

Morphological characteristics and phylogenetic analyses revealed four new species (Basidiomycota) in the Yunnan-Guizhou Plateau, China

Siyuan He^{1*}, Lu Wang^{1*}, Kaize Shen², Hongmin Zhou^{1,3}

¹ College of Forestry, Southwest Forestry University, Kunming 650224, China

² Yunnan Key Laboratory of Gastrodia and Fungi Symbiotic Biology, Zhaotong University, Zhaotong 657000, China

³ The Key Laboratory of Forest Resources Conservation and Utilization in the South-west Mountains of China Ministry of Education, Key Laboratory of National Forestry and Grassland Administration on Biodiversity Conservation in Southwest China, Yunnan Provincial Key Laboratory for Conservation and Utilization of In-forest Resource, Southwest Forestry University, Kunming 650224, China

Corresponding author: Hongmin Zhou (zhouhongmin@swfu.edu.cn)



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Abstract

Four new fungi, viz. *Clavulinopsis wumengshanensis* (Clavariaceae, Agaricales), *Henningsomyces bambusae* (Porothleaceae, Agaricales), *Xenasma bisterigmatae*, and *X. guttulata* (Xenasmataceae, Russulales), from Yunnan Province in China, are proposed, based on a combination of morphological features and molecular evidence. Phylogenetic analyses were conducted using a combined dataset of internal transcribed space and nuclear ribosomal RNA large subunit sequences. The ITS+LSU analysis showed that *Clavulinopsis wumengshanensis* **sp. nov.** groups with *C. aurantiocinnabarina*, *Henningsomyces bambusae* **sp. nov.** forms a sister group with *H. candidus*, *Xenasma bisterigmatae* **sp. nov.** is clustered with *X. rimicola*, and *X. guttulata* **sp. nov.** is clustered with *X. pruinsum*. The morphology and multi-gene phylogenetic analyses confirmed the placement of the four new taxa. *Clavulinopsis wumengshanensis* is distinguished by buff-yellow to straw-yellow basidiomata, clavate to subcylindrical basidia with four sterigmata, and subglobose basidiospores with several guttules (7–8.5 × 6–7.5 µm); *Henningsomyces bambusae* is characterized by white to cream basidiomata with short cylindric to tubular colonies, cylindrical to subcylindrical basidia with two sterigmata and globose to subglobose basidiospores (6.5–8.5 × 6.5–8.5 µm); *Xenasma bisterigmatae* can be characterized by its membranaceous and ash-grey basidiomata, clavate to subcylindrical basidia with two sterigmata and ellipsoid to subglobose basidiospores (10–12.5 × 8–10.5 µm); *X. guttulata* is distinguished by membranaceous and white to cream basidiomata, clavate to subcylindrical basidia with two sterigmata and ellipsoid to narrowly ellipsoid basidiospores (7–9 × 5.5–7.5 µm).

Key words: 4 new taxa, Agaricales, biodiversity, Russulales, taxonomy; Yunnan province

Introduction

The phylum Basidiomycota R.T. Moore represents one of the major divisions in the fungal tree of life, with global estimates that it encompasses 1.4–4.2 million species in the phylum and the latest estimates of 0.7 to 1 million species, which

* These authors have contributed equally to this work and share the first authorship.

represent about 28–40% of all fungal diversity (Hyde 2022; He et al. 2024; Liu et al. 2024). The basidiomata of Basidiomycota exhibit complex forms, such as coralloid, corticioid, gilled, hydroid, poroid, and toothed basidiomata (Bernicchia and Gorjón 2010; He et al. 2019; Zhou et al. 2024a). Traditionally, Basidiomycota is typically characterized by the basidia and basidiospores and some variable morphological characters, such as diverse cellular constructions in hyphal systems and meiosporangia; the basidiomata reflect a profound evolutionary history at the various taxonomic levels within Basidiomycota (Zhao et al. 2016; Hyde et al. 2023; Dong et al. 2024). Nowadays, DNA sequence-based classification and identification have become the standard methodology in fungal taxonomy (Dai et al. 2021; Zhang et al. 2023; Dong et al. 2024; He et al. 2024).

The genus *Clavulinopsis* Overeem, classified within the family Clavariaceae (Agaricales, Basidiomycota), includes species that are widely distributed. It is characterized by yellow, orange, or creamy white basidiomata, with simple or regularly dichotomously branched, cylindric or fusoid stems; generative hyphae with obtuse, occasionally inflated hyphae with clamp connections; 2–4-spored basidia; and smooth or echinulate basidiospores occasionally with big guttules (Petersen 1996; Knudsen and Vesterholt 2012; Keleş and Kaya 2021; Yan et al. 2023). More than 171 taxon records of the genus currently are listed in the Index Fungorum database (<http://www.indexfungorum.org>; accessed on 2 November 2024), and approximately 84 species names are legitimately published (Yan et al. 2023). However, the phylogeny of *Clavulinopsis* is ambiguous due to a lack of molecular evidence and morphological data. Two similar genera, *Clavaria* and *Ramariopsis*, are easily confused with *Clavulinopsis* in clavarioid basidiomata. However, the micromorphology features are different between the three genera; viz., *Ramariopsis* has various basidiomata, but those in *Clavaria* and *Clavulinopsis* are simple; clamp connections are present on the basidia and hyphae in *Clavulinopsis* (Corner 1950, 1970; Petersen and Corner 1968; Yan et al. 2023). Furthermore, the outline of *Clavulinopsis* was defined by the basidiospore ornamentation, and the related taxa were examined by D.N. Pegler and T.W.K. Young. Applying the molecular phylogenetic methods generated considerable promotion in the generic definition of *Clavulinopsis*, gradually clarifying the classification boundaries among several closely related genera, particularly *Clavaria* and *Ramariopsis* (Furtado et al. 2016; Yan et al. 2023; He et al. 2024).

Henningsomyces Kuntze, a type of cyphelloid fungi first described by Kuntze (1898), belongs to the family Porotheleaceae (Agaricales) (He et al. 2024). Previously, cyphelloid fungi were classified in the family Cyphellaceae based on similar morphology. Subsequently, the name Porotheleaceae (Murrill 1916) was later established for this group (Cooke 1957, 1961). However, the phylogenetic relationship of many cyphelloid fungi remains ambiguous. The genus *Henningsomyces*, a typical cyphelloid fungus with cylindric basidiomata, is typified by *H. candidus* (Pers.) Kuntze and is characterized by annual basidiomata consisting of sparse or gregarious tubes, a monomitic hyphae system that typically exhibits both clamp connections and simple septa, an absence of cystidia, and globose to subglobose basidiospores (Wei and Qin 2009; Liu et al. 2023). Among the 50 records of the genus currently listed in the Index Fungorum database (<http://www.indexfungorum.org>; accessed on 2 November 2024), approximately 22 species names are legitimately published (Liu et al. 2023). Among those studies, *Henningsomyces* forms a monophyletic lineage and nests into

the order Agaricales (Moncalvo et al. 2006, Bodensteiner et al. 2004, Binder et al. 2005, Thorn et al. 2005, Baltazar et al. 2015, Lucas and Dentinger 2015, Moreno et al. 2017). However, the placement of *Henningsomyces* and related taxa has not yet been substantiated. In recent years, based on morphological examination and molecular phylogenetic analysis, six new species were described in China (Yan et al. 2023). Most mycologists focused on the poroid or corticioid species, but the cyphelloid species bearing cup-, bowl-, or tube-shaped “cyphelloid” hymenophores were rarely reported, such as the genus *Henningsomyces* bearing the cylindric basidiomata (Wei and Qin 2009).

Xenasma Donk, classified in the family Xenasmataceae (Russulales, Basidiomycota), was introduced in 1957 and is typified by *X. rimicola* (P. Karst.) Donk (Liberta 1960; Bernicchia and Gorjón 2010). This genus is characterized by the resupinate and smooth basidiomata, a monomitic hyphal system with clamps, generative hyphae, and globose to cylindrical, striate basidiospores (Liberta 1960; Bernicchia and Gorjón 2010). Among the 39 records of the genus currently listed in the Index Fungorum database (<http://www.indexfungorum.org>; accessed on 2 November 2024), only 11 species names are legitimately published (Bernicchia and Gorjón 2010; He et al. 2024). *Xenasma* Donk continues to intrigue mycologists due to its unique morphological characteristics and ecological roles (Bernicchia and Gorjón 2010). The genus is primarily found in temperate forest ecosystems, often growing on decaying wood and contributing to wood decomposition (Liu et al. 2024). Recent phylogenetic studies have expanded the understanding of its evolutionary relationships within the Russulales, highlighting the potential for undiscovered species in understudied regions (He et al. 2019, 2024). The morphology of the basidiome and hymenophore, together with habitat, are often regarded as important characters for the taxonomy of the order Russulales, and Xenasmataceae is the only family in which the smooth hymenophore configuration could be found (Larsson and Larsson 2003; Miller et al. 2006; He et al. 2024). In the latest study, there are only two genera in the family Xenasmataceae, namely *Xenasma* and *Xenosperma* Oberw, in which the genus *Xenasma* is a mystery genus, and no new taxon was reported from this genus for nearly half a century (He et al. 2024).

The specimens of the three genera collected in the Yunnan-Guizhou Plateau, China, which could not be assigned to any described species of the order. Therefore, four new species, viz. *Clavulinopsis wumengshanensis*, *Henningsomyces bambusae*, *Xenasma bisterigmatae*, and *X. guttulate*, are proposed with descriptions, illustrations, and phylogenetic analysis results.

Materials and methods

Morphology

Fresh fruiting bodies of the fungi were collected from Wumengshan National Nature Reserve in Zhaotong of Yunnan Province, China, and the important collection information was recorded (Rathnayaka et al. 2024). Specimens were dried in an electric food dehydrator at 40 °C (Hu et al. 2022), then sealed and stored in an envelope bag and deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. Macromorphological descriptions are based on field notes and photos captured in the field and lab. Color terminology follows Petersen (1996). Micromorphological data were

obtained from the dried specimens when observed under a light microscope following the previous study (Zhao et al. 2023; Zhou et al. 2024b). The following abbreviations are used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB- = acyanophilous, IKI = Melzer's Reagent, IKI- = both inamyloid and indextrinoid, Lm = mean spore length (arithmetic average for all spores), Wm = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied, and n = a/b (number of spores (a) measured from given number (b) of specimens).

Molecular phylogeny

The CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing) was used to obtain DNA from dried specimens, and PCR was performed according to the manufacturer's instructions with some modifications. ITS locus was amplified using the primer pairs ITS5/ITS4 (White et al. 1990). The nuclear LSU region was amplified with primer pair LR0R and LR7 (Vilgalys and Hester 1990). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 54 °C for 45 s, and 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for LSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 50 °C for 1 min, and 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. All newly generated sequences were submitted to GenBank and are listed in Table 1.

