

THE GENUS *POLYTRICHUM* SECT. *APOROTHECA* (POLYTRICHACEAE) IN RUSSIA
РОД *POLYTRICHUM* СЕКЦИЯ *APOROTHECA* (POLYTRICHACEAE) В РОССИИ

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Abstract

Revision of herbarium collections and analysis of *rps4* and *trnL-F* molecular sequence data supports the recognition in Russia of four species of *Polytrichum* sect. *Aporotheca*. Most specimens from the territory of Russia previously named as *P. formosum* are transferred to *P. densifolium*. The species status of the latter is resurrected and the distinction of *P. formosum* and *P. densifolium* is discussed. The four species are described based on the material from Russia, their distributions are summarised, diagnostic characters are illustrated, and a key to identification is provided.

Резюме

Ревизия гербарных коллекций и изучение последовательностей хлоропластных участков *rps4* и *trnL-F* выявило во флоре России четыре вида *Polytrichum* sect. *Aporotheca*. Большинство образцов с территории России, определенных как *P. formosum*, отнесено к другому виду, *P. densifolium*, статус которого восстановлен. Обсуждаются отличия между *P. formosum* и *P. densifolium*. Приводятся описания видов, ключ для определения видов секции, иллюстрации их диагностических признаков и данные о их распространении в России.

KEYWORDS: *Polytrichum*, taxonomy, phylogeny, phytogeography, Russia, *trnL-F*, *rps4*

INTRODUCTION

The present paper continues a series of taxonomic treatments of the Polytrichaceae in Russia. In the previous study (Ivanova *et al.*, 2014), the genus *Polytrichastrum* s. str. was reviewed; seven species were recognized, without taking into account section *Aporotheca*. This section was established within *Polytrichastrum* by Smith (1992) to accommodate a group of species around *Polytrichastrum longisetum* which were transferred from *Polytrichum* based on sporophytic characters. However, a subsequent molecular phylogenetic study of the Polytrichaceae by 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* (sect. *Polytrichastrum*). Within sect. *Aporotheca*, no taxonomic problems were previously discovered in Europe and North Asia; in most floras and checklists it is represented by three species, *i.e.*, *P. formosum*, *P. longisetum* and *P. pallidisetum* (Hill *et al.*, 2006; Ignatov, Afonina, Ignatova *et al.*, 2006; Savicz-Lyubitskaya

& Smirnova, 1970; Ignatov & Ignatova, 2003). The goal of this study was to critically examine these species concepts and check for any discrete genetic variation within the rather wide distribution of the taxa in the extensive area of Russia.

MATERIAL AND METHODS

Sampling for the molecular study focused on the representation of maximally distant populations of these species from different regions of Russia. The chloroplast *trnL-F* and *rps4* regions were selected, as they provided reasonable resolution in the study of *Polytrichastrum* (Ivanova *et al.*, 2014), and also contributed considerably to the broader analyses (Bell & Hyvönen, 2010a,b).

Sequences for 25 specimens were newly obtained (see Appendix 1) and six previously sequenced specimens were taken from GenBank. All trees were rooted on *Polytrichastrum altaicum*, a species of a closely related genus. *Polytrichum commune*, *P. juniperinum* and *P. strictum* were also included in the outgroup. DNA extractions and overall laboratory protocols were essentially as

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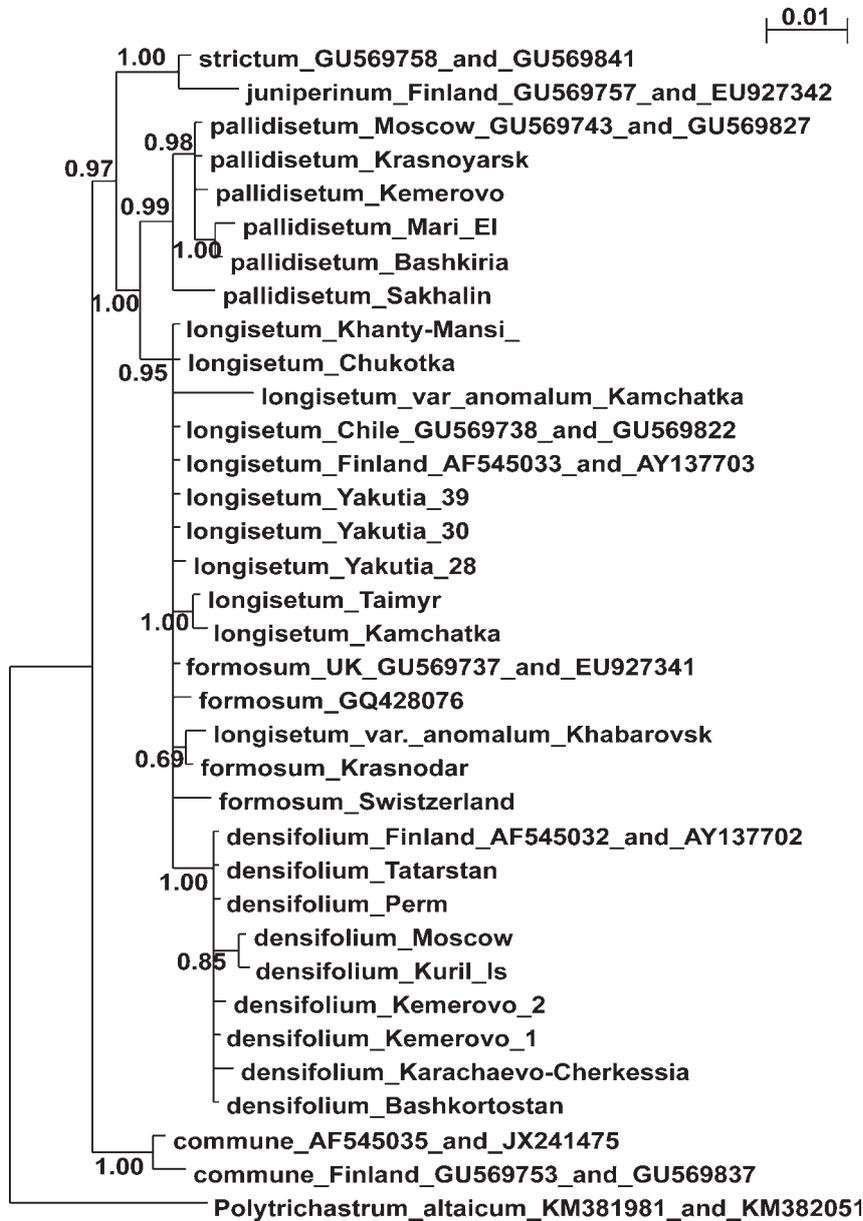


Fig. 1. Phylogenetic tree based on Bayesian analysis of *rps4* and *trnL-F* regions. Posterior probabilities are shown below branches.

in, *e.g.*, Gardiner *et al.* (2005). Sequences were aligned manually in Bioedit (Hall, 1999).

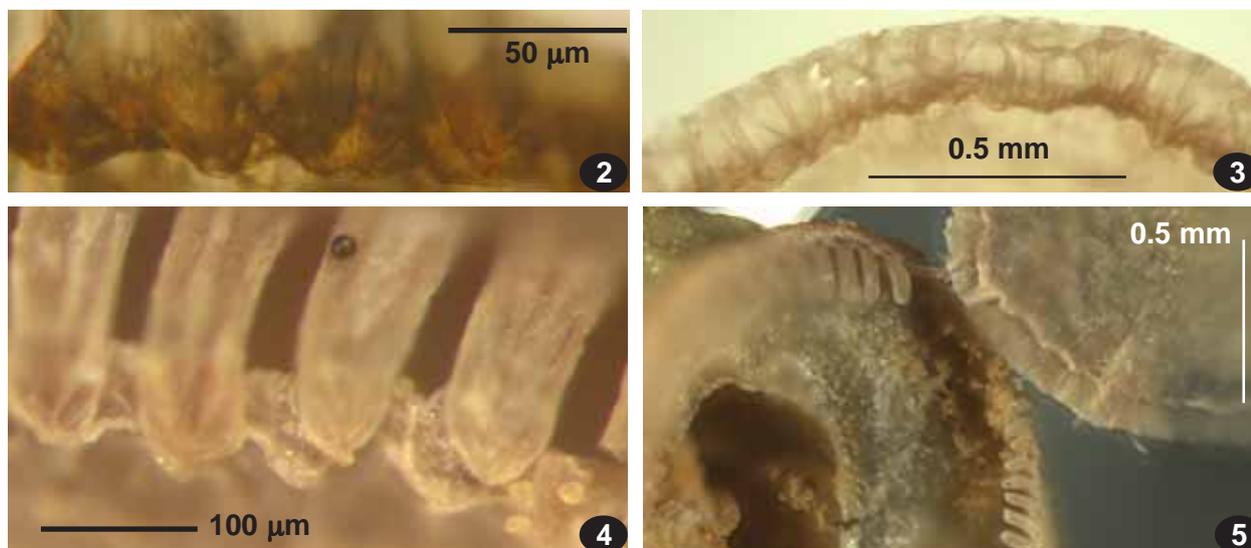
Bayesian analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) with two compartments for *rps4* DNA (the *rps4* coding region with the HKY+I model, 565 bp, and the *rps4* spacer with the HKY model, 274 bp), one compartment for the *trnL-F* region, 521 bp (HKY+I), and one compartment for all of the 22 indels together, 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 10000000 generations (2500 burnin), with trees sampled every 1000 generations, a temp parameter

value of 0.15 and parameters unlinked between partitions.

