

PHYLOGENETIC POSITION OF *HOMALOTHECIUM LAEVISETUM*
AND RELATIONSHIP WITH THE GENUS *PALAMOCLADIUM*
ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ *HOMALOTHECIUM LAEVISETUM*
И ЕГО РОДСТВО С РОДОМ *PALAMOCLADIUM*

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Abstract

Molecular phylogenetic analysis found *Homalothecium laevisetum*, a widespread East Asian and Malesian species, to be unrelated to other species of this genus and invoked resurrection of the genus *Oticodium*. The latter genus was described for one species, *O. celebesiae*, which is considered to be a synonym of *Homalothecium laevisetum*. *Oticodium* belongs to the subfamily Eurhynchioideae, and most closely related to *Eurhynchium* s.str. The specialized peristome of the epiphytic *Oticodium* seems to have evolved more abruptly from that in terrestrial *Eurhynchium* than in other epiphytic lineages of Brachytheciaceae, such as *Homalothecium* and *Palamocladium*, where the transition to a specialized peristome is more gradual. The superficially similar genus *Palamocladium* is briefly commented on.

Резюме

Результаты молекулярно-филогенетического анализа свидетельствуют о том, что широко распространенный восточноазиатский и малезийский вид *Homalothecium laevisetum* не является родственным другим видам этого рода, что приводит к необходимости восстановления родового статуса *Oticodium*. Этот род был описан как монотипный, включающий *O. celebesiae*, который сейчас считается синонимом *Homalothecium laevisetum*. *Oticodium* относится к подсемейству Eurhynchioideae; он наиболее близок к роду *Eurhynchium* s.str. Специализированный перистом *Oticodium*, по-видимому, эволюционировал гораздо более быстро, чем перистомы других эпифитных линий в Brachytheciaceae, таких как *Homalothecium* и *Palamocladium*, в которых переход к специализированному типу перистома более постепенный. Дан также краткий комментарий в отношении внешне сходного рода *Palamocladium*.

KEYWORDS: Eurhynchioideae, *Homalothecioideae*, *Oticodium*, phylogeny, morphological synapomorphies, taxonomy

INTRODUCTION

Homalothecium Bruch, Schimp. & W. Gümbel was among the first genera of Brachytheciaceae established in “Bryologia Europaea” by Bruch *et al.* (1851). The species in the genus typically have triangular, plicate leaves with small alar cells, and a glossy appearance. *Homalothecium* was revised by Hofmann (1998) and molecular phylogeny by Huttunen *et al.* (2008) confirmed the delimitation of the genus and included nine species. Two additional species have been described after that (Hedenäs *et al.*, 2009, 2014).

In revisions based on morphology, *Homalothecium* was often assumed to be closely related to *Palamocladium* Müll. Hal. (Lai *et al.*, 1991; Hofmann, 1997, 1998). That genus was erected by Müller (1896), but its species were

referred to the genus *Pleuropus* Griff., nom. illeg. (Griffith, 1842) until the middle of the 20th century. Later *Pleuropus* / *Palamocladium* species have also been included in *Homalothecium* by Grout (1928) and Ochyra & Pócs (1982), and Robinson (1962) even introduced *Homalothecium* subgen. *Palamocladium* (Müll. Hal.) H. Rob.

Homalothecium and *Palamocladium* share several morphological character states, such as dense terete foliage, narrowly triangular-lanceolate, deeply plicate leaves, relatively short laminal cells and a conspicuous alar cell region with small thick-walled quadrate alar cells, erect capsules in most species, and epiphytic and epilithic habitat preferences. However, molecular phylogenetic data (Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004) placed *Homalothecium* and *Palamocladium* in different

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subfamilies of the Brachytheciaceae: *Palamocladium* was resolved in the Eurhynchioideae, while *Homalothecium* was placed in the Homalothecioideae (Ignatov & Huttunen, 2002; Huttunen *et al.*, 2004).

In recent treatments the taxonomic position of *Homalothecium laevisetum* Sande Lac. has remained unsettled. The species was described by Sande Lacoste (1866) who placed it in the genus *Homalothecium* and compared it with *H. sericeum* (Hedw.) Schimp. *Homalothecium laevisetum* differs from other species in the genus by its temperate to tropical distribution, primarily in East Asia, and some morphological characters, such as a perfectly smooth seta, a hairy calyptra, and a reduced endostome (Hofmann, 1998). The species is morphologically variable and in a taxonomic revision of the East Asian Brachytheciaceae by Takaki (1955) and subsequent treatments in Japanese (Noguchi, 1991) and Chinese (Wang, 2008) moss floras two species were accepted, *H. laevisetum* and *H. leucodonticaule* (Müll. Hal.) Broth. In addition one more species, *H. celebesiae* (Müll. Hal.) Broth. has often been recognized in tropical Asia in Indonesia and Papua New Guinea (Brotherus, 1925; Enroth, 1993). However, in her revision of the genus *Homalothecium*, Hofmann (1998) concluded that the variation in Asian plants is so wide that no more than one species can be accepted, thus she synonymized both *H. celebesiae* and *H. leucodonticaule* with *H. laevisetum*.

In the first phylogenetic analyses *H. laevisetum* was resolved within the genus *Homalothecium* (Huttunen & Ignatov, 2004). However, in a molecular systematic study of *Homalothecium* (Huttunen *et al.*, 2008) the species appeared in the same subfamily as *Palamocladium*, which was revealed to be due to an erroneous ITS2 sequence (GenBank accession AF403616.1; now replaced with correct sequence data AF403616.2) in the first molecular systematic study. Thus far, taxonomic changes resulting from this new generic position of *H. laevisetum* have not been effected. In the present paper we aim to confirm the phylogenetic relationships of the species using both molecular and morphological data and to resolve the taxonomic position of the species.

MATERIAL AND METHODS

Taxon sampling included 53 accessions that belong to 37 species from the Brachytheciaceae subfamilies Brachythecioideae, Homalothecioideae, Helicodontioideae and Eurhynchioideae (Table 1; Ignatov & Huttunen, 2002). Earlier phylogenetic analysis of the Brachytheciaceae guided the taxon selection (Huttunen & Ignatov, 2004; Huttunen *et al.*, 2008). We aimed to include the closest relatives of *Homalothecium laevisetum* and taxa that were suggested to be closely related to it in earlier classifications. To confirm the phylogenetic relationships between *Palamocladium* and *H. laevisetum* and to test the monophyly of the morphologically diverse *Palamocladium leskeoides* (Hook.) E. Britton and *H. laevisetum*, we included several accession of these taxa, with

different morphological character state combinations and from different parts of the world.

A morphological data matrix was compiled for 76 characters using a morphological database by L. Hedenäs. The coding for each species is based on at least three herbarium specimens, mainly from S. The data matrix and descriptions of characters and their states are given in Appendix 1 (Supplementary material 1). Fifteen characters were continuous (characters 0-14 in Appendix 1) and 61 categorical variables (characters 15-75 in Appendix 1).

The molecular data consisted of five DNA sequence regions: four plastid regions, *rpl16*, *atpB-rbcL*, *trnD-T* and *trnL-F*, and a nuclear, ITS1-5.8S-ITS2. Laboratory work was mainly done in the Laboratory of Molecular Systematics, Swedish Museum of Natural History. Laboratory protocols and information about PCR primers are given in Huttunen & Ignatov (2010) and Huttunen *et al.* (2008).

