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Two new freshwater hyphomycetous species of *Sporoschisma* Berk. & Broome (Chaetosphaeriales) from Tibetan Plateau, China

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ABSTRACT
Four collections were isolated from submerged decaying wood in freshwater habitats. These species are characterized by scattered, capitate setae, straight, smooth, unbranched, brown conidiophores, phialidic conidiogenous cells, and cylindrical conidia. The phylogeny analysis using multi-gene sequences (ITS, LSU and TEF1-α) placed these isolates within *Sporoschisma* Berk. & Broome and formed a distinct clade separate from other species. Consequently, two new species, namely *S. lignicola* R.J.Xu & Q.Zhao, sp. nov. and *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov. were introduced, based on the phylogenetic analysis and morphological features. Illustrations of these species were provided and compared with the similar species.

KEY WORDS
Lignicolous freshwater fungi, Sordariomycetes, asexual morphology, new species.

RÉSUMÉ

Deux nouvelles espèces d'hyphomycètes d'eau douce de Sporoschisma *Berk. & Broome (Chaetosphaeriales) du plateau tibétain, Chine.*

Quatre collections ont été isolées à partir de bois en décomposition submergé dans des habitats d'eau douce. Ces espèces sont caractérisées par des sétacés épars et capitonnés, des conidiophores bruns, droits, lisses et non ramifiés, des cellules conidiogènes phialidiques et des conidies cylindriques. L'analyse phylogénique utilisant des séquences multigéniques (ITS, LSU et TEF1-α) a placé ces isolats au sein de *Sporoschisma* Berk. & Broome et a formé un clade distinct séparé des autres espèces. Par conséquent, deux nouvelles espèces, à savoir *S. lignicola* R.J.Xu & Q.Zhao, sp. nov. et *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov., ont été introduites, sur la base de l'analyse phylogénétique et des caractéristiques morphologiques. Des illustrations de ces espèces ont été fournies et comparées aux espèces similaires.

MOTS CLÉS
Champignons lignicoles d'eau douce, Sordariomycetes, morphologie asexuée, espèces nouvelles.

INTRODUCTION

Sporoschisma Berk. & Broome was introduced by Berkeley (1847) with *S. mirabile* Berk. & Broome as the type species. Hughes (1966) and Goh *et al.* (1997) have significantly revised the genus by presenting historical collection information and an illustrated account in *Sporoschisma*. Réblová (2014) transferred *Sporoschismopsis australiensis* Goh & K.D.Hyde to *Sporoschisma*, based on the characters of cylindrical conidia and presence of capitate setae. Réblová *et al.* (2016) synonymized *Melanochaeta* E.Müll., Harr & Sulmont to *Sporoschisma* and linked sexual of *Melanochaeta* with *Sporoschisma* based on cultural and molecular studies. In the recent research, *S. aquaticum* Z.L.Luo, K.D.Hyde & H.Y.Su was synonym of *S. juvenile* Boud. based on combined morphological and phylogenetic studies, and the accepted species within *Sporoschisma* were limited to 13 species, including *S. australiense* (Goh & K.D.Hyde) Réblová, *S. chiangraiense* N.G.Liu & K.D.Hyde, *S. daemonoropsis* (J.Fröhl. & K.D.Hyde) A.N.Mill., *S. hemipsilum* (Berk. & Broome) Zelski, A.N.Mill. & Shearer, *S. juvenile*, *S. longicatenatum* J.Yang, J.K.Liu & K.D.Hyde, *S. mirabile*, *S. nigroseptatum* D.Rao & P.Rag. Rao, *S. palauense* J.Yang, J.K.Liu & K.D.Hyde, *S. parcicuneatum* Goh & K.D.Hyde, *S. phaeocentron* W.H.Ho, K.D.Hyde & Goh, *S. taitense* (Mugambi & Huhndorf) A.N.Mill., and *S. uniseptatum* Bhat & W.B.Kendr. (Wu & Diao 2022). Later, Réblová *et al.* (2022) conducted an analysis using the ITS and LSU dataset that was curated by Gblocks. The results showed distinct and separate groups for *Chloridium* Link, *Adautomilanezia* Gusmão, S.S.Silva, Fiuza, L.A.Costa & T.A.B.Santos and *Sporoschisma*, and the phylogenetic placement of *Sporoschisma* in Chaetosphaeriaceae has been established.

