

New corticioid Russulales from China: bamboo-associated diversity and the establishment of *Camptocystidiellaceae* fam. nov.

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Abstract

Corticioid fungi in the Russulales are key decomposers in forest ecosystems, yet their diversity on specialized substrates, particularly bamboo, remains poorly understood. Based on extensive field collections across China with an emphasis on species of bamboo, morphological examinations and multi-loci phylogenetic analyses (ITS, nLSU, RPB2, and *tef1-α*) were employed to assess corticioid fungi in the Peniophoraceae, Stereaceae, and the *Gloeocystidiellum* complex. The phylogenies confirm the polyphyly of *Gloeocystidiellum* s. lat., resolving two distinct clades within the Russulales. The core clade, containing the type species *G. porosum*, is recognized within *Gloeocystidiellaceae*, while the second clade, distinct from the *Gloeocystidiellaceae*, is described here as a new family, *Camptocystidiellaceae* fam. nov., comprising one new genus, *Camptocystidiellum* gen. nov. Morphological and multi-loci phylogenetic analyses revealed 20 new species within nine genera, viz., *Acanthobasidium encrustans*, *A. septobasidium*, *Aleurodiscus subtropicus*, *Asterostroma bicyctidiatum*, *A. brevispinum*, *A. papillatum*, *Baltazaria massoniana*, *Camptocystidiellum flexuosum*, *Gloeocystidiellum monocotyledonum*, *Gloeomyces tapetiformis*, *Gloiothela bambusicola*, *G. spatulata*, *Vararia acanthocystidia*, *V. alpina*, *V. emeiensis*, *V. falcata*, *V. incarnata*, *V. miscanthi*, *V. septocystidiata*, and *V. subulata*. In addition, nine new combinations are proposed: *Baltazaria quintasiana*, *Confertotrama lojanense*, *Camptocystidiellum bisporum*, *C. kenyense*, *C. membranaceum*, *C. parvum*, *C. porosellum*, *C. purpureum*, and *C. yaoshanense*. Notably, monocots, particularly bamboos, appear to have served as recurrent arenas for ecological specialization across *Gloeocystidiellaceae*, *Peniophoraceae*, and *Stereaceae*, suggesting repeated independent transitions to these hosts across multiple lineages in East Asia. This pattern indicates that the region could be an important center for diversification on specialized substrates.

Keywords: Bamboo-associated fungi, Basidiomycota, East Asia, Phylogeny, Taxonomy

Citation: Zhang X, Dai Y, Li M, Zhao Y, Cui Y, et al. 2026. New corticioid Russulales from China: bamboo-associated diversity and the establishment of *Camptocystidiellaceae* fam. nov. *Mycosphere* 17: e015 <https://doi.org/10.48130/mycosphere-0026-0016>

Introduction

The corticioid fungi represent a morphologically and phylogenetically heterogeneous assemblage, unified by their resupinate basidiomata and hymenophores that range from smooth to tuberculate or odontoid^[1]. Phylogenetically, these fungi are widely distributed across numerous orders within the Agaricomycetes, including Agaricales, Amylocorticiales, Atheliales, Auriculariales, Canthareliales, Corticiales, Gloeophyllales, Hymenochaetales, Polyporales, Russulales, Thelephorales, Trechisporales, and Xenasmatellales^[2–15]. Ecologically, they function as essential primary decomposers in forest ecosystems, releasing lignocellulolytic enzymes that promote carbon cycling and nutrient mobilization^[16–20].

Within the order Russulales, species exhibiting corticioid morphology are predominantly concentrated in two families: the Stereaceae and Peniophoraceae^[21,22]. Members of both families typically possess gloeocystidia, predominantly amyloid basidiospores, and diverse sterile elements, such as acanthophyses, dichohyphae, and skeletocystidia^[1,23]. Peniophoraceae, typified by *Peniophora* Cooke, encompasses genera distinguished by specialized hyphal structures, such as *Asterostroma* Masee, characterized by stellate asteroetae, *Baltazaria* Leal-Dutra et al., featuring a dimitic hyphal system and dextrinoid skeletal hyphae, *Gloiothela* Bres. with gloeocystidia containing guttulate contents, and *Vararia* P. Karst. with dichotomously branched dichohyphae^[24–30].

Stereaceae, typified by *Stereum* Hill ex Pers., includes genera known for their varied sterile elements and basidial types, such as *Acanthobasidium* Oberw. with basidia bearing aculeate projections, *Aleurodiscus* Rabenh. ex J. Schröt. with discoid to resupinate basidiomata bearing various sterile elements, and *Gloeomyces* Sheng H. Wu with acanthophyses and simple-septate generative hyphae^[23,31–34]. The genus *Gloeocystidiellum* Donk s. lat. was originally placed in *Gloeocystidiellaceae*^[35], but species in the genus were later often assigned to Stereaceae due to morphological resemblances and insufficient molecular systematic sampling^[6,36–38]. The polyphyly of this genus has been demonstrated by recent phylogenetic investigations, which further confirmed that the core clade, harboring the generic type species *G. porosum* (Berk. & M.A. Curtis) Donk, belongs to the resurrected family *Gloeocystidiellaceae*^[21,39]. However, other lineages remain distributed across distinct families within Russulales, reflecting the long-standing complexity of this group.

Recent molecular studies have begun to clarify the generic boundaries within these families. The circumscriptions of *Peniophora* s. lat. and *Scytinostroma* Donk s. str. in Peniophoraceae have been revised, with *Dendrophora* (Parmasto) Chamuris and *Duportella* Pat. now merged into *Peniophora*^[40], and *Michenera* Berk. & M.A. Curtis nested within *Scytinostroma*^[41]. Within the Stereaceae, Xu et al.^[34] resolved 14 distinct lineages (including two new genera and nine new species from China) based on ITS + nLSU data. In

addition, detailed surveys in biodiversity hotspots like South-western China have uncovered a surprising diversity of species, particularly within *Vararia* and *Asterostroma*^[12,28–30,36,39,42–49]. Yet, comprehensive multi-gene phylogenies for both Stereaceae and Peniophoraceae remain limited, and the fungal diversity associated with specialized substrates, such as monocotyledons, is still poorly understood.

Bamboos (Poaceae, Bambusoideae) occupy a unique ecological niche for wood-inhabiting fungi. Unlike typical dicotyledonous woods, bamboo culms have unique anatomical and chemical characteristics, including high silica content, a distinct vascular bundle arrangement, and a specific lignin composition^[50,51]. China has the richest bamboo diversity in the world, with over 500 species distributed across tropical, subtropical, and temperate regions^[52], providing extensive habitats for bamboo-associated fungi^[53,54]. Numerous bambusicolous ascomycetes have been discovered in China recently^[54–58], and previous studies have revealed several bamboo-associated basidiomycetes within Russulales (e.g., *Acanthobasidium*, *Asterostroma*, *Vararia*, and *Scytinostroma*), suggesting that bamboo substrates harbor a distinctive and underexplored fungal community^[34,39,59–65].

During extensive field investigations across China, numerous corticioid specimens were collected, primarily from bamboos, many of which represent undescribed species. To determine their phylogenetic placements within Stereaceae and Peniophoraceae, we employed a multi-loci phylogenetic approach. The study aims to: (1) characterize the morphological diversity of these fungi; (2) infer their phylogenetic relationships; (3) formally describe new taxa with comprehensive documentation; and (4) explore host associations with monocots, with an emphasis on bamboo-associated taxa.

Materials and methods

Field sampling and herbarium specimen processing

Fresh basidiomata of corticioid fungi were obtained from 14 provinces (Anhui, Fujian, Guangdong, Guizhou, Hainan, Heilongjiang, Henan, Hunan, Jiangxi, Jilin, Shaanxi, Sichuan, Yunnan, and Zhejiang), three autonomous regions (Guangxi, Xinjiang, and Xizang), and two municipalities (Beijing and Chongqing) in China. Specimens were primarily collected from dead or decaying bamboo culms, including *Bambusa emeiensis*, *B. textilis*, *B. vulgaris*, *Dendrocalamus yunnanicus*, *Dendrocalamus* sp., *Fargesia spathacea*, *Indocalamus tessellatus*, *Indosasa crassiflora*, and *Phyllostachys heterocycla*; from other Poaceae (e.g. *Miscanthus* sp.); from Arecaceae (palms); from other dicotyledonous angiosperm wood, and from gymnosperm wood (including *Abies fabri*, *Pinus koraiensis*, and *P. massoniana*).

The specimens were photographed *in situ*, and detailed macroscopic characteristics of the fresh samples were recorded. The specimens were then dried at 38 °C in a mushroom dryer (Evermat, Finland) and sealed in ventilated bags. All examined materials were deposited in the Fungarium of the State Key Laboratory of Efficient Production of Forest Resources, Beijing Forestry University, China (BJFC).

Morphological studies

Macromorphological data were derived from field notes and laboratory observation. Color terminology follows Anonymous^[66] and Petersen^[67]. Microscopic examinations were performed on dried specimens mounted in 5% potassium hydroxide (KOH), 1% Congo Red solution; Melzer's reagent (IKI) and Cotton Blue (CB) were used

to test amyloid/dextrinoid reactions and cyanophily, respectively. Sections were observed under a Nikon Eclipse 80i light microscope (Tokyo, Japan) with phase contrast illumination, at magnifications up to 1,000×. For each specimen, at least 30 basidiospores were measured, mostly in CB, with the apiculus excluded; the upper and lower 5% of measurements are given in parentheses. Listed below are the abbreviations used: IKI = Melzer's reagent, IKI+ = amyloid; IKI[+] = dextrinoid; IKI– = neither amyloid nor dextrinoid; CB– = acyanophilous, and CB+ = cyanophilous. For all spores measured, L = mean length, W = mean width, Q = L/W length-to-width ratios (across all studied specimens), and *n* (a/b) = total spores (a) counted from specimens (b).

DNA extraction, amplification, and sequencing

Genomic DNA was isolated from dried specimens using the CTAB plant genomic DNA extraction kit DN14 (Aidlab Biotechnologies Co., Ltd, Beijing, China), according to the supplier's instructions but with minor modifications^[9,68]. Four gene regions were amplified for phylogenetic analyses: the internal transcribed spacer region (ITS)^[69], the large subunit of nuclear ribosomal RNA gene (nLSU)^[70], the translation elongation factor 1- α gene (*tef1- α*)^[71], and the second subunit of RNA polymerase II (RPB2)^[72]. Primer pairs employed for each marker are summarized in Table 1.

The following temperature and time settings were used for the polymerase chain reaction (PCR):

For ITS and *tef1- α* : 94 °C for 3 min (initial denaturation); 34 cycles of 94 °C for 40 s, 54 °C annealing for 45 s, 72 °C for 1 min; and a final extension at 72 °C for 10 min.

For nLSU: 94 °C for 1 min (initial denaturation); 35 cycles of 94 °C for 30 s, annealing at 50 °C for 1 min, 72 °C for 1.5 min; and a final extension at 72 °C for 10 min.

For RPB2: 94 °C for 2.5 min (initial denaturation); the first round comprised 10 cycles of 94 °C for 40 s, 60 °C for 40 s, and 72 °C for 1.5 min; a second round followed by 37 cycles of 94 °C for 45 s, 52–55 °C for 1 min, 72 °C for 1.5 min; and a final extension at 72 °C for 10 min.

The same primers were used to purify and sequence the PCR products at the Beijing Genomics Institute, China (BGI). The submission of all newly generated sequences to GenBank resulted in their listing in Supplementary Table S1.

Phylogenetic analysis

Newly generated sequences were initially checked using an NCBI BLAST search to verify their identities and to retrieve closely related sequences from GenBank. Additional sequences used were downloaded from GenBank based on recent publications and are listed in Table 2.

The assembly of a concatenated four-gene dataset (ITS + nLSU + RPB2 + *tef1- α*) was used to establish a phylogenetic framework for Russulales and determine the *Gloeocystidiellum* clade's position, including 103 samples representing 93 species, 47 genera, and 16

Table 1. Primers for PCR amplification.

Gene	Primer	Primer sequence (5'–3')	Ref.
ITS	ITS5	GGA AGT AAA AGT CGT AAC AAG G	[69]
	ITS4	TCC TCC GCT TAT TGA TAT GC	
nLSU	LR0R	ACC CGC TGA ACT TAA GC	[70]
	LR7	TAC TAC CAC CAA GAT CT	
RPB2	frPB2-5F	GAY GAY MGW GAT CAY TTY GG	[72]
	frPB2-7CR	CCC ATR GCT TGY TTR CCC AT	
<i>tef1-α</i>	<i>ef1</i> -983F	GCY CCY GGH CAY CGT CAY TTY AT	[71]
	<i>ef1</i> -1567R	ACH GTR CCR ATA CCA CCS ATC TT	

Table 2. Summary of estimated divergence times for the key nodes.

Node	Mean stem age in MCC tree (Mya)	95% HPD range (Mya)
A Russulales	199.48	142.29–276.26
B Peniophoraceae	118.3	83.3–168.41
C Camptocystidiellaceae	99.07	52.84–153.4
D Gloeocystidiellaceae	87.95	51.94–134.78
E Stereaceae	115.3	64.58–189
C1* Agaricales	112.85	90–152.96
C2* Hymenochaetales	144.15	125–190.66
C3* Ascomycota and Basidiomycota	410.48	400–445.29

families, with *Hydnum albomagnum* Banker and *Sistotrema coronilla* (Höhn.) Donk ex D.P. Rogers as outgroups. For Peniophoraceae, a two-gene (ITS + nLSU) dataset was assembled, including 154 samples representing 115 species and 13 genera, with *Amylostereum laevigatum* (Fr.) Boidin and *Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh. as outgroups. Another two-gene (ITS + nLSU) dataset was assembled for Stereaceae, including 124 samples representing 95 species and 16 genera, with *Laurilia sulcata* (Burt) Pouzar as an outgroup.

Multiple sequence alignments were conducted in MAFFT v7^[73] with default parameters, manually adjusted in BioEdit v7.0.9^[74], and combined in Mesquite v4.02^[75]. For each dataset, the best-fit partitioning scheme and substitution models for Bayesian inference (BI) were determined using ModelFinder^[76]. The corrected Akaike Information Criterion (AICc) was utilised for model selection with edge-unlinked partition models.

Maximum Likelihood (ML) phylogenies were inferred with RAXML v8.2.10^[77] employing rapid bootstrapping of 1,000 replicates under default parameters. The GTR + F + I + G4 model was applied with parameters estimated from the data.

Bayesian Inference (BI) analyses were performed with MrBayes v3.2.7^[78]. For the four-gene dataset, the alignment was partitioned by gene region, with the GTR + F + I + G4 model applied to ITS, nLSU, RPB2, and *tef1-α*. For these two ITS + nLSU datasets, the GTR + F + I + G4 model was applied to both genes. Two independent runs with four chains each were conducted for 50 (four-gene dataset), 300 (ITS + nLSU datasets for Peniophoraceae), and 10 million generations (ITS + nLSU datasets for Stereaceae), sampling every 1,000 generations. Analyses were run until convergence, evaluated by the average standard deviation of split frequencies (ASDSF) and effective sample sizes (ESS) of model parameters. According to the sampling range, an ASDSF below 0.05 was considered acceptable for the Peniophoraceae and the *Vararia* single-genus datasets, while for the other datasets the ASDSF dropped below 0.01; all parameters had ESS > 200 after discarding the first 25% of samples as burn-in. A 25% majority consensus tree was then constructed from the post-burn-in trees for all datasets.

Supplementary phylogenetic analyses

To provide higher resolution for within-genus relationships, additional datasets were analyzed, and the resulting trees are presented in the Supplementary Material (Supplementary Figs S1–S9). All ML and BI analyses for supplementary datasets followed the same substitution models and partitioning strategies as described for the main analyses.

Single-genus datasets were assembled for *Acanthobasidium*, *Asterostroma*, *Baltazaria*, the *Gloeocystidiellum* complex, *Gloeomyces*, and *Gloiothele* based on ITS + nLSU sequences. For these datasets, both ML (1,000 bootstrap replicates) and Bayesian (1.5–50 million generations) analyses were performed following the same parameter settings as described for the main datasets.

For *Vararia*, which exhibits extremely high sequence variability and polyphyly, three reduced datasets were constructed: ITS-only, LSU-only, and combined ITS + LSU. For the ITS-only dataset, both Bayesian and maximum likelihood analyses were performed, and the resulting trees are shown in Supplementary Fig. S7. For the LSU-only and combined ITS + LSU datasets, only maximum likelihood analyses were conducted; the resulting trees are shown in Supplementary Figs S8 and S9, respectively.

Visualization and editing of all the phylogenetic trees were carried out using FigTree v1.4.4 and iTOL v6. Branches were regarded as significantly supported if their ML bootstrap value reached ≥ 50% or their Bayesian posterior probability (BPP) reached ≥ 0.9. The alignment files and phylogenetic trees have been deposited in Figshare.

Divergence time estimation

Divergence times and their confidence intervals were inferred using BEAST v2.7.7^[79] under an uncorrelated lognormal relaxed molecular clock with a Yule speciation prior^[80–82], based on another concatenation of ITS, nLSU, RPB2, and *tef1-α* sequences, including 96 samples representing 95 species, 59 genera, 26 families, and 9 orders. Substitution models were simplified to GTR + G4 + I for all partitions.

Three fossil calibrations were employed as minimum age constraints, each assigned a gamma prior (shape = 1, scale = 20): *Archaeomarasmius leggetti* Hibbett et al.^[83] for the crown age of Agaricales at 90 Mya, *Quatsinoporites cranhamii* Smith et al.^[84] for Hymenochaetales at 125 Mya, and *Paleopyrenomycites devonicus* Taylor et al.^[85,86] for the divergence between Ascomycota and Basidiomycota at 400 Mya. The ucl. mean parameters were set to uniform^[7,11,68,87–89].

The Markov chain Monte Carlo (MCMC) analysis was performed over 102 million generations, sampling every 1,000 generations. Convergence was evaluated using Tracer v1.7^[90], and all parameters had ESS > 200 following a 10% burn-in. TreeAnnotator v2.7.7 was employed to summarize the maximum clade credibility (MCC) tree, applying median node heights and 95% highest posterior density (HPD) intervals^[79,91]. Visualization and editing of all the phylogenetic trees were carried out using FigTree v1.4.4 and iTOL v6.

Results

Phylogeny of Russulales derived from combined ITS + nLSU + RPB2 + *tef1-α* sequence data (Fig. 1)

The four-gene phylogeny recovered 14 major families within Russulales with strong support. Among these, Peniophoraceae (99% ML, 1 BPP; Fig. 1), Stereaceae (99% ML, 1 BPP; Fig. 1), Gloeocystidiellaceae (98% ML, 1 BPP; Fig. 1), and the newly described Camptocystidiellaceae fam. nov. (100% ML, 1 BPP; Fig. 1) each formed well-supported monophyletic clades.

Phylogeny of Peniophoraceae derived from combined ITS + nLSU sequence data (Fig. 2; Supplementary Figs S2, S3, S6–S9)

Within Peniophoraceae (Fig. 2), 11 genera were recovered, with the new species distributed across multiple lineages. Among them, *Asterostroma* and *Gloiothele* were resolved as monophyletic, while *Baltazaria* and *Vararia* appeared to be polyphyletic, with their species distributed across multiple lineages.

In *Asterostroma*, which formed a well-supported monophyletic group within Peniophoraceae (89% ML, 0.99 BPP; Fig. 2), three new species described below were placed in two infrageneric subclades (Supplementary Fig. S2) corresponding to morphological groups recognized in previous studies^[92]. *Asterostroma arundinicola* Li

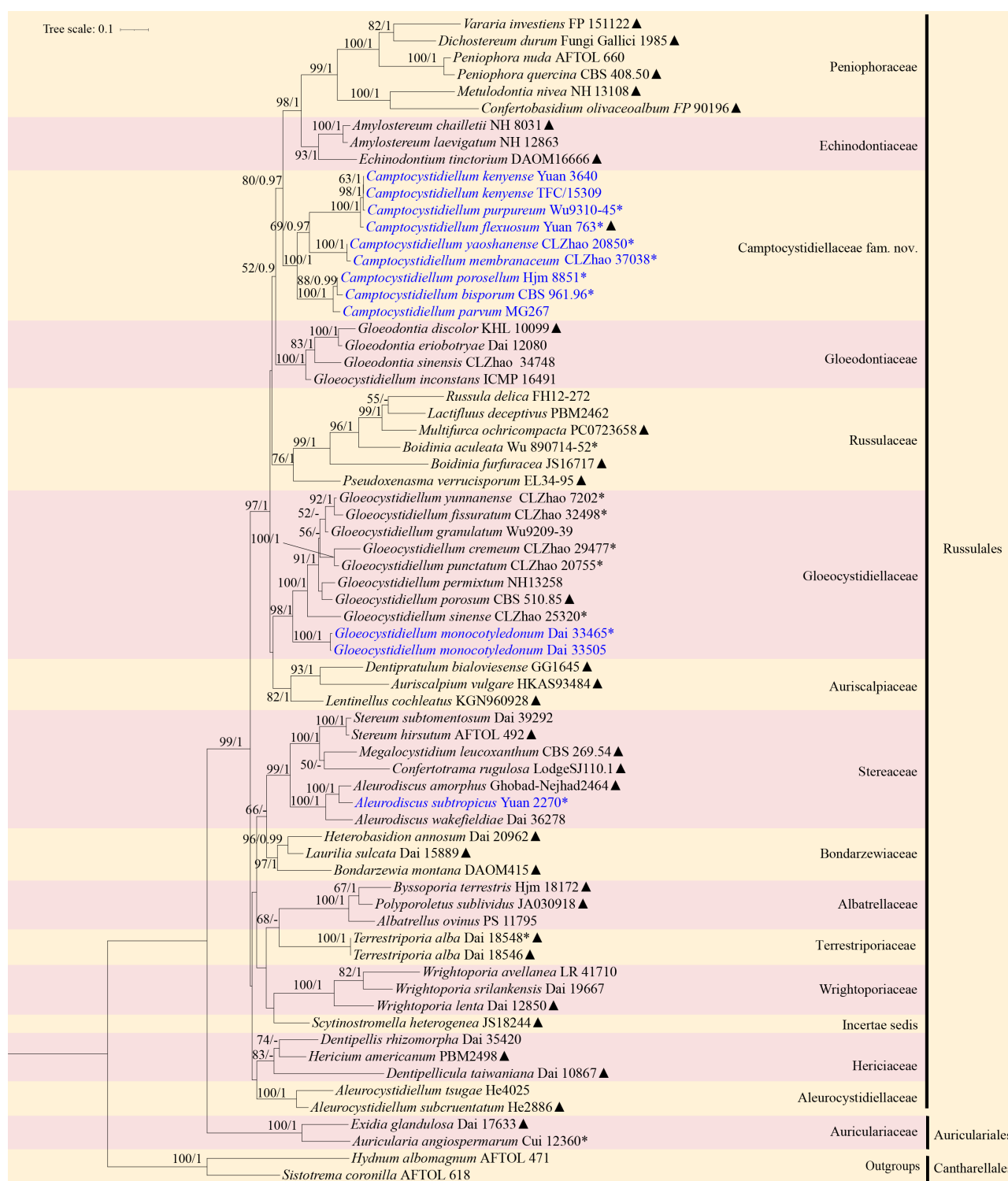


Fig. 1 The phylogeny of Russulales was reconstructed using Maximum Likelihood analysis of combined ITS + nLSU + RPB2 + *tef1-α* sequences. ML and BI analyses gave similar topologies (ASDSF = 0.008643; all parameters ESS > 200). Branch nodes are annotated with Bootstrap support (≥ 50%) and Bayesian posterior probabilities (≥ 0.9). Black triangle (▲) = type species; blue = new species/combinations; asterisk (*) = holotypes.

Wang & K.Y. Luo, *A. bicycidiatum* sp. nov., *A. brevispinum* sp. nov., *A. fimbriatum* Y.L. Deng & C.L. Zhao, and *A. medium* Bres. formed a well-supported clade within sect. *Asterostroma* (77% ML; [Supplementary Fig. S2](#)). *Asterostroma papillatum* sp. nov. was nested within sect. *Laevispora*, and sister to *A. andinum* Pat. ([Supplementary Fig. S2](#)).

