivea</i>	NH13108	AF506423	AF506423	Sweden	Larsson & Larsson 2003
<i>Michenera artocreas</i>	GHL-2016-Oct	MH204688	MH204691	USA	Liu <i>et al.</i> 2019
<i>Peniophora cinerea</i>	CBS:261.37	MH855905	MH867412	Belgium	Vu <i>et al.</i> 2019
<i>P. cinerea</i>	He3725	MK588769	MK588809	China	Unpublished
<i>P. incarnata</i>	CBS 430.72	MH860518	MH872230	Netherlands	Vu <i>et al.</i> 2019
<i>P. incarnata</i>	NH10271	AF506425	AF506425	Sweden	Larsson & Larsson 2003
<i>P. nuda</i>	LZ15-07	MT859929	—	China	Unpublished
<i>P. quercina</i>	CBS 407.50	MH856687	MH868204	France	Vu <i>et al.</i> 2019
<i>P. quercina</i>	CBS:410.50	MH856690	MH868207	France	Vu <i>et al.</i> 2019
<i>Scytinostroma acystidiatum</i>	He5646	MK625568	MK625494	China	Unpublished
<i>S. alutum</i>	CBS:762.81	MH861482	MH873221	France	Vu <i>et al.</i> 2019
<i>S. beijingensis</i>	He7768	OQ731943	OQ729731	China	Li <i>et al.</i> 2023
<i>S. boidinii</i>	He6911	OQ731934	OQ729724	China	Li <i>et al.</i> 2023
<i>S. duriusculum</i>	He3590	MK625571	MK625499	China	Unpublished
<i>S. hemidichophyticum</i>	CBS:702.84	MH861818	MH873509	Belgium	Vu <i>et al.</i> 2019
<i>S. renisporum</i>	CBS:771.86	MH862051	MH873738	Bali	Vu <i>et al.</i> 2019
<i>S. subrenisporum</i>	He4792	MK625566	MK625493	China	Unpublished
<i>Vararia abortiphysa</i>	CBS:632.81	MH861387	—	Gabon	Vu <i>et al.</i> 2019
<i>V. ambigua</i>	CBS 634.81	MH861388	MH873137	France	Vu <i>et al.</i> 2019
<i>V. amphithallica</i>	CBS:635.81	MH861389	MH873138	Gabon	Vu <i>et al.</i> 2019
<i>V. amphithallica</i>	CBS:687.81	MH861431	—	France	Vu <i>et al.</i> 2019
<i>V. aurantiaca</i>	CBS:642.81	MH861394	—	Gabon	Vu <i>et al.</i> 2019

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TABLE 1. (Continued)

