



Taxonomy and phylogeny of *Stereaceae* (*Russulales*, *Basidiomycota*): two new genera, nine new species and twenty new combinations

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molecular systematics
new taxa
white rot
wood-decaying fungi

Abstract: An in-depth study of the taxonomy and phylogeny of the *Stereaceae* was conducted. Specimens collected from East Asia were studied by using morphological and molecular systematic methods. The phylogenetic analyses were based on a concatenated ITS1-5.8S-ITS2 (ITS) and the D1–D2 domains of nuc 28S rDNA (LSU) sequence data of *Stereaceae* by using the maximum parsimony, maximum likelihood and Bayesian inference methods. Fourteen lineages including two new genera, *Confertotrama* and *Gelatinostereum*, are recognized in the phylogenetic tree. *Confertotrama*, typified by *Merulius rugulosus*, is segregated from *Gloeocystidiellum* s. lat. *Gelatinostereum* is sister to *Stereum* in the tree but differs in having gelatinous basidiomes and lacking thick-walled pseudocystidia. *Conferticium* is shown to be restricted to include species with smooth basidiospores, while species with ornamented basidiospores are nested within the *Gloeocystidiopsis* lineage. The delimitation of *Megalocystidium* is expanded based on the phylogenetic analyses. It includes species with or without clamp connections and acanthohyphidia and with a large variety of basidium size. *Neoaleurodiscus* is treated as a later synonym of *Aleurodiscus* sensu stricto, since their type species *N. fujii* and *A. amorphus* were nested within the same lineage. With this disposal, *Aleurodiscus* s. str. now includes species with smooth or ornamented basidiospores. The generic name, *Gloeomyces* is applied for the lineage of species of *Aleurodiscus* s. lat. with resupinate basidiomes, well-developed acanthohyphidia and smooth basidiospores, while *Acanthophysellum* is regarded as a synonym of *Xylobolus*. Nine new species, *Aleurodiscus globisporus*, *Conferticium subtropicum*, *Gelatinostereum phlebioides*, *Gloeocystidiopsis shenghuae*, *Gloeomyces subcerussatus*, *Megalocystidium brunneum*, *M. effusum*, *Stereum rhododendri* and *S. tropicum* are described and illustrated from China. Twenty new combinations, *Aleurodiscus fujii*, *Confertotrama aspella*, *Ca. macrospora*, *Ca. rugulosa*, *Ca. rajchenbergii*, *Gloeocystidiopsis ravum*, *Gs. tenuissimus*, *Gloeomyces bambusinus*, *G. bicornis*, *G. cerussatus*, *G. dextrinoideocerussatus*, *G. dextrinoideophyses*, *G. formosanus*, *G. parvisporus*, *G. persicus*, *G. thailandicus*, *G. thoenii*, *G. tropicus*, *Megalocystidium chinense* and *Xylobolus lividocoeruleus* are proposed. *Aleurodiscus isabellinus* is treated as a synonym of *Gloeomyces graminicola*. Morphological differences between closely related genera are discussed, and an identification key to all 14 genera of *Stereaceae* is presented.

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INTRODUCTION

The *Stereaceae*, typified by *Stereum*, formed a well-supported monophyletic clade in *Russulales* (Larsson & Larsson 2003, Miller *et al.* 2006, Larsson 2007). Species in the family are all saprobic, causing a white rot (or white pocket rot in some species) on both conifers and hardwoods. Although mushrooms and polypores are commonly present in different clades within the *Russulales*, so far *Stereaceae* contains only corticioid and stereoid wood-decaying fungi with a smooth or occasionally tuberculate or merulioid hymenophores. Micro-morphologically, all species in the family have gloeocystidia

(skeletocystidia in *Stereum*) and amyloid basidiospores with smooth or ornamented walls (Larsson & Larsson 2003, Bernicchia & Gorjón 2010).

Species in the family mostly belong to *Stereum*, *Xylobolus*, *Aleurodiscus* s. lat., and *Gloeocystidiellum* s. lat. While taxa of *Stereum* s. str. and *Xylobolus* formed monophyletic clades in published phylogenetic trees, the latter two genera were highly polyphyletic, which left the generic arrangements within *Stereaceae* partly unresolved (Wu *et al.* 2001, Larsson & Larsson 2003, Wu *et al.* 2010, Dai & He 2016, Phookamsak *et al.* 2019). Morphologically, species of *Aleurodiscus* s. lat. have cupulate, effused or effused-reflexed basidiomes, a



monomitic or dimitic hyphal system with simple-septate or clamped generative hyphae, smooth or ornamented, amyloid basidiospores and sterile organs such as acanthohyphidia, gloeocystidia and dendrohyphidia (Núñez & Ryvarden 1997). The genus is divided into several smaller genera according to different combinations of morphological characters, but their relationships are still unclear to a certain extent and some species formed single-species lineages without generic names. The situation in *Gloeocystidiellum* s. lat. is similar to *Aleurodiscus* s. lat., but its lineages have wider distributions in *Russulales* with only some species nested within *Stereaceae*. In recent years, many new taxa were described in *Stereaceae* from around the world (Gorjón *et al.* 2013, Dai & He 2016, 2017, Dai *et al.* 2017a, b, Ghobad-Nejhad & Langer 2018, Tian *et al.* 2018, Crous *et al.* 2019, Wu *et al.* 2019a, b, Cao & He 2020, Rajchenberg *et al.* 2021, Wu *et al.* 2022, Maekawa *et al.* 2023), but a complete taxonomy and phylogenetic study of the family focusing on the phylogenetic relationship at generic level is urgently needed. Thus, in the present study, we performed phylogenetic analyses of ITS-LSU sequences of *Stereaceae* that were newly generated from a large number of specimens collected from East Asia and combined with sequences from GenBank. We aim to build a natural and reasonable taxonomic system of *Stereaceae* based on the morphological and molecular evidence. This study is also a contribution to the exploration of species diversity of crust fungi in China.

MATERIALS AND METHODS

Morphological studies

Voucher specimens are deposited at the fungaria of Beijing Forestry University, Beijing, China (BJFC), Centre for Forest Mycology Research, U.S. Forest Service, Madison, Wisconsin, U.S.A. (CFMR), Iranian Research Organization for Science and Technology (ICH), and Beijing Museum of Natural History, Beijing, China (BJM). Freehand sections were made from dried basidiomes and mounted in 2 % (w/v) potassium hydroxide (KOH) with 1 % (w/v) phloxine, Melzer's reagent (IKI) or cotton blue (CB). Microscopic examinations were carried out with a Nikon Eclipse 80i microscope (Nikon Corporation, Japan) at magnifications up to 1000 ×. Drawings were made with the aid of a drawing tube. The following abbreviations are used: L = mean spore length, W = mean spore width, Q = L/W ratio, n (a/b) = number of spores (a) measured from number of specimens (b). Special colour terms follow Kornerup & Wanscher (1978). Fungarium code designations follow Index Herbarium (<http://sweetgum.nybg.org/science/ih/>).

DNA extraction and sequencing

A CTAB plant genomic DNA extraction kit DN14 (Aidlab Biotechnologies Co., Ltd, Beijing, China) was used to extract total genomic DNA from dried specimens, then amplified by the polymerase chain reaction (PCR), according to the manufacturer's instructions. The ITS1-5.8S-ITS2 region was amplified with the primer pair ITS5/ITS4 (White *et al.* 1990) using the following protocol: initial denaturation at 95 °C for

4 min, followed by 34 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and final extension at 72 °C for 10 min. The nrLSU D1–D2 region (LSU) was amplified with the primer pair LR0R/LR7 (Vilgalys & Hester 1990) employing the following procedure: initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min, and final extension at 72 °C for 10 min. DNA sequencing was performed at Beijing Genomics Institute, and the sequences generated in this study were deposited in GenBank (Table 1). BioEdit v. 7.0.5.3 (Hall 1999) was used to review the chromatograms and for contig assembly.

Phylogenetic analyses

The molecular phylogenetic analyses were inferred from a concatenated dataset of ITS and LSU sequences. *Laurilia sulcata* was selected as the outgroup. The ITS and LSU sequences were aligned separately using MAFFT v. 7 (Katoch *et al.* 2017) with the G-INS-I iterative refinement algorithm and optimized manually in BioEdit v. 7.0.5.3. The separate alignments were then concatenated using Mesquite v. 3.5.1 (Maddison & Maddison 2018). Sequence alignments were deposited at TreeBase (<https://treebase.org/treebase-web/home.html>; submission ID: 31514).

Maximum parsimony (MP), Maximum likelihood (ML) analyses and Bayesian inference (BI) were carried out by using PAUP v. 4.0b10 (Swofford 2002), RAxML v. 8.2.10 (Stamatakis 2014) and MrBayes v. 3.2.6 (Ronquist *et al.* 2012), respectively. In the MP analysis, trees were generated using 100 replicates of random stepwise addition of sequence and tree-bisection reconnection (TBR) branch-swapping algorithm with all characters given equal weights. Branch supports for all parsimony analyses were estimated by performing 1000 bootstrap replicates with a heuristic search of 10 random-addition replicates for each bootstrap replicate. In the ML analysis, statistical support values were obtained using rapid bootstrapping with 1000 replicates, with default settings used for other parameters. For BI, the best-fit substitution model was estimated with jModeltest v. 2.17 (Darriba *et al.* 2012). Four Markov chains were run for 8 M generations until the split deviation frequency value was lower than 0.01. Trees were sampled every 100 generations. The first quarter of the trees, which represented the burn-in phase of the analyses, were discarded, and the remaining trees were used to calculate posterior probabilities (BPP) in the majority rule consensus tree.

RESULTS

Phylogenetic analyses

The concatenated ITS-LSU dataset contained 103 ITS and 116 LSU sequences from 121 samples representing 87 *Stereaceae* taxa and the outgroup (Table 1). The dataset had an aligned length of 2122 characters, of which 551 were parsimony-informative. MP analysis yielded 5000 equally most parsimonious trees (TL = 3138, CI = 0.411, RI = 0.731, RC = 0.301, HI = 0.589). jModelTest suggested GTR+I+G to be the best-fit models of nucleotide evolution for BI. The average

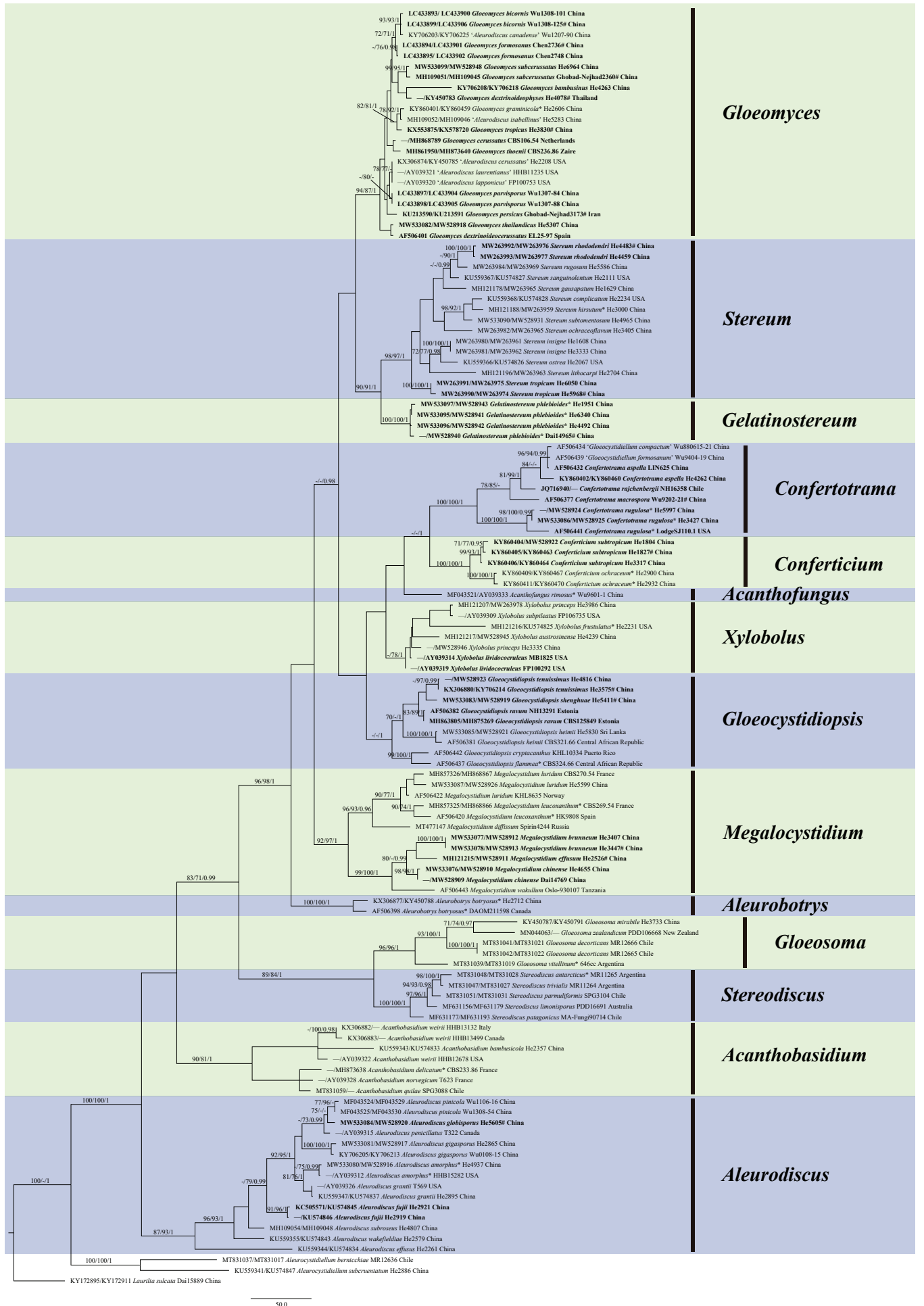


Fig. 1. Phylogenetic tree obtained from maximum parsimony analysis of ITS-LSU sequence data of Stereaceae. Branches are labelled with parsimony bootstrap values (≥ 70 %, first), maximum likelihood bootstrap values (≥ 70 %, middle) and Bayesian posterior probabilities (≥ 0.95, last). Type species of each genus are marked with an asterisk “*”. New taxa are shown in bold with type specimens marked with a number sign “#”.



Table 1. Species and sequences used in the phylogenetic analyses. New taxa are in **bold** with type specimens indicated with a number sign “#”.

Taxon	Voucher	Locality	ITS	LSU	Reference
<i>Acanthobasidium bambusicola</i>	He2357	China	KU559343	KU574833	Dai & He (2016)
<i>Ac. delicatum</i>	CBS 233.86	France	—	MH873638	Vu <i>et al.</i> (2018)
<i>Ac. norvegicum</i>	T623	France	—	AY039328	Wu <i>et al.</i> (2001)
<i>Ac. quiliae</i>	SPG3088	Chile	MT831059	—	Rajchenberg <i>et al.</i> (2021)
<i>Ac. weirii</i>	HHB13132	Italy	KX306882	—	Dai <i>et al.</i> (2017a)
	HHB13499	Canada	KX306883	—	Dai <i>et al.</i> (2017a)
	HHB12678	USA	—	AY039322	Wu <i>et al.</i> (2001)
<i>Acanthofungus rimosus</i>	Wu9601-1	China	MF043521	AY039333	Wu <i>et al.</i> (2019a)
<i>Aleurocystidiellium berricchiaiae</i>	MR12636	Chile	MT831037	MT831017	Rajchenberg <i>et al.</i> (2021)
<i>Al. subcruentatum</i>	He2886	China	KU559341	KU574847	Dai & He (2016)
<i>Aleurobotrys botryosus</i>	He2712	China	KX306877	KY450788	Dai <i>et al.</i> (2017b)
	DAOM211598	Canada	AF506398	AF506398	Larsson & Larsson (2003)
<i>Aleurodiscus amorphus</i>	He4937	China	MW533080	MW528916	This study
	HHB15282	USA	—	AY039312	Wu <i>et al.</i> (2001)
<i>A. canadensis</i>	Wu1207-90	China	KY706203	KY706225	Dai & He (2017)
<i>A. cerussatum</i>	He2208	USA	KX306874	KY450785	Dai <i>et al.</i> (2017a)
<i>A. effusus</i>	He2261	China	KU559344	KU574834	Dai & He (2016)
<i>A. fujii</i>	He2919	China	—	KU574846	Dai & He (2016)
	He2921	China	KC505571	KU574845	Dai & He (2016)
<i>A. gigasporus</i>	He2865	China	MW533081	MW528917	This study
	Wu0108-15	China	KY706205	KY706213	Dai & He (2017)
	He5605[#]	China	MW533084	MW528920	This study
<i>A. grantii</i>	T569	USA	—	AY039326	Wu <i>et al.</i> (2001)
	He2895	China	KU559347	KU574837	Dai & He (2016)
<i>A. isabellinus</i>	He5283	China	MH109052	MH109046	Tian <i>et al.</i> (2018)
<i>A. lapponicus</i>	FP100753	USA	—	AY039320	Wu <i>et al.</i> (2001)
<i>A. laurentianus</i>	HHB11235	USA	—	AY039321	Wu <i>et al.</i> (2001)
<i>A. penicillatus</i>	T322	Canada	—	AY039315	Wu <i>et al.</i> (2001)
<i>A. pinicola</i>	Wu1106-16	China	MF043524	MF043529	Wu <i>et al.</i> (2019a)
	Wu1308-54	China	MF043525	MF043530	Wu <i>et al.</i> (2019a)
<i>A. subroseus</i>	He4807	China	MH109054	MH109048	Tian <i>et al.</i> (2018)
<i>A. wakefieldiae</i>	He2579	China	KU559355	KU574843	Dai & He (2016)
<i>Conferticulum ochraceum</i>	He2900	China	KY860409	KY860467	Liu (2017)
	He2932	China	KY860411	KY860470	Liu (2017)

Table 1. (Continued).

