

## ON MOSS FAMILY LEMBOPHYLLACEAE IN THE RUSSIAN FAR EAST

### О МХАХ СЕМЕЙСТВА LEMBOPHYLLACEAE НА РОССИЙСКОМ ДАЛЬНЕМ ВОСТОКЕ

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Abstract

An integrative approach to the revision of the Lembophyllaceae in the Russian Far East, including molecular phylogenetic and morphological studies, revealed five species, three of *Dolichomitriopsis*, including one new species, *Dolichomitriopsis cherdantseviae*, and one species of *Dolichomitra*, one new genus *Dolichomitriadelphus* for the taxon commonly known as *Isothecium hakkodense*. The species known as *Isothecium subdiversiforme* is still not found in Russia, so it was analyzed based on Japanese material and also determined to be unrelated to any other species of Lembophyllaceae, thus it is segregated in a genus of its own, *Isotheciastrum*. The combined analysis of European, Asian and American species shows that the genus *Isothecium* has mostly Amphiatlantic distribution and combines species of *I. alopecurooides* affinity. The group of *Isothecium myosuroides* and related species form a clade sister to Asian *Dolichomitra*, *Dolichomitriopsis*, *Isotheciastrum*, and American *Bryolawtonia* and *Tripterocladium*. This fact suggests a resurrection of the genus *Pseudisothecium* Grout for *I. myosuroides*, *I. stoloniferum*, *I. interludens*, *I. prolixum*, *I. montanum*, *I. holtii*, *I. cardotii*, and *I. cristatum*. All species of the family from the Russian Far East are illustrated and the variation of their morphology is discussed.

Резюме

Интегративный подход к ревизии гербарных образцов Lembophyllaceae с российского Дальнего Востока, включающий молекулярно-филогенетический анализ и сравнение морфологических признаков, позволил выявить в регионе пять видов, три из которых относятся к роду *Dolichomitriopsis*, один из них новый для науки, *Dolichomitriopsis cherdantseviae*, а также один вид из рода *Dolichomitra* и один вид из нового рода *Dolichomitriadelphus*, ранее известный как *Isothecium hakkodense*. *Isothecium subdiversiforme*, пока не найденный в России, был также включен в анализ с использованием образцов из Японии; он оказался не родственником ни одному из известных видов Lembophyllaceae, и на этом основании он выделен в особый род *Isotheciastrum*. Комбинированный анализ европейских, азиатских и американских видов показал, что род *Isothecium* имеет б.ч. амфиатлантическое распространение и объединяет виды из родства *I. alopecurooides*. *Isothecium myosuroides* и родственные ему виды образуют кладу, сестринскую азиатским видам из родов *Dolichomitra*, *Dolichomitriopsis*, *Isotheciastrum*, а также американским видам из родов *Bryolawtonia* и *Tripterocladium*. Это предполагает восстановление рода *Pseudisothecium* Grout для *I. myosuroides*, *I. stoloniferum*, *I. interludens*, *I. prolixum*, *I. montanum*, *I. holtii*, *I. cardotii* и *I. cristatum*. Приводятся иллюстрации для всех российских дальневосточных видов семейства и обсуждается вариабельность их морфологических признаков.

KEYWORDS: bryophytes, molecular phylogeny, taxonomy, branch primordia, *Isotheciastrum*, *Dolichomitriadelphus*, *Dolichomitra*, *Dolichomitriopsis*, *Pseudisothecium*

#### INTRODUCTION

Recent check-list of the moss flora of Russia (Ignatov *et al.*, 2006) and of Far Eastern mosses (Cherdantseva *et al.*, 2018) mentioned only two species of the Lembophyllaceae in the Russian Far East: *Dolichomitriopsis diversiformis* (Mitt.) Nog. and *Isothecium hakkodense* Besch.

Even despite of only two, these species were not always correctly identified in herbaria. The difficulties in identification were caused by broad variation, absence of characters which are easy to present in manuals, and due to placement these two species into different genera, moreover, classified in different families and published in the

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“Illustrated moss flora of Japan” in different volumes (Noguchi & Iwatsuki, 1989; Noguchi *et al.*, 1991).

The species of *Isothecium* are widespread in Europe and Macaronesia, and two most common European species, *I. alopecuroides* (Lam. ex Dubois) Isov. and *I. myosuroides* Brid., extend to the western regions of European Russia, whereas species of *Isothecium* are absent in the territories east of the Caucasus and up to the Russian Far East, where *I. hakkodense* occurs. The original intention of this study was to check if the generic position of the latter species can be confirmed using a molecular phylogenetic approach.

However, it soon became clear that the East Asian Lembophyllaceae comprise a more puzzling complex, thus more groups of this family were involved in the study.

The circumscription of the family Lembophyllaceae is vague. It originally included four genera: *Camptochaete*, *Dolichomitra*, *Isothecium*, and *Lembophyllum* (Brotherus, 1907). The subsequent challenges in the scope of the family were overviewed by Tangney (1997), who accepted in it *Camptochaete*, *Fallaciella*, *Fifea*, *Lembophyllum* and *Weymouthia*, moving ten genera to other families. For example, *Isothecium* was placed in Brachytheciaceae and *Dolichomitriopsis* in Meteoriaceae.

The same circumscription of the family was accepted by Quandt *et al.* (2000), who considered it as a sister clade to Meteoriaceae; further Quandt *et al.* (2009) expanded it based on molecular phylogenetic reconstruction and included in the family a suite of lineages sister to the Lembophyllaceae sensu Tangney (1997). Their paper provides a historical overview of the Lembophyllaceae circumscription. Classification by Frey & Stech (2009) mostly follows Quandt *et al.* (2009); 14 genera are accepted in the Lembophyllaceae: *Bestia*, *Camptochaete*, *Dolichomitra*, *Dolichomitriopsis*, *Fallaciella*, *Fifea*, *Isothecium*, *Lembophyllum*, *Looseria*, *Neobarbella*, *Pilotrichella*, *Rigodium*, *Tripterocladium*, and *Weymouthia*. Goffinet *et al.* (2009) also included in the Lembophyllaceae the genera *Acrocladium* and *Orthostichella*, but did not include *Dolichomitra*, *Rigodium* and *Tripterocladium*. Since then, *Nogopterium* (= *Pterogonium*) appeared in some molecular phylogenetic analyses within the Lembophyllaceae (Troitsky *et al.*, 2008) or sister to that family (Huttunen *et al.*, 2012; Ignatov *et al.*, 2019) and thus it was placed in this family along with *Mawenzhangia*, newly described from Yunnan (Enroth *et al.*, 2018). *Orthostichella* was placed in a separate family (Enroth *et al.*, 2019). Finally, Ignatov *et al.* (2019) based on the molecular phylogenetic reconstruction of the Neckeraceae-Orthostichellaceae-Lembophyllaceae phylogeny suggested the inclusion of *Heterocladium* s.str. in the Lembophyllaceae. However, differences in the obtained topologies occurred from study to study, partly due to the differences in representation of the genera and partly due to different studied markers.

*Isothecium* was the only genus in focus of special molecular studies and therefore it was extensively sampled

(Draper *et al.*, 2007, 2015), but mostly European species were involved in these studies and thus affinities of Asian representatives of the genus were not comprehensively addressed until now. The aim of the present study was to consider Asian species of *Isothecium* and closely related genera in the broader molecular phylogenetic context and to estimate their affinities based on the obtained reconstructions.

## MATERIAL AND METHODS

### *Molecular phylogenetic studies*

The material used in the present study was sampled from MW and MHA and supplemented by sequences available in GenBank. For the molecular-phylogenetic study we used five markers, nuclear ITS1,2 and 5.8 rRNA gene, plastid *trnG* intron and *trnS-F* region, which were successfully used in phylogenetic studies of Lembophyllaceae and related families (Vanderpoorten *et al.*, 2002; Draper *et al.*, 2007, 2015; Olsson *et al.*, 2009; Quandt *et al.*, 2009; Hodgetts & Vanderpoorten, 2018, *etc.*). Besides the representatives of Lembophyllaceae from temperate areas of Asia, the closely related lineages of *Isothecium* were originally sampled for phylogenetic study. In total, 19 ingroup specimens were studied *de novo*. The obtained alignments were added by ITS, *trnG* and *trnL-F* sequences of *Isothecium* from GenBank, obtained by Draper *et al.* (2007, 2015), and by ITS & *trnL-F* (in some cases *trnT-trnF* or *trnS-trnF*) sequences of miscellaneous lineages of Lembophyllaceae obtained by Quandt *et al.* (2000, 2009) and Olsson *et al.* (2009). To provide representation of major clades of pleurocarpous mosses, both closely related groups and putative outgroups, sequences for suite of species well represented in GenBank were included based on the previously published reconstructions and our alignment designed for phylogenetic study of *Anomodon* and *Heterocladium* (Ignatov *et al.*, 2019). Vouchers of the newly studied specimens and GenBank accession numbers of all used sequences are compiled in Appendix 1.

The laboratory protocol was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005) and Hedenäs (2017). Sequences were aligned using MAFFT v. 7.402 (Katoh & Standley, 2013) with standard settings and then edited manually in BioEdit (Hall, 1999). At first, ITS (124 terminals, 792 bp), *trnG* (94 terminals, 616 bp), *trnL-F* (134 terminals, 431 bp) and *trnS-F* + *trnL-F* (56 terminals, 1938 bp), were analyzed separately to check their congruence. Since no supported conflict of topologies were observed among the trees inferred from these markers, the combined ITS - *trnG* - *trnS-F*, (including *trnL-F*) dataset (83 terminals, 3346 bp), divided into two partitions, for nr and cp data, was analyzed. In all analyses indels were coded using simple indel coding approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1 (Müller, 2005). An inversion in the *trnL-trnF* spacer was coded by binary code.

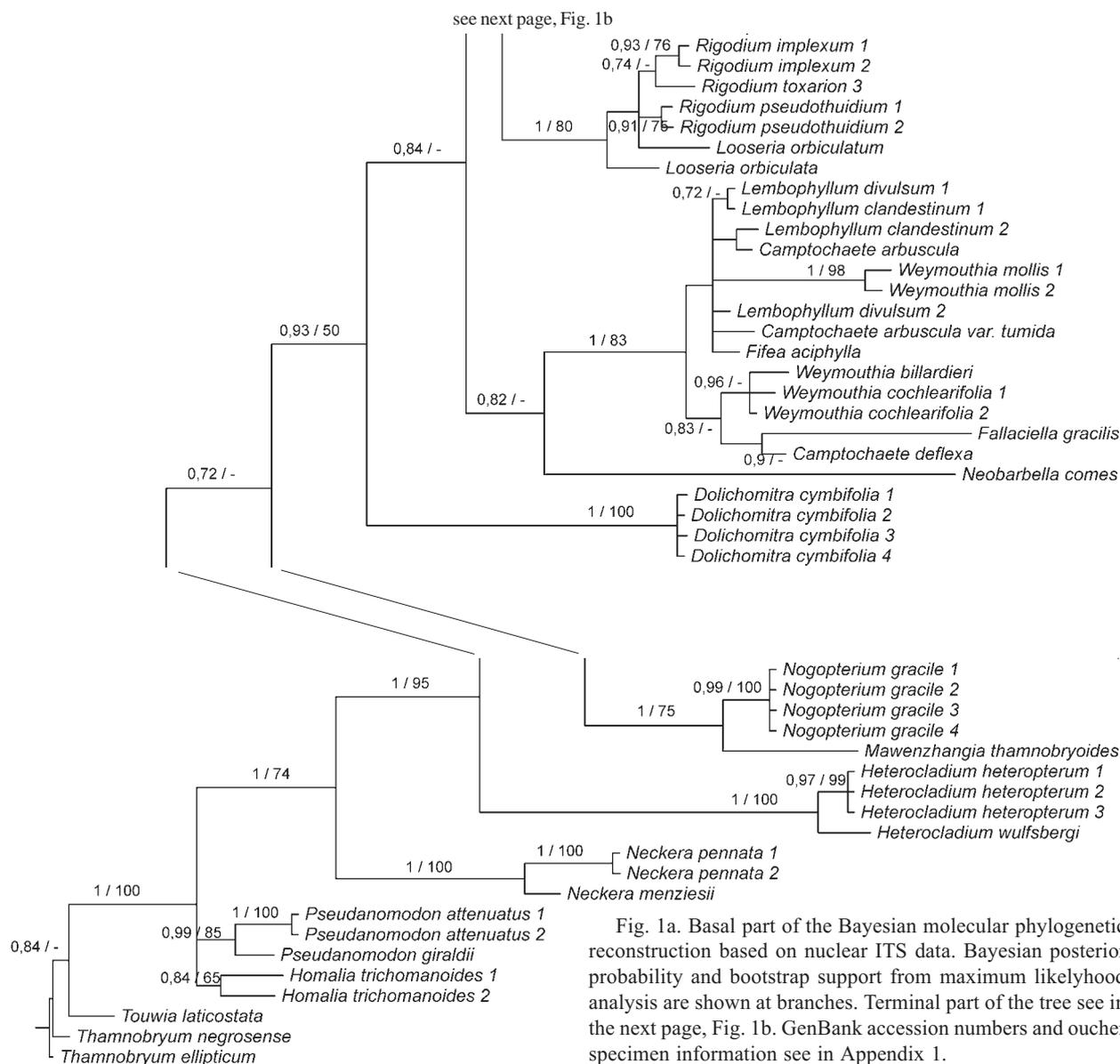


Fig. 1a. Basal part of the Bayesian molecular phylogenetic reconstruction based on nuclear ITS data. Bayesian posterior probability and bootstrap support from maximum likelihood analysis are shown at branches. Terminal part of the tree see in the next page, Fig. 1b. GenBank accession numbers and voucher specimen information see in Appendix 1.

Bayesian Analyses were performed by running two parallel analyses in MrBayes 3.2.7a (Ronquist *et al.*, 2012). For the single gene sets analyses each run consisted of six Markov chains, 10 000 000 generations with default number of swaps and sampling frequency one tree each 2500 generations. For the combined dataset the analysis consisted of eight Markov chains and 25 000 000 generations, with the default number of swaps and sampling frequency one tree each 5 000 generations was performed. The chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007). Consensus trees were calculated after omitting the first 25% trees as burn-in. 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 itera-

tions. Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>) on XSEDE (Miller *et al.*, 2010). The default outgroup for rooting the trees was evaluated using the previously published reconstructions of the backbone phylogeny of pleurocarpous mosses (Huttunen *et al.*, 2012).

