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THE GENUS POLYTRICHASTRUM (POLYTRICHACEAE) IN RUSSIA

РОД POLYTRICHASTRUM (POLYTRICHACEAE) В РОССИИ

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Abstract

Revision of herbarium collections and sequence study of *rps4* and *trn*L-F resulted in recognition in Russia of 7 species of the genus *Polytrichastrum* sensu stricto, *i.e.*, excluding sect. *Aporotheca*. The status of *Polytrichastrum sphaerothecium* is confirmed, and this species turns out to be the most isolated in the genus, not closely related to *P. sexangulare*. A group of rather closely related species is formed by *P. alpinum, P. fragile, P. septentrionale* (Brid) E.I. Ivanova, N.E. Bell & Ignatov comb. nov., and *P. altaicum.* Their morphological differentiation corresponds with sequence level characters, supporting their taxonomic recognition. One specimen from Chukotka has some characters of *P. papillatum* and is tentatively referred to this species, despite incomplete morphological and molecular congruence with the Himalayan material.

Резюме

Ревизия гербарных коллекций и изучение последовательностей хлоропластных участнов *rps*4 и *trn*L-F выявило во флоре России 7 видов *Polytrichastrum* s. str., т.е. без видов sect. *Aporotheca,* которые рассматриваются в роде *Polytrichum*. Подтвержден видовой статус *Polytrichastrum sphaerothecium*, который оказывается наиболее изолированным в роде, не являясь близким к *P. sexangulare*. Группу близкородственных видов образуют *P. alpinum, P. fragile, P. septentrionale* (Brid) E.I. Ivanova, N.E. Bell & Ignatov comb. nov. и *P. altaicum.* Небольшие, но устойчивые отличия в ДНК и морфологии подтверждают их статус как самостоятельных видов. Один образец с Чукотки предварительно отнесен к *P. papillatum* на основании сходства по морфологическим признакам, хотя генетически он отличается от гималайских растений этого вида.

KEYWORDS: *Polytrichastrum*, taxonomy, phylogeny, phytogeography, Russia, *trn*L-F, *rps*4

Introduction

The genus *Polytrichastrum* was introduced by Smith (1971) to solve a long-standing problem concerning the status of *Polytrichastrum alpinum,* which had been variously treated in *Polytrichum* or *Pogonatum* before this segregation. Although many authors placed it in the former genus (cf. Limpricht, 1896; Savich-Lyubitskaya & Smirnova, 1970; Podpera, 1954), placement in the latter was accepted by Lazarenko (1955), Lawton (1971) and Crum & Anderson (1981), amongst others.

Additional observations of sporophyte structure led Smith (1971) to conclude that there was a closer relationship between *P. alpinum* and the group of species around *Polytrichum longisetum* than between the latter and *P. commune*, the type of the genus *Polytrichum*. Thus, Smith (1971) placed *Polytrichum longisetum* and related species in *Polytrichastrum*, although in a separate sect. *Aporotheca.* This circumscription has been followed by most subsequent check-lists and floras (*e.g.*, Hill et al., 2006; Ignatov, Afonina, Ignatova et al., 2006; Iwatsuki, 2004; Smith Merrill, 2007).

However, recent advances in molecular phylogenetics have challenged this generic circumscription, and Bell & Hyvönen (2010a) suggested returning the members of *Polytrichastrum* sect. *Aporotheca* to the genus *Polytrichum,* retaining in *Polytrichastrum* only the taxa around *P. alpinum* and *P. sexangulare*.

A phylogenetic study of the genus has been published

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by Bell & Hyvönen (2010a). The present revision concentrates on the territory of Russia. It expands the sampling from northern areas, where problems of the status and distinction of some Polytrichaceae species are still awaiting solution.

We have mainly addressed elucidation of the status of species in pairs: *P. sexangulare–P. sphaerothecium*; *P. alpinum–P. fragile*, *P. alpinum–P. septentrionale* and *P. septentrionale–P. altaicum*. Most of these taxa have been variously treated by different authors. The recent treatment in the "Bryophyte flora of North America" accepted *P. sphaerothecium, P. fragile*, and *P. septentrionale* only at the level of varieties (Smith Merrill, 2007), which disagrees with the common practice in Russia, where most authors accept them as a separate species (Abramova et al., 1961; Savich-Lyubitskaya & Smirnova, 1970; Afonina & Czernyadjeva, 1995; Ignatov, Afonina, Ignatova et al., 2006). The related species *P. emodii* and *P. papillatum*, described from Himalayas, were also included in the study.

Material and Methods

Sample selection aimed for maximal coverage of environments and morphological differences, both in gametophyte and sporophyte structure. Sequences from the previous study of Bell & Hyvönen (2010a,b) were included for species known in Russia, as well as for *P. emodii* (*P. altaicum* was compared to *P. emodii* in its original description) and *P. papillatum* (known from the Himalayas and Alaska, thus a strong candidate for occurrence in eastern Russia).

Tests with two American species, *Polytrichastrum (Meiotrichum) lyallii* (Mitt.) G.L. Sm. (AF208423 and AF5450) and *P. tenellum* (Müll. Hal.) G.L. Sm. (GU569750 and GU569834) were conducted, but their inclusion reduced resolution within the group of *P. altaicum* and *P. septentrionale*, despite their being obviously far from both. Thus the final analysis did not include them.

In our previous studies, molecular data and nrITS sequences in particular helped considerably in the delimitation of some taxa. It confirmed the identifications of poorly developed *Oligotrichum* specimens and, among other things, resulted in expansion of the range of *Oligotrichum falcatum* by thousands of kilometers (Ivanova et al., 2005). However, a preliminary analysis of ITS for *Polytrichastrum* specimens gave poor results, while *trn*L-F and *rps*4 markers appeared to be more useful. Although both regions showed low variation, individual substitutions nicely correlated with morphology, and thus the main set of sequence data comprised these two chloroplast regions. As the *rps*4 sequences are longer, a number of specimens for which *trn*L-F could be successfully sequenced gave no PCR products for *rps*4 (especially older ones and those originating from polar deserts on arctic oceanic islands with harsh environments).

DNA extractions and overall laboratory protocols were essentially the same as in, *e.g.*, Gardiner et al. (2005). Sequences were aligned manually in Bioedit (Hall, 1999).

All trees were rooted on *Pogonatum urnigerum*, a species of a rather closely related genus.

Preliminary maximum parsimony analyses in TNT (Golobov et al., 2003) and Bayesian phylogenetic analyses gave similar results. Only the latter are shown here.

Bayesian analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003) with 2 compartments for *rps*4 DNA (the *rps*4 coding region with the HKY+I model, 537 bp, and the *rps*4 spacer with the HKY model, 275 bp), 1 compartment for the *trn*L-F region, 508 bp (HKY+I), and 1 compartment for all of the indels together (12 in *rps*4 + 29 in *trn*L-F = 41), using the restriction site (binary) model. The indels were coded as binary characters using the simple indel coding strategy of Simmons & Ochoterena (2000). The AIC criterion as implemented in MrModeltest 2.2 (Nylander, 2004) was used to determine the best fitting models. Three parallel runs were implemented, each with five chains and 30000000 generations (3000000 burnin), with trees sampled every 1000 generations, a temp parameter value of 0.15 and parameters unlinked between partitions.

The TCS program (Clement et al., 2000) was used to evaluate relationships among haplotypes using the same matrix as in the Bayesian analysis. Gaps were treated as missing data.

Results of the molecular phylogenetic analysis

Altogether 54 *trn*L-F sequences and 39 *rps*4 sequences were studied, including the outgroup *Pogonatum urnigerum*. Specimen data and accession numbers are in Table 1.

In the Bayesian analysis (Fig. 1), the earliest diverging clade is formed by *P. sphaerothecium* (PP=1), while two subsequent clades comprise *P. sexangulare* (PP=1) and the rest of the accessions (PP=1). A polytomy within the latter includes accessions of *P. septentrionale* as well as clades formed by accessions of *P. altaicum* + "*P. papillatum*2" (PP=0.77), and *P. emodii* + *P. papillatum* (PP=0.6). Note that the plant from Chukotka labelled "*P. papillatum*2" does not group with the Himalayan specimen of this species. The largest nested clade includes all accessions of *P. alpinum* and *P. fragile* (PP=1), comprising two subclades: one with five accessions of *P. alpinum* (PP=0.84) and another, bigger one (PP=1), within a large polytomy formed by accessions of *P. alpinum*. Eleven accessions of *P. alpinum* are unresolved, while 14 others occur in four clades with PP values of 0.86, 0.84, 0.77, and 0.75.

MP trees (not shown) have poorer resolution. The *rps*4 tree resolves *P. sphaerothecium* as the earliest diverging clade (BS=100), with *P. sexangulare* (BS=99) sister to rest of the accessions, these in turn forming a clade (BS=100) within which the remaining accessions are entirely unresolved. MP analysis of *trn*L-F region results

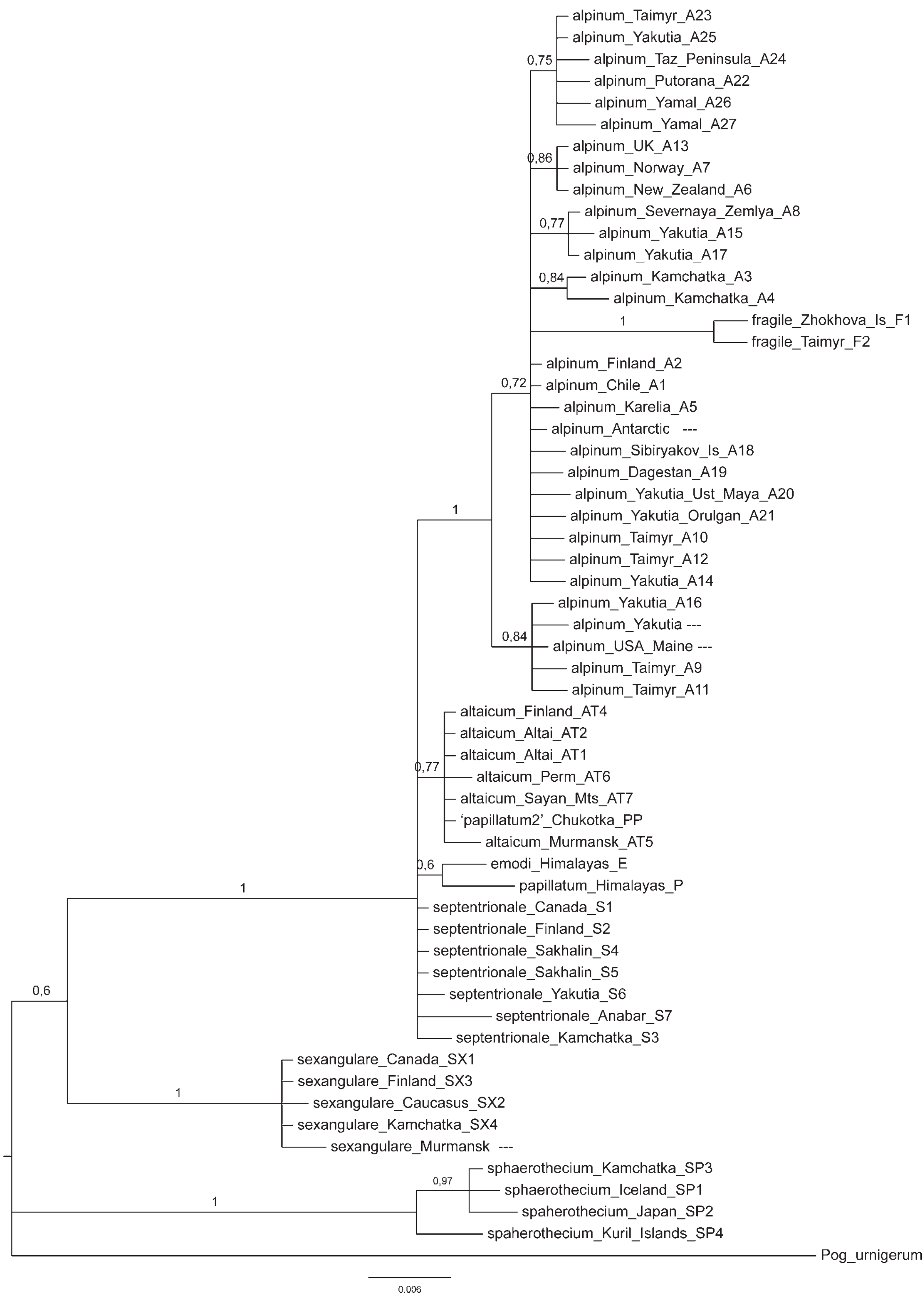
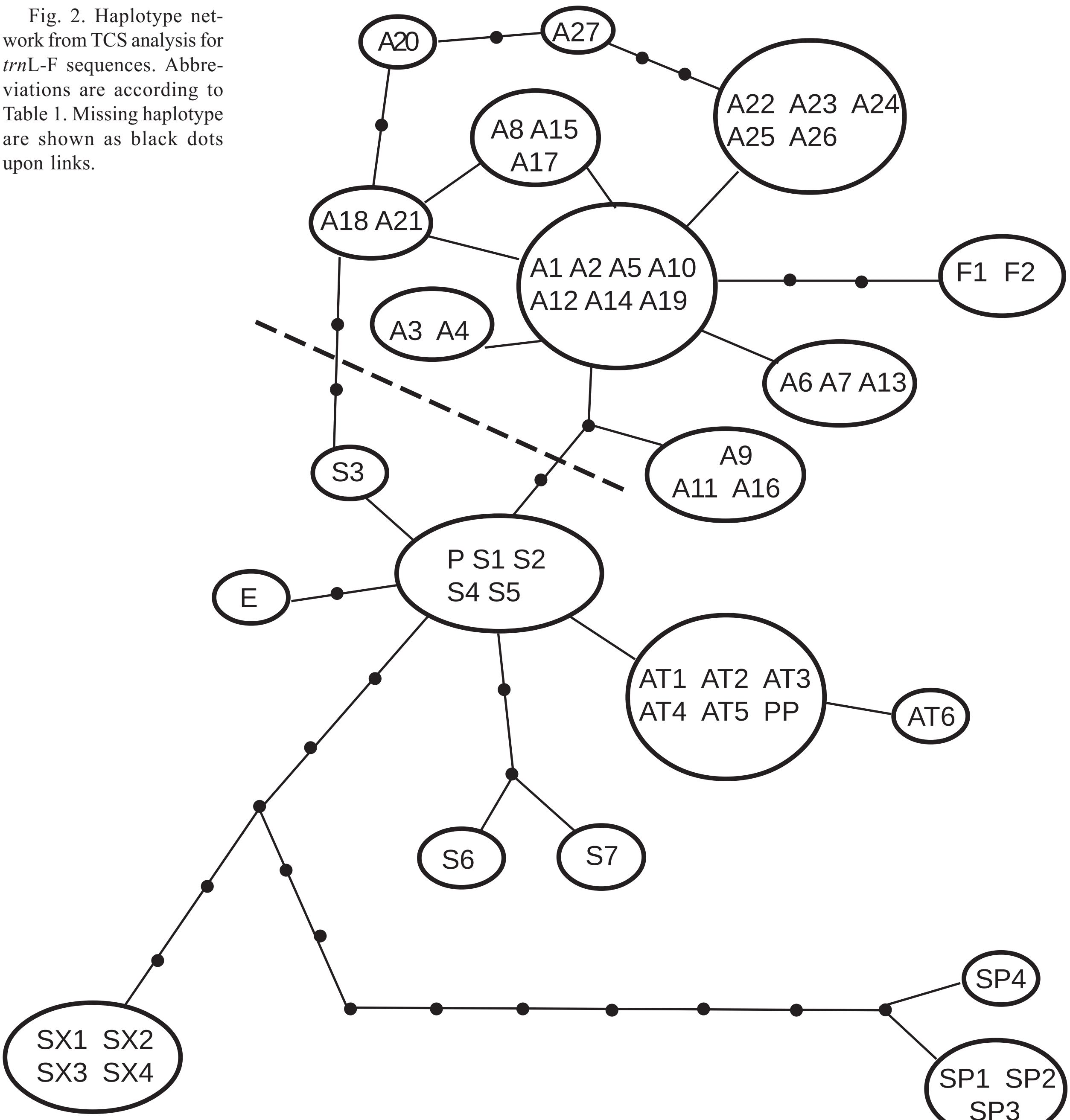


Fig. 1. Phylogenetic tree based on Bayesian analysis of *rps*4 and *trn*L-F regions. Posterior probabilities are shown above branches.