Sporoschisma is characterized by scattered, capitate setae, straight, smooth, unbranched, brown conidiophores; normally composed of a cylindrical stipe and a swollen venter and a long, cylindrical neck; phialidic conidiogenous cells; conidia cylindrical, mostly truncated at both ends and normally form in chains endogenously and in basipetal succession (Seifert *et al.* 2011; Yang *et al.* 2023). Species of *Sporoschisma* are widely distributed and occur on submerged wood in freshwater habitats, they were comprehensively discussed and extensively detailed in several studies (Hughes 1966; Goh *et al.* 1997; Ho *et al.* 2001, 2002; Réblová 2014; Zelski *et al.* 2014; Luo *et al.* 2016; Yang *et al.* 2016, 2023; Hyde *et al.* 2019; Shen *et al.* 2022; Wu & Diao 2022). Presently, there are 30 epithets in Index Fungorum (2024).

Four collections were isolated from submerged decaying woods in freshwater habitat of the Tibetan Plateau, China. The taxonomic position of two new species in *Sporoschisma* was determined through a phylogenetic analysis of combined ITS, LSU and TEF1-α sequencing data. The detailed description and illustration of these species as well as comparison between related species are provided.

MATERIAL AND METHODS

Collection, morphological examination and isolation of fungi

Specimens were collected in the Tibetan Plateau, China. Samples were observed and examined following the instruction outlined in Xu *et al.* (2023). Macroscopic and microscopic morphology of filamentous fungi (e.g. colonies, conidiomata, conidiophores or conidia) were examined using a stereomicroscope (SteREO Discovery.V12, Carl Zeiss Microscopy GmBH, Germany) and microphotographs were taken using a compound microscope (Nikon ECLIPSE 80i, Nikon, Japan) fitted with a NikonDS-Ri2 digital camera (Nikon, Japan). Measurements were made with the Tarosoft (R) Image Frame Work program and photographic plates used for figures were processed with Adobe Photoshop CS6 software (Adobe Systems, United States). Single spore isolation was carried out following the method described in Xu *et al.* (2023). All specimens were deposited in the Herbarium of Cryptogams of Kunming Institute of Botany, Chinese Academy of Sciences (HKAS), after natural air-drying. The living culture was deposited in the Kunming Institute of Botany Culture Collection (KUNCC), Kunming, China. Index Fungorum and Facesoffungi numbers were registered as mentioned in Index Fungorum (2023) and Jayasiri *et al.* (2015).

