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Morphology and multigene phylogeny reveal a new order and a new species of wood-inhabiting basidiomycete fungi (Agaricomycetes)

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Dead wood-associated fungi play an important role in wood degradation and the recycling of organic matter in the forest ecological system. Xenasmataceae is a cosmopolitan group of wood-rotting fungi that grows on tropical, subtropical, temperate, and boreal vegetation. In this study, a new fungal order, Xenasmatales, is introduced based on both morphology and multigene phylogeny to accommodate Xenasmataceae. According to the internal transcribed spacer and nuclear large subunit (ITS+nLSU) and nLSU-only analyses of 13 orders, Xenasmatales formed a single lineage and then grouped with orders Atheliales, Boletales, and Hymenochaetales. The ITS dataset revealed that the new taxon *Xenasmatella nigroidea* clustered into *Xenasmatella* and was closely grouped with *Xenasmatella vaga*. In the present study, *Xenasmatella nigroidea* collected from Southern China is proposed as a new taxon, based on a combination of morphology and phylogeny. Additionally, a key to the *Xenasmatella* worldwide is provided.

KEYWORDS

biodiversity, fungal systematics, ITS, LSU, new taxa, wood-decaying fungi, Xenasmatales, *Xenasmatella nigroidea*

Introduction

Among eukaryotic microorganisms, wood-decaying fungi interact positively with dead wood, playing a fundamental ecological role as decomposers of plants in the fungal tree of life (James et al., 2020). Wood-associated fungi are cosmopolitan and rich in diversity since they grow on tropical, subtropical, temperate, and boreal vegetation (Gilbertson and Ryvarden, 1987; Núñez and Ryvarden, 2001; Bernicchia and Gorjón, 2010; Dai, 2012; Ryvarden and Melo, 2014; Dai et al., 2015, 2021; Wu et al., 2020).

Xenasmataceae Oberw., a typical wood-associated fungal group mainly distributed in the tropics was discovered by Oberwinkler (1966), and typified by *Xenasma* Donk. Three genera, namely, *Xenasma*, *Xenasmatella* Oberw., and *Xenosperma* Oberw., have been accommodated in this family, however, higher-level classification of the order has not been designated. The tenth edition of the Dictionary of the Fungi showed that Xenasmataceae belongs to Polyporales Gäum., and consists of three genera (Kirk et al., 2008). MycoBank indicates that Xenasmataceae has a higher classification within Polyporales, although the Index Fungorum shows that Xenasmataceae belongs to the order Russulales.

High phylogenetic diversity among corticioid homobasidiomycetes suggests a close relationship among Radulomyces M.P. Christ., *Xenasmatella,* and *Coronicium* J. Erikss. and Ryvarden. *Xenasma pseudotsugae* (Burt) J. Erikss. nested into the euagarics clade, in which it grouped with *Coronicium* and *Radulomyces*. The three taxa of *Radulomyces* grouped together with *Phlebiella pseudotsugae* (Burt) K.H. Larss. and Hjortstam and *Coronicium alboglaucum* (Bourdot and Galzin) Jülich, and were composed of a rather confusing group with no obvious morphological features or ecological specialization to tie these three genera together (Larsson et al., 2004). The classification of corticioid fungi with 50 putative families from published preliminary analyses and phylogenies of sequence data showed that three species of *Xenasmatella* formed a single lineage with strong support within the unplaced Phlebiella family, in which this clade was unclaimed to any orders (Larsson, 2007). A higher-level phylogenetic classification of the Kingdom Fungi revealed that the Phlebiella clade and Jaapia clade do not show affinities within any orders (Hibbett et al., 2007). An outline of all genera of Basidiomycota with combined SSU, ITS, LSU, tef1, rpb1, and rpb2 datasets showed that *Xenasmatella* was assigned to Xenasmataceae within the order Russulales (He et al., 2019). Therefore, there is debate on the classification at the order level for the Xenasmataceae.

Recently, *Xenasmatella* has been studied deeply on the basis of morphology and phylogeny. *Phlebiella* P. Karst. was deemed to have not been legitimately published previously, and the name *Xenasmatella* was accepted (Duhem, 2010; Larsson et al., 2020; Maekawa, 2021). Molecular systematics involving *Xenasmatella* was carried out recently. On the basis of morphological and molecular identification, Zong et al. (2021) studied the sequences of 27 fungal specimens representing 24 species between the *Xenasmatella* clade and related orders; and the *Xenasmatella* clade formed a single lineage and three new species, namely, *X. rhizomorpha* C.L. Zhao, *X. tenuis* C.L. Zhao, and *X. xinpingensis* C.L. Zhao. Both the MycoBank database (http://www.MycoBank.org) and Index Fungorum (http://www.indexfungorum.org, accessed on June 20, 2022) have recorded 41 specific and infraspecific names in *Xenasmatella*. To date, the number of *Xenasmatella* species accepted worldwide has reached 25 (Oberwinkler, 1966; Stalpers, 1996; Hjortstam and Ryvarden, 2005; Bernicchia and Gorjón, 2010; Duhem, 2010; Larsson et al., 2020; Maekawa, 2021), of which, nine species have been found in China (Dai et al., 2004; Dai, 2011; Huang et al., 2019; Zong and Zhao, 2021; Zong et al., 2021).

In the present study, we verified the taxonomy and phylogeny of Xenasmataceae. In addition, we analyzed the species diversity of Xenasmataceae and constructed a phylogeny to the order level of this family on the basis of large subunit nuclear ribosomal RNA gene (nLSU) sequences, the internal transcribed spacer (ITS) regions, and ITS+nLSU analyses. Based on both morphology and phylogeny, we propose a new fungal order, Xenasmatales and a new species, *Xenasmatella nigroidea*. A key to the 25 accepted species of *Xenasmatella* worldwide is also provided.

The accepted species list

Xenasma Donk (1957).

1. *Xenasma Aculeatum* C.E. Gómez (1972).
2. *Xenasma Amylosporum* Parmasto (1968).
3. *Xenasma Longicystidiatum* Boidin and Gilles (2000).
4. Xenasma Parvisporum Pouzar (1982).
5. *Xenasma Praeteritum* (H.S. Jacks.) Donk (1957).
6. *Xenasma Pruinosum* (Pat.) Donk (1957).
7. *Xenasma Pulverulentum* (H.S. Jacks.) Donk (1957).
8. *Xenasma Rimicola* (P. Karst.) Donk (1957).
9. *Xenasma Subclematidis* S.S. Rattan (1977).
10. *Xenasma Tulasnelloideum* (Höhn. and Litsch.) Donk (1957).
11. Xenasma Vassilievae Parmasto (1965).

Xenasmatella Oberwinkler (1966).

1. *Xenasmatella Ailaoshanensis* C.L. Zhao ex C.L. Zhao and T.K. Zong (2021).
2. *Xenasmatella Alnicola* (Bourdot and Galzin) K.H. Larss. and Ryvarden (2020).
3. *Xenasmatella Ardosiaca* (Bourdot and Galzin) Stalpers (1996).
4. *Xenasmatella Athelioidea* (N. Maek.) N. Maek. (2021).
5. *Xenasmatella Bicornis* (Boidin and Gilles) Piatek (2005).
6. *Xenasmatella Borealis* (K.H. Larss. and Hjortstam) Duhem (2010).
7. *Xenasmatella Caricis-Pendulae* (P. Roberts) Duhem (2010).
8. *Xenasmatella Christiansenii* (Parmasto) Stalpers (1996).
9. *Xenasmatella Cinnamomea* (Burds. and Nakasone) Stalpers (1996).
10. *Xenasmatella Fibrillosa* (Hallenb.) Stalpers (1996).
11. *Xenasmatella Globigera* (Hjortstam and Ryvarden) Duhem (2010).
12. *Xenasmatella Gossypina* (C.L. Zhao) G. Gruhn and Trichies (2021).
13. *Xenasmatella Inopinata* (H.S. Jacks.) Hjortstam and Ryvarden (1979).
14. *Xenasmatella Insperata* (H.S. Jacks.) Jülich (1979).
15. *Xenasmatella Nasti* Boidin and Gilles ex Stalpers (1996).

TABLE 1 The list of species, specimens, and GenBank accession numbers of sequences used in this study.

Species Name	Specimen No.	GenBank Accession No.		References
		ITS	nLSU	
Albatrellus confluens	PV 10193	–	AF506393	Larsson et al., 2004
Aleurobotrys botryosus	CBS 336.66	MH858812	MH870451	Vu et al., 2019
Amaurodon viridis	TAA 149664	AY463374	AY586625	Larsson et al., 2004
Amphinema byssoides	EL 1198	–	AY586626	Larsson et al., 2004
Amylostereum areolatum	NH 8041	–	AF506405	Larsson and Larsson, 2003
Aphanobasidium pseudotsugae	NH 10396	–	AY586696	Larsson et al., 2004
Auriscalpium vulgare	EL 3395	–	AF506375	Larsson and Larsson, 2003
Athelia epiphylla	EL 1298	AY463382	AY586633	Larsson et al., 2004
Athelopsis subinconspicua	KHL 8490	AY463383	AY586634	Larsson et al., 2004
Bondarzewia dickinsii	Li 150909/19	KX263721	KX263723	Unpublished
Candelabrochaete septocystidia	AS 95	–	EU118609	Larsson, 2007
Chaetodermella luna	NH 8482	EU118615	–	Larsson, 2007
C. luna	CBS 305.65	–	MH870216	Vu et al., 2019
Chondrostereum purpureum	EL 5997	–	AY586644	Larsson et al., 2004
Clavulicium delectabile	KHL 11147	–	AY586688	Larsson et al., 2004
Clavulina cristata	EL 9597	AY463398	AY586648	Larsson et al., 2004
Columnocystis abietina	KHL 12474	EU118619	–	Larsson, 2007
Coronicium alboglaucum	NH 4208	–	AY586650	Larsson et al., 2004
Cystostereum murrayi	KHL 12496	EU118623	–	Larsson, 2007
Dacrymyces stillatus	CBS 195.48	MH856306	MH867857	Vu et al., 2019
Dacryopinax spathularia	Miettinen 20559	MW191976	MW159092	Unpublished
Erythricium laetum	NH 14530	AY463407	AY586655	Larsson et al., 2004
Exidia recisa	SL Lindberg 180317	–	MT664783	Unpublished
Exidiopsis calcea	KHL 11075	–	AY586654	Larsson et al., 2004
Gloeocystidiellum porosum	FCUG 1933	–	AF310094	Larsson and Hallenberg, 2001
Haplotrichum conspersum	KHL 11063	AY463409	AY586657	Larsson et al., 2004
Hydnocristella himantia	KUC 20131001-35	–	KJ668382	Unpublished
Hydnomerulius pinastri	412	–	AF352044	Jarosch and Besl, 2001
Hydnum repandum	420526MF0827	–	MG712372	Unpublished
Hygrophoropsis aurantiaca	EL 4299	–	AY586659	Larsson et al., 2004
Hymenochaete cinnamomea	EL 699	AY463416	AY586664	Larsson et al., 2004
Hyphodermella corrugate	KHL 3663	–	EU118630	Larsson, 2007
Hyphodontia aspera	KHL 8530	AY463427	AY586675	Larsson et al., 2004
Inonotus radiatus	TW 704	–	AF311018	Wagner and Fischer, 2001
Junghuhnia nitida	CBS 45950	–	MH868226	Vu et al., 2019
Kavinia alboviridis	EL 1698	–	AY463434	Larsson et al., 2004
Kavinia himantia	LL 98	AY463435	AY586682	Larsson et al., 2004
Lactarius volemus	KHL 8267	–	AF506414	Larsson and Larsson, 2003
Laetisaria fuciformis	CBS 18249	–	MH868023	Vu et al., 2019
Lentaria dendroidea	SJ 98012	EU118640	EU118641	Larsson, 2007
Lignosus hainanensis	Dai 10670	NR154112	GU580886	Cui et al., 2011
Merulicium fusisporum	Hjm s.n.	EU118647	–	Larsson, 2007
Mycoaciella bispora	EL 1399	–	AY586692	Larsson et al., 2004
Peniophora pini	Hjm 18143	–	EU118651	Larsson, 2007

