INTEGRATIVE TAXONOMIC REVISION OF THE GENUS CAMPYLOPUS
(LEUCOBRYACEAE, BRYOPHYTA) IN RUSSIA

РЕВИЗИЯ РОДА CAMPYLOPUS (LEUCOBRYACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus Campylopus in Russia is revisited based on molecular phylogenetic data, which included also European accessions originated from vicinities of the loci classici of several species. Eight species are proved to occur in Russia, among which C. schimperi is widespread in montane areas throughout the country, while other species are known from few localities in Kamchatka (5 species), southern part of Russian Far East (3 species), Caucasus (3 species) and Kaliningrad Province (1-3 species). Nuclear ITS allowed a reasonable delimitation of C. schimperi and C. subulatus; previously known differences in their morphology, ecology and distribution are confirmed. Molecular phylogenetic reconstruction, based on combined plastid trnS-trnF, mitochondrial Nad5 and nuclear ITS suggests that the genus Campylopus harbours at least three well morphologically and phylogenetically justified lineages, which could be considered as separate genera to prevent assigning Pilopogon to synonymy of Campylopus.

KEYWORDS: biodiversity, bryophytes, DNA-barcoding, integrative taxonomy, rare species, phyto-geography

INTRODUCTION

With ca. 175 accepted species, the genus Campylopus Brid. is one of the largest genera of Dicraniidae. General distribution of the genus stratches from Svalbard to continental Antarctic; at the same time, most representatives of the genus avoid xeric climatic conditions and concentrate in mild oceanic climates. The genus harbours C. introflexus (Hedw.) Brid., one of the “worst-known” invader moss species, spreading along roads, sandy seashores and otherwise disturbed ecotopes, and also a suite of thermophilous mosses which occur in the areas with high volcanic activity around geisers, hot springs, etc.

Although the genus was a subject of the lifetime interest of Jan-Peter Frahm, its very complex taxonomy remains insufficiently understood; due to characteristically high morphological variability, different treatments provide somewhat controversial morphological circum- scriptions even for the rather well known Holarctic species (cf. Smith, 2004; Frahm, 2007; Lüth, 2019, etc.). At the same time, phylogenetic studies dealing with the genus (Stech, 2004; Stech et al., 2010; Spagnuolo et al., 2014; Gama et al., 2016, 2017) are few and based on
very limited sampling, which does not include even all Campylopus species known from the Holarctic. Therefore, we decided to implement an integrative approach to the taxonomic treatment of Campylopus for the ongoing volume of the Moss flora of Russia, i.e. by involving molecular phylogenetic study.

According to the Check-list of mosses … (Ignatov et al., 2006), eight species of the genus Campylopus occur in Russia; two of them are known only from Kaliningrad Province, three only in the Russian Far East, and three have a wider distribution in mountain areas of the country. Another species, C. gracilis (Mitt.) A. Jaeger, was recorded for the neighbouring country of Ukraine. Recently the latter species with a predominantly European distribution was collected on Badzhal Mountains, Middle part of Khabarovsk Territory, ca. 200 km northward Khabarovsk City (Pisarenko et al., 2022). However, that did not seem impossible since its scattered localities were known from the Sino-Himalaya region and Pacific coast of North America. On the other hand, the identity of Russian records of C. atrovirens De Not. seemed dubious, since in Europe, where from it was described, it typically has a peculiar blackish coloration, which does not occur in plants from Kamchatka and the Caucasus. A report of tropical C. umbellatus (Arn.) Paris from thermal habitats of south Kamchatka (Ignatov & Samkova, 2006) was based solely on morphology, which may be very deceitful in Campylopus. Many samples from various regions of Russia referred to C. subulatus Schimp. ex Milde and largely corresponding to this species morphologically, had very dense and solid tomentose tufts, which contradicts the description of this species; however, in several cases ribbed dorsal costal surface did not allow immediate referring of these collections to C. schimperi Milde (for details of the differences between these two species see Frahm & Vitt, 1978). On the other hand, Asian plants assigned to C. pyriformis (Schultz) Brid. differed from those from North America and Europe in having shorter leaf cells and thus also could be problematic in distinguishing from the plants of C. schimperi – C. subulatus affinity. So the aim of the present study was to clarify the species identity in dubious cases. Finally, we had an opportunity to check morphological characters suggested by Frahm & Vitt (1978) for species delimitation within the C. schimperi – C. subulatus complex using molecular data.

MATERIALS AND METHODS

For molecular phylogenetic study nuclear ITS1,2 & 5.8 rRNA gene, which is rather well represented in GenBank for Campylopus, was added by plastid trnS-F region, where two usually used and thus also well represented in GenBank plastid markers, trnL-F and rps4 belong to, and by mitochondrial Nad5, often used for resolving backbone phylogeny of Dicranids. The ingroup of the molecular phylogenetic dataset included a selection of Campylopus species known to occur in Russia, added with few accessions for which at least (fragments of) two markers are presented in GenBank. For each species a selection of specimens including Russian and, where needed, also European samples representing proxies to the type, were studied. Since species assignments of many sequences in GenBank often are not correct, we used quite a limited number of GenBank accessions, which correspond to our data. For the ITS based analysis we involved broader selection of the GenBank accessions of the genus.

A set of outgroups, representing other lineages of Leucobryaceae was included based on data from GenBank; two accessions of Archidium Brid. were used for rooting the tree according to Bonfim-Santos & Stech (2017). ITS-based tree was rooted on the Brothera leana (Sull.) Müll. Hal. clade since ITS sequence of Archidium are not available and probably would not be possible to align with Leucobryaceae certainly.

