

ON THE TAXONOMY OF ANOMODONTACEAE AND *HETEROCLADIUM* (BRYOPHYTA)  
К СИСТЕМАТИКЕ ANOMODONTACEAE И *HETEROCLADIUM* (BRYOPHYTA)

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Abstract

A molecular phylogenetic analysis based on nuclear ITS, plastid trnS-F, rpl16, atpB–rbcL and mitochondrial nad5 revealed polyphyly in the genus *Anomodon*, and therefore its segregation into four genera is proposed. The largest clade includes *A. viticulosus*, the generic type of *Anomodon*, and all species with a broadly rounded leaf apex, including those with both pluripapillose (*A. minor*, *A. thraustus*, *A. dentatus*) and pseudounipapillose (*A. abbreviatus*, *A. solovjovii*) laminal cells. The species of *Haplohymenium* form a sister clade to *Anomodon*; however this clade is always maximally supported in Bayesian analyses, and thus *Haplohymenium* merits taxonomic recognition as a genus of its own. Two closely related species, *Anomodon attenuatus* and *A. giraldii*, were found deeply nested in the Neckeraceae, and thus they are segregated in the genus *Pseudanomodon* (Limpr.) Ignatov & Fedosov. *Anomodon rugelii* was found to be distant from the core *Anomodon* clade and is segregated into a new genus *Anomodontopsis* Ignatov & Fedosov within the Anomodontaceae. *Anomodon longifolius* has an erratic position in various analyses, appearing basal in the Anomodontaceae clade or sister to the *A. rugelii* clade in the organellar trees, or in a clade with *Heterocladium dimorphum*, closer to the Neckeraceae than to the Anomodontaceae, in the tree inferred from nuclear ITS. It is therefore referred to the new genus *Anomodontella* Ignatov & Fedosov in the Anomodontaceae. Likewise, *Heterocladium* species form two clades, centered around *H. dimorphum* and *H. heteropterum*. The latter group is referred to Lembophyllaceae, while *H. dimorphum* and related species form a fairly isolated group and are segregated in their own genus *Heterocradiella* Ignatov & Fedosov in the monogeneric family Heterocradiellaceae Ignatov & Fedosov. The genus *Herpetineuron* is excluded from the Anomodontaceae.

Резюме

Молекулярно-филогенетический анализ, основанный на последовательностях ITS ядерной ДНК, trnS-F, rpl16 и atpB–rbcL хлоропластной ДНК и nad5 митохондриальной ДНК, выявил полифилетичность рода *Anomodon*; предложено разделить его на 4 рода. Самая крупная клада молекулярно-филогенетического дерева включает *A. viticulosus*, который является типовым видом рода *Anomodon*, и все виды с широко закруленной верхушкой листа, как с мультитипиллозными клетками пластинки (*A. minor*, *A. thraustus*, *A. dentatus*), так и с “псевдоунипапиллозными” (*A. abbreviatus* и *A. solovjovii*). Виды рода *Haplohymenium* образуют кладу, сестринскую кладе *Anomodon* s.str.; эта клада имеет максимальную поддержку по результатам Байесова анализа, из чего следует, что *Haplohymenium* заслуживает таксономический статус самостоятельного рода. Два близкородственных вида, *Anomodon attenuatus* и *A. giraldii*, во всех реконструкциях оказываются в одной кладе с видами, относящимися к семейству Neckeraceae (вместе с *Homalia trichomanoides*); эти два вида выделены в отдельный род *Pseudanomodon* (Limpr.) Ignatov & Fedosov. Во всех вариантах анализа *Anomodon rugelii* занимает сестринское положение к высоко поддерживаемой кладе *Anomodon* s.str. + *Haplohymenium*, так что он выделяется в новый род *Anomodontopsis* Ignatov & Fedosov в семействе Anomodontaceae. Позиция *Anomodon longifolius* непостоянна: в деревьях, построенных по органеллярным маркерам, он оказывается в базальном положении к кладе *Anomodon* или формирует кладу с *A. rugelii*, тогда как в деревьях, построенных по ITS, он находится в кладе с *Heterocladium dimorphum*; на этом основании описан новый род *Anomodontella* Ignatov & Fedosov в семействе Anomodontaceae. Виды рода *Heterocladium* образует две клады, к одной из которых относится *H. dimorphum* и ко второй – *H. heteropterum*. Виды последней клады остаются в роде *Heterocladium*, но этот род предложено относить к семейству Lembophyllaceae, тогда как *H. dimorphum* и близкий к нему *H. procurrens*, образующие хорошо изолированную группу, выделены в новый род *Heterocradiella* Ignatov & Fedosov и семейство Heterocradiellaceae Ignatov & Fedosov. Род *Herpetineuron* исключен из Anomodontaceae.

KEYWORDS: *Anomodon*, *Heterocladium*, mosses, Hypnales, taxonomy, molecular phylogeny, new genera, new family, papillae.

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## INTRODUCTION

The Hypnales form the terminal clade in the phylogenetic tree of mosses (Newton *et al.*, 2000; Tsubota *et al.*, 2004; Shaw *et al.*, 2003; Lui *et al.*, 2019). This order is the largest among bryophytes, and also the most difficult for classification, as most characters valuable for taxonomy are homoplastic (Huttunen *et al.*, 2012). Many of them have been widely used because they look conspicuous and are easily observed. The molecular phylogenetic approach to taxonomy has already revealed many cases where morphological characters have been overvalued, overturning assumptions about the importance of, for example, the “Isobryalean peristome” (Buck *et al.*, 2000; Tsubota *et al.*, 2002), *Neckera*-like undulate leaves (Olsson *et al.*, 2011), *Drepanocladus*-like falcate-secund leaves with a costa (Vanderpoorten *et al.*, 2002); *Hypnum*-like falcate-secund leaves without a costa (Gardiner *et al.*, 2005; Ignatov *et al.*, 2007; Arikava *et al.*, 2008; Câmara *et al.*, 2018; Schlesak *et al.*, 2018), and a dendroid growth-form (Ignatov *et al.*, 2014). In this paper we will try to address one more such character, the papillosity of the laminal cells.

Acrocarpous mosses exhibit a great variety of papillose and mammillose cells, which occur in about half of the families, while pleurocarps usually have smooth laminal cells, which probably correlates with the prosenchymatous cell shape. Elongate multipapillose laminal cells are characteristics of only one family, the Meteoriaceae. In other families, papillose cells occur in species with short laminal cells, which has caused them to be combined together in genera and families.

For this reason, Brotherrus (1925) placed in the Thuidiaceae genera currently classified in different families: *Myurella* (Plagiotheciaceae), *Fauriella* (Pylaisiadelphaceae), *Anomodon* (Anomodontaceae), *Heterocladium* (Heterocladiaceae nom. illeg.), *Leptopterigynandrum* (Taxiphyllaceae), and *Miyabea* (Miyabeaceae).

The original aim of the present study was to address the classification of the genera *Anomodon* and *Heterocladium* for the Moss Flora of Russia. A previous analysis (Gardiner *et al.*, 2005) based on limited sampling has already revealed their non-monophyly. *Anomodon rostratus* was transferred to *Claopodium* (Ignatov *et al.*, 2006), while the distant positions of *A. attenuatus*, *A. giraldii*, *A. longifolius* and *A. rugelii* have not been discussed, even though some of them were confirmed in other publications, e.g. Tsubota *et al.* (2004), Ignatov *et al.* (2007), Olsson *et al.* (2009a,b). Among others, Olsson *et al.* (2009a) found *A. giraldii* nested in the Neckeraeae and indicated that its phylogenetic position would be discussed in later papers, but this has not yet happened. An isolated position of *Heterocladium* was revealed by Gardiner *et al.* (2005), and Ignatov & Ignatova (2004) had already segregated it in the family Heterocladiaceae. This family name is however illegitimate, as the red algae genus *Heterocladia* Decaisne, 1841

had previously been separated in a family with this name. The need to fix this nomenclatural problem for mosses remains, so we undertook the present analysis in order to solve it as well. In doing so, we paid special attention to papillae, which seemingly were described without adequate detail to be considered as a character of familial importance, as is usually assumed.

## MATERIAL AND METHODS

*Molecular phylogenetic studies*

The material used in the present study was sampled from MW and MHA and supplemented by sequences available in GenBank. For the molecular-phylogenetic study we used five markers, nuclear ITS1,2 and 5.8 rRNA gene, plastid region trnS-F, plastid rpl16 gene intron, plastid atpB-rbcL intergenic spacer and mitochondrial nad5, which have been used successfully in numerous studies of pleurocarpous moss phylogeny (Vanderpoorten *et al.*, 2002; Stech & Frey, 2008; Stech & Quandt, 2014; Olsson *et al.*, 2009a,b, 2011, etc.). Our sampling was mostly focused on our target groups and was intended to check the replication of results obtained in specimens sampled from remote areas of their distribution. Likewise we expanded the representation of the types of the genera to which these species have been assigned. In addition, the genera *Haplohymenium* and *Herpetineuron*, which are often placed in the Anomodontaceae (cf. Ignatov *et al.*, 2006), were included to check their affinity with *Anomodon*. In total 49 specimens were studied *de novo*. Sequences for a suite of species well represented in Genbank were included using the Blast facility and previously published reconstructions to provide representation of the major clades of pleurocarpous mosses, both closely related groups and putative outgroups, thereby placing our data in the context of a backbone phylogeny of pleurocarpous mosses. Vouchers of the newly sequenced specimens and GenBank accession numbers of all used sequences are compiled in Supplementary Materials 1.

The laboratory protocol was essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005), Hedenäs (2017). Sequences were aligned using MAFFT v. 7.402 (Katoh & Standley, 2013) with standard settings and then edited manually. For the highly variable ITS indels were considered as missing data, while in the less informative but unequivocally aligned organellar markers indels were coded using simple indel coding technique (Simmons & Ochoterena, 2000) in SeqState 1.4.1 (Müller, 2005). Highly homoplastic inversion in the trnL-trnF spacer was excluded from the analysis. At first, ITS (97 terminals, 1118 positions), trnS-F (93 terminals, 1995 positions), rpl16 (81 terminals, 864 positions), atpB (59 terminals, 705 positions) and nad5 (77 terminals, 1141 positions) were analyzed separately to check their congruence. Since no supported conflict of topologies was observed among the trees inferred from organellar markers, the sixth dataset represented the concatenated, trnS-F, rpl16, atpB and

nad5 sequences (97 terminals, 4711 bp), and indels were considered as missing data. The sixth dataset was divided into two partitions, for cp and mt data. Bayesian Analyses were performed by running two parallel analyses in MrBayes 3.2.6 (Ronquist et al., 2012). For the single gene set analyses, each run consisted of six Markov chains, 10 000 000 generations with the default number of swaps, and sampling frequency one tree each 2500 generations. For the concatenated dataset the analysis consisted of eight Markov chains and 25 000 000 generations, with the default number of swaps and sampling frequency one tree each 5 000 generations. The chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007). Consensus trees were calculated after omitting the first 25% trees as burn-in. Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>) on XSEDE (Miller et al., 2010). All trees were rooted on *Hookeria lucens* (Hedw.) Sm. or on *Hookeria lucens* and *Distichophyllum crispulum* (Hook. f. & Wilson) Mitt.

### Morphological observations

Material for SEM was prepared in two ways. Peristomes were coated with gold and observed under SEM Cambridge Instruments CamScan S2 without additional preparation. Some observations of the leaf and stem structures were made in a similar way (this is indicated on the photos). In other cases, shoots were wetted in phosphate buffers, fixed in 2% glutaraldehyde for 24 hours, washed in water, post-fixed with 2% osmium tetroxide in distilled water for 2 hours, washed in water, dehydrated through an ascending alcohol-acetone series, dried at critical point, covered with gold, and observed under SEM Cambridge Instruments CamScan S2.

Material for Confocal Laser Scanning Microscopy (CLSM) was taken from herbarium material. Shoots without fixation were stained by 0,1mM DAPI and berberin and investigated under an Olympus FV-1000, with 405 and 473 nm lasers.

## RESULTS

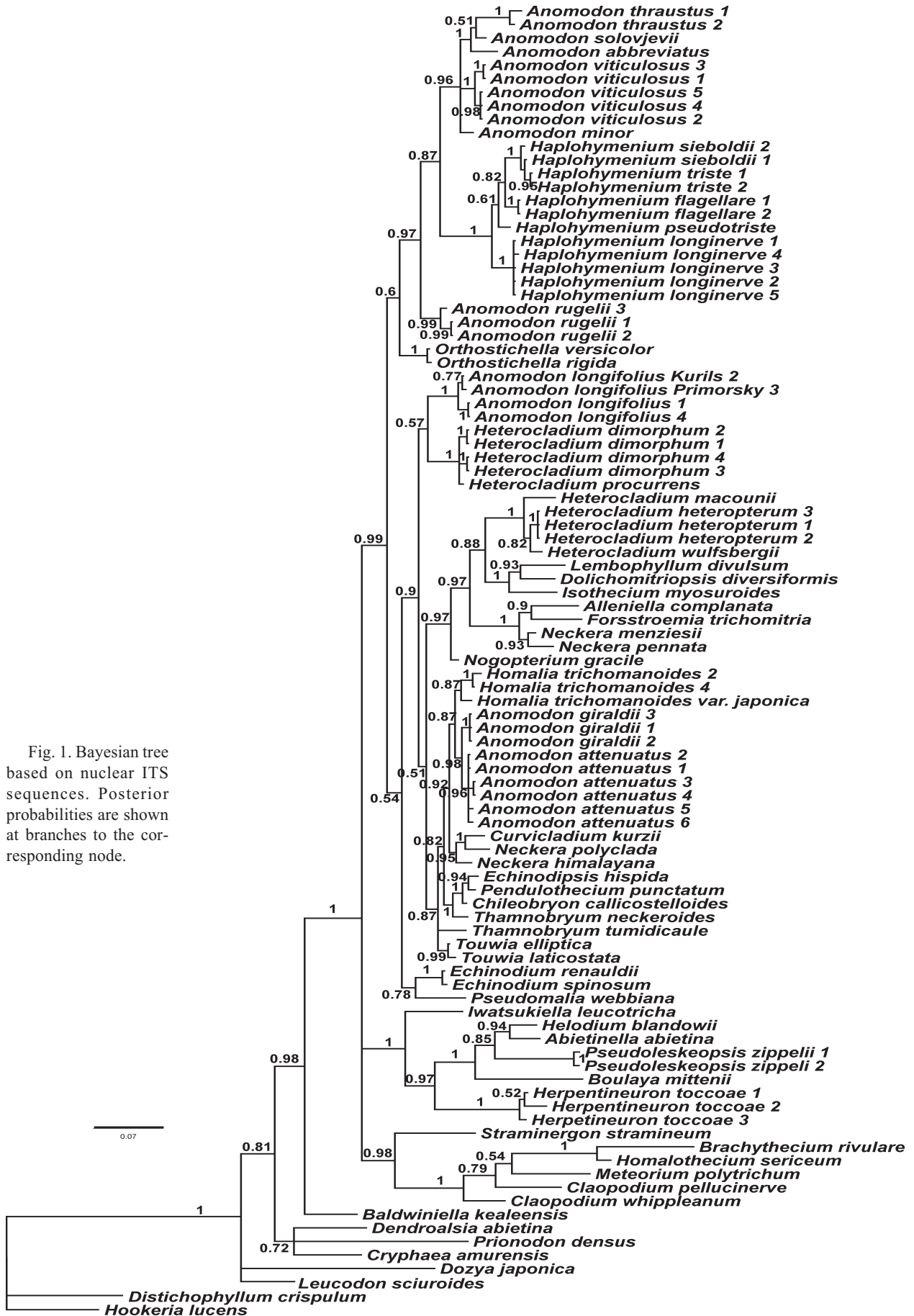
### Molecular phylogenetic analysis: single gene analyses

In general, the topologies inferred from analyses based on single gene datasets resemble each other, although they differ in resolution and in the statistical support of particular clades. In somewhat better resolved reconstructions inferred from ITS, trnSF and rpl16 *Baldwiniella kealeensis*, *Leucodon sciuroides*, *Dozya japonica*, *Prionodon densus*, *Cryphaea amurensis* and *Dendroalsia abietina* split in the basal portion of the trees forming grades or unsupported clades, while in reconstructions inferred from nad5 and AtpB sequences these species are found in polytomy with other major lineages of pleurocarpous mosses. The latter comprises a suite of more or less well defined and supported lineages, corresponding to Lembophyllaceae (*Isoetecium myosuroides*, *Lembophyllum divulsum*, *Dolichomitriopsis diversiforme*), Heterocladaceae s.str.

