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# *Xenasmatellales* ord. nov. and *Xenasmatellaceae* fam. nov. for *Xenasmatella* (*Agaricomycetes, Basidiomycota*)

Shi-Liang Liu[a], Hao-Wen Wei[a,b] and Li-Wei Zhou[a]

[a]State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; [b]College of Life Science, Liaoning University, Shenyang, China

**ABSTRACT**
In the era of molecular phylogeny as dominant evidence in fungal taxonomy, the taxonomic framework of fungi adopted from morphological characteristics has been largely updated. Compared with other fungal groups, macrofungi underwent fewer updates at the order and higher level. In this study, the taxonomic placement of a poorly known macro-basidiomycetous genus *Xenasmatella* is studied. Phylogenetic and molecular clock analyses inferred from a seven-locus dataset support that the genus represents an order rank lineage. Accordingly, a monotypic order *Xenasmatellales* and a monotypic family *Xenasmatellaceae* are newly introduced for *Xenasmatella* within *Agaricomycetes*. The species diversity and relationships of *Xenasmatella* are further clarified with the aid of the phylogenetic analysis inferred from a four-locus dataset. In association with morphological characteristics, a new species *Xenasmatella hjortstamii* is described. Moreover, the distribution of *Xenasmatella ailaoshanensis, X. gossypina*, and *X. wuliangshanensis* previously known only from type localities in Yunnan Province, China are expanded. In addition, two unnamed single-specimen lineages of *Xenasmatella* from Victoria State, Australia and Sichuan, China are revealed, likely representing two potential new species of this genus. In summary, the current study updates the taxonomic framework of *Agaricomycetes* and provides a crucial supplement for comprehensively understanding the evolutionary history of this fungal class.

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## 1. Introduction

Since Linnaeus's publication *Species Plantarum* in 1753, the taxonomy of fungi had long been based mainly on morphological traits (Linnaeus 1753). Until the 1990s, DNA sequence was brought into fungal taxonomy (White et al. 1990). With the development of molecular sequencing technology and its wide utilisation in fungal taxonomy, the taxonomic framework of fungi was largely updated, which was best exemplified by the milestone paper of Hibbett et al. (2007) which introduced the *Dikarya*. After that, more and more high-level taxa were newly erected (James et al. 2020).

Within *Dikarya*, compared with microfungi, macrofungi mostly in *Agaricomycetes, Basidiomycota* underwent fewer updates of taxonomic framework. For example, only six orders, viz. *Amylocorticiales* (Binder et al. 2010), *Jaapiales* (Binder et al. 2010), *Lepidostromatales* (Hodkinson et al. 2014), *Sistotremastrales* (Liu et al. 2022), *Stereopsidales* (Sjökvist et al. 2014) and *Tremellodendropsidales* (Vizzini 2014) were newly introduced for macro-basidiomycetes after the publication of Hibbett et al. (2007). This phenomenon may be partially caused by that macrofungi have more taxonomic morphological characteristics and thus provide more accurate taxonomic evidence in the era of morphology-based taxonomy. However, we cannot exclude the possibility that fewer studies focused on the reconsideration of certain macrofungal groups at higher taxonomic ranks. A recent example is the erection of *Sistotremastrales*. Its representative genus *Sistotremastrum* was placed in *Trechisporales* but had not been confirmed for its familial placement (Larsson 2007). Later, Spirin et al. (2021) segregated *Sertulicium* from *Sistotremastrum* and suggested that these two genera may be included in the so-called *Sistotremastrum* family as defined by Larsson (2007). Recently, when considering the phylogenetic position of *Sertulicium* and *Sistotremastrum* throughout the *Agaricomycetes*, Liu et al. (2022) raised these two genera to a new order rank beyond family. Therefore, more

**CONTACT** Li-Wei Zhou liwei_zhou1982@im.ac.cn
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efforts are needed to recognise the taxonomic framework of macro-basidiomycetes fully.

In the current study, the taxonomic placement of *Xenasmatella*, a poorly focused on macro-basidiomycetous genus, is explored. This corticioid genus, typified by *X. subflavidogrisea*, was erected by Oberwinkler (1966). Since the erection, *Xenasmatella* has long been buried in oblivion. Instead, some species of *Xenasmatella*, including the generic type, were placed in *Phlebiella*. Donk (1963) first stated that *Phlebiella* is an invalid genus name due to a lack of generic description when erected by Karsten (1890) and Piątek (2005) proposed that *Xenasmatella* should be the earliest valid name of genus for this fungal group. However, most taxonomists continued to use *Phlebiella* (Hjortstam and Larsson 1987; Boidin and Gilles 1989, 2000; Telleria et al. 1997; Larsson 2007; Bernicchia and Gorjón 2010; Huang et al. 2019; Zong and Zhao 2021), while only a few publications properly named species in *Xenasmatella* (Duhem 2010; Larsson et al. 2020; Maekawa 2021; Zong et al. 2021; Liu and Yuan 2022).

At the order level, previous studies successively placed *Xenasmatella* in *Xenasmatales* (Jülich 1981), *Polyporales* (Kirk et al. 2008), and *Russulales* (He et al. 2019). However, no widely accepted evidence can be found to support these taxonomic placements. The current phylogenetic analyses on the basis of multi-locus sequences undoubtfully support to place *Xenasmatella* in an independent, new lineage at the order level. Accordingly, a new order and a new family are erected to accommodate *Xenasmatella*. Moreover, a new species of *Xenasmatella* is described.

## 2. Materials & methods

### 2.1. Morphological examination

The studied specimens are preserved at the Fungarium, Institute of Microbiology, Chinese Academy of Sciences (HMAS), Beijing, China. The hymenophoral surface of basidiomes was examined with a Leica M125 stereomicroscope (Wetzlar, Germany) at a magnification of up to 100×. The microscopical characteristics were observed with an Olympus BX43 light microscope (Tokyo, Japan) at a magnification of up to 1,000×. The microscopic procedure followed Wang et al. (2021). Basidiome sections were prepared with Cotton Blue (CB), Melzer's reagent and 5% potassium hydroxide (KOH). All measurements were made from sections in CB. When presenting the variation of basidiospore sizes, 5% of the measurements were excluded from each end of the range and are given in parentheses. Drawings were made with the aid of a drawing tube. In the morphological description, L is short for mean basidiospore length (arithmetic average of all measured basidiospores), W for mean basidiospore width (arithmetic average of all measured basidiospores), Q for variation in the L/W ratios between the studied specimens, and (a/b) for a number of basidiospores (a) measured from a given number (b) of specimens. A Hitachi SU8010 scanning electron microscope (Tokyo, Japan) was used to further explore the ultrastructure of basidiospores following Liu et al. (2022).

