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THE GENUS *LEPTOPTERIGYNANDRUM* (TAXIPHYLLACEAE, BRYOPHYTA) IN RUSSIA

РОД *LEPTOPTERIGYNANDRUM* (TAXIPHYLLACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Leptopterigynandrum* in Russia includes 6 species (*L. austro-alpinum* Müll. Hal., *L. decolor* (Mitt.) Fleisch., *L. incurvatum* Broth., *L. piliferum* S. He, *L. subintegrum* (Mitt.) Broth. and *L. tenellum* Broth.) occurring in South Siberia from Transbaikalia to the Altai, in the Suntar-Khayata Range in Yakutia and in Chukotka. Most species can be separated by unique substitutions in nuclear ITS sequences, excepting *L. decolor* and *L. tenellum* represented by the same haplotype. The familial placement of *Leptopterigynandrum* is discussed and the new family Taxiphyllaceae is described to accomodate this genus together with *Taxiphyllum, Hondaella,* as well as with *Glossadelphus ogatae*. The genus *Taxiphyllum* is lectotypified with *Taxiphyllum taxirameum*.

Резюме

Род *Leptopterigynandrum* представлен в России 6 видами (*L. austro-alpinum* Müll. Hal., *L. decolor* (Mitt.) Fleisch., *L.incurvatum* Broth., *L. piliferum* S. He, *L. subintegrum* (Mitt.) Broth. и *L. tenellum* Broth.), которые распространены в Южной Сибири от Забайкалья до Алтая, на хребте Сунтар-Хаята в Якутии и на Чукотке. Большинство из этих видов имеют характерные замены в последовательностях ITS ядерной ДНК, за исключением *L. decolor* и *L. tenellum*, частично совпадающих по ITS. Обсуждается систематическое положение рода *Leptopterigynandrum*, описано новое семейство, Taxiphyllaceae, которое включает помимо этого рода *Taxiphyllum* и *Hondaella,* а также *Glossadelphus ogatae*. В качестве лектотипа рода *Taxiphyllum* выбран *Taxiphyllum taxirameum*.

KEYWORDS: flora, *Leptopterigynandrum*, molecular phylogeny, mosses, pleurocarpous mosses, Russia, Taxiphyllaceae, *Taxiphyllum*, taxonomy, typification

INTRODUCTION

The genus *Leptopterigynandrum* was established by Müller (1897) for a single simultaneously described species, *L. austro-alpinum* from South America. Later Fleischer (1923) transferred one East Asiatic species, *L. decolor,* to this genus, and after that a number of species from China and the Himalayas were either described or transferred to this genus by Brotherus (1924, 1925, 1929).

After a long gap in studies on this genus, Buck (1980) revealed it in North America, as he found that *Garysmithia bifurcata* Steere described shortly before by Steere (1977) from Alaska and Colorado is the same as the South American *L. austro-alpinum.*

These papers stimulated the search for this genus in Northern and Central Asia, successfully resulted in Russia, Chukotka (Abramova & Abramov, 1983), and Mongolia (Abramov & Abramova, 1983).

Later He (2005) undertook a worldwide revision, recognozong 10 species, but his suggestions were not accepted by some authors, for example by Weber (2008), *etc*. Ignatov *et al*. (2006) included 3 species of the genus in Check-list of mosses of East Europe and North Asia basing on data of He (2005).

As the species of the genus are rather rare and at the same time quite variable, it was difficult to understand if the observed morphological variation is infraspecific or it marks species differentiation. However, recent advances in DNA studies provide a new powerful tool for solving such problems. Among others, the study of ITS sequences has helped already in species delimitation in a number of pleurocarpous moss genera: *Lindbergia* (Ignatova *et al.*, 2010), *Brachythecium* (Ignatov & Milyutina, 2010), *Sciuro-hypnum (*Hedenäs *et al*., 2012)*, Thuidium* (Czernyadjeva *et al.*, 2006), *etc*. Therefore, we also applied this method to the genus *Leptopterigynandrum*.

MATERIAL AND METHODS

Morphological studies were based on collections from LE, MW, MHA, SASY. Molecular studies included the sequencing of nr ITS1-2 region. Specimens of *Leptopterigynandrym*, mainly from Russia and few from Mongolia and North America, were studied. Laboratory protocol was essentially the same as in some of our previous

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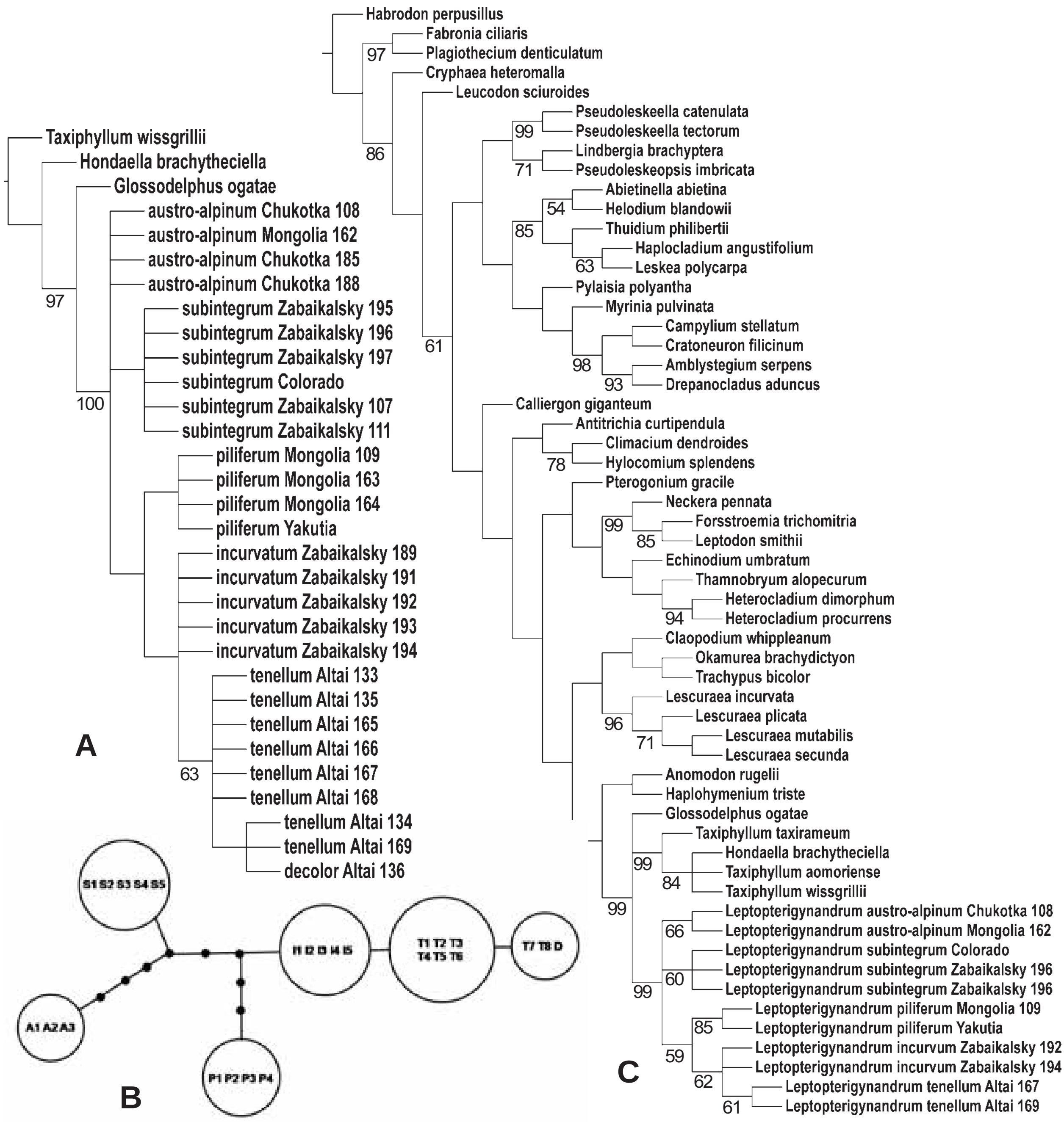


Fig. 1. A: strict consensus of 21 shortest trees found in ratchet MP analysis based on nr ITS1-2*;* support values >50% calculated by 1000 iterations in Nona, are indicated above branches. B: haplotype network for *Leptopterigynandrum* species. Species are abbreviated as: A – *austro-alpinum*; I – *incurvum*; D – decolor; P – *piliferum*; S – *subintegrum*; T – *tenellum* (T7-8 specimens are from Altai 134 &169, cf. also Fig. 1A). C: strict consensus of 4 shortest trees found in ratchet MP analysis based on nr ITS1-2*;* support values >50% calculated by 1000 iterations in Nona, are indicated above branches.

analyses (*e.g.* Gardiner *et al.*, 2005). Sequences were aligned manually in Bioedit (Hall, 1999). Maximum parsimony analysis was done with Nona (Goloboff, 1994) within the Winclada (Nixon, 1999a) shell. A multi-ratchet option was used (Nixon, 1999b). Jackknifing with 1000 replications including was performed with Nona within the Winclada shell.

First analysis addressed immediately *Leptopterigynandrum*, it included all its sequenced specimens. The tree was rooted on *Taxiphyllum,* which was found to be rather closely related to *Leptopterygynandrum* from previous analyses.

Second analysis included a broader outgroup taxa selection in order to find out the familial placement of the genus. Sequences of *Leptopterygynandrum* species were analyzed together with the data from the previous analysis of pleurocarps (Ignatov *et al.*, 2007). This previous set was reduced, so most taxa found in distant clades were excluded. Specimen vouchers and GenBank accessions are in Appendix 1.