(Continued)

TABLE 1 (Continued)

Species Name	Specimen No.	GenBank Accession No.		References
		ITS	nLSU	
Phanerochaete sordida	KHL 12054	–	EU118653	Larsson, 2007
Phellinus chrysoloma	TN 4008	–	AF311026	Wagner and Fischer, 2001
Phlebia nitidula	Nystroem 020830	–	EU118655	Larsson, 2007
Podoscypha multizonata	CBS 66384	–	MH873501	Vu et al., 2019
Polyporus tubiformis	WD 1839	AB587634	AB368101	Sotome et al., 2011
Porpomyces mucidus	KHL 11062	AF347091	–	Unpublished
P. mucidus	Dai 10726	–	KT157839	Wu et al., 2015
Pseudomerulius aureus	BN 99	–	AY586701	Larsson et al., 2004
Punctularia strigosozonata	LR 40885	AY463456	AY586702	Larsson et al., 2004
Rickenella fibula	AD 86033	–	AY586710	Larsson et al., 2004
Russula violacea	SJ 93009	AF506465	AF506465	Larsson and Larsson, 2003
Scopuloides hydnoides	WEI 17569	–	MZ637283	Chen et al., 2021
Sistotrema alboluteum	TAA 167982	AY463467	AY586713	Larsson et al., 2004
Sistotremastrum niveocremeum	MAFungi 12915	–	JX310442	Telleria et al., 2013
Sistotremastrum suecicum	KHL 11849	–	EU118667	Larsson, 2007
Sphaerobasidium minutum	KHL 11714	–	DQ873653	Larsson et al., 2006
Stereum hirsutum	NH 7960	AF506479	–	Larsson and Larsson, 2003
Tomentellopsis echinospora	KHL 8459	AY463472	AY586718	Larsson et al., 2004
Trametes suaveolens	CBS 279.28	MH855012	MH866480	Vu et al., 2019
Trechispora farinacea	KHL 8793	AF347089	–	Larsson et al., 2004
T. farinacea	MAFungi 79474	–	JX392856	Telleria et al., 2013
Tubulicrinis subulatus	KHL 11079	AY463478	AY586722	Larsson et al., 2004
Veluticeps abietina	HHB 13663	–	KJ141191	Unpublished
Veluticeps berkeleyi	HHB 8594	–	HM536081	Garcia-Sandoval et al., 2010
Vuilleminia comedens	EL 199	AY463482	AY586725	Larsson et al., 2004
Wrightoporia lenta	KN 150311	–	AF506489	Larsson and Larsson, 2003
Xerocomus chrysenteron	EL 3999	AF347103	–	Larsson et al., 2004
Xenasma praeteritum	ACD 0185	OM009268		Unpublished
Xenasma pruinosum	OTU 1299	MT594801		Unpublished
Xenasma rimicola	NLB 1571	MT571671		Unpublished
X. rimicola	NLB 1449	MT537020		Unpublished
Xenasmatella ailaoshanensis	CLZhao 3895	MN487105	–	Huang et al., 2019
X. ailaoshanensis	CLZhao 4839	MN487106	–	Huang et al., 2019
Xenasmatella ardosiaca	CBS 126045	MH864060	MH875515	Vu et al., 2019
Xenasmatella borealis	UC 2022974	KP814210	–	Rosenthal et al., 2017
X. borealis	UC 2023132	KP814274	–	Rosenthal et al., 2017
Xenasmatella christiansenii	TASM YGG 26	MT526341	–	Gafforov et al., 2020
X. christiansenii	TASM YGG 36	MT526342	–	Gafforov et al., 2020
Xenasmatella gossypina	CLZhao 4149	MW545958	–	Zong and Zhao, 2021
X. gossypina	CLZhao 8233	MW545957	–	Zong and Zhao, 2021
Xenasmatella nigroidea	CLZhao 18300	OK045679	OK045677	Present study
X. nigroidea	CLZhao 18333 *	OK045680	OK045678	Present study
Xenasmatella rhizomorpha	CLZhao 9156	MT832954	–	Zong et al., 2021
X. rhizomorpha	CLZhao 9847	MT832953	–	Zong et al., 2021
Xenasmatella tenuis	CLZhao 4528	MT832960	–	Zong et al., 2021

(Continued)

TABLE 1 (Continued)

Species Name	Specimen No.	GenBank Accession No.		References
		ITS	nLSU	
X. tenuis	CLZhao 11258	MT832959	–	Zong et al., 2021
Xenasmatella vaga	KHL 11065	EU118660	EU118661	Larsson, 2007
X. vaga	BHI-F 160a	MF161185	–	Haelewaters et al., 2018
Xenasmatella wuliangshanensis	CLZhao 4080	MW545962	–	Zong and Zhao, 2021
X. wuliangshanensis	CLZhao 4308	MW545963	–	Zong and Zhao, 2021
Xenasmatella xinpingensis	CLZhao 2216	MT832961	–	Zong et al., 2021
X. xinpingensis	CLZhao 2467	MT832962	–	Zong et al., 2021

*Indicates type materials.

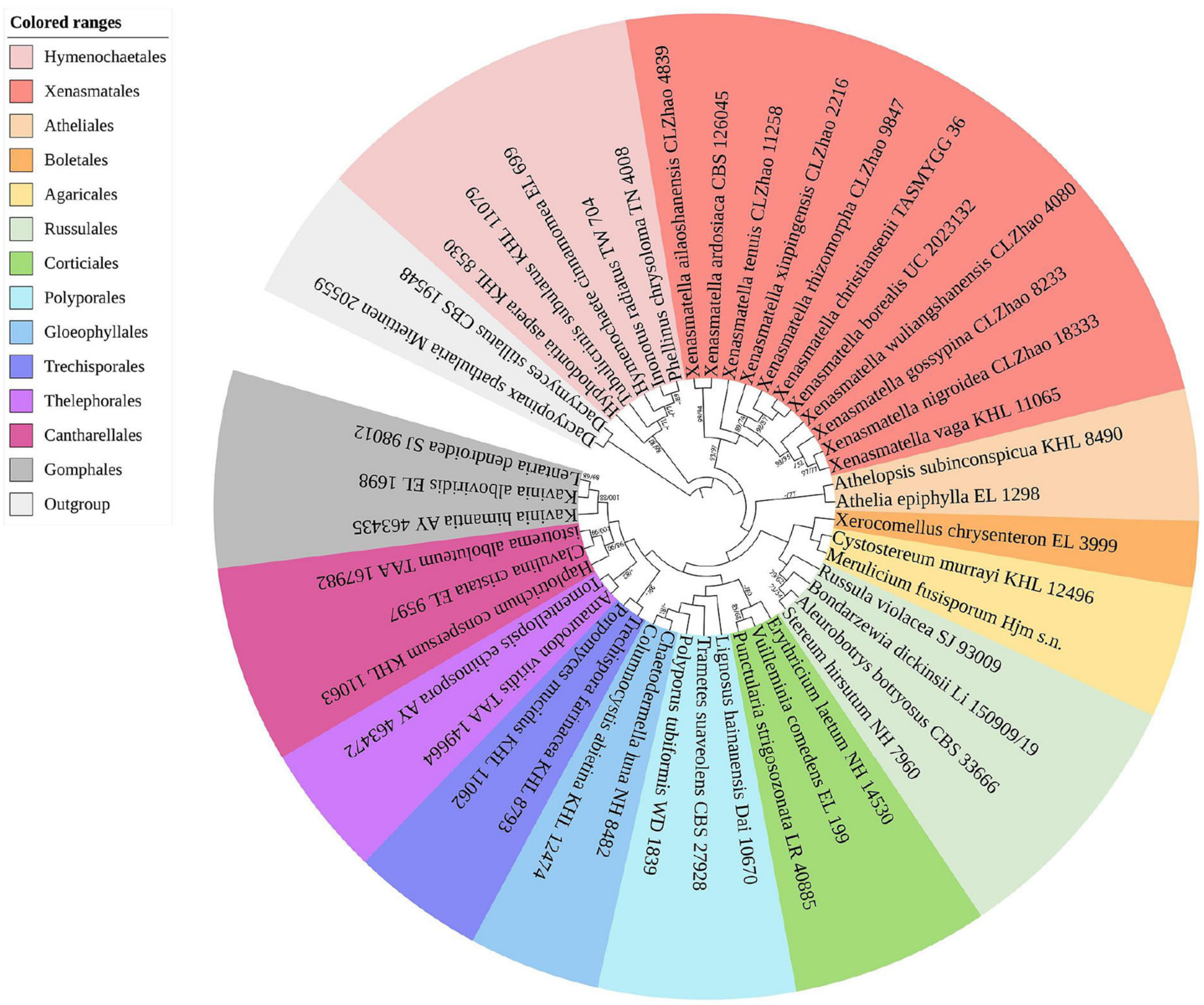

FIGURE 1
A maximum parsimony strict consensus tree illustrating the phylogeny of the new order Xenasmatales and related order in the class Agaricomycetes based on ITS+nLSU sequences. The orders represented by each color are indicated in the upper left of the phylogenetic tree. Branches are labeled with a maximum likelihood bootstrap value ≥ 70%, and a parsimony bootstrap value ≥ 50, respectively.

