



Sclerococcum glaucomarioides: a new geographical record from China

QING-FENG MENG^{1,2,3,8}, VINODHINI THIYAGARAJA^{1,4,9}, DAMIEN ERTZ^{5,6,10}, FIONA RUTH WORTHY^{4,11}, NATSARAN SAICHANA^{2,12} & SHAO-BIN FU^{7,13*}

¹Centre of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand

²School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand

³School of Public Health, Zunyi Medical University, Guizhou Province 563000, China

⁴Key Laboratory for Plant Biodiversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, Yunnan, China

⁵Meise Botanic Garden, Research Department, Nieuwelaan 38, 1860 Meise, Belgium

⁶Fédération Wallonie-Bruxelles, Service Général de l'Enseignement Supérieur et de la Recherche Scientifique, rue A. Lavallée 1, 1080 Bruxelles, Belgium

⁷School of Pharmacy, Zunyi Medical University, Guizhou Province 563000, China

⁸✉ qfmeng@126.com; <https://orcid.org/0000-0001-9814-8238>

⁹✉ vino.thiyagaraja@gmail.com; <https://orcid.org/0000-0002-8091-4579>

¹⁰✉ damien.ertz@jardinbotaniquemeise.be; <https://orcid.org/0000-0001-8746-3187>

¹¹✉ worthy@mail.kib.ac.cn; <https://orcid.org/0000-0003-0042-3110>

¹²✉ natsaran.sai@mfu.ac.th; <https://orcid.org/0000-0002-4357-7980>

¹³✉ fushb@126.com; <https://orcid.org/0000-0001-9932-1346>

*Corresponding author

Abstract

The lichenicolous species *Sclerococcum glaucomarioides* growing on the lichen *Ochrolechia akagiensis* is newly reported from China. This study provides an illustration and morphological description for this species, complemented by phylogenetic analyses based on ITS, LSU and mtSSU sequence data. The taxon is characterized by adpressed to sessile apothecia that are round to angular with black disc, hymenium with brownish color, 25–40 µm high, broadly cylindrical to subclavate 8-spored asci, 20–30 × 10–15 µm, with euamyloid apical cap and brown ascospores with 2–3 transverse septa.

Key words: Dactylosporaceae, multi-gene, new record, taxonomy

Introduction

Lichenicolous fungi are highly specialized organisms that grow on lichens as pathogens, saprotrophs or commensals, comprising over 2300 species (Diederich *et al.* 2018). Dactylosporaceae (Sclerococcales, Eurotiomycetes) was established by Bellem. & Hafellner (1982), and comprises of lignicolous, lichenicolous, and beetle-associated fungi (Bellemer and Hafellner 1982; Yang *et al.* 2023). The family comprised six genera namely *Cylindroconidiis* Huang Zhang & X.D. Yu, *Fusichalara* S. Hughes & Nag Raj, *Gamsomyces* Hern.-Restr. & Réblová, *Pseudobactrodesmium* H. Zhang, W. Dong & K.D. Hyde, *Rhopalophora*-Réblová, Unter. & W. Gams and the generic type *Sclerococcum* Fr. (Wijayawardene *et al.* 2022). Sclerococcaceae Réblová assigned as a type family within Sclerococcales Unter. & W. Gams, which was initially introduced by Réblová *et al.* (2017). In the past, Dactylosporaceae and Sclerococcaceae were distinct families within the same order Sclerococcales. Nevertheless, Diederich *et al.* (2018) found that the two type genera, *Dactylospora* Körb. and *Sclerococcum* Fr. from these two families appeared to form a monophyletic group in phylogenetic analyses. Consequently, the separation of these two genera became challenging. As a result, Diederich *et al.* (2018) proposed that Sclerococcaceae be considered as a new synonym, advocating for the reinstatement of Dactylosporaceae with *Sclerococcum* as the type genus. Subsequently, numerous species of *Dactylospora* were combined into the genus *Sclerococcum* (Diederich *et al.* 2013; Pino-Bodas *et al.* 2017; Réblová *et al.* 2017; Diederich *et al.* 2018).

