

AN ENIGMATIC SPECIES OF *SCHISTIDIUM* (GRIMMIACEAE, BRYOPHYTA)
FROM THE SAYAN MOUNTAINS, ASIAN RUSSIA

ЗАГАДОЧНЫЙ ВИД ИЗ РОДА *SCHISTIDIUM* (GRIMMIACEAE, BRYOPHYTA)
С САЯНА, АЗИАТСКАЯ ЧАСТЬ РОССИИ

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Abstract

During a field trip to Tunkinskie Goltsy Range, East Sayan Mountains, Republic of Buryatia a peculiar specimen of *Schistidium* with strongly concave, cucullate leaves was collected from rocks in a temporarily dry stream bed. It was identified as *Schistidium chenii* (Lin) Cao, Gao & Zhao. This species was previously known from two high mountain localities in China (Tibet and Xinjiang Uygur Autonomous Region). A molecular phylogenetic analysis of the Sayan specimen found its closest relative to be *S. occidentale*, a widespread western North American species, but recently discovered in Spain. The description based on specimen from Russia is provided; a comparison with *S. occidentale* and species similar to *S. chenii* in morphology is given.

Резюме

В ходе полевых исследований в Тункинских гольцах (Восточный Саян, Республика Бурятия) был собран необычный образец *Schistidium* с очень сильно вогнутыми листьями с колпачковидными верхушками; это растение было найдено на камнях в сухом русле временного водотока. Он был определен как *Schistidium chenii* (Lin) Cao, Gao & Zhao. Этот вид был до настоящего времени известен из двух местонахождений в высокогорьях Китая (в Тибете и Синьзянь-Уйгурском Автономном Районе). Согласно результатам молекулярно-филогенетического анализа, саянский образец наиболее близок к *S. occidentale*, виду, широко распространенному на западе Северной Америки и недавно найденному в Испании. Приводится описание *S. chenii*, сделанное по вновь найденному образцу, а также его сравнение с *S. occidentale* и другими видами, сходными с *S. chenii* по морфологии.

KEYWORDS: mosses, taxonomy, biogeography, Asian Russia

INTRODUCTION

Schistidium Brid. is a taxonomically difficult genus, with numerous taxa treated mainly at the infraspecific level during the 20th century. This tradition changed completely through the treatment of the *S. apocarpum* complex in Norway and Sweden (Blom, 1996) where many distinct species were defined. Most recent regional floras treat *Schistidium* as multispecific genus (Suárez & Muñoz, 2015; McIntosh, 2007; Weibull, 2006; Ignatova & Blom, 2017), and many European species have been illustrated by Lüth (2019).

The narrow species concept in *Schistidium* has been supported by ITS sequence analyses by Goryunov *et al.* (2007) and Milyutina *et al.* (2010). Most species found

in the vast territory of Russia were those already discovered by Blom (1996) in Scandinavia, but a considerable number were described in subsequent publications (Ignatova *et al.*, 2010, 2016; McIntosh *et al.*, 2017).

The present paper presents the elucidation of an enigmatic specimen collected on periodically submerged rocks in a stream bed in the vicinity of Mondy Sett., from the southern slope of Tunkinskie Goltsy Range of East Sayan Mts. This plant resembled *Schistidium sordidum* I. Hagen in having ovate leaves with rounded apices, but its leaves were stronger concave and did not have narrowly revolute margins characteristic for the latter species. No species with such character combination were known in the moss flora of Russia. Since the morpho-molecular

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approach showed promising results in revealing species affinities in previous studies of the genus *Schistidium*, we decided to apply it to the specimen from the Sayan mountains, as well as to search for appropriate name in literature.

MATERIALS AND METHODS

Dataset. Nuclear ITS1-2 was chosen, as most used plastid markers (*rps4*, *trnL-F*) are not variable enough to resolve affinities within the genus. Preliminary ITS sequence results showed that the East Sayan specimen is most closely related to *Schistidium occidentale* (E. Lawton) S.P. Churchill. Also the dataset was expanded to include other subaquatic taxa of the genus. Representatives of other main clades found in previous analyses were also included. In total, 62 accessions of 44 species were taken from GenBank and 4 sequences were obtained *de novo*. Two accessions of *S. sordidum* were used as an outgroup as it was done in our previous studies of the genus (e.g. Ignatova *et al.*, 2010). Sequences were automatically aligned using MAFFT v. 7.487 (Katoh & Standley, 2013) and the alignment was edited manually in Bioedit (Hall, 1999).

Sequence acquiring. The laboratory and sequencing protocols were essentially the same as in our previous moss studies, described in detail in other studies, e.g., Gardiner *et al.* (2005). Voucher data and GenBank accession numbers are given in Appendix 1.