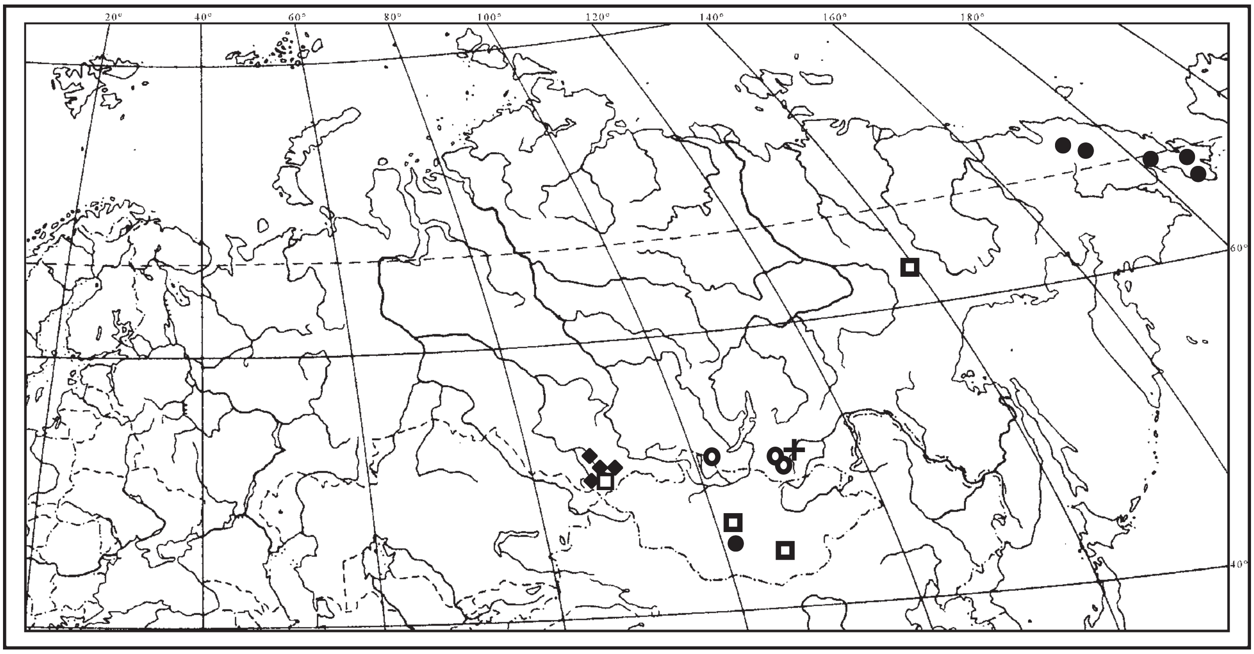


Fig. 2. Distribution of *Leptopterigynandrum* species in Russia (sequenced Mongolian specimens are also mapped). ● – *L. austro-alpinum*; □ – *L. decolor*; ✚ – *L. incurvatum*.; ◘ – *L. piliferum*; ⭘ – *L. subintegrum*; ◆ – *L. tenellum*.

Haplotype network analysis was performed in TCS 1.21 (Clement *et al*., 2000), with gap coding as a single event irrespective of their length with connection limit at 9 steps (95%).

Results

The genus *Leptopterigynandrum* was resolved as monophyletic in both analyses (Fig. 1A, C), in both cases with a high jackknife support, 100 and 99, respectively.

However, clades of individual species got no sufficient support. Their better differentiantion can be shown in TCS haplotype network (Fig. 1B).

The broader analysis revealed a high support for some familes or family groups: 85 for the Thuidiaceae+ Leskeaceae; 98 for Amblystegiaceae, 99 for Neckeraceae, 96 for Pseudoleskeaceae, and 99 for the clade formed by *Glossadelphus ogatae*, *Taxiphyllum*, *Hondaella* (which appeared nested within *Taxiphyllum*), and *Leptopterigynandrum*. Within the latter clade, the polytomy inculdes *Leptopterigynandrum* clade (support 98), *Taxiphyllum*+ *Hoondaella* clade (99), and *Glossadelphus ogatae.*

Discussion

The differences between species were found not to be big, but several substitutions usually provided a unique profile that appeared quite congruent with both morphology and distribution of species. This approach supports the narrow species concept suggested by He (2005). Poorly developed specimens whose affinity looks controversial from morphology only, can always be attributed to the "cores" formed by well-developed, "typical" phenotypes. Thus, as much as six species can be recognized in Russia.

Arguments in favor of species recognition

As the sampling covers mostly the territory of Russia only, and considering character deficit in morphology, the identity of Russian plants with those growing in type localities in Himalayn region or in South America still requires additional checking. At the same time, at least in two studied species, *L. austro-alpinum* and *L. subintegrum*, DNA sequences exhibit almost no variation between specimens from localities distant by more than 5000 km.

The strong geographical patterning might raise a suspect in clinal infraspecific variation. However, TCS analysis shows that morphologically most similar *L. subintegrum* and *L. tenellum* are not the closest, while *L. incurvatum*, one of the most distinct in morphology, differs from *L. tenellum* in a single substituion. In some groups of pleurocarps, however, one substitution in ITS may be stable and sharply demilit species almost throughout Holarctic (Hedenäs *et al*., 2012; Ignatov & Milyutina, 2010).

Leptopterigynandrum Müll. Hal., Hedwigia 36: 114. 1897.

Plants in loose interwolven mats, greyish- to brownish green, moderately glossy. Stem procumbent, irregularly to moderately regularly pinnate, densely terete foliate, all-sided to somewhat homomallous, central strand present, but often weak; proximal branch leaves lanceolate to ovate; axillary hairs 6-8-celled, including 2 basal colored cells. Leaves imbricate-appressed when dry, erect to spreading when moist, broadly to narrowly ovate-lanceolate, longly and rather abruptly acuminate, rounded to base, inconspicously decurrent; margin plane or narrowly recurved at leaf base, entire to weakly serrulate; costa double or more commonly forked, short to occasionally exceeding half upleaf; laminal cells moderately thick-walled, short rhomboidal-elongate, in extensive alar areas quadrate to transversely rectangular, at apex sometimes uniseriate, thus making leaf piliferous; cell surface at both sides of leaf

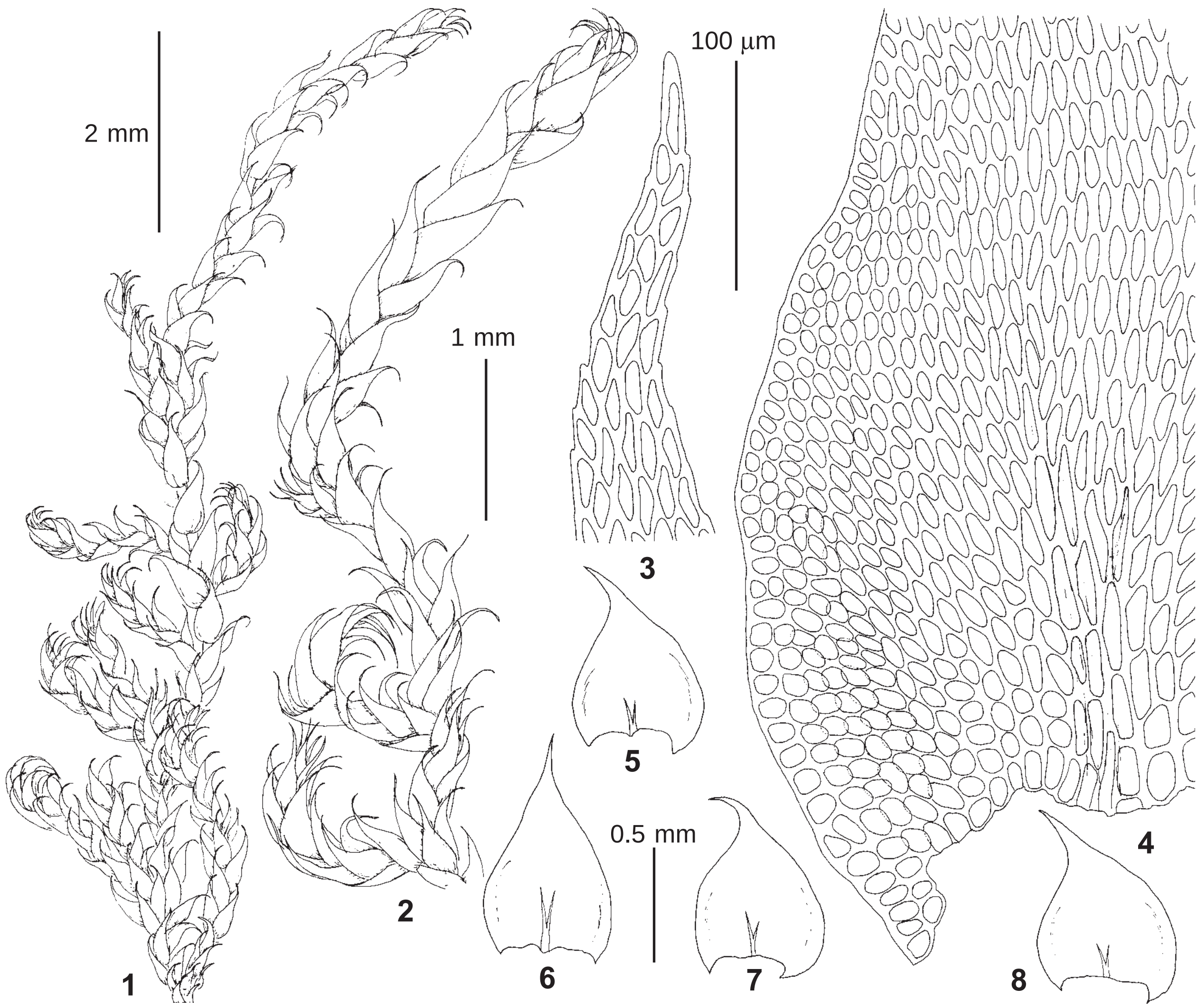


Fig. 3. *Leptopterigynandrum incurvatum* Broth. (from: Russia, Zabaikalsky Territory, *Afonina #A3010*, LE): 1-2 – habit, dry; 3 – upper laminal cells; 4 – median and basal laminal cells; 5-8 – leaves. Scale bars: 2 mm for 1; 1 mm for 2; 0.5 mm for 5-8; 100 μm for 3-4.

rough due to verrucose cuticular papillae. Dioicous. Perichaetial leaves with oblong basal part, enlarged after fertilization, with double costa or ecostate. Seta long, smooth. Capsule erect to suberect. Peristome double, well developed, although endostome segments slightly shorter than exostome teeth, narrow, cilia absent. Annulus weakly differentiated, separated by fragments. Operculum conic to shortly rostrate. Spores small, 14-23 μm.

