

## ***Sporastatia crassulata*, a new species from the Altai Mountains with a key to *Sporastatia* and remarks on some additional species**

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**Abstract:** *Sporastatia crassulata* Yakovchenko & Davydov sp. nov. is described and a phylogenetic analysis (mtSSU) is presented, confirming its distinctness and indicating a sister relationship with *S. testudinea*. The species is unique among *Sporastatia* species in having a distinctly squamulose, thick, uneven thallus composed of convex, rounded squamules irregularly ascending in the central part of the thallus. The new combination *Sporastatia karakorina* (Poelt & Obermayer) Davydov & Yakovchenko is proposed. The type specimen of *S. subasiatica* was examined. A key to the six species of *Sporastatia* is given. Mountainous Central Asia appears to be the centre of species diversity and endemism for *Sporastatia*.

**Key words:** Ascomycota, Asia, China, lichen, new taxon, *Rhizocarpaceae*, Russia, Siberia, Tuva

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### **Introduction**

*Sporastatia* A. Massal. is a small genus comprising four currently accepted species (Wijayawardene *et al.* 2017). Species of *Sporastatia* are arctic-alpine lichens occurring mostly on exposed hard siliceous or weakly calcareous rocks. Representatives of *Sporastatia* are long-lived and play an important role in the pedogenetic process (Favero-Longo *et al.* 2005). *Sporastatia testudinea* (Ach.) A. Massal. has been used in lichenometric studies (Haeberli *et al.* 1979). Two of the species, *S. testudinea* and *S. polyspora* (Nyl.) Grummann, are widely distributed throughout the Northern Hemisphere and are scattered in the Southern Hemisphere on subantarctic islands and in southern South America (Grube & Poelt 1993; Thomson 1997; Gilbert & Coppins 2009). The remaining two species, *S. asiatica* H. Magn. and *S. subasiatica* N. S. Golubk., are alpine endemics of Asia (Golubkova

1973, 1982). In addition, *S. testudinea* var. *karakorina* Poelt & Obermayer, described from the Karakorum in 1990, is unique within the genus in possessing thalloconidia. Grube & Poelt (1993) treated these three endemic taxa as morphotypes or races of one highly variable taxon, *S. testudinea* and suggested additional studies of this complex to delimit taxa satisfactorily.

*Sporastatia* is morphologically characterized by a crustose, areolate to effigurate placodioid thallus surrounded by a distinct black prothallus, lecideine, immersed apothecia with a rough or wrinkled disc, and 100–200-spored asci with hyaline, simple, ellipsoid to globose ascospores. Several species are hosts for lichenicolous fungi or lichens, especially the species *Rhizocarpon pusillum* Runemark, *R. asiaticum* Poelt and *Miriquidica invadens* Hafellner *et al.* (Poelt 1990; Rambold & Triebel 1992; Davydov *et al.* 2012; Hafellner *et al.* 2014).

The genus *Sporastatia* was established by Massalongo (1854) and Magnusson (1936) considered it to belong to the *Acarosporaceae*. The similarities between *Sporastatia* and *Catillaria* were noted by Hertel & Rambold (1988), who later placed the genus in *Catillariaceae* (Rambold & Triebel 1992) because of its *Catillaria*-type ascus. *Sporastatia* was recently classified in a separate family, *Sporastatiaceae* (Bendiksby & Timdal 2013), and

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was shown to be sister to *Rhizocarpaceae* (Miadlikowska *et al.* 2014). Several other taxa have been described but these have mostly been subsequently synonymized by different authors with the widespread species *S. testudinea* and *S. polyspora*. The taxonomic status of many taxa from the Southern Hemisphere (Dodge 1970) is not clear.

*Sporastatia testudinea* and *S. polyspora* are very common in the Altai Mts, especially in the upper mountain zone. This region remains underexplored (Davydov & Printzen 2012; Davydov *et al.* 2012). During fieldwork in 2014 in the Altai Mts, our attention was caught by an epilithic placodioid lichen resembling *Lecanora*. Anatomical investigation showed that the specimens had *Catillaria*-type asci with 100–200 hyaline, simple, ellipsoid to globose ascospores. Both morphological and molecular studies have independently confirmed its status as a new species, described here as *Sporastatia crassulata*. *Sporastatia testudinea* var. *karakorina* was also studied to determine whether it should be elevated to the level of species. In addition, the type specimen of *S. subasiatica* was examined.

## Materials and Methods

### Specimens and phenotypic studies

The core material for this study was collected by the authors and deposited in the herbaria ALTB and LE. Additionally, type specimens were revised in LE, GZU and S. Morphological observations were carried out using a dissecting microscope. Cross-sections of apothecia and thalli were hand cut with a razor blade and observed in water. Measurements are presented as follows: (minimum value)  $(\bar{x} - SD) - \bar{x} - (\bar{x} + SD)$  (maximum value), where  $\bar{x}$  is the (arithmetic) sample mean, and SD the sample standard deviation. The two extreme values are given to the nearest 0.5  $\mu\text{m}$ , and the sample mean to the nearest 0.1  $\mu\text{m}$ . The description below is based on nine specimens from four localities.

Secondary products were analyzed by applying standard thin-layer chromatography techniques (Culberson & Kristinsson 1970). Solvents A (toluene: 1,4-dioxane: acetic acid, 180: 45: 5), B (hexane: diethyl ether: formic acid, 140: 72: 18) and C (toluene: acetic acid, 170: 30) were used for the TLC analyses. The identification of insoluble lichen pigments follows the methods described by Meyer & Printzen (2000).

