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THE GENUS *MIELICHHOFERIA* (MIELICHHOFERIACEAE, BRYOPHYTA) IN RUSSIA

РОД *MIELICHHOFERIA* (MIELICHHOFERIACEAE, BRYOPHYTA) В РОССИИ

DOLGOR YA. TUBANOVA[1], OYUNA D. TUMUROVA[1] & ELENA A. IGNATOVA[2]

ДОЛГОР Я. ТУБАНОВА[1], ОЮНА Д. ТУМУРОВА[1], ЕЛЕНА А. ИГНАТОВА[2]

Abstract

A revision of the genus *Mielichhoferia* in Russia is performed basing on morphological and molecular phylogenetic study. Specimens were found in two major clades, corresponding to *M. mielichhoferiana* s.l. and *M. elongata* s.l. Each of these clades includes subclades corresponding to cryptic species. Interesting is that almost all cryptic species discovered in the analysis of Shaw (2000) for North America and Europe were also found in Russia. Mosses of two clades nested within the *M. elongata* s.l. major clade were found to be well delimited morphologically. One of them corresponds to *M. japonica*, which is characterized by strongly reduced peristome and narrowly acute leaves with recurved marginal teeth. Another morphotype, which is characterized by thick-walled cells, is described as a new species, *M. asiatica*. The latter is known only in Eastern Siberia and Sakhalin.

Резюме

На основе морфологических и молекулярно-филогенетических данных проведена ревизия рода *Mielichhoferia* на территории России. Отсеквенированные образцы и образцы из генбанка образовали в молекулярно-филогенетическом дереве две основные клады, соответствующие *M. mielichhoferiana* s.l. и *M. elongata* s.l. Внутри этих клад имеются подклады, соответствующие нескольким криптическим видам, б. ч. не отличающимися по морфологическим признакам. Почти все криптические виды, выявленные в анализе Shaw (2000) для Северной Америки и Европы, были обнаружены и в России. Две подклады, относящиеся к кладе *M. elongata* s.l., представлены образцами, хорошо отграниченными морфологически. Одна из этих групп образцов представляет *M. japonica*, которая характеризуется сильно редуцированным перистомом и узко заостренными листьями с отогнутыми зубцами по краю. Другой морфотип, характеризующийся б. м. толстостенными клетками листа, описан как новый для науки вид, *M. asiatica*, известный из Восточной Сибири и с Сахалина.

KEYWORDS: mosses, taxonomic revision, molecular phylogeny, cryptic species, new species

INTRODUCTION

The last check-list of mosses of the East Europe and North Asia (Ignatov, Afonina, Ignatova *et al*., 2006) reported from Russia four species of the genus *Mielichhoferia* Nees & Hornsch.: *M. elongata* (Hoppe & Hornsch. ex Hook.) Hornsch., *M. japonica* Besch., *M. macrocarpa* (Hook.) Bruch & Schimp., and *M. mielichhoferiana* (Funck) Loeske. One more species of this genus previously reported from Russia, *M. himalayana,* was placed in this checklist in the genus *Bryum*, as *B. caucasicum* (Schimp. ex Broth.) C.J. Cox & Hedd., following Cox & Hedderson (2003).

Mielichhoferia macrocarpa is considered now in the genus *Haplodontium* (Spence, 2007). The genus was recently revised for China, where four species are recognized now, but according to keys and descriptions of these authors (Zhang *et al*., 2007), the Siberian plants belong to *H. macrocarpum*.

Among other species, only *M. mielichhoferiana* was reported as a widespread species in the Caucasus, Siberia and Russian Far East, while *M. japonica* Besch. (*M. mielichhoferiana* var. *japonica* (Besch.) Wijk & Margad.) was reported only from the South Kuril Islands (Bardunov & Cherdantseva, 1984; Bakalin *et al*., 2009) and *M. elongata* (*M. mielichhoferiana* var. *elongata* (Hoppe & Hornsch. ex Hook.) Wijk & Margad.) was known until recently only from Vitimsky State Reserve, north of Baikal Lake (Bardunov, 2000).

In the course of bryoflorisctic exploration in the Mus-Khaya mountain area in Yakutia, Ignatova *et al*. (2011) found two contrastingly different phenotypes of *Mielichhoferia*, which were attributed to *M. mielichhoferiana* (common one), and *M. elongata* (rare in that area). The authors noted that the situation is opposite to that in North America, where *M. elongata* is reported as much more common than *M. mielichhoferiana* (Shaw, 2000, 2014).

1 – Institute of General and Experimental Biology SB RAS, Sakhjanovoy str., 6, Ulan-Ude, 670047 Russia – Россия 670047, Улан-Удэ, Сахьяновой, д. 6, Институт общей и экспериментальной биологии СО РАН. E-mail: tdolgor@mail.ru
2 – Lomonosov Moscow State University, Faculty of Biology, Geobotany Dept., Leninskie Gory Str. 1-12, Moscow 119234 Russia – Россия, 119234, Москва, Ленинские Горы, д. 1 стр. 12, Московский государственный университет, биологический факультет, кафедра геоботаники. E-mail: arctoa@list.ru

It is worthy noting that many authors thought that only *M. mielichhoferiana* occurs in Russia (Savicz-Lyubitskaya & Smirnova, 1970), and also many author thought that *M. elongata* is merely a variety of *M. mielichhoferiana* (Podpera, 1954; Anderson *et al*. 1990; Wijk & Margadant, 1961; Ireland *et al.*, 1987; Ignatov & Afonina, 1992), or combined as a single species (Shaw & Crum, 1984).

Later Shaw (1994) and Shaw & Rooks (1994) found that *M. mielichhoferiana* and *M. elongata* are well separated in isosyme analyses, and then Shaw (2000) came to the same conclusion in the study of ITS analysis of about 70 samples from the North America and Europe.

The present study aimed to test with DNA markers the status of the *Mielichhoferia* taxa from Russia.

Material and methods

The nuclear ITS data from the analysis of Shaw (2000) were used and 16 collections (14 from Russia) were added, so the sampling covers main areas where the species of *Mielichhoferia* occur in the country and includes most contrasting morphotypes. Vouchers of newly sequenced specimens and GenBank accession numbers are compiled in Appendix 1. *Pohlia nutans* was selected as an outgroup species, as another genus of the same family (Cox & Hedderson, 1999; Cox *et al*., 2000).

DNA extraction and amplification were done according to the laboratory protocols described in Gardiner *et al.* (2005) and Fedosov *et al.* (2016). Sequences were aligned manually in BioEdit (Hall, 1999). Bayesian analysis was conducted in MrBayes 3.1.2 (Ronquist *et al.*, 2012) using the GTR+G model, for 30,000,000 generations with sampling every 1000 generations. Three simultaneous runs were used. The first 25% of sampled trees were discarded for the burn-in.

The specimens from the obtained groups were studied by morphology in order to find stable differences and understand the reliability of characters used as a distinctions between taxa in the genus.

Observations of peristomes were done with the SEM Cambridge Instruments CamScan S2 and Jeol Scanning Microscope for specimens coated by gold without additional preparation.

Results

In the phylogenetic tree based on ITS sequence data rooted on *Pohlia nutans*, a representative of another genus of the family Mielichhoferiaceae, *M. pontaverdensis* is sister to all other species of the genus. These specimens were found in two clades: (1) one with maximal support, corresponding to *M. elongata* s.l., and another one (2), coresponding to *M. mielichhoferiana* s.l. The latter clade obtained a low support (P=0.66), but two its subclades have PP=1.0 and PP=0.99; they are denoted in Fig. 1 as M1 and M2 subclades.

M1 includes plants from Western North America, Alaska, Kamchatka and Sweden, while M2 is composed of specimens from North and Central Europe, Caucasus and Anabar Plateau (Southern Taimyr in northern Siberia).

The *M. elongata* s.l.–clade represents polytomy of four clades and one specimen from Tennessee that does not group with any of these clades.

E1 includes Colorado and Californian specimens; in terminal position within this clade there is a two-specimen clade of *M. japonica*, the latter with maximal support, whereas the whole E1 has low support of PP=0.70.

E2 includes five specimens from Siberia, segregated by their morphology to a separate species, *M. asiatica* (see below).

E3 includes samples from Transbaikalia, Yakutia, Alaska, Colorado and Sweden.

E4 is abbreviation for the single specimen from Tenessee.

E5 is the most "northern" clade, combining populations from Ellesmere, Alaska and NE regions of Yakutia.

Analysis of the concatenated dataset of nuclear and plastic regions with a limited sampling, mainly for Russian plants, revealed a principally similar topology with two differences: M1 and M2 appear as a grade, not clades, and E2 clade ('*M. asiatica*') is highly sipported, as well as *M. japonica* clade.

Morphological study confirmed a stable distinctions between two main clades, *i.e.*, *M. mielichhoferiana* s.l. and *M. elongata* s.l. Also it confirmed a reliable distinction of *M. japonica* (part of E1) from all other specimens of *M. elongata* s.l., and, finally, we revealed a group E2, formed by Siberian and Russian Far Eastern plants, that is also distinct in morphology. We failed to find a stable distinction between specimens of E3 and E5 clades available for us, probably due to a limited material. Subsequent study of more numerous material in herbaria supports the possibility to sort specimens between E2 and E3+E5 clades. The clade E1 is represented in Asia only by *M. japonica*, but American plants of this clade from Colorado and California appear to be more similar to E2, although not identical.