The laboratory protocol was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner et al. (2005), Fedosov et al. (2016) and Ignatov et al. (2020). Sequences were aligned using MAFFT v. 7.402 (Katoh & Standley, 2013) with standard settings and then edited manually in BioEdit (Hall, 1999). In trnS-trnF region and Nad5 gene indels were coded using simple indel coding approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1 (Müller, 2005), while quality of the ITS alignment was considered not reliable enough for indel coding. Since the ingroup topologies inferred from the nuclear (91 terminals, 1669 positions) and organellar (46 terminals, 3020 positions) data did not conflict, a combined dataset (47 accessions, 4689 positions) with 95 indels coded in organellar markers was analyzed. While compiling combined dataset, we included mostly those specimens for which all-three or at least two of three markers were available. In cases when the species/group was represented by organellar markers from one specimen/species and ITS from the other, we included only organellar data.

Bayesian analyses were performed by running two parallel analyses in MrBayes 3.2.7a (Ronquist et al., 2012). For the single gene sets analyses each run consisted of six Markov chains, 5 000 000 generations with sampling frequency one tree each 1000 generations. For the combined dataset the analysis consisted of eight Markov chains and 5 000 000 generations, with the default number of swaps and sampling frequency one tree each 1 000 generations was performed. The chain temperature was set at 0.02 in all analyses and GTR model with sampling throughout the model space (setting nst = mixed) was used in all analyses. Convergence of analyses was assessed via ESS values, checked using Tracer v.1.7.2. (Rambaut et al., 2018) to be higher than 200. Average deviation of split frequencies in all analyses excepting Nad5 reached 0.01 after 0.5 – 0.6 mln generations. Consensus trees were calculated after omitting the first 25% trees as burn-in. Molecular phylogenetic study
The genus Campylopus in Russia

Fig. 1. Bayesian tree of the genus Campylopus inferred from the nuclear ITS sequences
was supplemented by the revision of *Campylopus* collections in MW, MHA and L.E.

**RESULTS**

All the trees inferred from the single-gene analyses (ITS, *trn*S-F and Nad5) are well resolved and supported. Moreover, the topologies of all-three are very close and insufficient differences largely originate from different composition of the involved terminals. In the trees inferred from plastid *trn*S-F and mitochondrial Nad5, where larger set of outgroups was included, accessions of *Campylopus* formed a maximally supported clade sister to the clade composed of all other members of Leucobryaceae included in the analyses, except accessions of the genus *Pilopogon* Brid. and *Bryohumbertia subcomosa* (Dixon) J.-P. Frahm, which in both analyses were found nested in the *Campylopus*-clade. Likewise, the *Campylopus*-clade in the ITS-based tree comprises a nested *Pilopogon*-clade (Fig. 1). The topologies of the *Campylopus* clade in all three analyses also largely agree. At the first node the maximally supported clade composed of *C. brevipilus* splits. The next node represents a bifurcation of two major clades. First of these two includes GenBank accessions of *Pilopogon* forming a clade or grade crowned by grouping of originally studied accessions of three *Campylopus* species, *C. gracilis*, *C. subulatus* and *C. schimperi*. This clade is unresolved in the trees inferred from organellar markers and well resolved in the nr ITS based tree, where three clades corresponding to individual species appear (Fig. 1). The second major clade comprises all remaining *Campylopus* species included in the analysis and two accessions of *Bryohumbertia subcomosa*. Noteworthy, in the ITS-based tree the subclades formed by GenBank accessions of *C. subulatus* and *C. gracilis* fall in the second clade, although the originally studied European and Russian specimens of these species are in the third major clade (Fig. 1).
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The topology of the tree inferred from the concatenated combined dataset (Fig. 2) repeats the topologies of a single gene trees, demonstrating a fair support of the deep nodes. Within the *Campylopus* s.l. clade, three well supported clades corresponding to (1) “*Campylopus* 1” clade (*C. brevipilus*); (2) *Pilopogon* clade composed of two GenBank accessions, of *P. africanus* and *P. gracilis* plus “*Campylopus* 2” clade, which accommodates originally studied accessions of *C. gracilis*, *C. schimperi* and *C. subulatus*; (3) “*Campylopus* 3” clade composed of the accessions of *C. introflexus*, *C. umbellatus*, *C. atrovires*, *Bryohumbertia subcomosa*, *C. pyriformis*, *C. fragilis*, and *C. flexuosus*.

Noteworthy, nuclear ITS1,2 & 5.8 rRNA gene, which is very long and extremely variable in *Campylopus*, provides a sufficient signal for species delimitation within each of three major clades of *Campylopus* (thus, clades corresponding to particular species, including *C. schimperi*, *C. subulatus* and *C. gracilis*, are well supported), but is hard to align between specimens from different major clades.

**DISCUSSION**

The topologies of the obtained trees suggest a following inferences: (1) *Campylopus schimperi* and *C. subulatus* segregated by morphology according to Frahm & Vitt (1978) can be considered as separate species (following the topology inferred from ITS), although organelar markers do not support the delimitation of these two; (2) we confirm the identity of the eight GenBank accessions, of *P. africanus* and *P. gracilis* plus “*Campylopus* 2” clade, which accommodates originally studied accessions of *C. gracilis*, *C. schimperi* and *C. subulatus*; (3) “*Campylopus* 3” clade composed of the accessions of *C. introflexus*, *C. umbellatus*, *C. atrovires*, *Bryohumbertia subcomosa*, *C. pyriformis*, *C. fragilis*, and *C. flexuosus*.

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AY540859, AY373978 & AY373985, found in the ‘‘Campylopus 3’’ clade), since they definitely represent other species which might need an attention.

