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DOES *SCHISTIDIUM MARGINALE* OCCUR IN ASIAN RUSSIA?

ВСТРЕЧАЕТСЯ ЛИ *SCHISTIDIUM MARGINALE* В АЗИАТСКОЙ ЧАСТИ РОССИИ?

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Abstract

A combined molecular phylogenetic and morphological analysis revealed that specimens from Asian Russia previously referred to *Schistidium marginale* do not belong to that species. They are described as species new to science, *S. transbaicalense*. It is very similar to *S. marginale* superficially and shares with it some morphological characters, but it also differs in hair-point structure and transverse section of costa. In the molecular phylogenetic tree inferred from nrITS1-2 sequences it is resolved far from the terminal Confertum-clade where *S. marginale* is found, but in the basal grade in the tree rooted on *S. sordidum*, where *S. pulchrum* and *S. scabripilum* also occur. *Schistidium transbaicalense* is currently known from few localities in southern Siberia: Altai Republic, Kemerovo Province and SE of Zabaikalsky Territory, and further north, on Putorana Plateau in Krasnoyarsk Territory. Its description, illustrations, distribution, ecology and distinctions from similar species are provided.

Резюме

Комбинированный молекулярно-филогенетический и морфологический анализ показал, что образцы из азиатской части России, ранее отнесенные к *Schistidium marginale*, не принадлежат к этому виду. Они описаны как новый для науки вид *S. transbaicalense*. Этот вид очень сходен с *S. marginale* по внешнему виду растений и некоторым морфологическим признакам, однако отличается от него по строению гиалинового волоска и поперечному срезу жилки. В молекулярно-филогенетическом дереве, построенном по последовательностям ядерного ITS1-2, *S. transbaicalense* оказывается далеко от терминальной клады Confertum, в которую попадает *S. marginale*: в дереве, укорененном на *S. sordidum*, он находится в базальной граде, рядом с *S. pulchrum* и *S. scabripilum*. *Schistidium transbaicalense* в настоящее время известен из немногочисленных местонахождений в южной Сибири: в Республике Алтай, Кемеровской области и на юго-востоке Забайкальского края, а также на плато Путорана. Для него приводятся описание, иллюстрации, распространение, экология и отличия от морфологически сходных видов.

KEYWORDS: Grimmiaceae, Bryophyta, molecular phylogeny, nrITS, new species

Introduction

Ochyra & Bednarek-Ochyra (2015) fairly called *Schistidium* "a well defined and easily recognized genus", but "also one of the most troublesome, confusing, and taxonomically least understood of all moss genera". Before Blom's (1996) publication on the Scandianvian taxa of the *Schistidium apocarpum*-complex, only few species were usually accepted in this genus. Very diverse morphotypes, however, did not fit comfortably to these indefinitely broad species concepts. At present, when many more species are already described, it is also difficult to evaluate correctly numerous morphological characters and their variation, and apply a correct name to a particular plant.

Molecular phylogenetic studies confirmed the applicability of the Blom's narrow species concept since the earliest publications (Goryunov *et al.*, 2007; Milyutina *et al.,* 2010). However, it became clear that this genus is not over-split, but rather under-split and a worldwide revision is needed. Further studies based on the combined molecular and morphological approach resulted in the description of six new species: *S. sibiricum* Ignatova & H.H. Blom*, S. echinatum* Ignatova & H.H. Blom*, S. succulentum* Ignatova & H.H. Blom*, S. tenuinerve* Ignatova & H.H. Blom, and *S. bakalinii* Ignatova & H.H. Blom from Russia and *S. obscurum* H.H. Blom, Köckinger & Ignatova from Europe (Ignatova *et al.,* 2010). Few other species new for science were revealed later: *S. scabripi-*

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lum Ignatova & H.H. Blom and *S. austrosibiricum* Ignatova & H.H. Blom from Asian Russia (Ignatova *et al*., 2016) *S. relictum* T.T. McIntosh, H.H. Blom & Ignatova from NW North America and NE Asian Russia (McIntosh *et al.*, 2017); *S. memnonium* J. Guerra from the Iberian Peninsula (Guerra *et al*., 2020); and *S. foraminis-martini* Kiebacher, Köckinger & H.H. Blom from the European Alps (Kiebacher *et al*., 2021). Simultaneously, a number of new *Schistidium* species were described solely by morphology: *S. viride* H.H. Blom & Darigo from eastern North America (Blom & Darigo, 2009); *S. riparium* H.H. Blom, Shevock, D.G. Long & Ochyra and *S. mucronatum* H.H. Blom, Shevock, D.G. Long & Ochyra from China (Blom *et al.*, 2011); *S. ignatovae* C. Feng, X.L. Bai, J. Kou & W. Li from China (Feng *et al*., 2013); *S. splendens* T.T. McIntosh, H.H. Blom, D.R. Toren & Shevock and *S. squarrosum* T.T. McIntosh, H.H. Blom, D.R. Toren & Shevock from western North America (McIntosh *et al.*, 2015); and *S. marginale* from Europe (Blom *et al.*, 2016).