Discussion

The molecular phylogenetic analysis revealed a really complex situation within the genus *Mielichhoferia*, which includes many haplotypes, each of them being rather little variable across the circum-Holarctic range. However, *M. mielichhoferiana* s.l. and *M. elongata* s.l. differ from each other, as it was accepted in recent publications (Shaw, 2000, 2014), although the variation in characters that were thought to be diagnostic needs certain comments. It is usually assumed that the former species has dark green plants, which is correlated with rather thick-walled laminal cells, whereas in *M. elongata* plants are light and somewhat glaucous-green, glossy, and laminal cell are thin-walled. We found some exeptions in Asiatic plants, namely plants from clade E2, which have rather thick-walled cells. At the same time, we found that *M. mielichhoferiana* s.l. (M1+M2) and *M. elongata* s.l. (E1+E2+E3+E5, as E4 plants were not studied by

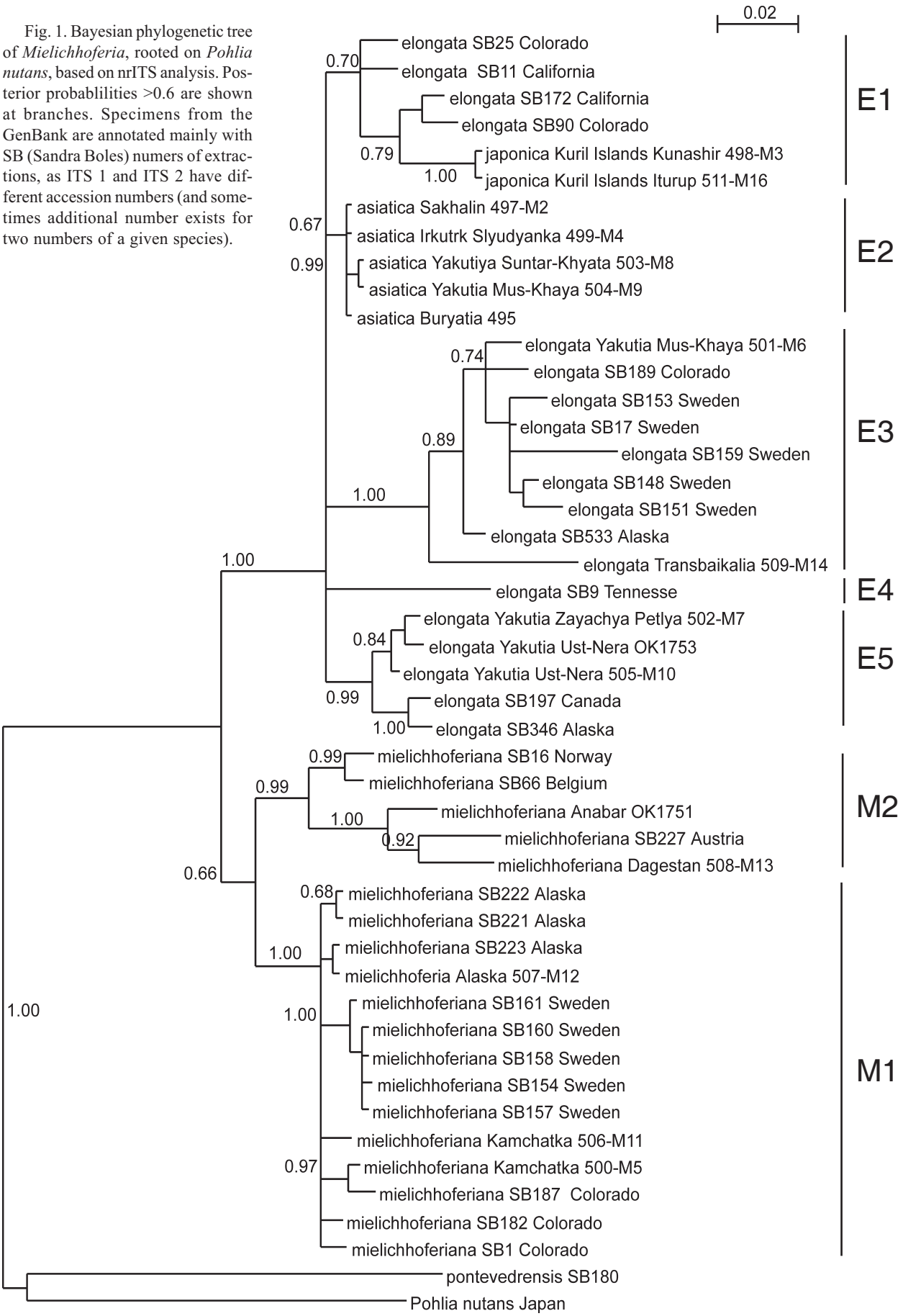


Fig. 1. Bayesian phylogenetic tree of *Mielichhoferia*, rooted on *Pohlia nutans*, based on nrITS analysis. Posterior probablilities >0.6 are shown at branches. Specimens from the GenBank are annotated mainly with SB (Sandra Boles) numers of extractions, as ITS 1 and ITS 2 have different accession numbers (and sometimes additional number exists for two numbers of a given species).

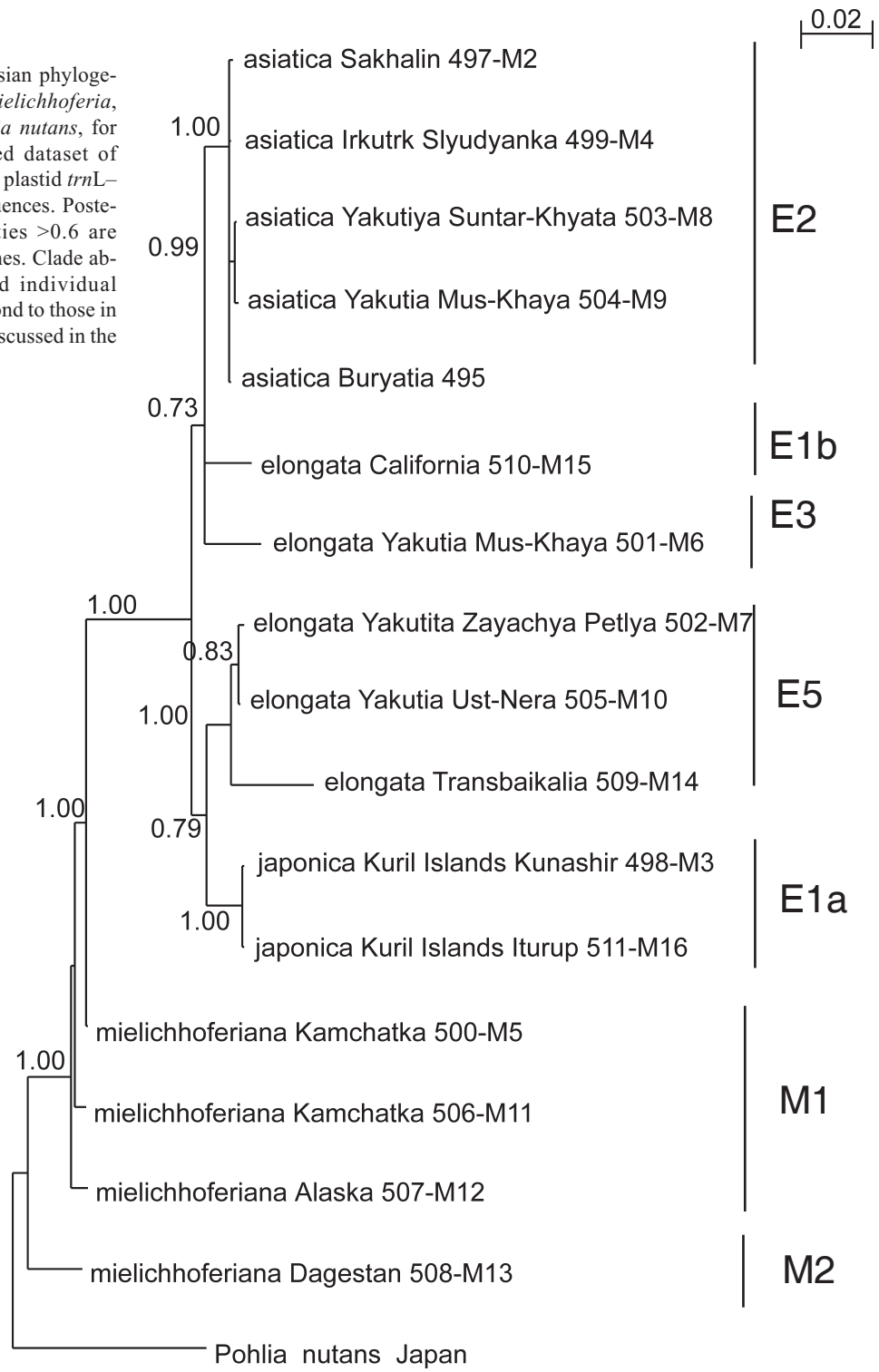


Fig. 2. Bayesian phylogenetic tree of *Mielichhoferia*, rooted on *Pohlia nutans*, for the concatinated dataset of nuclear ITS and plastid *trn*L–F and *rps*4 sequences. Posterior probablilities >0.6 are shown at branches. Clade abbreviations and individual species correspond to those in Fig. 1 and are discussed in the text.

ourselves) can be separated by stem cross sections: in the former groups, they are more or less distinctly pentagonal, with distinct central strand, while in the latter group stem cross sections are round or indistinctly pentagonal, and central strand is weak (Fig. 2).

