

Article



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Molecular phylogeny and morphology reveal a new species of *Gloeocystidiellum* (Stereaceae, Russulales) from Southwestern China

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Abstract

Gloeocystidiellum yaoshanense sp. nov., found in Yunnan Province, Southwestern China, is described here as a new species based on its morphology and phylogenetic analyses. Gloeocystidiellum yaoshanense is characterized by its membranaceous basidiomata with cracked, grandinioid hymenial surface, a monomitic hyphal system bearing simple septa on generative hyphae, and broadly ellipsoid to ellipsoid basidiospores measuring $4-4.6 \times 3-3.5 \mu m$. Phylogenetic analyses of the new species were carried out based on the nuclear ribosomal internal transcribed spacer (nrITS) and the nuclear large subunit (nrLSU) of ribosomal DNA. The phylogenetic analyses indicated that the new species belongs to the genus Gloeocystidiellum and forms a monophyletic lineage. A full description, illustrations, and phylogenetic analysis results of the new species are provided.

Key words: Biodiversity, Phylogenetically, Taxonomy, Wood-inhabiting fungi, Yunnan Province

Introduction

Fungi exhibit enormous species diversity in terms of morphological, ecological, and nutritional modes (Cui *et al.* 2018, Wu *et al.* 2016, Dai *et al.* 2021, Zhao *et al.* 2023b, Song *et al.* 2024). Wood-inhabiting fungi play a crucial role in ecosystem processes, particularly in the degradation of wood and the recycling of organic matter (Dong *et al.* 2024).

The corticioid genus *Gloeocystidiellum* Donk (1931: 156), belonging to the order Russulales, was established by Donk (1931) with *Gc. porosum* (Berk & MA Curtis) Donk (1931: 156) as its type species. The genus is characterized by resupinate, membranaceous or ceraceous basidiomata, smooth, rarely grandinioid or odontioid hymenial surface, a monomitic hyphal system with clamped or simple-septate generative hyphae, present gloeocystidia, subcylindrical to clavate basidia with four sterigmata and suballantoid, ellipsoid, subglobose or globose, verrucose or aculeate basidiospores (Donk 1931, 1957, Bernicchia & Gorjón 2010). The Index Fungorum (http://www.indexfungorum.org, accessed June 28, 2025) lists 38 species in the genus *Gloeocystidiellum* (Larsson & Larsson 2003, Gorjón & Hallenberg 2013, Zhao & Zhao 2023, Zhang *et al.* 2025).

Molecular studies involving the genus *Gloeocystidiellum* based on single-gene or multi-gene datasets have been carried out (Larsson & Hallenberg 2001, Larsson & Larsson 2003, Gorjón & Hallenberg 2013, Jaramillo-Riofrío *et al.* 2023, Zhao & Zhao 2023, Zhang *et al.* 2025, Zhou *et al.* 2025). Based on phylogenetic analyses of nuclear 5.8S, ITS2, and nrLSU rDNA genes, the taxa of *Gloeocystidiellum* formed two clades, where the generic type species, *Gc. porosum* is grouped into clade I (Larsson & Larsson 2003). The high phylogenetic diversity among corticioid

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homobasidiomycetes showed that the taxon *Gc. subasperisporum* (Litsch.) J. Erikss. & Ryvarden (1975: 443) nested into the russuloid clade and closely grouped with *Gloeodontia discolor* (Berk. & M.A. Curtis) Boidin (1966: 22) (Larsson *et al.* 2004). Molecular phylogenetic analyses based on nrITS+nrLSU sequences within the order Russulales indicated that the genus *Gloeocystidiellum* nested into the family Russulaceae and clustered with the genus *Gloeodontia* (Leal-Dutra *et al.* 2018). The result of phylogenetic analyses showed that the genus *Gloeodontia* formed a single clade grouped with *Gloeocystidiellum* within the order Russulales (Chen *et al.* 2020, Zhao & Zhao 2023). In a recent study, the genus *Gloeocystidiellum* was classified within the family Stereaceae, belonging to the order Russulales (He *et al.* 2024, Zhang *et al.* 2025).

During investigations on the corticioid fungi in Yunnan Province, southwestern China, two specimens of *Gloeocystidiellum* were collected. To clarify the placement and relationships of these specimens, we conducted a phylogenetic and taxonomic study on the genus *Gloeocystidiellum* based on combined nrITS and nrITS+nrLSU sequence data. These specimens are identified as a new species of *Gloeocystidiellum*. Detailed descriptions, illustrations, and phylogenetic analysis results of the new species are provided.