Sclerococcum is one of the species-rich lichenicolous genera (Diederich *et al.* 2018; Joshi 2021). It was originally introduced to accommodate a lichenicolous hyphomycete, *S. sphaerale* (Ach.) Fr. that was reported in its asexual

morph on saxicolous *Pertusaria corallina* (L.) Arnold (Fries 1819; Hawksworth 1975). Diederich *et al.* (2018) listed 64 species of *Sclerococcum*, which included 46 new combinations of lichenicolous species that had previously been assigned to *Dactylospora* (Diederich *et al.* 2018). In the past five years, eight new species and five new combinations belonging to lichenicolous fungi of this genus have been published (Elix *et al.* 2019; Flakus *et al.* 2019; Fryday 2019; Olariaga *et al.* 2019; Spribille *et al.* 2020; Joshi 2021; Zimmermann and Berger 2021; Zhurbenko 2022; Paz-Bermúdez *et al.* 2023). The sexual morph of *Sclerococcum* has superficial to stalked black apothecia, and amyloid asci with an apical gelatinous cap whereas the asexual morph has blackish sporodochial-stromatic conidiomata, dark brown uni- to multi-cellular conidia (Diederich *et al.* 2013; Olariaga *et al.* 2019; Joshi 2021). The members of *Sclerococcum* include both lichenicolous taxa and also saprotrophs on bark, wood and liverworts (Joshi 2021).

Ochrolechia A. Massal. is a widespread lichen genus, which usually grows on bark, mosses or soil detritus and mainly siliceous rocks (Cannon *et al.* 2021). This lichen genus contains 58 species (Ertz *et al.* 2016) and hosts more than 40 lichenicolous fungi and two lichenicolous lichens (Diederich *et al.* 2018; Zhurbenko *et al.* 2018). The present study provides the first geographical record of *Sclerococcum glaucomarioides* from China. The species was delineated based on maximum likelihood and Bayesian phylogenetic analyses coupled with morphological analysis.

Materials & methods

Sample collection & morphological studies

The specimen was collected from Anhui Province, Yangtianwo, Yaoluoping National Nature Reserve and deposited in the Lichen Herbarium of the Kunming Institute of Botany, Chinese Academy of Science (KUN-L). Its macromorphological structures were observed with a stereomicroscope (Olympus ZX-16) and photographed with a digital camera (Nikon D750). The apothecia were sectioned, transferred into a water droplet on a clean slide, covered with a cover-glass, then observed with a compound-microscope (Olympus BX-53). Photos were taken with the built-in camera. Photo plates were made with Adobe Photoshop CC 2019 software (Adobe Systems, USA).

DNA extraction, PCR amplification & sequencing

The total genomic DNA of *S. glaucomarioides* was extracted from the fruiting structures using a Forensic DNA Kit (Omega Bio-tek, Norcross, Georgia) following the manufacturers' instructions. The primer pairs ITS1f/ITS4 for internal transcribed spacer (ITS) (White *et al.* 1990), LR0R/LR5 for the large subunit ribosomal RNA gene (LSU) (Vilgalys and Hester 1990) and mtSSU1/mtSSU3R for mitochondrial small subunit ribosomal RNA gene (mtSSU) (Zoller *et al.* 1999) were selected for polymerase chain reaction (PCR). The procedures of PCR amplification were conducted on a Mastercycler (Bio-RAD T-100) in 25- μ L reactions with 1.0 μ L of DNA template, 12.5 μ L of 2 \times dNTPs Mix (Solarbio), 1.0 μ L (10mM) of each primer and 9.5 μ L of double-distilled water (ddH₂O). The parameters of PCR amplification are displayed in Table 1. The PCR products were sequenced by Shanghai Sangon Company (Chengdu, Sichuan Province, China).