Phylogenetic analyses. DNA sequence data were edited and aligned manually with PhyDE® v0.9971 (Müller *et al.*, 2005). Inversion events were included in the phylogenetic analyses by coding presence of inversion events as a binary data matrix. Due to possible phylogenetic information in substitution events in the inversion regions, inverted fragments were included in the analyses in the reverse complement form (Quandt *et al.*, 2003). Information in the indel events was also included in phylogenetic analyses as a binary matrix generated using simple indel coding (Simmons & Ochoterena, 2000) in the program SeqState (Müller, 2005).

Phylogenetic analyses were performed for two data sets. First, a molecular data set with 53 terminals was analyzed to test the species delimitation within *Palamocladium* and *Homalothecium laevisetum*. Phylogenetic analyses for 53-terminal data set were run with two optimality criteria: parsimony (MP) as implemented in the program TNT (Goloboff *et al.*, 2008), and maximum likelihood (ML), using the program RAXML (Stamatakis, 2006; Stamatakis *et al.*, 2008). With both methods analyses were performed both with and without the information in the indel events (Fig. 1).

The second data set comprised combined molecular and morphological data with 35 terminals, one accession per species (Fig. 2). Only parsimony analysis was performed with TNT which is able to handle continuous characters in combination with other types (DNA and categorical) of data.

All TNT analyses were run using the default setting in a new technology search (NTS) except that alignment gaps in DNA sequence data were always treated as missing data and the search was terminated after a minimum length tree was found five times. Bootstrap support (BS) for clades was calculated using 1000 bootstrap replications. Trees for bootstrapping were obtained from analysis similar to the original NTS for the most parsimonious tree.

RAxML analysis with the 53-terminal data set were run in CIPRES Science Gateway (Miller *et al.*, 2010). DNA sequence data was divided in analysis into five partitions following DNA sequence regions, *rpl16*, *atpB-rbcL*, *trnD-T*, *trnL-F*, and ITS1-5.8S-ITS2. We used rapid bootstrap analysis including a search for the tree with the best ML score (-fa). The bootstrapping step included 1000 iterations. The GTRgamma model was used for all DNA sequence partitions and the Lewis model with correction for ascertainment bias was applied for the binary coded indel data matrix.

Ancestral state reconstruction and synapomorphies for major clades. Ancestral character state reconstruction for morphological characters and search for synapomorphic character states were done with TNT using topology from the analysis of the 35-terminal data set (Fig. 2). In addition to morphological characters, information on habitat (character 76; Appendix 1) was compiled and ancestral character state reconstructed to show as background information for some morphological character state changes (Fig. 2b)

RESULTS

Molecular data

The aligned length of five sequenced regions was 3370 positions including 853 bp from ITS1-5.8S-ITS2 region, 700 bp from *rpl16*, 632 bp from *atpB-rbcL*, 745 bp from *trnD-T*, and 440 bp from *trnL-F*. In the *trnD-T* 47 bp were excluded from phylogenetic analysis including a 20 bp long poly-T repeat at the end of the *trnE-Y* spacer (see Shaw *et al.*, 2005; Huttunen & Ignatov, 2010) that hampered sequencing over the region. Additionally, a 6 bp long poly-T repeat and 21 bp region covering an inversion were excluded. In the ITS1-5.8S-ITS2 region 44 bp were excluded due to ambiguities in the alignment (40 bp) or because of poly-C repeat (4 bp). In plastid regions a 3 bp long poly-A repeat in *rpl16*, a 6 bp inversion region in the *trnL-F* spacer, and a 3 bp long poly-A repeat and a 4 bp long poly-T repeat in *atpB-rbcL* region were also excluded from all analyses. The total length of the alignment that was used in the phylogenetic analyses was thus 3264 bp including 626 positions from *atpB-rbcL*, 698 positions for *trnD-T*, 434 positions for *trnL-F*, 697 positions for *rpl16*, and 809 positions for the ITS1-5.8S-ITS2 region. In *rpl16* 15.6 % of the positions were variable and 8.0 % parsimony informative (PI), while in other regions these numbers were 15.2 % and 7.3 % for *trnD-T*, 10.4 % and 4.6 % for *trnL-F*, 11.2 % and 5.0 % for *atpB-rbcL*, and 22.3 % and 12.0 % for ITS1-5.8S-ITS2. Simple indel coding resulted in a data matrix with 240 characters, of which 37 characters were derived from *rpl16*, 31 from *trnD-T*, 11 from *trnL-F*, 17 bp from *atpB-rbcL*, and 144 from ITS1-5.8S-ITS2.

Phylogenetic relationships

Strict consensus topologies from parsimony analyses of the 53-terminal data set with and without indel data as well as topologies of best scoring ML trees are very

similar with only minor differences in branches lacking significant support. With both optimality criteria some nodes mainly within a *Plasteurhynchium* – *Palamocladium* clade and in *Homalothecium* are better resolved or have higher support in analyses including indel data (Fig. 1). The parsimony analysis with indel coding yielded 27 shortest trees with a length of 1235 steps. The analysis excluding indel coding resulted in 34 shortest trees with 861 steps.

Both analysis methods and all datasets suggested that all three subfamilies are monophyletic (Eurhynchioideae, maximum BS support both with MP and ML; Helicodontioideae, BS MP without/with indel data 99/99, ML without/with indel data 100/100 [first dataset/second dataset values]; Homalothecioideae, no significant support), as well as all included genera. The position of *Scleporodidium obtusifolium* (Mitt.) Kindb., that has tentatively been included in the subfamily Brachythecioideae (Ignatov & Huttunen, 2002), is in all analyses resolved as sister to a Eurhynchioideae + Helicodontioideae clade (BS: MP 84/52, ML 87/93). Within the Eurhynchioideae, generic relationships remain mostly unresolved, but *Homalothecium laevisetum* is resolved as sister to *Eurhynchium* Schimp. with high support (BS: MP 96/98, ML 98/99). A well-supported *Palamocladium* (BS: MP 84/96, ML 92/98) is found together with a monophyletic *Plasteurhynchium* M. Fleisch. ex Broth. which lacks significant support within a well-supported clade (BS: MP 84/89, ML 81/91). The Homalothecioideae includes a monophyletic *Brachytheciastrum* Ignatov & Huttunen (BS: MP 98/98, ML 99/100) and a *Homalothecium* clade (BS: MP 97/94, ML 100/100) that includes all *Homalothecium* species except *H. laevisetum* and *H. arenarium* (Lesq.) E. Lawton. The position of *H. arenarium* remains unsupported in all analyses based only on molecular data, and outside both the Homalothecioideae and the Eurhynchioideae + Helicodontioideae clade.

Parsimony analysis of the 35-terminal data set including morphological data and indel data resulted in one most parsimonious tree with a length of 1800.82¹ steps (Fig. 2). Support for most clades is lower than in the analysis based on the 53-terminal data set. Subfamilies Eurhynchioideae (BS 100) and Helicodontioideae (BS 100) are well supported, while in Homalothecioideae the only well-supported clade is *Brachytheciastrum* (BS 100). In the Eurhynchioideae, clades with high or moderate support include *Eurhynchium* (BS 81), *Palamocladium* (BS 94) and *Scorpiurium* Schimp. (BS 100). A close relationship of *Plasteurhynchium* and *Palamocladium* also gets significant support (BS 85). Relationships at the genus level are similar to the 53-terminal data set (Fig. 1). *Homalothecium arenarium* is, however, resolved within *Homalothecium* s. str. as sister to the rest of this genus, though without significant support.

¹ – tree length in TNT may be non-integer when continuous characters are analyzed.

