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TAXONOMY OF THE *PLAGIOTHECIUM LAETUM* COMPLEX (PLAGIOTHECIACEAE, BRYOPHYTA) IN RUSSIA

СИСТЕМАТИКА КОМПЛЕКСА *PLAGIOTHECIUM LAETUM* (PLAGIOTHECIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

A revision of the complex of *Plagiothecium laetum* and related species revealed a neglected species in East Europe, with some localities in Russian Far East, *Plagiothecium rossicum*. It differs from West European and North American *P. laetum* in sequences of both nuclear ITS and chloroplast rpl16 and in morphology. Plants identical with West European *P. laetum* occur in Russia only in the Black Sea coastal area of Caucasus and one locality in lowland European Russia (Kaluga Province). Asiatic plants characterized by abruptly tapered leaves with more or less piliferous acumen are referred to *P. svalbardense*, which therefore appeared to be a common plant throughout Siberia and Russian Far East. *Plagiothecium curvifolium* is also distinct from *P. rossicum*, in both DNA sequence and morphology; it is not confirmed by molecular markers in Russia east of the Urals.

Резюме

Ревизия комплекса видов, близких к *Plagiothecium laetum,* выявила ранее не распознанный вид, довольно широко распространенный в лесной зоне Восточной Европы, и с рядом местонахождений на Дальнем Вотоке России, *Plagiothecium rossicum*. Он отличается от западноевропейского и североамериканского *P. laetum* s.str. по последовательностям ядерных (ITS) и хлоропластных (rpl16) участков ДНК, а также по морфологии. Растения, идентичные западноевропейскому *P. laetum,* были найдены в России только в районе черноморского побережья Кавказа и в одном местонахождении в Калужской области. Азиатские растения с относительно быстро суженным у верхушки листом, часто выглядящие как имеющие гиалиновый волосок, отнесены к *P. svalbardense*, который, таким образом, оказывается частым видом в Сибири и на Дальнем Востоке. *Plagiothecium curvifolium* имеет четкие отличия от *P. rossicum* и по каждому из изученных молекулярных маркеров, и по морфологии; он не был найден в России восточнее Урала.

KEYWORDS: *Plagiothecium*, Russia, taxonomy, new species, nrITS, rpl16, molecular phylogenetics

Introduction

The circumscription of the genus *Plagiothecium* Bruch, Schimp. & W. Gümbel was changed considerably since its original description in "Bryologia Europaea" (Bruch *et al.*, 1851), when it included species classified now in *Herzogiella* Broth. and *Isopterygiopsis* Z. Iwats. in most treatmens (Hill *et al*., 2006; Huttunen *et al.*, 2013; Ireland, 2014; Wynns *et al*., 2018). Recent studies based on molecular phylogenetic approach have resulted in a narrower definition of the genus, with more distantly related groups segregated as *Rectithecium* Hedenäs & Huttunen (Huttunen *et al*., 2013)*, Struckia* Müll. Hal. (Ignatov *et al.*, 2007; Huttunen *et al.*, 2013); and *Ortholimnobium* Dixon (Wynns & Schröck, 2018). Three other genera have been described for species less deviated from core *Plagiothecium* and they are only rarely recognized as separate genera: *Saviczia* Abramova & I.I. Abramov (typified with *Plagiothecium obtusissimum* Broth.), *Buckiella* Ireland (typified with *Plagiothecium undulatum* (Hedw.) Bruch, Schimp. & W. Gümbel), and *Philoscia* Berk. (typified with *Plagiothecium latebricola* Bruch, Schimp. & W. Gümbel). Most recent taxonomic treatments (e.g. Huttunen *et al.,* 2013; Wynns *et al.,* 2018) retain them in the genus *Plagiothecium*.

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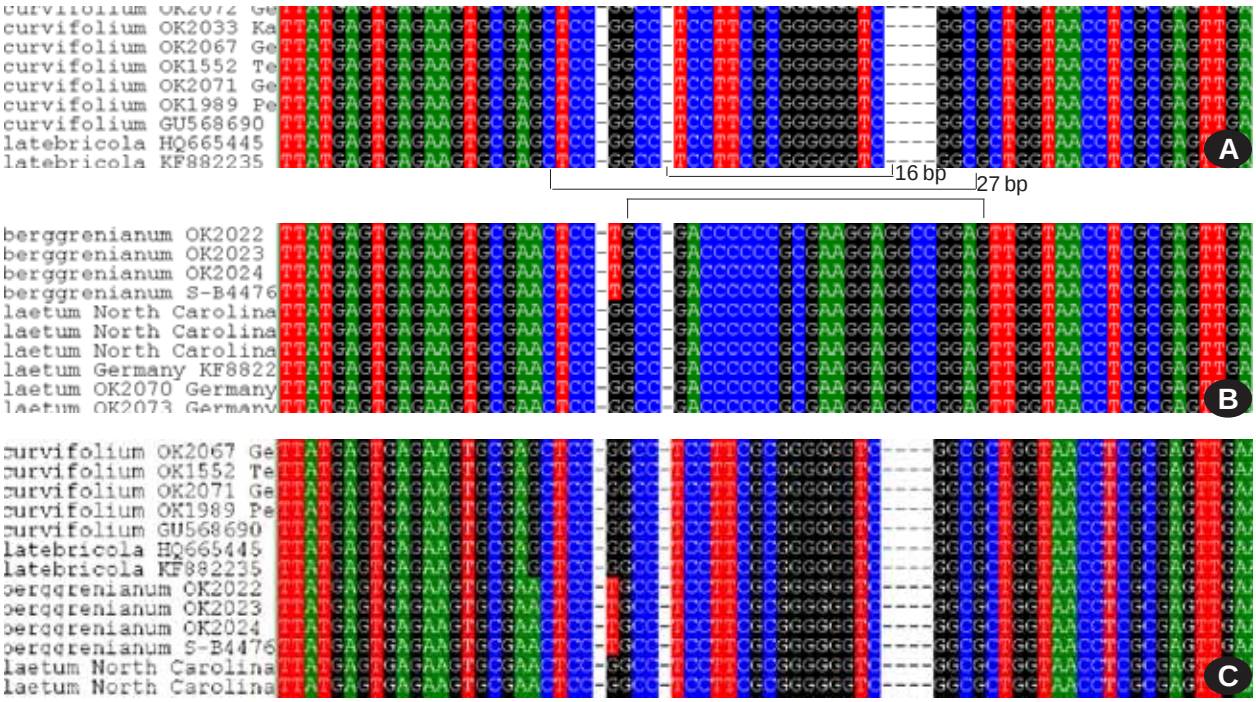

Fig. 1. Part of alignment of *Plagiothecium*: A and B are parts of original alignment, showing inversion in ITS1, and C shows how it was coded for the analysis, in addition to coding the fact of inversion in a separate partition.

The terminal position in evolution of Plagiotheciaceae, as it was found in various analyses (Pedersen & Hedenäs, 2001, 2002; Huttunen *et al.*, 2013; Wynns *et al.*, 2018) keeps the genus *Plagiothecium* s. str. Despite including not so great number of species, it remains a difficult genus, causing problems for bryologists who need to identify numerous collections for flora inventory and ecological studies every day. *Plagiothecium* includes about five circum-holarctic species and about ten otherwise widespread ones in the temperate part of Northern Hemisphere, with a number of less widespread species in the Southern Hemisphere and mountains in subtropical and tropical regions (Wynns *et al.,* 2018). At the same time, authors from different regions accepted different species, e.g. Noguchi *et al.* (1994) in Japan accepted *P. curvifolium* and did not include *P. laetum*. Both these species are treated as their own in Russia (Ignatov *et al.*, 2006) and Europe (Hill *et al.*, 2006), but in North America the former species is synonymized with the latter (Ireland, 2014).

In the course of our study of the Asian Russian moss flora, especially its permafrost regions, we found *Plagiothecium piliferum*-like plants, which, according to identification keys, however, came out to *P. laetum*. The great variation of plants in these populations forced us to report it as *P. laetum* in a number of publications concerning regional moss diversity (Ignatov *et al.*, 2001, 2014; Ignatova *et al.*, 2011, 2013; Ivanova *et al.*, 2016), due to the absence of any other apparently appropriate names. Recently, in the course of the revision of *Plagiothecium* for the Moss Flora of Russia, we studied these morphotypes with nuclear ITS and found an obvious difference between Siberian and European plants. By this reason we undertook an expanded analysis, which results are presented here.

Materials and Methods

Molecular markers. Nuclear ITS and chloroplast rpl16 were chosen. The former is the most common and was used already in most analyses of Plagiotheciaceae, providing the strongest phylogenetic signal compared to other regions (Huttunen *et al.*, 2012, 2013). Rpl16 is not so universal, but as it was used in previous expanded analysis by Wynns *et al.* (2018), and provided specific motifs for all *Plagiothecium* species, it was also used for the present analysis.

Sampling. The sampling was addressed mainly to fix the number of species and better understand differences and distribution in Russia for entities that coming out of molecular phylogenetic analysis. The main attention was addressed to *Plagiothecium laetum* and putatively related species, although we included representatives of the *P. cavifolium* group as well, in order to check the consistency of name usage, especially with the comprehensive analysis of Wynns *et al.* (2018). Expansion of set proceeded slowly by adding specimens from regions where from this or that "molecular entity" was still not represented and for checking hypotheses on the identity of specimens of ambiguous morphology.

Laboratory protocol and sequencing were rather standard, e.g. as in Gardiner *et al.* (2005).

Aligning and coding. Sequences were aligned in Bioedit (Hall, 1999) by built-in Clustal program and then

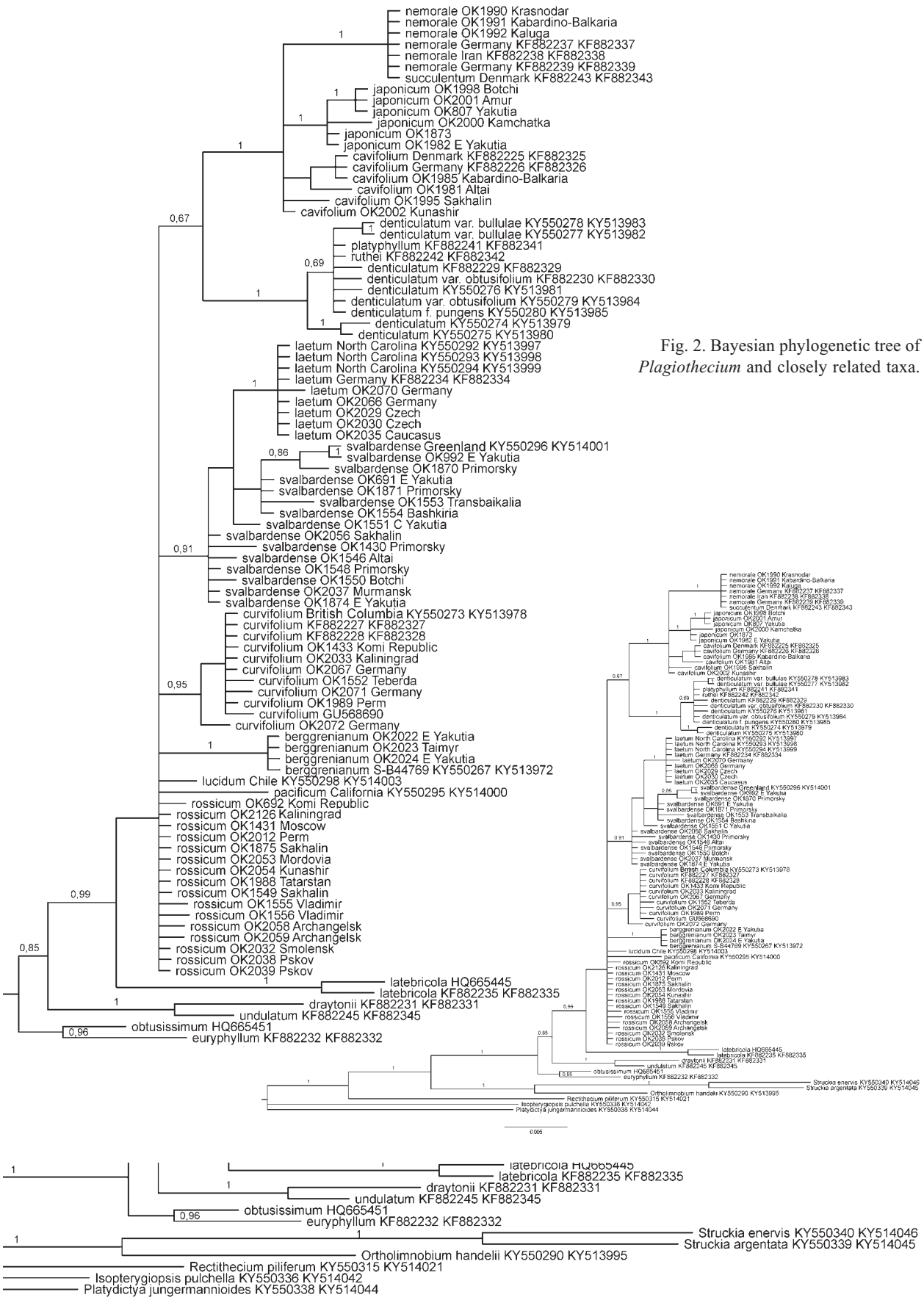

Fig. 2. Bayesian phylogenetic tree of *Plagiothecium* and closely related taxa.