Taxon	Voucher	Locality	ITS	LSU	Reference
<i>Cm. subtropicum</i>	He1827 [#]	China	KY860405	KY860463	Liu (2017)
	He1804	China	KY860404	MW528922	This study
	He3317	China	KY860406	KY860464	Liu (2017)
	He4262	China	KY860402	KY860460	Liu (2017)
<i>Conferotrama aspella</i>	LIN625	China	AF506432	AF506432	Larsson & Larsson (2003)
	Wu9202-21 [#]	China	AF506377	AF506377	Larsson & Larsson (2003)
<i>Ca. macrospora</i>	NH16358	Chile	JQ716940	—	Gorjón & Hallenberg (2013)
<i>Ca. rajchenbergii</i>	He5997	China	—	MW528924	This study
<i>Ca. rugulosa</i>	He3427	China	MW533086	MW528925	This study
<i>Gelatinostereum phlebioides</i>	LodgeSJ110.1	USA	AF506441	AF506441	Larsson & Larsson (2003)
	He1951	China	MW533097	MW528943	This study
	He6340	China	MW533095	MW528941	This study
	He4492	China	MW533096	MW528942	This study
	Dai14965 [#]	China	—	MW528940	This study
	Wu880615-21	China	AF506434	AF506434	Larsson & Larsson (2003)
	Wu9404-19	China	AF506439	AF506439	Larsson & Larsson (2003)
<i>Gloeocystidiopsis cryptacanthus</i>	KHL10334	Puerto Rico	AF506442	AF506442	Larsson & Larsson (2003)
	CBS 324.66	Central African Republic	AF506437	AF506437	Larsson & Larsson (2003)
<i>Gs. flammea</i>	He5830	Sri Lanka	MW533085	MW528921	This study
<i>Gs. heimii</i>	CBS 321.66	Central African Republic	AF506381	AF506381	Larsson & Larsson (2003)
	NH13291	Estonia	AF506382	AF506382	Larsson & Larsson (2003)
<i>Gs. ravum</i>	CBS 125849	Estonia	MH863805	MH875269	Vu <i>et al.</i> (2018)
<i>Gs. shenghuae</i>	He5411 [#]	China	MW533083	MW528919	This study
	He4816	China	—	MW528923	This study
<i>Gs. tenuissimus</i>	He3575 [#]	China	KX306880	KY706214	Dai <i>et al.</i> (2017a)
	He4263	China	KY706208	KY706218	Tian <i>et al.</i> (2018)
<i>Gloeomyces bambusinus</i>	Wu1308-101	China	LC433893	LC433900	Wu <i>et al.</i> (2022)
	Wu1308-125 [#]	China	LC433899	LC433906	Wu <i>et al.</i> (2022)
<i>G. cerussatum</i>	CBS 106.54	Netherlands	—	MH868789	Vu <i>et al.</i> (2018)
<i>G. dextrinoideocerussatus</i>	EL25-97	Spain	AF506401	AF506401	Larsson & Larsson (2003)
<i>G. dextrinoideophyses</i>	He4078 [#]	Thailand	—	KY450783	Dai <i>et al.</i> (2017b)
	Chen2736 [#]	China	LC433894	LC433901	Wu <i>et al.</i> (2022)
<i>G. formosanus</i>	Chen2748	China	LC433895	LC433902	Wu <i>et al.</i> (2022)
<i>G. graminicola</i>	He2606	China	KY860401	KY860459	Liu (2017)



Table 1. (Continued).

Taxon	Voucher	Locality	ITS	LSU	Reference
<i>G. parvisporus</i>	Wu1307-84	China	LC433897	LC433904	Wu <i>et al.</i> (2022)
	Wu1307-88	China	LC433898	LC433905	Wu <i>et al.</i> (2022)
<i>G. persicus</i>	Ghobad-Nejhad3173*	China	KU213590	KU213591	Ghobad-Nejhad & Langer (2018)
<i>G. subcerussatus</i>	He6964	China	MW533099	MW528948	This study
	Ghobad-Nejhad2360*	China	MH109051	MH109045	Tian <i>et al.</i> (2018)
<i>G. thailandicus</i>	He5307	China	MW533082	MW528918	This study
<i>G. thoenii</i>	CBS 236.86	Zaire	MH861950	MH873640	Vu <i>et al.</i> (2018)
<i>G. tropicus</i>	He3830*	China	KX553875	KX578720	Dai <i>et al.</i> (2017a)
<i>Gloeosoma decorticans</i>	MR12666	Chile	MT831041	MT831021	Rajchenberg <i>et al.</i> (2021)
	MR12665	Chile	MT831042	MT831022	Rajchenberg <i>et al.</i> (2021)
<i>Ga. mirabilis</i>	He3733	China	KY450787	KY450791	Dai <i>et al.</i> (2017b)
<i>Ga. zealandicus</i>	PDD106668	New Zealand	MN044063	—	—
<i>Ga. vitellinum</i>	646cc	Argentina	MT831039	MT831019	Rajchenberg <i>et al.</i> (2021)
<i>Megalocystidium brunneum</i>	He3407	China	MW533077	MW528912	This study
	He3447*	China	MW533078	MW528913	This study
<i>M. chinense</i>	He4655	China	MW533076	MW528910	This study
	Dai14769	China	—	MW528909	This study
<i>M. diffissum</i>	Spirin 4244 (H)	Russia	MT477147	MT477147	Spirin <i>et al.</i> (2021)
<i>M. effusum</i>	He2526*	China	MH121215	MW528911	Zhao (2018)
<i>M. leucoxanthum</i>	CBS 269.54	France	MH857325	MH868866	Vu <i>et al.</i> (2018)
	HK9808	Spain	AF506420	AF506420	Larsson & Larsson (2003)
<i>M. luridum</i>	KHL8635	Norway	AF506422	AF506422	Larsson & Larsson (2003)
	CBS 270.54	France	MH857326	MH868867	Vu <i>et al.</i> (2018)
	He5599	China	MW533087	MW528926	This study
<i>M. wakullum</i>	Oslo-930107	USA	AF506443	AF506443	Larsson & Larsson (2003)
<i>Stereodiscus antarcticus</i>	MR11265	Argentina	MT831048	MT831028	Rajchenberg <i>et al.</i> (2021)
<i>St. limonisporus</i>	PDD16691	Australia	MF631156	MF631179	Unpublished
<i>St. parmuliniformis</i>	SPG3104	Chile	MT831051	MT831031	Rajchenberg <i>et al.</i> (2021)
<i>St. patagonicus</i>	MA-Fungi 90714	Chile	MF631177	MF631193	—
<i>St. trivialis</i>	MR11264	Argentina	MT831047	MT831027	Rajchenberg <i>et al.</i> (2021)
<i>Stereum complicatum</i>	He2234	USA	KU559368	KU574828	Dai & He (2016)
<i>S. gausapatum</i>	He1629	China	MH121178	MW263965	Zhao (2018)
<i>S. hirsutum</i>	He3000	China	MH121188	MW263959	Zhao (2018)
<i>S. insigne</i>	He1608	China	MW263980	MW263961	Cao (2022)

Table 1. (Continued).

Taxon	Voucher	Locality	ITS	LSU	Reference
	He3333	China	MW263981	MW263962	Cao (2022)
<i>S. lithocarp</i>	He2704	China	MH121196	MW263963	Zhao (2018)
<i>S. ochraceoflavum</i>	He3405	China	MW263982	MW263965	Cao (2022)
<i>S. ostrea</i>	He2067	USA	KU559366	KU574826	Dai & He (2016)
<i>S. rhododendri</i>	He4483[#]	China	MW263992	MW263976	This study
	He4459	China	MW263993	MW263977	This study
<i>S. rugosum</i>	He5586	China	MW263984	MW263969	Cao (2022)
<i>S. sanguinolentum</i>	He2111	USA	KU559367	KU574827	Dai & He (2016)
<i>S. subtomentosum</i>	He4965	China	MW533090	MW528931	This study
<i>S. tropicum</i>	He5968[#]	China	MW263990	MW263974	This study
	He6050	China	MW263991	MW263975	This study
<i>Xylobolus annosus</i>	He3986	China	MH121207	MW263978	Cao & He (2020)
<i>X. austrosinense</i>	He4239	China	MH121217	MW528945	Cao & He (2020)
<i>X. frustulatus</i>	He2231	USA	MH121216	KU574825	Dai & He (2016)
<i>X. lividocoeruleus</i>	MB1825	USA	—	AY039314	Wu et al. (2001)
	FP100292	USA	—	AY039319	Wu et al. (2001)
<i>X. princeps</i>	He3335	China	—	MW528946	This study
<i>X. subpileatus</i>	FP106735	USA	—	AY039309	Wu et al. (2001)
Outgroup					
<i>Laurilia sulcata</i>	Dai15889	China	KY172895	KY172911	Liu et al. (2017)



standard deviation of split frequencies of BI was 0.008871 at the end of the run. The ML and BI analyses resulted in almost identical tree topologies compared to the MP analysis. Only the MP tree is provided in Fig. 1 with the parsimony bootstrap values ($\geq 70\%$, first), maximum likelihood bootstrap values ($\geq 70\%$, middle) and Bayesian posterior probabilities (≥ 0.95 , last) labelled along the branches. In the tree, 14 distinct lineages, viz. *Acanthobasidium*, *Acanthofungus*, *Aleurobotrys*, *Aleurodiscus* s. str., *Conferticium*, *Confertotrama*, *Gelatinostereum*, *Gloeocystidiopsis*, *Gloeomyces*, *Gloeosoma*, *Megalocystidium*, *Stereodiscus*, *Stereum* and *Xylobolus* were recognized. Nine new species, namely *Aleurodiscus globisporus*, *Conferticium subtropicum*, *Gelatinostereum phlebioides*, *Gloeocystidiopsis shenghuae*, *Gloeomyces subcerussatus*, *Megalocystidium brunneum*, *M. effusum*, *Stereum rhododendri* and *S. tropicum*, formed distinct lineages.

Taxonomy

In cases where confusion could arise due to the use of the same first letter abbreviation for the genus name, the following abbreviations are used in the text: *Acanthophysellum* (Ap.), *Acanthophysium* (Am.), *Aleurodiscus* (A.), *Conferticium* (Cm.), *Confertotrama* (Ca.), *Corticium* (C.), *Gelatinostereum* (Ge.), *Gloeocystidiopsis* (Gs.), *Gloeomyces* (G.), *Gloeosoma* (Ga.), *Stereodiscus* (St.), and *Stereum* (S.).

Key to genera of Stereaceae

- | | |
|---|---|
| 1a. Basidiospores ornamented..... | 2 |
| 1b. Basidiospores smooth | 10 |
| 2a. Generative hyphae simple-septate..... | 3 |
| 2b. Generative hyphae nodose-septate | 6 |
| 3a. Acanthohyphidia absent | 4 |
| 3b. Acanthohyphidia present | 5 |
| 4a. Basidiospores $\leq 12 \mu\text{m}$ long | <i>Gloeocystidiopsis</i> |
| 4b. basidiospores $\geq 12 \mu\text{m}$ long | <i>Aleurodiscus amorphus</i> |
| 5a. Acanthohyphidia with an amyloid reaction..... | <i>Aleurobotrys</i> |
| 5b. Acanthohyphidia without an amyloid reaction..... | <i>Aleurodiscus pinicola</i> |
| 6a. Acanthohyphidia absent | 7 |
| 6b. Acanthohyphidia present | 8 |
| 7a. Basidiospores $< 20 \mu\text{m}$ long | <i>Confertotrama</i> |
| 7b. Basidiospores $> 20 \mu\text{m}$ long | <i>Aleurodiscus grantii</i> |
| 8a. Basidiomes resupinate, usually on monocotyledons..... | <i>Acanthobasidium</i> |
| 8b. Basidiomes discoid, cupulate to resupinate, usually on dicotyledons | 9 |
| 9a. Distributed in Northern Hemisphere | <i>Aleurodiscus</i> spp., <i>Gloeosoma mirabile</i> |
| 9b. Distributed in Southern Hemisphere..... | <i>Gloeosoma</i> |

Stereaceae Pilát, *Hedwigia* 70: 34. 1930.

Type genus: Stereum Hill ex Pers. 1794.

Basidiomes annual or perennial, effused, resupinate, cupulate to effuse-reflexed to pileate, adnate, membranaceous, coriaceous, ceraceous, or gelatinous. *Pilei* (if present) initially tomentose, in most species becoming glabrous with age. *Hymenophore* smooth or tuberculate. *Hyphal system* monomitic or dimitic, generative hyphae simple-septate or nodose-septate, skeletal hyphae thick-walled, hyaline to yellowish. *Subiculum* indistinct or absent in some genera. *Gloeocystidia* present in all genera, *acanthohyphidia*, *skeletocystidia* and *acutocystidia* present in some species. *Basidia* clavate to subcylindrical, smooth or with spines, thin- to thick-walled, with two or four sterigmata. *Basidiospores* usually cylindrical, allantoid or ellipsoid, thin- to thick-walled, smooth or ornamented, amyloid, acyanophilous.

Notes: Species in *Stereaceae* are saprotrophs causing a white rot on various deciduous and coniferous trees. The *Stereaceae* clade received strong support values in the phylogenetic analyses of *Russulales* (Larsson & Larsson 2003, Miller *et al.* 2006, Larsson 2007). In the present study, 14 lineages within *Stereaceae*, viz. *Acanthobasidium*, *Acanthofungus*, *Aleurobotrys*, *Aleurodiscus*, *Conferticium*, *Confertotrama*, *Gelatinostereum*, *Gloeocystidiopsis*, *Gloeomyces*, *Gloeosoma*, *Megalocystidium*, *Stereodiscus*, *Stereum* and *Xylobolus*, were supported as monophyletic genera. Although several lineages of *Aleurodiscus* s. lat. are confirmed, this group still needs further analysis with more taxa to be sequenced and analysed.

10a. Basidiospores thick-walled	<i>Aleurodiscus fujii</i>
10b. Basidiospores thin-walled.....	11
11a. Acanthohyphidia absent.....	12
11b. Acanthohyphidia present	17
12a. Basidia repetitive	<i>Conferticum</i>
12b. Basidia not repetitive	13
13a. Basidiomes strictly resupinate.....	14
13b. Basidiomes resupinate, cupulate to stereoid.....	15
14a. Basidiomes subceraceous with a tight context.....	<i>Confertotrama rugulosa</i>
14b. Basidiomes membranaceous with a rather loose context	<i>Megalocystidium</i>
15a. Basidiospores $\geq 12 \mu\text{m}$ long	<i>Stereodiscus</i>
15b. Basidiospores $< 12 \mu\text{m}$ long	16
16a. Basidiomes coriaceous; pseudocystidia present.....	<i>Stereum</i>
16b. Basidiomes gelatinous when juvenile; pseudocystidia absent	<i>Gelatinostereum</i>
17a. Generative hyphae nodose-septate	18
17b. Generative hyphae simple-septate.....	20
18a. Basidiomes pulvinate, thick	<i>Acanthofungus</i>
18b. Basidiomes effused, thin	19
19a. Basidiomes usually with a bluish tint	<i>Xylobolus lividocoeruleus</i>
19b. Basidiomes usually without a bluish tint	<i>Gloeomyces</i>
20a. Subiculum thin	21
20b. Subiculum well-developed.....	22
21a. Causing a white pocket rot	<i>Xylobolus</i>
21b. Causing a typical white rot.....	<i>Gloeomyces</i>
22a. Basidiospores cylindrical, large	<i>Megalocystidium</i>
22b. Basidiospores ellipsoid to cylindrical, relatively small.....	<i>Stereum</i>

Aleurodiscus fujii (Sheng H. Wu) S.H. He & Y.L. Xu, **comb. nov.** MB 844714.