**Morphological studies** were conducted by a standard method, with additional attention to the structure of branch primordia, and especially proximal branch leaves. Previous studies of Spirina & Ignatov (2015) found them to have diverse and unusual structure, thus we studied them with the goal to find additional characters, important as morphological distinctions between genera that are not contrasting enough in the Lembophyllaceae. For SEM study we took several branches of one specimen selected as "typical" for the species after ordinary observation under light microscope. Chosen herbarium samples were soaked in wa-

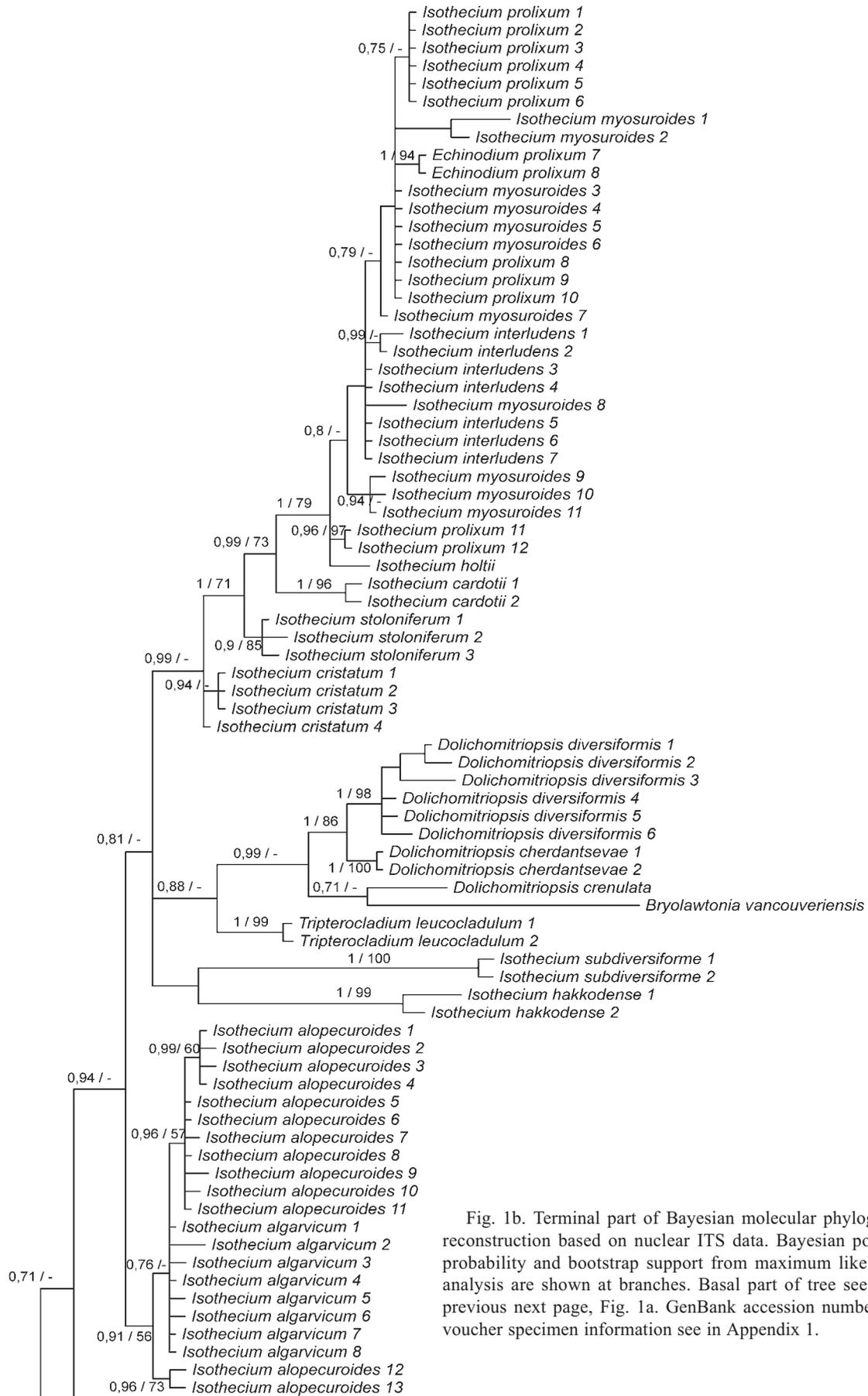


Fig. 1b. Terminal part of Bayesian molecular phylogenetic reconstruction based on nuclear ITS data. Bayesian posterior probability and bootstrap support from maximum likelihood analysis are shown at branches. Basal part of tree see in the previous next page, Fig. 1a. GenBank accession numbers and voucher specimen information see in Appendix 1.

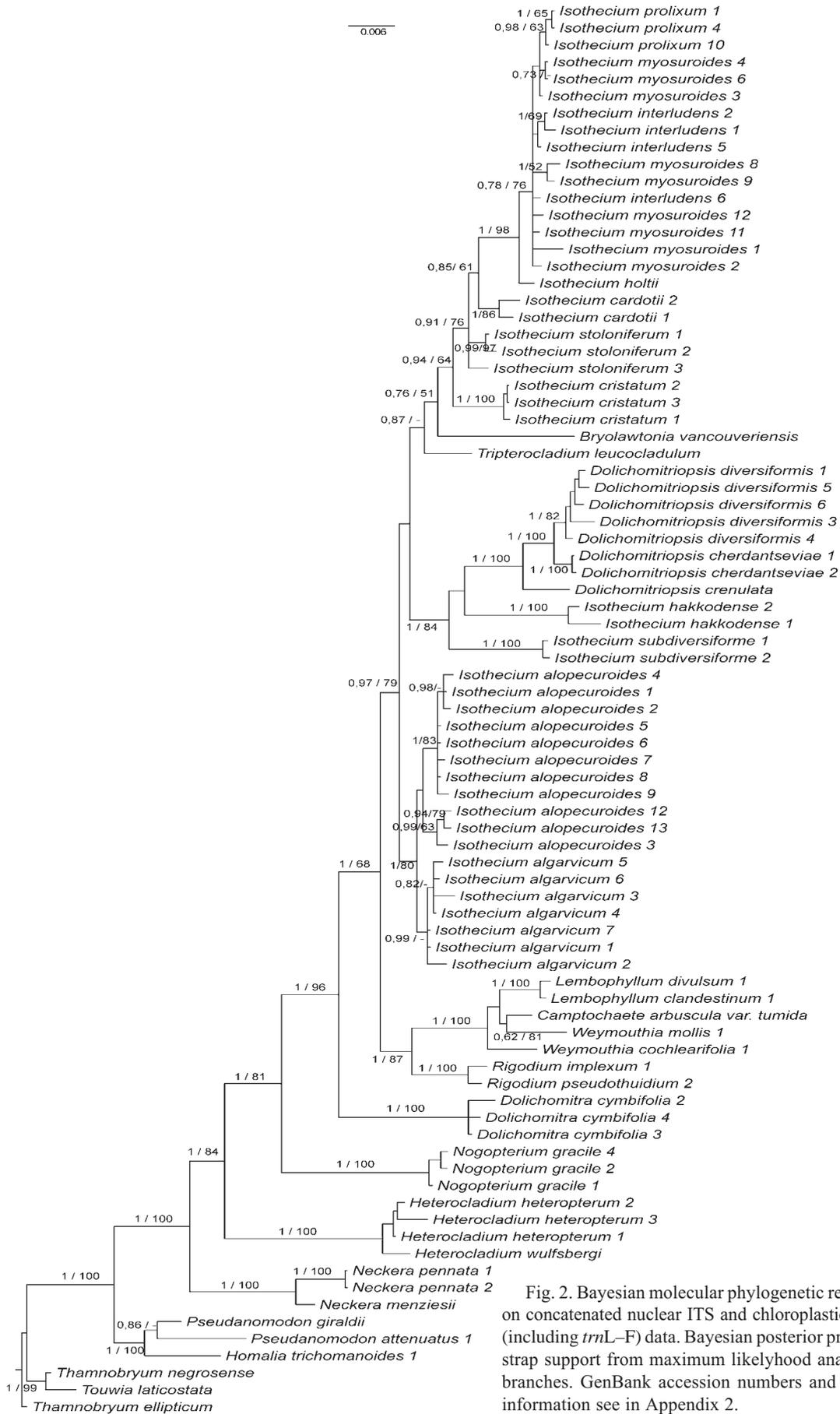


Fig. 2. Bayesian molecular phylogenetic reconstruction based on concatenated nuclear ITS and chloroplastic ITS-trnG-trnS-F (including trnL-F) data. Bayesian posterior probability and bootstrap support from maximum likelihood analysis are shown at branches. GenBank accession numbers and voucher specimen information see in Appendix 2.

ter for 24 hours, then fixed in 2,5% glutaraldehyde for 24 hours, post-fixed with 1% osmium tetroxide, water solution, for 3 hours. Then material was dehydrated through a graded ethanol/acetone series to 100% acetone and dried at a critical point, covered by gold and observed under SEM Jeol 6380. Partly previously done SEM images are used here: they were obtained under a similar preparation, under SEM LEO-430.

## RESULTS

### **Molecular phylogeny.**

Lembophyllaceae s.l., including *Heterocladium* and *Nogopterium*+*Mawenzhangia* were resolved as monophyletic, originating from the Neckeraceae s.l. ancestral groups. The difference between ITS and ITS+trnS-F+trnG analyses refer to the support values for two basal lineages, *Heterocladium* and *Nogopterium*+*Mawenzhangia*. The high statistical support in the ITS tree was found only for Lembophyllaceae s.l. (PP=1, ML=96), while the clade without these three genera, Lembophyllaceae s. str., has low support (PP=0.93, ML=50). The concatenated tree has higher support for Lembophyllaceae s. str. (PP=1, ML=96) than for Lembophyllaceae s.l. (PP=1, ML=84).

The most basal lineage in the Lembophyllaceae s. str. is the East Asian monospecific genus *Dolichomitra*. Next in the grade are mostly South Hemispheran clades of *Rigodium* and “core Lembophyllaceae” (in ITS tree, Fig. 1); which are combined in one clade in the concatenated tree (Fig. 2), and terminal clade is composed of *Isothecium* and related taxa, most of them were earlier treated in the genus *Isothecium*. The genera of intermediate clade, *Camptochaete*, *Fallaciella*, *Fifea*, *Lembophyllum*, *Looseria*, *Neobarbella*, *Rigodium*, and *Weymouthia* are included in the present analysis to be certain that the species of the Far Eastern Lembophyllaceae do not relate to any of them; this is obvious from the topology in Figs. 1 and 2, therefore, we do not address this group in detail.

The terminal, “*Isothecium* s.l.”-clade, is low supported in ITS tree (PP=0.94 / BS<50), and only a little more in concatenated tree (PP=0.97 / BS=79). The tree inferred from the analysis of combined dataset revealed in “*Isothecium* s.l.”-clade three subclades, where clade (1) *Isothecium alopecuroides* + *I. algarvicum* W.E. Nicholson & Dixon, with PP=1, BS=80, is sister to the join clade of other taxa, though the latter has very short branch and no support (PP<70, BS<50). This join clade is formed of two subclades: (2) “East Asian” clade (PP=1, BS=84), including species of the East Asian genus *Dolichomitriopsis* and two East Asian species treated as *Isothecium*, *I. hakkodense* and *I. subdiversiforme* Broth., and (3) the clade of species around *Isothecium myosuroides*. The latter includes several North American species, *I. stoloniferum* Brid., *I. cardotii* Kindb., and *I. holtii* Kindb., Macaronesian *I. prolixum* (Mitt.) M. Stech, Sim-Sim, Tangney & D. Quand and West European *I. interludens* Stirt. and also two North American genera from Pacific North-West, *Bryolawtonia* and *Tripterocladium*.

In ITS tree *Bryolawtonia* and *Tripterocladium* occur in a different position, clustering with East Asian species as follows. The East Asian group is not resolved as a clade, but as two clades in tritomy, where the third is the clade of species around *Isothecium myosuroides*. One of clades (without support) includes two highly supported clades of two specimens of *Isothecium hakkodense* and of two specimens of *Isothecium subdiversiforme*. The second clade has a low support as a whole (PP=0.88, <50), it includes a clade of two specimens of *Tripterocladium* (PP=1, ML=99), which is sister to moderately supported clade of *Dolichomitriopsis*+*Bryolawtonia* (P=0.99, ML<50). In the latter *Bryolawtonia* forms the almost unsupported clade with *Dolichomitriopsis crenulata* S. Okamura (P=0.71, ML<50), sister to the rest of *Dolichomitriopsis* (P=1, ML=86), composed of two clades, one of six specimens of *D. diversiformis* (PP=1, ML=98) and of two specimens of a new species described below (PP=1, ML=100).

### **Observation on branch primordia morphology**

The SEM pictures in Figs. 3–5 show polymorphism seen even within one sample, providing difficulties in their descriptions. Below we describe proximal branch leaves and branch primordia structures following terminology explained in detail in Spirina & Ignatov (2015).

In *Dolichomitra*, Figs. 3A–C, the first and second proximal branch leaves are compound, with their parts sometimes spaced, short triangular to oblate or just in a shape of low ridge, entire to serrate and incised. The third or sometimes also fourth and fifth proximal branch leaves are shallowly bilobed. Overall branch primordium shape is low hemispheric, with rather remote position of outer elements.

In *Lembophyllum*, Figs. 3D–F, the first proximal branch leaf is steadily reduced but the second one is developed, it is entire or slightly dissected, while the third one is divided into 2 or 3 lobes almost to the base. Leaves are obtuse and overall shape of branch primordium is about compact hemispheric.

In *Camptochaete*, Figs. 3G–I, the first or the first and second proximal branch leaves are reduced. If the second leaf is present it is either dissected into 2–4 lobes or entire. The third leaf often is bilobed or rarely entire. Overall branch primordium shape is low hemispheric.

*Rigodium brachypodium* (Müll. Hal.) Paris, Figs. 3J–L, has constant reduction of the first leaf and occasional presence of the compound second one, with closely arranged 3–5 triangle segments, often without apparent connection to each other at the level of stem surface. The third leaf is hood-like, entire or bilobed and dissected almost to the base and sometimes even compound. Branch primordium is low hemispheric, moderately compact.

