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Molecular phylogeny and morphology reveal a new *Lyomyces* species (Hymenochaetales, Basidiomycota) from Yunnan Province, China

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Abstract

The wood-inhabiting fungi play an important role in forest ecosystem processes and functions. Hymenochaetales is one of the fungal orders mainly composed of wood-inhabiting macrofungi within the class Agaricomycetes, Basidiomycota. A new wood-inhabiting fungus, *Lyomyces ruiliensis*, found in Yunnan Province, Southwestern China, is proposed based on a combination of morphological features and molecular evidence. *Lyomyces ruiliensis* is characterized by its coriaceous and slightly cracked basidiomata, a monomitic hyphal system with clamped generative hyphae, and ellipsoid basidiospores measuring 4.5–5 × 3–3.5 µm. Phylogenetic analyses of the new species are carried out based on the nuclear ribosomal internal transcribed spacer (ITS) and the nuclear large subunit (nLSU) of ribosomal DNA. Based on the ITS+nLSU sequences, the phylogenetic trees indicate that the new species belongs to the genus *Lyomyces*, and is retrieved as a sister to *L. juniperi*. A description, illustrations, and phylogenetic analysis results for the new species are provided. The present study contributes to understanding the species diversity, taxonomy, and phylogeny of *Lyomyces* in southwestern China.

Key words: Biodiversity, Classification, New taxon, Wood-inhabiting fungi

Introduction

The wood-inhabiting fungi, a diverse group in terms of morphology, phylogeny, and ecology, are integral to wood degradation and the carbon cycle in the ecosystem. They are considered the "key player" in wood decomposition, as they produce a variety of enzymes that break down woody lignin, cellulose, and hemicellulose, thus playing a crucial role in the ecological system (Dai 2010, Si *et al*. 2011, Wang *et al*. 2013, Zhao *et al*. 2023, Liu *et al*. 2025).

The family Schizoporaceae Jülich (1982: 389) (Hymenochaetales Oberw.) is an important group in wood-inhabiting fungi (Larsson *et al.* 2006, Wu *et al*. 2022a). Its type genus is *Schizopora* Velen. (1922: 638); however, *Xylodon* (Pers.) Gray (1821: 649) is a prior synonym of *Schizopora*; the previous family name Schizoporaceae, typified by *Schizopora* (Jülich 1981), was adopted to accommodate *Fasciodontia* Yurchenko & Riebesehl (2020: 178), *Lyomyces* P. Karst. (1881: 23) and *Xylodon* (Wang *et al*. 2023a). It encompasses many variations in the fruiting body types, including hydnoid, corticioid, and polyporoid basidiomata with diverse hymenophoral and cystidial morphologies (Yurchenko & Wu 2016, Riebesehl & Langer 2017, Yurchenko *et al.* 2017, Cui *et al*. 2019, Riebesehl *et al*. 2019, Wu *et al*. 2022a, b). In addition, species of Schizoporaceae have been described from various countries, and most can cause white rot (Langer 1994).

The genus *Lyomyces* is typified by the species *L. sambuci* (Pers.) P. Karst. (1882: 153) and belongs to the family Schizoporaceae. It is characterized by resupinate to effused basidiomata with a smooth to odontioid hymenophore, a monomitic hyphal system with generative hyphae bearing clamp connections, while the cystidia are thin-walled with

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tapering, cylindrical, subcapitate, or capitate apical parts and with smooth, thin-to slightly thick-walled basidiospores (Karsten 1881, Bernicchia & Gorjón 2010, Yurchenko *et al*. 2024). That crystalline deposits on hyphae and hymenial elements are a distinguishing feature of most *Lyomyces* species, and the size and arrangement of crystals in the hymenium can serve as additional morphological characters for species delimitation, although the shape of the crystals does not consistently play a defining role (Yurchenko *et al*. 2024). The members of *Lyomyces* grow on dead, still-attached, or fallen branches of angiosperms, wooden, or herbaceous stems, and occasionally on gymnosperm wood (Yurchenko *et al.* 2017, Chen & Zhao 2020, Yurchenko *et al*. 2024).

Given the frequent inclusion of DNA sequence data in many phylogenetic studies, the classification of wood-inhabiting fungi has been continuously updated (Yurchenko *et al*. 2020, Dai *et al*. 2021, Wang *et al*. 2024, Zhao *et al*. 2024). The genus *Hyphodontia* s.l. was indicated to be a polyphyletic group, in which the genera *Xylodon* and *Kneiffiella* P. Karst. (1889: 371) included the largest number of species (Yurchenko & Wu 2016, Riebesehl & Langer 2017, Riebesehl *et al*. 2019). Molecular data are insufficient to clearly distinguish many genera in Schizoporaceae, necessitating the acceptance of a broad concept of *Hyphodontia* s.l. (Yurchenko & Wu 2016, Riebesehl & Langer 2017, Riebesehl *et al*. 2019). Phylogenetic studies of *Hyphodontia* s.l., based on nuclear DNA sequence data, identified six well-distinguished clades—the *Hastodontia*, *Hyphodontia*, *Lagarobasidium*, *Kneiffiella*-*Alutaceodontia*, *Xylodon*-*Lyomyces*-*Rogersella*, and *Xylodon*-*Schizopora*-*Palifer* clades—with the genus *Lyomyces* nesting within the *Xylodon*-*Lyomyces*-*Rogersella* clade (Yurchenko & Wu 2013). This research led to the division of the broad genus *Hyphodontia* s.l. into six genera: *Hastodontia* (Parmasto) Hjortstam & Ryvarden (2009: 49), *Hyphodontia* J. Erikss. (1968: 101), *Kneiffiella*, *Lagarobasidium* Jülich (1974: 84), *Lyomyces* and *Xylodon*, in which thirty-five new combinations were proposed, including fourteen *Lyomyces* species (Riebesehl & Langer 2017). Based on sequences of the internal transcribed spacer (ITS) and the nuclear large subunit (nLSU) ribosomal DNA gene, the phylogenetic analysis revealed that the *L. sambuci* complex comprises four new species (Yurchenko *et al*. 2017). The generic concept and its phylogenetic reconstruction of *Lyomyces* were clarified by Riebesehl *et al.* (2019), and the species *L. sambuci* was found to be sister to *L. crustosus* (Pers.) P. Karst. (1881: 23). In recent years, the fungal diversity of the genus *Lyomyces* was analyzed, during which 31 new species were described based on a combination of morphological and molecular evidence (Guan *et al*. 2023, Yuan *et al.* 2024, Yurchenko *et al.* 2024, Deng *et al.* 2025).

During investigations of wood-inhabiting fungi from southwest China, six *Lyomyces* specimens could not be assigned to any described species. To clarify the placement and relationships of these specimens, we conducted a phylogenetic and taxonomic study of *Lyomyces* based on combined ITS+nLSU and ITS sequence analyses. These specimens are identified and described as a new species of *Lyomyces* (*L. ruiliensis*), here.