Molecular analysis. Phylogenetic reconstructions under Bayesian inference (BI) were performed using MrBayes v.3.2.7 (Ronquist *et al.*, 2012), with two parallel runs each consisting of six Markov chains, 5 000 000 generations with default number of swaps and sampling frequency one tree each 1000 generations, the chain temperature was set at 0.02. and models were sampled throughout the GTR model space (nst = mixed). Consensus tree was calculated after omitting the first 25% of trees as burn-in. The convergence between runs previously assessed as an average split deviation frequency lower than 0.01 was reached after 0.5–1.5 million generations. Additionally, ESS values were checked using Tracer v.1.7.2 (Rambaut *et al.* 2018) to be higher than 200.

Best-scoring maximum likelihood (ML) trees were estimated using IQtree (Trifinopoulos *et al.*, 2016) with GTR+G+I model. Robustness of the nodes was assessed using 1000 pseudoreplications of the ultrafast bootstrapping algorithm as implemented in IQtree. Trees were rooted on *S. sordidum* according to topology published by Ignatova *et al.* (2010), and visualized using FigTree 1.4.3.

Morphological studies. Light microscope observations were made under a stereomicroscope (Olympus SZX7) equipped with an Infinity 8-8 digital camera, and compound light microscope Olympus CX-43 with an Infinity 1-2 digital camera. Stacked micrographs using several optical sections were composed using the software package HeliconFocus 4.50 (Kozub *et al.*, 2008).

RESULTS

Using the root *S. sordidum* the phylogenetic tree comprises a clade formed by (1) *S. pulchrum* H.H. Blom+*S. grandirete* H.H. Blom+*S. platyphyllum* (Mitt.) H. Perss., and (2) *S. frivollianum* H.H. Blom, and (3) a weakly supported terminal clade with three subclades, I, II and III. The subclade I represents the maximally supported *Atrofuscum* clade with two species, *S. atrofuscum* (Schimp.) Limpr. and *S. viride* H.H. Blom & Darigo. Not supported subclade II is formed by poorly supported groups, where a high support for non-monospecific clades have (a) the clade of *S. occidentale* (Lawton) Churchill and the enigmatic plant from the Sayan Mts; (b) the maximally supported clade of *S. austrosibiricum* Ignatova & H.H. Blom+*S. relictum* T.T. McIntosh, H.H. Blom & Ignatova; and (c) the maximally supported *Robustum* clade with seven species.

The subclade III includes mostly the already analyzed sequences, and its subclades mostly correspond to informal groups suggested by Blom: the *Apocarpum*-group (represented here by *S. apocarpum* (Hedw.) Bruch, Schimp. & W. Gümbel, *S. papillosum* Culm., *S. pruinosum* (Wilson) G. Roth., *S. strictum* (Turn.) Loeske ex Mårtensson, *etc.*) and the *Confertum*-group (*S. confertum* (Funck) Bruch, Schimp. & W. Gümbel, *S. flaccidum* (De Not.) Ochyra, *S. marginale* H.H. Blom, Bedn.-Ochyra & Ochyra, *etc.*).

Subaquatic species were found in this tree, beside its root (*S. sordidum*), in a clade within the basal grade (*S. platyphyllum*), and in subclade II in two unrelated subclades: *S. agassizii* Sull. & Lesq. and *S. foraminis-martini* Kiebacher, Kockinger & H.H. Blom (in a clade with *S. dupretii* (Thér.) W.A. Weber, *S. robustum* (Nees & Hornsch.) H.H. Blom, *S. submuticum* Broth. ex H.H. Blom, *S. frigidum* H.H. Blom, and *S. tenerum* (J.E. Zetterst.) Nyholm); and *S. occidentale* with an enigmatic plant from the Sayan Mts. Subclade III has even more scattered subaquatic lineages: *S. abrupticostatum* (Bryhn) Ignatova & H.H. Blom in a rather isolated position, and a clade with *S. cinclidonteum* (Müll. Hal.) B. Bremer, *S. lewis-smithii* Ochyra, *S. falcatum* (Hook. f. & Wilson) B. Bremer, *S. rivulare* (Brid.) Podp.

DISCUSSION

Blom (1996) dealt only with the *Schistidium apocarpum* complex, which includes species that are characteristic of dryer habitats, vs. those found along streams (rheophytes). He recognized several informal groups which later were proved to be congruent with the clades obtained by the molecular phylogenetic analysis in Ignatova *et al.* (2010). Some of these informal groups were recognized by Ochyra *et al.* (2003) as sections within the subgenus *Apocarpa* Vahl.: *Apocarpiformia* (Kindb.) Ochyra, *Robusta* Ochyra, *Conferta* (Vahl.) Ochyra, and *Atrofusca* Ochyra. He also included into this subgenus section *Rivularia* Ochyra with one species, *S. rivulare*, due to its sharply keeled leaves, whereas another aquatic