Fig. 2. Haplotype network from TCS analysis for *trn*L-F sequences. Abbreviations are according to Table 1. Missing haplotype are shown as black dots upon links.



in a polytomy with only a few clades composed of: 1) *P. sphaerothecium* (BS=99); 2) *P. fragile* (BS=80); 3) *P. sexangulare* (BS=80); and 4) *P. altaicum* (BS=63), while lower support was found for two clades comprising 6 and 3 accessions of *P. alpinum*.

The TCS network was built with and without the gap coding partition. Although results were principally the same, only the network without the gap partition is shown (Fig. 2), as the other one has more missing haplotypes, making the picture more difficult to observe.

The TCS analysis placed *P. sphaerothecium* in the most isolated position. It appears to be distinct from both the *P. alpinum*-complex and from *P. sexangulare.* The latter species is the second most isolated based on missing haplotypes in TCS, which is consistent with the MP and Bayesian analyses of both studied gene regions.

The remaining haplotypes occur in two groups, as in the Bayesian *trn*L-F tree. The first includes *P. septentrionale, P. altaicum, P. papillatum, 'P. papillatum2',* and *P. emodii,* while the second is composed of *P. fragile* and *P. alpinum* (Fig. 2).

Within the *P. fragile* and *P. alpinum* group, a number of haplotypes occur. One of them (F1 and F2 in Fig. 2) correlates with the morphologically distinct *P. fragile.* Unfortunately, sequencing of additional samples from the Arctic islands was not successful, as material was old and scanty. However, both successfully sequenced specimens have three characteristic substitutions (seen

Table 1. Abbreviations used in haplotype network (TCS), in Bayesian tree (BI), specimen data and GenBank accession numbers of *Pogonatum urnigerum* and *Polytrichastrum* species.

TCS	Name in Bayesian tree	Specimen data	*trn*L-F	*rps*4
–	Pogonatum urnigerum	Russia, Putorana Plateau, July 1984 Czernyadjeva #54 (LE)	KM381958	KM382040
A1	alpinum Chile	Chile, Bell 1788 (H)	GU569730	GU569815
A2	alpinum Finland	Finland, 2 July 2006 Bell #3 (H)	GU569733	GU569818
A3	alpinum Kamchatka A3	Russia, Kamchatka, 5 Aug 2002 Czernyadjeva #40 (MHA ex LE)	KM381960	KM382042
A4	alpinum Kamchatka A4	Russia, Kamchatka, 5 Aug 2002 Czernyadjeva #40 (SASY ex LE)	KM381961	–
A5	alpinum Karelia	Russia, Karelia, 19 Aug 1970 Volkova s.n. (LE)	KM381962	KM382043
A6	alpinum New Zealand	New Zealand, 2 March 2008 Bell #5 (H)	GU569831	GU569816
A7	alpinum Norway	Norway, 1 July 2006 Bell #13 (H)	GU569732	GU569817
A8	alpinum Severnaya Zemlya	Russia, Severnaya Zemlya, 22 Aug 1991 Safronova s.n. (LE)	KM381964	KM382044
A9	alpinum Taimyr A9	Russia, Taimyr, Fedosov #05-212 (MW)	KM381970	–
A10	alpinum Taimyr A10	Russia, Taimyr, 3 July 2002 Varlygina s.n. (MW)	KM381966	–
A11	alpinum Taimyr A11	Russia, Polar Ural, 14 July 1999 Czernyadjeva #16 (MHA ex LE)	KM381967	–
A12	alpinum Taimyr A12	Russia, Taimyr, 17 July 1972 Matveeva s.n. (LE)	KM381968	–
A13	alpinum UK	UK, 30 April 2006 Bell # 1(H)	GU569729	EU927340
A14	alpinum Yakutia A14	Russia, Yakutia, 10 July 2006 Ivanova s.n. (MHA ex SASY)	KM381972	KM382047
A15	alpinum Yakutia A15	Russia, Yakutia, 20 July 2009 Sofronov s.n. (SASY)	KM381973	–
A16	alpinum Yakutia A16	Russia, Yakutia, 16 July 1994 Ivanova s.n. (SASY)	KM381974	KM382048
A17	alpinum Yakutia A17	Russia, Yakutia, 4 Aug 1991 Baryshev s.n. (SASY)	KM381975	KM382049
A18	alpinum Sibiryakov Is	Russia, Sibiryakov Is., Kuvaev & Kozhevnikova #1471-9 (MW)	KM381965	–
A19	alpinum Dagestan	Russia, Dagestan, Fedosov #13-1-147 (MW)	KM381959	–
A20	alpinum Yakutia A20	Russia, Yakutia, Ignatov #00-723 (MHA)	KM381976	–
A21	alpinum Yakutia A21	Russia, Yakutia, Ignatov #11-4198 (MHA)	KM381977	–
A22	alpinum Putorana A22	Russia, Putorana Plateau, 25 July 1982 Czernyadjeva #107 (LE)	KM381963	–
A23	alpinum Putorana A23	Russia, Taimyr, July 1983 Czernyadjeva #27 (LE)	KM381969	KM382045
A24	alpinum Taz Peninsula	Russia, Taz Peninsula, 14 Aug 1986 Rebristaya s.n. (LE)	KM381971	–
A25	alpinum Yakutia A25	Russia, Yakutia, 17 July 2009 Sofronov s.n. (SASY)	KM381978	KM382050
A26	alpinum Yamal A26	Russia, Yamal Peninsula, 5 Aug 1991 Rebristaya s.n. (MHA ex LE)	KM381979	–
A27	alpinum Yamal A27	Russia, Yamal Peninsula, 14 July 1977 Andreeva s.n. (LE)	KM381980	–
–	alpinum Maine	USA, Maine, 26 Oct 2000 Ledlie P. # 1066 (MO)	–	AY908013
–	alpinum Antarctic	Antarctic, King George Is., Hyoungseok Lee KGI-HS0001 (KOPRI)	–	KM361635
–	alpinum Yakutia A30	Russia, Yakutia, 10 July 1991 Ivanova s.n. (SASY)	–	KM382046
AT1	altaicum Altai AT1	Russia, Altai, 25 July 1993 Ignatov # 36/361 (MHA)	KM381981	KM382051
AT2	altaicum Altai AT2	Russia, Altai, I25 July 1993 gnatov # 36/361 (H)	GU569734	GU569819
AT4	altaicum Finland	Finland, 3 July 2006 Bell #7 (H)	GU569740	GU569824
AT5	altaicum Murmansk	Russia, Murmansk Prov., 31 July 2004 Filin s.n. (MW)	KM381982	–
AT6	altaicum Perm	Russia, Perm Territory, 8 July 1998 Bezgodov #252 (LE)	KM381983	KM382052
AT7	altaicum Sayan Mts.	Russia, Sayan Mts., 3 July 1961 Bardunov s.n. (LE)	KM381984	KM382053
E	emodi Bhutan	Bhutan, G. & S. Miehe #00-381-22 (H)	GU569736	GU569821
F1	fragile Zhokhova Is.	Russia, De Longa Archipelago, Zhokhova Island, 1989 Samarsky s.n. (MHA ex LE)	KM381986	–
F2	fragile Taimyr	Russia, Taimyr, 5 July 2003 Varlygina s.n. (MW)	KM381985	–
P	papillatum Bhutan	Bhutan, G. & S. Miehe # 00-183-17 (H)	GU569744	GU569828
PP	papillatum Chukotka	Russia, Chukotka, 19 July 1989 Afonina s.n. (LE)	KM381987	KM382054
S1	septentrionale Canada	Canada, Hedderson #1877 (H)	GU569741	GU569825
S2	septentrionale Finland	Finland, 2 July 2006 Bell #8 (H)	GU569739	GU569829
S3	septentrionale Kamchatka	Russia, Kamchatka, Czernyadjeva #107 (MHA)	KM381989	–
S4	septentrionale Sakhalin S4	Russia, Sakhalin, 15.VIII.2006 Ignatov & Teleganova (MHA)	KM381990	KM382055
S5	septentrionale Sakhalin S5	Russia, Sakhalin, 11 Sept 2009 Pisarenko op03179 (MHA)	KM381991	KM382056
S6	septentrionale Yakutia	Russia, Yakutia, 6 Aug 1987 Volotovsky s.n. (SASY)	KM381992	KM382057
S7	septentrionale Anabar	Russia, Taimyr, Fedosov #13-3-0355 (MW)	KM381988	–
SP1	sphaerothecium Iceland	Iceland, Blockeel #34/418 (E)	GU569749	GU569833
SP2	sphaerothecium Japan	Japan, Nishimura #11697 (H)	GU569748	GU569832
SP4	sphaerothecium Kuril Is	Russia, 14 Sept 2006 Ignatov s.n. (H)	GU569747	GU569831
SP3	sphaerothecium Kamchatka	Russia, Kamchatka, 3 Aug 1990, Czernyadjeva s.n. (LE)	KM381995	KM382060
SX1	sexangulare Canada	Canada, Belland #5727 (H)	GU569746	GU569830
SX2	sexangulare Caucasus	Russia, Karachaevo-Cherkessia, 15 Aug 2009 Kurbatova s.n.(SASY)	KM381993	KM382058
SX3	sexangulare Finland	Finland, 3 July 2006 Bell #4 (H)	GU569745	GU569823
SX4	sexangulare Kamchatka	Russia, Kamchatka, 25 Aug 2002 Czernyadjeva #680 (LE)	KM381994	KM382059
–	sexangulare Murmansk	Russia, Murmansk Prov., Ignatov & Ignatova #12-89 (MHA)	–	KM392104

in Fig. 2) in addition to a specific four nucleotide insertion in *trn*L-F (not illustrated, as gaps do not affect the diagram).

Within *P. alpinum* there are several haplotypes that do not appear to correlate with morphology, except in the case of five specimens that are represented in the TCS analysis by a group (A22, 23, 24, 25, 26 in Fig. 2) and also form a clade in the *trn*L-F Bayesian tree (Fig.1). These plants also usually have fragile leaves, but in a manner that differs from *P. fragile* (see discussion under *P. fragile*). This character state is not consistent in all six collections, however, and also occasionally occurs in plants of other haplotypes. Thus we do not think that this group merits taxonomic recognition, at least based on the present sampling.

The *P. septentrionale* group appears in the TCS analysis as an ancestral polytomy from which *P. alpinum* has evolved. Two Himalayan species, *P. emodii* and *P. papillatum* s.str., belong to this group, and the latter is identical to the most common haplotype of *P. septentrionale.*

The differentiation of *P. altaicum* from *P. septentrionale* is supported by TCS analysis of *trn*L-F (Fig. 2), as well as by Bayesian analysis of combined sequence data of *trn*L-F and *rps*4 (Fig. 1). The present analysis included considerably more specimens than in the study of Bell & Hyvönen (2010a,b) and provides a much better understanding of this rare species.

The occurrence of one collection from Chukotka with the *P. papillatum* morphology within the haplotype of *P. septentrionale* poses a problem. This exception is difficult to place within a wider context as material for additional sampling from Chukotka and Himalays was unavailable for the present study. The morphological background for the referral of the Chukotkan plant to *P.* cf. *papillatum* is discussed under this species.

There are two unique substitutions in *P. emodii* differentiating it from *P. septentrionale*, whereas *P. papillatum* s. str. differs from the latter species only by indels, thus placing it in the same haplotype in the TCS analysis (Fig. 2).

The overall interpretation of these sequence data is compatible with a number of taxonomic scenarios. Undoubtedly, there is sharp differentiation between *P. sexangulare*, *P. sphaerothecium* and the rest of *Polytrichastrum* as represented in the analysis. The ultimate lumper might suggest combining all of the taxa except the two former species, and including the Himalayan species, in one polymorphic *P. alpinum* s.l. However, for all of the named entities we found at least small but stable molecular differences that correlate with morphological characters, albeit usually relatively weak ones. In our view, this supports their recognition as species. At the same time, some haplotypes, even those corresponding to clades in the Bayesian tree with PP values of 0.84–0.96, are left without taxonomic recognition, as no morphological characters were found to separate them.

TAXONOMIC TREATMENT

Polytrichastrum G. L. Sm., Mem. New York Bot. Gard. 21(3): 35. 1971. Holotype: *Polytrichum alpinum* Hedw.

