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# ON *DICRANUM ELONGATUM* AND *D. GROENLANDICUM* IN RUSSIA

# О *DICRANUM ELONGATUM* И *D. GROENLANDICUM* В РОССИИ

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Abstract

Distinction between *Dicranum elongatum* and *D. groenlandicum* was tested with molecular markers. Molecular phylogenetic analysis of nuclear ITS1-2 and chloroplast *trn*L-F sequences confirmed separate status of these species. The importance of width of costa for their delimitation was confirmed; however, cell length in distal and proximal parts of leaves appeared to be variable in both species. Leaf apex in *D. groenlandicum* is occasionally acute and margins are denticulate near apex in some specimens, contrary to the statement in most handbooks that they are invariably entire and that leaf apex is always obtuse. *Dicranum elongatum* and *D. groenlandicum* have similar distribution in Russia. They occur in northern provinces of European Russia and Urals, are known by few records in the Caucasus and are widely distributed in Asian Russia, from Arctic regions to Southern Siberia.

Резюме

С помощью молекулярных маркеров уточнены границы между *Dicranum elongatum* и *D. groenlandicum*. Анализ последовательностей ITS1-2 ядерной и *trn*L-F хлоропластной ДНК подтвердил их видовую самостоятельность. Было показано, что наиболее устойчивым морфологическим признаком, позволяющим разграничивать эти виды, является ширина жилки, тогда как длина клеток в верхней и нижней части листа варьирует у обоих видов. Верхушка листа *D. groenlandicum* может быть заостренной, а края в верхней части листа иногда бывают пильчатыми, вопреки распространенному во многих определителях утверждению, что у этого вида верхушка всегда туповатая, а края листа цельные. *Dicranum elongatum* и *D. groenlandicum* имеют сходное распространение в России. В европейской части они встречаются в северных областях и на Урале и известны по единичным находкам на Кавказе, а в Азиатской части оба вида широко распространены от Арктики до гор южной Сибири.

KEYWORDS: *Dicranum*, Dicranaceae, mosses, taxonomy, ITS, *trn*l-F, Russia

## INTRODUCTION

*Dicranum elongatum* Schleich. ex Schwägr. and *D. groenlandicum* Brid. were reported from Russia in 19th century (Lindberg & Arnell, 1890; Brotherus & Saelan, 1890). However, first comprehensive taxonomic publication where both species were described and compared was the treatment of Brotherus (1918) in the series "Flora of Asian Russia" published for both vascular and spore plants by Fedchenko. In this publication, *Dicranum elongatum* was keyed out together with four other species: *D. tundrae* Lindb. & Arnell*, D. atratum* Geh.*, D groenlandicum* and *D. angustum* Lindb. Two of them, *D. tundrae* and *D. atratum*, were described in this flora using translations of original descriptions, with brief comments that they are very close to *D. elongatum* and merely are not a separate species. However, Brotherus preferred to retain them, not synonymizing until the additional data will be available.

Subsequent floras of the USSR (Abramova *et al.*, 1961; Savicz-Lyubitskaya & Smirnova, 1970) accepted three species in this group, *D. elongatum, D groenlandicum* and *D. angustum*, while *D. tundrae* was referred to *D. elongatum,* and *D. atratum* was simply not treated. However, being congruent in this overall resolution, the two latter treatments differed in character evaluation. For example, *D. elongatum* var. *sphagni* T. Jensen, that differs from the typical *D. elongatum* primarily by narrow costa, was referred to the synonymy of *D. elongatum* by Abramova *et al*. (1961), following Brotherus (1918) and many other authors, while Savicz-Lyubitskaya & Smirnova (1970) referred *D. elongatum* var. *sphagni* to *D. groenlandicum*. Although the latter synonymization is less common, it is not unique: for example, in the Moss flora of China *D. elongatum* var. *sphagni* is also included to the synonymy of *D. groenlandicum* (Gao *et al.*, 1999).

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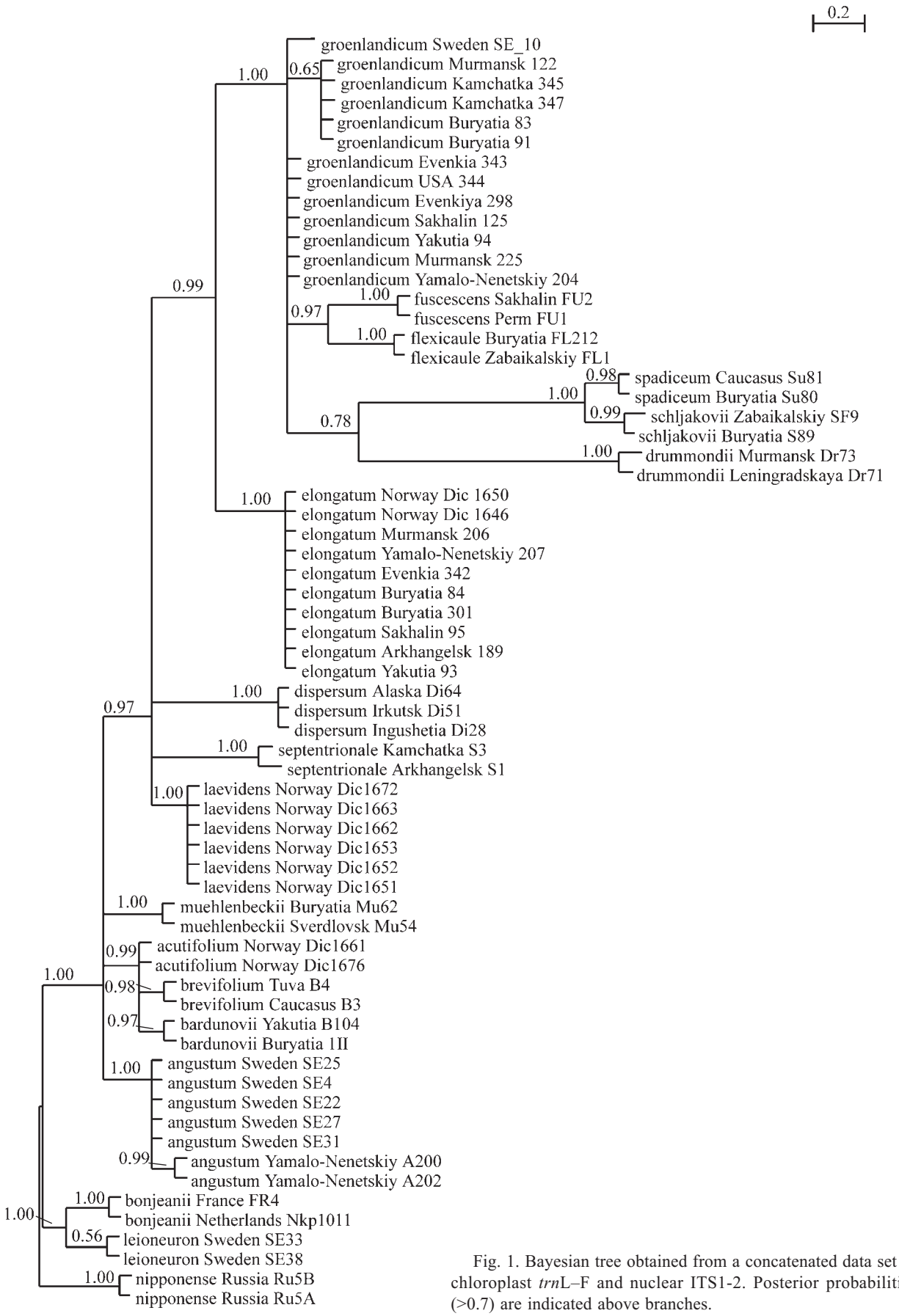


Fig. 1. Bayesian tree obtained from a concatenated data set of chloroplast *trn*L–F and nuclear ITS1-2. Posterior probabilities (>0.7) are indicated above branches.

Different estimation of some distinctive characters of these species led some authors to conclusion that the distinctions between *D. elongatum* and *D groenlandicum* are not absolute, thus *D. groenladicum* was accepted only as a subspecies of *D. elongatum* (Moenkemeyer, 1927; Podpera, 1954, Ignatov & Afonina, 1992). In recent floras these taxa are mostly accepted at species level (Ireland, 2007; Hallingbäck *et al.*, 2006; Noguchi & Iwatsuki, 1987); however, incongruence in the treatment of the most important diagnostic characters still remains, causing problems with their identification.

Although molecular data indicated considerable difference between these two species (Lang *et al*., 2014), this study included only one specimen referred to *D. groenlandicum*, and authors did not extensively discuss morphological distinctions between them.

Thus the aim of the present paper is to check if molecular markers are congruent with morphology for the delimitation between *D. elongatum* and *D groenlandicum*, as well as to find out which characters of these species are stable and which are variable in cases of poorly developed plants and marginal phenotypes.

In addition, plants with morphotype of *D. atratum* (from the type locality) and of *D. tundrae* were involved, as the possibility of their distinction form *D. elongatum* and recognition at least at infraspecific level was considered (Ignatova, 2005).

Another objective of this study is clarifying of the distribution of *D. groenlandicum*. There were no doubts about its generally Arctic distribution, but its presence in southern regions of Asian Russia remained questionable. Bardunov (1974) cited one record of Brotherus (1918) from Western Sayan Mts, but did not include this species into 'Handbook of mosses of Central Siberia' (Bardunov, 1969), likely keeping caution due to uncertainty of its distinction from "atypical *D. elongatum*". However, we observed a number of specimens from South Siberia in UUH, MHA and MW that fitted the description of *D. groenlandicum* rather than *D. elogatum*. They we also included into the present study.

## Material and Methods

***Sampling***. After an extensive herbarium study, eight specimens of *Dicranum elongatum* were selected, so different parts of Russian territory and different morphotypes were included. Eleven specimens of *D. groenlandicum* also cover Russia from its western border to Sakhalin in the East, and one specimen from Alaska was included (as no fresh material from Chukotka was available). The obtained sequences from these specimens were embedded to the data previously obtained by ourselves, as well as by other authors (Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011; Ignatova *et al.*, 2015; Lang *et al.*, 2014).

***DNA studies.*** ITS and *trn*L-F markers widely applied in moss phylogenetic studies were used. Extractions and overall laboratory protocols were essentially the same as in, *e.g.*, Fedosov *et al.* (2016). Amplified DNA fragments were sequenced partially in Novosibirsk (Center of collective use "Genomics") and Moscow ("Syntol"). Sequences were aligned manually in Bioedit (Hall, 1999).

We attempted to sequence also *rps*4, but as only a few specimens were successfully sequenced, these data are discussed separately.

***Phylogenetic analysis***. Trees were rooted on *Dicranum nipponense*, a systematically distant species of the same genus. Bayesian analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) with one compartment (5.8S) analysed with HKY+I model, and ITS1, ITS2 and *trn*L-F with GRT+I+G model. Three parallel runs were implemented, each with five chains and 15,000,000 generations (375 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*. (2014).

***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 all sequenced specimens of *D. elongatum* and *D. groenlansicum*. The measurements were made under the stereomicroscope CarlZeiss Stemi 2000-C in AxioVision Rel. 4.8 program.

## Results

***Molecular phylogenetic data.***

The Bayesian tree (Fig. 1) is rooted on *Dicranum nipponense*, a species of *Dicranum scoparium* affinity. Two other representatives of the same group, *D. bonjeanii* and *D. leioneuron*, are forming a clade sister to all other species included in the analysis.

Then the tree forms paraphyletic grade of two polytomies and two terminal clades: **(1 polytomy)** *D. acutifolium*, *D. angustum*, *D. bardunovii*, *D. brevifolium*, *D. muehlenbeckii*; **(2 polytomy)** *D. laevidens, D. septentrionale, D. dispersum*; **(3 clade)** *D. elongatum* specimens only; **(4 clade)** *D. drummondii, D. flexicaule, D. fuscescens, D. spadiceum, D. schljakovii, D. groenlandicum*.

The clade of *D. elongatum* is maximally supported, and the same support has the clade 4. The latter includes polytomy of *Dicranum groenlandicum* with nested **(1)** clade of *D. flexicaule* + *D. fuscescens* (PP=0.97) where subclades of individual species have both PP=1.0; **(2)** clade of *D. drummondii, D. spadiceum, D. schljakovii* (PP=0.78), with subclades of *D. drummondii* (PP=1.0) and subclade of two other species (PP=1.0); **(3)** clade of several specimens of *D. groenlandicum*, with weak support (PP=0.65).