Schistidium marginale H.H. Blom, Bedn.-Ochyra & Ochyra was described from the Austrian Alps (Blom *et al*., 2016). Among its diagnostic morphological characters were listed: strongly thickened, 2–4-stratose and (1–) 2–5-seriate leaf margins; coarse, 2–4-stratose costa which is 'trapezoid, subrectangular or irregularly angular in outline' in transverse section; and 'straight and rather stiff, ± flattened in lower part, not decurrent, coarsely spinulose' hair-points. This acidophilous saxicolous moss was reported also from Switzerland, Italia, Macedonia, and Spain in Europe and from Turkey and Georgia (Blom *et al.*, 2016), but also from Russian Caucasus (Ignatova *et al*. (2010) as a provisional name.

Later on, *S. marginale* was revised for the Moss Flora of Russia by Ignatova & Blom (2017). They reported this species from the Caucasus where it has been confirmed by DNA sequence data, and also from Asian Russia (Putorana Plateau, Altai Republic, Kemerovo Province, and Zabaikalsky Territory), based on non-sequenced specimens. Plants from southern Siberia possessed many characters similar to the Caucasian and Austrian plants of *S. marginatum* (i.e., bistratose, 2–4-seriate leaf margins, stiff hair-points and 2–4-stratose, ovate in transverse section costae), but they also had slightly wider middle stem leaves which resemble those of *S. pulchrum* H.H. Blom, and very short, 0.05–0.2 mm long, hair-points, flattened and decurrent (the latter character made them similar to *S. scabripilum*, which, however, has longer, to 0.6 mm, hair-points). The aim of the present paper is to explore these discrepances and confirm or reject the presence of *S. marginale* in Asian Russia. Some other specimens from Asian Russia putatively named as *S. marginale*, but different from the south Siberian plants, were also included into the analysis.

MATERIALS AND METHODS

Dataset. The dataset is compiled to include *S. marginale* from Europe and the Caucasus, as well as species morphologically similar to 'Asian' *S. marginale* (*S. pulchrum, S. scabripilum, S. echinatum*); representatives of the main clades corresponding to the informal groups recognized by Blom (1996) or the sections established by Ochyra *et al*. (2003) were also selected. In total, 33 accessions of 26 species were taken from GenBank and 9 sequences were obtained de novo. Accession numbers and voucher data are in Appendix 1. One accession of *S. sordidum* I. Hagen was 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. For the nuclear ITS1-2 the laboratory and sequencing protocols were essentially the same as in our previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005).

Molecular analysis. Bayesian analysis was performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with four parallel runs each consisting of six Markov chains, with 10 000 000 generations, chain temperature 0.02, GTR model, reaching all PSRF equal to 1.000, and ESS>1000. Maximum likelyhood analysis was done at W-IQ-TREE server (Trifinopoulos *et al*., 2016), with GTR+G+I model, 1000 replications and otherwise default parameter, 1000 replications. Trees were rooted on *S. sordidum* according to topology published by Ignatova *et al.* (2010).

Morphological studies. Light microscope observations were made under a stereomicroscope (Olympus SZX7) equipped with an Infinity 8-8 digital camera, and a 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

Molecular data. The basal grade of the tree rooted on *S. sordidum* includes two fully supported monospecific clades, of 'south Siberian *S. marginale*'and of *S. pulchrum*; unsupported clade of *S. scabripilum* + *S. austrosibiricum* (each species fully supported); single accessions of *S. liliputanum* (Müll. Hall.) Deguchi and *S. frisvollianum* H.H. Blom; and a moderately supported clade of *S. sibiricum* + *S. sinensiapocarpum* (Müll. Hall.) Ochyra. They are followed by a fully supported Apocarpum clade (5 species) and Atrofuscum clade (5 species + one accession of the 'Yacutian *S. marginale*'), and two sister terminal clades: a fully supported Robustum clade (4 species) and a moderately supported (0.94) Confertum clade which consists of one accession of *S. flaccidum* (De Not.) Ochyra and fully supported clade of 4 species, including three accessions of *S. marginale* from Europe and Caucasus.

