

ON THE *BRYOXIPHIMUM NORVEGICUM* AND *B. JAPONICUM*
(BRYOXIPHIACEAE, BRYOPSIDA)

О *BRYOXIPHIMUM NORVEGICUM* И *B. JAPONICUM*
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Abstract

Bryoxiphium japonicum was accepted as a subspecies of *B. norvegicum* in the world revision of the genus by Á. Löve & D. Löve (1953) and treated in the recent literature at this rank. However, ITS sequence data indicate a strong genetic difference between plants from the southern part of Russian Far East (mainland, Sakhalin and Kuril Islands), Japan and China, and plants from the northern part of Russian Far East (Chukotka, Kamchatka, Commander Islands), Transbaikalia Siberia, south-east Yakutia, and also from North America and Iceland. Low genetic variation over the expanded range of *B. norvegicum* s. str. and its sharp differentiation of sequences from East Asian plants suggest the resurrection of *Bryoxiphium japonicum* as a separate species. Additional comparison of these two taxa confirmed the diagnostic value of previously used morphological characters and revealed new ones, allowing the identification of plants in sterile state. *Bryoxiphium japonicum* differs from *B. norvegicum* in longer filiform awns in perichaetial and perigonal leaves with sharply serrate vs. slightly crenulate or subentire margins, higher dorsal lamellae in stem leaves, presence of attenuate filiform acumen in stem leaves, and shorter cells at the base of stem leaves.

Резюме

Bryoxiphium japonicum рассматривался в качестве подвида *B. norvegicum* в мировой ревизии рода (Löve & Löve, 1953), и в этом ранге он трактовался в недавно опубликованных региональных Флорах. В то же время, данные по последовательностям ITS ядерной ДНК показывают существенные отличия между растениями с юга Российского Дальнего Востока (включая материковую часть, Курильские острова и Сахалин), Японии и Китая с одной стороны, и растениями с севера Российского Дальнего Востока (Чукотка, Камчатка, Командорские острова), из Забайкалья, юго-восточной Якутии, а также из Северной Америки и Исландии, с другой. Почти идентичные последовательности ITS в пределах очень широкого ареала *B. norvegicum* s. str. и резко отличающиеся последовательности этого маркера у восточноазиатских растений предполагают восстановление статуса самостоятельного вида для *Bryoxiphium japonicum*. Изучение морфологических признаков отсеквенированных образцов позволило подтвердить диагностическое значение признаков, использовавшихся ранее для различения подвигов, а также выявить новые признаки, позволяющие различать растения в стерильном состоянии. *Bryoxiphium japonicum* отличается от *B. norvegicum* более длинными узкими верхушками перихециальных и перигонийных листьев, остро пильчатыми краями этих верхушек (у *B. norvegicum* они почти цельные), более высокими пластиночками на дорсальной стороне жилки в стеблевых листьях, наличием б.м. длинного оттянутого кончика в стеблевых листьях (у *B. norvegicum* жилка оканчивается в верхушке или очень коротко выбегает) и обширной зоной коротких квадратных клеток в основании стеблевых листьев (у *B. norvegicum* клетки основания листа менее дифференцированы, б.ч. прямоугольные).

KEYWORDS: mosses, Russia, taxonomy, ITS1-2, trnL-F

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INTRODUCTION

Bryoxiphium norvegicum (Brid.) Mitt. was originally described in the genus *Phyllogonium* subgenus *Eustichia* and later segregated in a separate genus *Bryoxiphium* by Mitten (1869). Bescherele (1892) established a separate family for the genus, and the subsequent elevation of its rank to the order Bryoxiphiales was suggested by Crum & Anderson (1981). Molecular phylogenetic data support highly isolated position of *Bryoxiphium* within the basal paraphyletic grade of haplolepidous lineage (Goffinet *et al.*, 2001; Cox *et al.*, 2010; Stech *et al.*, 2012; Fedosov *et al.*, 2016); however, its taxonomy and systematic position at the species level remain insufficiently known.

The world revision of Löve & Löve (1953) resulted in the acceptance of only two species in the genus, the Macaronesian endemic *B. madeirense* Á. Löve & D. Löve, and the widespread *Bryoxiphium norvegicum* with two subspecies: subsp. *norvegicum* (including its type variety in Iceland, Greenland and North America, and var. *mexicanum* (Besch.) Sharp in Central America and Mexico) and subsp. *japonicum* (Berggr.) Á. Löve & D. Löve in East Asia. A strongly disjunct distribution of the genus was in the focus of a biogeographical discussion of Steere (1937), Löve & Löve (1953) and Patiño *et al.* (2016).

Steere (1937) noted that the material from Japan and Korea called *B. japonicum* is probably very close and perhaps indistinguishable from *B. norvegicum*. The same conclusion was made by Löve & Löve (1953).

In Russia, *Bryoxiphium* was first revealed in Sakhalin by Savicz (1936) who published it under the name *B. savatieri* (Husn.) Mitt., a species synonymized subsequently by Löve & Löve (1953) with *Bryoxiphium norvegicum* subsp. *japonicum*. Lazarenko (1936) reported the same species in his “Handbook of mosses of the Soviet Far East”, citing Savicz’s personal communication. However, later he compared American and Asian Far Eastern material, and concluded their species identity. Hence, in the “Annotated list of mosses of the Soviet Far East”, he reported *Bryoxiphium norvegicum* in a number of localities from Kamchatka and southern part of mainland Far East in Primorsky Territory (Lazarenko, 1940). Savicz-Lyubitskaya & Smirnova (1970) continued to refer all material from the Russian Far East to *B. savatieri*, and Bardunov & Cherdantseva (1982, 1984) followed them, as well as some other authors who dealt with the Russian moss flora.

Afonina (2004) was the first to conclude that *Bryoxiphium* plants from the Chukotka, northern Kamchatka and Yakutia are not the same with plants from the southern Russian Far East, and referred the former to *B. norvegicum* s. str. Thus, in the “Check-list of mosses of East Europe and North Asia”, Ignatov, Afonina, Ignatova *et al.* (2006) reported two taxa for Russia. However, their distribution and diagnostic characters remained unclear, hence, Czernyadjeva (2012) kept only one taxon in the ‘Moss

flora of Kamchatka’, *Bryoxiphium norvegicum* subsp. *japonicum*, pending the revision of all material from the region.

Molecular phylogenetic studies have not been specially addressed at the species level taxonomy of the genus. Tsubota *et al.* (2004) found *B. norvegicum* subsp. *japonicum* nested in clade of *B. norvegicum* based on *rbcL* sequences. Recently Patiño *et al.* (2016) studied distribution patterns of the genus using four cpDNA loci from 39 specimens of *Bryoxiphium*, covering almost the entire range of the genus. They found that East Asian *Bryoxiphium* comprises three groups of haplotypes, one being sister to all other specimens. Unfortunately, they did not recognize any subordinate taxa of the genus, thus, their results cannot be correlated with any taxonomic units.

The present study aims to estimate molecular differentiation between plants referred to *Bryoxiphium norvegicum* subsp. *norvegicum* and subsp. *japonicum*, revise their taxonomical status, evaluate characters useful for the taxa delimitation and identification and clarify their distribution in the Russian Far East.

MATERIAL AND METHODS

Nuclear ITS and chloroplastic *trnL-F* markers were used for our molecular phylogenetic study, because they provided stronger phylogenetic signals and were successfully used in similar study in the related group (Ignatova *et al.*, 2015). Laboratory protocol was essentially the same as reported in previous moss studies and described in detail by, *e.g.*, Gardiner *et al.* (2005). ITS1 was used as a forward primer for ITS amplification and sequencing, since commonly used ITS L did not provide the PCR product. The primer ITS3 was used in order to amplify ITS2 region in cases where the primer ITS1 also did not provide amplification. Sequences were aligned manually using BioEdit 7.0 (Hall, 1999). Molecular distances were estimated using Mega 7 (Kumar *et al.*, 2015). Analyses were conducted using the Maximum Composite Likelihood model (Tamura *et al.*, 2004).

Alignment of sequences as well as a preliminary phylogenetic analysis have shown a low variability of *trnL-F* (only two informative positions), thus, it was excluded from the analysis. Totally, 21 sequences (11 for subsp. *norvegicum* and 10 for subsp. *japonicum*) with a total length 335–595 bp were obtained *de novo*. Voucher information for specimens used in molecular study and accession numbers are provided in Appendix 1. One sequence of subsp. *japonicum* (FJ572409) taken from the GenBank was added to the alignment. For eleven specimens, partial sequences of ITS1, complete sequences of 5.8S rRNA gene and partial sequences of ITS 2 were used. Total length of obtained alignment was 689 bp (1–234 partial ITS1 sequences; 235–393 complete 5.8S rRNA gene sequences; 394–689 partial ITS2 sequences). As we faced the problem with amplification and sequencing of ITS1 in subsp. *japonicum*, molecular dis-

