Arctoa (2008) **17**: *63-83*

SPECIES OF DICRANUM (DICRANACEAE, BRYOPHYTA) WITH FRAGILE LEAVES IN RUSSIA

ВИДЫ РОДА DICRANUM (DICRANACEAE, BRYOPHYTA) С ЛОМКИМИ ЛИСТЬЯМИ В РОССИИ

ELENA A. IGNATOVA[1] & VLADIMIR E. FEDOSOV[1]

Е. А. ИГНАТОВА[1], В. Э. ФЕДОСОВ[1]

Abstract

Three species of *Dicranum* with fragile leaves were usually recognized in Russia: *D. fragilifolium*, *D. tauricum* and *D. viride*. However, our revision based on morphology and nrITS sequences reveals that two more species were overlooked. Collections from the Russian Far East, including both mainland and the Kuril Islands, usually treated as *D. viride* were found to be different from the european *D. viride,* thus supporting the resurrection of *D. hakkodense* Cardot that was synonymised with *D. viride* and not accepted for a long time as a distinct species. In addition to the resurrection of *D. hakkodense*, its distributional range is much expanded. One more species, *Dicranum pacificum* sp. nov. was revealed among the collections from Kamchatka, Sakhalin and the Kuril Islands. It is clearly separated from the superficially similar *D. fragilifolium,* although probably not closely related to it. Phylogenetic analysis reveals that the group of *Dicranum* with fragile leaves is not monophyletic.

Резюме

В большинстве работ по флоре мхов России для территории страны признавали 3 вида *Dicranum* с ломкими листьями: *D. fragilifolium*, *D. tauricum* и *D. viride*. Однако в результате ревизии группы по морфологическим и молекулярно-генетическим данным с использованием ITS выявлено еще два вида. ‘Дальневосточный *D. viride*’, как выяснилось, является самостоятельным видом; ранее он был описан как *D. hakkodense* Cardot из Японии, но потом был синонимизирован с *D. viride* и в качестве самостоятельного вида не рассматривался. Восстанавливая видовой статус *D. hakkodense,* мы также и значительно расширяем его ареал. Описан еще один вид, *Dicranum pacificum* sp. nov., который был выявлен в коллекциях с Камчатки, Сахалина и Курильских островов, ранее определенных как *D. fragilifolium*. При значительном внешнем сходстве эти виды, однако, вероятно не являются близкородственными. Филогенетический анализ группы показывает ее полифилетичность в пределах рода.

KEYWORDS: mosses, *Dicranum*, taxonomy, molecular phylogenetics, ITS, Russia, phytogeography

INTRODUCTION

Three species of *Dicranum* with strongly fragile leaf apices were known in the territory of Russia: *D. fragilifolium* Lindb., *D. tauricum* Sapjegin and *D. viride* (Sull. & Lesq.) Lindb.

Dicranum fragilifolium is a circumboreal species known in Europe only in Scandinavia and northern European Russia, being rather common in the latter in boreal zone. It is equally common throughout Siberia and at places in the Russian Far East; a similar northern distribution is known in North America (Ireland, 2007). It occurs com-

[1] – Department of Geobotany, Biological Faculty, Moscow State University, Moscow 119991 Russia – Россия 119991, Москва, Московский университет, Биологический факультет, каф. геоботаники

Table 1. Accession numbers of ITS1-2 sequences and voucher information of specimens of *Dicranum* used in the present analysis.

Species	Specimen	GenBank #
Dicranoloma		
menziesii		DQ464184
Dicranum		
fragilifolium Arkhangelsk	Arkhangelsk Prov., 3.VII.2001, *Churakova s.n.* (MW)	FJ952597
fragilifolium Vologda	Vologda Prov., 12.VIII.2001, *Ignatov & Ignatova s.n.* (MW)	FJ952596
fragilifolium Kamchatka	Kamchatka, 7.VIII.2006, *Czernyadjeva #9* (LE)	FJ952595
fragilifolium Irkutsk	Irkutsk Prov., 2007, *Seregin et al.* (MW)	FJ952598
fragilifolium Zabaikalsky	Zabaikalsky Territory, 16.VII.2005, *Afonina s.n.* (MW)	FJ952599
hakkodense Primorsky	Primorsky Territory, *Ignatov et al. #06-2624* (MHA)	FJ952601
hakkodense Kuril Islands	Kuril Islands, Kunashir, *Ignatov #06-1411* (MHA)	FJ952600
pacificum Kamchatka 1	Kamchatka, 16.IX.2005, *Samkova #31* (MW)	FJ952605
pacificum Kuril Islands	Kuril Islands, Kunashir, *Ignatov #06-1226* (MHA)	FJ952602
pacificum Kamchatka 2-5	Kamchatka, 26.VII.2004 *Czernyadjeva #25* (LE), clone5	FJ952603
pacificum Kamchatka 2-7	Kamchatka, 26.VII.2004, *Czernyadjeva #25* (LE), clone7	FJ970929
pacificum Kamchatka 3	Kamchatka, 28.VII.2002, *Czernyadjeva #32* (LE)	FJ952604
pacificum Sakhalin	Sakhalin, *Ignatov & Teleganova #06-301* (MHA)	FJ952606
polysetum		AF144113
scoparium 1		DQ294335
scoparium 2		DQ294327
scoparium var. orthophyllum	*Klazenga #6105* (MEL 2226718)	DQ485166
tauricum Kursk	Kursk Prov., 23.V.1995, *Popova s.n.* (MHA)	FJ952591
tauricum North Ossetia	North Ossetia, *Korotkov #02-3560* (MW)	FJ952594
tauricum Karachaevo-Cherkessia	Karachaevo-Cherkessia, *Ignatov & Ignatova #05-3342* (MW)	FJ952593
tauricum Oregon	USA, Oregon, 14.VIII.1989, *Ignatov s.n.* (MHA)	FJ952592
viride Moscow	Moscow, 20.VII.1990, *Ignatov s.n.* (MHA)	FJ952608
viride Tatarstan	Tatarstan, 17.VIII.2003, *Ignatov & Ignatova s.n.* (MW)	FJ952607

monly on rotten wood, occasionally on siliceous rocks.

The distribution area of *Dicranum tauricum* includes most European countries, Algeria, Turkey, Caucasus and Crimea, western North America; in European Russia it grows in the forest-steppe zone in the lowland and also in Caucasus, on tree trunks and rotten wood in broad-leaved and conifer forests; it was reported for Asia outside Caucasus and the Middle East only in Kamchatka (Czernyadjeva, 2005), based on unconfirmed records of Möller (1927) and Persson (1970), and in China (but no material was found from this country).

Dicranum viride was reported from Europe, South Siberia, the southern part of the Russian Far East, Japan, Korea, China, and eastern North America. The typical habitat of this species in European Russia are trunks of *Quercus, Tilia, Ulmus, Acer, Fraxinus* in old-growth broad-leaved forests.

One more species with fragile leaf apices, *Dicranum hakkodense* Cardot was described from Japan and Korea; it was later treated as a variety, *D. viride* var. *hakkodense* (Cardot) Takaki (Noguchi, 1987), and then Iwatsuki (2004) synonymized it with *D. viride* without any taxonomic recognition.

The recent extensive collecting in the Russian Far East raises doubt regarding the identity of European and Far Eastern plants of '*D. viride*'. In addition to different morphology, the latter were usually collected in the boreal belt of mountains, mostly on rocks, and more rarely on trunks, but in the latter case only on conifers, such as, *Abies, Pinus pumila* and *P. koraiensis*.

To check if this difference agrees with genetic differentiation, we studied DNA sequences of the nrITS region that has proved to be useful for resolving species-level problems in mosses (Ivanova et al., 2005; Goryunov et al., 2007; Ignatov & Milyutina, 2007, etc.).

MATERIALS AND METHODS

Morphological studies were based on collections of MHA, MW, LE, VLA. Five species were in the focus of the study; *Dicranum fulvum* Hook. was used for comparison, but was not specially studied, as it has fragile leaves only occasionally.

Species selection for molecular phylogenetic studies included 'typical' as well as fairly deviating

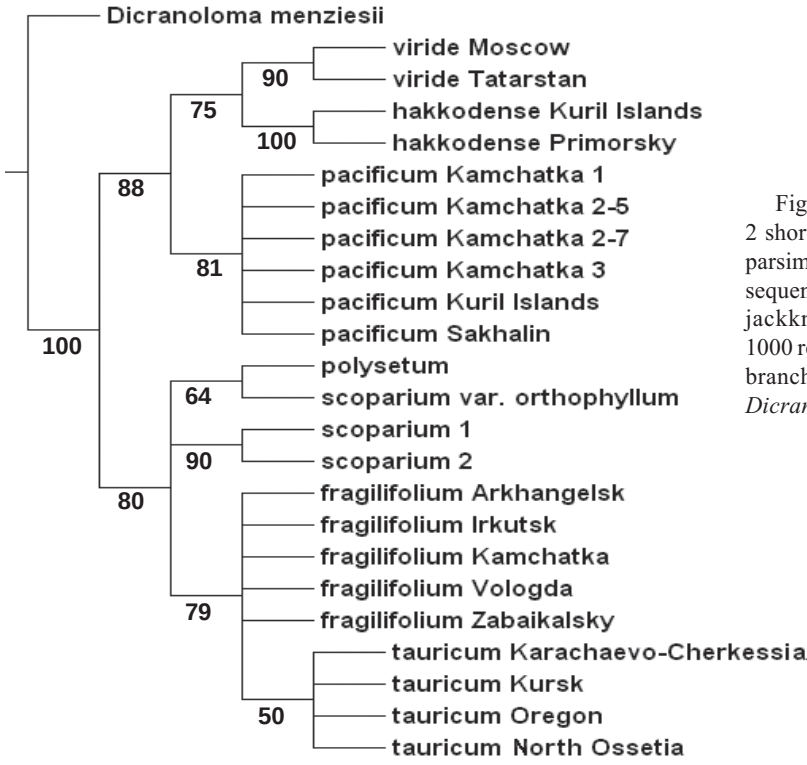


Fig. 1. Strict consensus tree of 2 shortest trees (L=188) found in parsimony ratchet analysis of ITS sequences (L=421; RI=1; CI=0); jackknife values calculated for 1000 replications are shown below branches. Data on specimens of *Dicranum* are given in Table 1.