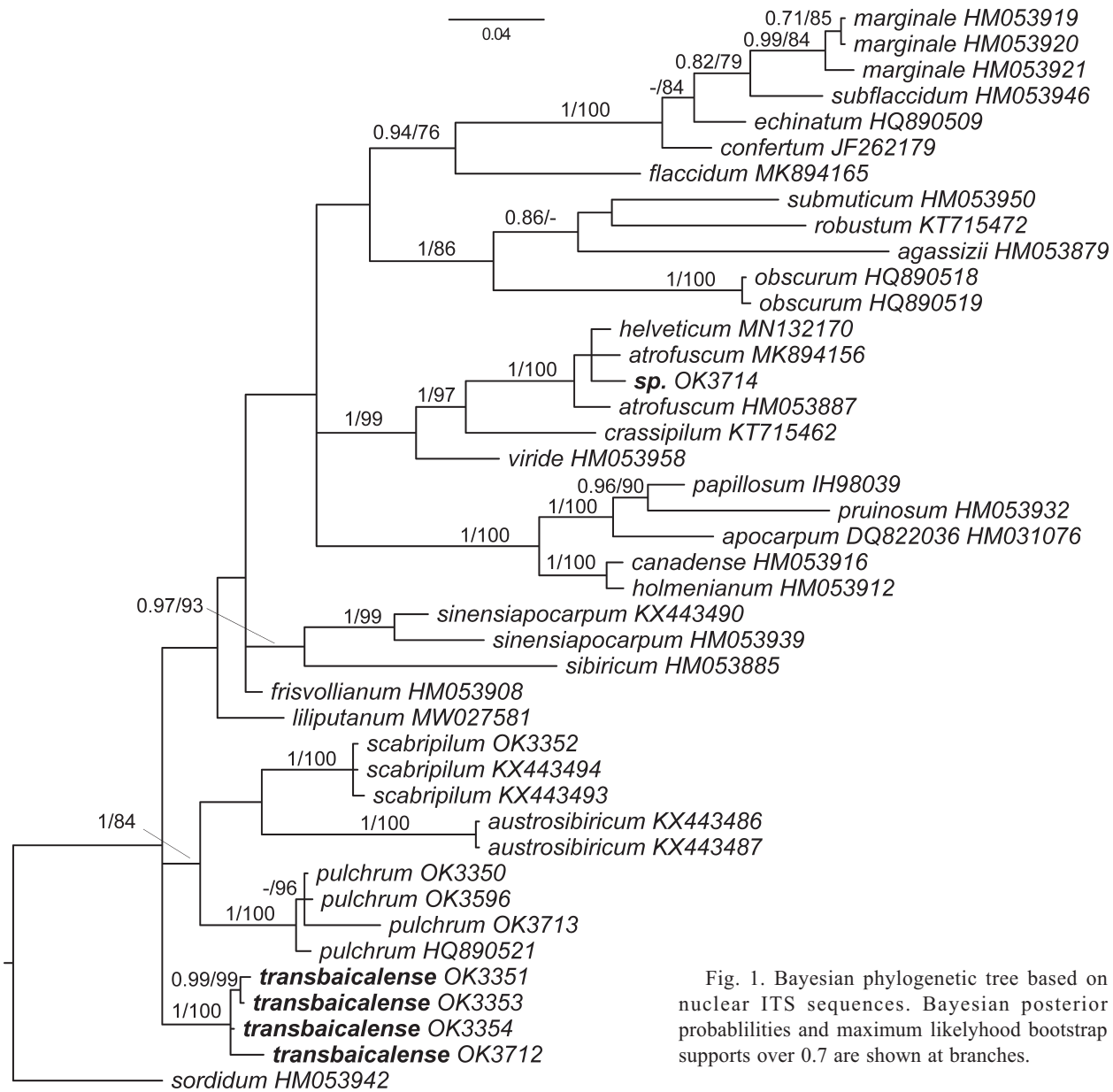

Fig. 1. Bayesian phylogenetic tree based on nuclear ITS sequences. Bayesian posterior probablilities and maximum likelyhood bootstrap supports over 0.7 are shown at branches.

Morphology. A comparison of sequenced south Siberian specimens of '*S. marginale*' with specimens of this species from the Caucasus and Austria revealed that they possess constant differences in the shape of costa in transverse section; the decurrency of hyaline hair-points; presence of bistratose spots in leaf lamina; and perforation of peristome teeth. These differences are discussed in detail in the taxonomy section.

Discussion

Previous molecular phylogenetic exploration of *Schistidium* already revealed several cases when the morphologically similar plants appeared to belong to unrelated lineages. One example is the pair *S. frigidum* H.H. Blom and *S. obscurum*: they have very similar leaf structure and cell areolation but differ in size, plant color and distribution. Another pair of species sharing such morphological traits as flattened, densely spinulose hair-points is *S. echinatum* and *S. scabripilum*; they were initially treated as a one species, but the former appeared to belong to Confertum clade, whereas the latter was found in the basal polytomy. The present analysis reveals a similar situation with *S. marginale* from Europe and south Siberian specimens previously referred to this species. The former is nested in the Confertum clade, whereas the latter appears in the basal grade. Since they can be separated by minor but constant morphological distinctions, we describe the south Siberian '*S. marginale*' as a species new for science.