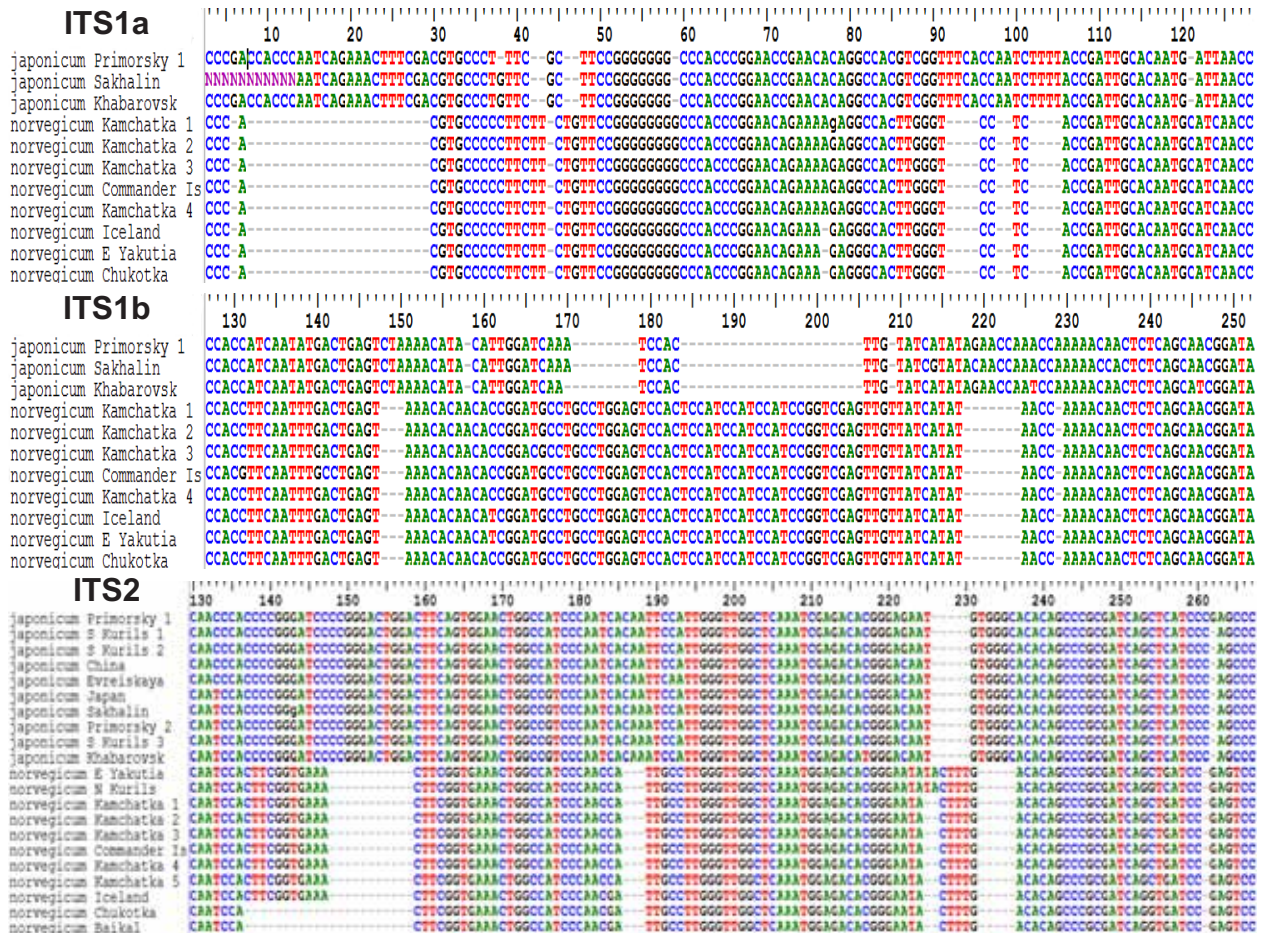


Fig. 1. Parts of ITS1 (in two halves) and ITS2 alignment, showing differentiation of *B. japonicum* and *B. norvegicum*. Alignment of ITS1 includes fewer specimens, due to difficulties in their sequencing.

tances were calculated for partial 5.8S rRNA sequences and partial ITS2 sequences.

Two sequences of *Scouleria* (KP308306 & KP308296) and one of *Drummondia prorepens* (Hedw.) E. Britton (KF135315) were used as an outgroups, as these taxa have been revealed to be the rather close relatives of *Bryoxiphium* in most of recently published molecular phylogenetic studies (cf. Cox *et al.*, 2010). *Dolotortula mnifolia* (Sull.) R.H. Zander (GQ339748) was also included as an outgroup using Blast facility (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>) since it was found to have closest ITS sequence to *Bryoxiphium*.

As the sequencing of ITS1 appeared to be very difficult and only three specimens were successful, two datasets were used for phylogenetic analysis, ITS1-2 (15 sequences, 702 positions) and ITS2 (25 sequences, 462 positions). The datasets were separated into three and two unlinked partitions, corresponding to ITS1, 5.8S rRNA gene and ITS2.

Bayesian analysis was performed using MrBayes (Huelsenbeck & Ronquist, 2001), version 3.2.2, running in two parallel analyses, consisting each of six Markov chains of 25,000,000 generations with a sampling frequency of one tree each ten thousand generations and the chain temperature at 0.05. Parameters of the substitution model

were estimated during the analysis (six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). Convergence of the analyses was evaluated using Tracer 1.4.1 (Rambaut & Drummond, 2007) to check that ESS values were all greater than 200 (default burning). The consensus tree was then combined after first 25% of trees were discarded as a burn-in.

Supplementary maximum parsimony analysis was performed in Nona (Goloboff, 1994) in Winclada shell (Nixon, 1999), with bootstrap calculated for 2000 iterations.

We revised all *Bryoxiphium* specimens from LE, MHA, MW, and VLA aiming to find useful morphological characters for the delimitation of subsp. *norvegicum* and subsp. *japonicum*. Several specimens from ICEL representing type locality of *Bryoxiphium norvegicum* were also studied. Several characters selected after examination of herbarium material and preparation of illustrations were studied, with special attention given to specimens used for DNA study. They include: (1) the length of filiform leaf acumen of perichaetial/perigonal leaves; (2) the length/width ratio of basal leaf cells; (3) height and length of dorsal lamella; (4) shape of leaf apex; (5) spore size (it was measured in ten specimens due to rare sporophyte occurrence).

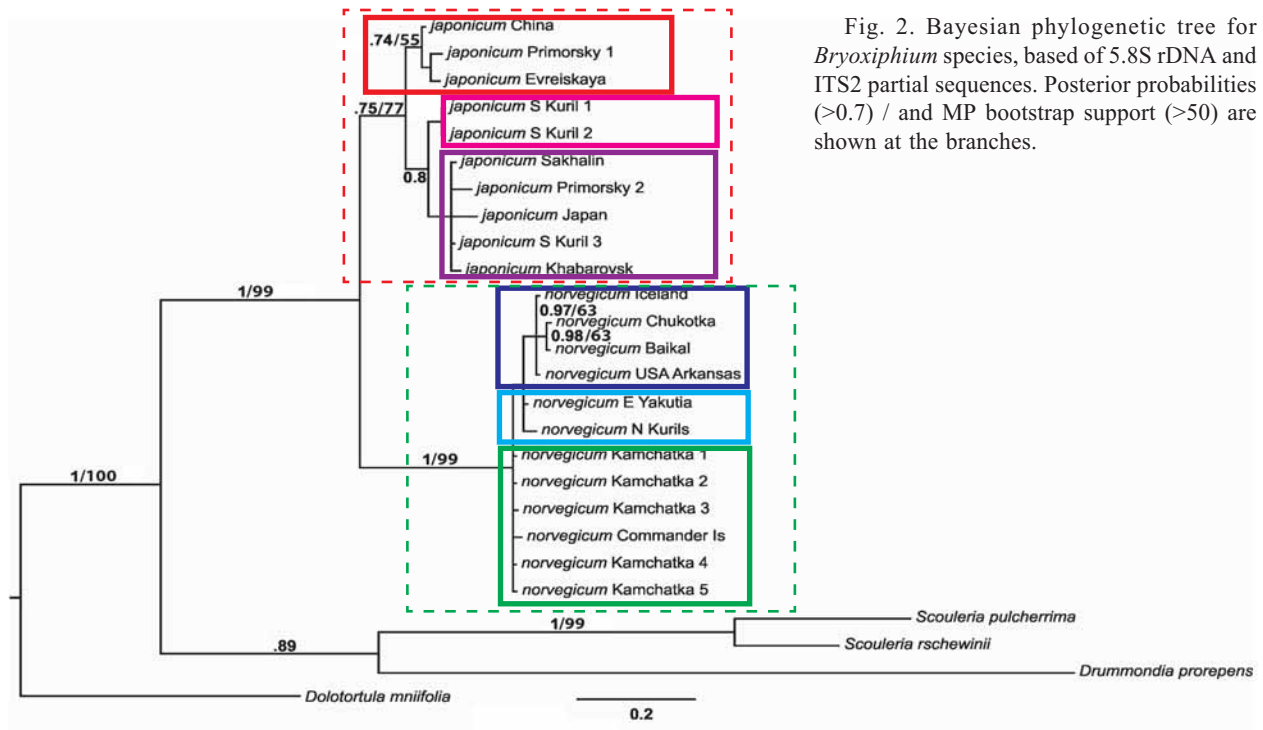


Fig. 2. Bayesian phylogenetic tree for *Bryoxiphium* species, based of 5.8S rDNA and ITS2 partial sequences. Posterior probabilities (>0.7) / and MP bootstrap support (>50) are shown at the branches.

lands, whereas the polytomy of specimens from the Kamchatka Peninsula and Commander Islands is paraphyletic. A highly supported nested clade includes four specimens obtained from the most marginal areas among those included in the present study: from Baikal area in inland Siberia, Chukotka, Arkansas in southern U.S.A., and Iceland in the North Atlantic (Fig. 3). Two specimens from northern Kurils and from East Yakutia (ca. 300 km from sea coast) form a paraphyletic grade to the mentioned terminal clade.

The clade of subsp. *japonicum* includes three weakly supported subclades: (1) three specimens (from Evrejskaya AP, Primorsky Territory, and Chang Bai Mt. in China); (2) two specimens from Kunashir; (3) the rest of specimens from both continental and insular localities. The first subclade comprises only mainland samples, whereas the larger clade has a mixture of island and mainland specimens.

The specimens that form large clades, in most cases, were previously referred to subsp. *norvegicum* (“northern clade”) and subsp. *japonicum* (“southern clade”), but several specimens from Kamchatka Peninsula originally identified as subsp. *japonicum* were found in northern clade.

Morphology

Three characters appeared to be especially useful for the delimiting subsp. *norvegicum* and subsp. *japonicum*.

(1) The length/width ratio of basal leaf cells in *Bryoxiphium* was never discussed before, as far as we know, but it seems to be the most useful character, helpful even for the identification of sterile plants. The basal cells in subsp. *norvegicum* are considerably shorter than in subsp. *japonicum* (Fig. 4A). The use of this character requires a certain caution, as in southern populations with the shorter basal leaf cells, some individual cells are

‘under divided’, hence about twice longer than neighboring ones. However a sufficient number of measurements makes this distinction highly statistically supported, despite of a broad variation (Fig. 5).

(2) The dorsal lamella is conspicuously higher in subsp. *japonicum* than in subsp. *norvegicum* (Fig. 4B). This character clearly separates these taxa when studied in the best developed leaves. Of course, in any collection, it is possible to find a few poorer developed leaves with low dorsal lamella.

(3) The filiform awns of perichaetial/perigonal leaves are considerably longer in subsp. *japonicum*. In subsp. *norvegicum* it never exceeds 5 mm, and usually is shorter than 3.5 mm, while in a well developed plants of subsp. *japonicum* the awns of 6–12 mm long are common. This character is useful as it is almost always well expressed in subsp. *japonicum*. However, when plants are sterile, the character cannot be evaluated.