Materials and methods

Sample collection and herbarium specimen preparation

Fresh basidiomata of the fungus growing on angiosperm branches were collected from Dehong of Yunnan Province, P.R. China. The samples were photographed *in situ* using a Jianeng 80D camera, and collection details were recorded (Rathnayaka *et al.* 2025). The samples were then taken to the laboratory, where fresh macroscopic details were recorded. All photos taken in the field were focus-stacked and merged using Helicon Focus Pro 7.7.5. Specimens were dried in an electric food dehydrator at 40 °C (Hu *et al.* 2022). They were then sealed in an envelope and deposited in the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, China.

Morphology

Macromorphological descriptions were based on field notes and photos captured in the field and lab. Color terminology follows Petersen (Petersen 1996). The micromorphological data were obtained from dried specimens after observation under a light microscope at 10×100 magnification (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). The new species was registered in the MycoBank database (http://www.mycobank.org).

DNA extraction and sequencing

The CTAB rapid plant genome extraction kit DN14 (Aidlab Biotechnologies Co. Ltd., Beijing) was used to extract genomic DNA from dried specimens according to the manufacturer's instructions. The extracted DNA was maintained at –20 °C for long-term storage. Two molecular markers were investigated, i.e., internal transcribed spacer (ITS), the ITS region was amplified with the primer pair ITS5 and ITS4 (White *et al.* 1990), and nuclear large subunit ribosomal RNA (nLSU), the nLSU region with primer pair LR0R and LR7 (Vilgalys & Hester 1990, Hopple 1994). The PCR procedure was as follows: initial denaturation at 95 °C for 3 min; followed by 35 cycles of 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 (Dong *et al.* 2024). The PCR procedure for nLSU was as follows: an 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 at 72 °C for 10 min. The PCR products were purified and directly sequenced at the Kunming Tsingke Biological Technology Ltd. Co. (Yunnan, P.R. China). All newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

TABLE 1. A list of species, specimens, and GenBank accession numbers of sequences used in this study. The new species is in bold. [* Indicates type materials and – refers to the data unavailability].

Species Name	Specimen No.	GenBank Accession No.		Country	References
		ITS	nLSU		
Fasciodontia brasiliensis	MSK-F 7245a	MK575201	MK598734	Brazil	Yurchenko *et al.* 2020
Fasciodontia bugellensis	KAS-FD 10705a	MK575203	MK598735	France	Yurchenko *et al.* 2020
Fasciodontia bugellensis	MSK-F 7353	MK575205	MK598736	Belarus	Yurchenko *et al.* 2020
Fasciodontia yunnanensis	CLZhao 6280	MK811275	MZ146327	China	Luo & Zhao 2021
Fasciodontia yunnanensis	CLZhao 6385	MK811277	–	China	Luo & Zhao 2021
Hyphodontia daweishanensis	CLZhao 18444	PP819710	PP826264	China	Unpublished
Hyphodontia daweishanensis	CLZhao 18536	PP819711	PP826265	China	Yang *et al.* 2025
Lyomyces albofarinaceus	CLZhao 33479	PQ523359	–	China	Dai *et al.* 2025
Lyomyces albofarinaceus	CLZhao 26661	PQ523360	–	China	Dai *et al.* 2025
Lyomyces albomarginatus	CLZhao 22551	PQ644120	PQ644121	China	Dai *et al.* 2025
Lyomyces albopulverulentus	CLZhao 21478	OP730712	OP730724	China	Guan *et al.* 2023
Lyomyces allantosporus	KAS-GEL4933	KY800401	KY795965	France	Yurchenko *et al.* 2017
Lyomyces allantosporus	FR-0249548	KY800397	KY795963	France	Yurchenko *et al.* 2017
Lyomyces bambusinus	CLZhao 4808	MN945970	–	China	Chen & Zhao 2020
Lyomyces bambusinus	CLZhao 4831	MN945968	MW264919	China	Chen & Zhao 2020
Lyomyces boquetensis	EYu 190727-12	PP471797	–	Panama	Yurchenko *et al.* 2024
Lyomyces cremeus	CLZhao 4138	MN945974	MW264922	China	Chen & Zhao 2020
Lyomyces cremeus	CLZhao 8295	MN945972	–	China	Chen & Zhao 2020
Lyomyces crustosus	LWZ 20170815-23	MT319465	MT319201	China	Wang *et al.* 2021

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TABLE 1. (Continued)

Species Name	Specimen No.	GenBank Accession No.		Country	References
		ITS	nLSU		
Lyomyces crystallina	LWZ 20190810-6b	OQ540901	–	China	Liu *et al*. 2024
Lyomyces daweishanensis	CLZhao 18344	OR094474	OR449934	China	Dong *et al*. 2024
Lyomyces densiusculus	Ryvarden 44818	OK273853	OK273853	Uganda	Viner *et al*. 2021
Lyomyces denudatus	Ryvarden 19256	ON980759	–	Argentina	Viner & Miettinen 2022
Lyomyces denudatus	Ryvarden 19436	ON980760	–	Argentina	Viner & Miettinen 2022
Lyomyces elaeidicola	LWZ20180411-19	MT319457	MT319190	China	Wang *et al*. 2021
Lyomyces elaeidicola	LWZ20180411-20	MT319458	NG_153910	China	Wang *et al*. 2021
Lyomyces erastii	TASM:YG 022	MF382992	–	Uzbekistan	Gafforov *et al*. 2017
Lyomyces erastii	23cSAMHYP	JX857800	–	Spain	Unpublished
Lyomyces fimbriatus	Wu910620-7	MK575209	–	China	Yurchenko *et al*. 2020
Lyomyces fimbriatus	Wu 911204-4	MK575210	MK598740	China	Yurchenko *et al*. 2020
Lyomyces fimbriatus	Wu911204-4	MK575210	MK598740	China	Yurchenko *et al*. 2020
Lyomyces fissuratus	CLZhao 4352	MW713742	MW713732	China	Luo *et al*. 2021b
Lyomyces fissuratus	CLZhao 4291	MW713738	MW713730	China	Luo *et al*. 2021b
Lyomyces fumosus	CLZhao 8188	MW713744	MW713736	China	Luo *et al*. 2021b
Lyomyces gatesiae	LWZ20180515-3	MT319447	MT319181	China	Wang *et al*. 2021
Lyomyces gatesiae	LWZ20180515-32	MT319448	MT319182	China	Wang *et al*. 2021
Lyomyces granulosus	KAS-GEL1662	PP471799	–	Costa Rica	Yurchenko *et al*. 2024
Lyomyces griseliniae	KHL 12971 (GB)	DQ873651	DQ873651	Costa Rica	Larsson *et al*. 2006
Lyomyces guttulatus	LWZ 20200921-29a	OQ540899	OQ540859	China	Liu *et al*. 2024
Lyomyces guttulatus	LWZ 20190810-20b	OQ540898	OQ540858	China	Liu *et al*. 2024
Lyomyces hengduanensis	CLZhao 20627	OR793233	PP657611	China	Yuan *et al*. 2024
Lyomyces hengduanensis	CLZhao 25551	OR658999	PP657610	China	Yuan *et al*. 2024
Lyomyces hengduanensis	CLZhao 32713	OR899153	–	China	Yuan *et al*. 2024
Lyomyces hengduanensis	CLZhao 32714	OR899154	–	China	Yuan *et al*. 2024
Lyomyces hengduanensis	CLZhao 32782	OR899155	PP657612	China	Yuan *et al*. 2024
Lyomyces incanus	CLZhao 22813	OR094480	OR449935	China	Dong *et al*. 2024
Lyomyces incanus	CLZhao 22900	OR094481	OR449936	China	Dong *et al*. 2024