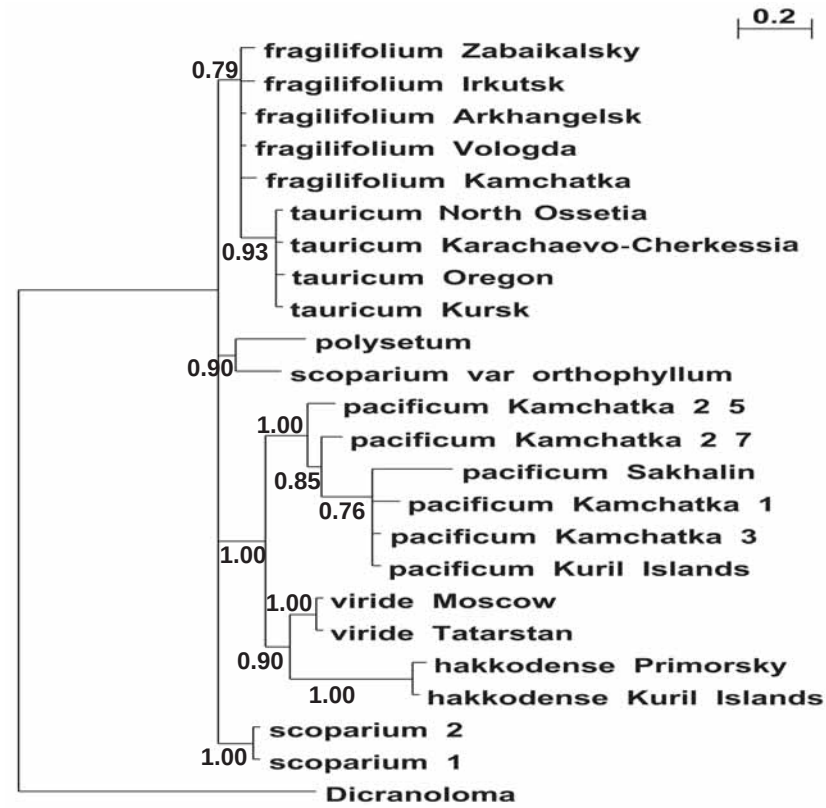


Fig. 2. Bayesian tree, showing posterior probabilities. Data on specimens of *Dicranum* are given in Table 1.

```
tau Kur  CCC--AGGGA GTC-TCCCTC TCTCC----A TATGGATGGG G-GGG---AA CTCTGGCT-C CCTGGGGCAA AA-CCCAA--
tau Ore  CCC--AGGGA GTC-TCCCTC TCTCC----A TATGGATGGG G-GGG---AA CTCTGGCT-C CCTGGGGCAA AA-CCCAA--
tau K-C  CCC--AGGGA GTC-TCCCTC TCTCC----A TATGGATGGG G-GGG---AA CTcTGGCT-C CCTGGGGCAA AA-CCCAA--
tau Oss  CCC--AGGGA GTC-TCCCTC TCTCC----A TATGGATGGG G-GGG---AA CTcTGGCT-C CCTGGGGCAA AA-CCCAA--
fra Kam  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TATGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCAA--
fra Vol  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TATGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCAACC
fra Ark  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TATGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCAACC
fra Irk  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TATGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCAACC
fra Zab  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TATGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCAACC
vir Tat  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TGTGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCACAA
vir Mos  CCC--AGGGA GTC-TCCCTC CCTCCCTCCA TGTGGATGGG GTGGGGGGAA CTCTG-CT-C CCTGGGGCAA AA-CCCACAA
hak Kur  CCCCCAGGGA GTC-TCCC-- ---------- ---------- ---------- -------T-C CCTGGGGCAG AA-CCCACAA
hak Pri  CCCCCAGGGA GTC-TCCC-- ---------- ---------- ---------- -------T-C CCTGGGGCAG AA-CCCACAA
pac Kur  CCC--AGGGA GTC-TCCCTC CC-CCC---A TGTGGATGGG GCGGGGGGAA CTCCG-CT-C CCTGGGGCAA AAACCCACAA
pac Ka2  CCC--AGGGA GTC-TCCCTC CC-CCC---A TGTGGATGGG GCGGGAGGAA CTCCG-CT-C CCTGGGGCAA AAACCCACAA
pac Ka3  CCC--AGGGA GTC-TCCCTC CC-CCC---A TGTGGATGGG GCGGGGGGAA CTCCG-CT-C CCTGGGGCAA AAACCCACAA
pac Ka1  CCC--AGNGA GTC-TCCCTC CC-CCC---A TGTGGATGGG GCGGGGGGAA CTCCG-CT-C CCTGNGGCAA AAACCCACAA
pac Sak  CCC--AGGGA GTC-TCCCTC CC-CCC---A TGTGGATGGG GCGGGGGGAA CTCCG-CT-C CCTGGGGCAA AAACCCACAA

tau Kur   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGG-CC-- ACGCCCCGGG AC----TTCG
tau Ore   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGG-CC-- ACGCCCCGGG AC----TTCG
tau K-C   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGG-CC-- ACGCCCCGGG AC----TTCG
tau Oss   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGG-CC-- ACGCCCCGGG AC----TTCG
fra Kam   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
fra Vol   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
fra Ark   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
fra Irk   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
fra Zab   AGCT-----C GACTGGG--A GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
hak Kur   GGCCCGCGCC GACTGGG--A GTGCGACCTG AGTGGAACYG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG ACACACTTGG
hak Pri   GGCCCGCGCC GACTGGG--A GTGCGACCTG AGTGGAACYG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG ACACACTTGG
vir Tat   AGCT-----C GACTGGGGAA GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
vir Mos   AGCT-----C GACTGGGGAA GTGCGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
pac Kur   AGCT-----C GACTGGG--A GTGGGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
pac Ka2   AGCT-----C GACTGGG--A GTGGGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
pac Ka3   AGCT-----C GACTGGG--A GTGGGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
pac Ka1   AGCT-----N GAGTGGG--A GTGGGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
pac Sak   AGCT-----C GACTGGG--A GTGGGAC-TG AGTGAAACTG GCCATCCGGA TGGGGGCC-- ACGCCCCGGG AC----TTCG
```

Fig. 3. Two relatively variable parts of alignment of ITS1 (above) and ITS2 (below) of 5 *Dicranum* species with fragile leaf tips (names abbreviated, compare with Table 1).

plants of fragile-leaved *Dicranum* from different parts of Russia (Table 1). GenBank accessions of *D. scoparium* Hedw. var. *scoparium, D. scoparium* var. *orthophyllum* Brid. and *D. polysetum* Sw. were added, and the tree was rooted on *Dicranoloma menziesii* (Hook. f. & Wils.) Par., also from GenBank. The protocol used was the same as in the study of Gardiner et al. (2005). GenBank accession numbers and information on voucher specimens are given in Table 1.

Sequences were aligned manually. We performed parsimony ratchet analysis with NONA (Goloboff, 1994) within the Winclada (Nixon, 1999a) shell. A multi-ratchet option was used (Nixon, 1999b). The jackknife support was calculated for 1000 replications.

The highest liklihood score according to AIC 1 measure was for HKY + Γ model which was used for Baesian inference performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2005) with three partitions (ITS1, ITS2, and 5.8S rDNA). Node confidences were determined by sampling 7,500 trees (four chains; 1,000,000 generations; burn-in set to 2,500 trees). Trees were rooted on *Dicranoloma.*

RESULTS

The resulting topologies of the maximum parsimony (MP) and Bayesian analyses (MB) are principally similar (Figs. 1-2), with one exception. Two main clades were found in MP. One of them includes polytomy of three clades fromed by (1) *Dicranum scoparium*; (2) *D. polysetum* and *D. scoparium* var. *orthophyllum*; and (3) *D. fragilifolium* and *D. tauricum*, while another clade

is formed by *D. viride, D. hakkodense* and *D. pacificum.* MB tree however, found all four clades in a polytomy. In both analyses, however, the contents of clades was identical.

In both analyses there is a clade formed by *D. viride, D. hakkodense* and *D. pacificum* sp. nov. (see below), each forming its own clade, and another clade formed by *D. fragilifolium* and *D. tauricum,* with the latter species forming a clade nested in the former species.

European and Far Eastern *Dicranum viride* were found in one clade, but with rather low support (75 in MP, 0.90 in MB), while the support for individual clades of both *D. viride* and *D. hakkodense* (= 'Far Eastern *D. viride*') was 90 and 100 in MP and 1.00 for both in MB trees.

A preliminary analysis of *D. fragilifolium* placed one specimen from Kamchatka in a surprising position, in the clade otherwise formed by *D. viride* and *D. hakkodense*. This specimen differs morphologically from *D. fragilifolium*, and additional revision of material from Kamchatka and neigbouring areas revealed a number of collections of this putatively new species. Sequences of four additional specimens confirmed that they are homogeneous genetically; in MP and MB trees these formed a clade sister to *D. hakkodense* plus *D. viride*, with supports of 81 and 1.00 respectively, thus supporting the hypothesis that eastern Russia has a so far undescribed species, *Dicranum pacificum* sp. nov., previously not separated from widespread *D. fragilifolium*. In Kamchatka, the latter species is restricted to the northern and central parts, whereas all collections from the southern part belong to *D. pacificum,* like all collections of '*D. fragilifolium*' from Sakhalin and the Kuril Islands.

Thus, most of the morphologically delimited species were supported by molecular phylogenetic data (except that the clade of *D. tauricum* was nested within *D. fragilifolium* in both analyses). All five taxa have a number of specific substitutions (s) and/or indels (i), (count for set of 5 species): *D. hakkodense* – 10s, 12i; *D. viride* – 4i; *D. pacificum* – 2s; *D. tauricum* – 4s, 3i; *D. fragilifolium* – 1i. The visual analysis of alignments (Fig. 3) provides an even more sound delimitation of the five fragile-leaved *Dicranum* by a combination of substitutions and indels.

The variation within each species was found to be low, although *D. pacificum* was rather variable, and two clones of one specimen differ from each other in 5 s and 2 i (plus one 'N'). These two clones where found in an unresolved group with other specimens of the species in MP and in a basal position to other specimens in MB.

In addition, *D. hakkodense*, *D. viride*, and *D. pacificum* are similar in the probable presence of a hair-pin in the 278 position of the alignment, near the 5'-end of ITS1. At this position the signal (as it appear in chromatogram from sequenator) suddenly dropped, not allowing further reading. This putative hair-pin remains unknown, but nothing similar was observed in the species of the other clade.

Discussion

At the moment only a few species of *Dicranum* have published ITS data and not much can be concluded about their phylogeny. Preliminary results allow to suggest that fragile-leaved *Dicranum* species are not monophyletic, but high support (80 in MP) of the close relationships of *D. polysetum* and *D. scoparium* with *D. fragilifolium* and *D. tauricum* got no support in MB analysis, where these taxa were found outside this clade.

Much more definitive is the conclusion about the presence in Russia of five species, one not recognized previously. All five have quite clear morphological circumscriptions. At the same time, the groups found in the present analysis, i.e. *D. fragilifolium–D. tauricum* and *D. viride–D. hakkodense–D. pacificum* are less clearly morphologically differentiated. Some characters considered rather important in the systematics of the group, such as capsule curved vs. almost straight seem to be unimportant, since straight capsules occur in *D. tauricum, D. viride,* and *D. hakkodense*, that belong to different clades. Consequently, the present data do not confirm the segregation of the genus *Orthodicranum* on the basis of sporophytic characters. However, some morphological differences between the clades were observed: *D. fragilifolium* and *D. tauricum* long basal laminal cells, whereas all representatives of the other clade are characterized by short rectangular to subquadrate basal laminal cells.

Two species, *D. fragilifolium* and *D. tauricum* were represented in this analysis by specimens

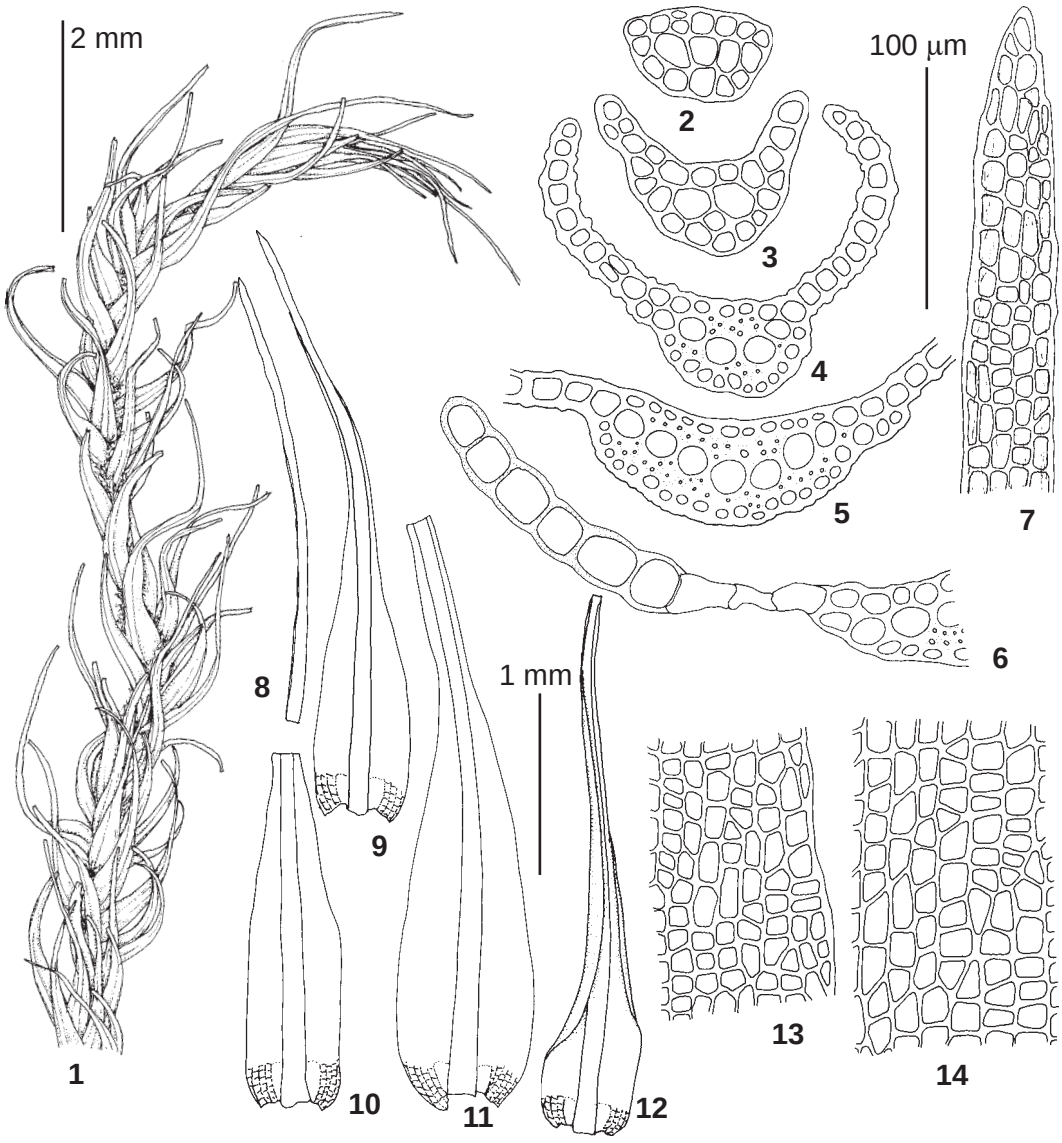


Fig. 4. *Dicranum viride* (from Russia, Tatarstan, 17.VIII.2003, *Ignatov & Ignatova s.n.*, MHA): 1 – habit, dry; 2-6 – leaf transverse sections; 7 – cells of leaf apex; 8 – broken leaf tip; 9-12 – leaves; 13 – median laminal cells; 14 – basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 8-12; 100 μm for 2-7, 13-14.

from rather remote areas, and they do not show any grouping that may correspond to their places of origin. Both species are rather variable in ITS sequences, and this causes rather low supports of the main clade and the clade of *D. tauricum*.