The shape of stem leaf apices also seems to be quite useful. In both species leaves are somewhat obtuse, but in subsp. *norvegicum* they are only occasionally notched, while the notching is often conspicuous in subsp. *japonicum* (Figs. 6, 7). The awn in subsp. *norvegicum* is formed by only shortly excurrent costa or costa plus dorsal lamella. In subsp. *japonicum*, the excurrent costa and dorsal lamella also constitute the awn, which, however, is often flanked also by extensions of the leaf lamina (Figs. 6, 7), and therefore the awn near its base has a transverse section of a three-pointed star.

Spore size measured in ten specimens has been found to be overlapping: 14–19(–21) μm in subsp. *norvegicum* and (17–)19–23 μm in subsp. *japonicum*, so being moderately helpful for species identification.

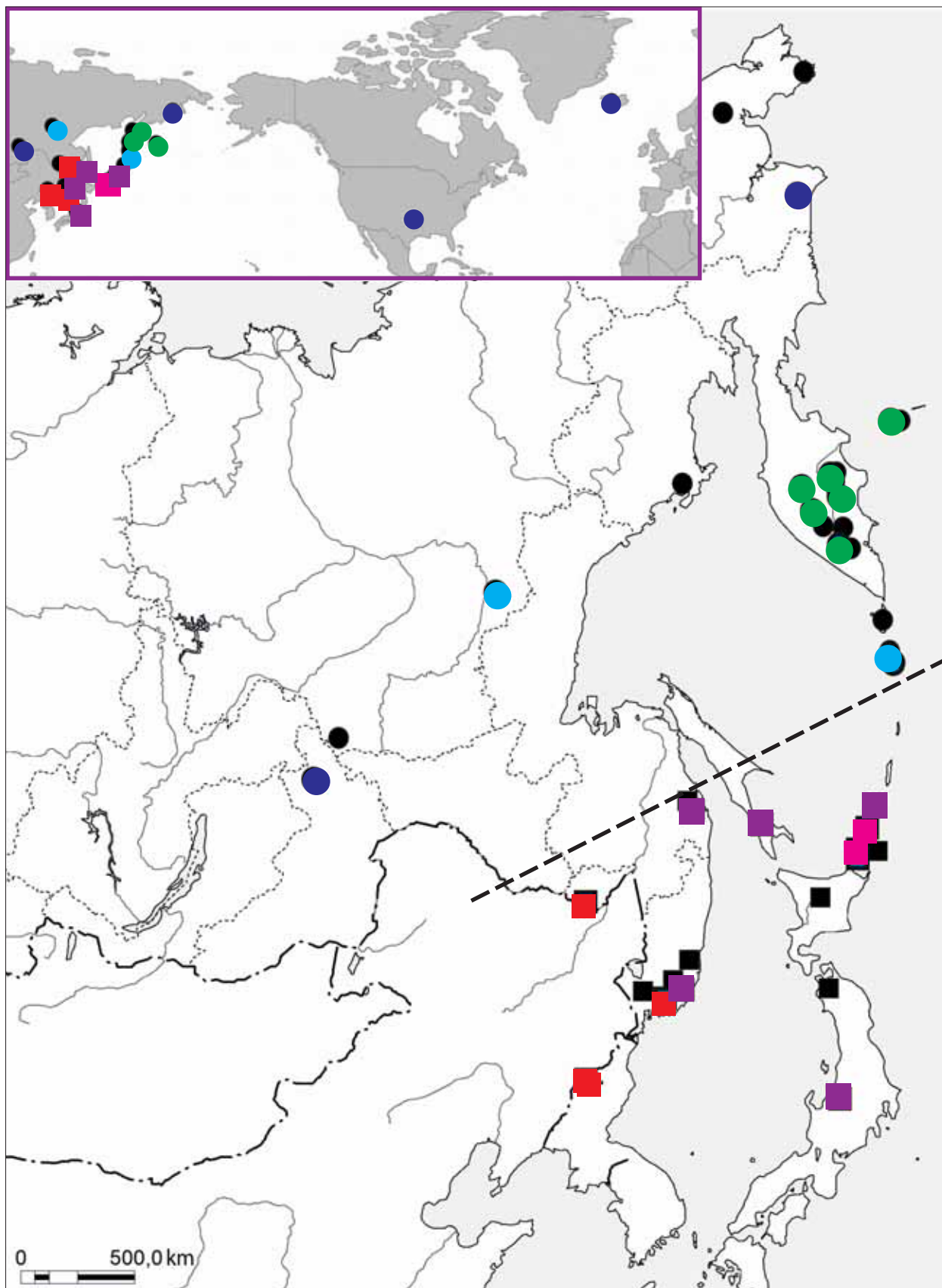


Fig. 3. Distribution of *Bryoxiphium* in Russia, showing also localities from other areas where from specimens were sequenced. In color are given specimens from the better supported clades, shown in Fig. 2.

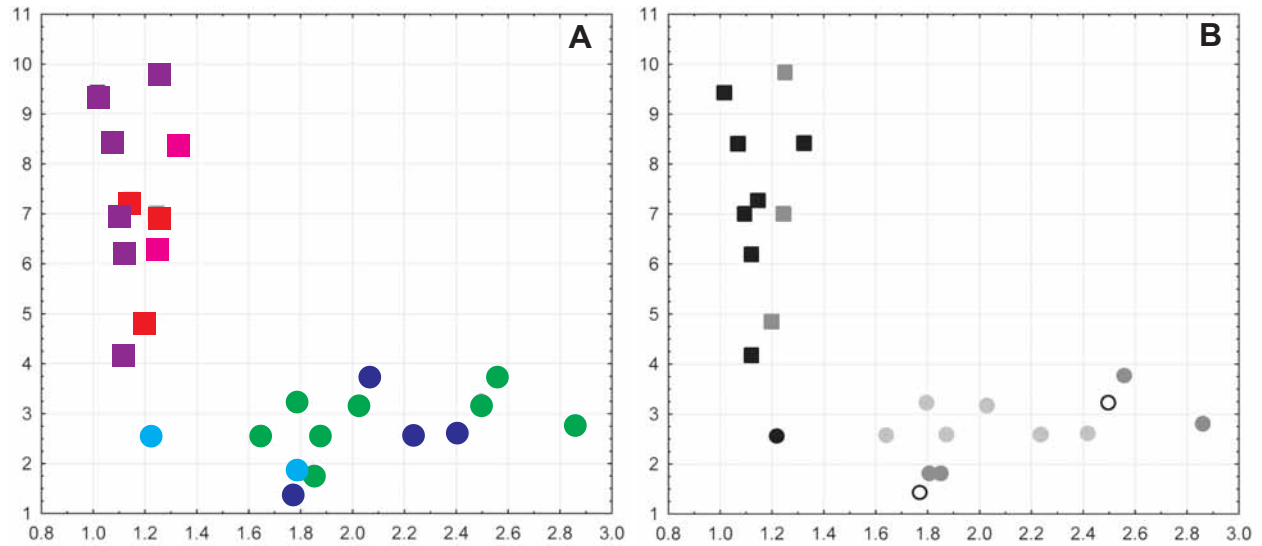


Fig. 4. Scatterplot of morphological characters of *Bryoxiphium* specimens studied for DNA. Axis X is the length/width ratio of the basal leaf cells; Axis Y is and length of filiform awns in perichaetial/perigonal leaves. Squares and circles indicate the region of specimen origin, from the 'norvegicum-area' and from the 'japonicum-area' respectively (cf. Fig. 3). Colors in A correspond to clades in Fig. 2 and localities in Fig. 3. Note the absence of any obvious correspondence between genetic entities and morphological characters within *B. norvegicum* and *B. japonicum*. Grey intensity in B indicates the height of dorsal lamella: black: 4 cells high; gray: 3, light gray: 2; open circle 0–1 cell high.

DISCUSSION

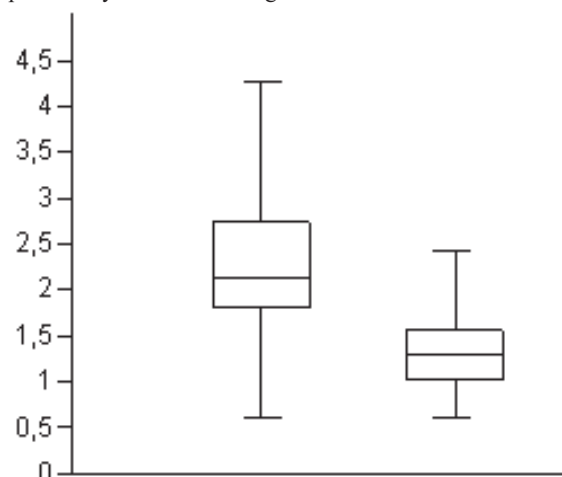
Phylogeny and Phylogeography

The level of genetic divergence between subsp. *norvegicum* and subsp. *japonicum*, in combination with rather clear morphological distinction, indicates a sharp genetic isolation and acceptance of these two taxa as a separate species. The subclade differentiation within the clades is contrastingly lower in support (Table 1) and does not correspond to any difference seen in their morphology.

However, the fact that the most marginally occurring plants among the studied populations appeared to be in one clade is quite unexpected and it requires an explanation.

The previous phylogeographic analysis of the genus

Fig. 5. Box diagram of length/width ratio of basal leaf cells (axis Y) in *Bryoxiphium norvegicum* (left) and *B. japonicum* (right); N=108 and 151 respectively, means 2.32 and 1.29, and 95% intervals of them are (1.25–1.38) and (2.15–2.43). The probability that data belong to the same set is <0.0001.



based on chloroplastic DNA markers (Patiño *et al.*, 2016) presented a picture only partly congruent with our study results. Their analysis indicated a previous, wider distribution of *Bryoxiphium*, strongly fragmented now, and its ability to long-distance dispersal. Also, their study pointed at the East Asia as an important centre from which *Bryoxiphium* migrated northward. Consequently, at least two events leading to the Alaskan colonization by *Bryoxiphium* took place by two different East Asian haplotypes.

At the same time, the Iceland and North American chloroplastic sequences were found by these authors to be related to different groups of East Asian plants. Instead, our ITS results demonstrate the low genetic difference between the Iceland, Arkansas, Chukotka and Baikal populations, the latter being the most inland population in the world, at ca. 1000 km from any sea coasts. *Bryoxiphium* has primary an oceanic distribution, with only few inland findings. There are good reasons to consider these inland populations as some of the most ancient in origin (Koponen *et al.*, 2004).