TABLE 1. Primer pairs and settings for PCR.

Locus	Primer	Initial Denaturation	Denaturation	Annealing	Elongation	Final Extension	Hold	References
ITS	ITS1f/ITS4	95°C/3 min	95°C/45 s	55°C/90s	72°C/1 min	72°C/10min	4°C/+∞	White <i>et al.</i> 1990
LSU	LR0R/LR5	95°C/3 min	95°C/45 s	55°C/90s	72°C/1 min	72°C/10min	4°C/+∞	Vilgalys and Hester 1990
mtSSU	mtSSU1/mtSSU3R	95°C/3 min	95°C/45 s	53°C/90s	72°C/1 min	72°C/10min	4°C/+∞	Zoller <i>et al.</i> 1999

Taxon sampling and Phylogenetic analyses

The newly generated sequences were subjected to BLAST search (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to check the phylogenetical position and to check for potential sample contamination. A total of 55 strains including 114 DNA sequences were used in this study (Table 2), and the outgroup taxa were selected based on Thiyagaraja *et al.* (2022).

Single-locus sequences were aligned using the online multiple alignment program MAFFT v.7 (<http://mafft.cbrc.jp/alignment/server>) employing default settings and trimmed with ‘gappyout’ method by TrimAl (Capella-Gutierrez *et al.* 2009), then further checked visually and improved manually where necessary using program AliView (Larsson 2014). ML and BI analyses were performed through the CIPRES Science Gateway V 3.3 (Miller *et al.* 2010). The ML analyses were conducted with RAxML-HPC2 on XSEDE (8.2.8) (Stamatakis 2014) using a GTRGAMMA approximation with rapid bootstrap analysis followed by 1000 bootstrap replicates. Twenty-two common DNA substitution models with rate heterogeneity were tested by ModelFinder (Kalyaanamoorthy *et al.* 2017). The best-fit model for each gene was selected by Bayesian information criterion (BIC), as follows: ITS/TNe+G4; LSU/TN+F+I+G4; mtSSU/TVM+F+G4. Bayesian Inference phylogenies were inferred using MrBayes v3.2.7a (Ronquist *et al.* 2012) (two parallel runs, 50,000,000 generations), in which the initial 25% of sampled data were discarded as burn-in. The resulting trees were drawn in FigTree v1.4.4, then edited in Adobe Illustrator CC2019 software.

TABLE 2. Taxa names, strain numbers and corresponding GenBank accession numbers used in the phylogenetic analyses. New sequences from this study are shown in bold front.