Speciesname	SpecimenNo.	GenBank accession No.		Country	References
		ITS	nLSU		
<i>V. aurantiaca</i>	CBS:641.81	MH861393	—	France	Vu <i>et al.</i> 2019
<i>V. breviphysa</i>	CBS:643.81	MH873144	MH873144	Gabon	Vu <i>et al.</i> 2019
<i>V. breviphysa</i>	CBS:644.81	MH861396	—	Gabon	Vu <i>et al.</i> 2019
<i>V. calami</i>	CBS:646.81	MH861398	—	France	Vu <i>et al.</i> 2019
<i>V. calami</i>	CBS:648.81	MH861399	—	France	Vu <i>et al.</i> 2019
<i>V. callichroa</i>	CBS:744.91	MH874000	MH874000	France	Vu <i>et al.</i> 2019
<i>V. cinnamomea</i>	CBS:641.84	MH861794	—	Madagascar	Vu <i>et al.</i> 2019
<i>V. cinnamomea</i>	CBS:642.84	MH873488	MH873488	Madagascar	Vu <i>et al.</i> 2019
<i>V. cremea</i>	CBS:651.81	MH873147	MH873147	France	Vu <i>et al.</i> 2019
<i>V. daweyshanensis</i>	CLZhao 17911	OP380613	—	China	Zou <i>et al.</i> 2022
<i>V. daweyshanensis</i>	CLZhao 17936	OP380614	—	China	Zou <i>et al.</i> 2022
<i>V. dussii</i>	CBS:652.81	MH873148	MH873148	France	Vu <i>et al.</i> 2019
<i>V. dussii</i>	CBS:655.81	MH861405	—	France	Vu <i>et al.</i> 2019
<i>V. ellipsospora</i>	HHB-19503	MW740328	—	New Zealand	Zou <i>et al.</i> 2022
<i>V. fissurata</i>	CLZhao 5218	OQ025218	OR539502	China	Deng <i>et al.</i> 2024
<i>V. fissurata</i>	CLZhao 8171*	OQ025219	OR539503	China	Deng <i>et al.</i> 2024
<i>V. fragilis</i>	CLZhao 16475	OP380612	—	China	Zou <i>et al.</i> 2022
<i>V. fragilis</i>	CLZhao 2628	OP380611	—	China	Zou <i>et al.</i> 2022
<i>V. fusispora</i>	PDD:119539	OL709443	—	New Zealand	Zou <i>et al.</i> 2022
<i>V. gallica</i>	CBS 234.91	MH862250	MH873932	Canada	Vu <i>et al.</i> 2019
<i>V. gallica</i>	CBS 656.81	MH861406	MH873152	France	Vu <i>et al.</i> 2019
<i>V. gillesii</i>	CBS:660.81	MH873153	MH873153	Netherlands	Vu <i>et al.</i> 2019
<i>V. gomezii</i>	CBS:661.81	MH873154	MH873154	France	Vu <i>et al.</i> 2019
<i>V. intricata</i>	CBS:673.81	MH861418	—	France	Vu <i>et al.</i> 2019
<i>V. investiens</i>	FP-151122ITS	MH971976	—	USA	Liu <i>et al.</i> 2019
<i>V. investiens</i>	UC2023140	KP814286	—	USA	Rosenthal <i>et al.</i> 2017
<i>V. isabellina</i>	CLZhao 22852	OR048789	OR506350	China	Deng <i>et al.</i> 2024
<i>V. isabellina</i>	CLZhao 22887	OR048788	OR506351	China	Deng <i>et al.</i> 2024
<i>V. lincangensis</i>	CLZhao 22791*	OR048819	OR506348	China	Deng <i>et al.</i> 2024
<i>V. lincangensis</i>	CLZhao 22799	OR048818	OR506349	China	Deng <i>et al.</i> 2024
<i>V. malaysiana</i>	CBS:644.84	MH873490	MH873490	Singapore	Vu <i>et al.</i> 2019
<i>V. ochroleuca</i>	JS24400	AF506485	AF506485	Norway	Larsson & Larsson 2003
<i>V. perplexa</i>	CBS:695.81	MH861438	—	France	Vu <i>et al.</i> 2019
<i>V. pirispora</i>	CBS:720.86	MH862016	—	France	Vu <i>et al.</i> 2019
<i>V. punctata</i>	CLZhao 22439*	OR048812	OR510675	China	Deng <i>et al.</i> 2024
<i>V. rosulenta</i>	CBS:743.86	MH862028	—	France	Vu <i>et al.</i> 2019
<i>V. rugosipora</i>	CBS:697.81	MH861440	—	Gabon	Vu <i>et al.</i> 2019
<i>V. sigmatospora</i>	CBS:748.91	MH874001	MH874001	Netherlands	Vu <i>et al.</i> 2019
<i>V. sinensis</i>	CLZhao 25160*	OR102494	OR510678	China	Deng <i>et al.</i> 2024
<i>V. sinensis</i>	CLZhao 25161	OR102495	OR510679	China	Deng <i>et al.</i> 2024
<i>V. sphaericospora</i>	CBS:700.81	MH873185	MH873185	Gabon	Vu <i>et al.</i> 2019
<i>V. sphaericospora</i>	He4847	MK625592	MK625521	China	Unpublished
<i>V. trinidadensis</i>	CBS:650.84	MH873495	MH873495	Madagascar	Vu <i>et al.</i> 2019
<i>V. trinidadensis</i>	CBS:651.84	MH861803	—	Madagascar	Vu <i>et al.</i> 2019
<i>V. tropica</i>	CBS 704.81	MH861447	MH873189	France	Vu <i>et al.</i> 2019

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TABLE 1. (Continued)

Speciesname	SpecimenNo.	GenBank accession No.		Country	References
		ITS	nLSU		
<i>V. tuberculata</i>	CLZhao 42458	—	PX072009	China	Present study
<i>V. tuberculata</i>	CLZhao 41375	PX097866	PX072010	China	Present study
<i>V. tuberculata</i>	CLZhao 41662	PX097867	PX072011	China	Present study
<i>V. tuberculata</i>	CLZhao 41669	PX097868	PX072012	China	Present study
<i>V. tuberculata</i>	CLZhao 41731	PX097869	PX072013	China	Present study
<i>V. tuberculata</i>	CLZhao 41768	PX097870	PX072014	China	Present study
<i>V. tuberculata</i>	CLZhao 41792	PX097871	PX072015	China	Present study
<i>V. tuberculata</i>	CLZhao 41830	PX097872	—	China	Present study
<i>V. tuberculata</i>	CLZhao 41861	PX097873	PX072016	China	Present study
<i>V. tuberculata</i>	CLZhao 41885*	PX097865	PX072017	China	Present study
<i>V. tuberculata</i>	CLZhao 41890	PX097874	PX072018	China	Present study
<i>V. tuberculata</i>	CLZhao 42151	PX097875	PX072019	China	Present study
<i>V. tuberculata</i>	CLZhao 42185	—	PX072020	China	Present study
<i>V. tuberculata</i>	CLZhao 42228	PX097876	—	China	Present study
<i>V. tuberculata</i>	CLZhao 42233	PX097877	PX072021	China	Present study
<i>V. tuberculata</i>	CLZhao 42673	PX097878	PX072022	China	Present study
<i>V. tuberculata</i>	CLZhao 42901	PX097879	PX072023	China	Present study
<i>V. tuberculata</i>	CLZhao 42927	PX097880	PX072024	China	Present study
<i>V. tuberculata</i>	CLZHao 42997	PX097881	—	China	Present study
<i>V. tuberculata</i>	CLZhao 43002	PX097882	PX072025	China	Present study
<i>V. tuberculata</i>	CLZHao 44011	PX097883	PX072026	China	Present study
<i>V. tuberculata</i>	CLZhao 44003	PX097884	PX072027	China	Present study
<i>V. tuberculata</i>	CLZHao 44049	PX097885	PX072028	China	Present study
<i>V. tuberculata</i>	CLZHao 44051	PX097886	PX072029	China	Present study
<i>V. vassilievae</i>	UC2022892	KP814203	—	USA	Unpublished
<i>V. verrucosa</i>	CBS:706.81	MH861449	MH861449	France	Vu <i>et al.</i> 2019
<i>V. yaoshanensis</i>	CLZhao 20565	PP091675	PP091683	China	Deng <i>et al.</i> 2024
<i>V. yaoshanensis</i>	CLZhao 20693*	PP091665	PP091684	China	Deng <i>et al.</i> 2024

