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WHEN THE PLANT SIZE MATTERS: A NEW SEMI-CRYPTIC SPECIES OF *DICRANUM* FROM RUSSIA

КОГДА РАЗМЕРЫ ИМЕЮТ РЕШАЮЩЕЕ ЗНАЧЕНИЕ: НОВЫЙ ПОЛУСКРЫТЫЙ ВИД РОДА *DICRANUM* ИЗ РОССИИ

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Abstract

The analysis of nuclear ITS1-2 and chloroplastic *trn*L-F DNA sequences revealed an undescribed species closely related to *D. spadiceum*, and it is described as *Dicranum schljakovii* Ignatova & Tubanova, *sp. nova*. Its distinctive characters include the smaller size of plants and leaves, and a different leaf shape. Its distribution area covers the southern part of Asian Russia, Yakutia, Russian Far East (Primorsky Territory, Kamchatka, Sakhalin and Kuril Islands) and Urals, plus few localities in Taimyr and a single disjunct locality in Murmansk Province. The distinction of *D. spadiceum* var. *spadiceum* and var. *subscabrifolium* is not confirmed by the molecular markers used in the study. Morphological chracteristics of *D. spadiceum* are corrected by the addition of some characters of var. *subscabrifolium*. Synonymization of *D. angustum* and *D. laevidens* with *D. spadiceum* is not confirmed as well, and these two species are not closely related to each other. Descriptions and illustrations for *D. spadiceum* and *D. schljakovii* are provided, their distribution and ecology are reviewed, and a key to the identification of species of *Dicranum* sect. *Muehlenbeckia* with the addition of *D. laevidens* is given.

Резюме

Анализ последовательностей ITS1-2 ядерной ДНК и trnL-F хлоропластной ДНК выявил не описанный вид, близкий к *D. spadiceum*. Он описан в данной статье как *Dicranum schljakovii* Ignatova & Tubanova sp. nova; его основные отличия от *D. spadiceum* заключаются в меньших размерах растений и листьев, а также в форме листьев. Этот вид распространен в основном на юге азиатской России, от Камчатки, Сахалина и Курильских островов до Алтая, в Якутии, на Урале, редок на Таймыре и один раз собран в Мурманской области. Таксономическая значимость морфологических отличий между *D. spadiceum* var. *spadiceum* и var. *subscabrifolium* не подтверждается с помощью изученных молекулярных маркеров. Морфологическая характеристика *D. spadiceum* дополнена признаками, соответствующими var. *subscabrifolium*. Синонимизация *D. angustum* и *D. laevidens* с *D. spadiceum* также не подтверждается, кроме того, два последних вида, согласно молекулярным данным, не являются близкими. Даны описания и иллюстрации для *D. spadiceum* и *D. schljakovii*, охарактеризована их экология и распространение; предложен ключ для определения видов секции *Muehlenbeckia*, с добавлением *D. laevidens*.

KEYWORDS: mosses, *Dicranum spadiceum*, taxonomy, ITS, trnl-F, new species, Russia

Introduction

The genus *Dicranum* is one of the largest in the moss flora of Russia, including 35 species (Ignatov, Afonina, Ignatova *et al*., 2006; Ignatova & Fedosov, 2008; Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011; Tubanova, 2013). Most of them occur in the Arctic and alpine ecosystems, where several species of the genus often grow together. Being quite variable, plants provide difficulties for a taxonomic identification, and some species remained for a long time a point of disagreement between taxonomists. For example, *D. fuscescens* Turner and *D. flexicaule* Brid. (previously named *D. congestum* Brid.) are

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considered conspecific and reduced to synonyms, or accepted as varieties in different combinations: *Dicranum congestum* subsp. *fuscescens* (Turner) J.J. Amann and *D. fuscescens* var. *flexicaule* (Brid.) Wilson.

Recent advances in molecular phylogeny using the DNA sequence variation resulted in a more definite delimitation of some taxa. Rather minor and even partly overlapping morphological differences, which are, at the same time, stable between distant populations have proved to be taxonomically important. In the past years, several molecular markers were tested for their discrimination capacity in *Dicranum* species collected from Arctic ecosystems where a great variability of morphological characters is expressed under extreme environmental conditions making the identification of some specimens difficult or even impossible (Lang *et al.*, 2014a). These authors concluded that DNA barcoding may improve the species delimitation; however, a combination of different markers is necessary for better and more reliable results, and the most promising of the molecular markers are ITS1, *trn*L-F and *rps*4-*trn*T. At the same time, one of the markers, nrITS1-5.8S-ITS2, was applied solely for the species discrimination in *Dicranum* with fragile leaves (Ignatova & Fedosov, 2008) and in *Dicranum acutifolium*-complex (Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011). These authors considered that even small but stable differences in the DNA sequences that coincide with a set of morphological characters can provide a testimony for a species distinction. For example, three species, *D. pacificum* Ignatova & Fedosov, *D. septentrionale* Tubanova & Ignatova, and *D. bardunovii* Tubanova & Ignatova were described as new for science from the territory of Russia, and the taxonomic status of *D. hakkodense* Cardot was resurrected recently (Ignatova & Fedosov, 2008; Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011). *D. septentrionale* Tubanova & Ignatova was separated from *D. brevifolium* (Lindb.) Lindb. on the basis of slightly longer and short rectangular leaf cells vs. quadrate cells in distal part of leaf. Their molecular differences, albeit without high statistical support, were demonstrated by a single marker, ITS1-2 (Tubanova *et al.*, 2010), and subsequently confirmed by the study of additional chloroplast regions which provided much better support (Lang *et al.*, 2014 b).

Some other groups of species in *Dicranum* are also waiting for a revision, in particular, those taxa having taxonomic disagreements between North American and European authors. One of these includes *Dicranum spadiceum* J.E. Zetterst., *D. angustum* Lindb. and *D. laevidens* R.S. Williams. Bellolio-Trucco & Ireland (1990), in their taxonomic treatment of the genus in Ontario and Quebec, synonymized *D. angustum* with *D. spadiceum*, in particular, because the type specimens of these species were found to be identical. At the same time, they pointed to a putative distinctiveness of *D. laevidens* (described from Yukon Territory of Canada). Later, Ireland (2007) in his publication in Moss Flora of North America confirmed the identity of *D. angustum* with *D. spadiceum* and added *D. laevidens* into the synonymy of the latter species. This species concept has been accepted in the Tropicos database (http://www.tropicos.org) and The Plant List project (http://www.theplantlist.org) by accession dated in 2013-August 2015. At the same time, in European floras and other treatments and checklists (*e.g.*, Nyholm, 1987; Hedenäs & Bizang, 2004; Hill *et al*., 2006) these three species are recognized as separate ones. In the Russian Handbooks (Abramova *et al.*, 1961; Savicz-Lyubitskaya & Smirnova, 1970), *D. spadiceum* is treated as a separate species, while *D. laevidens* is included in the synonymy of *D. angustum*.

Ignatova (2005), following Nyholm (1986) and Hedenäs & Bizang (2004), suggested that *D. laevidens* and *D. angustum* can be recognized in herbarium collections from Russia, and the former species was found to be much more common in Russia than the latter one, particularly in the Arctic and Subarctic regions. All these taxa are included in the moss checklist of East Europe and North Asia (Ignatov, Afonina, Ignatova *et al.*, 2006). The molecular distinction of *D. spadiceum*, *D. angustum* and *D. laevidens* was demonstrated recently by Lang *et al.* (2014a) who used five chloroplast loci and the nuclear ITS1-2 region.

In addition, the Russian Handbooks also included *D. spadiceum* var. *subscabrifolium* Schljakov. The variety was described by Schljakov (1951) who noted that some of his collections from Khibiny Mts looking like *D. spadiceum* could not be identified by the European keys to a species, as the specimens had densely serrulate distant leaf margins (described as almost entire for *D. spadiceum* in most floras) and also scabrous dorsal side of costa and dorsal leaf lamina in the distal leaf portion (while smooth or weakly scabrous costa and smooth lamina were usually mentioned for *D. spadiceum*). The descriptions of the species in handbooks and floras at that time did not mention such a variation for *D. spadiceum*. Therefore, Schljakov (l.c.) described the var. *subscabrifolium* to accommodate these specimens, though he expressed a strong opinion that the specimens definitely fall within the species concept of *D. spadiceum*. This variety was accepted by Savicz-Lyubitskaya & Smirnova (1970) and Ignatov & Ignatova (2003). It was not treated as a separate taxon in the Checklist of Mosses of East Europe and North Asia (Ignatov, Afonina, Ignatova *et al.*, 2006) solely by the reason of insufficient knowledge of its distribution, although its possible position at a higher taxonomic rank was pointed out.

The original aim of the present study was to check if the molecular markers would support the distinction of *D. spadiceum* var. *subscabrifolium* from var. *spadiceum*, and to clarify their morphological delimitation and distribution. However, the preliminary results had led us to adopt a broader sampling approach in order to resolve a bigger systematic problem.

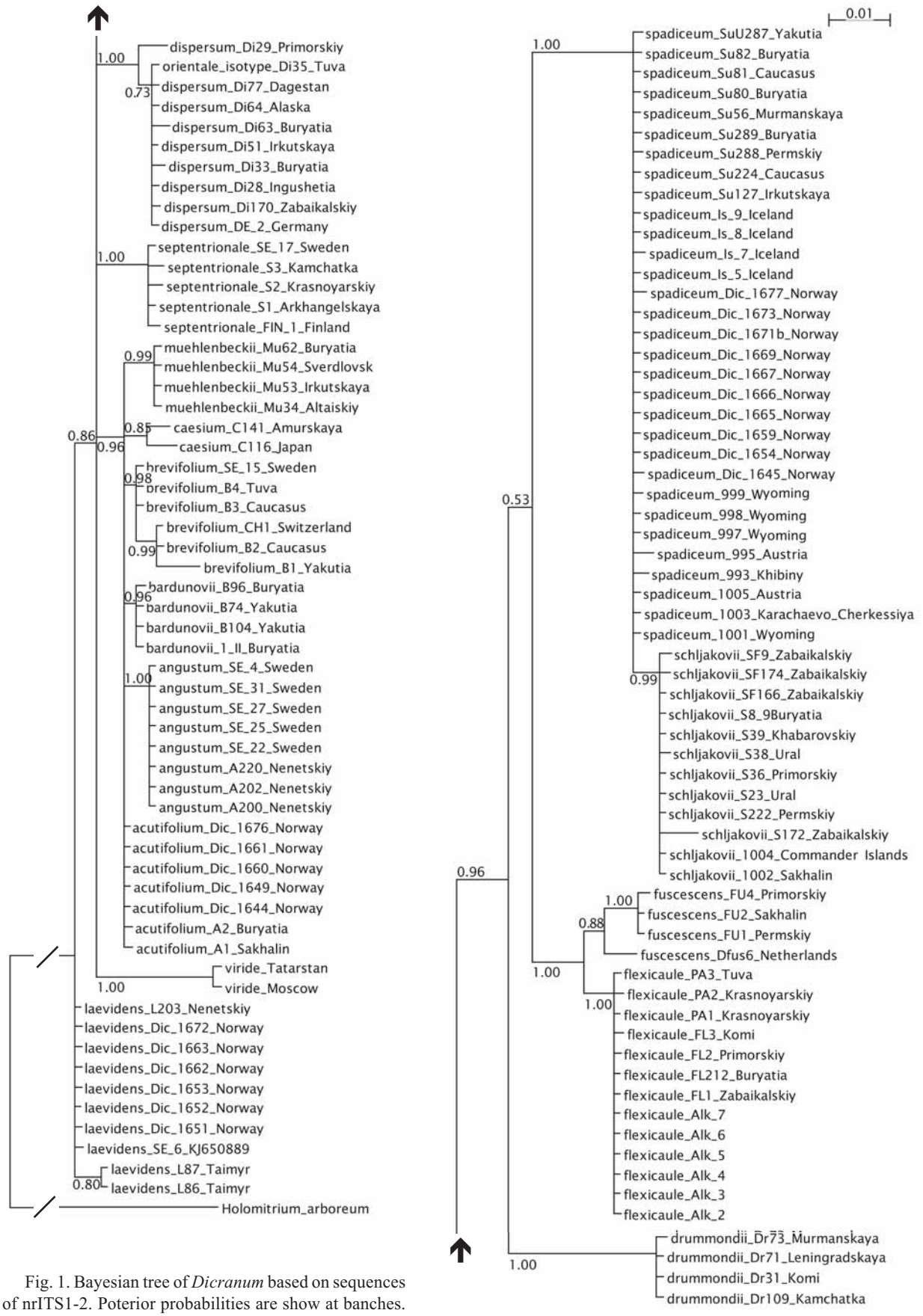


Fig. 1. Bayesian tree of *Dicranum* based on sequences of nrITS1-2. Poterior probabilities are show at banches. Specimens data are in Appendix 1.