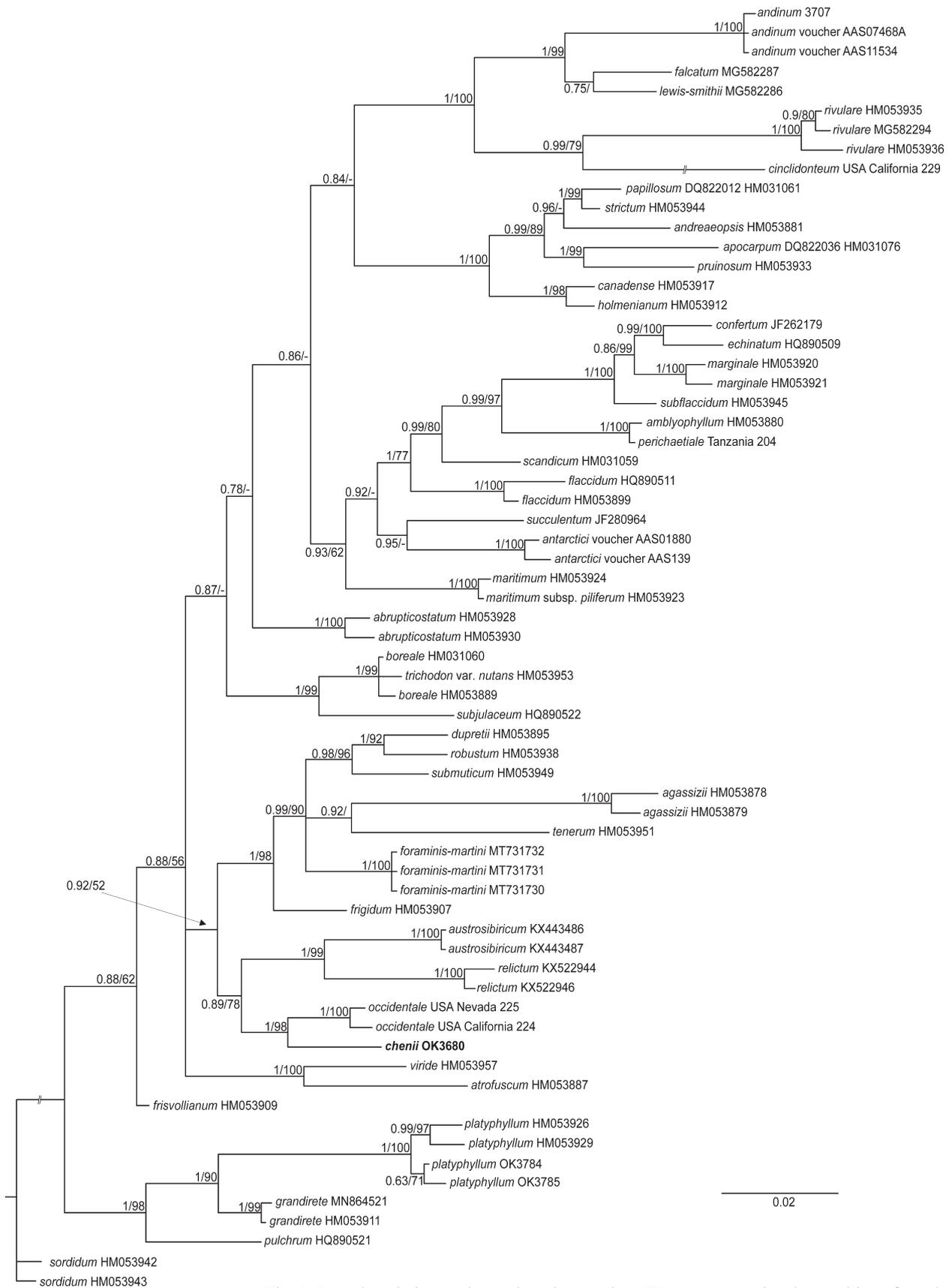


Fig. 1. Bayesian phylogenetic tree based on nuclear ITS sequences, showing position of specimen of *Schistidium chenii*. The posterior probabilities from Bayesian inference / Bootstrap supports from the maximum likelihood analysis are shown on the branches.

species, *S. agassizii*, was placed into a separate subgenus *Canalicularia* Ochyra based on canaliculate leaves with U-shaped cross sections. However, the results of Ignatova *et al.* (2010) did not confirm the close relationship of *S. rivulare* with the species of *S. apocarpum* group.

A brief overview of *Schistidium* subg. *Canalicularia* was provided by Ochyra & Bednarek-Ochyra (2015) who discovered that the mainly western North American *S. occidentale* was recognized as a form 27 years before its description at the species rank. The representatives of this subgenus are characterized by having broadly concave leaves with erect and plane margins. Many of these species are rheophytes.

The dataset in the present study includes four rheophytic species of the subgenus *Canalicularia* (*S. agassizii*, *S. lewis-smithii*, *S. falcatum*, and *S. cinclidontum*) and four other rheophytes (*S. sordidum*, *S. rivulare*, and *S. platyphyllum*). Most terrestrial species were resolved in the mentioned groups, while rheophytic species were scattered in many clades of the phylogenetic tree, often performing the earliest divergent lineages in smaller clades composed by terrestrial species.

