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Research Article

Morphology and multigene phylogeny revealed four new species of *Xylodon* (Schizoporaceae, Basidiomycota) from southern China

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Abstract

Fungi are one of the most diverse groups of organisms on Earth, amongst which wood-inhabiting fungi play a crucial role in ecosystem processes and functions. Four new wood-inhabiting fungi, Xylodon cremeoparinaceus, X. luteodontioides, X. poroides and X. wumengshanensis are proposed, based on morphological features and molecular evidence. Xylodon cremeoparinaceus is distinguished by a cream hymenial surface with a pruinose hymenophore, a monomitic hyphal system with clamped generative hyphae and ellipsoid basidiospores. Xylodon luteodontioides is characterised by flavescens hymenophore surface with odontioid hymenophore, monomitic hyphal system with clamped generative hyphae and ellipsoid basidiospores. Xylodon poroides bears coriaceous basidiomata with a poroid hymenophore surface, monomitic hyphal system with clamped generative hyphae and ellipsoid basidiospores. Xylodon wumengshanensis is a distinct taxon by its grandinoid hymenophore surface, monomitic hyphal system with clamped generative hyphae and ellipsoid basidiospores. Sequences of ITS and nLSU rRNA markers of the studied samples were generated and phylogenetic analyses were performed using the Maximum Likelihood, Maximum Parsimony, and Bayesian Inference methods. The phylogram, based on the ITS+nLSU rDNA gene regions, included three genera within the Schizoporaceae as Fasciodontia, Lyomyces and Xylodon. The four new species were grouped into the genus Xylodon. The topology, based on the ITS sequences, revealed that Xylodon cremeoparinaceus was grouped closely with X. pruinosus, X. detriticus and X. ussuriensis. The taxon X. luteodontioides was sister to X. nesporii. The species X. poroides separated from X. pseudotropicus, while X. wumengshanensis was grouped with four taxa: X. patagonicus, X. radula, X. subtropicus and X. taiwanianus.

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

Introduction

Fungi are well-known as a diverse group of microorganisms that play important roles in forest ecosystems (Phookamsak et al. 2019). Wood-inhabiting fungi are essential to natural ecosystems for nutrient cycling and maintaining plant

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diversity (Drinkwater et al. 2017; Horwath 2017; Hyde et al. 2018; Wu et al. 2022a, b; Guan et al. 2023; Yuan et al. 2023; Deng et al. 2024a, b; Zhang et al. 2024). Schizoporaceae Jülich includes many variations of the fruiting body types amongst Hymenochaetales Oberw. (Larsson et al. 2006; Wu et al. 2022a; Guan et al. 2023; Zhang et al. 2024), in which it comprises many representative wood-inhabiting fungal taxa, including hydnoid, corticioid and polyporoid basidiomes with diverse hymenophoral and cystidial morphology (Yurchenko and Wu 2016; Riebesehl and Langer 2017; Yurchenko et al. 2017; Cui et al. 2019; Riebesehl et al. 2019; Jiang et al. 2021; Wu et al. 2022a, b; Guan et al. 2023; Deng et al. 2024a, b; Zhang et al. 2024). In addition, members of Schizoporaceae are widely distributed, causing white rot (Langer 1994; Luo et al. 2022; Guan et al. 2023; Zhang et al. 2024).

Xylodon (Pers.) Gray is a large genus of corticioid fungi, having a cosmopolitan distribution (Bernicchia and Gorjón 2010; Guan et al. 2023; Yurchenko et al. 2024; Zhang et al. 2024). Species of Xylodon inhabit dead wood of various sizes, from twigs several millimetres in diameter to large fallen trunks and cause white rot (Girometta et al. 2020; Greslebin and Rajchenberg 2000; Kotiranta and Saarenoksa 2000; Guan et al. 2023). Sometimes basidiomata of Xylodon species appear on living parts of trees (Yurchenko 2008) and non-woody plant remains, for example, fern rachises (Kotiranta and Saarenoksa 2000), herb stems and fallen leaves (Viner et al. 2018) and dead polypore basidiomata (Viner et al. 2023). The genus is known from almost all types of world biomes where wooden plant debris occurs, from humid to semi-arid and from seashore to the upper limit of wooden vegetation in altitudinal gradients (Yurchenko et al. 2024). This genus is typified by X. quercinus (Pers.) Gray (Bernicchia and Gorjón 2010) and characterised by the resupinate or effuse basidiomata with a smooth, tuberculate, grandinioid, odontioid, coralloid, irpicoid or poroid hymenophore; a monomitic or dimitic hyphal system with clamped generative hyphae; the presence of different types of cystidia; utriform or suburniform basidia; and cylindrical to ellipsoid to globose basidiospores (Gray 1821; Bernicchia and Gorjón 2010; Zhang et al. 2024). Based on the MycoBank database (http://www.mycobank.org, accessed on 19 May 2024) and the Index Fungorum (http://www. indexfungorum.org, accessed on 19 May 2024), Xylodon has been registered with 234 specific and infraspecific names and the actual number of the species has reached 109 species (Chevallier 1826; Kuntze 1898; Wu 1990, 2000, 2001, 2006; Hjortstam and Ryvarden 2007, 2009; Xiong et al. 2009, 2010; Bernicchia and Gorjón 2010; Tura et al. 2011; Dai 2012; Lee and Langer 2012; Yurchenko et al. 2013; Yurchenko and Wu 2014a, b; Zhao et al. 2014; Chen et al. 2016; Kan et al. 2017a, b; Riebesehl and Langer 2017; Wang and Chen 2017; Viner et al. 2018; Riebesehl et al. 2019; Shi et al. 2019; Dai et al. 2021; Luo et al. 2021a, 2022; Qu and Zhao 2022; Qu et al. 2022; Viner and Miettinen 2022; Guan et al. 2023; Wang and Zhou 2024; Yurchenko et al. 2024; Zhang et al. 2024).

