

THE GENUS *CAMPYLOPHYLLOPSIS* (BRYOPHYTA) IN RUSSIA REVISITED

РОД *CAMPYLOPHYLLOPSIS* (BRYOPHYTA) В РОССИИ

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Abstract

The genus *Campylophyllopsis* in Russia is revised based on morphology and the molecular phylogenetic analysis of nuclear (ITS) and plastid (*trnL-F* and *rbcL-atpB*) markers. The main problem tested was the position of ‘*Campylium squarrosulum*’, an East Asian species that is similar in aspect to *Campylophyllopsis sommerfeltii* but has single leaf costa, which was never reported for other species of this genus. Molecular data support its position in the genus, showing its close relationships to *Campylophyllopsis sommerfeltii*. Two specimens from the Russian Far East also similar in aspect to *Campylophyllopsis* were found to be strongly different in DNA sequences from all *Campylophyllopsis* species; they also differ from *Campylophyllopsis* in having a well differentiated stem hyalodermis and median leaf cells with prominent papillae above the distal cell ends. The latter features are rare in the Amblystegiaceae and are diagnostic for the genus *Podperaea*. These plants, however, were found to be quite unrelated to *Podperaea* phylogenetically, but were resolved in the clade with *Campylophyllopsis*, *Pseudocampylium*, *Serpoleskea*, *Pseudoamblystegium*, and *Hygrohypnum*, being most closely related to *Hygrohypnum styriacum*. They are described as new species and genus, *Jankuceraea pacifica* Ignatov & Ignatova.

Резюме

Проведена ревизия рода *Campylophyllopsis* в России на основе морфологического изучения образцов и молекулярно-филогенетического анализа ядерного (ITS) и хлоропластных (*trnL-F* and *rbcL-atpB*) маркеров. Основной целью этого исследования было определение таксономического положения ‘*Campylium squarrosulum*’, восточно-азиатского вида, внешне похожего на *Campylophyllopsis sommerfeltii*, но имеющего листья с простой жилкой, тогда как у всех других видов этого рода жилка короткая двойная. Молекулярные данные подтверждают его принадлежность к этому роду, показывая наиболее близкое родство с *Campylophyllopsis sommerfeltii*. Кроме того, два образца с российского Дальнего Востока, также внешне сходные с *Campylophyllopsis*, оказались сильно отличающимися по молекулярным маркерам от всех видов этого рода; они также отличаются от *Campylophyllopsis* наличием гиалодермиса в стебле и клетками листа с папиллозно выступающими верхними углами. Оба эти признака очень редко встречаются у видов Amblystegiaceae и являются диагностическими для рода *Podperaea*. Однако изученные растения оказались филогенетически совершенно не родственными *Podperaea*, но образовали общую кладу с родами *Campylophyllopsis*, *Pseudocampylium*, *Serpoleskea*, *Pseudoamblystegium* и *Hygrohypnum*, будучи наиболее близкими к *Hygrohypnum styriacum*. Они описаны как новый вид и род *Jankuceraea pacifica* Ignatov & Ignatova.

KEYWORDS: taxonomy, new species, *Hygrohypnum*, *Jankuceraea*

INTRODUCTION

Recent advances in moss taxonomy elucidated species distinctions and relationships in many moss genera. Most commonly they confirmed a monophyly of genera, while a number of molecular phylogenetic analyses revealed that a traditional generic placements were wrong and a genus had to be moved to another family, e.g., the genera *Donrichardsia* H.A. Crum & L.E. Anderson and *Sciaromiopsis* Broth. from the Amblystegiaceae to the Brachytheciaceae (Wynns *et al.*, 2009; Sheng *et al.*, 2022)

and *Pseudanomodon* (Limpr.) Ignatov & Fedosov from the Anomodontaceae or Thuidiaceae to the Neckeraceae (Ignatov *et al.*, 2019). However, some other genera remain in an indefinite position awaiting molecular phylogenetic analyses.

Among them is the genus *Campylophyllopsis* W.R. Buck. It includes mostly small autoicous pleurocarpous mosses with reflexed leaves, mainly epixylic, and widespread in boreal and hemiboreal forests. In the middle of 20th century the Russian taxonomic literature referred

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these plants to *Campyllum hispidulum* (Brid.) Mitt. and *C. sommerfeltii* (Myrin) Lange (Abramova *et al.*, 1961, Lazarenko, 1955), both considered widespread. Later Crundwell & Nyholm (1962) excluded *Campyllum hispidulum* from the European flora, and recognized in Europe two species of small-sized *Campyllum*, *C. sommerfeltii* (Myrin) Lange and *C. calcareum* Crundw. & Nyholm. Hedenäs (1997) confirmed this and additionally elucidated the taxonomy of the genus *Campyllum* (Sull.) Mitt., although two East Asiatic taxa, *C. rishiriense* Kanda and *C. squarrosulum* (Besch. & Cardot) Kanda, were left out of this decision; for *C. rishiriense* a tentative suggestion has been made with respect to its relation to *Pseudocampyllum radicale* (P. Beauv.) Vanderp. & Hedenäs (following modern nomenclature). Also Hedenäs synonymized *C. pulchrum* Kanda described from Japan with *C. hispidulum*, thus extending the distribution of *C. hispidulum* to Asia.

In East Asia, the revision of the genus *Campyllum* was done in the course of revision of Amblystegiaceae by Kanda (1975a). Kanda segregated large *Campyllum* species to the genus *Campyliadelphus* (Kind.) R.S. Chopra, leaving in *Campyllum* (as he defined it) five species: *C. hispidulum*, *C. pulchrum* Kanda, *C. sommerfeltii*, *C. squarrosulum*, and *C. rishiriense*. Later, Noguchi (1994) reduced *C. rishiriense* to the synonymy of *C. squarrosulum*.

Campyllum squarrosulum has a scattered distribution in Russia (Bardunov & Cherdantseva, 2006; Bakalin *et al.*, 2009); thus, in the course of work on the Moss Flora of Russia, we faced a need to find the correct genus for its placement. This species differs from other species of *Campylophyllopsis* by having leaves with single costae and therefore its position requires elucidation. The potential occurrence of *C. hispidulum* s.str. in Russia also required a revision of collections from Russian Far East. Molecular phylogenetic analysis was used for finding answers to these questions.

MATERIAL AND METHODS

Sampling

The selection of samples was done so various regions of Russia were represented, and for the type species of the genus, *C. hispidulum*, we used the material from North America where from it was first described. Sequences were supplemented by the most similar ones from GenBank using the BLAST search (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>, on March 2002). As some sequenced samples were similar in morphology to the genus *Podperaea* Z. Iwats. & Glime, the dataset was expanded to include this genus and genera usually grouped with it in some previous analyses: *Campylophyllum* (Schimp.) Fleisch., *Arvernella* Hugonnot & Hedenäs, *Drepanium* (Schimp.) Lange & C.E.O. Jensen, *Tomentypnum* Loeske, *Myrinia* Schimp., *Platyhypnum* Loeske.

In addition to the nuclear ITS, which is the most commonly used in phylogenetic reconstructions of pleurocarps (Kučera *et al.*, 2019), we sequenced plastid *atp-*

rbcL and *trnL-trnF* regions, copiously represented in Genbank.

Amplification and sequencing

The laboratory protocol was essentially the same as in previous moss studies, described in detail by, *e.g.*, Gardiner *et al.* (2005). Primers used for amplification are given in Ignatov & Kuznetsova (2021).

