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Savoryella claviformis (*Savoryellaceae*), a new freshwater hyphomycetous species from the Tibetan Plateau, China

Rong-Ju Xu[1,2,3], Saranyaphat Boonmee[1,2], Wei Dong[4], Yi-Yun Guo[3], Qing-Yun Yang[3,5], Kevin D. Hyde[1,2,3*] and Qi Zhao[3*]

[1] *School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand*
[2] *Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand*
[3] *Yunnan Key Laboratory of Fungal Diversity and Green Development & Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China*
[4] *Innovative Institute for Plant Health / Key Laboratory of Green Prevention and Control on Fruits and Vegetables in South China, Ministry of Agriculture and Rural Affairs, Zhongkai University of Agriculture and Engineering, Guangzhou 510225, Guangdong, China*
[5] *Yunan Forestry Technological College, Kunming 650224, Yunnan, China*
* Corresponding authors, E-mail: kdhyde3@gmail.com; zhaoqi@mail.kib.ac.cn

Abstract

During an investigation of lignicolous freshwater fungi on the Tibetan Plateau, China, two collections were obtained from submerged wood in freshwater habitats. The morphological examinations and phylogenetic analysis using LSU, SSU, and ITS sequence data have identified that the two collections represent a novel species within the genus *Savoryella*, namely *S. claviformis*. *Savoryella claviformis* forms a distinct clade within *Savoryella*, and possesses unique characteristics compared with existing asexual species in having semi-micronematous, solitary, cylindrical conidiophores, terminal, determinate conidiogenous cells, and acrogenous, claviform, rostrate conidia. Detailed descriptions and illustrations of this species are provided.

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Introduction

In recent years, there has been a significant increase in research focusing on the taxonomy and phylogeny of saprobic fungi worldwide. These include an extensive examination of the diversity of lignicolous freshwater fungi in China[1–8]. The Tibetan Plateau, as the largest and most unique geographical region on Earth encompasses a remarkable range of endemic diversity[9–11]. Recent advancements in the study of lignicolous freshwater fungi on the Tibetan Plateau have led to the discovery of an increasing number of species, underscoring its critical importance for global biodiversity conservation and scientific research[12–14].

Savoryella was introduced by Jones & Eaton[15] with *S. lignicola* as the type species. The sexual morphs of *Savoryella* are characterized by immersed, partly immersed, or superficial, globose, subglobose, or ellipsoidal ascostromata, typically 8-spored, occasionally 2-spored, cylindrical or clavate, unitunicate asci, and ellipsoidal, three-septate ascospores[16–18]. By contrast, the asexual morphs are characterized by glistening, punctiform colonies; micronematous, mononematous conidiophores; holoblastic, determinate, integrated, terminal, and intercalary conidiogenous cells, and solitary or aggregated, pyriform to obovoid, septate conidia[19]. Zhang et al.[19] synonymized *Trichocladium nypae* with *Savoryella nypae* and introduced an asexual species, *S. sarushimana*, into the genus *Savoryella*, based on morphological and phylogenetic analyses. Subsequently, Tian et al.[20] reported two additional asexual species, *S. cocois*, and *S. chiangraiensis*, collected from decaying leaves of the *Arecaceae*, based on phylogenetic analysis and morphological characters. *Savoryella*, recognized as a holomorphic genus predominantly inhabits submerged, decaying woody debris within both aquatic and terrestrial ecosystems. It has been systematically described and illustrated by mycologists worldwide[15,18,21–25].

During the investigation of the diversity of lignicolous freshwater fungi on the Tibetan Plateau, two collections were made from freshwater habitats of taxa in their hyphomycetous forms. Multigene phylogenetic analysis showed that these two isolates belong to *Savoryella*. In this study, one new species, *Savoryella claviformis*, is introduced with morphological description and phylogenetic placement. These discoveries further add to the diversity of freshwater fungi on the Tibetan Plateau.