Thus, the presence of *S. marginale* in Asian Russia is not currently confirmed. However, this species was re-

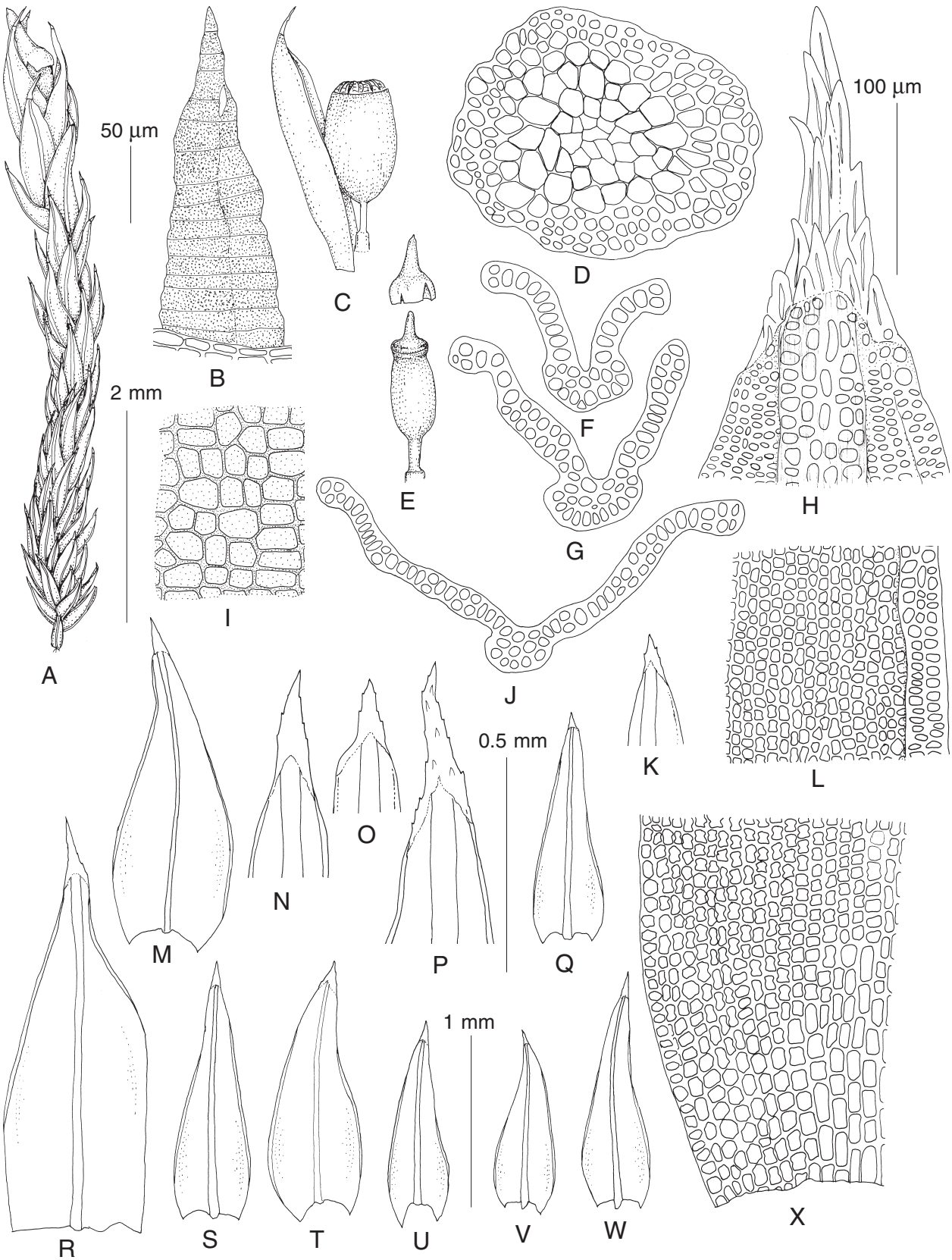

Fig. 2. *Schistidium transbaicalense* (from holotype). A: habit, dry; B: peristome; C: capsule and perichaetial leaf; D: stem transverse section; E: operculate capsule and calyptra; F–G, G: leaf transverse sections; H: upper leaf cells; I: exothecial cells; K, N–P: leaf apices: L: mid-leaf cells; M, Q–W: stem leaves; R: perichaetial leaf; X: basal leaf cells. Scale bars: 2 mm for A; 1 mm for M, Q–W; 0.5 mm for K, N–P; 50 µm for B, I; 100 µm for D, F–H, J, L, X.

cently reported for Xinjiang Uygur Autonomous Area, China (Sulayman *et al.*, 2022), the neighbouring region to Altai Mountains in Russia. The photos in that paper, including the trapezoid costa in transverse section, convince us that it is identified correctly. So, the possibility of finding *S. marginale* in the mountains of southern Siberia should be kept in mind.