Plants small to robust, in loose tufts, dark green, brownish with age. Leaves with differentiated sheath and blade, the blade appressed, erect to somewhat spreading when dry, widely spreading when wet; sheath ovate to elliptic or obovate, hyaline-margined, entire, often highly nitid (polished and glossy), a well-developed hinge tissue present; blade linear-lanceolate, gradually or abruptly tapered to apex or, more rarely, apex cucullate, margins sharply toothed to entire, teeth multicellular, usually formed of 2-4 cells; costa typically short-excurrent, scabrous, or (especially in perichaetial leaves) prolonged into a toothed awn. Lamellae numerous, closely-spaced, occupying most of the blade width, their margins smooth, finely striolate, or coarsely papillose, ± entire to regularly crenulate in profile, the marginal cells differentiated in size and/or shape and/or papillosity. Dioicous (or monoicous, but appearing unisexual). Male plants with inconspicuous rosettes. Seta solitary. Capsules terete or, more rarely, distinctly 6-angled or irregularly slightly 5-6 angled, the apophysis not or shallowly delimited from the urn. Operculum rostrate. Exothecium smooth, the cells sometimes (*P. sexangulare*) with an indistinct thin spot in the outer wall, irregularly polygonal, but in general arranged in longitudinal rows. Peristome teeth about 50 due to fusion of some neighboring teeth in paired teeth (original number of teeth 64), more rarely regularly 32, whitish, not keeled. Epiphragm readily detached, generally with erect tooth-like processes opposite the peristome teeth and attached to their inner face. Spores 13-26 mm diam., finely papillose. Calyptra with a rather loosely interwoven felt of hairs, covering only the upper portion of capsule.

KEY TO THE *POLYTRICHASTRUM* SPECIES IN RUSSIA

1. Margins of lamellae papillose; leaves sharply serrate, more rarely subentire; capsule terete 2
— Margins of lamellae smooth; leaves entire or subentire; capsule angled or terete 5
2. Upper cell of lamellae knobbed, with a crown of papillae crowded at the cell top; one collection from Chukotka .... *P. papillatum*
— Upper cells of lamellae ovate, with papillae rather even upon their distal part; widespread 3
3. Leaf blade abruptly constricted at junction to sheathing base and leaves are strongly fragile at this junction; high Arctic .... *P. fragile*
— Leaf blade gradually transits to sheathing base, leaves not fragile or fragile at different levels, usually below the junction of blade and sheathing base, widespread 4
4. Leaves incurved, entire to bluntly toothed above, seta 1-1.5 cm; capsule ovoid to subglobose; spores 17-22 mm .... *P. septentrionale*

— Leaves straight, usually sharply serrate (except strongly depressed arctic plants); seta (1-)3-5 cm; capsule cylindric to ovoid; spores 14-20 mm.......... .... *P. alpinum*

5. Plants small, growing on vertical walls with leaves pointed downwards; stem cortex thick-walled; leaves with poorly developed sheathing base; seta 0.3-0.5 mm, curved; capsule subglobose to globose, sometimes very weakly 5-6-angled; peristome teeth 32; on volcanic rocks in Pacific coastal area .... *P. sphaerothecium*

— Plants small to large, growing mostly orthotropously; stem cortex thin-walled; leaves with well-developed sheathing base; seta 1-3 mm, straight; capsule subglobose to cylindric, angled or smooth; peristome teeth 50 to 64; widespread 6

6. Costa subpercurrent, leaf apex blunt and sub-cucullate; marginal cells of lamellae ovate to pyriform; upper edge of lamellae from side view smooth, strongly incrassate along the edge; capsule (4-)6-angled, often only obtusely; exothecial cells each with a diffuse thin spot on the outer wall ....*P. sexangulare*

— Costa short-excurrent, leaf apex with an apiculate tip; marginal cells of lamellae slenderly tapering to a knob-like tip; upper edge of lamellae from side view slightly crenulate, moderately incrassate along the edge; capsule round in transversal section, not angled; exothecial cells lacking thin spots .... *P. altaicum*

1. Polytrichastrum alpinum (Hedw.) G.L. Smith, Mem. New York Bot. Gard. 21(3): 37. 1971.

Polytrichum alpinum Hedw., Sp. Musc. Frond. 92. pl. 19: f. 2b. 1801.

Figs. 3, 4, 7

Plants medium-sized to large. Stems from 2 cm (in exposed arctic and high alpine habitats) to 5-10(-20) cm tall, occasionally branched. Leaves erect-spreading and inrolled when dry, spreading when moist, 6-15×0.5-1.9 mm; blade narrowly tapered to a short, toothed awn; sheath obovate to elliptic, with tapering shoulders, ± nitid, broadly hyaline-margined especially conspicuopus in shoulders; marginal lamina erect, 3-5 cells wide, coarsely serrate with 1-3-celled multicellular teeth almost throughout the blade, rarely blade weakly serrulate distally and subentire proximally. Lamellae 25-35(-40), in profile ± entire, 5-8 cells high, marginal cells moderately to coarsely papillose (papillae being rather even on their surfaces), in cross-section ovate to narrowly ovate, outer wall strongly thickened, lumen pentagonal, walls often yellowish to brown, occasionally colorless. Blade marginal cells subquadrate, 15-20 µm; sheath median cells 40-65(-80)×6-15 µm, elongate-rectangular, mostly 3-8(-10):1. Seta (1-)2-4(-5) cm. Capsules pale to dark brown, suberect to inclined, terete, cylindric, ovate-cylindric, occasionally subglobose or pyriform-ventricose ("*Psilopilum*-shaped"), 1.0-1.5 µm wide, 2-4 mm long. Spores 14-20 µm.

Differentiation and variation. Within forest areas and otherwise sheltered habitats plants of *Polytrichastrum alpinum* are tall and robust, only slightly smaller than *Polytrichum commune*, from which they are differentiated in the field by cylindric capsules, a somewhat glaucous color and growth on rocks (as opposed to soil as is typical for *P. commune* in Russia). Among microscopic characters, the multicellular marginal teeth are sufficient to separate *P. alpinum* from all *Polytrichum* species, which have unicellular teeth. Smaller alpine and arctic plants require study of leaf cross sections, the characteristic shape and papillosity of the lamellar apical cells being essential in this case. Attention is called for also in distinguishing between *P. alpinum* and *Pogonatum urnigerum* var. *integrifolium*, which is sympatric in the Arctic with small phenotypes of *P. alpinum*. The upper wall of the apical cell in this variety is more convex than in *P. urnigerum* var. *urnigerum*, resulting in confusion with *P. alpinum* and some misidentification in herbaria. However this variety of *Pogonatum* has broader upper cells that is still less convex at distal end than in any phenotype of *P. alpinum*.

Arctic plants of *P. alpinum* are often more or less fragile, which is a common phenomenon in many groups of mosses in severe conditions. This fact made dubious the distinction between *P. alpinum* and *P. fragile*, which has often not been accepted as an entity distinct from *P. alpinum*. However, the above results from DNA analysis do not support the lumping of all fragile *Polytrichastrum* plants under a single species. The distinction between fragility patterns is illustrated in Figs. 4-7 and discussed under *P. fragile*. Differentiation from *P. septentrionale* and *P. papillatum* is discussed under those species.

The variation in capsule shape in *P. alpinum* is considerable. Most collections from Russia are large plants with cylindric, suberect capsules, corresponding to *Polytrichastrum alpinum* var. *sylvaticum* as accepted by Smith Merrill (2007). Capsules of Arctic and alpine plants are usually shorter, ovate-cylindric to ovate. Some plants from northern Yakutia and Chukotka have "*Psilopilum*-shaped" capsules, while in SE Yakutia plants with globose capsules occur. The absence of genetic differences as well as the great variation observed in some populations do not allow considering these characters as taxonomically important.

Distribution and ecology. *Polytrichastrum alpinum* is widespread from the Arctic and mountainous regions of the Holarctic southward to the Caucasus, the mountains of Central Asia, the Himalayas and Japan, and in North America to the southern states and Mexico. It also occurs in South Africa, southern South America, Antarctic, Australia, New Zealand and New Guinea. As a rule, *P. alpinum* is absent in lowland areas such as central European Russia and most of West Siberia, although some records exist from regions with an oceanic climate near sea level. In the southern mountains, *e.g.*, the Altai

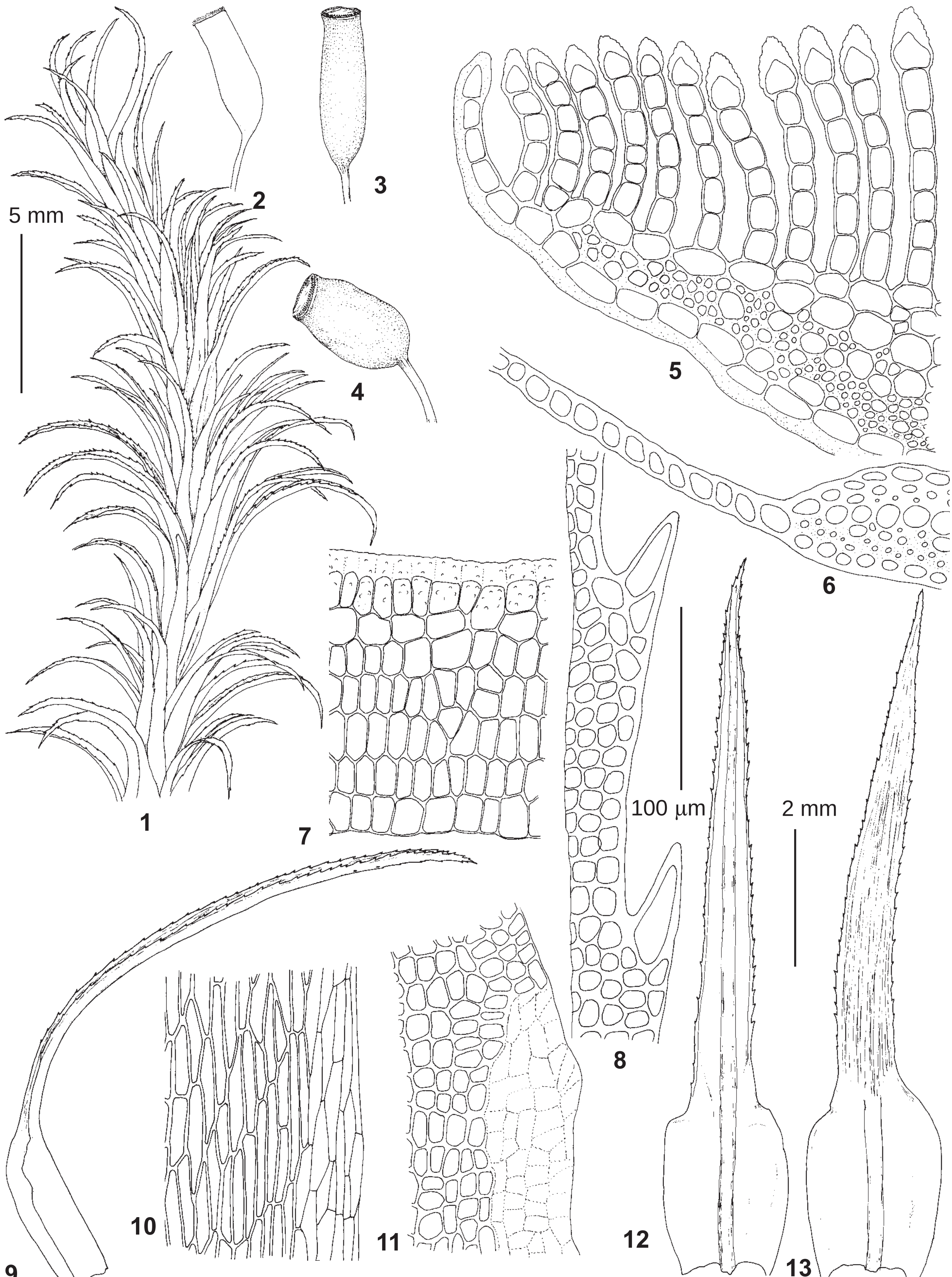


Fig. 3. *Polytrichastrum alpinum* (Hedw.) G. L. Smith (1-2, 5-13 – from: Russia, Perm Province, Basegi, *Ignatov & Bezgodov 69*, MW; 3 – from: Yakutia, Orulgan, *Ignatov 11-3745*, MHA; 4 – from: Yakutia, Orulgan, *Ignatov 11-4198*, MHA): 1 – habit, dry; 2-4 – capsules; 5-6 – leaf transverse sections; 7 – side view of lamella; 8 – leaf margin; 9, 12-13 – leaves; 10 – basal laminal cells; 11 – cells at leaf shoulder. Scale bars: 5 mm for 1-4; 2 mm for 9, 12-13; 100 μm for 5-8, 10-11.