Classification of taxa in the kingdom *Fungi* has been updated continuously, based on the frequent inclusion of data from DNA sequences in many phylogenetic studies (Yurchenko et al. 2020). For the past few years, the genus *Xylodon* was generally studied by molecular systematics and it was included in the *Hyphodontia* s.l. (Hjortstam and Ryvarden 2009; Yurchenko and Wu 2016; Riebesehl and Langer 2017; Wang and Chen 2017; Riebesehl et al. 2019; Qu et al. 2022; Guan et al. 2023). *Hyphodontia* s.l. was shown to be a polyphyletic

genus and a broad concept employed by some mycologists due to a lack of rDNA sequences for many taxa, in which Xylodon and Kneiffiella P. Karst included rich species (Hjortstam and Ryvarden 2009; Riebesehl and Langer 2017; Riebesehl et al. 2019; Luo et al. 2022; Zhang et al. 2024). Based on the molecular systematics research, two clades, the Xylodon-Lyomyces-Rogersella and the Xylodon-Schizopora-Palifer clades were described and the related species of Lyomyces P. Karst., Palifer Stalpers & P.K. Buchanan, Rogersella Liberta & A.J. Navas Schizopora Velen. and Xylodon, within both clades were suggested to be mixed (Yurchenko et al. 2013). The research comprised the representative sequences and taxa of Hyphodontia s.l., such as Lyomyces, Palifer, Rogersella, Schizopora and Xylodon, in which the result demonstrated that it was hard to distinguish the two genera Xylodon and Schizopora on the basis of the morphological and phylogenetic information; therefore, the authors proposed that the related species of Schizopora should be united into the genus Xylodon (Riebesehl and Langer 2017). For the phylogenetic relationship of Xylodon species, it was confirmed that the two genera Lagarobasidium Jülich and Xylodon should be synonymous, based on the molecular data from the ITS and nLSU regions, in which the three species X. pumilius (Gresl. & Rajchenb.) K.H. Larss., X. magnificus (Gresl. & Rajchenb.) K.H. Larss. and X. rickii (Gresl. & Rajchenb.) K.H. Larss. were combined into Xylodon (Viner et al. 2018). All the taxa of the genera Odontipsis Hjortstam & Ryvarden and Palifer were placed in the genus Xylodon, based on the molecular analyses of 28S and ITS data, in which they proposed four new species of Xylodon as X. exilis Yurchenko, Riebesehl & Langer, X. filicinus Yurchenko & Riebesehl, X. follis Riebesehl, Yurchenko & Langer and X. pseudolanatus Nakasone, Yurchenko & Riebesehl (Riebesehl et al. 2019). Based on the multiple loci in Hyphodontia s.l., Fasciodontia Yurchenko& Riebesehl, Hastodontia (Parmasto) Hjortstam & Ryvarden, Hyphodontia J. Erikss., Lyomyces, Kneiffiella and Xylodon in Hymenochaetales, they were divided into four clades and three new taxa were found from China, in which X. gossypinus C.L. Zhao & K.Y. Luo and X. brevisetus (P. Karst.) Hjortstam & Ryvarden grouped together (Luo et al. 2021a). Based on the morphological descriptions and molecular analyses, three new species, namely Xylodon angustisporus Viner & Ryvarden, X. dissiliens Viner & Ryvarden and X. laxiusculus Viner & Ryvarden, were described in Africa and placed in the genus Xylodon (Viner et al. 2021). A phylogenetic and taxonomic study focusing on the genus Xylodon (Hymenochaetales) newly described one species of this genus from southern China and this research enriched the fungal diversity worldwide (Zhang et al. 2024). Since the 1810s, a total of 234 species have been proposed for the genus Xylodon (http://www.indexfungorum.org/Names/Names. asp?pg=1, accessed on 19 May 2024). Inspiringly, new species have been described in the genus at an accelerated pace after the inflection point around the year 1890 and 2007 on the trend curve of species number (Fig. 1), which is due to advances in morphological taxonomy and molecular phylogeny (Luo et al. 2022; Qu et al. 2022; Guan et al. 2023; Yurchenko et al. 2024; Zhao et al. 2024; Zhang et al. 2024).

During investigations on the wood-inhabiting fungi in the Yunnan Province of China, samples representing four additional species belonging to *Xylodon* were collected. To clarify the placement and relationships of these species, we carried out a phylogenetic and taxonomic study on *Xylodon*, based on the ITS and



Figure 1. Trends in the accumulative number of species of Xylodon recorded in the world and China.

nLSU sequences. These specimens are identified as four undescribed species of *Xylodon* and the detailed description, illustrations and phylogenetic analysis results of the new species are provided here.