No clades with more than two species have exclusively rheophytic ones, and only one clade includes as much as four rheophytic species. This clade comprises three species from the subg. *Canalicularia*: *S. cinclidontum*, *S. lewis-smithii*, and *S. falcatum*; in addition, *S. rivulare* is also resolved within this clade, and in the terminal position there is one terrestrial Subantarctic species with hyaline hairpoints, *S. andinum* (Ochyra *et al.*, 2008). Furthermore, another species from the subg. *Canalicularia*, *S. occidentale*, was not resolved with these three species but in a separate small clade which also included the unknown species from the Sayan Mts. This plant also has ovate, strongly concave leaves with erect and flat margins, and may be considered among the species of this subgenus. It shares with *S. occidentale* 2–4-seriate, bistratose marginal cells forming a fleshy limbidium, and small spores, but its short, almost orbicular leaves contrast sharply with the linear-lanceolate, gradually long-acuminate, and usually falcate-secund leaves of *S. occidentale*. However, perichaetial leaves of *S. occidentale* are ovate, strongly concave with rounded apices (Lawton, 1971; see also Fig. 2J), being very similar to the stem leaves of the Sayan plant.

Ochyra & Bednarek-Ochyra (2015) included thirteen species in the subgenus *Canalicularia* and presented a key to their identification. In this key, one species attracted our attention due to its character combination strikingly similar to those of the East Sayan plant. This is *Schistidium cribrodontium* (Herzog) Ochyra described in 1937 from the high alpine zone in Ruwenzori Mts, Central Africa. It also has strongly concave, ovate leaves broadly rounded at their apices, and similar peristome teeth, mostly joined in pairs and strongly perforate. Other characters, such as presence or absence of bistratose patches along the leaf margins or other parts of lamina were not available in the original

description and illustration of *S. cribrodontium* (Herzog, 1937) and in the Ochyra & Bednarek-Ochyra (2015) key. This species is apparently known only by the type material. The plant from Sayan Mts differs from it in having wider leaves, 1.5–2.0×1.1–1.3 mm vs. ca. 2.0×0.7 mm, with L/W ratio 1.2–1.5:1 vs. ca. 3:1.

There are some other species with somewhat similar character combination, but also having some differences from the plant from Sayan Mts. One of them is recently described from the European Alps *Schistidium foraminemartini* (Kiebacher *et al.*, 2021). It also has concave and muticous leaves and strongly thickened leaf margins, but its leaves are more elongate, leaf margins are partially recurved, mid-leaf cells have sinuose walls, peristome teeth are truncate, not perforated, and filiform innovation shoots are occasionally present.

However, the possible proper name for the enigmatic Siberian plant was suggested by Hans Blom (l.c.). It is *Schistidium chenii* (Lin) Cao, Gao & Zhao, described by P.C. Chen in 1962 from high altitude in Himalayan region under the name *Grimmia himalayana* Chen. The latter name, however, appeared to be invalid and was replaced later by *Grimmia chenii* Lin. Thirty years later it was found for the second time in NW China, Xinjiang Uygur Autonomous Region; this collection contained more sporophytes than were in the rather poor type specimen, so the description of this species was supplemented by detailed sporophytic characters and, based on them, it was transferred into the genus *Schistidium* (Cao *et al.*, 1992). Illustration of the Xinjiang plant (l.c.) is very similar to the plant from the Sayan Mts, including leaf shape, laminal cell areolation, leaf transverse sections, and peristome teeth. But Cao *et al.* (1992) also provided a plate of line drawings made from the holotype of *Grimmia himalayana*, which caused some uncertainty – are the plants from Tibet and Xinjiang the same species or not. It showed leaves of different shape, less concave, with larger length/width ratio, and with margins bistratose only in a one row of cells. Fortunately, a small duplicate of Xinjiang collection preserved in MHA was available for our study. It was too small and in poor condition, and we failed to obtain DNA from it. However, in habit, leaf shape, cell areolation and leaf transverse sections it appeared to be intermediate between the holotype of *S. chenii* (as it is illustrated by Cao *et al.* 1992) and the plant from the Sayan Mts. Since all morphological traits of Chinese and Siberian plants are the same, differing only in minor details, and their ecological preferences are very similar, we prefer at present to refer the plant from Sayan Mts to *S. chenii*.

In summary, it is worth noting that rheophytic species likely evolved several times in various lineages of *Schistidium*. The relationships within the subgenus *Canalicularia* remain not fully resolved since there is no molecular data for eight of its species: *S. crassithecium* H.H. Blom ex B.H. Allen, *S. cribrodontium*, *S. deguchianum* Ochyra & Bedn.-Ochyra, *S. flexifolium* (Hampe) Ochyra,



Fig. 2. A–J: *Schistidium chenii* (A–C, E, F, H, I from Russia, Sayan Mts., Fedosov 23-02-0370, MW9092497; D, G from China, Xinjiang, Zhao 2434, MHA); J: *S. occidentale* (from U.S.A., California, Shevock 24388, MHA); K: *S. platyphyllum* (from Russia, Sayan Mts, Fedosov 23-02-0072, MW9092498). A–B: plants in their habitat; C–D: wet plants; E–K: habit of dry plants from herbarium collections, with the special attention to leaf shape.