Sequences generated for this study were aligned, with additional sequences downloaded from GenBank. Sequences were aligned using MAFFT v.7 (<https://mafft.cbrc.jp/alignment/server/>), adjusting the direction of nucleotide sequences according to the first sequence (accurate enough for most cases) and selecting the G-INS-i iterative refinement method (Katoh et al. 2019). Alignments were manually adjusted to maximize alignment and minimize gaps with BioEdit v.7.0.9 (Hall 1999). A dataset of concatenated ITS and LSU sequences was used to determine the phylogenetic position of the new species. Maximum likelihood (ML) analysis was performed using the CIPRES Science Gateway (Miller et al. 2010) based on the dataset using the RA × ML-HPC BlackBox tool, with the setting RA × ML halt bootstrapping automatically and 0.25 for maximum hours and obtaining the best tree using ML search. Other parameters in ML analysis followed default settings, and statistical support values were obtained using nonparametric bootstrapping with 1,000 replicates. Maximum parsimony (MP) analyses were applied to the combined three datasets following the methods outlined in a previous study (Zhao and Wu 2017), and the tree construction procedure was performed in PAUP* version 4.0b10 (Swofford 2002). Bayesian inference (BI) analysis based on the dataset was performed using MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003). The best substitution model for the dataset was selected by ModelFinder (Kalyaanamoorthy et al. 2017) using a Bayesian information criterion, and the model was used for Bayesian analysis. Four Markov chains were run from random starting trees. Trees were sampled every 1,000th generation. The first 25% of sampled trees were discarded as burn-in, whereas other trees were used to construct a 50% majority consensus tree and for calculating Bayesian posterior probabilities (BPPs). The bootstrap support for ML is greater than or equal to 70%, and Bayesian posterior probabilities greater than or equal to 0.95 are indicated on the branches in the phylogenetic tree, respectively.

Table 1. Names, voucher numbers, references, and corresponding GenBank accession numbers of the taxa used in the phylogenetic analyses. [* Indicates type materials;—indicates sequence unavailability].

| Taxa | Locality | Voucher no. | GenBank accession no. | | References |
|---|--------------------|----------------------|-----------------------|-----------------|-------------------------------|
| | | | ITS | 28S | |
| <i>Clavaria apulica</i> | Italy | AMB 150 | MT853065 | MT853066 | Agnell and Papetti 2020 |
| <i>Clavulinopsis amoena</i> | Australia | PBM3381 | — | HQ877702 | Hyde et al. 2016 |
| <i>Clavulinopsis aspersa</i> | China | MHHNU10153 | OQ703777 | OQ703794 | Yan et al. 2023 |
| <i>Clavulinopsis aspersa</i> | China | MHHNU10342* | OQ703778 | OQ703795 | Yan et al. 2023 |
| <i>Clavulinopsis aurantiaca</i> | Brazil | URM<BRA>:84212* | — | KX227749 | Hyde et al. 2016 |
| <i>Clavulinopsis aurantiaca</i> | Brazil | URM<BRA>:84216 | KC348464 | NG058946 | Hyde et al. 2016 |
| <i>Clavulinopsis bicolor</i> | China | MHHNU10381* | OQ703780 | OQ703797 | Yan et al. 2023 |
| <i>Clavulinopsis bispora</i> | China | MHHNU11188 | OQ703782 | OQ703799 | Yan et al. 2023 |
| <i>Clavulinopsis bispora</i> | China | MHHNU11181* | OQ703781 | OQ703798 | Yan et al. 2023 |
| <i>Clavulinopsis corallinorosea</i> | Australia | PBM3380 | KP257144 | HQ877707 | Hyde et al. 2016 |
| <i>Clavulinopsis corniculata</i> | USA | TENN064106 | KP257145 | HQ877713 | Hyde et al. 2016 |
| <i>Clavulinopsis erubescens</i> | China | MHHNU10290 | OQ703784 | OQ703801 | Yan et al. 2023 |
| <i>Clavulinopsis erubescens</i> | China | MHHNU8040* | OQ703783 | OQ703800 | Yan et al. 2023 |
| <i>Clavulinopsis fusiformis</i> | USA | PBM 2804 | — | EF535273 | Hyde et al. 2016 |
| <i>Clavulinopsis fusiformis</i> | USA | TENN064110 | — | HQ877717 | Hyde et al. 2016 |
| <i>Clavulinopsis gracillima</i> | Canada | MO 215748 | KY706170 | — | Hay et al. 2019 |
| <i>Clavulinopsis incarnata</i> | China | MHHNU11331 | OQ703788 | OQ703805 | Yan et al. 2023 |
| <i>Clavulinopsis incarnata</i> | China | MHHNU11330* | OQ703787 | OQ703804 | Yan et al. 2023 |
| <i>Clavulinopsis miyabeana</i> | China | ZP-2118 | MK427059 | — | Chen and Zhang 2019 |
| <i>Clavulinopsis sulcata</i> | Australia | PBM3379 | — | HQ877709 | Hyde et al. 2016 |
| <i>Clavulinopsis sulcata</i> | New Zealand | PDD78241 | — | DQ284904 | Dentinger and McLaughlin 2006 |
| <i>Clavulinopsis trigonospora</i> | China | MHHNU9186 | OQ703789 | OQ703806 | Yan et al. 2023 |
| <i>Clavulinopsis trigonospora</i> | Italy | AMB: 18557* | NR176720 | NG088120 | Franchi and Marchetti 2021 |
| <i>Clavulinopsis tropicalis</i> | China | MHHNU10721 | OQ703792 | OQ703809 | Yan et al. 2023 |
| <i>Clavulinopsis tropicalis</i> | China | MHHNU10722* | OQ703793 | OQ703810 | Yan et al. 2023 |
| <i>Clavulinopsis wumengshanensis</i> | China | CLZhao 29651 | PQ408630 | PQ408635 | Present Study |
| <i>Clavulinopsis wumengshanensis</i> | China | CLZhao 29612* | PQ408629 | PQ408634 | Present Study |
| <i>Clitocybula familia</i> | Slovakia | BRNM 736053 | JF730328 | JF730323 | Antonín et al. 2011 |
| <i>Clitocybula intervenosa</i> | São Tomé | BAP 613 SFSU* | MH414561 | MH385335 | Cooper 2018 |
| <i>Clitocybula lacerata</i> | Italy | AMB 18779 | OM422757 | OM423633 | Consiglio et al. 2022 |
| <i>Clitocybula lacerata</i> | Czech Republic | PRM 915404 | LT854054 | LT854030 | Antonín et al. 2019 |
| <i>Clitocybula oculus</i> | USA | PBM 1156 | DQ192178 | DQ151452 | Matheny et al. 2006 |
| <i>Gerronema keralense</i> | India | CAL 1666* | NR159832 | NG064531 | Latha et al. 2018 |
| <i>Gerronema kuruense</i> | India | CAL 1665* | NR159831 | NG064530 | Latha et al. 2018 |
| <i>Gerronema xanthophyllum</i> | Czech Republic | PRM 924657 | LT854023 | LT854023 | Antonín et al. 2019 |
| <i>Henningsomyces bambusae</i> | China | CLZhao 33024 | PQ408626 | — | Present study |
| <i>Henningsomyces bambusae</i> | China | CLZhao 33085 | PQ408627 | — | Present study |
| <i>Henningsomyces bambusae</i> | China | CLZhao 33088* | PQ408628 | — | Present study |
| <i>Henningsomyces candidus</i> | France | PB338 | AY571044 | AY571008 | Bodensteiner et al. 2004 |
| <i>Henningsomyces candidus</i> | Canada | T156 | AY571043 | — | Bodensteiner et al. 2004 |
| <i>Henningsomyces hengduanensis</i> | China | LWZ 20190807-22b | OR557251 | OR527277 | Liu et al. 2024 |
| <i>Henningsomyces hengduanensis</i> | China | LWZ 20190807-11b* | OR557250 | OR527276 | Liu et al. 2024 |
| <i>Hydropodia subalpina</i> | Italy | AMB 18784 | OM422761 | OM423638 | Consiglio et al. 2022 |
| <i>Hydropodia subalpina</i> | Italy | AMB 18785 | OM422762 | OM423639 | Consiglio et al. 2022 |
| <i>Hydropodia subalpina</i> | Turkey | OKA TR-K364 | MN701620 | MN700170 | Kaygusuz et al. 2020 |
| <i>Leucoinocybe lenta</i> | Italy | AMB 18837 | OM422765 | OM423643 | Consiglio et al. 2022 |
| <i>Leucoinocybe taniae</i> | Italy | AMB 18838 | OM422766 | OM423644 | Consiglio et al. 2022 |
| <i>Leucoinocybe taniae</i> | Italy | AMB 18839 | OM422767 | OM423645 | Consiglio et al. 2022 |
| <i>Porotheleum albodescendens</i> | New Zealand | PDD 96321* | OL998343 | OL998382 | Consiglio et al. 2022 |
| <i>Porotheleum domingense</i> | Dominican Republic | JBSD 131801* | OM422768 | OM423646 | Consiglio et al. 2022 |
| <i>Porotheleum fimbriatum</i> | France | CBS 465.50 | MH856711 | — | Vu et al. 2019 |
| <i>Porotheleum parvulum</i> | Dominican Republic | JBSD 131802* | OM422783 | OM423657 | Consiglio et al. 2022 |

| Taxa | Locality | Voucher no. | GenBank accession no. | | References |
|-------------------------------------|----------------|-----------------------|-----------------------|----------|--------------------------|
| | | | ITS | 28S | |
| <i>Pseudohydropsus commenticius</i> | New Zealand | PDD 86984* | OL998339 | OL998379 | Consiglio et al. 2022 |
| <i>Pseudohydropsus floccipes</i> | Czech Republic | BRNM 816173 | OM422758 | OM423634 | Consiglio et al. 2022 |
| <i>Pseudohydropsus parafunebris</i> | New Zealand | PDD 87227* | JQ694112 | — | Consiglio et al. 2022 |
| <i>Pterula echo</i> | USA | AFTOL-ID 711 | DQ494693 | — | Matheny et al. 2006 |
| <i>Radulomyces copelandii</i> | China | Dai 15061 | KU535664 | KU535672 | Zhao et al. 2016 |
| <i>Radulotubus resupinatus</i> | China | Cui 8383* | KU535660 | KU535668 | Zhao et al. 2016 |
| <i>Rectipilus afibulatus</i> | UK | K(M)189533* | KT893457 | — | Lucas and Dentinger 2015 |
| <i>Xenasma bistaminatae</i> | China | CLZhao 32542* | PQ408631 | — | Present study |
| <i>Xenasma bistaminatae</i> | China | CLZhao 32600 | PQ408632 | — | Present study |
| <i>Xenasma guttulata</i> | China | CLZhao 32193* | PQ408633 | — | Present study |
| <i>Xenasma praeteritum</i> | USA | Alden Dirks:ACD0185 | OM009268 | — | Unpublished |
| <i>Xenasma pruinosum</i> | Japan | OTU1299 | MT594801 | — | Unpublished |
| <i>Xenasma rimicola</i> | Australia | N.L. Bougher NLB 1449 | MT537020 | — | Unpublished |
| <i>Xenasma rimicola</i> | Australia | N.L. Bougher NLB 1571 | MT571671 | — | Unpublished |

Results

The phylogeny of *Clavulinopsis*

The dataset included ITS+LSU sequences from 27 samples representing 17 taxa. The datasets had an aligned length of 2,467 characters, of which 1,775 characters are constant, 273 are variable and parsimony-uninformative, and 419 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious tree (TL = 1359, CI = 0.6799, HI = 0.5829, RI = 0.7129, RC = 0.4847). BI analysis yielded a similar topology to ML analysis, with an average standard deviation of split frequencies of 0.012252; trees were sampled every 1,000th generation, 0.4 million in total. The effective sample size (ESS) for Bayesian analysis across the two runs is double the average ESS (avg ESS) = 201. Branches that received bootstrap support for ML \geq 70%, MP \geq 50%, and BI \geq 0.95 were considered significantly supported, respectively. The ML tree was provided (Fig. 1). The phylogenetic tree (Fig. 1) reveals that the new species *Clavulinopsis wumengshanensis* is nested into the genus *Clavulinopsis* and has a close relationship with *C. aurantio-cinnabarina* (Schwein.) Corner with full support (100/100/1.00).

