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ON THE GENERA *ISOPTERYGIOPSIS* AND *ISOPTERYGIELLA*, GEN. NOV. (PLAGIOTHECIACEAE) IN RUSSIA
О РОДАХ *ISOPTERYGIOPSIS* И *ISOPTERYGIELLA*, GEN. NOV. (PLAGIOTHECIACEAE) В РОССИИ

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Abstract

The results of molecular phylogenetic analysis and morphological characters suggest that Asian plants previously referred to *Isopterygiopsis muelleriana* are not conspecific with European plants of this species. The description of *Orthothecium catagonioides* Broth. clearly fits character combination of Asian plants. This name was synonymized with *Isopterygiopsis muelleriana* when the genus *Isopterygiopsis* Z. Iwats. was established. We resurrect it and make a new combination in *Isopterygiopsis*. Molecular markers also demonstrate that *I. muelleriana* and *I. catagonioides* do not group with *I. pulchella* and *I. alpicola*. Therefore we establish a new genus, *Isopterygiella*, for the latter two species. Descriptions of genera *Isopterygiella* and *Isopterygiopsis* and their comparison are given; descriptions, illustrations and distribution data are provided for two species of *Isopterygiopsis*. *Isopterygiopsis muelleriana* is known in Russia from two localities in the Caucasus and one disjunct locality in the Russian Far East; *I. catagonioides* is common in Asian Russia, while in its European part it was found only in the Polar Urals.

Резюме

Результаты молекулярно-филогенетического анализа и совокупность морфологических признаков свидетельствуют о том, что растения из Азиатской России и сопредельных территорий, ранее относимые к *Isopterygiopsis muelleriana,* существенно отличаются от европейских растений этого вида. Описание *Orthothecium catagonioides* Broth. хорошо соответствует комбинации морфологических признаков азиатских растений. Это название было помещено в синонимы *Isopterygiopsis muelleriana* при описании рода *Isopterygiopsis* Z. Iwats. Мы восстанавливаем это название для азиатских растений и делаем новую комбинацию в роде *Isopterygiopsis*. Анализ молекулярных маркеров также показывает, что *I. muelleriana* и *I. catagonioides* не группируются с *I. pulchella* и *I. alpicola*. На этом основании мы выделяем два последних вида в особый род, *Isopterygiella*. Даны описания родов, их сравнение; приводятся также описания, иллюстрации и данные о распространении в России для видов рода *Isopterygiopsis*. *Isopterygiopsis muelleriana* известен в России из двух иестонахождений на Кавказе и одного изолированного местонахождения на Дальнем Востоке; *I. catagonioides* обычен в азиатской части России, тогда как в европейской части он был найден только на Полярном Урале.

KEYWORDS: mosses, ITS, *trn*L-F, new genus, new combination

Introduction

The genus *Isopterygiopsis* was established to accommodate one species, *I. muelleriana* (Schimp.) Z. Iwats. This species was previously referred to the genus *Isopterygium* Mitt.; however, Iwatsuki (1970) found that it has a structure of branch primordia different from other members of this genus, *i.e.* lacking pseudoparaphyllia. Later on, he transferred to *Isopterygiopsis* one more species of *Isopterygium*, *I. pulchellum* (Hedw.) A. Jaeger (Iwatsuki, 1987), and shortly after that *Isopterygium alpicola* (Hedw.) Nyholm was also added to *Isopterygiopsis* (Hedenäs, 1988). All three species of this genus occur in Russia; their distribution in its territory with literature references was summarized in the Check-list of mosses of East Europe and North Asia (Ignatov *et al.*, 2006). *Isopterygiopsis muelleriana* was known mainly in the Asian part of Russia, being restricted to the northernmost areas in its European part. In the course of preparing of the treatment of the family Plagiotheciaceae for the 5th volume of the "Moss Flora of Russia" a revision of herbarium collections was undertaken, supplemented also with testing samples with strongly deviated mor-

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phology by molecular markers. Among others, a problematic specimen from Dagestan was included in such an analysis, and resolved in a clade of GenBank accessions of *I. muelleriana* from Europe, while all specimens from Asian Russia which we referred to that species formed another clade. These unexpected results raised the question on the species identity of Asian plants. This was the first aim of the present paper.

However, preliminary results showed that the generic delimitation may also need attention, despite the molecular circumscription of the family and its genera have been already addressed in a number of publications by Pedersen & Hedenäs (2002), Hedenäs & Pedersen (2002), Huttunen *et al*. (2013), Zuo *et al*. (2011), Wynns *et al.* (2018).

In the analysis of Huttunen *et al*. (2013), *Isopterygiopsis muelleriana* was resolved apart of *I. pulchella* plus *I. alpicola*, which were found in a weakly supported clade with species of *Herzogiella*. Absence of close relationship between *I. pulchella* and *I. muelleriana* was also mentioned by Wynns *et al.* (2018) who focused on the genus *Plagiothecium*, so only one specimen of *I. pulchella* and three of *I. muelleriana* were included into that analysis based on one nuclear and two plastid loci. In the tree based on plastid loci and on concatenated sequences, these two species were resolved in a sister position, while in the ITS tree *I. muelleriana* was found in a grade formed by *Herzogiella* and *Pseudotaxiphyllum*, and *I. pulchella* occupied a position sister to *Plagiothecium*. Wynns *et al.* (2018) pointed that *I. muelleriana* is more similar to *Plagiothecium* in having flattened stems and apparently distichous foliation but differ in non-decurrent leaves; *I. pulchella* is not especially *Plagiothecium*-like, but it is more closely related to this genus according to molecular data. Wynns *et al.* (l.c.) also suspected that "*I. pulchella* and its relatives would be better placed in a separate genus, which may already been described", but no taxonomic implications were made until now. Wider sampling of these groups and resolving this problem was a second aim of the present study.

MATERIALS AND METHODS

DNA regions and sampling. The usage of nuclear ITS is straightforward, as in mosses, and pleurocarps especially, it helps in species delimitation in more cases than any other molecular marker. In general, ITS alone was found to be sufficient for solving problems at species-level taxonomy. For the genus-level study we added plastid *trn*L-F and mitochondrial *nad*5.

The sampling was addressed to determine species identity of Asian specimens referred to *I. muelleriana,* and also to define the volume of the genus *Isopterygiopsis* and its relationships within the Plagiotheciaceae. For the present study sequences of 14 specimens of *Isopterygiopsis* were obtained (Appendix 1) and aligned with GenBank accessions. The datasets were formed by selecting in GenBank most similar groups by BLAST search, with addition of taxa that seem to be missing, but relevant for the analysis based on previously published results. As samples represented different isolates in many cases, we did not form a concatenated dataset, but performed here three separate analyses, as the main purpose of the study was not a phylogenic reconstruction, but rather confirming genetic distinctions of particular groups.

DNA PCR and sequencing. Laboratory protocol and sequencing were rather standard, e.g. as described in Gardiner *et al.* (2005). PCR products were sequenced using the ABI PRISM © BigDye™ Terminator v. 3.1 and further analyzed on an automated sequencer (Applied Biosystems) 3730 DNA Analyzer in common use facility "Genom".

Phylogenetic analysis. Sequences were aligned in Bioedit (Hall, 1999) by built-in Clustal program and then corrected manually. The specimen vouchers and GenBank accession numbers for newly sequenced specimens are given in Table 1.

Bayesian Analyses were performed in MrBayes 3.2.6 (Ronquist *et al*., 2012), with 20,000,000 generations, four runs, 25% trees burn-in, and chain temperature 0.02. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007). Maximum Likelihood (ML) trees were estimated using RaxML 8.2.12 (Stamatakis, 2014) from 1000 independent searches each starting from distinct random trees. Robustness of the nodes was assessed using standard non-parametric bootstrap with 1000 iterations. Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE (Miller *et al.*, 2010).