Materials and methods

Morphology

Fresh basidiomata of the fungi growing on the angiosperm branches were collected from the Honghe, Lincang, Puer, Wenshan and Zhaotong of Yunnan Province, P.R. China. Specimens were dried in an electric food dehydrator at 40 °C (Hu et al. 2022), then sealed and stored in an envelope and deposited in the Herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macromorphological descriptions were based on field notes and photos captured in the field and lab. Colour terminology followed Petersen (1996). Micromorphological data were obtained from the dried specimens when observed under a light microscope following the previous study (Guan et al. 2023). 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 phylogeny

The EZNA HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming, China) was used to extract DNA with some modifications from the dried specimens. 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, with a final extension of 72 °C for 10 min. The nuclear nLSU region was amplified with primer pair LR0R and LR7 (Rehner and Samuels 1994). The PCR procedure for nLSU 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 with a final extension of 72 °C for 10 min. The PCR procedure for ITS and nLSU followed a previous study (Zhao and Wu 2017). All newly-generated sequences were deposited in NCBI GenBank (https://www.ncbi.nlm.nih.gov/ genbank/) (Table 1).

The sequences were aligned in MAFFT version 7 (Katoh et al. 2019) using the G-INS-i strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). Sequences of *Hymenochaete ochromarginata* P.H.B. Talbot and *H. rubiginosa* (Dicks.) Lév. retrieved from GenBank were used as the outgroups in the ITS+nLSU analysis (Fig. 2); Sequences of *Lyomyces sambuci* (Pers.) P. Karst. retrieved from GenBank were used as the outgroups in the ITS analysis (Fig. 3) (Guan et al. 2023; Zhang et al. 2024).

Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were applied to the combined three datasets following a previous study (Zhao and Wu 2017). All 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 1000 pseudo replicates (Felsenstein 1985). Descriptive tree statistics - tree length (TL), composite consistency index (Cl), composite retention index (RI), composite rescaled consistency index (RC) and composite homoplasy index (HI) - were calculated for each maximum parsimonious tree generated. The combined dataset was also analysed using Maximum Likelihood (ML) in RAxML-HPC2 through the CIPRES Science Gateway (Miller et al. 2012). Branch support (BS) for the ML analysis was determined by 1000 bootstrap pseudo replicates.

MrModelTest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each dataset for the purposes of Bayesian Inference (BI) which was performed using MrBayes 3.2.7a with a GTR+I+G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist et al. 2012). A total of four Markov chains were run for two runs from random starting trees for 1.3 million generations for ITS+nLSU (Fig. 2) and 16 million generations for ITS (Fig. 3) with trees and parameters sampled every 1,000 generations. The first quarter of all of the 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 \geq 70%, a maximum parsimony bootstrap support value (BT) of \geq 70% or a Bayesian posterior probability (BPP) of \geq 0.95.

 Table 1. Names, specimen numbers, references and corresponding GenBank accession numbers of the taxa used in this study.

Species name	Specimen No.	GenBank accession No.		References
		ITS	nLSU	-
Fasciodontia brasiliensis	MSK-F 7245a	MK575201	MK598734	Yurchenko et al. (2020)
F. bugellensis	KAS-FD 10705a	MK575203	MK598735	Yurchenko et al. (2020)
F. bugellensis	MSK-F 7353	MK575205	MK598736	Yurchenko et al. (2020)
F. yunnanensis	CLZhao 6280	MK811275	MZ146327	Luo and Zhao (2021)
F. yunnanensis	CLZhao 6385	MK811277	_	Luo and Zhao (2021)
Hymenochaete ochromarginata	He 47	KU978861	JQ279666	Unpublished
H. rubiginosa	He 458	JQ279580	_	He and Li (2013)
Lyomyces albopulverulentus	CLZhao 21478	OP730712	OP730724	Guan et al. (2023)
L. niveus	CLZhao 6431	MZ262541	MZ262526	Luo et al. (2021b)
L. niveus	CLZhao 6442	MZ262542	MZ262527	Luo et al. (2021b)
L. ochraceoalbus	CLZhao 4385	MZ262535	MZ262521	Luo et al. (2021b)
L. ochraceoalbus	CLZhao 4725	MZ262536	MZ262522	Luo et al. (2021b)
L. sambuci	KAS-JR7	KY800402	KY795966	Yurchenko et al. (2017)
L. sambuci	83SAMHYP	JX857721		Yurchenko et al. (2017)
L. yunnanensis	CLZhao 9375	OP730710		Guan et al. (2023)
L. yunnanensis	CLZhao 10041	OP730709	_	Guan et al. (2023)
X. asiaticus	CLZhao 10368	OM959479	_	Zhang et al. (2024)
X. attenuatus	Spirin 8775	MH324476	_	Wang et al. (2021)
X. asperus	Spirin 11923	OK273838		Viner et al. (2021)
X. apacheriensis	Canfield 180	KY081800		Wang et al. (2021)
X. acuminatus	Larsson 16029	ON197552		Viner et al. (2023)
X. acystidiatus	LWZ 20180514-9	MT319474		Wang et al. (2021)
X. afromontanus	H 7006811	00645463	_	Yurchenko et al. (2024)
X. angustisporus	Rvvarden 50691b	0K273831		Viner et al. (2021)
X. astrocvstidiatus	TNM F24764	NR154054	_	Yurchenko and Wu (2014b)
X. australis	LWZ 20180509-8	MT319503	_	Wang et al. (2021)
X. bambusicola	CLZhao 11310	MW394660		Ma and Zhao (2021)
X. borealis	JS 26064	AY463429		Larsson et al. (2004)
X. brevisetus	JS 17863	AY463428	_	Larsson et al. (2004)
X. cremeoparinaceus	CLZhao 23388	PP537951	_	Present study
X. crystalliger	KUN 2312	NR166242		Viner et al. (2018)
X. cymosus	Miettinen 19606	ON197554	_	Viner et al. (2023)
X. cystidiatus	FR-0249200	MH880195	_	Wang et al. (2021)
X. damansaraensis	I WZ 20180417-23	MT319499	_	Wang et al. (2021)
X daweishanensis	Cl Zhao 18357	0P730715		Guan et al. (2023)
X detriticus	Zíbarová 30 10 17	MH320793		Wang et al. (2021)
X dissiliens	Ryvarden 44817	OK273856		Viner et al. (2021)
X echinatus	OM 18237	00645464		Yurchenko et al. (2024)
X filicinus	MSK-F 12869	MH880109		Wang et al. (2021)
X fissuratus	Cl Zhao 9407	0P730714		Guan et al. (2023)
X flavinorus	FR-02/0707	MH880201		Wang et al. (2023)
X flocoulosus	Cl 7hao 18342	MW080776		Ou and Zhao (2022)
X. noccurosus	ER-02/081/	MH880301		Wang et al. (2021)
X. doeocystidiifer	BLS M-5232	00645467		Yurchenko et al. (2024)
	CI Zhao 8375	MZ663804		Luc et al. (2021a)
X. grandineus	CLZhao 6425	OM338090		Luo et al. (20270)

