

A MORPHOLOGICAL AND MOLECULAR PHYLOGENETIC STUDY OF THE GENUS  
*CALLIERGON* (CALLIERGONACEAE, BRYOPHYTA) IN RUSSIA

МОРФОЛОГИЧЕСКОЕ И МОЛЕКУЛЯРНО-ФИЛОГЕНЕТИЧЕСКОЕ ИЗУЧЕНИЕ РОДА  
*CALLIERGON* (CALLIERGONACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Calliergon* is usually accepted in the Northern Hemisphere with only four widespread species and 1–2 less well-known ones, but nevertheless practical identification work often ends with specimens that are difficult to identify. This is especially so in Asian Russia, where combinations of character states in many plants do not always fit the classical treatments for Europe and North America. Especially problematic are dioicous plants with large alar groups and a thin costa. Such morphotypes prevail in some northern regions of Siberia. A molecular phylogenetic tree based on ITS and *rpl16* placed such plants in a grade with clades of *C. giganteum* s.str. and *C. megalophyllum* nested within. The differences from *C. giganteum* and *C. megalophyllum* are moderately sharp and stable, thus we suggest segregation the northern Siberian plants as a subspecies, *C. giganteum* subsp. *sibiricum* Ignatova & Czernyadjeva. *Calliergon cordifolium* populations from high Arctic are differentiated by nrITS, and some of these plants have very broad leaves and fit the concept of *C. orbicularicordatum*, but other plants of the same haplotype are morphologically identical to *Calliergon cordifolium* s.str., precluding acceptance of *C. orbicularicordatum* at the species level. Far Eastern populations of *Calliergon cordifolium* s.l. appeared to be most sharply differentiated in both ITS, *rpl16* and morphology by exceptionally well differentiated leaf borders. However, taxonomic segregation seems unwise due to enormous variation in these populations.

Резюме

Обычно считается, что в Северном полушарии род *Calliergon* представлен четырьмя широко распространенными видами, и иногда выделяются еще 1–2 вида. Тем не менее, при определении образцов нередко встречаются такие, которые невозможно уверенно отнести ни к одному из этих видов. Это особенно часто бывает с образцами из азиатской России, которые имеют комбинацию морфологических признаков, не соответствующую классическим обработкам рода для Европы и Северной Америки. Наиболее проблематичными являются двудомные растения, имеющие листья с крупными группами ушковых клеток и узкой жилкой. Этот морфотип часто встречается в некоторых регионах Сибири. В молекулярно-филогенетических деревьях, полученных при анализе ядерного ITS и хлоропластного *rpl16*, эти образцы образуют граду, внутри которой располагаются клады *C. giganteum* s.str. и *C. megalophyllum*. Такие растения умеренно резко, но стабильно отличаются от *C. giganteum* и *C. megalophyllum*, и мы предлагаем выделять их в ранге подвида, *C. giganteum* subsp. *sibiricum* Ignatova & Czernyadjeva. Популяции *Calliergon cordifolium* из высокой Арктики имеют определенные отличия в ядерном ITS, некоторые из них характеризуются очень широкими листьями и хорошо соответствуют *C. orbicularicordatum*, но к этому гаплотипу относятся и растения, морфологически идентичные *Calliergon cordifolium* s.str., что не позволяет выделять *C. orbicularicordatum* как особый вид. На Дальнем Востоке России также встречаются растения *Calliergon cordifolium* s.l., наиболее сильно отличающиеся по обоим изученным молекулярным маркерам, ITS и *rpl16*, а также имеющие очень резко дифференцированную кайму по краю листа. Однако их выделение в отдельный таксон также представляется невозможным из-за сильной морфологической вариабельности растений в этих популяциях.

KEYWORDS: mosses, taxonomy, ITS, *rpl16*, new subspecies

INTRODUCTION

Pleurocarpous mosses form a terminal clade in moss evolution, and their relatively recent diversification is usually considered as a reason for the poor morphologi-

cal differentiation of many species. For taxonomy, this caused instability of generic circumscriptions. In the middle of 20th century, the genus *Calliergon* (Sull.) Kindb. (Podpera, 1954) included some species that are

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now classified in other genera: *Calliergon trifarium* (F. Weber & D. Mohr) Kindb. is now in *Drepanocladus* (Müll. Hal.) G. Roth (Amblystegiaceae), *C. sarmentosum* (Wahlenb.) Kindb. in *Sarmentypnum* Tuom. & T.J. Kop. (Calliergonaceae), and *C. stramineum* (Dicks. ex Brid.) Kindb. in *Straminergon* Hedenäs (Calliergonaceae), according to recent nomenclature (Hodgetts *et al.*, 2020).

The modern circumscription, however, was developed before the molecular phylogenetic studies started. The main revisions that rectified the concept of the genus were conducted by Karczmarz (1971), Tuomikoski & Koponen (1979) and Hedenäs (1993), and the taxonomy of widespread species of this genus did not change later on.

However, despite these treatments, practical identification of *Calliergon* specimens from the Russian territory is not always easy, as critical character states occasionally occur in combinations that are missed in identification keys. Especially difficult to interpret are dioicous plants with a narrow leaf costa (i.e. excluding *C. giganteum*) and alar group almost reaching the costa (i.e. excluding *C. megalophyllum*). The primary aim of the present study was to address to such phenotypes. In addition, other unusual morphotypes from different parts of Russia were included, for example, to shed light on the status and distribution of *C. orbicularicordatum* (Renauld & Cardot) Broth., a species reported from the North American Arctic, although remaining poorly known (Hedenäs, 1993, 2014).

#### MATERIAL AND METHODS

At first, collections from LE, MW, and MHA were studied, and the difficult phenotypes were selected for sequencing, along with a few ‘typical’ representatives of all species. The dataset was then supplemented to test the hypothesis that arose from the preliminary analysis.

#### *Molecular phylogenetic study*

We sequenced nuclear ITS region, as the most informative one for phylogenetic reconstructions of pleurocarps (Huttunen *et al.*, 2012), and the plastid *rpl16*, as these were found to be useful in other studies of the Calliergonaceae (Hedenäs, 2006, 2011), and are also available in GenBank for dataset extension. Species of all other genera of the family Calliergonaceae were used as the outgroup.

The laboratory protocol for ITS was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005). For ITS amplification the primers ‘ITS1’ and ‘ITS-B’ (White, 1990; Sahin *et al.*, 2007) and for *rpl16* region the primers ‘F71’ and ‘RI661’ (Jordan *et al.*, 1996) were used.

Sequences were aligned using MAFFT v. 7.402 (Kato & Standley, 2013) with standard settings.

Vouchers of newly sequenced specimens and GenBank accession numbers of all used sequences are compiled in Appendix 1.

At first the ITS (1135 bp) and *rpl16* (1098 bp) datasets were analysed separately to check their congruence. No supported conflicts were detected in preliminary Baye-

sian analyses and therefore a concatenated dataset was built and analysed.

Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), in each case with four runs, six chains, 10,000,000 generations, 25% burnin, chain temperature 0.02, and GTR+G model. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007). Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>) on XSEDE (Miller *et al.*, 2010).

Maximum parsimony analysis was performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculation for 2000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

#### *Morphological study*

The morphological study of the dioicous *Calliergon* species was conducted after molecular phylogenetic analysis sorted these into three groups (two clades and one grade), somewhat expected from preliminary morphological studies, i.e. ‘typical’ *C. giganteum* with stout costa, ‘typical’ *C. megalophyllum* with thin costa and small alar groups, and problematic specimens with a thin costa and large alar groups.

Measurements were done for two sets of samples. The first set included only sequenced specimens: 30 samples, 5 well-developed leaves taken from one stem from each sample, thus 150 leaves were measured.

The second set had about an equal number of measurements, but we took more samples, measuring 3 leaves in each of them, thus 53 samples and 159 leaves were studied. The second set was taken from LE herbarium specimens, identified previously as *C. giganteum* and *C. megalophyllum* and putatively a third undescribed species, characterised by thin costa and alar cells reaching or almost reaching the costa.

The following characters were used for measurements: (1) leaf length, mm; (2) leaf width, mm; (3) costa width at leaf base,  $\mu\text{m}$ ; (4) costa width at 1/3 the leaf length,  $\mu\text{m}$ ; (5) costa length, % of leaf length; (6) alar group extending % of distance to costa; (7) mid-leaf cell length,  $\mu\text{m}$ ; (8) mid-leaf cell width,  $\mu\text{m}$ . Ten cells were measured in each leaf and their mean length and width were used for the analysed dataset.

Four additional values were calculated for comparison of species and putative species:

- (1):(2) leaf length to width ratio;
- (3):(4) costa width at base to its width at 1/3 leaf length;
- (7):(8) cell length to width ratio;
- (7):(1) ratio cell length in  $\mu\text{m}$  to leaf length in mm, as this character was found to be useful in *Drepanocladus* (Hedenäs, 1998, 2014).

Specimen data and measurements are available as a Supplementary Materials.

The morphological data were processed with PAST (Hammer *et al.*, 2001).

## RESULTS

**Molecular phylogenetic study**

Separate Bayesian analyses of ITS and *rp16* datasets revealed no supported conflicts. The plastid marker is less variable and, expectedly, the *rp16* based tree has lower resolution: the *Calliergon* clade was almost unresolved with only two clades nested in the polytomy: (1) two-specimen clade of Far Eastern *C. cordifolium* (marked in the tree in Fig. 1 as *C. cordifolium* A), and (2) the rest of *C. cordifolium* accessions. Specimens of dioicous species of *Calliergon* and *C. richardsonii* form a polytomy.

The ITS tree is resolved almost identically to that of concatenated tree, thus only the latter is shown here in Fig. 1. The basal grade of the tree rooted on *Loeskypnum* includes, sequentially, species of *Straminergon*, *Warnstorfia*, *Sarmentypnum*, and the terminal clade of *Calliergon*. The latter has a maximal Bayesian posterior probability, while in MP analysis its bootstrap support is non-significant (PP=1, BS=50). The *Calliergon* clade includes two subclades: one is formed by *C. richardsonii* (PP=1, BS=96), and another (PP=1, BS=100) with all other species.

