

*GRIMMIA BERINGIENSIS* SP. NOVA (GRIMMIACEAE, BRYOPHYTA),  
A PUTATIVE CASE OF INTRAGENERIC HYBRIDIZATION

*GRIMMIA BERINGIENSIS* SP. NOVA (GRIMMIACEAE, BRYOPHYTA),  
ВОЗМОЖНЫЙ МЕЖРОДОВОЙ ГИБРИД

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Abstract

Molecular phylogenetic analysis of the nuclear ITS revealed four monophyletic entities within the group of species closely related to *Grimmia leibergii*–*G. jacutuca*, often considered within a separate genus *Dryptodon*. This group includes: (1) *G. jacutica*, widespread species in northern Asia and penetrating to Alaska in North America; (2) *G. beringiensis*, sp. nov., known from several localities in Chukotka; (3) *G. arcuatifolia*, a species of the northern part of the Pacific Northwest, from British Columbia to Alaska; and (4) *G. leibergii*, that occurs in a more southern range, from California to British Columbia. Three out of these four species fully agree with their position in *Grimmia* subg. *Dryptodon* (or genus *Dryptodon*), by morphology, ITS and also chloroplastic *trnL*, whereas *G. beringiensis* has *trnL*-F sequence almost identical with *G. elatior* from the subg. *Grimmia*. This is the second case of incongruence in topology between trees based on nuclear and chloroplastic markers in *Grimmia* s.l. It differs from the previous one, with *G. tergestina*, in that the putative hybridization involves a more distantly related taxa, sometimes classified in separate genera, *Dryptodon* and *Grimmia*. The broad circumscription of the *Grimmia* seems to be more appropriate to avoid nomenclatural problems.

Резюме

Анализ последовательностей ITS1-5.8S-ITS2 ядерной ДНК позволил выявить четыре независимых таксона среди образцов, относящихся к группе близких видов *Grimmia leibergii*–*G. jacutuca*, часто рассматриваемых в пределах рода *Dryptodon*. К этой группе относятся: (1) *G. jacutica*, широко распространенная на севере Азиатской России и проникающая на Аляску в Северной Америке; (2) *G. beringiensis* sp. nov., известная из нескольких местонахождений на Чукотке; (3) *G. arcuatifolia*, встречающаяся на севере западного побережья Северной Америки, от Британской Колумбии до Аляски; (4) *G. leibergii*, распространенная несколько южнее на западе Северной Америки, от Калифорнии до Британской Колумбии. Положение трех видов в *Grimmia* subg. *Dryptodon* (или в роде *Dryptodon*) вполне подтверждается их морфологическими особенностями, а также данными по последовательностям ITS ядерной ДНК и *trnL*-F хлоропластной ДНК; в то же время последовательности *trnL*-F у *G. beringiensis* оказались очень похожими на таковые у *G. elatior*. Это второй случай несогласованности топологий молекулярно-филогенетических деревьев, построенных по ядерным и хлоропластным маркерам, в роде *Grimmia* s.l. Предположительно этот таксон имеет гибридогенное происхождение, он образовался в результате гибридизации между не близкородственными видами, иногда относимыми даже к разным родам. Этот случай свидетельствует в пользу помещения всех видов в род *Grimmia*, что поможет избежать номенклатурных проблем.

KEYWORDS: *Grimmia*, mosses, ITS, *trnL*-F, infrageneric hybridization

INTRODUCTION

The genus *Grimmia* recently received a considerable attention of taxonomists. Three revisions were published in a world-wide scope (Muñoz & Pando, 2000; Greven, 2003; Maier, 2010) and a number of regional treatments have covered expanded territories, including Russia (Ignatova & Muñoz, 2004), Central Europe (Greven, 1995;

Maier & Geissler, 1995), China (Cao *et al.*, 2003), Japan (Deguchi, 1978), Himalayas (Maier, 2002, 2010), U.S.A. and Canada (Hastings & Greven, 2007), Latin America (Muñoz, 1999b), and Neotropics (Delgadillo-Moya, 2015).

In the course of the preparation of a taxonomic revision of the genus *Grimmia* in Russia, one species was

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found to be undescribed, despite it is a quite widespread taxon. It was described under the name *G. jacutica* Ignatova, Bednarek-Ochyra, Afonina & J. Muñoz (Ignatova *et al.*, 2003). Its range covers ca.4000 km in Siberia, from Yenisei River and Baikal Lake to Chukotka, and also penetrates to Alaska. At the same time, several collections from Chukotka were noticed as being somewhat different, approaching in some characters to *G. leibergii* Paris. The latter species was described from California and was thought to be the closest relative of *G. jacutica* (Ignatova *et al.*, 2003). The Chukotkan specimens, however, were left without taxonomic recognition of any level.

Hastings & Greven (2007) reduced *G. jacutica* into the synonymy of *G. leibergii*, arguing that it is a very polymorphic species in Western North America, and characters separating it from *G. jacutica* are not enough stable to accept these species as distinct. On the other hand, E. Maier revised some collections of *G. jacutica* from Russia, including the holotype, and referred it to *G. decipiens* (Schultz) Lindb. (determinations in MW herbarium).

Finally, it is worthy mentioning that *G. leibergii* itself was for a long time treated as merely a synonym of *G. trichophylla* Grev. (Lawton, 1971; Anderson *et al.*, 1990), a species that has 28 synonyms according to Muñoz & Pando (2000).

*Grimmia leibergii* was resurrected from the oblivion by Muñoz (1999 a) together with another forgotten North American species, *G. arcuatifolia* Kindb., which is closely related to the former species. Hastings & Greven (2007) accepted both *G. leibergii* and the species called by Muñoz *G. arcuatifolia*, although using another name for the latter, *G. attenuata* (Müll. Hal. & Kindb.) Kindb. The usage of the earlier name *G. arcuatifolia*, was rejected because Hastings & Greven (2007) referred it to *G. lisae* De Not., without any discussion. The illustrations of the type specimen of *G. arcuatifolia* presented by Muñoz (1999 a), however, better agree with the plants called *G. attenuata* by Hastings & Greven (2007), rather than with *G. lisae*. In particular, the multistratose costa and, especially, thick-walled and porose basal juxtacostal cells are not characteristics of *G. lisae*. For this reason we follow Muñoz (1999a) in synonymization of *G. attenuata* with *G. arcuatifolia* and use of the latter name.

As the DNA sequences provide now a powerful method for solving taxonomic puzzles, we applied it to check which opinion corresponds more to the molecular barcoding patterns. In Grimmiaceae it was successfully applied to the whole family (Tsubota *et al.*, 2003; Hernández-Maqueda *et al.*, 2008b), *Grimmia* (Hernández-Maqueda *et al.*, 2008a, b; Streiff, 2006), *Coscinodon* (Ignatova *et al.*, 2008), *Schistidium* (Goryunov *et al.*, 2007; Ignatova *et al.*, 2010; Milyutina *et al.*, 2010), and *Racomitrium* (Larraín *et al.*, 2013; Stech *et al.*, 2013). We used ITS and *trnL*-F as markers, as they proved to be maximally useful in species-level taxonomy of Grimmiaceae in the above mentioned studies.

