

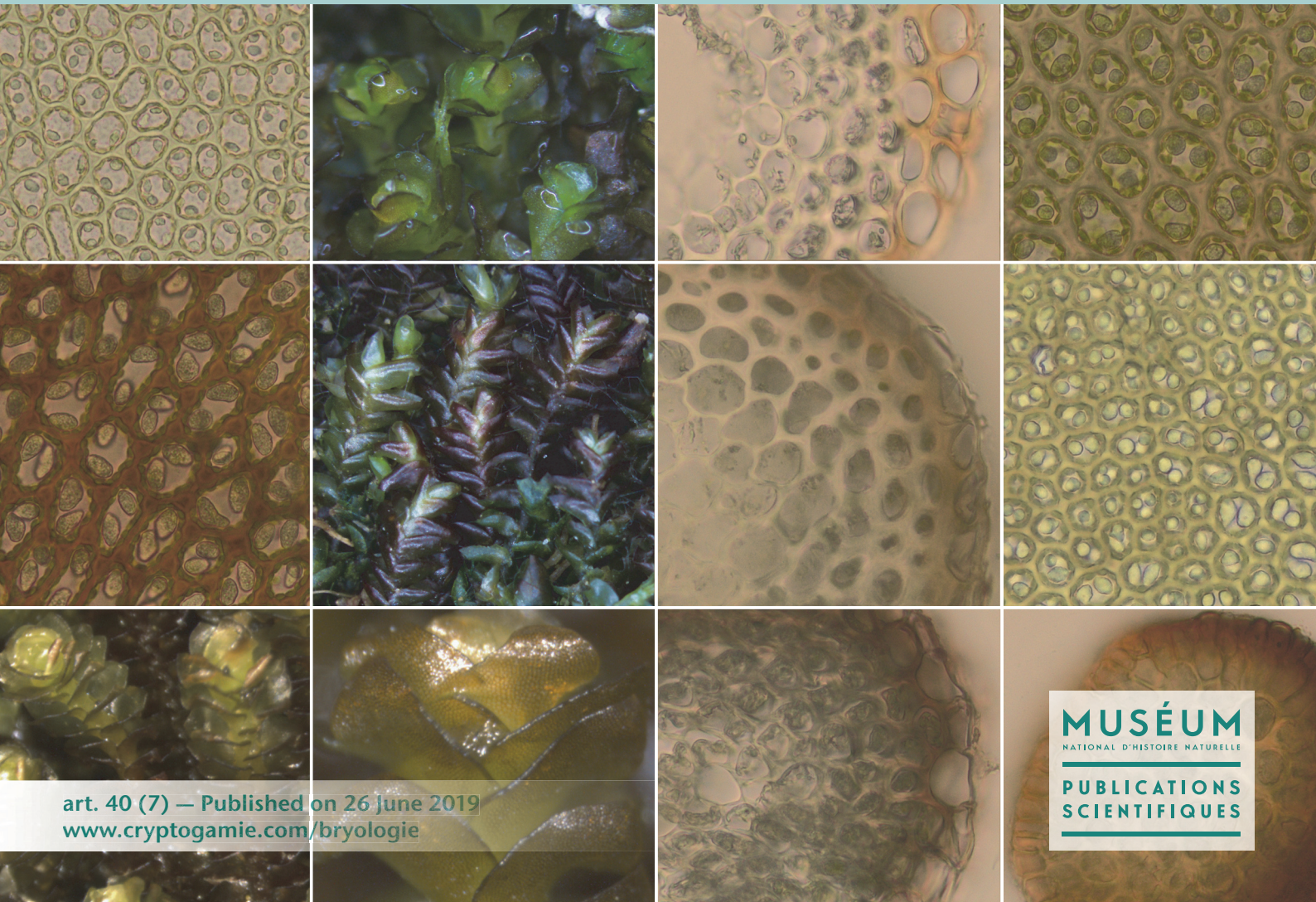
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Integrative taxonomic revision of *Marsupella* (Gymnomitriaceae, Hepaticae) reveals neglected diversity in Pacific Asia

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ABSTRACT

Molecular phylogenetic study of the genus *Marsupella* based on the dataset enriched by morphologically diverse specimens from Pacific Asia, the region with highest diversity of the genus, but still underexplored, reveals three new species: northern Indochinese *M. vietnamica* Bakalin & Fedosov, sp. nov., strictly Korean *M. koreana* Bakalin & Fedosov, sp. nov., and disjunctive amphi-Atlantic-amphi-Pacific *M. submarginata* Bakalin & Fedosov, sp. nov. Furthermore, obtained results suggest that some infraspecific taxa deserve species level recognition, thus, two new combinations are introduced: Japanese *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov., and East to South-East Asian–Papuanian *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. The species status for *M. apertifolia* is confirmed. The subgeneric system that implies 5 sections within the genus *Marsupella* (one founded on a new combination) is proposed based on the obtained topology. The key to identify all worldwide recognized *Marsupella* is provided. Our results indicate that distribution patterns (“geographic species concept”) may help to reveal taxa of species rank within the “integrative taxonomy” conception.

KEY WORDS

East Asia,
Gymnomitriaceae,
Hepaticae,
Marsupella,
geographic species
concept,
new combinations,
new species.

RÉSUMÉ

La révision taxonomique intégrative de Marsupella (Gymnomitriaceae, Hepaticae) révèle une diversité négligée dans l'Asie du Pacifique.

L'étude phylogénétique moléculaire du genre *Marsupella* basée sur des données enrichies de spécimens morphologiquement diversifiés de l'Asie du Pacifique, région où le genre est le plus diversifié, mais encore inexplorée, révèle trois nouvelles espèces : *M. vietnamica* Bakalin & Fedosov, sp. nov., du nord de l'Indochine, *M. koreana* Bakalin & Fedosov, sp. nov., coréenne stricte et *M. subemarginata* Bakalin & Fedosov, sp. nov., espèce disjointe amphi-atlantique-amphi-pacifique. En outre, les résultats obtenus suggèrent que quelques taxons infraspécifiques sont de niveau spécifique ; ainsi, deux nouvelles combinaisons sont proposées : *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov., du Japon et *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., de l'Asie Est-Sud-Est-Papouasie. Le statut d'espèce pour *M. apertifolia* est confirmé. Le genre *Marsupella* est divisé en cinq sous-genres (dont l'un est fondé sur une nouvelle combinaison) sur la base de la topologie obtenue. Une clé d'identification des *Marsupella* connus à travers le monde est proposée. Nos résultats indiquent que les modes de distribution (« concept géographique spécifique ») peuvent aider à révéler des taxons de niveau spécifique dans une conception de taxonomie intégrative.

MOTS CLÉS

Asie Est,
Gymnomitriaceae,
Hepaticae,
Marsupella,
concept géographique
spécifique,
combinaisons nouvelles,
espèces nouvelles.

INTRODUCTION

According to the last revision of the Gymnomitriaceae (Váňa *et al.* 2010), 26 species of *Marsupella* are known worldwide. Later Söderström *et al.* (2016) returned *Marsupella miniata* (Lindenb. & Gottsche) Grolle, to *Gymnomitrium* (as *G. miniatum* Lindenb. et Gottsche). Among the species diversity within *Marsupella*, less than half of them have circumpolar or sub-circumpolar distribution, others have more narrow ranges, with two noticeable diversity centers: 1) temperate mountainous Pacific part of Sino-Japanese region (slightly extending southward to subtropical zone, where it is associated with oro-temperate belt of the mountains); and 2) Himalayan region with its spur descending southeastward as far as to Indochina. Some regional specificities are also seen in Atlantic Europe and some other areas, although much less pronounced. The paper by Váňa *et al.* (2010) advanced our understanding of this genus compared with other treatments published before by a consistent acceptance of a more narrow generic concept in *Marsupella*, and therefore, the transfer of all former perianth-less “*Marsupella*” to *Gymnomitrium*. However, if *Gymnomitrium* in this concept becomes morphologically and genetically too voluminous it may deserve further splitting into some more narrower genera but this question is for another study. The nomenclature of *Marsupella* in the World checklist (Söderström *et al.* 2016) follows Váňa *et al.* (2010) with the exception of merging *Apomarsupella* with *Gymnomitrium* that are treated as separate genera in the latter.

Whereas “northern” circumpolar *Marsupella* were reviewed several times including some well-known and valuable examples by Schuster (1974), Schljakov (1981), Paton (1999), Damsholt (2002) and Müller (1956), the taxonomy of Himalayan and Pacific East Asian species of the genus remains relatively poorly understood. The only revision for Gymnomitriaceae of Japan was published by Kitagawa (1963), thus 55 years ago and without the insights now provided

by molecular data. Only scattered information is available for Himalayan, meta-Himalayan (the term cf. Bakalin *et al.* 2018) and South East Asian *Marsupella* (Schiffner 1898, 1900; Grolle 1966; Kitagawa 1967; Hattori 1975; Long & Grolle 1990; Gao & Wu 2007; etc.). Among taxa listed in “synopsis” of the genus by Váňa *et al.* (2010) there are taxa with very complex infraspécific nature where the status of some of them may be doubtful (conspecific with others or, on the contrary, requires the separation at the species level). Within the last 15 years the first author studied many specimens of the genus in living conditions and observed oil bodies that might provide additional features for taxa separation. Several populations were noted in the previous laboratory studies as potentially new taxa, differing both morphologically and ecologically. This inspired us to test the status of several taxa or morphological “phases” and reveal their affinities using the molecular phylogenetic approach that was the main goal of the present paper. The main focus of the present paper is the genus *Marsupella* in East Asia and some adjacent lands – the area poorly investigated in this respect until now.

MATERIAL AND METHODS

The main amount of the material is from East and South-East Asia – the areas still not so well investigated. All Holarctic species of the genus (according to Váňa *et al.* 2010) were included in the molecular phylogenetic study. In total, 64 sequences from 32 specimens representing 19 species of the genus *Marsupella* were obtained *de novo* (see Appendix 1), 20 sequences from 8 species were downloaded from GenBank, thus in total 22 in-group species were represented by 42 specimens (84 sequences). The set of outgroups was compiled from sequences, downloaded from GenBank. It included representatives of the genus *Gymnomitrium* Corda (14 sequences, 7 specimens, 4 species) and the family Sole-

nostomataceae Stotler & Crand.-Stotl. (8 sequences from 4 specimens and 4 species). Thus, in total 106 sequences from 53 specimens were included in final analyses. Initially some problematic East Asian species had larger vouchers, but were not included in final analyses to avoid unequal representation of different taxa.

Total genomic DNA was extracted from dry plants using the NucleoSpin Plant DNA extraction kit (Macherey-Nagel, Germany). For this study we used two DNA regions: internal transcribed spacer 1-2 (ITS1-2) and trnL-trnF intergenic spacer (*trnL-F*). The ITS1-2 region was amplified with ITS1 (TCCGTAGGTGAACCTGCG) and ITS2 (GATATGCTTAACTCAGCGG) and sequenced with the same primers. The *trnL-F* region was amplified with trnL C (CGAAATCGGTAGACGCTACG) and trnL F (ATTTGAAGTGGTGACACGAG) and sequenced with trnL C. Primers used for PCR were synthesized and purified in PAAG by Syntol Ltd. (Moscow, Russia). PCR was conducted in 20 µl aliquots containing 4 µl of the Ready-to-Use PCR MasterMIX based on “hot-start” SmarTaq DNA Polymerase (Dialat Ltd., Moscow, Russia), 13 µl of deionized water, 5 pmol of each primer, and about 1.5–2 ng of template DNA in a MJ Research PTC-220 DNA Engine Dyad Thermal Cycler (BioRad Laboratories, USA) under the following conditions: 95°C–3' (initial denaturation); 95°C–20", 58°C–20", 72°C–40" (34 cycles); 72°C–5' (final extension step). Amplification products were separated in 1% agarose gel in 1xTAE with ethidium bromide staining and purified using MinElute © Gel Extraction Kit (Qiagen, Germany). Purified PCR products were sequenced using the ABI PRISM © BigDye™ Terminator v. 3. kit (Applied Biosystems) and further analyzed on an ABI PRISM 3730 automated sequencer (Applied Biosystems) at the “Genom” Common Facilities Centre. Sequences were aligned for each gene independently using MUSCLE (Edgar 2004), with subsequent manual editing in BioEdit v. 7.0.9.0 (Hall 1999). Absent positions at 3' & 5'-ends were treated as missing data. Three analyses were performed. At first, ITS (911 positions) and trnL (437 positions), were analyzed separately to evaluate robustness of resulting trees and to check them for incongruence. The third analysis was performed on the concatenated ITS and trnL sequences (1348 positions). The ITS alignment was divided into 3 unlinked partitions, ITS1, 5.8rRNA gene and ITS2. The trnL alignment was divided into 4 unlinked partitions, corresponding to trnL-intron, trnL-exon, trnL-trnF spacer and trnF-exon. The concatenated ITS-trnL dataset was separated into seven unlinked partitions.

Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML v. 8.2.10 (Stamatakis 2014) from 100 independent searches each starting from distinct random trees. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein 1985) with 1000 iterations. Bayesian analyses (BA) were performed running two parallel analyses in MrBayes v. 3.2.6 (Ronquist *et al.* 2012). Analyses consisted of two runs of 6 chains of MCMC with the default temperatures for 25 million generations,

sampling every 5000 trees. All phylogenetic analyses were calculated on the CIPRES Science Gateway v. 3.3 (Miller *et al.* 2010). Convergence of each analysis was evaluated using Tracer v. 1.4.1 (Rambaut & Drummond 2007) to check that all ESS values exceeded 200. Consensus tree was calculated after omitting the first 25% trees as burn-in. Obtained topologies and nodal statistical support values were visualized and configured in FigTree v. 1.4.2. All trees were rooted on Solenostomataceae according to the topology of the main clades of Jungermanniidae, published by Vilnet *et al.* (2010).

RESULTS

Since the topologies of phylogenetic trees based on ITS, trnL and concatenated dataset were nearly identical, only the latter one is presented here (Fig. 1). In all three cases the specimens from the family Gymnomitriaceae (i.e. the genera *Marsupella* and *Gymnomitrium*) formed maximally supported clade. The specimens from the genus *Gymnomitrium* formed maximally supported clade in trnL-based tree and the one based on the concatenated dataset, while in ITS based topology the genus is represented by three maximally supported clades, sister to the *Marsupella* clade. The latter has lower bootstrap support though in all Bayesian analyses obtained posterior probabilities are 1. Patterns of *Marsupella* phylogenetic trees branching differ slightly in different analyses in order of main lineages splitting, but do not present any case of supported conflict of topologies. These stable and rather well supported lineages get high statistical support in reconstruction, obtained from combined dataset. These are 1) *M. stoloniformis* N.Kitag. and *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. (PP=1, BS=100); 2) *M. disticha* Steph., *M. funckii* (F.Weber & D.Mohr) Dumort., *M. sphacelata* (Giesecke ex Lindenb.) Dumort. and *M. sprucei* (Limpr.) Bernet (PP=1, BS=100); and 3) *M. apiculata* Schiffn. and *M. condensata* (Ångstr. ex C.Hartm.) Lindb. ex Kaal. (PP=1, BS=100), *M. boeckii* (Austin) Lindb. ex Kaal. (PP=1, BS=100) and “core *Marsupella* clade” (PP=1, BS=99), which comprises rest of the involved species. The latter starts with *M. arctica* (Berggr.) Bryhn & Kaal. splitting; on the next node (PP=0.96, BS=90) two large branches. One of these two has moderate support (PP=96, BS=64) and comprises clades, corresponding to *M. apertifolia* Steph., *M. aquatica* (Lindenb.) Schiffn., *M. submarginata* Bakalin & Fedosov, sp. nov., and *M. tubulosa* Steph. It is sister to not supported one with three clades: 1) *M. alata* S.Hatt. & N.Kitag., *M. yakushimensis* (Horik.) S.Hatt., *M. koreana* Bakalin & Fedosov, sp. nov., and *M. pseudofunckii* S.Hatt. (PP=0.98, BS=58); 2) monospecific clade of *M. patens* (N. Kitag) Bakalin & Fedosov, comb. nov., stat. nov. (PP=1, BS=100); and 3) *M. emarginata* Bakalin & Fedosov, sp. nov., and *M. vietnamica* Bakalin & Fedosov, sp. nov. (PP=0.83, BS=42). Most clades corresponding to individual species have high or maximal support.