Basionym: *Neoaleurodiscus fujii* Sheng H. Wu, *Mycologia* **102**: 219. 2010.

Notes: Wu *et al.* (2010) described the new genus, *Neoaleurodiscus*, based on the type species *N. fujii* collected from Mount Fuji in Japan on *Rhododendron*, and later Dai & He (2016) also found it in southwestern China. Morphologically, the genus mainly differs from *Aleurodiscus* s. str. by having thick-walled smooth basidiospores. However, the phylogenetic results of the present study and Rajchenberg *et al.* (2021) showed that *N. fujii* was nested within the *Aleurodiscus* s. str. lineage with strong support values. According to the above phylogenetic delimitation of *Aleurodiscus* s. str., the genus is still morphologically heterogenous with simple- or nodose-septate hyphae, smooth or ornamented basidiospores, and with or without acanthohyphidia. More evidence is needed to prove whether this delimitation of *Aleurodiscus* s. str. is natural and reasonable.

Aleurodiscus globisporus S.H. He, **sp. nov.** MB 843409. Fig. 2.

Etymology: The species epithet “*globisporus*” refers to the globose basidiospores.

Typus: **China**, Guizhou Province, Yinjiang County, Fanjingshan Nature Reserve, on dead branch of *Taxus chinensis*, 12 Jul. 2018, S.H. He, He 5605 (**holotype** BJFC 026667).

Basidiomes annual, resupinate, cupulate to effuse-reflexed with slightly elevated margin, adnate, easily separated from the substrate, coriaceous, small, up to 2 cm long, 1 cm wide, 400–500 μm thick. **Hymenophore** smooth, pruinose, light orange [5A(3–4)] to greyish orange [5B(3–6)], turning reddish brown in KOH, uncracked; **margin** slightly elevated and curved towards the hymenophore after drying, thinning out, slightly fimbriate, paler or concolourous with hymenophore.

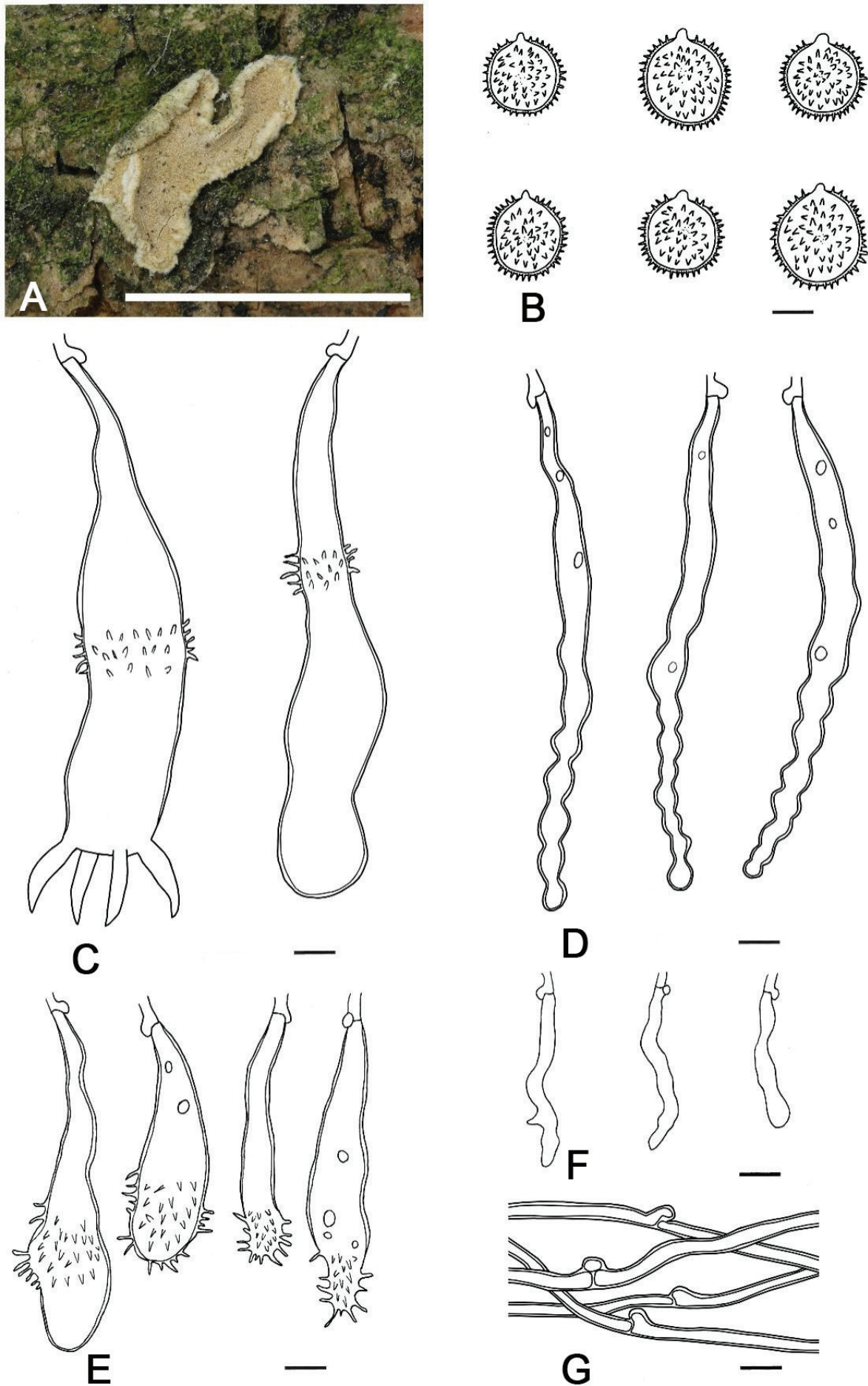


Fig. 2. *Aleurodiscus globisporus* He 5605 (BJFC 026667, holotype). **A.** Basidioma. **B.** Basidiospores. **C.** Basidium and a basidiole. **D.** Acanthocystidia. **E.** Gloeocystidia. **F.** Hyphidia. **G.** Generative hyphae from subiculum. Scale bars: A = 1 cm; B–G = 10 μ m.

Context greyish white, up to 0.4 mm thick. *Hyphal system* monomitic; all hyphae with clamp connections. *Subiculum* indistinct; hyphae colourless, thick-walled, smooth, loosely interwoven, rarely branched, moderately septate, 2–4 µm diam. *Subhymenium* distinct, thickening; hyphae colourless, slightly thick-walled, smooth, moderately branched and septate, interwoven, more or less vertically arranged, 3–4 µm diam. *Gloeocystidia* moniliform, with several contractions at the apex, colourless, slightly thick-walled, smooth, with a basal clamp connection, SA–, embedded, 65–140 × 8–10 µm. *Acanthocystidia* numerous, variable in shape and size, mostly clavate, with many spines at the apical part, colourless, slightly thick-walled, with a basal clamp connection, embedded, 50–85 × 5–25 µm. *Hyphidia* numerous, colourless, thin-walled,

smooth, rarely branched. *Basidia* clavate, with many spines at the middle part, colourless, slightly thick-walled, with four sterigmata up to 25 µm long, with a basal clamp connection, 80–120 × 20–28 µm; *basidioles* numerous, in shape similar to basidia, but slightly smaller. *Basidiospores* subglobose to globose, with a prominent apiculus, colourless, with walls up to 1 µm thick, distinctly echinulate, strongly amyloid, acyanophilous, 18–24 × 17.5–22 µm, L = 20.4 µm, W = 19.7 µm, Q = 1.04 (n = 30/1).

Notes: *Aleurodiscus globisporus* is characterized by cupulate basidiomes, clamped generative hyphae, moniliform gloeocystidia, acanthocystidia and large, globose and echinulate basidiospores. In the phylogenetic tree, *A.*

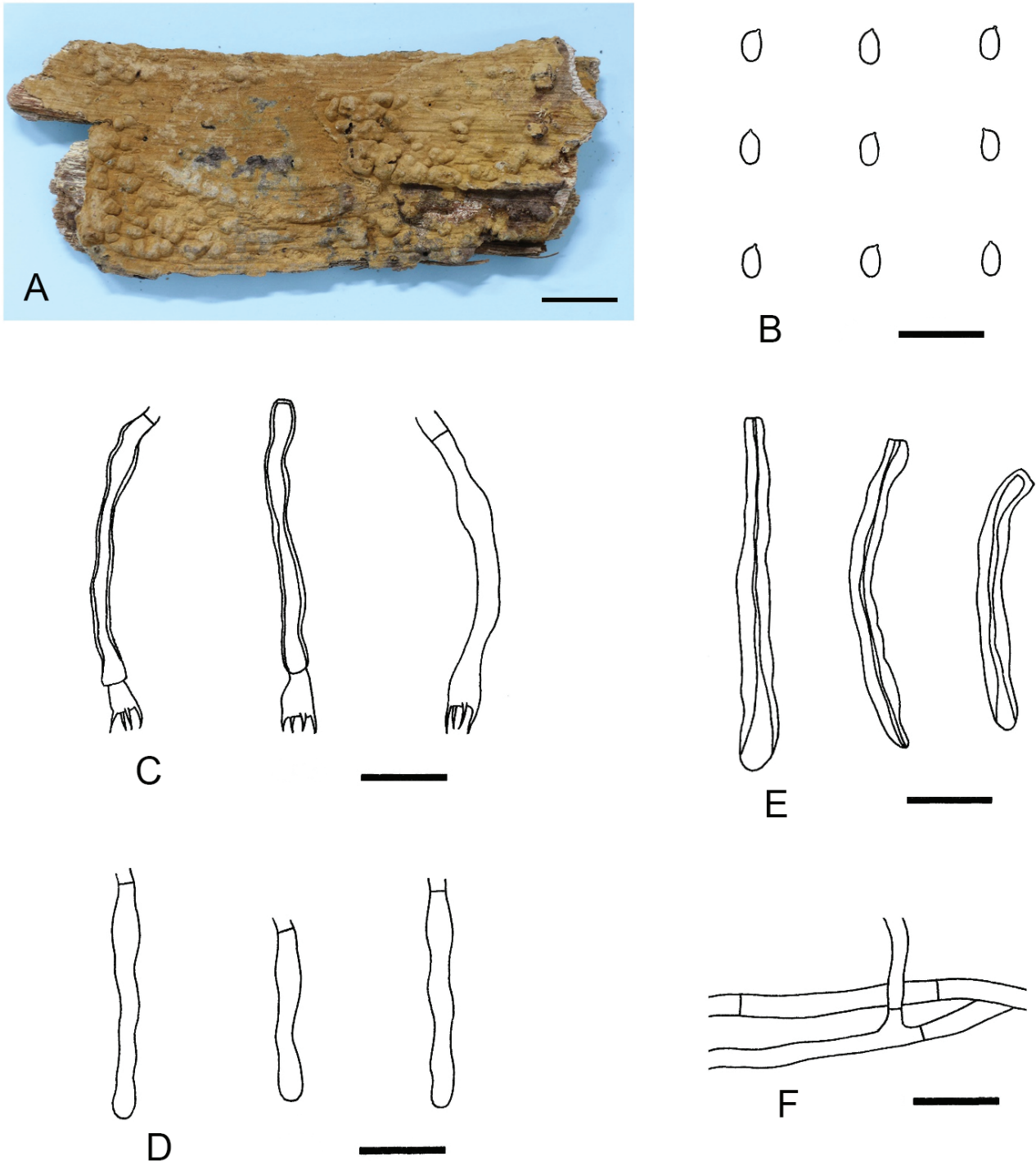


Fig. 3. *Conferticum subtropicum* He 1827 (BJFC 016294, holotype). **A.** Basidiomes. **B.** Basidiospores. **C.** Basidia. **D.** Basidioles. **E.** Pseudocystidia. **F.** Generative hyphae from subiculum. Scale bars: A = 1 cm; B–F = 10 µm.



globisporus nested within the *Aleurodiscus* s. str. lineage, and is closely related to *A. pinicola* and *A. penicillatus*. *Aleurodiscus pinicola* is similar to *A. globisporus* in many aspects but differs in having simple-septate hyphae and slightly larger basidiospores (22.5–27.5 × 19–24 µm; Wu *et al.* 2019a). *Aleurodiscus penicillatus* differs from *A. globisporus* by having less distinct and shorter moniliform gloeocystidia (50–75 µm long) and smaller basidiospores (15–20 × 13–17 µm; Núñez & Ryvarden 1997).

Conferticum subtropicum S.H. He & S.L. Liu, *sp. nov.* MB 843411. Fig. 3.

Etymology: The species epithet “*subtropicum*” refers to the distribution in subtropical areas in southern China.

Typus: **China**, Zhejiang Province, Kaihua County, Gutianshan Nature Reserve, on fallen angiosperm trunk, 13 Aug. 2013, S.H. He, He 1827 (**holotype** BJFC 016294, **isotypes** in BJM, CFMR).

Basidiomes annual, resupinate, effused, closely adnate, inseparable from substrate, coriaceous to crustose, up to 40 cm long, 6 cm wide, 100–200 µm thick. *Hymenophore* smooth to slightly tuberculate with scattered small tubercles, greyish orange [6B(3–6)], brownish orange [6C(4–8)] to light brown [6D(4–8)], immediately turning black in KOH, uncracked or densely cracked with age; *margin* thinning out, indistinct, usually indeterminate, concolourous with hymenophore. *Hyphal system* monomitic; all hyphae without clamps. *Subiculum* indistinct; *subhymenium* thickening, with a compact texture; *generative hyphae* colourless, thin-walled, smooth, interwoven, moderately branched and septate, 2–4 µm diam. *Pseudocystidia* numerous, originated from the base of subhymenium, stretched to hymenium, hyphoid, colourless to pale yellow, distinctly thick-walled, with a narrow lumen often enlarged at apex, smooth, dextrinoid, cyanophilous, vertically arranged, 5–6 µm diam. *Basidia* clavate, colourless, thin- to thick-walled, smooth, repetitive, often projecting beyond the hymenium, with one to several constrictions, with four sterigmata and a basal simple septum, 35–55 × 4–6 µm; *basidioles* dominant, in shape similar to basidia, but slightly smaller. *Basidiospores* ellipsoid, colourless, thin-walled, smooth, amyloid, acyanophilous, (4–)4.5–5 × 2.5–3 µm, L = 4.7 µm, W = 2.7 µm, Q = 1.7 (n = 40/2).

Additional specimens examined: **China**, Hunan Province, Dong'an County, Shunhuangshan Nature Reserve, on fallen angiosperm branch, 13 Jul. 2015, S.H. He, He 2387 (BJFC 020841, CFMR); Jiangxi Province, Lianping County, Jiulianshan Nature Reserve, on fallen angiosperm trunk, 14 Aug. 2016, S.H. He, He 4373 (BJFC 023814, CFMR); Yunnan Province, Lushui County, Gaoligongshan Nature Reserve, on fallen angiosperm trunk, 28 Nov. 2015, S.H. He, He 3317 (BJFC 021712, CFMR); Binchuan County, Jizhushan Nature Reserve, on stump of *Quercus*, 30 Aug. 2015, S.H. He, He 2814 (BJFC 026769) & He 2833 (BJFC 026770); Zhejiang Province, Kaihua County, Gutianshan Nature Reserve, on fallen angiosperm trunk, 12 Aug. 2013, S.H. He, He 1804 (BJFC 016271).

Notes: *Conferticum subtropicum* is characterized by yellow to brown basidiomes, numerous pseudocystidia and smooth basidiospores. In the phylogenetic tree (Fig. 1), *Cm. subtropicum* formed a strongly supported lineage sister to *Cm. ochraceum*, the type species of the genus. Morphologically, *Cm. ochraceum* differs from *Cm. subtropicum* by having typical gloeocystidia, enclosed basidia and a distribution in temperate areas mainly on gymnosperm trees (Wu 1996).

Confertotrama Nakasone & S.H. He, *gen. nov.* MB 843412.

Etymology: The genus epithet “*Confertotrama*” refers to the compact and agglutinated context.