Species name	Specimen No.	GenBank accession No.		References
		ITS	nLSU	-
X. hastifer	K(M) 172400	NR166558	_	Riebesehl and Langer (2017)
X. heterocystidiatus	Wei 17-314	MT731753	_	Unpublished
X. hjortstamii	Gorjon 3187	ON188816	_	Unpublished
X. hyphodontinus	KAS-GEL9222	MH880205	_	Riebesehl et al. (2019)
X. jacobaeus	MA-Fungi 91340	MH430073	—	Wang et al. (2021)
X. kunmingensis	TUB-FO 42565	MH880198	_	Wang et al. (2021)
X. laceratus	CLZhao 9892	OL619258	_	Qu et al. (2022)
X. lagenicystidiatus	LWZ 20180515-14	MT319633	-	Wang et al. (2021)
X. lagenicystidiatus	LWZ 20180513-16	MT319634	_	Wang et al. (2021)
X. lanatus	CFMR FP-101864-A	0Q645474	_	Yurchenko et al. (2024)
X. laxiusculus	Ryvarden 44877	OK273827	_	Viner et al. (2021)
X. lenis	Wu 890714-3	KY081802	_	Yurchenko et al. (2024)
X. luteodontioides	CLZhao 3207	MH114740	-	Present study
X. luteodontioides	CLZhao 18494	PP505422	-	Present study
X. macrosporus	CLZhao 10226	MZ663809	_	Luo et al. (2021a)
X. magallanesii	MA: Fungi:90397	MT158729		Fernandez-Lopez et al. (2020)
X. mantiqueirensis	MV 529	OQ645478	_	Yurchenko et al. (2024)
X. mollissimus	LWZ 20160318-3	KY007517	_	Kan et al. (2017)
X. montanus	CLZhao 8179	OL619260	_	Qu et al. (2022)
X. neotropicus	MV 580	OQ645479	_	Yurchenko et al. (2024)
X. nesporii	LWZ 20180921-35	MT319655	_	Wang et al. (2021)
X. nesporii	LWZ 20190814-17a	ON063679	_	Wang et al. (2023)
X. niemelaei	LWZ 20150707-13	MT319630	_	Wang et al. (2021)
X. nongravis	GC 1412-22	KX857801	—	Wang et al. (2021)
X. nothofagi	ICMP 13842	AF145583	_	Wang et al. (2021)
X. ovisporus	LWZ 20170815-31	MT319666	—	Wang et al. (2021)
X. papillosus	CBS 114.71	MH860026	—	Vu et al. (2019)
X. paradoxus	Dai 14983	MT319519	—	Wang et al. (2021)
X. patagonicus	ICMP 13832	AF145581	_	Wang et al. (2021)
X. poroides	CLZhao 17845	PP505420	PP657608	Present study
X. pruinosus	Spirin 2877	MH332700	—	Wang et al. (2021)
X. pruniaceus	Ryvarden 11251	OK273828	_	Viner et al. (2021)
X. pseudolanatus	FP-150922	MH880220	_	Wang et al. (2021)
X. pseudotropicus	Dai 10768	KF917543	—	Wang et al. (2021)
X. pseudotropicus	Dai 16167	MT326536	_	Wang et al. (2021)
X. puerensis	CLZhao 8142	OP730720	—	Guan et al. (2023)
X. punctus	CLZhao 17691	OM338092	—	Luo et al. (2022)
X. punctus	CLZhao 17908	OM338093	_	Luo et al. (2022)
X. punctus	CLZhao 17916	OM338094	—	Luo et al. (2022)
X. quercinus	Spirin 12030	OK273841	—	Viner et al. (2021)
X. raduloides	FCUG 2433	AF145570	_	Wang et al. (2021)
X. ramicida	Spirin 7664	NR138013	_	Unpublished
X. reticulatus	Wu 1109-178	KX857805	—	Wang et al. (2021)
X. reticulatus	GC 1512-1	KX857808	_	Wang et al. (2021)
X. rimosissimus	Ryberg 021031	DQ873627	-	Wang et al. (2021)
X. rhizomorphus	Dai 12367	NR154067	—	Zhao et al. (2014)
X. rhododendricola	LWZ 20180513-9	MT319621	_	Wang et al. (2021)
X. serpentiformis	LWZ 20170816-15	MT319673	_	Wang et al. (2021)
X. sinensis	CLZhao 9197	MZ663810	—	Luo et al. (2021a)