## MATERIAL AND METHODS

### Sampling strategy

The sampling was focused on rather confirming or rejecting the conclusions made by taxonomists using the classical morphological approach on the identity of *Grimmia jacutica* and *G. leibergii*. A number of specimens labeled with the latter name, however, appeared to represent two genetic entities at the stage of preliminary aligning. One of them, after additional studies, has been referred to *G. arcuatifolia*, which is morphologically similar and fairly confusing with *G. leibergii*. Thus we tried to obtain data for both of them.

Deviated Chukotkan plants, mentioned in the original description of *G. jacutica*, were represented by rather few samples. Available material for them was rather old, of 1970s, with few specimens of early 1980s, when Chukotka was actively explored by bryologists. DNA was successfully amplified only from three specimens, providing two sequences of ITS and two of *trnL*-F.

Specimen data and Genbank accession numbers are given in Appendix 1.

Total genomic DNA was extracted from herbarium specimens using the NucleoSpin Plant DNA extraction kit (Macherey-Nagel, Germany). The chloroplast *trnL*-F was amplified with primers C (CGA AAT CGG TAG ACG CTA CG) and F (ATT TGA ACT GGT GAC ACG AG) and sequenced with the same primers (Taberlet *et al.* 1991). The nuclear ITS1-5.8S-ITS2 region was amplified with primer ITS1(CC GTA GGT GAA CCT GCG) and ITSB (GAT ATG CTT AAA CTC AGC CTA CG) and sequenced with the same primers. In cases of short reading, we additionally used internal primers: p2(GCT GCG TTC TTC ATC GAT GC) and p3(GCA TCG ATG AAG AACGCA GC) for sequenced ITS1-5.8S-ITS2 region (White *et al.*, 1990). PCR was conducted in 20 IL aliquots containing 4 IL Ready-to-Use PCR MasterMIX based on 'hot-start' SmarTaq DNA polymerase (Dialat Ltd., Moscow, Russia), 13 IL deionized water, 5 pmol each primer and c. 1.5–2.0 ng template DNA in an MJ Research PTC-220 DNA Engine Dyad Thermal Cycler (BioRad Laboratories, Hercules, CA, USA). PCR program: for both region was the same: 94°C –3'(initial denaturation), 58°C – 30", 72°C – 1'; then 32 cycles: 94°C –30", 58°C – 30", 72°C – 1', and 72°C – 5' (final extension step). Amplification products were separated on a 1% garose gel in 19 TAE buffer with ethidium bromide staining and purified using the MinElute Gel Extraction Kit (Qiagen, Hilden, Germany). Purified PCR products were sequenced using the ABI PRISM BigDye Terminator v. 3. kit (Applied Biosystems) and further analysed on an ABI PRISM 3730 automated sequencer (Applied Biosystems, Waltham, MA, USA) at the 'Genom' Common Facilities Centre (Mocsov).

Sequences were aligned in Bioedit (Hall, 1999), using built-in aligning program ClustalW (Hall, 1999), with subsequent manual correction.

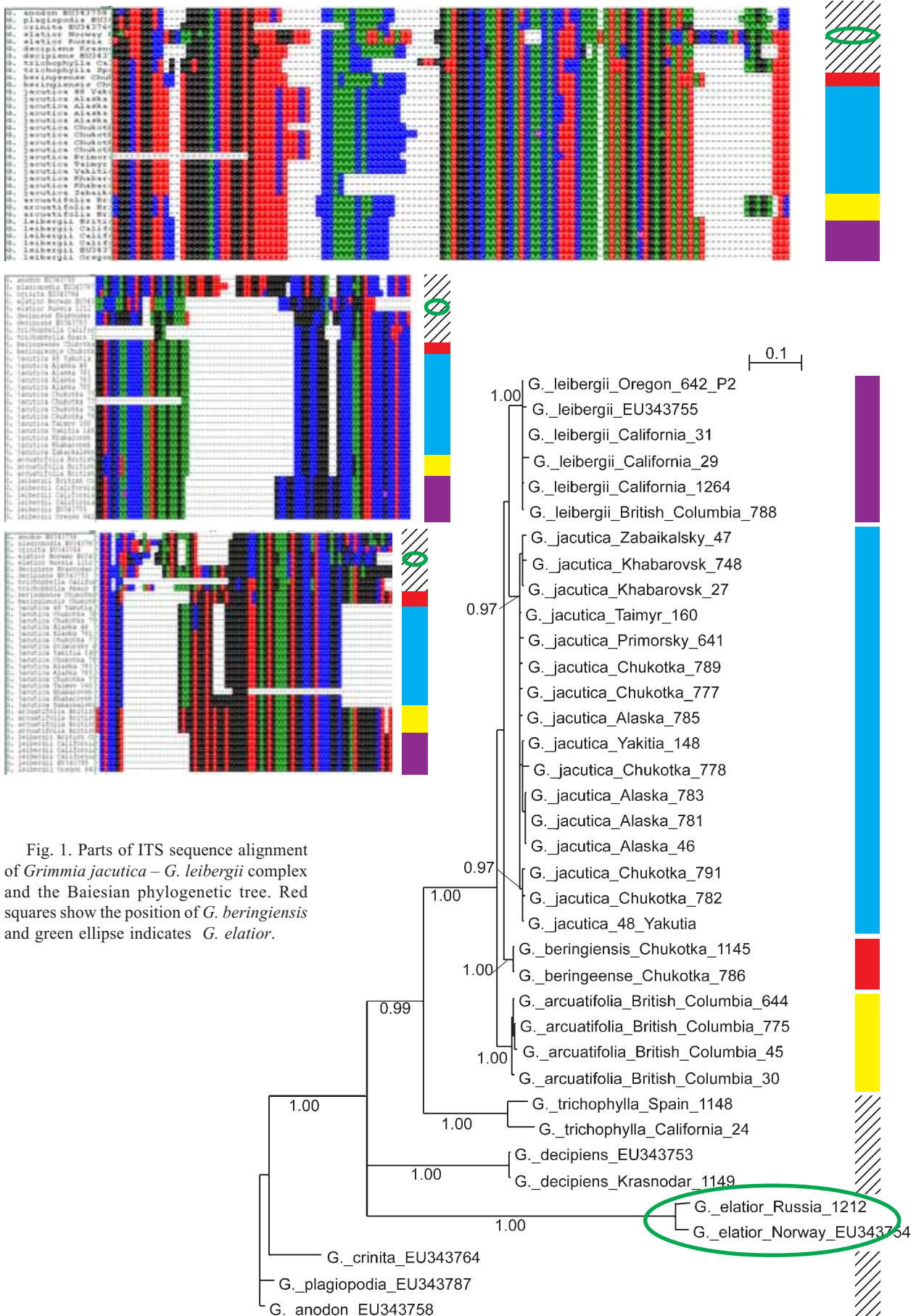


Fig. 1. Parts of ITS sequence alignment of *Grimmia jacutica* – *G. leibergii* complex and the Bayesian phylogenetic tree. Red squares show the position of *G. beringiensis* and green ellipse indicates *G. elatior*.