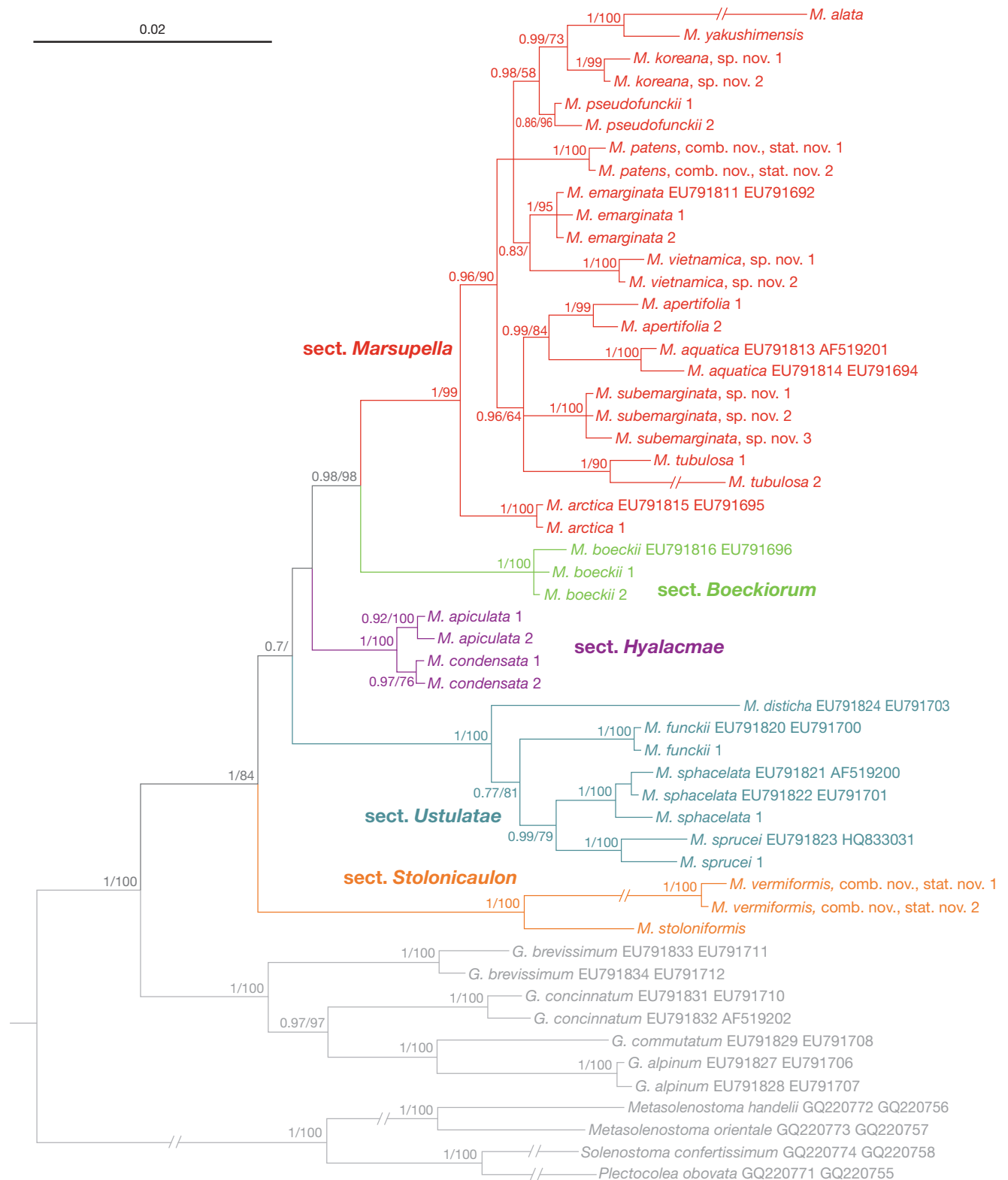


FIG. 1. — Bayesian tree obtained from the concatenated ITS and trnL sequences. Posterior probabilities (>70) / BS support (>50) from the best RAxML likelihood tree (if applicable) are indicated.

DISCUSSION

The clades, obtained as the result of this work in the most cases are properly explained by the relationships of morphology and/or distribution and possible related speciation. These clades show both probable infrageneric structure and taxon status. The obtained results fall into the following observation categories:

1) As is evident from the phylogenetic tree, some taxa, which for a long time were considered at infraspecific level (like *Marsupella emarginata* subsp. *tubulosa* var. *patens*) in fact are distinct comparably with related species of these complex (like *M. emarginata* and *M. pseudofunckii*). The similar situation is with *M. emarginata* ssp. *tubulosa* var. *apertifolia*, it was found as the member of clade another than that to which *M. emarginata* s.str. belongs. *Marsupella stoloniformis* subsp. *vermiformis* is quite distinct from *M. stoloniformis* s.str., and genetic distance between these taxa is higher than between many species of the genus.

2) There are several species being neglected until present. The robust difference was observed between *Marsupella pseudofunckii* and new taxon *M. koreana* Bakalin & Fedosov, sp. nov., that using existing keys would be identified as the former. *Marsupella subemarginata* Bakalin & Fedosov, sp. nov., is the taxon first recognized purely on genetic results obtained in the course of our work. We then examined those specimens to search for distinctive morphological features. The newly described *M. vietnamica* Bakalin & Fedosov, sp. nov., is superficially similar to *Gymnomitrium rubidum* and could be keyed out to the latter taxon, if generative structures are neglected.

3) The obtained clades of the first order are nearly corresponded to already known sections and subgenera and seem to be correlated with ecology and distribution patterns rather than with pure morphology. For instance, it is quite troublesome to substantiate why so morphologically unlike taxa like *Marsupella vietnamica* Bakalin & Fedosov, sp. nov., and *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov., fall into the same clade, whereas *M. disticha* and *M. alata* were found as exceedingly distanced. The analyzed diversity of *Marsupella* may be interpreted in the view of morphology, ecology and distribution as follows (here the asterisk marks species newly evaluated in the present paper, see taxonomical section):

Sect. *Marsupella* is split into three subclades. Subclade A (*alata-yakushimensis-koreana**-*pseudofunckii-patens**-*emarginata-vietnamica*) represent taxa most often with easily develop red pigmentation. This subclade also includes the circumpolar *M. emarginata* and its purely East Asian oro-boreal and oro-temperate relatives (exclusion if *M. vietnamica* Bakalin & Fedosov, sp. nov., that is oro-subtropical). Subclade B (*apertifolia**-*aquatica-subemarginata**-*tubulosa*) includes taxa distributed strictly in the areas with high air moisture year round, two of them are unable to develop red or purple pigmentation (*M. subemarginata* Bakalin & Fedosov, sp. nov., *M. apertifolia**), although two are able to do this (*M. tubulosa*, *M. aquatica*). These taxa are also similar due to mostly thickened cell walls in the leaf middle and ability to develop shortly bistratose leaf base (except *M. tubulosa*). Subclade C includes the only highly specialized Arctic *M. arctica*. All subclades are taxa preferring

bedrock (with somewhat exclusion for *M. arctica*); other features may include more or less rigid shoots with commonly recurved leaf margins and moderate to large (among other *Marsupella*) size – the features that are difficult to supply with exact definitions.

Sect. *Boeckiorum* as represented in the phylogenetic tree by one species that is quite polymorphic genetically. *Marsupella boeckii* is characterized by small size among other *Marsupella* (a few exceptions from sect. *Ustulatae* and both taxa of sect. *Stolonicaulon*). Other peculiar traits include small, distanced and spreading leaves. The taxon prefers bedrock in mild climates with high air humidity.

Sect. *Hyalacmae* includes two taxa of arctic-alpine distribution, *Gymnomitrium*-like habit with commonly densely imbricate leaves making stems invisible. A peculiar trait is that both sometimes have discolored leaf margins (constantly in *M. apiculata* where the leaf margin is commonly erose). The taxa of the section prefer fine soils.

Sect. *Ustulatae* provides the biggest problem. However two striking features are in hand: most of the taxa included here are unable to develop purple or red pigmentation (questionable in *M. disticha*) and prefer fine soils instead of bedrock. The studied taxa possess an amphi-oceanic distribution that varies from temperate East Asian to nearly circumpolar, arctoboreomontane and arctic-alpine.

Sect. *Stolonicaulon** is highly distinctive from the other bulk of *Marsupella* (and forms the basal branch to other *Marsupella*) in number of features, including a subequatorial distribution (East Asia, South Asia, South East Asia and Papuaia), very rigid shoots, strongly distanced, scale-like and appressed to the stem leaves and meso-xerophilous habitat that contradict to the majority of other *Marsupella*.

The obtained results require discussion in four ways: subgeneric division of the genus, clarification of status of already known subspecific taxa, evaluation of the new taxa, described here and discussion on the possible speciation within the genus in the view of their distribution patterns.

EVALUATION OF THE NEW TAXA

Due to obtained results, several taxa are different enough to warrant recognition at the species rank. They are described below.

Marsupella subemarginata Bakalin & Fedosov, sp. nov.
(Figs 2; 5A-C)

Plants greenish brownish to rusty, without purple pigmentation. Stem cross section with outer layer cells larger, with thickened cell walls. Leaves transversely inserted, shortly decurrent dorsally, leaf margin plane or revolute, concave-canaliculate, midleaf cells relatively small. Dioicous.

TYPE. — Russia. Kamchatka Territory, Ganalsky Range, Bakening Volcano area, upper course of Pravaya Kamchatka River, 53°56'45"N, 158°01'56"E, 900 m alt., moist boulder near temporary stream in alpine belt, field no. K-44-16-15, 04.VIII.2015, leg. Bakalin V. A. (holo-, VBG1; iso-, MW).

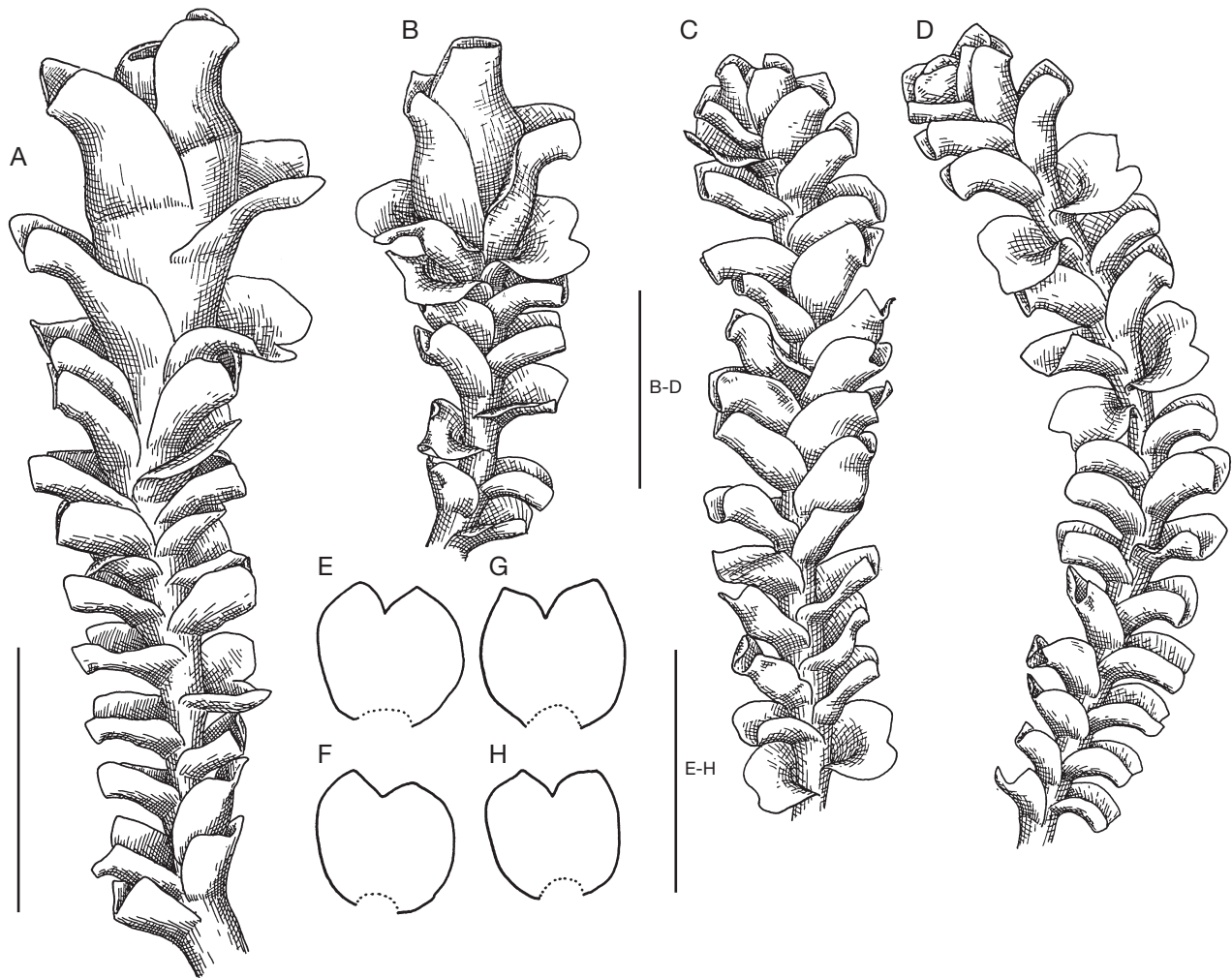


FIG. 2. — *Marsupella submarginata* Bakalin & Fedosov, sp. nov.: **A, B**, perianthous plants, dorsal view; **C**, male branch, dorsal view; **D**, sterile branch, dorsal view; **E-H**, leaves. Types: **A**, from holotype K-44-16-15, VBGI; **B-H**, from paratype K-44-14-15, VBGI. Scale bars: A, 1 mm; B-D, 1 mm; E-H, 1 mm.

PARATYPES. — **Russia.** Kamchatka Territory, Ganalsky Range, Bakening Volcano area, upper course of Pravaya Kamchatka River, 53°56'45"N, 158°01'56"E, 900 m alt., moist boulder near temporary stream in alpine belt, field no. K-44-14-15 (virtually the same site as the type), 04.VIII.2015, leg. Bakalin V. A. (VBGI). — **Switzerland.** Canton de Valais, Val d'Arpette, near Champex, 46°01'44"N, 07°05'24"E, 1700-2200 m alt., wet stone, field no. Sw-48-2-13, 28.IX.2013, leg. Bakalin V. A. (VBGI, MW). — **Japan.** Honshu, Yamanashi Prefecture, eastern slope of Senjo-ga-dake Mt., 35°45'46"N, 138°11'19"E, 2600 m alt., *Abies-Tsuga diversifolia* mountain forest in the valley, field no. J-89-31-15, 2.X.2015, leg. Bakalin V. A. (VBGI, MW).

