

ON THE TAXONOMY OF DICRANUM ACUTIFOLIUM AND
D. FUSCESCENS COMPLEXES (DICRANACEAE, BRYOPHYTA) IN RUSSIA

О ТАКСОНОМИИ КОМПЛЕКСОВ DICRANUM ACUTIFOLIUM И
D. FUSCESCENS (DICRANACEAE, BRYOPHYTA) В РОССИИ

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Abstract

ITS sequences of taxonomically difficult complexes in the genus *Dicranum*, *D. fuscescens*–*D. flexicaule* and *D. brevifolium*–*D. acutifolium*–*D. pseudacutifolium*, are analyzed. Type specimens of *D. pseudacutifolium* are found to be poorly developed specimens of *D. flexicaule* and therefore the former name is synonymized with the latter. At the same time, several specimens previously identified as *D. brevifolium* were found to be in a separate clade; they also have morphological differences and are described as a new species, *D. septentrionale* sp. nova.

Резюме

Проанализированы последовательности ITS сложных в систематическом отношении комплексов видов *Dicranum fuscescens*–*D. flexicaule* и *D. brevifolium*–*D. acutifolium*–*D. pseudacutifolium*. Показано, что типовые образцы *D. pseudacutifolium* не отличаются по этому маркеру от *D. flexicaule* и представляют собой, вероятно, не вполне развитые образцы последнего вида. В то же время ряд образцов, уклоняющихся сходным образом в группе *D. brevifolium*, оказывается четко изолированным генетически, представляя собой ранее не распознававшийся скрытый вид: *D. septentrionale* sp. nova.

KEYWORDS: *Dicranum*, ITS, mosses, new species, new synonym, Russia.

INTRODUCTION

The genus *Dicranum* remains a relatively poorly studied group in the Russian moss flora. There are a number of doubtful taxa, as well as specimens whose identification poses a serious difficulties. The application of molecular studies with ITS for the *Dicranum viride*-group (Ignatova & Fedosov, 2008) demonstrated that this is a rather promising tool in this genus, as well as in many other moss families.

In the present paper this approach is used to elucidate the status of a recently described species, *Dicranum pseudacutifolium* Otnyukova (Otnyukova, 2007) and its relationships with the taxa, which are known as a difficult complex of species: *D. acutifolium* (Lindb. & Arnell) C.E.O. Jensen, *D. brevifolium* (Lindb.) Lindb., *D. flexicaule* Brid. and *D. fuscescens* Turner. The two latter species were not always considered as distinct (cf. Hedenäs & Bisang, 2004; Ireland, 2007).

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Table 1. Data on specimens used in phylogenetic analysis and GenBank accession numbers

| Species of <i>Dicranum</i> | TCS code | Specimen | GenBank # |
|--|----------|---|----------------------|
| <i>acutifolium</i> Sakhalin | A1 | Sakhalin, <i>Ignatov</i> # 06-18 (MHA) | HQ830322 |
| <i>acutifolium</i> Buryatia | A2 | Buryatia, <i>Tubanova</i> # Ok-01/08 (UUH) | HQ830323 |
| <i>acutifolium</i> NE Yakutia | A3 | Yakutia, 26.VII.2007 <i>Isakova s.n.</i> (MHA) | HQ830324 |
| <i>brevifolium</i> Tuva | B4 | Tuva, 12.VI.2007 <i>Otnyukova s.n.</i> (KRF) | HQ830341 |
| <i>brevifolium</i> Karachaevo-Cherkessia | B2 | Karachaevo-Cherkessia, 27.VII.1996 <i>Egorov s.n.</i> (MW) | HQ830342 |
| <i>brevifolium</i> North Ossetia | B3 | North Ossetia, 6.IX.2002 <i>Korotkov s.n.</i> (MW) | HQ830343 |
| <i>brevifolium</i> South Yakutia | B1 | Yakutia, 3.VIII.2000 <i>Kuznetzova s.n.</i> (MW) | HQ830344 |
| <i>brevifolium</i> / <i>septentrionale</i> Kamchatka | S3 | Kamchatka, 4.VIII.2007 <i>Neshataeva</i> #986 (LE) | HQ830338 |
| <i>brevifolium</i> / <i>septentrionale</i> Arkhangelsk | S1 | Arkhangelsk Province, <i>Churakova</i> # 864 (MW) | HQ830339 |
| <i>brevifolium</i> / <i>septentrionale</i> Putorana | S2 | Krasnoyarsk Territory, Putorana, 21.VII.1969 <i>Kuvaev</i> # 46-8 (MW) | HQ830340 |
| <i>cf. pseudacutifolium</i> / <i>acutifolium</i> Buryatia | PS1 | Buryatia, <i>Tubanova</i> # Ok-01/08 (UUH) | HQ830325 |
| <i>cf. pseudacutifolium</i> / <i>acutifolium</i> SE Yakutia | PS2 | Yakutia, <i>Ignatov</i> # 00-813 (MHA) | HQ830326 |
| <i>cf. pseudacutifolium</i> / <i>acutifolium</i> NE Yakutia | PS3 | Yakutia, 26.VII.2007 <i>Isakova s.n.</i> (MHA) | HQ830327 |
| <i>flexicaule</i> Zabaikalsky | FL1 | Zabaikalsky Territory, 4.VIII.2006 <i>Dudareva s.n.</i> (IRK) | HQ830331 |
| <i>flexicaule</i> Primorsky | FL2 | Primorsky Territory, <i>Ignatov</i> # 06-2637 (MHA) | HQ830332 |
| <i>flexicaule</i> Komi | FL3 | Komi, 4.VII.2007 <i>Kucherov s.n.</i> (MW) | HQ830333 |
| <i>fuscescens</i> Perm | FU1 | Perm Province, 2005 <i>Bezgodov & Shkaraba s.n.</i> (MHA) | HQ830334 |
| <i>fuscescens</i> Sakhalin | FU2 | Sakhalin, <i>Ignatov</i> # 06-14 (MHA) | HQ830335 |
| <i>fuscescens</i> Sverdlovskaya | FU3 | Sverdlovskaya Province, <i>Braslavskaya</i> # DKT64 (MW) | HQ830336 |
| <i>fuscescens</i> Primorsky | FU4 | Primorsky Territory, <i>Ignatov</i> # 06-2588 (MHA) | HQ830337 |
| <i>pseudacutifolium</i> / <i>flexicaule</i> Tuva | PA3 | Tuva, 23.VII.1995 <i>Molokova s.n.</i> (KRF) | HQ830328 |
| <i>pseudacutifolium</i> / <i>flexicaule</i> Putorana 1 | PA2 | Krasnoyarsk Territory, Putorana, 29.VII.1991 <i>Otnyukova s.n.</i> (MHA) Isotype of <i>D. pseudacutifolium</i> | HQ830329 |
| <i>pseudacutifolium</i> / <i>flexicaule</i> Putorana 2 | PA1 | Krasnoyarsk Territory, Putorana, 29.VII.1991 <i>Otnyukova s.n.</i> (KRF) Holotype of <i>D. pseudacutifolium</i> | HQ830330 DQ294335 |
| <i>scoparium</i> | | | DQ294335 |

MATERIAL AND METHODS

Morphological studies were based on collections from MHA, MW, KRF, UUH, LE, IRK.

Molecular phylogenetic analysis was focused on *D. pseudacutifolium*, as well as on *D. flexicaule* and *D. fuscescens*. Three of 'the most typical' specimens of *D. acutifolium* were included in the study. Seven samples of *D. brevifolium*, which came from distant localities were selected. Preference was given to the morphotypes that somewhat differed from others in cell areolation. Data on voucher specimens and Genbank accession numbers are provided in Table 1. Species names are given as they were identified by morphology.

