Arctoa (2009) **19**: *195-233*

ON THE GENUS SCHISTIDIUM (GRIMMIACEAE, MUSCI) IN RUSSIA

О РОДЕ SCHISTIDIUM (GRIMMIACEAE, MUSCI) В РОССИИ

E.A. IGNATOVA[1], H.H. BLOM[2], D.V. GORYUNOV[3] & I.A. MILYUTINA[4]

Е.А. ИГНАТОВА[1], Х.Х. БЛОМ[2], Д.В. ГОРЮНОВ[3], И.А. МИЛЮТИНА[4]

Abstract

A phylogenetic analysis of ITS1-2 sequences from 117 specimens of *Schistidium* from Eurasia and North America revealed several new taxa within the genus. *Schistidium sibiricum* Ignatova & H.H. Blom, *S. obscurum* H.H. Blom, Köckinger & Ignatova, *S. tenuinerve* Ignatova & H.H. Blom, *S. bakalinii* Ignatova & H.H. Blom, *S. echinatum* Ignatova & H.H. Blom and *S. succulentum* Ignatova & H.H. Blom are described as new for science. Three new combinations are made: *S. canadense* (Dupr.) Ignatova & H.H. Blom, *S. abrupticostatum* (Bryhn) Ignatova & H.H. Blom and *S. konoi* (Broth.) Ignatova & H.H. Blom. Illustrations are provided for new species. A preliminary key for the identification of *Schistidium* species known in Russia is given.

Резюме

Филогенетический анализ ITS1-2 последовательностей, полученных из117 образцов *Schistidium* из Евразии и Северной Америки, выявил несколько новых таксонов в этом роде. *Schistidium sibiricum* Ignatova & H.H. Blom, *S. obscurum* H.H. Blom, Köckinger & Ignatova, *S. tenuinerve* Ignatova & H.H. Blom, *S. bakalinii* Ignatova & H.H. Blom, *S. echinatum* Ignatova & H.H. Blom и *S. succulentum* Ignatova & H.H. Blom описаны как новые для науки. Сделаны три новые комбинации: *S. canadense* (Dupr.) Ignatova & H.H. Blom, *S. abrupticostatum* (Bryhn) Ignatova & H.H. Blom и *S. konoi* (Broth.) Ignatova & H.H. Blom. Для новых видов даны иллюстрации. Приводится предварительный ключ для определения видов рода, известных на настоящий момент в России.

KEYWORDS: Grimmiaceae, molecular phylogeny, new combinations, new species, Russia, *Schistidium*, taxonomy

INTRODUCTION

Schistidium is a taxonomically difficult genus; the species concept within it changed significantly in recent years, especially after the treatment of *S. apocarpum* complex in Norway and Sweden (Blom, 1996). This narrow species approach was supported by the preliminary analysis of ITS1 sequences of 28 specimens representing 8 species published by Goryunov et al. (2007). This region of nuclear DNA was found to be a good marker in *Schistidium*, as its infraspecific variability appeared to be much lower than between species. A subsequent study of ITS1-2 from 112 specimens of 41 *Schistidium* species additionally confirmed these results (Milyutina et al., 2007). At the same time, the growing number of studied specimens allowed to conclude that the genus is not oversplit, but rather undersplit.

[1] – Moscow State University, Biological Faculty, Vorob'ovy gory 1-12, Moscow 119991 Russia – Россия 119991 Москва, Московский государственный университет, Биологический факультет; arctoa@list.ru

[2] – Norwegian Forest and Landscape Institute, Fanaflaten 4, 5244 Fana, Norway; blh@skogoglandskap.no

[3] – Main Botanical Garden of Russian Academy of Sciences, Botanicheskaya 4, Moscow 127276 Russia – Россия, 127276 Москва, Ботаническая, 4, Главный ботанический сад РАН; denis.goryunov@mail.ru

[4] – A.N.Belozersky' Research Institute of Physico-Chemical Biology, Moscow State University, Moscow 119991 Russia – Россия 119991 Москва, МГУ, НИИ Физико-химической биологии им. А.Н. Белозерского; iramilyutina@yandex.ru

MATERIALS AND METHODS

117 specimens of 40 taxa (38 species and 2 subspecies) were studied, many of them were taken from the previous study, but additional sampling was done for groups of *S. lancifolium*, *S. confertum* and *S. flaccidum*. Specimen data are given in Appendix 1. ITS extraction, amplification and sequencing used the standard protocols as in our previous studies (e.g. Gardiner et al., 2005), and maximum parsimony analysis was performed in Nona (Goloboff, 1994) in Winclada shell (Nixon, 1999a). Gaps were treated as missing data. Strict consensus was built from 3960 shortest trees (L=965) found in parsimony ratchet analysis (Nixon, 1999b). Jackknife support was calculated in Nona for 2000 iterations, and shown in strict consensus tree. Tree was rooted on *S. sordidum*, as this species is likely the most basal in the genus according to chloroplastic data analysis (Milyutina et al., 2010).

For Bayesian analysis the general time-reversible model with invariable sites and a gamma-distributed rate heterogeneity parameter (GTR+G +I) was selected. Sequence alignment was divided into three partitions: ITS1, 5.8S, ITS2. Each of these partitions was separately assigned the GTR+G+I model, gamma distributions were approximated using four categories. The analysis was performed in MrBayes v 3.1.2. (Ronquist & Huelsenbeck, 2003). Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run includes three heated chains and one unheated, and two starting trees were chosen randomly. The number of generations was 6,000,000, and trees were saved once every 100 generations. The first 45000 trees were discarded in each run, and 15000 trees from both runs were sampled after burning. Consensus trees were calculated after omitting the 10% of trees in strict consensus algorithm. When the log likelihood scores were found to stabilize, a consensus trees were calculated with the strict consensus algorithm after 5% of trees were omitted as burn in. Bayesian posterior probabilities were calculated as branch support values.

RESULTS

The obtained phylogenetic MP tree (Fig. 1) has a general topology similar to that found in previous studies (Milyutina et al., 2010), i.e. includes the basal grade (*S. sordidum, S. platyphyllum, S. grandirete, S. pulchrum, S. sinensiapocarpum, S. sibiricum, S. frisvollianum*) and terminal group subdivided into four main clades: Atrofuscum-clade (*S. elegantulum, S. atrofuscum, S. crassipilum, S. viride*), Apocarpum-clade (*S. abrupticostatum, S. subjulaceum, S. boreale, S. trichodon* var. *nutans, S. maritimum, S. rivulare, S. papillosum, S. apocarpum, S. lancifolium, S. canadense*), Confertum-clade (*S. scandicum, S. succulentum, S. flaccidum, S. subflaccidum, S. marginale, S. confertum, S. echinatum*), and Frigidum-clade (*S. frigidum, S. tenerum, S. cryptocarpum, S. umbrosum, S. tenuinerve, S. bakalinii, S. obscurum, S. dupretii, S. agassizii, S. submuticum*).

Unfortunately, the bootstrap support was found to be high mostly for ultimate clades composed of one or few species, while the mentioned bigger clades were not supported by ITS data, except Atrofuscum-clade.

The topology of Bayesian tree is generally the same as of MP tree (Fig. 2), with posterior probabilities 1.00 for Atrofuscum-clade, 0.98 for Apocarpum-clade and 0.94 for Confertum-clade. As the purpose of the paper is mainly the elucidation of species delimitation in taxonomically difficult groups, the general tree topology is not discussed here; it will be discussed elsewhere.

TAXONOMY

Schistidium apocarpum subsp. ***canadense*** (Dupr.) H.H. Blom ex B.H. Allen & Pursell, a taxon previously known only from eastern North America, was recently recorded for Asiatic Russia (Blom et al., 2006). It is characterized by the absence of hair-point, instead the leaf apex is made up of a yellowish green, chlorophyllose awn, which is short in lower leaves and comparatively long, up to 0.2 mm, in upper and perichaetial leaves. Other both gametophytic and sporophytic characters of the species agree with those of *S. apocarpum*. However, the comparison of ITS1-2 sequences revealed a considerable difference between specimens obtained from Russia and North America. The three specimens from southeastern Siberia (Zabaikal'sky Territory) and northern European Russia (Murmansk Province) form a highly supported clade with-

in the basal grade, whereas the North American specimens referred to *S. apocarpum* subsp. *canadense* were found in the *S. lancifolium* clade (Figs. 1-2). Within the latter, these four North American specimens and one from European Russia, Karelia formed a clade in some MP analyses (not shown), and in Bayesian analysis they are in terminal part of *S. lancifolium* clade (Fig. 2). The Karelian specimen agrees with *S. apocarpum* subsp. *canadense* in morphological characters and is clearly different from other sequenced specimens of *S. lancifolium* from Russia, which all have short hair-points typical for that species.

The sequenced specimens of North American "*S. apocarpum* subsp. *canadense"* are very similar to the plants from the type locality of *Grimmia apocarpa* forma *canadensis* annotated by the author of this taxon (St.-Hilaire Mt., 17 Oct. [19]24, coll. & det. Dupret, MT), see Figs. 7, *5:3*. (The protologue indicates a Dupret specimen from the same locality, without date, but with collector number 502 and note that the type is in Thériot Herbarium).

The phylogenetic analysis clearly indicates a much closer affinity of *S. apocarpum* subsp. *canadense* with *S. lancifolium* than with of *S. apocarpum*. *S. apocarpum* subsp. *canadense* differs from *S. lancifolium* in possessing distinctly larger plants with wider leaves and longer peristome teeth which are narrower in their apical part, in addition to the yellowish green awn at leaf apex. Therefore a new combination is proposed:

Schistidium canadense (Dupr.) Ignatova & H.H. Blom comb. nov. – *Grimmia apocarpa* var. *canadensis* Dupr., Contr. Lab. Bot. Univ. Montréal 25: 20. 1934. — *Schistidium apocarpum* subsp. *canadense* (Dupr.) H.H. Blom ex B.H. Allen & Pursell, Maine Mosses [shedae] [17]. 2005.

The Karelian specimen (Sortavala, *Maksimov & Maksimova #62-339,* MW, PTZ) is the only one representing this taxon in Eurasia up to now.

At the same time, plants of "*S. apocarpum* subsp. *canadense"* from the South Siberia and Murmansk Province form a clade within the basal grade and obviously belong to another species that apparently is undescribed, and consequently recognized here as *S. sibiricum* sp. nov.

Schistidium sibiricum Ignatova & H.H. Blom sp. nov. Figs. 3-4

A S. apocarpo similis sed mucro flavo-viridi, haud hyalino differt. A S. apocarpum ssp. canadense mucro angustioribus, cylindico, pauce serrulato vel laeve, reflexo versus triangulare, complanato, serrulato, stricto.

Type: Russia, Zabaikal'sky Territory, Aginskyi Buryatskyi Autonomous District, Alkhanai National Park, sothern slope of Alkhanai Mt., Ubzholgos Creek valley, 50°50'N – 113°24'E, forest belt, on rocks near stream, 20.VII.2005, Afonina #3005 (holotype LE, isotypes MW, MHA).

Additional illustrations: Blom et al., 2006: 188.

Plants medium-sized, in loose or dense tufts or mats, olivaceus-green or yellowish green, sometimes ferrugineous. Stems (0.5-)1-2.5 cm, slightly irregularly branched, central strand absent. Leaves appressed when dry, erect-spreading to widely spreading when moist, slightly falcato-secund, ovate-lanceolate to ovate-triangular, sharply keeled in upper part, acuminate, 2.0-3.0×0.6-0.8 mm; hyaline hair-point absent; margins recurved to shortly below leaf apex, denticulate in upper part, bistratose or 3-4-stratose in upper part; costa strongly projecting dorsally, 3-4-layered in distal part, 4-6-layered in proximal part, smooth, excurrent, forming stout, slightly denticulate, chlorophyllose mucro or awn, short in lower stem leaves and becoming longer, up to 0.2 mm, in upper and perichaetial leaves, straight or often recurved when dry; lamina unistratose, in upper part often with bistratose strips; upper lamina cells irregular in shape, subquadrate to transversely elongate, 7-10×8-10 μm, thick-walled, not sinuose; median cells subquadrate to short rectangular, 8-12×8-10 μm, weakly to moderately sinuose; basal cells rectangular, 12-25×11-12 μm, thick-walled, not or slightly porose, basal marginal cells subquadrate to transversely rectangular. Perichaetial leaves oblong, 3-3.5×0.6-0.9 mm. Urn shortly and broadly oblong, 0.8-0.9×0.6-0.7 mm, length/width ratio ca. 1.2; exothecial cells predominantly subquadrate to shortly rectangular with admixture of transversely rectangular cells; peristome teeth ca 500 μm, slightly or strongly perforated in upper part, patent to spreading, oblique, densely papillose. Spores ca. 15-17 μm.

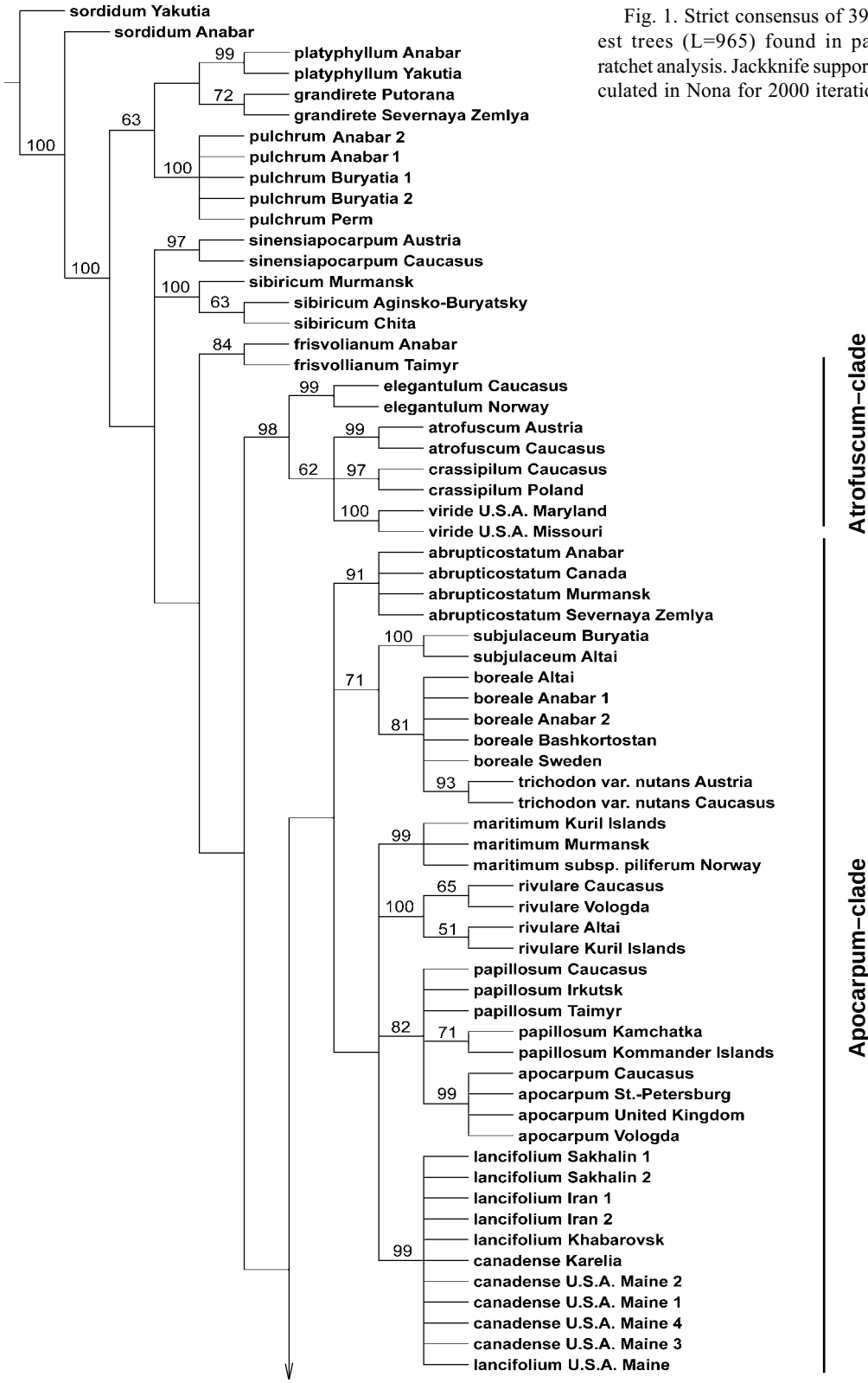
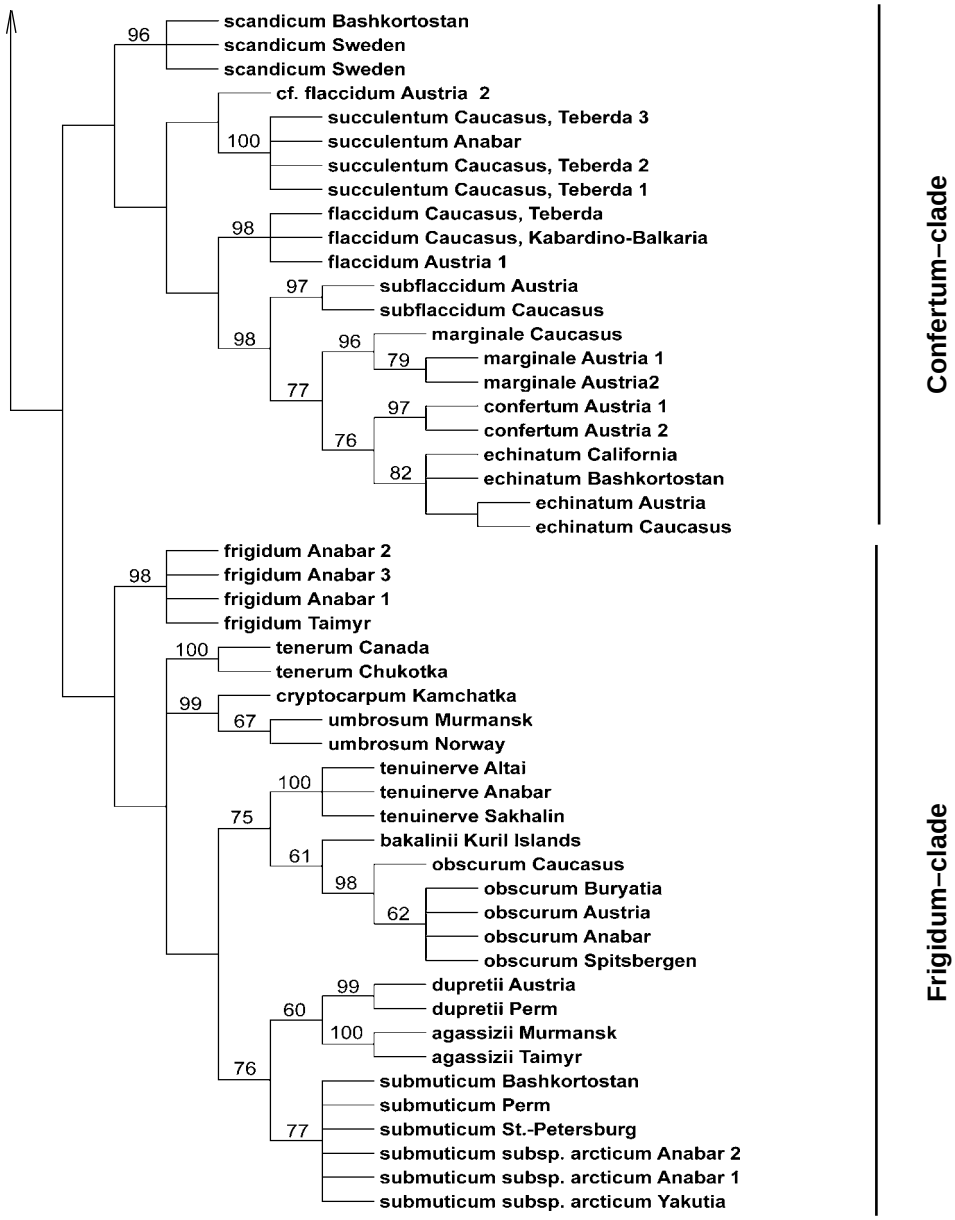


Fig. 1. Strict consensus of 3960 shortest trees (L=965) found in parsimony ratchet analysis. Jackknife support was calculated in Nona for 2000 iterations.



Differentiation. The main character differentiating *S. sibiricum* from most species of the genus in Russia is the absence of hyaline hair-points and costa excurrent into a stout chlorophyllose awn. In habit, as well as in leaf shape, the denticulate upper leaf margins and often strongly perforated peristome teeth, it is similar to *S. apocarpum*. However, in the latter species hyaline hair-points of variable length are usually present, at least in uppermost leaves, and its urns are mostly longer, with length/width ratio ca. 1.2-2.0 (vs. 1.2 in *S. sibiricum*).