Molecular phylogenetic studies

For ITS we used alignment built for Kučera *et al.* (2019) with addition of newly generated sequences. Gaps were not coded. In *atp-rbcL* and *trnL-trnF* regions indels were coded as one substitution irrespective the length of indel if it was not variable.

Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012). For the analyses four rounds were used, six Markov chains, and 10 000 000 generations; GTR+G model was applied in all cases. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007). Consensus trees were calculated after omitting the first 25% trees as burn-in.

RESULTS

The preliminary tests with molecular phylogenetic analyses of separate datasets gave slightly different topologies, therefore, we provide here the results of three analyses. All of them are similar in subdividing the Amblystegiaceae into basal grade (*Campylophyllum*, *Arvernella*, *Drepanium*, *Tomentypnum*, *Myrinia*, *Platyhypnum*) and the clade of core Amblystegiaceae. The latter was supported in all analyses, although not always highly: in nuclear ITS (PP=1, BS=99), in plastid *atp-rbcL* (PP=1, BS=54) and *trnL-F* (PP=1, BS=82). Only the core Amblystegiaceae clade is discussed below because its monophyly is unequivocal and the main inconsistencies occur within it.

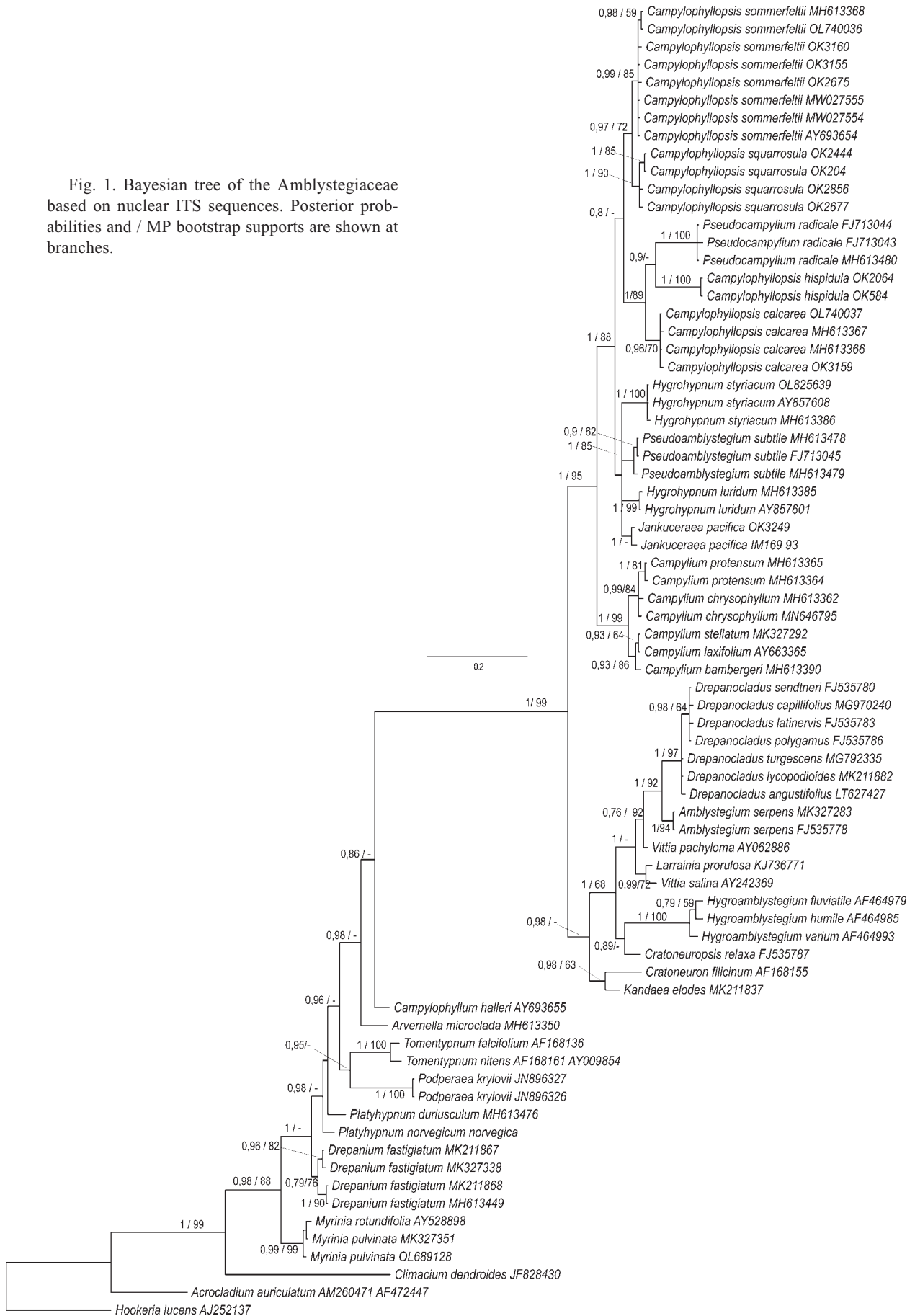
ITS, Fig. 1

Within the core Amblystegiaceae, the first branch off is a clade of *Drepanocladus*+*Amblystegium*+*Hygroamblystegium*+*Cratoneuron*+some other smaller genera. Next in the tree is the clade of *Campyllum* (PP=1 BS=99), which sister clades (PP=1 BS=88) include *Campylophyllopsis*, *Hygrohypnum*, *Pseudoamblystegium*, *Pseudocampyllum* and *Podperaea*-like plants.

All three studied *Campylophyllopsis* species were found in a poorly supported clade (PP=0.80 BS<50) that includes also *Campyllum squarrosulum* and *Pseudocampyllum radicale*. *Campyllum squarrosulum* forms a moderately supported clade with *Campylophyllopsis sommerfeltii* (PP=0.97 BS=72), and individual clades of these species have still higher supports (PP=1 BS=90) and (PP=0.99 BS=85).

The clade sister to *Campyllum squarrosulum*+*Campylophyllopsis sommerfeltii* clade is rather high supported (PP=1 BS=89), and its individual subclades are moderately (for *Campylophyllopsis calcarea*, PP=0.96, BS=70), or maximally (for *Pseudocampyllum radicale* and *Campylophyllopsis hispidula*, PP=1 BS=100) supported.

Fig. 1. Bayesian tree of the Amblystegiaceae based on nuclear ITS sequences. Posterior probabilities and / MP bootstrap supports are shown at branches.