Basidiomes annual, resupinate, effused, closely adnate, subceraceous to crustose. *Hymenophore* smooth or tuberculate, yellow, orange to ochraceous, uncracked or densely cracked with age; *margin* determinate, abrupt or thinning out, sometimes loosening from the substrate, paler or concolourous with hymenophore. *Context* yellowish white, with compact and agglutinated texture. *Hyphal system* monomitic; all *hyphae* with clamps, colourless, thin- to slightly thick-walled, smooth, rarely branched, moderately septate. *Gloeocystidia* numerous, vesicular, tubular to subulate, large, thin- to thick-walled, smooth, often with yellowish contents, turning bluish black in sulphovanillin, embedded or slightly projecting beyond the hymenium. *Basidia* clavate, colourless, thin-walled, smooth, with four sterigmata and a basal clamp. *Basidiospores* ellipsoid, oblong ellipsoid to cylindrical, colourless, thin-walled, smooth or ornamented, distinctly amyloid, acyanophilous.

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

Notes: Larsson & Larsson (2003) indicated that *Megalocystidium chelidonium*, *Boidinia macrospora*, *Gloeocystidiellum aspellum*, *Gm. compactum* and *Gm. formosanum* formed a strongly supported lineage (/ *chelidonium*) in *Stereaceae*. Our phylogenetic analyses also recovered this lineage (Fig. 1). Morphologically, these species have some similar characteristic features, such as yellowish basidiomes with compact texture, clamped generative hyphae and numerous large gloeocystidia with a positive sulphovanillin reaction. Basidiospores are reported as smooth in *M. chelidonium* and verrucose to indistinctly verrucose in the other species (Wu 1996, Boidin *et al.* 1997). Since there are no other morphological characters that can be used to separate *M. chelidonium* from other species in this lineage, we treat the lineage as a single genus and propose the new generic name *Confertotrama*.

Confertotrama aspella (Hjortstam) Nakasone & S.H. He, *comb. nov.* MB 843413. Figs 4A, B.

Basionym: *Gloeocystidiellum aspellum* Hjortstam, *Mycotaxon* 28: 27. 1987.

Specimens examined: **China**, Anhui Province, Qimen County, Guniujiang Nature Reserve, 10 Aug. 2013, S.H. He, He 1773 (BJFC 016240); Fujian Province, Wuyishan County, Wuyishan Nature Reserve, on fallen angiosperm trunk, 17

Aug. 2016, *S.H. He*, He 4466 (BJFC 023907), 6 Apr. 2018, *S.H. He*, He 5370 (BJFC 026431); Guangdong Province, Renhua County, Danxiashan Nature Reserve, on fallen angiosperm trunk, 4 Jun. 2019, *S.H. He*, He 5852 (BJFC 030727); Hubei Province, Wufeng County, Chaibuxi Forest Park, on dead angiosperm branch, 15 Aug. 2017, *S.H. He*, He 5049 (BJFC 024567); Jiangxi Province, Yifeng County, Guanshan Nature Reserve, on fallen angiosperm trunk, 10 Aug. 2016, *S.H. He*, He 4262 (BJFC 023704); Taiwan, Nantou County, Nandongyan Mountains, on fallen angiosperm branch, 7 Dec. 2016, *S.H. He*, He 4613 (BJFC 024055); Zhejiang Province, Qingyuan County, Tiantang Mountains, on fallen angiosperm trunk, Aug. 2013, *S.H. He*, He 2041 (BJFC 016510). **Vietnam**, Lam Dong Province, Bi Doup Nui Ba National Park, on fallen trunk of *Quercus*, 14 Oct. 2017, *S.H. He*, He 5247 (BJFC 024765), He 5262 (BJFC 024780), He 5266 (BJFC 024784) & He 5270 (BJFC 024788).

Notes: The species was originally described from Africa and is distinguished in *Gloeocystidiellum* s. lat. by its large ornamented basidiospores (Hjortstam 1987). Wu (1996) reported it from Taiwan, and here we record it from mainland China and Vietnam. However, whether the Asian specimens are identical with African ones needs further study. Larsson & Larsson (2003) showed that sequences of *Gm. compactum* and *Gm. formosanum*, both described from Taiwan, are almost identical with *Gm. aspellum* from Asia. Differences among the three species are mainly found in basidiospore size and culture incompatibility (Wu 1996). Thus, we leave the species complex of *Gm. compactum* and *Gm. formosanum*

for future studies, and refrain from proposing taxonomic changes at this time.

Confertotrama macrospora (Sheng H. Wu) Nakasone & S.H. He, **comb. nov.** MB 843414.

Basionym: *Boidinia macrospora* Sheng H. Wu, *Mycotaxon* **58**: 20. 1996.

Notes: The species is characterized by thin basidiomes and large, cylindrical, indistinctly ornamented basidiospores, and has been reported only in the type locality in Taiwan (Wu 1996). The type was sequenced and nested within the *Confertotrama* lineage in phylogenetic trees (Larsson & Larsson 2003; Fig. 1).

Confertotrama rajchenbergii (Gorjón & Hallenb.) Nakasone & S.H. He, **comb. nov.** MB 843415.

Basionym: *Gloeocystidiellum rajchenbergii* Gorjón & Hallenb., *Mycol. Progr.* **12**: 186. 2013.

Notes: The species was recently described from Chile and is morphologically similar to other species of *Confertotrama* by having compact texture, thick-walled gloeocystidia and narrowly ellipsoid to cylindrical basidiospores (Gorjón & Hallenberg 2013). In the published ITS tree and our present phylogenetic analyses, the species formed a strongly supported lineage with *Gloeocystidiellum aspellum*, *Gm. compactum* and *Gm. formosanum* (Gorjón & Hallenberg 2013). Thus, we propose this combination here.



Fig. 4. Basidiomes of *Confertotrama* spp. **A.** *Ca. aspellum* He 4262 (BJFC 023704). **B.** *Ca. aspellum* He 5262 (BJFC 024780). **C.** *Ca. rugulosa* He 5997 (BJFC 030873). **D.** *Ca. rugulosa* He 3427 (BJFC 021823). Scale bars = 1 cm.



Confertotrama rugulosa (Berk. & M.A. Curtis) Nakasone & S.H. He, **comb. nov.** MB 843416. Fig. 4C, D.

Basionym: *Merulius rugulosus* Berk. & M.A. Curtis, *J. Linn. Soc., Bot.* **10**(no. 46): 323. 1869.

Synonyms: *Corticium rugulosum* (Berk. & M.A. Curtis) Pat., *Bull. Soc. Mycol. France* **15**: 151. 1899.

Sesia rugulosa (Berk. & M.A. Curtis) Kuntze, *Revis. gen. pl.* (Leipzig) **2**: 870. 1891.

Lopharia rugulosa (Berk. & M.A. Curtis) Hjortstam, *Mycotaxon* **54**: 188. 1995.

Corticium chelidonium Pat., *Bull. Soc. Mycol. France* **16**(4): 180. 1900.

Vesiculomyces chelidonium (Pat.) Boidin & Lanq. [as 'chelidonium'], *Mycotaxon* **16**(2): 493. 1983.

Stereum chelidonium (Pat.) Höhn. & Litsch., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1* **116**: 741. 1907.

Megalocystidium chelidonium (Pat.) Boidin *et al.*, *Bull. Trimestriel Soc. Mycol. France* **113**(1): 62. 1997.

Specimens examined: **Brazil**, Parana, Parque Nacional de Iguacu, Foz do Iguacu, on decayed branch of dicot tree, 6 Jan. 1993, A.A.R. de Meijer 2415 (CFMR). **China**, Hainan Province, Changjiang County, Bawangling Nature Reserve, on fallen angiosperm branch, 4 Jul. 2019, S.H. He, He 5997 (BJFC 030873); Yunnan Province, Baoshan County, Gaoligongshan Nature Reserve, Baihualing, on fallen angiosperm trunk, 30 Nov. 2015, S.H. He, He 3427 (BJFC 021823, CFMR) & He 3442 (BJFC 021838); Ruili County, Moli Tropical Rainforest Park, on dead angiosperm tree, 2 Dec. 2015, S.H. He, He 3492 (BJFC 021889, CFMR). **Cuba**, ad cort, C. Wright 245, Fungi cubenses wrightianae no. 337 (FH-HUH00599534, HUH00304218 **isotypes** of *M. rugulosus*). **France**, Guadeloupe, Ravine-Chaude, on *Mammea americana* L., 1901, Duss s.n. (FH-HUH00304216, **holotype** of *C. chelidonium*; NY-NY01929719, NY01929719 **isotypes**); **USA**, Virgin Islands. St. John, Cinnamon Bay ruins, near Danish community, on bark of fallen tree, 6 Jan. 1994, D.J. Lodge, SJ-110.1 (CFMR, NY); Florida, Brickell Hammock, March 1923, W.A. Murrill (BPI-0257165).

Notes: Types of *Merulius rugulosus* and *Corticium chelidonium* were examined and found to be conspecific. The species has been reported in USA, Venezuela, Costa Rica, France (Guadeloupe), Gabon, South Africa, Thailand and India (Boidin *et al.* 1997), and here in China. Recent descriptions of *Ca. rugulosa* are available in Ginns (1971, as *M. rugulosus*) and Hjortstam & Ryvarden (2007, as *Megalocystidium chelidonium*).

Gelatinostereum S.H. He, S.L. Liu & Y.C. Dai, **gen. nov.** MB 843417.

Etymology: The genus epithet "*Gelatinostereum*" refers to the gelatinous and stereoid basidiomes; "*Gelatino-*": from gelatinous; "*stereum*": from the genus *Stereum*.

Basidiomes annual, resupinate to effused-reflexed, adnate, separable, gelatinous, hygrophanous, soft when fresh, becoming ceraceous to cartilaginous, brittle after drying. *Pilei* small, often radiately plicate, with abhymenial surface glabrous, light brown, golden brown to dark brown, indistinctly

zonate and sulcate. *Hymenophore* smooth, tuberculate to merulioid, greyish orange, brownish orange, light brown to brown, uncracked or densely cracked with age; *margin* determinate, abrupt, adnate or slightly elevated and curved towards the hymenophore, white when juvenile, slightly paler or concolourous with hymenophore when mature. *Context* brownish orange, with a compact and agglutinated texture. *Hyphal system* dimitic. *Generative hyphae* simple-septate, colourless, thin- to thick-walled with a wide lumen, smooth, rarely branched, moderately septate. *Skeletal hyphae* colourless, distinctly thick-walled, smooth, unbranched, not septate, with walls swelling in KOH. *Gloeocystidia* numerous, tubular, subclavate or subulate, colourless, thin-walled, smooth, embedded. *Hyphidia* numerous, unbranched, colourless, thin- to slightly thick-walled, smooth. *Basidia* clavate, colourless, thin-walled, smooth, with four sterigmata and a basal septum. *Basidiospores* cylindrical to suballantoid, colourless, thin-walled, smooth, amyloid, acyanophilous.

Type species: *Gelatinostereum phlebioides* S.H. He, S.L. Liu & Y.C. Dai

Notes: *Gelatinostereum* is similar to *Stereum* by sharing effused-reflexed basidiomes, a dimitic hyphal system with simple-septate generative hyphae and smooth amyloid basidiospores but differs in having gelatinous and brittle basidiomes with a smooth to merulioid hymenophore and thickened subhymenium, thin-walled gloeocystidia and numerous hyphidia. In the phylogenetic tree, *Gelatinostereum* formed a sister lineage to *Stereum* with high support values (90/91/1, Fig. 1).

Gelatinostereum phlebioides S.H. He, S.L. Liu & Y.C. Dai, **sp. nov.** MB 843418. Figs 5, 6.

Etymology: The species epithet "*phlebioides*" refers to the phlebia-like hymenophore when fresh.

Typus: **China**, Guizhou Province, Jiangkou County, Fanjingshan Nature Reserve, on fallen trunk of *Rhododendron*, 24 Nov. 2014, Y.C. Dai, Dai 14965 (**holotype** BJFC 018078, **isotypes** in BJM, CFMR).

Basidiomes annual, resupinate to effused-reflexed, adnate, separable, gelatinous, hygrophanous, soft when fresh, becoming ceraceous to cartilaginous, brittle after drying, up to 30 cm long, 5 cm wide, 500 µm thick. *Pilei* small, often radiately plicate; abhymenial surface glabrous, light brown, golden brown to dark brown, indistinctly zonate and sulcate. *Hymenophore* smooth, tuberculate to merulioid, greyish orange [5B(3–6)], brownish orange [5C(4–6)], light brown [5D(4–8)] to brown [5E(4–8)], slightly darkening in KOH, uncracked or densely cracked with age; *margin* determinate, abrupt, adnate or slightly elevated and curved towards the hymenophore, white when juvenile, slightly paler or concolourous with hymenophore when mature. *Context* brownish orange, with a compact and agglutinated texture, up to 0.4 mm thick. *Hyphal system* dimitic; all hyphae without clamps. *Subiculum* distinct, with a compact texture, composed of tightly agglutinated and parallelly arranged hyphae; *generative hyphae* colourless, thin- to thick-walled

with a wide lumen, smooth, rarely branched, moderately septate, 3–4.5 μm diam. *Skeletal hyphae* colourless, distinctly thick-walled, smooth, unbranched, not septate, with walls swelling in KOH, 4–6 μm diam. *Subhymenium* thickening with age; *generative hyphae* colourless, thin-walled, smooth, interwoven, agglutinated, 2–4 μm diam. *Gloeocystidia* numerous, tubular, subclavate or subulate, colourless, thin-walled, smooth, mostly embedded, (35–)60–130 \times 7–12(–14) μm . *Hyphidia* numerous, colourless, thin to slightly thick-walled, smooth, 25–35 \times 2–3.5 μm . *Basidia* clavate, colourless, thin-walled, smooth, with four sterigmata and a basal septum, 20–40 \times 4–5.5 μm . *Basidiospores* cylindrical to subballantoid, colourless, thin-walled, smooth, amyloid, acyanophilous, (5.5–)6–7.8(–8.3) \times 2–3(–3.8) μm , L = 6.8 μm , W = 2.6 μm , Q = 2.6–2.7 (n = 90/3).

Additional specimens examined: **China**, Fujian Province, Wuyishan County, Wuyishan Nature Reserve, on dead branch of *Rhododendron*, 17 Aug. 2016, S.H. He, He 4492 (BJFC 023933); Jiangxi Province, Lianping County, Jiulianshan Nature Reserve, On dead branch of *Rhododendron*, 14 Aug. 2016, S.H. He, He 4383 (BJFC 023824); Yunnan Province, Jingdong County, Ailaoshan Nature Reserve, On dead branch of *Rhododendron*, 15 Oct. 2013, S.H. He, He 1951 (BJFC 016419); Yulong County, Laojunshan Nature Reserve, on fallen trunk of *Rhododendron*, 1 Sep. 2015, S.H. He, He 2918 (BJFC 021348); Fuyuan County, Shibilianshan Nature Reserve, on dead branch of *Rhododendron*, 19 Nov. 2019, S.H. He, He 6340 (BJFC 033284).

Notes: *Gelatinostereum phlebioides* is the only species in the genus so far. It is similar to species of *Stereum* s. str., which, however, differs in non-gelatinous basidiomes and thick-walled gloeocystidia.

Gloeocystidiopsis ravum (Burt) S.H. He & Y.F. Cao, **comb. nov.** MB 843419.

Basionym: *Corticium ravum* Burt, *Ann. Mo. Bot. Gdn* **13**(3): 251. 1926.

Synonyms: *Conferticum ravum* (Burt) Ginns & G.W. Freeman, *Biblioth. Mycol.* **157**: 31, 1994.

Gloeocystidium karstenii Bourdot & Galzin, *Hyménomyc. de France* (Sceaux): 254. 1928. (1927).

Gloeocystidiellum karstenii (Bourdot & Galzin) Donk, *Fungus*, Wageningen **26**: 9. 1956.

Conferticum karstenii (Bourdot & Galzin) Hallenb., *Mycotaxon* **11**: 448. 1980.

Notes: Phylogenetic analyses and published morphological descriptions indicate that this species belongs to *Gloeocystidiopsis* (Wu 1996; Larsson & Larsson 2003; Fig. 1).

Gloeocystidiopsis shenghuae S.H. He & Y.F. Cao, **sp. nov.** MB 843420. Fig. 7.

Etymology: The species epithet “*shenghuae*” is named to honour the mycologist Dr. Sheng-Hua Wu (National Museum of Natural Science, Taiwan) who contributed to the taxonomy of *Gloeocystidiellum* s. lat.

Typus: **China**, Guizhou Province, Bijie County, Bailidujuan Forest Park, on dead angiosperm branch, 5 Jul. 2018, S.H. He, He 5411 (**holotype** BJFC 026472, **isotype** in BJM).