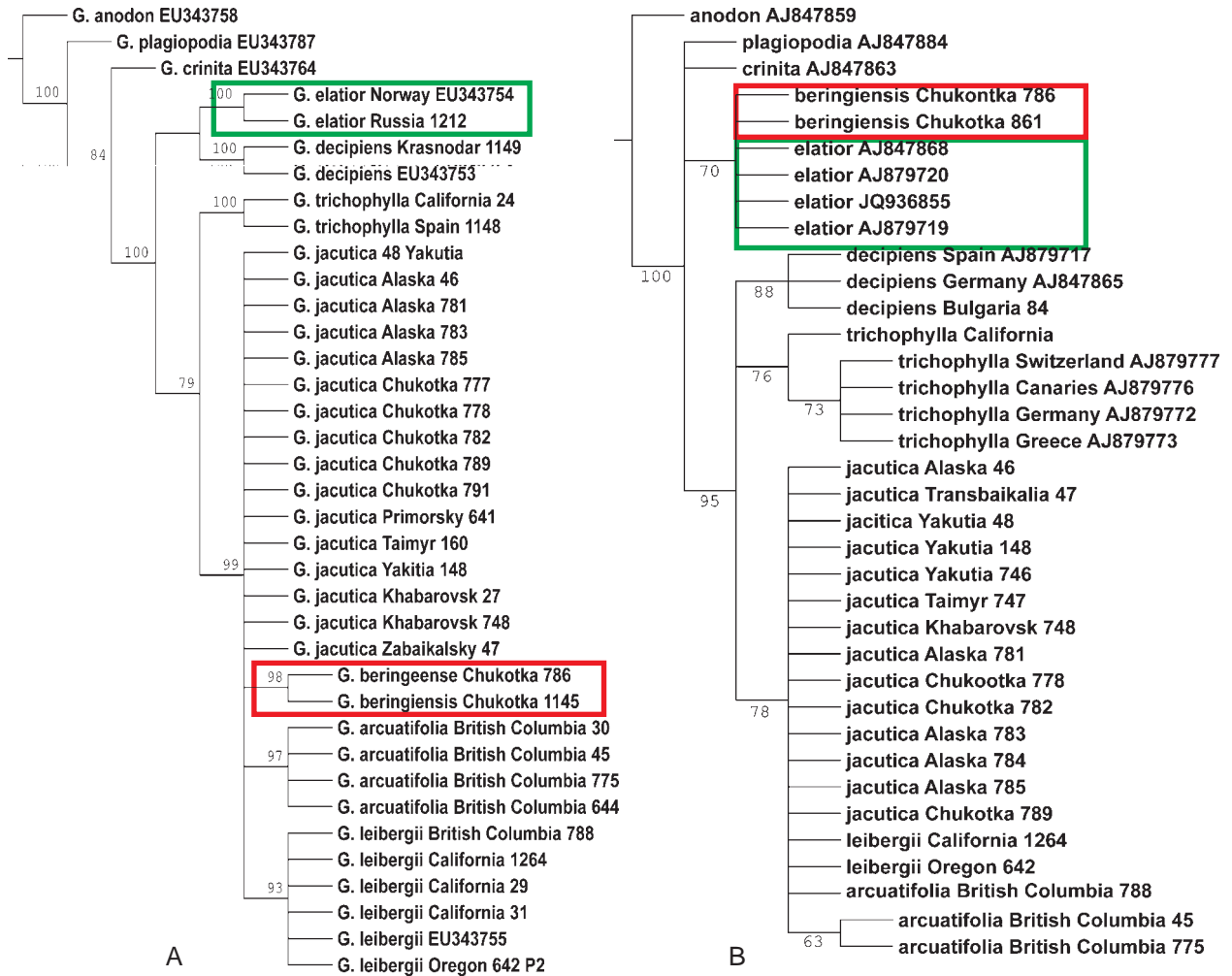
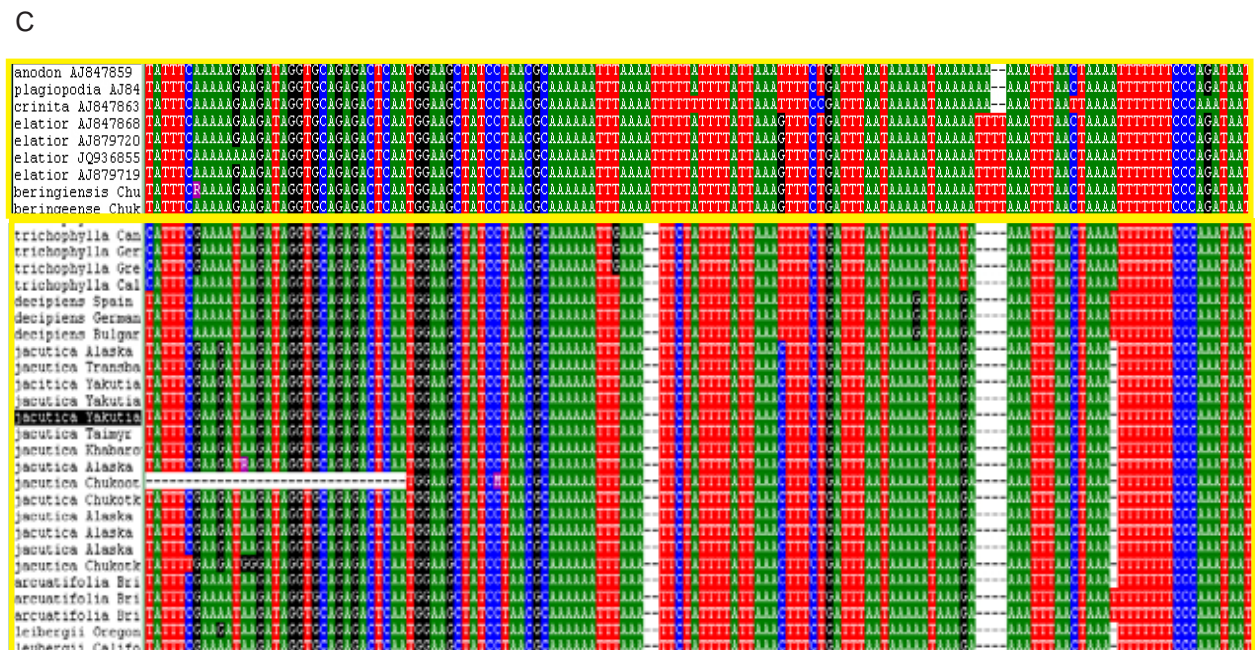


Fig. 2. Maximum parsimony phylogenetic trees based on nuclear ITS (A) and chloroplastic *trnL-F* sequences, and a part of *trnL-F* sequence alignment (C) of *Grimmia jacutica* – *G. leibergii* complex. In the trees, red frames show the position of *G. beringiensis* and green of *G. elatior*. In the alignment, yellow frames separate *Grimmia* (above) and *Dryptodon* (below).