(*Heterocladium heteropterum*, *H. wulfsbergii* & *H. macounii*), Neckeraceae s.str. (*Neckera pennata*, *N. menziesii*, *Forsstroemia trichomitria* & *Alleniella complanata*), “Neckeraceae II” (*Chileobryon*, *Pendulothecium*, *Thamnobryum*, *Homalia*, *Anomodon* p.p., etc.), *Orthostichella* (*O. rigida* & *O. versicolor*), Anomodontaceae s.str. (*Anomodon viticulosus*, *A. thraustus*, *A. abbreviatus*, *A. solovjovii*, *A. minor*, *Haplohymenium* spp. & *Anomodon rugelii*), Thuidiaceae s.str. (*Abietinella*, *Helodium*, *Pseudoleskeopsis* & *Boulaya*), some poorly represented major lineages (Brachytheciaceae, Meteoriaceae, Calliergonaceae, etc.) and other groups, whose putative phylogenetic affinity varies depending on the marker (*Anomodon longifolius*, *Claopodium* spp., *Herpetineuron toccoae* and *Iwatsukiella*). Since sampling in this study was aimed at revealing the affinities of a few particular lineages, concentrated within the “Anomodontaceae s.l. & Lembophyllaceae & Orthostichellaceae & Neckeraceae s.l. clade”, inferred from better resolved trees based on ITS and trnS-F, this group will be discussed in more detail.

Most of the groups at familial level were found to be monophyletic, except for Anomodontaceae, Heterocladaceae and Neckeraceae. Species placed in the Anomodontaceae (the genera *Anomodon*, *Herpetineuron* and *Haplohymenium*) are found in three or four unrelated clades in the trees obtained. Five species of the genus *Anomodon* form a moderately to highly supported clade sister to the *Haplohymenium* clade. The clade with *Anomodon rugelii* in most reconstructions was found in a sister clade to the *Anomodon* s.str. & *Haplohymenium* clade, and their common clade is mostly well supported. In reconstructions inferred from organellar markers, the clade with *Anomodon longifolius* splits on the next deeper node and this node lacks statistical support, while in the ITS based reconstruction it forms an unsupported grouping with the *Heterocladium dimorphum* clade, which is sister to the “Neckeraceae s.l.” clade. The clades corresponding to *A. attenuatus* and *A. girdalii* are deeply nested within the Neckeraceae s.str. clade, close to each other and *Homalia trichomanoides*. In the reconstructions inferred from ITS and rpl16, the clades with *A. attenuatus* and *A. girdalii* form a well-supported clade sister to the *Homalia trichomanoides* clade. In the reconstruction based on trnS-F these three unispecific clades are found in polytomy, while in the atpB-based reconstruction the *Anomodon attenuatus* clade occupies a sister position to the *Homalia trichomanoides* clade, and their joined clade is sister to the *A. girdalii* clade. Finally, the clade of *Herpetineuron* occupies an isolated position in reconstructions inferred from trnS-F and atpB, but forms a well-supported clade with the Thuidiaceae clade in the ITS-based reconstruction, and shows ambiguous affinity with the core *Anomodon* clade in the nad5-based reconstruction.

In most reconstructions inferred from the single gene datasets the species placed in the genus *Heterocladium* form two compact highly supported clades,



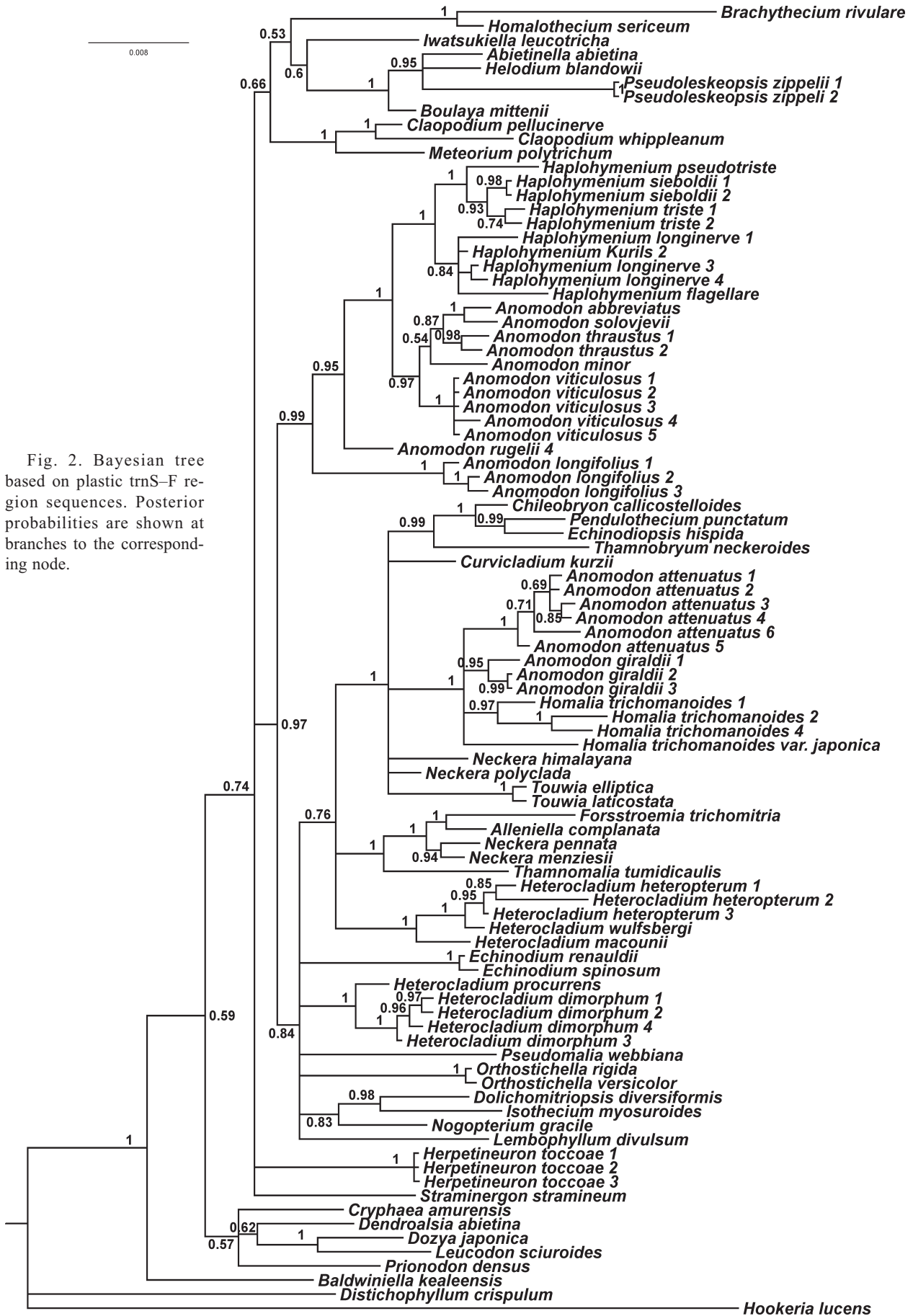


Fig. 2. Bayesian tree based on plastic trnS-F region sequences. Posterior probabilities are shown at branches to the corresponding node.

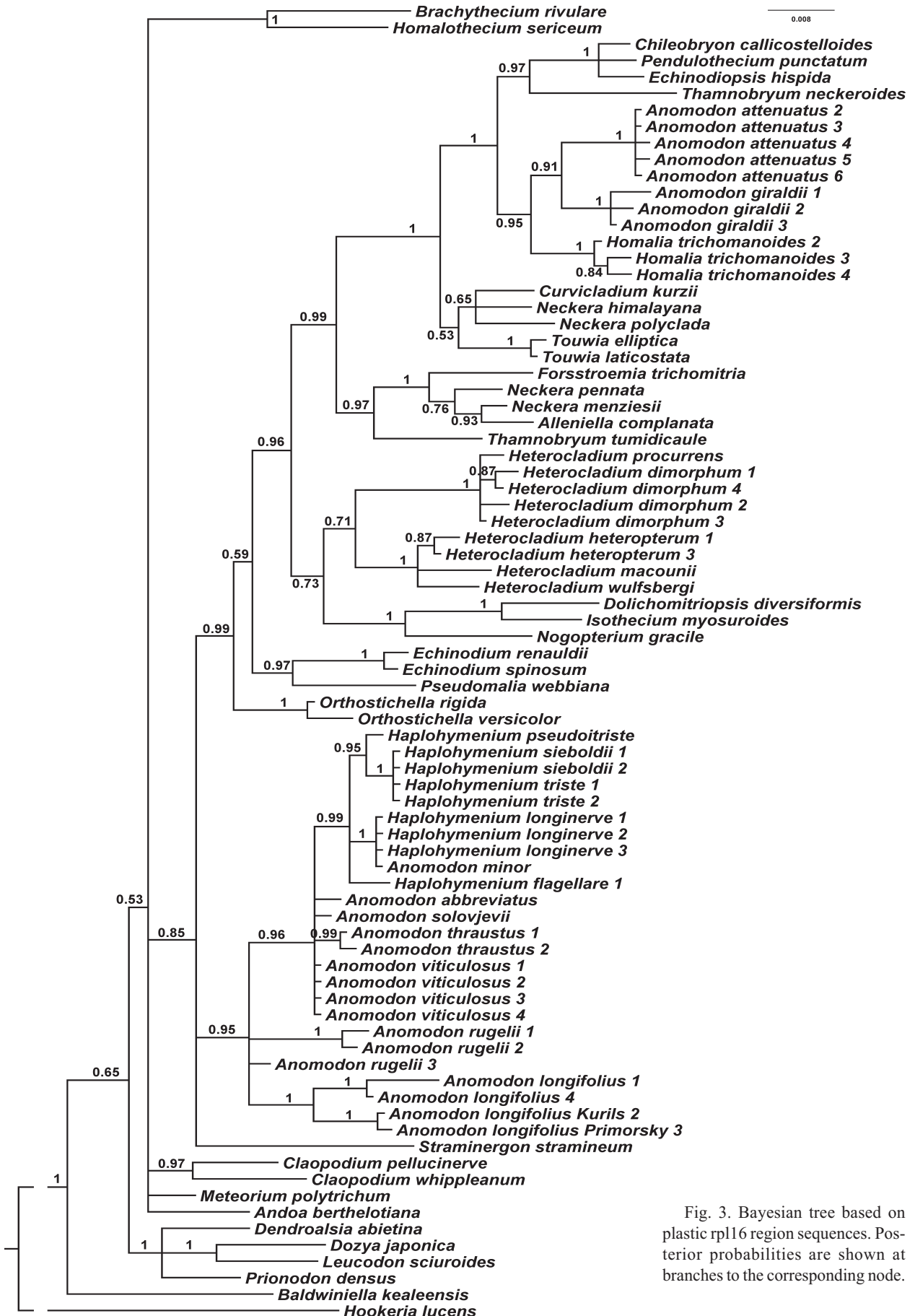


Fig. 3. Bayesian tree based on plastic rpl16 region sequences. Posterior probabilities are shown at branches to the corresponding node.

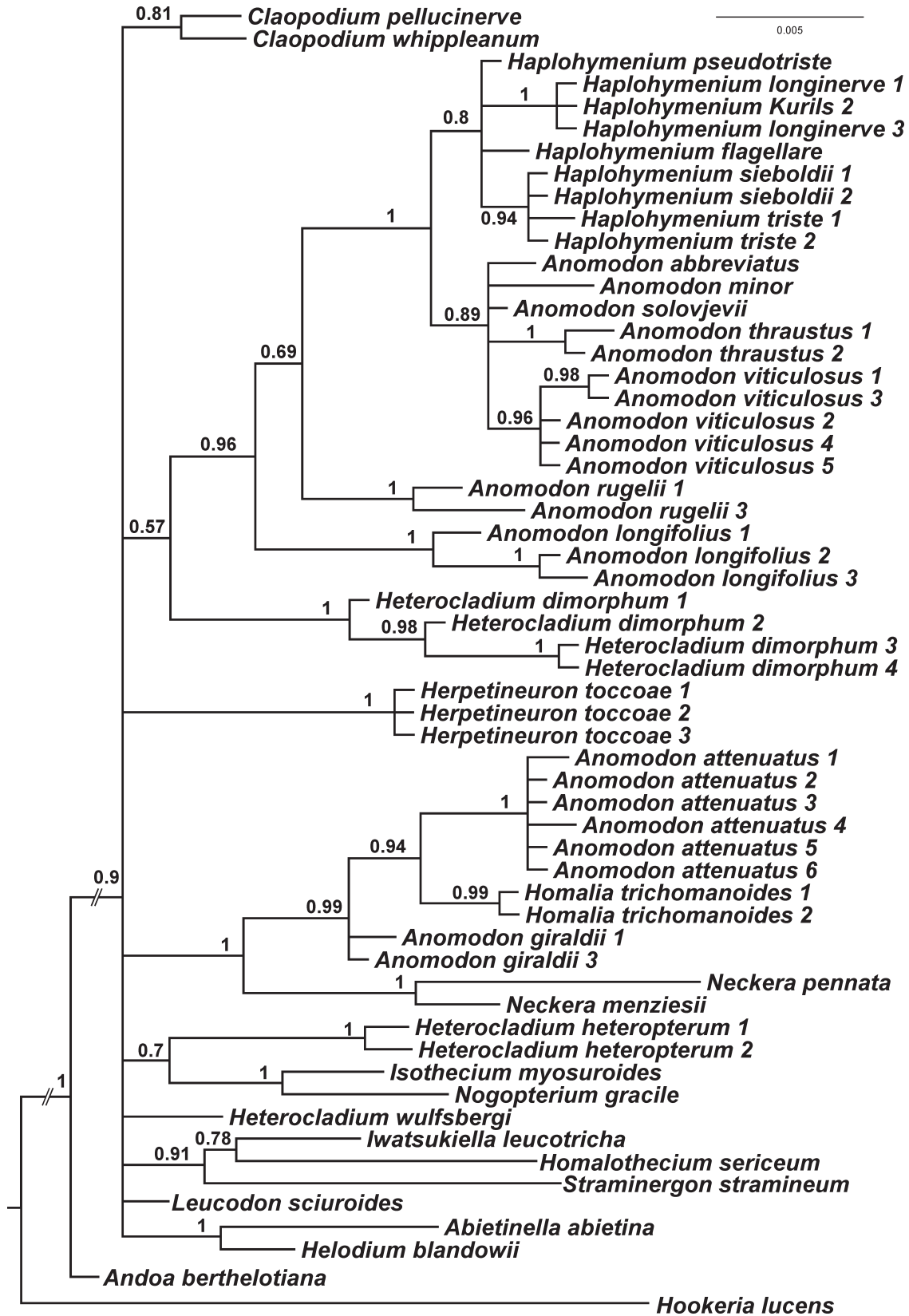


Fig. 4. Bayesian tree based on plastic atpB-rbcL region sequences. Posterior probabilities are shown at branches to the corresponding node.