Within both subclades of *M. mielichhoferiana* s.l., M1 and M2, there are populations from Russia. These subclades are highly supported and are potentially good species. They also have certain differences in morphology: at least Caucasian plants (M2, Dagestan) differ from plants of M1 (Kamchatka) in blunt, almost entire leaves and weaker stem central strand. By blunt leaves this species is more similar to *M. elongata* and *M. asiatica*, than to *M. mielichhoferiana,* but it differs from them by distinct pentagonal stem in transverse section. However, these distinctions are not stable, *e.g.* leaves in Siberi-

an plants from M2 clade, from the Anabar Plateau, are more similar to the Kamchatkan plants from M1 clade than to Dagestan plants from M2 clade (Fig. 2). Also, the status of M1 and M2 clades requires a special study aiming to identify to which of these two clades the type of *M. mielichhoferiana* belongs, as the broad variation precludes easy interpretation of specimens only by morphology.

Some haplotype groups of *M. elongata* s.l., *i.e.* E1 to E5, also have a broad distribution as follow:

E1: Colorado, California, Kuril Islands [and Japan] (it corresponds to clade A in Shaw, 2000).

E2: from Baikal Lake area to Eastern Yakutia and Sakhalin.

E3: Transbaikalia, Yakutia, Alaska, Colorado, Sweden (it corresponds to the clade C in Shaw, 2000).

E4: Tenessee (specimen found in basalmost position in clade A in Shaw, 2000)

E5: Alaska, Ellesmere, Yakutia (corresponds to the clade B in Shaw, 2000, which also includes specimens from Maine and New York).

Considering an obvious differentiation of E2 clade in morphology and its high support in concatinated analysis, we separate it as a species of its own (see below). Rest clades of *Mielichhoferia elongata* s.l. can be separated from this E2 clade, including numerous collections from Europe, where from *M. elongata* was described. Thus, we recognize four species of *Mielichhoferia* in Russia, although subsequent studies may find morphological delimitation of cryptic species and more species may be recognized, which is especially likely for M1 and M2 clades.

TAXONOMY

Mielichhoferia Nees & Hornschuch,

Plants small, in loose or dense, low, occasionally large tufts, green, glaucous, yellowish- or brownish-green, often brown below, dull or golden shiny, more or less tomentose below. *Stems* often fragile, irregularly branched, round or pentaginal in transverse section,with weak or strong central strand. *Leaves* appressed when dry, erect or slightly flexuose, erect or erect-spreading when wet, triangular-lanceolate or ovate-lanceolate; lamina unistratose; margins plane or narrowly recurved, serrulate or serrate, marginal teeth unicellular, blunt or acute, erect or reflexed; costa weak or more or less strong, ending below leaf apex, with differentiated ventral epidermis of two large cells, guide cells absent, stereid band small, dorsal epidermis weakly delimited or absent. *Dioicous,* male and female plants often growing in the same tuft. *Perigonia* large, bud-like. *Sporophytes* solitary, lateral. *Perichaetial leaves* longer than stem leaves, occasionally with weakly rcurved margins. *Setae* long, erect, flexuose or cygneous. *Capsules* erect, inclined or pendent, ovate or pyriform, with long neck. *Opercula* low conic, blunt. *Annulus* of 1–2 cell rows, deciduous. *Exostome* teeth 16, pale, long and narrow or short, strongly reduced, with low basal membrane; endostome absent. *Spores* 12–20 μm, papillose. *Calyptra* cucullate.

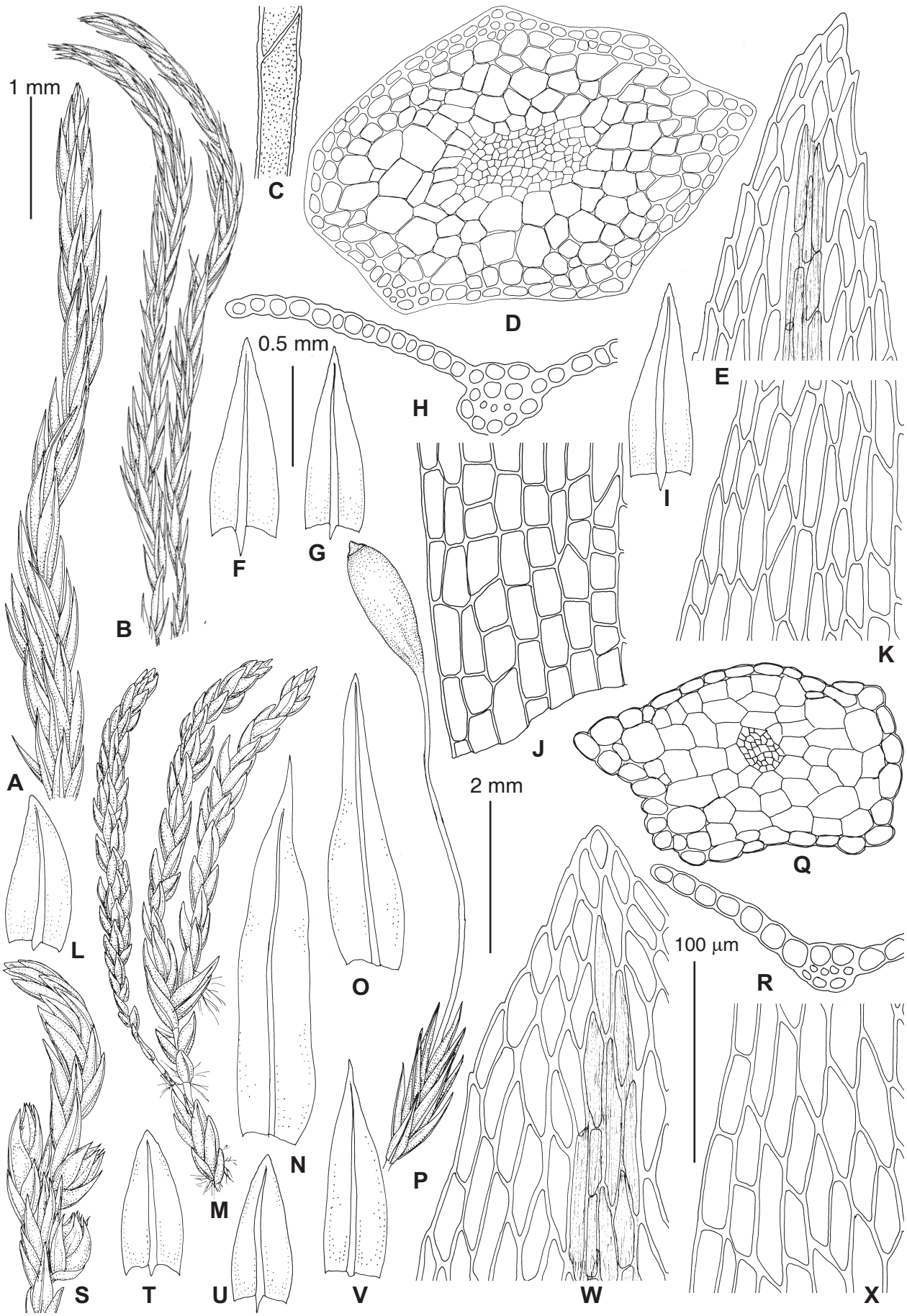
Lectotype of the genus not selected. The genus includes 45 species, distributed mainly in tropical areas. In Russia there are 5 species. The name of the genus is given in honor of Mathias Mielichhofer (1772–1847), Austrian mining geologist, mineralogist and botanist, who studied flora of Austrian Alps.

1. Stems in cross sections distinctly pentagonal, central strand strong or weak; leaves narrowly triangular, not or only slightly narrowed to the insertion; laminal cells thick-walled .. *M. mielichhoferiana* s.l.
— Stems in cross sections round or indistinctly pentagonal, central strand weak; leaves narrowly ovate, narrowed to the insertion; laminal cells thin- or firm-walled 2
2. Leaf marginal teeth long, sharp, straight to reflexed; distal laminal cells prorate; exostome teeth shorter than 100 μm, smooth to finely papillose .... *M. japonica*
— Leaf marginal teeth somewhat sharp or blunt, not deflexed or few teeth near leaf apex are reflexed; laminal cells smooth or sometimes few subapical cells prorate; exostome teeth 250–350 μm, more or less papillose 3
3. Leaves (0.4–)0.6–1.0×0.25–0.38 mm; margins finely serrulate to subentire; laminal cells thin-walled, occasionally firm-walled; rhizoids pale, smooth the finely granulose ..... *M. elongata*
— Leaves 0.4–0.7×0.18–0.25(–0.3) mm; margins serrulate, uppermost marginal teeth short and often reflexed; laminal cells firm-walled; rhizoids brownish to reddish, coarsely papillose ..... *M. asiatica*

1. **Mielichhoferia mielichhoferiana** (Funck) Loeske, Stud. Morph. Laubm. 126. 1910. — *Weissia mielichhoferiana* Funck, Crypt. Gew. Fichtelgeb. 24: 2. 1818. — *Mielichhoferia mielichhoferi* Wijk & Margad. Besch., Taxon 10: 24. 1961. Figs. 3; 6: F; 8

Plants small, in low, dense or loose, easily disintegrated tufts, green, yellowish, shiny. *Stems* 1–2 cm long, branched, in transverse section pentangular, often with sharp ribs, with strong or, rarely, weak central strand;

Fig. 3 (on page 171). *Mielichhoferia mielichhoferiana* (A–K – from: Kamchatka, 10.VIII.2006, *Czernyadjeva, Bryophyta Rossica exs.* (*2006*) *#231,* MHA; L–X – from: Dagestan, 25.VIII.2011, *Kotseruba s.n.,* LE). A–B, M, S: habit, dry (sterile plants); P – habit, dry (plant with sporophyte); C – rhizoid; D, Q – stem transverse sections; E, W – distal laminal cells; F–I, L, T–V – stem leaves; J – basal laminal cells; K, X – median laminal cells; N–O – perichaetial leaves. Scale bars: 2 mm for B, P; 1 mm for A, M, S; 0.5 mm for F–I, L, N–O, T–V; 100 μm for C–E, H, J–K, Q–R, W–X.


