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., Xenasmata, and Coronicium J. Eriks. and Ryvarden. Xenasma pseudotsugae (Burt) J. Eriks. nested into the euagarics clade, in which it grouped with Coronicium and Radulomyces. The three taxa of Radulomyces grouped together with Phlebiella pseudosugae (Burt) K.H. Larss. and Hjortstam and Coronicium alboglabrum (Bourd 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 Xenasmata assigned 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, rp1, and rp2 datasets showed that Xenasmata 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, Xenasmata 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 Xenasmata was accepted (Duhem, 2010; Larsson et al., 2020; Maekawa, 2021). Molecular systematics involving Xenasmata 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 Xenasmata clade and related orders; and the Xenasmata 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 Xenasmata. To date, the number of Xenasmata 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 funga order, Xenasmatales and a new species, Xenasmata nigroidea. A key to the 25 accepted species of Xenasmata worldwide is also provided.

### The accepted species list

**Xenasma Donk (1957).**

1. *Xenasma Aculeatum* C.E. Gómez (1972).
2. *Xenasma Amyloporum* Parmasto (1968).
3. *Xenasma Longicytistidatum* Boidin and Gilles (2000).
4. *Xenasma Parviporum* 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 Rinciola* (P. Karst.) Donk (1957).
9. *Xenasma Subclematidis* S.S. Rattan (1977).
10. *Xenasma Tulasielloideum* (Höhn. and Litsch.) Donk (1957).
11. *Xenasma Vassilieviae* Parmasto (1965).

