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THE GENUS *BRYOERYTHROPHYLLUM* (POTTIACEAE, BRYOPHYTA) IN RUSSIA

РОД *BRYOERYTHROPHYLLUM* (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

Eight species of *Bryoerythrophyllum* are currently known in Russia: *B. alpigenum, B. brachystegium* (new for Russia), *B. ferruginascens, B. inaequalifolium, B. latinervium* (Holmen) Fedosov & Ignatova comb. nov., *B. recurvirostrum, B. rotundatum,* and *B. rubrum*. The study of nrITS region demonstrated that *B. latinervium* (*B. recurvirostrum* var. *latinervium*) is clearly distinct from *B. recurvirostrum*. *Bryoerythrophyllum alpigenum,* often treated as *B. recurvirostrum* var. *dentatum*, is also confirmed to be a distinct species. *Bryoerythrophyllum rubrum* was found in a separate clade, although one dioicous sample was proved to be *B. recurvirostrum*, which poses a problem of reconsideration of differential characters of these taxa. Key for identification, species descriptions, maps and species illustrations are provided.

Резюме

В настоящий момент в России известны восемь видов рода *Bryoerythrophyllum*: *B. alpigenum, B. brachystegium* (новый для флоры России), *B. ferruginascens, B. inaequalifolium, B. latinervium* (Holmen) Fedosov & Ignatova comb. nov., *B. recurvirostrum, B. rotundatum, B. rubrum*. Анализ ITS участка ядерной ДНК указывает на самостоятельность *B. latinervium* (*B. recurvirostrum* var. *latinervium*) и *B. alpigenum* (*B. recurvirostrum* var. *dentatum*). *Bryoerythrophyllum rubrum* также образует отдельную кладу, однако один из двудомных образцов был выявлен в составе клады *B. recurvirostrum*, что ставит вопрос об уточнении отличительных признаков этих двух внешне сходных видов. Приводятся ключ для определения и описания видов, а также иллюстрации и карты распространения в России.

KEYWORDS: mosses, *Bryoerythrophyllum*, taxonomy, molecular phylogenetics, ITS, Russia, phytogeography

INTRODUCTION

Savicz-Lyubitskaya & Smirnova (1970) reported in Russia five species of *Bryoerythrophyllum*: *B. alpigenum, B. ferruginascens, B. recurvirostrum, B. rotundatum,* and *B. rubrum.* One more species, *B. inaequalifolium* was added by Ignatov (1992); a second find of this species in Russia was published by Afonina (2008). Ignatova & Ignatov (2001) expanded the distribution of *B. ferruginascens* in Russia, demonstrating that this species is not very rare in some areas of Siberia. Fedosov et al. (2007) published a preliminary molecular phylogenetic analysis that demonstrated the species status of *B. recurvirostrum* var. *latinervium*, but without making a nomenclatural combination. Later, Fedosov & Ignatova (2008) discussed the distribution of this interesting species in Asia. *Bryoerythrophyllum brachystegium*, East Asian species known from Japan and China has been collected recently in Kuril Islands, in Kunashir by Ignatov in 2006 and in Iturup by Bakalin in 2008 (VLA, MHA), and one specimen from Iturup was identified in herbarium collection.

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The present paper summarizes the data on the genus in Russia, along with the discussion on its classification as it is suggested from DNA sequences of nuclear ITS region.

MATERIALS AND METHODS

All eight taxa of *Bryoerythrophyllum* known from Russia were studied (Table 1). *Barbula unguiculata* Hedw. and *Pseudocrossidium hornschuchianum* (Schultz) Zander were taken as outgroup, using GenBank data. The protocol used was the same as in the study of Gardiner et al. (2005).

Sequences were aligned manually in Bioedit (Hall, 1999). The length of the ITS region varied from 671-673 bp in *Bryoerythrophyllum inaequalifolium* to 776 bp in *B. brachystegium*. Acquired alignment consists of 966 positions, however the last 35 positions were not possible to align unambiguously, so they were excluded from the final analysis.

Parsimony ratchet analysis was implemented with NONA (Goloboff, 1994) within the Winclada (Nixon, 1999a,b) shell. Jackknife support was calculated for 2000 replications.

The highest liklihood score according to AIC 1 measure was for HKY + Γ model which was used for Baesian inference performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2005) with three partitions (ITS1, ITS2, and 5.8S rDNA). Node confidences were determined by sampling 12,500 trees (four chains; 1,500,000 generations; burn-in set to 2,500 trees). Trees were rooted on *Pseudocrossidium.*

RESULTS

The ITS region, and especially ITS 1, was found quite variable, with many specific substitutions (s) and indels (i) unique (among studied *Bryoerythrophyllum*) for individual species: *B. inaequalifolium* – 5s, 16i; *B. brachystegium* – 1s,

Table 1. Accession numbers of ITS1-2 sequences and voucher information of specimens of *Bryoerythrophyllum* used in the present analysis

Barbula unguiculata	MUB 10325	AY437129
Pseudocrossidium hornshuchianum	MUB 9053	AY437128
B. alpigenum Altai	Russia, Altai Mts., 1.VI.1989 *Ignatov s.n.* (MW)	FJ952621
B. alpigenum Austria 2	Austria, Carinthia, *Köckinger #12 306* (MW)	FJ952622
B. alpigenum Austria 1	Austria, Styria, *Köckinger #94-551* (MW)	FJ952620
B. brachystegium Kuril Islands	Russia, Kunashir, *Ignatov # 06-1918* (MHA)	FJ952609
B. inaequalifolium Altai	Russia, Altai Mts. 20.VIII.1989 *Zolotukhin s.n.* (MHA)	FJ952615
B. inaequalifolium Zabaikalsky	Russia, Zabaikalsky Territory, *Afonina # 4006* (LE)	FJ952614
B. latinervium Mongolia	Mongolia, *Ignatov #01-984* (MHA)	FJ952618
B. latinervium Taimyr	Russia, Taimyr, *Fedosov #06-287a* (MW)	FJ952617
B. latinervium Alaska	U.S.A., Alaska, *Murray #10987* (MO)	FJ952619
B. latinervium Zabaikalsky	Russia, Zabaikal'sky Territory, 25.VIII.2006, *Yakovchenko s.n.* (LE)	FJ952616
B. ferruginascens Taimyr 1	Russia, Taimyr, *Fedosov #07-395* (MW)	FJ952612
B. ferruginascens Taimyr 2	Russia, Taimyr, *Fedosov # 05-20* (MW)	FJ952610
B. ferruginascens Altai	Russia, Altai Mts., 4.VIII.2000 *Ignatova s.n.* (MW)	FJ952611
B. recurvirostrum Maine	U.S.A., Maine, *Allen #27744* (MO)	FJ952632
B. recurvirostrum Switzerland	Switzerland, 7.VIII.2001 *Ulanova s.n.* (MW)	FJ952633
B. recurvirostrum Primorsky	Russia, Primorsky Territory, *Ignatov et al. #06-2545* (MW)	FJ952631
B. recurvirostrum Italy 1	Italy, 6.VIII.2002 *Werner* (MUB 15351)	AY437130
B. recurvirostrum Italy 2	Italy, 30.VII.2002 *Ros & Werner* (MUB 15334)	AY437131
B. recurvirostrum Arkhangelsk	Russia, Arkhangelsk Province, *Churakova # 933* (MW)	FJ952630
B. recurvirostrum Taimyr	Russia, Taimyr, *Fedosov # 06-287b* (MW)	FJ952634
B. recurvirostrum Antarctic	Antarctic, *Skotnicki #T576* (MHA)	AY613334
B. recurvirostrum Irkutsk	Russia, Irkutsk Prov.,8.VI.2005, *Ignatov s.n.* (MHA)	FJ952635
B. rubrum Austria 2	Austria, Carinthia, *Köckinger # 01-184* (MW)	FJ952624
B. rubrum Caucasus	Russia, Caucasus, *Onipchenko #35/02* (MW)	FJ952627
B. rubrum Taimyr	Russia, Taimyr, *Fedosov #Brer 2* (MW)	FJ952625
B. rubrum Austria 1	Austria, Salzburg, *Köckinger # #12304* (MW)	FJ952623
B. rubrum Austria 3	Austria, Styria, *Köckinger #12348* (MW)	FJ952626
B. rotundatum Taimyr 1	Russia, Taimyr, *Fedosov #06-510* (MW)	FJ952628
B. rotundatum Taimyr 2	Russia, Taimyr, *Fedosov #08-659* (MHA)	FJ952629

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bra Kur   G---GTTCC- -ACCTGCTTG CCGC--TCTA ACTGATCACT AGT--TTGG- -CAGG----T GGTTGGACG- -
fer Alt   A---GTTTC- -ATCTGCTTG CCGC--TCTA GCTGATCACT AG---TTGG- -CAGG----T GGTTGGACG- -
fer Ta2   A---GTTTC- -ATCTGCTTG CCGC--TCTA GCTGATCACT AG---TTGG- -CAGG----T GGTTGGACG- -
fer Ta1   A---GTTTC- -ATCTGCTTG CCGC--TCTA GCTGATCACT AG---TTGG- -CAGG----T GGTTGGACG- -
ina Zab   A--AGTTTC- -ATCCGCTTG CCAC----TA ACTGATCATT GG---TTGG- -CAGG----T GGTTGGGCG- -
ina Alt   A--AGTTTC- -ATCCGCTTG CCAC----TA ACTGATCATT GG---TTGG- -CAGG----T GGTTGGGCG- -
lat Tai   A---GTTTCA TATCTCCTTG CCCCCA-CTA ATTGATCGTT AGTACTTGG- -CAGGGA--T GGTTGAACGC G
lat Ala   A---GTTTCA TATCTCCTTG CCACCA-CTA ATTGATCGTT AGTACTTGG- -CAGGGA--T GGTTGAACGC G
lat Zab   A--AGTTTCA TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGAACGC G
lat Mon   A--AGTTTCA TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGAACGC G
alp Au1   AGTAGTTTCA TATCTCCTCG CCACC----A ACTGATCGTT GG---TTGG- -CAGGGGTGT GCTTGGACGC G
alp Alt   AGTAGTTTCA TATCTCCTCG CCACC----A ACTGATCGTT GG---TTGG- -CAGGGGTGT GCTTGGACGC G
alp Au2   AGTAGTTTCA TATCTCCTCG CCACC----A ACTGATCGTT GG---TTGG- -CAGGGGTGT GCTTGGACGC G
rub Au1   A---GTTATC TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGG----T GGTTGGACGC G
rub Au2   A---GTT-GA TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGG--TGT GATTGGACGC G
rub Tai   A---GTT--- -ATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGGC ACAGG----T GGTTGGACGC G
rub Au3   A---GTATAA TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGG----T GGTTGGACGC G
rub Cau   A---GTTATA TATCTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGG----T GGTTGGACGC G
rot Ta1   A---GTTTTC ---CTCCTTG CCACCA-CTA ATTGATCGTT AG---TTGG- -CAGGG-TGT GGTTGGACGC G
rot Ta2   A---GTTTTC ---CTCCTTG CCACCA-CTA ATTGATCGTT AG---TTGG- -CAGGG-TGT GGTTGGACGC G
rec It1   AGTTGTTT-- ----TCCTTG CCAC----TG ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Ark   AGTTGTTT-- ---CTCCTTG CCAC----TG ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC g
rec Pri   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Ant   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Mai   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec It2   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Swi   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Tai   AGTTGTTT-- ---CTCCTTG CCAC----TA ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G
rec Irk   AGTTGTTT-- ---CTCCTTG CCAC-----G ATTGATCGTT AG---TTGG- -CAGGG---T GGTTGGACGC G