1 mm
A
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rhizoids brown or reddish-brown, coarsely papillose. *Leaves* loosely appressed when dry, erect-spreading when wet, (0.35–)0.6–1.0(–1.5)×0.25–0.27 mm, lanceolate or narrowly triangular, gradually tapered; margins plane or narrowly recurved on both sides, serrulate in distal portion of leaf; *costa* ending below leaf apex, gradually tapered from base to upper part, without or with incomplete dorsal epidermis, ventral epidermis 2 cells wide, stereid band small; leaf lamina smooth; upper and median laminal cells phomboidal or hexagonal, (26–)36–55 (–66)×(6.5–)7–10(–11) μm, more or less thick-walled; basal laminal cells short rectangular and quadrate, (13–) 16–20(–40)×(9–)10–13(–15) μm, thin-walled. *Perichaetial leaves* elongate-rectangular. *Sporophytes* rare, present in two collections in the territory of Russia (Dagestan and Yakutia). *Setae* 10–13 mm, reddish. *Capsules* erect or slightly inclined, oblong-pyriform, 3.5 mm long. *Exostome teeth* pale yellow, papillose or smooth, on low basal membrane. *Spores* 14–18 μm, brownish-yellow, finely papillose.

Distribution and ecology. *Mielichhoferia mielichhoferiana* was described from the Central European Alps. It is also known from Africa and North America. Shaw (1994) has showed that it is much rarer than *M. elongata*. In Russia, we confirm its presence in the Caucasus (Dagestan, North Ossetia, Karachay-Circassian Republic, Krasnodar Territory), southern Taimyr, Yakutia (Mus-Khaya Mt. area), Magadan Province, Chukotka, and Kamchatka (Klyuchevskie Volcanoes). In the Caucasus it is more frequent than *M. elongata*, which was found only once, and it is the only species of the genus in Kamchatka. However, in Yakutia, in Mus-Khaya Mt. surroundings it was found growing together with *M. asiatica* and *M. elongata*; in this area, *Mielichhoferia* is especially abundant due to high content of heavy metals in rocks. In other areas, *M. mielichhoferiana* was collected on shists and volcanic rocks, often in moist places near waterfalls and along creeks.

Selected specimens examined: CAUCASUS: **Dagestan Republic**: Agulsky District, Tsirkhe Settl. surroundings, 44°55'N, 47°36'E, 2040 m a.s.l., 25.VIII.2011, *Kotseruba s.n.* (LE 15693); Dagestania australis, versus fontes fluvii Samur, inter Koffur & Virgull, 15.VII.1860. *Ruprecht s.n.* (LE). **Ossetia**: Lars, 24.V.1881, *A.E. & V.F. Brotherus s.n.* (LE). Karachay-Circassian Republic: Teberda State Reserve, North Klukhor Gorge, spurs of Buulgen Ridge, 3000 m a.s.l., 12.IX.1994, *Onipchenko 208/94* (MW). **Krasnodar Territory**: Caucasian State Reserve: Atseukho Mt., VII.1951, *Ariskina 26* (LE); slope of Fisht Mt. to Belaya River, 19.VIII.1999, *Ignatov s.n.* (MHA). ASIAN RUSSIA: **Krasnoyarsk Territory**: Taimyrsky Municipal District, Khatanga Settl. surroundings, Merkyu River 4 km upstream its mouth, *Fedosov 11-335* (MW). **Republic Sakha/Yakutia**: Oimyakon District, Suntar-Khayata Mt. System, Mus-khaya Mt., Knorij Creek, ca. 61°34'N, 141°01'E, 1575 m a.s.l., *Ignatov & Ignatova 11-3110*; same place, 13.VII.2011, *Ivanov s.n.* (MHA). **Magadan Province**: Yagodninsky District, upper course of Sukhahy River, Bolshoy Annachag Range, 62°10'N, 149°18'E, 1600 m a.s.l., 29.VII.2014, *Pisarenko op05445* (MW). **Chukotsky Autonomous Okrug**: Egvekinot Settl. surroundings, Krest Bay, 17.VIII.1977, *Afonina s.n.* (LE). **Kamchatsky Territory**: Klyuchevskie Volcanoes, Ushkovsky Volcano, 55°58'N, 165°15'E, 1000 m a.s.l., 15.VIII.2004, *Czernyadjeva 78* (LE); same place, 1250 m, 23.VIII.2005, *Czernyadjeva 65* (LE); same place, 1500 m a.s.l., 21.VIII.2004, *Czernyadjeva 111* (LE); Ostry Tolbachik Volcano, Vodopadny Creek, 55°46'N, 169°15'E, 1350 m a.s.l., 10.VIII.2006, *Czernyadjeva, Bryophyta Rossica exs. (2006) #231* (MHA, MW).

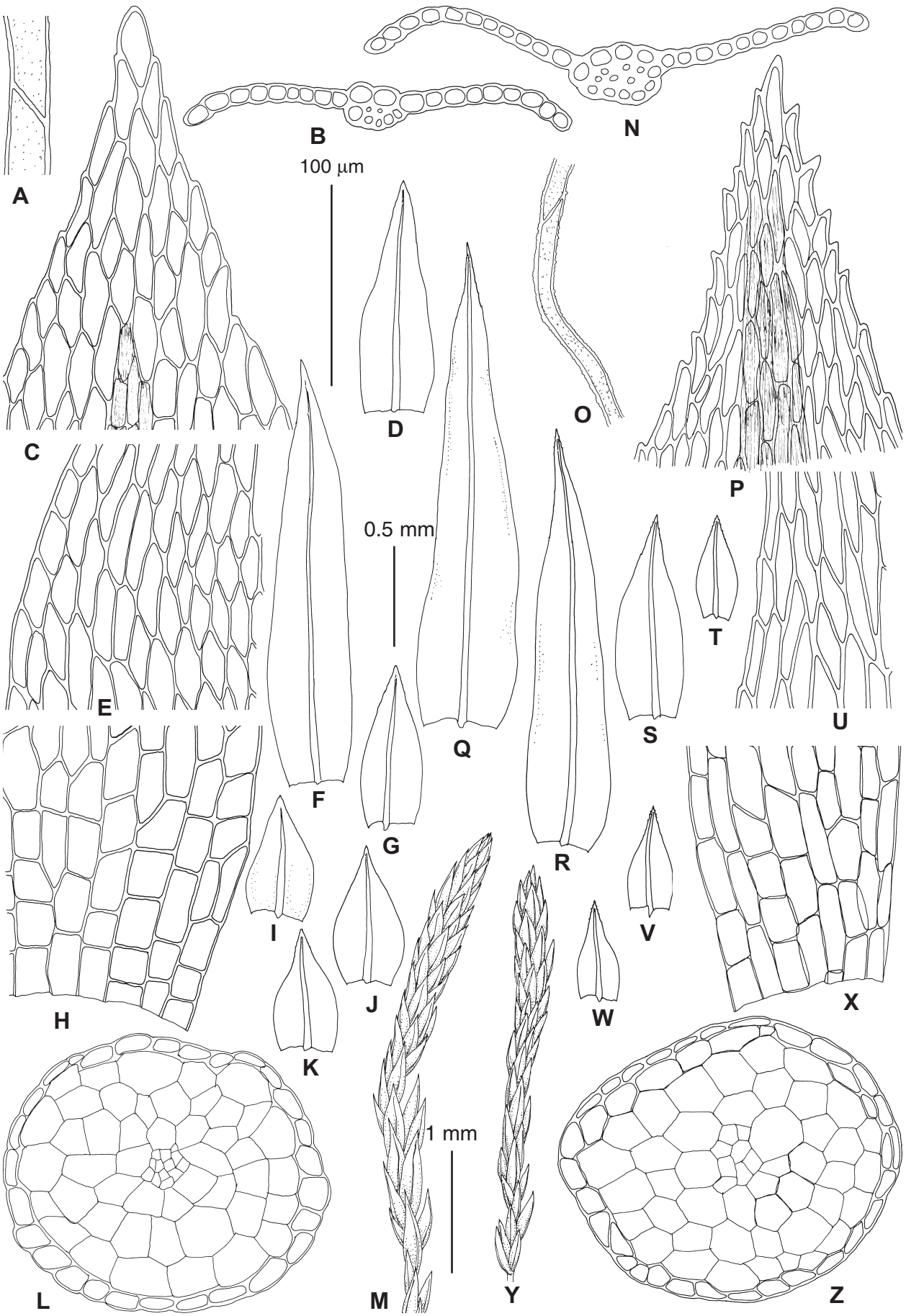
Differentiation. Stem transverse section is a good character separating *M. mielichhoferiana* from all other species of the genus: it is always pentagonal, often with sharp ribs and usually with large central strand, while in *M. elongata*-group it is round or elliptical, rarely indistinctly pentagonal, with weak central strand. Leaves of *M. mielichhoferiana* are narrowly triangular, widest at insertion or slightly above it and scarcely narrowed to the insertion, contrary to leaves widest well above insertion in other species; its leaves are less appressed when dry than in other species and, occasionally, falcate-secund (the latter is never observed in *M. elongata* and *M. asiatica*). Its cells are firm-walled, similarly to *M. asiatica*, but the latter species has shorter leaves, 0.4–0.7 mm vs. (0.65–)0.8–1.0(–1.5) mm long. Thin-walled cells of *M. elongata* were always used as a most important character separating this species from *M. mielichhoferiana*; it is true for *M. elongata* s.str. The distinction of *M. japonica* is discussed in comments to that species.