**Xenasmata Oberwinkler (1966).**

1. *Xenasmata Ailaoshanensis* C.L. Zhao ex C.L. Zhao and T.K. Zong (2021).
2. *Xenasmata Aplinicolia* (Bourd and Galzin) K.H. Larss. and Ryvarden (2020).
3. *Xenasmata Ardosiaca* (Bourd and Galzin) Stalpers (1996).
4. *Xenasmata Athelioidea* (N. Maek.) N. Maek. (2021).
5. *Xenasmata Bicorns* (Boidin and Gilles) Piatek (2005).
6. *Xenasmata Borealis* (K.H. Larss. and Hjortstam) Duhem (2010).
7. *Xenasmata Caricis-Pendulac* (P. Roberts) Duhem (2010).
8. *Xenasmata Christianseni* (Parmasto) Stalpers (1996).
9. *Xenasmata Cinnamomea* (Burds. and Nakasone) Stalpers (1996).
10. *Xenasmata Fibrillosa* (Hallenb.) Stalpers (1996).
11. *Xenasmata Globigera* (Hjortstam and Ryvarden) Duhem (2010).
12. *Xenasmata Gossypina* (C.L. Zhao) G. Gruhn and Trichies (2021).
13. *Xenasmata Inopinata* (H.S. Jacks.) Hjortstam and Ryvarden (1979).
14. *Xenasmata Inesperata* (H.S. Jacks.) Jülich (1979).
15. *Xenasmata Nasti* Boidin and Gilles ex Stalpers (1996).
| Species Name                  | Specimen No. | GenBank Accession No. | References                      |
|-------------------------------|--------------|-----------------------|---------------------------------|
| Albatrellus confinis         | PV 10193     | –                     | AF506393 Larsson et al., 2004   |
| Alectorobryce botryosus      | CBS 336.66   | MH858812              | MH870451 Vu et al., 2019        |
| Amaurodon viridis            | TAA 149664   | AY463374              | AY586625 Larsson et al., 2004   |
| Amphipnema hyssoides         | EL 1198      | –                     | AY586626 Larsson et al., 2004   |
| Amylostereum areolatum       | NH 8041      | –                     | AF506405 Larsson and Larsson, 2003 |
| Aphanobasidium pseudotugatae| NH 10396     | –                     | AY586696 Larsson et al., 2004   |
| Auriscalpium vulgar           | EL 3395      | –                     | AY506375 Larsson and Larsson, 2003 |
| Atheleopsis subconspicua     | EL 1298      | AY463382              | AY586633 Larsson et al., 2004   |
| Boudarzewia dickinsii        | KHL 8490     | AY463383              | AY586634 Larsson et al., 2004   |
| Candelabrochae septocystita  | AS 95        | –                     | EU118609 Larsson, 2007          |
| Chaetoderma 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 detectabile      | KHL 11147    | –                     | AY586688 Larsson et al., 2004   |
| Clavulina cristata           | EL 9597      | AY463398              | AY586648 Larsson et al., 2004   |
| Colomnocyctis abietina       | KHL 12474    | EU118619              | – Larsson, 2007                 |
| Cronwicum alboglascum        | NH 4208      | –                     | AY586650 Larsson et al., 2004   |
| Cystoestereum miry             | KHL 12496    | EU118623              | – Larsson, 2007                 |
| Dacryopinax spathularia      | CBS 195.48   | MI856306              | MI867857 Vu et al., 2019        |
| Dacryopinax spathularia      | MI856306     | –                     | MI867857 Vu et al., 2019        |
| Erythricium laetum           | NH 14530     | AY463407              | AY586655 Larsson et al., 2004   |
| Exidia resea                 | SL Lindberg 180317 | – | MT664783 Unpublished |
| Exidiopsis calaepx           | KHL 11075    | –                     | AY586654 Larsson et al., 2004   |
| Gloeocystidellum porosum     | FCUG 1933    | –                     | AF310094 Larsson and Hallenberg, 2001 |
| Haplotrichia conspersus      | KHL 11063    | AY463409              | AY586657 Larsson et al., 2004   |
| Hydnocystella himantia       | KUC 20131001-35 | – | KJ663832 Unpublished |
| Hydnomarulius pinastri       | 412          | –                     | AF352044 Jarosch and Besl, 2001 |
| Hydnocystella himantia       | 420526MF0827 | –                     | MG712372 Unpublished            |
| Hygrophoras aurantiaca       | EL 4299      | –                     | AY586659 Larsson et al., 2004   |
| Hymenochaete cinnamomos      | EL 699       | AY463416              | AY586664 Larsson et al., 2004   |
| Hypodermella corrugata       | KHL 3663     | –                     | EU118630 Larsson, 2007          |
| Hyphodontia aspera           | KHL 8530     | AY463427              | AY586675 Larsson et al., 2004   |
| Innotetis radiatus           | TW 704       | –                     | AF311018 Wagner and Fischer, 2001 |
| Junghuhnia nitida            | CBS 45950    | –                     | MI868226 Vu et al., 2019        |
| Kavinia alboviridis          | EL 1698      | –                     | AY463434 Larsson et al., 2004   |
| Kavinia himantia             | LL 98        | AY463435              | AY586682 Larsson et al., 2004   |
| Lactarius volvus             | KHL 8267     | –                     | AF506414 Larsson and Larsson, 2003 |
| Lactarius fasciformis         | CBS 18249    | –                     | MI868023 Vu et al., 2019        |
| Lentaria dendroidea          | Sj 98012     | EU118640              | EU118641 Larsson, 2007          |
| Lignosus hainanensis         | Dui 10670    | NR154112              | GUS80886 Cui et al., 2011      |
| Merulicium fusciporum        | Hjm s.n.     | EU118647              | – Larsson, 2007                 |
| Mycocybea bispora            | EL 1399      | –                     | AY586692 Larsson et al., 2004   |
| Peniophora pini              | Hjm 18143    | –                     | EU118651 Larsson, 2007          |