Materials and methods

Sample collection and herbarium specimen preparation

The fresh basidiomata were collected from fallen angiosperm branches in Zhaotong, Yunnan Province, southwest China. The samples were photographed in situ, and fresh macroscopic details, as well as other important collection information, were recorded (Rathnayaka *et al.* 2024). The photographs were recorded using a Nikon D7100 camera. All the photos were focus stacked using Helicon Focus software. Macroscopic details were recorded and transported to a field station, where the basidiomata were dried on an electronic food dryer at 40 °C (Hu *et al.* 2022). Once dried, the specimens were placed in a labeled envelope and then put in zip-lock plastic bags (Dong *et al.* 2024). The dried specimens were deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. The MycoBank number was registered in the MycoBank database (http://www.mycobank.org).

Morphology

The macro-morphological descriptions were based on field notes and photos captured in the field and lab. Petersen (1996) was followed in the use of color terminology. The micro-morphological data were obtained from dried specimens observed under a light microscope with a magnification of 1000° oil (Zhao *et al.* 2023a, Dong *et al.* 2024, Zhang *et al.* 2025). Sections mounted in 5% KOH and 2% phloxine B ($C_{20}H_2Br_4C_{14}Na_2O_5$), and other reagents were also used, including Cotton Blue and Melzer's reagent to observe micro-morphology following Wu *et al.* (2022a). To show the variation in spore sizes, 5% of measurements were excluded from each end of the range and shown in parentheses. At least thirty basidiospores from each specimen were measured. Stalks were excluded from basidia measurements, and the hilar appendage was excluded from basidiospore measurements. The following abbreviations are used: KOH = 5% potassium hydroxide water solution, CB— = acyanophilous, CB+ = cyanophilous, CB+ = both inamyloid and non-dextrinoid, CB+ = mean spore length (arithmetic average for all spores), CB+ mean spore width (arithmetic average for all spores), CB+ expanding the average CB+ of basidiospores measured CB+ standard deviation, and CB+ along the field and CB+ are appeared to the average CB+ acyanophilous and CB+ acyanophilous are used.

Molecular phylogeny

The CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain genomic DNA from the dried specimens according to the manufacturer's instructions. The nuclear ribosomal internal transcribed spacer (nrITS) region was amplified with ITS5 and ITS4 primers (White *et al.* 1990), while the nuclear large subunit (nrLSU) region was amplified with the LR0R and LR7 primer pair (Vilgalys & Hester 1990, Rehner & Samuels 1994). The PCR procedure for nrITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles of denaturation at 94 °C for 40 s, annealing at 58 °C for 45 s, extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for nrLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 48 °C for 1 min, extension at 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company (Yunnan Province, P.R. China). The newly generated sequences were deposited in NCBI GenBank (Table 1).