The above conclusions, despite the limited coverage of material, suggest the following taxonomical treatment.

KEY FOR IDENTIFICATION OF SPECIES OF *DICRANUM* WITH FRAGILE LEAVES IN RUSSIA

1. Leaf apices almost entire or with few blunt teeth; costa mostly smooth on abaxial side 2
— Leaf apices sharply denticulate or serrulate; costa more or less scabrose on abaxial side in distal part of leaf 4
2. Basal laminal cells short-rectangular, 20-35(-45) μm long ..... 1. *D. viride*
— Basal laminal cells elongate-rectangular, 40-80(-120) μm long 3
3. Costa in lower 1/2 of leaf with stereid bands,

often with differentiated abaxial epidermal layer, or rarely with substereids (cells with thick walls and large lumen); adaxially from guide cells in 2(-3) layers; capsules arcuate ..... 5. *D. fragilifolium*

— Costa in lower 1/2 of leaf on both sides of guide cells with substereids; epidermal layers not differentiated; adaxially from guide cells in 1(-2) layers; capsules straight .... 4. *D. tauricum*

4(1). Costa in lower 1/2 of leaf with stereid bands, well-differentiated abaxial and adaxial epidermal layers or sometimes with only abaxial epidermis differentiated 5

— Costa in lower 1/2 of leaf without stereid bands and differentiated epidermal layers, with substereids on both sides of guide cells 6

5. Leaves only occasionally fragile, crisped when dry; basal laminal cells short-rectangular, 20-35 μm long ..... [*D. fulvum*]

— Leaves moderately fragile, straight or slightly falcate-secund when dry; basal laminal cells elongate-rectangular, 25-50 μm long .... 2. *D. hakkodense*

6. Basal laminal cells linear, 40-80(-120) μm long, with moderately thickened and slightly porose walls ..... 4. *D. tauricum*

— Basal laminal cells rectanugular, 20-40(-50) μm long, with thin and smooth walls .... 3. *D. pacificum*

1. **Dicranum viride** (Sull. & Lesq.) Lindb., Hedwigia 2: 70. 1863. — *Campylopus viridis* Sull. & Lesq. in Sull., Musci Hep. U.S. (repr.) 103. 1856. — Fig. 4, 14.

Plants in dense or loose tufts, dark-green, not glossy. Stems 1-3 cm, moderately tomentose. Leaves erect-spreading or slightly falcate-secund in lower part of stem and flexuose in its upper part when dry, moderately to strongly fragile, with most apices broken off or intact in upper leaves, 4-5(-6)×0.5-0.7(-0.8) mm, from lanceolate base gradually tapering into long and narrow fragile acumen, concave below, canaliculate above; leaf margins with few blunt teeth near apex or entire; costa strong, occupying 1/5–1/4 the width of leaf base, 80-160 μm wide at base, filling distal part of leaf acumen or most of its width, smooth on dorsal side or, rarely, slightly rough near leaf apex, in transverse section in proximal part with 1 row of guide cells, two stereid bands, sometimes thin and weakly developed, not extending above mid-leaf, with differentiated adaxial and abaxial epidermal layers or sometimes adaxial epidermal layer indistinct, cell walls between laminal cells not or slightly bulging, rarely strongly bulging; lamina smooth, unistratose, sometimes with few bistratose patches in distal part; upper laminal cells subquadrate, 10-14×8-12 μm; median laminal cells subquadrate to short-rectangular, 10-20×8-12 μm; basal laminal cells short-rectangular, with moderately thickened, non-porose walls, 20-35(-45)×10-12 μm; alar cells unistratose or bistratose at places, large, with moderately thickened walls, brownish, extending or almost extending to costa. Sexual condition dioicous, male plants as large as female. Sporophytes rare. Setae solitary, 1-1.5 cm. Capsules erect and straight, urns 1.5-2 mm long, slightly furrowed when dry. Operculum 1-1.5 mm. Spores 10-19 μm.

Distribution. *Dicranum viride* occurs in the broad-leaved forest zone of European Russia and it was also reported from Caucasus (Akatova, 2002; Ignatov & al., 2002). It is rare in most areas, becoming more frequent in foothills of the Ural Mts. in Bashkortostan. The only record from Asian Russia is from the Kemerovo Province. It is rather rare in Western and Central Europe, rapidly decreasing in some areas and included in Red Data Books for some regions. All records of *D. viride* from the Russian Far East belong to *D. hakkodense*; its occurrence in Japan, Korea and China, as well as in Alaska seems to be doubtful, but *D. viride* is not rare in the eastern North America.

Ecology. In shady forests on bark of old broad-leaved trees, mostly on *Ulmus, Tilia, Querqus*, rarely also on *Betula* and fresh logs.

Differentiation. *Dicranum viride* and *D. fragilifolium* are quite different habitually (Fig. 11: 1-2); the former species usually has leaves falcate-secund or flexuose when dry, while the leaves of the latter are almost always straight and often appressed when dry. The basal laminal cells are shorter in *D. viride,* 20-35(-45) μm long vs. 40-60(-80) μm, and in addition the cell walls are not porose in *D. viride,* while in *D. fragilifolium* they are quite often porose. Hedenäs & Bisang (2004)

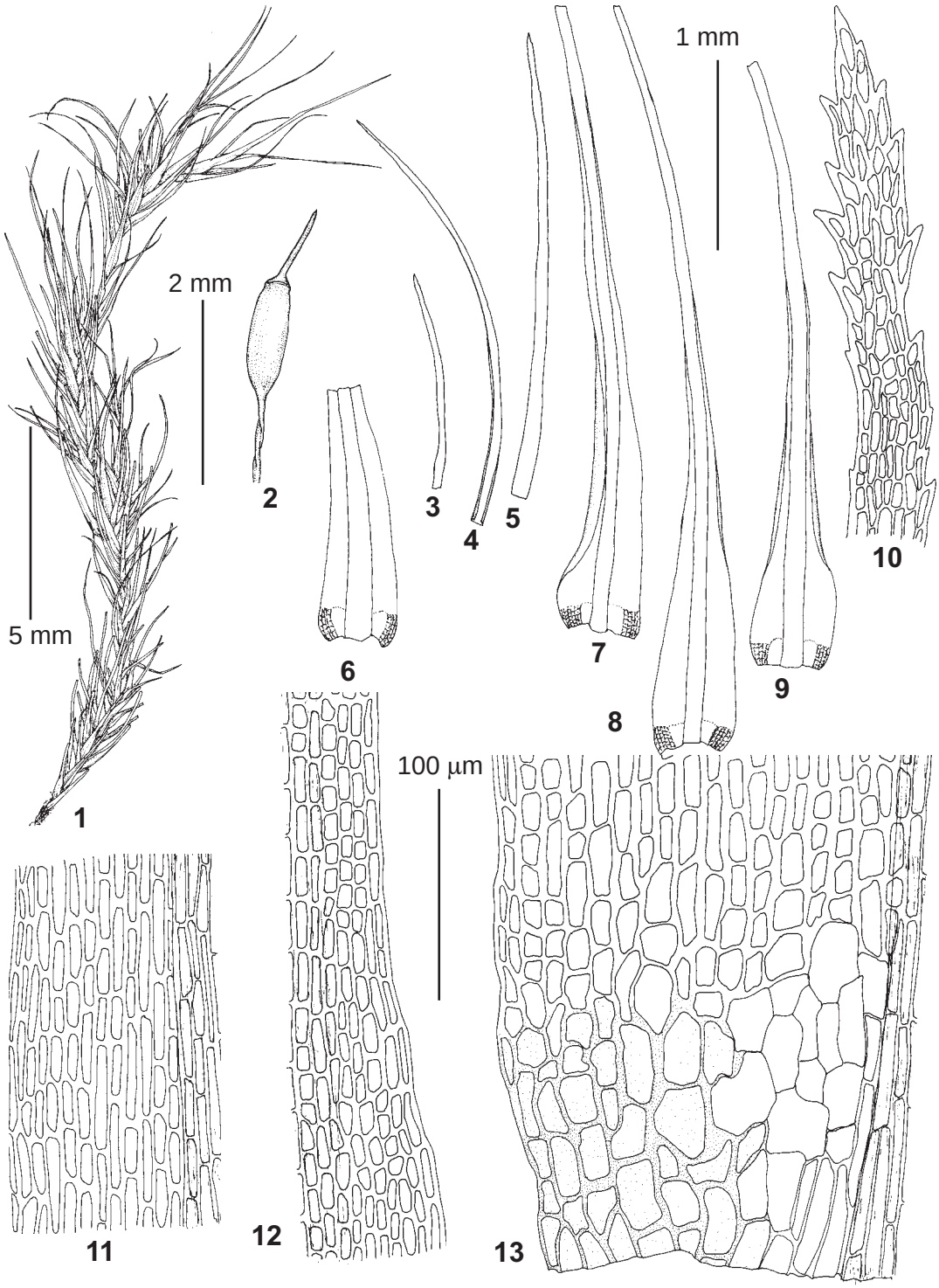


Fig. 5. *Dicranum hakkodense* (1, 3-13 – from: Russia, Primorsky Territory, *Ignatov #07-233*, MHA; 2 – from: Russia, Kuril Islands, Shikotan Island, *Bakalin #K-47-33-07*, MHA): 1 – habit, dry; 2 – capsule; 3-5 – broken leaf tips; 6-9 – leaves; 10 – upper laminal cells; 11, 13 – basal laminal cells; 12 – median laminal cells. Scale bars: 5 mm for 1; 2 mm for 2; 1 mm for 3-9; 100 μm for 10-13.

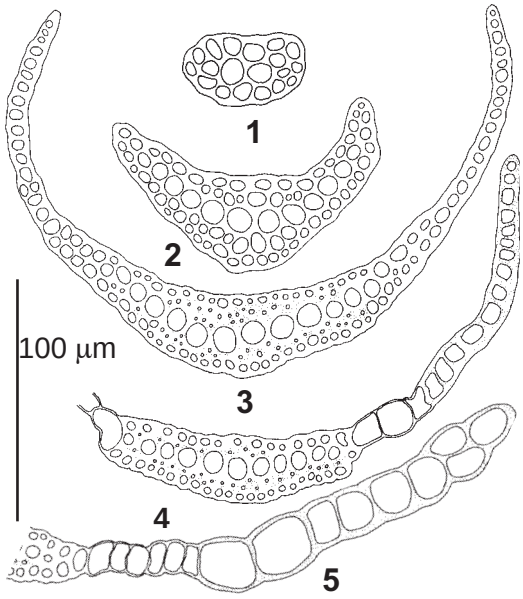


Fig. 6. *Dicranum hakkodense* (from: Russia, Primorsky Territory, *Ignatov #07-233*, MHA): 1-5 – leaf transverse sections. Scale bar: 100 μm for 1-5.

stated that another differentiating character is the absence of well-differentiated abaxial epidermis in *D. fragilifolium* (that is always well-differentiated in *D. viride*); we found however that this character has a limited use, as many populations of *D. fragilifolium* from Russia have it quite distinctly expressed (cf. Fig. 10.1c). Similarly, the adaxial epidermal cells are never clearly differentiated in *D. fragilifolium*, as they are in *D. viride* (cf. Fig. 10.1 and 10.2), although there are cases where all cells ventral from the guide cells are of the same size and thickness in the latter species, with moderately large lumens, not allowing certain interpretation. Hedenäs & Bisang (2004) also suggest to use bulging cell walls between laminal cells in leaf transverse section of *D. viride* for differentiation from *D. fragilifolium*; however, Ireland (2007) mentions that cell walls are bulging or not in *D. viride* and slightly bulging in *D. fragilifolium*; our observations found this character to be rather variable in both species. There are some differences in ecology: in European Russia *D. viride* grows almost exclusively on bark of living and recently fallen broad-leaved trees (i.e. those with subneutral bark reaction), and *D. fragilifolium* prefers rotten wood in boreal forests and sometimes grows at base of *Betula* trunks (which has acidic bark reaction). In eastern North America *D. viride* was reported from broader range of habitats, including decidous and coniferous trees, especially on *Thuja*, rotten wood, and both acidic and calcareous rocks (Ireland, 2007).