Holotype: *L. austro-alpinum* Müll. Hal.

Ca. 10 species are known in mountain Pacific regions of North and South America and in East Asia.

KEY TO SPECIES IDENTIFICATION

1. Leafy stems 0.5-0.8 mm wide when dry; leaves (0.9-) 1.0-1.3 mm long .... *L. austro-alpinum*
— Leafy stems 0.2-0.4(-0.5) mm wide when dry; most leaves less than 1.0 mm long 2
2. Branches and ends of stems curved to circinate; leaves distinctly falcate-secund; laminal cell lumens 25-30×6-8 μm .... *L. incurvatum*
— Branches and ends of stems not regularly curved; leaves straight or asymmetric, occasionally slightly one-sidedly turned; laminal cell lumens wider, or, if 6-8 μm wide, then lumens longer, 30-40 μm long . 3
3. Leaves shortly acuminate, uniseriate apex usually 1, rarely 2 cells long 4
— Leaves ± longly acuminate, uniseriate apex in many leaves > 2 cells long 5
4. Shoots with leaves usually 0.25-0.3(-0.4) mm wide; leaves mostly 0.6-0.7 mm long, with ovate basal part; sporophytes unknown .... *L. subintegrum*
— Shoots with leaves usually 04-0.5 mm wide; leaves 0.6-0.8(-1.0) mm long, with rounded-ovate to cordate basal part; sporophytes occasionally present ... .*L. decolor*
5. Uniseriate leaf apical part 3-7(-10) cells long; leaves from rounded-ovate base suddenly acuminate, 0.5-0.6 mm wide; leaf length/width ratio 1.6-1.8 .... *L. piliferum*

— Uniseriate leaf apical part 2-3 cells long; leaves variable in shape, from narrowly or widely ovate base ± gradually acuminate, 0.3-0.5 mm wide; leaf length/width ratio 1.6-2.3 .... *L. tenellum*

Variation of diagnostic characters observed in the material from Russia is summarized in Table 1.

1. **Leptopterigynandrum incurvatum** Broth., Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl., Abt. 1, 133: 577. 1924. Figs. 2-3.

Plants medium-sized, in compact or loose mats, green or yellowish green, not glossy. Stems 1-3 cm long, (0.3-) 0.4-0.5 mm wide with leaves, irregularly to subpinnately branched, stem and branches distinctly curved to circinate. Main stem leaves (0.6-)0.7-1.0[-1.3]×(0.4-)0.5-0.7 mm, with length/width ratio 1.4-1.6, erect-spreading and one-sidedly turned when moist, imbricate and falcate-secund when dry, often asymmetric, moderately concave, from ovate or rounded-ovate and occasionally widely decurrent base suddenly acuminate, acumen ca. 1/4–1/3 the leaf length; costa double or furcate near leaf base, to 1/5–1/4 the leaf length; margins plane, serrulate near apex, entire in basal and middle part of leaf; leaf cells moderately thick-walled, rhomboidal to elongate-rhomboidal in mid-leaf, laminal cell lumens (20-)25-30(-35)×6-7(-8) μm, lumens with rounded ends, verrucose cuticular papillae fine, occasionally hardly seen, alar cells in 4-7 rows toward costa quadrate and transversely rectangular.

Dioicous. Both male and female plants are present in collections from Russia. Sporophyte unknown in Russia (its description is given by He, 2005).

He (2005) describes specimens of *L. incurvatum* from China as having considerably larger leaves, 1.3-1.5×0.5-0.7 mm. However, in other diagnostic characters of gametophyte, *i.e.* circinate branches, falcate-secund leaves, narrow cell lumens, specimens from Russia (Zabaikalsky Territory) fit the description of this species.

Specimens examined: RUSSIA: Zabaikalsky Territory, Sokhondinsky Biosphere Reserve: Enda River, Kukhe-Baytsa Creek, 49°28'17"N, 110°51'58"E, 1214 m alt., *Afonina #7511* (LE); Enda River, 49°26'N, 110°53'E, 1239 m alt., *Czernyadjeva #56-11* (LE). See also Appendix 1.

Distribution and ecology. The species was known only from Central and SW China (Sichuan, Yunnan, Xizang), growing at 2800-4800 m alt. on rock surfaces and tree trunks (He, 2005). In Russia, it was revealed it one locality in a rather dry area east from the Baikal (represented by numerous collections), where it grows at 1100-1280 m alt., on rocks in mesic to rather xeric conditions, on open rocky slopes with steppe vegetation and in a birch forest.

Differentiation. Curved to circinate branches and stem tips, usually falcate-secund leaves and comparatively small mid-leaf cell lumens, mostly 20-30×6-7 μm, with rounded ends of lumen separate *L. incurvatum* from other species known in Russia. Slender forms of *L. incurvatum* with longer acuminate apical parts of leaf and longer uniseriate apex, 2-4 cells long, were seen in collections from Zabaikalsky Territory; they are similar habitually to some collections of *L. tenellum* from the Altai. The latter species has also mid-leaf cells with rather narrow lumens, 6-8 μm wide and comparatively thick cell walls. In such cases more or less curved branches and short mid-leaf cell lumens, 20-30 μm long in most cells, separate *L. incurvatum* from *L. tenellum*, which has mostly straight branches and usually longer cell lumens, 25-40 μm long.

2. **Leptopterigynandrum austro-alpinum** Müll. Hal., Hedwigia 36: 114. 1897. Figs. 2, 4.

Plants medium-sized, in compact tangled mats, yellowish green, greyish green or brownish, not glossy. Stems 1-4 cm long, 0.5-0.7(-0.8) mm wide with leaves, irregularly branched, straight or slightly curved in distalmost part. Main stem leaves (0.9-)1.0-1.3×0.5-0.6(-0.7) mm, with length/width ratio 2.1-2.4, erect-spreading to spreading when moist, imbricate when dry, often with recurved apices, occasionally slightly one-sidedly turned, symmetric or asymmetric, occasionally falcate, moderately concave, from oblong-ovate base long acuminate, acumen ca. 1/3 the leaf length, with uniseriate end of 1-2(-3) cells; costa furcate well above leaf base, to 1/3-1/2 the leaf length, rarely longer; margins plane or narrowly recurved at leaf base, serrulate near apex, entire in basal and middle part of leaf; leaf cells with moderately thickened walls, rhomboidal to elongate-rhomboidal in mid-leaf, laminal cell lumens 30-40(-45)×(7-)8-10(-11) μm, lumens with ± angular ends, verrucose cuticular papillae conspicouos, cells of acumen elongate-rhomboidal, alar cells in 6-9 rows toward costa transversely rectangular and quadrate.

Table 1. Diagnostic morphological characters of *Leptopterigynandrum* species.

species	width of leafy stem (dry)	leaf length, mm	leaf width, mm	mid-leaf cell lumen length, μm	mid-leaf cell lumen width, μm	number of cells of uniseriate apex
L. austro-alpinim	0.5-0.7(-0.8)	(0.9-)1.0-1.3	(0.4-)0.5-0.65(-0.7)	(25-)30-45	8-10(-11)	1-2(-3)
L. incurvatum	0.3-0.5	0.7-1.0	0.5-0.6(-0.7)	20-30	6-7(-8)	1-2
L. subintegrum	0.25-0.3(-0.4)	0.6-0.7(-0.8)	0.3-0.5(-0.55)	20-30(-35)	(7-)8-9	1
L. decolor	0.4-0.5	0.6-0.8(1.0)	0.45-0.6(0.7)	25-30(-35)	8-9	1-2
L. tenellum	0.2-0.3(-0.4)	0.5-0.9(-1.2)	0.3-0.5(-0.55)	25-40	6-8	(1-)2-3
L. piliferum	0.4(-0.5)	0.8-0.9	0.5-0.6	20-25	6-9	3-7(-10)