The protocol of DNA extraction, PCR and sequencing of ITS data were the same as de-

scribed by Gardiner et al. (2005). Sequences were aligned manually in BioEdit (Hall, 1999). Parsimony analysis was done with Nona (Goloboff, 1994) within the Winclada shell (Nixon, 1999) and bootstrap support was calculated with 3000 replications (mult*N 10, hold 10, do max). The tree was rooted on *Dicranum scoparium*.

Haplotype network analysis was performed in TCS 1.21 (Clement et al., 2000), with various parameters discussed below.

RESULTS

Phylogenetic analysis resulted in a bootstrap tree (Fig. 1) where *Dicranum fuscescens*, *D. flexicaule* and three specimens of *D. pseudacutifolium* (including parts of the isotype and holotype) appeared in the terminal clade. Sister to this ter-

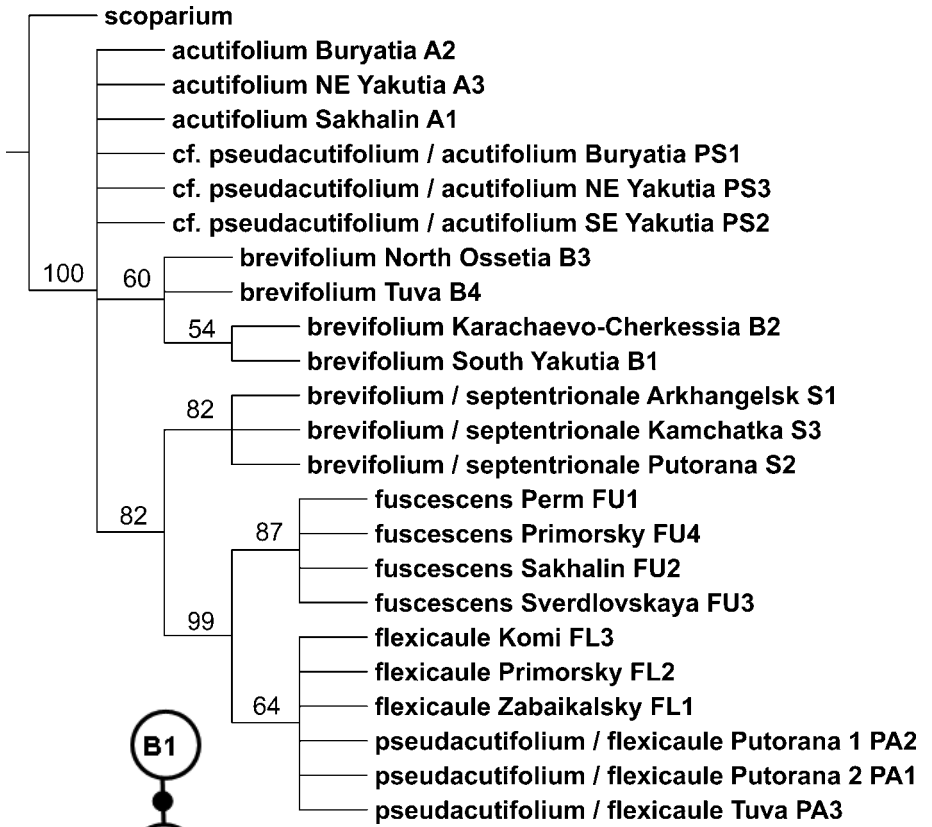


Fig. 1. Bootstrap tree for the species of *Dicranum acutifolium* and *D. fuscescens* complexes with *D. scoparium* as an outgroup Support values >50, calculated by 3000 iterations in Nona, are indicated above branches.

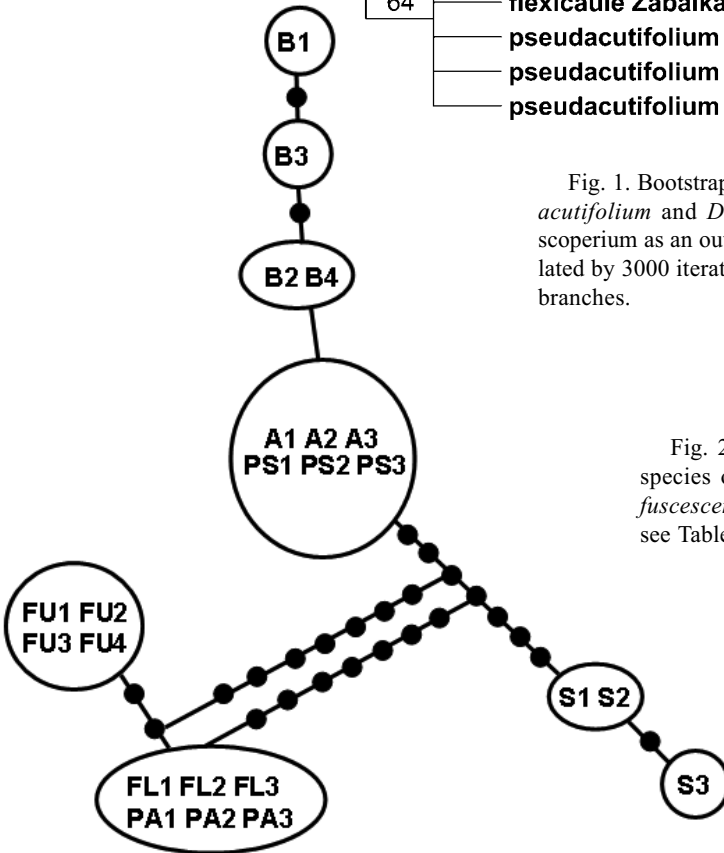


Fig. 2. ITS haplotype network for the species of *Dicranum acutifolium* and *D. fuscescens* complexes. For abbreviations see Table 1 and Fig. 1.

minimal clade is a clade formed by three northern specimens of *D. brevifolium*. Basal polytomy includes *Dicranum acutifolium*, three specimens identified as *D. cf. pseudacutifolium*, and a clade of four specimens of *D. brevifolium*.

Bootstrap support was found to be high for the whole terminal clade formed by *D. flexicaule*, *D. pseudacutifolium* and *D. fuscescens* (99) and within it also for the clade of *D. fuscescens* (87). The clade of *D. flexicaule* and *D. pseudacutifolium* was low supported (64), despite the fact that the visual analysis of the alignment found not one parsimony informative substitution within this group of 6 specimens. Also, the high bootstrap value (82) was found for the clade of three northern specimens of *D. brevifolium*.

TCS analysis with a connection limit at 12 steps (94%), with the gap as missing data and no gap coding resulting in a haplotype network (Fig. 2), shows delimited groups in a certain way similar to that in the phylogenetic tree in Fig. 1. The gap coding as a singular event regardless of gap length (not shown), gave the subidentical network that differs mainly in larger numbers of missing haplotypes between taxa, up to 20 between *D. flexicaule* and *D. acutifolium*.

The TCS analysis shows the position in the same haplotype for *D. flexicaule* and *D. pseudacutifolium* (type and Tuva specimens), as well as for *D. acutifolium* and *D. cf. pseudacutifolium* (one of specimens of *D. acutifolium* has one insertion of one adenine nucleotide, which separates it in the analysis with the second variant of gap coding).

DISCUSSION

The present analysis confirms neither the separate position of the type specimens of the *Dicranum pseudacutifolium* from the earlier described and widespread *D. flexicaule*, nor the homogeneity of the former species. Specimens identified as *D. pseudacutifolium* are found in two clades, together with *D. flexicaule* and with *D. acutifolium*, the species which were considered the most similar to *D. pseudacutifolium* by Otnyukova (l.c.).

