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

РЕВИЗИЯ РОДА *CAMPYLOPUS* (LEUCOBRYACEAE, BRYOPHYTA) В РОССИИ

VLADIMIR E. FEDOSOV [1,2], ALINA V. FEDOROVA[3] & ELENA A. IGNATOVA[1]

ВЛАДИМИР Э. ФЕДОСОВ[1,2], АЛИНА В. ФЕДОРОВА[3], ЕЛЕНА А. ИГНАТОВА[1]

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 *trn*S-*trn*F, mitochondrial *Nad*5 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*.

Резюме

Проведена ревизия рода *Campylopus* в России с помощью молекулярно-филогенетических методов, в которой были использованы для сравнения данные по образцам из Европы, собранным вблизи *loci classici* нескольких видов. На территории России выявлено 8 видов, среди которых наиболее широко распространенным является *C. schimperi*, встречающийся в горных регионах по всей стране, в то время как остальные виды известны из немногочисленных местонахождений на Камчатке (5 видов), в южной части российского Дальнего Востока (3 вида), на Кавказе (3 вида) и в Калининградской области (1-3 вида). Ядерный участок ITS позволил хорошо разграничить *C. schimperi* и *C. subulatus* и подтвердить ранее известные отличия между ними в морфологии, экологии и распространении. Молекулярно-филогенетическая реконструкция, основанная на объединенных последовательностях пластидного *trn*S-*trn*F, митохондриального *Nad*5 и ядерного ITS маркеров позволяет предположить, что в роде *Campylopus* имеются по меньшей мере три морфологически и филогенетически хорошо разграниченные линии, которые могут быть выделены в качестве самостоятельных родов, чтобы избежать включения рода *Pilopogon* в синонимы *Campylopus*.

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

INTRODUCTION

With ca. 175 accepted species, the genus *Campylopus* Brid. is one of the largest genera of Dicranidae. General distribution of the genus stratches from Svalbard to continental Antarctic; at the same time, most repersentatives 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 circumscriptions 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

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[1] – Lomonosov Moscow State University, Faculty of Biology, Leninskie Gory Str. 1–12, Moscow 119234 Russia; E-mails: fedosov_v@mail.ru; arctoa@list.ru. ORCID (VF): 0000-0002-5331-6346; (EI): 0000-0001-6287-5660

[2] – Botanical Garden-Institute, FEB RAS, Makovskogo Street, 142, Vladivostok, 690024 Russia

[3] – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia. E-mail: alina_77777@mail.ru. ORCID: 0000-0001-7362-2124

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 (Ignatova & 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 *trn*S-F region, where two usually used and thus also well represented in GenBank plastid markers, *trn*L-F and *rps*4 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 *trn*S-*trn*F 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 oganellar (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

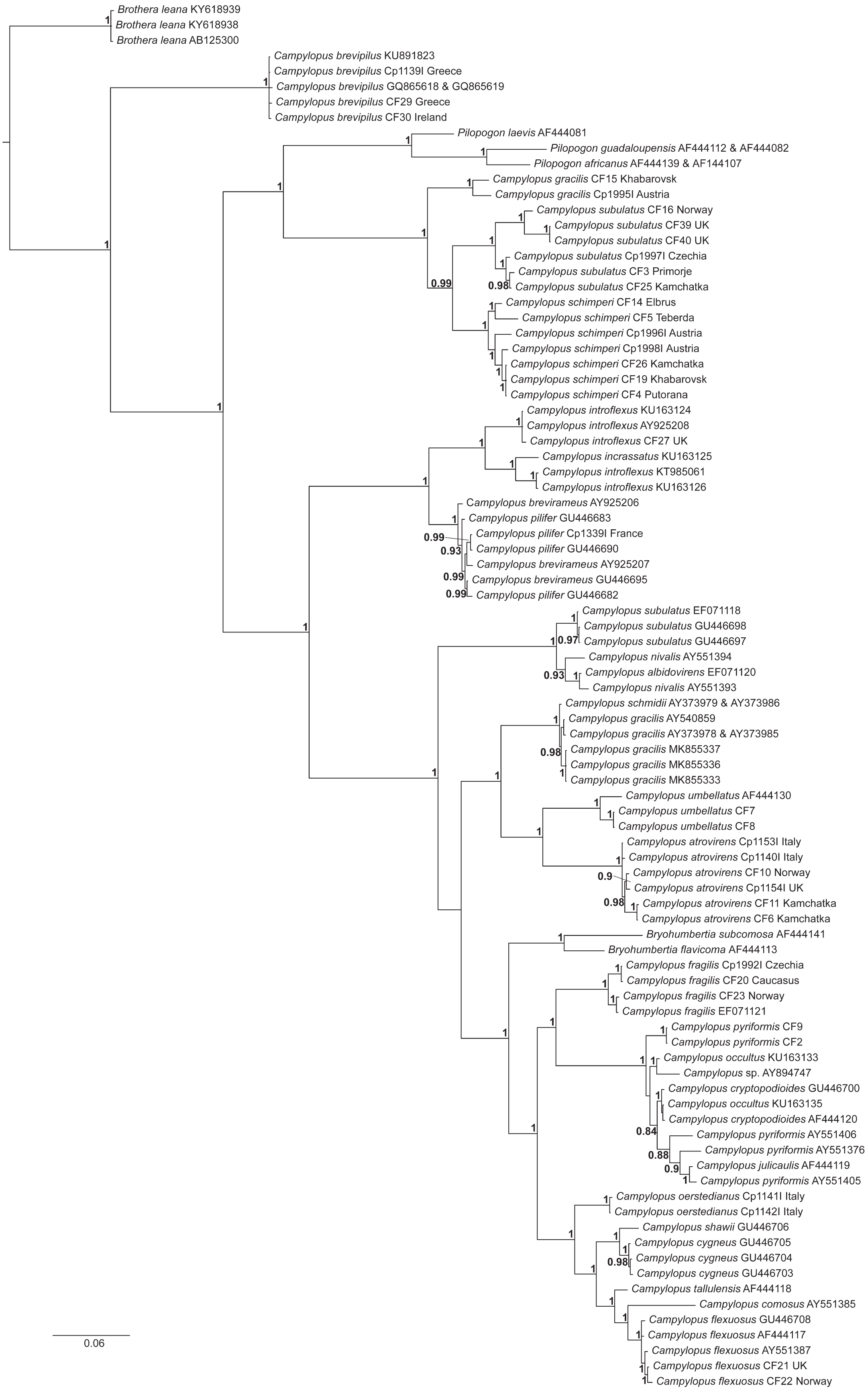

Fig. 1. Bayesian tree of the genus *Campylopus* inferred from the nuclear ITS sequences

