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ON THE TAXONOMY OF THE SUBFAMILIES PALLAVICINIOIDEAE AND PODOMITRIOIDEAE OF THE FAMILY PALLAVICINIACEAE (MARCHANTIOPHYTA)

К ТАКСОНОМИИ ПОДСЕМЕЙСТВ PALLAVICINIOIDEAE И PODOMITRIOIDEAE СЕМЕЙСТВА PALLAVICINIACEAE (MARCHANTIOPHYTA)

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Abstract

Integrative study of species of the genus *Podomitrium* confirmed the monophyly of the genus and its close phylogenetic affinity to the genus *Pallavicinia*. As a result, the subfamily Podomitrioideae is proposed to be a synonym of subfamily Pallavicinioideae. A high level of molecular divergence between the specimens of *Podomitrium malaccense* suggests its complicated infraspecific structure. *Pallavicinia xiphoides* is raised to the rank of a separate genus, while the section *Subciliatae* is raised to the subgenus rank.

Резюме

Интегративное изучение видов рода *Podomitrium* подтвердило монофилию этого рода и его близкое филогенетическое родство с родом *Pallavicinia*. Предложена синонимизация подсемейства Podomitrioideae с подсемейством Pallavicinioideae. Высокий уровень молекулярной дивергенции между образцами *Podomitrium malaccense* позволяет предположить сложную внутривидовую структуру этого вида. *Pallavicinia xiphoides* выделена в самостоятельный род, ранг секции *Subciliatae* повышен до подрода.

KEYWORDS: *Podomitrium*, *Pallavicinia*, integrative taxonomy

INTRODUCTION

Despite of many studies including molecular ones (Forrest & Crandall-Stotler, 2004; Forrest *et al.*, 2005; Schaumann *et al*., 2004, 2005; Mamontov *et al.*, 2015) the taxonomy of the Pallaviciniaceae remains controversial in cases of the genera *Pallavicinia* Gray and *Podomitrium* Mitt. Indeed, molecular studies on Pallaviciniaceae Mig. by Forrest & Crandall-Stotler (2004) and Forrest *et al.* (2005) revealed the phylogenetic affinity between *Podomitrium phyllanthus* (Hook.) Mitt. and some species of the genus *Pallavicinia*, namely *P. lyellii* (Hook.) Gray and *P. xiphoides* (Hook. f. & Taylor) Trevis. However, the study by Schaumann *et al*. (2005) showed that *Podomitrium phyllanthus* is nested in a sister relationship with the subfamily Symphyogynoideae R.M.Schust. ex Grolle (l.c.: Fig. 2, 3). Discussing these controversial results, Schaumann *et al.* (2005) noted that sequencing of further *Podomitrium* specimens will be important to clarify molecular relationships of the genus. Two other taxonomic inconsistencies are related to species *Pallavicinia levieri* Schiffn. and *P. xiphoides* (Hook. f. & Taylor) Trevis., which are representatives of *Pallavicinia* subg. *Podomitriopsis* R.M.Schust. and *Pallavicinia* subg. *Pallavicinia* sect. *Dentigerae* R.M.Schust., respectively (Schuster, 1991). The molecular studies mentioned above revealed remote affinity between *P. xiphoides* and species of *Pallavicinia* subg. *Pallavicinia*, namely *P. lyellii* (Hook.) Gray and *P. subciliata* (Austin) Steph. (Schaumann *et al*., 2005), while *P. levieri* has been found in a sister relationship with both *P. lyellii* and *P. subciliata* (Mamontov *et al.*, 2015). To resolve these issues, we attempted to obtain and analyze the nuclear ribosomal ITS1-2 and chloroplast *trn*L-F sequences from specimens of *P. levieri*, *Podomitrium phyllanthus* and *P. malaccense* (Steph.) Campb., to compare the morphology of the studied specimens, and to discuss the taxonomy of the subfamilies Pallavicinioideae and Podomitrioideae R.M. Schust. in response to the data on morphology and molecular phylogeny.

MATERIAL AND METHODS

Morphological study

The specimens of *Podomitrium phyllanthus* and *P. malaccense* were studied and photographed using stereomicroscopes and light microscopes equipped with a digital camera Nikon D700. To better illustrate three-dimensional features, the stacks of photomicrographs obtained from several optical sections were combined using the stacking software HeliconFocus.

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Taxa sampling

Three specimens of the genus *Podomitrium* (one of *P. phyllanthus* and two of *P. malaccense*) were selected for estimation of its phylogenetic affinity. As nucleotide markers the ITS2 nrDNA and *trn*L-intron cpDNA were chosen due to their representation for the majority of Pallaviciniineae: the datasets produced for current estimation included 28 specimens from Schaumann *et al*. (2005), four specimens from Mamontov *et al*. (2015), a single specimen from Konstantinova *et al*. (2021) and *trn*L-intron of *P. phyllanthus* from Forrest *et al*. (2005). Additionally, *trn*L-F sequences were obtained for three specimens of *Pallavicinia levieri,* the ITS2 sequence data for them was published in Mamontov *et al*. (2015). The voucher information and GenBank accession numbers for specimens are shown in Appendix 1.

DNA isolation, amplification and sequencing

DNA was extracted from dried specimens using the DNeasy Plant Mini Kit (Qiagen, Germany). The primers suggested by White *et al*. (1990) for ITS2 and Taberlet *et al*. (1991) for *trn*L-F were used for amplification and sequencing reactions.

PCRs were carried out in 20 µl volumes according to the following procedure: 3 min at 94 °C, 30 cycles (30 s 94 °C, 40 s 56 °C, 60 s 72 °C) and 2 min of extension time at 72 °C. Amplified fragments were visualized on 1 % agarose TAE gels by EtBr staining, purified using the QIAquick Gel Extraction Kit (Qiagen, Germany), and then used as a template for sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analyses

New sequences were assembled and then included in ITS2 and *trn*L-intron datasets with downloaded accessions in BioEdit 7.0.1 (Hall, 1999). Alignment was produced with ClustalW option and then manually edited, all positions were taken in estimation, absent ITS2 sequence for the specimen of *Podomitrium phyllanthus* from Forrest *et al*. (2009) were coded as missing. Each dataset was preliminarily estimated by maximum likelihood (ML) with PhyML v.3.0 (Guindon *et al.*, 2010) in case of congruence: conflict nodes with sufficient support were not detected by visual inspection. The combined ITS2+*trn*L-intron datasets were produced and then analyzed by ML and Bayesian approach with MrBayes v. 3.2.1 (Ronquist *et al*., 2012). The selection of the best-fit evolutionary model of nucleotide substitutions was provided in ModelGenerator (Keane *et al.*, 2006); the estimation of stopping frequency criterion for bootstrapping (Pattengale *et al.*, 2010) – in RAxML v7.2.6 (Stamatakis, 2006). Thus, ML analysis was run with K80+I+G model, 350 replicates of bootstrap procedure and gamma distribution of the rate heterogeneity among sites with four rate categories.