**TAXONOMIC TREATMENT**

*Campylopus* Brid., Muscol. Recent. Suppl. 4: 71.

Plants in loose to dense, green or brownish tufts or cushions. Stems (1–)2–4–(6.5) cm, simple or forked, not tomentose or with brownish tomentum, with weak or very strong central strand and scleroderms, in species with weak scleroderms the stem section is composed of thin-walled parenchymatose cells. *Leaves* 3–8 mm long, appressed when dry, spreading when wet, linear lanceolate to nearly subulate; *costa* strong, filling (1/3–) 2/5–3/4 the leaf base, excurrent as chlorophylllose or hyaline mucro, smooth or denticulate above, in transverse section with guide cells usually adjacent to the adaxial layer of hyalocysts, extensive dorsal band of substereids or stereids, on dorsal side smooth or ribbed due to projecting cells; upper and median *laminal cells* thick-walled, short rectangular, rounded, rhomboid or vermicular; basal leaf cells elongate-rectangular, thin-walled, hyaline, or subquadrate, irregularly elongate or rectangular, thick-walled, concolorous with median laminal cells, along margins often narrower, forming a distinct border; alar cells large, inflated, or scarcely differentiated. *Specialized asexual reproduction* by decidual leaves or stem tips [other types not seen in collections from Russia]. *Capsules Dioicous. Perichaetial leaves* with sheathing base. *Setae* 7–13 mm, [arcuate when young]. *Capsules* weakly asymmetric, furrowed when empty; annulus weakly developed; operculum rostrate; peristome dihidian. *Spores* small. *Calyptra* cucullate.

**KEY TO IDENTIFICATION SPECIES OF THE GENUS CAMPYLOPUS FROM FLORA OF RUSSIA:**

1. *Leaves with hyaline hair points* .................................. 2
   - *Leaves with concolorous point* .................................. 3
2. *Hyaline hairpoints upward directed, leaf apex often cucullate; laminal cells in basal leaf portion subquadrate, cells in distal portion of leaf lamina elongate, alar region weakly differentiated* .... 1. *C. atrovirens*
   - *Hyaline hairpoints reflexed, leaf apex not cucullate; laminal cells in basal leaf portion laminal cells in basal leaf portion elongate, subquadrate, cells in distal portion of leaf lamina rounded, alar region strongly differentiated* ............. 2. *C. introflexus*
3. *Leaves ovate-lanceolate; transverse section of costa with dorsal and ventral stereid bands; exclusively in thermal habitats* ............. 3. *C. umbellatus*
   - *Leaves lanceolate to linear-lanceolate, rarely ovate lanceolate (but then the plants are alpine); ventral side of costa is formed by hyalocysts/guide cells* .. 4
4. *Dorsal side of costae is formed by stereids with strongly incrassate walls* .................................. 5
   - *Dorsal side of costae is formed by substereids with weakly to moderately incrassate cell walls* .......... 6
5. *Leaves widest at 1/3–1/4 of a leaf length, gradually narrowed to insertion; cells at base of leaf lamina elongate-rectangular, thin-walled, sharply delimited from the subquadrate median laminal cells* .......................................................... 4. *C. fragilis*
   - *Leaves widest at a leaf base, gradually narrowed distally; cells at base of leaf lamina subquadrate, gradually or rather sharply becoming longer and narrower distally ........................................ [C. flexuosus]
6. *Costae very wide, occupying ca. 3/4 of the leaf base width; alar cells remarkably differentiated, forming inflated group, projecting into costa* .. 5. *C. gracilis*
   - *Costae narrower, rarely reaching 3/4 of the leaf base width; alar weakly differentiated, not inflated* ...... 7
   - *Lowland plants forming loose not tomentose tufts* ...................... 8. *C. subulatus*

*Campylopus atrovirens* De Not., Syllab. Musc. 221. 1838.

*Plants* in compact pure tufts, blackish proximally, dirty-olivaceous distally. *Stems* 1.5–3 cm, simple or forked. *Leaves* 3–5(-6)×0.45–0.6 mm, straight, narrow lanceolate, ending in a denticate hyaline hair-point to 0.5 mm long, composed of thick-walled cells; *costa* filling 1/3–2/3 the leaf base width, in transverse section with ventral hyalocysts of the same height as following guide cells, and dorsal stereids, weakly ribbed on dorsal surface; distal and median *laminal cells* 25–33×5–8 μm, elongate to vermicular, with incrassate walls, basal laminal cells 20–45×12–20 μm, short rectangular to subquadrate, gradually becoming rhomboid upward, moderately thick-walled, along margins in 3–4 rows narrower, not forming a distinct border; alar cells scarcely to moderately differentiated, composed of weakly inflated, moderately thick-walled cells, hyaline or brown. *Specialized asexual reproduction* by fragile stem tips. *Sporophytes* unknown in Russia.

**Differentiation.** Typical, well developed *C. atrovirens* is a large (up to 10 cm) black plant growing near cold springs and waterfalls. However, Russian specimens, both from the Caucasus and Kamchatka, are remarkably smaller and have dirty olivaceous coloration. At the same time, they are distinguished from all other Russian species of *Campylopus* due to the presence of straight hyaline hair points. According to Frahm (2007), leaves of *C. atrovirens* occasionally may lack hyaline hair points. In such cases, this species can be recognized by having leaves with cucullate apices and long, vermicular upper laminal cells.