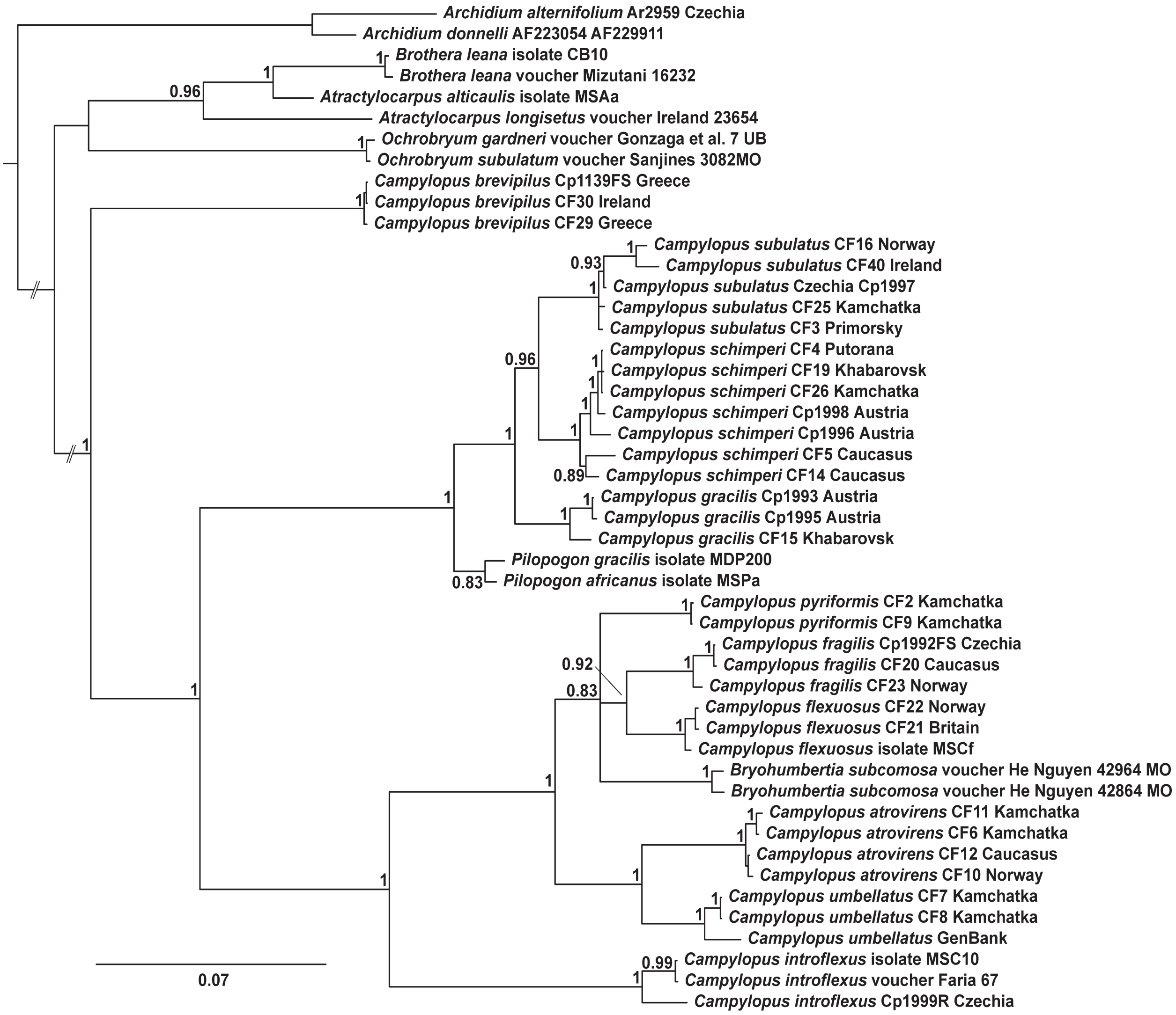

Fig. 2. Bayesian tree of the genus *Campylopus* inferred from the combined sequences of plastid *trn*SF, mitochondrial Nad5 and nuclear ITS.

was supplemented by the revision of *Campylopus* collections in MW, MHA and LE.

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).

Table 1. Voucher data of the originally studied specimens (their GenBank Accession numbers are in bold) and GenBank accession numbers of specimens included in combined dataset (GenBank accession numbers of GenBank specimens used in the analysis of ITS dataset are depicted in Fig. 1).