Morphological studies. The total revision of material of *Isopterygiopsis* in MW and MHA and partial revision of specimens from LE was done. Special search of specimens from the Caucasus was undertaken.

RESULTS

Three datasets, for nuclear, plastid and mitochondrial markers, were analysed separately. The ITS tree (Fig. 1) comprises the grade of (1) *Pseudotaxiphyllum*-clade; (2) *Isopterygiopsis muelleriana* s.l. clade; (3) *Platydictya+Myurella+Orthothecium*-clade; (4) terminal clade that includes *Herzogiella*, *Isopterygiopsis alpicola+I. pulchella*-clade, and *Plagiothecium* and related genera, *Struckia, Ortholimnobium,* and *Rectithecium.*

Isopterygiopsis muelleriana s.l. clade has rather high sipport (PP=1, BS=82) and is subdivided into two subclades: the first one includes mainly Asian specimens and one North American specimen (PP=1, BS=100); the second one comprises mainly European and few Asian specimens (PP=1, BS=99).

Isopterygiopsis alpicola+I. pulchella-clade is sister to the clade of species previously referred to *Plagiothecium*, but now some of them are usually segregated to *Rectithecium*, *Struckia*, and *Ortholimbidium* (PP=1, BS=94). The *Isopterygiopsis alpicola+I. pulchella*-clade ilself is

Fig. 1. Bayesian tree of Plagiotheciaceae based on nuclear ITS sequences. Posterior probabilities and / ML bootstrap supports are shown at branches.

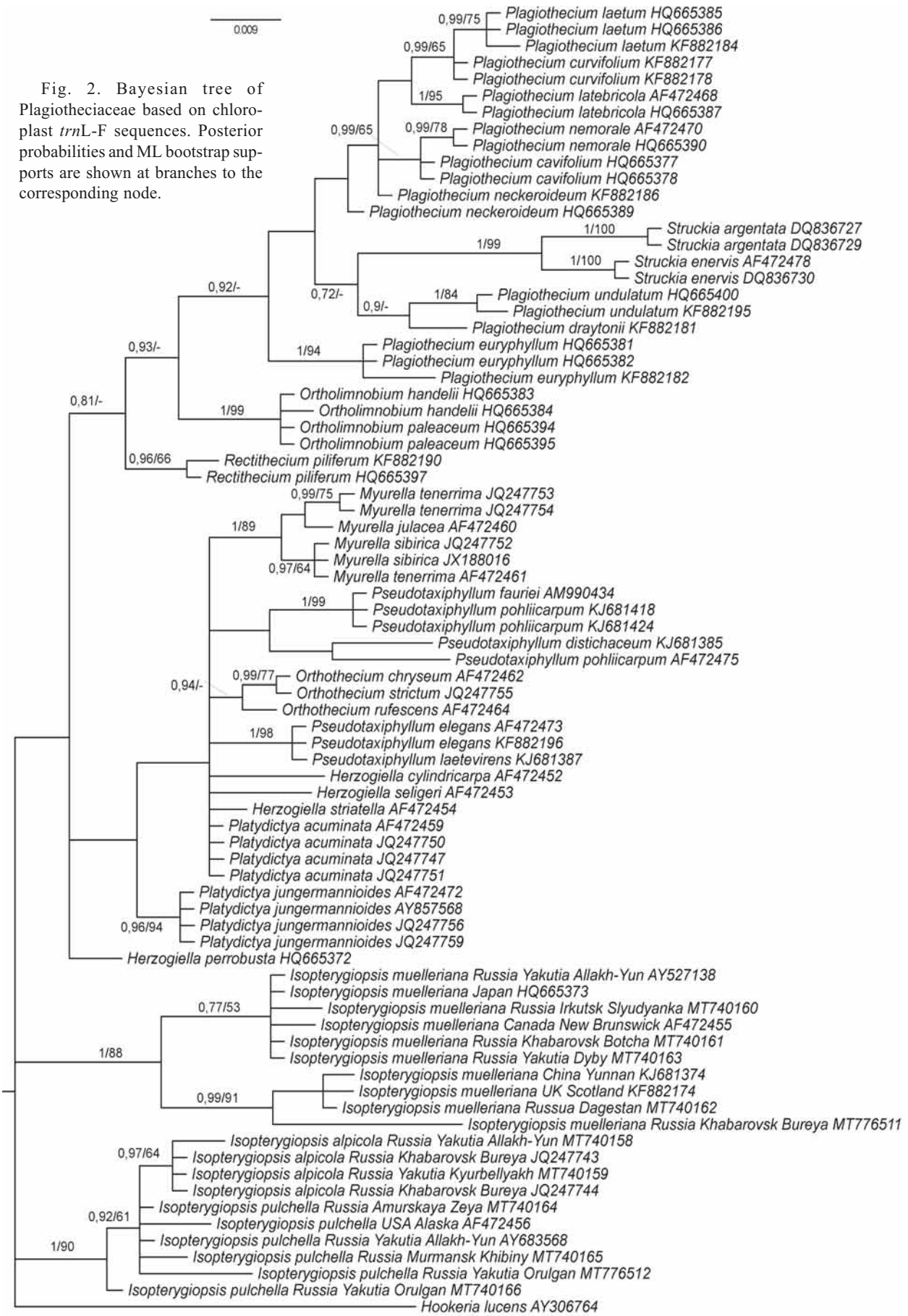

Fig. 2. Bayesian tree of Plagiotheciaceae based on chloroplast *trn*L-F sequences. Posterior probabilities and ML bootstrap supports are shown at branches to the corresponding node.

