Arctoa (2005) **14**: *1-11*

ON THE MORPHOLOGICAL AND MOLECULAR DIFFERENCES BETWEEN OLIGOTRICHUM HERCYNICUM AND O. FALCATUM (POLYTRICHACEAE, BRYOPHYTA)

О МОРФОЛОГИЧЕСКИХ И МОЛЕКУЛЯРНЫХ ОТЛИЧИЯХ OLIGOTRICHUM HERCYNICUM И O. FALCATUM (POLYTRICHACEAE, BRYOPHYTA)

E. I. Ivanova[1], M. S. Ignatov[2], I. A. Milyutina[3] & V. K. Bobrova[3]

Е. И. Иванова[1], М. С. Игнатов[2], И. А. Милютина[3] и В. К. Боброва[3]

Abstract

Morphological differences between two arcto-alpine species of *Oligotrichum, O. hercynicum* and *O. falcatum* (Polytrichaceae) are rather few, overlapping and not always expressed, thus problems with their distribution in Asia remain. In the present study we found that morphology of these species corresponds well with the six characteristic substitutions in nrITS1, providing more robust ground for delimitation of these two species. *Oligotrichum hercynicum* occurs in relatively oceanic climates in Northern Europe, mountains of Central Europe, Caucasus, Kuznetskij Alatau in South Siberia, Kamchatka, Chukotka, and northern North America. Contrary to that, *Oligotrichum falcatum* has the Beringian distribution, in a broad sense. It is known from mountains of South Siberia (westwards to Altai), Yakutia, xeric regions of North-East Asia and Arctic North America, including Western Greenland, and also reported from Tibet.

Резюме

Морфологические отличия двух аркто-альпийских видов *Oligotrichum, O. hercynicum* и *O. falcatum* далеко не всегда хорошо выражены, во многом перекрываются, так что угнетенные растения этих видов (что нередко имеет место в Арктике) оказывается практически невозможно определить. Изучение нуклеотидных последовательной ядерного внутреннего транскрибируемого спейсера ITS1 выявило в нем 6 замен, четко разделяющих эти два вида. Это позволило уточнить диагностические признаки видов и их распространение. *Oligotrichum hercynicum* встречается преимущественно в районах с более влажным климатом: на севере Европы, в горах Центральной Европы, Кавказа, Кузнецком Алатау, затем после дизъюнкции на Камчатке и Чукотке, а также на севере Северной Америки. *Oligotrichum falcatum* связан в целом с континентальными районами и имеет берингийское (в широком смысле) распространение: горы Южной Сибири (на запад до Алтая), Якутия, аридные районы северо-восточной Азии и арктической Северной Америки, включая западную Гренландию; он также указан для Тибета.

Introduction

The genus *Oligotrichum* includes 17-24 species with an almost worldwide distribution (Smith Merill, 2005). The genus was never monographed, thus even widespread species with non- or little-overlapping ranges were insufficiently compared, just in the course of regional studies. *Oligotrichum falcatum* Steere and *O. hercynicum* (Hedw.) Lam. et DC. were both included in the descriptive flora "Mosses of USSR. Acrocarpous mosses" (Savicz-Lyubitskaya & Smirnova, 1970), but they were referred at that time to different gen-

[3] — Institute of Biology of Permafrost-Zone, Lenina str. 41, Yakutsk 677890 Russia – Россия 677890 Якутск, пр. Ленина, 41, Институт Биологических проблем криолитозоны СО РАН

[2] – Main Botanical Garden of Russian Academy of Sciences, Botanicheskaya 4, Moscow 127276 Russia – Россия 127276 Москва, Ботаническая 4, Главный ботанический сад РАН

[3] — A. N. Belozersky' Institute of physicochemical biology, Moscow State University, Moscow 119992 Russia – Россия 119992 Москва, Московский государственный университ, НИИ физико-химической биологии им. А. Н. Белозерского.

era: *Oligotrichum falcatum* was considered to be a member of *Psilopilum*. Thus, they were not included in one key and the comparison of their morphological descriptions provided just a few differences without pointing out which ones are important for species delimitation. The original description of *O. falcatum* by Steere (1958), as well as subsequent publications of Steere (1978) and Steere & Smith (1976) never mentioned *O. hercynicum*.

Later on, Long (1985) and Smith Merill (2005) in their treatments of Polytrichaceae for Greenland and North America respectively discussed both species. The differences between them were described as follows: *O. hercynicum* has leaves ±straight when dry, erect-spreading when wet, arcuate-incurved; costa with dorsal lamellae usually present, often extending to below mid-leaf, whereas *O. falcatum* has leaves strongly falcate-secund; costa smooth abaxially or with low abaxial lamellae or teeth near apex (Smith Merill, 2005). Long (1985) noted in species descriptions also a difference in leaf base that is not decurrent in *O. hercynicum*, but slightly decurrent in *O. falcatum*. These characters are certainly helpful for distinguishing well-developed plants. However, according to our observations, the variation in populations can be quite misleading. For example in Yakutia, *O. falcatum* has strongly falcate leaves only in rather sheltered habitats, contrasting with plants from open places, exposed to very severe conditions, especially in winter (below minus 60°C combined with weak or almost no snow). The latter plants are small, with leaves which are difficult to evaluate regarding falcate vs. non-falcate and decurrent vs. not decurrent. This variation raises certain doubts over the species independence. There are a number of moss species where leaves can be falcate or straight, but this character is not considered as taxonomically important: e. g. *Hygrohypnella* (*Hygrohypnum*) *polare* (Lindb.) Ignatov & Ignatova vs. *Hygrohypnum ehlei* Lindb. et Arnell (Czernyadjeva, 2003), etc. There is one more difficulty in the application of the character of leaf falcateness: according to Steere & Smith (1976) falcate leaves are characteristic of female plants of *O. falcatum*, whereas the male ones have almost straight leaves.

The nuclear ITS region has been shown to be very helpful for solving problems at the species level in mosses (e. g. Stech & Frahm, 1999; Frahm & Mьller, 2000) and it was chosen here to elucidate the situation in these two species of *Oligotrichum*.

METHOD AND MATERIAL

Morphological studies are based mainly on collections from Russia in IRK, LE, MHA, MW, PTZ, SASY, and some specimens were borrowed also from KRAS and bryophyte herbarium of the geobotany Dept. of Central Siberian Botanical Garden. Collections from North America and Central and Northern Europe were studied in H, LE, MHA, MW, but no attempts were made to examine complete material from European and American herbaria.

Molecular analysis included 10 specimens from geographically distinct populations (see Table 2) of both species. Both typical and atypical expressions of *O. falcatum* were taken, to find out if leaf falcateness is an important character.

The protocols of DNA extraction, PCR and sequencing were the same as described in Budyakova & al. (2003).