bra Kur   G---CAAA-- CCCGGAA-CT CAAA-CGTGC GT-CGGTTGT GGCGCCCAGT --TGGTCGGA C-TCC-AAAA G
fer Alt   G---CAAA-- CCCGGAA-CT CAAA-CGTGC GT-CGGTTGT GGCGCCCAGT --TGGTCGGA C-TCC-AAAA G
fer Ta2   G---CAAA-- CCCGGAA-CT CAAA-CGTGC GT-CGGTTGT GGCGCCCAGT --TGGTCGGA C-TCC-AAAA G
fer Ta1   G---CAAA-- CCCGGAA-CT CAAA-CGTGC GT-CGGTTGT GGCGCCCAGT --TGGTCGGA C-TCC-AAAA G
ina Zab   G-TTCAAAAA CCTGGAA-CT CAAA-CGTGC GT-CGGTTGT GGGGCCCAGT --TGGTCGGA C-TCC--AAA G
ina Alt   G-TTCAAAAA CCTGGAACCT CAAAGCGTGC GT-CGGTTGT GGGGCCCAGT --TGGTCGGA C-TCCTCAAA G
lat Tai   CCTT-AGAGA CCCGGAA-CT CAAATCGTGC GTGCGGCCGT GGCACCCAGT --TGGTCGGA CCTCC--AAA G
lat Ala   CCTT-AGAGA CCCGGAA-CT CAAATCGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
lat Mon   CCTT-AGAGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
lat Zab   CCTT-AGAGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
alp Au1   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
alp Alt   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
alp Au2   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
rub Au1   CCTT-AGAGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
rub Au2   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA C-TCC--AAA G
rub Tai   CCTT-AGCGA CCCGGAA-CT CAAAACGTGC GT-CGGCCGT GGCACCCAGT -CTGGTCGGA C-TCC--AAA G
rub Au3   CCTT-AGCGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT TCTGGTCGGA C-TCC--AAA G
rub Cau   CCTT-AGCGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT TCTGGTCGGA C-TCC--AAA G
rot Ta1   CCTT-AGGGA TCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rot Ta2   CCTT-AGGGA TCCGGAAACT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec It1   CCCT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Ark   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Pri   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Ant   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Mai   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec It2   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Swi   CCTT-AGGGA CCCGGAA-CT CAAAACGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Tai   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
rec Irk   CCTT-AGGGA CCCGGAA-CT CAAA-CGTGC GT-CGGCCGT GGCACCCAGT --TGGTCGGA G-TCC--AAA G
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Fig. 1. Two relatively variable parts of alignment of ITS1 (above) and ITS2 (below) of *Bryoerythrophyllum* species (names abbreviated, compare with Table 1).

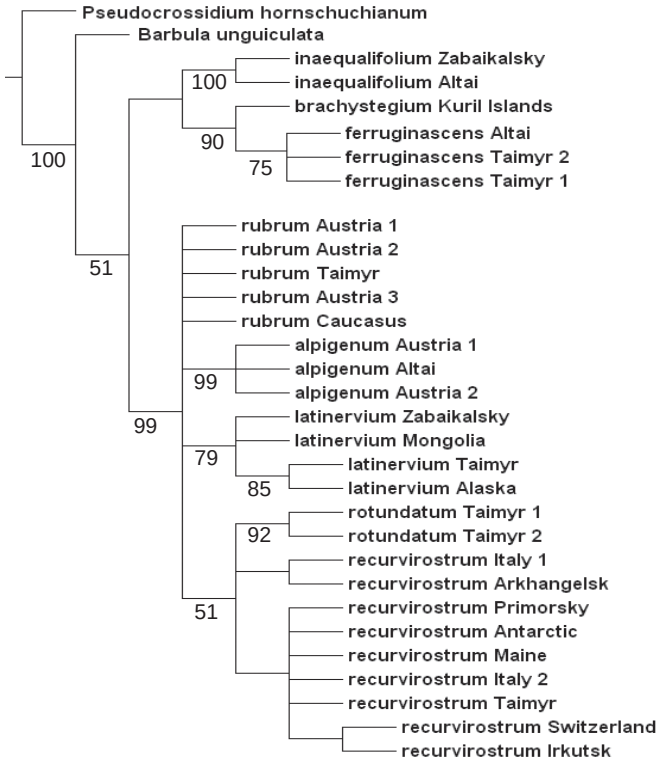

Fig. 2. Strict consensus of 131 shortest trees (L=215) found in parsimony ratchet analysis (L=226, CI=0, RI=0). Jackknife values (>50) calculated for 2000 replications are shown below branches. Data on specimens of *Bryoerythrophyllum* are given in Table 1.

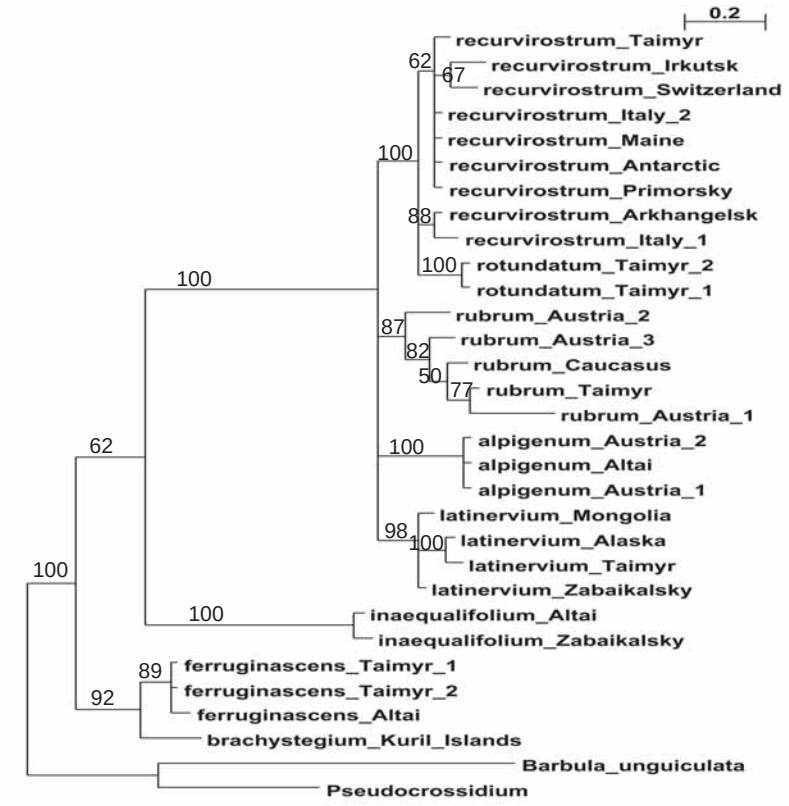

Fig. 3. Bayesian tree, showing posterior probabilities. Data on specimens of *Bryoerythrophyllum* are given in Table 1.

2i; *B. ferruginascens* – 2s, 1i; *B. alpigenum* – 3s, 4i; *B. rubrum* – 0; *B. rotundatum* – 3s, 3i; *B. recurvirostrum* 1i, *B. latinervium* 1s ,5i (Fig.1).

Phylogenetic analyses performed in MP (NONA) and MB (MrBayes 3.1.2) programs resulted in principally similar tree topologies (Figs. 2-3).

The genus *Bryoerythrophyllum* was found to be monophyletic, but with low support, 52, in MP analysis, while 1.00 in MB. The genus includes one big clade (clade 1) formed by *B. rubrum, B. alpigenum, B. latinervium, B. rotundatum* and *B. recurvirostrum*, and the rest of species form another clade 2 in MP tree or a grade in MB tree. In the latter, *B. brachystegium* and *B. ferruginascens* are forming a clade sister to all other species of the genus, and the second clade, sister to Clade 1, includes *B. inaequalifolium*. When contrasted with the MP analysis, this is not a great difference, as the clade 2 as a whole has no statistical support, joining two subclades that have high support each: one formed by *B. inaequalifolium*, another by *B. brachystegium* plus *B. ferruginascens*.

The clade 1 includes 5 species, and three of them, *B. rotundatum*, *B. latinervium* and *B. alpigenum*, were resolved monophyletically in both analyses. MB analysis also found *B. rubrum* in a separate clade, whereas MP analysis left it in a polytomy. Finally, *B. rotundatum* was nested within *B. recurvirostrum* in both analyses. Support of clades formed by 4 samples of *B. latinervium* and 3 samples of *B. alpigenum* was high (79 and 99 in MP correspondingly, and 0.98 and 1.00 in MB). Two samples of *B. rotundatum* from the same area (but collected at ca. 200 km from each other) form a high-supported clade in both analyses. The groups in the *B. recurvirostrum*-clade do not exhibit any correlation with the geography of specimens: plants from a very broad range (eastern North America, Europe, Siberia, Russian Far East, and Antarctic) were found to be nearly identical, while two specimens (from south and north Europe) were detected in a separate clade. Four positions in alignment in these two specimens are similar to those of *B. rotundatum* and different from other studied specimens of *B. recurvirostrum*.

Discussion

The formal infrageneric classification of the genus *Bryoerythrophyllum* has never been published, although the systematic order in monographs of Brotherus (1924), Zander (2007), etc., groups species in informal assemblages demonstrating the species relationships. The results of the present phylogenetic analysis agree rather well with such groupings. Species of the clade 2 differ from most representatives of clade 1 in small size of the plants, obtuse and entire leaf apices (in 2 of 3 species), and presence of asexual reproduction (in 2 of 3 species), as well as distributional pattern. All species in this group are dioicous.

In contrast, clade 1 includes mostly autoicous plants with the exception of the dioicous *B. rubrum*, rarely dioicous *B. recurvirostrum*, and apparently dioicous B. *latinervium*. Leaves in 3 of 5 species of this group are toothed above (to almost throughout in *B. alpigenum*). The clade 1 includes the widespread and polymorphous *B. recurvirostrum* and some others with problematic taxonomic status, sometimes considered to be synonyms or infraspecific taxa of *B. recurvirostrum*.

Bryoerythrophyllum rotundatum differs from *B. recurvirostrum* in ovate leaves with rounded apex and the peristome absence. Its ITS data add a number of molecular synapomorphies, and the high statistical support of the small clade of *B. rotundatum* is also in favor of its species independence. But this is a rare species, currently known from only four records in the north of Eastern Siberia. However, Zander (2007), who accepted *B. recurvirostrum* in North America in a broad circumscription, mentioned occasional occurrence of plants with completely reduced peristome or with subobtuse leaf apices (in latter case normal leaves can be also found). Comparison of them with the Siberian plants of *B. rotundatum* will be important for final evaluation of the status of this taxon.

Another species, *B. alpigenum,* sometimes also treated as a variety of *B. recurvirostrum,* was studied using three specimens, from Central Europe and South Siberia. They differ from 9 specimens of *B. recurvirostrum* in 3 substitutions and 4 indels, and phylogenetic programs found high support for its clade. Morphologically this species is distinct primarily by strong margin serration often almost throughout the leaf (better seen in young leaves, being masked by marginal recurvation in older ones). All these facts support *B. alpigenum* to be a good species.

The third problematic taxon is *B. recurvirostrum* var. *latinervium.* Its molecular synapomor-

phies include 1 substitution and 11 indels. MP and MB analyses demonstrate rather high support of its clade. Four specimens included in the analysis cover the broad range, including Alaska, north of East Siberia, Transbaikalia and Mongolia. Morphologically this species is quite different from *B. recurvirostrum*, and some specimens in herbaria were misidentified as *Pseudocrossidium*, which is similar in broadly revolute leaf margins. This suggests the treatment at specific level, thus the new combination is proposed below.