### Sequences and phylogenetic reconstructions

To test the phylogenetic relationships of the putative new species, SSU nrDNA sequences of our fresh material and other sequences retrieved from the NCBI database (GenBank) were used for molecular phylogenetic analysis. We also sequenced ITS nrDNA. Sequences of *S. testudinea* and *S. polyspora* were obtained from GenBank. The Asian endemic species of *Sporastatia*, *S. asiatica* and *S. subasiatica*, were not included in the phylogenetic work because we were unable to obtain fresh material of these species and the specimens available in herbaria were too old to allow successful DNA extraction. Our sampling comprised 10 species of *Rhizocarpaceae* including *Sporastatia*, *Toensbergia*, and *Rhizocarpon*, as well as five species of *Umbilicariales* as an outgroup. This selection is based on the studies of Bendiksy & Timdal (2013) and a five-gene analysis by Miadlikowska *et al.* (2014) in which *Umbilicariales* form a sister clade to *Rhizocarpaceae*. Information on these samples along with the GenBank Accession numbers are given in Table 1.

DNA extraction, amplification and sequencing followed the methods of Davydov & Yakovchenko (2017). The Hasegawa-Kishino-Yano parameter with proportion of invariable sites and gamma-distribution (HKY + I + G) was inferred as the optimal substitution model. The matrix consisted of 725 sites, 203 of which were variable and used for RAxML and Bayesian analyses. Bayesian inference with the Markov chain Monte Carlo (BMCMC) method (Larget & Shimon 1999) was performed using MrBayes 3.2.3 (Ronquist *et al.* 2012). Three parallel Bayesian analyses were run in six chains and every 200th generation was sampled. Convergence of the chains was inferred by calculating the average standard deviation of split frequencies every 100 000 generations using a burn-in fraction of 0.5 and the runs terminated when the standard deviation of split frequencies dropped below 0.001. This was the case after 5.9 M generations. The first 50% of trees were discarded as burn-in and a 50% majority-rule consensus tree was calculated from the remaining trees of three runs with the sumt command implemented in MrBayes 3.2.3. Bootstrap support values and BMCMC posterior probability were noted on the best scoring tree. The most likely tree and 1000 bootstrap replicates were calculated using RAxML 8.0.26 (Stamatakis 2014) by raxmlGUI software version 1.3.1 (Silvestro & Michalak 2012), applying the GTRGAMMA model of substitution to the subsets because RAxML does not support the HKY model.

## Results

ITS and mtSSU sequences were successfully obtained from two specimens of the putative new species, described below as *Sporastatia crassulata*; mtSSU sequences were used for reconstruction of the phylogeny in *Rhizocarpaceae*. As the Bayesian 50% majority-rule

TABLE 1. Sample numbers and their GenBank Accession numbers for the phylogenetic analyses in this study. New sequences are indicated in bold.

| Species  | Source: collection location, and collection number or reference                | GenBank Accession no. |                 |
|--|--|-----------------------|-----------------|
|  |  | ITS                   | mtSSU           |
| <i>Boreoplaca ultrafrigida</i> Timdal                          | Korea, Gangwon-do, <i>Yakovchenko</i> 1265 (NIBR)                              |                       | <b>MG993049</b> |
| <i>Catolechia wahlenbergii</i> (Ach.) Körb.                    | AFTOL-ID 1743  |                       | DQ986811        |
| <i>Fuscidea intercincta</i> (Nyl.) Poelt                       | <i>Bjelland</i> 59 (BG)  |                       | AF483172        |
| <i>Rhizocarpon atroflavescens</i> Lyngé                        | Russia, <i>Davydov</i> 14341 & <i>Yakovchenko</i> (ALTB)                       |                       | KY680782        |
| <i>R. disporum</i> (Nägeli ex Hepp) Müll. Arg.                 | Russia, Republic of Tuva, <i>Davydov</i> 14807 & <i>Yakovchenko</i> (ALTB)     |                       | <b>MG993051</b> |
| <i>R. geographicum</i> (L) DC.                                 | Norway, <i>Ihlen</i> 941 (BG)  |                       | AF483187        |
| <i>R. norvegicum</i> Räsänen                                   | Russia, <i>Davydov</i> 14810 & <i>Yakovchenko</i> (ALTB)                       |                       | KY680781        |
| <i>R. smaragdulum</i> <i>Davydov &amp; Yakovchenko</i>         | Russia, <i>Davydov</i> 14339 & <i>Yakovchenko</i> , holotype                   |                       | KY680780        |
| <i>Sporastatia crassulata</i> <i>Yakovchenko &amp; Davydov</i> | Russia, Republic of Tuva, <i>Davydov</i> 14814 & <i>Yakovchenko</i> , holotype | <b>MG993046</b>       | <b>MG993054</b> |
|  | Russia, Republic of Tuva, <i>Davydov</i> 14812 & <i>Yakovchenko</i> , paratype | <b>MG993047</b>       | <b>MG993053</b> |
| <i>S. polyspora</i> (Nyl.) Grunmann                            | AFTOL-ID 395   |                       | AY584724        |
| <i>S. testudinea</i> (Ach.) A. Massal.                         | AFTOL-ID 396, <i>Glew</i> 980808-34 (hb. of <i>Glew</i> )                      |                       | AY584725        |
| <i>Toensbergia leucococca</i> (R. Sant.) Bendiksby & Timdal    | Norway, <i>E. Timdal</i> 12328 (O L-170828)                                    |                       | KF360433        |
| <i>Umbilicaria aprina</i> Nyl.                                 | Antarctica, Dronning Maud Land, <i>Andreev</i> 38075 (ALTB)                    |                       | <b>MG993052</b> |
| <i>U. pustulata</i> (L.) Hoffm.                                | Sweden, 5 June 2001, <i>Wedin</i> (UPS)  |                       | AY300890        |
| <i>Xylospora friesii</i> (Ach.) Bendiksby & Timdal             | Russia, Murmansk Region, <i>Urbanavichus</i> (INEP-48)                         |                       | <b>MG993050</b> |

consensus tree had the same topology as RAxML, both phylograms are combined in Fig. 1.