### 2.2. Molecular sequencing

Dried specimens were taken for DNA extraction using CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) and the crude DNA was used as templates for PCR amplification. The nSSU, ITS, nLSU, mtSSU, *tef1α, rpb1* and *rpb2* regions were amplified with primer pairs PNS1/NS41 (Hibbett 1996), ITS5/ITS4 (White et al. 1990), LR0R/LR7 (Vilgalys and Hester 1990), MS1/MS2 (White et al. 1990), 983 F/1567 R (Rehner and Buckley 2005), RPB1-Af/RPB1-Cr (Matheny et al. 2002), and RPB2-f5F/RPB2-b7.1 R (Liu et al. 1999; Matheny 2005), respectively. The PCR procedures were as follows: initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, 53 °C (for nSSU region)/54 °C (for ITS and *tef1α* regions)/52 °C (for mtSSU region) for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 10 min for nSSU, ITS, mtSSU and *tef1α* regions; 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 for nLSU region; initial denaturation at 94 °C for 2 min, followed by 10 cycles at 94 °C for 45 s, 60 °C for 45 s (minus 1 °C per cycle) and 72 °C for 1.5 min, followed by 36 cycles at 94 °C for 45 s, 53 °C for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min for *rpb1* and *rpb2* regions. The PCR products were sequenced using the same primers as those used in PCR amplification at the Beijing Genomics Institute, Beijing, China. All newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/; Table 1).

### 2.3. Phylogenetic analyses

Besides the newly generated sequences, additional molecular sequences were downloaded from GenBank for phylogenetic analyses (Table 1). To explore the phylogenetic position of *Xenasmatella* within *Agaricomycetes*, a seven-locus dataset of nSSU, ITS, nLSU, mtSSU, *tef1α, rpb1* and *rpb2* including all 23 known orders within *Agaricomycetes* and two species from *Dacrymycetales, Dacrymycetes* as ingroup taxa and two species from *Tremellales, Tremellomycetes* as outgroup taxa were utilised according to He et al. (2019) and Liu et al. (2022). To clarify the species diversity and relationships of *Xenasmatella*, a four-locus dataset of nSSU, ITS, nLSU and mtSSU with *Heterobasidion annosum* and *Xenasma rimicola* as outgroup taxa were selected. Each locus in these two datasets was separately aligned using MAFFT 7.110 (Katoh and Dm 2013) under the G-INS-i option (Katoh et al. 2005). Then, the resulting alignments were concatenated into two individual alignments corresponding to the two datasets (Supplementary files 1 and 2).

jModelTest 2 was used to estimate the best-fit evolutionary models for these two alignments under the corrected Akaike information criterion (Guindon et al. 2003; Posada 2008). Following the estimated models, maximum likelihood (ML) and Bayesian inference (BI) algorithms were performed for phylogenetic analyses. The ML algorithm was conducted using raxmlGUI 2.0 (Stamatakis 2014; Edler et al. 2021), and the bootstrap (BS) replicates were calculated under the auto FC option (Pattengale et al. 2010). The BI algorithm was conducted using MrBayes 3.2.6 (Ronquist et al. 2012), which employed two independent runs each with four chains and starting from random trees. In the BI algorithm, trees were sampled every 1000th generation. Of the sampled trees, the first 25% were removed as burn-in and the remaining 75% were retained for constructing a 50% majority consensus tree and calculating Bayesian posterior probabilities (BPPs). Tracer 1.7 (Rambaut et al. 2018) was used to judge whether the chains converged.

The alignment resulting from the seven-locus dataset was subjected to the estimation of divergence times based on fossil calibrations using BEAST 2.6.3 (Bouckaert et al. 2019). The lognormal relaxed molecular clock and the Yule speciation prior were set in the calibration process. According to the hitherto known fossil records, 90 million years (myr) as the minimum age of *Agaricales* (Hibbett et al. 1997) and 113 myr as the minimum age of *Hymenochaetales* (Smith et al. 2004) were set for calibration of time points, while the mean age of *Agaricomycetes* was set as 290 myr following the phylogenomic analyses (Floudas et al. 2012). The analyses were conducted with 200 million MCMC iterations. The first 10% of the trees sampled every 1000th generation were removed as burn-in, while the remaining trees were used to estimate the maximum-clade-credibility tree using TreeAnnotator 2.6.3 (Bouckaert et al. 2019). Tracer 1.7 (Rambaut et al. 2018) was used to assess the convergence of parameter values and age estimates with effective sample sizes over 200.

## 3. Results

### 3.1. Phylogenetic analysis

In this study, a total of 19 nSSU, 24 ITS, 20 nLSU, 20 mtSSU, one *tef1α*, two *rpb1* and three *rpb2* sequences were newly generated from all 26 studied specimens (Table 1). The alignment of the seven-locus dataset included 54 taxa and contained 7,469 characters. Its best-fit evolutionary model was estimated as GTR + I + G. The ML search stopped after 200 bootstrap replicates. All chains in BI converged after one million generations, which is indicated by the effective sample sizes of all parameters above 1,000 and the potential scale reduction factors close to 1.000. ML and BI algorithms constructed similar topologies that differed only at several poorly supported nodes. The topology resulting from the ML algorithm is shown along with BS values of more than 50% and BPPs of more than 0.8 at the nodes (Figure 1). In the current phylogeny (Figure 1), the genus of *Xenasmatella* formed an independent lineage from previously known orders within *Agaricomycetes* (BS = 100%, BPP = 1). After 200 million generations, the chains in the molecular clock analysis converged, indicated by the effective sample size of each parameter above 200. The mean stem age for the independent clade of *Xenasmatella* was estimated as 162.79 myr with the 95% highest posterior density ages of 136–183.45 myr (Figure 2). These times fall within the previously estimated divergence times of orders (108–259 myr) and families (27–259 myr) within *Agaricomycetes* (He