Our present data may be interpreted as follow: the first wave of spreading of population of *Bryoxiphium* from East Asia involved a single ITS haplotype, and it retained in the most remote inland areas, while populations from Kamchatka underwent changes brought by the subsequent invasions of another East Asian haplotypes. Beyond the level of dash-line in a map shown in Fig. 3, the invasion of the second wave of haplotype on the originally installed population was only moderate in impact.

Thus, the statistically supported monophyly of Baikal, Chukotka, Arkansas and Iceland plants based on ITS sequences can be also assumed as a case of monochrony of their origin.

Table 2. Comparison of the main diagnostic characters of *Bryoxiphium norvegicum* and *B. japonicum*

	<i>Bryoxiphium norvegicum</i>	<i>Bryoxiphium japonicum</i>
Length of filiform awns in perichaetial/perigonal leaves, mm	1–3(–5)	(4–)5–12
Margin serration	subentire to slightly crenulate	serrate
Shape of basal leaf cells	short rectangular, hardly differentiated	subquadrate, ± differentiated
Length/width ratio of basal leaf cells	1.6–3.0:1	1–1.4:1
Dorsal lamella height, cell number	(0–)1–3	3–4(–5)
Dorsal lamella length	only in upper part of leaf	descending far below, often to the leaf base
Shape of middle stem leaf apex	obtuse, occasionally notched, mostly with short apiculus formed by excurrent costa and dorsal lamella or solely by costa, rarely with filiform awns to 0.2 mm long	obtuse, often notched, suddenly narrowed into filiform awn to 0.4 mm long, formed by lamina, costa and dorsal lamella
Spore size, µm	14–19(–23)	(17–)19–24

Accepting this scenario, the East Asian origin of modern populations for the Holarctic range of the species becomes obvious. However, the minimal difference between Iceland and Baikal populations (10 000 km from each other, opposite parts of the globe in Northern Hemisphere) poses necessarily a difficulty of explanation: (1) either the DNA structure of this haplotype is so conservative that allows no afterward variation, or, (2) both of these populations are the result of very recent spreading, and the time of divergence between North American and East Asian populations evaluated by Patiño *et al.* (2016) as about 10 million years is an overestimation; or (3) hybridization events in East Asia took place so fast that they resulted in a lack of variation of ITS sequences in *Bryoxiphium*, which looks like an outstanding phenomenon. Naturally, a combination of these explanations and other possible ones cannot be excluded.

The known distribution ranges of *B. norvegicum* and *B. japonicum* in Russia do not seem to overlap. However, Gao (1999) reported both species for China, although the two published distribution maps are almost identical. Based on our study, the confirmed species identity of *Bryoxiphium* in China data belongs to *B. japonicum*, and no confirmed record of *B. norvegicum* is known within the East Asian floristic region of Holarctic as defined by Takhtajan (1986).

Morphology

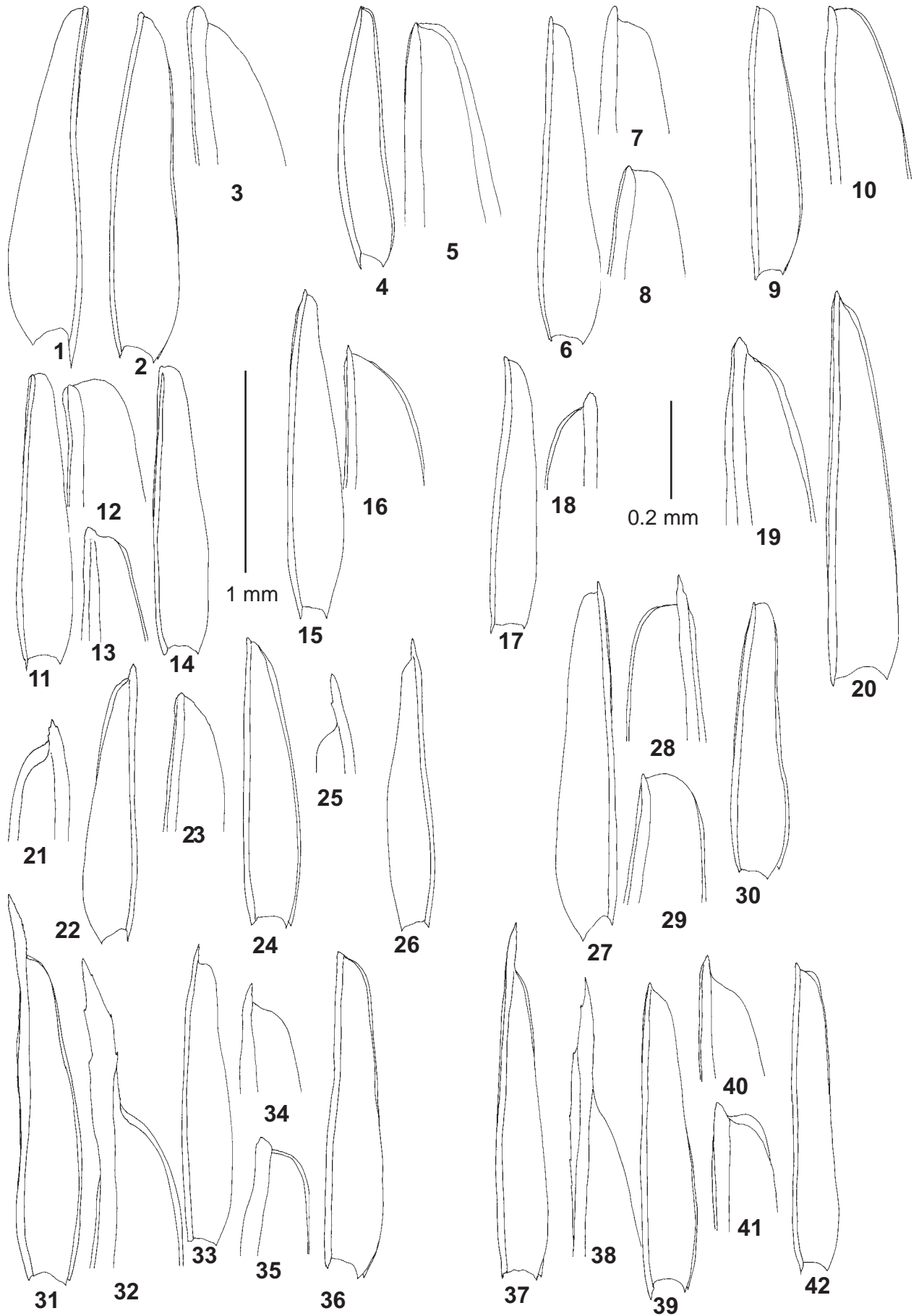
Á. Löve & D. Löve (1953) mentioned the serrate margins of filiform awns in perichaetial leaves as one of the most prominent, if not the only, character separating subsp. *japonicum* from subsp. *norvegicum*, while the latter subspecies has only weakly crenulate to subentire awn margins. Our observations confirm the high diagnostic value of this character, being stable in both perichaetial and perigonal leaves of *Bryoxiphium*. In stem leaves, the serration of leaf margins in distal portion is also better expressed in *B. japonicum*; however, it was found to be rather variable in both species. Note also that the overall structure of filiform awns of perichaetial and perigonal leaves is sim-

ilar in both species. They consist of narrow lamina with the costa extending almost to the awn apex and dorsal lamella (Figs. 8–9).

The length of filiform awns in perichaetial and perigonal leaves has been also confirmed as a reliable character for the separation of *B. norvegicum* from *B. japonicum* (Table 2). However, it apparently depends on fertilization and sporophyte development, in some cases complicating its uses in taxonomy.

Height of dorsal lamella was used by Gao (1999) for the separation of subsp. *norvegicum* and subsp. *japonicum* in Chinese material, in addition to the reported serrate vs. subentire margins of leaf awn of perichaetial leaves. In Russian specimens, a remarkable difference in both height and length of dorsal lamella between these two species was also observed. In *B. japonicum*, dorsal lamella was usually clearly seen, 3–4 cells high, extending far below from stem leaf tip and often reaching leaf base. In *B. norvegicum*, it was usually hardly visible in profile, often only one cell high, usually slightly higher near leaf tip in stem leaves and not descending to the leaf base. However, a variability of dorsal lamella height was observed in some specimens of *B. norvegicum*. An unusually high lamella, up to four cells high, has been seen in some leaves of plants from Kamchatka (Bannaya River) and Onkotan Island specimens, whereas the other leaves from the same specimens have dorsal lamella of 1–2 cells high, which is more typical for this species. At the same time, other characters of leaves with high dorsal lamella well agreed with *B. norvegicum*, *i.e.*, having very short apiculus and rectangular basal cells.

Stem leaves in both *B. norvegicum* and *B. japonicum* can vary in shape within one shoot. They are scaly in its proximal portion, oblong-lanceolate and obtuse in middle part of stem, and gradually change distally, becoming acute to acuminate below the perichaetium or perigonium. At the same time, we observed a rather clear and stable difference in the shape of apical portion of middle stem leaves between *B. japonicum* and *B. norvegicum*.