16. *Xenasmatella Odontioidea* Ryvarden and Liberta (1978).
17. *Xenasmatella Palmicola* (Hjortstam and Ryvarden) Duhem (2010).
18. Xenasmatella Rhizomorpha C.L. Zhao (2021).
19. *Xenasmatella Romellii* Hjortstam (1983).
20. Xenasmatella Sanguinescens Svrček (1973).

21. *Xenasmatella Subflavidogrisea* (Litsch.) Oberw. ex Jülich (1979).
22. *Xenasmatella Tenuis* C.L. Zhao (2021).
23. *Xenasmatella Vaga* (Fr.) Stalpers (1996).
24. *Xenasmatella Wuliangshanensis* (C.L. Zhao) G. Gruhn and Trichies (2021).
25. Xenasmatella Xinpingensis C.L. Zhao (2021).

Xenosperma Oberw. (1966).

1. *Xenosperma Hexagonosporum* Boidin and Gilles (1989).
2. *Xenosperma Ludibundum* (D.P. Rogers and Liberta) Oberw. ex Jülich (1979).
3. *Xenosperma Murrillii* Gilb. and M. Blackw. (1987).
4. *Xenosperma Pravum* Boidin and Gilles (1989).

Materials and methods

Sample collection and herbarium specimen preparation

Fresh fruit bodies of fungi growing on the stumps of angiosperms were collected from Honghe, Yunnan Province, P.R. China. The samples were photographed *in situ*, and macroscopic details were recorded. Field photographs were taken by a Jianeng 80D camera. All photographs were focus stacked and merged using Helicon Focus software. Once the macroscopic details were recorded, the specimens were transported to a field station where they were dried on an electronic food dryer at 45°C. Once dried, the specimens were

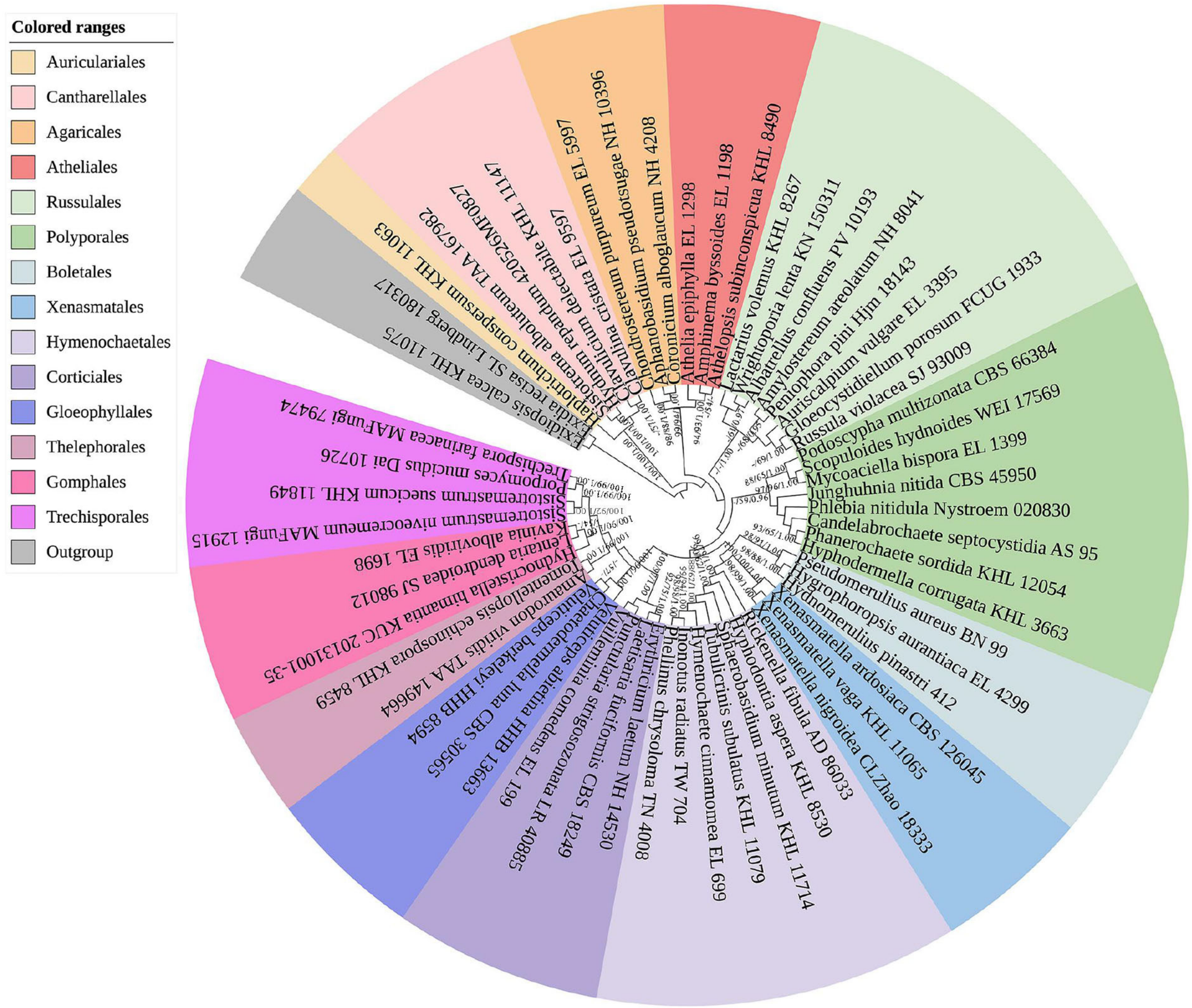

FIGURE 2
A maximum parsimony strict consensus tree illustrating the phylogeny of the new order Xenasmatales and related order in the class Agaricomycetes based on nLSU sequences. The orders represented by each color are indicated in the upper left of the phylogenetic tree. Branches are labeled with a maximum likelihood bootstrap value ≥ 70%, a parsimony bootstrap value ≥ 50%, and Bayesian posterior probabilities ≥ 0.95, respectively.

labeled and sealed in envelopes and plastic bags. The dried specimens were deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China.

Morphology

The macromorphological descriptions were based on field notes and photos captured in the field and laboratory. The color, texture, taste, and odor of fruit bodies were mostly based on the authors' field trip investigations. Rayner (1970) and Petersen (1996) were used for the color terms. All materials were examined under a Nikon 80i microscope. Drawings were made with the aid of a drawing tube. The measurements and drawings were made from slide preparations stained with cotton blue (0.1 mg aniline blue dissolved in 60 g pure lactic acid), melzer's reagent (1.5 g potassium iodide, 0.5 g crystalline iodine, 22 g chloral hydrate, and aq. dest. 20 ml), and 5% potassium hydroxide. Spores were measured from the sections of the tubes; and when presenting spore size data, 5% of the measurements excluded from each end of the range are shown in parentheses (Wu et al., 2022). The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB = cotton clue, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both inamyloid and indextrinoid, L = means spore length (arithmetic average for all spores), W = means 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 CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, P.R. China) was used to obtain genomic DNA from the dried specimens following the manufacturer's instructions (Zhao and Wu, 2017). The nuclear ribosomal ITS region was amplified with the primers ITS5 and ITS4 (White et al., 1990). The nuclear nLSU region was amplified with the primer pairs LR0R and LR7 (http://lutzonilab.org/nuclear-ribosomal-dna/, accessed on September 12, 2021). The PCR procedure used 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 PCR procedure used 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, and a final extension of 72°C for 10 min. The PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company (Yunnan Province, P.R. China). All the newly generated sequences were deposited in the National Center

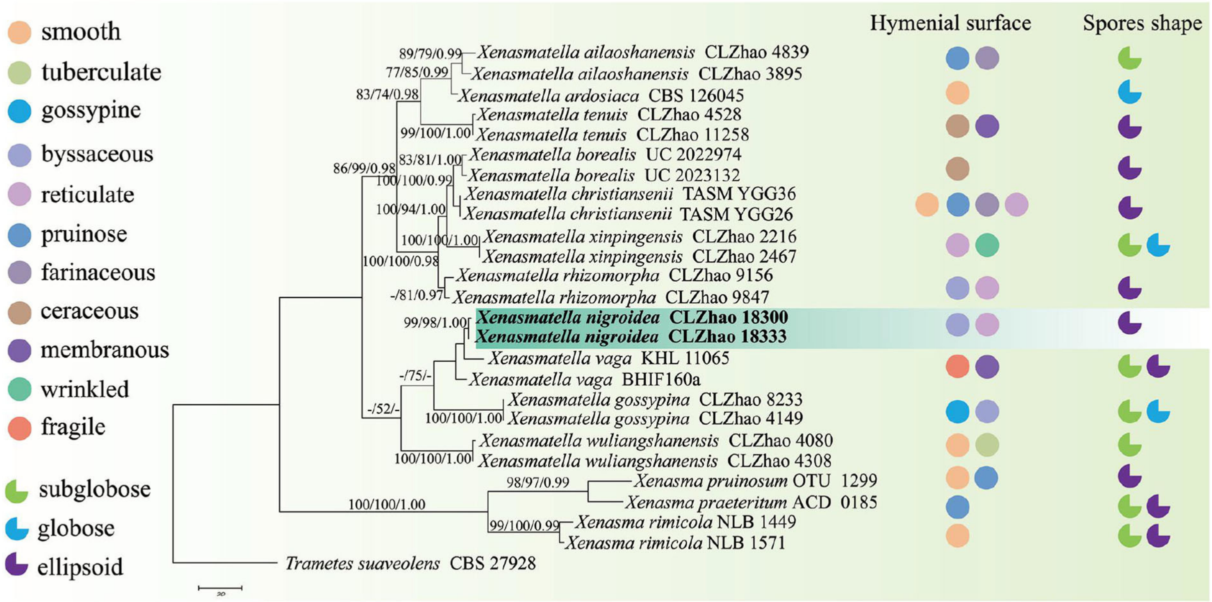

FIGURE 3
A maximum parsimony strict consensus tree illustrating the phylogeny of a new species and related species in *Xenasmatella* and *Xenasma* based on ITS sequences. Branches are labeled with a maximum likelihood bootstrap value $\geq$ 70%, a parsimony bootstrap value $\geq$ 50%, and Bayesian posterior probabilities $\geq$ 0.95, respectively. The new species are in bold.

for Biotechnology Information (NCBI) GenBank (https://www.ncbi.nlm.nih.gov/genbank/, accessed on September 12, 2021) (Table 1).