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

Species Name	Sample No.	GenBank Accession No.		Country	References
		ITS	nrLSU		
Aleurobotrys botryosus	He 2712	KX306877	KY450788	China	Maekawa et al. 2023
Aleurobotrys botryosus	Wu 9302-61	_	AY039331	China	Maekawa et al. 2023
Aleurodiscus bambusinus	He 4261	KY706207	KY706219	China	Dai & He 2017
Aleurodiscus canadensis	Wu1207-90	KY706203	KY706225	China	Dai & He 2017
Conferticium heimii	LY/CBS321.66	AF506381	AF506381	Central African Republic	Jaramillo-Riofrío et al. 202
Conferticium heimii	CBS321.66	MH858805	MH858805	Central African Republic	Vu et al. 2019
Conferticium ravum	CBS:125849	MH863805	MH875269	Estonia	Vu et al. 2019
Conferticium ravum	NH13291	AF506382	AF506382	USA	Larsson & Larsson 2003
Conferticium tuberculatum	CLZhao 29376	PQ166602	PQ295861	China	Wang et al. 2025
Conferticium tuberculatum	CLZhao 29390	PQ166603	PQ295862	China	Wang et al. 2025
Gloeocystidiellum aspellum	LIN 625	AF506432	_	China	Larsson & Lrsson 2003
Gloeocystidiellum bisporum	CBS/961.96	AY048875	AY048875	Sweden	Jaramillo-Riofrío et al. 202
Gloeocystidiellum bisporum	KHL11135	AY048877	AY048877	Norway	Larsson & Lrsson 2003
Gloeocystidiellum clavuligerum	GB/NH11185	AF310088	AF310088	Spain	Jaramillo-Riofrío et al. 202
Gloeocystidiellum cremeum	CLZhao 33623	PQ287847	PQ295864	China	Wang et al. 2025
Gloeocystidiellum cremeum	CLZhao 33690	PQ287848	_	China	Wang et al. 2025
Gloeocystidiellum fissuratum	CLZhao 32247	PQ287849	PQ295865	China	Wang et al. 2025
Gloeocystidiellum fissuratum	CLZhao 32303	PQ287850	PQ295866	China	Wang et al. 2025
Gloeocystidiellum formosanum	Wu9404-19	AF506439	_	China	Maekawa et al. 2023
Gloeocystidiellum kenyense	TFC/15278	FR878082	_	Portugal	Jaramillo-Riofrío et al. 202
Gloeocystidiellum kenyense	TFC/15309	FR878083	_	Portugal	Jaramillo-Riofrío et al. 202
Gloeocystidiellum lojanense	HUTPL(F)/2181	OP377059	_	Ecuador	Jaramillo-Riofrío et al. 202
Gloeocystidiellum lojanense	HUTPL(F)/550	OP377083	_	Ecuador	Jaramillo-Riofrío et al. 202
Gloeocystidiellum luridum	HK9808	AF506421	_	Germany	Maekawa et al. 2023
Gloeocystidiellum porosum	CBS/51085	AF310097	AF310097	Netherlands	Jaramillo-Riofrío et al. 202
Gloeocystidiellum porosum	NH 10434	AF310094	AF310094	Denmark	Larsson & Hallenberg 200
Gloeocystidiellum rajchenbergii	GB/NH16353	JQ734555	_	Chile	Jaramillo-Riofrío <i>et al</i> . 202
Gloeocystidiellum rajchenbergii	GB/NH16348	JQ734554	_	Chile	Jaramillo-Riofrío <i>et al.</i> 202
Gloeocystidiellum sinense	CLZhao 25040	PQ453516	PQ453518	China	Zhang et al. 2025
Gloeocystidiellum sinense	CLZhao 25320	PQ453517	PQ453519	China	Zhang et al. 2025
Gloeocystidiellum triste	KHL10334	AF506442	_	Sweden	Maekawa et al. 2023
Gloeocystidiellum vaoshanense	CLZhao 20850*	PV682890	PV682892	China	Present study
Gloeocystidiellum vaoshanense	CLZhao 45465	PV682891	PV682893	China	Present study
Gloeocystidiellum vunnanense	CLZhao 7165	MZ710569	MZ710571	China	Zhao & Zhao 2023
Gloeocystidiellum vunnanense	CLZhao 7202	MZ710570	MZ710572	China	Zhao & Zhao 2023

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TABLE 1. (Continued)

Species Name	Sample No.	GenBank Accession No.		Country	References
		ITS	nrLSU	_	
Lentinellus cochleatus	GB/KGN96- 09-28	AF506417	_	Sweden	Jaramillo-Riofrío et al. 2023
Megalocystidium diffissum	V.Spirin4244	MT477147	MT477147	Sweden	Maekawa et al. 2023
Megalocystidium leucoxanthum	HK9808	AF506420	AF506420	Sweden	Maekawa et al. 2023
Neoaleurodiscus fujii	He 2921	KU559357	KU574845	China	Dai et al. 2017
Neoaleurodiscus fujii	Wu0807-41	_	FJ799924	China	Dai et al. 2017
Stereum complicatum	He 2234	KU559368	KU574828	China	Maekawa et al. 2023
Stereum hirsutum	Wu1109—127	LC430906	LC430909	China	Maekawa et al. 2023
Stereum sanguinolentum	He 2111	KU559367	KU574827	China	Maekawa et al. 2023
Vararia investiens	FP-151122	MH971976	_	USA	Liu & He 2018
Xylobolus frustulatus	He 2231	KU881905	KU574825	China	Maekawa et al. 2023
Xylobolus subpileatus	FP-106735	_	AY039309	USA	Maekawa et al. 2023

^{*} is shown type material, holotype; — means the data unavailability.