Dicranum pseudacutifolium and *D. flexicaule*

According to the original description, the distinctions of *D. pseudacutifolium* from *D. flexicaule* include straight and thin lamina cell walls vs. "not straight" and thick lamina cell walls (which is not always so in *D. flexicaule*, accord-

ing to our observations). Also, included are leaves "keeled-channeled, looking like a pair of tongs in leaf cross section" vs. "keeled-tubulose" in *D. flexicaule*. However, the illustrations of the holotype by Otnyukova (l.c.) are variable for the latter character, showing both patterns. Other distinguishing characters listed in the table are numerous and still more variable so that any of them may occur in *D. flexicaule*.

Although the clade formed by three specimens of *D. pseudacutifolium* and three of *D. flexicaule* has only moderate support (64, cf. Fig. 1), the lack of genetic difference (cf. Fig. 2), indicates that by ITS these six specimens are more similar to each other, than e.g. *D. flexicaule* to *D. fuscescens*. Two latter species consistently differ in two substitutions, despite (1) *D. flexicaule* and *D. fuscescens* are often considered to be very closely related and sometimes treated as infraspecific taxa of one species; (2) both species were represented in analysis by specimens from European Russia and Russian Far East, with the distance between the localities over 5000 km.

The analysis of morphology indicates that the type of *D. pseudacutifolium* was selected among not very typical plants of *D. flexicaule* with quite thin cell walls and less falcate leaves. Therefore *D. pseudacutifolium* is synonymized here with *D. flexicaule*. A similar variation in these characters occurs in many species of *Dicranum*, especially in the severe climate in Siberia.

The problem, however, should not be oversimplified, as the part of the specimens identified originally as *D. pseudacutifolium* (called here as *D. cf. pseudacutifolium*) were found within the basal polytomy formed by *D. acutifolium*. These specimens, i.e. *D. cf. pseudacutifolium*, are morphologically more similar to the plants of the type of *D. pseudacutifolium* than to 'typical' *D. acutifolium*, which was revealed to be its closest relative by ITS data (Figs. 3-7).

Our attempts to find any stable discriminative morphological character or combination of characters between *D. pseudacutifolium* and *D. cf. pseudacutifolium* were not successful. A number of herbarium specimens (especially from the Eastern Siberia) were left with a question mark since we were not able to decide if they belong to thin-walled *D. flexicaule* (i.e. like the type of *D. pseudacutifolium*) or to *D. cf. pseudacutifolium*. At the same time (as discussed below), there is a

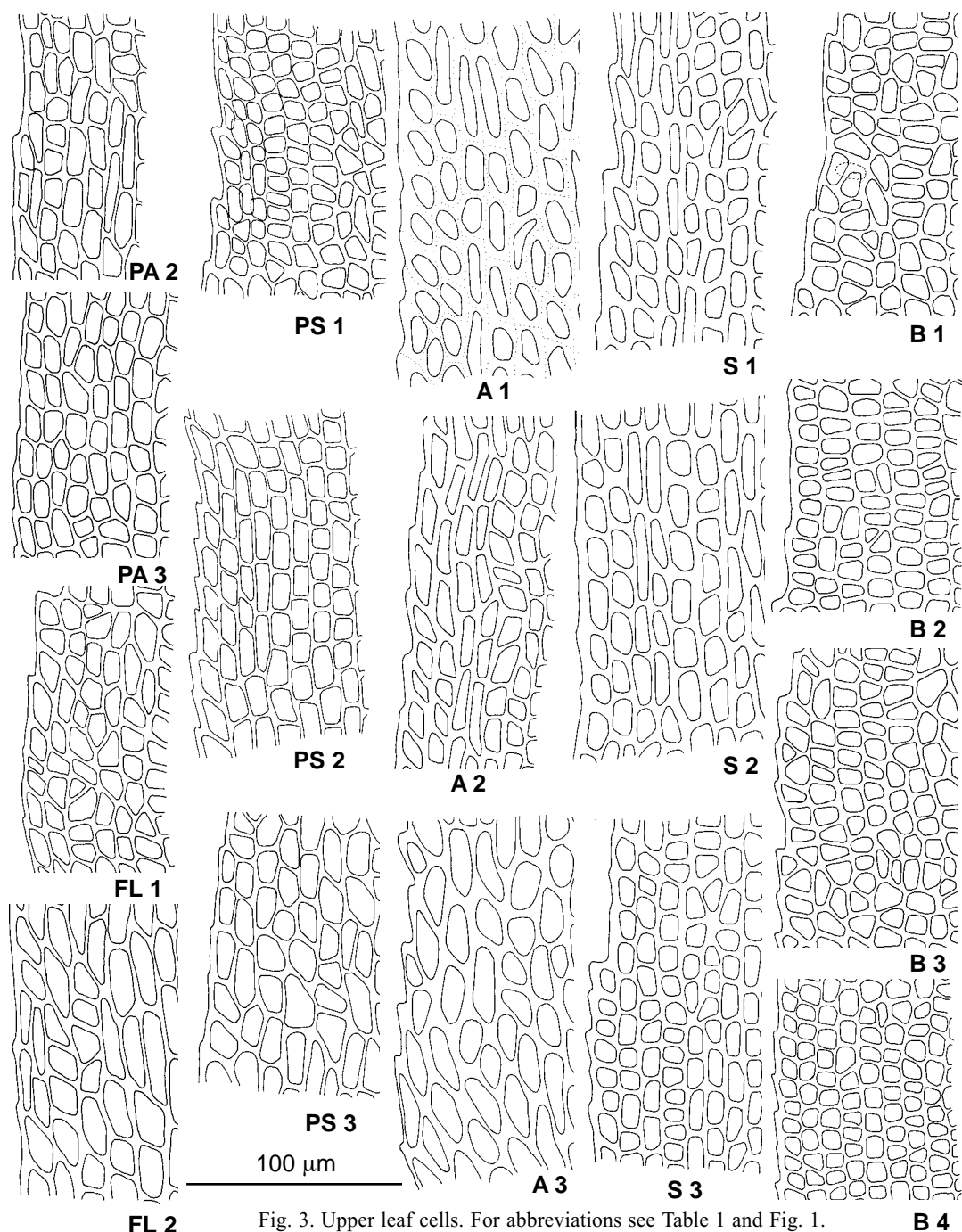


Fig. 3. Upper leaf cells. For abbreviations see Table 1 and Fig. 1.

certain difference in morphology between *D. cf. pseudacutifolium* and *D. acutifolium*.

***Dicranum pseudacutifolium*
and *D. acutifolium***

According to the original description, *Dicranum pseudacutifolium* differs from *D. acutifoli-*

um primarily in the absence of bulges between the cell walls as it is seen in leaf cross sections (Otnyukova, l.c.). However, many authors describe this character in *D. acutifolium* as very variable and there is also an inconsistency among authors in this respect, e.g. Hedenäs & Bisang