RESULTS

The sequence of ITS1 and gene 5.8S RNA consists of 546 positions, of which only seven are variable and six of them appeared to be parsimoniously informative (Fig. 1). All these six positions invariably divide the 10 studied specimens in two groups (composed of 5 and 5 specimens) by their characteristic substitutions.

One of these two groups appears to be relatively homogeneous in having prominent dorsal lamellae and non-falcate leaves, thus corresponding to *O. hercynicum*. The second group includes plants with both falcate and almost straight leaves, without or with dorsal lamellae, although in the latter case they were usually just 1(-2) cell high. However, ITS homogeneity supports the view, that they represent just one species, *O. falcatum*.

Searching for the characters separating these two groups, we found that the outline of lamellae in side view is different between these two groups, and rather constant within each of them (Fig. 6). This character can probably be rather useful for separating poorly developed material of *Oligotrichum* and also *Psilopilum*.

```
                              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                                  5          15         25         35         45         55         65         75         85         95
O. falcatum, Alaska          ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. falcatum, Khabarovsk      ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. falcatum, SE Yakutia      ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. falcatum, SW Yakutia      ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. falcatum, Sayany          ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. hercynicum, Kola          ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. hercynicum, Caucasus      ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. hercynicum, Kuzn.Alat     ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. hercynicum, Kamchatka     ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
O. hercynicum, Chukotka      ACACACGATG CAGCTAACTC GCGAACTGTG TTTGTCCCCC AAACCACCCC AAACTCGAGG GGCCGCACTT GGAGGTGCGG CTGCGAGCGC GCATGTCCGA
                   101 - 200
O. falcatum, Alaska          CTCCCGTCCG ATGGGACGGG GGTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. falcatum, Khabarovsk      CTCCCGTCCG ATGGGACGGG GGTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. falcatum, SE Yakutia      CTCCCGTCCG ATGGGACGGG GGTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. falcatum, SW Yakutia      CTCCCGTCCG ATGGGACGGG GGTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. falcatum, Sayany          CTCCCGTCCG ATGGGACGGG GGTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. hercynicum, Kola          CTCCCGTCCG AAGGGACGGG GTTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. hercynicum, Caucasus      CTCCCGTCCG AAGGGACGGG GTTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. hercynicum, Kuzn.Alat     CTCCCGTCCG AAGGGACGGG GTTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. hercynicum, Kamchatka     CTCCCGTCCG AAGGGACGGG GTTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
O. hercynicum, Chukotka      CTCCCGTCCG AAGGGACGGG GTTCCTCGCT TCCGGGAGCG CGAGCGAGCG TGGCATGTCG TTTGCGGGGC GCCTGCGCTG GCTCTCGTCG CGGCCTTCGG
                   201 - 300
O. falcatum, Alaska          GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GTCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACCATGCCA
O. falcatum, Khabarovsk      GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GTCTTCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACCATGCCA
O. falcatum, SE Yakutia      GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GTCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACCATGCCA
O. falcatum, SW Yakutia      GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GTCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACCATGCCA
O. falcatum, Sayany          GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GTCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACCATGCCA
O. hercynicum, Kola          GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GCCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACAATGCCA
O. hercynicum, Caucasus      GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GCCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACAATGCCA
O. hercynicum, Kuzn.Alat     GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GCCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACAATGCCA
O. hercynicum, Kamchatka     GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GCCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACAATGCCA
O. hercynicum, Chukotka      GTCCGGCGAC GCGGGTGCCC CCCTCCCCCA TCCTAGTGCC CCGTCCTCGA GCCATCGGGT GCCGGGAACG CTAAGGTGGG GCCGCTTATG CACAATGCCA
                   301 - 400
O. falcatum, Alaska          AACATTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT CGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. falcatum, Khabarovsk      AACATTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT CGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. falcatum, SE Yakutia      AACATTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT CGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. falcatum, SW Yakutia      AACATTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT CGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. falcatum, Sayany          AACATTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT CGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. hercynicum, Kola          AACGTTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT TGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. hercynicum, Caucasus      AACGTTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT TGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. hercynicum, Kuzn.Alat     AACGTTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT TGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. hercynicum, Kamchatka     AACGTTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT TGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
O. hercynicum, Chukotka      AACGTTTACG ACTGAGTATT ATTGTGACCG ACGCGGCAGA CCGCCCGAGA GGGTGAGAGT TGCGTCGGGA CAAGAGAGTT AAACATAAAC AACTCTCAGC
                   401 - 500
O. falcatum, Alaska          AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. falcatum, Khabarovsk      AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. falcatum, SE Yakutia      AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. falcatum, SW Yakutia      AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. falcatum, Sayany          AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. hercynicum, Kola          AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. hercynicum, Caucasus      AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. hercynicum, Kuzn.Alat     AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. hercynicum, Kamchatka     AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
O. hercynicum, Chukotka      AACGGATATC TTGGCTCTTG CAACGATGAA GAACGCAGCG AAATGCGATA CGTAGTGTGA ATTGCAGAAT TCCGCGAATC ATCGAGTCTT TGAACGCAAG
                   501 - 546
O. falcatum, Alaska          TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. falcatum, Khabarovsk      TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. falcatum, SE Yakutia      TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. falcatum, SW Yakutia      TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. falcatum, Sayany          TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. hercynicum, Kola          TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. hercynicum, Caucasus      TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. hercynicum, Kuzn.Alat     TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. hercynicum, Kamchatka     TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
O. hercynicum, Chukotka      TTGCGCCCGA GGCTCGTCCG AGGGCATTCC TGCCTGAGCG TCATCG
```

Fig. 1. Alignment of the ITS1 region of 5 specimens of *Oligotrichum falcatum* and 5 specimens of *O. hercynicum*. Variable positions are marked above column. Specimen details are in Table 2 and Fig. 4.