Also, one specimen from Yakutia similar to *S. marginale* in having leaves with 2(3)-stratose, 2–5-seriate margins and lamina with bistratose spots, is resolved in an *Atrofuscum* clade. This fact is of particular interest, because species of this group occur usually in southern regions and were never recorded from the permafrost area in NE Asia. This plant possesses some distinguishing morphological characters and likely deserves recognition as a separate species. However, only few old sporophytes occur in this single collection, so we postpond its description until an additional material will be found.

Taxonomy

Schistidium transbaicalense Ignatova, species nova. Type: Russia, Zabaikalsky Territory, Shelopuginsky District, Borshchovochny Mt. Range, southern spur, vicinity of Vershino-Shakhmatibsky Settlement, 51°19'36"N, 117°49'12"E, 880 m a.s.l., rock-field in larch forest, on rock. 20 July 2012, coll. I.V. Czernyadjeva 21-12. Holotype LE, isotype MHA. DNA: Isolate OK3353, GenBank OR949069 (ITS). Figs. 2, 3(I–T), 4(A)

Diagnosis. *Schistidium transbaicalense* is similar to *S. marginale* H.H. Blom, Bedn.-Ochyra & Ochyra in habit of plants, 2(3)-stratose, 2–5-seriate leaf margins, leaf lamina with bistratose spots, and costa flattened on abaxial side, but differs from it in decurrent hyaline hair-points, leaf lamina with more numerous bistratose spots and striae, and costa transversely ovate to elliptical vs. trapezoid in transverse section.

Etymology. The species name refers to Transbaikalia (Zabaikalsky Territory), an area SE of Baikal Lake, where from the type specimen was collected.

Description. *Plants* small to medium-sized, in compact tufts, olive or yellowish-green, faintly glossy. *Stems* 0.8–1.6 cm, moderately branched, densely foliate, with weak central strand. *Stem leaves* straight, appressed when dry, erect-spreading when wet, 1.3–1.6×0.4–0.6 mm, lower and median leaves narrowly lanceolate, subperichaecial leaves ovate-lanceolate, with shoulders, concave at base, keeled in upper half; margins entire, smooth, narrowly recurved in lower 1/3–3/4 on one side and plane or recurved at shorter distance on the other side; *hyaline hair-points* 0–0.2(–0.3) mm, stiff, widened and flattened at base, decurrent, denticulate at margins, sharply spinulose on dorsal surface with short, straight spines; *costa* smooth dorsally, strongly protruding on dorsal side, (2–)3–4-stratose, slightly flattened, transversely ovate in transverse section; *leaf lamina* smooth, unistratose and in upper 2/3 of leaf with numerous bistratose spots and striae, at margins 2(3)-stratose in 2–4(–6) cell rows, forming fleshy limbidium; upper laminal cells thick-walled, round and transversely ovate, 4–8 μm wide, with esinuose walls; mid-leaf cells short-rectangular, with moderately thick, slightly sinuose walls, 10–15×6–10 μm; basal juxtacostal cells rectangular, 20–30×5–8 μm, with moderately thick, straight walls, basal marginal cells shorter, in 4–8 rows quadrate and transversely ovate, with thicker transverse walls. *Autoicous*, sporophytes usually present but very few. *Perichaetial leaves* larger than stem leaves, ca. 2.0×0.8–0.9 mm, with oblong base formed of thin-walled rectangular cells and short, triangular acumen formed of thick-walled, round and elliptical cells 10–30×7–12 μm, hyaline hair-points 0.05–0.20 mm. *Setae* 0.2–0.3 mm. *Capsules* immersed, urns yellowish- or grayish-brown, slightly glossy, ovate-cylindrical, 0.9–1.1×0.5–0.7 mm; exothecial cells thin-walled, quadrate and transversely rectangular, with an admixture of rectangular cells, stomata few at urn base. *Operculi* low conic, with long, narrow, straight beaks. *Peristome teeth* 220–250 μm long, orange-brown to dark red, straight, not twisted along their axes, spreading or recurved and appressed to the urn wall, acute or subobtuse at tips, entire or with few slit-like perforations, densely and finely papillose or papillose-striolate at places, with horizontal and oblique striae. *Spores* 8–10 μm, looking almost smooth in light microscope. *Calyptrae* mitrate.