Sequences of *Sporastatia crassulata* clustered with the sequences of *S. testudinea* and *S. polyspora* in a clade with 78/0.97 support values (bootstrap/posterior probability) in the phylogenetic tree (Fig. 1). Therefore, it is highly likely, based on DNA results as well as morphology, that *S. crassulata* belongs in *Sporastatia*.

The two mtSSU sequences of *S. crassulata* are identical. The genetic difference between sequences of *S. crassulata* and *S. testudinea* (including gap vs. non-gap) is 10 residues in

mtSSU excluding gap versus non-gap or 24 residues including gaps (2.8%). *Sporastatia crassulata* is closest morphologically to *S. testudinea* but clearly differs in thalline and apothecial characters, as described below.

### ***Sporastatia crassulata* Yakovch. & Davydov sp. nov.**

Mycobank No.: MB 824361

Thallus squamulose, placodioid, uneven, thick (1–2 mm), pale to medium brown, delimited by the well-developed black hypothallus; squamules usually ascending at the central part of the thallus, convex, rotund, usually marginally pruinose, surface rugose; apothecia lecideine, sunken, fertile areoles with

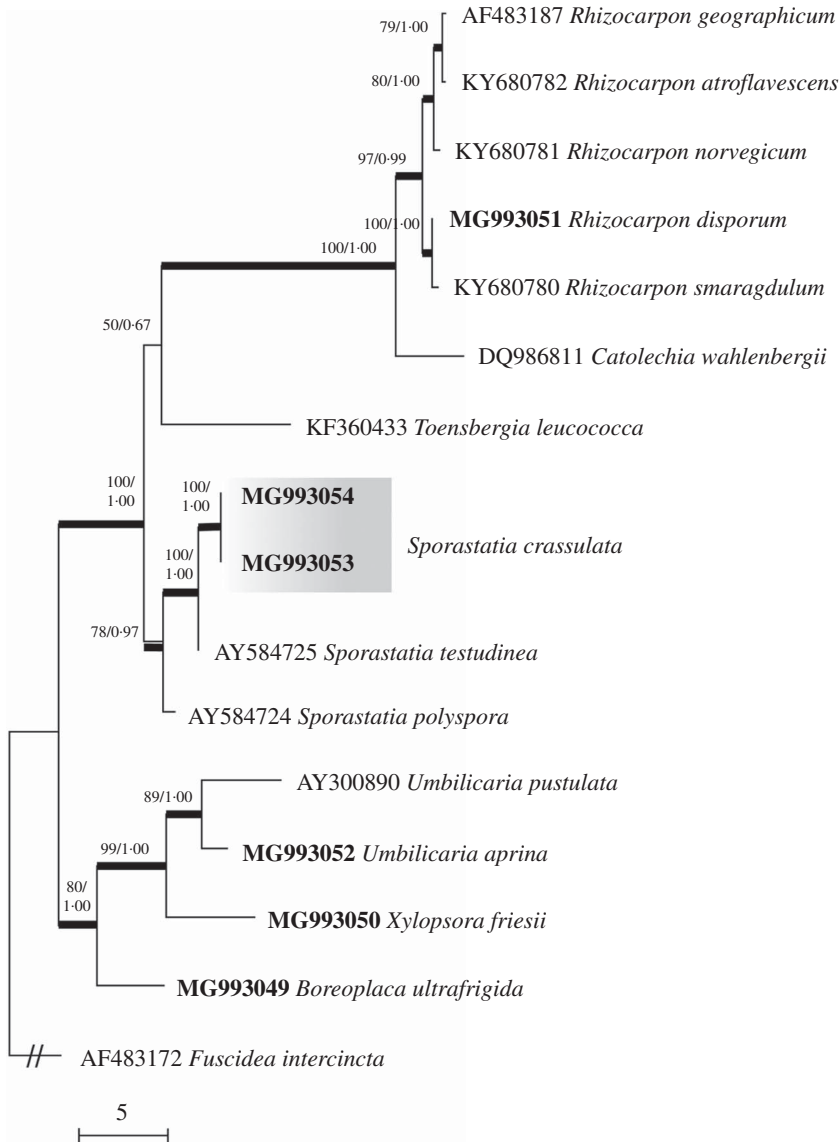


FIG. 1. Maximum likelihood phylogeny of selected *Rhizocarpaceae* mtSSU. Numbers at nodes indicate bootstrap values of ML (left of slash) and BMC MC posterior probabilities (right of slash) (only values  $\geq 50\%$  and  $\geq 0.50$ , respectively, are depicted). Thicker branches indicate when the bootstrap value of ML is  $\geq 70\%$  or the BMC MC posterior probability is  $\geq 0.95$ . GenBank Accession numbers are given as OTU names (see Table 1). New sequences are in bold.

ascending margins wrapping the disc forming a pseudo-lecanorine margin; epihymenium Cinereorufa-green with Atra-red patches.

