THE GENUS POLYTRICHASTRUM (POLYTRICHACEAE) IN RUSSIA

POD POLYTRICHASTRUM (POLYTRICHACEAE) В РОССИИ

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INTRODUCTION

The genus Polytrichastrum was introduced by Smith (1971) to solve a long-standing problem concerning the status of Polytrichum 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; Ivatsuki, 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) hyalli (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 Polytraichastrum specimens gave poor results, while trnL-F and rps4 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 rps4 sequences are longer, a number of specimens for which trnL-F could be successfully sequenced gave no PCR products for rps4 (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 rps4 DNA (the rps4 coding region with the HKY+1 model, 537 bp, and the rps4 spacer with the HKY model, 275 bp), 1 compartment for the trnL-F region, 508 bp (HKY+1), and 1 compartment for all of the indels together (12 in rps4 + 29 in trnL-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 trnL-F sequences and 39 rps4 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. papillatum2” (PP=0.77), and P. emodii + P. papillatum (PP=0.6). Note that the plant from Chukotka labelled “P. papillatum2” does not group with the Himalayan specimens 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 rps4 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 trnL-F region results
Fig. 1. Phylogenetic tree based on Bayesian analysis of rps4 and trnL-F regions. Posterior probabilities are shown above branches.
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 *trnL*-F tree. The first includes *P. septentrionale*, *P. altaicum*, *P. papillatum*, ‘*P. papillatum2*’, and *P. emodi*, 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.

<table>
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<th>TCS Name in Bayesian tree</th>
<th>Specimen data</th>
<th>GenBank accession numbers</th>
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<td></td>
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<td>A1 alpinum Chile</td>
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<td>GU569733 GU569818</td>
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The genus *Polytrichastrum* (Polytrichaceae) in Russia

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TAXONOMIC TREATMENT


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 papilllose, + entire to regularly crenulate in profile, the marginal cells differentiated in size and/or shape and/or papillosity. Dioicus (or monoicus, 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. sexangularare*) 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 μm...........

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. sphaerocladum

— 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-cuculate; marginal cells of lamellae ovate to pyriform; upper edge of lamellae from side view smooth, strongly incassate 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 slightly crenulate, moderately incassate along the edge; capsule round in transversal section, not angled; exothecial cells lacking thin spots .................. P. altaicum


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-spread 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 conspicuously 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 papillosate (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 cylindrical 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...
The genus Polytrichastrum (Polytrichaceae) in Russia

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 Province, 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.
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.

Plants small to medium-sized. Stems 2-8 cm tall, almost unbranched, with many broken-off leaves. Leaves erect-splaying to somewhat incurved when dry, spreading to reflexed when moist, 3-5(-7)x0.4-0.7 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 ± nitid, broadly hyaline-margined; marginal lamellae 20-30, in profile ± entire, 5-7 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 their blade shapes are irregular, usually through the upper part of the sheath.

Furthermore, *P. fragile* has strongly papillose and incrustate 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 very 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 Dist., Sparaifevka Island, 12.IX.1980 Blagodatskikh (LE); Republic Sakha/Yakutia: Tiksi, 6.IX.1956 Katenin 73 (LE); Al-

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Figs. 5-6.
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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.
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. Ivano-

va, N.E. Bell & Ignatov comb. nov.


Fig. 8

This species has been accepted in the genus Polytrichastrum under the name Polytrichum 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 Polytrichum alpinum, not Polytrichum septentrionale. Ignatov & Smith Merrill (1995) stated that the type of Polytrichum norwegicum is a form of Polytrichum alpinum, not identical with Polytrichum 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 ±in-curved, 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 Polytrichum 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 Polytrichum alpinum in its somewhat larger spores (17-22 μm, average 20 μm vs. 14-20 μm, average 17 μm in Polytrichum 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 incrasstate distal walls, whereas they are...
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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 *trnL-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 incurred 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

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Fig. 8. *Polytrichastrum septentrionale* (Brid) E.I. Ivanova, N.E. Bell & Ignatov (from: Russia, Sakhalin Island, Nabylsky Mt. Range, Ignatov & Telezhanova #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.
The 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.