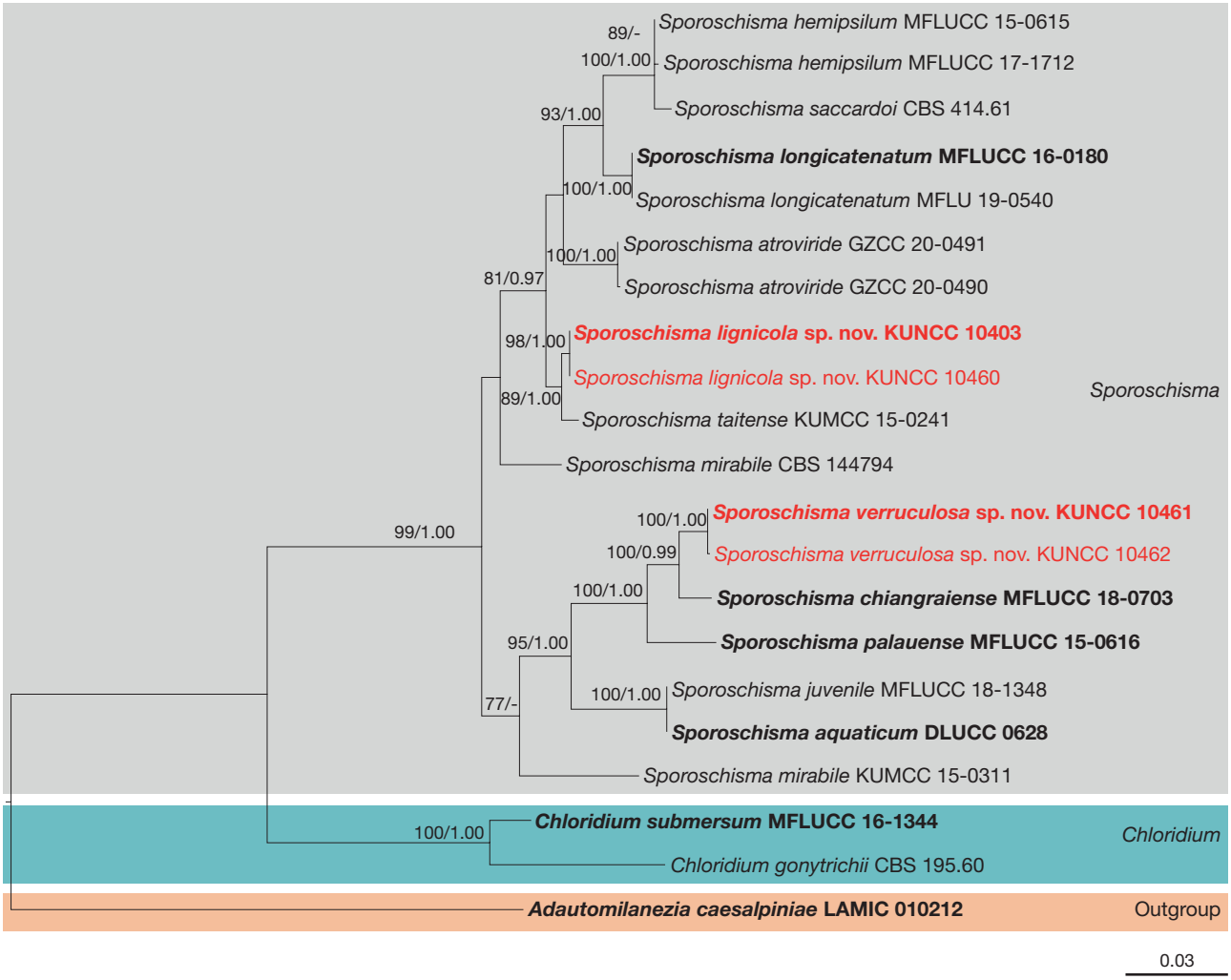

FIG. 1. — RAxML tree based on analysis of combined ITS, LSU and TEF1-α sequences. Bootstrap support values for maximum likelihood (ML) equal to or greater than 75% were given above the nodes (**left**). Bayesian posterior probability (PP) equal to or greater than 0.95 were given above the nodes (**right**) and hyphen (**-**) were marked as values below 0.95. The tree was rooted to *Adautomilanezia caesalpiniae* LAMIC 010212. The type strains were shown in **bold**, and the newly generated isolates were shown in **red**.

MOLECULAR PHYLOGENY

Protocols for DNA extraction, PCR, and sequencing followed the procedures described in Xu *et al.* (2023). All additional sequences used in the analyses followed recent molecular studies (Luo *et al.* 2016; Yang *et al.* 2016, 2023) and were retrieved from GenBank (Table 1). Multiple sequence alignments were aligned with MAFFT v.7 (http://mafft.cbrc.jp/alignment/server/index.html, Katoh *et al.* 2019) and automatically trimmed by using TrimA1 (http://phylemon.bioinfo.cipf.es/utilities.html, Capella-Gutiérrez *et al.* 2009). A combined sequence dataset was performed with the SquenceMatrix v.1.7.8 (Vaidya *et al.* 2011). Maximum likelihood (ML) analysis was performed by RAxML-HPC2 v.8.2.12 (Stamatakis 2014) in the CIPRES Science Gateway web server (http://www.phylo.org/portal2, Miller *et al.* 2010) by using 1000 rapid bootstrap replicates and the GTRGAMMA+I model.

The model of evolution for the Bayesian inference (BI) analysis was performed by using MrModeltest v2.3 (Nylander *et al.* 2004; Ronquist *et al.* 2012). HKY+G was selected as the best-fitting model for ITS, GTR+I+G was selected as the best-fitting model for LSU, and GTR+I was selected as the best-fitting model for TEF1-α dataset. Nucleotide substitution model BI analysis was conducted by Markov chain Monte Carlo sampling (BMCMC) to assess posterior probabilities (PP) by using MrBayes v.3.2.7 (Ronquist *et al.* 2012). Six simultaneous Markov chains were run for random trees for 1 000 000 generations and trees were sampled every 200th generation. Bootstrap support values for ML equal to or greater than 75% and Bayesian posterior probabilities (PP) equal to or greater than 0.95 were given above the nodes in the phylogenetic tree (Fig. 1). Phylogram was visualized by using FigTree v1.4.0 (Rambaut 2012) and rearranged in Adobe Photoshop CS6 software (Adobe Systems, United States). The new sequences were deposited into GenBank (Table 1) and the final alignment and phylogenetic tree were registered in TreeBASE under the submission ID: 30542 (http://www.treebase.org/).

TABLE 1. — Taxa used in the phylogenetic analyses and their corresponding GenBank accession numbers. The newly generated sequences are indicated in **red**. The ex-type strains are in **bold** and "**–**" indicate unavailable sequences.