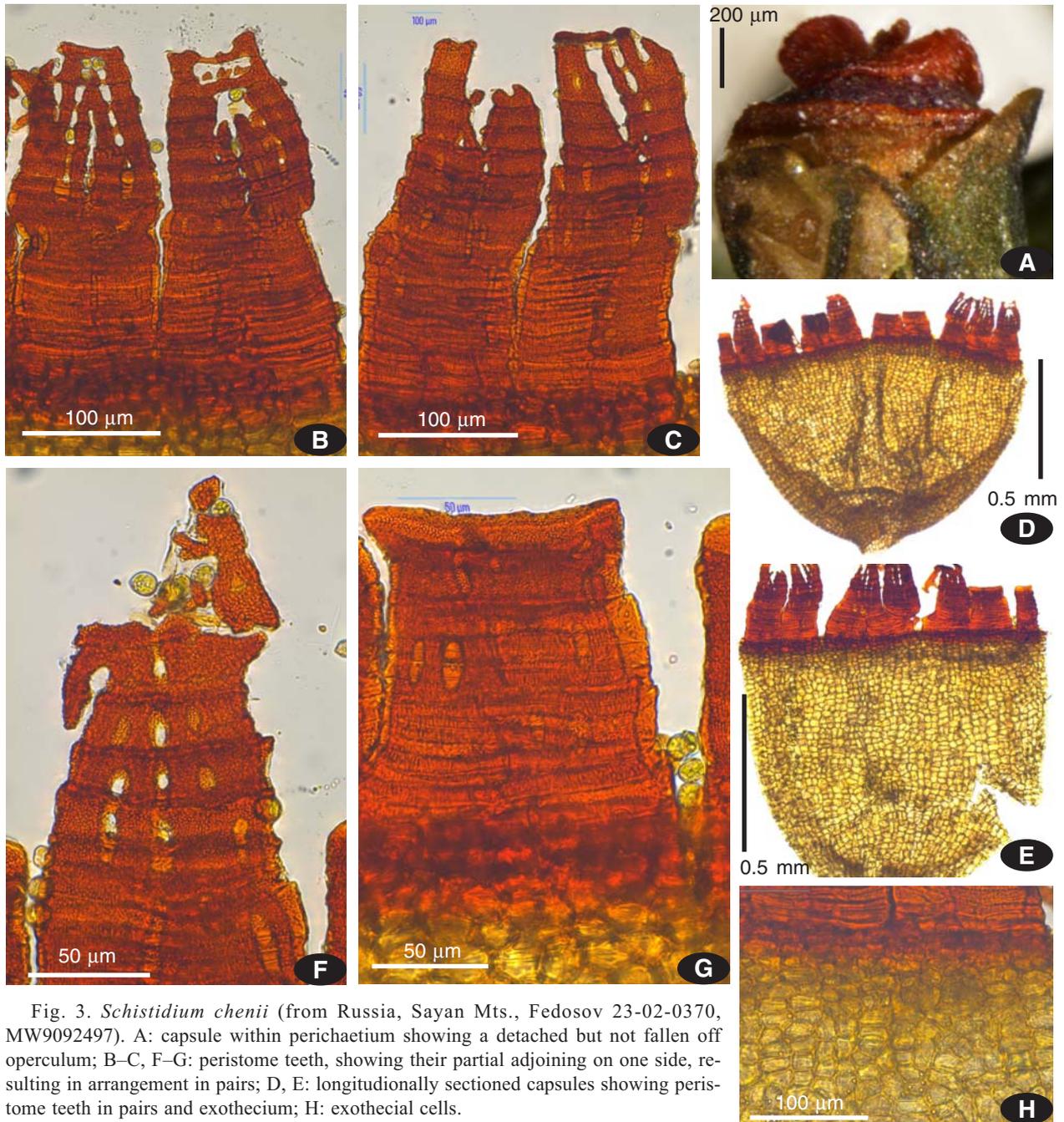


Fig. 3. *Schistidium chenii* (from Russia, Sayan Mts., Fedosov 23-02-0370, MW9092497). A: capsule within perichaetium showing a detached but not fallen off operculum; B–C, F–G: peristome teeth, showing their partial adjoining on one side, resulting in arrangement in pairs; D, E: longitudinally sectioned capsules showing peristome teeth in pairs and exothecium; H: exothecial cells.

S. frahmianum Ochyra & Afonina, *S. malacophyllum* Herzog, *S. mucronatum* H.H. Blom, Shevock, D.G. Long & Ochyra, and *S. riparium* H.H. Blom, Shevock, D.G. Long & Ochyra. It would be especially interesting to find out if the species which share several morphological traits, like *S. chenii* and *S. cribrodontium*, are related to each other genetically, or these traits appeared independently due to habitat influence.