The incongruence in ITS and *trnL-F* became apparent from the preliminary alignments (Figs. 1-2), thus the analysis for these two regions was done independently. Trees for both regions were rooted on *Grimmia anodon*, and few other species were added, including *G. decipiens* and *G. trichophylla* (which were recently thought to be identical with *G. jacutica* and *G. leibergii*, correspondingly).

Maximum parsimony (MP) analyses were performed in Nona (Goloboff, 1994) in Winclada shell (Nixon, 1999). Gaps were treated as missing data, not coded. Bootstrap trees were calculated in Nona for 1000 iterations.

Bayesian analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) with ITS divided into three partitions (ITS1, 5.8S rRNA, ITS2), with GTR+G+I model, for ITS1 and ITS2, and HKY+I model for 5.8S rRNA coding region. One compartment for the *trnL-F* region was analysed with HKY+I model. The AIC criterion as implemented in MrModeltest 2.2 (Nylander, 2004) was used to determine the best fitting models. Three parallel runs were implemented, each with five chains and 10,000,000 generations (25% burnin), a “temp” parameter value of 0.15 and parameters unlinked between partitions.

#### RESULTS

Bayesian analyses (Fig. 1) found a maximal support for the group *G. jacutica–G. leibergii*. Moreover, the maximal support was obtained for clades composed of *G. arcuatifolia*, *G. leibergii*, and specimens from the Chukotka Peninsula (Fig. 1), and the high support was found also for *G. jacutica* (PP=0.97). The branch lengths for these four subclades were contrastingly shorter than the lengths for species, e.g. *G. trichophylla* and *G. decipiens*.

MP analyses of ITS (Fig. 2A) recovered a quite similar topology, with the high support (BS=99) for *G. jacutica–G. leibergii* clade. This clade includes polytomy of specimens of *G. jacutica* and three nested clades, same as in Bayesian tree, i.e., *G. arcuatifolia*, *G. leibergii*, and specimens from the Chukotka Peninsula, with a rather high support (BS=97, 93, and 98, correspondingly).

The *trnL-F* analyses, both Bayesian (not shown) and MP (Fig. 2B), resulted in the topology similar to ITS tree for almost all taxa, but with one exception. The Chukotkan specimens were found in common clade with *Grimmia elatior* Bruch ex Bals.-Criv. & De Not. (with moderate support, BS=70), not within *G. jacutica–G. leibergii* clade, where they were resolved in ITS analyses. At the same time, *G. jacutica–G. leibergii–G. arcuatifolia* clade was moderately supported (BS=78) in the MP analysis of *trnL-F* (Fig. 2B); and with *G. decipiens* and *G. trichophylla* it forms a larger clade of high support (BS=95).

*Grimmia elatior* was resolved in ITS analyses either in polytomy with *G. decipiens* and clade that includes *G. trichophylla+G. jacutica–G. leibergii*-clade (Fig. 1, ), or in unsupported clade with *G. decipiens*, and their common clade was sister to *G. jacutica–G. leibergii* clade + *G. trichophylla* (Fig. 2A). The latter topology was the same

in *trnL-F* analyses, with the only difference in the position of Chukotkan plants (Fig. 2A, as ‘*beringiensis*’), which were sharing polytomy with specimens of *G. elatior*.

#### DISCUSSION

The first aim of the study was to solve the taxonomic status of *G. jacutica* and *G. leibergii*. Their close relationship was confirmed by this study, however, their distinction was greater than between *G. jacutica* and *G. arcuatifolia* (Bayesian tree in Fig. 1). Such situation would have two possible solutions: accepting a single species with three infraspecific taxa, or treating all three of them at the species level. We suggest the latter due to support from molecular phylogenetic analyses and the presence of morphological differences (Figs. 4–5, Table 1).

The Chukotkan plants, however, appeared to be much more interesting. A considerable incongruence between *trnL-F* and ITS datasets suggests its hybrid origin. ITS tree topology provided a strong signal that one of its ancestors is obviously a representative of the group of *G. jacutica–G. leibergii*. However, choosing one of the three species, *G. jacutica*, *G. leibergii* or *G. attenuata* as its most probable progenitor is not possible at present due to rather insufficient sampling.

The *G. jacutica–G. leibergii* group in the overall phylogeny of the genus *Grimmia* (Streiff, 2006; Hernandez-Maqueda *et al.*, 2008a) was found within the *G. trichophylla* group, in a monophyletic clade sister to the genus *Grimmia*, which would support the segregation of the genus *Dryptodon* (Hernandez-Maqueda *et al.*, 2008a).

However, the present *trnL-F* tree topology (Fig. 2 B), as well as the alignment (Fig. 2 C), indicate a quite remote position of the Chukotkan specimens from the *G. jacutica–G. leibergii* group. Instead, *trnL-F* sequences of the former are almost identical to *G. elatior* and also very similar to other species representing the main *Grimmia* clade by both Streiff (2006) and Hernandez-Maqueda *et al.* (2008 b). However, the variation of *trnL-F* marker is low within *Grimmia*, thus defining which would be the second putative ancestor is not clear.

The cases of reticulate evolution are not frequent in mosses, but already known in *Grimmia*. Hernandez-Maqueda *et al.* (2008a) found a similar incongruence in the position of *Grimmia tergestina* Tomm. ex Bruch *et al.* in chloroplast and ITS trees. The present case involves more distantly related groups (according to phylogeny of Hernandez-Maqueda *et al.*, 2008a), often recognized as two genera, *Grimmia* and *Dryptodon* (Ochyra *et al.*, 2003). A number of putative hybridogeneous species are known in *Sphagnum* (Cronberg & Natcheva, 2002; Ricca & Shaw, 2010), and a putative hybrid of taxa from different families has been found by Ignatov & Milyutina (2011).

The practical suggestion from the present result on putative hybridization, is a warning against an acceptance of the genus *Dryptodon*. Thus the Chukotkan plants are described here in the genus *Grimmia*.