Species	Isolate no.	GenBank accession no.		
		ITS	LSU	TEF
Adautomilanezia caesalpiniae Gusmão, S.S.Silva, Fiuza, L.A.Costa & T.A.B.Santos	LAMIC 010212	**KX821777**	**KU170671**	–
Chloridium gonytrichii (F.A.Fernández & Huhndorf) Réblová & Seifert	CBS 195.60	MH857954	MH869503	–
C. submersum Z.L.Luo, K.D.Hyde & H.Y.Su	MFLUCC 16-1344	**MN860551**	**MN860556**	–
Sporoschisma aquaticum Z.L.Luo, K.D.Hyde & H.Y.Su	DLUCC 0628	**KX455863**	**KX455856**	–
S. atroviride J.Yang, J.K.Liu & K.D.Hyde	GZCC 20-0490	OP377817	OP377916	OP472997
S. atroviride	GZCC 20-0491	OP377818	OP377917	OP472998
S. chiangraiense N.G.Liu & K.D.Hyde	MFLUCC 18-0703	**MH883032**	**MH883030**	–
S. hemipsilum (Berk. & Broome) Zelski, A.N.Mill. & Shearer	MFLUCC 15-0615	KX505869	KX358074	OP473070
S. hemipsilum	MFLUCC 17-1712	MK828616	MK835816	–
S. juvenile Boud.	MFLUCC 18-1348	MK828619	MK835819	MN194072
S. lignicola R.J.Xu & Q.Zhao, sp. nov.	KUNCC 10403	**OP626326**	**OR131044**	**OR136724**
S. lignicola R.J.Xu & Q.Zhao, sp. nov.	KUNCC 10460	OR131039	OR131045	OR136725
S. longicatenatum J.Yang, J.K.Liu & K.D.Hyde	MFLU 19-0540	MN513036	MN511738	–
S. longicatenatum	MFLUCC 16-0180	**KX505871**	**NG059700**	**OP473071**
S. mirabile Berk. & Broome	KUMCC 15-0311	KX455864	KX455857	–
S. mirabile	CBS 144794	MW987830	MW987825	–
S. palauense J.Yang, J.K.Liu & K.D.Hyde	MFLUCC 15-0616	**KX505870**	**KX358075**	**OP473072**
S. saccardoi E.W.Mason & S.Hughes	CBS 414.61	MH858104	MH869677	–
S. taitense (Mugambi & Huhndorf) A.N.Mill.	KUMCC 15-0241	KX455865	KX455858	–
S. verruculosa R.J.Xu & Q.Zhao, sp. nov.	KUNCC 10461	**OR098539**	**OR131046**	**OR136726**
S. verruculosa R.J.Xu & Q.Zhao, sp. nov.	KUNCC 10462	OR131040	OR131047	OR136727

RESULTS

PHYLOGENETIC ANALYSES

The concatenated sequence datasets of ITS, LSU and TEF1-α gene regions comprise 21 strains and one outgroup taxa, *Adautomilanezia caesalpiniae* Gusmão, S.S.Silva, Fiuza, L.A.Costa & T.A.B.Santos (LAMIC 010212) (Yang *et al.* 2023). The datasets contain 4869 characters including gaps after alignment (ITS = 1-469 bp, LSU = 470-1243 bp, TEF1-α = 1244-2013 bp). The RAxML analysis of the combined dataset yielded a best scoring tree with a final ML optimization likelihood value of –5911.724601. The aligned sequence matrix comprises 339 distinct alignment patterns with 22.90% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.214525, C = 0.290860, G = 0.307366, T = 0.187249, with substitution rates AC = 0.967050, AG = 2.278810, AT = 1.126234, CG = 1.233882, CT = 7.781256, GT = 1.000000, gamma distribution shape parameter α = 0.0010000000.

The tree topologies of combined sequence data obtained from ML and BI analyses were not significantly different. The phylogenetic analysis showed that the two collections of *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. (KUNCC 10403 and KUNCC 10460) formed a sister clade with *S. taitense* (KUMCC 15-0241) with 89% ML/1.00 PP support. Two collections of *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov. (KUNCC 10461 and KUNCC 10462) formed a sister clade with *S. chiangraiense* (MFLUCC 18-0703) with 100% ML/0.99 PP support (Fig. 1).

TAXONOMY

Family CHAETOSPHAERIACEAE
Réblová, M.E.Barr & Samuels
Genus *Sporoschisma* Berk. & Broome

Sporoschisma lignicola R.J.Xu & Q.Zhao, sp. nov.
(Fig. 2)

TYPE MATERIAL. — **China** • Yunnan Province, Shangri-La City, Napa Lake; 27°50'58.9"N, 99°38'17.9"E; alt. 3273 m; saprobic on submerged decaying wood in a freshwater lake; 26.XII.2020; R.J. Xu; *MD-207*; holotype: HKAS[HKAS 129208]; ex-type living culture: KUNCC 10403.

