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PROBLEMATIC GROUPS OF BRACHYTHECIUM AND EURHYNCHIASTRUM (BRACHYTHECIACEAE, BRYOPHYTA) AND TAXONOMIC SOLUTIONS SUGGESTED BY nrITS SEQUENCES

ПРОБЛЕМНЫЕ ГРУППЫ РОДОВ BRACHYTHECIUM И EURHYNCHIASTRUM (BRACHYTHECIACEAE, BRYOPHYTA) И ВОЗМОЖНЫЕ ТАХОНОМИЧЕСКИЕ РЕШЕНИЯ НА ОСНОВЕ ПОСЛЕДОВАТЕЛЬНОСТЕЙ nrITS

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Abstract

The revision of *Brachythecium* from Russia that use both traditional morphological appoach in combination with nuclear ITS study reveals three undescribed species in Asian part of the country. They are described here as *B. baicalense, B. boreale,* and *B. extremiorientale*. The species status of *B. udum, B. acutum, B. brandegei, B. rotaeanum* is discussed. *Brachythecium digastrum* is synonymized with *B. laetum*. New combinations: *Eurhynchiastrum pulchellum* var. *barnesii* and *Sciuro-hypnum delicatulum* are suggested. *Brachythecium buchananii* is revealed in Europe. ITS data allow to reduce the ambiguity of taxonomic decisions in the group, although sometimes good species has no difference in ITS between species, e.g. in group of *B. salebrosum+B. erythrorrhizon +B.brandegei+B.glareosum*.

Резюме

Изучение рода *Brachythecium* с помощью классических морфологических методов при использовании данных по нуклеотидным последовательностям ядерных ITS позволило выявить три новых для науки вида, которые и описываются в статье: *B. baicalense, B. boreale, B. extremiorientale.* Обсуждается также видовая самостоятельность *B. udum, B. acutum, B. brandegei, B. rotaeanum*. *Brachythecium digastrum* отнесен в синонимы к *B. laetum*. Предложены новые комбинации: *Eurhynchiastrum pulchellum* var. *barnesii* и *Sciuro-hypnum delicatulum*. *Brachythecium buchananii* впервые выявлен для Европы. Изучение последовательностей ITS позволяет существенно уменьшить уровень неопределенности таксономических решений. Вместе с тем, некоторые группы, например *B. salebrosum+B. erythrorrhizon+B.brandegei+B.glareosum* не имеют отличий в ITS.

KEYWORDS: mosses, *Brachythecium*, Brachytheciaceae, taxonomy, ITS, molecular phylogenetics, Russia, North America

INTRODUCTION

Brachythecium is one of the largest genera in the Northern Hemisphere and its species are often considered quite difficult to identify. Morphological variation within species is high, diagnostic characters are not constantly persent, and although taxonomic treatments from different parts of the world use the same names, they circumscribe the taxa in different ways.

The revision of the genus in Russia has faced many difficulties. In many cases, our attempts at species identification, especially from Asia, re-

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mained ‘hanging’, as European, Japanese, Chinese and North American treatments did not provide satisfactory solutions. In the course of the work on the moss flora of North America, additional problems have appeared as no correlation of names has been undertaken between these continents in recent decades.

In addition to morphological studies, we also studied nr ITS sequences, as they have proved to be powerful tools for taxonomic elucidation at various levels, including for species (Fedosov & Ignatova, 2008; Goryunov et al., 2007; Ignatova & Fedosov, 2008, etc.). However, the family Brachytheciaceae is not easy in this regard because ITS variation within genera is very low (e.g. Ignatov & Milyutina, 2007). Nevertheless, unique substitutions in combination with the use of morphological characters allows a better delimitation of at least some taxa. Many problems remain and their solution will need additional fieldwork and sampling, so only a preliminary analysis is possible now. However, this analysis solves a few problems, supports some nomenclatural suggestions, and indicates especially poorly understood groups that need further investigation.

MATERIAL AND METHODS

Since a preliminary phylogenetic study has been completed for *Brachythecium* (Huttunen & Ignatov, 2004; Huttunen et al., 2007), we here attempt here to test affinities of ‘untypical’ specimens (i.e., where morphology admits quite alternative interpretations) using ITS data. Selection of material was made in the course of identification of collections from different parts of the circumboreal zone in the Northern Hemisphere, especially from Russia. After a certain amount of data had been accumulated and outlines of some previously unrecognized groups appeared, additional sampling of specimens morphologically similar to the latter was undertaken. Another aim of the work was to check the identity of Eurasian and North American plants traditionally referred to the same or related species.

As some specimens studied for DNA long ago have only ITS1 or only ITS2 data, two analyses were performed: a smaller dataset included 51 specimens of *Brachythecium* that have both ITS1 and ITS2 data, while a larger dataset was supplemented by 13 additional specimens that have either ITS1, or ITS2 data.

The protocol of DNA extraction, PCR and sequencing of ITS data was the same as described by Gardiner et al. (2005). Sequences were aligned manually in Bioedit (Hall, 1999). Parsimony analysis was completed with Nona (Goloboff, 1994) within the Winclada shell (Nixon, 1999a). A multiratchet option with five sequential parsimony ratchet runs was employed (Nixon, 1999b). Jackknifing with 1000 replications was performed with Nona within the Winclada shell.

Type material of some studied taxa is commented when necessary, and in a few cases we discuss the taxonomy of species that were not sequenced due to lack of fresh material.

RESULTS

Sequence variation of is rather low and some species have no single molecular synapomorphy. The jackknife values in the analysis of the larger dataset were rather high, 85, only for a clade formed by *B. frigidum*, *B. asperifolium* and *B. baicalense,* and moderately high, 74, for a clade formed by four specimens of the here newly described here *B. boreale*. A strict consensus tree (not shown) received very poor resolution, and the 50% majority tree (Fig. 1) has many clades that are not resolved in the strict consensus. However, many of these poorly supported clades join specimens of morphologically circumscribed species, and are therefore worth of discussing.

The analysis of the smaller dataset results in a very similar topology, and as this dataset did not include incomplete data, the support of many clades raises. The main polytomy includes (1) *Brachythecium auriculatum*; (2) *B. campestre*; (3) The *B. rivulare–rutabulum–frigidum*–group; (4) A clade that includes species of the *B. salebrosum*–group, the *B. buchananii*–group, and species around *B. laetum* and *B. mildeanum*. The latter clade #4 received a high support, 99. The high support was found mostly for individual species, and for pairs: *B. rivulare–B. rutabulum* (99), *B. asperrimum–B. frigidum* (96), *B. asperrimum–B. frigidum–B. baicalense* (84), *B. campestre–B. complanatum* (98), *B. mildeanum–B. acutum* (98); the whole *B. buchananii*–group got a almost no support of 66, as well as clade of *B. rotaeanum* – 57, but two specimens of *B. rotaeanum*, from SE Europe and eastern North America, form a smaller clade with support of 76.

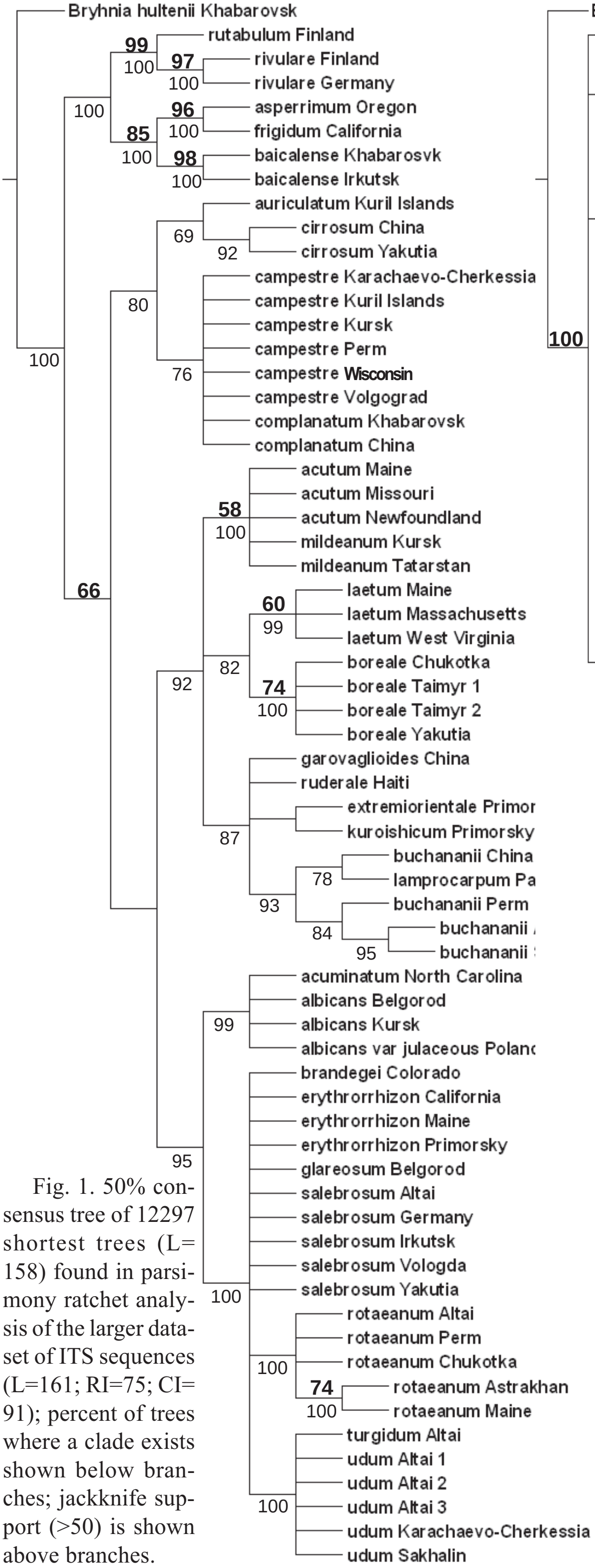


Fig. 1. 50% consensus tree of 12297 shortest trees (L=158) found in parsimony ratchet analysis of the larger dataset of ITS sequences (L=161; RI=75; CI=91); percent of trees where a clade exists shown below branches; jackknife support (>50) is shown above branches.

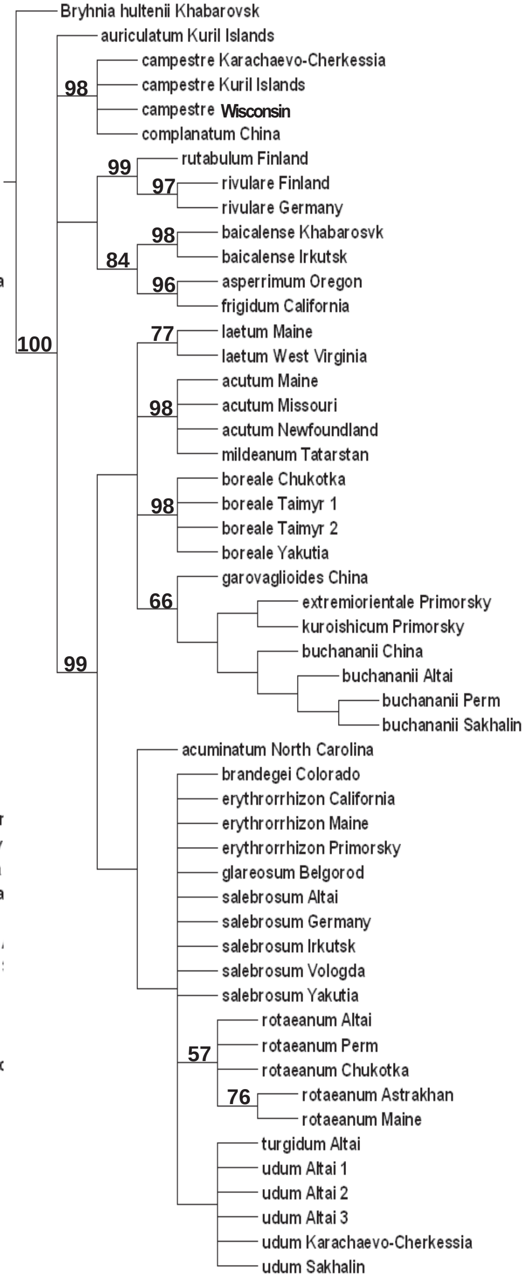


Fig. 2. Strict consensus tree of 221 shortest trees (L=149) found in parsimony ratchet analysis of the smaller dataset of ITS sequences (L=154; RI=79; CI=93); jackknife support (>50) is shown above branches. Data on specimens are given in Table 1.

Table 1. Data on specimens used in phylogenetic analysis.