In *Isothecium subdiversiforme*, Figs. 3M–O, the proximal branch leaves at early stage are oblate, widely rounded and clearly bilobed, with the first proximal branch leaf occasionally reduced. More developed proximal branch leaves are distally truncate and serrulate

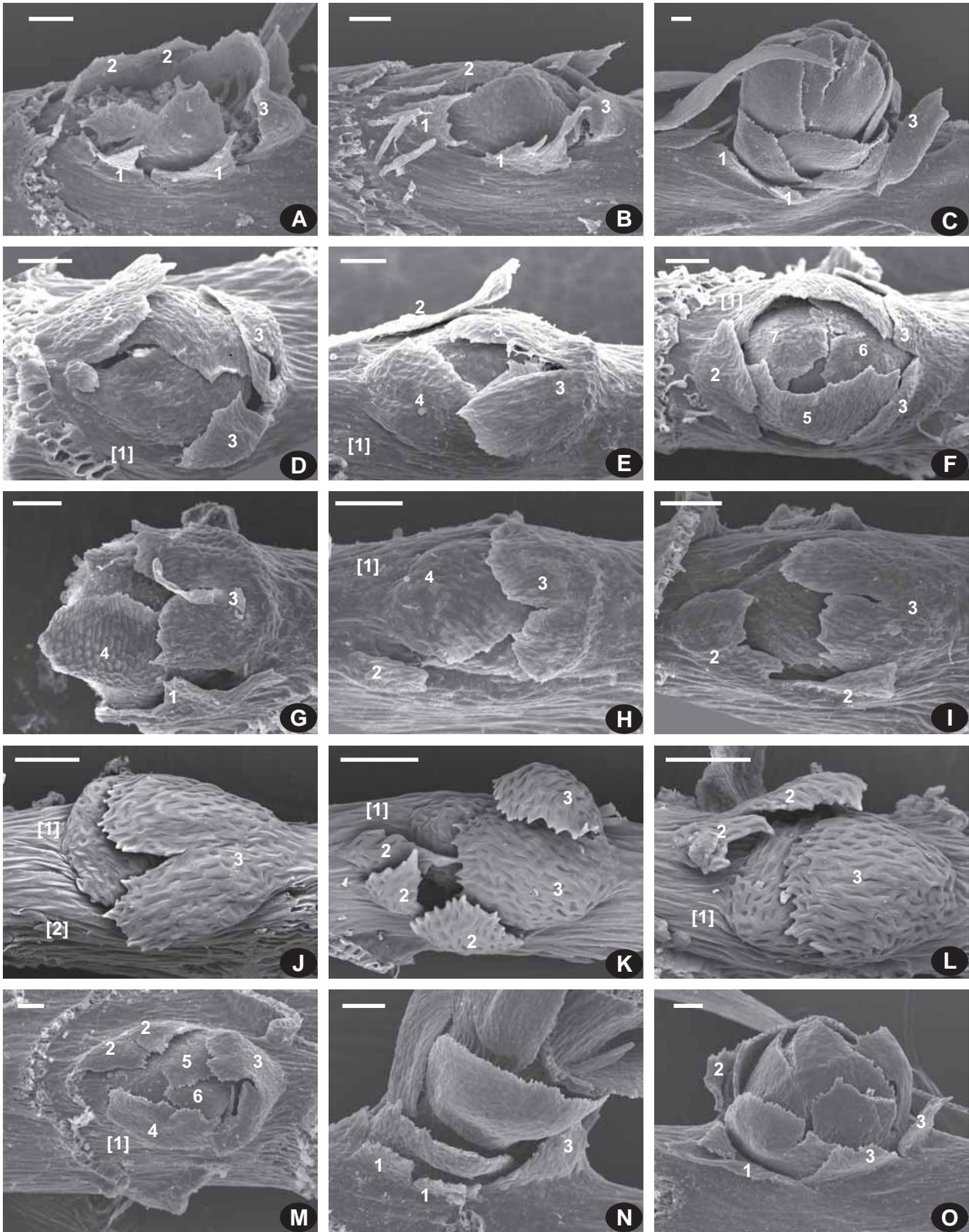


Fig. 3. Branch initials with proximal branch leaves of species of the Lembophyllaceae: A–C: *Dolichomitra cymbifolia* (Kuril Islands, *Bakalin K-45-29-07* MHA); D–F: *Lembophyllum divulgum* (Hook. f. & Wilson) Lindb. (Australia, *Streimann 59035* MHA); G–I: *Camptochaete arbuscula* (Sm.) Reichardt (Australia, *Streimann 49126* MHA); J–L: *Rigodium brachypodium* (Chile, *Crosby 11893* MHA); M–O: *Isoetes subdiversiforme* (Japan, *Ignatov & Ignatova 98-580* MHA). Scale bar: 50  $\mu$ m for all. Numerals indicate the proximal leaf number (cf. explanation in Spirina & Ignatov, 2015), with numbers of reduced leaves given in brackets and parts of compound leaves marked by the same numeral. Stem apex is on the right hand side.

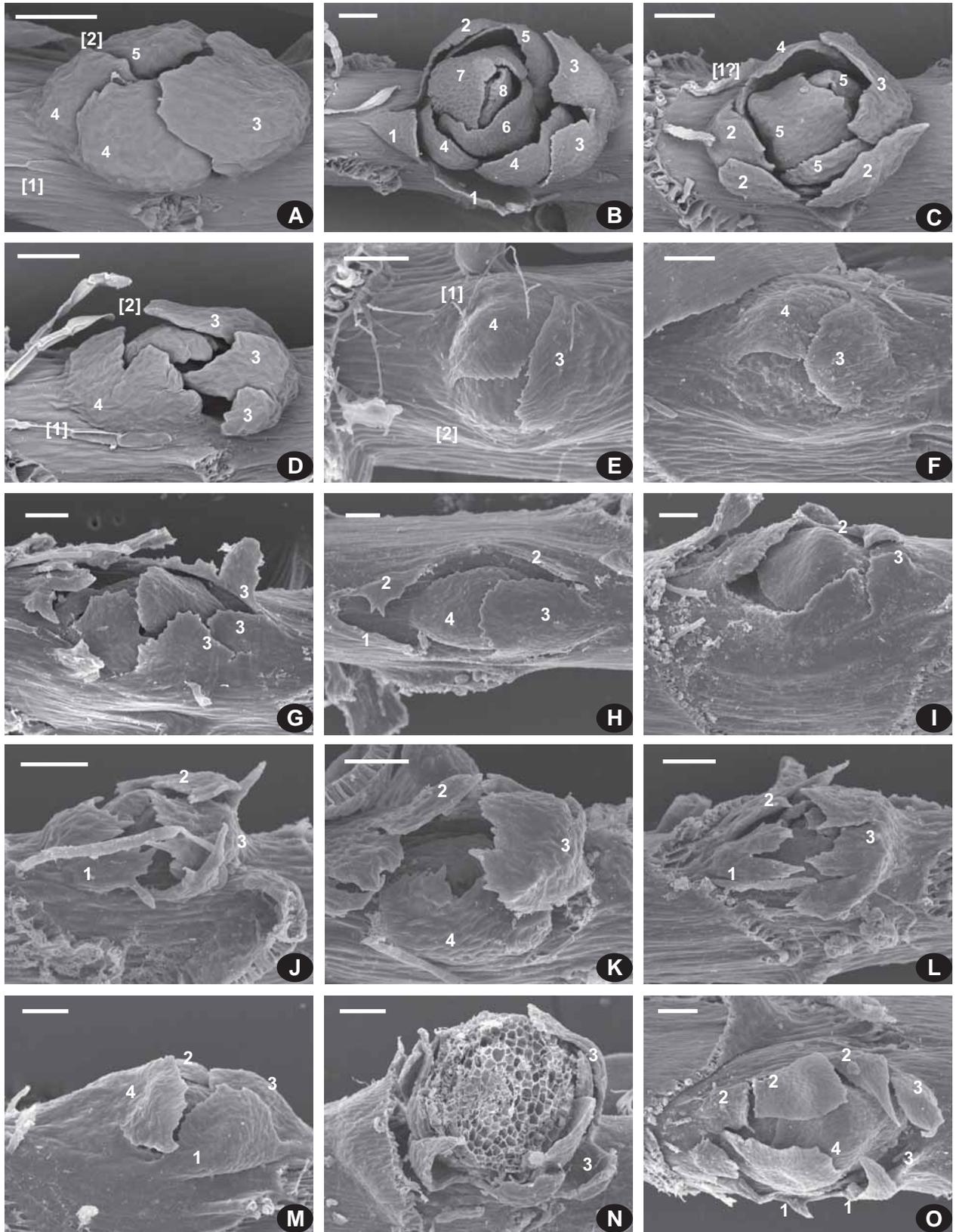


Fig. 4. Branch initials with proximal branch leaves of species of the Lemnophyllaceae: A–D: *Isothecium alopecuroides* (Russia, Ignatov & Ignatova 56/2, MHA9038346); E–F: *Pseudisothecium cristatum* (USA, 7 Aug 1989 Ignatov s.n., MHA 9055205); G–I: *Pseudisothecium stoloniferum* (USA, Shevock 31779, MHA 9055241); J–L: *Pseudisothecium myosuroides* (Krasnodar, Teplov 2015-029, MHA9038401); M–O: *Isothecium hakkodense* (Russia, Kuril Islands, Ignatov 06-1125, MHA9109600). Scale bar: 50  $\mu$ m for all. Numerals indicate the proximal leaf number (cf. explanation in Spirina & Ignatov, 2015), with numbers of reduced leaves given in brackets and parts of compound leaves marked by the same numeral. Stem apex is on the right hand side.

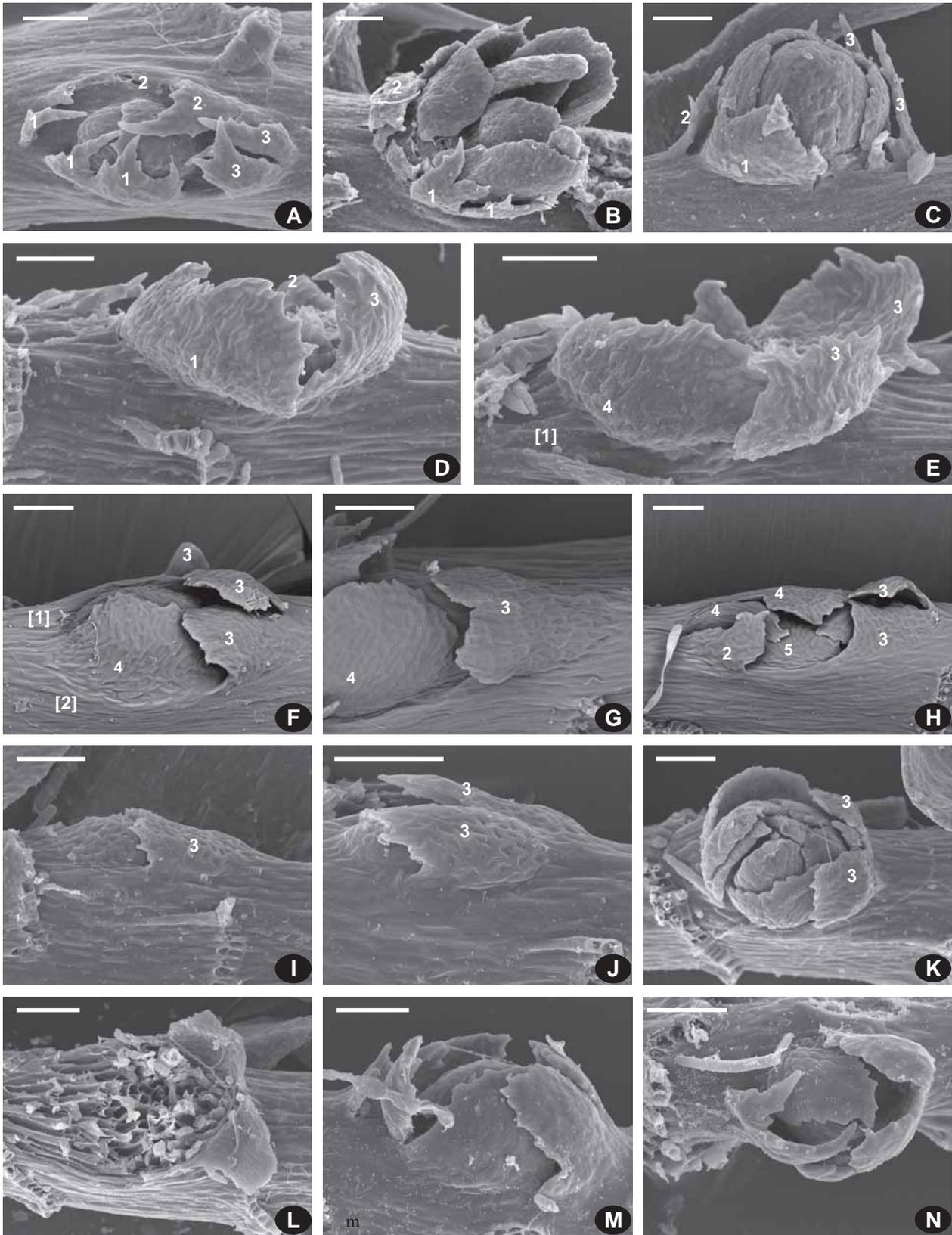


Fig. 6. Branch initials with proximal branch leaves of species of the Lembophyllaceae: A–C: *Dolichomitriopsis diversiformis* (Russia, Koroteeva 15-10/4-3, MHA); D–E: *Dolichomitriopsis cherdantseviae* (Russia, Kuril Islands, Ignatov 06-2107, MHA); F–H: *Dolichomitriopsis crenulata* (Japan, 19 Nov. 1961, Ikegami s.n., MHA); I–L: *Bryolawtonia vancouverensis* (USA, 8 Aug 1989, Ignatov & Norris s.n., MHA9051011); M–N: *Tripterocladium leuocladum* (Canada, 23 Apr 1979 Schofield s.n., MHA9059395). Scale bar: 50 μm for all. Numerals indicate the proximal leaf number (cf. explanation in Spirina & Ignatov, 2015), with numbers of reduced leaves given in brackets and parts of compound leaves marked by the same numeral. Stem apex is on the right hand side.

along the margin. Branch primordium is hemispheric, moderately compact.

In *Isothecium alopecuroides*, Figs. 4A–D, the proximal branch leaves are broadly ovate to suborbicular, and even if they are strongly divided into lobes, e.g., in Figs. 4C–D, their parts look broad and obtuse. The outermost and subsequent leaves are similar, so when the first or first and second proximal branch leaves are reduced, the existing leaves form the same shape, so branch primordium as a whole looks compact hemispheric.

In *Isothecium cristatum* (Hampe) H. Rob., Figs. 4E–F, the proximal branch leaves are broad, entire, and the first one is in 12 o'clock position, indicating that first and second proximal branch leaves are reduced. Overall shape of branch primordium is low hemispheric.

In *Isothecium stoloniferum*, Figs. 4G–I, the proximal branch leaves are entire, bilobed, incised to compound, reduced to low ridges beside primordium to well-developed, crenulate along margins. Overall shape of branch primordium is loose hemispheric or it is represented by an open group of low elements.

In *Isothecium myosuroides*, Figs. 4J–L, the proximal branch leaves are incised, lacinate to compound, entire, bilobed, incised to compound, reduced to low ridges beside primordium to well-developed, crenulate along margins. Overall shape of branch primordium is loose hemispheric or it is represented by an open group of low elements.