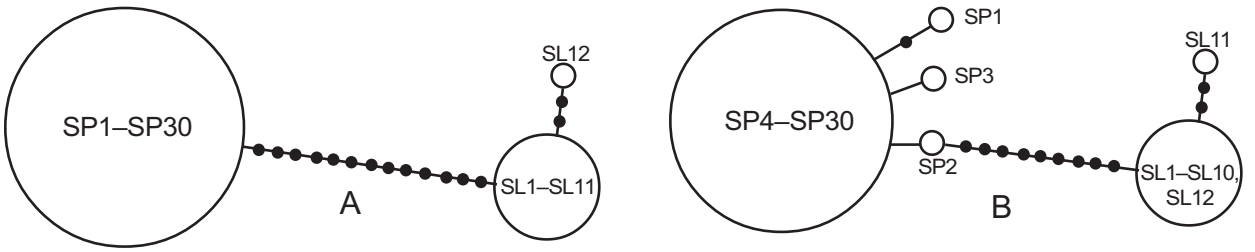


Fig. 2. *trn*l-F (A) and ITS (B) haplotype networks appeared from TCS analysis for the species of *D. spadiceum*–clade, including 30 specimens of *D. spadiceum* s.str. (SP) and 12 of *D. schljakovii* (SL). Specimen information is in Appendix 1, while deviated haplotypes are as following: SL11 KT580764 / SL12 KT580701 / SP1 KF423595 / SP2 KT580768 / SP3 KJ650880 (cf. Appendix 1)

MATERIAL AND METHODS

DNA sequences of 94 reference specimens comprising 16 taxa were compiled from earlier studies (Ignatova & Fedosov, 2008; Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011; Lang *et al.*, 2014a, b), and from the Genbank: *D. acutifolium* (8), *D. angustum* (5), *D. bardunovii* (4), *D. brevifolium* (6), *D. laevidens* (7), D. septentrionale (5), *D. spadiceum* (14) and *D. viride* (2). Additional sequences were newly generated for this study (voucher data are given in Appendix 1): *Dicranum angustum* (3), *D. caesium* (2), *D. dispersum* (9), *D. drummondii* (4), D. *flexicaule* (1), *D. laevidens* (3), *D. muehlenbeckii* (4), *D. spadiceum* (17), and *D. schljakovii* (12, selected as *D. spadiceum*). Specimens for molecular study were selected from geographically distant populations (12 from European Russia, 25 from Siberia and 5 from the Russian Far East).

DNA extractions and overall laboratory protocols were essentially the same as in, *e.g.*, Gardiner *et al*. (2005). Amplified DNA fragments were sequenced partially in Novosibirsk (Center of collective use "Genomics") and Moscow ("Genom"). Sequences were aligned manually in Bioedit (Hall, 1999). Trees were rooted on *Holomitrium arboreum*.

Bayesian analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) with two compartments (5.8S and *trn*L-F region) analysed with HKY+I model, and ITS1 and ITS2 with GRT+I+G model. Three parallel runs were implemented, each with five chains and 20,000,000 generations (5000 burnin), with trees sampled every 1000 generations, a temp parameter value of 0.10 and parameters unlinked between partitions.

Positions near hairpins in ITS1 were cut off, to be congruent with GenBank data deposited for the publication of Lang *et al*. (2014ab).

Haplotype network analysis was performed in TCS 1.21 (Clement *et al.*, 2000), with gap coding as one mutational event irrespective to its length. TCS was run for *trn*L-F with parameter: connection limit 95%, fit connection limit at 15 steps, gaps=5th state.

Morphological studies were based on herbarium collections from H, IRK, KPABG, KRF, LE, MHA, MW, S, SASY and UUH.

Measurements of leaf length and width were provided for plants selected as *D. spadiceum*. Three well-developed plants were selected in each specimen; five largest leaves were taken from the middle part of each shoot. The measurements were made under the stereomicroscope CarlZeiss Stemi 2000-C in AxioVision Rel. 4.8 program. In total, 570 leaves were measured. The data were analyzed in Microsoft Excel Program and in PAST Program (Hammer *et al.*, 2008).

RESULTS

The Bayesian tree (Fig. 1) represents a polytomy formed by specimens of *D. laevidens* and a clade nested in it with all other species. This clade also comprises a polytomy of five well-supported clades formed by **(1)** *D. viride,* PP=1.0; **(2)** *D. septentrionale,* PP=1.0; **(3)** *D. dispersum,* PP=1.00; **(4)** polytomy of 6 species: *D. acutifolium* (unresolved), *D. angustum* (PP=1.0), *D. bardunovii* (PP=0.96), *D. brevifolium* (PP=0.98), *D. muehlenbeckii* (PP=0.99), and a moderately supported clade of two specimens of *D. caesium* (PP=0.88); **(5)** clade of three supported subclades of *D. drummondii* (PP=1.0), *D. flexicaule* + *D. fuscescens* (PP=1.0), and a terminal subclade (PP=1.00) formed by specimens previously identified as *D. spadiceum* (*D. spadiceum* s.l.-clade).

The latter clade represents a polytomy of specimens of *D. spadiceum* and a highly supported clade (PP=0.99) containing specimens from Asian Russia and Urals that corresponds to the new species described as *D. schljakovii* Ignatova & Tubanova (see below). No difference was found between phenotypes of *D. spadiceum* var. *spadiceum* and var. *subscabrifolium*.

The two TCS analyses of specimens of *D. spadiceum* s.l.-clade performed separately using the *trn*L-F and for ITS regions gave a similar pictures of haplotype networks (Figs. 2A and 2B). In both cases specimens were separated in a subidentical way, proving the distinctiveness of *D. schljakovii* from *D. spadiceum.*

Morphological differences of the plants from the two entities representing specimens of *D. schljakovii* and *D. spadiceum* were sought for, but nothing more reliable than the measurements of leaf length and width were found. However, these differences were overlapping (Table 1 and Figs. 3-4), but in general, allowing the identification of most specimens, although some collections (especially scanty specimens) may be difficult or even impossible to name based solely on the morphology. Costa width in relation to leaf width is also suggestive of a differentiating morphological character, but this charac-

Fig. 3. A-D – *Dicranum spadiceum* J.E. Zetterst. (habit, dry): A – from: Austria, *Ignatov & Schanzer 05-5054*, MHA; B – from: Russia, Murmansk Province, Khibiny Mts, *Ignatov & Ignatova 12-124*, MHA; C – from: Russia, Caucasis, Kabardino-Balkaria, 29.VII.2004, *Ignatov et al. s.n.*, MHA; D – from: Russia, Altai Republic, Taldura Creek, *Ignatov & Ignatova 12-597*, MHA. E-H – *D. schljakovii* Ignatova & Tubanova (habit, dry): E – from: Russia, North Urals, Perm Territory, Vishersky Reserve, 9.VII.2009, *Bezgodov 341*, PPU; F – from holotype: Russia, Buryatia, Dzherginsky Nature Reserve, 13.VII.2003, *Anenkhonov Rel. Ku-42/03*, UUH; G – from: Russia, Khabarovsk Territory, Bureinskij Reserve, 14.VII.1992, *Borisov 92-1*, MW; H – from: Russia, Sakhalin, *Ignatov & Teleganova 06-760*, MHA.

ter is rather a "secondary" one, as both species have costae of nearly the same width, and its relative width depends of the leaf length.

Cell dimensions were found to be even more variable, least helpful for a practical specimen identification. Alar and epidermal characters were found also of little use for the taxa discrimination. Leaf serration and flexuosity have a weak tendency to be more expressed in *D. spadiceum* than in *D. schljakovii* (Figs. 4D-E), but the variation is strong in these characters.

Discussion

Despite of the unresolved relationships between some groups of species, the present phylogenetic analysis allows the confirmation and rejection of at least some of the previous taxonomic conclusions.

1. Nine specimens of *D. dispersum* Engelmark from Europe, Asia and North America form a well-supported clade (PP=0.93). Among others, it includes the isotype specimen of *D. orientale* Otnyukova described from South Siberia a year after the description of *D. dispersum*. This confirms the taxonomic identity of these taxa suggested by Otnyukova & Ochyra (2003). Morphologically, this species is similar to *D. muehlenbeckii* and *D. caesium*, but, according to our obtained phylogeny, it is not especially closely related to any of the two.

2. The doubtful status of *D. spadiceum*, which was not accepted as a species of the first sort by, *e.g.*, Corley *et al*. (1981), has no ground of support. Likewise, the inclusion of *Dicranum angustum* and *D. laevidens* in the synonymy of *D. spadiceum* (Ireland, 2007) can not be accepted. The present study indicates that these two species are far from *D. spadiceum*, as well as from each other, in their position on the molecular tree. Our data confirm the conclusion of Lang *et al.* (2014a) about the distinction of these species. However, additional analysis on a more expanded sampling is still required. For their morphological comparison see Fig. 8 and the discussion under *D. spadiceum*.

3. No distinction was found between the plants with morphology of *D. spadiceum* var. *subscabrifolium* collected near the type locality in Khibiny Mountains and the plants referred as *D. spadiceum* var. *spadiceum* collected from

Table 1. Statistical data based on measurements of leaf length and width of *Dicranum spadiceum* and *D. schljakovii* (for details see Material and Methods).

	Dicranum spadiceum		*Dicranum schljakovii*	
Number of measurements	300	300	270	270
	Leaf length, mm	Leaf width, mm	Leaf length, mm	Leaf width, mm
Mean	5,7851	1,05998	3,80901	0,62428
Standard deviation	1,23932	0,164124	0,681404	0,117687
Min	3,095	0,586	2,576	0,407
Max	9,946	1,462	6,015	0,956

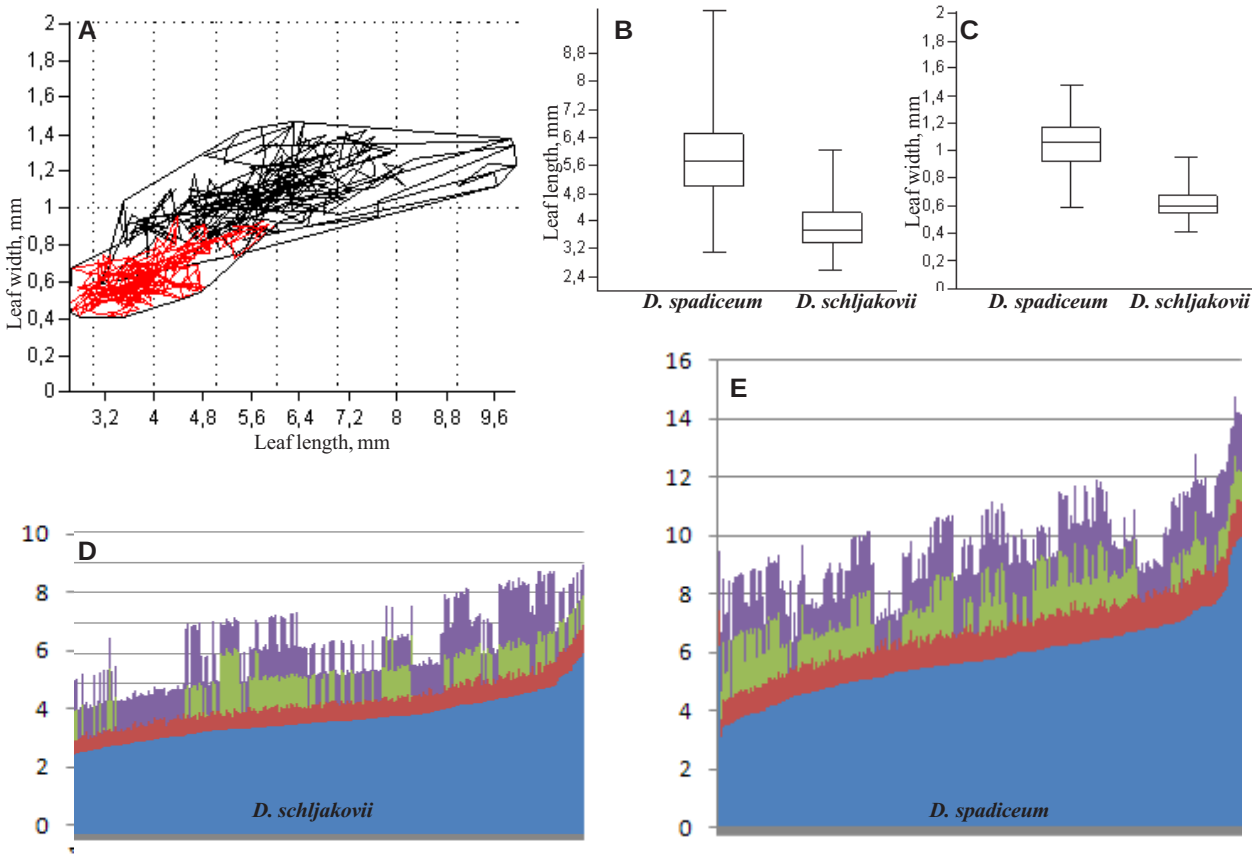


Fig. 4. A-C – plots showing the difference in leaf length and width between *D. spadiceum* and *D. schljakovii* based on measurements of plants from 40 specimens given in Table 1. In A red color marks *D. schljakovii* and black – *D. spadiceum*. D and E – plots demonstrating an integrate characteristics of *D. schljakovii* and *D. spadiceum*, respectively, based on the same sampling. In axis Y arbitrary units are shown. Blue color indicates leaf length; red – leaf width; green – leaf margin serration and dorsal leaf surface scabrosity (0 – absent, 1 – slight, 2 – strong); violet – flexuosity of leaves in dry state (0 – absent, 1 – slight, 2 – strong).