Brachytheciastrum			
collinum (Müll. Hal.) Ignatov & Huttunen	EF617553	EF617553	Russia, Astrakhan Prov., Suragina 5.V.2002 (MHA)
Brachythecium			
B. acuminatum (Hedw.) Austin	GQ246810	AF403654	U.S.A., North Carolina, Anderson 24257 (H)
B. acutum (Mitt.) Sull.	GQ246821	GQ246821	U.S.A., Maine, Allen 28201 (MO)
B. acutum	GQ246822	GQ246822	U.S.A., Missouri, Allen 26741 (MO)
B. acutum	GQ246823	GQ246823	Canada, Newfoundland, Buck 52529 (NY)
B. albicans (Hedw.) Bruch et al.	GQ246811	—	Russia, Belgorod Prov., Ignatov 13.V.1999 (MHA)
B. albicans	GQ246812	—	Russia, Kursk Prov., Ignatov 20.V.1999 (MHA)
B. albicans var. *julaceum* Warnst.	GQ246813	—	Poland, Ochyra 13.IV.1987 (MHA)
B. asperrimum (Mitt. ex Müll.Hal.) Sull.	GQ246824	GQ246824	U.S.A., Oregon, Darigo 3977 (MO)
B. auriculatum A.Jaeger	DQ497446	DQ497446	Russia, Kuril Is., Bardunov 10.IX.1980 (MHA ex IRK)
B. baicalense Ignatov	GQ246825	GQ246825	Russia, Khabarovsk Territory, Bureya, Ignatov 97-1115 (MHA)
B. baicalense	GQ246826	GQ246826	Russia, Irkutsk Prov., Slyudyanka, Ignatov & Kazanovsky 05-6010 (MHA)
B. boreale Ignatov	GQ246827	GQ246827	Russia, Chukotka, Afonina 20.VIII.2001 (MHAex LE)
B. boreale	GQ246828	GQ246828	Russia, Yakutia, Ignatov 00-1074 (MHA)
B. boreale Taimyr 1	GQ246829	GQ246829	Russia, Taimyr, Fedosov, 05-31 (MW)
B. boreale Taimyr 2	GQ246830	GQ246830	Russia, Taimyr, Fedosov 05-650 (MW)
B. brandegei (Austin) H.Rob.	GQ246831	GQ246831	U.S.A., Colorado, Weber B-114286 (MHA ex COLO)
B. buchananii (Hook.) Jaeger	GQ246832	GQ246832	Russia, Perm Prov., Bezgodov N176 11.VIII.2005 (MHA)
B. buchananii	DQ200075	AF403595	China, Koponen et al. 53972 (H)
B. buchananii	GQ246833	GQ246833	Russia, Altai, Ignatov 29/29 (MHA)
B. buchananii	GQ246834	GQ246834	Russia, Sakhalin, Ignatov 06-196 (MHA)
B. cirrosum (Schwaegr.) Schimp.	—	AF403641	China, Xianjing, Tan 93-846 (H)
B. cirrosum	—	AF403641	Russia, Yakutia, Ignatov 00-26 (H ex MHA)
B. campestre (Müll. Hal.) Bruch et al.	GQ246814	—	Russia, Perm Prov., Bezgodov 682 (MHA)
B. campestre	GQ246835	GQ246835	Russia, Kuril Is., Ignatov 06-1560 (MHA)
B. campestre	GQ246815	—	Russia, Kursk Prov., Ignatov 14.VIII.1996 (MHA)
B. campestre	GQ246836	GQ246836	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova 05-3789 (MW)
B. campestre	GQ246816	—	Russia, Volgograd Prov., Ignatov 10.VIII.1999 (MHA)
B. campestre	GQ246837	GQ246837	U.S.A., Wisconsin, Bowers 11-10-1990 (MO)
B. complanatum Broth.	—	AY166444	Russian, Khabarovsk Territory, Bureya, Ignatov 97-172 (MHA)
B. complanatum	GQ246838	GQ246838	China, Cao Tong 040063 (MHA)
B. erythrorhizon Bruch et al.	GQ246817	—	Russia, Arkhangelsk , Churakova 1148 (MHA)
B. erythrorhizon	GQ246839	GQ246839	U.S.A., Maine, Allen 28225 (MO)
B. erythrorhizon	GQ246840	GQ246840	Russia, Primorsky Territory, Ignatov et al. 06-2122 (MHA)
B. erythrorhizon	GQ246841	GQ246841	U.S.A., California, Ignatov 27-8-1989 (MHA)
B. extremiorientale Ignatov	GQ246842	GQ246842	Russia, Primorsky Territory, Ignatov & Ignatova 06-2935 (MHA)
B. frigidum (Müll. Hal.) Besch.	DQ336898	AF403638	USA, California, Düll, 23.IV.1981 (H)
B. garovaglioides Müll. Hal.	DQ497445	DQ497445	China, Fuan 960785 (PE ex MHA)
B. glareosum (Bruch ex Spruce) Bruch et al.	GQ246843	GQ246843	Russia, Belgorod Prov., Ignatov14.V.1999 (MHA)
B. kuroishicum Besch.	DQ497444	DQ497444	Russia, Primorsky Territory, Cherdantseva 15.IV.1991 (MHA ex VLAD)
B. laetum (Brid.) Bruch et al.	GQ246818	—	U.S.A., Massachusetts, Tan 91-501 (MHA)

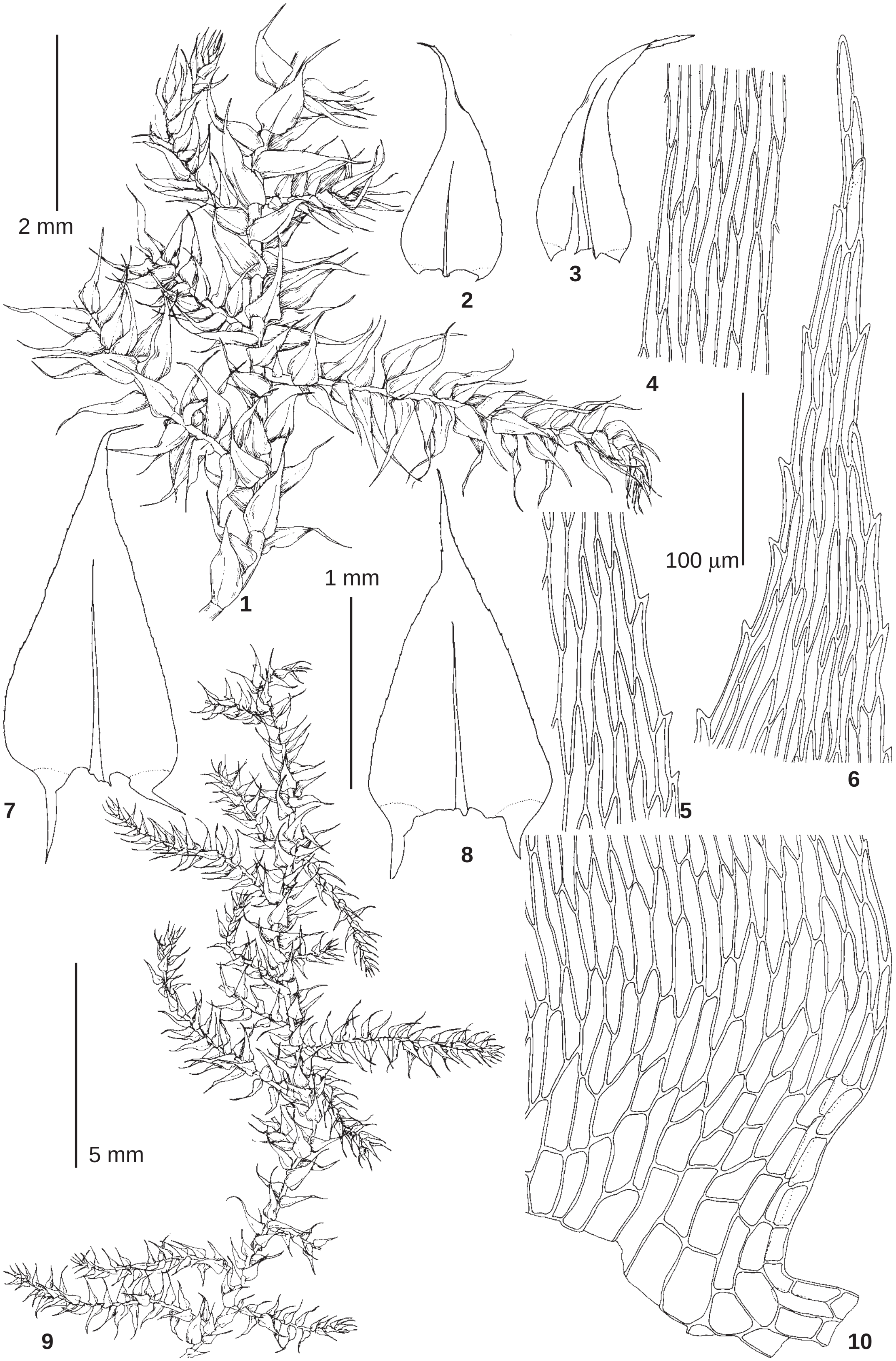
B. laetum (morphotype '*digastrum*')	GQ246844	GQ246844	U.S.A., West Virginia, Buck 36983 (NY)
B. laetum	GQ246845	GQ246845	U.S.A., Maine, Allen 28393 (MO)
B. lampocarpum (Müll.Hal.) A.Jaeger	—	AF403584	Papua New Guinea, Koponen 28748 (H)
B. mildeanum (Schimp.) Schimp.	—	AY166441	Russia, Kursk Prov., Ignatov 20.V.1999 (MHA)
B. mildeanum	GQ246846	GQ246846	Russia, Tatarstan, Ignatov & Ignatova 18.VIII.2003 (MHA)
B. rivulare Bruch et al.	DQ200076	AF403651	Finland, Parnela 19.V.1996 (H)
B. rivulare	DQ200077	DQ200077	Germany, Frahm 19.VI.1999 (BONN)
B. rotaeanum De Not.	GQ246847	GQ246847	Russia, Chukotka, Afonina 24.VIII.2001 (MHA ex LE)
B. rotaeanum	GQ246848	GQ246848	Russia, Astrakhan Prov., Suragina 5.V.2002 (MHA)
B. rotaeanum	GQ246849	GQ246849	Russia, Altai, Ignatov 0/3004 (MHA)
B. rotaeanum	GQ246850	GQ246850	Russia, Perm Prov., Bezgodov 20.IX.2003 #65 (MHA)
B. rotaeanum	GQ246851	GQ246851	U.S.A., Maine, Allen 28536 (MO)
B. ruderale (Brid.) Buck	—	AF503535	Haiti, Buck 4826 (H)
B. rutabulum (Hedw.) Bruch et al.	DQ200078	AF403644	Finland, Huttunen 1415 (H)
B. salebrosum (F. Web. & D. Mohr) Bruch et al.	GQ246852	GQ246852	Russia, Irkutsk Prov., Ignatov 8.VI.2005 (MHA)
B. salebrosum	GQ246819	—	Russia, Bashkortostan, Zolotov 08-6 (MHA)
B. salebrosum	GQ246853	GQ246853	Russia, Altai, Ignatov 14/61 (MHA)
B. salebrosum	GQ246854	GQ246854	Russia, Vologda Prov., Ignatov & Ignatova 12.VIII.2001 (MHA)
B. salebrosum	GQ246855	GQ246855	Russia, Yakutia, Ignatov 00-866 (MHA)
B. salebrosum	AY654609	AY654609	Germany, Goffinet 4723
B. turgidum (Hartm.) Kindb.	GQ246856	GQ246856	Russia, Altai, Ignatov 31/291 (MHA)
B. udum I. Hag. Altai 1	GQ246857	GQ246857	Russia, Altai, Ignatov 0/444 (MHA)
B. udum Altai 2	GQ246858	GQ246858	Russia, Altai, Ignatov 15/112 (MHA)
B. udum Altai 3	GQ246859	GQ246859	Russia, Altai, Ignatov 31/297 (MHA)
B. udum	GQ246860	GQ246860	Russia, Karachaevo-Cherkessia, Ignatova 07-156 (MW)
B. udum	GQ246861	GQ246861	Russia, Sakhalin, Ignatov & Teleganova 21.VIII.2006 (MHA)
Bryhnia			
hultenii E.D.Bartram	GQ246820	GQ246820	Russia, Khabarovsk Territory, Bureya Ignatov 97-1282 (MHA)
Eurhynchiastrum			
pulchellum (Hedw.) Ignatov & Huttunen France1	AY737470	AY737470	France, Sotiaux 14737
pulchellum France2	AY737465	AY737465	France, Sotiaux 13234
pulchellum	AY737468	AY737468	Italy, Blockeel 26/519
pulchellum	FM161101	FM161101	Finland, Koponen & Huttunen 1321 (H)
pulchellum	GQ254298	GQ254298	Canada, British Columbia, Vitt 35808a [admixture to 35808] (MHA)
pulchellum var. *barnesii* (Renauld & Cardot) Ignatov	GQ254299	GQ254299	Canada, British Columbia, Schofield 85054 (UBCU)

DISCUSSION

The overall topology of the phylogenetic tree obtained in the present study is similar to previous results (e.g. Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004; Huttunen et al., 2007, etc.). The group of hygrophilous species around *B. rivulare* with rough setae is basal, whereas the group with smooth setae (usually named as sect. *Salebrosa*) is in a terminal position. The *B. salebrosum* group was not resolved in the present analysis as ITS has no synapomorphies for the *salebrosum–erythrorrhizon–glareosum-brandegei*–complex. Only a few contrastingly different species in this group are commented on here.

At the same time, some species, e.g. *B. rotaeanum* and *B. udum* differ from 'average *B. salebrosum*' in only one or two substitutions, but they are consistently present in all of the studied specimens and consistently agree with morphology. This fact forces us to analyze even singular substitutions.

In several cases, the positions of 'enigmatic specimens' were resolved by molecular data, en-


2 mm
1
2
3
4
100 μm
1 mm
5
6
7
8
9
5 mm
10

couraging the description of new species, especially when they aer clearly distinct from species resolved as their closest relatives.

1. ***Brachythecium baicalense*** Ignatov sp. nov. Figs. 3, 9.

Species haec habitu, ITS sequentia, foliis ovato-lanceolatis vel lanceolatis, margine serratis, cellulis laminae angustis et cellulis alaribus paucis, hyalinis inflatisque Brachythecio asperrimo similis, sed inflorescentiis monoicis et setis glabris differt.