In *Baltazaria*, which appeared polyphyletic, distinct clades were recovered within the genus ([Fig. 2](#); [Supplementary Fig. S3](#)). The

Baltazaria s. str. clade, containing the type *B. galactina* (Fr.) Leal-Dutra et al., formed a fully supported clade (100% ML, 1 BPP; [Supplementary Fig. S3](#)) together with the new species *B. massoniana* sp. nov. and two specimens of *Scytinostroma quintasianum* (Bres. & Roum.) Nakasone (CBS 749.86 and CBS 750.86; proposed as a new combination in *Baltazaria* below). The second clade, comprising *B. eurasiaticogalactina* (Boidin & Lanq.) Leal-Dutra et al. and *B.*

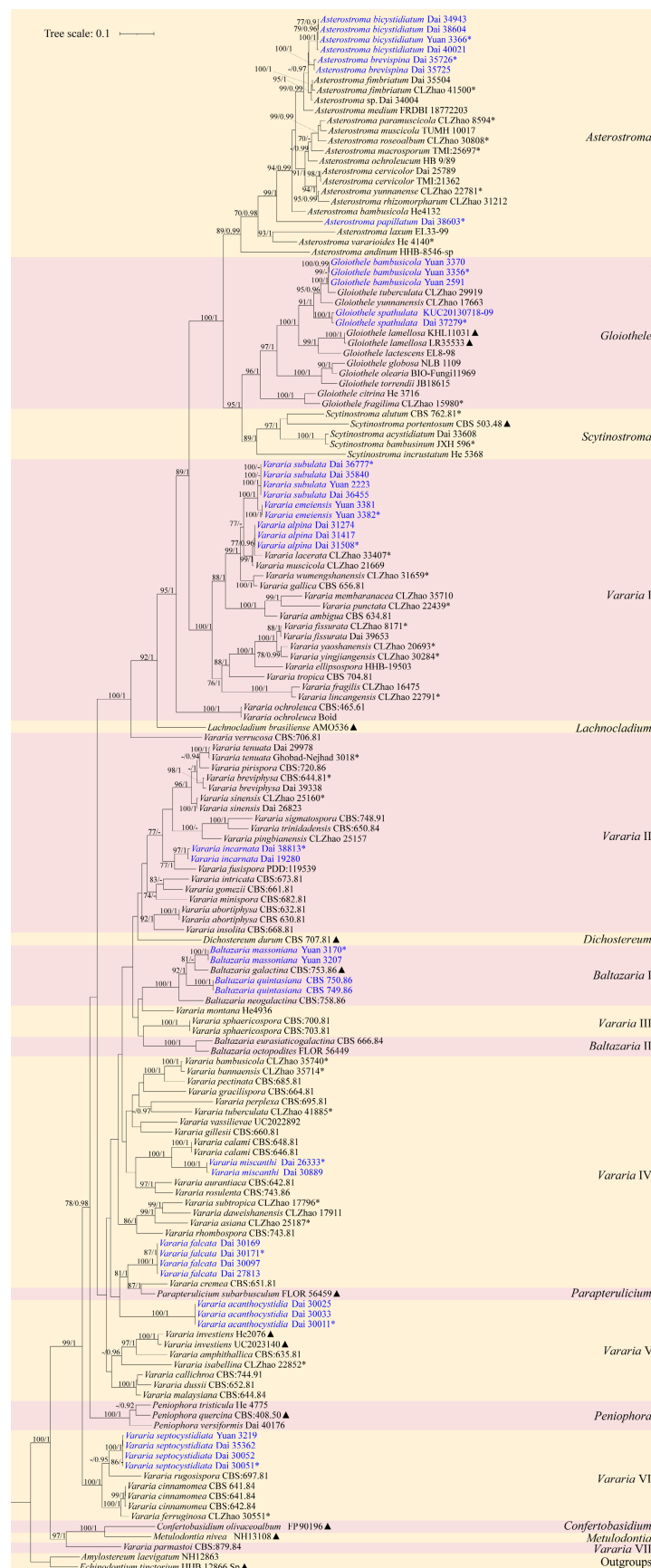


Fig. 2 The phylogeny of Peniophoraceae was reconstructed using Maximum Likelihood analysis of combined ITS + nLSU sequences. ML and BI analyses gave similar topologies (ASDSF = 0.01319; all parameters ESS > 200). Branch nodes are annotated with Bootstrap support ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.9). Black triangle (▲) = type species; blue = new species/combinations; asterisk (*) = holotypes. Major clades are labelled with roman numerals.

octopodites (Corner) Leal-Dutra et al., formed a strongly supported clade (100% ML, 1 BPP; [Supplementary Fig. S3](#)). The third clade includes *B. pingbianensis* Y.L. Deng & C.L. Zhao (100% ML, 1 BPP; [Supplementary Fig. S3](#)).

In *Gloiothele*, also recovered as monophyletic (96% ML, 1 BPP; [Fig. 2](#)), two new species were placed in distinct positions. *Gloiothele bambusicola* sp. nov. formed a well-supported clade with *G. tuberculata* Y.L. Deng & C.L. Zhao (97% ML, 1 BPP; [Supplementary Fig. S6](#)), while *G. spathulata* sp. nov. grouped with *G. lactescens* (Berk.) Hjortstam (69% ML, 1 BPP; [Supplementary Fig. S6](#)). An additional sequence from South Korea (KUC20130718-09) clustered with *G. spathulata* with less than 1.5% ITS sequence divergence and was identified as this species.

In *Vararia*, which was also polyphyletic, eight new species were distributed across multiple lineages within the genus ([Fig. 2](#)). *Vararia acanthocystidia* sp. nov. and *V. falcata* sp. nov. each formed an independent lineage (100% ML, 1 BPP; [Supplementary Fig. S7](#)). *Vararia alpina* sp. nov. and *V. muscicola* Y.L. Deng & C.L. Zhao formed a strongly supported clade (70% ML, 0.98 BPP; [Supplementary Fig. S7](#)), that was sister to another supported clade containing *V. emeiensis* sp. nov., *V. lacerata* Y.L. Deng & C.L. Zhao, and *V. subulata* sp. nov. (64% ML, 0.97 BPP; [Supplementary Fig. S7](#)). *Vararia incarnata* sp. nov. formed an independent, well-supported lineage (100% ML, 1 BPP; [Supplementary Fig. S7](#)) within a larger stable clade (78% ML, 1 BPP; [Supplementary Fig. S7](#)) comprising *V. breviphysa* Boidin & Lanq., *V. pirispora* Boidin et al., *V. sinensis* Y.L. Deng & C.L. Zhao, and *V. tenuata* Ghobad-Nejhad. *Vararia miscanthi* sp. nov. formed a well-supported clade with the African palm-associated *V. calami* Boidin & Lanq. (100% ML, 1 BPP; [Supplementary Fig. S7](#)). *Vararia septocystidiata* sp. nov. formed a well-supported clade with *V. ferruginosa* Y.L. Deng & C.L. Zhao and another African species, *V. cinnamomea* Boidin et al. (88% ML, 1 BPP; [Supplementary Fig. S7](#)). These within-genus relationships are further resolved in the single-genus trees of *Vararia* (ITS-only, LSU-only, and combined ITS + LSU), which are provided in [Supplementary Figs S7–S9](#).

Phylogeny of Stereaceae derived from combined ITS + nLSU sequence data ([Fig. 3](#); [Supplementary Figs S1, S5](#))

Within Stereaceae ([Fig. 3](#)), 16 genera were recovered, with the new species distributed across multiple lineages. Most genera, such as *Acanthobasidium*, *Aleurodiscus* s. str., *Confertotrama*, and *Gloeomyces*, were resolved as monophyletic with strong support following previous studies [[34](#)].

In *Acanthobasidium*, which formed a well-supported monophyletic group (100% ML, 1 BPP; [Fig. 3](#)), two new species were placed in a well-supported clade with the previously described *A. bambusicola* L.D. Dai & S.H. He (100% ML, 1 BPP; [Supplementary Fig. S1](#)). *Acanthobasidium encrustans* sp. nov. and *A. septobasidium* sp. nov. formed a sister relationship within this clade.

Aleurodiscus is represented here by its core *Aleurodiscus* s. str. clade, which was recovered as monophyletic (94% ML, 0.96 BPP; [Fig. 3](#)). *Aleurodiscus subtropicus* sp. nov. was nested within this clade, sister to *A. pinicola* Sheng H. Wu (0.98 BPP; [Fig. 3](#)).

Gloeomyces was resolved as monophyletic (93% ML, 0.94 BPP; [Fig. 3](#)). *Gloeomyces tapetiformis* sp. nov. was recovered as sister to *G. dextrinoideophyses* (S.H. He) S.H. He with strong support (52% ML; [Supplementary Fig. S5](#)).

Confertotrama formed a monophyletic group (99% ML, 1 BPP; [Fig. 3](#)). The type sequence of *Gloeocystidiellum lojanense* A.C. Jaram. et al. (HUTPL(F) 2181, holotype) was nested within *Confertotrama*, sister to *C. aspella* (Hjortstam) Nakasone & S.H. He and *C. rajchenbergii* (Gorjón & Hallenb.) Nakasone & S.H. He. Based on this phylogenetic evidence, a new combination in *Confertotrama* is proposed below.

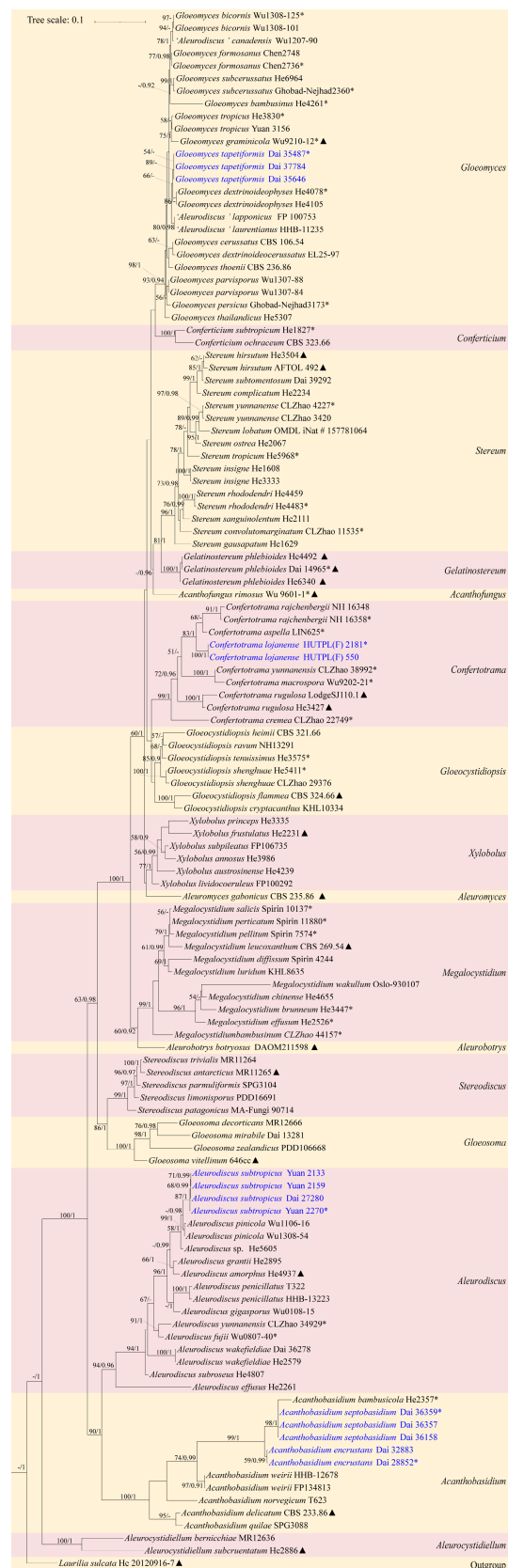


Fig. 3 The phylogeny of Stereaceae was reconstructed using Maximum Likelihood analysis of combined ITS + nLSU sequences. ML and BI analyses produced similar topologies (ASDSF = 0.009606; all parameters ESS > 200). Branch nodes are annotated with Bootstrap support ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.9). Black triangle (▲) = type species; blue = new species/combinations; asterisk (*) = holotypes.

Extensive sampling of the *Gloeocystidiellum* complex derived from combined ITS + nLSU sequence data (Supplementary Fig. S4)

Gloeocystidiellum was confirmed to be polyphyletic, with species distributed across two distinct clades within Russulales (Fig. 1; Supplementary Fig. S4). The core *Gloeocystidiellum* s. str. clade formed a well-supported clade (99% ML, 1 BPP; Supplementary Fig. S4) and is recognized here within Gloeocystidiellaceae. This clade contains *G. porosum* (the type species of *Gloeocystidiellum*), *G. permixtum* (Boidin, Lanq. & Gilles) E. Larss. & K.H. Larss, *G. sinense* Q.Y. Zhang & Yuan Yuan, *G. cremeum* Lu Wang & C.L. Zhao, *G. fissuratum* Lu Wang & C.L. Zhao, *G. yunnanense* Y.L. Zhao & C.L. Zhao, and the new species *G. monocotyledonum* sp. nov.

The second well-supported clade (90% ML, 1 BPP; Supplementary Fig. S4) is treated here as a single new genus, *Camptocystidiellum*. This clade includes *Boidinia parva* Ghobad-Nejhad et al., *Gloeocystidiellum bisporum* Boidin et al., *G. clavuligerum* (Höhn. & Litsch.) Nakasone, and *G. kenyense* Hjortstam, *G. membranaceum* Y.L. Deng & C.L. Zhao, *G. porosellum* Hjortstam, *G. purpureum* Sheng H. Wu, *G. yaoshanense* Y.J. Zhu & C.L. Zhao, and a new species described below as *Camptocystidiellum flexuosum* sp. nov. All these species are transferred to *Camptocystidiellum* as described below, except for *G. clavuligerum*.

Divergence of *Camptocystidiellaceae* fam. nov. derived from combined ITS + nLSU + RPB2 + *tef1-α* sequence data (Fig. 4)

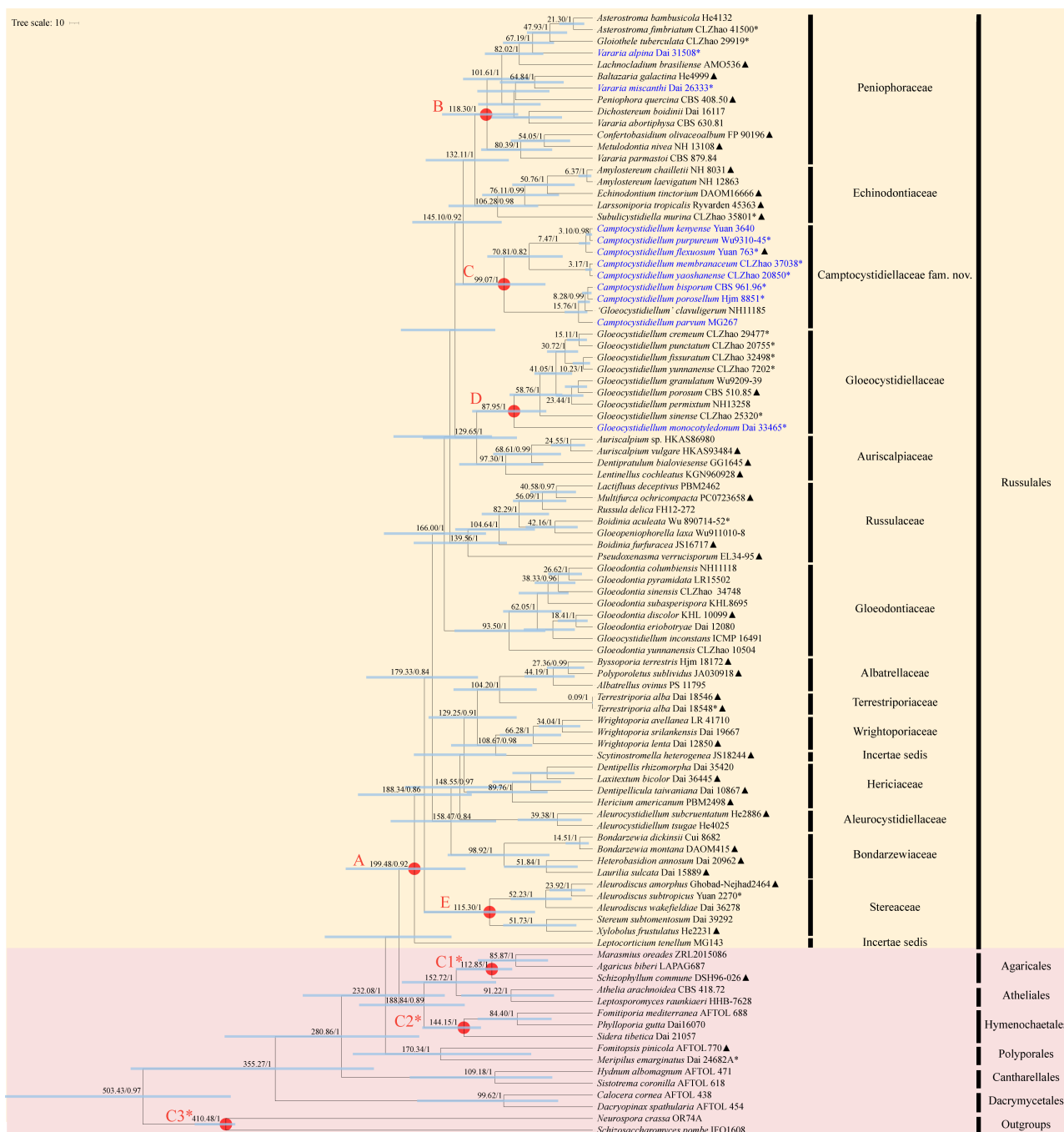


Fig. 4 Estimated divergence times of Russulales families were calculated using a four-gene dataset (ITS + nLSU + RPB2 + *tef1-α*). Node supports were assessed with Bayesian posterior probabilities (≥ 0.8). Mean ages (Mya) are shown with 95% HPD intervals represented as horizontal bars. Black triangle (▲) = type species; blue = new species/combinations; asterisk (*) = holotypes.

The mean stem age of the new family *Camptocystidiellaceae*, which contains the single genus *Camptocystidiellum*, was estimated at 99.07 Mya (52.84–153.4 Mya, 95% HPD) during the Late Cretaceous, distinguished from *Gloeocystidiellaceae* (87.95 Mya; 51.94–134.78 Mya, 95% HPD) following the initial diversification of Russulales (199.48 Mya; 142.29–276.26 Mya, 95% HPD). The three fossil calibration points used in this analysis (C1* Agaricales: 112.85 Mya, 90–152.96 Mya, 95% HPD; C2* Hymenochaetales: 144.15 Mya, 125–190.66 Mya, 95% HPD; C3* Ascomycota and Basidiomycota: 410.48 Mya, 400–445.29 Mya, 95% HPD) yielded age estimates compatible with previous studies^[39,87,93–95]. The estimated divergence times for all major nodes are summarized in Table 2.

Taxonomy

Order Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David

Index Fungorum number: IF90569.

Type family – Russulaceae Lotsy

Family Camptocystidiellaceae Xin Zhang, Y.C. Dai & Yuan Yuan, fam. nov.

Index Fungorum number: IF905320.

Type genus – *Camptocystidiellum* Xin Zhang, Y.C. Dai & Yuan Yuan, gen. nov.

Etymology – Refers to the type genus *Camptocystidiellum*.

Description – Basidiomata annual, resupinate, adnate, membranous to coriaceous. Hymenial surface smooth to slightly cracked, yellowish (1A2–4A2) to cream (4A3) or buff (4A4). Hyphal system monomitic; generative hyphae with clamp connections or simple septa, colorless, thin- to slightly thick-walled, IKI–, CB–. Gloeocystidia abundant, mostly subcylindrical to tubular, straight to flexuous, sometimes constricted, moniliform, or with a schizopapillate apex. Basidia subcylindrical to clavate or urniform, with 2–4 sterigmata. Basidiospores ellipsoid to subglobose, mostly verrucose or rarely smooth, strongly IKI+, CB–.

Notes – *Gloeocystidiellum* has long been recognized as a polyphyletic assemblage within Russulales^[21,35,39,96,97]. In the present study, this new family is proposed on the basis of phylogenetic analyses (Fig. 1; Supplementary Fig. S4), which recover it as a well-supported clade (100% ML, 1 BPP; Fig. 1), separated from *Gloeocystidiellaceae*.

Both *Camptocystidiellaceae* and *Gloeocystidiellaceae* contain a single genus, but they differ in several morphological traits. *Gloeocystidiellum* (type genus of *Gloeocystidiellaceae*) possesses mostly clamped hyphae and straight to slightly curved gloeocystidia. In contrast, *Camptocystidiellum* (type genus of *Camptocystidiellaceae*) exhibits both clamped and simple-septate hyphae, and its gloeocystidia range from straight to strongly flexuous—a feature not found in *Gloeocystidiellaceae*. The genus *Camptocystidiellum* currently includes eight species, occurring on gymnosperm and angiosperm wood in montane to lowland forests across Africa, Asia, Europe, and North America^[35,38,39,98–102]. In contrast to *Gloeocystidiellaceae*, no association with monocotyledonous hosts is currently known for *Camptocystidiellaceae*. A morphological comparison of *Camptocystidiellaceae* with related families is provided in Table 3.

Camptocystidiellum Xin Zhang, Y.C. Dai & Yuan Yuan, gen. nov.

Index Fungorum number: IF905232.

Type species – *Camptocystidiellum flexuosum* Xin Zhang, Y.C. Dai & Yuan Yuan

Etymology – *Camptocystidiellum* (Lat.), from *camptos* (Greek, bent) + *cystidiellum* (cystidium), refers to the distinctly flexuous gloeocystidia.

Description – Basidiomata annual, resupinate, adnate, membranous to coriaceous. Hymenial surface smooth to slightly cracked, white (–A1) to cream (4A3) or buff (4A4). Hyphal system monomitic;

generative hyphae with clamp connections or simple-septate, colorless, thin- to slightly thick-walled, IKI–, CB–. Gloeocystidia abundant, subulate to tubular, straight to distinctly flexuous (winding), sometimes constricted, moniliform, or with a schizopapillate apex. Basidia subcylindrical to clavate or urniform, with 2–4 sterigmata. Basidiospores ellipsoid to subglobose, mostly verrucose or rarely smooth, strongly IKI+, CB–.

Notes – *Camptocystidiellum* is established based on phylogenetic and morphological evidence (Fig. 1, Supplementary Fig. S4), including eight species: the new species *C. flexuosum* (type species) and seven new combinations, *C. kenyense* (= *Gloeocystidiellum kenyense*), *C. purpureum* (= *G. purpureum*), *C. bisporum* (= *G. bisporum*), *C. parvum* (= *Boidinia parva*), *C. porosellum* (= *G. porosellum*), *C. yaoshanense* (= *G. yaoshanense*), and *C. membranaceum* (= *G. membranaceum*).

The eight species are divided into two groups based on hyphal septation: four with clamped hyphae and four with simple-septate hyphae. *Camptocystidiellum flexuosum*, *C. kenyense*, *C. purpureum*, and *C. parvum* share a monomitic hyphal system with clamp connections and verrucose basidiospores^[99,101,102]. *Camptocystidiellum flexuosum* (the type species), known only from high-elevation temperate forests of Xinjiang and Xizang (2,158–3,925 m) in Western China on gymnosperm and angiosperm wood. *Camptocystidiellum kenyense*, originally described from Kenya, is distinguished by subfusiform and generally straight gloeocystidia^[99]. It is distributed across high-elevation habitats in East Africa (2,200–2,400 m)^[99] and Sichuan, China (2,867 m; on *Pinus yunnanensis*), contrasting with lower elevations in the Atlantic islands (380–485 m)^[100]. *Camptocystidiellum purpureum*, known only from Taiwan, China (1,950 m), is characterized by flexuous gloeocystidia with a purplish reaction in sulphovanillin, and its transfer is based on the sequence from the type material (Wu 9310-45)^[21,101]. *Camptocystidiellum parvum*, known only from Jilin, China (1,020 m), is distinguished by obclavate gloeocystidia, with its holotype specimen (BJFC012115) and corresponding sequence data available^[102].