**Distribution and ecology.** *Campylopus atrovirens* has predominantly Holarctic, amphioceanic distribution. It
occurs throughout UK, in south-western Scandinavia, mountains of Central and Western Europe, an isolated locality in the Caucasus, in Kamchatka Peninsula (Fig. 9) and Japan, in Labrador, Newfoundland, and Appalachian Mts in North Carolina, along the western coast of North America, from Washington to Alaska, and in a few localities in the middle Aleutians. Russian localities of the species are remarkably distant from the closest areas where the species grows and originate from the areas with volcanogenic ecotopes. In the Caucasus it was collected in lava fields of Elbrus Mt. in Kabardino-Balkaria, in Kamchatka in the thermal fields near Pauzhetskaya Settlement (south of the peninsula).

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Distr., Pauzhetska Settl. vicinity, Eastern Pauzhetskoe thermal field, Samkova 3 (MHA9011779).


This species was found in Russia for the first time in Kaliningrad Province by Razgulyaeva et al. (2001) who described and illustrated these specimens; it was also discussed by Dolnik & Napreenko (2007). It is currently known from three localities on Kuronian Spit. Although the climate warming promoted a remarkable

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*Fig. 4. Campylopus fragilis* (from: Russia, Republic of Kabardino-Balkaria, Ignatov, Ignatova & Kharzinov s.n., MHA9011782). A: habit, dry; B: upper leaf cells; C–E: leaves; F: cells at leaf shoulder; G: basal leaf cells; H–J: leaf transverse sections. Scale bars: 2 mm for A; 1 mm for C–E; 200 μm for G; 100 μm for B, F, H–J.
range extent of several western species eastwards, no additional reports of this invasive species from Russia have appeared since that time, so we do not consider it here in more details.


This tropical species was revealed in Russia in three localities on thermal fields in the south of Kamchatka, in Pauzhetka settlement surroundings (Ignatova & Samkova, 2006); these specimens were described and illustrated in this paper, so we do not consider this species here in more details, except the note that our DNA data confirm the species identification, at least, our sequences of nuclear ITS region form a clade with GenBank sequence AF444130 assigned to *C. umbellatus* and our trnSF sequences form a clade with the GenBank sequences AF226764 (rps4) and AF231171, assigned to the same species.

**Campylopus fragilis** (Brid.) Bruch & Schimp., Bryol. Eur. 1: 164 (fasc. 41. Monogr. 4). 1847. — *Dicranum fragilis* Brid., J. Bot. (Schrader) 1800(2): 296. 1801.  Fig. 4.

*Plants* in loose tufts, green above, yellowish below. **Stems** 0.5–1 cm, simple, densely foliate. **Leaves** 4–5×0.45–0.55 mm, ovate-lanceolate, widest at 1/4 of their length and shallowly narrowed toward insertion, narrowed into long, concolorous subula; **costa** filling 1/2–2/3 of leaf width, short excurrent, slightly serrate at tip, in transverse section with very high ventral hyalocysts, filling half of the costa height, guide cells and dorsal stereids, regularly ribbed on dorsal surface due to protruding cells; distal and median laminal cells 10–28×5–10 μm, quadrate or rhomboidal, thick-walled, sharply differentiated from hyaline, translucent rectangular basal laminal cells; basal laminal cells 50–90(–160)×13–20 μm; alar cells not differentiated, basal marginal cells narrower, in transition zone form rather well differentiated border. **Specialized asexual reproduction** and sporophytes unknown in Russia.

**Differetiation.** *Campylopus fragilis* differs from most other Russian species of the genus in possessing well developed stereids in transverse section of the costa. Although as much as five species in the key above have this trait, *D. fragilis* is distinguished from most of them by the lack of hyaline hair point, lack of ventral stereids and leaves widest well above the insertion. According to Ignatov et al. (2006), in Russia *C. fragilis* occurs in the Caucasus, southern Siberia and the southern part of Far East. However, most specimens referred to this species were reidentified as *C. schimperi* or *C. subulatus*, excepting the specimen from Kabardino-Balkaria, which suits well to *S. fragilis* morphologically and which identity was proved by DNA sequencing. Among the other characteristic traits of *C. fragilis*, asexual reproduction by small leaves in upper leaf axils was not seen in the specimen from Russia. The transverse section of costa in this species shows very high adaxial hyalocysts, occupying ca. half of its height.

**Distribution and ecology.** *Campylopus fragilis* has a wide, disjunctive distribution in the areas with rather warm oceanic climate, which, however, might need a revision. In Holarctic it occurs throughout Western and Central Europe, UK and Macaronesia, southern part of Scandinavia, but do not occur or is very rare in East Europe and xeric Mediterranean areas. According to Frahm (2007), in North America it occurs only in two areas: British Columbia in Canada, and Arkansas in the USA. A single Russian collection from the Caucasus is the easternmost in Europe (Fig. 9); the species might be expected also in warm and wet coastal areas of the Black Sea around Sochi and also in Teberda Nature Park (Karachaevo-Cherkessia), but has not been so far revealed there despite the extensive moss collecting in both areas.

**Specimens examined.** RUSSIA: Republic of Kabardino-Balkaria, Bezengi Mountain area, Cherek Bezengiysky River valley 1 km upstream Dumala Creek mouth, ca. 1650 m alt., 31 Aug 2004, Ignatov, Ignatova & Kharzinov s.n. (MHA9011782).


This species was mentioned to occur in the Kaliningrad Province of Russia by Ignatov et al. (2006) based on the data by Napreenko (unpublished). Actually, this species was recorded by Groß (1914) from wetlands around the raised bog on the Kuronian spit, but it was not collected later (Dolnik & Napreenko, 2007). World distribution of this species resembles that of *C. fragilis*; it can occur in Kaliningrad Province of Russia. An easternmost European locality of *C. flexuosus* is in Poland (Hodgetts & Lochart, 2020).