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

RESULTS

In the Bayesian analysis the two accessions of *Polytrichum commune* were grouped, as were the two closely related species *P. juniperinum* and *P. strictum*, in both cases with maximal support (PP=1.00). All accessions of *P. pallidisetum* appeared in a single clade (PP=0.99), sister to a larger clade of the specimens kept in herbaria under the names *P. longisetum* and *P. formosum*. The topology of this clade was unexpected: within the almost unresolved polytomy formed by these two species (*P. longisetum* and part of *P. formosum*), appeared two clades with P=1.00. One of them included only two specimens from the geographically distant localities of Kamchatka



Figs. 2–5: Peristome and epiphragm in *Polytrichum* sect. *Aporotheca*. 2–4: *P. densifolium* (from Russia, Perm Territory, 12.VII.1997, *Bezgodov 172*, MW); 5: *P. formosum* (from: Czech Republic, Karlovy Vary, 28.VIII.2011, *Donskov s.n.*, MHA). 2–3: inner edge of epiphragm showing hints of sacculi; 4: portion of peristome and outer edge of epiphragm showing short teeth on epiphragm opposite the peristome teeth; 5: portion of peristome and inner edge of epiphragm showing absence of sacculi and presence of “annulus”.

and Taimyr, while the other combined plants from nine localities spanning almost the whole of Russia identified previously as *P. formosum*.

More precisely, two groups of *P. formosum* were resolved as follows: one (inseparable form *P. longisetum* by the chloroplast DNA markers) including plants from the UK, Switzerland, and the Caucasus (Black Sea coastal areas only), and another including plants from the Kuril Islands, the South Siberian mountains, the Urals, Finland, and the Caucasus, although in the latter case only from middle elevations dominated by conifer forest. The latter plants are named in the tree as *P. densifolium* for the reasons explained below.

The maximum parsimony analysis found no bootstrap support for these entities, although simple visual inspection of the alignment revealed two substitutions in *rps4* and one substitution and one indel in the *trnL-F* region, with these differences being completely consistent between the two clades.

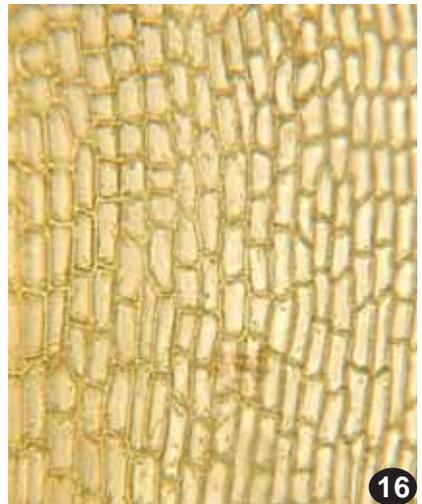
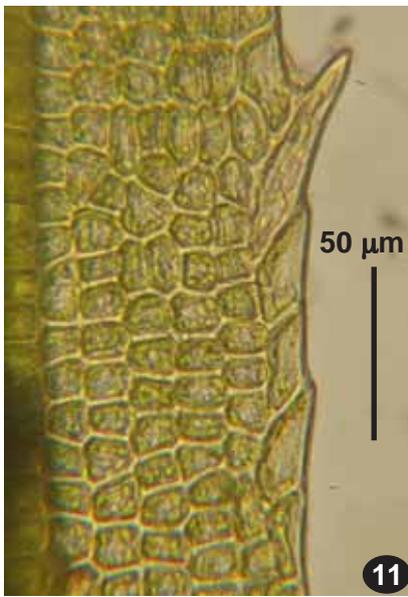
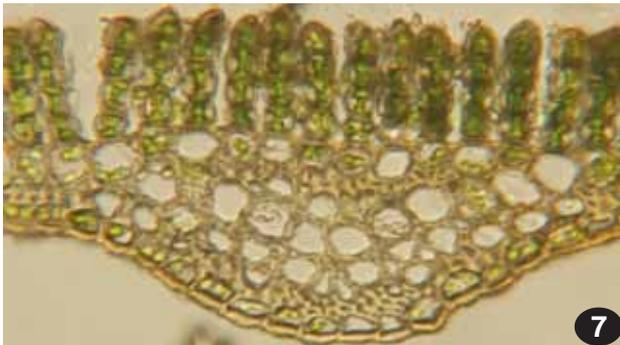
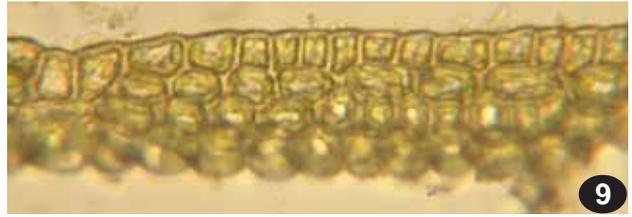
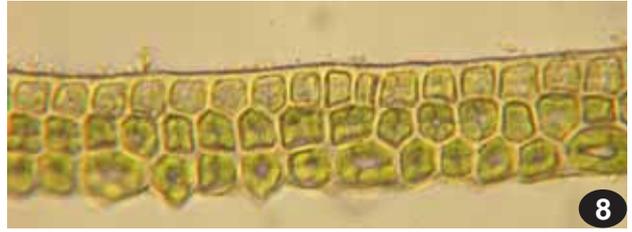
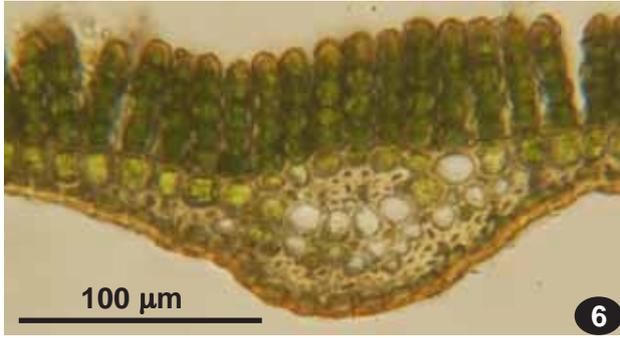
A targeted search for morphological differences between these two entities revealed rather many differentiating characters, as described below under *P. formosum*. In fact, these differences have previously been discussed by American (Smith, 2007) and Japanese (Osada, 1966) authors, who in addition to *P. formosum* also recognized *P. densifolium*, although only at the varietal level.