The greatest similarity is observed between *S. sibiricum* and *S. canadense,* and it is not surprising that the former species was previously referred to the latter taxon. These two taxa may be considered as semi-cryptic ones. However, molecular data, both nuclear and chloroplast, show their different affinities and suggest convergent morphological resemblance (Figs. 1-2; see also Milyutina et al., 2010: 1003). Furthermore, minor morphological differences between them can

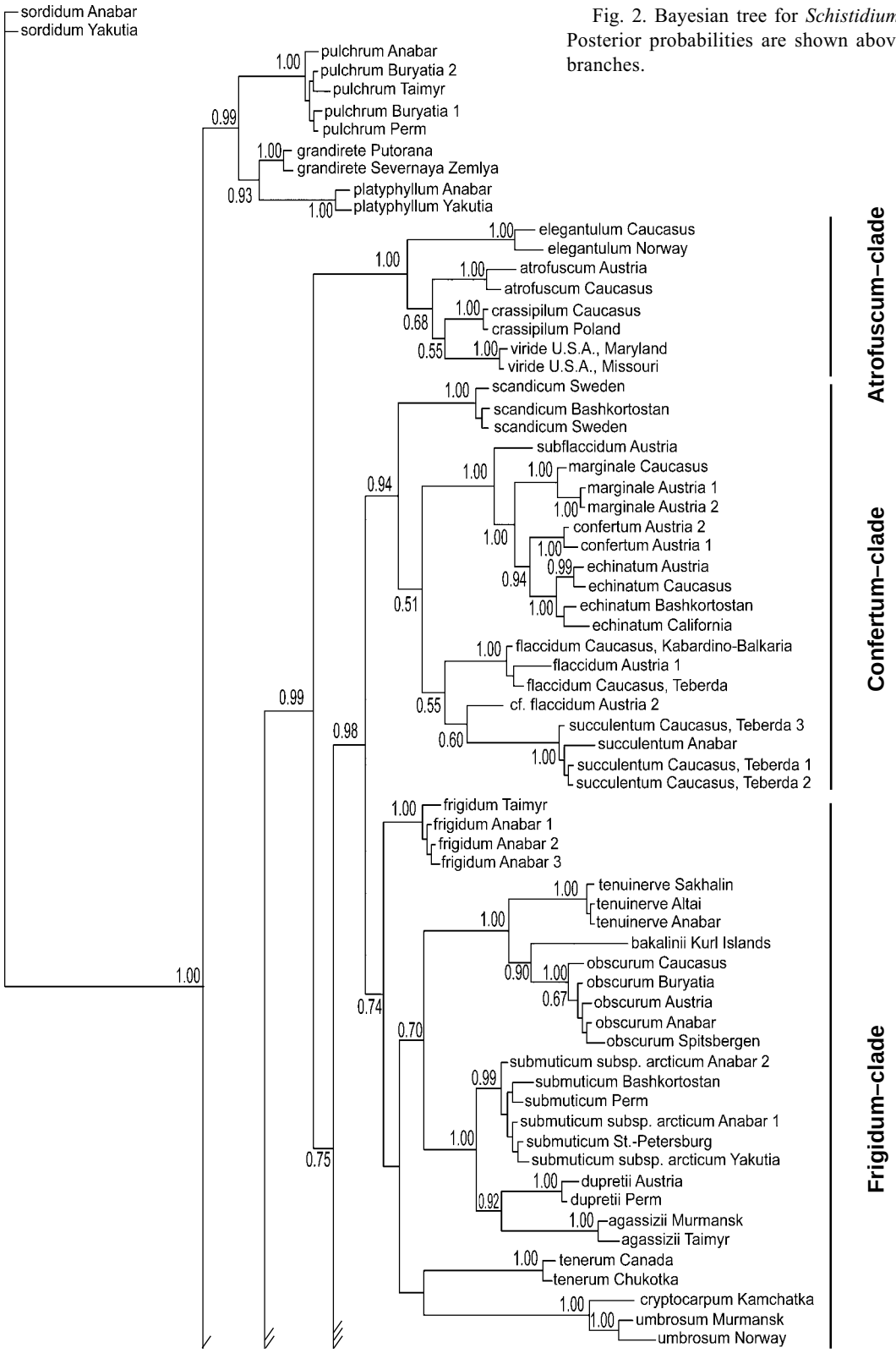
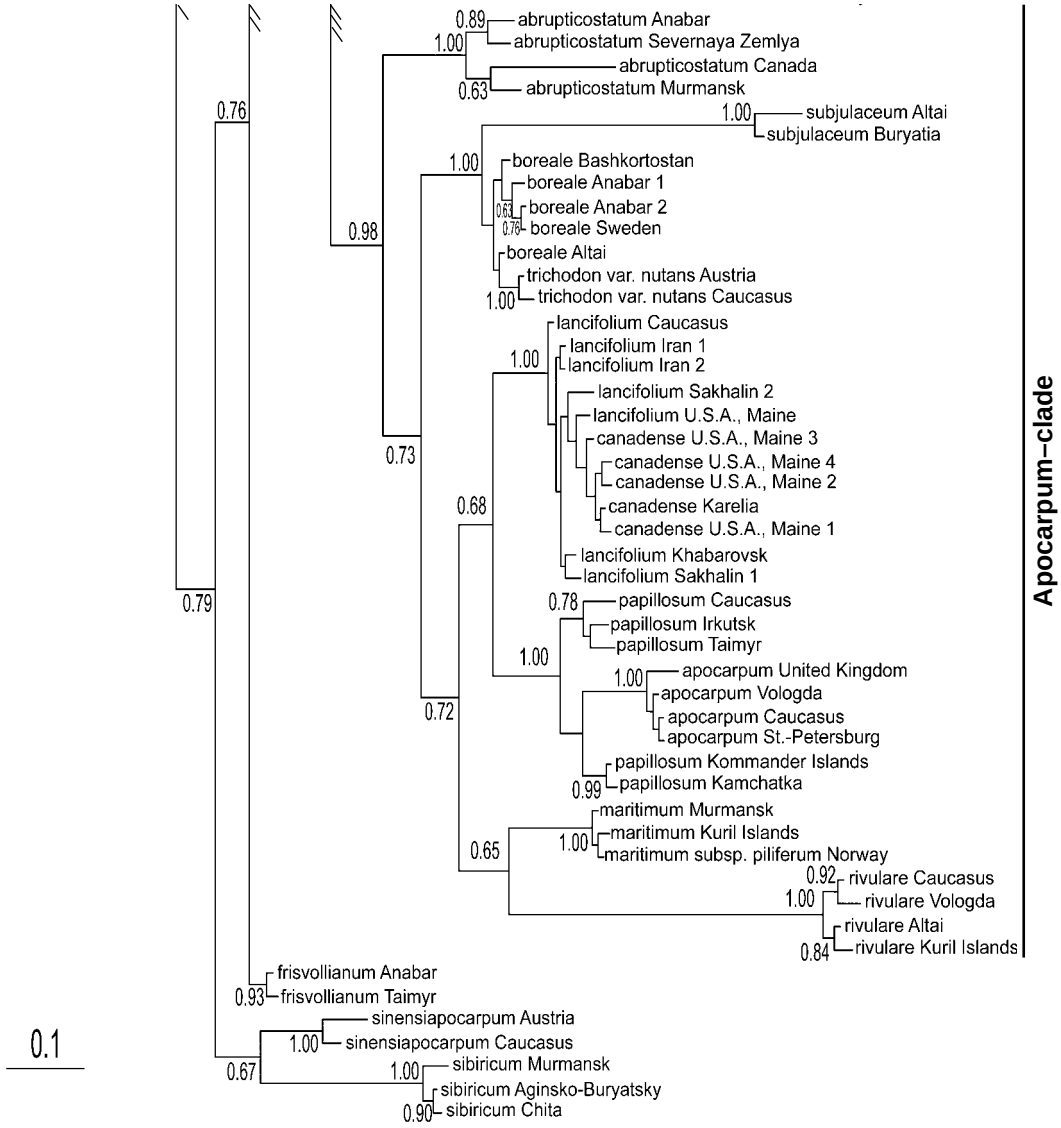


Fig. 2. Bayesian tree for *Schistidium*. Posterior probabilities are shown above branches.



be found. The upper and perichaetial leaves of *S. canadense* possess more strongly dentate distal margins and often papillose-denticulate dorsal side of costa vs. slightly denticulate upper margins and mostly smooth dorsal side of costa in *S. sibiricum*. The chlorophyllose awn is similarly variable in length in both taxa, being longer in upper and perichaetial leaves; however, in *S. canadense* it is always straight, mostly flattened and widened at base, and rather strongly dentate and spinulose dorsally whereas it is often recurved when dry in the upper leaves, narrower, less flattened and slightly to moderately denticulate in *S. sibiricum* (see Fig. 5: *1-3*). The median lamina cells are wider (10-14 vs. 8-10 μm) and more strongly sinuose in *S. canadense* (Figs. 6, 7), and, in addition, the peristome teeth of *S. canadense* are tapering to a fine, narrow point but they are more widely acute in *S. sibiricum* (Figs. 4, 6-7). According to our present knowledge, these taxa have different distributions: *S canadense* is mainly an eastern North American species (Fig. 8) whereas the main distribution area of *S. sibiricum* stretches from the southern part of Russian Far East and Transbaikalia to Tyva, and only in NW European Russia both taxa are recorded (Karelia and southern part of Murmansk Province respectively) (Fig. 9).

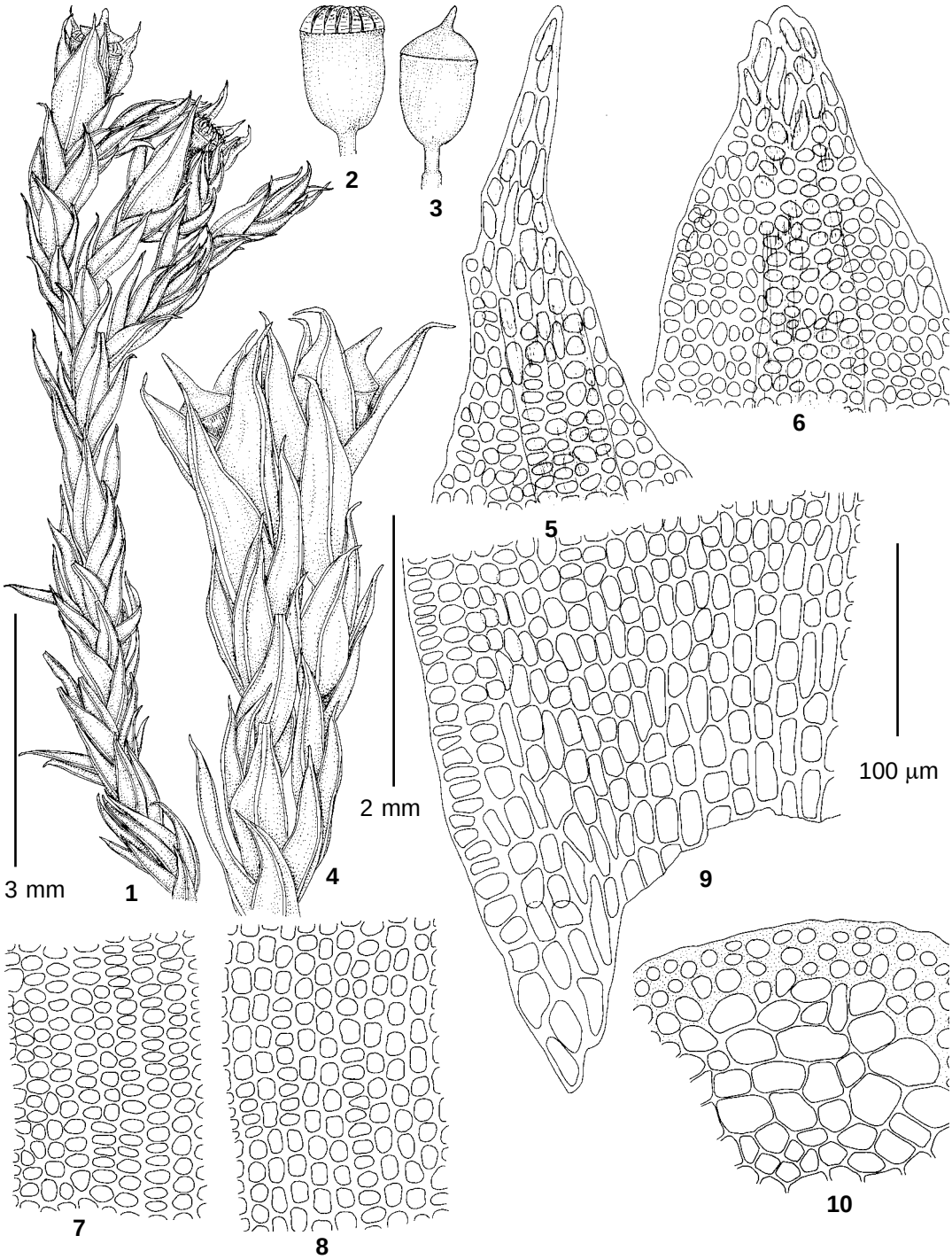


Fig. 3. *Schistidium sibiricum* sp. nov. (1-2, 4-10 – from Russia, Zabaikal'sky Territoty, *Afonina #3005*, LE; 3 – from Russia, Primorskij Territory, *Cherdantseva s.n.*, MW). 1, 4 – habit, dry; 3-4 – capsules, wet; 5 – apical part of subperichaetial leaf; 6 – apical part of stem leaf; 7 – upper lamina cells; 8 – median lamina cells; 9 – basal lamina cells; 10 – stem transverse section. Scale bars: 3 mm for 1; 2 mm for 2-4, 100 μm for 5-10.

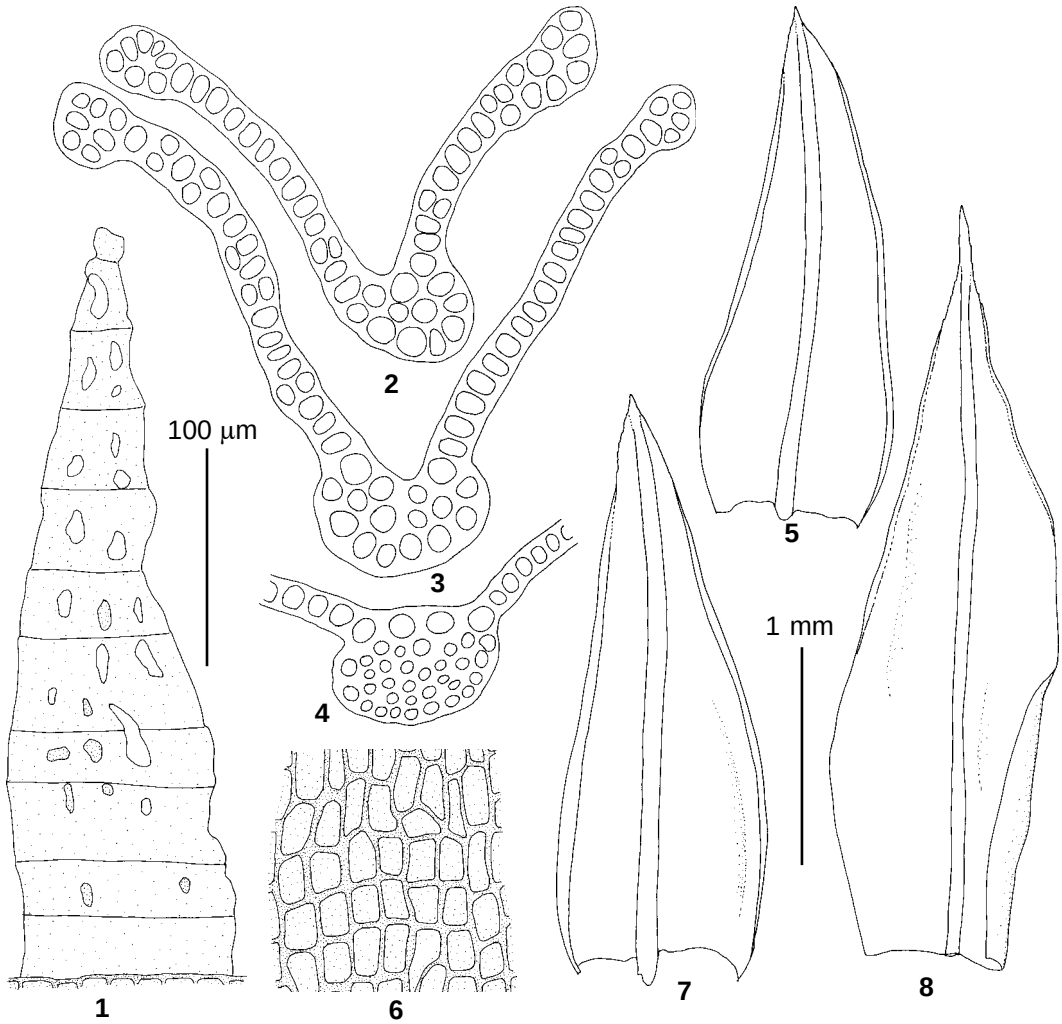


Fig. 4. *Schistidium sibiricum* sp. nov. (from Russia, Zabaikal'sky Territoty, *Afonina #3005*, LE). 1 – peristome tooth; 2-4 – leaf transverse sections; 5, 7 – stem leaves; 6 – exothecial cells; 8 – perichaetial leaf. Scale bars: 1 mm for 5, 7-8; 100 μm for 1-4, 6 .

Ecology. Usually on rocks near creeks and lakes, in dry stream beds, occasionally on rocks on slopes; in most places in rather wet habitats.

Selected specimens examined: ASIATIC RUSSIA: **Tyva Republic**, Todzha depression, western end of Kadysh Lake, northern shore, on rocks near the lake, 30.VIII. 1999, *Otnyukova s.n.* (MW, ex. KRAS). **Buryatia Republic**, NW shore of Baikal Lake, Kovrizhka Cape, on boulders at the lake shore, 27.VIII.1957, *Bardunov s.n.* (MW, ex. IRK). **Irkutsk Province**, Baikal Lake, Aya Gulf, on boulders at the lake shore, 29.VIII.1956, *Bardunov s.n.* (MW, ex IRK). **Zabaikal'sky territory**: 35 km N of Kyra, 1300 m alt., 16.VIII. 2006, *Afonina* (LE, MW). **Amurskaya Province**, Zeya District, Zeya State Reserve, Motovaya Creek upper course, on boulders, *Petelin #157* (MW). **Primorskiy Territory**, Sikhote-Alinskij Nature Reserve, Serebryanka, S-facing slope, on rocks, IX.1980, *Flyagina s.n.* (VLA, MW).EUROPEAN RUSSIA: **Murmansk Province***,* Kovda, *Kučera #11338* (MW).

"Alpine Schistidium frigidum"

Schistidium frigidum H.H. Blom has been considered to have a circumpolar arctic-alpine distribution (Blom, 1996). The species is very common in non-calcareous habitats in the Arctic in Eurasia and North America and was also reported from the Alps in Europe and from the Rocky Mountains in western North America. The species is very variable morphologically, and es-

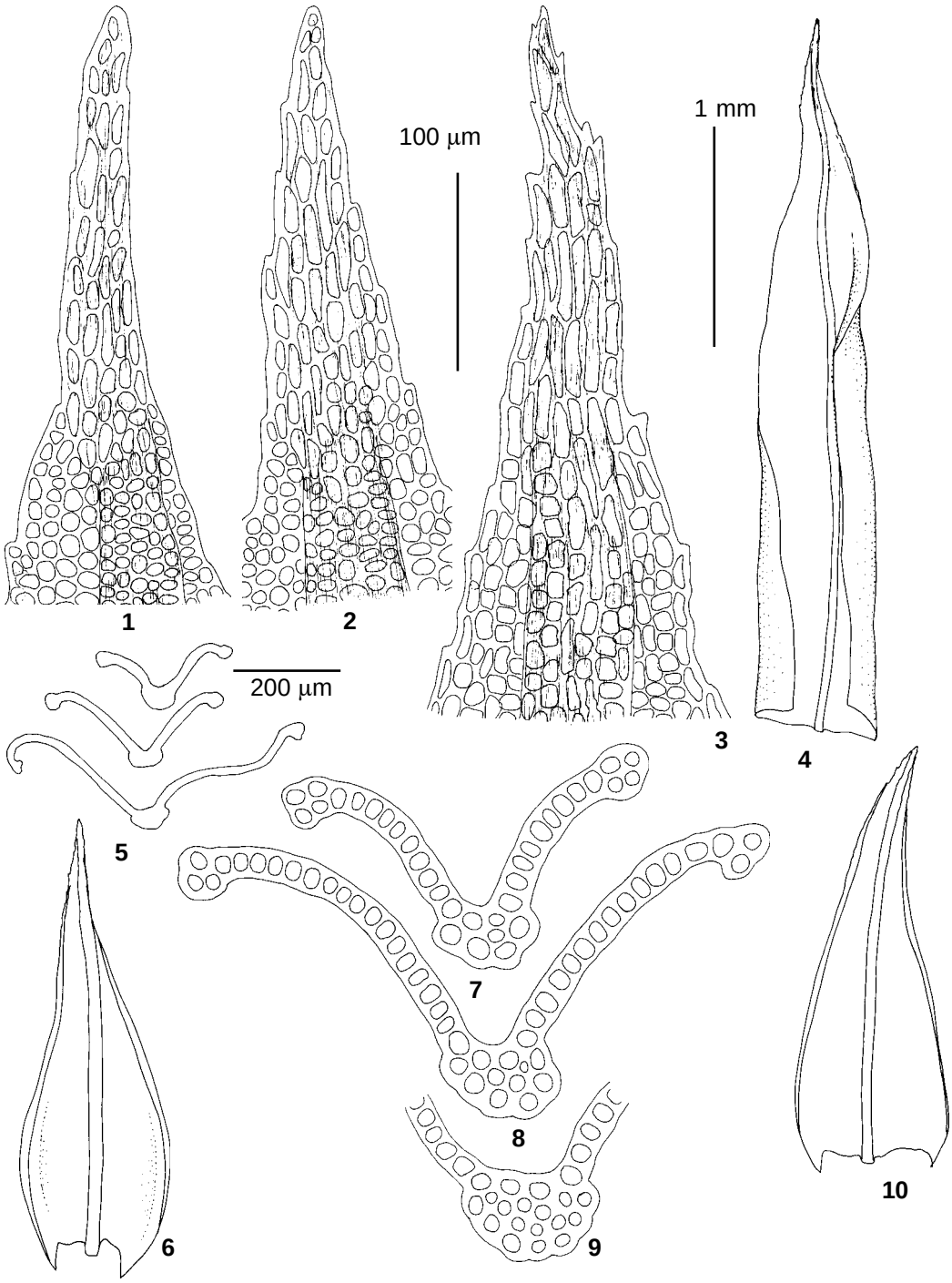


Fig. 5. 1-2 – *Schistidium sibiricum* sp. nov. (from Russia, Zabaikal'sky Territory, *Afonina #3005,* LE); 3-10 – *S. canadense* comb. nov. (3 – from Canada, St.-Hilaire, 17.X.1294 *Dupret s.n.*, MT; 4-10 – from Russia, Karelia, *Maksimov & Maksimova #62-339,* MW). 1, 3 – apical parts of perichaetial leaves; 2 – apical part of subperichaetial leaf; 4 – perichaetial leaf; 5, 7-9 – leaf transverse sections; 6, 10 – leaves. Scale bars: 1 mm for 4, 6, 10; 200 μm for 5; 100 μm for 1-3, 7-9.