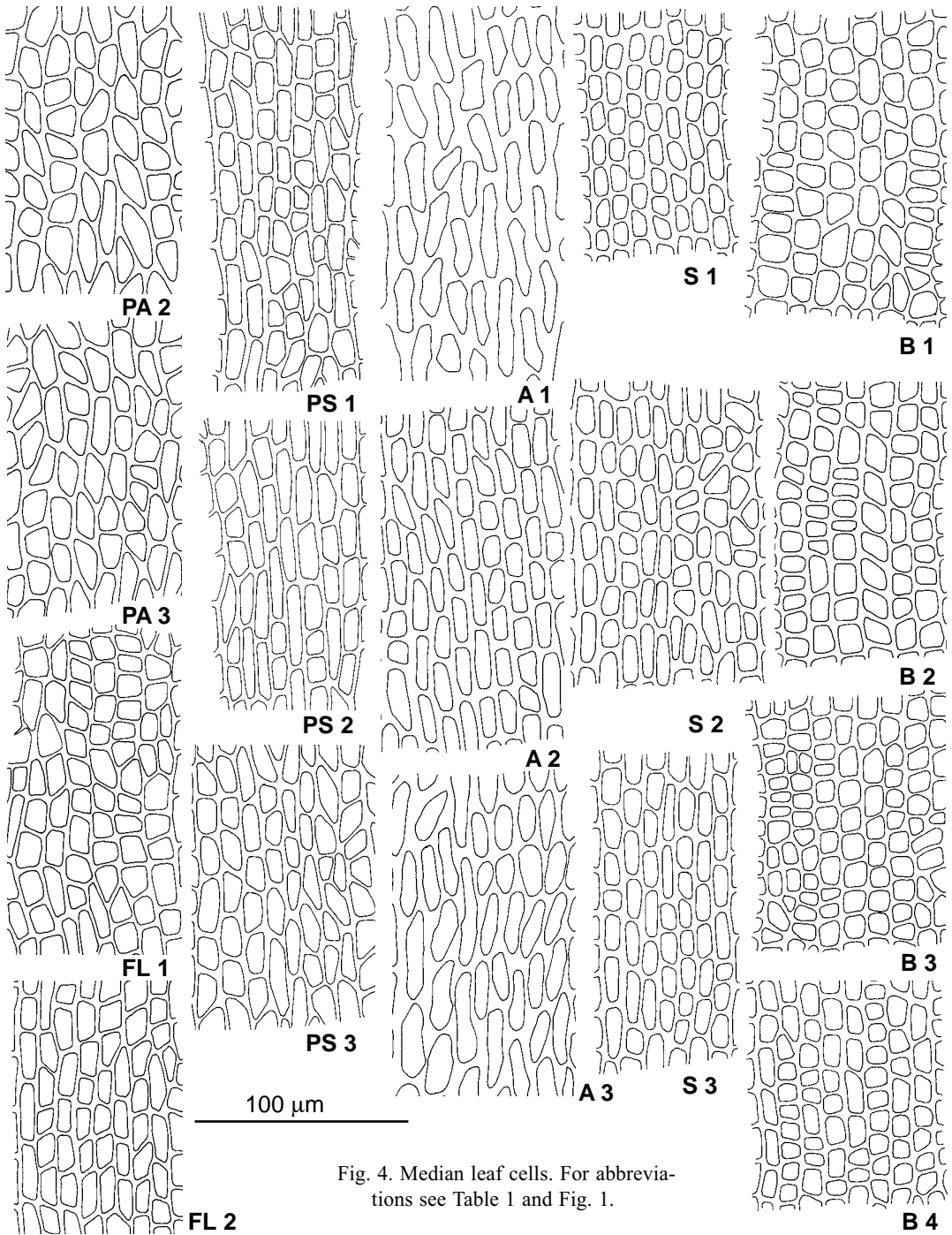


Fig. 4. Median leaf cells. For abbreviations see Table 1 and Fig. 1.

(l.c.) reported their presence, while Ireland (l.c.) reported cell walls of *D. acutifolium* to be smooth or slightly bulging. Our observation found mostly very weak to completely absent bulgings in *D. acutifolium* in most of Siberian specimens, thus

this character may hardly be considered of a great importance. In all sequenced specimens of the latter species these bulges are weak to almost absent (Fig. 7: A1-3), while other diagnostic characters of *D. acutifolium*, i. e. thick-walled and

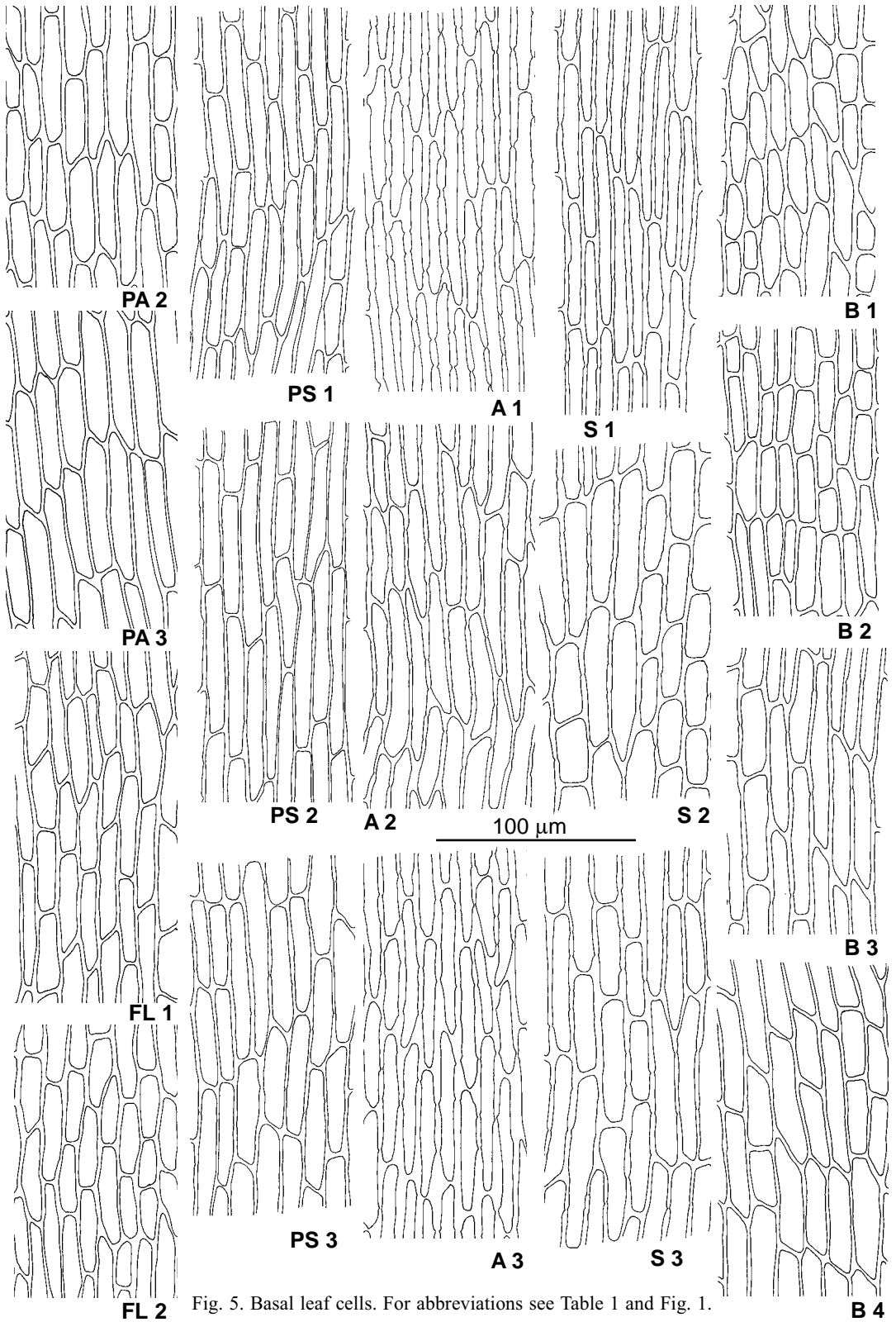


Fig. 5. Basal leaf cells. For abbreviations see Table 1 and Fig. 1.