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Species name	Specimen No.	GenBank accession No.		References
		ITS	nLSU	
X. sinensis	CLZhao 11120	MZ663811	_	Luo et al. (2021a)
X. spathulatus	LWZ 20180804-10	MT319646	-	Wang et al. (2021)
X. subclavatus	F0 42167	MH880232	-	Wang et al. (2021)
X. subflaviporus	TNM F29958	NR184880	-	Chen et al. (2017)
X. submucronatus	Renvall 1602	OK273830	_	Viner et al. (2021)
X. subserpentiformis	LWZ 20180512-16	MT319486	_	Wang et al. (2021)
X. subtilissimus	Spirin 12228	ON188818	_	Unpublished
X. subtropicus	LWZ 20180510-24	MT319541	_	Wang et al. (2021)
X. taiwanianus	CBS 125875	MH864080	_	Vu et al. (2019)
X. tropicus	CLZhao 3351	OL619261	_	Qu et al. (2022)
X. ussuriensis	KUN 1989	NR166241	_	Unpublished
X. verecundus	KHL 12261	DQ873642	-	Wang et al. (2021)
X. victoriensis	LWZ 20180510-29	MT319487	-	Wang et al. (2021)
X. wenshanensis	CLZhao 15729	OM338097	-	Luo et al. (2022)
X. wumengshanensis	CLZhao 32517	PP645439	PP826351	Present study
X. xinpingensis	CLZhao 9174	MW394657	_	Ma and Zhao (2021)
X. yarraensis	LWZ 20180510-5	MT319639	_	Wang et al. (2021)
X. yunnanensis	LWZ 20180922-47	MT319660	-	Wang et al. (2021)



Figure 2. Maximum Parsimony strict consensus tree illustrating the phylogeny of four new species and related species in *Xylodon* within Schizoporaceae, based on ITS+nLSU sequences. Branches are labelled with Maximum Likelihood boot-strap values \geq 70%, parsimony bootstrap values \geq 50% and Bayesian posterior probabilities \geq 0.95, respectively.



Figure 3. Maximum parsimony strict consensus tree illustrating the phylogeny of the four new species and related species in *Xylodon*, based on ITS sequences. Branches are labelled with Maximum Likelihood bootstrap values \ge 70%, parsimony bootstrap values \ge 50% and Bayesian posterior probabilities \ge 0.95, respectively.

Results

Molecular phylogeny

The ITS+nLSU dataset (Fig. 2) comprised sequences from 36 fungal specimens representing 27 taxa. The dataset had an aligned length of 2130 characters, of which 1312 characters were constant, 301 were variable and parsimony-uninformative and 517 were parsimony-informative. Maximum parsimony analysis yielded three equally parsimonious trees (TL = 2445, CI = 0.5051, HI = 0.4949, RI = 0.6113 and RC = 0.3088). The best model of nucleotide evolution for the ITS+nLSU dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.005704 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 337. The phylogram, based on the ITS+nLSU rDNA gene regions (Fig. 2), included three genera viz. *Fasciodontia, Lyomyces* and *Xylodon*, within the family Schizoporaceae (Hymenochaetales), in which four new species were grouped into the genus *Xylodon*.

The ITS+nLSU dataset (Fig. 3) comprised sequences from 98 fungal specimens representing 88 taxa. The dataset had an aligned length of 748 characters, of which 219 characters were constant, 168 were variable and parsimony-uninformative and 361 were parsimony-informative. Maximum parsimony analysis yielded 100 equally parsimonious trees (TL = 3719, CI = 0.2533, HI = 0.7467, RI = 0.4268 and RC = 0.1081). The best model of nucleotide evolution for the ITS dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.015679 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 3443. The phylogenetic tree (Fig. 3), inferred from the ITS+nLSU sequences, highlighted that X. cremeoparinaceus was grouped closely with X. pruinosus (Bres.) Spirin & Viner, X. detriticus (Bourdot) K.H. Larss., Viner & Spirin and X. ussuriensis Viner. The taxon X. luteodontioides was sister to X. nesporii (Bres.) Hjortstam & Ryvarden. The species X. poroides was sister to X. pseudotropicus (C.L. Zhao, B.K. Cui & Y.C. Dai) Riebesehl, Yurch. & Langer. The species X. wumengshanensis was grouped with four taxa: X. patagonicus J. Fernández-López, Telleria, M. Dueñas & M.P. Martín, X. radula (Fr.) Tura, Zmitr., Wasser & Spirin, X. subtropicus (Che C. Chen & Sheng H. Wu) Che C. Chen & Sheng H. Wu and X. taiwanianus (Sheng H. Wu) Hjortstam & Ryvarden.

Taxonomy

Xylodon cremeoparinaceus Q. Yuan & C.L. Zhao, sp. nov.

MycoBank No: 854061 Figs 4, 5

Holotype. CHINA. Yunnan Province, Zhaotong, Zhaoyang District, Fenghuang Mountain Forest Park, GPS coordinates 27°29'N, 103°68'E, altitude 2872 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 24 August 2022, CLZhao 23388 (SWFC).

Etymology. *cremeoparinaceus* (Lat.): referring to the cream hymenial surface with pruinose hymenophore.