The phylogeny of *Henningsomyces*

The dataset included ITS sequences from 31 samples representing 23 taxa. The datasets had an aligned length of 2,375 characters, of which 1,204 characters are constant, 525 are variable and parsimony-uninformative, and 646 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious tree (TL = 2,997, CI = 0.5706, HI = 0.4294, RI = 0.5875, RC = 0.3352). The BI analysis yielded a similar topology to the ML analysis, with an average standard deviation of split frequencies of 0.007176; trees were sampled every 1,000th generation, 0.4 million in total. And the effective sample size (ESS) for Bayesian analysis across the two runs is double the average ESS (avg ESS) = 349. Branches that received bootstrap support for ML \geq 70%, MP \geq 50%, and BI \geq 0.95 were considered significantly supported, respectively. The ML tree was provided (Fig. 2). The phylogenetic tree (Fig. 2) reveals the new species *Henningsomyces bambusae* nested into the genus *Henningsomyces* and has a close relationship with *H. candidus* (Pers.) Kuntze with full support (100/100/1.00).

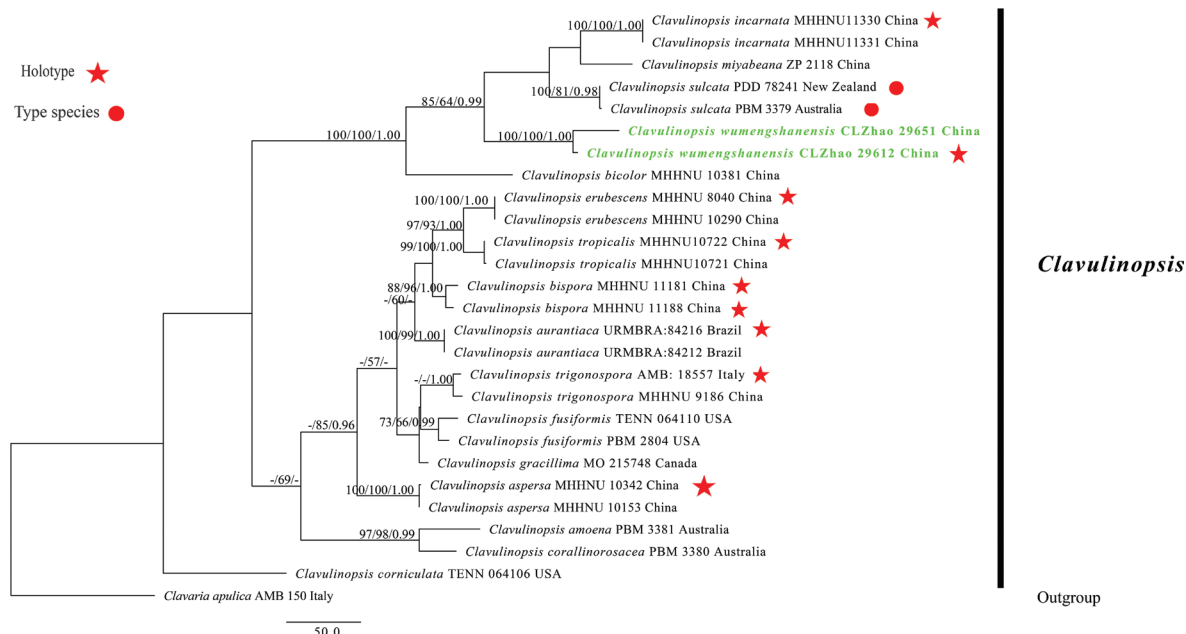


Figure 1. Phylogeny of species in *Clavulinopsis* generated by maximum likelihood based on ITS+LSU sequence data. Branches are labeled with maximum likelihood bootstrap $\geq 70\%$, a reduced lead value greater than 50%, and Bayesian posterior probabilities ≥ 0.95 , respectively.

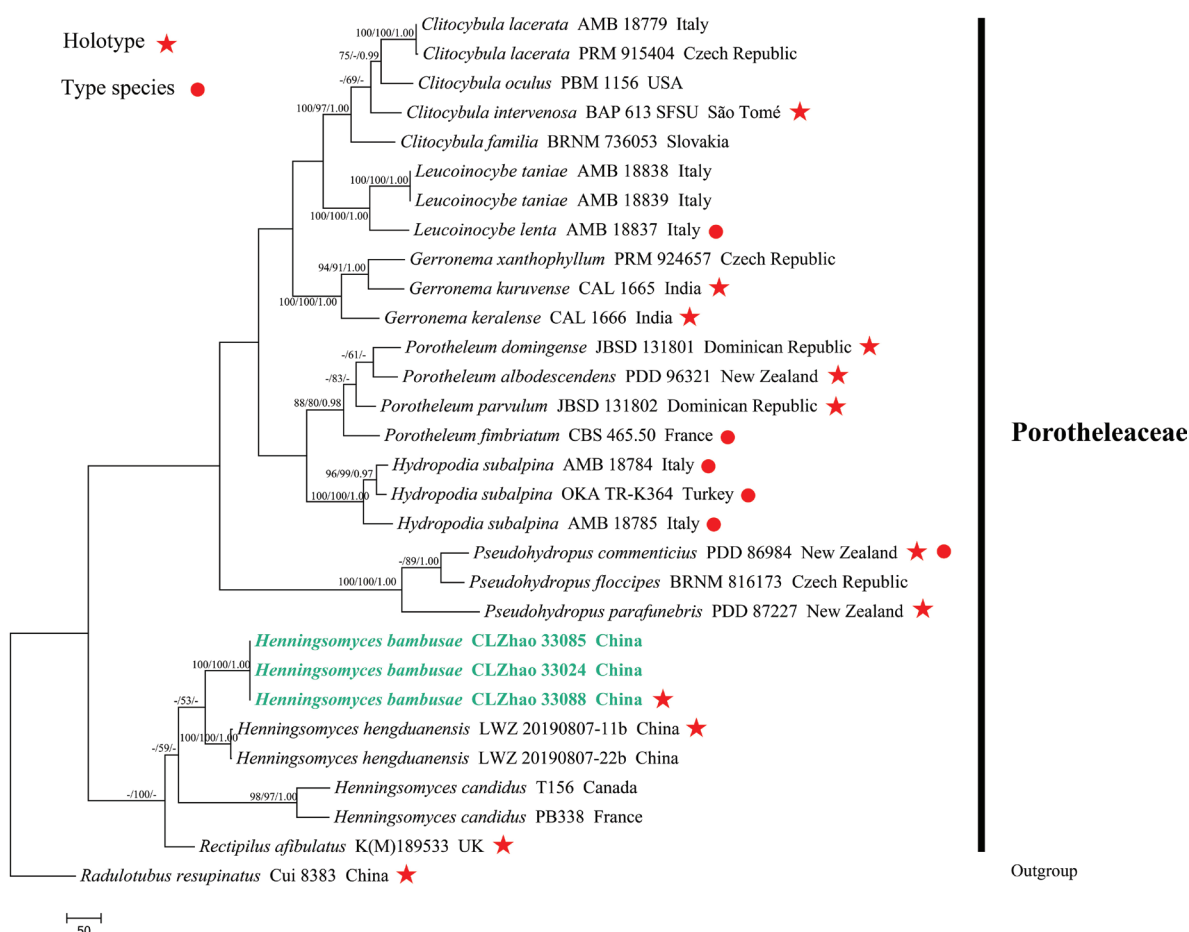


Figure 2. Phylogeny of species in *Henningsomyces* generated by maximum likelihood based on ITS sequence data. Branches are labeled with maximum likelihood bootstrap $\geq 70\%$, a reduced lead value greater than 50%, and Bayesian posterior probabilities ≥ 0.95 , respectively.

The phylogeny of *Xenasma*

The dataset included ITS sequences from nine samples representing seven taxa. The datasets had an aligned length of 944 characters, of which 574 characters are constant, 154 are variable and parsimony-uninformative, and 216 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious tree (TL = 520, CI = 0.8942, HI = 0.1058, RI = 0.8243, RC = 0.7371). The BI analysis yielded a similar topology to the ML analysis, with an average standard deviation of split frequencies of 0.007297; trees were sampled every 1,000th generation, 0.4 million in total. And the effective sample size (ESS) for Bayesian analysis across the two runs is double the average ESS (avg ESS) = 768.5. Branches that received bootstrap support for ML $\geq 70\%$, MP $\geq 50\%$, and BI ≥ 0.95 were considered significantly supported, respectively. The ML tree was provided (Fig. 3). The phylogenetic tree (Fig. 3) reveals the two new species, *Xenasma bisterigmatae* and *X. guttulata*, nested into the genus *Xenasma*. The taxon *X. bisterigmatae* has a close relationship with *X. rimicola* (P. Karst.) Donk, while the taxon *X. guttulata* has a close relationship with *X. pruinsum* with strong support (97/100/0.96). The BLAST result of four new species for the closest top 10 taxa and their corresponding parameters are given (Table 2).

The BLAST result of four new species for the closest top 10 taxa and their corresponding parameters are given (Table 2).