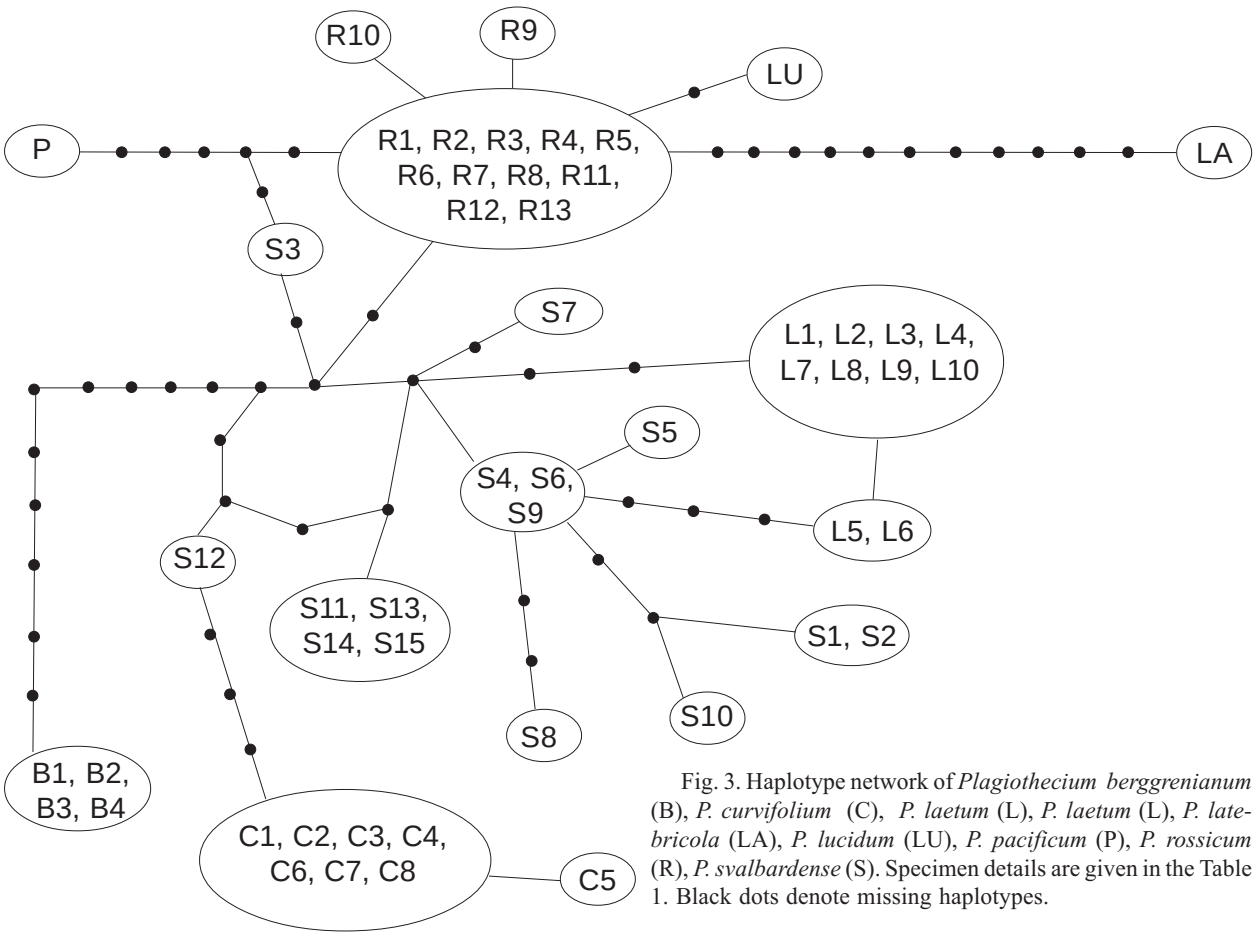

Fig. 3. Haplotype network of *Plagiothecium berggrenianum* (B), *P. curvifolium* (C), *P. laetum* (L), *P. laetum* (L), *P. latebricola* (LA), *P. lucidum* (LU), *P. pacificum* (P), *P. rossicum* (R), *P. svalbardense* (S). Specimen details are given in the Table 1. Black dots denote missing haplotypes.

Fig. 3. Haplotype coding of species of *Plagiothecium laetum– complex*: (code/ species name/ isolate and region for newly generatad sequences or GenBank accession numbers, ITS and rpl16, and region where known).

B1 *berggrenianum* OK2022 E Yakutia
B2 *berggrenianum* OK2023 Taimyr
B3 *berggrenianum* OK2024 E Yakutia
B4 *berggrenianum* S-B44769 KY550267 KY513972
LU *lucidum* Chile KY550298 KY514003
C1 *curvifolium* British Columbia KY550273 KY513978
C2 *curvifolium* KF882227 KF882327
C3 *curvifolium* KF882228 KF882328
C4 *curvifolium* OK1433 Komi Republic
C5 *curvifolium* OK2072 Germany
C6 *curvifolium* OK2033 Kaliningrad
C7 *curvifolium* OK2067 Germany
C8 *curvifolium* OK1989 Perm
LA *latebricola* KF882235 KF882335
R1 *rossicum* OK2126 Kaliningrad
R2 *rossicum* OK1431 Moscow
R3 *rossicum* OK2012 Perm
R4 *rossicum* OK1875 Sakhalin
R5 *rossicum* OK2053 Mordovia
R6 *rossicum* OK2054 Kunashir
R7 *rossicum* OK1988 Tatarstan
R8 *rossicum* OK1549 Sakhalin
R9 *rossicum* OK1555 Vladimir
R10 *rossicum* OK1556 Vladimir
R11 *rossicum* OK2032 Smolensk
R12 *rossicum* OK2038 Pskov
R13 *rossicum* OK2039 Pskov
P *pacificum* California KY550295 KY514000
L1 *laetum* North Carolina KY550292 KY513997
L2 *laetum* North Carolina KY550293 KY513998
L3 *laetum* North Carolina KY550294 KY513999
L4 *laetum* Germany KF882234 KF882334
L5 *laetum* OK2070 Germany
L6 *laetum* OK2073 Germany
L7 *laetum* OK2066 Germany
L8 *laetum* OK2029 Czech
L9 *laetum* OK2030 Czech
L10 *laetum* OK2035 Caucasus
S1 *svalbardense* Greenland KY550296 KY514001
S2 *svalbardense* OK992 E Yakutia
S3 *svalbardense* OK991 N Sakhalin
S4 *svalbardense* OK691 E Yakutia
S5 *svalbardense* OK1547 Anabar
S6 *svalbardense* OK1871 Primorsky
S7 *svalbardense* OK1551 C Yakutia
S8 *svalbardense* OK1553 Transbaikalia
S9 *svalbardense* OK1554 Bashkiria
S10 *svalbardense* OK1870 Primorsky
S11 *svalbardense* OK2056 Sakhalin
S12 *svalbardense* OK1430 Primorsky
S13 *svalbardense* OK1548 Primorsky
S14 *svalbardense* OK2037 Murmansk
S15 *svalbardense* OK1874 E Yakutia

corrected manually. The main difference from Wynns *et al.*'s (2018) analysis was a somewhat different coding of inversion in the ITS1of *Plagiothecium laetum* s.str., *P. berggrenianum* Frisvoll and *P. svalbardense* Frisvoll. Wynns *et al.* (2018) had coded the fact of 16-bp inversion, whereas we coded "unequally inverted" fragment of 27 bp, flanked at the sides of the insertion at the 5'-end by a substitution in *P. laetum* s.str., *P. berggrenianum* and *P. svalbardense*, and at the 3'-end by a substitution only in *P. berggrenianum* (Fig. 1). Therefore, we inverted it as shown in Fig. 1, so this region appears the same as in all other *Plagiothecium* species. The fact of the presence of inversion was coded as additional partition one nucleotide long, as C if inversion is present and T for inversion absence.

Phylogenetic analysis.

Bayesian analyses were conducted following a Bayesian Markov Chain Monte Carlo approach using MrBayes 3.2.6 (Ronquist *et al.*, 2012). The four partitions (ITS1, 5.8S RNA, ITS2, rpl16) were analyzed with the GTR+G model and the indel partition was analyzed using the restriction site (binary) model. Four parallel runs were implemented, each with six chains and 40,000,000 generations, with trees sampled every 1000 generations. Burn-in was set to exclude 25% generations. The chain temperature was set at 0.02 in all analyses. The stationary phases of analyses were tested by Tracer 1.6 (Rambaut *et al.*, 2014). Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE.

Haplotype network analysis was performed in TCS 1.21 (Clement *et al.*, 2000), with gap coding as a single event irrespective of length with connection limit at 15 steps and coding gaps as missing data. TCS analysis included only species of *Plagiothecium* sect. *Leptophyllum* with exception for *P. berggrenianum*, a putative hybrid of *P. svalbardense* and *P. denticulatum* var. *obtusifolium* (Wynns *et al.*, 2018).

Morphological studies. Although the specimens were always studied when being selected for sequencing, the total revision of material in MW, MHA and LE, and partly from other herbaria was done based on characters elucidated after the preliminary sorting of material.

RESULTS

The tree inferred from the Bayesian analysis (Fig. 2) found *Rectithecium* sister to the *Plagiothecium*+*Struckia* +*Ortholimnobium*-clade with high support, and after branching off *Struckia*+*Ortholimnobium,* the terminal clade of *Plagiothecium* was resolved with maximal support. This terminal clade starts from the grade of *P. eurysphyllum* and *P. obtusissimum* (sect. *Saviczia*), then *P. undulatum* and *P. draytonii* (sect. *Lycambium*), then clade of *P. latebricola,* and finally the terminal clade composed of a broad polytomy of the species from sect. *Leptophyllum, Orthophyllum* and *Plagiothecium*. The two latter sections form clades with maximal support, while species of the group of *P. laetum* form a polytomy of individual specimens of the East European new species, *P. pacificum, P. lucidum*, monospecific clades of *P. berggrenianum* (PP=1) and *P. curvifolium* (PP=0.95), and a moderately supported (P=0.91) clade of *P. svalbardense* and *P. laetum*, where a nested clade of the latter has maximal support.

The TCS haplotype network (Fig. 3) shows another side of diversity in sect. *Leptophyllum*. Fairly isolated positions are shown for *P. latebricola, P. pacificum* and *P. berggrenianum*, represented by a limited number of specimens. *Plagiothecium curvifolium, P. laetum* (as defined here) and a new species from the East Europe *(P. rossicum*, described below) form rather compact groups with a few slightly different haplotypes around the main groups, whereas specimens referred here to *P. svalbardense* form a loose cloud. The main reason to refer these specimens to *P. svalbardense* is their morphology.

Although being somewhat apart from the mainstream of the present study, *Plagiothecium* sect. *Orthophyllum* is resolved as monophyletic with maximally supported nested clades of *P. nemorale* and *P. japonicum,* and a basal polytomy of *P. cavifolium*. One Genbank specimen of *P. platyphyllum* (an autopolyploid of *P. denticulatum* s.l. according to Wynns *et al*. (2018)) and one of *P. ruthei* were found in a clade with *P. denticulatum*, which comprises an unresolved polytomy of these three species (Fig. 2).

DISCUSSION

The finding of a widespread entity (Fig. 4) well delimited by molecular markers was surprising in itself; and it is even more interesting that it appeared to have rather clear morphological distinction, which became apparent during a comparison of morphology of sequenced specimens. It turned out that a narrowly recurved leaf margin occurs in all specimens with inversion in ITS1. Among them, *P. berggrenianum* with its reflexed acumen and a relatively robust stature is a species easily recognizable in the field, and in addition it has unique substitutions both in ITS and rpl16.

Other specimens with the inversion are different in leaf shape: longer and gradually narrowing in European plants, and more abruptly contracted to a narrow or filiform acumen in Siberian plants (see below, Figs. 8–10). These two groups do not differ in ITS at all, but have a number of differences in plastid rpl16.

Plants without the inversion from Russia split into three groups. First, *P. latebricola* is a well-known plant, the only species, at least in Northern Hemisphere, with subapical brood body production, so it is segregated by some authors in a separate genus; it possesses apomorphies in both ITS and rpl16. The others, *P. curvifolium* and *P. rossicum* (see below), in addition to morphological characters have also substitutions in both studied DNA regions being always present in all studied specimens. Therefore the East European plants are described below as a new species (additional localities of this species were revealed also in Russian Far East).

