

On moss genera *Hylocomiadelphus* Ochyra & Stebel and *Rhytidiadelphus* (Limpr.) Warnst.

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Abstract: The moss family Hylocomiaceae is studied for the generic level taxonomy within a molecular phylogenetic approach. We confirm segregating of the species formerly known as *Rhytidiadelphus triquetrus* to *Hylocomiadelphus* Ochyra & Stebel from the genus *Rhytidiadelphus*. *Hylocomiadelphus* forms a clade with *Loeskeobryum* and *Meteoriella*, sharing with both genera cordate to auriculate leaf bases and non-squarrose leaves, and with the former undulate leaves and reticulate exostome teeth ornamentation. However, *Loeskeobryum* differs from *Hylocomiadelphus* in having paraphyllia, while *Meteoriella* has a straight capsule and reduced peristome, likely caused by its epiphytic ecology. In the group of species closely related to *R. squarrosus*, in addition to *R. subpinnatus*, the third species with North Pacific distribution is described as *R. pacificum*. *Macrothamnium* is found deeply nested in *Rhytidiadelphus*, although no nomenclatural implications are suggested at the moment due to insufficient sampling. *Hylocomium splendens* var. *splendens* and var. *obtusifolium* were found intermingled in the phylogenetic tree, indicating no correlation between morphology and variation in ITS region, thus supporting a view that these taxa are merely environmentally induced morphs.

Key words: bryophytes, *Rhytidiadelphus*, *Hylocomiadelphus*, *Hylocomium*, Hylocomiaceae, taxonomy, molecular phylogeny, phytogeography, new species, new genera, nomenclature

Introduction

Despite that the moss family Hylocomiaceae M. Fleisch. is rather small, with 50-70 species worldwide, its systematics at both the generic and species level remains the point of disagreements, as well as the family circumscription itself. The comprehensive revision of Hylocomiaceae has been done by Rohrer (1985a, 1985b), and later it was the focus of morphological cladistic analysis by Hedenäs (2004). It is not surprising that subsequent molecular phylogenetic studies suggested some alternatives for the family systematics, similarly to those in many other bryophyte groups (Ignatov & Huttunen 2002; Olsson *et al.* 2011; Fedosov *et al.* 2016). For example, *Rhytidium rugosum* (Hedw.) Kindb. included by Rohrer in the family has subsequently been found unrelated to it (Tsubota *et al.* 2004; Gardiner *et al.* 2005). Also, already early molecular results, e.g. Gardiner *et al.* (2005) found a rather distant position of *Rhytidiadelphus triquetrus* (Hedw.) Warnst. from other species of this genus. Basing on these results, Ignatov & Ignatova (2004) suggested to split *Rhytidiadelphus* (Limpr.) Warnst. and to segregate *R. squarrosus* (Hedw.) Warnst. and related taxa in the genus *Rhytidiastrum* Ignatov & Ignatova, considering typification of the genus *Rhytidiadelphus* by *R. triquetrus* (Abramov & Savicz-Lyubitskaya 1963). Doing this, Ignatov and Ignatova, however, overlooked earlier lectotypification of the genus *Rhytidiadelphus* by *R. squarrosus* (Grout, 1928). Therefore, Ochyra & Stebel (2008) described the new genus *Hylocomiadelphus* Ochyra & Stebel for *H. triquetrus*. This suggestion remains not widely accepted (Huttunen *et al.* 2012; Rohrer 2014), so the main aim of the present study was to obtain robust evidence for or against such a segregation.

In the present study, we concentrated on the phylogeny within the core Hylocomiaceae, i.e. *Hylocomium* Schimp., *Hylocomiastrum* M. Fleisch. ex Broth., *Rhytidiadelphus*, and *Loeskeobryum* M. Fleisch. ex Broth., supplementing new sequences with relevant data from Genbank for other genera of Hylocomiaceae (as defined by Rohrer 1985b). Species of Antitrichiaceae Ignatov and Ignatova and Climaciaceae Kindb. were added as representatives of families often considered as closely related to Hylocomiaceae. For *Rhytidiadelphus* and *Hylocomium* species we studied specimens from a broad geographical range in order to exclude possible influence from marginal haplotypes. It also made possible to address, besides the main focus of the study, two other problems in the taxonomy of Hylocomiaceae around *Rhytidiadelphus squarrosus* and *Hylocomium splendens* (Hedw.) Schimp.

Material and Methods

Internal spacers of nuclear ribosomal operon (ITS 1 and ITS2) were chosen as quickly evolving markers which provide a suitable signal to resolve phylogeny of pleurocarpous mosses on both intrageneric and intergeneric levels and thus is successfully used in other groups, combined with other markers or alone (Olsson *et al.* 2009; Ignatov & Milyutina 2010; Ignatov *et al.* 2007, 2014; Ignatova *et al.* 2017). For ITS region the laboratory protocol was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005). The dataset includes 66 sequences from 18 species of Hylocomiaceae, 43 of them newly obtained, the specimen data is given in Table 1. Sequences were aligned manually in Bioedit (Hall 1999). *Climacium dendroides* and *Pleuroziopsis ruthenica* were used as outgroup, as representatives of a closely related family Climaciaceae, often discussed along with Hylocomiaceae (Hedenäs 2004). Alignment of 825 positions was divided in three partitions, ITS1, 5.8rRNA gene and ITS2. Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML 8.2.10 (Stamatakis 2006) from 1000 independent searches each starting from distinct random trees. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein 1985) with 1000 iterations. Bayesian Analyses (BA) were performed in MrBayes 3.2.6 (Ronquist *et al.* 2012) with each run consisted of six Markov chains and 10,000,000 generations. The sampling frequency was one tree each 2 500 generations, and the chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond 2007) to check that all ESS values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Phylogenetic analyses were performed on the Cipres Science Gateway ([http:// www.phylo.org/portal2](http://www.phylo.org/portal2)) on XSEDE. In addition, the maximum parsimony analysis was completed with Nona (Goloboff 1994) within the Winclada shell (Nixon 1999), with a bootstrap calculation with 2000 replications.