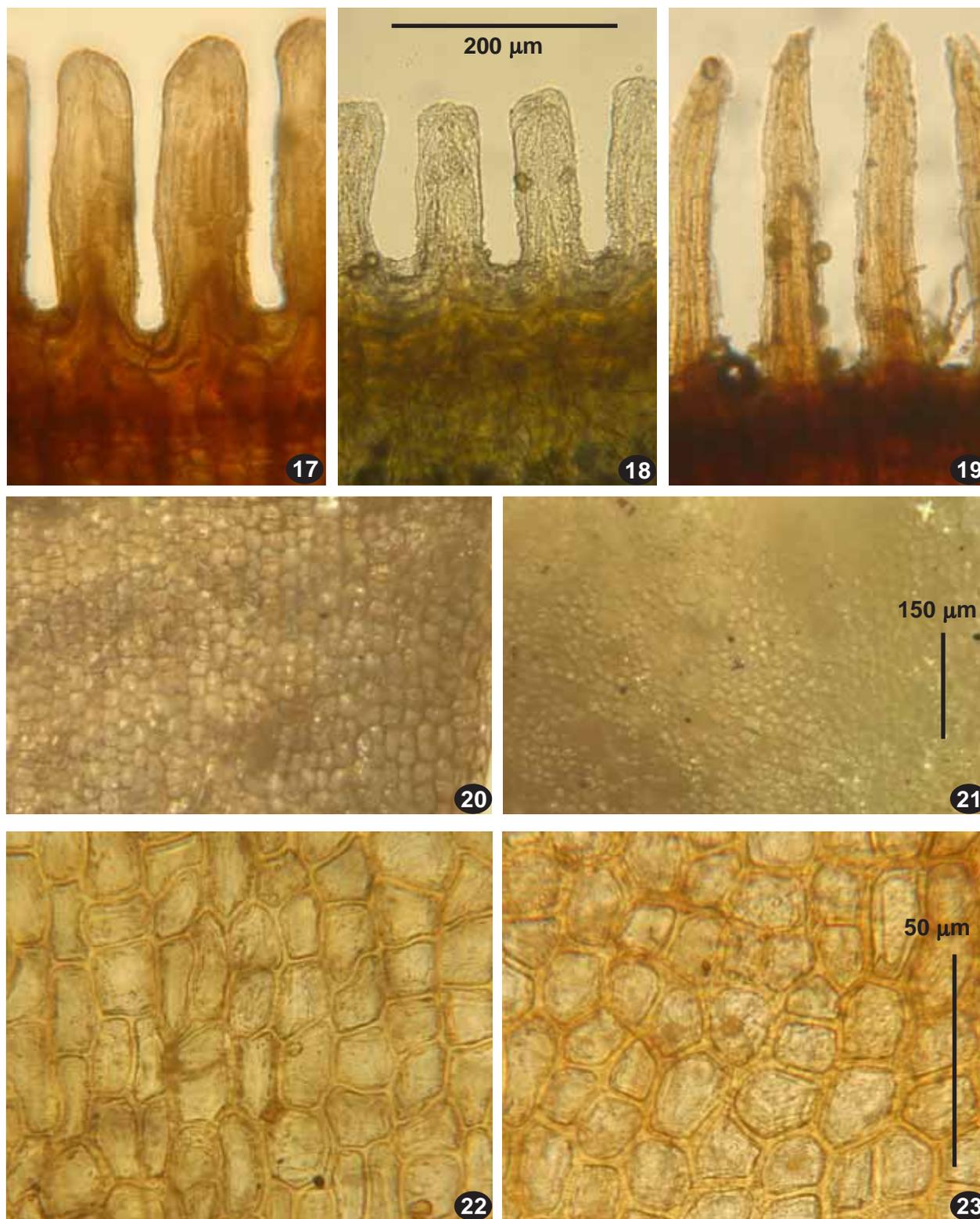
According to our molecular data the difference between these entities is not great (3 substitutions and 1 indel), but this is significant considering that there is no difference at all in our markers between *P. formosum* and *P. longisetum*. Given that these molecular characters are associated with a significant number of stable morphological differences, independent species status is justified for *P. densifolium*.

TAXONOMIC TREATMENT

Polytrichum Hedw., Sp. Musc. Frond. 88. 1801. Lectotype: *Polytrichum commune* Hedw.

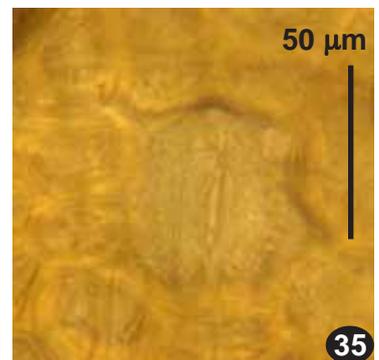
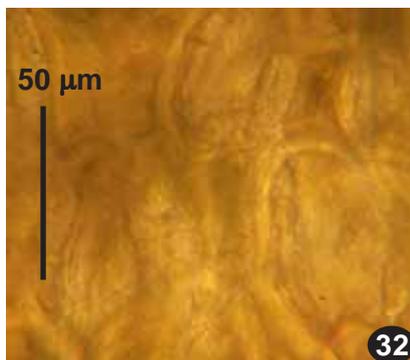
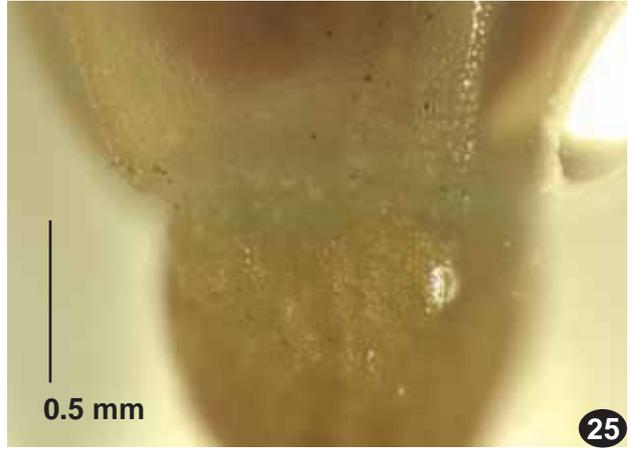
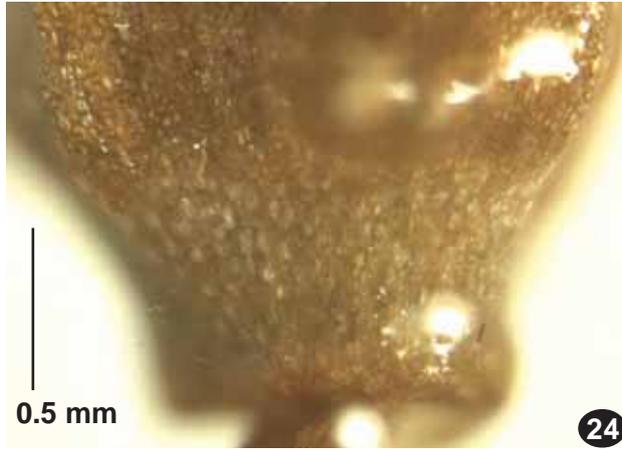
Plants medium-sized to robust, in loose or dense tufts. Stems erect. Leaves with differentiated sheath and blade, the blade erect to somewhat spreading when dry, erect, widely spreading or recurved when wet; sheath hyaline-margined, entire, often highly nitid (polished and glossy), hinge tissue well-developed or, rarely, not strongly developed; blade unbordered, sharply toothed to entire at margins, sometimes filmy, plane, erect or, sometimes, abruptly inflexed and covering ventral lamellae; costa typically short-excurrent, scabrous, or (especially in perichaetial leaves) prolonged into a toothed awn, awn reddish-brown or hyaline. Lamellae numerous, closely-spaced, occupying most of the blade width, their margins smooth, ± entire to regularly crenulate in profile, the marginal cells undifferentiated or sharply distinct in size and/or shape. Dioicous (or, rarely, monoicous). Male plants with inconspicuous rosettes. Seta solitary. Capsules acutely or obtusely 4-angled or sometimes variably 4–6 or 5–6-angled, the apophysis sharply or shallowly delimited from the urn. Exothecium smooth or bulging-mammillose and papillose, the cells without thin spots in the outer wall, irregularly polygonal, but in general arranged in longitudinal rows. Peristome teeth 64, generally simple, but often somewhat fewer, usually with some teeth compound, not keeled at back, with or without ridges and spurs inside, not deeply pigmented. Epiphragm persistent or, more rarely, readily detached, without erect tooth-like processes opposite the peristome teeth or with short processes; with or without sacculi on ventral side alternating with peristome teeth, or with solid ridge-like circular “annulus” on ventral edge of





Figs. 17-23: Peristome and exothecium in *Polytrichum* sect. *Aporotheca*. **17, 20, 22:** *Polytrichum densifolium* (from Russia, Perm Territory, 12.VII.1997, *Bezgodov 172*, MW); **18, 21, 23:** *P. formosum* (from: Czech Republic, 28.VIII.2011, *Donskov s.n.*, MHA); **19:** *P. longisetum* (from: Russia, Ryazan Province, 30.IX.1999, *Ignatov s.n.*, MHA). **17-19:** portion of peristome; **20-23:** exothecium in the middle part of urn.

Figs. 6-16 (opposite page): Leaf characters of *Polytrichum* sect. *Aporotheca*. **6, 8, 12, 15:** *P. formosum* (from: Czech Republic, 28.VIII.2011, *Donskov s.n.*, MHA); **7, 9-11, 14:** *P. densifolium* (from Russia, Perm Territory, 12.VII.1997, *Bezgodov 172*, MW); **13, 16:** *P. longisetum* (from: Russia, Ryazan Province, 30.IX.1999, *Ignatov s.n.*, MHA). **6-7:** leaf transverse sections; **8-10:** side view of lamellae; **11-13:** cells of unistratose part of blade; **14-16:** cells in the middle part of sheath leaf base.



the epiphragm. Spores 13–26 µm, finely papillose. Calyptra with a rather loosely interwoven felt of hairs, covering only the upper portion of capsule.

Polytrichum sect. *Aporotheca* (Limpr.) N.E. Bell & Hyvönen, Amer. J. Bot., 97(4): 577. 2010. — *Polytrichum* subgen. *Aporotheca* Limpr., Laubm. Deutschl. 2: 615. 1893. — *Polytrichastrum* sect. *Aporotheca* (Limpr.) G. L. Merr., Bryologist 95: 271. 1992.