Central Europe. A broader sampling approach resulted in a topology where plants with entire leaf margins and smooth leaves and those with serrate margins and variously scabrous leaves were severely intermingled. Thus the distinction of *D. spadiceum* var. *subscabrifolium* has no support from the studied molecular markers.

A similar variation of leaf margin serration and scabrosity of dorsal costa and lamina was also observed in *D. elongatum* (Savicz-Lyubitskaya & Smirnova, 1970; Ignatova, 2005). Some specimens of *D. majus* also possess spinosely projected upper cell ends on dorsal side in distal portion of leaf (Hedenäs & Bizang, 2004; authors' observations). Another example is the case of *Dicranum scoparium* var. *integrifolium* Lindb. that has variable subentire to entire leaf margins. This was a long known subject of confusion for students. The variation occurs throughout the species range and is usually neglected in taxonomic treatments. The variation most likely represents no more than an environmental response.

On the other hand, the mammillose dorsal surface of leaf costa and lamina comprises the main morphological distinction of *D. bardunovii* from *D. acutifolium*. This difference between the two taxa was supported by molecular data (Tubanova *et al.*, 2011; Lang *et al.*, 2014b).

4. While the present study suggested the submerging of *D. spadiceum* var. *subscabrifolium* in a synonymy of *D. spadiceum* var. *spadiceum,* it emerged another entity within *D. spadiceum* which was not noticed earlier. The obtained topology found a clade nested within a basal grade.

A morphological comparison of plants from these two entities revealed that they did share the most essential morphological characters of *D. spadiceum*, *i.e.*, tubular leaves with round cross-section, a narrow costa with differentiated ventral epidermis, and a similar leaf areolation. However, representatives of the grade and the nested clade differ in their plant size (Fig. 3). The measurements in Table 1 and Fig. 4 demonstrate the differences in leaf length and width between the two groups of specimens. There are also some differences in their leaf shape: leaves are gradually tapering to the apex in smaller plants vs. they are more or less suddenly narrowing from basal part to the narrow acumen in larger ones, at least in well-developed plants.

The grade with larger plants includes specimens from Central Europe, Iceland and Svalbard, Kola Peninsula, Caucasus, Urals, Asian Russia and from North America (Wyoming). Leaf size of these plants falls within the morphological description of *D. spadiceum* and is in agreement with the leaf size of type specimens of both

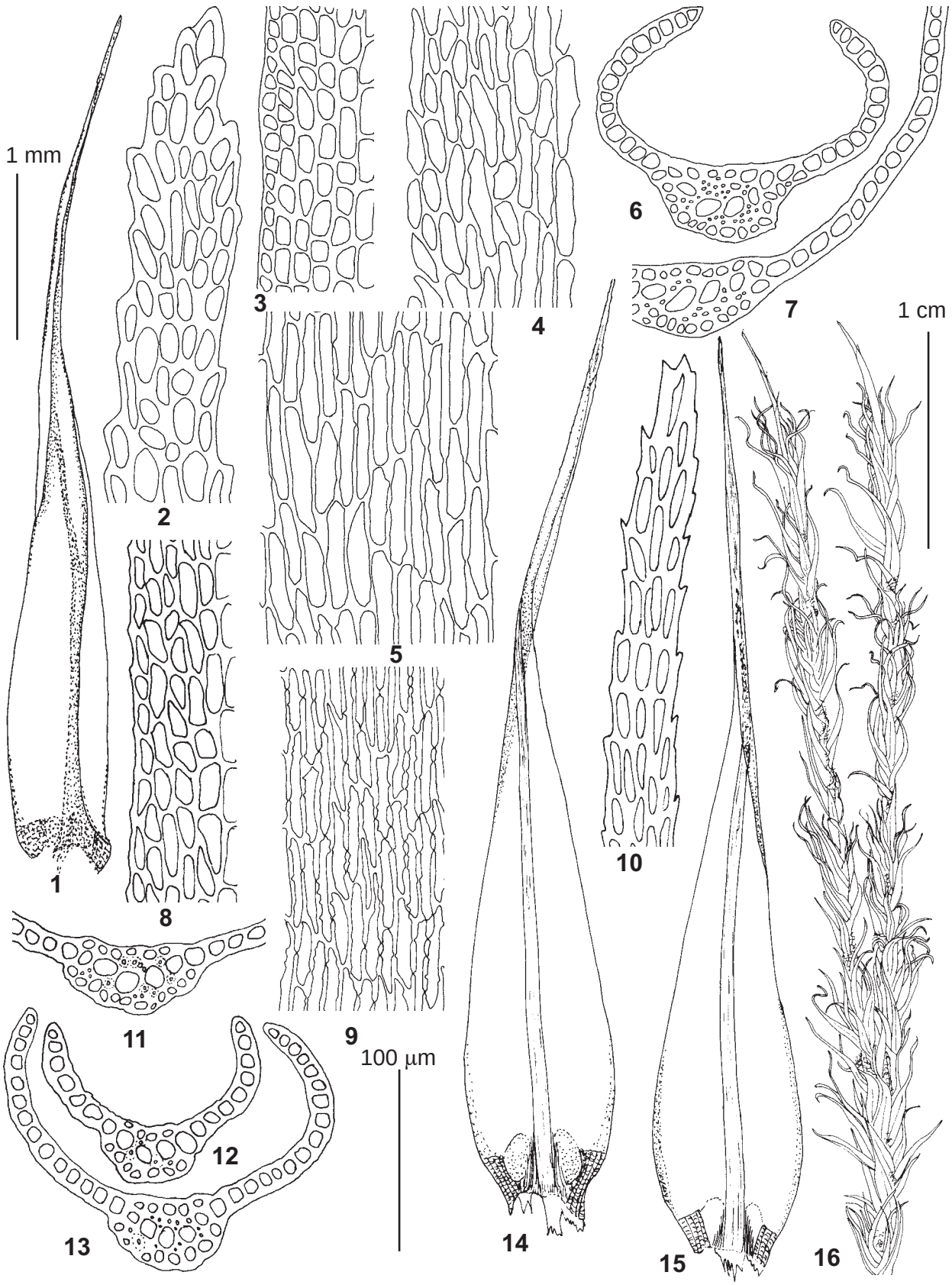


Fig. 5. *Dicranum spadiceum* J.E. Zetterst. (1-7 – from lectotype: Pyrénées, port(?) de Vènasque, 1856, *J. E. Zetterstedt*, S; 8-16 – from: Russia, Kabardino-Balkaria, Shkhelda Creek, 29.VII.2004, *Ignatov et al. s.n.*, MHA). 1, 14-15 – leaves; 2, 10 – cells of leaf tip; 3, 8 – upper laminal cells; 4 – median laminal cells; 5, 9 – basal laminal cells; 6-7, 11-13 – leaf transverse sections; 16 – habit, dry. Scale bars: 1 cm for 16; 1 mm for 1, 14-15; 100 μm for 2-13.

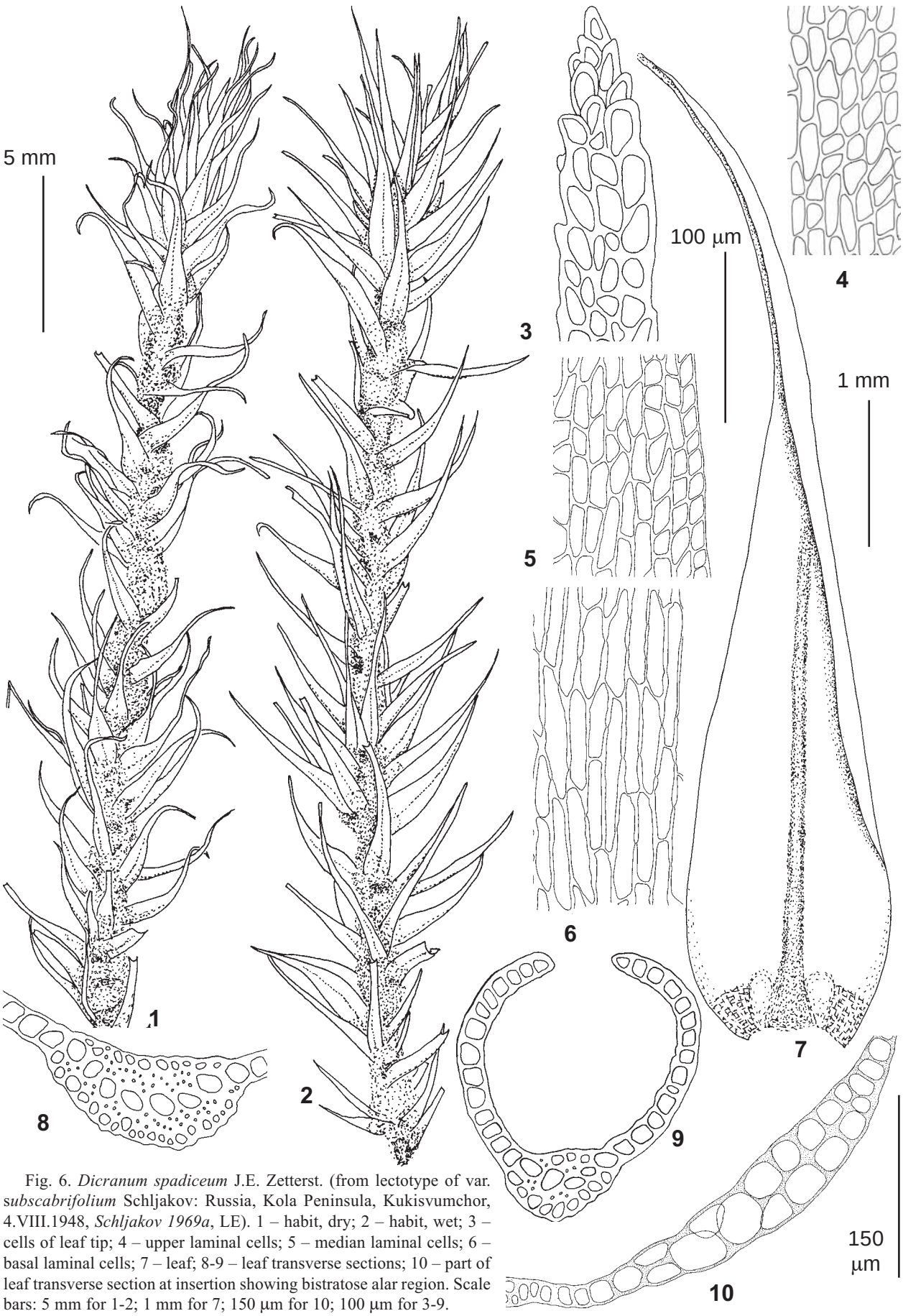


Fig. 6. *Dicranum spadiceum* J.E. Zetterst. (from lectotype of var. *subscabrifolium* Schljakov: Russia, Kola Peninsula, Kukisvumchor, 4.VIII.1948, *Schljakov 1969a*, LE). 1 – habit, dry; 2 – habit, wet; 3 – cells of leaf tip; 4 – upper laminal cells; 5 – median laminal cells; 6 – basal laminal cells; 7 – leaf; 8-9 – leaf transverse sections; 10 – part of leaf transverse section at insertion showing bistratose alar region. Scale bars: 5 mm for 1-2; 1 mm for 7; 150 µm for 10; 100 µm for 3-9.

varieties (Fig. 5: 1-7 and Fig. 6), which were described from Pyrénées and from Kola Peninsula, respectively

The other clade with smaller plants is formed by specimens mostly collected from Asian Russia (Commander Islands, Sakhalin, mainland Far East, Transbaikalia, Yakutia) and westward to Ural Mts (both southern and northern).

The results obtained from the use of molecular markers indicate that the differences of larger and smaller plants are no less sound than the differences between, *e.g.*, *D. flexicaule* and *D. fuscescens.* Therefore, considering the large plants as *D. spadiceum*, we suggest to segregate the small plants as a new, semi-cryptic species to be named *D. schljakovii* (see below). It is quite unusual that the smaller plant size appears to be so taxonomically valuable, being almost the only diagnostic character of the new species. Naturally, quantitative characters usually possess some variations, and of course, in the case of *D. schljakovii*. There is a number of herbarium specimens with intermediate dimensions, but they are the few, and in most cases plants can be identified for sure.

Taxonomic treatment

Dicranum spadiceum J.E. Zetterst., Kongl. Svenska Vetensk. Acad. Handl., n.s. 5(10): 20. 1865. — *D. neglectum* Jur. ex De Not., Atti Reale Univ. Genova 1: 613. 1869. — *D. muehlenbeckii* var. *spadiceum* (J.E.Zetterst.) Podp., Consp. Musc. Eur. 143. 1954. — *Dicranum spadiceum* var. *subscabrifolium* Schljak., Bot. Mater. Otd. Sporov. Rast., Bot. Inst. Komarova Akad Nauk SSSR 7: 242. pl. 3: 1: [g–e]. 1951. Figs. 3A-D, 5-6, 8A,F,R, 9.