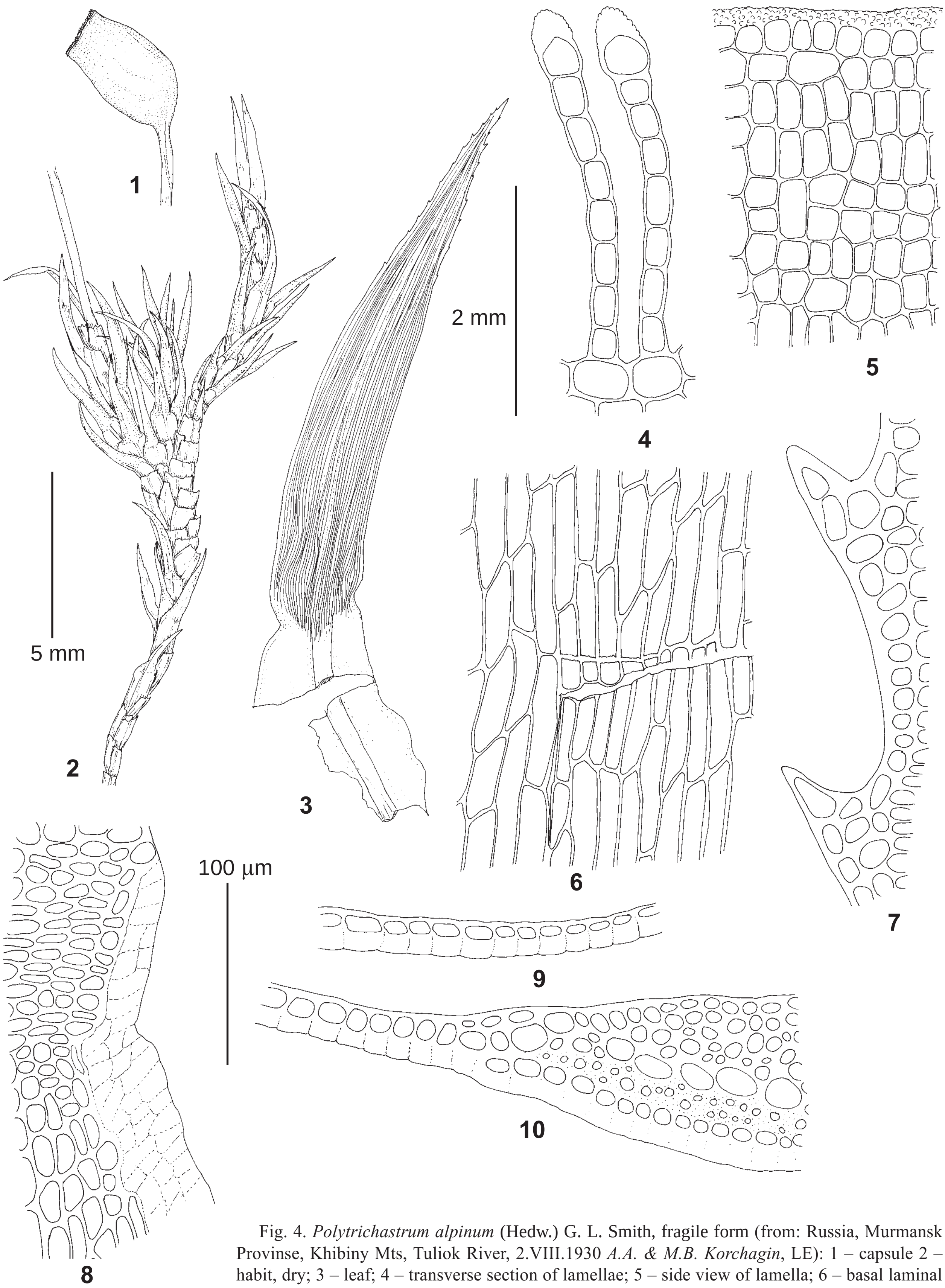


Fig. 4. *Polytrichastrum alpinum* (Hedw.) G. L. Smith, fragile form (from: Russia, Murmansk Provinse, Khibiny Mts, Tuliok River, 2.VIII.1930 *A.A. & M.B. Korchagin*, LE): 1 – capsule 2 – habit, dry; 3 – leaf; 4 – transverse section of lamellae; 5 – side view of lamella; 6 – basal laminal cells; 7 – lamina margin at midleaf; 8 – cells at leaf shoulder; 9-10 – leaf transverse sections at leaf base. Scale bars: 5 mm for 1-2; 2 mm for 3; 100 µm for 4-10.

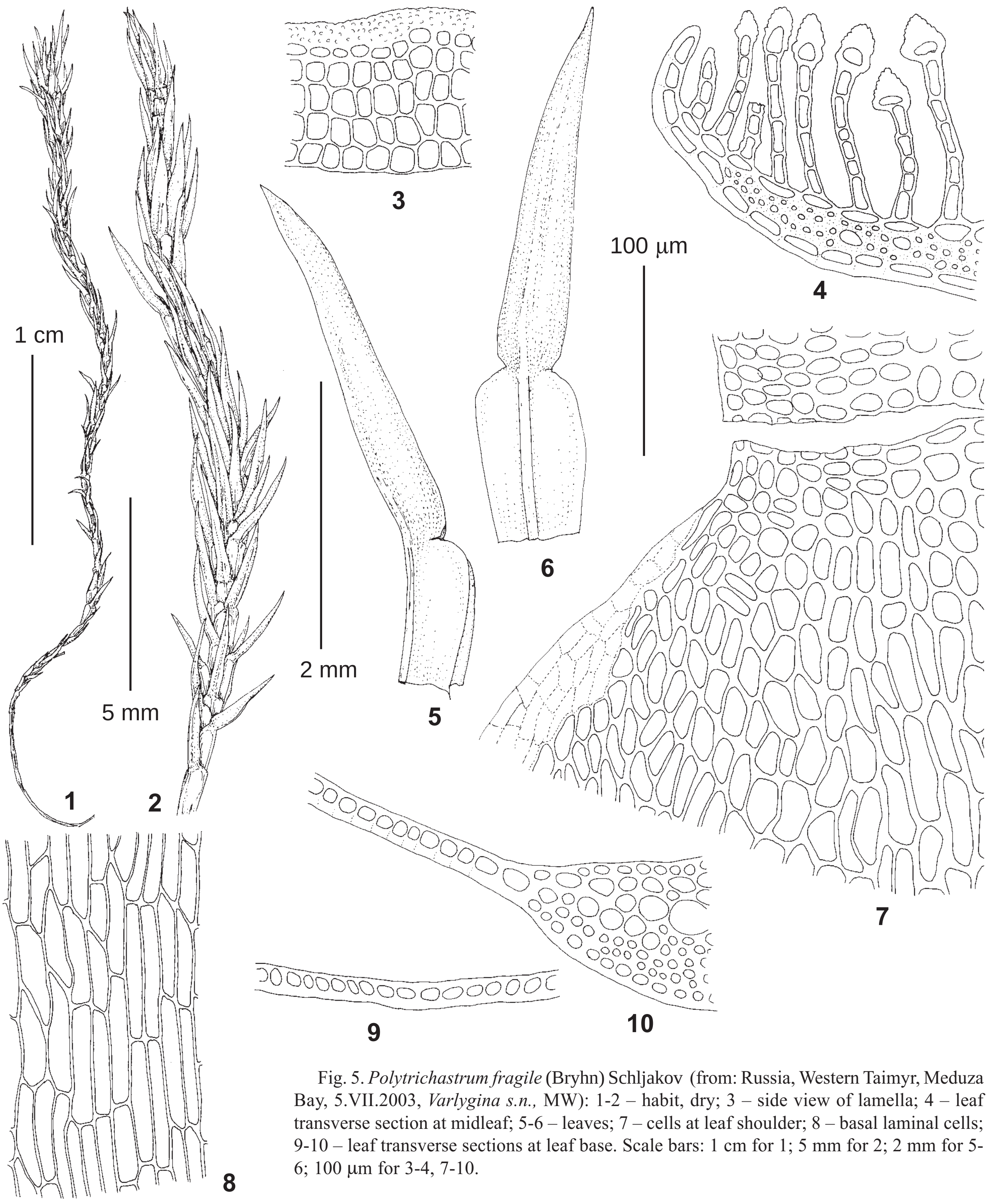


Fig. 5. *Polytrichastrum fragile* (Bryhn) Schljakov (from: Russia, Western Taimyr, Meduza Bay, 5.VII.2003, *Varlygina s.n.,* MW): 1-2 – habit, dry; 3 – side view of lamella; 4 – leaf transverse section at midleaf; 5-6 – leaves; 7 – cells at leaf shoulder; 8 – basal laminal cells; 9-10 – leaf transverse sections at leaf base. Scale bars: 1 cm for 1; 5 mm for 2; 2 mm for 5-6; 100 μm for 3-4, 7-10.

and Caucasus mountains, the species occurs not only in the high mountains, but also rather commonly at lower elevations on rock outcrops (especially in deep canyons, near waterfalls, *etc.*). In the Arctic and alpine areas it grows on soil in a wide range of tundra and nival habitats, within shrub communities, as well as on rocks.

***Selected specimens examined*: EUROPAEAN RUSSIA: Republic of Karelia:** White Sea Biostation of Moscow State University, Kindo Peninsula, 15.VI.1964, *Vekhov* (MW), S+; **Murmansk Province:** Khibiny Mts, 5.IX.1957, *Schljakov* (LE, #919); **Nenetskij Autonomous District**: Ad'zva River, *Ivanov & Donskov 09-253* (MHA); **Komi Republic**: Sosnogorsk Distr., 27.VI.2007 *Kucherov & Kutenkov 48* (MHA); **Perm Territory:** Vishersky Nature Reserve, 27.VI.1994, 7.VII.1994, 21.VII.1994, *Bezgodov 164, 391, 516a* (MW); Basegi State Reserve: Severnyj Baseg, 5.VI.1994, *Ignatov & Bezgodov 358* (MHA), S+; Yuzhnyj Baseg, 9.VI.1994, *Igna-*

tov & Bezgodov 69 (MHA), S+; Usva River, 4.VI.1994, *Ignatov & Bezgodov 301* (MHA); **Bashkortostan**: Bolshoi Shelom Mt., 4.VII.1998 *Muldashev* (UFA); **CAUCASUS**: **Adygeia**: Caucasian State Reserve, 7.VIII.1935 *Vasiljeva* (LE); **Dagestan**: Charodinsky Distr., *Fedosov 13-1-147* (MW); **Karachaevo-Cherkessia**: Teberda, 15.VIII.1986 *Ignatova* (LE); **Krasnodar Territory**: Krasnaya Polyana, 6.IX.2008 *Seregin et al.* (MW); **Stavropol Territory**: Beschtau, 11.VII.1843 *Kolenati* (LE); **ASIATIC RISSIA: Yamalo-Nenetskij Autonomous Distr.**: Kolguev Island, 29.VII.1935 *Savicz-Lyubitskaya* (SASY). **Krasnoyarsk Territory:** Taimyr, Ledyanaya Bay, 25.VI.2004 *Fedosov Pol4* (MW); Khatanga settl., *Fedosov 13-3-0864* (MW); Afanasjevskie Lakes, *Fedosov 06-157* (MW); Medvezhya River, *Fedosov 05-212* (MW); Putorana, 3.VIII.1969 *Kuvaev 147-4* (MW); **Evenkiya**: Central-Siberian Nature Reserve, 2.VIII.1992 *Szerbina* (MW); **Altai Republic:** Altai Mts., Bugusun Creek, 19.VIII.1993 *V. Pavlov* (MHA); **Kemerovo Province**: Kuznetsky Alatau 17.VI.2000 Pisarenko (NSK); **Irkutsk Province**: Sukachev et al. 208/2 (LE ex SASY); **Zabaikal'sky Terrritory**: Udokan Mt. Rang, 31.VII.1989, 3.VIII.1985, *Filin* (MW), S+; **Republic Sakha/Yakutia**: Nizhnekolymsk Distr., Alazea River, 13.IX.2008 *Efimova* (SASY #4564); Bulun Distr., Chekanovsky Ridge, 29.VII.1977 *Egorova* (SASY #4561); Olekma-Charsky Highlands, 16.VII.1999, *Ivanova* (SASY #4565); Allaikhovskoe Plateau, Punga Mt., 10.VIII.1978 *Perfiljeva* (SASY #4575); Tokinsky Stanovik Range, 13.VIII.1990 *Volotovsky* (SASY #4591); Aldan Plateau, Uchur River, 10 VII.1991 *Ivanova* (SASY #4594); Suntar-Khayata Mt. Range, Kyurbellakh Creek, *Ignatov & Ignatova 11-213* (MHA), S+; Suntar-Khayata Mt. Range, Mus-Khaya Mt., *Ignatov & Ignatova 11-3275* (MHA); Orulgan Range, Aenigan-Toloono Creek, *Ignatov 11-4591* (MHA); Ust-Maya Distr., Solnechnyj, *Ignatov 00-73* (MHA), S+; Zhigansky Distr., Natara River, 26.VI.1962, *Filin ВФ-960626-5* (MW), S+; Kular Range, 30.VII.1960 *Vekhov* (MW); Novosibirskie Islands, Bolshoj Lyakhovsky Island, 12.VIII.1980 *Karpov* (SASY); **Chukotksky Autonomous District:** Ayon Island, 9.VIII.1958 *Filin* (MW); **Magadan Province:** Nera Upland, *Ivanova 90/1* (SASY); **Kamchatsky Territory**: Ust-Bolsheretsky Distr., Poroj'istaya River, 10.IX.2005, 14.IX.2005 *Samkova 27, 19* (MHA); Commander Islands, Bering Island, *Fedosov 10-3-209, 10-3-1114* (MW); **Khabarovsk Territory**: Verkhnebureisky Distr., *Ignatov #97-543, 97-545, 97-55* (MHA), S+; **Amurskaya Province**: Zeya State Reserve, 27.VIII.1979 *Petelin 34* (MW); **Primorsky Territory:** Olkhovaya Mt., 2.X.2006 *Ignatov et al.* (MHA); **Sakhalinskaya Province:** Kuril Islands, Iturup Island, *Bakalin K-19-27-07* (MHA ex VLA), S+; Kunashir Island, *Ignatov 06-1736* (MHA); Shikotan Island, Nushko *Ш-15.2-06g* (MHA); Dolinsk Distr., Sokol, *Ignatov & Teleganova 06-288* (MHA); Smirnykh Distr., «Vaida Mountain», *Ignatov & Teleganova 06-33* (MHA), S+; Yuhno-Sakhalinsk, *Ignatov & Teleganova 06-364* (MHA); Tymovsky Distr., Nabilsky Mt. Range, *Ignatov & Teleganova 06-657* (MHA), S+.

2. **Polytrichastrum fragile** (Bryhn) Schljakov, Novosti Syst. Nizsh. Rast. 19: 209. 1982.

Polytrichum fragile Bryhn, Rep. Second Norweg. Arctic Exped. Fram 1898–1902 2(11): 122. pl. 1: f. 3. 1906.

Polytrichastrum alpinum var. *fragile* (Bryhn) D.G. Long, Meddel. Grønland, Biosci. 17: 30. 1985.

Figs. 5-6

Plants small to medium-sized. Stems 2-8 cm tall, almost unbranched, with many broken-off leaves. Leaves erect-spreading to somewhat incurved when dry, spreading to reflexed when moist, 3-5(-7)×0.4-0.7 mm; blade moderately abruptly tapered to apex, awn lacking or short, red-brown and smooth; constricted at the junction with obovate sheath and strongly fragile at this line; sheath ± nitid, broadly hyaline-margined; marginal lamina erect, 4-6 cells wide, subentire or slightly serrulate in distal half; lamellae 20-30, in profile ± entire, 5-7 cells high, marginal cells coarsely papillose (papillae being rather even on their surfaces), in cross-section ovate to narrowly ovate, outer wall strongly thickened, walls yellowish to deep brown. Blade marginal cells subquadrate, 13-16(-20) μm; sheath median cells 30-65×6-10 μm, elongate-rectangular, mostly 4-5(-7):1. Seta to 2 cm. Capsules pale to dark brown, inclined and somewhat curved, terete, 1.0-1.5 μm wide, 2-3 mm long. Spores 16-18 μm.

Differentiation. The distinctive habit of *P. fragile* is usually described as being a result of the fragile leaves, which is true, but almost 'leafless' plants do not always belong *P. fragile.* There are fragile-leaved forms of *P. alpinum* s.str., which differ from *P. fragile* in the way that the blade detaches from the sheathing base.