The *rps*4 was sequenced for four specimens of *D. elongatum* and four of *D. groenlandicum.* Three substitutions comprise the difference between these species (403 position: C/T, 512: G/A, 578: C/T respectively), without any other polymorphism.

## DISCUSSION

*Dicranum elongatum* and *D. groenlandicum* were usually recognized at species level in most recent Floras from Europe, Asia and North America; at the same time, most authors emphasized that typical specimens are easily distinguished, while 'intermediate' specimens difficult for identifications are also not rare. Among distinguishing characters, cell length in proximal and distal part of leaf, presence or absence of pores in cell walls, entire or denticulate leaf margins, shape of leaf apex, width of costa and shape of capsule were usually used. Character states of *D. elongatum* and *D. groenlandicum* from a number of handbooks and other treatments are summarized in Table 1; they are supplemented by our data obtaned from sequenced specimens. Some characters are differently treated by different authors; however, most of them agree that cells of *D. goenlandicum* are longer and more strongly pitted than in *G. elongatum*, and that costa of the former species is narrower than in the latter one. There also is an agreement that *D. elongatum* often has leaves with acute apices and denticulate margins, while leaf margins are always entire in *D. groenlandicum* and leaf apices are always narrowly obtuse.

According to our observations, cells in distal parts of leaves of *D. elongatum* are mainly short and not porose (Fig. 4: 5, 11); however, in some specimens short cells are mixed with elongate ones (Fig. 4: 2, 8), and occasionally elongate cells prevail, but their walls are usually not porose. Leaf acumens of *D. elongatum* are always narrow, acute, denticulate near apex, with percurrent costa. It also has comparatively wide costae and narrow laminae at leaf base, so costa occupies 1/6–1/3 of leaf width (Fig. 3: 5–12). Therefore, our circumscription of morphological charcters based on sequenced specimens of *D. elongatum* does not contradict a concept of this species applied in most taxonomic treatments.

Leaf lamina and costa are mainly smooth on abaxial side in upper part of leaf in *D. elongatum*, though specimens with more or less clearly scabrose distal portion of lamina and costa are also not rare. Scabrose leaves were attributed to *D. tundrae*. This species was described from Dudinka Settlement surroundings in lower course of Yenisey River (Lindberg & Arnell, 1890). Savicz-Lyubitskaya and Smirnova (1970) mentioned slightly different shape of distal laminal cells of *D. tundrae* (with quadrate, triangular and short rectangular lumens instead of round and ovate), but considered it merely as a synonym of *D. elongatum*. We also studied the specimen in H collected by Arnell in Dudinka and cited in the protologue and totally agree that it does not contradict *D. elongatum* in all essential characters.

We haven't seen types or any other specimens of *Dicranum atratum* Geh., but its distinguishing characters mentioned by the author (Geheeb, 1879), *i.e.*, sharply denticulate leaf apices, strong costa and blackish color of plants agree with the species concept of *D. elongatum*; this was already considered by Savicz-Lyubitskaya & Smirnova (1970).

Among most important charcters of *Dicranum groenlandicum*, obtuse leaf apices and entire leaf margins were used in all taxonomic treatments. Many authors also mentioned that distal laminal cells are often elongate and porose in this species. Such specimens occur in collections from Russia and some of them were included into the present set of sequenced plants; at the same time, a number of specimens with acute and denticulate apices were found in the grade of *D. groenlandicum*, together with its 'typical' specimens in the molecular-phylogenetic tree. Such plants, as well as plants with entire obtuse apices occasionally have short, not porose distal laminal cells. In North American Floras *D. groenlandicum* was placed in both branches of the key, separating species with short and elongate cells. This character was considered to be variable in *D. groenlandicum*, but porose cells above mid-leaf were thought to be important for its recognition. Our data do not confirm that this character is stable, as well as the difference in length of proximal laminal cells between *D. groenlandicum* and *D. elongatum* (see Table 1). At the same time, costa width was found to be the most important character distinguishing these species. *Dicranum groenlandicum* always has comparatively wide, ovate leaf base and costa occupying 1/11–1/7 of leaf width (Fig. 6). In case if plants of *D. elongatum*/*groenlandicum* habit have acute leaf apices, short, not porose distal leaf cells and, at the same time, narrow costa, they should be identified as *D. groenlandicum*. We have seen such specimens in herbaria referred to *D. elongatum*, because entire leaf margins were though to be most important character of *D. groenlandicum* and other characters were considered as variable. Our results point on costa width as the most stable distinguishing character of this species, while other mentioned characters may vary.

Despite occasional similarity in dentation of margin near leaf apex between these two species, there is a difference in costa height: it is percurrent in *D. elongatum* (ending at the extreme apex), but it usually ends several cells below the apex in *D. groenlandicum* (cf. Figs. 3: 1–4, 4: 1, 4, 7, 10 and Fig. 7: 1–6).

There is inconsistence in descriptions of sporophytes of both species by different authors (see Table 1). Sporophytes are not frequent in collections of *D. elongatum* and *D. groenlandicum* from Russia. However, in fruiting specimens of *D. elongatum* capsules were more or less curved, while in *D. groenlandicum* they were mostly erect, short, ovate-cylindric, slightly ribbed when dry (Fig. Fig. 5: 1–2), rather numerous in fertile specimens.

Tufts of *D. groenlandicum,* similarly to *D. elongatum*, are rather dense, but in most cases they are rather easily separating, contrary to very tight tufts of the latter species (this feature was very colorfully described by Crum & Anderson, 1980). Height of plants varies in both species; in *D. groenlandicum* they are often to 20 cm high, but sometimes they are moderately sized, ca. 4 cm high.

Table 1. Comparison of differential characters of *Dicranum elongatum* (E) and *D. groenlandicum* (G, shaded)

| | | North America (Bellolio-Trucco & Ireland, 1990; Ireland, 2007) | Europe (Nyholm, 1987; Hedenas & Bisang, 2014) | China (Gao *et al.*, 1999) | Russia (Abramova *et al.*, 1961; Savicz-Lyubitskaya & Smirnova, 1970) | Our observations |
|---|---|---|---|---|---|---|
| **Leaves** | E | (2.5–)3–4.5(–6)×0.3–0.5 mm leaf base lanceolate | leaf base lanceolate | lanceolate, 3–5×0.4–0.5 mm | 3–3.5×0.4–0.5 mm leaf base lanceolate | (2.5–)3–4.5(–6)×0.3–0.6 mm, leaf base lanceolate to narrowly ovate-lanceolate |
| | G | (2.5–)3–4(–6.5)×0.3–0.5 mm leaf base ovate-lanceolate | leaf base ovate-lanceolate | ovate-lanceolate, 3.0×0.6–0.8 mm | 3×0.6–0.8 mm leaf base oblong | (1.5–)2.5–5×(0.3–)0.4–0.7 mm, leaf base ovate-lanceolate |
| **Proximal laminal cells** | E | usually elongate, pitted, (14–)24–36(–49)×(2–)4–6(–9) μm | gradually elongate, strongly incrassate, smooth or slightly porose below | elongate, strongly thick-walled, porose | incrassate, elongate and narrow, porose or not porose | elongate, thick-walled, porose (14–)20–58(–100)×(3–)5–10(–12) μm, |
| | G | elongate-sinuose, incrassate strongly pitted, (36–)54–65(–98)×(2–)5–6(–9) μm | elongate strongly incrassate and porose | elongate, thick-walled, strongly porose | strongly incrassate, porose, linear, with the oblong lumens | elongate, thick-walled, porose (23–)33–59(–96)×(6–)8–11(–12) μm |
| **Distal laminal cells** | E | short-rectangular, quadrate, rounded, or sometimes irregularly shaped, incrassate, not pitted, (5–)12–17(–23)×(4–)6–8(–9) μm | strongly incrassate, rounded-quadrate, short rectangular or ovate, not porose | irregular, rounded quadrate or short-rectangular to slightly elongate, thick-walled, smooth, scarcely porose | incrassate, rounded-rectangular or partly rounded-quadrate | thick-walled, not porose, (8–)13–23(–34)×(7–)8–10(–13) μm |
| | G | elongate, incrassate and pitted, (11–)17–26(–42)×(2–)5–6(–12) μm | porose throughout the leaf rectangular or short rectangular, 8–10 μm wide | rounded rhomboidal, thick-walled, somewhat porose | strongly incrassate, porose, occasionally not porose, 10–12 μm, quadrate, triangular or rhomboidal, rounded | elongate, thick-walled and porose or short, not porose (13–)18–35(–57)×(7–)9–12(–14) μm |
| **Leaf apex** | E | smooth, usually acute sometimes blunt | sharp to blunt | acute or obtuse | slightly serrulate | acute, denticulate or entire |
| | G | narrowly obtuse, rarely acute | blunt or obtuse (rounded) | blunt apex without a sharp-pointed tip | blunt and entire | blunt, entire or denticulate |
| **Costa** | E | 1/6–1/4 the leaf width at base | broad | 1/5–1/4 the leaf width at base | 1/5–1/3 of the leaf width at base | (1/7)1/6-1/4 the leaf width at base |
| | G | 1/10–1/6 the leaf width at base | — | 1/10–1/8 the leaf width at base | 1/10–1/8 (1/7) the leaf width at base | 1/11 – 1/7 the leaf width at base |
| **Leaf margins** | E | entire, rarely slightly denticulate at apex | entire or nearly so | slightly serrulate at the apex | entire or slightly serrulate at apex | entire and slightly denticulate at apex |
| | G | entire | entire throughout, or with few obtuse denticles near apex | nearly entire throughout | entire | entire or denticulate at apex |
| **Capsule** | E | 1.2–1.8 mm, nearly straight and erect to slightly arcuate, striate when dry, yellowish brown | curved | erect to suberect, short-cylindric, 1.5–2.0 mm long, often slightly curved, furrowed when dry | slightly curved, small, ovate, humpy, furrowed | curved or slightly curved, 1–1,8 mm, slightly humpy |
| | G | 1.5–2 mm, nearly straight and erect to slightly arcuate, ± striate when dry, yellowish brown; | slightly curved | erect or slightly curved when dry, short-cylindric | erect, small to 4 mm long, almost cylindrical, slightly humpy, furrowed when dry | erect, short, oval-cylindric, 1,4–2 mm long, furrowed when dry, brown |