The remaining four species (*Camptocystidiellum bisporum*, *C. porosellum*, *C. yaoshanense*, and *C. membranaceum*) have simple-septate hyphae. *Camptocystidiellum porosellum* and *C. bisporum* are combined based on sequences derived from their respective type materials (Hjortstam 8851 and CBS 961.96) and morphological compatibility with the generic concept. *Camptocystidiellum porosellum*, known only from Europe, is characterized by gloeocystidia with a schizopapillate apex^[98]. *Camptocystidiellum bisporum*, known only from France, is unique within the genus by its two-spored basidia and elongated gloeocystidia^[35]. *Camptocystidiellum yaoshanense* and *C. membranaceum* are combined based on phylogenetic and morphological evidence, both recently described from Yunnan, China, with holotype specimens (CLZhao 20850 and CLZhao 26028) and corresponding sequence data available. *Camptocystidiellum yaoshanense* grows at high elevation (3,200 m) with a grandinoid hymenophore, tubular gloeocystidia^[38], whereas *C. membranaceum* is found at lower elevations (1,000–1,875 m) with a membranous hymenophore, cylindrical gloeocystidia, and smooth basidiospores—a unique feature within *Camptocystidiellum*^[39].

All species share a preference for montane to high-elevation habitats on gymnosperm and angiosperm wood across Africa, Asia, Europe, and North America, and all new combinations proposed herein are based on sequences derived from type specimens or authenticated reference strains. However, *Gloeocystidiellum clavuligerum* is retained in *Gloeocystidiellum* since no sequence data were available from the type material and no further specimens could be obtained. The following combinations are thus proposed:

Camptocystidiellum flexuosum Xin Zhang, Y.C. Dai & Yuan Yuan, sp. nov. Fig. 5

Table 3. Morphological comparison of Camptocystidiellaceae fam. nov. with related families in Russulales.

Character	Camptocystidiellaceae	Gloeocystidiellaceae	Gloeodontiaceae	Peniophoraceae	Russulaceae*	Stereaceae
Basidiomata	Resupinate, membranous to coriaceous	Resupinate, membranous	Resupinate to effused-reflexed, membranous to coriaceous	Resupinate, orbicular, discoid, effused-reflexed to clavarioid, often waxy or coriaceous	Resupinate, arachnoid to ceraceous or membranaceous	Resupinate, discoid, cupulate, steroid, auricularioid, effused-reflexed to pileate-sessile
Hymenial surface	Smooth to slightly cracked, sometimes grandinioid	Smooth, rarely grandinioid or odontoid	Smooth to odontoid	Smooth, grandinioid, tuberculate or raduloid	Smooth, odontoid, to tuberculate	Smooth, rugose to tuberculate
Hyphal system	Monomitic	Monomitic	Monomitic	Monomitic to dimitic	Monomitic	Monomitic to dimitic
Generative hyphae	With or without clamp connections	Mostly with clamp connections (rarely simple-septate)	With clamp connections	With or without clamp connections	With or without clamp connections (simple-septate in <i>Boidinia</i> ; clamped in others)	With or without clamp connections
Skeletal/binding hyphae	None	None	None	Present in many genera, often dextrinoid	None	Occasionally present
Gloeocystidia	Abundant, subcylindrical to tubular, straight to strongly flexuous	Abundant, straight to slightly curved	Present, often with apical projections	Present; variable	Present, often tubular to clavate	Present, often capitate or moniliform
Other sterile elements	None	None	None	Dendrohyphidia, dichohyphae, asterosetae, acanthophyses	Acanthophyses in <i>Gloeopeniophorella</i> ; none in others	Acanthophyses, acanthobasidia, dendrohyphidia
Basidia	Subcylindrical to clavate or urniform, 2–4 sterigmata	Subcylindrical to clavate, 4 sterigmata	Cylindrical to uniform, 4 sterigmata	Mostly clavate to subcylindrical, 4 sterigmata	Clavate to urniform (or pleurobasidia in <i>Pseudoxenasma</i>), 4 sterigmata	Mostly clavate to subcylindrical, 4 sterigmata
Basidiospores	Ellipsoid to subglobose, verruculose (rarely smooth), strongly IKI+, CB–	Ellipsoid to subglobose, verruculose to echinulate (rarely smooth), IKI+, CB–	Ellipsoid to globose, asperulate, IKI+, CB–	Variable (mostly ellipsoid to subglobose), smooth or ornamented, mostly IKI+, mostly CB–	Globose to ellipsoid, verrucose to echinulate, IKI+, CB–	Variable (mostly ellipsoid to subglobose), smooth or ornamented, mostly IKI+, mostly CB–
Ecology	On wood	On wood, rarely on monocots	On wood	On wood and monocots	On wood	On wood, occasionally on monocots
Distribution	Africa, Asia, Europe, North America	Asia, Europe, North America	Asia, Africa, Americas, Europe	Widespread	Widespread	Widespread

* Corticioid representatives, e.g., *Boidinia* Stalpers & Hjortstam, *Gloeopeniophorella* Rick, *Pseudoxenasma* K.H. Larss. & Hjortstam.

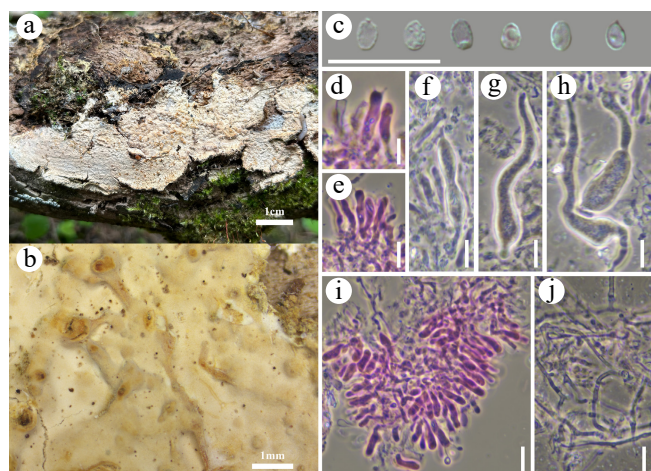


Fig. 5 *Camptocystidiellum flexuosum* (holotype, Yuan 763). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f)–(h) Gloeocystidia. (i) A section of hymenium. (j) Generative hyphae. Scale bars: (c)–(j) = 10 μ m.

Index Fungorum number: IF905231.

Etymology – *Flexuosum* (Lat.): refers to the species having winding cystidia.

Diagnosis – Characterized by the presence of distinctly flexuous (winding) gloeocystidia with a schizopapillate apex, ellipsoid, verruculose basidiospores measuring $3.7\text{--}4 \times 2.6\text{--}2.9 \mu\text{m}$, and growing on gymnosperm and angiosperm wood in high-elevation temperate forests of Western China.

Type – China, Xinjiang Autonomous Region, Yili, Tekes County, Kaladala, Qiongkushitai Village, 42.913632°N , 82.107869°E , elevation 2,158 m, on fallen angiosperm branch, leg. Yuan Yuan, 21 July 2023, Yuan 763 (BJFC041775).

Description – Basidiomata annual, resupinate, soft, membranous, closely adnate, up to 6.1 cm long, 1.7 cm wide, 150 μm thick at center. Hymenial surface smooth to locally tuberculate, slightly cracked, cream (4A3) to buff (4A4) and without odor and taste when fresh, buff (4A4) to olivaceous buff (4C4) when dry; margin white (–A1), thinning out, fimbriate.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin-walled, moderately branched and septate, IKI–, CB–, $1.2\text{--}3 \mu\text{m}$ in diam. Gloeocystidia abundant, subulate, mostly with many bends (or strongly flexuous), with guttulate content and a schizopapillate apex, hyaline, thin-walled, $55\text{--}100 \times 7\text{--}18 \mu\text{m}$. Basidia subcylindrical to clavate, thin-walled, with four sterigmata and a basal clamp connection, $17\text{--}30 \times 3\text{--}6 \mu\text{m}$; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores ellipsoid, hyaline, thin-walled, verruculose, IKI+, CB–, $(3.5\text{--})3.7\text{--}4(4.2) \times (2.5\text{--})2.6\text{--}2.9(3.1) \mu\text{m}$, $L = 3.94 \mu\text{m}$, $W = 2.82 \mu\text{m}$, $Q = 1.3\text{--}1.5$ ($n = 60/2$).

Additional specimens examined – China, Xizang Autonomous Region, Rikaze, Yadong County, along the road from Yadong Customs to Baxia Waterfall, 27.3172°N , 88.9698°E , elevation 3,925 m, on a fallen branch of *Abies fabri*, leg. Y.C. Dai, 18 October 2024, Dai 31934 (BJFC052193).

Known distribution – currently known from high-elevation temperate forests in Western China (Xinjiang and Xizang), found on fallen gymnosperm and angiosperm branches.

Notes – phylogenetically, *Camptocystidiellum flexuosum* formed a well-supported clade with *C. kenyense* and *C. purpureum* (99% ML, 1 BPP; [Supplementary Fig. S4](#)). Morphologically, *C. kenyense* is distinguished from *C. flexuosum* by its subfusiform and generally straight gloeocystidia, larger basidiospores ($4\text{--}4.5 \times 3\text{--}3.5 \mu\text{m}$ vs $3.7\text{--}4 \times$

$2.6\text{--}2.9 \mu\text{m}$), and distribution in Africa^[99]. *Camptocystidiellum purpureum* shares flexuous gloeocystidia with *C. flexuosum*, but is distinguished by having a purplish reaction of gloeocystidia in sulphovanillin and slightly larger basidiospores ($3.8\text{--}4.3 \times 2.9\text{--}3.4 \mu\text{m}$ vs $3.7\text{--}4 \times 2.6\text{--}2.9 \mu\text{m}$)^[101]. In addition, *C. flexuosum* is further distinguished by its distinctly winding gloeocystidia and high-elevation distribution in Western China.

Camptocystidiellum bisporum (Boidin, Lanq. & Gilles) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905235.

Basionym – *Gloeocystidiellum bisporum* Boidin, Lanq. & Gilles, Bull. Trimestriel Soc. Mycol. France 113(1): 33 (1997)

Known distribution – currently known from the type locality in France, growing on a fallen, decomposing branch of *Quercus robur*.

Camptocystidiellum kenyense (Hjortstam) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905234.

Basionym – *Gloeocystidiellum kenyense* Hjortstam, Mycotaxon 28(1): 29 (1987)

Specimen examined – China, Sichuan Province, Yajiang County, 318 National Highway near Shangzhongjiu, 30.070603°N , $101.147041^\circ \text{E}$, elevation 2,867 m, on a fallen branch of *Pinus yunnanensis*, leg. Yuan Yuan, 6 October 2025, Yuan 3640 (BJFC063186).

Known distribution – originally described from Kenya (Aberdare Mountains, 2,200–2,400 m), also recorded from China (Sichuan, 2,867 m), found on coniferous wood.

Camptocystidiellum membranaceum (Y.L. Deng & C.L. Zhao) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905239.

Basionym – *Gloeocystidiellum membranaceum* Y.L. Deng & C.L. Zhao, in Deng, Chen, Zhang, Wang, Liu, Qiu, Dou, Liu, Wijesinghe, Zhou, Jabeen & Zhao, Mycosphere 17: e003. (2026)

Known distribution – currently known from the type locality in Yunnan Province, China (1,000–1,875 m), found on a fallen angiosperm branch.

Camptocystidiellum parvum (Ghobad-Nejhad, S.L. Liu, Y.C. Dai & E. Langer) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905236.

Basionym – *Boidinia parva* Ghobad-Nejhad, S.L. Liu, Y.C. Dai & Langer, in Adamčík et al., Cryptog. Mycol. 36(2): 126 (2015)

Specimen examined – China, Jilin Province, Antu County, Erdaobaihe, Changbaishan Nature Reserve, Huangsongpu, on a fallen decorticated trunk, leg. Ghobad-Nejhad, Dai, Wu & Sohrabi, 6 September 2011, Ghobad-Nejhad 2236 (holotype of *Boidinia parva*, BJFC012115).

Known distribution – currently known from the type locality in Jilin Province, China (1,020 m), found on a fallen decorticated trunk.

Camptocystidiellum porosellum (Hjortstam) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905237.

Basionym – *Gloeocystidiellum porosellum* Hjortstam, Mycotaxon 19: 505 (1984)

Known distribution – currently known from Europe, found on a fallen trunk and branches of *Alnus*.

Camptocystidiellum purpureum (Sheng H. Wu) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905233.

Basionym – *Gloeocystidiellum purpureum* Sheng H. Wu, Mycotaxon 58: 44 (1996)

Known distribution – currently known only from the type locality in Taiwan, China (1,950 m), found on angiosperm wood.

Camptocystidiellum yaoshanense (Y.J. Zhu & C.L. Zhao) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905238.

Basionym – *Gloeocystidiellum yaoshanense* Y.J. Zhu & C.L. Zhao, in Zhu, Dong, Shen, Yang, Zhao & Zhan, Phytotaxa 725(1): 17 (2025)

Known distribution – currently known from the type locality in Yunnan Province, China, found on a fallen angiosperm branch at high elevation (3,200 m).

Family Gloeocystidiellaceae Jülich 1982

Index Fungorum number: IF81775.

Type genus – *Gloeocystidiellum* Donk

Gloeocystidiellum Donk

Index Fungorum number: IF17041.

Type species – *Gloeocystidiellum porosum* (Berk. & M.A. Curtis) Donk

Notes – *Gloeocystidiellum* was traditionally defined as a genus of resupinate corticioid fungi with a monomitic hyphal system, gloeocystidia, and amyloid basidiospores. However, the genus in its broad sense has long been recognized as polyphyletic, with species distributed across multiple clades within the Russulales^[21,39,96,97], which is consistent with our phylogenies (Fig. 1; Supplementary Fig. S4). Thus, two distinct *Gloeocystidiellum* clades are resolved.

The core clade is recognized here as belonging to the family Gloeocystidiellaceae (99% ML, 1 BPP; Supplementary Fig. S4); all species in this restricted genus have mostly clamped hyphae and straight to slightly curved gloeocystidia, with the exception of *G. sinense*, which has simple septa. The second well-supported clade is here accommodated in the newly described family Camptocystidiellaceae (90% ML, 1 BPP; Supplementary Fig. S4), and exhibits both clamped and simple-septate hyphae and more variable gloeocystidia (straight to strongly flexuous).

Accordingly, *Gloeocystidiellum* is now restricted to its core clade within Gloeocystidiellaceae, containing the type species *G. porosum* together with *G. cremeum*, *G. sinense*, *G. permixtum*, *G. fissuratum*, *G. yunnanense*, and a new species described below, *G. monocotyledonum*, which grows on monocotyledonous plants (palms and *Miscanthus*) in subtropical China. Information on the *Gloeocystidiellum* complex and the morphological comparison of the resulting families is provided in Table 3.

Gloeocystidiellum monocotyledonum Xin Zhang, Y.C. Dai, Y.L. Zhao & Yuan Yuan, sp. nov. Fig. 6

Index Fungorum number: IF905285.

Etymology – *Monocotyledonum* (Lat.): refers to the species growing on monocotyledonous plants.

Diagnosis – characterized by the presence of subcylindrical to subclavate, flexuous gloeocystidia, fusiform cystidioles, verruculose basidiospores measuring $5.6\text{--}6.7 \times 4.9\text{--}5.2 \mu\text{m}$, and growing only on monocotyledonous plants (palms and *Miscanthus*) in subtropical China.

Type – China, Zhejiang Province, Jinhua, Wuyi County, Qianzhangyan Scenic Spot, 28.766327° N, 119.900587° E, elevation 670 m, on dead palm, leg. Y.C. Dai, 20 March 2025, Dai 33465 (BJFC054457).

Description – basidiomata annual, resupinate, soft, membranous, closely adnate, up to 12 cm long, 3 cm wide, 75 μm thick at center. Hymenial surface smooth, rarely graninioid, uncracked, white (–A1) to grayish white (1B1) and without odor and taste when fresh, cream (4A3) to buff (4A4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin-walled, moderately branched and frequently septate, IKI–, CB–, $1.2\text{--}3.5 \mu\text{m}$ in diam. Gloeocystidia abundant, subcylindrical to subclavate, flexuous, with guttulate content, hyaline, thin-walled, $45\text{--}70 \times 5\text{--}10 \mu\text{m}$. Basidia subcylindrical to clavate, thin-walled, with four sterigmata and a basal

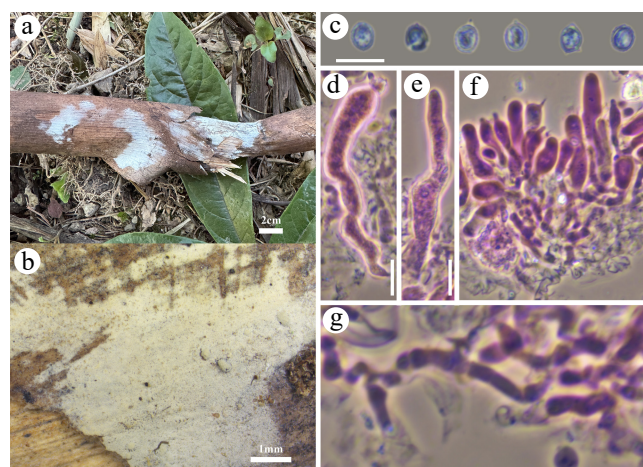


Fig. 6 *Gloeocystidiellum monocotyledonum* (holotype, Dai 33465). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Gloeocystidia. (f) A section of hymenium. (g) Generative hyphae. Scale bars: (c)–(g) = 10 μm .

clamp connection, $18\text{--}30 \times 4\text{--}7 \mu\text{m}$; fusiform cystidioles present; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores broadly ellipsoid to subglobose, hyaline, slightly thick-walled, verruculose, IKI+, CB–, $(5.4\text{--})5.6\text{--}6.7\text{--}(6.8) \times (4.8\text{--})4.9\text{--}5.2\text{--}(5.4) \mu\text{m}$, $L = 6.15 \mu\text{m}$, $W = 5.04 \mu\text{m}$, $Q = 1.1\text{--}1.3$ ($n = 90/3$).

Additional specimens examined – China, Zhejiang Province, Jinhua, Wuyi County, Hongsi Village, Lengjiang Pond, 28.73127° N, 119.551414° E, elevation 648 m, on dead *Miscanthus*, leg. Y.C. Dai, 22 March 2025, Dai 33505 (BJFC054497); Lishui, Baiyun National Forest Park, on dead *Miscanthus*, leg. Y.C. Dai, 27 April 2025, Dai 33840 (BJFC055102).

Known distribution – currently known from subtropical montane forests in Eastern China (Zhejiang), found on dead *Miscanthus* and palm.

Notes – phylogenetically, *Gloeocystidiellum monocotyledonum* occupies an independent, well-supported lineage within *Gloeocystidiellum* (100% ML, 1 BPP; Supplementary Fig. S4), and is sister to *G. sinense*. Morphologically, *G. sinense* shares similar basidia with *G. monocotyledonum*, but is distinguished by simple-septate generative hyphae, smaller basidiospores, and growth on angiosperm wood ($3.7\text{--}4.4 \times 2.8\text{--}3.2 \mu\text{m}$ vs $5.6\text{--}6.7 \times 4.9\text{--}5.2 \mu\text{m}$)^[37]. The type species *G. porosum* also resembles *G. monocotyledonum* in having a monomitic hyphal system with clamp connections, and verrucose basidiospores, but differs by its smaller basidiospores ($4.3\text{--}5 \times 2.8\text{--}3.2 \mu\text{m}$ vs $5.6\text{--}6.7 \times 4.9\text{--}5.2 \mu\text{m}$), and occurrence on diverse gymnosperm and angiosperm wood, and occasionally on bamboo^[1,35,96,97,101,103,104].

Family Peniophoraceae Lotsy

Index Fungorum number: IF81123.

Type genus – *Peniophora* Cooke

Asterostroma Massee

Index Fungorum number: IF17113.

Type species – *Asterostroma apalum* (Berk. & Broome) Massee

Notes – *Asterostroma* is a well-defined corticioid genus characterized by the presence of distinctive asterosetae (regular star-shaped or dichotomously branched) and amyloid basidiospores^[92,105]. This study, incorporating three new species from bamboos in China, supports and further elucidates these morphological groupings: *A. bicytidiatum* and *A. brevispinum* (echinulate basidiospores and regular star-shaped asterosetae) belong to sect. *Asterostroma* clade, while *A. papillatum* (smooth basidiospores and dichotomously branched asterosetae) represents sect. *Laevispora* clade.

Asterostroma bicycstidium Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 7

Index Fungorum number: IF905286.

Etymology – *Bicycstidium* (Lat.): refers to the species having two kinds of cystidia.

Diagnosis – characterized by the presence of two kinds of gloeocystidia (fusiform or sinuous), globose, echinulate basidiospores measuring $4.7\text{--}4.9 \times 4.3\text{--}4.7 \mu\text{m}$ with prominent spines (up to $1.2 \mu\text{m}$ long), and growing on bamboos in subtropical to warm-temperate China.

Type – China, Sichuan Province, Dujiangyan, Tongmagouzhuhai Park, 31.042187°N , $103.644348^\circ \text{E}$, elevation 728 m, on dead culm of *Bambusa emeiensis*, leg. Yuan Yuan, 29 September 2025, Yuan 3366 (BJFC062912).

Description – basidiomata annual, resupinate, soft, membranous, loosely adnate, up to 6 cm long, 3 cm wide, $150 \mu\text{m}$ thick at center. Hymenial surface smooth, uncracked, cottony to hypochnoid, cream (4A3) to buff (4A4), without odor or taste when fresh and dry; margin white (–A1), with distinct hyphal strands.

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin-walled, moderately branched and frequently septate, IKI–, CB–, $1.7\text{--}5 \mu\text{m}$ in diam. Asterosetae in subiculum abundant, predominant, dark brown, thick-walled, regularly star-shaped, weakly IKI(+), CB–, $3\text{--}6 \mu\text{m}$ in diam, rays up to $75 \mu\text{m}$ long, with acute tips; asterohyphidia in hymenium similar to asterosetae in subiculum, but smaller and less regularly shaped, weakly IKI(+), CB–, $3\text{--}5 \mu\text{m}$ in diam, rays up to $35 \mu\text{m}$ long, with acute tips. Gloeocystidia abundant, two types, one fusiform, another sinuous, both hyaline, thin-walled, with a basal simple septum, $30\text{--}60 \times 7\text{--}15 \mu\text{m}$; cystidioles absent. Basidia clavate with constricted middle, hyaline, thin-walled, with four sterigmata and a basal simple septum, $25\text{--}41 \times 4.2\text{--}5.3 \mu\text{m}$; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores globose, occasionally with a big oil drop, hyaline, thin-walled, echinulate, IKI+, CB–, $(4.5\text{--})4.7\text{--}4.9\text{--}(5) \times (4.2\text{--})4.3\text{--}4.7\text{--}(4.8) \mu\text{m}$, $L = 4.71 \mu\text{m}$, $W = 4.44 \mu\text{m}$, $Q = 1\text{--}1.1$ ($n = 60/2$); spines obtuse, up to $1.2 \mu\text{m}$ long.

Additional specimens examined – China, Guangxi Autonomous Region, Liuzhou, Rongshui County, Sirong, 25.1411°N , 109.1981°E , elevation 176 m, on dead culm of *Indocalamus tessellatus*, leg. Y.C. Dai, 27 October 2025, Dai 40021 (BJFC061278); Henan Province, Luoyang, Luanchuan County, Wangfuzuhai, 33.876175°N , $111.555185^\circ \text{E}$, elevation 925 m, on rotten bamboo, leg. Y.C. Dai, 20 October 2025, Dai 38604 (BJFC059863); Shaanxi Province, Ankang, Ningshan County, Huoditang, 33.372652°N , $108.337217^\circ \text{E}$,

elevation 907 m, on dead culm of *Fargesia spathacea*, leg. Y.C. Dai, 7 August 2025, Dai 34943 (BJFC056204); Sichuan Province, Dujiangyan, Tongmagouzhuhai Park, 31.041281°N , $103.649118^\circ \text{E}$, elevation 708 m, on dead culm of *Bambusa vulgaris*, leg. Yuan Yuan, 29 September 2025, Yuan 3354 (BJFC062900).

