THE GENUS POLYTRICHUM SECT. APOROTHECA (POLYTRICHACEAE) IN RUSSIA

ROD 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.

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 Polytrichum commune, P. juniperinum and P. strictum were also included in the outgroup. DNA extractions and overall laboratory protocols were essentially as
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. longietum 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.

Fig. 1. Phylogenetic tree based on Bayesian analysis of rps4 and trnL-F regions. Posterior probabilities are shown below branches.
The genus Polytrichum sect. Aporotheca (Polytrichaceae) in Russia 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 from *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


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. 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”.

50 μm

0.5 mm

100 μm

0.5 mm
The genus Polytrichum sect. Aporotheca (Polytrichaceae) in Russia


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


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 profile; 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*


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** dioicus. 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 deepolated capsules often absent. **Spores** (15–)18–23(–26) μm. **Opereculum** rostrate, the beak about 0.5 mm long. **Calyptra** hairy, yellowish to golden brown to fuscous, covering the upper portion of the capsule.

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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: from Czech Republic, Karlovy Vary, 28.VIII.2011, Donskov s.n., MHA; 31: from Czech Republic, Karlovy Vary, 22.IV.1957, Tyurennov s.n., MHA), 24-25: lower part of capsule showing apophysis, wet; 26-29: capsules showing 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, or 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 pestostome 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 China and Japan. In North America it occurs from Labrador to the mountains of Mongolia, Northern China, to Russia: Murmansk Province: Tetino, 24.VII.1927, Zinzinger 30 (LE, SASY), S+; Leningrad Province: Lenvokava River, 23.VII.1971, Vjunova 94 (LE), S+; Gluboke Lake, 9.VI.1974, Vjunova 474 (LE), S+; Peterhof, 6.IX.1975, Vjunova 533 (LE), S+; Tyumen Province: Lenina 1975: 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


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-

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-sprouting 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 brown pointed toothed, 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 ± isodiametric, with moderately thickened walls, (9–)10–13(–24) μm wide. Sexual condition dioicus. Seta stout, to 4 cm tall. Capsules short rectangular, ±acutely 4-angled, inclined to horizontal, yellowish brown to dark brown, 3.5×1.5 mm, with rather small round apophysis, ±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, 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, 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 (I. e.) mention an additional difference regarding sexual condition for var. formosum and var. densifolium, i.e., always dioicus 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. intercedens (Card.) Osada] was reported to be comparatively more frequent, than var. densifolium,
common on Honshu, Shikoku 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.


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, osseous when dry, widely spreading to reflexed when moist, ly 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** (30–345–50–60), 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; medium **cells** of sheath elongate rectangular, (50–)60–70–90(–9)(–9)–10–13(–15) μm; cells of the lamina near margin ± isodiametric to transversely widened, (10–)12–15(–15) μm wide, thin-walled. Sexual condition dioicous [or polyoicous]. **Seta** stout, 3–6 cm tall. **Capsules** elongate-rectangular, ± acute 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 sacculi on ventral side alternating with peristome teeth, and without teeth opposite peristome teeth on dorsal side or, occasionally, with small reduced teeth. **Opeculum** rostrate, with straight beak. **Spores** 12–15 μm, finely papillose. **Calytra** 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 Ganguee (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 Yakuishima 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 uprooted trunks 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.

from above, the marginal cells are convex, so that the edge file, the lamellae are distinctly crenulate. When viewed and truncate to shallowly retuse in cross-section; in protonemata, the lamellar marginal cells, which are broadened in much the same habitats. The species is best characterized by the lamellar marginal cells, though they are much weaker.

Differentiation. Polytrichastrum pallidisetum has a predominately 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 Sado Island (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: *Volgodon Province*: Sokol District, 532 rm of Hwy Moscow – Arkhangelsk, 21.9.1990, Ignatov n.s. (MHA); Totma District, Belyakhan, akha Village, 18.VII.1926, Korochkin & Gaze n.s. (MHA); *Tver Province*: Andreapoul District, 1 km N of Kozlovo Village, 04.VIII.1998, Notov n.s. (TVBG); Nelidovo District, Tsentralno-Lesnoi Nature Reserve, 1990, Ignatov n.s. (MHA); *Kostroma Province*: Manturovo District, vicinity of Khabuzh Village, 17.VII.2003, Fedosov n.s. (MHA); Moscovo District, Zvenigorod biological station, Ignatova 06-3 (MHA); *Nizhegorodskaya Province*, Bor District, Kozhensky Nature Reserve, 21.X.1998, Popov n.s. (MHA); *Perm Territory*: Grenyachinsk District, Rudysky Spioi Range, 19.V.2012, Bezgodov 30 (MHA); Republic of Bashkortostan: Beloretsky District, Maljy Iremel Mt., 31.VII.1990, Ignatova 25/M (MHA). ASIAN RUSSIA: *Krasnoyarsk Territory*: Taimyrsky District, Khantanga settlement outskirts, Kotujkan River in the vicinity of Burdur Creek mouth, Fedosov 07-341 (MWA); Shushensky District, Sayano-Shushensky Nature Reserve, mouth of Golaya River, 02.VII.2003, Ermakov n.s. (NSK); *Altai Republic*: Altichuk Creek, at mouth, 21.X.1989, Zolotukhin n.s. (MHA); Boshoye Istyube Creek, Ignatov 0/1355, 0/1360a, 18/43 (MHA); *Khabarovsk Territory*: Sovgavan District, Botchinsky Nature Reserve, Mokhovo Creek, 12.VIII.2013, Ignatov & Ignatova 13-335 (MHA); *Kamchatka Territory*: Sredniy Range, vicinity of Esso Settlement,
middle course of Irakan River, 06.VIII.2003, Zernyadjeva 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, Kiyypashchee Lake, 5.IX.2006, Ignatov 06-3163 (MHA); Kunashir Island, Runur Mt., Ignatov 06-1408 (MHA).

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LITERATURE CITED


APPENDIX 1.
GenBank accession number are given in the following order: rps4, trnL-F.