This maximally supported clade of *Calliergon* with long costa is subdivided into two subclades: one with autoicous plants (PP=1, BS=99) and another with dioicous (PP=0.85, BS=79). Autoicous plants, usually classified as one species, *C. cordifolium*, include a small clade of specimens from the Russian Far East (PP=1,

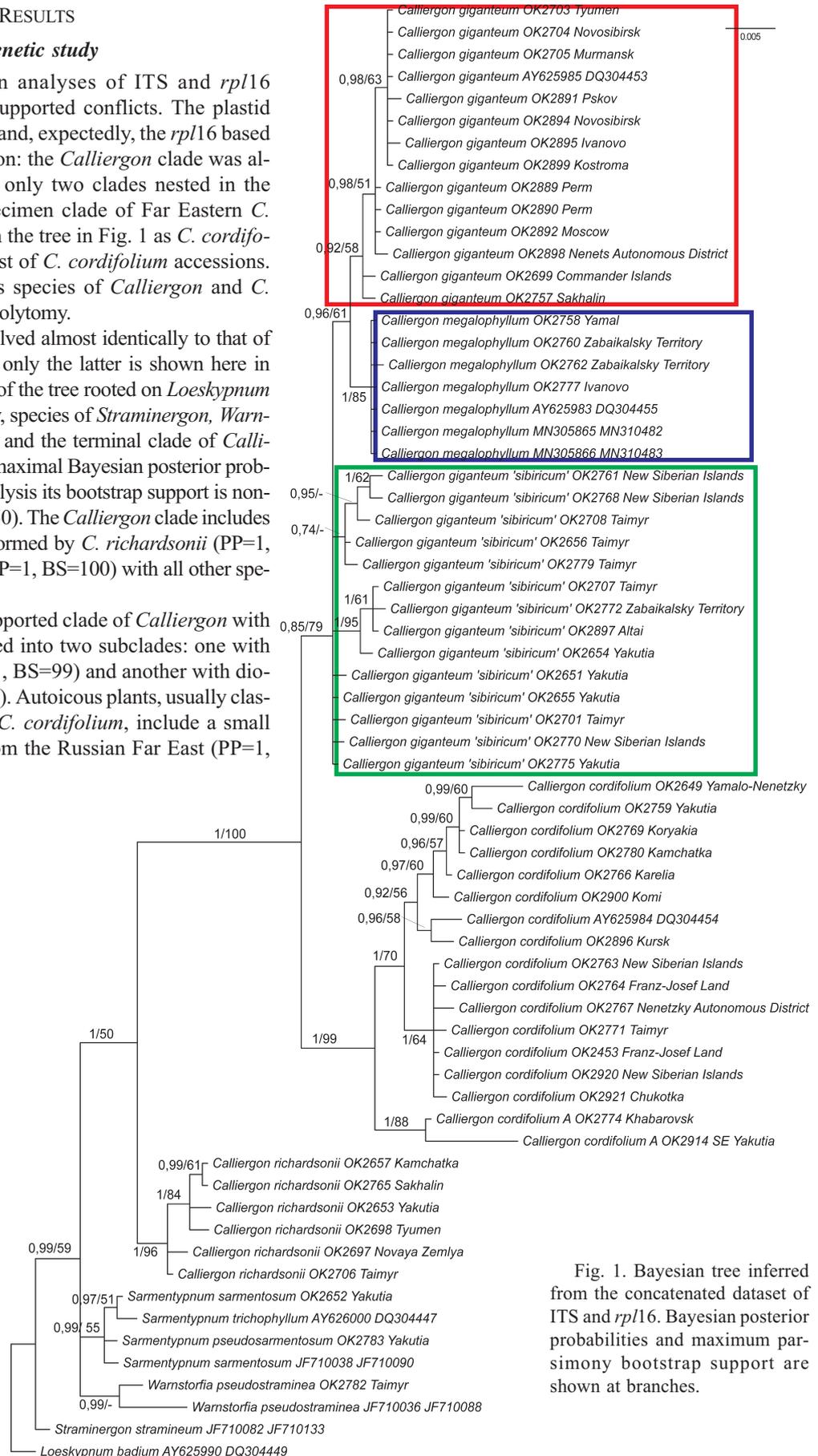


Fig. 1. Bayesian tree inferred from the concatenated dataset of ITS and *rp16*. Bayesian posterior probabilities and maximum parsimony bootstrap support are shown at branches.

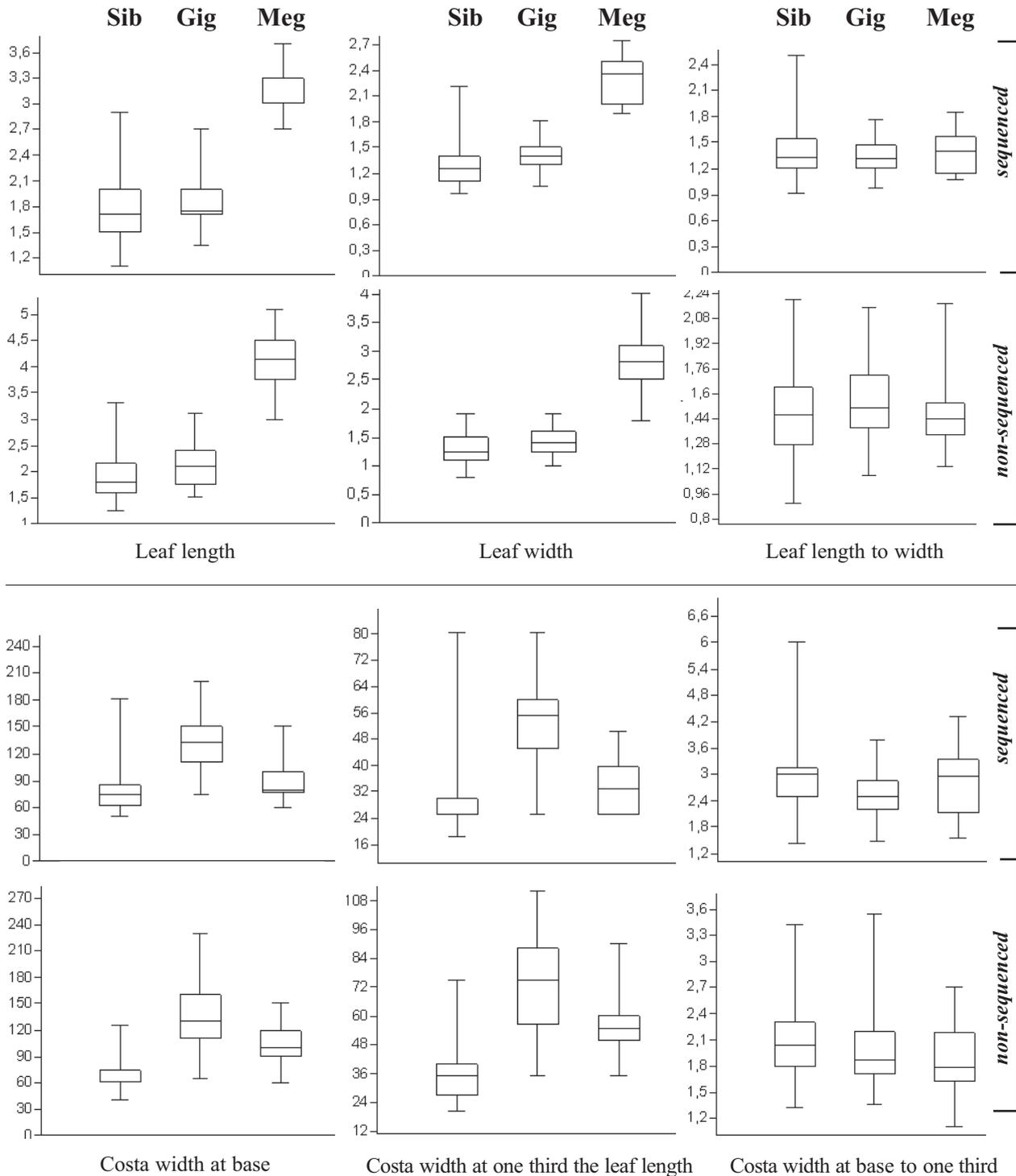


Fig. 2. Comparison of six morphological characters of three groups of *Calliergon* (**Sib**: *C. giganteum* 'sibiricum'; **Gig**: *C. giganteum* s.str.; **Meg**: *C. megalophyllum*), in two sets of morphometrical studies: sequenced and non-sequenced specimens.

BS=88) sister to other specimens of *C. cordifolium* (PP=1, BS=70), which is further subdivided into two clades: one with high Arctic species from Northern Siberia, some of which with the phenotype of *C. orbicularicordatus* (PP=1, BS=64), and another clade from scattered localities from Russia, including both eastern, western, southern, and Arctic populations, and also West European plants (PP=0.92, BS=56).

The dioecous species clade is poorly supported (PP=0.85, BS=79). It comprises a polytomy composed by plants with narrow costa, from Siberia, mostly from areas with permafrost, and this polytomy has four nested clades. Two of them include species from the same region as in the polytomy and combine species without any geographical or morphological peculiarity. The third nested clade includes *C. megalophyllum* (PP=1, BS=85),

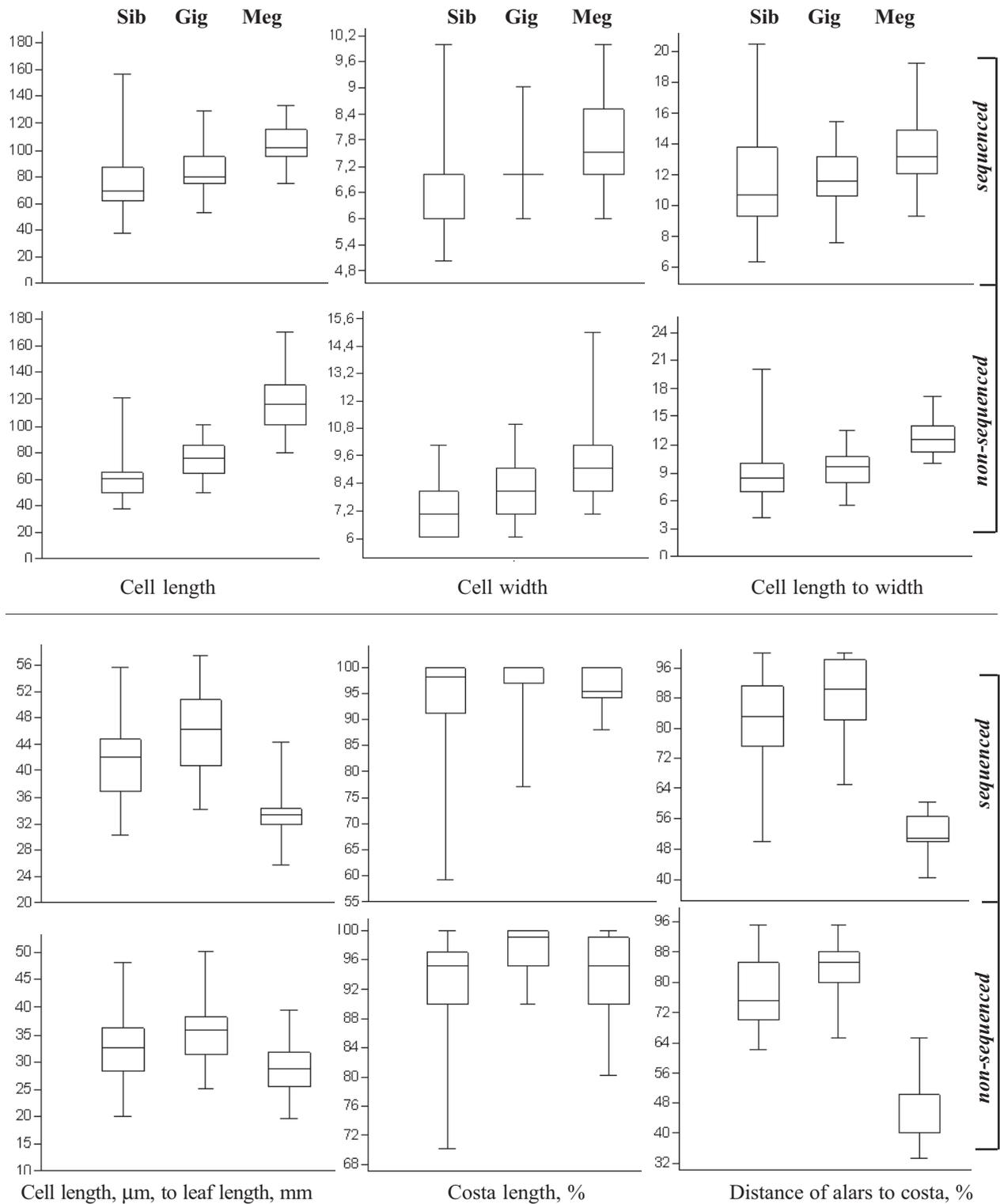


Fig. 3. Comparison of six morphological characters of three groups of *Calliargon* (**Sib**: *C. giganteum* 'sibiricum'; **Gig**: *C. giganteum* s.str.; **Meg**: *C. megalophyllum*), in two sets of morphometrical studies: sequenced and non-sequenced ones.

represented by seven accessions that form a polytomy. The last nested clade (PP=0.92, BS=58) includes *C. giganteum* s. str. (mostly with a broad costa) from different parts of Eurasia, mostly outside the permafrost region in Siberia.