Basidiomes annual, resupinate, effused, closely adnate, inseparable, membranaceous to coriaceous, at first as small patches, later confluent up to 3 cm long, 1.5 cm wide, 200–300 μm thick. **Hymenophore** smooth, pale orange (5A3), light

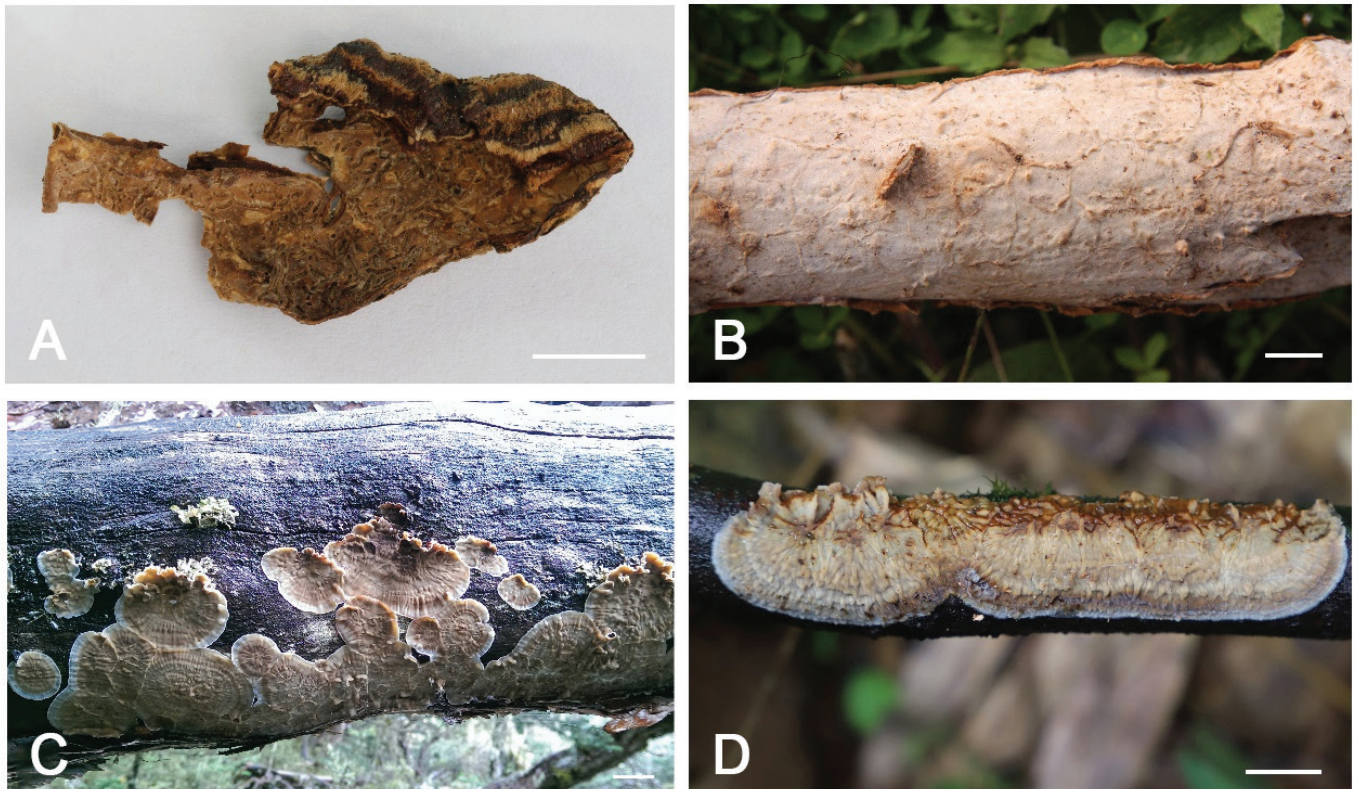


Fig. 5. Basidiomes of *Gelatinostereum phlebioides*. **A.** Dai 14965 (BJFC 018078, holotype). **B.** He 1951 (BJFC 016419). **C.** He 2918 (BJFC 021348). **D.** He 6340 (BJFC 033284). Scale bars = 1 cm.



orange [5A(4–5)] to greyish orange [5B(3–5)], unchanged in KOH, uncracked; *margin* thinning out, indistinct, concolourous with hymenophore. *Hyphal system* monomitic; all *hyphae* without clamps. *Subiculum* indistinct; *hyphae* colourless, slightly thick-walled, smooth, rarely branched, frequently septate, slightly agglutinated, more or less parallel to substrate, 1.8–2.6 μm diam. *Subhymenium* distinct; *hyphae* colourless, thin- to slightly thick-walled, smooth, rarely branched, moderately septate, interwoven, 1.5–2.2 μm diam. *Gloeocystidia* subfusiform to subulate, colourless, thick-walled, smooth, with one to several indistinct constrictions at the apex, embedded or slightly projecting, 60–80 \times 10–14 μm . *Hyphidia* scattered, colourless, thin-walled, smooth, unbranched. *Basidia* subclavate, often with a constriction, colourless, thin-walled, smooth, with four sterigmata and a basal simple septum, 30–45 \times 9–12 μm ; *basidioles* dominant, in shape similar to basidia, but slightly smaller. *Basidiospores* ellipsoid to broadly ellipsoid, colourless, thin-walled, finely echinulate, strongly amyloid, acyanophilous, (9–)10–12 \times 7–8.5(–8.9) μm , L = 11 μm , W = 7.9 μm , Q = 1.4 (n = 30/1).

Notes: *Gloeocystidiopsis shenghuae* was nested within the *Gloeocystidiopsis* lineage and is characterized by large basidiospores, which can be used to distinguish it from all other species in the clade ($\leq 8 \mu\text{m}$ long, $\leq 5 \mu\text{m}$ wide; Jülich 1982, Wu 1996, Boidin *et al.* 1997, Dai *et al.* 2017a).

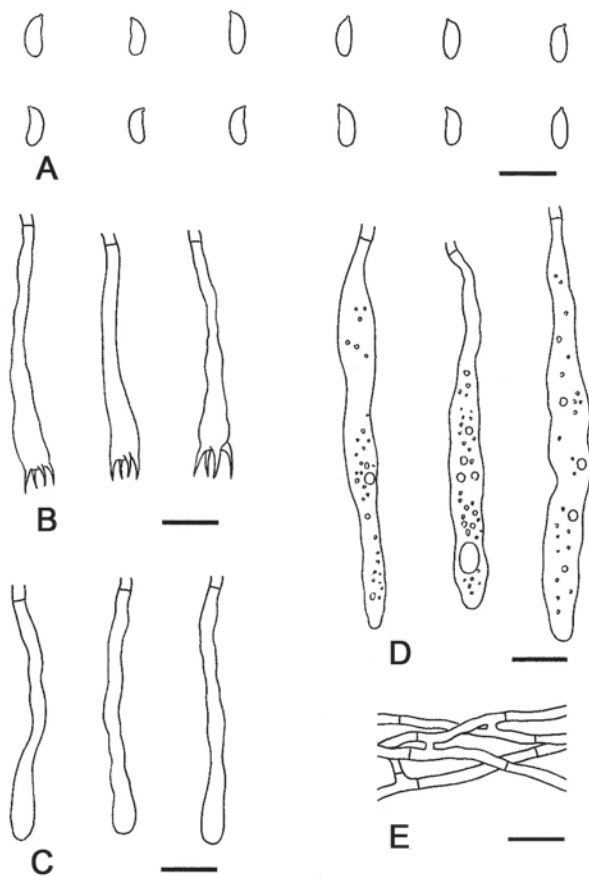


Fig. 6. Microscopic structures of *Gelatinostereum phlebioides* Dai 14965 (BJFC 018078, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Gloeocystidia. **E.** Generative hyphae from subiculum. Scale bars = 10 μm .

Gloeocystidiopsis tenuissimus (L.D. Dai & S.H. He) S.H. He & Y.F. Cao, **comb. nov.** MB 843421.

Basionym: *Aleurodiscus tenuissimus* L.D. Dai & S.H. He, *Mycoscience* **58**(3): 214. 2017.

Notes: The present phylogenetic analyses based on a more complete sampling of *Stereaceae* reveal that *Aleurodiscus tenuissimus* nested within the *Gloeocystidiopsis* lineage (Fig. 1). Furthermore, the morphology of the species fits well the *Gloeocystidiopsis* (Dai *et al.* 2017a). Thus, the combination is proposed here.

Gloeomyces Sheng H. Wu, *Mycotaxon* **58**: 47. 1996. **emend.**

Basidiomes annual, resupinate, effused, adnate, membranaceous, coriaceous or subcrustose. *Hymenophore* smooth or slightly tuberculate, greyish white, cream to yellowish-brown, not cracked or densely cracked with age; *margin* thinning out or abrupt, determinate, indistinct, adnate, paler than or concolourous with hymenophore. *Hyphal system* monomitic. *Generative hyphae* simple-septate or nodose-septate, colourless, thin- to slightly thick-walled. *Subiculum* usually indistinct or absent. *Subhymenium* thickening, composed of hyphae, gloeocystidia and acanthohyphidia. *Gloeocystidia* abundant, variable in shape, usually submoniliform with one to several contractions in the upper part, colourless, slight thick-walled. *Acanthohyphidia* numerous, variable in shape, usually hyphoid or vase shaped with a wide base, sometimes branched, typically colourless, thin-walled, with many small spines in upper part, in some species yellow to brown, thick-walled, with long spines or branches (resemble binding-hyphae), inamyloid, indextrinoid or dextrinoid in some species. *Basidia* clavate to subcylindrical, colourless, thin-walled, smooth, with two or four sterigmata, bearing a basal septum with or without a *clamp connection*. *Basidiospores* ellipsoid, colourless, thin-walled, smooth, amyloid, acyanophilous.

Type species: *Gloeomyces graminicola* Sheng H. Wu

Notes: In the phylogenetic tree, *Gloeomyces* formed a well-supported clade. Previously, several species in the clade were placed in *Acanthophysellum*, viz. *Ap. cerussatum*, *Ap. dextrinoideocerussatum* and *Ap. lapponicum*, but the type of the genus, *Ap. lividocoeruleum*, was nested within *Xylobolus* clade (Wu *et al.* 2001, Larsson & Larsson 2003). *Acanthophysium*, typified by *Am. apricans* and used for species with abundant acanthohyphidia and smooth basidiospores, is a possible name for this clade. Wu *et al.* (2000) treated *Acanthophysium* as a synonym of *Xylobolus* based on the simple-septate hyphae, smooth basidiospores, holocoenocytic nuclear behaviour and phenoloxidase negative reaction of *Am. apricans*. DNA sequences of *Am. apricans* are expected to clarify the phylogenetic relationship. Before this, we prefer to use *Gloeomyces* for the name of the clade, since its type species, *G. graminicola* was included (Fig. 1).

Morphologically, species of *Gloeomyces* are characterized by having resupinate basidiomes, well-developed acanthohyphidia and smooth basidiospores (Wu 1996, Núñez & Ryvar den 1997). The coloured thick-walled binding hyphae

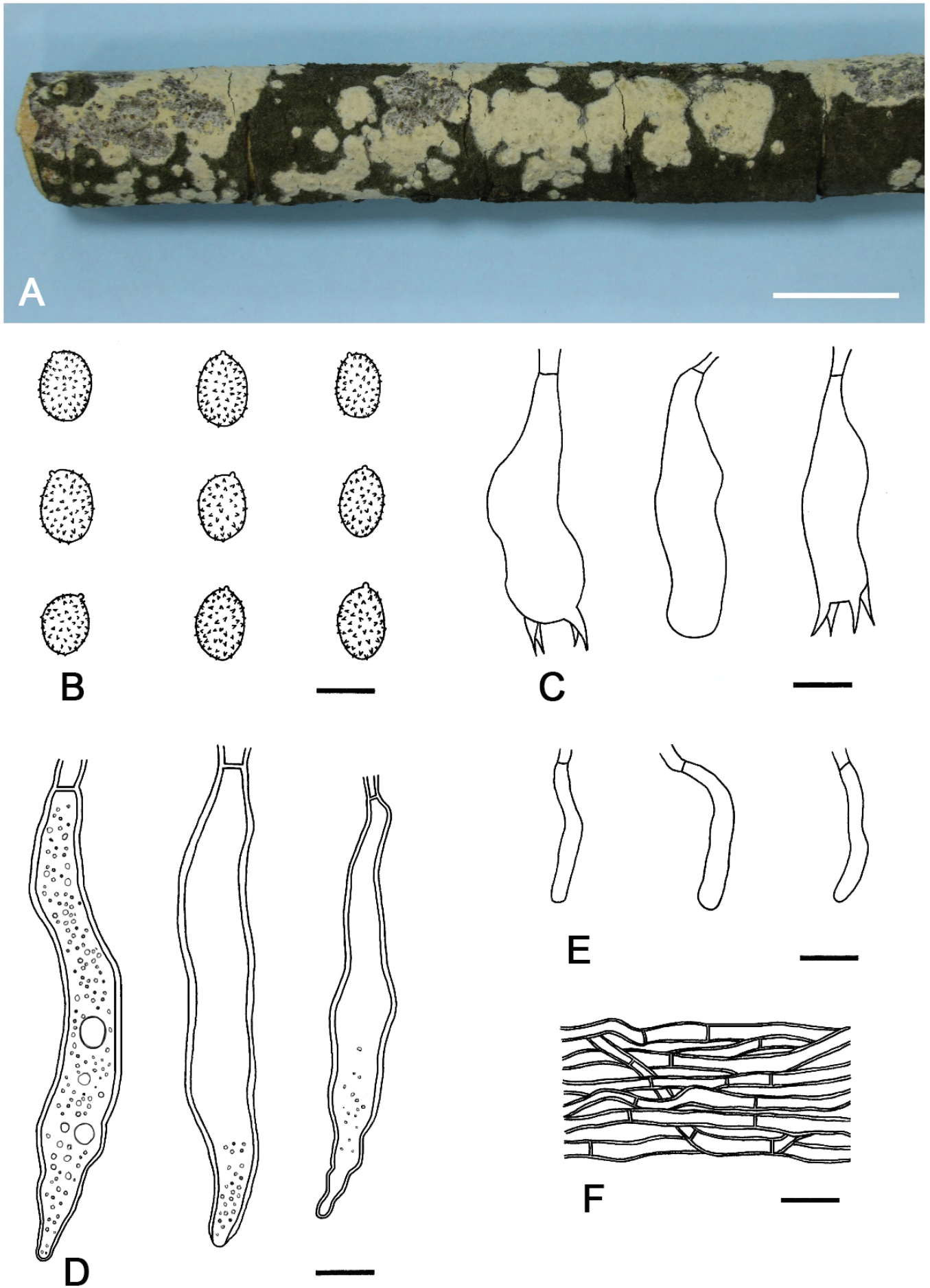


Fig. 7. *Gloeocystidiopsis shenghuae* He 5411 (BJFC 026472, holotype). **A.** Basidiomes. **B.** Basidiospores. **C.** Basidia and a basidiole. **D.** Gloeocystidia. **E.** Hyphidia. **F.** Generative hyphae from subiculum. Scale bars: A = 1 cm; B–F = 10 μ m.



in some species of the genus might be a special form of the acanthophyses. *Aleurodiscus* s. str. can be easily separated from *Gloeomyces* by possessing ornamented basidiospores or thick-walled smooth basidiospores in *A. fujii*.

Based on morphological and molecular evidence, a new species is described and illustrated, and 11 new combinations are proposed in *Gloeomyces*. We believe that more species of *Aleurodiscus* s. lat. will be moved to *Gloeomyces* after sequencing of authentic specimens.

The ITS similarity between MH109052 (from He 5283, paratype of *A. isabellinus*) and AF506448 (from Wu 9210-12, holotype of *G. graminicola*) is 99.2% with three differences of total 357 base pairs. *Gloeomyces graminicola* originally described from Taiwan was also found in Yunnan Province, southwestern China (Liu 2019), whereas *A. isabellinus* was reported only from Yunnan Province. Morphologically, the two species are similar to each other except that *A. isabellinus* has abundant colourless acanthohyphidia. However, this might be because that the specimens were at different stages, since the specimens without basidia usually have well-developed sterile organs. Thus, considering both molecular and morphological evidence, we treat *A. isabellinus* as a synonym of *G. graminicola*.

Gloeomyces bambusinus (S.H. He & Y.C. Dai) S.H. He, **comb. nov.** MB 844716.

Basionym: *Aleurodiscus bambusinus* S.H. He & Y.C. Dai, *MycKeys* **37**: 95. 2018.