Other specimens examined: RUSSIA: **Krasnoyarsk Territory**, Putorana Plateau, Kapchuk Lake, rock-field, on rock. July 1982 *Czernyadjeva #26* (MW9018071). **Zabaikalsky Territory**, Sretensk District, Borshchovochny Mt. Range, Kurenga River, 8 km from Sretensk Town, 52°07'18"N, 117°03'59"E, 470 m a.s.l., rock outcrops on N-faced slope, on rock. 19 July 2012 *Czernyadjeva 18-12* (LE, duplicate MHA). **Kemerovo Province**, Mariinsk District, vicinity of Mariinsk Town, Archekassky Ridge, 56°08'N, 87°49'E, 203 m alt., on surface of dry limestone. 8 June 2007 *Pisarenko op04666* (MW9077170). **Altai Republic**, Ulagan District, Chulyshman River near Katuyaryk winter huts, 50°55'N, 88°12'E, 750 m alt., E-faced cliffs, inclined rock surface under *Rhododendron*. 18 Aug 2012 *Ignatova 12-708* (MHA9135071).

Distribution and ecology. *Schistidium transbaicalense* is distributed mainly in the mountains of southern Siberia; is currently known from two close localities in Borshchovochny Range in SE Transbaikalia, on Archekassky ridge (at foothills of Kuznetsky Alatay Mts) in Kemerovo Province, and in the valley of Chulyshman River in Altai Mts. It is also found near Kapchuk Lake on Putorana Plateau, which is it northernmost locality. It was collected within altitudinal range 200–880 m a.s.l., on dry rocks (calcareous, sandstone or unknown) in larch or birch forest and among *Rhododendron* shrubs at base of xeric slope.

Differentiation. The differences of *S. transbaicalense* from *S. marginale* are given in the diagnosis. It is also worth to mention that in all studied specimens of *S. transbaicalense* it was difficult to find sporophytes despite its autoicous sexual condition, whereas in specimens of *S. marginale* sporophytes develop on most plants. Very short,