Figure 4. Basidiomata of Xylodon cremeoparinaceus (holotype). Scale bars: 1 cm (A); 2 mm (B).

Description. Basidiomata annual, resupinate, adnate, farinaceous, without odour or taste when fresh, up to 2.5 cm long, 1.5 cm wide, 50–80 um thick. Hymenial surface reticulate, white to cream when fresh, turning to cream upon drying. Sterile margin white, up to 1 mm wide.



Figure 5. Microscopic structures of *Xylodon cremeoparinaceus* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), capitate cystidia (**D**), a section of hymenium (**E**). Scale bars: 20 μm (**A**–**E**).

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thin-walled, frequently branched, interwoven, 1.5–2 μ m in diameter; IKI–, CB–, tissues unchanged in KOH. Numerous crystals present amongst generative hyphae.

Cystidia capitate, colourless, thin-walled, smooth, slightly constricted at the neck, with a globose tip, $18.5-25 \times 3.5-6.5 \mu m$; basidia subclavate, with 4 sterigmata and a basal clamp connection, $13.5-17.5 \times 3-3.5 \mu m$.

Basidiospores ellipsoid, colourless, thin-walled, smooth, with one drop, cyanophilous, IKI-, $3.5-4.5 \times 2.5-3.5 \mu m$, L = $3.71 \mu m$, W = $2.82 \mu m$, Q = 1.31 (n = 30/1).

Xylodon luteodontioides **Q. Yuan & C.L. Zhao, sp. nov.** MycoBank No: 854060

Figs 6, 7

Holotype. CHINA. Yunnan Province, Puer, Laiyanghe National Forestry Park, GPS coordinates 22°60'N, 101°00'E, altitude 1500 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 30 September 2017, CLZhao 3207 (SWFC).



Figure 6. Basidiomata of Xylodon luteodontioides (holotype). Scale bars: 1 cm (A); 2 mm (B).

Etymology. *luteodontioides* (Lat.): referring to the flavescent hymenophore surface with odontioid hymenophore.

Description. Basidiomata annual, resupinate, adnate, coriaceous, without odour and taste when fresh and up to 7 cm long, 4 cm wide, 100 μ m thick. Hymenial surface odontioid, buff when fresh, to buff to olivaceous-buff upon drying. Sterile margin slightly buff and up to 1 mm wide.



Figure 7. Microscopic structures of *Xylodon luteodontioides* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), schizopapillate cystidia (**D**), capitate cystidia (**E**), a section of hymenium (**F**). Scale bars: 20 μ m (**A**–**F**).

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thin-walled, branched, 2.5–3.5 μ m in diameter; IKI–, CB–, tissues unchanged in KOH. Cystidia of two types: (1) schizopapillate cystidia, colourless, thin-walled, smooth, $29.5-37 \times 2.5-3.5 \mu m$; (2) capitate cystidia, colourless, thin-walled, smooth, $38.5-44.5 \times 3.5-4 \mu m$; basidia subclavate, with 4 sterigmata and a basal clamp connection, $19.5-26 \times 3.5-4 \mu m$.

Basidiospores ellipsoid, colourless, thin-walled, smooth, CB–, IKI–, $3.5-4.5 \times 2.5-3.5 \mu$ m, L = 4.07 μ m, W = 2.92 μ m, Q = 1.39–1.45 (n = 60/2).

Additional specimens examined (*paratypes*). CHINA. Yunnan Province, Honghe, Pingbian Country, Daweishan National Nature Reserve, GPS coordinates 22°93'N, 103°69'E, altitude 1800 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 3 August 2019, CLZhao 18494 (SWFC).

Xylodon poroides Q. Yuan & C.L. Zhao, sp. nov.

MycoBank No: 854059 Figs 8, 9

Holotype. CHINA. Yunnan Province, Honghe, Pingbian Country, Daweishan National Nature Reserve, GPS coordinates 22°93'N, 103°69'E, altitude 1800 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 1 August 2019, CLZhao 17845 (SWFC).

Etymology. poroides (Lat.): referring to the poroid hymenophore surface.

Description. Basidiomata annual, resupinate, adnate, coriaceous, without odour and taste when fresh and up to 14 cm long, 4 cm wide, 200 µm thick. Hymenial surface poroid, pores angular, 4–5 per mm, cream to pink-buff when fresh, turn to flesh-pink to pink-buff upon drying. Sterile margin slightly buff and up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thin-walled, frequently branched, $2-3 \mu m$ in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia of two types: (1) fusoid cystidia, colourless, thin-walled, smooth, $17.5-24.5 \times 2.5-3 \mu m$, encrusted crystals; (2) capitate cystidia, colourless, thin-walled, smooth, $11.5-15.5 \times 3.5-4.5 \mu m$; basidia clavate, with 4 sterigmata and a basal clamp connection, $15.5-19 \times 3.5-5.5 \mu m$.

Basidiospores ellipsoid, colourless, thin-walled, smooth, CB-, IKI-, (3.5-)4-5.5 × 2.5-3.5(-5) µm, L = 4.82 µm, W = 2.95 µm, Q = 1.63 (n = 30/1).

Xylodon wumengshanensis Q. Yuan & C.L. Zhao, sp. nov.

MycoBank No: 854058 Figs 10, 11

Holotype. CHINA. Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates 27°77'N, 104°29'E, altitude 2900 m, on the fallen branch of angiosperm, leg. C.L. Zhao, 29 August 2023, CLZhao 32517 (SWFC).