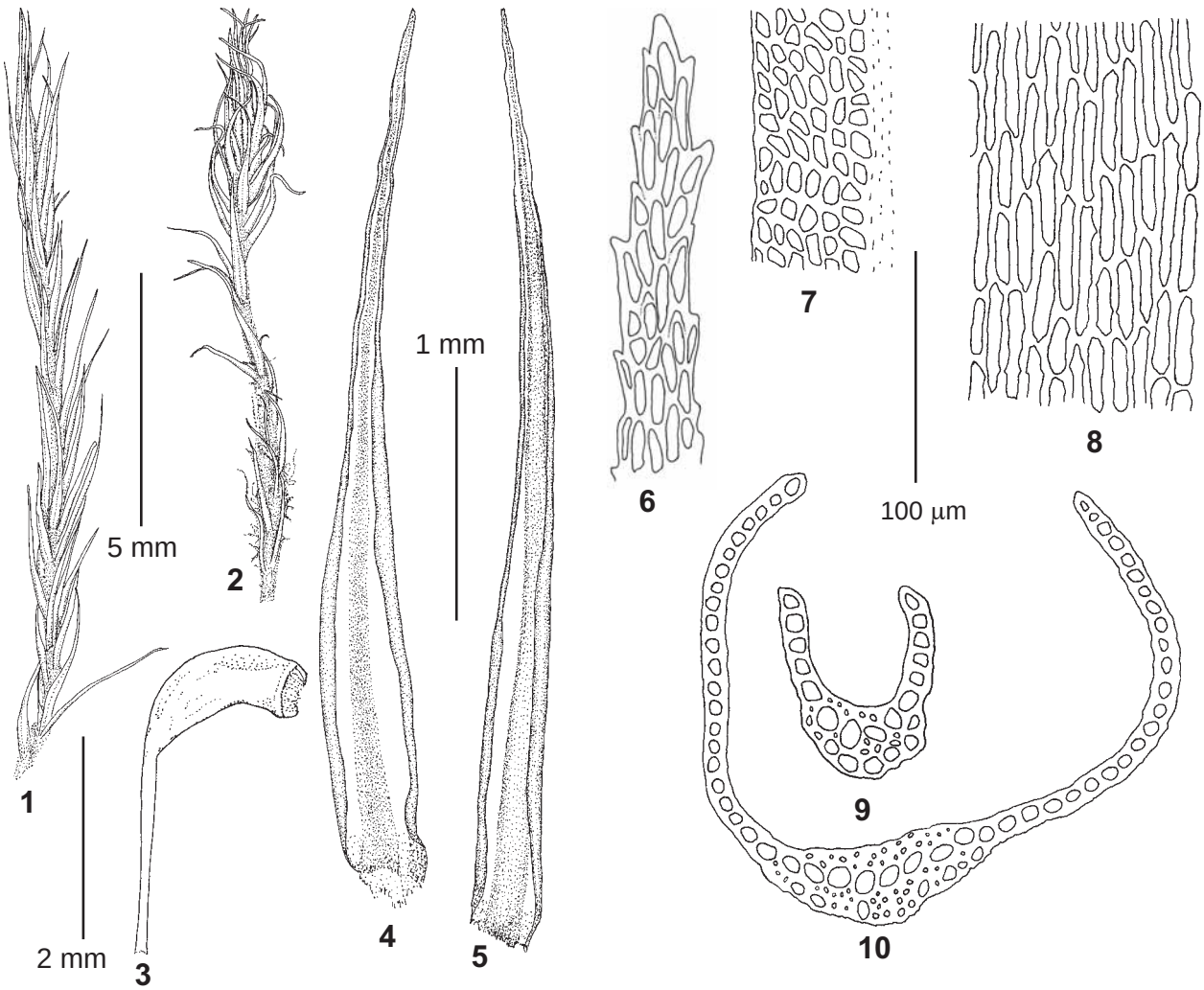


Fig. 2. *Dicranum elongatum* (from: Russia, Murmansk Province, Podpakhtinskiy Bay, 31.VII.2001, *Belkina 50-5-01*, KPABG). 1 – habit, wet; 2 – habit, dry; 3 – capsule; 4–5 – leaves; 6 – leaf apical part: 7 – upper leaf cells; 8 – basal leaf cells; 9–10 – leaf transverse sections. Scale bars: 5 mm for 1–2; 2 mm for 3; 1 mm for 4–5; 100 μm for 6–10.

Both *Dicranum elongatum* and *D. groenlandicum* can be confused with other species of the genus that have tubulose leaves, *i.e.*, *D. angustum*, *D. laevidens*, *D. spadiceum*, and *D. schljakovii*. However, all four latter species have more spreading leaves and their tufts are much less compact. Leaves of *D. angustum* and *D. laevidens* are not appressed, but erect-spreading to sptreading in dry and wet condition. Costa of both these species is weaker, with smaller number of cell layers and usually lacking stereid bands. In case of *D. spadiceum* and *D. schljakovii,* costa with well differentiated ventral and dorsal epidermal cells, having wider lumens, is the best character separating them from *D. elongatum* and *D. groenlandicum*.

TAXONOMIC TREATMENT

**Dicranum elongatum** Schleich. ex Schwägr., Sp. Musc. Frond., Suppl. 1: 171. pl. 43. 1811. — *D. tundrae* Lindb. & Arnell, Kongl. Svenska Vetensk. Acad. Handl., n.s 23(10): 82. 1890. — *D. atratum* Geh.,Flora 62: 473. 1879. Figs. 2–4.

Plants medium-sized, slender, but often tall, forming very dense, tight, hardly desintegrated tufts, yellowish, light green, slightly glossy. Stems 1–8(–16) cm long, with reddish-brown tomentum, sparsely foliose. Leaves appressed and slightly flexuose when dry, erect when wet, (2.5–)3–4.5(–6)×0.3–0.6 mm, from lanceolate or narrowly ovate-lanceolate base gradually tapered, narrowly acute, tubulose; margins unistratose, entire in proximal part of leaf, denticulate below apex; lamina unistratose, smooth or, occasionally, scabrose on dorsal side in distal leaf portion; costa wide, occupying (1/7–)1/6–1/3 of leaf width, percurrent or shortly excurrent, in transverse section with one row of guide cells and two stereid bands, dorsal and ventral epidermal cells not differentiated or, occasionally, with few dorsal surface cells with wider lumens, smooth or more or less scabrose on dorsal side in distal part of leaf; upper laminal cells short, round-quadrate or elliptic, occasionally with admixture of elongate cells, rarely elongate rectangular, (8–)13–23(–34) ×(7–)8–10(–13) μm, thick-walled, not porose; basal laminal cells elon-

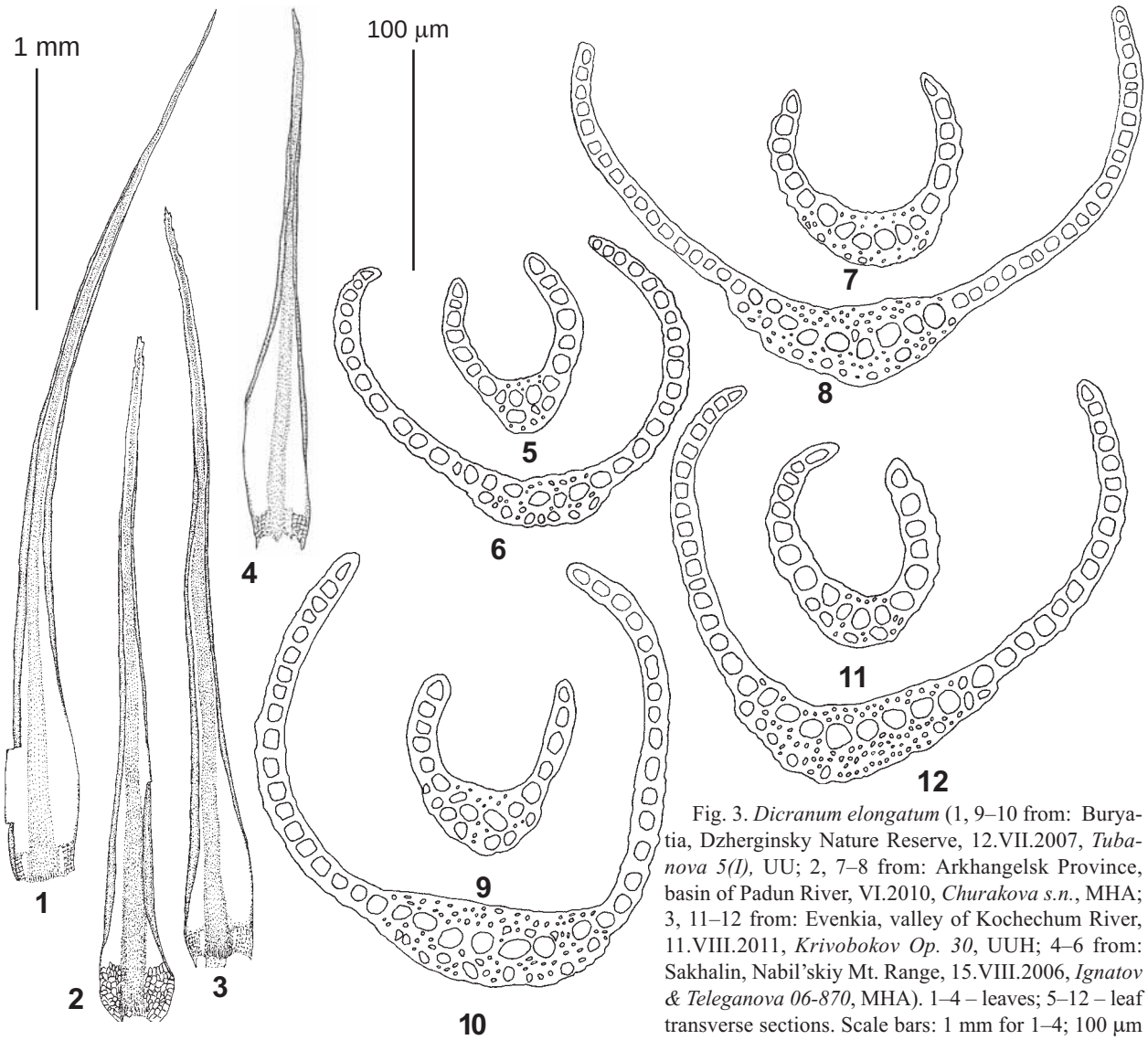


Fig. 3. *Dicranum elongatum* (1, 9–10 from: Buryatia, Dzherginsky Nature Reserve, 12.VII.2007, *Tubanova 5(I),* UU; 2, 7–8 from: Arkhangelsk Province, basin of Padun River, VI.2010, *Churakova s.n.*, MHA; 3, 11–12 from: Evenkia, valley of Kochechum River, 11.VIII.2011, *Krivobokov Op. 30*, UUH; 4–6 from: Sakhalin, Nabil'skiy Mt. Range, 15.VIII.2006, *Ignatov & Teleganova 06-870*, MHA). 1–4 – leaves; 5–12 – leaf transverse sections. Scale bars: 1 mm for 1–4; 100 μm for 5–12.

gate rectangular to linear, thick-walled, porose, (14–)20–58(–100)×(3–)5–10(–12) μm, gradually becoming shorter toward apex, with porose cells up to mid-leaf; alar cells brownish, unistratose, not reaching costa; thin-walled, hyaline cells between costa and alar group usually present. Dioicous. Setae yellowish, straight, 1–1.7 cm. Capsules 1–1.8 mm long, asimmetric, curved, smooth or furrowed when dry, occasionally slightly ribbed. Annuli of 2 rows of large cells. Spores 15–22 μm, papillose.

***Distribution.*** *Dicranum elongatum* is rather widespread and common in the Arctic and throughout Siberia, not rare in Russian Far East, Urals, north of European Russia (in Kola Peninsula), but becoming rarer in Arkhangelsk Province and Komi Republic and is rare in the Caucasus. In Asia it is known from Mongolia, China and Japan, in mountain regions and in northern Europe, Iceland, Greenland, and North America.

***Ecology.*** *Dicranum elongatum* grows in various types on arctic and mountain tundra, in bogs, on forest floor in larch, birch and mixed forests, occasionally on rotten wood, on fine soil and humus in crevices and on ledges of rock outcrops, on soil between rocks on rocky slopes, *etc*.

***Differentiation.*** The most constant distinctions of *D. elongatum* from the closest species, *D. groenlandicum* include wider costa, occupying 1/6–1/3 vs. 1/11–1/7 of leaf width; costa percurrent or shortly excurrent vs. ending few cells below leaf apex; and asymmetric, curved vs. usually straight capsules. Subtile morphotypes of *D. elongatum* can be confused with *D. schljakovii*. However, the latter species forms much more lax tufts and has differentiated ventral and dorsal epidermal cells with larger lumens. The latter character, as well as longer and wider leaves, is also helpful for separating *D. spadiceum* from *D. elongatum*.