(Continued)
| Species Name              | Specimen No. | GenBank Accession No. | References                       |
|--------------------------|--------------|-----------------------|----------------------------------|
| Phanerochaete sordida    | KHL 12054    | –                     | EU118653                         | Larson, 2007                               |
| Phellinus chrysoloma     | TN 4008      | –                     | AF311026                         | Wagner and Fischer, 2001                   |
| Phlebia nitidula         | Nystroem 020830 | –                     | EU118655                         | Larson, 2007                               |
| Podoscypha multizonata   | CBS 66384    | –                     | MIH873501                        | Vu et al., 2019                            |
| Polyporus tubiformis     | WD 1839      | AB587634              | AB586101                         | Sotome et al., 2011                        |
| Porphomyces mucidus      | KHL 11082    | AF347091              | –                                | Unpublished                                 |
| P. mucidus               | Dai 10726    | –                     | KT157839                         | Wu et al., 2015                            |
| Pseudomerulius aureus    | BN 99        | –                     | AY586701                         | Larson et al., 2004                        |
| Punctularia strigosozonata | LR 40885   | AY463456              | AY586702                         | Larson et al., 2004                        |
| Rickenella fibula        | AD 86033     | –                     | AY586710                         | Larson et al., 2004                        |
| Russula violacea         | SJ 93009     | AF506465              | AF506465                         | Larson and Larsson, 2003                   |
| Scopularioides hydnoides | WEI 17569    | –                     | MZ637283                         | Chen et al., 2021                           |
| Sistotrema albolaxatum   | TAA 167982   | AY463467              | AY586713                         | Larson et al., 2004                        |
| Sistotremastrum niveocremum | MAFungi 12915 | –                     | JX310442                         | Telleria et al., 2013                      |
| Sistotremastrum succixum | KHL 11149    | –                     | EU118667                         | Larson, 2007                               |
| Sphaerobasidium minutum  | KHL 11714    | –                     | DQ873553                         | Larson et al., 2006                        |
| Stereum hirsutum         | NH 7960      | AF506479              | –                                | Larson et al., 2003                        |
| Tomentellopsis echinospora | KHL 8459   | AY463472              | AY586718                         | Larson et al., 2004                        |
| Trametes suaveolens      | CBS 279.28   | MIH855012             | MIH866480                        | Vu et al., 2019                            |
| Trechispora farinacea     | KHL 8793     | AF347089              | –                                | Larson et al., 2004                        |
| Trechispora farinacea     | MAFungi 79474 | –                     | JX392856                         | Telleria et al., 2013                      |
| Tubularicrinis subulatus | KHL 11079    | AY463478              | AY586722                         | Larson et al., 2004                        |
| Veluticeps abietina      | HHB 13663    | –                     | KJ141191                         | Unpublished                                 |
| Veluticeps berkeleyi     | HHB 8594     | –                     | HM536801                         | Garcia-Sandoval et al., 2010               |
| Vuilleminia comedens     | EL 199       | AY463482              | AY586725                         | Larson et al., 2004                        |
| Wrighttoporia lenta      | KN 150311    | –                     | AF506489                         | Larson and Larsson, 2003                   |
| Xerocomus chrysenteron   | EL 3999      | AF347103              | –                                | Larson et al., 2004                        |
| Xenasma praeteritum      | ACD 0185     | OM009268              | Unpublished                      |                                      |
| Xenasma pruinicornum     | OTU 1299     | MT594801              | Unpublished                      |                                      |
| X. riniolae              | NLB 1571     | MT571671              | Unpublished                      |                                      |
| X. riniolae              | NLB 1449     | MT57020               | Unpublished                      |                                      |
| Xenasmatella ailaoshanensis | CLZhao 3895 | MN487103              | –                                | Huang et al., 2019                        |
| X. ailaoshanensis        | CLZhao 4839  | MN487106              | –                                | Huang et al., 2019                        |
| Xenasmatella ardisiaca   | 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 christianseni | TASM YGG 26 | MT526341              | –                                | Gaffarov et al., 2020                     |
| X. christiansensi        | TASM YGG 36  | MT526342              | –                                | Gaffarov 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                         |
TABLE 1 (Continued)

| Species Name              | Specimen No. | ITS GenBank Accession No. | nLSU GenBank Accession No. | References                  |
|---------------------------|--------------|---------------------------|----------------------------|-----------------------------|
| 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 4880 | 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.