DESCRIPTION

Plants greenish brownish to rusty, without distinct purple pigmentation, 5-20 mm long and 0.8-1.3 mm wide, merely soft. Rhizoids sparse, brownish, present in basal part of perianthous shoots only, obliquely spreading or united into unclear fascicles. Stem yellowish greenish to brownish, branching not seen (probably due to free sporophyte production and distribution by spores within cushions even); cross section transversely elliptic, c. 200 × 250 µm, hyaloderm distinct due to larger cells, but

cell walls are thickened, 15-20 µm along margin, scleroderma distinct, cell walls thickened, colorless, 11-15 µm in diameter, gradually becoming thinner to the middle. Leaves transversely inserted, shortly (to 1/3 of stem width) decurrent dorsally, transversely or arcuately inserted ventrally, loosely or not sheathing the stem, leaf margin plane or revolute (large leaves) in lower half of leaf only, concave-canaliculate, obliquely spreading, when flattened in the slide suborbicular to loosely ovate, 0.5-1.0 × 0.6-1.1 mm, divided by gamma- or widely V-shaped sinus into two subequal or slightly unequal (dorsal smaller) lobes with rounded to obtuse apices. Midleaf cells 12-30 × 12-18 µm, walls slightly thickened, trigones convex, moderate in size; cells in the base of lobe middle 10-17 × 10-15 µm, nearly thin-walled, trigones moderate to large in size, convex to triangular; cells along leaf margin 9-14 µm, slightly thick-walled, trigones moderate in size, concave (adjacent to external side) to slightly convex; cuticle smooth throughout; oil bodies in the midleaf cells relatively small, spherical to oblong, 2-7 × 2-4 µm, 2-3 per cell, grayish bluish, very finely granulate. Dioicous. Androecia intercalary, with 10-15 and more pairs of

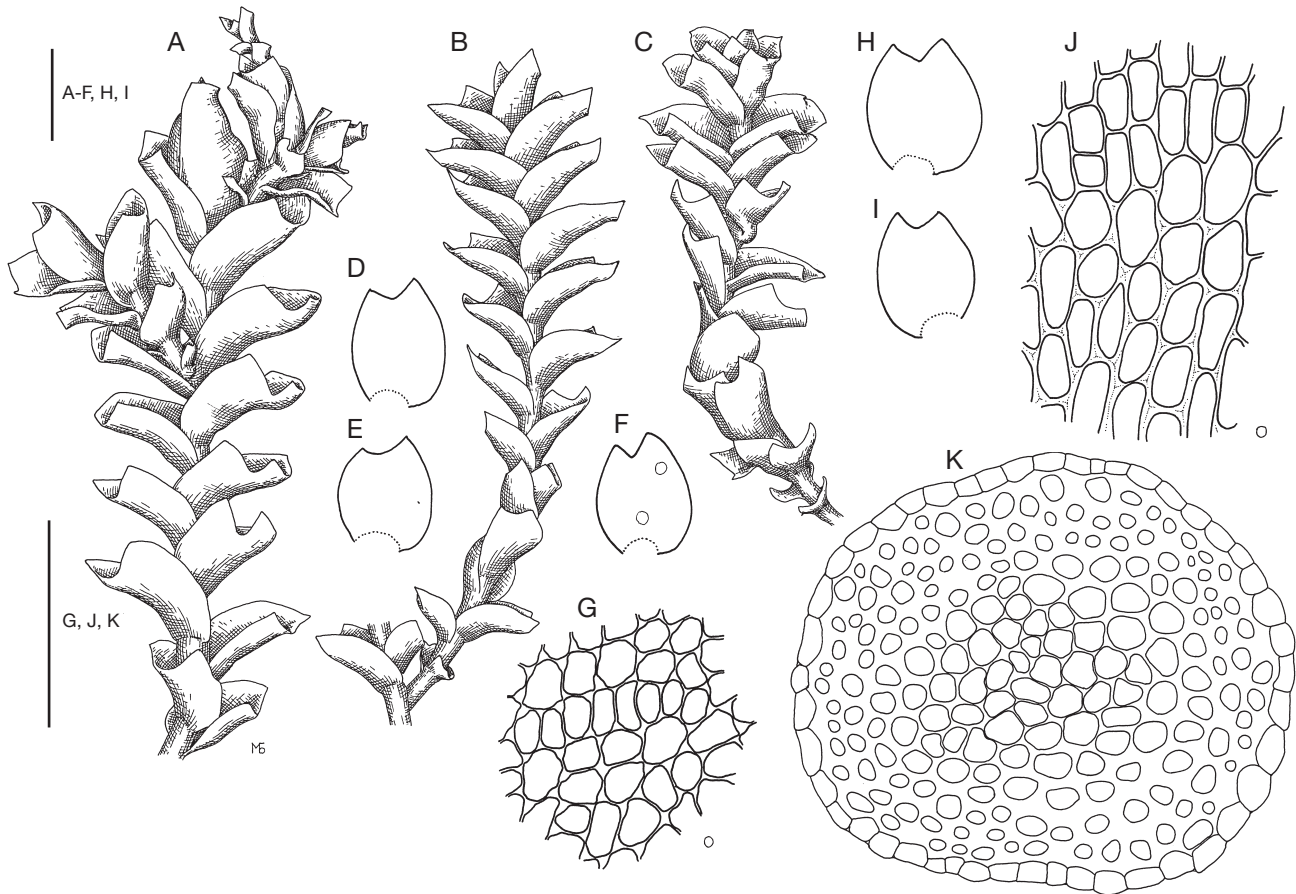


FIG. 3. — *Marsupella vietnamica* Bakalin & Fedosov, sp. nov.: **A**, perianthous plant, ventral view; **B**, sterile branch, dorsal view; **C**, male branch, ventral view; **D-F, H, I**, leaves; **G**, cells near leaf lobe base; **J**, cells in leaf base; **K**, stem cross section. Types: all from holotype V-2-101-16, VBGI. Scale bars: A-F, H, I, 1 mm; G, J, K, 100 μ m.

bracts, unfrequently becoming to sterile branch or die. Perianth conical, loosely beaked, 0.2-0.3 \times 0.6 mm, perigynium robust, 0.8-1.2 mm high, with 2 pairs of bracts; female bracts in lower pair sheathing the perigynium in the base and obliquely to erect spreading above and sometimes loosely reflexed, the axis of the upper pair of bracts subparallel to the stem and cover the perianth. Elaters bispiral, *c.* 100 \times 7 μ m. Spores brown, finely papillose, 10-12 μ m in diameter.

ECOLOGY

This is probably an oro-boreal species that occurs over temporarily wetted cliffs and boulders in areas with mild climate and smoothened distribution of precipitation around the year. In Switzerland it was observed in lighted subalpine dark coniferous forest in the cliff, where intermixed with *Pseudolophozia sudetica* (Nees ex Huebener) Konstant. & Vilnet and *Nardia scalaris* Gray. In two other tested specimens it forms pure patches (with some admixture of mosses). In Japan the specimen was collected in *Abies-Tsuga diversifolia* forest (called as subalpine in Japanese tradition, but is oro-boreal in European look). The habitat there is similar to the Switzerland one – moist open cliff. The gathering from Kamchatka was collected on moist boulder near temporary stream in mountain tundra environments and represent small phase of the taxon.

DISCUSSION

This is the most morphologically problematic semi-cryptic taxon that needs to be evaluated. In general appearance it is quite similar to true *M. emarginata* and our attention to this taxon was inspired first by the robust genetic differentiation of this taxon from *M. emarginata*. Morphological differences are minor and their stability is under suspicion. The most valuable difference is in the cell size, cells are relatively small and are only 12-18 μ m wide in the midleaf in *M. submarginata* Bakalin & Fedosov, sp. nov. Besides, the stem cross section, where the hyaloderm layer is composed by larger than scleroderm cells, looks as weakly differentiated due to thickened cell walls in *M. submarginata* Bakalin & Fedosov, sp. nov., contrary to uniformly thin cell walls of hyaloderm layer in *M. emarginata* (at least in its external wall). Another difference may be seen in midleaf and midlobe cells that are slightly thick-walled in *M. submarginata* Bakalin & Fedosov, sp. nov. (noticeably the same feature is observed in all taxa of the clade in phylogenetic tree: *M. apertifolia*, *M. aquatica*, *M. tubulosa*), contrary to thin-walled cells in *M. emarginata* midleaf and the leaf lobe middle. Moreover, *M. submarginata* Bakalin & Fedosov, sp. nov., apparently cannot produce clear red or purple pigmentation so the rusty or brown pigmentation is the main coloration type observed in this species. In this way, it may

be even more difficult to differ this taxon from *M. apertifolia*. *Marsupella subemarginata* Bakalin & Fedosov, sp. nov., differs from the latter in thickened hyaloderm cells in the stem cross section and prominent presence of rusty pigmentation (that may be regarded as the transition feature from inability to develop red and purple pigmentation. Another feature that differentiates this new taxon from both *M. apertifolia* and *M. emarginata* is the partly biconcentric oil bodies (less 20% of oil bodies in the leaf are biconcentric, with very small central eye), although observed just once (in holotype).

The geographic distribution provides one more distinct feature that may be usable in evaluation of this taxon. Similar to other taxa of the clade, this taxon is characterized by strictly suboceanic distribution (noticeable, it was not found even in Primorsky Territory and Korean Peninsula that are washed by Sea of Japan, but characterized by evident temperate monsoon (not oceanic) climate. The species was collected in the areas of Kamchatka and Japan that are strongly influenced by cyclones in the North Pacific and are characterized by smoothened seasonal variation with precipitation evenly distributed across the year. The similar situation is characteristic for Canton de Valais, Switzerland, where this taxon was collected in Europe, where the precipitation is evenly distributed over the year and average of air humidity varies from 60 to 85-90% (<https://weather-and-climate.com/average-monthly-Rainfall-Temperature-Sunshine-region-canton-of-valais-ch,Switzerland>). We may suggest this taxon is distributed much more widely than it may be estimated now and likely will be found in other areas of Eastern and North Eastern Asia as well as in temperate Atlantic Europe.

Marsupella vietnamica Bakalin & Fedosov, sp. nov.
(Figs 3; 5D-G)

Plants green to purple, without rusty pigmentation, rigid. Stem cross section with hyaloderm distinct, with external wall commonly destroying with time. Leaves subtransversely to virtually succubously inserted and oriented, strongly turned to ventral side, with plane margins, divided by sinus into 2 acute, subequal to unequal (ventral smaller) lobes. Dioicous.

TYPE. — **Vietnam**. Lao Cai province, Sapa district, Phan Xi Pang (also spelled Fansipan) National Park, 22°20'18"N, 103°46'39"E, 1900-2100 m alt., moist cliff in part shade, field no. V-2-101-16, leg. Bakalin V. A., 16.III.2016 (holo-,VBGI; iso-,MW)

PARATYPES. — There are several specimens from virtually the same place with the type: **Vietnam**. Lao Cai province, Sapa district, Phan Xi Pang (also spelled Fansipan) National Park, 22°20'18"N, 103°46'39"E, 1900-2100 m alt., moist cliff in part shade, field nos V-2-86a-16, V-2-91-16, V-2-98-16, 16.III.2016, leg. Bakalin V. A. (MW, VBGI).

DESCRIPTION

Plants greenish, yellowish greenish, deep green to (commonly) green purple, seems to be without rusty pigmentation, rigid, 10-40 mm long and 1.5-2.8 mm wide, in loose, mostly pure patches. Rhizoids virtually absent or very few, colorless and soft. Stem brownish, rigid, slightly glossy when dry, sparsely

ventrally branched (or with 1-3 lateral and ventral subfloral innovations); cross section transversely elliptic, c. 200 × 250 μm, hyaloderm distinct, cells 12-18 μm along margin, external wall thin and commonly destroying with time, tangential walls gradually becoming thicker inward, scleroderm very distinct, in 3-4 layers of cells, cell walls very thick than cell lumen sometimes obsolete, with well-visible median lamina, 6-15 μm in diameter (from middle lamina to middle lamina), inward suddenly become thinner (although never thin). Leaves subtransversely to virtually *succubously* inserted and oriented, with *plane* margins, insertion line arcuate dorsally and decurrent for ½ of stem width ventrally, obliquely spreading, loosely sheathing the stem in the base, strongly turned to ventral side, concave-canaliculate, when flattened in the slide ovate to slightly obliquely ovate, divided by U- to widely V-shaped sinus descending to ¼-½ of leaf length into 2 acute, subequal to unequal (ventral smaller) lobes, well developed leaves 1.3-1.5 × 1.0-1.5 mm. Midleaf cells 20-30 × 12-15 μm, distinctly thick-walled, trigones moderate in size, convex, middle lamina hardly visible, cells in the lobe middle base 17-25 × 12-20 μm, thick-walled, with moderate in size, convex trigones, cells along leaf margin 7-12 μm, thick-walled, with small, concave trigones, cells near leaf base in one layer, to 55 μm long, very thick-walled, with well-visible middle lamina; cuticle smooth throughout; oil bodies in the midleaf cells 2-3 per cell, large, nearly filling cell lumen, oblong, grayish, finely granulate. Dioicous (?). Perianth terminal, on main axis, hidden within bracts, with 1-3 lateral or ventral subfloral innovations, conical, 0.7-1.0 × 0.7-1.0 mm, loosely beaked; perigynium well developed, 1.0-1.5 of perianth length, with one pair of bracts; bracts closely sheathing the perianth in the base and overlap one another above. Otherwise not seen.

ECOLOGY

Acidophilic meso-hygrophite, preferring shaded to semi-open moist to wet cliffs (with enough amount of water even during so-called "dry season" in tropical zone) near stream. The species occurs in middle mountain elevations in southernmost tips of Tibetan spur stretching to Indochina. One of the species regularly occurring near (or contacting) patches of *Marsupella vietnamica* Bakalin & Fedosov, sp. nov., are *Cephalozia conchata* (Grolle & Vána) Vána and *Solenostoma suborbiculatum* (Amakawa) Vána & D. G. Long. The latter species may be intermixed with *Marsupella vietnamica* Bakalin & Fedosov, sp. nov., and other associates are rare including *Scapania undulata* (L.) Dumort. and *Scapania* sp., aff. *S. contorta* Mitt.