For the Bayesian analysis, each partition of the combined alignment was separately assigned the K80 model, gamma distributions were approximated using four rate categories. Two independent runs of the Metropolis-coupled ĔCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated, and two starting trees were chosen randomly. Chains were run for five million generations and trees were sampled every 1000th generation. The software tool Tracer (Rambaut & Drummond, 2007) revealed an effective sample size as 11071,7693 and auto-correlation time as 812,9685. As determined by Tracer, the first 500 trees in each run were discarded as burn-in. Thereafter 9000 trees were sampled from both runs. The average standard deviation of split frequencies between two runs was 0.003176 at the end of the estimation. Bayesian posterior probabilities were calculated from trees sampled after burn-in. The majority rule consensus tree was calculated after combining the runs without burn-in of 10% and the topology was illustrated with FigTree v.1.4.4. (http://tree.bio.ed.ac.uk/software/figtree/).

The infrageneric variability of ITS2 and *trn*L-intron for selected taxa were calculated as the average pairwise *p*-distances in Mega 5.1 (Tamura *et al*., 2011) using the pairwise deletion option for counting gaps.

RESULTS

For three specimens of the genus *Podomitrium* the ITS2 and *trn*L-F sequence data were newly obtained, for three specimens of *Pallavicinia levieri* – *trn*L-F sequences, totally nine accessions were deposited into GenBank.

The combined alignment for 40 specimens of Pallaviciniineae consists of 750 sites, of these 342 sites belong to ITS2 and 408 sites to *trn*L-intron.

The ML estimation recovered a tree with a Log likelihood of -6382.2475. Arithmetic means of Log likelihoods in Bayesian analysis for each sampling run were -6270.13 and -6268.57. Topology reconstructed by both methods are identical, thus Fig. 1 provides the ML topology with the indication of ML bootstrap values (BS) and Bayesian posterior probabilities (PP) for each node. The phylogeny obtained here is congruent with those produced for other datasets in Schaumann *et al.* (2005), Forrest *et al*. (2009), Mamontov *et al*. (2015) and Konstantinova *et al*. (2021).

The specimens of *Pallavicinia levieri* are nested within the supported subclade (BS=100% in ML, PP=1.00 in BA, or 100/1.00) of *Pallavicinia* species, whereas specimens of *P. xiphoides* are in remote affinity to the clade composed by *Pallavicinia* and *Podomitrium* species. Due to the molecular differences from other *Pallavicinia* species, as well as morphological distinctions by the shape of the thallus and the spore ornamentation, *Pallavicinia xiphoides* is raised to the rank of a new genus *Prionothallus* (see Discussion and Taxonomy sections).

