



Taxonomic and phylogenetic study of genus *Sarcogyne* (Acarosporales, Acarosporaceae) reveals two new species from Pakistan

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Abstract

Two new species, *Sarcogyne crispula* and *S. pakistanensis* are described and illustrated from Pakistan. *Sarcogyne crispula* is similar to *S. praetermissa*. Both have lecideine apothecia with smooth melanized margins which curl inward above the apothecial disc and grow on calcareous rock, but they differ especially in *S. crispula* having larger apothecia (2–3 mm wide vs. usually less than 1 mm) with thinner margins (50–70 vs. 70–120 µm) as well as differing in nrITS and mtSSU regions. *Sarcogyne pakistanensis* is similar to *S. similis*. Both grow on siliceous rocks and produce psoromic acid. *Sarcogyne pakistanensis* differs from *S. similis* especially in having a lower hymenium (55–85 vs. 100–125 µm), a thinner margin [ca. 100 vs. (100–)150–200 µm], a hypothecium with dark black area, as well as differing in their nrITS regions.

Keywords Asian lichens · Calciphytes · Dark hypothecium · Keys · Himalayas · Phylogeny

Introduction

Sarcogyne Flot. (Acarosporaceae) is a genus of crustose lichens with asci with usually a hundred or more simple hyaline ascospores. They have carbonized lecideine apothecia with their algal layer usually occurring in the substrate in an endolithic thallus (Magnusson 1935). They rarely have algae also in their base or lower part of apothecia. Only a few species have an epilithic thallus. They grow on calcareous and non-calcareous rock and rarely in soil crusts. Centers of diversity for *Sarcogyne* are Australia and western North America (McCarthy & Elix 2017). *Sarcogyne* species are especially adapted to desert and arid habitats because their thallus is endolithic and their algal partner is well protected

from insolation. The type of the genus is *Sarcogyne clavus* (DC.) Kremp., which due to complicated nomenclatural confusion, had to be proposed for conservation as the type of the genus and is expected to be confirmed (Knudsen et al. 2021a). In this paper we publish a key to 23 *Sarcogyne* species in Europe and Asia.

One should not confuse the genus *Sarcogyne* with the *Sarcogyne* clade in recent phylogenies (Westberg et al. 2015a; Knudsen et al. 2020). The *Sarcogyne* clade has a weak backbone and is non-monophyletic. Besides *Sarcogyne clavus* and the core group of lecideine species, it contains *Acarospora badiofusca* (Nyl.) Th. Fr. and *A. glaucocarpa* (Ach.) Körber and a number of species with elevated lecideine apothecia usually the color of the epilithic thallus. The *Sarcogyne* clade also includes species without lecideine apothecia like *A. cervina* A. Massal., *A. macrospora* (Hepp ex Nyl.) A. Massal. ex Bagl., *Gypholecia scabra* (Pers.) Müll. Arg., *A. oligospora* (Nyl.) Arnold and *A. scottii* K. Knudsen & Kocourk., all species that look like *Acarospora* with immersed or pseudolecianorine apothecia. Most species of *Sarcogyne* with lecideine apothecia and a *Polysporina*-type epihymenium with carbonized epihymenial accretions, like *Acarospora privigna* (Ach.) A. Schneid. (*Polysporina simplex*, nom. illeg.), were recovered in the *Acarospora* clade (Westberg et al. 2015a). The two species described as *Sarcogyne* in this paper as well as

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species in the key are *Sarcogyne* s. str. and would probably be recovered in the *Sarcogyne* clade if already sequenced.

While species of *Sarcogyne* are especially common and diverse in arid or desert habitats, the genus is less common in temperate and montane habitats. Pakistan had only two reports of *Sarcogyne*, *S. regularis* Körb. and *S. hypophaea* (Nyl.) Arnold (reported under the misapplied name *Sarcogyne privigna*) (Aptroot & Iqbal 2012). Both species have a holarctic distribution (Magnusson 1935; Knudsen & Standley 2007). In this paper we describe two new species of *Sarcogyne*, *S. crispula* Afshan, Fayyaz & K. Knudsen and *S. pakistanensis* R. Zulfiqar, Khalid & K. Knudsen. *Sarcogyne crispula* grows on limestone in the moist temperate pine and oak forests of the Himalaya. *Sarcogyne pakistanensis* grows in moist temperate forest, near a waterfall on enriched siliceous rock, in Khyber Pakhtunkhwa Province. While possibly more species can be discovered in these habitats, *Sarcogyne* is not expected to be a diverse genus in the temperate areas of Pakistan.