Taxa name	Strain/Voucher	GenBank Accessions Number		
		LSU	ITS	mtSSU
beetle-associated isolate	INB io4503Q	-	KM242300	
beetle-associated isolate	INB io4513J	-	KM242356	-
beetle-associated isolate	INB io4513L	-	KM242358	-
<i>Caliciopsis orientalis</i>	CBS 138.64	NG_058741	NR_145392	FJ190654
<i>Cylindroconidiis aquaticus</i>	MFLUCC 11-0294	MH236579	MH236576	-
<i>Fusichalara minuta</i>	CBS 709.88	KX537758	KX537754	KX537762
<i>Gamsomyces aquaticum</i>	MFLUCC 18-1015	MN335230	MN335228	-
<i>Gamsomyces Chiangmaiensis</i>	MFLUCC 18-0982	MN335229	MN335227	-
<i>Gamsomyces longisporus</i>	CBS 118.86	MT020877	MT020865	-
<i>Gamsomyces longisporus</i>	CBS 240.89	MT020878	MT020866	-
<i>Gamsomyces stilboideus</i>	CBS 146494	MT020879	MT020867	-
<i>Onygena corvina</i>	CBS 281.48	AB075355	-	FJ225792
<i>Pseudosclerococcum golindoi</i>	ARAN-Fungi 6619	NG_073673	NR_171236	MK759897
<i>Rhopalophora clavispora</i>	CBS 281.75	KX537756	KX537752	KX537760
<i>Rhopalophora clavispora</i>	CBS 129.74	KX537755	KX537751	KX537759
<i>Rhopalophora clavispora</i>	CBS 637.73	KX537757	KX537753	KX537761
<i>Sclerococcum ahtii</i>	RP23	KY661659	KY661630	KY661686
<i>Sclerococcum ahtii</i>	RP182	-	KY661622	-
<i>Sclerococcum Chiangraiensis</i>	MFLU 16-0570	NG_066422	NR_163755	-
<i>Sclerococcum deminutum</i>	RP235	-	KY661629	-
<i>Sclerococcum fusiformis</i>	MFLU 16-0593	NG_066423	NR_163756	-
<i>Sclerococcum fusiformis</i>	MFLU 18-0678	-	MH718442	-
<i>Sclerococcum glaucomarioides</i>	RP275	KY661660	KY661632	KY661683
<i>Sclerococcum glaucomarioides</i>	KUN-L 88756	OR033169	OQ991232	OR035764
<i>Sclerococcum haliotrephum</i>	AFTOL_ID 758	FJ176855	-	KJ766382
<i>Sclerococcum haliotrephum</i>	J.K.5129B	FJ713617	-	-
<i>Sclerococcum lobariellum</i>	Diederich 18109	MH698499	-	MH698503
<i>Sclerococcum lobariellum</i>	Diederich 17708	MH698498	-	MH698502
<i>Sclerococcum lobariellum</i>	ARAN-Fungi 10091	MK759891	-	MK759898
<i>Sclerococcum mangrovei</i>	AFTOL_ID 2108	FJ176890	-	KJ766383
<i>Sclerococcum martynii</i>	D. Haelew. F_1567b	MZ221620	MZ221612	-
<i>Sclerococcum martynii</i>	D. Haelew. F_1569a	MZ222283	MZ221614	-
<i>Sclerococcum martynii</i>	D. Haelew. F_1577a	MZ221619	MZ221610	-

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TABLE 2. (Continued)

Taxa name	Strain/Voucher	GeneBank Accessions Number		
		LSU	ITS	mtSSU
<i>Sclerococcum</i> sp.	RP391	KY661664	-	KY661689
<i>Sclerococcum parasiticum</i>	ARAN-Fungi 2724	MK759892	-	MK759899
<i>Sclerococcum parasiticum</i>	RP422	KY661666	KY661646	KY661690
<i>Sclerococcum parasiticum</i>	F283586	MK759894	-	MK759901
<i>Sclerococcum parasiticum</i>	F283587	MK759895	-	MK759902
<i>Sclerococcum parasiticum</i>	ARAN-Fungi A3044025	MK759893	-	MK759900
<i>Sclerococcum pseudobactrodesmium</i>	GZCC 23-0049	OR514702	OR514693	OR588036
<i>Sclerococcum pseudobactrodesmium</i>	GZCC 23-0055	OR514703	OR514694	OR588037
<i>Sclerococcum pseudobactrodesmium</i>	GZCC 23-0056	OR514704	OR514695	OR588038
<i>Sclerococcum pseudobactrodesmium</i>	GZCC 23-0057	OR514705	OR514696	OR588039
<i>Sclerococcum ricasoliae</i>	A.F.29132	MT153992	MT153963	MT153924
<i>Sclerococcum ricasoliae</i>	A.F.25967	MT153991	MT153962	MT153923
<i>Sclerococcum ricasoliae</i>	A.F. Fla6b	MT153993	MT153964	MT153925
<i>Sclerococcum ricasoliae</i>	A.F. 25611	MT153990	MT153961	MT153922
<i>Sclerococcum simplex</i>	MFLU 21-0117	MZ655912	MZ664325	MZ676669
<i>Sclerococcum sphaerale</i>	Diederich 17283	JX081673	-	JX081678
<i>Sclerococcum sphaerale</i>	Diederich 17279	JX081672	-	JX081677
<i>Sclerococcum sphaerale</i>	Ertz 17425 (BR)	JX081674	-	JX081676
<i>Sclerococcum stygium</i>	ARAN-Fungi 00823	-	MK759886	MK759904
<i>Sclerococcum stygium</i>	ARAN-Fungi 3395	MK759896	-	MK759903
<i>Sclerococcum stygium</i>	BHI-F312 (FH)	-	MF161218	-
<i>Sclerococcum tardum</i>	ICMP 24355	-	NR_176187	-
<i>Sclerococcum tardum</i>	PDD 91756	-	OL709435	-
<i>Sclerococcum tardum</i>	JAC13187	-	MK432753	-
<i>Sclerococcum vrijmoediae</i>	NTOU 4002	KC692153	NR_138396	-
<i>Trichocoma paradoxa</i>	CBS 788.93	FJ358290	JN899398	FJ225782