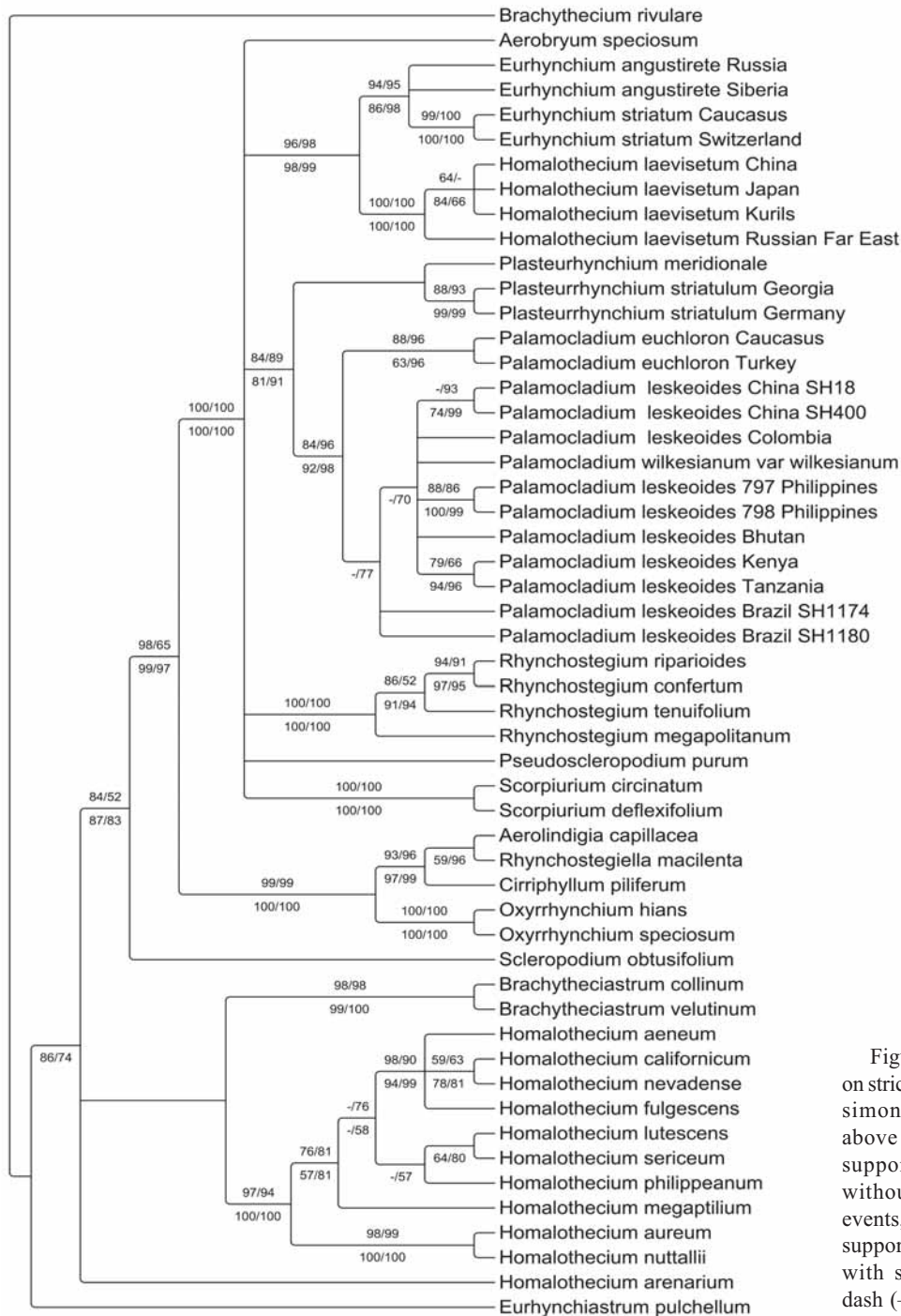


Figure 1. Phylogenetic tree based on strict consensus topology from parsimony analysis. Support values above branches indicate bootstrap support from parsimony analysis without/with sic coding for indel events, and below branch bootstrap support from ML analysis without/with sic coding for indel events; dash (-) indicates support < 50 %.

Ancestral state reconstruction and synapomorphies for major clades

Character states shared by *Homalothecium laevisetum* and the *Palamocladium* clade include only one sporophytic character, presence of reduced exostome PPL ridges. Analogous state changes in this character are concentrated in clades with epiphytic species (Fig. 2a).

The number of synapomorphic morphological character states for the major clades is low. Ancestral state reconstruction resolved a smooth seta (Fig. 2b) as a synapomorphy for the subfamily Eurhynchioideae and quad-

rate, rhombic or short rectangular alar cells (Fig. 2b) for the *Plasteurhynchium* – *Palamocladium* clade.

DISCUSSION

Our phylogeny resolves *Palamocladium* sister to a monophyletic *Plasteurhynchium*, while *Homalothecium laevisetum* is sister to a clade with *Eurhynchium angustirete* and *E. striatum* (i.e. *Eurhynchium* s. str., see Ignatov & Huttunen, 2002). The two clades, the *Plasteurhynchium* – *Palamocladium* clade and the *Eurhynchium* – *Homalothecium laevisetum* clade, share some similar trends in ecological, geographical and morphologi-