Materials and methods

Collection, morphological examination, and isolation of fungi

Submerged decaying wood samples were collected from freshwater habitats in the Tibetan Plateau, China. Samples were obtained from freshwater lakes and rivers, encompassing various substrates such as parts of tree trunks, branches, twigs, and litter. The specimens were studied following the methods of Senanayake et al.[26]. Microscopic structures were examined by using a stereomicroscope (SteREO Discovery.V12, Carl Zeiss

Microscopy GmBH, Germany), photographed by using a Nikon ECLIPSE 80i compound microscope fitted with a NikonDS-Ri2 digital camera, macro morphological characters were examined by using a dissection microscope (Nikon SMZ745T, Nikon Instruments Inc., Japan), photographed by using a Canon 6D Mark II camera, measured by using the Tarosoft (R) Image Frame Work program. The illustrated figures were processed by using Adobe Photoshop CS6 v. 10.0 software (Adobe Systems, San Jose, CA, USA).

Single spores were isolated on potato dextrose agar (PDA) plates using the techniques outlined in Senanayake et al.[26]. Both the holotype and pure cultures were deposited at the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), and the Kunming Institute of Botany Culture Collection (KUNCC), Kunming, China. Taxonomic novelties were submitted to the Faces of Fungi database[27] and Index Fungorum 2024[28].

DNA extraction, polymerase chain reaction (PCR) amplification, and sequencing

Fresh mycelia were scraped from colonies grown on PDA plates and transferred to a 1.5 mL microcentrifuge tube using a sterilized lancet for genomic DNA extraction. Fungal genomic DNA was extracted using the TOLOBIO Plant Genomic DNA Extraction Kit (Shanghai Co. Ltd, China), following the protocols in the manufacturer's instructions.

PCR amplifications were undertaken using the following primer pairs: ITS5/ITS4 for the internal transcribed spacer ribosomal DNA (rDNA) region, encompassing the 5.8S rDNA coding region (ITS); LR0R/LR5 for the 28S rDNA of the nuclear ribosomal large subunit (LSU); NS1/NS4 for the 18S rDNA of the nuclear ribosomal small subunit (SSU)[29,30]. DNA preparation was conducted in a 25 μL mixture, which included 21 μL of 1× Power Taq PCR Master Mix, 1 μL of each primer from a 10 μL stock, and 2 μL of genomic DNA, and amplification was performed in the BioTeke GT9612 thermocycler (Beijing, China). The PCR conditions for ITS, LSU, and SSU involved an initial denaturation at 98 °C for 3 min, followed by 35 cycles of 98 °C for 20 s for denaturation, 53 °C for 10 s for annealing, and 72 °C for 20 s for extension, and then the final extension at 72 °C for 5 min.

The PCR products were examined using 1% agarose gel electrophoresis with ethidium bromide staining. The presence of distinct bands was confirmed using the Compact Desktop UV Transilluminator Analyzer GL-3120 gel documentation system. The PCR products were sequenced by Tsingke Company (Beijing, China).

Phylogenetic analyses

Newly sequences were blasted to search for closely related taxa in GenBank database (www.ncbi.nlm.nih.gov/blast). Sequences generated from the ITS, LSU, and SSU gene regions were verified before further analyses, using BioEdit v. 7.0.9[31]. Sequences with high similarity percentages were determined to find the closest matches with taxa and from recently published data in Table 1[19–21]. Multiple sequence alignments were aligned with MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/index.html)[32] and automatically trimmed by using TrimA1 (http://phylemon2.bioinfo.cipf.es/index.html)[33]. A combined sequence dataset was performed with the SquenceMatrix v. 1.7.8[34].

A maximum likelihood (ML) analysis was conducted using RAxML-HPC2 v. 8.2.12[35] on the CIPRES Science Gateway web server[36] (www.phylo.org/portal2), employing 1,000 rapid bootstrap replicates and the GTRGAMMA + I model.

The model of evolution for the Bayesian inference (BI) analysis was performed by using MrModeltest v. 2.3[37,38]. GTR + I + G was selected as the best-fitting model for the ITS, LSU, and SSU dataset. For the 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[38]. 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). Phylograms were created using FigTree v. 1.4.0[39] and subsequently modified in Adobe Photoshop CS6 (Adobe Systems, USA). The completed alignments and phylogenetic trees were then submitted to TreeBASE, with the submission ID 31293 (www.treebase.org).