Results

Phylogenetic analyses

The concatenated sequence matrix comprised 59 strains with 2391 aligned characters including gaps (ITS: 540; LSU: 1088; mtSSU: 763). Figure 1 displays the best-scoring ML consensus tree with bootstrap values from ML analyses and posterior probabilities from MrBayes analysis shown at the nodes. Bootstrap support values for maximum likelihood higher than 75% and Bayesian posterior probabilities greater than 0.95 are indicated above the nodes. The strains of *Onygea corvina* (CBS 281.48), *Trichocoma paradoxa* (CBS 788.93) and *Caliciopsis orientalis* (CBS 138.64) were utilized as outgroup taxa.

The phylogenetic tree (Figure 1) inferred from maximum-likelihood and Bayesian inference analyses based on combined ITS, LSU and mtSSU sequence data comprised six genera of the family Dactylosporaceae (*Cylindroconidiis*, *Fusichalara*, *Gamsomyces*, *Pseudosclerococcum*, *Rhopalophora* and *Sclerococcum*) and the beetle associated isolates. All the *Sclerococcum* strains formed a well-supported clade, with the new collection clustering with *S. glaucomarioides*, having ML/PP = 100/1 statistical support. The topologies of the BI tree closely resembled the ML tree, except for the clade of *Sclerococcum haliotrephum* and *S. vrijmoediae* which was more closely related to the clade of *S. ricasoliae* and *S. lobariellum*. The other genera and outgroup each formed a well-supported clade.