**Table 1.** Information of collections used in phylogenetic analyses.

| Class/Order | Species name | Voucher No. | Accession No. nSSU | ITS | nLSU | mtSSU | *tef1a* | *rpb1* | *rpb2* |
|---|---|---|---|---|---|---|---|---|---|
| *Agaricomycetes/ Agaricales* | *Calocybe carnea* | CBS552.50 | DQ367418 | AF357028 | AF223175 | AF357097 | DQ367425 | DQ825423 | DQ825407 |
| | *Marasmius oreades* | ZRL2015086 | KY418930 | LT716048 | KY418864 | | KY419066 | KY418972 | KY419010 |
| | *Psathyrella candolleana* | ZRL20151400 | KY418945 | LT716063 | KY418879 | | KY419075 | KY418978 | KY419024 |
| /*Amylocorticiales* | *Amylocorticium cebennense* | HHB-2808 | GU187612 | GU187505 | GU187561 | | GU187675 | GU187439 | GU187770 |
| | *Anomoloma myceliosum* | MJL-4413 | GU187614 | GU187500 | GU187559 | | GU187677 | GU187441 | GU187766 |
| /*Atheliales* | *Athelia arachnoidea* | CBS 418.72 | GU187616 | GU187504 | GU187557 | | GU187672 | GU187436 | GU187769 |
| | *Leptosporomyces raunkiaerii* | HHB-7628 | GU187640 | GU187528 | GU187588 | | | GU187471 | GU187791 |
| /*Auriculariales* | *Auricularia heimuer* | Xiaoheimao | | LT716074 | KY418890 | | KY419083 | | KY419035 |
| | *Exidia* sp. | PBM2527 | | DQ241774 | AY700191 | | DQ408144 | | |
| /*Boletales* | *Coniophora arida* | FP104367 | GU187622 | GU187510 | GU187573 | | GU187684 | GU187445 | GU187775 |
| | *Serpula lacrymans* | REG-383 | GU187649 | GU187542 | GU187596 | | GU187752 | GU187485 | GU187809 |
| | *Hydnum albomagnum* | AFTOL 471 | AY665777 | DQ218305 | AY700199 | | DQ234568 | DQ234570 | DQ234553 |
| /*Corticiales* | *Punctularia strigosozonata* | AFTOL 1248 | AF518586 | DQ398958 | AF518642 | | DQ408147 | DQ831031 | DQ381843 |
| | *Vuillemenia comedens* | AFTOL-1247 | | DQ398959 | AF518666 | | | | DQ381844 |
| /*Geastrales* | *Schenella pityophilus* | OSC59743 | | | DQ218519 | DQ218694 | DQ219232 | | DQ219057 |
| | *Geasteroides taylorii* | OSC59760 | | | DQ218520 | | DQ219235 | | DQ219060 |
| /*Gloeophyllales* | *Gloeophyllum trabeum* | 1320 | HM536068 | HM536094 | HM536067 | | HM536113 | | HM536112 |
| | *Osmoporus protractum* | H-80 | HM536060 | HM536090 | HM536059 | | HM536108 | | HM536107 |
| /*Gomphales* | *Clavariadelphus truncatus* | OSC67280 | | | AY574649 | | DQ219240 | | DQ219064 |
| | *Kavinia alboviridis* | O102140 | | | AY574692 | | DQ219250 | | DQ219073 |
| /*Hymenochaetales* | *Coltricia abieticola* | Cui 10,321 | KY693761 | KX364785 | KX364804 | KY693823 | KY693911 | KX364828 | KX364876 |
| | *Hyphodontia zhixiangii* | LWZ 20170818–13 | | MT319420 | MT319151 | MT326424 | MT326397 | MT326361 | MT326270 |
| | *Sidera minutipora* | Cui 16,720 | MW418078 | MN621349 | MN621348 | MW424986 | MW446248 | MW526261 | MW505865 |
| /*Hysterangiales* | *Aroramyces gelatinosporus* | H4010 | | | DQ218524 | | DQ219118 | | DQ218941 |
| | *Chondrogaster pachysporus* | OSC49298 | | | DQ218538 | | DQ219136 | | DQ218958 |
| /*Jaapiales* | *Jaapia argillacea* | CBS 252.74 | AF518581 | GU187524 | GU187581 | | GU187711 | GU187463 | GU187788 |
| /*Lepidostromatales* | *Lepidostroma vilgalysii* | RV-MX16 | | JN698907 | JN698908 | | | | |
| | *Sulzbacheromyces caatingae* | Sulzbacher 1479 | | KC170320 | KC170318 | | | | |
| /*Phallales* | *Gelopellis* sp. | H4397 | | | DQ218630 | | DQ219269 | | DQ219090 |
| | *Phallus hadriani* | AFTOL 683 | AY771601 | DQ404385 | AY885165 | | DQ435792 | | DQ408114 |
| /*Polyporales* | *Polyporus squamosus* | Cui 10,595 | KU189840 | KU189778 | KU189809 | KU189960 | KU189925 | KU189892 | KU189988 |
| | *Fomitopsis pinicola* | AFTOL 770 | AY705967 | AY854083 | AY684164 | | AY885152 | AY864874 | AY786056 |
| | *Laetiporus sulphureus* | Cui 12,388 | KX354518 | KR187105 | KX354486 | KX354560 | KX354607 | MG867671 | KX354652 |
| /*Russulales* | *Heterobasidion annosum* | AFTOL-ID470 | | DQ206988 | AF287866 | U27042 | DQ028584 | DQ667160 | AH013701 |
| | *Echinodontium tinctorium* | DAOM16666 | | AY854088 | AF393056 | | AY885157 | AY864882 | AY218482 |
| | *Xenasma rimicola* | FP-133272-sp | AY293162 | | AY293220 | AY293249 | | | |
| /*Sebacinales* | *Sebacina* sp. | AFTOL 1517 | DQ521413 | DQ911617 | DQ521412 | | | | |
| | *Tremellodendron pallidum* | AFTOL 699 | AY766081 | DQ411526 | AY745701 | | DQ029196 | | DQ408132 |
| /*Sistotremastrales* | *Sistotremastrum* sp. | LWZ20191107-25 | | MW477771 | MW474864 | OM422784 | MW478703 | | MW478712 |
| /*Stereopsidales* | *Stereopsis radicans* | OLR45395 | | KC203496 | KC203496 | | KC203516 | | KC203502 |
| | *Stereopsis* sp. | OKHL15544 | | | | | KC203519 | | KC203505 |
| /*Thelephorales* | *Boletopsis leucomelaena* | PBM2678 | DQ435797 | DQ484064 | DQ154112 | | GU187763 | GU187494 | GU187820 |
| | *Thelephora ganbajun* | ZRL20151295 | KY418962 | LT716082 | KY418908 | | KY419093 | KY418987 | KY419043 |
| /*Trechisporales* | *Trechispora alnicola* | AFTOL 665 | AY657012 | DQ411529 | AY635768 | | DQ059052 | | DQ408135 |

(*Continued*)