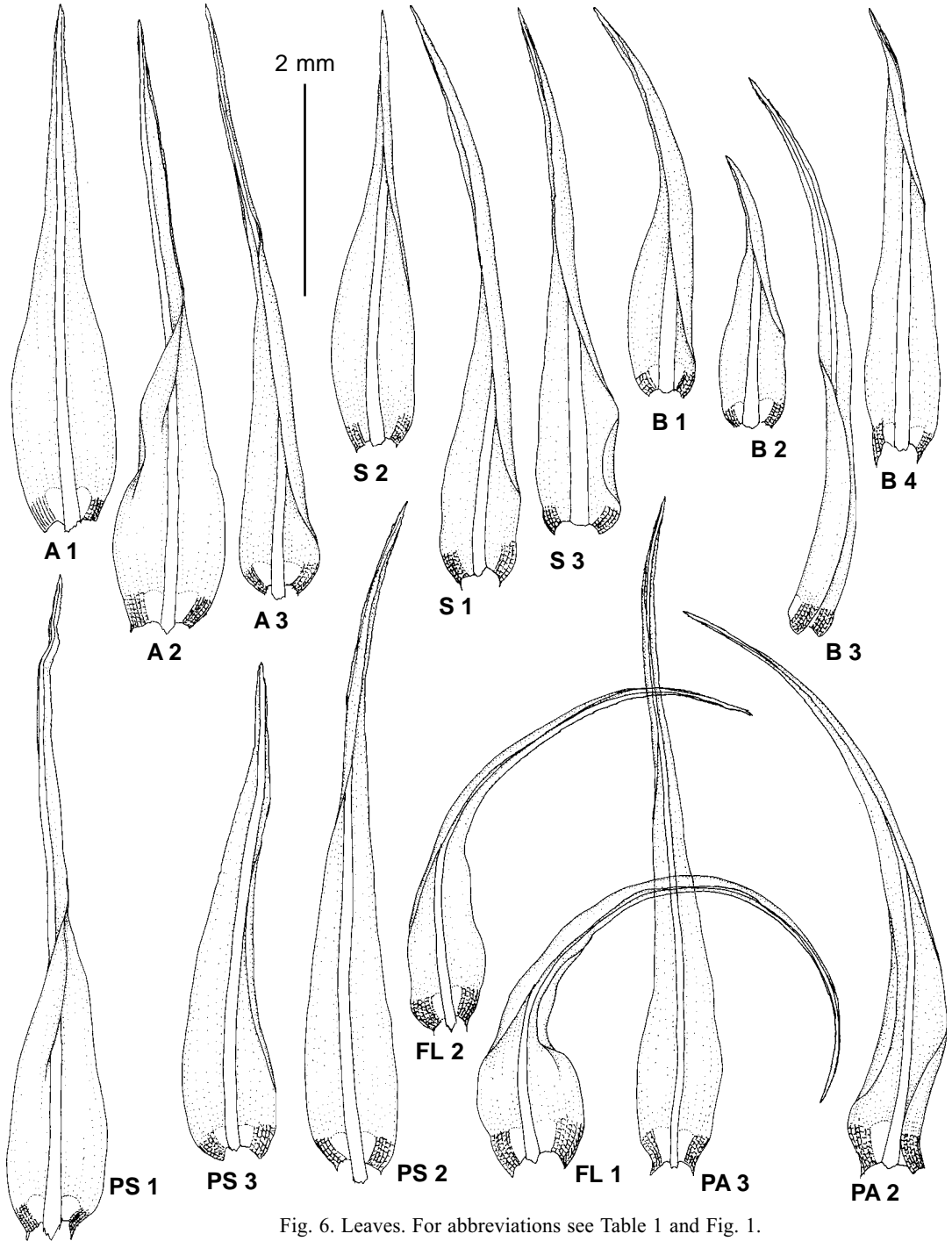


Fig. 6. Leaves. For abbreviations see Table 1 and Fig. 1.

irregularly shaped distal lamina cells and long, porose proximal cells, are more important for their identification (Figs. 3-5: A1-3).

Three specimens of *D. cf. pseudacutifolium* that appeared in the basal polytomy with *D. acuti-*

folium and *D. brevifolium* (in part) are rather distinct in cell areolation. They differ from two specimens of *D. acutifolium* (Figs. 3-4: A1, 3) in the contrastingly thin-walled distal lamina cells, mostly arranged in clear longitudinal rows ver-

sus the usually strongly thickened and irregular cells in *D. acutifolium*; although in one specimen (Figs. 3-4: A2) these characters have intermediate states.

The basal lamina cells are similar in shape in *D. cf. pseudacutifolium* and *D. acutifolium*, but in the former they are relatively thin-walled and weakly porose (Fig. 5 PS1-3), in contrast to the usually thick-walled and strongly porose basal cells in *D. acutifolium* (Fig. 5 A1 & A3, but not A2, which is intermediate).

Leaf shape is similar in *D. cf. pseudacutifolium* and *D. acutifolium*, with at best the only small difference. Specimens of *D. cf. pseudacutifolium* with longer leaves are somewhat curled when dry. Also all leaves have a distinct group of thin-walled, hyaline cells between alar region and costa.

The differences between *D. cf. pseudacutifolium* and *D. acutifolium* in areolation may be taxonomically significant, but an additional study is needed to confirm that the former is not just a marginal phenotype within the range of *D. acutifolium*. Before this possible formal recognition, we have chosen to keep the plants of *D. cf. pseudacutifolium* within *D. acutifolium*.

Dicranum flexicaule and *D. fuscescens*

These two species are considered to be hardly separable from each other due to the numerous specimens with intermediate characters, which are impossible to determine for certain. Hedenäs & Bisang (l.c.) express a doubt if they are really a good species, even if their extreme phenotypes are readily recognizable. Bellolio-Trucco & Ireland (1990) and Ireland (l.c.) treat *D. flexicaule* as a variety of *D. fuscescens*. Among differential characters of these species are usually listed: 1) densely and coarsely denticulate distal leaf margins of *D. fuscescens* vs. irregularly denticulate, with long entire portions to almost entire ones of *D. flexicaule*; 2) upper lamina cells relatively regularly quadrate, frequently mamillate vs. irregular in shape, only with scattered mamillae; 3) costa dorsally densely denticulate or rough in upper 2/5–4/5 of the costa vs. relatively distantly denticulate or rough in the upper 1/3 (Hedenäs & Bisang, l.c.); Ireland (2007) describes the costa as almost smooth on dorsal surface in var. *flexicaule* and adds that the length of seta is longer than 2.5 cm vs. less than 2.5 cm in

var. *fuscescens*. Savicz-Lyubitzskaya & Smirnova (1970) and Ignatov & Ignatova (2003) also mention the costa width, which is less strong in *D. flexicaule*, 1/10–1/7 vs. 1/7–1/5 the width of the leaf base in *D. fuscescens*.

Specimens used in the present analysis represent rather typical phenotypes of both species, except specimen of *D. flexicaule* FL1, Zabaikalsky Territory, which is similar to *D. fuscescens* habitually and in strongly rough costa in the distal half or more, and upper lamina cells densely mamillate distally. However, its leaf margins are strongly serrate only along a short distance near apex and below are quite slightly serrulate; distal lamina cells are thin-walled, rather regular but short rectangular (not quadrate); costa is narrow, ca. 1/10 the width of leaf base. In ITS1-2 this specimen does not differ from other specimens of *D. flexicaule*.

The analysis of ITS sequences of *D. fuscescens* and *D. flexicaule* found only two substitutions between them (Fig. 2), but this difference remains stable in a broad geographical range and consistently associated with morphology. Therefore the species status of *D. flexicaule* is more likely than just an infraspecific entity within *D. fuscescens*.

Dicranum brevifolium and *D. septentrionale*, sp. nov.

Seven specimens of *D. brevifolium* included in the analysis were resolved in two clades, one having a high bootstrap value (82), while another one was quite weakly supported (60). The former (group 1) is situated in a grade to *D. fuscescens*–*D. flexicaule* terminal clade, while the latter (group 2) appeared in an unresolved grade with *D. acutifolium* (Fig. 1).