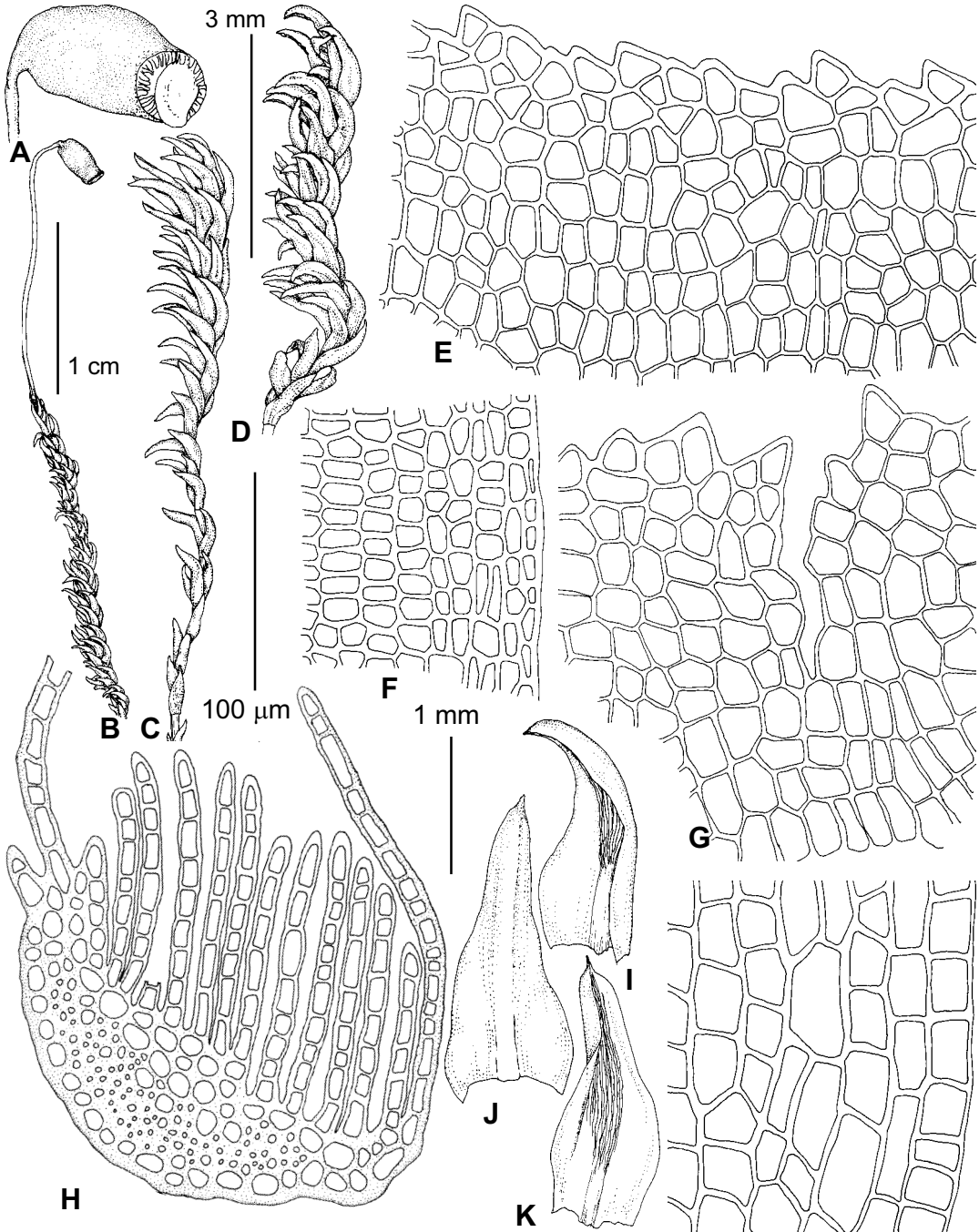
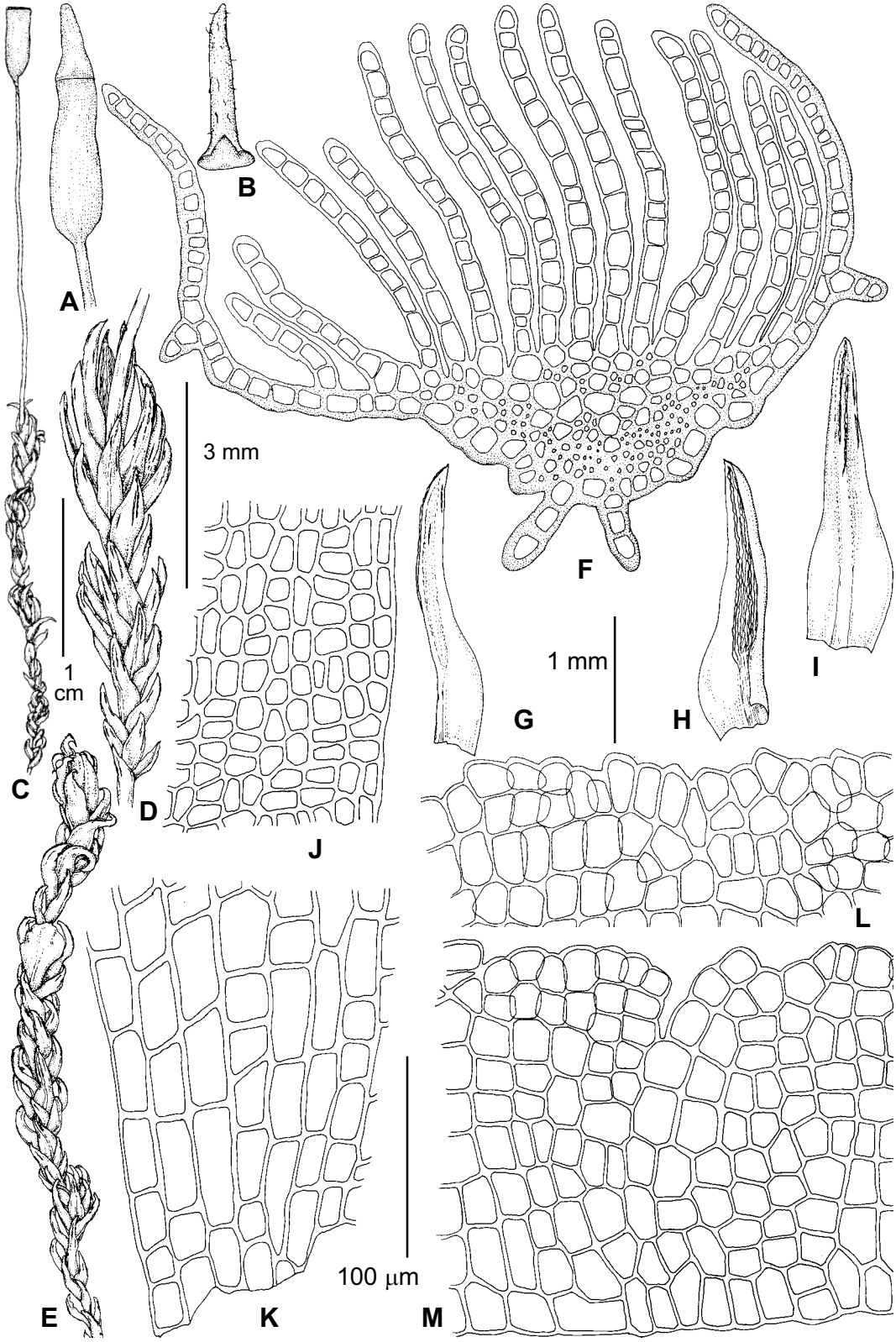


Fig. 2. *Oligotrichum falcatum* (from: Khabarovsk Territory, Upper Bureya River, Ignatov 97-525, MHA): A – capsule; B-D – habit, dry; E, G – lamella on side view; F – lamina cells of mid-leaf; H – leaf transverse section; I-K – leaves; L – basal leaf cells. Scale bars: 1 cm – B; 3 mm – A, C, D; 1 mm – I-K; 100 μm – E-H, L.