Typus: Siberia, Irkutsk Prov., Slyudyanka Distr., Slyudyanka Creek 7 km upstream from mouth, 51°37.5'N – 103°39'E, 650 m alt., on rotten log in valley, 8.VI.2005, M. Ignatov & S. Kazanovsky 05-6010 (holotypus MHA).

Plants medium-sized, in loose tufts, light green to yellowish or whitish green. Stems to 5 cm, prostrate to arching, terete foliate, irregularly to regularly pinnately branched; branches often deviating from stem with at about a right angle, to 5 mm, straight to slightly curved, terete foliate. Stem leaves erecto-patent to patent, 1.8-2.2 x 0.8-1.1 mm, ovate-triangular (broadest at about 1/10 of leaf length), gradually tapered to apex, and short or moderately long acuminate, rounded to insertion, conspicuously decurrent, not or weakly plicate; margins plane, serrate to strongly so; costa slender, reaching 0.6-0.75 of leaf length, ending in a small spine or not; laminal cells 70-120 x 5-8 μm; narrow almost to leaf base, cells to leaf corners enlarged, forming indistinctly delimited pellucid group. Branch leaves smaller to strongly and abruptly smaller, more strongly serrate. Sexual condition autoicous. Seta 15-20 mm, smooth. Capsule inclined to horizontal, somewhat curved, ca. 20 mm long, operculum unknown. Spores 15-17 μm.

Brachythecium baicalense forms a clade sister to North American *B. frigidum* and *B. asperrimum*. *Brachythecium frigidum* is very common in Pacific North-West of North America and was recently collected in Russian Far East (Bakalin, VLA, MHA). It is a highly variable species, but is usually easy to identify due to many characters that are otherwise rare in the genus: the leaves are rigid, strongly plicate, conspicously triangular (i.e., leaf margins are tapering to apex in straight lines), the marginal cells are short and form sharp serrations, the alar region is somewhat auriculate, the alar cells are large, and cells in one row across the whole base at insertion are conspicuously enlarged.

The sister species to *B. frigidum* is *B. asperrimum*, a species that was synonymized with *B. frigidum* in the Canadian check-list (Ireland et al., 1987), but considered a species in the North American checklist (Anderson et al., 1990). This synonymization was apparently based on assumption that *B. asperrimum* is a poorly developed *B. frigidum*. *Brachythecium asperrimum* is one of the most variable species in North America; it has been described under six different species names and Grout (1928) accepted three of them as species. It is variable in size from moderately small to rather robust, and forms loose to moderately dense tufts; its stems are creeping to arching, straight to flexuose, terete to subcomplanately foliate; its leaves are densely to very loosely arranged, erect to falcate-secund, ovate to lanceolate; and the leaf margins are distinctly serrate to occasionally subentire. However it can usualy be recognized by remote foliage, narrow leaves, enlarged basal cells, and by almost always having sharply serrate leaf margin.

These characteristics of *B. asperrimum* are provided here to parallel its variation pattern with *B. baicalense* that is gametophytically closest to *B. asperrimum*, and also exhibits great variation even among a limited number of specimens. Most collections are composed of slender, loosely foliate plants that habitually look like a depressed phenotyte of *B. salebrosum*. The differences from this species include enlarged alar cells, unusually strong marginal serration, and narrow and long laminal cells, reminiscent of *Sciuro-hypnum starkei* to which it was referred when collected by one of the authors, MI, for the first time in a sterile state (Ignatov et al., 2000). The important difference between *B. baicalense* and both *B. frigidum* and *B. asperifolium* is the monoicous sexual condition and smooth seta. The latter character and a contrastingly different habit distinguishes *B. baicalense* from *S. starkei*.

Fig. 3. *Brachythecium baicalense* (from holotype: Irkutsk Prov., Ignatov & Kazanovsky, 05-6010 MHA): 1, 9 – habit (dry); 2-3 – branch leaves; 4-5 – mid-leaf cells; 6 – upper leaf cells; 7-8 – stem leaves; 10 – basal leaf cells. Scale bars: 5 mm for 9; 2 mm for 1; 1 mm for 2-3, 7-8; 100 μm for 4-6, 10.

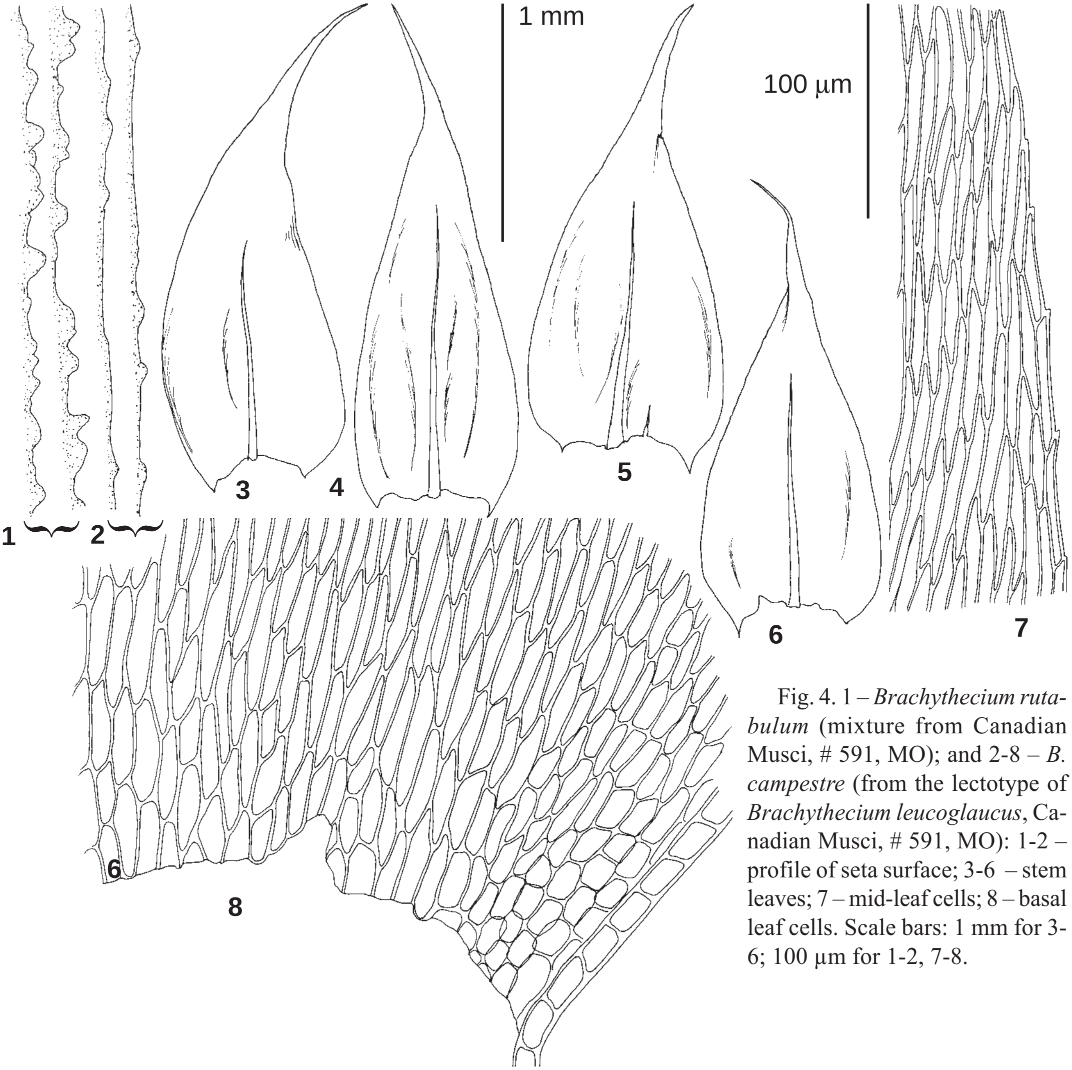


Fig. 4. 1 – *Brachythecium rutabulum* (mixture from Canadian Musci, # 591, MO); and 2-8 – *B. campestre* (from the lectotype of *Brachythecium leucoglaucus*, Canadian Musci, # 591, MO): 1-2 – profile of seta surface; 3-6 – stem leaves; 7 – mid-leaf cells; 8 – basal leaf cells. Scale bars: 1 mm for 3-6; 100 µm for 1-2, 7-8.

Poor collections of *B. baicalense* without gametangia are very difficult to differentiate from underdeveloped morphotypes of *B. salebrosum* from shaded habitats where small subquadrate cells in the leaf corners are not always clearly expressed. The comparison with *B. boreale* is given under that species.

Specimens examined: **Amurskaya Prov.**: Bureya River near Ostashino, year 1909, Fedchenko #527 (LE); **Irkutsk Prov.**: Slyudyanka, Ignatov & Kazanovsky, 05-6010 (MHA); **Khabarovsk Territory**, Levaya Bureya River, Ignatov 97-1113 (MHA), 97-313 (MHA), 97-310 (MHA); Chegdomyn, Ignatov 97-1115 (MHA); **Yakutia** (South-West), Vitim River, Ivanova 13.VI.2004 (SASY ex MHA); same 9.VI.2004 (SASY ex MHA).

Most collections of *B. baicalense* are from fallen logs in flood-valleys, at low elevations. In general this seems to be a rare species.

2. *Brachythecium campestre*. Fig. 4: 2-8.

Brachythecium campestre, as many authors have noted, is a very similar species to *B. salebrosum* and it is very difficult to separate them in many cases. Grout (1928) expressed some doubts that *B. campestre* is a good species and Crum & Anderson (1981) wrote that it “certainly cannot be considered a species of the first rank”. The controversial approaches to circumscription of this species in Europe were discussed by Hedenäs (1995), who considered this species as a close one to *B. albicans* and *B. salebrosum*, which is most likely from its morphology.

However, *B. campestre* (plus *'B. complanatum',* see below) was found to be one of the most distinct species in *Brachythecium* using molecular data. Some motifs are the same as in *B. rutabulum* and *B. rivulare*, while other are similar to the *B. salebrousum*–group, and, probably, *B. campestre* (n=11, 12, 16, 17) can be suspected of hybrid origin, although its morphological similarity with *B. salebrosum* (n=10, 12, 13) is more sound than with that of *B. rivulare* (most counts n=6). Chromosome data, however, are taken from the literature (Lazarenko et al., 1971; Fritsch, 1991), so combined molecular and karyological study is necessary to confirm or reject this hypothesis.

Even if the hypothesis of hybrid origin is correct, at the moment *B. campestre* is quite stable: plants from the Pacific coast of Asia, Central Asia, Europe, and Eastern North America are subidentical by ITS and also have similar morphologies. The main features differentiating *B. campestre* from *B. salebrosum* include: 1) leaves are concave and plicate, but the plicae are more or less parallel only in the more narrow and falcate leaves, while the broader, more deeply concave and straight leaves have crumpling surfaces with only shallow plicae in divergent directions; concave leaves make the plant foliage more julaceous, thus, superficially, *B. campestre* is often more like robust *B. albicans* than *B. salebrosum*; 2) cells in the leaf corners are subquadrate or short rectangular, forming a more or less extensive group (larger than in *B. salebrosum*), or, often, the group is rather small and compact (not larger than in *B. salebrosum*), but in this case it usually has a pellucid zone of supra-alar cells that form a conspicuous group along leaf margin, just above the small leaf corner cells, extending up to the broadest pertion of the leaf, almost forming auricles when well expressed; this pattern seems to correspond to the rather abrupt constriction, or 'rounding' to the leaf base, somewhat resembling that of *B. rutabulum*. Contrary to this, the leaves of *B. salebrosum* have much less constriction to the base, a smaller and a more distinctly delimited square group of cells in the leaf corners, and its leaves are either clearly longitudinally plicate or rather smooth when it is growing in wet and shady forests; 3) the seta of *B. campestre* is rough in most populations.