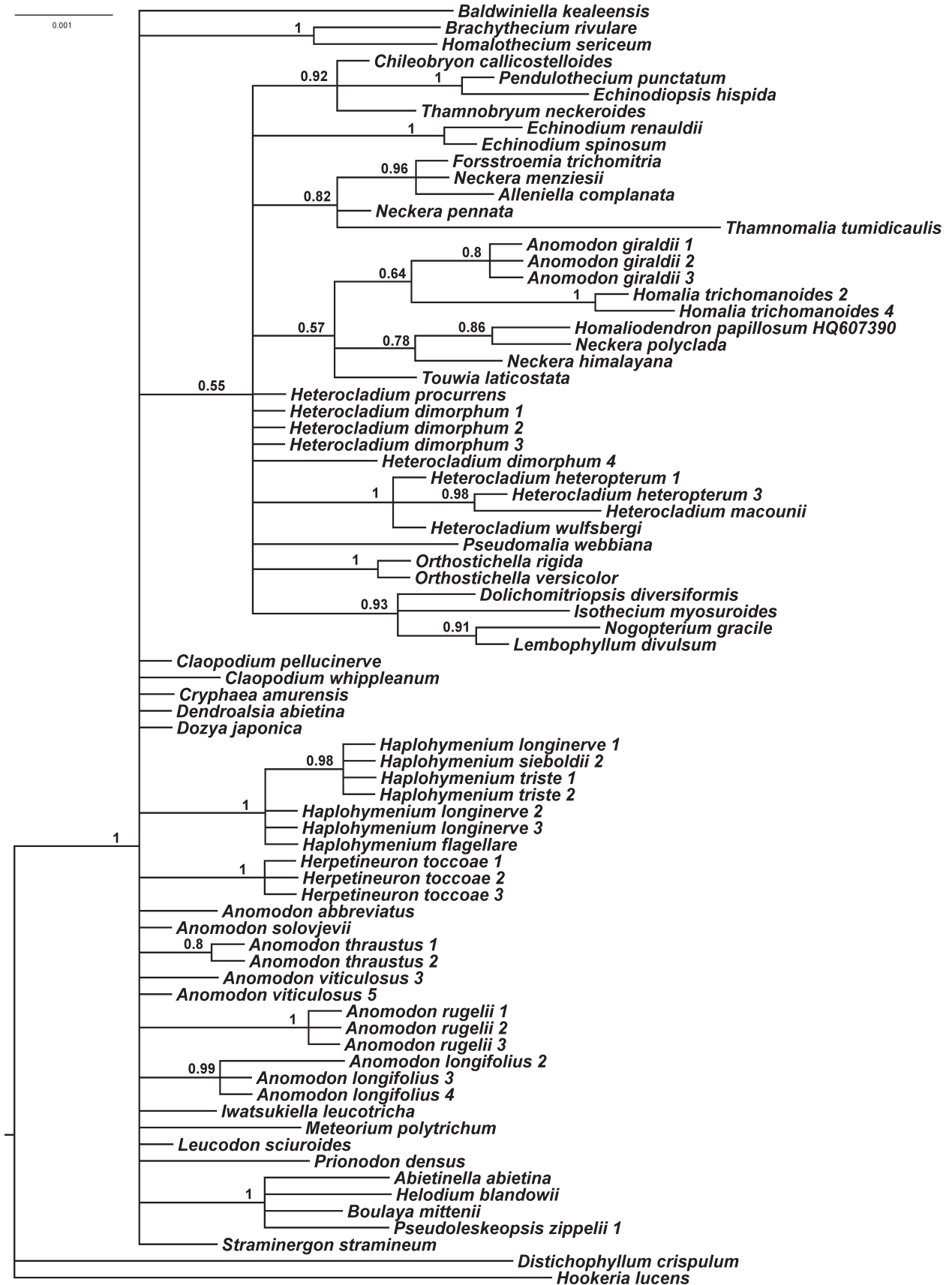


Fig. 5. Bayesian tree based on mitochondrial nad5 region sequences. Posterior probabilities are shown at branches to the corresponding node.





Fig. 6. Bayesian tree based on concatenated organellar sequences (trnS-F, rpl16, atpB-rbcL and nad5). Posterior probabilities are shown at branches to the corresponding node.

“*Heterocladium* s.str.” (*H. heteropterum*, *H. wulfsbergii* & *H. macounii*) and the *Heterocladium dimorphum* clade (*H. dimorphum* & *H. procurrens*). Only the topology based on the rpl16 sequences places these clades sister to each other, though their affinity is not supported statistically, while in reconstructions inferred from the ITS and atpB sequences the *Heterocladium* s.str. grouping forms a poorly supported clade with the Lembophyllaceae. Moreover, in the ITS-based topology, the weakly supported joint clade containing *Heterocladium* s.str. & Lembophyllaceae forms a moderately supported clade with Neckeraceae s.str. (*Neckera*, *Alleniella* & *Forsstroemia*), sister to *Nogopterium*. This topology conflicts with those obtained from the rpl16 and nad5 sequences, where the clade containing Neckeraceae s.l. (including *Anomodon attenuatus* and *A. giraldii* but without Lembophyllaceae and *Heterocladium* s.str.) is highly supported. The topology of the trnS-F and nad5 based trees are not informative on the affinity of the two *Heterocladium* lineages.

**Molecular phylogenetic analysis: concatenated organellar dataset analysis**

The topology of the concatenated organellar dataset mostly corresponds to the single gene-based organellar topologies considered above, but is better resolved and better supported statistically. All the target groups except *Herpetineuron toccoe* are found in the highly statistically supported “Anomodontaceae s.l. & Lembophyllaceae & Orthostichellaceae & Neckeraceae s.l. clade”; the former does not group with any other lineages included in the present dataset. The highly supported Anomodontaceae clade comprises clades corresponding to (1) *Anomodon* s.str. (generitype *A. viticulosus*) excluding *A. thraustus*; (2) *A. thraustus*; (3) *Haplohymenium*; (4) *Anomodon rugelii* & *A. longifolius*. The *Anomodon* s.str. clade lacks statistical support and distinctiveness (branch length), resulting in the separation of *A. thraustus*, while the *Haplohymenium* clade is well delineated and supported; clade 4 is moderately supported. The clades of *Anomodon attenuatus* and *A. rugelii* are found nested in the Neckeraceae, as in all single gene-based reconstructions; *Anomodon attenuatus* forms a moderately supported clade with *Homalia trichomanoides*, and this clade is sister to *A. giraldii*. The two clades of *Heterocladium* are not immediately related: The *Heterocladium* s.str. clade is found in an unsupported sister position to the Lembophyllaceae with nested *Nogopterium*, and their joint clade occupies a sister position to Neckeraceae s.l., with high statistical support, while the *Heterocladium dimorphum* clade is split on the previous node. To a large extent, the topology obtained for *Heterocladium* s.str., Lembophyllaceae and the *Heterocladium dimorphum* group resembles that inferred from the ITS-based reconstruction, but they differ in the position of the Neckeraceae and *Nogopterium*.

DISCUSSION

The present analysis has revealed or confirmed three facts that are new or have not been adequately discussed.

The first is the unexpected position of some *Anomodon* species within the Neckeraceae, which usually have smooth laminal cells, rarely bulging mammillose (in some species of *Thamnobryum*), and very rarely unipapillose (*Homaliiodendron papillosum*), but never multipapillose. The second is the incongruent position of some species, especially *Anomodon longifolius* and *Heterocladium dimorphum* in trees inferred from the nuclear ITS and organellar markers (Figs. 1-6). The third is the position of *Herpetineuron* distant to the Anomodontaceae.

The arrangement of the outgroup taxa was essentially the same in all analyses, more or less corresponding to numerous previously published trees (e.g. Ignatov *et al.*, 2007; Cox *et al.*, 2010; Huttunen *et al.*, 2012), and therefore we skip discussion of this basal part of the tree in general, with the exception of *Herpetineuron*, which is currently placed in the Anomodontaceae (Granzow-de la Cerda, 1997, 2014; Goffinet *et al.*, 2009; Frey & Stech, 2009). Thus, the following discussion is subdivided into sections dealing with the Anomodontaceae, *Heterocladium* and *Herpetineuron* respectively.

**Family Anomodontaceae and the position of *Anomodon attenuatus* and *A. giraldii***

The polyphyly of *Anomodon* found in the present molecular phylogenetic analysis may appear extreme, especially with *Anomodon attenuatus* and *A. giraldii* deeply nested in the Neckeraceae. Although *Anomodon* was originally segregated from *Neckera* (Hooker & Taylor, 1818), at that time the pleurocarp genera were very different from their modern circumscriptions. The familial classification of pleurocarps took shape in the mid XIX century and from the beginning papillose leaf cells were evaluated as a character of great weight: Schimper first segregated Leskeaceae (Schimper, 1856), and shortly after that Thuidiaceae (Schimper, 1860a). *Anomodon* was placed in Leskeaceae in the former publication of Schimper, but not transferred to Thuidiaceae. This was later done by Fleischer (1923) and Brotherus (1925), and most authors of 20th century (Podpera, 1954; Smith, 1978; Crum & Anderson, 1981) followed this placement until the publication of Buck & Vitt (1986). The latter authors crucially revised the whole pleurocarpous moss system, and among other changes placed *Anomodon* not only in its own family Anomodontaceae (originally segregated by Kindberg (1897) but disregarded for almost a century), but also in the order Leucodontales, whereas Thuidiaceae and Leskeaceae were referred to the Hypnales. Most subsequent floras and checklists accepted the family Anomodontaceae. Buck & Vitt (1986) included in Anomodontaceae the genera *Anomodon*, *Haplohymenium*, *Herpetineuron*, *Lindbergia*, *Myurella*, and *Thelia*, united mostly by their papillose laminal cells. Their placement in other families has already been mentioned, and the position of *Herpetineuron* will be discussed below.

Granzow-de la Cerda (1997) published a thorough worldwide revision of *Anomodon* (incl. *Haplohymenium*) and *Herpetineuron*, applying cladistic methodology based on morphology. He submerged *Haplohymenium* into a section *Haplohymenium* of *Anomodon*, along with sect. *Anomodon* and the newly described monospecific sect. *Thraustus*. More importantly, the genus *Anomodon* was subdivided in two subgenera; the first, subgen. *Anomodon*, included the three sections just mentioned, while the second, subgen. *Pseudanomodon* Limpr., included *A. attenuatus*, *A. giraldii*, *A. longifolius* and *A. rostratus*. Thus, Granzow-de la Cerda (1997) accepted the latter subgenus with almost the same circumscription as Limpricht (1895), adding only the East Asian *A. giraldii*.

Limpricht (1895) was the first author who found *Anomodon* heterogeneous in its current circumscription, and he subdivided it into two subgenera (although without a definite indication of rank). Subgen. *Pseudanomodon* ('*Pseud-anomodon*') included *A. attenuatus*, *A. longifolius* and *A. rostratus*, while *A. viticulosus*, *A. rugelii*, and *A. (Haplohymenium) triste* formed subgen. '*Euanomodon*'. The difference between these subgenera included: the presence vs. absence of a neck with an air space in the lower part of the capsules; mostly acuminate vs. broadly rounded leaf apices; and elongate and smooth vs. mostly isodiametric and papillose cells of the perichaetial leaves. Although *A. attenuatus* was characterized as a somewhat atypical member of the subgenus (the leaf is broadly acute), Granzow-de la Cerda (1997) selected this species as the type of *Pseudanomodon*. He also found other important distinctions in the branching pattern between *Anomodon* subg. *Pseudanomodon* and *Anomodon* s. str. (obtuse-leaved species related to *A. viticulosus*): only the species of *Pseudanomodon* have a truly "Isobryalean" branching architecture, i.e. have a clearly defined stoloniform "primary stem" giving rise to the secondary stems with much larger leaves and pinnate branching, contrary to the main stem of, e.g., *A. viticulosus*, albeit creeping and with smaller leaves, but having simple branches which never subdivide extensively. According to Granzow-de la Cerda (1997), this difference is clearly correlated with another character, the central strand, which appears to be absent in subgen. *Pseudanomodon* and also *Haplohymenium*; however, the latter genus is characterized by much smaller plants with thin stems, and accordingly may lack a central strand for that reason. In addition, Granzow-de la Cerda (1997) found the position of the perichaetia in *Anomodon attenuatus* and *A. giraldii* to be confined to older parts of the plants and never present beyond the last branching point. This character never occurs in other core *Anomodon* species and *Haplohymenium*, with the exception of *Haplohymenium sieboldii*. However, the free branching of the latter species makes evaluation of this character rather difficult,

and thus we refrain from confirming or rejecting it; moreover, this rare species never occurs with sporophytes in Russia (Czernyadjeva & Ignatova, 2019).