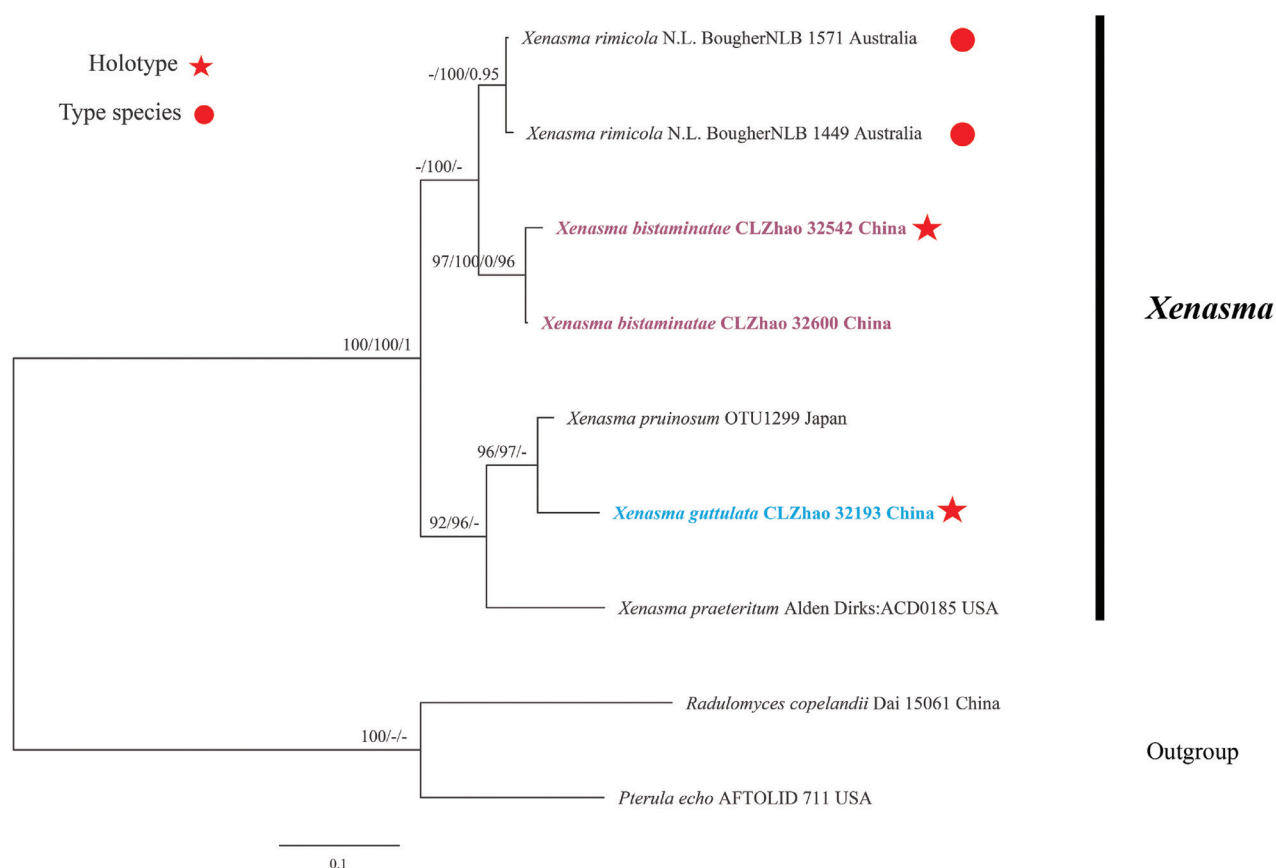


Figure 3. Phylogeny of species in *Xenasma* generated by maximum likelihood based on ITS sequence data. Branches are labeled with maximum likelihood bootstrap $\geq 70\%$, a reduced lead value greater than 50%, and Bayesian posterior probabilities ≥ 0.95 , respectively.

Table 2. The BLAST result of four new species for the closest top 10 taxa and their corresponding parameters.

| Scientific Name | Specimens | Sequence Number | Max score | Total score | Query cover | E value | Per. Ident. | Acc. len. | Accession |
|--------------------------------------|--------------|-----------------|-----------|-------------|-------------|---------|-------------|-----------|-----------|
| <i>Clavulinopsis wumengshanensis</i> | CLZhao 29612 | PQ408629 | 1123 | 1123 | 100% | 0 | 100% | 638 | PQ408629 |
| | | | 734 | 734 | 71% | 0 | 97.24% | 431 | PQ515870 |
| | | | 448 | 448 | 44% | 6e-121 | 96.68% | 295 | PQ453614 |
| | | | 911 | 911 | 93% | 0 | 95.94% | 573 | ON943319 |
| | | | 972 | 972 | 100% | 0 | 95.60% | 627 | PQ346233 |
| | | | 970 | 970 | 100% | 0 | 95.59% | 626 | PQ346239 |
| | | | 976 | 976 | 100% | 0 | 95.57% | 624 | PQ346237 |
| | | | 966 | 966 | 100% | 0 | 95.43% | 653 | PQ453611 |
| | | | 966 | 966 | 100% | 0 | 95.43% | 632 | PQ346229 |
| | | | 966 | 966 | 100% | 0 | 95.43% | 627 | PQ346265 |
| <i>Clavulinopsis wumengshanensis</i> | CLZhao 29612 | PQ408634 | 1024 | 1024 | 100% | 0 | 100.00% | 638 | PQ408629 |
| | | | 896 | 896 | 100% | 0 | 95.85% | 643 | PQ408630 |
| | | | 885 | 885 | 99% | 0 | 95.99% | 627 | PQ346233 |
| | | | 881 | 881 | 100% | 0 | 95.32% | 624 | PQ346237 |
| | | | 880 | 880 | 99% | 0 | 95.81% | 611 | PQ453612 |
| | | | 880 | 880 | 99% | 0 | 95.81% | 653 | PQ453611 |
| | | | 880 | 880 | 99% | 0 | 95.81% | 626 | PQ346239 |
| | | | 880 | 880 | 99% | 0 | 95.81% | 632 | PQ346229 |
| | | | 880 | 880 | 99% | 0 | 95.81% | 627 | PQ346265 |
| | | | 878 | 878 | 99% | 0 | 95.63% | 590 | PQ453613 |
| <i>Henningsomyces bambusae</i> | CLZhao 33088 | PQ408628 | 1282 | 1282 | 100% | 0 | 100.00% | 694 | PQ408628 |
| | | | 1253 | 1253 | 98% | 0 | 99.85% | 694 | PQ408626 |
| | | | 1223 | 1223 | 97% | 0 | 99.26% | 697 | PQ408627 |
| | | | 1081 | 1081 | 96% | 0 | 95.71% | 701 | LC774058 |
| | | | 1077 | 1077 | 96% | 0 | 95.56% | 733 | PP849903 |
| | | | 1072 | 1072 | 96% | 0 | 95.41% | 732 | MG707601 |
| | | | 1059 | 1059 | 96% | 0 | 95.1% | 745 | MK607599 |
| | | | 985 | 985 | 89% | 0 | 95.22% | 643 | AB847016 |
| | | | 950 | 950 | 89% | 0 | 94.38% | 622 | AY571057 |
| | | | 813 | 813 | 90% | 0 | 90.3% | 652 | OQ872100 |
| <i>Xenasma bisterigmatae</i> | CLZhao 32542 | PQ408631 | 1138 | 1138 | 100% | 0 | 100.00% | 616 | PQ408631 |
| | | | 1040 | 1040 | 99% | 0 | 97.55% | 611 | PQ408632 |
| | | | 846 | 846 | 92% | 0 | 93.58% | 634 | MT537020 |
| | | | 758 | 676 | 83% | 0 | 92.83% | 676 | MT571671 |
| | | | 597 | 597 | 60% | 6e-166 | 95.48% | 411 | LR819650 |
| | | | 597 | 597 | 60% | 6e-166 | 95.48% | 411 | LR602855 |
| | | | 508 | 508 | 72% | 3e-139 | 87.25% | 636 | JF691144 |
| | | | 503 | 503 | 91% | 1e-137 | 86.96% | 675 | PQ408633 |
| | | | 492 | 492 | 59% | 3e-134 | 90.98% | 638 | OM009268 |
| | | | 431 | 431 | 60% | 6e-116 | 87.47% | 417 | LR819360 |
| <i>Xenasma guttulata</i> | CLZhao 32193 | PQ408633 | 1247 | 1247 | 100% | 0 | 100.00% | 675 | PQ408633 |
| | | | 737 | 737 | 91% | 0 | 88.36% | 636 | JF691144 |
| | | | 634 | 634 | 91% | 5e-177 | 85.53% | 638 | OM009268 |
| | | | 592 | 592 | 55% | 3e-164 | 94.97% | 417 | LR819360 |
| | | | 592 | 592 | 55% | 3e-164 | 94.97% | 417 | LR602599 |
| | | | 586 | 586 | 55% | 1e-162 | 94.71% | 417 | LR602541 |
| | | | 586 | 586 | 55% | 1e-162 | 94.71% | 417 | LR819292 |
| | | | 558 | 558 | 55% | 3e-154 | 93.39% | 417 | LR602585 |
| | | | 558 | 558 | 55% | 3e-154 | 93.39% | 417 | LR819344 |
| | | | 507 | 507 | 47% | 1e-138 | 95.34% | 417 | MT852420 |

Taxonomy

***Clavulinopsis wumengshanensis* S.Y. He, H.M. Zhou & C.L. Zhao, sp. nov.**

MycoBank No: 855906

Figs 4, 5

Diagnosis. *Clavulinopsis wumengshanensis* differs from *C. aurantiocinnabarina* by buff-yellow to straw-yellow basidiomata and thick-walled, subglobose, and longer basidiospores (7–8.5 μm vs. 5.6–7.1 μm).