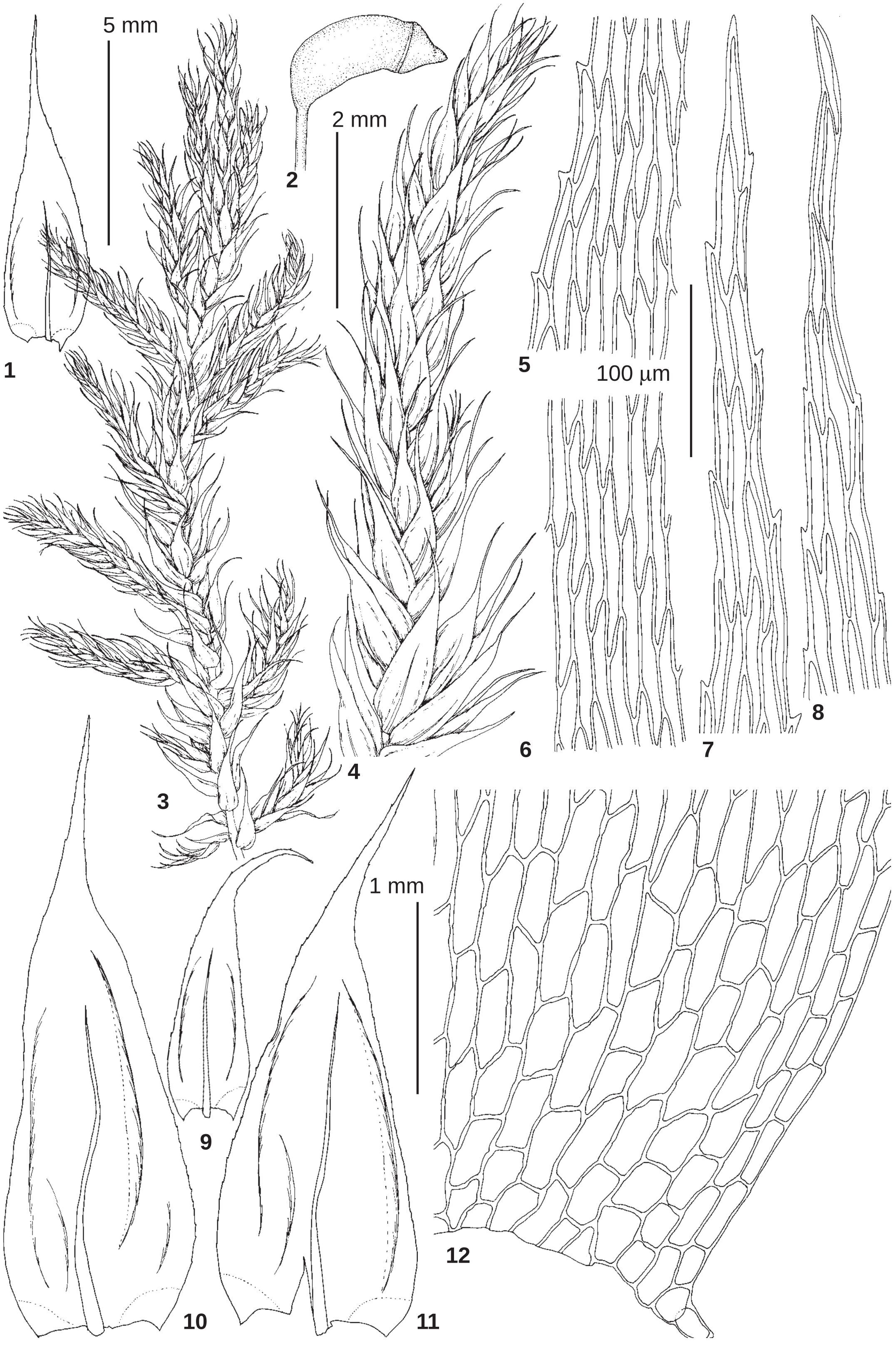
There are some small differences between European and American populations of *B. campestre*: American populations have, usually, narrower and more or less falcate leaves, while European plants have often relatively broad leaves that are usually straight, and the seta is usually more conspicuously rough in American plants than European ones where the seta is often almost or even totally smooth or with low mammillae. If future studies provide additional evidence for their separation, the appropriate name for the American *'B. campestre'* should be *Brachythecium leucoglaucum* Müll. Hal. & Kindb.

Brachythecium leucoglaucum, according to Grout (1928) and subsequent authors, is a synonym of *B. rutabulum*. This decision was apparently accepted because the type collection, the exsiccate #591 (specimen in MO), contains two plants, one of *B. rutabulum* and other *B. campestre* (Fig. 4). The description itself, as well as the name, refers to the latter one: plants of *B. rutabulum* are bright green (not 'whitish to subglaucous green', as stated in the protologue), have large alar cells (not 'alar cells small'), and have strongly rough seta (not 'faintly rough'). In addition, another exsiccate, of *B. leucoglaucus*, Canadian Mosses #297, includes only *B. campestre*. Thus the lectotype of *Brachythecium leucoglaucus* is selected here:

Brachythecium leucoglaucum Müll. Hal. & Kindb. Catalogue of Canadian Plants, Part VI, Musci 198. 1892.

Lectotype, designated here: Canadian Musci, Prepared by J. Macoun, 591. *Brachythecium leucoglaucum*, C.M. & Kindb., On loose Earth, Queens Co., N.B. [New Brunsvick] Sept. 10th, 1888, Coll. J. Moser (MO!) [plant in a separate envelope, annotated by M. Ignatov].

Selected North America specimen studied (with the state/province abbreviations of BFNA, specimens in MO, if otherwise not indicated): Man. (Bird 5774), N.B. (Allen 2141), Nfld. (Waghorne 23.???.1891), N.S. (King & Garvey B623), Ont. (Dupret March 28, 1910), Sask. (GN Jones 43477), Conn. (Pease 456), Del. (Reed 132429), Iowa (Allen 10896), Maine (Allen 22419), Mich. (Flowers 3209 (NY)), Minn. (Churchill 6295), Mo. (Darigo 4026), N.H. (Allen 24582), N.Y. (Allen 7908), R.I. (Allen 20438), S.Dak. (Churchill 11331), Wis. (Bowers 11.X.1990). Specimens from Russia are available from: http://gis-app.ict.nsc.ru/bio/search.php.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2a. ***Brachythecium complanatum*** Broth. remained for a long time a little-known species, while Ignatov (1998) and Ignatov & al. (2006) found it to be not so rare in south Siberia and occurring also in Japan.

This is a distinct species characterized by the following combination of characters: plants glossy, foliage somewhat subcomplanate in loose growth, while julaceous in dense growth, leaves strongly crumplingly plicate, margin coarsely serrate above, seta strongly rough, calyptra hairy (hairs few), sexuality dioicous.

This species grows usually in mesic or moist forests, while *B. campestre* is primarily a species of open habitats.

Its position in the clade formed mostly by *B. campestre* provides a novel idea of its affinity, but also indicates that morphologically distinct species may not be resolved by ITS (cf. Figs. 1&2 for *B. salebrosum* and near species).

3. ***Brachythecium buchananii***-group, including ***Brachythecium extremiorientale,*** sp. nova.

This group includes two widespread and polymorphic species, *B. buchananii* in East and South-East Asia and *B. ruderale*, ranging from the southern states of U.S.A. to West Indies and South America. Buck (1999) suggested that the widespread tropical African *B. implicatum* (Hornsch. ex Müll. Hal.) A. Jaeger is a synonym of *B. ruderale*; O'Shea (2006) continues to use the former name; regardless the final decision on their identity, these two taxa are closely related. This group includes also West Indian *B. zanonii* W.R.Buck, East Asian *B. kuroishicum* and *B. garovaglioides*, Malesian *B. lamprocarpum*, and a number of other species with principally temperate and tropical distribution.

Superficially, the plants of this group are distinct, in being strongly lustrous (i.e. more than usually in *B. albicans, B. salebrosum*, etc.) and in having a rather broad basal part of the leaf that tapers more or less abruptly to a narrow acumen. McFarland (1988) in his Ph.D. thesis segregated them in a separate section, but never formally validated it. In addition to leaf shape he mentioned as an important characters the little-differentiated annulus, which is true for most of its species. At the same time, a dioicous sexual condition is not a characteristic of all species of this group.

Field studies in Primorsky Territory in the Russian Far East revealed a locally common species that still has no name. By both appearance and ITS analysis, it belongs to this group. The fact that it had remained undescribed up to now is readily explained: in the key of *Brachythecium* for Japan and adjacent areas by Takaki (1955) it keys out as *B. salebrosum*, a species that appears to be absent or at least very rare in East Asia. Certainly, separation from this species would be difficult, considering the enormous variability of *B. salebrosum* globally. However, the rich golden-lustrous plants with non-plicate leaves (though plicae may appear in microscope slides due to concavities) with long acumina, along with the indistinct square group of smaller cells in the corners of the leaves, make this unnamed species rather distinct from *B. salebrosum*. In addition, ITS data also indicates that its position is in the '*buchananii*-group'.

Brachythecium extremiorientale Ignatov, sp. nov. Fig. 5, 9.

A habitu, plantis pernitentibus, foliis concavis abrupte acuminatis et ITS sequentia species haec appropinquat Brachythecium buchananii gregem, praecipue B. kuroishicum inflorescentiis monoicis, sed marginibus foliorum distincte serratis, sensim acuminatis et cellulis basalibus dilatatis iam dignoscenda.

Typus: 'Russian Far East, Primorsky Territory, Ussurijsky State Reserve, Kamenka Creek, 43°39'N – 132°21'E, 150 m alt., on rotten log, 28.IX.2006 M. Ignatov & E. Ignatova 06-2935' (holotypus MHA).

Plants moderately robust, in loose to moderately dense tufts, yellowish to brownish green. Stems to 6 cm, prostrate, or ascending in dense growth, terete foliate, irregularly to moderately regularly pinnate branching; branches often deviating from stem by a narrow angle, to 6 mm, straight, terete foliate. Stem leaves imbricate, erect to erect-appressed, with acumens usually straight, 2.5-3.2 x 0.9-1.3 mm, ovate-lanceolate (broadest at about

Fig. 5. *Brachythecium extremiorientale* (from the holotype, Ignatov & Ignatova #06-2935, MHA): 1, 9 – branch leaves; 2 – capsule; 3-4 – habit; 5-6 – mid-leaf cells; 7-8 – upper leaf cells; 10-11 – stem leaves; 12 – basal leaf cells. Scale bars: 5 mm for 3; 2 mm for 4; 1 mm for 1, 9-11; 100 µm for 5-8, 12.

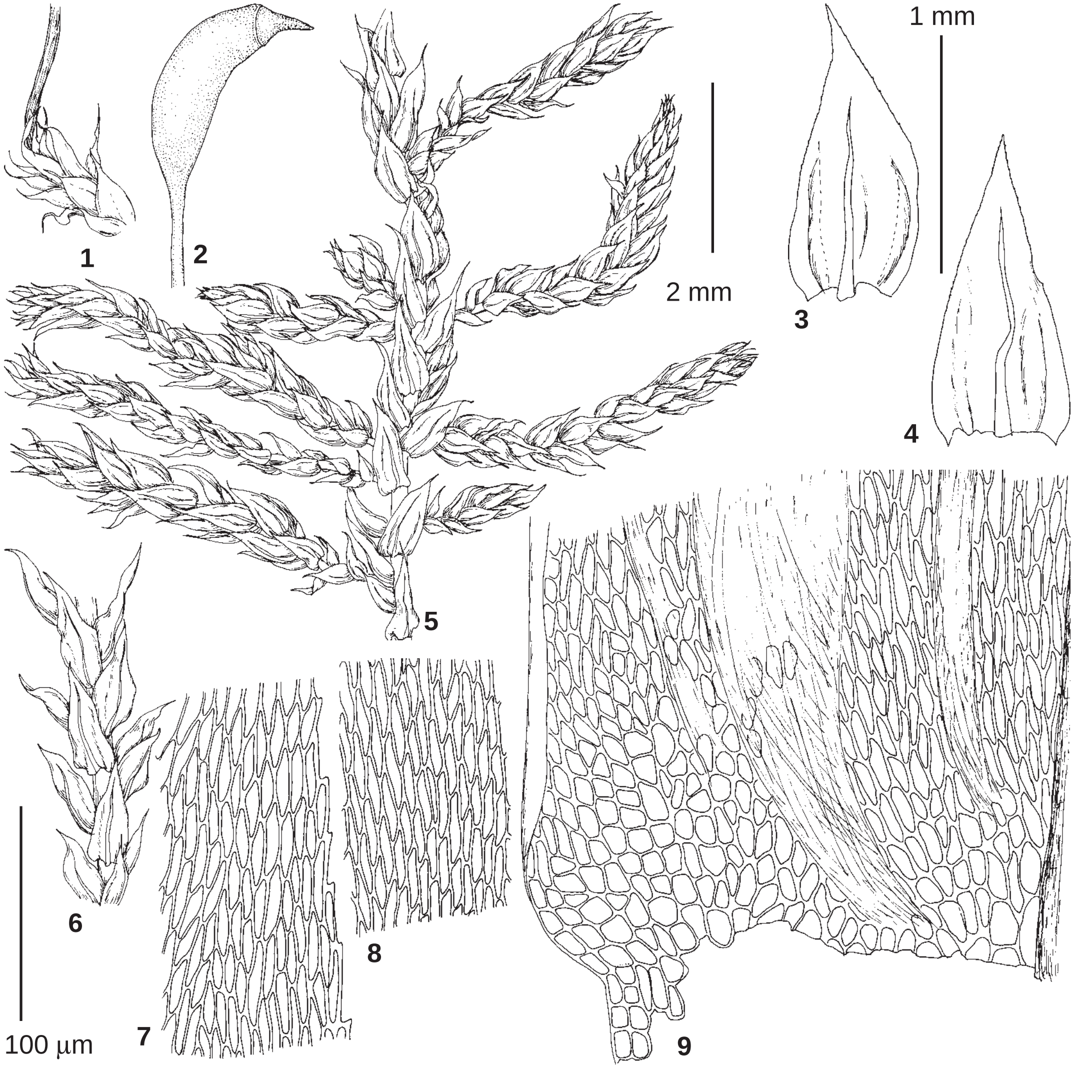


Fig. 6. *Brachythecium laetum* (from the lectotype of *Brachythecium digastrum*, CANM): 1 – perichaetium; 2 – capsule; 3-4 – stem leaves; 5-6 – habit, dry; 7-8 – mid-leaf cells; 9– basal leaf cells. Scale bars: 2 mm for 1-2, 5-6; 1 mm for 3-4; 100 μm for 7-9.

1/7 of leaf length), concave, gradually to abruptly acuminate, below broadest point of leaf only slightly and gradually narrowed to leaf insertion, narrowly decurrent and decurrencies rarely come off with detached leaves, concave, not to weakly plicate (but with stronger pseudo-plicae in slides); margins plane or occasionally recurved in some areas, serrulate to serrate; costa slender, reaching 0.5-0.7 of leaf length, ending without a spine; laminal cells 80-130 x 6-9 μm; basal cells homogeneous across whole leaf base, shorter, to 50-80 μm long, and quite broad, to 20-25 μm; basal cell walls thin, but looking rigid and somewhat pitted. Branch leaves smaller and narrower, usually more strongly serrate. Sexual condition autoicous. Seta 15-20 mm, smooth. Capsule inclined to horizontal, curved, short-elongate, ca. 15 mm long, operculum conic, annulus poorly developed and hardly separated. Spores 13-16 μm.