Lectotype of *D. spadiceum*: Pyrénées, port(?) de Vènasque (S, № B66312)!

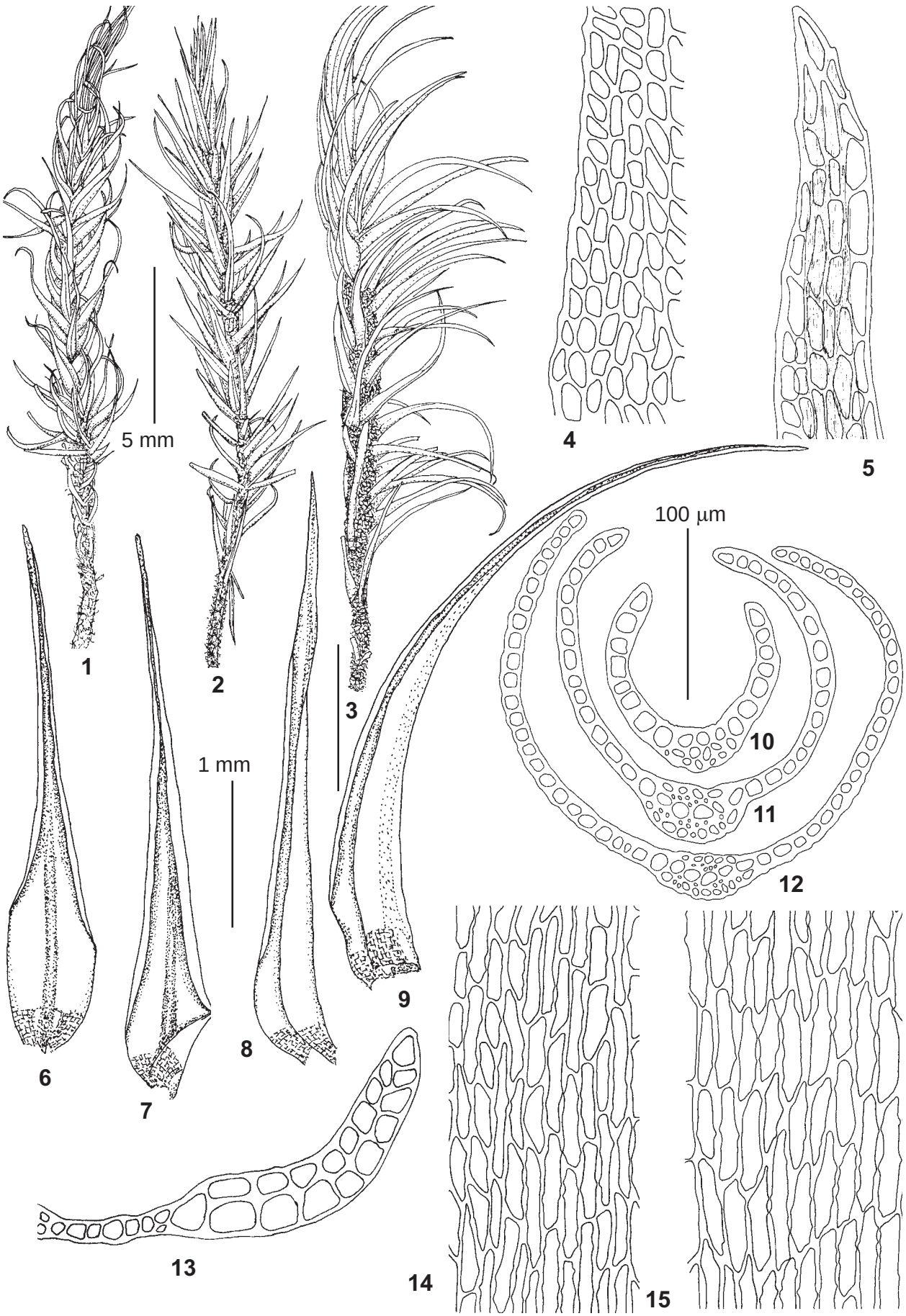
Lectotype of *D. subscabrifolium* (selected here): Russia, Kola Peninsula, Kukisvumchorr, valley of the left tributary of Kukisvumyok Creek, meadow in the lower part of a moraine hill slope, 4.VIII.1948, R.N. Schljakov 1969a (LE).

Plants medium-sized, in dense tufts, light brownish-green, slightly glossy. Stems 6–8(–12) cm, moderately tomentose. Leaves slightly to moderately flexuose, erect-spreading to loosely appressed when dry, straight and erecto-patent when wet, (4.5–)5.5–7(–8)×(0.9–)1.0–1.3 (–1.5) mm, from ovate base gradually to abruptly narrowed into long and narrow tubular acumen, semicircular in transverse section; leaf margins subentire, weakly serrulate or densely serrulate distally; costa narrow, occupies 1/12–1/9 of leaf base, percurrent to shortly excurrent, smooth or weakly to strongly mammillose dorsally in distal leaf portion, in transverse section with one row of guide cells, two stereid bands and differentiated dorsal and ventral epidermises formed by cells with wider lumens; leaf lamina unistratose, smooth or mammillose on dorsal side in leaf acumen; distal lamina cells (12–) 20–40(–66)×(5–)7–10 (–14) μm, isodiametric to rectangular, irregular in shape, thin- to moderately thick-walled, with rounded corners, usually slightly porose, occasionally isodiametric and short rectangular cells are restricted to the uppermost portion of acumen; mid-leaf cells gradually becoming longer; basal leaf cells elongate-rectangular to linear, (23–)47–77(–107)×(4.5–)6–10(–13) μm, with moderately thickened, porose walls, marginal cells in middle part of leaf base in two rows longer and narrower, forming weakly differentiated border; alar cells bistratose, inflated, brown; basal juxtacostal cells narrow and moderately thick-walled, similar to cells of basal portion of costa which makes it vaguely delimited; hyaline and thin-walled cells between costa and alar group absent or few. Phyllodioicous. Sporophytes rare. Seta single, 1.8–2 cm, yellowish. Capsule suberect to slightly inclined, weakly curved, furrowed, 2–2.5 mm long; operculum conic, longly rostrate. Spores 20–25 μm, finely papillose.

Distribution. The species is widespread in mountain areas in Europe, and according to Hedenäs & Bisang (2004), is probably overlooked in some places, especially in Central Europe. *D. spadiceum* is "fairly common in some parts of the Scandes mountains" and known from Iceland (Hallingbäck *et al.*, 2006), Svalbard (Lang *et al.*, 2014a), but absent in Britain (according to Smith, 2004). In European Russia it is rather frequent in Kola Peninsula and in the Caucasus, and known from few localities in Arkhangelsk Province and Komi Republic. Most records of the species from the Urals actually belong to the newly described *D. schljakovii*. In Asian Russia, *D. spadiceum* is common in southern Siberia from Altai Mts to Transbaikalia, and is sporadic in Yakutia and in Arctic and Subarctic areas of Asian Russia, from Subpolar Urals to Chukotka. In Russian Far East this species was reported, but most collections turned out to belong to *D. schljakovii*, although on Commander Islands and in Kamchatka *D. spadiceum* definitely occurs. *D. spadiceum* was also reported from Mongolia and Northern China, but additional revision of these collection is needed. In North America, it is difficult to evaluate the distribution area of *D. spadiceum* because the authors of several treatments of the genus have included *D. angustum* and *D. laevidens* in its synonymy (Bellolio-Trucco & Ireland, 1990; Ireland, 2007), but, at least in Rocky Mts. and NE North America (Newfoundland), *D. spadiceum* s.str. is confirmed.

Ecology. *D. spadiceum* is an arctic-montane species, growing in various types of tundras in the north and in forest reaching to alpine belt in the mountains, in mountain tundras, shrub communities, conifer forests and open stands near timberline, on alpine meadows and mires, in niches of rock-fields and rock outcrops, on cliff ledges, *etc.*

Differentiation. The differences of *D. spadiceum* from *D. schljakovii* are discussed under the latter species. *D. spadiceum* is also frequently confused with *D. muehlenbeckii*, as both species have tubular leaves and differentiated ventral epidermis in the transverse section of costa. Most authors suggest that the slightly curled to loosely appressed leaves in dry state vs. strongly curled ones, as well as weakly serrulate to subentire vs. strongly irregularly dentate distal leaf margins, are the main characters for their distinction (Hedenäs & Bisang, 2004;


5 mm
1
2
3
4
5
100 μm
10
11
12
1 mm
6
7
8
9
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14
15

Hallingbäck *et al*., 2006). However, it is more difficult to separate plants of *D. spadiceum* with serrate margins (previously referred to var. *subscabrifolium*) from *D. muehlenbeckii*, but even then leaves of *D. spadiceum* are less curled. Distal lamina cells irregular in shape vs. quadrate, short rectangular and transversely rectangular are additional helpful diagnostic character.

Synonymization of *D. angustum* and *D. laevidens* with *D. spadiceum* by North American authors suggests that some deviating specimens possess problems in their identification. We also face such problems with some specimens from Russia. All three species share such characters as tubular leaves and a narrow costa. Their distal leaf cells are characterized as ± isodiametric to short-rectangular in *D. spadiceum*, but such cells are occasionally restricted to the uppermost portion of leaf and such specimens may be confused with *D. laevidens* and *D. angustum* which typically have elongate distal lamina cells. However, costal structure in transverse section is different in *D. spadiceum* and in the other two species. The ventral and dorsal epidermis and the two stereid bands are well developed in *D. spadiceum*, while the ventral epidermis formed by cells with larger lumens is lacking in both *D. laevidens* and *D. angustum* (Fig. 8). The latter two species also have a more slender costa, with thinner stereid bands consisting of 1-2 cell layers (Fig. 8).