The sequences and alignment were adjusted manually using AliView version 1.27 (Larsson, 2014). The datasets were aligned with Mesquite version 3.51. The ITS+nLSU dataset and the nLSU-only sequence dataset were used to position a new order, Xenasmatales, and the ITS-only dataset was used to position a new species among the *Xenasmatella*-related taxa. Sequences of *Dacrymyces stillatus* and *Dacryopinax spathularia* retrieved from GenBank were used as the outgroup for the ITS+nLSU sequences (Figure 1) (He et al., 2019); sequences of *Exidia recisa* and *Exidiopsis calcea* retrieved from GenBank were used as the outgroup for the nLSU sequences (Figure 2) (Larsson, 2007); and the sequence of *Trametes suaveolens* was used as the outgroup for the ITS-only sequences (Figure 3) (Zong and Zhao, 2021).

The three combined datasets were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI), according to Zhao and Wu (2017), and the tree was constructed using PAUP* version 4.0b10 (Swofford, 2002). 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 5,000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using the bootstrap (BT) analysis with 1,000 replicates (Felsenstein, 1985). Descriptive tree statistics—tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI)—were calculated for each maximum parsimonious tree generated. In addition, multiple sequence alignment was analyzed using ML in RAxML-HPC2 through the Cipres Science Gateway (Miller et al., 2012). Branch support (BS) for ML analysis was determined by 1,000 bootstrap replicates.

MrModeltest 2.3 (Nylander, 2004) was used to determine the best-fit evolution model for each dataset of 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 4 Markov chains were run for 2 runs from random starting trees for 1 million generations for the ITS+nLSU dataset (Figure 1), 1.4 million generations for the nLSU-only sequences (Figure 2), and 0.5 million generations for the ITS-only sequences (Figure 3), with trees and parameters sampled every 1,000 generations. The first one-fourth of all generations was discarded as a burn-in. The majority rule consensus tree of all remaining trees was calculated. Branches were considered significantly supported if

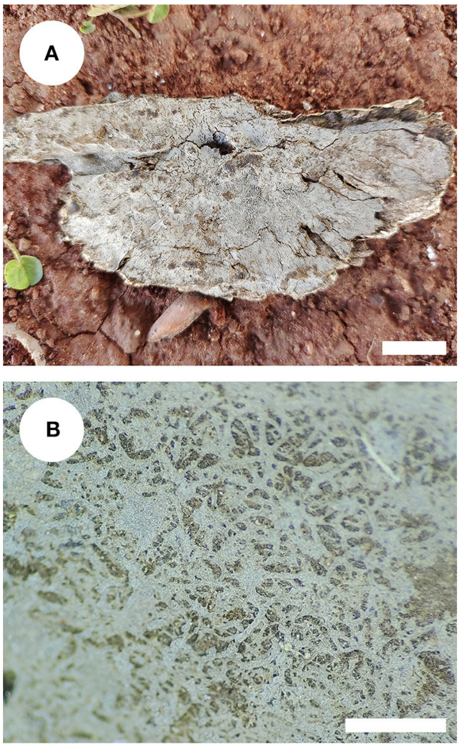

FIGURE 4
Basidiomata of *Xenasmatella nigroidea* (holotype). Bars: **(A)** 1 cm; **(B)** 1 mm.

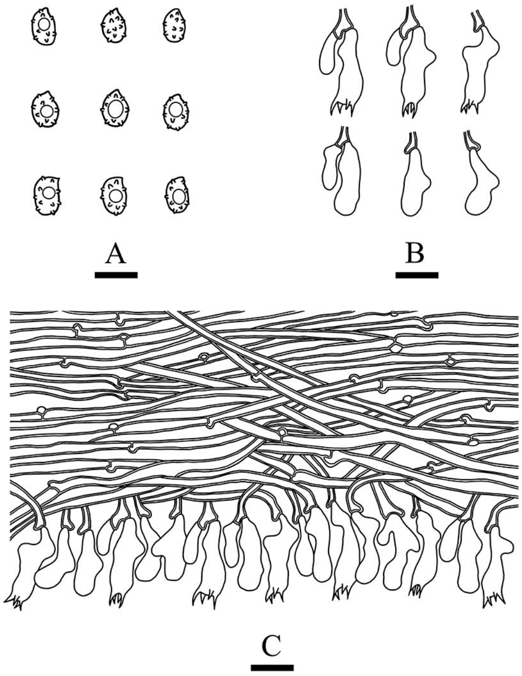

FIGURE 5
Microscopic structures of *Xenasmatella nigroidea* (drawn from the holotype). **(A)** Basidiospores. **(B)** Basidia and basidioles. **(C)** A section of hymenium. Bars: **(A)** 5 µm; **(B,C)** 10 µm.

they received a maximum likelihood bootstrap value (BS) ≥70%, a maximum parsimony bootstrap value (BT) ≥70%, or Bayesian posterior probabilities (BPP) ≥0.95.

Results

Phylogenetic analyses

The ITS+nLSU dataset (Figure 1) included sequences from 45 fungal specimens representing 45 species. The dataset had an aligned length of 3,095 characters, of which 1,910 characters are constant, 353 are variable and parsimony uninformative, and 832 are parsimony informative. Maximum parsimony analysis yielded 45 equally parsimonious trees (TL = 3,984, CI = 0.4666, HI = 0.5334, RI = 0.3909, and RC = 0.1824). The best model was GTR+I+G [lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1)]. Bayesian and ML analyses showed a topology similar to that of MP analysis with split frequencies equal to 0.009126 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 250.5.

The ITS+nLSU rDNA gene regions (Figure 1) were based on 13 orders, namely, Agaricales Underw., Atheliales Jülich, Boletales E.J. Gilbert, Cantharellales Gäum., Corticiales K.H. Larss., Gloeophyllales Thorn, Gomphales Jülich, Hymenochaetales Oberw., Polyporales, Russulales, Thelephorales Corner ex Oberw., Trechisporales, and Xenasmatales, while *Xenasmatella* was separated from the other orders.

The nLSU-alone dataset (Figure 2) included sequences from 58 fungal specimens representing 58 species. The dataset had an aligned length of 1,343 characters, of which 726 characters are constant, 176 are variable and parsimony-uninformative, and 441 are parsimony-informative. Maximum parsimony analysis yielded 3 equally parsimonious trees (TL = 2,864, CI = 0.3209, HI = 0.6791, RI = 0.4476, and RC = 0.1436). The best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR+I+G [lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1)]. The Bayesian and ML analyses

TABLE 2 Morphological characteristics of the relevant orders used in this study.

Order Name	Morphological characteristics	References
Agaricales	Hymenophore type gilled, poroid, ridged, veined, spinose, papillate, and smooth; spore deposit color white, pink, brown, purple-brown and black	Fries, 1821–1832, 1828, 1857–1863, 1874
Atheliales	Generally corticioid and athelioid, producing effused, crust like fruiting bodies that are loosely attached to the substrate and with non-differentiated margins	Eriksson et al., 1978, 1981, 1984
Boletales	Includes conspicuous stipitate-pileate forms that mainly have tubular and sometimes lamellate hymenophores or intermediates that show transitions between the two types of hymenophores. Also includes gasteromycetes (puffball-like forms), resupinate or crust-like fungi that produce smooth, merulioid (wrinkled to warted), or hydnoid (toothed) hymenophores, and a single polypore-like species, *Bondarcevomyces taxi*	Gilbert, 1931; Besl and Bresinsky, 1997; Jarosch, 2001; Larsson et al., 2004
Corticiales	Basidiomata resupinata, effuso-reflexa vel discoidea; hymenophora laevia; systema hypharum monomiticum; dendrohyphidia raro absentia; basidia saepe e probasidiis oriuntur. Cystidia presentia vel absentia. Sporae hyalinae, tenuitunicatae, albae vel aggregatae roseae.	Hibbett et al., 2007
Gloeophyllales	Basidiomata annua vel perennia, resupinata, effuso-reflexa, dimidiata vel pileata; hymenophora laevia, merulioidea, odontioidea vel poroidea. Systema hypharum monomiticum, dimiticum vel trimiticum. Hyphae generativae fibulatae vel efibulatae. Leptocystidia ex trama in hymenium projecta, hyalina vel brunnea, tenuitunicata vel crassitunicata. Basidiosporae laeves, hyalinae, tenuitunicatae, ellipsoideae vel cylindricae vel allantoideae, inamyloideae. Lignum decompositum brunneum vel album.	Hibbett et al., 2007
Gomphales	Basidiomata can be coralloid, unipileate or merismatoid (having a pileus divided into many smaller pilei); the pileus, if present, can be fan- to funnel-shaped	Gonzalez-Avila et al., 2017
Hymenochaetales	Hymenial structure (corticioid, hydnoid or poroid) and basidiocarps (resupinate, pileate or stipitate); the main characters are the xanthochroic reaction, the lack of clamps, the frequent occurrence of setae	Tobias and Michael, 2002
Thelephorales	Basidiospores tuberosae spinosaeque plus minusve coloratae	Oberwinkler, 1975
Trechisporales	Basidiomata resupinata, stipitata vel clavarioidea. Hymenophora laevia, grandinioidea, hydnoidea vel poroidea. Systema hypharum monomiticum vel dimiticum. Hyphae fibulatae, septa hypharum interdum inflata (ampullata). Cystidia praesentia vel absentia. Basidia 4-6 sterigmata formantia. Sporae laeves vel ornatae. Species lignicolae vel terricolae.	Hibbett et al., 2007
Xenasmatales	Basidiomata resupinate. Hyphal system monomitic, generative hyphae with clamp connections. Basidia pleural. Basidiospores colorless.	Present study

resulted in a topology similar to that of MP analysis with split frequencies equal to 0.009830 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 402.

The nLSU regions (Figure 2) were based on 13 orders, namely, Agaricales, Atheliales, Boletales, Cantharellales, Corticiales, Gloeophyllales, Gomphales, Hymenochaetales, Polyporales, Russulales, Thelephorales, Trechisporales, and Xenasmatales, while *Xenasmatella* was separated from the other orders.

The ITS-alone dataset (Figure 3) included sequences from 26 fungal specimens representing 15 species belonging to *Xenasma* and *Xenasmatella*. The dataset had an aligned length of 598 characters, of which 267 characters are constant, 74 are variable and parsimony-uninformative, and 257 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious tree (TL = 629, CI = 0.7329, HI = 0.2671, RI = 0.8301, and RC = 0.6084). The best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR+I+G [lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1)]. The Bayesian and ML analyses resulted in a topology similar to MP analysis with split frequencies equal to 0.007632 (BI), and the effective sample size (ESS) across the two runs is double that of the average ESS (avg ESS) = 300.5.

In the ITS sequence analysis (Figure 3), a previously undescribed species was grouped into *Xenasmatella* with a sister group to *X. vaga* (Fr.) Stalpers.