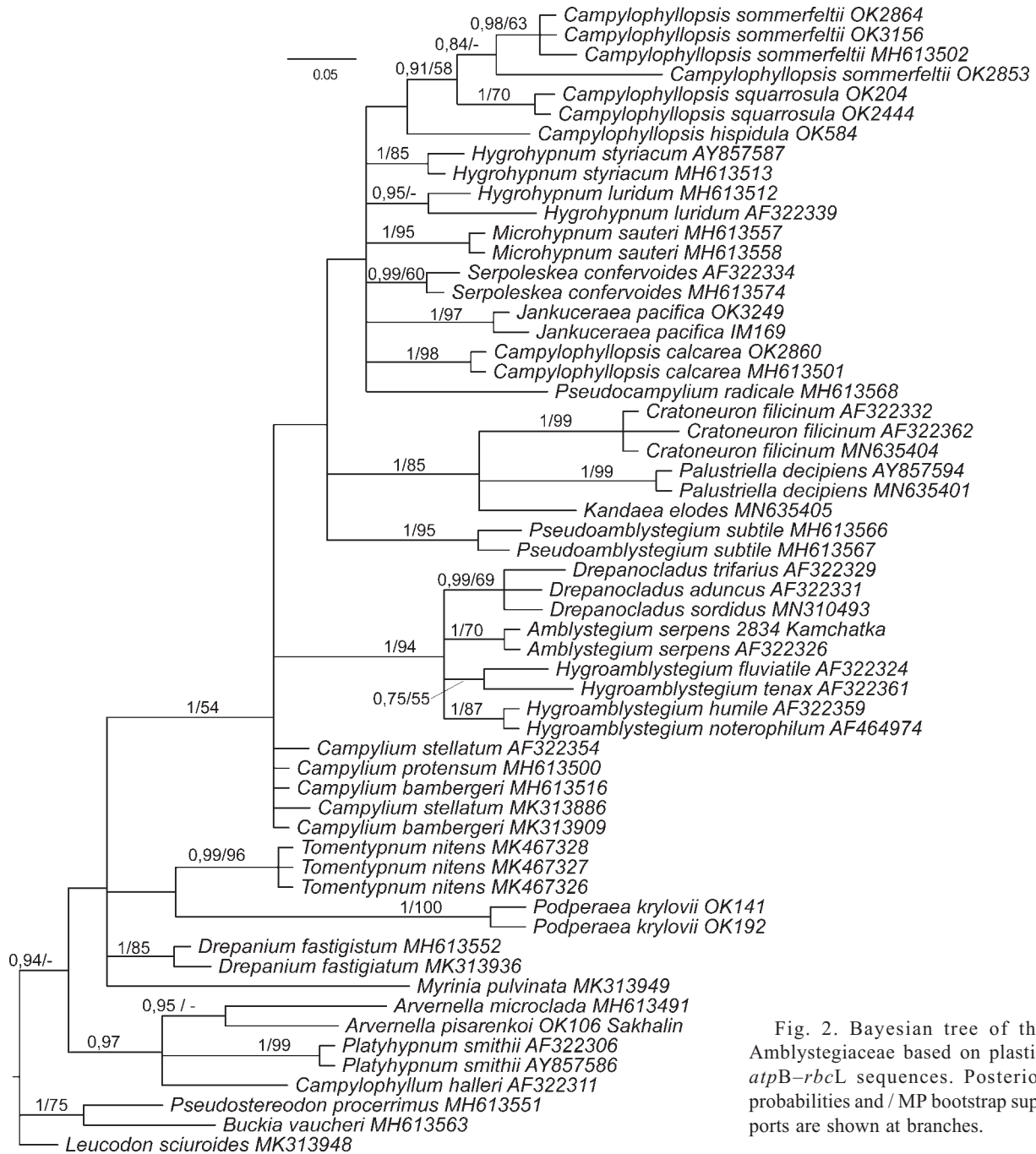


Fig. 2. Bayesian tree of the Amblystegiaceae based on plastid *atpB-rbcL* sequences. Posterior probabilities and / MP bootstrap supports are shown at branches.

Sister clade to the above mentioned mainly *Campylophyllopsis*-clade (5 species) is unsupported and includes four individual clades of *Hygrohypnum luridum*, *Hygrohypnum luridum* (PP=1 BS=99), *H. styriacum* (PP=1 BS=100), *Pseudoamblystegium subtile* (PP=1 BS=85) and *Podperaea*-like plants (PP=1 BS<50).

***atpB-rbcL*, Fig. 2**

The analysis of *atpB-rbcL* found 'core Amblystegiaceae' is, in most respect, similar to that in ITS. It includes (1) unresolved polytomy of *Campylium* spp.; (2) a clade of *Drepanocladus*+*Amblystegium*+*Hygroamblystegium* (PP=1 BS=94), and (3) an unsupported clade with three subclades: *Pseudoamblystegium* (PP=1

BS=95), *Cratoneuron*+*Palustriella*+*Kandaea* (PP=1 BS=85), and the unsupported clade with *Campylophyllopsis*, *Hygrohypnum*, *Pseudocampyllum*, *Serpoleskea*, *Microhypnum* and *Podperaea*-like plants. This latter clade includes mostly polytomy of clades with one species. The only non-monospecific clade was found for *Campylophyllopsis hispidula*, *C. sommerfeltii*, and *Campylium squarrosulum* (without support). Within it, *C. hispidula* is sister to two other species, which form a poorly supported mutual clade (PP=0.91 BS=58), where both *Campylophyllopsis sommerfeltii* and *Campylium squarrosula* individual clades were better supported.

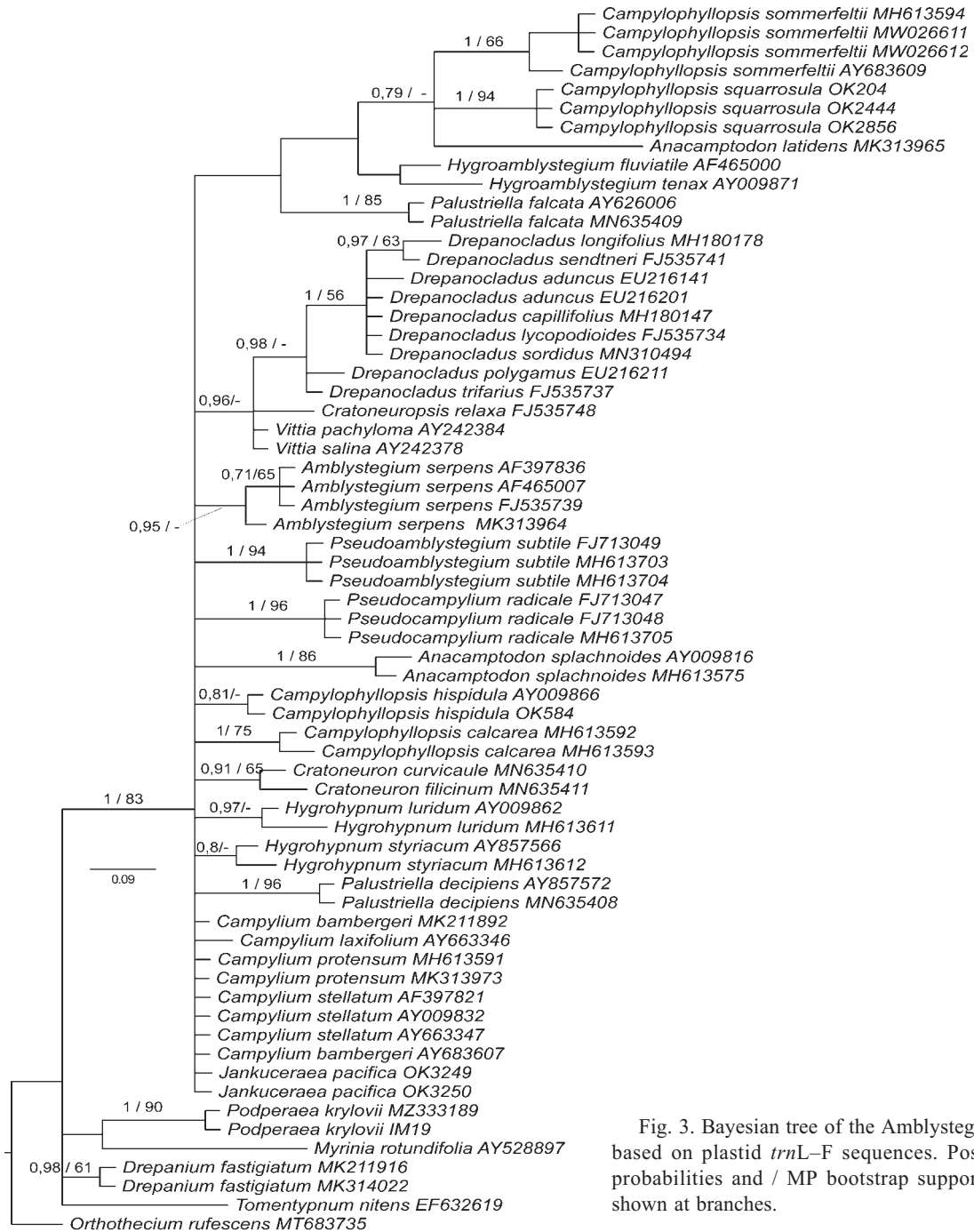


Fig. 3. Bayesian tree of the Amblystegiaceae based on plastid *trnL-F* sequences. Posterior probabilities and / MP bootstrap supports are shown at branches.