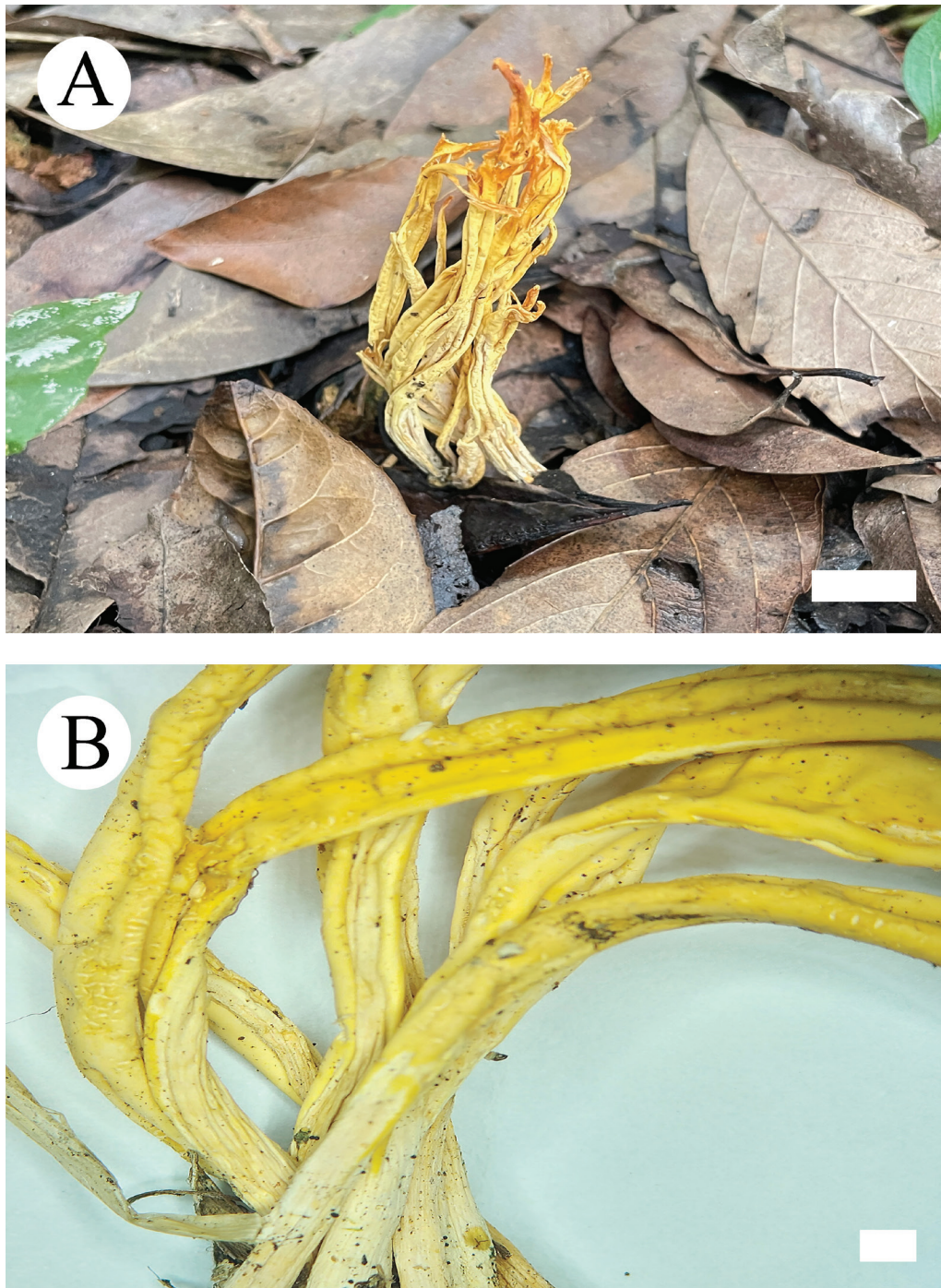


Figure 4. Basidiomata of *Clavulinopsis wumengshanensis* (holotype, CLZhao 29612). Scale bars: 1 cm (A); 1 mm (B).

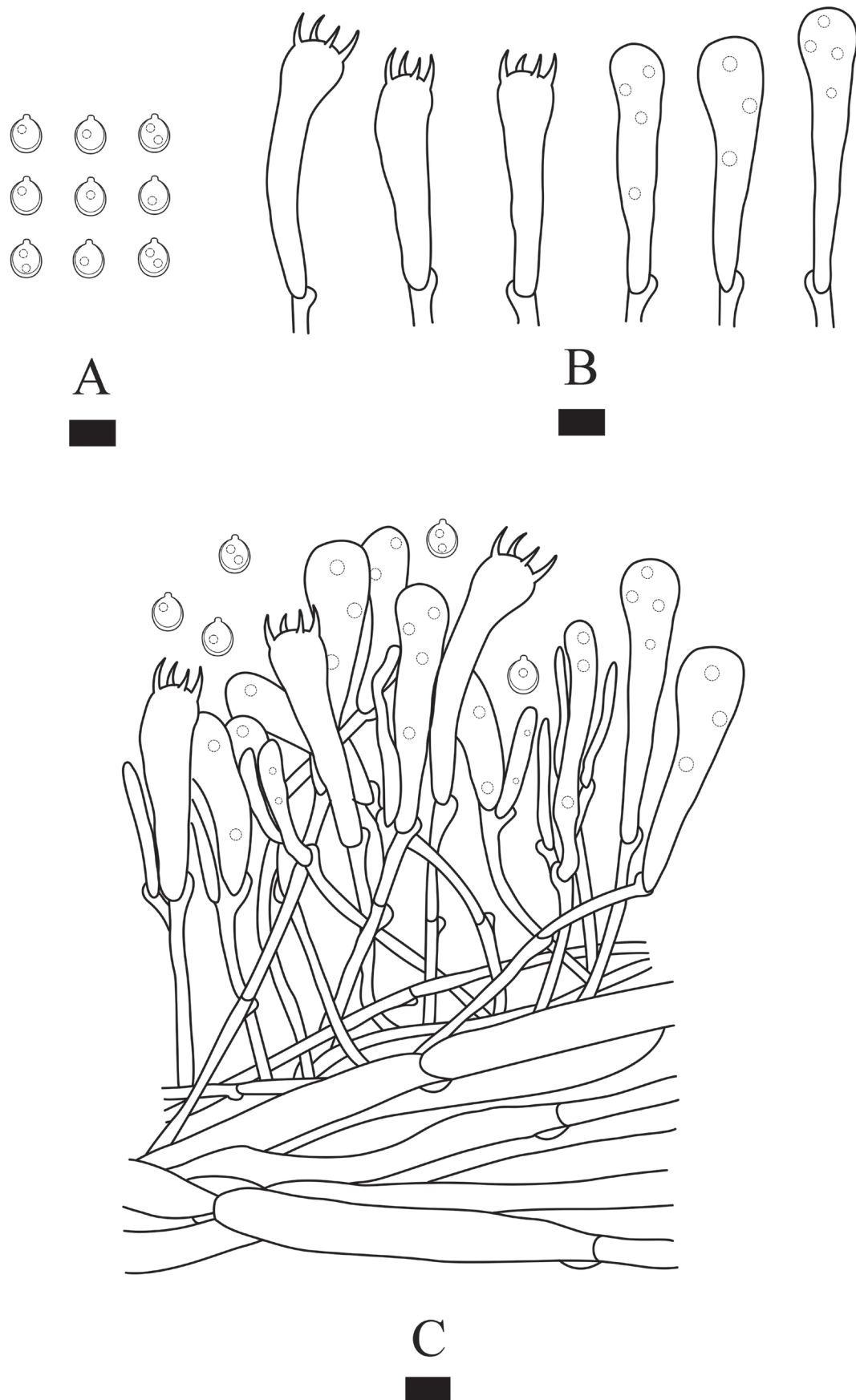


Figure 5. Microscopic structures of *Clavulinopsis wumengshanensis* (holotype, CLZhao 29612) **A** basidiospores **B** basidia and basidioles **C** a section of basidiomata. Scale bars: 10 μm (**A–C**).

Holotype. CHINA • Yunnan Province, Zhaotong, Yiliang County, Wumengshan National Nature Reserve, GPS coordinates 27°30'N, 104°12'E, elev. 1710 m asl., on the ground, leg. C.L. Zhao, 12 July 2023, CLZhao 29612 (SWFC).

Etymology. *Wumengshanensis* (Lat.) refers to the locality “Wumengshan National Nature Reserve” of the holotype.

Basidiomata. Basidiomes annual, clavarioid, without odor or taste when fresh, up to 8 cm long, 4 mm wide, and 400–800 µm thick. Fertile part subcylindrical to fusiform, occasionally slightly curved or flexuous and with a distinct longitudinal depression, buff-yellow (4A4) to straw-yellow (3A/B3) when dry. Apex rounded or obtuse acute when mature, concolourous or slightly paler.

Hyphal structure. Monomitic, generative hyphae with clamp connections, hyaline, thick-walled, parallel, interwoven, 2–3 µm in diam, some inflated to 13 µm in diam, IKI–, CB–; tissues unchanged in KOH. Cystidia absent. Basidia clavate to subcylindrical, hyaline, thin-walled, with four sterigmata and a basal clamp connection, 35–48.5 × 9–11.5 µm; basidioles in shape similar to basidia, with several guttules.

Spores. Basidiospores subglobose with a distinct apiculus, hyaline, thick-walled, smooth, with several guttules, IKI–, CB–, 7–8.5(–5) × (5.5–)6–7.5 µm, L = 7.59 µm, W = 6.54 µm, Q = 1.14–1.16 (n = 60/2).

Additional specimen examined (paratype). CHINA • Yunnan Province, Zhaotong, Yiliang County, Wumengshan National Nature Reserve, GPS coordinates 27°30'N, 104°12'E, elev. 1710 m asl., on the ground, leg. C.L. Zhao, 12 July 2023, CLZhao 29651 (SWFC).

Notes. Based on the ITS + LSU analysis (Fig. 1), the result showed that the new species *Clavulinopsis wumengshanensis* is grouped with *C. aurantiocinnabarina* (Schwein.) Corner. However, *C. aurantiocinnabarina* differs from *C. wumengshanensis* by its thin-walled basidiospores and narrower basidia (5.2–7.1 µm vs. 9–11.5 µm, Petersen 1978).

***Henningsomyces bambusae* S.Y. He, H.M. Zhou & C.L. Zhao, sp. nov.**

MycoBank No: 855907

Figs 6, 7

Diagnosis. *Henningsomyces bambusae* differs from *H. candidus* by its globose to subglobose and wider basidiospores (6.5–8.5 µm vs. 4–5 µm).

Holotype. CHINA • Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates 27°29'N, 103°55'E, elev. 1900 m asl., on dead bamboo, leg. C.L. Zhao, 18 September 2023, CLZhao 33088 (SWFC).

Etymology. *Bambusae* (Lat.) refers to the host genus *Bambusa*.

Basidiomata. Basidiomes forming loosely scattered colonies, short cylindric to tubular, sessile, up to 1–1.6 cm in length, 0.5–1 cm diam; external surface white (60) to cream (4A2/3), finely tomentose when dry; inner surface covered by a deeply concave, smooth hymenium.

Hyphal structure. Monomitic, generative hyphae with clamp connections and simple septa, thin- to thick-walled, IKI–, CB–; tissues unchanged in KOH. External hyphae slightly contorted, widest at the base, slightly tapering towards the obtusely rounded apex, hyaline, thick-walled to solid, occasionally with