Isolate	Species	Geographic origin	Specimen voucher	ITS	trnSF	Nad5
Ar2959	*Archidium alternifolium*			-	OQ094892	OQ094861
	Archidium donnelli		Risk 1536 (DUKE)	-	AF229911 & AF223054	AY908972
MSAa	*Atractylocarpus alticaulis*			-	KX580486 & AF129592	KX580404
	Atractylocarpus longisetus		Ireland 23654	-	KY619040 & KY619015	–
CB10	*Brothera leana*			FJ572390	FJ572594 & FJ572424	–
	Brothera leana		Mizutani 16232	KY618938	KY619031	AY908911
	Bryohumbertia subcomosa		Nguyen 42864 MO	-	KY619046	KY618930
	Bryohumbertia subcomosa		Nguyen 42964 MO	-	KY619045	KY619070
CF6	*Campylopus atrovirens*	Kamchatka	MW9027797	**OQ076709**	**OQ077923**	**OQ077891**
CF10	*Campylopus atrovirens*	Norway	MW9079021	**OQ076707**	**OQ077922**	**OQ077890**
CF11	*Campylopus atrovirens*	Kamchatka	MW9027793	**OQ076708**	**OQ077920**	**OQ077888**
CF12	*Campylopus atrovirens*	Caucasus, Elbrus	14.VIII.1993, Ukrainskaya LE	**-**	**OQ077921**	**OQ077889**
Cp1154	*Campylopus atrovirens*	UK Scotland Mt Suilven	CBFS 15672	**OQ076712**	**-**	**-**
Cp1140	*Campylopus atrovirens*	Italy Cicogna	Kučera 15149 CBFS	**OQ076710**	**-**	**-**
Cp1153	*Campylopus atrovirens*	Italy Cicogna	Kučera 15153 CBFS	**OQ076711**	**-**	**-**
CF29	*Campylopus brevipilus*	Greece	Blockeel 45/248	**OQ076731**	**OQ077949**	**OQ077917**
CF30	*Campylopus brevipilus*	Ireland	Blockeel 36/496	**OQ076732**	**OQ077950**	**OQ077918**
Cp1139	*Campylopus brevipilus*	Greece, Lesbos Island	Blockeel 42 220	**OQ076730**	**OQ077948**	**OQ077916**
CF21	*Campylopus flexuosus*	United Kingdom	MW9027805	**OQ076698**	**OQ077930**	**OQ077898**
CF22	*Campylopus flexuosus*	Norway	MW9079023	**OQ076699**	**OQ077929**	**OQ077897**
CF20	*Campylopus fragilis*	Caucasus	MHA9011782	**OQ076703**	**OQ077927**	**OQ077895**
CF23	*Campylopus fragilis*	Norway	MW9079024	**OQ076704**	**OQ077928**	**OQ077896**
Cp1992	*Campylopus fragilis*	Czechia, Broumovske steny	Kučera 12383 CBFS	**OQ076702**	**OQ077926**	**OQ077894**
CF15	*Campylopus gracilis*	Khabarovsk	MW9130218	**OQ076716**	**OQ077945**	**OQ077913**
Cp1993	*Campylopus gracilis*	Austria, Lake Filzsee	Kučera 12496 CBFS	**-**	**OQ077946**	**OQ077914**
Cp1995	*Campylopus gracilis*	Austria, Mt. Rossgruberkogel	Kučera 16854 CBFS	**OQ076717**	**OQ077947**	**OQ077915**
CF27	*Campylopus introflexus*	United Kingdom	MW9027850	**OQ076714**	**-**	**-**
Cp1141	*Campylopus oerstedianus*	Italy, Ghiffa	Kučera 15251 CBFS	**OQ076700**	**-**	**-**
Cp1339	*Campylopus pilifer*	France	Lüth 2619	**OQ076713**	**-**	**-**
CF2	*Campylopus pyriformis*	Kamchatka	MW9027887	**OQ073445**	**OQ077924**	**OQ077892**
CF9	*Campylopus pyriformis*	Kamchatka	MW9027889	**OQ073446**	**OQ077925**	**OQ077893**
CF4	*Campylopus schimperi*	Putorana	MW9079030	**OQ076729**	**OQ077942**	**OQ077910**
CF5	*Campylopus schimperi*	Caucasus, Teberda	MW9027928	**OQ076724**	**OQ077940**	**OQ077908**
CF14	*Campylopus schimperi*	Caucasus, Elbrus	16.VIII.1993, Ukrainskaya LE	**OQ076723**	**OQ077941**	**OQ077909**
CF19	*Campylopus schimperi*	Khabarovsk	MHA9011786	**OQ076726**	**OQ077943**	**OQ077911**
CF26	*Campylopus schimperi*	Kronotsky Reserve	MW9077875	**OQ076725**	**OQ077944**	**OQ077912**
Cp1998	*Campylopus schimperi*	Austria, Mt. Grosser Hafner	Kučera 12574 CBFS	**OQ076727**	**OQ077938**	**OQ077906**
Cp1996	*Campylopus schimperi*	Austria, Mt. Waldhorn	Kučera 12888 CBFS	**OQ076728**	**OQ077939**	**OQ077907**
CF3	*Campylopus subulatus*	Primorsky	MW9090384	**OQ076718**	**OQ077936**	**OQ077904**
CF16	*Campylopus subulatus*	Norway	MHA9057604	**OQ076715**	**OQ077934**	**OQ077902**
CF25	*Campylopus subulatus*	Kamchatka, Pauzhetka	MW9027943	**OQ076719**	**OQ077933**	**OQ077901**
CF39	*Campylopus subulatus*	Wales	Ottley 21031401	**OQ076721**	**-**	**-**
CF40	*Campylopus subulatus*	Ireland	Blockeel 48/420	**OQ076722**	**OQ077935**	**OQ077903**
Cp1997	*Campylopus subulatus*	Czechia, Zulova Hradilek	23.VII.2009 CBFS 13561	**OQ076720**	**OQ077937**	**OQ077905**
CF7	*Campylopus umbellatus*	Kamchatka	MW9027956	**OQ076705**	**OQ077931**	**OQ077899**
CF8	*Campylopus umbellatus*	Kamchatka	MW9027961	**OQ076706**	**OQ077932**	**OQ077900**
	Campylopus umbellatus				AF226764 & AF231171	-
	Ochrobryum gardneri		Gonzaga et al. 7 UB	-	KY619047	KY619069
	Ochrobryum subulatum		Sanjines 3082MO	-	KY619025	-
MSPa	*Pilopogon africanus*			-	KX580556 & AF129595	KX580433
MDP200	*Pilopogon gracilis*			-	AY908137	AY908907

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. atrovirens, 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 organellar markers do not support the delimitation of these two; (2) we confirm the identity of the eight *Campylopus* species from Russian moss flora, including seven well known from Holarctic species (*C. atrovirens, C. fragilis, C. gracilis, C. introflexus, C. pyriformis, C. schimperi,* and *C. subulatus*) and one predominantly tropical (*C. umbellatus*); (3) our results suggest that the genus *Campylopus* in its current delimitation may be paraphyletic. While the first and the second inferences do not need further discussion and thus are just accepted in the "taxonomy" section, the overall phylogeny of the genus *Campylopus* as obtained here deserves a brief consideration.

Already pioneer molecular phylogenetic studies (La Farge *et al.*, 2000) showed that the genus *Campylopus* might be paraphyletic. However, later study of the genus by Stech (2004) as well as the revision of the generic composition of Leucobryaceae by Bonfim Santos & Stech (2017) demonstrated a monophyly of the genus, which formed a clade sister to the *Pilopogon* clade in both studies. Although several other molecular phylogenetic studies dealt recently with *Campylopus,* even in the studies based completely on the plastid markers, accessions of *Pilopogon* were most often included for tree rooting, so, paraphyly of *Campylopus* could not be tested. In case of ITS, which is extremely variable and hard-to align even within *Campylopus*, involving more distant outgroup than *Pilopogon* indeed is problematic. On the other hand, the previous studies sampled neither *C. brevipilus*, nor representatives of the true *C. subulatus/C. schimperi/C. gracilis* lineage, which falls outside the "*Campylopus* 3" (= *Campylopus* s.str.) clade with the generitype, *C. flexuosus* in our analyses. Since we have no possibility to check the specimens of *Pilopogon gracilis* and *P. africanus*, from which the sequences involved in our study have originated, no taxonomic decisions are possible at the present stage. However, if their identity is correct, two decisions would be possible: (1) synonymization of *Pilopogon* with *Campylopus* or (2) split of *Campylopus* into at least three genera, since the type species of the genus *Pilopogon, P. gracilis,* is included in the dataset. Counting a degree of divergence of accepted genera within the "rest of Leucobryaceae clade" (the clade sister to *Campylopus* s.l. in the tree inferred from the concatenated dataset in Fig. 2), the second option would look more natural than preserving heterogeneous *Campylopus* s.l. by price of referring *Pilopogon* into the synonymy with it. The structure of costa may be used for morphological circumscription of the clades in the obtained topology. With rather weak costae lacking ventral hyalocysts, but with two well developed stereid bands instead (see Lüth, 2019), *Campylopus brevipilus* represents a discordant element in *Campylopus* and, according to the obtained topologies, deserves placing in a separate genus that, however requires studying the type specimen. On the other hand, in the majority of species within the "*Campylopus* 3" clade (excepting *C. pyriformis*) dorsal side of costa is formed by well developed stereids, while in all species of the "*Campylopus* 2" clade it is formed by substereids.

The clade "*Campylopus* 2" (*C. subulatus/C. schimperi/C. gracilis* lineage) forms a well supported clade sister to the *Pilopogon* clade. According to the revision of Frahm (1983), the genus *Pilopogon* includes eight species of predominantly neotropical mosses (one species in Africa). Molecular data existing for four species (*P. africanus, P. gracilis, P. guadalupensis,* and *P. laevis*) suggest the same affinity. Representatives of this clade share hyaline basal laminal cells and substereids rather then stereids on dorsal side of costa in the majority of *Pilopogon* species (as illustrated by Frahm, 1983). At the same time, according to Frahm' illustrations, several *Pilopogon* species also have ventral stereids instead of hyalocysts, as it is characteristic for *C. brevipilus*. Probably, several species accepted in *Pilopogon* by Frahm (1983) are not phylogenetically close to the group of "*Pilopogon* s. str." At the same time, placing *Campylopus subulatus*, *C. schimperi* and *C. gracilis* in the genus *Pilopogon* needs in additional morphological justification.