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; exothecal 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 Altai 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-Baikal 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 fields, along cold brooks, and on cliffs beside snow fields, in rocky tundras, new glaciers, the margins of late snow fields.

**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”.

**Specimens examined:** **EUROPEAN RUSSIA:** Murmansk Province: Khibiny Mts, 31.VII.2004, Filin (MW); Perm Territory: Molebnaya Kamen Range, 8.VII.1998 Bezdodov 252 (LE); **ASIATIC RUSSIA:** Altai Republic: Dvakhkarovaya 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 foliante above, leafless below. Leaves erect to apressed 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, slanderly 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 trnL-F and rps4 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.** 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-spread when moist, 3-6×0.5 mm; sheath broadly elliptic, hyaline-margined, strongly contracted to the blade; marginal lamina entire to remotely denticate, erect to narrowly inflexed in the distal half of the blade, 2-6 cells wide; costa perpendicular; apex blunt and ± ciliate. 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.
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**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 cylindrical 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 perfectly smooth in *P. sexangulare.*

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**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.
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, Lavrenenko & Kholod (LE); Indiga River, 30.VIII.2008, Lavrenenko & Kholod (LE); Komi Republic: Shchugor River, 11.VII.1928 Sochava (LE); CAUCASUS: North Ossetiya: Shulu Pass, 8.VIII.1925, Bush & Bush (LE);
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ASIATIC RUSSIA: Yamalo-Nenetsky Autonomous District: Sob River, 17.VII.1988 Czernyadjeva (LE); Khanty-Mansi Autonomous District: Berezovsky Dist., 9.VIII.1997, Zolotukhin & al. (MH); Bugiyauk Creek, 2800 m, Ignatov 0/193 (MH); Perevalnaya Creek, 1900 m, 11.VIII.1978 Zolotukhin & al. (MH); Sumulinskij Belok, 14.VIII.1923, Anonymous (LE); Talyzyki Belki. Pobedimova 672 (LE); Kemerovo Province: Kanyt Mt., 20.VII.1997 Pisarenko op02593 (NSK); Krasnoyarsk Territory: Taimyr Municipal Dist., Khantanga, Fedosov 13-3-0355 (MW); Khabarovsk Territory: Dusse-Alin, Medvez’e Lake, 9.VIII.1997 Ignatov 97-539 (MHA). Kamchatktsky Territory: Vodopadny Creek, 19.VIII.2006 Czernyadjeva 37 (LE); Bilchenok Glacier, 16.VII.2003 Czernyadjeva 18 (LE); Arbatun 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).


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-spread ing 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 cuneulate; 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 rounded-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 pend ent, 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 & Hyvönen (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 (nad5, rbcL, 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, Schjakov (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 Somnetilnaya 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 Auton omous District: Pekulneiske Lake, 7.VII.1984, Afonina (LE); Kamchatksky Territory: Shchapina River, VIII.1909, Savič (LE); Ushkovsky Volcano, 16.VII.2003 Czernyadjeva 18 (LE), S+; Tolbachik Volcano, 10.VII.2006, Czernyadjeva (LE), S+; Sakhalinskaya Province: Kurils Islands, Kunashir, Ignatov 06-1720 (MHA), S+.

ACKNOWLEDGMENTS

We are grateful to O.M. Afonina and E.A. Ignatova for arranging specimen loan from LE and MW, to O.Yu. Pisarenko and I.V. Czernyadjeva for recently collected specimens, and to Ignatova also for preparing illustrations. The work was partly supported by RFBR 12-04-98524 (for Ivanova) and 13-04-01592 (for Ignatov). The second author acknowledges support from Academy of Finland research fellowship no. 258554.

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