Taxonomy

Xenasmatales K.Y. Luo and C.L. Zhao, **ord. nov.**
MycoBank no.: MB 842882
Type family: Xenasmataceae Oberw.

Basidiomata resupinate. Hyphal systems are monomitic, generative hyphae with clamp connections. Basidia pleural. Basidiospores are colorless.

Xenasmataceae Oberw., Sydowia 19(1–6): 25 (1966).
MycoBank no.: MB 81527
Type genus: *Xenasma* Donk

Basidiomata resupinate, ceraceous to geletinous. Hyphal systems are monomitic, generative hyphae with clamp connections. Basidia pleural usually with 4 sterigmata and a basal clamp connection. Basidiospores are colorless.

TABLE 3 Morphological characteristic comparison of *Xenasmatella nigroidea* and other species.

Species name	Basidiomata	Hymenial surface	Basidia	Basidiospores	References
Xenasmatella nigroidea	Thin, very hard to separate from substrate	Smooth, byssaceous to reticulate under the lens	12–18 × 4.5–6 µm	Ellipsoid, 3.5–4.5 × 2.5–3.5 µm; asperulate with blunt spines up to 0.2 µm long	Present study
X. christiansenii	Fragile	Smooth, pruinose to farinaceous or more or less reticulate	6–7 × 4–4.5 µm	Ellipsoid, 6–7 × 4–4.5 µm; asperulate with blunt spines up to 1 µm long	Bernicchia and Gorjón, 2010
X. fibrillosa	Thin, fragile	Porulose to reticulate or formed by radially arranged, white to pale yellowish white	12–15 × 4–5 µm	Ellipsoid, 4.5–5.5 × 3–3.5 µm	Bernicchia and Gorjón, 2010
X. gaspesica	Small spots and becoming a closed coating, firmly attached	Resh smooth and somewhat gelatinous, light gray, dry waxy, white gray	7–11 × 4–4.5 µm	Ellipsoid, 8–10 × 2–2.5 µm	Grosse-Brauckmann and Kummer, 2004
X. gossypina	Cotton to flocculent	Cream to buff	14–23.5 × 4–7 µm	Subglobose to globose, 3.3–4.4 × 2.8–4 µm	Zong and Zhao, 2021
X. odontioidea	Colliculosa	Ceraceo-membranacea	17.5–20 × 4.5–5 µm	Ovale-ellipsoid, 2.5–3.5 µm	Ryvarden and Liberta, 1978
X. rhizomorpha	Presence of the rhizomorph	Clay-buff to cinnamon	10.5–17.5 × 3.5–6.5 µm	Ellipsoid, 3.1–4.9 × 2.3–3.3 µm	Zong et al., 2021
X. subflavidogrisea	Thin	White to grayish	10–12 × 4–5 µm	Ellipsoid, 3.5–4.5 × 2–2.5 µm	Bernicchia and Gorjón, 2010
X. vaga	Detachable	Grandinioid	15–20 × 5–6 µm	Ellipsoid, 5–5.5 × 4–4.5 µm	Bernicchia and Gorjón, 2010

Xenasma Donk, Fungus, Wageningen 27: 25 (1957).
MycoBank no.: MB 18755
Type species: *Xenasma rimicola* (P. Karst.) Donk.

Basidiomata resupinate, adnate, are ceraceous to gelatinous when fresh, membranaceous when dry, and have a hymenophore smooth. Hyphal system are monomitic, generative hyphae with clamp connections. Cystidia and cystidioles are present. Basidia are cylindrical to subclavate, pleural, usually with 4 sterigmata and a basal clamp connection. Basidiospores are globose to cylindrical, colorless, thin-walled, warted to striate, non-amyloid, and weakly dextrinoid.

Xenosperma Oberw., Sydowia 19(1–6): 45 (1966).
MycoBank no.: MB 18759
Type species: *Xenosperma ludibundum* (D.P. Rogers and Liberta) Oberw.

Basidiomata resupinate, closely adnate to the substratum, are gelatinous when fresh and pruinose when dry. Hyphal

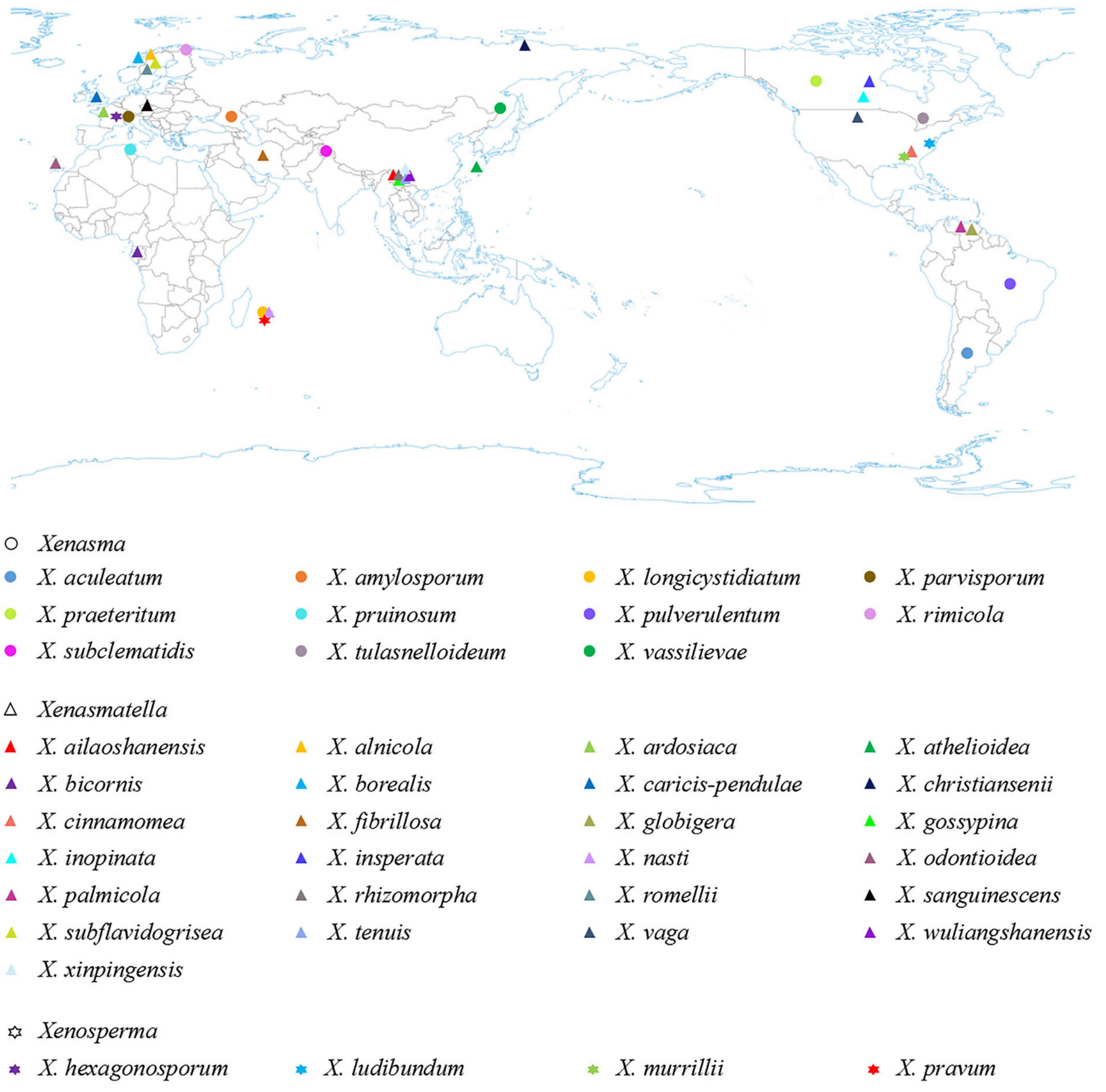

FIGURE 6
The geographic distribution of Xenasmataceae species (holotype) worldwide.

systems are monomitic, generative hyphae with clamp connections. Cystidia are absent. Basidia pleural, usually with 2–4 sterigmata and a basal clamp connection. Basidiospores are angular, colorless, thin-walled, tetrahedral, with some protuberances, IKI–, and CB–.

Xenasmatella Oberw., Sydowia 19(1–6): 28 (1966).
MycoBank no.: MB 18756
Type species: *Xenasmatella subflavidogrisea* (Litsch.) Oberw. ex Jülich.

TABLE 4 The geographic distribution and host-substratum of Xenasmataceae species (holotype).

Species name	Geographic distribution	Host-substratum	References
Xenasma aculeatum	Argentina	On fructifications of *Hypoxylon*	Gómez, 1972
X. amylosporum	Primorye	On rotten trunk of *Picea jezoensis*	Parmasto, 1968
X. longicystidiatum	Réunion	On *Rubus alcaefolius*	Boidin and Gilles, 2000
X. parvisporum	Czech Republic	On fallen branch of *Quercus petraea*	Pouzar, 1982
X. praeteritum	Ontario	On wood	Donk, 1957
X. pruinosum	Tunisia	On oak tree, bared and rotten	Donk, 1957
X. pulverulentum	Austria	On rotten wood	Donk, 1957
X. rimicola	Finland	On cracks in bark	Donk, 1957
X. subclematidis	Jammu-Kashmir	On log	Rattan, 1977
X. tulasnelloideum	America	On very rotten wood	Höhnel and Litschauer, 1908
X. vassilievae	Khabarovsk	On fallen trunk of *Taxus cuspidata*	Parmasto, 1965
Xenasmatella ailaoshanensis	Yunnan	On trunk of *Angiospermae*	Huang et al., 2019
X. alnicola	Allier	Sur bois humides, aune, saule blane	Bourdot and Galzin, 1928
X. ardosiaca	France	On decayed wood	Bourdot and Galzin, 1928
X. athelioidea	Japan	On rotten trunk of *Quercus*	Maekawa, 2021
X. bicornis	Gabon	Among shrubs on shore	Boidin and Gilles, 2004
X. borealis	Norway	On rotten *Pinus sylvestris*	Hjortstam and Larsson, 1987
X. caricis-pendulae	Great Britain	On dead attached leaf of *Carex pendula*	Roberts, 2007
X. christiansenii	Kamchatka	On fallen branch of *Larix kurilensis* var. *glabra*	Parmasto, 1965
X. cinnamomea	Florida	On *Magnolia*	Burdsall and Nakasone, 1981
X. fibrillosa	Iran	On decayed wood	Hallenberg, 1978
X. globigera	Venezuela	On hardwood	Hjortstam and Ryvarden, 2005
X. gossypina	Yunnan	On trunk of *Angiospermae*	Zong and Zhao, 2021
X. inopinata	Ontario	On *Tsuga canadensis*	Jackson, 1950
X. insperata	Ontario	On bark	Jackson, 1950
X. nasti	Reunion	Under Nastus borbonicus	Stalpers, 1996
X. odontioidea	Canary	On decayed wood	Ryvarden and Liberta, 1978
X. palmicola	Venezuela	On palm	Hjortstam and Ryvarden, 2007
X. rhizomorpha	Yunnan	On trunk of *Angiospermae*	Zong et al., 2021
X. romellii	Sweden	On deciduous wood	Hjortstam, 1983
X. sanguinescens	Czech Republic	On decayed wood	Svrcek, 1973
X. subflavidogrisea	Sweden	On rotten wood of *Pinus sylvestris*	Jülich, 1979
X. tenuis	Yunnan	On trunk of *Angiospermae*	Zong et al., 2021
X. vaga	Italy	On *Robinia pseudoacacia*	Stalpers, 1996
X. wuliangshanensis	Yunnan	On trunk of *Angiospermae*	Zong and Zhao, 2021
X. xinpingensis	Yunnan	On trunk of *Angiospermae*	Zong et al., 2021
Xenosperma hexagonosporum	France	On wood of *Platanus acerifolia*	Boidin and Gilles, 1989
X. ludibundum	Massachusetts	On bark of *Quercus* and decayed wood of *Chamaecyparis thyoides*	Jülich, 1979
X. murrillii	Florida	On branch of *Juniperus virginiana*	Gilbertson and Blackwell, 1987
X. pravum	Réunion	On dead branch	Boidin and Gilles, 1989