Variation. There is a considerable variation in leaf length between specimens of *M. mielichhoferiana*; the longest leaves, ca. 1.5 mm long, were observed in specimen from Yakutia, while the shortest leaves, 0.45–0.7 mm long, were seen in collection from Dagestan. The latter specimen was also remarkable in having obtuse leaves with almost entire margins in sterile plants, but plants with sporophytes had "normal" acute leaves with serrulate margins.

2. **Mielichhoferia elongata** (Hoppe & Hornsch.) Nees & Hornsch., Bryol. Germ. 2(2): 186. 1831. — *Weissia elongata* Hoppe & Hornsch., Musci Exot. 2: pl. 102. 1819.
Figs. 4: A–M, 6: C, E; 8

Plants small, in low, dense tufts, yellowish-green, slightly glossy. *Stems* 1–2 cm long, moderately branched, round-elliptical, rarely indistinctly pentagonal in transverse section; *rhizoids* straw-colored or pale brownish, almost smooth or finely papillose. *Leaves* loosely ap-

Fig. 4 (on page 173). A–M – *Mielichhoferia elongata* (from: Republic of Sakha/Yakutia, Mus-Khaya Mt., *Ignatov & Ignatova 11-3204*, MHA); N–Z – *Mielichhoferia asiatica* (from holotype). A, O – rhizoids; B, N – leaf transverse sections; C, P – distal laminal cells; D, S – stem leaves from fertile plants; F, Q–R – perichaetial leaves; E, U – median laminal cells; G, I–K, T–W – stem leaves from sterile plants; H, X – basal laminal cells; L, Z – stem transverse sections; M, Y – habit, dry. Scale bars: 1 mm for M, Y; 0.5 mm for D, F–G, I–K, Q–T, V–W; 100 μm for A–C, E, H, L, N–P. U, X, Z.


A
B
N
100 μm
C
D
O
P
0.5 mm
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F
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Y
Z

pressed when wet and dry, (0.5–)0.6–0.9(–1.1)×0.25–0.38 mm, lanceolate, narrowly acute; margins plane, weakly serrulate distally; costa ending below apex, gradually narrowing distally, with ventral epidermis, small stereid band and incomplete dorsal epidermis; leaf lamina unistratose, smooth; upper and median laminal cells rhomboidal or hexagonal, (45–)55–80(–100)×(9–)11–13(–15) μm, thin-walled; basal laminal cells short rectangular, (24–)36–60(–80)×(9–)10–14(–15) μm, thin-walled. *Sporophytes* frequent. *Setae* yellow, erect or cygneous, 4–5 mm. *Capsules* ovate or puriform, 1.5–2.0 mm long. *Exostome teeth* narrow, long, light yellowish, finely papillose, with low basal membrane. *Spores* 15–20 μm, pale, finely papillose.

Distribution and ecology. Similarly to *M. mielichhoferiana*, *M. elongata* was described from Central Europe; both species have similar distribution in Europe, Africa and North America. In Russia, contrary to North America, it is rarer, compared with *M. mielichhoferiana* and *M. asiatica*; the latter species is very close to *M. elongata* and partially substitutes it in Yakutia and Transbaikalia. *Mielichhoferia elongata* was found only once in the Caucasus (in Kabardino-Balkarian Republic, where other species of the genus are absent); it is also known from a single locality in southern Taimyr, in several places in Yakutia, one in Zabaikalsky Territory and one in Chukotka. Grows on wet rocks (ultrabasites and schists) rich in heavy metals.

Specimens examined: CAUCASUS: **Kabardino-Balkarian Republic**, northern futhills of Elbrus Mt., Dzhilysu Creek, 20.VII.2012, *Ukrainskaya s.n.* (LE 15524). ASIAN RUSSIA: **Krasnoyarsk Territory**: Taimyrsky Municipal District, 70.8105°N, 101.086°E, north of plateau 495 m alt., *Fedosov 09-446* (MW). **Republic Sakha/Yakutia**: Oimyakon District: Suntar-Khayata Mt. System, Mus-khaya Mt., Knorij Creek, ca. 61°35'N, 141°05'E, 1450 m a.s.l., *Ignatov & Ivanov 11-3587*; same place, 61°32'N, 141°01'E, 1652 m a.s.l., *Ignatov & Ignatova 11-3278* (MHA); 35 km E of Ust-Nera Settlement, 64°26'9"N, 143°57'20"E, 520 m a.s.l., *Ignatov & Ignatova 15-1553*; Tomponsky District, Suntar Khayata Mt. System, Setorym Creek, 63°12'26"N, 139°27'12"E, 1010 m a.s.l., *Ignatov & Ignatova 15-3204* (MHA). **Zabaikalsky Territory**: Kodar Mt. Range, 12.VI.2015, *Afonina 0915* (LE). **Chukotsky Autonomous Okrug**: Anyuiskoe Upland, Kytep-Guityryveem Creek, 15.VIII.1977, *Andreev s.n.* (LE).

Differentiation. Round or round-elliptical stem cross-sections and leaves with weakly serrulate margins and thin-walled cells separate *M. elongata* from *M. mielichhoferiana*. Differenses from *M. asiatica* and *M. japonica* are discussed under these species.

3. **Mielichhoferia asiatica** Tubanova & Ignatova sp. nova. Figs. 4: N–Z; 5: A–D; 6: A–B, D; 8.

Type: Russia, Republic Sakha/Yakutia, Oimyakon District, Mus-Khaya Mt., Knorij Creek (tributary of Kongor River), ca. 62°32'N, 141°01"E, 1652 m a.s.l., right tributary near mouth, wall of conglomerate, in crevices and on overhanging surfaces, Ignatov & Ignatova #11-3279 (Holotype MHA, lectotypes MW, LE).

Diagnosis. The new species is similar to *Mielichhoferia elongata* in having round or round-elliptical stem transverse sections with small central strand and ovate-lanceolate leaves, narrowed to the insertion; it differs from the latter species in having smaller leaves, 0.4–0.7×0.18–0.25(–0.3) mm vs. (0.4–)0.6–1.0×0.25–0.38 mm; sharper teeth at upper leaf margins, short, but often recurved at 90° vs. subentire to slightly serrulate margins with blunt teeth; firm-walled vs. thin-walled laminal cells; and coarsely vs. finely papillose rhizoids.

Plants small, in low, dense tufts, yellowish-green, glossy. *Stems* 1–5 mm long, moderately to strongly branched, round or round-elliptical in transverse section, with small central strand; *rhizoids* brownish, coarsely papillose. *Leaves* appressed when wet and dry, on sterile shoots and innovations (0.35–)0.4–0.7(–0.8)×(0.1–)0.15–0.25(–0.3) mm, ovate-lanceolate, acute; margins plane, serrulate above, teeth short, sharp, often recurved at 90°; leaves of fertile shoots gradually becoming larger from base of stem to perichartium; *costa* ending just below apex, slightly narrowed distally, with differentiated ventral epidermis, small stereid band and incomplete dorsal epidermis; leaf lamina unistratose, smooth or often with protruding upper cell angles in distal leaf portion; upper and median laminal cells romboidal or hexagonal, (40–)50–65(–78)×8–11(–12) μm; basal laminal cells short rectangular and quadrate, (16–)25–42(–48)×(9.5–)11–16(–18) μm. Sporophytes frequent. *Perichaetial leaves* ca. 1.75×0.25 mm. *Setae* yellow, 5–6 mm, flexuose or curved when dry, cygneous when wet. *Capsules* oblong-ovate to pyriform, 1.7–2.5 mm long. *Exostome teeth* 350–450 μm long, whitish, coarsely papillose, with low basal membrane. *Spores* 15–20 μm, yellowish, finely papillose.

Distribution and ecology. *Mielichhoferia asiatica* is most frequent in East Siberia, including Yacutia, Irkutsk Province, Zabaikalsky Territory and Buryatia; it is also known from Sakhalin Island in Russian Far East. Like other species of the genus, it grows on rock outcrops and cliffs along creeks and streams, often in crevices and on overhanging surfaces, forming extensive low tufts.