The distribution of *D. fragilifolium* is confined to northern European Russia and to its Asian territory, while *D. viride* has a more southern distribution and is known from a single record east of the Ural Mts., but their areas overlap in, e. g., Tver Province, Tatarstan, and Bashkortostan.

Dicranum viride differs from *D. tauricum*, which has a similar southern distribution in European Russia, in the differentiation of cells into stereid bands and epidermal layers in the costa, whereas in *D. tauricum* this differentiation is almost absent and 1-2(-3)-celled layers either ventral or dorsal from the guide cells are rather homogeneous. The basal laminal cells are very short in *D. viride* and much longer in *D. tauricum*: 20-35(-45) μm vs. 60-105(-120) μm. The latter species grows both on tree trunks and rotten wood.

Dicranum viride can also be confused with *D. fulvum* due to its dull dark-green color, flexuose leaves, short laminal cells and similar costa structure. However, the leaves of *D. fulvum* are less fragile and more strongly flexuose to crisped when dry (Fig. 11: 6); its laminal cells are slightly shorter and more strongly thick-walled (Fig.9: 6); the distinctly rough dorsal costa near the apex vs. the smooth or almost smooth one are also helpful for its differentiation from *D. viride.*

Differences from *D. hakkodense* are discussed under this species.

Selected specimens examined: EUROPEAN RUSSIA: **Moscow Province**: Moscow, Losiny Ostrov National Park, 3.VIII.1996, *Ignatov s.n.* (MW); **Orel Province**: Mtsensky Distr., Zheleznitsa, 18.VI.1988, *Vyshegorodskikh s.n.* (MHA); **Kursk Province**: Glushkovsky District, between Samarki and Oktyabr' villages, 24.VI. 2005, *Poluyanov #282b* (MW); **Tatarstan**: Volga-Kama Nature Reserve, Raifa, 17.VIII.2003, *Ignatov & Ignatova s.n.* (MW); **Krasnodar Territory**, Khosta, 12.VIII.2002, *Ignatov & Ignatova s.n.* (MHA); **Kabardino-Balkaria**, Nalchik surroundings, Belaya Rechka, *Ignatov & al. #05-1783* (MHA). ASIAN RUSSIA: **Kemerovo Province**: Promyshlennovsky Distr., Khristinovka surroundings, Kas'ma River valley, 19.VI.1992, *Pisarenko s.n.* (LE). Total number of studied specimens 102.

2. **Dicranum hakkodense** Cardot, Bull. Herb. Boiss. ser. 2, 7: 714. 1907. — *Dicranum viride* var. *hakkodense* (Cardot) Takaki, J. Hattori Bot. Lab. 35: 35. 1972. — Figs. 5-6, 15.

Lectotype (selected here): ''Corea: ile Quelpaert, leg. Faurie, 1905, n° 481'' (H).

Note: The specimen from South Korea represents a slender form of *D. hakkodense* with unusually flexuose leaves. However it is selected here to avoid possible further confusions, as Japanese material (not fully studied at moment by us), may have not only *D. hakkodense,* but also *D. pacificum*, which occurs in the South Kuril Islands, very close to Japan. Most characters mentioned in the treatments of Takaki (1964) and Noguchi (1987) agree better with *D. hakkodense* (thick-walled basal laminal cells), but other may belong to *D. pacificum* (Noguchi, 1987: most leaves broken off, it is difficult to find any intact leaf apices).

Plants in loose to dense tufts, yellowish-green or olivaceous, sometimes brownish below, glossy. Stems 1-2(-3) cm, not or slightly tomentose in lower part. Leaves erect-spreading or slightly falcate-secund, moderately fragile, with numerous intact apices in upper leaves and broken off in lower leaves, (4-)5-7(-8)×0.4-0.6 mm, from lanceolate base gradually tapering into long and narrow acumen, concave below, canaliculate above; leaf margins sharply denticulate near apex and in proximal part, entire or very slightly crenulate in mid-leaf; costa strong, occupying 1/5–1/4 the width of leaf base, 100-150 μm wide at base, filling distal part of leaf acumen, rough on dorsal side near leaf apex, smooth below, in transverse section in proximal part with 1 row of guide cells, two stereid bands not extending above mid-leaf, with differentiated adaxial and abaxial epidermal layers or rarely adaxial epidermal layer with few enlargered cells, cell walls between laminal cells not or slightly bulging; lamina smooth, unistratose; upper and median laminal cells rectangular, 20-35×6-10 μm; basal laminal cells rectangular, thick-walled, cell walls non-porose or rarely hardly porose, (20-)25-50(-60)×10-12 μm; alar cells unistratose or bistratose at places, large, thick-walled, brownish, not extending to costa, basal juxtacostal cells pellucid, thin-walled. Sexual condition dioicous, male plants as large as female, in different tufts or mixed with female plants. Sporophytes rare. Setae solitary, 1-1.5 cm. Capsules erect, straight or slightly curved, urns 1.5-2 mm long, smooth. Operculum 1-1.5 mm. Spores 15-20 μm.

Variability. Specimens from the Primorsky Territory usually have well-differentiated adaxial and abaxial epidermal layers in the costa, or occasionally an adaxial epidermis is only partially differentiated. At the same time, the adaxial epidermis of the costa is often indistinct in specimens from the Kuril Islands, as well as in the lectotype specimen from South Korea.

Noguchi (1987) stated that the leaves of *D. hakkodense* are strongly fragile, and that it is difficult to find leaves with intact apices. However, specimens from Japan (in LE) are very similar to plants from the Russian Far East, with numerous intact apices of their upper leaves. Collections from the Russian Far East are not strongly variable in this character and a presence of intact apices is helpful for differentiating *D. hakkodense* from *D. pacificum,* which always has most leaf apices broken off (see also comments to the latter species).

Distribution. *Dicranum hakkodense* is the only species of *Dicranum* with fragile leaves in the southern part of the Primorsky Territory (except *D. fulvum*, known from a single old collection), and is not rare from middle to upper elevations in mountains. It was also collected in the Kunashir, Iturup and Shikotan, often in the same places as *D. pacificum*. It is known by two collections from the Khabarovsk Territory and a single one from the southern part of Yakutia. *Dicranum hakkodense* was reported as the only species of the genus with fragile leaves from Japan (throughout the country, in montane and subalpine areas). It is also known from South Korea, and one specimen from China (Sichuan Province) was found during the revision of LE collections.

Ecology. *Dicranum hakkodense* was collected at 370-1850 m elev. in the mainland and at 200-1335 m in the Kuril Islands. It grows on rocks and fine soil between rocks and in cliff niches, on trunks of *Abies*, *Picea, Pinus koraiensis*, *P. pumila*, and more rarely on *Betula*. Collections from Japan and China are from tree trunks (*Abies, Fa-*

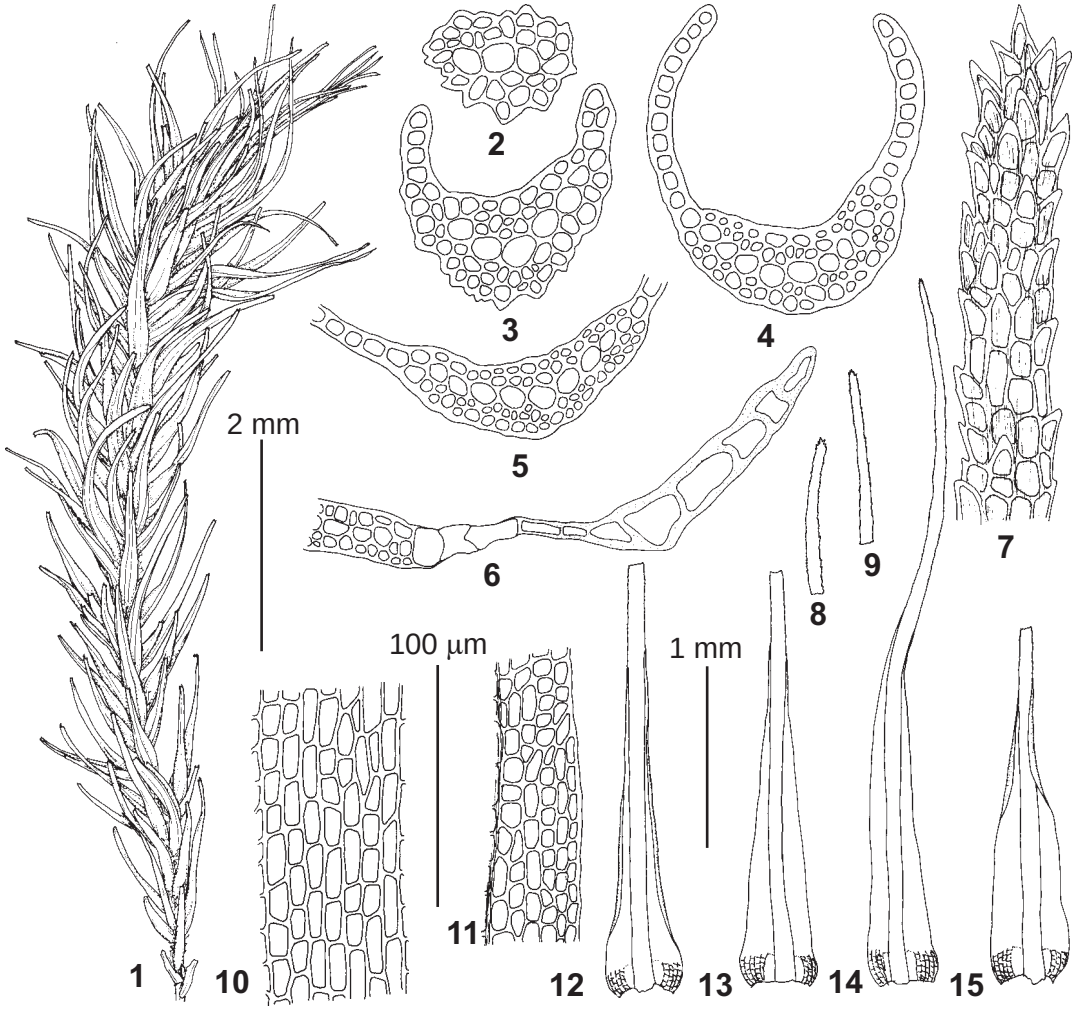


Fig. 7. *Dicranum pacificum* (from holotype: Russia, Sakhalin, *Ignatov & Teleganova #06-301*, MHA): 1 – habit, dry; 2-6 – leaf transverse sections; 7 – cells of leaf apex; 8-9 – broken leaf tips; 10 – basal laminal cells; 11 – median laminal cells; 12-15 – leaves. Scale bars: 2 mm for 1; 1 mm for 8-9, 12-15; 100 μm for 2-7, 10-11.

gus or label information is uncertain) at 1000-2400 m elev.

Differentiation. *Dicranum hakkodense* differs from *D. fragilifolium* by its sharply denticulate leaf apices vs. almost entire ones. Furthermore, its basal laminal cells have non-porose walls, whereas they are usually porose in *D. fragilifolium* (Fig. 9: 1,3).

Sharply denticulate leaf apices also help to differentiate *D. hakkodense* from *D. viride*; the latter species has leaf apices with a few blunt teeth or are almost entire (Fig. 8: 2,3). Plants of *D. hakkodense* are yellowish-green and glossy, with straight or slightly falcate-secund leaves, while plants of *D. viride* are dark-green, not glossy, with most leaves curved or flexuose. The basal laminal cells of *D. hakkodense* are more thick-walled and longer than that in *D. viride*, 25-50(-60) μm vs. 20-35(-45) μm. These two species also differ in ecology: *D. viride* grows almost exclusively on trunks of broad-leaved trees, and *D. hakkodense* was very rarely (never in Russia) collected in such habitats, it prefers trunks of conifer trees or rocky substrates.