Materials and methods

Morphological and chemical studies

Collections were made during a lichen survey of Azad Jammu and Kashmir and Parachinar in 2021. The specimens were examined macro- and micromorphologically using a stereomicroscope (Meiji Techno, EMZ-5TR, Japan) and compound microscope (SWIFT M4000-D) with a 9MP camera system, respectively. For anatomical investigation, sections of apothecia were made by hand and examined in water, KOH (10%) and Lugol's iodine solution (2% I). A minimum of twenty measurements in water and KOH were made for each diagnostic feature from the three specimens. The collected specimens were deposited in the herbarium of Institute of Botany, University of the Punjab, Lahore (LAH). The secondary chemistry was analyzed using spot tests which were performed using KOH (10%; K), sodium hypochlorite solution (C) and Lugol's iodine solution (2% IKI). Thin Layer Chromatography was carried out using Solvent System C, following standard methods (Orange et al. 2001).

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted directly from a portion of thallus with apothecia from each specimen using a modified 2% CTAB method (Gardes & Bruns 1993). The primer pair ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990) was used to amplify the internal transcribed spacer (ITS) region and the mtSSU using the primers following the amplification protocol of Khan et al. (2018). PCR

products were sent to BGI, China, where both strands were sequenced.

Sequences were assembled using BioEdit (Hall 1999). BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) analysis was used to retrieve highly similar sequences of the ITS region. Sequences' maximum query coverage and percent identity along with related taxa were noted. Sequences retrieved from GenBank and obtained from published literature were used in an initial alignment, which was then trimmed and realigned using web-PRANK with default settings (Löytynoja & Goldman 2010). On the CIPRES Portal (Miller et al. 2010), the HYK + G + I model was selected using jModelTest (Posada 2008). Using RAxML-HPC2 v. 8.1.11 on CIPRES Portal, maximum likelihood analysis (ML) was also implemented (Stamatakis 2014), using 1000 bootstraps for rapid bootstrapping. FigTree v 1.4.3 (Rambaut et al. 2014) was used for displaying the phylogeny reconstructed from the ML analysis.

Results

Phylogenetic analyses

ITS sequences of both specimens of *S. crispula* were identical. The final dataset of ITS consisted of 57 sequences including *Pycnora sorophora* (Vain.) Hafellner (OK333010) as outgroup (Westberg et al. 2015a). The aligned ITS1-5.8S-ITS2 region comprised 569 sites, of which 378 were conserved and 179 variable; 156 sites were parsimony-informative. In our phylogram, the sequences of *Sarcogyne crispula* (CKR-16 and CKR-17) formed a well-supported lineage sister to *S. algoviae* H. Magn. The sequences of *S. pakistanensis* (PC-03 and PC-06) were discovered as a well-supported clade sister to *S. praetermissa* K. Knudsen & Kocourk (Fig. 1).

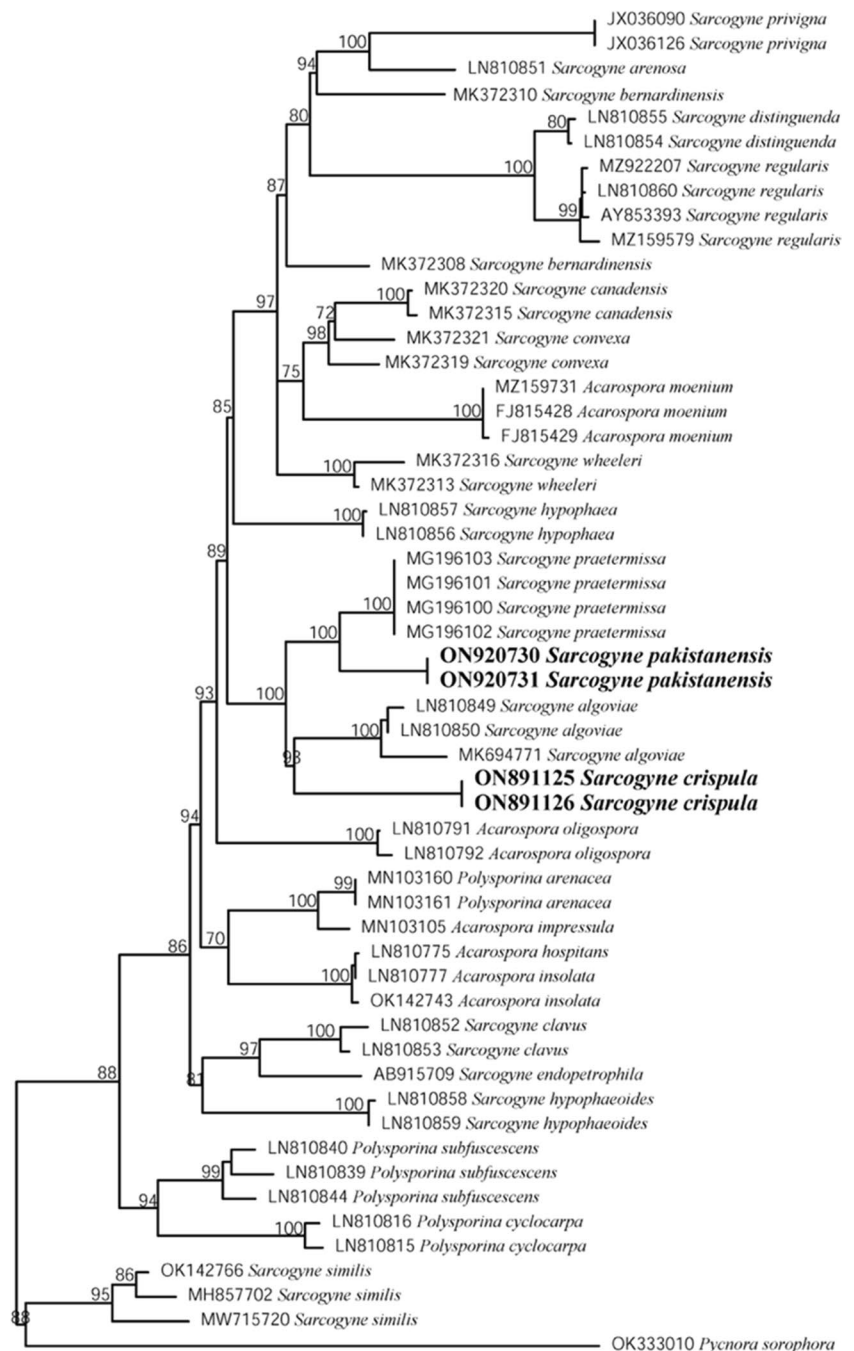
The mtSSU final dataset is composed of 29 sequences including *Pycnora sorophora* (Vain.) Hafellner (OQ646413) as outgroup (Westberg et al. 2015a). In the tree resulting from analysis of the SSU region (Fig. 2) *Sarcogyne crispula* formed a well-supported lineage sister to *S. algoviae*. The molecular phylogenetic analysis strongly supported the taxonomic delimitation of the new species.