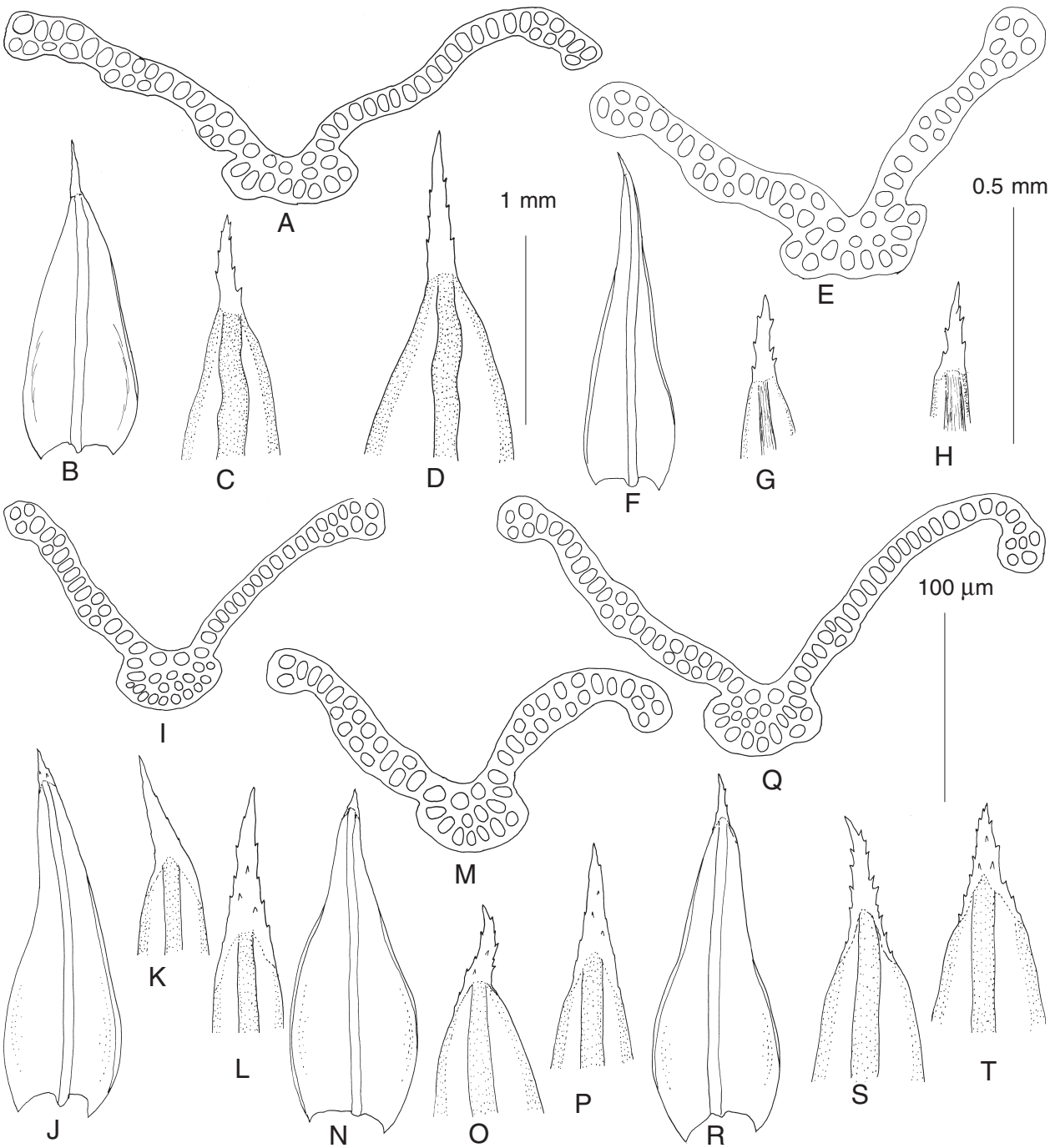

Fig. 3. A–H: *Schistidium marginale* (A–D: from Russia Teberdinsky Nature Park, isolate OK 3711; E–H: from Austria, HM053920); I–T: *S. transbaicalense* (I–L: from Russia, Altai, isolate 0K3351; M–P: from Zabaikalsky Territory, isolate OK3354; Q–T: from Kemerovo Province, isolate OK3712). A, E, I, M, Q: leaf transverse sections; B, F, J, R: stem leaves; C–D, G–H, K–L, O–P, S–T: apical portions of leaves. Scale bars: 1 mm for B, F, J, R; 0.5 mm for C–D, G–H, K–L, O–P, S–T; 100 µm for A, E, I, M, Q.

to 0.2 mm, hyaline hair-points of *S. transbaicalense* are also helpful in its separating from *S. pulchrum* and *S. scabripilum* (both these species have hair-points to 0.6–0.7 mm long). Leaf lamina of *S. pulchrum* is usually unistratose except for one row at margins, whereas it often has numerous bistratose spots in *S. scabripilum*. Both these species differ from *S. transbaicalense* in having costa semicircular in transverse section and arcuate, twisted peristome teeth. Short and flattened hyaline hair-point is also the case of *S. umbrosum* (J.E. Zetterst.) H.H. Blom, but at least in perichaetial leaves of this species it is longer, to 0.4 mm, and it also differs from *S. transbaicalense* in having unistratose leaf lamina, costa semicircular in transverse section, and strongly perforate peristome teeth. In Russia *S. umbrosum* is known from few localities in northern Asia and Murmansk Province in NW European Russia, while currently known distribution of *S. transbaicalense* is generally confined to xeric areas of south-