Brachythecium kuroishicum, a moderately rare moss and rather strictly confined to the Pacific coastal zone in Asia, is most similar to *B. extremioientale* in both habit and autoicous sexuality that is relatively rare in this group. However *B. kuroishicum* has leaves more abruptly tapered to linear, ‘cirriphylloid’ acumina, subentire leaf margins, and large cells confined to the leaf corners, not across the whole leaf base.

Basal cells that are rather even across the leaf base are somewhat similar to those of *B. garovaglioides*, but this species is much more robust, has leaves with broadly ovate basal part and is dioicous.

Specimens examined: **Primorsky Territory**: Usurijsky State Reserve Ignatov & Ignatova 06-2335, 2340, 2345 (MHA); Chuguevsky Distr., Ignatov 07-557 (MHA); **Sakhalin Province**: Kuril Islands, Kunashir, Ignatov 06-1793; 06-3161; 06-3189 (MHA).

Brachythecium extremiorientale grows at low elevations, usually 100-700 m, on tree bases and fallen logs and stumps in forest (usually in mixed north-temperate type) in shallow valleys, and in the Kuril Islands on *Hydrangea* stems within *Sasa* communities.

3a. ***Brachythecium buchananii*** new to Europe.

The species is very common in China and Japan, but the fact that it was recognized in Russia only recently (Ignatov & Afonina, 1992) clearly indicates the low level of exchange of taxonomic concepts across biogeographic and sometimes also political borders. After its first records from south Siberia, this species was found to be common in the southern part of Asian Russia, penetrating as far north as Central Kamchatka (Czernyadjeva, 2005) and central Yakutia, 61°N (Krivoshapkin et al., 2001). The known western limit of the species was in Altai in Russia, Uzbekistan in Middle Asia (Ignatov & Ignatova, 2003), and Pakistan (Nishimura & Higuchi, 1993).

Collections of the species from the Middle Ural Mountains in Perm Province were made recently by Andrey Bezgodov. *Brachythecium buchananii* was collected on the banks of Chusovaya River, along a stretch of ca. 6 km on several individual cliffs formed by Upper Devonian limestone, on cliff bases and ledges. They are represented by very small plants, especially similar to those from Altai and Kamchatka, and would be difficult to interpret by morphology only. As all the leaves are narrow and similar to branch leaves of more southern populations, and have more serrulate margins (again, a similarity to branch leaves). Takaki (1955) described a similar morphotype as *B. buchananii* var. *gracile* Broth.; its real taxonomic value, however, needs further studies in the context of the study of the ‘*buchananii*-group’ as a whole.

Specimens examined from Europe: Perm Province, Lys’va Distr., Chusovaya River downstream from Kyn-Zavod: cliff “Stenovoy”, 57°53’N–58°41E, 260 m alt., 9.VIII.2005 Bezgodov #111; cliff “Pechka”, 57°52’N–58°42’E, 200 m alt., 11.VIII.2005 Bezgodov # 176; cliff “Velikan”, 57°52’N–58°42.5’E, 280 m alt., 9.VIII.2005 Bezgodov #79; cliff “Ostryak”, 57°53’N– 58°44’E, 240 m alt., 12.VIII.2005 Bezgodov #184; cliff “Denezhnyy”, 57°52’N–58°41’E, 180 m alt., 9.VIII.2005 Bezgodov #61 (all in MHA and PPU).

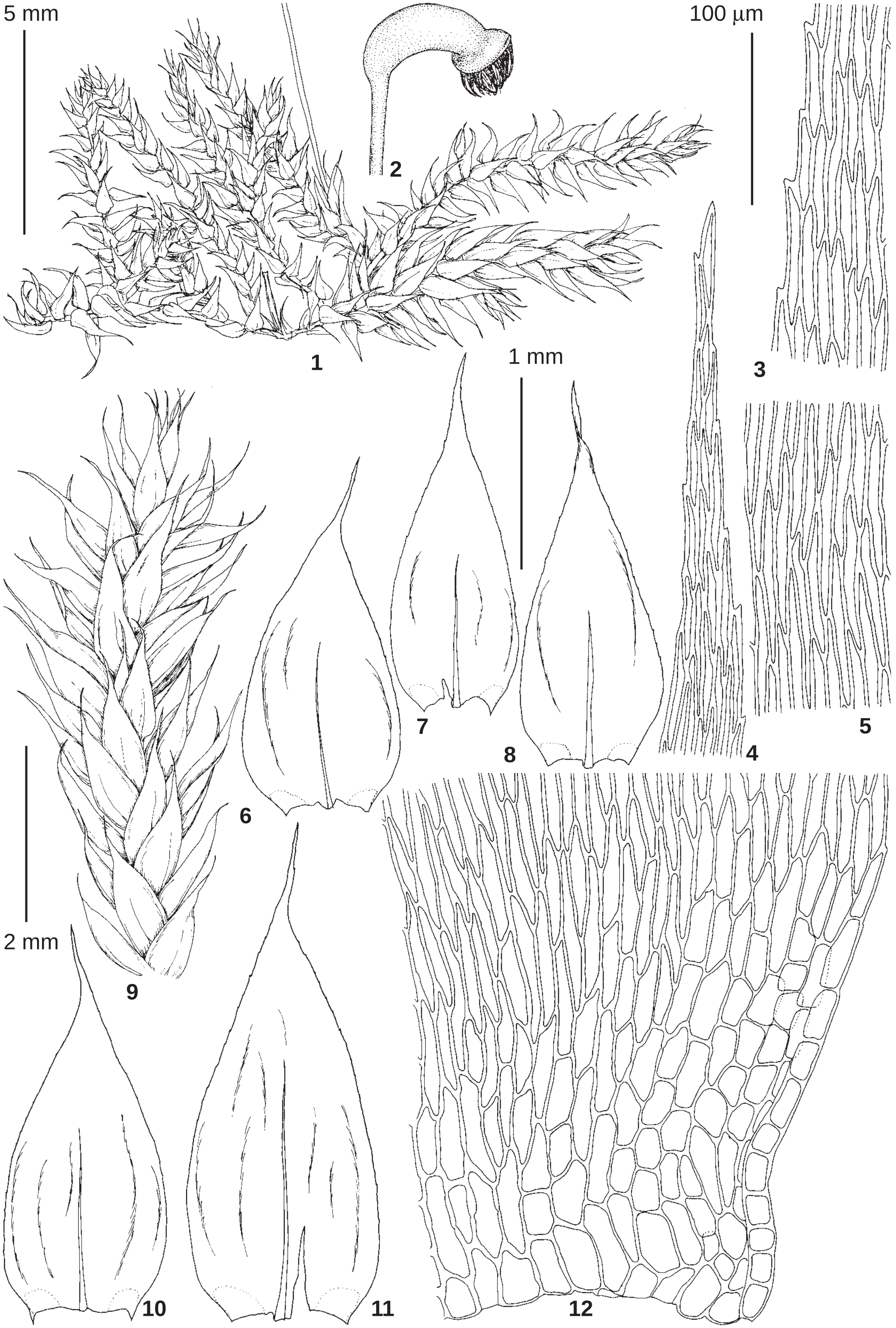
4. ***Brachythecuim laetum*** and ***B. digastrum,*** Fig. 6.

Brachythecium laetum (Brid.) Bruch, Schimp. & Gümbel, Bryologia Europaea 6: 24. Fig. 554. 1853. – *Hypnum laetum* Brid., Bryologia Universa 2: 479. 1827.

Brachythecium digastrum Müll. Hal. ex Kindb., *Catalogue of Canadian Plants, Part VI, Musci* 190. 1892. Lectotype (designated here): “North American Mosses, Herbarium of Columbia College, Named By ~~E.G.Britton~~ A.J.Grout, 345. Brachythecium digastrum CM & K. On earth, McKay’s Bush, Ottawa, Ont., Oct. 12th 1889 *J. Macoun* (CANM!)”. *Syn. nov.*

Brachythecium digastrum was described by Carl Müller and Kindberg in Macoun’s Catalogue of Canadian plants (Macoun, 1892). It was compared with *B. biventrosum* (Müll. Hal.) A. Jaeger (=*B. acuminatum*), from which it differs in more robust plants, and with *B. laetum*. The differences of *B. digastrum* from the latter species include leaves that in *B. digastrum* are short acuminate (vs. long acuminate in *B. laetum*), rigid (vs. soft), not shining (vs. shining) and, when dry, loosely appressed or sub-imbricate (vs. patent). All these characters are highly variable in *B. laetum* and can hardly be sufficient for the segregation of a separate species. Plants from dry places usually have shorter leaves and such short cells that their separation in a sterile state from *B. acuminatum* may be quite difficult. This resulted, among others, in the misinterpretation of the type of *Hypnum (Brachythecium) oxycladon,* (cf. Robinson & Ignatov, 1997).

The protologue of *B. digastrum* mentioned that the species is monoicous, but sexuality was not used to distinguish it from *B. laetum*, because *B. laetum* was also considered by those authors to be monoicous. Moreover, they poined out that Lesquereaux & James were wrong in describing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B. laetum as a dioicous species, and that it is in fact autoicous). It is not clear why the sexuality of these species was so confusing. One of the possible explanations could be that undeveloped 'branch buds' of *B. laetum* are superficially quite similar to perigonia. Soon after, the sexual condition of *B. laetum* was correctlt described by Grout (1897), who, however, did not totally reject the opinion of Carl Müller and Kindberg, and described *B. laetum* (sub. *B. oxycladon*) as 'dioicous, rarely monoicous'. All subsequent authors do not mention that a monoicous condition in this species is possible. At the same time, the characteristic of *B. digastum* as monoicous remains in Grout (1897), as well as in all subsequent publications (Grout, 1928; Robinson, 1962; Crum & Anderson, 1981, etc.), and was used as an additional or the main evidence for recognition of this taxon. The holotype of *Hypnum digastrum* has only female plants, thus leaving no character for separation it from *B. laetum*. And finally, one specimen from West Virginia with typical '*B. digastrum* appearance' was included in our molecular analysis and appeared within the clade with two 'typical *B. laetum*'.

5. **Brachythecium boreale** Ignatov sp. nov. Fig. 7, 9.

Species haec habitu, marginibus foliorum ubique serrulatis et inflorescentiis monoicis Sciuro-hypno oedipodio similis, sed tamen ITS sequentia et setis glabris genero Brachythecium, praecipue B. mildeano affinis, sed ab altero marginibus folii serrulatis, foliis abrupte acuminatis et cellulis alaribus magis delimitatis recedit.

Type: 'East Siberia, Republic Saha/Yakutiya, Ust-Maya District, Solnechny, Tom Creek, 60°14'N – 139°39'E, 650 m alt., on rotten log in *Larix* forest, 2.IX.2000 M. Ignatov 00-1074' (holotype in MHA).

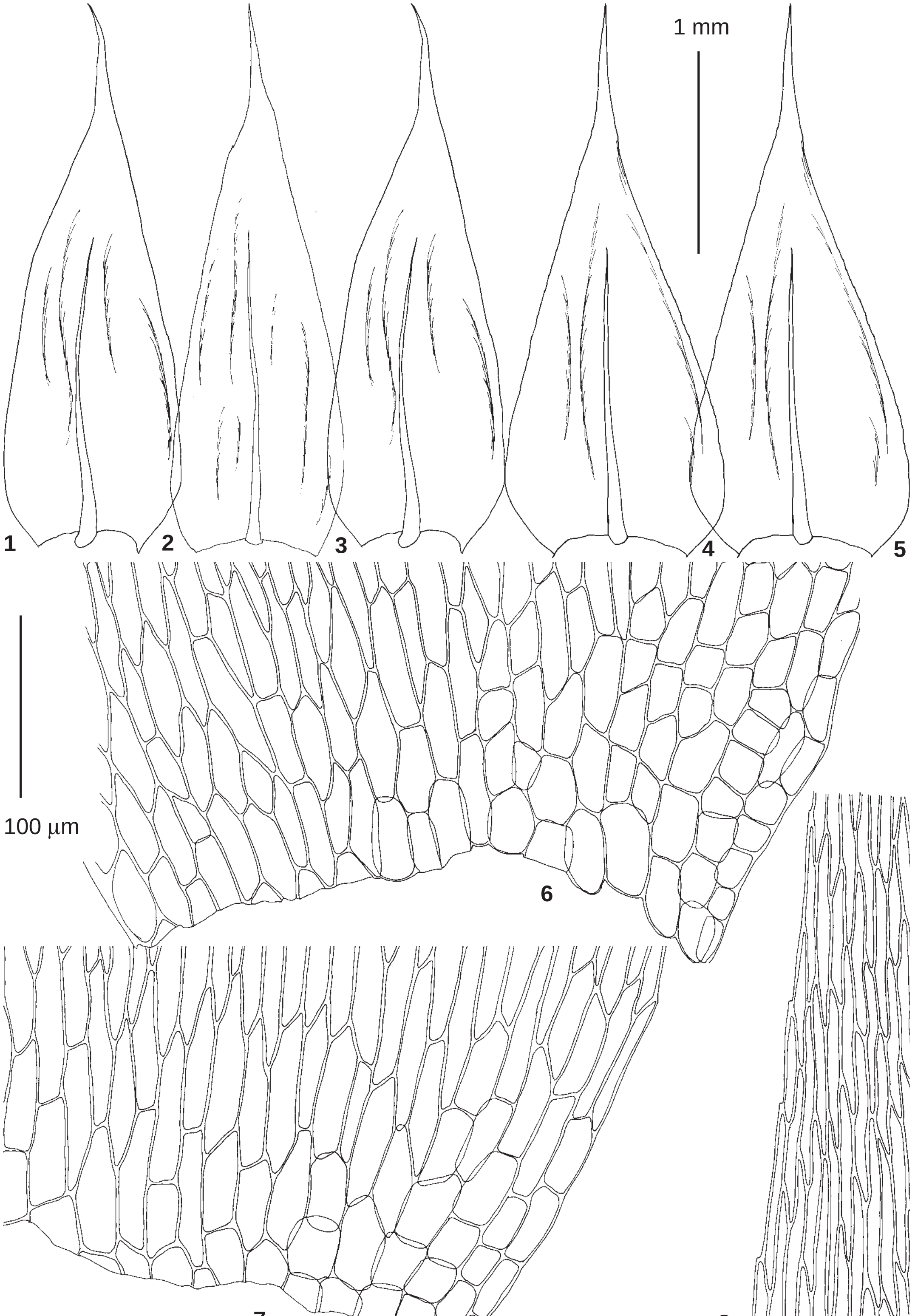
Plants medium-sized to moderately robust, in loose to moderately dense tufts, yellowish to brownish-green, in exposed habitats fading to stramineous. Stems to 6 cm, prostrate, rarely ascending, terete foliate, irregularly, often fasciculately branching; branches to 6 mm, straight, terete foliate. Stem leaves imbricate, erect to erecto-patent, 1.8-2.4 x 0.6-0.9 mm, ovate (broadest at about 1/7 of leaf length), abruptly acuminate, below the broadest point of leaf rounded to leaf insertion, narrowly and shortly decurrent, decurrencies rarely come out with detached leaves, concave, not to strongly plicate; margins plane or recurved in some areas, serrulate all around; costa slender, reaching 0.4-0.6 of leaf length, ending in a small spine or without it; laminal cells 45-80 x 6-8 μm; basal cells near costa broader and shorter in a few rows, large in leaf corners, forming an indistinctly delimited conspicuous, pellucid group. Branch leaves somewhat smaller, but otherwise similar. Sexual condition autoicous. Seta 15-20 mm, smooth. Capsule inclined to horizontal and curved, ca. 20 mm long, operculum conic, annulus separated at places. Spores ca. (18-)20-25 μm.