Fig. 3 (page 5). *Oligotrichum hercynicum* (from: Murmansk Prov., Khibiny: B – Ignatov 29.VI.1990, MHA; the rest – Smirnova & Katenin 4.VIII.1948 (LE exsiccate # 133): A – capsule; B – calyptra; C-E – habit, dry; F – leaf transverse section; G-I – leaves; J – lamina cells of mid-leaf; K – basal leaf cells; L-M – lamellae on side view. Scale bars: 1 cm – C; 3 mm – A, B, D, E; 1 mm – G-I; 100 μm – F, J-M.


A
B
C
D
E
F
G
H
I
J
K
L
M
1 cm
3 mm
1 mm
100 μm

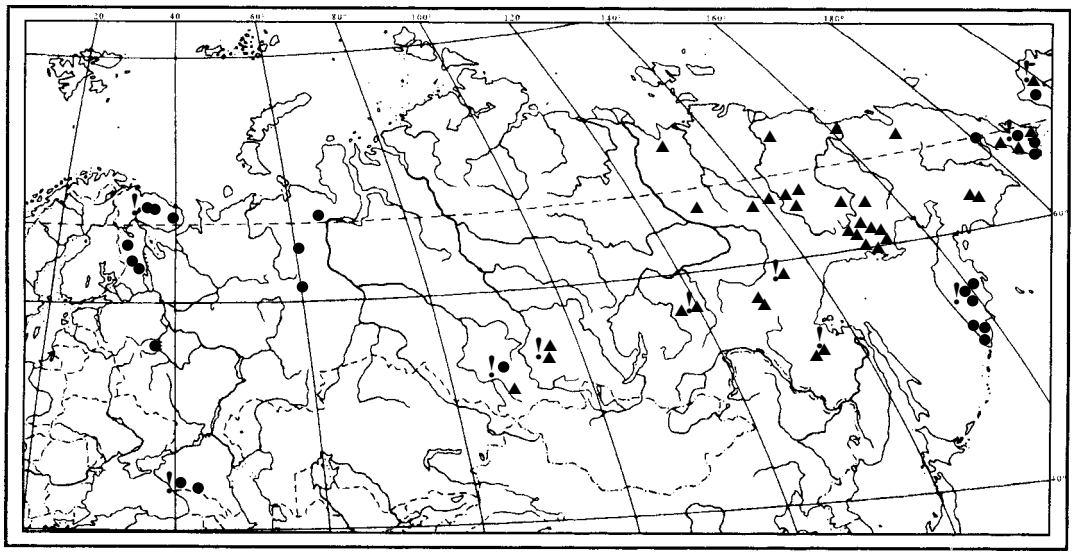
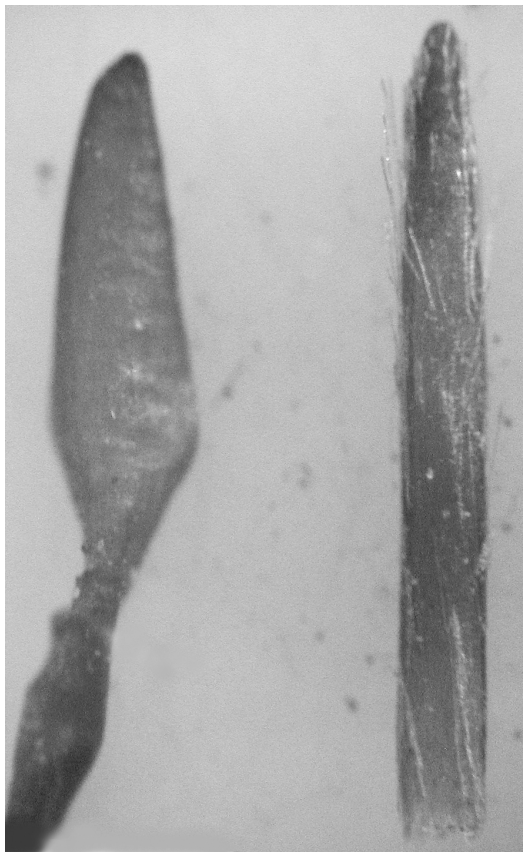


Fig. 4. Distribution of *Oligotrichum falcatum* (triangles) and *O. hercynicum* (circles) in Russia; ! – specimens used for DNA study.

Fig. 5. Calyptrae of *Oligotrichum falcatum* (left, from Magadan Prov., Blagodatskikh 25.VII.1972, LE) *and O. hercynicum* (right, from Karelia, Marsimov 7.VII.2005, PTZ).



DISCUSSION AND TAXONOMIC IMPLICATIONS

The present example demonstrates one more case where molecular data provide relatively solid evidence in favour of one of two possible taxonomic solutions in a situation where morphological differentiation is rather subtle. Again, our analysis confirms that the ITS1 region can be an useful locus for studies at the species level in mosses.

This study shows that leaf falcateness is a variable character and sometimes may not be expressed even in female plants of *O. falcatum*, expecially from Arctic and high mountain environments.

Dorsal lamellae are usually much better expressed in *O. hercynicum* than in *O. falcatum* (cf. Figs. 2 & 3), but the quantitative application of this character is also problematic due to the broad range of variation. At least their height up to 2 cells is common in *O. hercynicum*, and not impossible in *O. falcatum* (cf. Figs. 2 & 3).

However, quite stable is the difference in hairiness of the calyptra, at least as far as we could find in material from Russia, but this character can not be applied to the vast majority of sterile collections, and moreover, a naked calyptra is reported to be rarely occurring in *O. hercynicum* too (e. g. Savicz-Lyubitskaya & Smirnova, 1970). Table 1 presents the characters which are useful for the separation of *Oligotrichum falcatum* from *O. hercynicum*, and also from *Psilopilum* species, which are similar to *Oligotrichum falcatum* in the

Table 1. Comparison of *Oligotrichum hercynicum, O. falcatum, Psilopilum laevigatum,* and *P. cavifolium* (based on material from Russia).