Specimens examined: ASIAN RUSSIA: **Republic of Sakha/Yakutia**: Tomponsky District: Suntar-Khayata Mt. Range, ca. 63°07'N, 130°00'E, 890 m a.s.l., Sukhaya Creek, *Ignatov & Ignatova 15-36* (MHA, MW); Oimyakon District, 35 km E of Ust-Nera Settlement, 64°26'9"N, 143°57'20"E, 520m a.s.l., *Ignatov & Ignatova 15-1551* (MHA). **Irkutsk Province**: Slyudyanka Districy, Slyudyanka Creek 7 km upstream from mouth, 51°37.5'N, 103°39'E, 650 m a.s.l., 8.VI.2005, *Ignatov & Kazanovsky*, Mosses of Russia Exs. #128 (MHA, MW); Bodaibo District, Vitimsky Nature Reserve, 10.VII.1984, *Bardunov s.n.* (LE); Nizhneudinsky District, East Sayan Mountains, Kara-Buren Creek (right tributary of Uda River), 1000 m a.s.l., 12.VII.1961, *Bardunov*, Hepaticae et Musci URSS exs. #176 (MHA, MW). **Republic of Buryatia**: East Sayan Mountains: Okinsky District, middle course of Obtoi Creek, 52°48'50.4"N, 99°30'25.1E, 1892 m a.s.l., 9.VII.2015, *Tubanova O1504/09* (UUH); Tunka District: Arshan, 1100 m a.s.l., 21.IX.1966, *Bar-*

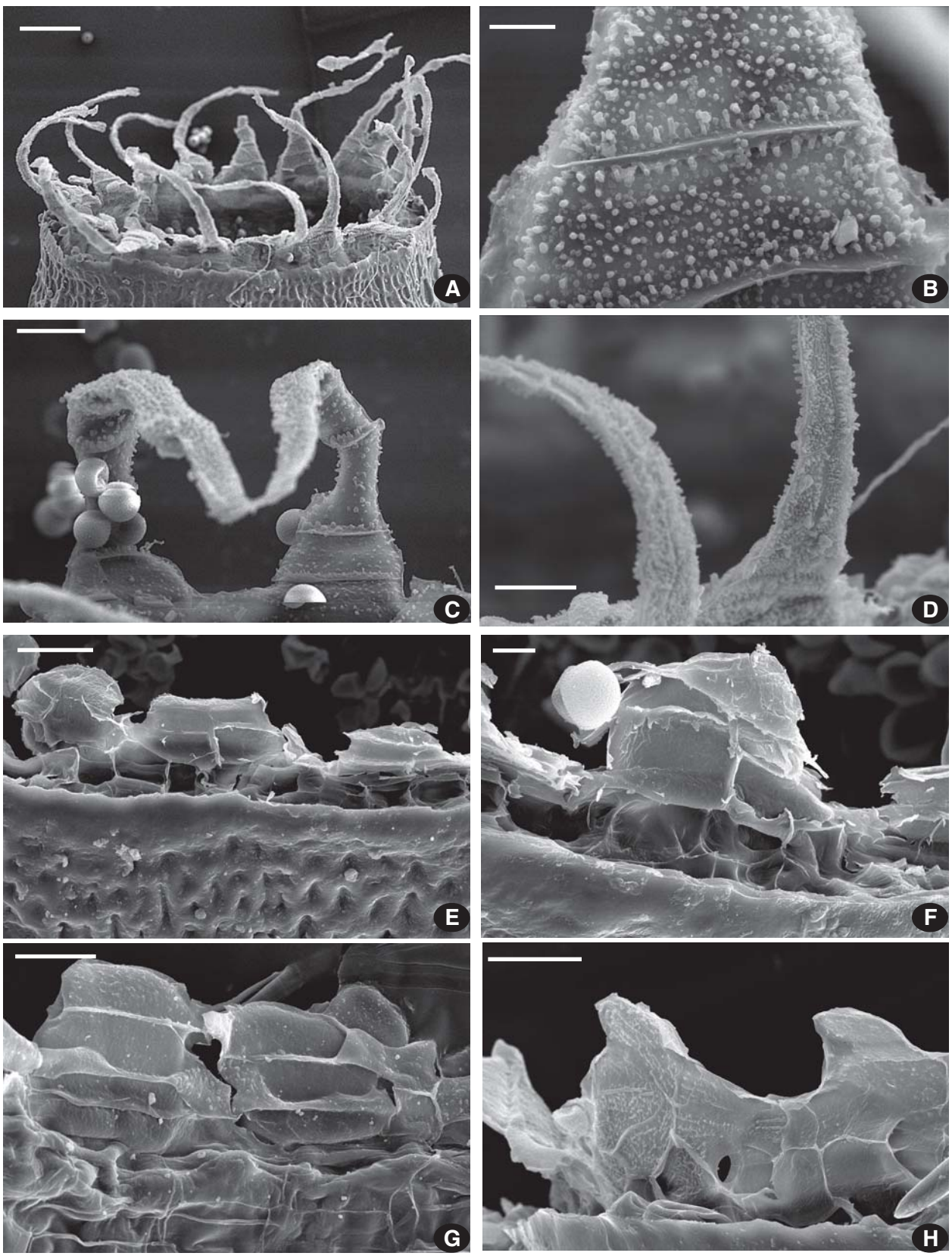

Fig. 5. SEM images of *Mielichhoferia* peristomes. A–D – *Mielichhoferia asiatica* (from: Yakutia, *Ignatov & Ignatova 15-1557*, MW) and E–H – *Mielichhoferia japonica* (from: Kuril Islands, *Ignatov 06-1616*, MHA). A: general view; B–C: inner surface of teeth; D–H: outer surface of teeth. Scale bars: 100 μm for A; 30 μm for C–E, G–H; 10 μm for B, F.

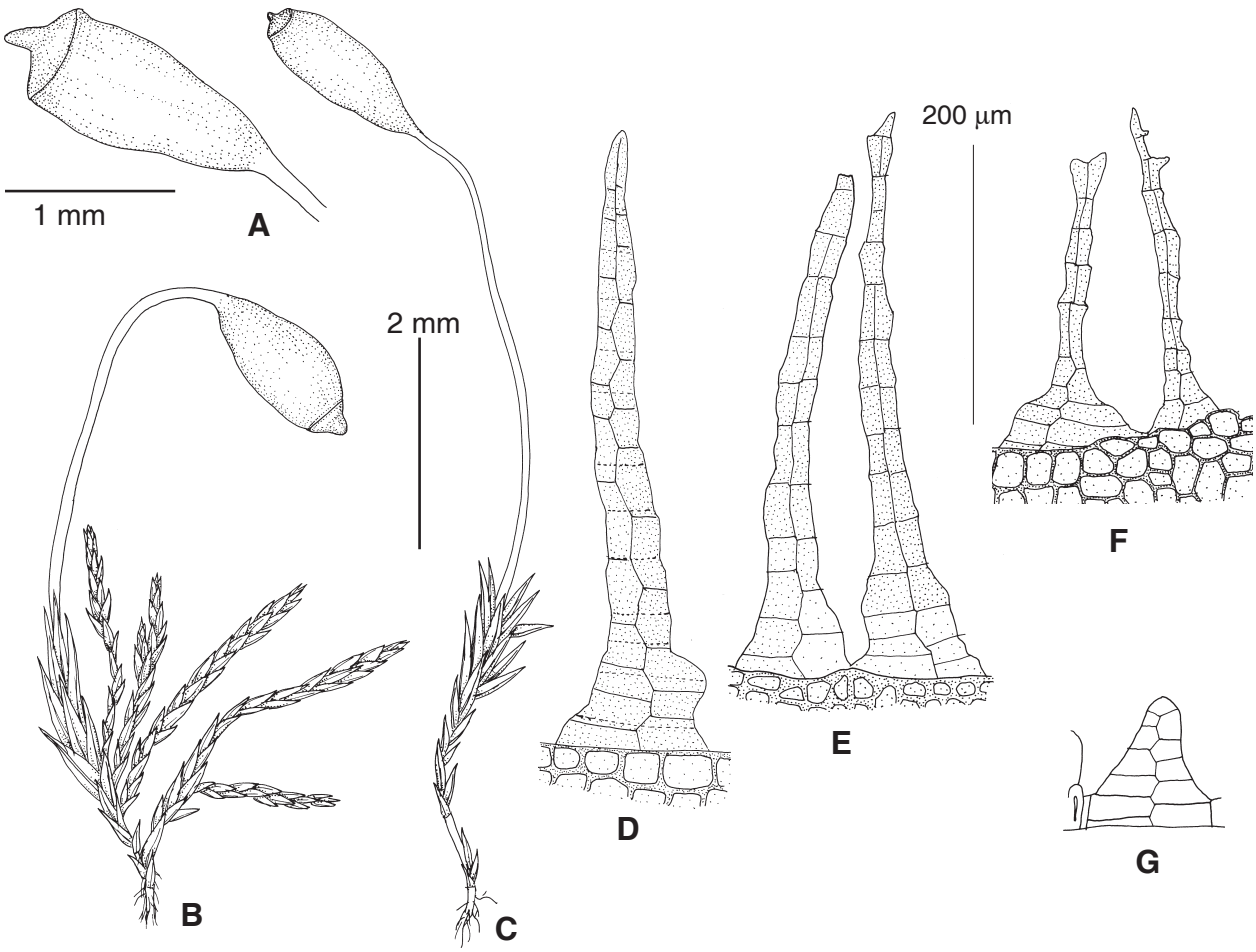

Fig. 6. Plants with sporophytes and peristomes of *Mielichhoferia*. A–B, D: *M. asiatica* (from holotype), C, E: *M. elongata* (from Republic of Sakha/Yakutia, Mus-Khaya Mt., *Ignatov & Ignatova 11-3204*, MHA), F: *M. mielichhoferiana* (Dagestan, 25.VIII.2011, *Kotseruba s.n.,* LE); C: D: *M. japonica* (from Kuril Islands, *Ignatov 06-1616*, MHA). Scale bars: 2 mm for B–C; 1 mm for A; 200 μm for D–G.

dunov s.n. (MHA); Mondy, 2000 m a.s.l., 22.VIII.1960, *Bardunov s.n.* (LE); Cheremkhovo District, Urik River near Zegen-Tol Creek mouth, 850 m a.s.l., 9.VIII.1959, *Bardunov s.n.* (LE). **Zabaikalsky Territory**: Borzya District, Kharanor railway station, 18.VI.1989, *Bardunov s.n.* (LE). **Sakhalinskaya Province**: Sakhalin, Aleksandrovsk-Sakhalinsky District, Khodzhi Cape, Due, 550'N, 14206'E, 30 m a.s.l., 6.IX.2009, *Pisarenko op03215* (MHA).