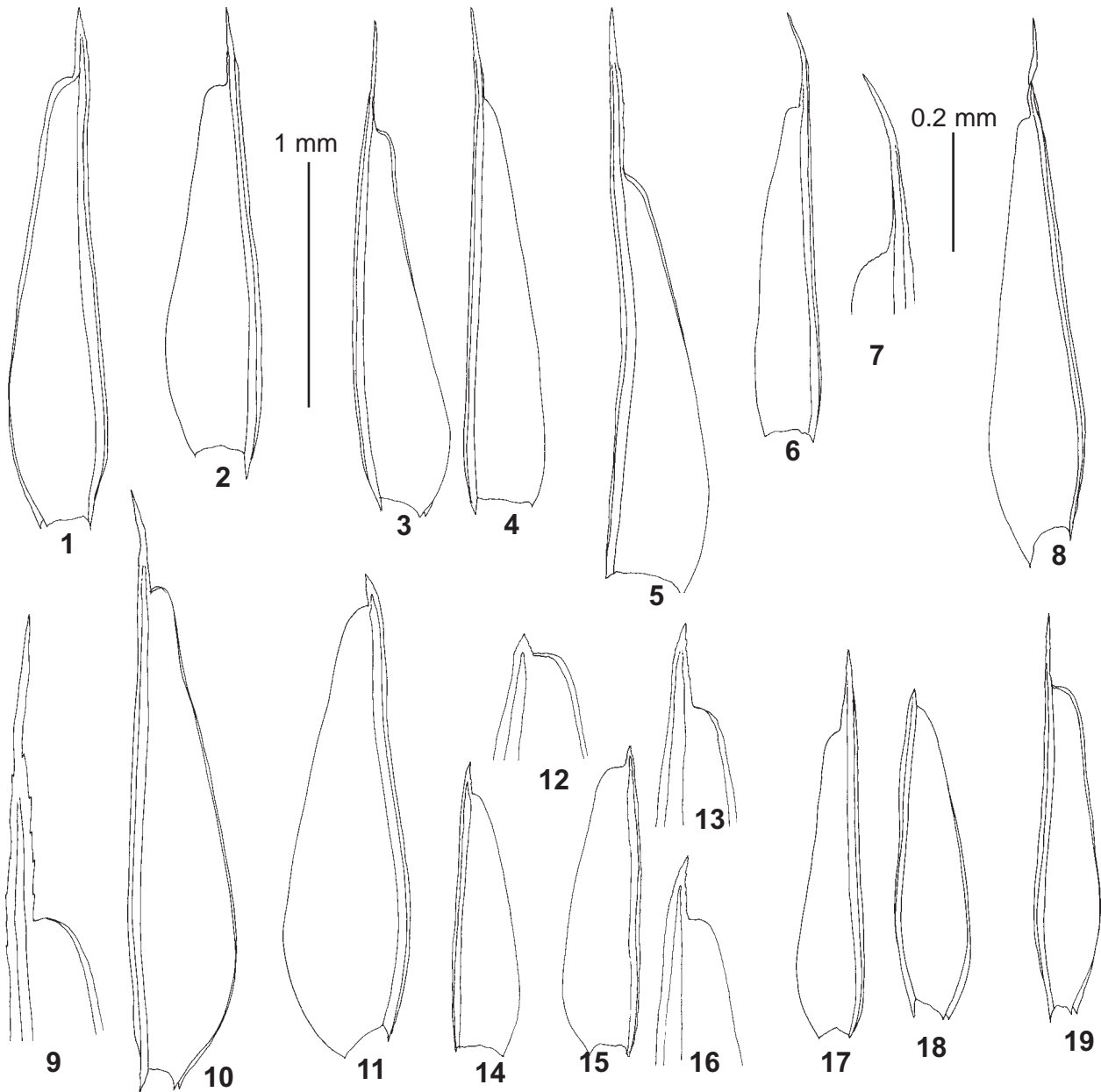


Fig. 7. *Bryoxiphium japonicum* (Berggr.) E. Britton (from: 1 – Japan, Honshu, *Deguchi 33030*, MHA; 2 – Russia: Kuril Islands, Shikotan Island, 6.IX.2006, *Nyushko III-4.2-06a*, MHA; 3–4 – Kunashir Island, *Ignatov 06-1308*, MHA; 5 – Iturup Island, *Bakalin K-22-1-07*, MHA; 6–7 – Sakhalin, *Ignatov & Teleganova 06-780*, MHA; 8 – Khabarovsk Territory, Sovgavan District, *Ignatov & Ignatova 13-915*, MHA; 9–10 – Primorsky Territory, Kit Bay near Glazkovo Settlement, *Ignatov 07-378*, MHA; 11 – Primorsky Territory, Valentin Bay, 12.IX.1977, *Bardunov & Cherdantseva s.n.*, VLA; 12–16 – Primorsky Territory, Pidán Mt., *Ignatov & Ignatova 06-2290*, MW; 17–18 – Jewish Autonomous Province, VII.1997, *Nedoluzhko & Rubtsova s.n.*, LE; 19 – China, Jilin Province, 22.IX.1981, *Koponen s.n.*, MHA). 1–6, 8, 10–11, 14–15, 17–19 – middle stem leaves; 7, 9, 12–13 – apices of middle stem leaves. Scale bars: 1 mm for 1–6, 8, 10–11, 14–15, 17–19; 0.2 mm for 7, 9, 12–13.

Fig. 6 (previous page). *Bryoxiphium norvegicum* (Brid.) Mitt. (from: 1–3 – Iceland, 3 IX.1950, *Löve & Löve 2-805*, MHA; 4–5 – U.S.A., Arkansas, 24.04.1993, *Redfearn & Redfearn*, LE; 6–8 – U.S.A., Washington, VIII.1977, *B.R. Jenkinson*, MHA; 9–10 – Russia: Commander Islands, Bering Island, *Fedosov 10-3-494*, MHA; 11–14 – Kamchatka, Icha Volcano, 4.VIII.2007, *Czernyadjeva 6*, LE; 15–16 – Kamchatka, Ushkovsky Volcano, 15.VIII.2004, *Czernyadjeva 78*, LE; 17–18 – Kamchatka, Esso, 30.VIII.2001, *Czernyadjeva 47*, LE; 19–20 – Kamchatka, Bannaya River, 2.VIII.2002, *Czernyadjeva 67*, LE; 21–26 – Zabaikalsky Territory, Mamontov 506/1, LE; 27–30 – Onkotan Island, 12.VII.1981, *Barkalov s.n.*, LE; 31–36 – Koryakia, 10.VIII.1984, *Afonina s.n.*, LE; 37–42 – Yakutia, Yst-Maya District, 18.VI.2001, *Krivoshapkin s.n.*, MW). 1–2, 4, 6, 9, 11, 14–15, 17, 20, 22, 24, 26–27, 30–31, 33, 36–37, 39, 42 – middle stem leaves; 3, 5, 7–8, 10, 12–13, 16, 18–19, 21, 23, 25, 28–29, 32, 34–35, 38, 40–41 – apices of middle stem leaves. Scale bars: 1 mm for 1–2, 4, 6, 9, 11, 14–15, 17, 20, 22, 24, 26–27, 30–31, 33, 36–37, 39, 42; 0.2 mm for 3, 5, 7–8, 10, 12–13, 16, 18–19, 21, 23, 25, 28–29, 32, 34–35, 38, 40–41.

In the former species, middle stem leaves are obtuse and often notched at apex and always have a narrow attenuate awn up to 0.4 mm long, consisting of leaf lamina, costa and dorsal lamella and often being serrate at margins (Fig. 7). In *B. norvegicum*, middle stem leaves are obtuse at apex, occasionally notched, and shortly apiculate; the apiculus is formed solely by very shortly excurrent costa or, more often, by costa and slightly extended dorsal lamella (Fig. 6). Exceptionally long awns, to 0.2 mm, were seen in some leaves obtained from three specimens collected from Koryakia, Yakutia and Zabaikalsky Territory. In all cases, only a few leaves possessed such unusually long awns, while other leaves were shortly apiculate. Long awns of *B. norvegicum* look stouter than awns of *B. japonicum*, being formed mostly by excurrent costa (Fig. 6: 31, 37). And again, other characters of these unusual leaves (height of dorsal lamella and basal laminal cells) agreed with *B. norvegicum* rather than with *B. japonicum*.

Difference was also detected in shape of basal cells of stem leaves, which can be used for the delimitation of *B. norvegicum* and *B. japonicum*. In the former species, basal laminal cells are mainly short rectangular, hardly delimited from the rest of lamina, while in the latter, they look shorter, mostly subquadrate, which makes the lamina areolation dim in basal portion, contrasting with the rest of lamina. This visual difference was generally confirmed by cell measurements (see Table 2 and Figs. 4 and 5). The estimation of cell length/width ratio apparently depended on cell sampling and was affected by the rather high variability of cell shape and size (caused by numerous irregular cell divisions). However, even this rather rough estimation showed a considerable difference between species (Table 2, Fig. 5).

TAXONOMY

Bryoxiphium Mitt., J. Linn. Soc., Bot. 12: 24, 850. 1869.

Plants small to medium-sized, light-green, golden-green to brownish-green, often shiny, forming loose or dense tufts. Stems 5–20[–50] mm long, erect or pendent, simple or sometimes irregularly branched, moderately tomentose basally, with large central strand and small incrassate epidermal cells; axillary hairs of 3–4(–7) cells, hyaline or with rose-violet basal cell. Leaves strongly distichous, appressed, strongly keeled, imbricate and partly covering each other, ovate-lanceolate, blunt or apiculate, becoming longer distally, acute or aristate; costa single, percurrent, short or long excurrent, with dorsal lamella, in cross-section showing a solid stereid band, well differentiated ventral epidermis and weakly differentiated dorsal epidermis; margin plane, entire, crenulate or minutely serrate near apex; lamina unistratose, cells smooth and firm-walled, with stronger thickened dorsal walls and plane to somewhat convex ventral walls, along margins in 10–25 rows longer and narrower, with thinner walls. Dioicous. Perichaetia and perigonia terminal. Perichaetial

leaves from ovate-lanceolate base narrowed into a long, flexuose, hyaline, yellowish to brownish filiform awn with serrate, crenulate or entire margins. Setae shorter than perichaetial leaves, erect, curved or flexuose. Capsules spherical to ovate or obovate, symmetric, erect or \pm inclined. Annulus not differentiated. Peristome absent. Operculum remains attached to the elongated columella after dehiscence, shortly and obliquely rostrate. Spores spherical, faintly roughened. Calyptra cucullate.

KEY TO THE SPECIES OF *BRYOXIPHIMUM* IN RUSSIA

1. Filiform awns in perichaetial and perigonial leaves 1–3(–5) mm long, with finely crenulate or subentire margins; middle stem leaves mostly obtuse, occasionally notched, shortly apiculate, apiculus formed mainly by shortly excurrent costa and partially by dorsal lamella; basal laminal cells short rectangular, with length/width ratio of 1.6–3, weakly differentiated; dorsal lamella mostly 1–2 cells high, not descending to the leaf base; spores 14–19(–23) μ m *B. norvegicum*
- Filiform awns in perichaetial and perigonial leaves (4–)6–12 mm long, with sharply serrate margins; middle stem leaves obtuse, often notched and suddenly narrowed into awn to 0.4 mm long, awn consisting of lamina, costa and dorsal lamella; basal laminal cells subquadrate, with length/width ratio of 1–1.4, forming large, more or less distinct group; dorsal lamella mostly 3–4 cells high, often reaching leaf base; spores (17–)19–22(–24) μ m *B. japonicum*

Bryoxiphium norvegicum (Brid.) Mitt., J. Linn. Soc., Bot. 12: 580. 1869. — *Phyllogonium norvegicum* Brid., Bryologia Universa 2: 674. 1827. — *Eustychia norvegica* (Brid.) Brid., Bryologia Universa 2: 789. 1827. — *Eustychia norvegica* (Brid.) Bruch et al., Bryologia Europaea 2: 161. 195. 1849. Figs. 6, 8.