Results

The Bayesian, ML and MP trees have similar topologies, thus we present here Bayesian tree only (Fig. 1), adding support values from ML and MP analyses and discussing the difference wherever relevant. Basal grade in the tree is formed by *Pleurozium schreberi* (Brid.) Mitt., *Antitrichia curtipendula* (Hedw.) Brid. and *Neodolichomitra yunnanensis* (Besch.) T.J. Kop. Two latter genera are resolved in low supported clade in ML and MP trees, and form a polytomy in Bayesian analysis (Fig. 1)

Core Hylocomiaceae, i.e. *Hylocomium*, *Hylocomiastrum*, *Rhytidiadelphus* and *Loeskeobryum* are resolved in a well supported clade, which includes also *Leptohymenium* Schwägr., *Leptocladiella* M. Fleisch., *Orontobryum* Mitt. ex M. Fleisch., *Meteoriella* S. Okamura and *Macrothamnium* M. Fleisch. This clade is subdivided in the tree inferred from Bayesian analysis into two subclades: (1) maximally supported in Bayesian and ML analyses and with BS=99 in MP, *Rhytidiadelphus* sensu Ochrya & Stebel (2008) clade, which includes also *Macrothamnium*, and (2) other core Hylocomiaceae-clade, with all other genera and *Hylocomiadelphus triquetrus*, having high to moderate support in Bayesian and ML analyses (PP=99, BS=84), but not resolved in MP where its groups form a polytomy of smaller clades.

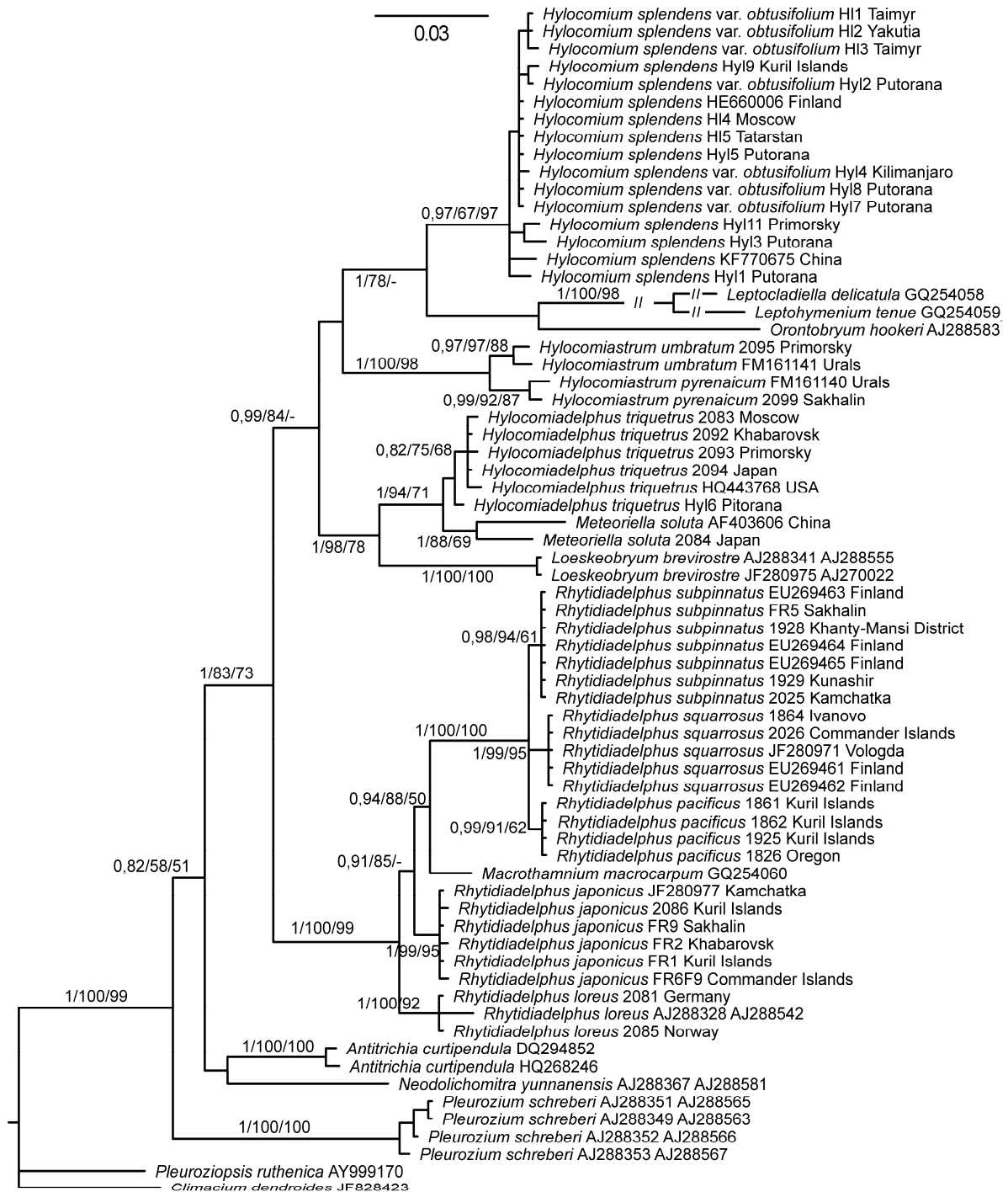


Fig 1: Bayesian tree based on nuclear ITS sequences. Support values are shown at branches: Bayesian posterior probability / ML bootstrap support / MP bootstrap support.