Characters	*Oligotrichum falcatum*	*Oligotrichum hercynicum*	*Psilopilum laevigatum*	*Psilopilum cavifolium*
Stem height, cm	(0.5-)0.8-2.5(-4.0)	(0.5-)1.0-2.0(-2.3)	1.0-3.5	0.5-1.5
Leaves when dry	falcate-secund to curved inwards, cucullate, loosely imbricate	curved inwards to contorted, not cucullate, not imbricate	curved inwards, cucullate, loosely imbricate	curved inwards, cucullate, loosely imbricate
Leaves when wet	almost as dry	spreading	almost as dry	almost as dry
Leaf length, mm	(1.2) 1.5 - 2.5 (-2.75)	(-1.7) 2.0 - 3.0 (-3.7)	1.2-3.0	1.2-3.0
Leaf width, mm	0.5-0.7	0.5-1.2	0.9-1.1	0.9-1.1
Dorsal lamellae	absent or rare, short and low, usually on costa	2-5, reaching mid-leaf, 1-4 cell high, on costa and lamina	absent	absent (present in var. *anomala*)
Laminal cells width, μm	(8.0-)10.0-15.0(-17.0)	(14.0-)16.0-20.0	(16-)19-21(-25)	(15-)21-24(-27)
Border of rhombic cells	absent	absent	always distinct	distinct to indistinct
Leaf base	shortly decurrent	not decurrent	not decurrent	not decurrent
Costa	shortly excurrent, rarely percurrent	ending below apex to percurrent	ending below apex to percurrent	ending below apex to percurrent
Ventral lamellae	8-16	8-12	8-14	7-10
Ventral lamella height	6-13	4-12	8-16	8-14
Upper edge of lamella on side view	serrate	coarsely crenate	obtusely, but strongly denticulate	entire to slightly serrulate
Spores, μm	15.5-19.5	[10-]12.0-13.0[-15]	21-26	24-28
Calyptra	naked	hairy	naked	naked
Capsule	straight	straight	strongly curved	± curved

sterile condition and a number of misidentifications were found in herbaria.

Descriptions and differentiation of *Oligotrichum falcatum* and *O. hercynicum*

Oligotrichum falcatum Steere, Bryologist 61: 115. f. 1-9. 1958.

Plants in loose tufts or growing as well-spaced individuals, bright green to red-brown, sometimes slightly glaucous. Stem ascending to erect, in dry habitats 5-10, in wet – 8-25(-40) mm high, simple, rarely branched by innovations, densely foliate, in larger plants often with thread-like lower part (up to 5-8 mm long), bearing very small leaves. Leaves loosely appressed to falcate-secund both when dry and wet, 1.2-2.5(-2.75)* x 0.5-0.7 mm, asymmetric, ovate to ovate-lanceolate, strongly concave and cucullate above, at base slightly decurrent; margin entire or serrulate, sometimes with few more prominent teeth near the apex; costa shortly excurrent or percurrent, with large thick-walled apical cells or few-celled point, often reflexed from cucullate apex; dorsal lamina smooth or with low teeth or solitary short dorsal lamellae (usually 1(-2) per cross section) in upper 1/4–1/3 of leaf. Ventral lamellae 8-16, reaching from apex to about 1/5 of leaf length, straight or more commonly strongly undulate, 6-13 cells high, in transverse section with undifferentiated upper cell, in lateral view irregularly serrulate and notched, the marginal cells in section undifferentiated, smooth; median laminal cells ± isodiametric, from transverse-rectangular to short-rectangular, (8.0-)10-15(-17) μm wide, thick-walled; marginal cells ± rectangular, with cell walls ± perpendicular to the margin; basal cells short rectangular, sometimes with small groups of enlarged alar cells; leaves of male plants only weakly falcate. Dioicous (sporophytes only in 4 specimens from Chukotka, Yakutia, Magadan

* – Leaves are ranging from 1.2-1.5 mm long in dry places and in tundra up to 1.6-2.5(-2.75) in wet sheltered habitats

Prov., and Khabarovsk Territory (Bureya)). Perigonial leaves not seen in collections from Russia. Perichaetial leaves up to 4.0 mm, straight. Seta 1-1.5 cm, yellow-reddish, twisted above, rather thick. Capsule symmetric, straight to horizontal and pendent when mature, 2.3-4.0 mm long, 1.0-1.2 mm wide, cylindric to irregularly 6-8-angulate, widest at the base and tapering towards the mouth, brownish; stomata present; operculum conic with a short beak; peristome teeth ca. 32, brownish, finely papillose. Spores 15.5-19.5 μm, mature in late July–August. Calyptra naked.

Some quantitative characters in North American plants are reported as being larger, e. g. spore size – 19-21 μm (Smith Merill, 2005; Long, 1985).

Differentiation. Differences between *O. falcatum* and *O. hercynicum* are summarized in Table 1. In problematic cases with identificaltion of undeveloped plants, the most reliable difference is probably, the profile of lamellae (cf. Figs. 2&3).

Low sterile plants of *Oligotrichum falcatum*, commonly found in dry exposed habitats, are superficially very similar to species of *Psilopilum* (leaves closely imbricate, symmetric, very concave, cucullate, dorsal lamellae absent). We found in herbaria a number of misidentifications of *O. falcatum* as *Psilopilum* spp., especially from Yakutia and South Siberian mountains. At the moment, all the studied specimens called *Psilopilum* from South Siberia and South Yakutia were found to be erroneous. At the same time, in the Arctic *O. falcatum* is sometimes misidentified as *Psilopilum* (the latter is common there).

Psilopilum differs from *Oligotrichum* in capsule shape: in the former the capsule is curved, whereas in *Oligotrichum* it is cylindric. In *Psilopilum* capsules are not so rare as in *Oligotrichum*.

Psilopilum cavifolium is easier to recognize by its almost entire lamellae in lateral view. In *P. laevigatum* the lamellae are rather similar to those of *Oligotrichum falcatum* and the most reliable character for their differentiation is probably the border of rhombic cells along the leaf margin in its lower half. This border is not always very well expressed in *P. cavifolium*, but in Russian collections of *P. laevigatum* it is usually quite conspicuous.

Also in *Oligotrichum falcatum* the costa often forms an apiculus, whereas it always ends below the leaf apex in *Psilopilum* species.

Low dorsal lamellae occur in *Psilopilum cavifolium* var. *anomalum* (I. Hag.) Broth., but this variety can be differentiated from *O. hercynicum* by the well-developed border of rhombic cells.

Additional characters are shown in Table 1.

Ecology. Acidophilous species, growing on wet rocky substrates, including late snow beds and temporarily flooded places in tundra.

Distribution. Greenland, Canada (Labrador, Yukon), USA (Alaska), Russia (Sibeira and Russian Far East – see Fig. 4 and specimens examined).