#### Morphological study

A partial genetic and geographic differentiation of plants from the permafrost region of Siberia raised a necessity to check if they can be identified by morphology. Results of the measurements are displayed in Figs. 2 and

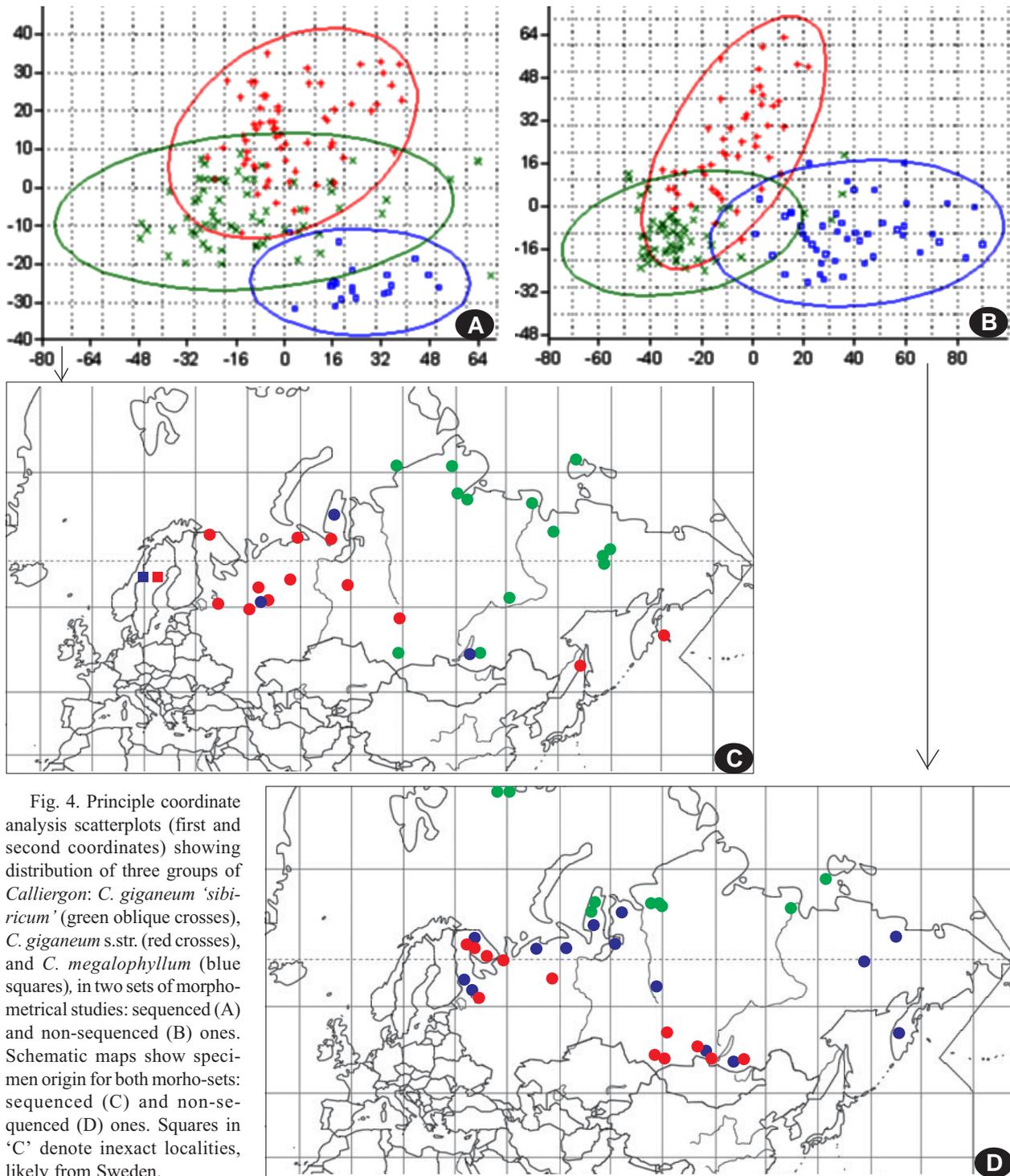


Fig. 4. Principle coordinate analysis scatterplots (first and second coordinates) showing distribution of three groups of *Calliergon*: *C. giganteum* 'sibiricum' (green oblique crosses), *C. giganteum* s.str. (red crosses), and *C. megalophyllum* (blue squares), in two sets of morphometrical studies: sequenced (A) and non-sequenced (B) ones. Schematic maps show specimen origin for both morho-sets: sequenced (C) and non-sequenced (D) ones. Squares in 'C' denote inexact localities, likely from Sweden.

3, showing twelve studied characters for pairs of sequenced and non-sequenced plants. These characters show rather similar patterns, that differ mostly for *C. megalophyllum* which was measured in sequenced dataset only in four specimens.

The box plots in Figs. 2 and 3 point to five characters that differentiate taxa of three groups better than others: leaf length, leaf width, cell length, width of costa at one third leaf length, and alar group (extension towards costa).

Using these five characters, the two morphological

datasets were compared by the Principal coordinate analysis in PAST (Hammer *et al.*, 2001), Fig. 4. The overlap between 'typical *C. giganteum*' and 'typical *C. megalophyllum*' is absent in the dataset of sequenced plants (Fig. 4A) or is very small in second set of non-sequenced plants (Fig. 4B). The putative third species (denoted in Fig. 1 as *C. giganteum* 'sibiricum') overlaps strongly with the two mentioned taxa, and in the scatterplot of sequenced plants (Fig. 4A) this overlap is greater than in non-sequenced ones (Fig. 4B).

## DISCUSSION

*Dioicous species*

The molecular phylogenetic tree found dioicous plants of *Calliergon* rather poorly resolved, with only two clades of high support: one (PP=1, BS=95) combines four specimens that are separated from other plants of the group neither in morphology, nor in geography. Another well supported clade (PP=1, BS=95) joins seven specimens of *C. megalophyllum*.

The clade sister to *C. megalophyllum* is poorly supported (PP=0.92, BS=58), but at the same time it is more or less consistent in morphology with 'typical *C. giganteum*': most plants of this clade have a broad, stout costa, whereas dioicous *Calliergon* outside this clade almost never have such costa. Therefore, the North Siberian plants with thin costa and large alar groups, which identity was in the main focus of the present study, receive genetic support (albeit poor) for their segregation. Interestingly, such plants were found so far mostly in the area of permafrost in Siberia, with a few finds in the high mountains of Altai and Transbaikalia. A number of specimens from the Urals and West Siberian lowland with a comparatively thin costa and large alar groups similar to North Siberian plants of *C. giganteum* 'sibiricum' were found in the *C. giganteum* clade.

The interpretation of these results is not straightforward. The first possibility would be to combine all dioicous *Calliergon* in one species as there are specimens that are impossible to identify by morphology, i.e. sort between two known species: *C. giganteum* and *C. megalophyllum*. However, an inconsistency between molecular and morphological groupings of specimens occur in some other genera of the family Calliergonaceae. In expanded analysis of the genus *Sarmentypnum* Hedenäs (2011, 2015) found few such inconsistencies, which nevertheless require special study and being infrequent, 1-3%, do not preclude recognition of species which are well recognizable in most cases. Similarly, *C. giganteum* and *C. megalophyllum* in Europe rarely provide identification problems.

The Asian plants called *C. giganteum* 'sibiricum' in Fig. 1 overlap strongly with other species. However, the overlap with *C. giganteum* is obviously greater than with *C. megalophyllum* (Fig. 4A,B), so further discussion of the possible inclusion of *C. giganteum* 'sibiricum' in *C. megalophyllum* is not necessary. The status of *C. giganteum* 'sibiricum' therefore needs to be decided only relative to *C. giganteum*.

One could argue for the segregation of *C. giganteum* 'sibiricum' as a separate species as follows: (1) an almost allopatric distribution; (2) genetic differentiation in ITS; (3) differentiation in most cases by the combination of thin costa and large alar groups; (4) a costa that occasionally ends far below the leaf apex. At the same time, the main difference for practical identification will be in the width of the costa, which overlaps rather strongly and suboptimally developed plants of *C. giganteum* (cf. Fig. 5) will likely cause many cases of misidentifications.

One more problem with recognising *C. giganteum* 'sibiricum' as a species based on the mentioned two features, the thin costa and large alar groups, can be seen in Fig. 4A, B. The molecular circumscription of *C. giganteum* 'sibiricum' in Fig. 4A is obviously wider than the morphologically defined group in Fig. 4B. The much broader variation in Fig. 4A raises suspicion that it is easy to misidentify outlying morphotypes, that genetically belong to the *C. giganteum* 'sibiricum', as *C. giganteum* or *C. megalophyllum*. Figure 5 includes both typical and outlying morphotypes of *C. giganteum* s. str., *C. giganteum* 'sibiricum', and *C. megalophyllum*, illustrating the difficulties of making a certain identification in some cases.

On the other hand, a simple inclusion of *C. giganteum* 'sibiricum' into *C. giganteum* provides a considerable difficulty to circumscribe *C. giganteum* s.l., and its differentiation from *C. megalophyllum* only by the alar group size.

We suggest the formal recognition and description of *C. giganteum* 'sibiricum' as a subspecies, that will make possible to sort out this morphotype in many cases (and continue searching for additional characters differentiating these plants), while it makes possible to accept *C. giganteum* sensu lato for equivocally looking plants, and to retain the name, that is abundantly represented in studies of the vegetation science.

*Calliergon giganteum* subsp. *sibiricum* Ignatova & Czernyadjeva, subsp. nov. Figs. 6, 5: E–L, 7.