TAXONOMY

Schistidium chenii (Lin) Cao, Gao & Zhao, J. Hattori Bot. Lab. 71: 69. 1992. — *Grimmia chenii* S.H. Lin, Biolo. Bull. Dept. Biol. Coll. Sci. Tunghai Univ. 60: 67. 1984. — *Grimmia himalayana* P.C. Chen nom. illeg.,

Zhumulangma Feng Diqu Kexue Kaocha Baogao 227. 1962. Figs. 2(A–C, E, F, H, I), 3–4, 5(A–Q)

Plants in loose tufts, bright green above, dark green to blackish-green below. *Stems* 0.7–1.3 cm long, simple or repeatedly branched; central strand well developed, cortex (1)2-layered. *Leaves* loosely appressed to imbricate when dry, erect-spreading when wet, 1.5–2.0×1.1–1.3 mm, broadly ovate, strongly concave, broadly rounded at apex, cucullate; margins entire, flat or widely incurved; costa thin, 60–75 µm wide at base, hardly narrowed distally, ending well below the apex; lamina unistratose except margins, often with few narrow bistratose strips or patches, 2–4 rows of marginal cells 2(3)-stra-

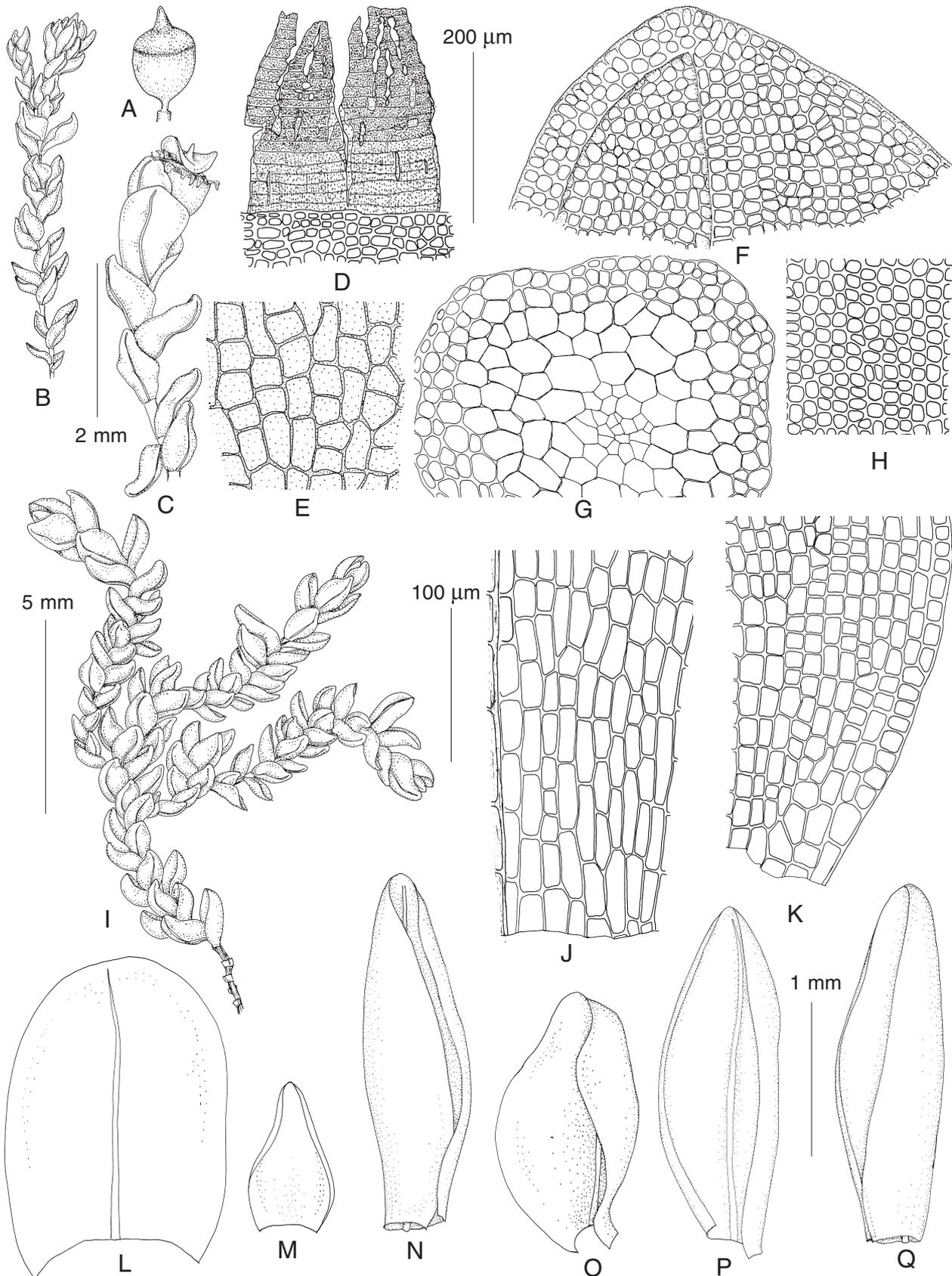


Fig. 4. *Schistidium chenii* (from Russia, Sayan Mts., Fedosov 23-02-0370, MW9092497). A: capsule; B–C: habit, dry; D: peristome; E: exothecial cells; F: upper leaf cells; G: stem transverse section; H: mid-leaf cells; I: habit, wet; J: basal juxtacostal cells; K: basal marginal cells; L: perichaetial leaf; M: perigonal leaf; N–Q: stem leaves. Scale bars: 5 mm for B, I; 2 mm for A, C; 1 mm for L–Q; 200 μm for D; 100 μm for E–H, J–K.