*Selected specimens examined*: EUROPEAN RUSSIA: **Murmansk Province**: Iokanga River Basin, Sukhaya Creek east of Semuzh'ya River,24.VII.1965, *Shljakov & Avdymuratova 515* (MW, IRK), S+; near Iokanga Village, 12.VII.1928, *Tsinzer-*

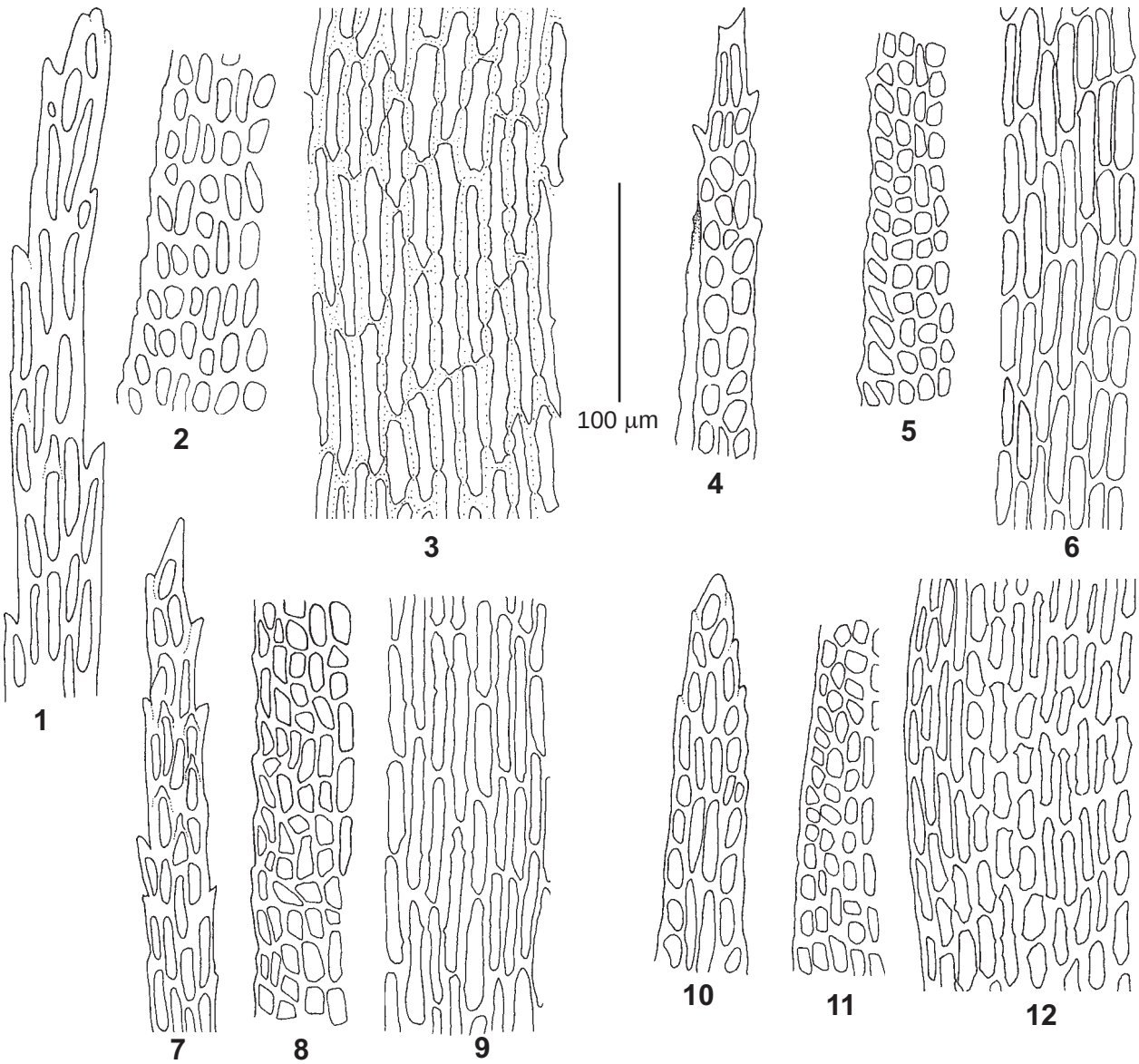


Fig. 4. *Dicranum elongatum* (1–3 from: Russia, Buryatia, Dzherginsky Nature Reserve, 12.VII.2007, *Tubanova 5(I)*, UUH; 4–6 from: Arkhangelsk Province, basin of Padun River, VI.2010, *Churakova s.n.*, MHA; 7–9 from: Evenkiya, valley of Kochechum River, 11.VIII.2011, *Krivobokov Op. 30*, UUH; 10–12 from: Sakhalin, Nabil'skij Mt. Range, 15.VIII.2006, *Ignatov & Teleganova 06-870*, MHA). 1, 4, 7, 10 – leaf apices; 2, 5. 8. 11 – upper laminal cells; 3, 6, 9. 12 – basal laminal cells. Scale bars: 100 μm for all.

*ling s.n.* (LE); Khibiny Mts, Vudjavrchorr Mt., Botanichesky Cirque, 20.VII.1948, *Shljakov 1881* (LE); Laplandsky Nature Reserve, Sal'nye Tundry, northern slope of Zasteid 2nd Mt., 26.IX.1986, *Andreeva 2A260786* (LE) and 28.VII.2003, *Belkina Б117-1-03* (KPABG); Lapponia murmanica, Rynda, 31.VII.1927, *Savicz 4115* (LE); White Sea bay near Umba Settlement, 66°40'30''N, 34°18'35''E, 20 m alt., 29.VI.2012, *Ignatov & Ignatova 12-134* (MW); Tersky District, Kandalaksha Bay of the White Sea, Porjya Guba: Bolshoj Skalistyj Island, 66.69256°N, 33.86770°E, 24.IX.2009, *Kozhin M-M-0534* (MW), S+; Pedunov Cape, 66.70631°N, 33.62948°E, 25.VIII.2008, Kozhin *M-M-028* (MW); Malyj Sedlovatyj Island, 66.70143°N, 33.68057°E, 25.VIII.2008, *Kozhin # M-M-0289* (MW); Medvezhij Island, 66.72141°N, 33.69188°E, 18.VII.2011, *Golovina 42-1* (MW); Ploskaya Luda Island, 66.78121°N, 33.63121°E, 02.08.2012, *Golovina 77-3* (MW), S+; Pechengsky District, Rybachij Peninsula, Bolshaya Volokovaya Bay, 69.840903°N, 32.008836°E, 14.VIII.2008, *Popova 404* (p-59) (MW); coast of the Barents Sea, Podpakhtinsky Bay, 6 km SE of Voronjya River mouth, 31.VII.2001, *Belkina 50-5-01* (KPABG). **Republic of Karelia**: Kandalaksha Bay, Kindo Peninsula, 15.VII.1993, *Notov s.n.* (MW); same place, 22.VIII.1985, *Abramova L.I. 26* (MW). **Arkhangelsk Province**: Kotkino Settlement, 12.VII.1973, *Sander s.n.* (LE), S+; Primorsky District, Paduk River basin, VI.2010, *Churakova s.n.* (MHA); Solovetsky District, Bolshaya Muksalma Island, 13.VII.1998, *Churakova 876* (MW); Franz Josef Land Archipelago, Northbrook Island, 79°56'50.3"N, 50°06'56.5"E, 18 m alt., 24.VIII.2012, *Kholod 76* (LE). **Nenets Autonomous District**: Bolshezemelskaya tundra, right bank of Neruyu river, near pipeline Cherpayu-Salyukayu, 67°08'43"N, 59°47'03"E, 19.VII.2006, *Batalov 06-34* (MW); Bolshezemelskaya tundra, 09.VIII.1931, *Sambuk, Gaze & Dushechkin s.n.* (MW) and 1932,

*Gorodkov s.n.* (LE); Kolguev Island, Bugrino, 21.VIII.1930, *Smirnova 12*, exsiccati Decas II (1957) (LE), S+. **Komi Republic**: Vorkuta surrounding, 25 km N of Vorga-Shor Settlement, Yaneity Lake, 11.VII.1976, *Druzhinina s.n.* (MW), S+; Lyapin River basin, 14.VI.1927, *Sochava s.n.* (MW); upper course of Selym-yu River, 09.VIII.1932, *Govorukhin s.n.* (MW); Kozhim River basin, 10.IX.1949, *Kuvaev 483* (MW). **Sverdlovskaya Province**: Kytlym, 03.07.1962, *Storozheva s.n.* (LE). Caucasus: **Kabardino-Balkaria**, Elbrus Mt., 43°24'N, 42°30'E, 2950 m alt, 22.VII.2011, *Ukrainskaya 15646* (LE), S+. **Karachaevo-Cherkessia**, Dukka riverhead, near Semitzvetnoye (Seven Colors) Lake, 2420 m alt., 25.VIII.2000, *Korotkov s.n.* (MW). ASIAN RUSSIA: **Yamalo-Nenetz Autonomous District**: Polar Urals, Sob' River bank near railway station 134 km, 725 alt., 6.VII.1976, *Kuvaev & Vostryakov 456-3* (MW); near railway station129 km, 20.VII.1988, *Czernyadjeva 68* (LE); upper course of Khulga River tributaries, Perna-yu and East Dyolya-Yu Creeks, 1146 alt., 10.VII.1949, *Kuvaev 480* (MW); Yamal Peninsula: lower course of Eryakh Creek, 68°10'N, 72°50'E, 11.VII.1978, *Andreeva s.n.* (LE), S+; Stynyaj-Sale Settlement, 66°55'N, 71°20'E, 28.VII.1996, *Czernyadjeva & Kuzmina 15* (LE); middle course of Matyuyakha River, 70°55'N, 70°20'E, 19.VIII.1983, *Rebristaya s.n.* (LE); Khadyta-Yakha River, 09.VIII.1972, *Meltzer 32* (IRK); Ngaranato Lake, 70°17'N, 68°57'E, 10.VIII.1991, *Czernyadjeva 35* (LE); Bolshaya Khadyta River, 1999, *Smirnova 39* (MW); Khadutte River, 67°25'15"N, 76°25'44"E, 29.VII.2014, *Bezgodov 287* (MW); Yamburg, 67°56'30''N, 74°50'E, 25.VII.2014, *Bezgodov 229* (MW); Pur District, 0.5 km NE of the bridge on Enayakha River, 67°16'07''N, 76°26'23''E, 29.VII.2014, *Bezgodov 297* (MW); Tazovsky District, Malaya Kheyakha River, 67°00' N, 079°28' E, 11.VII.2010, *Pisarenko op06253, N10-09f* (NSK); south of Tazovsky Settlement, 67°25' N, 078°39' E, 12.VII.2010, *Pisarenko op06256, N10-10b* (NSK), S+; Tazovskaya Guba, Pur, 15.VI.1925, *Yurovskaya s.n.* (MW), S+. Gydansky Peninsula: 6 km N of Anti-Bayuta, 18.VIII.1971, *Meltzer 56* (IRK); Sydy-Yakha River, 24.08.1972, *Meltzer 73* (IRK); between Neshayakha and Yarukha Rivers, 27.VII.1971, *Meltzer 18* (IRK); bear mouth of Nyavu-yaga River, Gyda0yam Bay, 18.VII.1927, *Gorodkov s.n.* (LE); Novo-Nadymsky District, Pangoda Settlement, *Sedova s.n.* (MW). **Khanty-Mansijsky Autonomous District**: Surgut District, Tromjegan River, 62°08' N, 073°38' E, 08.VII.2010, *Pisarenko op06254, N10-05* (NSK). **Altai Republic**: Kurkure Range, Kayakkatuyarykskiy Creek Basin, near first (lower) lake, 51°06'N, 88°09'E, 1760 m alt., 02.VII.1990, *Ignatov 8/3* (IRK), S+; Ukok Plateau, Kanas River valley, 26.VII.1955, *Kuminova & Listova 127* (IRK), S+; Taldura River at Dzhelo Creek mouth, 49°57'N, 87°50'E, 2200 alt., 11.VIII.2012, *Ignatov & Ignatova 12-600* (MW); Kosh-Agach District: Kapchil' River, 29.VIII.1936, *Kalinina & Sokolova 408*, (LE); 7.5 km S of Chibit Settlement, Oroj River, 1990 alt., 30.VII.2008, *Seregin & Seregina M-2196* (MW). **Krasnoyarsk Territory**: Putorana Plateau: Lama Lake, 17.VII.1984, *Czernyadjeva 35* (LE), S+; Ayan Lake, 07.VIII.1983, *Czernyadjeva 112* (LE), S+ and 28.VII.1984, *Czernyadjeva 44* (LE), S+; Bel'dumchana Lake, 350 m alt., 30.VII.1971, *Bardunov s.n.* (IRK), S+; Western Taimyr: Willem Barentz Biostation, Meduza Bay, 73°22'N, 80°32'E, 05.VII.2003, *Varlygina s.n.* (MW); Byrranga mt. Range, 09.VII.1989, *Varvarchuk s.n.* (IRK), S+; Baikura-Turku Bay of Taimyrskoe Lake, 74°00'N, 99°10'E, 1990, *Pospelova s.n.* (MW); Pyasina River, Tareya Settlement, 01.VIII.1969, *Blagodatskikh s.n.* (LE); middle course of Novaya River, Ary-Mas, 17.VII.1972, *Usorin s.n.* (LE); Anabar Plateau: 70°7875'N, 101°047'E, 21.VI.2009, *Fedosov 09-299* (MW), S+; Epishkina Gora, 70°8668'N, 101°968'E, 30.VI.2009, *Fedosov 09-220* (MW), S+; State Biosphere Natural Reserve Taimyrsky, Medwezhya River, 71°1131'N, 102°433'E, 18.VII.2005, *Fedosov 05-584* (MW); Anabar Plateau, Fomich River mouth, 72°1251'N, 110°338'E, 10.VII.2008, *Fedosov 08-462* (MW); Fomich River, 71°40'N, 108°15'E, 19.VIII.2003, *Pospelov s.n.* (MW), S+; Kotuikan River 4 km downstream Arbyn Creek mouth, 70.2951°N, 106.2328°E, 27.VII.2011, *Fedosov 11-1501* (MW); Kotuikan River at Vyurbyur Creek mouth, 30.VII.2011, *Fedosov 11-951* (MW); Evenkia, Nizhnyaya Tunguska River, 64°09.760'N, 100°28.381'E, 226 m alt., 12.VIII.2014, *Krivobokov 15-14* (UUH), S+, and 64°12'32.8''N, 100°27'04.7''E, 186 m alt., 13.VIII.2011, *Krivobokov 41* (UUH), S+; Severnaya Zemlya, Bolshevik Island, 78°13'N, 103°15'E, 07.VIII.1997, *Matveeva s.n.* (LE). **Tyva Republic**: Erzinsky District, Sangilen Plateau, upper course of Balyktyg-Khem River, 50°19' N, 096°28' E, 2200 m alt., 18.VII.2013, *Pisarenko op06247, Tv13-4h* (NSK). **Republic Sakha-Yakutia**: Kobyaisky District, upper course of Kele River, Keshin Krest Mt., 25.VII.1986, *Nikolin 33* (IRK); Syntar District, Vilyuj River 5 km downstream Ulakhan-Vava, 15.VII.1958, *Kil'dyushevsky 27/5* (LE); Nizhnekolymsk District, Kamenka, 19.VII.1975, *Stepanova 3/12* (LE); Allaikhovsky District, lower course of Indigirka River, 'Kytalyk' Protected Area, VII.2009, *Sofronov s.n.* (MHA); Chersky Mt. System, Khatys-Yuryakh River, 1490 m alt., 12.VII.1971, *Garashchenko s.n.* (IRK); Tomponsky District: 2 km W of Teplyj Klyuch Settlement, 62°46'19"N, 136°47'42"E, 265m alt., 07.VII.2011, *Ignatov & Ignatova 11-2068* (MW); Sette-Daban Range, Sehenyakh Creek, 63°03,5'N, 137°56,5'E, 700 m alt., 16.VII.2015, *Ignatov & Ignatova 15-473* (MW), S+; Kyurbelyakh Creek, 63°07'N,139°02'E, 900 m alt., 09.VII.2011, *Ignatov & Ignatova 11-2246* (MW); Oimyakon Districy: Mus-Khaya Mt.,Knorij Creek, 62°34'N, 141°02'E, 1520 m alt., 12.VII.2011, *Ivanov 6381-84* (MW); East-Siberian Sea, Medvezh'I Ostrova Archipelago, Chetyrehstolbovoi Island, 70°37'N, 162°27'E, VIII.1980, *Zaslavskaja s.n.* (LE). **Irkutsk Province**: Vitimsky Nature Reserve: Kodar Range, Olen'ya Creek at the sources of Levaya Sygykta River, 1200 m alt., 27.VIII.1991, *Chechetkina s.n.* (IRK, UUH); Vitim River near Verkhnij Yuryakh Creek mouth, 18.VII.1984, *Bardunov s.n.* (IRK); Oron Lake, Kultuchnaya Creek, 30.VII.1984, *Bardunov s.n.* (IRK), S+; **Republic of Buryatia**: Barguzinsky District, Baikal Lake, Svyatoj Nos Peninsula: Baklanij Island, 11.VIII.1998, *Budaeva s.n.* (IRK, UUH); Chevyrkujskij Bay, Burtuj River, 53°37'19.5''N, 108°55'19.4''E, 473 m alt., 30.VI.2014, *Tubanova B14018/07* (UUH) and 02.07.2014, *Czernyadjeva 34-14* (LE), S+; Kurumkanskij District, Dzherginskij Nature Reserve, winter hut '81th km', hill 361 m, 02.VII.1998, *Tubanova 22(I)* (UUH), S+; Oka District: Sorok River valley, 52°34'N, 100°06'E, 1805 m alt., 08.VII.2008, *Tubanova Ок-14/0829* (UUH), S+; Zhakhna River valley, 52°32'N, 099°55'E, 1703 m alt., 05.VII.2008, *Tubanova Ок-07/0805* (UUH); NE Baikal Lake, 2 km S of Bolshaya Chermshanaya River mouth, 27.VII.1956, *Bardunov s.n.* (IRK). **Zabaikalsky Territory**: National Park "Alhanai", near Ara-Ilja Settlement, 50°56'N, 113°12'E, 870 m alt., 06.VII.2006, *Afonina 0606* (LE); Kyra District, Sokhondinsky Nature reserve, upper course of Agutsa River, 15.VII.2013, *Czernyadjeva 33-13* (LE), S+, and 49°48'28.3"N, 111°12'20.3"E, 15.07.2013, *Afonina 4813* (LE); Stanovoe Upland, Charskaya Depression, 2 km NW of Kyust-Kemda Village, 05.VIII.1975,