In *Isothecium hakkodense*, Figs. 4M–O, the proximal branch leaves are broadly ovate to compound of also highly variable parts, from oblate to narrowly triangular, irregularly crenulate along margins. Overall shape of branch primordium is low hemispheric.

*Dolichomitriopsis diversiformis*, Figs. 5A–C, has compound outermost proximal branch leaves, with incised segments; in observed specimens no complete reduction was observed, i.e. the first proximal leaf was in 4 o'clock position. Overall shape of branch primordium is hemispheric.

In *Dolichomitriopsis* [new species], Figs. 5D–E, the first and second outer branch leaves may be reduced or present, but in both cases the outermost proximal branch leaves are broadly oblate, serrate, bilobed or entire. Overall shape of branch primordium is low, moderately compact hemisphere.

In *Dolichomitriopsis crenulata*, Figs. 5F–H, the first and second proximal branch leaves are usually completely reduced, although rarely small lamina of the second leaf is developed; third leaf is bilobed, sometimes with more lobes; overall shape of branch primordium is low hemispheric.

*Bryolawtonia*, Figs. 5I–K, has relatively invariable branch primordia with the outermost proximal branch leaf in 12 o'clock position, which means the reduction of the first and second proximal branch leaves, typical for Brachytheciaceae (Ignatov, 1999). Contrary to Brachytheciaceae, however, this outermost leaf is bilobed. Branch primordium is flat at early stage to compact hemispheric later.

ciaceae, however, this outermost leaf is bilobed. Branch primordium is flat at early stage to compact hemispheric later.

In *Tripterocladium*, Figs. 5L–N, proximal branch leaves are deeply bilobed, with narrow to broad-ovate lobes; branch primordium in hemispheric, moderately compact.

#### DISCUSSION

Lembophyllaceae were found monophyletic both *sensu lato*, including *Heterocladium* and *Nogopterium*+*Ma-wenzhangia*, and *sensu stricto*, without these three genera. As the present sampling was not focused specifically on the whole Lembophyllaceae, the controversy of these results cannot be properly discussed here. The more distal position of *Heterocladium* from Lembophyllaceae was found in some other analyses, e.g. Wang & Jia (2019). As it was already mentioned in Material and Method section, few ITS sequences strongly different from “typical” (i.e. widely represented in GenBank) were not included in the analyses, though few identical sequences occur in GenBank as well. They are so different that appear in the tree outside not only *Isothecium* and Lembophyllaceae s.str., but also Lembophyllaceae s.l. The reason of such a hyper-variability is interesting, but it requires a special study. Leaving out those sequences, the phylogeny of Lembophyllaceae looks consistent with earlier phylogenies, based on representation of taxa by one or few specimens, and with morphological circumscription of taxa.

The position of the East Asian monospecific *Dolichomitra* in the basal most position in the Lembophyllaceae s. str. is in agreement with the previously published reconstruction of Quandt *et al.* (2009) and highly distinctive peristome structure of *Dolichomitra*: exostome teeth narrow, on dorsal surface smooth below and with high ridges of OPL cell remnants, densely papillose distally; endostome segments narrow and unperforiated, cilia lacking. In addition, the outermost proximal branch leaves in branch primordia are compound and their lobes at early stage of development are spaced, which occurs in some Neckeraceae (Spirina & Ignatov, 2015) and *Heterocladium* (Ignatov *et al.*, 2019).

The genera of “core Lembophyllaceae” and some mostly South Hemispheran genera, i.e., *Camptochaete*, *Fallaciella*, *Fifea*, *Lembophyllum*, *Looseria*, *Neobarbella*, *Rigodium*, and *Weymouthia*, were found in intermediate clade (Fig. 2) or grade (Fig. 1); such position confirms their distant relationship with any of “*Isothecium* s.l.”-clade, which was the main objective of their inclusion in the present analysis.

The terminal, “*Isothecium* s.l.”-clade will be in the main focus of further discussion. First of all, the temptation to accept *Isothecium* s.l. so to include all the species of “*Isothecium* s.l.”-clade seems not appropriate, as two out of its three subclades have much better support than when joined as a clade. Second, the genera *Bryolawtonia* and *Tripterocladium* have little in common in morphology with either *Isothecium alopecuroides*, the type

of the genus, or with the plants of *I. myosuroides* group. It is worthy mentioning, that the large part in the third subclade, around *I. myosuroides*, also has high support in both trees.

Such phylogenetic reconstruction commonly leads to splitting genera into more natural entities, as it was suggested for *Eurhynchium* (Ignatov & Huttunen, 2002), *Neckera* (Olsson *et al.*, 2009), *Hypnum* (Kučera *et al.*, 2019).

The major splitting for the genus *Isothecium* was suggested already by Grout (1929). Grout found that taxa of the *I. myosuroides* complex in North America have too little in common with European *I. alopecuroides*, as the latter species has perfectly erect and symmetric capsules, stronger reduced peristome with poor striolation on dorsal surface of the exostome, low basal membrane, narrow segments and lack of cilia, contrary to *Pseudisotheceium* Grout, in which capsules are slightly inclined to inclined, slightly asymmetric to asymmetric, and the peristome is perfect, with well-developed striolation; endostome has high basal membrane, more broad segments, one or two cilia that can be short to well-developed. In addition, leaves are coarsely serrate all around in species of *I. myosuroides* affinity vs. subentire in *I. alopecuroides*. There is also a fairly contrasting difference in proximal branch leaves in branch primordia between *I. alopecuroides* and *I. myosuroides*, as in the latter species they are compound, divided into narrow lobes; however, this character is not consistent throughout the *I. myosuroides* lineage. In *I. cristatum*, the most basal species in the grade to “core *I. myosuroides*”, proximal branch leaves are entire. The suggestion of Grout on *Pseudisotheceium* did not meet wide acceptance; only Podpera (1954) accepted this genus in Europe. The distinctions between *Isothecium* and *Pseudisotheceium* are not hundred-percent stable: e.g., *I. algarvicum*, sister to *I. alopecuroides*, possesses endostome ciliae (Hedenäs, 1992), while *I. cristatum* has julaceous habit and less serrate leaves, habitually resembling *I. alopecuroides* rather than *I. myosuroides*.

However, the tree topologies and the nested position of *Bryolawtonia* and *Tripterocladium* within the Lembophyllaceae provide an evidence for the necessity of the *Pseudisotheceium* segregation. *Bryolawtonia* is least similar to other Lembophyllaceae due to subcomplanate foliage, so it was occasionally considered within the Neckeraeae (Norris, 2014). An evidence from morphology for its placement in the Lembophyllaceae is the bilobed proximal branch leaves (Fig. 51–L).

*Tripterocladium* is a moss without a strong single costa, so it was historically placed in various families, e.g., in the Sematophyllaceae. This is a small plant, contrary to most other Lembophyllaceae (although some *Rigodium* species and *I. algarvicum* comprise other examples of Lembophyllaceae with small plant size).

The East Asian species are habitually similar to North American and European plants; the general difference of East Asian taxa includes the persistent annulus in all

species referred to *Dolichomitriopsis* and *Isothecium* (*I. hakkodense* and *I. subdiversiforme*). Proximal branch leaves do not show anything distinct, except the case of *I. subdiversiforme*, where proximal branch leaves at early stage are oblate, widely rounded and clearly bilobed, while more developed proximal branch leaves are distally truncate, evenly denticulate along margin. Sporophyte of *I. subdiversiforme* is “maximally Hypnoid”: capsules are strongly curved, exostome teeth are striolate below on the dorsal side, and endostome has perforated segments and developed cilia.

*Isothecium hakkodense* is variable and sometimes it is difficult to distinguish it from some phenotypes of *Dolichomitriopsis*; however, its moderately developed peristome, exostome teeth striolate below and endostome having ciliae, in addition to separate position in phylogenetic analysis, also suggests segregating it into a separate genus, rather than placing it in either *Isothecium*, *Pseudisotheceium*, *Dolichomitriopsis*, or in the genus segregated for *I. subdiversiforme* (cf. Table 1).

#### TAXONOMY

The formal recognition of lineages discussed above are as follow:

**1. Dolichomitriadelphus** Ignatova, Fedosov & Ignatov, gen nov.

Type: **Dolichomitriadelphus hakkodensis** (Besch.) Ignatova, Fedosov & Ignatov, comb. nov.

Basionym: *Isothecium hakkodense* Besch., Ann. Sci. Nat., Bot., sér. 7, 17: 371. 1893. Type: Nippon Nord, montagne d’Hakkoda, 5 juillet 1893, Faurie 826 (holotype in PC, high-resolution scan: <https://science.mnhn.fr/taxon/species/isothecium/hakkodense>; isotype in H-BR!).

Etymology. The name means related to *Dolichomitra*, an East Asian genus of the Lembophyllaceae.

**Diagnosis.** Differs from *Dolichomitra*, *Dolichomitriopsis* and *Isothecium* in combination of (1) leaves ovate, with obtuse apices and serrulate margins vs. various in shape, mostly acuminate or, if with obtuse apices, then leaves are oblong-ovate and margins indistinctly crenulate; (2) costa thin, extending to 1/3–1/2 the leaf length vs. stout, extending above midleaf; (3) alar group weakly delimited, small vs. well-delimited, medium sized; (4) capsules slightly inclined, slightly asymmetric vs. erect, symmetric.

Species included: monospecific genus.

**Dolichomitriadelphus hakkodensis** (Besch.) Ignatova, Fedosov & Ignatov. — *Isothecium hakkodense* Besch., Ann. Sci. Nat., Bot., sér. 7, 17: 371. 1893.

Plants robust, yellowish-green, glossy. Secondary stems erect to ascending, to 5 cm long, dendroid, irregularly branched; stipe short; attenuate flagelliform branches absent. Secondary stem leaves imbricate when dry and wet, 1.3–1.5×0.7–0.9 mm, ovate, widest at 1/6–1/3 the leaf length, obtuse or bluntly acute, concave; costa single or forked, thin, extending to 1/2–3/4 the leaf length; margins serrulate in upper 1/2, entire below; upper laminal cells 15–20×6–7 μm, moderately thick-walled, slightly

Table 1. Comparison of genera of the *Isothecium* s.l.-clade

	<u><i>Dolichomitriopsis</i></u>	<u><i>Dolichomitriadelephus</i></u>	<u><i>Isotheciastrum</i></u>	<u><i>Pseudisothecium</i></u>	<u><i>Isothecium</i></u>	<u><i>Tripterocladium</i></u>	<u><i>Bryolavtonia</i></u>
Plant size	medium to large	medium to large	medium	medium to large	small to large	small	medium
Branching	irregular	irregular	irregular to pinnate	irregular to pinnate	irregular	pinnate	pinnate
Foliage	julaceous or not	julaceous	not julaceous	julaceous or not	julaceous or not	not julaceous	subcomplanate
Foliage density	loose to dense	loose to dense	loose	loose, rarely dense	dense, rarely loose	loose to dense	loose
Leaf shape	ovate	ovate	ovate-lanceolate	ovate to triangular	ovate to obovate	ovate-lanceolate	ovate
Leaf concavity	rather strong	rather strong	moderately strong	strong to weak	rather strong	weak	weak
Leaf apex	acuminate	acute	narrow acute	acute to acuminate	short acuminate	narrow acute	acute
Leaf margin serration	weak	weak	strong	strong	weak	weak	strong
Alar group	moderate	poor	moderate	moderate to conspicuous	moderate	moderate	moderate
Costa	long	long	long	long	long	short	long
Cells	elongate	elongate	elongate	elongate or short	elongate	elongate	short
Cell walls	thick and porose	thin	thick	thick	thick	thick	thick
Capsule	erect	slightly inclined	strongly inclined	sl-str inclined	erect or inclined	inclined	
Annulus	persistent	persistent	persistent	deciduous	deciduous	deciduous	deciduous
Exostome teeth below	papillose	striolate	striolate	striolate	striolate	striolate	striolate
Cilia	0	1-2	1-2	1-3	0-1	1-2	1-2
Calyptra	smooth	smooth	with few hairs	smooth	smooth	?	smooth

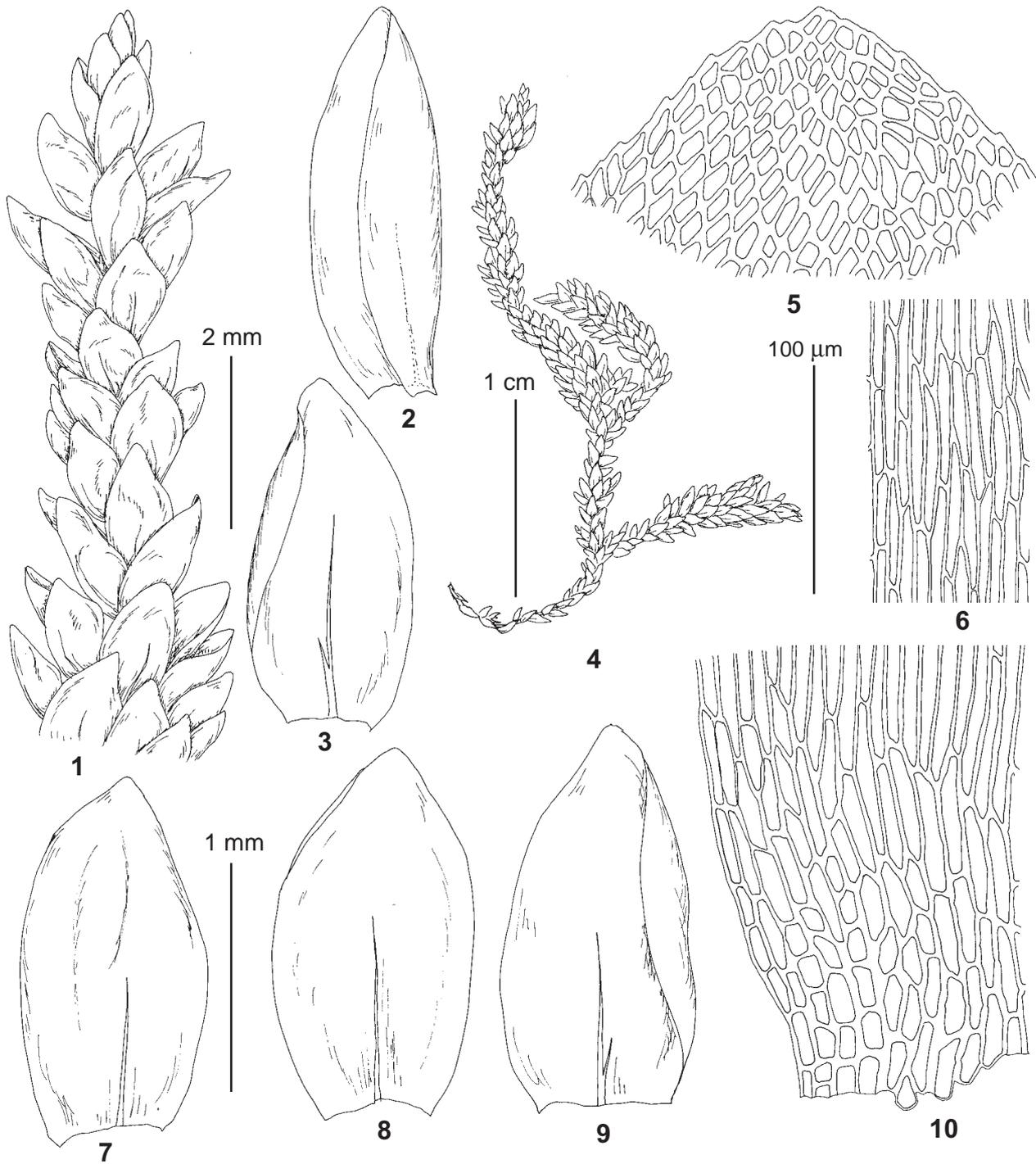


Fig. 2. *Dolichomitriadelphus hakkodensis* (from: Russia, Kuril Islands, Kunashir, Ignatov 06-1284, MHA): 1, 4 – habit, dry; 2-3 – branch leaves; 5 – upper laminal cells; 6 – mid-leaf cells; 7-9 – stem leaves; 10 – basal laminal cells. Scale bars: 1 cm for 4; 2 mm for 1; 1 mm for 2-3, 7-9; 100  $\mu\text{m}$  for 5-6, 10.