Basidiomata resupinate with a gelatinous. Hyphal system with clamped generative hyphae. Cystidia are absent. Basidia pleural, usually with 4 sterigmata and a basal clamp connection. Basidiospores are hyaline, thin-walled, warted, IKI–, and CB–.

Xenasmatella nigroidea K.Y. Luo and C.L. Zhao, **sp. nov.**
MycoBank no.: MB 842470, Figures 4, 5.

Holotype—China. Yunnan Province, Honghe, Pingbian County, Daweishan National Nature Reserve, GPS coordinates 23°42′ N, 103°32′ E, altitude 1,500 m asl., on angiosperm stump, leg. C.L. Zhao, August 3, 2019, CLZhao 18333 (SWFC).

Etymology—*nigroidea* (Lat.): refers to the black hymenial surface.

Basidiomata: Basidiomata are annuals, resupinate, thin, very hard to separate from substrate, odorless or tasteless when fresh, grayish when fresh, gray to black and brittle when dry, up to 7.5 cm long, 3.5 cm wide, 70–150 µm thick. Hymenial is surface smooth, and byssaceous to reticulate under the lens. Sterile margin indistinct, black, up to 1 mm wide.

Hyphal system: monomitic, generative hyphae with clamp connections, thick-walled, unbranched, 2.5–4 µm in diameter, IKI–, CB–, and tissues unchanged in KOH.

Hymenium: cystidia and cystidioles are absent; basidia are pleural, clavate, with 4 sterigmata and a basal clamp connection, 12.0–18.0 × 4.5–6 µm; basidioles are shaped similar to basidia but slightly smaller.

Basidiospores: ellipsoid, colorless, thin-walled, warted throughout, asperulate with blunt spines up to 0.2 µm long, with one oil drop inside, IKI–, CB–, 3.5–4.5 × 2.5–3.5 µm, L = 4.07 µm, W = 2.87 µm, Q = 1.38–1.45 (*n* = 60/2).

Type of rot: White rot.

Additional specimen examined: CHINA, Yunnan Province, Honghe, Pingbian County, Daweishan National Nature Reserve, GPS coordinates 23°40′ N, 103°31′ E, altitude 1,500 m asl., on the angiosperm stump, leg. C.L. Zhao, August 3, 2019, CLZhao 18300 (SWFC).

Discussion

There have been debates among mycologists regarding the order level taxonomic status of the Xenasmataceae. Corticioid homobasidiomycetes have a high phylogenetic diversity. Thus, an accurate place for the taxa of Xenasmataceae has not been decided. However, it was only assigned to euagarics clade (Larsson et al., 2004). Later, the Phlebiella family was proposed by Larsson (2007) on the basis of corticioid fungi; however, this group was not placed under any order. Recently, Xenasmataceae was placed under Russulales by He et al. (2019). Zong et al. (2021) studied the specimens and sequences from China and treated this group as *Xenasmatella* as the phylogenetic datasets showed that this clade does not belong

TABLE 5 Key to 25 accepted species of *Xenasmatella* worldwide.

1. Gloeocystidia present	*X. inopinata*
1. Cystidia absent	2
2. Basidia with 2, 3 sterigmata	*X. bicornis*
2. Basidia with 4 sterigmata	3
3. Basidia sterigmata > 5 µm in length	*X. nasti*
3. Basidia sterigmata < 5 µm in length	4
4. Basidiospores > 5 µm in length	5
4. Basidiospores < 5 µm in length	12
5. Basidiospores > 4 µm in width	6
5. Basidiospores < 4 µm in width	9
6. Basidiospores globose	*X. ardosiaca*
6. Basidiospores ellipsoid	7
7. Basidia < 6 µm in width	*X. vaga*
7. Basidia > 6 µm in width	8
8. Growth on dead angiosperm	*X. caricis-pendulae*
8. Growth on the trunk of gymnosperm	*X. christiansenii*
9. Basidiospores < 2 µm in width	*X. athelioidea*
9. Basidiospores > 2 µm in width	10
10. Hymenial margin with fimbriae	*X. romellii*
10. Hymenial margin without fimbriae	11
11. Hymenial surface arachnoid or byssoid	*X. borealis*
11. Hymenial surface smooth	*X. insperata*
12. Basidiospores subglobose to globose	13
12. Basidiospores ellipsoid to subcylindrical	17
13. Basidiospores thick-walled	*X. globigera*
13. Basidiospores thin-walled	14
14. Hymenial surface clay-pink to saffron	*X. wuliangshanensis*
14. Hymenial surface white to grayish or cream to buff	15
15. Generative hyphae thick-walled, unbranched	*X. xinpingensis*
15. Generative hyphae thin-walled, branched	16
16. Hymenial surface gossypine to byssaceous	*X. gossypina*
16. Hymenial surface pruinose to farinaceous	*X. ailaoshanensis*
17. Generative hyphae thick-walled	18
17. Generative hyphae thin-walled	19
18. Hymenial surface gray to black	*X. nigroidea*
18. Hymenial surface clay-buff to cinnamon	*X. rhizomorpha*
19. Growth on palm	*X. palmicola*
19. Growth on other plant	20
20. Growth on the bark of magnolia	*X. cinnamomea*
20. Growth on other wood	21
21. Basidiospores slightly thick-walled	*X. alnicola*
21. Basidiospores thin-walled	22
22. Basidia barrel-shaped	*X. tenuis*
22. Basidia cylindrical	23
23. Basidiomata ochreous	*X. odontioidea*
23. Basidiomata white to gray	24
24. Basidiospores > 3 µm in width	*X. fibrillosa*
24. Basidiospores < 3 µm in width	*X. subflavidogrisea*

to any order. In the present study (Figure 1), the ITS+nLSU analyses of 13 orders, namely, Agaricales, Atheliales, Boletales, Cantharellales, Corticiales, Gloeophyllales, Gomphales, Hymenochaetales, Polyporales, Russulales, Thelephorales, Trechisporales, and Xenasmatales showed that the taxa of Xenasmataceae form a single lineage with the sequences of Hymenochaetales and Atheliales; and this is similar to the results of Larsson (2007). In the present study (Figure 2), the nLSU analysis showed that the taxa of Xenasmataceae form a single lineage with the sequences of Hymenochaetales and Boletales; and this is similar to the results of Larsson (2007). In the present study (Table 2), we have enumerated morphological differences among the related orders. Therefore, a new fungal order, Xenasmatales, is proposed on the basis of morphological and molecular identification.

Phlebiella was not deemed to be a legitimately published genus (Duhem, 2010), and transferring to *Xenasmatella* was proposed. Later, Larsson et al. (2020) studied corticioid fungi (Basidiomycota and Agaricomycetes) and agreed with Duhem (2010), who suggested accepting the genus *Xenasmatella*. Recently, several mycologists have suggested the replacement of the invalid genus *Phlebiella* with *Xenasmatella* on the basis of morphology and molecular analyses (Maekawa, 2021; Zong et al., 2021).

On the basis of ITS dataset, a previous study showed that nine species of *Xenasmatella* have been reported, of which 6 new species were found in China, namely, *X. ailaoshanensis* C.L. Zhao ex C.L. Zhao and T.K. Zong, *X. gossypina*, *X. rhizomorpha*, *X. tenuis*, *X. wuliangshanensis*, and *X. xinpingensis*. According to our sequence data, *Xenasmatella nigroidea* was nested into *Xenasmatella* with strong statistical support (Figure 3), and formed a sister group with *X. vaga*. However, *X. nigroidea* is morphologically distinguished from *X. vaga* by larger basidiospores (5–5.5 × 4–4.5 µm). In addition, it turns dark red or purplish with KOH (Bernicchia and Gorjón, 2010).

Morphological comparisons of *Xenasmatella nigroidea* and other species are included in Table 3. *Xenasmatella nigroidea* is similar to *X. christiansenii* (Parmasto) Stalpers, *X. fibrillosa* (Hallenb.) Stalpers, *X. gossypina*, and *X. rhizomorpha* C.L. Zhao by having gossypine, byssaceous to reticulate hymenial surface, however, *X. christiansenii* is distinguished from *X. nigroidea* by its larger basidiospores (6–7 × 4–4.5 µm) and asperulate with blunt spines (up to 1 µm long; Bernicchia and Gorjón, 2010). *Xenasmatella fibrillosa* differs from *X. nigroidea* due to the presence of a white to pale yellowish white hymenial surface and longer basidiospores (4.5–5.5 µm; Bernicchia and Gorjón, 2010). *Xenasmatella gossypina* can be distinguished from *X. nigroidea* because it has cotton to flocculent basidiomata with a cream to buff hymenial surface and subglobose to globose basidiospores (Zong and Zhao, 2021). *Xenasmatella rhizomorpha* is separated from *X. nigroidea* by the clay-buff to cinnamon hymenial surface and the presence of the rhizomorphs (Zong et al., 2021).