These distinctions help to explain the strange position of subgen. *Pseudanomodon* in the Neckeraceae, namely in a supported clade with *Homalia*, as already mentioned by Tsubota *et al.* (2002) and Olsson *et al.* (2009a). The Neckeraceae as a whole, and *Homalia* in particular, have a sharp differentiation between creeping stoloniform "primary stems" and pinnately branched secondary stems. The presence of papillae in the leaf cells makes *Anomodon* quite an odd member of the Neckeraceae; however, the '*Pinnatella*-lineage' of the Neckeraceae (Olsson *et al.*, 2009a) includes *Homali dendron papillosum*, a moss with distinctly unipapillose laminal cells. We failed to include material of it in our own study, but the *nad5* sequence from GenBank points towards a considerable similarity with *Anomodon attenuatus* and *A. giraldii* (cf. Fig. 5).

Summing up, there is no alternative to the placement of two latter species in a separate genus within the Neckeraceae, and raising the subgenus *Pseudanomodon* to generic level is obviously a preferable solution.

***Pseudanomodon*** (Limpr.) Ignatov & Fedosov, stat. nov. – Basionym: *Anomodon* [unranked] *Pseudanomodon* ('*Pseud-Anomodon*'), Laubm. Deutschl. 2: 774. 1895. Lectotype (selected by Granzow-de la Cerda, 1997): *Anomodon attenuatus* (Hedw.) Huebener.

Species included:

***Pseudanomodon attenuatus*** (Hedw.) Ignatov & Fedosov, comb. nov. – Basionym: *Leskea attenuata* Hedw., Sp. Musc. Frond. 230. 1801.

***Pseudanomodon giraldii*** (Müll. Hal.) Ignatov & Fedosov, comb. nov. – Basionym: *Anomodon giraldii* Müll. Hal., Nuovo Giorn. Bot. Ital., n.s. 3: 117. 1896.

**Diagnosis:** Plants rather large, yellowish green. Primary stem creeping, without central strand, stoloniform, proximal branch leaves broad (wider than long); secondary stems with much larger leaves, arcuate, attenuate, pinnately branched, foliage subcomplanate; leaves ligulate, broadly acute, entire or with a few teeth near apex; costa ending shortly below apex; laminal cells moderately to sparsely papillose, papillae not pedicellate. Gametangia only on old axes. Perichaetial leaves with smooth or slightly papillose cells of elongate shape. Capsules symmetric, cylindrical, with neck. Annulus not differentiated; operculum obliquely short-rostrate. Exostome teeth striolate proximally, finely papillose distally. Endostome with segments about as long as teeth, cilia reduced or occasionally developed, short. Spores small. Calyptra smooth.

The original description of the subgenus *Pseudanomodon* included also *A. rostratus* and *A. longifolius*. The former species was found nested in a clade of *Claopodium* (Gardiner *et al.*, 2005), and accordingly was placed

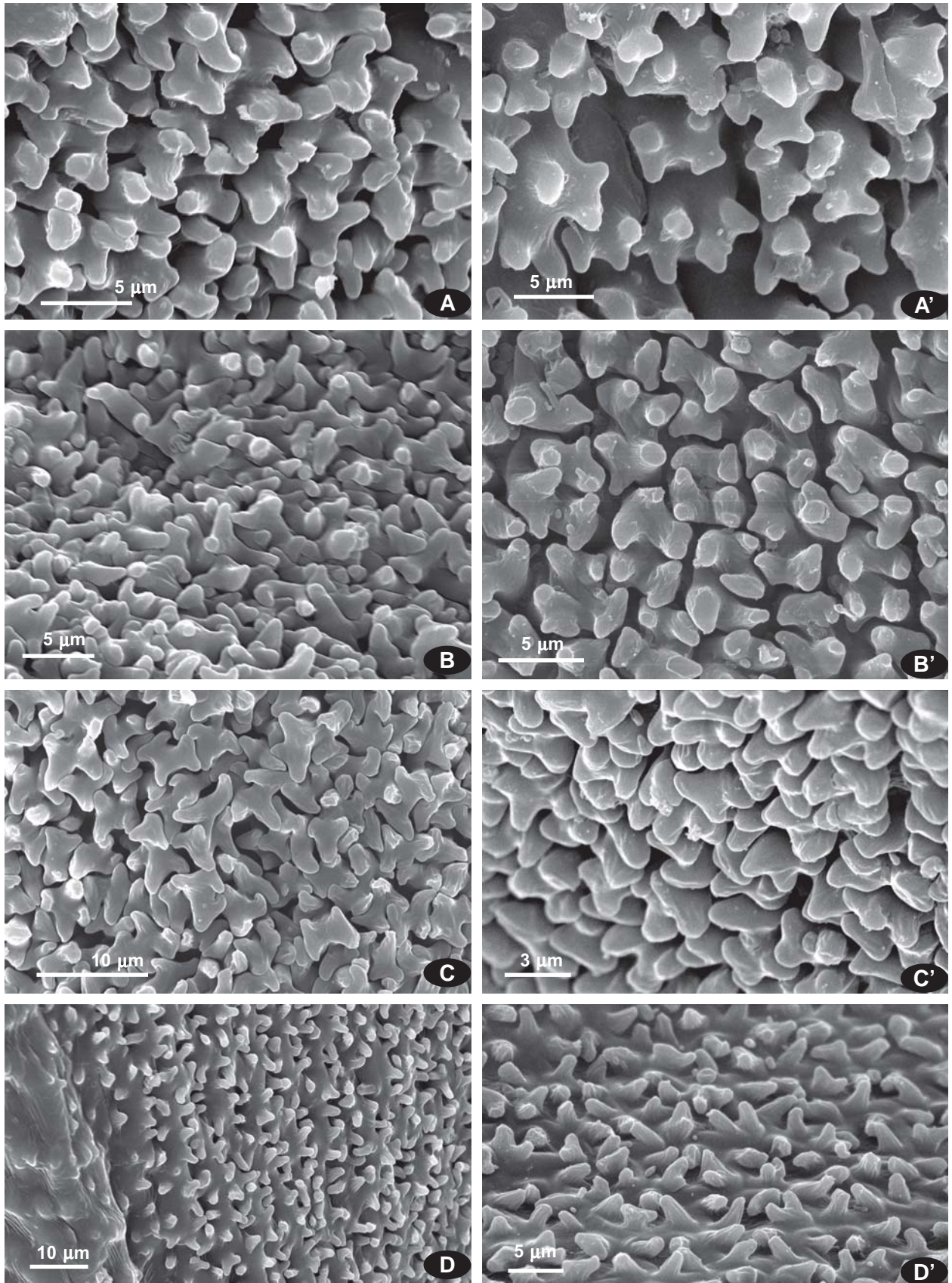


Fig. 7. Laminal cell papillae (SEM images from dry herbarium material [ABCD] and material dried at critical point [A'B'C'D']): A: *Anomodon viticulosus* (MHA9001940); B: *Anomodontopsis rugelii* (MHA9001791); C: *Pseudanomodon attenuatus* (Ukraine, Voronkova, 11.XI.2018, MHA); D: *Pseudanomodon giraldii* (MHA9001740).

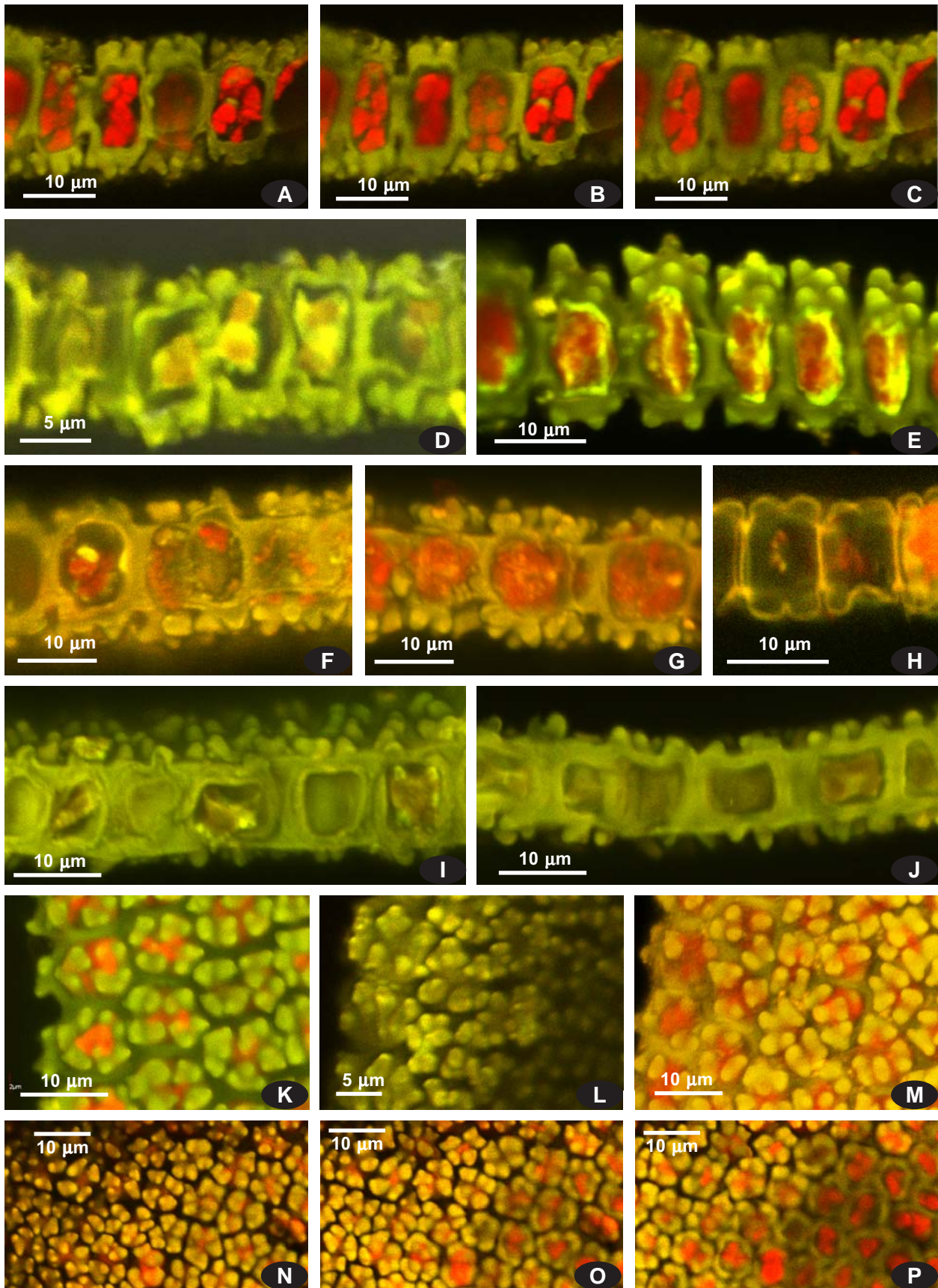


Fig. 8. Lamina cell papillae of species previously referred to *Anomodon s.l.* A–C, K, N–P: *Anomodontopsis rugelii* (MHA9001791); D, L: *Anomodon viticulosus* (MHA9001940); E: *Haplohymenium triste* (MW9090494); F–H, M: *Pseudanomodon attenuatus* (Ukraine, Voronkova, 11.XI.2018, MHA); I–J: *P. giraldii* (MHA9001740). See also Fig. 7. CLSM images.

in that genus (Ignatov *et al.*, 2006). *Anomodon longifolius* will be discussed in more detail below.

The two species referred here to *Pseudanomodon* form a clade in ITS and rpl16, whereas in the concatenated dataset and in atpB-rbcL analyses *Homalia trichomanoides* appears to be closer to *P. attenuatus* than to *P. giraldii*. We do not intend to give a detailed analysis of this puzzling situation; a detailed discussion was promised some time ago by Olsson *et al.* (2009a), and presumably will appear as a comprehensive special study. It seems worthy mentioning that in the same *Pinnatella*-clade Enroth *et al.* (2010) revealed a species more similar to *Homaliadelphus* than to *Pinnatella* and any related genera.

Among the additional characters differentiating both species of *Pseudanomodon* from the Anomodontaceae (*Anomodon* and *Haplohymenium*) is the much better developed endostome.

At the same time, we must note a considerable difference in the proximal branch leaves, which are compound (sensu Ignatov & Spirina, 2012) in *P. giraldii*, and much more similar to some Neckeraceae (Spirina & Ignatov, 2015), while *P. attenuatus* has proximal branch leaves similar to *Anomodon* (Figs. 12–13). The papillae in *Pseudanomodon* are different from the massive papillae of *Anomodon* (Fig. 8), which was noted by Granzow-de la Cerda (1997), who also pointed out that the papillae in *P. giraldii* and *P. attenuatus* are quite different. As shown in Fig. 8, *P. attenuatus* has rather thin cell walls and small papillae which are occasionally forked, while the papillae in *P. giraldii* are more scattered, always simple, and the dorsal and ventral cell surfaces are thickened. In *Anomodon* and *Haplohymenium* the cell outlines are convex, thus the outlines of the dorsal and ventral surfaces are crenate, while they are plane in both of the *Pseudanomodon* species.

#### **A new circumscription of the genus *Anomodon* and family Anomodontaceae**

The controversial topologies inferred from the analyses of different DNA regions obviously cannot be followed literally and require a compromise solution.

The core group of *Anomodon*, i.e. *A. viticulosus*, *A. minor*, *A. thraustus*, *A. abbreviatus* and *A. solovjovii* form a maximally supported clade in most analyses, and only a few comments regarding the two latter species are needed. Their laminal cells have papillae of a very unusual shape (Fig. 9) among other *Anomodon*. Iwatsuki (1963) segregated them in a separate section, whereas Granzow-de la Cerda (1997) lowered their status to subsectional. The present molecular phylogenetic results showed only a slight segregation, thus supporting the latter view. Although appearing very peculiar, the cells in *A. abbreviatus* and *A. solovjovii* are in fact pluripapillose, i.e. the same as in other core *Anomodon* species, although one papilla “branch” overtops the others and in most parts of the leaf each cell has one papilla much larger than the rest (Fig. 9). A somewhat similar

case is observed in *Haplohymenium longinerve* (Czernyadjeva & Ignatova, 2019). Closer to the leaf margin (Fig. 9C, D) and just above the smooth basal cell area (Fig. 9F) the multipapilosity of *Anomodon solovjovii* is especially apparent.

Granzow-de la Cerda (1997) included *Haplohymenium* in *Anomodon* subgen. *Anomodon*, as a separate section. It seems that this decision was quite adequate for his study, in demonstrating that *Haplohymenium* is much closer to *Anomodon* than to *Pseudanomodon* and *Claopodium rostratum*. However, as Granzow-de la Cerda did not put his study in the broader context of pleurocarp systematics at familial level, any recognition that these taxa did not belong to *Anomodon* at all was impossible. The data available now are rather in favor of the recognition of *Haplohymenium* as a separate genus. It has a distinct morphology and its clade is situated on a long branch and has maximal support in most analyses (Figs. 1–6). The only odd topology was found in rpl16, where *Anomodon minor* fell within the *Haplohymenium longinerve* clade, which we cannot explain based on the present limited sampling. However, the independent status of the genus *Haplohymenium* requires a fuller discussion, with decisions regarding the statuses of *Anomodon longifolius* and *A. rugelii*.