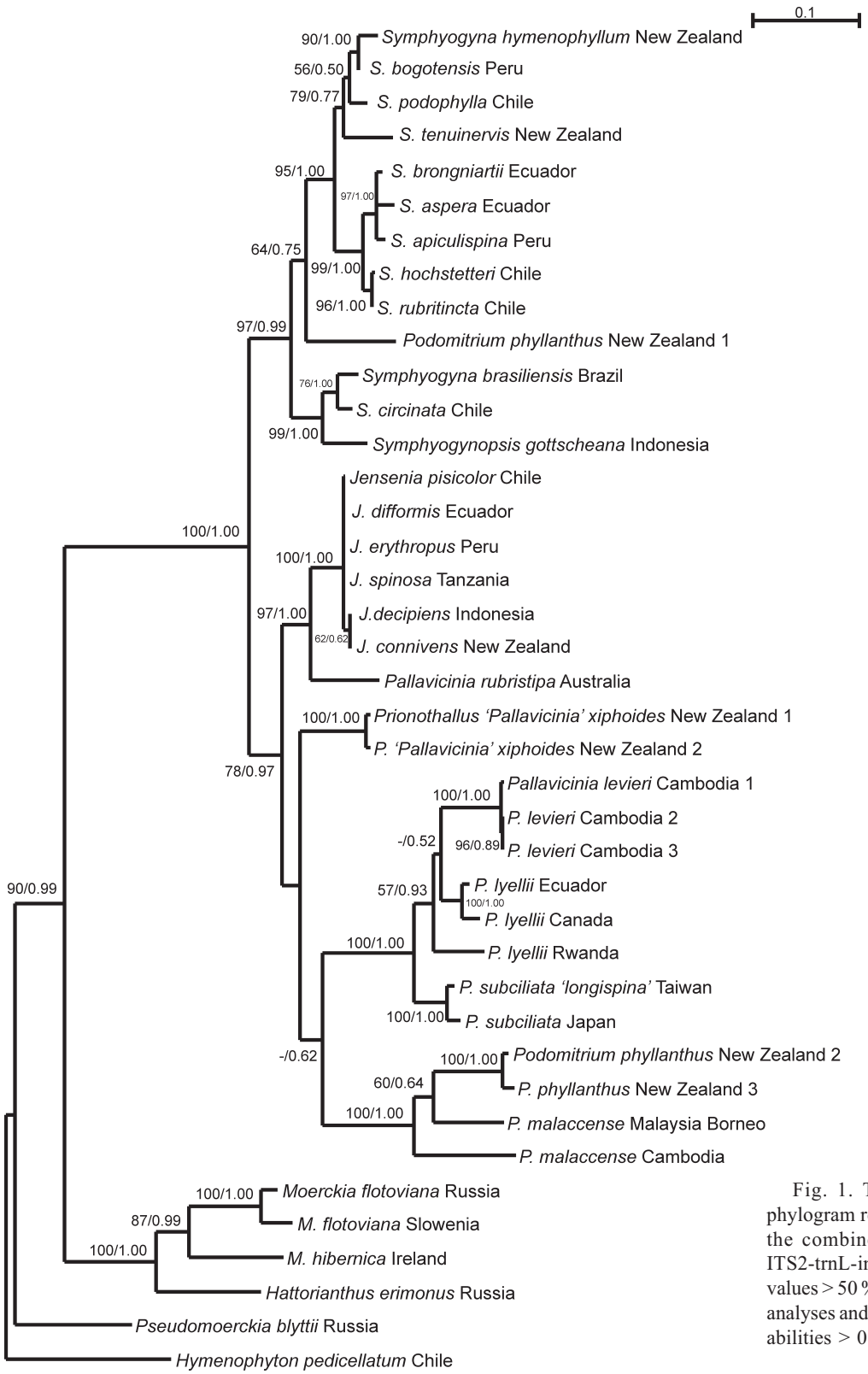

Fig. 1. The single most likely phylogram resulting from analysis of the combined molecular data sets ITS2-trnL-intron. Bootstrap support values > 50 % of maximum likelihood analyses and Bayesian posterior probabilities > 0.5 are indicated.

One of the specimens of *Podomitrium phyllanthus* (New Zealand 2) is located in the same subclade (100/1.00) as the second specimen of this species (New Zealand 3) (Fig. 1). The specimen of *P. malaccense* from Borneo revealed the sister relation with both *P. phyllanthus* specimens (60/0.64), while the next relation is composed of the specimen of *P. malaccense* from Cambodia (100/1.00). This *Podomitrium*-subclade forms a clade together with the *Pallavicinia*-subclade, but without sufficient support in both analyses (-/0.62). The third specimen of *Podomitrium phyl-*

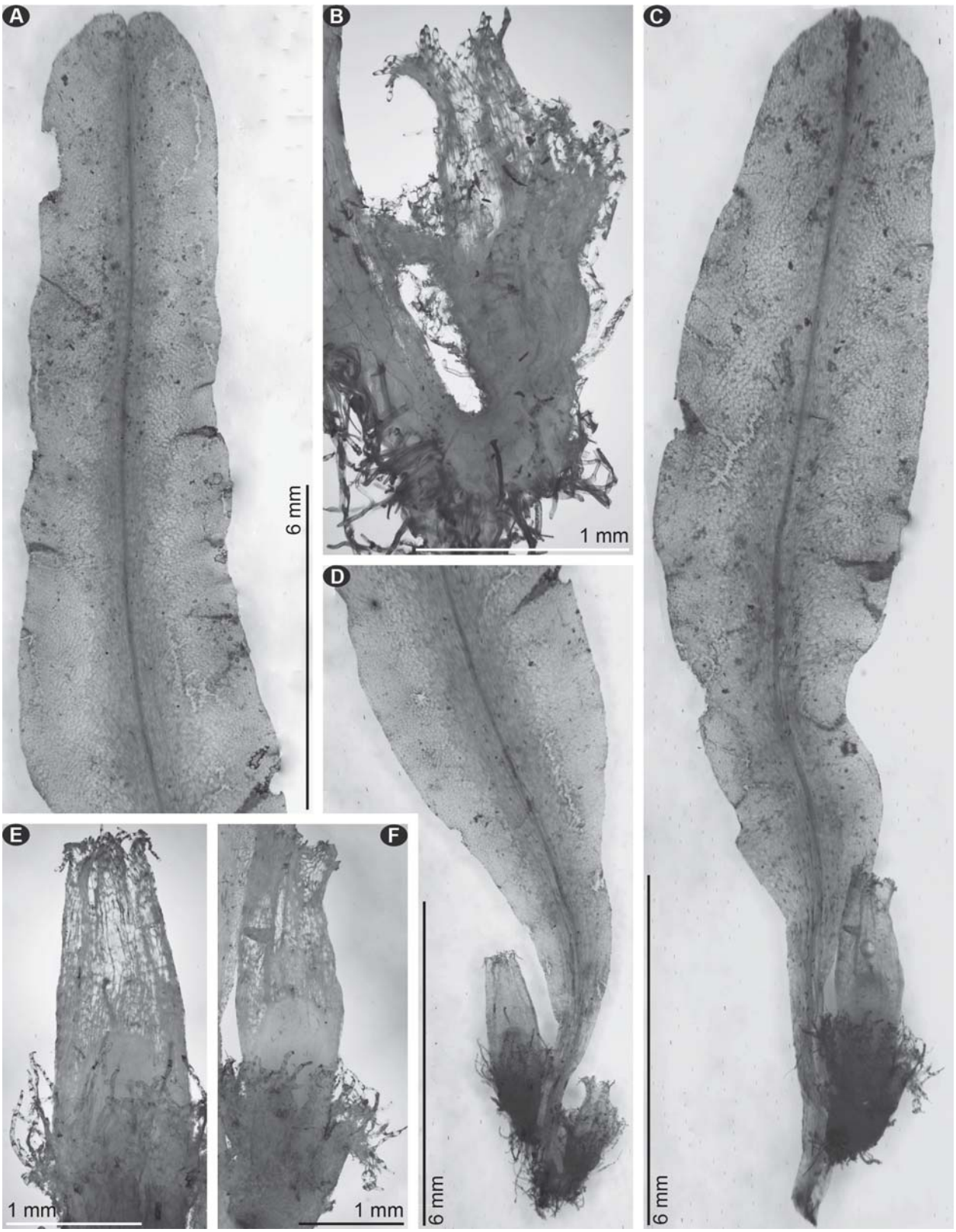

Fig. 2. *Podomitrium phyllanthus*: A, D: parts of the same female shoot (ventral view). C: female shoot (ventral view). B, E, F: female branchlets. All from *Schäfer-Verwimp & Verwimp 14090* (MHA).

lanthus (New Zealand 1) kept its position (64/0.75) within the clade of the genus *Symphyogyna* Nees & Mont. s.l. (that is *Symphyogyna* + *Symphyogynopsis* Grolle) as it was achieved by Schaumann *et al*. (2005). This specimen appears to be an unknown taxon of the genus *Symphyogyna* or the subfamily Symphyogynoideae.