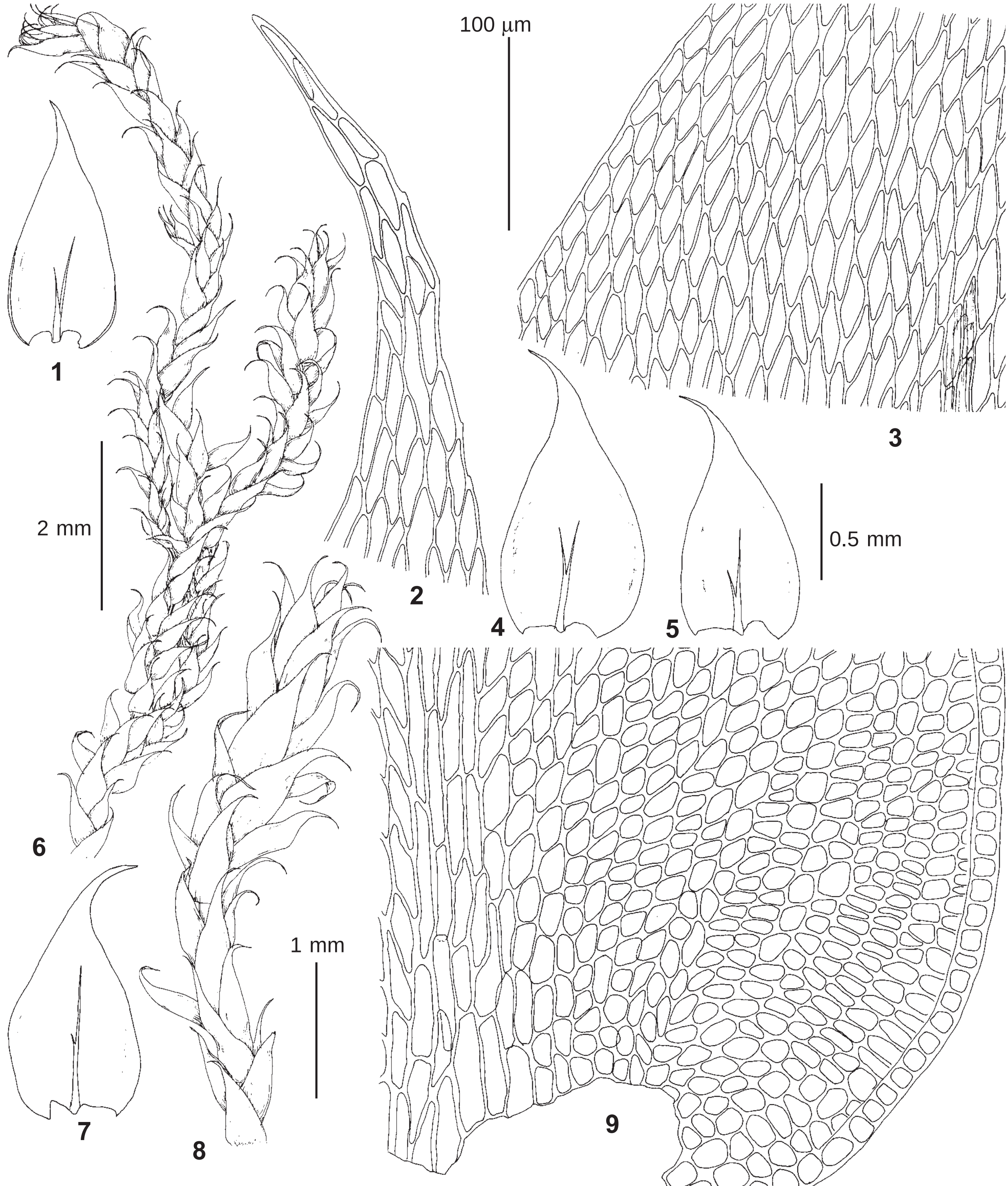


Fig. 4. *Leptopterigynandrum austro-alpinum* Müll. Hal. (from: Russia, Chukotka, 17.VII.1981, *Afonina s.n.*, LE): 1, 4-5, 7 – leaves; 2 – upper laminal cells; 3 – median laminal cells; 6, 8 – habit, dry; 9 – basal laminal cells. Scale bars: 2 mm for 6; 1 mm for 8; 0.5 mm for 1, 4-5, 7; 100 μm for 2-3, 9.

Sporophyte unknown in Russia (its description is given by He, 2005). Specimens from Chukotka without gametangia.

He (2005) reports for *L. austro-alpinum* smaller size of median laminal cells, 28-32×7-8 μm based on lectotype specimen; moreover, Wu *et al.* (2002) use smaller size of lamina cells as a character differentiating *L. austro-alpinum* from *L. incurvatum* for Chinese material. Plants from Chukotka have larger median laminal cells, with lumen mostly 30-40×9-10 μm. However, the largest plant size, leafy stems 05-0.7 mm wide, costa furcate well above leaf base and moderately thickened cell walls

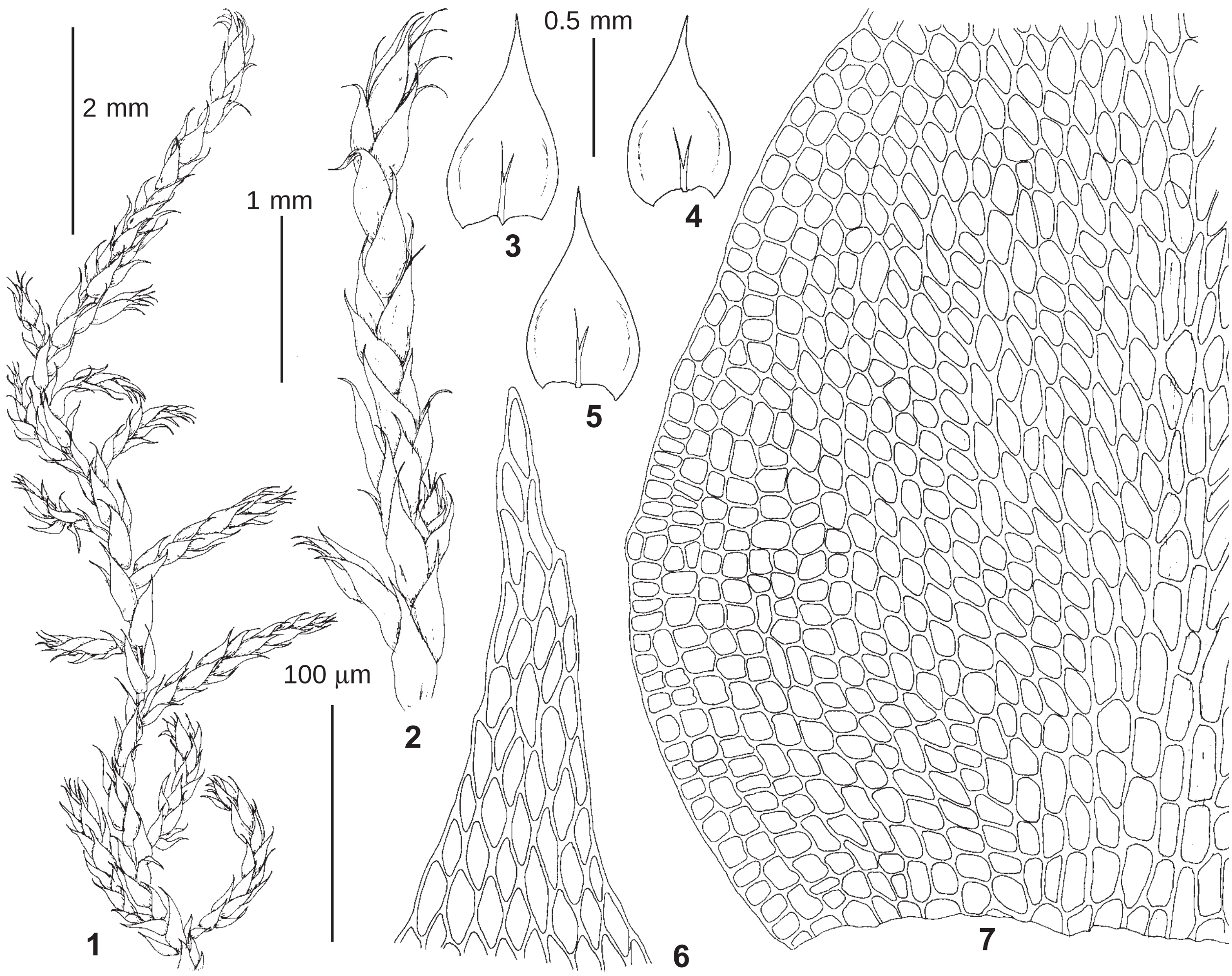


Fig. 5. *Leptopterigynandrum subintegrum* Broth. (from: Russia, Zabaikalsky Territory, *Afonina #08307*, LE): 1-2 – habit, dry; 3-5 – leaves; 6 – upper laminal cells; 7 – median and basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 2; 0.5 mm for 3-5; 100 µm for 6-7.

making lumens angular, suggest their placement into *L. austro-alpinum*.

He (2005) lists several specimens from Russia, including Chukotka, the Altai and Eastern Sayan Mts, and Sakhalin. However, the specimen from the Altai (the Chulcha River, Ignatov s.n., *exsiccatae* 194) is characterized by slender plants, with leafy stems ca. 0.2 mm wide, leaves 0.5-0.6 mm long and 0.35-0.45 mm wide, and cell lumens 20-30×7-8 µm. It does not differ in diagnostic characters from other specimens from the Altai used in the molecular analysis and should be referred to *L. tenellum*. Plants of the specimen from the Eastern Sayan (27.VII.1961, Bardunov s.n.) are slightly larger, with leafy stems ca. 0.3 mm wide, but its stem leaves are comparatively small, 0.6-0.7 mm long and 0.45-0.55 mm wide, with cell lumens ca. 20-39×7-9 µm. It most likely belongs to *L. subintegrum* which grows rather close to the Eastern Sayan Mts, in Zabaikalsky Territory. We were unable to study a specimen from Sakhalin; this record seems to be doubtful.

Afonina (2009) reported *L. austro-alpinum* from Sokhondinsky Biosphere Reserve (Zabaikalsky Territory). According to the present study, this record should be referred to *L. subintegrum*.

Specimens examined: RUSSIA: Chukotka: Anadyr River basin: Baranje Lake, 6.VIII.1980, *Afonina s.n.* (LE); upper course of Tanyurer River, Golubaya Creek, 17.VII.1981, *Afonina s.n.* (LE). MONGOLIA: Bayan-Hongor Province, Bogd Somon, Ikh-Bogd Mt., 45°00'N, 100°20'E, 3100 m alt., *Ignatov #01-412* (MHA).

Distribution and ecology. *L. austro-alpinum* is known as having disjunct distribution from mountains of South America (Bolivia, Peru, Argentina, Chile) and Alaska in North America to Asiatic Russia, Mongolia, and China (He, 2005). Our study confirms presence of the species in Chukotka. It grows on rock surface of rock outcrops on rather dry steep slopes and on rocky slopes.

Differentiation. *L. austro-alpinum* is the largest species in the genus, with leaves mostly 1.0-1.2 mm long and 05-0.6(-0.7) mm wide, as well as with larger laminal cells, the lumen being mostly 30-40×9-10 µm and with conspicuous angulose-rhombic shape. Leaves of *L. incurvatum* often reach also 1.0 mm long and 0.7 mm wide, but they are less oblong, with length/width ratio 1.4-1.6 vs. 2.1-2.4 in *L. austro-alpinum*; in addition, *L. incurvatum* has much smaller mid-leaf cell lumens, mostly 25-30×6-7 µm. Differences from *L. decolor* and *L. subintegrum* are discussed under these species.

3. **Leptopterigynandrum subintegrum** (Mitt.) Broth., Nat. Pflanzenfam. (ed. 2), 11: 309. 1925. Figs. 2, 5.