**Table 1.** (Continued).

| Class/Order | Species name | Voucher No. | Accession No. | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | nSSU | ITS | nLSU | mtSSU | *tef1a* | *rpb1* | *rpb2* |
| */Tremellodendropsidales* | *Tremellodendropsis tuberosa* | KU900852 | KU900854 | KU900857 | KU900857 | | | | |
| */Xenasmatellales* | *Xenasmatella ailaoshanensis* | CLZhao 4839 | | MN487106 | | | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20170909–4 | | **OQ738207** | | | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20170909–6 | | **OQ738203** | **OQ674459** | **OQ758254** | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20180510–7 | | **OQ738209** | **OQ674457** | | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20190811–37a | **OQ733194** | **OQ738201** | **OQ692633** | **OQ758238** | | **OQ683407** | **OQ683411** |
| | *Xenasmatella ailaoshanensis* | LWZ 20190811–40a | **OQ733198** | **OQ738204** | **OQ692634** | **OQ758241** | | **OQ683408** | **OQ683412** |
| | *Xenasmatella ailaoshanensis* | LWZ 20200921–25a | **OQ733195** | **OQ738206** | **OQ674445** | | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20200925–10a | **OQ733201** | **OQ738205** | | **OQ758244** | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20200926–4b | **OQ733207** | **OQ738202** | **OQ674455** | **OQ758251** | | | |
| | *Xenasmatella ailaoshanensis* | LWZ 20210922–22b | | **OQ738208** | | | | | |
| | *Xenasmatella ailaoshanensis* | Zhao 3895 | | MN487105 | | | | | |
| | *Xenasmatella ardosiaca* | CBS 126045 | | MH875515 | | | | | |
| | *Xenasmatella* aff. *ardosiaca* | KHL 12928 | | EU118658 | | | | | |
| | *Xenasmatella christiansenii* | KHL 11689 | | EU118659 | EU118659 | | | | |
| | *Xenasmatella christiansenii* | YG-G22 | | MT526340 | | | | | |
| | *Xenasmatella gossypina* | CLZhao 4149 | | MW545958 | | | | | |
| | *Xenasmatella gossypina* | CLZhao 8233 | | MW545957 | | | | | |
| | *Xenasmatella gossypina* | LWZ 20190819–18b | **OQ733203** | **OQ738197** | **OQ674452** | **OQ758247** | | | |
| | *Xenasmatella gossypina* | LWZ 20190819–3a | | **OQ738198** | **OQ674451** | **OQ758246** | | | |
| | *Xenasmatella gossypina* | LWZ 20200818–25b | **OQ733191** | **OQ738196** | **OQ674442** | **OQ758235** | | | **OQ683410** |
| | *Xenasmatella hjortstamii* | LWZ 20200819–29a | **OQ733192** | **OQ738199** | **OQ674443** | **OQ758236** | **OQ683409** | | |
| | *Xenasmatella hjortstamii* | LWZ 20200819–30a | **OQ733193** | **OQ738200** | **OQ674444** | **OQ758237** | | | |
| | *Xenasmatella nigroidea* | CLZhao 18,300 | | OK045679 | OK045677 | | | | |
| | *Xenasmatella nigroidea* | CLZhao 18,333 | | OK045680 | OK045678 | | | | |
| | *Xenasmatella rhizomorpha* | CLZhao 9156 | | MT832954 | | | | | |
| | *Xenasmatella rhizomorpha* | CLZhao 9847 | | MT832953 | | | | | |
| | *Xenasmatella roseobubalina* | Dai 20,506 | | OM855607 | | | | | |
| | *Xenasmatella tenuis* | CLZhao 11,258 | | MT832959 | | | | | |
| | *Xenasmatella tenuis* | CLZhao 4528 | | MT832960 | | | | | |
| | *Xenasmatella vaga* | KHL 11065 | | EU118660 | EU118661 | | | | |
| | *Xenasmatella wuliangshanensis* | CLZhao 4080 | | MW545962 | | | | | |
| | *Xenasmatella wuliangshanensis* | CLZhao 4308 | | MW545963 | | | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20170909–5 | **OQ733206** | **OQ738215** | **OQ674454** | **OQ758250** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20171014–14 | **OQ733205** | **OQ738219** | | **OQ758249** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20180416–14 | **OQ733209** | **OQ738218** | **OQ674458** | **OQ758253** | | | |

(*Continued*)

**Table 1.** (Continued).

| Class/Order | Species name | Voucher No. | Accession No. nSSU | ITS | nLSU | mtSSU | *tef1a* | *rpb1* | *rpb2* |
|---|---|---|---|---|---|---|---|---|---|
| | *Xenasmatella wuliangshanensis* | LWZ 20180804–25 | **OQ733197** | **OQ738212** | **OQ674447** | **OQ758240** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20190726–16 | **OQ733204** | **OQ738213** | **OQ674453** | **OQ758248** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20190915–7 | **OQ733202** | **OQ738214** | **OQ674450** | **OQ758245** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20210626–15b | **OQ733200** | **OQ738216** | **OQ674449** | **OQ758243** | | | |
| | *Xenasmatella wuliangshanensis* | LWZ 20210928–5 | **OQ733199** | **OQ738217** | **OQ674448** | **OQ758242** | | | |
| | *Xenasmatella xinpingensis* | CLZhao 2216 | | MT832961 | | | | | |
| | *Xenasmatella xinpingensis* | CLZhao 2467 | | MT832962 | | | | | |
| | *Xenasmatella* sp. | LWZ 20180509–23 | **OQ733208** | **OQ738210** | **OQ674456** | **OQ758252** | | | |
| | *Xenasmatella* sp. | LWZ 20200819–9b | **OQ733196** | **OQ738211** | **OQ674446** | **OQ758239** | | | |
| *Dacrymycetes/ Dacrymycetales* | *Calocera cornea* | AFTOL 438 | AY771610 | AY789083 | AY701526 | | AY881019 | AY857980 | AY536286 |
| | *Dacryopinax spathularia* | AFTOL 454 | AY771603 | AY854070 | AY701525 | | AY881020 | AY857981 | |
| *Tremellomycetes/ Tremellales* | *Bullera alba* | CBS 501 | X60179 | AF444368 | AF075500 | | KF037016 | KF036334 | KF036745 |
| | *Dioszegia antarctica* | CBS 10920 | KF036667 | DQ402529 | FJ640575 | | KF037129 | KF036444 | KF036858 |

Newly generated sequences are in boldface.

et al. 2019). Taking the unique morphological characteristics of *Xenasmatella* into consideration, we raise the clade of *Xenasmatella* to an order rank. Accordingly, a new order and a new family are described to accommodate *Xenasmatella*.

The alignment of the four-locus dataset included 46 taxa and contained 3,372 characters. Its best-fit evolutionary model was estimated as GTR + I + G. The ML search stopped after 250 bootstrap replicates. All chains in BI converged after ten million generations, which is indicated by the effective sample sizes of all parameters above 1,000 and the potential scale reduction factors close to 1.000. ML and BI algorithms constructed similar topologies that differed only at several poorly supported nodes. The topology resulting from the ML algorithm is shown along with BS values of more than 50% and BPPs of more than 0.8 at the nodes (Figure 3). In the current phylogeny (Figure 3), two newly sequenced specimens, viz. LWZ 20200819–29a and LWZ 20200819–30a from Sichuan Province, China, grouped together (BS = 100%, BPP = 1) as an independent lineage from other sampled species within *Xenasmatella*. In association with morphological characteristics, these two specimens are described as a new species of *Xenasmatella*.

### *3.2 Taxonomy*

***Xenasmatellales*** L.W. Zhou & S.L. Liu, ord. nov.

*Fungal names number*: FN 571316

*Etymology: Xenasmatellales* (Latin), refers to the type genus *Xenasmatella.*

*Type genus: Xenasmatella* Oberw., Sydowia 19 (no. 1–3): 28 (1966).

*Type species: Xenasmatella subflavidogrisea* (Litsch.) Oberw. ex Jülich, Persoonia 10 (no. 3): 335 (1979).

*Description*: Basidiomes resupinate, effused, thin, soft membranous to ceraceous. Hymenophore smooth to grandinioid; margin fibrillose with hyphal strands. Hyphal system monomitic, all septa with clamp connections. Cystidia absent. Basidia usually pleural, cylindrical or broadly clavate, with four sterigmata. Basidiospores aculeate, thin to slightly thick-walled, subglobose to ellipsoid, inamyloid, indextrinoid, acyanophilous. On wood.