The sequences were aligned using MAFFT version 7 (Katoh et al. 2019) with the G-INS-i strategy, and then manually adjusted using AliView version 1.27 (Larsson 2014). After trimming, the sequences of nrITS and nrLSU were combined using Mesquite version 3.51. Sequence of *Vararia investiens* (Schwein.) P. Karst. (1898: 32). The sequence obtained from GenBank was used as an outgroup to root trees in the nrITS+nrLSU analysis for the family Stereaceae (Fig. 1, Zhao & Zhao 2023), and *Lentinellus cochleatus* (Pers.) P. Karst. (1879: 247) was used as an outgroup in the nrITS analysis in the genus *Gloeocystidiellum* (Fig. 2, Zhang et al. 2025).

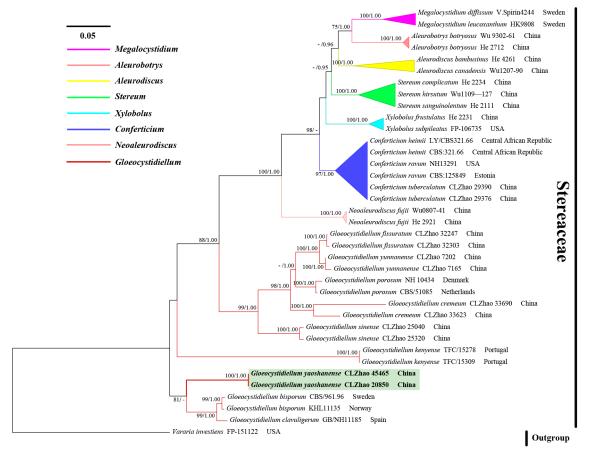


FIGURE 1. Maximum Likelihood strict consensus tree illustrating the *Gloeocystidiellum* and related genera in the family Stereaceae based on the combined nrITS+nrLSU sequences. Branches are labeled with Maximum Likelihood bootstrap values equal to or above 70% and Bayesian posterior probabilities equal to or above 0.95. The new species is in bold.

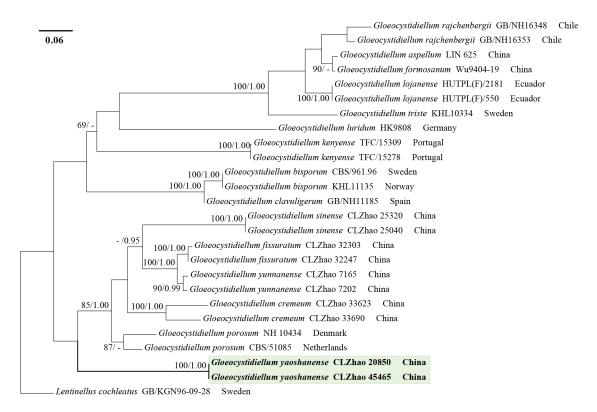


FIGURE 2. Maximum Likelihood strict consensus tree illustrating the phylogeny of the new species *Gloeocystidiellum yaoshanense*, and related species in the genus *Gloeocystidiellum* based on nrITS sequences. Branches are labeled with Maximum Likelihood bootstrap values equal to or above 70% and Bayesian posterior probabilities equal to or above 0.95.

Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were applied to the combined two datasets following a previous study (Dong *et al.* 2024). Maximum Likelihood (ML) analysis was performed using RAxML-HPC BlackBox in the CIPRES Science Gateway (https://www.phylo.org/portal2/login!input.action, Miller *et al.* 2012) with a GTRCAT model of evolution and 1,000 bootstrap replicates (Felsenstein 1985). jModelTest v2 (Darriba *et al.* 2012) was used to determine the best-fit evolution model for each dataset for the purposes of Bayesian inference (BI), Bayesian inference was performed using MrBayes 3.2.7a (Ronquist *et al.* 2012). Four Markov chains were run from random starting trees. Trees were sampled every 1,000 generations. The first 25% of sampled trees were discarded as burn-in, while the remaining trees were used to construct a 50% majority consensus tree and to calculate Bayesian posterior probabilities (BPP).

Phylogenetic trees were visualized and adjusted using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree), and the exports were edited using Adobe Illustrator CS6 software (Adobe Systems, USA). Branches were considered significantly supported if they received a maximum likelihood bootstrap value (BS) of \geq 70%, Bayesian posterior probabilities (BPP) of \geq 0.95.