Type: Russia, Republic of Tuva, Mongun-Taiginsky District, Mongun-taiga massif, right side of the Khairykan

River valley at 4 km upstream from its mouth (Mugur River),  $50^{\circ}18'11''\text{N}$ ,  $90^{\circ}11'55''\text{E}$ , alt. 2540 m a.s.l., stone-fields within alpine meadows and mountain tundra, on stones, 11 July 2014, *E. A. Davydov* 14814 & *L. S. Yakovchenko* (LE-L13175—holotype; ALTB—isotype).

(Fig. 2A–E)

*Life habit* lichenized, not lichenicolous. *Thallus* squamulose, placodioid, round to irregular in outline, up to 5 cm in diam., 1–2 mm thick, uneven, beige, greyish-yellow, pale-brown to medium brown, paler at margins, colour unchanged when wet, *prothallus* usually distinct, black, forming a rim around the thallus and sometimes visible between the squamules, *vegetative propagules* absent. *Squamules* in the central part of the thallus convex, rotund or irregular in outline (but not angular), usually ascending, (0.25–) 0.65–1.00–1.35(–2.35) mm ( $n=74$ ). Fertile squamules larger and prominent, with margins wrapping the disc forming a pseudolecanorine margin. Marginal squamules elongated, convex, attached, extended and notched at the ends, (1.10–) 1.65–2.00–2.50(–3.75) mm ( $n=67$ ). *Surface* rimose, wrinkled, rugose to scabrose, rarely  $\pm$  smooth, matt to shiny, with white pruina forming a rim around each squamule and heavy on the periphery of the thallus, rarely the whole thallus pruinose or entirely without pruina. *Upper cortex* (37.5–) 42.5–70.5–98.0(–125.0)  $\mu\text{m}$  thick ( $n=13$ ), hyaline to brownish yellow, opaque due to the presence of crystals, sometimes covered by an epinecral layer (7.5–) 14.5–17.5–20.5(–25.0)  $\mu\text{m}$  tall ( $n=11$ ). *Algal layer* continuous, (62.5–) 74.0–98.0–122.0(–187.5)  $\mu\text{m}$ , tall ( $n=10$ ). *Photobiont*: *Myrmecia* sp., algal cells up to 12.5  $\mu\text{m}$  diam. *Medulla* up to 1–2 mm tall, grey with unclear structure, granular, with perpendicular thick-walled hyphae (3.5–) 4.5–5.0–5.5(–7.5)  $\mu\text{m}$  thick ( $n=10$ ).

*Apothecia* lecideine, (0.25–) 0.60–0.80–1.10(–1.65) mm ( $n=71$ ), common, numerous in the centre of the thallus, sunken, 1–3 per squamule, rarely separated from the thallus by cracks; *disc* black to dark brown-black, colour unchanged when wet, plane, angular, rarely roundish, cracked to roughened, slightly pruinose or without pruina; *margin* thin, black, at the same level as disc or higher, sometimes excluded. *Exciple* extended in uppermost part, (22.5–) 37.5–55.0–72.5(–87.5)  $\mu\text{m}$  thick ( $n=15$ ), brown-black, of rounded cells (5.0–) 6.5–7.5–8.5(–10.0)

$\mu\text{m}$  diam. ( $n=12$ ), lateral exciple (12.5–) 16.5–19.5–22.5(–25.0)  $\mu\text{m}$  thick ( $n=11$ ), of elongated cells, hyaline to brown, basal exciple indistinct and scarcely distinguishable from the hypothecium, brown, (12.5–) 13.0–30.0–47.0(–62.5)  $\mu\text{m}$  thick ( $n=10$ ). *Hypothecium* (25.0–) 46.0–68.5–91.0(–112.5)  $\mu\text{m}$  thick ( $n=15$ ), hyaline, ochraceous to brown toward the exciple, I+ blue. *Hymenium* (75.0–) 88.0–99.0–110.0(–137.5)  $\mu\text{m}$  thick ( $n=15$ ), hyaline, always with Atra-red lines of sterile hyphae, I+ blue. *Epithecium* Cinereorufa-green with Atra-red patches (see Meyer & Printzen 2000). *Paraphyses* septate, simple to weakly branched, (1.6–) 1.6–1.8–2.0(–2.4)  $\mu\text{m}$  thick ( $n=9$ ) in mid-hymenium with cylindrical or narrowly clavate tips, (2.1–) 2.3–2.6–2.9(–3.2)  $\mu\text{m}$  thick ( $n=11$ ). *Asci* *Catillaria*-type, 100–200-spored, clavate, unitunicate, thick-walled, (75.0–) 76.0–79.0–84.5(–90.0)  $\times$  (25.0–) 24.5–26.5–28.5(–30.0)  $\mu\text{m}$  ( $n=16$ ); *ascospores* (3.5–) 3.7–3.9–4.2(–4.5)  $\times$  (3.2–) 3.2–3.4–3.6(–4.0)  $\mu\text{m}$  ( $n=35$ ), hyaline, simple, broadly ellipsoid to globose, thin walled, without a distinct perispore.

*Pycnidia* not seen.

*Chemistry*. Thallus K–, C+ red, KC+ red; gyrophoric and lecanoric acids by TLC.

*Etymology*. The name refers to the thick squamulose thallus.

*Ecology*. *Sporastatia crassulata* was found abundantly in dry conditions on exposed siliceous rocks in the upper mountain belt (c. 2400–3100 m a.s.l.).