Notes: The species was recently described from southern China on dead bamboo (Tian *et al.* 2018). The paratype specimen (He 4263) was nested within the *Gloeomyces* clade and has typical morphological structures of the genus.

Gloeomyces bicornis (Sheng H. Wu) S.H. He, **comb. nov.** MB 844717.

Basionym: *Aleurodiscus bicornis* Sheng H. Wu, *Mycol. Progr.* **21**(1): 150. 2022.

Notes: The species is characterized by 2-sterigmate basidia and is similar to *Aleurodiscus canadensis* that, however, differs in having acanthobasidia, smaller basidiospores and a distribution in North America (Núñez & Ryvarden 1997, Wu *et al.* 2022). The sample Wu 1207-90 collected from northeastern China was identified as *A. canadensis* by Dai & He (2017). It formed a distinct lineage with *A. bicornis* in Wu *et al.* (2022) but was nested within the *G. bicornis* lineage with strong support values in the present study. We believe that the studied Chinese specimens represent one species, but more evidence, especially DNA sequences of *A. canadensis*, is needed to resolve the relationship between *G. bicornis* and *A. canadensis*.

Gloeomyces cerussatus (Bres.) S.H. He, **comb. nov.** MB 844718.

Basionym: *Corticium cerussatum* Bres., *Fung. Trident.* **2**(8–10): 37. 1892.

Synonyms: *Kneiffia cerussata* (Bres.) Bres., *Ann. Mycol.* **1**(2): 104. 1903.

Aleurodiscus cerussatus (Bres.) Höhn. & Litsch., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1* **116**: 808. 1907.

Acanthophysellum cerussatum (Bres.) Parmasto, *Eesti NSV Tead. Akad. Toim., Biol. seer* **16**(4): 378. 1967.

Acanthophysium cerussatum (Bres.) Boidin, *Bull. Trimestriel Soc. Mycol. France* **101**(4): 340. 1986. (1985).

Notes: The species has been reported in many countries but may represent a species complex (Núñez & Ryvarden 1997, Bernicchia & Gorjón 2010, Rajchenberg *et al.* 2021). Since *Corticium cerussatum* was originally described from Europe, we chose the lineage of the sample of CBS 106.54 from Netherlands to represent this species. In our phylogenetic tree (Fig. 1), three samples from USA, identified as *Aleurodiscus cerussatus*, *A. laurentianus* and *A. lapponicus*, respectively, formed a strongly supported lineage. The three species are morphologically similar to each other and represent a species complex that needs further study.

Gloeomyces dextrinoideocerussatus (Manjón *et al.*) S.H. He, **comb. nov.** MB 844719.

Basionym: *Aleurodiscus dextrinoideocerussatus* Manjón *et al.*, *Mycotaxon* **39**: 351, 1990.

Synonyms: *Acanthophysellum dextrinoideocerussatum* (Manjón *et al.*) Sheng H. Wu *et al.*, *Mycotaxon* **76**: 160. 2000.

Basionym: *Acanthophysium dextrinoideocerussatum* (Manjón *et al.*) Tellería, *Nova Hedwigia* **57**: 208. 1993.

Notes: We propose this combination based on morphological and molecular evidence (Fig. 1). The dextrinoidity of dendrohyphidia of this species is also seen in other species and can be regarded as an interspecific difference in the genus. In the phylogenetic tree (Fig. 1), *G. dextrinoideocerussatus* formed a lineage with *G. thailandicus*. Morphologically, *G. dextrinoideocerussatus* can be easily separated from *G. thailandicus* by having nodose-septate generative hyphae, dextrinoid dendrohyphidia and slight longer basidiospores (Bernicchia & Gorjón 2010).

Gloeomyces dextrinoideophyses (S.H. He) S.H. He, **comb. nov.** MB 844720.

Basionym: *Aleurodiscus dextrinoideophyses* S.H. He, *Cryptog. Mycol.* **38**: 231. 2017.

Notes: The species is characterized by dextrinoid dendrohyphidia and a habitat on bamboos in tropical areas. We tried many times to obtain the ITS of this species but failed.

Gloeomyces formosanus (Sheng H. Wu) S.H. He, **comb. nov.** MB 844723.

Basionym: *Aleurodiscus formosanus* Sheng H. Wu, *Mycol. Progr.* **21**: 150. 2022.

Notes: It is a recently described species from Taiwan. The type was nested within the *Gloeomyces* clade and has the typical morphological characteristics of the genus (Fig. 1).

Gloeomyces parvisporus (Núñez & Ryvarden) S.H. He, **comb. nov.** MB 844724.

Basionym: *Aleurodiscus parvisporus* Núñez & Ryvarden, *Syn. Fung.* **12**: 117. 1997.

Notes: The species was originally described from Japan and recently redescribed and sequenced based on materials from China (Wu *et al.* 2022). We propose this combination based on morphological and molecular evidence (Fig. 1).

Gloeomyces persicus (Ghob.-Nejh.) S.H. He, *comb. nov.* MB 844725.

Basionym: *Aleurodiscus persicus* Ghob.-Nejh., *Phytotaxa* **351**: 265. 2018.

Notes: The species was described from Iran based on morphological and molecular evidence (Ghobad-Nejhad & Langer 2018). It is similar to *G. cerussatus* in macro- and microscopic structures and is in the *Gloeomyces* clade (Fig. 1).

Gloeomyces subcerussatus S.H. He & Ghob.-Nejh., *sp. nov.* MB 843410. Figs 8, 9.

Etymology: The species epithet “*subcerussatus*” refers to the morphological similarity to *A. cerussatus*.

Typus: **China**, Jilin Province, Antu County, Changbaishan Nature Reserve, on branches of dead standing planted

angiosperm tree, 9 Sep. 2011, *M. Ghobad-Nejhad*, Ghobad-Nejhad 2360 (**holotype** BJFC 012135; **isotypes** in ICH).

Basidiomes annual, resupinate, effused, closely adnate or loosening with age, inseparable from substrate or easily detached with age, coriaceous, at first as small patches, later confluent up to 4 cm long, 1 cm wide, 80–400 µm thick in section. *Hymenophore* smooth, pale orange (5A3), light orange [5A(4–5)] to greyish orange [5B(3–5)], slightly darkening in KOH, not cracked when juvenile, densely and deeply cracked when mature; *margin* thinning out, indistinct, concolourous with hymenophore. *Hyphal system* monomitic, all hyphae with clamps. *Subiculum* indistinct; hyphae colourless, thin- to slightly thick-walled, smooth, loosely interwoven, more or less parallel to substrate, moderately branched and septate, 2–5 µm diam. *Subhymenium* thickening, composed of vertically arranged hyphae, gloecystidia and acanthohyphidia. *Gloecystidia* abundant, variable in shape and size in different stages, narrowly clavate to subcylindrical when mature, slightly thick-walled, 55–95 × 7–10 µm. *Acanthohyphidia* numerous, colourless, variable in shape and size, hyphoid or arising from a clavate base, mostly branched, with numerous spines, transitional forms from smooth subclavate cystidia-like structures to well-developed acanthohyphidia present, 25–55 × 2–6 µm (spines excluded). *Basidia* not seen; *basidioles* rare, scattered among acanthohyphidia, clavate to subcylindrical. *Basidiospores* ellipsoid, colourless, thin-walled, smooth, amyloid, acyanophilous, 5.8–7.0 × 2.8–4.0 µm, L = 6.7 µm, W = 3.2 µm, Q = 2.1 (n = 10/2), only few spores observed.

Additional specimens examined: **China**, Beijing, Huairou District, Labagoumen Forest Park, on fallen angiosperm branch, 25 Aug. 2020, *S.H. He*, He 6847 (BJFC 033796); Pinggu District, Xiniujiangyuan Village, on fallen angiosperm branch, 16 Sep. 2020, *S.H. He*, He 6964 (BJFC 033913).

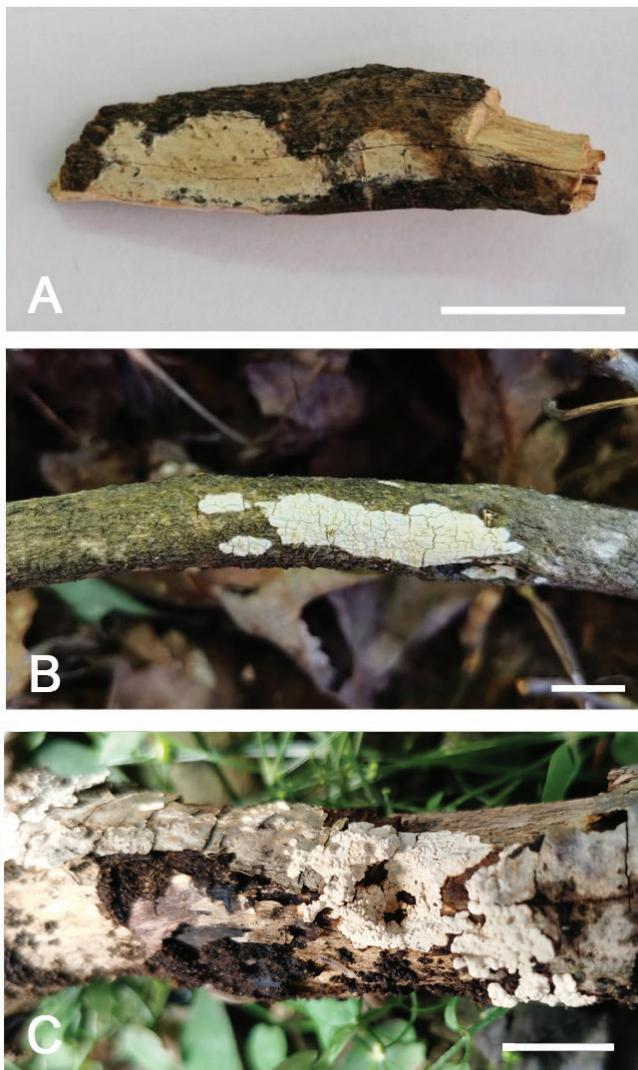


Fig. 8. Basidiomes of *Gloeomyces subcerussatus*. **A.** Ghobad-Nejhad 2360 (BJFC 012135, holotype). **B.** He 6847 (BJFC 033796). **C.** He 6964 (BJFC 033913). Scale bars = 1 cm.

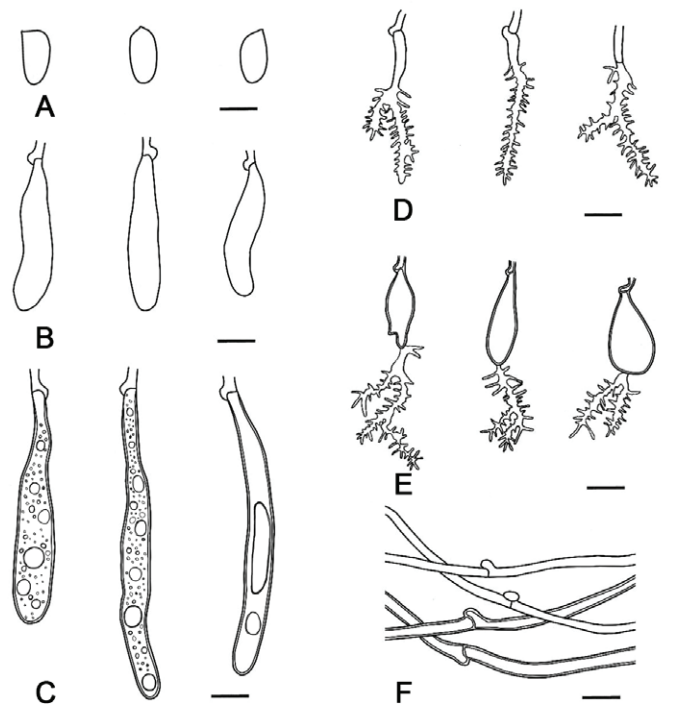


Fig. 9. Microscopic structures of *Gloeomyces subcerussatus* Ghobad-Nejhad 2360 (BJFC 012135, holotype). **A.** Basidiospores. **B.** Basidioles. **C.** Gloecystidia. **D, E.** Acanthohyphidia. **F.** Generative hyphae from subiculum. Scale bars = 10 µm.



Notes: *Gloeomyces subcerussatus* is characterized by clamped generative hyphae, numerous acanthohyphidia, variably shaped and sized gloecystidia and a habitat on angiosperm branches. In the tree, *G. subcerussatus* formed a lineage sister to *G. bambusinus* and *G. dextrinoideophyses*, both of which differ by having simple-septate generative hyphae and growing on bamboo in subtropical to tropical areas (Dai *et al.* 2017b, Tian *et al.* 2018). *Gloeomyces parvisporus* is similar to *G. subcerussatus* by sharing thickened subhymenium, clamped generative hyphae and well-developed gloecystidia and acanthohyphidia but differs in having subglobose basidiospores $5\text{--}6 \times 4\text{--}5 \mu\text{m}$ (Núñez & Ryvarden 1997). *Gloeomyces cerussatus* differs from *G. subcerussatus* by having distinctly larger basidiospores ($10\text{--}12 \times 6\text{--}7 \mu\text{m}$; Núñez & Ryvarden 1997).

Gloeomyces thailandicus (S.H. He) S.H. He, **comb. nov.** MB 844726.

Basionym: *Aleurodiscus thailandicus* S.H. He, *Cryptog. Mycol.* **38**: 234. 2017.

Notes: The species was originally described from Thailand and later found in China. It is similar to *G. graminicola* by having yellow acanthohyphidia in subhymenium; phylogenetically, it clustered with other *Gloeomyces* species (Fig. 1).

Gloeomyces thoenii (Boidin *et al.*) S.H. He, **comb. nov.** MB 844727.

Basionym: *Acanthophysium thoenii* Boidin *et al.*, *Bull. Trimestriel Soc. Mycol. France* **101**(4): 356. 1986.

Synonyms: *Aleurodiscus thoenii* (Boidin, Lanq. & Gilles)

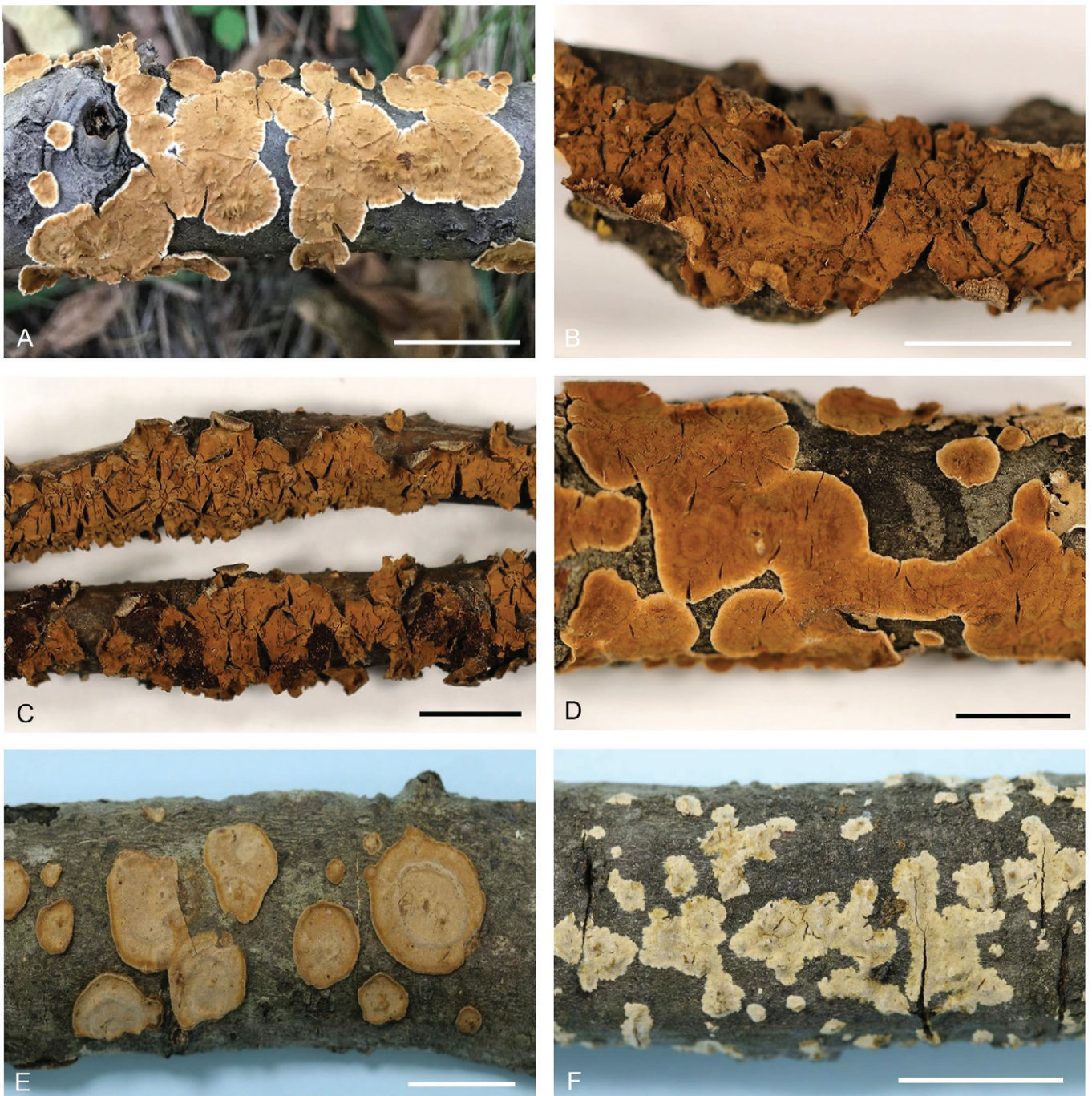


Fig. 10. Basidiomes of *Megalocystidium* spp. **A.** *M. chinense* He 5119 (BJFC 024637). **B.** *Eichleriella chinensis* Licent 718 (PRM 501018, syntype). **C.** *Stereum peculiare* TAA 10185 (LY 8630, isotype). **D.** *Stereum peculiare* TAA 101891 (BPI 0349308, paratype). **E.** *M. brunneum* He 3447 (BJFC 021843, holotype). **F.** *M. effusum* He 2526 (BJFC 020979, holotype). Scale bars = 1 cm.