The fourth species, *B. rubrum* has main distributional range in Europe; it was known in Russia by few old records in Caucasus and also few old and recent collections from Siberian Arctic and Subarctic. This species is said to be different in dioicous sexual condition (autoicous in *B. recurvirostrum*), but this character is not always easy to apply because antheridia do not occur in all inflorescences of the latter species (see also comments on *B. recurvirostrum* by Zander, 2007). In Europe *B. rubrum* is usually rather easily distinguished from *B. recurvirostrum* by larger plant size, longer leaves (to 4-5 mm vs. 2-3 mm), slightly longer urns (to 3 mm vs. 1.5-2 mm), and often entire leaf margins (vs. usually dentate at apex). Limpricht (1890) mentioned also peristome teeth being whitish in *B. rubrum* versus usually reddish in *B. recurvirostrum* (our observations suport this in most cases, although exceptions exist). However, one specimen from Caucasus with leaves ca. 2.5 mm long and another one from Taimyr (Subarctic East Siberia) with leaves 1.5-1.7 mm long were resolved by phylogenetic analysis among 3 specimens of *B. rubrum* from Austria that exhibit quite 'typical' phenotype, representing 'typical' states of all characters. Both Caucasian and Siberian specimens are dioicous, and they have leaves very gradually tapering to the apex, with strongly recurved margins. Such small morphotypes of *B. rubrum* are also known from alpine habitats in Austrian Alps (H. Köckinger, pers. comm.). Among the studied specimens of *B. recurvirostrum* one from Primorsky Territory was apparently dioicous (no antheridia were found by special search), but its morphology agrees with this species in all other details (Fig. 7: 7,9). However, there are cases, especially for sterile plants from Arctic, when the choice between *B. recurvirostrum* and *B. rubrum* will be incredibly difficult, if at all possible.

TAXONOMIC TREATMENT

Bryoerythrophyllum P.C. Chen, Hedwigia 80: 4. 1941. Type: *Bryoerytherophyllum recurvirostrum* (Hedw.) P.C. Chen

Plants small to medium-sized, in loose or moderately dense tufts, usually green or yellowish green in upper part and red-brown below, sometimes reddish brown or brownish throughout. Stem occasionally branching, usually with strong or, rarely, weak central strand, without hyalodermis. Leaves appressed, flexuose to crispate when dry, erecto-patent to spreading when wet, ovate, ovate-lanceolate or lanceolate, usually widened at base, acute, acuminate or rounded-obtuse at apex, margins recurved in mid-leaf and plane in distal 1/2 of leaf or recurved almost to the apex, entire or dentate in distal part, often with few teeth only near leaf apex; costa usually strong, percurrent or ending several cells below leaf apex, adaxially flat or slightly grooved, sometimes slightly convex, abaxially strongly convex, with one row of guide cells, two stereid bands, ventral epidermis clearly differentiated, dorsal epidermis clearly or unclearly differentiated; surface cells on adaxial side of costa subquadrate, densely papillose, surface cells on abaxial side of costa rectangular, densely or more sparsely papillose; leaf lamina unistratose throughout; upper and median laminal cells mostly rounded-quadrate, with thin or moderately thickened walls, densely papillose, papillae bifid or multifid, c-shaped in lateral view, 4-6 per cell, obscuring cell lumen; cells at leaf base clearly differentiated, smooth, thin-walled, short rectangular to elongate rectangular, subhyaline or often orange-colored, more short in several rows at margin of leaf base; KOH-reaction red or orange-red. Monoicous or dioicous. Outer perichaetial leaves longer than stem leaves, with longer sheathing base; innermost perichaetial leaves narrow triangular, subhyaline. Seta long, single in perichaetium. Urn cylindric, erect or slightly curved, reddish-brown or light brownish. Annulus of 1-2 rows of vesiculose cells, revoluble and deciduous. Operculum conic to short-rostrate. Peristome teeth 16, entire or deeply bifid, filiform, sometimes on low basal membrane, erect to twisted, or reduced to none. Spores small, slightly papillose. Calyptra cucullate. Asexual reproduction occasional, by means of unicellular gemmae in mass in leaf axils or multicellular rhizoidal gemmae that are irregular in shape.

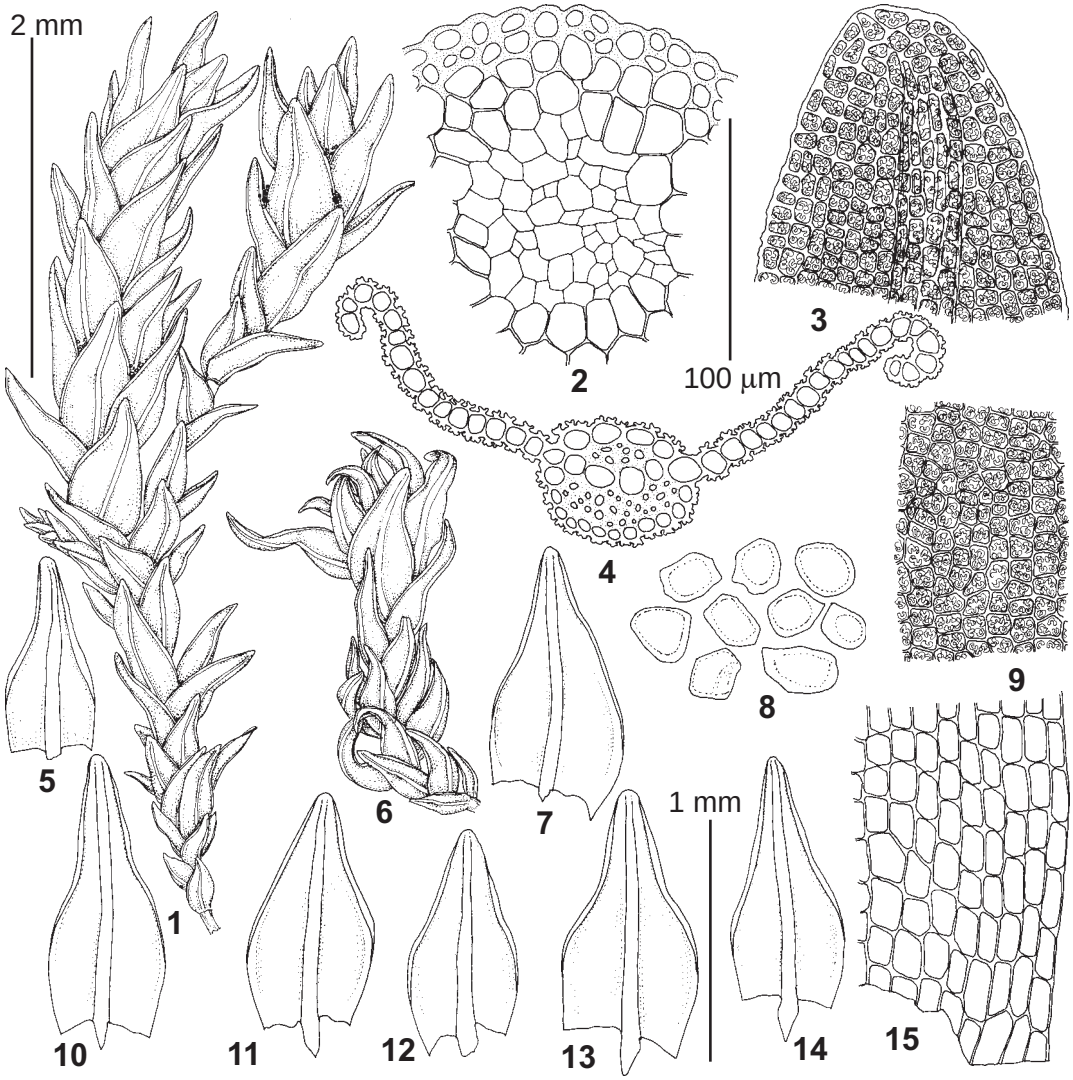

Fig. 4. *Bryoerythrophyllum inaequalifolium* (Taylor) R.H. Zander (from Altai Mts., 20.IX.1989 *Zolotukhin s.n.,* MHA): 1 – habit, wet; 2 – stem transverse section; 3 – upper laminal cells; 4 – leaf transverse section; 5, 7, 10-14 – stem leaves; 6 – habit, dry; 8 – gemmae; 9 – median laminal cells; 15 – basal laminal cells. Scale bars: 2 mm for 1, 6; 1 mm for 5, 7, 10-14; 100 μm for 2-4, 8-9, 15.

Number of accepted species 27 (Zander, 1993); 8 species in Russia.

KEY FOR IDENTIFICATION OF SPECIES OF BRYOERYTHROPHYLLUM

1. Leaves with rounded or obtuse apex, sometimes with small apiculus 2
— Leaves acute or acuminate at apex 4
2. Unicellular gemmae present in mass in leaf axils ..... 1. *B. inaequalifolium*
— Gemmae in leaf axils absent 3
3. Plants autoicous; leaves ovate, 1.0-1.3 x 0.6 mm; north of Eastern Siberia ..... 6. *B. rotundatum*
— Plants dioicous; leaves ovate-lanceolate, 1.2-1.5 x 0.4 mm; southern Far East .... 2. *B. brachystegium*
4. Plants small, stem leaves 1.0-1.3 mm long; rhizoidal multicellular gemmae usually present ..... 3. *B. ferruginascens*
— Plants medium-sized, stem leaves 1.5-4.0 mm long; rhizoidal gemmae absent 5
5. Leaves appressed and spirally twisted when dry; costa very strong, 120-200 μm wide at base (rarely ca. 75 μm), leaf margins strong-