To determine the phylogeny, we compiled an ITS+nLSU dataset. In the combined dataset, Sequences of *Confertobasidium olivaceoalbum* (Bourdot & Galzin) (1987: 58) Jülich and *Metulodontia nivea* (P. Karst.) Parmasto (1968: 18) retrieved from GenBank were used as the outgroups in the ITS+nLSU analysis (Figure 1); Sequences of *Peniophora incarnata* (Pers.) P. Karst. (1889: 27) and *P. nuda* (Fr.) Bres. (1897: 114) retrieved from GenBank were used as the outgroups in the ITS+nLSU analysis (Figure 2) (Deng *et al.* 2024). The sequences were initially aligned with MAFFT (<https://mafft.cbrc.jp/alignment/server/>) using the “G-INS-I” strategy (Katoh *et al.* 2019), and then manually optimized in AliView version 1.27 (Larsson 2014). Finally, the two gene fragments were concatenated with Mesquite v3.70 (Maddison & Maddison 2021, <https://www.mesquiteproject.org/>) for further phylogenetic analyses.

Maximum parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were applied to the combined datasets following a previous study (Dong *et al.* 2024), and the tree construction procedure was performed in PAUP* version 4.0b10 (Swofford 2002). All of the characters were equally weighted, and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max trees were set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1,000 replicates (Felsenstein 1985). Descriptive tree statistics, tree length (TL), the consistency index (CI), the retention index (RI), the rescaled consistency index (RC), and the homoplasy index (HI) were calculated for each maximum parsimonious tree generated. The multiple sequence alignment was also analyzed using maximum likelihood (ML) in RAxML-HPC2 (Miller *et al.* 2012). Branch support (BS) for ML analysis was determined by 1,000 bootstrap replicates.

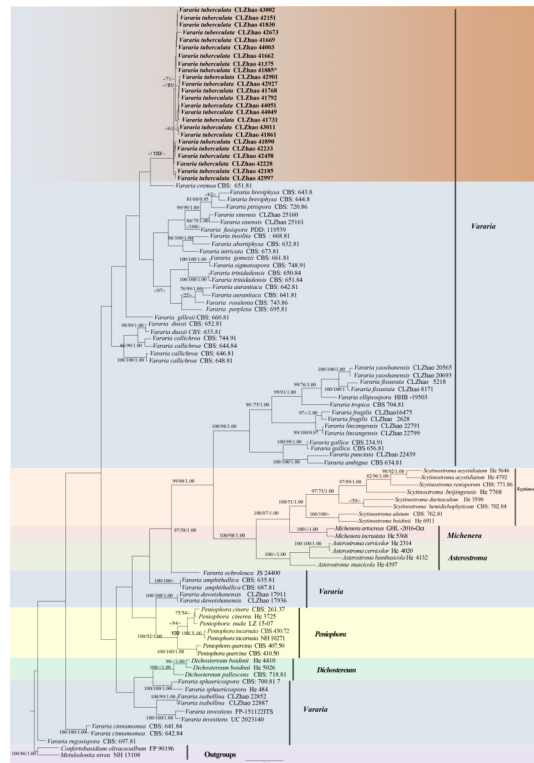


FIGURE 1. Maximum parsimony strict consensus tree illustrating the phylogeny of the new species *Vararia tuberculata* and related species in the family Peniophoraceae within the order Russulales based on ITS+nLSU sequences. The branch is labeled with a maximum-likelihood lead value of 70% or higher, a reduced lead value of 50% or higher, and a Bayesian posterior probability of 0.95 or higher.