Known distribution – widely distributed in subtropical and warm-temperate regions of Central to Southwestern China (Sichuan, Shaanxi, Henan, and Guangxi), found on dead or decaying culms of various bamboo species.

Notes – phylogenetically, *Asterostroma bicycstidium* belongs to the sect. *Asterostroma* clade and formed a well-supported clade with *A. arundinicola*, *A. brevispinum*, *A. fimbriatum*, and *A. medium* (77% ML; Supplementary Fig. S2). Morphologically, it is distinguished by the presence of two types of gloeocystidia (fusiform and sinuous)—a feature not observed within this genus. *Asterostroma bicycstidium*, *A. brevispinum*, and *A. fimbriatum* share a similar macromorphology, globose basidiospores and the growth on bamboo species in China, but *A. brevispinum* differs from *A. bicycstidium* in having subulate gloeocystidia and larger basidiospores ($5.6\text{--}6 \times 5.5\text{--}5.8 \mu\text{m}$ vs $4.7\text{--}4.9 \times 4.3\text{--}4.7 \mu\text{m}$) with much shorter spines (up to $0.5 \mu\text{m}$ long vs up to $1.2 \mu\text{m}$ long); *A. fimbriatum* differs from *A. bicycstidium* by having only one kind of cystidia and bigger basidiospores with conical echinulae ($4.9\text{--}6 \times 4.8\text{--}6 \mu\text{m}$ vs $4.7\text{--}4.9 \times 4.3\text{--}4.7 \mu\text{m}$)^[39]. Additionally, *A. bicycstidium* is further distinguished by its wide distribution on various bamboos in subtropical to warm-temperate China (Sichuan, Shaanxi, Henan, and Guangxi).

Asterostroma brevispinum Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 8

Index Fungorum number: IF905287.

Etymology – *Brevispinum* (Lat.): refers to the basidiospores of the species with short spines.

Diagnosis – characterized by fusiform cystidioles, globose, echinulate basidiospores measuring $5.6\text{--}6 \times 5.5\text{--}5.8 \mu\text{m}$ with short spines (up to $0.5 \mu\text{m}$ long), and growing on *Bambusa* in subtropical China.

Type – China, Guizhou Province, Guiyang, Qianling Mountain Park, 26.605301°N , $106.697464^\circ \text{E}$, elevation 1,116 m, on living culm of *Bambusa*, leg. Y.C. Dai, 7 July 2025, Dai 35726 (BJFC056987).

Description – basidiomata annual, resupinate, soft, membranous, loosely adnate, up to 7.8 cm long, 4.6 cm wide, $65 \mu\text{m}$ thick at center. Hymenial surface smooth, uncracked, cottony to hypochnoid, cream (4A3) to buff (4A4), without odor or taste when fresh and dry; margin white (–A1), with distinct hyphal strands.

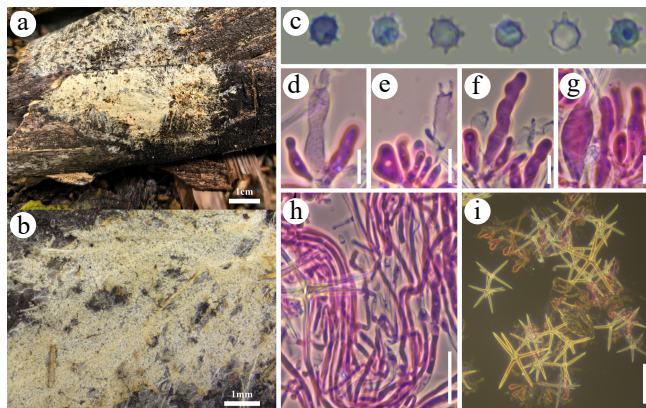


Fig. 7 *Asterostroma bicycstidium* (holotype, Yuan 3366). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f), (g) Gloeocystidia. (h) Generative hyphae. (i) Asterosetae and Asterohyphidia. Scale bars: (c)–(h) = $10 \mu\text{m}$; (i) = $50 \mu\text{m}$.

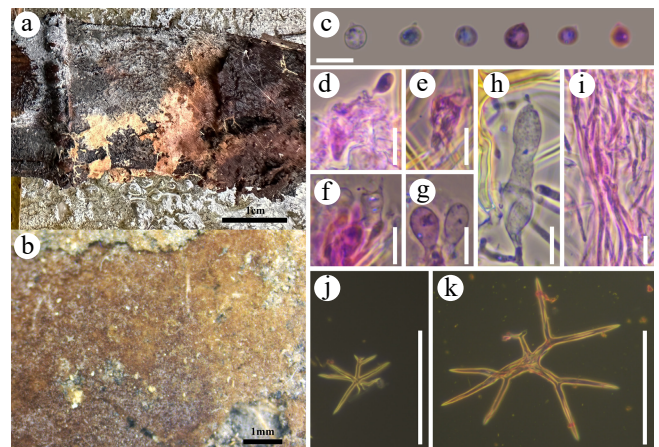


Fig. 8 *Asterostroma brevispinum* (holotype, Dai 35726). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f) Gloeocystidia and cystidioles. (g) Generative hyphae. (h) Asterosetae and Asterohyphidia. Scale bars: (c)–(g) = $10 \mu\text{m}$; (h) = $50 \mu\text{m}$.

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin-walled, frequently branched and septate, IKI–, CB–, 2–4 μm in diam. Asterosetae in subiculum abundant, predominant, dark brown, thick-walled, regularly star-shaped, weakly IKI(+), CB–, 3.2–6.4 μm in diam, rays up to 125 μm long, with acute tips; astero-hyphidia in hymenium similar to asterosetae in subiculum, but smaller and less regularly shaped, weakly IKI(+), CB–, 3–5 μm in diam, rays up to 77 μm long, with acute tips. Gloeocystidia occasionally present, subcylindrical, hyaline, slightly thick-walled, with a basal simple septum, 40–60 $\times$ 7–10 μm ; fusiform cystidioles occasionally present. Basidia clavate with constricted middle, usually with a few guttules, hyaline, thin-walled, with four sterigmata and a basal simple septum, 33–45 $\times$ 4.3–6.2 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores globose, occasionally with a big oil drop, hyaline, thin-walled, echinulate, IKI+, CB–, (5.5–)5.6–6(–6.2) $\times$ (5.4–)5.5–5.8(–6) μm , L = 5.72 μm , W = 5.54 μm , Q = 1–1.1 ($n = 60/2$); spines obtuse, up to 0.5 μm long.

Additional specimens examined – China, Guizhou Province, Guiyang, Qianling Mountain Park, 26.605029° N, 106.697994° E, elevation 1,103 m, on sheath of *Bambusa*, leg. Y.C. Dai, 7 July 2025, Dai 35725 (BJFC056986).

Known distribution – currently known only from subtropical bamboo forests in Southwestern China (Guizhou), found on culms and sheaths of *Bambusa*.

Notes – phylogenetically, *Asterostroma brevispinum* forms an independent lineage within the sect. *Asterostroma* clade (99% ML, 1 BPP; [Supplementary Fig. S2](#)), sister to *A. arundinicola*, *A. bicycidiatum*, *A. fimbriatum*, and *A. medium*. Morphologically, *A. arundinicola* has cream to flesh-pink hymenial surface, lacks cystidia, and grows on *Arundo donax*^[48]; *A. bicycidiatum* is easily distinguished from *A. brevispinum* by having two kinds of gloeocystidia (fusiform or sinuous); *A. medium* is distinguished from *A. brevispinum* by its subglobose, tuberculate basidiospores (with sparse tubercles up to 1.5 μm long vs dense spines up to 0.5 μm long) and growing on wood of *Quercus* and *Pinus pinea* in Europe^[1]; *A. fimbriatum* differs by its subglobose to globose basidiospores (with conical echinulae vs dense spines up to 0.5 μm long), shorter, subulate to fusiform gloeocystidia (15.6–24.7 $\times$ 4.6–8.2 μm vs 40–60 $\times$ 7–10 μm)^[39]. Additionally, *A. fimbriatum* was described on dead bamboo in Yunnan, China, while *A. brevispinum* occurs on living culms and sheaths of *Bambusa* in Guizhou, China.

Asterostroma papillatum Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. [Fig. 9](#)

Index Fungorum number: IF905288.

Etymology – *Papillatum* (Lat.): refers to the gloeocystidia of the species with a schizopapillate tip.

Diagnosis – characterized by the presence of dichotomously branched asterosetae, clavate gloeocystidia with a distinctly constricted zone in the middle and a schizopapillate tip, subglobose, smooth basidiospores measuring 6.3–6.7 $\times$ 5.2–6.2 μm , and growing on bamboo in warm-temperate China.

Type – China, Henan Province, Luoyang, Luanchuan County, Wangfuzuhai, 33.876185° N, 111.555178° E, elevation 925 m, on rotten bamboo culm, leg. Y.C. Dai, 20 October 2025, Dai 38603 (BJFC059862).

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 5 cm long, 2 cm wide, 80 μm thick at center. Hymenial surface smooth, uncracked, cottony to hypochnoid, cream (4A3) to salmon (6A4) and without odor or taste when fresh, cinnamon buff (4B4) to reddish brown (9E7) when dry; margin white (–A1), with distinct hyphal strands.

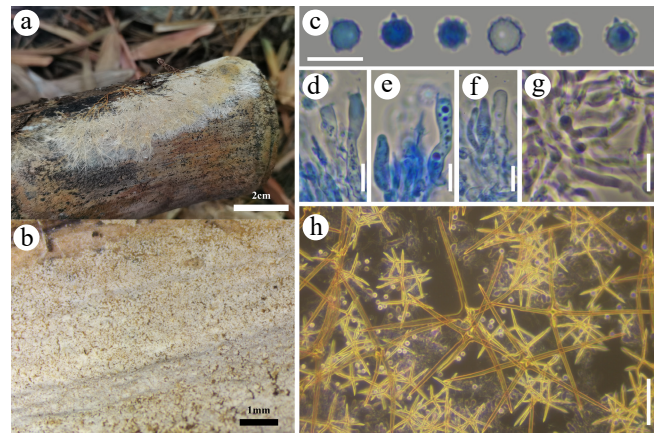


Fig. 9 *Asterostroma papillatum* (holotype, Dai 38603). (a), (b) Basidiomata. (c) Basidiospores. (d)–(g) Basidia and basidioles. (h) Gloeocystidia. (i) Generative hyphae. (j), (k) Dichohyphae from subiculum. Scale bars: (c)–(i) = 10 μm ; (j), (k) = 50 μm .

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin-walled, moderately branched and septate, IKI–, CB–, 2–5.9 μm in diam. Asterosetae in subiculum abundant, predominant, dark brown, thick-walled, dichotomously branched, weakly IKI(+), CB–, 7–9 μm in diam, terminal branches up to 128 μm long, with acute tips; astero-hyphidia in hymenium similar to asterosetae in subiculum, but smaller and with shorter branches. Gloeocystidia occasionally present, clavate, with a distinctly constricted zone in the middle and a schizopapillate apex, hyaline, thin-walled, with a basal simple septum, 27–40 $\times$ 7–10 μm ; cystidioles absent. Basidia subcylindrical to clavate, hyaline, thin-walled, with four sterigmata and a basal simple septum, 11–18.7 $\times$ 4–7 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores subglobose, hyaline, thin-walled, smooth, IKI+, CB–, (6.2–)6.3–6.7(–7) $\times$ 5.2–6.2(–6.3) μm , L = 6.48 μm , W = 5.76 μm , Q = 1–1.2 ($n = 30/1$).

Known distribution – currently known only from a warm-temperate mountain forest in Central China (Henan), found on rotten bamboo culm.

Notes – phylogenetically, *Asterostroma papillatum* was nested within the sect. *Laevispora* clade, forming an independent lineage, sister to *A. andinum*, *A. vararioides*, and *A. laxum* ([Supplementary Fig. S2](#)). Morphologically, *A. papillatum* resembles *A. andinum*, *A. vararioides*, and *A. laxum* by sharing dichotomously branched asterosetae and smooth, amyloid basidiospores. However, *A. andinum* differs from *A. papillatum* by having narrower gloeocystidia (4–5 μm vs 7–9 μm in width) and a wide geographic distribution across North America, the Caribbean, Sri Lanka, and New Zealand^[106]; *A. vararioides* differs from *A. papillatum* by having longer basidia (30–65 μm vs 11–18.7 μm in length) and growing on angiosperms in tropical Thailand^[61]; *A. laxum* is distinguished from *A. papillatum* by larger gloeocystidia (40–100 $\times$ 6–10 μm vs 27–40 $\times$ 7–10 μm), longer basidia (40–80 μm vs 11–18.7 μm in length) and growing on *Picea abies* in Europe^[1,107].

Baltazaria Leal-Dutra, Dentinger & G.W. Griff.

Index Fungorum number: IF825233.

Type species – *Baltazaria galactina* (Fr.) Leal-Dutra, Dentinger & G.W. Griff.

Notes – *Baltazaria* was established recently by Leal-Dutra et al. to accommodate several species formerly placed in *Scytinostroma* Donk and *Parapterulicium* Corner. The genus is characterized by coriaceous to membranous basidiomata when fresh, becoming hard and whitish when dry, and a dimittic hyphal system dominated by

thick-walled, dextrinoid skeletal-binding hyphae. In this study, we broaden the taxonomic and ecological distribution of *Baltazaria* by describing a new species, *B. massoniana*, from subtropical China, and proposing a new combination, *B. quintasiana* comb. nov. from West Africa^[108].

This combination is supported by phylogenetic analyses, in which sequences obtained from the paratypes of *Corticium quintasianum* Bres. & Roum. (CBS 749.86 and CBS 750.86) formed a well-supported sister lineage within the clade (67% ML; [Supplementary Fig. S3](#)) containing *Baltazaria massoniana* and *B. galactina*. Morphologically, it corresponds to the generic diagnosis by having a dimitic hyphal system with clamped generative hyphae and gloeocystidia^[108]. The combination is thus proposed.

Baltazaria massoniana Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. [Fig. 10](#)

Index Fungorum number: IF905289.

Etymology – *Massoniana* (Lat.): refers to the species growing on *Pinus massoniana*.

Diagnosis – characterized by uniform basidia, oblong-ellipsoid, inamyloid basidiospores measuring $5\text{--}5.3 \times 3.1\text{--}3.4\ \mu\text{m}$, and growing on dead *Pinus massoniana* in subtropical China.

Type – China, Guangdong Province, Zhaoqing, Fengkai County, Heishiding Nature Reserve, 23.433333°N , 111.883333°E , elevation 445 m, on a fallen trunk of *Pinus massoniana*, leg. Yuan Yuan, 6 July 2025, Yuan 3170 (BJFC062716).

Description – basidiomata annual, resupinate, soft, coriaceous, adnate, up to 14 cm long, 4 cm wide, 120 μm thick at center. Hymenial surface smooth to locally tuberculate, uncracked, white (–A1) and without odor or taste when fresh, cream (4A3) to buff (4A4) when dry; margin white (–A1), with distinct hyphal strands.

Hyphal system dimitic; generative hyphae with clamp connections, hyaline, thin-walled, moderately branched and septate, IKI–, CB–, $2\text{--}3.4\ \mu\text{m}$ in diam; skeletal hyphae dominant, frequently dichotomously branched, aseptate, tortuous, interwoven, thick-walled, IKI(+), CB–, $1.8\text{--}3\ \mu\text{m}$ in diam. Gloeocystidia occasionally present, capitate, hyaline, thin-walled, $23\text{--}30 \times 3.6\text{--}4.5\ \mu\text{m}$. Basidia uniform, thin-walled, with four sterigmata and a basal clamp connection, $10\text{--}15 \times 3\text{--}5\ \mu\text{m}$; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores oblong-ellipsoid, hyaline, thin-walled, smooth, IKI–, CB–, $(4.9\text{--})5\text{--}5.3(5.4) \times$

$(3\text{--})3.1\text{--}3.4(3.6)\ \mu\text{m}$, $L = 5.15\ \mu\text{m}$, $W = 3.31\ \mu\text{m}$, $Q = 1.4\text{--}1.6$ ($n = 60/2$).

Additional specimens examined – China, Guangdong Province, Zhaoqing, Dinghu District, Dinghushan National Nature Reserve, 23.159571°N , 112.538344°E , elevation 511 m, on a fallen branch of *Pinus massoniana*, leg. Yuan Yuan, 7 July 2025, Yuan 3207 (BJFC062753).

Known distribution – currently known from subtropical montane coniferous forests in Southern China (Guangdong), found on dead *Pinus massoniana*.

Notes – phylogenetically, *Baltazaria massoniana* formed a well-supported clade (67% ML; [Supplementary Fig. S3](#)) with *B. galactina* and *B. quintasiana* ($\equiv$ *Scytinostroma quintasianum*). Morphologically, the three species share the generic characteristics, including a dimitic hyphal system with frequently dichotomous skeletal hyphae and subcylindrical, capitate gloeocystidia^[26]. However, *B. galactina* is distinguished from *B. massoniana* by clavate to subcylindrical and longer basidia ($20\text{--}40 \times 3\text{--}4\ \mu\text{m}$ vs $10\text{--}15 \times 3\text{--}5\ \mu\text{m}$), longer gloeocystidia ($40\text{--}60 \times 2\text{--}5\ \mu\text{m}$ vs $23\text{--}30 \times 3.6\text{--}4.5\ \mu\text{m}$), and growing on various angiosperm and gymnosperm wood throughout North America^[1,109]; *B. quintasiana* differs from *B. massoniana* by having shorter basidiospores ($3.8\text{--}4.5\ \mu\text{m}$ vs $5\text{--}5.3\ \mu\text{m}$ in width) with a small amyloid apiculus and growing on angiosperm wood from West Africa^[110]. In addition, BLAST searches using the ITS sequence of *B. massoniana* revealed high similarity to two sequences (LC852187: 98.9% identity, AB470241: 98.7% identity). Although these two accessions are labelled as *Scytinostroma* sp., we consider them to represent the same species, *B. massoniana*, based on their near-identical sequences and consistent phylogenetic placement ([Supplementary Fig. S3](#)).

Baltazaria quintasiana (Bres. & Roum.) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905290.

Basionym – *Corticium quintasianum* Bres. & Roum., Rev. Mycol., Toulouse 12(no. 45): 36 (1890)

$\equiv$ *Scytinostroma quintasianum* (Bres. & Roum.) Nakasone, Cryptog. Mycol. 29(3): 239 (2008)

Known distribution – currently known from West Africa, found on dead angiosperm wood in tropical forests.

Gloiothele Bres.

Index Fungorum number: IF17678.

Type species – *Gloiothele lamellosa* (Henn.) Bres.

Notes – the genus *Gloiothele* is defined by a monomitic hyphal system with simple septa, the presence of gloeocystidia (often with guttulate contents), and smooth, weakly amyloid basidiospores^[1,23]. This study introduces two new species, notably documenting its first occurrence on bamboo and extending its distribution into temperate East Asia. *Gloiothele bambusicola* is characterized by constricted basidia, subulate gloeocystidia, oblong-ellipsoid basidiospores, and growth on both bamboo and angiosperm trees in subtropical to temperate China. *Gloiothele spathulata* is characterized by spatulate basidia and globose basidiospores, and grows on *Quercus mongolica* in temperate China, with evidence of occurrence in mixed forests in South Korea, representing a new temperate East Asian lineage.

Gloiothele bambusicola Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. [Fig. 11](#)

Index Fungorum number: IF905291.

Etymology – *Bambusicola* (Lat.): refers to the species growing on *Bambusa*.

Diagnosis – characterized by the presence of a distinct constriction on the basidia, oblong-ellipsoid basidiospores, and growing on both bamboo and angiosperm wood.

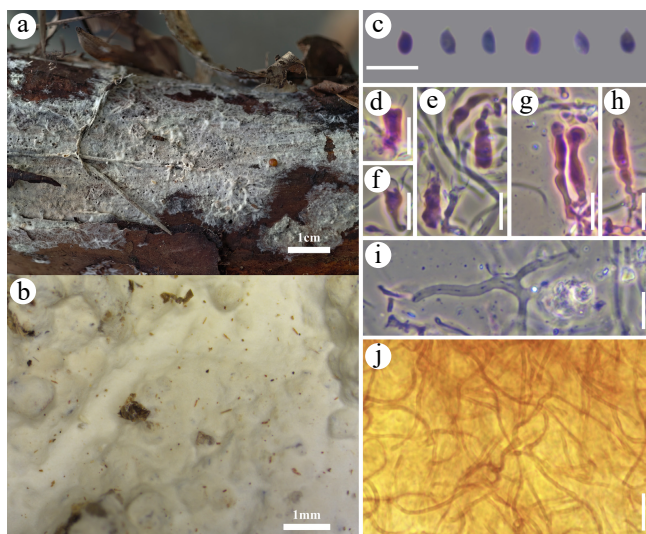


Fig. 10 *Baltazaria massoniana* (holotype, Yuan 3170). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (g), (h) Gloeocystidia. (i) Dichotomously branched hyphae. (j) Hyphal system in Melzer's reagent. Scale bars: (c)–(j) = 10 μm .

Type – China, Sichuan Province, Dujiangyan, Tongmagouzuhai Park, 31.041175° N, 103.649225° E, elevation 714 m, on dead culm of *Bambusa emeiensis*, leg. Yuan Yuan, 29 September 2025, Yuan 3356 (BJFC062902).

Description – basidiomata annual, resupinate, ceraceous, adnate, up to 4.3 cm long, 3.6 cm wide, 120 µm thick at center. Hymenial surface smooth, uncracked, cream (4A3) to buff yellow (ca. 4A4) and without odor and taste when fresh, buff yellow (ca. 4A4) to olivaceous buff (4C4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin-walled, moderately branched and septate, IKI–, CB–, 2–3.2 µm in diam. Gloeocystidia frequent, more or less subulate, flexuous, distinctly and strongly swollen at base and tapering to tip without guttulate content when juvenile, becoming clavate and often curved with guttulate content when mature, hyaline, thin-walled, 55–150 × 7–10 µm. Basidia urniform, with a strong median constriction, thin-walled, with four sterigmata and a basal simple septum, 22–27.6 × 5–7.9 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores oblong-ellipsoid, occasionally with oil drops, hyaline, thick-walled, smooth, weakly IKI+, CB–, (8–)8.2–9(–9.2) × (5.4–)5.5–5.7(–5.9) µm, L = 8.73 µm, W = 5.61 µm, Q = 1.4–1.6 (n = 60/2).

Additional specimens examined – China, Beijing, Xishan Experimental Forest Farm, Heilongtan Sub-farm, on a dead standing angiosperm tree, leg. Yuan Yuan, 23 August 2024, Yuan 2591 (BJFC062137); Dongbeiwang Sub-farm, on angiosperm trunk, leg. Yuan Yuan, 3 September 2024, Yuan 2698 (BJFC062244); Sichuan Province, Dujiangyan, Tongmagouzuhai Park, 31.041281° N, 103.649118° E, elevation 708 m, on dead culm of *Bambusa emeiensis*, leg. Yuan Yuan, 29 September 2025, Yuan 3370 (BJFC062916).

Known distribution – currently known only from temperate to subtropical China (Beijing and Sichuan), found on dead culms of *Bambusa emeiensis* and angiosperm wood.

Notes – phylogenetically, *Gloiothele bambusicola* formed a strongly supported lineage (94% ML, 1 BPP; [Supplementary Fig. S6](#)) sister to *G. tuberculata*, but *G. tuberculata* differs by having a tuberculate hymenial surface and broadly ellipsoid to globose basidiospores^[39]. Morphologically, *G. ventricosa* Ghobad-Nejhad resembles *G. bambusicola* by having constricted basidia, but *G. ventricosa* differs by its globose to subglobose basidiospores^[111].

Gloiothele lactescens (Berk.) Hjortstam also resembles *G. bambusicola* by having oblong-ellipsoid basidiospores, but *G. lactescens* differs by having longer basidia (40–55 × 6–7 µm vs 22–28 × 5–8 µm)^[1,112]. In addition, *Gloiothele bambusicola* exhibits a broad substrate range, growing on both bamboo (subtropical China) and angiosperm wood (temperate China), while *G. tuberculata* grows on fallen angiosperm branches in subtropical China, *G. ventricosa* grows on angiosperm wood in Réunion Island, and *G. lactescens* grows on angiosperm wood in temperate and subtropical regions^[1,39,111,112].