The topology of *Rhytidiadelphus*-clade is almost the same in all analyses: it includes the grade of *R. loreus* (Hedw.) Warnst., *R. japonicus* (Reimers) T.J. Kop., *Macrothamnium macrocarpum* (Reinw. & Hornsch.) M. Fleisch., and terminal clade of *R. subpinnatus* (Lindb.) T.J. Kop., *R. squarrosus* and a new species described below, *R. pacificus*. Support for the clades of three latter species is moderate to low, although visual analysis of the alignment ensures that these three entities have stable differences (Fig. 2). Altogether species of *R. squarrosus*-group

share 11 substitutions and one indel of 2 bp, differing them from both *R. loreus* and *R. japonicus*. Each of three clades within *R. squarrosus*-group also has unique substitutions: *R. squarrosus* has three, new species two, and *R. subpinnatus* one (Fig. 2). Since *R. squarrosus* and *R. subpinnatus* are represented by specimens from West Europe to Pacific coast, such distinction has to be considered as very stable. The third species includes sequenced specimens also from areas nearly 8000 km one from another, thus its two substitutions in ITS and morphological differentiation seems no less sound than between *R. squarrosus* and *R. subpinnatus*, thus requiring the same status of a separate species, not just as a locally presented haplotype.

Larger subclade of Hylocomiaceae in Bayesian and ML analyses has identical topology of two further subclades: one with *Hylocomiastrum*+*Orontobryum*+*Leptocladiella*+*Leptohymenium*+*Hylocomium*, and another formed by *Loeskeobryum*+*Hylocomiadelphus*+*Meteoriella*. The former clade has poor support as a whole, but its subclades formed by species of *Hylocomiastrum* and *Hylocomium* have a rather high support.

The *Loeskeobryum*+*Hylocomiadelphus*+*Meteoriella* clade is maximally to highly supported in all analyses (PP=1, ML BS=98, MP BS=78). Within this clade *Loeskeobryum* keeps basal position, while *Hylocomiadelphus* forms a clade with *Meteoriella* with high to low support (PP=1, ML BS=94, MP BS=71).

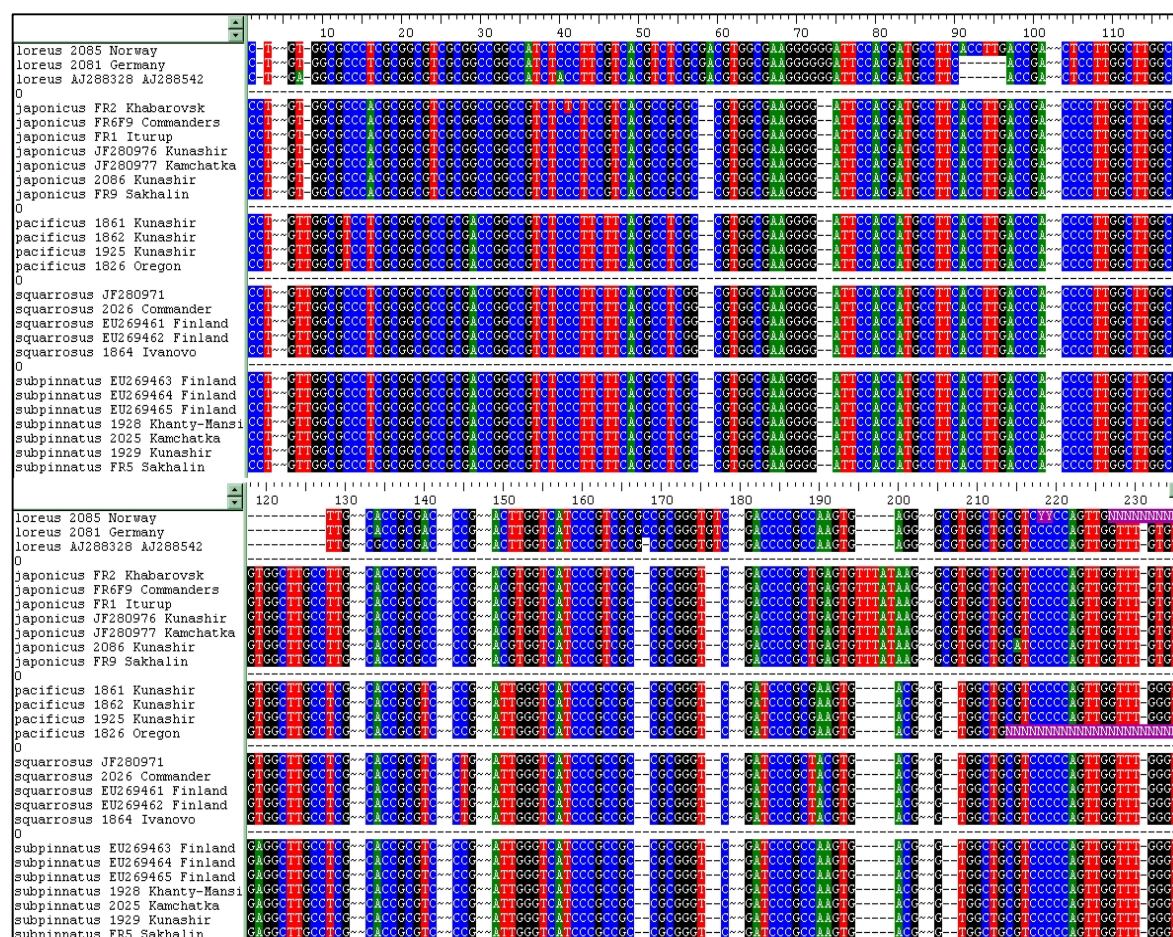


Fig 2: Parts of nuclear ITS alignment of five species of *Rhytidiadelphus*, with omitted invariable parts, substituted by double space columns.