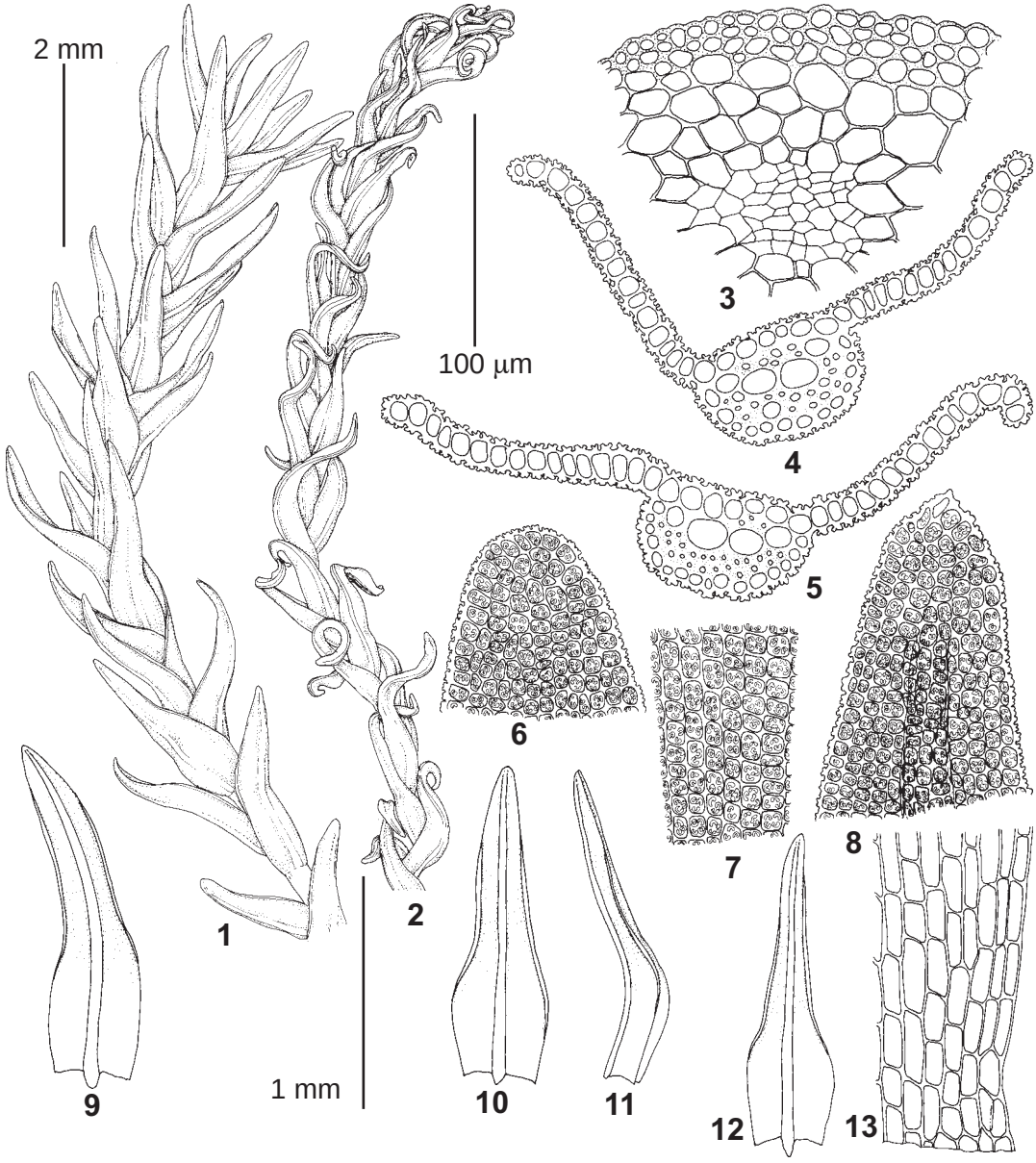

Fig. 5. *Bryoerythrophyllum brachystegium* (Besch.) K.Saito (from Kuril Islands, Kunashir, *Ignatov #06-1918,* MHA): 1 – habit, wet; 2 – habit, dry; 3 – stem transverse section; 4-5 – leaf transverse sections; 6, 8 – upper laminal cells; 7 – median laminal cells; 9-12 – stem leaves; 13 – basal laminal cells. Scale bars: 2 mm for 1-2; 1 mm for 9-12; 100 μm for 3, 6-8, 13.

ly revolute, always entire . 5. *B. latinervium*

— Leaves contorted to crisped, not spirally twisted when dry; costa less strong, 50-85 μm wide at base; leaf margins recurved to mid-leaf or almost to leaf apex or less strongly revolute, usually dentate at apex 6

6. Leaf margins recurved to mid-leaf, plane and dentate in distal 1/2 ..... 8. *B. alpigenum*

— Leaf margins recurved almost to leaf apex, with few teeth at leaf tip or entire 7

7. Plants dioicous; leaves rigid, with strongly recurved margins, very gradually tapering to the apex ..... 4. *B. rubrum*

— Plants autoicous; leaves soft, with narrowly recurved margins, more abruptly tapering at the apex ..... 7. *B. recurvirostrum*

1. **Bryoerythrophyllum inaequalifolium** (Taylor) R.H. Zander, Bryologist 83:232. 1980. — *Barbula inaequalifolia* Taylor, London J. Bot. 5: 49. 1846. — *Tortula inaequalifolia* (Taylor) Wilson, London J. Bot. 5: 454, 15D. 1846.

Illustrations: Figs. 4, 10; Ignatov, 1992 (p. 96).

Plants small, in loose or moderately dense tufts, yellowish-green or reddish-green in upper part, brownish in lower part. Stem 1-4(-6) mm, not or irregularly branched, with weak or moderately strong central strand. Leaves incurved or slightly spirally twisted when dry, erect-spreading when wet, ovate to ovate-lanceolate, obtuse at apex, concave, (0.5-)0.8-1.0×(0.3-)0.4-0.5 mm, margins entire, strongly recurved from above leaf base to near apex; costa strong, 50-60 μm wide proximally, not narrowing distally, ending few cells below apex, convex on adaxial side; upper laminal cells subquadrate and short rectangular, 6-10 μm wide, median laminal cells 7-14×10-12 μm, basal laminal cells near costa 20-25×10-12 μm, sparsely papillose, smooth only at extreme base, basal marginal cells quadrate and transversely rectangular, or subquadrate papillose cells occupy whole leaf base. Dioicous. Sporophytes unknown from the territory of Russia. [Seta 12-15 mm long. Urn 2-3 mm long, slightly curved. Peristome teeth bifid, red, on low basal membrane, filamentose, spirally twisted, densely spiculose. Annulus of 2-3 rows of vesiculose cells. Operculum long-conic, 1 mm. Spores 8-12 μm, finely papillose (from Allen, 1994)]. Asexual reproduction by unicellular gemmae formed in mass on stem in leaf axils, brown when mature, irregular in shape, angular-ovate, 25-30×15-20(-25) μm.

Differentiation. Presence of unicellular angular-ovate brown gemmae in leaf axils readily differentiates *B. inaequalifolium* from other species with obtuse apices (*B. brachystegium*, *B. rotundatum*). Leaves of *B. inaequalifolium* are slightly shorter than in both other species (05-1.0 mm vs. 1.0-1.5 mm); short and sparsely papillose basal laminal cells are also unique for *B. inaequalifolium*.

Ecology. In all three Siberian localities, *B. inaequalifolium* was collected at middle elevations: 660 m in Altai and 772 m in Zabaikal'sky Territory, on loamy bank of moraine and on vertical walls of eroded cliffs; all places have quite xeric environments.

Distribution. The species has wide distributional range, mostly in tropical and temperate zones, but it is rare in many parts of its area. It is currently known from Western and Northern South America, Central America, Mexico and southeastern U.S.A., northeastern Africa, Macaronesia, in Europe only in Spain, China (many localities), India, Malesia (Allen, 1994; Gallego, 2006; Li Xing-jiang et al., 2001).

Specimens examined: ASIAN RUSSIA: **Altai Republic**, Artyshtu Creek 0.3 km upstream from joint with Chul'cha River, 20.VIII.1989, *Zolotukhin s.n.* (MHA); **Zabaikal'sky Territory**, Agin-Buryat Autonomous District, 5 km E of Dul'durga settlement, Elo-Rakhanai Mt., *Afonina #4006* (LE); **Buryatia**, Selenga River left slope near Novoselenginskoe, *Afonina #00507* (LE).

2. **Bryoerythrophyllum brachystegium** (Besch.) K. Saito, J. Jap. Bot. 47:14. 1972. — *Gymnostomum brachystegium* Besch., J. Bot. (Morot.) 12: 281. 1898. — *Didymodon brachystegius* (Besch.) Broth., Nat. Pflanzenfam. 1(3): 406. 1902.

Illustrations: Figs. 5, 10.

Plants small to medium-sized, in dense tufts, yellowish green in upper part, reddish brown below. Stem 7-10(-15) mm, not or irregularly branched, with moderately strong central strand. Leaves flexuose to contorted when dry, spreading when wet, narrowly ovate-lanceolate to lanceolate, obtuse at apex or with small apiculus, widely keeled distally, concave proximally, (0.8-)1.0-1.4×0.25-0.35 mm, margins entire, recurved in mid-leaf, often on one side, plane at base and in distal part; costa strong, 50-60 μm wide proximally, not narrowing distally, percurrent or ending few cells below apex, flat on adaxial side; upper laminal cells subquadrate and transversely rectangular, 6-8 μm wide, median laminal cells 8-10×6-8 μm, basal laminal cells near costa 25-35×10-12 μm, smooth, basal marginal cells more short and narrow. Dioicous. Sporophytes unknown from the territory of Russia. [Urn 1-1.5 mm long. Peristome teeth reduced, short and fragile. Spores 13-16 μm, verrucose (from Noguchi, 1988)]. Asexual reproduction absent.

Differentiation. Distinctions from *B. inaequalifolium* and *B. rotundatum* are discussed under these species. *Bryoerythrophyllum ferruginascens,* which is similar to *B. brachystegium* in plant size and habit and is most closely related according to molecular data, differs in narrowly acute leaf apices, wider leaves (0.4-0.5 mm vs. 0.25-

0.35 mm wide) and presence of multicellular orange gemmae on rhizoids.

Ecology. Rocks along streams and wet cliffs in forest belt, at low altitudes, 20-55 m.

Distribution. Newly found in Russia in Kuril Islands, in one locality in Kunashir and two close localities in Iturup. *B. brachystegium* is currently known from Japan (Hokkaido, Honshu) and China (many localities in mountain areas) (Noguchi, 1988; Li Xing-jiang et al., 2001).

Specimens examined: ASIAN RUSSIA: **Sakhalinskaya Province**: Kuril Islands: Kunashir, Ruruy Mt., *Ignatov #06-1918* (MHA); Iturup: *Bakalin #K-34-10-07*, *#K-10-8-07* (VLA, MHA, MW); Reidovo, 30.IX.1980, *Bardunov s.n.* (KPABG).

3. **Bryoerythrophyllum ferruginascens** (Stirt.) Giacom., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser. 5, 4: 210. 1947. — *Barbula ferruginascens* Stirt., Ann. Scot. Nat. Hist. 9(35): 176. 1900.

Barbula botelligera Mönk. in Murr, Allg. Bot. Zeitschr. 20: 24. 1914.

Barbula rubella var. *ruberrima* Ferg. in Braithw., Brit. Moss. Fl. 1: 261. 1887.

Illustrations: Fig. 10; Ignatova & Ignatov, 2001 (p. 153); http://arctoa.ru/Flora/taxonomy-ru/bryoerythrophyllum-ill.pdf

Plants small to medium-sized, in loose to moderately dense tufts, on sandy substrates partly buried into sand, yellowish-green or reddish-brown in upper part, or reddish-brown throughout. Stem 7-17 mm, evenly foliate with upper leaves slightly larger, simple or rarely branched, central strand well-developed. Leaves appressed-incurved to weakly twisted when dry, erect-spreading when wet, 1.0-1.3×0.4-0.5 mm, ovate-lanceolate, rather abruptly contracted above broad (in upper leaves – sheathing) base, gradually acuminate, and in leaf tip with 1-3-celled apiculus, composed of smooth or slightly papillose cells, obtusely keeled in upper part; margins entire, plane in upper part, distinctly recurved in mid-leaf; costa strong, ca. 60 μm wide at base, gradually narrowing distally, flat on adaxial side; upper and median laminal cells subquadrate, 9-10 μm, basal cells short rectangular, to 25×12-13 μm, slightly papillose to smooth. Dioicous, sporophytes (very young + very old, partly decomposed) found in only one collection from Khabarovsk Territory. Perichaetial leaves to 2 mm long, sheathing base to 1 mm long, costa percurrent. Seta 5-6 mm long, red-brown; urn ca. 1.0 mm long, elliptic, brown, smooth, operculum ca. 0.5 mm long. Peristome none or rudimentary, ca. 25 μm long. Calyptra cucullate. Rhizoidal gemmae usually present, more numerous on rocky substrates, red-brown, ovoid to irregular in shape, sometimes branching, 50-115(-185)×30-70(-110) μm, multicellular, opaque.

Differentiation. *Bryoerythrophyllum ferruginascens* differs from *B. recurvirostrum* in smaller plants, shorter acumen, margin recurved only in mid-leaf (vs. nearly to the apex), margins entire (vs. with few teeth near apex). Presence of rhizoidal gemmae is also helpful for easy recognition of *B. ferruginascens*. Difference from *B. brachystegium* is discussed under this species.

Ecology. Rock surfaces, rocks covered with alluvium in flood-valleys, sandy and gravely river banks, mostly in mountain areas with calcareous soils, at 300-2400 m a.s.l., usually in forest belt, more rarely above timberline. Collections from the Vrangel Island (Chukotka) were done in wet shrubby-mossy tundra, along temporary stream bed. Recently found in two localities in Caucasus, at 2000-2200 m a.s.l., in rock crevice at splash zone of waterfall and on soil.