Lectotype (Smith, 1971): *Polytrichum formosum* Hedw.

Section *Aporotheca* is characterized by 4-angled capsules with not very sharp angles or by obtusely and variably 4–6 or 5–6 angled ones, the absence of ridges and spurs on the inner sides of the peristome teeth and by a ± weakly delimited apophysis. Sacculi are mostly absent on the ventral edge of the epiphragm or, in case of *P. densifolium*, there are intermediate structures (hints of sacculi), otherwise a fleshy annulus is present. Epiphragm teeth are absent or, if present, are shorter than wide. For the detailed characteristics of the section see Bell & Hyvönen (2010b).

KEY TO IDENTIFICATION OF SPECIES OF *POLYTRICHUM*
SECT. *APOROTHECA* IN RUSSIA

1. Lamellar marginal cells strongly differentiated, broader than high, cuneate, flat-topped to shallowly retuse; lamellae crenulate in profile *P. pallidisetum*
— Lamellar marginal cells ± undifferentiated, rounded in cross-section or slightly taller than cells beneath; lamellae entire or slightly and distantly crenulate in profile 2
2. Sheath cells short-rectangular (3–4:1); marginal lamina 4–9(–20) cells wide; capsule obtusely 5–6-angled; epiphragm easily detached, often missing in older open capsules; spores 15–23 µm *P. longisetum*
— Sheath cells rectangular (5–9:1); marginal lamina 2–4 cells wide; capsules ± sharply 4-angled; epiphragm moderately firmly attached, persistent in open capsules; spores 12–15 µm 3
3. Sheath cells 70–80(–110) µm long; lamellae entire in profile; capsules short rectangular, with short, ± sharply delimited apophysis; stomata small, round, restricted to a narrow, shallowly grooved zone between urn and lower part of apophysis; peristome teeth pale, 170–185 µm long and 48–55 µm wide; epiphragm without sacculi on ventral side; Eastern, Central and NW Europe, lowland Caucasus and southern European Russia *P. formosum*
— Sheath cells 60–70(–90) µm long; lamellae slightly and distantly crenulate or, occasionally, entire in pro-

file; capsules elongate rectangular, with long, weakly delimited apophysis; peristome teeth yellowish brown, with reddish brown base, 220–305 µm long and 60–100 µm wide; epiphragm with hints of sacculi on ventral side alternating with peristome teeth; East and NE Europe, European Russia, highland Caucasus, southern Siberia, southern Far East, Chukotka *P. densifolium*

Polytrichum longisetum Sw. ex Brid., J. Bot. (Schrader) 1800(1): 286. 1801. — *Polytrichastrum longisetum* (Sw. ex Brid.) G. L. Smith, Mem. New York Bot. Gard. 21(3): 35. 1971. Figs. 13, 16, 19

Plants medium to large, dark green, in loose tufts. Stems to 3–5(–10) cm, erect, mostly unbranched. **Leaves** loosely appressed, erect and somewhat twisted when dry, widely spreading when moist, (4–)5–6(–8) mm long; sheath (0.9–)1.3–1.5(–1.8) mm wide, rather short, oblong, yellowish, often not as distinctly delimited as in other species of the genus (almost lacking in var. *anomalum*), the hinge-tissue not strongly developed; blade lanceolate to linear-lanceolate; marginal lamina plane to erect, 4–9 cells wide (to 20 cells wide in var. *anomalum*), sharply toothed (less often bluntly toothed to merely denticulate); **costa** excurrent, ending in a short yellowish awn; **lamellae** (12–)20–45, in profile entire or finely serrulate, (2–)4–5(–7) cells high, the lamellar marginal cells almost undifferentiated in shape and size, ovate to elliptic in cross-section, taller than wide, sometimes slightly thicker-walled; median **cells** of sheath short-rectangular, (30–)50–60(–70) × (12–)14–18(–25) µm, (2–)3–5(–6):1; cells along the margins of the lamina ± isodiametric, hexagonal, (13–)15–18(–20) µm wide (in var. *anomalum* the cells of the broad lamina larger, to 22–25 µm). **Sexual condition** dioicous. Seta to 4(–7) cm tall, often exceeding the leafy shoots in length. **Capsules** inclined, ovoid, obtusely (4–)5–6-angled, yellowish brown, 2–3 × 1.5–2 mm, with a ± rounded apophysis more than 1/2 the capsule diam., differentiated by a shallow groove; exothecial cells irregularly rectangular, stomata numerous, small, round, distributed throughout the surface of short apophysis; **peristome** with low basal membrane, teeth ca. 50, light yellowish-brown, more deeply colored along the median line, long and narrow, ca. 300 µm long and 50–55 µm wide, the space between the teeth appearing wider than width of the teeth; **epiphragm** with well-developed tooth-like processes, readily detached, in deoperculate capsules often absent. **Spores** (15–)18–23(–26) µm. **Operculum** rostrate, the beak about 0.5 mm long. **Calyptra** hairy, yellowish to golden brown to fuscous, covering the upper portion of the capsule.

Figs. 24–35 (opposite page): Apophyses and stomata of *Polytrichum* sect. *Aporotheca*. **24, 26, 28, 30, 32**: *P. densifolium* (**24, 26, 28, 30**: from Russia, Perm Territory, 12.VII.1997, *Bezgodov* 172, MW; and **32**: from Russia, Tatarstan, *Ignatov & Ignatova* 03-64, MHA); **25, 27, 29, 31, 33–35**: *Polytrichum formosum* (**25, 27, 29, 33–35**: from Czech Republic, Karlovy Vary, 28.VIII.2011, *Donskov s.n.*, MHA; **31**: from Czech Republic, Karlovy Vary, 22.IV.1957, *Tyuremnov s.n.*, MHA). **24–25**: lower part of capsule showing apophysis, wet; **26–29**: capsules showing apophysis shape, dry; **30–31**: lower parts of capsule showing apophysis and stomata distribution, dry; **32–35**: stomata.

Differentiation. *Polytrichastrum longisetum* is similar to *P. formosum* and *P. densifolium* in having undifferentiated upper lamellar cells. Differences include flexuose leaves in the dry condition that become widely spreading when moist (vs. more rigid, not or only slightly flexuose leaves when dry, becoming reflexed when moist), the rather short, less strongly delimited sheath and short-rectangular sheath cells, and the broader lamina margins. If capsules are present, *P. longisetum* is readily recognized by the rather short, obtusely 5–6-angled urn and comparatively wide and short, shallowly delimited apophysis, long and narrow, widely spaced peristome teeth and an easily detached epiphragm.

Distribution. *Polytrichastrum longisetum* is a widespread species, occurring mostly in cool climates. It is known in the mountains of central and northern Europe, including Iceland; in Asia, it is common in arctic and boreal zones and in the mountains of Mongolia, Northern China and Japan. In North America it occurs from Labrador to Minnesota, south to Pennsylvania and Illinois, and in Alaska and Colorado. Reported also for southernmost South America, South Africa, and New Zealand.

Ecology. In Russia, the species occurs almost throughout the territory, being most common in the taiga zone. It grows in two rather different types of habitats: 1) on rich humus soil at the bases of fallen trees in mesic coniferous forests, in the lowlands and at lower and middle elevations in the mountains, and 2) on bare peat in bogs in the lowlands and at upper elevations in the mountains.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province:** Tetrino, 24.VII.1927, *Zinserling 30* (LE, SASY), S+; **Leningrad Province:** Lemovka River, 23.VII.1971, *Vjunova 94* (LE), S+; Glubokoe Lake, 9.VI.1974, *Vjunova 474* (LE), S+; Peterhof, 6.IX.1975, *Vjunova 531* (LE), S+; Vyborg, 22.VIII.2002, *Kurbatova s.n.* (LE), S+; **Arkhangelsk Province:** Arkhangelsk, 8.VII.1983, *Volkova s.n.* (LE), S+; **Komi Republic:** Pechora, 23.V.1899, *Puring s.n.* (LE), S+; **Sverdlovsk Province:** Kytlym, 4.VII.1960, *Storozheva s.n.* (LE), S+; **Pskov Province:** Sebez National Park, 7.V.2000, *Andreeva s.n.* (LE), S+; **Moscow Province:** Zvenigorod, 24.VI.1996, *Filin s.n.* (MW); **Ryazan Province:** Oksky Nature Reserve, 30.IX.1999, *Ignatov s.n.* (MHA); **Voronezh Province:** Voronezh Nature Reserve, 29.VI.1975, *Krasnoshtanova s.n.* (LE), S+. CAUCASUS: **Republic of Karachaevo-Cherkessia:** 14.VIII.1993, *Ukrainskaya 14460* (LE). ASIAN RUSSIA: **Yamal-Nenetsky Autonomous District:** Verkhnetazovskiy National Park, 4.VIII.1997, *Czernyadjeva 10* (LE), S+; **Tyumen Province:** Surgut, 18.IX.1999, *Taran 00704* (NSK, SASY); Surgut, 9.VIII.2000, *Czernyadjeva & Kuzmina 73* (LE); Laryak, 29.VII.2000, *Czernyadjeva & Kuzmina 31* (LE); Agan River 25.VII.1923, *Mitusova s.n.* (LE), S+; **Kemerovo Province:** Kuznetsky Alatau Mts, 13.IX.2004, *Pisarenko 00039, 00710, 00712* (NSK, SASY); **Altai Republic:** Kukol Lake, 24.VII.1989, *Ignatov 01/1357* (MHA); **Krasnoyarsk Territory:** Yenisey River, 4.VII.1876, *Arnell s.n.* (LE), S+; Putorana Plateau, Kapchuk Lake, 19.VII.1982, *Czernyadjeva 86* (LE); Ayan Lake, 14.VIII.1983, *Czernyadjeva 109* (LE), S+; Anabar Plateau, Medwez'ya River, *Fedosov 05-422* (MW); **Irkutsk Province:** Karam, 17.VIII.1912, *Aleksandrova 1528* (LE), S+; Baikal Lake, 26.VII.1915, *Tsinzerling s.n.* (LE), S+; Vitimsky Nature Reserve, Oron Lake,