Results

Phylogenetic analyses

Best-scoring RA x ML tree for *Savoryellaceae* based on analysis of the combined LSU, SSU, and ITS datasets. The combined dataset comprised 51 strains with 3,268 characters including gaps (LSU: 1–1,845 bp; SSU: 1,846–2,759 bp; ITS: 2,760–3,268 bp). The tree is rooted with *Pleurotheciella aquatica* (MFLUCC 17-0464) and *P. erumpens* (CBS 142447)[18] and has a final ML likelihood value of −22,514.850213. The matrix had 1,326 distinct alignment patterns, with 36.62% undetermined characters or gaps. The estimated base frequencies were A = 0.226977, C = 0.268195, G = 0.306489, T = 0.198339; the substitution rates were AC = 1.307677, AG = 2.608024, AT = 1.966100, CG = 0.982783, CT = 6.087648, and GT = 1.000000; and the gamma distribution shape parameter α = 0.0010000000. The tree topologies of combined sequence data obtained from ML. BI analyses were not significantly different (Fig. 1).

Phylogenetic analysis showed that *Savoryella claviformis* (KUNCC 10408 and KUNCC 10495) formed a distinct lineage within the genus, and formed a distinct and sister group (100% ML, 1.00 BIPP) with *S. bambusicola* (UESTCC 22-0057 and CGMCC 3.23775) (Fig. 1).

Taxonomy

Savoryella claviformis R.J. Xu, S. Boonmee, K.D. Hyde & Q. Zhao, ***sp. nov.*** (Fig. 2)

MycoBank: MB853230; *Facesoffungi number*: FoF 15685

Etymology: The specific epithet 'claviformis' refers to the claviform conidia.

Holotype: HKAS 133191

Saprobic on decaying stems of wood submerged in a freshwater stream habitat. **Asexual morph**: *Colonies* effuse, scattered, brown to dark brown. *Mycelium* immersed, subhyaline to pale brown, composed of branched, septate hyphae. *Conidiophores* 66–151 × 3–6 μm ($\overline{x}$ = 99 × 4 μm, n = 20), semi-micronematous, mononematous, straight or slightly flexuous, solitary, cylindrical, smooth-walled, septate, unbranched, pale brown to brown, guttulate, truncate at the apex. *Conidiogenous cells* holoblastic, monoblastic, terminal, determinate, cylindrical, dark brown to brown, smooth. *Conidia* 55–160 × 6–12 μm ($\overline{x}$ = 102 × 9 μm, n = 25), acrogenous, solitary, fusiform, claviform, rostrate, straight or slightly curved, tapering at apex, truncated

Table 1. Taxa used in the phylogenetic analyses and their corresponding GenBank accession numbers.