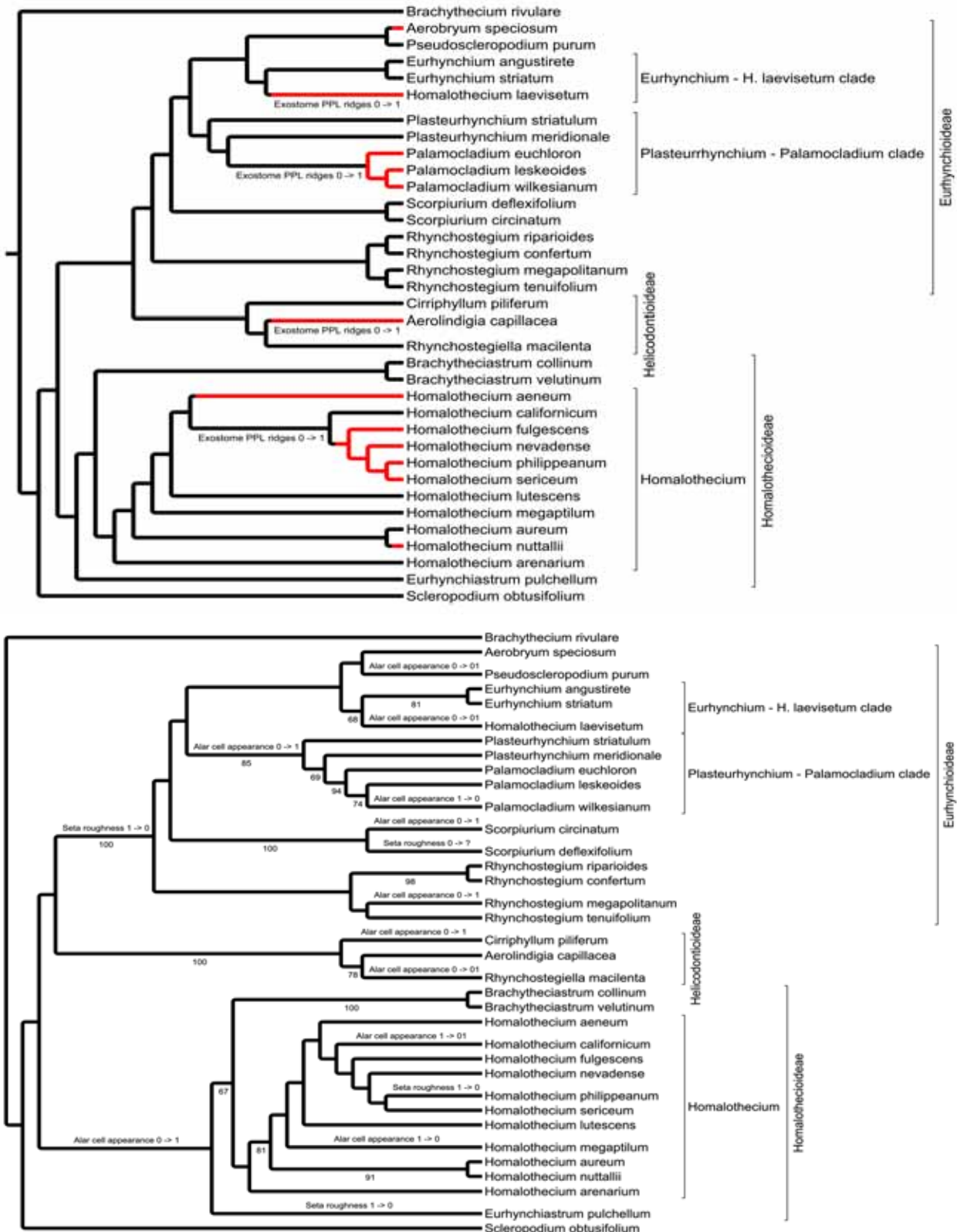


Figure 2. The single most parsimonious tree from analysis of combined molecular and morphological data. Bootstrap support for nodes with > 50 % support is presented below the branches. a) Ancestral character state reconstruction for preference of epiphytic habitats (red branches) and character state changes for a character state (exostome PPL ridges (0) normal, well developed or (1) reduced) that are shared by the *Eurhynchium* – *H. laevisetum* clade and the *Plasteurhynchium* – *Palamocladium* clade. b) Morphological synapomorphies of the Eurhynchioideae (seta roughness (0) smooth or (1) rough) and the *Palamocladium* – *Plasteurhynchium* clade (alar cells appearance (0) rectangular, elongate, or linear; (1) quadrate, rhombic, or short rectangular) with their character state changes along the branches.



Fig. 3. Habits of *Oticodium laevisetum*, from Kuril Islands (A), *Homalothecium sericeum*, Caucasus (B), *Eurhynchium striatum*, Caucasus (C) and *Palamocladium euchloron*, Caucasus (D).

cal evolution: the cool temperate genera *Plasteurhynchium* and *Eurhynchium*, with unspecialized morphology and growing on soil, rock and tree bases, are sister to the warm temperate to tropical taxa *Palamocladium* and *Homalothecium laevisetum*, respectively, which are both morphologically specialized epiphytes (Fig. 3). The distribution area of *Eurhynchium* concentrates to the western part of temperate Eurasia with only a few occurrences in the east where it is sympatric with the warm temperate to tropical *H. laevisetum* (Fig. 7). A similar pattern exists in the *Plasteurhynchium* – *Palamocladium* clade although the total distribution of the warm temperate to tropical *Palamocladium* species is much wider and pantropical (Hofmann, 1997).

Like at the family level in the Brachytheciaceae, epiphytism has evolved independently in several lineages within the subfamily Eurhynchioideae and in *Homalothecium* (Fig. 2a). The epiphytic *Palamocladium* and *H. laevisetum*, as well as epiphytic *Homalothecium* lineages, including *H. nuttallii*, *H. aeneum* and a *Homalothecium* crown clade with *H. fulgescens*, *H. nevadense*, *H. philippeanum* and *H. sericeum*, have several sporophytic characters such as reduced exostome, endostomial cil-

ia that are reduced or absent, and orthotropous capsules that are more frequently present in epiphytic species and which evolution is most likely associated with epiphytic habitats (Hedenäs, 2012, Huttunen *et al.*, 2004, 2012). However, despite shared overall habitus of species, *Palamocladium* and *H. laevisetum* share only one character state, presence of a reduced exostome ridges in the primary peristomial layer (PPL) (Fig. 2a, 4). Height of projecting trabecular varies even in species with reduced PPL, the most extreme cases occurring in epiphytic *Homalothecium* s.str. species. Reduced peristomes in general may show rather different character combinations in different lineages in Brachytheciaceae.

The repeated evolution of several character states makes it difficult to find morphological synapomorphies in many pleurocarpous taxa. According to our data, the only morphological synapomorphy for Eurhynchioideae is the smooth seta (Fig. 2b). The smooth seta in *Palamocladium* and *Homalothecium laevisetum* thus supports placement in the Eurhynchioideae, contrasting with the rough setae in most species of the Homalothecioideae, where only in *Homalothecium philippeanum* setae are smooth. The *Plasteurhynchium* – *Palamocladium* clade