COMMENT

Among *Marsupella* species this is a very distinctive taxon due to leaves strongly turned to ventral side, concave-canaliculate leaves with acute lobes and very thick-walled cells in the leaf base with visible middle lamina. Genetically this taxon was found to be closely related to *M. emarginata*, from which it, however, easily differs morphologically due to plane leaf margin and acute lobes. By the appearance this taxon resembles not *Marsupella*, but *Apomarsupella*, treated now (Söderström

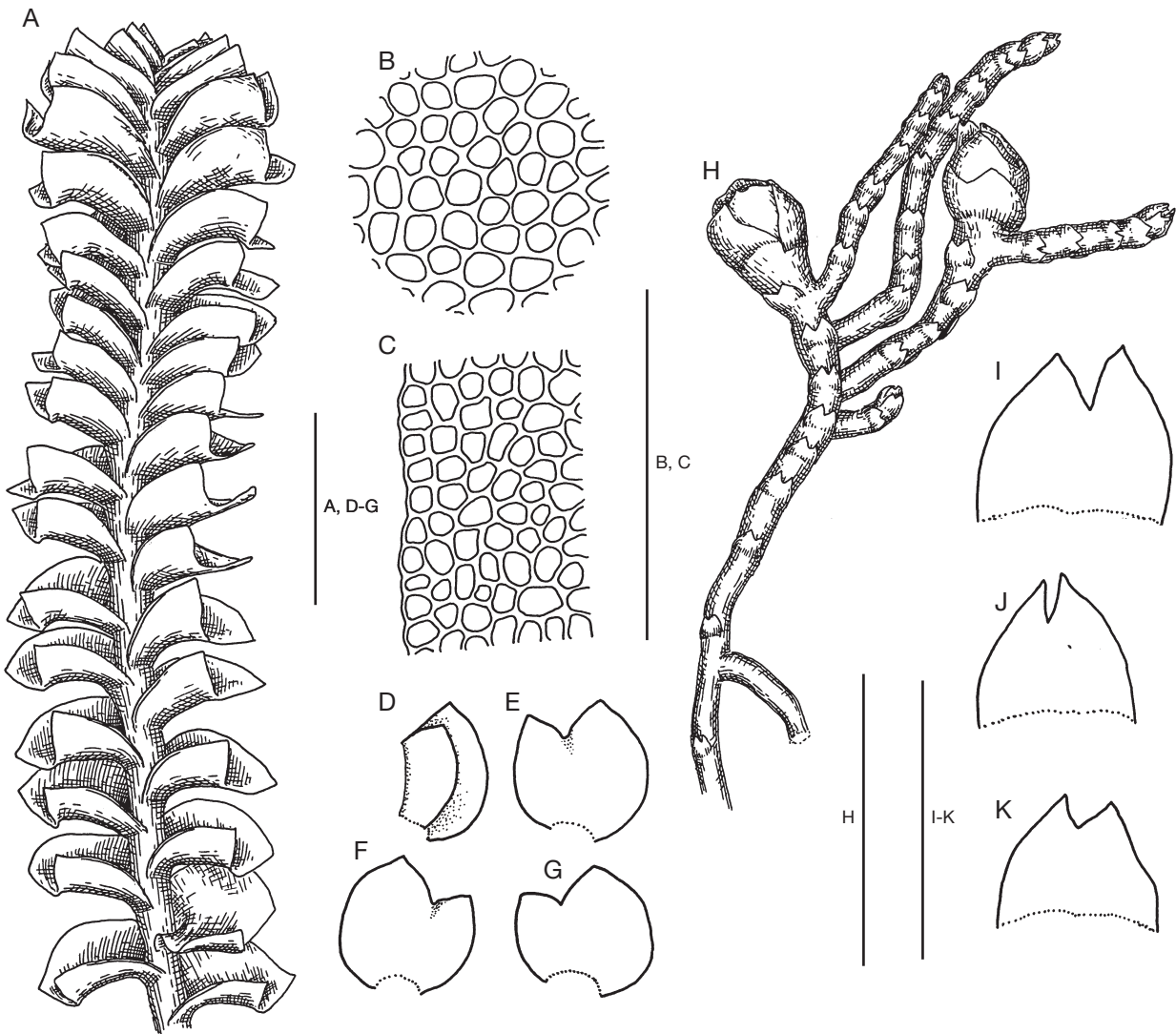


FIG. 4. — **A-G**, *Marsupella koreana* Bakalin & Fedosov, sp. nov.: **A**, plant habit, **B**, cells in leaf middle, **C**, cells in the leaf margin, **D-G**, leaves; **A-G**, types from holotype Kor-23-18-15 (VBGI); **H-K**, *Marsupella vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov.: **H**, plant habit; **I-K**, leaves; **H-K**, types from Choi-120911, VBGI. Scale bars: A, D-G, 1 mm; B,C, 100 μ m; H, 1 mm; I-K, 200 μ m.

et al. 2016), and probably hastily as the part of *Gymnomitrium*. Within “*Apomarsupella*” *Gymnomitrium rubidum* (Mitt.) Vána is most closely morphologically related to *Marsupella vietnamica* Bakalin & Fedosov, sp. nov. However, there are differences in fundamental generic features, such as well-developed perianth and perigynium in *M. vietnamica* Bakalin & Fedosov, sp. nov., vs their absence in *Gymnomitrium* s.l. Other differences are in smaller size of plants (less 1.0-1.5 mm wide), narrowly recurved leaf margin and brown blackish to rusty-brown pigmentation of plants in *Gymnomitrium rubidum*, vs larger size, plane leaf margin and common purple pigmentation of plants in *M. vietnamica* Bakalin & Fedosov, sp. nov. The position of *Gymnomitrium rubidum* in *Gymnomitrium* s.l. was tested and confirmed genetically by Shaw *et al.* (2015).

The general distribution patterns of this new species are difficult to estimate due to the limited material available.

We may suggest the species should occur more widely than currently found. Although we did not see androecia nor sporophytes, the species is quite abundant locally in middle elevation of Phan Xi Pang (also spelled Fansipan) Mt. that is quite a unique place in the view of taxonomic diversity. We think this species should be found in, at least, adjacent areas of Yunnan, China, where natural environments are somewhat similar to those observed in North Vietnam.

Marsupella koreana Bakalin & Fedosov, sp. nov.
(Figs 4A-G; 5H-K)

Plants strongly distichous, brownish green to deep green. Leaves distichously arranged, transversely to subtransversely inserted, narrowly canaliculate, divided by gamma-shaped sinus into two strongly unequal gibbous lobes, slightly revolute in margins. Dioicous.

TYPE. — **Republic of Korea.** KyongNam Province, Chiri Mts. National Park, south-eastern part of the park, the stream descending southward of the main peak, 35°19'42"N, 127°43'07"E, 1300-1600 m alt., moist cliff in part shade in mixed coniferous (*Picea abies*)-broadleaved deciduous forest in steep slope, field no. Kor-28-4-15, 7.V.2015, leg. Bakalin V. A. (holo-, VBGI; iso-, MW)

PARATYPES. — Only selected specimens are cited, the full list will be completed in the treatment of Korean Gymnomitriaceae: **Republic of Korea.** KyongNam Province, Chiri Mts. National Park, 35°19'54"N, 127°44'03"E, 1500-1600 m alt., 5.V.2015, Bakalin V. A. (MW, VBGI). — Chuncheonnam-do Province, Mt. Daedun, 36°08'02.9"N, 127°18'29.1"E, 343 m, 31.III.2009, S. S. Choi 3407 (JNU). — Gyeongsangnam-do Province, Mt. Gaya, 35°49'14.8"N, 128°07'27.5"E, 1313 m, 8.IX.2009, S. S. Choi (JNU). — Jeju-do Province, S. S. Choi 111147 (JNU). — Jeollabuk-do Province, Mt. Deogyu, 22.V.2008, S. S. Choi 509 (JNU). — Jeollanam-do Province, Mt. Dureun, 5.II.2009, S. S. Choi 3058 (JNU).

DESCRIPTION

Plants in loose mats, more or less rigid, strongly distichous, brownish green to deep green, brownish greenish and yellowish brownish, rarely brown with rusty tint to brown-purple, 500-1100 µm wide and 10-25 mm long. Rhizoids absent or very few, but common in geotropic stolons, colorless to grayish, obliquely to erect spreading. Stem rarely produces normal ventral branches, more commonly with ventral geotropic leafless stolons, almost always with 1-2 subfloral ventral or dorsal innovations; stem cross section differentiated into strata, nearly rounded to slightly transversely elliptic, with outer layer cells 10-20 µm along margin, mostly thin, rarely slightly unequally thickened, but with thin and easily destroying external side, with moderate to small concave trigones; scleroderm well developed, in 2-3 layers, walls very thick, sometimes with visible median lamina, 7-10 µm in diameter, but with lumen only 3-6 µm in diameter, trigones moderate to large, concave; inner cells irregular in shape, 10-15 µm in diameter, walls thickened, trigones moderate, concave. Leaves distichously arranged, transversely to subtransversely inserted, obliquely spreading and subtransversely oriented, margins commonly narrowly recurved in the both (dorsal and ventral) sides, narrowly canaliculate (but not distinctly conduplicate) with "keel" line slightly arched or nearly straight (in poorly developed phases), divided by gamma-shaped sinus into two strongly unequal gibbous lobes, lobe apices acute to obtuse. Cells in the midleaf mostly oblong, rarer subsodiametric, 7-20 × 7-13 µm, walls thickened, trigones large, triangle to convex, cuticle smooth, cells along lobe margin 5-10 µm, with unequally thickened walls, trigones small to moderate in size, concave, cuticle smooth; cells in the lobe middle 7-15 × 7-12 µm, with walls thickened to thin, trigones large and convex, sometimes confluent; oil-bodies (1-)(2-)(3) per midleaf cell, nonbiconcentric, finely granulate, spherical to oblong, c. 5-7.5 × 5 µm. Dioicous. Androecia intercalary,

with 2-3 pairs of bracts (but adjacent 1-2 pairs of leaves are similar with bracts that gives expression of more long androecious part), spicate, bracts cupped to spoon-shaped, with recurved margin, suborbicular and lacerate when flattened in the slide, divided by gamma-shaped sinus into two almost equal gibbous lobes, 750-875 × 825-1050 µm, 2-3-androus, antheridium stalk biserial, 100-200 µm long, body nearly spherical c. 100-120 µm in diameter. Perianth hidden within bracts or shortly exerted, onion-shaped, c. 250 × 600 µm; perigynium well developed, 600-800 µm long (when archegonia fertilized), with two pairs of bracts, bracts sheathing perianth, with lobes incurved to perianth or very narrowly spreading. Elaters entirely bispiral, c. 200 × 7-8 µm, with narrowed (sometimes even homogenous as in "*Plectocolea*-type") ends. Spores brown, papillose, spherical, 10-11 µm in diameter.

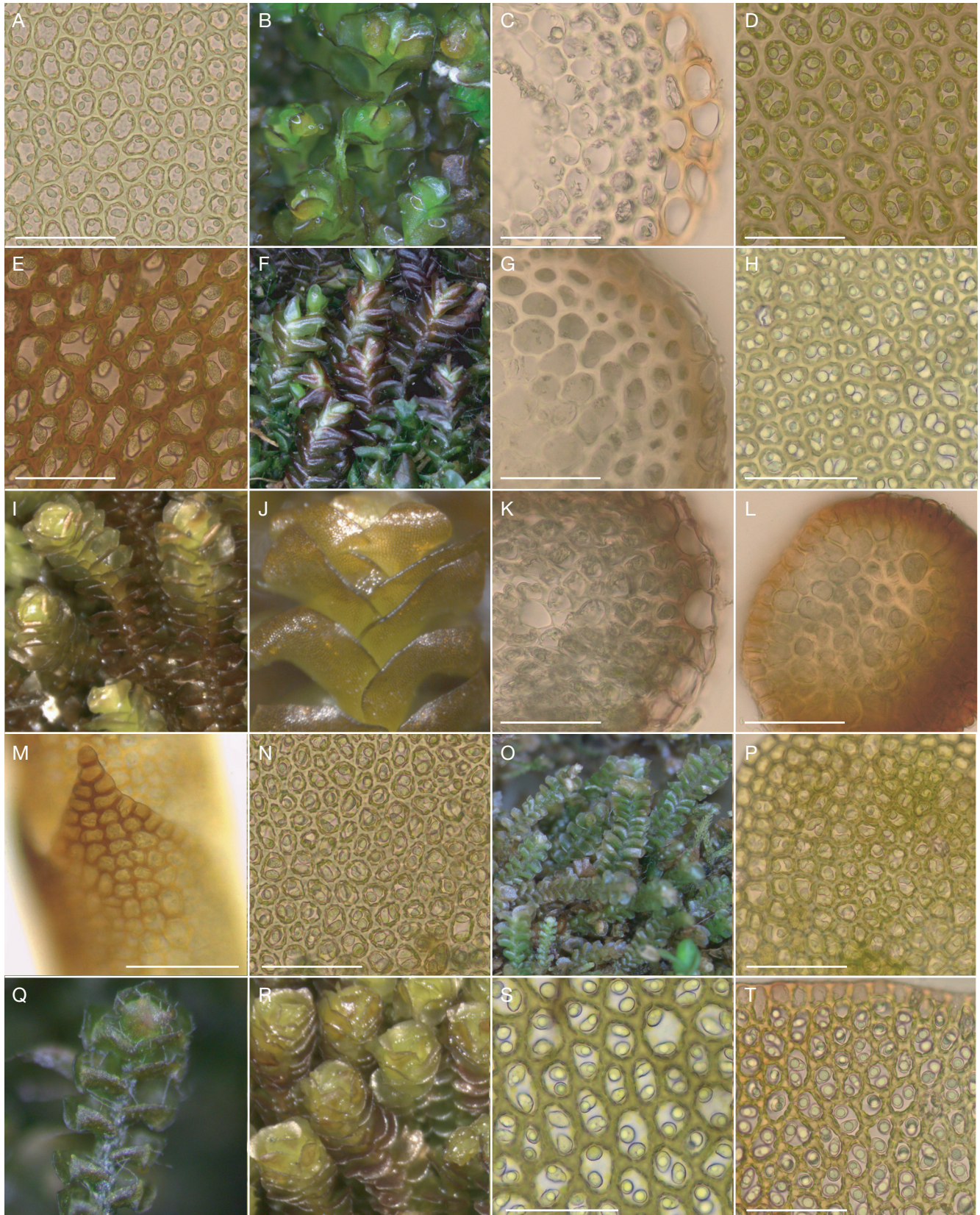
ECOLOGY

Acidophilic to neutro-tolerant meso- to hygrophyte. The ecology of this species is somewhat related to *Marsupella pseudofunckii*. It occupies mesic, rarer moist or dry substrata in open to partly shaded places. Among common associates in drier habitats are *Sphenolobus minutus*, in open alpine stations it sometimes growing together with *Gymnomitrium commutatum* (Limpr.) Schiffn. Wetter habitats are occupied by this species together with *Marsupella tubulosa*, *Cephalozia otaruensis* Steph., or, as exotic admixture, with *Hattoria yakushimensis* (Horik.) R.M.Schust.

COMMENT

This is probably an endemic species of strictly Korean distribution that is quite common there and very malleable in morphology. We have seen no specimens that would confirm its occurrence in Japan, Russian Far East and other adjacent areas. The species exhibits conduplicate leaves - the feature characteristic to the all taxa of the group "*pseudofunckii-patens*", weaker than in *M. alata*, *M. yakushimensis* and *M. pseudofunckii*, but stronger than in *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov. (where the leaves are only canaliculate, sometimes weakly so). *Marsupella yakushimensis*, *M. pseudofunckii* and *M. koreana* Bakalin & Fedosov, sp. nov., unlike *M. alata* and *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov., possess to develop red or purple pigmentation. *Marsupella koreana* Bakalin & Fedosov, sp. nov., and *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov., are able to develop a slightly revolute leaf margin - this feature is much more common in the former than in the latter. Due to its relatively small size three species are superficially most closely morphologically related to one another: *M. alata*, *M. koreana* Bakalin & Fedosov, sp. nov., and *M. pseudofunckii*. *Marsupella alata* differs from *M. koreana* Bakalin & Fedosov, sp. nov., in commonly winged leaves with lobes commonly subequal

FIG. 5. — **A-C**, *Marsupella submarginata* Bakalin & Fedosov, sp. nov.: **A**, cells in the midleaf; **B**, plant habit; **C**, stem cross section fragment; **A, B**, types from K-44-14-15; **C**, types, from Sw-48-2-1, VBGI; **D-G**, *Marsupella vietnamica* Bakalin & Fedosov, sp. nov.: **D**, cells in the leaf lobe base; **E**, cells in the midleaf; **F**, plant habit (dorsal view); **G**, stem cross section fragment; **D-G**, types from V-2-101-16, VBGI; **H-K**, *Marsupella koreana* Bakalin & Fedosov, sp. nov.: **H**, cells



in the midleaf; **I**, plant habit; **J**, upper part of the branch; **K**, stem cross section fragment; **I-K**, types from *Kor-23-18-15*, VBGI; **L, M**, *Marsupella vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov.: **L**, stem cross section fragment; **M**, leaf fragment; **L, M**, types from *Choi 120911*, VBGI; **N-Q**, *Marsupella pseudofunkii* N.Kitag.: **N**, cells in the midleaf; **O**, plant habit; **P**, cells in lobe base; **Q**, upper part of branch; **N, O**, types from *J-88-23-15*, VBGI; **P, Q**, types from *Prim-16-34-16*, VBGI; **R-T**, *Marsupella tubulosa* Steph.: **R**, plant habit; **S**, cells in the midleaf; **T**, cells along leaf margin; **R, S**, types from *Kor-23-12-15*, VBGI; **T**, types from *K-66-7-15*, VBGI. Scale bars: 50 µm.

and the absence of red or purple pigmentation. *Marsupella pseudofunckii* (Fig. 5N-Q) differs from *M. koreana* Bakalin & Fedosov, sp. nov., in strongly conduplicate (vs rather conduplicate-canaliculate to canaliculate-concave) leaves and shoots strongly dilated to the perianth. It is worth to note that *M. pseudofunckii* in its original description was estimated as olive green to brownish green, although the plant in one specimen studied here (J-7-10-14) is able to develop red-brown pigmentation.