These differences are illustrated in Figs. 4-7: *P. fragile* has a conspicuous constriction at the junction of the blade and sheath, and also the blade is more or less swollen, whereas in *P. alpinum* fragile leaves have no or only a slight constriction at this point and the fractures are irregular, usually through the upper part of the sheath.

Furthermore, *P. fragile* has strongly papillose and incrassate walls in the distal cells of the lamellae and in subentire leaf margins. The former character serves to distinguish it from *P. septentrionale*, where the distal cells of the lamellae are usually rather weakly papillose. Although strongly papillose cells are not rare in *P. alpinum*, its leaves are strongly serrate.

Distribution and ecology. As is also the case for *P. septentrionale*, the distribution of *P. fragile* is imperfectly known. Moreover its "key character", fragile leaves in the broadest sense, also occur in other species. Smith Merrill (2007) reported it from Alaska in the USA, Northwest Territories in Canada, Greenland, Scandinavia and northern Siberia. Podpera (1954) did not accept it at any rank. In the studied collections, the species has been found mostly on the islands of the Arctic Ocean and rather close to the coast in the continental Arctic. The data in the literature are unreliable, as quite a number of putative specimens in herbaria represent fragile forms of *P. alpinum*.

Specimens examined: **EUROPEAN RUSSIA: Arkhangelsk Province**: Frants-Josef Land, Hooker Island, 14.VIII.1979 *Safronova* (LE). **ASIATIC RUSSIA: Krasnoyarsk Territory:** Dickson Island, 7.VIII.1959, *Dorogostaiskaya* (LE); Taimyr, Ary-Mas, 13.VIII.1972, *Norin* (LE). **Magadan Province:** Ola Distr., Sparafieva Island, 12.IX.1980 *Blagodatskikh* (LE); **Republic Sakha/Yakutia**: Tiksi, 6.IX.1956 *Katenin 73* (LE); Al-

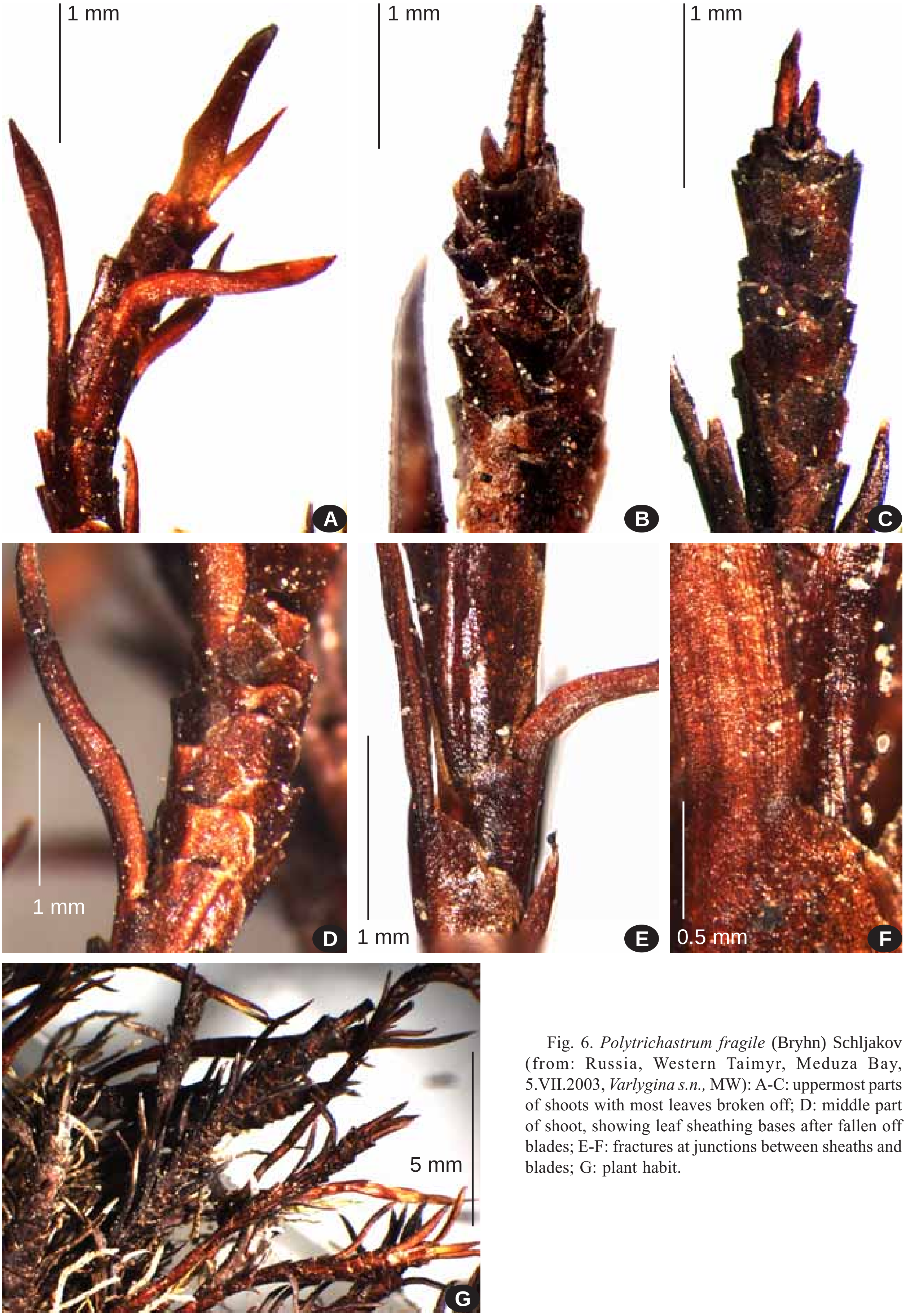


Fig. 6. *Polytrichastrum fragile* (Bryhn) Schljakov (from: Russia, Western Taimyr, Meduza Bay, 5.VII.2003, *Varlygina s.n.,* MW): A-C: uppermost parts of shoots with most leaves broken off; D: middle part of shoot, showing leaf sheathing bases after fallen off blades; E-F: fractures at junctions between sheaths and blades; G: plant habit.

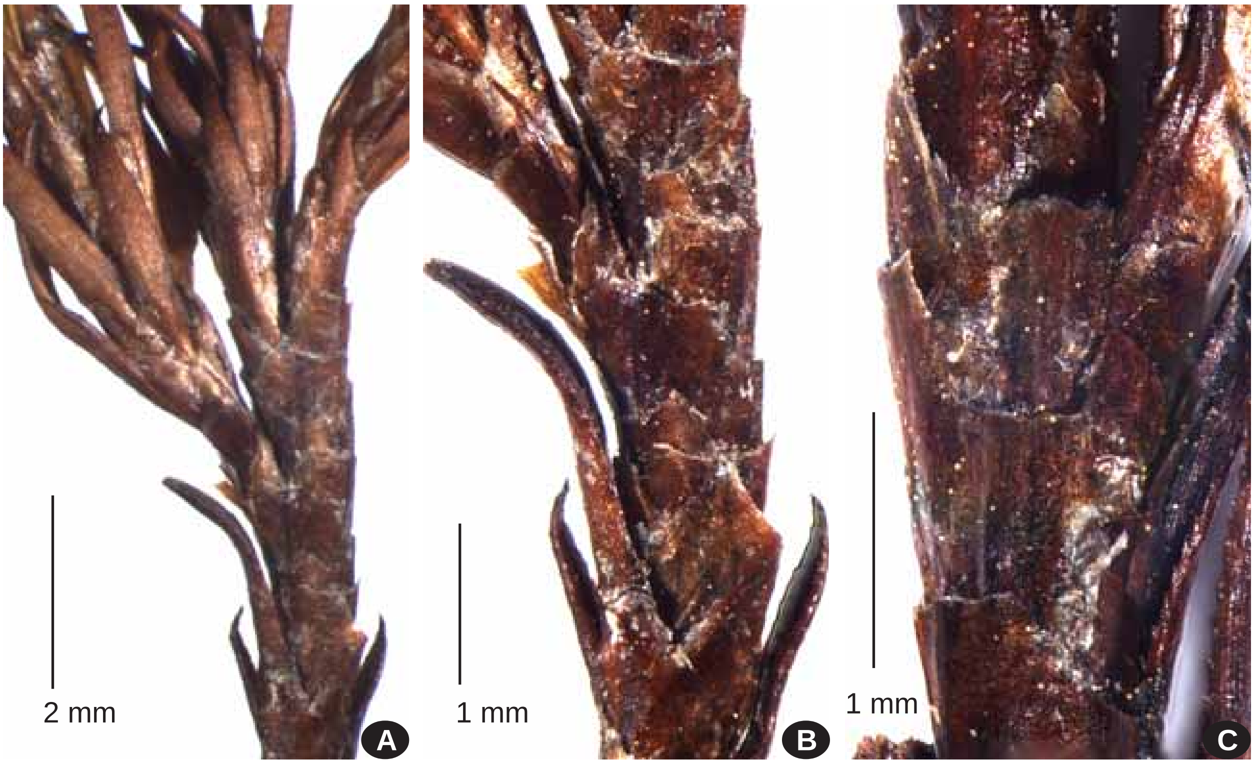


Fig. 7. *Polytrichastrum alpinum* (Hedw.) G. L. Smith, fragile form (from: Russia, Murmansk Provinse, Khibiny Mts, Tuliok River, 2.VIII.1930, *A.A. & M.B. Korchgin*, LE): A-C: shoots of Arctic plants of *P. alpinum*, showing irregular fractures of blades from sheaths. Compare with Figs. 5-6.

laikhovsky Distr., East-Siberian Sea coast, 25 km NW from the left shore of Kolymskaya Guba, 17.VIII.1976 *Perfiljeva* (SASY #4643); Bulun Distr., 60 km SW of Dunai Island, 20.VIII.1982 *Anonym* (SASY #4642); Severnaya Zemlya Archipelago, Bolshevik Island, VII-VIII.1978 *Matveeva* (LE); **Chukotsky Autonomous District:** Vankarem Cape, 28.VII.1934 *Gorodkov* (LE); Kolyuchin Island, 25.VII.1938 *Gorodkov* (LE).

3. **Polytrichastrum septentrionale** (Brid.) E.I. Ivanova, N.E. Bell & Ignatov comb. nov.

Polytrichum septentrionale Brid., J. Bot. (Schrader) 1800 (1): 285. 1801.

Polytrichastrum alpinum var. *septentrionale* (Brid.) G.L. Smith, Mem. New York Bot. Gard. 21(3): 37. 1971. Fig. 8

This species has been accepted in the genus *Polytrichastrum* under the name *P. norwegicum* (Hedw.) Schljakov. However this name cannot be applied to this species. Smith (1971, expanded footnote on page 37) lectotypified *Polytrichum norwegicum* Hedw. with an illustration by Oeder (of *P. oederi*) in Flora Danica (Fl. Dan. 2(5): 9, t. 297, 1766). This illustration depicts capsules that are inclined-horizontal, quite elongated and smooth-cylindrical, thus resembling *P. alpinum*, not *P. septentrionale*. Ignatov & Smith Merill (1995) stated that the type of *P. norwegicum* is a form of *P. alpinum*, not identical with *P. alpinum* var. *septentrionale*.

Plants medium-sized. Stems 1-3(-8) cm tall, usually unbranched. Leaves erect to inrolled when dry, spreading when moist, 3-5×0.4-0.75 mm; blade rather abruptly tapered to a short, smooth awn or subcucullate apex; sheath short obovate, with tapering shoulders, ±nitid, hyaline-margined distally; marginal lamina erect to ±incurved, 2-5 cells wide, subentire, with few small blunt teeth distally and occasionally to the middle of the blade. Lamellae 18-26, in profile ±entire to slightly wavy, 6-9 cells high, marginal cells slightly or, more rarely, coarsely papillose (papillae being rather even on their surfaces), in cross-section ovate to narrowly ovate, outer walls strongly thickened, lumen pentagonal, walls often yellowish to brown, occasionally colorless. Blade marginal cells round-quadrate, 12-15 μm, in proximal portion of blade often thick-walled and transversely elongate; sheath median cells 30-50×6-10 μm, rectangular, mostly 4-6:1. Seta 1-2 cm. Capsules ±dark brown, inclined to almost pendent, ovate-cylindric to subglobose, ca. 1.0-1.5 mm wide, 1.5-2 mm long. Spores 17-22 μm.

Differentiation. *P. septentrionale* often occurs without capsules; in this case it can be differentiated from *P. alpinum* only by the weak serration of the leaf margin. However, this isolated character appears to be consistently supported genetically. In addition, *P. septentrionale* differs from *P. alpinum* in its somewhat larger spores (17-22 μm, average 20 μm vs. 14-20 μm, average 17 μm in *P. alpinum*), usually subglobose capsules, smaller plant size, and its distribution in the Arctic, more rarely in the alpine zone of high mountains, with a clear tendency to occur in regions with an oceanic climate.