Although our taxon sampling is very scarce, a comparison of our data with the previously published ones suggest a need for careful reexamination of the European and especially Macaronesian specimens previously assigned to *Campylopus subulatus* (three identical ITS sequences, GU446698, GU446697, EF071118 found in the "*Campylopus* 3" clade) and *C. gracilis* (five identical sequences, MK855333, MK855336, MK855337, 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 sclerodermis, in species with weak sclerodermis the stem cross 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 chlorophyllose 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 deciduous leaves or stem tips [other types not seen in collections from Russia]. *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 dicranoid. *Spores* small. *Calyptra* cucullate.

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

1. Leaves with hyaline hair point 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

7. Alpine, rarer lowland plants forming dense tomentose tufts .... 6. *C.schimperi*
Lowland plants forming loose not tomentose tufts 8

8. Dorsal surface of costae smooth .... 7. *C. pyriformis*
– Dorsal surface of costae strongly ribbed due to round projecting cells .... 8. *C. subulatus*

Campylopus atrovirens De Not., Syllab. Musc. 221. 1838. Fig. 3.

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 denticulate 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

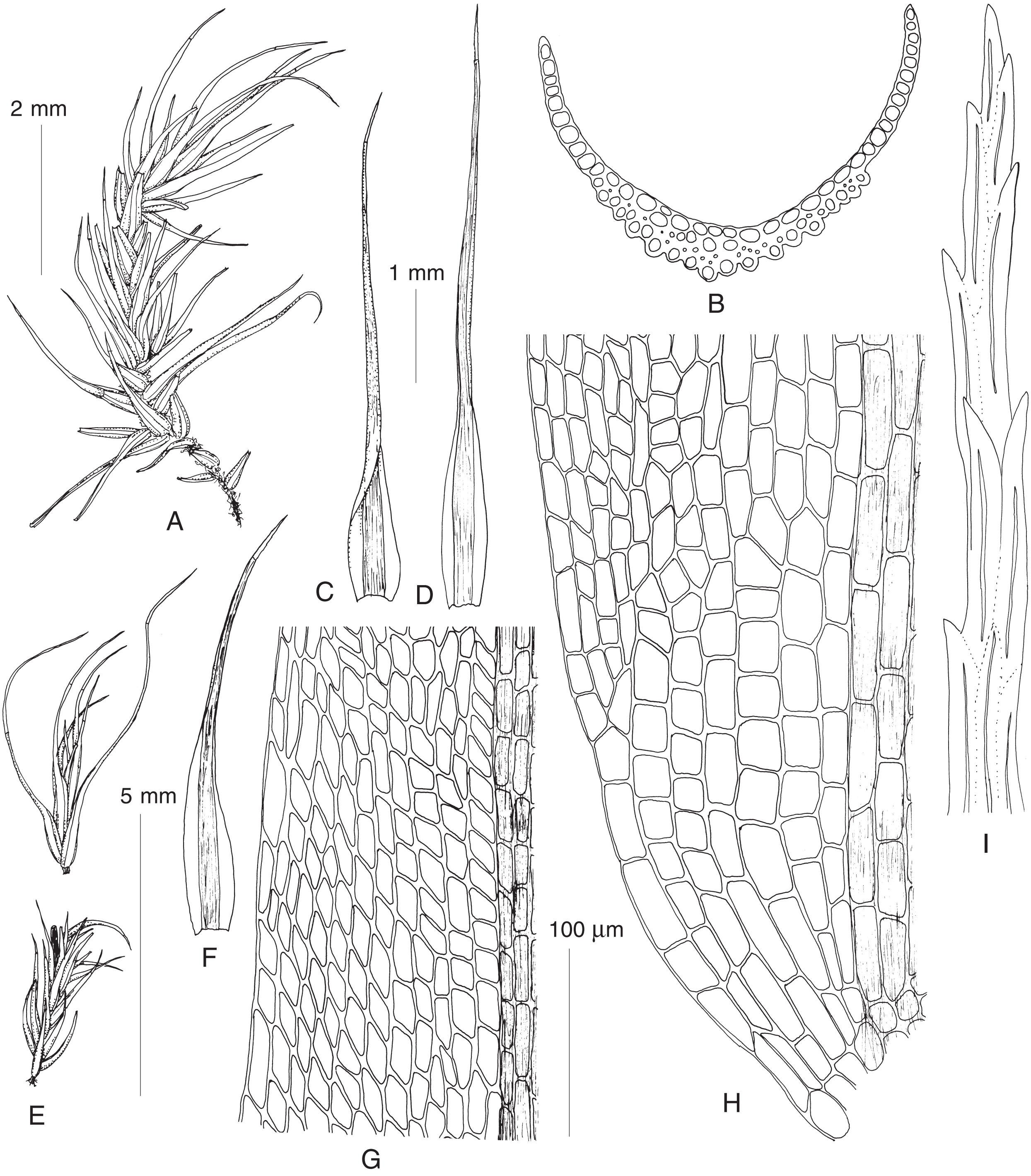

Fig. 3. *Campylopus atrovirens* (from: Russia, Kamchatka, *Samkova 14*, MHA9011785). A: habit, dry; B: leaf transverse section; C–D, F: leaves; E: plant with broken upper part, dry; G: mid-leaf cells; H: basal leaf cells; I: upper leaf cells. Scale bars: 5 mm for E; 2 mm for A; 1 mm for C–D, F; 100 µm for B, G–I.

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 Pauzhetka Settlement (south of the peninsula).

Specimens examined: RUSSIA: **Kabardino-Balkaria Republic**: Elbrus Mt slope alt., 14 Aug 1993, *Doroshina* (LE, dupl. in MW). **Kamchatsky Territory**: Ust'-Bolsheretsky