Two samples of *Podperaea*-like plants form well-supported clade (PP=1 BS=97), being thus similar to clades of *Pseudocampyllum*, *Serpoleskea*, *Microhypnum*, etc., and also *Campylophyloopsis calcarea*, that was not monophyletic with other congeneric species.

trnL-F, Fig. 3

This plastid region has the lowest variation and its phylogenetic tree is poorest in resolution. Species either form monospecific clades or samples of one species even remain in polytomy, not forming any clades (species of *Campylium* and *Podperaea*-like plant). Only three clades

are non-monospecific, all poorly supported: (1) *Cratoneuron filicinum*+*C. curvicaule*; (2) species of *Drepanocladus*, *Vittia* and *Cratoneurosis*; (3) *Palustriella falcata*, *Hygroamblystegium* spp., *Anacamptodon latidens*, *Campylophyloopsis sommerfeltii* and *Campylium squarrosulum*. Three latter species form a terminal clade without support.

Similar to the *atpB-rbcL* analysis, *Campylophyloopsis calcarea* is not monophyletic with *C. sommerfeltii*, and contrary to the *atpB-rbcL* analysis, *C. hispidula* also is not resolved as monophyletic with *C. sommerfeltii*.

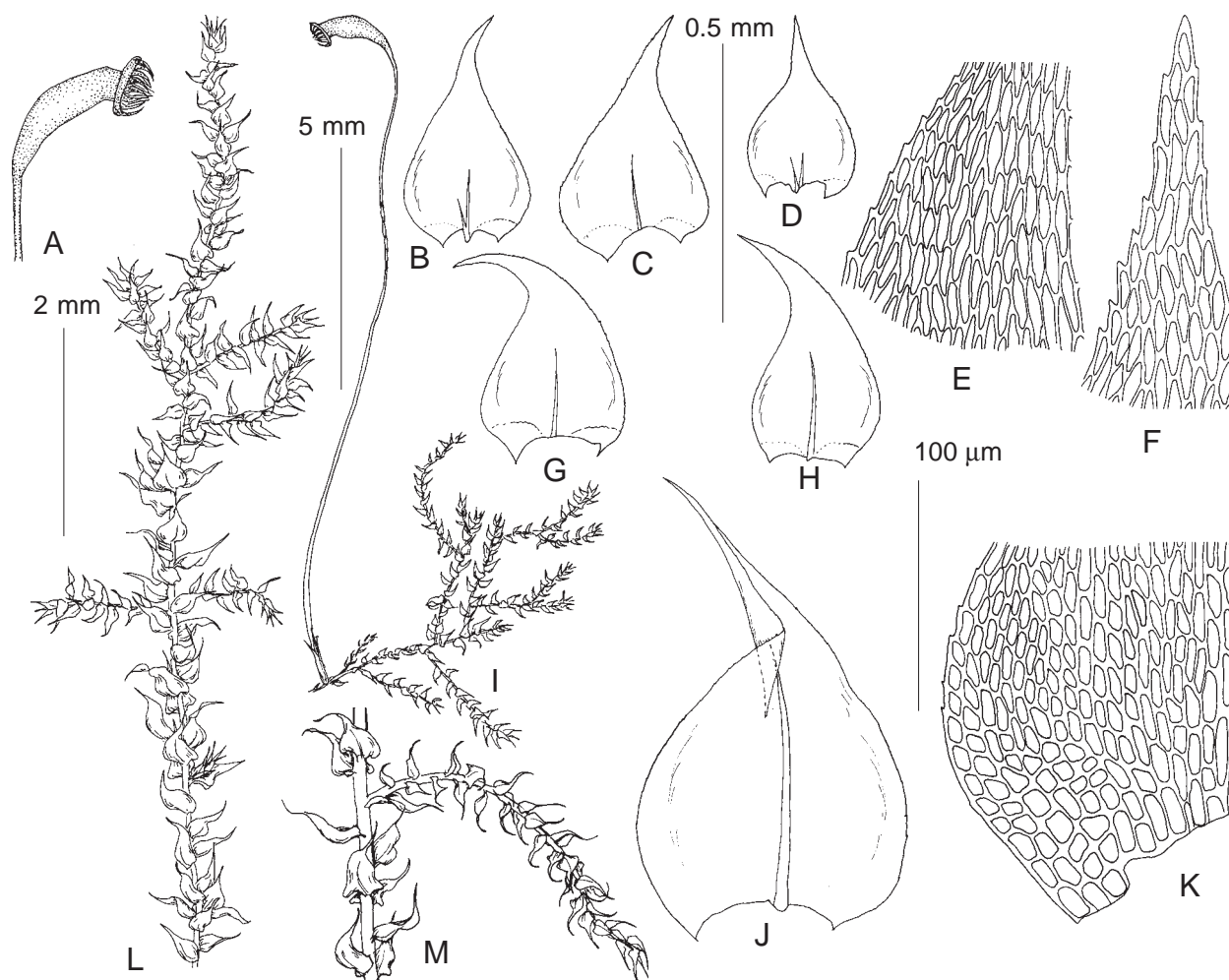


Fig. 4. *Campylophyllopsis squarrosula* (from Primorsky Territory, Vladivostok, Ignatov et al. 06-3371, MHA): A: capsule; B–D: branch leaves; E: mid-leaf cells; F: upper leaf cells; G–H, J: stem leaves; I, L–M: habit, dry; K: basal leaf cells. Scale bars: 5 mm for I; 2 mm for A, L–M; 0.5 mm for B–D, G–H, J; 100 µm for E–F, K.

DISCUSSION

The present amount of data does not achieve the exhaustive resolving of the phylogeny of the genus *Campylophyllopsis*. It obviously includes several ancient lineages, and their relationships each to another are seen only partly. Pending a complete revision for further research of a sufficiently bigger dataset, we, however, are able now to come to conclusions about the species which were in the main focus of the study.

TAXONOMY

All three phylogenetic analyses resolved *Campylium squarrosulum* as sister to *C. sommerfeltii*. Thus by now, the placement of *Campylium squarrosulum* in the genus *Campylophyllopsis* seems to be most appropriate, so it will be at least congeneric with its closest relative, *C. sommerfeltii*.

Campylophyllopsis squarrosula (Besch. & Cardot) Ignatov, comb. nov.

Basionym: *Amblystegium squarrosulum* Besch. & Cardot, Bull. Soc. Bot. Genève 5: 320. 1913. Type: Japan (not seen, illustrations of syntype are given by Kanda, 1975).