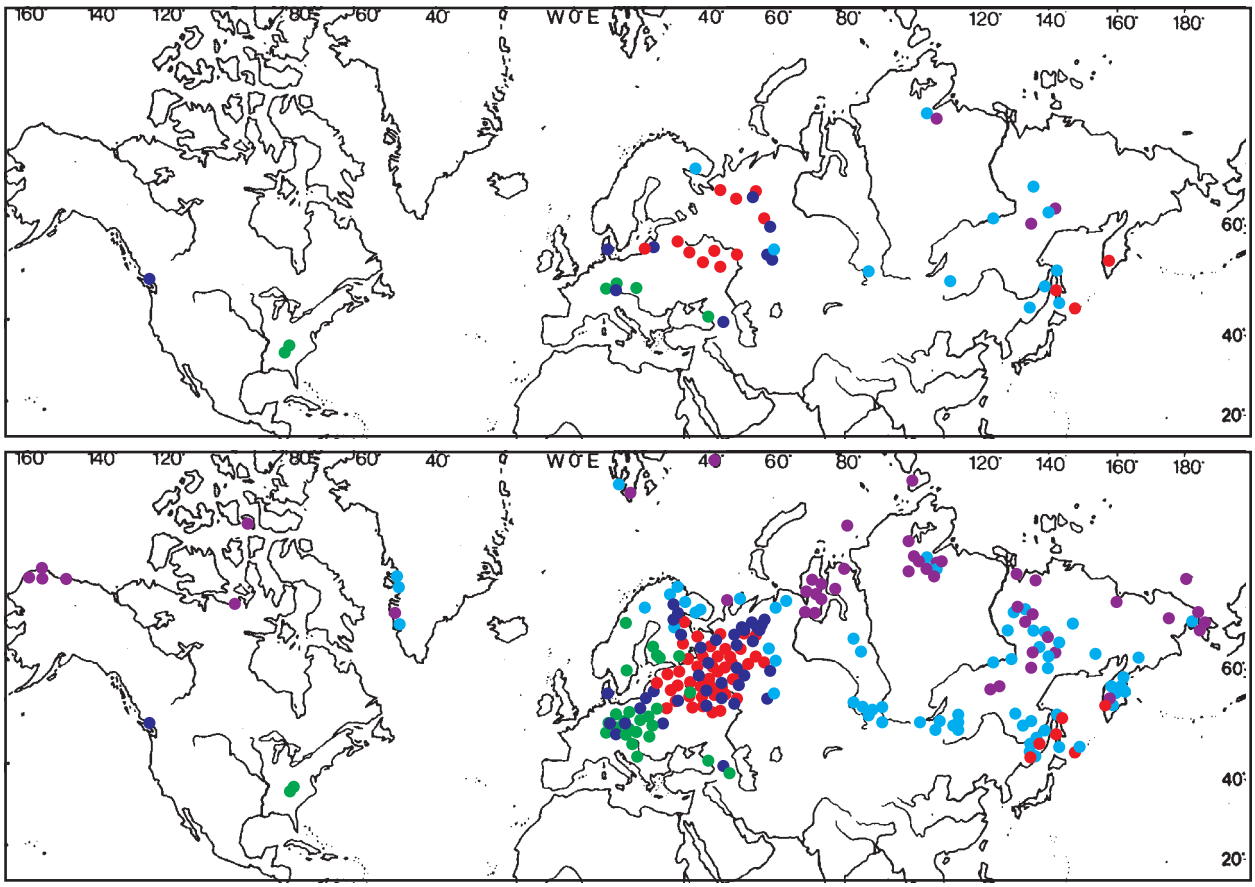

Fig. 4. Distribution of *Plagiothecium P. laetum* (●), *P. svalbardense* (●), *P. berggrenianum* (●), *P. curvifolium* (●) and *P. rossicum* (●) in Russia (with few dots outside Russia, based mostly on sequenced specimens). A: sequenced specimens, B: all studies specimens, and for *P. berggrenianum* with dots from Ireland (1986), and Ukrainskaya (1996) and for *P. berggrenianum* and *P. svalbardense* by localities from Wynns (pers. corr.), listed after specimens examined.

TAXONOMY

Plagiothecium rossicum Ignatov & Ignatova, sp. nov. Figs. 5–6.

Type: Russia, Pskov Province, Nevel'sk Distr., vicinities of Ustavnoe Settl. (near Yazno Lake), pine forest, at base of pine trunk, 26.IX.2001, Zolotov P504 (Holotype MHA9041611).

Etymology: the name refers the country, Russia, the main area where the species occurs.

Diagnosis: *Plagiothecium rossicum* is distinguished from *P. laetum*, *P. curvifolium* and *P. svalbardense* by always flat leaf margins, contrary to narrowly recurved margins in all these species, partially or almost thoroughout. *Plagiothecium rossicum* is most similar to *P. laetum* in only slightly concave, ovate leaves gradually tapered to the apex or shortly apiculate, and flattened shoots forming flat mats, but the size of its plants is somewhat smaller and its leaves are more strongly asymmetrical than in *P. laetum*. From *P. curvifolium* it differs in smaller size of plants, leaves more or less flat vs. usually curved towards substrate, and narrower laminal cells, 6–7 vs. 8–9 µm wide. Capsules are commonly symmetrical and straight or slightly curved and inclined in *P. rossicum*, similar to *P. laetum* and *P. svalbardense*, but not *P. curvifolium*, which usually has curved and inclined capsules. *Plagiothecium pacificum* from western North America is a larger plant with leaves 1.4–1.9(–2.2) mm long, smaller spores, 9–10 µm, and sometimes with rhizoids in subapical position (never so in *P. rossicum*). Southern Hemispheran *P. lucidum* is most closely related genetically, but in addition to too faraway distribution, it differs in somewhat larger plants, leaves to 2.1 mm long, longly attenuate leaf apex and sporadically rhizomatous leaves (Allen, 2018), and its closely related species have even larger leaves, to 3.1 mm long (Wynns *et al.*, 2018).

Description. Plants small, in flat lustrous mats. Stems creeping, 0.6–1 cm long, slightly branched; foliage distinctly complanate; central strand present. Leaves forming 40–100° angle with stem, spreading, asymmetric, (0.7–)0.9–1.4(–1.6) × 0.35–0.5(–0.6) mm, ovate-lanceolate, tapered to a narrowly acute or shortly acuminate apex, decurrent, cells of decurrencies in 2–3 rows, rectangular; leaf margins flat, entire or minutely denticulate at apex; costa short and double; laminal cells (70–)100–130 × 6–7 µm. Gemmae of 3–4 quadrate or short rectangular cells occasionally present. Autoicous. Perigonial leaves ovate, acuminate to apiculate; perichaetial leaves 1.0–1.5 mm long, oblong-lanceolate, shortly acuminate. Setae 5–7 mm long; capsules straight and erect or slightly curved and

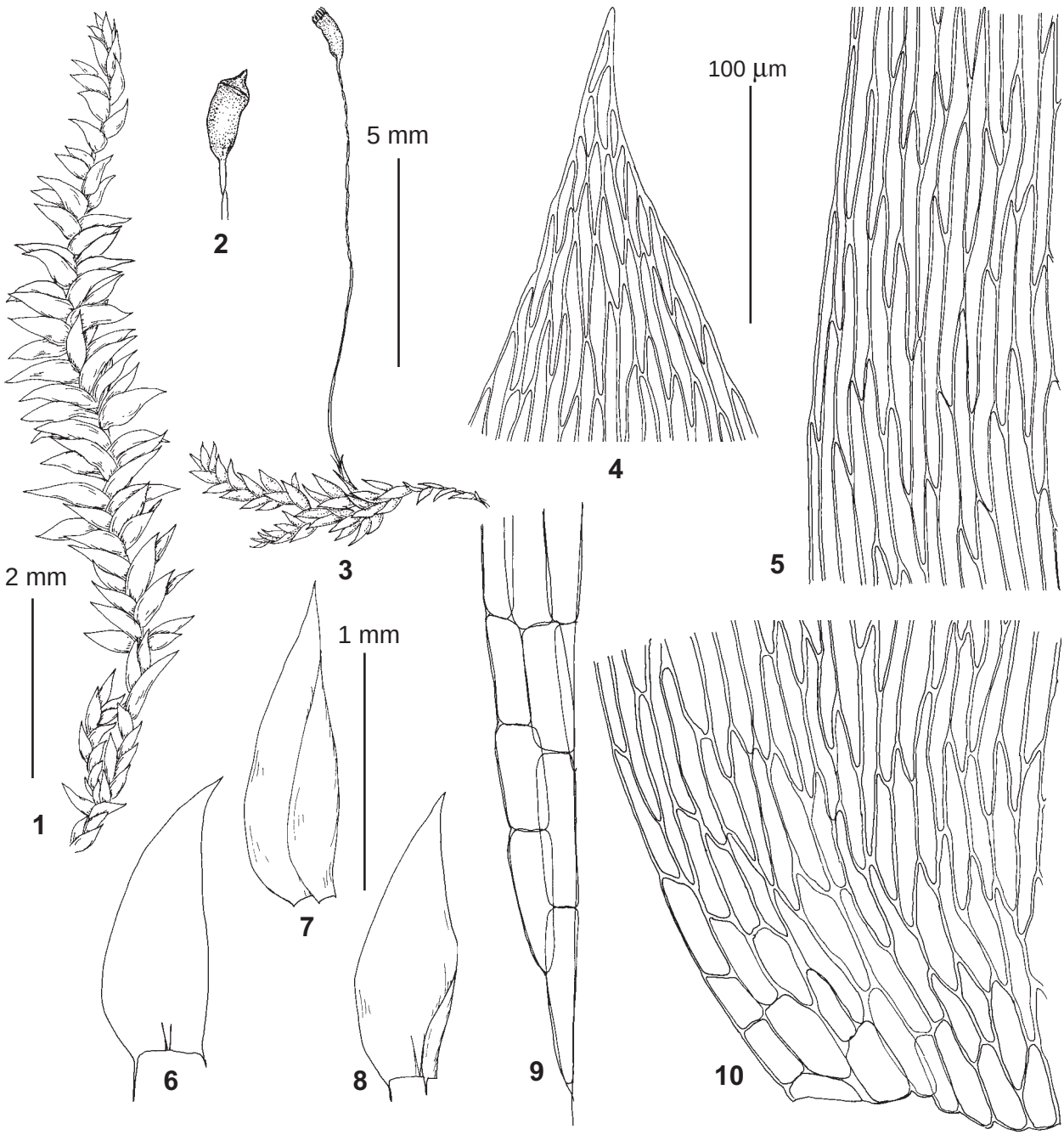

Fig. 5. *Plagiothecium rossicum* (from holotype): 1, 3 – habit, dry; 2 – capsule; 4 – upper leaf cells; 5 – mid-leaf cells; 6–8 – leaves; 9 – cells of leaf decurrency; 10 – basal leaf cells. Scale bars: 5 mm for 2; 2 mm for 12; 1 mm for 6–8; 100 µm for 4–5, 9–10.

more or less inclined, 1–1.2 mm long; annulus differentiated; operculum conic-apiculate; peristome pale yellowish; teeth 370–400 µm long, cross-striolate below, hyaline and papillose in upper half; endostome 400 µm long, basal membrane 120–130 µm high, segments narrow, narrowly perforated along keel or entire, cilia 1, slightly shorter than segments, nodose. Spores 11–13(–17) µm.

Distribution and ecology. The species in common in boreal and hemiboreal forests of European Russia, growing at trunk bases, fresh logs, stumps, sometimes of sandy soil on vertical banks along roads, near rock outcrops, and on siliceous rocks. In forest regions of European Russia it is much more common than *P. curvifolium*. The westernmost localities we were able to find are from Poland. The second area where *P. rossicum* was found is the Russian Far East, including Sakhalin and Kurils, SE of Khabarovsk Territory, Primorsky Territory, and Kamchatka Peninsula. Although such a pattern looks strange, the occurrence in islands after disjunction from much more western regions is characteristic for some other forest species like *Leucodon sciuroides, Anomodon longifolius*, *etc*. We failed so far to find any locality of this species in South Siberia. The habitats in Far East are about the same as in European Russia.

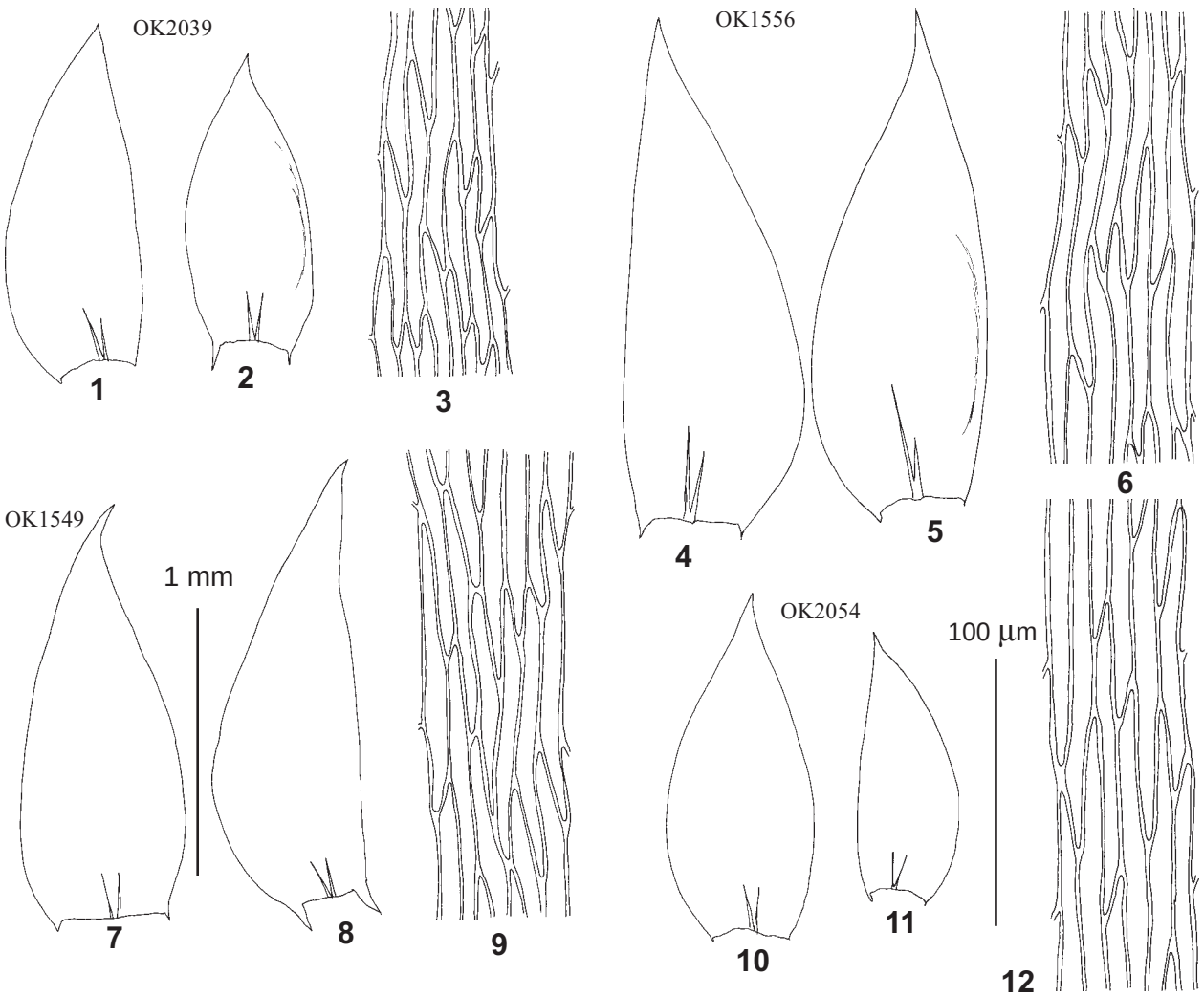

Fig. 6. *Plagiothecium rossicum* (from: 1–3: Russia, Pskov Province, *Zolotov P88*, MHA9041613; 4–6: Russia, Vladimir Province, *Kokoshnikova 19-9-2007*, MW 9055352; 7–9: Russia, Sakhalin, *Ignatov & Teleganova 06-723*, MW9055480; 10–12: Russia, Kunashir, *Ignatov 06-1090*, MW9055478): 1–2, 4–5, 7–8, 10–11 – leaves; 3, 6. 9, 12 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10–11; 100 µm for 3, 6. 9, 12.