Plants small to medium-sized, in loose or compact mats, greyish green to yellowish green, not glossy. Stems 1-2 cm long, 0.2-0.3(-0.4) mm wide with leaves, irregularly to subpinnately branched, straight, occasionally with numerous short branchlets, branches julaceous. Main stem leaves erect-spreading to spreading when moist, imbricate when dry, slightly concave, 0.6-0.8×(0.3)0.4-0.5(-0.55) mm, straight, symmetric, from ovate or widely ovate base rather gradually or abtuptly acuminate, acumen ca. 1/3 the leaf length, with uniseriate end of 1 cell; costa comparatively strong, furcate well above leaf base, to 1/3-1/2 the leaf length; margins plane, entire or weakly serrulate near apex; leaf cells with moderately thickened walls, rhomboidal in mid-leaf, laminal cell lumens 20-30(-35)×(7-)8-9(-10) μm, lumens with angular ends, verrucose cuticular papillae fine to conspicouos, cells of acumen elongate-rhomboidal, alar cells in 6-10 rows toward costa transversely rectangular and quadrate.

Sporophyte unknown. Gametangia not seen.

Specimens examined: RUSSIA: Zabaikalsky Territory: Sokhondinsky Biosphere Reserve, Enda River, Schanarichi Creek, 49°27'50"N, 110°52'11"E, 1214 m alt., *Afonina #8111* (LE); National Park "Alkhanai", Ubzholgoe River, 50°50'N, 113°22 'E, 1048 m alt., *Afonina #08307* (LE); Eastern Sayan, Udinsky Mt. Range, Bolshoj Khongorok Creek, 1300 m alt., 27.VII.1961, *Bardunov s.n.* (LE).

Distribution and ecology. In Eurasia, *L. subintegrum* is known from SW China (Quinghai, Sichuan, Yunnan, Xizang), India, Mongolia. Its records from the Altai Mts in Russia (He, 2005) belong to *L. tenellum*, however, our study revealed new localities in the Baikal area. Its disjunct localities are known also from South Africa, South America (Bolivia), and North America (Colorado, Alaska). According to literature data, it grows on tree trunks, rotten wood and rocks (He, 2005). Russian collections were made from rock outcrops, including limestone ones, and from boulders on slope to a creek.

Differentiation. Comparatively thin-walled cells with lumens 8-10 μm wide and strong costa branching well above leaf base make *L. subintegrum* similar to some extent to *L. austro-alpinum*. However, plants of the former species are distinctly smaller, with leafy shoots ca. 0.2-0.3(-0.3) mm wide vs. 0.4-0.7 mm wide in the latter one. In addition, leaves of *L. austro-alpinum* are usually larger, 1.0-1.3×0.5-0.8 mm, while in Russian collections of *L. subintegrum* they are mostly 0.6-0.7×0.4-0.5 mm. Their length/width ratio is also different, 2.1-2/4 in *L. austro-alpinum* and 1.2-1.7(1.9) in *L. subintegrum*. He (2005) and Wu (2002) describe cells of *L. austro-alpinum* as having smaller size then those of *L. subintegrum*. At the same time, in collections from Russia, larger size of plants and leaves in specimens of *L. austro-alpinum* from Chukotka correlate with longer cells, *i.e.* lumens 30-50×8-10 μm vs. mostly 20-30×8-9 μm in *L. subintegrum*. Numerous short branchlets also separate *L. subintegrum* from *L. austro-alpinum* which has irregulary branching shoots with comparatively long branches.

It is rather difficult to separate *L. subintegrum* from *L. decolor*. These species share shortly acuminate leaves with comparatively short and wide lumens of mid-leaf cells. They can be recognized by width of leafy shoots, 0.25-0.3(-0.4) mm in *L. subintegrum* vs. 0.4-0.5 mm in *L. decolor*, and shape of leaf base, ovate vs. rounded-ovate or cordate. In populations from Russia, plants of *L. subintegrum* have comparatively short leaves, 0.6-0.7, rarely 0.8 mm long, while leaves of *L. decolor* occasionally reach 1.0 mm long (being mostly 0.6-0.8 mm long).

Differences from *L. tenellum* are discussed under this species.

4. **Leptopterigynandrum decolor** (Mitt.) Fleisch., Musci Buitenzorg 4: 1496. 1923. Figs. 2, 6.

Plants medium-sized, in compact mats, pale green to green, not glossy. Stems 1.5-3.0 cm long, 0.4-0.5 mm wide with leaves, irregularly to subpinnately branched, branches numerous, julaceous. Main stem leaves erecto-patent when moist, imbricate when dry, concave, 0.6-0.8(-1.0)×0.45-0.6 (-0.7) mm, straight or one-sidedly turned, symmetric or asymmetric, from widely ovate or cordate base suddenly

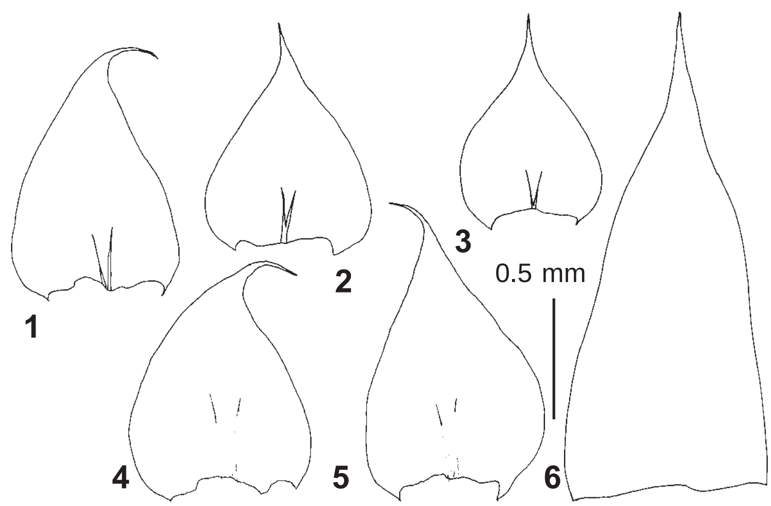
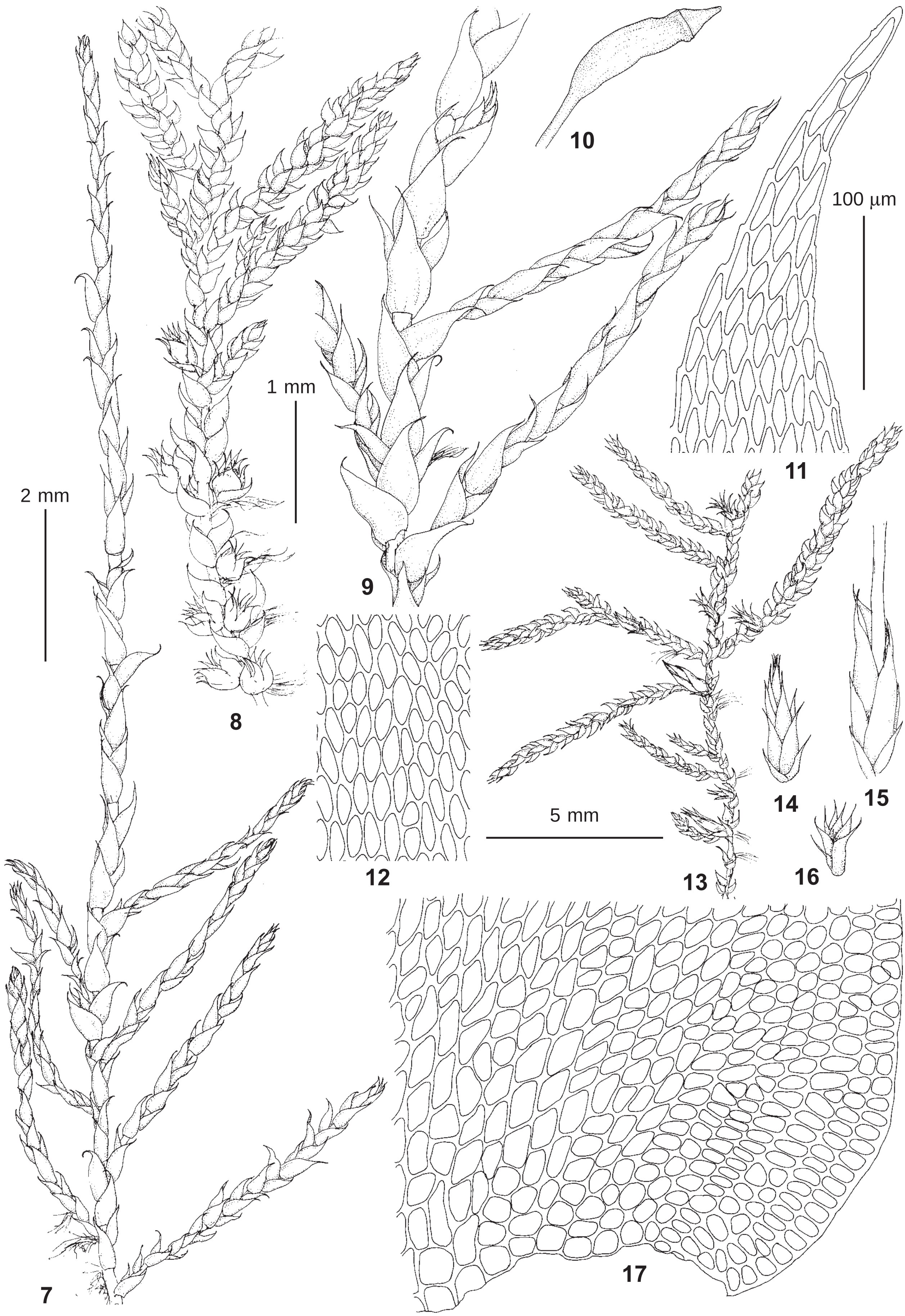


Fig. 6. *Leptopterigynandrum decolor* (Mitt.) Fleisch. (from: Russia, Altai, *Ignatov #36/272*, MHA): 1-5 – leaves; 6 – perichaetial leaf (bottom of this page).