*Notes*: *Xenasmatellales* is characterised by a combination of corticioid hymenophores, soft membranous to ceraceous basidiomes, fibrillose margin with hyphal strands, the absence of cystidia, aculeate basidiospores and growth on wood. *Sistotremastrales* is another order exclusively producing corticioid basidiomes in *Basidiomycota*; however, species of *Sistotremastrales* have hard texture of basidiomes,

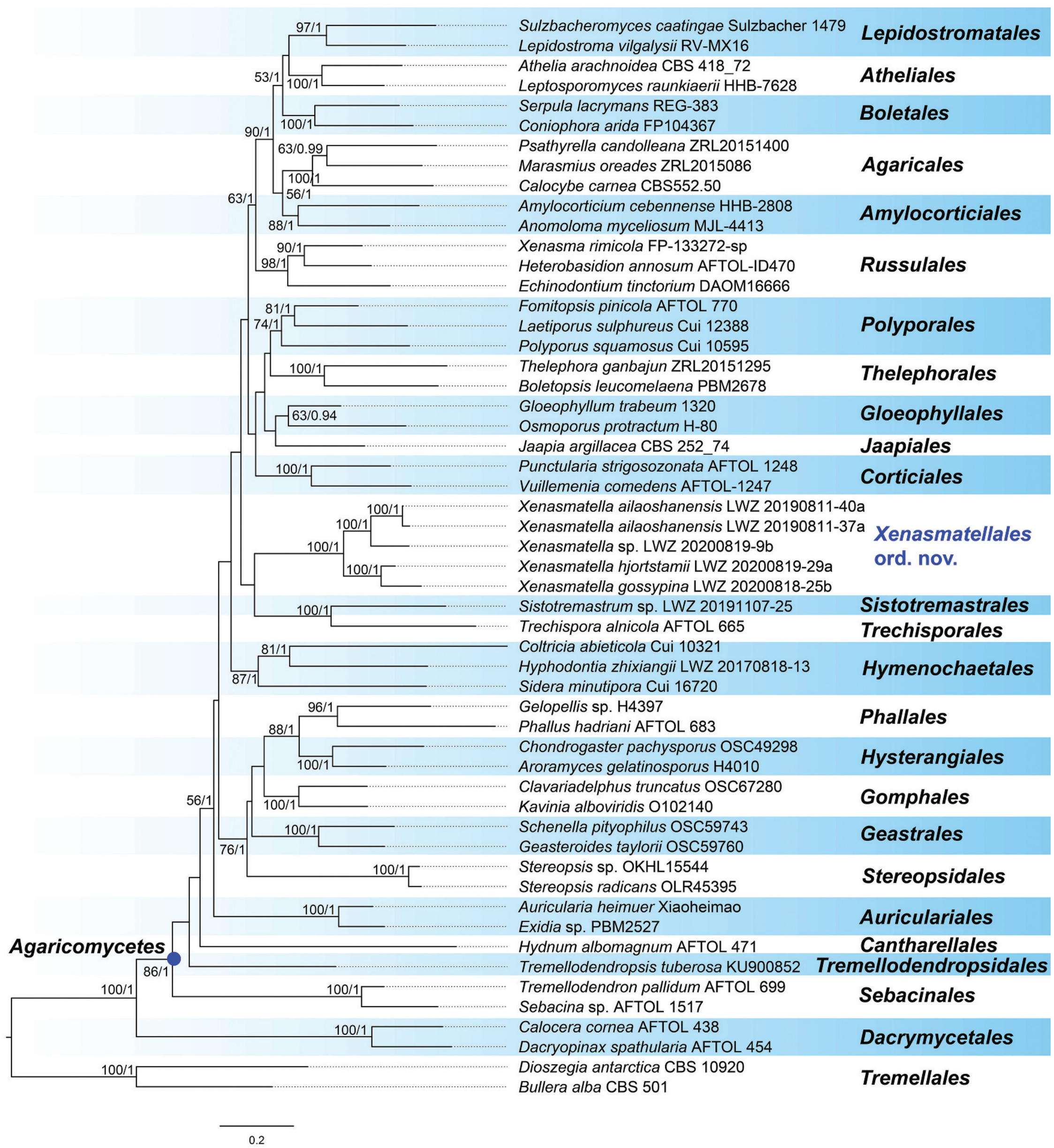


**Figure 1.** Phylogenetic position of *Xenasmatella* within *Agaricomycetes* inferred from a seven-locus dataset of nSSU, ITS, nLSU, mtSSU, *tef1a, rpb1* and *rpb2* regions. The topology is generated from the maximum likelihood algorithm. Bootstrap values and Bayesian posterior probabilities simultaneously above 50% and 0.8, respectively, are presented at the nodes.

basidia with four to eight sterigmata and smooth basidiospores (Liu et al. 2022).

***Xenasmatellaceae*** L.W. Zhou & S.L. Liu, fam. nov.

*Fungal names number*: FN 571254

*Etymology: Xenasmatellaceae* (Latin), refers to the type genus *Xenasmatella*.

*Type genus: Xenasmatella* Oberw., Sydowia 19 (no. 1–3): 28 (1966).

*Type species: Xenasmatella subflavidogrisea* (Litsch.) Oberw. ex Jülich, Persoonia 10 (no. 3): 335 (1979).

*Description*: Basidiomes resupinate, effused, thin, soft membranous to ceraceous. Hymenophore smooth to grandinioid; margin fibrillose with hyphal strands. Hyphal system monomitic, all septa with clamp connections. Cystidia absent. Basidia usually pleural, cylindrical or broadly clavate, with four sterigmata. Basidiospores aculeate, thin to slightly thick-walled, subglobose to ellipsoid, inamyloid, indextrinoid, acyanophilous. On wood.