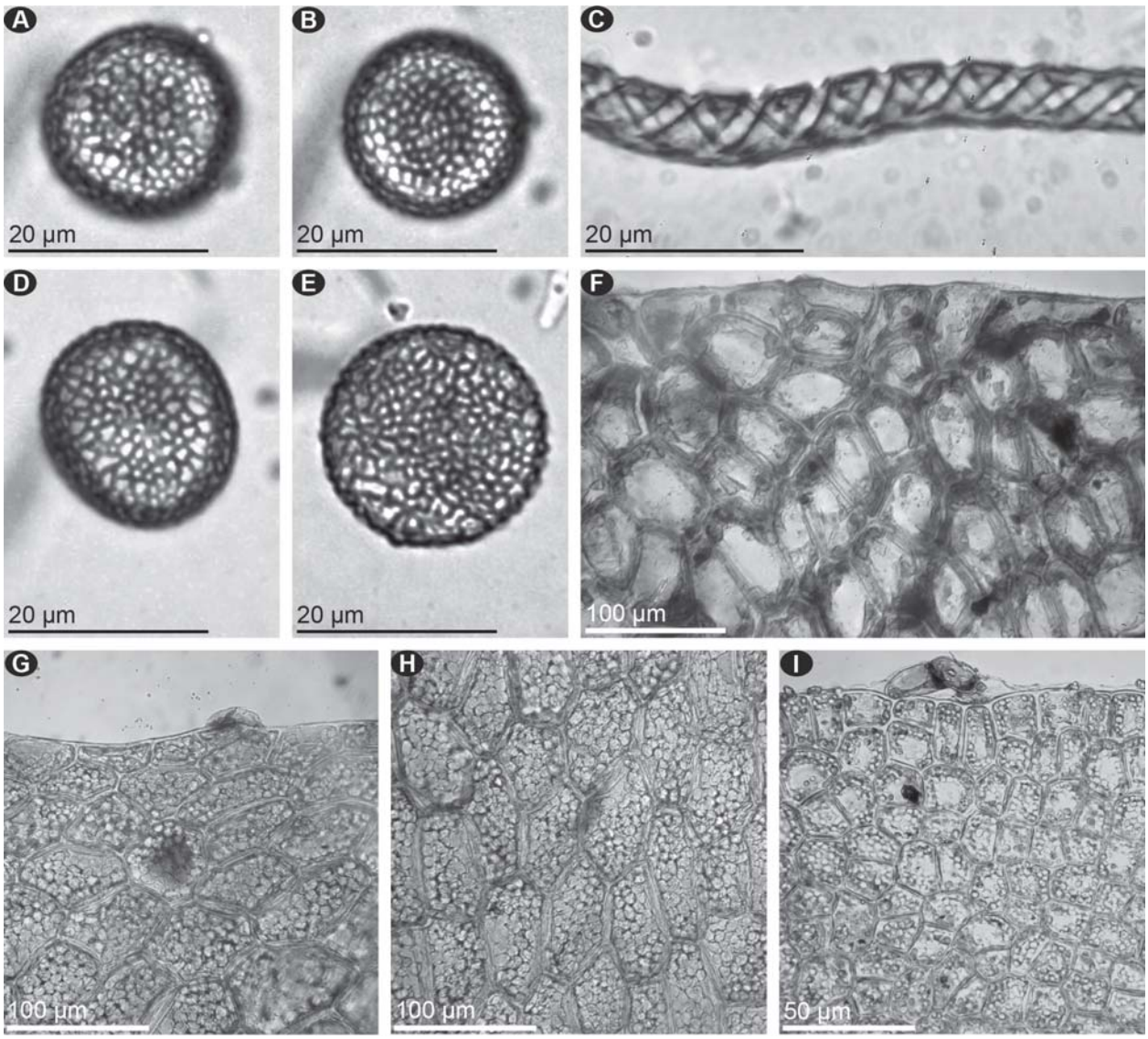

Fig. 3. *Podomitrium phyllanthus*: A, B, D, E: spores. C: elatere fragment. G: cells of thallus margin. H: cells of thallus wing near the midrib. *Podomitrium malaccense*: F, I: cells of thallus margin. A–E, G, H from *Schäfer-Verwimp & Verwimp 14090* (MHA). F from type, *Ridley s.n.* (G-00067976). I from *Bakalin Cam-81-107-11* (KPABG).

The *p*-distance estimation suggested differences of 1.2% in *trn*L-intron sequences between two sister related *Podomitrium phyllanthus* specimens New Zealand 2 and New Zealand 3, whereas two specimens with *P. malaccense* morphology are different from one another by 7.7% in *trn*L-intron and 17.5% in ITS2 (see "The values of p-distance, %, calculated for tested taxa from *trn*L-intron (page 1) and ITS2 (page 2) datasets" in the Supplementary file). At the same time, *P. phyllanthus* New Zealand 2 diverged from both specimens of *P. malaccense* from 17.0% to 22.1% in ITS2, and *p*-distances by *trn*L-intron among two samples of *P. phyllanthus* and two samples of *P. malaccense* varied from 4.4% to 7.9%. This molecular divergence exceeds that of the other genera of Pallaviciniaceae and suggests a complicated infrageneric and infraspecific structure of *Podomitrium*.

Discussion

Pallavicinia

It was shown in Mamontov *et al*. (2015) that ITS1-2 sequences of *Pallavicinia levieri* specimens are nested in a sister relationship with *P. lyellii* and *P. subciliata* and form a supported (BS=100% in both ML and MP) clade. Involving *trn*L-F sequences of three *P. levieri* specimens did not change the previous results in the sense that *P. levieri* remains in a supported sister relation with *P. lyellii* and *P. subciliata* (Fig. 1). Grolle & Piippo (1986) described the section *Subciliatae* Grolle to include species *P. subciliata*, *P. ambigua* (Mitt.) Steph. and *P. xiphoides*, based on the shortly ciliate thallus margin. However, Schuster (1991) separated a monospecific subgenus *Podomitriopsis* R.M.Schust. of the genus *Pallavicinia* to include *P. levieri*, since "In *Podomitriopsis*, as in the remotely allied genus *Podomitrium*, gametangia