*Distribution*. *Sporastatia crassulata* is currently known from several localities in the Altai Mountains, both in South Siberia and in adjacent territory of China (Fig. 3). The distance between the two most remote localities is c. 500 km.

*Additional material examined*. **Russia**: Republic of Altai: Ust'-Koksinsky District, Katunsky Range, upper reaches of the Ioldo River, 49°49'37.5"N, 86°15'58.7"E, alt. 2574 m a.s.l., stonefields and rocks, on stones, 2008, E. A. Davydov 10677 (ALTB). Republic of Tuva: Mongun-Taiginsky District, Mongun-taiga Massif, right side of the Khairykan River valley at 3 km upstream from its mouth (Mugur River), 50°18'3"N, 90°12'23"E, alt. 2400–2500 m a.s.l., alpine meadows and mountain tundra with stones, on stones, 2014, E. A. Davydov 14812 & L. S. Yakovchenko

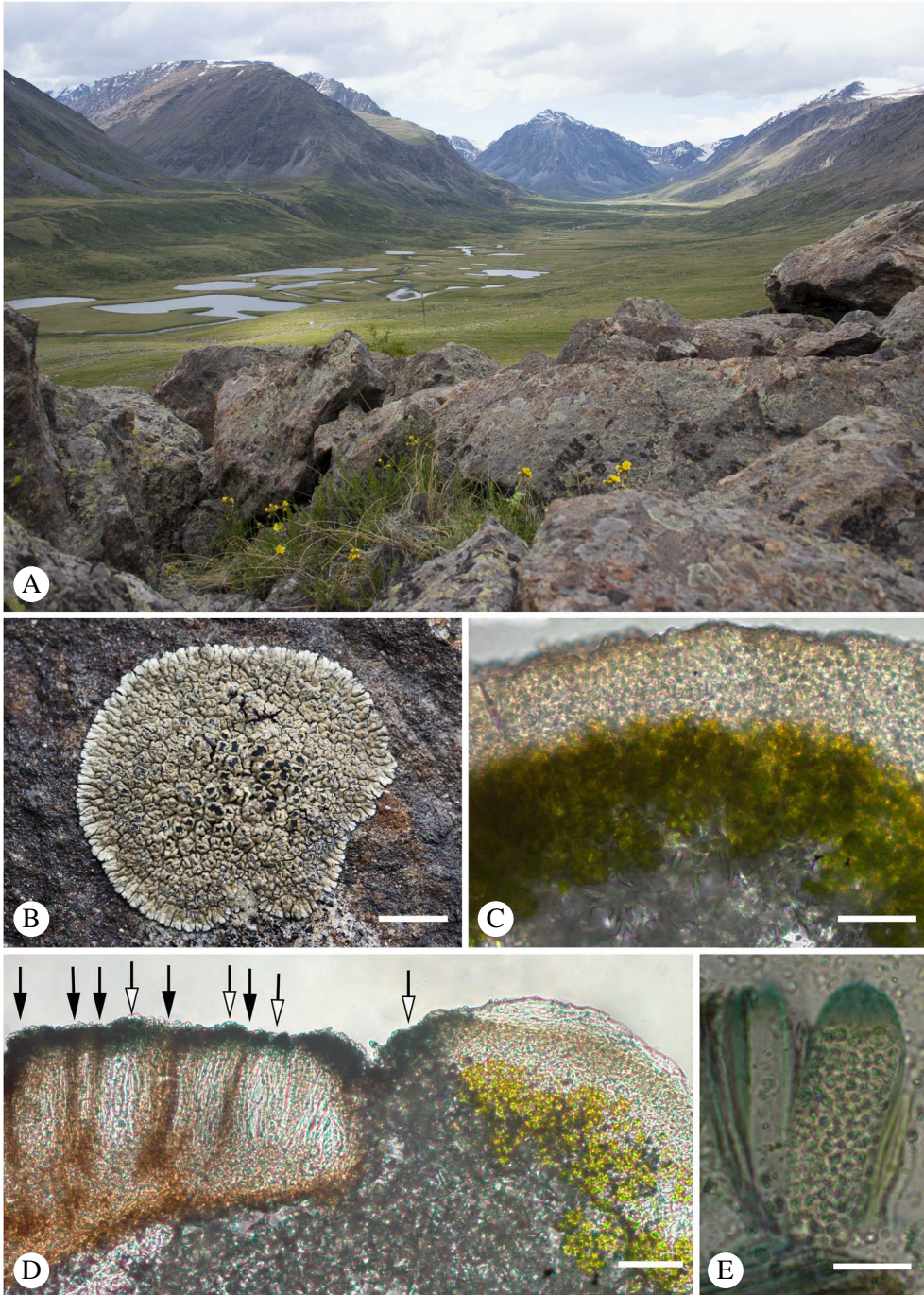


FIG. 2. *Sporastatia crassulata*. A, type locality, Mongun-Taiga Massif, Khairkan River basin; B, type specimen (field photograph); C, section of thallus showing the continuous algal layer; D, section of apothecium with Cinereorufa-green (white arrows) and Atra-red (black arrows) pigments; E, multisporous ascus of *Catillaria*-type (in KI). Scales: B = 1 cm; C & D = 50  $\mu\text{m}$ ; E = 20  $\mu\text{m}$ . In colour online.