Selected specimens examined: **EUROPE:** SLOVAKIA: Belanského Tatry Mt., ca. 1690 m a.s.l., 6.VIII.1958, *Pilous 170* (LE). FINLAND: Lapponia enontekiensis, Ridnitshohka, ca. 1250 m. a.s.l., 12.VIII.1958, *Loila & H. Roivainen s.n.* (LE). ICELAND: *Kristbjörn Egilsson 44012*, *43998, 41447*, *43804*, *44012, 43998, 41447, 43804* (ICEL). POLAND: Tatry Zachodnie, Czerwone Wierchu, polnocae zbocze kopy kondrackiej, 1800 m a.l.s., 30.VIII.1956, *S.Lisovski* 605 (LE). EUROPEAN RUSSIA: **Murmansk Province**: Kukisvumchorr, western slope of the southern spur, 04.VIII.1948, *Schljakov 1974* (KPABG); Lovozero Mts, left slope of the gorge, the W slope of Elmarayok, *Belkina 87-34-84* (KPABG); Lovozero Mts, *Belkina 82-10-84* (KPABG); Tolbnyunuay Gorge, 24.VIII.1982, *Belkina & Likhachev 99/3* (KPABG); Voron'ya River basin, Tumannaya River Valley, 2.VIII.1977, *Schljakov 675-77* (KPABG); Khibiny Mts: Poachvumlok River valley, Ramsay Gorge, 11.VII.1948, *Schljakov 1738* (KPABG); upper course of Vuonkemnok River valley, 03.VII.1948, *Schljakov 1642* (KPABG); Kukisvum River valley, Kukisvumchorr, 21.VIII.1947, *Schljakov 1355a* (KPABG); Lovchorr, Botanicheskij Cirque, 12.VIII.1948, *Schljakov 2122* (KPABG); middle part of Tumgok River valley, 30.VII.1930, *Korchagin & Korchagina 165* (KPABG); Yukspor, 12.VII.1930, *Gaze 14753k* (KPABG); Ganeshin cirque slope to the lake Malyj Vudyavr, 21.VII.1947, *Smirnova s.n.* (KPABG); Vudyavrchorr Mt., Vorkunets Stream valley, 19.VII.1947, *Schljakov RS-156-47* (KPABG); Botanicheskij cirque, 03.IX.1947, *Medvedev RM-95-47* (KPABG); Yukspor near Loparskaya pass, 2.VII.1970, *Schljakov* 14754k (KPABG); Kukisvumchorr, 26.VII.1947, *Schljakov 657a* (KPABG); Rasvumchorr, 14.VIII.1947, *Schljakov 1162* (KPABG); Rasvumchorr, 28.VIII.1948, *Schljakov 2231* (KPABG); Rasvumchorr, 14.VIII.1947, *Schljakov 14757k* (KPABG). **Perm Territory:** Vishera Nature Reserve: Kuryksar Ridge, 850 m a.s.l. (61°01'N, 58°51'E), 24.VI.1995, *Bezgodov & Selivanov* 363 (PPU); Oshe-N'yor Ridge: 840 m a.s.l. (61°36'N, 59°24'E), 10.VII.2009, *Bezgodov 364* (PPU); 820 m a.s.l. (61°37'N, 059°20'E), 11.VII.2009, *Bezgodov 411* (PPU). **Bashkortostan Republic**: Beloretzk District, Iremel Mt., Tygynskoe bog (54°31'N, 58°53'E), 994 m a.s.l., 17.VII.2006, *Baisheva 82* (MW); same place, Bolshoi Iremel Mt., 1439 m a.s.l., 19.VII.2006, *Baisheva 87* (MW). CAUCASUS**: Dagestan:** Gunib, 24.05.2009, *Ukrainskaya s.n.* (LE); same place, *Ignatov & Ignatova 09-705* (MW); Charoda District, Gunukh, *Ignatov & Abakarova 11-226* (MW). **Kabardino-Balkaria**: Shkhel'da river, 29.VII.2004, *Ignatov et al. s.n.* (MHA). **Karachaevo-Cherkessia:** Daut River valley, 5.VIII.1993, *Ukrainskaya 14499* (LE); Gudgora, 2200 m a.s.l. (43°43'N, 42°19'E), 14.VII.2010, *Ukrainskaya & Shilnikov* 14643 (LE); the sources of Bermamyt River, 2240 m a.s.l. (43°42'N, 42°27'E), 9.VII.2009, *Ukrainskaya & Shilnikov 14741* (LE); Teberdinsky Nature Reserve, Malaya Khatipara, 13.IX.1999, *Onipchenko 26/99* (MW); same place, Goralykol River, I*gnatova 07-121* (MW). **Severnaya Ossetia/Alania**: North Ossetian Nature Reserve, Tsei River upper course, 1800 m a.s.l., 25.VII.1976, *Abramova L.I. s.n.* (MW). **ASIA**: ASIAN RUSSIA: Yamal-Nenets Autonomous District, Ngaranato Lake (70° 17' N, 68° 57' E), 12.08.1992, *Czernyadjeva 19* (LE). **Khanty-Mansiisk Autonomous District**: Berezovo District, Subpolar Ural Mts., Ner-Oika Mt., Shaitanka River, 2.VIII.2013, *Lapshina 13-103* (MHA); same place, Kabyla-Yu River (64°33'N, 59°37.5'E), 703 a.s.l., 4.VIII.2013, *Lapshina 13-137* (MHA). **Altai Republic**: Ak-Turu, ca. 2400 m a.s.l., 18.VII.1966, *Bardunov* s.n. (IRK) (fr.); Tyuguryuk, ca. 2200 m a.s.l., 23.VI.1966, *Bardunov s.n*. (IRK); Kosh-Agach District, Taldura Creek (49°57'N, 87°50'E), 2360 m a.s.l., *Ignatov & Ignatova 12-597* (MHA). **Khakasia:** Western Sayan**,** the upper reaches of the Malya Ona river, 4.VII.1968, *Bardunov s.n.* (IRK); upper reaches of Karasu River, ca. 2200 m a.s.l., 06.VII.1968, *Bardunov s.n.* (IRK). **Krasnoyarsk Territory**: Taimyr, Byrranga Mts., Bolshaya Bootonkaga River, 7.VIII.1991, *Kuvaev 2071-1* (MW); Western Taimyr, Dikson Settlement, 13.VII.2001, *Varlygina s.n.* (MW); Sibiryakov Island, 2.VIII.1989, *Kuvaev & Poleshchuk 1346-2* (MW); Western Taimyr, Pyasina River, Kresty Settlement, 18.VIII/1976, *Matveeva 592* (LE, MHA); Bikada River lower course (74°50'N, 106°10'E); 16.VIII.1989, *Pospelova s.n.* (MW); Ledyanaya Bay of Taimyrskoe Lake, 13.VIII.2004, *Fedosov Dicr8* (MW); Taimyrsky Nature Reserve, Afanasjevskie Lakes, Fomich River, Fedosov *06-586* (MW); Medvezhjya River, Arydzhang Plateau, *Fedosov 05-203* (MW); Medvezhjya River, Aeterin-Tumus Plateau, *Fedosov 05-12* (MW); Kotujkan River 7 km upstream Merkyu River mouth, *Fedosov 11-947* (MW); Putorana, Nyakshingda Lake, 820 m a.s.l., 23.VII.1968, *Kuvaev 137* (MW); Putorana, Negnekit River, 705 m a.s.l., 12.VIII.1970, *Kuvaev 105* (MW);. **Irkutsk Province:** Baikal'skiy Ridge, the upper part of Lena river opposite Solntsepad, 21.VIII.1995, *Kazanovsky 1278* (IRK). **Buryatia**: Baikal Lake, sources of the river Snezhnaya, 20.VIII.1912, *Smirnov 662* (IRK); Eastern Sayan

Fig. 7 (opposite page). *Dicranum schljakovii* Ignatova & Tubanova (1-2, 4-8, 10-14 – from holotype: Russia, Buryatia, Dzherginsky Nature Reserve, 13.VII.2003, *Anenkhonov Rel. Ku-42/03*, UUH; 3, 9 – from: Russia, Southern Siberia. Zabaikalsky Territory, National Park "Alhanai", 7.VII. 2006, *Afonina 1106*, LE). 1 – habit, dry; 2-3 – habit, wet; 4 – upper laminal cells; 5 – cells of leaf tip; 6-9 – leaves; 10-12 – leaf transverse sections; 13 – part of leaf transverse section at insertion showing bistratose alar region; 14 – median laminal cells; 15 – basal laminal cells. Scale bars: 5 mm for 1-3; 1 mm for 6-9; 100 μm for 4-5, 10-14.

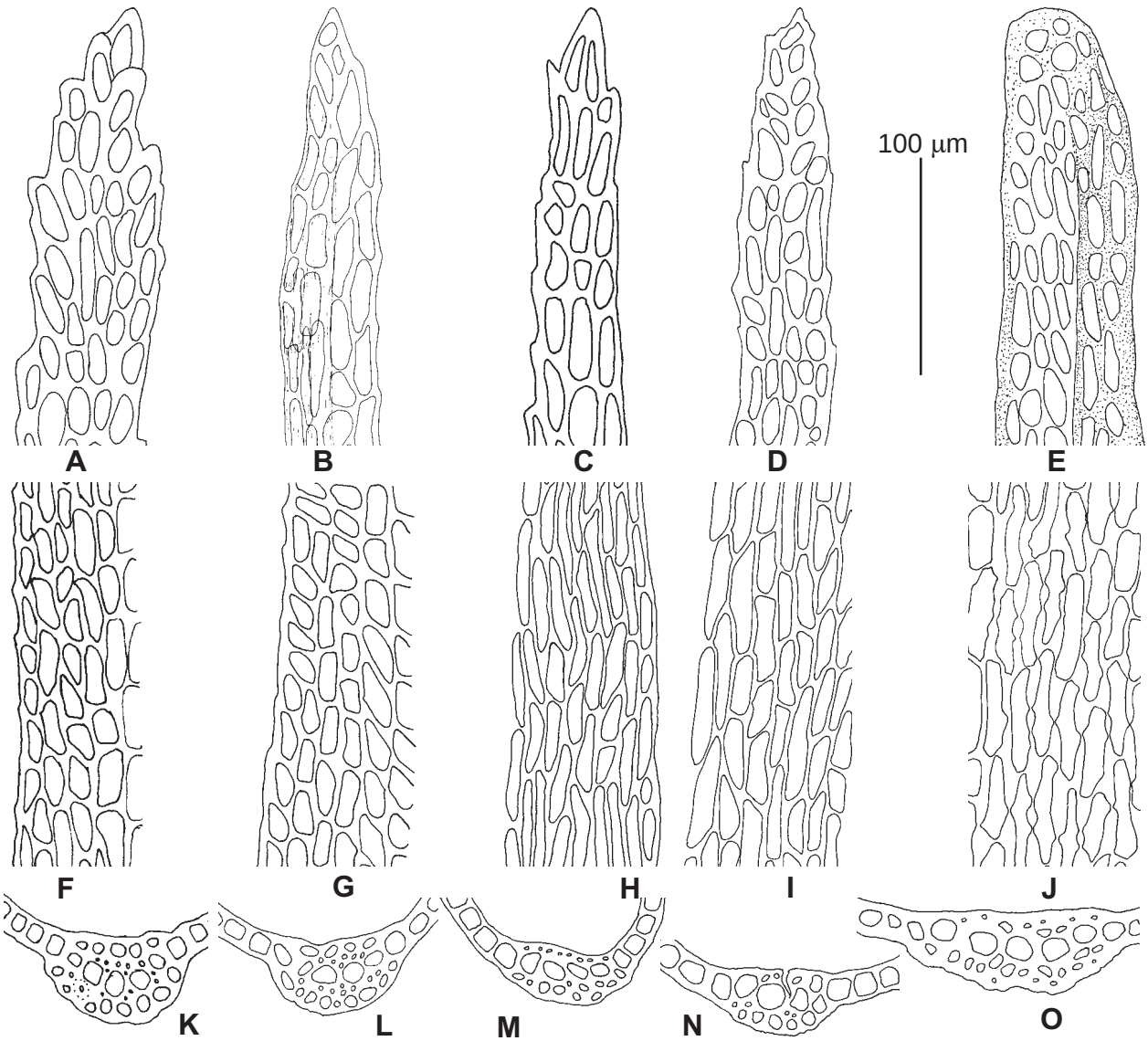

Fig. 8. A comparison of lamina areolation and costa structure of four species of *Dicranum*: A, F, K – *D. spadiceum* J.E. Zetterst.*;* B, G, L – *D. schljakovii* Ignatova & Tubanova; C-D, H-I, M-N – *D. angustum* Lindb.; E, J, O – *D. laevidens* R.S. Williams (A – from lectotype of *D. spadiceum*: Pyrénées, port(?) de Vènasque, 1856, *J. E. Zetterstedt*, F, K – from: Russia, Kabardino-Balkaria, Shkhelda Creek, 29.VII.2004, *Ignatov et al. s.n.*, MHA; B, G, L – from holotype of *D. schljakovii*, Russia, Buryatia, Dzherginsky Nature Reserve, 13.VII.2003, *Anenkhonov Rel. Ku-42/03*, UUH; C, H, M – from holotype of *D. angustum*, Lappovaara, 27 June 1877, *Hjelt & Hult*, H; D, I, H – from Russia, Yamal-Nenetz Autonomous District, Yamburg, 27.VII.2013, *Bezgodov 400*, PPU; E, J, O – from Russia, western Taimyr, Meduza Bay, 6.VII.2003, *Varlygina s.n.*, MW). A-E – cells of leaf tips; F-J – distal laminal cells; K-O – parts of leaf transverse sections. Scale bars: 100 μm for all.

Mts, sources of Burgutuy Creek, ca. 1800 m a.s.l., 12.VIII.1961, *Bardunov s.n.* (IRK); Bolshoj Shibit River, ca. 2080 m a.s.l. 29.VI.1961, *Bardunov s.n.* (IRK); Tunkinskie Goltsy, sources of the river Tunka, 10.VIII.1926, *Smirnov 60* (IRK); Kurumkansky District, Dzherginsky Reserve: 9 km NNW from the source Dzhirga River, ca. 1900 m a.s.l. (55°02'N, 111°41'E), 16.VII.2002, *Tubanova 23(IX)* (UUH); 1.2 km east of Moil, ca. 1960 m a.s.l. (55°05'N, 111°31'E), 12.VII.2002, *Anenkhonov* Op.Ku-02/18 (UUH); 9 km NSW from the sources of Dzhirga River, ca. 1950 m a.s.l. (55°02'N, 111°41'E), 16.VII.2002, *Anenkhonov Op.Ku-02/33, Op.Ku-02/32, Op.Ku-02/28, Op.Ku-02/30* (UUH); Birankur–Ilantakan, ca. 2100 m a.s.l. (55°00'N, 111°36'E), 13.VII.2003, *Anenkhonov Op. Ku-35/03* (UUH); Barguzin Nature Reserve, Valley of Seven Lakes, 1610 m a.s.l. (54°21'233"N, 109°51'702"E), 14.VII.2009, *Krivobokov Op.7-Bar09* (UUH). **Zabaikalsky Territory:** Onon River sources, 1.VIII.1913, *Smirnov 3102*(IRK); vicinity of Akshinsk, sources of Bal'dhzi River, 1913, *Smirnov 3103* (IRK). **Republic of Sakha/ Yakutia:** Tomponsky District: Tukulan River basin, Temirdeekh Creek, 1009 m a.s.l., 9.VI.1990, *Ivanova s.n.* (MHA); Verkhoyanskiy Range, sources of Tompo River, 22.VIII.1956, *V. Ivanova 141/31, 144/29, 144/31* (MHA); Ridge Suntar-Khayata, vicinity Mus-Khaya Mt., Knoriy Creek, 1870 m a.s.l. (62°30'N, 140°58'E), 15.VII.2011, *Ignatov & Ignatova 11-3363* (MHA); Aldan Distr., Yakokit, 23.VII.1995 *Ivanova s.n.* (SASY 2370); Bulun Distr., Tiksi, Suonanakh Creek, 13.VIII.[1987] *Perfilieva s.n.* (SASY 2377); Bulun Distr., Sokol, 14.VIII.1987 *Perfilieva s.n.* (SASY 2374); Allaikhovsky Distr., Gusinaya Guba, *Stepanova s.n.*