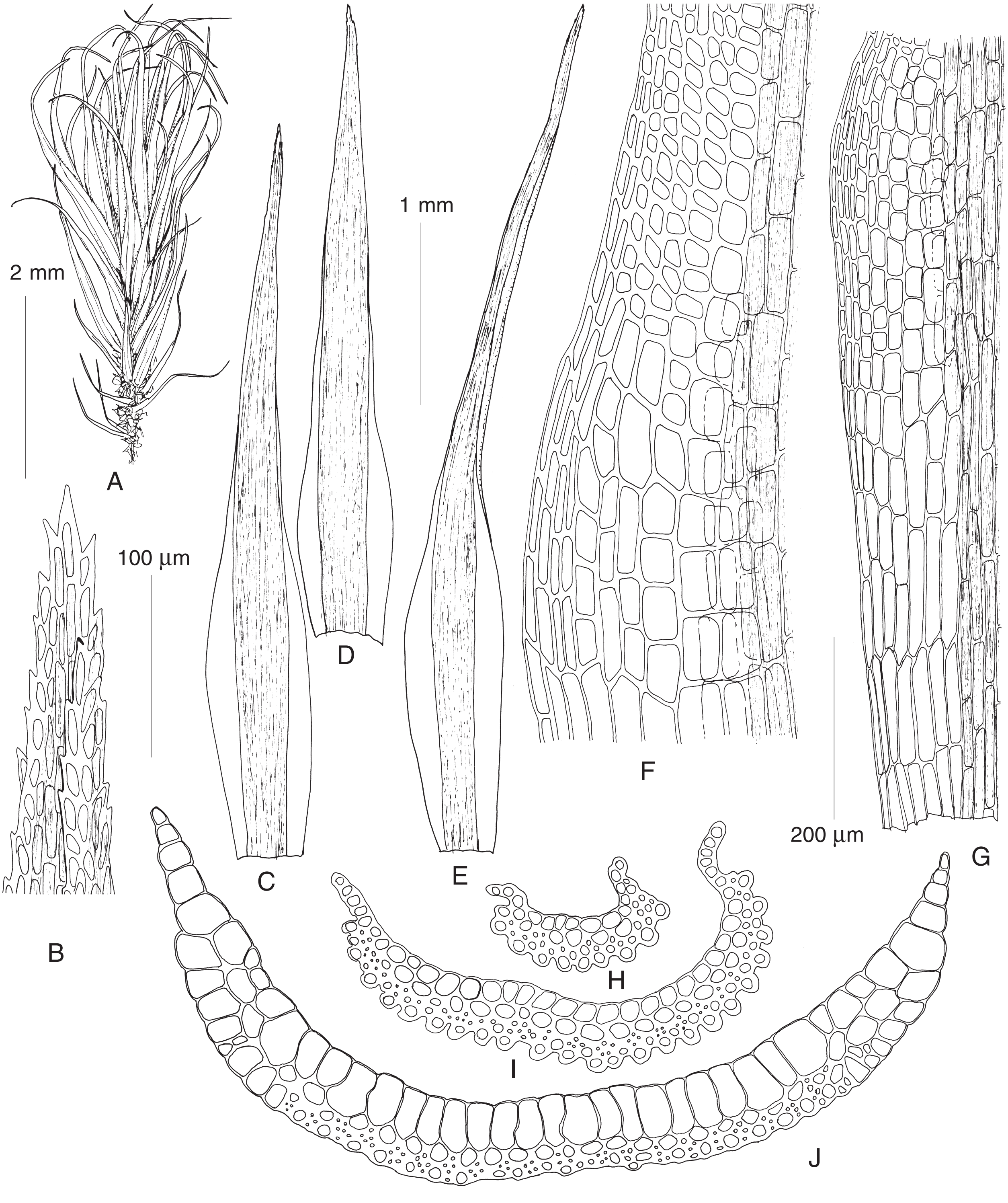

Fig. 4. *Campylopus fragilis* (from: Russia, Republic of Kabardino-Balkaria, *Ignatov, Ignatova & Kharzinov s.n.*, MHA9011782). A: habit, dry; B: upper leaf cells; C–E: leaves; F: cells at leaf shoulder; G: basal leaf cells; H–J: leaf transverse sections. Scale bars: 2 mm for A; 1 mm for C–E; 200 µm for G; 100 µm for B, F, H–J.

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

Campylopus introflexus (Hedw.) Brid., Muscol. Recent. Suppl. 4: 72. 1819[1818]. – *Dicranum introflexum* Hedw., Sp. Musc. Frond. 147. 29 f. 1–7. 1801.

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 range extention 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.

Campylopus umbellatus (Arn.) Paris, (Arn.) Paris, Index Bryol. 264. 1894. – *Thysanomitrion umbellatum* Arn., Disp. Méth. Mousses 34. 1825.

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 *trn*SF sequences form a clade with the GenBank sequences AF226764 (*rps*4) and AF231171, assigned to the same species.

Campylopus fragilis (Brid.) Bruch & Schimp., Bryol. Eur. 1: 164 (fasc. 41. Monogr. 4). 1847. — *Dicranum fragile* 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 at1/4 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).

Campylopus flexuosus (Hedw.) Brid., (Hedw.) Brid., Muscol. Recent. Suppl. 4: 71. 1819[1818]. – *Dicranum flexuosum* Hedw., Sp. Musc. Frond. 145. 38 f. 1–4. 1801.

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).

Campylopus gracilis (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1870–71: 427 (Gen. Sp. Musc. 1: 131). 1872. — *Dicranum gracile* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 17. 1859. Fig. 5