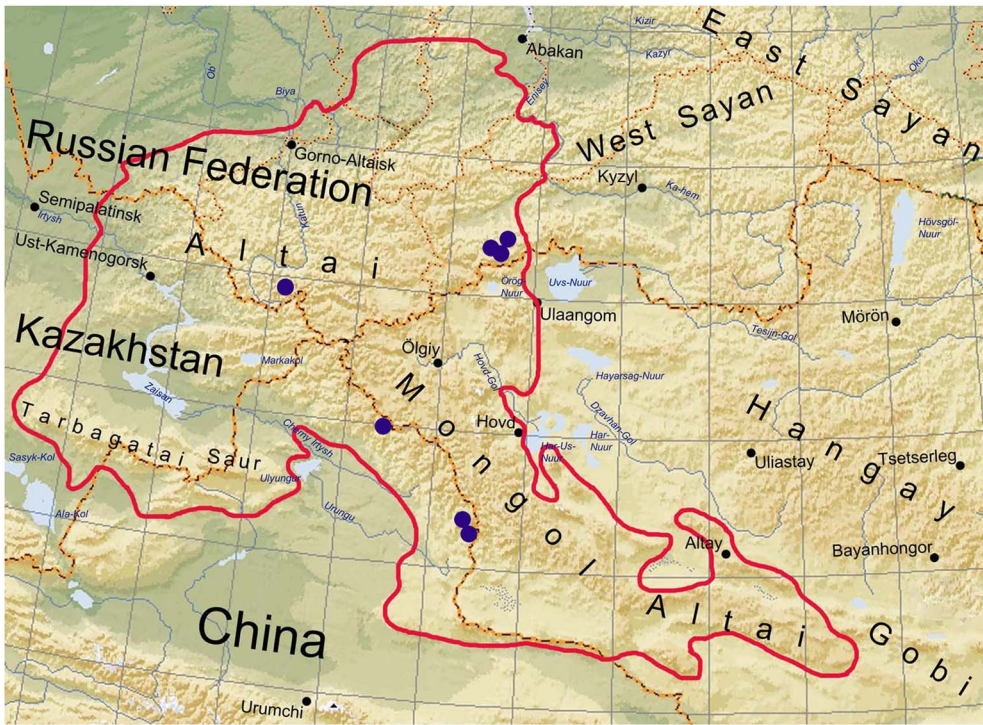


FIG. 3. Distribution of *Sporastatia crassulata*. Solid line indicates the outline of the Altai region. In colour online.

(ALTB); same massif, left side of the Toolaity River valley at 2.7 km upstream from the Eski-Toolaity lake, 50°10'1"N, 90°09'05"E, alt. 2670 m a.s.l., mountain tundra, stonefield, on stones, 2014, *E. A. Davydov* 14813 & *L. S. Yakovchenko* (ALTB); same valley, 5 km upstream from the Eski-Toolaity lake, 50°11'3"N, 90°08'46"E, alt. 2550 m a.s.l., mountain tundra, stonefield, on stones, 2014, *E. A. Davydov* 16521 & *L. S. Yakovchenko* (ALTB).— **China:** *Xinjiang:* Mongol'sky Altai Range, SE slope of Mt. Keshtau (3511 m), 46°45'18"N, 90°50'15"E, alt. 3136 m a.s.l., gravelly tundra, on rocks, 2007, *E. A. Davydov* 17335 (ALTB); same range, upper reaches of Khara-Belchir-he, west slope of Kara-Balchigtau Mt. (3215 m), 46°42'0"N, 90°56'49"E, 2656 m a.s.l., *Larix sibirica* forest, steppe slopes with *Juniperus* spp., on rocks, 2007, *E. A. Davydov* 17336 (ALTB); same range, Kungeytytau Mts, upper reaches of Yelt-gol, 15 km up from the mouth of Duntsa-he, 48°03'37"N, 88°51'25"E, alt. 2800–3040 m a.s.l., subalpine and alpine meadows, near the snow, on rocks, 2007, *E. A. Davydov* 17337 (ALTB).

### Discussion

*Sporastatia crassulata* is unique within the genus in having a distinctly squamulose, thick, uneven thallus composed of convex,

not angular squamules irregularly ascending in the central part of the thallus. It is also unusual among *Sporastatia* species in that its apothecia are below the thallus level and the prominent fertile squamules have ascending margins sometimes surrounding the disc as a pseudolecanorine margin. Thus, in the field *S. crassulata* resembles a species of *Lecanora* s.l. *Sporastatia crassulata* shows wide morphological variability throughout its distribution. Russian populations characteristically have an effigurate thallus, delimited by a well-developed black prothallus with squamules ascending in the central part of the thallus, and with the upper surface matt, pruinose, wrinkled, and rugose to scabrous. The Chinese populations of the species differ by their less well-developed prothallus, marginal lobes weakly elongated (1.1–1.5(–2.5) mm) and central squamules weakly ascending, and by the darker, glossier, non-pruinose, ± smooth upper surface. These regional differences are within the variability of the species

and appear to be due merely to climatic factors. *Sporastatia crassulata* and the widely distributed species *S. testudinea* are both brown-coloured with a radiate thallus delimited by a black, well-developed prothallus. However, the thallus of *S. testudinea* is thin, crustose-areolate, composed of plane, angular areoles with apothecia at the same level as the thallus. *Sporastatia crassulata* clearly differs from *S. polyspora* by its squamulose radiate (vs. non-effigurate), brown (vs. grey), thick and uneven (vs. thin and plain) thallus. *Sporastatia crassulata* may slightly resemble *S. asiatica* (Fig. 4E) and *S. subasiatica* (Fig. 4F) in the presence of pruina, and by having an uneven, rugose to scabrous upper surface (distinctions given below).