**Holotype:** Right bank of Tirektyakh River in middle course, west of Mramornaya Mt., 64°52'43"N, 146°31'13"E, 1240 m alt., flat depression with lakes, flooded site with *Carex stans* between lakes, 14 July 2018, Ignatov & Ignatova 18-1525 (Holotype: MHA9028275!, isotype MW9091937!). Figs. 6, 7.

**Diagnosis:** Dioicous *Calliergon*, differs from *C. giganteum* in weak costa and from *C. megalophyllum* in large alar groups.

**Description:** Plants medium-sized, green or olivaceous-green. Stems 3–7(–15) cm long, simple, irregularly branched or, rarer, pinnately branched. Stem leaves appressed to erect, (1.2–)1.7–2.7(–3.3)×(0.9–)1.2–1.4(–2.2) mm; ovate or ovate-triangular, rounded at apex, cordate at base, concave; costa thin, reaches 0.9–1.0 leaf length, rarely in largest leaves only 0.7 the leaf length, often indistinct in upper portion, (50–)60–80(–180) μm wide at base, (20–)25–40(–60) μm wide at one third the leaf length; median laminal cells (40)50–65(–120)×(4.5–)6–7.5(–10) μm, with moderately thickened walls; alar cells large, thin-walled, forming large, sharply delimited group reaching (0.5–)0.7–0.9(–1.0) the distance from leaf margin to costa. Dioicous, sporophytes rare. Male plants not seen. Inner perichaetial leaves 2.25–2.5×0.9–1.2 mm, straight, not plicate, oblong-triangular, strongly concave, subobtusate at apex, with entire margins, costa single, thin, reaching 0.65–0.95 of leaf length. Setae 3–4 cm long, reddish-brown. Capsules inclined to horizontal, oblong, curved, occasionally with mouth turned down-

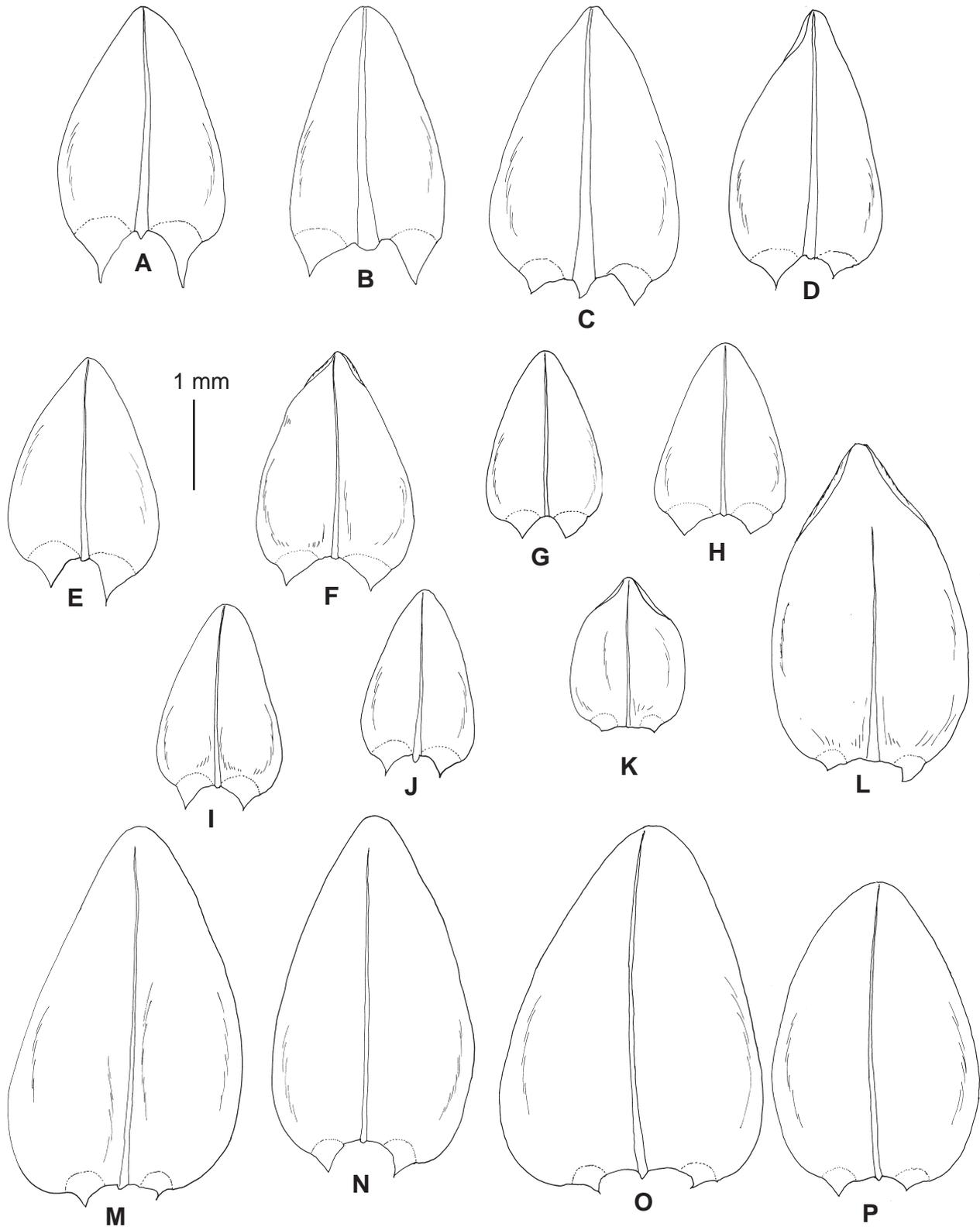


Fig. 5. Leaves of three dioicous taxa of the genus *Calliergon*, showing their variation. A–D – *Calliergon giganteum* subsp. *giganteum* (A: OK2699, Commander Islands; B: OK2703, Tyumen Province; C: OK2704, Novosibirsk Province; D: OK2705, Murmansk Province); E–L – *C. giganteum* subsp. *sibiricum* (E: OK2654, central Yakutia; F: OK2701, Taimyr; G: OK2655, eastern Yakutia; H: OK2651, eastern Yakutia; I: OK2708, Taimyr; J: OK2707, Taimyr; K: OK2702, Taimyr; L: OK2656, Taimyr); M–P – *C. megalophyllum* (M: OK2760, Zabaikalsky Territory; N: OK2762, Zabaikalsky Territory; O: OK2758, Yamal; P: OK2777, Ivanovo Province). Scale bars: 1 mm for all.

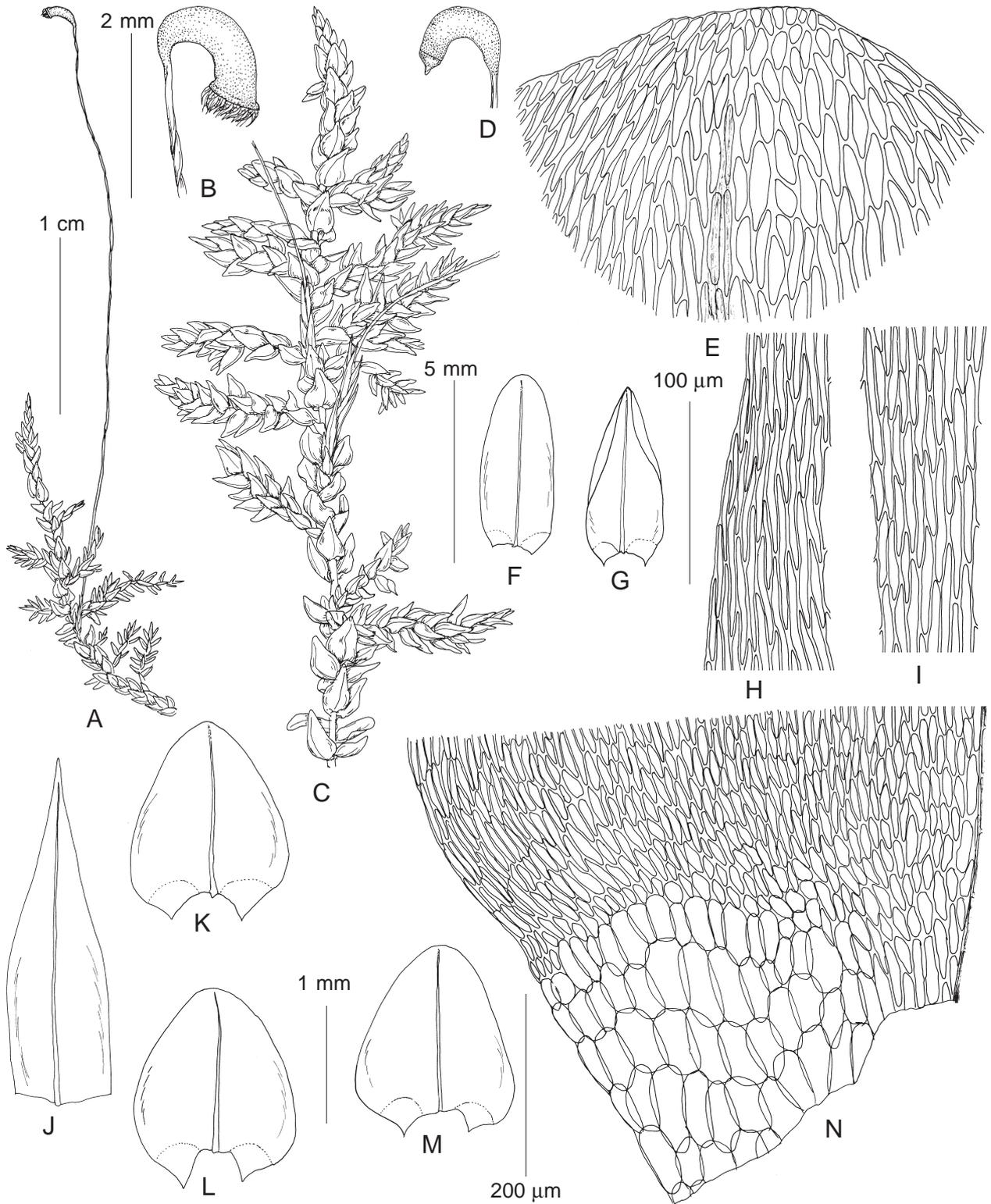


Fig. 6. *Calliergon giganteum* subsp. *sibiricum* (from holotype): A, C: habit, dry; B, D: capsules; E: upper leaf cells; F–G: branch leaves; H–I: median laminal cells; J: inner perichaetial leaf; K–M: stem leaves; N: basal laminal cells. Scale bars: 1 cm for A; 5 mm for C; 2 mm for B, D; 1 mm for F–G, J–M; 200 µm for N; 100 µm for E, H–I.