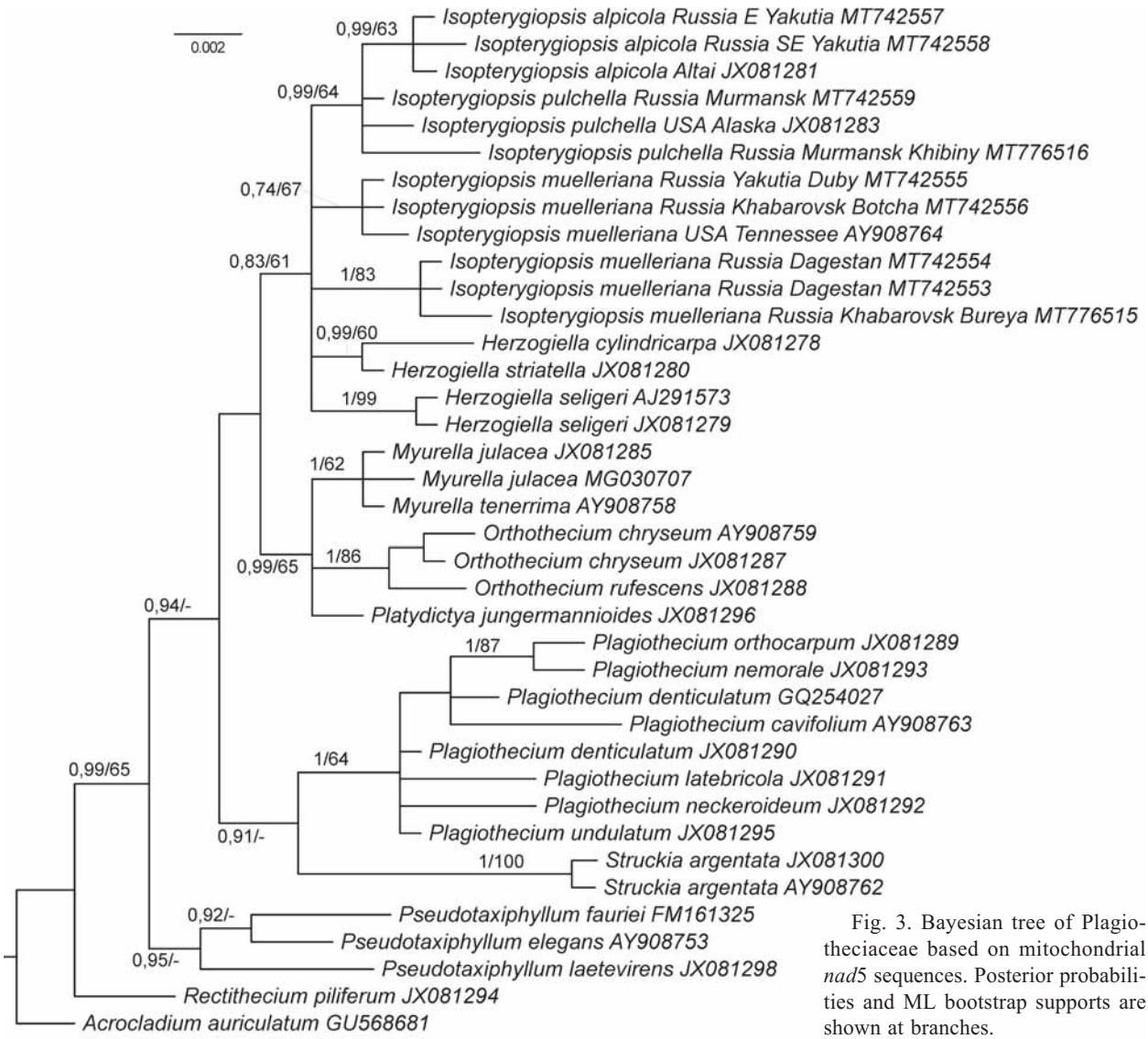

Fig. 3. Bayesian tree of Plagiotheciaceae based on mitochondrial *nad*5 sequences. Posterior probabilities and ML bootstrap supports are shown at branches.

only moderately supported (PP=0.98, BS=72), but two its subclades have a high support: PP=1, BS=90 for *I. pulchella* and PP=0.98, BS=85 for *I. alpicola*.

The *trn*L-F tree inferred from the Bayesian analysis (Fig. 2) is poorer resolved. It comparises a grade formed by clades of individual genera with moderate to maximal support. Species of *Isopterygiopsis* are resolved in two clades: (1) *I. muelleriana* (PP=1, BS=88), and (2) *I. pulchella* + *I. alpicola* (PP=1, BS=90), and in the latter, specimens of *I. alpicola* form a weakly supported clade (PP=0.97, BS=64) nested within *I. pulchella*.

Table 1. Specimens used in the molecular analyses, with newly obtained GenBank accession numbers.

Species	Isolate	Province	Voucher	ITS	*trn*L–F	*nad*5
I. alpicola	OK2517	Russia, Yakutia, Allakh-Yun	*Ignatov 00-297,* MHA9038097	MT731347	MT740158	MT742558
I. alpicola	OK2522	Russia, Khabarovsk, Botchi	*Ignatov & Ignatova 13-829,* MHA9038070	MT731348	-	-
I. alpicola	OK2515	Russia, Yakutia, Kyurbellyakh	*Ignatov & Ignatova 15-927,* MHA9038233	MT765092	MT740159	MT742557
I. catagonioides	OK2511	Russia, Khabarovsk, Botchi	*Ignatov & Ignatova 13-176,* MHA9038158	MT731352	MT740161	MT742556
I. catagonioides	OK2509	Russia, Yakutia, Dyby	*Ignatov & Ignatova 17-503,* MHA9025548	MT731353	MT740163	MT742555
I. catagonioides	OK2507	Russia, Khakassia	*Ignatov & Spirina 11-5001,* MHA9102630	MT731354	-	-
I. catagonioides	OK2523	Russia, Irkutsk, Slyudyanka	*Ignatov et al. 18-4014,* MHA9026003	MT731355	MT740160	-
I. pulchella	OK2476	Russia, Yakutia, Orulgan	*Isakova 449*, 4 Aug 2011, MHA	MT731349	MT776512	MT776516
I. pulchella	OK2412	Russia, Amurskaya Prov.,	*Dudov & Kotelnikova 2013_Br_0460*, MW	MT731350	MT740164	-
I. pulchella	OK2513	Russia, Yakutia, Orulgan	*Ignatov 11-4421,* MHA9038200	MT731351	MT740166	-
I. pulchella	OK2514	Russia, Primorsky, Lozovyi	*Ignatov et al. 06-2746*, MHA9038267	MT765093	-	-
I. pulchella	OK2520	Russia, Murmansk Prov.,Khibiny	*Ignatov & Ignatova 12-48,* MHA9038199	MT776905	MT740165	MT742559
I. muelleriana	OK2411	Russia, Khabarovsk, Bureya	*Ignatov 97-1127*, MHA9038067	MT731356	MT776511	MT776515
I. muelleriana	OK2505	Russia, Dagestan, Charodinsky Distr.	*Ignatov & Abakarova 11-2015*, MHA	MT731357	-	MT776517
I. muelleriana	OK2497	Russia, Dagestan, Charodinsky Distr.	*Ignatov & Abakarova 11-2015a,* MHA	MT731358	MT740162	MT742553