Discussion

1. Phylogenetic position of *Hylocomiadelphus triquetrus*

The present analysis do not contradict previously published molecular phylogenetic analyses, although the latter were generally less complete, and therefore can be compared only by parts (Chiang & Schaal, 2000; Vanderpoorten *et al.*, 2003; Tsubota *et al.*, 2004; Gardiner *et al.*, 2005; Ignatov *et al.*, 2007; Wang *et al.*, 2010; Cox *et al.*, 2010; Huttunen *et al.*, 2012). Poor sampling in previous studies likely was the main reason why *Hylocomiadelphus triquetrus* continued to be accepted in the genus *Rhytidiadelphus*, despite molecular phylogenetic analysis that mildly indicated the opposite. The present analysis unequivocally supports the acceptance of the genus *Hylocomiadelphus* Ochyra & Stebel.

Our data also point that the closest relative of *Hylocomiadelphus* is *Loeskeobryum brevirostre* (Brid.) M. Fleisch.; it shares with *Hylocomiadelphus* rigid, erect, non-reflexed leaves, which are plicate and undulate, have auriculate base and long double costa reaching beyond the mid-leaf, as well as reticulate ornamentation of exostome teeth from outside.

Obviously, the presence of paraphyllia was a character which was thought to be of crucial importance for a long time. It can be reminded that less than 40 years ago in the Check-list of mosses of Europe by Corley *et al.* (1981), all the Hylocomiaceae with paraphyllia were classified in just one genus *Hylocomium*, and only after the revision by Rohrer (1985a, 1985b) this genus was split, and molecular data now fully support that it is reasonable. *Hylocomium* s.str., *Hylocomiastrum* and *Loeskeobryum* do not form a clade (Fig. 1), but are intermingled in clades with genera without paraphyllia: *Loeskeobryum* forms a clade with eparaphyllose *Meteoriella* and *Hylocomiadelphus*, while between *Hylocomiastrum* and *Hylocomium* are eparaphyllose *Leptohyenum* and *Leptocladiella*, and not always paraphyllose *Orontobryum*.

It might be worth noting that in the Climaciaceae, a family sharply delimited morphologically by dendroid plant habit, as in of *Climacium* and *Pleuroziopsis*, molecular phylogeny also revealed a subaquatic plant, formerly classified as a *Hygrohypnum* or *Leptodictyum*; it was independently resolved within Climaciaceae by three molecular markers, and thus placed within the family despite of average hypnoid habit (Ignatov *et al.*, 2014).

The genus *Meteoriella* was found even closer to *Hylocomiadelphus* in all analyses, however, this tropical epiphytic plant has strongly deviated morphology, especially in sporophyte structure, and only auriculate leaf base seems to be a character shared by three genera forming this clade, i.e. *Loeskeobryum*, *Meteoriella* and *Hylocomiadelphus*. The cases when molecular markers reveal the relationship between epiphytic genera and terrestrial genera of "average" morphology were found recently in many phylogenetic lineages (Huttunen *et al.*, 2004, 2012), providing highly unexpected examples of rapid modification of sporophytes, and the pair *Meteoriella*+*Hylocomiadelphus* is one more such example. Therefore the conclusion by Hedenäs (2004) about the important differentiation of tropical and temperate lineages related to Hylocomiaceae has to be reconsidered, especially concerning the position of *Leptocladiella*, *Leptohyenum* and *Macrothamnium*, also found intermingled with common boreal mosses.

2. Taxonomy of *Rhytidiadelphus squarrosus* complex

There is a noteworthy discrepancy between European and American taxonomists in their approaches to *R. squarrosus* and *R. subpinnatus* complex. In Europe, the latter species was recognized for a long time as *R. squarrosus* var. *calvescens* (Lindb.) Warnst., but it was almost invariably mentioned in treatments; e.g., Limpricht (1896) included it in the general key for species. Koponen (1971) clearly described the difference between *R. squarrosus* and *R. subpinnatus* and introduced the species status of the latter. Contrary to this, Grout (1928), Crum & Anderson (1981) and Rohrer (1985b) stated that in North America this variety and, later, species, *R. subpinnatus*, can not always be successfully separated, or even it was not

mentioned at all (Lawton, 1971). Later Rohrer (2014) accepted *R. subpinnatus* as a species, basing on molecular evidence published by Vanderpoorten *et al.* (2003) and Korpelainen *et al.* (2008), although still noting that sometimes these species are difficult to distinguish by morphology. Although the latter is sometimes difficult, we presume that this view of North American bryologists may be partly explained also by the presence of the third species revealed in our molecular analysis. Below is its description.

Rhytidiadelphus pacificus* Ignatov, Ignatova & Fedosov, *sp. nova

Type: Russia, Sakhalinskaya Province, Kuril Islands, Kunashir Island, 2 km north of Yuzhno-Kurilsk, 44°3'N, 145°50'E, 10 m alt., on dunes at sea shore, 9.IX.2006, *Ignatov 06-3207* (holotype MHA9049126). Figs. 3-12, 14, 16, 17.

Diagnosis: *Rhytidiadelphus pacificus* differs from *R. subpinnatus* in having irregularly branched stems and more densely arranged stem leaves with ovate vs. triangular basal part; it differs from *R. japonicus* by more densely arranged stem leaves with longer acumens, shorter costae and thin- vs. thick-walled alar cells; the differences from *R. squarrosus* include sharply differentiated stem and branch leaves; it also differs from all three species in having very finely serrulate vs. serrate margins of stem and branch leaves and by nuclear ITS sequence as shown in Fig. 2.