Differentiation. Differences of *M. asiatica* from the closest species, *M. elongata*, are given in the diagnosis. It is also similar to *M. mielichhoferiana* in having firm-walled cells and short, but sharp teeth at leaf margins; however, leaves of *M. asiatica* are smaller, 0.4–0.7 mm vs. 0.6–1.0(–1.5) mm long, and they are distinctly narrowed to the insertion, while in *M. mielichhoferiana* leaves are widest at the insertion; stem transverse section is also very helpful for their separating, as it is round-elliptical, rarely indistinctly pentagonal, with weak central strand in *M. asiatica* and sharply pentagonal in *M. mielichhoferiana. Mielichhoferia japonica* has longer teeth at leaf margins and longer laminal cells; furthermore, its peristome is vestigal, scarcely exceeding annulus, whereas in *M. asiatica* exostome teeth are ca. 450 μm long.

4. **Mielichhoferia japonica** Besch., J. Bot. (Morot) 12: 299. 1898. Figs. 6: G; 7; 8

Plants small, in low, dense tufts, green or yellowish, glossy. *Stems* 1–5 mm long, moderately branched, round-elliptical in transverse section, with small central strand; *rhizoids* pale or brownish, finely papillose. *Leaves* loosely appressed when dry and wet, (0.3–)0.45–0.6(–0.9) ×0.1–0.2 mm, lanceolate, gradually tapered to the apex; margins plane, sharply serrulate distally, with straight and slightly recurved teeth; costa ending just below apex, gradually narrowing distally, with ventral epidermis, very small stereid band and dorsal epidermis; lamina unistratose, smooth in proximal part and with weakly protruding upper cell angles above; upper and median laminal cells elongate-rhomboidal to linear, (48–)4–77(–91)×(9–)10–12(–13) μm; basal laminal cells rectangular, gradually transiting to median cells, (24–) 29–54(–67)×(9.5–)12–17(–19) μm, thin-walled. Sporophytes frequent. *Seta* yellow, 5–6 mm, erect. *Capsules* yellowish, elongate, pyriform, 2.0–2.5 mm long. *Exostome teeth* pale, rudimentary, ca. 80–90 μm long, on low basal membrane, finely papillose. *Spores* 12–17 μm, finely papillose.

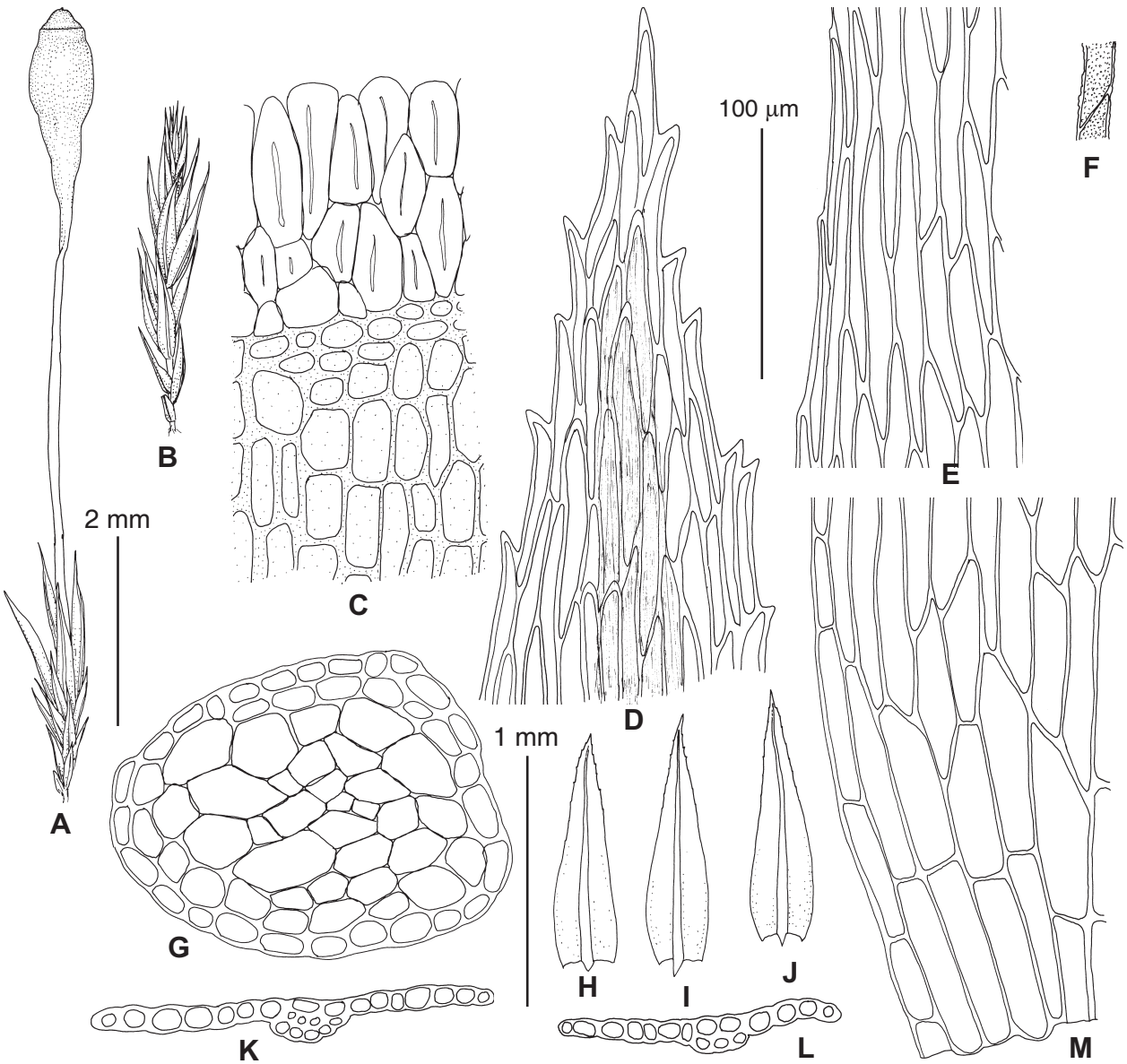

Рис. 7. *Mielichhoferia japonica* (from: Sakhalinskaya Province, Kuril Islands, Rurui Volcano, *Ignatov 06-1616*, MHA). A–B – habit, dry; C – operculum; D – upper laminal cells; E– median laminal cells; F – part of rhizoid; G – stem transverse section; H–J – stem leaves; K–L – leaf transverse sections; M – basal laminal cells. Scale bars: 2 mm for A–B; 1 mm for H–J; 100 μm for C–G, K–M.

Distribution and ecology. *Mielichhoferia japonica* was described from Japan; it is also known from few localities in Taiwan. In Russia, it was found in southern Kuril Islands (Kunashir and Iturup), at elevations from 700 to 1300 m, on slopes of old volcanoes. It grows on acid volcanic rocks; in Kunashir it was collected in a cave on slope, while in Iturup it grew on rocks in a bed of temporary brook.

Specimens examined: Asian Russia: **Sakhalinskaya Province**: Kuril Islands: Kunashir Island, NW slope of Ruruj Mt., 44°29'N, 146°8'E, 1250 m a.s.l., *Ignatov 06-1616* (MHA, MW); same place, 1300 m a.s.l., *Ignatov 06-1551* (MHA, MW); Iturup Island, N-faced slope of Kudryavy Volcano, 45.393°N, 148.822°E, 700 m a.s.l., *Pisarenko op05820* (MHA).

Disfferentiation. *Mielichhoferia japonica* belongs to *M. elongata*-group of species; it shares with *M. elongata* and *M. asiatica* round or round-elliptical stem transverse section. It differs from both of these species by narrowly lanceolate vs. ovate-lanceolate leaves, longer laminal cells and longer, sharper and stronger recurved marginal teeth. Round vs. sharply pentagonal stem transverse section helps to separate *M. japonica* from *M. mielichhoferiana*. If mature sporophytes are present, *M. japonica* is immideately recognized due to its strongly reduced peristome, hardly exceeding above the large, decidous annulus and looking like absent. All other species of *Mielichhoferia* known in Russia have well-developed peristome with teeth longer than 150 μm.