![Colored ranges graph](image)

**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 Svrcék (1973).
21. Xenasmata Subflavidogrisea (Litsch.) Oberw. ex Jülich (1979).
22. Xenasmata Tenuis C.L. Zhao (2021).
23. Xenasmata Vaga (Fr.) Stalpers (1996).
24. Xenasmata Wuliangshanensis (C.L. Zhao) G. Gruhn and Trichies (2021).
25. Xenasmata 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...
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 Xenasmata-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 reicisa 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
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 parsimony informative, and 832 are parsimony uninformative. 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 [iset 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., Corticales 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 parsimony informative, and 441 are parsimony uninformative. 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 [iset 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 athelid, producing effused, crust like fruiting bodies that are loosely attached to the substrate and with non-differentiated margins. | Eriksson et al., 1978, 1981, 1994 |
| 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 gastromycetes (puffball-like forms), resupinate or crust-like fungi that produce smooth, meruloid (wrinkled to warded), or hydnoid (toothed) hymenophores, and a single poly pore-like species, Bondarcevomyces taxi | Gilbert, 1931; Beal and Bresinsky, 1997; Jarosch, 2001; Larsson et al., 2004 |
| Corticales | 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, alvae vel aggregatae roseae. | Hibbett et al., 2007 |
| Gloeophyllales | Basidiomata annua vel perennia, resupinata, effuso-reflexa, dimidiata vel pileata; hymenophora laevia, meruloidia, odontiodae vel poroidae. Systema hypharum monomiticum, dimiticum vel triniticum. Hyphae generativa e fibulatae vel elfibulatae. Leptocystidia ex trama in hymenium projecta, hyalina vel brunnea, tenuitunicata vel crassitunicata. Basidiospora laeves, hyalinae, tenuitunicatae, ellipsoidae vel cylindraceae vel allantoideae, imamylodeae. Lignum decompositum bruneum 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 (corticoid, hydnid or porid) and basidioceps (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 | Basidiospora tuberose spinosaeque plus minusve colorateae. | Oberwinkler, 1975 |
| Trechisporales | Basidiomata resupinata, stipitata vel clavariae. Hymenophora laevia, grandinioidea, hydnoida vel poroidae. Systema hypharum monomiticum vel dimiticum. Hyphae fibulatae, septa hypharum interdum inflata (ampullata). Cystidia praesentia vel absentia. Basidia 4-6 sterigmatu 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, Corticii, Gloeophyllales, Gomphales, Hymenochaetales, Polyporales, Russulales, Thelephorales, Trechisporales, and Xenasmatales, while Xenasmata 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 Xenasmata. 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 Xenasmataella 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 gelatinous. 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 *Xenasmataella nigroidea* and other species.

| Species name                  | Basidiomata        | Hymenial surface                                          | Basidia                          | Basidiospores                                      | References                          |
|-------------------------------|--------------------|-----------------------------------------------------------|----------------------------------|----------------------------------------------------|-------------------------------------|
| *Xenasmataella nigroidea*     | Thin, very hard to | Smooth, hypsaceous 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 × 2.8–4.5 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         | Grandinoid                                                  | 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

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**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.