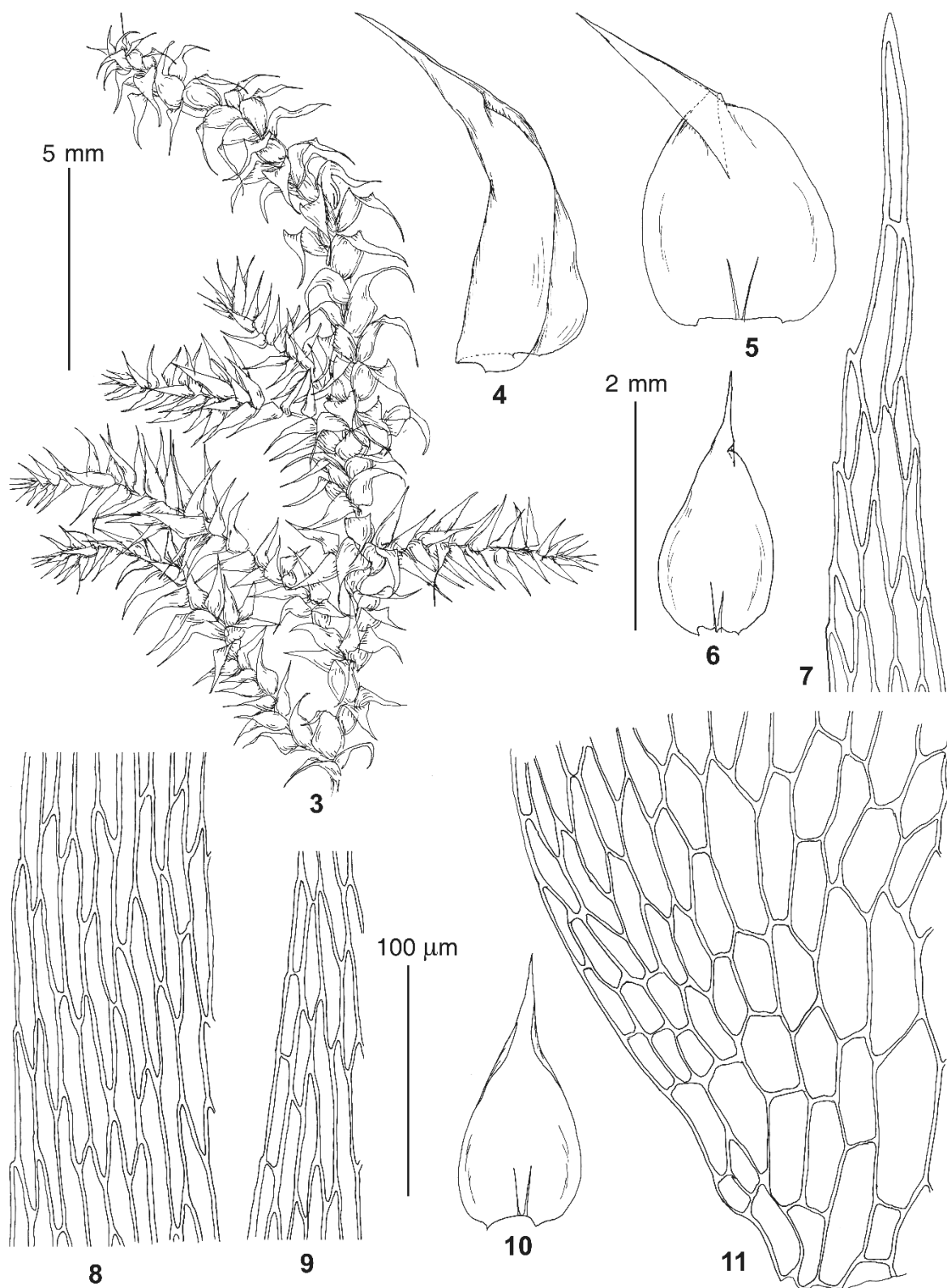
Etymology: the species indicates the distribution of the species along the coast of Pacific Ocean both in Asia and North America.

Description: Plants in loose mats, light green, slightly glossy. Stems ascending, to 15 cm long, 4 mm wide with leaves, irregularly branched, branches to 1.5 cm long, stem reddish-brown, in transverse section 5-angled, without hyalodermis, with 1–2-layered sclerodermis formed by cells with moderately thickened, brown-colored walls, thin-walled medullar cells and indistinct central strand consisting of few smaller cells. Stem leaves crowded, more or less sheathing, stem hardly visible between them, widely spreading to reflexed, $2.5\text{--}3.7 \times 1.0\text{--}1.7$ mm, from broadly ovate base abruptly narrowed into long acumen, widely rounded to the insertion, not plicate or undulate; margins very finely serrulate almost throughout; costa double, ca. 1/4 the leaf length; median leaf cells $55\text{--}80 \times 6\text{--}7$ μm , with moderately thickened, weakly porose walls; alar cells differentiated, rectangular, $15\text{--}17$ μm wide, thin-walled, forming quadrate or rectangular group not reaching the costa. Branch leaves sharply differentiated from stem leaves, erect-spreading, not sheathing, ovate-lanceolate, $2.0\text{--}2.3 \times 0.5\text{--}0.75$ mm, margins finely serrulate. Dioicous. Only female plants seen. Outer perichaetial leaves ovate, $1.0\text{--}1.3 \times 0.4\text{--}0.6$ mm, inner perichaetial leaves longer, sharply reflexed at their middle, $1.5\text{--}2.0 \times 0.5\text{--}0.6$ mm, ecostate, with fine serrulation in mid-leaf, at area of maximal curvature. Male plants and sporophytes not seen.