17.VIII.1976 (SASY 2373); Ust-Yana Distr., 232 km W of Ust-Kujga, 23.VII.1978 *Stepanova s.n.* (SASY 2380); same 22.VII.1978 (SASY 2371); Zhigansk Distr., Undyulyung River at mouth of Atalakha, 30.VI.1990 *Ivanova s.n.* (SASY 2386); Tomponsky Distr., Tukulan River, 6.IX.1990 *Ivanova s.n.* (SASY 2387); Tomponsky Distr., Sanar River, 8.VIII.1954 *Kuvaev 106/2* (SASY); same 13.VIII.1954 *Kuvaev 122/15* (SASY); Kobyaisky Distr., Keshin Krest Mt., 30.II.1986 *Nikolin s.n.* (SASY 2397); Tomponsky Distr., Sukhalag River (Adycha River tributary), 20.VII.1955 *Dobretsova 132* (SASY); Zhigansk Distr., Undyulyung River at Imgadan Creek mouth, 7.VII.1990 *Nikolin s.n.* (SASY 2382, 2382); Kobyaisky Distr., Kele River, 1843 m alt., 1.VIII.1986 *Nikolin s.n.* (SASY 2384); same, 27.VI.1986 *Nikolin s.n.* (SASY 2403); Kobyaisky Distr., Bytantai River, 12.VI.1990 *Nikolin s.n.* (SASY 2402); Yansky Distr., Selirichen Creek (Bytantai River tributary), 15.IX.1955 *Perfilieva 134/1* (SASY). **Kamchatskaya Province**: Kamchatka Peninsula, Sredinny Range, Irakan River (55°49'N, 158°46'E), 1070 m a.s.l., 11.08.2003, *Czernyadjeva 92* (LE);Aleutsky District, Bering Island, *Fedosov 10-3-173* (MW). **Chukotsky Autonomous District**: Provideniya Bay (64°21'N, 172°36'), 23.VIII.2001, *Afonina s.n.* (LE); Palyavaam River middle course, 13.VII.1989, *Afonina s.n.* (LE); Pekul'nei Range, 18.VII.1979, *Afonina s.n.* (LE); Vrangel Island, Somnitel'naya Bay (70°56'N, 179°37'W), 2.VIII.1985, *Afonina s.n.* (LE). **MONGOLIA**: Mongolian Altai, Bayan-Ulgii District, 37 km N of the Lake Dayan Nuur, ca. 2500 m a.s.l., 29.VI.1973, *Maksimovich 8741* (IRK); Bayan-Hongorsky District, west of the Khukh-Nur Lake, 18.VII.1972, *Banzragch et al. 3993* (LE); Ubsa Nursky District, vicinity of Turun Village, Khan Khukhei Ridge, 22.VII.1945, *Junatov s.n.* (LE); Khubsugul District, S slope Erchmiyn nuru Ridge, Dankhor, 2430 m a.s.l., 29.VII.1974, *Tsegmed s.n.* (LE); Arkhangai District, Solongot Mt., 1.VIII.1972, *Banzragch et al. 4184* (LE). **NORTH AMERICA**: **U.S.A.**: Cook Harbor, White Bay (54°33'N, 55°53'W), 15.VII.1949, *Tuomikoski 3477* (LE).

Dicranum schljakovii Ignatova & Tubanova sp. nova. Figs. 3E-H, 7, 8B, G, L, 9.

Type: Russia, Buryatia, Dzherginsky Nature Reserve, 13.VII.2003, *Anenkhonov Rel. Ku-42/03* (holotype UUH, isotype MW).

Plants small, in low, loose or compact tufts, brownish-green, slightly glossy. Stems 2–4(–6) cm, loosely tomentose. Leaves loosely appressed and slightly flexuose when dry, occasionally falcate-secund, erect-spreading when moist, (3.0–)3.5–4.5(–5.5)×(0.6–)0.7–0.8(–0.9) mm, from ovate base gradually tapering to narrow tubular acumen; margins subentire, slightly serrulate or densely serrate distally; costa narrow, occupies 1/8–1/6 the width of leaf base, percurrent or shortly excurrent, smooth or mammillose dorsally in distal portion, in transverse section with one row of guide cells, two stereid bands, but occasionally ventral stereid band do not reach distal part of costa, and with a differentiated dorsal and ventral epidermises; lamina unistratose, smooth or occasionally mammillose on dorsal side in distal part of leaf; upper lamina cells (10–)14–18(–22)×8–10(–12) μm, irregular in shape, isodiametric to short rectangular, thin- to moderately thick-walled, gradually transiting to longer meadian lamina cells; cells of leaf base elongate-rectangular to linear, (27–)38–64(–83)×(7–)8–10(–13) μm, with moderately thickened, porose walls, occasionally thin-walled and almost without pores; alar cells bistratose, inflated, brownish; cells between costa and alar group like in *D. spadiceum,* weakly delimited from cells of costa, rarely few cells thin-walled and hyaline. Pseudomonoicous? Sporophytes very rare, 1(–2) from perichaetium, perichaetia 1–2(-4) on one plant. Seta 1-1.5 mm. Capsule suberect to slightly inclined, weakly curved, furrowed, ca. 2 mm long; operculum conic, longly rostrate. Spores (15–)20–22 μm, finely papillose.

Etymology. The species name is given in honour of Roman Nikolaevich Schljakov (1912-1999), famous Russian hepaticologist and bryologist, who, in particular, paid a special attention to the genus *Dicranum*.

Variability. Leaf cells of *D. schljakovii* show a considerable variability in cell wall thickness and pitting. The species also possesses both smooth and scabrous dorsal side of costa and lamina in distal part of leaf, representing a parallel pattern with *D. spadiceum*.

Distribution. *D. schljakovii* is known from mountain areas of southern Siberia, Yakutia and Russian Far East, including its continental part and Sakhalin and Kuril Islands, extending to the west to the Urals and known from single locality in Khibiny Mts (Kola Peninsula). Several dijunct localities are also known in Taimyr.

Ecology. This is a mountain species which occurs mostly in subalpine and alpine belts, rarely found below timberline, in open larch and birch forests, and in *Alnus* stands. Grows in various types of mountain tundra, in niches of rock-fields, on mires and meadows.

Differentiation. The species can usually be distinguished from *D. spadiceum*, even visually, without the study of microscopic slides (see Fig 3). The differences between these two species are almost solely quantitative, including their leaf length, (3.0–)3.5–4.5(–5.5) mm vs. (4.5–)5.5–7(–8) mm and leaf width, (0.6–)0.7–0.8(–0.9) mm vs. (0.9–)1.0–1.3(–1.5) mm. *D. schljakovii* never possesses leaves that are rather abruptly tapering from ovate base to a narrow acumen which is frequently observed in plants of *D. spadiceum*. Its costa has a width similar to that of *D. spadiceum*, but it occupies a greater portion of leaf width due to narrower leaves: 1/8–1/6 vs. 1/12–1/9.

Specimens of *D. schljakovii* with thin-walled and almost not porose cells can be confused with *D. angustum*. In such case, the enlarged cells on ventral side of costa in transverse section help to separate the former species from the latter one which does not have a differentiated ventral epidermis. Another helpful character is the absence of hyaline cells between costa and the alar group in *D. schljakovii* and their presence in *D. angustum*.

In plant size and leaf shape, *D. schljakovii* resembles *D. elongatum*, especially in specimens of the latter species with curled leaves and scabrous lamina. However, *D. elongatum* has a much wider costa, occupying to 1/2 of leaf width, and lacks the differentiated ventral epidermis in the transverse section of costa.

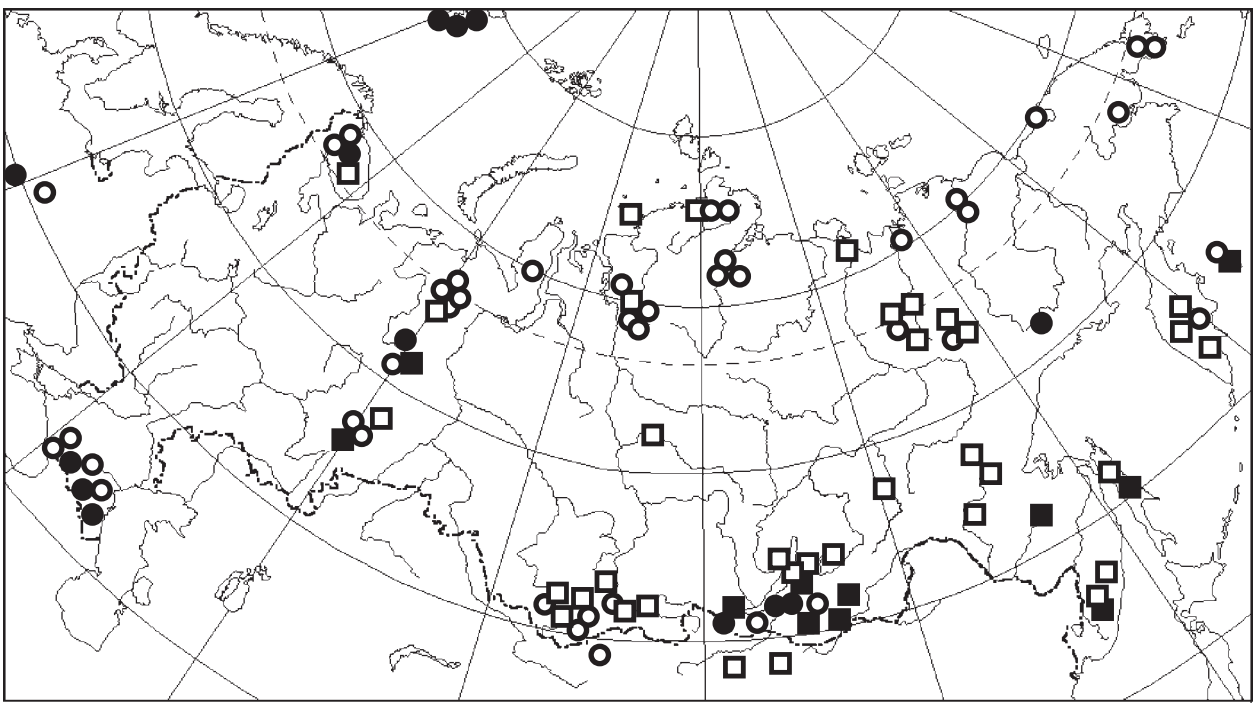

Fig. 9. Distribution of *Dicranum spadiceum* based on specimens sequenced (solid circles) and specimens studied in herbaria (open circles) and *D. schljakovii* based on specimens sequenced (solid squares) and specimens studied in herbaria (open squares).