Differentiation. *Plagiothecium rossicum* is more likely to be confused with *P. laetum* (see the diagnosis); however, flat vs. narrowly recurved leaf margins and often strongly asymmetrical vs. moderately asymmetrical leaves are helpful for separating them. Straight vs. curved to the substrate leaves provide the distinction between *P. rossicum* and *P. curvifolium.* In slides, under cover glass leaves of *P. rossicum* have only small lateral plicae, often only on one side, due to slight concavity, whereas leaves of *P. curvifolium* are often more deeply and irregularly plicate and folded. An additional diagnostic character is flat vs. narrowly recurved leaf margin. It is unlikely to confuse *P. rossicum* with *P. svalbardense* due to numerous differences between them: flat, appressed vs. loose mats; scarcely vs. subpinnately or irregularly branched stems; flat vs. recurved almost throughout leaf margins; leaves gradually tapered to the apex or shortly acuminate vs. suddenly narrowed into a longer apiculus; always narrow, 5–7 µm wide, laminal cells vs. cells rather variable in width, 5–10 µm wide. These species have rather different distributions (Fig. 4), though they occasionally grow in the same habitats in the Urals, northern European Russia and Russian Far East.

Selected specimens examined: EUROPEAN RUSSIA: **Republic of Karelia**: Loukhi District, biostation Kartesh, 21.VII.2017 *Zakharchenko s.n.* (MW9110798); **Arkhangelsk Province**: Nature Reserve "Pinezhsky" 2.VIII.1988, *Ignatov s.n.* (MHA9041582); **Komi Republic**: Sosnogorsk Distr., Nizhny Odes, 27.VI.2007, *Kucherov & Kutenkov 50* (MHA9041602); **Kaliningrad Prov.**: 3.IV.2005, *Rozhina s.n.*, (MHA); **Novgorod Province**: Valdai Distr., Valdaiskoe forestry, VIII.1979, *Morozova s.n.* (MHA9041617); **Vologda Province**: Permas, 11.VIII.2001, *Ignatov & Ignatova s.n.* (MHA9040772); Verkhny Dvor, 16.VIII.2001, *Ignatov & Ignatova s.n.* (MHA9041596); **Perm Territory**: Gainsky Distr., Shumino, 5.VIII.2012, *Bezgodov 285* (MHA9023476); **Sverdlovsk Province**: Nature Reserve "Denezhkin Kamen", 10.VIII.2014 *Smirnova DKS-14-74* (MW9055391); Kirovograd Distr., Nature Reserve "Visimsky", 15.VII.2005, *Smirnova 129* (MHA9041630); **Smolensk Province**: Sapsho Lake, 16.VII.2004, *Ignatov s.n.*

(MHA9041634); **Kaluga Province**: National Park "Ugra", *Teleganova 06-184* (MHA9041636); **Tver Province**: Zentralno-Lesnoy Nature Reserve, 1974, *L.I. Abramova s.n.* (MW9055331); Oleninsky Distr., Kozino, 6.VII.2000, *Notov s.n.* (MW9055349); **Moscow Province**: Zvenigirod Biostation of MSU, 17.VI.2004, *Ignatova s.n.* (MW9055372); **Ivanovo Province**: Ples, 23.XI.2008, *Sorokin 247* (MHA9041609); **Kostroma Province**: Mezhevsky Distr., Rodinskoe Forestry, 4.VII.2003, *Tikhonova & Prokazina s.n.* (MW9055334); Manturovo Distr., Kostromskaya biostation, 13.VI.1998 *Popov 1-98* (MHA9041637); **Vladimir Province**: Vladimir, *Seregin M-199* (MW9055333); Murom Distr., Strigino, 27.VI.2006, *Kokoshnikova s.n.* (MW9055353); **Ryazan Province**: Oksky Nature Reserve, 29.IX.1999, *Ignatov s.n.* (MW9066336); **Nizhegorodskaya Province**: Nature Reserve "Kerzhensky", 15.X.1998, *Popov s.n.* (MHA9041624); **Republic of Mordovia**: Smol'ny, 26.VI.2008, *Kobozeva 86* (MW9055434); **Republic of Chuvashia**: Nature Reserve "Prisursky", V.1999, *Moshkovsky s.n.* (MHA9041639); **Republic of Tatarstan**: Nature Reserve "Volzhsko-Kamsky": Raifa, 14.VIII.2003, *Ignatov & Ignatova s.n.* (MW9066026); Saraly, *Ignatov & Ignatova 05-2220* (MHA9041642); **Republic of Bashkortostan**: Beloretsk Distr., Maly Iremel' Peak, *Ignatova 2/142* (MHA9041657); Salavat Distr., Lagerevo Village, 3.VIII.1988, *Solomeshch s.n.* (MHA9041666); **Orel Province**: Naryshkinsky forest, 22.IV.1990, *Popova s.n.* (MHA9055925).

POLAND: Bryotheca Polonica 1096, Lisowski 3.IV.1959 (LE); Musci Macr. Med. poloniae Exs. 89, Zarnoviec 30.VIII.1981 (LE).

ASIAN RUSSIA: **Khabarovsk Territory**: Sovgavan Distr., Botchinsky State Reserve, *Ignatov & Ignatova 11-1053* (MW9055028); **Primorsky Territory**: Chuguevka Distr., ridge S of Pravaya Sokolovka Creek, *Ignatov 07-394* (MHA9041677); Partizansk Distr., Olkhovaya Mt., *Ignatov, Ignatova & Cherdantseva 06-2868* (MHA9041679); **Sakhalinskaya Province**: Sakhalin, Okha Distr., *Pisarenko op03393* (MHA 9041461); Korsakov Distr., Mereya River, *Ignatov & Teleganova 06-723* (MW9055480); Kunashir Island, Golovin Volcano, *Ignatov 06-1090* (MHA9055478).

Plagiothecium curvifolium Schlieph. ex Limpr., Laubm. Deutschl. 3: 269. 1897. — *Plagiothecium denticulatum* var. *curvifolium* (Schlieph. ex Limpr.) Meylan, Bull. Soc. Vaud. Sci. Nat. ser. 5, 41: 151. 1905. Fig. 7.

Description. Plants medium-sized, in more or less dense, somewhat rigid lustrous mats. Stems creeping, 1–3 cm long, foliage complanate to more commonly subcomplanate due to homomallous leaves. Leaves forming 30–50° angle with stem, curved towards substrate by their distal part, 1.3–2.0(–2.2) × 0.55–0.9 mm; ovate-oblong, more or less symmetric to slightly asymmetric, concave (in slides plicate and crumpled), tapered to acute apex or shortly acuminate, decurrent in 2–4 rows of rectangular to almost quadrate cells; leaf margins narrowly recurved on one or both sides, occasionally flat, entire or faintly denticulate at apex; costa short and double; laminal cells 80–150 × 6–10 μm. Gemmae rarely present, of 3–4 quadrate or short rectangular cells. Autoicous. Sporophytes usually present. Setae 15–20 mm long; capsules curved, inclined to horizontal, 1.5–2.0 mm long. Exostome teeth ca. 500 μm long; basal membrane of endostome ca. 200 μm high, segments slightly longer than exostome teeth, cilia 2, 300 μm long, distinctly nodose. Spores 9–12 μm.

Distribution and ecology. The species is rather common in European Russia, although more rare compared to *P. denticulatum* and *P. rossicum*. It occurs in boreal and hemiboreal forests of European Russia, partly in broadleaved forests, and in the Caucasus. No specimens were seen from the Asian Russia, except for eastern slope of subpolar Ural Mts. The species grows on trunk bases, fresh logs, stumps, sometimes of sandy soil on vertical banks along roads, occasionally on rocks. The habitat where this species is more common than other species of the genus are exserted roots of *Pinus sylvestris* in mesic to moderately dry forest types.

Differentiation. Specimens of *P. curvifolium* are usually easy to identify due to their characteristic foliage: leaves of this species are curved towards substrate, not flattened and therefore are usually variously plicate and folded in slides under cover glass (Fig. 7). This feature is combined with partially recurved leaf margins and leaf cells variable in width (6–10 μm). Capsules of *P. curvifolium* are the longest within the *P. laetum* complex and are usually markedly curved and inclined; the exostome teeth are also longer than in other species of the group, ca. 500 μm long. However, some sequenced specimens with less markedly curved leaves were resolved within the *P. curvifolium* clade. They could most likely be confused with *P. laetum*, which is most similar in leaf shape (moderately asymmetrical, with acute or very shortly attenuate apical portion, and partially recurved margins). In such cases, leaf cell width may be helpful (6–10 μm in *P. curvifolium* vs. 6–8 μm in *P. laetum*). If sporophytes are present, distinctly curved capsules up to 2 mm long are characteristic for *P. curvifolium* rather than for *P. laetum*, which often has shorter capsules, straight and erect or slightly curved and inclined. As for the other two species of the *P. laetum* complex, *P. rossicum* is distinguished from *P. curvifolium* by flat leaf margins and narrower, 6–7 μm wide, leaf cells, while *P. svalbardense* differs from it by its smaller size, usually stronger branched stems, and a distinctly attenuate leaf apex.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province**: Tersky Distr., Porja Guba, *Kozhin M-M-1785* (MW9077455); **Arkhangelsk Province**: Pinega Nature Reserve, 8.VIII.1988, *Ignatov s.n.* (MHA9041583); Bolshoi Solovetsky Island, 20.VII.1998, *Churakova 235* (MW9055387); **Komi Republic**: Sosnogorsk Distr., Nizhny Odes, 26.VI.2007, *Kucherov & Kutenkov 14* (MHA 9041603); Pechoro-Ilychsky Nature Reserve, *Smirnova 87* (MW9055022); **Perm Province**: Dobryansky Distr., Verkh-Kvazhva Setl., 3.VIII.2005, *Bezgodov & Shkaraba 36* (MW9055024); **Moscow Province**: Zvenigorod biostation of Moscow State University, 19.VI.2018, *Ignatov s.n.* (MW9110620); **Vladimir Province**: Aleksandrov, *Seregin M-382* (MW9055015); Torfoprodukt, 10.IX.2008, *Kokoshnikova s.n.* (MW9055016). CAUCASUS: **Republic of Karachaevo-Cherkessia**: Teberda Nature Reserve, Severny Klukhor Gorge, 8.IX.1994, *Onipchenko 174/94* (MW9055444). ASIAN RUSSIA: **Khanty-Mansiisk Autonomous District**: Berezov