Opposite page: 7, 9 – habit, dry, 8, 13 – habit, wet; 10 – capsule, wet; 11 – upper laminal cells; 12 – median laminal cells; 14-15 – perichaetia; 16 – perigonium; 17 – basal laminal cells. Scale bars: 5 mm for 13; 2 mm for 7-8, 10, 14-16; 1 mm for 9; 0.5 mm for 1-6; 100 μm for 11-12, 17.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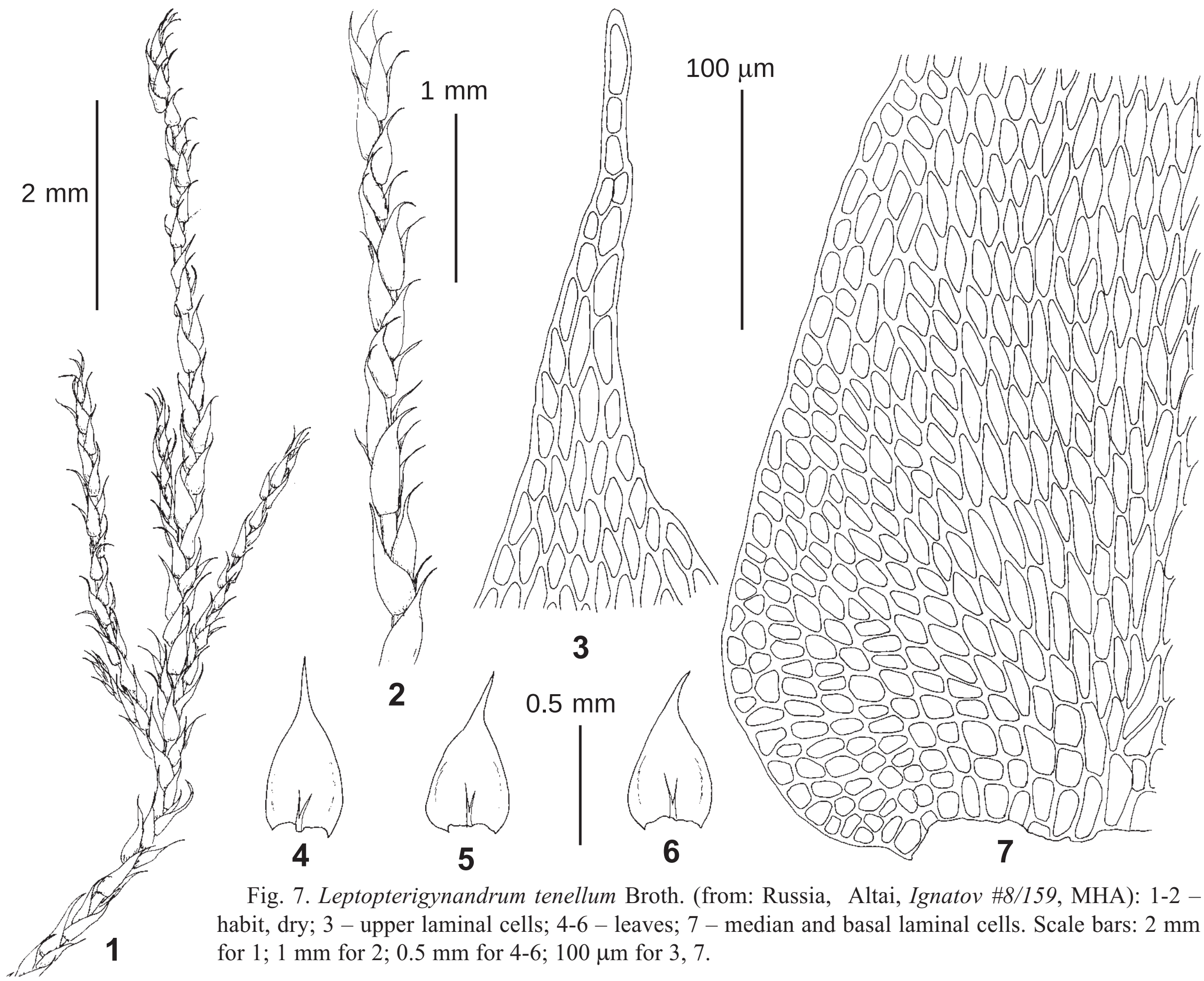

Fig. 7. *Leptopterigynandrum tenellum* Broth. (from: Russia, Altai, *Ignatov #8/159*, MHA): 1-2 – habit, dry; 3 – upper laminal cells; 4-6 – leaves; 7 – median and basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 2; 0.5 mm for 4-6; 100 µm for 3, 7.

shortly acuminate, acumen ca. 1/3 the leaf length, with uniseriate end of 1-2 cells; costa short, double or furcate near leaf base, to 1/5 the leaf length; margins plane, minutely serrulate near apex, entire below; leaf cells with moderately thickened walls, rhomboidal in mid-leaf, laminal cell lumens 25-35×8-9 µm, cells of acumen elongate-rhomboidal, alar cells in 4-7 rows toward costa transversely rectangular and quadrate.

Immature sporophytes present in several collections. Perichaetial leaves erect, concave, not plicate, 1.5-1.7 mm long and 0.5-0.6 mm wide at base, from oblong base gradually acuminate, margins weakly serrulate near apex, costa absent or indistinct. Seta 8-9 mm. Capsule erect to weakly inclined, urn cylindrical, ca. 2 mm long. Exostome teeth inserted well below urn mouth, narrow, 350-370 µm long, finely papillose throughout. Endostome basal membrane ca. 100 µm high, segments short, cilia absent. Spores 12-15 µm, finely papillose. Operculum conic to low conic, with short, erect or curved beak. Calyptrae not seen.

Sequenced specimen of *L. decolor* belongs in ITS to the same haplotype with two specimens of *L. tenellum,* which represent quite typical for the species slender plants with narrow leaves (Altai Mts, Ignatov #8/152 & Zolotukhin, 28.VI.1990). However, the former specimen is distinct from the latter two in larger size of plants, wider leaves with cordate basal part and wider lumens of mid-leaf cells. In leaf shape and cell width, as well as in perichaetial leaves and sporophyte characters, it fits the description of *L. decolor*; at the same time, its leaves are shorter than it is indicated by He (2005), 0.6-1.0 mm vs. 1.2-1.4 mm long, which corresponds with shorter lumens of mid-leaf cells, 25-35 µm vs. 35-40 µm long. It can be explained by extremely dry conditions of its locality in the Altai, and its northern position in comparison with Chinese and Indian localities.

Specimens examined: RUSSIA: **Altai Republic**, Bogoyash River upper basin, Tokpak Creek in middle course, *Ignatov ##36/270, 36/271, 36/272, 36/277* (MHA).

Distribution and ecology.The species was known from India (Sikkim) and China (Sichuan), where it grows on rocks at 3000-3900 m alt. In Russia, it was collected in one locality in the Altai Mts, at 1950 m, on side surfaces of boulders in a dry open larch forest on a slope to the creek.

Differentiation. Rather wide shoots of *L. decolor*, 0.4-0.5 mm with leaves, make it similar to *L. austro-alpinum* and *L. incurvatum*. However, *L. austro-alpinum* differs in longer leaves, 1.0-1.3 mm long, with length/width ratio 2.1-2.4 vs. 1.3-1.4 in *L. decolor*, and longer lumens of mid-leaf cells, 30-45 µm vs. 25-35 µm long. *L. incurvatum* can be separated by regularly curved branches and narrower cell lumens, 6-7 μm wide. Differences from *L. subintegrum* and *L. tenellum* are discussed under these species.

5. **Leptopterigynandrum tenellum** Broth., Symb. Sin. 4: 96. 4 f. 1. 1929. Figs. 2, 7.

Plants slender, in loose mats, green to yellowish green, not or slightly glossy. Stems 1.5-3.0 cm long, 0.2-0.3(-0.4) mm wide with leaves, irregularly and remotedly branched, occasionally subpinnately branched, straight, branches subjulaceous. Main stem leaves erectopatent when moist, loosely appressed when dry, often with recurved tips, slightly concave, (0.5-)0.6-0.9(-1.2)×0.25-0.45(-0.55) mm, straight, symmetric or slightly asymmetric, variable in shape, from narrowly or widely ovate base slendery acuminate, acumen ca. 1/3 the leaf length, with uniseriate end of (1-)2-3 cells; costa short, double or furcate near leaf base, to 1/5 the leaf length; margins plane, entire or minutely serrulate near apex; leaf cells with moderately thickened walls, rhomboidal in mid-leaf, laminal cell lumens 25-40×6-8 μm, cells of acumen elongate-rhomboidal, alar cells in 4-7 rows toward costa transversely rectangular and quadrate.

Sporophytes unknown.

Type specimen of *L. tenellum* is illustrated by He (2005). It has very narrow and long leaves, to 1 mm long and 0.2-0.25 mm wide. Such plants were never seen in collections from Russia. Specimens identified by Si He as *L. tenellum* (Altai, Ignatov ##0/681 & 8/152), have leaves 0.6-0.95 mm long and 0.25-0.4 mm wide. Numerous collections from the Altai represent great variability in leaf length and width and leaf length/width ratio (1.4-2.2), but they share comparatively narrow cell lumens, 6-7(-8) μm wide, slender habit of plants and usually rather long uniseriate apiculus, 2-3 cells in many leaves. They are represented by two haplotypes in ITS that differ from each other in one substitution. One of these haplotypes is shared also with *L. decolor*, which, however, is distinct in morphology (see comments under this species).