ADDITIONAL MATERIAL. — **China** • Shangri-La City, Giligu River; 27°47'53.7"N, 99°54'49.9"E; alt. 3423 m; saprobic on submerged decaying wood in a freshwater river; 25.XII.2020; R.J. Xu; *SW-807*; HKAS[HKAS 129209]; living culture: KUNCC 10460.

ETYMOLOGY. — Referring to this taxon dwelling on wood.

INDEX FUNGORUM. — IF 900719.

FACESOFFUNGI. — FoF 14351.

DESCRIPTION

Saprobic on submerged decaying wood in a freshwater habitat. Sexual morph: Undetermined. Asexual morph: Colonies superficial, effuse, dark brown. Mycelium immersed, composed of pale to dark brown hyphae. Setae 81-135 × 4-5 µm ($\bar{x}$ = 103 × 4 µm, n = 15), arising from the bulbous base, often

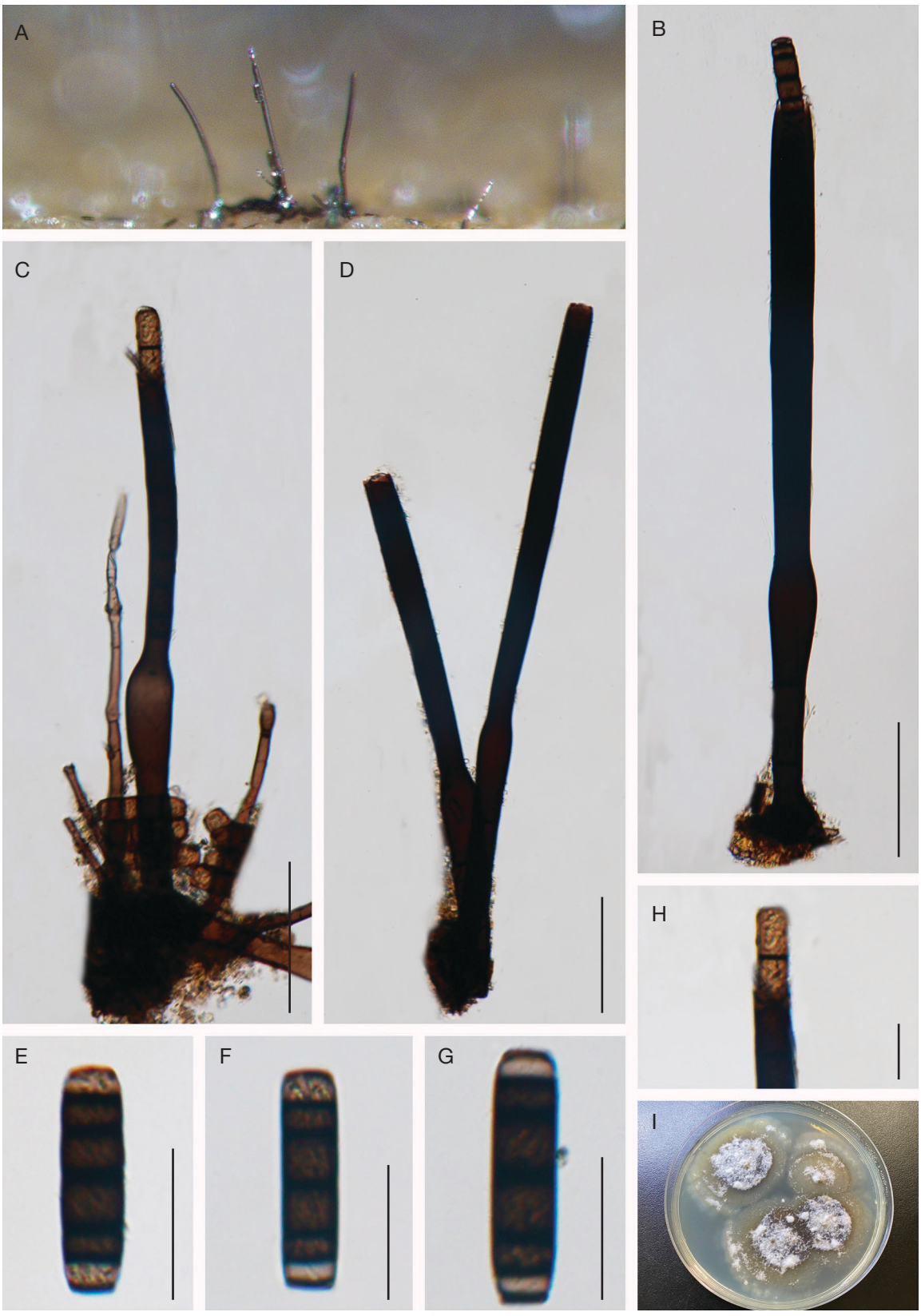

Fig. 2. — *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. (holotype, HKAS 129208): **A**, colonies on substrate; **B**, **D**, conidiophores with conidia; **C**, conidiophores with setae; **E**-**G**, conidia; **H**, conidiogenous cell; **I**, culture on PDA. Scale bars: B-D, 50 µm; E-H, 20 µm.