Campylium squarrosulum (Besch. & Cardot) Kanda, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 15: 258. 1975[1976].

Plants in loose low tufts, light-green. *Stems* 1–3 cm long, loosely or densely foliate. *Stem leaves* terete, occasionally homomalous, 0.3–1.0×0.2–0.5 mm, broadly ovate and rather abruptly tapered to short lanceolate acumina ca. 1/3 the leaf length; margins serrulate almost throughout, costa single or in some leaves double or forked; laminal cells 18–40×5–6(–7) µm; alar cells quadrate to short rectangular, indistinctly delimited from laminal cells, occasionally looking more pellucide. *Sporophytes* frequent. *Setae* 1.4–2 cm. *Capsules* 1.5 mm long. *Spores* 8–10 µm.

Distribution. *Campylophyllopsis squarrosula* is an East Asiatic species. It is rare in Russia and found only in the southern part of the Russian Far East, growing in forests on tree bases, rotten logs and rocks. It resembles *Campylophyllum halleri* in having somewhat dense foliage and rigidly squarrose leaves. It is more similar to the American *Campylophyllopsis hispidula*, and likely has been confused with it, since depauperate plants may have

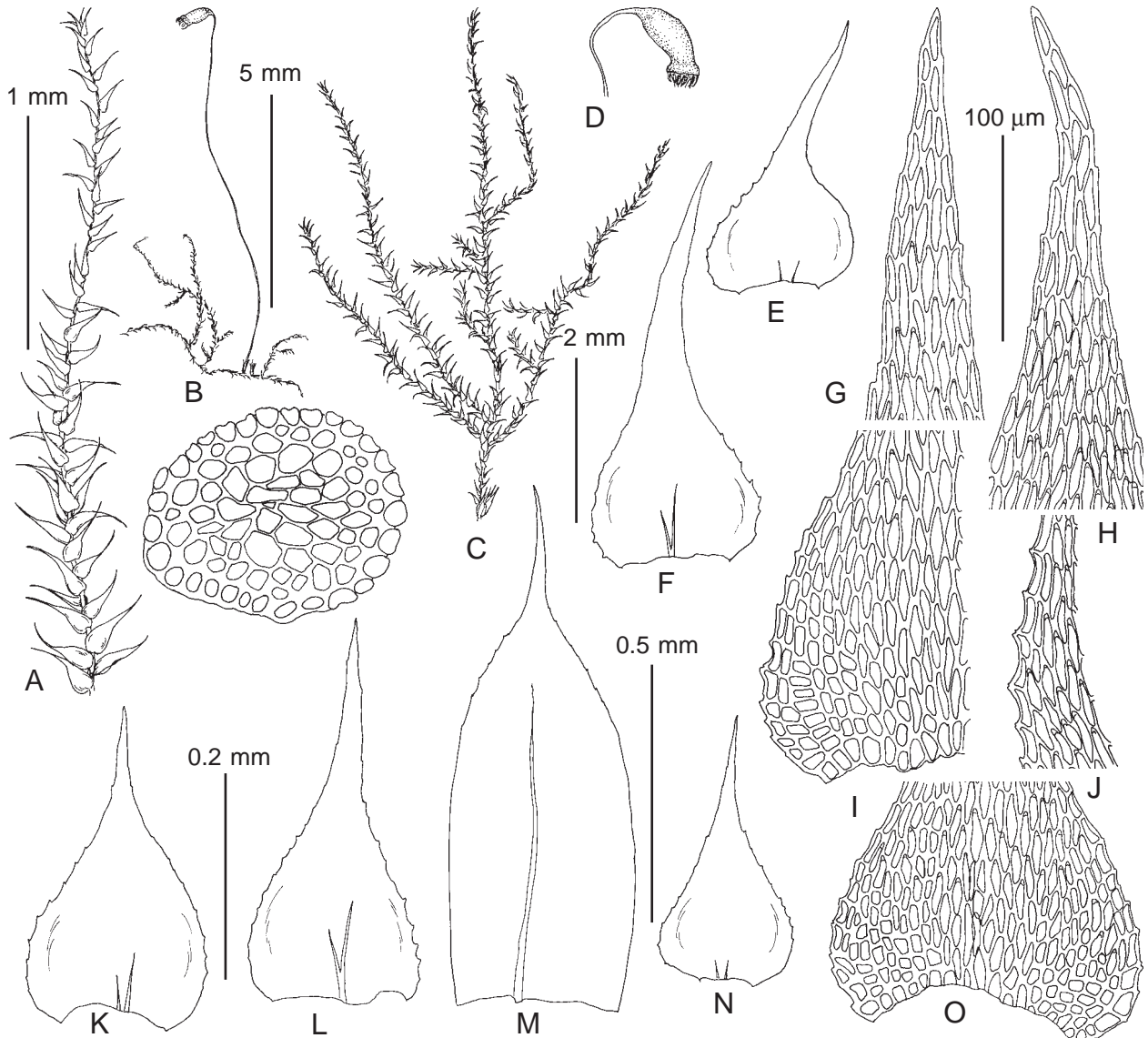


Fig. 5. *Jankuceraea pacifica* (from holotype): A–C: habit, dry; D: capsule; E, N: branch leaves; F, K–L: stem leaves; G–H: upper leaf cells; I, O: basal leaf cells; J: mid-leaf cells; M: perichaetial leaf. Scale bars: 5 mm for B; 2 mm for C; 1 mm for A, D; 0.5 mm for M; 0.2 mm for E–F, K–L, N.

a double costa in many leaves. However, normally developed *C. squarrosula* differs from all these species in having long, single costae on most leaves.

Podperaea-like moss

In addition to the problem of *Campylium squarrosulum*, the current analysis revealed another moss that needs attention.

Being superficially similar to a very small *Campylium* (Figs. 5–7), it has three features that are sub-unique in the Amblystegiaceae, being known only in the genus *Podperaea*. Likewise *Podperaea*, this moss has a stem hyalodermis (unknown in any other Amblystegiaceae in their current circumscription), leaf margins with double teeth formed by the projecting upper end of the lower cell and the projecting lower end of cell above; also, it has prominent papillae above the distal cell ends (Fig. 6).

However, all three phylogenetic analyses found no

relationships between this plant and *Podperaea krylowii*, the only species of the genus, as the second one has been segregated in a separate genus *Redfearnia* (Wynns, 2020). Therefore this species is described as a new genus and species.

Jankuceraea Ignatov & Ignatova gen. nov.

Monospecific genus

Jankuceraea pacifica Ignatov & Ignatova, sp. nov.

Type: Russian Far East, Primorsky Territory, Dalnegorsk District, ca. 5 km N of Sedaya Mt., 44°36'40.1"N, 135°16'47.8"E; 650 m alt., mixed forest along the road, on rocky soil at roadside, 31 Aug 2013, Ignatov & Ignatova 13-1552. Holotype MHA9011432, isotype MW8027413. Isolate OK3249.