More problematic is differentiation between *Polytrichastrum septentrionale* and *P. altaicum*. The apical cells of the lamellae in the former species are papillose with more or less incrassate distal walls, whereas they are

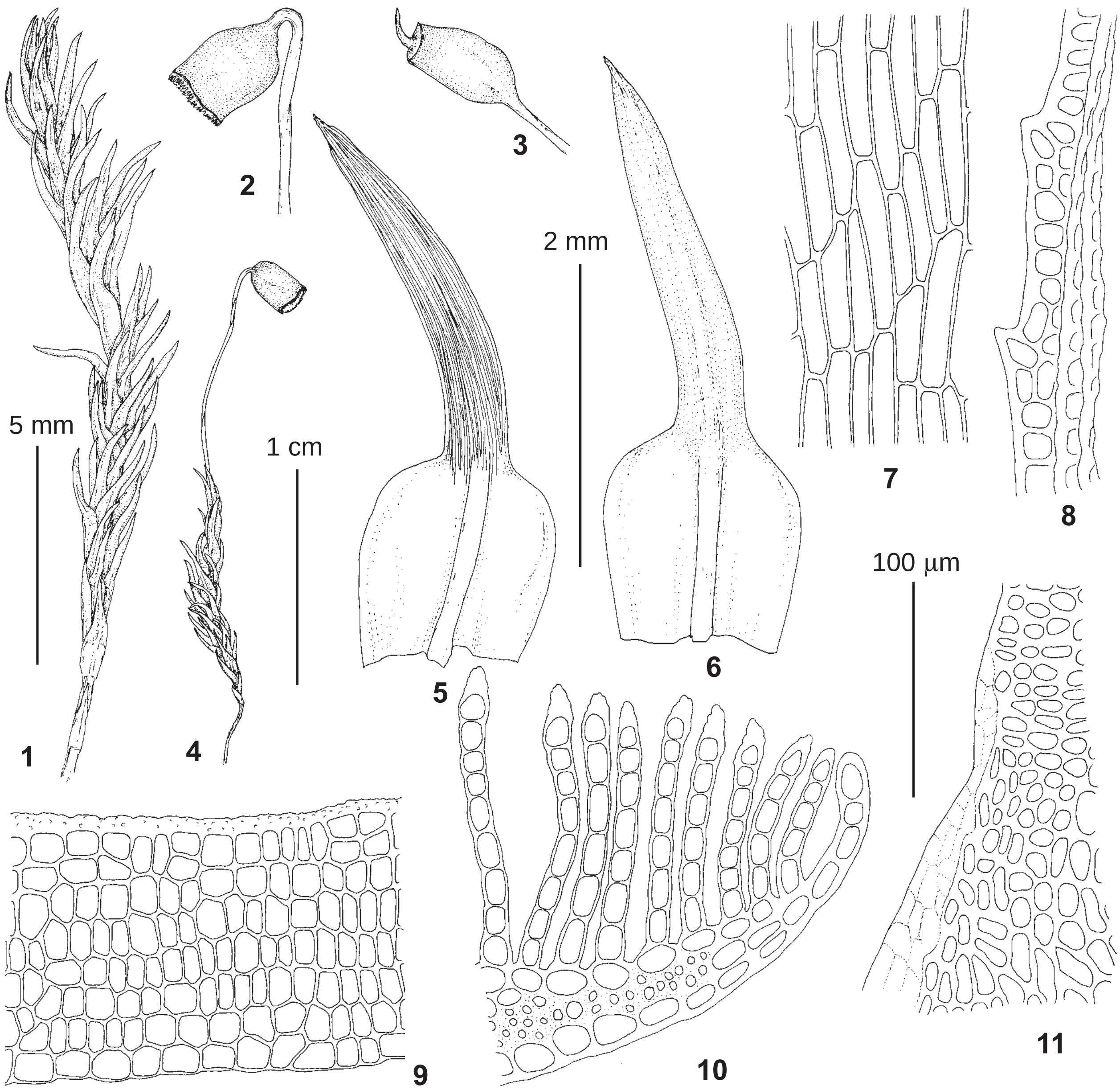


Fig. 8. *Polytrichastrum septentrionale* (Brid) E.I. Ivanova, N.E. Bell & Ignatov (from: Russia, Sakhalin Island, Nabylsky Mt. Range, *Ignatov & Teleganova #06-591*, MHA): 1 – habit, wet; 2-3 – capsules; 4 – habit, dry; 5-6 – leaves; 7 – basal laminal cells; 8 – median laminal cells at leaf margin; 9 – side view of lamella; 10 – leaf transverse section; 11 – cells at leaf shoulder. Scale bars: 1 cm for 4; 5 mm for 1-3; 2 mm for 5-6; 100 μm for 7-11.

perfectly smooth in the latter, with walls less strongly thickened distally, and in addition cells of the sheathing base are slightly longer, 4-6:1 vs. 3-5:1 in *P. altaicum*. Also *P. altaicum* has a tendency to somewhat more inrolled leaf margins and more subcucullate leaf apices. Genetically *P. altaicum* is very close to *P. septentrionale* (only one substitution in *trn*L-F and no differences in *rps4*), but the differences in both morphology and sequence data are about the same as between some other taxa of this complex, *e.g.*, the Himalayan *P. emodii* and the Himalayan-Beringian *P. papillatum.*

Polytrichastrum septentrionale differs from *P. sexangulare* in its not distinctly cucullate leaf apices, less incurved blade margins, papillose apical lamellar cells, at least a few blunt marginal teeth in the distal part of the leaf, and a capsule that is perfectly round in transverse section (vs. ±angular).

Distribution and ecology. Due to previous recognition at the infraspecific level, as well as the subtlety of its differentiating characters and absence of unanimous acceptance, the distribution of this species is rather approximately known. It is generally known from the Arctic, but also occurs in high mountains: in North America south to California, Utah and Colorado (Smith Merrill, 2007), in Western Europe to Spain and the Caucasus (Podpera, 1954). The Russian collections indicate that the

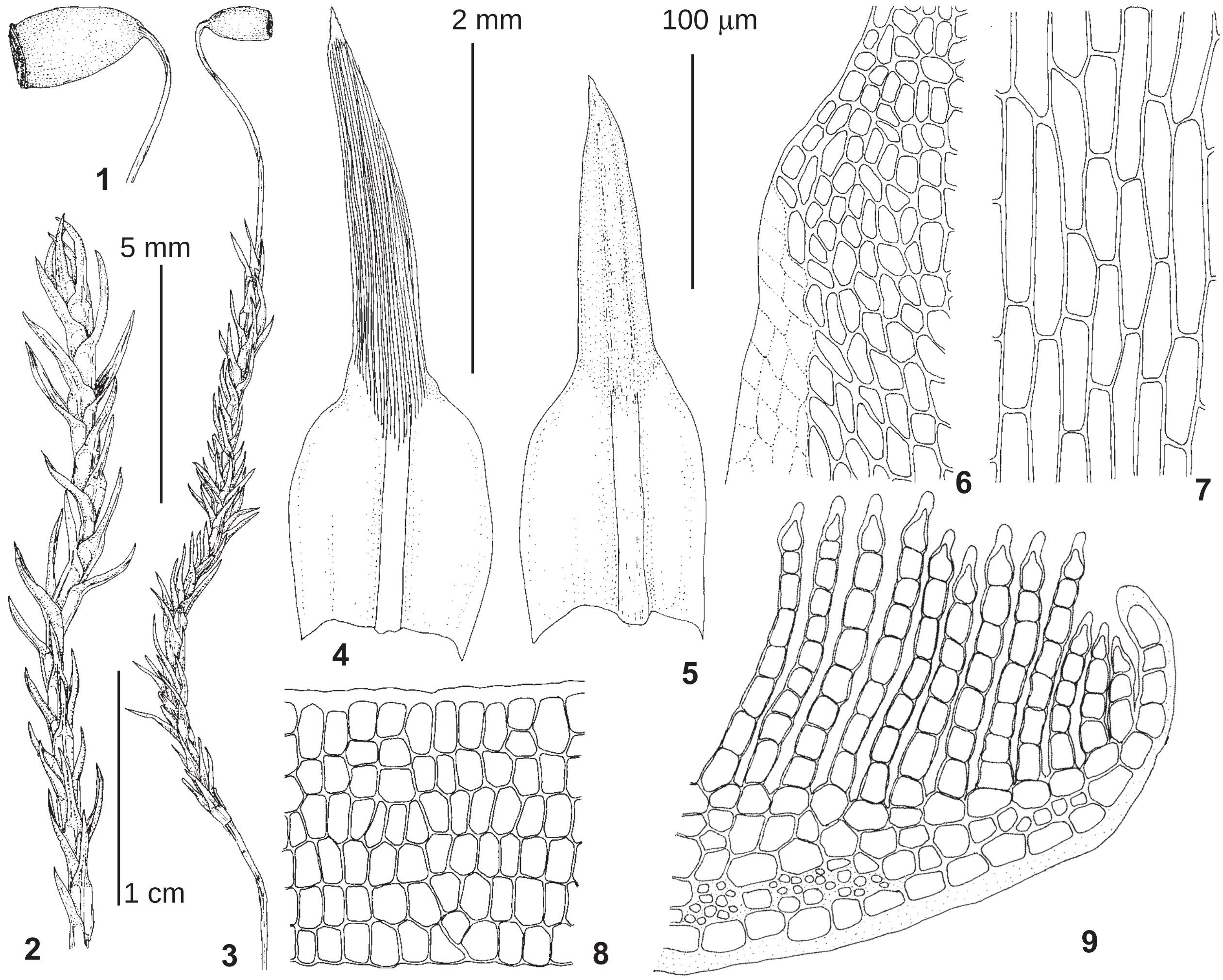


Fig. 9. *Polytrichastrum altaicum* Ignatov & G.L. Sm. (from: Russia, Altai Republic, Dvukhkarovaya Creek, *Ignatov #36/361*, MHA): 1 – capsule; 2 – habit, dry; 3 – habit, wet; 4-5 – leaves; 6 – cells at leaf shoulder; 7 – basal laminal cells; 8 – side view of lamella; 9 – leaf transverse section. Scale bars: 1 cm for 3; 5 mm for 1-2; 2 mm for 4-5; 100 µm for 6-9.

species is more common and penetrates further to the south in regions with oceanic climates, although solitary records from inland mountains (*e.g.*, Altai) are also known. The species grows on soil and rocks in a wide range of habitats, mostly in open areas.

Specimens examined: **EUROPEAN RUSSIA: Murmansk Province:** Kola Peninsula, 12.VIII.1885, *Brotherus* (LE #356), S+; Khibiny Mts: Vudyavrchorr Mt., 18.VII.1947, *Schljakov* (LE); Rasvumchorr Mt., 9.VIII.1949, *Schljakov* (LE); S+; Takhtarvumchorr Mt., 11.VII.1973, *Schljakov* (LE); **Nenetsky Autonomous District**: Franz Jopsef Land, 26.VII.1930 *V. Savicz* (LE #1997, 1484); same place, 30.VII.1930 *V. Savicz* (LE №755); same place, 1.VIII.1930 *V. Savicz* (LE #1877); Vise Island, 14.VIII.1930 *V. Savicz* (LE #1571). **ASIATIC RUSSIA: Yamalo-Nenetsky Autonomous District**: Yamal, 30.VIII.1982, *Rebrisaya* (SASY #199); Yamal, 13.VII.1977, *Andreeva* (LE); **Altai Republic:** Malaya Kokorya River, *Ignatov 36/53* (MHA), S+; **Krasnoyarsk Territory:** Taimyr, 14.VII.1901, *Birulya* (LE), S+; Putorana, Kapchuk Lake, 25.VII.1982, *Czernyadjeva 98* (LE); Khatanga settl. outskirts, *Fedosov 11-1298, 13-3-0355* (MW, as *Polytrichastrum sexangulare*); Odichincha Mt., *Fedosov 07-303* (MW); Sibiryakov Island, 6.VIII.1989, 14.VII.1990, *Kuvaev 1357-23, 1471-9* (MW), S+; **Republic Sakha/Yakutia:** Novaya Sibir Island, 5-18.VI.1902, *Birulya* (LE), S+; same loc., 12-25.VII.1902, *Birulya* (LE), S+; *same loc.*, 31.VII.1903, *Brusnew* (LE), S+; Olenek River lower course, 1.VIII.1932, *Sochava* (LE), S+; Bolshoi Lyakhvsky Island, 17.VI.1956, 14.VIII.1956, 26.VIII.1956, *Aleksandrova* (LE); same loc., 24.VIII.1956, *Pigulevskaya* (MHA), S+; Tokinsky Stanovik Range, 6.VIII.1987, 22.VII.1990, *Volotovsky* (SASY); Tarbagannakh Creek, *Ignatov 00-722* (MHA); same loc., 25.VIII.2001, *Ivanova* (SASY); **Chukotksky Autonomous District:** Chaplino Hot Springs, 29.VIII.1956, *Tikhomirov* (LE); same loc., 5.VIII.1957, *Gavrilyuk* (LE); Chaplin Cape, 6.IX.1956, *Tikhomirov* (LE); 32 km of road Aegvekinot – Iultin, 18.VIII.1967, *Zimarskaya* (LE); Provideniya Bay, 6.VII.1969, 11.VII.1969, *Afonina* (LE); Nunligran, 26.VI.1970, 1.VII.1970, 9.VII.1970, *Afonina* (LE); Aerguveem River, 3.VIII.1970, *Afonina* (LE), S+; Achchen Lake, 14.VII.1970, 17.VII.1970, *Afonina* (LE), S+; Getlyanen River, 31.VII.1976, *Afonina* (LE); Arakamchechen Island, 15.VIII.1976, 16.VIII.1976, *Afonina* (LE); Televeem River, 23.VII.1979, *Afonina* (LE), S+; Pekulney Lake, 27.VII.1986, *Kuzmina* (LE); **Kamchatsky Territory:** sine loco, 3.VI.1908, *Ramensky* (LE), S+; Ushkovsky Volcano, 25.VII.2003, 20.VIII.2004 *Czernyadjeva 70, 102*(LE),