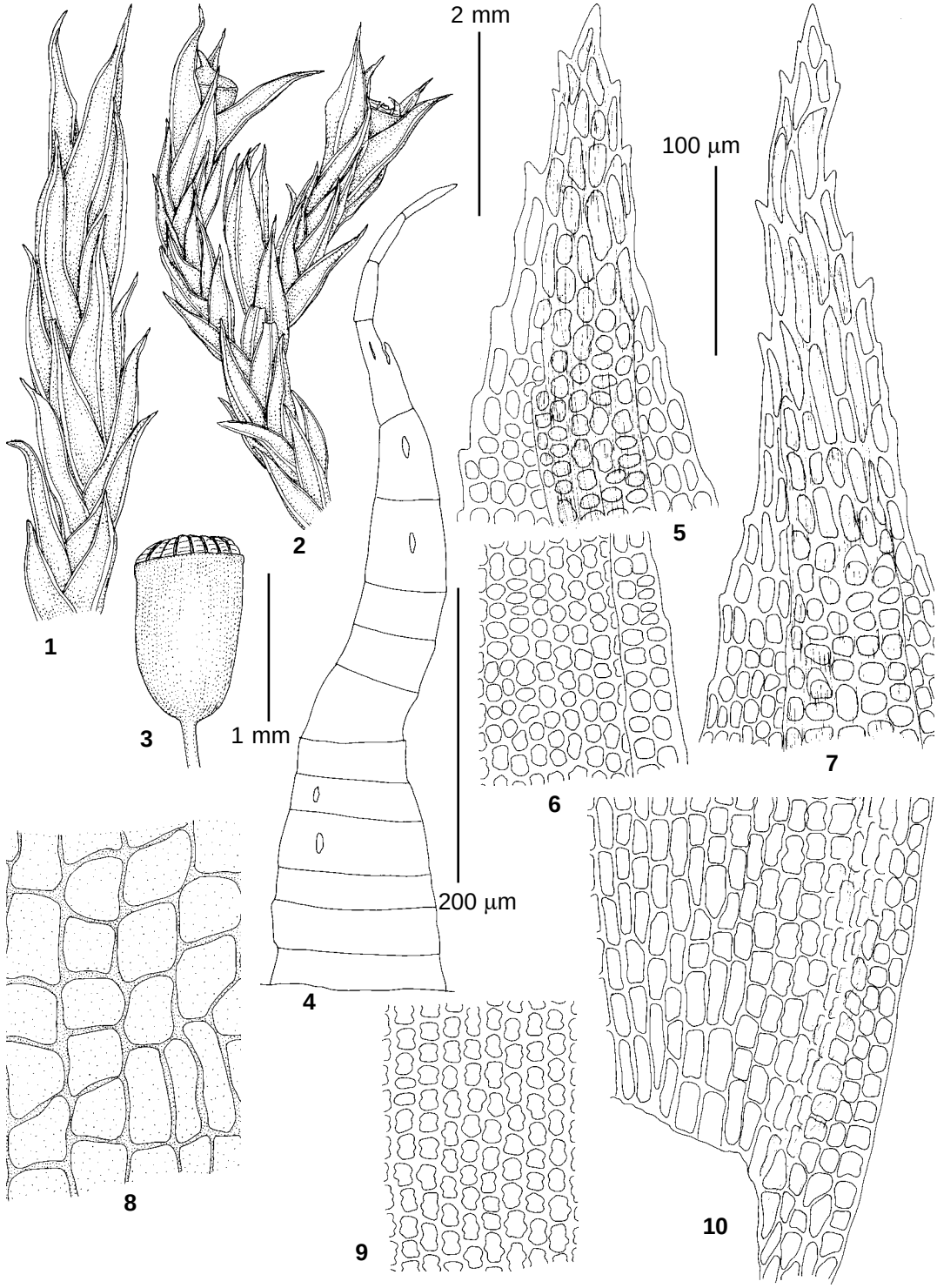


Fig. 6. *Schistidium canadense* comb. nov. (from Russia, Karelia, *Maksimov & Maksimova #62-339,* MW). 1-2 – habit, dry; 3 – capsule; 4 – peristome tooth; 5 – apical part of stem leaf; 6 – upper lamina cells; 7 – apical part of perichaetial leaf; 8 – exothecial cells; 9 – median lamina cells; 10 – basal lamina cells. Scale bars: 2 mm for 2; 1 mm for 1, 3; 200 μm for 4; 100 μm for 5-10.

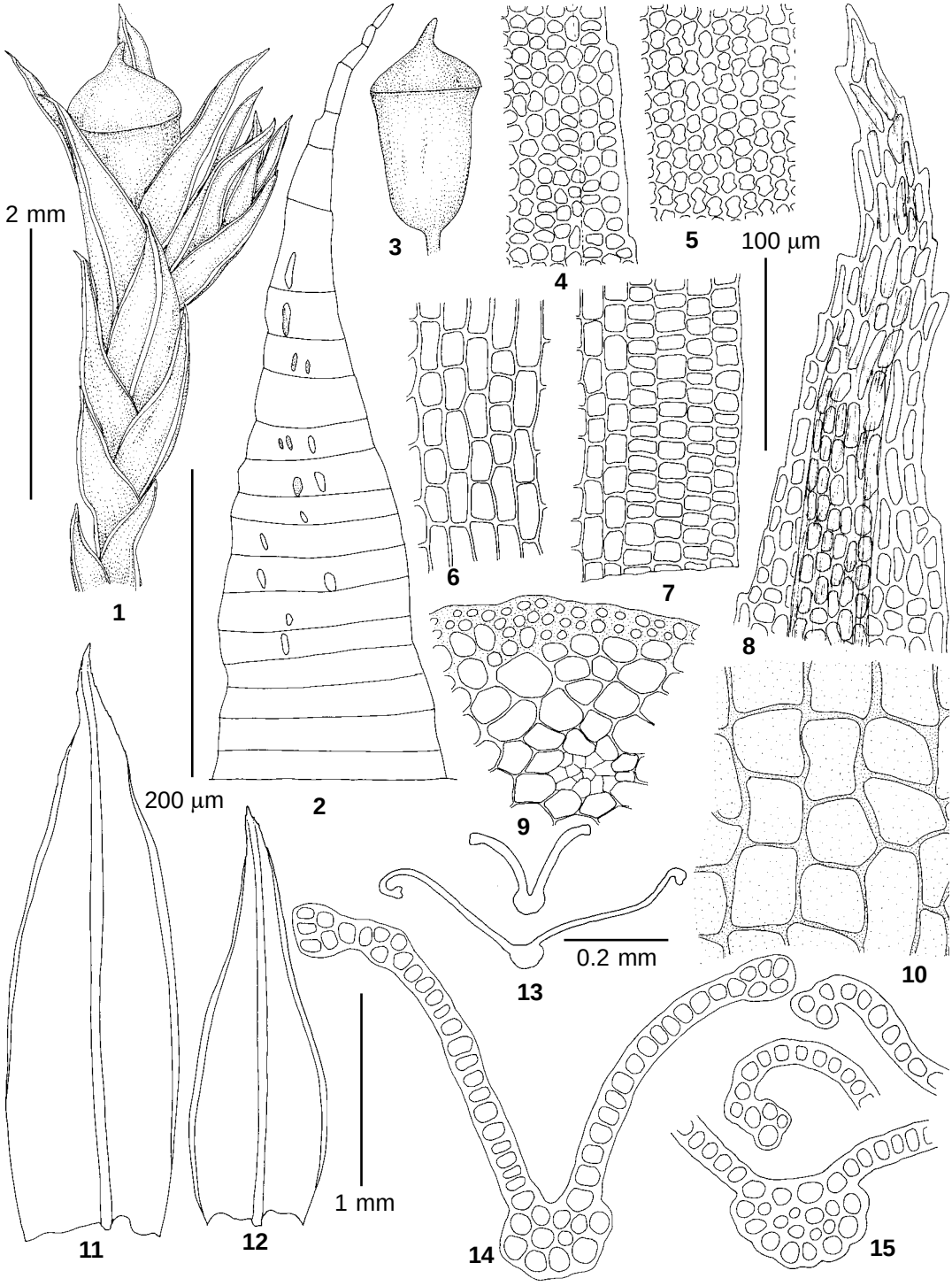


Fig. 7. *Schistidium canadense* comb. nov. (from Canada, St.-Hilaire, 17.X.1294 *Dupret s.n.*, MT). 1 – habit, dry; 2 – peristome tooth; 3 – capsule; 4 – upper lamina cells; 5 – median lamina cells; 6 – basal juxtacostal cells; 7 – basal marginal cells; 8 – apical part of perichaetial leaf; 9 – stem transverse section; 10 – exothecial cells; 11 – perichaetial leaf; 12 – stem leaf; 13-15 – leaf transverse sections. Scale bars: 2 mm for 1, 3; 1 mm for 11-12; 0.2 mm for 13; 200 μm for 2; 100 μm for 4-10, 14-15.

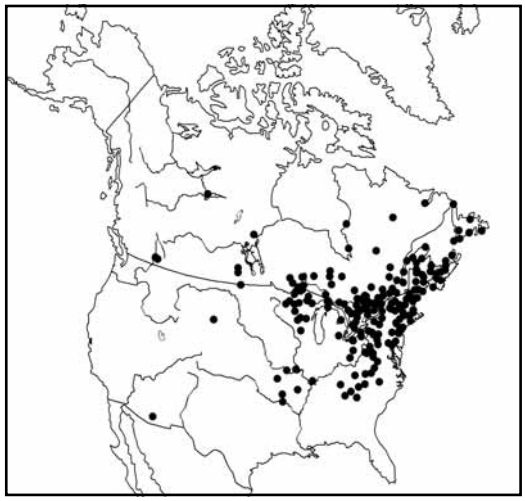


Fig. 8. Distribution of *Schistidium canadense* in North America.

pecially a large range of variation in gametophyte characters was reported for its alpine populations, which have among others smaller plant size, shorter leaves, narrow hair-point and moderately sinuose leaf cells (Blom, 1996). Molecular analysis revealed a sharp difference between specimens from the Siberian Arctic and Subarctic from one side, and alpine forms from the Alps, Caucasus, and southern Siberia from the other side. In addition, two other specimens, one from the Siberian Subarctic and one from Svalbard were resolved in a clade with the latter group of specimens. Their morphology that looked somewhat odd for *S. frigidum* appeared to fit perfectly alpine plants described below.

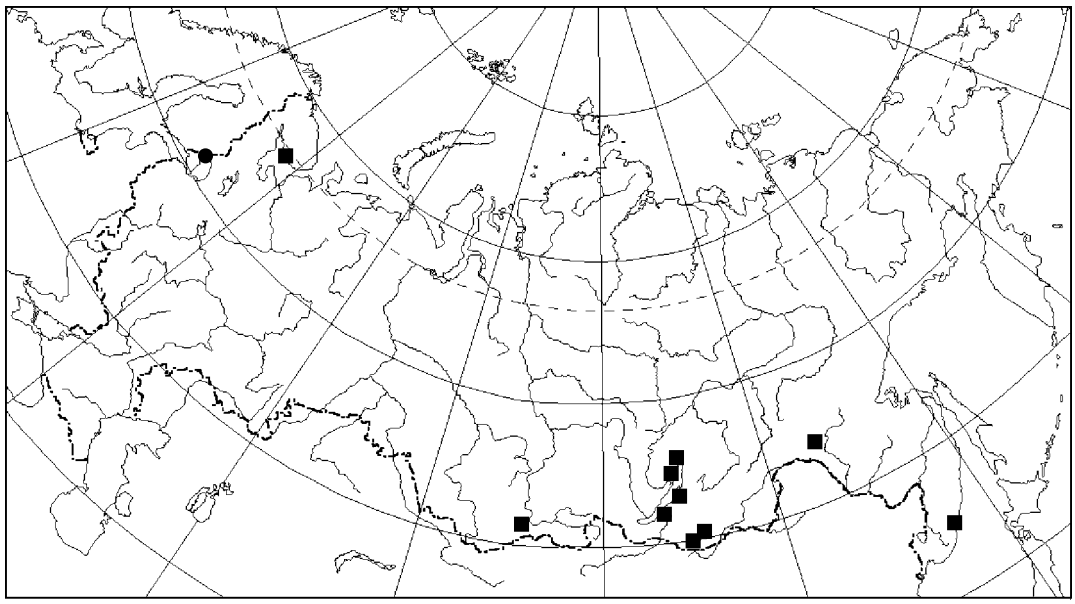
Schistidium obscurum H.H.Blom, Köckinger & Ignatova sp. nov. Figs. 10-11

A species S. frigido proximum, autem coloribus atrato et dimensionibus minoribus. Foliis brevioribus 0.75-1.5 mm lg. versus1.4-2.1 mm lg., parietibus cellularibus minus incrassates et obscure coloratis differt.

Type: Austria, Carinthia, Kreuzeckgruppe Mts., Kreuzeck Mt., northern slope of the summit, ca. 2680 m a.s.l., N-facing rock ledge, amphibolite, 7.IX.2006, Köckinger #12244 (holotype MW, isotypes MHA, KL, E).

Plants small to medium-sized, in rather dense tufts, dull, greyish green or olivaceous-green in uppermost tips of shoots, jet-black or more rarely brownish below (dull olivaceous-green in deep shade). Stems up to 15 mm, not or freely branched, central strand absent or indistinct. Leaves straight and imbricate when dry, erect-spreading when moist, narrowly to rather broadly ovate-lanceolate, obtusely keeled in upper part, 0.75-1.5×0.25-0.4 mm, with length/width ratio 2.5-

Fig. 9. Distribution of *Schistidium sibiricum* (square) and *S. canadense* (circle) in Russia.



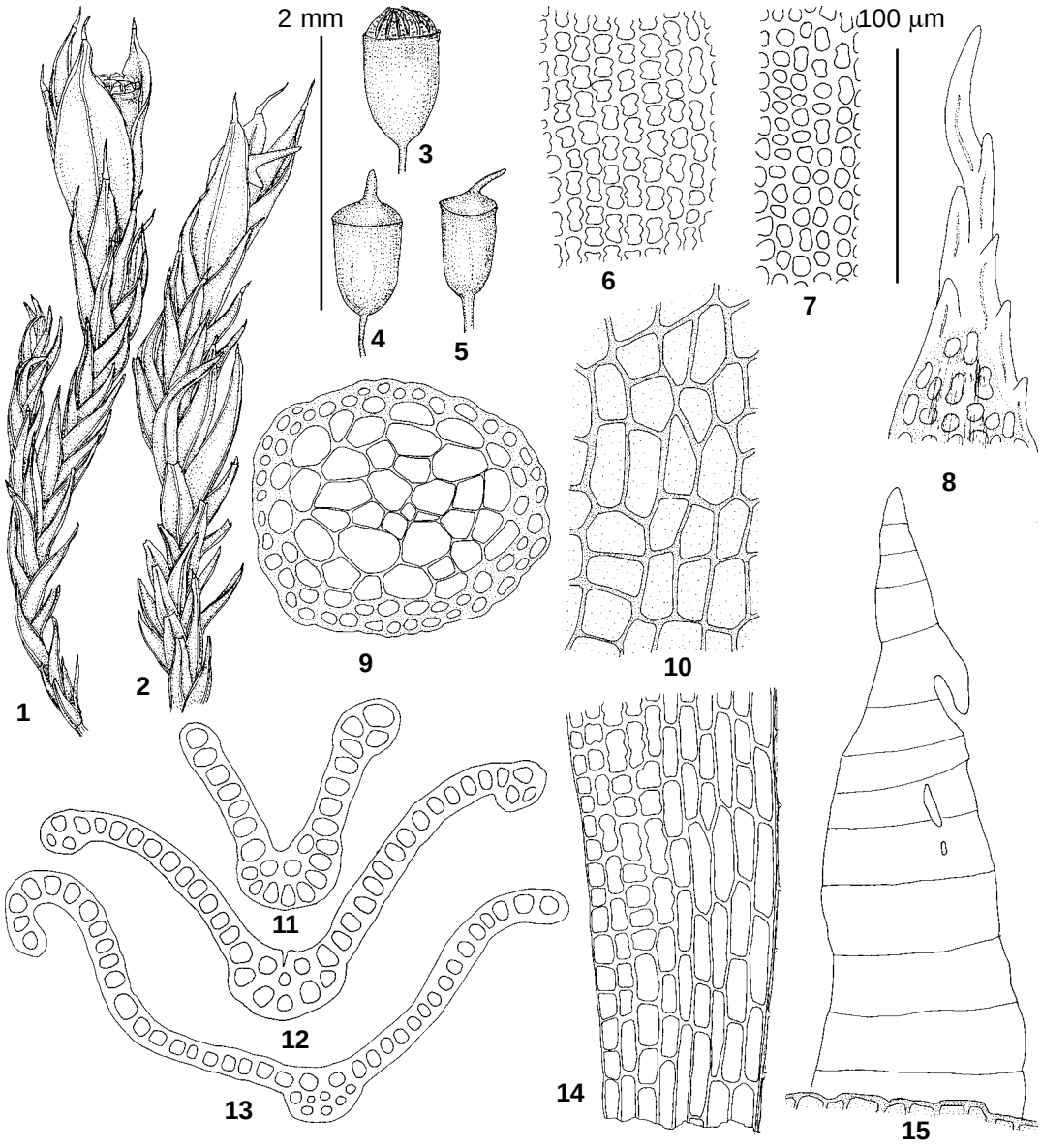


Fig. 10. *Schistidium obscurum* sp. nov. (1, 15 – from Russia, Buryatia, *Tubanova #Ky24/03*, MW; 2-14 – from Austria, *Köckinger #12244,* MW). 1, 2 – habit, dry; 3-5 – capsules; 6 – median lamina cells; 7 – upper lamina cells; 8 – hyaline hair-point; 9 – stem transverse section; 10 – exothecial cells; 11-13 – leaf transverse sections; 14 – basal leaf cells; 15 – peristome tooth. Scale bars: 2 mm for 1-5; 100 µm for 6-15.

4.0, widest at ca. 1/3 from leaf base, apex blunt when epilose or often rather broadly triangularly pointed, not evenly tapering into hair-point; hyaline hair-point 0-0.3 mm, straight or bent, narrow, terete, not or shortly decurrent, with short, blunt, distant spinulae; margins narrowly recurved from above the base to near the apex, 2-stratose in one row distally, smooth; costa weakly projecting dorsally, 2(-3)-layered distally, semicircular in transverse section, smooth; lamina unistratose, smooth; cell walls dark-colored, upper lamina cells round, oval and transversely oval, 7-9 µm wide, thick-walled, not sinuose; median lamina cells short rectangular, 8-20×8-10 µm; thick-walled, ± strongly sinuose; basal cells well-differentiated, rectangular, 25-40×8-10 µm, with

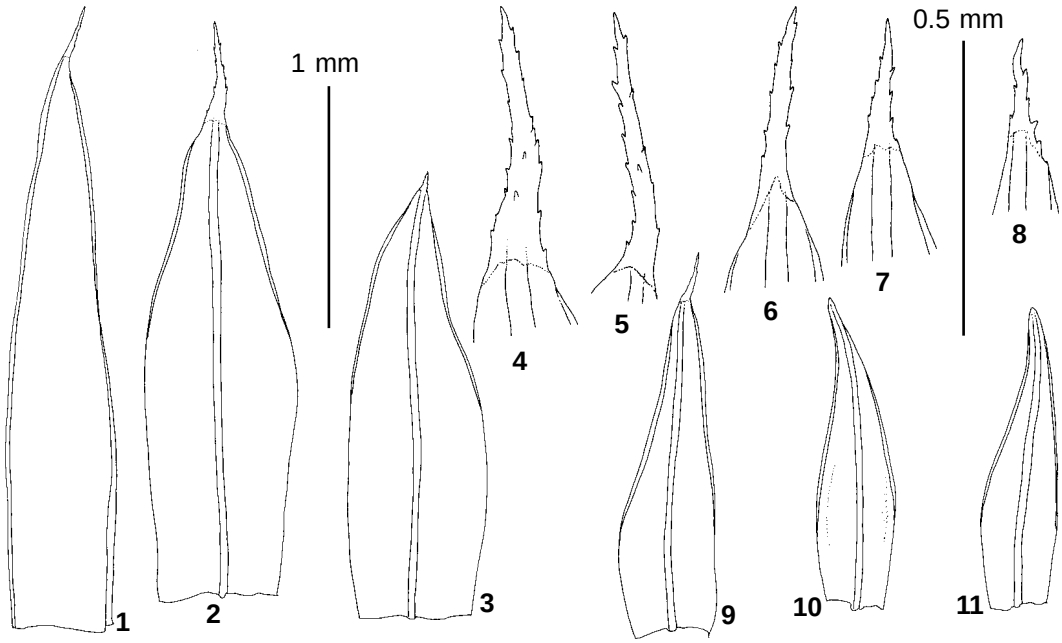


Fig. 11. *Schistidium obscurum* sp. nov. (from Austria, *Köckinger #12244,* MW). 1-2 – perichaetial leaves; 3 – subperichaetial leaf; 4-8 – leaf apices; 9-11 – stem leaves. Scale bars: 1 mm for 1-3, 9-11; 0.5 mm for 4-8.