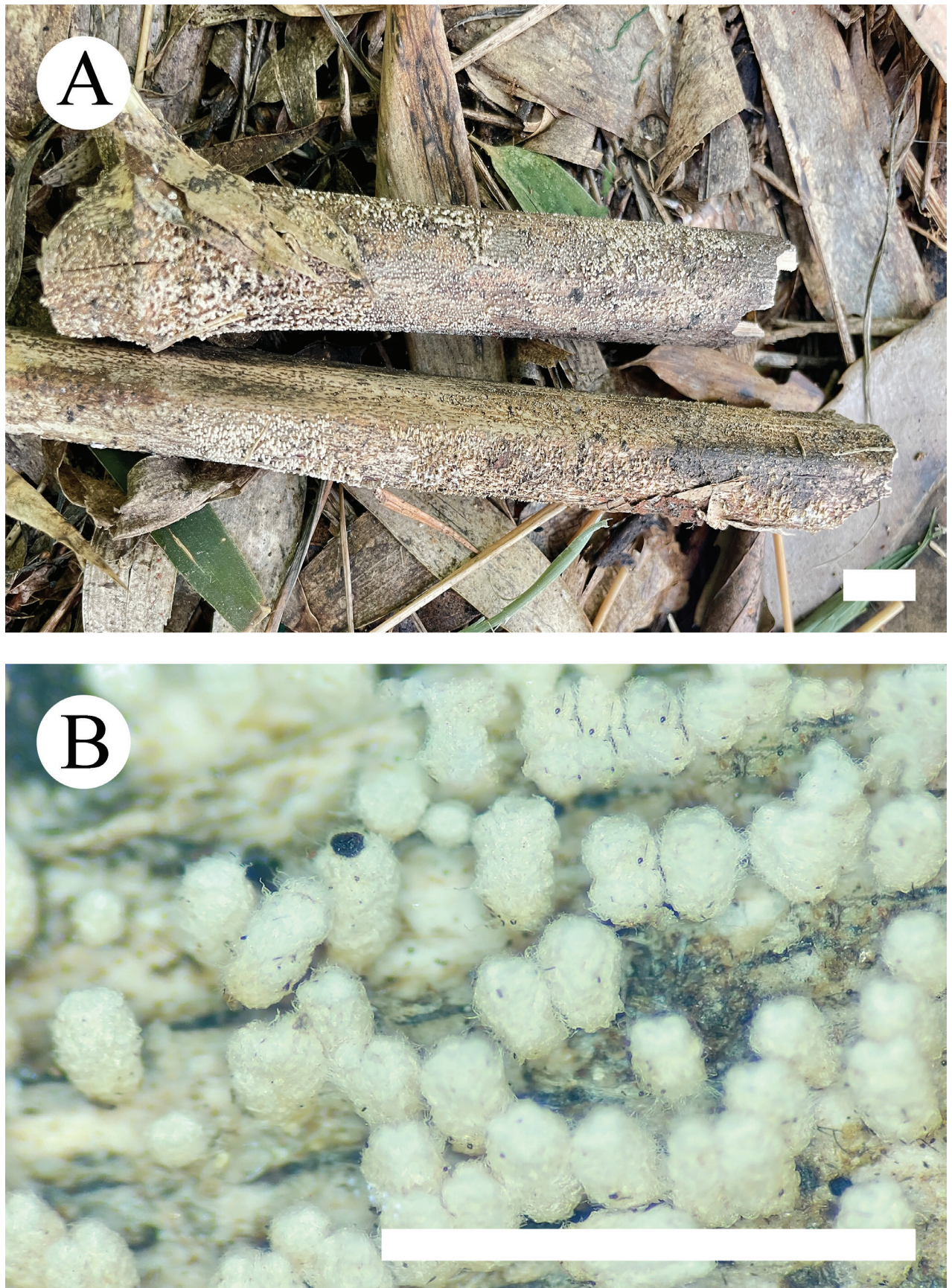


Figure 6. Basidiomata of *Henningsomyces bambusae* (holotype, CLZhao 33088). Scale bars: 1 cm (A); 1 mm (B).

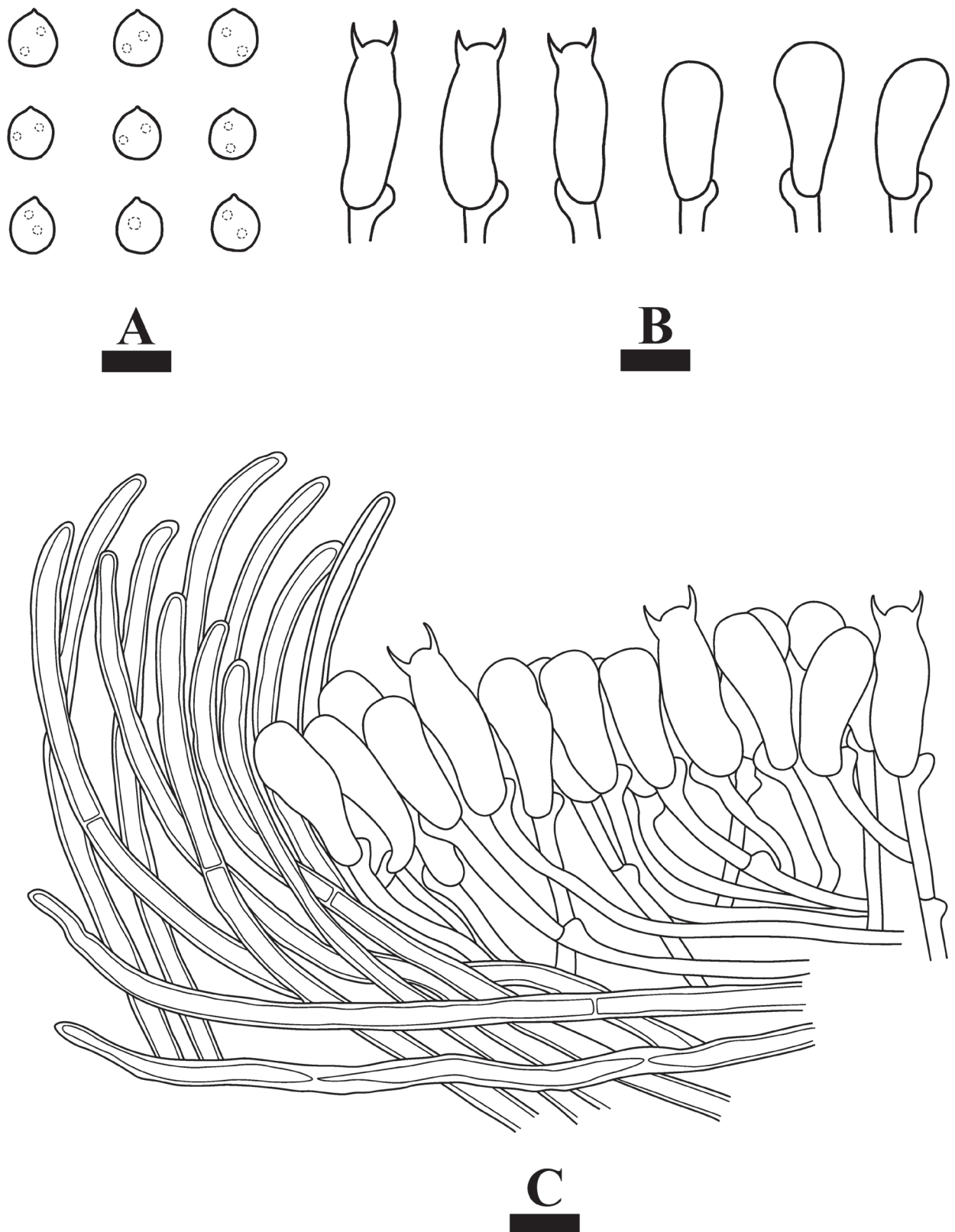


Figure 7. Microscopic structures of *Henningsomyces bambusae* (holotype, CLZhao 33088) **A** basidiospores **B** basidia and basidioles **C** a section of basidiomata. Scale bars: 10 μm (**A–C**).

simple septa, frequently unbranched, dextrinoid, CB–, 3–4 μm diam; tramal hyphae hyaline, thin-walled, with clamp connections, IKI–, 2.5–3 μm diam. Cystidia absent. Basidia cylindrical to subcylindrical, hyaline, thin-walled, with two

sterigmata and a basal clamp connection, $19.5\text{--}22.5 \times 7\text{--}8.5\text{ }\mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller.

Spores. Basidiospores globose to subglobose, hyaline, thin-walled, smooth, with guttules, IKI–, CB–, $6.5\text{--}8.5(-9) \times (6\text{--})6.5\text{--}8.5(-9)\text{ }\mu\text{m}$, $L_m = 7.61\text{ }\mu\text{m}$, $W_m = 7.45\text{ }\mu\text{m}$, $Q = 1.02\text{--}1.04$ ($n = 60/2$).

Additional specimens examined (paratypes). CHINA • Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates $27^{\circ}29'N$, $103^{\circ}55'E$, elev. 1900 m asl., on a dead bamboo, leg. C.L. Zhao, 18 September 2023, CLZhao 33024; CLZhao 33085 (SWFC).

Notes. Based on the ITS analysis (Fig. 2), the new taxon *Henningsomyces bambusae* grouped within the genus *Henningsomyces* and formed a sister group with *H. candidus* (Pers.) Kuntze. However, *H. candidus* can be delimited from *H. bambusae* by its narrower basidiospores ($4\text{--}5\text{ }\mu\text{m}$ vs. $6\text{--}8\text{ }\mu\text{m}$; Gilbertson and Blackwell 1985).

***Xenasma bisterigmatae* S.Y. He, H.M. Zhou & C.L. Zhao, sp. nov.**

MycoBank No: 855908

Figs 8, 9

Diagnosis. *Xenasma bisterigmatae* differs from *X. rimicola* by its ellipsoid to subglobose and larger basidiospores ($8.5\text{--}10.5 \times 4.5\text{--}7\text{ }\mu\text{m}$ vs. $10\text{--}12.5 \times 8\text{--}10.5\text{ }\mu\text{m}$), two-sterigmata basidia.

Holotype. CHINA • Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates $27^{\circ}29'N$, $103^{\circ}55'E$, elev. 1900 m asl., on fallen angiosperm branch, leg. C.L. Zhao, 29 August 2023, CLZhao 32542 (SWFC).

Etymology. *Bisterigmatae* (Lat.) refers to two-sterigmata basidia of the holotype.

Basidiomata. Basidiomes annual, resupinate, smooth, without odor or taste when fresh, up to 6.5 cm long, 2.3 cm wide, and 100 μm thick. Hymenial surface smooth, membranaceous, ash-grey (19C2) when dry; sterile margin indistinct.

Hyphal structure. Monomitic, generative hyphae with clamp connections, thin-walled, branched, interwoven, with dense crystal, $3.2\text{--}3.5\text{ }\mu\text{m}$ diam, IKI–, CB–; tissues unchanged in KOH. Cystidia abundant, tubular with obtuse apex, with slightly thick walls in the basal part that appears frequently collapsed, often with an apical amorphous globule, $64.5\text{--}93 \times 5.5\text{--}7.5\text{ }\mu\text{m}$. Cystidioles absent. Basidia clavate to subcylindrical, thin-walled, with two sterigmata and a basal clamp connection, with several guttules, $21.5\text{--}28 \times 10\text{--}12\text{ }\mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid to subglobose, thick-walled, verrucose, IKI–, CB–, $10\text{--}12.5 \times 8\text{--}10.5(-11)\text{ }\mu\text{m}$, $L_m = 11.15\text{ }\mu\text{m}$, $W_m = 9.3\text{ }\mu\text{m}$, $Q = 1.19\text{--}1.27$ ($n = 60/2$).

Additional specimens examined (paratype). CHINA • Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates $27^{\circ}29'N$, $103^{\circ}55'E$, elev. 1900 m asl., on fallen angiosperm branch, leg. C.L. Zhao, 29 August 2023, CLZhao 32600 (SWFC).

Notes. Based on the ITS analysis (Fig. 3), the new species *Xenasma bisterigmatae* was clustered with *X. rimicola* (P. Karst.) Donk. However, *X. rimicola* differs from *X. bisterigmatae* by its four-sterigmata basidia (Cunningham 1963).