The species is the most common in the central Yakutia, growing on soil in *Larix* and *Alnus* forests, while in the Arctic it grows among willow shrubs. Most collections are from the forest belt (which has an upper limit at ca. 700 m in this region at 60°N), but occasional collections are from as high as 1600 m (in sheltered places near cliffs).

The northern populations of this species are superficially similar to *Sciuro-hypnum oedipodium* and sometimes even *S. curtum* due to the triangular and more or less spreading leaves. The autoicous sexual condition and enlarged basal cells also support such a relationship and the plants were first thought to be an unusual *Sciuro-hypnum* with a smooth seta. More southern populations, however, have longer and more concave leaves, resulting in a 'cirriphylloid' appearance; in habit they are somewhat similar to *B. udum* (see below), but that species has subentire leaves, a character that has been never observed in *B. boreale*.

Poorly developed *Brachythecium boreale* with relatively narrow leaves can be confused with *B. baicalense*, as both are autoicous, have enlarged cells in the leaf corners and serrulate leaf margin. In the presence of sporophytes, the former species can be recognized by large spores, 20-25 vs. 15-17 μm. When plants are sterile, the most reliable characters are relatively short cells in *B. boreale*, rarely longer than 80 μm while in *B. ba-*

Fig. 7. *Brachythecium boreale* (from the holotype, Yakutia, Ignatov 00-1074, MHA): 1, 9 – habit, dry; 2 – capsule; 3, 5 – mid-leaf cells; 4 – upper leaf cells; 6-8 – branch leaves; 10-11 – stem leaves; 12 – basal leaf cells. Scale bars: 5 mm for 1; 2 mm for 2, 9; 1 mm for 6-8, 10-11; 100 μm for 3-5, 12.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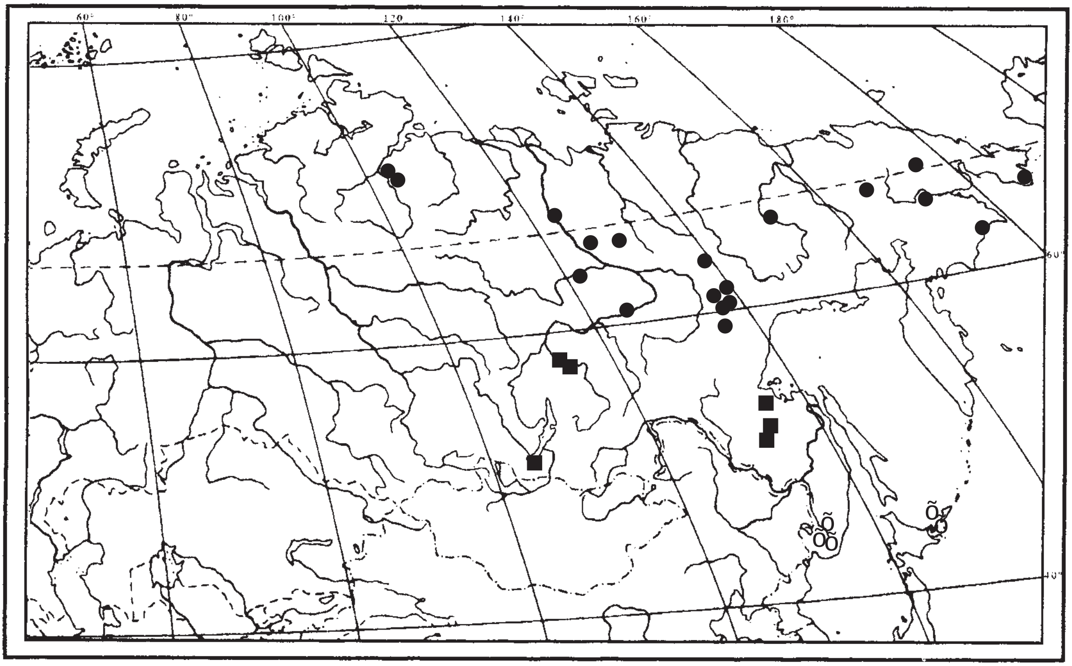


Fig. 9. Distribution of new species: *Brachythecium baicalense* (■), *B. boreale* (●), and *B. extremiorientale* (õ).

icalense many median laminal cells are longer than 100 µm. Also leaf serration is different: teeth in the former species are of moderate size and fairly regular along the leaf margin, whereas in the latter the marginn is sharply serrate. In addition the decurrency in *B. boreale* is inconspicuous compared with *B. baicalense* (cf. Figs. 3 and 7).

ITS data clearly indicate the position of *B. boreale* near *B. laetum, B. acutum* and *B. mildeanum*. The morphological justification of such a grouping is absent as these species have little in common (except for *B. acutum* and *B. mildeanum*).

Specimens examined: **Chukotksy Autonomous District**: Inachpak Cape, Afonina 29.VIII.1001 (MHA ex LE); Anadyr Distr., Yuzhny Pekulneiveem, Afonina 5.VIII.1979, 13.VIII.1979 (MHA ex LE); Anadyr Distr., Yuzhny Pekulneiveem, Afonina 22.VII.1979 (MHA ex LE); upper course of Tanyurer River, Afonina 15.VII.1979 (MHA ex LE); Baran'e Lake, Afonina 25.VII.1980 (MHA ex LE); Yablon River, Afonina 10.VIII.1982 (MHA ex LE). **Yakutia**: Khangalassky Distr., Lenskie Stolby, Ignatov 00-831, 00-790 (MHA); Kobyaisky Distr., upper course of Undyulyung River, Imgalan Creek, E.V. Baryshev 8.VII.1990 (SASY ex MHA); Tomponsky Distr.: Suntar-Khayata, 227 km from Khandyga to Oimyakon, Ivanova & Krivoshapkin, 18.VI.1999 (MHA); Ust-Maya Distr.: Khatun-Yuryakh Creek, Ignatov 00-1068, 00-1069 (MHA); Solnechnyy, Ignatov 00-1064, 00-1070 (MHA); Tarbagannakh Creek, Ignatov 00-1068 (MHA); Tom Creek, Ignatov 00-1066, 00-1074 (MHA); Yugorenok Creek, Ignatov 00-1058, 00-1059 (MHA); Verkhnekolymsky Distr., Kolyma River near Ochegino Creek mouth, E.I.Ivanova 31.VII.1992 (SASY ex MHA); Vilyuj Distr., A. Permyakova & L. Dobretsova 1958 (SASY ex MHA); Zhigansk Distr., lower course of Undyulyung River, E.V.Ivanova 24.VI.1990 (SASY ex MHA); Zhigansk Distr., Lena River near Kystatemka Creek mouth, L. Dobretsova 25.VI.1958 (SASY ex MHA). **Taimyr Municipal District**: Anabar Plateau, Medvezhya River, Fedosov 05-31, 05-650 (MW); Fomich River, Fedosov 06-604 (MW).

6. ***Brachythecium mildeanum*** and ***B. acutum***. Fig. 8.

The identity of *B. acutum* that was described from eastern North America was controversial. European authors either included *B. acutum* in *B. mildeanum* (Limpricht, 1896), or considered the former to be a variety of the latter (Podpera, 1954). Most North American publications, however, included *B. acutum* in *B. salebrosum* (Robinson, 1962; Crum & Anderson, 1981) .

Fig. 8. *Brachythecium acutum* (1-3, 7 – from Illinois, Allen, 6157, MO; 4-6, 8 – from New York State, Leonardi BB-50, MO): 1-5 – stem leaves; 6-7 – basal leaf cells; 8 – mid-leaf cells. Scale bars: 1 mm for 1-5; 100 µm for 6-8.

Grout (1928) discussed these two species, concluding that the North American *B. acutum* is distinct from the common and widespread European *B. mildeanum* in its usually loose foliage and flaccid branches (*B. mildeanum* has dense foliage and turgid branches). This is generally true, although the variation of both species overlaps. Also *B. acutum* is autoicous, and only rarely polyoicous, while *B. mildeanum* is usually described as polyoicous: plants can be synoicous, autoicous, and unisexual, and then usually male; however, many collections of both species are sterile, and many collections from Asian Russia and Western Europe are autoicous.

One more characteristic and constant feature of *B. acutum* is the unusually long seta, 3-4 cm long; most collections of *B. mildeanum* from Europe have setae 2(-2.5) cm, although Limpricht (1896) gave its length as 'usually 2(-2.5) cm, rarely 4 cm', and especially mentioned one locality where this *B. m.* var. *longiseta* Warnst. occurs. Plants with setae of 3.5-4 cm were issued in Bryophyta Danica Esc. #283 (coll. Hesselbo 3.IX.1907, LE!).

The study of herbarium collections from North America revealed that *B. acutum* is no less distinct from *B. salebrosum* than *B. mildeanum*. Certainly, all three species are extremely variable. Sometimes, especially in dry habitats, *B. acutum* has rather small cells in the leaf corners, resembling those of *B. salebrosum*. Similar variation is known in *B. mildeanum* as well. At the same time, most *Brachythecium* species growing in very wet or flooded habitats develop alar cells that are larger than usual; a good example of this was shown in cultivation experiments with *Brachythecium rutabulum* (Wigh,1975).

A rather constant character in *B. acutum* is the pattern of serration: each marginal cell ends in a small but distinct tooth, whereas in *B. mildeanum* the leaves are entire, subentire, or very rarely slightly serrulate, but without a regular pattern.

ITS data clearly demonstrate the close affinity of *B. acutum* with *B. mildeanum*, as well as their distant position from *B. salebrosum* (Fig. 1). However, if the latter statement seems rather clear (mostly due to good correspondence with morphology), the position of *B. acutum* and *B. mildeanum* in one common clade should probably not be interpreted in favor of their immediate synonymy. The analysis (Fig. 1) combined *B. campestre* with *B. complanatum*, *B. salebrosum* with *B. erythrorrhizon*, *B. brandegei*, and *B. glareosum*; and *B. turgidum* with *B. udum*; the species status of all or at least most of them is unquestionable.

The present data just point out the necessity of a thorough comparison between the species, and if they were confirmed as two independent species, then their distribution has to be elucidated, as the present observations do not exclude the occurrence of *B. acutum* in Europe.

In North America, *B. acutum* has a scattered distribution, mainly in the eastern regions, from Newfoundland and Nunavut southward to Missouri and Illinois, while in the mountains of the West it penetrates to the south into Utah and California (in the latter maybe recently introduced). It grows on wet soil and peat in fens or swamps, occasionally on rotten logs in swampy forests at 0–1000 m elev.; one collection from 3650 m in Colorado is also tentatively attributed to this species.

Selected specimen studied (with the state/province abbreviations of BFNA, specimens in MO, if otherwise not indicated): B.C. (Grout, North American Musci Perfecti,# 15), Man.(Hand 932), Nfld. (Buck 52529), Nunavut(Sutton, year 1930), Ont. (Macoun, Canadian Mosses #288), Que. (Dupret 2.I.1926), Sask. (Bourgeau, year 1985), Yukon(North American Mosses, R.S.Willams #716), Alaska (Trelease & Saunders 14.VI.1899), Calif. (Habeeb 1411, on lawn in Los Angeles), Colo. (Grout, North American Musci Perfecti 447; Hermann 27141), Del. (Reed 131703), Idaho (McFadden 19102), Ill. (Allen 6157), Ind. (Flowers 3040, NY), Iowa (Conard 23.VI.1942), Maine (Allen 27503), Mo. (Allen 26741), Mont. (Montana mosses, R.S. Williams 385), Nebr. (Churchhill 11878), N.J. (Austin, Musci Appalachiani 316), N.Y. (Grout, North American Musci Perfecti 213), N.Dak. (Ikenberry 218), Ohio (Environm. Control Group 5, 6-20.V.1972), Pa. (Rau, s.n.), S.Dak. (Allen 3601), Utah (Flowers 3244), Wyo (Nelson 1698).