*Plants* in loose tufts, light green, glossy. **Stems** 1–2 cm, forked. **Leaves** (4–)5–7×0.35–0.5 mm, erect when wet, appressed when dry, narrowly lanceolate, ending in a very long, slightly flexuose, concolorous, serrate subula; **costa** very broad, occupying 3/4–4/5 of leaf width, long-excurrent, in transverse section with ventral hyalocysts of the same size as following guide cells and somewhat smaller substereids forming massive band on a dorsal side, with dorsal surface ribbed due to protruding cells; distal and median laminal cells 20–37×6–8 μm, rectangular or elongate-rhomboidal, with oblique transverse walls, basal laminal cells 30–55×8–15 μm, rectangular, hyaline and translucent, along margins well differentiated, narrower, forming a border extending to mid-leaf; alar cells sharply hyaline, thin-walled, forming inflated
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**Fig. 5.** *Campylopus gracilis* (from: Russia, Khabarovsk Territory, Fedosov & Pisrenko, MW9130218). A: habit, dry; B–C: leaf transverse sections; D: mid-leaf cells; E: upper leaf cells; F–H: leaves; I: basal leaf cells. Scale bars: 5 mm for A; 1 mm for F–H; 100 μm for B–E, I.

Group, projecting into the costa; basal laminal cells hyaline, thin-walled, long-rectangular. *Specialized asexual reproduction* unknown. *Sporophytes* not seen in collections from Russia.

**Differentiation.** In having combination of a very broad costa bearing substereids with longitudinal ribs on dorsal side and short cells in upper portion of the leaf lamina, *C. gracilis* can resemble the only one another Rus-
sian *Campylopus, C. subulatus*. Although in most manuals *C. subulatus* is treated as having costa that occupies a half of the leaf base width, this character is very variable, and plants with broader costae may occur; moreover, basal laminal cells in *C. subulatus* usually are hyaline, not forming well delimited, inflated alar groups, but, according to Frahm & Vitt (1978), this species possesses well-differentiated group, composed of reddish-brown, inflated alar cell. However, a combination of very wide costa and inflated hyaline alar group projecting into the costa occurs only in *C. gracilis*. One more remarkable trait of this species is a rather well differentiated narrow cells, forming a border in a basal leaf portion.

**Distribution and ecology.** *Campylopus gracilis* is an oceanic species with a disjunctive distribution, largely associated with western coasts of Eurasia (UK, southwestern part of Norway, the Alps) and North America (British Columbia). In addition, this species occurs in Asia: in China and neighbouring areas of Sino-Himalayan Region within Nepal, India, Myanmar and Thailand. A single Russian collection originates from the middle part of Khabarovsk Territory (Fig. 9), where the species was found in subalpine belt at elevation of about 1500 m, on humus in cliff crevice (for details see Pisarenko et al., 2022). DNA-barcoding supports an identification based on morphology, although an Asian specimen has somewhat different sequences from the European ones.

**Specimens examined:** Russia, Khabarovsk Territory. Badzhal Mountains in the Yarap River middle course, 4 Aug 2016, Fedosov (MW9130218).

Fig. 6.

Plants in compact tufts, yellowish-green above, brownish-tomentose below. **Stems** 0.5–3 cm, simple or
repeatedly branched. Leaves (1.3–)2.2–3.5(–5.0)×0.3–0.4 mm, appressed, from an ovate-lanceolate base gradually narrowed to short acuminate, straight, concolorous subula; costa filling 1/2, rarer up to 2/3 of leaf width, short excurrent, in transverse section with large ventral halyocysts, somewhat smaller guide cells and large group of substereids, usually with rhomboid lumens, forming dorsal side of costa, almost smooth to distinctly ribbed at dorsal surface; upper and median laminal cells 10–32×5–7 μm, chlorophyllose, elongate-rectangular, rarely short-rectangular or elongate, thick-walled; basal laminal cells 45–80×8–16 μm, thin-walled, hyaline and translucent, rectangular, along margins well differentiated, narrower; alar cells not or weakly differentiated, wider and shorter. Specialized asexual reproduction not found in Russia. Sporophytes unknown in Russia.

**Differentiation.** Campylopus schimperi differs from the other species of the genus in growing in dense, tomentose tufts, having leaves with rather narrow costa (1/2 of the leaf base width or a little broader) with substereids forming its dorsal side, thin-walled rectangular basal laminal cells, not or weakly differentiated alar cells, and elongate-rectangular medium and upper laminal cells. Differentiation of this species from the closely related *C. subulatus* is considered in details by Frahm and Vitt (1978) based on American and European specimens. Our molecular-phylogenetic study largely confirmed the distinctiveness of *C. subulatus* and *C. schimperi* based on this treatment. However, several traits suggested by these authors as useful, do not work in specimens from Asia. For instance, several Asian specimens of *C. schimperi* have well developed ridges on dorsal side of costa. On the other hand, cells in upper part of leaf lamina may be rather short in several, mostly Far Eastern specimens of *C. schimperi*, and the values of cell length/width ratio overlap those of *C. subulatus*, although general trend is the same: in *C. schimperi* upper laminal cells are elongate, with the width/length ratio ca. (1/2.5–)1/3–1/4, while in *C. subulatus* they are generally shorter, with the width/length ratio 1/1.5–2/5(–1/3). Likewise, the width of laminal cells which was found rather suggestive for the delimitation of *C. schimperi* by Frahm & Vitt (1978), in several cases does not work for Far Eastern plants, although in most Caucasian and Siberian plants of *C. schimperi* upper laminal cells are indeed narrower than 6 μm. In such cases, additional traits, such as longer leaves with stronger denticulate acumina in *C. subulatus* vs. shorter leaves with weakly denticulate ones in *C. schimperi* can be used. The most useful trait for their distinguishing in Asia is the growth in dense, tomentose tufts, characteristic for *C. schimperi* vs. loose tufts and shoots with scarce rhizoids of *C. subulatus*. Also, these species differ in their ecology and distribution. *C. schimperi* occurs in the mountains nearly throughout Russia, while *C. subulatus* is a thermophylic species, which occurs only in the Russian Far East, in thermal habitats of Kamchatka Peninsula and at lower elevations in the southern part of Primorsky Territory (however, in the southern Kuril Islands *C. schimperi* occurs along seashores instead of *C. subulatus*).