Specimens examined from Russia: **Altai Republic:** *Kurkure Range, Kayakkatuyarykskij Creek*, 1950 m alt., Ignatov 4/14 (MHA). **Krasnoyarsk Territory:** *West Sayan Mts, Kulumys Range*, 1450 m alt., 17.VIII.2005, N.V. Stepanov (KRAS, MHA); *Ergaki Range*, 1650 m alt., 17.VIII.2002, Muldiyarov (MHA). **Irkutsk Prov.:** *Vitimsky Reserve, Oron Lake*, 27.VIII.1984 Bardunov (IRK, as *Psilopilum laevigatum* var. *anomala*). **Yakutia**: *Neryungri Distr., Bolshoe Toko Lake,* 5.VIII.1987, 8.VII.1986, 26.VIII.1987, 30.VIII.1989 Volotovsky (SASY); 23.VII.1987 (SASY, LE as *Psilopilum laevigatum*); *Udokan Range, Upper course of At-Bastaakh River*, 12.VII.2002, Sofronova (SASY, MHA); 2000, Bakalin (SASY); *Nizhnekolymsky Distr., Kamenka Island*, Stepanova, 22.VII.1975 (SASY, as *Psilopilum cavifolium*); *Oimyakon Distr., Indigirka River near Ust-Nera*, 29.VII.1960, Dobretsova (LE, SASY, as *O. hercynicum*); *Silyansky Range,* 24.VI.1976, Afonina (LE); *Aercha River,* 2.VIII.1974, 5.VIII.1974, 9.08.1974, Afonina (LE); *Momsky Distr., Indigirka River Basin, Ulakhan-Chistai Range, upper course of Gyrban'ya River*, 22.VII.2003, 24.VII.2003, Sofronova (SASY); *Zhigansk Distr., upper course of Undyulyung River*, 11.VII.1990, Nikolin (SASY); *Tomponsky Distr., Tinkirkan River*, 19.VII.1956, Kildyushevsky (LE as *O. hercynicum*); *upper course of Tompo River*, 25.VII.1956, V. Ivanova (SASY); *Ust-Maya Distr., Tarbagannakh*, 27.VIII.2000, E. Ivanova & M. Ignatov (SASY, MHA). **Khabarovsk Territory**: *Bureinsky State Reserve*, 97-526, 97-525, 97-521 Ignatov (MHA). **Magadan Prov.**: (selected): *Tenkinsky Distr., Pdumai Pass*, 25.VII.1972, Blagodatskikh (LE); *Omchak,* 5.VIII.1972, Blagodatskikh (LE); *Stokovyj,* 1.VII.1973, Blagodatskikh (LE); *Sibit-Tyaellakh*, 13.VIII.1976, Blagodatskikh (LE). *Magadan Distr., Marchekanskaya Hill*, 25.VII.1972, Blagodatskikh (LE); *Magadan City*, 8.IX.1972, 19.VII.1978, Blagodatskikh (LE); *Khasynskij Distr.,Khuraendzhi River,* 5.IX.1972, Blagodatskikh (LE). *Olskij Distr., Khuraendzhi River*, 5.IX.1972, Blagodatskikh (LE). *Chaunskij Distr., Niti Mt.,* 15.VIII.1977, Blagodatskikh (LE); *Chaun River,* 15.VIII.1977, Blagodatskikh (LE). *Chukotskij Distr., Lorinskie hot springs*, 13.VIII.1974, Blagodatskikh (LE). *Omsunganskij Distr., Ayam,* 16.VIII.1980, Blagodatskikh (LE). **Chukotskij Autonomous District**: *Provideniya Zalif, Aemma Bay,* 13.VII.1938, Gorodkov (LE); *Aerguveem River*, 6.VIII.1970, 8.VIII.1970, Afonina (LE, as *Oligotrichum hercynicum*); *Amguaema River*, 18.VIII.1970, Afonina (LE); *Inchoun*, 2.VIII.1975, 4.VIII.1975, Afonina (LE); *Kresta Zalif,* 17.VIII.1977, Afonina (LE); *Tanyurer River,* 11.VII.1979, 14.VII.1981, 17.VII.1981, 20.VII.1981, 30.VII.1981, 6.VIII.1981, Afonina (LE); *Arakamchechen Island,* 20.VII.1976;

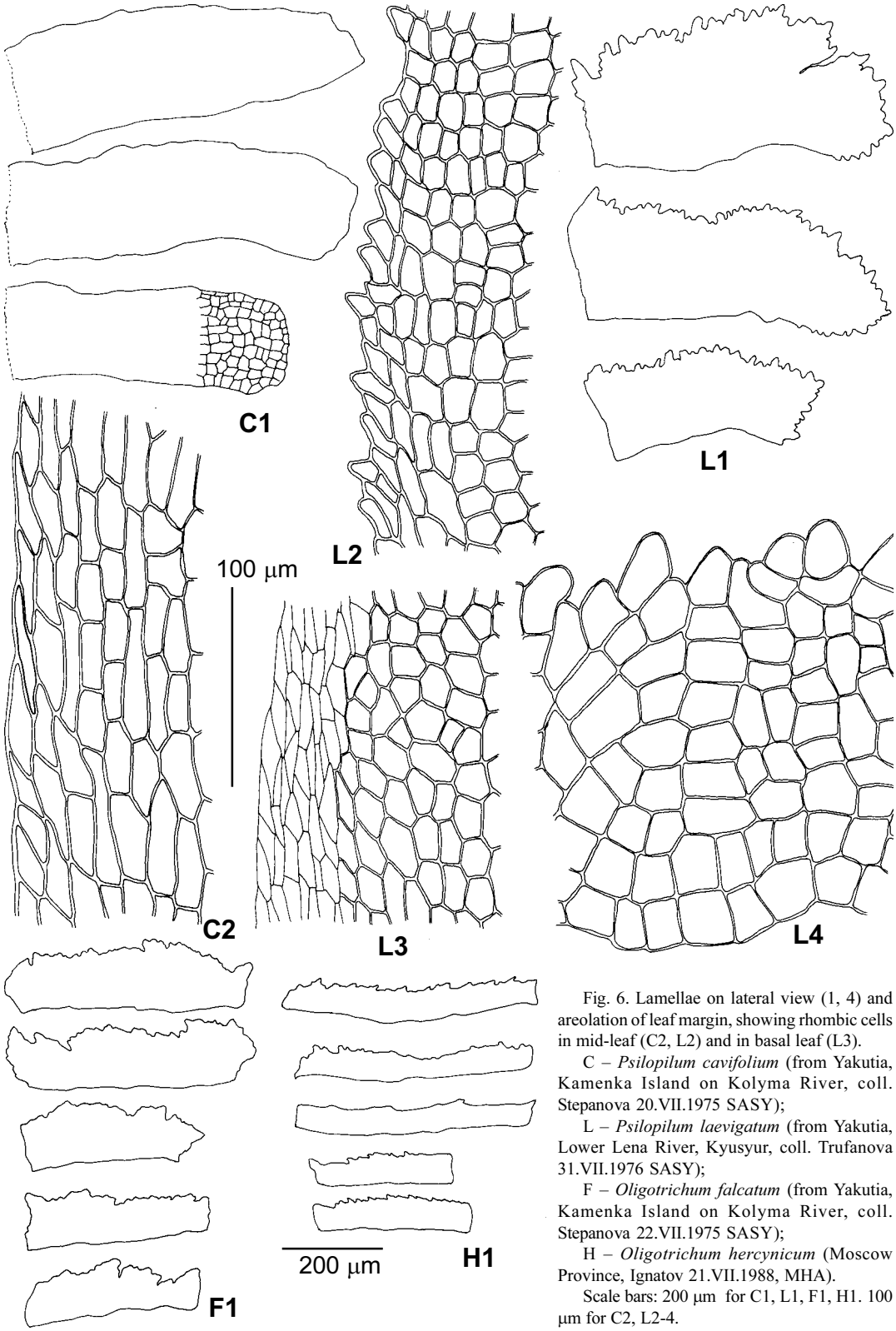


Fig. 6. Lamellae on lateral view (1, 4) and areolation of leaf margin, showing rhombic cells in mid-leaf (C2, L2) and in basal leaf (L3).