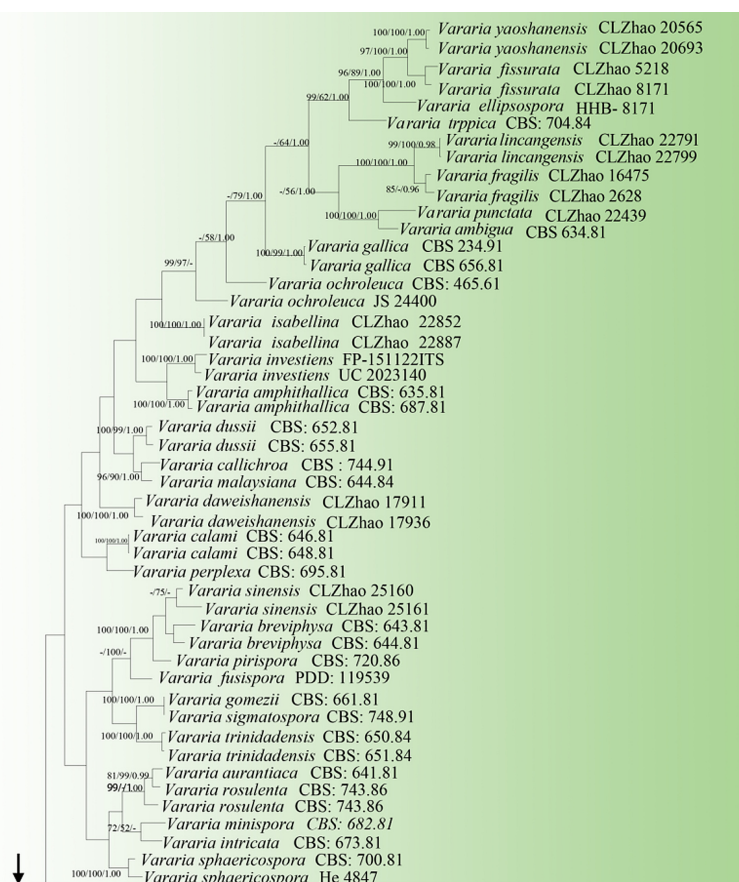


FIGURE 2. Maximum parsimony strict consensus tree illustrating the phylogeny of the new species *Vararia tuberculata* and related species in the genus within the family Peniophoraceae based on ITS+nLSU sequences. The branch is labeled with a maximum-likelihood lead value of 70% or higher, a reduced lead value of 50% or higher, and a Bayesian posterior probability of 0.95 or higher.

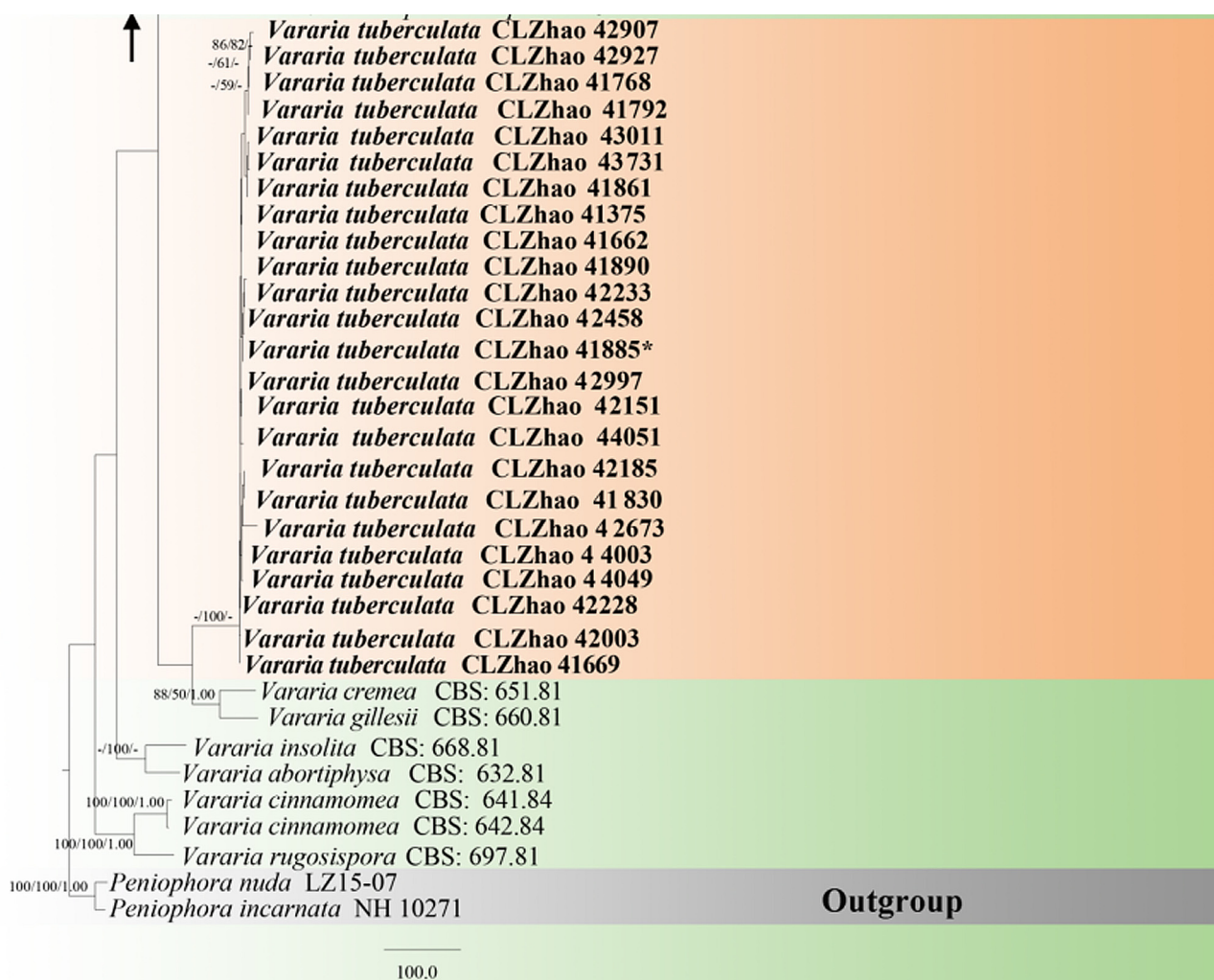


FIGURE 2. Maximum parsimony strict consensus tree illustrating the phylogeny of the new species *Vararia tuberculata* and related species in the genus within the family Peniophoraceae based on ITS+nLSU sequences. (Continued)

Bayesian Inference (BI) phylogenies were inferred using MrBayes v3.2.7a with a general time-reversible model of DNA substitution and a gamma distribution rate variation across sites (Ronquist *et al.* 2012). Four Markov chains were run twice from a random starting tree, for 5.76 million generations of the datasets (Figure 1) and 2.56 million generations of the datasets (Figure 2), with trees and parameters sampled every 1,000 generations. The first one-fourth of all generations was discarded as burn-in. The majority rule consensus tree of all remaining trees was calculated. Branches were considered significantly supported if they received a maximum likelihood bootstrap value (BS) $\geq 70\%$, a maximum parsimony bootstrap value (BT) $\geq 50\%$, or a Bayesian posterior probability (BPP) ≥ 0.95 .