Gloiothele spathulata Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. [Fig. 12](#)

Index Fungorum number: IF905292.

Etymology – *Spathulata* (Lat.): refers to the species having spathulate basidia.

Diagnosis – characterized by the presence of spathulate basidia, globose basidiospores, and growing on *Quercus mongolica*.

Type – China, Heilongjiang Province, Wuchang, Chenxiangdian Forest Farm, 44.957241° N, 127.727710° E, elevation 212 m, on fallen branch of *Quercus mongolica*, leg. Y.C. Dai, 30 August 2025, Dai 37279 (BJFC058538).

Description – basidiomata annual, resupinate, ceraceous, adnate, up to 6.5 cm long, 6 cm wide, 63 µm thick at center. Hymenial surface smooth, uncracked, irregularly and indistinctly tuberculate, white (–A1) to cream (4A3) and without odor and taste when fresh, straw yellow (3B3) to cream (4A3) when dry; margin white (–A1), thinning out, fimbriate.

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin-walled, frequently branched and moderately septate, IKI–, CB–, 2–3.8 µm in diam. Gloeocystidia frequent, tubular to narrowly clavate, some with guttulate content, hyaline, thick-walled, with guttulate content, 55–70 × 5–8.5 µm. Basidia more or less spathulate, thin-walled, with four sterigmata and a basal simple septum, 29–50 × 5–9 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores globose, hyaline, thin-walled, smooth, weakly IKI+, CB–, (5.7–)5.9–6.3(–6.4) × (5.4–)5.5–6(–6.2) µm, L = 5.91 µm, W = 5.77 µm, Q = 1–1.1 (n = 30/1).

Known distribution – currently known only from a temperate broadleaved forest in Northeast China (Heilongjiang), found on a fallen branch of *Quercus mongolica*, and indicated by sequence data from mixed forest in Gangwon, South Korea.

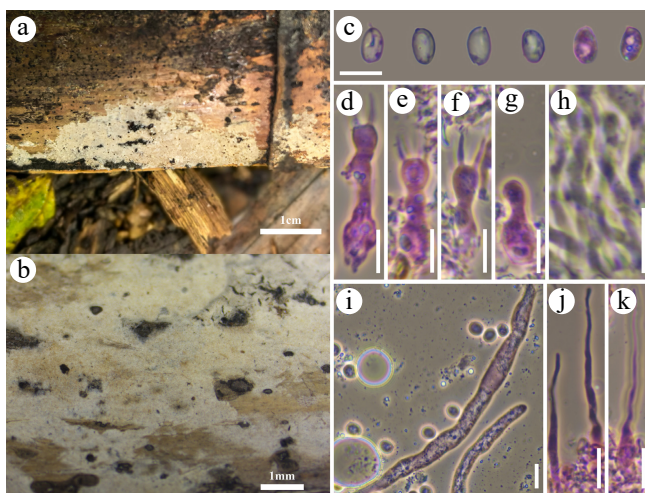


Fig. 11 *Gloiothele bambusicola* (holotype, Yuan 3356). (a), (b) Basidiomata. (c) Basidiospores. (d)–(g) Basidia and basidioles. (h) Generative hyphae. (i) Gloeocystidia when mature. (j), (k) Gloeocystidia when juvenile. Scale bars: (c)–(k) = 10 µm.

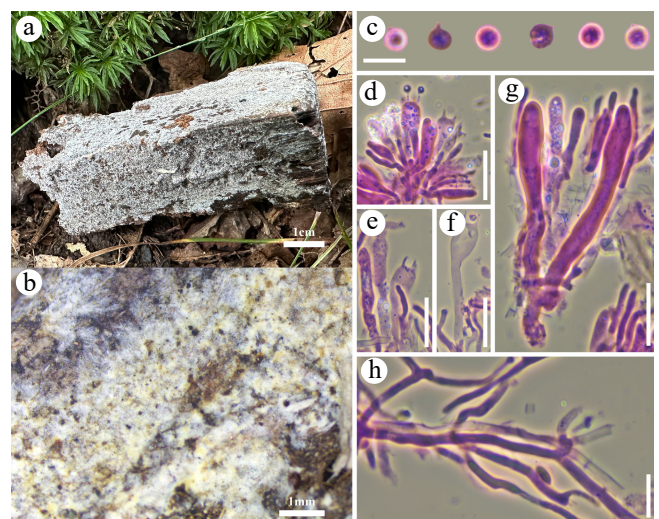


Fig. 12 *Gloiothele spathulata* (holotype, Dai 37279). (a), (b) Basidiomata. (c) Basidiospores. (d)–(f) Basidia and basidioles. (g) Gloeocystidia. (h) Generative hyphae. Scale bars: (c)–(h) = 10 µm.

Notes – phylogenetically, *Gloiothle spathulata* was recovered within a well-supported clade with *G. lactescens* (69% ML, 1 BPP; Supplementary Fig. S6), but *G. lactescens* differs from *G. spathulata* by its longer basidia ($45\text{--}66 \times 6.5\text{--}7.5 \mu\text{m}$ vs $29\text{--}50 \times 5\text{--}9 \mu\text{m}$) and longer gloecystidia ($180\text{--}270 \mu\text{m}$ vs $55\text{--}70 \mu\text{m}$ in length)^[99]. In addition, *G. spathulata* is strongly supported and includes an additional sequence (KUC20130718-09, GenBank: KJ668539) from South Korea, which exhibits less than 1.5% ITS sequence dissimilarity. The sample KUC20130718-09 was collected in a mixed coniferous and deciduous forest in Odaesan National Park, South Korea, which has a similar ecology to our collection in Heilongjiang, China^[113]. Therefore, we treat KUC20130718-09 as *G. spathulata*.

Vararia P. Karst.

Index Fungorum number: IF18724.

Type species – *Vararia investiens* (Schwein.) P. Karst.

Notes – the genus is defined by resupinate basidiomata, a dimitic hyphal system, generative hyphae with or without clamp connections, with more or less dextrinoid dichohyphae, the presence of gloecystidia, and smooth basidiospores^[1]. The genus has long been recognized as polyphyletic^[22,24,25,27,29,39,47], and our phylogeny confirms this (Fig. 2). Our study expands the morphological, ecological, and geographical scope of the genus by describing eight new species from China. These species are recovered in different lineages across the tree (Fig. 2), but all conform morphologically to *Vararia*, which can be grouped into several distinct ecological groups: a subtropical bamboo-associated clade (*V. emeiensis* and *V. subulata*), a subtropical grass-associated lineage (*V. miscanthi*), a tropical bamboo- and grass-associated clade (*V. falcata* and *V. acanthocystidia*), a tropical palm/rattan lineage (*V. septocystidiata*), a high-altitude temperate bamboo- and wood-associated lineage (*V. alpina*), and a high-altitude temperate wood-associated lineage (*V. incarnata*). A key to the species of *Vararia* in China is provided at the end of the manuscript.

Vararia acanthocystidia Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 13

Index Fungorum number: IF905293.

Etymology – *Acanthocystidia* (Lat.): refers to the species having acanthocystidia.

Diagnosis – characterized by the presence of urniform to clavate acanthocystidia densely covered with tuberculate spines, oblong-ellipsoid basidiospores measuring $7.9\text{--}9.1 \times 4.1\text{--}5.2 \mu\text{m}$, and growing on rotten bamboo in tropical forests of Hainan, China.

Type – China, Hainan Province, Qiongzong County, Limushan National Forest Park, 19.176944°N , $109.747526^\circ \text{E}$, elevation 784 m, on rotten bamboo, leg. Y.C. Dai, 22 September 2024, Dai 30011 (BJFC050270).

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 13.4 cm long, 2.2 cm wide, 65 μm thick at center. Hymenial surface smooth, uncracked, white (–A1) to cream (4A3) and without odor and taste when fresh, buff (4A4) to olivaceous buff (4C4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin- to slightly thick-walled, moderately branched and frequently septate, loosely interwoven, IKI–, CB–, $1.5\text{--}3 \mu\text{m}$ in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI[+], CB+, stem $1.5\text{--}3.5 \mu\text{m}$ wide, upper branches narrow and thin-walled. Acanthocystidia occasionally present, urniform to clavate, densely covered with short, tuberculate spines over the upper part, hyaline, thin-walled, $15\text{--}45 \times 6\text{--}9 \mu\text{m}$. Basidia subcylindrical to urniform, thin-walled, with four sterigmata and a basal simple septum, $15\text{--}30 \times 4\text{--}9 \mu\text{m}$; basidioles morphologically resembling basidia, yet

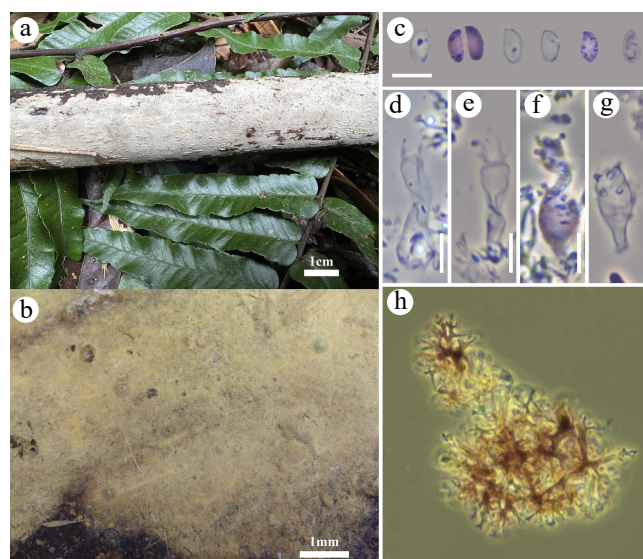


Fig. 13 *Vararia acanthocystidia* (holotype, Dai 30011). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia. (f), (g) Acanthocystidia. (h) Dichohyphae in subiculum (Melzer's reagent). Scale bars: (c)–(h) = 10 μm .

slightly smaller in size. Basidiospores oblong-ellipsoid, hyaline, thin-walled, smooth, occasionally with oil drops, IKI–, CB–, $(7.8\text{--})7.9\text{--}9.1(–9.4) \times (4\text{--})4.1\text{--}5.2(–5.4) \mu\text{m}$, $L = 8.87 \mu\text{m}$, $W = 4.78 \mu\text{m}$, $Q = 1.7\text{--}1.9$ ($n = 160/4$).

Additional specimens examined – China, Hainan Province, Qiongzong County, Limushan National Forest Park, 19.176944°N , $109.747526^\circ \text{E}$, elevation 784 m, on rotten bamboo, leg. Y.C. Dai, 22 September 2024, Dai 30009 (BJFC050268); 19.176932°N , $109.747802^\circ \text{E}$, elevation 793 m, on rotten bamboo, leg. Y.C. Dai, 22 September 2024, Dai 30025 (BJFC050284) and Dai 30033 (BJFC050292).

Known distribution – currently known only from tropical forests in Southern China (Hainan), found on rotten bamboo.

Notes – phylogenetically, *Vararia acanthocystidia* formed an independent, well-supported lineage within *Vararia* (100% ML, 1 BPP; Supplementary Fig. S7). Morphologically, *V. abortiphysa* Boidin & Lanq. resembles *V. acanthocystidia* in having similar basidia, but *V. abortiphysa* differs by having fusiform to narrowly ellipsoid basidiospores and lacking acanthocystidia^[24]. In addition, *Vararia acanthocystidia* is currently known only from rotten bamboo in the tropical forests of Hainan, China, while *V. abortiphysa* is recorded from dead wood in tropical Africa^[24].

Vararia alpina Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 14

Index Fungorum number: IF905294.

Etymology – *Alpina* (Lat.): refers to the species occurring in high mountainous areas.

Diagnosis – characterized by ellipsoid basidiospores measuring $7.5\text{--}8.1 \times 4.6\text{--}5.0 \mu\text{m}$ and growing on diverse substrates including bamboo, angiosperm and gymnosperm wood at high-elevation temperate forests of Xizang, China.

Type – China, Xizang Autonomous Region, Rikaze, Yadong County, Yadong Customs Site, 27.4247°N , 88.9319°E , elevation 2,875 m, on dead bamboo, leg. Y.C. Dai, 15 October 2024, Dai 31508 (BJFC051767).

Description – basidiomata annual, resupinate, soft, membranous to coriaceous, adnate, up to 12.2 cm long, 3.9 cm wide, 130 μm thick at center. Hymenial surface smooth, cracked, white (–A1) to cream

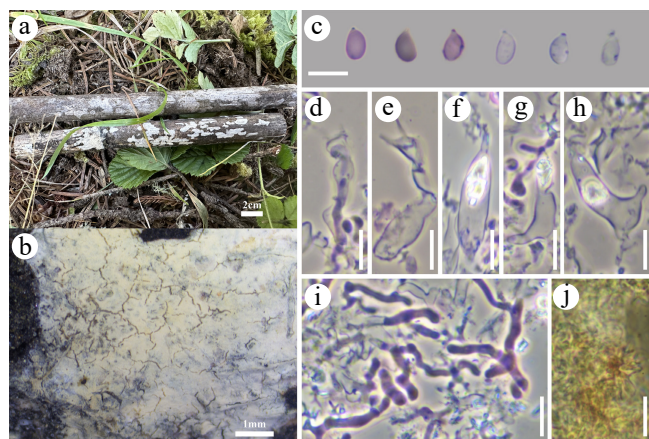


Fig. 14 *Vararia alpina* (holotype, Dai 31508). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia. (f)–(h) Gloeocystidia. (i) Generative hyphae. (j) Dichohyphae in subiculum (Melzer's reagent). Scale bars: (c)–(j) = 10 µm.

(4A3) and without odor and taste when fresh, buff yellow (ca. 4A4) to buff (4A4) when dry; margin white (–A1), thinning out, fimbriate.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin- to slightly thick-walled, frequently branched and septate, interwoven, IKI–, CB–, 2–3.5 µm in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI[+], CB+, stem 1.5–2.5 µm wide, upper branches narrow and thin-walled. Gloeocystidia occasionally present, subulate, with a schizopapillate apex, with guttulate content often aggregated in the central or upper part, hyaline, thin-walled, 25–40 × 5–9 µm. Basidia clavate, thin-walled, with four sterigmata and a basal simple septum, 20–45 × 5–9 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores ellipsoid, hyaline, thin-walled, smooth, IKI–, CB–, (7.4–)7.5–8.1(–8.3) × (4.4–)4.6–5(–5.1) µm, L = 7.81 µm, W = 4.85 µm, Q = 1.5–1.7 (n = 180/6).

Additional specimens examined – China, Xizang Autonomous Region, Rikaze, Yadong County, along the road from Lower Yadong to Baxia Waterfall, 27.4121° N, 88.9482° E, elevation 2,838 m, on a fallen angiosperm twig, leg. Y.C. Dai, 14 October 2024, Dai 31274 (BJFC051533); Renqinggang Village, Lower Yadong, 27.4247° N, 88.9319° E, elevation 2,875 m, on a rotten bamboo, leg. Y.C. Dai, 15 October 2024, Dai 31417 (BJFC051676), Dai 31418 (BJFC051677), and Dai 31419 (BJFC051678); Yadong Customs Site, 27.4274° N, 88.9019° E, elevation 3,322 m, on a fallen gymnosperm branch, leg. Y.C. Dai, 15 October 2024, Dai 31507 (BJFC051766), and on a fallen angiosperm branch, leg. Y.C. Dai, 15 October 2024, Dai 31514 (BJFC051773).

Known distribution – currently known only from high-elevation temperate forests in Southwestern China (Xizang), found on various substrates including bamboo and angiosperm and gymnosperm wood.

Notes – phylogenetically, *Vararia alpina* formed a well-supported clade with *V. muscicola* (70% ML, 0.98 BPP; [Supplementary Fig. S7](#)). However, *V. muscicola* is distinguished by having two kinds of gloeocystidia (subcylindrical to fusiform, and cylindrical to subclavate), fusiform to subcylindrical, flexuous basidia, and growing only on angiosperm branches in subtropical montane forests of Yunnan, China. (2,600 m)^[39].

Vararia emeiensis Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. **Fig. 15**

Index Fungorum number: IF905295.

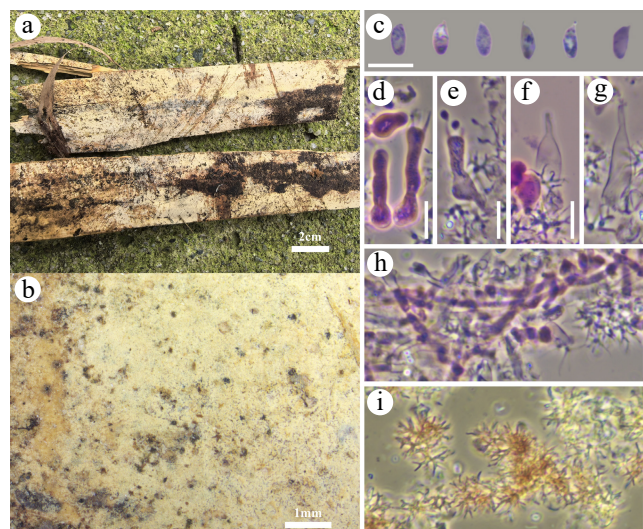


Fig. 15 *Vararia emeiensis* (holotype, Yuan 3382). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f), (g) Gloeocystidia. (h) Generative hyphae. (i) Dichohyphae in subiculum (Melzer's reagent). Scale bars: (c)–(i) = 10 µm.

Etymology – *Emeiensis* (Lat.): refers to the species growing on *Bambusa emeiensis*.

Diagnosis – characterized by oblong-ellipsoid basidiospores measuring 7–7.9 × 3.1–3.6 µm and growing only on *Bambusa emeiensis* in subtropical Southwestern China.

Type – China, Sichuan Province, Dujiangyan, Tongmagouzhuhai Park, 31.042008° N, 103.647461° E, elevation 724 m, on dead culm of *Bambusa emeiensis*, leg. Yuan Yuan, 29 September 2025, Yuan 3382 (BJFC062928).

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 12.2 cm long, 3.9 cm wide, 130 µm thick at center. Hymenial surface smooth, uncracked, cream (4A3) to buff yellow (ca. 4A4) and without odor and taste when fresh, buff yellow (ca. 4A4) to olivaceous buff (4C4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin-walled, moderately branched and frequently septate, interwoven, IKI–, CB–, 1.5–3.5 µm in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI[+], CB+, stem 1.5–3 µm wide, upper branches narrow and thin-walled. Gloeocystidia occasionally present, subulate, with a schizopapillate apex, hyaline, thin-walled, 30–50 × 6–10 µm. Basidia urniform to clavate, thin-walled, with four sterigmata and a basal simple septum, 20–30 × 5.5–7.8 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores oblong-ellipsoid, occasionally with oil drops, hyaline, thin-walled, smooth, IKI–, CB–, 7–7.9(–8.1) × (3–)3.1–3.6(–3.8) µm, L = 7.56 µm, W = 3.46 µm, Q = 2–2.5 (n = 60/3).

Additional specimens examined – China, Sichuan Province, Dujiangyan, Tongmagouzhuhai Park, 31.041971° N, 103.647 550° E, elevation 722 m, on dead culm of *Bambusa emeiensis*, leg. Yuan Yuan, 29 September 2025, Yuan 3381 (BJFC062927).

Known distribution – currently known only from subtropical montane bamboo forests in Southwestern China (Sichuan, Chongqing), found on dead culms of *Bambusa emeiensis*.

Notes – phylogenetically, *Vararia emeiensis* formed a strongly supported clade with *V. subulata* (100% ML, 1 BPP; [Supplementary Fig. S7](#)). Morphologically, it is characterized by oblong-ellipsoid basidiospores, an uncracked hymenophore, and growing only on *Bambusa emeiensis* in subtropical China. *Vararia subulata* has similar

urniform basidia and an uncracked hymenophore, but differs by having ellipsoid basidiospores ($8.1\text{--}9.2 \times 4\text{--}4.9 \mu\text{m}$, $Q = 1.6\text{--}2$ vs $7\text{--}7.9 \times 3.1\text{--}3.6 \mu\text{m}$, $Q = 2\text{--}2.5$) and the presence of projecting paraphyses. *Vararia emeiensis* also resembles *V. alpina* in having subulate gloeocystidia, but *V. alpina* differs from *V. emeiensis* by having broader basidiospores ($4.6\text{--}5.0 \mu\text{m}$ vs $3.1\text{--}3.6 \mu\text{m}$ in width), a cracked hymenophore, and growth on bamboo, angiosperm, and coniferous wood in Xizang.

Vararia falcata Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov.
Fig. 16

Index Fungorum number: IF905296.

Etymology – *Falcata* (Lat.): refers to the species having falcate basidiospores.

Diagnosis – characterized by sickle-shaped basidiospores measuring $11\text{--}15.7 \times 1.8\text{--}2.5 \mu\text{m}$, subulate gloeocystidia with a schizopapillate apex, and growing on rotten bamboo and *Miscanthus* in tropical southern China.

Type – China, Hainan Province, Baisha County, Qingsong, 19.241425°N , $109.393279^\circ \text{E}$, elevation 369 m, on rotten bamboo, leg. Y.C. Dai, 24 September 2024, Dai 30171 (BJFC050430).

Description – Basidiomata annual, resupinate, soft, coriaceous, adnate, up to 10.6 cm long, 3.7 cm wide, $75 \mu\text{m}$ thick at center. Hymenial surface smooth, uncracked, white (–A1) to grayish white (1B1) and without odor and taste when fresh, white (–A1) to cream (4A3) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin- to slightly thick-walled, occasionally branched and septate, interwoven, IKI–, CB–, $2\text{--}5 \mu\text{m}$ in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI[+], CB+, stem $1.5\text{--}3 \mu\text{m}$ wide, upper branches narrow and thin-walled. Gloeocystidia occasionally present, subulate, with guttulate content and a schizopapillate apex, hyaline, thin-walled, $35\text{--}65 \times 8\text{--}13 \mu\text{m}$; fusiform cystidioles occasionally present. Basidia clavate, thin-walled, with four sterigmata and a basal simple septum, $20\text{--}35 \times 4\text{--}7.5 \mu\text{m}$; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores sickle-shaped, often aggregated in pairs or quartets, occasionally with oil drops, hyaline, thin-walled, smooth, IKI–, CB–,

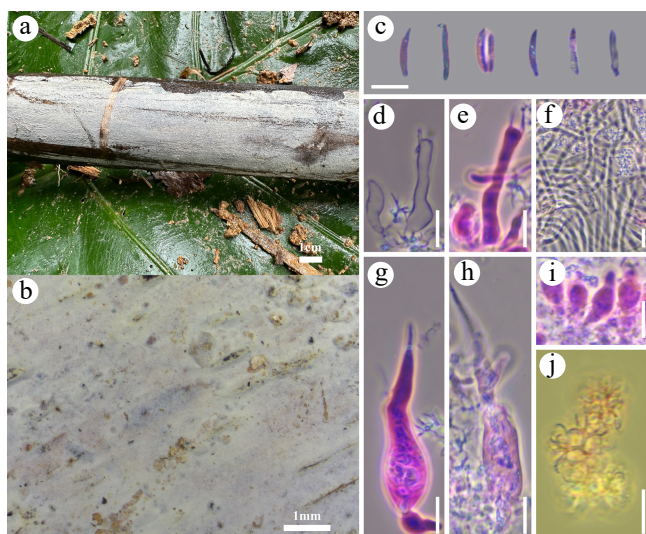


Fig. 16 *Vararia falcata* (holotype, Dai 30171). (a), (b) Basidiomata. (c) Basidiospores. (d) Basidia and cystidioles. (e) Basidia and basidioles. (f) Generative hyphae. (g), (h) Gloeocystidia. (i) Cystidioles and basidioles. (j) Dichohyphae in subiculum (Melzer's reagent). Scale bars: (c)–(j) = $10 \mu\text{m}$.

$(10.8\text{--})11\text{--}15.7\text{--}(16) \times (1.7\text{--})1.8\text{--}2.5\text{--}(2.6) \mu\text{m}$, $L = 12.99 \mu\text{m}$, $W = 2.23 \mu\text{m}$, $Q = 4.5\text{--}9$ ($n = 210/7$).