with 1-2 at the side of conidiophores, capitate, 2-3-septate, brown, slightly constricted at some septa. Conidiophores 131-278 µm long, stipes 9-11 µm wide below venter and 9-15 µm wide above, 13-20 µm wide at the venter, macronematous, mononematous, erect, straight or slightly flexuous, solitary or 2-3 group, smooth-walled, dark brown to black, cylindrical, a cylindrical stipe and a swollen venter with a long cylindrical neck. Conidiogenous cells monophialidic, integrated, terminal, determinate, dark brown, lageniform, with a tubular collarette and swollen venter, flared margin at free end. Conidia 28-34 × 7-10 µm ($\bar{x}$ = 30 × 9 µm, n = 20), catenate, emerging in a chain inside the tubular collarette, develop basipetally, cylindrical, truncate at both ends, 5-septate, with conspicuously darkened septa, hyaline when young, brown to dark brown when mature, with pale brown to subhyaline end cells.

Culture characteristics

Conidia germinating on PDA within 48 hours and germ tubes produced from both ends. Colonies on PDA reaching 7-10 mm diam at 30 days, with dense, greyish, sparse mycelium on surface initially, white grey at the undulant edge; in reverse with a brown middle and sparse, light brown margin.

Notes

Morphologically, *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. is highly similar to *S. atroviride* J.Yang, J.K.Liu & K.D.Hyde, *S. longicatenatum*, and *S. nigroseptatum* in having capitate setae scattered or in groups among conidiophores, cylindrical conidiophores and catenate, cylindrical, septa, with hyaline end cells conidia (Goh *et al.* 1997; Yang *et al.* 2016, 2023). However, *S. lignicola* R.J.Xu & Q.Zhao, sp. nov. differs from *S. atroviride* in having shorter conidiophores (131-278 vs 275-390 µm) and smaller conidia (28-34 × 7-10 vs 36-49(-53) × (13-)14-15.5(-16) µm) (Yang *et al.* 2023). *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. differs from *S. longicatenatum* in having smaller sized conidia (28-34 × 7-10 vs 35-45.5 × 9-11 µm) and cylindrical, brown conidia (Yang *et al.* 2016). *Sporoschisma nigroseptatum* differs from *S. lignicola* R.J.Xu & Q.Zhao, sp. nov. in having longer conidiophores (300-410 vs 131-278 µm) and doliiform conidia (Goh *et al.* 1997).

Phylogenetic analysis showed that *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. is located in a distinct clade within *Sporoschisma*, and formed a sister lineage with *S. taitense* with 89% ML/1.00 PP support (Fig. 1). However, comparison of the ITS gene region between the ex-holotype of *Sporoschisma lignicola* R.J.Xu & Q.Zhao, sp. nov. (KUNCC 10403) and *S. taitense* (KUMCC 15-0241) revealed a 2.1% (11/536 bp, excluding gap) difference (Jeewon & Hyde 2016; Luo *et al.* 2016). In addition, *S. lignicola* R.J.Xu & Q.Zhao, sp. nov. is distinguished from *S. taitense* by having shorter setae (81-135 vs 192-204 µm), shorter conidiophores (131-278 vs 299-322 µm), and cylindrical to doliiform conidia (Luo *et al.* 2016).

Sporoschisma verruculosa R.J.Xu & Q.Zhao, sp. nov. (Fig. 3)

Type material. — **China** • Tibet, Zayu County, Xiachayu Town; 28°29'39.2"N, 96°59'35.25"E; alt. 1537 m; saprobic on submerged decaying wood in a freshwater stream; 14.VII.2022; R.J. Xu; *MD-634*; holotype: HKAS[HKAS 129210]; ex-type living culture: KUNCC 10461.

Additional material. — **China** • Zayu County, Guyu Town; 28°53'19.64"N, 97°27'49.23"E; alt. 2805 m; saprobic on submerged decaying wood in a freshwater stream; 14.VII.2022; R.J. Xu; *MD-634-2*; HKAS[HKAS 129211]; living culture: KUNCC 10462.