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TABLE 1. (Continued)

Species Name	Specimen No.	GenBank Accession No.		Country	References
		ITS	nLSU		
Lyomyces juniperi	FR-0261086	KY081799	–	France	Riebesehl & Langer 2017
Lyomyces lancangjiangensis	CLZhao 25280	OR844489	OR891517	China	Li *et al*. 2024
Lyomyces lancangjiangensis	CLZhao 25338	OR844490	OR891518	China	Li *et al*. 2024
Lyomyces lincangensis	CLZhao 22966	OR094487	OR449937	China	Dong *et al*. 2024
Lyomyces luteoalbus	CLZhao 18211	OR094485	OR449938	China	Dong *et al*. 2024
Lyomyces macrosporus	CLZhao 4516	MN945977	MW264920	China	Chen & Zhao 2020
Lyomyces mascarensis	KAS-GEL4833	KY800399	KY795964	France	Yurchenko *et al*. 2020
Lyomyces napoensis	EYu 190720-18	PP471800	PP471820	Ecuador	Yurchenko *et al*. 2024
Lyomyces microfasciculatus	CLZhao 5109	MN954311	MW264921	China	Chen & Zhao 2020
Lyomyces. *niveomarginatus*	CLZhao 16360	PP537949	PP657607	China	Yuan *et al*. 2024
Lyomyces niveus	CLZhao 6431	MZ262541	MZ262526	China	Luo *et al*. 2021b
Lyomyces niveus	CLZhao 6442	MZ262542	MZ262527	China	Luo *et al*. 2021b
Lyomyces ochraceoalbus	CLZhao 9819	MZ262538	MZ262524	China	Liu *et al*. 2024
Lyomyces ochraceoalbus	CLZhao 4385	MZ262535	MZ262521	China	Luo *et al*. 2021b
Lyomyces orientalis	KAS-GEL 3376	DQ340325	DQ340351	Germany	Yurchenko *et al*. 2017
Lyomyces pantropicus	EYu 190727-23b	PP471808	PP471825	Panama	Yurchenko *et al*. 2024
Lyomyces pruni	Ryberg 021018 (GB)	DQ873624	DQ873625	Sweden	Yurchenko *et al*. 2020
Lyomyces pruni	KAS-GEL 2327	DQ340312	DQ340349	Germany	Yurchenko *et al*. 2020
Lyomyces punctatomarginatus	CLZhao 11629	OR844491	OR891519	China	Li *et al*. 2024
Lyomyces punctatomarginatus	CLZhao 22699	OR844492	OR891520	China	Li *et al*. 2024
Lyomyces qujingensis	CLZhao 27462	OR167768	OR449940	China	Dong *et al*. 2024
Lyomyces ruiliensis	**CLZhao 44431**	**PV750812**	**PV990085**	**China**	**Present study**
Lyomyces ruiliensis	**CLZhao 44469**	**PV750813**	**PV990086**	**China**	**Present study**
Lyomyces ruiliensis	**CLZhao 44587 ***	**PV750811**	**PV990087**	**China**	**Present study**
Lyomyces ruiliensis	**CLZhao 44647**	**PV750814**	**PV990088**	**China**	**Present study**
Lyomyces ruiliensis	**CLZhao 44648**	**PV750810**	**–**	**China**	**Present study**
Lyomyces ruiliensis	**CLZhao 44667**	**PV750809**	**PV990089**	**China**	**Present study**
Lyomyces sambuci	KAS-JR 7	KY800402	KY795966	Sweden	Yurchenko *et al*. 2017
Lyomyces sambuci	LWZ 20180905-1	MT319444	MT319178	China	Wang *et al*. 2021

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TABLE 1. (Continued)

Species Name	Specimen No.	GenBank Accession No.		Country	References
		ITS	nLSU		
Lyomyces sceptrifer	KAS-Ec661	PP471811	–	Ecuador	Yurchenko *et al.* 2024
Lyomyces sinensis	CLZhao 27391	OR167769	OR449941	China	Dong *et al*. 2024
Lyomyces sinensis	CLZhao 27464	OR167770	OR449942	China	Dong *et al*. 2024
Lyomyces subcylindricus	EYu 190727-25	PP471817	–	Panama	Yurchenko *et al.* 2024
Lyomyces tasmanicus	LWZ 20180515–17	OQ540900	–	China	Liu *et al*. 2024
Lyomyce vietnamensis	TNM F9073	JX175044	KX857814	China	Yurchenko & Wu 2014
Lyomyce vietnamensis	He 3260	MW507086	MW507028	China	Yurchenko *et al.* 2017
Lyomyces wuliangshanensis	CLZhao 4108	MN945980	–	China	Chen & Zhao 2020
Lyomyces wuliangshanensis	CLZhao 4167	MN945979	–	China	Chen & Zhao 2020
Lyomyces wumengshanensis	CLZhao 29374	OR803021	PP657613	China	Yuan *et al*. 2024
Lyomyces wumengshanensis	CLZhao 32800	OR899211	PP657614	China	Yuan *et al*. 2024
Lyomyces wumengshanensis	CLZhao 32915	OR899213	PP657615	China	Yuan *et al*. 2024
Lyomyces wumengshanensis	CLZhao 31486	OR899208	–	China	Yuan *et al*. 2024
Lyomyces yunnanensis	CLZhao 2463	OP730711	OP730723	China	Guan *et al*. 2023
Lyomyces yunnanensis	CLZhao 9375	OP730710	–	China	Guan *et al*. 2023
Lyomyces yunnanensis	CLZhao 10041	OP730709	–	China	Guan *et al*. 2023
Xylodon afromontanus	O-F-904012	OQ645463	–	Rwanda	Yurchenko *et al.* 2024
Xylodon bamburesupinus	CLZhao 23088	OR167773	OR449943	China	Dong *et al*. 2024
Xylodon bamburesupinus	CLZhao 23123	OR167774	OR449944	China	Dong *et al*. 2024
Xylodon daweishanensis	CLZhao 18446	OP730717	OP730725	China	Guan *et al*. 2023
Xylodon daweishanensis	CLZhao 18492	OP730719	OP730727	China	Guan *et al*. 2023
Xylodon filicinus	MSK-F 12869	MH880199	NG067836	Germany	Wang *et al*. 2021
Xylodon flaviporus	FR-0249797	MH880201	–	Germany	Wang *et al*. 2021
Xylodon flaviporus	MA-Fungi 79440	MH260071	MH260066	Spain	Fernández-López *et al*. 2018
Xylodon hyphodontinus	KAS-GEL9222	MH880205	MH884903	Germany	Riebesehl *et al.* 2019
Xylodon lagenicystidiatus	LWZ 20180515-14	MT319633	–	China	Wang *et al*. 2021
Xylodon luteodontioides	CLZhao 3207	MH114740	–	China	Yuan & Zhao 2024