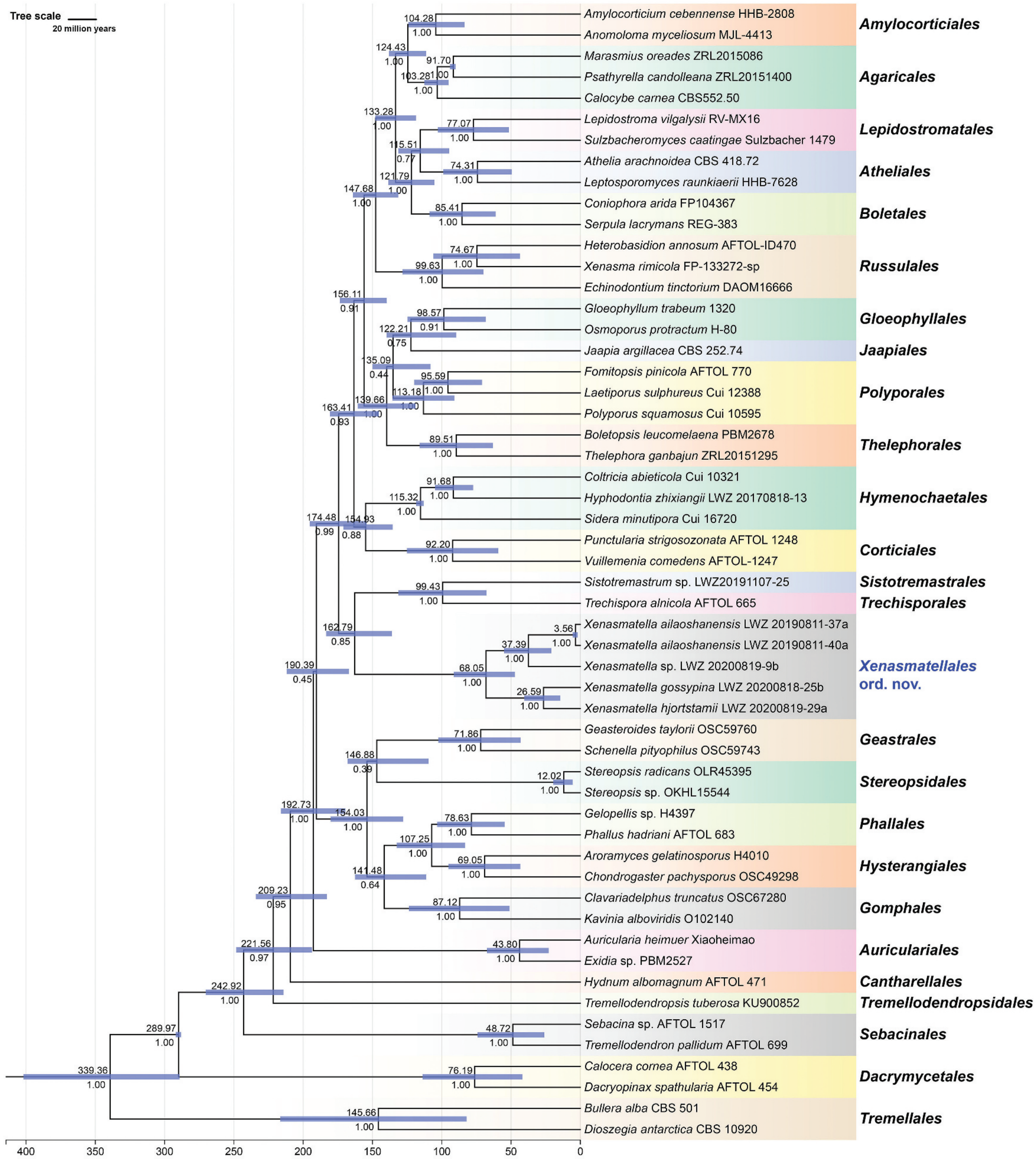


**Figure 2.** Maximum-clade-credibility chronogram and estimated divergence times of orders within *Agaricomycetes* inferred from a seven-locus dataset of nSSU, ITS, nLSU, mtSSU, *tef1a, rpb1* and *rpb2* regions. The estimated divergence times of 95% highest posterior density for all clades are indicated as node bars. The mean divergence times of clades and Bayesian posterior probabilities above 0.8 are presented above and below the branches, respectively, at the nodes.

*Notes*: *Xenasmatellaceae* is the single family within *Xenasmatellales* and accommodates a single genus *Xenasmatella*.

***Xenasmatella hjortstamii*** S.L. Liu & L.W. Zhou, sp. nov. Figures 4, 5, 6a

*Fungal names number*: FN 571320

*Etymology: hjortstamii* (Latin), refers to the Swedish mycologist, Kurt Hjortstam, who made significant contributions to the taxonomy of *Xenasmatella*.

*Diagnosis*: Differs from other species of *Xenasmatella* in the cinnamon colour of hymenophoral surface upon drying and growth on bamboo.

*Description*: Basidiomes annual, resupinate, without odour or taste, soft membranous when fresh, smooth or somewhat wrinkled upon drying, up to 12 cm long, 5 cm wide, 0.3 mm thick. Hymenophoral surface pale mouse-grey to clay buff when fresh, cinnamon colour upon drying; margin sterile, thinning out, fimbriate, brownish, sometimes fibrillose. Underneath of the

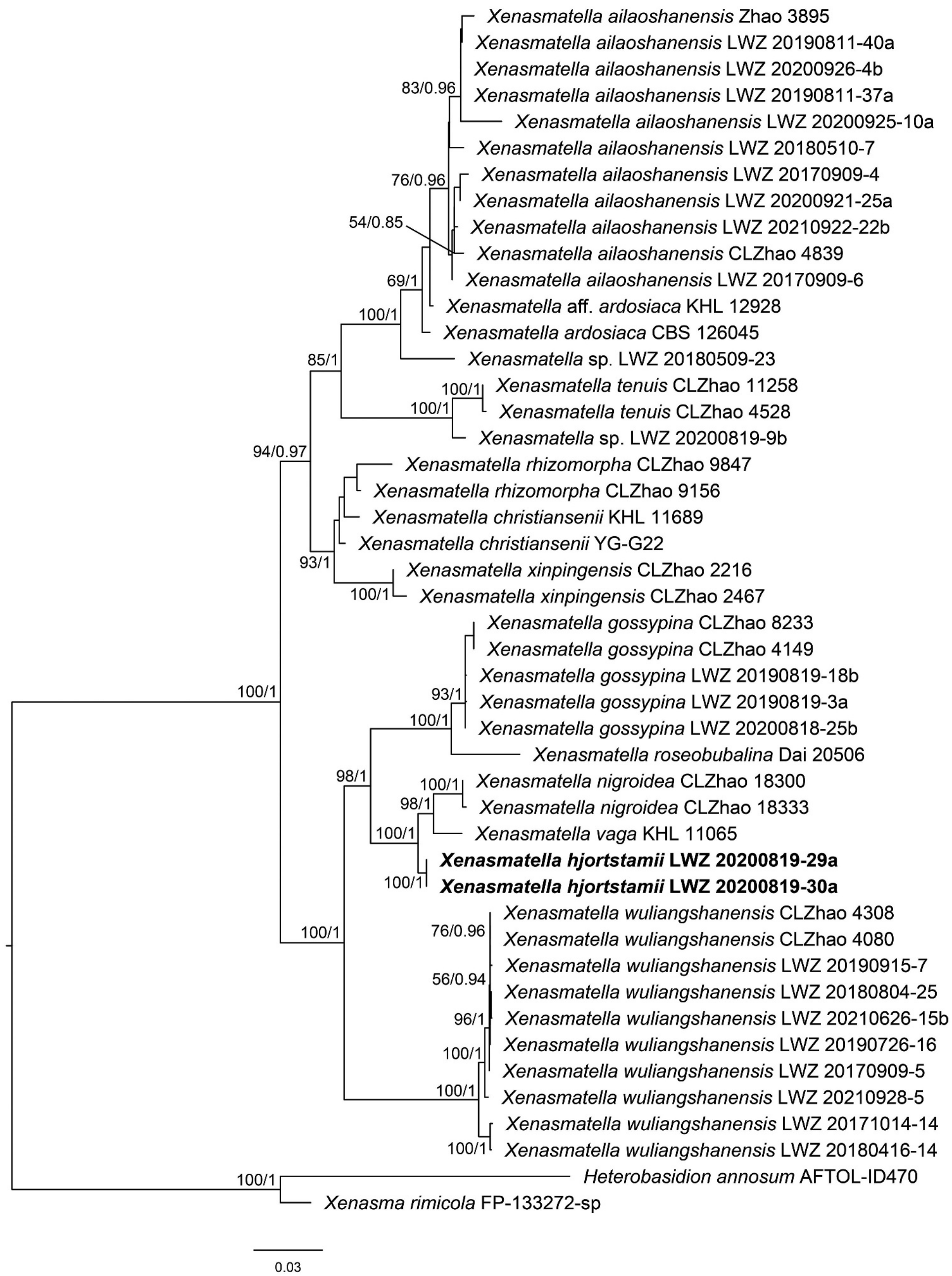


**Figure 3.** Phylogenetic relationship among species of *Xenasmatella* inferred from a four-locus dataset of nSSU, ITS, nLSU and mtSSU regions. The topology is generated from the maximum likelihood algorithm. Bootstrap values and Bayesian posterior probabilities simultaneously above 50% and 0.8, respectively, are presented at the nodes. The new species is in boldface.

basidiomes with thin, concolorous to cinnamon hyphal cordons. Hyphal system monomitic; generative hyphae with clamp connections, slightly thick-walled, yellowish to brownish, unbranched or rarely branched, normally 3–5 µm in diam., sometimes 6–7 µm in diam., inamyloid, indextrinoid, acyanophilous; tissues unchanged in KOH. Cystidia and cystidioles absent. Basidia pleural or broadly clavate, with 4 sterigmata and a basal clamp connection, 14–22 × 5–9 µm; basidioles dominant, in shape similar to basidia, but slightly smaller. Basidiospores ellipsoid to subglobose, yellowish, thin-walled, aculeate, inamyloid, indextrinoid, acyanophilous, 4–5 × 3–3.8(–4) µm, L = 4.4 µm, W = 3.3 µm, Q = 1.3 (n = 60/2).