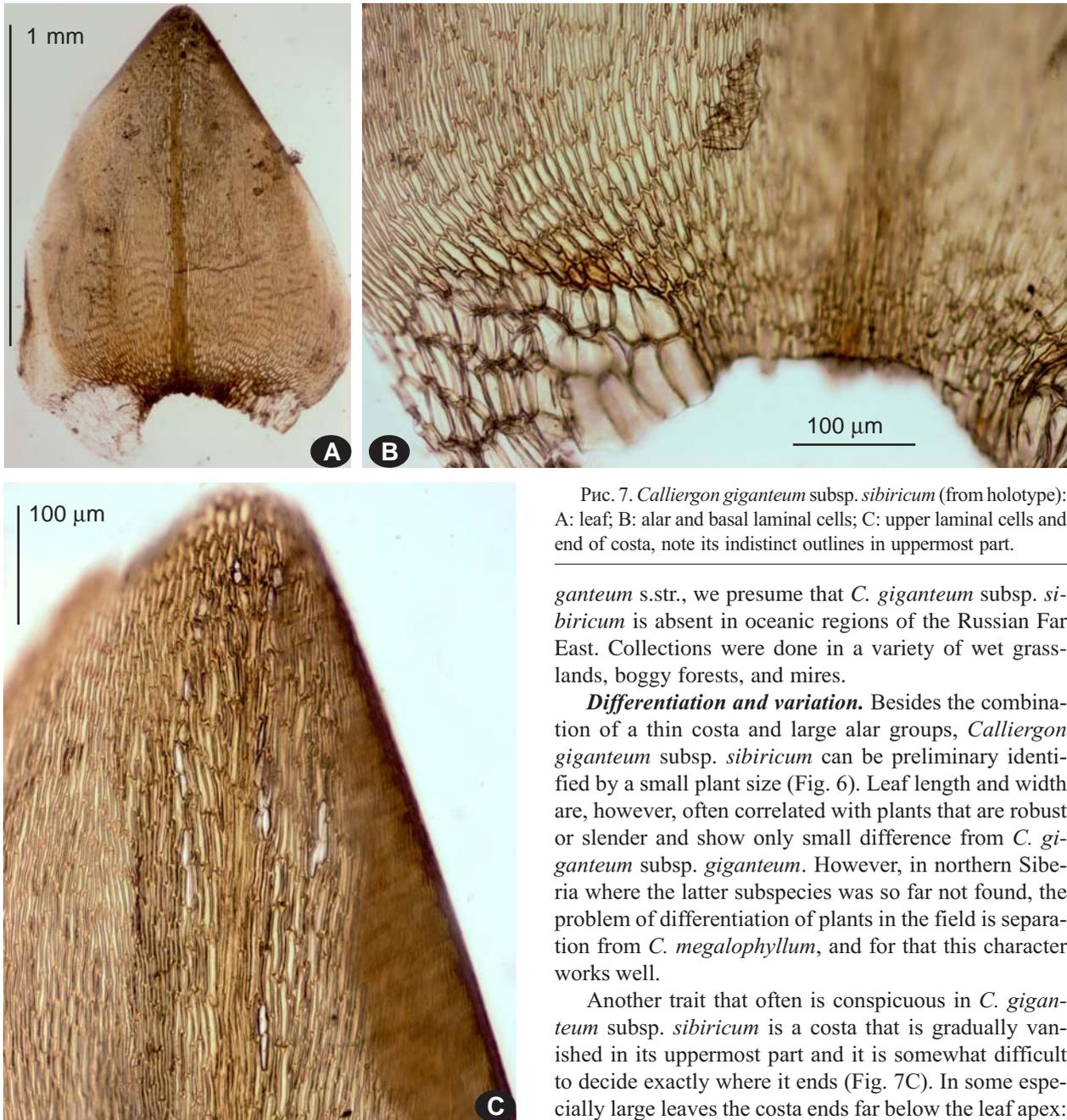


FIG. 7. *Calliergon giganteum* subsp. *sibiricum* (from holotype): A: leaf; B: alar and basal laminal cells; C: upper laminal cells and end of costa, note its indistinct outlines in uppermost part.

*giganteum* s.str., we presume that *C. giganteum* subsp. *sibiricum* is absent in oceanic regions of the Russian Far East. Collections were done in a variety of wet grasslands, boggy forests, and mires.

**Differentiation and variation.** Besides the combination of a thin costa and large alar groups, *Calliergon giganteum* subsp. *sibiricum* can be preliminary identified by a small plant size (Fig. 6). Leaf length and width are, however, often correlated with plants that are robust or slender and show only small difference from *C. giganteum* subsp. *giganteum*. However, in northern Siberia where the latter subspecies was so far not found, the problem of differentiation of plants in the field is separation from *C. megalophyllum*, and for that this character works well.

Another trait that often is conspicuous in *C. giganteum* subsp. *sibiricum* is a costa that is gradually vanished in its uppermost part and it is somewhat difficult to decide exactly where it ends (Fig. 7C). In some especially large leaves the costa ends far below the leaf apex: one such leaf is shown in Fig. 5L. Such plants could be identified as *C. richardsonii*, so DNA was re-extracted and re-sequenced to confirm the identity of this specimen with most other specimens of *C. giganteum* subsp. *sibiricum*.

**Specimens examined:** (other than those in Appendix 1, with sequenced samples).

**Selected specimens examined:** RUSSIA: **Altai Territory:** Biisky Okrug, Malyi Ad mire, 27 Jul 1928, *Sheludyakova s.n.* (LE). **Amur Province,** Bysa River, 25 Aug 1927, *Kuzeneva 88* (LE); Zeya River basin, Bomnak River, 28 Aug 1910, *Abramov 121* (LE). **Arkhangelsk Province:** Franz Josef Land, Meibl Island, 28 Jul 1979, *Safronova s.n.* (LE); Franz Josef Land, Hooker Island, 80°20'18.7"N, 52°47'27.6"E, 29 Jul 2019, *Konoreva 913* (LE). **Buryatia Republic,** West Sayan, Oka River, 52°34'N, 100°07'E, 9 Jul 2008, *Afonina 02808* (LE);

wards, ca. 2 mm long, brownish. *Operculum* conic, with short obtuse beak. *Peristome* perfect; *exostome teeth* 600–700 µm long, light brownish, on dorsal surface finely striolate-reticulate below, finely papillose above; endostome with high basal membrane, segments about the same length as exostome teeth, perforated, finely papillose, cilia 2–3, long, nodose to shortly appendiculate. *Spores* 13–18 µm, finely papillose. *Calyptrae* not seen.

**Distribution and ecology.** The subspecies occurs in the tundra zone and in mires in permafrost regions of the boreal zone, occasionally in the upper belts of high mountains in continental areas. Fig. 4C–D shows approximate limits of the species distribution; preliminary attempts to find it in Europe failed. Because the easternmost localities of dioicous *Calliergon* belong to *C. gi-*

Mukhorshibirsky District, Bolshoy Sibilduy River, 50°48'57"N, 107°20'18"E, 25 Aug 2018, *Afonina s.n.* (LE, #1218). **Chukotsky Autonomous District:** Ioni Lake, 3 Jul 1977, *Afonina s.n.* (LE); Yanrakynnot Settlement, 20 Jul 1976, *Afonina s.n.* (LE); Amguema River, 17 Aug 1970, *Afonina s.n.* (LE); Aion Island, 19 Jul 1983, *Afonina CH-00064* (LE); Il'myneiveem River, 30 Jul 1978, *Afonina s.n.* (LE); Vrangal Island, Somnitelnaya Bay, 23 Jul 1985, *Afonina s.n.* (LE). **Krasnoyarsk Territory:** Kureika station, 17 Sept 1933, *Sokolov s.n.* (LE, #26); **Archipelago Severnaya Zemlya,** Island of the October Revolution, 24 Aug 1975, *Safronova s.n.* (LE); **Evenkia,** Turukhansk Region, Lower Tunguska River, 9 Jul 1932, *Rubin & Maskil s.n.* (LE); Chunya River, 9 Jul 1931, *Rubin s.n.* (LE); **Taimyr Autonomous District:** mouth of Malaya Logata River, 98°24'N, 73°25'E, 5 Aug 1988, *Pospelova s.n.* (MW9026350); Lake Syrutaturku, 73°35'N, 97°30'E, *Pospelova 94/55 & 94/66* (MW9026351, MW9026352); West Taimyr, Willem Barentz Biostation, Meduza Bay, 20 Jul 2001, *Varlygina s.n.* (MW9026276); Afanas'evskie Lakes, 71.5896°N, 106.117°E, *Fedosov 06-64* (MW9026280); between Afanas'evskie Lakes and Fomich River, 71.6208°N, 106.315°E, *Fedosov 06-442* (MW9026274); mouth of Kogotok Creek, 70.8195°N, 100.983°E, *Fedosov 09-227* (MW9026273); Nyurai-tar Creek – left tributary of Bikada River, 17 Aug 1978, *Sokolova s.n.* (MW9026284); northern edge of Anabar Plateau, watershed of Popigai and Anabarka Rivers, 72.1283°N, 110.702°E, *Fedosov 08-305* (MW9010425); Taimyr, Dixon Island, 7 Aug 1954, Dorogostaiskaya (LE); Uboinaya River, 19 Aug. 1988, *Kannukene s.n.* (LE, #14975); Mamontova River, 12 Aug. 1949, *Tikhomirov & Uvarov s.n.* (LE); Kresty Settlement, Aug. 1976, *Matveeva s.n.* (LE); Tareya Settlement, 22 Jul 1970, *Blagodatskikh s.n.* (LE); Novaya River, Ary-Mas, 1 Aug. 1972, *Afonina s.n.* (LE); Plateau Putorana, Ayan Lake, 23 Jul 1983, *Czernyadjeva 88* (LE); Plateau Putorana, Lama Lake, Jul 1984, *Czernyadjeva 65* (LE). **Kamchatsky Territory:** Paratunka River, 25 June 1957, *anonym* (LE). **Khabarovsk Territory,** Nikolaevsky District, Kulchi Settlement, 13 Aug 1964, *Ganeka s.n.* (LE). **Magadan Province:** Chaunsky District, 18 Jul 1977, *Blagodatskikh s.n.* (LE); Olsky District, Atargan Settlement, 29 Jul 1978, *Blagodatskikh s.n.* (LE). **Zabaikalsky Territory:** vicinity of Nerchinsk Town, 4 Jul 1908, *Novopokrovskij 1564* (LE); Sokhondinski Reserve, 49°27'N, 110°51'E, 11 Jul 2010, *Czernyadjeva 8-10* (LE); Gazimuro-Zavodskiy District, 52°14'48"N, 119°23'22"E, 22 Jul 2012, *Afonina 2912* (LE); Kalarsky District, Naminga Settlement, 56°36'N, 118°32'E, 2 Aug 1985, *Filin s.n.* (LE, MW); Alkhanay National Park, 50°48'N, 113°03'E, 16 Jul 2005, *Afonina 1005* (LE). **Tuva Republic:** East Tannu-Ola Range, 50.90890°N, 94.32896°E, 30 Jun 2018, *Pisarenko tv18-5d* (LE). **Yamalo-Nenetsky Autonomous District:** Yamal, Junto Lake, 67°40'N, 68°00'E, 10 Aug 1993, *Czernyadjeva 56* (LE); Yamal, vicinity Syunyaj-Sale Settlement, 66°55'N, 71°20'E, 26 Jul 1996, *Czernyadjeva 42* (LE). **Republic of Sakha/Yakutia:** Momsy District: Ulakhan-Chistai Mt. Range, west of Mramornaya Mt., 64°52'43"N, 146°31'13"E, *Ignatov & Ignatova 18-1523* (MHA9028171); middle course of Tirektyakh River, Ulakhan-Chistai Mt. Range, 64°54'28"N, 146°25'52"E, *Ignatov & Ignatova 18-1897* (MHA9092425); lower course of Tirektyakh River, Tymny-Ulakh Creek, 64°10'33"N, 146°45'09"E; *Ignatov & Ignatova 18-2498* (MHA9029134); Khangalassky District: Ulakhan Keteme Creek near road to Tit-Ary, 61°15'50"N, 128°05'09"E, *Ignatov & Ignatova 16-165* (MHA9022144); Tomponsky Dis-