*Anomodon longifolius* was referred to *Pseudanomodon* (as a subgenus) by both Limpricht (1895) and Granzow-de la Cerda (1997), though sharing only a few characters with *A. attenuatus* and *A. giraldii*: the presence of flagelliform branches, the absence of perichaetia beyond the point of last branching (although in *A. longifolius* only thin branches occur on the stem distally from the perichaetia), and elongate cells in the perichaetial leaves. The papillae of *Anomodon longifolius* are different from the core species of *Anomodon*, *Pseudanomodon*, and probably from any other pleurocarp (Figs. 10). Higher magnification of moist leaf cells shows that the papillae are not centered over the cell lumen, as is usually assumed, but paired. SEM images taken from young leaves (Fig. 10A, B) and from dry herbarium material (Fig. 10C, D), show the papillae of two neighboring cells originating from the wall between these two cells (sometimes a longitudinal, sometimes a transverse one). In the dry state (Fig. 10C, D), the papillae are inclined towards the center of the lumen and their tips cover the concavities that appear as a result of cell drying.

The proximal branch leaves of *Anomodon longifolius* are narrow and occasionally compound, sometimes similar to those in *Anomodon rugelii* and *Heterocladium dimorphum* and related species, while they are broad in *Anomodon*, *Haplohymenium* and *Pseudanomodon* (Figs. 12).

The peristome of *Anomodon longifolius* differs strongly from the peristomes of core *Anomodon*: its exostome teeth are relatively narrow, transversely striolate below, longi-

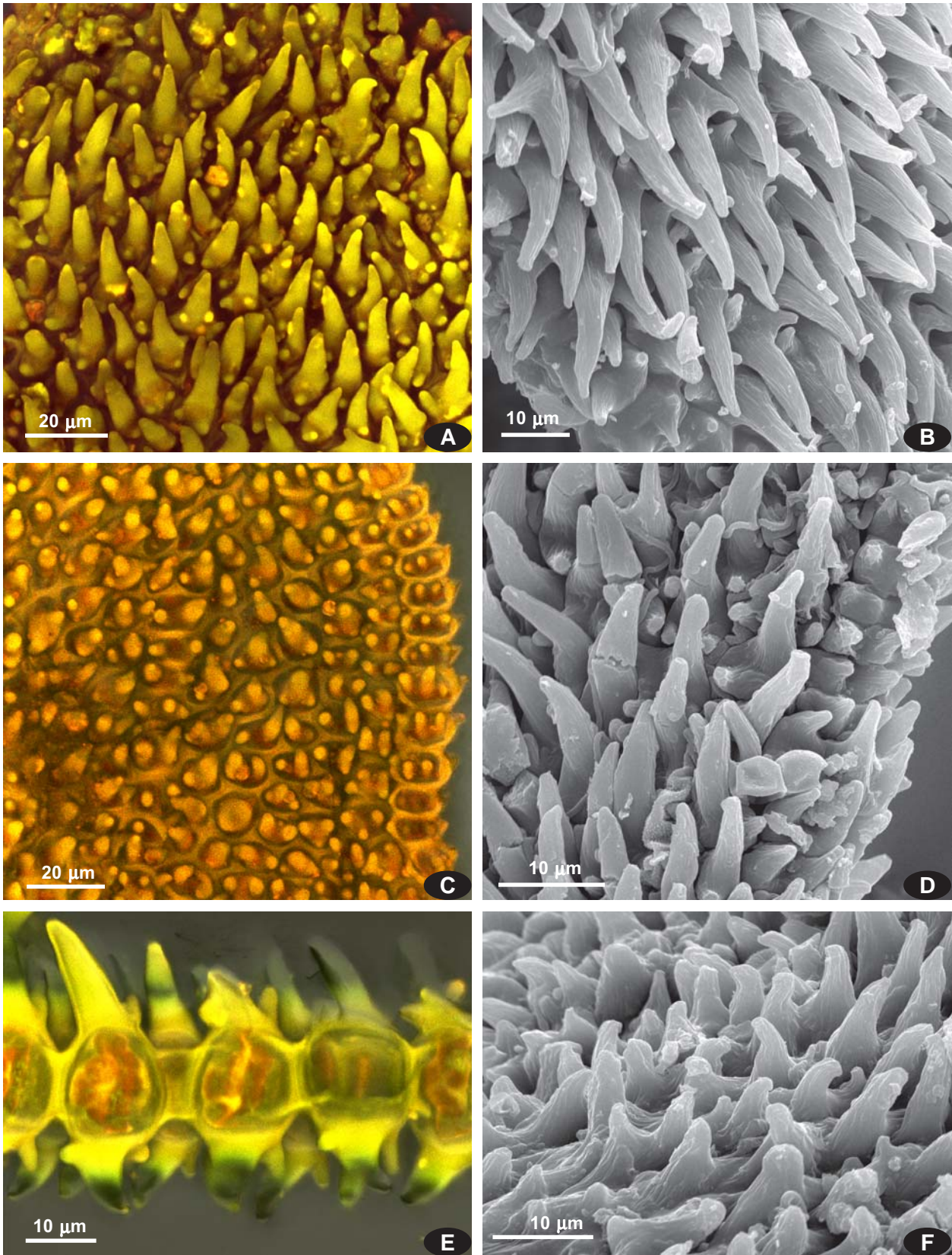


Fig. 9. *Anomodon solovjvii* (MW9001945): papillae shown in CLSM (A, C, E) and SEM (B, D, F) images. A, B: subapical part of leaf; C: lower part of leaf; E: transverse leaf section.

tudinally striolate to prominently papillose above, and finely papillose on the inner surface, whereas in core *Anomodon* the teeth are massive, smooth below on the outer surface and indistinctly papillose above (Figs. 14).

The position of *Anomodon longifolius* in ITS trees in the Neckeraceae–Lembophyllaceae–Echinodiaceae–Ortostichellaceae clade, and in some analyses sister to *Heterocladium dimorphum* (albeit with very low support), and its basalmost position in organellar trees (or sister to *A. rugelii*, both keeping a basal position in this case) indicate the necessity of excluding *A. longifolius* from the genus *Anomodon*. Therefore it is separated here in its own genus. Its familial placement requires further study, but for now, in a view of the topologies of the organellar trees, we retain it in the Anomodontaceae.

**Anomodontella** Ignatov & Fedosov, gen. nov.

Type species: ***Anomodontella longifolia*** (Schleich. ex Brid.) Ignatov & Fedosov, comb. nov. – Basionym: *Pterigynandrum longifolium* Schleich. ex Brid., Muscol. Recent. Suppl. 4: 128. 1819[1818]. Monospecific genus.

**Etymology:** diminutive of *Anomodon*.

**Diagnosis:** *Anomodontella* differs from other Anomodontaceae in: laminal cells unipapillose on both surfaces, with papillae on the ventral surface more prominent than on the dorsal, and from all other pleurocarps in the paired, “geminat” arrangement of the papillae; compound proximal branch leaves (occurring in Anomodontaceae only in *A. rugelii*); long acuminate leaves; smooth and elongate cells in perichaetial leaves; exostome teeth striolate on outer surface in proximal half and highly papillose distally.

Additional differentiating features of *Anomodontella* are the very loose tufts composed of numerous attenuate, flagelliform branches (similar in habit to *Heterocladium*), and the dark to yellow-green color of the plants, not glaucous as in most *Anomodon* and *Haplohymenium* species. Such a color is not unique in the Anomodontaceae, occurring e.g. in *Haplohymenium flagellare* and *H. longinerve*.

\* \* \*

The species closer to *A. viticulosus* than *Anomodontella longifolia* from three groups: (1) *Anomodon* s. str. (*A. viticulosus*, *A. minor*, *A. thraustus*); (2) *Haplohymenium* species; and (3) the monospecific clade of *Anomodon rugelii* (or, in some trees forming a clade with *A. longifolius*). One of the possible taxonomic solutions is to lump all the species in the genus *Anomodon*, following Granzow-de la Cerda (1997). At the same time, the acceptance of *Haplohymenium* at generic level seems to us reasonable: these much smaller plants with papillose and hairy calyptrae are well delimited and form a highly supported clade in most analyses. This unity is somewhat surprising, as *Haplohymenium* includes plants highly polymorphic in papillae structure (representing essentially most types known in *Anomodon* in its new circumscription).

The acceptance of *Haplohymenium* however implies the necessity of separating *Anomodon rugelii*. In most trees it keeps a position sister to the clade of *Anomodon* s. str. + *Haplohymenium* (Figs. 1, 2, 4) or forms a clade with *Anomodontella* (Fig. 6).

Iwatsuki (1963) suggested its segregation in a separate section, i.e. at the same level as *Anomodontella*. The phylogenetic analysis by Granzow-de la Cerda (1997) did not find sufficient morphological distinction in *A. rugelii*, although the author acknowledged its unique auriculate leaf base (Fig. 11), the compound proximal branch leaves (“pseudoparaphyllia present” in his terminology), and the golden to rusty color of the costa.

Additional characters distinguishing *A. rugelii* from the core *Anomodon* species include narrow peristome teeth, with the plates markedly narrower than the trabeculae and papillose on both surfaces, and also the apiculate leaf apex. The latter character is not present in every leaf, and Granzow-de la Cerda (1997) wrote that it is unreliable, although even its occasional presence is important, as it never occurs in *Anomodon* s. str. However, an apiculus occurs in *Haplohymenium*, being especially conspicuous in *H. triste*, although similarly not in every leaf and every shoot.

Therefore we segregate *A. rugelii* in its own monospecific genus.

**Anomodontopsis** Ignatov & Fedosov, gen. nov.

Type species: ***Anomodontopsis rugelii*** (Müll. Hal.) Ignatov & Fedosov. – Basionym: *Hypnum rugelii* Müll. Hal., Syn. Musc. Frond. 2: 473. 1851.

**Etymology:** alluding similarity to the genus *Anomodon*.

**Diagnosis.** Similar to *Anomodon* in the broadly rounded leaf apex and leaf shape, but differs in the compound proximal branch leaves, and the auriculate leaf base, as well as in molecular data (Figs. 1–6).

Additional characters: North American, European and West Asian plants are dark green to rusty brown, which alone allows the species to be recognized in the field. In East Asia there are probably two infraspecific taxa, one of which was recognized by Iwatsuki as *A. rugelii* var. *ferrugineus* (Besch.) Z. Iwats. However, this form is the same as plants from America, from where *A. rugelii* was described. Also in the Russian Far East there is another form of *A. rugelii*, which is slightly different molecularly and has more or less glaucous shoots, less different from species such as *A. viticulosus* and *A. thraustus*; in such plants the leaves are contorted, but not so conspicuously incurved as in North American and European plants. Granzow-de la Cerda (1997) found transitions and did not recognize these forms at all. Further molecular studies with expanded sampling may reveal that in East Asia there are two taxa of *Anomodontopsis*.

**Description:** Plants medium-sized, in rather dense mats, dark green, brownish or, in some populations, somewhat glaucous-green. Stems erect-ascending, weakly ir-



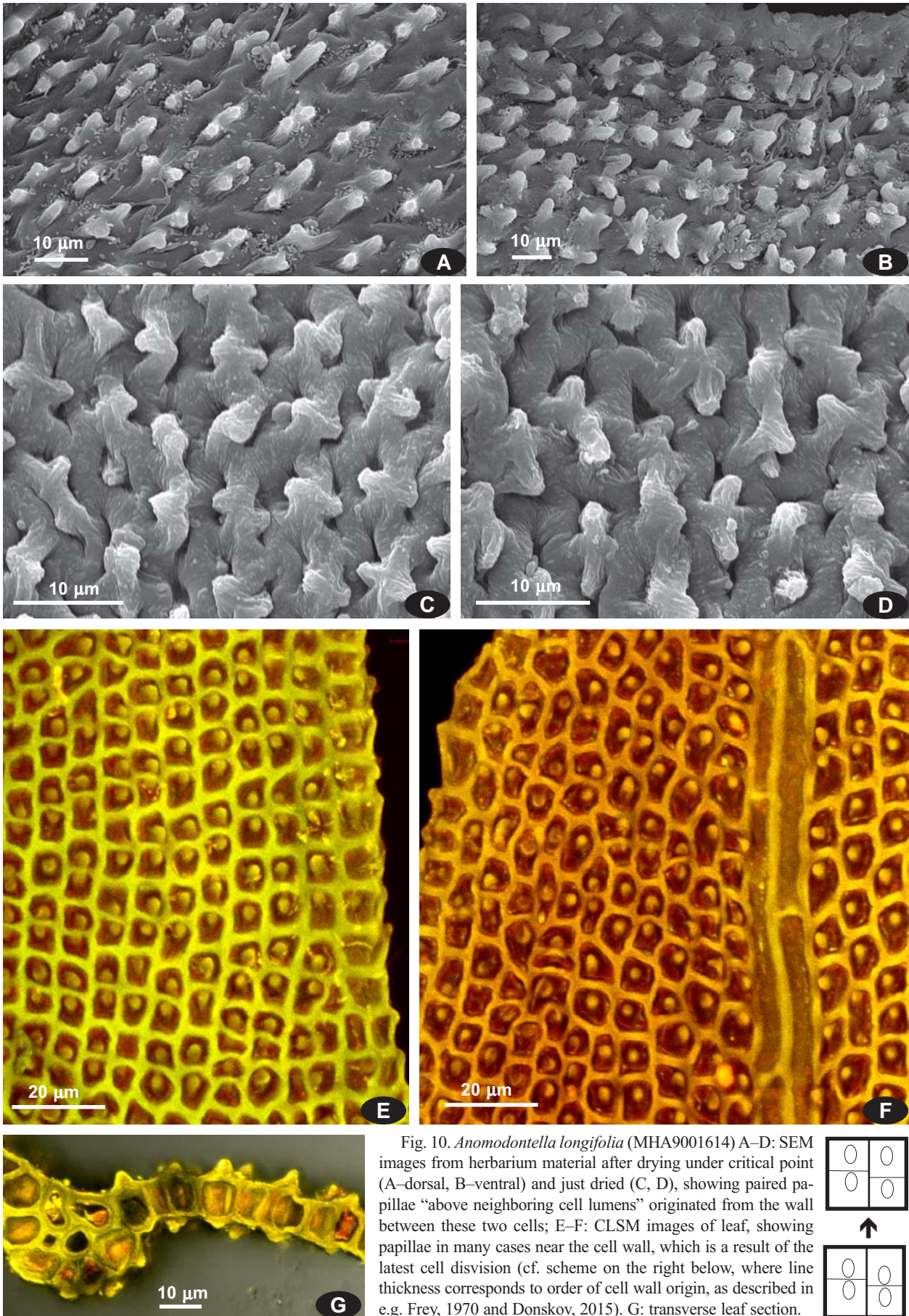


Fig. 10. *Anomodontella longifolia* (MHA9001614) A–D: SEM images from herbarium material after drying under critical point (A–dorsal, B–ventral) and just dried (C, D), showing paired papillae “above neighboring cell lumens” originated from the wall between these two cells; E–F: CLSM images of leaf, showing papillae in many cases near the cell wall, which is a result of the latest cell division (cf. scheme on the right below, where line thickness corresponds to order of cell wall origin, as described in e.g. Frey, 1970 and Donskov, 2015). G: transverse leaf section.