Etymology: The generic name is in honor of Jan Kučera (born 1972), an outstanding bryologist from Czech Republic who contributed a lot to the molecular phylogene-

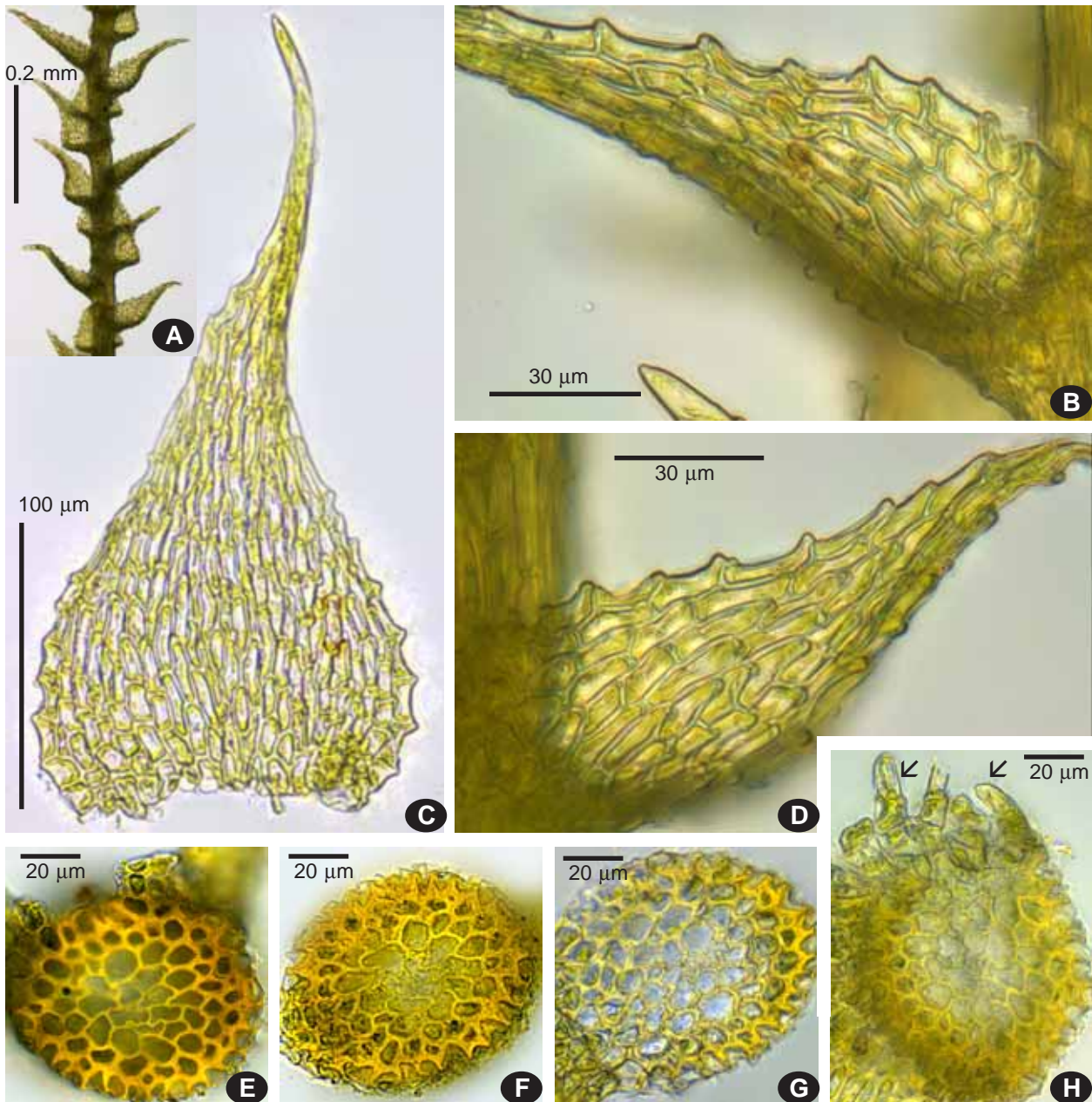


Fig. 6. *Jankuceraea pacifica* (from holotype): A: distal part of shoot, with not the largest leaves, cf. Fig. 5A; B–D: stem leaves (from ‘A’), showing prorate upper cell angles; E–H: stem transverse sections, showing hyalodermis and proximal branch leaves, arrowed (H).

tic studies of mosses. The species name refers to the region where the type specimen was collected.

Diagnosis: *Jankuceraea* shares with the genus *Podperaea* the following character combination: 1) stems with well-differentiated hyalodermis; 2) leaf margins with “compound” teeth formed of projected angles of two contiguous cells; 3) leaf cells with distinct papillae in the upper end of each cell. Its distinctions from *Podperaea* include: 1) smaller size of plants; 2) widely spreading, concave, rigid leaves with canaliculate acumina vs. reflexed, soft, flexuose, weakly concave leaves; 3) almost straight or only slightly curved vs. arcuate capsules.

Description: *Plants* small, green or yellowish-green, in small loose mats. *Stems* prostrate, to 1 cm long, irreg-

ularly pinnate, distantly foliate; branches 3–5 mm long; hyalodermis well-developed, central strand weak; axillary hairs 2-celled, upper cell 13–25×5 µm long; proximal branch leaves of branch primordia narrow lanceolate or subulate. *Stem leaves* distantly arranged, widely spreading to weakly reflexed, rigid, 0.2–0.4×0.12–0.17 mm, from ovate or widely ovate base ± abruptly tapered into long, narrow lanceolate acumina, rounded to the insertion, concave, canaliculate distally; margins plane or incurved distally, serrate throughout, with simple and “double” (formed of projecting angles of two contiguous cells) teeth; *costae* short, double; *cells* elongate-rhomboidal, 15–30×5–6 µm, 3–6:1, prorate or with distinct papillae in the upper end of each cell on dorsal surface, alar cells