**Figure 4.** Basidiomes of *Xenasmatella hjortstamii*. a, b: LWZ 20200819–30a (holotype); c, d: LWZ 20200819–29a (paratype). Bar: d = 1 mm.

*Materials examined*: China. Sichuan Province, Pingshan County, Baxianshan Scenic Spot, on root of bamboo, 19 August 2020, *L.W. Zhou*, LWZ 20200819–30a (holotype in HMAS 257912); Pingshan County, Baxianshan Scenic Spot, on root of bamboo, 19 August 2020, *L.W. Zhou*, LWZ 20200819–29a (HMAS 257913).

*Notes*: The cinnamon colour of hymenophoral surface makes *Xenasmatella hjortstamii* similar to *X. cinnamomea* and *X. vaga*. However, *X. cinnamomea* differs in its mostly hyaline generative hyphae, slightly shorter basidiospores (2.5–3.5 μm in length) and growth on magnolia (Burdsall and Nakasone 1981), and *X. vaga* in its colliculose to grandinioid basidiomes, frequently branched and anastomosing hyphal threads, larger basidiospores (5–5.5 × 4–4.5 μm) and growth on a variety of conifers and hardwood trees (Stalpers 1996; Bernicchia and Gorjón 2010). *Xenasmatella hjortstamii* may be confused with species of *Laxitextum* in *Russulales*, but differs in the absence of gloeocystidia and inamyloid basidiospores (Bernicchia and Gorjón 2010).

## 4. Discussion

In this study, the taxonomic placement of *Xenasmatella* is for the first time clarified based on multilocus phylogenetic analyses. Moreover, the species diversity and relationships of *Xenasmatella* are also further explored.

When erection, *Xenasmatella* was placed in a new family *Xenasmataceae* together with *Acanthobasidium, Litschauerella, Xenasma* the family type, and *Xenosperma* (Oberwinkler 1966). Later, Jülich (1981) erected a new

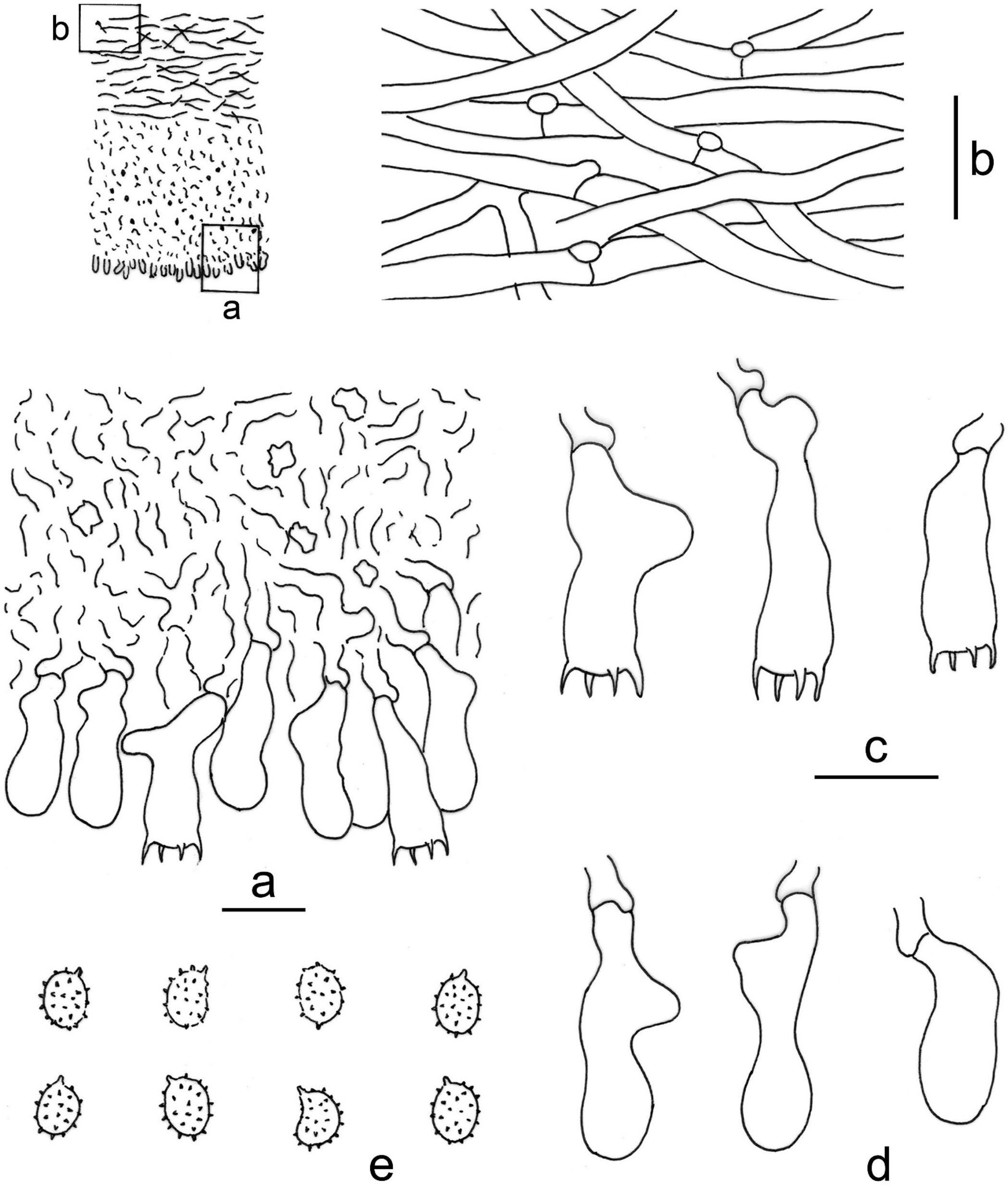


**Figure 5.** Microscopic structures of *Xenasmatella hjortstamii* (drawn from LWZ 20200819–30a, holotype). a: A vertical section of basidiomes; b: Hyphae from subiculum; c: Basidia; d: Basidioles; e: Basidiospores. Bars: 10 µm.