*Garashchenko Г-42* (IRK); Kalar District, Udokan Mt. Range: 1500 m alt., 20.VII.1977, *Otnyukova s.n.* (IRK); 2 km S of Udokan Settlement, 55°45'N, 118°19'E, VII.1985, *Filin 28* (MW); 23 km SSW of Nizhnyaya Chara Settlement, upper course of Levyj Nirungnakan River, Sekushchij Creek, 1900 m alt., 10.VIII.1987, *Filin s.n.* (MW). **Chukotskij Autonomous District**: Chaunskaya Guba, Ajon Island, 69°55'N, 167°58'E, 13.VII.1983, *Afonina CH-00104* (LE); Provideniya Bay, 600 m alt., 13.VII.1938, *Gorodkov 4* (LE); Vrangel Island: Somnitelnaya Bay, 02.VIII.1985, *Afonina s.n.* (LE); Lednikovaya River, 28.VII.1985, *Afonina B-16(I)* (LE), S+. **Kamchatsky Territory**: western coast, Mikoyanovskoe Bog, 01.VII.1953, *Sventikhovskaya s.n.* (MW); Elizovo District, Pinachevskij pass, 53.44931°N, 158.64073°E, 1200 m alt., 18.VIII.2015, *Pisarenko op06224, K15-15c* (NSK); Mil'kovo District, Bakening Volcano, 53.91357°N, 158.08276°E, 1850 m alt., 05.VIII.2015, *Pisarenko op06226, K15-3c* (NSK). **Magadan Province**: Khasynsky District, Ol'skoe Plateau, Skif Mt., 60°38' N, 151°22' E, 1460 m alt., 07.VIII.2014, *Pisarenko op06214, m14-8a* (NSK), S+; Yagodninskij Distric, Yagodnoe Settlement, Debin River, 62°27' N, 149°49' E, 480 m alt., 03.VIII.2014, *Pisarenko op06217, m14-6f* (NSK). **Sakhalinskaya Province**: Sakhalin Island, Tymovsky District, Nabil'skij Range, 50°45'N, 143°17-18,5'E, 1300-1511 m alt., 15.VIII.2006, *Ignatov & Teleganova 06-870* (MW). **Khabarovsk Territory**: Ayano-Majskij District, Dzhugdzhur Range, Uchur River valley, 55.77919°N, 134.17844°E, 1058 m alt., 06.VIII.2010, *Dudov 24* (MW);b Solnechnyj District, Etkil'-Yankan Range, watershed between Amgun; and Nilan Rivers, 1500 m alt., 51°49'N, 135°39'E, 31.VIII.1995, *Ukrainskaya U. 95-23* (MW).

GEORGIA: Borzhomi District, Bakuriani Settlement, Tskhra-Tskaro Mt., 41°42'N,43°27'E, 19.IX.1956, *Abramova & Abramov*, exsiccati Fasc. V, #122 (LE, MW. IRK).

MONGOLIA: Uri-gol River Basin, Naryn-Gol, 1925, *Smirnov 78* (IRK), S+.

**Dicranum groenlandicum** Brid., Muscol. Recent. Suppl. 4: 68. 1819[1818]. — *Dicranum elongatum* subsp. *groenlandicum* (Brid.) Mönk., Laubm. Eur. 210. 1927. — *D. elongatum* var. *sphagni* T. Jensen, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1858(1–4): 58. 1858. — *Dicranum groenlandicum* var. *sachalinense* S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36(7): 7. pl. 4. 1915. Figs. 5–7.

Plants medium-sized to large, forming dense, but easily desintegrating tufts, light green to brownish green, slightly to moderately glossy. Stems 4–8(–20) cm long, tomentose, sparsely or densely foliate. Leaves appressed, sraight or slightly flexuose when dry, erect when wet, (1.5–)2.5–5×(0.3–)0.4–0.7 mm, from ovate-lanceolate base gradually tapered, narrowly obtuse or acute at apex, tubulose; margins unistratose, entire or denticulate at apex; lamina unistratose, smooth; costa narrow, occupying 1/11–1/7 of leaf length, endingh few cells below apex or percurrent, in transverse section with one row of guide cells and two stereid bands, ventral and dorsal epidermal cells not differentiated or few dorsal cells with larger lumens, smooth; upper laminal cells elongate, thick-walled, porose, or short, almost isodiametric, with moderately thickened, not porose walls, (13–)18–35(–57)×(7–)9–12(–14) μm; basal laminal cells elongate rectangular to linear, thick-walled, porose, (23–)33–59 (–96)×(6–)8–11(–12) μm, porose cells extend to the distal part of leaf or to its middle; alar cells brownish, 1–2-stratose, not reaching costa; thin-walled, hyaline cells between costa and alar group usually present. Dioicous. Sporophytes, if present, numerous. Setae yellowish, straight, 1.5–2 см cm. Capsules 1.4–2 mm long, ovate-cylindrical, straight, furrowed when dry, occasionally weakly curved. Annuli of 2 rows of large cells. Spores 15–20 μm, papillose.

***Distribution.*** *Dicranum groenlandicum* is widespread in Siberia; it has more restricted distribution compared with *D. elongatum*, but is rather locally frequent in the Arctic and in Russian Far East; in European Russia, it is sporadic in Murmansk Province and rare in Arkhangelsk Province and Perm Territory; few records are known from the Caucasus. It is also known from China and Mongolia in Asia, Europe, Greenland and North America.

***Ecology.*** *Dicranum groenlandicum* grows on soil in various types of tundra, on forest floor in larch forests (mainly open and more or less boggy), dark conifer, mixed and small-leaved forests, in wet pine forests, bushy communities and Siberian dwarf pine thickets; it also occurs in oligotrophic bogs, between rocks of rock-fields on mountain slopes, occasionally near snowbeds, in alpine meadows, in heathberry communities and on rotten wood.

***Differentiation.*** Differences from *D. elongatum* are discussed under that species. *Dicranum groenlandicum* is rather frequently confused with *D. laevidens* due to similar leaves with narrowly obtuse apices and often elongate, porose cells throughout leaf lamina. However, tufts of *D. laevidens* are much more lax, leaves are erect spreading both in dry and wet condition, costa is weaker, often lacking stereid bands, capsules are curved, and peristome teeth are smooth at ends. *Dicranum angustum* is also considered as close to *D. groenlandicum,* but its tufts are lax and look quite different from dense tufts of the latter species. Leaves of *D. angustum* are erect-spreading or spreading, capsules are curved, and laminal cells are elongate and thin-walled throughout the lamina.