The mentioned triplet of taxa also possesses somewhat different distribution patterns. *Marsupella alata* is Kurils-North Japanese (seems to middle Honshu) oro-boreal species. *Marsupella koreana* Bakalin & Fedosov, sp. nov., is strictly Korean as mentioned above. *Marsupella pseudofunckii* is oro-temperate (or oro-hemiboreal) species, with a more mysterious, however, understandable distribution. It is distributed in middle to southern Japan (Honshu, Shikoku, Kyushu, cf. Yamada & Iwatsuki 2006) and then re-occurs in southern Sikhote-Alin, although probably absent or rare in the Korean Peninsula (although it was many times recorded from there, cf. Yamada & Choe (1997), Kim & Hwang (1991), but in review of more than 200 so named specimens in Korean herbaria all of them are actually *M. koreana* Bakalin & Fedosov, sp. nov., and not *M. pseudofunckii*). The floristic relationships of Japanese archipelago and alpine flora of Sikhote-Alin were discussed in Vyshin (1990) for vascular plants. The cited paper provides arguments that Sikhote-Alin was floristically “connected” with Japan via its northern extremities and Sakhalin Island rather than via the Korean Peninsula and East-Manchurian Mountains. The similar results—complicated contacts between mountain flora of Korean Peninsula with Sikhote-Alin—were obtained for liverworts too (Bakalin 2015; Bakalin *et al.* 2017). If this point of view were to be adopted, the following scenario could be proposed: *M. pseudofunckii* has migrated from (or vice versa) Japan via Sakhalin Island to Sikhote-Alin Range and then survived in southern part of the area where the climate conditions are more favorable for it. The latter way may be however criticized since when the land bridge between Japan-Sakhalin and Asian mainland existed the climatic conditions were relatively cold, which makes chances for this temperate or hemiboreal taxon to migrate (another question: from Japan or to Japan!) via this bridge relatively low.

STATUS OF THE ALREADY KNOWN SUBSPECIFIC TAXA

The last revision of Gymnomitriaceae (Vána *et al.* 2010) provides infraspecific categories for three species: *Marsupella sparsifolia*, *M. stoloniformis* and *M. emarginata*. *Marsupella sparsifolia* var. *childii* is from Australia and New Zealand, its status is somewhat unclear and probably deserves recognition as a separate species. On the contrary, *M. stoloniformis* and *M. emarginata* are known from or near the area under treatment here.

INFRASPECIFIC STRUCTURE OF *MARSUPELLA STOLONIFORMIS*

Marsupella stoloniformis subsp. *stoloniformis* was recorded by Vána *et al.* (2010) for the Indian subcontinent and Malesia whereas *M. stoloniformis* ssp. *vermiformis* R.M.Schust. was recorded from Eastern Asia, Malesia and Papuaia (unfortunately that voluminous revision never cites original sources for distributional data they provide, especially for poorly known taxa). The record from East Asia probably refers to China, since the only mention we were able to find in the literature is the one presented in Shaw *et al.* (2015) where they cite the accession of *M. stoloniformis* (no reference to subspecific status) from Yunnan. Our specimen from Jeju-do (Halla-san) corresponds well to the description (type cited at F, but not located, and therefore, was not studied) and regarding subsp. *vermiformis* is well distinct both in genetic and morphological terms from subsp. *stoloniformis*. This evidence required a re-evaluation of this taxon at the species level:

Marsupella vermiformis

(R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov.
(Figs 4H-K; 5L-M)

Marsupella stoloniformis subsp. *vermiformis* R.M.Schust., *The Journal of the Hattori Botanical Laboratory* 80: 72, fig. 13 (1996) (The type RMS 67-5379 is cited for F, but was not located). Since the original description of this taxon is very short (only two lines) we provide a detailed morphological diagnosis of the species based on the material seen from Korea.

SPECIMENS EXAMINED. — **Republic of Korea**, Jeju-do, Mt. Halla, 33°21'42.1"N, 126°32'02.8"E, 1861 m, 21.IX.2012, S. S. Choi 120911, 120897, 120898 (JNU, VBG).

DESCRIPTION

Plants strongly vermicular, forming loose patches, deep green when fresh then turning to brown to blackish brown in the herbarium, without red or purple pigmentation, orbicular in cross section, 100-140 µm in diameter, 3-6 mm long, freely ventrally branched, from leafless “rhizome”, brownish to whitish in color, densely ventrally branched. Rhizoids virtually absent, to solitary, colorless, obliquely spreading, short (less than 100 µm long). Stem 100-140 µm in diameter, orbicular in cross section, outer layer cells with external wall thin to obscurely thickened, tangential walls subequally thickened, trigones small, concave, walls brown in color, 6-10 µm in diameter, inner cells with walls unequally thickened, walls colorless, trigones moderate, concave. Leaves appressed to the stem (lacerate into two parts when try to detach), transversely inserted and oriented, not decurrent, widely triangular, 75-110 µm long and 125-175 µm wide, divided by V-shaped sinus descending to 2/5-1/2 of leaf length into two subequal triangle lobes with acute apices. Cells in the midleaf 5-10 × 5-8 µm, walls moderately thickened, trigones small, concave; cuticle smooth; oil-bodies 1-2 per cell, spherical, 2-3 µm in diameter. Dioicous. Pants suddenly dilated to the perianth,

to form the head-like structure, perianth completely hidden within bracts, nearly conical, 75–100 µm long and 200–230 µm wide, smooth, perigynium 120–150 µm long, with one pair of bracts; bracts nearly orbicular to orbicular-triangular in shape, *c.* 250 × 250 µm, covering perianth and then occlude one with another.

ECOLOGY

Acidophilic meso-xerophyte. This is a rare and poorly known species and the data on its ecology may be incomplete. It occupies dry well exposed rocks in large block gravelly barrens in crater rim of Halla Mt. The similar habit type may be suggested and for classic locality if the taxon. *Marsupella vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., forms pure patches or grows with slight admixture of *Gymnomitrium concinnatum* or dwarf xeric form of *Marsupella tubulosa*.

COMMENT

This very distinctive species resembles with hand lens the poorly developed *Gymnomitrium pacificum* Grolle due to vermicular shoots and never spreading but closely appressed leaves, forming in female branches “head-like” structures (these shoots are somewhat subclavate). From aforementioned *G. pacificum* the present species is clearly different in having much smaller leaves, with normally developed cells along margin and in such fundamental features as the presence of distinct perianth and perigynium. This species, if found in northern part of East Asia, may probably be mistaken with the northern arctic-alpine *Marsupella boeckii* (more probably due to its dwarf forms from relatively xeric habitats), to that it is remotely allied due to small size. However, the two species distinctly differ in the following: 1) never spreading leaves in *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., vs commonly squarrose or, at least, slightly spreading in perianthous shoots in *M. boeckii*; 2) smaller shoot size, not exceeding 140 µm in diameter (vs 200–500 µm); 3) small and brown cells with thickened tangential walls of epidermal stem cells in cross section (vs large and hyaline); 4) total absence of red pigmentation (vs such pigmentation commonly present); 5) smaller leaves, reaching at maximum 175 µm wide (vs 200–300 µm wide); 6) very small leaf cells, 5–10 × 5–8 µm (vs 12–20 × 12–20 µm); and 7) smooth and small oil bodies, 2–3 µm in diameter, (vs “granular-botryoidal” (Schuster 1974), 3–8 × 3–7 µm).

The most closely related taxon, both in genetic and a morphological sense is *Marsupella stoloniformis* s.str. The differentiation features were provided by Schuster (1996) and may be summarized as following: *M. stoloniformis* s.str. has nearly ovate, longer than wide unlobed or shallowly emarginate leaves, vs wider than long and always incised sterile leaves in *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. The same may be said on female bracts, that are distinctly acute in *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., and obtuse to rounded in *M. stoloniformis*. It is also worth noting that the two taxa formally exhibit a distinctly sym-

patric distribution, with *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., showing a latitudinal wider range, from 32°N in Jeju-do to 5°S in Mt. Wilhelm in Papua New Guinea. However, in fact, the two taxa probably never occur at the same community type. *Marsupella stoloniformis* is probably mostly an oro-subtropical to oro-south-temperate taxon, never leaving evergreen forest environments. On the contrary, *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., is oro-cool-temperate to, even, oro-boreal taxon. In the type locality (Papua New Guinea) this species was collected in the elevation exceeding 4000 m a.s.l. that may mean peculiar cold alpine environments. Presumably both taxa are also different in water dependency with *M. stoloniformis* growing in open to slightly shaded wet to moist cliffs, whereas *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., confined to dry (virtually meso-xeric) sites in open shallow cliff crevices.

INFRA-SPECIFIC STRUCTURE OF *MARSUPELLA EMARGINATA*

The most complex question is infraspecific structure of *Marsupella emarginata* for which Váňa *et al.* (2010) list four infraspecific taxa: subsp. *emarginata* and subsp. *tubulosa* (Steph.) N.Kitag., including three varieties: var. *apertifolia* (Steph.) N.Kitag., var. *patens* N.Kitag. and var. *tubulosa* (Steph.) N.Kitag. The cited paper (Váňa *et al.* 2010) marks certain advance in recognition of some infraspecific taxa at the species level. *Marsupella aquatica* before was uniformly treated as the variety within *M. emarginata* (noticeable exclusions are the treatments by Schljakov (1981) and Grolle (1976), where it is the species; major works published at the end of 19th and the beginning of 20th century also recognized it as the taxon of species rank, cf. Schuster 1974).

Another complex taxon that after description was rarely treated as an independent species is *Marsupella tubulosa*. The only examples in the second half of the 20th century known to the authors are in Schljakov (1981) and Grolle (1976) although the latter only references to Schljakov's (1973) record from North Ural and cannot be regarded as independent finding. These listed papers as well as Schuster (1974) have introduced the usage of this name (regardless as variety or as the species) outside of Sea of Japan Basin which we suggest was a mistake. Originally *Marsupella tubulosa* is viewed from Japan. The study of dry material (also by Kitagawa 1963) could hardly reveal the stable distinction characters. The mentioned main differentiation characters (cf. Schljakov 1981; Schuster 1974) as the leaves asymmetry, more acute leaf sinus, and even (Schuster 1974, for subsp. *tubulosa* var. *laticus* R.M.Schust.) supposed absence of red pigmentation (although type in G is red colored). Later, as it was shown in Japanese literature, *Marsupella tubulosa* in its narrow sense (e.g. var. *tubulosa*) is characterized by distinctly biconcentric oil bodies (Iwatsuki 2001) (Fig. 5R–T), a feature remained neglected outside of Japan. Our study

of fresh material from East Asia has revealed this is the species of Japanese-Korean distribution, stretching the area to the Kurils and Kamchatka and, probably, as evident rarity, occurs in Sikhote-Alin. In any way, this taxon could hardly expand beyond Pacific Eastern Asia especially to the areas with a continental climate. Taking into account the genetic differences, this taxon needs to be recognized as a separate species. It is also worth to mention that the status of two varieties distinguished within "*M. emarginata* subsp. *tubulosa*", by Kitagawa (1963) as var. *apertifolia* and var. *patens* require further discussion that is provided below.

Kitagawa (1963) treated the latter two taxa (var. *apertifolia* (Steph.) N.Kitag. and var. *patens* N.Kitag.) as varieties within *Marsupella emarginata* ssp. *tubulosa* (Steph.) N.Kitag. based on supposedly intergrading character of differentiation features. To some degree, we may agree with him, because such features as the presence of red coloration and other features may not be easily observed in some depauperate plants or populations from shady habitats. On the other hand, the genetic analysis displayed robust distances between all these three taxa that even some "small" difference should help to recognize the taxa morphologically.

Indeed *M. apertifolia* possesses somewhat similar characters that differentiates it from *M. tubulosa* as do *M. aquatica* when compared with *M. emarginata*. These differences are in larger size, not so deeply lobed leaves, less recurved leaf margin, thick-walled cell walls in the midleaf and sometimes shortly bistratose leaf base (although not noted in the literature for *M. apertifolia*, but observed in our and type material). Kitagawa suggested both *M. aquatica* and *M. apertifolia* as independent derivatives from *M. emarginata* ssp. *emarginata* and *M. emarginata* subsp. *tubulosa* correspondingly. However, the results of comparison of genetic structure show the opposite situation. These taxa (*M. aquatica* and *M. apertifolia*) are more closely related to one another than to any *M. emarginata* or *M. tubulosa*. The former pair of taxa is better to regard as the result of more recent divergence probably due to geographic gap in distribution: both taxa show distinct amphi-oceanic tendencies in distribution, where *M. aquatica* is generally a sub-Atlantic taxon, whereas *M. apertifolia* is an oro-boreo-temperate West Pacific taxon. The morphological differences between these two taxa we were able to find are the absence of red pigmentation in *M. apertifolia*, whereas this coloration is common in *M. aquatica*, and distinctly (at least sometimes) striolate leaf cuticle in *M. apertifolia* (noted by Schuster (1996) as the peculiar feature of *Apomarsupella* within Gymnomitriaceae!), vs constantly smooth cuticle in *M. aquatica*. According to the obtained topology, the closest relative of *M. apertifolia* in fact is *M. aquatica*, not *M. tubulosa*; these species form highly supported clade and are similar morphologically. Thus, *M. apertifolia* cannot be considered an infraspecific taxon of *M. tubulosa* and should be either regarded as a separate species, or synonymized with *M. aquatica*. However, the distance between two clades in a genetic sense (Fig. 1) and the robust difference in distribution and somewhat morphology (absence of red or purple

pigmentation in *M. apertifolia*) suggest a re-establishment of this taxon as a distinct species under the name *Marsupella apertifolia* Steph. (*Bulletin de l'herbier Boissier*, sér. 2, 1 [2]: 162 [23], 1901; holotype: Japan, Miyo Kosan, U., 1897, *Faurie* 75, G9469/00065015!).

Principally another situation is with "*Marsupella emarginata* subsp. *tubulosa* var. *patens*" that is characterized strongly by unequally bilobed leaves that even "look like to *Diplophyllum*" (Kitagawa 1963: 90). Further Kitagawa (1963) noted the resemblance of var. *patens* with *Marsupella pseudofunkii*, from which, however, the species differ in larger size, rounded leaf lobes and not so prominently complicate leaves. Indeed, the genetic results have shown the strong relationship of this taxon with another group of other strictly East Asian taxa with unequal lobes and folded leaves: *M. alata*, *M. yakushimensis*, *M. koreana* Bakalin & Fedosov, sp. nov., and *M. pseudofunkii*. In our opinion, there are no reasons to merge this taxon with *M. tubulosa* and it should be regarded as the taxon of species rank. It easily differs from the other bulk of listed taxa in strongly unequal leaf lobes (by this feature joined with *M. pseudofunkii*, *M. koreana* Bakalin & Fedosov, sp. nov.), greenish to brown pigmentation without the red color (joined with *M. alata*, *M. pseudofunkii*), not keeled leaves (joined with *M. pseudofunkii* and *M. koreana* Bakalin & Fedosov, sp. nov.) and rounded leaf lobes. Therefore a new combination is needed:

Marsupella patens

(N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov.

Marsupella emarginata subsp. *tubulosa* var. *patens* N.Kitag., *Memoirs of the College of Science, Kyoto Imperial University. Series B. Biology* 27: 77 (1960) (Kitagawa 1960). — Type: Japan, Mie Prefecture, Mitsukuchi-dani, between Mt. Gozaisho-yama and Mt. Kamagatake, near Yunomine, moist rocks, field no. 37, 10.V.1958, leg. Iwatsuki Z & N. Kitagawa, (holo-, KYO!, s. n.).