Originally all these plants were identified as *D. brevifolium* because they have more or less strongly crispate leaves in dry condition, distal lamina cells are arranged in clear longitudinal rows, distal lamina cells are moderately thick-walled and have distinct bulgings upon longitudinal walls as it is seen in a leaf transverse section.

However, plants have also a number of characters specific for each of these two clades. Plants of the group 1 have mostly rectangular cells in distal and median lamina vs. predominantly isodiametric and transversely rectangular in group 2. The basal lamina cells are longer, (2.5-)4-6(-10):1 and clearly porose in group 1 vs. comparatively

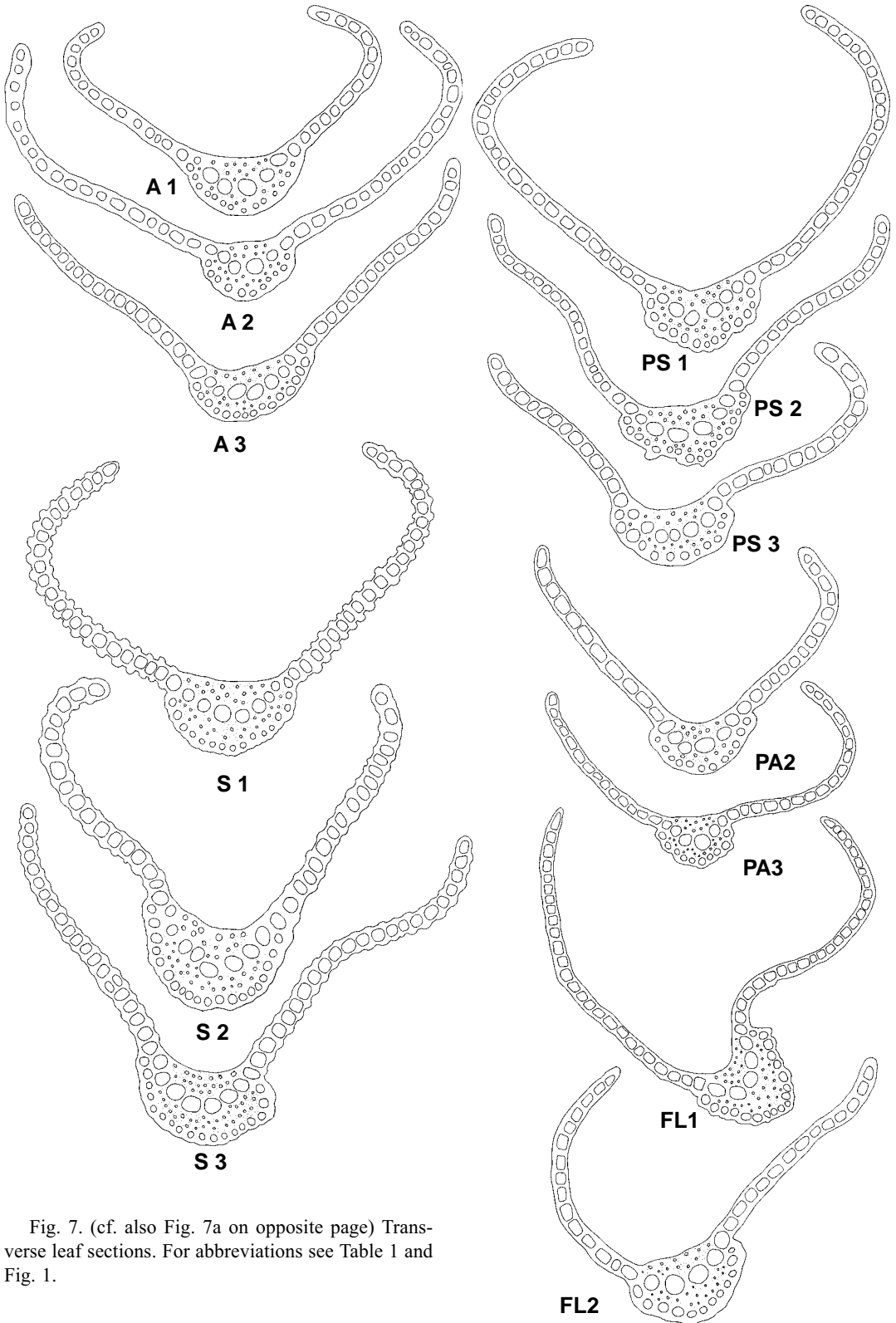


Fig. 7. (cf. also Fig. 7a on opposite page) Transverse leaf sections. For abbreviations see Table 1 and Fig. 1.

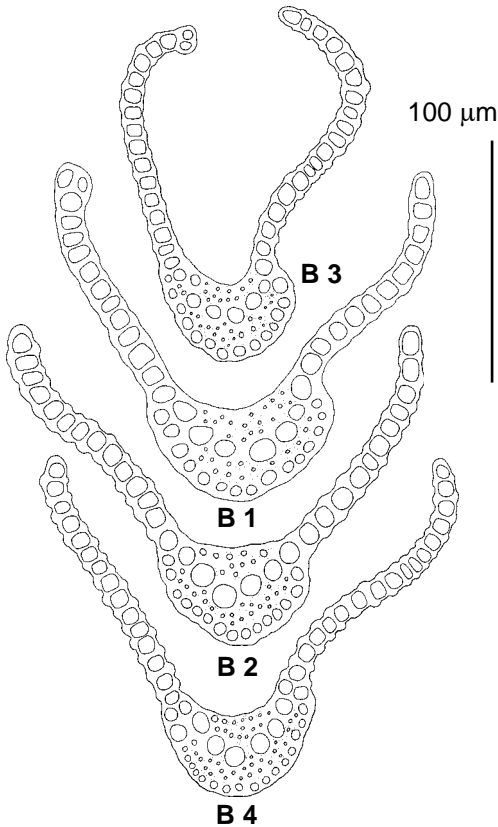


Fig. 7a (cf. opposite page). Transverse leaf sections. For abbreviations see Table 1 and Fig. 1.

short, (1.6-)3-4(-8):1 and not or very slightly porose in group 2. Basal lamina cells are not sharply delimited from rectangular median cells in group 1 vs. contrastingly differ from more opaque quadrate median cells in group 2. Leaves of group 2 have distinct thin-walled hyaline cells between alars and costa, while this is not always the case in group 1. Plants of group 2 fit well the description of *D. brevifolium* and agree with the holotype in all essential characters (Fig. 8 and Figs. 3-7: B1-4). Therefore the name *D. brevifolium* should be applied to the group 2 in our study, while the group 1 needs to be described as a new species, *D. septentrionale* (see below).

Though *D. acutifolium* and *D. brevifolium* have very weak difference in ITS, morphologically these species are quite distinct. Their differentiating characters include: 1) almost straight or slightly flexuose when dry leaves, not secund when moist in *D. acutifolium* vs. \pm strongly curled when dry leaves, usually secund when moist in *D. brevi-*

folium; 2) distal lamina cells irregular in shape, mostly elongate, usually strongly thick-walled, not arranged in longitudinal rows vs. predominantly isodiametric, \pm quadrate, moderately thick-walled cells in clear longitudinal rows; 3) longitudinal cell walls not or weakly bulging vs. clearly, occasionally conspicuously bulging; 4) basal lamina cells (3.5-)5-7(-10):1 and clearly porose vs. (1.6-)3-4(-8):1 and not or very slightly porose.