flexuose, eporose; median laminal cells linear,  $40\text{--}60 \times 5\text{--}7 \mu\text{m}$ , with moderately thickened walls, porose; basal laminal cells elongate rectangular,  $30\text{--}40 \times 6\text{--}7 \mu\text{m}$ , with moderately thickened walls, porose; alar group small, weakly delimited, consisting of rectangular cells. Branch leaves similar to secondary stem leaves but smaller. Dioicous. Gametangia and sporophytes not seen in specimens from Russia. [Setae  $0.8\text{--}1.2 \text{ cm}$ , curved or flexu-

ose. Capsules inclined, oblong, symmetric or slightly asymmetric. Exostome teeth ca.  $600 \mu\text{m}$  long, striolate below, papillose distally; basal membrane low, segments narrowly perforated, cilia 1-2, short. Spores  $12\text{--}15 \mu\text{m}$ .]

**Distribution and ecology.** This species occurs in Japan (Hokkaido, Honshu) and in South Kuril Islands in the Russian Far East. In Russia it grows at altitudes  $200\text{--}500 \text{ m}$ , on rocks and cliffs along streams.

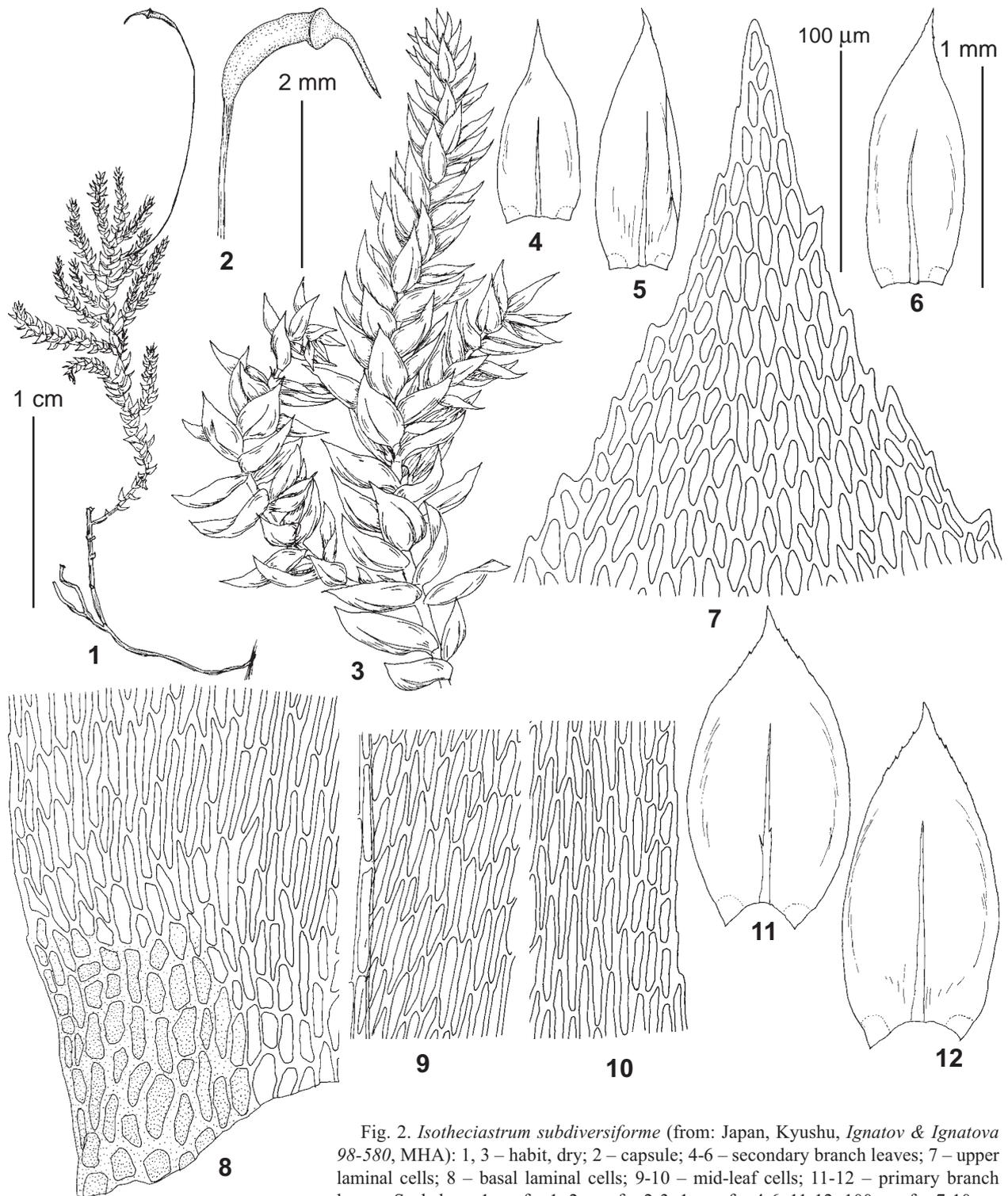


Fig. 2. *Isotheciastrum subdiversiforme* (from: Japan, Kyushu, Ignatov & Ignatova 98-580, MHA): 1, 3 – habit, dry; 2 – capsule; 4-6 – secondary branch leaves; 7 – upper laminal cells; 8 – basal laminal cells; 9-10 – mid-leaf cells; 11-12 – primary branch leaves. Scale bars: 1 cm for 1; 2 mm for 2-3; 1 mm for 4-6, 11-12; 100 µm for 7-10.

*Specimens examined:* Russia, Sakhalinskaya Province, Kunashir Island, Ruruj Mt., NW-faced slope, Dal'nij Creek, 44°28'N, 46°06', 250 m alt., Ignatov 06-1284 (MHA9038396); same place, 500 m alt., Ignatov 06-1188 (MHA9038398).

**Differentiation.** The distinction from *Dolichomitriopsis crenulata* is discussed under this species. Other species of *Dolichomitriopsis* from the Russian Far East

have leaves with attenuate apices, while leaf apex in *D. hakkodense* is obtuse, rounded or, rarely, bluntly acute. *D. hakkodense* was also confused with *Dolichomitra cymbifolia* due to imbricate foliage and strongly concave leaves with rounded-obtuse apices; however, they can be recognized by ovate vs. wide elliptical leaves and upper leaf margins serrulate vs. irregularly dentate.

**Isotheciastrum** Ignatova, Fedosov & Ignatov, gen. nov.

Type: **Isotheciastrum subdiversiforme** (Broth.) Ignatova, Fedosov & Ignatov

Basionym: *Isothecium subdiversiforme* Broth., Hedwigia, 38: 237. 1899. Holotype: Nippon Nord, montagne d'Hakkoda, 5 juillet 1893, Faurie 826 (in H-BR!).

Etymology. The name means related to *Isothecium*, widespread genus of the Lembophyllaceae.

**Diagnosis.** Differs from *Dolichomitria*, *Dolichomitriopsis* and *Isothecium* in combination of (1) erect-spreading vs. mostly imbricate leaves; (2) leaf margins strongly dentate vs. serrulate, crenulate to subentire or, if dentate, leaf apices rounded; (3) capsules inclined, clearly asymmetric vs. erect or slightly inclined, symmetric or slightly asymmetric; calyptra occasionally with few hairs at base; endostome cilia 1–2, short vs. lacking, rudimentary or, rarely, well-developed. Broadly rounded to truncate proximal branch leaves (Fig. 3M–O) also differentiate it from other species of *Isothecium*-clade.

Species included: monospecific genus.

**Isotheciastrum subdiversiforme** (Broth.) Ignatova, Fedosov & Ignatov, comb. nova — *Isothecium subdiversiforme* Broth., Hedwigia 38: 237. 1899.

Plants slender, rigid, pale green, slightly glossy. Secondary stems erect to ascending, to 2–5 cm long, dendroid, irregularly to subpinnately branched; stipe short; attenuate flagelliform branches absent. Secondary stem leaves erect-spreading when dry and wet, 1.3–1.5×0.6–0.7 mm, ovate-lanceolate, widest at mid-leaf, acuminate, moderately concave; costa single, stout, gradually narrowing, occasionally forked, extending to 2/3–3/4 the leaf length; margins sharply serrate in upper 1/3–1/2, serrulate almost to the base; upper laminal cells 20–30×8–10 μm, slightly flexuose, thick-walled, eporose; median laminal cells sublinear, 25–45×7–8 μm, not flexuose, thick-walled, weakly porose; basal laminal cells long rectangular, 30–50×7–8 μm, thick-walled, weakly porose; alar group small to medium sized, well delimited, consisting of isodiametric, irregular in shape, thick-walled, dark colored cells. Branch leaves similar to secondary stem leaves but smaller. Dioicous. Setae 1.0–1.5 cm, flexuose. Capsules inclined, asymmetric, narrowly oblong-cylindric, brown. Exostome teeth 500–600 μm long, striolate below, papillose above; endostome basal membrane low, segments perforated, cilia 1–2, short. Spores 12–17 μm. Calyptra occasionally with few hairs at base.

**Distribution and ecology.** This species is widespread in Japan and is also known from Taiwan and southern provinces of China. It is not found in Russia yet; we consider it as a provisional species which can be found in South Kuril Islands. Grows on humus or rocks, rarely on tree bases.

*Specimens examined:* Japan, Kyushu: Kagoshima Prefecture, Ohnami Lake in Kirishima Range, 31°56'N, 131°22'E, Ignatov & Ignatova 98-619 (MW9046234); Miyazaki Prefec-

ture, Inohae Valley north of Nichinan, 31°40'N, 130°51'E, Ignatov & Ignatova 98-589 (MW9046235); same place, Ignatov & Ignatova 98-580 (MW9046237); Miyazaki, Minaminaka, Kitago, IV.1946 Noguchi & Hattori, Musci Japonici Ser. 1 (1947), #6 (MW9046236).

**Differentiation.** *Isotheciastrum subdiversiforme* can be easily recognized due to a unique combination of morphological characters, i.e. erect-spreading leaves with acuminate apices and strongly dentate upper margins, and asymmetric, inclined capsules.

**Dolichomitriopsis** S. Okamura, Bot. Mag. (Tokyo) 25: 66. 1911.

Type: **Dolichomitriopsis crenulata** S. Okamura

The genus is characterized by ovate-lanceolate or oblong-ovate leaves, mainly acuminate, except for the type species of the genus which has leaves with widely obtuse apices. Other diagnostic characters of the genus include (1) erect, symmetric capsules; (2) calyptra extending to the middle of capsule; (3) annulus persistent (consisting of small cells); (4) exostome teeth evenly and densely papillose; (5) endostome basal membrane low, segments not perforated, cilia lacking.

**Dolichomitriopsis crenulata** S. Okamura, Bot. Mag. (Tokyo) 25: 66. 3. 1911.

Plants medium-sized, yellowish-green, slightly glossy, forming loose tufts. Secondary stems ascending, to 5 cm long, irregularly branched, stipe indistinct; branches occasionally flagelliform-attenuate. Secondary stem leaves imbricate when dry and wet, 1.6–1.8(–2.0)×0.8–1.0 mm, oblong-ovate or obovate, widest at 1/3–2/3 the leaf length, widely obtuse, strongly concave; costa single, stout, gradually narrowing, occasionally forked, extending to 2/3–4/5 the leaf length; margins widely incurved, crenulate or almost entire in upper 1/2, slightly uneven below; upper laminal cells vermiform, 20–30×8–10 μm, thick-walled, eporose; median laminal cells sublinear, flexuose, forming oblique rows, 35–50×6–7 μm, with moderately thickened walls, eporose; basal laminal cells sublinear, 40–55×8–9 μm, thick-walled, eporose or indistinctly porose; alar group small to medium-sized, well-delimited, consisting of isodiametric, irregular in shape, thick-walled, dark colored cells. Branch leaves similar to secondary stem leaves but smaller.

Dioicous. Gametangia and sporophytes unknown in Russia. [Perichaetia on secondary stems. Setae flexuose when dry, 5–7 mm long. Capsules erect, symmetric, oblong-cylindric, smooth, brown. Annulus consisting of small cells. Exostome teeth ca. 300 μm long, papillose throughout; endostome basal membrane low. Spores 10–13 μm].

**Distribution and ecology.** This species was considered as an endemic of Japan (Hokkaido, Honshu). It is newly reported from Russia, South Kuril Islands, Iturup Island. It was collected in dwarf-shrub & herb dominated tundra in place with late snow melting, in crevices between boulders.