**Distribution and ecology.** Campylopus schimperi was described from Europe, where it occurs in montane areas of UK, Iceland, Scandinavia, the Alps, Tatras and Pyrenees. In the genus Campylopus it presents an outstanding example of circumpolar distribution in Holarctic. Unlike all other species of the genus, *C. schimperi* occurs in most continental mountain regions of North Asia, including quite xeric Transbaikalia and Suntar-Khayata in Yakutia (Fig. 9); however, it apparently absent in Karelia, Kola Peninsula and the Ural Mts. Although in most areas it is rare, it may be quite abundant in suitable places (e.g., in the locality on Putorana Plateau); in some areas, e.g. in Teberda Nature Park in the Caucasus and in Transbaikalia it is apparently a frequent species. Campylopus schimperi occurs from low to high elevations on soil in mountain tundra and heaths, among rock outcrops; it also colonizes a disturbed or non-durable ecotopes like bare ground along roads (Transbaikalia) or silty alluvium at lake shores (Putorana Plateau). North American distribution of the species mapped by Frahm and Vitt (1978) largely agrees with our data, although most records are spread along the coastal areas, most of them are concentrated between 60° and 70° parallels, e.g., on the northern slope of Brooks Range in Alaska or Baffin Island, in cool and xeric environments, while in North Asia the species is more frequent in mountains of South Siberia southwards of 60th parallel.

**Specimens examined.** RUSSIA: CAUCASUS: Adygeya Republic: Maykop Dist., Belaya River basin, Abago Mt. northern slope, ca. 2200 m alt., 25 June 1999 Akatov (MHA); the same area, Armyskany Range, 2020 m alt., 16 Aug 1999, Akitova (MHA); Pshekhish Range, 2200 m alt., 23 July 1992 Akatov (MHA), same place, 2100 m alt., 01 Aug 1999 Eskin (MHA).

**Karakach-Cherkess Republic:** MaloKarakhaevsky Dist., Hudes River upper course, 2400 m alt., 22 Sept 2002 Onipchenko 38/02 (MW9027918); the same area, Tokhana Gorge, 2450 m alt., 31 Sept 2002 Onipchenko 30/02 (MW9027921); Zelenchu River basin, Pastukhova Mt., 2300 m alt., 27 Aug 1999, Korotkov (MW9027919); Daut Sanctuary, Ephik, 3040 m alt., 10 July 1995, Onipchenko 31/95 (MW9027937); the same place, 3010 m alt., 22 Aug 2009, Onipchenko & Ezhelev (MW9027922); Teberdinsky State Reserve, Kyskhadzher, 3370 m alt., 10 Aug 1995 Zenyakin (MW9027934); Malaya Khati-para Mt., 3100 m alt., 29 July 2001 Onipchenko 1/01 (MW9027926); same place, 2750 m alt., Onipchenko 84/95 (MW9027935); 2900 m alt., 22 Aug 1993 Onipchenko 75/93 (MW9027924); Baduk, 2660 m alt., 31 July 1996, Egorov 53/96 (MW9027933); Musa-Achitara Mt., 3150 m alt., Ignatov & Ignatova 05-3636 (MW9027928); Gonachhir River valley near Kluchor Creek Mouth, Ignatov & Ignatova 05-1107 (MW9027929); Ariuchat Gorge, Goro, 2000 m alt., 6 Sept 1994 Onipchenko 163/94 (MW9027936); same place, 2850 m alt., 3 Sept 1998, Onipchenko 27/98 (MW9027930); Ullo-Murudzhu River valley, Goluboe Lake, 2900 m alt., Ignatov & Ignatova 05-3911 (MW9027927); Nazalykol Gorge, Goro, 2700 m alt., 4 July 1998 Volkov & Zenyakin z-53 (MW9027932), same place, 2430 m
alt., 5 Aug 1998, Volkov & Ženyakin z-55 (MW9027931); same place, 2750 m alt., 24 Aug 1996, Egorov 153/96 (MW9027925); watershed of Hasaut and Eshkakon Rivers, 2305 m alt., 13 July 2010 Ukrainskaya 14658 (LE); Kabardino-Balkarian Republic: Adyl-Su River valley, near its mouth, 1700 m alt., 27 July 2004 Ignatov, Ignatova & Kharzinov (MHA); Baksan River valley near Adyl-Su River mouth, 1700 m alt., 30 July 2004 Ignatov, Ignatova & Kharzinov (MHA); Elbrus, 15 Aug 1993 Ukrainskaya (LE); Ingushetia: Tersky Range, 600 m alt., on soil, 29 June 2004 Bersanova (MHA).