5.VII.1984, *Bardunov s.n.* (LE); **Zabaikal'sky Territory:** Chikoy River, 2.VII.1913 & 6.VII.1913, *Smirnov s.n.* (LE); Mudirikan River, 5.VIII.1979, *Otnyukova s.n.* (LE); Kudaldu River, 25.VIII.1939, *Siplivinsky s.n.* (LE), S+; **Republic Sakha/Yakutia:** Indigirka River, Shandrin, 5.VII.1974, *Afonina s.n.* (LE); Nizhnekolymsk Distr., Alazea River, 14.VIII.2009, *Efimova s.n.* (SASY), S+; Lampuchka River, 16.VIII.1985, *Volotovskiy 16/8* (SASY), S+; Chara River, At Bastakh Lake, 18.VII.1994, *Ivanova s.n.* (SASY); Vilyuj River, Ulakhan Vava Creek, 9.VII.1958, *Kuldyushevskiy 10/2* (SASY), S+; **Chukotsky Autonomous District:** Pekulney Range, 5.VIII.1979, *Afonina s.n.* (LE), S+; Yanrakhynnot, 28.VIII.1976, *Afonina s.n.* (LE), S+; **Magadan Province:** Tenkenskiy Distr., Maldan Lake, 26.VIII.1988, *Katenin s.n.* (LE); Chemodan, 24.VI.1982, *Blagodatskykh s.n.* (LE); **Primorsky Territory:** Olchi, 28.VII.1930, *Shishkin s.n.* (LE), S+.

Specimens matching the expression known as *P. longisetum* var. *anomalum* are occasionally collected throughout the area of type variety. They are distinctive in appearance, looking more like an *Atrichum* or *Timmia* than a *Polytrichum*. No sporophytes were observed in such forms. Leaf cells in marginal lamina are slightly larger than in typical *P. longisetum*, 22–25 µm vs. (13–)15–18(–20) µm wide, and the leaf sheath is more weakly developed. Transitional plants are also occasionally found. Although no evidence of any distinction of such plants was obtained from the molecular data, these varieties can be distinguished morphologically as follows:

1. Lamellae 20–45, occupying most of blade width, (2–) 4–7 cells high; marginal lamina narrow, 4–9 cells wide; sheath oblong-ovate, rather short var. *longisetum*
- Lamellae 15–20, occupying ca. 1/2 of the width of the blade, 1–3 cells high, flanked by a broad, unistratose lamina up to 20 cells wide; sheath weakly developed, almost obsolete var. *anomalum*

Polytrichum longisetum var. *anomalum* (Milde) G.L. Sm., *Phytologia* 18: 403. 1969. — *Polytrichastrum longisetum* var. *anomalum* (Milde) Ignatov & G. L. Merr., comb. nov. — *Atrichum anomalum* Milde, *Hedwigia* 8: 161. 1869. — *Polytrichum gracile* var. *anomalum* (Milde) I. Hagen, *Tromsø Mus. Aarsh.* 21-23(3): 265. 1905. — *Polytrichastrum longisetum* fo. *anomalum* (Milde) Schljakov, *Novosti Sist. Niz. Rast.* 19: 209. 1982. — *Pogonatum manchuricum* Horik., *J. Jap. Bot.* 12: 24. 1936. — *Oligotrichum sibiricum* Bardunov, *Novosti Sist. Niz. Rast.* 1968: 303. 1968.

Unistratose lamina broad, up to 20 cells wide; leaf base not or only slightly broader than the blade; lamellae 12–20, confined to the median portion of the leaf, 1–3 cells high; cells along the margins of the lamina to 22–25 µm wide.

The variety typically occurs on soil walls and upturned roots of fallen trees, and is occasionally found on *Sphagnum* mires, on ledges of calcareous cliffs and rocks covered with soil. In mountain areas, it usually grows at lower altitudes.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province:** Lavna-Tundra Mt., 6.VIII.1987, *Belkina 267-*

7-87 (KPABG); Kandalakshsky Nature Reserve, Porja Bay, Bolshoi Yagodnyi Island, 14.VIII.1991, *Likhachev* 164-5-91 (KPABG); Lovozerskie Mts, Seidozero Lake, 28.VIII.1984, *Belkina* 95-9-84 (KPABG); Ponoj River basin, Krasnoshchelje Settlement, 21.VII.1965, *Schljakov* \check{R} 492-65 (KPABG); **Tver Province**: Nelidovo District, Tsentral'no-Lesnoj Nature Reserve, 31.VIII.1993, *Minaeva* 356, 357, 365 (MW). ASIAN RUSSIA: **Altai Republic**: Adylda Creek, *Ignatov* 34/16 (MHA); Ayukol Lake, *Ignatov* 0/1358 (MHA); Teletskoe Lake, Bolshoye Istyube Creek, *Ignatov* 0/1360 (MHA); **Amurskaya Province**: Selemdzhinsky District, Selemdzha River valley, 19.VI.2011, *Bezgodov* 327 (MHA); **Khabarovsk Territory**, Botchinsky Nature Reserve, *Ignatov & Ignatova* 13-560 (MHA); **Kamchatkaya Province**: Ust-Bolsheretsky District, Pauzhetka River, 1.VIII.2006, *Samkova* 13-1 (MHA).

Polytrichum formosum Hedw., Sp. Musc. Frond. 92. pl. 19: f. 1a. 1801. — *Polytrichastrum formosum* (Hedw.) G. L. Smith, Mem. New York Bot. Gard. 21(3): 37. 1971. Figs. 5-6, 8, 12, 15, 18, 21, 23, 25, 27, 29, 31, 33-35.

Plants medium to large, robust, green to dark olive-green, rigid. **Stems** to 10 cm, mostly unbranched. **Leaves** erect or erect-spreading and tubular when dry, recurved when moist, 7–8 mm long, sheath 1.4–1.5(–1.7) mm wide, erect, elliptic, yellowish-brown, clasping the stem; blade linear-lanceolate; marginal lamina erect, 3–4 cells wide, sharply toothed nearly to the base of the blade; **costa** short excurrent, ending in a brownish to reddish brown toothed point, toothed at back near tip; **lamellae** 45–50(–60), in profile entire, 3–4 cells high, the lamellar marginal cells almost undifferentiated in shape and size, in cross-section rounded, with moderately thickened outer walls; median **cells** of sheath linear, (60–)70–80(–110)×(8–)10–12(–14) μm , 5–12:1; cells of the lamina near margin \pm isodiametric, with moderately thickened walls, (9–)10–13(–24) μm wide. **Sexual condition** dioicous. **Seta** stout, to 4 cm tall. **Capsules** short rectangular, \pm acutely 4-angled, inclined to horizontal, yellowish brown to dark brown, 3.5×1.5 mm, with rather small round apophysis, \pm sharply delimited by a shallow groove; exothecium smooth, the cells not bulging, irregularly rectangular, 35–45(–50) μm wide; stomata small, rounded, becoming “stellate” with age, restricted to a narrow groove between the lower part of urn and apophysis; **peristome** with high basal membrane, teeth 64, regular in form, pale, light brownish at base only, weakly papillose, 175–185 μm long and 48–55 μm wide; **epiphragm** moderately firmly attached, persistent, without teeth on dorsal side or sacculi on ventral side, and with fleshy “annulus” on ventral side. **Spores** 13–15 μm , finely papillose. **Calyptra** hairy, covering the upper portion of the capsule.