trict: between Khandyga and Teplyi Klyuch Settlements, 62°45'28"N, 136°28'19"E, *Ignatov & Ignatova 18-1214* (MHA9027704); New Siberian Islands, Stolbovoi Island, 74°10'31.2"N, 135°27'36.6"E, 3 Aug 2019, *Czernyadjeva 8-19* (LE); New Siberian Islands, Kotelny Island, 25 May 1947, *Gorodkov s.n.* (LE); New Siberian Islands, Bolshoi Lyakhovskiy Island, 73°20'N, 140°00'E, 25 Aug 1956, *Pigulevskaya s.n.* (LE); Tiksi, 71°40'42.6"N, 128°51'7.1"E, 30 Jul 2019, *Czernyadjeva 3-19* (LE); delta of Lena River, Samoillovskiy Island, 72°22'N, 126°29'E, Aug 1998, *Zhurbenko s.n.* (LE); lower course of Indigirka River, 17 Aug 1974, *Afonina s.n.* (LE); Medvezhji Islands Archipelago, Chetyrekhtolbovoi Island, 70°37'N, 162°27'E, 7 Aug 1980, *Zaslavskaja s.n.* (LE); Nizhnekolymsk District, Pokhodsk Village, 6 Aug. 1973, *Stepanova 2/6* (LE); Suntarsky District, Vilui River basin, 5 Aug. 1958, *Kildyushevsky 77/5* (LE); Indigirka River basin, Moma River, 66.5°N, 30 May 1936, *Sheludyakova s.n.* (LE); Lensk District, Dzerba River basin, 60°29'N, 116°50'E, 20 Jul 2000, *Ivanova s.n.* (LE); Tomponsky District, Delinnaya River, 28 Jun 1955, *V. Ivanova s.n.* (LE); Olekminsk District, Tokko River, 20 Jul 1995, *Krivoshapkin 02.04.01.09* (LE).

**Comment on the subspecies' distribution.** The distribution of dioicous taxa of *Calliergon giganteum* group (Figs. 4C–D; 8) shows that subsp. *sibiricum* appears to be restricted mostly to areas with permafrost, and it is absent in the extensive boggy lowland of West Siberia and oceanic regions along Pacific coast of Asia where *Calliergon giganteum* subsp. *giganteum* occurs (Figs. 4C–D; 8). Interestingly, in the severe climate of the Transbaikalia, with local (though not rare) permafrost spots, *Calliergon giganteum* subsp. *sibiricum* appears to be much more common than subsp. *giganteum*.

**Comment on phytogeography.** In general, the known distribution of *Calliergon giganteum* subsp. *sibiricum* is similar to some common Yakutian species, e.g. *Tomentypnum involutum* (Limpr.) Hedenäs & Ignatov (Hedenäs *et al.*, 2020). However, in contrast to *T. involutum*, which populations in Yakutia are sympatric with *T. nitens*, a widespread Holarctic species, the distributions of *C. giganteum* subsp. *sibiricum* and subsp. *giganteum* hardly overlap.

A more similar situation has been found by Hedenäs (2009) for *Scorpidium cossonii*–*S. scorpioides* complex. *Scorpidium scorpioides* has obviously evolved inside basal *S. cossonii*; similarly, *Calliergon megalophyllum* originated from *C. giganteum* s.l., that gave also a lineage of *C. giganteum* s.str. In both cases 'ancestral' grades (of *S. cossonii* and *C. giganteum* subsp. *sibiricum*) have Arctic to northern distributions. In both cases the derivatives, *S. scorpioides* and *C. megalophyllum* received a rather strong morphological difference and bigger size, and also both latter species often grow submerged, at least for larger parts of their bodies.

Hedenäs (2009) estimated that *S. cossonii* must have evolved before the general cooling of the climate started in Pliocene, earlier than the Arctic region expanded. As the complex of the dioicous *Calliergon* taxa received a stronger genetic differentiation, we may suggest that it is likely no less ancient; moreover, *C. giganteum* was re-

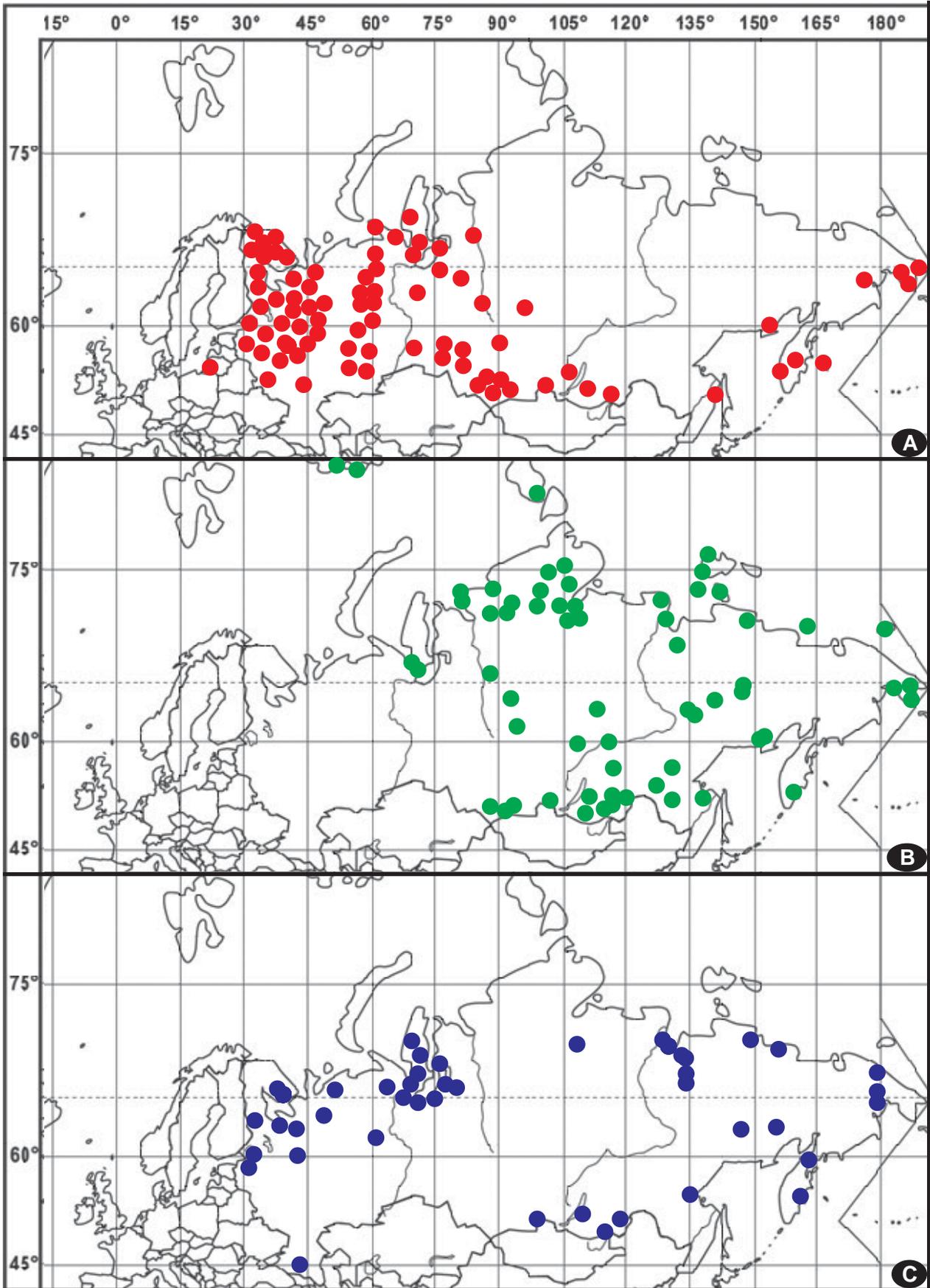


Fig. 8. Distribution of *Calliergon giganteum* subsp. *giganteum* (A), *C. giganteum* subsp. *sibiricum* (B), and *C. megalophyllum* (C), based on specimens in LE, MHA, and MW.