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TABLE 1. (Continued)

Species Name	Specimen No.	GenBank Accession No.		Country	References
		ITS	nLSU		
Xylodon luteodontioides	CLZhao 18494	PP505422	–	China	Yuan & Zhao 2024
Xylodon macrosporus	CLZhao 10226	MZ663809	MZ663817	China	Luo *et al*. 2021a
Xylodon ovisporus	LWZ 20170815-31	MT319666	–	China	Wang *et al*. 2021
Xylodon ovisporus	LWZ 20190817-6b	ON063680	ON063880	China	Wang *et al*. 2023a
Xylodon pingbianensis	CLZhao 19029	OR096208	OR449949	China	Dong *et al*. 2024
Xylodon puerensis	CLZhao 8142	OP730720	OP730728	China	Guan *et al*. 2023
Xylodon puerensis	CLZhao 8639	OP730721	OP730729	China	Guan *et al*. 2023
Xylodon quercinus	Larsson 11076 (GB)	KT361633	–	Sweden	Larsson *et al*. 2004
Xylodon quercinus	Spirin 12030	OK273841	OK273841	Finland	Viner *et al*. 2021
Xylodon quercinus	KHL 11076	KT361633	AY586678	Sweden	Larsson *et al*. 2004
Xylodon ramicida	Spirin 7664	NR138013	–	Russia	Unpublished
Xylodon rimosissimus	LWZ 20180904-28	ON063682	ON063882	China	Wang *et al*. 2023a
Xylodon sinensis	CLZhao 9197	MZ663810	–	China	Luo *et al*. 2021a
Xylodon sinensis	CLZhao 11120	MZ663811	–	China	Luo *et al*. 2021a

Phylogenetic analyses

The sequences were aligned in MAFFT version 7 using the G-INS-i strategy (Katoh *et al.* 2019). The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). Each dataset was aligned separately at first, and then the ITS and nLSU regions were combined with Mesquite version 3.51. The sequence alignments were deposited in figshare (DOI: 10.6084/m9.figshare.29979055). The sequence of *Hyphodontia daweishanensis* Yang Yang & C.L. Zhao (2025: 279) obtained from GenBank was used as an outgroup to root trees in the ITS+nLSU analysis for the family Schizoporaceae (Fig. 1). The sequence alignments were deposited in figshare (DOI: 10.6084/m9.figshare.29979055). Sequences of *Xylodon quercinus* (Pers.) Gray (1821: 649) and *Xylodon ramicida* Spirin & Miettinen (2015: 229) were selected as the outgroup in the ITS analysis (Fig. 2) by a previous study (Guan *et al.* 2023).

Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were applied to the combined two datasets. Maximum Likelihood (ML) analysis in the CIPRES Science Gateway (https://www.phylo.org/portal2/login!input.action, Miller *et al*. 2012) was applied to the combined ITS+nLSU dataset following a previous study (Fig. 1, Dong *et al*. 2024). Maximum Likelihood (ML) analysis was performed with RAxML-HPC BlackBox in CIPRES Science Gateway using a GTRCAT model of evolution with 1,000 bootstrap replicates (Felsenstein 1985). Phylogenetic trees were visualized and adjusted using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree), and the final phylogenetic tree was edited in Adobe Illustrator CS6 (Adobe Systems, USA).

Maximum parsimony (MP), maximum likelihood (ML), and Bayesian Inference (BI) analyses were applied to the three combined datasets. Maximum parsimony analysis in PAUP* version 4.0b10 (http://phylosolutions. com/paup-test/) was applied to the ITS dataset following a previous study (Zhao & Wu 2017). All of the characteristics were equally weighted, and gaps were treated as missing data. Max-trees were set to 5,000, branches of zero length were collapsed, and almost all most-parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1,000 replicates (Felsenstein 1985).

MrModeltest 2.3 was used to determine the best-fit evolution model for each dataset for the purposes of Bayesian inference (BI) (Nylander 2004), which was performed with MrBayes 3.2.7a using a GTR+I+G model of DNA substitution and a gamma distribution of rate variation across sites (Ronquist *et al.* 2012). A total of four Markov chains were run for 2 runs from random starting trees, each for 1.5 million generations for ITS+nLSU (Fig. 1) and 2.5 million generations for ITS (Fig. 2), with trees and parameters sampled every 1,000 generations. The first one-fourth generations were discarded as burn-in. A majority rule consensus tree was computed from the remaining trees. Branches were considered as significantly supported if they received a maximum likelihood bootstrap support value (BS) of ≥ 70%, a maximum parsimony bootstrap support value (BT) of ≥ 50% or a Bayesian posterior probability (BPP) of ≥ 0.95.