Specimens examined: EUROPEAN RUSSIA: **Murmansk Province**: Khibiny, Aikuyavenchorr Mt., 498 m a.s.l., 67°35'26" N, 33°42'12"E, 28.VII.2012, *Tubanova KП-3/12* (UUH). **Perm Territory:** Vishersky Nature Reserve: northern slope of Isherim Mt., ca. 900 m a.s.l. (61°11'N, 59°10'E), 4.VII.1998, *Bezgodov 188a* (PPU, MHA, MW); Lop'insky Stone Ridge, peak 931.9 m, ca. 900 m a.s.l. (61°30'30"N, 59°06'E), 28.VII.2009, *Bezgodov 731* (PPU); Oshe-N'yor Ridge, western part, ca. 820 m a.s.l. (61°37'N, 59°20'E), 11.VII.2009, *Bezgodov 441* (PPU); Gornozavodskoy District, Khmeli Mt. sources of Vil'va River, 19.VIII.1987, *Ban'kovsky s.n.* (SYKO); Basegi Nature Reserve, 9.VI.1994, *Ignatov s.n.* (MW). **Bashkortostan**: Beloretsk District, Yuzhnoural'skij Nature Reserve, Mashak Ridge: 30.VI.1996, *Solomeshch 18* (MW); 31.07.1996, *Solomeshch Op.19* (MW); Beloretzk District, Bolshoi Iremel Mt. (54°31'10.5"N, 58°49'50.2"E), 1500 m a.s.l., 19.VII.2006, *Baisheva 91* (MW). **Chelyabinsk Province**: Satka District, Bolshoj Nurgush Mt. (54°49'N, 59°09'E), 1320 m a.s.l., 16.VIII.1997, *Kulikov 20* (MW). **ASIA:** ASIAN RUSSIA: **Khanty-Mansiisk Autonomous District**: Berezovo District, Subpolar Ural Mts., Ner-Oika Mt., Shaitanka River, 2.VIII.2013, *Lapshina 13-98* (MHA). **Republic of Altai:** Altaiskij Nature Reserve, Shantal Ridge, Yankul' Mt., ca. 3010 m a.s.l., 18.VIII.1977, *Zolotukhin & Makhatkov s.n.* (IRK); Karakem River, Kobiguayuk Creek (50°30'N, 89°10'E), 2908 m a.s.l., 19.VI.1989, *Ignatov 0/423* (MHA); same place, Ayulyuyuzyuk Creek, 2300 m a.sl., 16.VI.1989, *Ignatov 0/526* (MHA). **Republic of Khakassia**: Western Sayan Mts., at the border between Tyva and Khakassia, road Abakan – Ak-Dovurak, 6.VIII.2004, *Grigor'eva s.n.* (MW); Western Sayan, Osevoj Sayansky Range, 2230 m a.s.l., 21.VIII.1991, *Kuvaev 2099-6* (MW); Ordzhonikidzhevsky District, Zolotogorsky Settlement, 1600 m a.s.l., 13.VII.1970, *Vasiljev s.n.* (IRK, MHA). **Krasnoyarsk Territory**: Gydanskij Peninsula, 10.VIII.1970, *Meltzer 56(b)* (IRK); Western Taimyr, Willem Barentz Biostation, Meduza Bay, 22.VII.2003, *Varlygina s.n.* (MW); Taimyr, Ledyanaya Bay of Taimyrskoe Lake, 6.VII.2004, *Fedosov Dicr14* (MW); Putorana Plateau: Kapchuk Lake, 25.VII.1982, *Czernyadjeva 98* (LE); Beldunchana Lake, ca. 800 m a.s.l., 2.VIII.1971, *Bardunov s.n.* (IRK); Turukhansk District, 26.VII.1913, *Pole s.n.* (IRK); Baikit District, Central Siberian Nature Reserve, Podkamennaya Tunguska, 8.VII.1994, *Shcherbina 272* (MW); Chistye Klyuchi Railway station between Krasnoyarsk and Abakan, 14.VII.1993, *Shcherbina s.n.* (MW). **Irkutsk Privince:** Vitimsky Nature Reserve: Vitim, near the river Amalyk, 26.VI.1984, *Bardunov s.n.* (IRK); Levaya Sygykta Creek, ca. 1400 m a.s.l., 9.VII.1991, *Bardunov s.n.* (IRK); Lednikovaya River, Sygykty Creek, ca. 1840 m a.s.l., 23.VII.1990, *Anisimova 68* (IRK); Amalyk Creek, ca. 1000 m a.s.l., 10.VIII.1986, *Bardunov s.n.* (IRK); NW Baikal area, Solontsovaya Creek, 1600 m a.s.l., 12.VII.1957, *Bardunov s.n.* (IRK, MHA); Baikal'skiy Ridge, upper course of Lena River opposite Solntsepad, 21.VIII.1995, *Kazanovsky 1278* (IRK). **Republic of Buryatia**: NE Baikal area, Svyatoj Nos, 27.VI.1956, *Bardunov s.n.*, plants with sporophytes (IRK, MHA); NE Baikal area, Bolshaya Rechka, 3.VII.1956, *Bardunov s.n.* (IRK, MHA); Dzherginsky Nature Reserve: 7 km NNW from the sources Dzhirga River, Saddle Ridge, ca. 1980 m a.s.l. (55°02'N, 111°41'E), 17.VII.2002, *Anenkhonov Ku-02/40* (UUH); Barguzin Nature Reserve, Valley of Seven Lakes, 1702 m a.s.l. (54°21,567'N, 109°52,052'E), 14.VII.2009, *Krivobokov 10-Bar09* (UUH); NE Baikal, Bolshaya River, 3.VII.1956, *Bardunov s.n.* (IRK) (fr.); Tunkinskie Goltsy, sources of Tunka River, 10.VII.1926, *Smirnov 60* (IRK); East Sayan Mts: upper course of Oka River, valley of Sorok River, 1703 m a.s.l. (52°33'N, 100°07'E), 06.VII.2008, *Afonina 02008* (LE); vicinity of Arshan Resort, ca. 1800 m a.s.l., 15.VI.1957, *Bardunov s.n.* (IRK); Bolshoj Shibit River, ca. 2080 m a.s.l. 29.VI.1961, *Bardunov s.n.* (IRK); Bolshoj Hangorok Creek, tundra belt, ca. 2000 m a.s.l., 26.VII.1961, *Bardunov s.n.* (IRK); Bel'sky Ridge, Urik River, Chertova Mt., ca. 1860 m a.s.l., 8.VII.1959, *Bardunov s.n.* (IRK). **Zabaikalsky Territory**: Kalar District, vicinity of Kuanda Settlement, 556 m a.s.l. (56°13'54,1"N, 116°08'45.6"E), 04.VIII.2012, *Afonina 6413* (LE) (fr.); Udokan Range, mouth of Scol'skiy Creek,

Namingnakan River, ca. 1400 m a.s.l., 23.VII.1977, *Otnyukova s.n.* (IRK); Kalar District, spur of Udokan Range, deserted settlement Nirungnakan, 17.VIII.1987, *Kozhevnikova & Filin s.n.* (MW); Pass of Menza in Chikoy, Atsinsky Ridge, 13.VII.2006, *Galanin s.n.* (LE); Sokhondinsky Biosphere Reserve, Upper Bukukun River: 4.VIII.2000, *Galanin & Belikovich* s.n. (LE) (fr.); 1977 m a.s.l. (49°39'N, 111°03'E), 29.VII.2008, *Afonina 308708a* (LE). **Republic of Sakha/ Yakutia**: Aldan District, opposite Kurungkhokhoyo Aryta Island, lower course of Uchur River, ca. 550-650 m a.s.l., 1.VIII.1991, *Ivanova E.I. s.n.* (MW); Olekminsk District, Toko River, 23.VII.1995, *Krivoshapkin 02.04.07.20* (MHA); Tomponsky District: Tukulan River, Temirdeeh Creek, 1009 m a.s.l., 9.VI.1990, *Ivanova E. s.n.* (MHA); Bulun Distr., Sokol, 14.VIII.1987 *Perfilieva s.n.* (SASY 2376); same place, 11.VIII.1987 *Perfilieva s.n.* (SASY 2375); Ust-Yansky Distr., 50 km W of Kular, 23.VII.1978 *Stepanova s.n.* (SASY 2379); Ust-Yana Distr., 238 km W of Ust-Kujga, 23.VII.1978 *Stepanova s.n.* (SASY 2372); Verkhoyansk Distr., Verkhoyansk, 6.VII.2007, *Isakova s.n.* (SASY 2395); Verkhoyansk Distr., Kisilyakh Mts., 15.VII.2007, *Isakova s.n.* (SASY 2393, 2394); Verkhoyansk Distr., Elgetsk, 7.VIII.2007, *Isakova s.n.* (SASY 2392); Kobyaisky Distr., Ilderkey Lake, 20.VII.1986 *Nikolin s.n.* (SASY 2388); Kobyaisky Distr., Kele River, 1.VIII.1986 *Nikolin s.n.* (SASY 2381); same, 4.VIII.1986 Nikolin (SASY 2385); Zhigansk Distr., Undyulyung at mouth of Byrandya, 986 m alt., 14.VII.1990 *Kirillina s.n.* (SASY 2390); same, 14.VII.1990 *Akimova s.n.* (SASY 2399); Zhigansk Distr., Undyulyung River upper course, 12.VI.1990 *Nikolin s.n.* (SASY 2398); Tomponsky Distr., Talchan Creek (Barai River – tributary in Lower course of Aldan River), 11.IX.1957 *Dobretsova s.n.* (SASY); Tomponsky Distr., Aenykchan (tributary of Anman-Dykan), 19.VIII.1955 *Dobretsova 189/1* (SASY); Tomponsky Distr., Tukulan River, 6.IX.1990 *Ivanova s.n.* (SASY 2405); Tomponsky Distr., Chukoman Creek (Menkule River Basin), 25.VIII.1956 *Ivanova 152/56* (SASY). **Khabarovsk Territory**: Bureya Nature Reserve: 14.VII.1992, *Borisov 92-1* (MW); Medvezh'e Lake, 12.VIII.1997, *Ignatov 97-992* (MHA); Geran Ridge, ca. 1500 m a.s.l., 18.VII.1975, *Shlotgauer & Bardunov s.n.* (IRK). **Kamchatskaya Province**: Shiveluch volcano, ca. 150 m a.s.l. (56°27'N, 161°01'E), 18.VII.2001, *Czernyadjeva 18* (LE) (fr.); Kluchevskaya group of volcanoes: Ostryj Tolbachik volcano, Tolbinsky dol, vicinity of Lesnaya Mt., 660 m a.s.l. (55°40'N, 160°23 'E), 05.IX.2007, *Neshataeva 1139* (LE); NW macroslope of Ushkovskij Volcano, valley of the glacier Bilchenok, ca. 1000 m a.s.l. (56°11'N, 160°21'E), 24.VII.2003, *Czernyadjeva 65* (LE); Aleutsky District, Bering Island, *Fedosov 10-3-165* (MW). **Primorsky Territory**: Oblachnaya Mt., 1840 m a.s.l., 18.VIII.2007, *Ignatov 07-280* (MHA). MONGOLIA: Ubsanursky District, vicinity Turgen Village, N slope of Turgen Mt., ca. 2600 m a.s.l., 08.VII.1973, *Tsegmed 427* (LE); Central District, Batu Sumbur village, SW Khentei, 5 km NW of Asaralgu Hayrkan Mt., 15.VI.1943, *Yunatov 17451* (LE).

KEY TO IDENTIFICATON OF SPECIES OF *DICRANUM* SECT. *MUEHLENBECKIA*, WITH ADDITION OF *D. LAEVIDENS*

1. Costa without differentiated ventral epidermis in transverse section; distal lamina cells rectangular to elongate-rectangular 2
— Costa with differentiated ventral epidermis formed by cells with wide lumens in transverse section; distal lamina cells subquadrate, short-rectangular or irregular in shape 3
2. Leaves soft, slightly flexuose, with acute apices; distal leaf margins weakly serrulate; costa 1/9-1/10 of the leaf base width; lamina cells with thin or slightly thickened walls, not porose throughout, or only weakly porose at basal part of leaf ..... *D. angustum*
— Leaves rigid, straight, with obtuse apices; costa 1/13–1/10 of the leaf base width; lamina cells thick-walled and strongly porose ..... *D. laevidens*
3. Stems densely tomentose throughout, tomentum rusty or brownish-colored; plants in dense and compact tufts; leaves crisped when dry; leaf margins serrate distally; costa 1/6–1/5 the width of leaf base; distal lamina cells subquadrate ..... *D. muehlenbeckii*
— Stems loosely tomentose, tomentum whitish or pale brownish; leaves slightly flexuose when dry, occasionally falcate-secund; leaf margins subentire to densely serrulate; costa 1/9–1/6 the width of leaf base; distal lamina cells short rectangular or isodiametric and irregular in shape 4
4. Plants small, leaves (3.0–)3.5–4.5(–5.5) × (0.6–)0.7–0.8(–0.9) mm, flexuose when dry, occasionally falcate-secund; costa 1/8–1/6 of leaf base width .... *D. schljakovii*
— Plants medium-sized, leaves (4.5–)5.5–7(–8)×(0.9–)1.0–1.3(–1.5) mm, flexuose when dry; costa 1/12–1/9 of leaf base width ..... *D. spadiceum*

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Appendix 1: Species of *Dicranum* and *Holomitrium arboreum* used in analyses, with GenBank accession numbers and voucher information for specimens from Russia. The numbers of newly generated sequences are boldfaced.

Species	# in tree	nrITS1-2	*trn*L-F	Specimen data (for newly generated sequences)
Holomitrium arboreum	PA17b	KF423640	KF423994	Brasil
acutifolium	A1	HQ830322	–	Russia, Sakhalin, *Ignatov 06-18* (MHA)
acutifolium	A2	HQ830323	–	Russia, Buryatia, 07.VII.2008, *Tubanova Ok-01/08* (UUH)
acutifolium	Dac	KJ650881	–	Finland
acutifolium	Dic_1676	KJ650879	KJ651084	Norway
acutifolium	Dic_1661	KJ650866	KJ651070	Norway
acutifolium	Dic_166	KJ650865	KJ651069	Norway
acutifolium	Dic_1649	KJ650858	KJ651061	Norway
acutifolium	Dic_1644	KJ650855	KJ651057	Norway
angustum	SE_31	KJ650894	KJ651094	Swedwen
angustum	SE_27	KJ650893	KJ651093	Swedwen
angustum	SE_22	KJ650892	KJ651092	Swedwen
angustum	SE_4	KJ650891	KJ651091	Swedwen
angustum	SE_25	KJ650890	KJ651090	Swedwen
angustum	A220	**KT580732**	**KT580678**	Russia, Yamalo-Nenetskiy AD, 29. VII.2013, *Bezgodov 463a* (PPU)
angustum	A200	**KT580730**	**KT580676**	Russia, Yamalo-Nenetskiy AD, 27. VII.2013, *Bezgodov 400* (PPU)
angustum	A202	**KT580731**	**KT580677**	Russia, Yamalo-Nenetskiy AD, 23. VII.2013, *Bezgodov 335* (PPU)
bardunovii	1_II	KJ796547	KJ796597	Russia, Buryatia, 12.07.2000, *Krivobokov On. 262* (UUH)
bardunovii	B74	JN897274	KJ796600	Russia, South Yakutia, 20.06.1985, *Volotovskiy on.II* (MW)
bardunovii	B104	JN897273	KJ796599	Russia, Yakutia (Sakha), 01.08.1991, *Ivanova s.n.* (MW)