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

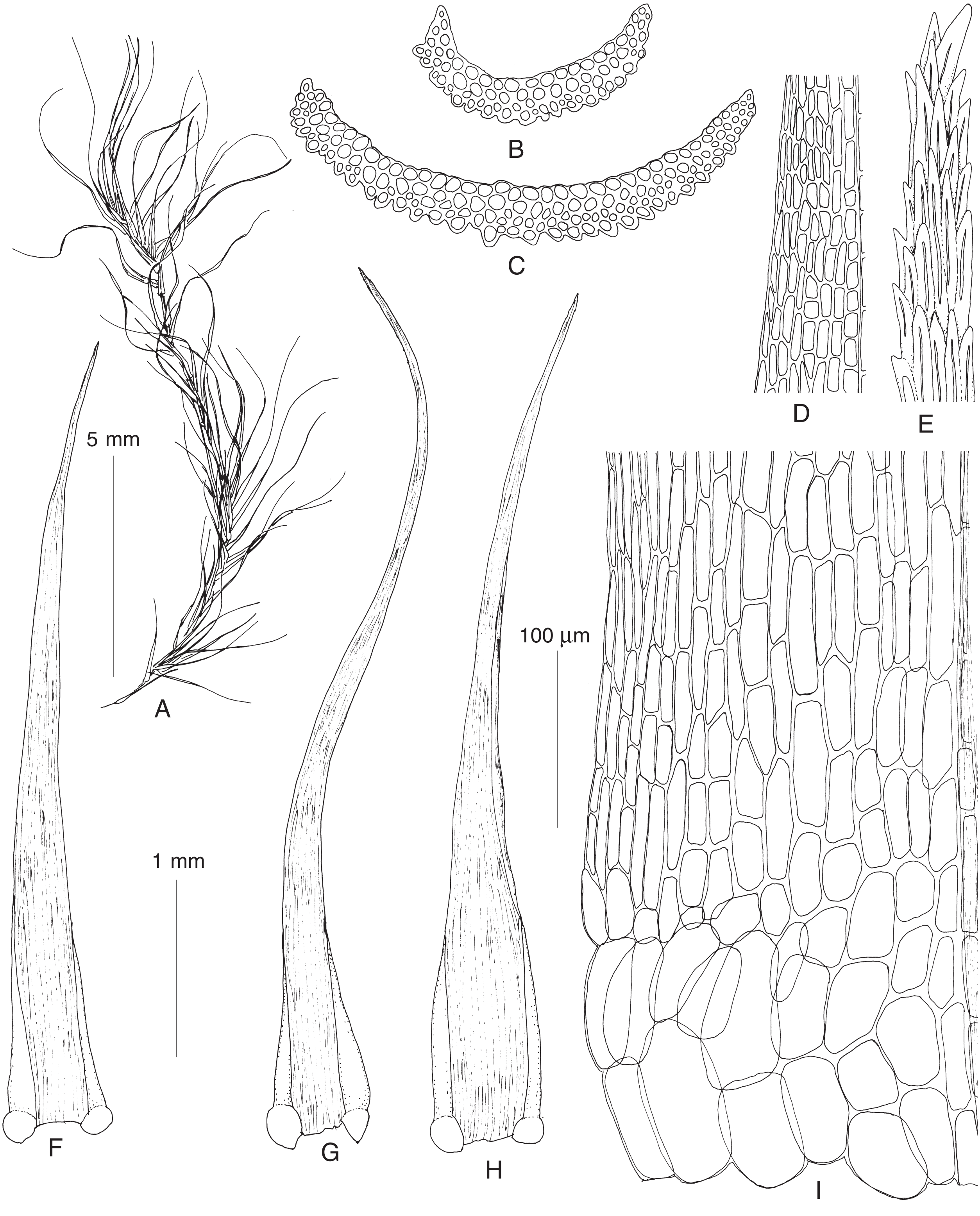

Fig. 5. *Campylopus gracilis* (from: Russia, Khabarovsk Territory, *Fedosov & Pisrenko*, MW9130218). A: habit, dry; B–C: leaf transverse sections; D: mid-leaf cells; E: upper leaf cells; F–H: leaves; I: basal leaf cells. Scale bars: 5 mm for A; 1 mm for F–H; 100 µm for B–E, I.

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-

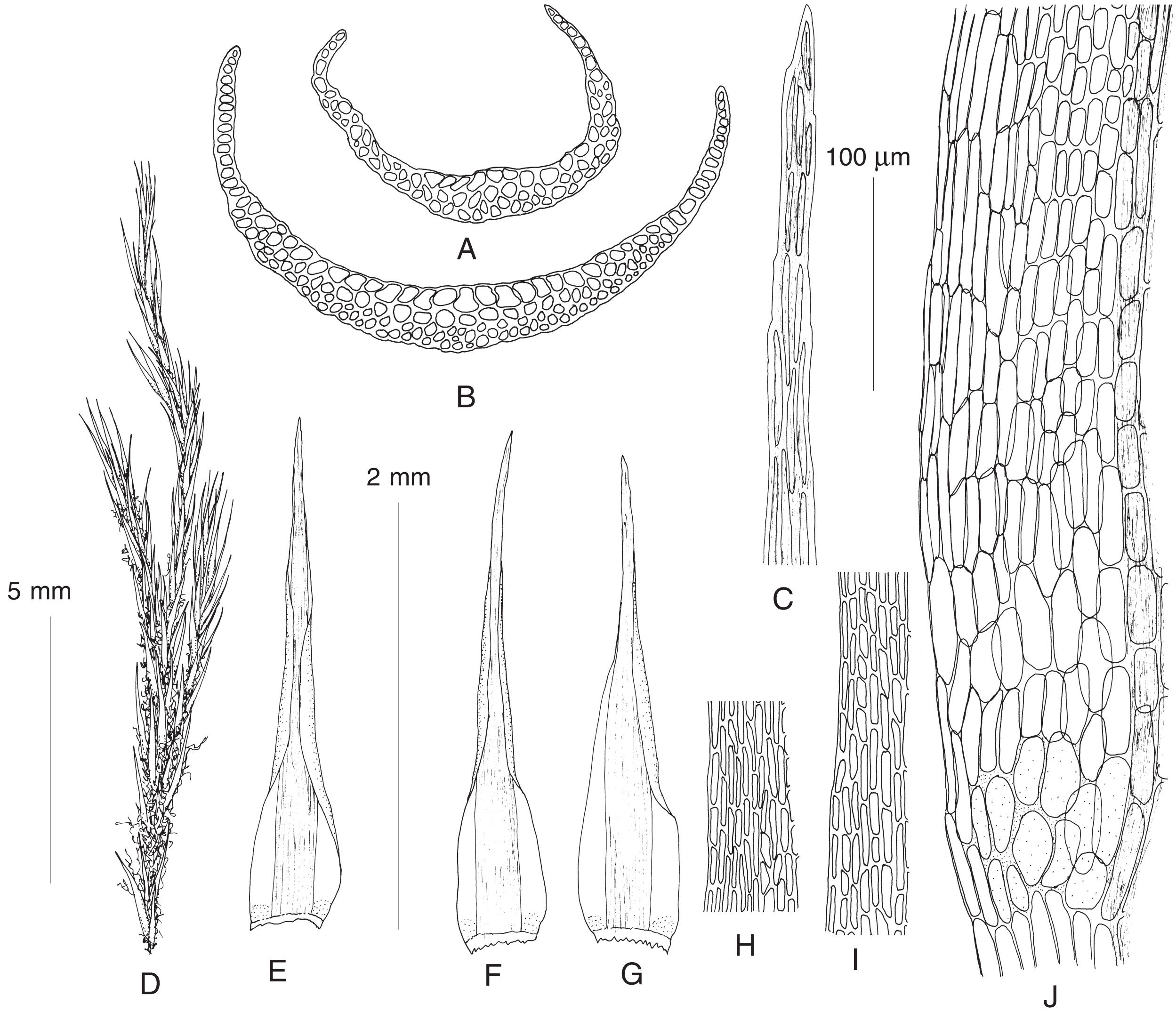

Fig. 6. *Campylopus schimperi* (from: Russia, Khabarovsk Territory, *Pisarenko s.n.*, MW9115373). A–B: leaf transverse sections; C: upper leaf cells; D: habit, dry; E–G: leaves; H–I: mid-leaf cells; J: basal leaf cells. Scale bars: 5 mm for D; 2 mm for E–G; 100 µm for A–C, H–J.

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).

Campylopus schimperi Milde, Bryoth. Eur. 14: no. 658. 1864. 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 hyalocysts, 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 authours 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 1/1.5–1/2.5(–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, althought 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 thermophylous 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 absents 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 60th and 70th 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 Distr., Belaya River basin, Abago Mt. northern slope, ca. 2200 m alt.,25 June 1999 *Akatov* (MHA); the same area, Armyansky Range, 2020 m alt., 16 Aug 1999, *Akatova* (MHA); Pshekish Range, 2200 alt., 23 July 1992 *Akatova* (MHA), same place, 2100 m alt., 01 Aug 1999 *Eskin* (MHA). **Karachay-Cherkess Republic**: Malokarachaevsky Distr., Hudes River upper course, 2400 m alt., 22 Sept 2002 *Onipchenko 38/02* (MW9027918); the same area, Tokhana Gorge, 2450 m alt., 21 Sept 2002 *Onipchenko 30/02* (MW9027921); Zelenchuk River basin, Pastukhova Mt., 2300 m alt., 27 Aug 1999, *Korotkov* (MW9027919); Daut Sanctuary, Epchik, 3040 m alt., 10 July 1995, *Onipchenko 51/95* (MW9027937); the same place, 3010 m alt., 22 Aug 2009, *Onipchenko & Ezhelev* (MW9027922); Teberdinsky State Reserve, Kyshkadzher, 3370 m alt., 10 Aug 1995 Zenyakin (MW9027934); Malaya Khatipara 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), Mussa-Achitara Mt., 3150 m alt., *Ignatov & Ignatova 05-3636* (MW9027928); Gonachhir River valley near Kluchor Creek Mouth, *Ignatov & Ignatova 05-1107* (MW9027929); Ariuchat Gorge, 2900 m alt., 6 Sept 1994 *Onipchenko 163/94* (MW9027936), same place, 2850 m alt., 3 Sept 1998, *Onipchenko 27/98* (MW927930); Ullu-Murudzhu River valley, Goluboe Lake, 2900 m alt., *Ignatov & Ignatova 05-3911* (MW9027927); Nazalykol Gorge, 2700 m alt., 4 July 1998 *Volkov & Zenyakin z-53* (MW9027932), same place, 2430 m