Differences from *D. pacificum* and *D. tauricum* are discussed under these species.

Selected specimens examined: ASIAN RUSSIA: **Primorsky Territory**: Shkotovo Distr., Pidan (Liva-

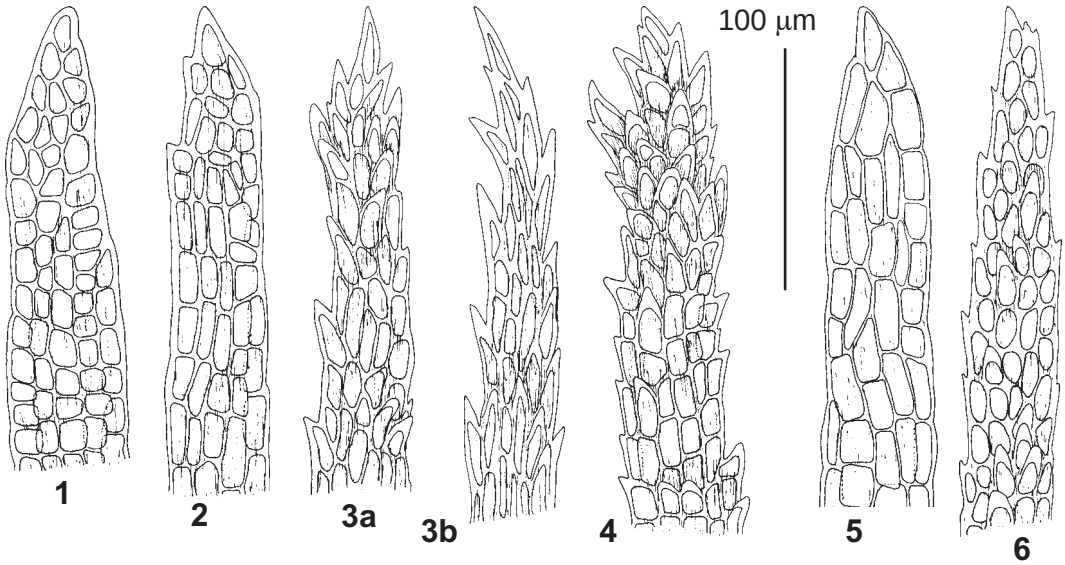


Fig. 8. Leaf apices of *Dicranum*: 1 – *D. fragilifolium* (Kamchatka, 7.VIII.2006 *Czernyadjeva #9*, LE); 2 – *D. viride* (Tatarstan, Volga-Kama Nature Reserve, 17.VIII. 2003, *Ignatov & Ignatova s.n.*, MW); 3a – *D. hakkodense* (Kuril Islands, Kunashir Island, *Ignatov #06-1411*, MHA); 3b – *D. hakkodense* (Primorsky Territory, Olkhovaya Mt., *Ignatov et al. #06-2624*, MHA); 4 – *D. pacificum* (Kamchatka, 16.IX.2005, *Samkova #31*, MW); 5 – *D. tauricum* (Caucasus, Kabardino-Balkaria, Adyl-Su River, 29.VII.2004, *Ignatov & Ignatova s.n.*, MW); 6 – *D. fulvum* (Caucasus, Kabardino-Balkaria, 31.VII.2004, *Ignatov et al. s.n.*, MW). Scale bar: 100 μm for 1-6.

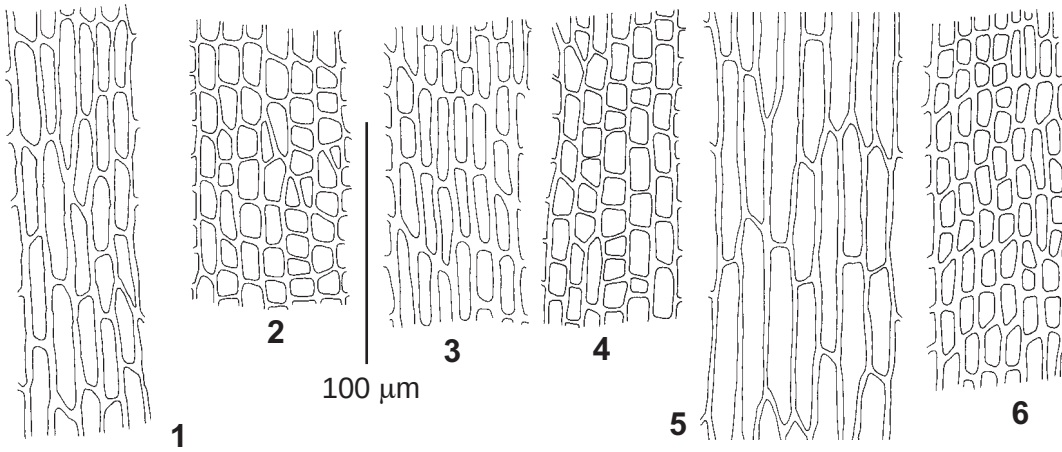


Fig. 9. Basal laminal cells of *Dicranum*: 1 – *D. fragilifolium* (Kamchatka, 7.VIII.2006 *Czernyadjeva #9*, LE); 2 – *D. viride* (Tatarstan, Volga-Kama Nature Reserve, 17.VIII.2003, *Ignatov & Ignatova s.n.*, MW); 3 – *D. hakkodense* (Kuril Islands, Kunashir Island, *Ignatov #06-1411*, MHA); 4 – *D. pacificum* (Kamchatka, 16.IX.2005, *Samkova #31*, MW); 5 – *D. tauricum* (Caucasus, Karachaevo-Cherkessia, Teberda Nature Reserve, *Ignatov & Ignatova #05-3342*, MW); 6 – *D. fulvum* (Caucasus, Kabardino-Balkaria, 31.VII.2004, *Ignatov et al. s.n.*, MW). Scale bar: 100 μm for 1-6.

dijskaya) Mt., *Ignatov & Ignatova #06-2115* (MHA); Chuguevka Distr., Beryozovy Brook, *Ignatov #07-233* (MHA); Chuguevka Distr., Oblachnaya Mt., *Ignatov #07-291* (MHA); Olkhovaya Mt., *Ignatov et al. #06-2624* (MHA); Ol'ga Distr., waterfall on Milogradovka Creek, *Ignatov #07-419* (MHA); Partizanskij Distr., Olkhovaya Mt., *Ignatov et al. #06-2654* (MHA); **Republic Sakha/Yakutia:** Tokinskij Stanovik Range, *Volotovsky s.n.* (SASY, MW); **Khabarovsk Territory**: Verkhnebureinsky Distr., Bure-

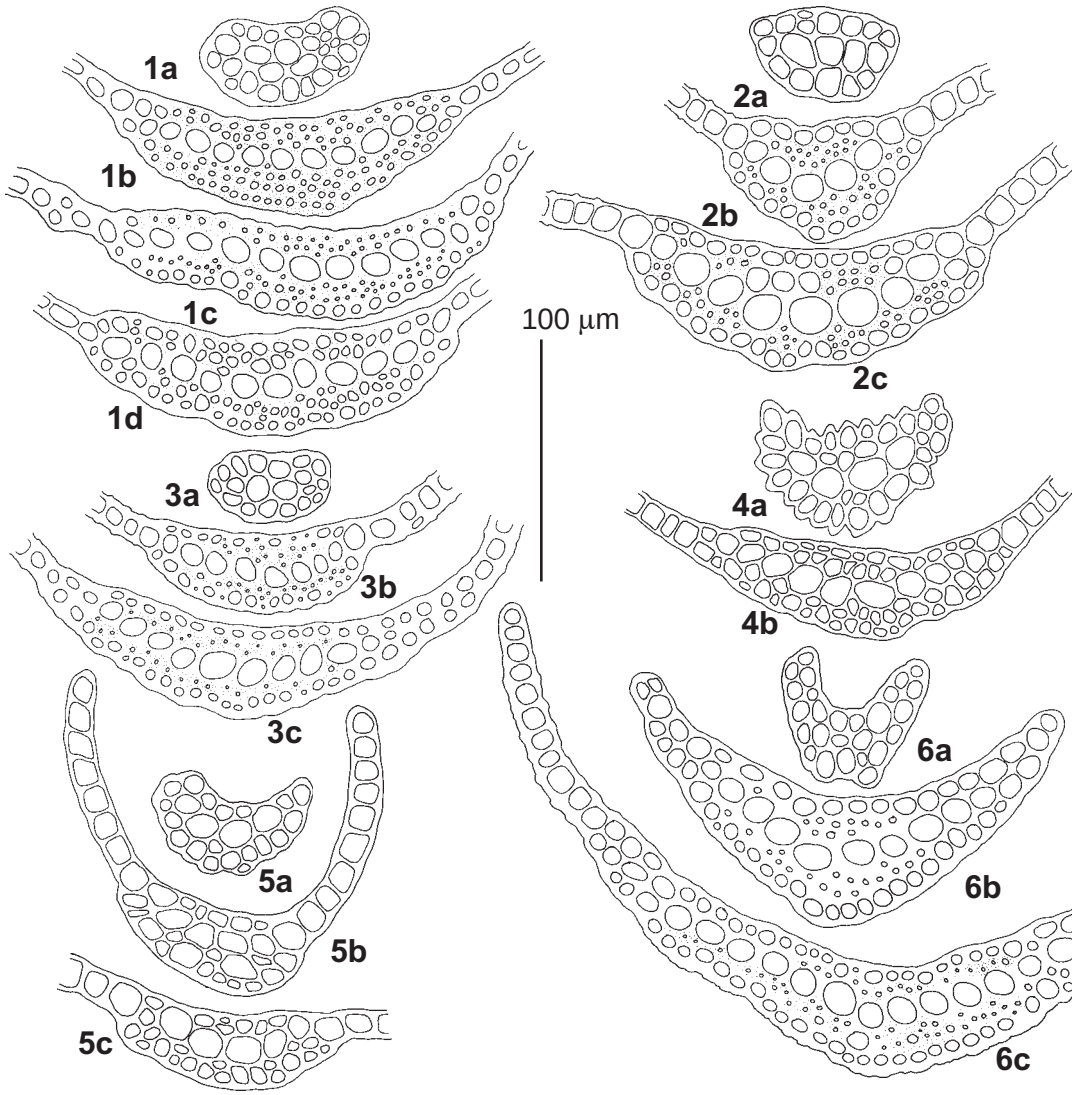


Fig. 10. Leaf transverse sections of: 1a,b - *Dicranum fragilifolium* (Kamchatka, 7.VIII.2006 *Czernyadjeva #9*, LE); 1c – *D. fragilifolium* (Altai Mts., *Ignatov #8/212,* MHA); 1d – *D. fragilifolium* Kamchatka, 6.VIII.2003 *Czernyadjeva #85*, LE); 2a-c – *D. viride* (Tatarstan, Volga-Kama Nature Reserve, 17.VIII. 2003, *Ignatov & Ignatova s.n.*, MW); 3b – *D. hakkodense* (Kuril Islands, Kunashir Island, *Ignatov #06-1411*, MHA); 3a,c – *D. hakkodense* Cardot (Primorsky Territory, Olkhovaya Mt., *Ignatov et al. #06-2624*, MHA); 4a,b – *D. pacificum* (Kamchatka, 16.IX.2005, *Samkova #31*, MW); 5a-c – *D. tauricum* (Caucasus, Karachaevo-Cherkessia, Teberda Nature Reserve, *Ignatov & Ignatova #05-3342*, MW); 6a-c – *D. fulvum* (Caucasus, Kabardino-Balkaria, 31.VII.2004, *Ignatov et al. s.n.*, MW). Scale bar: 100 μm for 1-6.

insky Nature Reserve, *Grigorjeva #89-M-231* (MW); Medvezh'e Lake, 1450 m, *Ignatov #97-959* (MHA); **Sakhalinskaya Province**: Kunashir Island, Ruruj Mt., *Ignatov #06-1411, 06-1171* (MHA); Iturup Island, Bogatyr' Range, near Burevestnik Mt., *Bakalin #K-15-7-07, K-15-26-07* (MHA); Shikotan Island: Ploskaya Mt., *Bakalin #K-47-33-07* (MHA); Notoro Mt., *Bakalin #K-41-18-07* (MHA).