*Selected specimens examined*: EUROPEAN RUSSIA: **Murmansk Province**: Murmansk Biological Station, VIII.1905, *Elenkin s.n.* (LE); Terskij District, Kandalahshskij Bay of the White Sea, Porjya Gyba: Ozerchanka Island, 66.67796°N, 33.88643°E, 17.VII.2013, *Golovina M-M-1094* (MW). **Arkhangelsk Province**, Solovetskij District, Bolshaya Mukasalma Island, 13.VII.1998, *Churakova 4* (MW). **Nenetz Autonomous District**: Bolshezemelskaya Tundra, 02.VIII.1931, *Gorodkov s.n.* (MW). **Perm Territory**: Visherskij Nature Reserve, Olkhovochnyj Range, 61°05'N, 59°06'E, 860 m alt., 31.VII.1994, *Bezgodov 628* (MW). Caucasus: **Krasnodar Territory**, Caucasian State Reserve, Tygba Mt., 29.VII.1929, *Vasiljeva s.n.* (LE), S+. ASIAN RUSSIA: **Yamalo-Nentzkij Autonomous District**: Nadym District, Yamburg Settlement, 67°56'30"N, 74°50'E, 25.VII.2014, *Bezgodov 228 & 236* (MW); Pur District, 0.5 km NE of the bridge on enayakha River, 67°16'07"N, 76°26'23"E, 29.07.2014, *Bezgodov 295 & 297a* (MW); Tazovsky District. 1 km W of Yazovsky Settle-

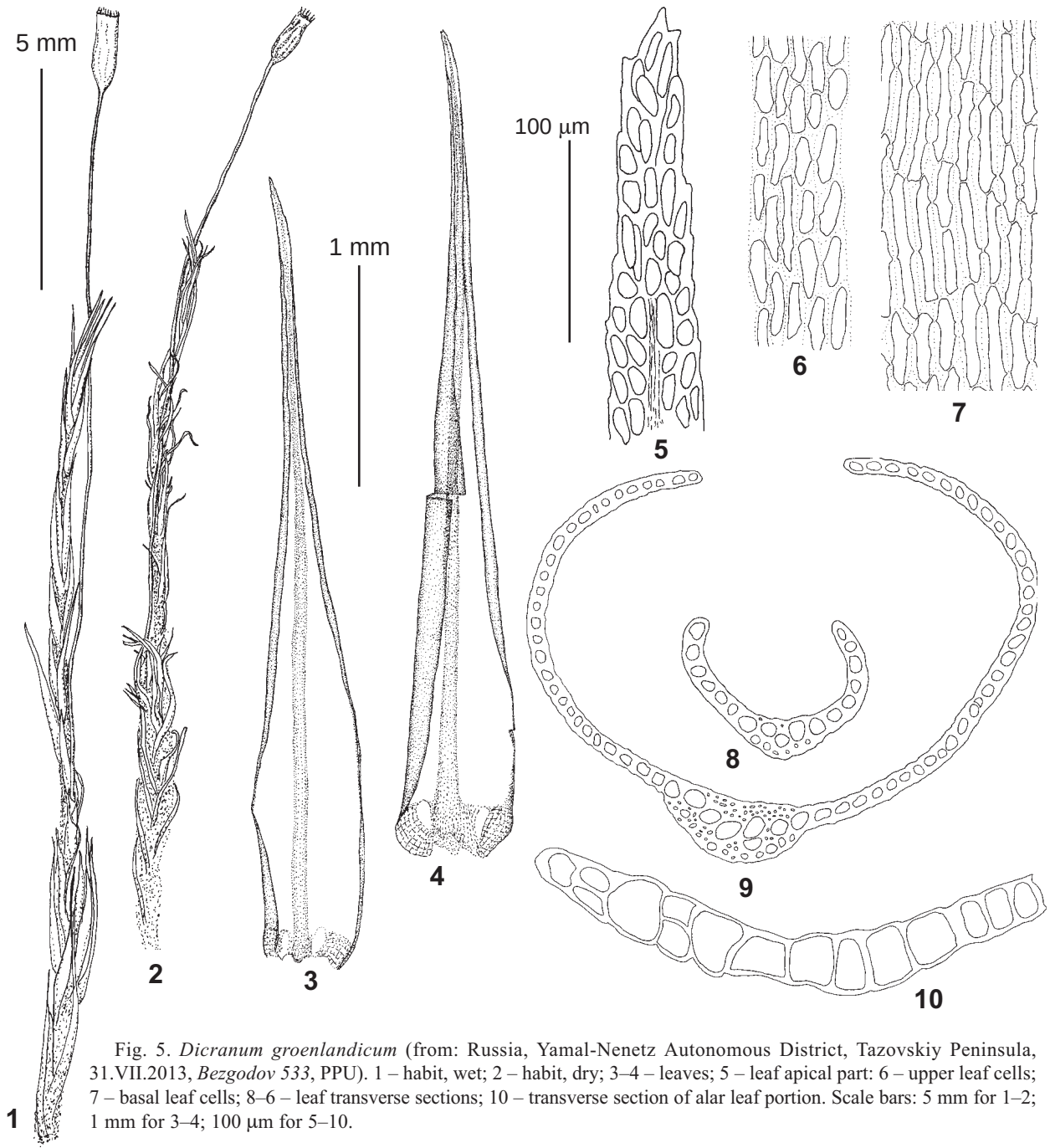


Fig. 5. *Dicranum groenlandicum* (from: Russia, Yamal-Nenetz Autonomous District, Tazovskiy Peninsula, 31.VII.2013, *Bezgodov 533*, PPU). 1 – habit, wet; 2 – habit, dry; 3–4 – leaves; 5 – leaf apical part: 6 – upper leaf cells; 7 – basal leaf cells; 8–6 – leaf transverse sections; 10 – transverse section of alar leaf portion. Scale bars: 5 mm for 1–2; 1 mm for 3–4; 100 μm for 5–10.

ment, 67°28'35"N, 78°41'E, 31.VII.2013, *Bezgodov 533* (PPU), S+; near Novyj Port Settlement, 06.VII.1938, *Katz & Katz s.n.* (LE); Pyasyadejyakha River, 22.VII.2003, *Voronova WS-922 & WS-929* (IRK); middle course of Yuribej River, 12-15 km SW of Voiborl-to Lake, 20.VIII.1976, *Gribova s.n.* (LE); eastern coast of middle Yamal, 17.IX.1932, *Andreev, Savkina & Nekrasova 620* (LE); lower course of Khutyyakha River, 68°45'N, 70°30'E, 18.VII.1977, *Andreeva s.n.* (LE); Subpolar Urals, Khosaj-yol Creek, a tributary of Verkhnyaya Dyokya-Yu (Khulga River basin), 304 m alt., 15.VIII.1949, *Kuvaev 481* (MW); Tazovskaya Guba, Tazovskaya winter hut, 22.VII.1925, *Yurovskaya s.n.* (MW); Yamburgskaya winter hut, 13.VII.1925, *Yurovskaya s.n.* (MW); Krasnyj Kamen' railway station of Labytnangi Railway, 05.VIII.1966, *Voronov s.n.* (MW). **Altai Republic**: Sailyugem Range, Bluty Lake, 30.VII.1926, *Baranov s.n.* (LE), S+; Shavla Argutskaya river basin, 18.VII.1908, *Vereshchagin 893* (LE), S+; Chulyshman River basin, upper course of Bogoyash River, 12.VII.1955, *Pavlova & Fedulina 15* (IRK), S+; Archaly Creek – tributary of Koksu River, 27.VII.1931, *Shishkin, Chilikina & Sumnevich s.n.* (LE), S+. **Krasnoyarsk Territory**: Putorana Plateau, Talnakh Settlement,, 22.VI.1982, *Czernyadjeva VIIIc* (LE), S+; Ayan Lake, 16.VIII.1983, *Czernyadjeva 130* (LE, UUH), S+; between Nikshingda and Vivi Lakes, 31.VII.1969, *Boldyrev 127-7* (MW); Western Taimyr: Dikson District, Sibiryakova Island, 13.VII.1930, *Kuvaev & Kozhevnikova 1470-5* (MW); Willem Barentz Biostation, Meduza bay, 73°22'N, 80°32'E, 03.VII.2003, *Varlygina s.n.* (MW); Pyasina River, Tareya Set-

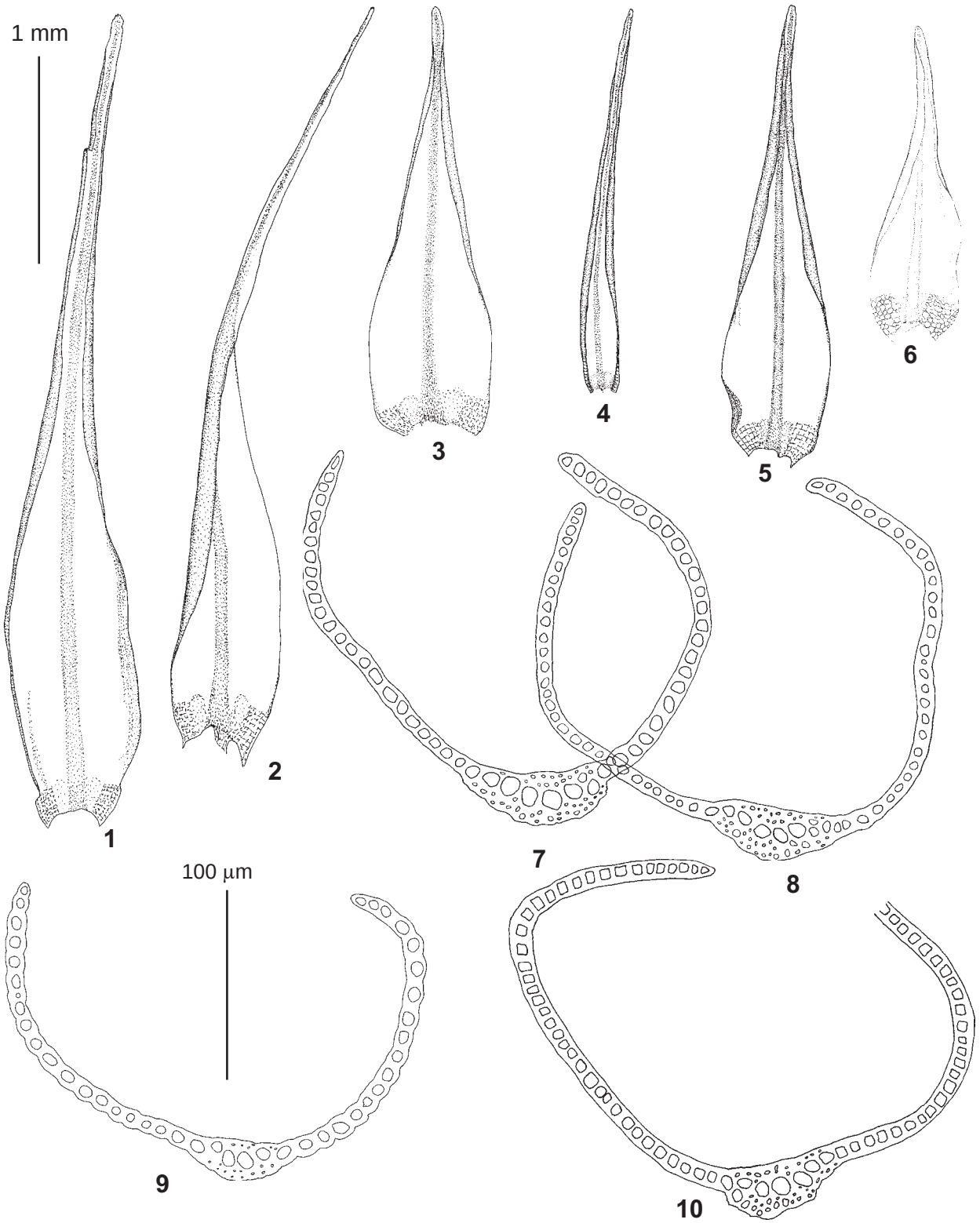


Fig. 6. *Dicranum groenlandicum* (1 from: Buryatia, Dzherginsky Nature Reserve, 16.VII.2007, *Anenkhonov Op. Ku-02/29*, UUH; 2, 8 from: Yakutia/Sakha, Lenskie Stolby, 18.VIII.2000, *Ignatov 00-83*, MHA; 3, 10 from: Murmansk Province, Lumbovskiy Bay, 20.VII.2007, *Belkina B172-3-07*, KPABG; 4, 9 from: Evenkiya, valley of Kochechum River, 10.VIII.2012, *Krivobokov Op. 18*, UUH; 5 from: Sakhalin, Pil'tun Bay, 03.IX.2009, *Pisarenko op03452*, NSK; 6–7 from: Buryatia, ravine "Botyskaya Yama", 18.VII.2010, *Tubanova Kaykh-5/10*, UUH). 1–6 – leaves; 7–10 – leaf transverse sections. Scale bars: 1 mm for 1–6; 100 μm for 7–10.