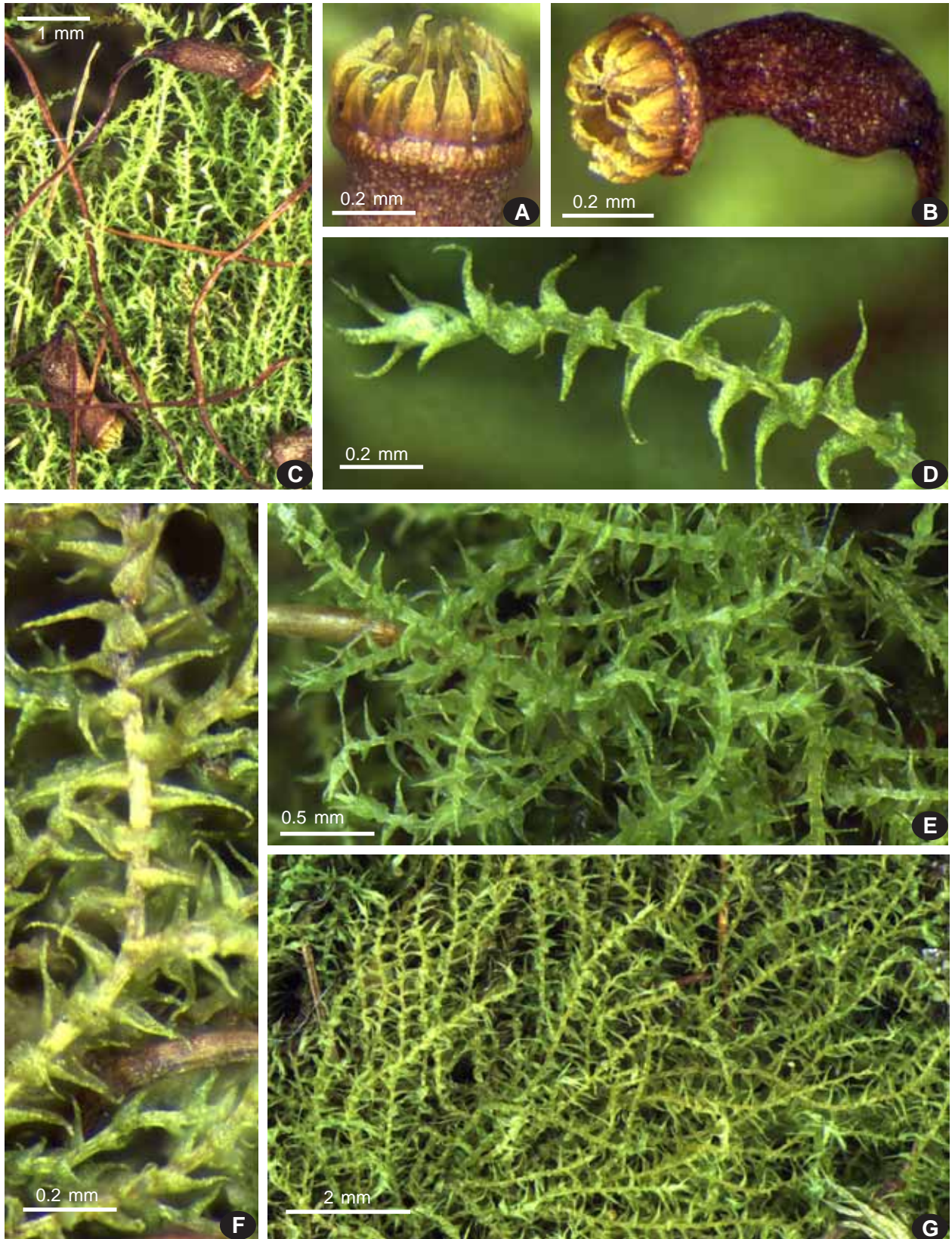


Fig. 7. *Jankuceraea pacifica* (from holotype): A–B: capsules; C–G: habit, dry.

small, quadrate and short rectangular, in a small, indistinctly delimited groups. *Autoicous*. *Inner perichaetial leaves* 1.0×0.35 mm, straight, oblong, wide, abruptly con-

stricted into short, narrow lanceolate acumina, smooth; margins plane, entire; costae single, thin, to 0.7 the leaf length. *Setae* 1.0–1.5 cm, reddish-brown. *Capsules* ca. 1 mm



Fig. 8. Habitat of *Jankuceraea pacifica*. A–B: Primorsky Territory, surroundings of Sedaya Mt.; C–D: Kunashir Island (site where the species has been collected is arrowed).

long, reddish-brown, inclined or pending, almost straight or slightly curved, cylindrical, constricted below mouth when empty, smooth. *Operculi* conic. *Annuli* deciduous by fragments. *Peristome* perfect: *exostome* teeth ca. 320 μm long, striolate below, papillose above; *endostome* with basal membrane ca. 150 μm high, segments wide, keeled, slightly shorter than *exostome* teeth, cilia long, appendiculate. *Spores* 12–15 μm .

Other specimen examined: Russia, Kuril Islands, Kunashir Island, NW slope of Ruruj Volcano, Dalny Creek, 50 m alt., fir forest, on steep slope to stream, on rocks and on soil nearby. 27 Aug 2006, *Ignatov 06-1901* (MHA9011335, MW9056505).

Differentiation: Superficially, *Jankuceraea pacifica* looks like a small *Campylophyllopsis sommerfeltii*: such small leaves may occur in the latter species at shoot ends, especially in plants growing in deep shade or otherwise unfavorable conditions. However, in *Jankuceraea* such foliage is uniform throughout a tuft, and also its leaves are uniformly remote. Differences of *J. pacifica* from *Podperaea krylovii* are given in the diagnosis. In addition, stem leaves of *J. pacifica* are shorter: 0.3–0.4 mm vs. 0.4–0.9 mm long, as well as leaf cells: 15–28 μm vs. 30–55(–75) μm long.

The maximally similar structure, according to description of Kanda (1975) has *Campylium pulchrum* Kanda,

a moss from Hokkaido, known by holotype. The detailed illustrations of Kanda show only simple teeth along the leaf margin. The type of this species was been studied by Hedenäs (1997), who found it conspecific with *Campylophyllopsis hispidula*, which supports the absence of any outstanding features in this taxon. Hedenäs (1997) also found some inconsistencies between the holotype and the description in protologue.

Distribution. Our first specimen of the *Jankuceraea* was collected in 2006 in Kunashir Island, South Kuril Islands. This was a strongly depauperate thin plant, which however had clear double teeth at leaf margins and distantly papillose cells, and therefore it was identified and reported as *Podperaea krylovii* (Bakalin *et al.*, 2009).

Later this specimen was sequenced and turned out to be strikingly different form *Podperaea*, but closer to *Campylophyllopsis*. The imperfect collection did not allow us to decide if this is simply an abnormal morphotype or something else.

In the course of the further studies, we collected a large sample of this species in the Primorsky Territory, which helped to reveal its taxonomic identity.

Two localities of *Jankuceraea* have rather little in common and both look rather average in the Far Eastern region. In Kunashir, the shore of the Sea of Okhotsk is steep

(Fig. 8C), with narrow canyons, and *Jankuceraea* was collected on rocks in open fir forest at 50 and 200 m elev. In Primorsky Territory, Middle Sikhote-Alin mountain range, the species was collected on gravelly soil bank not far from a road in the conifer (*Pinus*, *Larix*) forest, at 650 m elev. (Fig. 8A, B). *Campylophyllopsis sommerfeltii* was as an admixture in some collections of this species.

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Other Species of *Campylophyllopsis* in Russia

KEY TO IDENTIFICATION OF *CAMPYLOPHYLLOPSIS* SPECIES IN RUSSIA

1. Costae single, reaching mid-leaf in most leaves, rarely double or forked *C. squarrosula*
- Costae double or forked with lower, single part shorter than 0.2 the leaf length; very rarely costae single, up to 1/3 the leaf length 2
2. Leaf acumina 0.55–0.75 the leaf length *C. calcarea*
- Leaf acumina 0.40–0.60 the leaf length *C. sommerfeltii*

Campylophyllopsis sommerfeltii (Myrin) Ochyra, Moss. Pieniny Range 99. 2010. — *Hypnum sommerfeltii* Myrin, Årsberätt. Bot. Arbeten Upptäckter 1832: 328. 1832. — *Campylium hispidulum* var. *sommerfeltii* (Myrin) Lindb., Contr. Fl. Crypt. As. 279. 1872.

Campylium calcareum f. *latifolia* Schljak., Novosti Syst. Nizsh. Rast. 32: 183. 1998. Type: Altai, Chermal Creek, 3 km from mouth. Mixed forest in flood vallet, on boulder in open place. 51°23'N – 86°04'E, 450 m alt. 12 July 1993. Coll. M. Ignatov & E. Ignatova 34/182 (LE, isotype MHA9011517). syn nov.

This form was not compared with *C. sommerfeltii*, but we see no difference from it, except maybe that some leaves have rectangular alar cells.

Campylophyllopsis sommerfeltii is widespread throughout Russia, except the Arctic and southern xeric areas near the Caspian Sea. It is very variable and alar cells are sometimes transversely rectangular, resembling those of *C. hispidula*. A limited number of the studied American material (including siquences ones) have usually plants with denser foliage American However their apical part is never as short and broad as in American *C. hispidula* s. str., which almost never occurs in *C. sommerfeltii*.