Species	# in tree	nrITS1-2	*trn*L-F	Specimen data (for newly generated sequences)
bardunovii	B96	JN897272	–	Russia, Buryatia, 12.07.2000, *Krivobokov On. 262* (UUH)
brevifolium	CH1	KJ650895	KJ651095	Switzerland
brevifolium	B3	HQ830343	KJ796589	Russia, North Ossetia, 6.IX.2002, *Korotkov s.n.* (MW)
brevifolium	B4	HQ830341	KJ796588	Russia, Tuva, 12.VI.2007, *Otnyukova s.n.* (KRF)
brevifolium	B2	HQ830342	KJ796587	Russia, Karachaevo-Cherkessia, 27.VII.1996, *Egorov s.n.* (MW)
brevifolium	B1	HQ830344	–	Russia, Yakutia (Sakha) , 3.VIII.2000, *Kuznetzova s.n.* (MW)
brevifolium	SE_15	KJ650896	KJ651096	Sweden
caesium	C141	**KT580733**	**KT580680**	Russia, Amurskaya Province, 08.VI.2011, *Bezgodov 60* (PPU)
caesium	C116	–	**KT580679**	Japan, Shikoku, 27.XI.1999, *Deguchi 204* (LE)
dispersum	Di170	**KT580734**	–	Russia, Zabaikalskiy Territory, 09.VIII.2012, *Afonina 8912* (LE)
dispersum	Di 29	**KT580746**	**KT580692**	Russia, Primorskiy Territory, 17.X.2008, *Ignatov 08-317* (MHA)
dispersum	Di 77	**KT580740**	**KT580686**	Russia, Dagestan, 19.V.2009, *Ignatov & Ignatova 09-189* (MHA)
dispersum	Di 64	**KT580739**	**KT580685**	USA, Alaska, 10.VII.2004, *Breen T001-3B* (LE)
dispersum	Di 63	**KT580738**	**KT580684**	Russia, Buryatia, 18.VII.2010, *Tubanova Kях-6/10* (UUH)
dispersum	Di 51	**KT580737**	**KT580683**	Russia, Irkutsk Province, 10.VIII.2004, *Dudareva 04-35* (IRK)
dispersum	Di 33	**KT580736**	**KT580682**	Russia, Buryatia, 27.VII.1999, *Krivobokov on.113* (UUH)
dispersum	Di 28	**KT580735**	**KT580681**	Russia, Ingushetia, 19.VII.2005, *Bersanova s.n.* (MHA)
drummondii	Dr109	**KT580741**	**KT580687**	Russia, Kamchatka, 10.VIII.2007, *Neshataeva Op.1022* (LE)
drummondii	Dr 73	**KT580744**	**KT580690**	Russia, Murmansk Province, 30.VII.2009, *Kozhin & Leonova M-M-0542* (MW)
drummondii	Dr 71	**KT580743**	**KT580689**	Russia, Leningrad Province, 11.VIII.2006, *Kurbatova 211* (LE)
drummondii	Dr 31	**KT580742**	**KT580688**	Russia, Komi, 05.VII.2007, *Kucherov 169* (MHA)
flexicaule	FL212	**KT580745**	**KT580691**	Russia, Buryatia, 14.07.2009, *Krivobokov Op.10-Bar09* (UUH)
flexicaule	PA1	HQ830330	KJ796582	Russia, Krasnoyarsk Territory, Putorana, 29.VII. 1991 *Otnyukova s.n.* (KRF)
flexicaule	PA3	HQ830328	KJ796581	Russia, Tuva, 23.VII.1995 *Molokova s.n.* (KRF)
flexicaule	FL1	HQ830331	KJ796583	Russia, Transbaikalia, 4.VIII. 2006 *Dudareva s.n.* (IRK)
flexicaule	FL2	HQ830332	KJ796584	Russia, Primorie, *Ignatov 06-2637* (MHA)
flexicaule	FL3	HQ830333	–	Russia, Komi, 4.VII.2007 *Kucherov s.n.* (MW)
flexicaule	PA2	HQ830329	–	Russia, Putorana, 29.VII. 1991, *Otnyukova s.n.* (MHA)
flexicaule	Alk_7	KJ650854	KJ651056	Norway?
flexicaule	Alk_6	KJ650853	KJ651055	Norway?
flexicaule	Alk_5	KJ650852	KJ651054	Norway?
flexicaule	Alk_4	KJ650851	KJ651053	Norway?
flexicaule	Alk_3	KJ650850	KJ651052	Norway?
flexicaule	Alk_2	KJ650849	KJ651051	Norway?
fuscescens	Dfus6	KJ650898	KJ651098	Netherlands
fuscescens	FU1	HQ830334	KJ796578	Russia, Perm Province, 2005 Bezgodov & Shkaraba *s.n.* (MHA)
fuscescens	FU4	HQ830337	KJ796579	Russia, Primorsky Territory, *Ignatov 06-2588* (MHA)
fuscescens	FU2	HQ830335	KJ796580	Russia, Sakhalin, *Ignatov 06-14* (MHA)
laevidens	Dic_1672	KJ650876	KJ651081	Norway
laevidens	Dic_1663	KJ650868	KJ651072	Norway
laevidens	Dic_1662	KJ650867	KJ651071	Norway
laevidens	Dic_1653	KJ650862	KJ651065	Norway
laevidens	Dic_1652	KJ650861	KJ651064	Norway
laevidens	Dic_1651	KJ650860	KJ651063	Norway
laevidens	L87	**KT580748**	**KT580695**	Russia, Taimyr, 29.VI.2009, *Fedosov 09-253* (MW)
laevidens	L86	**KT580747**	**KT580694**	Russia, West Taimyr, 06.VII.2003, *Varlygina s.n.* (MW)
laevidens	L203	–	**KT580693**	Russia, Yamalo-Nenetskiy AD, 29.VII.2013, *Bezgodov 471* (PPU)
laevidens	SE_6	KJ650889	–	Norway?
muehlenbeckii	Mu62	**KT580752**	**KT580699**	Russia, Buryatia, 18.VII.2010, *Tubanova Kaykh-6/10* (UUH)
muehlenbeckii	Mu54	**KT580751**	**KT580698**	Russia, Sverdlovsk Province, 12.VII.1996, *Nikonova s.n.* (MW)
muehlenbeckii	Mu53	**KT580750**	**KT580697**	Russia, Irkutsk Province, 05.VII.2003, *Dudareva 593* (IRK)
muehlenbeckii	Mu34	**KT580749**	**KT580696**	Russia, Altai Territory, 1992-1993, *Ignatov & Ignatova 24/34* (MHA)
***orientale* (type)**	Di 35	**KT580753**	**KT580700**	Russia, Tyva, 01.VIII.1995, *Otnyukova s.n.* (MHA)
schljakovii	SF166	**KT580762**	**KT580709**	Russia, Zabaikalskyi Territory, 11.VIII.2012, *Afonina 9312* (LE)
schljakovii	SF174	**KT580763**	**KT580710**	Russia, Zabaikalskyi Territory, 13.VII.2006, *Afonina 1106* (LE)
schljakovii	SF9	**KT580764**	**KT580711**	Russia, Zabaikalskyi Territory, 01.VIII.2006, *Dudareva s.n.* (IRK)
schljakovii	S38	**KT580758**	**KT580705**	Russia, Ural, 09.VI.1994, *Ignatov s.n.* (MHA)
schljakovii	S172	**KT580754**	**KT580701**	Russia, Zabaikalskiy Territory, 06.VIII,2012, *Afonina 7212* (LE)
schljakovii	S222	**KT580755**	**KT580702**	Russia, Perm Territory, 09.VII.2009, *Bezgodov 341* (PPU)
schljakovii	S36	**KT580757**	**KT580704**	Russia, Primorskiy Territory, 18.VIII.2007, *Ignatov 07-280* (MHA)
schljakovii	S89	**KT580761**	**KT580708**	Russia, Buryatia, 13.VII.2003, *Anenkhonov Op.Ku-42/03* (UUH)

Species	# in tree	nrITS1-2	*trn*L-F	Specimen data (for newly generated sequences)
schljakovii	S39	**KT580759**	**KT580706**	Russia, Khabarovsk Territory, VII.1992, *Borisov 92-1* (MW)
schljakovii	S23	**KT580756**	**KT580703**	Russia, Bashkortostan. 30.VI.1996, *Solomesh* 18 (MW)
schljakovii	1002	**KT580775**	**KT580721**	Russia, Sakhalin, *Ignatov & Teleganova 06-760* (MW)
schljakovii	1004	**KT580776**	**KT580722**	Russia, Commander Is., Bering I., *Fedosov 10-3-165* (MW)
septentrionale	FIN_1	KJ796546	KJ796596	Finland
septentrionale	SE_17	KJ796545	KJ796595	Sweden
septentrionale	S1	HQ830339	KJ796586	Russia, Arkhangelsk Province, *Churakova* 864 (MW)
septentrionale	S3	HQ830338	KJ796585	Russia, Kamchatka, 4.VIII.2007 *Neshataeva s.n.* (LE)
septentrionale	S2	HQ830340	–	Russia, Krasnoyarsk Territory, Putorana, 21.VII.1969 *Kuvaev s.n.* (KRF)
spadiceum	Is_9	KF423595	KF423950	Iceland
spadiceum	Is_8	KF423594	KF423949	Iceland
spadiceum	Is_7	KF423593	KF423948	Iceland
spadiceum	*Is_5*	*KF423592*	*KF423947*	*Iceland*
spadiceum	Dic_1677	KJ650880	KJ651085	Norway, Svalbard
spadiceum	Dic_1673	KJ650877	KJ651082	Norway, Svalbard
spadiceum	Dic_1671b	KJ650873	KJ651079	Norway, Svalbard
spadiceum	Dic_1669	KJ650872	KJ651077	Norway, Svalbard
spadiceum	Dic_1667	KJ650871	KJ651075	Norway, Svalbard
spadiceum	Dic_1666	KJ650870	KJ651074	Norway, Svalbard
spadiceum	Dic_1665	KJ650869	KJ651073	Norway, Svalbard
spadiceum	Dic_1659	KJ650864	KJ651068	Norway, Svalbard
spadiceum	Dic_1654	KJ650863	KJ651066	Norway, Svalbard
spadiceum	Dic_1645	KJ650856	KJ651058	Norway, Svalbard
spadiceum	Su224	**KT580766**	**KT580713**	Russia, Caucasus, 14.VII.2010, *Ukrainskaya*, #14644 (LE)
spadiceum	Su127	**KT580765**	**KT580712**	Russia, Irkutsk Province, 21.VIII.1995, *Kazanovskiy 1278* (IRK)
spadiceum	Su289	**KT580768**	**KT580715**	Russia, Buryatia, 16.VII.2002, *Anenkhonov Op.Ku-02/28* (UUH)
spadiceum	Su82	**KT580772**	**KT580719**	Russia, Buryatia, 16.VII.2002, *Anenkhonov Op.Ku-02/33* (UUH)
spadiceum	Su288	**KT580767**	**KT580714**	Russia, Perm Territory, 10.VII.2009, *Bezgodov 364* (PPU)
spadiceum	Su287	**KT580773**	**KT580720**	Russia, Yakutia (Sakha) 15.VII.2011, *Ignatov & Ignatova 11-3363* (MHA,MW)
spadiceum	Su81	**KT580771**	**KT580718**	Russia, Kabardino-Balkariya, 29.VII.2004, *Ignatov, Ignatova & Kharzinov s.n.* (MHA)
spadiceum	Su80	**KT580770**	**KT580717**	Russia, Buryatia, 14.VII.2009, *Krivobokov Op.07-Bar09* (UUH)
spadiceum	Su56	**KT580769**	**KT580716**	Russia, Murmansk Province, 30.VII.2006, *Ignatova s.n.* (MW)
spadiceum	1001	**KT580777**	**KT580723**	USA Wyoming, Beartooth Plateau, *Kosovich-Anderson 2394* (MHA ex herb. Kosovich-Anderson)
spadiceum	1003	**KT580778**	**KT580724**	Russia, Karachaevo-Cherkeyssya, Daut, *Onipchenko 21/00* (MW)
spadiceum	1005	**KT580779**	**KT580725**	Austria, *Köckinger 14-989* (Herb. Köckinger)
spadiceum	993	**KT580780**	**KT580726**	Russia, Murmansk Province, Khibiny, Aykuayvenchorr, *Ignatov & Ignatova 12-124* (MHA)
spadiceum	995	**KT580781**	**KT580727**	Austria, Schneeberg, 1700 m, *Ignatov & Schanzer 05-5054*(MHA)
spadiceum	997	**KT580782**	**KT580728**	USA, Wyoming, Beartooth Plateau, *Kosovich-Anderson 38-04* (MHA ex US)
spadiceum	998	**KT580783**	**KT580729**	USA Wyoming, Beartooth Plateau, *Kosovich-Anderson 2344* (MHA ex herb. Kosovich-Anderson)
spadiceum	999	**KT580784**	–	USA Wyoming, Beartooth Plateau, *Kosovich-Anderson 2356* (MHA ex herb. Kosovich-Anderson)
viride	Tatarstan	FJ952607	–	Tatarstan 17.VIII.2003 *Ignatov & Ignatova s.n.* (MHA)
viride	Moscow	FJ952608	–	Moscow 20.VII.1990 *Ignatov s.n.* (MHA)