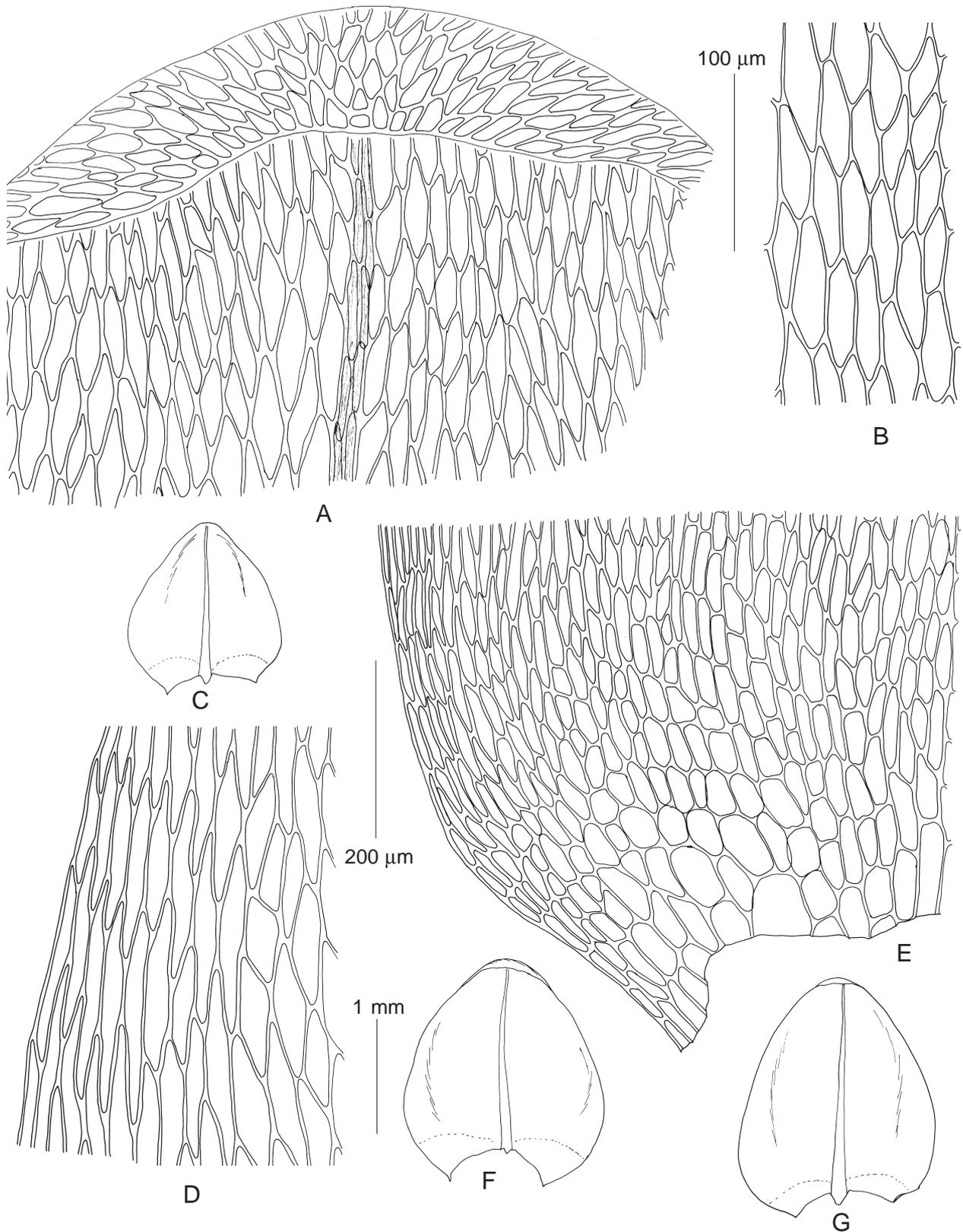


Fig. 9. *Calliergon cordifolium*, high Arctic morphotype corresponding to *C. orbicularicordatum* (from: Russia, Franz-Josef Land, 23 Aug 2012, *Kholod* #71, LE). A: upper leaf cells; B, D: median laminal cells; C: branch leaf; E: basal laminal cells; F–G: stem leaves. Scale bars: 1 mm for C, F–G; 200 μm for E; 100 μm for A–B, D.

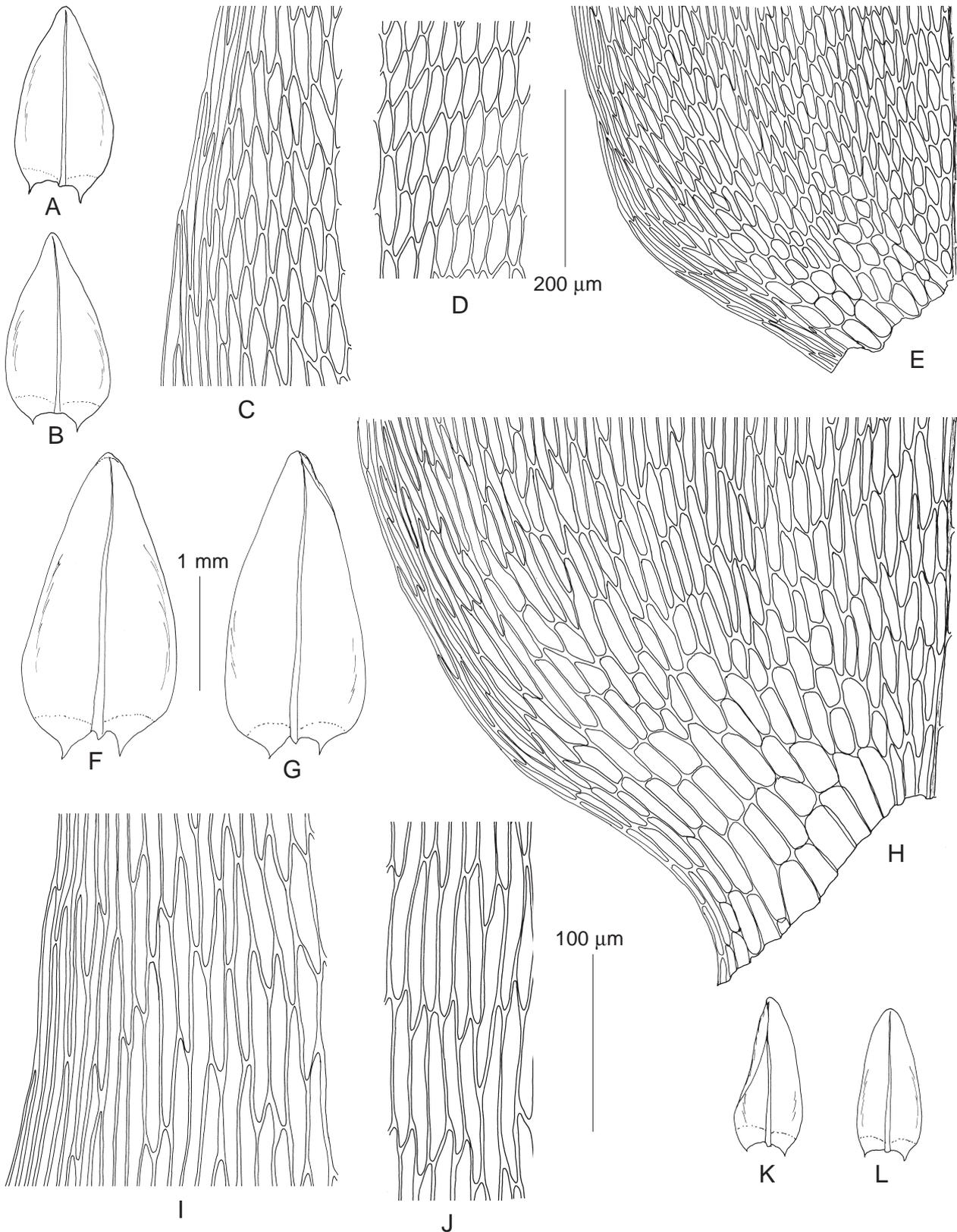


Fig. 10. *Calliergon cordifolium*, Far Eastern morphotype with sharply delimited leaf border, showing variation (from: Russia, Yakutia, Yugorenok, *Ignatov 00-901*, MHA9010447). A–B, F–G: stem leaves; C–D, I–J: median laminal cells; E, H: basal laminal cells; K–L: branch leaves. Scale bars: 1 mm for A–B, F–G, K–L; 200 μm for E, H; 100 μm for C–D, I–J.

ported from Late Miocene or Pliocene deposits of Beaufort Formation (Kuc & Hills, 1971; Kuc, 1973). Although the overlap in distribution of *C. giganteum* subsp. *giganteum* and subsp. *sibiricum* is considerably smaller compared to that for haplotypes of *Scorpidium cossonii* (Hedenäs, 2009), the genetic isolation between these *C. giganteum* subspecies seems to be not strict.

#### *Autoicous species*

The autoicous species of *Calliergon* in Eurasia are usually treated as two species, *C. richardsonii* and *C. cordifolium* (Hodgetts *et al.*, 2020; Ignatov *et al.*, 2006).

The former is a northern species, and usually providing no problems with identification because its leaf costa ends far below the leaf apex. A short costa rarely occurs in *C. giganteum* subsp. *sibiricum* (cf. Fig. 5L) but in this species the short costa is not constant: study of many leaves from several shoots would find some (and usually a majority) leaves with a costa reaching leaf apex or almost so (>0.95 distance to apex).

The present analysis found a certain incongruence regarding *C. richardsonii*: in the ITS tree *C. richardsonii* is sister to the rest of the genus, and low support for the whole *Calliergon*-clade (BS=50) contrasts with the maximal support of a clade that includes *Calliergon* specimens other than *C. richardsonii*. Thus, even a position of *C. richardsonii* in the genus *Calliergon* is not unequivocal based on the MP analysis. However, a separate analysis of plastid *rpl16* does not resolve *C. richardsonii* at all, leaving its specimens in polytomy intermingled with dioicous species of *Calliergon*.

The second autoicous species, *Calliergon cordifolium*, appeared to be quite heterogeneous molecularly (Fig. 1). The present study revealed that plants from Arctic (Fig. 9) form a separate lineage with high to moderate support (PP=1, BS=64, see Fig. 1), and some plants of this genotype have characters considered diagnostic for *C. orbicularicordatum*: short and broad laminal cells and differentiated border of narrow cells in the lower part of the leaf (Fig. 10).

*Calliergon orbicularicordatum* was described from Hudson Bay in Canada, an area with a severe climate equivalent to that of continental areas in northern Russia. There were no records of this species in Eurasia yet, although northern plants fit it rather well (cf. Fig. 9) in having very broad leaves with a distinct leaf border of narrow cells. The alar cells in such plants form a large group, but the transition to laminal cells is less distinct than in most plants of *C. cordifolium*. Thus, how far they extend towards the costa is described differently by different authors. However, not all plants of this high Arctic ribotype possess this combination of traits, and some specimens with the identical sequences are indistinguishable from the most common morphotype of *C. cordifolium* from the forest zone. Thus, our present observations do not support a taxonomic segregation of high Arctic plants of *C. cordifolium* affinity and their relationship to

the North American plants of *C. orbicularicordatum* remains to be studied.

An even stronger morphological and genetic variation was found in Far Eastern plants of *C. cordifolium* (PP=1, BS=88, see Fig. 1), with ovate (not orbicular) leaves having an especially conspicuous border of narrow cells along the leaf margin, often extending almost to the leaf apex and fairly contrasting with the laminal cells further inwards, which are rhomboidal, with a length to width ratio of ca. 4:1 (Fig. 10). However, again, this morphology is not stable and in some shoots of the same collection (that looks otherwise homogeneous), we saw in some leaves a very distinct border, while a border was almost absent in other leaves. Such variation seems to depend on an extreme plasticity in a species adapted to growth in habitats with highly variable moisture conditions.

Kanda (1975) discussed *C. cordifolium* var. *japonicum* Card. and confirmed the conclusion of Karczmarz (1971) that this variety cannot be distinguished from var. *cordifolium*. The distinctions of this variety include smaller size of plants and sparse branching, which coincides with the Russian Far Eastern plants of the genotype mentioned above. Kanda did not mention a border of narrow cells, but it is illustrated in his publication and is contrasting with short mid-leaf cells (Kanda, 1975, figs. 49-6 and 49-7). Thus, it is likely that the eastern genotype found in the present study and shown in Fig. 10 occurs in Japan. However, Karczmarz (1971), in his key to the genus *Calliergon*, used the border of narrow cells and short mid-leaf cells as diagnostic only for *C. orbicularicordatum*, thus we are pending the applicability of the name *C. cordifolium* var. *japonicum* to the plants of the mentioned eastern genotype).

The morphological variation does not support taxonomic segregation in *Calliergon cordifolium* s.l., although it might be considered for future investigations based on data on haplotype distributions and modelling of the species distribution (e.g., Hedenäs, 2019).