Additional specimens examined – China, Guangxi Autonomous Region, Chongzuo, Longzhou County, Nonggang National Nature Reserve, on rotten bamboo, leg. Y.C. Dai, 29 May 2024, Dai 27813 (BJFC048073); Hainan Province, Baisha County, Qingsong, 19.241425°N , $109.393279^\circ \text{E}$, elevation 369 m, on rotten bamboo, leg. Y.C. Dai, 24 September 2024, Dai 30169 (BJFC050428); 19.249437°N , $109.389240^\circ \text{E}$, elevation 456 m, on rotten bamboo, leg. Y.C. Dai, 24 September 2024, Dai 30196 (BJFC050455); and on rotten bamboo leaf, leg. Y.C. Dai, 24 September 2024, Dai 30194 (BJFC050453); Wuzhishan County, Shuiman, 18.813533°N , $109.646510^\circ \text{E}$, elevation 577 m, on rotten *Miscanthus*, leg. Y.C. Dai, 23 September 2024, Dai 30092 (BJFC050351), Dai 30093 (BJFC050352), and Dai 30097 (BJFC050356).

Known distribution – currently known only from tropical forests in Southern China (Guangxi, Hainan), found on rotten bamboo and *Miscanthus*.

Notes – *Vararia falcata* formed a phylogenetically distinct lineage (100% ML, 1 BPP; [Supplementary Fig.S7](#)). The sickle-shaped basidiospores of *V. falcata* are unique within the genus, contrasting with the fusiform to ellipsoid basidiospores of tropical relatives such as *V. aurantiaca* Boidin & Lanq. (Central Africa), *V. rosulenta* Boidin et al. (New Caledonia), *V. gomezii* Boidin & Lanq., *V. intricata* Boidin & Lanq., and *V. insolita* Boidin & Lanq. (tropical Africa and the Americas), all of which grow on angiosperm wood^[24,114]. Ecologically, *V. falcata* is currently known from rotten bamboo and *Miscanthus* in tropical Southern China (Hainan, Guangxi).

Vararia incarnata Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov.
Fig. 17

Index Fungorum number: IF905297.

Etymology – *Incarnata* (Lat.): refers to the species having a flesh-pink hymenophore when fresh.

Diagnosis – characterized by the flesh-pink hymenophore when fresh, fusiform basidiospores measuring $15.8\text{--}17.5 \times 5.9\text{--}7.0 \mu\text{m}$, the bush-like, blunt-tipped dichohyphidia in the hymenium, and growing on both angiosperm and gymnosperm wood in high-elevation temperate to subalpine forests of Southwestern China.

Type – China, Xizang Autonomous Region, Linzhi, Bayi District, near the 318 National Highway, 29.8150°N , 94.7426°E , elevation 3,130 m, on a fallen angiosperm branch, leg. Y.C. Dai, 7 October 2025, Dai 38813 (BJFC060072).

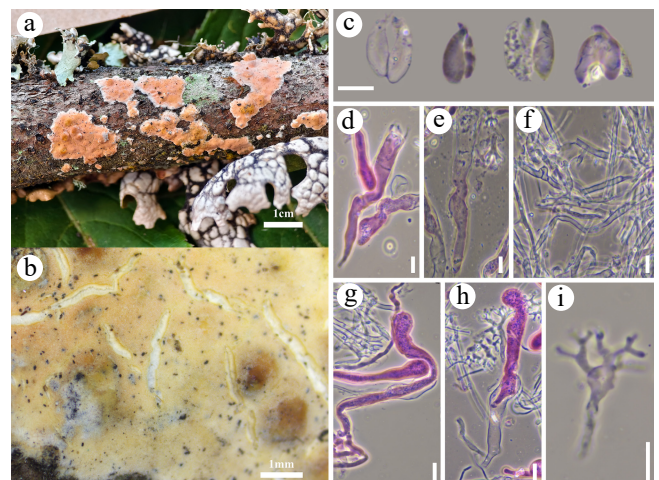


Fig. 17 *Vararia incarnata* (holotype, Dai 38813). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f) Generative hyphae. (g), (h) Gloeocystidia. (i) Dichohyphidia. Scale bars: (c)–(i) = $10 \mu\text{m}$.

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 6 cm long, 1.2 cm wide, 310 μm thick at center. Hymenial surface smooth to locally tuberculate, cracked, flesh pink (9A4) and without odor or taste when fresh, buff (4A4) to reddish brown (9E7) when dry; margin white (–A1), thinning out, fimbriate.

Hyphal system dimitic; generative hyphae with clamp connections, hyaline, thin- to slightly thick-walled, moderately branched and septate, loosely interwoven, IKI–, CB–, 2.5–4.5 μm in diam; skeletal hyphae infrequent, rarely branched, interwoven, hyaline, thick-walled, 2–3 μm in diam, IKI–, CB–. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI–, CB+, stem 2–3 μm wide, upper branches narrow and thin-walled; dichohyphidia present, in shape similar to dichohyphae, but with shorter and blunter upper branches. Gloeocystidia occasionally present, mostly capitate, more or less curved at the middle, some with guttulate content, hyaline, slightly thick-walled, 60–120 $\times$ 9–15 μm . Basidia clavate and slightly curved, thin-walled, with four sterigmata and a basal clamp connection, 60–85 $\times$ 7.5–13 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores fusiform, hyaline, thin-walled, smooth, commonly aggregated in pairs or quartets, IKI–, CB–, (15.5–)15.8–17.5(–17.7) $\times$ (5.6–)5.9–7(–7.2) μm , L = 16.9 μm , W = 6.6 μm , Q = 2.4–2.9 (n = 40/2).

Additional specimens examined – China, Yunnan Province, Kunming, Luquan County, Jiaozishan Forest Park, elevation 2,950 m, on a dead standing tree of *Abies georgei*, leg. Y.C. Dai, 4 November 2018, Dai 19280 (BJFC027748).

Known distribution – currently known only from high-elevation temperate to subalpine forests in Southwestern China (Xizang, Yunnan), found on fallen angiosperm branches and dead *Abies* trees.

Notes – phylogenetically, *Vararia incarnata* formed an independent, well-supported lineage (100% ML, 1 BPP; Supplementary Fig. S7) within a larger stable clade comprising *V. breviphysa*, *V. pirispora*, *V. sinensis*, and *V. tenuata* (78% ML, 1 BPP; Supplementary Fig. S7). Morphologically, *V. incarnata* and *V. sinensis* share a cracked hymenial surface when mature and a dimitic hyphal system with clamp connections^[28]. However, *V. sinensis* differs from *V. incarnata* by its smaller basidiospores (6–11 $\times$ 4–6 μm vs 15.8–17.5 $\times$ 5.9–7.0 μm)^[28]. *Vararia tenuata*, originally described from Thailand and also recorded here from Hainan, China (Dai 29978), differs by having smaller fusiform basidiospores (13.5–15 $\times$ 5–6 μm vs 15.8–17.5 $\times$ 5.9–7.0 μm), and smaller gloeocystidia (28–40 $\times$ 7–10 μm vs 60–120 $\times$ 9–15 μm)^[115]. *Vararia breviphysa*, known from Gabon, is distinguished from *V. incarnata* by having shorter gloeocystidia (30–70 $\times$ 6–12 μm vs 60–120 $\times$ 9–15 μm), and narrower basidiospores (4–5.5 μm vs 5.9–7.0 μm in width)^[24]. *Vararia pirispora*, described from Réunion on dead wood, differs by its distinctly piriform basidiospores^[114].

Ecologically, *V. incarnata* grows on both angiosperm and coniferous wood in high-elevation temperate to subalpine forests of Southwestern China (Xizang, Yunnan, 2,950–3,130 m), whereas its relatives occur in lower-elevation forests of Thailand and China (*V. tenuata* on bamboo)^[115], and tropical Africa (*V. breviphysa* and *V. pirispora* on wood)^[114].

Vararia miscanthi Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 18

Index Fungorum number: IF905298.

Etymology – *Miscanthi* (Lat.): refers to the species growing on *Miscanthus*.

Diagnosis – characterized by the presence of cylindrical basidiospores measuring 12.3–15.5 $\times$ 2–3 μm and subclavate gloeocystidia densely encrusted with crystals, and growing on dead *Miscanthus* in Zhejiang, subtropical China.

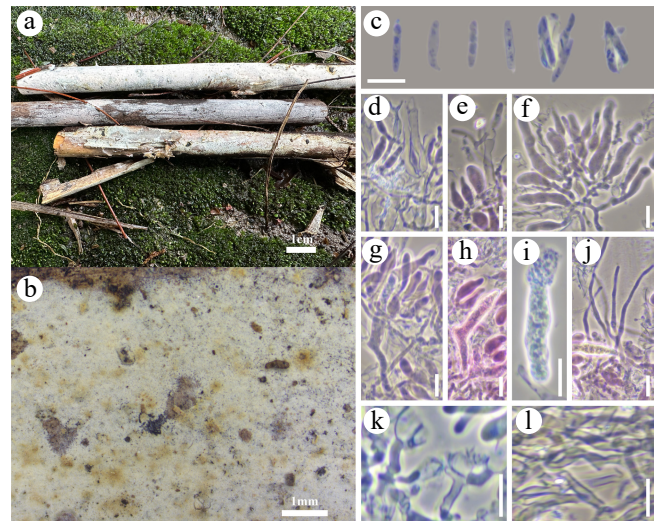


Fig. 18 *Vararia miscanthi* (holotype, Dai 26333). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f) A section of hymenium. (g)–(i) Gloeocystidia. (j) Paraphyses. (k) Dichohyphae in subiculum. (l) Generative hyphae. Scale bars: (c)–(l) = 10 μm .

Type – China, Zhejiang Province, Jinhua, Wuyi County, Yuyuan, Dahuanglingtou Village, 28.753447° N, 119.658151° E, elevation 240 m, on dead *Miscanthus*, leg. Y.C. Dai, 13 October 2023, Dai 26333 (BJFC043883).

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 13 cm long, 0.9 cm wide, 65 μm thick at center. Hymenial surface smooth to locally tuberculate, uncracked, white (–A1) to grayish white (1B1) and without odor and taste when fresh, buff (4A4) to olivaceous buff (4C4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system dimitic; generative hyphae with clamp connections, hyaline, thin- to slightly thick-walled, moderately branched and frequently septate, interwoven, IKI–, CB–, 1.5–3 μm in diam. Dichohyphae rarely present, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI–, CB–, stem 1.5–2.5 μm wide, upper branches narrow and thin-walled. Paraphyses present, cylindrical, slightly projecting, 1.5–2 μm wide. Gloeocystidia occasionally present, more or less subulate, often obtusely bent near the base, hyaline, thin-walled, densely encrusted with crystals, 55–100 $\times$ 4–7 μm , IKI+, CB+. Basidia clavate to suburniform, thin-walled, with four sterigmata and a clamp connection, 20–40 $\times$ 3.5–8 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores cylindrical, hyaline, thin-walled, smooth, occasionally with oil drops, commonly aggregated in quartets, IKI–, CB–, (12–)12.3–15.5(–15.7) $\times$ (1.8–)2–3(–3.2) μm , L = 13.63 μm , W = 2.41 μm , Q = 4.3–7.5 (n = 60/2).

Additional specimens examined – China, Zhejiang Province, Jinhua, Wuyi County, Yuyuan, 28.753425° N, 119.658148° E, elevation 230 m, on dead *Miscanthus*, leg. Y.C. Dai, 8 October 2024, Dai 30889 (BJFC051148).

Known distribution – currently known only from a subtropical forest in Eastern China (Zhejiang), found on dead *Miscanthus*.

Notes – phylogenetically, *Vararia miscanthi* formed a strongly supported clade with *V. calami* (100% ML, 1 BPP; Supplementary Fig. S7). Morphologically, *V. calami* resembles *V. miscanthi* by sharing a dimitic hyphal system with clamp connections on generative hyphae, and a substrate preference for dead monocot stems, but *V. calami* differs by having thicker basidiospores (3.5–4 μm vs 2–3 μm in width) and lacking crystal-encrusted gloeocystidia^[24]. Besides,

Vararia miscanthi is known from dead *Miscanthus* in subtropical China, while *V. calami* occurs on palms in tropical Africa^[24].

Vararia septocystidiata Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 19

Index Fungorum number: IF905299.

Etymology – *Septocystidiata* (Lat.): refers to the species having septocystidia.

Diagnosis – characterized by two distinct cystidia (tubular gloeocystidia and septocystidia with 3–5 septa), oblong-ellipsoid basidiospores measuring $11\text{--}13.1 \times 4.7\text{--}5.3\ \mu\text{m}$, and growth on diverse substrates including palm, rattan, angiosperm and gymnosperm wood in tropical to subtropical China.

Type – China, Hainan Province, Qiongzong County, Limushan National Forest Park, 19.176177°N , 109.744454°E , elevation 651 m, on rotten palm, leg. Y.C. Dai, 22 September 2024, Dai 30051 (BJFC050310).

Description – basidiomata annual, resupinate, soft, membranous, adnate, up to 6.8 cm long, 0.9 cm wide, 60 μm thick at center. Hymenial surface smooth, uncracked, cream (4A3) to buff (4A4), without odor and taste when fresh, buff (4A4) to honey yellow (5B4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin- to slightly thick-walled, moderately branched and septate, interwoven, IKI–, CB–, 2–4 μm in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI+, CB+, stem 2–4 μm wide, upper branches narrow and thin-walled. Cystidia of two kinds: gloeocystidia abundant, more or less subulate, winding, with guttulate content, hyaline, thin-walled, $70\text{--}125 \times 5\text{--}9\ \mu\text{m}$; septocystidia occasionally present, subulate, some with guttulate content, hyaline, slightly thick-walled, with 3–5 distinct septa, $60\text{--}85 \times 5\text{--}10\ \mu\text{m}$. Basidia clavate, thin-walled, with four sterigmata and a basal simple septum, $40\text{--}60 \times 7\text{--}11\ \mu\text{m}$; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores oblong-ellipsoid, occasionally with oil drops, hyaline, thin-walled, smooth, IKI–, CB–, $(10.8\text{--})11\text{--}13.1\text{--}(13.3) \times (4.5\text{--})4.7\text{--}5.3\text{--}(5.5)\ \mu\text{m}$, $L = 11.64\ \mu\text{m}$, $W = 5.11\ \mu\text{m}$, $Q = 2.2\text{--}2.5$ ($n = 120/4$).

Additional specimens examined – China, Fujian Province, Zhangzhou, Tianzhushan National Forest Park, 24.599587°N ,

117.869454°E , elevation 131 m, on a fallen angiosperm branch, leg. Y.C. Dai, 14 July 2025, Dai 35362 (BJFC056623); Guangdong Province, Zhaoqing, Dinghu District, Dinghushan National Nature Reserve, on a fallen twig of *Pinus massoniana*, leg. Yuan Yuan, 8 July 2025, Yuan 3219 (BJFC062765); Hainan Province, Qiongzong County, Limushan National Forest Park, 19.176177°N , 109.744454°E , elevation 651 m, on rotten rattan, leg. Y.C. Dai, 22 September 2024, Dai 30052 (BJFC050311).

Known distribution – currently known only from tropical to subtropical China (Hainan, Guangdong, Fujian), found on various substrates including rotten palm, rattan, and fallen angiosperm and gymnosperm branches.

Notes – phylogenetically, *Vararia septocystidiata* formed a well-supported clade with *V. cinnamomea* and *V. ferruginosa* (88% ML, 1 BPP; Supplementary Fig. S7). Morphologically, all three species share a dimitic hyphal system with simple-septate generative hyphae^[25,39]. However, *V. cinnamomea* differs by having subcylindrical basidia and growing on dead wood in tropical Africa^[25]; *V. ferruginosa* differs by having ellipsoid basidiospores, obclavate gloeocystidia without septa, and growing on angiosperm branches in Yunnan, Southwestern China^[39].

Vararia subulata Xin Zhang, Y.C. Dai, M.R. Li & Yuan Yuan, sp. nov. Fig. 20

Index Fungorum number: IF905300.

Etymology – *subulata* (Lat.): refers to the species having subulate gloeocystidia.

Diagnosis – characterized by the presence of subulate gloeocystidia, projecting paraphyses, and ellipsoid basidiospores with a tapering apiculus.

Type – China, Chongqing Municipality, Yongchuan District, Yinshan Forest Farm, 29.325276°N , 105.698251°E , elevation 373 m, on dead culm of *Bambusa emeiensis*, leg. Y.C. Dai, 14 November 2025, Dai 36777 (BJFC058036).

Description – basidiomata annual, resupinate, soft, coriaceous, adnate, up to 16 cm long, 4.1 cm wide, 65 μm thick at center. Hymenial surface smooth, uncracked, white (–A1) to pale cream (3A2), without odor and taste when fresh, buff yellow (ca. 4A4) to buff (4A4) when dry; margin white (–A1), thinning out, fimbriate.

Hyphal system dimitic; generative hyphae with simple septa, hyaline, thin-walled, moderately branched and septate, loosely

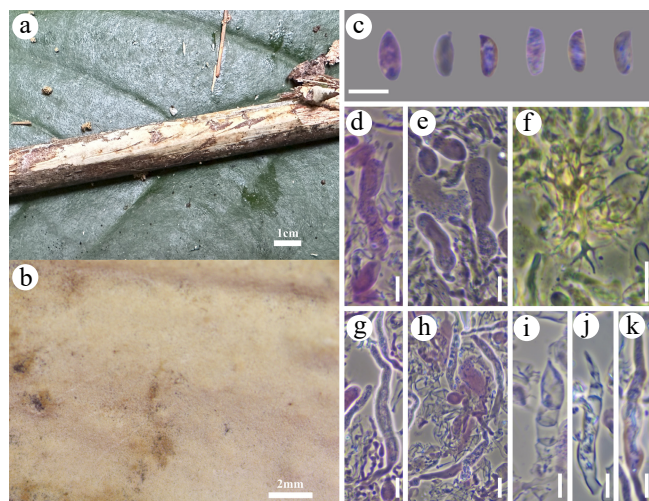


Fig. 19 *Vararia septocystidiata* (holotype, Dai 30051). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f) Dichohyphae in subiculum (Melzer's reagent). (g), (h) Gloeocystidia. (i)–(k) Septocystidium. Scale bars: (c)–(k) = 10 μm .

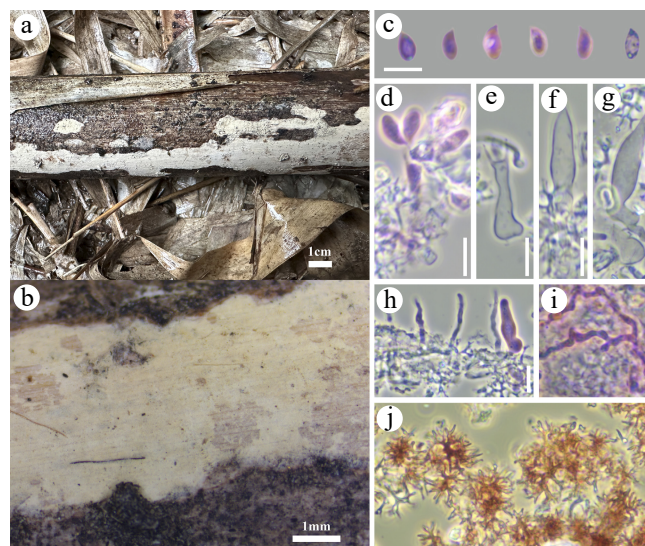


Fig. 20 *Vararia subulata* (holotype, Dai 36777). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia. (f), (g) Gloeocystidia. (h) Paraphyses. (i) Generative hyphae. (j) Dichohyphae in subiculum (Melzer's reagent). Scale bars: (c)–(j) = 10 μm .

interwoven, IKI–, CB–, 1.7–3.3 μm in diam. Dichohyphae predominant, bush-like at apex with acute tips, dichotomously to irregularly branched, thick-walled, IKI[+], CB+, stem 1.5–2 μm wide, upper branches narrow and thin-walled. Paraphyses present, cylindrical, slightly projecting, 1.5–2 μm wide. Gloeocystidia occasionally present, subulate, with a schizopapillate apex, hyaline, thin-walled, 35–50 $\times$ 4–6 μm . Basidia urniform, thin-walled, with four sterigmata and a basal simple septum, 15–25 $\times$ 5–9 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores ellipsoid, tapering to an apiculus, hyaline, thin-walled, smooth, occasionally with oil drops, IKI–, CB–, (8–)8.1–9.2(–9.5) $\times$ (3.8–)4–4.9(–5) μm , L = 8.61 μm , W = 4.49 μm , Q = 1.6–2 (n = 210/7).

Additional specimens examined – China, Anhui Province, Liuan, Jinzhai County, Tianma Nature Reserve, 31.123471° N, 115.683911° E, elevation 325 m, on a fallen branch of *Phyllostachys heterocycla*, leg. Y.C. Dai, 18 September 2025, Dai 35840 (BJFC057101); Chongqing, Yongchuan District, Chashanzhuhai National Forest Park, 29.402084° N, 105.917336° E, elevation 737 m, on dead culms of *Bambusa emeiensis*, leg. Y.C. Dai, 13 November 2025, Dai 36738 (BJFC057997), Dai 36719 (BJFC057978); Guangxi Autonomous Region, Guilin, Ziyuan County, Meixi, Bajiaozhai Scenic Spot, 26.180258° N, 110.671014° E, elevation 429 m, on dead bamboo culm, leg. Y.C. Dai, 11 May 2025, Dai 36455 (BJFC057714); Hunan Province, Changsha, Hunan Botanical Garden, 28.104948° N, 113.024667° E, elevation 89 m, on dead culm of *Bambusa textilis*, leg. Yuan Yuan, 25 April 2025, Yuan 2223 (BJFC061769).

Known distribution – currently known only from subtropical bamboo forests in subtropical China (Anhui, Guangxi, Hunan, and Chongqing), found on various bamboo species. It is characterized by ellipsoid basidiospores tapering to an apiculus, the presence of projecting paraphyses, and growth on various bamboo species in subtropical China.

Notes – phylogenetically, *Vararia subulata* formed a strongly supported clade with *V. emeiensis* (100% ML, 1 BPP; Supplementary Fig. S7). However, *V. emeiensis* differs by having oblong-ellipsoid basidiospores, lacking paraphyses and growing only on *Bambusa emeiensis* in Sichuan, whereas *V. subulata* exhibits a broader host range, occurring on multiple bamboo genera (e.g., *Bambusa* and *Phyllostachys*) across subtropical China. *Vararia subulata* may be confused with *V. alpina* in basidiospore shape; however, *V. alpina* differs by having slightly shorter basidiospores, not tapering to an apiculus (7.5–8.1 $\times$ 4.6–5.0 μm vs 8.1–9.2 $\times$ 4–4.9 μm), a cracked hymenophore, and occurrence on diverse substrates at high elevations.

Family Stereaceae Pilát

Index Fungorum number: IF81424.

Type genus – *Stereum* Hill ex Pers.

Acanthobasidium Oberw.

Index Fungorum number: IF17002.

Type species – *Acanthobasidium delicatum* (Wakef.) Oberw. ex Jülich

Notes – the genus *Acanthobasidium* historically circumscribed within *Aleurodiscus* s. lat., is defined by resupinate, corticioid basidiomata typically on monocotyledons, a monomitic hyphal system with clamp connections on generative hyphae, the presence of basidia with lateral protuberances (acanthobasidia), acanthophyses, and amyloid basidiospores^[31,94,116,117]. Our study expands the morphological and ecological scope of the genus by describing two new species from rotten bamboo in subtropical China (Guangxi): *A. encrustans* (characterized by crystal-encrusted gloeocystidia) and *A. septobasidium* (characterized by phragmobasidiate basidia developing 2–4 horizontal septa at maturity).

Acanthobasidium encrustans Xin Zhang, Y.L. Zhao & Yuan Yuan, sp. nov. Fig. 21

Index Fungorum number: IF905301.

Etymology – *Encrustans* (Lat.): refers to the species having encrusted gloeocystidia.

Diagnosis – characterized by the presence of crystal-encrusted gloeocystidia, variable acanthophyses, dendrohyphidia, globose, thick-walled, echinulate, amyloid basidiospores with a big oil drop measuring 8.5–9.2 $\times$ 8–8.7 μm , and growing on rotten bamboo in subtropical China.