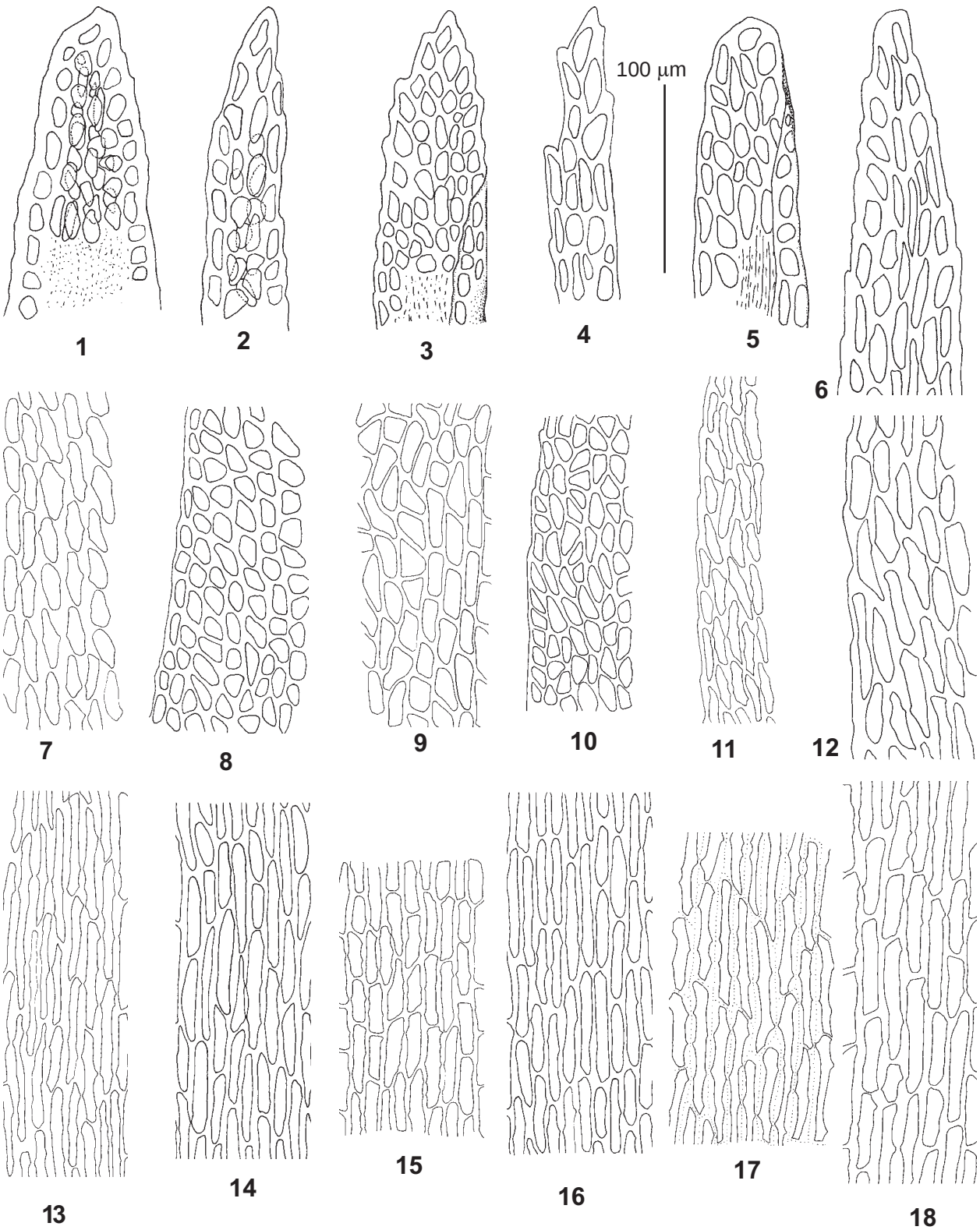


Fig. 7. *Dicranum groenlandicum* (1, 7, 13 from: Buryatia, Dzherginsky Nature Reserve, 16.VII.2007, *Anenkhonov Op. Ku-02/29*, UUH; 2, 8, 14 from: from Buryatia, ravine "Botyskaya Yama", 18.VII.2010, *Tubanova Kaykh-5/10*, UUH; 3, 9, 15 from: Murmansk Province, Lumbovskiy Bay, 20.VII.2007, *Belkina B172-3-07*, KPABG; 4,10, 16 from: Yakutia/Sakha, Lenskie Stolby, 18.VIII.2000, *Ignatov 00-83*, MHA; 5, 11, 17 from: Sakhalin, Bay Pil'tun, 03.IX.2009, *Pisarenko op03452*, NSK; 6, 12, 18 from: Evenkiya, valley of Kochechum River, 10.VIII.2012, *Krivobokov Op. 18*, UUH). 1–6 – leaf apical parts; 7–12 – upper leaf cells; 13–18 – basal leaf cells. Scale bars: 100 μm for all.

tlement, 11.VIII.1965, *Matveeva 18* (MW) and 02.08.1970, *Matveeva 121(2)* (LE); Burranga Range: Bolshaya Bootankaga River, 300 m alt., 08.VIII.1991, *Kuvaev & Voropanov 2078-8* (MW) and 400 m alt., 05.VIII.1991, *Kuvaev 2092-6* (MW); Bootankaga River 2.5 km upstream the mouth of Geologicheskij Creek, 80 m alt., 10.VII.1991, *Kuvaev 1757-7* (MW) and 110 m alt., 08.VII.1991, *Kuvaev 1750-5* (MW); State Biosphere Natural Reserve Taimyrsky, Ledyanaya Bay of Taimyrskoe Lake, 74°4602'N, 99°699'E, 01.VII.2004, *Fedosov Dicr2* (MW); Anabarskoe Plateau, mouth of Fomich River, Fomich-Lonktokhoto Mt., 72°0626'N,110°21'E, 12.VII.2008, *Fedosov 08-11* (MW); Popigaj River 15 km downstream Fomich River, 72.2593°N, 110.779°E, 12.VIII.2008, *Fedosov 08-525* and *08-595* (MW); Medvezhlya River mouth, Lagernaya Mt., 71.1541°N, 102.674°E, 18.VI.2005, *Fedosov 05-172* (MW); Afanasjevskie Lakes, Eriechka River valley, 71.6053°N, 105.283°E, 14.VIII.2006, *Fedosov 06-653* (MW). Evenkia: Tura, Kochuchem River valley, 147 m alt., 64°19'39.9"N, 100°13'19.2"E, 09.VIII.2011, *Krivobokov 20* (UUH), S+; Nizhnyaya Tunguska River, 64°12'32.8"N, 100°27'04.7"E, 186 m alt., 13.VIII.2011, *Krivobokov 41* (UUH), S+, and 64°12'57.3''N, 100°25'16.0''E, 125 m alt., 05.VIII.2014, *Krivobokov 01-14* (UUH), S+. **Tyva Republic**: East Sayan Mts, Kutyrga-Hol Lake, 1640 m alt., 28.VI.1961, *Bardunov s.n.* (IRK). **Republic of Sakha/Yakutia**: Anabarskij District: 75 km E of Ebbelyakh River mouth, 13.VIII.1981, *Stepanova s.n.* (MW); Kogda-Taasa Hill at the left bank of Utzha River, 13.VIII.1981, *Stepanova s.n.* (MW); Bulun District: Lena River 60 km SW of Dunaj Lake, 20.VIII.1981, *Zakharova s.n.* (MW); Kobyajskij District, Kele River, Kyunkyu-nyur Creek mouth, 28.VII.1987, *Nikolin 11* (MW); Mirnyj District: Vilyuj River 10 km downstream Lokharchan River mouth, 31.VII.1990, *Isaev 4* (MW); Nizhnekolymsk District: 500 m SW of Pokhodsk Settlement, 25.VII.1972, *Stepanova 3/1* (MW); Rogovatka Settlement 40 km of Pokhodsk, 07.VII.1972, *Stepanova 2/15* (MW); Suntar District, Vilyuj River at the mouth of Ulakhan River, 11.VII.1959, *Kildyushevskij 18/3* (MW); Ust-Yanskij District: Alyta River - tributary of Smoloj River 180 km of Ust-Kujva Settlement, 23.VI.1978, *Stepanova s.n.* (MW); 'Perevalnyj Quarry of Tenkali mine, 17.VI.1991, *Protopopov s.n.* (MW); Tomponskij District, middle course of Barykchan River – tributary of Yuge-Syakh River, 24.VIII.1939, *Ivanova V. s.n.* (LE), S+; Ust-Maya, 02.IX.2000, *Ignatov 00-937* (MHA); Allaikhovskij District, 50 km of Chokurdakh Settlement, 07.VIII.1978, *Egorova s.n.* (MW); Verkhoyansk District: Batagaj Settlement, 192 m alt., 67°38'N, 134°38'E, 01.VIII.2007, *Isakova s.n.* (MW); 'Tuostakh' Protected Area, 30 km W of Tabalakh Settlement, Tuostakh River, 02.VIII.2008, *Isakova 1* (MW); Zhigansk District, upper course of Sobolokh-Mayan River, near Kuolanda River mouth, 26.VIII.1991, *Kirillina s.n.* (MW); Kobyaskij District, upper course of Bytantaj River, 6.VI.1990, *Nikolin s.n.* (MW); Olekminsk District, right bank of Lena River opposite Markha River mouth, 28.VIII.1952, *Sheludyakova s.n.* (LE), S+; Oimyakon District: Ust-Nera Settlement, Tas-Kystabyt Range, 64°39.5'N, 142°32.5'E, 1270 m alt., VIII.2015, *Balburov 33* (MW); Chersky Mt. System: Tuora-Tas River, 64°39'32"N, 142°32'27"E, 900 m alt., 01.VIII.2015, *Ignatov & Ignatova 15-1087* (MW); Khatys-Yuryakh River, 1170 m alt., 17.07.1971, *Garashchenko s.n.* (IRK), S+; Tomponskij District, Sette-Daban Range, Vostochnaya Khandtga River valley, 63°04.3'N, 137°46,3'E, 460 m alt., 18.VII.2015, *Ignatov & Ignatova 15-644 & 15-697* (MW); Eveno-Bytantaiskij District, watershed of Sobolokh-Mayan and Bytantaj Rivers, Lybalakh Lake, 1407 m alt., 04.VIII.1991, *Gabyshev s.n.* (MW); SE of Yano-Oimyakonskoe Upland, Syrylakh River - left tributary opf Indigirka River, 800 m alt., 17.VIII.1971, *Garashchenko s.n.* (IRK), S+. **Irkutsk Province**: Stanovoe upland, Bodaibo District, Vitimskih Nature reserve, Verkhnee Lake, 1200 m alt., 14.VII.1987, *Vlasenko, Ivanova & Anisimova M-3* (IRK, UUH). **Republic of Buryatia**: Barguzinskj District, Ina River 4,5 km S of Urzhil Village, 940 m alt., 13.VII.2000, *Krivobokov 269* (UUH), S+; spurs of Severo-Mujskij Range, Koira River, 04.VIII.1982, *Otnyukova s.n.* (IRK, UUH), S+; Kurumkan District, Dzherginskij Nature reserve: 9 km NNW of Dzhirga River sourses, 1900 m alt., 55°02'N, 111°41'E, 16.VII.2002, *Anenkhonov Ky-02/29* (UUH), S+; 2 km SW of Gramnakan River mouth, 11.VII.2004, *Anenkhonov Ky-04/11* (UUH), S+; W of winter hut '81th km', 01.VII.1998, *Tubanova 13(VI)* (UUH); 66 km of road Tazy-Uoyan, 1120 m alt., 12.VII.2004, *Anenkhonov Ky-04/12* (UUH), S+; 8 km NNW of Dzhirga River sourses, 2000 m alt., 55°02' N, 111°41' E, 17.VII.2002, *Anenkhonov Ky-02/36* (UUH), S+; Ukshaka River valley, 55°13.348'N, 111°29.393'E, 1028 m alt., 13.VII.2015, *Krivobokov 9-15 & 11-15* (UUH); Birankur winter hut, 08.VII.1999, *Tubanova 32(III)* (UUH), S+; Malan-Zurkhen Mt., 07.VII.1998, *Tubanova 70(IV)* (UUH), S+; Lovokton River 1 km E of Gramnakan River mouth, 1120 m alt., 11.VII.2004, *Anenkhonov Ky-04/6* (UUH), S+; Lovokton River mouth, 02.VII.1998, *Tubanova 22(VI)* (UUH); Amatkhan River mouth, 02.VII.2000, *Tubanova 33(I)* (UUH), S+; Kyakhtinskij District, 'Botyjskaya Yama', *Tubanova Кях-5/10* (UUH); Oka District, Orlik Settlement, 52°30' N, 099°50' E, 1402 m alt., 1.VII.2008, *Tubanova Ок-01/0810* (UUH); Baikal Lake, Svyatoj Nos Peninsula, 13.VIII.1991, *Anenkhonov s.n.* (IRK), S+; Tunkinskij District, 4 km N of Nilova Pustyn' Settlement, 15.X.1997, *Kosovich s.n.* (IRK); Khamar-Daban Range, Khokhryukh-Gol – Tsakirka River Tributary, 28.07.1956, *?50* (LE), S+. **Zabaikalskij Territory**: Trotitskosavskij District, Snezhnaya River sourses, 1912, *Smirnov 3469* (MW); Kalar District: Naminga Settlement, 56°40'N, 118°32'E, 1000 m alt., 11.VIII.1987, *Kozhevnikova & Filin s.n.* (MW); S+; naer abandoned Nirungnakan Settlement, Sekulit Creek, 56°37'N, 118°26'E, 1900 m alt., 10.VIII.1987, *Kozhevnikova & Filin s.n.* (MW); Kyra District, Sokhondinskij Nature reserve: Sopkoyan Mt., 49°75'N, 111°E, 1900 m alt., VI.1990, *Arbuzova s.n.* (MW); Agutsa River, Larionov Klyuch Creek, 13.VII.2013, *Czernyadjeva 28-13* (LE), S+. **Magadan Province**: Kolyma Upland, Boltuonakh, sources of Verina River, 63°17'31.4"N, 151°25'29.3"E, 1316 m alt., 23.VIII.2011, *Malashkina Mg-6-30-11* (VBGI, UUH), S+; Magadan, Marchekanskaya Sopka Hill, 59°30' N, 150°47' E, 500 m alt., 13.VIII.2014, *Pisarenko op06216, m14-9m* (NSK); Okhotskoe Sea near Magadan, Nedorazumeniya Island, 59,5816° N, 150,4016° E, 10 m alt., 10.VIII.2014, *Pisarenko op06211* (NSK); Khasynskij District, Olskoe Plateau, watershwd between Ola and Bolshaya Khaya Rivers, 60°39' N, 151°29' E, 1090 m alt., 05.VIII.2014, *Pisarenko op06208, m14-7a* (NSK); Yagodninskij District, Bolshoj Annachag Range, Jack London Lake, 62°07'N, 149°29'E, 1100 m alt., 26.VII.2014, *Pisarenko op05549* (MW). **Amurskaya Province**: Zeya District, Zejskij Nature reserve, Peak 1442 m, 54°08'N, 126°55'E, 1400 m alt., 22.VIII.1980, *Abramova L.I. 293* (MW), S+. **Khabarovsk Territory**: Verkhnebureinskij District, Bureinskj Nature Reserve, Lednikovyj Creek, 52°8'N, 134°25'E, 1560 m alt., 19.VII.1991, *Petelin П-4* (MW); Sovgavan District, Botchinskij Nature Reserve, Mulpa River, 48°17'N, 139°31'E, 245