SUBGENERIC DIVISION

The last revision of Gymnomitriaceae (Váňa et al. 2010) does not descend to subgeneric level, and therefore, the last and most consistent treatment of subgeneric structure of *Marsupella* may be found in the works by Grolle (1976), Schuster (1974), Müller (1956) and others published about half of century before. The modern infrageneric system was substantiated in general traits by Müller (1956). It was then slightly clarified by Grolle (1976), Schuster (1974) and Schljakov (1981). The recent and "genetically" based research that firstly obviously showed that perianth-less *Marsupella* are not "true" *Marsupella* was published by Vilnet et al. (2010) who does not use subgeneric classification units. Schuster (1974) provides as robust as it was possible morphological evidence to separate *Marsupella* into subgeneric entities and may be briefly discussed as following. First, Schuster split *Marsupella* into two subgenera: *Marsupella* and *Nardiocalyx* (Lindb.) R.M.Schust., with the latter limited to the only type species (*Gymnomitrium condensatum* Ångstr. that is homotypic

synonym of *Marsupella condensata*). Then, further, Schuster split the remained bulk of taxa into several sections that are mostly based on Müller's (1956) system:

Sect. *Ustulatae* Müll.Frib. ex R.M.Schust. (type species *M. ustulata*), to include "all of the small, dark, often scorched-appearing northern *Marsupella* in one section" (Schuster 1974: 23) and uniting it with Müller's (1956) sect. *Adustae*. As it was seen, the morphological features are of quantitative nature and could be hardly evaluated in the terms of exact meaning.

Sect. *Funckiae* Müll.Frib. ex R.M.Schust., including beside the type species (*M. funckii*) also *M. alpina* (Gottsche ex Husn.) Bernet (synonym of *Gymnomitrium alpinum* (Gottsche ex Husn.) Schiffn.), *M. commutata* (Limpr.) Bernet (synonym of *G. commutatum* (Limpr.) Schiffn.) and *M. badensis* Schiffn. (synonym of *M. funckii*), to unite blackish to dark brown plants of moderate size, non-Arctic distribution, dioicous inflorescence and lobes apices and sinus acute.

Sect. *Marsupella*, including, as the type species *M. emarginata* along with several vigorous European, North American, circumpolar and East Asian taxa: *M. paroica*, *M. sphacelata*, *M. arctica*, *M. pseudofunckii*, *M. yakushimensis*, *M. disticha*, *M. alata* and *M. minutissima* (the latter with question mark, following to Kitagawa 1963).

Sect. *Revolutae* Müll.Frib. ex R.M.Schust. with the type species *Marsupella revoluta* (Nees) Dumort. (synonym of *G. revolutum* (Nees) H.Philib.) and one additional taxon *Marsupella rubida* (Mitt.) Grolle (synonym of *Gymnomitrium rubidum* (Mitt.) Váňa, Stotl.-Crand. & Stotler).

Sect. *Boeckiae* Müll.Frib. ex R.M.Schust. for small, *Cephaloziella*-like plants with remote leaves; with type species *M. boeckii* and British *M. stableri*.

Moreover the *Gymnomitrium* sect. *Apiculatum* should be mentioned in this context. The latter was described (Schuster 1974) solely to separate *G. apiculatum* (Schiffn.) Müll. Frib. (synonym of *M. apiculata*) from the other bulk of *Gymnomitrium* taxa. Besides Schuster (1996) additionally described *Marsupella* subg. *Nanocaulon* R.M.Schust. to separate *M. microphylla* (the subgenus treated as monotypic), *Marsupella* subgen. *Micromarsupella* R.M.Schust., for *Marsupella minutula* Hässel, synonym of *Gymnomitrium minutulum* (Hässel) Váňa and evaluated *Marsupella* subgen. *Nanomarsupella* R.M.Schust. to the genus *Nanomarsupella* (R.M.Schust.) R.M.Schust.

The same subgeneric division was followed by Grolle (1976), with the addition of *Marsupella* sect. *Alpinae* for *Marsupella alpina* and *M. commutata* (synonym of *Gymnomitrium alpinum* and *G. commutatum* correspondingly) and acceptance of species level for *Marsupella tubulosa* and *M. aquatica*. This scheme latterly adopted by Schljakov (1981) who also described the new sect. *Pseudohyalacme* Schljakov for Schuster's sect. *Nardiocalyx* and Müller's sect. *Hyalacme* as *nomen novum* due to the confusing story of interpretation: the type of sect. *Hyalacme* (Lindberg 1878) was based on description that corresponds to *Marsupella apiculata* (also present in the type of *M. condensata*), but not on *M. condensata*. However, since the type species of the new subgenus (under *Nardia*

subgen. *Hyalacme* Lindb.) was correctly indicated by Lindberg (1878), this name should block the name proposed by Schljakov (1981) as an earlier homonym, and thus, the correct name should be *Marsupella* sect. *Hyalacme*. Another thing was acceptance of *Marsupella* subg. *Homocraspis* (Schiffn.) Grolle for solely *Marsupella brevissima* (Dumort.) Grolle (synonym of *Gymnomitrium brevissimum* (Dumort.) Warnst.). With minor alterations the latter scheme was adopted by Damsholt (2002) and Hong (1982).

Among other attempts to classify the genus, that by Kitagawa should be mentioned. Kitagawa (1963) uncritically accepted Müller's (1956) infrageneric system and added (with question mark) the only *Marsupella minutissima* to the sect. *Marsupella*. Later Kitagawa (1967) described *Marsupella* subg. *Neomarsupella* for solely *Marsupella integra* N.Kitag. (synonym of *Gymnomitrium subintegrum* (S. W.Arnell) Váňa) and subg. *Stolonicaulon* for *Marsupella stoloniformis*.

As it is obvious from the recent molecular phylogenetic studies (Vilnet *et al.* 2010), these schemes are out of date now, especially in the mixture of the taxa of different genera. The latter advance is reflected in recent monograph of Gymnomitriaceae (Váňa *et al.* 2010). Unfortunately, both mentioned works do not provide infrageneric division within *Marsupella*. Since in our work the dataset of taxa is larger than it was available before and includes the main bulk of taxa within the genus, this question may now be discussed again. Five clades of the first grade are found within the genus: 1) *disticha-funckii-sphacelata-sprucei*; 2) *apiculata-condensata*; 3) *M. emarginata* and its close morphological relatives and *M. arctica*; 4) *M. boeckii*; and 5) *M. vermiformis*-*M. stoloniformis* (Fig. 1). These five main branches, it seems, may be adopted as independent sections that correspond to previously known entities in general traits. Now we avoid to split the genus into subgenera and then to sections because from the practical point of view the difference between subgenera and sections could be hardly be evaluated morphologically and, additionally, because not all known taxa of *Marsupella* were involved into study. Nonetheless, that does not permit as to consider this scheme as the final one.

If to "cut off" the taxa now known as *Gymnomitrium* the infrageneric structure is described below. The taxa marked by asterisk were not tested genetically and therefore their position may remain somewhat doubtful. The list includes some taxa described here as new or evaluated here as independent species. The concept accepted in the present paper is incorporated to the Appendix 2 along with historic summary of the genus subdivision in several works mentioned above.

THE SYNOPSIS OF MARSUPELLA

Marsupella sect. *Marsupella*

Marsupella sect. *Emarginatae* Müll.Frib., *Hedwigia* 81: 113 (1942), nom. inval. (Art. 32. 1.d; no description).

TYPE SPECIES. — *Marsupella emarginata* (Ehrh.) Dumort.

DESCRIPTION

Plants moderate in size to large, rarely small in size, commonly with leaf margin narrowly revolute, green to brown and purple with red coloration frequent.

INCLUDED SPECIES

Marsupella alata S.Hatt. & N.Kitag., *Memoirs of the College of Science, Kyoto Imperial University. Series B. Biology* 27: 79 (1960).

Marsupella apertifolia Steph., *Bulletin de l'herbier Boissier* (sér. 2) 1 (2): 162 (23) (1901).

Marsupella aquatica (Lindenb.) Schiffn., *Deutsch-naturwissenschaftlich-medizinischer Verein für Böhmen "Lotos" in Prag* 44 (8): 267 (1896) [1897].

Marsupella arctica (Berggr.) Bryhn et Kaal., *Report of the Second Norwegian Arctic Expedition in the "Fram" 1898-1902* 11: 26 (1906).

**Marsupella bolanderi* (Austin) Underw., *Zoe* 1 (12): 365 (1891)

Marsupella emarginata (Ehrh.) Dumort., *Recueil d'Observations sur les Jungermanniacées*: 24 (1835).

Marsupella koreana Bakalin & Fedosov, sp. nov.

**Marsupella minutissima* N.Kitag., *Memoirs of the College of Science, Kyoto Imperial University. Series B. Biology* 27: 81 (1960).

**Marsupella paroica* R.M.Schust., *Bryologist* 60 (2): 145 (1957)

Marsupella patens (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov.

Marsupella pseudofunckii S.Hatt., *The Journal of the Hattori Botanical Laboratory* 4: 63 (1950).

Marsupella subemarginata Bakalin & Fedosov, sp. nov.

Marsupella tubulosa Steph., *Bulletin de l'herbier Boissier* 5 (2): 99 (1897).

Marsupella vietnamica Bakalin & Fedosov, sp. nov.

Marsupella yakushimensis (Horik.) S.Hatt., *Bulletin of the Tokyo Science Museum* 11: 80 (1944).

Marsupella sect. *Boeckiorum* R.M.Schust.

In *The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian* 3: 102 (1974) "Boeckiae".

Marsupella sect. *Boeckiorum* Müll.Frib., *Hedwigia* 81: 113 (1942) (see Müller 1942), nom. inval. (Art. 32. 1.d; no description), "Boeckiae".

TYPE SPECIES. — *Marsupella boeckii* (Austin) Lindb. ex Kaal.

DESCRIPTION

Plant small, filiform with leaves contiguous to distant, red coloration frequent, in well-developed shoots leaf apices somewhat squarrose.

INCLUDED SPECIES

Marsupella boeckii (Austin) Lindb. ex Kaal., *Nytt Magazin for Naturvidenskapene* 33 (4/5): 409 (1893).

**Marsupella stableri* Spruce, *Revue bryologique* 8 (6): 96 (1881).

Marsupella sect. *Stolonicaulon* (N.Kitag.) Váša

In *Bryobrothera* 5: 226 (1999).

Marsupella subgen. *Stolonicaulon* N.Kitag., *The Journal of the Hattori Botanical Laboratory* 30: 203 (1967) (see Kitagawa 1967).

Marsupella subgen. *Nanocaulon* R. M.Schust., *The Journal of the Hattori Botanical Laboratory* 80: 75 (1996) syn. nov.

TYPE SPECIES. — *Marsupella stoloniformis* N.Kitag.

DESCRIPTION

Plants filiform, small, leaves distant, scale-like, appressed to the stem, red or purple coloration unknown.

INCLUDED SPECIES

**Marsupella microphylla* R.M.Schust., *Phytologia* 39 (4): 249 (1978).

Marsupella stoloniformis N.Kitag., *The Journal of the Hattori Botanical Laboratory* 30: 201 (1967).

Marsupella vermiformis (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov.

Marsupella sect. *Hyalacme* Bakalin & Fedosov, comb. nov.

Nardia subgen. *Hyalacme* Lindb., *Helsingfors Dagblad* 1878 (38) 9 Feb.: 2 (1878).

Marsupella subgen. *Hyalacme* (Lindb.) Lindb., *Finland* 1885 (290) 13 Dec.: 2 (1885).

Gymnomitrium sect. *Hyalacme* (Lindb.) Schljakov, *Novosti Sistematiki Nizshikh Rastenii* 18: 100 (1981).

Nardiocalyx Lindb. ex Jørg., *Bergens Museums Skrifter* n. s. 16: 74 (1934). — Type: *Nardiocalyx apiculata* (Schiffn.) Jørg. (synonym of *Marsupella apiculata* Schiffn.).

Cesius A *Nardiocalyx* Lindb., *Musci Scandinavici in systemate novo naturali dispositi*: 9 (1879), nom. inval. (32. 1.d; no description).

Gymnomitrium subgen. *Nardiocalyx* (Lindb. ex Jørg.) S. W.Arnell, *Illustrated Moss Flora of Fennoscandia: Hepaticae. I.*: 225 (1956).

Marsupella sect. *Hyalacme* Müll.Frib., *Die Lebermoose Europas. Eine Gesamtdarstellung der europäischen Arten*: 759 (1956), nom. inval. (Art. 32. 1.d; no description, non subgen.) *Hyalacme* Lindb.

Marsupella subgen. *Pseudohyalacme* Schljakov, *Pechenochnyye Mkh Severa SSSR* 4: 96 (1981).

Gymnomitrium sect. *Apiculatae* R.M.Schust., *The Hepaticae and Anthocerotae of North America east of the hundredth meridian* 3: 122. 129 (1974). — Type: *Gymnomitrium apiculatum* (Schiffn.) Müll.Frib. (synonym of *Marsupella apiculata* Schiffn.).

TYPE SPECIES. — *Nardia condensata* (Ångstr. ex C.Hartm.) Lindb. (synonym of *Marsupella condensata* (Ångstr. ex C.Hartm.) Lindb. ex Kaal.).

DESCRIPTION

Plants small to moderate in size, densely leaved, leaves imbricate (one leaf covers 2-3 or more above situated leaves), rusty

coloration common (no distinct red or purple pigmentation), leaf margin commonly discolored (more obviously near apices).

INCLUDED SPECIES

Marsupella apiculata Schiffn., *Oesterreichische botanische Zeitschrift* 53 (6): 249 (1903)

Marsupella condensata (Ångstr. ex C.Hartm.) Lindb. ex Kaal., *Nytt Magazin för Naturvidenskapene* 33 (4/5): 420 (1893).

Marsupella sect. *Ustulatae* R.M.Schust.

In *The Hepaticae and Anthocerotae of North America east of the hundredth meridian* 3: 23, 1974

Marsupella sect. *Funckiorum* Müll.Frib., *Hedwigia* 81: 113 (1942), nom. inval. (Art. 32. 1.d; no description) “*Funckiae*”.

Marsupella sect. *Ustulatae* Müll.Frib., *Hedwigia* 81: 113 (1942) nom. inval. (Art. 32. 1.d; no description).

Marsupella sect. *Funckiorum* R.M.Schust., *The Hepaticae and Anthocerotae of North America east of the hundredth meridian* 3: 45 (1974) “*Funckiae*”. — Type: *Marsupella funckii* (F.Weber & D.Mohr) Dumort.

TYPE SPECIES. — *Marsupella ustulata* Spruce (synonym of *Marsupella sprucei* (Limpr.) Bernet).

DESCRIPTION

Plants moderate to small in size, leaves contiguous to somewhat distant, red pigmentation, rarely present (*M. sparsifolia* and *M. disticha* only, Schuster (1974) provide purplish black pigmentation for “*M. ustulata*” (synonym of *M. sprucei*), but we never observed it in the latter species)

INCLUDED SPECIES

**Marsupella andreaeoides* (Lindb.) Müll.Frib., *Repertorium specierum novarum regni vegetabilis* 54 (2/3): 214 (1951).

Marsupella disticha Steph., *Bulletin de l'herbier Boissier* (sér. 2) 1 (2): 164 (25) (1901).

Marsupella funckii (F.Weber & D.Mohr) Dumort., *Recueil d'Observations sur les Jungermanniacées*: 24 (1835).

**Marsupella neesii* Sande Lac. ex Schiffn., *Conspectus Hepaticarum Archipelagi Indici*: 70 (1898).

**Marsupella profunda* Lindb., *Revue bryologique* 14 (2): 19 (1887).

**Marsupella sparsifolia* (Lindb.) Dumort., *Bulletin de la Société royale de Botanique de Belgique* 13: 128 (1874).

Marsupella sphacelata (Giesecke ex Lindenb.) Dumort., *Recueil d'Observations sur les Jungermanniacées*: 24 (1835).

**Marsupella spiniloba* R.M.Schust. & Damsh., *Phytologia* 63 (5): 326 (1987).

Marsupella sprucei (Limpr.) Bernet, *Catalogue des hépatiques de sud-ouest de la Suisse et de la Haute-Savoie*: 33 (1888).