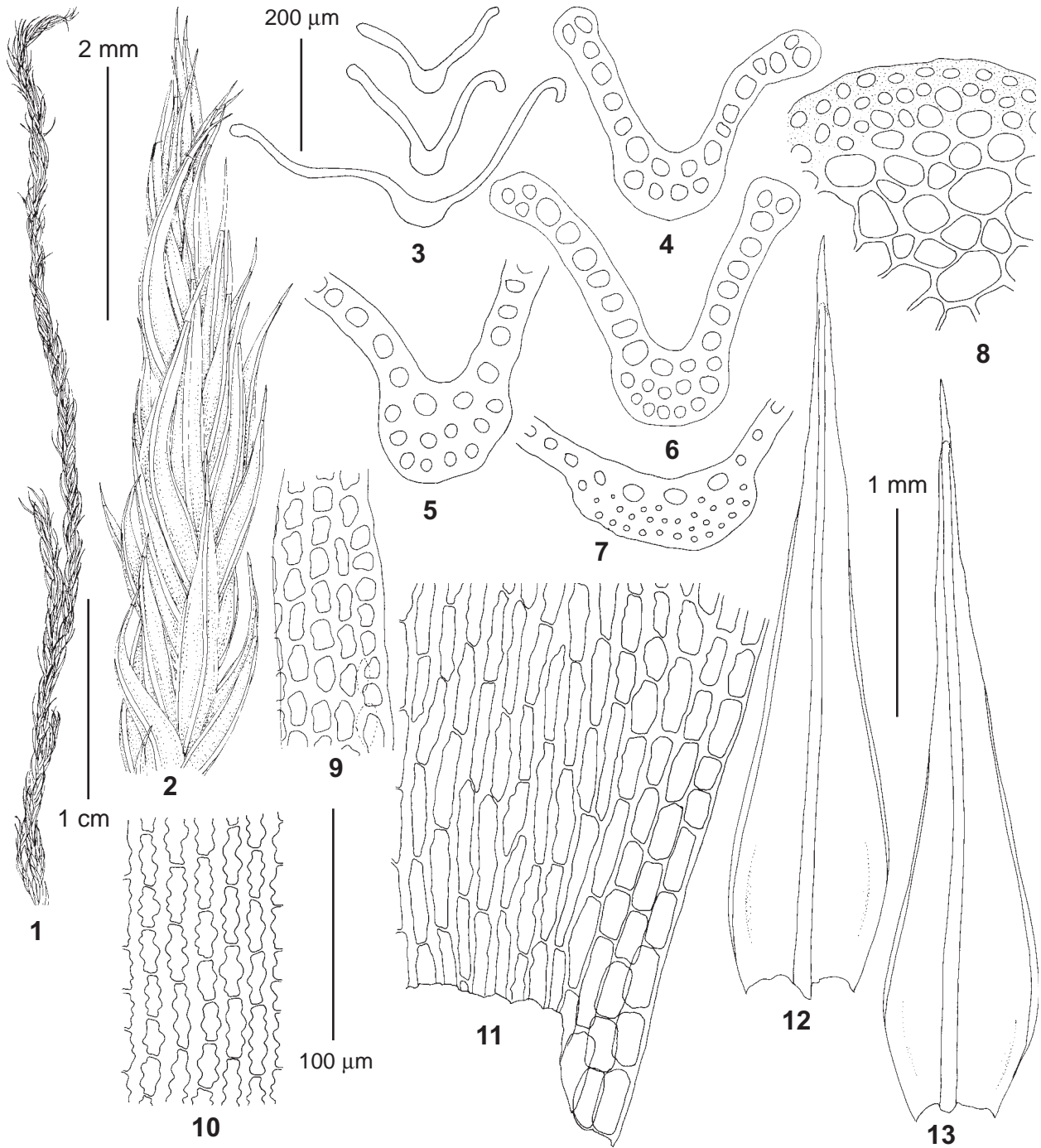


Fig. 3. *Grimmia beringiensis* Ignatova & Ignatov (from holotype). 1, 2 – habit, dry; 3–7 – leaf transverse sections; 8 – stem transverse section; 9 – upper lamina cells; 10 – median lamina cells; 11 – basal lamina cells; 12–13 – leaves. Scale bars: 1 cm for 1; 2 mm for 2; 1 mm for 12–13; 200 µm for 3; 100 µm for 4–11.

#### TAXONOMY

***Grimmia beringiensis*** Ignatova & Ignatov, sp. nov.  
Figs. 3, 4.

Similar to *Grimmia jacutica*, differs in appressed leaves with straight vs. recurved hair-points, costa (2–) 3–4-layered vs. 2-layered in transverse section and growing on soil among rocks in tundras vs. on rocks.

Type: Russia, south-east of Chukotka Peninsula, northern shore of Senyavin Strait near Yanrakynnot Set-

tlement, rocky calcareous tundra with patchy *Dryas* and lichens, 23.VII.1976, Afonina s.n. (Holotype MW, Isotypes LE, MHA).

Plants medium-sized to large, growing in extensive, dense, but easily separating cushions, yellowish-green at tips of shoots, brownish below, dull. Stems 2–8 cm, ascending to straight, sparsely branching, densely foliate, without central strand. Leaves appressed when dry, straight or slightly twisted around



Table 1. Some diagnostic morphological characters of *Grimmia* (*Dryptodon*) species with costa reniform in cross-section and arcuate seta.

Species	<i>G. jacutica</i>	<i>G. beringiensis</i>	<i>G. leibergii</i>	<i>G. arcuatifolia</i>	<i>G. decipiens</i>	<i>G. lisae</i>
leaf lamina length, mm	2–2.5	2–3	2–3.1	3–3.5	2.5–3	1.5–2
hair-point length, mm,	0–0.5	0–0.8	0.45–1.1	0–0.45	0.5–1.5	0–0.5
decurrency	decurrent	decurrent	decurrent	not decurrent	decurrent	decurrent
and serration	fine, distant	fine, distant	fine, distant	sharp, distant	strong, dense	sharp, dense
costa width at base, $\mu\text{m}$	60–85	50–75	80–100	130–175	60–70	50–75
number of cell layers in costa:						
distal	2	2–3	2	3	2	3
median	2	3	3	3–5	2	3(–4)
basal	2	3–4	3–4	4–5	2	3(–4)
cell wall thickness	strong	strong	median	median	median	median
cell size, $\mu\text{m}$ :						
distal, width	7–12	8–13	5.5–8.5	7–9.5	9–13	5–7
distal, length	9–25	13–25	7–15	6–12	10–14	4–9.5
median, width	8.5–12	9–13	7–10.5	7–11	9–12	5–8.5
median, length	12–30	18–33	9–20	7.5–15(–20)	15–25	9–16
basal juxtacostal cell walls	thick, porose	thick, porose	thick, porose	thick, porose	thick, porose	thin, not porose
basal marginal transverse cell walls	thick	thick	thick	thin	thick	thick
sexual condition	dioicous	dioicous	dioicous	dioicous	autoicous	dioicous
sporophyte frequency	rare	unknown	frequent	rare	frequent	rare