Taxa	Vouchers/strains/isolates	GenBank accession numbers		
		ITS	LSU	SSU
Aquabispora sp.	MFLU 18-1002	MK421951	MK421953	MK421952
Aquabispora setosa	**GZCC 20-0492**	**OP377819**	**OP377918**	**OP378003**
Ascotaiwania latericolla	**ICMP 22739**	**MN699390**	**MN699407**	**–**
Ascotaiwania lignicola	NIL 00005	HQ446341	HQ446364	HQ446284
Ascotaiwania lignicola	NIL 00006	HQ446342	HQ446365	HQ446285
Bactrodesmium abruptum	CBS 145967	MN699393	MN699410	MN699367
Bactrodesmium diversum	CBS 142448	MN699352	MN699412	MN699369
Bactrodesmium diversum	CBS 144080	MN699355	MN699415	MN699371
Bactrodesmium leptopus	CBS 144542	MN699388	MN699423	MN699374
Bactrodesmium obovatum	CBS 144407	MN699397	MN699426	MN699377
Bactrodesmium pallidum	CBS 142449	MN699363	MN699428	MN699379
Bactrodesmium pallidum	CBS 145349	MN699364	MN699429	MN699380
Canalisporium jinghongense	SS 03491	GQ390287	GQ390272	GQ390257
Canalisporium kenyense	MFLU17-1086	MH701998	MH701999	–
Canalisporium krabiense	**MFLU 16-1888**	**MH275051**	**MH260283**	**–**
Canalisporium pallidum	**SS 00498**	**GQ390295**	**GQ390280**	**GQ390265**
Canalisporium paulopallidum	NCYU-106A2-3-1	MT946658	–	–
Canalisporium paulopallidum	**NCYU-106A2-3-2**	**MT946659**	**–**	**–**
Canalisporium pulchrum	SS 03773	GQ390293	GQ390278	GQ390263
Canalisporium sichuanense	CGMCC 3.23926	OQ428270	OQ428262	OQ428254
Canalisporium sichuanense	UESTCC 22.0060	OQ428271	OQ428263	OQ428255
Canalisporium taiwanense	**NCYU-108ZQ-D1-1-1**	**MT946663**	**–**	**–**
Canalisporium taiwanense	NCYU-108ZQ-D1-1-2	MT946664	–	–
Canalisporium thailandense	MFLU 16-1900	MH275052	MH260284	–
Dematiosporium aquaticum	CBS 144793	MN699402	MN699433	MN699385
Dematiosporium bambusicola	**CGMCC 3.23774**	**OQ428268**	**OQ428260**	**OQ428252**
Dematiosporium bambusicola	UESTCC 22.0059	OQ428273	OQ428265	OQ428256
Neoascotaiwania fusiformis	**MFLUCC 15-0621**	**MG388215**	**KX550893**	**–**
Neoascotaiwania limnetica	CBS 126576	KY853452	KY853513	KT278689
Neoascotaiwania terrestris	**CBS 142291**	**KY853454**	**KY853515**	**KY853547**
Pleurotheciella aquatica	**MFLUCC 17-0464**	**MF399236**	**MF399253**	**MF399220**
Pleurotheciella erumpens	**CBS 142447**	**MN699406**	**MN699435**	**MN699387**
Savoryella appendiculata	NF 00206	HQ446350	–	HQ446293
Savoryella aquatica	SS 03801	HQ446349	HQ446372	HQ446292
Savoryella bambusicola	**CGMCC 3.23775**	**OQ428269**	**OQ428261**	**OQ428253**
Savoryella bambusicola	UESTCC 22.0057	OQ428267	OQ428259	OQ428251
Savoryella claviformis	**KUNCC 10408**	**OP626331**	**PP577958**	**PP577960**
Savoryella claviformis	KUNCC 10495	PP580830	PP577959	PP577961
Savoryella fusiformis	SS 00783	HQ446351	–	HQ446294
Savoryella lignicola	NF 00204	HQ446357	HQ446378	HQ446300
Savoryella longispora	SAT 00320	HQ446358	HQ446379	HQ446301
Savoryella nypae	MFLUCC 18-1570	MK543219	MK543210	MK543237
Savoryella paucispora	SAT 00867	HQ446361	HQ446382	HQ446304
Savoryella sarushimana	**NBRC 105262**	**–**	**MK411004**	**MK411005**
Savoryella verrucosa	SS 03331	HQ446355	HQ446376	HQ446298
Savoryella yunnanensis	**MFLUCC 18-1395**	**–**	**MK411422**	**MK411423**
Savoryella sp.	NF 00205	HQ446362	–	HQ446305
Savoryella cocois	**MFLU 23-0227**	**OR581911**	**OR438867**	**OR458366**
Savoryella cocois	GZAAS 23-0589	OR581912	OR438868	OR458367
Savoryella chiangraiensis	GZAAS 23-0590	OR581914	OR438870	OR458369
Savoryella chiangraiensis	**MFLU 23-0228**	**OR581913**	**OR438869**	**OR458368**

The newly generated sequences are indicated in blue. The ex-type strains are in bold and '–' indicates unavailable sequences.

at the base, 4–6-septate, smooth, guttulate, brown when young, dark brown to black when mature. **Sexual morph**: Undetermined.

Culture characteristics: Conidium germinated on PDA within 48 h. Mycelia superficial, velvet, irregular, circular, raised near the center, surface villiform, dense, grey mycelium in the center, brown to grey from above, dark brown from below, becoming sparse and paler at the entire margin.