± thin, straight, non-porose walls; basal marginal cells slightly shorter, equally thin-walled, usually >10 cells along margin in 1(-2) rows pellucid. Perichaetial leaves much larger than stem leaves, oblong, 1.25-2.25×0.6-0.9 mm, hyaline hair-point to 0.3 mm. Urn light orange-brown, cylindrical, 0.8-0.9×0.5 mm, length/width ratio 1.6-1.7; exothecial cells predominantly rectangular, thin-walled, with corner thickenings, stomata at base of urn; peristome teeth small, orange-brown to more often reddish brown, straight, spreading, later reflexed, ca. 250 μm long, not perforated or with few narrow perforations in upper part, finely and densely papillose-striolate. Operculum low conic, with mostly oblique, more rarely straight rostrum ca. 0.2 mm long. Spores ca.10 μm, smooth.

Differentiation. *Schistidium obscurum* has much in common with *S. frigidum*, and previously it has been considered to be a dark form of the latter species restricted to the Alps and the Caucasian mountains. These species have a similar cell areolation: thick-walled and strongly sinuose median lamina cells, a large group of long and smooth basal cells and a marginal row of thin-walled pellucid cells. Hair-point structure and sporophyte characters are also similar. However, ITS, as well as *trn*T-D sequences indicate that these taxa are good species. The following main differentiating characters should be listed: 1) smaller size of plants of *S. obscurum*, stems up to 1.5 cm, and leaves to 1.5 mm long and not arranged in distinct rows vs. more variable stem length, up to 5 cm, in *S. frigidum* and leaves to 2.1 mm long and usually arranged in rows; 2) usually jet-black or dark-brown color of plants vs. mainly olivaceous tufts; 3) leaves with a usually rather broadly triangular apex vs. a mostly narrow apex; 4) cell walls a little less strongly thickened, less elongated and dark-colored vs. usually very thick, nearly uncolored (lighter than content of cells); 4) hyaline hair-points comparatively short, up to 0.3 mm vs. variable in lengh, 0-0.8 mm; 6) peristome teeth orange-brown to often reddish brown vs. orange .

Blom (1996: 183) described a great variation in the gametophyte of *S. frigidum* and mentioned difficult specimens, particularly those growing in fissures of rock walls, which may belong to *S. obscurum*. Clearly, from our present knowledge, material of *S. frigidum* from the Scandinavian mountains as well as from N America should be re-examined.

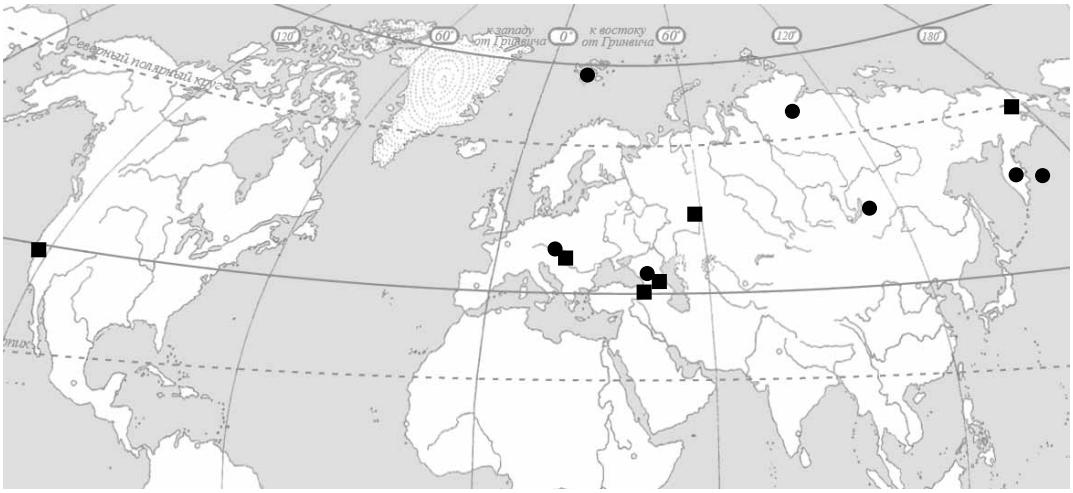


Fig. 12. Distribution of *S. obscurum* (circle) and *Schistidium echinatum* (square).

From the two closely related species, *S. tenuinerve* and *S. bakalinii*, which have similar cell areolation, *S. obscurum* can be separated by dark color of plants and narrow, terete hyaline hair-points.

Variation. Among the five sequenced specimens two, from Austria and Buryatia, are very similar in all characters, including jet-black color of plants and large group of more translucent, elongate-rectangular basal cells with straight walls and pellucid marginal cells. Three other specimens are more light-colored, brownish (Spitsbergen and Taimyr) or green in upper part (Caucasus), the group of smooth basal cells is smaller, and the marginal row of pellucid cells is often inconspicuous.These alterations, however, could be explained by an unusually shady habitat. Similar plants occur also in the Alps, where its variability is much better known.

Ecology and distribution. In the Caucasus, the species was collected in the alpine belt, at 2800 m a.s.l., in small crevices of NW-facing dry cliffs. In a similar habitat, a crevice of dolerite cliff on a steep rocky slope with nival vegetation near a mountain top it grows in southern Taimyr, the altitude is ca. 500 m. In Buryatia, it grows also above the tree line, at 1720 m a.s.l., on rocks above a brook but not influenced by water. In Spitsbergen, the species occupies the surface of a rock outcrop on a steep SW-facing slope. All reports of *S. frigidum* from the Alps (Blom, 1996; Grims, 1999; Köckinger et al., 2008) seemingly belong to *S. obscurum*. Especially in the central ranges of the Eastern Alps the species proved to be widespread, although definitely nowhere frequent and usually occuring only in few small cushions. Its altitudinal amplitude ranges from the alpine to the nival zone, where it is growing mainly on rock-walls and ledges of base-rich mica-schist or amphibolite, usually in N-exposure and somewhat protected, only in the highest sites tolerating also S-facing and more exposed habitats. Contrary to *S. frigidum* it was never found on boulders. Typical associates include *S. papillosum*, *S. trichodon* var. *nutans*, *S. umbrosum*, *Hymenoloma crispulum* and *Tortella fragilis*.

Other specimens examined: RUSSIA: Caucasus, **Karachaevo-Cherkessian Republic**, Teberda Nature Reserve, Khatipara Range northern spur, 2800 m a.s.l., *Ignatov & Ignatova #05-3200* (MW). **Buryatia Republic**, Kurumkan District, Dzherginsky Nature Reserve, sources of Levyj Birankur River, 1720 m a.s.l., *Tubanova #Ky-24/03* (MW). **Krasnoyarsk Territory**, Taimyrsky Municipal District, Khatanga surroundings, SE slope of Longdoko Mt. near the top of mountain, ca. 500 m a.s.l., steep rocky slope, nival communities with *Saxifraga* spp. and mosses, in crevice of dolerite cliff, *Fedosov #06-683* (MW); **Kamchatskaya Province**: Mil'kovo Distr., Kostina Mt., *Fedosov #10-4-5, 10-4-15* (MW); Aleutsky Distr., Bering Island, *Fedosov #10-3-10* (MW).

NORWAY: Spitsbergen Archipelago, Western Spitsbergen Island, Is-fjord, Gren-fjord, Barentzburg surroundings, Gladdalen Gorge, ca. 120 m a.s.l., *Belkina #B128/1-06* (KPABG, MW).

***Schistidium confertum* group**

Schistidium confertum is characterized by small size of plants, costa flattened and strongly exserted dorsally, hyaline hair-point flattened, broadened to its base, with prominent recurved teeth. There are a number of collections from Caucasus and Urals Mountains that are rather similar to it, but with somewhat different structure of hyaline hair-point (cf. Fig. 15: *1-3*). Molecular phylogenetic analysis demonstrated that they form a clade sister to typical *S. confertum* (Figs. 1-2); comparison of the alignment found 11 substitutions and indels differentiating two specimens of *S. confertum* from Austrian Alps and 4 accessions from a broad geographical range: Ural, Caucasus, Austria and California. Although morphological distinction is not large, there is a quite stable difference in hyaline hair-point structure: it is formed by cells with strongly exerted upper angles that are numerous and blunt, "finger-like", whereas in typical *S. confertum* teeth are fewer, massive and sharp, "tooth-like". Thus plants from the latter clade are described here as a new species, *S. echinatum*.

Schistidium confertum (Funck) Bruch & Schimp. has been repeatedly reported from many regions of Russia (Savicz-Lyubitskaya & Smirnova, 1970; Ignatov & Afonina, 1992), but subsequent revision of herbarium collections revealed that nearly all of them were erroneous. The species is not rare in mountains of Central Europe, southern Sandinavia and western North America; scattered localities are known in Turkey, Trans-Caucasian region, China, and India. The only confirmed collection from Russia is a Brotherus' specimen from Caucasus, Ossetia, near Lars.

Schistidium echinatum Ignatova & H.H.Blom sp. nov. Figs. 13-15

A S. conferti sed spina pili longiore obtusis dentibus obtusiusculus margine ad pilo recurvato differt.

Type: Russia, Bashkortostan Republic, Ishimbaisky District, Makarovskoe Forestry, Fareikin settlement, northern slope of Uryuk River valley, rock outcrops in pine-birch forest, on limestone rock covered by fine soil, 13.VI.2001, Zolotov #07-1 (holotype MHA).

Plants small, in loose tufts, slightly glossy, green, olivaceus-green or dark-green in upper part, brownish below. Stems 4-10 mm, repeatedly branching, with narrow central strand. Leaves appressed when dry, erecto-patent when moist, ovate-lanceolate to ovate-triangular, sharply keeled in upper part, 0.8-1.8×0.3-0.6(-0.7) mm, with length/width ratio 2.2-2.5, hyaline hair-point 0-0.25 mm, in lower leaves usually very short, consisting of few cells, with 2-3 sharp teeth, in upper leaves longer and slightly widened at base, densely spinulose, not or shortly decurrent; margins recurved from above the base to near the apex, 2-3 (-4)-stratose in 2(-3) rows in upper part, smooth; costa strongly projecting dorsally, 2-3-layered distally, flattened, trapezoid in transverse section, smooth; lamina with numerous bistratose strips distally, smooth; upper lamina cells round-oval to transversely oval, 5-7×5-10 μm, with moderately thickened walls, not sinuose; median cells subquadrate to short rectangular, 8-15×8-10 μm, with moderately thickened walls, slightly to moderately sinuose; basal cells rectangular, 12-20×10-12 μm, with moderately thickened, straight, non-porose walls; basal marginal cells in 5-8 rows subquadrate, short rectangular and transversely rectangular, with more thickened transverse walls. Perichaetial leaves with oblong base and short to long triangular acumen, 1.7-2.0×0.8-0.9 mm, hyaline hair-point 0.3-0.5 (-0.6) mm, weak and flattened, densely spinulose at margins and dorsally, spinulae short and blunt or longer and narrower, blunt. Urn light orange brown, short-cylindrical, ca. 0.8-0.9×0.5-0.6 mm, length/width ratio 1.5-1.8; exothecial cells predominantly oblong, irregular in shape, with admixture of isodiametric, rounded-rectangular and transversely rectangular cells, thin-walled, stomata at base of urn; peristome teeth orange, straight, 240-260 μm, strongly perforated, occasionally irregular in shape, fragile, finely striolate-papillose. Operculum low conic, with straight beak ca. 0.2 mm long. Spores 12-15 μm, very finely papillose.

Differentiation. *Schistidium echinatum* is similar to *S. confertum* in plant size, partially bistratose leaf lamina, weak and flattened, strongly spinulose-denticulate hair-points, often with recurved spinulae, costa strongly prominent and flattened dorsally and the strongly perforated peristome teeth. It differs from the latter one ina structure of hair-point teeth that are "finger-like",

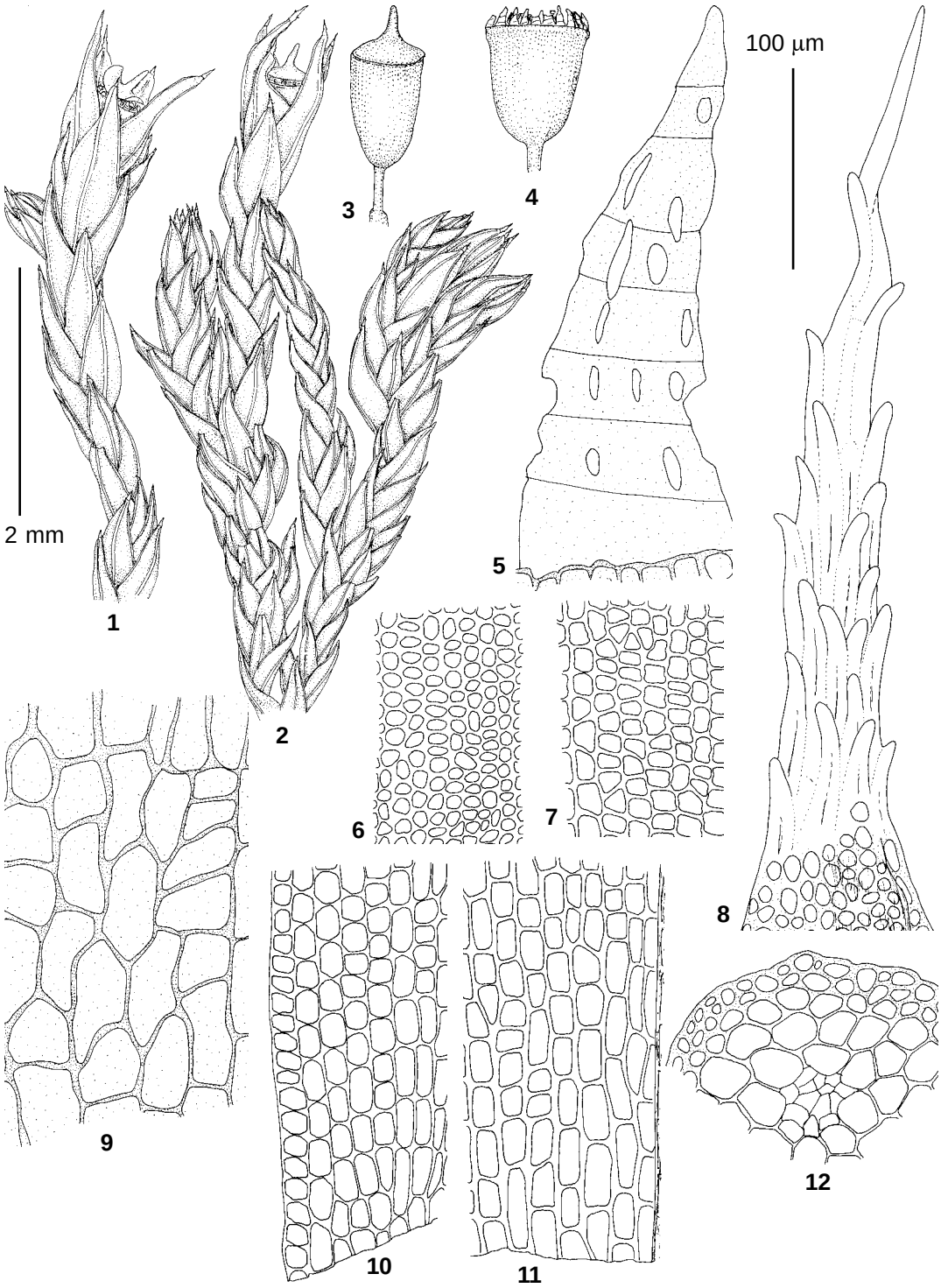


Fig. 13. *Schistidium echinatum* sp. nov. (from Russia, Bashkortostan, *Zolotov #07-1,* MHA). 1-2 – habit, dry; 3-4 – capsules; 5 – peristome tooth; 6 – upper lamina cells; 7 – median lamina cells; 8 – hyaline hair-point; 9 – exothecial cells; 10 – basal marginal cells; 11 – basal juxtacostal cells; 12 – stem transverse section. Scale bars: 2 mm for 1-4; 100 μm for 5-12.

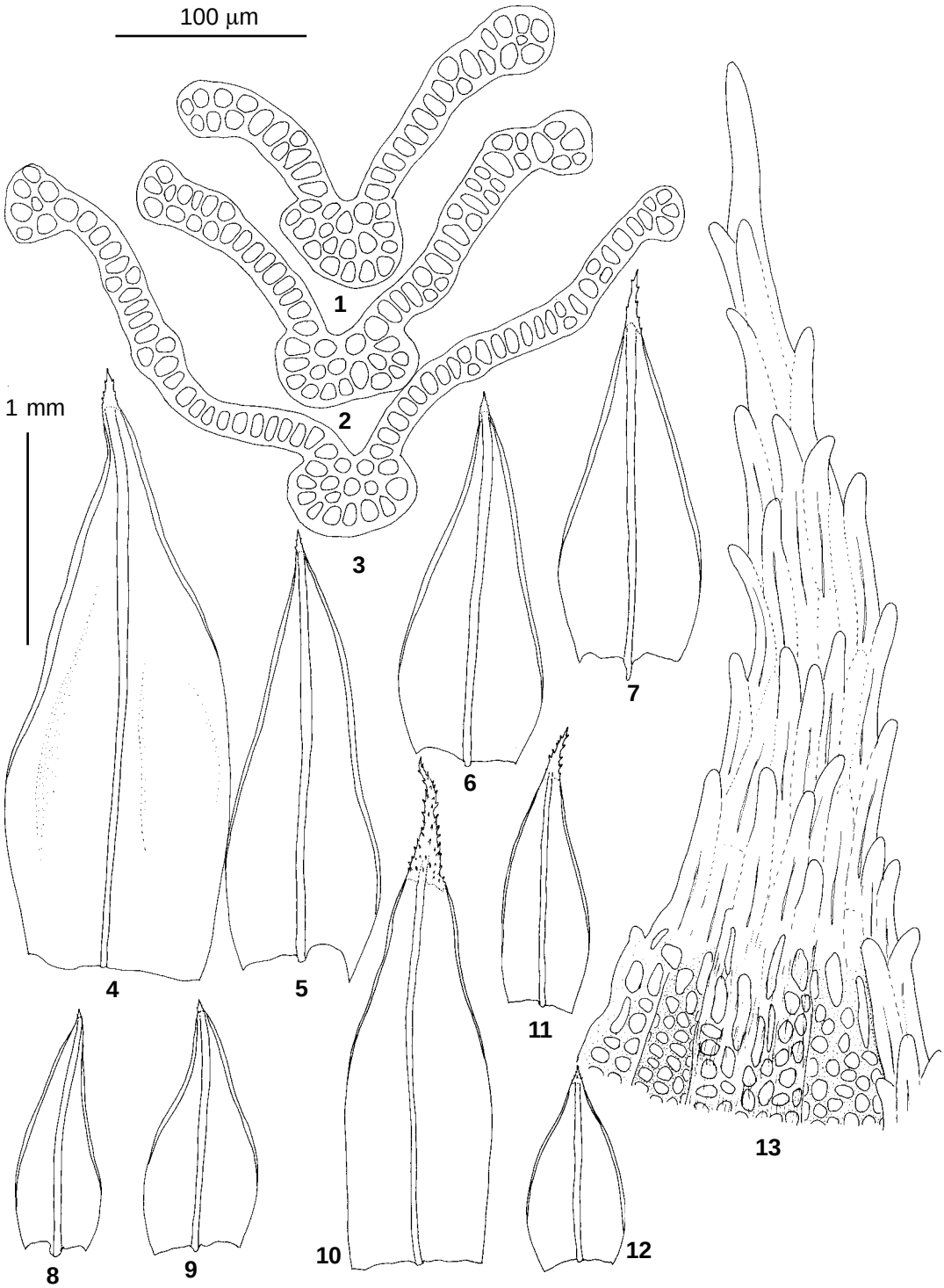


Fig. 14. *Schistidium echinatum* sp. nov. (1-9, 13 – from Russia, Bashkortostan, *Zolotov #07-1,* MHA; 10-12 – from Russia, Karachaevo-Cherkessian Republic, *Ignatov & Ignatova #05-3902,* MW). 1-3 – leaf transverse sections; 5-9, 11-12 – stem leaves; 4, 10 – perichaetial leaves; 13 – hyaline hair-point of perichaetial leaf. Scale bars: 1 mm for 4-12; 100 µm for 1-3, 13.