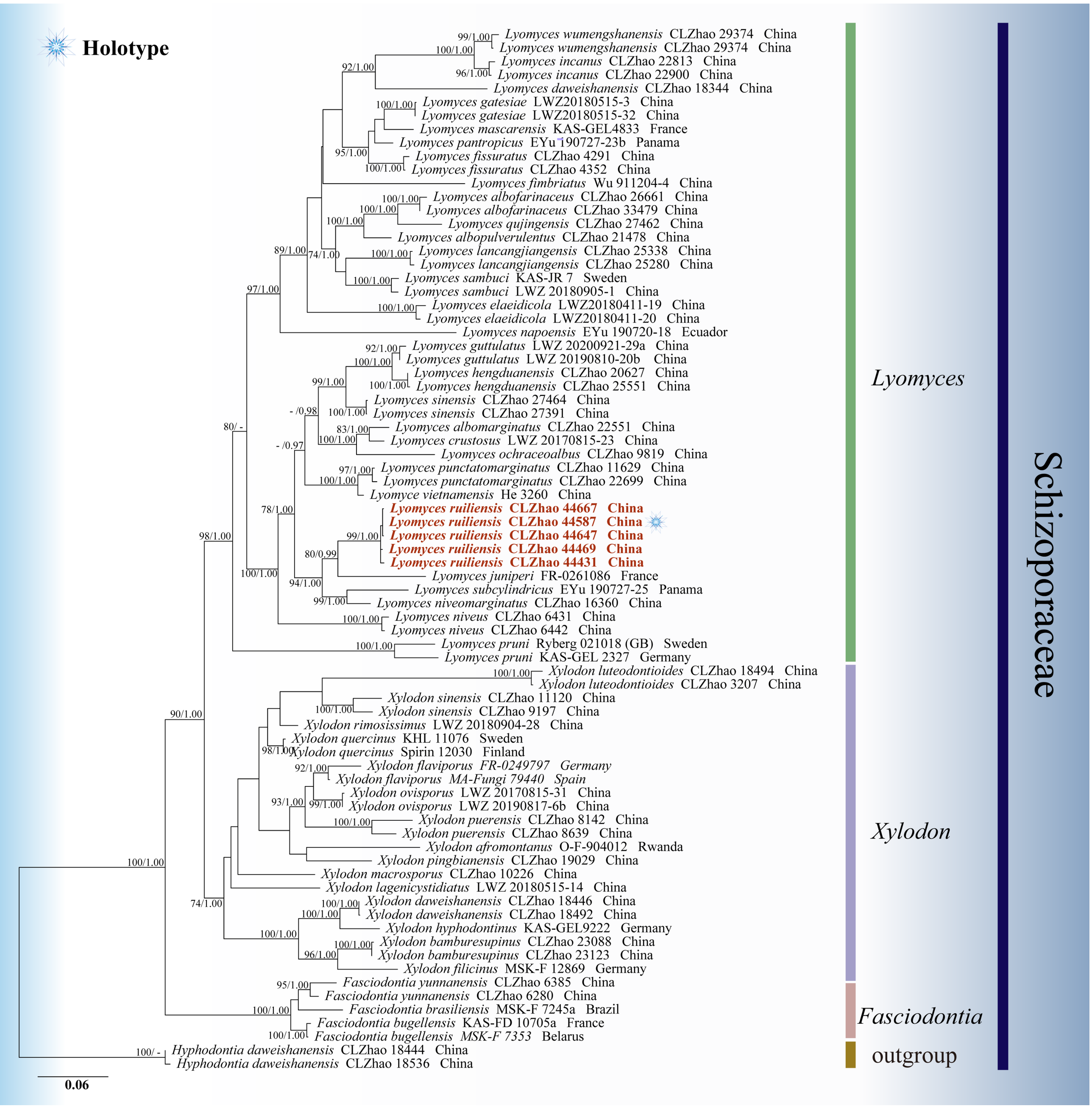

FIGURE 1. Maximum Likelihood strict consensus tree illustrating the *Lyomyces* and related genera in the family Schizoporaceae based on the combined ITS+nLSU sequences. Branches are labeled with Maximum Likelihood bootstrap values ≥ 70% and Bayesian posterior probabilities ≥ 0.95. The newly generated sequences are in red bold.

Results

Molecular phylogeny

The aligned ITS+nLSU dataset comprised 74 specimens representing 48 species. Four Markov chains were run for 2 independent runs from random starting trees, each for 1.5 million generations, using the combined ITS+nLSU dataset (Fig. 1), with trees and parameters sampled every 1,000 generations. The best model for the ITS+nLSU dataset, estimated and applied in the Bayesian analysis, was GTR+I+G. Maximum Likelihood (ML) and Bayesian Inference (BI) analyses yielded similar topologies, with average standard deviations in split frequencies of 0.008558 (BI). The effective sample size (ESS) for Bayesian analysis across the two runs was approximately double the average ESS (avg. ESS) = 136.

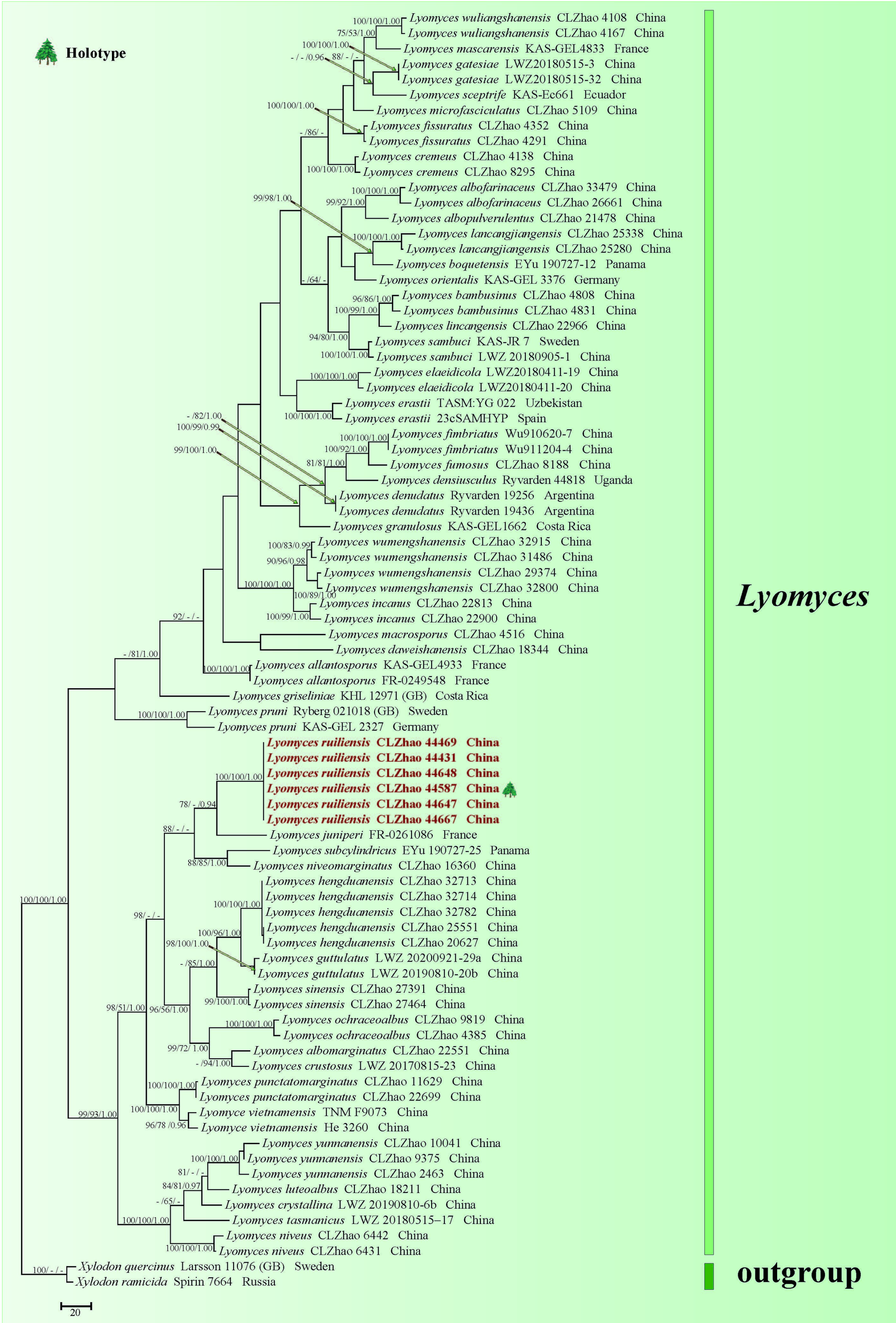

FIGURE 2. Maximum Parsimony strict consensus tree illustrating the *Lyomyces ruiliensis* and related species in the genus *Lyomyces* based on the combined ITS sequences. Branches are labeled with Maximum Likelihood bootstrap values ≥ 70%, parsimony bootstrap values ≥ 50%, and Bayesian posterior probabilities ≥ 0.95. The newly generated sequences are in red bold.