Results

Phylogenetic analyses

The dataset, based on ITS+nLSU (Figure 1), comprises sequences from 103 fungal specimens representing 59 different species. The dataset had an aligned length of 2,428 characters, of which 1,242 characters were constant, 247 were variable and parsimony-uninformative, and 939 were parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 6,618, CI = 0.3293, HI = 0.6707, RI = 0.6418, RC = 0.2113). Bayesian analysis and ML analysis yielded a similar topology to the MP analysis, with an average standard deviation of split frequencies of 0.009970 (BI), and the effective sample size (ESS) across the two runs was double the average ESS (avg ESS) = 2765. The phylogenetic tree inferred from ITS+nLSU sequences revealed that the new species *Vararia tuberculata* was nested within the genus *Vararia* within the family Peniophoraceae (Russulales), and sister to *V. cremea* Boidin, Lanq. & Gilles (1980: 301).

The dataset, based on ITS+nLSU (Figure 2), comprises sequences from 81 fungal specimens representing 38 different species. The dataset had an aligned length of 2,254 characters, of which 1,309 characters were constant, 208 were variable and parsimony-uninformative, and 737 were parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 4,620, CI = 0.3582, HI = 0.6418, RI = 0.6463, RC = 0.2315). Bayesian analysis and ML analysis yielded a similar topology to the MP analysis, with an average standard deviation of split frequencies of 0.009992 (BI), and the effective sample size (ESS) across the two runs was double the average ESS (avg ESS) = 1,757. The phylogenetic tree inferred from ITS+nLSU sequences revealed that the new species *Vararia tuberculata* was nested within the genus *Vararia* within the family Peniophoraceae (Russulales), forming a sister species to *V. cremea* Boidin, Lanq. & Gilles (1980: 301) and *V. gillesii* Boidin & Lanq. (1976: 461).

Taxonomy

Vararia tuberculata K.S. Wang & C.L. Zhao, *sp. nov.* Figs. 3 and 4
MycoBank no.: MB860681

Etymology:—*Tuberculata* (Lat.) refers to the tuberculate hymenophore of the type specimen.

Holotype:—CHINA. Yunnan Province, Dehong, Ruili County, Nongdao Town, Tongbiguan Provincial Nature Reserve, GPS coordinates 23°38' N, 97°51' E, altitude 1,500 m asl., on the fallen angiosperm branch, leg. C.L. Zhao, 23 November 2024, CLZhao 41885 (SWFC 00041885).

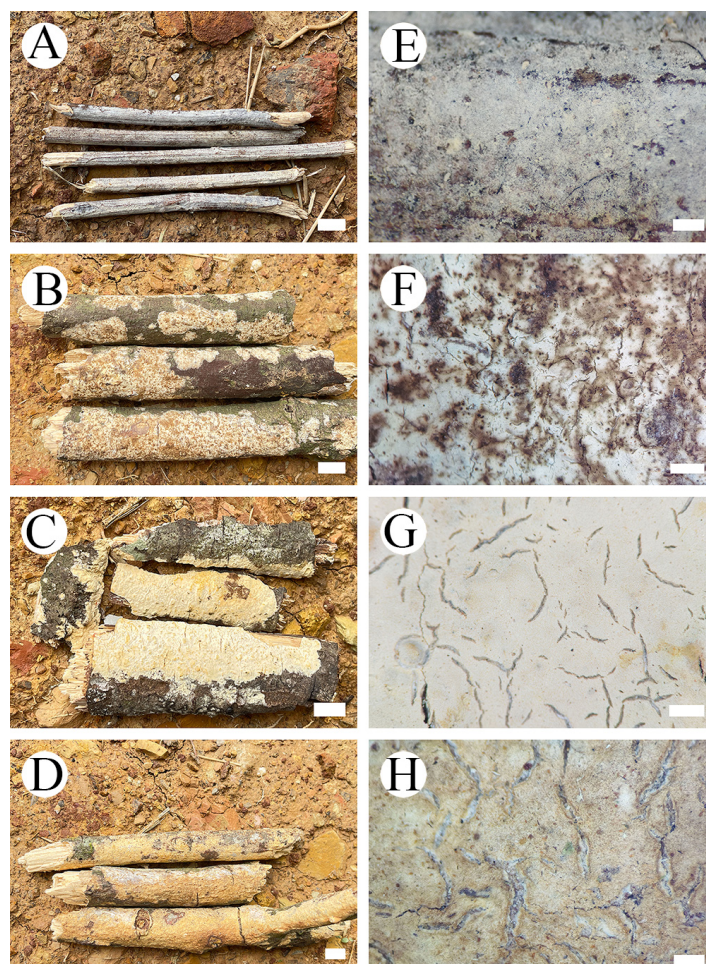


FIGURE 3. *Vararia tuberculata* (holotype, CLZhao 41885): basidiomata on the substrate (A–D), macroscopic characteristics of hymenophore (E–H). Bars: (A–D) = 1 cm and (E–H) = 1 mm.