| Species name                  | Geographic distribution | Hostsubstratum                                      | References          |
|-------------------------------|-------------------------|-----------------------------------------------------|---------------------|
| **Xenasma aculeatum**         | Argentina               | On fructifications of *Hypoxylon*                   | Gómez, 1972         |
| **X. amylosporum**            | Primorye                | On rotten trunk of *Picea jezoensis*                 | Parmasto, 1968      |
| **X. longicyrtidatum**        | Reunion                 | On *Rubus alcefolius*                                | Boidin and Gilles, 2000 |
| **X. parvisporum**            | Czech Republic          | On fallen branch of *Quercus petraea*               | Pouzar, 1982        |
| **X. praeterritum**           | Ontario                 | On wood                                             | Donk, 1957          |
| **X. pruinum**                | 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. subclamatisidis**        | Jammu-Kashmir           | On log                                              | Rattan, 1977        |
| **X. tulasnelloideum**        | America                 | On very rotten wood                                  | Hohnel and Litschauer, 1988 |
| **X. vasileevae**             | Khabarovsk              | On fallen trunk of *Taxus cuspidata*                 | Parmasto, 1965      |
| **Xenasmatella ailaoshanensis**| Yunnan                  | On trunk of *Angiospermae*                          | Huang et al., 2019  |
| **X. athnicola**              | Allier                  | Sur boss humides, aune, saule blane                 | Bourdot and Galzin, 1928 |
| **X. ardisiaca**              | France                  | On decayed wood                                      | Bourdot and Galzin, 1928 |
| **X. athelioidea**            | Japan                   | On rotten trunk of *Quercus*                        | Maekawa, 2021       |
| **X. bicorvis**               | Gabon                   | Among shrubs on shore                                | Boidin and Gilles, 2004 |
| **X. borealis**               | Norway                  | On rotten *Pinus sylvestris*                         | Hjortstam and Larsson, 1987 |
| **X. carici-pendulae**        | Great Britain           | On dead attached leaf of *Carex pendula*             | Roberts, 2007       |
| **X. christiansensi**         | Kamchatka               | On fallen branch of *Larix kurilensis var. glabra*  | Parmasto, 1965      |
| **X. cinnaeomea**             | Florida                 | On *Magnolia*                                        | Burdall 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 *Typha canadensis*                                | Jackson, 1950       |
| **X. inopinata**              | Ontario                 | On bark                                              | Jackson, 1950       |
| **X. inunis**                 | 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                                      | Srzvek, 1973        |
| **X. subflavidogrisea**        | Sweden                  | On rotten wood of *Pinus sylvestris*                 | Jülich, 1979        |
| **X. tenus**                  | Yunnan                  | On trunk of *Angiospermae*                          | Zong et al., 2021   |
| **X. vagi**                   | Italy                   | On *Robinia pseudocacica*                            | Stalpers, 1996      |
| **X. wulianghanensis**        | Yunnan                  | On trunk of *Angiospermae*                          | Zong and Zhao, 2021 |
| **X. xinginsensis**           | Yunnan                  | On trunk of *Angiospermae*                          | Zong et al., 2021   |
| **Xenosperma hexagonosporum**  | France                  | On wood of *Platanus acerifolia*                     | Boidin and Gilles, 1989 |
| **X. ludidii**                | 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**                 | Reunion                 | 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 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°42′ 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 worldwide.

| 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 |
| 3. Basidia with 4 sterigmata | 3 |
| 3. Basidia sterigmata > 5 µm in length | X. naesi |
| 4. Basidiospores > 5 µm in length | 4 |
| 4. Basidiospores < 5 µm in length | 5 |
| 5. Basidiospores > 4 µm in width | 6 |
| 5. Basidiospores < 4 µm in width | 9 |
| 6. Basidiospores globose | X. ardosiaea |
| 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. caricos-pendulac |
| 8. Growth on the trunk of gymnosperm | X. christiansenii |
| 9. Basidiospores < 2 µm in width | X. atheliosidea |
| 9. Basidiospores > 2 µm in width | 10 |
| 10. Hymenial margin with fimbriae | X. romelli |
| 10. Hymenial margin without fimbriae | 11 |
| 11. Hymenial surface arachnoid or byssoid | X. borealis |
| 11. Hymenial surface smooth | X. inopinata |
| 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. wuiangshanhanensis |
| 14. Hymenial surface white to grayish or cream to buff | 15 |
| 15. Generative hyphae thick-walled, unbranched | X. xipengensis |
| 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 ochrous | 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, Corticales, Gloeophyllales, Gomphales, Hymenochaetales, Polyporales, Russulales, Thelephorales, Trechisporales, and Xenasmataceae 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. wuiliangshanensis, 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 (5.5–4.5 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. christianseni (Parmasto) Stalpers, X. fibrillosa (Hallenb.) Stalpers, X. gossypina, and X. rhizomorpha C.L. Zhao by having gossypine, byssaceous to reticulate hymenial surface, however, X. christianseni is distinguished from X. nigroidea by its larger basidiospores (6.7 × 4.45 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. gasepica (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. gasepica 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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