C – *Psilopilum cavifolium* (from Yakutia, Kamenka Island on Kolyma River, coll. Stepanova 20.VII.1975 SASY);

L – *Psilopilum laevigatum* (from Yakutia, Lower Lena River, Kyusyur, coll. Trufanova 31.VII.1976 SASY);

F – *Oligotrichum falcatum* (from Yakutia, Kamenka Island on Kolyma River, coll. Stepanova 22.VII.1975 SASY);

H – *Oligotrichum hercynicum* (Moscow Province, Ignatov 21.VII.1988, MHA).

Scale bars: 200 μm for C1, L1, F1, H1. 100 μm for C2, L2-4.

Table 2 Accession number of ITS1 sequence and vaucher information of specimens of *Oligotrichum hercynicum* and *O. falcatulum* used in the present analysis

O. falcatum Alaska	USA, Alaska, Seward Peninsula, Afonina 65-20-16314 (LE)(KRAS)	DQ333442
O. falcatum Bureya	Russia, Khabarovsk Territory, Bureya River, Ignatov 97-522 (MHA)	DQ333438
O. falcatum SE Yakutiya	Russia, Yakutiya, Ignatov 00-689 (MHA)	DQ333439
O. falcatum SW Yakutiya	Russia, Yakutiya, Udokan, Sofronova 12.VII.2002 (SASY)	DQ333440
O. falcatum Sayan	Russia, Krasnoyarsk Territory, Sayany, N.V. Stepanov, 17 VIII 2005	DQ333443
O. hercynicum Chukotka	Russia, Chukotka, Afonina 2.VII.1989 (LE)	DQ333436
O. hercynicum Kamchatka	Russia, Kamchatka, Czernyadjeva 1.IX.2001; #24 (LE)	DQ333445
O. hercynicum Kuzn-Alat.	Russia, Kuznetsky Ala-Tau, Pisarenko 00-707 (Novosibirsk)	DQ529252
O. hercynicum Kola	Russia, Murmansk Province, Khibiny, Likhachev 23.VIII.1994 (MHA)	DQ333444
O. hercynicum Caucasus	Russia, Krasnodar territory, Achishkho, Akatova 218-96 (MHA)	DQ529253

17.VIII.1976, Afonina (LE); *Ionii Mt.,* 10.VII.1977, Afonina (LE); *Il'mnejveem River*, 4.V1II.1978, Afonina (LE); *Anadyr River, Baranie Lake*, 24.VII.1980, 27.VII.1980, 2.VIII.1980, 6.VIII.1980, Afonina (LE); *Velikaya River,* 19.VIII.1983, Afonina (LE); *Palyavaam River,* 2.VII.1989, 19.VII.1989, 22.VII.1989, Afonina (LE).

Oligotrichum hercynicum (Hedw.) Lam. et DC., Fl. Franc. ed. 3, 2: 491. 1805. – *Polytrichum hercynicum* Hedw., Sp. Musc. Frond. 94. 1801.

Plants in loose tufts or growing as well-spaced individuals, bright to olive green, obtaining reddish pigmentation with age, especially in sunny habitats. Stem ascending to erect, in arctic and alpine regions 5-10 mm, in forest zone – 10-23 mm high, simple or rarely forking, densely to rather sparsely foliate, in larger plants often with thread-like lower part (up to 5-8 mm long), bearing very small leaves. Leaves when dry almost straight and appressed (in small plants), to incurved-appressed, or in less rigid plants from shady habitats strongly incurved to contorted (cf. Ignatov & Ignatova, 2003, Fig. 59), when wet – more or less spreading to erect-incurved; 1.7-3.0(-3.7)* x 0.5-1.2 mm, lanceolate from a weakly sheathing base without decurrencies; margins plane to more or less incurved, entire to distantly serrulate above or up to the base; costa ending below apex to percurrent, the dorsal leaf surface with (0-)2-4 lamellae on laminae and (1-)2-5 lamellae on costa, lamellae 1-4 cells high, more numerous above, extending downwards almost to the sheathing base. Ventral lamellae 8-12, 6-12 cell high, straight or more rarely undulate (restricted to the costa or one or two lamella situated on lamina close to costa), in transverse section with undifferentiated upper cell, on lateral view serrulate to serrate with blunt teeth and with few rather deep sinuses; median laminal cells isodiametric, 14-20 μm [14-16.5 μm in Arctic, 17-20 μm in Kamchatka], smaller towards margins, towards the base rectangular, 2-4:1. Dioicous [sporophytes rare, seen from Kola Peninsula, Karelia, Caucasus and Kamchatka]. Perigonial leaves broadly ovate, abruptly tapered to apex, widely spreading. Perichaetial leaves to 3.5 mm long. Seta 1-2(-2.5) cm, yellow-reddish, twisted above, rather thick. Capsule symmetric, straight to horizontal and pendent when mature, 2-4 mm long, 1.0-1.2 mm wide, cylindric to slightly angled and sometimes slightly contracted below mouth; stomata numerous; operculum conic or distally contracted into indistinct beak; peristome teeth about 32, finely papillose, pale brownish, contrasting with dark colour of urn. Spores 12-13 μm [mature spores seen and measured here only in Karelia, reported as 10-15 μm], mature in August. Calyptra with relatively sparse hairs.

Differentiation. Well developed plants of *O. hercynicum* have numerous and rather high lamellae and provide problems with differentiation from *O. aligerum (*occurs in Russia in Far East). The latter species is different in its larger size, leaf margin serrate to base (not or more strongly above), lower ventral lamellae (up to 9, not 12 cell high) and higher dorsal lamellae (often 3-4, not usually 1-2(-4)), and more narrow leaf without a differentiated sheathing base.