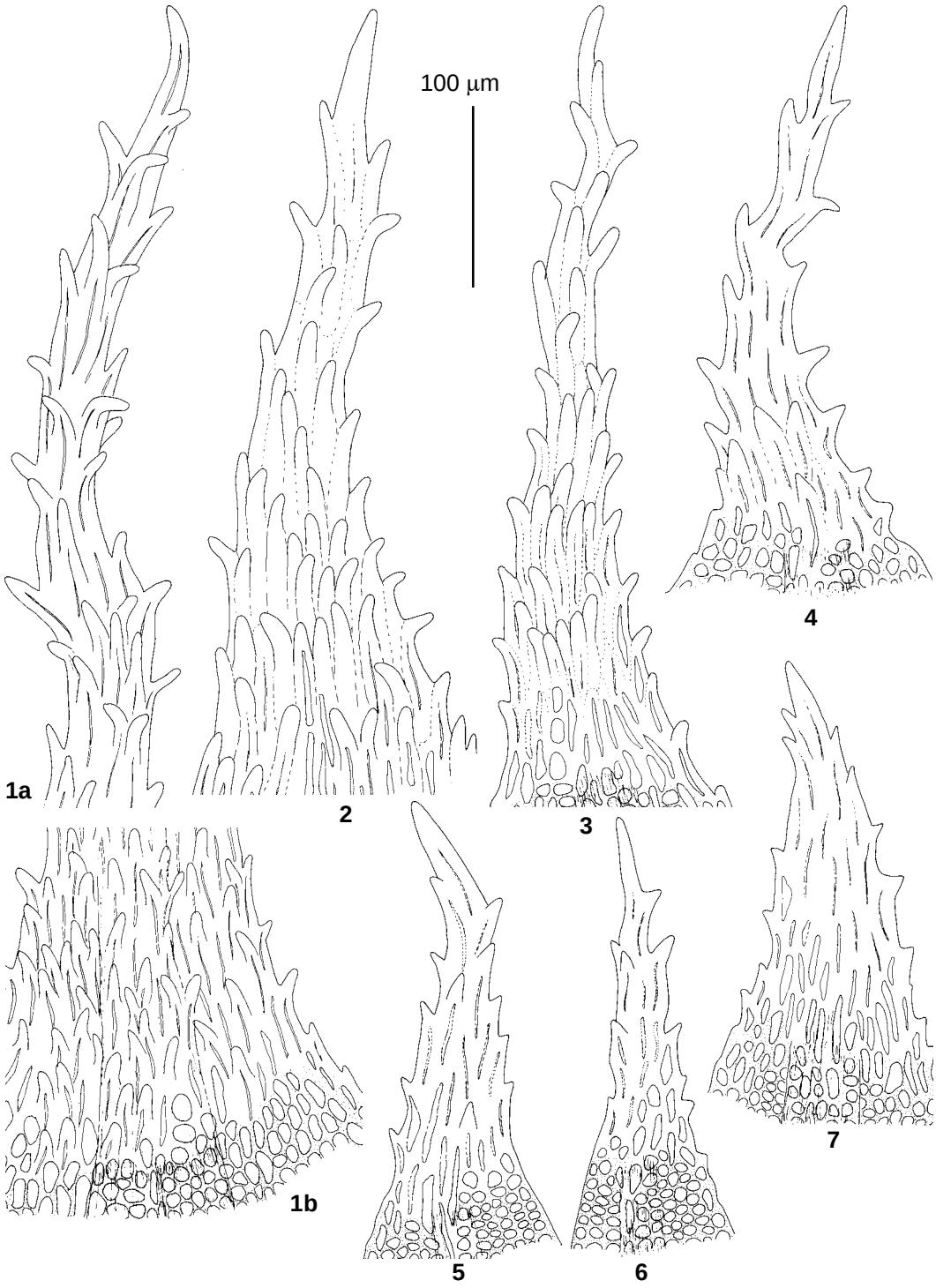


Fig. 15. 1-3 – *Schistidium echinatum* sp. nov. (1 – from Russia, Karachaevo-Cherkessian Republic, *Ignatov & Ignatova #05-3902,* MW; 2 – from Austria, *Köckinger #96-937,* MW; 3 – from California, *Toren #9500b,* MW); 4-7 – *S. confertum* (4 – from Georgia, Imeretia, *Brotherus,* H-Br #1880017; 5 – from Austria, *Köckinger #93-1312,* MW; 6-7 – from Austria, *Köckinger #12251,* MW). 1-7 – hyaline hair-points. Scale bars: 100 μm for 1-7.

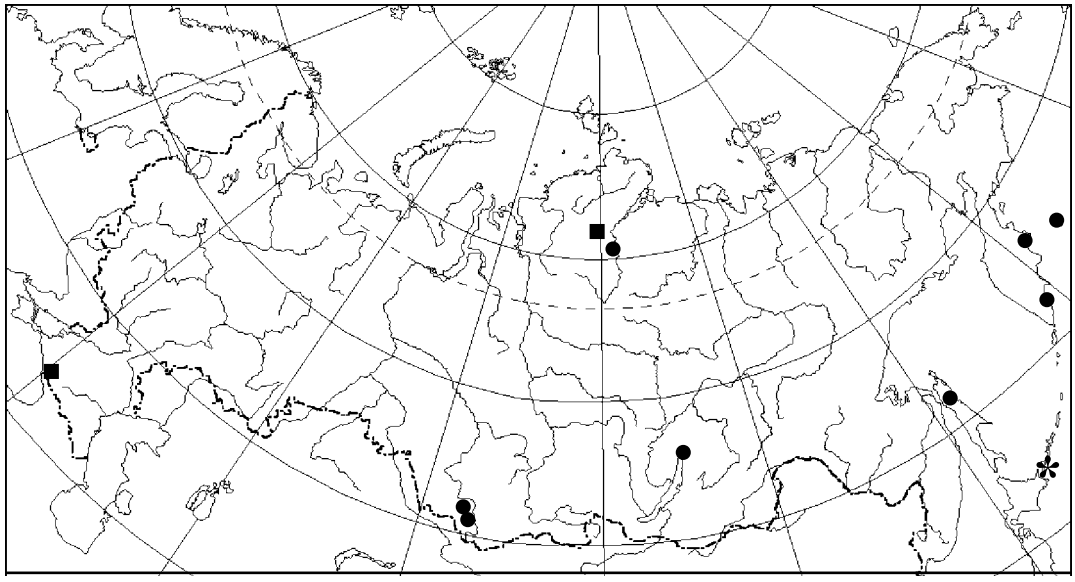


Fig. 16. Distribution of *Schistidium bakalinii* (asterisk), *S. succulentum* (square), *S. tenuinerve* (circle).

less massive, narrow, formed by upper part of protruding cell, without deep depressions between them (Fig. 15: *1-3*). Contrary to this the hair-point teeth of *S. confertum* are "tooth-like", large, wide at base, consisting of upper half of a cell, with deep depressions between them, making outline of the hair-point irregular (Fig. 15: *4-7*). In addition, in *S. echinatum* leaf margins are recurved to near the apex, while in *S. confertum* they are more shortly recurved, up to 3/4 of leaf length.

Schistidium liliputanum (Müll. Hal.) Deguchi also has strongly spinulose hair-points with narrow and often recurved spinulae; however, its hair-points are narrow and terete, and the spinulae are more distant than in *S. echinatum*. Furthermore, *S. liliputanum* often has rusty color of plants, which is never observed in *S. echinatum*, and its leaf lamina is predominantly unistratose, except several rows of marginal cells, whereas the leaf lamina is partially bistratose in *S. echinatum*.

Schistidium spinosum H.H. Blom & M. Lüth differs from *S. echinatum* in its terete hair-points with longer spinulae and the shorter obovoid urns (length/width ratio 0.9-1.3 vs. 1.5-1.8 in *S. echinatum*).

Differences between *S. echinatum* and *S. flaccidum* include: 1) strongly and densely spinulose-denticulate hair-points vs. finely and distantly denticulate ones; 2) partially bistratose vs. unistratose leaf lamina; 3) costa flattened, trapezoid in transverse section vs. semicircular one; 4) cylindrical vs. cyathiform urns; 5) operculum mamillate vs. rostrate.

The peculiar hair-point structure of *S. echinatum,* with dense "finger-like" teeth, resembles to some extent that of recently described *Grimmia horrida* J. Muños & H. Hespanhol from Iberian Peninsula; the latter species is dioicous, and its sporophytes are unknown; it has even longer, cilia-like teeth of hair-points (cf. Muños et al., 2009: 327) and differs from *S. echinatum* in leaf shape and areolation.

Variation. The species varies with regard to height of plants, and stems are shorter in populations from the alpine belt. Even within the few known specimens hair-point length of perichaetial leaves varies considerably; the longest hair-points were observed in small plants from high altitude in Caucasus.

A specimen from California (*Toren #9500b*, duplicate in MW) can be referred to *S. echinatum* based on its ITS sequence, and it has the same hair-point structure as in specimens from Russia. However, it differs from Russian plants in leaf shape: the stem leaves are narrower, ovate-lanceolate with length/width ratio >3, and occasionally possess more shortly recurved leaf margins. We tentatively refer it to *S. echinatum*; however, its final position must await the study of more material from North America.

Ecology and distribution. The species grows on shaded limestone outcrops in the forest at low altitude in the Ural Mts., on sandsone in Chukotka and on volcanic rocks in the alpine belt in Caucasus, at 2790-2950 m a.s.l. In the Alps it is definitely rare with hitherto only one record from Eastern Tyrol (Austria), growing on calcareous schist in the subnival belt.

Specimens examined: AUSTRIA: Tyrol, Hohe Tauern Mts., Mt. Muntanitz, *Köckinger #96-937* (MW); RUSSIA: Caucasus: **Karachaevo-Charkessian Republic**, Teberda Nature Reserve, left slope of Ullu-Murudzu River Valley, Goluboe Lake, *Ignatov & Ignatova #05-3902* (MW); **Kabardino-Balkarian Republic**, Balkaria, Terskol Ridge, 29.VIII.2004, *Korotkov s.n.* (MW); **North Ossietian (Alania) Republic**, North-Ossetian Nature Reserve, upper course of Tsej River, 25.VII.1977, *Abramova s.n.* (MW). **Chukotka**, Anadyr Distict, upper course of Tanyurer River, Televeem Creek, 23.VII.1979 *Afonina s.n.* (LE).

? North America, U.S.A., California, Lake Co., Mendocino National Forest, *Toren #9500b* (duplicate in MW).

***Schistidium flaccidum* group**

Schistidium flaccidum (De Not.) Ochyra up to recent time was considered as a species easiest for identification due to combination of small plant size, flattened hyaline hair-point, short cup-like capsule with flat and very shortly beaked operculum, plicate perichaetial leaves and reduced peristome. The latter character sometimes was considered as the most important and used in keys, although Blom (1996) noted the variation in degree of reduction from complete to only weak, so teeth occasionally reaching 220 μm long.

During our study among the plants with reduced peristome were found a number of plants with rather long beak; another group of plants from Caucasus had bistratose and slightly mamillose to papillose leaf. Molecular data also show heterogenity in *S. flaccidum* s.l., which is resolved in four clades (Figs. 1-2), each characterized by a combination of morphological characters. *Schistidium flaccidum* s. str. is represented in the analysis by three specimens, among which two from Caucasus have peristome longer than 100 μm, while Austrian plant has peristome almost totally lacking, almost unseen above the mouth. However, these specimens have no difference in ITS. One more specimen from Austria with a well developed peristome and larger plant size, but flat operculum (cf. *flaccidum*) was found somewhat outside. This taxon needs further studies.

Three other clades represent species never recognized before, and therefore described here as new species: *S. succulentum, S. tenuinerve, S. bakalinii*.

Schistidium succulentum Ignatova & H.H.Blom sp. nov. Fig. 17-18.

Species haec capsula a S. subconferto similis, sed folia partim bistratosa et interdum papillosa, foliis perichaetialibus non plicatis et apici angusto differt.

Type: Russia, Karachaevo-Cherkessian Republic, Teberda Nature Reserve, Khatipara Range northern spour, 2850 m a.s.l., NW-facing rock outcrops, on open rock surface, Ignatov & Ignatova 05-3150 (holotype MW).

Plants small, in loose or dense tufts, dull, green or olivaceus-green at uppermost shoot tips, brownish below. Stems 7-10 mm, repeatedly branched, central strand narrow, occasionally weakly differentiated. Leaves slightly incurved and appressed when dry, erecto-patent when moist, occasionally spirally ranked, ovate-lanceolate with narrow acumens, subobtuse at apex, sharply keeled in upper part, 1.0-1.5×0.3-0.4 mm, with length/width ratio 2.4-2.8; hyaline hair-point absent; margins recurved almost throughout on one side, plane at base and recurved to shortly below leaf apex at the other side, or equally recurved from shortly above base to apex on both sides, 2-3-stratose in 2-3 rows in upper part, smooth or occasionally papillose-crenulate distally; costa strongly projecting dorsally, 2-3-layered, often flattened dorsally, trapezoid or rarely semicircular in transverse section, smooth or papillose; lamina unistratose, with bistratose strips or completely bistratose distally, occasionally with few 3-stratose spots, smooth or slightly to moderately papillose; upper lamina cells irregular in shape and size, round-oval or irregularly angular, 6-8 (10) μm, thick-walled, not or slightly sinuose; median cells subquadrate to short rectangular, 10-16×10-12 μm; thick-walled, sinuose; basal cells clearly differentiated, translucent, light brownish, rectangular, 15-25×8-12 μm, with moderately thickened, straight, non-porose walls; basal marginal cells not differentiated or slightly shorter, with equally thickened walls or with more

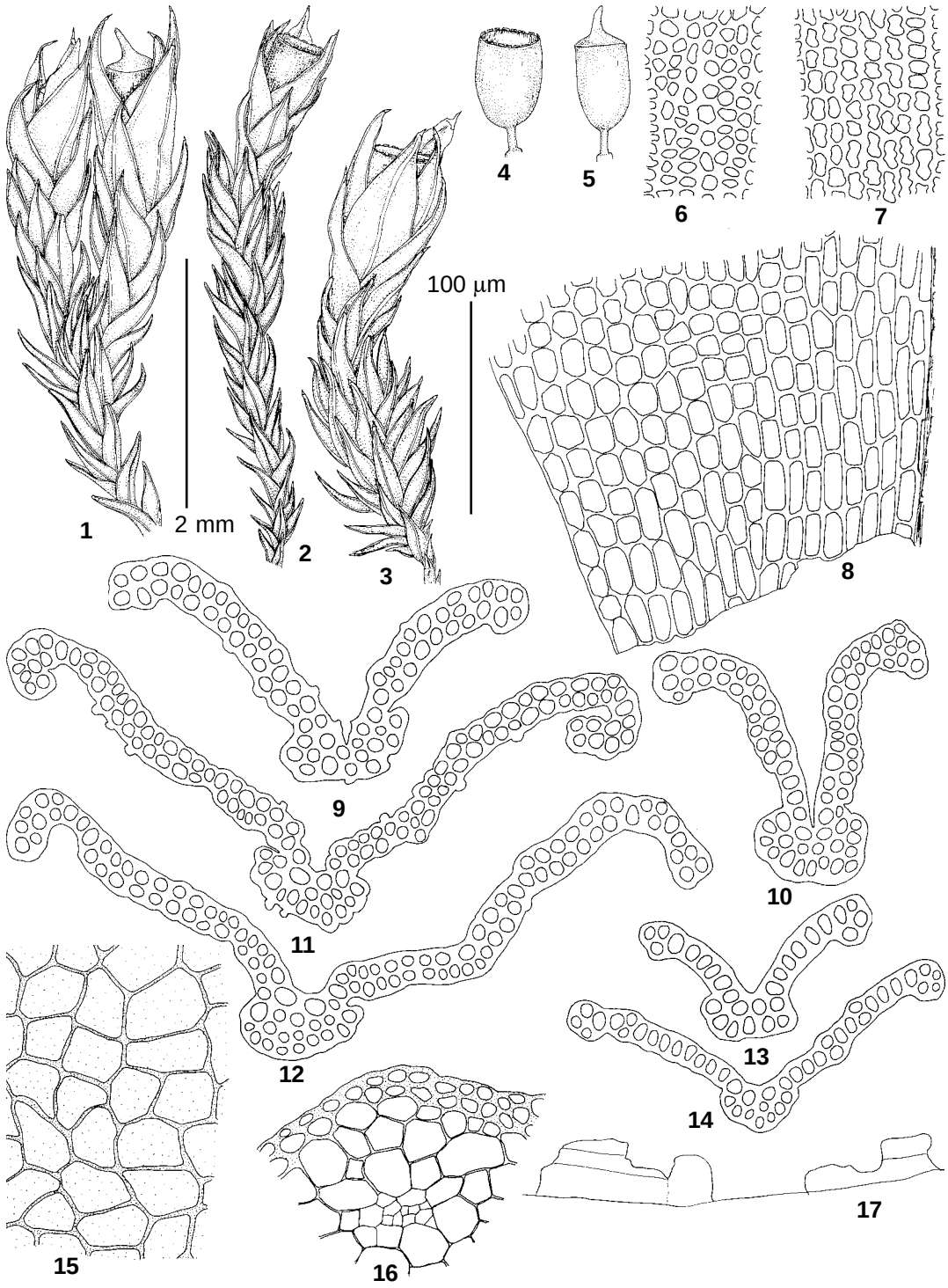


Fig. 17. *Schistidium succulentum* sp. nov. (from Russia, Teberda Reserve, *Ignatov & Ignatova,* MW: 1-2, 6-9, 12, 15-16 – *#05-3057*; 3-5, 13, 14, 17 – *#05-3208*; 10-11 – *Zolotov #05-3612*). 1-3 – habit, dry; 4-5 – capsules; 6 – upper lamina cells; 7 – median lamina cells; 8 – basal leaf cells; 9-14 – leaf transverse sections; 15 – exothecial cells; 16 – stem transverse section; 17 – perisrome. Scale bars: 2 mm for 1-5; 100 μm for 6-17.

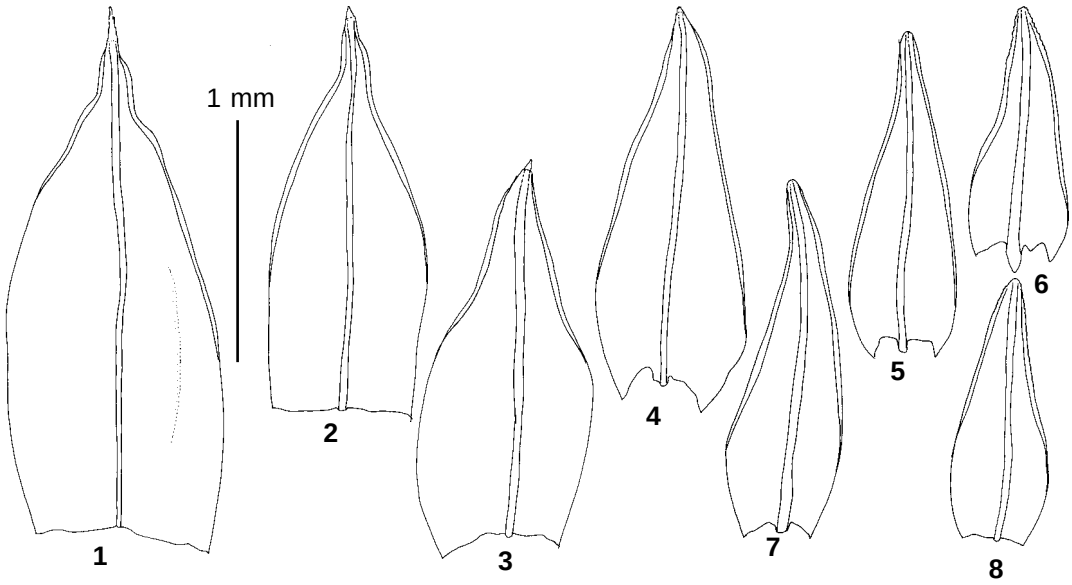


Fig. 18. *Schistidium succulentum* sp. nov. (from Russia, Teberda Reserve, MW: 1-2, 4-5, 7 – *Ignatov & Ignatova #05-3057*; 3, 6, 8 – *Zolotov #05-3612*). 1-3 – perichaetial leaves; 4-8 – stem leaves. Scale bars: 1 mm for 1-8.

thickened transverse walls. Subperichaetial leaves to 1.7×0.6 mm, with very short hyaline apiculus. Perichaetial leaves oblong, suddenly narrowed into short and narrow apiculus, 1.6-2.2×0.7-0.9 mm, with short and narrow, non-decurrent, terete hyaline hair-point to 0.2 mm long, with distant blunt spinulae. Urn light brown, oblong-cylindrical or ovoid when open, 0.8-1.0×0.55-0.65 mm, length/width ratio 1.5-1.7; exothecial cells predominantly subquadrate and transversely rectangular, thin-walled, stomata at base of urn; peristome teeth strongly reduced, 25-30 μm long, truncate, finely papillose or striolate-papillose. Operculum low conic, with long and narrow, straight or slightly oblique beak ca. 0.25 mm long. Spores 10-12 μm, finely papillose.

Differentiation. *Schistidium succulentum* differs from *S. flaccidum* in both gametophyte and sporophyte characters: 1) partially or totaly bistratose and occasionally papillose leaf lamina vs. usually unistratose and smooth one; 2) blunt apices of stem leaves without hair-point vs. acute ones, usually with hair-point; 3) hyaline hair-points of perichaetial leaves stiff, terete, narrow, to 0.2 mm vs. weak, flattened and broad, to 1.0 mm; 4) perichaetial leaves non-plicate vs. usually plicate; 5) urn cylindrical, with length/width ratio 1.5-1.7 vs. hemisphaerical or cyatiform, with length/width ratio 0.9-1.3; 6) operculum rostrate vs. mamillate. In sporophyte characters it is most similar to *S. subconfertum* (Broth.) Deguchi, which also has an oblong-cylindrical urn and operculum with long beak. However, leaf lamina of the latter species is unistratose except margins which are bistratose in one row, and always smooth, while it is partially or predominantly bistratose and often papillose in *S. succulentum*; furthermore, the perichaetial leaves of *S. subconfertum* are usually obtuse at apex, whereas they end in a short apiculus with a narrow hair-point in S. *succulentum*. The Antarctic *S. lewis-smithii* Ochyra is quite similar to *S. succulentum* in sporophytic characters including a vestigal peristome, but can be readily distinguished by its plane leaf margins. *Schistidium cryptocarpum* Mogensen & H.H. Blom, another species with strongly reduced peristome, is readily differentiated by its cyatiform urn and unistratose leaf lamina.