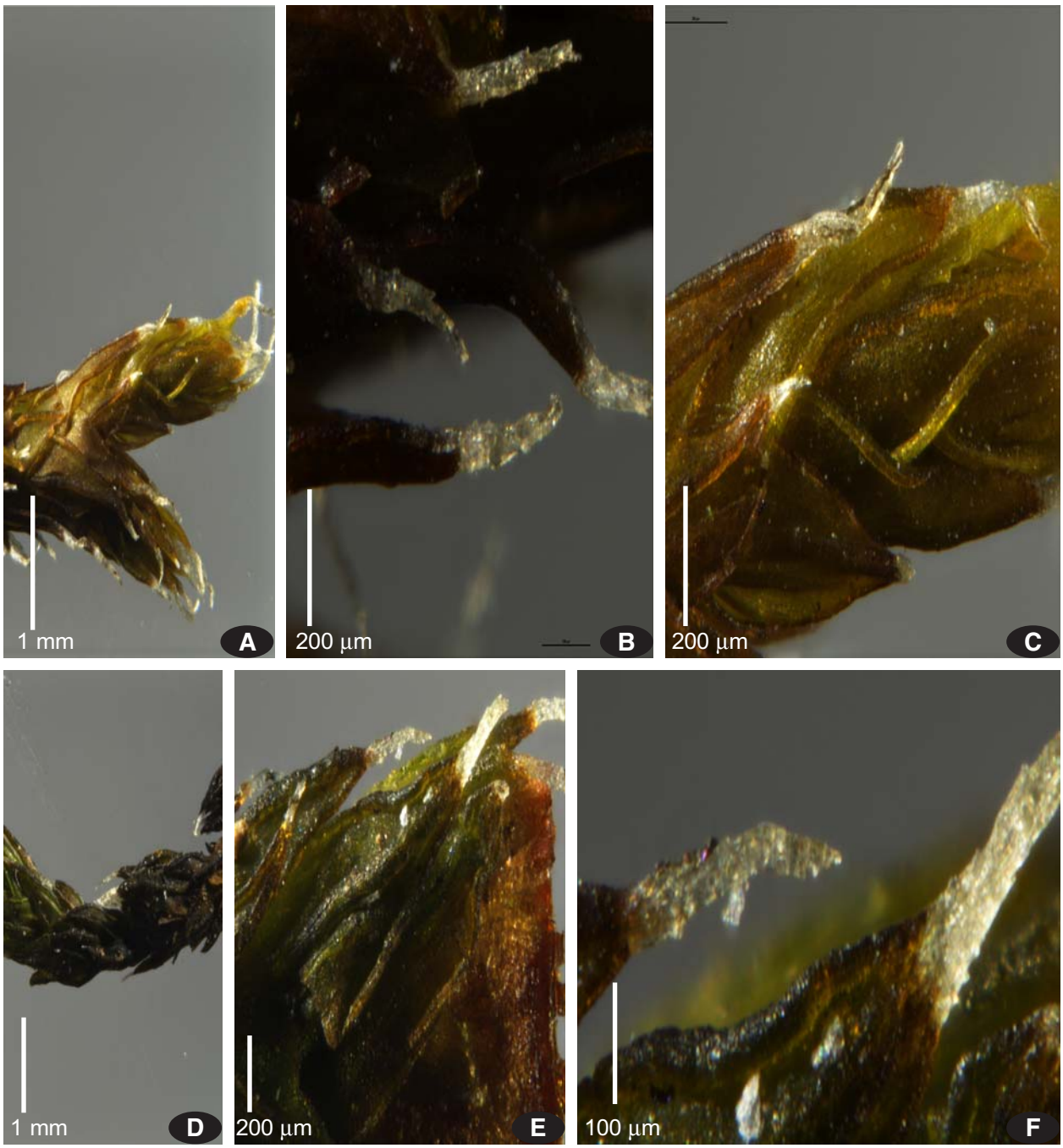

Fig. 4. A–C: *Schistidium transbaicalense* (from Russia, Altai Republic, *Ignatov & Ignatova 12-708*, isolate OK3351); D–F: *Schistidium marginale* (from Russia, Caucasus, Karachaevo-Cherkessia, *Ignatov & Ignatova 05-3500*, MW9018066).

ern Siberia. There also is some similarity between *S. transbaicalense* and another xeric species, *S. helveticum* (Schkuhr) Deguchi, since the latter species also has hyaline hair-points to 0.2 mm long, predominantly bistratose leaf lamina, and costa elliptical to trapezioid in transverse section. However, its hair-points are scarcely widened at base and not decurrent; its leaves are longer, 1.7–2.6 mm long, ovate-triangular, without shoulders, and predominantly totally bistratose; its plants usually are jet-black; and its peristome teeth are strongly perforate. Some specimens from Asian Russia were erroneously named as *S. helveticum*, but its occurrence in Russia is currently confirmed only for Dagestan Republic in the Russian Caucasus.

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

Species	Isolate	Locality	Voucher	GenBank acc. number
Schistidium pulchrum	OK 3350	Russia, Republic of Yakutia	Ignatov #11-3875, MHA	OR949064
S. pulchrum	OK 3596	Russia, Altai Republic	Pisarenko #op04659, MHA (dupl. from NVS)	OR949065
S. pulchrum	OK 3713	Russia, Republic of Yakutia	Balakirev #17-28, MHA9005417	OR949066
S. scabripilum	OK 3352	Russia, Republic of Yakutia	Ignatov & Ignatova #15-1055, MHA	OR949067
S. transbaicalense	OK 3351	Russia, Altai Republic	Ignatov & Ignatova #12-708, MHA	OR949068
S. transbaicalense	OK 3353	Russia, Zabaikalsky Territory	Czernyadjeva #21-12, 20 July 2012, MHA (dupl. from LE)	OR949069
S. transbaicalense	OK 3354	Russia, Zabaikalsky Territory	Czernyadjeva #18-12, 19 July 2012, MHA (dupl. from LE)	OR949070
S. transbaicalense	OK 3712	Russia, Kemerovo Province	Pisarenko #op04666, MW9077170 (dupl. from NVS)	OR949071
S. sp	OK 3714	Russia, Republic of Yakutia	Ignatov #00-985, MW9077186	OR949072

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