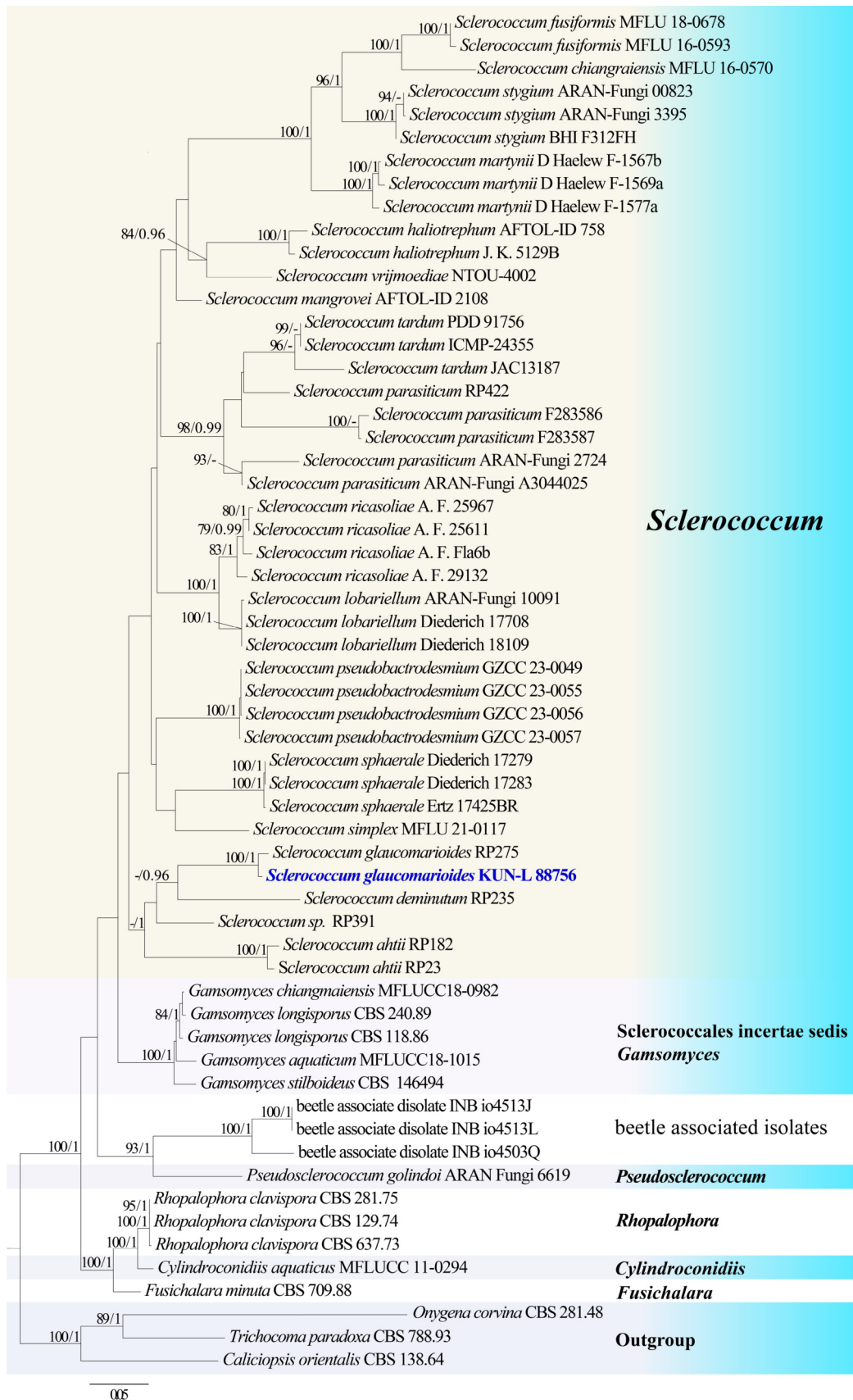


FIGURE 1. Phylogenetic relationships among Sclerococcales resulting from RAxML analysis and verified by MrBayes analysis based on combined LSU, ITS and mtSSU sequence data. Bootstrap support values of maximum likelihood (ML)>75%, and Bayesian posterior probabilities (PP)≥0.95 are given near the nodes as ML/PP. *Onygea corvina* (CBS 281.48), *Trichocoma paradoxa* (CBS 788.93) and *Caliciopsis orientalis* (CBS 138.64) were used as outgroup taxa. The newly generated sequences from this study are shown in blue bold font.