Taxonomy

Sarcogyne crispula Afshan, Fayyaz & K. Knudsen, **sp. nov.** (Figs. 1–3).

Holotype Pakistan. Azad Jammu and Kashmir, Garhi Dupatta (34°36' N, 73°35' E), 817 m alt., on rock, October 02 2021, N. S. Afshan and A. R. Niazi (CKR-16) (LAH37424) (ITS GenBank accession number ON891125) (SSU GenBank accession number ON921012).

Fig. 1 Phylogenetic relationships of *Sarcogyne* species based on a Maximum Likelihood analyses of the ITS region



0.03

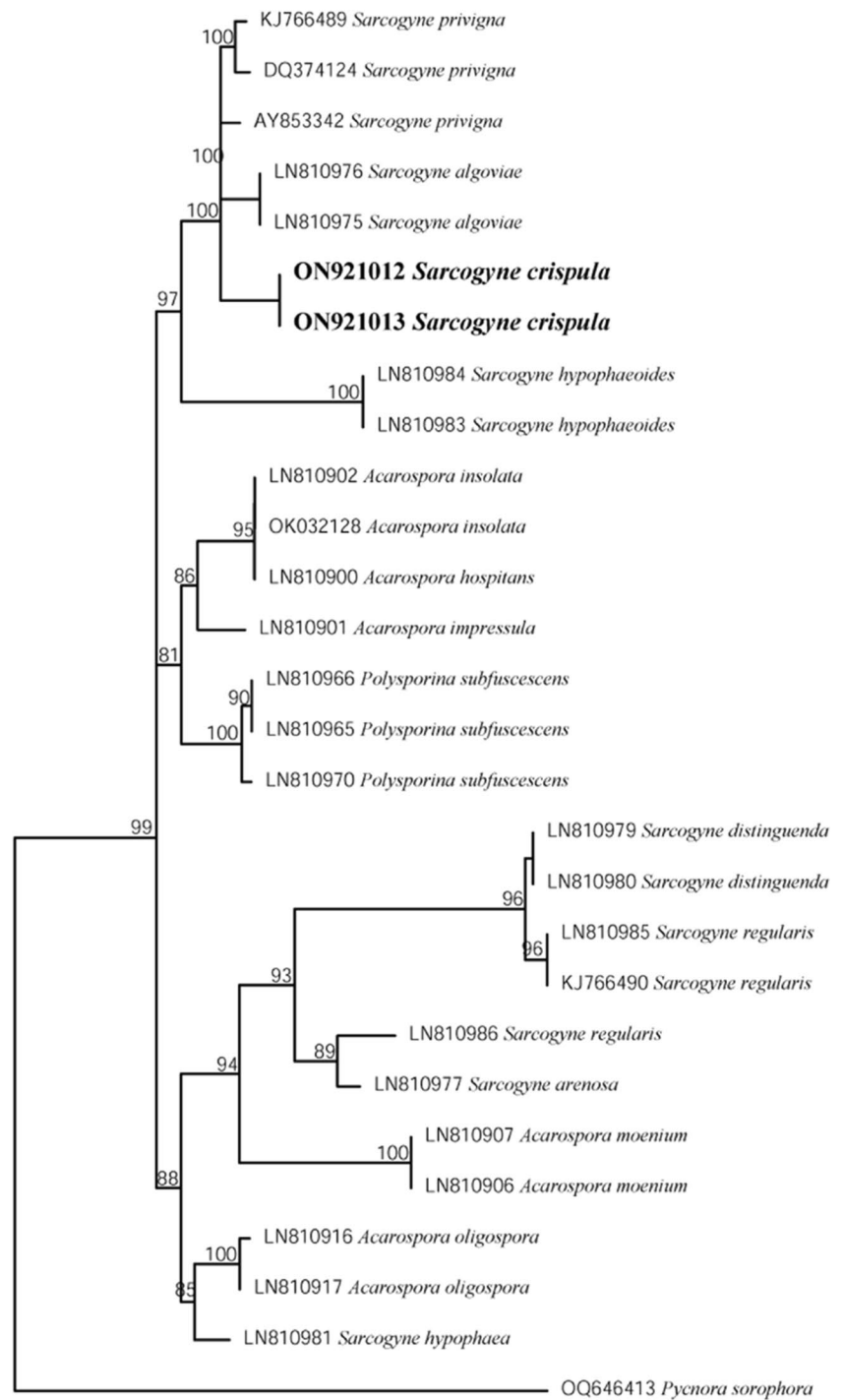
Mycobank number MB844747.