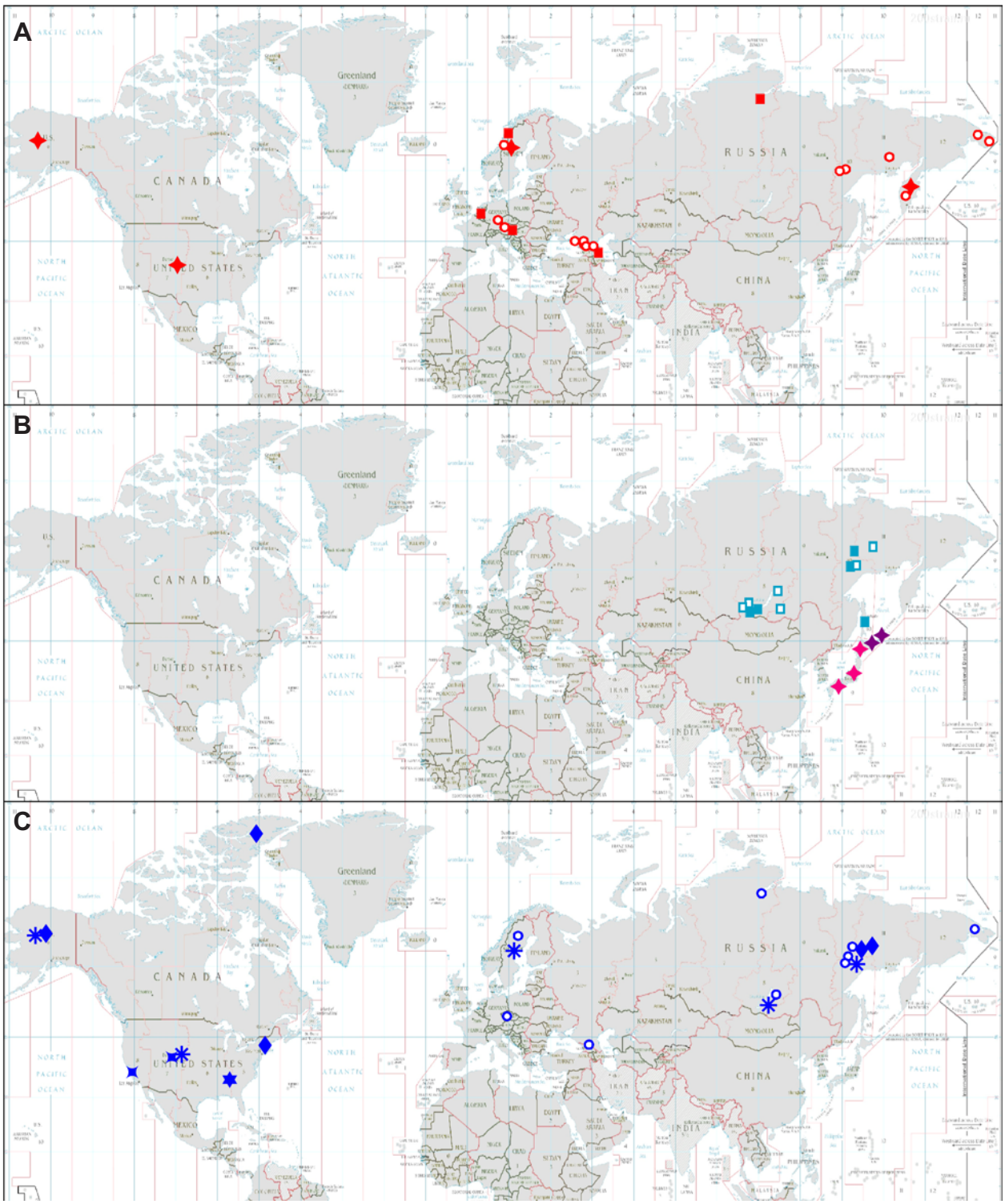

Fig. 8. Distribution of four *Mielichhoferia* species known in Russia, using data on haplotypes found by Shaw (2000). A: *M. mielichhoferiana*: four-pointed stars – M1 haplotype; solid squares – M2 haplotype; open circles – specimens referred to M. *mielichhoferiana* by morphology. B: *M. asiatica* (solid squares – sequenced, E2 haplotype; open squares – referred by morphology) and *M. japonica* (dark stars – sequenced; light stars – referred by morphology and literature records). C: *M. elongata* (four-pointed star – E1 haplotype; eight-pointed star – E3 haplotype; six-pointed star – E4 haplotype; diamonds – E5 haplotype; open circles – referred by morphology). Marks outside Russia are put partly with the country/state level of exactness.

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Appendix 1. Species of *Mielichhoferia* and *P. nutans* used in analyses, with GenBank accession numbers and voucher information for specimens from Russia. The numbers of newly generated sequences are boldfaced.

Species	# / isolate	nrITS1-2	trnL-F	rps4	Specimen data (for newly generated sequences)
mielichhoferiana	508-M13	**MG707202**	**MG707219**	**MG719364**	Russia, Caucasus, Dagestan, 25.VIII.2011, *Kozeruba s.n.* (MHA ex LE)
mielichhoferiana	OK1751	**MG707203**	**-**	**-**	Russia, Anabar, *Fedosov 11-335* (MW9048191)
mielichhoferiana	506-M11	**MG707204**	**MG707220**	**MG719365**	Russia, Kamchatka, Zhupanovsky Volcano, 18.VII.2006, *Makarova 50* (MHA ex LE)
mielichhoferiana	500-M5	**MG707205**	**MG707221**	**MG719366**	Russia, Kamchatka, 10.VIII.2006, *Czernyadjeva s.n.* (Bryophyta Rossica #231, LE)
mielichhoferiana	507-M12	**MG707206**	**MG707222**	**MG719367**	USA, Alaska, 15.VII.1993, *Afonina s.n.* (MHA ex LE)
japonica	511-M16	**MG707207**	**MG707223**	**MG719368**	Russia, Kuril, Islands, Iturup, *Pisarenko 05820* (MHA ex NVS)
japonica	498-M3	**MG707208**	**MG707224**	**MG719369**	Russia, Kuril Islands, Kunashir, *Ignatov 06-1616* (MHA)
asiatica	495	**MG707209**	**MG707225**	**MG719370**	Russia, Buryatia, 09.VII.2015, *Tubanova O1504/09* (UUH)
asiatica	504-M9	**MG707210**	**MG707226**	**MG719371**	Russia, Yakutia_Mus-Khaya, *Ignatov & Ignatova 11-3279* (MHA)
asiatica	503-M8	**MG707211**	**MG707227**	**MG719372**	Russia, Yakutia, Suntar-Khayata, Sukhaya Creek, *Ignatov & Ignatova 15-38* (MHA)
asiatica	499-M4	**MG707212**	**–**	**MG719373**	Russia, Irkutsk Province, 08.VI.2005, *Ignatov & Kazanovsky s.n.* (Mosses of Russia 128, MHA)
asiatica	497-M2	**MG707213**	**MG707228**	**MG719374**	Russia, Sakhalin, *Pisarenko 03215* (MHA)
elongata	509-M14	**MG707214**	**MG707229**	**MG719375**	Russia, Transbaicalia, Kodar, 12.VI.2015, *Afonina 0915* (MHA ex LE)
elongata	505-M10	**MG707215**	**MG707230**	**MG719376**	Russia, Yakutia, Ust-Nera, *Ignatov & Ignatova 15-1553* (MHA)
elongata	OK1753	**MG707216**	**-**	**-**	Yakutia, Yakutia, Ust-Nera, *Ignatov & Ignatova 15-1553* (MHA)
elongata	502-M7	**MG707217**	**MG707231**	**MG719377**	Russia, Yakutia, Zayachya Petlya, *Ignatov & Ignatova 15-324* (MHA)
elongata	501-M6	**MG707218**	**MG707232**	**MG719378**	Russia, Yakutia, Mus-Khaya, *Ignatov & Ignatova 11-3278* (MHA)
pontevedrensis	SB180	AF144205	–	–	Spain
shevockii	SB169	AF144204	–	–	USA
elongata	SB346	AF144180	–	–	Canada, Alaska Dean
elongata	SB197	AF144173	–	–	Canada, Ellesmere Island
elongata	SB151	AF144179	–	–	Sweden
elongata	SB159	AF144175	–	–	Sweden
elongata	SB153	AF144174	–	–	Sweden
elongata	SB17	AF144176	–	–	Sweden
elongata	SB148	AF144177	–	–	Sweden
elongata	SB533	AF144181	–	–	USA, Alaska
elongata	SB11	AF144134	–	–	USA, California
elongata	SB13	AF144136	–	–	USA, California
elongata	SB172	AF144145	–	–	USA, California
elongata	SB90	AF144168	–	–	USA, Colorado
elongata	SB25	AF144153	–	–	USA, Colorado
elongata	SB185	AF144154	–	–	USA, Colorado
elongata	SB189	AF144159	–	–	USA, Colorado
elongata	SB9	AF144163	–	–	USA, Tennessee
mielichhoferiana	SB227	AF144202	–	–	Austria, Tirol
mielichhoferiana	SB66	AF144195	–	–	Belgium, Vielsalm
mielichhoferiana	SB16	AF144191	–	–	Norway
mielichhoferiana	SB154	AF144186	–	–	Sweden
mielichhoferiana	SB157	AF144187	–	–	Sweden
mielichhoferiana	SB160	AF144188	–	–	Sweden
mielichhoferiana	SB158	AF144189	–	–	Sweden
mielichhoferiana	SB161	AF144190	–	–	Sweden
mielichhoferiana	SB221	AF144199	–	–	USA, Alaska
mielichhoferiana	SB222	AF144200	–	–	USA, Alaska
mielichhoferiana	SB223	AF144201	–	–	USA, Alaska
mielichhoferiana	SB1	AF144192	–	–	USA, Colorado
mielichhoferiana	SB182	AF144194	–	–	USA, Colorado
mielichhoferiana	SB187	AF144197	–	–	USA, Colorado
Pohlia nutans	J013	EU878201		FJ593886	Japan.