In addition to morphology, *D. acutifolium* and *D. brevifolium* have a rather contrasting distribution. *Dicranum acutifolium* is an arctic-alpine species, and it is more common in northern territories including Subarctic and Arctic in Russia; *D. brevifolium*, as appeared after a revision of collections in MW, MHA, LE and UUH, occurs in NW European Russia, Caucasus, South Siberia, and in Yakutia (only in southern part). There are many records of *D. brevifolium* from the Arctic and Subarctic in Russia (e.g. Ignatov et al., 2006), but at least most of them must be excluded from *D. brevifolium* and put in *D. septentrionale*.

Dicranum septentrionale Tubanova & Ignatova sp. nov.

Type: Russia, Arkhangelsk Province, Pinega Nature reserve, 19.VII.2000, Churakova #864. (Holotype MW, Isotype in MHA. Figs. 3-7 (S1-3), 9.

A D. brevifolio affinis, sed cellulis folii superioribus et mediocrius rectangularibus et cellulis basilibus valde elongates et porosis differt.

Plants medium-sized, in dense tufts, dull yellowish green in upper part, dull brownish below. Stems 5-7 cm, densely tomentose almost to apex, rhizoids of tomentum reddish brown. Leaves curled when dry, falcate-secund when moist, occasionally slightly undulate distally, lanceolate, narrowly acute, 4-6 mm long, 0.7-0.8 mm wide at base, concave proximally, keeled distally, with incurved margins, in transverse section like a pair of tongs; costa strong, occupies ca. 1/5 the width of leaf base, 150-200 μ m wide at base, strongly projecting dorsally in distal part, weakly roughened dorsally in distal 1/3 (-1/2) to smooth, with one row of guide cells, two thick stereid bands extending to almost the apex, adaxial epidermal cells not differentiated, abaxial epidermal layer differentiated; margins entire in proximal 1/3-1/2, serrulate distally and more strongly serrate near apex, occasion-

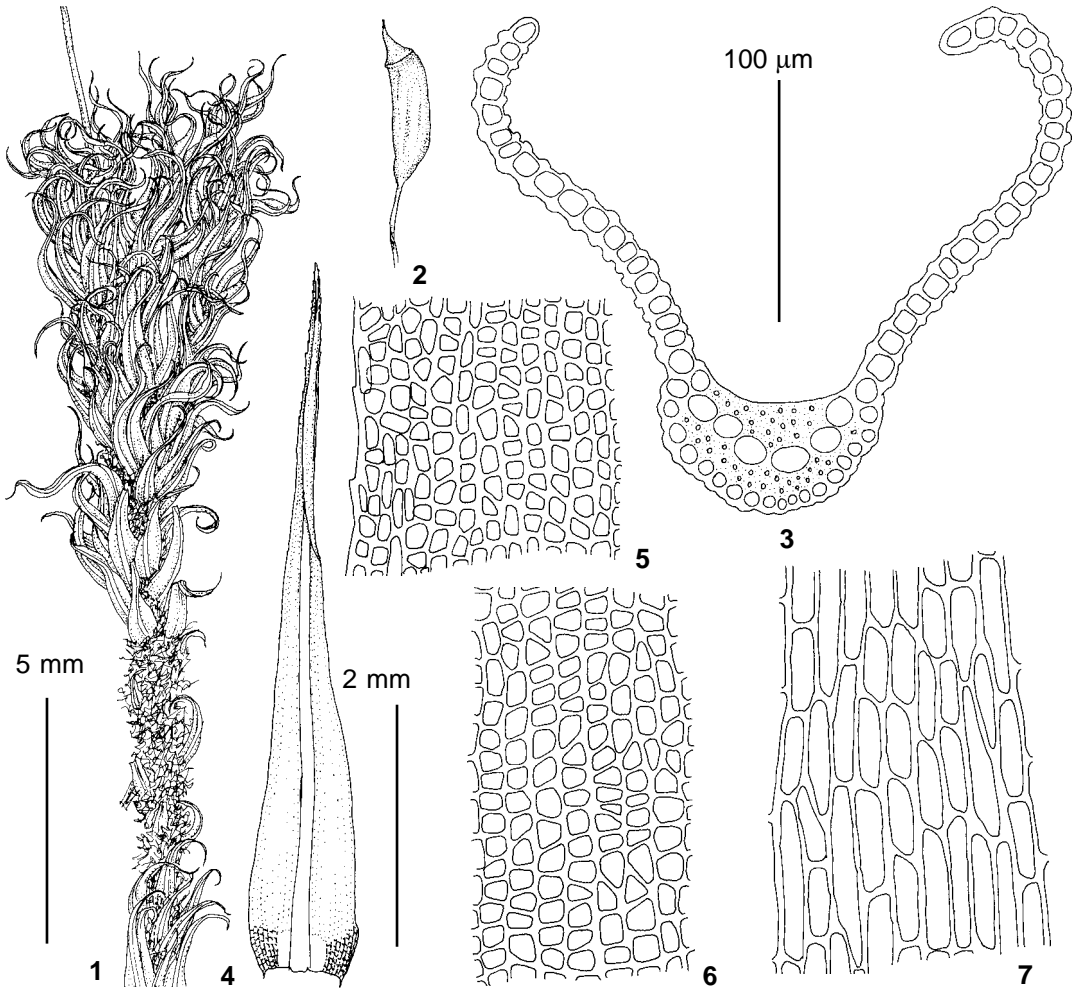


Fig. 8. *Dicranum brevifolium* (from holotype: Norvegia, N.M.Blytt, H-SOL #667026); 1 – habit, dry; 2 – capsule; 3 – leaf transverse section; 4 – leaf; 5 – upper lamina cells; 6 – median lamina cells; 7 – basal lamina cells. Scale bars: 5 mm for 1-2; 2 mm for 4; 100 µm for 3, 5-7.

ally almost entire; lamina unistratose or occasionally bistratose at places at margins distally and with few bistratose patches near costa; distal lamina cells short-rectangular or elongate rhomboidal with small admixture of isodiametric cells, (7-)10-25×10-12 µm, moderately thick-walled, not porose, arranged in clear longitudinal rows, with bulging longitudinal walls, occasionally papillae-like in transverse section; median lamina cells similar to distal cells, 10-30×10 (-12) µm; basal lamina cells long rectangular, (2.5-)4-6(-10):1, 40-100×(8-)11-14(-16) µm, with small admixture of shorter cells, ±strongly porose; alar cells bistratose, dark brown, cells between alar group and costa short-rectangular, comparatively thin-walled, light

brownish or few cells hyaline, occasionally not differentiated from basal lamina cells.

Apparently dioicous; sporophytes very rare; male plants not seen. Sporophytes single in perichaetium; capsules inclined; spores 20-25 µm.