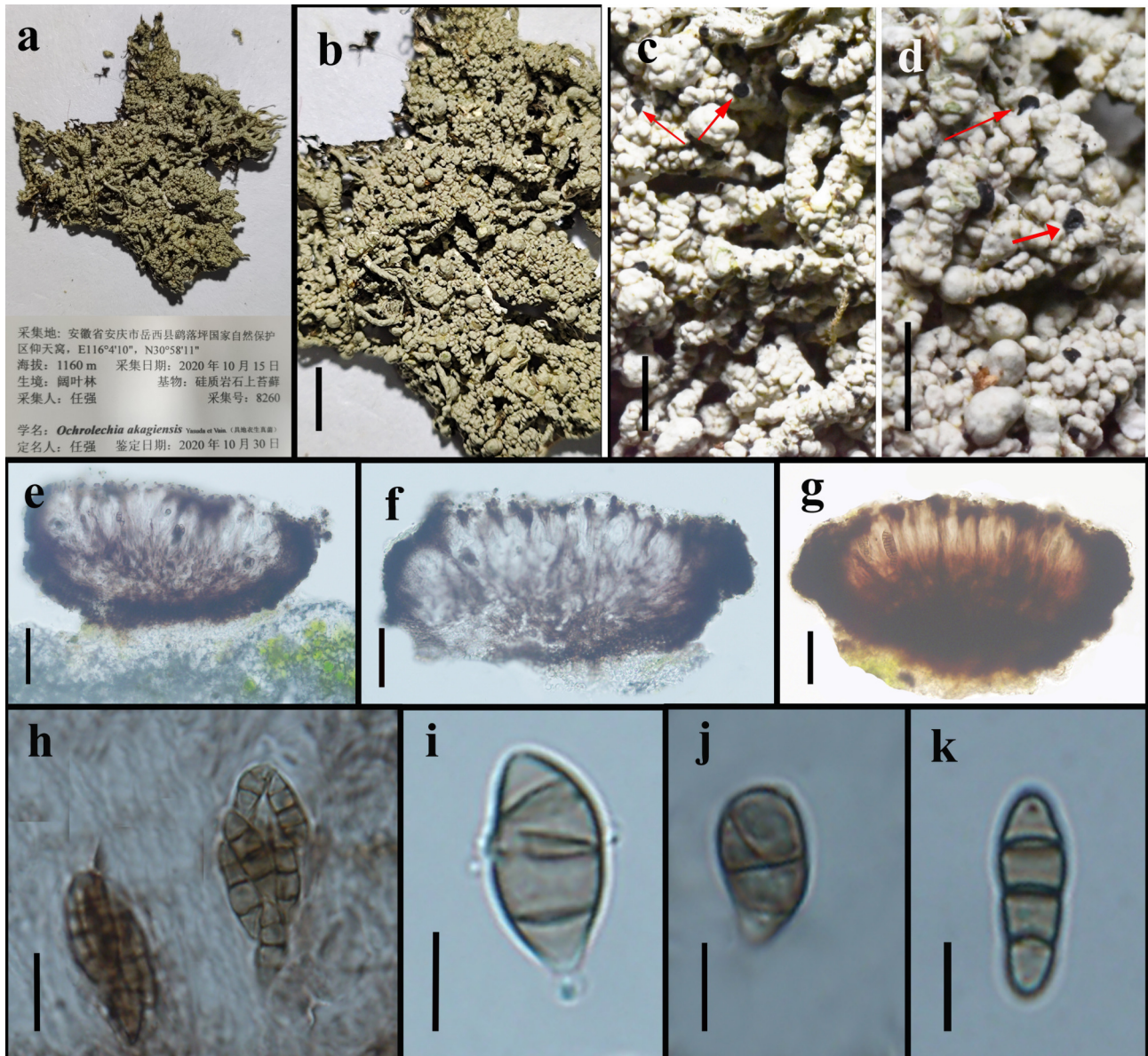


FIGURE 2. *Sclerococcum glaucomarioides* (KUN-L 88756) on the lichen thallus of *Ochrolechia akagiensis*. **a–d** Host substrate. **e–g** Vertical section of apothecia in water. **h** Asci and ascospores in water. **i–k** Ascospores in water. Scale bar: **b** = 5 mm, **c–d** = 2.5 mm, **e–g** = 20 μ m, **h** = 10 μ m, **i–k** = 5 μ m.

Taxonomy

Sclerococcum glaucomarioides (Willey ex Tuck.) Ertz & Diederich, *The Bryologist* 121 (3): 398 (2018) [MB#827718].

Figure 2

Family: Sclerococcaceae R blov , Unter. & W. Gams, *Mycol. Progr.* 16(1): 35 (2016).

=*Dactylospora glaucomarioides* (Tuck.) Hafellner.

=*Buellia glaucomarioides* Tuck.