Material examined: CHINA, Xinjiang Province, Bayingoleng Mongolian Autonomous Prefecture, Kaidu River, 41°52'4.8" N, 86°43'39.8" E, 1049 msl, saprobic on submerged decaying wood in freshwater habitats, 22 July 2021, R.J. Xu, MD-325 (HKAS 133191, holotype), ex-type culture KUNCC 10408. Bayingoleng Mongolian Autonomous Prefecture, Bosten Lake, 42°3'4.69" N, 87°8'47.71" E, 1051 msl, saprobic on submerged decaying wood

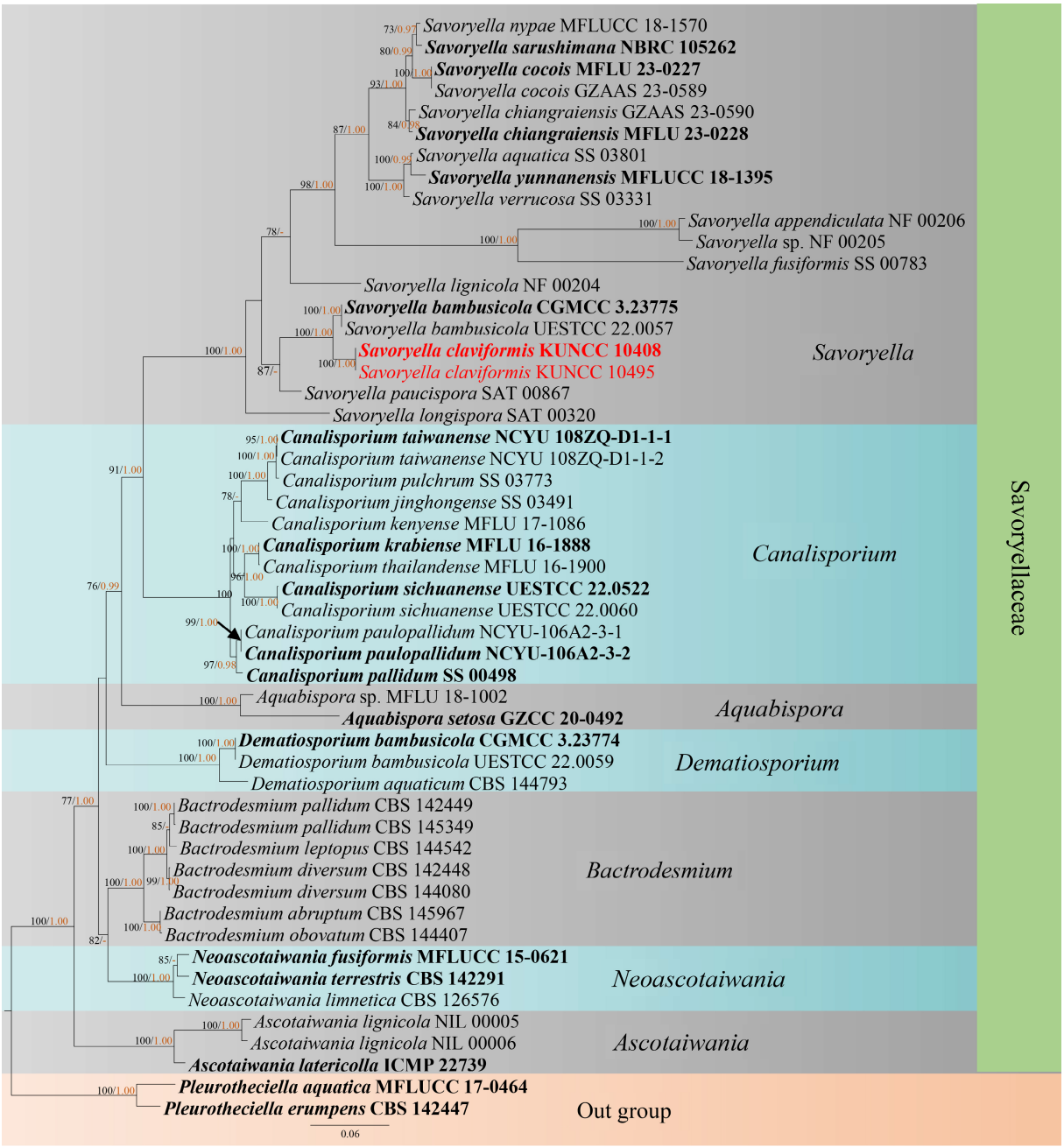

Fig. 1 RAxML tree based on analysis of a combined LSU, SSU, and ITS sequences for *Savoryellaceae*. Bootstrap support values for maximum likelihood (ML) equal to or greater than 75% were given above the nodes (left). Bayesian posterior probability (BIPP) equal to or greater than 0.95 were given above the nodes (right) and hyphen (–) were marked as values below 0.95. The tree was rooted to *Pleurotheciella aquatica* (MFLUCC 17-0464) and *P. erumpens* (CBS 142447)[18]. Two new isolates were shown in red, and ex-type strains are bold.

in freshwater habitats, 22 July 2021, R.J. Xu, MD-376 (HKAS 133192), living culture KUNCC 10495.

Notes: *Savoryella claviformis* can be distinguished from all asexual species in *Savoryella* by its semi-micronematous conidiophores, terminal, determinate conidiogenous cells, and acrogenous, solitary, fusiform, claviform, rostrate conidia[19,20]. Additionally, phylogenetic analysis showed that *S. claviformis* clustered into a distinct subclade and is sister to *S. bambusicola*, with (100% ML/1.00 BIPP) bootstrap support (Fig. 1). Since only the sexual morph of *S. bambusicola* has been discovered, it is not possible to compare their morphological differences[18]. Further comparisons of ITS sequences demonstrate a 7.9% (33/417 bp, excluding gaps) difference between *S. claviformis* and *S. bambusicola*. Therefore, following the guidelines of Chethana et al.[40,41], *S. claviformis* has been identified as a new species, supported by both morphological and phylogenetic evidence.

Discussion

Savoryellaceae currently comprises seven genera: *Aquabispora*, *Ascotaiwania*, *Bactrodesmium*, *Canalisporium*,