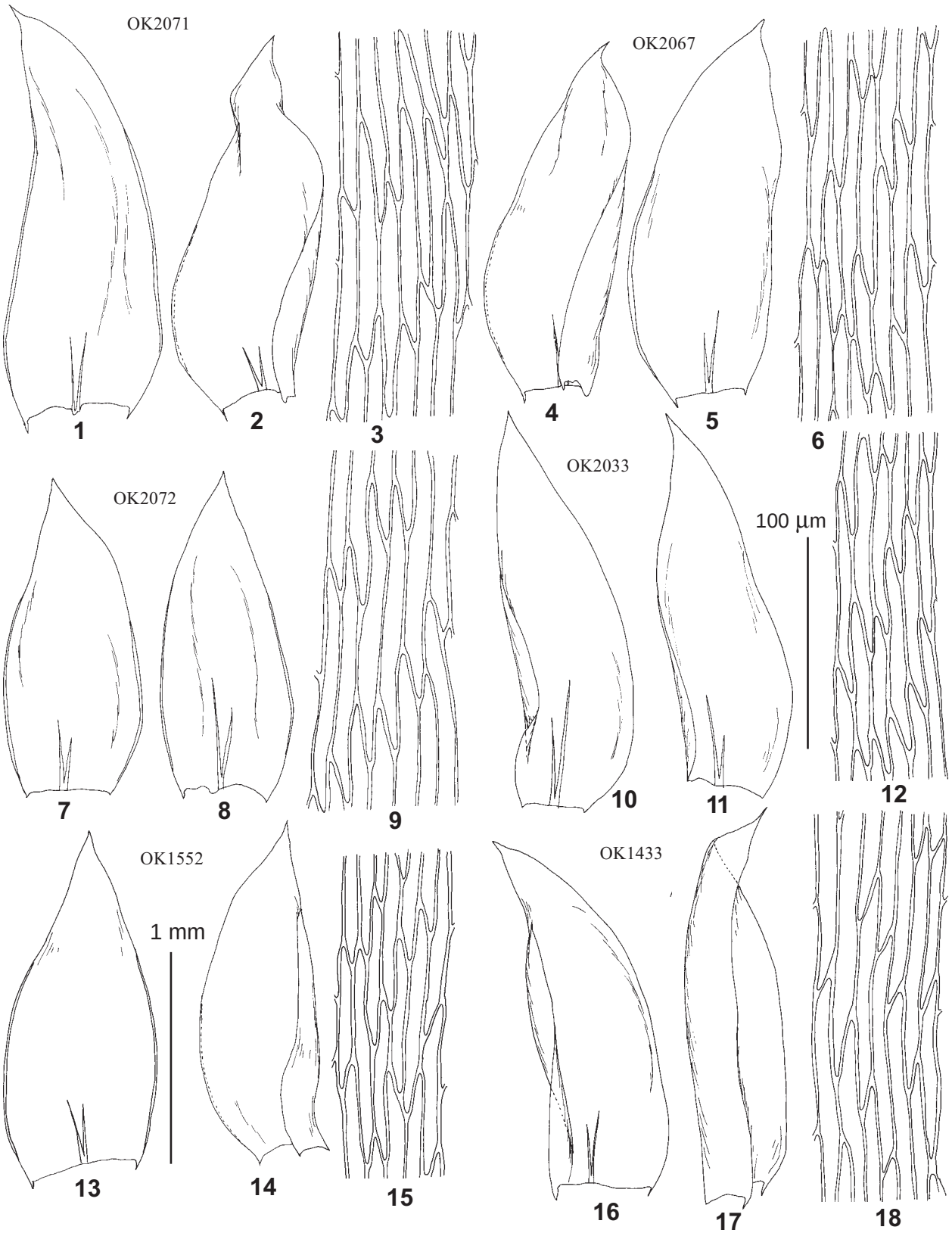

Fig. 7. *Plagiothecium curvifolium* (from: 1–3: Germany, Mosses of Saarlandes 2573, 6.IV.1991, *Caspari s.n.*, SAAR; 4–6: Germany, Mosses of Saarlandes 7591, 28.XII,2011, *Caspari s.n.*, SAAR; 7–9: Germany, Mosses of Saarlandes 7495, 26.X.2006, *Caspari s.n.*, SAAR; 10–12: Russia, Kaliningrad Province, 3.IV.2005, *Rozhina s.n.*, MHA9041610; 13–15: Russia, Caucasus, Karachaevo-Cherkessia, *Onipchenko 174/94*, MW9055444; 16–18: Russia, Komi Republic, *Kucherov & Kutenkov 175*, MHA9023477): 1–2, 4–5, 7–8, 10–11, 13–14, 16–17 – leaves; 3, 6. 9, 12, 15, 18 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10–11, 13–14, 16–17; 100 µm for 3, 6. 9, 12, 15, 18.

distr., subpolar Urals, Neroika Mt., 64°33'08.3"N, 50°42'50.4"E, 9.VIII.2013, *Lapshina 13-589* (MHA9023468).

UKRAINE: Volyn Province, Seltsy Gornitskie, 18.VII.1949, *Bradis s.n*. (MW9055303). **GERMANY**: Hessen, XI.1900 *Roth s.n.* (E. Nauer, MEE 670; MW9055009). **POLAND**: Silesia Inferior, Walbrzych, 23.VIII.1979 *Berdowski 1274* (MW9055012); Warmian-Masurian Voivodeship, Olsztyn, S*eregin & Kolodziej* M-3131 (MW9055011).

Plagiothecium laetum Bruch, Schimp. & W. Gümbel, Bryol. Eur. 5: 185. *495.* 1851. Fig. 8.

Description. Plants medium-sized, in rather dense, soft, lustrous mats. Stems creeping, 1–3 cm long, foliage complanate. Leaves forming 20–70° angle with stem, (1.1–)1.3–1.7 × 0.5–0.7 mm, ovate-oblong, more or less symmetric to slightly asymmetric, slightly concave, tapered to acute apex or shortly apiculate, decurrent in 2–4(–5) rows of rectangular cells; leaf margins entire, narrowly recurved almost throughout or at lower 3/4, in more asymmetric leaves occasionally recurved on one side; costa short and double; laminal cells 70–140 × 6–8 μm. Gemmae rarely present, of 3–4 short rectangular cells. Autoicous. Sporophytes usually present. Setae 10–15 mm long; capsules erect, straight or inclined, 1.0–1.5 mm long. Exostome teeth 400 μm long; endostome basal membrane 130 μm high, segments slightly shorter than exostome teeth, cilia 1–2, short, nodose. Spores 11–13 μm.

Distribution and ecology. Contrary to previous publications, plants identical with Central European plants are very rare in Russia. *Plagiothecium laetum* s. str. was collected twice in the Caucasus, at low and middle elevations. One old specimen from Kaluga Province was also seen in the herbarium; it was collected on sandstone outcrops in a place where some rare species of mosses and vascular plants are found. Data on species ecology is scarce. According to the label information, it grows on tree bases and stumps in pine and broadleaved forests.

Differentiation. *Plagiothecium laetum* differs from *P. rossicum* in always narrowly recurved leaf margins, at least partially. Flattened foliage is helpful for separating it from *P. curvifolium* (see also discussion under that species). From *P. svalbardense* it differs in larger size of plants; slightly larger leaves (1.3–1.7 × 0.5–0.7 mm in *P. laetum* vs. 1.2–1.6 × 0.35–0.6 mm in *P. svalbardense*); leaves acute or shortly apiculate vs. distinctly attenuate in the apical portion; less variable width of laminal cells (6–8 μm vs. 5–10 μm); and less branched stems on creeping shoots forming flat mats vs. stronger branched stems and loose mats. In addition, these two species have different distributions, never growing in same localities (see comments under both of them). In Eurasia, *P. laetum* grows in Europe, with a few localities in the Caucasus, while *P. svalbardense* is mainly a North Asian taxon, distributed in Europe only in its northern regions.

Selected specimens examined: EUROPEAN RUSSIA: **Kaluga Province**: Chertovo Gorodishche, 3.IX.1924, *Zhadovsky s.n.* (MW9055355). CAUCASUS: **Republic of Ingushetia**: Dzheirakh Distr., Nature Reserve "Erzi", 42°49'57.2"N, 44°55'06.8"E, 22.IV.2018, *Bersanova 18-159* (MW9090994); **Krasnodar Territory**: Nature Reserve "Kavkazsky", Babuk, Shakhe Creek valley, 43°50'N, 39°50'E, 23.VIII.1990, *Ignatov s.n.* (MHA9041733).

AUSTRIA: VII.1914, [coll. unclear] (LE). **BOSNIA AND HERZEGOVINA**: 10.VI.1979, *Rusinska s.n.* (LE). **CZECH REPUBLIC**: Karlovy Vary, 12.IV.1957, *Tyuremnov s.n.* (MW9055294, MW9055295). **FINLAND**: 20.VII.1930, *Railonsalo s.n.* (LE). **GERMANY**: Lorenzer Wald bei Nürnberg, 24.VI.1921, *H. Paul s.n.* (MW9055300). **HUNGARY**: 14.VII.1955, *Boros s.n.* (LE). **NORWAY**: 25.VI.1972, *Frisvoll s.n.* (LE). **POLAND**: 20.VII.1972, *Flora Silesia exs. 1171*, *Bedrowski s.n.* (LE). **SWEDEN**: 29.VIII.1909, *Möller s.n.* (LE); 9.VII.1904, *Arnell s.n.* (LE).

Plagiothecium svalbardense Frisvoll, Norsk Polarinst. Skr. 198: 103. 1996. Figs. 9–10.

Description. Plants small, lustrous, in somewhat loose mats formed by variously directed stems. Stems 0.6–2 cm long, subpinnately or irregularly branched, foliage indistinctly complanate. Leaves forming a 30–70° angle with stem, symmetric to strongly asymmetric, concave, (0.7–)1.2–1.6 × 0.35–0.6 mm, ovate, gradually tapered to the apex, with attenuate apiculus, sometimes almost piliferous; cells of decurrencies in 2–3 rows, rectangular; leaf margins entire or minutely denticulate shortly below the apex, narrowly recurved almost throughout; costa short and double, occasionally extending beyond midleaf; laminal cells 70–130 × 5–10 μm. Gemmae of 3–4 short rectangular cells, occasionally present. Autoicous. Sporophytes occasionally present. Setae 5–10 mm long; capsules straight and erect or slightly curved and more or less inclined, 1–1.2 mm long. Exostome teeth 400–450 μm long; basal membrane of endostome ca. 130 μm high, segments slightly shorter than exostome teeth, cilia 2, 150 μm long, nodose. Spores 10–12 μm.

Distribution and ecology. *Plagiothecium svalbardense* occurs throughout the territory of Asian Russia: in permafrost zone of Yakutia and Taimyr, Amur Province, Khabarovsk and Primorsky Territories, Sakhalin, Kamchatka, mountain areas of southern Siberia, and West Siberia; in European Russia, it grows in the Urals and northern areas of lowland part (Arkhangelsk and Murmansk Provinces, Karelia). *Plagiothecium svalbardense* grows on various substrates, including cliffs, rock outcrops, rocks, tree bases, stumps, and rotten wood.

Differentiation. According to the original description, *P. svalbardense* is characterized by subjulaceus foliation, ovate and distinctly apiculate leaves, and leaf cells 7–10 × 80–110 μm. Frisvoll in Frisvoll & Elvebakk (1996) emphasized that leaves of *P. svalbardense* are ovate and fairly suddenly narrowed into apiculus, while in *P. laetum* the leaves are more evenly narrowed into the short apex. He also stated that the majority of leaves in *P. svalbardense* are quite or almost symmetrical, while in *P. laetum* they are distinctly asymmetrical. In addition, he mentioned often subjulaceus and rarely complanate shoots

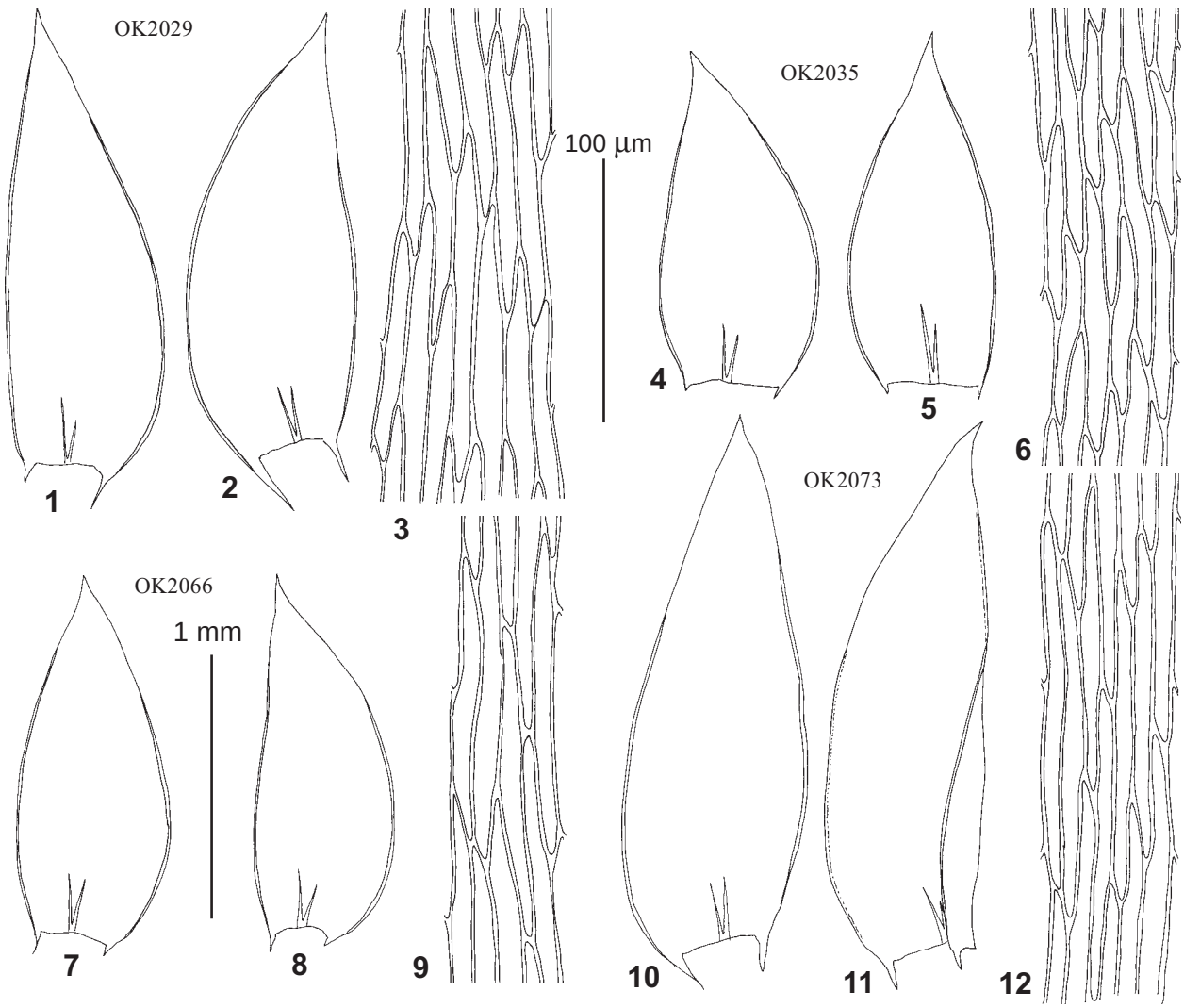

Fig. 8. *Plagiothecium laetum* (from: 1–3: Czech Republic, Karlovy Vary, 28.VII.2011, *Donskov s.n.,* MHA9055918; 4–6: Russia, Krasnodar Territory, 23.VIII.1999, *Ignatov s.n.*, MHA 9041733; 7–9: Germany, Mosses of Saarlandes 3103, 1.IX.1996, *Caspari s.n.*, SAAR; 10–12: Germany, Mosses of Saarlandes 5382, 24.XII.1995, *Caspari s.n.*, SAAR): 1–2, 4–5, 7–8, 10–11 – leaves; 3, 6. 9, 12 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10–11; 100 µm for 3, 6. 9, 12.