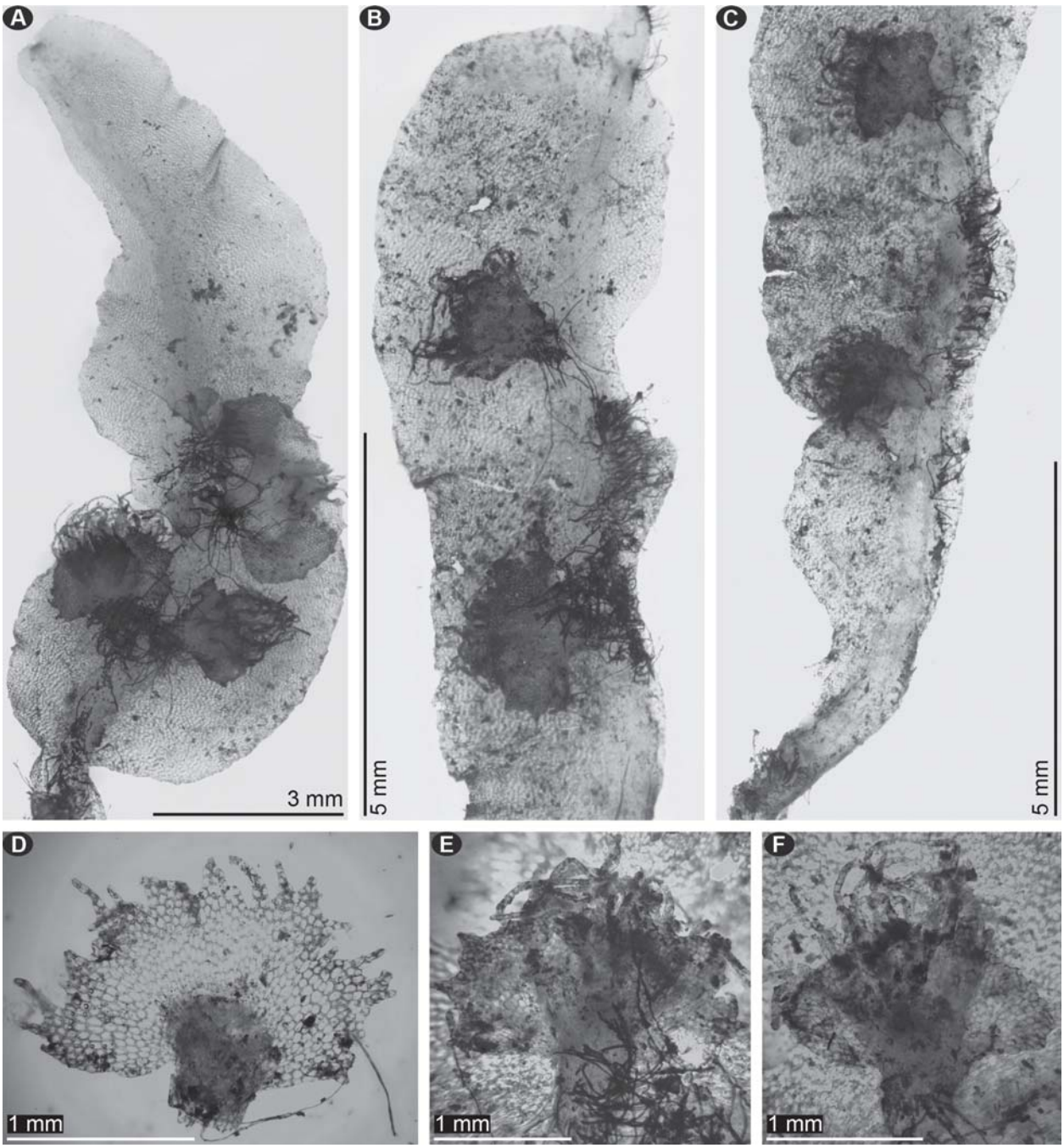

Fig. 4. *Podomitrium malaccense*: A–C: shoot fragments showing female branchlets (ventral view). D–F: female branchlets (ventral view). All from *Bakalin Cam-81-107-11* (KPABG).

tend to be restricted to the basal portions of stipitate-based ventral or lateroventral branches" (l.c.: 146). Concerning this feature, it should be noted that the type plants of *Pallavicinia levieri* studied by Grolle & Piippo (1986: 62) and Mamontov *et al*. (2015: 110, Fig. 7) bear gametangia on the dorsal surface of the main thallus, and the gametangia are not restricted to the basal portions of branches. However, Schuster (1991: 146) also noted that the antheridia in *P. levieri* "occur axillary in scales found irregularly scattered over the entire costal surface", which is a characteristic feature of the type of this species (Mamontov *et al*., 2015: 110, Fig. 7). The phylogenetic trees obtained in Mamontov *et al*. (2015) and Konstantinova *et al.* (2021) show an unsupported relationship between *P. lyellii* and *P. subciliata*, whereas the presented here tree (Fig. 1) shows an unsupported clade composed by *P. lyellii* and *P. levieri*. Nevertheless, these three species form a supported group that corresponds to the genus *Pallavicinia* sensu Grolle & Piippo (1986), excluding *P. xiphoides* (see below). The species within this group share the reticulate spore surface but differ from one another by the shape of the thallus margin or by the type of distri-