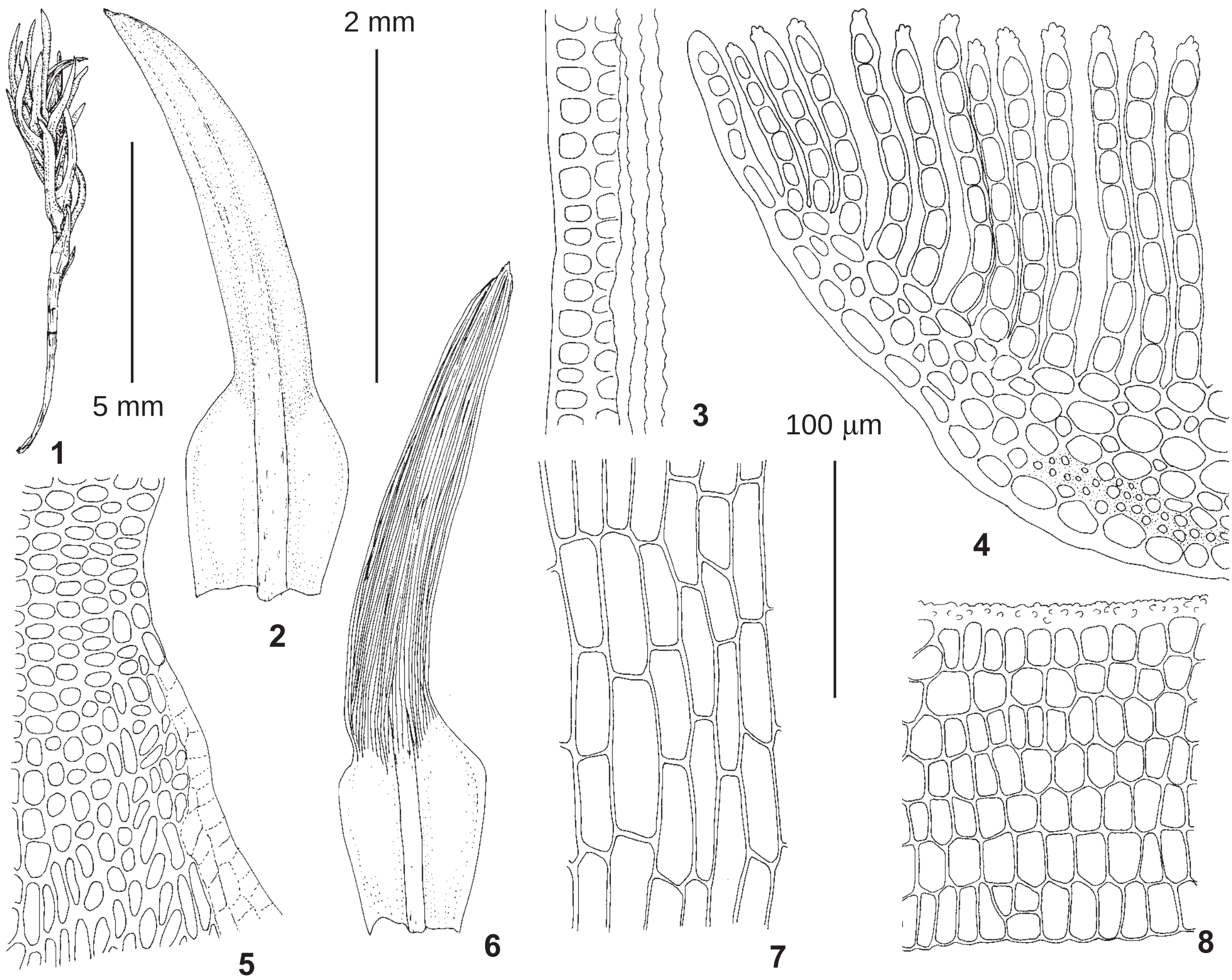


Fig. 10. *Polytrichastrum* cf. *papillatum* G.L. Sm. (from: Russia, Chukotka, Palyavaam River, 19.VII.1989 *Afonina s.n.*, LE): 1 – habit, dry; 2, 6 – leaves; 3 – median laminal cells at leaf margin and lamellae; 4 – leaf transverse section; 6 – cells at leaf shoulder; 7 – basal laminal cells; 8 – side view of lamella. Scale bars: 5 mm for 1; 2 mm for 2, 6; 100 µm for 3-5, 7-8.

S+; Commander Islands, Bering Island, *Fedosov 10-3-1114* (MW); **Sakhalinskaya Province**: Sakhalin, Nabylsky Mt. Range, *Ignatov & Teleganova 06-591* (MHA); Okha Distr., *Pisarenko 03179* (MHA), S+.

4. **Polytrichastrum altaicum** Ignatov & G.L. Smith Merril, Arctoa 5: 76, fig. 29. 1995. Fig. 9.

Plants small to medium-sized for the genus, in moderately dense but easily separating tufts, green to red-brown with age. Stem 1-4(-6) cm, unbranched, densely foliate above, leafless below. Leaves erect-spreading to somewhat curved when dry, spreading when moist; sheath 2×1.5 mm, broadly elliptic, hyaline-margined, blade narrowly triangular, straight to subfalcate, 2-4×0.3-0.5 mm; marginal lamina 4-5 cells wide, entire (or in some leaves with a few irregular teeth above); costa ending in a shortly apiculate or subcucullate tip. Lamellae (22-)26-30(-34), in profile ±entire or a little wavy, 6-9 cells high, marginal cells smooth, in cross-section narrowly pyriform, slenderly tapering and ending in a thickened knob, distal wall only moderately thickened. Median sheath cells rectangular, 32-40×10-13 µm. Seta rather stout, 0.5-2 cm long. Capsules ovoid-cylindric to short elliptic, or occasionally globose erect to inclined, 2-2.5×1.5-2 mm; exothecial cells smooth, irregularly rectangular, lacking thin spots. Operculum rostrate, beak about 0.5 mm long. Peristome 0.2 mm long, divided to 0.6 of its length, the teeth ca. 50, reddish brown except for the margins. Spores 16-18 µm, finely papillose.

Differentiation and variation. By habit, *Polytrichastrum altaicum* does not differ greatly from the moderately developed *P. alpinum* or *P. septentrionale* or *P. sexangulare.* The short subglobose capsules occur rarely in *P. alpinum* as well, however perfectly smooth distal lamellar cells and subentire leaves are too odd for *P. alpinum.* Smooth lamellar margins occur in *P. sexangulare*, another high mountain species, which also has entire leaf margins. However, *P. sexangulare* has (4-)6-angled capsules on generally longer setae, leaves bluntly and very distinctly cucullate at the apex, and difference in upper cells of lamellae as explained in the key. In addition, molecular differentiation between *P. altaicum* and *P. sexangulare* is very distinct. Relatively short, terete capsules and entire leaf margins are characteristic of *P. septentrionale,* which however has distal cells of lamellae papillose and with stronger incrassate walls. Despite these differences, *P. septentrionale* and *P. altaicum* are closely related taxa according to our molecular results. The Himalayan *P. emodi* G.L. Sm. also has lamellae with smooth apical cells, but it differs from *P. altaicum* in its toothed leaves and cylindric capsules.

Distribution and ecology. The species was described from a single collection, and a revision of additional Altaian collections did not reveal more specimens. However, it has subsequently been found in northern Finland, the Kola Peninsula, the Ural Mts, and the East Sayan Mts (Cis-Baical Region). Records are few, and obviously it is a rare species, restricted mostly to inland areas (somewhat unlike *P. septentrionale*, which is known from Pacific coastal regions in many areas). The species grows in rocky tundras, new glaciers, the margins of late snow beds, along cold brooks, and on cliffs beside snow fields, at and above the timber-line.

Specimens examined: **EUROPEAN RUSSIA**: **Murmansk Province**: Khibiny Mts, 31.VII.2004, *Filin* (MW); **Perm Territory:** Molebny Kamen Range, 8.VII.1998 *Bezdodov 252* (LE); **ASIATIC RUSSIA: Altai Republic:** Dvukhkarovaya Creek, *Ignatov 36/361* (MHA); **Irkutsk Province**: Udinsky Range, 3.VII.1961, *Bardunov* (LE).

FINLAND: Lapland, 3.VII.2006, *Bell 7* (H).

5. **Polytrichastrum** cf. **papillatum** G.L. Sm., J. Hattori Bot. Lab. 38: 633. f. 12–24. 1974. Fig. 10

Plants small for the genus, in moderately dense tufts, green to red-brown with age. Stems 1 cm, unbranched, densely foliate above, leafless below. Leaves erect to appressed when dry, spreading when moist, 3.5-4.0×0.5 mm; sheath 1-1.5×1 mm, broadly elliptic to obovate, hyaline-margined, blade lanceolate, straight to subfalcate, to 2×0.5 mm; marginal lamina 4-5 cells wide, entire (or, in some leaves, with a few irregular teeth above); costa ending in a shortly apiculate tip. Lamellae 28-31, in profile ±entire or somewhat wavy, 7-8 cells high, lamellar marginal cells in cross-section narrowly pyriform, slenderly tapering and ending in a knob, with papillae crowded near the top of the knob, otherwise cell walls thin and smooth. Median sheath cells rectangular, 50-70×20-25 μm. Sporophytes unknown in Russian material.

Differentiation and variation. *Polytrichastrum papillatum* has a specific crown-like papillae arrangement on top of the 'knob' on the distal cell of the lamellae. The second diagnostic character for this species is the wavy outline of the lamellae when viewed laterally (Smith, 1974); this is not always apparent in Russian material, or it occurs only in certain places, while in other places the lamellae are totally entire. We tentatively place the only specimen from Chukotka in this species, for both morphological and phytogeographical reasons. Most significant is the pattern of crowded papillae, quite distinct from any other species of the genus occurring in Russia. The recent discovery of *P. papillatum* in Alaska (Smith Merrill, 2007), close to Chukotka, is additional evidence in that at least a peculiar *P. papillatum*-like morphotype occurs in the Beringian region.

Two points are against the immediate placement of plants from Chukotka in *P. papillatum*: (1) certain differences in *trn*L-F and *rps*4 sequences, which place plants from Chukotka and the Himalayas in different, albeit very close, haplotypes, cf. Fig. 2, and (2) smooth to only slightly wavy distal margins of lamellae, as seen in the lateral view. At the moment, it is impossible to determine based on the available material if these difference are caused by variation within one species, or if the Beringian plants comprise an undescribed rare northern species.

Distribution and ecology. Following its description in 1974 the species had been considered a Himalayan endemic until Smith Merrill (2007) reported it from Alaska, where it has been found at only one site in a sterile condition. Its discovery in the present study was equally unexpected. The plant was collected in "nival tundra on rocky slope".

Specimen examined: **ASIATIC RUSSIA: Chukotsky Autonomous District**: Palyavaam River middle course, 19.VII.1989, *Afonina* (LE).

Polytrichastrum sexangulare (Floerke ex Brid.) G.L. Sm., Mem. New York Bot. Gard. 21(3): 35. 1971.

Polytrichum sexangulare Floerke ex Brid., J. Bot. (Schrader) 1800(1): 285. 1801.

Fig. 11

Plants rather small and wiry, green to reddish brown with age, densely leafy, to 3(-6) cm high. Leaves erect and broadly incurved when dry, erect-spreading when moist, 3-6×0.5 mm; sheath broadly elliptic, hyaline-margined, strongly contracted to the blade; marginal lamina entire to remotely denticulate, erect to narrowly inflexed in the distal half of the blade, 2-6 cells wide; costa percurrent; apex blunt and ± cucullate. Lamellae 6-7(-8) cells high, in profile weakly crenulate, the lamellar marginal cells in cross-section narrowly ovoid to slightly pyriform, smooth, with a thickened outer wall, only slightly wider than the cells beneath. Median sheath cells rectangular, 24-80×9-14(-18) μm; cells of the marginal lamina quadrate to hexagonal, rather thick-walled, 11-14 μm wide and long. Seta stout, yellowish brown, to 4 cm long. Capsules obtusely (4-)6-angled to distictly 6-angled (rarely almost terete and subglobose), erect to somewhat inclined, 3×1.5 mm, with a small apophysis delimited by a shallow or occasionally quite sharp groove. Exothecial cells smooth, irregularly rectangular, with an elongate lighter area in the cell centre due to a pit in the inner cell wall. Operculum rostrate. Peristome 0.3 mm high, divided to 0.3-0.5 of its length, the teeth ca. 50, simple, rather slender, at times somewhat colored in the median portion. Epiphragm with well-developed tooth-like processes. Spores 16-18 μm, finely papillose.

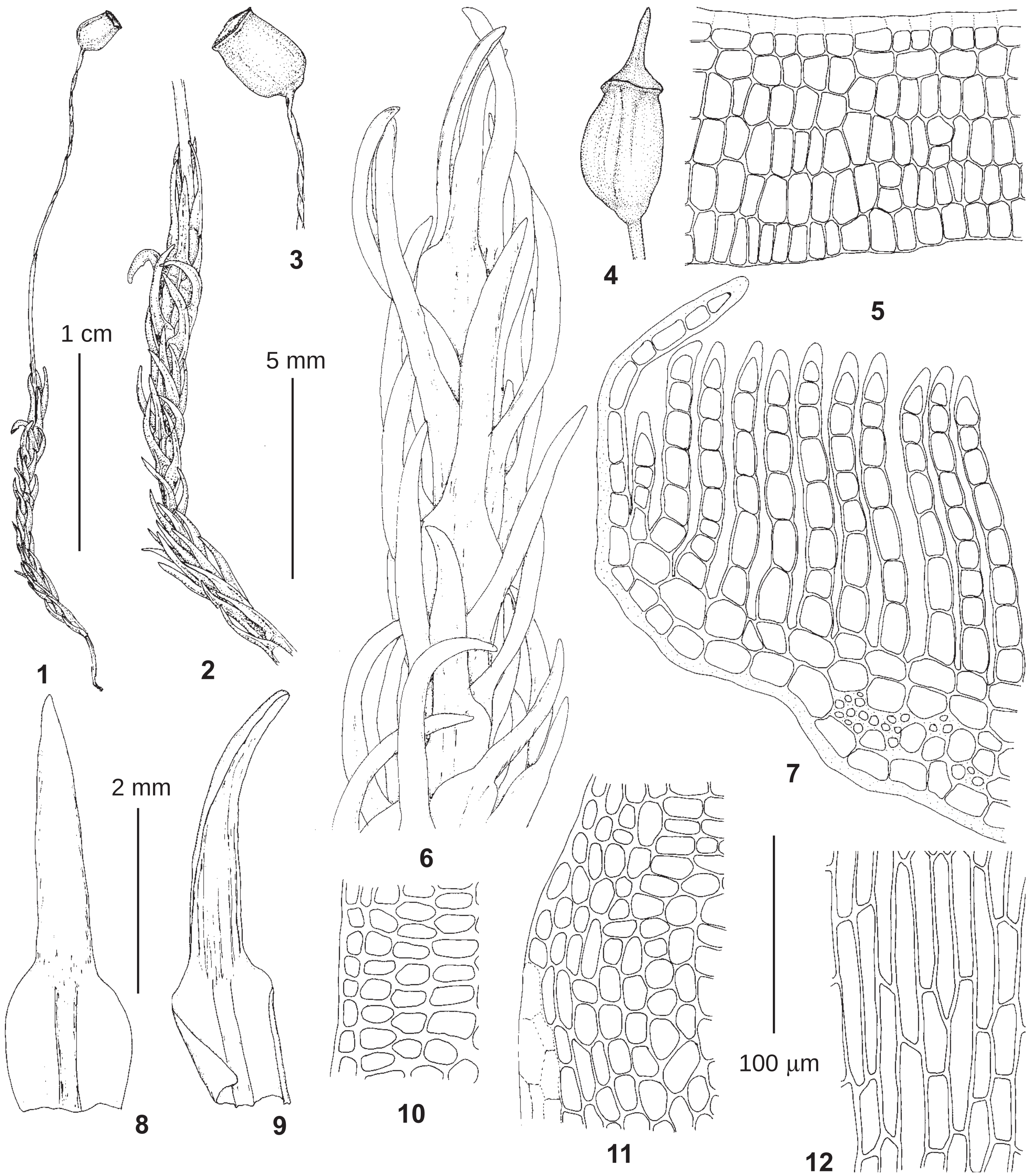


Fig. 11. *Polytrichastrum sexangulare* (Floerke ex Brid.) G.L.Smith (1-3, 5, 11 – from: Russia, Karachaevo-Cherkessia, Teberda Reserve, 3.IX.2005 Ignatov & Ignatova, MW; 4, 6-10, 12 from: Russia, Perm Province, North Ural, 19.VII.1878 Krylov (H): 1-2, 6 – habit, dry; 3-4 – capsules; 5 – side view of lamella; 7 – leaf transverse section; 8-9 – leaves; 10 – median laminal cells at leaf margin; 11 – cells at leaf shoulder; 10 – basal laminal cells. Scale bars: 1 cm for 1; 5 mm for 2-3; 2 mm for 4, 6, 8-9; 100 μm for 5, 7, 10-12.