Type: Krýsuvík, Iceland, A. Mörch, 1820 (C, not seen).

Stems 1–15 mm long. Leaves in the middle part of stem 1.2–2.1 \times 0.5–0.8 mm, oblong-lanceolate, obtuse and occasionally notched at apex, blunt or shortly apiculate, rarely with stout awn to 0.2 mm long; costa percurrent or shortly excurrent, with dorsal lamella 1–2(–3) cells high, usually hardly visible in profile, reaching leaf tip, but not descending to the leaf base; margin entire, crenulate, rarely minutely serrulate at leaf apex; cells in upper and middle part of leaf 9–16 μ m wide and 12–20 long, short rectangular, triangular, rhomboidal or hexagonal, firm-walled, along margins in 10–15 rows narrower, elongate, 4–6 μ m wide and 28–50 μ m long, thin-walled, gradually transiting to mid-leaf cells; basal laminal cells larger, 11–18 μ m wide and 16–40 μ m long, with length/width ratio (1.2–)1.6–3(–4), short rectangular, weakly differentiated from the rest of lamina. Perichaetial and perigonial leaves from ovate-lanceolate base gradually narrowed into a flexuose and twisted, yellowish, brownish or hya-

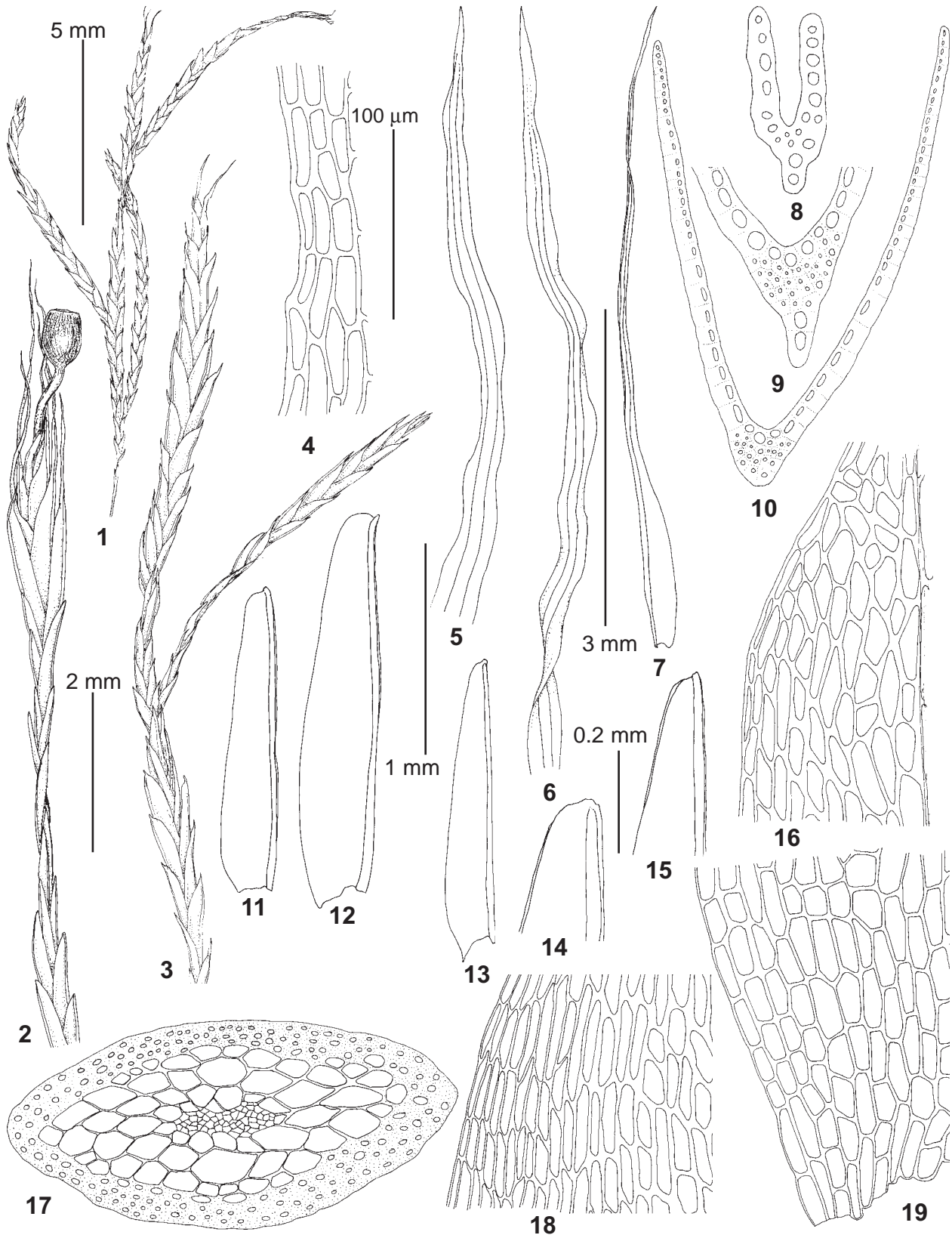


Fig. 8. *Bryoxiphium norvegicum* (Brid.) Mitt. (from: Russia, Kamchatka, 12.VIII.2002, *Czernyadjeva* 67, LE). 1–3 – habit, dry; 4 – margin of filiform awn of perichaetial leaf; 5–6 – filiform awns of perichaetial leaves; 7 – perichaetial leaf; 8 – transverse section of filiform awn of perichaetial leaf; 9–10 – leaf transverse sections; 11–13 – stem leaves; 14–15 – distal portions of stem leaves; 16 – upper laminal cells of stem leaf; 17 – stem transverse section; 18 – median laminal cells of stem leaf; 19 – basal laminal cells of stem leaf. Scale bars: 5 mm for 1; 3 mm for 7; 2 mm for 2–3; 1 mm for 11–13; 0.2 mm for 5–6, 14–15; 100 μm for 4, 8–10, 16–19.

line filiform awn 1–3(–5) mm long, with entire to crenulate margins. Seta 1.5–2.5 mm. Urn ca. 1 mm long. Spores 14–19(–21) μm .

Distribution. *Bryoxiphium norvegicum* s. str. is distributed mainly in humid areas of Northern Hemisphere. It is known from Europe (Iceland), North America (Greenland, U.S.A.) and Asia (Russia and China). The identity of Macaronesian, Mexican, Dominican and Indonesian populations needs further study. Distribution area of *B. norvegicum* in Russia (Fig. 3), includes northern Far East: Chukotka Autonomous District, Magadan Province, Kamchatka Peninsula and Kommander Islands (Afonina, 2004; Czernyadjeva, 2012, as *Bryoxiphium norvegicum* subsp. *japonicum*; Fedosov *et al.*, 2012; Pisarenko *et al.*, 2015). Scattered records were also reported from continental regions of Siberia: Yakutia and Zabaikalsky Territory (Ivanova *et al.*, 2005; Afonina *et al.*, 2015). All specimens from Kamchatka Peninsula previously referred to *B. japonicum*, in fact, represent *B. norvegicum*, and molecular data confirm this identification.

Ecology. The species occurs on bare cliffs and boulders composed of acidic to basic volcanic rocks, and on sandstone; it grows on cliff surfaces, in crevices and niches, and on mineral soil and humus between rocks. In most cases it occurs near lakes, creeks or along sea coasts. In Chukotka Peninsula it also grows in rocky tundra. The species often forms pure carpets, especially extensive in shaded niches, or grows intermixed with *Distichium capillaceum* (Hedw.) Bruch *et al.*, *Ditrichum flexicaule* (Schwägr.) Hampe, *Eurhynchiastrum pulchellum* (Hedw.) Ignatov & Huttunen, *Amphidium lapponicum* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw., *Pohlia cruda* (Hedw.) Lindb., *Polytrichastrum alpinum* (Hedw.) G.L.Sm., *Mnium* spp., *etc.* Four specimens from Kamchatka Peninsula and one from Onkotan Island (North Kurils) contained plants with sporophytes.

Specimens examined. ICELAND: Gullbringusysla: Kleifarvatn, Innro Stapi (63°55'N, 22°00'W), 150 m alt., 3 IX.1950 *Askel & Doris Löve 2-805* (ICEL, dupl. MHA); Southwest Iceland, Sveifluhals, 26.VI.1964, *Steere s.n.* (LE); Kleifarvatn auf Reykjanes, Sudvesturland, 26.VI.1973, *Frahm s.n.* (LE). DENMARK: Northeast Greenland, Wollaston Foreland, 14.VIII.1949, *Holmen s.n.* (LE).

RUSSIA: SIBERIA: **Zabaikalsky Territory**, Kalar Distr., Stanovoye Upland (56°14'36.4'N, 117°26'23.8'E), 1516 m alt., 26.VIII.2014, *Mamontov 506/1* (LE). **Yakutia**: Olekminskij Distr., Udokan Range, 1200 m. alt., 29.VII.2001, *Kuznetsova s.n.* (SASY); Ust-Majskij Distr., Aldan River valley, 18.VI.2001, *Krivoshapkin s.n.* (SASY, MW). FAR EAST: **Magadan Province**, vicinity of Magadan City (59°34'N, 150°39'E), 330 m alt., 10.VIII.2014, *Pisarenko 05358* (VBGI, LE, MW). **Chukotka Autonomous District**: Iultinskij Distr., vicinity of Egvekinot Settl. (66°20'N, 179°07'W), 21.VI.1970, *Afonina s.n.* (LE); Providenskij Distr., vicinity of Yanrakynnot Settl. (64°53'N, 172°30'W), 27.VII.1976, *Afonina s.n.* (LE); Anadyrskij Distr., vicinity of Pekulnejskoe Lake, Kakanaut Gulf (62°43'N, 176°58'E), 15.VIII.1984, *Afonina s.n.* (LE); the same area, Byanranaj Mt. (62°43'N, 176°58'E), 10.VIII.1984, *Afonina s.n.* (LE). **Kamchatsky Territory**: Kamchatka: Ust'-Kamchatskij Distr., Klyuchevskaya group of volca-