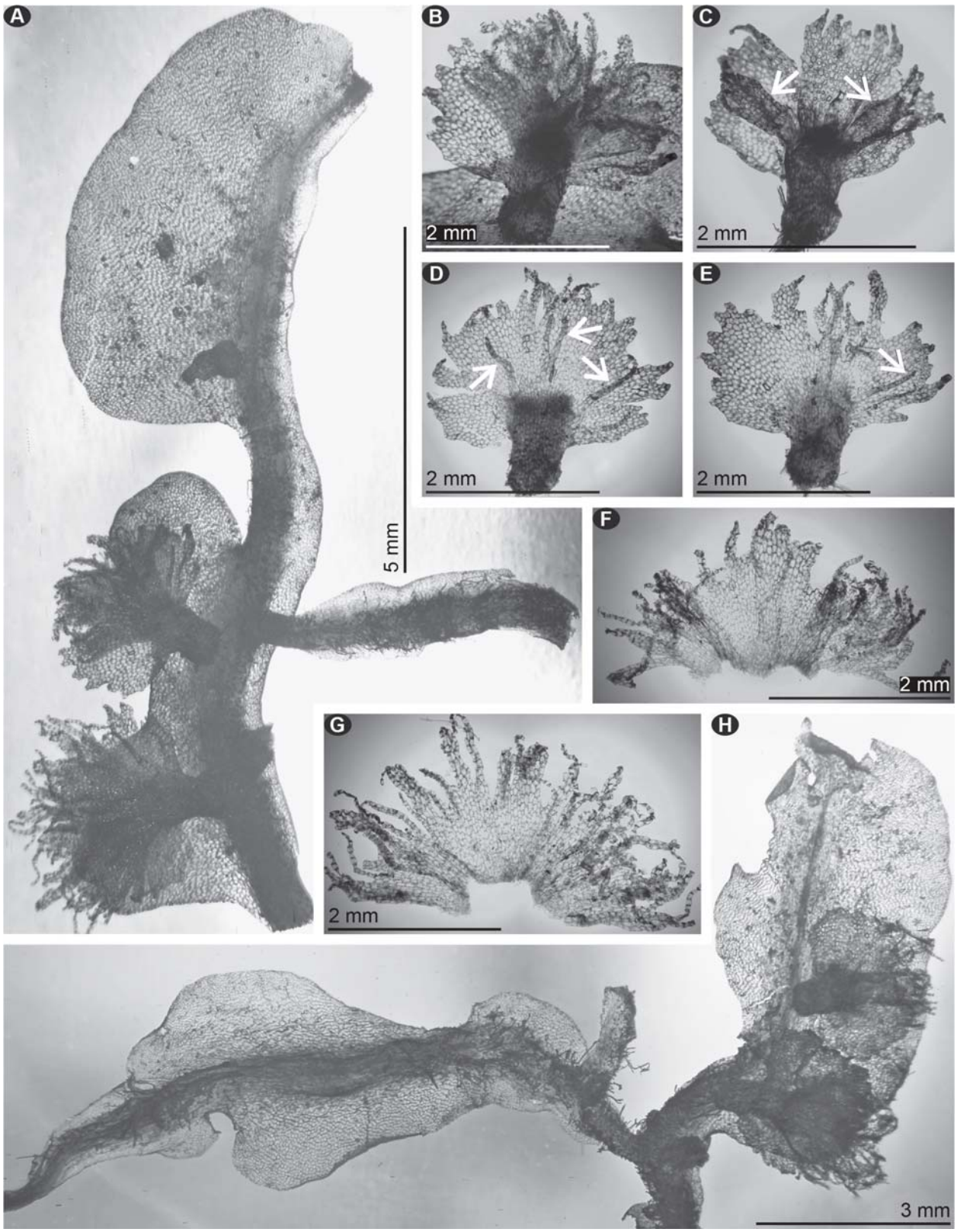

Fig. 5. *Podomitrium malaccense*: A, H: shoot fragments showing female branchlets (ventral view). B: female branchlet (ventral view). C–E: female branchlets with detached outer involucre (ventral view). F, G: outer female involucres. All from type, *Ridley s.n.* (G-00067976).

bution of the androecia over the dorsal surface of the thallus. The phylogenetic relationships within this genus remains unresolved since the position of these three species (*P. levieri*, *P. lyellii* and *P. subciliata*) to one another is unsupported within the presented phylogeny. Due to the unresolved phylogeny of *Pallavicinia,* as well as the presence of species with ambiguous affinity (*P. ambigua* (Mitt.) Steph., *P. pseudolyellii* R.M. Schust. & J.J. Engel, *P. rubristipa* Schiffn.) and significant molecular divergence within *P. levieri* and *P. lyellii* (see Mamontov *et al.*, 2015: 100, 101, Fig. 1, 2), it seems appropriate to maintain the subdivisions of the genus. We do accept *Podomitriopsis* as a subgenus, following Schuster (1991), and accordingly raise the section *Subciliatae* to the same subgeneric rank. Therefore, the genus *Pallavicinia* includes the following subdivisions: *P.* subg. *Pallavicinia* (type *P. lyellii*), *P.* subg. *Podomitriopsis* R.M. Schust. (type *P. levieri*), and *P.* subg. *Subciliatae* (Grolle) Mamontov, Vilnet & Schäfer-Verwimp, *stat. nov*. (type *P. subciliata*). The necessary combination for the subgenus *Subciliatae* is provided in the Taxonomy section.

Schuster (1991) also separated section *Dentigerae* R.M.Schust. of the subgenus *Pallavicinia* to include *P. xiphoides* based on the (1) presence of conspicuous marginal teeth, (2) free furcated branching, and (3) granular-papillate spores. Concerning the first characteristic it should be noted that the thalli of *P. subciliata* also bear conspicuous (sometimes rather long) marginal teeth, although these teeth are not numerous, only in (3–)5–9 (rarely more) opposite pairs (Mamontov *et al.*, 2015). Whereas the thalli of *P. xiphoides* have regular and numerous marginal teeth, so that the thalli are conspicuously serrate-dentate at margins (Hässel de Menéndez, 1961: 269, Fig. 3; Schaumann *et al*., 2005: 29, Fig. 1:4). Moreover, the granular-papillate spores distinguish *P. xiphoides* from all other species of *Pallavicinia*, excluding *P. innovans* Steph. The latter species, however, was proposed by Frey *et al*. (2010) to be a synonym of *P. xiphoides* on the base of the phylogenetic and morphological affinity between the sequenced specimens (Schaumann *et al*., 2005). As it was stressed in the Results section, *P. xiphoides* specimens remain in remote affinity to the clade composed by *Pallavicinia* and *Podomitrium* species (Fig. 1). In Forrest *et al.* (2005), *P. xiphoides* is nested in a supported clade together with *Podomitrium phyllanthus*, whereas in Schaumann *et al*. (2005) *Pallavicinia xiphoides* is nested in an unsupported clade together with species of the genus *Jensenia*. Due to the molecular and morphological differences between *Pallavicinia xiphoides* and other *Pallavicinia* species, the section *Dentigerae* (with the type species *P. xiphoides*), in our opinion, deserves the rank of a separate genus. Since the name *Dentigerae* coincides with a Latin technical term in use in morphology and was published after 1 January 1912, it cannot be used as the name of a genus (ICN Art. 20.2). Therefore, a new name *Prionothallus* is proposed here to use as a generic name of the former section *Dentigerae.* The necessary combination for this name is provided in the Taxonomy section.