Basidiomata:—Annual, membranous, thin, adnate, without odor or taste when fresh, up to 14 mm long, 2 mm wide, and 120 µm thick. Hymenial surface tuberculate, white when fresh, cream to isabelline to slightly brown, cracked when dry. Sterile margin thinning out, white to cream, and up to 1 mm wide.

Hyphal structure:—Hyphal system dimitic; generative hyphae bearing simple septa, colorless, thin-walled, frequently branched, interwoven, 3–4 µm in diameter; skeletal hyphae thick-walled, colorless, 3.5–4.5 µm in diameter; IKI–, CB–; tissues unchanged in KOH.

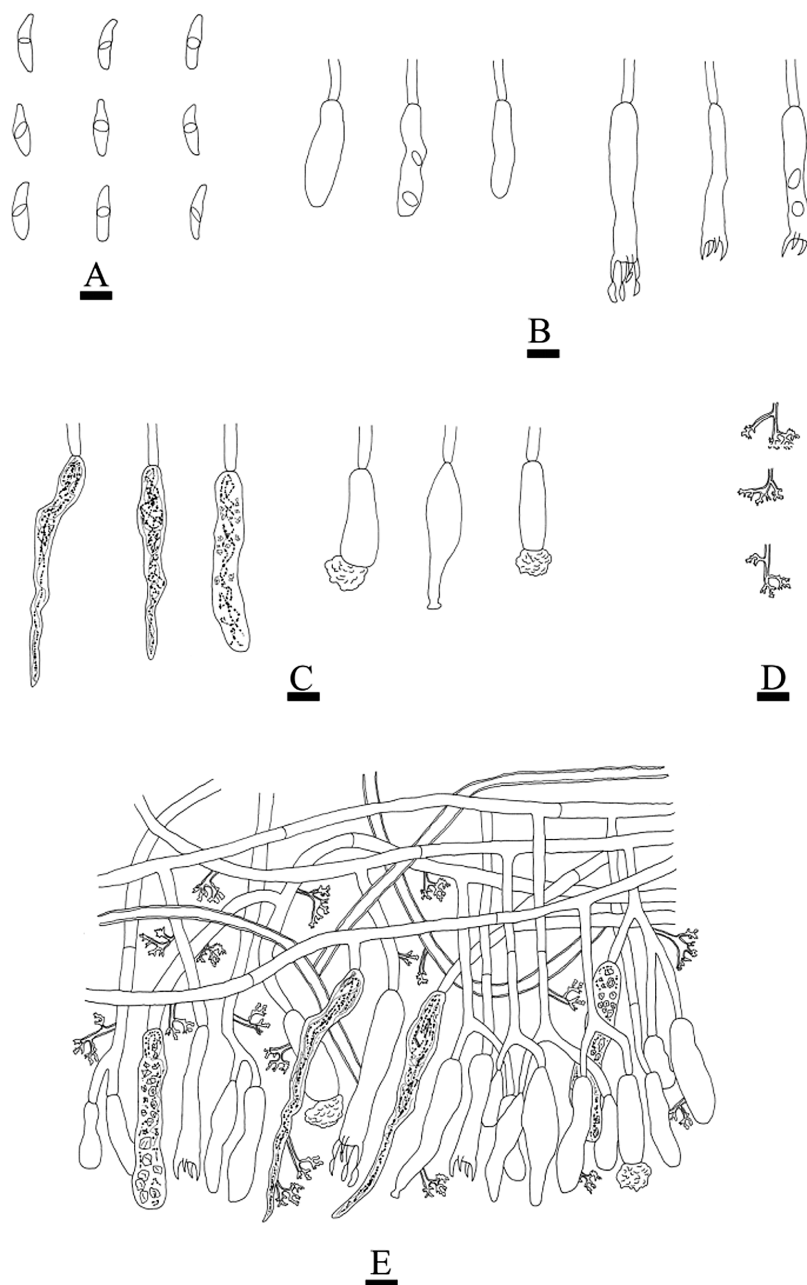


FIGURE 4. Microscopic structures of *Vararia tuberculata* (holotype, CLZhao 41885): basidiospores (A), basidia and basidioles (B), gloecystidia (C), skeletal hyphae (D), a section of hymenium (E), Bars: A–E= 10 µm.

Hymenium:—Cystidia three types: (1) cylindrical, filled with refractive matter, colorless, thin-walled, smooth, $24\text{--}83 \times 6\text{--}10$ µm; (2) subulate, with a swollen base, slender in the upper part, filled with refractive matter, colorless, thin-walled, smooth, $26\text{--}75 \times 7\text{--}13$ µm; (3) cylindrical to bottle-shaped, with an irregularly clustered apical structure, colorless, thin-walled, smooth, $23\text{--}45 \times 9\text{--}13$ µm. Dendrohyphidia predominant, colorless, thick-walled, irregularly branched with main branches up to 4 µm in diameter and with blunt tips, IKI–, CB–; tissues unchanged in KOH. Basidia cylindrical, with four sterigmata and a basal simple septum, contain oil droplets, $29\text{--}56 \times 5.5\text{--}10$ µm; basidioles dominant, in shape similar to basidia but slightly smaller.

Spores:—Basidiospores fusiform, colorless, thin-walled, smooth, containing oil droplets, IKI–, CB–, $(12.7\text{--})13.5\text{--}15.1(15.8) \times (3.3\text{--})4.0\text{--}5.0(5.2)$ µm, $L = 14.43$ µm, $W = 4.54$ µm, $Q = 3.02\text{--}3.30$ ($n = 210/7$).