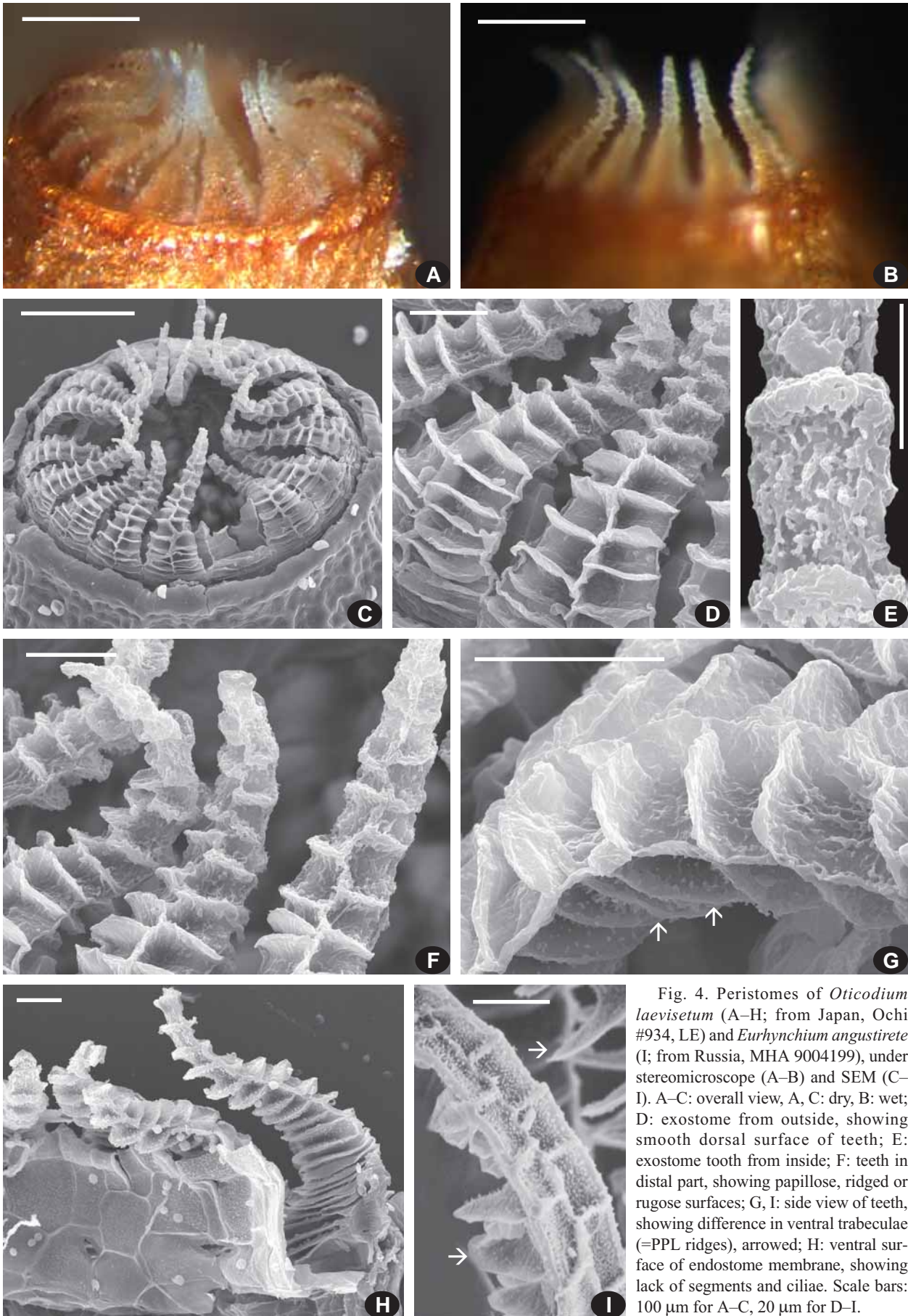


Fig. 4. Peristomes of *Oticodium laevisetum* (A–H; from Japan, Ochi #934, LE) and *Eurhynchium angustirete* (I; from Russia, MHA 9004199), under stereomicroscope (A–B) and SEM (C–I). A–C: overall view, A, C: dry, B: wet; D: exostome from outside, showing smooth dorsal surface of teeth; E: exostome tooth from inside; F: teeth in distal part, showing papillose, ridged or rugose surfaces; G, I: side view of teeth, showing difference in ventral trabeculae (=PPL ridges), arrowed; H: ventral surface of endostome membrane, showing lack of segments and cilia. Scale bars: 100 μm for A–C, 20 μm for D–I.

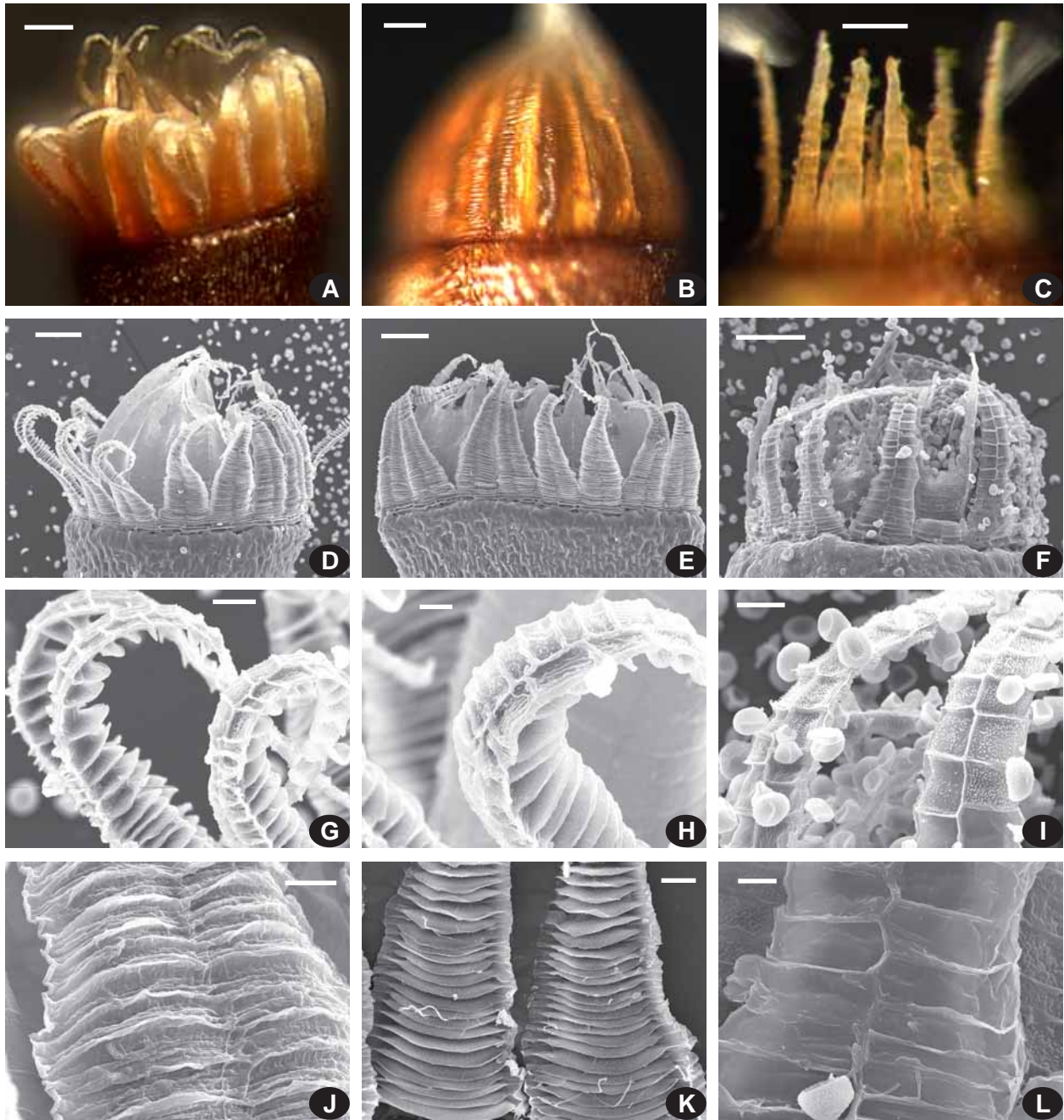


Fig. 5. Peristomes of *Palamocladium euchloron* (A–B, D–E, G–H, J–K; from Russia, Caucasus, MHA 9038527) and *Homalothecium philippeanum* (C, F, I, L; Russia, Caucasus, MHA9026760). Photos under stereomicroscope (A, dry, B–C, wet) and SEM (D–L); A–F: general views; G–H: side view, showing smooth ventral trabeculae and variously ornamented outer surface of distal part of teeth; I: exostome teeth in the middle, showing papillose distal part and smooth surface below; J: proximal part of tooth from outside, the surface smooth to rugose; K: proximal part of tooth from inside, showing densely arranged ventral trabeculae and wide membranaceous marginal zone; L: proximal part of tooth from outside, the surface smooth. Scale bars: 10 μm for A–F, 20 μm for G–L.

is also supported by a single synapomorphy, the rectangular, quadrate, or rhombic alar cells, while no synapomorphic morphological state was found for the *Eurhynchium* – *H. laevisetum* clade. In the original description of the subfamily Eurhynchioideae, the group was described as large plants with pale green to yellowish-green color and a characteristic, whitish color and silky gloss, cf. Fig. 3 (Ignatov & Huttunen, 2002). Axillary hairs are often long and their upper cells are more

strongly colored than the basal cells. The sexual condition in the Eurhynchioideae can be either autoicous (e.g. *Rhynchostegium*) or dioicous, but, similar to the Homalothecioideae, in the *H. laevisetum* – *Eurhynchium* and *Palamocladium* – *Plasteurhynchium* clades, all species are at least facultatively phyllo dioicous. The seta is always smooth, and the operculum has most often a sharply delimited beak. The peristome is usually perfect, but some epiphytic species in *Rhynchostegium* s. l. (*Eri-*