Unknown species

**Marsupella shimizuana* S. Hatt. (see explanation concerning this species in Váňa *et al.* 2010).

GEOGRAPHIC DIFFERENTIATION AND SPECIATION OF EAST ASIAN MARSUPELLA

Taking into account the position of taxa displayed in phylogenetic trees, some observation on speciation may be made in the following ways:

SECT. *MARSUPELLA*

This section bears four main lineages (based on analyzed taxa, but the real number may be higher). The basal branch is formed by *Marsupella arctica* — one of a few taxa that could be regarded as real arctic species in the global liverwort flora. This species does not go far from the tundra zone and does not occur even in higher mountains above timberline in the southern Hemi-arctic. This species is a highly specialized taxon within the genus that is confirmed by entire or shallowly retuse leaves, absence of brown coloration and peculiarly cupped, imbricate leaves.

The clade *M. alata-yakushimensis-koreana-pseudofunckii-patens* has very distinct regional attribute: all taxa of this group are distributed in East Asian floristic Province, moreover in the areas adjacent to the Pacific Ocean. The most “continental” locality was found for *M. pseudofunckii* as far as c. 50 km from Ocean coast in Primorsky territory where climate has a monsoon character. All other localities are under strong influence of oceanic climates (Váňa *et al.* 2010, recorded *M. pseudofunckii* for China, but we do not know which paper this report is based from). Within Korean-Japanese distribution these species exhibit regional differentiation: *M. yakushimensis* — the southernmost representative; *M. alata* — the northernmost in this group, extending area to the southern Kurils; *M. pseudofunckii* — oro-temperate taxon of middle Japan and south Sikhote-Alin Range; and *M. koreana* Bakalin & Fedosov, sp. nov. — strictly Korean taxon.

The clade *M. apertifolia-aquatica-submarginata-tubulosa* exhibits distinct amphioceanic distribution patterns, with taxa distributed in the areas of distinct oceanic (or, at least nearly so) climates. *Marsupella submarginata* Bakalin & Fedosov, sp. nov., is distributed in both amphi-Pacific and amphi-Atlantic areas (and probably the oldest taxon of the group due to strong malleability in morphology, the “intermediate” character of features between other species of the clade, presence of rusty pigmentation within absence of distinct purple color), other taxa show more distinct longitudinal patterns. *Marsupella apertifolia* and *M. tubulosa* are East Asian amphi-Pacific, although easily going northward to Hemi-arctic (e.g. in Kamchatka Peninsula). *Marsupella aquatica*, if to simplify, is purple European analogue of East Asian *M. apertifolia* and may be the more recent derivative of something similar to *M. submarginata* Bakalin & Fedosov, sp. nov., (if to regard red pigmentation as advanced feature).

The heterogeneous both in geographical and morphological sense in the clade that includes by now only two species: *Marsupella emarginata* Bakalin & Fedosov, sp. nov., and *M. vietnamica* Bakalin & Fedosov, sp. nov. *Marsupella emarginata* has very large arcto-boreal mountain circumpolar range (seems avoid “High Arctic”), and easily going southward by moun-

tain ranges, where appropriate air moisture correspond to this taxon requirements. The only exception is in East Asia due to the substitution of this taxon by closely morphologically and ecologically related (but more sensitive to air moisture) *M. tubulosa*. Another taxon of this morphologically heterogeneous group, *M. vietnamica* Bakalin & Fedosov, sp. nov., likely exhibits a meta-Himalayan range. This species shows distinct parallelism with the morphological appearance of *Apomarsupella* that probably was stimulated by similar environmental conditions (the highest taxonomic diversity of *Apomarsupella* is in meta-Himalaya and adjacent areas).

SECT. *BOECKIAE*

The only *Marsupella boeckii* now could be convincingly included to this section, although *M. stableri* likely belongs to this section too. This is arctic-alpine taxa, of which *M. boeckii* exhibits some regional variation (that may require further attention), distributed in subarctic mountains, in wet places of areas of oceanic and suboceanic climate. It seems to be absent in the areas with continental and especially ultracontinental climates.

SECT. *STOLONICAULON*

Both species *M. stoloniformis* and *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. may be convincingly included to this section based on genetic analysis; the third taxon – South American *M. microphylla* – is referred to this section with some doubts. Due to their small size these species could somewhat resemble *M. boeckii*, although both in shoot organization, distribution patterns and ecological requirements they are noticeably different. Both taxa of the section are growing in monsoon to tropical oceanic climates, although prefer well-insolated places. Especially characteristic are somewhat xeric habitats of *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov., both above 4000 m a.s.l. in locus classicus in Papua New Guinea and in insolated and free of vegetation crater rim of Halla-san in Jeju-do above 1800, in the northern “extreme” of the area. The species was also recorded from Yakushima Island (Miyanoura Peak) at the elevation 1420 m a.s.l., where the habitat of the species

was not clearly defined (Yokoyama *et al.* 2006). *Marsupella stoloniformis* is somewhat more water-dependent and prefers moist cliffs in open to slightly shaded areas. In the many cases where we observed *M. stoloniformis* in North Vietnam, the cliffs where it was observed were only temporarily wet and likely become dry in the dry season.

SECT. *HYALACME*

This section includes two very distinct morphologically (see above) and in distributional aspect taxa. Both are highly specialized in their habitats: moist fine soil and fine soils in various cliff crevices in tundra zone or alpine belt, only as very rare exception they occur in subalpine belt. Both taxa show circumpolar Hemiartic ranges. *Marsupella apiculata* seems to be more advanced than *M. condensata*, if the leaf margin characters are taken into account.

SECT. *FUNCKIAE*

The section includes nine taxa, only four of them were tested genetically (and therefore the position of the remained ones may be questioned). This section probably includes the most primitive group of the genus (no red pigmentation, simplified organization of the shoot, variation in elater spiral number). Moreover, the representatives of this group in several features somewhat resemble *Poeltia campylata*, that may be regarded as one of the most simplified member of the Gymnomitriaceae (especially if one excludes *Nardia* with well-developed underleaves). The representatives of this section are circumpolar Hemiartic to circumpolar oro-boreo-temperate areas or European (*M. profunda*), East Asian (*M. disticha*) or, even, Malesian (*M. neesii*). Most taxa of this section are growing on fine soil with disturbed vegetation cover (as again similar to *Poeltia*!).

As it is seen from the data presented above, not only species, but also sections show some regularity in distribution patterns. This difference in distribution is, highly probably, the consequence of geographic isolation of populations. The geographic isolation could stimulate speciation. The evidences presented here highly correspond to previous findings that describe and discuss geographic factors toward speciation in Biological Species Concept (BSC) (Mayr 1942, 1996).

KEY TO SPECIES

Since no keys currently exists to key out all known *Marsupella* and, certainly, the taxa described or evaluated in the present paper, we provide a key to all *Marsupella* recognized in the synopsis provided above.

1. Plants filiform, when leaved narrower 0.5 mm (sterile branches commonly narrower 0.3 mm wide), leaves in sterile axis strongly distant 2
- Plants not filiform, although sometimes small, mostly wider 0.5 mm wide, with leaves in sterile axis contiguous to imbricate (rarely distant in basal portions) 6
2. Plants paroicous, stem cross section with 2 layers of larger and somewhat thick-walled cells, scleroderm not differs from medulla, medulla composed by cells 1.6-2.0 times smaller than outer cells, very thick-walled [Latin American taxon] *M. microphylla* R.M.Schust.
- Plants dioicous, stem cross section with distinct hyaloderm or hyaloderm not distinct and cells of outer layer as similarly thick-walled as inner and sometimes become larger inside [Circum-hemiartic to circum arctic-alpine taxa and East to South-East Asian and Papuasian taxa, not occurring in Latin America] 3

3. Plants with somewhat spreading, distant, but somewhat contiguous near sterile branch apices, easily detaching leaves, stem cross section with hyaloderm cells distinctly different in size from inner (although sometimes with somewhat thickened walls) [Circum-hemiarctic to circum arctic-alpine or North amphi-Atlantic taxa] 4
 - Plants with leaves strongly remote, strongly appressed to the stem, difficult to detach, stem cross section with hyaloderm absent, inward cells commonly slightly larger than outer layer [East Asia, South-East Asia and Papuasias] 5
4. Leaves concave, when flattened in the slide somewhat rounded, androecial bracts concave, with lobes turned inward, 1-3-androus [subcircumpolar arctic-alpine seems to be amphi-oceanic taxon, southward to East Asia and Indian subcontinent] *M. boeckii* (Austin) Lindb. ex Kaal.
 - Leaves somewhat canaliculate, when flattened in the slide ovate, androecial bracts canaliculate-concave, with lobe apices squarrose to spreading, uniformly monandrous [North amphi-Atlantic] *M. strableri* Spruce
5. Leaves (especially well developed ones) wider than long, distinctly incised by narrow V-shaped sinus, lobe apices acute *M. vermiformis* (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov.
 - Leaves longer than wide, with rounded to emarginate apex, if shortly retuse, lobe apices rounded *M. stoloniformis* N.Kitag.
6. Plants vermiform, leaves in sterile shoots imbricate, strongly appressed and overlapping lower part of 1-5 leaves situated above, leaf margin commonly discolored and erose, especially in upper portions of leaf lobes, leaves very shortly (to $\frac{1}{10}$ - $\frac{1}{8}$ of leaf length) incised by crescentic sinus 7
 - Plants with leaves spreading, not vermiform, sometimes overlapping lower half of above situated leaf, but never so strongly appressed, leaf margin not erose and not discolored, leaves mostly more deeply incised ... 8
7. Leaf margin composed by thin-walled and easily destroying cells along the whole margin *M. apiculata* Schffn.
 - Leaf margin composed by more thick and although sometimes discolored in apical part, but never along the whole margin and not to hardly erose *M. condensata* (Ångstr. ex C.Hartm.) Lindb. ex Kaal.
8. Leaves in sterile axis strongly turned to ventral side, somewhat incubously oriented and inserted, dorsal lobe larger than ventral one [meta-Himalayan taxon] *M. vietnamica* Bakalin & Fedosov, sp. nov.
 - Leaves transversely or obliquely inserted and oriented, never turned to ventral side, lobes subequal or dorsal lobe smaller [various areas, also including meta-Himalayan region] 9
9. Plants with distinctly conduplicate leaves sometimes with distinct keel wing, or leaves with strongly unequal lobes giving scapanioid appearance [East Asian] 10
 - Plants with lobes equal to subequal, never strongly conduplicate, nor keeled [various areas, including East Asia] 15
10. Lobes subequal 11
 - Lobes distinctly unequal 13
11. Keel wing commonly distinctly developed, plants 0.7-1.2 mm wide *M. alata* S.Hatt. & N.Kitag.
 - Keel wing absent 12
12. Leaves with margin plane (never undulate), leaf lobes rounded, smaller plants 0.4-0.7 mm wide *M. disticha* Steph.
 - Leaves with margins commonly undulate, leaf lobes acute, larger plants wider than 1.0 mm wide *M. yakushimensis* (Horik.) S.Hatt.
13. Leaves canaliculate (sometimes loosely so) with dorsal lobe somewhat vertically oriented (turned to dorsal direction) *M. patens* (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov.
 - Leaves conduplicate to conduplicate-canaliculate, with dorsal lobe at the same plane with stem 14
14. Plants with purple pigmentation common, leaf margin commonly narrowly revolute (at least in some areas like leaf base), plants loosely dilated to the perianth [Korea] *M. koreana* Bakalin & Fedosov, sp. nov.
 - Plants with purple pigmentation absent, leaf margin always plane, plants distinctly dilated to the perianth [Japan and southern Sikhote-Alin] *M. pseudofunckii* S.Hatt.
15. Leaves cupped, only shallowly retuse with sinus less $\frac{1}{10}$ of leaf length, lacerate when flattened in the slide [strictly Arctic] *M. arctica* (Berggr.) Bryhn & Kaal.
 - Leaves concave-canaliculate to canaliculate, sinus $\frac{1}{8}$ - $\frac{2}{5}$ of leaf length, never lacerate when flattened in the slide [various areas including Arctic] 16

16. Sterile plants wider 1.0 mm wide, red or purple pigmentation commonly present, leaf margin commonly narrowly recurved along whole or part leaf margin, leaves distinctly spreading, never subimbricate 17
- Sterile plants narrower 0.7-1.0 mm wide, red or purple pigmentation rare, leaf margin never revolute, leaves commonly subimbricate, rarer spreading 23
17. Plants paroicous, green to brownish (never purplish or black) [Eastern North America]
..... *M. paroica* R.M.Schust.
- Plants dioicous, variously colored [various areas, including Eastern North America] 18
18. Leaves somewhat undulate, sheathing stem in lower half, margin plane (never revolute), sinus descending to $\frac{2}{3}$ of leaf length, leaf lobes rounded, plants greenish to brownish-blackish, never red or purple
..... *M. sphacelata* (Giesecke ex Lindenb.) Dumort.
- Leaves never undulate, not sheathing the stem, margin plane or revolute, sinus descending to $\frac{1}{4}$ of leaf length, leaf lobes rounded to acute, plants variously colored with some taxa commonly red or purple 19
19. Plants with red or purple pigmentation common 20
- Plants never purplish or reddish 22
20. Leaves bistratose very near to the base, sinus descending less than $\frac{1}{5}$ of leaf length [amphi-Atlantic]
..... *M. aquatica* (Lindenb.) Schiffn.
- Leaves unistratose to base, sinus descending for $\frac{1}{5}$ - $\frac{1}{4}$ of leaf length [circumpolar or East Asian amphi-Pacific] 21
21. Oil bodies nonbiconcentric, leaf lobes nearly equal in size [arctic-alpine circumpolar]
..... *M. emarginata* (Ehrh.) Dumort.
- Oil bodies biconcentric, leaf lobes subequal in size [East Asian, in strictly oceanic climates]
..... *M. tubulosa* Steph.
22. Stem hyaloderm with slightly thickened walls, leaves unistratose to the base, plants with common rusty pigmentation, midleaf cells 12-18 μ m wide [Eurasian amphi-oceanic]
..... *M. subemarginata* Bakalin & Fedosov, sp. nov.
- Stem hyaloderm with thin walls, leaves bistratose very near to base, midleaf cells commonly wider 18 μ m [East Asian, in strictly oceanic climates] *M. apertifolia* Steph.
23. Plants dioicous, distributed mostly in oro-boreal and more southern communities 24
- Plants monoicous (paroicous to synoicous), distributed mostly in arctic-alpine environments 27
24. Plants commonly tinged with red or purple, only slightly dilated to the perianth 25
- Plants brownish to blackish, never red or purple, distinctly dilated to the perianth 26
25. Cells in lobe middle 13-15 \times 11-14 μ m [East Asia] *M. minutissima* N.Kitag.
- Cells in leaf middle larger 15-20 μ m in diameter [Western North America]
..... *M. bolanderi* (Austin) Underw.
26. Leaves divided for $\frac{1}{3}$ - $\frac{1}{2}$ of the length, perianth exerted [Malesia (Java, Sumatra)]
..... *M. neesii* Sande Lac. ex Schiffn.
- Leaves divided to $\frac{1}{3}$ of leaf length, perianth hidden [amphi-oceanic arcto-boreo-montane to oro-boreal]
..... *M. funckii* (F.Weber & D.Mohr) Dumort.
27. Leaves distinctly longer than wide, subimbricate (giving aspect *Gymnomitrium commutatum*!), elaters 3-4-spirals
..... *M. andreaeoides* (Lindb.) Müll.Frib.
- Leaves nearly as long as wide, spreading, elaters 2-spiral 28
28. Plants 0.5-1.5 mm wide, only slightly dilated to the perianth, cells width in the midleaf 16-20 μ m, leaves loosely sheathing the stem near base *M. sparsifolia* (Lindb.) Dumort.
- Plants commonly under 0.7-0.8 mm wide, strongly dilated to the perianth, cells width in the leaf middle 8-17 μ m, leaves not sheathing the stem near base 29
29. Leaf lobes obtuse to rounded [strictly southern Atlantic (Portugal, Madeira, British Isles)]
..... *M. profunda* Lindb.
- Leaf lobes acute, rarely rounded [Arctic to arctic-alpine European-North American to circumpolar]
..... 30
30. Leaf lobes somewhat squarrose, distinctly diverging, midleaf cells 9-14 μ m wide, plants somewhat pectinate-distichous *M. spiniloba* R.M.Schust. & Damsh.
- Leaf lobes not squarrose, straight, midleaf cells 12-17 μ m wide, plants more terete, never distichous
..... *M. sprucei* (Limpr.) Bernet.