Type – China, Guangxi Autonomous Region, Laibin, Jinxiu County, Liugang, Daling Village, 23.940620° N, 110.070302° E, elevation 650 m, on rotten bamboo, leg. Y.C. Dai, 15 July 2024, Dai 28852 (BJFC049111).

Description – basidiomata annual, resupinate, soft, coriaceous, closely adnate, up to 7.5 cm long, 2.5 cm wide, 65 μm thick at center. Hymenial surface smooth, uncracked, snow white (–A1) and without odor and taste when fresh, pale yellow (3A4) to curry yellow (4B8) when dry; margin white (–A1), thinning out as byssoid.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin- to slightly thick-walled, occasionally branched and septate, loosely interwoven, IKI–, CB–, 1.5–4.5 μm in diam. Acanthophyses abundant, variable in shape, mostly clavate with a swollen apex, with several to many blunt and cylindrical spines up to 7 μm long at apex, hyaline, slightly thick-walled, IKI–, CB–, 20–35 $\times$ 3–9 μm . Acanthohyphidia numerous, bearing several to many acute protuberances (spines) up to 3 μm long, hyaline, thin-walled, IKI–, 60–130 $\times$ 4–9 μm . Dendrohyphidia numerous, frequently branched at apex, hyaline, thin-walled, IKI–, CB–. Gloeocystidia occasionally present, more or less pyriform, slightly thick-walled, densely encrusted with fine crystals, 40–65 $\times$ 7–17 μm . Basidia subclavate, with many short and blunt spines at base, slightly thick-walled, with four sterigmata and a basal clamp connection, 35–60 $\times$ 11–17 μm ; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores globose, hyaline, thick-walled, with numerous blunt cylindrical spines up to 4 μm long, echinulate, with a big oil drop, IKI+, CB+, (8.4–)8.5–9.2 $\times$ (7.9–)8–8.7(–8.8) μm , L = 8.77 μm , W = 8.39 μm , Q = 1–1.1 (n = 60/2).

Additional specimens examined – China, Guangxi Autonomous Region, Fangchenggang, Shangsi County, Shiwandashan National

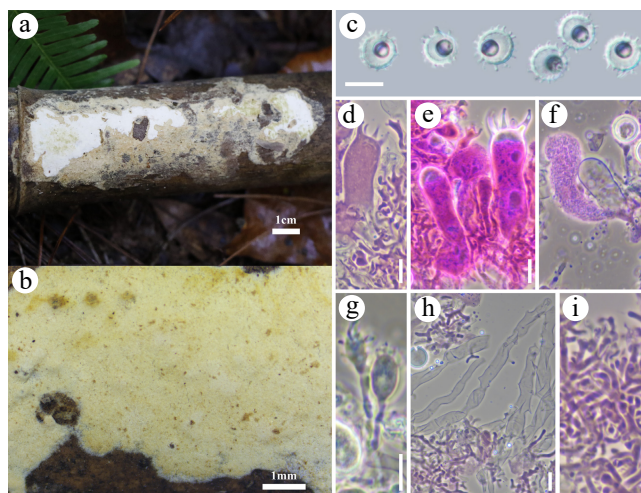


Fig. 21 *Acanthobasidium encrustans* (holotype, Dai 28852). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f) Gloeocystidia. (g) Acanthophyses. (h) Acanthohyphidia. (i) Dendrohyphidia. Scale bars: (c)–(i) = 10 μm .

Forest Park, 21.89932° N, 107.905843° E, elevation 317 m, on rotten bamboo, leg. Y.C. Dai, 4 September 2024, Dai 32883 (BJFC053142).

Known distribution – currently known only from subtropical forests in Southern China (Guangxi), found on rotten bamboo.

Notes – *Acanthobasidium encrustans* is phylogenetically sister to the clade containing *A. septobasidium* and *A. bambusicola* (Supplementary Fig. S1). Morphologically, *A. encrustans* shares with *A. septobasidium* and *A. bambusicola* the presence of variable acanthophyses and globose, thick-walled, echinulate, amyloid basidiospores, as well as growth on bamboo in Southern China. However, *A. septobasidium* and *A. bambusicola* can be distinguished from *A. encrustans* by non-encrusted gloeocystidia and basidiospores without a big oil drop^[32].

Acanthobasidium septobasidium Xin Zhang, Y.C. Dai, Y.L. Zhao & Yuan Yuan, sp. nov. Fig. 22

Index Fungorum number: IF905302.

Etymology – *Septobasidium* (Lat.): refers to the species having septate basidia.

Diagnosis – characterized by the presence of 2–4 horizontal septa in mature basidia; acanthophyses; gloeocystidia; globose, echinulate, amyloid basidiospores, and growth on dead culms of *Indosasa crassiflora* in subtropical China.

Type – China, Guangxi Autonomous Region, Guilin, Maoershan National Nature Reserve, 25.885672° N, 110.484717° E, elevation 1,182 m, on dead culm of *Indosasa crassiflora*, leg. Y.C. Dai, 10 May 2025, Dai 36359 (BJFC057616).

Description – basidiomata annual, resupinate, soft, coriaceous, closely adnate, up to 9 cm long, 3.5 cm wide, 300 µm thick at center. Hymenial surface smooth, slightly cracked, pale grayish white (1A1) and without odor and taste when fresh, becoming curry yellow when bruised, buff (4A4) to cinnamon (6D6) when dry; margin thinning out as byssoid, paler or concolorous with the hymenophore.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin- to slightly thick-walled, occasionally branched and septate, more or less regularly arranged to loosely interwoven, IKI–, CB–, 1.5–4 µm in diam. Acanthophyses abundant, variable in shape, mostly racket-shaped, with several to many blunt and cylindrical spines up to 2 µm long at apex, hyaline, slightly thick-walled, IKI–, CB–, 20–45 × 7–15 µm. Acanthohyphidia numerous, bearing several to many acute protuberances (spines) up to 3.5 µm long, hyaline, some with guttulate content, thin-walled, IKI–, CB–, 45–80 × 4–8 µm. Dendrohyphidia predominant, frequently

branched at apex, hyaline, thin-walled, IKI–, CB–. Gloeocystidia occasionally present, spatulate, slightly thick-walled, 25–65 × 10–20 µm. Basidia clavate, with many short and blunt spines at base, slightly thick-walled, initially aseptate, developing 2–4 horizontal septa at maturity, with four sterigmata and a basal clamp connection, 40–75 × 11–17 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores globose, hyaline, thick-walled, with numerous blunt cylindrical spines up to 4 µm long, echinulate, IKI+, CB+, (9.6–)9.7–10.2 × (9.2–)9.3–10(–10.2) µm, L = 10.09 µm, W = 9.72 µm, Q = 1–1.1 (n = 120/4).

Additional specimens examined – China, Guangxi Autonomous Region, Guilin, Maoershan National Nature Reserve, 25.863445° N, 110.493975° E, elevation 886 m, on dead culm of *Indosasa crassiflora*, leg. Y.C. Dai, 8 May 2025, Dai 36155 (BJFC057414) and Dai 36158 (BJFC057417); 25.885054° N, 110.485055° E, elevation 1,146 m, on dead culm of *Indosasa crassiflora*, leg. Y.C. Dai, 10 May 2025, Dai 36357 (BJFC057618).

Known distribution – currently known only from a subtropical montane forest in Southern China (Guangxi), found on dead culms of *Indosasa crassiflora*.

Notes – phylogenetically, *Acanthobasidium septobasidium* formed a well-supported clade with *A. bambusicola* (87 ML%, 1 BPP; Supplementary Fig. S1), and together they are sister to *A. encrustans*. These three species share a monomitic hyphal system with clamp connections, the presence of acanthophyses, gloeocystidia, globose, echinulate, amyloid basidiospores, and all are associated with bamboo in Southern China^[32]. *Acanthobasidium septobasidium* occurs on dead culms of *Indosasa crassiflora* in Guangxi, distinguished by a unique feature within the genus: its basidia develop 2–4 horizontal septa at maturity; *A. encrustans* differs by its crystal-encrusted gloeocystidia, while *A. bambusicola* is characterized by two distinct kinds of gloeocystidia and lacks dendrohyphidia^[32].

Aleurodiscus Rabenh. ex J. Schröt.

Index Fungorum number: IF17041.

Type species – *Aleurodiscus amorphus* (Pers.) J. Schröt.

Notes – the genus *Aleurodiscus* is morphologically defined by resupinate to discoid basidiomata, various sterile elements (e.g., acanthophyses, dendrohyphidia), gloeocystidia, and amyloid basidiospores^[1,31,116,118,119]. Recent phylogenetic studies have revealed that this broad concept comprises several distinct lineages, leading to the restriction of *Aleurodiscus* to a core clade^[34,118]. Notably, *Neoeurodiscus* Sheng H. Wu, characterized by thick-walled smooth basidiospores, is also nested within this core clade^[34,94]. Thus, *Aleurodiscus* s. str. remains morphologically heterogeneous, comprising taxa with simple- or nodose-septate hyphae, smooth or ornamented basidiospores, and with or without acanthohyphidia^[34]. Our new species, found on *Pinus massoniana* in subtropical China, is phylogenetically nested within the *Aleurodiscus* s. str. clade (Fig. 3), and contributes to its documented morphological and ecological diversity.

Aleurodiscus subtropicus Xin Zhang, Y.C. Dai, Y.L. Zhao & Yuan Yuan, sp. nov. Fig. 23

Index Fungorum number: IF905303.

Etymology – *Subtropicus* (Lat.): refers to the species having a distribution in subtropical China.

Diagnosis – characterized by resupinate to effuse-reflexed basidiomata, the presence of clavate acanthophyses with blunt apical spines; moniliform gloeocystidia; ellipsoid, verruculose basidiospores measuring 10–12 × 8.2–9.8 µm, and growth on *Pinus massoniana* in subtropical China.

Type – China, Jiangxi Province, Nanchang, Shengshuitang National Forest Park, 28.992633° N, 115.535941° E, elevation 258 m,

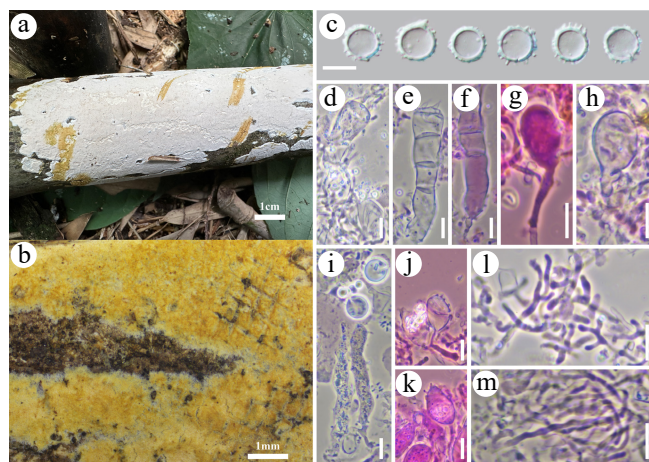


Fig. 22 *Acanthobasidium septobasidium* (holotype, Dai 36359). (a), (b) Basidiomata. (c) Basidiospores. (d)–(f) Basidia. (g), (h) Gloeocystidia. (i) Acanthohyphidia. (j), (k) Acanthophyses. (l) Dendrohyphidia. (m) Generative hyphae. Scale bars: (c)–(m) = 10 µm.

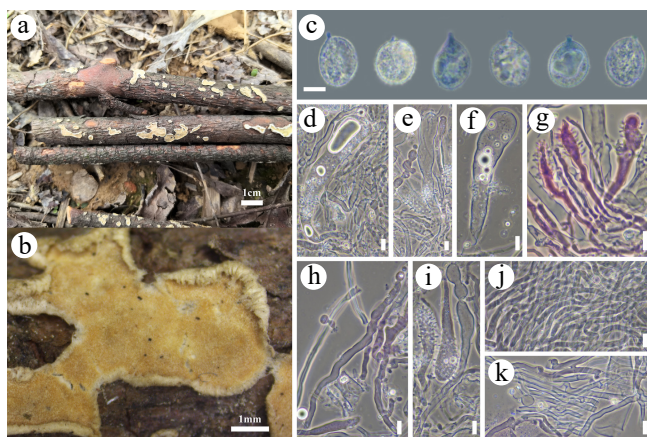


Fig. 23 *Aleurodiscus subtropicus* (holotype, Yuan 2270). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia. (f) Basidioles. (g) Acanthophyses. (h), (i) Gloeocystidia. (j), (k) Generative hyphae. Scale bars: (c)–(k) = 10 µm.

on fallen branches of *Pinus massoniana*, leg. Yuan Yuan, 26 April 2025, Yuan 2270 (BJFC061816).

Description – basidiomata annual, resupinate to effuse-reflexed, soft, membranous to coriaceous, easily separated from the substrate, up to 1.3 cm long, 0.4 cm wide, 400 µm thick at center. Hymenial surface smooth, pruinose, uncracked, cream (4A3) to buff yellow (ca. 4A4) and without odor and taste when fresh, buff (4A4) to clay buff (6D4) when dry; margin incurved, thinning out, fimbriate, paler with the hymenophore.

Hyphal system monomitic; generative hyphae with clamp connections, hyaline, thin- to slightly thick-walled, moderately branched and septate, more or less regularly arranged to loosely interwoven, IKI–, CB–, 2–6 µm in diam. Acanthophyses abundant, variable in shape, mostly clavate, with several to many blunt and cylindrical spines up to 3.5 µm long at apex, hyaline, slightly thick-walled, IKI–, CB–, 40–65 × 4–9 µm. Hyphidia numerous, hyaline, thin-walled, IKI–, CB–, 45–130 × 3–7 µm. Gloeocystidia occasionally present, moniliform, slightly thick-walled, 75–160 × 5–12 µm. Basidia clavate, with many short and blunt spines in the middle, slightly thick-walled, with four sterigmata and a basal clamp connection, 65–130 × 13–25 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores broadly ellipsoid, hyaline, slightly thick-walled, verruculose, IKI+, CB+, (9.7–)10–12(–12.2) × (8–)8.2–9.8(–10) µm, L = 11.26 µm, W = 9.28 µm, Q = 1.1–1.3 (*n* = 120/4).

Additional specimens examined – China, Hunan Province, Hengyang, Hengshan Scenic Spot, 27.248327° N, 112.732913° E, elevation 122 m, on fallen branches of *Pinus massoniana*, leg. Yuan Yuan, 24 April 2025, Yuan 2133 (BJFC061679); on fallen trunk of *Pinus massoniana*, leg. Yuan Yuan, 24 April 2025, Yuan 2146 (BJFC061692); on fallen twigs of *Pinus massoniana*, leg. Yuan Yuan, 24 April 2025, Yuan 2158 (BJFC061704) and Yuan 2159 (BJFC061705); Zhejiang Province, Jinhua, Wuyi County, Tongqin, Xiaxie Village, Wuniu Mountain, on a fallen branch of *Pinus massoniana*, leg. Y.C. Dai, 15 April 2024, Dai 27280 (BJFC047540).

Known distribution – currently known only from subtropical montane coniferous forests in Eastern China (Jiangxi, Hunan, and Zhejiang), found on fallen trunks, branches, and twigs of *Pinus massoniana*.

Notes – phylogenetically, *Aleurodiscus subtropicus* occupies an independent position within the core *Aleurodiscus* s. str. clade, which is sister to *A. pinicola* (0.98 BPP; Fig. 3). Morphologically, *A. pinicola* shares the presence of moniliform gloeocystidia,

acanthophyses, amyloid basidiospores, and growth on *Pinus* with *A. subtropicus*^[119]. However, *A. pinicola* differs from *A. subtropicus* by its larger basidiospores (23–27 × 19–23 µm vs 10–12 × 8.2–9.8 µm) and its occurrence in high-elevation temperate forests (2,580–3,250 m vs 122–258 m)^[119].

Confertotrama Nakasone & S.H. He

Index Fungorum number: IF27592.

Type species – *Confertotrama rugulosa* (Berk. & M.A. Curtis) Nakasone & S.H. He

Notes – the genus *Confertotrama* was established to accommodate corticioid fungi characterized by yellowish basidiomata with compact texture, clamped generative hyphae, numerous large gloeocystidia with a positive sulphovanillin reaction, and ellipsoid to cylindrical, smooth or ornamented, amyloid basidiospores^[34]. In our phylogenies (Fig. 3), species of *Confertotrama* are recovered as a well-supported monophyletic clade distinct from *Gloeocystidiellum* s. str.

In this present study, the new combination is proposed on the basis of phylogenetic analyses (Fig. 3). *Gloeocystidiellum lojanense* A.C. Jaram. et al. was originally described from Ecuador^[104]. In the original phylogeny based on ITS and LSU sequences, *G. lojanense* formed a strongly supported clade with *G. aspellum* Hjortstam, *G. compactum* Sheng H. Wu, *G. formosanum* Sheng H. Wu, and *G. rajchenbergii* Gorjón & Hallenb.^[104]. These species have subsequently been transferred to *Confertotrama*^[34]. Our phylogenetic analyses confirmed that *G. lojanense* is nested within *Confertotrama*, sister to *C. aspellum* and *C. rajchenbergii* (Fig. 3). Morphologically, *G. lojanense* shares the diagnostic features of *Confertotrama*, including yellowish basidiomata, the presence of clamped generative hyphae, gloeocystidia with granular protoplasmic contents, and ellipsoid, verrucose, amyloid basidiospores^[104]. The combination is thus proposed.

Confertotrama lojanense (A.C. Jaram., D. Cruz & Decock) Xin Zhang, Y.C. Dai & Yuan Yuan, comb. nov.

Index Fungorum number: IF905304.

Basionym – *Gloeocystidiellum lojanense* A.C. Jaram., D. Cruz & Decock, in Jaramillo-Riofrío, Decock, Suárez, Benítez, Castillo & Cruz, J. Fungi 9(1, no. 54): 9 (2023).

Known distribution – currently known from the type locality in Ecuador, growing on a fallen, decomposing branch of an unknown tree in tropical montane rainforest.

Gloeomyces Sheng H. Wu

Index Fungorum number: IF27592.

Type species – *Gloeomyces graminicola* Sheng H. Wu

Notes – the genus *Gloeomyces* is characterized by resupinate, corticioid basidiomata, a monomitic hyphal system with simple-septate generative hyphae, the presence of distinctive sterile elements such as acanthophyses, and smooth basidiospores^[101]. It is phylogenetically and morphologically distinct from *Aleurodiscus* s. str., which typically has thick-walled, ornamented or smooth basidiospores^[34,118]. Our new species, *G. tapetiformis*, grows on bamboo as well as other woody substrates, further expanding the ecological diversity known within this genus.

Gloeomyces tapetiformis Xin Zhang, Y.C. Dai, Y.L. Zhao & Yuan Yuan, sp. nov. Fig. 24

Index Fungorum number: IF905305.

Etymology – *Tapetiformis* (Lat.): refers to the species having acanthophyses tapering to the apex.

Diagnosis – characterized by the presence of hyphoid acanthophyses tapering from the base to a frequently branched apex, ellipsoid, amyloid basidiospores measuring 3.8–4.4 × 2.6–2.9 µm, and occurrence on various substrates (bamboo, gymnosperm and angiosperm wood) in temperate to tropical China.

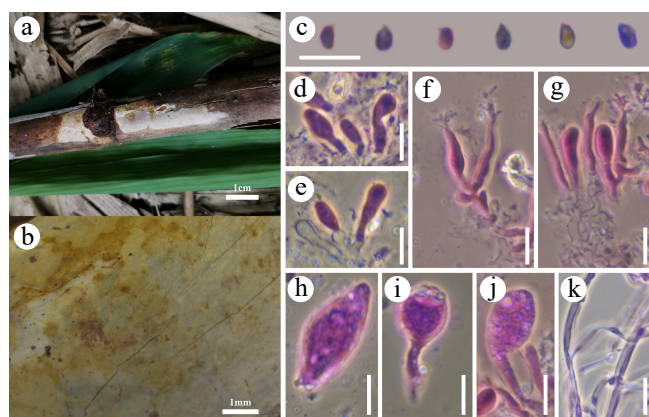


Fig. 24 *Gloeomyces tapetiformis* (holotype, Dai 35487). (a), (b) Basidiomata. (c) Basidiospores. (d), (e) Basidia and basidioles. (f), (g) Acanthophyses. (h)–(j) Gloeocystidia. (k) Generative hyphae. Scale bars: (c)–(k) = 10 µm.

Type – China, Yunnan Province, Xishuangbanna, Jinghong City, along G219 National Highway from Jinghong to Menglun, 22.007047° N, 101.033348° E, elevation 871 m, on fallen branches of *Dendrocalamus yunnanicus*, leg. Y.C. Dai, 1 July 2025, Dai 35487 (BJFC056748).

Description – basidiomata annual, resupinate, soft, coriaceous, adnate, up to 6 cm long, 1.5 cm wide, 65 µm thick at center. Hymenial surface smooth, uncracked, white (–A1) to cream (4A3) and without odor and taste when fresh, pale yellow (3A4) to buff (4A4) when dry; margin thinning out, indistinct, concolorous with the hymenophore.

Hyphal system monomitic; generative hyphae with simple septa, hyaline, thin- to slightly thick-walled, moderately branched and septate, loosely interwoven, IKI–, CB–, 1.2–2.5 µm in diam. Acanthophyses abundant, variable in shape, mostly hyphoid, tapering to apex, frequently branched at apex, hyaline, slightly thick-walled, IKI–, CB–, 15–25 × 2–5 µm. Hyphidia numerous, unbranched, hyaline, thin-walled, IKI–, CB–, 13–18 × 2–4 µm. Gloeocystidia occasionally present, mostly fusiform, slightly thick-walled, with guttulate content, 18–35 × 7–18 µm. Basidia clavate, thin-walled, with four sterigmata and a basal simple septum, 15–25 × 4–7 µm; basidioles morphologically resembling basidia, yet slightly smaller in size. Basidiospores ellipsoid, tapering to an apiculus, hyaline, thin-walled, smooth, IKI+, CB–, (3.6–)3.8–4.4(–4.6) × (2.3–)2.6–2.9(–3) µm, $L = 4.17$ µm, $W = 2.63$ µm, $Q = 1.6$ –1.7 ($n = 120/4$).

Additional specimens examined – China, Jilin Province, Baishan, Fusong County, Lushuihe, Korean Pine Virgin Forest, 42.482319° N, 127.868987° E, elevation 804 m, on a fallen branch of *Pinus koraiensis*, leg. Y.C. Dai, 12 September 2025, Dai 37784 (BJFC059043); Yunnan Province, Xishuangbanna, Jinghong, near Daizhai Viewing Platform along G219 National Highway, 21.981136° N, 101.166855° E, elevation 939 m, on dead culm of *Dendrocalamus* sp., leg. Y.C. Dai, 4 July 2025, Dai 35646 (BJFC056907).

Known distribution – currently known from temperate to tropical forests in Northern to Southwestern China (Jilin and Yunnan), found on various substrates including bamboo and coniferous wood.

Notes – phylogenetically, *Gloeomyces tapetiformis* is closely related to *G. dextrinoideophyses* (52% ML; [Supplementary Fig. S5](#)). Both species share simple-septate generative hyphae, the presence of acanthophyses, clavate basidia, and smooth, amyloid basidiospores^[34,60]. However, *G. dextrinoideophyses* is distinguished from *G. tapetiformis* by its dextrinoid acanthophyses, larger basidiospores (5–7 × 3–4 µm vs 3.8–4.4 × 2.6–2.9 µm), and growing in tropical Thailand and only on bamboo^[60].

Discussion

The order Russulales encompasses a remarkable diversity of basidiomata forms, with corticioid species mainly in Peniophoraceae and Stereaceae^[1,3,21,22,34,36,39,120–122]. Our multi-loci phylogenetic analyses provide a well-resolved framework for reassessing these families and the *Gloeocystidiellum* complex by establishing a new family. The results also suggest multiple independent transitions to monocotyledonous hosts, particularly bamboo, in China, suggesting that the region could represent a center of ecological specialization.