Etymology. — "verruculosa" referring the verruculose conidia.

Index Fungorum. — IF900720.

Facesoffungi. — FoF 14352.

Description

Saprobic on submerged decaying wood in a freshwater stream. Sexual morph: Undetermined. Asexual morph: Colonies superficial, effuse, dark brown, with long chains of conidia. Mycelium immersed, composed of pale to dark brown hyphae. Setae 116-204 × 5-9 µm ($\bar{x}$ = 161 × 6 µm, n = 15), arising from the bulbous base, often with 1-2 at the side of conidiophores, capitate, 2-4-septate, brown, slightly constricted at some septa. Conidiophores 130-320 µm long, stipes 10-18 µm wide below venter and 16-22 µm wide above, 17-33 µm wide at the venter, macronematous, mononematous, erect, straight or slightly flexuous, solitary or 2-3 group, smooth-walled, dark brown to black, cylindrical, a cylindrical stipe and a swollen venter with a long cylindrical neck. Conidiogenous cells monophialidic, integrated, terminal, determinate, dark brown, lageniform, with a tubular collarette and swollen venter, flared margin at free end. Conidia 36-52 × 10-16 µm ($\bar{x}$ = 42 × 14 µm, n = 25), catenate, emerging in a chain inside the tubular collarette, develop basipetally, guttulate, verruculose, cylindrical, slightly rounded at both ends, with conspicuously darkened septa, hyaline, 0-septate when young, brown to dark brown, 3-septate, when mature, all the cells are the same length.

Culture characteristics

Conidia germinating on PDA within 48 hours and germ tubes produced from both ends. Colonies on PDA reaching 7-10 mm diam at 30 days, with dense, grey, sparse mycelium on surface initially, white grey at the entire; in reverse with a light brown middle and white grey margin.

Notes

Morphologically, *Sporoschisma verruculosa* R.J.Xu & Q.Zhao, sp. nov. shares common characteristics with *S. aquaticum* in having capitate setae scattered or in groups among conidiophores, cylindrical conidiophores and catenate, cylindrical, brown to dark brown septa, conidia (Goh *et al.* 1997; Luo *et al.* 2016). However, *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov. differs from *S. aquaticum* by having larger sized conidia (36-52 vs 26-32 µm) and verruculose conidia (Luo *et al.* 2016). Phylogenetically, *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov. forms