Xenasmatella nigroidea is similar to *X. gaspesica* (Liberta) Hjortstam, *X. odontioidea* Ryvarden & Liberta, *X. subflavidogrisea* (Litsch.) Oberw. ex Jülich, and *X. vaga* (Fr.) Stalpers due to the presence of the ellipsoid or narrowly ellipsoid basidiospores. However, *X. gaspesica* differs from *X. nigroidea* because it has smaller basidia (7–11 × 4–4.5 µm) and larger basidiospores (8–10 × 2–2.5 µm; Grosse-Brauckmann and Kummer, 2004). *Xenasmatella odontioidea* can be distinguished from *X. nigroidea* by its colliculosa hymenial surface and shorter basidiospores (2.5–3.5 µm; Ryvarden and Liberta, 1978). *Xenasmatella subflavidogrisea* is separated from *X. nigroidea* due to the presence of a white to grayish hymenial surface, turning dark reddish brown in KOH and narrower basidiospores (2–2.5 µm; Bernicchia and Gorjón, 2010). *Xenasmatella vaga* differs from *X. nigroidea* due to its grandinioid hymenial surface and larger basidiospores (5–5.5 × 4–4.5 µm; Bernicchia and Gorjón, 2010).

Based on the geographical distribution in America, Asia, and Europe, and ecological habits, white-rot causing Xenasmataceae have been reported in angiosperms and gymnosperms (Figure 6 and Table 4) (Stalpers, 1996; Dai et al., 2004; Hjortstam and Ryvarden, 2005; Bernicchia and Gorjón, 2010; Duhem, 2010; Dai, 2011; Huang et al., 2019; Larsson et al., 2020; Maekawa, 2021; Zong and Zhao, 2021; Zong et al., 2021). Key to 25 accepted species of *Xenasmatella* worldwide in Table 5. Many wood-decaying fungi have been recently reported worldwide (Zhu et al., 2019; Angelini et al., 2020; Gafforov et al., 2020; Zhao and Zhao, 2021). According to the results of our study on *Xenasmatella*, all these fungi can be classified into a new taxon (Figure 3). In addition, this study contributes to the knowledge of the fungal diversity in Asia.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Author contributions

C-LZ: conceptualization, resources, supervision, project administration, and funding acquisition. C-LZ and K-YL: methodology, software, validation, formal analysis, investigation, writing—original draft preparation, writing—review and editing, and visualization. Both authors have read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Angelini, C., Vizzini, A., Justo, A., Bizzi, A., and Kaya, E. (2020). First report of a neotropical agaric (lepiota spiculata, agaricales, basidiomycota) containing lethal α-amanitin at toxicologically relevant levels. *Front. Microbiol.* 11, 1833. doi: 10.3389/fmicb.2020.01833

Bernicchia, A., and Gorjón, S. P. (2010). *Fungi Europaei 12: Corticiaceae s.l.* Alassio: Edizioni Candusso.

Besl, H., and Bresinsky, A. (1997). Chemosystematics of suillaceae and gomphidiaceae (suborder Suillineae). *Plant Syst. Evol.* 206, 223–242. doi: 10.1007/BF00987949

Boidin, J., and Gilles, G. (1989). Les Corticiés pleurobasidiés (Basidiomycotina) en France. *Cryptogamic Bot.* 1, 70–79.

Boidin, J., and Gilles, G. (2000). Basidiomycètes Aphyllophorales de l'ile de La Reunion. XXI - Suite. *Mycotaxon* 75, 357–387.

Boidin, J., and Gilles, G. (2004). Homobasidiomycètes Aphyllophorales non porés à basides dominantes à 2 (3) stérigmates. *Bull. Trimest. Soc. Mycol. Fr.* 119, 1–17.

Bourdot, H., and Galzin, A. (1928). *Hyménomycètes de France : Hétérobasidiés. Homobasidiés gymnocarpes / par MM. l'abbé H. Bourdot et A. Galzin.* Paris: Bibliothèque nationale de France, département Sciences et techniques, 786.

Burdsall, H. H., and Nakasone, K. K. (1981). New or little known lignicolous aphyllophorales (Basidiomycotina) from southeastern United States. *Mycologia* 73, 454–476. doi: 10.1080/00275514.1981.12021368

Chen, C. C., Chen, C. Y., and Wu, S. H. (2021). Species diversity, taxonomy and multi-gene phylogeny of phlebioid clade (Phanerochaetaceae, Irpicaceae, Meruliaceae) of polyporales. *Fungal Divers.* 111, 1–106. doi: 10.1007/s13225-021-00490-w

Cui, B. K., Du, P., and Dai, Y. C. (2011). Three new species of *Inonotus* (Basidiomycota, Hymenochaetaceae) from China. *Mycol. Prog.* 10, 107–114. doi: 10.1007/s11557-010-0681-6

Dai, Y. C. (2011). A revised checklist of corticioid and hydnoid fungi in China for 2010. *Mycoscience* 52, 69–79. doi: 10.1007/S10267-010-0068-1

Dai, Y. C. (2012). Polypore diversity in China with an annotated checklist of Chinese polypores. *Mycoscience* 53, 49–80. doi: 10.1007/s10267-011-0134-3

Dai, Y. C., Cui, B. K., Si, J., He, S. H., Hyde, K. D., Yuan, H. S., et al. (2015). Dynamics of the worldwide number of fungi with emphasis on fungal diversity in China. *Mycol. Prog.* 14, 62. doi: 10.1007/s11557-015-1084-5

Dai, Y. C., Wei, Y. L., and Zhang, X. Q. (2004). An annotated checklist of non-poroid Aphyllophorales in China. *Ann. Bot. Fennici* 41, 233–247.

Dai, Y. C., Yang, Z. L., Cui, B. K., Wu, G., Yuan, H. S., Zhou, L. W., et al. (2021). Diversity and systematics of the important macrofungi in Chinese forests. *Mycosystema* 40, 770–805.

Donk, M. A. (1957). Notes on resupinate Hymenomycetes IV. *Fungus* 27, 1–29.

Duhem, B. (2010). Deux corticiés nouveaux méditerranéens à spores allantoïdes. *Cryptogam. Mycol.* 31, 143–152.

Eriksson, J., Hjortstam, K., and Ryvarden, L. (1978). *Corticiaceae of North Europe Volume 5: Mycoaciella-Phanerochaete*. Oslo: Fungiflora.

Eriksson, J., Hjortstam, K., and Ryvarden, L. (1981). *Corticiaceae of North Europe Volume 6: Phlebia-Sarcodontia*. Oslo: Fungiflora.

Eriksson, J., Hjortstam, K., and Ryvarden, L. (1984). *Corticiaceae of North Europe Volume 7: Schizopora-Suillosporium*. Oslo: Fungiflora.

Felsenstein, J. (1985). Confidence intervals on phylogenetics: an approach using bootstrap. *Evolution* 39, 783–791. doi: 10.1111/j.1558-5646.1985.tb00420.x

Fries, E. (1821–1832). *Systema Mycologicum, Sistens Fungorum Ordines, Generaet Species Hucusque Cognitas*. Gryphiswaldiae: Ernestus Mauritius.

Fries, E. (1828). *Elenchus Fungorum. Vols. I and II*. Germany: Greifswald.

Fries, E. (1857–1863). *Monographia Hymenomycetum Sueciae. Vols. I and II. Leffler, C. A.* Uppsala: Nabu Press.

Fries, E. (1874). *Hymenomycetes Europaei*. Berling; Uppsala: Typis descripsip Ed. p. 755.

Gafforov, Y., Ordynets, A., Langer, E., Yarasheva, M., de Mello Gugliotta, A., Schigel, D., et al. (2020). Species diversity with comprehensive annotations of wood-inhabiting poroid and corticioid fungi in Uzbekistan. *Front. Microbiol.* 11, 598321. doi: 10.3389/fmicb.2020.598321

Garcia-Sandoval, R., Wang, Z., Binder, M., and Hibbett, D. S. (2010). Molecular phylogenetics of the Gloeophyllales and relative ages of clades of Agaricomycotina producing a brown rot. *Mycologia* 103, 510–524. doi: 10.3852/10-209

Gilbert, J. E. (1931). *Les Bolets, in les livres du Mycologue*. Paris: Le Village du Livre. p. 254.

Gilbertson, R. L., and Blackwell, M. (1987). Notes on wood-rotting fungi on *Junipers* in the Gulf Coast region. II. *Mycotaxon* 28, 369–402.

Gilbertson, R. L., and Ryvarden, L. (1987). *North American Polypores 1-2.* Fungiflora; Oslo: Lubrecht and Cramer Ltd. p. 1–433.

Gómez, C. E. (1972). *Xenasma* y géneros afines de los alrededores de Buenos Aires (Aphyllophorales). *Bol Soc Argent Bot* 14, 269–281.

Gonzalez-Avila, A., Contreras-Medina, R., Espinosa, D., and Luna-Vega, I. (2017). Track analysis of the order Gomphales (Fungi: Basidiomycota) in Mexico. *Phytotaxa* 316, 22–38. doi: 10.11646/phytotaxa.316.1.2

Grosse-Brauckmann, H., and Kummer, V. (2004). Fünf bemerkenswerte Funde corticioider Pilze aus Deutschland. *Feddes Repert.* 115, 90–101. doi: 10.1002/fedr.200311029

Haelewaters, D., Dirks, A. C., Kappler, L. A., Mitchell, J. K., Quijada, L., Vandegrift, R., et al. (2018). A preliminary checklist of fungi at the Boston Harbor Islands. *Northeast. Nat.* 25, 45–76. doi: 10.1656/045.025.s904

Hallenberg, N. (1978). Wood-Fungi (Corticiaceae, Coniophoraceae, Lachnocladiaceae, Thelephoraceae) in N. Iran. I. *Iran. J. Plant Pathol.* 14, 38–87.

He, M. Q., Zhao, R. L., Hyde, K. D., Begerow, D., Kemler, M., Yurkov, A., et al. (2019). Notes, outline and divergence times of Basidiomycota. *Fungal Divers.* 99, 105–367. doi: 10.1007/s13225-019-00435-4

Hibbett, D. S., Binder, M., Bischoff, J. F., Blackwell, M., Cannon, P. F., Eriksson, O. E., et al. (2007). A higher-level phylogenetic classification of the Fungi. *Mycol. Res.* 111, 509–547. doi: 10.1016/j.mycres.2007.03.004

Hjortstam, K. (1983). Notes on Corticiaceae (Basidiomycetes). XII. *Mycotaxon* 17, 577–584.

Hjortstam, K., and Larsson, K. H. (1987). Additions to *Phlebiella* (Corticiaceae, Basidiomycetes), with notes on *Xenasma* and *Sistotrema*. *Mycotaxon* 29, 315–319.

Hjortstam, K., and Ryvarden, L. (2005). New taxa and new combinations in tropical corticioid fungi, (Basidiomycotina, Aphyllophorales). *Synop. Fungorum* 20, 33–41.