Specimens examined: **Altai Republic** (altitude in meter; # – collector number of Ignatov; specimens in MHA): Tabozhok Peak, 2700 m, # 31/221a; Yakhansoru Lake, 1870 m, 28.VI.1990 *Zolotukhin*; same, 1940 m, 26.VI.1990 *Zolotukhin*; Yazula, 1600 m, # 0/1089; same, 1700 m, # 0/1092; Berekhtuyaryk, 1640 m, # 0/1094; Kukol, 1750 m, # 0/1097; same, 1850 m, # 0/1095; same, 2000 m, # 0/680; Kayakkatuyarykskij Creek, 1850 m # 8/159; same, 1860 m, # 8/30; same, 1900 m, # 8/152; same, 1950 m, # 8/150, # 8/299, # 8/322, # 8/325; Kobiguayuk Creek, 2050 m, # 0/1096, # 0/681; same, 2200 m, # 0/143; same, 2300 m, # 0/1090, # 0/1091; same, 2400 m, # 0/1093; Kokorya Creek, 2100 m, *Ignatov & Ignatova # 0/2066a*, # 32/33, # 33/14, # 33/15; Tabozhok Creek, 2250 m, *Ignatov & Ignatova* # 30/79; Chulcha River, 1000 m, # 9/28, # 9/3, # 9/46; same, 1100 m, # 9/169, # 9/66; same, # 9/132; same, 750 m, *Ignatov & Ignatova #12-1*.

Distribution and ecology.The species is rather common in the Altai Mts, from 750 to 2400 m alt., and known also from the Mongolian Altai and Khentei Region of Mongolia; type is from Sichuan. He (2005) recorded the species from Bolivia. However he also identified some Altaian collections as *L. subintegrum*, while according to DNA, all Altaian collections are subidentical and different from plants from Transbaikalia and Colorado in North America. Thus we consider records of *L. subintegrum* from the Altai to be *L. tenellum*. The species usually grows on moderately shaded vertical walls of big rocks in the forest zone or shortly above the timber-line (the area where it was found at 2400 m has scattered forests to 2300 m).

Differentiation. The species has slender plants and leaves that are the narrowest in the genus, so in many collections all leaves are less than 0.3 mm wide. The species is closest to *L. subintegrum* which, however, has stiffer plants, slightly wider laminal cells and shorter branches.

Shoots of *L. decolor* are considerably wider, 0.4-0.5 mm vs. 0.25-0.3(-0.35) mm, and leaves differ in rounded-ovate or cordate basal part and shorter acumen, as well as wider cell lumens, 8-9 μm vs. 6-7(-8) μm.

6. **Leptopterigynandrum piliferum** S. He, J. Hattori Bot. Lab. 97: 22. f. 111–124. 2005. Figs. 2, 8.

Plants medium-sized, in loose mats, greyish green to green, not glossy. Stems 1-2(-3) cm long, 0.4-0.5 mm wide with leaves, irregularly to subpinnately branched, straight, branches subjulaceous. Main stem leaves erect-spreading when moist, loosely appressed when dry, slightly concave, 0.8-0.9[-1.3]×0.5-0.6 mm, straight, symmetric, from widely ovate base abruptly acuminate, acumen ca. 1/3 the leaf length, with uniseriate end of 3-7(-10) cells; costa short, double or furcate near leaf base, to 1/5-1/4 the leaf length; margins plane, entire; leaf cells comparatively thick-walled, rhomboidal in mid-leaf, laminal cell lumens 20-25×6-9 μm, lumens with rounded ends, verrucose cuticular papillae fine, cells of acumen elongate-rhomboidal to oblong, alar cells in 5-8 rows toward costa transversely rectangular and quadrate.

Sporophyte unknown in this species.

In the original description the species was characterized by a piliferous leaf apex, less julaceous foliage, and also a relatively regular branching. The piliferous leaves are indeed a conspicous character in well-developed plants, however in harsh environments of Mongolia this character is not always well expressed. We collected this species (as was confirmed from the ITS identity with the holotype of *L. piliferum*) in Mongolian Gobi Desert in one small *Betula* forest, highly isolated from any other places suitable for bryophyte, excepting unltraxeric ones (Ignatov *et al.*, 2004). We sequenced one specimen from rock and one from nearby growing *Betula microphylla* trunk, the latter exposed to stronger drought.

Specimens examined: RUSSIA: Yakutia, Suntar-Khayata, Kyurbellyakh, 19.VI.1991, *Ivanova s.n.* (MHA). MONGOLIA: 15.VIII.1975, *Tsegmed s.n.* (LE #2660, MHA); Gobi, Gurvan-Saikhan National Park, *Ignatov #01-435, 01-365* (MHA).

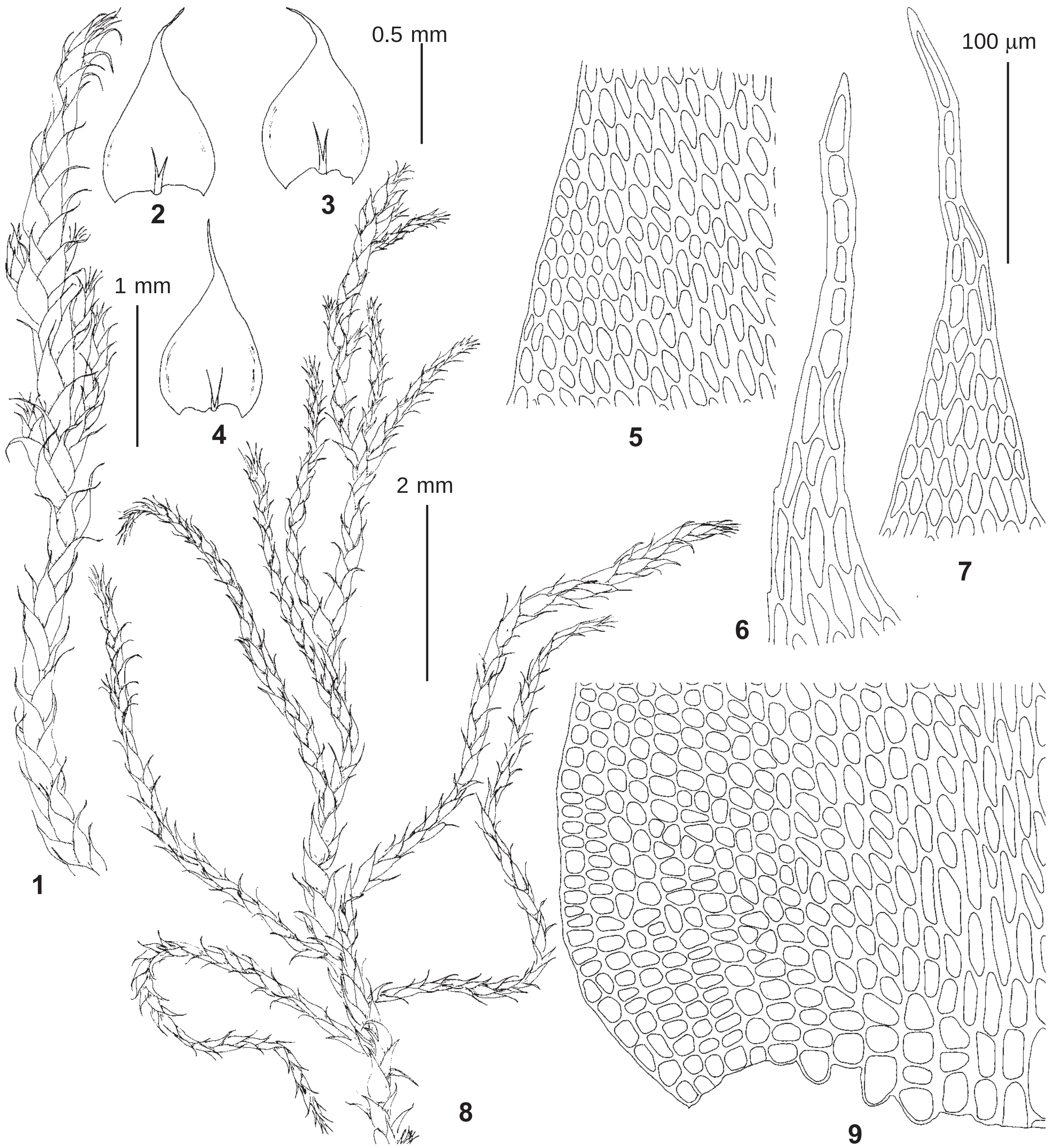

Fig. 8. *Leptopterigynandrum piliferum* S. He (from: Russia, Yakutia, Kyurbelyakh, 19.VI.1991 *Ivanova s.n.*, MHA): 1, 8 – habit, dry; 2-4 – leaves; 5 – median laminal cells; 6-7 – upper laminal cells; 9 – basal laminal cells. Scale bars: 1 mm for 1; 2 mm for 8; 0.5 mm for 2-4; 100 μm for 5-7, 9.

Distribution and ecology.The species was described from Khangai Region of Mongolia, and He (2005) reported it also from SW China (Sichuan). We found additional localities in the easternmost part of Gobi in Monglia, in Gurvan-Saikhan National Park, and a single collection in Russia, from Suntar-Khayata Range. It grows on rock surfaces and occasionally on tree trunks.

Differentiation. Typical forms of *L. piliferum* with long uniseriate apical part of leaf are easily separated from all other species of the genus. Plants with shorter leaf apices from harsh environments can be recognized by shoots with loosely appressed leaves, rounded-ovate leaf base and comparatively short and moderately thick-walled laminal cells.

Systematic position of *Leptopterigynandrum*

The genus *Leptopterigynandrum* was placed in the Thuidiaceae: Heterocladioideae (Brotherus, 1925), and later in the Leskeaceae (Buck & Goffinet, 2000), where it was retained by He (2005) and Goffinet *et al.* (2009). Recent molecular phylogenetic analyses have found *Lep-*

topterigynandrum in a quite unrelated position to this family and revealed its affinity to *Taxiphyllum* and *Glossadelphus ogatae* Broth. & Yasuda (Ignatov *et al.*, 2007; Troitsky *et al.*, 2008; Olsson *et al.*, 2009). Close relationship of *Taxiphyllum* and *Glossadelphus ogatae* was found by Tsubota *et al.*, 2004) and Arikawa *et al.* (2008) who also added to this group *Hondaella.*

Nuclear ITS analysis of a small set of pleurocarpous genera shown in Fig. 1C additionally illustrates the situation, and basing on all these results we propose segregation of the above mentioned taxa in the Taxiphyllaceae.

Taxiphyllaceae Ignatov, fam. nov.