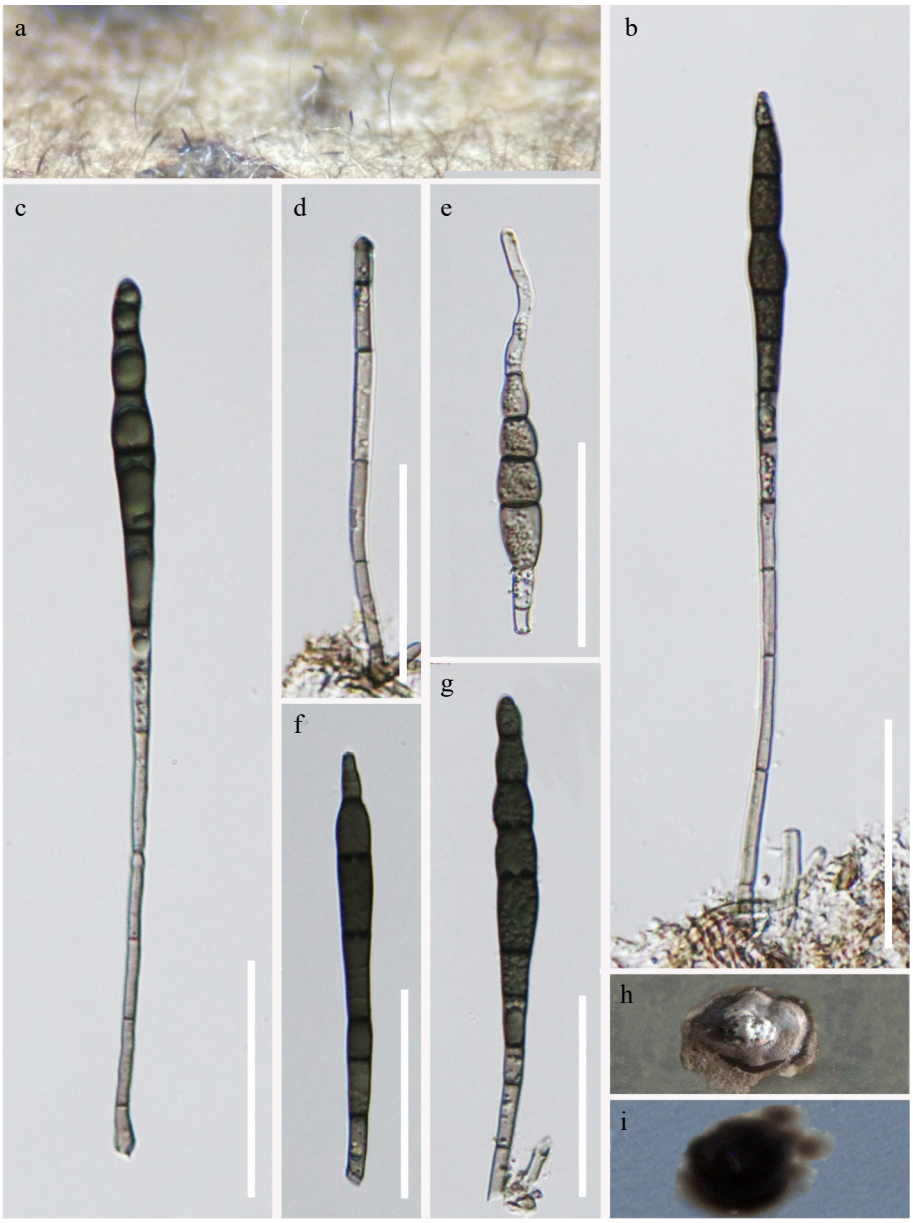

Fig. 2 *Savoryella claviformis* (HKAS 133191, holotype). (a) Colony on nature substrates. (b), (c) Conidiophores and apical conidia. (d) Conidiophore. (e)–(g) Conidia. (h) Culture colony on PDA medium, from surface. (i) Culture colony on PDA medium, from reverse. Scale bars: (b)–(g) = 50 μm.

Dematiosporium, *Neoascotaiwania*, and *Savoryella*[7,17,18,21,42–44]. The asexual morphs of these genera are typically characterized by micronematous, often reduced to undifferentiated hyphal conidiophores and monodictys-like conidia. Specifically, *Ascotaiwania*, which has terminal, blastic, globose, dictyosporous conidia; *Bactrodesmium* known for its sporodochium-like conidiomata; *Canalisporium* is characterized by dark brown and muriform conidia; *Dematiosporium* is known for monodictys-like conidia; and *Neoascotaiwania*, recognized for its fusiform, dark brown, transversely septate conidia[17,21,42–45].

The specimens described in this study were collected from freshwater habitats on the Tibetan Plateau in China, increasing our understanding of fungal diversity in this region and enabling comparisons across a north-south gradient in Asia[1]. In addition, among the 17 accepted species in *Savoryella*, only four species, including *S. cocois*, *S. chiangraiense*, *S. nypae*, and *S. sarushimana*, are known as asexual morphs[19,20]. *Savoryella limnetica* was observed producing an asexual morph in culture, as reported by Réblová et al.[46]. However, based on molecular data and culture characteristics, it was synonymized with *Neoascotaiwania limnetica* by Hernández-Restrepo et al.[47].

This study exposes a new ascomycetous taxon from the freshwater ecosystems of the Kaidu River and Bosten Lake in Xinjiang, China, marking a new discovery in the region's fungal diversity. Originating from elevations above 4,000 m on the Tibetan Plateau, the unique geographical and climatic conditions of the Kaidu River and Bosten Lake create distinctive niches that support a rich biodiversity, including previously undocumented fungal species. This discovery enriches our understanding of ascomycetes in freshwater ecosystems.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Xu RJ, Hyde KD, Zhao Q; data collection: Xu RJ, Guo YY, Yang QY; analysis and interpretation of results: Xu RJ, Dong W, Boonmee S; draft manuscript preparation: Xu RJ. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The authors of the manuscript confirm that data supporting our study findings are available in the article. Data regarding species/specimen DNA sequences are publically available on the accession provided in Table 1, in the GenBank data base of NCBI.

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Conflict of interest

The authors declare that they have no conflict of interest.

Dates

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