Etymology The specific epithet “**crispula**” (Latin) refers to the way the margins curl inward above the apothecial disk.

Diagnostic characters Similar to *S. praetermissa* in having lecideine apothecia with smooth melanized margins

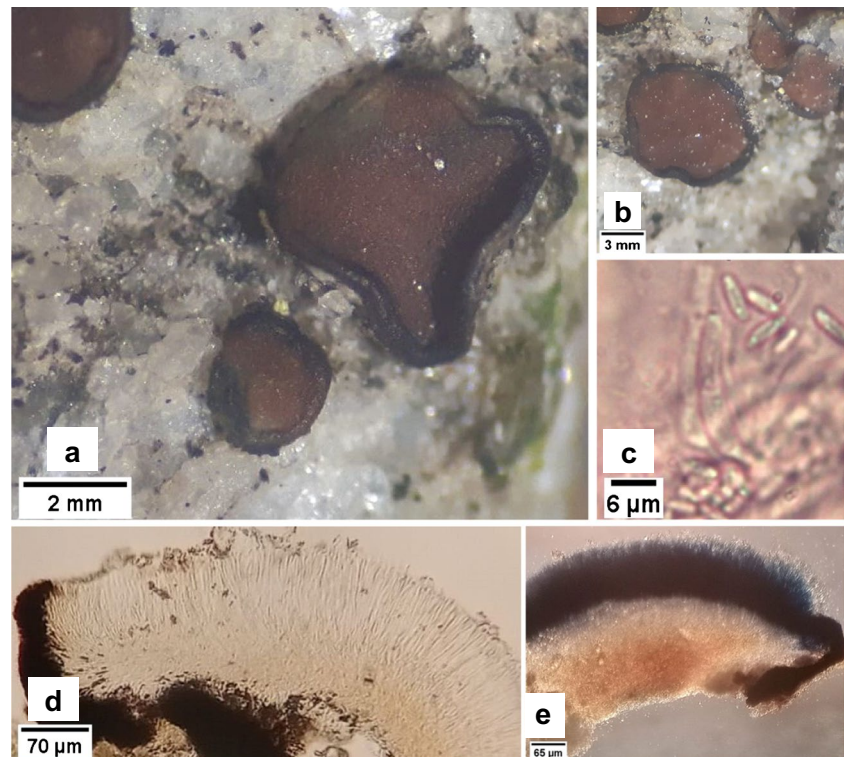
which curl inward above the apothecial disc, but differing especially in having larger apothecia (2–3 mm wide vs. usually less than 1 mm) with thinner margins (50–70 vs. 70–120 μm).