JAPAN: **Honshu**: Yamanashi-ken, Mt. Fuji, 6.IX.1987, *T. & K. Osada s.n.* (Crypt. exsiccatae edite a Museo Hist. Nat. Vindobonensi #4945, LE); Mie Pref., Hirakura Experimental Forest, 21.VIII.1963, *Nakajima s.n.* (Musci Japonici Exsiccatae Ser. 19 #909, LE); Tottori Pref., Mt. Daisen, 23.VII.1958, *Mizutani s.n.* (Musci

Fig. 11. Habits of: 1 – *Dicranum fragilifolium* (Zabaikal'sky Territory, 16.VII. 2005, *Afonina s.n.,* MHA); 2 – *D. viride* (Tatarstan, Volga-Kama Nature Reserve, 17.VIII. 2003, *Ignatov & Ignatova s.n.*, MW); 3 – *D. hakkodense* (Primorsky Territory, Olkhovaya Mt., *Ignatov et al. #06-2624*, MHA); 4 – *D. pacificum* (Kamchatka, 18.VIII.2001, *Czernyadjeva #113,* LE); 5 – *D. tauricum* (Caucasus, Karachaevo-Cherkessia, Teberda Nature Reserve, *Ignatov & Ignatova #05-3938*, MW); 6 – *D. fulvum* (Caucasus, Kabardino-Balkaria, 31.VII.2004, *Ignatov et al. s.n.*, MW). Scale bar: 2 mm for 1-6.

Japonici Exsiccatae Ser. 14 #680, LE); **Kyushyu**: Fukuoka Pref., Suburi Mt., 2.IV.1965, *Osada s.n.* (Musci Japonici Exsiccatae Ser. 23 #1114, LE).

CHINA: **Sichuan Prov.**, Namchuan Co., Mt. Jinfu, 2100 m, X.Y. Hu #0100 (sub *D. fulvum*, LE)

SOUTH KOREA: ile Quelpaert, leg. Faurie, 1905, n°481 (H).

Total number of studied specimens 25.

3. **Dicranum pacificum** Ignatova & Fedosov, sp. nov. – Figs. 7, 15.

Species haec fabrica costae Dicrano taurico affinis, sed cellulis basalibus laminae brevioribus, 20-40(-50) μm vice 40-80 (-120) μm longis, apicibus foliorum recedit.

Holotype: Russia, Sakhalinskaya Province,

Sakhalin, Dolinsk distr., Sokol, valley of Belaya creek 4-5 km upstream from Biological station, 47° 15' N – 142° 49'E, 50 m alt., on rock in fir forest, 12.VIII.2006, Ignatov & Teleganova #06-301 (MHA). Isotype in MW.

Plants in dense or loose tufts, dull-green or yellowish-green, not glossy. Stems 0.5-1.5(-2) cm, moderately tomentose below. Leaves spreading to erect-spreading and incurved or slightly falcate-secund when dry, strongly fragile, with most apices broken off, more rarely apices intact in upper leaves, 3-5×0.4-0.7(-0.8) mm, from lanceolate base gradually tapering into long and narrowly subulate acumen, concave below, canaliculate above; leaf margins sharply denticulate near apex, minutely crenulate or entire in mid-leaf, entire below; costa strong, occupying ca. 1/5 the width of leaf base, 75-100 μm wide at base, filling subulate leaf acumen, densely mammillose on dorsal side or on both sides in distal part, in transverse section in proximal part with 1 row of guide cells, 2 rows of substereids on adaxial side, 2-3 rows of substereids on abaxial side, adaxial and abaxial epidermal layers not differentiated, cell walls between laminal cells not bulging; lamina smooth, unistratose; upper laminal cells subquadrate to short-rectangular, 7-12×6-10 μm; median laminal cells subquadrate to short-rectangular, 8-20×8-12 μm; basal laminal cells rectangular, with thin or moderately thickened, non-porose walls, (15-)20-40(-50)×10-12 μm; alar cells unistratose, large, with moderately thickened walls, brownish, extending or almost extending to costa, sometimes with small group of thin-walled cells between alar cells and costa. Sexual condition dioicous. Sporophytes unknown.

Variability. The foliage of the shoots vary from loose, with leaves more spreading when dry, to more tight, when the leaves are erect-spreading (Figs. 7.1, 11.4). The uppermost leaf acumen is strongly rough on both sides, with projecting upper ends of most cells, but the density of teeth varies.

In most cases the laminal cell walls are rather thin, allowing easy differentiation of *D. pacificum* from *D. hakkodense,* but occasionally they are thicker. In such cases laminal areolation alone is not sufficient for their separation.

Distribution. *Dicranum pacificum* is known mainly from the southern part of Kamchatka, where its area extends to ca. 53° N, whereas *D. fragilifolium* was collected from more northern localities (only two collections of *D. pacificum* are from 55-56° N, from the same localities as *D. fragilifolium*). *Dicranum pacificum* was also found in Sakhalin and the Kuril Islands (Kunashir and Iturup). It may occur in Japan (see notes on *D. hakkodense*). No collections of *D. pacificum* from the Primorsky Territory have been seen yet, and a single specimen was found among specimens of *D. fragilifolium* from the Khabarovsk Territory (Bureinsky Nature Reserve).

Ecology. In Kamchatka, *D. pacificum* grows at altitudes between 30-560 m, and it was collected at 550 m in the Khabarovsk Territory. In Sakhalin and the Kuril Islands it was found in the same altitudinal range, but with two collections at 1100-1200 m (in Iturup and Kunashir). It grows on trunks of deciduous trees (*Alnus, Betula, Chosenia*), more rarely on stumps and rotten logs or on rocks; one collection in southern Kamchatka is from *Pinus pumila*, and in the northernmost localities in Kamchatka the species grows on soil.

Differentiation. *Dicranum pacificum* is similar to *D. tauricum* in costa structure: both species lack stereid bands and differentiated epidermal layers in the costa. However, they differ in the number of cell layers adaxially from the guide cells, 2(-3) vs. 1(-2). They also have very different basal laminal cells, (15-)20-40(-50) μm in *D. pacificum* vs. 40-80(-120) μm in *D. tauricum*. The mature leaves of *D. tauricum* are mostly subentire close to the apices, whereas they are scabrose in *D. pacificum*. The leaves of *D. pacificum* are more or less spreading and slightly incurved or falcate-secund when dry, while they are straight and erect to erect-appressed in *D. tauricum*.

Dicranum pacificum is readily distinguished from *D. fragilifolium* by the sharply denticulate upper leaf acumina (vs. entire) and its shorter, non-porose basal laminal cells (vs. usually porose). In these two characters, *D. pacificum* is similar to *D. hakkodense*, but the cell walls of the latter are usually much thicker (Fig. 9), it has clear stereid bands in the costa and at least an abaxial epidermal layer of enlargered cells. However, plants from more southern populations of *D. pacificum* in Kunashir Island have thicker cell walls; in this case, the curved, loosely arranged

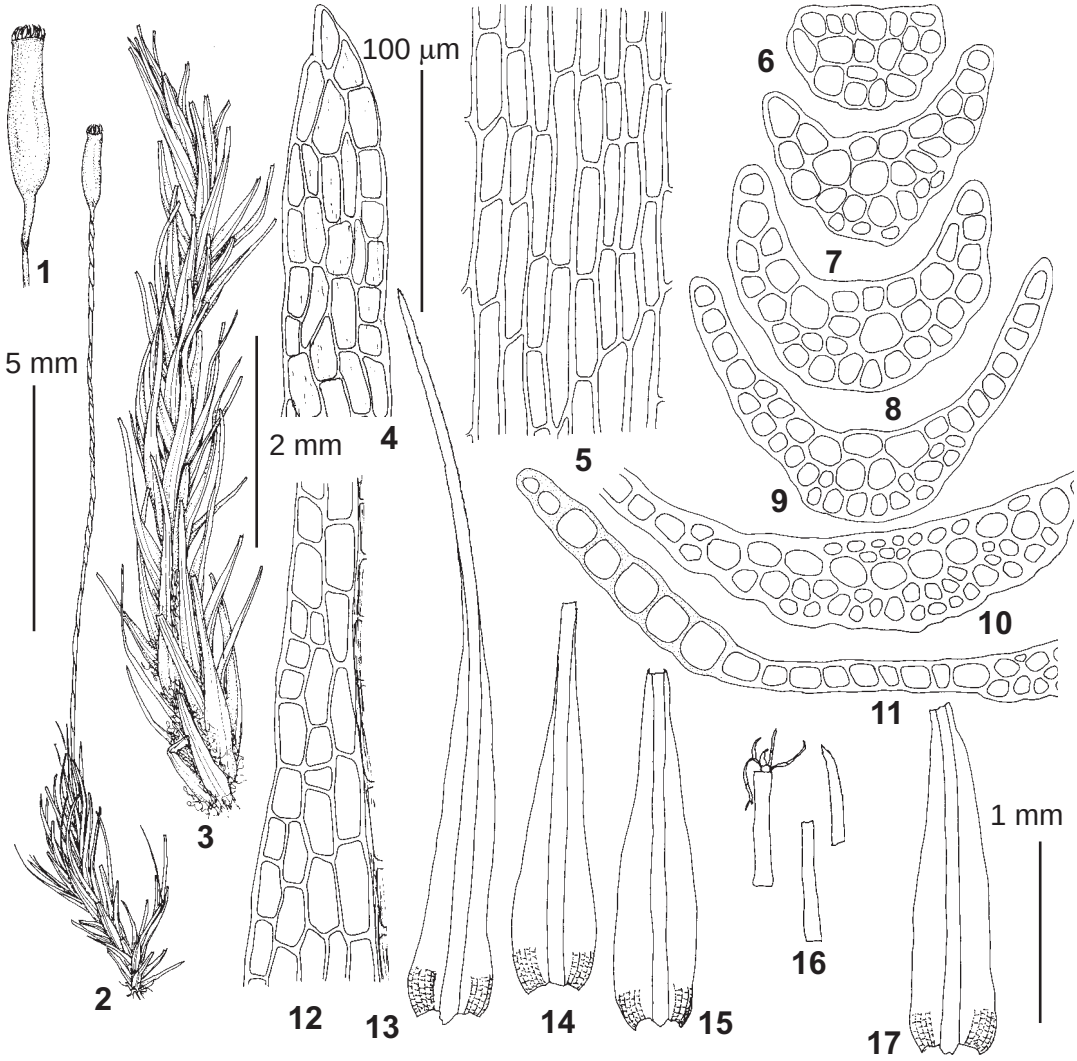


Fig. 12. *Dicranum tauricum* (1-2 – from: Russia, Karachaevo-Cherkessia, *Ignatov & Ignatova #05-3342*, MW; 3 – from: Russia, Karachaevo-Cherkessia, *Ignatov & Ignatova #05-3938*, MW): 1 – capsule, dry; 2-3 – habit, dry; 4 – cells of leaf apex; 5 – basal laminal cells; 6-11 – leaf transverse sections; 12 – median laminal cells; 13-15, 17 – leaves; 16 – broken leaf tips. Scale bars: 5 mm for 2; 2 mm for 1, 3; 1 mm for 13-17; 100 μm for 4-12.

leaves with most apices broken off are helpful for its recognition from *D. hakkodense*, which has straighter leaves with many intact apices in the distal part of shoots.

Specimens examined: ASIAN RUSSIA: **Kamchatskaya Province**: middle course of Bannaya River, 5.VIII. 2002. *Czernyadjeva #41* (LE); Lewyj Kikhchik River basin, 17.VIII.2001, *Czernyadjeva #109* (LE); Pravyj Kikhchik River basin, 26.VII.2004, *Czernyadjeva #25* (LE); Khodutka Bay, Pravaya Khodutka Creek lower course, 28.VII.2002, *Czernyadjeva #32* (LE);Ust-Bol'sheretzky District, Porozhistaya River basin, 16.IX.2005, *Samkova #31* (MW); Sredinnyj Range, Esso, Bystraya River, 6.VIII.2003, *Czernyadjeva #85* (LE); Klyuchevskaya group of volcanoes, Tolbachik Volcano, Tolbachinsky Dol, Vysokaya Mt., 7.VIII.2006, *Czernyadjeva #10* (LE); **Sakhalinskaya Province**: Sakhalin, Dolinsky Distr., Sokol, *Ignatov & Teleganova #06-301* (MHA); Kunashir Island, Ruruj Mt., *Ignatov #06-1599, 06-1226, 06-1143, 06-1576* (MHA); Iturup Island: vicinity of Kuril'sk, *Bakalin #K-9-17-07* (MW); Bogatyr' Range, *Bakalin #K-13-9-07* (MW); **Khabarovsk Territory**: Verkhnebureinsky District, Bureinsky Nature Reserve, *Ignatov #97-957* (MHA).