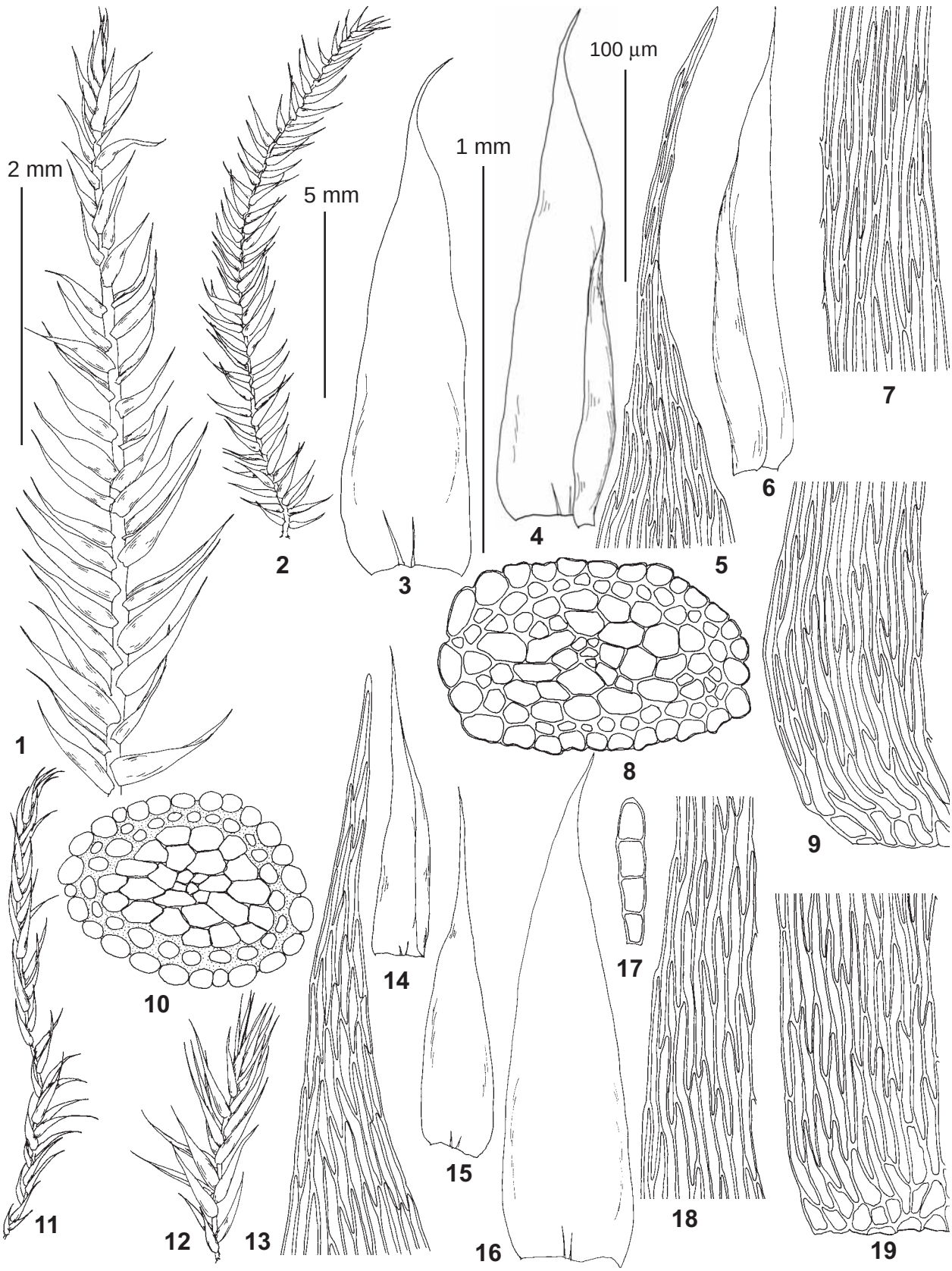

Fig. 4. *Isopterygiopsis muelleriana* (1-9 – from: Germany, Tegernsee, 6.I.1919, *Herzog, Paul & Schellenberg s.n.,* MW; 10, 16-17 – from: Russia, Karachayevo-Circassian Republic, 5.VIII.1999, *Ukrainskaya 13913*, LE; 11-15, 18-19 – from: Russia, Dagestan, *Ignatov & Abakarova 11-2015*, MHA). 1-2, 11-12 – habit, dry; 3-4, 6, 14-16 – stem leaves; 5, 13 – upper laminal cells; 7, 18 – median laminal cells; 8, 10 – stem transverse sections; 9, 19 – basal laminal cells; 17 – gemma. Scale bars: 5 mm for 2; 2 mm for 1, 11-12; 1 mm for 3-4, 6, 14-16; 100 µm for 5, 7-9, 13, 17-19.

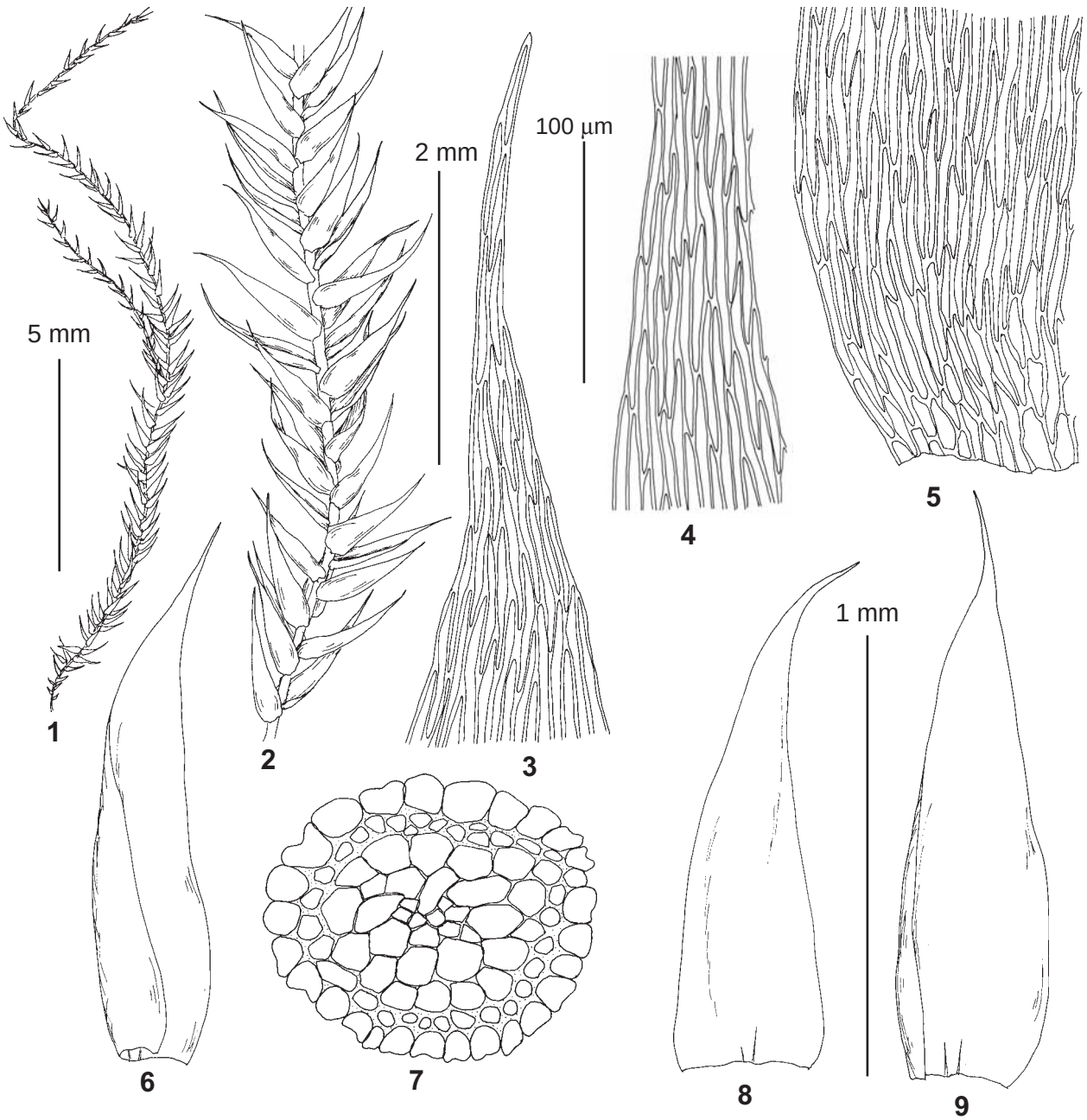

Fig. 5. *Isopterygiopsis muelleriana* (from: Russia, Khabarovsk Territory, *Ignatov 97-1125,* MHA9038067). 1-2 – habit, dry; 3 – upper laminal cells; 4 – median laminal cells; 5 – basal laminal cells; 6, 8-9 – stem leaves; 7 – stem transverse section. Scale bars: 5 mm for 1; 2 mm for 2; 1 mm for 6, 8-9; 100 µm for 3-5, 7.

Within the clade of *I. muelleriana* two sister subclades were found: one of them (PP=0.99, BS=91) includes four specimens, from Scotland, Russian Caucasus, China (Yunnan), and Bureya River in Khabarosk Territory, Russian Far East; the second, mainly Asian clade, is weakly supported (PP=0.77, BS=53).

Tree based on mitochondrial marker *nad*5 is also poorly resolved, with only one moderately supported clade other than monogeneric, i.e. *Myurella*+*Platydictya*+*Orthothecium* (PP=0.99, BS=65).

A similar level of support is for *Isopterygiopsis pulchella*+*P. alpicola*-clade (PP=0.99, BS=64), and for *P. alpicola*-clade (PP=0.99, BS=63) that is nested among *Isopterygiopsis pulchella.*

Isopterygiopsis muelleriana is resolved in two clades. The Asian+American clade lacks support, while another one, formed by plants from the Caucasus (two sequences form different isolates of one collection) and Khabarovsk (one sequence) has a high support (PP=1, BS=83).

Morphological studies. Most Asian plants appeared to be distinct from and European ones in several characters discussed in Taxonomy section. A limited observations on North American plants support their identity with Asian ones.