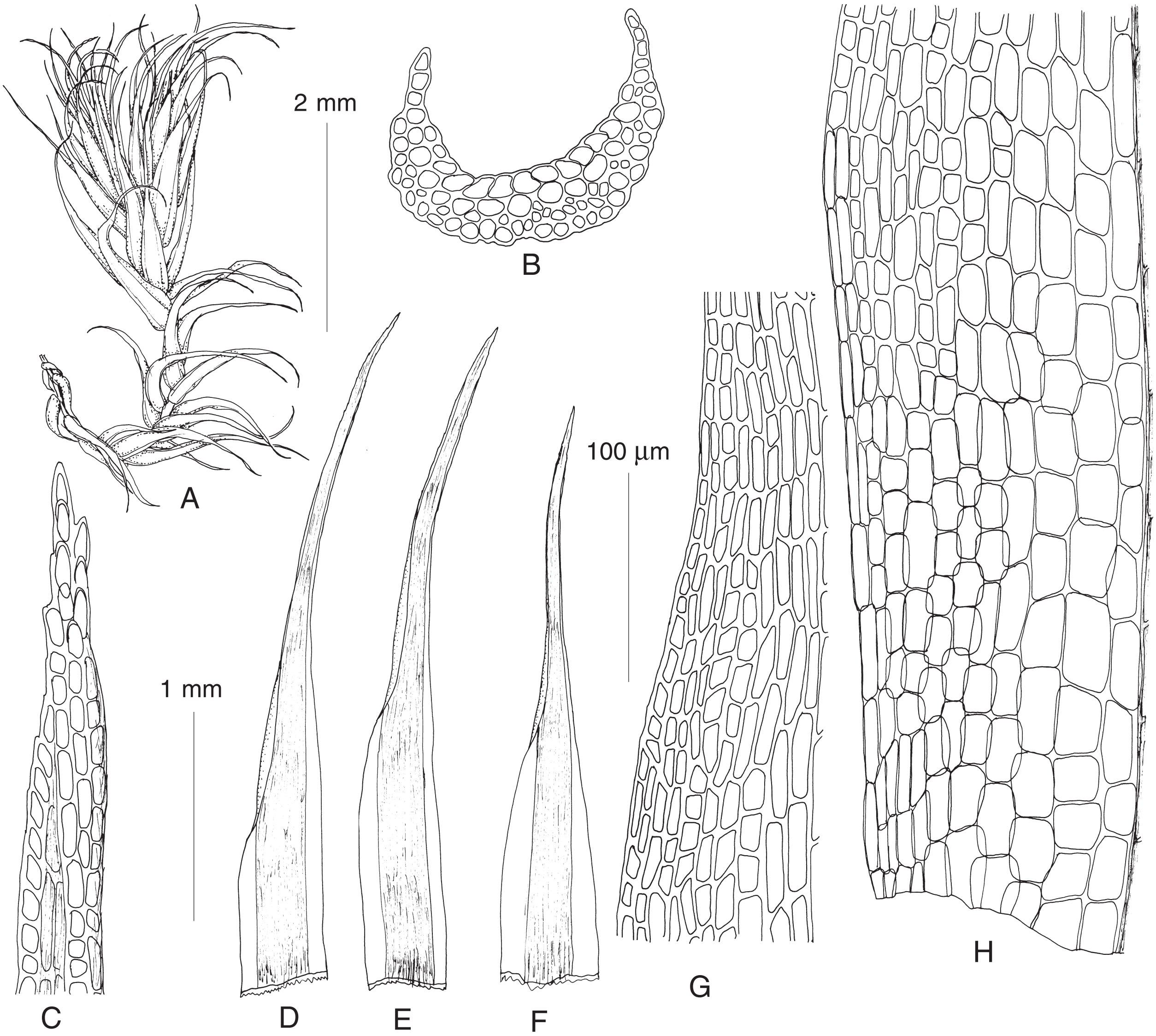

Fig. 7. *Campylopus pyriformis* (from: Russia, Kamchatka, *Samkova 13-3*, MW9027889). A: habit, dry; B: leaf transverse section; C: upper leaf cells; D–F: leaves; G: mid-leaf cells; H: basal leaf cells. Scale bars: 2 mm for A; 1 mm for D–F; 100 µm for B–C, G–H.

alt., 5 Aug 1998, *Volkov & Zenyakin 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-Chuysky Ridge northern spurs, Baksara Creek basin, 2200 m alt., on dry rocks, 27 June 2008 *Seregin & Seregina M-2102* (MW9027938); Bashkaus River, in upper course, 25 July 1993 *Ignatov* (MHA). **Krasnoyarsk Territory**, Taimyr District, Putorana 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, Kululbey 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, 1178m 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 A5910* (LE); Larionov Kluch, 1364 m alt., 13 July 2013 *Afonina 4113* (LE); Upper Bukukun River, Tsagan-Ula Mt., 1747m alt., 19 Aug 2011 *Afonina 4911* (LE); the same place, 2138m 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, 2000m alt., 19 Aug 2011, *Czernyadjeva 32-11* (LE). **Yakutia**: Oymyakonsky Distr., Suntar-Khayata Range, Mus-

Khaya Mt., Knoriy Creek (tributary of Kongor Creek), *Ignatov & Ignatova 11-3415* (MHA). **Amur Province**: Zeya District, Tokinsky-Stanovoy National Park, Tok River valley 4 km upstream 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 Kamenisty Creek right tributary, 1770 m alt., 8 Aug 2016 *Pisarenko* (NSK, dupl. MW). **Primorsky Territory**: Chuguevka Distr., 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). **Chukotsky Autonomous District**: Beringian Chukotka, Hot springs on Gil'mimli River 15 km Seward Ioni Lake, 23 July 1977, *Afonina* (LE), Krauze Cape, NW extremity of the Lavrentiya Gulf, 2 Sept 1976 *Afonina* (LE). **Kamchatsky Territory**: West-Kamchatian Lowland, Levij Kikhchik River basin, 500 m alt., 19 Aug 2001 *Chernyadjeva 116* (LE); Sredinnij Range, Esso Settl. outskirts, 1000 m alt., 01 Aug 2001 *Czernyadjeva 54* (LE); Klyuchevskaya volcano group, Ushkovsky Dol, Shirokij Creek upper course, 1050 m alt., 19 Aug 2004, *Chernyadjeva 100* (LE); Ostry Tolbachik volcano western slope, Tolbachinsky Dol, upper course of Vodopadny 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. Starg. 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-spreading, slightly contorted to flexuose when dry, occasionally falcate, from lanceolate base gradually narrowed into a long concolorous, canaliculate subula with few blunt teeth near apex; *costa* filling 1/3–1/2 of leaf width, excurrent, in transverse section with large ventral hyalocysts, guide cells and rather small and lax group of substereids on dorsal side, smooth or nearly so on dorsal surface; distal and median *laminal cells* 15–25×7–9 μm, thick-walled, elongate-rectangular; basal laminal cells 45–65×8–15 μm, translucent, thin-walled, quadrate to rectangular, along margins in 2–3 rows narrower, alar cells not differentiated. *Specialized asexual reproduction* absent. *Sporophytes* unknown in Russia.