Differentiation. *Polytrichastrum sexangulare* can usually be distinguished even with a hand-lens due to the cucullate apex and entire leaf margins. Unlike *Polytrichum juniperinum*, the marginal lamina is narrow and erect, or narrowly inflexed, scarcely exceeding the lamellae in height, and not hyaline.

This species is at times difficult to distinguish from *P. septentrionale* and *P. altaicum*, which also have subentire leaf margins. The former species differs in cylindric or globose capsule, while *P. sexangulare* has angular capsules, which are highly diagnostic but rather rarely produced; under microscope a reliable character of *P. septentrionale* is papillose distal cells on the lamellae, which are parfectly smooth in *P. sexangulare*.

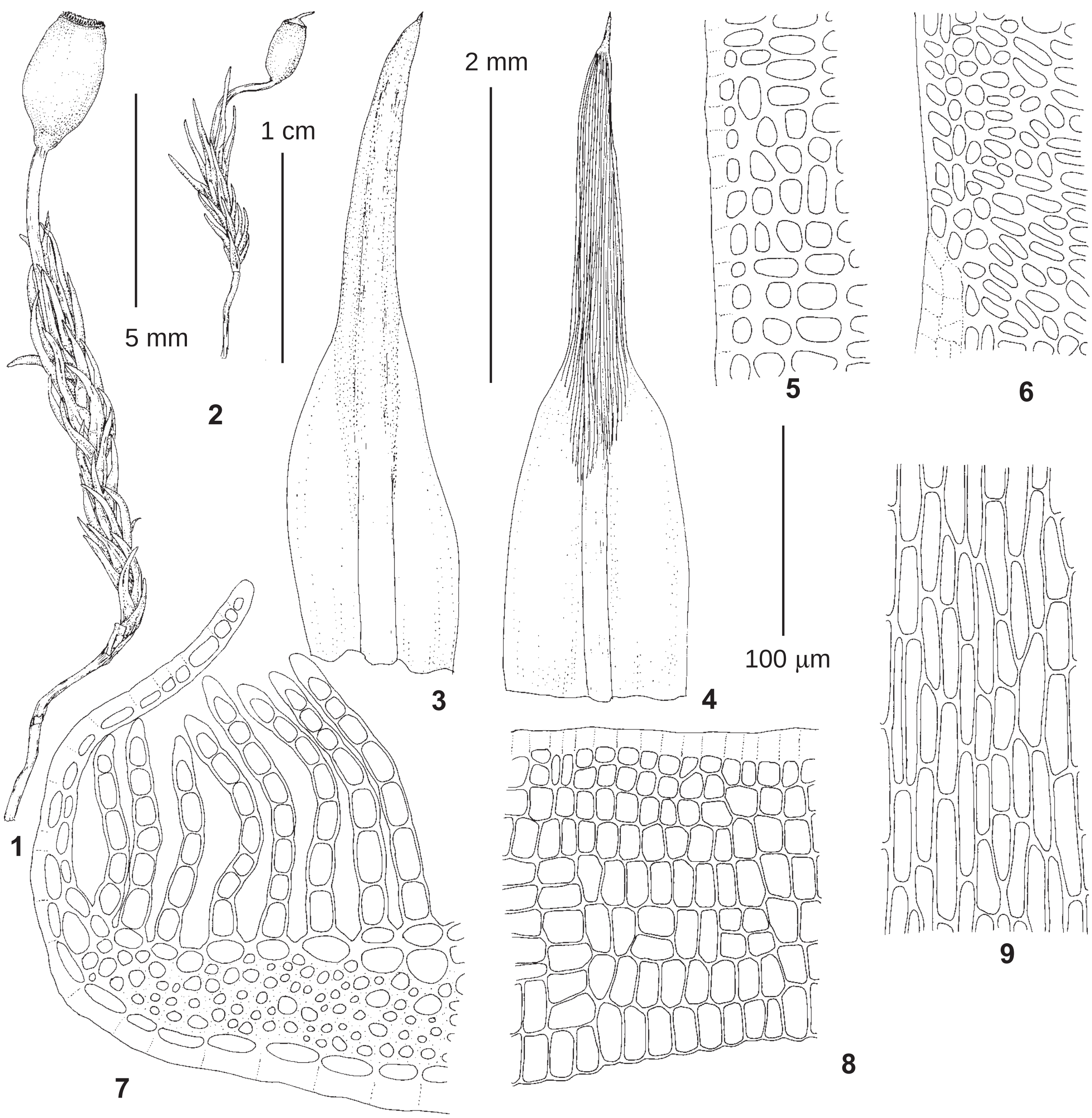


Fig. 12. *Polytrichastrum sphaerothecium* (Besch.) J.-P. Frahm (from: Russia, Kamchatka, *Fedosov #12-351*, MHA): 1 – habit, wet; 2 – habit, dry; 3-4 – leaves; 5 – median laminal cells at leaf margin; 6 – cells at leaf shoulder; 7 – leaf transverse section; 8 – side view of lamella; 8 – basal laminal cells. Scale bars: 1 cm for 2; 5 mm for 1; 2 mm for 3-4; 100 µm for 5-9.

When mature capsules are available, the differentiation of *P. altaicum* from *P. sexangulare* is easy, and the former species has capsule cylindric or globose. For sterile plant essential are the difference the shape of upper cells of lamellae as it is seen on transverse section and pattern of its thickening, as it is seen on side view of lamellae (cf. Figs. 9 and 11).

Distribution and ecology. *P. sexangulare* has a rather scattered distribution in cool and especially montane regions of the Holarctic. It is known from Northern Europe (including Svalbard and Iceland), Central Europe, the Caucasus, Turkey, the Northern Urals, the mountains of southern Siberia, the basin of the Okhotsk Sea (Kamchatka and the Northern Kuril Islands), the Chukotka Peninsula, Japan, and Pacific and Arctic North America. In many regions *P. sexangulare* is not a common species. It grows in various types of tundra, especially rocky ones, often close to late snow beds, as well as in alpine meadows.

Specimens examined: **EUROPEAN RUSSIA: Murmansk Province**: Khibiny, *Ignatov & Ignatova 12-89* (MHA); **Nenetskij Autonomous District**: Kamennaya Viska River, 5.IX.2008, *Lavrinenko & Kholod* (LE); Indiga River, 30.VIII.2008, *Lavrinenko & Kholod* (LE); **Komi Republic:** Shchugor River, 11.VII.1928 *Sochava* (LE); **CAUCASUS: North Ossetiya**: Shulu Pass, 8.VIII.1925, *Bush & Bush* (LE);

Karachaevo-Cherkessian Republic: Teberda, Malaya Khatipara, 2800 m, 3.IX.2005, *Ignatov & Ignatova* (MHA, S-B114225); Pshish River, 25.VIII.1988, *Akatova* (MHA, CSR); Dombay, 18.VIII.1947, *Tumadzhanov* (LE, 12881). **Krasnodar Territory**: Bambak Camp, 14.VIII.1927, *Kosenko* (LE #12883). **ASIATIC RUSSIA: Yamalo-Nenetsky Autonomous District**: Sob River, 17.VII.1988 *Czernyadjeva* (LE); **Khanty-Mansi Autonomous District**: Berezovsky Distr., 9.VIII.1949 *Kuvaev* (LE); **Altai Republic**: Balaktykol Lake, 2.VIII.1915 *Krylov* (LE); Bystraya Creek, 1800 m, 20.VII.1968 *Krylov & Rechan* (LE); Karatumysh, 2110 m, 14.VIII.1978 *Zolotukhin & al.* (MHA); Kobiguayuk Creek, 2800 m, *Ignatov 0/193* (MHA); Perevalnaya Creek, 1900 m, 11.VII.1984 *Zolotukhin & al.* (MHA); Sumultinskij Belok, 14.VIII.1923, *Anonymous* (LE); Talyzkiye Belki, *Pobedimova 672* (LE); **Kemerovo Province**: Kanym Mt., 20.VII.1998 *Pisarenko op02593* (NSK); **Krasnoyarsk Territory**: Taimyr Municipal Distr., Khatanga, *Fedosov 13-3-0355* (MW); **Khabarovsk Territory**: Dusse-Alin, Medvezh'e Lake, 9.VIII.1997 *Ignatov 97-539* (MHA). **Kamtchatsky Territory**: Vodopadny Creek, 19.VIII.2006 *Czernyadjeva 37* (LE); Bilchenok Glacier, 16.VII.2003 *Czernyadjeva 18* (LE); Arbunat Lake, 8.VIII.2007 *Czernyadjeva 17* (LE); Commander Islands, Bering Island, *Fedosov 10-3-355* (MW); **Sakhalinskaya Province**: Granichnaya Mt., 15.VIII.2006 *Ignatov & Teleganova 06-591* (MHA); Kuril Islands, Iturup, *Bakalin K-18-14-07* (MHA).

Polytrichastrum sphaerothecium (Besch.) J-P. Frahm, Kleine Kryptogamenfl. (ed. 6) 4: 142. 1995.

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Polytrichum sexangulare var. *vulcanicum* C.E.O. Jensen, Bot. Tidsskr. 20: 109. 1896.

Polytrichastrum sexangulare var. *vulcanicum* (C.E.O. Jensen) G.L. Merr., Bryologist 95: 270. 1992.

Fig. 12

Plants small to medium-sized. Stems 1-2(-3) cm, usually unbranched, curved towards substrate. Leaves erect to inrolled and appressed to stem when dry, erect-spreading when moist, 2.5-4.5×0.4-0.8 mm; sheath ovate, weakly differentiated, with tapering shoulders, hyaline-margined along most of its length; blade lanceolate, rather abruptly tapered to apex or to short and smooth or slightly serrulate awn, apex cucullate; marginal lamina erect to ±incurved, 6-10 cells wide, entire. Lamellae 18-30, in profile ±entire, 6-8 cells high, marginal cells smooth, in cross-section ovate, outer wall strongly thickened, lumen pentagonal, walls pellucid. Blade cells irregularly round-quadrate, (8-)10-18(-20) µm, thick-walled; sheath median cells 25-40×6-9 µm, rectangular, mostly 4-5:1. Sporophytes often present. Seta 0.3-0.5 cm, curved when mature. Capsules brown to ±dark brown, inclined to pendent, subglobose to almost globose, sometimes faintly and obtusely 5-6-angled, ca. 1,8-2,3×1,2-1,8 mm. Peristome teeth 32. Spores 15-18 µm.

Differentiation. Some authors have considered this species, described from Japan, to be a variety of *P. sexangulare*, *Polytrichum norwegicum* var. *vulcanicum* (Osada, 1965; Noguchi, 1987). The latter variety has been described from Iceland, and Schofield (1966) suggested its identity with the North Pacific plants. Bell & Hyvonen (2010a) accepted *P. sphaerothecium* as a separate species. The present analysis suggests that it is the earliest diverging species in the genus, based on MP and Bayesian analyses (Fig. 1) and the most isolated, as seen from the TCS network (Fig. 2). A similar tree topology was found in the analysis of Bell & Hyvönen (2010a), while the more distant taxon sampling and inclusion of other gene regions (*nad*5, *rbc*L, 18S) left *P. sphaerothecium* and *P. sexangulare* even unresolved in relation to the group of *Polytrichastrum alpinum* & *P. septentrionale* (Bell & Hyvönen, 2010b).

Among the unique characters in the genus are: (1) thick-walled stem cortex; (2) leaves with poorly developed sheath; (3) peristome teeth regularly 32 in number, not in between 32 and 64 (usually around 50), as in other species of the genus.

In the field, it is easy to recognize the species by its specific occurrence on volcanic rocks, where it is usually abundant and forms pure stands (based on our observations in the Kuril Islands, and also by Czernyadjeva, 2012). Sporophytes are commonly numerous, with very short setae which are turned upwards, while the shoots (at least when growing on vertical to more or less inclined surfaces) are bent towards the substrate, in a manner similar to *Oligotrichum falcatum*.

Distribution and ecology. The species was reported for the first time in Russia by Bardunov (1982), from Iturup in the Kuril Islands, and was subsequently found in Paramushir and Kunashir (Cherdantseva, 1986; Bakalin & Cherdantseva, 2006; Bakalin et al., 2009) and Kamchatka (Cherdantseva, 1989; Czernyadjeva, 2012). Revising material of *P. sexangulare* in LE, Schljakov (unpubl., reported by Afonina, 2004) found *P. sphaerothecium* also in Chukotka, the Kolyma Upland in Magadan Province and in new localities in Kamchatka. Records from Vrangel Island (Afonina, 2006) were based on specimens from the Somnitelnaya and Getlyanen Rivers; both collections in LE were subsequently identified as *Polytrichastrum sexangulare.* Outside of Russia, the species occurs in north-western North America (British Columbia and Alaska), eastern Asia (Japan, NE China and Korea), and on Iceland in the northern Atlantic. It grows on volcanic rock outcrops, in cliff crevices, and on more or less sheltered rock faces (Afonina, 2006; Czernyadjeva, 2012; Bakalin et al., 2009, Smith Merrill, 2007).

***Specimens examined*: RUSSIA**: **Magadan Province:** Pyagina Peninsula, 10.IX.1938 *Vasiljev* (LE); **Chukotsky Autonomous District:** Pekulneiskoe Lake, 7.VII.1984, *Afonina* (LE); **Kamchatsky Territory:** Shchapina River, VIII.1909, *Savicz* (LE); Ushkovsky Volcano, 16.VII.2003 *Czernyadjeva 18* (LE), S+; Tolbachik Volcano, 10.VIII.2006, *Czernyadjeva* (LE), S+; **Sakhalinskaya Province:** Kuril Islands, Kunashir, *Ignatov 06-1720* (MHA), S+.

JAPAN: Mt. Yatsugatake, 9.IX.2001, *Itouga* (MHA), S+.

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