Fig. 2 Phylogenetic relationships of *Sarcogyne* species based on a Maximum Likelihood analyses of the mtSSU region



0.02

Fig. 3 *Sarcogyne crispula* (LAH37424): (a & b): Crustose thallus with abundant apothecia; (c): Ascospores; (d & e): Cross section of an apothecium (without and with IKI test respectively)



Thallus endolithic, algae in substrate. *Apothecia* lecidine, 2–3 mm wide, broadly attached. *Disc* epruinose, flat to strongly concave, usually round, dark brown to black, red brown or orange when wetted. *Margins* black, raised above surface of disc, curled inward, smooth, without incisions. *Proper exciple* of radiating hyphae, black and carbonized in outer part, paler within, 50–70 μm wide, *Epithecium* light brown, 12–15 μm thick. *Hymenium* hyaline, 60–75 μm high, hymenial gel IKI+ dark blue, euamyloid. *Subhymenium* 30–35 μm high, IKI+ persistent dark blue, euamyloid. *Hypothecium* continuous with proper exciple and attaching hyphae, interspersed, light in thin section, dark in section at least 90 μm thick. *Paraphyses* coherent, simple or sparingly branched in upper part, 1–2.5 μm thick, capitate, apices barely expanded in a gel cap, *Asci* > 100-spored, cylindrical-clavate, 59–70 × 15–22 μm. *Ascospores* 1-celled, hyaline, narrowly ellipsoid, 4–7 × 0.9–1.8 μm. No pycnidia observed.

Chemistry K–, C–, KC–, No lichen substances detected by TLC.

Substrate & Ecology

The known collections of the new species are from moist temperate forest of the Himalaya in Azad Jammu and Kashmir, Pakistan. This is a mixed forest dominated by *Pinus roxburghii* Sarg., *Pyrus pashia* L., *Quercus oblongata* D. Don and *Q. glauca* Thumb. The maximum daily temperature of

the region varies from 20 °C to 30 °C during the summer and averages 4 °C during the winter, with moderate rainfall.

Additional specimens examined Azad Jammu and Kashmir, Ganga Choti (34°15' N, 73°25' E), 2960 m alt., on rock, December 02 2021, I. Fayyaz, N. S. Afshan and A. R. Niazi (CKR-17) (LAH37425) (ITS GenBank accession number ON891126) (SSU GenBank accession number ON921013).