m alt., 14.VIII.2013, *Ignatov & Ignatova 13-517* (MW), S+; Chumikanskij District, Tylskij Cape, 3.IX.1962 (MW). **Chukotskij Autonomous District**: Iultinkij District, Kresta Bay, 22.VII.1951, *Gribova s.n.* (MW); Anadyr District, Anadyrskij Bay coast, 29.VII.1950, *Rapoport s.n.* (MW); Tanyurer River 50 km upstream its mouth, 17.VIII.1941, *Avramchik 68* (LE); Uelkalskij District, 21.VII.1950, *Rapoport s.n.* (MW). **Kamchatskij Territory**: Kamchatka, 5.VII.1958, *Korenev s.n.* (MW); Aleutskij District, Commander Islands, Bering Island:Lodyginskaya River, 20.VIII.2010, *Fedosov 10-3-713* (MW); depression between Malaya and Bolshaya Stolovaya Mts., 20.VIII.2010, *Fedosov 10-3-570* (MW); Koryakia, Karaginskij District, watershed of Levaya Ozernaya and Khomut Rivers, 570 m alt., 24.VIII.2006, *Samkova 63* ((MW); Lanpanovayam River, 29.VIII.1952, *Filippova s.n.* (LE); **Sakhalinskaya Province**: Sakhalin Island, Uanga River, 52°07'31.5"N, 141°53'50.2"E, 34 m alt., 16.VII.2014, *Tubanova & Tumurova S14003/18* (UUH).

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Appendix 1: Species of Dicranum 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 | trnL-F | Rps4 | Country or specimen for new sequences |
|---|---|---|---|---|---|
| acutifolium | Dic1661 | KJ650866 | KJ651070 | – | Norway |
| acutifolium | Dic1676 | KJ650879 | KJ651084 | – | Norway |
| angustum | SE25 | KJ650890 | KJ651090 | – | Sweden |
| angustum | SE4 | KJ650891 | KJ651091 | – | Sweden |
| angustum | SE22 | KJ650892 | KJ651092 | – | Sweden |
| angustum | SE27 | KJ650893 | KJ651093 | – | Sweden |
| angustum | SE31 | KJ650894 | KJ651094 | – | Sweden |
| angustum | A200 | KT580730 | KT580676 | | Russia, Yamalo-Nenetskiy AD |
| angustum | A202 | KT580731 | KT580677 | – | Russia, Yamalo-Nenetskiy AD |
| bardunovii | B104 | JN897273 | KJ796599 | – | Russia, Yakutia (Sakha) |
| bardunovii | 1 II | KJ796547 | KJ796597 | – | Russia, Buryatia |
| brevifolium | B3 | HQ830343 | KJ796589 | – | Russia, North Ossetia |
| brevifolium | B4 | HQ830341 | KJ796588 | – | Russia, Tuva |
| bonjeanii | FR4 | KF423583 | KF423939 | – | France |
| bonjeanii | Nkp1011 | KF423608 | KF423965 | – | Netherlands |
| dispersum | Di64 | KT580739 | KT580685 | – | USA, Alaska |
| dispersum | Di51 | KT580737 | KT580683 | – | Russia, Irkutsk Province |
| dispersum | Di28 | KT580735 | KT580681 | – | Russia, Ingushetia |
| drummondii | Dr73 | KT580744 | KT580690 | – | Russia, Murmansk |
| drummondii | Dr71 | KT580743 | KT580689 | – | Russia, Leningrad |
| elongatum | Dic1650 | KJ650859 | KJ651062 | – | Norway |
| elongatum | Dic1646 | KJ650857 | KJ651059 | – | Norway |
| **elongatum** | **206** | **KY296851** | **KY296870** | **KY296885** | Russia, Murmansk Province, 31.VII.2001, *Belkina50-5-01* (KPABG) |
| **elongatum** | **207** | **KY296846** | **KY296869** | **KY296884** | Russia, Yamalo-Nenetskiy AD, 27.VII.2013, *Bezgodov 395* (PPU) |
| **elongatum** | **342** | **KY296849** | **KY296871** | – | Russia, Evenkiya, 11.VIII.2011, *Krivobokov Op. 30* (UUH) |
| **elongatum** | **84** | **KY296850** | **KY296868** | – | Russia, Buryatia, 13.VII.2007, *Anenkhonov Op. Ku-02/21* (UUH) |
| **elongatum** | **301** | **KY296848** | **KY296867** | – | Russia, Buryatia, 12.VII.2007, *Tubanova 5(I)* (UUH) |
| **elongatum** | **95** | **KY296847** | **KY296866** | **KY296886** | Russia, Sakhalin, 15.VIII.2006, *Ignatov, Teleganova 06-870* (MHA) |
| **elongatum** | **189** | **KY296845** | **KY296865** | – | Russia, Arkhangelsk Province, VI.2010, *Churakova s.n.* (MHA) |
| **elongatum** | **93** | **KY296844** | **KY296864** | **KY296887** | Russia, Yakutia (Sakha), VII.2009, *Sofronov s.n.* (MHA) |
| flexicaule | FL212 | KT580745 | KT580691 | – | Russia, Buryatia |
| flexicaule | FL1 | HQ830331 | KJ796583 | – | Russia, Transbaikalia |
| fuscescens | FU1 | HQ830334 | KJ796578 | – | Russia, Perm |
| fuscescens | FU2 | HQ830335 | KJ796580 | – | Russia, Sakhalin |
| groenlandicum | SE10 | KJ650888 | KJ651089 | – | Sweden |
| **groenlandicum** | **122** | **KY296859** | **KY296877** | – | Russia, Murmansk Province, 20.VII.2007, *Belkina B172-3-07* (KPABG) |
| **groenlandicum** | **345** | **KY296862** | – | – | Russia, Kamchatka, 24.VII.2013, *Neshataeva 105* (LE) |
| **groenlandicum** | **347** | **KY296861** | – | – | Russia, Kamchatka, 15.VIII.2014, *Ovcharenko, Neshataeva 223* (LE) |
| **groenlandicum** | **83** | **KY296863** | **KY296879** | **KY296882** | Russia, Buryatia, 16.VII.2007, *Anenkhonov Op. Ku-02/29* (UUH) |
| **groenlandicum** | **91** | **KY296860** | **KY296878** | **KY296883** | Russia, Buryatia, 18.VII.2010, *Tubanova Kaykh-5/10* (UUH) |
| **groenlandicum** | **343** | **KY296858** | – | – | Russia, Evenkiya, 13.VIII.2011, *Krivobokov Op. 39* (UUH) |
| **groenlandicum** | **344** | **KY296857** | – | – | USA, Alaska, 23.VII.1993, *Afonina 932306606* (LE) |
| **groenlandicum** | **298** | **KY296856** | **KY296876** | – | Russia, Evenkiya, 10.VIII.2012, *Krivobokov Op. 18* (UUH) |
| **groenlandicum** | **125** | **KY296855** | **KY296875** | – | Russia, Sakhalin, 03.IX.2009, *Pisarenko op03452* (NSK) |
| **groenlandicum** | **94** | **KY296854** | **KY296874** | **KY296881** | Russia, Yakutia/Sakha, 18.VIII.2000, *Ignatov 00-83* (MHA) |
| **groenlandicum** | **225** | **KY296853** | **KY296873** | – | Russia, Murmansk Province, 22.VII.2007, *Belkina B176-1a-07* (KPABG) |
| **groenlandicum** | **204** | **KY296852** | **KY296872** | **KY296880** | Russia, Yamalo-Nenetskiy AD, 31.VII.2013, *Bezgodov 533* (PPU) |
| laevidens | Dic1672 | KJ650876 | KJ651081 | – | Norway |
| laevidens | Dic1663 | KJ650868 | KJ651072 | – | Norway |
| laevidens | Dic1662 | KJ650867 | KJ651071 | – | Norway |
| laevidens | Dic1653 | KJ650862 | KJ651065 | – | Norway |
| laevidens | Dic1652 | KJ650861 | KJ651064 | – | Norway |
| laevidens | Dic1651 | KJ650860 | KJ651063 | – | Norway |
| leioneuron | SE33 | KJ650905 | KJ651105 | – | Sweden |
| leioneuron | SE38 | KJ650906 | KJ651106 | – | Sweden |
| muehlenbeckii | Mu62 | KT580752 | KT580699 | – | Russia, Buryatia |
| muehlenbeckii | Mu54 | KT580751 | KT580698 | – | Russia, Sverdlovsk |
| nipponense | Ru5B | KF423625 | KF423982 | – | Russia, Far East |
| nipponense | Ru5A | KF423624 | KF423981 | – | Russia, Far East |
| schljakovii | SF9 | KT580764 | KT580711 | – | Russia, Zabaikalskyi |
| schljakovii | S89 | KT580761 | KT580708 | – | Russia, Buryatia |
| septentrionale | S1 | HQ830339 | KJ796586 | – | Russia, Arkhangelsk |
| septentrionale | S3 | HQ830338 | KJ796585 | – | Russia, Kamchatka |
| spadiceum | Su81 | KT580771 | KT580718 | – | Russia, Kabardino-Balkariya |
| spadiceum | Su80 | KT580770 | KT580717 | – | Russia, Buryatia |