Differentiation. *Polytrichum formosum* was hitherto understood in a wider sense, including specimens which we refer here to *P. densifolium*. However, these two species have clear differences, especially in sporophytic characters, *i.e.*, short rectangular capsules in *P. formosum* vs. elongate rectangular ones in *P. densifolium*; \pm well delimited round apophysis vs. not well delimit-

ited, narrow and elongate one; small round stomata restricted to a shallow groove between the urn and apophysis vs. more numerous, larger, ovate stomata, distributed throughout apophysis; absence vs. presence of hints of sacculi on ventral side of epiphragm; peristome teeth pale and short and narrow, 175–185×48–55 μm vs. deeper colored, yellowish-brown, and longer and wider, 220–305×60–100 μm . Differentiation of sterile plants is more problematic, although possible; *P. formosum* can be recognized by more rigid stems with straight, appressed leaves with recurved tips when dry and stronger reflexed leaves when moist, while plants of *P. densifolium* are less rigid, with leaves slightly flexuose when dry and widely spreading to reflexed when moist; the cells of the sheathing base are slightly longer in *P. formosum*, (60–)70–80(–110) μm vs. (50–)60–70(–90) μm in *P. densifolium*, and the marginal cells of the lamellae are rounded with thicker outer walls in *P. formosum*, while they are slightly longer than wide and thin-walled in *P. densifolium*; furthermore, the lamellae are slightly higher in *P. formosum*, 4–5 cells high vs. 3–4 cells. Osada (1966) also considered the entire margin of the lamellae (vs. crenulate in var. *densifolium*) as an important differentiating character; this is repeated by Smith (2007), although he admits that there are exceptions. In the material from Russia, distantly crenulate margins were also observed for *P. densifolium*, while *P. formosum* always possesses entire lamellae. Both Smith and Osada (*l.c.*) mention an additional difference regarding sexual condition for var. *formosum* and var. *densifolium*, *i.e.*, always dioicous in the former variety and polyoicous (polygamous) in the latter one (male, female and, very rarely, monoicous with both inflorescences on one stem). However, we did not observe monoicous plants in the collections of *P. densifolium* from Russia. There is also some difference in the height of the lamellae in *P. densifolium* between North American plants and those from Russia, *i.e.*, 5–7 vs. 4–5 cells high.

The differences from *P. longisetum* are discussed under that species.

Distribution. *Polytrichum formosum* was previously reported as widely distributed throughout the temperate regions of Eurasia. However, our data indicate that it is very rare in Russia, being represented in herbaria only by a few collections from the lowland Caucasus and a single collection from Belgorod Province (southern European Russia). By contrast, in Europe it is one of the most common *Polytrichum* species, known from practically all countries (although according to our data at least some records from NE Europe actually belong to *P. densifolium*). At the same time, the species is apparently absent in most areas of European Russia and in its Asian part, being replaced by its vicariant, *P. densifolium*. A similar pattern was revealed in North America, where var. *formosum* is reported to be much rarer than var. *densifolium* (Smith, 2007). However, in Japan, var. *formosum* [=var. *intersedens* (Card.) Osada] was reported to be comparatively more frequent, than var. *densifolium*,

common on Honshu, Sikoku and Kyushu, but rather rare in Hokkaido, being distributed from the lowlands to the subalpine region (Osada, 1966; Noguchi, 1987). Similarly, in China, var. *formosum* has been reported from many provinces, mainly in central and southern parts of the country, but not in the north, close to the boundary of Russia (Wu & Wang, 2005). *Polytrichum formosum* was also listed in the moss flora of Mongolia (Abramov & Abramova, 1983; Tsegmed, 2010), but these records apparently belong to *P. densifolium*.

Ecology. The species grows on soil in broad-leaved forests.

Specimens examined: EUROPE: **Czech Republic:** Karlovy Vary, 28.VIII.2011, *Donskov s.n.* (MHA); same place, 22.IV.1957, *Tyuremnov s.n.* (MHA). EUROPEAN RUSSIA: **Belgorod Province:** Belogorje Reserve, 18.V.2003, Nemykin 341 (LE). CAUCASUS: **Stavropol Territory:** Zheleznovodsk, 14.IX.1928, *Steinberg s.n.* (LE); **Krasnodar Province:**, Sochi District, Lazarevskoye, 29.I.2012, *Ignatov & Ignatova 12-51* (MW).

Polytrichum densifolium Wilson ex Mitt., J. Proc. Linn. Soc., Bot., Suppl. 2: 155. 1859. — *Polytrichum formosum* var. *densifolium* (Wilson ex Mitt.) Osada, J. Jap. Bot. 41: 80. 1966. — *Polytrichastrum formosum* var. *densifolium* (Wilson ex Mitt.) Z. Iwats. & Nog., J. Hattori Bot. Lab. 37: 389. 1973.

Figs. 2-4, 7, 9-10, 11, 14, 17, 20, 22, 24, 26, 28, 30, 32.

Plants medium-sized to robust, dark green, forming dense and wide tufts. **Stems** 5–10 cm high, mostly unbranched. **Leaves** loosely appressed and slightly flexuose when dry, widely spreading to reflexed when moist, (5)–6–8(–9) mm long; sheath 1.5–1.8 mm wide, erect, elliptic, yellowish-brown, clasping the stem; blade linear-lanceolate; marginal lamina erect, 3–5(–6) cells wide, sharply toothed nearly to the base of the blade; **costa** short excurrent, ending in a brownish to reddish brown toothed point, toothed at back near tip; **lamellae** (30)–45–50(–60), in profile finely and distantly crenulate, 4–5 cells high, the lamellar marginal cells almost undifferentiated in shape and size, in cross-section narrowly conic to elliptic, somewhat taller than broad, thin-walled; median **cells** of sheath elongate rectangular, (50)–60–70(–90)×(9)–10–13(–15) µm; cells of the lamina near margin ± isodiametric to transversely widened, (10)–12–13(–15) µm wide, thin-walled. Sexual condition dioicous [or polyoicous]. **Seta** stout, 3–6 cm tall. **Capsules** elongate-rectangular, ±acutely 4-angled or, rarely, 5-angled, inclined to horizontal, yellowish-green to dark brown, 3–5(–6) × 1.5–2.5 mm, with weakly delimited, narrow and elongate apophysis 1/4 of the diameter of the capsule; exothecial cells irregularly 4–5-angled, 40–60(–75) µm wide, stomata numerous, large, elliptic, distributed over the entire surface of the apophysis; **peristome** with high basal membrane, teeth 50–64, sometimes irregular in appearance, yellowish-brown, reddish-brown at base, 220–305 µm long and 40–60(–100) µm wide, weakly papillose; **epiphragm** moderately firmly attached, persistent, with hints of sac-

culi on ventral side alternating with peristome teeth, and without teeth opposite peristome teeth on dorsal side or, occasionally, with small reduced teeth. **Operculum** rostrate, with straight beak. **Spores** 12–15 µm, finely papillose. **Calyptra** hairy, covering the upper portion of the capsule.

Differentiation. Differences between *Polytrichum densifolium* and *formosum* are discussed under the latter species. Osada (1966) also noted a difference in chromosome number between the varieties [14 in var. *densifolium* and 7 in var. *intersedens* (=var. *formosum*)].

Distribution. *Polytrichum densifolium* was described in 1859 from Sikkim. In India, it was also reported from SE Tibet by Gangulee (1969) who considered the species to be Indo-Chinese. It was subsequently recognized in Japan, being treated at the varietal rank, being known from alpine and subalpine mountain belts in Honshu and Hokkaido and disjunctively from Yakushima Island (Osada, 1966). In China, it is known only from Sichuan (in the forest belt) and Taiwan (Wu & Wang, 2005). The species was thought to be restricted to India, China and Japan, until Smith (2007) in his treatment of the Polytrichaceae in the Flora of North America referred most North American specimens previously identified as *P. formosum* to *Polytrichastrum formosum* var. *densifolium*. Similarly, our study revealed the wide distribution of the species in Asian Russia (southern Siberia from Altai to Transbaikalia, the southern Russian Far East, and Chukotka), and in most of the territory of European Russia and the highland Caucasus. It also occurs in E and N Europe, *i.e.*, in the Baltic countries and Finland. More detailed studies are needed to outline the boundary between the distribution areas of *P. densifolium* and *P. formosum*.