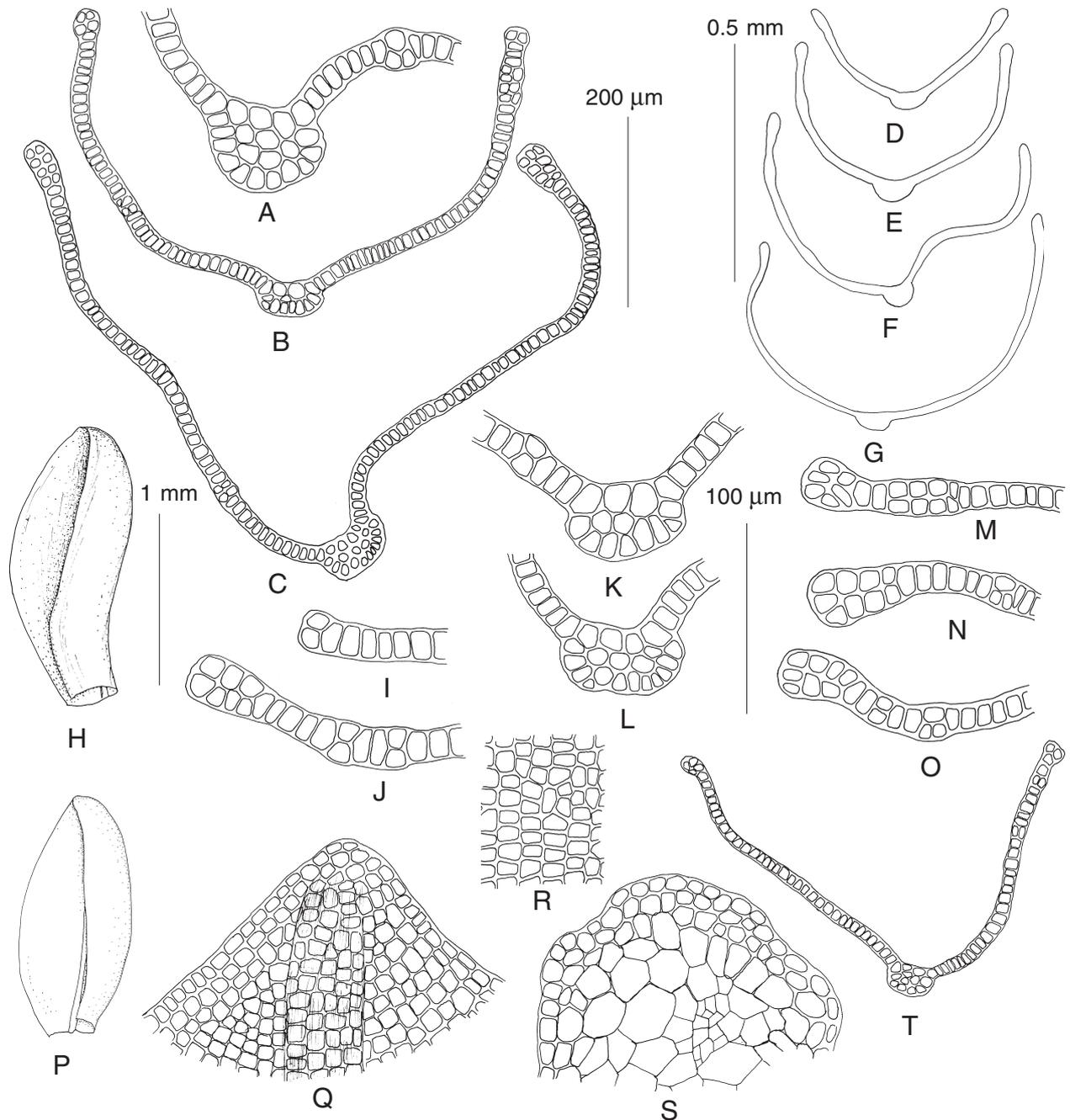


Fig. 5. *Schistidium chenii* (A–Q: from Russia, Sayan Mts., Fedosov 23-02-0370, MW9092497; R–T: from China, Xinjiang, Zhao 2434, MHA). A–G, I–O, T: leaf transverse sections; H, P: leaves; Q: upper leaf cells; R: mid-leaf cells; S: stem transverse section. Scale bars: 1 mm for H, P; 0.5 mm for D–G; 200 µm for B–C, T; 100 µm for A, I–O, Q–S.