Variation. Leaf lamina of Caucasian specimens is variously bistratose, most common with numerous bistratose strips and patches, more rarely completely bistratose and with few 3-stratose patches, and very rarely predominantly unistratose with few bistratose strips. The papillosity of leaf lamina is also variable: usually it is moderately papillose, but occasionally papillae are more numerous or rarely

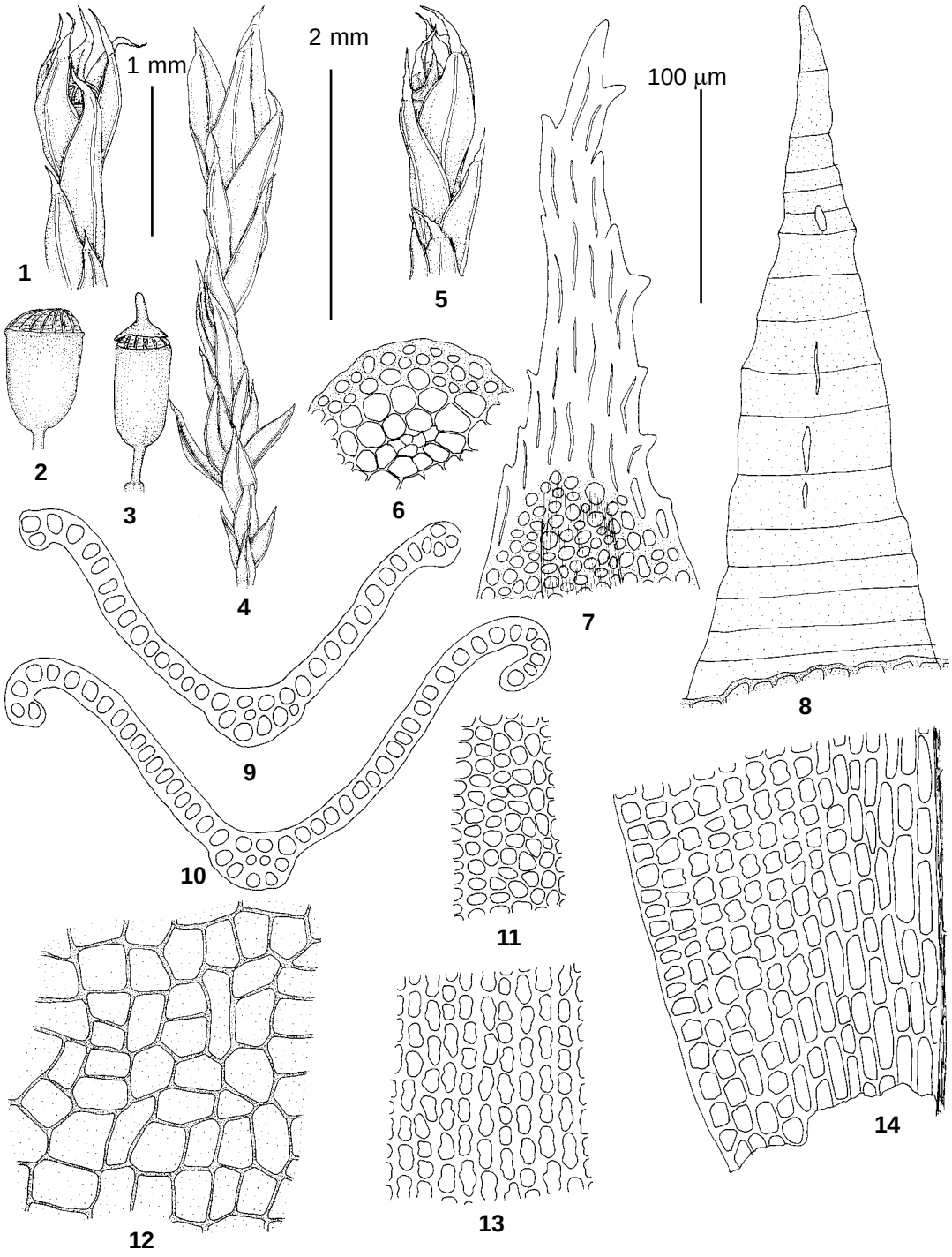


Fig. 19. *Schistidium teninerve* sp. nov. (from Russia, Sakhalin, *Pisarenko #03275,* MW). 1, 5 – perichaetia; 2-3 – capsules; 4 – habit, dry; 6 – stem transverse section; 7 – hyaline hair-point; 8 – peristome tooth; 9-10 – leaf transverse sections; 11 – upper lamina cells; 12 – exothecial cells; 13 – median lamina cells; 14 – basal leaf cells. Scale bars: 2 mm for 4; 1 mm for 1-3, 5; 100 μm for 6-14.

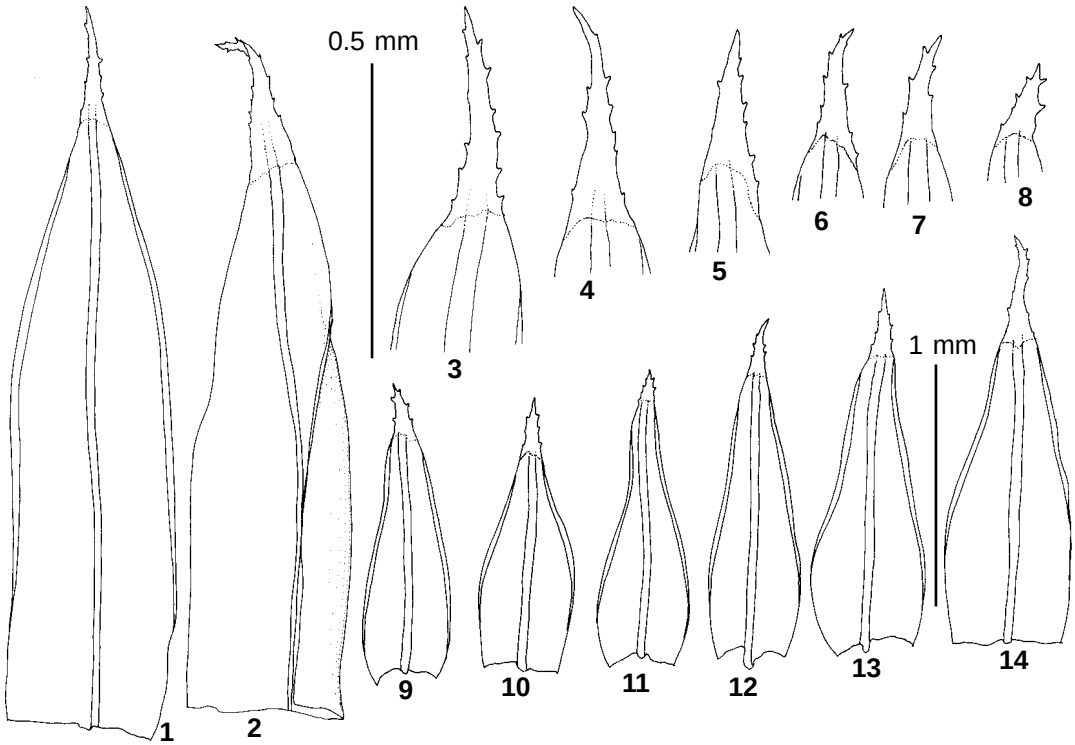


Fig. 20. *Schistidium tenuinerve* sp. nov. (from Russia, Sakhalin, *Pisarenko #03275,* MW). 1-2 – perichaetial leaves; 3-8 – hair-points; 9-14 – stem leaves. Scale bars: 1 mm for 1-2, 9-14; 0.5 mm for 3-8.

completely lacking. Distal leaf margins are smooth or slightly papillose-crenulate in stem leaves and often weakly denticulate or papillose-crenulate in perichaetial and subperichaetial leaves.

Ecology and distribution. In the Caucasus, *Schistidium succulentum* grows in the alpine belt, at 2650-3000 m a.s.l., mostly on N-facing slopes, on rock outcrops of granite and schists near ridge tops and in alpine meadows, both on rock surfaces and in small crevices. It is locally not rare in Teberda Nature Reserve where bryophyte flora is rather well-explored; one distant locality is known in the north of Asiatic Russia, in Anabar Plateau.

Specimens examined: EUROPEAN RUSSIA: Caucasus, **Karachaevo-Cherkessian Republic**, Teberda Nature Reserve: Khatipara Range northern spour, *Ignatov & Ignatova #05-3057, 05-3208* (MW); Kyshkadzher River upper course, *Onipchenko #57/94* (MW); Goralykol River upper course, *Onipchenko #112/94* (MW); Gitche-Murudzhu gorge, *Onipchenko #183/94* (MW); Mussa-Achitara Mt., *Zolotov #05-3612* (MW). ASIATIC RUSSIA: **Krasnoyarsk Territory**, Taimyrsky District, Anabar Plateau, *Fedosov #7-2-47* (MW).

Schistidium tenuinerve Ignatova & H.H.Blom sp. nov. Figs. 19-20.

A S. flaccidum similis, sed theca cylindrica, operculo longirostro et dentibus peristomo longiore differt.

Type: Russia, Sakhalin Island, Makarov District, southern part of Zhdanko Range, ridge top, rock fields, 537 m a.s.l., 29.VIII.2009, Pisarenko #03275 (holotype MW, isotype MHA).

Plants small, in dense or loose tufts, slightly glossy, yellowish-green or olivaceous-green in upper part, brownish below. Stems 4-10 mm, slightly to moderately branched, with narrow or indistinct central strand. Leaves appressed when dry, erecto-patent when moist, ovate-lanceolate, widely and obtusely keeled in upper part, 0.8-1.4×0.3-0.5 mm, with length/width ratio 2.3-2.8, hyaline hair-point 0.1-0.4 mm, present in most leaves, weak and flattened, not or shortly decurrent, distantly and finely denticulate with short, but sometimes recurved teeth; margins recurved from above the base to near the apex, 2-stratose in 1-2 rows, smooth; costa narrow, weakly projecting dorsally, 2-3-layered distally, semicircu-

lar in transverse section, smooth; lamina unistratose, smooth; upper lamina cells round, oval and transversely oval, 5-8 μm wide, moderately thick-walled, not sinuose; median cells short rectangular, 8-15×8-10 μm; thick-walled, moderately sinuose; basal cells rectangular, 12-30×8-10 μm, with moderately thickened, straight, non-porose walls; basal marginal cells in 4-7 rows subquadrate and short-rectangular, with more thickened transverse walls. Perichaetial leaves much larger than stem leaves, with oblong base and short to long triangular acumen, 2.0-2.4×0.7-0.8 mm, hyaline hair-point to 0.5 mm, denticulate as in stem leaves. Urn light orange brown, short-cylindrical, ca. 0.6-0.8×0.5-0.6 mm, length/width ratio 1.2-1.4; exothecial cells predominantly subquadrate and transversely rectangular, with admixture of rectangular cells, thin-walled, stomata at base of urn; peristome teeth reddish brown, straight, recurved when old, ca. 250 μm, with few longitudinal perforations, finely striolate-papillose throughout. Operculum low conic, with straight beak ca. 0.2 mm long. Spores 10-12 μm, smooth.

Differentiation. *Schistidium tenuinerve* is similar to *S. flaccidum* in gametophyte characters, such as leaf size and shape, unistratose leaf lamina, thick-walled and moderately sinuose median lamina cells, and weak and flattened, slightly denticulate hair-points. The differences between these species include: 1) costa weakly projecting dorsally vs. strongly projecting in distal part of leaf; 2) non-plicate vs. distinctly plicate perichaetial leaves; 3) operculum with long straight beak vs. with very short and obtuse rostrum; 4) normally developed, narrow triangular peristome teeth vs. vestigal or irregular shaped teeth.

Schistidium venetum H.H. Blom shares with *S. tenuinerve* the dorsally weakly projecting costa and the weak and flattened, slightly denticulate hair-points. However, it is readily separated by predominantly bistratose leaf lamina, mostly rectangular exothecial cells and longer (300-440 μm vs. ca. 250 μm), more strongly perforated peristome teeth.

The thick-walled and distinctly sinuose median lamina cells and the oblong, smooth basal leaf cells of *S. tenuinerve* indicate an affinity to *S. obscurum*. However, the latter species has usually narrow, terete hair-points vs. weak and flattened ones of *S. tenuinerve*.

Variation. In few studied specimens of *S. tenuinerve* the hyaline hair-points show some variation with regard to denticulation: within one tuft leaves both with weakly denticulate and more strongly denticulate hair-points with larger teeth can be found; however, finely denticulate hair-points are more common.

Ecology and distribution. The species grows in alpine belt in the mountains and in treeless area of rocky plateaus, at altitude 380-2000 m a.s.l., on dry rock surface and on fine soil in rock crevices. It is sporadically distributed in Asiatic Russia, from Anabar Plateau in its northern part to southern Siberia (Irkutsk Province and Altai); several localities are known in Kamchatka and Commander Islands.

Other specimens examined: ASIATIC RUSSIA: **Krasnoyarsk Territory**, Taimyrsky Municipal District, northern edge of Anabar Plateau, near Fomich River mouth, S-facing slope of plateau, *Fedosov #08-466* (MW). **Irkutsk Province**, NE Baikal, Bolsodej Bay, mountain tundra, 800 m a.s.l., 28.VIII.1957, *Bardunov s.n.* (IRK, MW). **Altai Republic**, Karakem River basin, Kobiguayuk Creek, 2000 m a.s.l., *Ignatov #0/953* (MHA). **Kamchatskaya Province**: Khodutka, 24.VII.2002, *Czernyadjeva #23* (LE); Bystraya River basin, 10.VIII.2005, *Czernyadjeva #29* (LE); Mil'kovsky Dist., Kostina Mt., *Fedosov #10-4-6, 10-4-11* (MW); Aleutsky Distr., Bering Island, *Fedosov #10-3-375, 10-3-573, 10-3-1015* (MW).

Schistidium bakalinii Ignatova & H.H.Blom sp. nov. Figs. 21-22.

Folia unistratose, paries celluli mediocre foliorum incrassatis et flexuosis, pilum hyalinum complanatum, pauce serrulatum, longissimus, ad 1.2 mm longa, dentes peristomii irregularis, truncatis, 200-230 μm longa, operculum rostratum, rostrum strictum.

Type: Russia, Kuril Islands, Shikotan Island, northern slope of Ploskaya Mt., 200 m a.s.l., 28.VIII.2007, Bakalin #K-49-7-07 (holotype MHA, isotypes MW, LE).

Ethymology: in honor of Vadim A. Bakalin, bryologist from Russia.

Plants small, in dense tufts, slightly glossy, hoary, green or olivaceous-green in upper part, brownish or blackish below. Stems 4-8 mm, slightly to moderately branched, with well-developed central strand. Leaves appressed when dry, erecto-patent when moist, narrowly ovate-

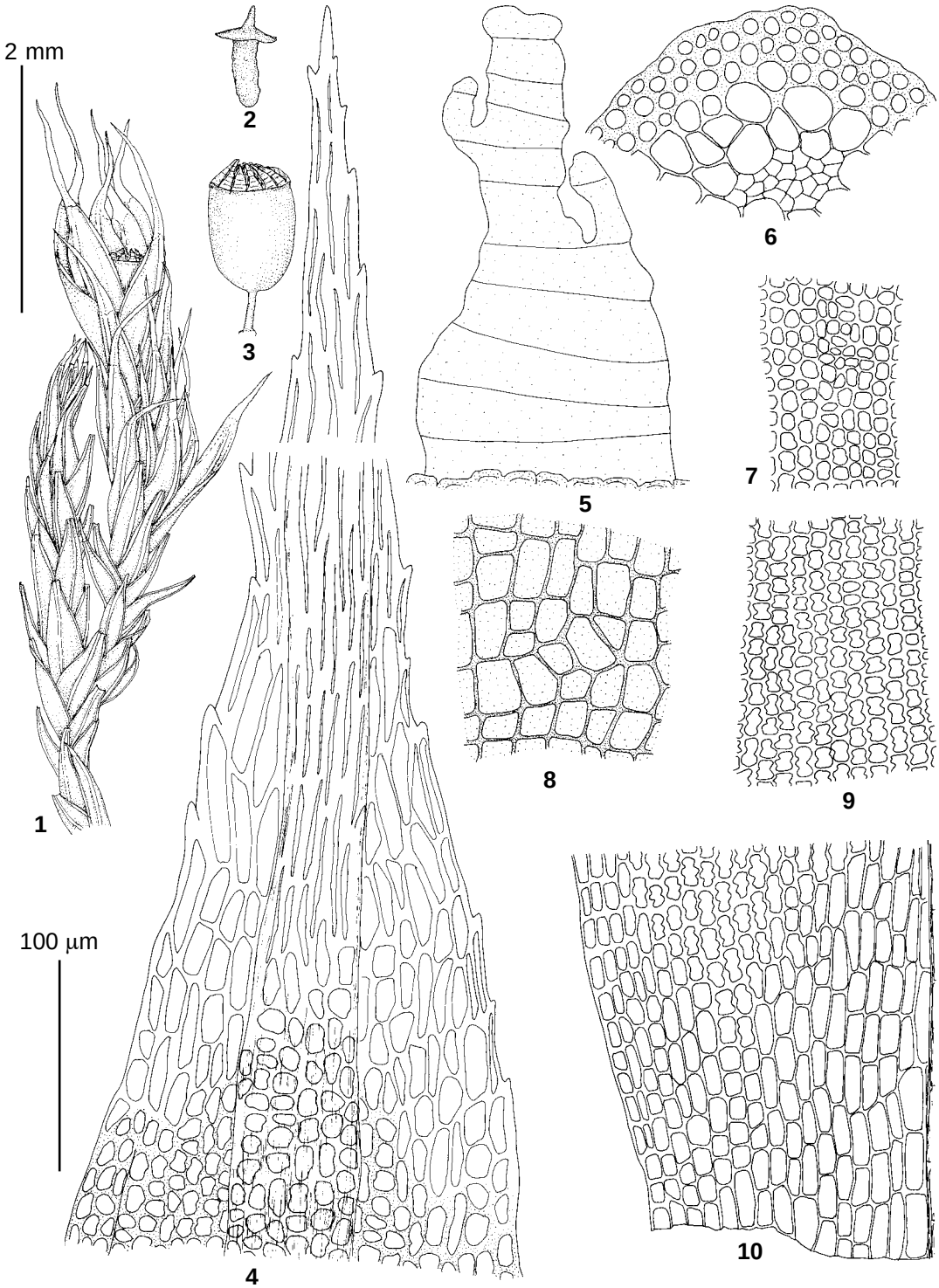


Fig. 21. *Schistidium bakalinii* sp. nov. (from Russia, Kuril Islands, Shikotan, *Bakalin #K-49-7-07,* MW). 1 – habit, dry; 2 – operculum; 3 – capsule; 4 – hair-point; 5 – peristome tooth; 6 – stem transverse section; 7 – upper lamina cells; 8 – exothecial cells; 9 – median lamina cells; 10 – basal leaf cells. Scale bars: 2 mm for 1-3; 100 μm for 4-10.