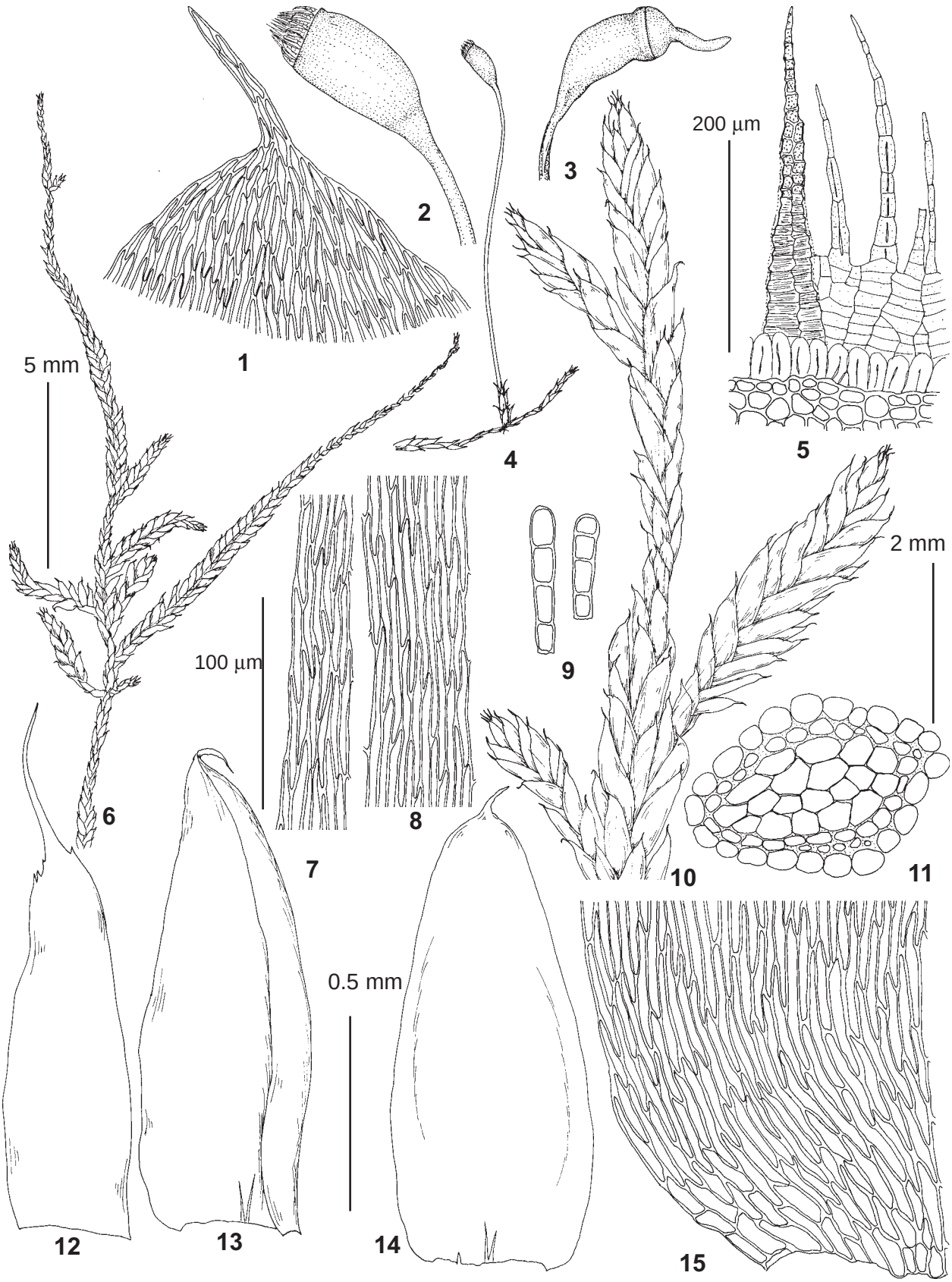

Fig. 6. *Isopterygiopsis catagonioides* (1, 6-11 – from: Russia, Khabarovsk Territory, Bureinsky Reserve, 14.VIII.1997 *Ignatov s.n.*, MHA; 2-5 – from: Khabarovsk Territory, Tardoki-Yani Mt., *Ermolenko 1-17*, MHA). 1 – upper laminal cells; 2-3 – capsules; 4, 6, 10 – habit; dry; 5 – peristome; 7-8 – median laminal cells; 9 – gemmae; 11 – stem transverse section; 12 – perichaetial leaf; 13-14 – stem leaves; 15 – basal laminal cells. Scale bars: 5 mm for 4, 6; 2 mm for 2-3, 10; 0.5 mm for 12-14; 200 µm for 5; 100 µm for 1, 7-9, 11, 15.

Discussion

Since the time when the genus *Isopterygiopsis* has been segregated by Iwatsuki (1970) from aggregate genus *Isopterygium*, Asian specimens were referred to as *Isopterygiopsis muelleriana*. They were exhaustively described and illustrated by Iwatsuki (l.c.), and almost all specimens from Russia are in full agreement with this description. Noteworthy is that in the protologue of the new genus Iwatsuki mentioned that the type of *I. muelleriana* was not studied, and among specimens examined only Japanese and Siberian collections are mentioned. No special comparison of Asian and European populations of *I. muelleriana* was undertaken, or at least never published, despite some noticable discrepancies exist. For example, Iwatsuki (1970) described the genus *Isopterygiopsis* as having no stem central strand, whereas illustrated floras, *e.g.*, Nyholm (1965) and treatment of the genus in Flora Iberica (Cano, 2018) show distinct central strand in European plants referred to *I. muelleriana*. Likewise the only herbarium specimen from Europe (Germany) which was available for our study also has central strand (Fig. 4: 8).

The heterogeneity of *I. muelleriana* was not discerned until now, likely due three reasons: first, the bryologists who studied local floras usually dealt with uniform material, either in Europe or Asia or North America; second, only few specimens of this genus were involved into molecular phylogenetic analyses of pleurocarps (Huttunen *et al*., 2012, 2013; Wynns *et al.*, 2018, *etc*.); and third, it is a rare species in Europe. In Russia, the 'Asian *I. muelleriana*' occurs in its Asian part, being reported from European Russia only in Polar Urals by few old records (there are more collections from the East-faced slope of Urals).

The Caucasus is the only area in Russia where only European *I. muelleriana* s.str. occurs, but it is very rare, known only from two localities: one in Karachayevo-Circassian Republic (not published), and another in Dagestan, represented in our molecular analysis. There is one more enigmatic collection of European *I. muelleriana* s.str. in Asia, in Khabarovsk Territory, Bureya River, the area rich in 'Asian *I. muelleriana*'. This sample was recognized in the field as having anomalous morphology, and was going to be described, but finally was just reported as an anomalous form, perhaps influenced by regular flooding (Ignatov *et al.*, 2000). Its sequence and the presence of central strand are consistent with its identification as *I. muelleriana* s.str.

The eastern border of *I. muelleriana* s.str. is diffuse, as in addition to the Khabarovsk specimen, there is a sequence of a collection from Yunnan that perfectly fits sequences of plants from Western Europe, Caucasus, and Khabarovsk Territory (Bureya).

Phylogenetic trees inferred from all three studied DNA regions, ITS, *trn*L-F, and *nad*5 showed high to moderate statistical support for separation mainly European and mainly Asian *I. muelleriana* at the species level. Morphologically they differ in leaf shape (ovate-lanceolate, gradually acuminate vs. ovate, abruptly contracted into piliferous apiculus ca. 0.1 mm long), foliage (leaves ± distantly arranged, erect-spreading vs. closely arranged, erect, imbricate), and presence vs. absence of stem central strand. In addition, plants of mainly Asian lineage usually have only one subepidermal layer below hyalodermis, with rather moderately incrassate cell walls, while in mainly European plants the thick-walled cells in transverse stem section often form two layers and have especially thick walls adjacent to hyalodermis cells. Length of laminal cells in Asian and European plants is overlapping, but the maximal values seen in European plants (60–100 (–120) μm) were never observed by us in Asian plans (their length is 55–90 μm). Thus, the distinction of these two lineages obviously merits recognition at the species level.