Etymology. *wumengshanensis* (Lat.): referring to the locality (Wumengshan) of the type specimen.

Description. Basidiomata annual, resupinate, adnate, coriaceous, without odour and taste when fresh and up to 4.5 cm long, 1.5 cm wide, $100-200 \mu m$ thick. Hymenial surface grandinoid, cream when fresh; turn to cream to buff upon drying. Sterile margin distinct, cream, up to 1 mm wide.



Figure 8. Basidiomata of Xylodon poroides (holotype). Scale bars: 1 cm (A); 2 mm (B).

Hyphal system monomitic, generative hyphae with clamp connections, colourless, thick-walled, rarely branched, $2-3.5\,\mu m$ in diameter; IKI–, CB–, tissues unchanged in KOH.

Qi Yuan & Changlin Zhao: Four new species of Xylodon





Cystidia of two types: (1) capitate, colourless, thin-walled, smooth, slightly constricted at the neck, with a globose head, $24.5-29.5 \times 5-6 \mu m$; (2) fusoid, colourless, thin-walled, smooth, $14.5-22 \times 5.5-6.5 \mu m$; basidia clavate, with 4 sterigmata and a basal clamp connection, $22.5-33 \times 5-5.5 \mu m$.

Basidiospores ellipsoid, colourless, thin-walled, smooth, with one oil drop, CB-, IKI-, (4.5-) 5-6.5(-7) × 4-5.5 μ m, L = 5.55 μ m, W = 4.39 μ m, Q = 1.26 (n = 30/1).



Figure 10. Basidiomata of *Xylodon wumengshanensis* (holotype). Scale bars: 1 cm (A); 2 mm (B).

Discussion

Many recently-described wood-inhabiting fungal taxa have been reported in the subtropics and tropics, including in the genus *Xylodon* (Xiong et al. 2009; Chen et al. 2017; Kan et al. 2017a, b; Riebesehl and Langer 2017; Viner et al. 2018; Chen and Zhao 2020; Luo et al. 2021a, b, c; Luo et al. 2022; Qu and Zhao 2022; Qu et al. 2022; Viner and Miettinen 2022; Guan et al. 2023; Deng et al. 2024a, b; Zhang et al. 2024). Prior to this study, the following forty-five *Xylodon* species were report-

ed from China. The present study reports four new species in *Xylodon*, based on a combination of morphological features and molecular evidence.

Phylogenetically, based on the multiple loci in Schizoporaceae, three genera Fasciodontia, Lyomyces and Xylodon were located in this family (Wang et al. 2021). In the present study, the phylogram inferred from the ITS+nLSU data, four new species grouped into the genus Xylodon (Fig. 2). Based on ITS topology (Fig. 3), Xylodon cremeoparinaceus grouped closely with three species viz. X. detriticus, X. pruinosus and X. ussuriensis. The taxon X. luteodontioides was sister to X. nesporii. The species X. poroides was sister to X. pseudotropicus. The taxon X. wumengshanensis grouped with four taxa viz. X. patagonicus, X. radula, X. subtropicus and X. taiwanianus. However, morphologically, X. detriticus can be delimited from X. cremeoparinaceus by its smooth or warted, farinaceous hymenial surface and its wider basidia (13.1-20.0 × 3.4-5.0 µm; Viner et al. (2018)); X. pruinosus can be delimited from X. cremeoparinaceus by its grandinioid to odontoid hymenial surface and its larger basidiospores (4.5-5.9 × 3.7-4.8 µm; Viner et al. (2018)); X. ussuriensis can be delimited from X. cremeoparinaceus by its grandinioid to odontoid hymenial surface and its larger basidiospores (5.1–6.0 × 3.8–4.6 µm; Viner et al. (2018)). Xylodon nesporii can be delimited from X. Iuteodontioides by its subcylindrical basidia (15–25 × $4-5 \,\mu\text{m}$) and its longer and narrower basidiospores ($4.5-6 \times 2-2.5 \,\mu\text{m}$; Hjortstam and Ryvarden (2009)); X. pseudotropicus can be delimited from X. poroides by its shorter basidia $(9-12.5 \times 3-5 \mu m)$ and its oblong-ellipsoid basidiospores (4.3-4.9 × 2.8-3 µm; Zhao et al. (2014)); X. patagonicus can be delimited from X. wumengshanensis by its poroid to labyrinthiform hymenial surface and its narrower basidiospores $(4-5.5 \times 2.5-3.5 \mu m;$ Fernández-López et al. (2019)); X. radula can be delimited from X. wumengshanensis by its subclavate to subcylindrical basidia ($20-25 \times 4-6 \mu m$) and its longer and narrower basidiospores $(9-11 \times 3-3.5 \mu m)$; Eriksson and Ryvarden (1975)); X. subtropicus can be delimited from X. wumengshanensis by its poroid hymenial surface and its smaller basidiospores (13-18 × 4-4.5 µm; Chen et al. (2018)); X. taiwanianus can be delimited from X. wumengshanensis by its poroid hymenial surface and its smaller basidia $14-20 \times 4-5 \mu m$; Wu (2001)).