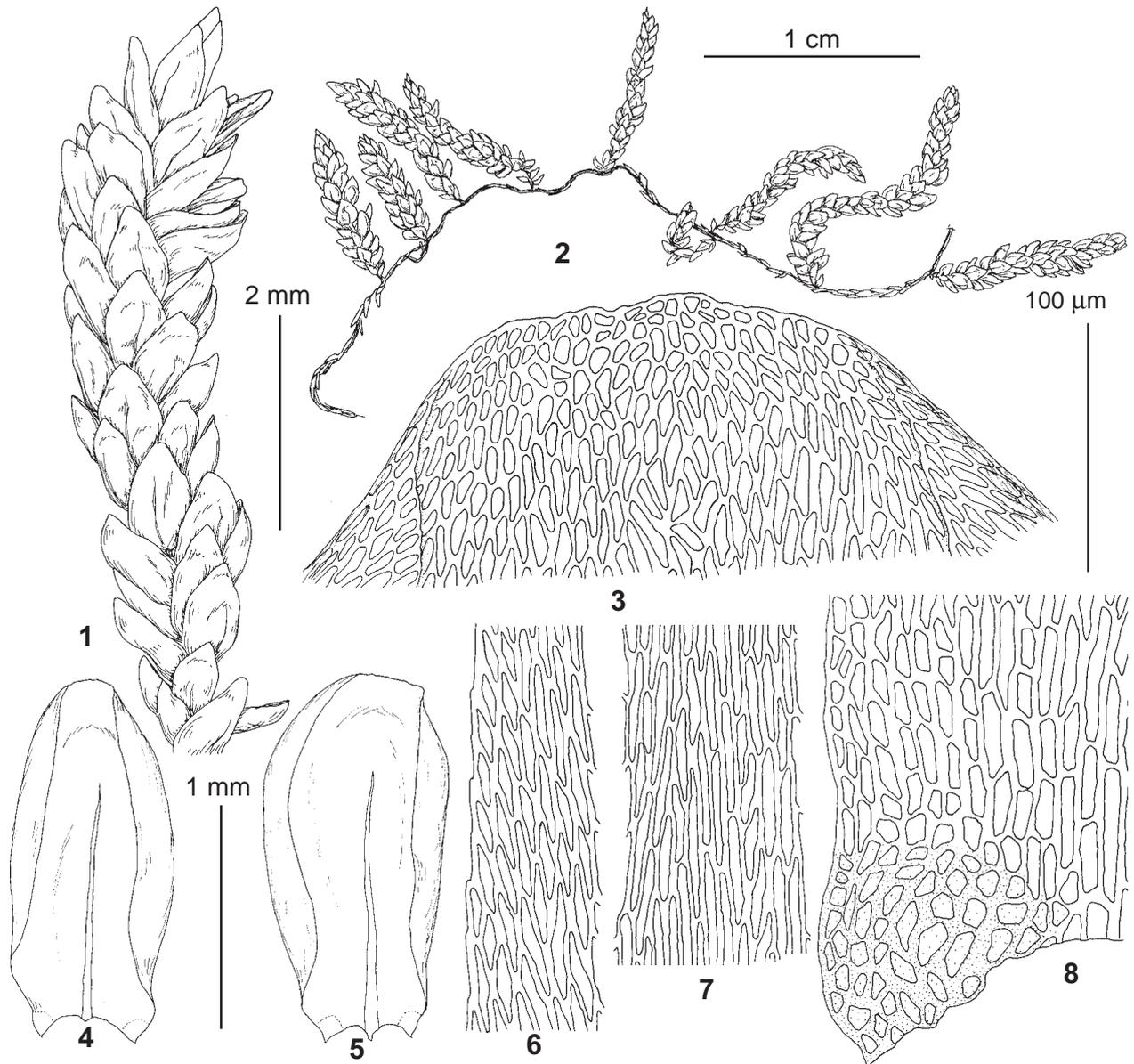


Fig. 2. *Dolichomitriopsis crenulata* (from: Russia, Kuril Islands, Iturup, *Bakalin K-16-45-07*, MHA9038397): 1-2 – habit, dry; 3 – upper laminal cells; 4-5 – leaves; 6-7 – mid-leaf cells; 8 – basal laminal cells. Scale bars: 1 cm for 2; 2 mm for 1; 1 mm for 4-5; 100 µm for 3, 6-8.

*Specimen examined*: Russia, Sakhalinskaya Province, Iturup Island, Bigatyr Range NW-faced macroslope, *Bakalin K-16-45-07* (MHA9038397).

**Differentiation.** In leaf shape (oblong-ovate, widely obtuse, strongly concave) and imbricate foliage *D. crenulata* is similar to *Dolichomitra cymbifolia*; however, leaf margins are indistinctly crenulate in *D. crenulata* vs. strongly and irregularly dentate in the latter species. *D. crenulata* was also confused with *Dolichomitriadelphus hakkodense*; the differences between these two species include strongly vs. moderately concave leaves; oblong-ovate or obovate vs. ovate leaf shape; widely vs. narrowly obtuse leaf apices; and indistinctly crenulate vs. serrulate upper leaf margins.

***Dolichomitriopsis cherdantsevae*** Ignatov & Ignatova, sp. nov.

**Type:** Russia, Primorsky Territory, Livadijskaya (Pidan) Mt., left tributary of Pryamoj Klyuch, 43°06'N, 132°41'E, alt. 450 m, on rocks in forest, 28.VIII. 2007, Ignatov 07-160. Holotype MW9037078, isotypes MHA9109603, LE.

**Diagnosis.** Differs from *Dolichomitriopsis diversiformis* in loose vs. dense tufts; secondary stems longer, to 10 cm vs. 3–4 cm long, subpinnate vs. dendroid branching; secondary stem and branch leaves erect-spreading vs. imbricate when dry; secondary stem and branch leaves not variable in shape, widest at 1/4–1/2 the leaf length

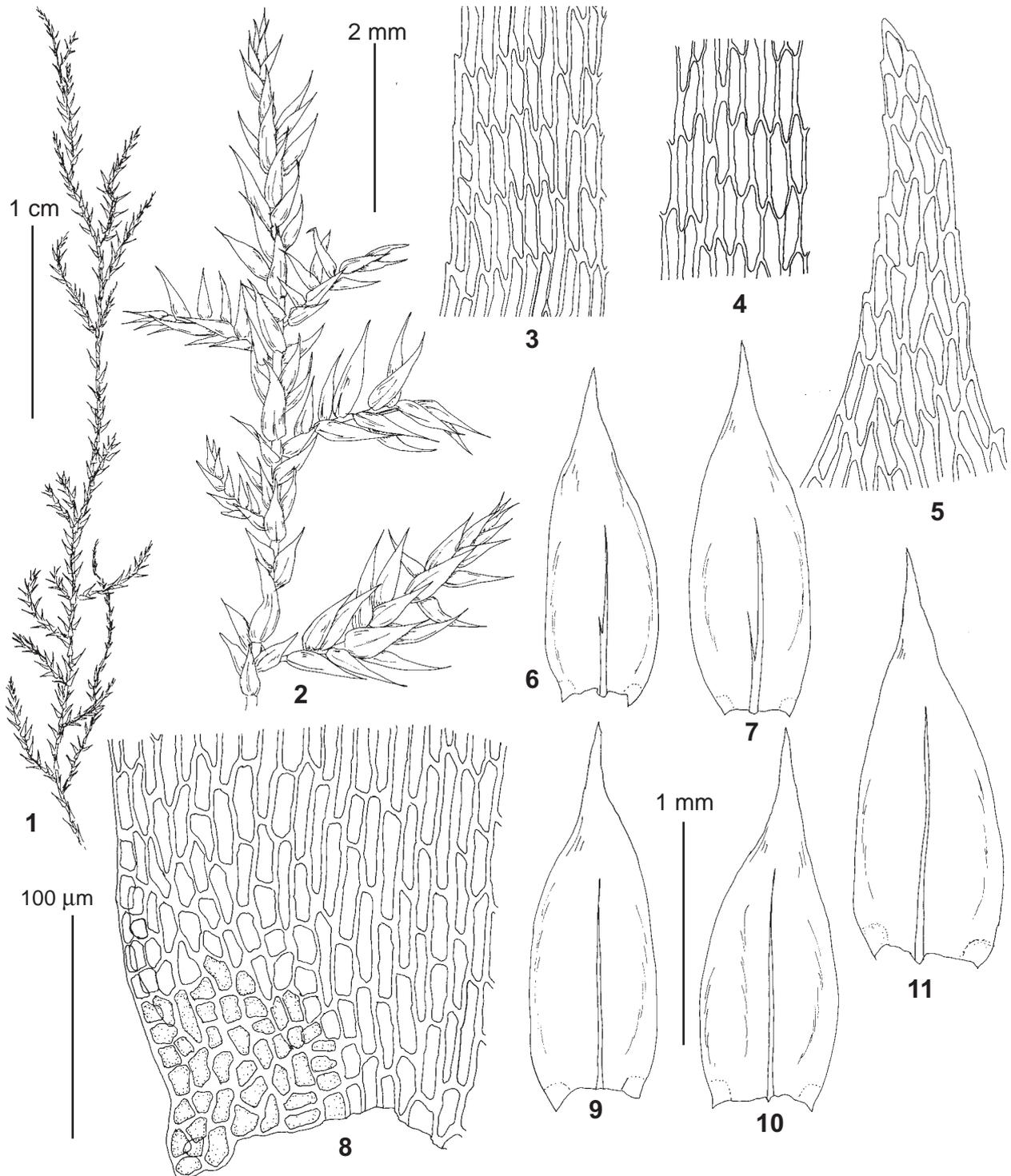


Fig. 2. *Dolichomitriopsis cherdantsevae* (from: Russia, Primorsky Territory, Pidan Mt., Ignatov & Ignatova 06-2397, MW9037075): 1-3 – habit, dry; 3-4 – mid-leaf cells; 5 – upper laminal cells; 6-7 – branch leaves; 8 – basal laminal cells; 9-11 – stem leaves. Scale bars: 1 cm for 1; 2 mm for 2; 1 mm for 6-7, 9-11; 100 µm for 3-5, 8.

vs. variable in shape, widest at 1/3– 2/3 the leaf length; and attenuate flagelliform branches present vs. absent.

**Etymology.** The species name is given in honor of Valentina Yakovlevna Cherdantseva (1939–2013), Russian bryologist who worked in Vladivostok and made a great impact into the knowledge of the moss flora of Primorsky Territory.

Plants slender, pale-green, slightly glossy, forming loose tufts. Secondary stems erect to ascending, to 10 cm long, irregularly to subpinnately branched; stipe short or absent; attenuate-flagelliform branches often present. Secondary stem leaves erect-spreading when dry and wet, 1.5–1.8×0.5–0.6 mm, ovate-lanceolate, acuminate, slightly concave in lower half; costa single, gradually narrow-

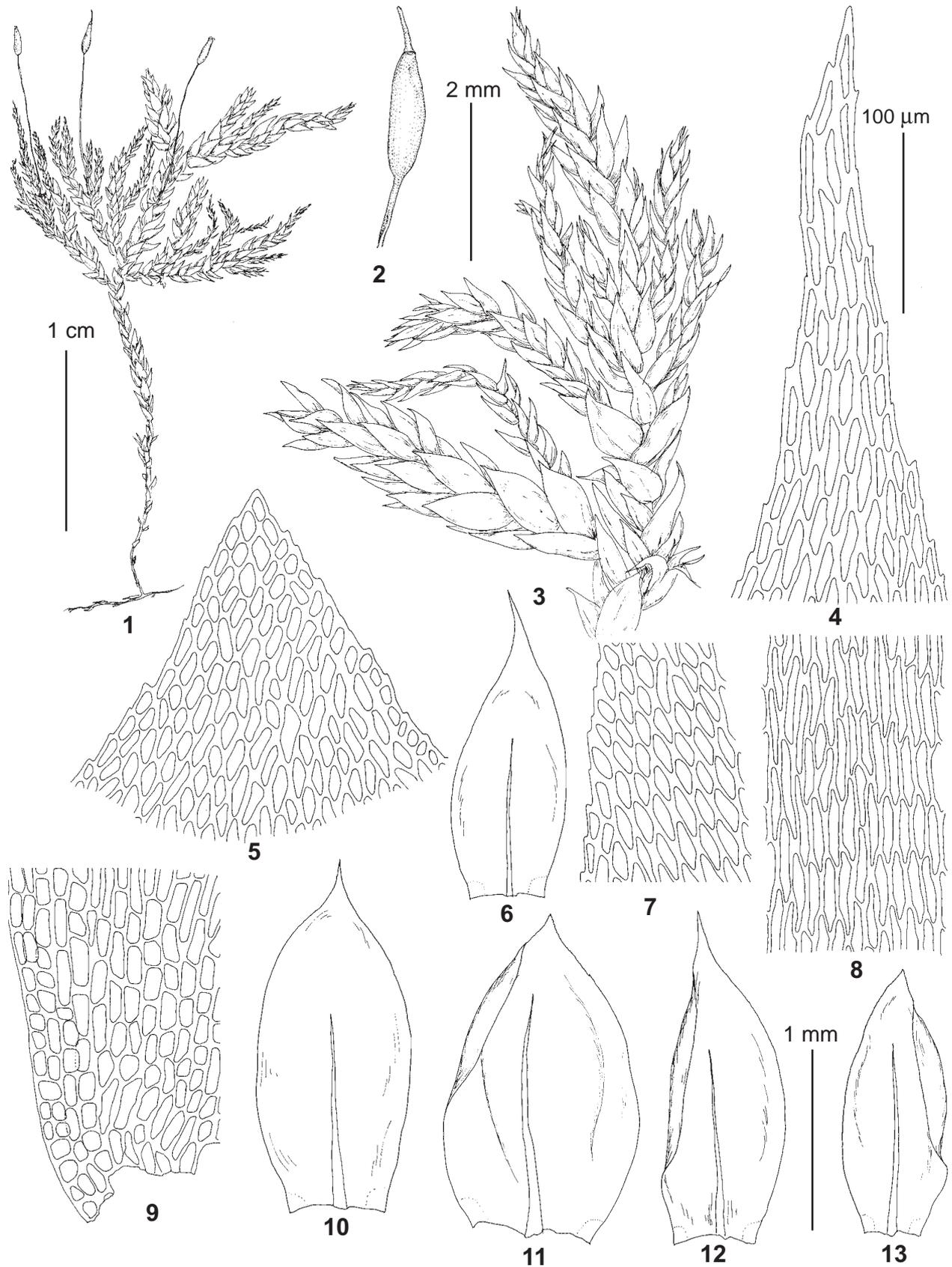


Fig. 2. *Dolichomitriopsis diversiformis* (from: Russia, Kuril Islands, Kunashir, Ignatov 06-1847, MHA): 1, 3 – habit, dry; 2 – capsule; 4-5 – upper laminal cells; 6, 12-13 – branch leaves; 7-8 – mid-leaf cells; 9 – basal laminal cells; 10-11 – stem leaves. Scale bars: 1 cm for 1; 2 mm for 2-3; 1 mm for 6, 10-13, 7-9; 100 µm for 4-5, 7-9.

ing, occasionally forked, extending to 1/2–3/4 the leaf length; margins plane, serrulate in upper 1/2, weakly serrulate almost to the base; upper and median laminal cells linear, 40–80×7–8 µm, thick-walled, eporose or weakly porose; basal laminal cells long rectangular, 40–70×7–9 µm, thick-walled, weakly porose; alar group well delimited, consisting of isodiametric, irregular in shape, thick-walled, dark colored cells. Branch leaves similar to secondary stem leaves but smaller.