order *Xenasmatales* to accommodate *Xenasmataceae* being composed of *Acanthobasidium, Aphanobasidium, Lepidomyces, Xenasma, Xenasmatella* and *Xenosperma*, and a new monotypic family *Litschauerellaceae* typified by *Litschauerella*. Noteworthily, Luo and Zhao (2022) recently republished the previously known order name *Xenasmatales* Jülich as *Xenasmatales* K.Y. Luo & C.L. Zhao based on the same type. According to International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) (Turland et al. 2018), this later isonym should be disregarded and treated as a discarded name. In the latest edition of the dictionary of the fungi, the circumscription of *Xenasmataceae* was narrowed to three genera, viz. *Xenasma, Xenasmatella,* and *Xenosperma*; meanwhile this family was moved to *Polyporales* (Kirk et al. 2008). Similarly, this circumscription of the family was followed by a recent outline of *Basidiomycota* (He et al. 2019), which, however, placed *Xenasmataceae* in *Russulales*. Whichever order *Xenasmataceae* belongs to, all these studies considered

*Xenasma* and *Xenasmatella* in a single family. Nevertheless, the current seven-locus based phylogeny clearly indicates the separation of these two genera: *Xenasma* fell within *Russulales*, while *Xenasmatella* represents an independent lineage from all 23 known orders of *Agaricomycetes* (Figure 1). Moreover, the divergence time of *Xenasmatella* (Figure 2) is not contrary to previously estimated times of orders and families in *Agaricomycetes* (He et al. 2019), and to our knowledge no other known order and family names have been assigned for *Xenasmatella*. Therefore, as the type genus, *Xenasma* is accepted to belong to *Xenasmataceae* in *Russulales*, while a new monotypic order *Xenasmatellales* and a new monotypic family *Xenasmatellaceae* are introduced to accommodate *Xenasmatella*.

At the species level, including *Xenasmatella hjortstamii*, a total of 27 species are accepted in this genus with 11 species distributed in China (Liu and Yuan 2022; Luo and Zhao 2022). *Xenasmatella ailaoshanensis* (Figure 6b), *X. gossypina* (Figure 6c) and *X. wuliangshanensis* (Figure 6d) were previously known only from their type localities in Yunnan Province, China. Based on the current morphological and phylogenetic analyses, the distribution of these three species is expanded. The distribution of *X. ailaoshanensis* is newly recognised in three provincial regions in China, viz. Beijing (LWZ 20170909–4 and LWZ 20170909–6), Hubei (LWZ 20210922–22b) and Sichuan (LWZ 20190811–37a, LWZ 20190811–40a, LWZ 20200921–25a, LWZ 20200925–10a and LWZ 20200926–4b), and also in Victoria State, Australia (LWZ 20180510–7). According to the topology in the phylogenetic tree of *Xenasmatella* (Figure 3), the current concept of *X. ailaoshanensis* may be a species complex that needs to be further clarified. Three newly examined specimens of *X. gossypina*, viz. LWZ 20190819–3a, LWZ 20190819–18b and LWZ 20200818–25b were collected from Sichuan Province, China. Regarding *X. wuliangshanensis*, four provincial regions in China, viz. Beijing (LWZ 20170909–5, LWZ 20180804–25 and LWZ 20190726–16), Guizhou (LWZ 20210928–5), Jiangxi (LWZ 20210626–15b), and Sichuan (LWZ 20190915–7) are recognised as its new distribution. Furthermore, two specimens from Malaysia (LWZ 20180416–14) and Viet Nam (LWZ 20171014–14) forming a separate lineage from other representatives of *X. wuliangshanensis* are tentatively identified to be *X. wuliangshanensis* mainly due to morphological consistency (Figure 3). Moreover, two unnamed single-specimen lineages of *Xenasmatella*, viz. LWZ

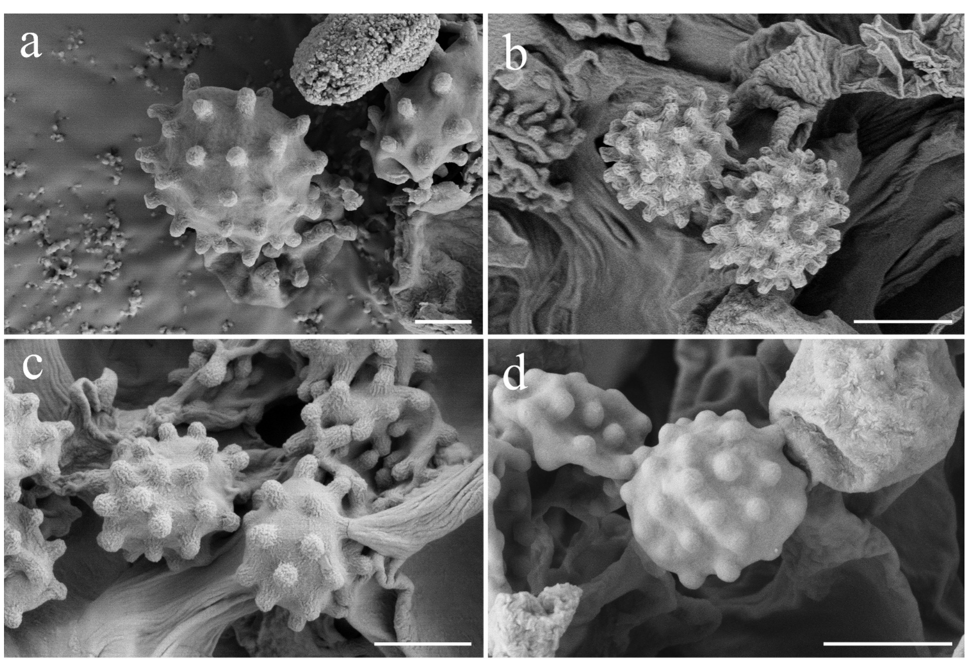


**Figure 6.** Scanning electron micrographs of basidiospores of *Xenasmatella*. a: *X. hjortstamii* (LWZ 20200819–30a, holotype); b: *X. ailaoshanensis* (LWZ 20200925–10a); c: *X. gossypina* (LWZ 20190819–18b); d: *X. wuliangshanensis* (LWZ 20210928–5). Bars: 2 μm.

20180509–23 from Victoria State, Australia and LWZ 20200819–9b from Sichuan Province, China are revealed (Figure 3), and they may represent two potential new species of this genus but more samples need to be examined before making this taxonomic proposal. Given the above, more species of *Xenasmatella* await to be described worldwide.

## 5. Conclusion

In summary, the taxonomy and phylogeny of *Xenasmatella* are explored with the aid of multilocus phylogenetic analyses for the first time. Accordingly, a monotypic order *Xenasmatellales* and a monotypic family *Xenasmatellaceae* are newly introduced for *Xenasmatella* within *Agaricomycetes*, and a new species *X. hjortstamii* is described. These taxonomic proposals update the taxonomic framework of *Agaricomycetes* and provide a crucial supplement for comprehensively understanding the evolutionary history of this fungal class.

## Disclosure statement

No potential conflict of interest was reported by the authors.


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## Availability of data and materials

All sequence data generated for this study can be accessed via GenBank: https://www.ncbi.nlm.nih.gov/genbank/.

## Supplementary files

Supplementary file 1. The alignment resulted from a seven-locus dataset of nSSU, ITS, nLSU, mtSSU, *tef1a, rpb1* and *rpb2* regions.

Supplementary file 2. The alignment resulted from a four-locus dataset of nSSU, ITS, nLSU and mtSSU regions.

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