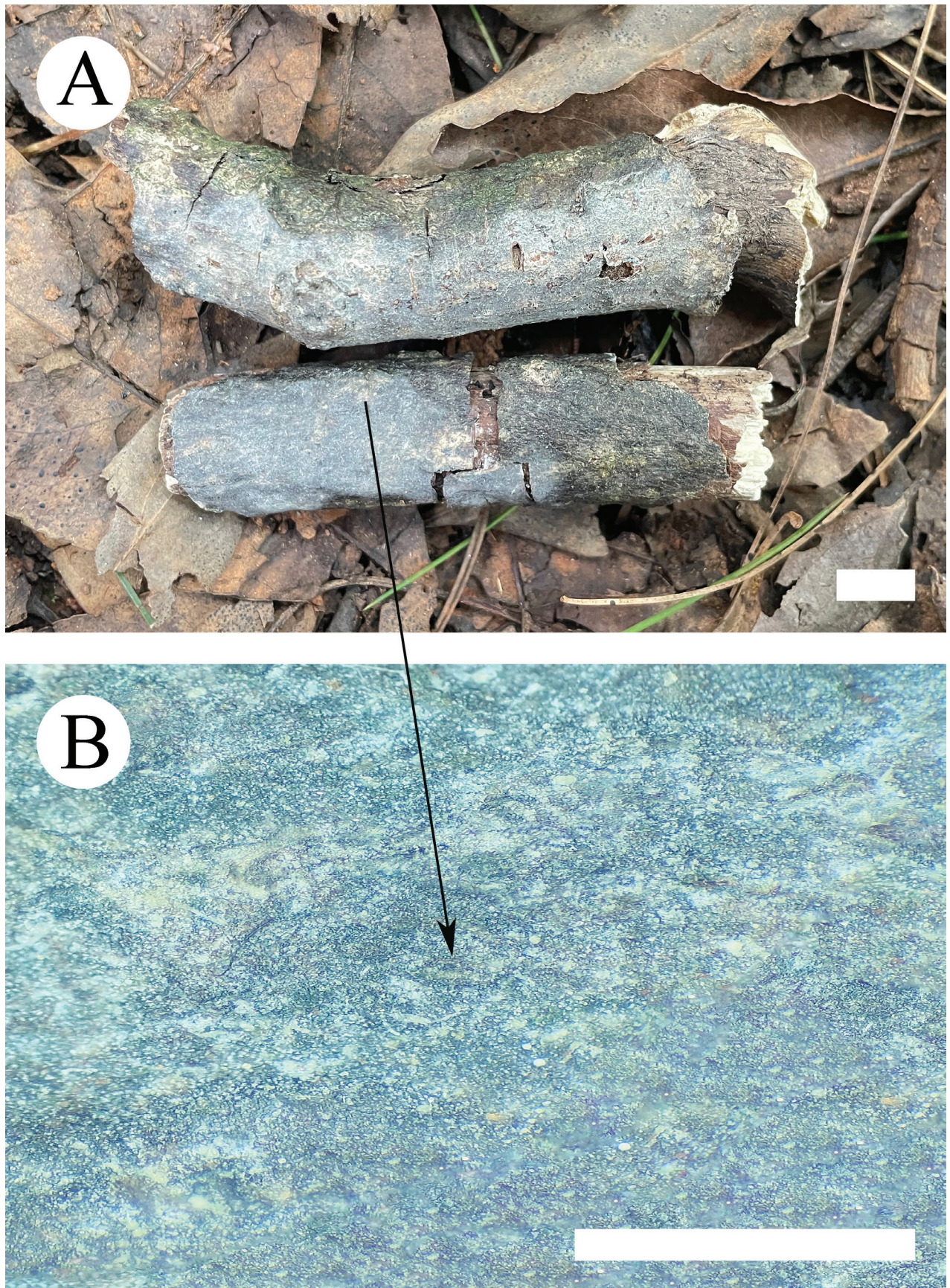


Figure 8. Basidiomata of *Xenasma bisterigmatae* (holotype, CLZhao 32542). Scale bars: 1 cm (**A**); 1 mm (**B**).

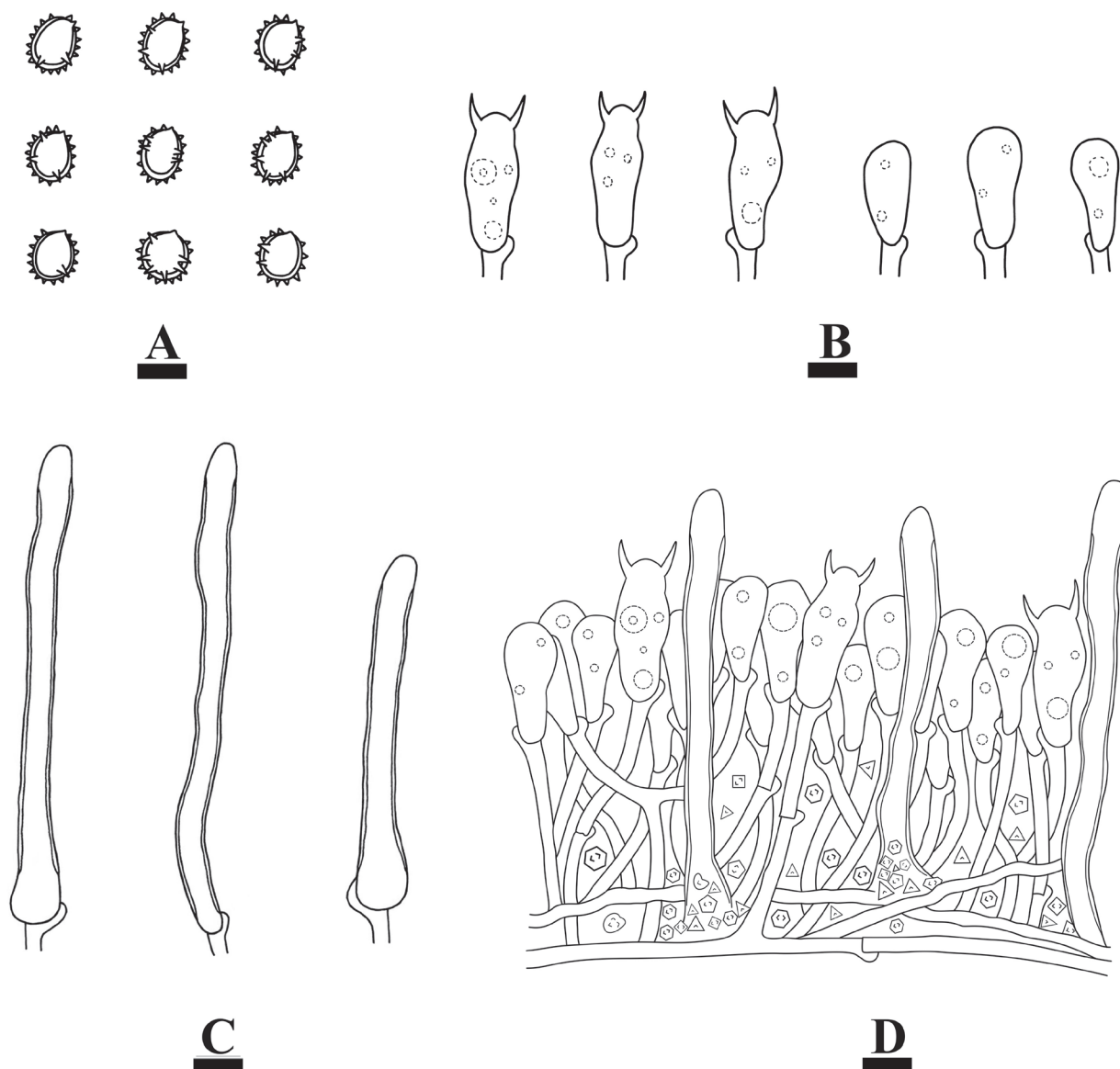


Figure 9. Microscopic structures of *Xenasma bisterigmatae* (holotype, CLZhao 32542) **A** basidiospores **B** basidia and basidioles **C** cystidia **D** a section of basidiomata. Scale bars: 10 μ m (**A–C**).

***Xenasma guttulata* S.Y. He, H.M. Zhou & C.L. Zhao, sp. nov.**

MycoBank No: 855909

Figs 10, 11

Diagnosis. *Xenasma guttulata* differs from *X. pruinsum* by its membranaceous basidiomata with a white to cream hymenial surface and larger basidiospores ($6\text{--}7 \times 3\text{--}4 \mu\text{m}$ vs. $7\text{--}9 \times 5.5\text{--}7.5 \mu\text{m}$).

Holotype. CHINA • Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates $27^{\circ}29'N$, $103^{\circ}55'E$, elev. 1900 m asl., on a fallen angiosperm branch, leg. C.L. Zhao, 29 August 2023, CLZhao 32193 (SWFC).

Etymology. *Guttulata* (Lat.) refers to the basidiospores with guttules in the holotype.

Basidiomata. Basidiomes annual, resupinate, closely adnate, without odor or taste when fresh, up to 2.5 cm long, 1.5 cm wide, and 100 μ m thick. Hymenial

surface smooth, membranaceous, white (60) to cream (4A2/3) when dry; sterile margin indistinct.

Hyphal structure. Monomitic, generative hyphae with clamp connections, thin-walled, occasionally branched, interwoven, with dense crystal, $3.3\text{--}3.5\ \mu\text{m}$ diam, IKI–, CB–; tissues unchanged in KOH. Cystidia abundant, cystidia tubular with obtuse apex, $75\text{--}91.5 \times 4\text{--}8.5\ \mu\text{m}$, with slightly thick walls in the basal part that appears frequently collapsed, often with an apical amorphous globule.