Ecology. It is an acidophilous species, growing often on bare soil as a pioneer, sometimes submerged in permanent and late pools. In the European North locally frequent along roads and trenches and in clear-cuttings, on sandy soil. In

* – Leaves are ranging from 1.7-2.3 mm long in Arctic to 2.0-3.0(-3.7) in forest zone (reported – up to 5 mm long).

the Arctic and alpine zone it occurs in various tundra communities, near late snow beds, among rocks on rocky slopes, cliff crevices, etc. In Kamchatka, it occurs on eroded slopes within the forest belt and also tundra, including nival communities, along brooks and on lake bars. It is commonly associated with *Polytrichum piliferum, Pogonatum dentatum, Pohlia crudoides* and *Leptobryum pyriforme.*

Distribution. Northen Europe, including Iceland, mountains [1500-3000 m] of Central and South Europe (southwards to Bulgaria and Italy), Turkey, Georgia, China (Xizang and Yunnan), Japan [2400-2900 m], Greenland [up to 2200 m], North America [up to 1700 m], Russia (see Fig 4 and specimen examined). Recently found as spreading southwards in Karelia (Bakalin, Maksimov, unpubl.), and recorded in Moscow Province in Central Russia in 1980s (Ignatov & Ignatova, 2003) which is obviously a result of recent introduction.

Specimens examined from Russia: **Murmansk Prov**. (selected): Lebyazhya River, 31.VII.1989, Czernyadjeva (LE); Pacha River, 5.VIII.1989, Czernyadjeva (LE); Polar-Alpine Botanical Garden, 18.VII.1947, Smirnova (LE); Malyj Vudjavr Lake, 23.VII.1930, Gaze (LE); Aikost River, 1981, Volkova (LE); Takhtarvymchorr Range, 23.VIII.1994, Likhachev (LE). **Karelian Republic:** Kostomuksha, 10.VIII.1997, Boichuk (LE); Kostomuksha, 21.VII.1998, Boichuk (PTZ); Latvozero, 10.VIII.1998, Boichuk (PTZ), Elmozero Lake, 24.VIII.2000, Maksimov & Maksimova (PTZ) S+; Lendery, 25.X.2003, Maksimov & Maksimova (PTZ); Tulos Lake, 20.VIII.2004, 7.VII.2005, Maksimov & Maksimova (PTZ), S+; Khiisjarvi Lake, 7.VII.2004, Maksimov, (PTZ). **Moscow Prov.** *Vysokovsk,* 21.VII.1988, Ignatov (MHA). **Krasnodar Territory Krasnodar Territory,** Western Caucasus, Achishkho Range, 2100 m alt., Akatova 218-96 (MHA)**; Karachaevo-Cherkesskaya Republic:** Teberda Reserve 1750 m, Ignatov & Ignatova 05-3437 (MHA); Teberda Reserve 2900 m, Ignatov & Ignatova 05-3912 (MHA); **Komi Republic:** North Urals, Subpolar Urals, Sablya Peak, 14.VII.1954 Gorchakovsky (LE); **Perm Prov.:** *North Urals, Vishera Reserve,* 3.VII.1998, Bezgodov (LE). **Tyumen Prov.:** *Polar Ural, Sob River*, VII.1988, Czernyadjeva (LE); *Puiva River,* 31.VIII.1950, Kildyushevsky (LE); *Lyapin River,* 11.VIII.1950, Kildyushevsky (LE). **Kemerovo Prov.**: *Kuznezky Alatau Range, Chernyj Iyus*, 1300 m alt., 20.VII.1998, Pisarenko, 00-707 (herbarium of Geobotany Dept. of Central Siberian Bot. Garden (Novosibirsk), LE, MHA, SASY). **Chukotskij Autonomous Distr.** *Provideniya Settlement* 8.VII.1992 & 23.VIII.2001, Afonina (LE); *Kresta Zalif*, 25.VII.1969 Afonina (LE); *Arakamchechen Island,* 20.VIII.1976 Afonina (LE); *Chigitun River,* 13.VIII.1991, Afonina (LE). **Kamchatskaya Prov.**: Koshelevsky Volcano, Czernyadjeva № 4S+,26,36,518 S+ (LE).

ACKNOWLEDGEMENTS

We are grateful to Olga Afonina for providing us some specimens for sequencing, to Elena Ignatova for preparing illustrations, and to David Long for revision of English of manuscript. This work was partly supported by RFBR grant 05-04-48780 and 03-04-48960.

LITERATURE CITED

BUDYAKOVA, A. A., M. S. IGNATOV, S. P. YATSENTYUK & A. V. TROITSKY 2003. Systematic position of Habrodon (Habrodontaceae, Musci) as inferred from nuclear ITS1 and ITS2 and chloroplast trnL intron and trnL-trnF spacer sequence data. – *Arctoa* 12: *137-150.*

[CZERNYADJEVA, I. V.] ЧЕРНЯДЬЕВА, И. В. 2003. Род Hygrohypnum (Amblystegiaceae, Musci) в России. – [The genus Hygrohypnum (Amblystegiaceae, Musci) in Russia] *Arctoa* 12: *25-58.*

[CZERNYADJEVA, I. V.] ЧЕРНЯДЬЕВА, И. В. 2005. О находке редкого листостебельного мха Oligotrichum aligerum (Polytrichaceae) на полуострове Камчатка. – [On the record of the rare moss Oligotrichum aligerum (Polytrichaceae) on Kamchatka Pensinsula] Бот. журн. [Bot. Zhurn.] 90(1): *60-63*.

FRAHM, J.-P. & K. MьLLER 2000. The taxonomic status of Eurhynchium crassinervium from river banks based on ITS sequence data. – *J. Bryol.* 22: 291-292.

[IGNATOV, M.S. & E.A. IGNATOVA] ИГНАТОВ М, С., Е. А. ИГНАТОВА 2003-2004. Флора мхов средней части Европейской России. – [Bryophyte flora of Middle Part of European Russia]. КМК, *M.* [*Moskva*], *960.*

LONG, D.1985. Oligotrichum. – *Meddelelser om Gronland, Bioscience*. 17: 15-19.

[SAVICZ-LYUBITSKAYA, L.I. & Z.N. SNIRNOVA] САВИЧ-ЛЮБИЦКАЯ, Л.И., З.Н. СМИРНОВА. 1970. Определитель листостебельных мхов СССР. Верхоплодные мхи. – [The Handbook of mossesof the USSR. The acrocarpous mosses] *Л., Наука* [*Leningrad, Nauka*], *826 pp.*

SMITH MERILL, G. L. 2005. Oligotrichum. – *Bryophyte Flora of North America, Provisional Publication, Missouri Botanical Garden:* http://www.mobot.org/plantscience/BFNA/bfnamenu.htm.

STECH, M. & J.-P. FRAHM 1999. The status of *Platyhypnidium mutatum* Ochyra & Vanderpoorten and the systematic value of the Donrichardsiaceae based on molecular data. – *J. Bryol.* 21: 191-195.

STEERE, W. C. 1958. Oligotrichum falcatum, a new species from Arctic Alaska. – *Bryologist* 61: *115-118.*

STEERE, W. C. 1978. The mosses of Arctic Alaska. – *Bryoph. Bibl.* 14: *1-508.*

STEERE, W. C. & G. L. SMITH 1976. The sporophyte of Oligotrichum falcatum. – *Bryologist* 79: *447-451.*