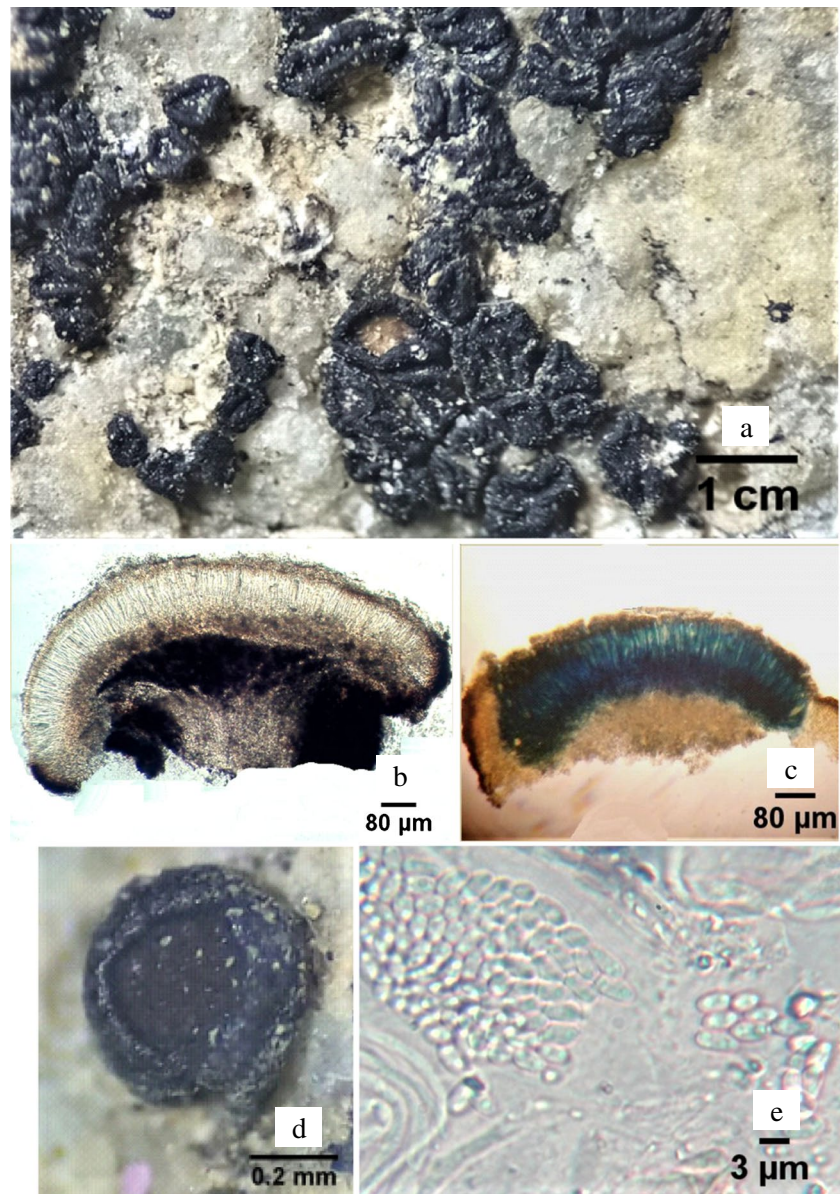
Discussion

The superficially most similar species to *Sarcogyne crispula* is *S. praetermissa* (Knudsen & Kocourková 2018). Both are calciphytes with smooth melanized margins which curl inward above the apothecial disc, but they differ especially in *S. crispula* having larger apothecia (2–3 mm wide vs. usually less than 1 mm) with thinner margins (50–70 μm vs. 70–120 μm). The most closely related species to *S. crispula* is *S. algoviae* H. Magn. It differs from *S. algoviae* in having non-incised/smooth melanized margins vs. incised carbonized margins, larger apothecia (2–3 mm wide vs. 0.3–1.8 mm wide), shorter hymenium (60–75 μm high vs. 65–105 μm high), and larger ascospores (4–7 × 0.9–1.8 μm vs. 2.5–4 × 1.5 μm) (Westberg et al. 2015b).

Sarcogyne pakistanensis R. Zulfiqar, Khalid & K. Knudsen, **sp. nov.** (Figs. 1 & 4).

Mycobank number MB844739.

Fig. 4 *Sarcogyne pakistanensis* (LAH37443): (a): Crustose-endolithic thallus with abundant apothecia; (b & c): Cross section of an apothecium (without and with IKI test, respectively); (d): Close-up of an apothecium; (e): Ascospores



Holotype Pakistan. Khyber Pakhtunkhwa Province, district Kurram, Parachinar 1705 m a.s.l, August 18 2018, A. N. Khalid & K. Habib, (PC-03) (LAH37443) (ITS GenBank accession number ON920730).

Etymology The specific epithet “**pakistanensis**” refers to the type locality ‘Pakistan’ from where the sample was collected.

Diagnostic characters Similar to *S. similis* H. Magn. in producing psoromic acid and growing on siliceous rock but differing especially in having a lower hymenium (55–85 vs. 100–125 μm), a thinner margin [ca. 100 vs. (100–) 150–200 μm], and hypothecium with dark black areas.

Thallus endolithic, or chasmolithic and/or epilithic, reduced to mostly beneath the apothecia, rimose-areolate and white where visible, intermingled with rock particles

and algae, up to 6 cm across and 0.2–0.3 mm thick. *Areoles* indistinct, or very few centrally, initially rounded becoming irregular, fertile areoles having one apothecium, usually larger when sterile, 0.2–0.9 mm in diameter. *Upper surface* pruinose, fissured, smooth, non-farinose, ecorticate. *Color* pale brown to off-white or whitish when dry, no change when wet. *Apothecia* broadly attached with mycelial base, sometimes semi-immersed or immersed in pits in the substrate, replicating by division, forming clusters, rarely solitary, 0.2–0.5 mm in diameter. *Disc* pruinose, dark brown to blackish brown, initially rounded to irregular or angular with age, unchanged when wetted. *Margins* thick, smooth, glossy, often elevated above the disc, not incised. *Proper exciple* 80–100 μm thick, of radiating hyphae, continuous with hypothecium and mycelial base, black, melanized outer

layer thinner than hyaline inner layer. *Epihymenium* reddish brown, 10–20 µm thick. *Hymenium* hyaline, 55–85 µm tall, hymenial gel IKI + persistent dark blue, euamyloid. *Subhymenium* inspersed, 30–60 µm tall, IKI + slowly turning dark blue, euamyloid. *Hypothecium* continuous with proper exciple and mycelial base, with black areas. *Paraphyses* hyaline, septate, 2–3 µm wide at mid height, apices swollen to 3–4 µm wide. *Asci* clavate, 60–80 µm × 15–20 µm. *Ascospores* narrowly ellipsoid, hyaline, 3–4 × 1–2 µm. *Pycnidia* not found.

Secondary chemistry K–, C–, KC–, **TLC:** 2'-O-demethylpsoromic acid, psoromic acid detected.

Substrate & ecology

Sarcogyne pakistanensis was found on nutrient enriched siliceous rocks near waterfalls, in moist temperate forest at an altitude of 1,705 m, temperature ranges between –2–37 °C, average annual rainfall 1,500–1,650 mm, with dominant tree species *Cedrus deodara* (Roxb. ex Lambert) G. Don, *Pinus walllichiana* A. B. Jacks., *Picea smithiana* Boiss., *Abies pindrow* Royle., *Quercus incana* W. Bartram, *Q. dilatata* Lindl. ex Royle. and *Q. semecarpifolia* Sm. It occurred both as an endolithic lichen and as a chasmolith or epilithic lichen with a thin, ecorticate, rimose-areolate thallus.

Additional specimen examined Pakistan, Khyber Pakhtunkhwa Province, district Kurram, Parachinar 1705 m a.s.l, August 20 2018, A. N. Khalid & K. Habib, (PC-04) (LAH37444) (ITS GenBank accession number ON920731).