Podomitrium

This genus was described for *Jungermannia phyllanthus* Hook., originally from New Zealand, to separate it from the genus *Steetzia* Lehm. (now a synonym of the genus *Pallavicinia*) "in the ventral origin of its perianth and its pedicellate male spikes" (Mitten, in Hooker 1855). Schuster (1984) separated the subfamily Podomitrioideae for this genus based on its characteristic feature, namely the development of highly reduced latero-ventral, intercalary, gametangial branches from lower, stipe-like sectors of sterile fronds. As was stressed before, the sequences of one specimen of *Podomitrium phyllanthus* from New Zealand were found by Forrest *et al.* (2005) in a close supported affinity to the clade of *Pallavicinia xiphoides*, while another New Zealand specimen of *Podomitrium phyllanthus* was found by Schaumann *et al.* (2005) in a sister relation to species of the genera *Symphyogyna* and *Symphyogynopsis*. In the specimen *Podomitrium phyllanthus* New Zealand 2 sequenced here (Fig. 2), the gynoecia are developed ventrally, on female branchlets in lower sectors of sterile fronds, the wings of the branchlets are reduced to dentate scales and the pseudoperianth with laciniate-dentate mouth is present. The capsule valves are apically coherent, the epidermal capsule-wall cells are without nodular thickening, and the spores are finely reticulate (Fig. 3A, B, D, E), as in species of the genus *Pallavicinia*. In our opinion, the mentioned morphological characteristics of the studied shoots of *P. phyllanthus* New Zealand 2 specimen fit well to the description and illustrations of the type of *Jungermannia phyllanthus* Hook. (Hooker, 1818: Pl. 95, Tab. XCV [https://www.biodiversitylibrary.org/page/11156667#page/193/mode/1up]). We therefore consider this specimen to belong to *Podomitrium phyllanthus.* We did not study the specimen *P. phyllanthus* New Zealand 3, which was sequenced by Forrest *et al*. (2005), however, the close phylogenetic affinity between the sequences of *P. phyllanthus* New Zealand 2 and New Zealand 3 allows us to regard both specimens as belonging to the same species. The close phylogenetic affinity between the specimen *P. phyllanthus* New Zealand 1, which was sequenced by Schaumann *et al*. (2005), and the genera *Symphyogyna* and *Symphyogynopsis* will remain a puzzle until a morphological investigation of this specimen is performed. When the shoots of *P. phyllanthus* New Zealand 1 bear gametangia on ventral-intercalary reduced branchlets, this specimen could be a representative of an unknown species and possibly a new genus.

All sequenced species (including *Xenothallus vulcanicola* R.M.Schust.), which are known to bear massive shoot calyptra instead of reduced pseudoperianth, have been revealed to have a close phylogenetic affinity to

Symphyogyna (Forrest & Crandall-Stotler, 2004; Schaumann *et al*., 2005), including *S. hochstetteri* Nees & Mont., the type species of this genus. Since the lineage of *Symphyogyna* and its allied genera *Symphyogynopsis* and *Xenothallus* is invariably supported in all the published phylogenies, we do recognize the subfamily Symphyogynoideae to include the mentioned genera. On the other hand, according to molecular data all other genera of Pallaviciniaceae, namely *Jensenia*, *Pallavicinia*, *Podomitrium* and *Prionothallus* can be considered as representatives of the type subfamily Pallavicinioideae (Mig.) Grolle. This subfamily therefore unites the species which bear pseudoperianth. The subfamily Podomitrioideae, which was separated by Schuster (1991), in this case should be treated as a synonym of Pallavicinioideae. Another solution is to recognize each of the four abovementioned genera as belonging to separate subfamilies. However, it seems not to be warranted by the present molecular and morphological data.

As was stressed in the Results section, two sequenced specimens of *Podomitrium malaccense* reveal the sister relation with the New Zealand 2 and New Zealand 3 specimens of *P. phyllanthus* (Fig. 1), that show a monophyly of the genus *Podomitrium* in the sense of Grolle & Piippo (1986). However, comparatively high divergence between *P. phyllanthus* and *P. malaccense* (17.0–22.1% in ITS2, 4.4–7.9% in *trn*L-intron) can indicate the necessity of further taxonomic separation of these two lineages, at least at the subgeneric level. Moreover, the specimens determined as *P. malaccense* have a comparatively high molecular divergence from one another – 7.7% in *trn*L-intron, and 17.5% in ITS2. These great molecular distinctions may possibly be caused from the island isolation of the *P. malaccense* populations during a long time. However, these differences may also indicate the presence of undescribed taxa within the *P. malaccense*-complex, similar to the case of *Moerkia hibernica* (Hook.) Gottsche and *M. flotoviana* (Nees) Schiffn. (Konstantinova *et al*., 2021). Morphologically, the shoots of the sequenced specimen *Podomitrium malaccense* from Cambodia (Fig. 4) are somewhat different from the type plants of this species from Singapore (Fig. 5) by the shape of the wings of the female branchlets. In the Cambodia specimen the studied female branchlets have no scale-like outgrowths on the ventral surface of the wings (Fig. 4D–F), whereas in the type plants of *P. malaccense* the wings of the female branchlets bear scale-like outgrowths, which are narrow and entire (Fig. 5D, E, arrows), or rather broad, plane to involute, laciniate-dentate (Fig. 5C, arrows) in their upper half. However, the correlation between the morphological differences and molecular divergence within *P. malaccense*-complex remains in need of further investigation based on sampling of specimens from other areas of the distribution of *P. malaccense*.

Taxonomy

Pallavicinioideae (Mig.) Grolle = Podomitrioideae R.M.Schust., Phytologia 56(2): 66. 1984, **syn. nov.**

Pallavicinia subg. **Subciliatae** (Grolle) Mamontov, Vilnet & Schäfer-Verwimp, **stat. nov.** – Basionim: *Pallavicinia* sect. *Subciliatae* Grolle, Acta Bot. Fenn. 133: 62, 1986. Type: *Steetzia subciliata* Austin ȶ *Pallavicinia subciliata* (Austin) Steph.

Prionothallus Mamontov, Vilnet & Schäfer-Verwimp, **nom. et stat. nov. pro** *Pallavicinia* subg. *Pallavicinia* sect. *Dentigerae* R.M.Schust., J. Hattori Bot. Lab. 70: 146, 1991 (ICN Art 20.2). Type: *Jungermannia xiphoides* Hook. f. & Taylor ȶ *Prionothallus xiphoides* (Hook. f. & Taylor) Mamontov, Vilnet & Schäfer-Verwimp, *comb. nov.* Etymology: The name refers to the serrate-dentate thallus margin, a characteristic feature of the genus.