of *P. svalbardense*, which is contrasting with really complanate shoots of *P. laetum*. All these observations were made solely on Svalbard material, wherefrom *P. svalbardense* was known that time. Later Wynns *et al.* (2018) cited a specimen of Holmen and Mogensen from Greenland which they referred to *P. svalbardense*. Since a large number of specimens from Russia, mainly from its Asian part, grouped in the molecular phylogenetic analysis based on sequences of nuclear and plastid DNA with this specimen from Greenland, it made us confident that *P. svalbardense* has a much wider distribution than it was thought before. Our specimens agree with *P. svalbardense* in most habitual and morphological characters mentioned by Frisvoll (1996) and detailed description and illustration of "*P. laetum*, Svalbard plant" given by Frisvoll (1981), except for always quite or almost symmetrical leaves: in many of our specimens, both symmetrical ("dorsal") and strongly asymmetrical ("lateral") leaves can be found (see Figs. 9–10). Actually, the descriptions of leaf symmetry by Frisvoll (1981) and by Frisvoll & Elvebakk (1996) are in some disagreement: in the former work leaves are described as both symmetrical and asymmetrical, sometimes strongly so, while in the latter publication it is stressed that leaves are more often symmetrical. Frisvoll (1981) writes that leaves of Svalbard plants are more or less gradually tapered, while later he emphasized a suddenly narrowed leaf acumen (Frisvoll & Elvebakk, 1996). In our material from the wider distributional range, leaf shape (ovate leaves with suddenly narrowed acumen, sometimes resembling *Rectithecium piliferum*) is a very stable character of this species, as well as hardly flattened shoots. Leaf margins are always narrowly recurved in *P. svalbardense*, often up to the base of attenuate apiculus (described as "narrowly recurved from base to apex" by Frisvoll, 1981). Width of laminal cells appeared to be even more variable in our material, 5–10 µm, as well as cell length, 70–130 µm. Sporophytes were not described by Frisvoll, apparently being absent in Sval-

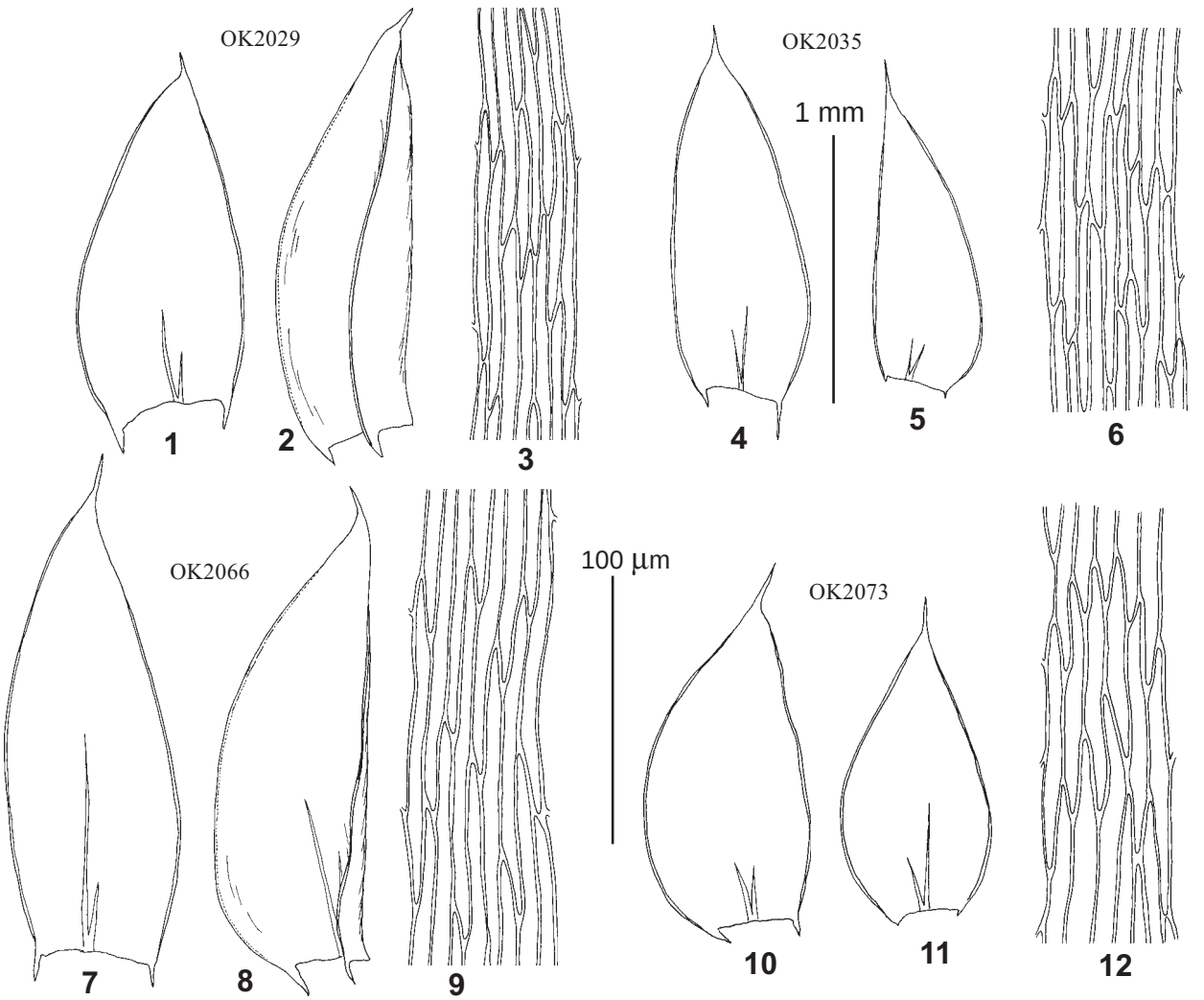

Fig. 9. *Plagiothecium svalbardense* (from: 1–3: Russia, Khabarovsk Territory, Sovgavan Distr., *Ignatov & Ignatova 13-247*, MW9055475; 3; 4–6: Russia, Khabarovsk Territory, Sovgavan Distr., *Ignatov & Ignatova 13-780*, MHA9041672; 7–9: Russia, Primorsky Territory, Olkhovaya Mt., *Ignatov et al. 06-2706*, MW9055481; 10–12: Russia, Murmansk Province, Tersky Distr., *Ignatov & Ignatova 12-140*, MHA9041614). 1–2, 4–5, 7–8, 10–11 – leaves; 3, 6. 9, 12 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10–11; 100 µm for 3, 6. 9, 12.

bard material. Thus, they are described above for the first time.

There is some resemblance in morphological traits between *P. svalbardense* and *P. berggrenianum* (ovate leaves with margins recurved from base to near the apex and suddenly narrowed apical part); however, the leaves of *P. berggrenianum* are much wider (0.8–0.9 mm vs. 0.35–0.6 mm), always symmetrical, leaf margins are more widely recurved, and the attenuate apical part is strongly curved and hook-shaped.

There is no problem to separate *P. svalbardense* from *P. rossicum* due to always narrowly recurved leaf margins in the former species and flat margins in the latter one; in addition, shoots of *P. rossicum* are hardly branched and distinctly flattened, while *P. svalbardense* has much more branched, scarcely flattened shoots. Regarding *P. curvifolium*, Frisvoll (1981) mentions the similarity of "Svalbard *P. laetum*" (=*P. svalbardense*) with the former species in cell width, color of plants and structure of leaf decurrencies; at the same time, he states that *P. curvifolium* is a larger plant, it has different shape and orientation of leaves, and its distribution in Scandinavia is strictly confined to the range of conifer forest. These statements agree well with our observations of Russian material.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province**: Umba, *Ignatov & Ignatova 12-140* (MW9055491); Porja Guba, *Kozhin M-M-0519* (MW9055309); Alakurtti 30.VII.1971, *Konstantinova s.n.* (MW9055318); **Republic of Karelia**: Loukhi Distr., biostation "Kartesh", 19.VII.2017, *Zakharchenko s.n.* (MW9110792); Kostomukshsky Nature Reserve, 9.VII.1992, *V.N. Korotkov s.n.* (MW9055311); **Arkhangelsk Province**: Pinega Nature Reserve, 5.VIII.2006, *Stepanov II-2* (MW9055023); same place, 30.VII.1988, *Ignatov s.n.* (MHA9041588); **Komi Republic**: Pechoro-Ilychsky Nature Reserve, *Seregin & Zakharov M-3425* (MW9055632); Sosnogorsk Distr., Nizhny Odes, 5.VII.2007, *Kucherov &*

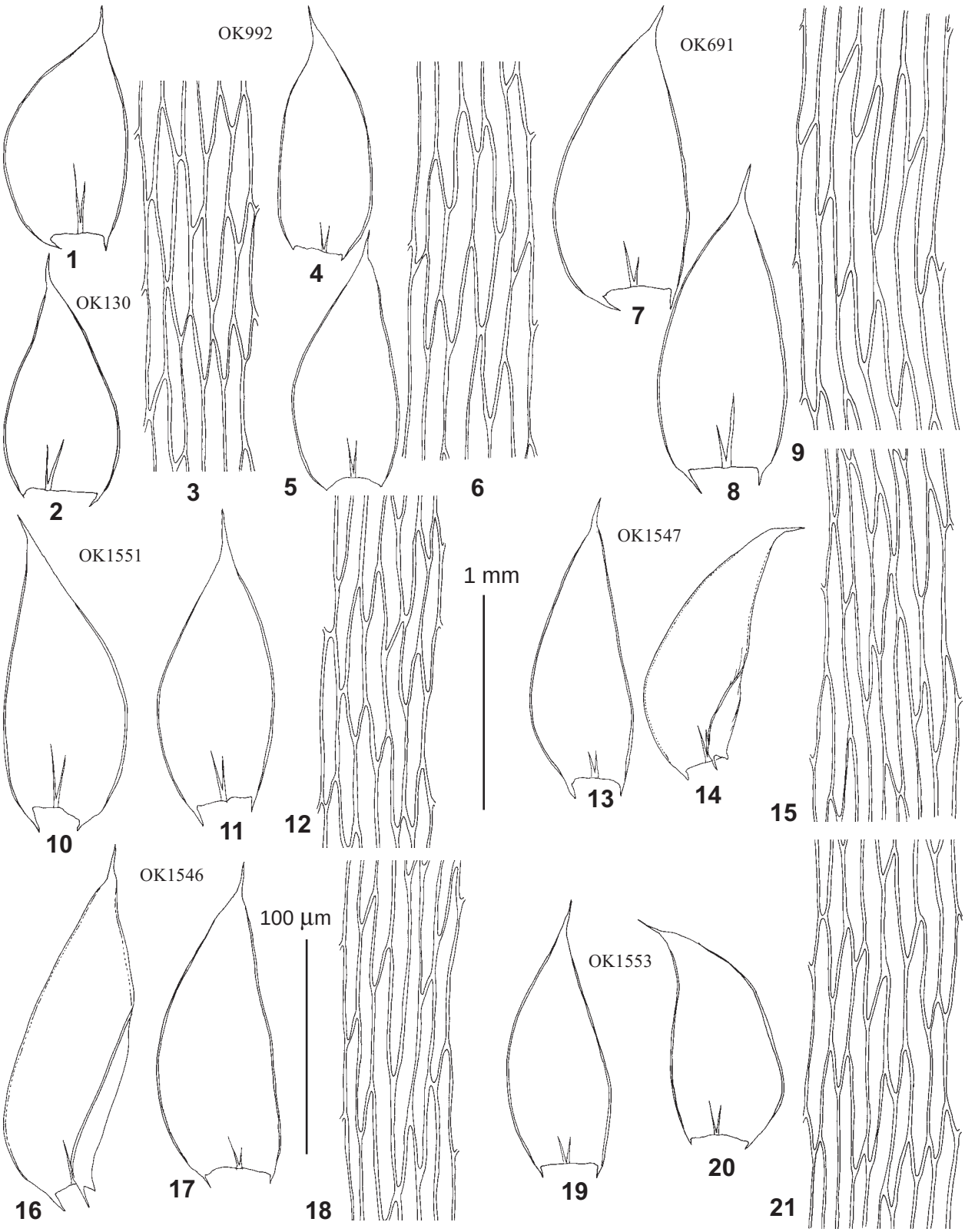

Fig. 10. *Plagiothecium svalbardense* (from: 1–3: Russia, Yakutia, Mus-Khaya Mt., *Ignatov & Ignatova 11-3467*, MHA9041919; 4–6: Russia, Yakutia, Mus-Khaya Mt., *Ignatov & Ignatova 11-3022*, MHA9041464, SAAR; 7–9: Russia, Yakutia, Ust-Maya Distr., *Ignatov 00-878*, MHA9041471; 10–12: Russia, Yakutia, Lena Pillars, *Ignatov & Ignatova 16-330*, MW9077452; 13–15: Russia, Taimyr, Anabar Plateau, *Fedosov 07-286*, MW9055460; 16–18: Russia, Altai Republic, Kyga River, 25-8-2000, *Zolotukhin s.n.*, MW9055448; 19–21: Russia, Zabaikalsky Territory, Kalarsky Distr., 25.VII.1989, *Filin s.n.*, MW9055464). 1–2, 4–5, 7–8, 10–11, 13–14, 16–17, 19–20 – leaves; 3, 6. 9, 12, 15, 18, 21 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10–11, 13–14, 16–17, 19–20; 100 µm for 3, 6. 9, 12, 15, 18, 21.