The ITS dataset (Fig. 2) included sequences from 81 fungal specimens representing 46 species belonging to three genera and related to *Lyomyces* in the family Schizoporaceae. The aligned length of the data set was 676 characters, of which 297 characters were constant, 44 were variable and parsimony-uninformative, and 335 were parsimony-informative. Maximum parsimony analysis yielded three equally parsimonious trees (TL = 2060, CI = 0.3286, HI = 0.674, RI = 0.7367, RC = 0.2421). The best-fit model for the ITS alignment estimated and applied in BI was GTR+I+G. At the end of the BI runs, the average standard deviation of split frequencies was 0.009717 (BI), and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 140.

The phylogram based on the combined ITS+nLSU sequences (Fig. 1) indicated that the new species *Lyomyces ruiliensis* was assigned to the genus *Lyomyces*. The phylogenetic tree (Fig. 2), inferred from the ITS sequences, retrieved the new species *L. ruiliensis* as a sister to *L. juniperi* (Bourdot & Galzin) Riebesehl & Langer (2017: 647).

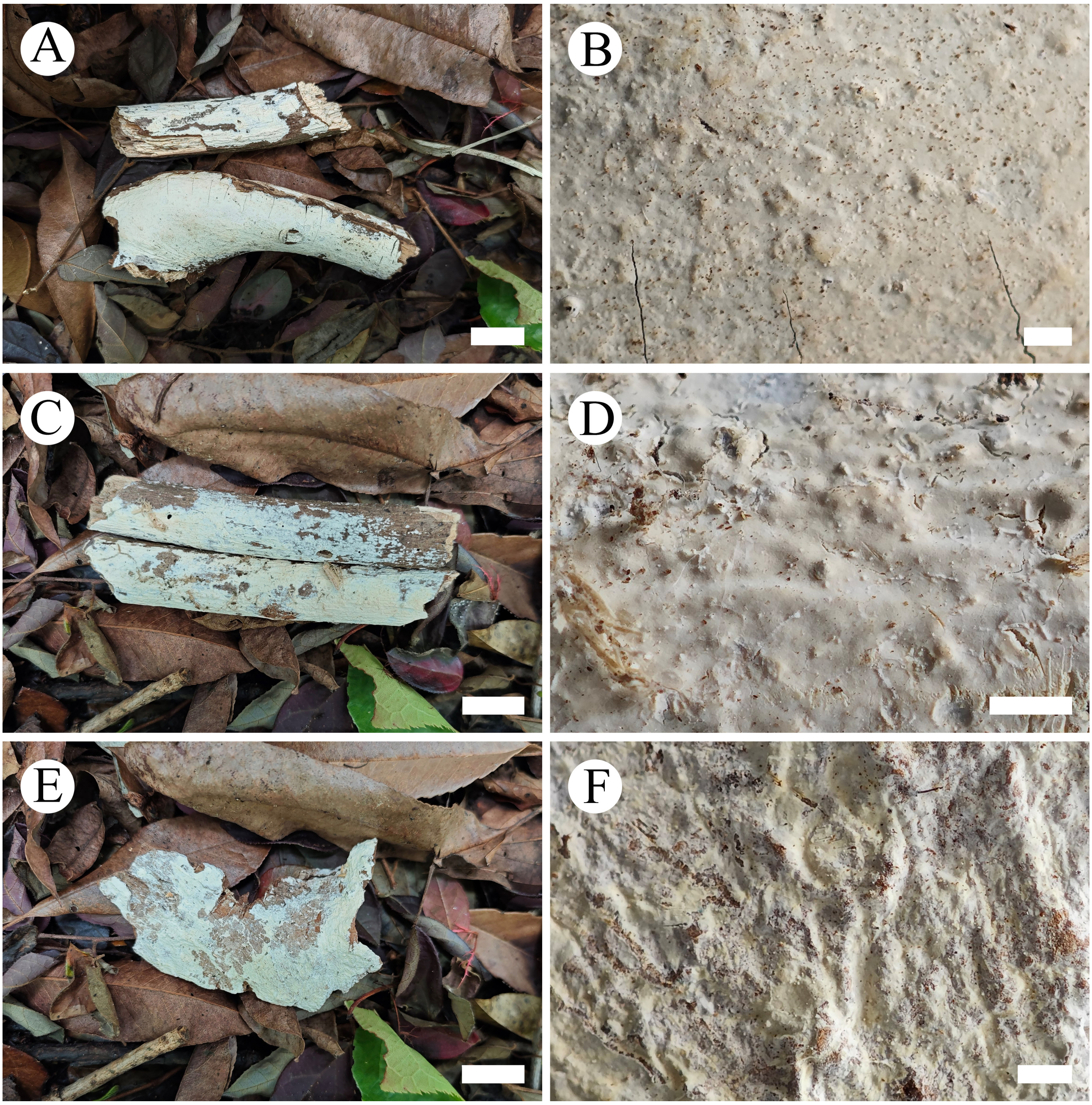

FIGURE 3. Basidiomata of *Lyomyces ruiliensis* (A, B) CLZhao 44431; (C, D) CLZhao 44587 (holotype); (E, F) CLZhao 44647. Scale bars: A, C, E = 2 cm; B, D, F = 2 mm.

Taxonomy

Lyomyces ruiliensis Q.Q. Jiang & C.L. Zhao, *sp. nov*. Figs. 3–5
MycoBank no.: MB 860246

***Etymology*:**—*Ruiliensis* (Lat.): refers to the type locality, Ruili County.

***Diagnosis*:**—Differs from other species of *Lyomyces* by its coriaceous basidiomata with white to cream hymenial surface, a monomitic hyphal system with clamped generative hyphae; subhymenial hyphae densely covered by larger crystals and ellipsoid basidiospores measuring 4.5–5 × 3–3.5 µm.

***Holotype*:**—CHINA. Yunnan Province, Dehong, Ruili County, Tongbiguan Nature Reserve, GPS coordinates 23°38′N, 97°32′E, altitude 850 m asl., on a fallen angiosperm branch, leg. C.L. Zhao, 15 January 2025, CLZhao 44587 (SWFC).

***Basidiomata*:**—Annual, resupinate, adnate, coriaceous, without odor or taste when fresh, becoming slightly cracking upon drying, up to 20 cm long, 5 cm wide, and 50–100 µm thick. Hymenial surface smooth, white when fresh, turning white to cream when drying. Sterile margin white, thinning out, up to 3 mm wide.

***Hyphal structure*:**—Hyphal system monomitic, generative hyphae with clamp connections, colorless, thick-walled, frequently branched, 2–3.5 µm in diameter; IKI–, CB–; tissues unchanged in KOH; subhymenial hyphae densely covered by larger crystals.