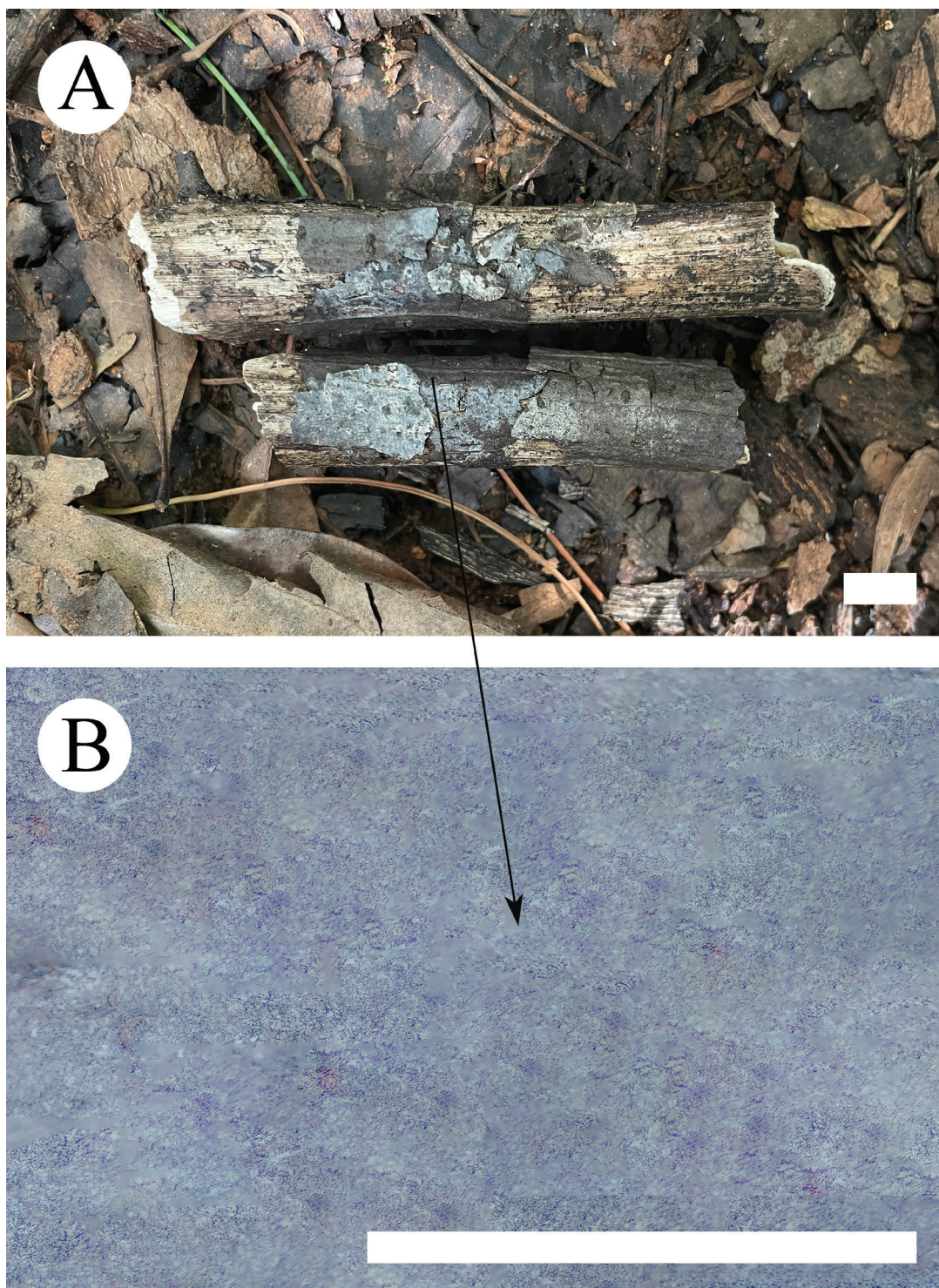


Figure 10. Basidiomata of *Xenasma guttulata* (holotype, CLZhao 32193). Scale bars: 1 cm (A); 1 mm (B).

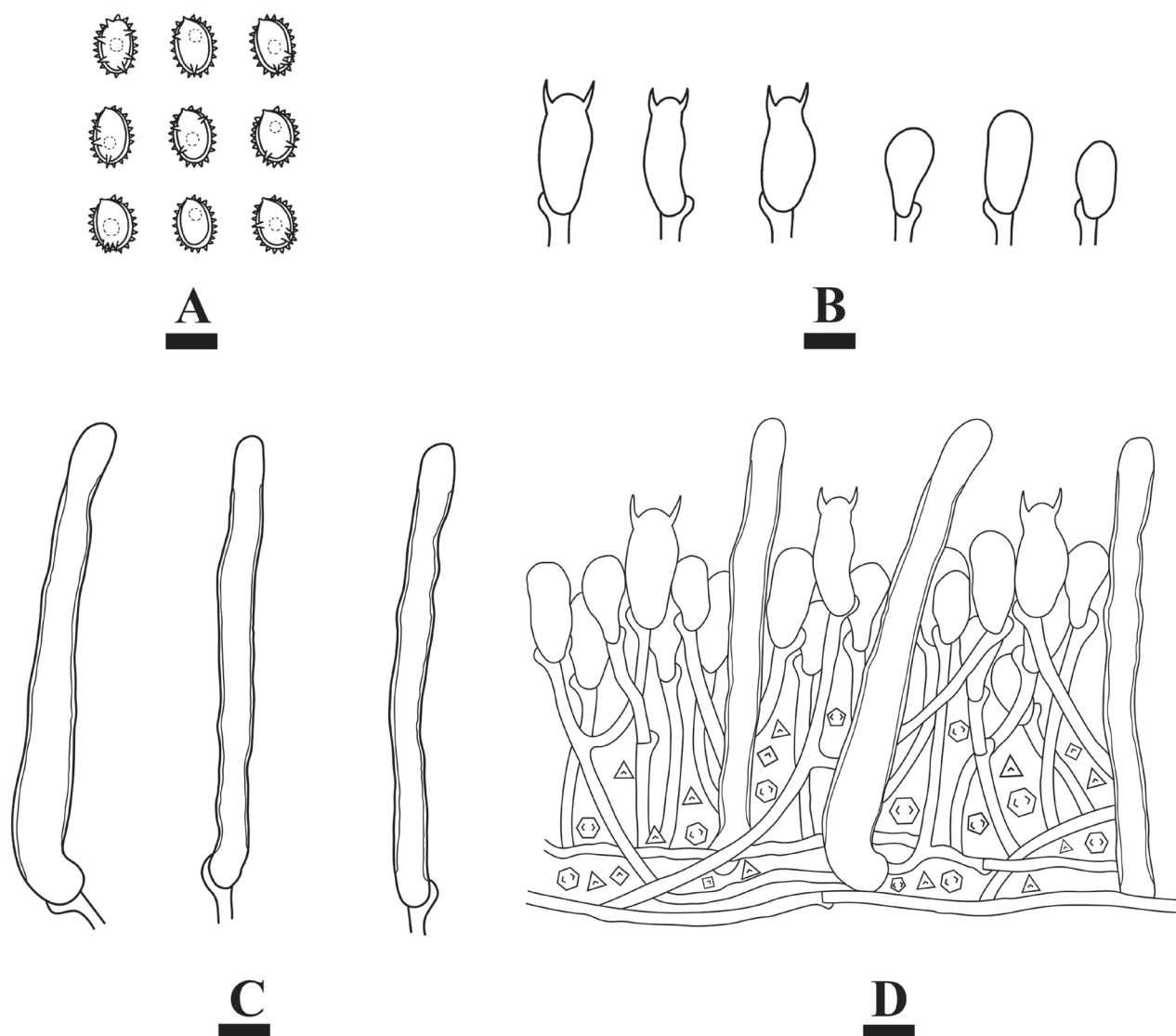


Figure 11. Microscopic structures of *Xenasma guttulata* (holotype, CLZhao 32193) **A** basidiospores **B** basidia and basidioles **C** cystidia **D** a section of basidiomata. Scale bars: 10 μm (**A–C**).

Cystidioles absent. Basidia clavate to subcylindrical, thin-walled, with two sterigmata and a basal clamp connection, $18.5\text{--}24 \times 7.5\text{--}11 \mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller.

Spores. Basidiospores ellipsoid to narrowly ellipsoid, thick-walled, verrucose, with several guttules, IKI–, CB–, $7\text{--}9 \times 5.5\text{--}7.5 \mu\text{m}$, $L_m = 8.05 \mu\text{m}$, $W_m = 6.52 \mu\text{m}$, $Q = 1.23$ ($n = 30/1$).

Notes. Based on the ITS analysis (Fig. 3), the new species *Xenasma guttulata* was clustered with *X. pruinsum* (Pat.) Donk. However, *X. pruinsum* can be distinguished from *X. guttulata* by its smaller basidiospores ($6\text{--}7 \times 3\text{--}4 \mu\text{m}$ vs. $7\text{--}9 \times 5.5\text{--}7.5$; Donk 1957; Bernicchia and Gorjón 2010).

Discussion

The multilocus (ITS+LSU) analysis (Fig. 1) showed that the new species *Clavulinopsis wumengshanensis* groups with *C. aurantiocinnabarina* (Schwein.) Corner. However, *C. aurantiocinnabarina* differs from *C. wumengshanensis* by its

thin-walled basidiospores and narrower basidia (5.2–7.1 μm vs. 9–11.5 μm) (Petersen 1978). Morphologically, *Clavulinopsis fusiformis* (Sowerby) Corner and *C. incarnata* P. Zhang & Jun Yan are similar to *C. wumengshanensis* by both having smooth, globose to subglobose basidiospores (Keleş and Kaya 2021; Yan et al. 2023). However, *C. fusiformis* differs in its pale yellow basidiomata, and *C. incarnata* differs in its pinkish basidiomata (Keleş and Kaya 2021; Yan et al. 2023).

Based on the ITS locus phylogenetic analysis (Fig. 2), the new taxon *Henningsomyces bambusae* forms a sister group with *H. candidus* (Pers.) Kuntze. However, *H. candidus* can be delimited from *H. bambusae* by its narrower basidiospores (4–5 μm vs. 6–8 μm , Gilbertson and Blackwell 1985). Morphologically, *Henningsomyces hengduanensis* S.L. Liu & L.W. Zhou and *H. minimus* (Cooke and W. Phillips) Kuntze are similar to *H. bambusae* by both having thin-walled, smooth, subglobose basidiospores (Wei and Qin 2009; Liu et al. 2023). However, *H. hengduanensis* differs in its cream basidiomata and broadly clavate basidia with four sterigmata (Liu et al. 2023); *Henningsomyces minimus* differs in its shorter (11–15 μm vs. 19.5–22.5 μm), broadly clavate basidia with four sterigmata (Wei and Qin 2009).

Based on the combined ITS locus phylogeny (Fig. 3), *X. rimicola* (P. Karst.) Donk differs from the new species *X. bisterigmatae* by its four-sterigmata basidia (Cunningham 1963); *X. pruinsum* (Pat.) Donk can be distinguished from the new species *X. guttulata* by its smaller basidiospores (6–7 \times 3–4 μm vs. 7–9 \times 5.5–7.5, Donk 1957; Bernicchia and Gorjón 2010). Morphologically, *X. pruinsum* is similar to *X. bisterigmatae* by having tubular cystidia with an apical amorphous globule and slightly thick walls in the basal part (Donk 1957; Bernicchia and Gorjón 2010). However, *X. pruinsum* differs in its smaller basidiospores (6–7 \times 3–4 μm vs. 7–9 \times 5.5–7.5 μm ; Donk 1957; Bernicchia and Gorjón 2010). *Xenasma rimicola* is similar to *X. guttulata* by having tubular cystidia and slightly thick walls in the basal part (Donk 1957). However, *X. rimicola* differs in its subclavate basidia with four sterigmata (Donk 1957).

Yunnan Province is located in the southwest of China. The climate in Yunnan offers conducive environments for the speciation and diversification of various life forms, and this climatic diversity in Yunnan creates varied landscapes with multiple habitats, resulting in a high species diversity, with over 6,000 recorded fungal species up to now (Wang and Cai 2022; Dong et al. 2024; Wang et al. 2024; Zhou et al. 2024b). Therefore, focusing on the diversity of fungi in the Yunnan-Guizhou Plateau of China is of great significance. Based on the present study, the results not only enrich the species diversity of fungi worldwide but also contribute to the branches of the fungal tree of life.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: HSY, WL, ZHM. Formal analysis: HSY, WL, SKZ, ZHM. Methodology: HSY, ZHM. Software: HSY, ZHM. Writing—original draft: HSY, WL, SKZ. Writing—review and editing: ZHM.

Author ORCIDs

Siyuan He  <https://orcid.org/0009-0005-2478-0624>

Lu Wang  <https://orcid.org/0009-0004-6274-5953>

Hongmin Zhou  <https://orcid.org/0000-0002-0724-5815>

Data availability

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

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