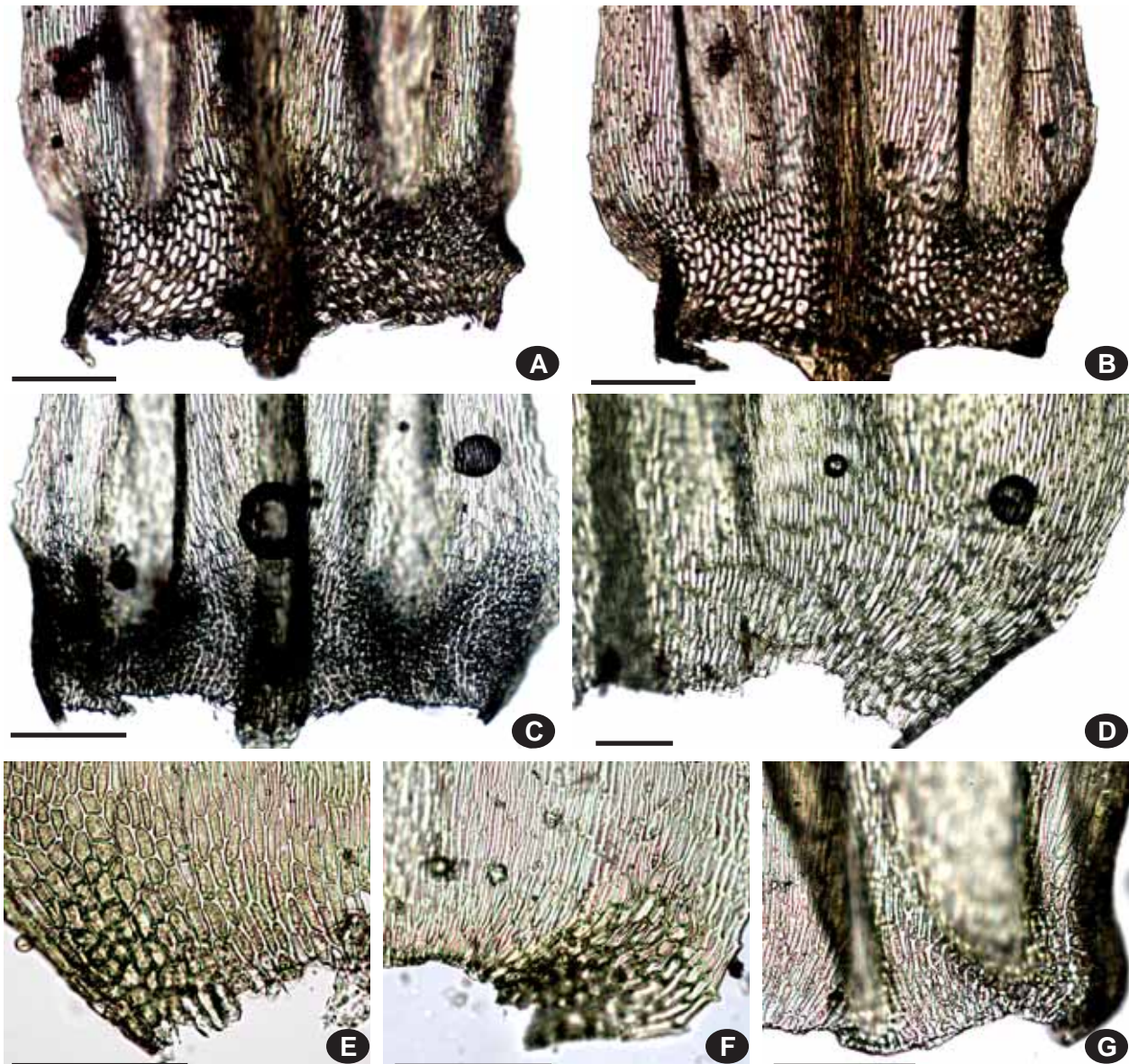


Fig. 7. Leaf bases of A–B: *Oticodium laevisetum* (Papua New Gunia, Streimann 23080, MHA 9054435), C: *Oticodium laevisetum* (Russia, MHA 9036174), D: *Eurhynchium angustirete* (Russia, MHA 9004199), E: *Palamocladium euchloron* (Russia, Caucasus, MHA 9038527); F: *Palamocladium leskeoides* (China, Sichuan, MHA 9051234); G: *Homalothecium philippeanum* (Russia, Caucasus, MHA 9026760) Scale bars: 100 μ m for all.

odon, *Eurhynchiella*) and *Palamocladium* have a rather strongly modified peristome structure. In the molecular data, the *Eurhynchium* – *H. laevisetum* clade shares a 19 bp long insertion in the *trnY-D* spacer of the *trnD-T* region.

Despite the large morphological variation within *Palamocladium leskeoides*, the species appears monophyletic but lacks significant support and includes the Hawaiian endemic *P. wilkesianum*. The position of *P. wilkesianum* should not be surprising; according to Hoffmann (1997), *P. leskeoides* and *P. wilkesianum* cannot be distinguished from each other with certainty based on gametophytic characters. Sporophytic characters differentiating them include lack of cross-striolation at the base

of the exostome teeth and 3–5 rows of rectangular exothecial cells below the capsule mouth in *P. wilkesianum*, contrasting with cross-striolate bases of exostome teeth and only 2–3 rows of rectangular exothecial cells in *P. leskeoides* (Hoffman, 1997). Branch lengths within the *P. leskeoides* clade are extremely short, and other methods than DNA sequence data are needed to study whether *P. wilkesianum* and taxa that have earlier been distinguished within the *P. leskeoides*, should be recognized at the species level. In early treatments of *P. leskeoides* s.l., the species delimitations followed geographical distributions. The taxon was thus split into the East Asiatic *P. nilgheriense*, the African *P. sericeum* and the American *P. leskeoides* s.str. The present results agree to a cer-

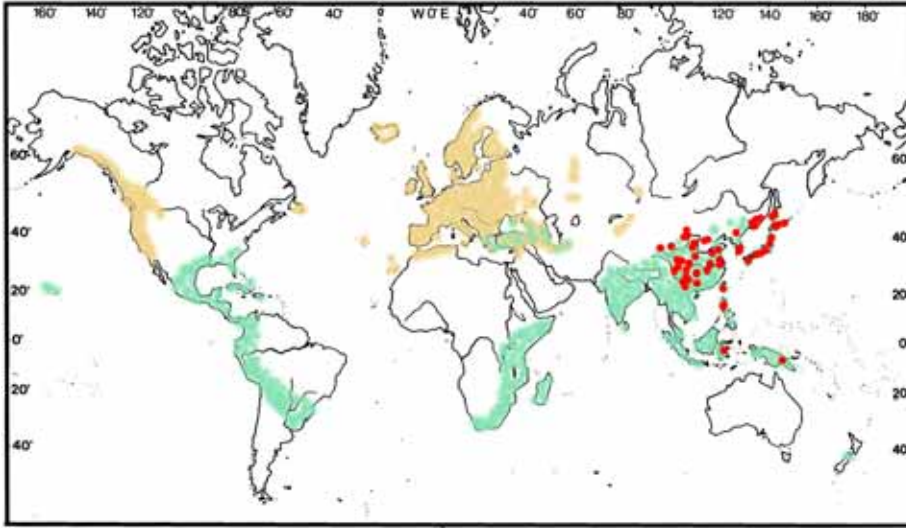


Fig. 7. Distribution of *Oticodinium* (red dots). Brown shading indicates *Homalothecium* species, and green one – *Palamocladium* species. Expanded from Hofmann (1997, 1998), with addition from Wang (2008), and database of moss Flora of Russia (<http://arctoa.ru/Flora/basa.php>).

tain extent with these geographic patterns (Fig. 1), although with low support for both the (1) African *P. leskeoides*, and (2) African + Asian *P. leskeoides* + *P. wilkesianum* clades. This lends support to Hofmann's (1997) synonymization of *P. nilgheriense* and *P. sericeum* with *P. leskeoides*.