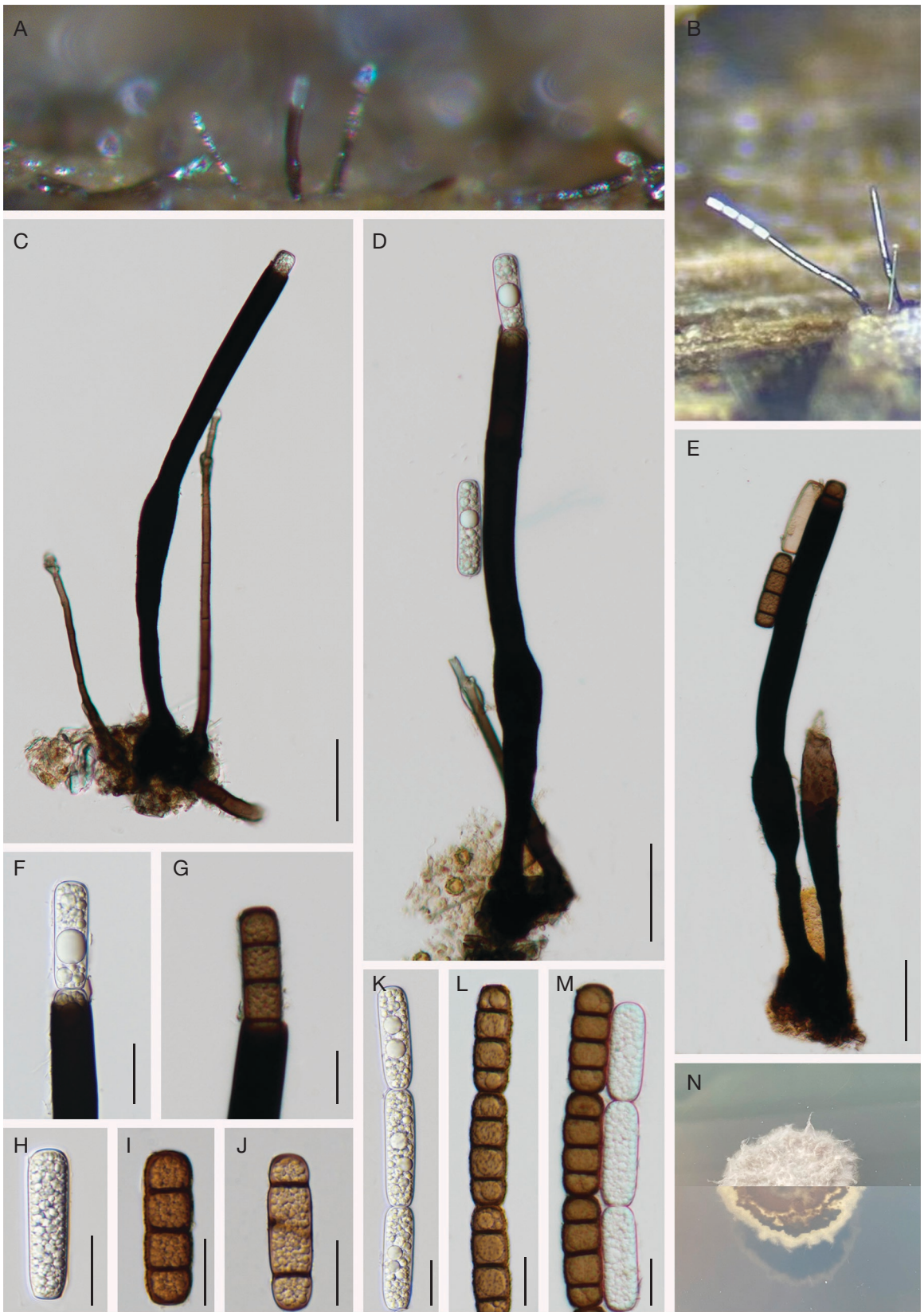

Fig. 3. — *Sporoschisma verruculosa* R.J.Xu & Q.Zhao, sp. nov. (holotype, HKAS 129210): **A**, **B**, colony on wood with long conidia chains; **C**, **D**, conidiophores with setae; **E**, conidiophores with conidia; **F**, **G**, conidiogenous cell with a conidium; **H**-**M**, conidia; **N**, culture on PDA. Scale bars: C-E, 50 µm; F-M, 20 µm.

a sister lineage with *S. chiangraiense* with 100% ML/0.99 PP support (Fig. 1). However, *S. verruculosa* R.J.Xu & Q.Zhao, sp. nov. differs from *S. chiangraiense* by having 3-septate and verruculose conidia (Hyde *et al.* 2019).

DISCUSSION

Species of *Sporoschisma* are morphologically remarkably similar, sharing characteristics such as capitate setae, cylindrical conidiophores and catenate, cylindrical, septa conidia (Hughes 1949, 1966; Goh *et al.* 1997; Sivichai *et al.* 2000; Réblová 2014; Zelski *et al.* 2014; Luo *et al.* 2016; Réblová *et al.* 2016; Yang *et al.* 2016, 2023; Hyde *et al.* 2019). Among these species, some have 3-septate conidia, including *S. aquaticum*, *S. australiense*, *S. juvenile* and *S. mirabile* (Goh *et al.* 1997; Réblová 2014; Luo *et al.* 2016). Additionally, species with 5-septate conidia include *S. atroviride*, *S. hemipsilum*, *S. nigroseptatum*, and *S. saccardoi* (Goh *et al.* 1997; Luo *et al.* 2016; Yang *et al.* 2023). However, their positions in the phylogenetic tree are not correlated (see Fig. 1). Interestingly, the conidia with 3-septate are slightly rounded at both ends, except for *S. australiense*. Conversely, 5-septate conidia typically have truncate ends, with the cells at both ends appearing hyaline to pale brown (Hughes 1949, 1966; Goh *et al.* 1997; Sivichai *et al.* 2000; Réblová 2014; Zelski *et al.* 2014; Luo *et al.* 2016; Réblová *et al.* 2016; Yang *et al.* 2016, 2023; Hyde *et al.* 2019).

Sporoschisma is a cosmopolitan genus that is commonly found in freshwater habitats. Recently, 12 species have been reported on submerged wood in freshwater environments, including *S. aquaticum*, *S. atroviride*, *S. australiense*, *S. chiangraiense*, *S. hemipsilum*, *S. juvenile*, *S. longicatenatum*, *S. nigroseptatum*, *S. palauense*, *S. parcicuneatum*, *S. phaeocentron* and *S. uniseptatum* (Hughes 1949, 1966; Goh *et al.* 1997; Sivichai *et al.* 2000; Réblová 2014; Luo *et al.* 2016; Réblová *et al.* 2016; Yang *et al.* 2016, 2023; Hyde *et al.* 2019; Bao *et al.* 2021).

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