the stem, erecto-patent when wet, lamina 2–3 mm long, 0.45–0.6 mm wide, narrowly lanceolate; hair-points 0–0.6(–0.8) mm long, with very short distant spinulae to almost smooth, short to long decurrent; costa 50–75  $\mu\text{m}$  wide at leaf base, moderately projecting dorsally, reniform in transverse section, with 3–6 cells exposed on ventral surface, 2–3-layered distally, 3-layered in mid-leaf and 3–4-layered at base; margin recurved in proximal 2/3–3/4 on one side of leaf and shorter recurved on the other side, plane and slightly uneven distally; lamina smooth, unistratose except one bistratose marginal or submarginal row of cells; distal lamina cells rectangular, (12–)15–25(–28)  $\mu\text{m}$  long and (8–) 10–12(–13)  $\mu\text{m}$  wide, thick-walled, walls slightly sinuose; median lamina cells elongate-rectangular, (18–)21–30(–35)  $\mu\text{m}$  long and 9–11(–13)  $\mu\text{m}$  wide, with strongly thickened and strongly sinuose longitudinal walls and thin transverse walls; basal juxtacostal cells linear, 12–13  $\mu\text{m}$  wide and 30–50(–70)  $\mu\text{m}$  long, thick-walled and porose, basal marginal cells short rectangular, with thickened transverse walls, occasionally pellucide. Sexual condition dioicous, gametangia lateral. Sporophytes unknown.

*Specimens examined*: RUSSIA: **Chukotka**: Yanrakynnot Settlement surroundings, 20.VII.1976, *Afonina s.n.* (LE, MW); Ushkligran Settlement outskirts, 6.VII.1970, *Afonina s.n.* (LE, MW); NW shore of Penkigney Bay near Peszovaya Creek mouth, 11.VII.1978, *Afonina s.n.* (LE, MW).

**Distribution and ecology**. The species was collected in several rather close localities in south-eastern Chukotka. It grows at low altitudes not far from sea coast, on

soil in rocky tundras in an area with calcareous bedrocks, along patchy *Dryas* communities with extensive moss and lichen cover; it was also once collected in *Alnus fruticosa* stands on calcareous slopes of a hill.

**Differentiation**. Leaves of *G. beringiense* are slightly longer than those of *G. jacutica*, with lamina length up to 3 mm vs. to 2.5 mm. Its hair-point length and decurrency, and lamina areolation are very similar or practically identical with *G. jacutica* (Fig. 4, see also illustrations in Ignatova *et al.*, 2003). However, these two species can be recognized with a hand-lens or under stereomicroscope by their different leaf arrangement and hair-point orientation: leaves are straight, occasionally only slightly twisted and with straight hair-points in *S. beringiense*, while in *G. jacutica* leaves are often secund and usually have hair-points recurved at right angle, resembling *Racomitrium laetum* in this character. Furthermore, *Grimmia jacutica* grows mostly on rocks, often on and between boulders of rock-fields, whereas *G. beringiense* was collected on soil in tundras. Plants of *G. jacutica* are in most cases yellowish-olivaceous in a considerable distal portion, whereas plants of *G. beringiense* have only uppermost leaves yellowish-green and with most part of the shoots brown. Among microscopic characters, costa transverse section alone is important, being always bistratose throughout in *G. jacutica* and 3–4-stratose in *G. beringiense* at least at leaf base.

*Grimmia beringiense* differs from *G. leibergii* in considerably larger laminal cells with much thicker longitudinal walls (Table 1, Figs. 4–5). Costa of *G. leibergii* is 3–4-stratose in transverse section, like in *G. beringien-*