Homalothecium laevisetum differs from other *Homalothecium* species by its strongly modified peristome with high dorsal trabeculae, endostome almost lacking not only ciliae but also segments (cf. Figs. 4–5), a smooth seta, hairy calyptra, and larger area of more homogeneous cells across the whole leaf base (Fig. 6). The plants lack the golden green color that is typical for other *Homalothecium* species (Fig. 3). The distribution of the eleven species in *Homalothecium* s.str. covers western parts of both the Palearctic (non-tropical Eurasia and North Africa) and North America (Fig. 7) while the distribution of *H. laevisetum* is restricted to the eastern parts of subtropical and tropical Asia. The only area where *Homalothecium* occurs in an eastern part of continent is Newfoundland, with populations of *Homalothecium sericeum* that are putatively introduced from Europe (Ignatov, 2014). On the other hand, ampho-Atlantic distributions occur in a number of other bryophyte taxa (Schuster, 1983; Hedenäs, 2008), suggesting that such distributions have in most cases natural explanations. Based on the position of the species in the molecular analyses, as well as morphological and biogeographical differences, we suggest to transfer *Homalothecium laevisetum* to another genus, *Oticodinium* (Müll. Hal.) Kindb. (see below).

TAXONOMY

Genus *Oticodinium* (Müll. Hal.) Kindb., Enum. Bryin. Exot. 27. 1888.

Hypnum sect. *Oticodinium* Müll. Hal., Ber. Thätigk. St. Gallischen Naturwiss. Ges., 1876–77: 303. 1978.

Type: *Hypnum celebesiae* Müll. Hal. = *Oticodinium celebesiae* (Müll. Hal.) Kindb.

Oticodinium laevisetum (Sande Lac.) comb. nov.

Basionym: *Homalothecium laevisetum* Sande Lac. in

Miquel, Annales Musei Botanici Lugduno-Batavi 2: 298. pl. 9. 1866. Type: Japonia, leg. Textor (Lectotype in L.).

Hypnum celebesiae Müll. Hal., Linnea 39:469. 1875 (Lectotype in L!, selected in Hofmann, 1998).

Other species included: none.

In early treatments *Homalothecium celebesiae* and *H. laevisetum* have been distinguished from each other based on thicker and distinctly porose cell walls at the base of the leaf (Piippo, 1987; Enroth, 1993; Hofmann, 1998; Fig. 6). However, Hofmann (1998) transferred the name *H. celebesiae* under synonymy of *H. laevisetum* because although these characters show a wide variation and the differences in between the specimens do not allow distinguishing the two taxa.

Unfortunately, we were unable to find fresh material of typical *H. celebesiae* and could not test phylogenetic relationships of the two morphotypes. As morphologically diverse samples of populations from different parts of the distribution area of *H. laevisetum* form a monophyletic unit (Fig. 1), we feel that using the genus name *Oticodinium* for this taxon is still safe.

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Table 1. Voucher specimens used for molecular studies and GenBank/EMBL accession numbers for sequences.

Species	Sample N	<i>rpl16</i>	<i>atpB-rbcL</i>	<i>trnD-T</i>	<i>trnL-F</i>	ITS1-5.8S-ITS2	Voucher specimen (Herbarium: herbarium id)
<i>Aerobryum speciosum</i> (Doz. & Molk.) Doz. & Molk.	SH13	MK138456	MK138422	FM244767	AF397780	AF403619	China, Hunan prov., T. Koponen & al. 52753, 9.X.1997 (H) & FM242657
<i>Aerolindigia capillacea</i> (Hornch.) Menzel	SH31	-	MK138423	FM244763	AY044072	AF395634	Ecuador, Loja prov., D. H. Norris 92175 & M. Bolivar, & DQ200070 18.XII.1997 (H)
<i>Brachytheclastrum collinum</i> (Schleich. ex Müll. Hal.) Ignatov & Huttunen	SH232	EF531025	EF530960	MK138389	DQ336923	DQ200954	Russia, Kamchatka, Czemyadievk #53, 21.VII.2003 (MHA) & DQ200071
<i>B. velutinum</i> (Hedw.) Ignatov & Huttunen	SH78	EF531033	EF530965	MK138390	AF397832	AF403667	Finland, Karjalohja, M. Kirikki, 23.VIII.1988 (H) & EF585538
<i>Brachytheclium rivulare</i> Schimp.	SH131	EF531018	EF530950	FM244742	AF397866	FM161081	Finland, Hyrynsalmi, A. Parnela, 19.V.1996 (H)
<i>Cirriphyllum piliferum</i> (Hedw.) Grout	SH33	EF531017	EF530949	FM244761	AF397799	AF403608	Finland, Lohja, T. Koponen & S. Huttunen 1324, 24.V.1999 (H) & DQ200081
<i>Eurhynchiastrum pulchellum</i> (Hedw.) Ignatov & Huttunen	SH34	EF531024	EF530956	-	AY044069	FM161101	Finland, Lohja, T. Koponen & S. Huttunen 1321, 24.V.1999 (H)
<i>Eurhynchium angustirete</i> (Broth.) T.Kop.	SH66	MK138457	MK138424	FM244771	AF397825	AF403621	Russia, Moscow prov., M. Ignatov, 3.VII.1998 (MHA) & DQ200086
<i>E. angustirete</i>	SH795	MK138458	MK138425	MK138391	MK138488	MK120836	Russia, South Siberia, Kemerovo Prov., O. Yu. Pisarenko 22.VII.2007 (S; B158498)
<i>E. striatum</i> (Schreb. ex Hedw.) Schimp.	SH147	MK138460	MK138427	FM244772	AY184788	FM242661	Russia, Caucasus, Makridin, 13.VII.1998 (MHA)
<i>E. striatum</i>	SH796	MK138461	MK138428	MK138392	MK138489	MK120837	Switzerland, Kt. Tessin, L. Hedenäs 14.IV.2006 (S; B111448)
<i>Homalothecium aeneum</i> (Mitt.) Lawton	SH349	EF531044	EF530986	MK138393	MK138490	EF617574	Canada, British Columbia, W. B. Schofield 117349, 18.V.2001 (UBC; B186983)
<i>H. arenarium</i> (Lesq.) E. Lawton	SH343	EF531034	EF530966	MK138394	MK138491	EF617554	Canada, British Columbia, P. Henderson 12, 22.IV.2003 (UBC; B185615)
<i>H. aureum</i> (Spruce) H. Rob.	SH302	EF531082	EF530970	MK138395	MK138492	EF617557	Cyprus, Trodos, L. Hedenäs, 29.XI.1995 (S; B106846)
<i>H. californicum</i> Hedenäs & al.	SH432	EU684459	EU684452	-	EU697738	EU697738	USA, California, J. R. Shevock 29193, 28.X.2006 (S; B148197)
<i>H. fulgens</i> (Mitt. ex Müll. Hal.) A. Jaeger	SH363	EF531039	EF530979	MK138396	EF531039	EF530979	Canada, British Columbia, W. B. Schofield & R. J. Belland 93259, 18.IV.1989 (UCB)
<i>Homalothecium laevisetum</i> Sunde Lac.	SH792	MK138462	MK138429	MK138397	MK138493	MK120838	Japan, Tochigi Prov., M. Higuchi 1208, 5.V.1999 (S; B138825)
<i>H. laevisetum</i>	SH808	MK138464	MK138431	MK138399	MK138495	MK120840	Russia, Primorsky territory, M. Ignatov & E. Ignatov #06-2953, 29.IX.2006 (MHA)
<i>H. laevisetum</i>	SH809	MK138463	MK138430	MK138398	MK138494	MK120839	Russia, Kuril Islands, M. Ignatov #06-1870, 27.VII.2006 (MHA)
<i>H. laevisetum</i>	SH67	EF531023	EF530955	FM244773	AF397820	FM242663	China, Hunan prov., T. Koponen & al. 54066, 30.VII.1998 (H)
<i>H. lutescens</i> (Hedw.) H. Rob.	SH321	EF531050	EF530973	MK138400	MK138496	EF617559	Denmark, Jylland, L. Hedenäs, 20.IV.2005 (S; B101271)
<i>H. megaptilium</i> (Sullivant) Schofield	SH344	EF531036	EF531014	MK138401	MK138497	EF617568	U.S.A., Washington, W. B. Schofield 119346, 11.IV.2002 (UBC)
<i>H. nevadense</i> (Lesq.) Renaud & Cardot	SH355	EF531047	EF530988	MK138402	MK138498	EF617576	U.S.A., Idaho, W. B. Schofield 118833, 25.IX.2001 (UBC; B189551)
<i>H. nuttallii</i> (Wilson) A. Jaeger	SH362	EF531078	EF530991	MK138403	MK138499	EF617579	Canada, British Columbia, W. B. Schofield & al. 87599, 26.III.1987 (UBC)
<i>H. philippianum</i> (Spruce) Schimp.	SH310	EF531074	EF531000	MK138404	MK138500	EF617584	Kazakhstan, Alma Ata, B. Allen 10715, 17.VII.1991 (S; B106957)
<i>H. sericeum</i> (Hedw.) Schimp.	SH319	EF531066	EF531012	MK138405	MK138501	EF617595	France, Cabernet, G. Een, 3.X.1998 (S; B107454)
<i>Oxyrrhynchium hians</i> (Hedw.) Loeske	SH1140	MK138465	MK138432	MK138406	MK138502	MK120841	Finland, Turku, J. Issakainen & al., X.2011 (TUR; TUR 120943)
<i>O. speciosum</i> (Brid.) Wamst.	SH1097	MK138466	MK138433	MK138407	MK138503	MK120842	Sweden, Gotland, K. Hylander 2992, 26.X.2002 (S; B107577)
<i>Palamocladium euchloron</i> (Bruch ex Müll. Hal.) Wijk & Margad.	SH93	-	-	FM244774	AF397851	FM242672	Russia, Caucasus, M. Ignatov, 23.VIII.1999 (MHA)
<i>P. euchloron</i>	SH407	MK138467	MK138434	MK138408	MK138504	MK120843	Turkey, Trabzon prov., E. Nyholm 14782, 8.X.1982 (S; B101851)
<i>P. leskeoides</i> (Hook.) Britt.	SH1180	MK138476	MK138443	MK138416	MK138512	MK120851	Brasil, Parana, D. F. Peralta & al. 12710, 17.XI.2012 (TUR; TUR 118674)
<i>P. leskeoides</i>	SH1174	MK138475	MK138442	MK138415	MK138511	MK120850	Brasil, Rio Grande do Sul, D. F. Peralta 10470, 14.IV.2010 (TUR; TUR 118683)
<i>P. leskeoides</i>	SH18	MK138468	MK138435	FM244775	AF397791	FM242673	China, Hunan prov., T. Koponen & al. 52596, 10.X.1997 (H)
<i>P. leskeoides</i>	SH400	MK138469	MK138436	MK138409	MK138505	MK120844	China, Hunan prov., T. Koponen & al. 51817 (H)
<i>P. leskeoides</i>	SH403	MK138470	MK138437	MK138410	MK138506	MK120845	Colombia, Norte de Santander, S. P. Churchill & al., 24.I.1995 (S)