Results

Molecular phylogeny

The aligned nrITS+nrLSU dataset comprised 37 specimens representing 24 species. Four Markov chains were run for two independent runs from random starting trees, each for one million generations, using the combined nrITS+nrLSU (Fig. 1) data set, with trees and parameters sampled every 1,000 generations. The best model for the nrITS+nrLSU dataset, estimated and applied in the Bayesian analysis, was SYM+I+G. Maximum Likelihood (ML) and Bayesian Inference (BI) analysis yielded a similar topology, with an average standard deviation of split frequencies of 0.002328 (BI). The effective sample size (ESS) for Bayesian analysis across the two runs was approximately double the average ESS (avg. ESS) of 246.5.

The aligned nrITS dataset comprised 24 specimens representing 16 species. Four Markov chains were run for

two runs from random starting trees, each for 0.3 million generations, for the nrITS-only (Fig. 2) data set with trees and parameters sampled every 1000 generations. The best model for the nrITS dataset, estimated and applied in the Bayesian analysis, was HKY+G. Maximum Likelihood (ML) and Bayesian Inference (BI) analysis yielded a similar topology, with an average standard deviation of split frequencies of 0.006831 (BI). The ESS for Bayesian analysis across the two runs was approximately double the average ESS (avg. ESS) of 210.5.

The phylogram based on the combined nrITS+nrLSU sequences (Fig. 1) indicated that the new species *Gloeocystidiellum yaoshanense* was assigned to the genus *Gloeocystidiellum*. The topology based on nrITS sequences (Fig. 2) revealed that the new species *Gc. yaoshanense*, formed a monophyletic lineage.

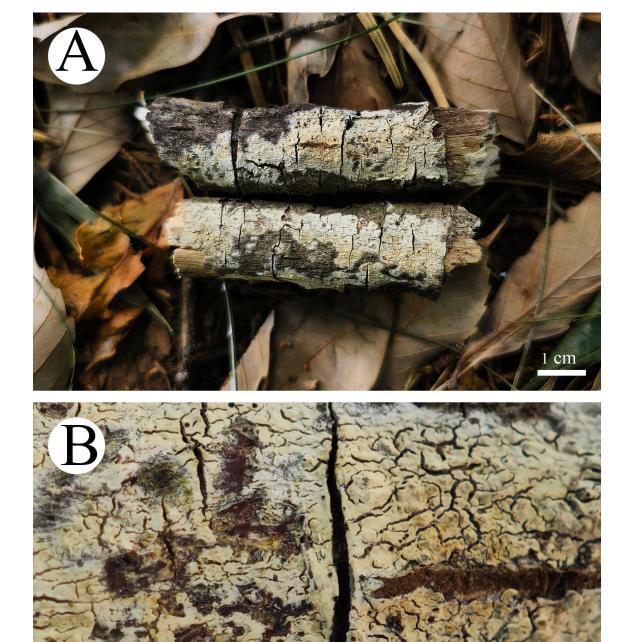


FIGURE 3. Basidiomata of Gloeocystidiellum yaoshanense (holotype, CLZhao 20850).

Taxonomy

Gloeocystidiellum yaoshanense Y.J. Zhu & C.L. Zhao, sp. nov. Figs. 3-5.

MycoBank no.: MB859528

Etymology:—yaoshanense (Lat.) refers to the type locality, Yaoshan National Nature Reserve.

Diagnosis:—Differs from *Gloeocystidiellum porosum* by its grandinoid hymenial surface, septate generative hyphae, and broadly ellipsoid to ellipsoid basidiospores $(4-4.6 \times 3-3.5 \mu m)$.

Holotype:—CHINA. Yunnan Province, Zhaotong, Qiaojia County, Yaoshan Town, Yaoshan National Nature Reserve, 27°15′52″N, 103°07′11″E, elev. 3,200 m, on the fallen angiosperm branch, 23 August 2020, CLZhao 20850 (SWFC!).

Basidiomata:—Annual, resupinate, adnate, membranaceous, becoming hard coriaceous upon drying, very hard to separate from substrate, without odor or taste when fresh, up to 15 cm long, 3 cm wide, 100–150 μm thick. Hymenial surface grandinioid, cracked with numerous crevices, cream (4A2) when fresh, turning to pinkish buff (5A3) to straw yellow (3A/B3) upon drying. Sterile margin narrow, cream (4A2), up to 1 mm wide.