4. **Dicranum tauricum** Sapjegin, Bot. Jahrb. Syst. 46: 10. *f. 2: 19.* 1911. — *Orthodicranum tauricum* (Sapjegin) Smirnova, Novosti Sist. Niz. Rast. 6: 256. 1969 [1970]. — *Dicranum strictum* Schleich. ex D. Mohr, Ann. Bot. 2: 542. 1806. nom. illeg. — Fig.12, 14.

Plants in dense tufts, light-green or yellowish-green, not or slightly glossy. Stems 0.5-3 cm, tomentose below. Leaves straight, erect-spreading to appressed when dry, strongly fragile, 4-6×0.3-0.5 mm, from lanceolate base gradually tapering into long and narrowly subulate acumen, concave below, canaliculate above; leaf margins subentire or, more rarely, serrulate near apex, entire or uneven in mid-leaf, entire below; costa 1/6–1/4 the width of leaf base, 60-100(-120) μm wide at leaf base, filling subulate leaf acumen, smooth or finely scabrose dorsally in distal part, in transverse section in middle and proximal part with one row of guide cells, 1(-2) rows of substereids with large lumen on ventral side of guide cells and 2(-3) rows of substereids on dorsal side, cells of epidermal layers not enlarged; leaf lamina unistratose or rarely with small bistratose patches; upper and median laminal cells subquadrate or short-rectangular, 12-35×9-12 μm, thin-walled; basal laminal cells elongate-rectangular to linear, 40-80(-120) ×10-14 μm, thin-walled, nonporose or very slightly porose; alar cells unistratose, with slightly thickened walls, brownish, not extending to costa, basal juxtacostal cells chlorophyllose, similar to cells above. Sexual condition dioicous, sporophytes infrequent. Male plants as large as female. Inner perichaetial leaves with sheating base and subulate acumen. Setae 1.5-2.5 cm. Capsules erect, straight, urns 1.4-2.5 mm long, smooth or slightly furrowed when dry. Spores 12-18 μm.

Distribution. *Dicranum tauricum* is known in Europe from Portugal to Spitsbergen, in North Africa, Crimea, Caucasus, Turkey and western North America. Several collections from the forest-steppe and steppe zones of European Russia were made in last decades of the XX century, and very recently it was found in hemiboreal zone near Moscow (Teplov & Ignatova, 2008). The species was also found in the Russian part of Caucasus (Karachaevo-Cherkessia, Kabardino-Balkaria, North Ossetia), where it is infrequent. Old records (middle of XIX century) from the Leningrad Province are not confirmed by herbarium material.

Our data do not confirm the occurrence of *D. tauricum* in Kamchatka. However, some problematic specimens with substereids in the costa and entire upper leaf portions were found among collections of *D. fragilifolium*. They differ from *D. tauricum* by shorter basal laminal cells, resembling those of *D. pacificum*; entire upper leaf acumina differentiate these from *D. pacificum*. Probably, records of *D. tauricum* in Kamchatka (Müller, 1927; Persson, 1970) were based on such specimens. However, a number of species from Pacific North-West of North America are known from Kamchatka (and Chukotka) and there are examples when 'Western–Western' disjunctive species have unique localities in this part of Asia (e. g., *Plagiothecium undulatum*).

Ecology. *Dicranum tauricum* grows on rotten logs and stumps, at trunk bases of pine and birch trees. In Caucasus it was collected at middle elevations, ca. 1600-2100 m, in fir and pine forests, and it is absent in coastal areas of the Black Sea.

Differentiation. The differentiation of *D. tauricum* from *D. viride* and *D. pacificum* is discussed under these species. *Dicranum tauricum* differs from *D. fragilifolium* in the absense of stereid bands in the costa vs. presense of dorsal and ventral sterid bands in the latter species. Sometimes, e.g. in some collections from Kamchatka (Fig. 10: 1d), the costa of *D. fragilifolium* consists of substereids similar to those of *D. tauricum*; in this case the number of cell layers adaxially from the guide cells is helpful, (1(-2) in *D. tauricum* vs. 2(-3) in *D. fragilifolium*). The alar cells are unistratose in the former species and at least partially bistratose in the latter. The capsules of *D. tauricum* are straight and erect, but usually curved and inclined in *D. fragilifolium*. The distributions of these two species do not overlap in the territory of Russia.

Dicranum tauricum differs from *D. hakkodense* in its usually subentire upper leaf acumina vs. sharply denticulate ones, longer basal laminal cells (40-80 μm vs. 25-50 μm), absence of stereid bands and undifferentiated epidermal layers.

Selected specimens examined: EUROPEAN RUSSIA: **Moscow Province**: Mytishchi Distr., between Veshki and Moscow, 15.II.2009, *Teplov s.n.* (MHA);

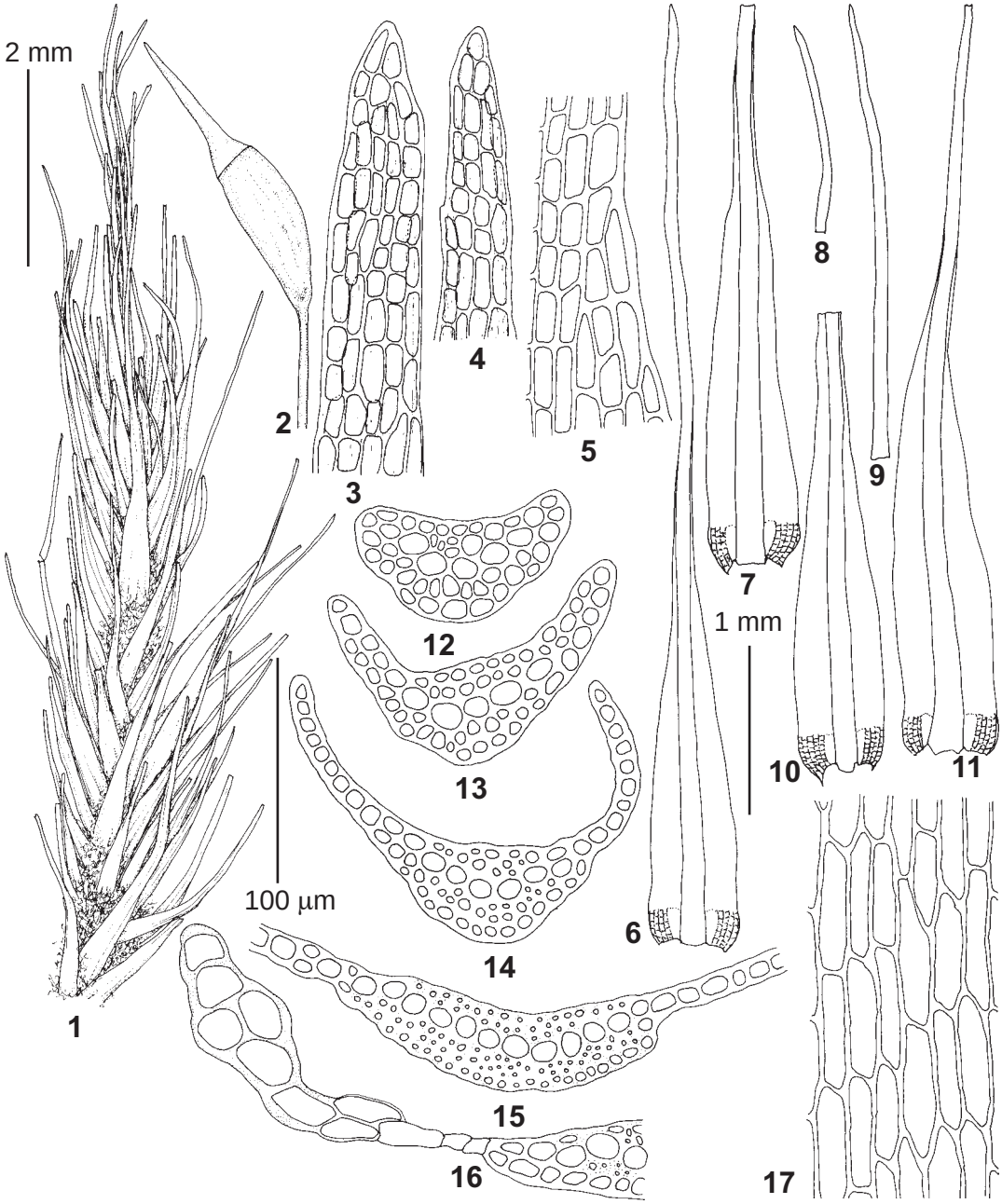


Fig. 13. *Dicranum fragilifolium* (1, 3-17 – from: Russia, Zabaikal'sky Territory, 16.VII. 2005, *Afonina s.n.,* MHA; 2 – from: Karelia, 14.VIII.1993, *Notov s.n.,* MW): 1 – habit, dry; 2 – capsule; 3-4 – cells of leaf apex; 5 – median laminal cells; 6-7, 10-11 – leaves; 8-9 – broken leaf tips; 12-16 – leaf transverse sections; 17 – basal laminal cells. Scale bars: 2 mm for 1-2; 1 mm for 6-11; 100 μm for 3-5, 12-17.

Kursk Province: Kursk Distr., Mokva, 23.V.1995, *Popova s.n.* (MHA); **Kabardino-Balkaria**: Baksan River basin, Adyl-Su Creek, 29.VII.2004, *Ignatov et al. s.n.* (MW); **Karachaevo-Cherkessia**: Teberda Nature Reserve, *Ignatov & Ignatova #05-3342* (MW); **North Ossetia**: Digoria, Karaugom River, 6.IX.2002, *Korotkov s.n.* (MW).

NORTH AMERICA: U.S.A., **Oregon**: Curry Co., Eagle Mt., 14.VIII.1989, *Ignatov & Norris s.n.* (MW).

Total number of studied examined 42.

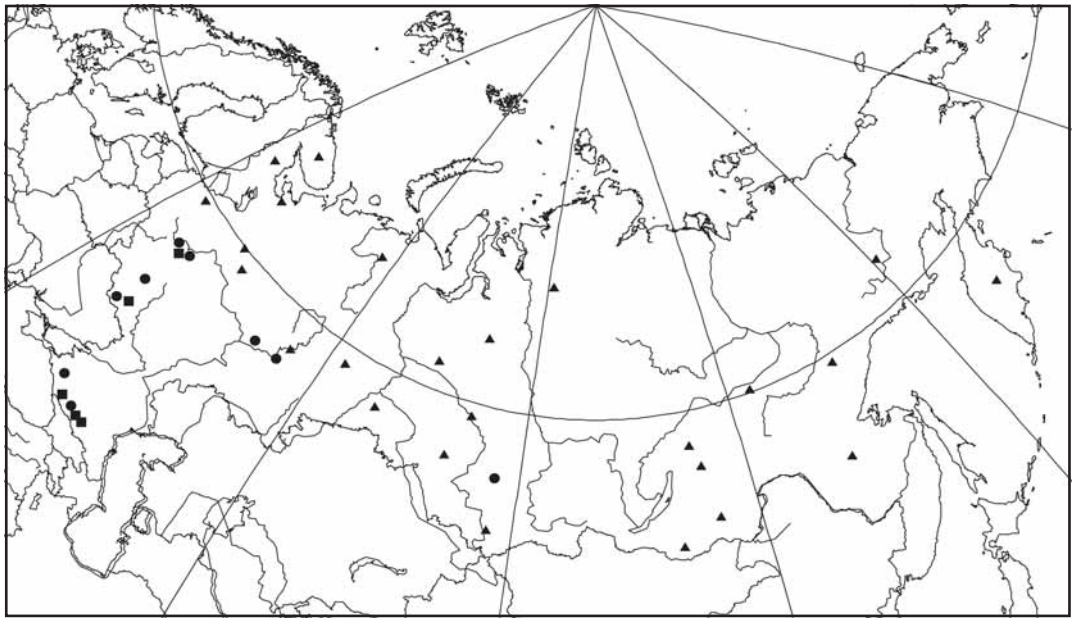
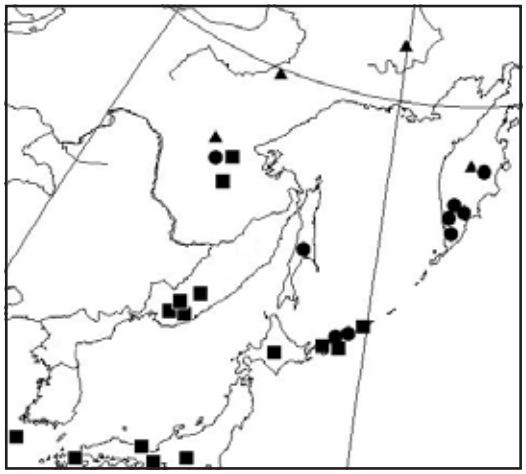


Fig. 14. Distribution of *Dicranum fragilifolium* (triangles), *D. viride* (circles), *D. tauricum* (squares) in Russia based on selected specimens (usually one for province/territory/republic).