Morphologically, *Xylodon cremeoparinaceus* resembles *X. fissuratus*, *X. flocculosus*, *X. grandineus*, *X. laceratus*, and *X. wenshanensis* K.Y. Luo & C.L. Zhao by ellipsoid basidiospores. However, *X. fissuratus* differs from *X. cremeoparinaceus* due to its grandinioid hymenial surface and its shorter capitate cystidia $(11.5-16.5 \times 3-4.5 \mu m;$ Guan et al. (2023)); *X. flocculosus* differs from *X. cremeoparinaceus* due to its grandinioid hymenial surface and its barrel-shaped basidia $(11-20 \times 3.3-4.8 \mu m;$ Qu and Zhao (2022)); *X. grandineus* differs from *X. cremeoparinaceus* due to its grandinioid hymenial surface and by possessing subulate cystidia $(11-19 \times 3-5 \mu m;$ Luo et al. (2022)); *X. laceratus* differs from *X. cremeoparinaceus* due to its grandinioid hymenial surface and by possessing fusiform cystidia $(20.3-26.8 \times 5.3-6.4 \mu m;$ Qu et al. (2022)); *X. wenshanensis* differs from *X. cremeoparinaceus* due to its grandinioid hymenial surface and by possessing fusiform cystidia $(6-11 \times 3-6.5 \mu m;$ Luo et al. (2022)).

Morphologically, X. luteodontioides resembles X. fissuratus, X. laurentianus J. Fernández-López, Telleria, M. Dueñas & M.P. Martín, X. puerensis C.L. Zhao, X. subflaviporus Che C. Chen & Sheng H. Wu and X. wenshanensis due to the capitate cystidia. However, X. fissuratus differs from X. luteodontioides due to

its shorter capitate cystidia (11.5–16.5 × 3–4.5 µm) and its shorter basidia (10.5–16.5 × 2–4 µm; Guan et al. (2023)); *X. laurentianus* differs from *X. lute-odontioides* due to its poroid to labyrinthiform hymenial surface and its wider basidia (18–26 × 4.5–5.5 µm) and its longer basidiospores (5–6 × 2.5–3.5 µm; Fernández-López et al. (2019)); *X. puerensis* differs from *X. luteodontioides* due to its poroid hymenial surface and its larger basidiospores (6–7 × 4.5–5.5 µm; Guan et al. (2023)); *X. subflaviporus* differs from *X. luteodontioides* due to its poroid hymenial surface and its shorter, wider basidia (8–18 × 4–5 µm; Chen et al. (2018)).

Morphologically, X. poroides resembles X. daweishanensis, X. fissuratus, X. laceratus and X. wenshanensis by the capitate cystidia. However, X. daweishanensis differs from X. poroides due to its odontioid hymenial surface and its shorter basidia (11–15.5 × 2.5–4 μ m; Guan et al. (2023)); X. fissuratus differs from X. poroides due to its grandinioid hymenial surface; X. laceratus differs from X. poroides due to its grandinioid hymenial surface and its longer capitate cystidia (15.4–24.7 × 3.8–4.7 μ m; Qu et al. (2022)); and X. wenshanensis differs from X. poroides due to its grandinioid hymenial surface and its shorter basidia (15.4–24.7 × 3.8–4.7 μ m; Qu et al. (2022)); and X. wenshanensis differs from X. poroides due to its grandinioid hymenial surface and its shorter basidia (8–15.5 × 3–5 μ m; Luo et al. (2022)).

Morphologically, X. wumengshanensis is similar to X. asiaticus, X. laceratus, X. puerensis, X. punctus and X. wenshanensis by having the ellipsoid basidiospores. However, X. asiaticus differs from X. wumengshanensis due to its hydnoid hymenial surface and its narrower basidiospores (4–5.2 × 2.8–3.5 µm; Zhang et al. (2024)); X. laceratus differs from X. wumengshanensis due to its shorter basidia (11–17.5 × 3.2–5.5 µm) and its narrower basidiospores (3.9– $5.3 \times 2.6-4.1 \mu$ m; Qu et al. (2022)); X. puerensis differs from X. wumengshanensis due to its poroid hymenial surface and its shorter basidia (14.5–20 × $5-7 \mu$ m; Guan et al. (2023)); X. punctus differs from X. wumengshanensis due to its smooth hymenial surface and its smaller basidiospores (2–4 × 1.5–2.5 µm; Luo et al. (2022)); and X. wenshanensis differs from X. wumengshanensis due to its smaller basidia (8–15.5 × 3–5 µm) and its smaller basidiospores (3–5 × 2–3.5 µm; Luo et al. (2022)).

Wood-inhabiting fungi, a unique group of Basidiomycota, have been identified through morphological, phylogenetic and cytological studies in China (Wu et al. 2020). Currently, forty-five species of *Xylodon* have been documented in China (Riebesehl and Langer 2017; Viner et al. 2018; Riebesehl et al. 2019; Shi et al. 2019; Luo et al. 2021a; Ji et al. 2022; Guan et al. 2023; Liu et al. 2023; Zhang et al. 2024; Zhao et al. 2024). However, the species diversity of *Xylodon* in China, particularly in the subtropical and tropical regions, remains largely unexplored. This paper contributes to our understanding of fungal diversity in these areas and underscores the urgent need for further fieldwork and molecular analyses to discover new taxa.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization, C.Z.; methodology, C.Z. and Q.Y.; software, C.Z.; validation, C.Z. and Q.Y.; formal analysis, C.Z. and Q.Y.; investigation, C.Z. and Q.Y.; resources, C.Z.; writing—original draft preparation, C.Z. and Q.Y.; writing—review and editing, C.Z. and Q.Y.; visualization, C.Z. and Q.Y.; supervision, C.Z.; project administration, C.Z.; funding acquisition, C.Z. All authors have read and agreed to the published version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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