Ecology. In Russia, *P. densifolium* is most common in the southern taiga and mixed conifer and deciduous forests, mostly on upturned roots of fallen trees in mesic forests and on soil in various other disturbed places (along forest roads, *etc.*), occasionally also on the bases of tree trunks and on rocks covered with soil.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province:** Khibiny Mts., 2.VIII.1949, *Schljakov 2335* (LE); **Republic of Karelia:** Vodla River, 29.VIII.1976, *Volkova s.n.* (LE); **Leningrad Province:** Vyborg Reserve, 31.VII.2005, *Leusina 152* (LE); **Perm Province:** Dzerzhinsky District, 12.07.1997, *Bezgodov 172* (MW); Vishersky Nature Reserve, Kvarush Mts, 7.VII.1998, *Bezgodov 339* (MW); **Pskov Province:** Pushkinogorje, 15.VIII.2005, *Afonina 170205* (LE); **Novgorod Province:** 9.VII.2000, *Borisova s.n.* (MW); **Tver Province:** Centralno-Lesnoy Nature Reserve, 12.VIII.1994 & 17.VIII.1994, *Kuraeva 564.1 & 509.1* (MW); **Kostroma Province:** Halbuzh, 07.VIII.1999, *Zhukov s.n.* (LE); **Moscow Province:** Zvenigorod, 8.VIII.2010, *Fedosov 10-1-70* (MW), S+; **Ryazan Province:** Oksky Nature Reserve, 26.VIII.1972, *Samarin s.n.* (MW); **Republic of Tatarstan:** Volga-Kama Nature Reserve, 18.VIII.2003, *Ignatov & Ignatova 03-64* (MW); **Republic of Bashkortostan:** Kailysh, 2.VII.1996, *Baishева s.n.* (LE, MHA), S+. CAUCASUS: **Karachaev-Cherkessia:** *Ignatov & Ignatova 05-3480* (MW). ASIAN RUSSIA: **Altai Re-**

public, Teletskoye Lake, 14.VI.1905, *Vereshchagin 111* (LE); Kanga River Valley, 6.VI.1989, *Ignatov 0/90* (LE, MHA); **Kemerovo Province**: Kuznetskiy Alatau Mts, 22. VI.2002, *Pisarenko 00709* (NSK, SASY); **Zabaikal'sky Territory**: Sokhondinsky Biosphere Reserve, 28.VII.1982 & 08.VII.2010, *Afonina s.n.* (LE), S+; **Chukotsky Autonomous District**: Yanrakyntot, 28.VIII.1976, *Afonina s.n.* (LE), S+; **Sakhalinskaya Province**: Kuril Islands, Kunashir, 17.IX.2006, *Ignatov 06-1388* (MW); **Primorsky Territory**: Southern Sikhote-Alin Mts, 15.VIII.1958, *Ponomarenko 317* (LE).

Polytrichum pallidisetum Funck, Krypt. Gew. Fichtelgeb. 3: 55. 1802. — *Polytrichastrum pallidisetum* (Funck) G. L. Smith, Mem. New York Bot. Gard. 21(3): 35. 1971. — *Polytrichum decipiens* Limpr., Rabenhorst Krypt-Fl. 4(2): 618. 1893.

Plants medium-sized to large, dark green, in loose tufts. **Stems** to 8 cm, not or sparingly branched. **Leaves** erect spreading when dry, the blade widely spreading but not sharply reflexed when moist, 6–10 mm long; sheath 1.1–1.7 mm wide, with tapering shoulders, hyaline or yellowish in color; blade linear-lanceolate; marginal lamina plane, 3–9 cells wide, sharply toothed from the apex almost to base of blade; **costa** excurrent, ending in short, reddish, toothed awn; **lamellae** 20–40, crenulate in profile, 4–6 cells high, the lamellar marginal cells in cross-section broader than the cells beneath, cuneate (obtrapezoidal), flat-topped to shallowly retuse, typically somewhat variable in shape in the same leaf cross-section, frequently tinged with brown; median **cells** of sheath elongate-rectangular, (60–)70–80(–100)×9–12 μm, ca. 5–7:1; marginal laminal cells ± isodiametric, 12–16 μm wide. **Sexual condition** dioicous. **Seta** yellowish, to 5 cm tall. **Capsules** acutely 4-angled, suberect to inclined, pale yellowish brown, slender and somewhat curved, 3–5×1.0–1.5 mm, tapering to the base (particularly when old and empty), apophysis not or only weakly differentiated; exothecial cells irregularly angular to subquadrate, 25–50 μm wide; stomata numerous, large, elliptic, distributed over entire area of short apophysis; **peristome** with high basal membrane, the teeth ca. 50, pale, 170–200 μm long and 55–70 μm wide; epiphragm persistent, without well-developed tooth-like processes or sacculi. **Operculum** rostrate, with straight beak. **Spores** ca. 12–16 μm, finely papillose. Calyptra hairy, covering the upper portion of the capsule.

Differentiation. In the field, *Polytrichum pallidisetum* most closely resembles *P. densifolium*, and they occur in much the same habitats. The species is best characterized by the lamellar marginal cells, which are broadened and truncate to shallowly retuse in cross-section; in profile, the lamellae are distinctly crenulate. When viewed from above, the marginal cells are convex, so that the edge of the lamella resembles a string of beads, in contrast to *P. formosum* and *P. longisetum*, in which the lamellae are narrow, ± sharp-edged, and straight-sided when viewed from above. *Polytrichum densifolium* also has crenulate lamellar margins, though they are much weaker.

The species can be also confused with *P. swartzii*, since both species have retuse lamellar marginal cells. However, in the latter species the lamellar marginal cells are even more irregular in shape within the same cross-section, and the lamellae are entire vs. crenulate in profile.

Distribution. *Polytrichastrum pallidisetum* has a predominantly Holarctic distribution, being rather scattered in most regions. In Europe it is known from the mountains of central Europe and Scandinavia, with a few records from Belorussia and Ukraine. In Russia, it occurs sporadically in the southern taiga zone of European Russia, in the Urals and the Caucasus, and in the mountainous areas of South Siberia and the Russian Far East, including its continental part, as well as the Sakhalin and Kuril Islands. In China and Japan it has been reported as *P. ochioense* (Ren. & Card.) G.L. Smith (Wu & Wang, 2005; Osada, 1966; Noguchi, 1987), although the latter species has been shown to be endemic to North America (Smith, 2007). In Japan the species is known from Hokkaido, Honshu and Sikoku (Osada, 1966), while in China it is rather rare, known from a few scattered localities in Chongqing, Heilongjiang, Jilin, and Yunnan (Wu & Wang, 2005). The species is also common in eastern North America, where it grows in coniferous or northern hardwood forests, from Labrador and Newfoundland to northern Michigan and Minnesota, Wisconsin, Ohio, and Pennsylvania, and southward to the mountains of North Carolina and Tennessee (Smith, 2007).

Ecology. In Russia, *P. pallidisetum* is sporadically distributed in the taiga zone, being common in some areas (e.g., Tver province in European Russia). It grows on soil rich in humus on the roots of fallen trunks, on rotten stumps, and on soil-covered rocks in conifer forests.

Selected specimens examined: EUROPEAN RUSSIA: **Vologda Province**: Sokol District, 532 rm of Hwy Moscow – Arkhangelsk, 21.IX.1990, *Ignatov s.n.* (MHA); Tot'ma District, Bryukhanikha Village, 18.VII.1926, *Korchagin & Gaze s.n.* (MHA); **Tver Province**: Andreapol District, 1 km N of Kozlovo Village, 04.VIII.1998, *Notov s.n.* (TVBG); Nelidovo District, Tsentralno-Lesnoi Nature Reserve, 1990, *Ignatov s.n.* (MW); **Kostroma Province**: Manturovo District, vicinity of Khalbuzh Village, 17.VII.2003, *Fedosov s.n.* (MHA); **Moscow Province**: Odintsovo District, Zvenigorod biological station, *Ignatova 06-3* (MHA); **Nizhegorodskaya Province**, Bor District, Kerzhensky Nature Reserve, 21.X.1998, *Popov s.n.* (MHA); **Perm Territory**: Gremyachinsk District, Rudyansky Spoi Range, 19.V.2012, *Bezgodov 30* (MHA); **Republic of Bashkortostan**: Beloretzky District, Malyy Iremel Mt., 31.VIII.1990, *Ignatova 2/5* (MHA). ASIAN RUSSIA: **Krasnoyarsk Territory**: Taimyrsky District, Khatanga settlement outskirts, Kotujkan River in the vicinity of Burdur Creek mouth, *Fedosov 07-341* (MW); Shushensky District, Sayano-Shushensky Nature Reserve, mouth of Golaya River, 02.VIII.2003, *Ermakov s.n.* (NSK); **Altai Republic**: Atkichu Creek, at mouth, 21.X.1989, *Zolotukhin s.n.* (MHA); Bolshoye Istyube Creek, *Ignatov 0/1355, 0/1360a, 18/43* (MHA); **Khabarovsk Territory**: Sovgavan District, Botchinsky Nature Reserve, Mokhovoi Creek, 12.VIII.2013, *Ignatov & Ignatova 13-335* (MHA); **Kamchatsky Territory**: Sredinny Range, vicinity of Esso Settlement,

middle course of Irakan River, 09.VIII.2003, *Czernyadjeva s.n.* (LE); **Primorsky Territory**: Partizansk District, Lazovsky Pass, *Ignatov et al. 06-3303* (MHA); **Sakhalinskaya Province**: Sakhalin, Korsakov District, Mereya River 2 km upstream its mouth, *Ignatov & Teleganova 06-702* (MHA); Kuril Islands, Kunashir Island, Kipyashchee Lake, 5.IX.2006, *Ignatov 06-3165* (MHA); Kunashir Island, Ruruj Mt., *Ignatov 06-1408* (MHA).