Hyphal structure:—Hyphal system monomitic, generative hyphae with simple septa, colorless, thin-walled, branched, interwoven, 2–3 μm in diameter, IKI–, CB–; tissues unchanged in KOH.

Hymenium:—Gloeocystidia numerous, tubular, colorless, thin-walled, $17-25 \times 3.5-5$ µm; cystidioles absent. Basidia subclavate, occasionally sinuous or constricted in the middle, with four sterigmata, and a basal simple septum, $14-18 \times 3-5$ µm; basidioles dominant, similar to basidia in shape, but slightly smaller.

Basidiospores:—Broadly ellipsoid to ellipsoid, colorless, verrucose, slightly thick-walled, IKI+, CB+, (3.8–)4–4.6(–4.8) \times 3–3.5(–3.7) μ m, L = 4.34 μ m, W = 3.31 μ m, Q = 1.21–1.43, Q_m = 1.31 \pm 0.07 (n = 60/2).

Additional specimen examined:—CHINA. Yunnan Province, Zhaotong, Qiaojia County, Yaoshan Town, Yaoshan National Nature Reserve, 27°15′52″N, 103°07′11″E, elev. 3,200 m, on the fallen angiosperm branch, 25 April 2025, CLZhao 45465 (SWFC!).

Discussion

In the present study, a new species, *Gloeocystidiellum yaoshanense*, is described based on phylogenetic analyses and morphological characteristics.

Phylogenetically, the combined nrITS+nrLSU sequences (Fig. 1) indicated that the new species, *Gloeocystidiellum* yaoshanense, was assigned to the genus *Gloeocystidiellum*. The topology based on nrITS sequences (Fig. 2) revealed that the new species *Gc. yaoshanense*, formed a monophyletic lineage, and it seems that the new species is not related to other taxa in *Gloeocystidiellum*. The species *Gloeocystidiellum yaoshanense* has 75 base differences with the type species *Gc. porosum* in the genus *Gloeocystidiellum* based on the nrITS sequences. However, *Gc. porosum* can be distinguished from *Gc. yaoshanense* by its smooth hymenial surface, longer basidia $(20-25 \times 3.5-4.5 \mu m vs. 14-18 \times 3-5 \mu m)$, and thin-walled, longer basidiospores $(5-6 \times 2.5-3 \mu m vs. 4-4.6 \times 3-3.5 \mu m)$, Bernicchia & Gorjón 2010).

Morphologically, the species *Gloeocystidiellum yaoshanense* resembles *Gc. fimbriatum* Burds. *et al.* (1981: 422), *Gc. lojanense* A. Jaram. *et al.* (2023: 9), *Gc. rajchenbergii* Gorjón & Hallenberg (2013: 186) and *Gc. sinense* S.C. Zhang & C.L. Zhao (2025: 6) in sharing the ellipsoid basidiospores. However, *Gloeocystidiellum fimbriatum* is different from *Gc. yaoshanense* by its fimbriate sterile margin, larger basidia (18–26 × 5–6.5 μm *vs.* 14–18 × 3–5 μm) (Ginns & Freeman 1994). The species *Gc. lojanense* differs from *Gc. yaoshanense* by having a ceraceous basidiomata with smooth and slightly tuberculate hymenial surface, larger basidia (25–35 × 5–6 μm *vs.* 14–18 × 3–5 μm) and thinwalled, longer basidiospores (6.5–8 × 3.4–4.5 μm *vs.* 4–4.6 × 3–3.5 μm, Jaramillo-Riofrío *et al.* 2023). The taxon *Gc. rajchenbergii* differs from *Gc. yaoshanense* by having a ceraceous basidiomata with the smooth hymenial surface, wider basidia (15–20 × 5–5.5 μm *vs.* 14–18 × 3–5 μm) and longer basidiospores (6–7 × 3–3.5 μm *vs.* 4–4.6 × 3–3.5 μm, Gorjón & Hallenberg 2013). The species *Gc. sinense* can be distinguished from *Gc. yaoshanense* by its coriaceous basidiomata and thin-walled, smooth basidiospores (Zhang *et al.* 2025).