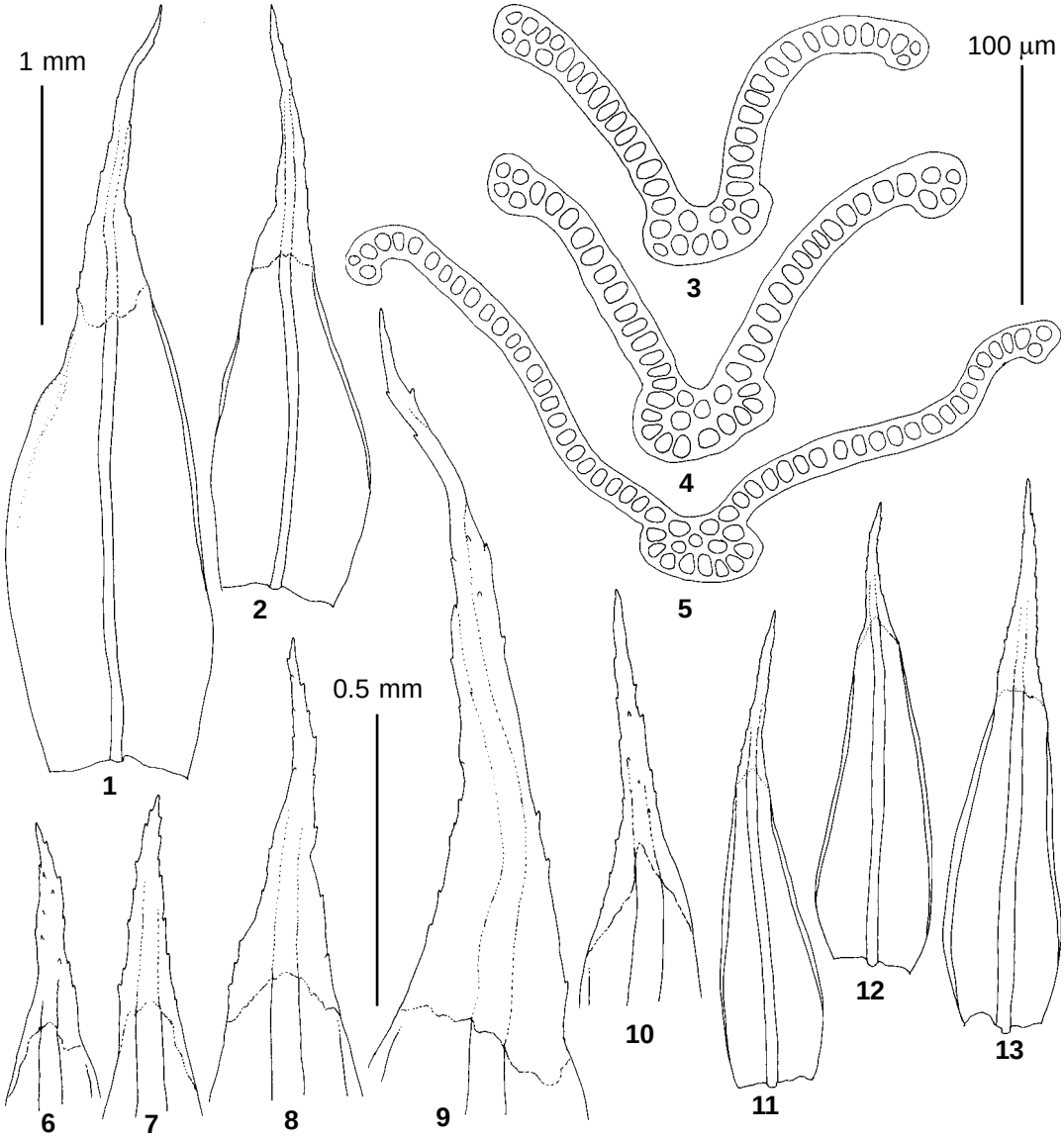


Fig. 22. *Schistidium bakalinii* sp. nov. (from Russia, Kuril Islands, Shikotan, *Bakalin #K-49-7-07,* MW). 1-2 – perichaetial leaves; 3-5 – leaf transverse sections; 6-10 – hair-points; 11-13 – stem leaves. Scale bars: 1 mm for 1-2, 11-13; 0.5 mm for 6-10; 100 μm for 3-5.

lanceolate, sharply keeled in upper part, 1.0-1.3×0.35-0.5 mm, with length/width ratio (2.3-) 2.6-3.4, hyaline hair-point 0.1-0.7 mm, present in most leaves, flattened, but rather stiff due to thickened central part formed by excurrent costa, straight when dry, not or moderately decurrent, with lower part formed by cells with wide lumen and clearly visible walls, distantly and finely denticulate; margins ± widely recurved from above the base to near the apex, 2-stratose in 1-2(-3) rows, smooth; costa strong, strongly projecting dorsally, 2-3-layered distally, flattened, ovate or trapezoid in transverse section, smooth; lamina unistratose, smooth; upper lamina cells round-oval and transversely oval, 5-8 μm wide, moderately thick-walled, not sinuose; median cells short rectangular, 8-15×8-10 μm; thick-walled, moderately to strongly sinuose; basal cells

yellowish brown, well differentiated, rectangular, 15-30×10-12 μm, with ± thin, straight, non-porose walls; basal marginal cells in 3-7 rows subquadrate and short-rectangular, with more thickened transverse walls, occasionally sinuose cells almost reaching leaf base at margins. Perichaetial leaves much larger than stem leaves, oblong, 1.8-2.0×0.7-0.8 mm, hyaline hair-point to 1.2 mm, wide at base, embracing parts of the upper lamina, mostly not decurrent, with thickened central part (continuing costa) coming high up. Urn light orange-brown, short-cylindrical, 0.9-1.0×0.8-0.9 mm, length/width ratio 1.0-1.2; exothecial cells predominantly subquadrate, with admixture of rectangular cells, thin-walled, stomata at base of urn; peristome teeth orange, straight, recurved when old, 200-230 μm, not perforated, irregular in shape, often truncate, finely striolate-papillose. Operculum low conic, with straight beak ca. 0.2 mm long. Spores 10-15 μm, finely papillose.

Differentiation. The very long, flattened hair-points which are embracing a part of the upper lamina are reminiscence of *S. bryhnii* Hag., a local endemic of Norway. It differs from *S. bakalinii* in widely ovate-lanceolate leaves with length/width ratio ca. 1.9-2.5 (vs. 2.6-3.4) and weaker hair-points which are strongly flexuose when dry (vs. stiff ones, ± straight when dry), oblong-cylindrical urns with length/width ratio 1-7-2.4 (vs. 1.0-1.2), and longer peristome teeth, 330-420 μm (vs. 200-230 μm).

Flat and weakly denticulate hair-points and sinuose median lamina cells are also shared by *S. bakalinii* and *S. tenuinerve*; their close relationship is supported also by ITS sequences. However, the latter species never has such long hair-points in the perichaetial leaves, reaching only 0.5 mm (vs. 1.2 mm); its costa is weaker and only slightly projecting dorsally; the urns are more elongate, with length/width ratio 1.2-1.4 (vs. 1.0-1.2); and peristome teeth are narrow triangular (vs. irregular in shape).

Schistidium bakalinii readily differs from *S. obscurum* in long and flat hair-points (vs. comparatively short, narrow, terete ones).

Ecology and distribution. The species was collected on forested N-facing slope, at 200 m a.s.l., in crevices of tufa cliff.

Schistidium bakalinii is only known from a single collection.

Schistidium abrupticostatum (Bryhn) Ignatova & H.H. Blom comb. nov. — *Schistidium apocarpum* var. *abrupticostatum* Bryhn, Rep. 2. Norw. Arct. Exp. Fram 2(11): 64. 1907.

Among others, the present analysis found *S. platyphyllum* and *S. platyphyllum* subsp. *abrupticostatum* in a fairly distant places: the former being sister to *S. grandirete* in a clade with PP=0.99 (Fig. 2) within the basal grade, while the latter was found within the terminal clade (PP=0.98, cf. Fig. 2), and in it in a basal position to Apocarpum-clade, although without high support. The taxa are similar in sporophyte structure, leaf areolation, poor development of hair-point, structure of costa transverse section, and leaf margins recurved almost to the apex. However, the leaves are widely triangular in the former (vs. narrowly triangular, «*Didymodon*-like» in the latter), margins bistratose (vs. often unistratose at places); plants dark green, blackish or yellow-olivaceous, rarely reddish (vs. often reddish or ferrugineous). In addition, these taxa have different distributions: *S. platyphyllum* is a widespread species, while *S. platyphyllum* subsp. *abrupticostatum* is restricted to the Arctic and Subarctic. These differences indicate the species status of the latter.

KEY TO IDENTIFICATION OF THE GENUS SCHISTIDIUM IN RUSSIA

1. Dioicous, sporophytes very rare; plants very small, shoots filiform, julaceous; hair-points coarsely spinulose; upper lamina partly bistratose ..... *S. tenerum*
— Autoicous; combination of characters different 2
2. Leaves stiff, lanceolate; costa usually with 1-2 stereid bands and often with guide cells in transverse section 3
— Leaves soft, not lanceolate (except *S. agassizii*); costa without guide cells and stereid bands 4
3. Leaf margins recurved; lamina often partly bistratose distally, occasionally mamillose and/or papillose; costa percurrent or excurrent as a short hyaline tip, with guide cells and often with 2 stereid bands; in the spray zone on sea shores ..... *S. maritimum*
— Leaf margins plane; lamina unistratose,

smooth; costa excurrent as a fleshy multistratose apiculus; along water courses .... *S. frahmianum*

4. Upper leaf lamina papillose on dorsal side 5
— Upper leaf lamina smooth on dorsal side (but leaf margins and dorsal side of costa may be papillose) 10
5. Upper leaf lamina with bistratose patches or striae or predominantly bistratose; central strand distinct 6
— Upper leaf lamina unistratose; central strand absent or indistinct 8
6. Peristome strongly reduced, <50 μm long . ..... *S. succulentum*
— Peristome perfect, >250 μm long 7
7. Upper and central leaf cells 6-9 μm wide, round and oval, esinuose or slightly sinuose; hair-points stiff ..... *S. pruinosum*
— Upper and central leaf cells 8-11 μm wide, oblong at least in central part, sinuose; hair-points weak ..... *S. confusum*

8(5). Hair-points papillose dorsally in lower part, coarsely spinulose; papillae on lamina broad ..... *S. frisvollianum*
— Hair-points not papillose dorsally, finely and distantly spinulose-denticulate; papillae on lamina not very broad 9
9. Leaf cells with strongly sinuose, dark reddish walls; plants mostly dull black, leaf lamina without reddish patches; peristome teeth 220-330 μm ..... *S. boreale*
— Leaf cells with moderately sinuose, not dark reddish walls; plants olivaceous or reddish, leaf lamina often with reddish patches; peristome teeth 220-500 μm ..... *S. papillosum*

10(4). Costa excurrent as an yellowish chlorophyllose awn 11
— Costa ending well below apex, percurrent or excurrent as an hyaline hair-point 12
11. Awns finely denticulate, often recurved when dry; upper leaf cells isodiametric and transversely oval; median leaf cells slightly sinuose ..... *S. sibiricum*
— Awns sharply denticulate, straight when dry; upper leaf cells short rectangular; median leaf cells ± strongly sinuose ..... *S. canadense*
12. Plants robust, dark reddish or black, in extensive tufts or mats on soil in arctic tundra and fens 13
— Plants medium-sized or small, rarely robust, various in color, growing mostly on rocks 14
13. Costa strongly projecting dorsally, 3-5-stratose in mid-leaf; upper leaf cells subquadrate, not sinuose; cell walls not dark reddish ..... *S. holmenianum*
— Costa weakly projecting dorsally, 2(-3)-stratose in mid-leaf; upper leaf cells rectangular, sinuose; cell walls dark reddish .... *S. andreaeopsis*
14. Peristome rudimentary, less than 150 μm 15
— Peristome perfect, more than 200 μm 18
15. Apex of stem leaves obtuse or rounded, occasionally with stiff, very short and narrow hyaline apiculus; lamina partly bistratose 16
— Apex of stem leaves acute, with weak and flattened hyaline hair-point; lamina unistratose 17
16. Plants jet-black; leaf margins plane distally; urns short-cylindrical; exothecial cells predominantly oblong in central and lower part of urn ..... *S. atrofuscum*
— Plants dark green; leaf margins recurved to shortly below leaf apex; urns cylindrical; exothecial cells predominantly isodiametric and transversely rectangular in lower part of urn ..... *S. succulentum*
17. Leaf margins unistratose; leaf cells with strongly thickened walls; perichaetial leaves not plicate; operculum with long beak .... *S. cryptocarpum*
— Leaf margins bistratose; leaf cells with moderately thickened walls; perichaetial leaves plicate; operculum with very short beak .... *S. flaccidum*

18(14). Capsule length/width ratio 0.8-1.3, urns short cylindrical or cupulate 19
— Capsule length/width ratio > 1.3, urns oblong cylindrical 32
19. Exothecial cells incrassate, irregularly angular; hair-points absent 20

— Exothecial cells thin-walled, subquadrate or rectangular; hair-points usually present .. 22

20. Leaves linear-lanceolate or lingulate, weakly keeled distally ..... *S. agassizii*
— Leaves ovate-lanceolate or ovate, sharply keeled distally 21

21. Plants robust; leaves acute at apex; margins distantly denticulate at upper part, bistratose, recurved in lower1/2–3/4 or to near the apex; lamina often with bistratose patches ..... *S. rivulare*
— Plants slender; leaves rounded at apex; margins smooth, unistratose, recurved to near the apex; lamina unistratose ..... *S. sordidum*

22(19). Hair-points wide and distinctly flattened 23
— Hair-points coarse, narrow or widened at base 26

23. Operculum with very short beak; perichaetial leaves plicate ..... *S. flaccidum*
— Operculum with long beak; perichaetial leaves not distinctly plicate 24

24. Hair-points with strong and sharp, often recurved teeth ..... *S. confertum*
— Hair-points finely denticulate or denticulate-spinulose, with blunt spinulae 25

25. Hair-points very long, to 1.2 mm in perichaetial leaves, embracing a part of lamina; costa strongly projecting dorsally, trapezoid in transverse section ..... *S. bakalinii*
— Hair-points moderately long, to 0.5 mm in perichaetial leaves, not embracing a part of lamina; costa weakly projecting dorsally, semicircular in transverse section ..... *S. tenuinerve*

26(22). Spores 15-25 μm 27
— Spores 8-13 μm 29

27. Costa papillose dorsally; upper leaf cells 11-14 μm wide; exothecial cells predominantly isodiametric and transversely rectangular . ..... *S. grandirete*
— Costa smooth dorsally; upper leaf cells 8-11 μm wide; exothecial cells predominantly oblong 28

28. Leaves widely triangular, 1.4-2.3×0.5-1.0 mm; margins bistratose; plants dark green, blackish or yellow-olivaceous, rarely reddish ..... *S. platyphyllum*
— Leaves narrowly triangular (*Didymodon*-like), 1.4-2.0×0.5-0.8 mm; margins often with unistratose patches; plants often reddish or ferrugineous ..... *S. abrupticostatum*

29(26). Exothecial cells predominantly oblong in central and lower part of urn .... *S. submuticum* subsp. *arcticum*
— Exothecial cells predominantly isodiametric and transversely rectangular in central and lower part of urn 30

30. Hair-points long and narrow, with distant, sharp, often recurved teeth; costa semicircular in transverse section ..... *S. liliputanum*
— Hair-points short, finely denticulate, occasionally absent; costa often trapezoid or irregular in outline in transverse section ... 31

31. Plants small; stem central strand distinct; upper leaf margins smooth; costa trapezoid in transverse section, smooth dorsally .... *S. umbrosum*
— Plants medium-sized; stem central strand indistinct; upper leaf margins denticulate; costa irregular in transverse section, usually papillose dorsally ..... *S. konoi*[1]

32(18). Upper leaf margins denticulate or papillose-crenulate distally 33
— Upper leaf margins smooth 40

33. Exothecial cells predominantly oblong in central and lower part of urn 34
— Exothecial cells predominantly isodiametric and transversely rectangular in central and lower part of urn 36

34. Lamina partially bistratose distally .... *S. crassipilum*
— Lamina unistratose 35

35. Leaf margins recurved to near the apex, coarsely papillose-denticulate in upper part of leaf; alar region not differentiated .... *S. crenatum*
— Leaf margins plane distally, finely denticulate in upper part of leaf; basal marginal cells in 5-7 rows enlargered, wider than upper cells, forming an alar group .... *S. relictum* (provisional name)

---

[1]**Schistidium konoi** (Broth.) Ignatova & H.H. Blom, comb. nov. — *Grimmia konoi* Broth, Bot. Mag. (Tokyo) 20: (79). 1906.

36(33). Peristome teeth narrowly acuminate, erect, with incurved apices, forming a dome; columella persistent 37
— Peristome teeth acute, erectopatent, not forming a dome; columella falling with the operculum 38

37. Plants jet-black; urn length/width ratio 1.3-2.1; shoots straight ..... *S. trichodon* var. *trichodon*
— Plants olivaceous or brownish; urn length/width ratio 1.6-2.4; shoots arcuate, secund ..... *S. trichodon* var. *nutans*

38. Upper leaf margins strongly and irregularly denticulate to dentate; costal papillae tall .. .. *S. lancifolium*
— Upper leaf margins finely denticulate; costal papillae low or tall 39

39. Plants usually robust, olivaceous or brownish, without rusty color; hair-points flexuose, finely spinulose-denticulate, 0-0.8 mm; costa semicircular in transverse section, with scattered low papillae on dorsal side .... *S. apocarpum*
— Plants medium-sized, brownish, often with rusty color; hair-points stiff, rather strongly spinulose, 0-0.3 mm; costa irregular in transverse section, distinctly papillose dorsally, papillae often tall ..... *S. konoi*

40(32). Leaf margins recurved to near the apex 41
— Margins plane in distal 1/5–1/2 leaf length 57

41. Hair-points broad and distinctly flattened 42
— Hair-points narrow, not flattened, occasionally widened at base 47

42. Basal leaf cells thin-walled, oblong and smooth, sharply delimited from thick-walled and strongly sinuose median leaf cells; basal marginal cells forming a hyaline border .... *S. frigidum*
— Basal leaf cells not sharply delimited from median leaf cells; basal marginal cells not forming a hyaline border 43

43. Hair-points finely denticulate 44
— Hair-points strongly denticulate or spinulose 46

44. Leaves 0.8-1.4×0.3-0.5 mm; hair-points 0.1-0.5 mm; costa weakly projecting dorsally ... . *S. tenuinerve*
— Leaves 1.5-2.5×0.4-0.7 mm; hair-points 0-0.65 mm; costa strongly projecting dorsally 45

45. Exothecial cells predominantly isodiametric and transversely rectangular in central and lower part of urn; median leaf cells strongly sinuose ..... *S. flexipile*
— Exothecial cells predominantly oblong in central and lower part of urn; median leaf cells weakly sinuose ..... *S. scandicum*

46(43). Leaf margins broadly recurved; hair-ponts up to 0.3 mm, with wide teeth; median leaf cells strongly sinuose; costa semicircular in transverse section ..... *S. recurvum*
— Leaf margins narrowly recurved; hair-points variable in length, in upper leaves occasionally to 0.6 mm, with narrow finger-like spinulae; median leaf cells weakly sinuose; costa flattened, trapezoid in transverse section ..... *S. echinatum*

47(41). Exothecial cells predominantly subquadrate and transversely rectangular in central and lower part of the urn 48
— Exothecial cells predominantly oblong in central and lower part of the urn 52

48. Hair-points coarsely and densely spinulose-denticulate; costa papillose on dorsal side . ..... *S. sinensiapocarpum*
— Hair-points finely denticulate or sharply and distantly spinulose; costa smooth on dorsal side 49

49. Leaf cells thick-walled and strongly sinuose; basal leaf cells sharply delimited, oblong, thin-walled; basal marginal cells forming a hyaline border ..... *S. frigidum*
— Leaf cells with moderately thickened and variously sinuose walls; basal laminal cells not sharply delimited; basal marginal cells not forming a hyaline border 50

50. Leaf margins 2-4-stratose in 2-3 rows distally; distal lamina often with bistratose patches; median leaf cells not or weakly sinuose ..... *S. marginale* (provisional name)
— Leaf margins 2-stratose in 1 row distally; lamina usually unistratose; median leaf cells moderately to strongly sinuose 51

51. Perichaetial leaves similar to stem leaves, 0.8-1.1 mm wide at base, urns not exposed laterally; hair-points 0-0.7 mm, widened at base, decurrent; peristome teeth erectopatent to patent ..... *S. pulchrum*
— Perichaetial leaves differentiated, long and narrow, 0.5-0.6 mm wide at base, urns exposed laterally; hair-points 0-0.2 mm, narrow throughout, not decurrent; peristome teeth squarrose ..... *S. dupretii*

52(47). Perichaetial leaves long and narrow, 0.5-0.6 mm wide at base, urns exposed laterally ..... *S. dupretii*
— Perichaetial leaves wider, 0.6-1.25 mm wide at base, urns not exposed laterally 53

53. Leaf cells thick-walled and strongly sinuose; basal laminal cells sharply delimited, oblong, thin-walled; basal marginal cells forming a hyaline border 54
— Leaf cells with moderately thickened and variously sinuose walls; basal laminal cells not sharply delimited; basal marginal cells not forming a hyaline border 55

54. Plants olivaceous in upper part, medium-sized, stems up to 5 mm, leaves to 2.1 mm; cell walls light-colored, strongly thick-walled; hair-points variable in length, 0-0.8 mm ..... *S. frigidum*
— Plants jet-black or dark brown in upper part, rarely olivaceous, small, stems up to 1.5 mm, leaves to 1.3 mm; cell walls dark-colored, moderately to strongly thick-walled; hair-points short, 0-0.3 mm ..... *S. obscurum*

55. Upper leaves of fertile shoots appressed, subsheathing; perichaetial leaves 0.75-1.25 mm wide at base; hair-points thin, denticulate ..... *S. subjulaceum*
— Upper leaves of fertile shoots erect or erectopatent, without sheathing base; perichaetial leaves 0.6-1.0 mm wide at base; hair-points coarse, strongly spinulose 56

56. Leaves 1.9-2.5 mm long; median leaf cells strongly sinuose; perichaetial leaves similar to stem leaves in shape; hair-points decurrent ..... *S. robustum*
— Leaves 1.2-1.5 mm long; median leaf cells slightly sinuose; perichaetial leaves differentiated, oblong; hair-points widened at base but not decurrent ..... *S. subflaccidum*

57(40). Leaf lamina predominantly unistratose 58
— Leaf lamina usually with bistratose patches or predominantly bistratose 59

58. Plants dull-brown; costa irregular in outline in transverse section; leaf cells with strongly thickened walls; basal marginal cells in 5-7 rows enlargered, wider than upper cells, forming an alar group; perichaetial leaves acute, costa excurrent, hair-points usually present, short ..... *S. relictum* (provisional name)
— Plants olivaceous or brownish black in upper part; costa semicircular in transverse section; leaf cells thin-walled; alar cells not differentiated; perichaetial leaves widely acute, costa percurrent, hair-points often absent ..... *S. submuticum*

59. Hair-points weak and flattened 60
— Hair-points terete 61

60. Hair-points finely denticulate; lower leaf cells arranged in oblique rows ..... *S. venetum*
— Hair-points densely spinulose; lower leaf cells not arranged in oblique rows .. *S. echinatum*

61. Leaves with ridge-like plicae, often shouldered ..... *S. brunnescens* subsp. *griseum*
— Leaves without ridge-like plicae, not shouldered 62

62. Hair-points widened at base 63
— Hair-points not widened at base 64

63. Plants small, dull brown; leaves not in spiral rows; hair-points not decurrent; peristome teeth strongly perforated to cribrose ..... *S. brunnescens* subsp. *brunnescens*
— Plants medium-sized to small, dark olivaceous or brownish; leaves occasionally in spiral rows; hair-points decurrent; peristome teeth entire or with few perforations in vertical rows ..... *S. crassipilum*

64. Leaves ovate-lanceolate, 2.2-3.0×0.5-0.8 mm; hair-points 0.3-1.0 mm, distantly spinulose-denticulate; peristome teeth entire or with few perforations ..... *S. elegantulum*
— Leaves ovate-triangular, 1.75-2.6×0.6-0.9 mm; hair-points 0-0.2 mm, densely and coarsely spinulose; peristome teeth strongly perforate to cribrose in upper part ..... *S. helveticum*

ACKNOWLEDGEMENTS

We thank Heribert Köckinger, Bruce Allen, Olga Afonina, Olga Belkina, Vadim Bakalin, David Toren and Jan Kučera for providing specimens for our study; curators of ALTA, CANM, COLO, DUKE, MICH, NFLD, MO, QFA, NY, TENN, UBC, WTU for loan of material for Blom. We are grateful to Heribert Köckinger for helpful comments and suggestions, to Vladimir Fedosov for the help with some sequences and maps, to Alexander Fedosov for the help with Bayesian analysis, and to Vladimir P. Prokhorov for the Latin diagnoses. The work of Ignatova, Goryunov and Milyutina was partially supported by RFBR grants ##09-04-01324 and 10-04-00678, Biodiversity Program of the Russian Academy of Science and by Federal program «Scientific and Educational personalities of innovative Russia 2009-2013 years» (government contracts #14.740.11.0165 & 16.740.111.0177).