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LITERATURE CITED

- [ABRAMOV, I.I. & A.L. ABRAMOVA] АБРАМОВ И.И., А.Л. АБРАМОВА. 1983. Конспект флоры мхов Монгольской Народной Республики. – [Conspect of moss flora of Mongolian People Republic] *Л., Наука [Leningrad, Nauka]*, 222 pp.
- BELL, N.E. & J. HYVÖNEN. 2010. Phylogeny of the moss class Polytrichopsida (Bryophyta): generic-level structure and incongruent gene trees. – *Molec. Phylogen. Evol.* **55**(2): 381–398.
- BELL, N.E. & J. HYVÖNEN. 2010. A phylogenetic circumscription of *Polytrichastrum* (Polytrichaceae): reassessment of sporophyte morphology supports molecular phylogeny. – *Am. J. Bot.* **97**(4): 566–578.
- GANGULEE, H.C. 1969. Mosses E. India. Vol. 1. – *Privately published, Calcutta*: 1–170.
- GARDINER, A., M. IGNATOV, S. HUTTUNEN & A. TROITSKY. 2005. On resurrection of the families Pseudoleskeaceae Schimp. and Pylaisiaceae Schimp. (Musci, Hypnales). – *Taxon* **54**: 651–663.
- HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucl. Acids. Symp. Ser.* **41**: 95–98.
- HILL, M.O., N. BELL, M.A. BRUGGEMAN-NANNENGA, M. BRUGUÉS, M.J. CANO, J. ENROTH, K.I. FLATBERG, J.-P. FRAHM, M.T. GALLEGU, R. GARILLETI, J. GUERRA, L. HEDENÄS, D.T. HOLYOAK, J. HYVÖNEN, M.S. IGNATOV, F. LARA, V. MAZIMPAKA, J. MUÑOZ & L. SÖDERSTRÖM. 2006. An annotated checklist of the mosses of Europe and Macaronesia. – *J. Bryol.* **28**: 198–267.
- IGNATOV, M.S., O.M. AFONINA, E.A. IGNATOVA et al. 2006. Checklist of mosses of East Europe and North Asia. – *Arctoa* **15**: 1–130.
- [IGNATOV, M.S. & E.A. IGNATOVA] ИГНАТОВ М.С., Е.А. ИГНАТОВА. 2003. Флора мхов средней части европейской России. Т. 1. – [Moss flora of the Middle European Russia. Vol. 1] *М., КМК [Moscow, KMK]*: 1–608.
- IVANOVA, E. I., N. E. BELL, O. I. KUZNETSOVA, H.-S. LEE, M. PARK & M. S. IGNATOV. 2014. The genus *Polytrichastrum* (Polytrichaceae) in Russia. – *Arctoa* **23**: 164–184.
- NOGUCHI, A. & Z. IWATSUKI. 1987. Illustrated Moss Flora of Japan. Vol. 1. – *Hattori Bot. Lab., Nichinan*, 1–242.
- OSADA, T. 1966. Japanese Polytrichaceae. II. The genera *Polytrichum*, *Oligotrichum*, *Bartramiopsis* and *Atrichum* and phytogeography. – *J. Hattori Bot. Lab.* **29**: 1–52.
- [SAVICZ-LYUBITSKAYA, L.I. & Z.N. SMIRNOVA] САВИЧ-ЛЮБИЦКАЯ Л.И., З.Н. СМІРНОВА. 1970. Определитель листостебельных мхов СССР. Верхлоплодные мхи. – [Handbook of mosses of the USSR. The acrocarpous mosses] *Л., Наука [Leningrad, Nauka]*, 822 pp.
- SMITH, G.L. 1971. A conspectus of the genera of Polytrichaceae. – *Mem. New York Bot. Garden* **21**: 1–83.
- SMITH MERRILL, G.L. 2007. *Polytrichastrum*. – In: *Flora of North America Editorial Committee (Eds.), Flora of North America North of Mexico, vol. 27. Bryophytes: Mosses, Part 1. Oxford University Press, New York*, 124–133.
- [TSEGMED, TS.] ЦЭГМЭД Ц. 2010. Флора мхов Монголии. – [Moss Flora of Mongolia] *М. [Moscow]*, 634 pp.
- WU, P. & M. WANG. 2005. Polytrichaceae. – In: *Wu Peng-cheng, M.R. Crosby & S. He (eds.), Moss Flora of China. Vol. 8. Sematophyllaceae–Polytrichaceae. Science Press & Missouri Botanical Garden, Beijing, New York & St. Louis*, 385 pp.

APPENDIX 1.

GenBank accession number are given in the following order: *rps4*, *trnL-F*.

Polytrichum densifolium Tatarstan (Russia, Tatarstan, 18.VIII.2003, *Ignatov & Ignatova 1*, MHA): KP342501, KP342481; *P. densifolium* Perm (Russia, Perm Province, 2.VII.1995, *Bezgodov & Selivanov 466*, MHA): KP342502, KP342482; *P. densifolium* Moscow (Russia, Moscow Province, *Fedosov 10-1-70*, MW): KP342503, KP342483; *P. densifolium* Kuril Is. (Russia, Kunashir, *Ignatov 06-1388*, MW): KP342504, KP342484; *P. densifolium* Kemerovo 1 (Russia, Kemerovo Province, *Pisarenko 00503*, SASY): KP342506, KP342486; *P. densifolium* Kemerovo 2 (Russia, Kemerovo Province, 22.VI.2002, *Pisarenko s.n.*, SASY): KP342505, KP342485; *P. densifolium* Karachaevo-Cherkessia (Russia, Karachaevo-Cherkessia, *Ignatov & Ignatova 05-3480*, MW): —, KP342487; *P. densifolium* Bashkortostan (Russia, Bashkortostan, 2.VII.1996, *Baisheva s.n.*, MW): KP342508, KP342488; *P. formosum* Krasnodar (Russia, Krasnodar Territory, *Ignatov & Ignatova 12-51*, MW): KP342500, KP342479; *P. formosum* Switzerland (Switzerland, 7.VIII.2001, *Ulanova s.n.*, MW): —, KP342480; *P. longisetum* Chukotka (Russia, Chukotka, 5.VIII.1976, *Afonina s.n.*, LE): KP342493, KP342472; *P. longisetum* Yakutia 28 (Russia, Yakutia 18.VII.1994, *Ivanova s.n.*, SASY): KP342496, KP342476; *P. longisetum* Yakutia 30 (Russia, Yakutia, 16.VIII.1985, *Volotovskiy 16/8*, SASY): KP342495, KP342475; *P. longisetum* Yakutia 39 (Russia, Yakutia, 14.VIII.2009, *Efimova s.n.*, SASY): KP342494, KP342474; *P. longisetum* Taimyr (Russia, Taimyr, Putorana, 4.VIII.1983, *Czernyadjeva 109*, LE): KP342497, KP342477; *P. longisetum* Kamchatka (Russia, Kamchatka, 13.VIII.2005, *Czernyadjeva 36*, LE): KP342498, KP342478; *P. longisetum* Khanty-Mansi (Russia, Khanty-Mansi District, Surgut, 9.VIII.2000, *Czernyadjeva & Kuzmina 73*, LE): KP342492, KP342471; *P. longisetum* var. *anomalum* Khabarovsk (Russia, Khabarovsk Territory, *Ignatov & Ignatova 13-619*, MHA): KP342499, —; *P. longisetum* var. *anomalum* Kamchatka (Russia, Kamchatka, 1.VIII.2006, *Samkova 4*, MW): —, KP342473; *P. pallidisetum* Krasnoyarsk (Russia, Krasnoyarsk, 2.VIII.2003, *Ermakov s.n.* (SASY): KP342489, KP342466; *P. pallidisetum* Kemerovo (Russia, Kemerovo Province, 22.VI.2002, *Pisarenko 00137* (SASY): KP342490, KP342467; *P. pallidisetum* Mari-El (Russia, Mari El, 15.X.1999, *Popov & Bogdanov s.n.*, LE): —, KP342468; *P. pallidisetum* Bashkiria (Russia, Bashkortostan, 23.VII.1995, *Solometch 4*, LE): KP342491, KP342469; *P. pallidisetum* Sakhalin (Russia, Sakhalin, *Ignatov & Teleganova 06-709*, MHA): —, KP342470.