Kutenkov 168 (MHA9041472); **Perm Province**: Basegi Nature Reserve, *Ignatov & Bezgodov 743* (MW9055417); Vishersky Nature Reserve, 5.VII.1994, *Bezgodov 379* (MW9055427); **Republic of Bashkortostan**: Beloretzky Distr., projected Nature Park "Inzer", 8.VII.2005, *Shirokikh 222A* (MW9055447); Zuyakovo Settl., 1.VIII.1990, *Muldashev 89* (MW9055446); Bolshoy Iremel' Peak, *Ignatova 6/11* (MHA9041659). ASIAN RUSSIA: **Tymen Province**: Uvatsky Distr., Bartak River, 3.V.2013, *Bezgodov 123* (MW9055451); **Altai Republic**: Kaitanak, *Ignatov & Ignatova 12-628* (MW9055449); Ayulyuyuzyuk, *Ignatov 0/384* (MHA9041722); Yailyu, *Ignatov 0/622* (MHA9041717); **Krasnoyarsk Territory**: Taimyr Distr.: Kotuy River, *Fedosov 13-3-1087* (MW9055633); Ereechka River, *Fedosov 13-3-0869* (MW9055454); Baikit Distr., Stolbovaya River, 1992, *Shcherbina s.n.* (MW9055461); **Zabaikalsky Territory** [Chita Province]: Naminga, 26.VII.1989, *Filin s.n.* (MW9055465); **Republic of Buryatia**: Bol'shoy Mamai Creek, *Ignatov et al. 18-4057* (MW9090527); **Republic of Sakha/Yakutia**: Tomponsky Distr., Dyby River, *Ignatov & Sofronova 17-366* (MW9090011); Sette-Daban, between Ulakh and Nadezhda Creeks, *Ignatov & Ignatova 16-1045* (MW9078473); Kyurbelyakh Creek, 63°08'N, 139°04'E, 8.VII.2011, *Ignatov & Ignatova 11-2164* (MW9055468); Ulakhan-Chistai Mt. Range, *Ignatov & Ignatova 18-2123* (MHA9028887); Orulgan Mt. Range, Tumara, *Ignatov 11-4468* (MW9055466); Oimyakon Distr., Mus-Khaya Mt., *Ignatov & Ignatova 11-3022* (MW9055467); Ust-Maya Distr., Allakh-Yun, *Ignatov 00-878* (MHA9041471); Nature Park "Lena Pillars", *Ignatov & Ignatova 16-330* (MW9077452); **Amurskaya Province**: Zeya Nature Reserve, *Dudov & Kotelnikova 2014_Br_9139* (MW9079826); Norsky Nature Reserve, 6.VII.2010, *Bezgodov 228* (MHA9041681); **Khabarovsk Territory**: Bureinsky Nature Reserve, 8.VIII.1992 *Borisov s.n.* (MW9055482); Botchi State Reserve, *Ignatov & Ignatova 13-60* (MW9055474); **Primorsky Territory**: Shkotovo Distr., Pidan Mt., *Ignatov & Ignatova 06-2111* (MW9055479); Chuguevka Distr., Berezovy Creek, *Ignatov 07-232* (MW9055477); Terney Distr., Isakov Creek, *Ignatov & al 13-1820* (MW9055029); **Kamchatsky Territory**: Kamchatka Peninsula, Elovka River, 29.VIII.2003, *Czernyadjeva 115* (MHA9041706); **Sakhalinskaya Province**: Sakhalin Island, Nogliki Distr., Gortachie Klyuchi station, *Pisarenko op03391* (MHA9041462).

Localities confirmed by J.Wynns (pers. corr. May 2019): ***GREENLAND**: *K. Holmen & G. Mogensen 71-1916*, sub *P. laetum*; Kangerdluatslaq, Arveprinsens Ejland [W5], 69°52'N, 50°47'W, 12 Aug 1971, C; *K. Holmen & G. Mogensen 71-2531*, Ivnaq, Arveprinsens Ejland, 69°48'N, 51°14'W, 14 Aug 1971, sub *P. piliferum*, C; *K. Holmen & G. Mogensen 71-2532*, idem, sub *P. laetum*, C; *K. Holmen & G. Mogensen 71-2538*, idem, C; *K. Holmen & G. Mogensen 71-2552*, idem, sub *P. denticulatum*, C; *J. Lewinsky 73-948*, Kilaersarfik, Ameragdla, GodthÍb distr. [W3], 64°15'N, 50°12'W, 1 Aug 1973, sub *P. laetum*, C. **NORWAY**: *Musci Spetsbergenses Exsic. 122* p.p., Parrys I, Spitsbergen [Svalbard], 1868, UC no. 1752324. **SWEDEN**: *T. Westergren 204*, Kvikkjokk, Lapponia Lulensis, original specimen of *P. westergrenii*, HBG.

Plagiothecium berggrenianum Frisvoll, Lindbergia 7(2): 96–98, f. 2. 1981[1982]. Fig. 11.

Description. Plants medium-sized to large, in loose lustrous mats, often growing by individual shoots in tufts of other mosses or hanging down a cliff surface. Stems 1–3 cm long, poorly branched, foliage julaceous. Leaves appressed, directed upwards, symmetric, strongly concave (in slides plicate and crumpled), 1.4–1.6 × 0.8–0.9 mm, broadly ovate, cucullate at apex, abruptly narrowed to a hooked, reflexed apiculus, longly decurrent, cells of decurrencies in 2–4 rows, rectangular, sometimes round close to leaf base; leaf margins entire or minutely serrulate shortly below apex, more or less widely recurved almost throughout; costa short and double, occasionally extending beyond midleaf; laminal cells 75–130 × 7–9 μm, thick-walled. Gemmae of 3–4 short rectangular cells, occasionally present. Autoicous. Setae 2–2.2 mm long; capsules straight and erect or slightly curved and more or less inclined, 1–1.2 mm long. Exostome teeth ca. 450 μm long; cross-striolate below, slightly papillose in upper half; endostome basal membrane ca. 180 μm long, segments slightly longer than exostome teeth; cilia 2, up to as long as segments, nodose to appendiculate. Spores 15–21 μm.

Distribution and ecology. This northern species is not rare in permafrost areas of Asian Russia (Taimyr Peninsula and adjacent areas, Yakutia, Chukotka, Magadan Province); it extends southward up to ca. 61°N (Ust-Maya District of Yakutia). It is also known from islands of the Arctic Ocean, Svalbard and Franz Josef Land. In North America it is confined to the northernmost areas, including Greenland, Alaska and NW Territories. Grows on wet cliffs and rocks along water courses, in shady niches under boulders, on moist turf and humus in shady places, in tundra and *Sphagnum* bogs, occasionally on rotten wood. Forms pure mats or grows as solitary shoots in tufts of other mosses.

Differentiation. *Plagiothecium berggrenianum* is a conspicuous plant due to a combination of such morphological characters as large size of plants and appressed, symmetrical, ovate, strongly concave leaves with distinctly recurved margins and hook-shaped apiculus. It makes unlikely its confusing with any species of the *P. laetum* complex (see, however, discussion under *P. svalbardense*). Sporophytes and gametangia of *P. berggrenianum* were unknown from Svalbard and not described in the protologue. Later sporophytes of this species were found in the Russian Arctic (West Siberia, Yamal) and described by Ukrainskaya (1996), who mentioned a dioicous sexual condition, erect or slightly inclined capsules, absence of cilia and large size of spores (15–17 μm). Sporophytes of *P. berggrenianum* were also illustrated by Ignatov *et al.* (2001), who found this species in Ust-Maya District of Yakutia (one of southernmost localities). Cilia were drawn as short, and sexual condition was described as autoicous (at least some shoots with both antheridia and archegonia were observed). Since that time more collections of *P. berggrenianum* were made in Asian Russia. According to our observations, an autoicous sexual condition is confirmed; cilia of endostome may be almost as

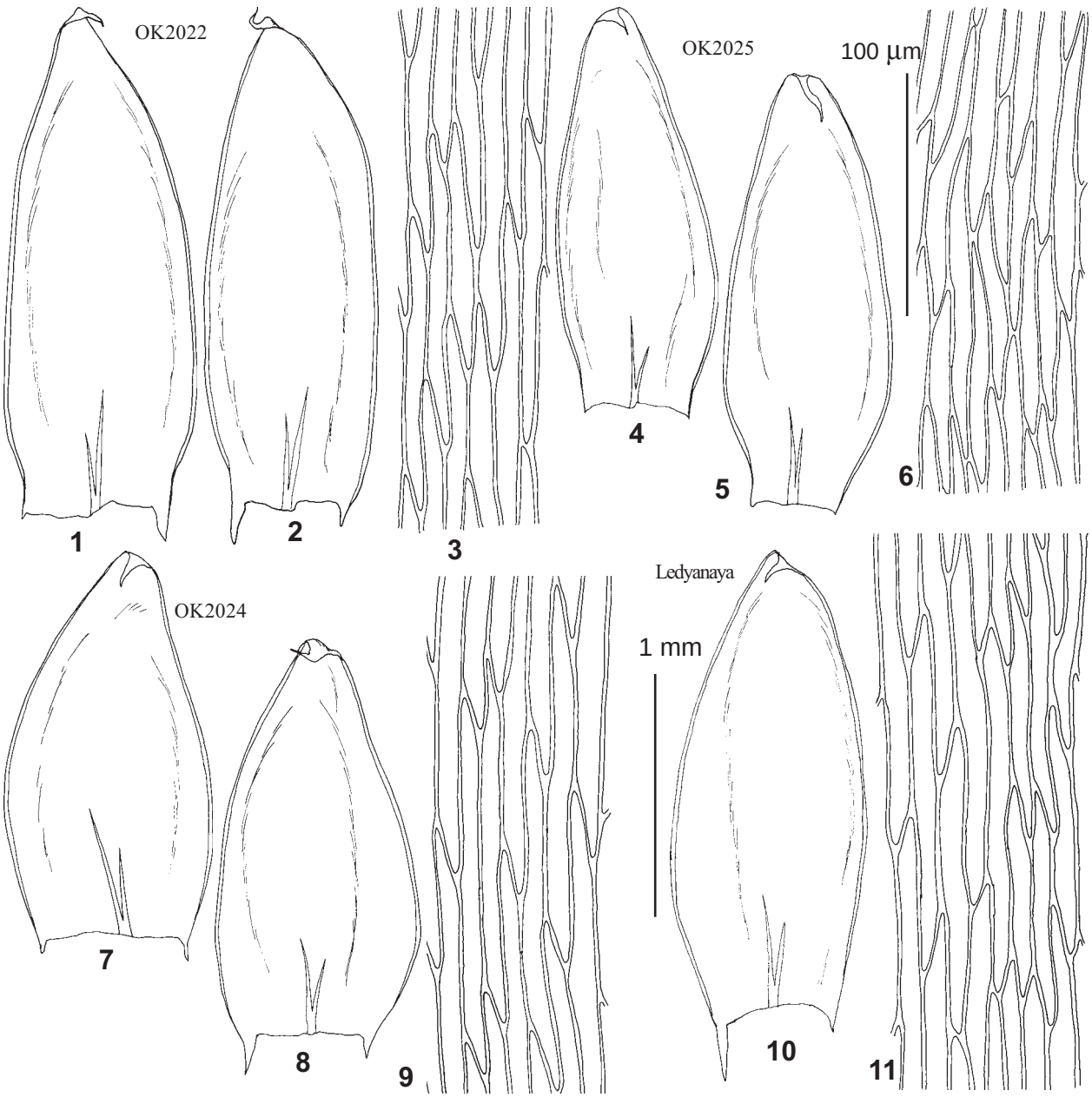

Fig. 11. *Plagiothecium berggrenianum* (from: 1–3: Russia, Ust-Nera, *Ignatov & Ignatova, 15-1222*, MW9054799; 4–6: Russia, Taimyr, Anabar Plateau, *Fedosov 11-1222,* MW9054782; 7–9: Russia, Yakutia, Mus-Khaya Mt., *Ignatov & Ivanov 11-3584,* MW9054804; 10–11: Russia, Taimyr, Ledyanaya Bay of Taimyrskoe Lake, *Fedosov Plt17*, MW9054797). 1–2, 4–5, 7–8, 10 – leaves; 3, 6. 9, 11 – midleaf cells. Scale bars: 1 mm for 1–2, 4–5, 7–8, 10; 100 µm for 3, 6. 9, 11.

long as segments, nodose to almost appendiculate; and spores are sometimes even larger, 15–21 µm.