The Wood-inhabiting fungi are an extensively studied group of Basidiomycota, which includes a number of poroid, smooth, grandinioid, odontioid and hydnoid basidiomata, and previously many new taxa were described from China (Dai 2010, Cui *et al.* 2019, Wu *et al.* 2020, 2022a, b, Wang *et al.* 2021, 2023, 2024, Liu *et al.* 2022, 2023, 2024, Zhao *et al.* 2023a, 2024, Yuan *et al.* 2023, Zhou *et al.* 2023, 2024, Dong *et al.* 2025a, b, Liu *et al.* 2025a, b, Qin

et al. 2025). Fungi are closer to humans than to plants, and therefore can be treated as a kind of strategic biological resource (Ming et al. 2023). Scientific research on the biodiversity of fungi and their applications is important, as it may lead to the development of new products (Wu et al. 2019, Hyde et al. 2024a, b). Therefore, for future utilization, it is now urgent to recognize and conserve fungi. The species diversity of Gloeocystidiellum is still poorly understood in China, particularly in the subtropical region. This paper enriches our knowledge of fungal diversity in this area, and it is likely that more new taxa will be found with further fieldwork and molecular analyses.

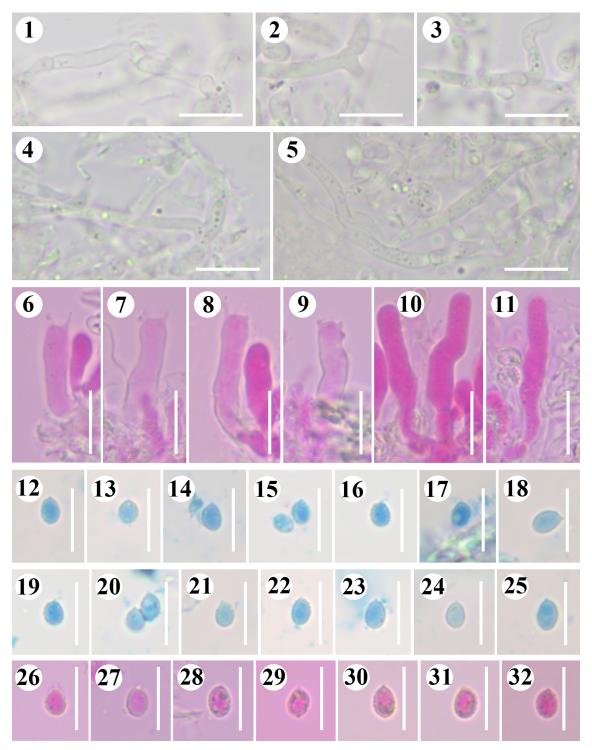


FIGURE 4. Sections of the hymenium of *Gloeocystidiellum yaoshanense* (holotype, CLZhao 20850). (1–5) Hyphae; (6–9) Basidia; (10–11) Gloeocystidia; (12–32) Basidiospores. Scale bars: 1–32 = 10 µm.

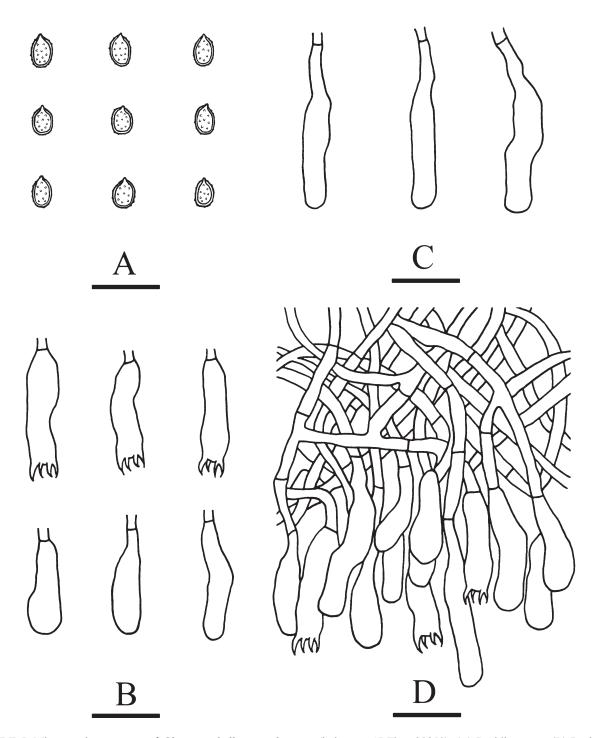


FIGURE 5. Microscopic structures of *Gloeocystidiellum yaoshanense* (holotype, CLZhao 20850). (A) Basidiospores; (B) Basidia and basidioles; (C) Gloeocystidia; (D) Part of the vertical section of the hymenium. Scale bars: A–D = 10 µm.

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