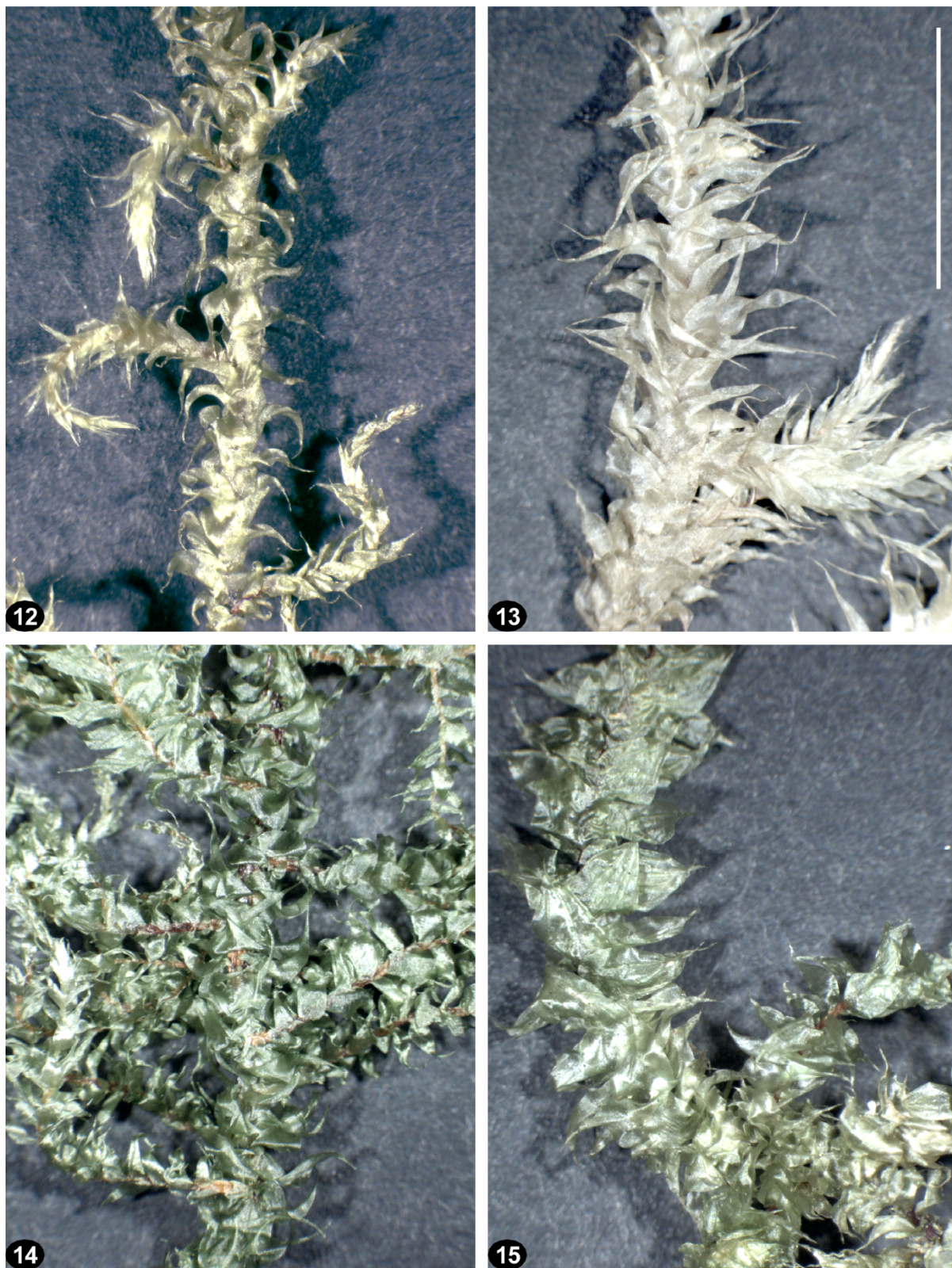
Distribution and ecology: According to label information and personal observation, in Kunashir Island *R. pacificus* grows on soil in boggy meadows and on dunes covered with grass vegetation at sea shore, at altitude 4–10 m, while in Oregon it was collected at elevation 350 m, in coniferous forest (*Abies concolor*, *Tsuga heterophylla* and *Pseudotsuga*), on diffusely lit soil layer over outcrops. Presumably the species occurs also in Japan, at least an illustration of *R. subpinnatus* in Noguchi (1994) much better fits *R. pacificus*, than *R. subpinnatus*.

Specimens examined: Russia: Sakhalinskaya Province, Kunashir Island, Lagunnoe Lake, 44°3'4"N, 145°48'4"E. 4 m alt., 15.VIII.2015 *Koroteeva 15-12-1* (MHA 9049129); same place, *Koroteeva 15-12-8* (MHA9049128). U.S.A., Oregon, Linn Co., 1 mile north of US Forest Service Road 11 (2 miles west of Quartzville), 44°33'N, 122°23'W, Willamette National Forest, 4.X.1994 *Norris 83956* (MHA9057426).