Lichenicolous, grows on the thallus of crustose lichen *Ochrolechia akagiensis*

Description: *Sexual morph:* Apothecia superficial, growing dispersed on the lichen tuberculates or in the gap between the tuberculates, adpressed to sessile, disc black, 0.4–0.6 (0.8) mm diam., round to irregularly round, flat or not. *Epihymenium* blackish, paraphysis tips bond in cluster with brown-blackish granular structure, excipulum thin 2–4 μ m thick. *Hymenium* with brownish color, 25–40 μ m high. *Hypothecium* brownish-black, hymenium transparent with somewhat brownish hyphae tissue. *Paraphyses* thin, 1.5–2 μ m wide, with apices expanded, mostly 2–3 μ m wide.

Exciple dark brownish to blackish, pseudoparenchymatous, 8–15 µm thick. *Asci* broadly cylindrical to crassly clavate, 20–30 × 10–15 µm, 8-spored. *Ascospores* ellipsoid or oblong, brownish, 3–4-locules with 2–3 lenticular or linear transverse septate, occasional with one longitudinal septate, (6) 8–12 × 5–7 µm, overlapping, multiseriate in asci.

Asexual morph: Not observed.

Specimens examined: Yuexi country, Anqing city, Anhui Province: Yangtianwo, Yaoluoping National Nature Reserve, elev. 1160m, E116°4'10", N30°58'11", 15th October 2020, collected by Qiang Ren, Collection No. 8260 (KUN-L 88756). The host lichen grows with moss on siliceous rock.

Discussion

The newly obtained sequence clustered together with *Sclerococcum glaucomarioides*, in the multi-gene phylogenetic tree with high bootstrap support. Morphologically, this new collection shares similarities with *S. glaucomarioides*, featuring adpressed to sessile, round to angular, black disc apothecia. The hymenium is hemiamyloid, 50–65 µm in height, and the asci are broadly cylindrical to subclavate, 8-spored, with dimensions of 48–60 × 14–20 µm. The asci possess an euamyloid apical cap, and ascospores are brown, 12.5–19 × 5.5–7.5 µm, with 3–4 (–7) transverse septate (Joshi *et al.* 2010). However, it is noteworthy that the new sample exhibits a brownish-colored hymenium and slight variations from *S. glaucomarioides*. These differences include a smaller height of hymenium (25–40 µm vs. 50–65 µm high), smaller asci (20–30 × 10–15 µm vs. 48–60 × 14–20 µm), and smaller ascospores ((6) 8–12 × 5–7 µm vs. 12.5–19 × 5.5–7.5 µm). *S. glaucomarioides* was originally described as *Buellia glaucomarioides*. In the original description, the spores shared a similar shape and septa but were larger (12–16 × 5–7 µm). It was reported to grow on different host lichens, viz. *Ochrolechia tartarea* (sub. *Lecanora tartarea*) (Tuckerman 1888).

Sclerococcum glaucomarioides has been documented in several regions, including Iceland (Svane and Alstrup 2004), North America (Hafellner 1979; Hodkinson *et al.* 2009; Lendemer 2010), North Korea (Huneck *et al.* 1994), Russia (Zhurbenko 2004, 2009; Zhurbenko and Ohmura 2019), and South Korea (Joshi *et al.* 2010). Research on lichenicolous fungi in China has been limited, with only 48 species reported in the past 20 years. Among these reported species, only *S. simplex*, belonging to the genus *Sclerococcum*, was recorded last year (Thiyagaraja *et al.* 2022). Notably, *S. glaucomarioides* had previously been reported growing on *Ochrolechia akagiensis*, *O. tartarea* and *O. yasudae*, with the host lichen found on bark, rock and moss (Tuckerman 1888; Joshi *et al.* 2010; Pino-Bodas *et al.* 2017), as well as on *Megaspora verrucosa* in tundra (Zhurbenko 2009). Therefore, this marks the first recorded geographical occurrence of this species in China, specifically on the host lichen *Ochrolechia akagiensis* on siliceous rocks.

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