Type of rot:—White rot.

Additional specimens examined (paratypes):—CHINA. Yunnan Province, Dehong, Ruili County, Nongdao Town, Tongbiguan Provincial Nature Reserve, GPS coordinates 23°38' N, 97°51' E, altitude 1,500 m asl., on the fallen angiosperm branch, leg. C.L. Zhao, 21 November 2024, CLZhao 41375 (SWFC 00041375); 22 November 2024, CLZhao 41662 (SWFC 00041662), CLZhao 41669 (SWFC 00041669), CLZhao 41731 (SWFC 00041731), CLZhao 41768 (SWFC 00041768), CLZhao 41792 (SWFC 00041792), CLZhao 41793 (SWFC 00041793), CLZhao 41830 (SWFC 00041830), CLZhao 41861 (SWFC 00041861), CLZhao 41890 (SWFC 00041890); 23 November 2024, CLZhao 42151 (SWFC 00042151), CLZhao 42185 (SWFC 00042185), CLZhao 42228 (SWFC 00042228), CLZhao 42233 (SWFC 00042233), CLZhao 42458 (SWFC 00042458); 24 November 2024, CLZhao 42673 (SWFC 00042673), CLZhao 42901 (SWFC 00042901), CLZhao 42927 (SWFC 00042927), CLZhao 42997 (SWFC 00042997), CLZhao 43002 (SWFC 00043002), CLZhao 44011 (SWFC 00044011); 14 January 2025, CLZhao 44003 (SWFC 00044003), CLZhao 44049 (SWFC 00044049), CLZhao 44051 (SWFC 00044051).

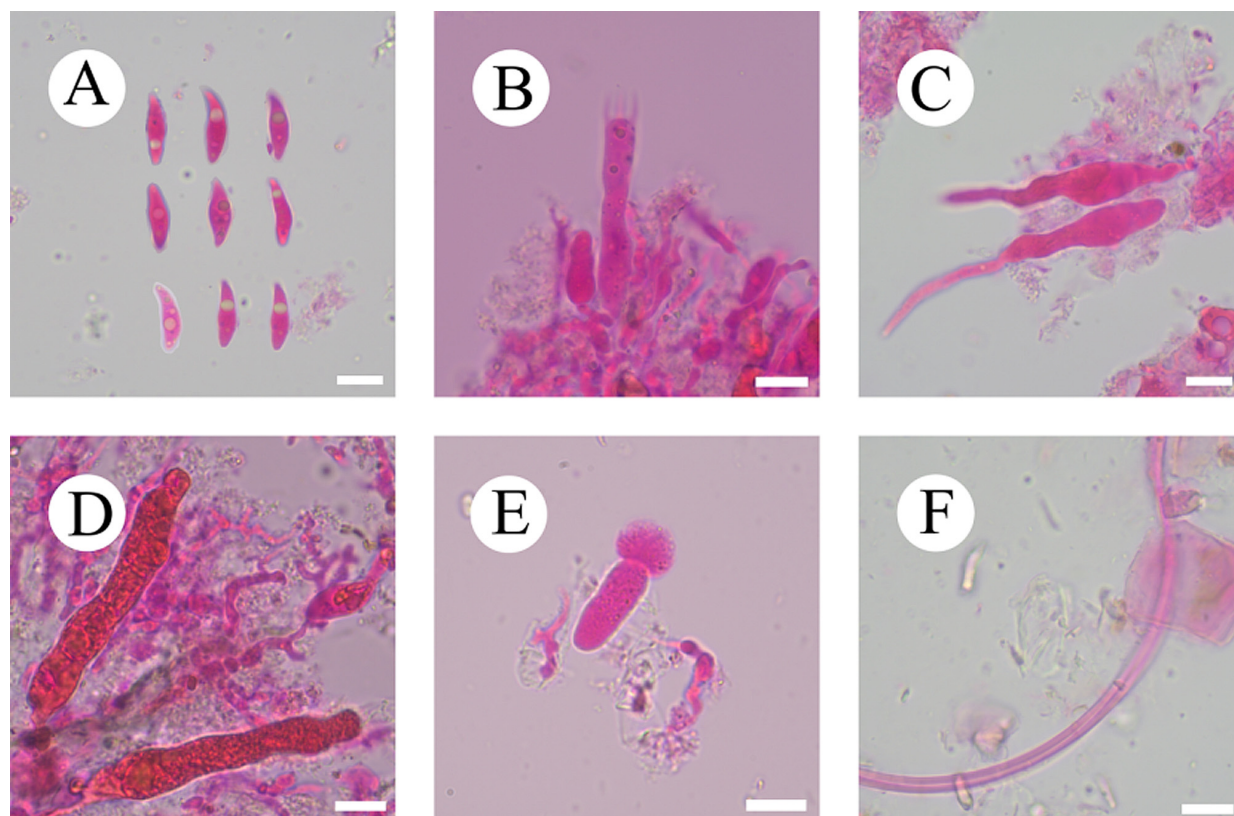


FIGURE 5. Microscopic structures of *Vararia tuberculata* (holotype, CLZhao 41885): basidiospores (A), basidia (B), gloeocystidia (C–E), skeletal hyphae (F) Bars: A–F = 10 μ m.