Campylophyllopsis calcarea (Crundw. & Nyholm) Ochyra, Moss. Pieniny Range 99. 2010. — *Campylium calcareum* Crundw. & Nyholm, Trans. Brit. Bryol. Soc. 4: 198, f. 2. 1962[1963].

The distribution of this species species in Europe is relatively well known and it was confirmed from most

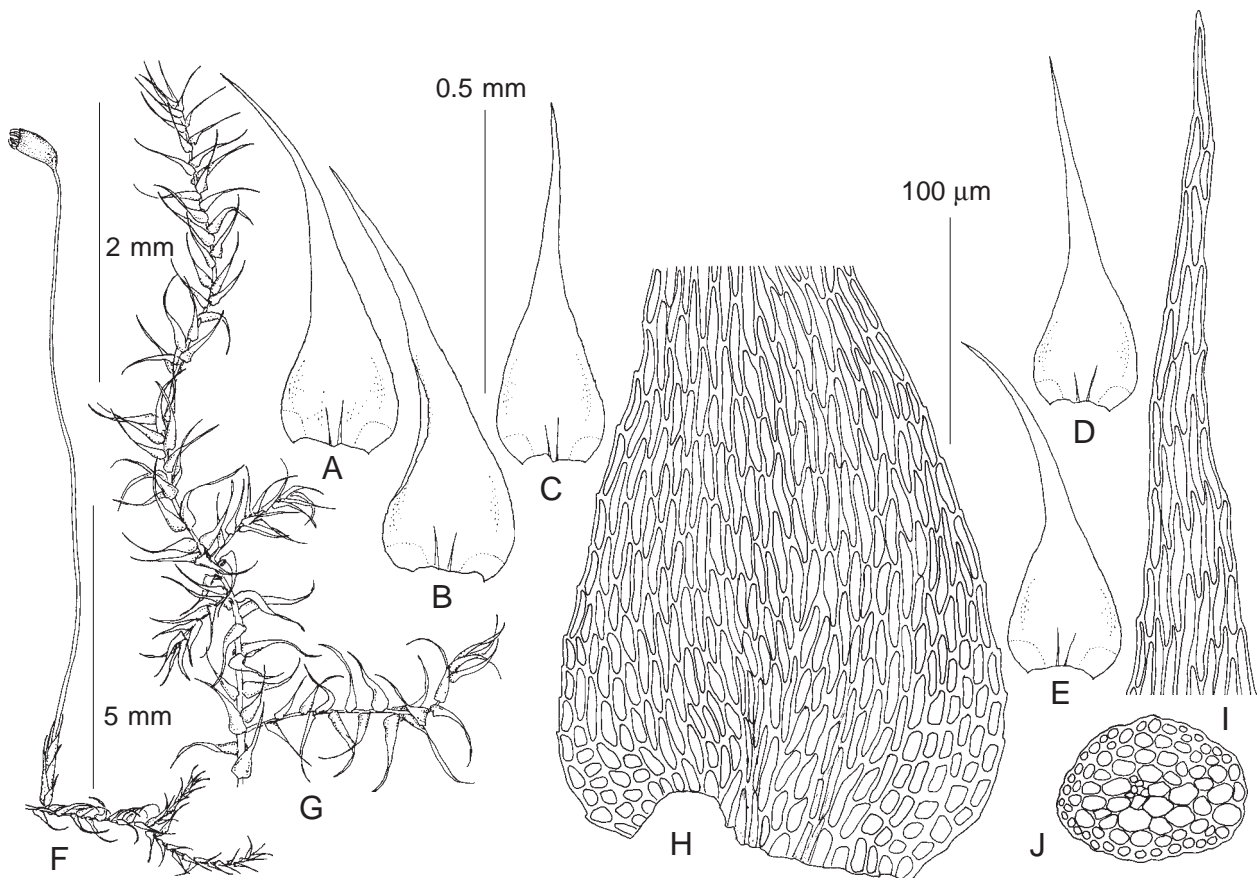


Fig. 9. *Campylophyllopsis calcarea* (from: Russia, Yakutia, Sette Daban Mts., Ignatov & Ignatova 16-716, MHA9131653). A–E: stem leaves; F–G: habit, dry; H: mid-leaf & basal leaf cells; I: upper leaf cells; J: stem transverse section. Scale bars: 5 mm for F; 2 mm for G; 0.5 mm for A–E; 100 μm for H–J.

European countries (Hodgetts & Lockart, 2020). Hedenäs (1997) confirmed its occurrence from Europe only.

Schljakov (1998) reported from Altai *Campylophyllopsis calcarum* f. *latifolia*, which we refer to *C. sommerfeltii*.

In Asia, where limestone is less widespread, we confirmed specimens from Yakutia (Fig. 8).

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APPENDIX

Newly sequenced samples with Genbank (ITS, atpB–rbcL, trnL–F) and Isolate numbers [all except *Campylophyllopsis hispidula* are from Russia]:

Amblystegium serpens ----- ON681592 -----
 OK2834: Kamchatka, Fedosov 10-3-1085, MW9001219;
Jankucea pacifica ON653197 ON681593 ON677255
 OK3249: Primorsky Territory, Sedaya Mt., Ignatov & Ignatova 13-1552, MW8027413; ON653198 MZ333207
 ON677256 OK3250 (IM169): Kuril Islands, Kunashir, Ruruj, Ignatov 06-1901, MHA9011335: *Campylophyllopsis squarrosula* ON653201 ON681595 ON677257
 OK204: Primorsky Krai, Ignatov 07-143, MHA; ON653200 ON681601 ON677258 OK2444 Primorsky Territory, Ignatov 07-143, MHA 9011586; -----
 ON681596 ----- OK2674: Primorsky Territory, Vladivostok, Ignatov et al. 06-3371, MW9027430; ON653202 -----
 ----- OK2677: Primorsky Territory, Ignatov et al. 06-2434, MW9027424; ON653199 ----- ON677259
 OK2856: Primorsky Territory, Vladivostok, Ignatov et al., 06-3510, MW9027516; *Campylophyllopsis sommerfeltii* -----
 ON681598 ----- OK302: Kamchatka, Czernyadjeva 30 July 2001 #49, MHA; ----- ON681597 -----
 ----- OK2853: Sakhalin, Tymovsk Distr., Pisarenko 03737, MHA9011491; ----- ON681599 -----
 OK2864: Bashkortostan, Zolotov 08-86, MHA9011756; ON653204 -----
 ----- OK3155: Tatarstan, Ignatov & Ignatova 19 Aug 2003, MHA9011412; -----
 ON681600 ----- OK3156: Nenets Autonomous Distr., Adzva, Ivanov & Donskov, 09-276, MHA9011409; ON653203 -----
 ----- OK3160: Kuril Islands, Shikotan, Bakalin K-46-5-07, MHA9011498; ON653205 -----
 ----- OK2675: Kuril Islands, Shikotan, Bakalin K-46-5-07, MW9027429; *Campylophyllopsis calcar-
 ea* ----- ON681594 ----- OK2860: Dagestan, Gunib, Ignatov & Ignatova 09-726, MHA9011362; ON653206 -----
 ----- OK3159: Vologda Province, Ignatov & Ignatova 16 Aug 2001, MHA 9012085; *Campylophyllopsis hispidula* ON653207 ON681602 ON677254
 OK584: USA, South Carolina, Buck 31579, NY00306671; ON653208 -----
 ----- OK2064: USA, Georgia, Buck 30618, NY00306610.

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