Discussion

Sarcogyne pakistanensis and *Sarcogyne similis* H. Magn. from North America are the only described species of the *Sarcogyne* group producing psoromic acid. *Sarcogyne pakistanensis* differs from *S. similis* especially in having a lower hymenium (55–85 vs. 100–125 µm), a thinner margin [100 vs. (100–) 150–200 µm], a hypothecium with dark black areas, and euamyloid vs. hemiamyloid hymenial gel (persistent dark blue vs. light blue turning red in IKI). Both species can form chasmolith or a thin ecorticate epilithic thalli. But *S. pakistanensis* differs in producing areoles divided by thin cracks which become individual apothecia which eventually form clusters of apothecia by division. *Sarcogyne pakistanensis* also differs in having an inspersed subhymenium, which slowly reacts to IKI to become euamyloid, and a black hypothecium. (Lendemeyer et al. 2022).

The species *Sarcogyne pakistanensis* is most closely related to *S. praetermissa*. *Sarcogyne pakistanensis* grows on siliceous rock while *S. praetermissa* grows on calcareous rock. *Sarcogyne pakistanensis* especially differs from *S. praetermissa* in producing psoromic acid and in having black regions in the hypothecium and a densely inspersed

subhymenium. Seven lecideine *Acarosporaceae* species have a dark or black hypothecium, *Acarospora brodoana* K. Knudsen, Kocourk. & M. Westb., *Sarcogyne austroafricana* (Zahlbr.) H. Magn., *Sarcogyne clavus*, *S. clavulus* (Stiz.) H. Magn., *S. endopetrophila* Tokiz. & Y. Ohmura, *S. giberella* (Nyl.) H. Magn., and *S. hypophaeoides* Vain. but all differ in not producing psoromic acid (Knudsen et al. 2016; Magnusson 1937; Tokizawa et al. 2015). *Acarospora brodoana* from California differs from *Sarcogyne pakistanensis* in having epihymenial melanized accretions (Knudsen et al. 2015). The Holarctic *Sarcogyne clavus* differs in having a crenulate margin and large apothecia to 4 mm wide. *Sarcogyne endopetrophila* from Japan has a hypothecium with black or pale brown areas similar to *S. pakistanensis* but differs especially in having larger apothecia (0.5–2.0 vs. 0.2–0.5 mm). *Sarcogyne hypophaeoides* from Europe and North America differs especially in having a solid black hypothecium and finely incised margins. All differ also in occurring on non-calcareous rock.

A key for *Sarcogyne* of Europe and Asia

This key is only for species of *Sarcogyne* and not all species currently recovered in the *Sarcogyne* clade (see introduction). They have lecideine apothecia with a carbonized or melanized margin without melanized epihymenial accretions. (Knudsen et al. 2021a). They were once treated as *Sarcogyne* but most taxa are now in *Acarospora* and a few others are in unstable clades with some provisionally treated as *Sarcogyne* until phylogenetic analysis (Westberg et al. 2015a).

- 1-Species with epilithic thallus.....2
- 1-Species without an epilithic thallus.....6
- 2-Hypothecium dark, Italy.....*Sarcogyne coronata* (Nimis 2016)
- 2-Hypothecium hyaline.....3
- 3-Epilithic thallus thick (usually 1 mm), Europe.....*Sarcogyne cretacea* (see Poelt 1964; photograph, Knudsen et al. 2016)
- 3-Epilithic thallus thin (0.05–0.5 mm).....4
- 4-Hymenium 85–130 µm high, ascospores broadly ellipsoid, mostly 7 × 3 µm, Europe and North Africa*Sarcogyne algerica* (Knudsen & Etayo 2009)
- 4-Ascospores globose to broadly ellipsoid less than 5 µm long.....5
- 5-Hymenium 85–110 µm high, ascospores globose to broadly ellipsoid, 3–3.5 µm to 4 × 3 µm, Europe.....*Sarcogyne nivea* (Magnusson 1935)
- 5-Hymenium 110–180 µm high, ascospores globose to broadly ellipsoid, 3–4.5 × 3.0–3.5 µm, Europe.....*Sarcogyne distinguenda* (Magnusson 1935)