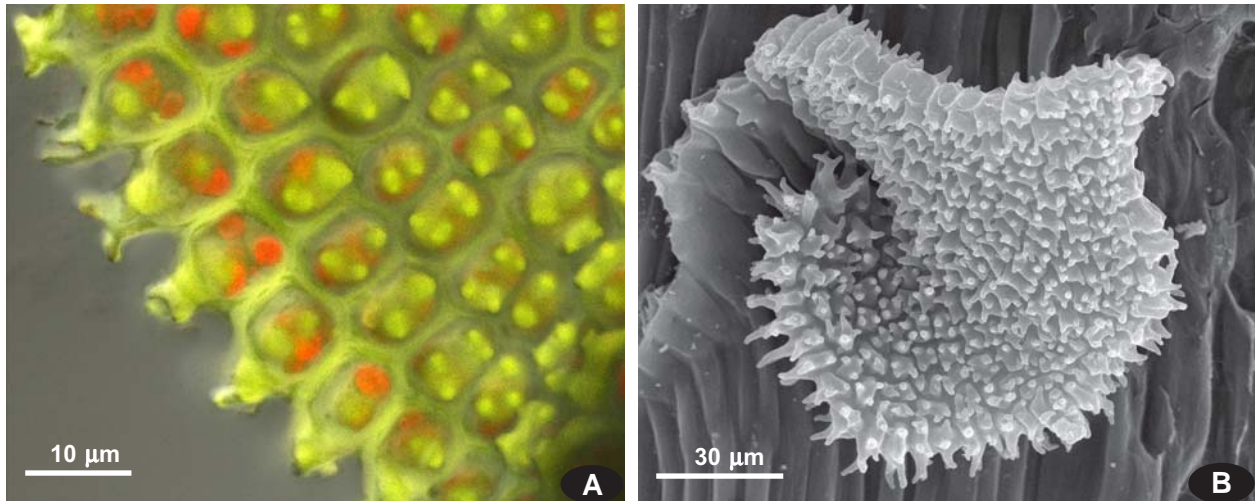


Fig. 11. Auriculate leaf bases of *Anomodontopsis rugelii* (MHA9001791); the marginal cells are multipapillose, although they may appear unipapillose at margin (A: CLSM; B: SEM).

regularly branched, central strand differentiated; proximal branch leaves compound; rhizoids often abundant. Branch leaves in dry state contorted and often incurved, when wet erect-spreading to subcomplanate, broadly oblong-ligulate, conspicuously auriculate, with auricles papillose on the side facing the stem; margins plane, almost entire; apex broadly rounded or occasionally apiculate; costa strong, pellucid, white or with golden to rusty pigmentation, ending shortly below apex, often flexuose, sometimes with lateral offshoots and forked at apex, epidermal cells smooth; laminal cells isodiametric, small, thick-walled, with high, usually pedicellate papillae on both surfaces, basal juxtacostal cells elongate, pellucid, smooth, occupying half of leaf width. Dioicous. Perichaetia at ends of terminal secondary branches; perichaetial leaves from broad base abruptly constricted to narrowly lanceolate apex, laminal cells papillose. Capsule exerted on a long seta, symmetric, cylindrical. Annulus persistent; operculum obliquely short-rostrate, exostome teeth papillose or indistinctly striolate proximally, endostome with short basal membrane, segments short, irregular or absent. Spores small, 9–14  $\mu\text{m}$ . Calyptra smooth. Capsules mature in mid-autumn.

The other species of the genus currently accepted in the Tropicos database all belong to the genus *Anomodon* s. str.: *A. dentatus* C. Gao is accepted by Granzow-de la Cerda (1997) and Wu *et al.* (2002), *Anomodon perlingulatus* Broth. ex P.C. Wu & Y. Jia is accepted by Wu *et al.* (2002), while *Anomodon rotundatus* Paris & Broth. was tentatively synonymized with *A. thraustus* (Wu *et al.*, 2002) and *A. grandiretis* Broth. was placed into synonymy with *Anomodon minor* (Wu *et al.*, 2002).

#### Taxonomy of the genus *Heterocladium*

The genus *Heterocladium* Bruch, Schimper & W. Gumbel was described for two species, *H. dimorphum* and *H. heteropterum*, but the type species of the genus in

unclear (it is not indicated in Tropicos, accessed on 19 May 2019). Different authors have reported one or other of the two species as the type: *H. dimorphum* was mentioned as the type of the genus by Watanabe (1972) and Ignatov & Ignatova (2004), whereas Grout's (1928) typification, supposedly the earliest one, was with *H. heteropterum* (cf. also Enroth *et al.*, 2019). For a long time the genus was placed in the Thuidiaceae (Fleischer, 1923; Broth. 1925), but later Buck & Crum (1990) suggested transferring it to the Pterigynandraceae (along with *Myurella*, *Habrodon*, *Iwatsukiella* and *Leptohymenium*), where it is accepted in some recent publications (Magill, 2014).

The early analysis of Gardiner *et al.* (2005) showed that *Heterocladium* was unrelated to the Thuidiaceae, where it was traditionally placed, but at the same time without any apparent affinity. Thus Ignatov & Ignatova (2004) segregated it in a family Heterocladiaceae. Limited sampling did not allow any further splitting, so despite low support all the species were assumed to form one lineage. Most subsequent analyses have separated the *Heterocladium* species in two different clades, and *Heterocladium* s. str. (the species grouped around *H. heteropterum*) has usually been placed within the Neckeraceae or Lembophyllaceae or between them in a grade (cf. Enroth *et al.*, 2019), while the species related to *H. dimorphum* were usually in a more distant position.

The family has been accepted in some floras, e.g. by Hedenäs *et al.* (2014), but recently it was pointed out that the earlier name Heterocladiaceae Decaisne for a family of red algae has been overlooked (Enroth *et al.*, 2019). This family is based on the genus *Heterocladia* Nageli, which is still in current use and therefore the name cannot be a subject for conservation.

The present analyses of different loci resulted in somewhat different topologies regarding the position of these

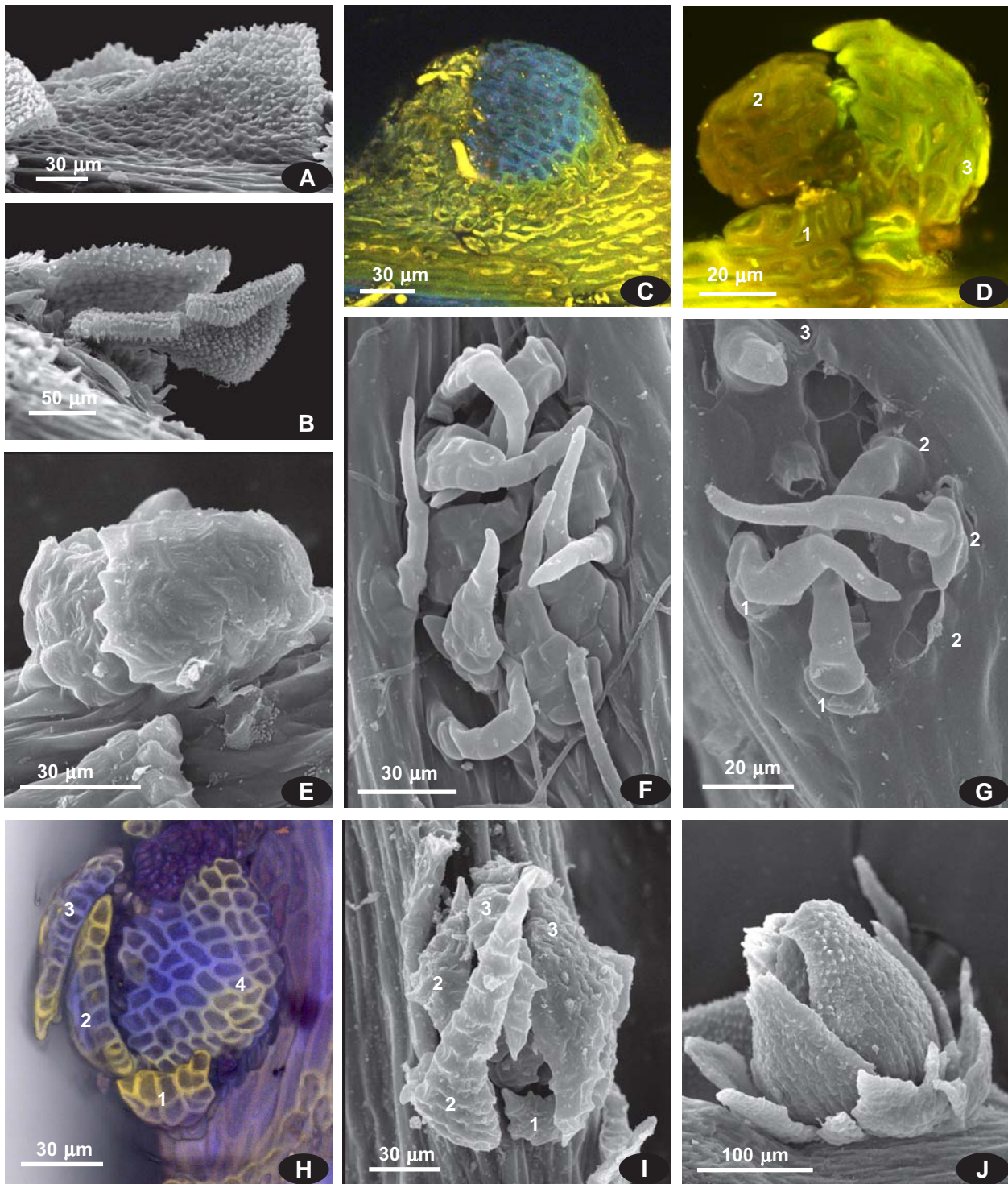


Fig. 12. Proximal branch leaves of A, B: *Anomodon viticulosus* (MHA9001940), C: *Anomodon thraustus* (MHA9002034), D–E: *Haplodymenium longinerve* (MHA9035366), F–G: *Anomodontopsis rugelii* (MHA9001791), H–J: *Anomodontella longifolia* (MHA9001614). Numerals in figures D, G, H, I denote number of compound branch leaves or their parts (cf. Berthier, 1971; Spirina & Ignatov, 2008, 2015). (C, D, H: CLSM; A, B, E–G, I, J: SEM).

two groups of *Heterocladium*. The ITS and *atpB* analyses resolve *Heterocladium* s.str. in a clade with the Lembophyllaceae; *rpl16* shows the same, but in this case the *H. dimorphum* clade is found sister to the *Heterocladium* s.str. clade. The analysis of *trnS-F* found the *Heterocladium* s.str. clade in the grade from

Lembophyllaceae to Neckeraceae, between the core clade of the Neckeraceae and the “*Pinnatella*-clade”. It seems that the position of *Heterocladium* in the Lembophyllaceae would be the best solution in the present state of knowledge.

The similarity in morphology between *Heterocladium*

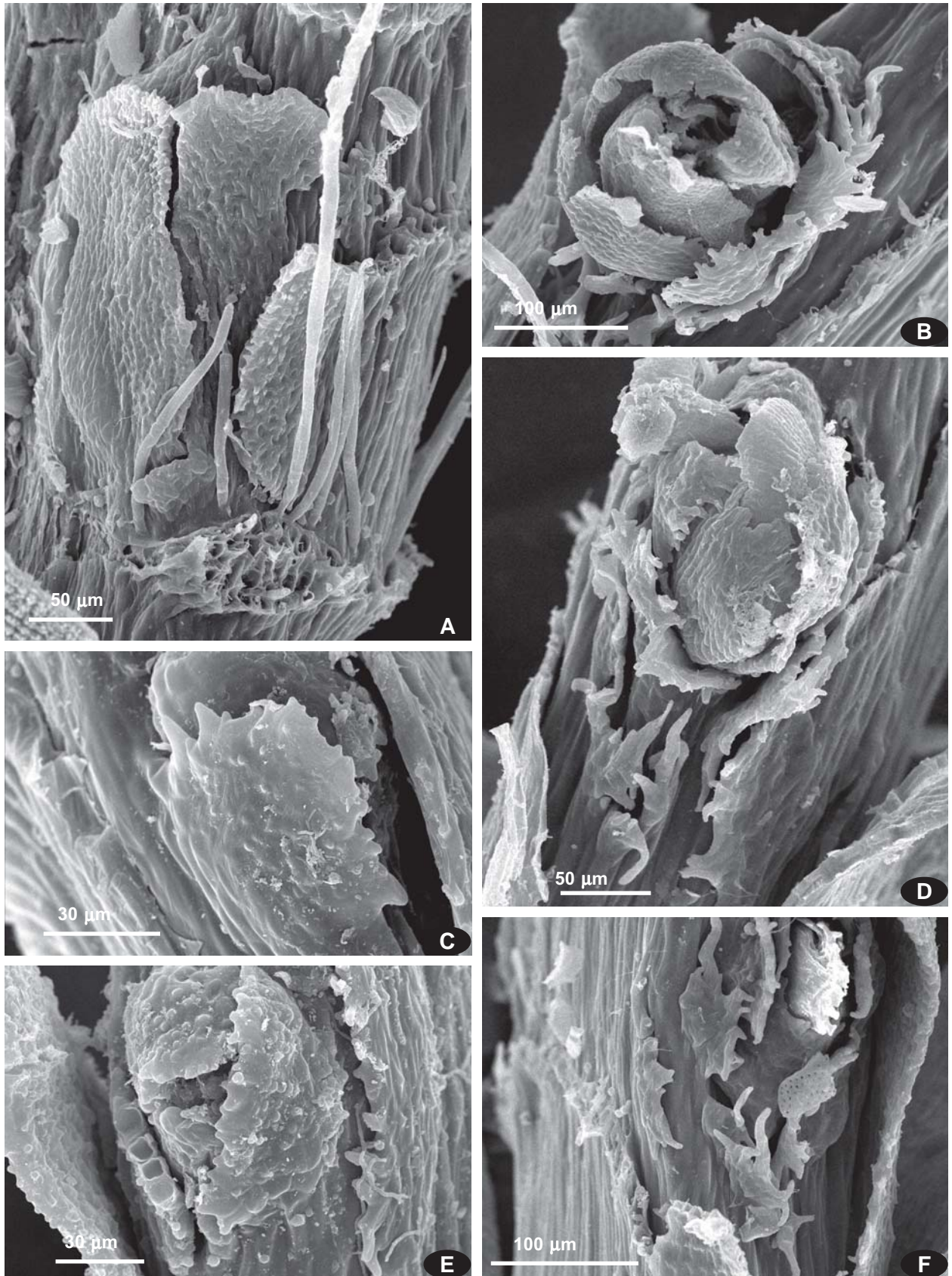


Fig. 13. SEM images of proximal branch leaves of *Pseudanomodon attenuatus* (A, C, E from Ukraine, Voronkova, 11.XI.2018, MHA) and *P. giraldii* (B, D, F, from MHA9001740). The branch buds of the former species are similar to those of most pleurocarps, including *Anomodon* s.str. in having broad proximal branch leaves tightly covering the branch apical cell, whereas in *P. giraldii* the outermost proximal branch leaves are compound, as in many neckeraceae and related families (cf. Spirina & Ignatov, 2015).