Differentiation. *Campylopus pyriformis* differs from other *Campylopus* species in Russian flora in having combination of substereids rather than stereids on transverse section of costa, not differentiated alar groups, and concolorous, short-quadrate basal cells of leaf lamina. In addition, *C. pyriformis* has smooth dorsal surface of costa – the trait shared with only one species, *C. schimperi*. From the later species *C. pyriformis* differs in growth in loose, not tomentose tufts (vs. very dense, tomentose) and concolorous basal leaf portion. Due to having leaves with the costae smooth on dorsal side, *C. pyriformis* may be confused with representatives of several other Dicranoid mosses.

Campylopus pyriformis is a very polymorphic species, so the traits useful for its identification in several areas do not work in the other ones. For instance, both Europen and North American plants of *C. pyriformis* have leaves with very long, subulate acumina, which is not neccessary 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 south 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'sheretsky Distr., 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 powerplant, 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-spreading 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, excurrent in a

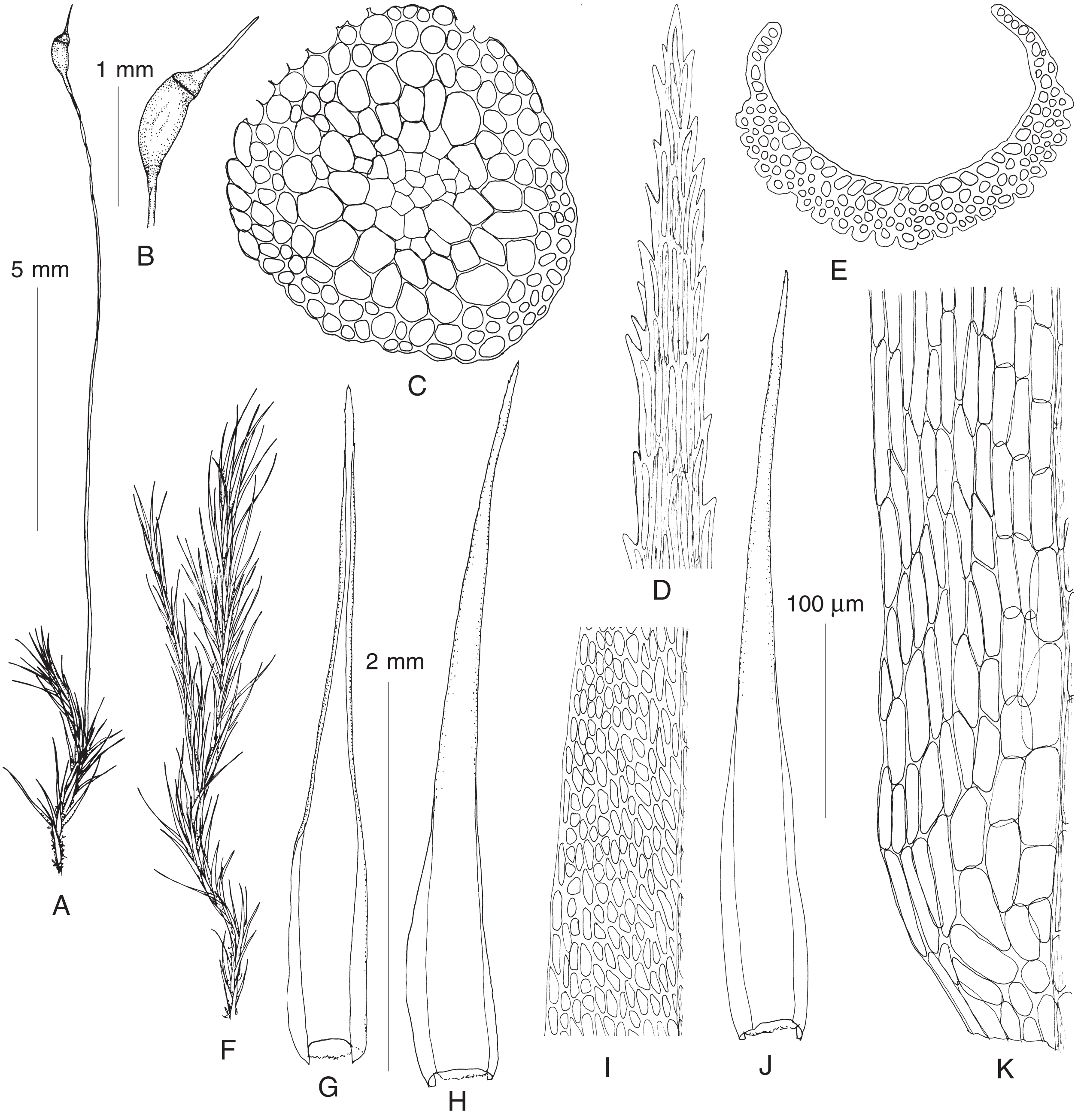

Fig. 8. *Campylopus subulatus* (from: Russia, Primorsky Territory, *Fedosov* & *Pisarenko e2016-30*, MW9090384). A, F: habit, dry; B: capsule; C: stem transverse section; D: upper leaf cells; E: leaf transverse section; G-H, J: leaves; I: mid-leaf cells; K: basal leaf cells. Scale bars: 5 mm for A; 1 mm for B; 2 mm for G–H, J; 100 μm for C–E, I, K.

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 longitudinual rows of projecting cells; distal and median *laminal cells* 12–15×5–8 μm, thick-walled, subquadrate, 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 subuatus* 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-

Fig. 9. Distribution of *Campylopus* species in Russia.

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 Kronotzky State Reserve.

Specimens examined: **Primorsky Territory**: Olga Distr., Timofeevka settlement surroundings, the coastal area of Vladimira Bay (ca. 30 m alt.), on disturbed sandy soil in moist meadow (in abandoned wheel tracks), 28 Aug 2016, *Fedosov & Pisarenko* (MW9090384, 9115372, MHA, LE); Khasansky Distr., Ryazanovka near the field station of DVGU, roadside near creek, 14 Sept 1985 *Ignatov* (MHA). **Kamchatsky Territory**: Ust'-Bolsheretsky Distr., 800 m southwards from Pauzhetka Settl., upper heothermal field, 170 m alt., 1 Oct 2001, *Samkova 3* (MW9027943); Elizovo Distr., Kronotsky State Reserve, Geyzerov valley, thermal fields, 27 Sept 1961 *Lescshina* (MW9027942, 9027944).

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