Distribution. World range of the species is very wide, including arctic, temperate and tropical areas: subarctic America, western Canada, northwestern and southeastern U.S.A., Mexico, Central America, northern, southwestern and middle Europe, Caucasus, Siberia, China (Inner Mongolia), Eastern Asia, northeastern and eastern tropical Africa, Indian subcontinent, Malesia (Allen, 1994; Zhao, 2008; Kharzinov et al., 2004; Ignatova et al., 2008). However, it is not so frequent as *B. recurvirostrum* and is known from limited number of localities in many parts of its area.

Specimens examined: EUROPEAN RUSSIA: **Kabardino-Balkaria**: Bezengi River Gorge, Mizhirgi Creek, 2.VIII.2004 *Ignatov et al. s.n.* (MHA); **Karachaevo-Cherkessia**: Teberda State Nature Reserve, *Ignatov & Ignatova #05-3174* (MW). ASIAN RUSSIA: **Republic Altai**: Bogoyash Creek, 27.VII.1993 *Ignatov s.n.* (MHA); Karakem Creek, 24.VI.1989 *Ignatov s.n.* (MHA); Chemal, 2.VIII.2000 *Ignatova s.n.* (MW); Malyj Yaloman, 4.VIII.2000 *Ignatova s.n.* (MW)**; Krasnoyarsk Territory:** Taimyrsky Municipal District, *Fedosov #07-395, # 05-20* (MW); **Republic Sakha/Yakutiya**: eastern part, Ust-Maya District, *Ignatov #00-1061, 00-1080, 00-671b* (MHA);

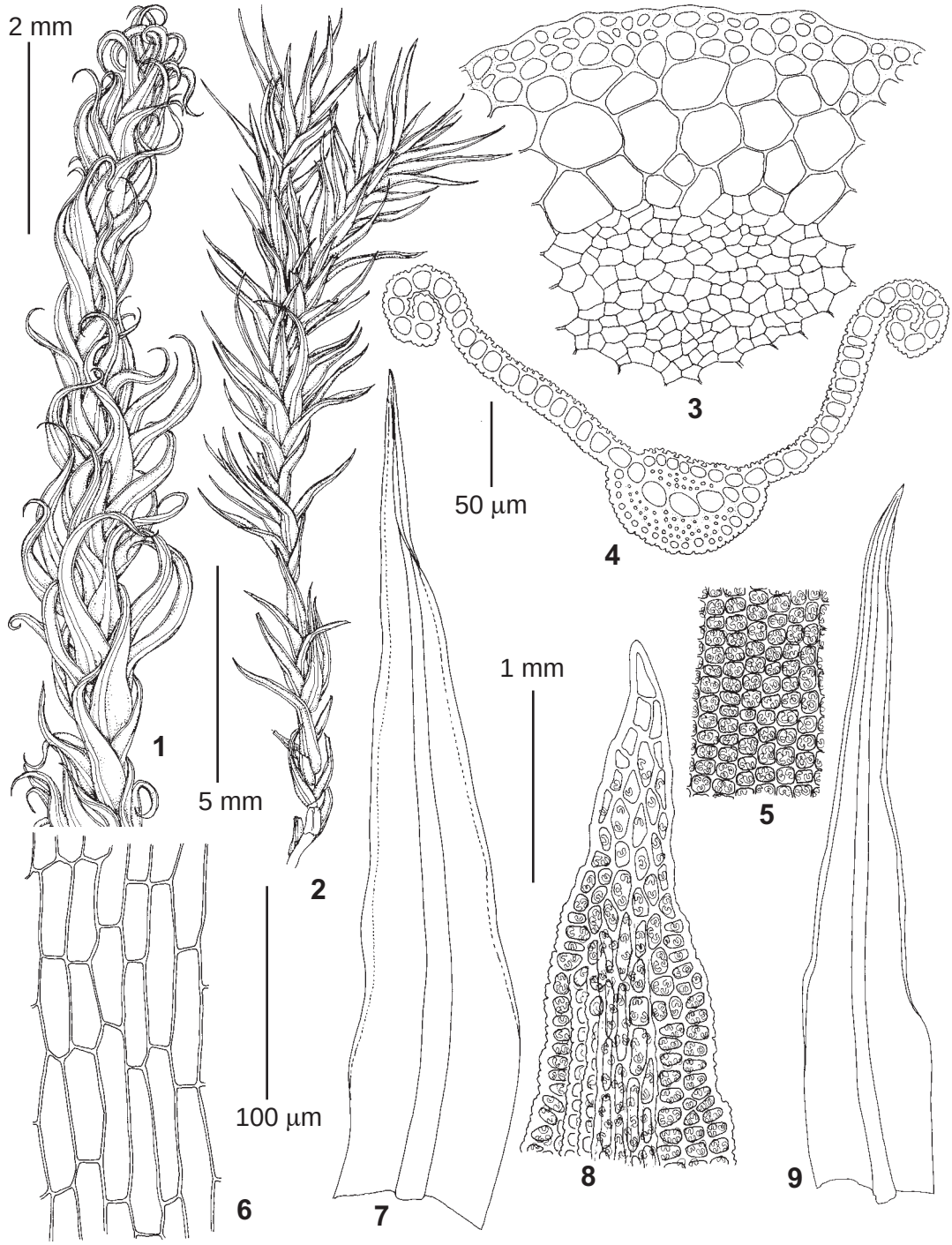

Fig. 6. *Bryoerythrophyllum rubrum* (Jur. ex Geh.) P.C. Chen (from Austria, Salzburg, *Köckinger #12304,* MW): 1 – habit, dry; 2 – habit, wet; 3 – stem transverse section; 4 – leaf transverse section; 5 – median laminal cells; 6 – basal laminal cells; 7, 9 – leaves; 8 – upper laminal cells. Scale bars: 5 mm for 2; 2 mm for 1; 1 mm for 7, 9; 50 μm for 4; 100 μm for 3, 5-6, 8.

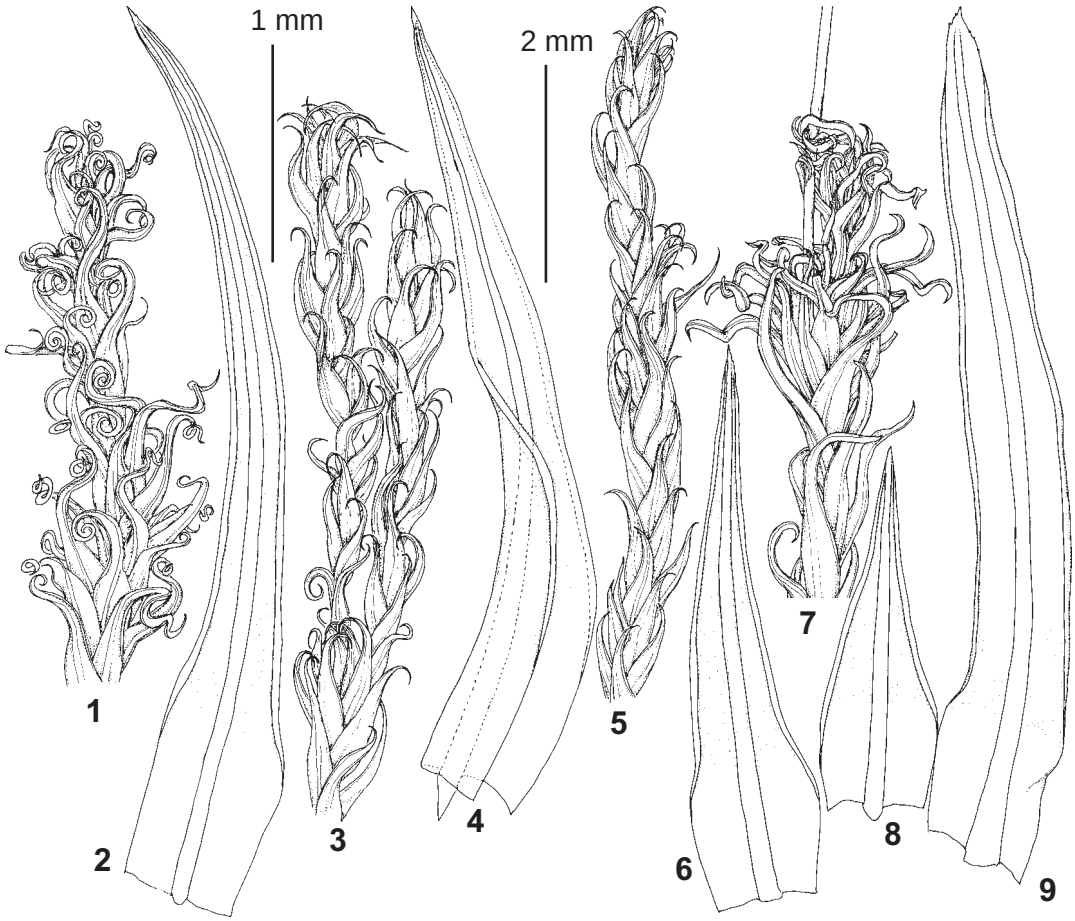

Fig. 7. *Bryoerythrophyllum rubrum* (Jur. ex Geh.) P.C. Chen (1, 2 – from Switzerland, 8.IX.1904 *Culmann:*E. Bauer, Musci europaei exsiccati #153, MW; 3, 6 – from Russia, Caucasus, Karachaevo-Cherkessia, *Onipchenko #35/02*, MW; 4 – from South Ossetia, *Brotherus #965,* H; 5, 8 –from Russia, Taimyr, *Fedosov #Brer-2*, MW); *Bryoerythrophyllum recurvirostrum* (Hedw.) P.C. Chen (7, 9 – from Russia, Primorsky Territory, *Ignatov #07-54,* MW): 1, 3, 5, 7 – habit, dry; 2, 4, 6, 8-9 – leaves. Scale bars: 2 mm for 1, 3, 5, 7; 1 mm for 2, 4, 6, 8-9.

Khabarovsk Territory: Upper Bureya River, *Tan #97-150* (MHA); *Ignatov #97-1126* (MHA). **Chita Province:** Kyra Distr., Onon-Baldzhinsky Range, *Afonina #7805* (LE); **Zabaikal'sky Territory:** Alkhanai National Park, *Afonina #1906* (LE); **Kamchatskaya Province**: Klyuchevskie volcanoes, Ushkovsky volcano slope, 13.VIII.2004 *Czernyadjeva #66* (LE); Ostryj Tolbachik volcano, 21.VIII.2001 *Czernyadjeva #21* (LE); Esso, 28.VII.2001 *Czernyadjeva #44* (LE);

4. **Bryoerythrophyllum rubrum** (Jur. ex Geh.) P.C. Chen, Hedwigia 80: 5. 1941. — *Didymodon ruber* Jur. ex Geh., Rev. Bryol. 5:28. 1878.

Bryoerythrophyllum cavernarum (Molendo) Podp., Consp. Musc. Eur. 219. 1954. — *Didymodon rubellus* var. *cavernarum* Molendo, Ber. Naturalist. Vereins Augsburg 18: 143. 1865.

Illustrations: Figs. 6, 7, 10.

Plants medium-sized to large, rigid, in moderately dense tufts, green in upper part, reddish-brown below. Stem 1.5-6(-7) cm, with strong central strand. Leaves appressed and slightly contorted when dry, sometimes with strongly twisted apices, spreading when wet, from oblong base narrowed into long lanceolate acumen, gradually narrowing to the apex, (1.5-)4-6×(0.5-)0.6-0.8 mm, margins entire or with few teeth at apex, narrowly recurved from above leaf base to near the apex; costa 70-100 μm wide at base, slightly narrowed to the apex, percurrent or ending few cells below apex, weakly convex or flat on adaxial side; upper and median laminal cells 8-10 μm; basal laminal cells near costa elongate-rectangular, (40-)60-

100×10-12 μm, thin-walled, slightly bulging, basal marginal cells in several rows narrower. Dioicous. Only female plants were seen. Sporophytes absent in collections from Russia. [Seta reddish, 1.0-1.5 cm. Urn to 3 mm long, straight or slightly curved; operculum conic, with short obtuse beak; peristome teeth bifid, straight, whitish, papillose. Spores 14-18 μm (from Savicz-Lyubitskaya & Smirnova, 1970)]. Asexual reproduction absent.