Differentiaton. *Dicranum septentrionale* resembles *D. acutifolium* in areolation due to mostly elongate, rather irregular distal and median lamina cells and long, porose basal lamina cells. However, upper cells of the former species are arranged in longitudinal rows which is uncommon for *D. acutifolium*, and usually moderately to strongly bulging longitudinal cell walls vs. mostly plane or indistinctly bulging cell walls also separate these species. In addition, leaves of *D. sep-*

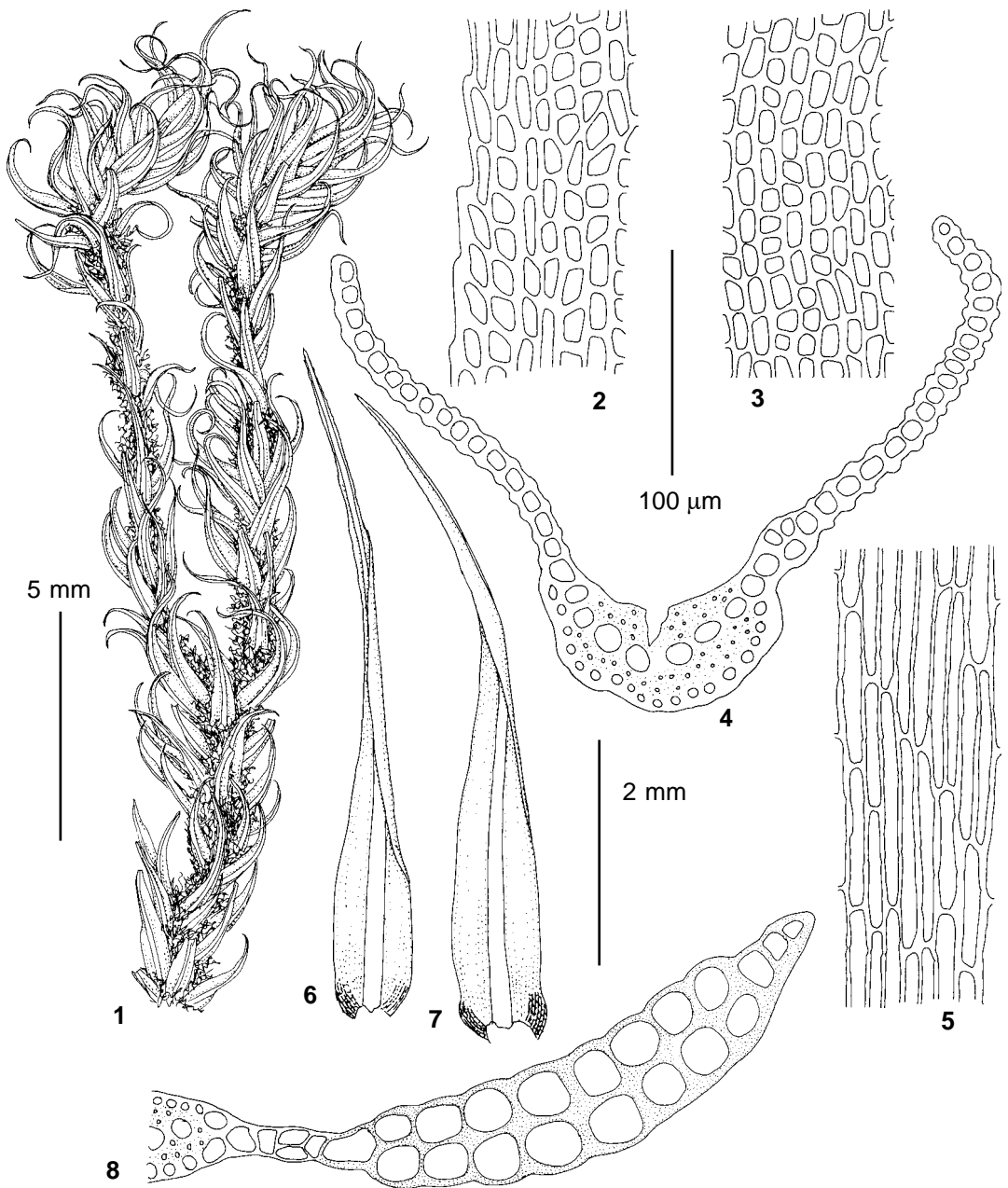


Fig. 9. *Dicranum septentrionale* sp. nov. (from holotype); 1 – habit, dry; 2 – upper lamina cells; 3 – median lamina cells; 4 – leaf transverse section; 5 – basal lamina cells; 6-7 – leaves; 8 – transverse section of alar region. Scale bars: 5 mm for 1; 2 mm for 6-7; 100 μ m for 2-5, 8.

septentrionale are curled or crisped when dry whereas they are mostly almost straight or slightly bent in *D. acutifolium*. *Dicranum brevifolium* is more similar in appearance, but it is distinct in predominantly isodiametric distal and median lamina cells and usually shorter basal cells (cf. Figs. 3-5).

Ecology. The species grows mostly in mountains from foothills to 1330 m, or more rarely in lowlands, on soil and rocks in birch, pine and pine-larch forests, rarely in spruce forests, in *Alnus* stands, different types of mountain tundra and in meadows; collected once on thermal field.

Distribution. As it was revealed from collections in LE, MW and MHA, *D. septentrionale* has a wide distribution in northern Eurasia, being apparently rare in most regions, except Kamchatka, where there are numerous collections. The species occurs either in the mountains or in lowland areas with numerous rock outcrops (e.g. Pinega in Arkhangelsk Province). It occurs both in Subarctic (Chukotka, Putorana Plateau, Polar Urals, and Khibiny Mts. in Murmansk Province), as well as southwards to Primorsky Territory, north of Irkutsk Province, and mostly in mountains of the South Urals. Distribution areas of *D. septentrionale* and *D. brevifolium* do not strongly overlap, as the latter has a more southern distribution, except NW European Russia. *Dicranum brevifolium* is rather common in Kola Peninsula where *D. septentrionale* is known only from two collections in the Khibiny Mts. On the other hand, in Kamchatka the situation is just the opposite with *D. septentrionale* being more common, while *D. brevifolium* is represented by a single collection.

Other specimens examined: EUROPEAN RUSSIA: **Murmansk Province:** Khibiny Mts., Tulijok River valley, s-facing slope of Kukisvumchorr Mt., 2.VIII.1930, A.A.Korchagin & M.V. Korchagina s.n. (LE); Khibiny Mts., Loparka River valley, E-facing slope of Apatitovaya Mt., 7.VIII.1930 A.A. & M.V. Korchaginy s.n. (LE). **Karelia:** Petrozavodsk District, VI.1914, *Dingelshedt s.n.* (LE). **Bashkortostan:** Burzyan District, 2 km S of Magadeevo, *Ignatova #9/12* (MHA); Bashkirskiy Nature Reserve, upper course of Belaya River, South Kraka Range, 10.VIII.1945, 8.IX.1945, 14.VI.1946, 28. IX.1946, 3.VII.1948, *Selivanova-Gorodkova s.n.* (LE). ASIATIC RUSSIA. **Krasnoyarsk Territory:** Putorana Plateau, Kapchuk Lake, 4.VII.1982, *Czernyadjeva #122* (LE); Jenisei, Dudinka, 69°35' n. lat., 30.VII.1876, *Arnell s.n.* (LE). **Irkutsk Province:** Tutura River valley, 1910, *Kuznetsov #328* (LE). **Khanty-Mansy Autonomous District:** Northern (subpolar) Urals, Lysaya Gora Mt. at right slope; of Serania-el Creek (Khulga River right tributary), ca. 480 m a.s.l., 23.IX.1949, *Kuvaev #484* (MW); **Kamchatka:** Elovka River, 25.VIII.2003, *Czernyadjeva #110* (LE); Ushkovskiy Volcano, Bilchenok Glacier valley, 15.VII.2003, *Czernyadjeva #9* (LE); Bystraya River basin, Uvalnaya Mt., 10.VIII.2005, *Czernyadjeva #30* (LE); Esso surroundings, Ubojnyj Creek sources, 4.VIII.2003, *Czernyadjeva #78* (LE); Klyuchevskoj Dol surroundings, 19.VIII. 2004, *Czernyadjeva #99* (LE); Ostryj Tolbachik Volcano, Vodopadnyj Creek sources, 11.VIII.2006, *Czernyadjeva #22* (LE); Alnej Mt., Kirevna River, 23.VIII.201, *Czernyadjeva #24* (LE). **Chukotka:** Achchen Lake surroundings, 8.VII.1970, *Afonina s.n.* (LE).

Primorsky Territory: Southern Sikhote-Alin, Tskhamodynza Mt., 5.IX.1959, *Ponomarenko #372* (LE).

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