#### KEY TO *CALLIERGON* SPECIES IN RUSSIA

1. Costa in most leaves to (0.4–)0.5–0.8 the leaf length ..... 1. *C. richardsonii*
- Costa in most leaves to 0.9–1.0 the leaf length ... 2
2. Alar cells gradually grading into other laminal cells; autoicous; leaf marginal cells often form more or less distinct border ..... 2. *C. cordifolium*
- Alar cells rather abruptly delimited from other laminal cells; dioicous; leaf marginal cells never form border ..... 3
3. Stem leaves (2.5–)3.0–4.0(–5.0)×1.5–2.0(–3.0) mm; alar group reaching 0.4–0.7 of distance to costa .... 3. *C. megalophyllum*
- Stem leaves (1.2–)1.5–2.7(–3.3)×0.9–1.5(–2.2) mm; alar group reaching (0.5–)0.7–1.0 of distance to costa ..... 4

4. Plants medium-sized; costa weak, (45–)60–80(–130)  $\mu\text{m}$  wide at base; stem leaves (1.5–)1.7–2.5(–3.3)  $\times$  (0.9–)1.2–1.4(–2.2) mm; alar cells extend to (0.5–)0.7–0.9(–1.0) of distance to costa .....  
 ..... 4a. *C. giganteum* subsp. *sibiricum*
- Plants medium-sized to large; costa strong, being (80–)110–160(–210)  $\mu\text{m}$  wide at base; stem leaves (1.5–)1.7–2.7(–3.0)  $\times$  (0.9–)1.2–1.5(–1.8) mm; alar cells extend to 0.8–1.0 of distance to costa .....  
 ..... 4b. *C. giganteum* subsp. *giganteum*

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## Appendix 1. Newly sequenced specimens, with voucher information and GenBank accession numbers.

Species	Isolate	Region	Voucher	ITS	rpl16
<i>Calliargon cordifolium</i>	OK2900	Russia, Komi Republic	Kucherov & Kutenkov 28 June 2007 #65d (MHA9010504)	MZ333478	MZ395587
<i>C. cordifolium</i>	OK2920	Russia, New Siberian Islands	Czernyadjeva 34-19a (LE)	MZ333479	MZ395588
<i>C. cordifolium</i>	OK2921	Russia, Chukotka	Afonina, 15 Aug 1969 (LE)	MZ333480	MZ395589
<i>C. cordifolium</i>	OK2774	Russia, Khabarovsk	Ignatov & Ignatova 13-295 (MW9026045)	MZ333481	MZ395590
<i>C. cordifolium</i>	OK2914	Russia, Yakutia	Ignatov 00-901 (MHA9010447)	MZ333482	MZ395591
<i>C. cordifolium</i>	OK2453	Russia, Franz-Josef Land	Kholod 23-8-2012 #71 (LE)	MZ333483	MZ395592
<i>C. cordifolium</i>	OK2759	Russia, Yakutia, Ust-Maya Distr.	Ignatov 00-908 (MHA9010448)	MZ333484	MZ395593
<i>C. cordifolium</i>	OK2763	Russia, New Siberian Islands	Czernyadjeva 34-19 (MHA9130370)	MZ333485	MZ395594
<i>C. cordifolium</i>	OK2764	Russia, Franz-Josef Land	Moseev 25 Aug 2016 (MHA9130368)	MZ333486	MZ395595
<i>C. cordifolium</i>	OK2766	Russia, Karelia	Zakharchenko bm-16-3 (MW9111418)	MZ333487	MZ395596
<i>C. cordifolium</i>	OK2767	Russia, Nenetsky Autonomous District	Lavrinenko #12, 11 Aug 2013 (MHA9130374)	MZ333488	MZ395597
<i>C. cordifolium</i>	OK2769	Russia, Koryakia	Kuzmina 18 Jul 2014		
			Bryophyta Rossica #414 (MW9073540)	MZ333489	MZ395598
<i>C. cordifolium</i>	OK2771	Russia, Taimyr	Pospelova 42 9 Jul 1992 (MW9026038)	MZ333490	MZ395599
<i>C. cordifolium</i>	OK2780	Russia, Kamchatka	Kozhin & Budanova Kam-M-859 (MW9091931)	MZ333491	MZ395600
<i>C. giganteum</i>	OK2892	Russia, Moscow Province	Ignatov & Notov 08-55 MHA9010459	MZ333492	MZ395601
<i>C. giganteum</i>	OK2889	Russia, Perm Province	Bezgodov 1 Aug 2012 #166 MHA9010497	MZ333493	MZ395602
<i>C. giganteum</i>	OK2890	Russia, Perm Province	Bezgodov 17 Aug 2004 #166 MHA9010496	MZ333494	MZ395603
<i>C. giganteum</i>	OK2891	Russia, Pskov Province	Zolotov lz82 MHA9010484	MZ333495	MZ395604
<i>C. giganteum</i>	OK2894	Russia, Novosibirsk Province	Lapshina op00906 MHA9010564	MZ333496	MZ395605
<i>C. giganteum</i>	OK2895	Russia, Ivanovo Province	Sorokin & Ivanov 4 June 2013 MHA9010482	MZ333497	MZ395606
<i>C. giganteum</i>	OK2898	Russia, Nenets Autonomous District	Ivanov & Donskov 09-284 MHA9010478	MZ333498	MZ395607
<i>C. giganteum</i>	OK2899	Russia, Kostroma Prov.	Sorokin et al. 30 June 2009 MHA 9010476	MZ333499	MZ395608
<i>C. giganteum</i>	OK2699	Russia, Commander Is., Bering Island	Fedosov 10-3-66 (MW9026322)	MZ333500	MZ395609
<i>C. giganteum</i>	OK2703	Russia, Tyumen	Bezgodov #198 19 July 2014 (MW9007247)	MZ333501	MZ395610
<i>C. giganteum</i>	OK2704	Russia, Novosibirsk	Pisarenko op04433 (MW9007246)	MZ333502	MZ395611
<i>C. giganteum</i>	OK2705	Russia, Murmansk	Kozhin M-M-0014 (MW9026092)	MZ333503	MZ395612
<i>C. giganteum</i>	OK2757	Russia, Sakhalin	Pisarenko op03552 (MHA9010538)	MZ333504	MZ395613
<i>C. g. subsp. sibiricum</i>	OK2897	Russia, Altai	Ignatov 36/239 MHA9010577	MZ333505	MZ395614
<i>C. g. subsp. sibiricum</i>	OK2651	Russia, Yakutia	Ignatov & Ignatova 18-2498 (MHA9092120)	MZ333506	MZ395615
<i>C. g. subsp. sibiricum</i>	OK2654	Russia, Yakutia	Ignatov & Ignatova 16-334 (MHA9021332)	MZ333507	MZ395616
<i>C. g. subsp. sibiricum</i>	OK2655	Russia, Yakutia	Ignatov & Ignatova 18-1525 (MHA9028275)	MZ333508	MZ395617
<i>C. g. subsp. sibiricum</i>	OK2656	Russia, Taimyr	Fedosov 08-602 (MHA9010599)	MZ333509	MZ395618
<i>C. g. subsp. sibiricum</i>	OK2701	Russia, Taimyr	Varlygina s.n., 15 July 2001 (MW9026283)	MZ333510	MZ395619
<i>C. g. subsp. sibiricum</i>	OK2707	Russia, Taimyr	Fedosov 05-213 (MW9026029)	MZ333511	MZ395620
<i>C. g. subsp. sibiricum</i>	OK2708	Russia, Taimyr	Fedosov 15 June 2004 (MW9026339)	MZ333512	MZ395621
<i>C. g. subsp. sibiricum</i>	OK2761	Russia, New Siberian Islands	Czernyadjeva 14-19 (MHA9130375)	MZ333513	MZ395622
<i>C. g. subsp. sibiricum</i>	OK2768	Russia, New Siberian Islands	Czernyadjeva 26-19 (MHA9130372)	MZ333514	MZ395623
<i>C. g. subsp. sibiricum</i>	OK2770	Russia, New Siberian Islands	Czernyadjeva 22-19 (MHA9130369)	MZ333515	MZ395624
<i>C. g. subsp. sibiricum</i>	OK2772	Russia, Zabaikalsky Territory	Afonina 1406 (MHA9130366)	MZ333516	MZ395625
<i>C. g. subsp. sibiricum</i>	OK2775	Russia, Yakutia	Czernyadjeva 5-19 (MHA9130371)	MZ333517	MZ395626
<i>C. g. subsp. sibiricum</i>	OK2779	Russia, Taimyr	Fedosov 08-602 (MHA9010599)	MZ333518	MZ395627
<i>C. megalophyllum</i>	OK2758	Russia, Yamal	Czernyadjeva & Kuzmina 29 July 1996		
			Bryophyta Rossica #111 (MW9026335)	MZ333519	MZ395628
<i>C. megalophyllum</i>	OK2760	Russia, Zabaikalsky Territory	Afonina 03107 (MHA9130365)	MZ333520	MZ395629
<i>C. megalophyllum</i>	OK2762	Russia, Zabaikalsky Territory	Czernyadjeva 13-10 (MHA9130373)	MZ333521	MZ395630
<i>C. megalophyllum</i>	OK2777	Russia, Ivanovo	Sorokin & Nosov 779 (MHA9010585)	MZ333522	MZ395631
<i>C. richardsonii</i>	OK2653	Russia, Yakutia	Ignatov & Ignatova 18-1895 (MHA9028117)	MZ333523	MZ395632
<i>C. richardsonii</i>	OK2657	Russia, Kamchatka	Czernyadjeva 15 Aug 2004		
			(Bryophyta Rossica #208 (MHA9010601))	MZ333524	MZ395633
<i>C. richardsonii</i>	OK2697	Russia, Novaya Zemlya	Beldiman NZ-2016-52 (MW9111380)	MZ333525	MZ395634
<i>C. richardsonii</i>	OK2698	Russia, Tyumen	Bezgodov #205, 19 July 2014 (MW9007250)	MZ333526	MZ395635
<i>C. richardsonii</i>	OK2706	Russia, Taimyr	Fedosov Calln3, 21 June 2004 (MW9026415)	MZ333527	MZ395636
<i>C. richardsonii</i>	OK2765	Russia, Sakhalin	Pisarenko op03553 (MHA9010623)	MZ333528	MZ395637
<i>C. richardsonii</i>	OK2698	Russia, Tyumen	Bezgodov #205, 19 July 2014 (MW9007250)	MZ333526	MZ395635
<i>C. richardsonii</i>	OK2706	Russia, Taimyr	Fedosov Calln3, 21 June 2004 (MW9026415)	MZ333527	MZ395636
<i>C. richardsonii</i>	OK2765	Russia, Sakhalin	Pisarenko op03553 (MHA9010623)	MZ333528	MZ395637
<i>Sarmentypnum pseudosarmentisum</i>	OK2783	Russia, Yakutia	Ivanova 36-37 (MHA9111773)	MZ333529	MZ395638
<i>S. sarmentosum</i>	OK2652	Russia, Yakutia	Ignatov & Ignatova 17-70 (MHA9025792)	MZ333530	MZ395639
<i>Warnstorfia pseudostraminea</i>	OK2782	Russia, Taimyr	Pospelova #43, 16 Aug 1989 (MHA9111777)	MZ333531	MZ395640