*Sporastatia crassulata* is currently known from several localities throughout the Altai Mountains (South Siberia and adjacent China). In Russia, this species occurs in the Katunsky Range (Central Altai) and in five localities through the high mountain massif Mongun Taiga (south-east Altai) (Fig. 3). In China, it is known from the Mongolian Altai Range. *Sporastatia crassulata* grows together with *S. testudinea* and *S. polyspora* at all localities. We have seen intermixed populations of the first two taxa in the Altai where the differences in thallus morphology cannot be the result of different ecology. The distribution of *S. crassulata* in the Altai appears to be restricted to alpine environments at elevations of 2400–3100 m a.s.l. Other endemic species of *Sporastatia* also occur in high Asian mountains. Mountainous Central Asia therefore appears to be the centre of species diversity and endemism for *Sporastatia*.

### Additional Species Reported

#### ***Sporastatia karakorina* (Obermayer & Poelt) Davydov & Yakovch. comb. & stat. nov.**

Mycobank No.: MB 824362

*Sporastatia testudinea* (Ach.) Massal. var. *karakorina* Obermayer & Poelt, *Herzogia* 8: 278 (1990); type: China, Xinjiang Prov., Karakorum, östlich des K2-Gletschers oberhalb der Einmündung des Siang-kiang-Gletschers (35° 58'N, 76°27'E), c. 490 m, großer Sandstein/Quarzit-Block,

Exp. Nordwest 80°, 24 Sept. 1986, B. Dickoré Nr. F24 (GZU!—holotype).

(Fig. 4C & D)

*Notes.* Examination of the type material of *Sporastatia testudinea* var. *karakorina* and its description in the protologue suggested that this taxon required recognition at the species level. In morphology it resembles *S. testudinea* but differs by having globose ascospores (i.e. length/width ratio: 1.0–1.05(–1.1) (vs. ellipsoid to broadly ellipsoid, length/width ratio 1.2–1.7)) and possessing characteristic mitosporic dispersal units, so-called ‘thalloconidia,’ on the prothallus (Fig. 4D). Thalloconidia as defined by Hestmark (1990) may develop in various lichen families (Hasenhüttl & Poelt 1978; Poelt & Obermayer 1990) but they are most commonly formed by members of the *Umbilicariaceae*. Thalloconidia in various taxa were shown to be non-homologous and to have a highly species-specific morphology (Hasenhüttl & Poelt 1978; Hestmark 1991; Davydov *et al.* 2017b). Within *Sporastatia*, true thalloconidia are so far known only in *Sporastatia karakorina*. Poelt & Obermayer (1990) mentioned that some specimens of *S. testudinea*, collected higher than 2500 m in the Alps, show a tendency to produce thalloconidia but true thalloconidia were not observed. In the Altai Mountains, specimens collected above 2800–3000 m also have a better developed rough prothallus but never produce thalloconidia. The presence of thalloconidia alone is not necessarily a distinguishing trait at the species level (Poelt & Obermayer 1990; Davydov *et al.* 2017a) but as this trait is geographically localized and correlated to other characters (in this case globose ascospores), we propose the species level for this taxon.

#### ***Sporastatia subasiatica* N. S. Golubk.**

*Nov. Sist. Niz. Rast.* 10: 202 (1973); type: [Tadjikistan], East Pamir, Murgabsky District, valley of Kul'-Nambed River, alt. 4200 m a.s.l., on siliceous boulder with lime intrusions, 26 July 1966, Golubkova N. S. 809 (LE-L497!—holotype).

(Fig. 4F)

*Sporastatia subasiatica* was described from the Pamir Mountains (Golubkova 1973).