continued on next page

Table 1 (cont.). Voucher specimens used for molecular studies and GenBank/EMBL accession numbers for sequences.

<i>P. lamocladium leskeoides</i> (Hook.) Britt.	OK797	MK138472	MK138439	MK138412	MK138508	MK120847	Philippines, Mindanao prov., F. Schumm & U. Uwe Schwarz 4578, 10.VIII.1999 (MHA)
<i>P. leskeoides</i>	OK798	MK138473	MK138440	MK138413	MK138509	MK120848	Philippines Mindanao prov., F. Schumm & U. Uwe Schwarz 4579, 10.VIII.1999 (MHA)
<i>P. leskeoides</i>	OK800	MK138474	MK138441	MK138414	MK138510	MK120849	Bhutan, G. & S. Miehle 00-086-02, 2000 (MHA)
<i>P. leskeoides</i>	SH788	MK138477	MK138444	MK138417	MK138513	MK120852	Kenya, Mount Elgon National Park, T. Pocs & al. 9211/BV, 11-27.I.1992 (H; H3204174)
<i>P. leskeoides</i>	SH789	MK138478	MK138445	MK138418	MK138514	MK120853	Tanzania, Nguru Mountains, G. Kis & T. Pocs 9105/B, 30.I.1991 (H)
<i>P. wilkxstanum</i> (Sull.) Müll. Hal.	SH408	MK138471	MK138438	MK138411	MK138507	MK120846	Hawaii, Oahu, W. J. Hoe 3336, 2.I.1975 (S)
<i>Plasteurhynchium meridionale</i> (Schimp.) M.Fleisch.	SH410	MK138459	MK138426	FM244770	FM242060	FM242660	France, Alpes Maritimes, G. & P. Een, 26.IX.2001 (S; B62881)
<i>P. striatulum</i> (Spruce) Schimp.	SH153	MK138479	MK138446	FM244776	AY184792	FM242656	Georgia, Abkhazia, M. Ignatov, 1.VIII.1987 (MHA)
<i>P. striatulum</i>	SH411	MK138480	MK138447	MK138419	MK138515	-	Germany, Baden-Württemberg, L. Hedenäs, 17.IV.1998 (S; B6358)
<i>Pseudoxleropodium purum</i> (Hedw.) M.Fleisch	SH21	MK138482	MK138449	FM244768	AF397797	FM242678	Czech Republic, Central Bohemia, J. Vana & J. Enroth, 30.IV.1999 (H)
<i>Rhynchostegiella macilenta</i> (Renauld & Cardot) Cardot	SH101	MK138483	FJ262464	FM244758	AF397781	AF403570	Portugal, Madeira, L. Hedenäs, 13.V.1993 (S; B4503)
<i>Rhynchostegium confertum</i> (Dicks.) Bruch & al.	SH29	-	MK138450	FM244795	AF397837	AF403622	Georgia, Caucasus, M. Ignatov, 27.VIII.1987 (MHA)
<i>R. megapolitanum</i> (Blandow ex F. Weber & D. Mohr) Schimp.	SH388	MK138484	MK138451	FM244810	FM242078	FM242692	Portugal, Alentejo Baixo, G. & P. Een, March 18.III.1999 (S; B18444)
<i>R. riparioides</i> (Hedw.) Dixon	SH220	MK138481	MK138448	FM244783	DQ336931	DQ200969	Finland, S. Huttunen 1683, 29.VIII.2002 (H)
<i>R. tenuifolium</i> (Hedw.) Reichardt	SH335	MK138485	MK138452	FM244816	FM242080	FM242694	Australia, Australian Capital Territory, H. Streimann 50179, 20.X.1992 (H)
<i>Scleropodium obtusifolium</i> (Brid.) L.	SH40	-	MK138453	MK138420	AF397793	AF403615	USA, California, M. Ignatov & D. H. Norris, 13.VIII.1989 (MHA)
<i>Scorpiurium circinnatum</i> (Brid.) M.Fleisch.	SH354	MK138486	MK138454	FM244769	FM242081	FM242695	Portugal, Coimbra, L. Hedenäs, 22.IX.2000 (S; B44524)
<i>S. deflexifolium</i> (Solms.) M.Fleisch. & Loeske	SH102	MK138487	MK138455	MK138421	AF397844	AF403599	Portugal, Madeira, L. Hedenäs & I. Bisang, 21.XI.1999 (S; B22455)