Dioicous. Perichaetia numerous on secondary stems. Perichaetial leaves from oblong sheathing base narrowed into long triangular acumen, acumina spreading. Male plants and sporophytes not seen.

**Distribution and ecology.** This species is endemic for the Russian Far East. It was collected several times at one locality, on slope of Pidán (Livadijskaya) Mt., at 450–900 m alt., in mixed conifer & broadleaved forest, on rocks covered with mosses.

*Other specimen examined:* Russia, Primorsky Territory, Pidán (Livadijskaya) Mt., 43°05'N, 132°41', 900 m alt., *Ignatov & Ignatova 06-2107* (MHA9109604 & MW9037077); same place, 43°06'N, 132°41'E, alt. 400–500 m, *Ignatov & Ignatova 06-2397* (MW9037075).

**Dolichomitriopsis diversiformis** (Mitt.) Nog., J. Jap. Bot 22: 83. 1948.

Plants medium-sized, pale-green or yellowish-green, slightly glossy, forming dense tufts. Secondary stems erect, 3.5–4 cm long, dendroid, stipe short; stoloniform branches absent. Secondary stem leaves imbricate when dry and wet, 1.2–1.3(–1.7)×0.6–0.7(–0.9) mm, ovate, oblong or obovate, widest at 1/3–2/3 the leaf length, acuminate, concave; costa single, stout, gradually narrowing, occasionally forked, extending to 1/2–5/6 the leaf length; margins plane, serrulate in upper 1/2, entire below; upper laminal cells rhomboidal to oblong-elliptical, 12–20×8–10 µm, thick-walled, eporose; median laminal cells sublinear, slightly flexuose, 20–40×5–6 µm, thick-walled, eporose; basal laminal cells long rectangular, 25–45×6–7 µm, thick-walled, eporose; alar group small to medium-sized, well-delimited, consisting of isodiametric, irregular in shape, thick-walled, dark colored cells. Branch leaves similar to secondary stem leaves but smaller.

Dioicous. Perichaetia numerous on secondary stems and branches. Perichaetial leaves from oblong sheathing base narrowed into long triangular acumen, acumina spreading. Setae straight, 7–10 mm long. Capsules erect, symmetric, oblong-cylindric, smooth, reddish-brown. Annulus consisting of small cells. Exostome teeth 250 (–300) µm long, papillose throughout; endostome basal membrane low; segments narrow, not perforated; cilia absent. Spores 14–18 µm.

**Distribution and ecology.** In the Russian Far East *D. diversiformis* is known from the South Kuril Islands and Primorsky Territory; it grows at altitudes from sea level to 695 m, in broadleaved, conifer and mixed forests, and occasionally on meadows. It was collected from

tree bases (of *Sorbus*, *Alnus*, *Betula*, *Quercus*, and *Abies*), as well as on rocks and rock outcrops.

*Specimens examined:* Russia: Sakhalinskaya Province, Island Kunashir: 5–6 km east of Golovnino, 43°45'N, 145°34'E, 18.VII.1990 *Nedoluzhko s.n.* (MHA9109601); cape Mysovyj, 44°17'N, 146°17'E, 40 m alt., *Ignatov 06-1847* (MW9037073); vicinities of Tretjakovo Settlement, 43°58'N, 145°39'E, 123 m alt., *Koroteeva 15-10/7-7 & 15-10/4-3* (MHA9049327 & MHA9049325); Bay Aerodromnaya, on hill top, 43°48'N, 146°45'E, 11.IX.2006 *Nyushko Sh-28-06f* (MHA 9109597); Ruruy Mt., 44°28'N, 146°06'E, 450m alt., *Ignatov 06-1125* (MHA9109600); Island Shikotan: area of Malokurilsk Village, 43°52'N, 146°51'E, 100 m alt., *Bakalin K-37-3-07* (MHA9109598); Primorsky Territory: Vladivostok Area, near Lyanchikhe Settl., 26.IX.1950 *Voroshilov s.n.* (MHA9109605); Lazo Distr., Elomovsky Creek, 43°14'N, 133°43'E, 695 m alt., *Ignatova & Ignatova 13-1742* (MHA9109599).

**Differentiation.** Differences between *D. diversiformis* and *D. cherdantsevae* are given in the diagnosis of the latter species. *Isotheciastrum subdiversiforme* has leaves of similar shape; however, in that species leaves are erect-spreading vs. imbricate in *D. diversiformis*, with sharply serrate vs. serrulate margins; furthermore, if sporophytes are present, these species are easily recognized due to asymmetric, inclined vs. symmetric, erect capsules.

**Dolichomitra** Broth., Nat. Pflanzenfam. 1(3): 867. 1907.

The genus is characterized by combination of robust plants; imbricate foliage; widely ovate, strongly concave leaves with rounded apices and irregularly dentate upper margins; erect, symmetric capsules; deciduous annulus; exostome teeth smooth below, densely papillose in upper 2/3; endostome basal membrane moderately low, segments not perforated, cilia lacking.

The genus includes single species.

**Dolichomitra cymbifolia** (Lindb.) Broth., Nat. Pflanzenfam. 1(3): 868. 636. 1907.

Plants robust, pale-green or yellowish-green, forming loose tufts. Secondary stems erect, to 8 cm long, curved above, irregularly branched, stipe distinct; flagelliform-attenuate branches occasionally present. Secondary stem leaves imbricate when dry and wet, 1.6–2.0×1.6–1.3 mm, broadly oblong, oblong-elliptical or almost round, widest at mid-leaf, widely obtuse, strongly concave; costa single, stout, gradually narrowing, often forked, extending to 2/3–3/4 the leaf length; margins widely incurved, irregularly dentate at rounded apical part, serrate at upper 1/3, entire below; upper laminal cells vermiform, 20–25×8–10 µm, with unevenly thickened walls, with pores near cell ends; median laminal cells sublinear, not flexuose, 35–45×6–7 µm, thick-walled, strongly porose; basal laminal cells sublinear, 40–50×8–9 µm, thick-walled, strongly porose; alar group indistinct or weakly differentiated, small. Branch leaves similar to secondary stem leaves.

Dioicous. Archegonia on secondary stems. Male plants and sporophytes unknown in Russia. [Setae flex-

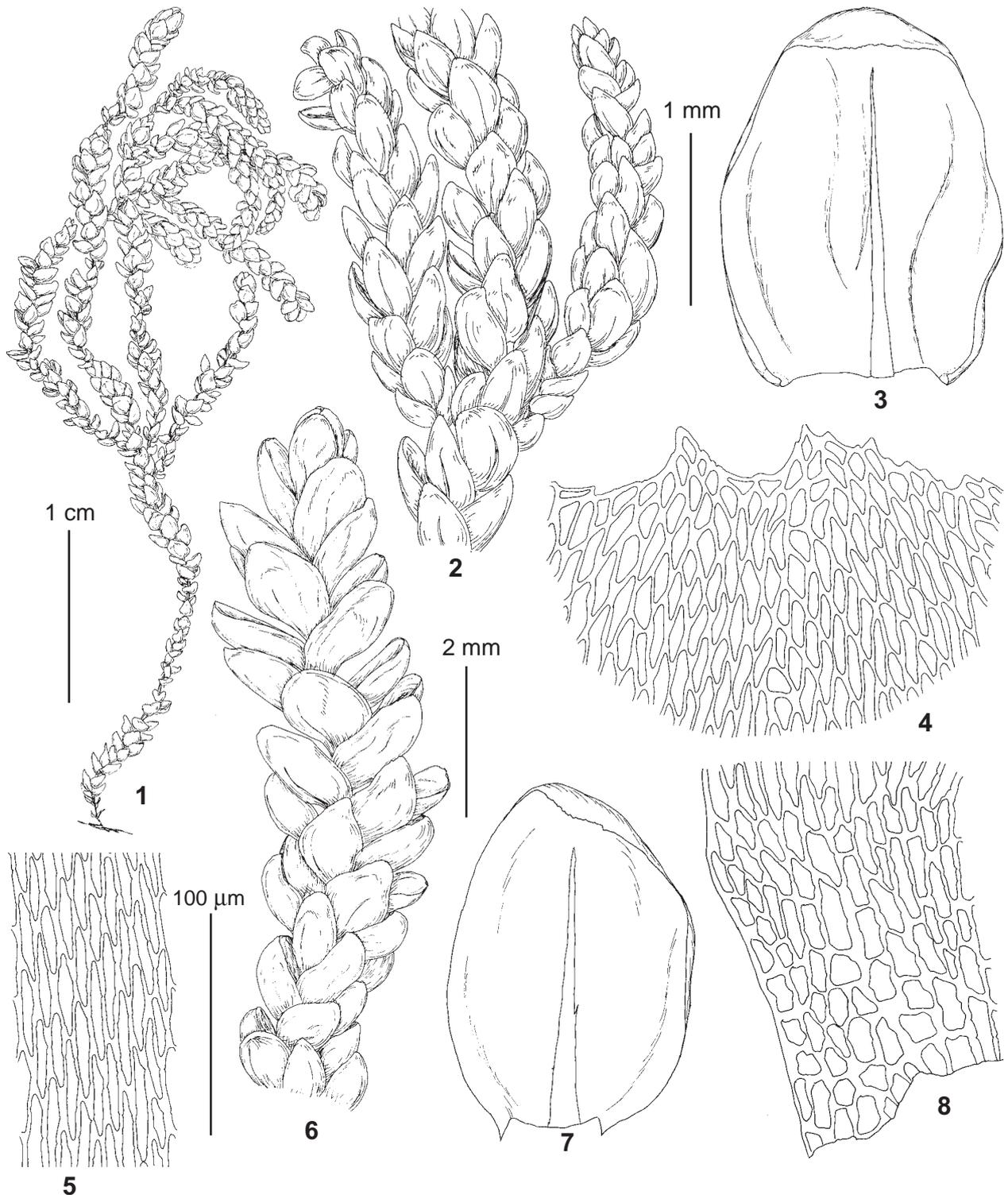


Fig. 2. *Dolichomitra cymbifolia* (from: Russia, Kuril Islands, Shikotan, *Bakalin K-42-4-07*, MW9046187): 1-2, 6 – habit, dry; 3, 7 – branch leaves; 4 – upper laminal cells; 5 – mid-leaf cells; 8 – basal laminal cells. Scale bars: 1 cm for 1; 2 mm for 2, 6; 1 mm for 3, 7; 100  $\mu$ m for 4, 5, 8.

uose when dry, 2.0–2.5 cm long. Capsules erect, symmetric, oblong-cylindric, smooth, brown. Annulus deciduous. Exostome teeth ca. 500  $\mu$ m long, smooth below, papillose in upper 2/3; endostome basal membrane low, segments keeled, not perforated, cilia lacking. Spores 10–15  $\mu$ m].

**Distribution and ecology.** *Dolichomitra cymbifolia* is known from Japan, Korea, China, and Taiwan; it is newly reported from South Kuril Islands in Russia. Grows in forests, on rocks covered with humus layer; in Shikotan Island it was collected at 250 m a.s.l., in grass community intermingled with *Juniper* thickets, on a ledge of wet cliff.

*Specimens examined:* Russia, South Kuril Islands, Shikotan Island, Notoro Mt., 43°47'N, 146°44'E, 250 m alt., *Bakalin K-45-29-07* (MHA, MW9046191).

**Differentiation.** *Dolichomitra cymbifolia* can be recognized by robust plants; imbricate foliage; oblong-elliptical to almost round, strongly concave leaves with widely incurved margins; widely obtuse apices; leaf margins irregularly serrate only at apex and serrulate in upper 1/2; and almost indistinct alar groups; strongly porose median and basal cells are also unique for *Dolichomitra* among the Lembophyllaceae in the Russian Far East. Differences from *Dolichomitriadelphus hakkodensis* are discussed under that species.

KEY FOR IDENTIFICATION OF LEMBOPHYLLACEAE IN THE RUSSIAN FAR EAST AND NEIGHBORING TERRITORIES

1. Leaves ovate, wide elliptical, round or oblong-ovate, rounded at apex ..... 2
- Leaves ovate-lanceolate or ovate, rarely obovate, acute or acuminate ..... 4
2. Leaves wide elliptical or round, irregularly dentate at apex; laminal cells strongly porose .....  
..... *Dolichomitra cymbifolia*
- Leaves ovate or oblong-ovate, serrulate or crenulate to almost entire at apex; laminal cells eporose or weakly porose ..... 3
3. Leaves oblong-ovate, cymbiform, crenulate to almost entire at apex ..... *Dolichomitriopsis crenulata*
- Leaves ovate, cochleariform, serrulate at apex .....  
..... *Dolichomitriadelphus hakkodensis*
- 4(1). Leaves strongly dentate in distal part; capsules inclined, asymmetric .....  
..... [*Isotheciastrum subdiversiforme*]
- Leaves serrulate in distal part; capsules erect, symmetric or sporophytes absent ..... 5
5. Leaves imbricate when dry, widest at 1/3–2/3 the leaf length; attenuate-flagelliform branches absent; capsules erect, symmetric .....  
..... *Dolichomitriopsis diversiformis*
- Leaves erect-spreading when dry, widest at 1/3–1/2 the leaf length; attenuate-flagelliform branches occasionally present; sporophytes unknown .....  
..... *Dolichomitriopsis cherdantsevae*

OTHER PROPOSED NOMENCLATURE CHANGES

**Pseudisotheceum** Grout Moss Fl. N. Amer. 3: 12. 1928. Type: *Pseudisotheceum myosuroides* (Brid.) Grout

Plants medium-sized to robust. Secondary stems dendroid to pinnately branched, branches often arching downward, in some species attenuate-flagelliform. Leaves ovate to ovate-lanceolate or ovate-triangular, acute or acuminate; margins serrate to coarsely so, rarer serrulate; laminal cells short-elongate to elongate, thick-walled, alar cells numerous. Capsules suberect to inclined, more or less symmetric to distinctly curved; operculum rostrate; annulus deciduous; exostome teeth striolate be-

low, papillose above; basal membrane high, segments narrow, perforated, ciliae 1–3, usually long.

Other species included:

**Pseudisotheceum cardotii** (Kindb.) Ignatova, Fedosov & Ignatov, comb. nov. — *Isotheceum cardotii* Kindb., Cat. Canad. Pl., Musci 275–276. 1892.

**Pseudisotheceum cristatum** (Hampe) Ignatova, Fedosov & Ignatov, comb. nov. — *Leptohymenium cristatum* Hampe, Linnaea 30(4): 459–460. 1860. — *Isotheceum cristatum* (Hampe) H. Rob., Bryologist 65(2): 95. 1962 [1963].