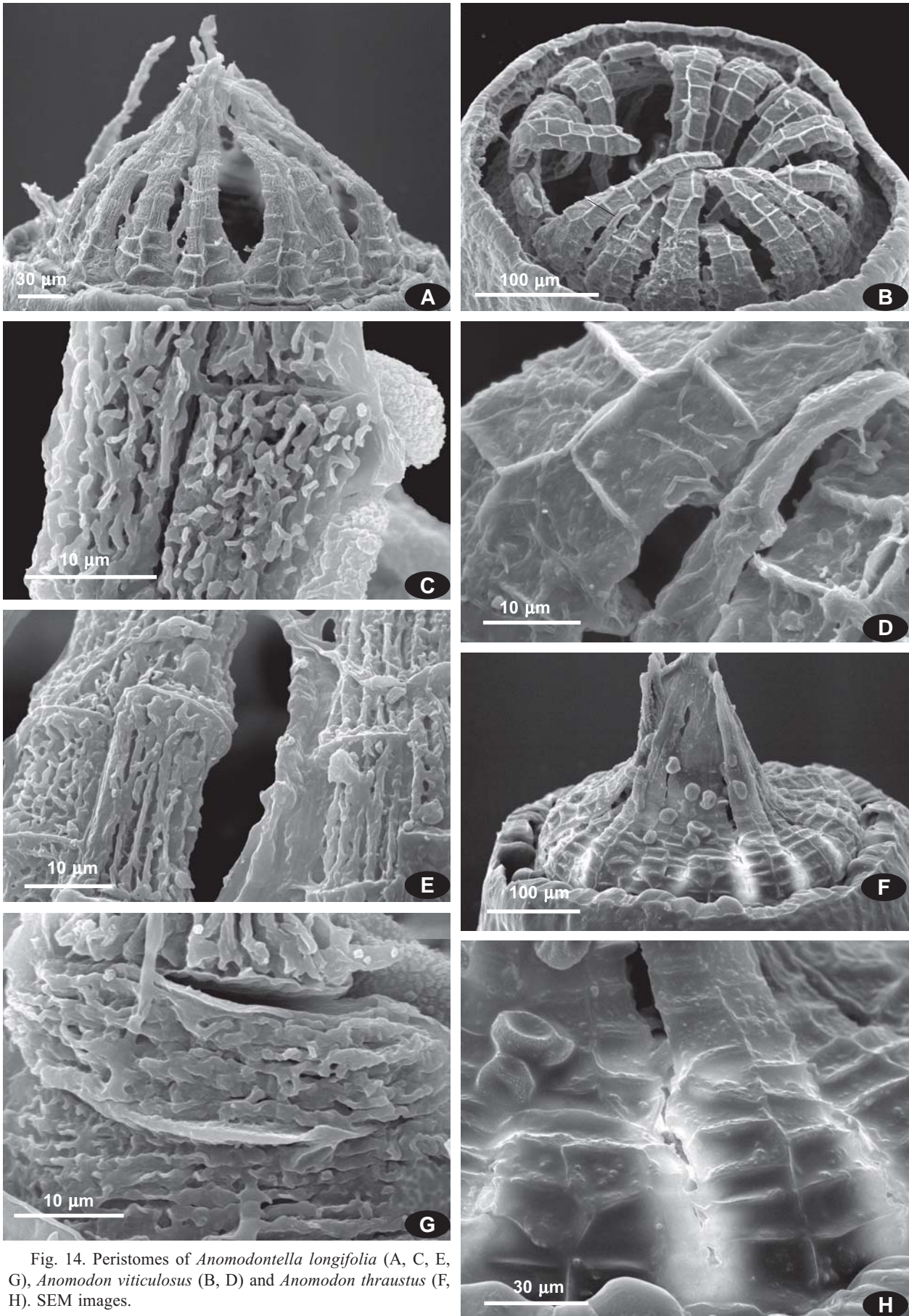


Fig. 14. Peristomes of *Anomodontella longifolia* (A, C, E, G), *Anomodon viticulosus* (B, D) and *Anomodon thraustus* (F, H). SEM images.

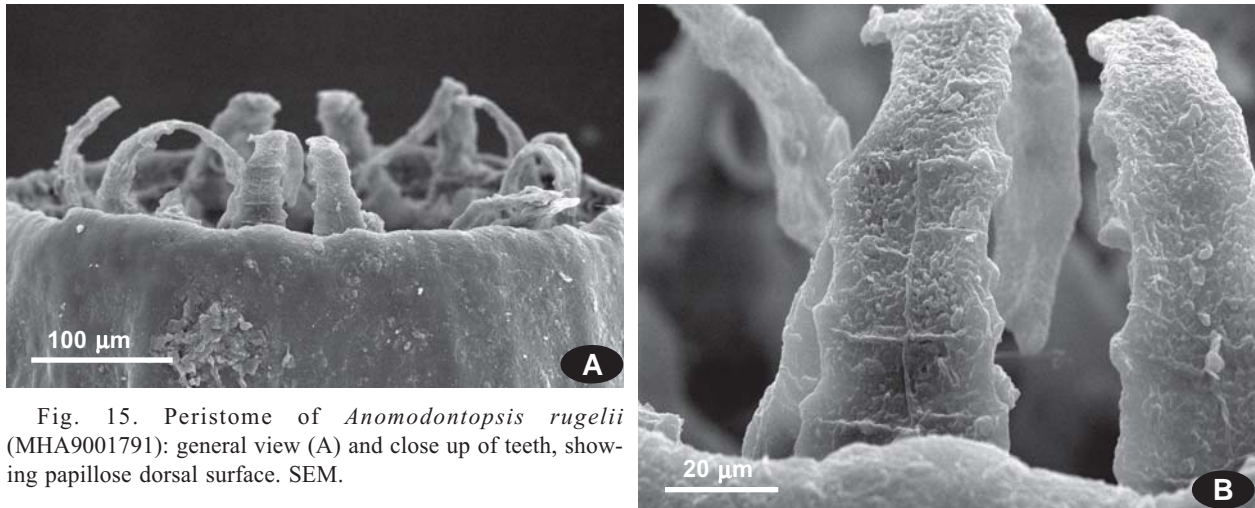


Fig. 15. Peristome of *Anomodontopsis rugelii* (MHA9001791): general view (A) and close up of teeth, showing papillose dorsal surface. SEM.

s. str. and core Lembophyllaceae (Tangney, 1997; Quandt *et al.*, 2009) is not very high; however, some other marginal groups which have been referred to the family based on molecular phylogenetic inference have likewise not much in common with the core of the family, e.g. *Nogopterium* and *Mawenzhangia* (Enroth *et al.*, 2018). Multipapillose laminal cells, especially conspicuous in *H. macounii*, would be odd in the new circumscription of the family; it may be inconvenient, but the loss of the “smooth laminal cell” character from the diagnosis of the Lembophyllaceae has so much in parallel with the case of *Pseudanomodon* that it is already not surprising. Note that in contrast to the Anomodontaceae, the papillae in *Heterocladium* occur only on the dorsal leaf surface, as in the Thuidiaceae and Leskeaceae.

\* \* \*

The position of the *Heterocladium dimorphum* group is more indefinite. It forms clades with *Anomodontella* in the ITS tree (with low support, Fig. 1) and with *Heterocladium* in the rpl16 analysis (Fig. 3), but more commonly keeps a separate position in polytomy or grade near Ortostichellaceae, Echinodiaceae, Lembophyllaceae and Neckeraceae (Figs. 2-6), being in most cases maximally supported. Considering such genetic differentiation, we suggest segregating the *H. dimorphum*-group of species in a separate genus and family.

#### **Heterocladialaceae** Ignatov & Fedosov, fam. nova

Monogeneric family, type: *Heterocladia* Ignatov & Fedosov

**Diagnosis.** Stems rather regularly pinnately branched, densely foliate; central strand present; epidermal cells smooth; paraphyllia absent, proximal branch leaves often compound. Stem leaves squarrose, from broadly ovate, appressed base tapered to triangular acute acumen, broadly decurrent; margins serrate to serrulate; costa short, double; laminal cells quadrate to rhomboidal, on dorsal surface with a massive papilla closer to distal end of cell, on ventral surface smooth. Branch leaves dis-

tinctly differentiated, erect to spreading, ovate, broadly acute. Dioicous. Capsule horizontal, short-cylindrical, curved. Operculum conic-apiculate. Peristome perfect, cilia long. Spores small.

#### **Heterocladia** Ignatov & Fedosov, gen. nov.

Type species: **Heterocladia dimorpha** (Bridel) Ignatov & Fedosov, comb. nov. – Basionym: *Hypnum dimorphum* Brid., Muscol. Recent., suppl. 2: 149. 1812.

Species included: **Heterocladia procurrens** (Mitt.) Ignatov & Fedosov, comb. nov. – Basionym: *Pterogonium procurrens* Mitt., J. Linn. Soc., Bot. 8: 37. 1864.

**Description:** Leaves spreading to erect-appressed when dry, erect-spreading when moist; stem leaves to 1 mm; margins serrate to serrulate; apex acute; costa usually double and short to just below mid leaf; laminal cells papillose, papillae single, in distal end of cell; basal cells smooth.

**Differentiation:** The morphological distinction between *Heterocladia* and *Heterocladium* includes (1) branching pattern: more or less regularly unipinnate in *Heterocladia* and strongly to moderately irregularly repeatedly branched in *Heterocladium*; (2) always smooth stem cells in *Heterocladia* vs. occasionally papillose in *Heterocladium*; (3) laminal cells smooth to multipapillose on dorsal surface in *Heterocladium* vs. smooth to unipapillose on dorsal surface in *Heterocladia*; (4) leaves appressed at their bases and then reflexed to squarrose in *Heterocladia* vs. leaves somewhat spreading from stem at their bases in *Heterocladium*. Hedenäs & Bisang (2011) found that species of *Heterocladia* have both large and dwarf males, whereas dwarf males in *Heterocladium* s. str. have not been observed.

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According to the Tropicos database (accessed 2 May 2019), there are nine species of the genus currently accepted. Two are referred here to *Heterocladia*, and none of the other species accepted by Tropicos belong to this

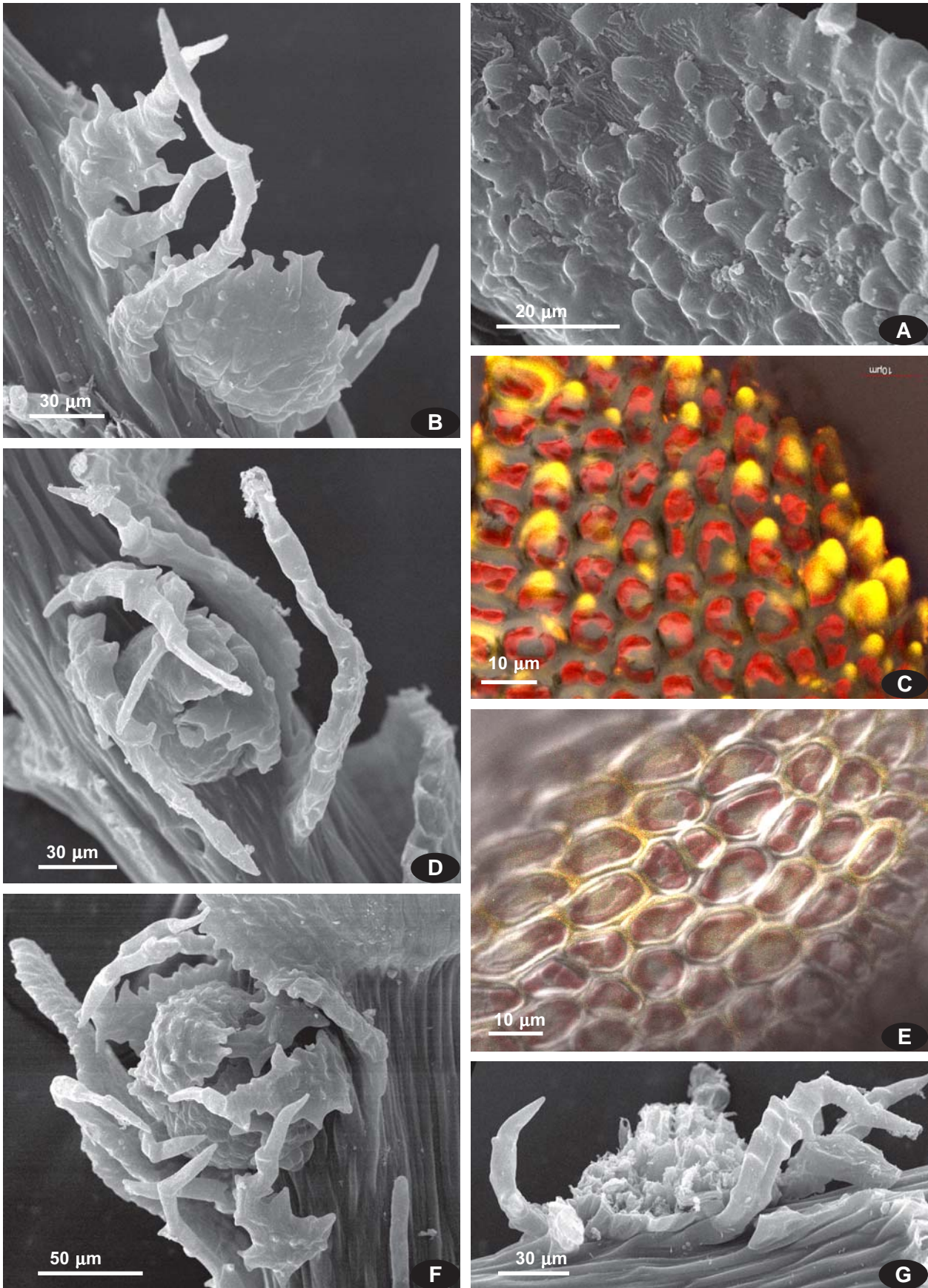


Fig. 16. *Heterocladia dimorpha* (MW9043335): Leaf surface (A and C dorsal, and E ventral) and incised and compound proximal branch leaves of (B, D, F, G).