LITERATURE CITED

BLOM, H.H., E.A. IGNATOVA & O.M. AFONINA 2006. New records of Schistidium (Grimmiaceae, Musci) in Russia. – *Arctoa* **15**: *187-194*.

BLOM, H.H. 1996. A revision of the Schistidium apocarpum complex in Norway and Sweden. – *Bryophyt. Biblioth.* **49**: *333 pp*.

GARDINER, A., M. IGNATOV, S. HUTTUNEN & A. TROITSKY 2005. On resurrection of the families Pseudoleskeaceae Schimp. and Pylaisiaceae Schimp. (Musci, Hypnales). – *Taxon* **54**: *651-663*.

GOLOBOFF, P. A. 1994. *NONA: A Tree Searching Program. Program and documentation*. Argentina, Tucumán, published by the author.

GORYUNOV, D.V., E.A. IGNATOVA, M.S. IGNATOV, I.A.MILYUTINA & A.V. TROITSKY 2007. Support from DNA data for a narrow species concept in Schistidium (Grimmiaceae, Musci). – *J. Bryol.* **29**: *98-103*.

GRIMS, F. 1999. Die Laubmoose Österreichs. Catologus Florae Austriae, 2 Teil, Bryophyten (Moose), Heft. 1, Musci (Laubmoose). – *Wien: Österreich. Akad. Wiss., 418 pp.*

KÖCKINGER, H., M. SUANJAK, A. SCHRIEBL & C. SCHRÖCK 2008. Die Moose Kärntens. – *Sonderreihe Natur Kärnten, Band 4. Verl. Natur. Ver. Kärnten, Klagenfurt., 320 pp.*

[MILYUTINA, I.A., D.V. GORYUNOV, M.S. IGNATOV, E.A. IGNATOVA & A.V. TROITSKY] МИЛЮТИНА И.А., Д.В. ГОРЮНОВ, М.С. ИГНАТОВ, Е.А. ИГНАТОВА, А.В. ТРОИЦКИЙ 2010. Филогения мхов рода *Schistidium* (Bryophyta, Grimmiaceae) по нуклеотидным последовательностям и вторичной структуре внутренних транскрибируемых спейсеров ядерной рДНК. – [The phylogeny of *Schistidium* (Bryophyta, Grimmiaceae) based on the primary and secondary structure of nuclear rDNA internal transcribed spacers] *Молекулярная биология* [*Molecular biology*] **44**(6): *994-1009*.

MILYUTINA I.A., E.A. IGNATOVA, D.V. GORYUNOV, M.S. IGNATOV, R. HERNANDEZ-MAQUEDA & A.V. TROITSKY 2007. Nuclear ITS data allow discriminating between the narrow and broad species concepts in Schistidium (Grimmiaceae, Musci). – *Computational phylogenetics and molecular systematics, Moscow, 16-19 November 2007: 173-176.*

MUÑOS, J., H. HESPANHOL, K. CEZÓN & A. SÉNECA 2009. Grimmia horrida (Grimmiaceae), a new species from the Iberian Peninsula. – *Bryologist* **112**(2): *325-328.*

NIXON, K.C. 1999a. *Winclada (BETA) ver. 0.9.9*. available at http://www.cladistics.com/about_winc.html.

NIXON, K.C. 1999b. The parsimony ratchet, a new method for rapid parsimony analysis. – *Cladistics* **15**: *407-414*

RONQUIST, F., & J.P. HUELSENBECK 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. – *Bioinformatics* **19**: *1572-1574*.

Appendix 1. Specimen data and Genbank accession numbers.

Species	Region as appear in trees	Specimen data	GenBank # for ITS
		Виды рода *Schistidium*	
abrupticostatum (Bryhn) Ignatova & H.H. Blom	Anabar	Russia, Anabar Plateau, Fedosov #08-218 (MW) (as *S. platyphyllum* subsp. *abrupticostatum*)	HM053930
abrupticostatum (Bryhn) Ignatova & H.H. Blom	Canada	Canada, NWT, Cornwallis, 6.VIII.1999, Daniels (MO) (as *S. platyphyllum* subsp. *abrupticostatum*)	HM053931
abrupticostatum (Bryhn) Ignatova & H.H. Blom	Murmansk	Russia, Murmansk Province, 9.VIII.2006, Ignatova s.n.(MW) (as *S. platyphyllum* subsp. *abrupticostatum*)	HM053927
abrupticostatum (Bryhn) Ignatova & H.H. Blom	Severnaya Zemlya	Russia, Severnaya Zemlya, 3.VIII.2006, Matveeva s.n.(LE) (as *S. platyphyllum* subsp. *abrupticostatum*)	HM053928

agassizii Sull. & Lesq.	Murmansk	Russia, Murmansk Province, 4.VIII.2006, Ignatova s.n. (MW)	HM053878
agassizii Sull. & Lesq.	Taimyr	Russia, Taimyr, Fedosov #67A-1-15 (MW)	HM053879
andreaeopsis (Müll. Hal.) Laz.	Anabar	Russia, Anabar Plateau, Fedosov #06-63 (MW)	HM053881
andreaeopsis (Müll. Hal.) Laz.	Canada	Canada, 25.VII.2005, Matveeva s.n. (MW ex LE)	HM053882
apocarpum (Hedw.) Bruch et al.	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3764 (MW)	DQ822033 HM031074
apocarpum (Hedw.) Bruch et al.	St.-Petersburg	Russia, St.-Petersburg, 25.X.1996, Ignatov s.n. (MHA)	DQ822034 HM031075
apocarpum (Hedw.) Bruch et al.	United Kingdom	United Kingdom, 8.IX.2004, Ignatov s.n. (MHA)	HM031076
apocarpum (Hedw.) Bruch et al.	Vologda	Russia, Vologda Province, 14.VIII.2001, Ignatov & Ignatova s.n. (MHA)	DQ822035 HM031077
atrofuscum (Schimp.) Limpr.	Austria	Austria, Köckinger #12258 (MW)	HM053886
atrofuscum (Schimp.) Limpr.	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3313 (MW)	HM053887
bakalinii Ignatova & H.H. Blom	Kuril Islands	Russia, Kuril Islands, Bakalin #K-49-7-07 (MW)	HQ890504
boreale Poelt	Altai	Russia, Altai, Ignatov #0/285 (MHA)	DQ822025 HM031060
boreale Poelt	Anabar 1	Russia, Anabar Plateau, Fedosov #06-208 (MW)	HM053888
boreale Poelt	Anabar 2	Russia, Anabar Plateau, Fedosov #06-694 (MW)	HM053889
boreale Poelt	Bashkortostan	Russia, Bashkortostan, VI-2000, Martynenko #14 (MW)	DQ822024 HM031069
boreale Poelt	Sweden	Sweden, 20.VII.990, Hedenäs & Aronsson #B1748 (S)	HM053890
canadense (Dupr.) Ignatova & H.H. Blom	Karelia	Russia, Karelia, Maksimov & Maksimova #62-339 (MW ex PTZ) (as *S. lancifolium*)	DQ822016 HM031067
canadense (Dupr.) Ignatova & H.H. Blom	USA, Maine1	U.S.A., Maine, Allen #16385 (MO) (as *S. lancifolium*)	HM053915
canadense (Dupr.) Ignatova & H.H. Blom	USA, Maine 2	U.S.A., Maine, Allen #15716 (MO) (as *S. lancifolium*)	HM053914
canadense (Dupr.) Ignatova & H.H. Blom	USA, Maine 3	U.S.A., Maine, Allen #27860 (MO) (as *S. lancifolium*)	HM053917
canadense (Dupr.) Ignatova & H.H. Blom	USA, Maine 4	U.S.A., Maine, Allen #24480 (MO) (as *S. lancifolium*)	HM053916
confertum (Funck) Bruch et al.	Austria 1	Austria, Köckinger #12251 (MW)	HM053891
confertum (Funck) Bruch et al.	Austria 2	Austria, Köckinger #93-1312 (MW)	JF262179
crassipilum H.H. Blom	Caucasus	Russia, Krasnodar Territory, Seregin #M-564 (MW)	DQ822021 HM031070
crassipilum H.H. Blom	Poland	Poland, 10.III.1995 Ignatov & Ochyra, s.n. (MHA)	DQ822020 HM031073
cryptocarpum Mogensen & H.H. Blom	Kamchatka	Russia, Kamchatka, 24.VII.2003 Chernyadjeva s.n. (MHA)	HM053893
dupretii (Thér.) W.A. Weber	Austria	Austria, Köckinger #12243 (MW)	HM053894
dupretii (Thér.) W.A. Weber	Perm	Russia, Perm Province, 6.VIII.1995, Bezgodov #630 (MW)	HM053895
echinatum Ignatova & H.H. Blom	Bashkortostan	Russia, Bashkortostan, Zolotov #07-1 (MHA)	HQ890507
echinatum Ignatova & H.H. Blom	California	U.S.A., California, Toren #9500b (MHA)	HQ890506

echinatum Ignatova & H.H. Blom	Caucasus	Russia, Karachaevo-Cherkessia, Teberda, Ignatov & Ignatova #05-3902 (MW)	HQ890508
echinatum Ignatova & H.H. Blom	Austria	Austria, Köckinger #96-937 (MW)	HQ890509
elegantulum H.H. Blom	Caucasus	Russia, Krasnodar Territory, 5.VIII.1002, Ignatov &Ignatova s.n. (MHA)	DQ822022 HM031071
elegantulum H.H. Blom	Norway	Norway, Bergen, 2002 Ignatov & Ignatova #06-5062 (MW)	DQ822023 HM031072
flaccidum (De Not.) Ochyra	Caucasus, Kabardino-Balkaria	Russia, Kabardino-Balkaria, 28.VII.2004, Ignatov & Ignatova s.n.(MW)	HM053896
flaccidum (De Not.) Ochyra	Caucasus, Teberda	Russia, Karachaevo-Cherkessia, Teberda, Ignatov & Ignatova #05-470 (MW)	HM053899
flaccidum (De Not.) Ochyra	Austria 1	Austria, Köckinger #14897 (MW)	HQ890510
cf. *flaccidum* (De Not.) Ochyra	Austria 2	Austria, Köckinger #97-1257 (MW)	HQ890511
frigidum H.H. Blom	Anabar 1	Russia, Anabar Plateau, Fedosov #07-2-28 (MW)	HM053904
frigidum H.H. Blom	Anabar 2	Russia, Anabar Plateau, Fedosov #06-771 (MW)	HM053906
frigidum H.H. Blom	Anabar 3	Russia, Anabar Plateau, Fedosov #07-1-8 (MW)	HM053905
frigidum H.H. Blom	Taimyr	Russia, Taimyr, 3.VII.2004 Fedosov Sch25 (MW)	HM053907
frisvollianum H.H. Blom	Anabar	Russia, Anabar Plateau, Fedosov #06-295 (MW)	HM053908
frisvollianum H.H. Blom	Taimyr	Russia, Taimyr, 23.VII.2004, Fedosov #Sch14 (MW)	HM053909
grandirete H.H. Blom	Putorana	Russia, Putorana, VI-VII.1996, Matveeva s.n. (LE)	HM053910
grandirete H.H. Blom	Severnaya Zemlya	Russia, Severnaya Zemlya, 4.VIII.2000, Matveeva s.n. (LE)	HM053911
lancifolium (Kindb.) H.H. Blom	Caucasus	Russia, Caucasus, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3721 (MW)	DQ822019 HM031064
lancifolium (Kindb.) H.H. Blom	Iran 1	Iran, Veisar forest, Zare s. n. (MW)	HQ890514
lancifolium (Kindb.) H.H. Blom	Iran 2	Iran, Cheten forest, Zare s.n. (MW)	HQ890515
lancifolium (Kindb.) H.H. Blom	Khabarovsk	Russia, Khabarovsk Territory, Pisarenko #03263 (MHA)	HQ890516
lancifolium (Kindb.) H.H. Blom	Sakhalin 1	Russia, Sakhalin, Pisarenko #03254 (MW)	HQ890512
lancifolium (Kindb.) H.H. Blom	Sakhalin 2	Russia, Sakhalin, Pisarenko #03261 (MW)	HQ890513
lancifolium (Kindb.) H.H. Blom	U.S.A., Maine	U.S.A., Maine, Allen #24447 (MO)	HQ890517
marginale (provisional name)	Austria 1	Austria 1, Köckinger #12239 (MW)	HM053919
marginale (provisional name)	Austria 2	Austria 2, Köckinger #12240 (MW)	HM053920
marginale (provisional name)	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-1092 (MW)	HM053921
maritimum (Sm. ex R. Scott) Bruch et al.	Kuril Islands	Russia, Kuril Islands, Ignatov 06-1528 (MHA)	HM053924
maritimum (Sm. ex R. Scott) Bruch et al.	Murmansk	Russia, Murmansk Province, 5.VIII.2006 Sukhova s.n. (MW)	HM053922
maritimum subsp. *piliferum* (I. Hagen) B. Bremer	Norway	Norway, year 2002 Blom s.n. (MW)	HM053923
obscurum H.H. Blom, Köckinger & Ignatova	Anabar	Russia, Anabar Plateau, Fedosov #06-683 (MW) (as *S. flexipile*)	HM053900
obscurum H.H. Blom, Köckinger & Ignatova	Austria	Austria, Köckinger #12244 (MW)	HQ890519
obscurum H.H. Blom, Köckinger & Ignatova	Buryatia	Russia, Buryatiya, Tubanova # Ky-24/03 (MW)	HQ890518

obscurum H.H. Blom, Köckinger & Ignatova	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3200 (MW) (as *S. flexipile*)	HM053902
obscurum H.H. Blom, Köckinger & Ignatova	Spitsbergen	Norway, Spitsbergen, Belkina #B128/1-06 (KPABG) (as *S. flexipile*)	HM053903
papillosum Culm.	Caucasus	Russia, Kabardino-Balkaria, 27.VII.2004, Ignatov & Ignatova s.n. (MW)	DQ822012 HM031061
papillosum Culm.	Irkutsk	Russia, Irkutsk Province, 8.VI.2005, Ignatov & Kazanovsky s.n. (MHA)	DQ822013 HM031062
papillosum Culm.	Kamchatka	Russia, Kamchatka, 31.VIII.2003, Czernyadjeva	DQ822014
		#120 (MW)	HM031063
papillosum Culm.	Kommander Islands	Russia, Kommander Islads, Bering Island, Fedosov #1-3-177 (MW)	HQ890520
papillosum Culm.	Taimyr	Russia, Taimyr, 15.VI.2004, Fedosov #Sch7 (MW)	DQ822015 HM031065
platyphyllum (Mitt.) Perss.	Anabar	Russia, Anabar Plateau, Fedosov #07-2-1 (MW)	HM053926
platyphyllum (Mitt.) Perss.	Yakutia	Russia, Yakutia, Ignatov #00-321 (MHA)	HM053929
pulchrum H.H. Blom	Anabar 1	Russia, Taimyr, ITS1 – Fedosov 05-573 (MW); ITS2 – Fedosov #06-545 (MW)	DQ822031 HM031050
pulchrum H.H. Blom	Buryatia 1	Russia, Buryatia 1, 11.VII.2003, Tubanova s.n. (MW ex UUH)	DQ822028 HM031051
pulchrum H.H. Blom	Buryatia 2	Russia, Buryatia 2, 14.VII.2002, Tubanova #5(V) (MW ex UUH)	DQ822032 HM031052
pulchrum H.H. Blom	Perm	Russia, Perm Province, 9.VIII.2005,	DQ822030
		Bezgodov #78 (MW)	HM031053
pulchrum H.H. Blom	Anabar 2	Russia, Taimyr, 18.VIII.2004, Fedosov #HK-9 (MW)	HQ890521
rivulare (Brid.) Podp.	Altai	Russia, Altai, 7.VIII.2008, Ignatova s.n. (MW)	HM053934
rivulare (Brid.) Podp.	Caucasus	Russia, Karachaevo-Cherkessia, Ignatova #07-229 (MW)	HM053935
rivulare (Brid.) Podp.	Kuril Islands	Russia, Kuril Islands, Bakalin #K-10-6-07 (MHA)	HM053936
rivulare (Brid.) Podp.	Vologda	Russia, Vologda Province, 20.VII.2001, Chemeris & Bobrov (MW)	HM053937
scandicum H.H. Blom	Bashkortostan	Russia, Bashkortostan, Zolotov #07-38 (MHA)	DQ822026 HM031054
scandicum H.H. Blom	Sweden	Sweden, 15.XII.1988 Hedenäs s.n. (S)	DQ822027 HM031059
sibiricum Ignatova & H.H. Blom	Aginsko-Buryatsky	Russia, Aginsko-Buryatsky Autonom. District, Afonina #3005 (LE)	HM053883
sibiricum Ignatova & H.H. Blom	Chita	Russia, Chita Province, Afonina #11706 s.n. (LE)	HM053884
sibiricum Ignatova & H.H. Blom	Murmansk	Russia, Murmansk Prov., Kučera #11338 (MW)	HM053885
sinensiapocarpum (Müll. Hal.) Ochyra	Austria	Austria, Köckinger #12255 (MW)	HM053939
sinensiapocarpum (Müll. Hal.) Ochyra	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3773 (MW)	HM053940
sordidum I. Hagen	Anabar	Russia, Anabar Plateau, Fedosov #08-458 (MW)	HM053942
sordidum I. Hagen	Yakutia	Russia, Yakutia, 11.VII.2006, Ivanova s.n. (MW)	HM053943
subflaccidum (Kindb.) H.H. Blom	Austria	Austria, Köckinger #12254 (MW)	HM053945

subflaccidum (Kindb.) H.H. Blom	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3973 (MW)	HM053946
subjulaceum H.H. Blom	Altai	Russia, Altai, 4.VIII.1992, Ignatov s. n. (MHA)	HQ890522
subjulaceum H.H. Blom	Buryatia	Russia, Buryatia, 11.VII.2002, Tubanova #1(V) (MW ex UUH)	HM053947
submuticum Broth. ex H.H. Blom	Bashkortostan	Russia, Bashkortostan, Zolotov #14-29 (MW)	DQ822011 HM031055
submuticum Broth. ex H.H. Blom	Perm	Russia, Perm Prov., 20.IX.1980, Ignatov s.n. (MHA)	DQ822010 HM031056
submuticum Broth. ex H.H. Blom	St.-Petersburg	Russia, St.-Petersburg, 13.III.2004, Kurbatova s.n. (MW)	DQ822009 HM031058
submuticum subsp. *arcticum* H.H. Blom	Anabar 1	Russia, Anabar Plateau, Fedosov #06-443 (MW)	HM053949
submuticum subsp. *arcticum* H.H. Blom	Anabar 2	Russia, Anabar Plateau, Fedosov #06-476 (MW)	HM053948
submuticum subsp. *arcticum* H.H. Blom	Yakutia	Russia, Yakutia, 19.VII.1988, Filin (MW)	HM053950
succulentum Ignatova & H.H. Blom	Anabar	Russia, Anabar Plateau, Fedosov #07-2-47 (MW) (as *S.* cf. *flaccidum)*	HM053875
succulentum Ignatova & H.H. Blom	Caucasus, Teberda 1	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3057 (MW) (as *S. flaccidum*)	HQ890523 HM053897
succulentum Ignatova & H.H. Blom	Caucasus, Teberda 2	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3057 (MW) (as *S. flaccidum*) – second extraction from previous specimen	HM053898
succulentum Ignatova & H.H. Blom	Caucasus, Teberda 3	Russia, Caucasus, Teberda, Zolotov #05-3612 (MW)	JF280964
tenerum (J.E. Zetterst.) Nyholm	Canada	Canada, Yukon, Readfern #36434 (MO)	HM053951
tenerum (J.E. Zetterst.) Nyholm	Chukotka	Russia, Chukotka, 12.VII.1989, Afonina s.n. (LE)	HM053952
tenuinerve Ignatova & H.H. Blom	Altai	Russia, Altai, Ignatov #0/953 (MHA)	HQ890525
tenuinerve Ignatova & H.H. Blom	Anabar	Russia, Anabar Plateau, Fedosov #08-466 (MW) (as *S. flexipile*)	HM053901
tenuinerve Ignatova & H.H. Blom	Sakhalin	Russia, Sakhalin, Pisarenko #03275 (MW)	HQ890524
trichodon var. *nutans* H.H. Blom	Austria	Austria, Köckinger #12261 (MW)	HM053953
trichodon var. *nutans* H.H. Blom	Caucasus	Russia, Kabardino-Balkaria, Kharzinov #1721 (MW)	HM053954
umbrosum (J.E. Zetterst.) H.H. Blom	Murmansk	Russia, Murmansk Province, Kučera #11499 (MW)	HM053955
umbrosum (J.E. Zetterst.) H.H. Blom	Norway	Norway, 23.VII.2001, Hedenäs s. n. (S)	HM053956
viride H.H. Blom	USA, Maryland	U.S.A., Maryland, Darigo #4201 (MO)	HM053958
viride H.H. Blom	USA, Missouri	U.S.A., Missouri, Allen #27405 (MO)	HM053957