Pleurocarpous mosses of medium size to robust, terrestrial, aquatic or epiphytic. Branch primordia of *Climacium*-type. Leaves ovate to lanceolate, obtuse, acute or acuminate. Laminal cells smooth or rough due to minute verrucose cuticular papillae, elongate to almost isodiametric. Costa double to short and forked. Mostly dioicous, rarely autoicous. Perichaetial leaves smooth. Seta long, smooth. Capsule inclined to horizontal with perfect hypnoid peristome or erect with somewhat reduced peristome; stomata round-pored.

Type genus: *Taxiphyllum* M. Fleisch., Musci Buitenzorg 4: 1434. 1922[1923]. Lectotype: *T. taxirameum* (Mitt.) M. Fleisch. (selected here).

The proposed lectotype is the first species discussed in the original description of the genus; it is a widespread tropical-temperate moss, described in many Asitic and American floras, resolved with other species of the genus in molecular phylogenetic analyses with high support (*e.g.* Fig. 1C).

Other genera included: *Hondaella, Leptopterigynandrum*. Also, *Glossadelphus ogatae* belongs to this family, but molecular phylogenetic analyses revealed the genus *Glossadelphus* to be polyphyletic, and *G. glossoides* (Bosch & Sande Lac.) M. Fleisch., one of possible lectotypes of the genus, was found quite unrelated to *G. ogatae*. So the systematics and nomenclature of species currently kept in *Glossadelphus* require futher study.

Leptopterigynandrum differs from *Taxiphyllum* in shorter leaf cells, straight capsule and slightly reduce peristome, which is a common trend along the transitoin from terrestrial to epiphytic growth (Huttunen *et al*., 2004), charactersitic for *Leptopterigynandrum* in southern regions.

ACKNOWLEDGEMENTS

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Appendix 1. Genbank accession numbers and voucher specimen data for *Leptopterigynandrum* speces.

L. austro-alpinum	Chukotka 1	Russia, Chukotka, 17.VII.1981, *Afonina s.n.* (LE)	KC121274
L. austro-alpinum	Chukotka 2	Russia, Chukotka, 2.VII.1980, *Afonina s.n.* (LE)	KC121275
L. austro-alpinum	Chukotka 3	Russia, Chukotka, Anadyr, 6.VIII.1980, *Afonina s.n.* (LE)	KC121276
L. austro-alpinum	Mongolia	Mongolia, Ikh-Bogd, 30.VII.2001, *Ignatov #01-412* (MHA)	KC121277
L. decolor	Altai 8	Russia, Altai, *Ignatov #36/272* (MHA)	KC121296
L. incurvum	Zabaikalsky 1	Russia, Zabaikalsky Territory, 10.VII.2010, *Afonina #A1210* (LE)	KC121284
L. incurvum	Zabaikalsky 2	Russia, Zabaikalsky Territory, 15.VII.2010, *Afonina #A3010a* (LE)	KC121285
L. incurvum	Zabaikalsky 3	Russia, Zabaikalsky Territory, 27.VIII.2010, *Afonina #A2010* (LE)	KC121286
L. incurvum	Zabaikalsky 4	Russia, Zabaikalsky Territory, 15.VII.2010, *Afonina #A3010b* (LE)	KC121287
L. incurvum	Zabaikalsky 5	Russia, Zabaikalsky Territory, 10.VII.2010, *Afonina #A1110* (LE)	KC121288
L. tenellum	Altai 1	Russia, Altai, *Ignatov #33/14* (MHA)	KC121289
L. piliferum	Mongolia 1	Mongolia, 15.VIII.1975, *Tsegmed s.n.* (MHA)	KC121298
L. piliferum	Mongolia 2	Mongolia, *Ignatov #01-435* (MHA)	KC121299
L. piliferum	Mongolia 3	Mongolia, *Ignatov # 01-365* (MHA)	KC121300
L. piliferum	Yakutia	Russia, Yakutia, Kyurbelyakh, 19.VI.1991 *Ivanova s.n.* (MHA)	KC121301
L. subintegrum	Zabaikalsky 1	Russia, Zabaikalsky Territory, 29.VIII.2011, *Afonina #8111* (LE)	KC121278
L. subintegrum	Zabaikalsky 2	Russia, Zabaikalsky Territory, 23.VII.2000, *Urbanavichyus s.n.* (LE)	KC121279
L. subintegrum	Zabaikalsky 3	Russia, Zabaikalsky Territory, 24.VII.2007, *Afonina #08307* (LE)	KC121280
L. subintegrum	Zabaikalsky 4	Russia, Zabaikalsky Territory, 18.VII.2010, *Afonina #A3719a* (LE)	KC121281
L. subintegrum	Zabaikalsky 5	Russia, Zabaikalsky Territory, 18.VII.2010, *Afonina #A3710a* (LE)	KC121282
L. subintegrum	Colorado	U.S.A., Colorado, 24 June 1977, *Hermann s.n.* (MHA)	KC121283
L. tenellum	Altai 2	Russia, Altai, *Ignatov #9/169* (MHA)	KC121290
L. tenellum	Altai 3	Russia, Altai, *Ignatov #0/1093* (MHA)	KC121291
L. tenellum	Altai 4	Russia, Altai, *Ignatov #0/1094* (MHA)	KC121292
L. tenellum	Altai 5	Russia, Altai, *Ignatov #0/1097* (MHA)	KC121293
L. tenellum	Altai 6	Russia, Altai, *Ignatov #8/150* (MHA)	KC121294
L. tenellum	Altai 7	Russia, Altai, *Ignatov #8/159* (MHA)	KC121295
L. tenellum	Altai 9	Russia, Altai, 28.VI.1990 *Zolotukhin s.n.* (MHA)	KC121297

Appendix 2. GenBank accession numbers for outgroup taxa; voucher specimen data are given for new sequences only.

Abietinella abietina (Hedw.) M. Fleisch. AY009802; *Amblystegium serpens* (Hedw.) Bruch et al. AF168152; *Anomodon rugelii* (Müll. Hal.) Keissl. AJ288420/AJ277232; *Antitrichia curtipendula* (Hedw.) Brid. (ITS1: Caucasus, Krasnodar Territory, *Ignatov & Ignatova #05-89*, MHA) KC249953/AY010300; *Calliergon giganteum* (Schimp). Kindb. AF168144; *Campylium stellatum* (Hedw.) C. Jens. AF168151; *Claopodium whippleanum* (Sull.) Renauld & Card. AY173470; *Climacium dendroides* (Hedw.) F. Weber & D. Mohr AJ288355/AJ288569; *Cratoneuron filicinum* (Hedw.) Spruce AY009812; *Cryphaea heteromalla* (Hedw.) D. Mohr (ITS1: Caucasus, Krasnodar Territory, 9.VIII.2002, *Ignatov & Ignatova s.n.*, MHA) KC249954/AF543549; *Drepanocladus aduncus* (Hedw.) Warnst. AF180949; *Echinodium umbratum* (Mitt.) A. Jaeger AY999172; *Fabronia ciliaris* (Brid.) Brid. AY528883; *Forsstroemia trichomitria* (Hedw.) Lindb. AY999173; *Glossodelphus ogatae* Broth. & Yasuda AY999169; *Habrodon perpusillus* (De Not.) Lindb. AY528880; *Haplocladium angustifolium* (Hampe & Müll. Hal.) Broth. AY528884/AY528885; *Haplohymenium triste* (Ces.) Kindb. AY568551; *Helodium blandowii* (F. Weber & D. Mohr) Warnst. AY009803; *Heterocladium dimorphum* (Brid.) Bruch & al. AY695757/AY695771; *Heterocladium procurrens* (Mitt.) A. Jaeger AY695756/AY695782; *Hondaella caperata* (Mitt.) Ando, B.C. Tan & Z. Iwats. (ITS1-2 Japan, Hokkaido, *Deguchi 36754*, MHA) KC249956; *Hylocomium splendens* (Hedw.) Bruch et al. AJ288336/AJ270021; *Leptodon smithii* (Hedw.) F. Web.& D. Mohr AY999171; *Lescuraea incurvata* (Hedw.) Lawt. AY693661; *Lescuraea mutabilis* (Brid.) I. Hag. AY695738/AY695792; *Lescuraea plicata* (Schleich. ex F. Weber & D. Mohr) Schimp. AY695740/AY695765; *Lescuraea secunda* Arnell AF516164/AF516150; *Leskea polycarpa* Hedw. AY528889/AF516151; *Leucodon sciuroides* (Hedw.) Schwägr. HQ268285; *Lindbergia brachyptera* (Mitt.) Kindb. AY695760/AY695763; *Myrinia pulvinata* (Wahlenb.) Schimp. AY528886/AY528887; *Neckera pennata* Hedw. AY009809; *Okamurea brachydictyon* (Card.) Noguchi AF516161/AF503537; *Plagiothecium denticulatum* (Hedw.) Bruch & al. AY528892/AY528893; *Pseudoleskeella catenulata* (Brid. ex Schrad.) Kindb. AY695747/AF516154; *Pseudoleskeella tectorum* (Funck ex Brid.) Kindb. ex Broth. AF516168/AY695776; *Pseudoleskeopsis imbricata* (Hook. & Wilson) Thér. AY693653; *Pterogonium gracile* (Hedw.) Sm. (ITS1-2 Turkey, 1999, *Konovalova s.n.* MHA) KC249957; *Pylaisia polyantha* (Hedw.) Schimp.AY528881; *Taxiphyllum aomoriense* (Besch.) Z. Iwats. FM161217; *Taxiphyllum taxirameum* (Mitt.) M. Fleisch. AJ862522; *Taxiphyllum wissgrillii* (Garov.) Wijk & Marg. AY999168; *Thamnobryum alopecurum* (Hedw.) Gang. (ITS1 Caucasus, Kabardino-Balkaria, 3.VIII.2004, *Ignatov & Ignatova s.n.*, MHA) KC249955/AY010304; *Thuidium assimile* (Mitt.) A. Jaeger AJ416442; *Trachypus bicolor* Reinw. & Hornsch. DQ200118/AF395624.