Phylogenetic complexity, morphological diversity, and substrate associations in the *Gloeocystidiellum* complex: resolving into Camptocystidiellaceae and Gloeocystidiellaceae

Previous placements of species, such as *Gloeocystidiellum sinense*, *G. cremeum*, *G. fissuratum*, and *G. yaoshanense*, within Stereaceae were based on limited phylogenetic sampling and an incomplete understanding of the polyphyly of the *Gloeocystidiellum* complex, leading to their misplacement^[36–38]. Our multi-gene phylogeny resolves the *Gloeocystidiellum* complex into two distinct families within Russulales ([Fig. 1](#)): Camptocystidiellaceae and Gloeocystidiellaceae, consistent with recent phylogenetic evidence^[21,39,96,97].

Camptocystidiellaceae is a phylogenetically distinct and morphologically more diverse group, comprising a single genus, *Camptocystidiellum*. Within this genus, species exhibit variation in hyphal septation (clamped or simple-septate), gloeocystidial morphology (straight to slightly curved or flexuous), basidiospore ornamentation (verrucose or smooth), substrate preference, and geographic distribution^[38,39,96,98,99,101,102]. Unlike Gloeocystidiellaceae, none of the Camptocystidiellaceae species show affinity for monocots; instead, they occur on gymnosperm and angiosperm wood across diverse ecosystems in Africa, Asia, America, and Europe.

Gloeocystidiellaceae contains a single genus, *Gloeocystidiellum*, characterized by mostly clamped hyphae and straight to slightly curved gloeocystidia^[35–37,101,123,124]. Species of this family are distributed across the Northern Hemisphere, with particularly notable diversity in East Asia, particularly in China, where at least six species are now documented. The type species, *G. porosum*, has a wide distribution in the Northern Hemisphere, recorded from Asia, Europe, and North America, occurring on diverse woody substrates and occasionally on bamboo (*Phyllostachys* in France)^[1,35,96,97,101,104,110]. Beyond the widespread *G. porosum* and the European species *G. permixtum*^[35], an unexpected richness of *Gloeocystidiellum* has recently been documented in China, including *G. sinense*, *G. cremeum*, *G. fissuratum*, *G. yunnanense* from Yunnan^[36,37,124], and our new species *G. monocotyledonum* from Zhejiang. All these Chinese representatives share clamped generative hyphae, with the exception of *G. sinense*, which has simple-septate generative hyphae^[37]. These four species, described from Yunnan, are known only from their type localities at elevations of 900–1,900 m, showing variation in gloeocystidia (straight to slightly curved) and basidiospores (smooth or verrucose), occurring on angiosperm wood, with *G. fissuratum* also on *Picea*^[36,37,124]. In contrast, *G. monocotyledonum* grows on palms and *Miscanthus* in subtropical Eastern China (Zhejiang), representing the first monocot specialist within *Gloeocystidiellum*. Morphologically, it is characterized by subcylindrical to subclavate, flexuous gloeocystidia, fusiform cystidioles, and broadly ellipsoid to subglobose, verruculose basidiospores (5.6–6.7 × 4.9–5.2 µm), which are notably larger than those of its close relatives.

The recognition of two families within the former *Gloeocystidiellum* complex resolves its long-standing polyphyly. Moreover, the discovery of *Gloeocystidiellum monocyledonum* in Gloeocystidiellaceae suggests a possible specialization on monocots, having larger basidiospores, fusiform cystidioles, and flexuous gloeocystidia, compared to its wood-associated relatives. Whether these morphological differences are linked to host shift remains to be investigated.

Peniophoraceae: morphological diversity and substrate associations of *Asterostroma*, *Baltazaria*, *Gloiothele*, and *Vararia*

Within Peniophoraceae, *Vararia*, *Asterostroma*, *Gloiothele*, and *Baltazaria* differ in substrate associations and morphological traits. *Vararia* stands out with the highest diversity on monocotyledonous hosts, with seven of the eight new species showing some degree of monocotyledonous associations. *Asterostroma* follows a similar trend, with three new species emerging on bamboo across both sections within this genus.

Historically, *Vararia* species outside Asia are predominantly found on woody plants, with only rare monocotyledonous records such as *V. dussii* Boidin & Lanq. on *Philodendron* in the West Indies and *V. gallica* on *Phyllostachys* in Europe^[24,125]. In striking contrast, the eight new species exhibit remarkable morphological diversity alongside varied substrate associations. Six are strictly monocot-associated: *V. emeiensis* and *V. subulata* on bamboo, *V. miscanthi* on *Miscanthus*, *V. falcata* on bamboo, *Miscanthus* and *V. septocystidiata* on palms and rattans, and *V. acanthocystidia* on bamboo. In addition, *V. alpina* occurs on both bamboo and woody plants, while *V. incarnata* is restricted to angiosperm and gymnosperm wood in high-elevation forests. These ecological shifts appear to be accompanied by lineage-specific morphological traits: sickle-shaped basidiospores in *V. falcata*, septocystidia in *V. septocystidiata*, acanthocystidia in *V. acanthocystidia*, and crystal-encrusted gloeocystidia in *V. miscanthi*.

Among the strictly bamboo-associated species, *Vararia emeiensis* and *V. subulata* share urniform basidia and subulate gloeocystidia, but differ in more details and host range: *V. emeiensis* has oblong-ellipsoid basidiospores ($7\text{--}7.9 \times 3.1\text{--}3.6 \mu\text{m}$) and grows only on *Bambusa emeiensis* in Sichuan, while *V. subulata* has ellipsoid basidiospores ($8.1\text{--}9.2 \times 4\text{--}4.9 \mu\text{m}$) with tapering apiculus and projecting paraphyses, occurring on multiple bamboo genera across subtropical China. *Vararia acanthocystidia*, also bamboo-associated, is distinguished by unique, urniform to clavate acanthocystidia densely covered with tuberculate spines, and oblong-ellipsoid basidiospores ($7.9\text{--}9.1 \times 4.1\text{--}5.2 \mu\text{m}$) in tropical Hainan.

Species on other monocots show further morphological divergence. *Vararia falcata* possesses unique sickle-shaped basidiospores ($11\text{--}15.7 \times 1.8\text{--}2.5 \mu\text{m}$) and subulate gloeocystidia with a schizopapillate apex, growing on both bamboo and *Miscanthus* in tropical Hainan and Guangxi. *Vararia miscanthi* is characterized by cylindrical basidiospores ($12.3\text{--}15.5 \times 2\text{--}3 \mu\text{m}$) and crystal-encrusted gloeocystidia, and growth only on *Miscanthus* in Zhejiang. *Vararia septocystidiata* is distinguished by two cystidia types: subulate gloeocystidia and septocystidia with 3–5 septa—a feature reported here for the first time within *Vararia*. It has oblong-ellipsoid basidiospores ($11\text{--}13.1 \times 4.7\text{--}5.3 \mu\text{m}$) and grows on palms, rattans, and woody plants in tropical to subtropical China. *Vararia alpina*, characterized by ellipsoid basidiospores ($7.5\text{--}8.1 \times 4.6\text{--}5.0 \mu\text{m}$) and subulate gloeocystidia, occurs on both bamboo and woody plants in high-elevation Xizang, representing a broad ecological tolerance.

Vararia incarnata stands apart from all other new species, found on angiosperm and gymnosperm wood in high-elevation forests of Xizang and Yunnan. It is characterized by fusiform basidiospores

($15.8\text{--}17.5 \times 5.9\text{--}7.0 \mu\text{m}$), a flesh-pink hymenophore when fresh, and bush-like, blunt-tipped dichohyphidia.

A parallel yet contrasting pattern occurs in *Asterostroma*. Species worldwide are predominantly wood-associated, with occasional exceptions such as *A. cervicolor* on sugarcane and *A. spinosporum* on *Agave*^[35]. The three new species described here are all bamboo-associated and are distributed across both sections of *Asterostroma*. Unlike *Vararia*, however, these species retain the diagnostic basidiospore ornamentation of their respective sections, suggesting that transitions to bamboo occurred without altering fundamental basidiospore architecture. Among the bamboo-associated species in sect. *Asterostroma*, characterized by echinulate basidiospores and regularly star-shaped asterosetae, three species form a well-supported bamboo-associated subclade in Southern China (0.97 BPP; Fig. 2). *Asterostroma bicystidiatum*, distinguished by two types of gloeocystidia (fusiform and sinuous), is widely distributed across multiple bamboo genera from Sichuan to Guangxi. *Asterostroma brevispinum*, distinguished by fusiform cystidioles, occurs on *Bambusa* in Guizhou, and *A. fimbriatum* was recently described from bamboo in Yunnan^[39]. Representing sect. *Laevispora*, *A. papillatum* is currently known only from bamboo in warm-temperate Henan, representing the northernmost distribution of bamboo-associated *Asterostroma* in China.

Turning to the remaining genera within Peniophoraceae, *Gloiothele* and *Baltazaria* show different trends. *Gloiothele* species have previously been recorded on angiosperm wood across Europe, North America, and tropical regions^[111,112]. *Gloiothele bambusicola* represents the first bamboo-associated species in the genus, characterized by distinctly constricted basidia, and occurs on both bamboo and angiosperms in China. A second new species, *G. spathulata*, possesses spathulate basidia and globose basidiospores, and grows on *Quercus mongolica* in temperate China and Korea. In contrast, *Baltazaria* shows no monocotyledonous associations. Species in this genus are predominantly found on gymnosperm and angiosperm wood across the Northern Hemisphere^[26,110]. *Baltazaria massoniana* follows this trend, occurring on *Pinus massoniana* from subtropical China, and is characterized by urniform basidia and oblong-ellipsoid, inamyloid basidiospores. The new combination *B. quintasiana*, based on sequences from paratypes of *Corticium quintasianum* (CBS 749.86, CBS 750.86), extends the genus to West Africa, showing an intriguing disjunct distribution^[82,109].

Together, these findings indicate that monocots, particularly bamboo, have been repeatedly colonized by different lineages of corticioid fungi in East Asia: *Vararia* shows considerable ecological and morphological diversification on monocots, with notable traits including sickle-shaped basidiospores, acanthocystidia, and septocystidia; *Asterostroma*, in contrast, shows repeated transitions to bamboo across both sections of *Asterostroma* yet retaining the diagnostic ornamentation basidiospores; *Gloiothele* gains its first bamboo-associated species in *G. bambusicola*, while *Baltazaria* remains strictly wood-associated with a disjunct intercontinental distribution^[1,26]. The repeated and independent transitions to bamboo and other monocots across multiple lineages differ from the predominantly wood-associated habits of these genera elsewhere, suggesting that East Asia may be a significant area for ecological specialization within Peniophoraceae.

Stereaceae: morphological diversity and substrate associations of *Aleurodiscus* s. str., *Acanthobasidium*, *Confertotrama*, and *Gloeomyces*

Turning to Stereaceae, a different pattern emerges: bamboo association is less widespread than in Peniophoraceae but

morphologically more striking. Within this family, four genera differ markedly in substrate preference and morphological traits.

Acanthobasidium, segregated from *Aleurodiscus* s. lat. by its distinctive acanthobasidia, has historically been recorded on gymnosperms and angiosperms, with only occasional bamboo records outside Asia, such as *A. phragmitis* in France^[110]. In striking contrast, our study shows that *Acanthobasidium* hosts the most concentrated bamboo-associated lineage in Stereaceae: *A. bambusicola* and two new species—*A. encrustans* and *A. septobasidium* formed a well-supported clade restricted to Southern China (Hunan and Guangxi), exhibiting remarkable morphological traits. *Acanthobasidium encrustans* possesses crystal-encrusted gloecystidia, a feature previously unreported in the genus, while *A. septobasidium* develops phragmobasidia with 2–4 transverse septa at maturity—a feature previously unknown in Stereaceae^[3,34,60,94]. The consistent presence of this trait across multiple collections from its specific host, *Indosasa crassiflora*, suggests biological significance rather than a developmental anomaly.

Gloeomyces, characterized by simple-septate generative hyphae, acanthophyses, and smooth, amyloid basidiospores, has long been known from diverse substrates including gymnosperms, angiosperms, and monocots across the Northern Hemisphere^[23,34,94]. Our new species *G. tapetiformis* expands this ecological breadth further, occurring on bamboo and conifers across temperate to tropical China. Its relative with the bamboo-restricted *G. dextrinoideophyses* in Thailand mirrors patterns observed in other genera, suggesting the evolutionary lability of substrate preference^[60].

Elsewhere in Stereaceae, bamboo association appears sporadically. *Aleurodiscus* s. str., historically obscured by a broad polyphyletic circumscription that included species on diverse woody plants and even monocotyledons^[31,118], has been restricted by recent phylogenies to a core clade^[34,39,94,118]. Within this restricted concept, the genus maintains a conservative morphology on coniferous hosts, with our new species *A. subtropicus* representing a low-elevation ecological counterpart to the high-elevation *A. pinicola*, extending the altitudinal range of the genus in China while showing no affinity for monocotyledonous hosts^[119].

Meanwhile, *Confertotrama*, recently established for species formerly in *Gloeocystidiellum* s. lat. with yellowish basidiomata, clamped generative hyphae, and ornamented amyloid basidiospores, was previously known only from Asia and North America^[34]. Our phylogenetic analysis confirms the transfer of *Gloeocystidiellum lojanense* to *Confertotrama*, based on its type sequence from Ecuador, adding the first South American record (Ecuador) and extending its distribution across two hemispheres^[104].

Thus, within Stereaceae, these contrasting patterns suggest how different lineages may have responded uniquely to ecological opportunities, with *Acanthobasidium* standing out as the most concentrated bamboo-associated clade, characterized by crystal-encrusted gloecystidia in *A. encrustans* and phragmobasidia with transverse septa in *A. septobasidium*—a feature novel to the family^[34,39].

Divergence time estimates and high intrageneric variation in *Vararia*.

Using the same three fossil calibrations (Agaricales, Hymenochaetales, and the Ascomycota–Basidiomycota split), Deng et al.^[39] estimated the crown age of Russulales at approximately 222.49 Mya and Camptocystidiellaceae at ca. 109.96 Mya. Our analysis, applying the same calibration points, yields comparable estimates: Russulales at ca. 199.48 Mya (142.29–276.26 Mya, 95% HPD), Camptocystidiellaceae at ca. 99.07 Mya (52.84–153.4 Mya, 95% HPD), Gloecystidiellaceae at ca. 87.95 Mya (51.94–134.78 Mya, 95% HPD). The relative divergence order of major families remains consistent with previous studies^[7,93,95].

A striking observation is the exceptionally high level of sequence variability within Peniophoraceae, and no genus exemplifies this more strikingly than *Vararia*. Long suspected to be polyphyletic^[22,24,25,29,39], *Vararia* is confirmed as such by our phylogeny (Fig. 2). Our divergence time tree (Fig. 4) also reveals that *Vararia* has experienced multiple independent divergence events at different evolutionary depths. For example, *V. parmasoi* Boidin & Lanquetin represents the earliest diverging lineage (ca. 80.39 Ma) among these species, followed by *V. abortiphysa* Boidin & Lanquetin (ca. 71.42 Ma), *V. alpina* (ca. 67.19 Ma) and *V. miscanthi* (ca. 64.84 Ma). These staggered divergence times suggest that the genus may have experienced a series of sequential speciation events rather than a single radiation event. The pattern matches the high level of sequence variability seen in *Vararia*, which further confirms its long-known polyphyly. The extreme sequence divergence within the genus, particularly in the ITS region, posed serious challenges for Bayesian convergence. However, the eight new species are always clearly defined in single-genus trees (Supplementary Figs S7–S9), and their species definition is strong. A future genus-level revision is needed. For now, we retain them in *Vararia* because they fit the traditional concept of the genus.

In summary, this study adds substantially to the documented diversity of corticioid fungi in China, contributing one new genus, 20 new species, and nine new combinations across Camptocystidiellaceae, Gloecystidiellaceae, Peniophoraceae, and Stereaceae. Our multi-gene phylogeny provided a robust framework for understanding evolutionary relationships within these families, with a particular focus on bamboo-associated taxa. Together, these findings suggest that monocots, particularly bamboo, may have served as recurrent arenas for ecological specialization across three distantly related families within Russulales: Gloecystidiellaceae, Peniophoraceae, and Stereaceae. The repeated, independent transitions to monocots across multiple lineages in East Asia—diverse in *Vararia*, repeated but conservative in *Asterotroma*, emergent in *Gloiothele*, and concentrated in *Acanthobasidium*—contrast sharply with the predominantly wood-associated habits elsewhere, suggesting the region may be a significant center for diversification. These patterns indicate possible directions for future research on host shifts.

Key to species of *Vararia* in China (35 species)

- | | |
|--|-------------------------|
| 1. Basidia with 2 sterigmata | 2 |
| 1. Basidia with 4 sterigmata | 3 |
| 2. Gloecystidia ventricose, thick-walled; basidiospores fusiform to cylindrical, 18–22 × 6–7.2 μm | <i>V. bispora</i> |
| 2. Gloecystidia subclavate to subcylindrical, sinuous, thin-walled; basidiospores ellipsoid to cylindrical, 10–13 × 4.2–5.2 μm | <i>V. amphithallica</i> |
| 3. Generative hyphae with clamp connections | 4 |
| 3. Generative hyphae with simple septa | 11 |
| 4. Basidiospores falcate, allantoid, or subcylindrical to cylindrical | 5 |
| 4. Basidiospores fusiform to broadly ellipsoid, or subglobose | 7 |
| 5. Gloecystidia densely encrusted with crystals | <i>V. miscanthi</i> |
| Gloeocystidia without crystals | 6 |

6. Basidiospores falcate; gloeocystidia subulate 35–65 × 8–13 µm	<i>V. falcata</i>
6. Basidiospores allantoid; gloeocystidia subcylindrical, elliptical to ovoid, 9–23 × 7–10.5 µm	<i>V. dawuishanensis</i>
7. Basidiospores with a suprahilar amyloid appendage	<i>V. investiens</i>
7. Basidiospores without amyloid appendage	8
8. Basidiospores > 15 µm long	9
8. Basidiospores ≤ 15 µm long	10
9. Basidiospores fusiform to ellipsoid, 15.8–17.5 × 5.9–7 µm; gloeocystidia capitate, 60–120 × 9–15 µm	<i>V. incarnata</i>
9. Basidiospores broadly ellipsoid with a beak-like extension, 18–23 × 9.5–13 µm; Gloeocystidia clavate, 50–100 × 4–9 µm	<i>V. montana</i>
10. Basidiospores ellipsoid, 7.5–9.5 × 4–5 µm; hymenial surface deeply cracked; gloeocystidia of two types (ventricose and obclavate)	<i>V. fissurata</i>
10. Basidiospores subglobose to spherical, 8–10 × 7.5–8.5 µm; gloeocystidia of one type (subcylindrical to fusiform)	<i>V. sphaericospora</i>
11. Basidiospores amyloid	12
11. Basidiospores inamyloid	20
12. Basidiospores > 20 µm long	<i>V. bambusicola</i>
12. Basidiospores ≤ 20 µm long	13
13. Rhizomorph present	<i>V. yunnanensis</i>
13. Rhizomorph absent	14
14. Basidiospores > 5 µm wide	15
14. Basidiospores ≤ 5 µm wide	19
15. Gloeocystidia thin-walled	16
15. Gloeocystidia thick-walled	17
16. Gloeocystidia urniform and fusiform	<i>V. membranacea</i>
16. Gloeocystidia subcylindrical to fusiform, and cylindrical to subclavate	<i>V. muscicola</i>
17. Gloeocystidia with 1–2 constrictions	<i>V. yingjiangensis</i>
17. Gloeocystidia without constrictions	18
18. Gloeocystidia clavate to cylindrical, with oil drops	<i>V. punctata</i>
18. Gloeocystidia subglobose and fusiform, without oil drops	<i>V. yaoshanensis</i>
19. Hymenial surface cream to buff, cracked; basidiospores broadly ellipsoid, 6–7.5 × 3.5–5 µm	<i>V. lacerata</i>
19. Hymenial surface white to cream, smooth; basidiospores subcylindrical to narrowly ellipsoid, 7.5–9.5 × 4–5 µm	<i>V. wumengshanensis</i>
20. Gloeocystidia of two or three types	21
20. Gloeocystidia of one type	23
21. Gloeocystidia of three types, cylindrical, subulate, and cylindrical to bottled shape	<i>V. tuberculata</i>
21. Gloeocystidia of two types	22
22. Basidiospores fusiform to ellipsoid, 11.8–16.1 × 5.6–7.7 µm	<i>V. bannaensis</i>
22. Basidiospores ellipsoid, 3.5–5.5 × 2.5–3.5 µm	<i>V. fragilis</i>
23. Acanthocystidia or septocystidia present	24
23. Acanthocystidia or septocystidia absent	25
24. Septocystidia present (with 3–5 transverse septa)	<i>V. septocystidiata</i>
24. Acanthocystidia present (densely covered with tuberculate spines)	<i>V. acanthocystidia</i>
25. Paraphyses present	<i>V. subulata</i>
25. Paraphyses absent	26
26. Basidiospores with a distinct beak-like extension	27
26. Basidiospores without a beak-like extension	28
27. Basidiospores subfusiform to navicular, 9–13 × 5–8 µm; gloeocystidia spindle to subcylindrical, 38–47 × 8–13 µm	<i>V. isabellina</i>
27. Basidiospores broadly ellipsoid, 6–11 × 4–6 µm; Gloeocystidia subulate, 17–35 × 6–7 µm	<i>V. sinensis</i>
28. Gloeocystidia subulate	29
28. Gloeocystidia not subulate	31
29. Basidiospores ≤ 7.5 µm long	<i>V. ambigua</i>
29. Basidiospores > 7.5 µm long	30
30. Basidiospores 7.5–8.1 × 4.6–5 µm; high altitude (ca. 2,600–2,875 m); on bamboo and wood	<i>V. alpina</i>
30. Basidiospores 7–7.9 × 3.1–3.6 µm; low altitude (ca. 700 m); strictly on <i>Bambusa emeiensis</i>	<i>V. emeiensis</i>
31. Gloeocystidia ≤ 25 µm long	32
31. Gloeocystidia > 25 µm long	<i>V. tenuata</i>
32. Basidia clavate or barrel-shaped	33
32. Basidia fusiform to subcylindrical	34
33. Basidia clavate, gloeocystidia subglobose, clavate to fusiform	<i>V. lincangensis</i>
33. Basidia barrel-shaped, gloeocystidia pyramidal	<i>V. pingbianensis</i>
34. Gloeocystidia fusiform to subcylindrical, basidiospores broadly ellipsoid, 2.5–4 × 1.5–2.5 µm	<i>V. asiana</i>
34. Gloeocystidia obclavate, basidiospores ellipsoid, 5.9–8.8 × 3.1–5.1 µm	<i>V. ferruginosa</i>

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Yuan Y; data collection: Yuan Y, Dai Y, Zhang X, Li M, Zhao Y, Cui Y, Luo K, Liu S, Zeng G, Wang C, Deng C, Li Z; analysis and interpretation of results: Zhang X, Dai Y, Li M, Zhao Y, Yuan Y; draft manuscript preparation: Zhang X, Dai Y, Yuan Y. All

authors reviewed the results and approved the final version of the manuscript.

Data availability

The phylogenetic datasets (including multiple sequence alignments for ITS, nLSU, RPB2, and *tef1-α*) and the resulting Maximum

Likelihood and Bayesian phylogenetic trees generated during the current study are available in the Figshare repository (doi: [10.6084/m9.figshare.31889623](https://doi.org/10.6084/m9.figshare.31889623))

Acknowledgments

This study was financed by the National Natural Science Foundation of China (Project Nos U23A20142, 32370013), the Yunnan Province Expert Workstation Program (No. 202205AF150014), the Yunnan Key Laboratory of Gastrodia and Fungi Symbiotic Biology, the Macrofungal Diversity of Qinghai Province (Project GHMB-2024-18), grants from the Hainan Province Science and Technology Special Fund (ZDYF2023RDYL01), the Hainan Institute of National Parks (HINP, KY-24ZK02), and the Key Laboratory of Breeding and Processing of Edible and Medicinal Mushrooms, Ministry of Agriculture and Rural Affairs, China.

Conflict of interest

Author Zhenhao Li was employed by the company Zhejiang Shouxiangu Pharmaceutical Co., Ltd. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary information accompanies this paper online at: <https://doi.org/10.48130/mycosphere-0026-0016>.

Dates

Received 9 April 2026; Revised 8 July 2026; Accepted 10 July 2026; Published online 18 August 2026

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