***Hymenium*:**—Cystidia fusiform, tapering, colorless, thin-walled, 14.5–22 × 2.5–4 µm. Basidia subutriform, slightly sinuous or constricted in the middle, colorless, with 4 sterigmata and a basal clamp connection, 9–16.5 × 3.5–5 µm; basidioles dominant, similar to basidia in shape, but slightly smaller.

Basidiospores:—Ellipsoid, colorless, thin-walled, smooth, occasionally with one bubble inside, IKI–, CB–, (4.3–)4.5–5(–5.4) × (2.5–)3–3.5 µm, L = 4.87 µm, W = 3.18 µm, Q = 1.52–1.54 (n = 180/6).

***Additional specimens examined*:**—CHINA. Yunnan Province, Dehong, Ruili County, Tongbiguan Nature Reserve, GPS coordinates 23°38′N, 97°32′E, altitude 850 m asl., on the dead bamboo, leg. C.L. Zhao, 15 January 2025, CLZhao 44431, CLZhao 44469, CLZhao 44647, CLZhao 44648, CLZhao 44667 (SWFC).

Discussion

Located in Yunnan Province, China, Dehong is characterized by its complex topography and diverse ecosystems, which support high biodiversity in flora and fauna. However, fungal diversity in this region remains understudied. Given the intricate associations between fungi and plants, further in-depth research on fungal diversity in Dehong is warranted. In the present study, a new species, *Lyomyces ruiliensis*, is described based on phylogenetic analyses and morphological characteristics.

Phylogenetically, DNA sequence-based classification and identification have become the standard approach in fungal taxonomy (Hibbett *et al*. 2007, Xu 2020, Sun *et al*. 2020, Lücking *et al*. 2021, Wang *et al*. 2023b, Zhou *et al.* 2023). In the present study, the combined ITS+nLSU sequences (Fig. 1) indicated that our collections belong to the genus *Lyomyces* and represent a distinct species. Based on ITS topology (Fig. 2), in which *L. ruiliensis* is grouped with *L. juniperi* and then closely grouped with *L. subcylindricus* Yurchenko & Riebesehl (2024: 160) and *L. vietnamensis* (Yurchenko & Sheng H. Wu) Riebesehl & Langer (2017: 651). However, morphologically, *L. juniperi* can be delimited from *L. ruiliensis* by its smooth hymenial surface with some scattered small granules, longer basidia (15–25 × 4–4.5 µm *vs*. 9–16.5 × 3.5–5 µm, Hjortstam & Ryvarden 2004) and larger basidiospores (5–7 × 3–4 µm *vs*. 4.5–5 × 3–3.5 µm, Riebesehl & Langer 2017); *L. subcylindricus* can be separated from *L. ruiliensis* by its minutely odontoid or warted hymenial surface and longer basidia (15–20 × 3.5–4.5 µm *vs*. 9–16.5 × 3.5–5 µm, Yurchenko *et al*. 2024). The taxon *L. vietnamensis* differs from *L. ruiliensis* by its aculeate hymenial surface and longer basidiospores (5.8–6.1 × 2.6–2.9 µm *vs*. 4.5–5 × 3–3.5, Yurchenko & Wu 2013).

Morphologically, *Lyomyces ruiliensis* is similar to *L. cremeus* C.L. Zhao (2020: 108), *L. denudatus* Viner (2022: 381), *L. mascarensis* Riebesehl, Yurchenko & Langer (2017: 870), and *L. niveomarginatus* Qi Yuan & C.L. Zhao (2024: 77) by the smooth hymenial surface and ellipsoid basidiospores. However, *L. cremeus* differs from *L. ruiliensis* by its the ceraceous basidiomata and wider basidiospores (4.5–5.6 × 3.3–4.3 µm *vs*. 4.5–5 × 3–3.5 µm, Chen & Zhao 2020); *L. denudatus* is separated from *L. ruiliensis* by its longer basidia (15–21.1 × 3.8–5.5 µm *vs*. 9–16.5 × 3.5–5 µm) and basidiospores (4.8–7 × 2.8–4.2 µm *vs*. 4.5–5 × 3–3.5 µm, Viner & Miettinen 2022); *L. mascarensis* can be