noes: Bilchenok glacier (56°11'N, 160°21'E), 1000 m alt., 16.VII.2003, *Czernyadjeva 18* (LE); the same area 950 m alt., 19.VII.2003, *Czernyadjeva 37, 64* (LE); the same area, 750 m alt., 22.VII.2003, *Czernyadjeva 53* (LE); Bilchenok River (56°11'N, 160°21'E), 550 m alt., 22.VII.2003, *Czernyadjeva 18* (LE); Ushkovsky volcano (55°58'N, 160°15'E), 1000 m alt., 19.VIII.2005, *Czernyadjeva 40* (LE); the same place, 15.VIII.2004, *Czernyadjeva 78* (LE); vicinity of Kozyrevsk Settl., valley of Kamchatka River, (56°00'N, 160°02'E), 220 m alt., 12.VIII.2004, *Czernyadjeva 63* (LE); Bystrinskij Distr., vicinity of Esso Settl. (55°55'N, 158°42'E), 700 m alt., 30.VII.2001, *Czernyadjeva 47* (LE); Middle Kamchatskij Range, Icha volcano (55°32'N, 157°37'E), 800 m alt., 4 & 5.VIII.2007, *Czernyadjeva 6, 10* (LE); Elizovo Distr., Kronotskij State Reserve, Death Valley in upper course of Geyzernaja River (54°28'N, 160°16'E), ca. 840 m alt., 7.IX.2012, *Fedosov 12-132* (MW); Ust'-Bol'sheretskij Distr., middle course of Bannaya River (52°54'N, 157°30'E), 250 m alt., 12.VIII.2002, *Czernyadjeva 67* (LE, MHA, MW); Aleutskij Distr., Kommander Islands, Bering Island, Nakoval'nya Mt. near Nikol'skoe settl. (55°13'N, 166°01'E), ca. 20 m alt., 5.VIII.2010, *Fedosov 10-3-494, 10-3-593, 10-3-1104* (MW). **Sakhalinskaya Province**: Northern Kuril Islands: Paramushir Island, vicinity Severo-Kurilsk Settlement (~50°23'N, 155°41'E), 4.VIII.1978, *Barkalov s.n.* (VLA); Onkotan Island, Nemo Bay (~49°27'N, 154°46'E), 12.VII.1981, *Barkalov s.n.* (VLA, LE); the same place, 29.VII.2008, *Koroteeva 0-32.2-08* (MHA); Shumshu Island, Bolshoe Lake (~50°45'N, 156°21'E), 22.VII.1978, *Zavorotniy s.n.* (VLA).

U.S.A.: Washington, Glacier Peak Wilderness Area, Kennedy Ridge above Pacific Crest Trail, VIII.1977, *B.R. Jenkinson s.n.* (MHA); Arkansas, Newton County, 24.IV.1993, *P.L. Redfearn, Jr. & A. Redfearn* (Mosses of the Interior Highlands Exsiccatae 36) (LE); Wisconsin Dells, Potsdam Sandstone, 19.VIII.1893, *Britton s.n.* (LE); Missouri, St. Clair County, 30.V.1973, *Redfearn 28522* (LE); Missouri, St. Clair County, 28.VII.1969, *Ireland 10092* (LE); Ohio, Hocking County, VI.1937, *Welch 208* (LE).

Bryoxiphium japonicum (Berggr.) E. Britton, Bull. Torrey Bot. Club 19: 24. 1892. — *Eustychia japonica* Berggr. in Geheeb, Flora 64: 290. 1881. — *Bryoxiphium norvegicum* subsp. *japonicum* (Berggr.) Å. Löve & D. Löve, Bryologist 56: 197. 1953. — *Bryoxiphium savatieri* (Husn.) Mitt., Trans. Linn. Soc. London, Bot. 3: 154. 1891. — *Eustychia savatieri* Husn., Revue Bryol. 10: 85. 1. 1883. Figs. 7, 9

Type: Near Kusatsu, Gumma Prefecture, Honshu, Japan, F. R. Kjellman 1879 (S).

Stems 1–20 mm long. Leaves in the middle part of stem 1.5–2.4×0.5–0.8 mm, oblong-lanceolate, often notched and suddenly narrowed into awn to 0.4 mm long, formed by lamina, costa and dorsal lamella; leaves in upper part stems up to 3.5 mm long, acute, with longer awns; costa extending into the awn, percurrent, on dorsal side with lamella 3–4(–5) cells high, extending to the awn and often descending to the leaf base; margin entire, crenulate or serrate at leaf apex; cells in upper and middle part of leaf 11–16 μm wide and 14–30 μm long, irregularly shortly rectangular, triangular, rhomboidal or hexagonal, firm-walled, at margins in 15–25 rows narrower, 3–5 μm wide and 40–65 μm long, linear, thin-

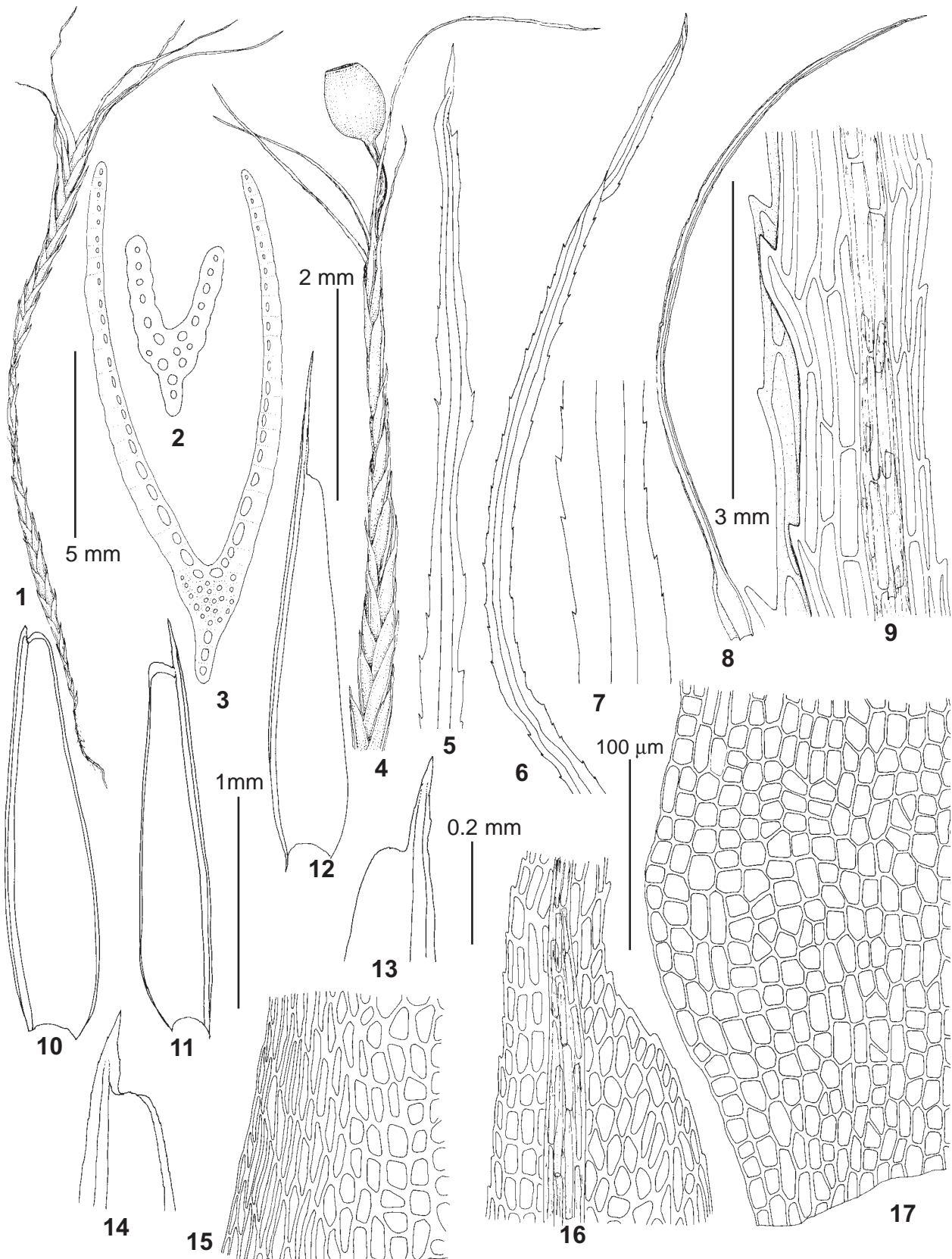


Fig. 9. *Bryoxiphium japonicum* (Berggr.) E. Britton (from: Russia, Khabarovsk Territory, Ignatov & Ignatova 13-915, MHA). 1, 4 – habit, dry; 2 – transverse section of filiform acumen of perichaetial leaf; 3 – stem leaf transverse section; 5–7, 9 – parts of filiform acumina of perichaetial leaves; 8 – perichaetial leaf; 10–12 – stem leaves; 13–14 – distal portions of stem leaves; 15 – median laminal cells of stem leaf; 16 – upper laminal cells of stem leaf; 17 – basal laminal cells of stem leaf. Scale bars: 5 mm for 1; 3 mm for 8; 2 mm for 4; 1 mm for 5–6, 10–12; 0.2 mm for 7, 13–14; 100 µm for 2–3, 9, 15–17.

walled; cells in basal part of leaf 9–20 µm wide and 10–34 µm long, with length/width ratio (0.8–)1–1.2(–1.4), subquadrate, dim, forming large, more or less distinct group. Perichaetial and perigonal leaves from ovate-lanceolate base gradually or abruptly narrowed into a pale yellowish or hyaline awn (4–)7–10(–12) mm long, with sharply serrate margins, wavy, flexuose and twisted. Seta 1.5–2.5 mm. Urn ca. 1 mm long. Spores (17–)19–23 µm.

Distribution. *Bryoxiphium japonicum* is an East-Asian species, distributed along the coast of Pacific Ocean (Fig. 3). It is known from Japan (Hokkaido, Honshu, Shikoku, Kyushu), Korea, China, Taiwan, Philippines (Noguchi, 1987; Gao, 1999). In Russia *B. japonicum* occurs in southern region of Far East: southern Kuril Islands, Sakhalin Island, coastal area in Khabarovsk Territory, Primorsky Territory, and Jewish Autonomous Province (Savicz, 1936; Bardunov & Cherdantseva, 1982, 1984; Nedoluzhko & Rubtsova 1998; Ignatov *et al.*, 2004; Bakalin *et al.*, 2009; Pisarenko *et al.*, 2012; Ignatova *et al.*, 2013). The specimens from Magadan Province (Cherdantseva & Bakalin, 2011) and north Kuril Islands (Cherdantseva, 1986; Nyushko *et al.*, 2008) referred to this species are re-identified here as *B. norvegicum*.