tose, forming a fleshy limbidium; upper laminal cells round-hexagonal and transversely ovate, with moderately thickened, esinuose walls, 7–11×10–13 µm; mid-leaf cells rounded-quadrate to rounded-hexagonal, firm-walled, esinuose, 8–14×10–12 µm; marginal cells larger, transverse rectangular, 10–11×15–16 µm; basal juxtacostal cells thin- to firm-walled, rectangular, 30–80×12–18 µm, basal marginal cells quadrate to short rectangular, 10–22×13–16 µm. *Autoicous*, sporophytes few. *Perichaetial leaves* broadly ovate, ca. 1.5×1.3 mm, flat above. *Capsules* deeply immersed, short cylindrical, ca. 0.8–0.9 mm

long, 0.7 mm wide; exothecial cells thin-walled, transversely rectangular, quadrate and short rectangular; peristome teeth usually grouped in pairs, joined at lower 1/10–1/6 of their length, 275–290 µm long, ca. 130 µm wide at base, usually with broken upper portions, bright orange, strongly cribrate, on outer surface finely papillose distally, longitudinally papillose-striolate in lower half. *Operculi* low conic, with short, thick beak. *Spores* 9–11 µm. *Calyptrae* not seen.

Specimen examined: Russia. Republic of Buryatia, Tunka District, 51.715376°N, 100.99654°E, 1850 m alt., ca. 4 km

north of Mondy Settlement, near trail to Hulugaysha Mt., rocky bed of seasonally dry mountain brook in open larch & siberian pine forest, on rock near temporarily dry waterfall, with *Hygrohypnella polaris* and *Blindia acuta*. 10 July 2023, leg. Fedosov & Ishchenko 23-02-0370, MW9092497, MHA 9135060).

Distribution and ecology. In China *Schistidium chenii* was found on wet or moist rocks near stream and near glaciers at high elevation, 3100 and 5450 m a.s.l. (Cao *et al.*, 1992). In Russia it is currently known from a single locality on southern slope of Tunkinskie Goltsy Mt. Range, in a forest zone, at 1850 m a.s.l. It grew on rocks in a bed of temporary brook. Generally the upper belt of Tunkinskie Goltsy Mountains, where the species occurs, is composed by acidic rocks, gneiss, granitoids and shists; however, many calciphylous mosses occur there as well. Although the area around Mondy Settlement was not extensively studied for bryophyte flora until 2023, episodic collections made here by L.V. Bardunov revealed several rare montane and central Asian mosses, such as *Aongstroemia julacea* (Hook.) Mitt., *Scopelophila ligulata* (Spruce) Spruce, and *Oreas martiana* (Hoppe & Hornsch.) Brid. Our exploration revealed many other interesting mosses, which will be considered in a separate papers.

Differentiation. Among the species of *Schistidium* known in Russia, the most similar is another rheophytic species, *S. sordidum*, due to its ovate leaves with rounded apices; furthermore, its unistratose but narrowly revolute leaf margins may look similar to the darker bistratose leaf margins of *S. chenii*. However, leaves of *S. sordidum* are narrower, 0.5–0.9 mm wide, less strongly concave, and totally unistratose; its exothecial cells are irregular in shape and thick-walled; its peristome teeth are longer, 330–440 µm, and not joined in pairs; and its spores are larger, 14–20 µm. Another species with rounded leaf apices, *S. agassizii*, has much longer, to 3.2 mm, lanceolate, almost flat leaves, unistratose leaf laminae, cupulate urns, thick-walled, irregular exothecial cells, longer, to 550 µm, peristome teeth, and larger, 14–20 µm, spores.

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Appendix 1. Voucher data and GenBank accession numbers for newly sequenced specimens.

Species	Isolate	Locality	Voucher data	ITS, GenBank acc. number
<i>Schistidium andinum</i>	OK 3707	Chile	Melik 217198, MHA	OR966507
<i>Schistidium cinclidoteum</i>	DG 229	U.S.A.: California	Shevock 32619, MHA	OR966508
<i>Schistidium perichaetiale</i>	DG 204	Tanzania	Pócs et al. 88135/c, MHA	OR966509
<i>Schistidium occidentale</i>	DG 224	U.S.A.: California	Shevock 32480, MHA	OR966510
<i>Schistidium occidentale</i>	DG 225	U.S.A.: Nevada	Shevock 30283, MHA	OR966511
<i>Schistidium chenii</i>	OK 3680	Russia: Buryatia	Fedosov & Ishchenko 23-02-0370, MW9092497	OR966512
<i>Schistidium platyphyllum</i>	OK 3784	Russia: Buryatia	Fedosov 23-02-0072, MW9092498	OR966513
<i>Schistidium platyphyllum</i>	OK 3785	Russia: Yakutia	Ignatov & Ignatova 11-3159, MHA9100205	OR966514

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