Hjortstam, K., and Ryvarden, L. (2007). Studies in corticioid fungi from Venezuela III (Basidiomycotina, Aphyllophorales). *Synop. Fungorum* 23, 56–107.

Höhnel, F., and Litschauer, V. (1908). Beiträge zur Kenntnis der Corticieen: III. *Sitz. K. Akad. Wiss. Math. Naturw. Klasse Abt. I.* 117, 1081–1124.

Huang, R. X., Chen, J. Z., Wu, J. R., and Zhao, C. L. (2019). *Phlebiella ailaoshanensis* sp. nov. (Polyporales, Basidiomycota) described from China. *Phytotaxa* 419, 105–109. doi: 10.11646/phytotaxa.419.1.8

Jackson, H. S. (1950). Studies of Canadian Thelephoraceae. VII. Some new species of *Corticium*, section Athele. *Can. J. Res.* 28, 716–725. doi: 10.1139/cjr50c-045

James, T. Y., Stajich, J. E., Hittinger, C. T., and Rokas, A. (2020). Toward a fully resolved fungal tree of life. *Annu. Rev. Microbiol.* 74, 291–313. doi: 10.1146/annurev-micro-022020-051835

Jarosch, M. (2001). Zur molekularen systematik der boletales: coniophorineae, paxillineae und suillineae. *Bibl. Mycol.* 191, 1–158.

Jarosch, M., and Besl, H. (2001). *Leucogyrophana*, a polyphyletic genus of the order boletales (Basidiomycetes). *Plant Biol.* 3, 443–448. doi: 10.1055/s-2001-16455

Jülich, W. (1979). Studies in resupinate Basidiomycetes - V. On some new taxa. *Persoonia* 10, 325–336.

Kirk, P. M., Cannon, P. F., David, J. C., Minter, D. W., and Stalpers, J. A. (2008). Ainsworth and bisby's dictionary of the fungi. 10th ed. Wallingford, Oxon, UK: CAB International Press, 783.

Larsson, A. (2014). AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30, 3276–3278. doi: 10.1093/bioinformatics/btu531

Larsson, E., and Hallenberg, N. (2001). Species delimitation in the *Gloeocystidiellum Porosum-Clavuligerum* complex inferred from compatibility studies and nuclear RDNA sequence data. *Mycologia* 93, 907–914. doi: 10.1080/00275514.2001.12063225

Larsson, E., and Larsson, K. H. (2003). Phylogenetic relationships of Russuloid Basidiomycetes with emphasis on *Aphyllophoralean* taxa. *Mycologia* 95, 1037–1065. doi: 10.1080/15572536.2004.11833020

Larsson, K. H. (2007). Re-thinking the classification of corticioid fungi. *Mycol. Res.* 111, 1040–1063. doi: 10.1016/j.mycres.2007.08.001

Larsson, K. H., Larsson, E., and Koljalg, U. (2004). High phylogenetic diversity among corticioid homobasidiomycetes. *Mycol. Res.* 108, 983–1002. doi: 10.1017/S0953756204000851

Larsson, K. H., Larsson, E., Ryvarden, L., and Spirin, V. (2020). Some new combinations of corticioid fungi (Basidiomycota. Agaricomycetes). *Synop. Fungorum* 40, 113–117.

Larsson, K. H., Parmasto, E., Fischer, M., Langer, E., Nakasone, K. K., and Redhead, S. A. (2006). Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98, 926–936. doi: 10.1080/15572536.2006.11832622

Maekawa, N. (2021). Taxonomy of corticioid fungi in Japan: present status and future prospects. *Mycoscience* 62, 345–355. doi: 10.47371/mycosci.2021.10.002

Miller, M. A., Pfeiffer, W., and Schwartz, T. (2012). The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources. *Assoc. Comput. Mach.* 39, 1–8. doi: 10.1145/2335755.2335836

Núñez, M., and Ryvarden, L. (2001). East Asian polypores 2. *Synop. Fungorum* 14, 165–522.

Nylander, J. A. A. (2004). *MrModeltest v2. Program Distributed by the Author.* Uppsala: Evolutionary Biology Centre; Uppsala Univeristy.

Oberwinkler, F. (1966). Primitive Basidiomyceten. Revision einiger Formenkreise von Basidienpilzen mit plastischer Basidie. *Sydowia* 19, 1–72.

Oberwinkler, F. (1975). Eine agaricoide Gattung der Thelephorales. *Sydowia* 28, 359–362.

Parmasto, E. (1965). Corticiaceae U.R.S.S. I. Descriptiones taxorum novarum. Combinationes novae. *Eesti NSV Tead. Akad. TOIM.* 14, 220–233. doi: 10.3176/biol.1965.2.06

Parmasto, E. (1968). *Conspectus Systematis Corticiacearum*. Spain: Euorpa Press. p. 1–261.

Petersen, J. H. (1996). *Farvekort. The Danish Mycological Society's Colour-Chart.* Greve: Foreningen til Svampekundskabens Fremme.

Piatek, M. (2005). A note on the genus *Xenosmatella* (Fungi, Basidiomycetes). *Polish Bot. J.* 50, 11–13.

Pouzar, Z. (1982). Taxonomic studies in resupinate fungi I. *Ceská Mykol.* 36, 141–145.

Rattan, S. S. (1977). The resupinate Aphyllophorales of the North Western Himalayas. *Bibl. Mycol.* 60, 1–427.

Rayner, R. W. (1970). *A Mycological Colour Chart*. Commonwealth Mycological Institute, Kew and British Mycological Society, Kew, United Kingdom. p. 1–34.

Roberts, P. J. (2007). Phlebiella caricis-pendulae: A new corticoid fungus from Wales. *Synop. Fungorum* 22, 25–26.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Hohna, S., et al. (2012). Mrbayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542. doi: 10.1093/sysbio/sys029

Rosenthal, L. M., Larsson, K. H., Branco, S., Chung, J. A., Glassman, S. I., Liao, H. L., et al. (2017). Survey of corticioid fungi in North American pinaceous forests reveals hyperdi-versity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. *Mycologia* 109, 115–127. doi: 10.1080/00275514.2017.1281677

Ryvarden, L., and Liberta, A. E. (1978). Contribution to the Aphyllophoralles of the Canary Islands 4. Two new species of *Trechispora* and *Xenmastella*. *Can. J. Bot.* 56, 2617–2619. doi: 10.1139/b78-314

Ryvarden, L., and Melo, I. (2014). Poroid fungi of Europe. *Synop. Fungorum* 31, 1–455.

Sotome, K., Hattori, T., and Ota, Y. (2011). Taxonomic study on a threatened polypore, *Polyporus pseudobetulinus*, and a morphologically similar species, *P. subvarius. Mycoscience* 52, 319–326. doi: 10.1007/S10267-011-0111-X

Stalpers, J. A. (1996). The aphyllophoraceous fungi II. Keys to the species of the Hericiales. *Stud. Mycol.* 40, 1–185.

Svrcek, M. (1973). Species novae *Corticiacearum* e Bohemia. *Ceská Mykol.* 27, 201–206.

Swofford, D. L. (2002). *PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10.* Sunderland, Massachusetts: Sinauer Associates.

Telleria, M. T., Melo, I., Duenas, M., Larsson, K. H., and Paz Martin, M. P. (2013). Molecular analyses confirm *Brevicellicium* in Trechisporales. *IMA Fungus* 4, 21–28. doi: 10.5598/imafungus.2013.04.01.03

Tobias, W., and Michael, F. (2002). Classification and phylogenetic relationships of *Hymenochaete* and allied genera of the Hymenochaetales, inferred from rDNA sequence data and nuclear behaviour of vegetative mycelium. *Mycol. Prog.* 1, 93–104. doi: 10.1007/s11557-006-0008-9

Vu, D., Groenewald, M., de Vries, M., Gehrmann, T., Stielow, B., Eberhardt, U., et al. (2019). Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Stud. Mycol.* 92, 135–154. doi: 10.1016/j.simyco.2018.05.001

Wagner, T., and Fischer, M. (2001). Natural groups and a revised system for the European poroid Hymenochaetales (Basidiomycota) supported by nLSU rDNA sequence data. *Mycol. Res.* 105, 773–782. doi: 10.1017/S0953756201004257

White, T. J., Bruns, T., Lee, S., and Taylor, J. (1990). "Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics," in *PCR protocols: A Guide to Methods And Applications*, eds Innis, M. A., Gelfand, D. H., Sninsky, J. J., and White, T. J. (San Diego, CA: Academic Press), 315–322.

Wu, F., Yuan, H. S., Zhou, L. W., Yuan, Y., Cui, B. K., and Dai, Y. C. (2020). Polypore diversity in South China. *Mycosystema* 39, 653–682.

Wu, F., Yuan, Y., and Zhao, C. L. (2015). *Porpomyces submucidus* (Hydnodontaceae, Basidiomycota), a new species from tropical China based on morphological and molecular evidence. *Phytotaxa* 230, 61–68. doi: 10.11646/phytotaxa.230.1.5

Wu, F., Zhou, L. W., Vlasák, J., and Dai, Y. C. (2022). Global diversity and systematics of Hymenochaetaceae with poroid hymenophore. *Fungal Divers.* 113, 1–192. doi: 10.1007/s13225-021-00496-4

Zhao, C. L., and Wu, Z. Q. (2017). *Ceriporiopsis kunmingensis* sp. nov. (Polyporales, Basidiomycota) evidenced by morphological characters and phylogenetic analysis. *Mycol. Prog.* 16, 93–100. doi: 10.1007/s11557-016-1259-8

Zhao, W., and Zhao, C. L. (2021). The phylogenetic relationship revealed three new wood-inhabiting fungal species from genus *Trechispora*. *Front. Microbiol.* 12, 650195. doi: 10.3389/fmicb.2021.650195

Zhu, L., Song, J., Zhou, J. L., Si, J., and Cui, B. K. (2019). Species diversity, phylogeny, divergence time and biogeography of the genus *Sanghuangporus* (Basidiomycota). *Front. Microbiol.* 10, 812. doi: 10.3389/fmicb.2019.00812

Zong, T. K., Wu, J. R., and Zhao, C. L. (2021). Three new *Xenasmatella* (Polyporales, Basidiomycota) species from China. *Phytotaxa* 489, 111–120. doi: 10.11646/phytotaxa.489.2.1

Zong, T. K., and Zhao, C. L. (2021). Morphological and molecular identification of two new species of *Phlebiella* (Polyporales, Basidiomycota) from southern China. *Nova Hedwig.* 112, 501–514. doi: 10.1127/nova_hedwigia/2021/0628