ASIAN RUSSIA: Altai Republic; Chulyshman Upland, Kayakkatuyarykskij Creek (Chulcha River Tributary), subalpine belt, 2100 m alt., 28 June 1991 Ignatov 4/16 & 4/6 (MHA); Kosh-Agach Distr., Severo-Chuyksky Ridge northern spurs, Baksara Creek basin, 2200 m alt., on dry rocks, 27 June 2008 Seregin & Seregin 2-2102 (MW9027938); Bashkau River, in upper course, 25 July 1993 Ignatov (MHA). Krasnoyarsk Territory, Taimyr District, Pur-torana Plateau, Lama Lake Lama Lake shore near Vekhikay Creek mouth, 45 m alt., 12 July 2016 Fedosov 16-0080, 16-0081 (MW9079030, 9079031); Zabaikalsky Territory: 20 km northward Achinsk, 04 July 1988 Bardunov (LE); Borzinsky District, Kulubey Range, 5 km NW of Perednyaya Byrka settlement, 880 m alt., 28 July 2012 Czernyadjeva 34-12 (LE); Kyrinsky Distr., Sokhondinsky Reserve, Ingoda River basin, 1413 m alt., 18 July 2013 Czernyadjeva 44-13 (LE); upper course of Ingoda River, 1178 m alt., 21 July 2013 Afonina 6313 (LE); Agutsa River basin, 1120 m alt., 21 July 2013 Czernyadjeva 47-13 (LE); the same area, 1098 m alt., 18 July 2010 Afonina A3610 (LE); the same place, 1126 m alt., 19 July 2010 Afonina A3910 (LE); the same place, 1100 m alt., 23 July 2010 Afonina A3910 (LE); Larionov Kluch, 1364 m alt., 13 July 2013 Afonina A4113 (LE); Upper Bukukan River, Tsagan-Ula Mt., 1747 m alt., 19 Aug 2011 Afonina A4911 (LE); the same place, 2138 m alt., 22 July 2008 Afonina 7008 (LE); the same area, 1884 m alt., 19 Aug 2011 Czernyadjeva 31-11 (LE); the same place, 2060 m alt., 19 Aug 2011 Czernyadjeva 36-11 (LE); the same area, 2000 m alt., 19 Aug 2011, Czernyadjeva 32-11 (LE).

Yakutia: Oymyakonsky Distr., Suntar-Khayat Range, Mus-
Khaya Mt., Knoriy Creek (tributary of Kongor Creek), Ignatov & Ignatova 11-3415 (MHA), Amur District, Tokinsky-Stanovoy National Park, Tok River valley up to the Ulyagir River mouth, 970 m alt., Dudov (MW).

Khabarovsk Territory: Upper Bureya River, Pravaya Bureya River 6 km upstream from the junction with Levaya Bureya River, 580 m alt., 27 Aug 1997 Ignatov 97-950 (MHA); Dusse-Alin Range, watershed of Levaya Bureya and Kuraygagna Rivers, 1620 m alt., 8 Aug 1992, Borisov (MW9027940, 9027941); Badzhal Mountains, Yarap River Basin in its watershed with Kamenny Creek right tributary, 1770 m alt., 8 Aug 2016 Pisarenko (NSK, dupl. MW).

Primorsky Territory: Chuguevka Dist., Oblachnaya Peak, 1700 m alt., 18 Aug 2007 Ignatov 07-192a (MHA); Sakhalin Province: Kuril Islands, Iturup Island, vicinity of Cirk Bay, ca. 15 m alt., Fedosov 15-2-084 (MW); Shikotan Island, vicinity of Ostrovnoy Cape, ca. 20 m alt., 21 Aug 2021 Fedosov (MW).


Kamchatsky Territory: West-Kamchatkan Lowland, Levij Kikkich River basin, 500 m alt., 19 Aug 2001 Chernyadjeva 116 (LE); Srednij Range, Esso Settl. outskirts, 1000 m alt., 01 Aug 2001 Chernyadjeva 54 (LE); Klyuchevskaya volcano group, Ushkovskiy Dol, Shirokij Creek upper course, 1050 m alt., 19 Aug 2004, Chernyadjeva 100 (LE); Ostry Tolbachik volcano western slope, Tolbachinsky Dol, upper course of Vodopady Creek, 1400 m alt., 11 Aug 2006 Chernyadjeva 19 (LE); Kronotsky State Reserve, Fedosov 12-490 (MW9077875).

Campylopus pyriformis (Schultz) Brid., Bryol. Univ. 1: 471. 1826. — Dicranum pyriforme Schultz, Prodr. Fl. Stang. Suppl. 73. 1819. Fig. 7

Plants in loose tufts, light to bright green. Stems 0.2–2.5 cm, simple or forked. Leaves 3–4×0.3–0.45 mm, erect-spreadling, slightly contorted to flexuose when dry, occasionally falcate, from lanceolate base gradually narrowed into a long, concolorous, ciliate subula with very long, conspicuous, subulate acumina, which is necessary for its identification in several areas does not work in the other ones. For instance, both European and North American plants of C. pyriformis have leaves with very long, subulate acumina, which is not necessary the case of plants from Kamchatka. At the same time, the molecular data proved that the plants from southern Kamchatka represent C. pyriformis s.l. Except Kamchatka, this species was reported from Kaliningrad Province (Ignatov et al., 2006, Dolnik & Napreenko, 2007) and Iturup Island (Bakalin et al., 2019). Although Dolnik & Napreenko (2007) noticed C. pyriformis as a common species on sandy dunes of Kuronian Spit, no specimens are available from that area for checking. Report of the species from Iturup Island (Bakalin et al., 2019) is based on misidentification of Dicranella cf. heteromalla, which resembles C. pyriformis in having leaves with very wide costae, guide cells opening on the ventral side of the costa, smooth dorsal surface of costa and concolorous, short rectangular laminal cells at leaf base. To differentiate such Dicranella specimens from Campylopus, transverse sections of costa in middle portion of leaf should be checked. In Campylopus, hyalocysts form ventral surface of costa throughout its length, while in Dicranella leaf cross section in the middle part of leaf shows ventral stereids and ventral epidermis.