Iwatsuki (1970) placed to the synonymy of *Isopterygiopsis muelleriana* a species described from Shaanxi, *Orthothecium catagonioides* Broth. However, since he considered, as it was mentioned above, only Asian material, it may be assumed as an evidence for identity of 'Asian *I. muelleriana* sensu Iwatsuki' with *O. catagonioides.* The protologue of *Orthothecium catagonioides* mentions complanate and dense foliage, concave, oblong-lanceolate leaves with piliferous acumen that characterize Asian, but not European plants. Furthermore, the species name and mentioning in the protologue the habitual similarity to south hemispheran species *Catagonium politum* (Hook. f. & Wilson) Dusén ex Broth. (=*C. nitens* (Brid.) Cardot) are in favor for applying this name to Asian plants. Thus with only a little hesitation we refer 'mainly Asian *I. muelleriana*' to *O. catagonioides* and make a combination for this species name in *Isopterygiopsis*.

Another question of the present study was if *Isopterygiopsis muelleriana* s.l. is congeneric with *I. pulchella* and *I. alpicola*. Their non-monophyly in the present analyses agree with some of the previous results (Huttunen *et al*., 2013; Wynns *et al.*, 2018), which suggest their placement in different genera. We failed to find any existing generic name for the latter two species; so the new genus, *Isopterygiella*, is described below to accommodate them.

Taxonomy

Isopterygiella Ignatov & Ignatova, gen nov.

Diagnosis. The new genus differs from *Isopterygiopsis* in having terete or indistinctly complanate vs. strongly complanate foliage; leaves often homomallous to falcate-secund vs. straight to slightly homomallous; plants autoicous or apparently dioicous (only one sex is known) vs. dioicous; operculum high conic vs. rostrate.

Type species: *Isopterygiella pulchella* (Hedw.) Ignatov & Ignatova (= *Leskea pulchella* Hedw.).

Fig. 7. *Isopterygiopsis muellariana* (A–B, D, F, I, L, M) and *I. catagonioides* (C, E, G–H, J–K, N–O). A–E: habit; F–O: stem transversal cross sections, N–O in addition showing leaves keeled in lower parts. Specimens (specimens from DNA barcoding are cited by isolate ##, cf. Table 1): **A, L**: Dagestan, OK2497; **B**: Khabarovsk, OK2411; **C, N**: Khabarovsk, OK2511; **D, F, I**: Germany, Tegernsee, 6.I.1919, *Herzog, Paul & Schellenberg s.n.,* MW; **E, H, K, O**: Urals, Khanty-Mansi, OK2524; **G, J, N**: Khakassia, OK2507; **M**: Karachayevo-Circassian Republic, 5.VIII.1999, *Ukrainskaya 13913*, LE.

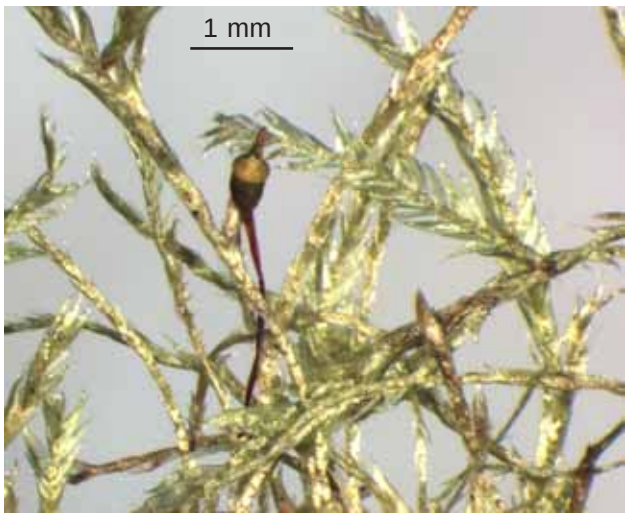

Fig. 8. *Isopterygiopsis catagonioides* (from: Russia, Khabarovsk Territory, Badzhal Range, *Fedosov 16-13*, MW): Plant with sporophyte.

Description. *Plants* small or minute, green or yellowish-green, silky glossy, in small soft patches. *Stems* terete-foliate or indistinctly complanate, sparsely and irregularly branched; central strand present; hyalodermis well-developed or absent, in the latter case epidermal cells with thinner outer walls; rhizoids axillary, purple, coarsely papillose. *Leaves* straight or slightly falcate-secund, ovate-lanceolate to lanceolate, narrowly acute or acuminate; margins entire or serrulate near apex or throughout; costa short, double; *laminal cells* linear, basalmost cells shorter and wider, alar cells not differentiated or few alar cells quadrate to short rectangular. *Specialized asexual reproduction* by axillary propagulae of 3–4 cells in one row. *Autoicous* or *apparently dioicous* (male plants unknown). *Inner perichaetial leaves* short. *Capsules* erect to inclined, cylindric to slightly, rarely moderately curved. *Operculum* conic, sometimes with an apiculus. *Annulus* revoluble, of 2–3 rows of cells. *Peristome* slightly reduced; exostome teeth whitish, striolate below, papillose above; basal membrane of endostome ca. 40% of exostome teeth length, segments narrow, not perforated, cilia 1–2, short to about as long as exostome teeth, nodose. *Spores* 10–15 μm. *Calyptra* cucullate.

The genus inclides two species.

Isopterygiella pulchella (Hedw.) Ignatov & Ignatova, comb. nova. — *Leskea pulchella* Hedw., Sp. Musc. Frond. 220. *55, 7-12.* 1801. — *Isopterygiopsis pulchella* (Hedw.) Z. Iwats., J. Hattori Bot. Lab. 63: 450. 1987. — *Isopterygium pulchellum* (Hedw.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 441 (Gen. Sp. Musc. 2: 1259). 1878.

Isopterygiella alpicola (Lindb.) Ignatov & Ignatova, comb. nova. — *Stereodon alpicola* Lindb., Kongl. Svenska Vetensk. Acad. Handl., n.s. 23(10): 153–154. 1890. — *Isopterygiopsis alpicola* (Lindb.) Hedenäs, J. Bryol. 15(2): 495. 1988. — *Isopterygium alpicola* (Lindb.) Nyholm, Ill. Moss Fl. Fennoscandia. II. Musci 776. 1969.

Isopterygiopsis Z. Iwats.

Plants small, green or yellowish-green, strongly silky glossy, in loose tufts. *Stems* strongly complanate, irregularly branched; central strand absent or present, occasionally consisting of few cells; hyalodermis well-developed, rhizoids axillary, purple, coarsely papillose. *Leaves* apparently distichous, very rarely slightly secund (when growing in inappropriate habitats), ovate-lanceolate to ovate, gradually acuminate or abruptly narrowed into piliferous apiculus, moderately to strongly concave, occasionally cucullate; margins entire; *costa* short, double; *laminal cells* linear, basal cells shorter and wider, alar cells not differentiated. *Specialized asexual reproduction* by axillary propagulae of 3–4 cells in one row. *Dioicous*. *Inner perichaetial leaves* short. *Capsules* erect, rarer inclined, cylindric or slightly curved. *Operculum* rostrate. *Annulus* of 1–2(–3) rows of cells. *Peristome* moderately reduced; *exostome teeth* whitish or yellowish, striolate below, papillose above; basal membrane of *endostome* low, ca. 30% of exostome teeth length, segments narrow, not perforated, cilia 1(–2). *Spores* 8–15(–17) μm. *Calyptra* cucullate.

Type species: *Isopterygiopsis muelleriana* (Schimp.) Z. Iwats. (typified by Z. Iwatsuki, who however treated this species in a wide sense, including '*Orthothecium catagonioides*' and keeping in mind solely Asian plants which we refer to a separate species).

The genus inclides two species.