Núñez & Ryvarden, *Syn. Fung.* (Oslo) 12: 139. 1997.

Acanthofungus thoenii (Boidin *et al.*) Sheng H. Wu *et al.*, *Mycotaxon* 76: 159. 2000.

Xylobolus thoenii (Boidin *et al.*) Tura *et al.*, *Biodiversity of the Heterobasidiomycetes and non-gilled Hymenomycetes (former Aphyllophorales) of Israel*: 323. 2011.

Note: The species was only reported from Zaire, and is morphologically similar and phylogenetically close to *G. cerussatus* (Núñez & Ryvarden 1997, Fig. 1).

Gloeomyces tropicus (L.D. Dai & S.H. He) S.H. He, **comb. nov.** MB 844728.

Basionym: *Aleurodiscus tropicus* L.D. Dai & S.H. He, *Mycoscience* 58: 215. 2017.

Notes: The species is reported from Hainan and Yunnan Provinces, China. It is similar to *G. graminicola* but differs by having larger basidiospores and lacking yellowish acanthohyphidia with long branches (Dai *et al.* 2017a, Tian *et al.* 2018). Phylogenetically, it is closely related to *G. graminicola* (Fig. 1).

Megalocystidium Jülich, *Persoonia* 10: 139. 1978. **emend.**

Basidiomes annual, effused to effused-reflexed, adnate, membranaceous, ceraceous to coriaceous. *Pilei* small, usually curved inwards when dried; abhymenial surface with dense tomentum when juvenile, becoming glabrous with age, greyish brown to dark brown, sulcate and zonate.

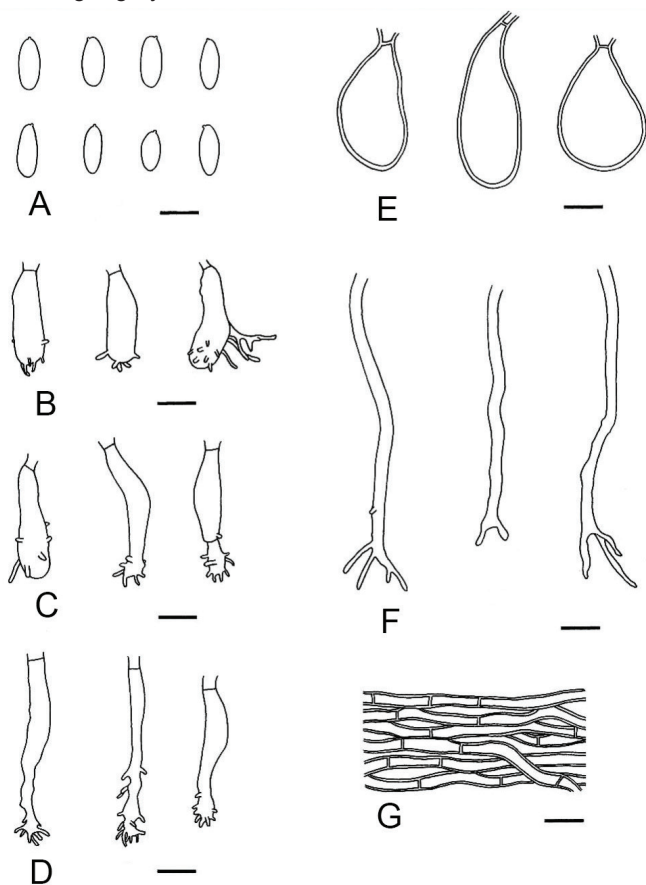


Fig. 11. Microscopic structures of *Megalocystidium brunneum* He 3447 (BJFC 021843, holotype). **A.** Basidiospores. **B–D.** Acanthohyphidia. **E.** Gloeocystidia. **F.** Hyphidia. **G.** Generative hyphae from subiculum. Scale bars = 10 µm.

Hymenophore smooth to tuberculate, greyish orange, light brown, greyish brown, golden brown to brown, not cracked or deeply cracked with age; *margin* byssoid or thinning out, adnate or slightly elevated, paler than or concolourous with hymenophore. *Hyphal system* monomitic or dimitic. *Generative hyphae* simple-septate or nodose-septate, colourless to pale yellow, thin- to thick-walled, smooth. *Gloeocystidia* present, tubular, vesicular or clavate, colourless to pale yellow, thin to slightly thick-walled, smooth, mostly embedded. *Acanthohyphidia* present or absent, subclavate to subcylindrical, colourless to pale yellow, thin- to thick-walled, with spines at the apical part. *Basidia* clavate to subcylindrical, colourless, thin-walled, smooth, with four sterigmata. *Basidiospores* ellipsoid to cylindrical, colourless, thin-walled, smooth or almost so, amyloid, acyanophilous.

Type species: *Megalocystidium leucoxanthum* (Bres.) Jülich

Notes: The genus was moderately supported in the tree (Fig. 1). Traditionally, *Megalocystidium* included species with effused basidiomes, nodose-septate generative hyphae, long basidia, large basidiospores and without acanthohyphidia (Wu 1996). Spirin *et al.* (2021) transferred *Peniophora diffissa* to the genus, which has abundant acanthohyphidia. In our phylogenetic analyses, *Megalocystidium chinensis*, *M. wakullum* and other two undescribed species with simple-septate generative hyphae and acanthohyphidia formed a sister subclade to *M. leucoxanthum* subclade. Moreover, Boidin *et al.* (1979) described *Stereum peculiare* (syn. *M. chinensis*, see below) as dimitic, whereas all other species are monomitic. Thus, at present, we prefer to treat the two subclades as a single genus because of the entangled morphological patterns.

Megalocystidium brunneum S.H. He, **sp. nov.** MB 843405. Figs 10E, 11.

Etymology: The species epithet “*brunneum*” refers to the brown basidiomes.

Typus: **China**, Yunnan Province, Baoshan County, Gaoligongshan Nature Reserve, on fallen angiosperm branch, 30 Nov. 2015, S.H. He, He 3447 (**holotype** BJFC 021843, **isotypes** in BJM, CFMR).

Basidiomes annual, resupinate, effused, adnate, easily separated from the substrate, coriaceous, brittle when dry, first as small round patches, later confluent. *Hymenophore* smooth, greyish brown [6B(3–6)], brownish orange [6C(3–8)] to light brown [6D(3–8)], turning reddish-black in KOH, uncracked; *margin* abrupt, slightly elevated, indistinct and concolourous with hymenophore. *Context* light brown, up to 1.5 mm thick. *Hyphal system* monomitic; all hyphae without clamps. *Subiculum* well-developed; hyphae colourless to pale yellow, thick-walled, smooth, rarely branched, moderately septate, tightly interwoven, more or less parallel to substrate, 2–3 µm diam. *Subhymenium* indistinct; hyphae colourless, thin- to thick-walled, smooth, tightly interwoven, 2–2.5 µm diam. *Gloeocystidia* vesicular to racket-shaped, colourless, slightly thick-walled, smooth, embedded, 25–40 × 15–25 µm. *Acanthohyphidia* numerous, variable in shape and size, mostly subclavate to subcylindrical, with few to many spines



at apex, colourless, thin- to slightly thick-walled, 20–40 × 2–6 μm. *Hyphidia* present, colourless, thin-walled, smooth, slightly branched. *Basidia* not seen; *basidioles* numerous, clavate, colourless, thin-walled, smooth, with a basal septum. *Basidiospores* subcylindrical to subfusiform, colourless, thin-walled, smooth, amyloid, acyanophilous, (9–) 10–12 (–12.7) × 4–5 μm, L = 11.3 μm, W = 4.7 μm, Q = 2.4 (n = 12/1).

Additional specimens examined: **China**, Yunnan Province, Baoshan County, Gaoligongshan Nature Reserve, on fallen angiosperm branch, 30 Nov. 2015, S.H. He, He3407 (BJFC 021803, CFMR); Yongde County, Daxueshan Nature Reserve, on fallen angiosperm branch, 28 Aug. 2015, S.H. He, He 2735 (BJFC 021173).

Notes: *Megalocystidium brunneum* is characterized by brown basidiomes, vesicular to racket-shaped gloeocystidia, numerous acanthohyphidia and large cylindrical basidiospores. *Megalocystidium chinense* is similar to *M. brunneum* by sharing basidioma colour and large cylindrical basidiospores but differs in having brown gloeocystidia and hyphidia (Boidin *et al.* 1979). *Megalocystidium wakullum* differs from *M. brunneum* by having subcylindrical gloeocystidia and smaller basidiospores (8–10 × 3–3.5 μm; Burdsall *et al.* 1981).

Megalocystidium chinense (Pilát) S.H. He & Nakasone, **comb. nov.** MB 843406. Figs 10A–D.

Basionym: *Eichleriella chinensis* Pilát, *Ann. Mycol.* **38**(1): 62. 1940.

Synonyms: *Stereum peculiare* Parmasto *et al.*, *Persoonia* **10**: 311. 1979.

Xylobolus peculiare (Parmasto *et al.*) Ryvarden, *Syn. Fung.* (Oslo) **40**: 86. 2020.

Additional specimens examined: **China**, Hebei Province, Zhulu County, Xiaowutaishan Nature Reserve, Yangjiaping Station, on dead branch of *Quercus*, 9 Sep. 2017, S.H. He, He 5119 (BJFC 024637); Jilin Province, Antu County, Changbaishan Nature Reserve, on fallen branch of *Tillia*, 10 Sep. 2014, Dai 14769 (BJFC 017873); on fallen branch of *Acer*, 10 Sep. 2014, Dai 14826 (BJFC 017940); Liaoning Province, Zhuanghe County, Xianrendong Forest Park, on fallen branch of *Quercus*, 5 Aug. 2017, S.H. He, He 4655 (BJFC 024174), He 4661 (BJFC 024180) & He 4667 (BJFC 024186). *Eichleriella chinensis*: **China**, Hebei Province, Zhulu County, Yangjiaping, on fallen trunk of *Quercus*, 11 Nov. 1950, leg. C. Yang, det. S. Teng (HMAS 18343); on fallen branch of *Quercus*, Apr. 1917, leg. Licent 718, det. Pilát (PRM 501018, **syntype**); leg. Licent 729, det. Pilát (PRM 501014, **syntype**). *Stereum peculiare*: **U.S.S.R.** Primorskij Terr., Kavalerovo Distr., Gornoretshensk, on fallen branch of *Quercus mongolica*, 9 Oct. 1977, E. Parmasto (TAA 10185, LY 8630, **isotype**); near the holotype's locality, on fallen branch of *Quercus mongolica*, 9 Oct. 1977, E. Parmasto (TAA 101891, LY 8629, BPI 0349308, **paratype**).

Notes: Pilát (1940) described *Eichleriella chinensis* from China without data on basidia and basidiospores. Later, Boidin *et al.* (1979) described *Stereum peculiare* based on specimens from U.S.S.R. and India. Malysheva & Spirin (2017) excluded *Eichleriella chinensis* from the genus but did not suggest any alternative classification. We re-studied types and authentic materials (Fig. 10A–D) of the two species and found them to be conspecific. The species is common in northern China, but specimens are usually sterile. See Pilát (1940) and Boidin *et al.* (1979) for descriptions and illustrations.

Megalocystidium effusum S.H. He, **sp. nov.** MB 843407. Figs 10F, 12.

Etymology: The species epithet “*effusum*” refers to the effused basidiomes.

Typus: **China**, Yunnan Province, Kunming, Yeyahu Park, on fallen angiosperm branch, 22 Aug. 2015, S.H. He, He 2526 (**holotype** BJFC 020979, **isotype** in BJM).

Basidiomes annual, resupinate, effused, adnate, inseparable from the substrate, coriaceous, first as small colonies, later confluent up to 5 cm long, 2 cm wide, 100–150 μm thick. **Hymenophore** smooth, pale orange [5A(3), light orange [5A(4–5)] to greyish orange [5B(3–6)], turning light brown in KOH, uncracked; **margin** thinning out, slightly fimbriate, indistinct, concolourous with hymenophore. **Hyphal system** monomitic; all hyphae without clamps. **Subiculum** indistinct; hyphae colourless, slightly thick-walled, smooth, rarely branched, moderately septate, more or less parallel to substrate, 2.5–5 μm diam. **Subhymenium** distinct; hyphae colourless, thin- to slightly thick-walled, smooth, densely interwoven, 2–3.5 μm diam. Cystidia of three kinds: (1) *pseudocystidia* scattered, subclavate to subcylindrical, with a papilla at the apex, colourless to pale yellow, slightly thick-walled, smooth, mostly embedded, up to 100 μm long, 7–10 μm wide; (2) *acutocystidia* numerous, subulate, colourless, thin-walled, smooth, 15–20 × 3–4.5 μm; (3) *acanthohyphidia* clavate or hyphoid, with few to many spines at the apex, colourless,

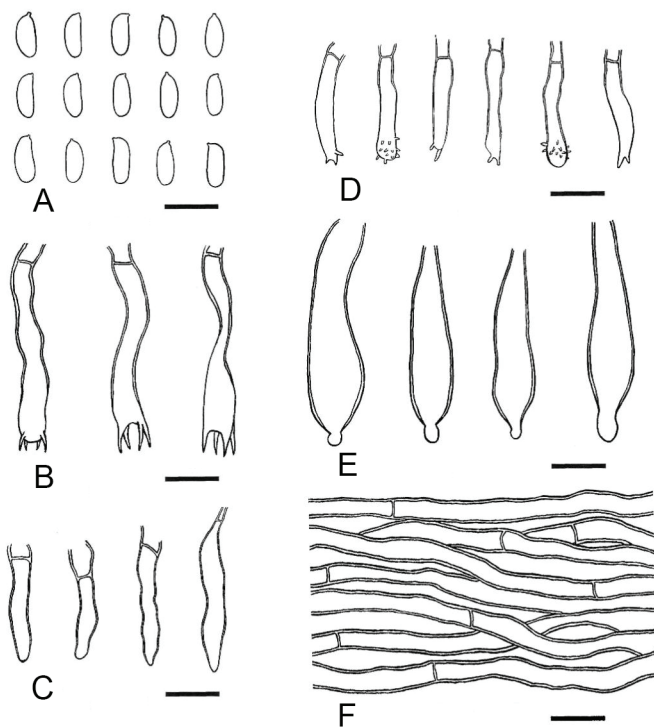


Fig. 12. Microscopic structures of *Megalocystidium effusum* He 2526 (BJFC 020979, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Acutocystidia. **D.** Acanthohyphidia. **E.** Pseudocystidia. **F.** Generative hyphae from subiculum. Scale bars = 10 μm.

thin-walled, $18\text{--}26 \times 3.5\text{--}6 \mu\text{m}$. *Basidia* cylindrical to clavate, colourless, slightly thick-walled toward the base, with 4 sterigmata and a basal simple septum, $30\text{--}35 \times 4\text{--}4.5 \mu\text{m}$; *basidioles* dominant, in shape similar to basidia, but slightly smaller. *Basidiospores* oblong ellipsoid to subcylindrical, colourless, thin-walled, smooth, amyloid, acyanophilous, $7.5\text{--}10 \times 2\text{--}3.5 \mu\text{m}$, $L = 8.4 \mu\text{m}$, $W = 2.9 \mu\text{m}$, $Q = 2.9$ ($n = 30/1$).