Selected specimens examined: ASIAN RUSSIA: **Yamalo-Nenetsky Autonomous Distr.**: Yamburg 25.VII.2014, *Bezgodov 239* (PPU6896); Yunto Lake, 2.VIII.1993, *Czernyadjeva 13* (LE); Gydan Peninsula, 11.VII.1991, *Czernyadjeva 24* (LE); Ngaranato Lake, 19.VIII.1992, *Czernyadjeva 21* (LE); middle course of Sebayakha River, 22.VII.1992, *Czernyadjeva s.n.* (LE); middle course of Khabeyakha River, 31.VII.1981, *Rebristaya 38* (LE); **Krasnoyarsk Territory**: Byrranga Mts., *Fedosov Plt7* (MW); Medusa Bay, 6.VII.2002, *Varlygina s.n.* (MW9054793); Ledyanaya Bay of Taimyrskoe Lake, *Fedosov P87* (MW9054797); Kotuikan River, *Fedosov 11-607* (MW9054787); Afanas'evskie Lakes, *Fedosov 06-589* (MW9054790); Ary-Mas biostation, *Fedosov 07A-1-17* (MW9054789); same place, 30.VII.1972, *Norin s.n.* (LE); Ereechka River, *Fedosov 13-3-0469* (MW9054785); **Republic of Sakha/Yakutia**: Orulgan Mt. Range, *Ignatov 11-4182* (MW9054800); Kyurbelyakh Creek, *Ignatov & Ignatova 11-2178* (MW9054802); Oimyakon Distr., Mus-Khaya Mt., *Ignatov & Ivanov 11-3582* (MW9054804); Ust-Nera Settl., Tas-Kystabyt Range, *Ignatov & Ignatova 15-1222* (MW9054799); Nizhnekolymsk Distr., 8.IX.1972, *Stepanova s.n.* (MW9054805); Lower course of Indigirka River, Malaya Ercha Creek, 2.VIII.1974, *Afonina s.n.* (LE); Anabar Distr.: Anabar River basin, *Andreev 8244/2* (SASY); Saskylakh Settl., *Andreev 8248/2* (SASY); upper course of Kele River, *Andreev 8246/2* (SASY); Verkhoy-

ansky Distr., Elgetsk, *Isakova 8250/2* (SASY); **Chukotsky Autonomous District**: Providensky Distr., Arakamchechem Island, *Afonina A-35* (LE); St. Laurence Bay, 25.VII.1934, *Gorodkov s.n.* (LE); Place of confluence of Chegitun and Khesmymken Rivers, 24.VIII.1982, *Katenin & Popov s.n.* (LE); Karvakyanskaya Creek, 27.VII.1982, *Afonina s.n.* (LE); Egvekinot, 16.VIII.1985, *Afonina s.n.* (LE); **Magadan Province**: Okhotskoe Sea coast, Kamenny Range, *Ermolenko op06803* (NSK2006803); **Kamchatsky Territory**: Sobolevsky Distr., Pravy Kikhchik River basin, 23.VII.2004, *Czernyadjeva 15* (LE).

Localities confirmed by J.Wynns (pers. corr. May 2019): *CANADA: NUNAVUT: Resolute Bay, Cornwallis Island, 74°41'N, 94°50'W, 10 m, 14 July 1990, *Mogensen 90-306,* C. **GREENLAND**: Egedesminde, Tupilak Island [W4], 68°42'N, 52°55'W, 30 June 1956, sub *P. laetum*, *Holmen 15554*, C. **USA** : ALASKA: vicinity of Point Barrow, SE of Laboratory, 71°40'N, 156°38'W, 2–3 m, 18 June 1973, *Steere et al. 73-1*, NY no. 159489; between National Arctic Research Laboratory and gas well, idem, 19 June 1973,*Steere et al. 73-2*, NY no. 159491; Meade River Post Office (Coal Mine), 70°28'N, 157°25'W, ca. 30 m, 12–15 July 1973, *Steere et al. 73-372*, NY no. 159490.

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Appendix 1. Vaucher specimens of sequenced *Plagiothecium* species and GenBank accession numbers.

Species	Country, locality, collector, collector number (or date), herbarium barcode	Isolate	ITS	rpl16
P. berggrenianum	Russia, Yakutia, Ust-Nera, coll. Ignatov & Ignatova, 15-1222, MW 9054799	OK2022	MK934639	MK941638
P. berggrenianum	Russia, Taimyr, coll. Fedosov 11-1222 MW9054782	OK2023	MK934640	MK941639
P. berggrenianum	Russia, Yakutia, Mus-Khaya, coll. Ignatov & Ivanov 11-3584 MW 9054804	OK2024	MK934641	MK941640
P. cavifolium	Russia, Kabardino-Balkaria, coll. Ignatov et al. 31-7-2004 MHA9041060	OK1985	MK934603	MK941607
P. cavifolium	Russia, Altai, coll. Ignatov & Ignatova 12-577 MHA9041029	OK1981	MK934604	MK941608
P. cavifolium	Russia, Sakhalin, coll. Pisarenko, 03373 MHA9041797	OK1995	MK934608	MK941612
P. cavifolium	Russia, Kunashir, coll. Ignatov 06-1781 MHA	OK2002	MK934611	MK941615
P. curvifolium	Russia, Komi Republic, coll. Kucherov & Kutenkov, 5 July 2007 #175 (MHA)	OK1433	MK934632	MK941633
P. curvifolium	Germany, coll. Caspari 26-Oct-2006 Mosses of Saarlandes 7495 (SAAR)	OK2072	MK934633	MK941634
P. curvifolium	Russia, Kaliningrad, coll. Rozhina, sn, 3-Apr-2005 MHA9041610	OK2033	MK934634	MK941635
P. curvifolium	Germany, coll. Caspari 28-Dec-2011 Mosses of Saarlandes 7591 (SAAR)	OK2067	MK934635	MK941636
P. curvifolium	Russia, Karachaevo-Cherkessiya, coll. Onipchenko 8-Sept-1994 174/94 (MW)	OK1552	MK934636	
P. curvifolium	Germany, coll. Caspari 6-Apr-1991 Mosses of Saarlandes 2.573 (SAAR)	OK2071	MK934637	
P. curvifolium	Russia, Perm, coll. Bezgodov, 3-Aug-2005 #36 MHA9040993	OK1989	MK934638	MK941637
P. japonicum	Russia, Kamchatka, coll. Fedosov, 10-3-1097 MHA9040932	OK2000	MK934605	MK941609
P. japonicum	Russia, Khabarovsk, Bureya, coll. Ignatov 97-699 MHA9041009	OK1873	MK934606	MK941610
P. japonicum	Russia, Yakutia, coll. Ignatov 00-475 MHA9040999	OK1982	MK934607	MK941611
P. japonicum	Russia, Khabarovsk, Botchi, coll. Ignatov& Ignatova 13-408 MHA9040909	OK1998	MK934609	MK941613
P. japonicum	Russia, Amur, coll. Bezgodov 5.07.2010 #155 MHA9040929	OK2001	MK934610	MK941614
P. japonicum	Russia, Yakutia, coll. Pisarenko 09/08 MHA	OK807	MK934612	MK941616
P. laetum	Germany, coll. Caspari 5-Sept-2007 Mosses of Saarlandes 6791 (SAAR)	OK2070	MK934642	MK941641
P. laetum	Germany, coll. Caspari 24-Dec-1995, Mosses of Saarlandes 5382 (SAAR)	OK2073	MK934643	
P. laetum	Germany, coll. Caspari 1-Sept-1996 Mosses of Saarlandes 3.103 (SAAR)	OK2066	MK934644	MK941642
P. laetum	Czech Republic, coll. Donskov, 28-July-2011 MHA9055918	OK2029	MK934645	MK941643
P. laetum	Czech Republic, coll. Donskov, 17-July-2012 MHA9055917	OK2030	MK934646	MK941644
P. laetum	Russia, Krasnodar, Shakhe, coll. Ignatov 23-8-1999 MHA9041733	OK2035	MK934647	MK941645
P. nemorale	Russia, Krasnodar, coll. Ignatov & Ignatova 12-96 MHA9041877	OK1990	MK934613	MK941617
P. nemorale	Russia, Kabardino-Balkaria, coll. Ignatov et al. 05-1784 MHA9041888	OK1991	MK934614	MK941618
P. nemorale	Russia, Kaluga, coll. Teleganova 07-530 MHA9041793	OK1992	MK934615	MK941619
P. rossicum	Russia, Komi Republic, coll. Kucherov #77b 29.VI.2007 (MHA)	OK692	MK934616	
P. rossicum	Russia, Kaliningrad, Tikhonova KK17-06 MW9110623	OK2126	MK934617	MK941620
P. rossicum	Russia, Moscow, coll. Ignatov & Ignatova s.n. 18July 2010 (MHA)	OK1431	MK934618	MK941621
P. rossicum	Russia, Perm, coll. Bezgodov 5 Aug 2012 # 285 (MHA)	OK1432	MK934619	MK941622
P. rossicum	Russia, Sakhalin, coll. Tubanova and Dorzhieva S14021/20 (MHA ex UUH)	OK1875	MK934620	MK941623
P. rossicum	Russia, Mordovia, coll. Kobozeva 26-7-2008 #86 MW9055434	OK2053	MK934621	MK941624
P. rossicum	Russia, Kunashir, coll. Ignatov 06-1090 MW9055478	OK2054	MK934622	MK941625
P. rossicum	Russia, Tatarstan, coll. Ignatov & Ignatova 03-47 MHA9040983	OK1988	MK934623	MK941626
P. rossicum	Russia, Sakhalin, coll. Ignatov, Teleganova, 06-723 (MW)	OK1549	MK934624	MK941627
P. rossicum	Russia, Vladimir, coll. Seregin, 7-11-2003, M-199 (MW)	OK1555	MK934625	MK941628
P. rossicum	Russia, Vladimir, coll. Kokoshnikova 19-9-2007 (MW 9055352)	OK1556	MK934626	MK941629
P. rossicum	Russia, Arkhangelsk, coll. Churakove 20-6-2000 MW9055385	OK2058	MK934627	
P. rossicum	Russia, Arkhangelsk, coll. Korotkov 1155 MW9055375	OK2059	MK934628	
P. rossicum	Russia, Smolensk, coll. Ignatov 17-7-2004 MHA9041632	OK2032	MK934629	MK941630
P. rossicum	Russia, Pskov, coll. Zolotov, P504 MHA9041611	OK2038	MK934630	MK941631
P. rossicum	Russia, Pskov, coll. Zolotov, P88 MHA9041613	OK2039	MK934631	MK941632
P. rossicum	Russia, Kamchatka, coll. Czernyadjeva 21-July-2002 # 11, LE	OK2230	MK934664	
P. svalbardense	Russia, Sakhalin, coll. Pisarenko 03391 (MHA)	OK991	MK934648	MK941646
P. svalbardense	Russia, Yakutia, Mus-Khaya, coll. Ignatov & Ignatova 11-3022 (MHA)	OK992	MK934649	MK941647
P. svalbardense	Russia, Yakutia, Ust-Maya Distr., coll. Ignatov s.n. 29.VIII.2000 (MHA)	OK691	MK934650	MK941648
P. svalbardense	Russia, Anabar, coll. Fedosov 07-286 (MW)	OK1547	MK934651	MK941649
P. svalbardense	Russia, Primorsky, Olkhvaya Mt., coll. Ignatov et al., 06-2706 (MHA9041680)	OK1871	MK934652	MK941650
P. svalbardense	Russia, Yakitia, Lenskie Stolby, coll. Ignatov and Ignatova #16-330 (MW)	OK1551	MK934653	MK941651
P. svalbardense	Russia, Zabaikalsky Territory, Kadar Distr., coll. Filin s.n. 25-July-1989 (MW)	OK1553	MK934654	MK941652
P. svalbardense	Russia, Bashkortostan, coll. Shirokikh #222A, 8-7-2005 (MW)	OK1554	MK934655	MK941653
P. svalbardense	Russia, Primorsky Territory,, coll. Tubanova #Pr15-1/24 MHA ex UUH	OK1870	MK934656	MK941654
P. svalbardense	Russia, Sakhalin, coll. Pisarenko #03392 MW55306	OK2056	MK934657	MK941655
P. svalbardense	Russia, Primorsky Territory, Terney Distr., coll. Ignatov et al., #13-1820 (MHA)	OK1430	MK934658	MK941656
P. svalbardense	Russia, Altai, Kyga, coll. Zolotukhin sn, 25-Aug-2000 (MHA)	OK1546	MK934659	
P. svalbardense	Russia, Primorsky, Olchovaya Mt., coll. Ignatov et al., #06-2706 (MW)	OK1548	MK934660	MK941657
P. svalbardense	Russia, Khabarovsk, Botchi, coll. Ignatov and Ignatova #13-247 (MW)	OK1550	MK934661	MK941658
P. svalbardense	Russia, Murmansk, Umba, coll. Ignatov and Ignatova, #12-140 MHA9041614	OK2037	MK934662	MK941659
P. svalbardense	Russia, Yakutia, Kuraanakh, coll. Ignatov Ignatova #17-119, MHA	OK1874	MK934663	MK941660