- 6-Species on calcareous rock.....7
- 6-Species on siliceous rock.....14
- 7-Hymenium 110–130 (–180) μm high, ascospores globose to broadly ellipsoid, 3–3.5 μm to 4 \times 3 μm , Europe.....*Sarcogyne fallax* (Magnusson 1935)
- 7-Hymenium lower, ascospores not globose.....8
- 8-Apothecia Pd+ orange cortex (salazinic acid?), Mongolia.....*Sarcogyne solitaria* (Magnusson 1944)
- 8-Apothecia Pd-.....9
- 9-Margin not incised, smooth.....10
- 9-Margin incised or segmented.....13
- 10-Hymenium ca. 100 μm high.....11
- 10-Hymenium less than 90 μm high.....12
- 11-Hymenium usually 90–100 (–120 μm) high, apothecia 0.4–1.0 mm wide, Holarctic.....*Sarcogyne regularis* K rb. (Knudsen et al. 2021)
- 11-Hymenium 85–100 μm high, apothecia 0.1–0.3 mm wide, Egypt, Afghanistan.....*Sarcogyne calcifraga* (Magnusson 1937)
- 12-Hymenium (50–)70–80 (–85) μm high, margin 50–70 μm wide, apothecia 1 mm or less wide, Europe.....*Sarcogyne praetermissa* (Knudsen & Kocourkov 2018)
- 12-Hymenium 60–75 μm , margin 70–120 μm wide, apothecia 1–2 mm wide, Pakistan.....*Sarcogyne crispula* (this paper)
- 13-Hymenium 65–105 μm high, margin incised, on soft calcareous schist, alpine, Europe.....*Sarcogyne algoviae* (see Westberg et al. 2015b)
- 13-Hymenium (50–)70–80 (–85) μm high, margin segmented, on hard calcareous rock, non-alpine, Holarctic.....*Sarcogyne hypophaea* (Knudsen et al. 2013)
- 14-Hypothecium hyaline or dark, PD+ yellow (psoromic acid).....15
- 14-Hypothecium hyaline or dark, PD- (psoromic acid).....16
- 15-Apothecia broadly attached, hypothecium black, not emerging from stromata. Pakistan.....*Sarcogyne pakistanensis* (this paper)
- 15-Apothecia stipitate, hypothecium hyaline, emerging from stromata, Greece.....*Sarcogyne poeltii* (Knudsen & Kocourkov 2020)
- 16-Hypothecium dark or black, (not to be confused with melanin buildup on lower margin or lower surface of apothecia).....17
- 16-Hypothecium hyaline.....20 (Magnusson 1935)
- 17-Apothecia with crenulate and cracked margin.....18
- 17-With smooth margin, incised or not.....19
- 18-Hymenium 85–115 μm high, apothecia 1–4 mm wide, hypothecium interspersed, dark brown, Holarctic.....*Sarcogyne clavus* (Magnusson 1935)
- 18-Hymenium 100–115 μm high, apothecia < 1 mm, Japan.....*Sarcogyne giberella* (Tokizawa et al. 2015)
- 19-Smooth margin with usually several shallow incisions, hypothecium black, Europe.....*Sarcogyne hypophaeoides* (Westberg et al. 2015b)
- 19-Smooth margin, no incisions, hypothecium dark brown, Japan.....*Sarcogyne endopetrophila* (Tokizawa et al. 2015)
- 20-Margin segmented, also on calcareous rock.....*Sarcogyne hypophaea*
- 20-Margin not segmented, smooth, not also on calcareous rock.....21
- 21-Hymenial gel IKI+ dark blue.....22
- 21-Hymenial gel IKI+ pale blue turning red or immediately red.....23
- 22-Margin 80–100 μm thick, apothecia 0.3–1.0 mm wide, not convex, often near the coast, Europe.....*Sarcogyne oceanica* (Knudsen et al. 2021)
- 22-Margin 100–120 μm thick, apothecia 0.5 mm wide, convex, China.....*Sarcogyne picea* (Magnusson 1944)
- 23-Apothecia 0.2–0.7 mm wide, ascospores 3–5 \times 2–3 μm , margin ca. 65 μm wide, hypothecium interspersed but not dark brown or black, blackish-brown melanized under surface, China.....*Sarcogyne parviascifera* (Wang & Wei 2016) (The species is possibly a synonym of *S. sinensis*)
- 23-Apothecia 0.2–0.5 mm, ascospores 5–7 \times 3.0 μm , margin 30–50 (–70) μm , hypothecium not observed interspersed, blackish-brown melanized under surface, Mongolia, China.....*Sarcogyne sinensis* (Magnusson 1940)

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Authors' contributions All authors contributed to this study conception and design. Material preparation, data collection and analysis were performed by [Iram Fayyaz], [Najam-ul-Sehar Afshan], [Rizwana Zulfiqar] and [Kerry Knudsen]. The first draft of the manuscript was written by [Iram Fayyaz, Rizwana Zulfiqar and Fatima Iftikhar] and all authors commented on previous versions of the manuscript. Dr. Abdul Rehman Khan Niazi also helps in the collection of the specimens that are used in this study. Dr. Kerry Knudsen also prepared the comprehensive key of this genus. Prof. Dr. Abdul Nasir Khalid supervised and validated the manuscript. All authors read and approved the final manuscript.

Data availability DNA sequence data that support the findings of this study have been deposited in the GenBank repository. Other data generated or analyzed during this study are included in this article.

Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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