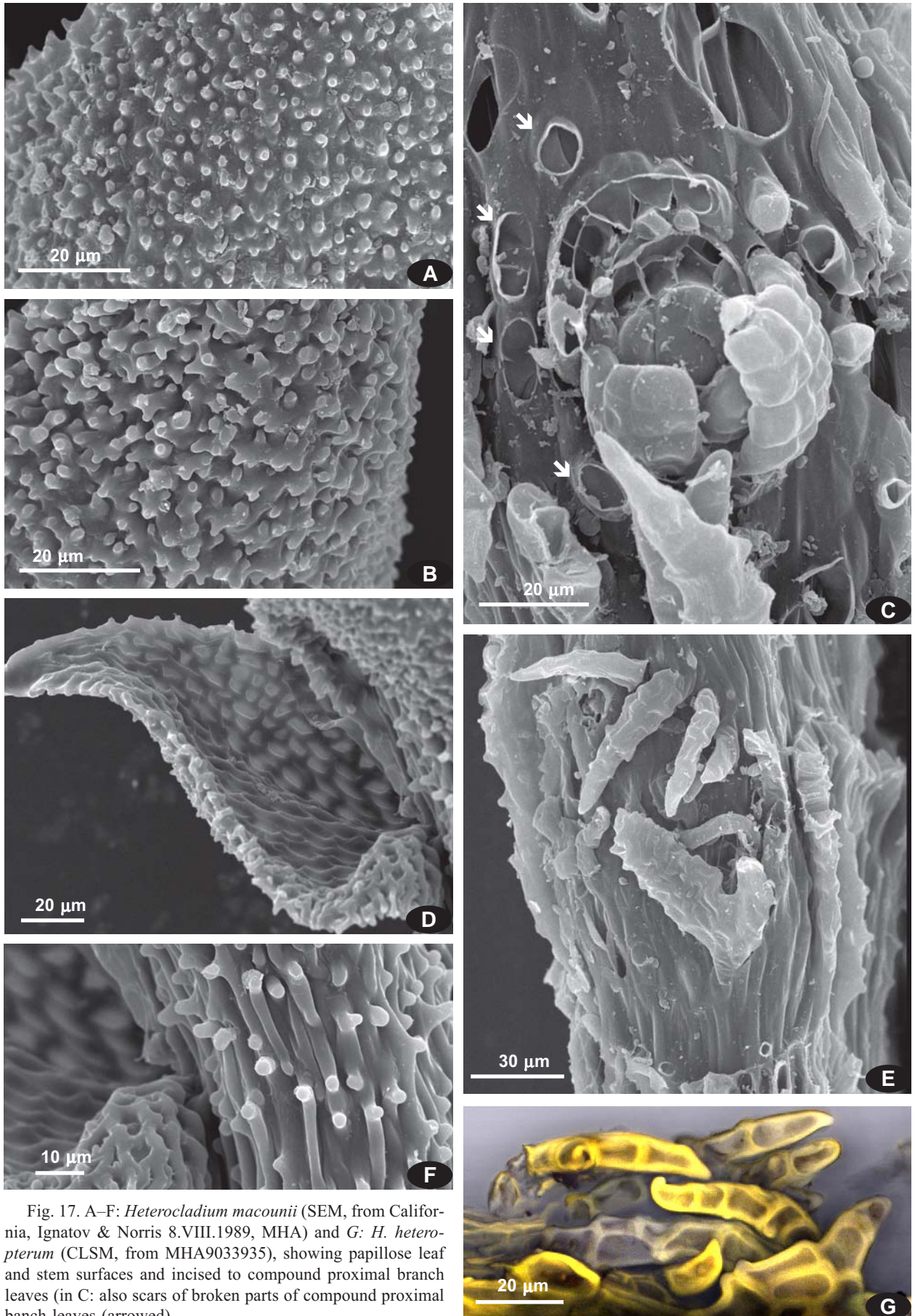


Fig. 17. A–F: *Heterocladium macounii* (SEM, from California, Ignatov & Norris 8.VIII.1989, MHA) and G: *H. heteropterum* (CLSM, from MHA9033935), showing papillose leaf and stem surfaces and incised to compound proximal branch leaves (in C: also scars of broken parts of compound proximal branch leaves (arrowed)).



genus. Three sequenced species of *Heterocladium* (*H. macounii*, *H. wulfsbergii*, *H. heteropterum*) were found to be monophyletic in most analyses. According to their species descriptions *Heterocladium angustifolium* (Dixon) R. Watan., *H. capillaceum* Broth. ex Ihsiba, *H. pilicuspis* Broth. ex Ihsiba and *H. tenellum* Deguchi & H. Suzuki belong to *Heterocladium* s. str.

#### Systematic position of *Herpetineuron*

The grouping of *Herpetineuron* with *Anomodon* was suggested by Brotherus (1907, 1925), who placed these genera in *Anomodontoideae* (one out of four subdivisions of the Thuidiaceae). Subsequent authors placed it in the Thuidiaceae, e.g. Watanabe (1972), Crum & Anderson (1981), Noguchi (1991). Buck & Vitt (1986) resurrected the Anomodontaceae, including *Herpetineuron* and some less closely related genera (discussed above). Granzow-de la Cerda (1997) provided a revision of *Anomodon* and *Herpetineuron*, but he avoided discussion of the family-level taxonomy.

Thus, no justification of the close relationship between *Herpetineuron* and *Anomodon* has ever been put forward. The molecular phylogenetic analysis (based on *rbcL*) of Tsubota *et al.* (2004) supported this position, whereas the analysis of Cox *et al.* (2010) (based on *rps4* and *nad5*) did not. Not one of five studied loci supported the relationship of *Herpetineuron* with *Anomodon*; most markers left *Herpetineuron* unresolved in the polytomy outside the *Anomodon*-clade and the Neckeraceae+Lembophyllaceae+Orthostichellaceae clade, and ITS indicated that its closest relationship was with the Thuidiaceae, with moderate support. In view of the isolated position of *Herpetineuron*, usually on very long branch, which reflects its strong divergence and peculiar morphology, we foresee that *Herpetineuron* needs its own family. However as sampling of the Thuidiaceae is not sufficient in the present study, we refrain from doing this now, and temporarily suggest returning *Herpetineuron* to the Thuidiaceae.

Some morphological features of *Herpetineuron* are remarkable. Its leaf structure is especially outstanding and merits a short comment here. The genus *Herpetineuron* includes only a single species, *H. toccoe* (Sull. & Lesq.) Cardot, a widespread pantropical moss penetrating to the temperate zone in the eastern sectors of both Eurasia and North America. It grows mostly in habitats which experience moderately long periods of severe desiccation, requiring the ability to incurve its leaf margins in the dry state (Fig. 18A, B, I) and spread them after wetting. The peculiarity of *Herpetineuron toccoe* is an exceedingly conspicuous ontogenetic sector of  $4 \times 4$ ,  $4 \times 8$ , and  $8 \times 8$  cells throughout the leaf (Fig. 18C–H). Such sectors are universal in mosses, as the moss leaf is always formed from a single cell by a number of divisions (Schimper, 1860b; Frey, 1970); they are usually masked by developmental irregularities, and far less apparent in fully de-

veloped leaves (Donskov, 2015). We don't know of any other moss whose ontogenetic sectors are so clearly apparent. Our tentative explanation of this expression is that the repeated leaf incurvation requires reliable joints, and the ontogenetic sectors in *Herpetineuron* are connected by efficient joints (e.g. Figs. 18L, N), often associated with papilla-like thickening (Figs. 18M, P). Note that in addition to incurved leaf margins, the leaves of *Herpetineuron* in the dry state are also incurved along their length.

\* \* \*

#### The occurrence of papillae and their structural variation within phylogenetic lineages

The present study found mosses with papillose laminal cells in two families where they were either unknown (Lembophyllaceae) or extremely rare (Neckeraceae).

It seems that the taxonomic value of papillae on the leaf lamina has been strongly overestimated in moss systematics. Some genera or species with papillose laminal cells, previously placed in various families based on this character, have already been found to have different affinities, like *Myurella* in the Plagiotheciaceae, while some other groups, e.g. *Claopodium*, actually a relative of Brachytheciaceae, are still awaiting a final verdict. The present analysis indicated that the latter genus has no affinity with either *Anomodon* or the Thuidiaceae, where it was traditionally placed.

Many pleurocarpous moss families include species with cells that are prominently prorate to “dorsally papillose in the distal cell end” but have not evolved further to a central-unipapillose or multipapillose state. Examples are found in the Brachytheciaceae (*Brachythecium* (*Bryhnia*) *novae-angliae*), Pseudoleskeellaceae (*Pseudoleskeella papillosa*), Amblystegiaceae (*Palustriella decipiens*), and Hylocomiaceae (*Hylocomiadelfus triquetrus*).

There are genera which, in different species, develop papillae at the distal end of the cell or in a central position (*Myurella*, *Haplocladium*, *Pseudoleskea*); note that in these cases (and maybe in most others) the papillae occur only on the dorsal leaf surface. This can lead to two trends in the complexity in the pattern of papillae, firstly from unipapillose to multipapillose (observed in *Claopodium* and *Thuidium*), and secondly from dorsally papillose to papillose on both surfaces. The latter trend is gradual, and papillosity on the ventral surface is often less prominent compared with the dorsal surface: it is more or less apparent in *Haplohymenium* (Fig. 8E). There are probably no cases where papillae are present on the ventral surface but absent on the dorsal, although sometimes the ventral papillae may be larger than the dorsal: *Anomodontella* provides one such example (Fig. 10A, B, G). A quite separate case consists of papillae in the corners of the ontogenetic sectors in *Herpetineuron*, comparable with e.g. *Atrichum*, but rare in pleurocarps.

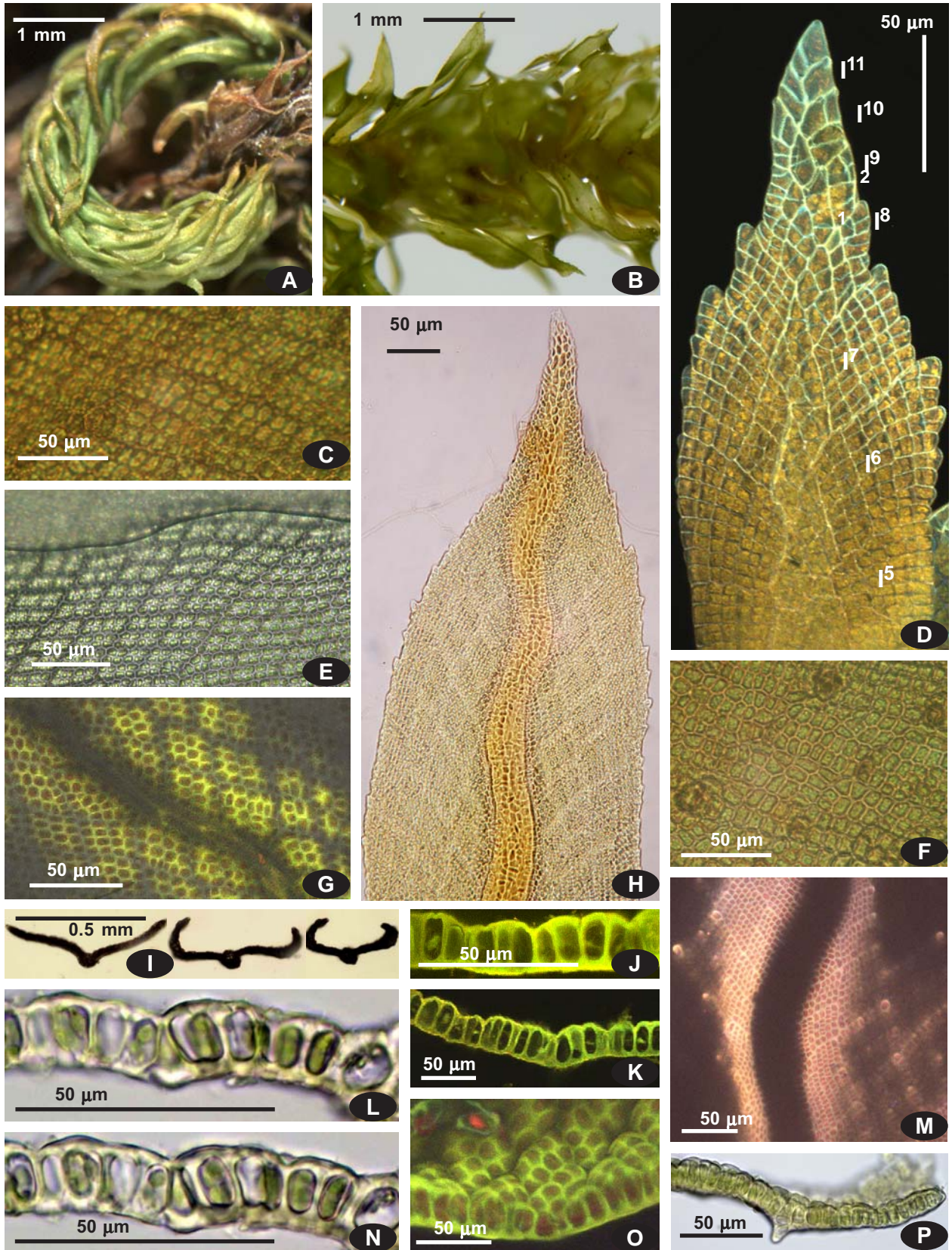


Fig. 18. *Herpetineuron toccoae* (MHA9035729): A: habit, dry, B: habit, wet, C, E–H, M: different views of lamina, showing ontogenetic sectors, and thickenings in corners of these blocks (E: recently dried leaf part where an air bubble has encroached under the cover glass as the slide dried); I: three views of the same transverse leaf section, in wet, half-dry and dry states; K–N, P: leaf transverse sections, showing ontogenetic sectors of four (eight) cells, and papillae at their joints (in P); O: 3D view of leaf surface, highlighting its tetragon pattern; D: young leaf, with numbered ontogenetic sectors, I5 to I11 following Frey's (1970) terminology.

In general, variation in the pattern of papillosity in genera and families is rather gradual, and the placement of the multipapillose *Heterocladium* in the Lembophyllaceae and *Pseudanomodon* in the Neckeraceae (discussed in the present paper) looks fairly odd, and further studies are needed to understand what lies behind this. In any case, our knowledge of variation in papillae structure is still far from complete and future study will certainly reveal many interesting details for a deeper understanding of pleurocarp evolution.

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