**Pseudisotheceum holtii** (Kindb.) Ignatova, Fedosov & Ignatov, comb. nov. — *Isotheceum holtii* Kindb., Rev. Bryol. 22: 83. 1895.

**Pseudisotheceum interludens** (Stirt.) Ignatova, Fedosov & Ignatov, comb. nov. — *Isotheceum interludens* Stirt., Ann. Scott. Nat. Hist. 9(35): 178. 1900.

**Pseudisotheceum montanum** (Draper et al.) Ignatova, Fedosov & Ignatov, comb. nov. — *Isotheceum montanum* Draper, Hedenäs, M. Stech, Tina Lopes & Sim-Sim, Bot. J. Linn. Soc. 177(3): 431. 2015.

**Pseudisotheceum prolixum** (Mitt.) Ignatova, Fedosov & Ignatov, comb. nov. — *Leskea prolixa* J. Proc. Linn. Soc., Bot. 8: 7. 1. 1864. — *Echinodium prolixum* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 1217. 1909. — *Isotheceum prolixum* (Mitt.) M. Stech, Sim-Sim, Tangney & D. Quandt, Organisms Diversity Evol. 8: 290. 2008.

**Pseudisotheceum stoloniferum** (Brid.) Grout.

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## Appendix 1. Specimens and accession number used in concatenated analysis.

Species	isolate and specimen for new sequences	ITS	trnG	trnSF(*-trnLF)
<i>Bryolawtonia vancouveriensis</i>	B222	FM161082	–	AM990349
<i>Camptochaete arbuscula</i>	s.n.	AF403629	–	–
<i>Camptochaete arbuscula</i> var. <i>tumida</i>	SH10	FM161087	–	AM990353
<i>Camptochaete deflexa</i>	s.n.	AF188057	–	–
<i>Dolichomitra cymbifolia</i> 1	s.n.	AF509855	–	–
<i>Dolichomitra cymbifolia</i> 2	Deguchi HIRO 79	LS999115	AY908344	LR130214 & AF509558

Species	isolate and specimen for new sequences	ITS	trnG	trnSF(*-trnLF)
<i>Dolichomitria cymbifolia</i> 3	OK2125 Shikotan, <i>Bakalin K-45-29-07</i> , MHA	MN854444	MN841342	–
<i>Dolichomitria cymbifolia</i> 4	OK2395 Shikotan, <i>Bakalin K-42-4-07</i> , MHA	MN854442	MN841341	MN841361
<i>Dolichomitriadelphus hakkodensis</i> 1	OK427 Kunashir, <i>Ignatov 06-1284</i> , MHA	MN854443	–	–
<i>Dolichomitriadelphus hakkodensis</i> 2	OK2396 Kunashir, <i>Ignatov 06-1125</i> , MHA	MN854438	MN841339	MN841357
<i>Dolichomitriopsis cherdantsevae</i> 1	OK2371 Primorsky, <i>Ignatov &amp; Ignatova 06-2397</i> , MW9037075	MN854430	MN841331	MN841349
<i>Dolichomitriopsis cherdantsevae</i> 2	OK2372 Primorsky, <i>Ignatov 07-160</i> , MW9037078	MN854431	MN841332	MN841350
<i>Dolichomitriopsis crenulatus</i>	OK2121 Iturup, <i>Bakalin K-16-45-07</i> , MHA9038397	MN854436	MN841337	MN841355
<i>Dolichomitriopsis diversiformis</i> 1	OK2122 Kunashir, <i>Ignatov 06-1847</i> , MHA	MN854433	MN841334	MN841352
<i>Dolichomitriopsis diversiformis</i> 2	s.n.	FM161098	–	–
<i>Dolichomitriopsis diversiformis</i> 3 (as <i>D. subdiversiformis</i> )	T11	DQ294917	DQ294781	–
<i>Dolichomitriopsis diversiformis</i> 4	OK2370 Primorsky, <i>Ignatov &amp; Ignatova 13-1742</i> , MW9037072	MN854432	MN841333	MN841351
<i>Dolichomitriopsis diversiformis</i> 5	OK2123 Primorsky, <i>Ignatov &amp; Ignatova 13-1742</i> , MW9037072	MN854434	MN841335	MN841353
<i>Dolichomitriopsis diversiformis</i> 6	OK2394 Kunashir, <i>Koroteeva 15-10/4-3</i> , MHA	MN854435	MN841336	MN841354
<i>Fallaciella gracilis</i>	s.n.	AF188058	–	–
<i>Fifea aciphylla</i>	s.n.	AF295041	–	–
<i>Heterocladium heteropterum</i> 1	B350	FM161116	–	AM990377
<i>Heterocladium heteropterum</i> 2	OK2224	MN030527	–	MN045120
<i>Heterocladium heteropterum</i> 3	OK2223	MN030526	–	MN045119
<i>Heterocladium wulfsbergi</i>	AnomF19	MN030542	–	MN045121
<i>Homalia trichomanoides</i> 1	B218	FM161126	–	AM990385
<i>Homalia trichomanoides</i> 2	OK2219	MN030524	–	–
<i>Isotheciastrum subdiversiforme</i> 1	OK2369 Japan, <i>Ignatov &amp; Ignatova 97-580</i> , MHA	MN854437	MN841338	MN841356
<i>Isotheciastrum subdiversiforme</i> 2	T57	DQ294918	DQ294827	–
<i>Isothecium algarvicum</i> 1	T52	DQ294867	DQ294822	–
<i>Isothecium algarvicum</i> 2	T53	DQ294868	DQ294823	–
<i>Isothecium algarvicum</i> 3	IP1	HQ380897	HQ380953	HQ381007*
<i>Isothecium algarvicum</i> 4	IP2	HQ380898	HQ380954	HQ381008*
<i>Isothecium algarvicum</i> 5	GO1	HQ380904	HQ380959	HQ381014*
<i>Isothecium algarvicum</i> 6	PA1	HQ380906	HQ380961	HQ381016*
<i>Isothecium algarvicum</i> 7	PA3	HQ380908	HQ380963	HQ381017*
<i>Isothecium algarvicum</i> 8	MD4	HQ380914	–	–
<i>Isothecium alopecuroides</i> 1	T23	DQ294879	DQ294793	–
<i>Isothecium alopecuroides</i> 2	T91	DQ294889	DQ294851	–
<i>Isothecium alopecuroides</i> 3	T31	DQ294915	DQ294801	–
<i>Isothecium alopecuroides</i> 4	AZ	HQ380916	HQ380971	HQ381034*
<i>Isothecium alopecuroides</i> 5	T25	DQ294881	DQ294795	–
<i>Isothecium alopecuroides</i> 6	T46	DQ294895	DQ294816	–
<i>Isothecium alopecuroides</i> 7	T38	DQ294903	DQ294808	–
<i>Isothecium alopecuroides</i> 8	T39	DQ294907	DQ294809	–
<i>Isothecium alopecuroides</i> 9	T74	DQ294909	DQ294840	–
<i>Isothecium alopecuroides</i> 10	T79	DQ294910	–	–
<i>Isothecium alopecuroides</i> 11	T81	DQ294911	–	–
<i>Isothecium alopecuroides</i> 12	OK2466 Ingushetia, <i>Ignatov et al. 2018</i> , MW 9090725	MN854426	MN841327	MN841345
<i>Isothecium alopecuroides</i> 13	T12	DQ294916	DQ294782	–
<i>Lembophyllum clandestinum</i> 1	SH103	FM161145	–	AM990401
<i>Lembophyllum clandestinum</i> 2	s.n.	AF403630	–	–
<i>Lembophyllum divulgum</i> 1	B295	FM161146	–	FM1611461
<i>Lembophyllum divulgum</i> 2	s.n.	AY009807	–	–
<i>Looseria orbiculata</i> 1	s.n.	AJ862691	–	–
<i>Looseria orbiculata</i> 2	s.n.	AF509860	–	–
<i>Mawenzhangia thamnobryoides</i>	sn	MG515239	–	–
<i>Neckera menziesii</i>	B161	FM161167	–	FM210305
<i>Neckera pennata</i> 1	NF48	MN854440	–	MN841359
<i>Neckera pennata</i> 2	NF50	MN854441	–	MN841360
<i>Neobarbella comes</i>	s.n.	AF395628	–	–
<i>Nogopterium gracile</i> 1	Buchbender 348	HE660012	–	HE717062*
<i>Nogopterium gracile</i> 2	Pt gr	HQ268249	–	–
<i>Nogopterium gracile</i> 3	s.n.	KC249957	–	–
<i>Nogopterium gracile</i> 4	B408	LS999114	–	LR130213
<i>Pseudanomodon attenuatus</i> 1	OK2209	MN030519	–	MN045086
<i>Pseudanomodon attenuatus</i> 2	OK2169	MN030517	–	–

Species	isolate and specimen for new sequences	ITS	trnG	trnSF(*-trnLF)
<i>Pseudanomodon giraldui</i>	Jiangxi3	KF770680	–	KF770518
<i>Pseudisothecium cardotii</i> 1	OK2472 California, <i>Shevock 51319</i> , MW9112752	MN854439	MN841340	MN841358
<i>Pseudisothecium cardotii</i> 2	CAN	HQ380917	HQ380972	HQ381038*
<i>Pseudisothecium cristatum</i> 1	USA	HQ380918	HQ380973	HQ381040*
<i>Pseudisothecium cristatum</i> 2	OK2469 California, <i>Shevock 53668</i> , MW9112676	MN854424	MN841325	MN841343
<i>Pseudisothecium cristatum</i> 3	OK2470 California, <i>Shevock 48391</i> , MW9075665	MN854425	MN841326	MN841344
<i>Pseudisothecium cristatum</i> 4	T54	DQ294919	–	–
<i>Pseudisothecium holtii</i>	T65	DQ294923	DQ294834	–
<i>Pseudisothecium interludens</i> 1	T67	DQ294926	DQ294836	–
<i>Pseudisothecium interludens</i> 2	T72	DQ294925	DQ294838	–
<i>Pseudisothecium interludens</i> 3	Hodgetts_6780	MH465612	–	–
<i>Pseudisothecium interludens</i> 4	Hodgetts_9099	MH465613	–	–
<i>Pseudisothecium interludens</i> 5	T66	DQ294921	DQ294835	–
<i>Pseudisothecium interludens</i> 6	GBR2	HQ380928	HQ380982	HQ381055*
<i>Pseudisothecium interludens</i> 7	Hodgetts_9099	MH465613	–	–
<i>Pseudisothecium myosuroides</i> 1	T60	DQ294927	DQ294830	–
<i>Pseudisothecium myosuroides</i> 2	T59	DQ294924	DQ294829	–
<i>Pseudisothecium myosuroides</i> 3	GO2	HQ380921	HQ380975	HQ381044*
<i>Pseudisothecium myosuroides</i> 4	GO3	HQ380922	HQ380976	HQ381045*
<i>Pseudisothecium myosuroides</i> 5	Kucera_15467	MK327347	–	–
<i>Pseudisothecium myosuroides</i> 6	TE1	HQ380923	HQ380977	HQ381046*
<i>Pseudisothecium myosuroides</i> 7	CAN1	HQ380919	–	–
<i>Pseudisothecium myosuroides</i> 8	AZ	HQ380925	HQ380979	HQ381050*
<i>Pseudisothecium myosuroides</i> 9	MD	HQ380926	HQ380980	HQ381051*
<i>Pseudisothecium myosuroides</i> 10		AY737479	–	–
<i>Pseudisothecium myosuroides</i> 11	OK2468 Norway <i>Ignatov &amp; Ignatova 06-5024</i> , MW 9046192	MN854427	MN841328	MN841346
<i>Pseudisothecium myosuroides</i> 12	T51	DQ294922	DQ294821	–
<i>Pseudisothecium prolixum</i> 1	MD1	HQ380934	HQ380989	HQ381062*
<i>Pseudisothecium prolixum</i> 2	s.n.	KF648790	–	–
<i>Pseudisothecium prolixum</i> 3	Cafifo 242201	KM676255	–	–
<i>Pseudisothecium prolixum</i> 4	MD7	HQ380940	HQ380994	HQ381068*
<i>Pseudisothecium prolixum</i> 5	s.n.	KM676258	–	–
<i>Pseudisothecium prolixum</i> 6	s.n.	KM676256	–	–
<i>Pseudisothecium prolixum</i> 7	s.n.	EU477598	–	–
<i>Pseudisothecium prolixum</i> 8	s.n.	KF648791	–	–
<i>Pseudisothecium prolixum</i> 9	s.n.	KM676261	–	–
<i>Pseudisothecium prolixum</i> 10	MD8	HQ380941	HQ380995	HQ381069*
<i>Pseudisothecium prolixum</i> 11	s.n.	KF64880	–	–
<i>Pseudisothecium prolixum</i> 12	s.n.	KM676257	–	–
<i>Pseudisothecium stoloniferum</i> 2	T56	DQ294920	DQ294826	–
<i>Pseudisothecium stoloniferum</i> 3	OK2471 California, <i>Shevock 53640</i> , MW9112640	MN854428	MN841329	MN841347
<i>Pseudisothecium stoloniferum</i> 1	OK2473 Oregon, 22 Aug 1989 <i>Ignatov s.n.</i> , MW9046232	MN854429	MN841330	MN841348
<i>Rigodium implexum</i> 1	Ri29	FM161209	AM990436	–
<i>Rigodium implexum</i> 2	s.n.	AF543551	–	–
<i>Rigodium pseudothuidium</i> 2	B559	FM161210	–	AM990437
<i>Rigodium pseudothuidium</i> 1	s.n.	AF509842	–	–
<i>Rigodium toxarion</i>	s.n.	AF509843	–	–
<i>Thamnobryum ellipticum</i>	B546	FM161220	–	FM210325
<i>Thamnobryum negrosense</i>	B420	FM161225	–	FM210327
<i>Touwia laticostata</i>	B261	FM161233	–	FM882221 & FM210330
<i>Tripterocladium leucocladulum</i> 1	SH431	FM161235	–	AM990450
<i>Tripterocladium leucocladulum</i> 2	s.n.	AY188175	–	–
<i>Weymouthia billardieri</i>	s.n.	AF188053	–	–
<i>Weymouthia cochlearifolia</i> 1	SZ	FM161236	AM990451	–
<i>Weymouthia cochlearifolia</i> 2	s.n.	AJ862693	–	–
<i>Weymouthia mollis</i> 1	DQ	FM161237	–	AM990452
<i>Weymouthia mollis</i> 3	s.n.	HQ380917	–	–
<i>Weymouthia mollis</i> 2	s.n.	AJ862694	–	–