Differentiation. Main diagnostic characters of *B. rubrum* include linear-lanceolate, gradually tapering, narrowly acuminate leaves, comparatively strongly recurved margins from above base to near the apex and dioicous sexual condition. Larger size of plants and leaves is also usually mentioned as a character differentiating *B. rubrum* from *B. recurvirostrum*. It is observed in many collections from european Alps. Plants are to 6-7 cm high, with leaves 4-5 mm long, comparatively rigid due to strongly recurved margins, and long and narrow leaf acumens are sometimes strongly spirally twisted when dry (Fig. 5:1). However, leaf length varies greatly in collections from Caucasus and Russian Arctic: from ca. 3.5-4 mm in specimen from Georgia (Fig. 5:4), ca. 2.5 mm in specimen from Karachaevo-Cherkessia to 1.5-1.7 mm in specimen from Taimyr (Fig. 5: 8). All these specimens are dioicous and have gradually acuminate narrow leaf apices. The latter character seems to be most important for recognizing of *B. rubrum* in case of unusually small plants. Contrary, unusually robust plants of *B. recurvirostrum* from Primorsky Territory with leaves ca. 4.5 mm long and only female inflorescences have wider leaf apices (Fig.5: 9) and softer leaves, flexuose when dry (Fig. 5: 7) vs. rigid leaves and spirally twisted apices (Fig.5: 1) or rigid and slightly contorted leaves (Fig.5:3, 5) of *B. rubrum*. Small morphotypes of *B. rubrum* from the Arctic can be confused with *B. ferruginascens*, but the latter species has smaller leaves (1.0-1.3 mm vs. ca. 1.5-1.7 mm) and peculiar rizhoidal tubers. Distinctions from *B. latinervium* are disussed under this species.

Ecology. In Caucasus, *B. rubrum* was collected in alpine belt in Karachaevo-Cherkessia, at 3100 m, on steep rocky talus slope. Arctic collections were reported in different types of tundras, in Severnaya Zemlya Archipelago (Afonina, 2002) and Vrangel Island (Afonina, 2004), and in Taimyr it grew on bare loamy substrate under limestone outcrop.

Distribution. The species is currently known mostly from mountain areas of Central Europe (Podpera, 1954); Podpera also mentions its occurence in Norway, probably basing on the record of Mönkemeyer (1927), but Nyholm (1989) did not include this species into Scandinavian Moss Flora. However, Sollman &Frahm (2007) found *B. rubrum* in Sweden and confirmed its occurence in Caucasus basing on collections of Brotherus in H. Handbooks of mosses of the former USSR (Abramova et al., 1961; Savicz-Lyubitskaya & Smirnova, 1970) recorded the species from Caucasus (indefinite if in Russia or Georgia) and Chukotka; voucher specimens however are absent in LE, where they supposed to be kept. Our data confirm the presence of *B. rubrum* in Russian part of Caucasus and Siberian Arctic, though it is very rare there comparatively with much more frequent *B. recurvirostrum*. *Bryoerythrophyllum rubrum* was also reported from China (Li Xing-jiang et al., 2001).

Specimens examined: SWITZERLAND: Bern, 8.IX.1904, *Culmann s.n.* (E.Bauer, Musci Europaei exsiccati #153, MW). AUSTRIA: Salzburg, *Köckinger #12304* (MW); Carinthia, *Köckinger #11378, 01-184* (MW); Styria, *Köckinger #12348* (MW). SOUTH OSSETIA: *Brotherus #965* (H). EUROPEAN RUSSIA: **Karachaevo-Cherkessia**: Malokarachaevsky District, Tokhana Gorge, Khudes Creek upper course, *Onipchenko #35/02* (MW). ASIAN RUSSIA: **Krasnoyarsk Territory**: Taimyrsky Municipal District, Taimyrsky State Nature Reserve, surroundings of Ledyanaya Bay of Taimyrskoe Lake, *Fedosov #Brer2* (MW).

5. **Bryoerythrophyllum latinervium** (Holmen) Fedosov & Ignatova, comb. n. — *Barbula recurvirostris* var. *latinervia* Holmen, Meddel. Groenland 163 (2): 37. 1960.

Bryoerythrophyllum recurvirostrum var. *latinervium* (Holmen) B.M. Murray, Bryobrothera 1: 14. 1992.

Illustrations: Fig. 10; Fedosov & Ignatova, 2008; http://arctoa.ru/Flora/taxonomy-ru/bryoerythrophyllum-ill.pdf

Plants medium-sized to small, in loose tufts, green or brownish green in upper part, brown in lower part. Stem (5-)10-20 mm, sparsely branched, with strong central strand. Leaves appressed and often slightly spirally twisted when dry, erect-

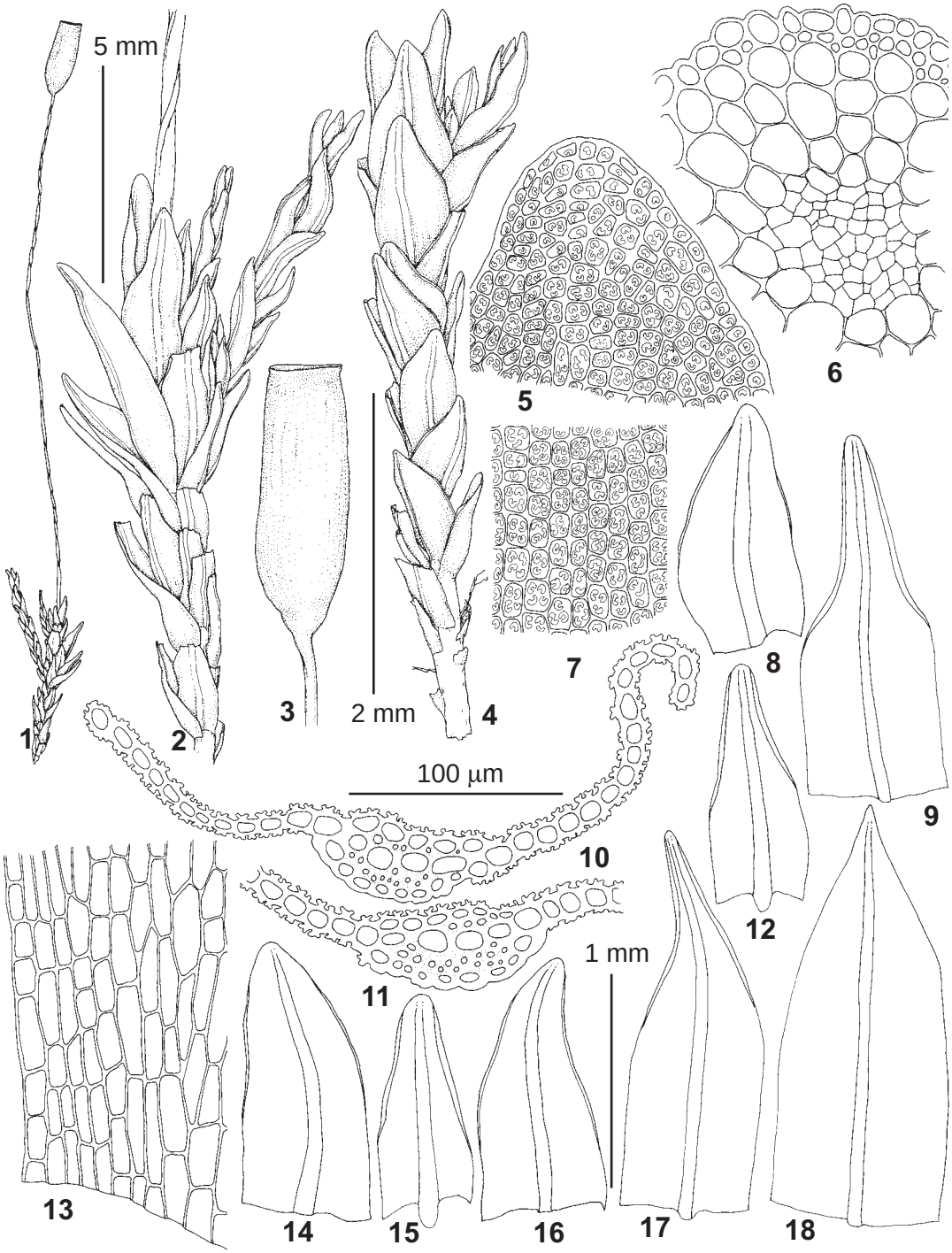

Fig. 8. *Bryoerythrophyllum rotundatum* (Lindb. & Arnell) Kindb. (1-8, 10-11, 13-14, 16 – from isotype specimen: Sibiria, Jenisei, Nikandrovskij ostrov, 70° 20' n. lat., 14.VIII.1876, *Arnell s.n.,*LE, ex S; 9, 12, 15, 17-18 – from Taimyrsky State Nature Reserve, vicinity of Afanasjevskie Lakes, *Fedosov #06-510,* MW): 1-2, 4 – habit, dry; 3 – capsule; 5 – upper laminal cells; 6 – stem transverse section; 7 – median laminal cells; 8-9, 12, 14-16 – stem leaves; 10-11 – leaf transverse sections; 13 – basal laminal cells; 17 – outer perichaetial leaf; 18 – inner perichaetial leaf. Scale bars: 5 mm for 1; 2 mm for 2-4; 1 mm for 8-9, 12, 14-18; 100 μm for 5-7, 10-11, 13.

spreading when wet, ovate-lanceolate to lanceolate, narrowly acute at apex or, rarely, subobtuse, 0.9-1.8×(0.4-)0.5-0.6 mm, margins entire, strongly revolute (to 360° or more) from above leaf base to near apex; costa very strong, occupying 1/3–1/4 of leaf base, (75-)120-200 μm wide proximally, gradually narrowing distally, percurrent, flat or slightly grooved on adaxial side, with (4-)5-6 guide cells; upper laminal cells subquadrate, 8-10 μm, median laminal cells 10-12×10-14 μm, basal laminal cells near costa 20-45×10-12 μm, with moderately thickened walls, basal marginal cells in several rows short rectangular to subquadrate. Dioicous (?), plants with archegonia were seen. Perichaetial leaves similar to stem leaves. Sporophytes unknown. Asexual reproduction absent.

Plants from Zabaikal'sky Territory are considerably smaller than those from Taimyr, they have subobtuse leaf apices and considerably less strong costa, ca. 75 μm wide at base, not narrowing distally, but strongly revolute leaf margins make them similar to other specimens of *B. latinervium*. They resemble greatly phenotype from Alaska described by Murray (1992).