Ecology. The species occurs on moist, mostly acidic volcanic rocks, in cliff niches and crevices near streams and along sea shores. In most cases it forms pure carpets, which reach extensive cover in moist niches and caves. It also grows intermixed with other mosses, *i.e.*, *Claopodium pellucinerve* (Mitt.) Besch., *Herzogiella adscendens* (Lindb.) Z. Iwats. & W.B. Schofield, *Hypnum cupressiforme*, *Myurella sibirica* (Müll. Hal.) Reimers, *Pohlia cruda*, *Mnium* spp., *etc.*

Specimens examined: RUSSIA: FAR EAST: **Khabarovsk Territory**, Sovgavansky Distr., Botchinsky State Reserve, (48°17'N, 139°30'E), 230 m alt., 11.VIII.2013, *Ignatov & Ignatova 13-160, 13-271, 13-677, 13-899, 13-915* (MHA, MW); the same area (48°17'N, 139°34'E), 293 m alt., 20.VIII.2013, *Ignatov & Ignatova 13-899* (MW). **Jewish Autonomous Province:** Amur River valley, (–48°36'N, 130°37'E), VII.1997, *Nedoluzhko & Rubtsova* (VLA, LE). **Primorsky Territory:** Lazovsky Distr., Valentin Bay (–43°07'N, 134°18'E), 12.IX.1977, *Bardunov & Cherdantseva* (VLA); Lazovsky Reserve (–43°14'N, 133°24'E), 2.III.1986, *Khokhryakov* (VLA); Lazovsky (=Sudzukhinsky) Reserve (–43°14'N, 133°24'E), 13.VII.1944, *Zhudova & Pokrovskaya s.n.* (LE); Elomovskij Creek (–43°13'N, 133°46'E), ca. 250 m alt., 6.IX.2013, *Malashkina & Ivanov s.n.* (MHA); Olga Distr., Proselochnaja (Chingousa) Bay (–43°40'N, 134°57'E), 5.IX.1936, *Kolesnikov s.n.* (LE); Kit Bay near Glazkovo (43°02'N, 134°09'E), less than 100 m alt., 22.VIII.2007, *Ignatov 07-378* (MW); Shkotovsky Distr., Bejchi River basin, 600 m alt., 29.IX.1946, *Kolesnikov s.n.* (LE); Tumannaja Mt. eastern slope (43°14'N, 132°48'E), 13.VII.1944, *Zhudova & Pokrovskaya s.n.* (MW); Pidan (Livadiyskaya) Peak, left tributary of Pryamoj Klyuch (43°06'N, 132°41'E), 400–500 m alt., 25.IX.2006, *Ignatov & Ignatova 06-2072* (MHA, MW). **Sakhalinskaya Province:** Sakhalin Island: 23.VIII & 1.X.1929, *Krishtophovich s.n.* (LE); Dolinsk Distr., Sokol, valley of Belaya Creek (47°15'N, 142°49'E), 50 m alt., 12.VIII.2006, *Ignatov & Teleganova 06-780* (MW, MHA); Iturup Island: vicinity of Rybaki

Settlement (–45°12'N, 147°51'E), 3.X.1956, *Vorob'ev & Koval 730* (LE); the same place (–45°12'N, 147°51'E), 18.IX.1974, *Blagodatskikh s.n.* (LE); Stokap Mt. (44°51'N, 147°20'E), 660 m alt., 13.VIII.2007, *Bakalin K-22-1-07* (VLA, MW); Burevestnik Mt. (44°53'N, 147°27'E), 1335 m alt., 9.VIII.2007, *Bakalin K-15-13-07* (VLA, MW); Kunashir Island: vicinity Yuzhno-Kurilsk Settlements, (–44°02'N, 145°51'E), VII.1978, *Cherdantseva s.n.* (VLA); Kisly stream, (–44°02'N, 145°51'E), 22.VIII.1978, *Cherdantseva s.n.* (VLA); 3.VII.1946, *Vorob'ev 31* (LE); vicinity of Alekhino, 14.IX.1956, *Koval 678* (LE, MHA); SSW slope of Tyatya Volcano (44°18'N, 146°18'E), ca. 100 m alt., 15.IX.2006, *Ignatov 06-1775* (MHA, MW); Ruruj Mt. (44°29'N, 146°06'E), 28.VIII.2006, *Ignatov 06-1178, 06-1241, 06-1295, 06-1308, 06-1424* (MHA, MW3); Shikotan Island: Gorobets River, (–43°49'N, 146°42'E), 30.VIII.1978, *Cherdantseva s.n.* (VLA); vicinity Krabozavodsk Settlement (–43°50'N, 146°45'E), 3.IX.1978 & 29.VIII.1978, *Cherdantseva s.n.* (VLA); Shikotan Island: Otradnaja Mt. (43°51'N, 146°45'E), 290 m alt., 6.IX.2007, *Bakalin* (MHA); Otradnaja Bay vicinity, 6.IX.2006, *Nyushko III-4.2-06a* (MHA); Ostrovnoy Cape Area (43°44'N, 146°35'E), 25 m alt., 30.VIII.2007, *Oleynikov K-53-7-07* (MHA).

JAPAN: Hokkaido: Kamikawa-gun, Kamikawa-cho, ca. 500 m alt. 11.VI.1978, *Sasaki s.n.* (MHA); Ishikari District, 10.VII.1971, *Koponen 21697* (LE); Saitama Prefecture, Chichibu, 27.V.1971, *Koponen 20002* (LE); Honshu: Aomori-ken, Towada-shi, Oirase Gorge, Kumoi-no-taki Falls, 280 m alt., 29.VII.1994, *Deguchi 33030* (MHA); Nagano-ken, Kami-inagun, Ihjima-cho, Shioji-daira, ca. 1300 m alt. 28.VII.1996 *Deguchi s.n.* (MHA); Tochigi Prefecture, 17.VI.1969, *Inoue* (Bryophyta selecta exsiccata 31) (LE); Fukushima Prefecture, 24.VIII.1994, *Higuchi & Ueno* (Bryophyta Selecta Exsiccata 1276) (LE); Nara-ken, Takaichi-gun, 19.VI.1966, *Kodama* (Musci Japonici Exsiccata 1410) (LE); Yamanashi Prefecture, 15.VII.1967, *Osada 1108* (LE); Gifu Prefecture, 17.X.1962, *Iwatsuki 963* (LE); Kyushu: Miyazaki Prefecture, 20.VI.1969, *Iwatsuki & Chuang, 1156* (LE); Ōita, Naoiri, VI.1946, *Noguchi* (Musci Japonici Exsiccata. 43) (LE).

CHINA: Jilin (Kirin) Prov., vicinity of Chang Bai Mt., Erdo-Baihu River valley (41°30'N, 128°10'E), 1700 m alt., on boulder in *Betula ermanii* dominated forest near small lake, 22.IX.1981, *Koponen s.n.* (MHA ex H); Si-kang Province, Yanan, IV.1955, *Li* (Musci sinici Exsiccata 61) (LE); China interior, provincia Schen-si, 1.IX.1896, *Giraldi 2024* (LE); Anhwei Province, montis Hwang-shan, 17.VIII.1961, *Tsang Mu 1045* (LE); Taiwan, Nantou County, 8.XI.2012, *Shevock 41534* (LE).

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Appendix 1. Specimens vaucher information and GenBank accessions numbers

Bryoxiphium norvegicum

Baikal	Zabaikalsky Territory, Kalar Distr., Stanovoye Upland, 26.VIII.2014, <i>Mamontov 506/1</i> (LE)	KX131278
E Yakutia	Ust-Majskij Distr., Aldan River valley, 18.VI.2001, <i>Krivoshapkin s.n.</i> (SASY, MW)	KX131270
Chukotka	Anadyrskij Distr., Byanranaj Mt. 10.VIII.1984, <i>Afonina s.n.</i> (LE)	KX131277
Kamchatka 1	Elizovo Distr., Kronotskij State Reserve, <i>Fedosov 12-132</i> (MW)	KX131271
Kamchatka 2	Ust'-Bol'sheretskij Distr., Bannaya River, 12.VIII.2002, <i>Czernyadjeva 67</i> (LE)	KX131272
Kamchatka 3	Bystrinskij Distr., vicinity of Esso Settl., 30.VII.2001, <i>Czernyadjeva 47</i> (LE)	KX131273
Kamchatka 4	Ust'-Kamchatskij Distr., Klyuchevskaya group of volcanoes, Bilchenok glacier, 22.VII.2003, <i>Czernyadjeva 53</i> (LE)	KX131276
Kamchatka 5	Middle Kamchatskij Range, Icha volcano, 5.VIII.2007, <i>Czernyadjeva 10</i> (LE)	KX235917
Iceland	<i>B. Jóhannsson 2-805</i> (ICEL)	KX131274
Commander Is.	Aleutskij Distr., Bering Island, <i>Fedosov 10-3-1104</i> (MW)	KX131275
N Kurils	Onekotan Island, 12.VII.1981, <i>Barkalov s.n.</i> (VLA, LE)	KX235916
USA Arkansas	Newton County, 24.IV.1993, <i>P.L. Redfearn, Jr. & A. Redfearn s.n.</i> (LE) (Mosses of the Interior Highlands Exsiccatae 36)	KX265438

Bryoxiphium japonicum

Evreiskaya	Jewish Autonomous District, VII.1997, <i>Nedoluzhko & Rubtsova s.n.</i> (VLA, LE)	KX235912
Khabarovsk	Khabarovsk Territory, Sovgavan Distr., Botchinsky State Nature Reserve, <i>Ignatov & Ignatova 13-677</i> (MHA, MW)	KX131268
Primorsky 1	Primorsky Territory: Pidan Mt., 25.IX.2006, <i>Ignatov 06-2072</i> (MHA, MW)	KX131266
Primorsky 2	Primorsky Territory: Elomovskij Creek, 6.IX.2013, <i>Malashkina & Ivanov</i> (MHA)	KX235914
Sakhalin	Sakhalin Island, Dolinsk Distr., Sokol, <i>Ignatov & Teleganova 06-780</i> (MW, MHA)	KX131269
S Kurils 1	Kunashir Island, Ruruj Mt., <i>Ignatov 06-1178</i> (MHA, MW)	KX131267
S Kurils 2	Kunashir Island, Ruruj Mt., <i>Ignatov 06-1424</i> (MHA, MW)	KX235913
S Kurils 3	Iturup Island, <i>Bakalin K-22-1-07</i> (VLA, MW)	KX235911
Japan	Honshu, 28.VII.1996 <i>H. Deguchi s.n.</i> (MHA)	KX235915
China	Jilin (Kirin) Prov., Chang Bai Mt. (sequence obtained from Genbank)	FJ572409