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APPENDICES

APPENDIX 1. — The list of taxa, specimen vouchers, and GenBank accession numbers used.

Taxon	Specimen voucher	GenBank accession number	
		ITS1-2 nrDNA	trnL-F cpDNA
<i>Marsupella alata</i> S.Hatt. & N.Kitag.	Republic of Korea, Seorak Mt., 11.V.2011, Bakalin, Kor-6-28a-11, VBGI	MH539833	MH539890
<i>Marsupella apertifolia</i> Steph. – 1	Russia, Sakhalin Province, 19.IX.2015, Bakalin, K-79-2-15, VBGI	MH539834	MH539891
<i>Marsupella apertifolia</i> – 2	Japan, Yamanashi prefecture, 30.IX.2015, Bakalin, J-87-25-15, VBGI	MH539835	MH539892
<i>Marsupella apiculata</i> Schiffn. – 1	Russia, Kamchatka Territory, 4.VIII.2015, Bakalin, K-44-7-15, VBGI	MH539839	MH539896
<i>Marsupella apiculata</i> – 2	Russia, Magadan Province, 10.VIII.2013, Bakalin, Mag-24-17-13, VBGI	MH539840	MH539897
<i>Marsupella arctica</i> (Berggr.) Bryhn & Kaal.	Russia, Magadan Province, 9.VIII.2011, Bakalin, Mag-54-13-11, VBGI	MH539841	MH539898
<i>Marsupella boeckii</i> (Austin) Lindb. ex Kaal. – 1	Russia, Khabarovsk Territory, 25.VIII.2016, Bakalin, Kh-41-1-13, VBGI	MH539842	MH539899
<i>Marsupella boeckii</i>	Russia, Magadan Province, 23.VII.2011, Bakalin, Mag-28-21-11, VBGI	none	none
<i>Marsupella boeckii</i> – 2	Russia, Magadan Province, 8.VIII.2014, Bakalin, Mag-33-16-14, VBGI	MH539843	MH539900
<i>Marsupella condensata</i> (Ångstr. ex C.Hartm.) Lindb. ex Kaal. – 1	Russia, Kamchatka Territory, 16.VIII.2015, Bakalin, K-60-30-15, VBGI	MH539844	MH539901
<i>Marsupella condensata</i> – 2	Russia, Magadan Province, 29.VII.2014, Bakalin, Mag-26-2-14, VBGI	MH539845	MH539902
<i>Marsupella emarginata</i> (Ehrh.) Dumort.	Russia, Khabarovsk Territory, 12.VIII.2016, Bakalin, Kh-27-8-16, VBGI	none	none
<i>Marsupella emarginata</i> – 1	Russia, Primorsky Territory, 15.X.2016, Bakalin & Klimova, Prim-16-14-16, VBGI	MH539848	MH539905
<i>Marsupella emarginata</i>	Russia, Khabarovsk Territory, 30.VII.2016, Bakalin, Kh-13-1-16, VBGI	none	none
<i>Marsupella emarginata</i>	Russia, Khabarovsk Territory, 4.VIII.2016, Bakalin, Kh-17-31-16, VBGI	none	none
<i>Marsupella emarginata</i> – 2	Russia, Khabarovsk Territory, 22.VIII.2016, Bakalin, Kh-34-7-13, VBGI	MH539849	MH539906
<i>Marsupella funckii</i> (F.Weber & D.Mohr) Dumort.	Georgia, Adjara, 14.V.2013, Bakalin, G-17-2-13, VBGI	MH539854	MH539911
<i>Marsupella koreana</i> Bakalin & Fedosov, sp. nov. – 1	Republic of Korea, KyongNam Province, 5.V.2015, Bakalin, Kor-23-18-15, VBGI	MH539850	MH539907
<i>Marsupella koreana</i> Bakalin & Fedosov, sp. nov. – 2	Republic of Korea, KyongNam Province, 7.V.2015, Bakalin, Kor-28-4-15, VBGI	MH539851	MH539908
<i>Marsupella patens</i> (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov. – 1	Japan, Fukuoka Prefecture, 16.III.2014, Bakalin, J-6-41-14, VBGI	MH539847	MH539904
<i>Marsupella patens</i> (N.Kitag.) Bakalin & Fedosov, comb. nov., stat. nov. – 2	Japan, Fukuoka Prefecture, 17.III.2014, Bakalin, J-7-26a-14, VBGI	MH539846	MH539903
<i>Marsupella pseudofunckii</i> S.Hatt. – 1	Japan, Yamanashi Prefecture, 1.X.2015, Bakalin, J-88-23-15, VBGI	MH539852	MH539909
<i>Marsupella pseudofunckii</i> – 2	Russia, Primorsky Territory, 15.X.2016, Bakalin & Klimova, Prim-16-34-16, VBGI	MH539853	MH539910
<i>Marsupella sphacelata</i> (Giesecke ex Lindenb.) Dumort.	U.S.A., Missouri State, 26.X.2014, Bakalin, US-41-91-14, VBGI	MH539855	MH539912
<i>Marsupella sprucei</i> (Limpr.) Bernet	Russia, Magadan Province, 26.VII.2011, Bakalin, Mag-38-39-11, VBGI	MH539856	MH539913
<i>Marsupella sprucei</i>	Russia, Murmansk Province, 14.VI.2015, Bakalin, Mur-32-5-15, VBGI	none	none
<i>Marsupella stoloniformis</i> N.Kitag.	Vientam, Lao Cai Province, 22.IV.2017, Bakalin & Klimova, V-11-11-17, VBGI	MH539859	MH539916
<i>Marsupella subemarginata</i> Bakalin & Fedosov, sp. nov. – 1	Japan, Yamanashi Prefecture, 2.X.2015, Bakalin, J-89-31-15, VBGI	MH539836	MH539893

APPENDIX 1. — Continuation.

Taxon	Specimen voucher	GenBank accession number	
		ITS1-2 nrDNA	trnL-F cpDNA
<i>Marsupella submarginata</i> Bakalin & Fedosov, sp. nov. – 2	Switzerland, Canton de Valais, 28.IX.2013, Bakalin, Sw-48-2-13, VBGI	MH539837	MH539894
<i>Marsupella submarginata</i> Bakalin & Fedosov, sp. nov. – 3	Russia, Kamchatka Territory, 4.VIII.2015, Bakalin, K-44-16-15, VBGI	MH539838	MH539895
<i>Marsupella tubulosa</i> Steph. – 1	Russia, Kamchatka Territory, 18.VIII.2015, Bakalin, K-66-7-15, VBGI	MH539860	MH539917
<i>Marsupella tubulosa</i> – 2	Republic of Korea, KyongNam Province, 5.V.2015, Bakalin, Kor-23-15-15, VBGI	MH539861	MH539918
<i>Marsupella vermiformis</i> (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. – 1	Republic of Korea, Jeju Province, 21.X.2012, Choi S.S., 120911, VBGI	MH539857	MH539914
<i>Marsupella vermiformis</i> (R.M.Schust.) Bakalin & Fedosov, comb. nov., stat. nov. – 2	Republic of Korea, Jeju Province, 21.X.2012, Choi S.S., 120911-1, VBGI	MH539858	MH539915
<i>Marsupella vietnamica</i> Bakalin & Fedosov, sp. nov. – 1	Vietnam, Lao Cai Province, 16.IV.2016, Bakalin, V-2-101-16, VBGI	MH539862	MH539919
<i>Marsupella vietnamica</i> Bakalin & Fedosov, sp. nov. – 2	Vietnam, Lao Cai Province, 16.IV.2016, Bakalin, V-2-86a-16, VBGI	MH539863	MH539920
<i>Marsupella yakushimensis</i> (Horik.) S.Hatt.	Republic of Korea, Gangwon Province, 11.X.2010, Choi S.S., 8347, VBGI	MH539864	MH539921

APPENDIX 2. — The distribution of *Marsupella* through subgeneric divisions of *Marsupella* and some taxa before regarded as *Marsupella*. The name authorities are in the synopsis.

Species	Schuster 1974, 1996	Müller 1956	Schljakov 1981	Kitagawa 1963, 1967	Hong 1982	Grolle 1976	Damsholt 2002	The present paper
<i>Gymnomitron adustum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Adustae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Adustae</i>	–	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	(not <i>Marsupella</i>)
<i>Gymnomitron alpinum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funkiae</i>	<i>Marsupella</i> sect. <i>Funckiae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Funkiae</i>	<i>Marsupella</i> sect. <i>Alpinae</i>	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Alpinae</i>	subg. <i>Homocraspis</i> sect. <i>Alpinae</i>	(not <i>Marsupella</i>)
<i>Gymnomitron brevissimum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Adustae</i> , nom. nud.	<i>Marsupella</i> subg. <i>Homocraspis</i>	–	<i>Marsupella</i> subg. <i>Homocraspis</i>	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	(not <i>Marsupella</i>)
<i>Gymnomitron commutatum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funckiae</i>	<i>Marsupella</i> sect. <i>Funckiae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Funkiae</i>	<i>Marsupella</i> sect. <i>Alpinae</i>	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Alpinae</i>	subg. <i>Homocraspis</i> sect. <i>Alpinae</i>	(not <i>Marsupella</i>)
<i>Gymnomitron revolutum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Revolutae</i>	<i>Marsupella</i> sect. <i>Revolutae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Revolutae</i>	<i>Marsupella</i> sect. <i>Revolutae</i>	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Revolutae</i>	subg. <i>Homocraspis</i> sect. <i>Revolutae</i>	(not <i>Marsupella</i>)
<i>Gymnomitron rubidum</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Revolutae</i>	<i>Marsupella</i> sect. <i>Revolutae</i> , nom. nud.	–	–	–	–	–	(not <i>Marsupella</i>)
<i>Gymnomitron subintegrum</i>	–	–	–	<i>Marsupella</i> subg. <i>Neomarsupella</i>	–	–	–	(not <i>Marsupella</i>)
<i>Marsupella alata</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella andraeoides</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Adustae</i> , nom. nud.	–	–	–	<i>Marsupella</i> subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	subg. <i>Homocraspis</i> sect. <i>Homocraspis</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella apertifolia</i>	–	–	–	–	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella apiculata</i>	<i>Gymnomitron</i> sect. <i>Apiculatae</i>	<i>Gymnomitron</i> subg. <i>Nardiocalyx</i>	<i>Gymnomitron</i> subg. <i>Apiculatae</i>	(not assigned, under <i>Gymnomitron</i>)	(not assigned, under <i>Gymnomitron</i>)	<i>Gymnomitron</i> sect. <i>Apiculata</i>	<i>Gymnomitron</i> subg. <i>Nardiocalyx</i>	<i>Marsupella</i> sect. <i>Hyalacmae</i>
<i>Marsupella aquatica</i>	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella arctica</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>

APPENDIX 2. — Continuation.

Species	Schuster 1974, 1996	Müller 1956	Schljakov 1981	Kitagawa 1963, 1967	Hong 1982	Grolle 1976	Damsholt 2002	The present paper
<i>Marsupella badensis</i> (synonym of <i>M. funckii</i>)	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funkiae</i>	<i>Marsupella</i> sect. <i>Funckiae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Funkiae</i>	—	—	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funckiae</i>	—	(species rank not accepted)
<i>Marsupella boeckii</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Boeckiae</i>	<i>Marsupella</i> sect. <i>Boeckiae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Boeckiae</i>	—	<i>Marsupella</i> sect. <i>Boeckiae</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Boeckiae</i>	subg. <i>Marsupella</i> sect. <i>Boeckiae</i>	<i>Marsupella</i> sect. <i>Boeckiorum</i>
<i>Marsupella bolanderi</i>	—	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella condensata</i>	<i>Marsupella</i> subg. <i>Nardiocalyx</i>	<i>Marsupella</i> sect. <i>Hyalacmae</i>	<i>Marsupella</i> subg. <i>Pseudo- hyalacmae</i>	—	<i>Marsupella</i> subg. <i>Hyalacmae</i>	<i>Marsupella</i> subg. <i>Hyalacmae</i>	subg. <i>Hyalacmae</i>	<i>Marsupella</i> sect. <i>Hyalacmae</i>
<i>Marsupella disticha</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	—	<i>Marsupella</i> sect. <i>Marsupella</i>	—	—	—	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella emarginata</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella funckii</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funkiae</i>	<i>Marsupella</i> sect. <i>Funckiae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Funkiae</i>	—	—	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Funkiae</i>	subg. <i>Marsupella</i> sect. <i>Funckiae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella koreana</i>	—	—	—	—	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella microphylla</i>	<i>Marsupella</i> subg. <i>Nanocaulon</i>	—	—	—	—	—	—	<i>Marsupella</i> sect. <i>Stolonicaulon</i>
<i>Marsupella miniata</i>	—	—	—	—	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella minutissima</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	—	<i>Marsupella</i> sect. <i>Marsupella</i>	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella neesi</i>	—	—	—	—	—	—	—	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella paroica</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	—	—	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella patens</i>	—	—	—	—	—	—	—	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella profunda</i>	—	—	—	—	—	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	—	<i>Marsupella</i> sect. <i>Ustulatae</i>

APPENDIX 2. — Continuation.

Species	Schuster 1974, 1996	Müller 1956	Schljakov 1981	Kitagawa 1963, 1967	Hong 1982	Grolle 1976	Damsholt 2002	The present paper
<i>Marsupella pseudofunckii</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella ramosa</i> (synonym of <i>M. funckii</i>)	–	–	–	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	–	(species rank not accepted)
<i>Marsupella shimizuana</i>	–	–	–	–	–	–	–	not known
<i>Marsupella sparsifolia</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Ustulatae</i>	–	<i>Marsupella</i> sect. <i>Ustulatae</i>	–	subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella sphacelata</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella spiniloba</i>	–	–	–	–	–	–	subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella sprucei</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i> , nom. nud.	<i>Marsupella</i> sect. <i>Ustulatae</i>	–	<i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i>
<i>Marsupella stableri</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Boeckiae</i>	<i>Marsupella</i> sect. <i>Boeckiae</i> , nom. nud.	–	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Boeckiae</i>	–	<i>Marsupella</i> sect. <i>Boeckiorum</i>
<i>Marsupella stoloniformis</i>	–	–	–	<i>Marsupella</i> subg. <i>Stolonicaulon</i>	–	–	–	<i>Marsupella</i> sect. <i>Stolonicaulon</i>
<i>Marsupella subemarginata</i>	–	–	–	–	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella tubulosa</i>	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella ustulata</i> (synonym of <i>M. sprucei</i>)	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	<i>Marsupella</i> sect. <i>Ustulatae</i> , nom. nud.	–	–	–	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Ustulatae</i>	–	(species rank not accepted)
<i>Marsupella vermiformis</i>	–	–	–	–	–	–	–	<i>Marsupella</i> sect. <i>Stolonicaulon</i>
<i>Marsupella vietnamica</i>	–	–	–	–	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>
<i>Marsupella yakushimensis</i>	<i>Marsupella</i> subg. <i>Marsupella</i> sect. <i>Marsupella</i>	<i>Marsupella</i> sect. <i>Emarginatae</i> , nom. nud.	–	<i>Marsupella</i> sect. <i>Marsupella</i>	–	–	–	<i>Marsupella</i> sect. <i>Marsupella</i>