Prionothallus xiphoides (Hook. f. & Taylor) Mamontov, Vilnet & Schäfer-Verwimp, **comb. nov.** – Basionim: *Jungermannia xiphoides* Hook. f. & Taylor, London Journal of Botany 3: 569. 1844. Type: New Zealand.

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Appendix 1. The list of specimens included in phylogenetic estimation with voucher details and GenBank accession numbers, boldfaced accessions were obtained in this study.

Taxon	Specimen voucher	GenBank accession number ITS2	*trn*L-F
Hattorianthus erimonus (Steph.) R.M.Schust. & Inoue	Russia, *Mamontov 107/1-10* (KPABG)	KJ577205	KJ577218
Hymenophyton pedicellatum Steph.	Chile, *Frey & Schaumann 01-145a* (VALD)	AY640221	AY368649
Jensenia connivens (Colenso) Grolle	New Zealand, *Frey & Pfeiffer 98-Mo11* (CHR)	AY763522	AY547540
J. decipiens (Mitt.) Grolle	Indonesia, *Hiepko & Schultze-Motel 2051* (B)	AY763523	AY547518
J. difformis (Nees) Grolle	Ecuador, *Kürschner et al. 02-619* (BSB)	AY547530	AY547514
J. erythropus (Gottsche) Grolle	Peru, *Frahm et al. 1043* (B)	AY547529	AY547513
J. pisicolor (Hook. f. & Taylor) Grolle	Chile, *Frey & Schaumann Mo 01-257* (BSB)	AY547527	AY547512
J. spinosa (Lindenb. & Gottsche) Grolle	Tanzania, Pocs et al., Ser. VIII, No. 197 (BONN)	AY547531	AY547515
Moerckia flotoviana (Nees) Schiffn.	Russia, *Borovichev BE-46-7-05* (KPABG)	KJ577211	KJ577215
M. flotoviana (Nees) Schiffn.	Slowenia, *Frahm 2.8.2003* (BONN)	AY763520	AY763543
M. hibernica (Hook.) Gottsche	Ireland, *Lockhart 2019-01a* (KPABG)	MN819065	MN829810
Pallavicinia levieri (Hook.) Gray	Cambodia, 1, *Bakalin Cam-83-37-11* (VBGI, KPABG-118157)	KP137574	**OK771593**
P. levieri (Hook.) Gray	Cambodia, 2, *Bakalin Cam-83-42-11* (VBGI, KPABG-118155)	KP137576	**OK771595**
P. levieri (Hook.) Gray	Cambodia, 3, *Bakalin Cam-83-44-11* (VBGI, KPABG-118156)	KP137575	**OK771594**
P. lyellii (Hook.) Gray	Ecuador, *Kürschner et al. 02-508* (H. Kürschner)	AY763530	AY763549
P. lyellii (Hook.) Gray	Canada, Bryophyte Exsicc. Terrae-Novae et Labrad., 176 (LE)	KJ577194	KJ577203
P. lyellii (Hook.) Gray	Rwanda, *Pocs 6434* (W. Frey)	AY547536	AY547522
P. rubristipa Schiffn.	Australia, *Fuhrer & Scott 4125* (B)	AY547539	AY547525
P. subciliata (Austin) Steph.	Japan, *Inoue 917* (B)	AY547535	AY547521
P. subciliata	Taiwan, *Yang, Kao et al. 1004-8* (B), as *P. longispina* Steph.	AY547533	AY547519
Podomitrium malaccense (Steph.) Campb.	Cambodia, *Bakalin Cam-81-107-11* (VBGI, KPABG-118160)	**OL304240**	**OK771596**
P. malaccense (Steph.) Campb.	Malaysia: Borneo, *Konstantinova 118161* (KPABG)	**OL304241**	**OK771597**
P. phyllanthus (Hook.) Mitt.	New Zealand 1, *Frahm 2-880* (W. Frey)	AY763531	AY763550
P. phyllanthus (Hook.) Mitt.	New Zealand 2, *Schäfer-Verwimp & Verwimp 14090* (MHA)	**OL304242**	**OK771598**
P. phyllanthus (Hook.) Mitt.	New Zealand 3, *Stotler & Crandall-Stotler 4517* (ABSH)	AY507551	no data

Taxon	Specimen voucher	GenBank accession number	
		ITS2	*trn*L-F
Prionothallus xiphoides (Hook. f. & Taylor) Mamontov, Vilnet & Schäfer-Verwimp	New Zealand 1, *Fife 10324* (CHR)	AY547538	AY547524
P. xiphoides '*innovans*'	New Zealand 2, *Frahm s.n. (*W. Frey)	AY763527	AY763545
Pseudomoerckia blyttii (Mørch) Vilnet, Konstant., D.G. Long, N. Lockh. & Mamontov	Russia, *Mamontov 53/8* (KPABG)	KJ577208	KJ577221
Symphyogyna apiculispina Steph.	Peru, *Frahm et al. 84* (BONN)	AY763535	AY763554
S. aspera Steph. ex F.A.McCormick	Ecuador, *Kürschner et al. 02-513* (H. Kürschner)	AY763537	AY763556
S. bogotensis Steph.	Peru, *Weigend et al. 256* (B)	AY763533	AY763552
S. brasiliensis Nees	Brazil, *Frahm 1792* (BONN)	AY289180	AY289156
S. brongniartii Mont.	Ecuador, *Kürschner et al. 02-531* (H. Kürschner)	AY763536	AY763555
S. circinata Nees & Mont.	Chile, *Frey & Schaumann 01-320* (W. Frey)	AY763538	AY763538
S. hochstetteri Nees & Mont.	Chile, *Frey & Frey 95-9* (W. Frey)	AY763534	AY763553
S. hymenophyllum (Hook.) Nees & Mont.	New Zealand, *Frey & Frey 94-182* (W. Frey)	AY289176	AY289152
S. podophylla (Thunb.) Mont. & Nees	Chile, *Frahm 1-20* (BONN)	AY289165	AY289141
S. rubritincta A.Evans	Chile, *Frey & Schaumann 01-236* (W. Frey)	AY289179	AY289155
S. tenuinervis (Hook. f. & Taylor) Grolle	New Zealand, *Frey & Pfeiffer 98-Mo42a* (CHR)	AY289178	AY289154
S. gottscheana (Mont. & Nees) Grolle	Indonesia, *Hiepko & Schultze-Motel 2033* (B)	AY289182	AY289158