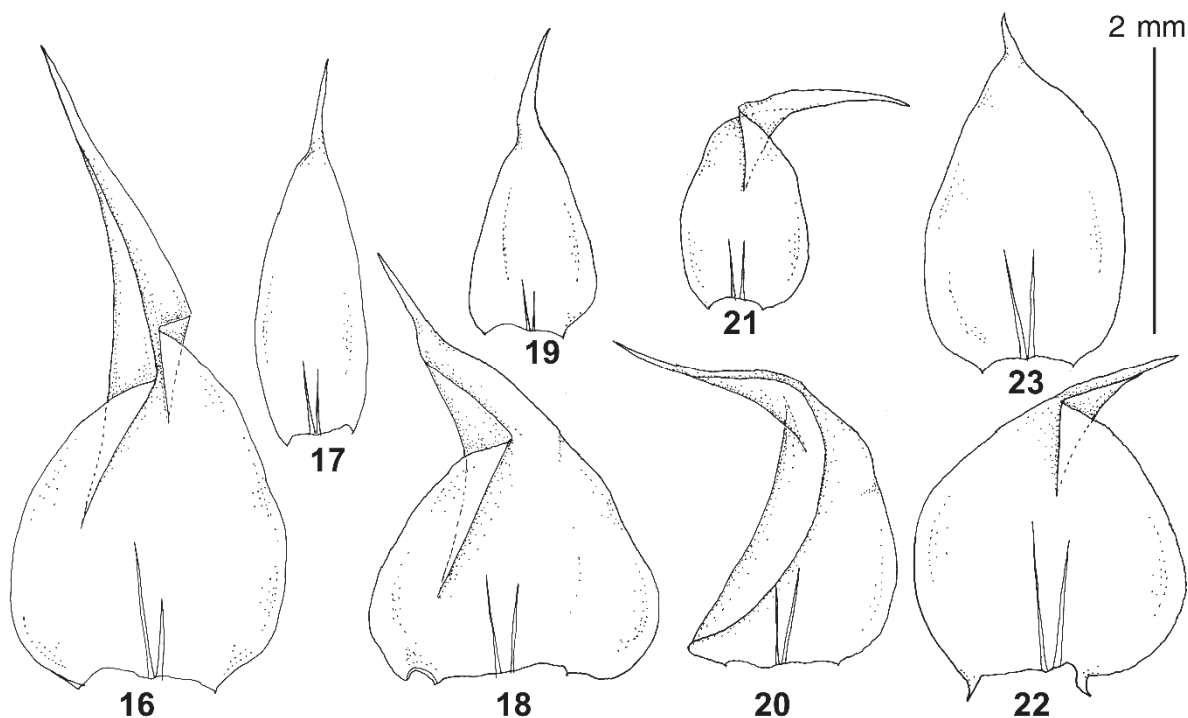
Rhytidiadelphus pacificus shares with *R. squarrosus* crowded, more or less sheathing leaves with ovate base and reflexed acumina; however, its branch leaves are more similar to those of *R. subpinnatus* and *R. japonicus*, since they are not similar to stem leaves – not sheathing, with straight apices, erect-spreading. At the same time, *R. pacificus* has crowded and sheathing stem leaves with an ovate base, while stem leaves of *R. subpinnatus* are more distantly arranged, not sheathing and have a triangular basal part. *Rhytidiadelphus pacificus* is also distinct from *R. japonicus* because this species has a shorter acumen in stem leaves, which are also distantly arranged, have longer costae and thick-walled alar cells. In addition, leaf margins of both stem and branch leaves of *R. pacificus* are only faintly serrulate, while they are sharply serrate in all three other species.



Figs 3-11: *Rhytidiadelphus pacificus* (from holotype): 3: habit; 4-5: stem leaves; 6 & 10: branch leaves; 7: apical cells; 8-9: median leaf cells; 11: basal leaf cells.



Figs 12-15: Photo of four species of *Rhytidiadelphus*: **12:** *R. squarrosus* (European Russia, Ivanovo, Sorokin, coll. 27.VI.2008 MHA); **13:** *R. pacificus* (holotype); **14:** *R. subpinnatus* (Primorsky Territory, Olchovaya Mt., Ignatov *et al.*, 06-2319, MHA); **15:** *R. japonicus* (Kuril Islands, Ignatov *et al.*, 06-1437, MHA). Scale bar 5 mm for all.



Figs 16-23: Stem (16, 18, 20, 22) and branch (17, 19, 21, 23) leaves of four species of *Rhytidiadelphus*: **16-17:** *R. pacificus* (holotype); **18-19:** *R. subpinnatus* (Primorsky Territory, Olchovaya Mt., Ignatov *et al.*, 06-2319, MHA); **20-21:** *R. squarrosus* (Ivanovo, European Russia, Sorokin, coll. 27.VI.2008 MHA); **22-23:** *R. japonicus* (Kurul Islands, Ignatov *et al.*, 06-1437, MHA). Scale bar 2 mm for all.

Key to identification of *Rhytidiadelphus* species in Russia

- | | | |
|----|--|-----------------------|
| 1. | Leaves plicate, at stem and branch apices falcate-secund; alar cells not differentiated | <i>R. loreus</i> |
| 1. | Leaves not plicate, not falcate-secund; alar cells clearly differentiated | 2 |
| 2. | Costa reaching 1/3–1/2 the leaf length; alar cells thick-walled; leaf acumens comparatively short | <i>R. japonicus</i> |
| 2. | Costa reaching not longer than 1/3 the leaf length; alar cells thin-walled; leaf acumens long | 3 |
| 3. | Branch and stem leaves similar, crowded, with spreading to reflexed acumina | <i>R. squarrosus</i> |
| 3. | Stem leaves crowded or distant, with reflexed acumina, branch leaves sharply differentiated, erect-spreading, with straight acumina | 4 |
| 4. | Stem leaves crowded, stem hardly visible between them; basal part of stem leaves ovate; margins of stem and branch leaves faintly serrulate | <i>R. pacificus</i> |
| 4. | Stem leaves more or less distant, stem visible between them at places; basal part of stem leaves triangular-ovate; margins of stem and branch leaves sharply serrate | <i>R. subpinnatus</i> |

3. *Hylocomium splendens* (Hedw.) Schimp. var. *splendens* and var. *obtusifolium* (Geh.) Paris (= *H. alaskanum* (Lesq. & James) Austin).

Most authors accepted these taxa as varieties, although Grout (1928) argued for the species status of *H. alaskanum*. The latter is an Arctic and high mountain taxon, differing from the type variety in branching pattern and stem leaf shape. On Putorana Plateau, vicinity of Sobach'e Lake this morphotype is common above the timberline, whereas within forest belt *Hylocomium splendens* s. str. occurs. Three specimens of these phenotypes from Putotana were compared with each other, as well as with a number of morphologically similar plants from other regions, from high Arctic to Kilimanjaro Mt. Although ITS sequences in *H. splendens* s.l. were found to be variable, their variation does not correlate with morphology of var. *obtusifolium* and

var. *splendens*. Furthermore, plants of different haplotypes grow in Putorana together. These results support a view that var. *obtusifolium* is merely an environmentally induced morph of *H. splendens*.

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Appendix.

Table 1: Newly sequenced specimens used in molecular phylogenetic analysis, with voucher information and GenBank accession numbers.