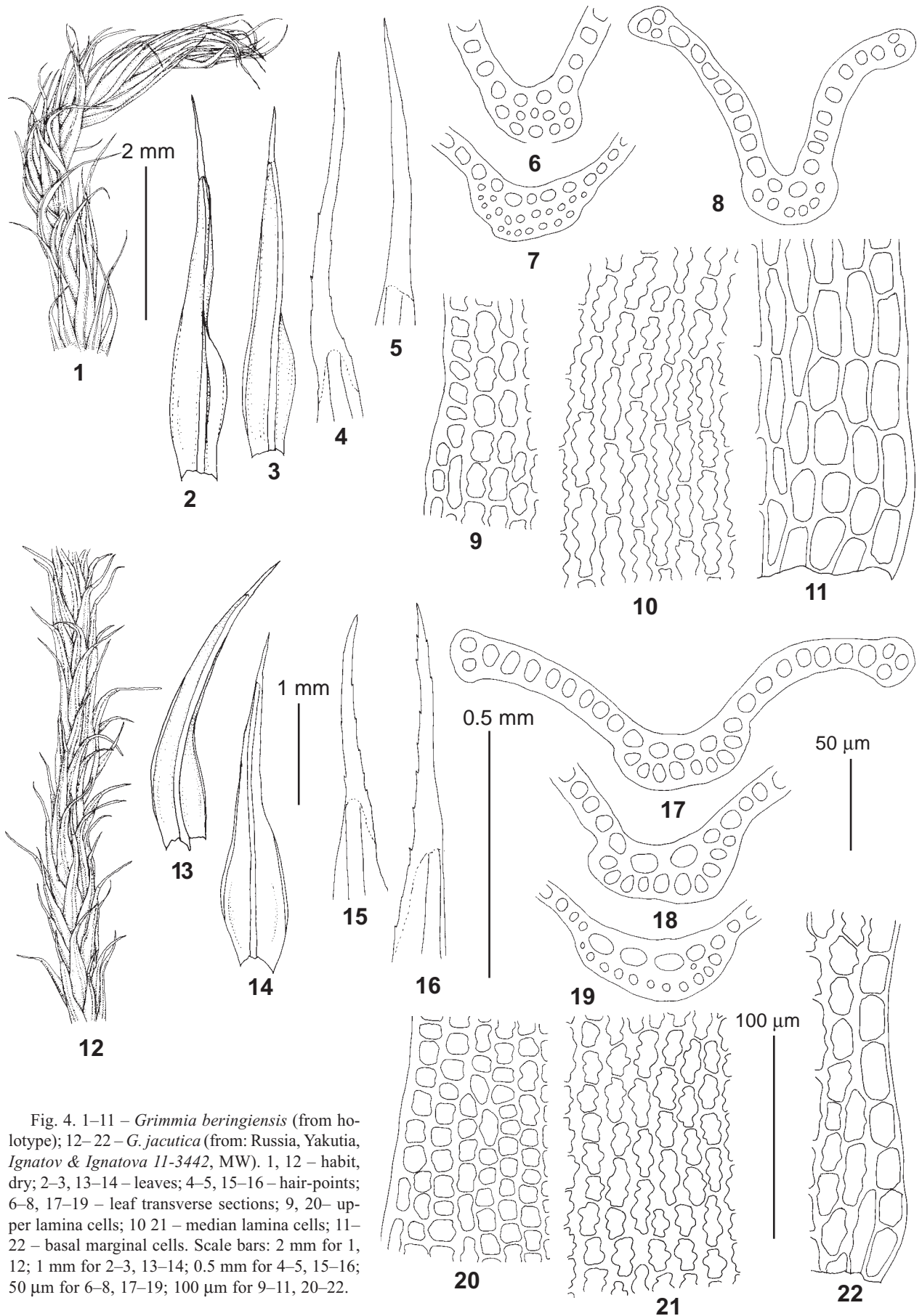


Fig. 4. 1–11 – *Grimmia beringiensis* (from holotype); 12–22 – *G. jacutica* (from: Russia, Yakutia, Ignatov & Ignatova 11-3442, MW). 1, 12 – habit, dry; 2–3, 13–14 – leaves; 4–5, 15–16 – hair-points; 6–8, 17–19 – leaf transverse sections; 9, 20 – upper lamina cells; 10, 21 – median lamina cells; 11–22 – basal marginal cells. Scale bars: 2 mm for 1, 12; 1 mm for 2–3, 13–14; 0.5 mm for 4–5, 15–16; 50 μm for 6–8, 17–19; 100 μm for 9–11, 20–22.



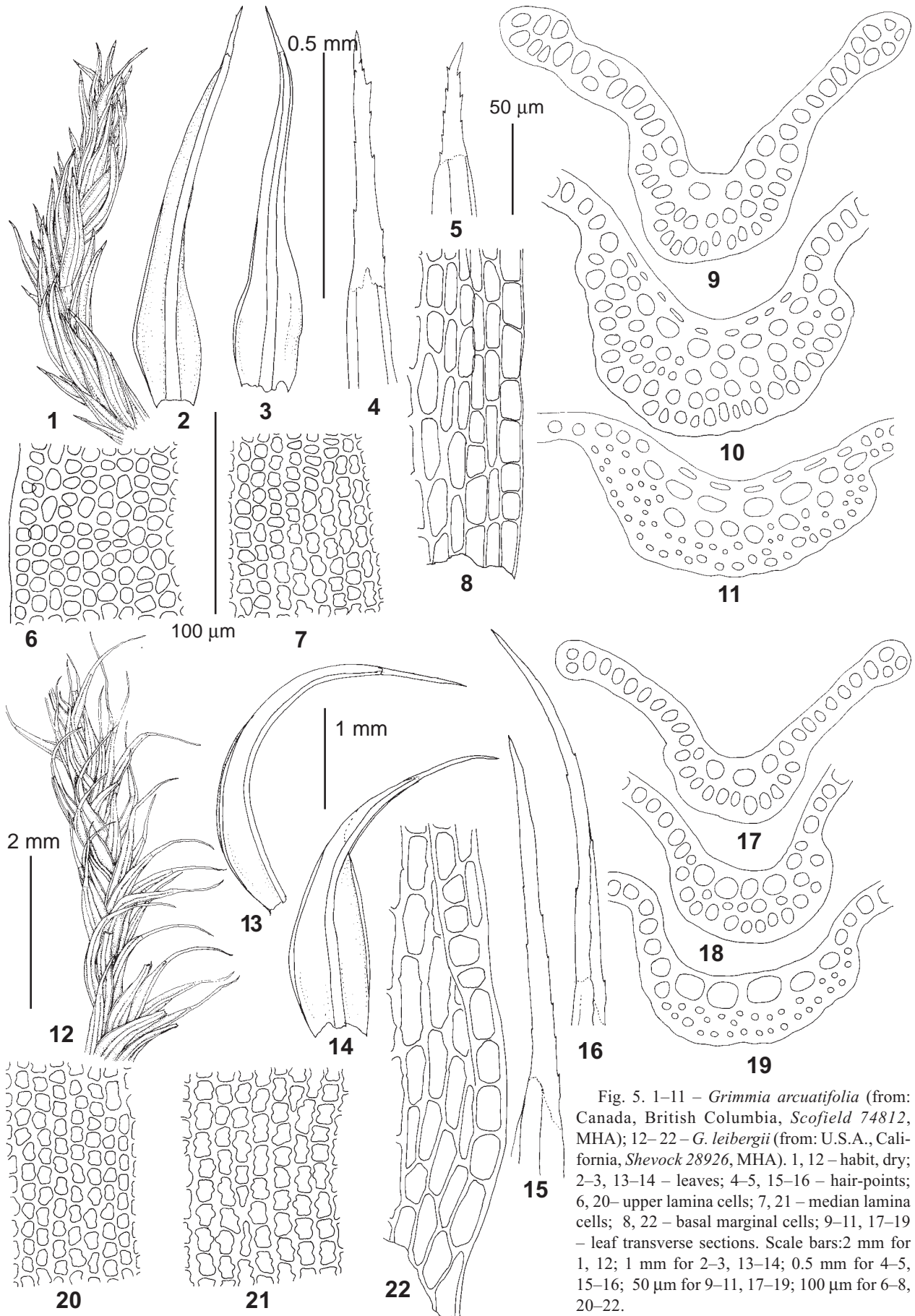


Fig. 5. 1–11 – *Grimmia arcuatifolia* (from: Canada, British Columbia, Scofield 74812, MHA); 12–22 – *G. leibergii* (from: U.S.A., California, Shevock 28926, MHA). 1, 12 – habit, dry; 2–3, 13–14 – leaves; 4–5, 15–16 – hair-points; 6, 20 – upper lamina cells; 7, 21 – median lamina cells; 8, 22 – basal marginal cells; 9–11, 17–19 – leaf transverse sections. Scale bars: 2 mm for 1, 12; 1 mm for 2–3, 13–14; 0.5 mm for 4–5, 15–16; 50  $\mu$ m for 9–11, 17–19; 100  $\mu$ m for 6–8, 20–22.

sis, but it is much wider in the former species, 80–100 µm vs. 50–75 µm, with greater number of cells on ventral surface and stronger differentiated ventral surface cells (Figs. 4–5). In addition, falcate-secund leaves, the plants usually fertile, and the dark-green colored plants, make *G. leibergii* contrastingly different from the brown plants with straight leaves of *G. beringiensis*, which sporophytes are still unknown.

*Grimmia attenuata* superficially resembles *G. beringiensis* in shoots with straight and appressed leaves and straight hair-points, but these two species have strikingly different lamina areolation (see Figs. 4–5 and Table 1). The exceedingly strong costa of *G. attenuata*, very wide (130–175 µm at base) and 3–5-stratose, the non-decurrent hair-points, and the thin-walled basal marginal cells, are the features distinguishing it from all three other species of this group.