Brachythecium acutum is distinct from *B. salebrosum* in having lax, homogeneous areolation across the leaf base (vs. differentiated small cells in leaf corners), straight and often conspicuously triangular leaves (Fig. 6: 4, 5), i.e., gradually tapered from the broadest point upward (vs. more or less falcate leaves that are usually narrow, and if broad, then acuminate), small but sharp teeth all along the leaf margins (vs. serrulate to serrate above), usually not or only weakly plicate leaves (vs. usually plicate), and unusually long setae, 3-4 cm long (vs. ca. 2 cm).

7. *Brachythecium rotaeanum*. Figs. 10-11.

Ignatov (1998) found that this species is very common in the Altai Mountains in Russia, whereas *B. salebrosum* is a rare in this region. Subsequent studies demonstrate that almost all collections from Asian Russia identified in herbaria as *B. salebrosum* belong to *B. rotaeanum*. The latter species is especially common in the hemiboreal zone of Asia, while *B. salebrosum* is rare in the eastern part of Asian Russia, having a scattered distribution mainly in boreal areas.

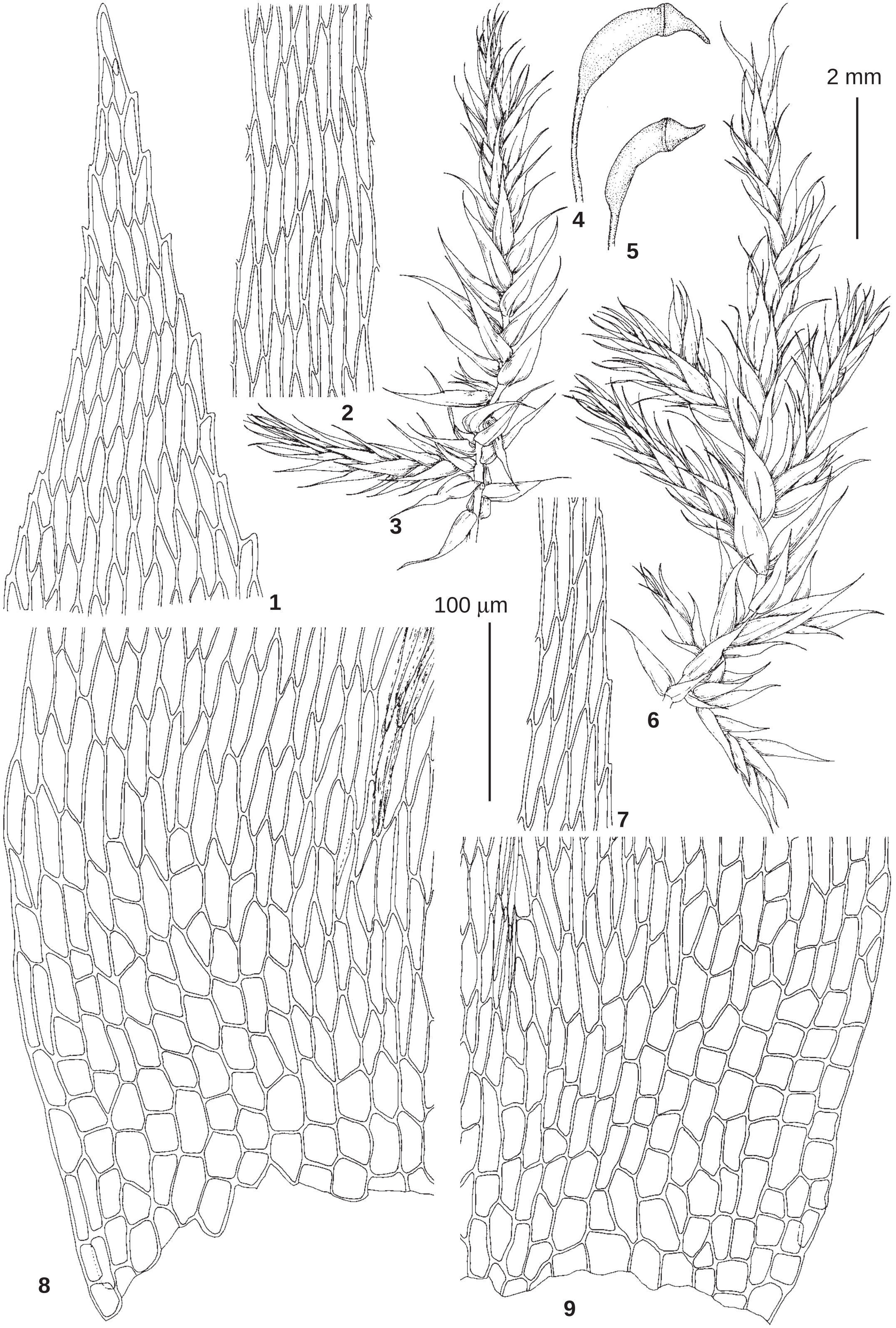
Most of the northern Chinese and Mongolian collections of *B. salebrosum* were also re-identified as *B. rotaeanum*. Finally, a similar situation was found also in eastern North America: *B. salebrosum* is more or less widespread in the West, but is a rare species in eastern North America, where it is confined to the northern areas (Newfoundland), while it is totally absent in the main part of the territory covered in Crum & Anderson's (1981) flora. Most of so-called herbarium collections from the latter area were sorted among *B. acutum* and *B. rotaeanum* (cf. Robinson, 1962). Being very common in the eastern North America, *B. rotaeanum* is occurs in western North America as well, but is uncommon there.

Selected North American specimen studied (with the state/province abbreviations of BFNA, specimens in MO, if otherwise not indicated): B.C. (Brinkman 15.V.1921 in McFadden Herb #19933), N.B. (Habeeb 21211), Ont. (Ireland 21876), Ala. (Earle & Baker, 4.X.1896), Alaska (Schofield 117749), Conn. (Allen 25996), Del. (Reed 126345), Fla. (Anderson & Crum 13678; Pursell 300MF5), Ill. (Schoil 319B), Ind. (Haines 160), Iowa (Allen 14973), Ky. (Risk 10233), La. (Reese 8172), Maine (Allen 10163, 21278 [Maine Mosses 70, as *B. salebrosum*]), Md. (Allen & Solomon 22938), Mich. (Ikenberry 16.VII.1936), Minn. (Holzinger 16.VI–7.VIII.1902), Mo. (Brant & O'Donnell 5343), N.Mex. (Weber B-44682), N.Y. (Redfearn 38177), N.C. (Anderson 12612 [Mosses of North America 921, as *B. salebrosum*]), N.Dak. (Ikenberry ND208-B), Ohio (Sullivant 1842), Tenn. (Clebsch 13148), Vt. (Grout 23.VII.1900 [North America Musci Pleurocarpi 127, as *B. salebrosum* var.]), Va. (Hunsucker 609), W.Va. (Gray 12.IX.1922), Wis. (Iltis 27848). Specimens from Russia are available from: http://gis-app.ict.nsc.ru/bio/search.php.

The fact that many collections of *B. rotaeanum* were identified as *B. salebrosum* is not surprising, as some handbooks did not separated them (e.g., Lawton, 1971; Nyholm, 1965), whereas other authors accepted *B. rotaeanum* with a rather narrow circumscription. For example, Crum & Anderson (1981) suggested that the most useful characters for separation of *B. rotaeanum* from *B. salebrosum* are the slightly curved and almost erect capsule and its smooth leaves. The latter seems to be based on observation mostly from southeastern U.S.A. where leaves of *B. rotaeanum* often have no plicae, but this is not a constant character throughout its range. Similarly, the slightly curved capsule is conspicuous in some populations, while its shape is variable in other, and sometimes all the sporophytes do not differ from those of *B. salebrosum*. Robinson (1962) separated *B. rotaeanum* from *B. salebrosum* mainly based on the homogeneous basal cells (parallels to *B. laetum*), and this approach is closer to the circumscription accepted here, although the basal cells should probably not be considered especially similar to *B. laetum* where they are small and opaque, while in *B. rotaeanum* they are rather large. When protected from direct light, *B. rotaeanum* has a pure green and slightly glaucous color, that is often useful for recognition of the plants in the field. This color is more similar to that of *B. laetum* (when it grows in shade which is not common) than to that of *B. salebrosum* (which is dirty yellow-green in moderate light to more dark-green in deep shade).

Thus, *B. rotaeanum* differs from *B. salebrosum* in: 1) an indistinctly delimited group of cells in the leaf corners vs. clearly delimited square group of small subquadrate cells; 2) often (but not always) slightly curved capsules vs. always more or less horizontal; 3) leaves lacking a tendency to be falcate vs. often more or less falcate-secund, at least to a some extent; 4) color (as described previously).

The variation of *B. rotaeanum* follows a somewhat different pattern than in *B. salebrosum*. In the latter the growth under xeric conditions usually results in a narrower leaves, whereas in *B. rotaeanum* growth under unfavourable conditions produces shorter leaves; the laminal cells are proportionally shorter as a consequence (as illustrated by Hedenäs (1998) for *Drepanocladus* species).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2 mm
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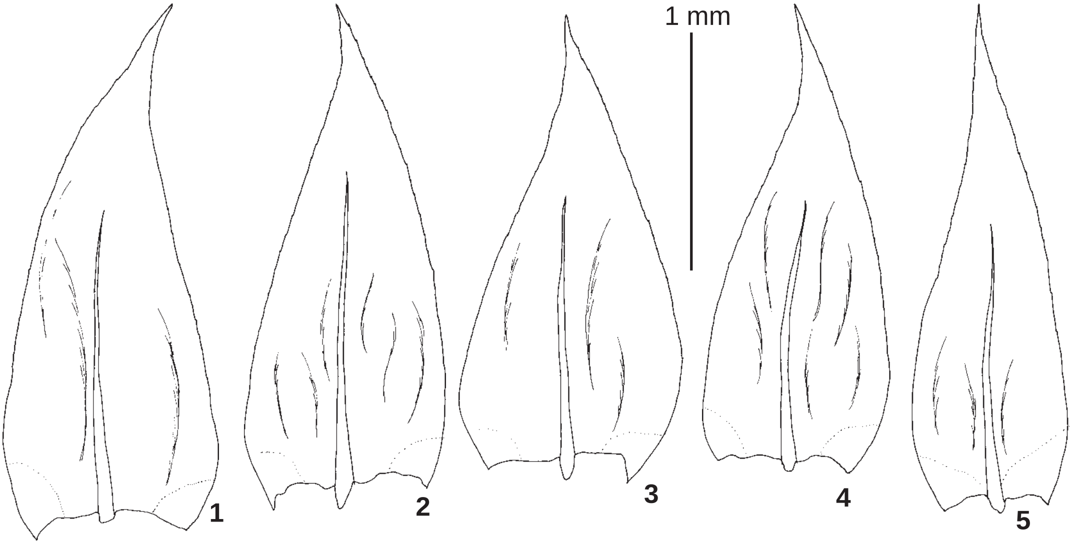

Fig. 11. *Brachythecium rotaeanum* (1-5 – from type of *Brachythecium rotaeanum*, Italy, FI); 1-5 – stem leaves. Scale bars: 1 mm for 1-5.

Fig. 10 (page 132). *Brachythecium rotaeanum* (1-4 – from type of *Brachythecium rotaeanum*, Italy, FI); 1-3, 8 – from Illinois, Allen, 6157, MO): 1 – upper leaf cells; 2, 7 – mid-leaf cells; 3, 6 – habit; 4-5 – capsules; 8-9 – basal leaf cells. Scale bars: 2 mm for 3-6; 100 µm for 1-2, 8-9.

A similar pattern of leaf shape variation is also noted in *B. laetum*, a species that was considered closely related to *B. rotaeanum* by Grout and Robinson. In addition, *B. salebrosum* has usually a rather consistently expressed leaf serration, whereas margins in *B. rotaeanum* are extremely variable in this character: usually they are serrulate to more strongly toothed in the acumen, but in many collections leaves along one shoot vary from subentire to coarsely serrate distally; however, even in such cases, at least some leaves have a rather distinct serration in their acumina.

In Asian Russia there is no problem recognising *B. rotaeanum* and *B. salebrosum*, and about 90% of the collections can be identified under a stereomicroscope (the latter species is rare and not especially variable in the area). In Europe, where *B. rotaeanum* is rare and *B. salebrosum* is common and extremely variable, it is more difficult to separate the two, which explain why most of European authors agree that this is a variety and not a species.

Worldwide revisions leave no doubt that *B. rotaeanum* is a valid species. Molecular data support this as well, because five specimens from distant localities (Ural Mountains, Caspian Sea area, Altai in cental Asia, Chukotka, and eastern North America), all have the same two substitutions in ITS2 and form a clade (Figs. 1, 2).

The species here called *Brachythecium rotaeanum* is often accepted under the name *B. capillaceum* (F.Weber & D. Mohr) Giac., Atti Ist. Bot. “Giovanni Briosi” ser. 5, 4: 268. 1947; – *Hypnum salebrosum* var. *capillaceum* Web. et Mohr, Bot. Taschenbuch 313. 1807. The type of this name is absent in B (letter of Ludwig Martins of 20 Dec 2007), and before its lectotypification it is safest to use the name *B. rotaeanum*, the type of the latter is illustrated here (Figs. 10-11) and clearly agrees with the present circumscription.