Differentiation. Zander (2007) synonymized *B. recurvirostrum* var. *latinervium* within var. *recurvirostrum,* attributing this to intergradation. However, we have not found plants with intermediate characters in herbarium collections from Russia, and our search for such an intermediates in NYBG and MO also gave no results. ITS sequences also confirm their distinction. In addition, a mixed collection of *B. latinervium* and *B. recurvirostrum* was found in Taimyr, and both species kept their characteristic morphological distinctions, making plants quite contrasting, which confirms the species status of the former species. Very strong costa, strongly revolute and always entire leaf margins, as well as appressed and spirally twisted leaves differentiate *B. latinervium* from *B. recurvirostrum*. The former species is apparently dioicous, sporophytes are unknown, whereas the latter one has sporophytes in most collections and in most cases its sexual condition is easily recognizable as synoicous or paroicous. *Bryoerythrophyllum rubrum* is similar to *B. latinervium* in dioicous sexual condition, and the small-sized morphotypes of the former species from Siberian Arctic also have rather strongly recurved leaf margins; however costa of *B. rubrum* is not as wide as in *B. latinervium*. Strongly revolute leaf margins give *B. latinervium* some similarity with *Pseudocrossidium hornschuchianum* or *P. obtusulum*, but the presence of ventral stereid band in costa vs. its absence, large stem central strand vs. small one, and red KOH-reaction vs. yellow readily differentiate *B. latinervium* from *Pseudocrossidium.*

Ecology. Calcareous rocks in xeric regions of Subarctic and boreal zone and also in xeric area in Mongolia. However, in the xeric areas in Zabaikal'sky Territory it was collected in wet dwarf birch community in flood-valley. In Taimyr it grew on limestone boulder covered with dry fine soil, in mixed stand with *Bryoerythrophyllum recurvirostrum*, *Encalypta longicollis, E. alpina, Distichium inclinatum, Pseudocrossidium obtusulum, Tortula mucronifolia.*

Distribution. *Bryoerythrophyllum latinervium* has widely disjunctive distribution in Asia and North America. It is currently known from northern Greenland (at ca. 82° N), from several localities in Alaska, one locality in southern Taimyr (NW part of Anabarskoe Plateau), one locality in Mongolia and one in Zabaikal'sky Territory. Such distribution probably represents remnants of more wide area of the species in Pleictocene.

Specimens examined: ASIAN RUSSIA: **Krasnoyarsk Territory**, Taimyrsky Municipal Area, Khatanga District, Afanas'evskie Lakes surroundings, 150 m a.s.l., *Fedosov # 06-287* (MW); **Zabaikal'sky Territory**, Sokhondinsky State Nature Reserve, Enda Creek, 25.VIII.2006, *Yakovchenko s.n.* (LE). MONGOLIA: Gobi-Altai District, 20 km E of Tsogt settlement, 2900 m a.s.l., *Ignatov # 01-984* (MHA); same place, 3000 m a.s.l., *Ignatov # 01-985* (MHA). GREENLAND: north coast of Independence Fjord, *Holmen #7128* (MO); Heilprin Land, Bronlund Fjord, *Holmen #277d* (MO). USA: Alaska, *Murray # 10987* (MO).

6. **Bryoerythrophyllum rotundatum** (Lindb. & Arnell) P.C. Chen, Hedwigia 80: 22. 1941. — *Barbula rotundata* Lindb. & Arnell, Kongl. Svenska Vetenskapsakad. Handl. 23 (10): 72. 1890. — *Dydimodon rotundatus* Paris, Index Bryol. 379. 1896.

Illustrations: Figs. 8, 10.

Plants small, in loose tufts or as individual shoots, reddish-brown. Stems to 1.5 cm, with moderately strong central strand. Leaves loosely appressed when dry, erect-spreading when wet, low-

er stem leaves ovate, rounded at apex, all almost equal in size, 1.0-1.2×0.4 mm, upper leaves ovate-lanceolate, obtuse at apex, 1.3-1.5×0.5-0.6 mm, margins recurved from above leaf base to near apex; costa 60-80 μm wide at base, slightly narrowed distally, ending well below leaf apex, flat on adaxial side; upper laminal cells isodiametric, 8-10 μm, median laminal cells subquadrate to shortly rectangular, 12-18× 8-12 μm; basal laminal cells near costa rectangular, thin-walled, orange, 25-30×10-12 μm, basal marginal cells in several rows more narrow. Synoicous. Inner perichaetial leaves 1.7-1.8×0.7-0.8 mm, from oblong base formed by smooth thin-walled rectangular cells gradually tapering to short triangular acumen. Sporophytes usually present. Seta reddish, 1.0-1.5 cm. Urn 0.9-1.0 mm long; annulus of 2 rows of vesiculose cells, revoluble; operculum 0.3-0.5 mm; peristome absent. Spores 15-20 μm. Asexual reproduction absent.

Differentiation. *Bryoerythrophyllum rotundatum* differs from *B. recurvirostrum* by rounded-obtuse leaf apices and completely absent perisome. *B. inaeqaulifolium* has similar leaf shape and size but it is dioicous, lacking sporophytes in the territory of Russia, and often produces numerous unicellular gemmae in leaf axils; it is also very rare in Russia, with more southern distribution in Siberia. Leaves of *B. brachystegium* are similar in shape to upper leaves of *B. rotundatum*, but the former species is dioicous, usually lacks sporophytes and is known in Russia only from Kuril Islands.

Ecology. Grows on pebbly river banks covered with alluvium.

Distribution. Rare species, endemic of Russia, currently known only from three localities in the north of Eastern Siberia.

Specimens examined: ASIAN RUSSIA: Sibiria, Jenisei, Nikandrovskij ostrov, 70° 20' n. lat., 14.VIII.1876, *Arnell s.n.* (LE, ex S); **Krasnoyarsk Territory**: Taimyrsky Municipal Area: Taimyrsky State Nature Reserve, Afanas'evskie Lakes, Fomich River right bank, *Fedosov #06-510* (MW); Popigaj River 10 km upstream Sopochnaya Creek, *Fedosov #08-659* (MHA).

7. **Bryoerythrophyllum recurvirostrum** (Hedw.) P.C. Chen, Hedwigia 80: 5. 1941. — *Weissia recurvirostris* Hedw., Sp. Musc. Frond. 71. 1801. — *Didymodon rubellus* Bruch et al., Bryol. Eur. 2: 137. *185*. 1846.

Illustrations: Ignatov & Ignatova, 2003, p. 277; http://arctoa.ru/Flora/taxonomy-ru/bryoerythrophyllum-ill.pdf

Plants medium-sized, in loose or moderately dense tufts, green in upper part, reddish below. Stem 0.5-2(-3) cm, with moderately strong central strand. Leaves flexuose to crisped when dry, spreading when wet, from ovate or oblong base narrowed into long lanceolate acumen, shortly or gradually acuminate at apex, 2-3×0.4-0.5 mm, margins narrowly recurved from above leaf base to near apex, usually with several teeth near apex; costa 50-75(-85) μm wide at base, slightly narrowed to the apex, percurrent or ending few cells below apex, weakly convex or flat on adaxial side; upper laminal cells 8-10 μm; basal laminal cells near costa elongate-rectangular, thin-walled, slightly bulging, basal marginal cells in several rows more short rectangular. Synoicous or/and paroicous. Sporophytes frequent, single per perichaetium, but perichaetia sometimes 2-3 crowded at the top of stem. Seta reddish, 0.6-1.6 cm. Urn 1.3-2.5 mm long; operculum 0.3-1.0 mm; peristome teeth irregularly cleft, straight, 100-250 μm, reddish or yellowish, finely papillose. Spores 14-20 μm. Asexual reproduction absent.

Differentiation. It is easy to recognize this species in the field because of the reddish or orange color of lower parts of tufts, long leaves, and usually numerous sporophytes. Among other characters, the synoicous or paroicous sexual condition, orange color of thin-walled basal laminal cells, leaf margins recurved almost throughout and few teeth at leaf apex (sometimes in not every leaf) are important for its identification. Zander (2007) mentions that antheridia are not found in all inflorescences of *B. recurvirostrum*, and our observations confirm this statement.

Ecology. Usually in rock crevices and steep soil banks, but also in many various habitats, e.g. logs and trunk bases covered by muddy alluvium, walls of caves, etc.; mostly on calcareous substrates, but in the areas where it is common it occurs on the fairly broad range of rock and soil types.

Distribution. Known from all continents, in polar, boreal and temperate zones and in mountains of tropics. In Russia it was reported from practically all the regions; it is very common in some areas of Siberia, Urals, not rare in Caucasus and lowland territories where calcareous rock is widespread, but it is almost absent in areas with sandy soils.

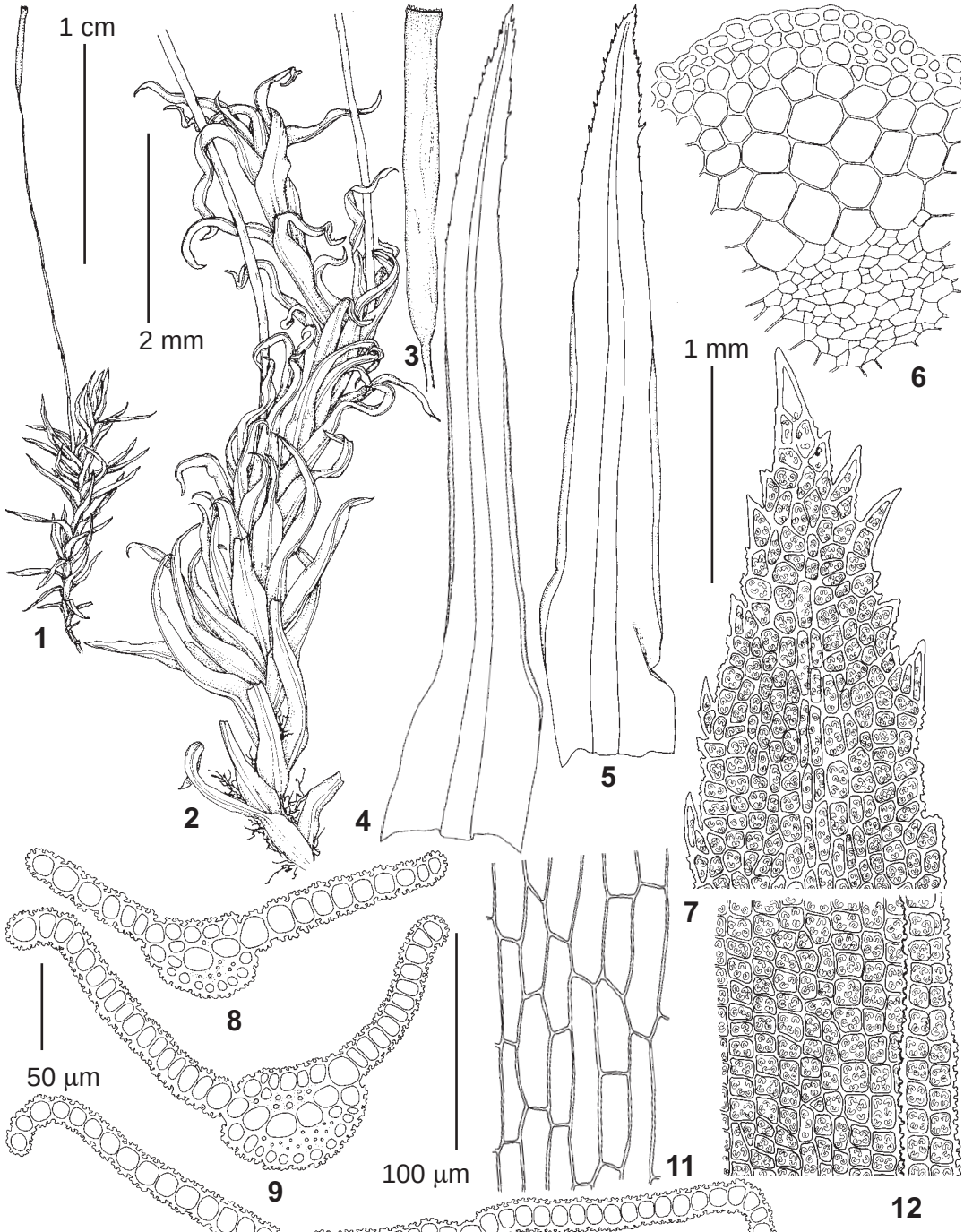

Fig. 9. *Bryoerythrophyllum alpigenum* (Venturi) P.C. Chen (from Altai Mts., 1.VI.1989 *Ignatov s. n.*, MHA): 1 – habit, wet; 2 – habit, dry; 3 – capsule; 4-5 – stem leaves; 6 – stem transverse section; 7 – upper laminal cells; 8-10 – leaf transverse sections; 11 – basal laminal cells; 12 – median laminal cells. Scale bars: 1 cm for 1; 2 mm for 2-3; 1 mm for 4-5; 50 μm for 6, 8-10; 100 μm for 7, 11-12.