Isopterygiopsis muelleriana (Schimp.) Z. Iwats., J. Hattori Bot. Lab. 33: 379. 1970. — *Plagiothecium muellerianum* Schimp., Syn. Musc. Eur. 584. 1860. — *Isopterygium muellerianum* (Schimp.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 441. (Gen. Sp. Musc. 2: 1259). 1878. Figs. 4, 5, 7A–B, D, F, I, L, M.

Stems to 2 cm long, central strand consisting of few cells present, rarer lacking. *Leaves* erect-spreading to spreading, loosely or densely arranged, (0.5–)1.0–1.5 ×(0.2–)0.3–0.4 mm, ovate-lanceolate, gradually attenuate, with 1–2-seriate apical portion 2–4 cells long, moderately concave, not cucullate; margins flat, entire; *laminal cells* 60–100(–120)×4–5 μm, alar cells not differentiated. *Specialized asexual reproduction* by axillary propagulae of 3–4 cells in one row. *Sporophytes rare*, unknown in Russia. [*Perichaetial leaves* gradually narrowed into narrow acumen with serrulate margins. *Setae* 1.2–1.5 cm. *Capsules* ca. 1.2 mm long, erect, straight to weakly curved. *Spores* 10–14 μm].

Distribution and ecology. *Isopterygiopsis muelleriana* is a mountainous species occurring in South and Central Europe and extending northward to the southern areas of Norway (Hodgetts & Lockhart, 2020); it was

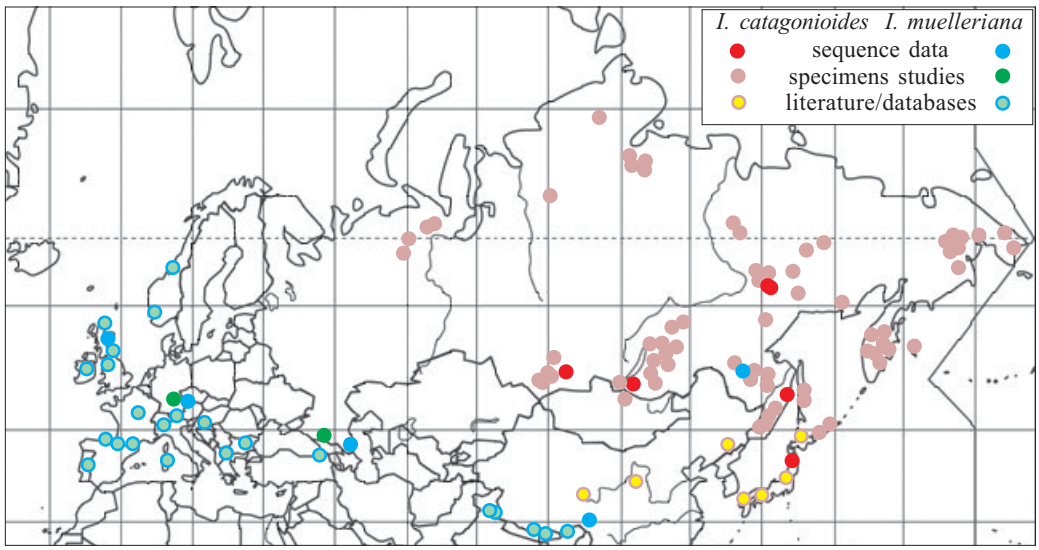

Fig. 8. Distribution of two speices of the genus *Isopterygiopsis I. catagonioides* and *I. muelleriana*. Mapping in Russia in according to Moss Flora of Russia database (Ivanov *et al.*, 2017), literature and database data are mostly with country- or province-level exactness from Ros et al. (2013) and Hodgetts & Lockhart (2020).

also reported from Turkey (Ros *et al.*, 2013), Africa (Kenya, Tanzania, Uganda) (O'Shea, 2006) and India (Gangulee, 1978-1980). *Isopterygium sericifolium* Dixon described from Kenya was synonymised with *Isopterygiopsis muelleriana* by Hedenäs (2001); specimen in BM (000674451) is habitually similar to European plants, as well as the drawing of leaf and shoot (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/4522883). Illustration in Gangulee (1978-1980) (Fig. 1014) also shows a plant similar to European specimens rather than North Asian ones.

Both *I. muelleriana* and *I. catagonioides* occur in China. The latter species was decribed from Shaanxi Province; illustrations in "Moss Flora of China" (Zhang & He, 2005) also show a stem transverse section without central strand and ovate leaves abruptly narrowed into short filiform apiculus. At the same time, molecular data confirm the presence of *I. muelleriana* in China (Yunnan) (Figs. 1 & 2).

Isopterygiopsis muelleriana is also considered to be widespread in eastern North America. However, its distribution in these areas needs confirmation because *I. catagonioides* was included into it. Illustrations in Flora of North America (Ireland Jr., 2014) likely represent *I. catagonioides* rather than *I. muelleriana.* Photograph of stem transverse section that lack central strand and has the whole cortex of rather few cells is provided by Faubert (2014), and illustrations in "Flora of Maine" by Allen (2014) also show plants which are much more similar to *O. catagonioides* than to *I. muelleriana* s.str. The only *trn*L-F sequence of *I. muelleriana* from North America in Genbank is also resolved within the clade of *O. catagonioides* (Fig. 2), as well as *nad*5 region (AY908764), cf. Fig. 3.

In European Russia *I. muelleriana* is known only in the Caucasus where it was collected in Dagestan and Karachayevo-Circassian Republics; collections from Dagestan represent strongly depressed plants with small leaves (Fig. 4: 11-12, 7A). These specimens were collected at altitudes 1900–2100 m on open slopes, on soil among grasses and rock outcrops. Plants from Karachayevo-Circassian Republic are better developed, similar to the specimen from Germany. Label data do not provide exact ecological information except for growing on soil. A single collection of *I. muelleriana* from Asian Russia was made in a valley of Bureya River, within forest zone, at 370 m elevation. It grew in a flood valley, on soil bank in forest, forming thin, lax patch and being represented mainly by tiny, depressed plants with small, distantly arranged leaves and attenuate stem and branch apices.

Additional specimens examined: EUROPE: GERMANY, Tegernsee, 6.I.1919, *Herzog, Paul & Schellenberg s.n.* (MW9045910). RUSSIA: **Karachayevo-Circassian Republic**: gorge of Daut River, 5.VIII.1999, *Ukrainskaya 13913* (LE). **Dagestan**: Charoda Distr., Gunukh, *Ignatov & Abakarova 11-206 & 11-218* (MHA 9038321 & 9038319).

Differentiation. *Isopterygiopsis muelleriana* has ovate-lanceolate leaves more or less gradually tapered and ending with narrow, filiform apiculus. In leaf shape it is similar to *Isopterygiella pulchella*. However, *Isopterygiopsis muelleriana* has well-developed stem hyalodermis and complanate foliage, while hyalodermis in stems of *Isopterygiella pulchella* is absent or scarcely recognized, its stems are terete-foliate or leaves are secund. The distinctions from *I. catagonioides* are discussed under that species. *Isopterygiella alpicola* is another plant with well-developed stem hyalodermis and gradually acuminate leaves; it differs from *Isopterygiopsis muelleriana* in smaller size of plants, with leaves 0.3–0.8×0.1–0.3 mm vs. 1.0–1.5×0.3–0.5 mm; terete foliate stems, often falcate-secund leaves; serrulate vs. entire leaf margins; and shorter laminal cells, 30–60×5–9 μm vs. 60–100(–120)×4–5 μm.

Isopterygiopsis catagonioides (Broth.) Ignatov & Ignatova, comb. nova. — *Orthothecium catagonioides* Broth., Nuovo Giorn. Bot. Ital., n.s. 13: 270. 1906. Figs. 6, 7C, E, G–H, J–K, N–O, 8.