Distribution and ecology. Broadly circumscribed, C. pyriformis has a worldwide distribution with most records concentrated in Europe and in moderate climate of southern hemisphere. Few currently known North American populations are considered as a result of rather recent dispersal from South America. The species was also reported from several provinces of China, including Jilin in north-east of the country close to the Russian border. According to Frahm (2007), C. pyriformis usually grows on eroded soil, including acidic sand; however, specimens from Kamchatka Peninsula available for our study originated from the thermal fields of southern Kamchatka (Fig. 9), where it grew together with C. atrovirens, C. subulatus and C. umbellatus (Ignatova & Samkova, 2006). Specimens examined: RUSSIA: Kamchatsky Territory: Ust’-Bol’shertsky Dist., vicinity of Pauzhetka settl., eastern Pauzhetskoe thermal field, Samkova 9-10 (MW9027886, MW9027888) (with C. umbellatus); the same area, ca. 500 m southward Pauzhetskaya geothermal power plant, upper thermal field, 01.VIII.2006 Samkova #13-4 (MW9027887).

Campylopus subulatus Schimp. ex Milde, Bot. Zeitung (Berlin) 20: 460. 1862. Fig. 8

Plants in loose tufts, light green, not tomentose. Stems 1–3.5 cm, simple or furcate. Leaves 2.5–4×0.3–0.4 mm, appressed when dry, erect-spreadling when wet, from lanceolate base narrowed into a long, straight subula; margins entire or bluntly serrulate below, serrate at apex; costa filling 1/2–2/3 of leaf base width, excrrent in a...
short concolorous mucro, in transverse section with ventral hyalocysts, guide cells which are only slightly larger than substereids, the latter in 2–3 layers on dorsal side, dorsal surface of costa strongly ribbed due to longitudinal rows of projecting cells; distal and median laminal cells 12–15×5–8 μm, thick-walled, subquadrangular, rounded-rectangular or rhomboidal; basal laminal cells 30–50×8–13 μm, narrow rectangular, slightly narrower along margins, thin-walled, hyaline and translucent, alar cells shorter and wider, not or slightly inflated, sometimes brownish. Specialized asexual reproduction unknown in Russia. Setae 1–1.3 cm. Capsules slightly inclined, ca. 0.8 mm long, ovate, slightly asymmetric, estrumose, weakly longitudinally sulcate. Operculum long rostrate, beak ca. 0.8 mm long.

Differentiation. Campylopus subulatus differs from the other species of the genus reported from Russia in having a combination of substereids filling the dorsal side of costa, ribbed dorsal surface of costa, short cells in upper portion of leaf lamina, narrow costa, and scarcely differentiated alar cells. Actually, alar groups in C. subulatus are usually better differentiated than in C. schimperi and may be inflated (moreover, they are usually inflated according to Frahm & Vitt, 1978); however, com-

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Fig. 8. Campylopus subulatus (from: Russia, Primorsky Territory, Fedosov & Pisarenko 2016-30, MW9090384). A, F: habit, dry; B: capsule; C: stem transverse section; D: upper leaf cells; E: leaf transverse section; G-H, J: leaves; I: mid-leaf cells; K: basal leaf cells. Scale bars: 5 mm for A; 1 mm for B; 2 mm for G–H, J; 100 μm for C–E, I, K.
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paring with *C. gracilis*, they are weaker delimited and never project into costa. Unlike *C. schimperi*, alar groups in *C. subulatus* often have red-brownish coloration. Differentiation of the later two species often may be tricky, and many specimens which represent *C. schimperi* were originally identified as *C. subulatus*. One of possible sources of such mistakes is that in Asian populations, which were proved by molecular data to represent *C. schimperi*, the dorsal surface of costa is often remarkably ribbed. For the distinction of these two species see Frahm & Vitt (1972) and comment to *C. schimperi*.

**Distribution and ecology.** *Campylopus subulatus* is widespread in Europe, where it occurs throughout UK, in south-western parts of Norway and Sweden, in Central and Western Europe, however, avoiding Mediterranean regions and Eastern Europe, like most other *Campylopus* species do. After molecular phylogenetic study and further revision of herbaria, it turns out that *C. subulatus*, which was reported from many areas of Russia, actually is known only from four localities in the Russian Far East (Fig. 9), while all other records should be referred to *C. schimperi*. Two known collections of *C. subulatus* originate from Primorsky Territory, where the species occurs on the seashore in Olginsky and Khasansky Districts. In Kamchatka it is from the thermal fields of Pauzhetka and in Kronotsky Reserve State.

**Specimens examined:** Primorsky Distr., Timofeevka settlement surroundings, the coastal area of Vladimir Bay (ca. 30 m alt.), on disturbed sandy soil in moist meadow (in abandoned wheel tracks), 28 Aug 2016, Fedosov & Pisarenko (MW900384, 9115372, MHA, LE); Khasansky Distr., Ryazanovka near the field station of DVGU, roadside near creek, 14 Sept 1985 Ignatov (MHA). Kamchatsky Territory: Ust’-Bolsheretsk Distr., 800 m southwards from Pauzhetka Settl., upper heothermal field, 170 m alt., 1 Oct 2001, Sankova 3 (MW9027943); Elizovo Distr., Kronotsky State Reserve, Geyzerov valley, thermal fields, 27 Sept 1961 Lescchina (MW9027942, 9027944).

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