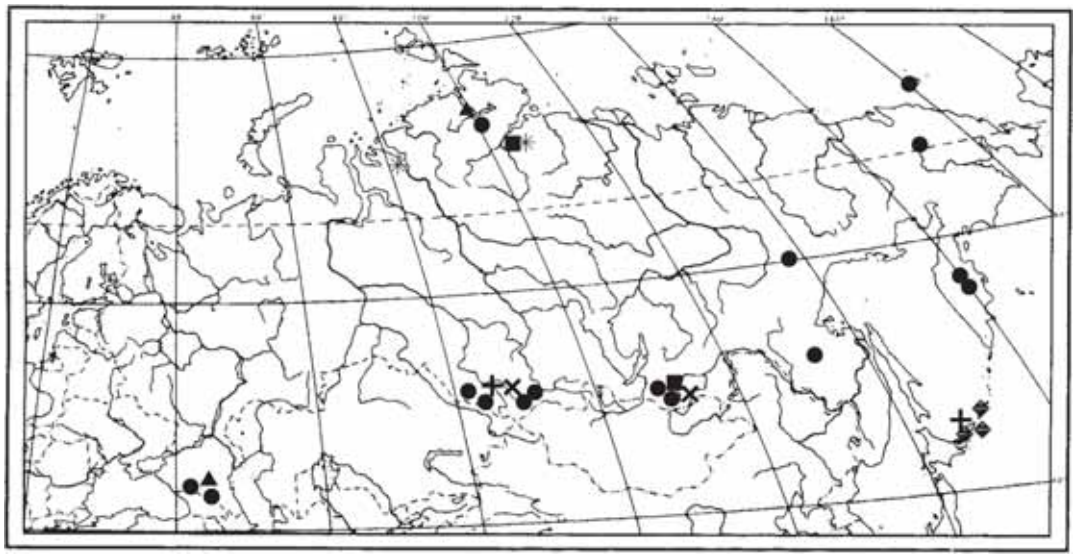

Fig. 10 Distribution in Russia of *Bryoerythrophyllum alpigenum* (cross), *B. brachystegium* (rhombs), *B. ferruginascens* (circle), *B. inaequalifolium* (oblique cross), *B. latinervium* (square), *B. rotundatum* (asterisk), *B. rubrum* (triangle).

Selected specimens examined: EUROPEAN RUSSIA: **Republic Karelia**: Prionezhsky Distr., Botanical Garden of Petrozavodsk University, *Bakalin & Bakalina #24* (MW); **Arkhangelsk Province**: Solovetsky Island, 1.VIII.1984, *Vekhov s.n.* (MW); **Komi Republic**: Pechoro-Ilychsky State Nature Reserve, *Bezgodov & Kucherov #415* (MW); **Perm Province**: Basegi State Nature Reserve, *Ignatov & Bezgodov #167* (MW); **Leningrad Province:** Tosno Distr., Sablino, 25.VI. 1954, *Abramov s.n.* (LE); **Pskov Province**: Izborsk, 9.XI.2003, *Ukrainskaya s.n.* (LE); **Novgorod Province**: Opechensky Distr., Rovny, 27.IX.1957, *Kil'dyushevsky s.n.* (LE); **Tver Province**: Staritsky Distr., Lipino, VI.1984, *Notov s.n.* (MW); **Nizhegorodskaya Province**: Gorbatov Distr., Dudenevo, 21.V.1915, *Shvetsov s.n.* (LE); VI.1984, *Notov s.n.* (MW); **Ekaterinburg**, VIII.1887, *Navashin s.n.* (LE); **Bashkortostan**, Burzyan District, Muradymovo, *Ignatova #11/191* (MW). **Kaluga Province**: Ferzikovo Distr., 7.5 km SSW of Ferzikovo, *Ignatov #08-168* (MHA, MW); **Smolensk Province**: Sapsho Lake, 16.VII. 2004, *Ignatov s.n.* (MHA, MW); **Moscow**, Kuntsevo, 27.IV. 1891, *Zikendrath s.n.* (MW); **Lipetzk Province**: Zadonsky Distr., Morozova Gora, 17.VIII. 1963, *Samsel' s.n.* (MW); **Belgorod Province**: "Les na Vorskle" Reserve, 27.VII. 1940, *Yakovleva s.n.* (LE); CAUCASUS: **Stravropol' Territory:** Stavropol' surroundings, Russkaya Lesnaya Dacha, 16.X.1955, *Skripchinsky s.n.* (LE); **Krasnodar Territory**: Adler Distr., Achishkho, 14.VII.1948, *Rapoport s.n.* (LE); **Dagestan**: Andsky Range, 18.VII. 1960, *Kateridze & Dylevskaya s.n.* (LE); **Kabardino-Balkaria**: Verkhnyaya Balkaria, *Ignatov et al. #05-1838* (MW); **Karachaevo-Cherkessia**: Teberda State Nature Reserve, *Ignatov & Ignatova # 05-3210* (MW); ASIAN RUSSIA: **Yamal**: Yunto Lake, 12.VIII. 1994, *Czernyadjeva #92* (LE); **Tymen' Province**: Verkhnetazovsky Reserve, 20.VIII.1997, *Czernyadjeva #51* (LE); **Republic Altai**: Malyj Yaloman, 4.VIII.2000, *Ignatova s.n.* (MW); **Krasnoyarsk Territory**: Taimyrsky District, Kotuj River 10 km downstream Kayak settlement, *Fedosov #07-18* (MW); Evenkia, Baikit Distr., Stolbovaya River lower course, 9.VI.1992, *Shzerbina s.n.* (MW); **Irkutsk Province**: Slyudyanka Distr., Slyudyanka Creek 5 km upstream from mouth, 8.VI.2005, *Ignatov & Kazanovsky s.n.* (MW); **Buryatia**, Tunka Distr., Tunkinsky National Park, *Seregin et al. #M-1986* (MW); **Sakha/Yakutia**: Olekminsky Distr., Tokko River midlle course, 5.VII.2006, *Ivanova s.n.* (MW); Severnaya Zemlya, Bol'shevik Island, VII.1997, *Matveeva s.n.* (LE); **Amurskaya Province**: Zeisky State Nature Reserve, Teplyi Klyuch, VIII.1979, *Petelin s.n.* (MW); **Khabarovsk Territory**: Verkhnebureinsky Distr., Bureinsky State Nature Reserve, Levaya Bureya River, 5.VIII.1994, *Petruk s.n.* (MW); **Primorsky Territory**: Partizansk Distr., Alekseevka Creek south of Olkhovaya Mt., *Ignatov et al. #06-2545* (MW); **Sakhalinskaya Province**: Kuril Islands, Iturup, *Bakalin #K-34-12-07* (MW); **Chukotka:** Anadyrsky Distr., Pekul'nej Range, 8.VIII.1979, *Afonina s.n.* (LE); **Magadan Province**: Ten'kinsky Distr., Stokovyj, 18.VIII. 1973, *Blagodatskikh s.n.* (LE); **Kamchatka**: Klyuchevskaya group of volcanoes, western slope of Ushkovski volcano, *Czernyadjeva #206* (MW).

8. **Bryoerythrophyllum alpigenum** (Vent.) P.C. Chen, Hedwigia 80: 5. 257. 53. 1941. — *Didymodon alpigenus* Vent., Laubm.-Fl. Oesterr.-Ung. 98. 1882. — *Bryoerythrophyllum recurvirostrum* subsp. *alpigenum* (Vent.) Giacom., Inst. Bot. R. Univ. R. Lab. Crittog. Pavia Atti 5(4): 210. 1947.

Bryoerythrophyllum recurvirostrum var. *dentatum* (Schimp.) H.A. Crum, Steere & L.E. Anderson, Bryologist 67: 163. 1964. — *Didymodon rubellus* var. *dentatus* Schimp., Syn. Musc. Eur. 131. 1860.

Illustrations: Figs. 9, 10.

Plants medium-sized to large, in loose tufts, dull-green in upper part, reddish below. Stem 1-3(-4) cm, with moderately strong central strand. Leaves contorted to crisped when dry, spreading when wet, from oblong base narrowed into long lanceolate acumen, shortly or gradually acuminate at apex, 3-4×0.6-0.7 mm, margins narrowly recurved from above leaf base to mid-leaf, plain in distal 1/2–1/3 of leaf, sharply dentate to far below the apex, teeth formed by one to several smooth or papillose cells; costa 80-100 μm wide at base, flat on adaxial side, slightly narrowed to the apex, percurrent or ending few cells below apex, weakly convex or flat on adaxial side; upper and median laminal cells 7-10 μm; basal laminal cells near costa elongate-rectangular, 40-100×10-15 μm, thin-walled, slightly bulging, smooth or sparsely papillose, basal marginal cells in several rows more narrow. Synoicous. Sporophytes frequent. Seta reddish, 1.5-2.0 cm. Urn ca 3 mm long, straight or slightly curved; operculum 0.3-1.0 mm; peristome teeth 16, straight, entire or irregularly cleft, 100-250 μm, reddish, finely papillose. Spores 14-16 μm. Asexual reproduction absent.

Differentiation. *Bryoerythrophyllum alpigenum* is considered by some authors (i.e. Nyholm, 1989) to be a variety of *B. recurvirostrum* or is even submerged into the latter species (Zander, 2007) due to intergradation, but it is treated as a separate species in the recent check-list of mosses of Europe and Macaronesia (Hill et al., 2006) and Moss Flora of China (Li Xing-jiang et al., 2001). Our data confirm its distinction. *Bryoerythrophyllum alpigenum* differs from *B. recurvirostrum* by larger size of plants, usually longer leaves (3-4 mm vs. 2-3 mm) and plane and strongly dentate leaf margins in distal 1/2–1/3 of leaf length. The small juvenile leaves (0.2-0.4 mm) are even more strongly dentate almost throughout.

Ecology. In the Altai Mts. *B. alpigenum* grows at 450-1300(-2100) m, mostly in forest belt, occasionally in subalpine belt, on wet rocks near streams and waterfalls (often associated with *Plagiobryum zieri, Cyrtomnium hymenophylloides, Sciuro-hypnum plumosum, Orthothecium spp*.). Collection in Kuril Islands was also from wet cliffs, at 50 m. In Austrian Alps the species was collected beside brooks.

Distribution. World range of *B. alpigenum* is insufficiently known because it was often treated at intraspecific level or included into *B. recurvirostrum*. It was recorded from Norway and Sweden (Nyholm, 1989), the Alps [Austria, Swiss] (Podpera, 1954), China (Li Xing-jiang et al., 2001).

Specimens examined: AUSTRIA: Styria, *Köckinger #94-551* (MW); Carinthia, *Köckinger #12306* (MW). RUSSIA: **Altai Republic**: Teletzkoe Lake, Bolshoe Istyube Creek, 1.VI.1989 *Ignatov s.n.* (MW); same place, *Ignatov #0/436* (MHA); Kamga Creek, *Ignatov #0/1631, 0/1633* (MHA); Sredny Shaltan Creek, *Ignatov #0/1632* (MHA); Teletzkoe Lake, *Ignatov #0/1630, 21/29* (MHA); Kayra River, *Ignatov #14/46, 13/2* (MHA); **Sakhalinskaya Prov.**, Kuril Islands, Iturup, *Bakalin #K-34-9-07* (MHA).

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