The differences between *G. beringiensis* and *G. decipiens* include finely and distantly vs. sharply and densely serrate hair-points, straight vs. falcate leaves, 3-stratose vs. 2-stratose costa and strongly vs. moderately thickened cell walls. *Grimmia lisae* differs from *G. beringiensis* in the smaller size of plants and leaves, strongly recurved vs. erecto-patent leaves in wet condition, and basal juxtacostal cells with thin and non porose walls vs. thick and strongly porose walls. Both *G. decipiens* and *G. lisae* were only recently found in Russia (Doroshina *et al.*, 2015; Bezdgodov *et al.*, 2016), and each of them is known from a single locality at the Black Sea coastal area in the West Caucasus.

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Appendix 1. Species of *Grimmia*, used for molecular phylogenetic analysis of nrITS and cp *trnL-F*.

			ITS	<i>trnL-F</i>
<i>G. arcuatifolia</i>	British Columbia 30	Canada, British Columbia, Schofield & Spence 84310 (MHA)	KX443539	-
<i>G. arcuatifolia</i>	British Columbia 643	Canada, British Columbia, Schofield & Djan-Chekar 104960 (MHA)	KX443542	-
<i>G. arcuatifolia</i>	British Columbia 644	Canada, British Columbia, Schofield 77506 (MHA)	KX443545	-
<i>G. arcuatifolia</i>	British Columbia 775	Canada, British Columbia, Schofield 74812 (MHA)	KX443540	KX443514
<i>G. arcuatifolia</i>	British Columbia 45	Canada, British Columbia, Schofield & Djan -Chekar 104960 (MHA)	-	KX443513
<i>G. arcuatifolia</i>	British Columbia 788	Canada, British Columbia, 9.VII.1990, Greven s.n. (MO)	KX443549	KX443511
<i>G. beringiensis</i>	Chukotka 861	Russia, Chukotka, Penzhigney Bay, 11.VII.1978, Katenin (LE)	-	KX443496
<i>G. beringiensis</i>	Chukotka 1145	Russia, Chukotka, 23.VII.1976, Afonina s.n. (LE, MW)	KX443538	-
<i>G. beringiensis</i>	Chukotka 786	Russia, Chukotka, Yanrakynnot, 20.VII.1976, Afonina s.n. (LE, MW)	KX443537	KX443517
<i>G. decipiens</i>	Bulgaria 84	Bulgaria, Seregin & Bocharnikov M-1046 (MHA)	-	KX443497
<i>G. decipiens</i>	Krasnodar 1149	Russia, Krasnodar Territory, Doroshina 16014 (LE, MW)	KX443520	-
<i>G. elatior</i>	Russia 1212	Russia, Perm Province, 27.VII.2009, Bezgodov 702 (MHA)	KX443519	KX443518
<i>G. jacutica</i>	Primorsky 641	Russia, Primorsky Territory, Ignatov et al. 13-1467 (MHA)	KX443544	-
<i>G. jacutica</i>	Chukotka 782	Russia, Chukotka, Anadyr, 23.VII.1981, Afonina s.n. (LE)	KX443523	KX443507
<i>G. jacutica</i>	Chukotka 777	Russia, Chukotka, Palyavaam, 13.VII.1989, Afonina s.n. (LE)	KX443532	-
<i>G. jacutica</i>	Chukotka 778	Russia, Chukotka, Palyavaam, 25.VII.1989, Afonina s.n. (LE)	KX443527	KX443506
<i>G. jacutica</i>	Chukotka 789	Russia, Chukotka, Palyavaam, 25.VII.1989, Afonina s.n. (LE)	KX443546	KX443512
<i>G. jacutica</i>	Khabarovsk 27	Russia, Khabarovsk Territory, Ignatov 97-2013 (MHA)	KX443533	-
<i>G. jacutica</i>	Khabarovsk 748	Russia, Khabarovsk Territory, Ignatov 97-2013 (MHA)	KX443531	KX443504
<i>G. jacutica</i>	Taimyr 160	Russia, Taimyr, Fedosov 05-317 (MW)	KX443530	-
<i>G. jacutica</i>	Taimyr 747	Russia, Taimyr, Khatanga, Fedosov 11-149 (MHA)	KX443548	KX443503
<i>G. jacutica</i>	Yakutia 746	Russia, Yakutia, Orulgan, Ignatov 11-4447 (MHA)	-	KX443502
<i>G. jacutica</i>	Yakutia 148	Russia, Yakutia, Suntar-Khayata, Ignatov & Ignatova 11-3442 (MHA)	KX443526	KX443501
<i>G. jacutica</i>	Yakutia 48	Russia, Yakutia, Suntar-Khayata, 14.VII.2003, Zolotov (MHA)	KX443525	KX443500
<i>G. jacutica</i>	Zabaikalsky 47	Russia, Zabaikalsky Territory, 21.VII.2005, Afonina s.n. (LE)	KX443534	KX443499
<i>G. jacutica</i>	Chukotka 791	Russia, Chukotka, Tanyurer, 10.VIII.1981, Afonina s.n. (LE)	KX443524	-
<i>G. jacutica</i>	Alaska 46	U.S.A., Alaska, 16.07.1993, Afonina s.n. (LE)	KX443547	KX443498
<i>G. jacutica</i>	Alaska 781	U.S.A., Alaska, 14.VIII.1993, Afonina s.n. (LE)	KX443528	KX443505
<i>G. jacutica</i>	Alaska 783	U.S.A., Alaska, 14.VII.1993, Afonina s.n. (LE)	KX443529	KX443508
<i>G. jacutica</i>	Alaska 784	U.S.A., Alaska, 13.VII.1992, Afonina s.n. (LE)	-	KX443509
<i>G. jacutica</i>	Alaska 785	U.S.A., Alaska, 14.VII.1993, Afonina s.n. (LE)	KX443543	KX443510
<i>G. leibergii</i>	Oregon 642	U.S.A., Oregon, Shevock 27918 (MHA)	KX443541	KX443515
<i>G. leibergii</i>	California 1264	U.S.A., California, Shevock 28926 (MHA)	KX443550	KX443516
<i>G. leibergii</i>	California 29	U.S.A., California, Shevock 28926 (MHA)	KX443535	-
<i>G. leibergii</i>	California 31	U.S.A., California, Toren 1460f (MHA)	KX443536	-
<i>G. trichophylla</i>	Spain 1148	Spain, Kučera 17547 (CBFS, MHA)	KX443521	-
<i>G. trichophylla</i>	California 24	U.S.A., California, 9.VIII.1989, Ignatov s.n. (MHA)	KX443522	-