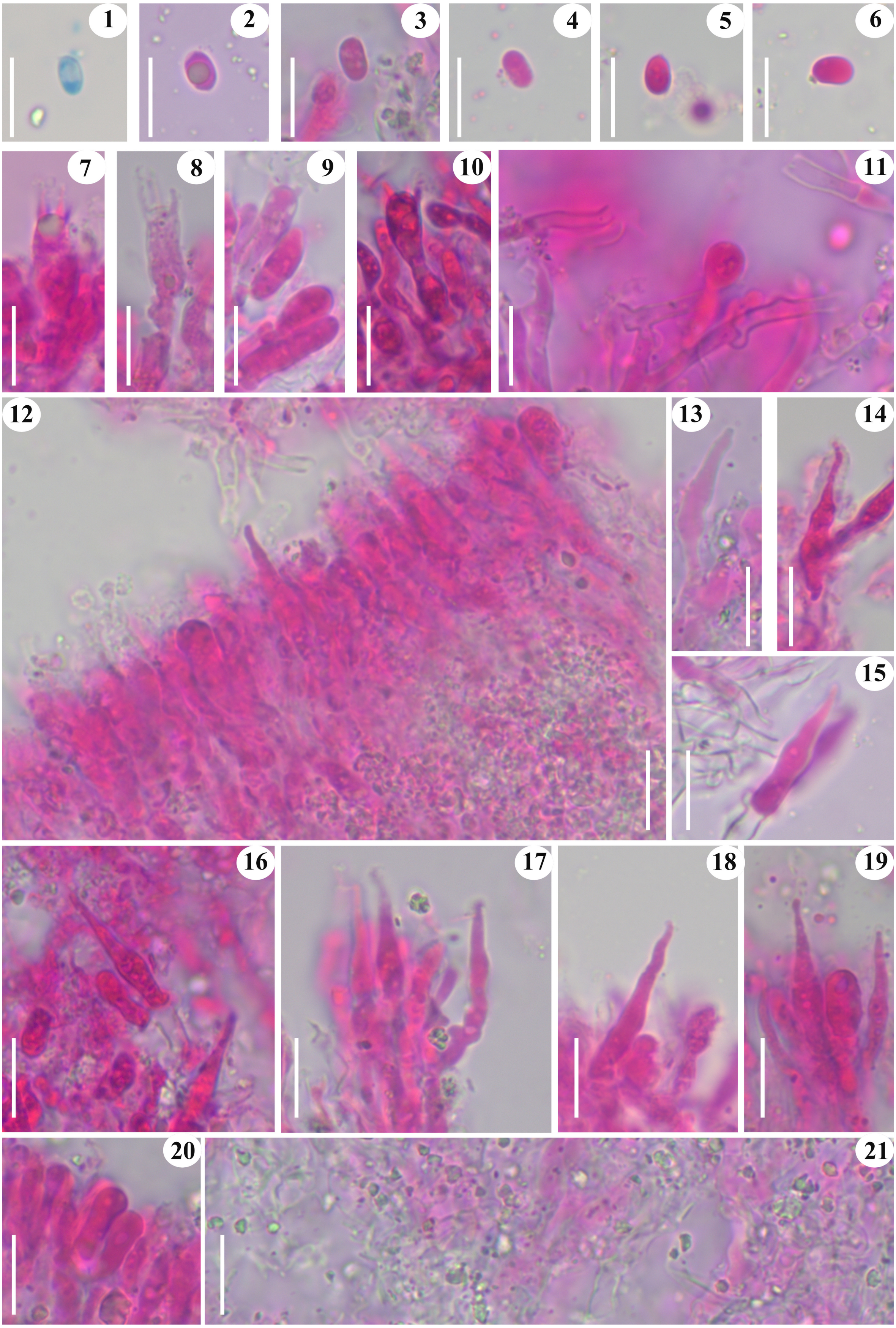

FIGURE 4. Sections of hymenium of *Lyomyces ruiliensis* (holotype, CLZhao 44587). (1–6) Basidiospores; (7–10) Basidia and basidioles; (11) Generative hyphae; (12) A section of the hymenium; (13–19) Cystidia; (20) Basidioles; (21) Subhymenial hyphae densely covered by larger crystals. Scale bars: 1–21 = 10 µm.

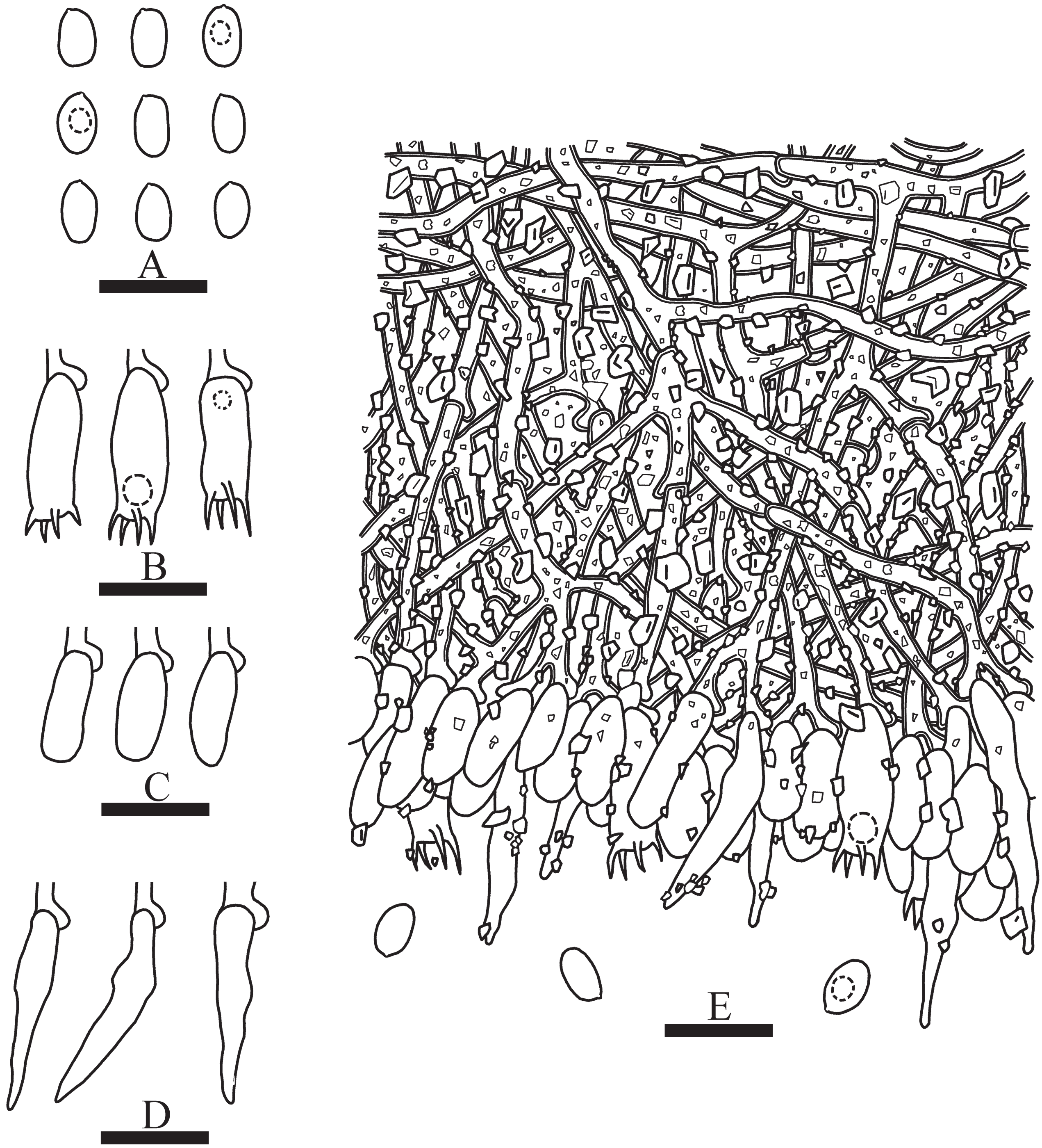

FIGURE 5. Microscopic structures of *Lyomyces ruiliensis* (holotype, CLZhao 44587). (A) Basidiospores; (B) Basidia; (C) Basidioles; (D) Cystidia; (E) A section of the hymenium. Scale bars: A–E = 10 µm.

delimited from *L. ruiliensis* by having thin-walled generative hyphae, longer basidia (16–17.5 × 3.5–4.5 µm *vs*. 9–16.5 × 3.5–5 µm) and cystidia with three types: capitate cystidia (17–38 × 3.5–6 µm), submoniliform cystidia (18–22 × 5–5.5 µm) and tapering cystidia (25–30 × 3.5–4.5 µm, Yurchenko *et al*. 2017). The species *L. niveomarginatus* differs from *L. ruiliensis* due to its cream to slightly buff hymenial surface and longer basidia (23–29 × 2.5–3.5 µm *vs*. 9–16.5 × 3.5–5 µm, Yuan *et al*. 2024).

The Yunnan Province is recognized as the "Ecological Security Barrier in Southwest China" and "Biodiversity Treasure", plays a crucial role in the national ecological safety and biodiversity conservation structure (Yan *et al*. 2021, Yuan *et al*. 2023, Qin *et al*. 2025). It is rich in woody plant species, providing excellent substrates for wood-inhabiting fungi. Hence, studying the diversity of wood-inhabiting fungi in Yunnan, China, is of great significance. Based on this study, one new species is identified from Yunnan Province, which will further enrich our knowledge of fungal diversity in this area, and the discovery of additional novel taxa within *Lyomyces* is anticipated with further fieldwork and comprehensive molecular phylogenetic analyses, the results not only enrich the species diversity of fungi worldwide but also contribute to the branches of the fungal tree of life.

Acknowledgements

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