Species	Voucher data	GenBank ##
<i>Hylocomiastrum umbratum</i>	Russia, Primorsky, Ignatov <i>et al.</i> 06-2235 MHA 9037087, isolate OK2095	MK463496
<i>Hylocomiastrum pyrenaicum</i>	Russia, Sakhalin, Ignatov & Teleganova 06-738 MHA 9037005, isolate OK2099	MK463497
<i>Hylocomiadelphus triquetrus</i>	Russia, Putorana, Fedosov 18-01-0001 MW, isolate Hyl6	MK463498
<i>Hylocomiadelphus triquetrus</i>	Russia, Moscow, Grigorovo, Ignatov and Ignatova, 11 Nov 2018, MHA, isolate OK2083	MK463499
<i>Hylocomiadelphus triquetrus</i>	Russia, Khabarovsk, Botchi, Ignatov and Ignatova 13-50 MHA, isolate OK2092	MK463500
<i>Hylocomiadelphus triquetrus</i>	Russia, Primorsky, Lazo, Ignatov and Ignatova 13-1392 MHA, isolate OK2093	MK463501
<i>Hylocomiadelphus triquetrus</i>	Japan, Inouga 9 Sept 2001, MHA, isolate OK2094	MK463502
<i>Meteoriella soluta</i>	Japan, Iwatsuki 6 Dec 1979 MHA 9061907, isolate OK2084	MK463503
<i>Hylocomium splendens</i>	Russia, Putorana, Fedosov 18-01-0005 MW, isolate Hyl1	MK463504
<i>Hylocomium splendens</i>	Russia, Kuril Islands, Shikotan, Bakalin 40-3-07 MW 9044945, isolate Hyl9	MK463505
<i>Hylocomium splendens</i>	Russia, Primorsky, Ignatov <i>et al.</i> 06-2322 MW 9044949, isolate Hyl11	MK463506
<i>Hylocomium splendens</i>	Russia, Moscow, Kozlova, sn MW 9044694, isolate HI4	MK463507
<i>Hylocomium splendens</i>	Russia, Tatarstan, Ignatov and Ignatova, 14 Aug 2003, MW 9044795, isolate HI5	MK463508
<i>Hylocomium splendens</i>	Russia, Putorana, Fedosov 18-01-0004 MW, isolate Hyl3	MK463509
<i>Hylocomium splendens</i>	Russia, Putorana, Fedosov 18-01-0003 MW, isolate Hyl5	MK463510
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Putorana, Fedosov 18-01-0002 MW, isolate Hyl2	MK463511
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Tanzania, Kilimandzharo, Ochyra sn KRAM 102388, isolate Hyl4	MK463512
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Taimyr, Meduza Fedosov MW 9045017, isolate Hyl6	MK463513
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Yakutia, Orulgan Ignatov MW 9045029, isolate HI2	MK463514
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Taimyr, Byrranga Fedosov MW 9045024, isolate HI3	MK463515
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Putorana, Fedosov 18-01-0007 MW, isolate Hyl8	MK463516
<i>Hylocomium splendens</i> var. <i>obtusifolium</i>	Russia, Putorana, Fedosov 18-01-0006 MW, isolate Hyl7	MK463517
<i>Rhytidiadelphus loreus</i>	Germany, Ignatov 16-2017 MHA, isolate OK2081	MK463518
<i>Rhytidiadelphus loreus</i>	Norway, Ignatov and Ignatova 06-5048 MHA 9057396, isolate OK2085	MK463519
<i>Rhytidiadelphus japonicus</i>	Russia, Kunashir, Ignatov 06-1059 MHA 9049037, isolate 2086	MK463520
<i>Rhytidiadelphus japonicus</i>	Russia, Sakhalin, Fedosov 8 Aug 2014, MW, isolate RF9	MK463521
<i>Rhytidiadelphus japonicus</i>	Russia, Khabarovsk, Ignatov and Ignatova 13-1227 MW, isolate FR2	MK463522
<i>Rhytidiadelphus japonicus</i>	Russia, Kuril Islands, Iturup, Fedosov 21 Sept 2015 MW, isolate FR1	MK463523
<i>Rhytidiadelphus japonicus</i>	Russia, Commander Islands, Bakalin 10-3-558 MW, isolate FR6	MK463524
<i>Rhytidiadelphus subpinnatus</i>	Russia, Sakhalin, Ignatov and Teleganova, 06-354 MW, isolate FR5	MK463525
<i>Rhytidiadelphus subpinnatus</i>	Russia, Khanty-Mansi Autonomous District, Lapshina 13-86 MHA, isolate OK1928	MK463526
<i>Rhytidiadelphus subpinnatus</i>	Russia, Kunashir, Ignatov 06-1816 MHA, isolate OK1929	MK463527
<i>Rhytidiadelphus subpinnatus</i>	Russia, Kamchatka, Fedosov, 12-107 MW 9063386, isolate OK2025	MK463528
<i>Rhytidiadelphus pacificus</i>	Russia, Kunashir, Koroteeva 15-12-8 MHA, isolate OK1861	MK463529
<i>Rhytidiadelphus pacificus</i>	Russia, Kunashir, Ignatov 06-3207 MHA, isolate OK1862	MK463530
<i>Rhytidiadelphus pacificus</i>	Russia, Kunashir, Koroteeva 15-12-1 MHA, isolate OK1925	MK463531
<i>Rhytidiadelphus pacificus</i>	USA, Oregon, Norris 83956 MHA9057426, isolate OK1826	MK463532
<i>Rhytidiadelphus squarrosus</i>	Russia, Ivanovo, Sorokin 27-6-2008 MHA, isolate OK1864	MK463533
<i>Rhytidiadelphus squarrosus</i>	Russia, Commander Islands, Fedosov, 10-3-286 MW 9063387, isolate OK2026	MK463534