Discussion

Many recently described wood-inhabiting fungal taxa have been reported in the subtropics and tropics, including those of the genus *Vararia* (Liu & He 2016, Deng *et al.* 2024). In the present study, a new species, *V. tuberculata*, is described based on phylogenetic analyses and morphological characteristics.

A phylogeny of corticioid species in the Russulales revealed that eight genera clustered in the Peniophoraceae (Leal-Dutra *et al.* 2018). In this study, the new species *V. tuberculata* clustered within the genus *Vararia* (Figure 1, 2) within Russulales and was closely related to *V. cremea* and *V. gillesii*. However, morphologically, the new species is easily separated from other known species of the genus *Vararia*. *V. cremea* is delimited from *V. tuberculata* by having tenuis, fragilis, a purple hymenial surface, subcylindrical gloeocystidia, and both narrower basidia ($25\text{--}35 \times 4\text{--}5 \mu\text{m}$) and basidiospores ($15\text{--}20 \times 2.7\text{--}3.5 \mu\text{m}$, Boidin *et al.* 1980). The taxon *V. gillesii* is distinguished from *V. tuberculata* by its generative hyphae with clamp connection, smaller basidia ($30\text{--}40 \times 6\text{--}7 \mu\text{m}$), and larger basidiospores ($14\text{--}17 \times 4\text{--}4.75 \mu\text{m}$, Boidin & Lanquetin 1975).

Morphologically, *Vararia tuberculata* resembles *V. fissurata*, *V. punctata*, *V. sinensis*, and *V. yaoshanensis* in having subcylindrical to cylindrical basidia. However, *V. fissurata* differs from *V. tuberculata* due to its smooth hymenial

surface, generative hyphae with clamp connections, smaller basidia ($20\text{--}27 \times 4\text{--}8 \mu\text{m}$ vs. $29\text{--}56 \times 5.5\text{--}10 \mu\text{m}$), and longer, ellipsoid to broadly ellipsoid basidiospores ($5\text{--}10 \times 3\text{--}7 \mu\text{m}$ vs. $13.5\text{--}15.1 \times 4.0\text{--}5.0 \mu\text{m}$, Deng *et al.* 2024). *Vararia punctata* is distinguished from *V. tuberculata* by its smooth hymenial surface, smaller gloecystidia ($12\text{--}21 \times 5\text{--}9 \mu\text{m}$ vs. $23\text{--}83 \times 6\text{--}13 \mu\text{m}$), shorter basidia ($11\text{--}25 \times 4\text{--}7 \mu\text{m}$ vs. $29\text{--}56 \times 5.5\text{--}10 \mu\text{m}$), and shorter, ellipsoid basidiospores ($6\text{--}10 \times 4\text{--}6 \mu\text{m}$ vs. $13.5\text{--}15.1 \times 4.0\text{--}5.0 \mu\text{m}$, Deng *et al.* 2024). *Vararia sinensis* differentiates from *V. tuberculata* by its smooth hymenial surface with a pinkish tinge, shorter basidia ($25\text{--}35 \times 6\text{--}7 \mu\text{m}$ vs. $29\text{--}56 \times 5.5\text{--}10 \mu\text{m}$), and smaller, sub-fusiform to navicular basidiospores ($6\text{--}11 \times 4\text{--}6 \mu\text{m}$ vs. $13.5\text{--}15.1 \times 4.0\text{--}5.0 \mu\text{m}$, Deng *et al.* 2024). *Vararia yaoshanensis* is distinct from *V. tuberculata* in having a smooth hymenial surface with a cinnamon-buff to pinkish buff tinge, slightly thick-walled generative hyphae, and smaller, ellipsoid, slightly thick-walled, amyloid basidiospores ($7.6\text{--}10.8 \times 5.7\text{--}7.8 \mu\text{m}$ vs. $13.5\text{--}15.1 \times 4.0\text{--}5.0 \mu\text{m}$; Deng *et al.* 2024).

Fungi are closer to humans than to plants and can therefore be considered a strategic biological resource (Manawasinghe *et al.* 2025). The application potential of fungi is as important as their natural attributes in recognizing fungi (Liu *et al.* 2025). Climate change and the destruction of natural habitats are also threatening species, and many may become extinct before they are even discovered (Hyde *et al.* 2024). Studies on fungal biodiversity and their applications are important, as they may lead to new products (Si *et al.* 2011, Wang *et al.* 2013, Hyde *et al.* 2024). Therefore, it is now urgent to recognize and conserve fungi for future utilization.

The wood-inhabiting fungi are an extensively studied group of Basidiomycota, which includes several poroid, smooth, grandinioid, odontoid, and hydroid basidiomata, and previously many new taxa were described from China (Cui *et al.* 2019, Wu *et al.* 2020, He *et al.* 2022, Yuan *et al.* 2023, Zhao *et al.* 2023, 2024, Dong *et al.* 2024, Wang *et al.* 2024, Qin *et al.* 2025, Yang *et al.* 2025). Based on our phylogenetic and morphological research results, 18 species of *Vararia* have been reported from China, including those newly described in the present study and other recently published papers in this country (Liu & He 2016, Liu 2019, Dai *et al.* 2021, Zou *et al.* 2022, Deng & Zhao 2023, Deng *et al.* 2024). Therefore, the diversity of *Vararia* species remains largely unknown in China, particularly in subtropical and tropical regions. This paper enhances our understanding of fungal diversity in this region, and further fieldwork and molecular analyses are likely to reveal additional taxa.

Acknowledgements

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