Stems 1–2(–2.5) cm long, central strand lacking. *Leaves* appressed, densely arranged, often imbricate, (0.8–)1.0–1.3×0.4–0.5 mm, ovate, abruptly contracted into filiform, flexuose to reflexed apiculus ca. 0.1 mm long, strongly concave, often cucullate; margins flat, entire; *laminal cells* 55–90×4–6 μm, alar cells not differentiated. *Specialized asexual reproduction* by axillary propagulae of 3–4 cells in one row sporadically present. *Dioicous. Sporophytes* rare. *Inner perichaetial leaves* 1.3–1.4×0.3 mm, abruptly contracted into long acumen, margins coarsely dentate above. *Setae* ca 0.8 cm. *Capsules* to 1.0 mm long, erect to slightly inclined, straight to slightly curved. *Spores* 13–17 μm.

Distribution and ecology. This species is sporadically distributed in mountain areas in Asian Russia, from the Arctic to southern Siberia and Far East. In European Russia it is known from Polar Urals. It also apparently occurs in China and North America (see comments to *I. muelleriana*; furthermore, one duplicate specimen of this species from Canada is stored in MHA). However, its distribution in these territories needs further study. *Isopterygiopsis catagonioides* grows in a wide altitudinal range, from sea level (in Iturup Island, Kurils) to 2000 m (in Altai Mts.), in shady cliff crevices and cracks, between rocks of rock-fields, on rock outcrops, in mountain tundra, on cliffs near waterfalls and more or less dry cliffs, in forests and on open slopes, rarely on tree bases, rotten wood and bare soil in forests; it prefers acidic and neutral rocks.

Additional selected specimens examined: EUROPE: RUSSIA: **Republic of Komi**: Subpolar Urals, Malaya Nyadokota River (tributary of Lemva River), 21.IV.1950, *Kil'dyushevsky s.n.* (LE); Subpolar Urals, Saranseda Creek (upper right tributary of Kozhim River), 19.IV.1950, *Kil'dyushevsky s.n.* (LE).

ASIA: RUSSIA: **Yamalo-Nenetzky Autonomous District**: Junto Lake, 14.VIII.1994, *Czernyadjeva 16* (LE); Polar Urals, middle course of Sob' River, railway station 110 km, 6.VII.1988, *Czernyadjeva 7* (LE). **Krasnoyarsk Territory**: Taimyr Municipal Distr.: Putorana Plateau, Glubokoe Lake, *Fedosov 15-0366* (MW9046852); vicinity of Khatanga Settl., valley of Merkyu River, *Fedosov 11-1382* (MW9046849); Anabar Plateau, near Fomich River mouth, *Fedosov 08-581* (MW9045911); Maimecha River at 11 km upstream Chopko Creek mouth, *Fedosov 09-416* (MW9045912); Kotuikan River at 7 rm upstream Merkyu River mouth, *Fedosov 11-1489* (MW9045916). **Republic of Buryatia**: Barguzinsky Distr., Barguzinsky Nature reserve, Davsha Settl., *Czernyadjeva 64-14* (MW9112304); Kabansk Distr., Khamar-Daban Range, valley of Bolshoy Mamai Creek, *Ignatov, Ignatova & Kolesnikova 18-4014* (MW9090512). **Zabaikalsky Territory**: Kalar Distr.: vicinity of Kuanda Settl., 4.VIII.2012, *Afonina s.n.* (MW9045918); vicinity of Udokan Settl., Udokan Range, 28.VII.1985, *Filin s.n.* (MW9045919). **Republic of Yakutia**: Oimyakon Distr., Suntar-Khayata Range, Mus-Khaya Mt., *Ignatov & Ignatova 11-3250* (MW9045925); Tomponsky Distr.: Suntar-Khayata Range, Kyurbelyakh Creek, *Ignatov & Ignatova 11-2233* (MW9045924); Dyby River, *Ignatov & Ignatova 17-430* (MW9090155); Momsky Distr., Ulakhan-Chistai Range, middle course of Tirekhtyakh River, Tas Creek, *Ignatov & Ignatova 18-2127* (MW9091656). **Khabarovsk Territory**: Verkhnebureinsky Distr.: Bureinsky State Reserve, Dusse-Alin Range, Medvezh'e Lake, 5*Ignatov 97-338* (MW9038116); left bank of Bureya River near "Tri Brata", *Ignatov 97-342* (MW9038115); Sovgavansky Distr.: Botchinsky State Reserve, Mulpa River opposite Podzemny Creek mouth, *Ignatov & Ignatova 13-167* (MW9045928); Badzhal Mts., Yarap River valley, *Fedosov 16-30* (MW9112951); North Sikhote-Alin, Tardoki-Yani Mt. Range, Sukhaya Pad' Stream, 28.VIII.2013 *Ermolenko 12-8* (MW9111159). **Amurskaya Province**: Zeya Distr., Zeisky Nature reserve, Tukuringra Range, Izyubriny Creek, 28.VI.2012, *Dudov Br_12_084* (MW9045931); Selemdzhinsky Distr., Norsky Nature Reserve, Meun River, 5.VII.2010, *Bezgodov 127* (MHA9038166). **Primorsky Territory**: Olga Distr., waterfall on Milogradovka Creek, *Ignatov 07-296* (MW9045930); Chuguevka Distr., Oblachnaya Mt., *Ignatov 07-263* (MW9045941); Partizansk Distr., Olkhovaya Mt., *Ignatov, Ignatova & Cherdantseva 06-2672* (MW9045940); Shkotovo Distr., Pidan (Livadijskaya) Mt., *Ignatov & Ignatova 06-2274* (MW9045937). **Sakhalinskaya Province**: Sakhalin: Dolinsk Distr., Sokol, Belaya Creek, *Ignatov & Teleganova 06-819* (MW9045938); Tymovsk Distr., Nabilsky Mt. Range, along a tributary of Khrebtovyj Creek, *Ignatov & Teleganova 06-902* (MW9045939); Kuril Islands: Iturup Island: Bogatyr Range, *Bakalin K-16-38-07* (MW9045943); vicinity of Circ Bay, 45.32366°N, 148.6187°E, *Fedosov 15-2-216* (MW9046853); Kunashir Island: atrio of Tyatya Volcano, *Ignatov 06-1754* (MW9045936). **Kamchatsky Territory**: Kamchatka Peninsula: Klyuchevskie Volcanoes, Ostryj Tolbachik Volcano, 6.VIII.2006, *Czernyadjeva 8* (MW9045952); Kronotskyj State Reserve, Krasheninnikov Volcano, *Fedosov 12-224* (MW9045953); Aleutsky Distr., Bering Island, Bolshaya Stolovaya Sopka, *Fedosov 10-3-1124* (MW9045955).

NORTH AMERICA: Canada, New Brunswick, Restigouche Co., 14 Aug 1970 Ireland (MHA9054883).

Differentiation. *Isopterygiopsis catagonioides* differs from *I. muelleriana* in having abruptly vs. gradually narrowed leaf acumina; strongly concave, often cucullate vs. moderately concave, not cucullate leaves; and densely vs. often ± sparsely foliate stems. Due to ovate leaves with abruptly attenuate apiculus, *I. catagonioides* can be confused with widespread Siberian *Plagiothecium svalbardense* and European *Rectithecium piliferum,* both having similar leaf shape. However, *I. catagonioides* differs from both these species in flat leaf margins and presence of stem hyalodermis vs. narrowly recurved margins from base to apiculus and hyalodermis not developed.

KEY TO IDENTIFICATION OF *ISOPTERYGIOPSIS* SPECIES

1. Leaves ovate, strongly concave to keeled at base, cucullate, abruptly acuminate; stem central strand absent ..... 2. *I. catagonioides*
— Leaves ovate-lanceolate, moderately concave, not keeled at base, not cucullate, gradually acuminate; stem central strand usually present .... 1. *I. muelleriana*

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