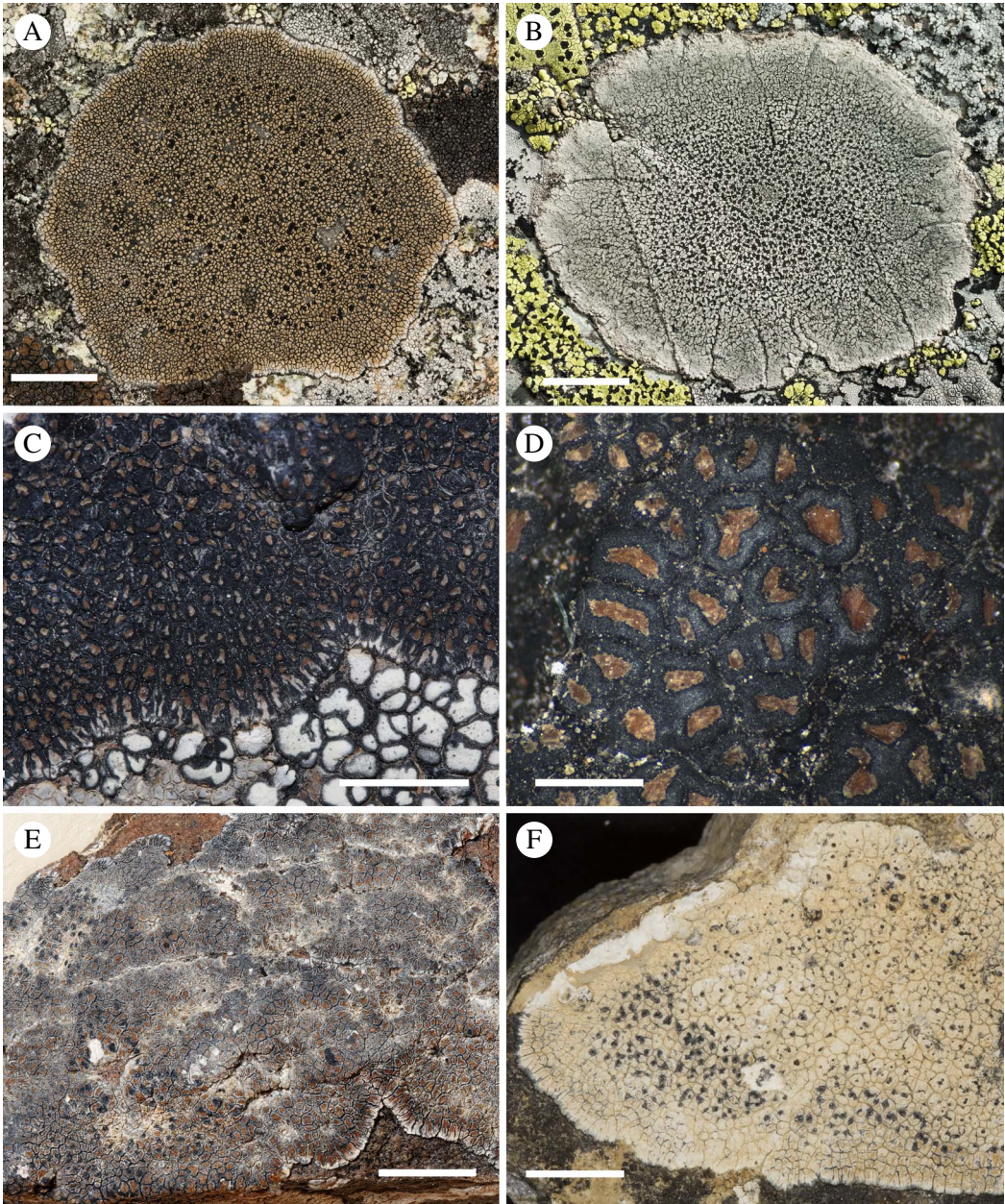


FIG. 4. A, *Sporastatia testudinea*, Altai Mts (field photograph); B, *S. polyspora*, Altai Mts (field photograph); C, *S. karakorina*, holotype; D, *S. karakorina*, holotype, note the thalloconidial rims around areoles; E, *S. asiatica*, holotype; F, *S. subasiatica*, holotype. Scales: A & B = 1 cm; C, E & F = 0.5 cm; D = 0.5 mm. In colour online.

This alpine species occurs at elevations up to 4200 m a.s.l. on siliceous rocks partly with calcareous modification. It is characterized by its thin, crustose, placodioid, whitish thallus, composed of plane angular areoles (central 0.3–0.9 mm diam., marginal 1.2–1.8 × 0.4–0.9 mm) with a pruinose scabrous to echinate upper surface, and delimited by a black prothallus. Apothecia are at the same level as the thallus, 0.2–0.7 mm diam., black, lecideine, pruinose, with a thin proper margin and rugose disc. Other characters include: green-black exciple, hyaline hymenium, (130–) 145–170 µm tall with violet epihymenium, hyaline to pale-brown hypothecium, 100–145 µm tall, and *Catillaria*-type asci with 100–200

hyaline, simple, ellipsoid ascospores, 5–6 × 2.5–3.0 µm. Thallus C+ red (gyrophoric and lecanoric acids), K–.

*Sporastatia subasiatica* differs from other *Sporastatia* species mainly by the presence of a violet epihymenium, green-black exciple, hymenium (130–)145–170 µm high and a pale, whitish thallus (largely due to the presence of dense pruina). The pigments in the epithecium (unknown in the classification of Meyer & Printzen (2000)) differ from those in *S. testudinea* and *S. crassulata*. They are brownish with a purple tint, KOH+ (purple intensive) – HCl (black to brown); HNO<sub>3</sub> (purple clearing) – KOH+ (black to purple) – HCl (brown).

### Key to *Sporastatia*

- 1 Thallus squamulose, 1–2 mm thick; squamules convex, rotund, usually ascending in the central part of the thallus ..... **Sporastatia crassulata** (Fig. 2B)  
Thallus crustose areolate, ± thin, 0.2–0.6 mm thick; areoles plane to concave, angular, closely attached ..... 2
- 2(1) Thallus pale, whitish; areoles with scabrous to echinate surface; upper hymenium with a purple tint; hymenium (130–)145–170 µm tall. On silicate (sometimes calcareous modified) rocks ..... **S. subasiatica** (Fig. 4F)  
Thallus pale to dark; areoles with smooth to cracked surface; epithecium dark green, brown-green, blue-green, brown to black-brown; hymenium up to 130 µm tall. On siliceous rocks only ..... 3
- 3(2) Thallus greyish, rarely distinctly effigurate, matt; epinecral layer lacking ..... **S. polyspora** (Fig. 4B)  
Thallus brownish, usually effigurate, partly or entirely shiny, cortex with an epinecral layer ..... 4
- 4(3) Prothallus lacking at the thallus margins, seldom visible between the areoles; areoles heavy pruinose along the margin ..... **S. asiatica** (Fig. 4E)  
Prothallus distinct at the thallus margins and between the areoles, forming a black rim; areoles not pruinose ..... 5
- 5(4) Thalloconidia developed on prothallus around the areoles; ascospores globose ..... **S. karakorina** (Fig. 4C)  
Thalloconidia absent; ascospores ellipsoid to broadly ellipsoid ..... **S. testudinea** (Fig. 4A)

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