8. ***Brachythecium udum***.

This species was described from Scandinavia and according to Hedenäs (pers. comm.) is rather common there in mountain areas. It is a northern species, probably absent in central Europe, and most of European authors did not recognize it as a separate species, but as a variety of *B. mildeanum* (Podpera, 1954). Both species are growing in wet places, have mostly upright shoots, entire or subentire leaf margins, and more or less homogeneous basal leaf cells. However, in contrast to *B. mildeanum, B. udum* is dioicous and has less evenly tapered leaves, so their shape is acuminate rather than narrowly acute. Cells in the leaf corners can

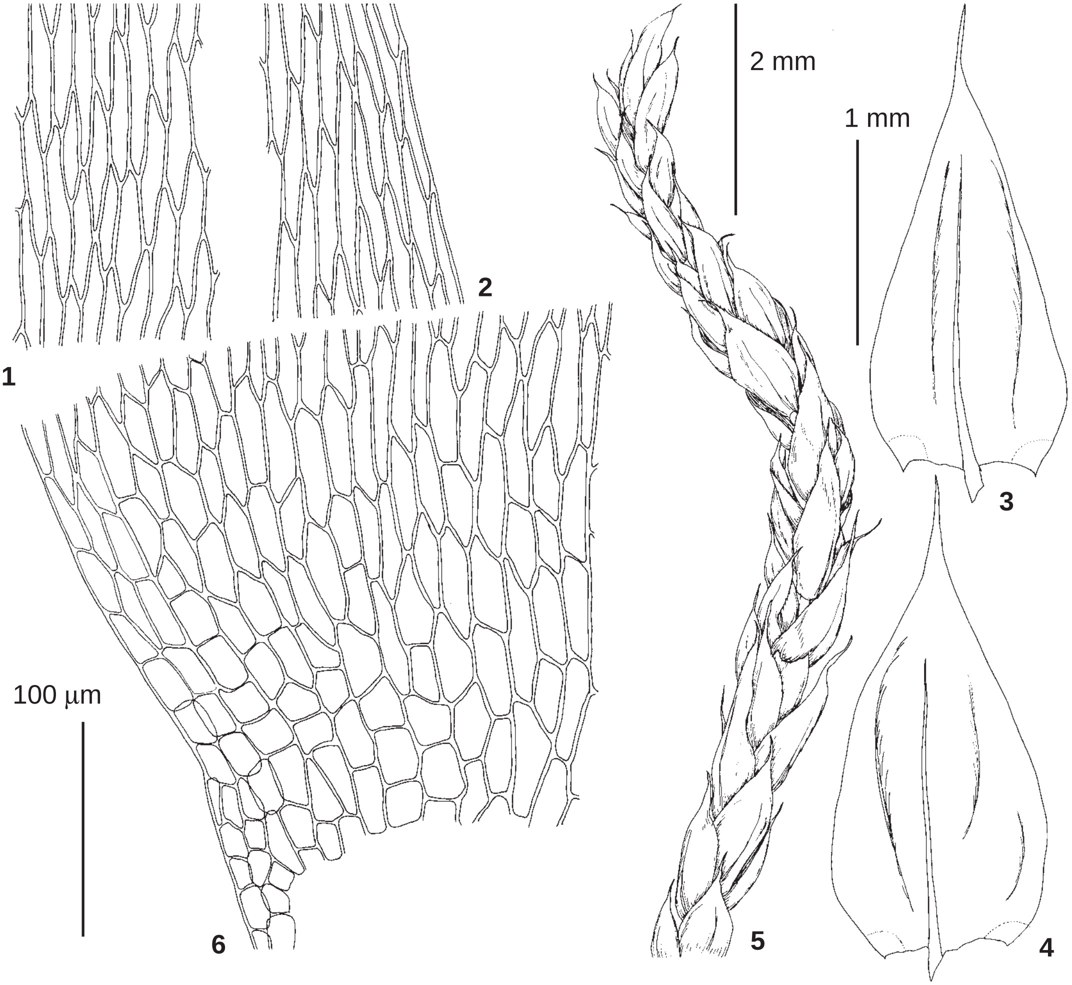

Fig. 12. *Brachythecium brandegei* (from U.S.A., Colorado, Weber B-114286 (MHA ex COLO); 1-2 – mid-leaf cells; 3-4 – leaves; 5 – habit; 6 – basal leaf cells. Scale bars: 2 mm for 5; 1 mm for 3-4; 100 µm for 1-2, 6.

be somewhat smaller than the juxtacostal cells, or somewhat larger, depending on the environmental conditions.

In Siberia, however, this species is much more common in relatively wet places in cold environments, often in high mountains near snowfields, along brooks, in tundra, etc. Some specimens may pose a question of their distinction from *B. mildeanum* (especially because of difficulty of sex identification in northern populations where gametangia are often absent). Ignatov (1998) failed to sort them based on morphology in the Altai region. However, further studies confirm their distinction and the present phylogenetic analysis places it in a rather distinct position from *B. mildeanum* within the *Brachythecium salebrosum*-group; one specimen of *B. turgidum* is in the same clade (Fig. 1). Both *B. udum* and *B. turgidum* differ from species of the *B. salebrosum*–group by the only one substitution in ITS2, but this substitution is consistently present in all 6 specimens studied.

Brachythecium udum differs from *B. turgidum* in: (1) sexual condition dioicous vs. autoicous sexual condition; 2) not or only moderately incrassate basal cell walls vs. incrassate to strongly so, and conspicuously pitted; 3) laminal cell walls 1.0-1.5 µm thick vs. 2.0-2.5 µm thick; 4) little or moderately plicate leaves vs. strongly plicate. In addition, *B. turgidum* has a usually easily-recognizable habit: plants are robust and have a more or less rich golden color, while *B. udum* has the size

Fig. 13. *Eurhynchiastrum pulchellum var. barnesii* (Canada, British Columbia, Schofield 85054, MHA ex UBCU, specimen used for sequensing) and *E. pulchellum* var. *pulchellum* (Tver Province, Ignatov, 13.VIII.1996, MHA): habit. Scale bar 2 mm for 1-2.

of 'average' *Brachythecium* species and is yellowish-green, similar to the 'average' *B. salebrosum* or *B. mildeanum*. When optimally developed, *B. turgidum* can hardly be misidentified as *B. udum*, but poorly developed plants of the former may be confusing.

Brachythecium boreale is a widespread species in the area where *B. udum* is also common, and superficially they are often similar. Their distinctions includes, first of all, a leaf margin that is serrulate in *B. boreale* and (sub)entire in *B. udum*. In addition, the presence of sporophytes or both perichaetia and perigonia in *B. boreale* usually allow to confirm the autoicous sexual condition, while perigonia in *B. udum* were never found in Siberia.

In addition to northern Eurasia, *Brachythecium udum* has been found in Steere's collections from Noluck Lake, Alaska, and apparently occurs also in northern Canada.

Selected specimens examined from Russia: **Khabarovsk Territory**: Verhnebureinsky Distr., Upper Bureya River, 1600 m, Ignatov 97-169 (MHA); 1700 m, Ignatov 97-167 (MHA); **Altai Republic**: Karakem River, 2300 m, Ignatov 0/379 (MHA); 2700 m, Ignatov 0/1664 (MHA); 2250 m, Ignatov 0/2037 (MHA); **Yakutia**: Algama River, tributary of Gonam River, 1420 m, Garashchenko 31.VIII.1970 (IRK ex MHA); Ust-Maya Distr., Allakh-Yun, 600 m, Ignatov 00-893 (MHA); Verkhnekolymsky Distr., Kolyma River 40 km downstream from Zyryanka, E.I.Ivanova 30.VII.1992 (SASY ex MHA).

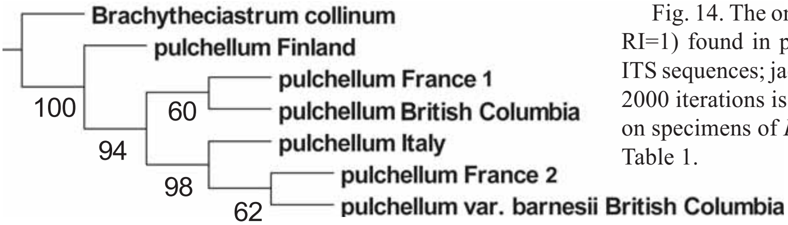

Fig. 14. The only shortest tree (L=50, CI=1, RI=1) found in parsimony ratchet analysis of ITS sequences; jackknife support calculated for 2000 iterations is shown below branches. Data on specimens of *Eurhynchiastrum* are given in Table 1.

9. **Brachythecium brandegei** (Austin) H. Rob. (*Cirriphyllum brandegei* (Austin) Grout). Fig. 12.

This species was described from the high mountains of Colorado and is still known from a small area near Summit Lake at Mount Evans in Park Co., Colorado, at 3850-3900 m alt., growing on cliffs and wet soil in mountain tundra. It was issued in exsiccates Crypt. Exs. Museo Hist. Natur. Vindobonensi, #4165, with the label indicating elevation as 4200 m. This is probably a result of inaccurate transmission of 12700 feet into meter, as according to the same label the species was collected on cliffs at the lake shore, which is at 3850 m.

It is characterized by erect growth, more or less julaceous foliage, concave leaves with short acumina, and lax areolation: the laminal cells are 40-80 x 8-12 µm; the basal cells are rather large and homogeneous across the base, and the cells in the leaf corners are somewhat differentiated, being moderately thin-walled and forming pellucid or moderately opaque alar groups of somewhat shorter cells.

Brachythecium brandegei is most similar to *B. udum*, but the single specific substitution that differentiates *B. udum* from the species around *B. salebrosum* is absent in the former species and it is found in the species more closely related to *B. salebrosum* and *B. erythrorrhizon* (cf. Fig. 1). However these two species have narrower cells, alar groups composed of small cells, the more or less falcate leaves, which suggest keeping *Brachythecium brandegei* as a separate species.

10. ***Eurhynchiastrum pulchellum*** var. ***barnesii***. Fig. 13.

The genus includes one species, *E. pulchellum*, that is universally accepted and several other taxa that are accepted as species by some authors and as infraspecific taxa by others. Some of them, for example, *E. pulchellum* var. *praecox*, seem to be ecology-dependent and occur throughout the range of this species in especially dry environments where plants develop morphotypes with closely julaceous foliage due to strongly appressed leaves that are shorter and more obtuse.

The North American flora, however, includes at least three other morphotypes that are beyond the variation of the species in at least the Russian territory (and apparently Eurasia as a whole). One of them is '*Eurhynchium strigosum* var. *scabrisetum* Grout'. It has seta surface at places with scattered shallow raisings, although far from definite mammillosity. Nevertheless, nothing similar was reported from the area outside of Nova Angliae. However, due to rather inconspicuous mammillosity and the difficulty of identifying material by this character, this variety is not accepted in the modern literature.

A second variety, *E. pulchellum* var. *robustum* (Roll) Jennings, occurs in southeastern North America and differs primarily in the larger size of plants. The largest plants observed (Georgia, Harper, 2053g, MO) have stem 5 cm long, branches 10 mm, stem leaves up to 1.4 x 0.75 mm, and branch leaves up to 1.25 x 0.5 mm. However, this variety is also usually not widely accepted because of the very gradual transition to the common morphotype that usually has stems 2-4 cm, branches 3-5 mm, stem leaves 0.5-1.0 x 0.4-0.7 mm, and branch leaves 0.2-0.8 x 0.2-0.4 mm. Our observations confirm the indistinctiveness of this taxon, so it hardly merits formal recognition, at least until its distinctiveness will be demonstrated.

The third taxon is especially distinct and it is accepted here: ***Eurhynchiastrum pulchellum*** var. ***barnesii*** (Renauld & Cardot) Ignatov, comb. nov. – *Eurhynchium strigosum* var. *barnesii* Renauld & Cardot, Revue Bryologique 15: 72. 1888.

This variety occurs in the mountains of western North America (Montana, British Columbia, Alberta). The largest specimen seen by us has stems to 8 cm, branches to 16 mm, stem leaves up to 2.6 x 1.8 mm and branch leaves 1.5 x 0.75 mm. Branch leaves of this size become longitudinally plicate. In addition to morphology, its distribution also supports this separation. It occurs in the area where many North American endemic and subendemic species of Brachytheciaceae occur (*Sciuro-hypnum hylotapetum* (N.L. Higinb. & B.L. Higinb.) Ignatov & Huttunen, *S. oedipodium*, (Mitt.) Ignatov & Huttunen, *Brachytheciastrum leibergii*(Grout) Ignatov & Huttunen, *Kindbergia oregana* (Sull.) Ochyra, *Homalothecium nevadense*(Lesq.) Renauld & Cardot, etc.). Comparison of ITS, however, does not support a strong distinction from other populations of the species, although this conclusion is a preliminary one. It is likely that further studies of ITS haplotype distribution may show local differentiation and paths of migration, but the reproductive isolation of them seems needs further studies.

11. ***Sciuro-hypnum delicatulum*** (Flowers) Ignatov, comb. nov. (basionum: *Brachythecium delicatulum* Flowers, Bryologist 76: 287. 1973). This peculiar moss is still known only from the type locality in Utah (Flowers, 1973). It is apparently not allied to any group of *Brachythecium*, but most likely related to *Scuiro-hypnum plumosum*, thus the combination is suggested to consider it within *Scuiro-hypnum*.

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