Additional specimen examined: **China**, Yunnan Province, Kunming, Yeyahu Park, on fallen angiosperm branch, 22 Aug. 2015, S.H. He, He 2514 (BJFC 020967, CFMR).

Notes: *Megalocystidium effusum* is characterized by resupinate and pale yellow basidiomes, papillate pseudocystidia and numerous acanthohyphidia. *Megalocystidium wakullum* is similar to *M. effusum* by sharing resupinate basidiomes, presence of three kinds of cystidia and same size of basidiospores but differ in having longer acutocystidia ($20\text{--}40 \mu\text{m}$), less distinctly papillate pseudocystidia and a distribution in southern USA (Burdall *et al.* 1981, Boidin *et al.* 1997). Moreover, the two species are recognized as independent lineages in the phylogenetic tree (Fig. 1).



Fig. 13. Basidiomes of *Stereum* spp. **A, B.** *S. rhododendri* He 4483 (BJFC 023924, holotype). **C–F.** *S. tropicum* He 5968 (BJFC 030843, holotype). Scale bars = 1 cm.



Stereum rhododendri S.H. He, Y.F. Cao & Y.L. Xu, *sp. nov.*
MB 844729. Figs 13A, B, 14.

Etymology: The species epithet “*Rhododendri*” refers to the host *Rhododendron*.

Typus: **China**, Fujian Province, Wuyishan Nature Reserve, on fallen *Rhododendron* branch, 17 Aug. 2016, S.H. He, He 4483 (**holotype** BJFC 023924).

Basidiomes annual, resupinate to slightly effused-reflexed, closely adnate, coriaceous, first as small patches, later confluent up to 17.5 cm long, 3.5 cm wide, 100 μm thick in section. **Hymenophore** smooth, white (5A1) to orange white (5A2) when fresh, pale orange (5A3) to greyish orange [5B(3–4)] when dry, turning reddish brown after bruised when fresh, becoming dark brown when dry, unchanged in KOH, not cracked; **margin** adnate or slightly elevated, distinct, paler or concolourous with hymenophore surface. **Hyphal system** monomitic. **Subiculum** distinct, pale brown, hyphae colourless to pale yellow, slightly to distinctly thick-walled, smooth, simple-septate, rarely branched and septate, more or less parallel to the substrate, 2.5–5 μm diam. **Subhymenium** thickening, composed of hyphae and collapsed hymenial elements. **Cystidia** of two types: (1) **acutocystidia** subfusiform, colourless, thin- to slightly thick-walled, smooth, usually with a tapered apex, embedded or rarely projecting beyond the hymenium, 15–35(–50) \times 3–6 μm ; (2) **gloeocystidia** fusiform or subclavate, thin-walled, smooth, often with yellow contents,

embedded, 20–60 \times 3–8 μm . **Basidia** clavate, colourless, thin-walled, with 4 sterigmata and a basal simple septum, 20–30 \times 3–6 μm ; **basidioles** dominant, in shape similar to basidia, but slightly smaller. **Basidiospores** ellipsoid to subcylindrical, colourless, thin-walled, smooth, amyloid, acyanophilous, (4.2–)5–7 \times 2–3 μm , L = 5.7 μm , W = 2.6 μm , Q = 2.1–2.3 (n = 60/2).

Additional specimens examined: **China**, Fujian Province, Wuyishan Nature Reserve, on fallen *Rhododendron* branch, 17 Aug. 2016, S.H. He, He 4459 (BJFC 023900); *ibid.*, He 4481 (BJFC023922).

Notes: *Stereum rhododendri* is characterized by resupinate to slightly effused-reflexed basidiomes, presence of acutocystidia and gloeocystidia, absence of thick-walled cystidia, relatively small basidiospores and host of *Rhododendron*. In the phylogenetic tree (Fig. 1), *S. rhododendri* formed a distinct lineage sister to *S. rugosum* and *S. sanguinolentum*. Morphologically, *S. rugosum* can be easily separated from *S. rhododendri* by having dimitic hyphal system, thick-walled pseudocystidia, and larger basidiospores (Chamuris 1988). *Stereum sanguinolentum* is similar to *S. rhododendri* by sharing resupinate to effused-reflexed basidiomes with hymenophore darkening when bruised, but differs in having acanthocystidia, thick-walled gloeocystidia, and slightly larger basidiospores (7–10 \times 3–4.5 μm), and growing on *Pinus* trees (Eriksson *et al.* 1984).

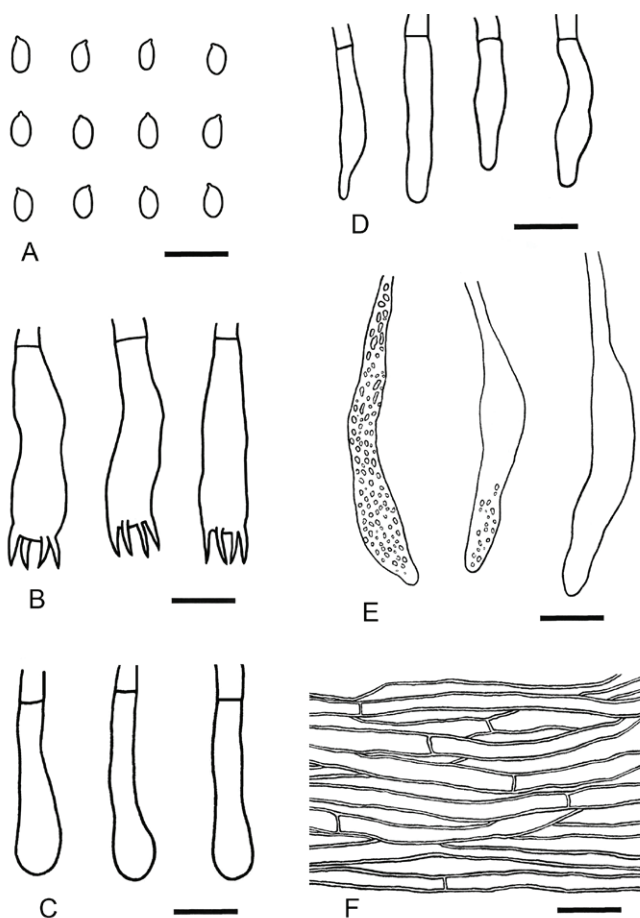


Fig. 14. Microscopic structures of *Stereum rhododendri* He 4483 (BJFC 023924, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Acutocystidia. **E.** Gloeocystidia. **F.** Generative hyphae from subiculum. Scale bars = 10 μm .

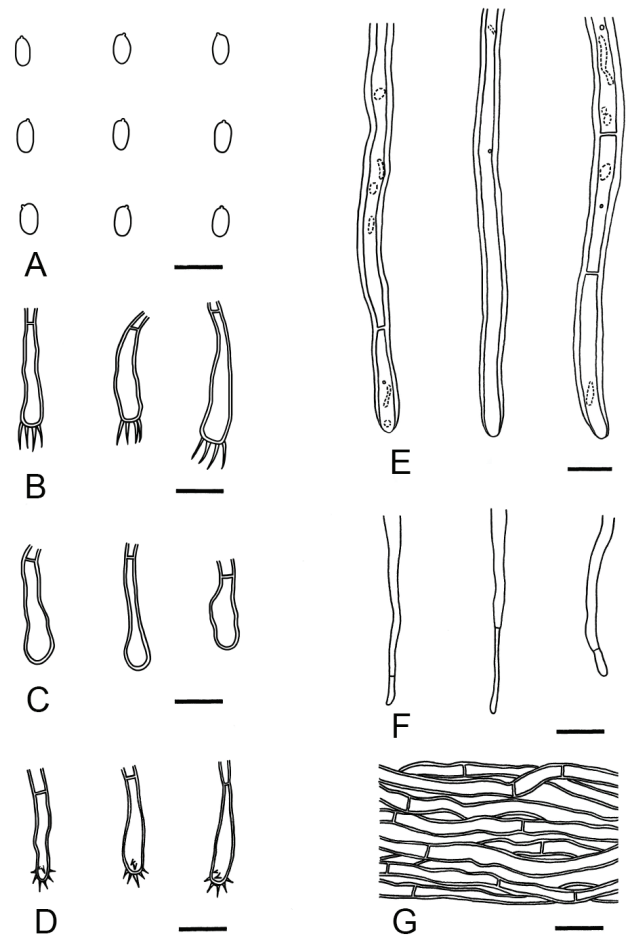


Fig. 15. Microscopic structures of *Stereum tropicum* He 5968 (BJFC 030843, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Basidioles. **D.** Acanthocystidia. **E.** Pseudocystidia. **F.** Acutocystidia. **G.** Generative hyphae from subiculum. Scale bars = 10 μm .

Stereum tropicum S.H. He, Y.F. Cao & Y.L. Xu, *sp. nov.* MB 844730. Figs 13C–F, 15.

Etymology: The species epithet “*tropicum*” refers to the tropical distribution.

Typus: **China**, Hainan Province, Lingshui County, Diaoluoshan Nature Reserve, on fallen angiosperm trunk, 2 Jul. 2019, S.H. He, He 5968 (**holotype** BJFC 030843).

Basidiomes annual, resupinate to effused-reflexed, adnate, separable from substrate, coriaceous to soft corky, at first as small circular patches, later confluent up to 30 cm long, 5 cm wide, 1.5 mm thick at base. *Reflexed parts* projecting up to 2 cm, abhymenial surface reddish brown [8D(5–8)], sulcate, zonate, glabrous; *margin* distinct, light orange [5A(4–5)]. *Hymenophore* smooth, brownish orange [6C(4–5)] when juvenile, becoming light brown (5D5) when dry, not bleeding when fresh, slightly darkening in KOH, not cracked; *margin* thinning out, distinct and white when juvenile, becoming indistinct and concolourous with hymenophore surface with age. *Context* light brown, corky, up to 1 mm thick. *Hyphal system* monomitic. *Subiculum* distinct, light brown, composed of horizontally arranged hyphae, with crystal masses; *hyphae* simple septate, colourless to pale brown, thick-walled, smooth, rarely branched and septate, 3–7 μm diam. *Subhymenium* thickening, composed of hyphae and collapsed hymenial elements. *Cystidia* of three types: (1) *Acanthocystidia* numerous, clavate, with a few protuberances at tip part, colourless, slightly thick-walled, embedded or slightly projecting beyond the hymenium, with a basal simple septum, 20–40 \times 3–5 μm . (2) *Pseudocystidia* tubular, colourless or pale brown, distinctly thick-walled except in the apex, embedded, 30–100 \times 4–7 μm . (3) *Acutocystidia* scattered, colourless, thin-walled, smooth, unbranched. *Basidia* clavate, colourless, thick-walled, with 4 sterigmata and a basal simple septum, 20–30 \times 4–6 μm ; *basidioles* dominant, in shape similar to basidia, but slightly smaller. *Basidiospores* ovoid to ellipsoid, colourless, thin-walled, smooth, amyloid, acyanophilous, 5–7 \times 3–4 μm , L = 6.1 μm , W = 3.4 μm , Q = 1.6–1.9 (n = 60/2).

Additional specimen examined: **China**, Hainan Province, Lingshui County, Diaoluoshan Nature Reserve, on dead angiosperm branch, 5 Jul. 2019, S.H. He, He 6050 (BJFC 030925).

Notes: *Stereum tropicum* is characterized by resupinate to effused-reflexed basidiomes not bleeding after bruising, a bright yellow hymenophore when fresh, and the presence of acanthocystidia, and acutocystidia. Morphologically, *S. rugosum* is similar to *S. tropicum* by sharing resupinate to effused-reflexed tough basidiomes and presence of acanthocystidia but differs in having larger basidia (30–50 \times 6–8 μm) and longer basidiospores (7–12 μm , Eriksson et al. 1984). *Stereum tropicum* is similar to *S. rhododendri* by having resupinate to effused-reflexed basidiomes, similar size of basidia and basidiospore length, but it is as a rule easy to determine by its thick and tough basidiomes and numerous tubular thick-walled pseudocystidia.

Xylobolus lividocoeruleus (P. Karst.) S.H. He & Y.L. Xu, *comb. nov.* MB 844731.

Basionym: *Corticium lividocoeruleum* P. Karst., *Not. Sällsk. Fauna et Fl. Fenn. Förh.* **9**: 370. 1868.

Synonyms: *Terana lividocoerulea* (P. Karst.) Kuntze, *Revis. gen. pl.* (Leipzig) **2**: 872. 1891.

Gloeocystidium lividocoeruleum (P. Karst.) Höhn. & Litsch., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt.* **1** 115: 1554. 1906.

Gloeocystidiellum lividocoeruleum (P. Karst.) Donk, *Fungus*, Wageningen **26**: 9. 1956.

Aleurodiscus lividocoeruleus (P. Karst.) P.A. Lemke, *Canad. J. Bot.* **42**: 253. 1964.

Acanthophysellum lividocoeruleum (P. Karst.) Parmasto, *Eesti NSV Tead. Akad. Toim., Biol. seer* **16**(4): 377. 1967.

Acanthophysium lividocoeruleum (P. Karst.) Boidin, *Bull. Trimestriel Soc. Mycol. France* **101**(4): 340. 1986.

Notes: *Corticium lividocoeruleum* is the type species of *Acanthophysellum*, but phylogenetic analyses showed that it nested within the *Xylobolus* lineage (Fig. 1). Morphologically, *X. lividocoeruleus* shares with other species in the genus a pseudo-parenchymatic subhymenium, numerous acanthohyphidia and smooth basidiospores, but is unique for its resupinate basidiomes, nodose-septate hyphae and typical gloeocystidia. With this disposition, *Acanthophysellum* becomes a synonym of *Xylobolus*.

DISCUSSION

According to the lineage delimitation, some genera are morphologically well-circumscribed, but some have wide ranges in several aspects. All genera have amyloid basidiospores and gloeocystidia, but most genera have its specific characteristics. *Acanthobasidium* is strongly supported and is characterized by basidia with spines and usually ornamented subglobose basidiospores. The monotypic genus *Acanthofungus* formed a sister lineage to *Gelatinostereum* and *Stereum* but their relationship was not well-supported. *Aleurobotrys* is monotypic and characterized by amyloid acanthohyphidia. *Aleurodiscus* s. str. is still a complex assemblage of species with diverse morphology. At present, we prefer to treat it in a rather broad sense to avoid more lineages and new names. One solution is to treat the subclade from *A. pinicola* to *A. grantii* as *Aleurodiscus* s. str. and *Neoaleurodiscus* as a distinct lineage. However, then generic names for *A. subroseus*, *A. wakefieldiae* and *A. effusus* may be in order. *Conferticum* s. str. contains only two species with repetitive basidia and smooth basidiospores. *Confertotrama* comprises species with abundant gloeocystidia and ornamented or smooth basidiospores. The monotypic genus *Gelatinostereum* is similar to *Stereum* but has gelatinous basidiomes, thin-walled gloeocystidia and hyphae. The *Gloeocystidiopsis* lineage was not well-supported, but species in this lineage have simple-septate hyphae and ornamented basidiospores. *Gloeomyces* includes species with strictly resupinate basidiomes, well-developed acanthohyphidia and relatively small, smooth basidiospores. *Gloeosoma* is characterized by cupulate basidiomes and large echinulate basidiospores. It is closely



related to *Stereodiscus* that has stereoid basidiomes, large smooth basidiospores and is only known in the Southern Hemisphere. The concept of *Megalocystidium* is expanded and it now comprises species with a monomitic or dimittic hyphal system, simple-septate or nodose-septate generative hyphae, with or without acanthohyphidia. *Stereum* is an old genus with many names, but only a few species remain in the core clade. *Stereum* species usually have effused-reflexed to pileate basidiomes, gloeocystidia, acutocystidia and smooth basidiospores but acanthohyphidia maybe present or absent. *Xylobolus* is well-characterized by the distinctly thickened subhymenium with vertically arranged hyphae, numerous acanthohyphidia, relatively small smooth basidiospores and usually causing a white pocket rot.

The present study resolved several important taxonomic and phylogenetic problems and provides a framework for further studies of the phylogeny of the *Stereaceae*. Additional taxa in the family should be added to phylogenetic analyses so that the generic delimitation will be better and more clearly defined. Meanwhile, investigations on the species diversity of the family would benefit from a focus on under-collected areas and hosts, for example, monocots in subtropical and tropical areas.

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Declaration on conflict of interest The authors declare that there is no conflict of interest.

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