5. **Dicranum fragilifolium** Lindb., Bot. Not. 1857: 147. 1857. — Fig.13-15.

Plants in dense, often compact tufts, green or brownish-green, slightly glossy. Stems to 2-3(-6) cm, moderately tomentose below. Leaves rigid, erect-spreading and appressed when dry, strongly fragile, with most apices broken off or apices of upper leaves intact, 5-7×0.4-0.5 mm, from lanceolate base gradually tapering into long subulate acumen, concave below, canaliculate above; leaf margins entire throughout or rarely with 1-2 blunt teeth at apex; costa strong, occupying 1/4–1/3 the width of leaf base, (100-)120-180 μm wide at leaf base, filling subulate leaf apex, smooth on abaxial side, in transverse section in middle and basal part of leaf with one row of guide cells, adaxial and abaxial stereid bands of 2-5 cell layers, adaxial epidermal layer not differentiated, abaxial epidermal layer differentiated or not; leaf lamina unistratose, rarely with few bistratose patches near costa; upper and median laminal cells isodiametric to short-rectangular, with moderately thickened, non-porose walls and rounded lumen, 10-35×7-12 μm; basal laminal cells elongate-rectangular, thick-walled, slightly porose, (25-)40-65(-80)×10-14 μm; alar cells unistratose or bistratose at places, moderately thick-walled, brownish, not extending to costa, basal juxtacostal cells thin-walled, chlorophyllose or pellucid. Sexual condition dioicous, male plants dwarfed or as large as female [observed in collections from Altai]. Sporophytes not frequent. Setae 7-15 mm. Capsules inclined, urns 1.5-2 mm long, curved, furrowed when dry. Spores 18-28 μm.

Fig. 15. Distribution of *Dicranum fragilifolium* (triangles), *D. pacificum* (circles), *D. hakkodense* (squares) in Far Eastern Russia, Japan, and South Korea.



Variability. The costa structure of *D. fragilifolium* is described in different ways by different

authors. Crum & Anderson (1981), Nyholm (1987) and Ignatov & Ignatova (2003) state that stereid bands are absent, but there are several rows of substereids (cells with thick walls and large lumen) on both sides of guide cells. Hedenäs & Bizang (2004) indicated the presence of stereid bands in costa, but the absence of epidermal layers. Ireland (2007) mentions two thin stereids bands (2-3 cell layers), adaxial and abaxial epidermal layers not differentiated or few cells enlargered on both surfaces. These differences reflect the real situation; it is often difficult to say what is seen in transverse sections of the costa of *D. fragilifolium* because the size of the lumen and the thickness of the cell walls are variable. These cells usually have a larger lumen than in the stereids of *D. viride* or *D. hakkodense* and sometimes resemble the substereids of *D. tauricum*. In most cases the cells are best called stereids; the dorsal epidermal layer of larger cells is also often differentiated, although the epidermal cells are often only slightly larger than the cells below them. The dorsal epidermis is thus usually fairly obscure.

Another problem is the level where sectioning is made. In species with fragile leaf apices, the costa in upper and middle part of leaf is filling a considerable part of leaf width and composed entirely or mostly by rather uniform cells. However, the adaxial and abaxial stereid bands are usually well-developed in the costa of *D. fragilifolium* at the distance from leaf base to ca. 1/3 of leaf length.

Most authors describe the upper leaf acumen of *D. fragilifolium* as entire or slightly serrulate. However, we did not find any specimens of *D. fragilifolium* from Russia with serrulate or serrate tips of mature leaves (juvenile leaves at the same plant may be scabrous). Specimens with serrulate leaf tips from the Russian Far East belong to *D. pacificum*.

Distribution. *Dicranum fragilifolium* is a circumboreal species, known in Europe only from Scandinavia, is relatively common in the boreal zone of European Russia and throughout Siberia, in the northern part of the Russian Far East (in Kamchatka north of 54°N, absent in the Kuril Islands and the southern part of the Primorsky Territory), Mongolia and China; in North America it is a rare boreal species. In European Russia it is frequent in the northern taiga zone, declining southward, rare in the hemiboreal zone and absent from broad-leaved forests and Caucasus.

Ecology. *Dicranum fragilifolium* grows mostly on decaying wood (rotten logs and stumps) in conifer forests, more rarely on siliceous rock outcrops, tree bases or soil.

Differentiation. Differences from *D. viride, D. hakkodense, D. pacificum* and *D. tauricum* are discussed under these species. Straight, appressed leaves in combination with entire leaf acumina are the most valuable character states for recognizing *D. fragilifolium* in the field or under the stereomicroscope. Furthermore, inclined and curved capsules are helpful for its differentiation from other species with fragile leaves.

Selected specimens examined: EUROPEAN RUSSIA: **Murmansk Province**: Khibiny Mts., 6.IX.1948, *Shlyakov s.n.* (LE); **Karelia**: Loukhi Distr., Biological Station of Moscow State University, 14.VIII.1993, *Notov s.n.* (MW); **Leningrad Province**: Luga Distr., Vedrovo, 26.VIII.1926, *Ganeshin s.n.* (LE); **Arkhangelsk Province**: Pinezhsky Nature Reserve, 30.VII. 1988, *Ignatov s.n.* (MW); **Vologda Province**: Velsky Distr., Kisheromskaya settlement, 3.VIII.1926, *Shennikov s.n.* (LE);**Kostroma Province**: Makarjev Distr., 19.VII.1907, *Elenkin s.n.* (LE); **Komi Republic**: Pechoro-Ilychsky Nature Reserve, 8.VII.2000, *Bezgodov & Kucherov #393* (MW); **Sverdlovsk Province**: Chusovaya River, Kamen' Boyarin, 30.IV. 1981, *Djachenko s.n.* (LE); **Bashkortostan**: Sredny Kraka Range, Uzyan River, 22.VII.1946, *Selivanova-Gorodkova #554* (LE); ASIAN RUSSIA: **Tyumen Province**: Berezov Distr., Lyapin River basin, 12.IX.1949, *Kil'dyushevsky s.n.* (LE); Verkhnetazovsky Nature Reserve, 1.VIII. 1997, *Czernyadjeva #3* (LE); Surgut surroundings, 2.VIII.2000, *Czernyadjeva & Kuzmina #47* (LE); **Novosibirsk Province**: Maslyaninsky Distr., Suenga Mt., VIII.1995, *Pisarenko s.n.* (LE); **Altai Republic**: *Ignatov #8/212* (MHA); **Tomsk Province**: Bakcharsky Distr., Yarya village, 11.VIII. 1966, *Kosacheva s.n.* (LE); **Krasnoyarsk Territory**: Putorana Plateau, 22.VII.1996, *Kuvaev #118* (MHA); **Sakha/Yakutia**: Verkhoyansky Distr., Biryul'ke village, 28.VIII. 1911, *Aleksandrov s.n.* (LE); Chara River basin, Byas-Kyuel', 6.VIII.1996, *Krivoshapkin s.n.* (MHA);Ust-Maya Distr., Solnechnyj, *Ignatov #00-688* (MHA); Khangalassky Distr., Lenskie Stolby, *Ignatov #00-74* (MHA); **Zabaikal'sky Territory**: Aginsky Buryatsky Autonomous Area, Alkhanai National park, 16.VII. 2005, *Afonina s.n.* (MHA); **Chita Province:** Kyra Distr., Sokhondo Nature Reserve, 5.IX.2008, *Korobkov s.n.* (LE); **Irkutsk Province**: Vitimsky Nature Reserve,

6.VII. 1984, *Bardunov s.n.* (LE); **Amurskaya Province**: Amur River basin, Zimovichi Creek, 8.IX.1910, *Kvashnin-Samarin s.n.* (LE); **Khabarovsk Territory**: Verkhnebureinsky Distr., Bureinsky Nature Reserve, 25.VII.1994, *Petelin #D-94-IX* (MHA); **Magadan Province**: Ol'sky Distr., Chelomdzhi River, 26.VI.1982, *Blagodatskikh s.n.* (LE); **Kamchatskaya Province**: Klyuchevskaya group of volcanoes, Ostryj Tolbachik volcano, 7.VIII.2006 *Czernyadjeva #9* (LE).

Total number of specimens examined is 328.

Acknowledgements

Authors are greatly indebted to Alexey V. Troitsky and Irina A. Milyutina for the help with laboratory work; to Irina V. Czernyadjeva and Olga M. Afonina for specimens loan, to R. Ochyra for checking Latin diagnosis and fruitful discussion, and to Lars Hedenäs for valuable comments on manuscript, including linguistic corrections. The work was partially supported by RFBR # 07-04-00013 and 06-04-49493, and Scientific School Programs НШ-1275.2008.4 and НШ-4243-2008.4.

Literature cited

[AKATOVA, T.V.] АКАТОВА Т.В. 2002. Листостебельные мхи Кавказского заповедника (Западный Кавказ, Россия). – [Moss flora of the Caucasian Nature Reserve (Western Caucasus, Russia)] *Arctoa* **11**: *179-204.*

CRUM, H.A. & L.E. ANDERSON 1981. Mosses of Eastern North America (Vol. 1-2). – *New York, Colombia University Press, 1328 pp.*

CZERNYADJEVA, I.V. 2004. *Anacamptodon kamchaticum*, a new species of Amblystegiaceae (Musci) from Far East. – *Arctoa* **13**: *5-8*.

GOLOBOFF, P. A. **1**994. *NONA: A Tree Searching Program. Program and documentation*. Argentina, Tucumán, published by the author.

GORYUNOV, D. V., E. A. IGNATOVA, M. S. IGNATOV, I. A. MILYUTINA & A. V. TROITSKY 2007. Support from DNA data for a narrow species concept in Schistidium (Grimmiaceae, Musci). – *J. Bryol*. **29**: *98-103.*

HEDENÄS, L. & I. BISANG 2004. Key to European Dicranum species. – *Herzogia* **17:** *179-197.*

HUELSENBECK, F. & F. RONQUIST 2005. MrBayes 3.1.2. http://mrbayes.csit.fsu.edu/index.php

IGNATOV, M.S., E.A. IGNATOVA, T.V. AKATOVA & N.A. KONSTANTINOVA 2002. Bryophytes of the Khosta' Taxus and Buxus Forest (Western Caucasus, Russia). – *Arctoa* **11**: *205-214.*

[IGNATOV, M.S. & E.A. IGNATOVA] ИГНАТОВ М.С., Е.А. ИГНАТОВА 2003. Флора мхов средней части европейской России. Т. 1. – [Moss flora of the Middle European Russia. Vol. 1] *M., KMK [Moscow, KMK]: 608 pp.*

IRELAND, R.R. 2007. Dicranum. – In: Flora of North America. Vol. 27. Mosses, part. 1. *New York, Oxford, Oxford Univ. Press: 397-420.*

IVANOVA, E.I., M.S. IGNATOV, I.A. MILYUTINA & V.K. BOBROVA 2005. On the morphological and molecular differences between Oligotrichum hercynicum and O. falcatum (Polytrichaceae, Bryophyta). – *Arctoa* **14**: *1-11.*

IWATSUKI, Z. 2004. New catalog of the mosses of Japan. – *J. Hattori Bot. Lab.* **96**: *1-182*.

MÖLLER, H. 1927. Die Laubmose Kamtschatkas. – *Hedwigia* **67**: *86-98.*

NIXON, K.C. 1999a. *Winclada (BETA) ver. 0.9.9*. available at http://www.cladistics.com/about_winc.html.

NIXON, K.C. 1999b. The parsimony ratchet, a new method for rapid parsimony analysis. – *Cladistics* **15**: *407-414.*

NOGUCHI, A. 1987. Illustrated moss flora of Japan. Pt. 1 – *Hattori Botanical Laboratory, Nichinan*: *1-242.*

NYHOLM, E. 1987. *Illustrated flora of Nordic Mosses, Fasc. 1. Fissidentaceae-Seligeriaceae. Copenhagen & Lund: Nordic Bryological Society.*

PERSSON, H. 1970. Contribution to the bryoflora of Kamtchatka. – *Rev. bryol. lichénol., n.s.* **37** (2): *209-221.*

TAKAKI, N. 1964. A revision of Japanese Dicranum. – *J. Hattori Bot. Lab*. **27**: *73-123*.

TEPLOV, K.U. & E.A. IGNATOVA 2008. New moss records from Moscow Province. 1. – *Arctoa* **17**: *200.*