

Phylogeny and morphological evolution of *Macrothamnium* M. Fleisch. and related taxa (Bryopsida: Hypnaceae)

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(Received February 27, 1995; Accepted June 5, 1995)

Abstract. Three species of *Macrothamnium* M. Fleisch., two species of *Leptohyphenium* Schwaegr., two species of *Leptocladia* M. Fleisch., and one species of *Orontobryum* M. Fleisch. were revised. *Macrothamnium submacrocarpum* Renauld & Cardot and *M. longirostre* Dix. were synonymized with *M. macrocarpum* (Reinw. & Hornsch.) M. Fleisch. *Macrothamnium hylocomioides* M. Fleisch. and *Chaetomitriopsis diversifolia* Zanten were considered identical to *M. javense* M. Fleisch. A new combination, *Hypnum flagellaris* (T. J. Kop. & D. H. Norris) T.Y. Chiang, was proposed and excluded from genus *Leptocladia*. The phylogeny of *Macrothamnium* and the related genera was reconstructed based on ontogenetic transformations of paraphyllia, axillary hairs, central strand, and other morphological characters. Whole ontogenetic transformations, instead of instantaneous stages, were recognized as characters and polarized by outgroup comparison. To test the phylogenetic relationship (familial position), *Hypnum lindbergii* Mitt. and *Gollania ruginosa* (Mitt.) Broth. of the Hypnaceae and *Hylocomium splendens* (Hedw.) B.S.G. and *Loeskeobryum cavifolium* (Lac.) M. Fleisch. of Hylocomiaceae were chosen as outgroups. The monophyly of the clade of *Macrothamnium*, *Leptohyphenium*, and *Orontobryum* was supported, with a bootstrapping value of 96%, and was characterized by sharing regularly pinnate branching pattern, amplified costa, and a lack of foliose pseudoparaphyllia, whereas *Macrothamnium* appeared to be a paraphyletic group, in which *M. leptohyphenioides* Nog. is more related to *Leptohyphenium* than it is to any other species of *Macrothamnium*. The three genera are more related to the Hypnaceae than to the Hylocomiaceae. In contrast, *Leptocladia* appears to be a genus of Hylocomiaceae. Patterson's tests were applied to the homology of the horn-type paraphyllia of *Hylocomium splendens* and *Loeskeobryum cavifolium*, and the foliose-type paraphyllia of *Orontobryum hookeri*. They passed the similarity and conjunction tests, but failed the congruence test. This suggests that the two types of paraphyllia are homoplastic—that is, they evolved independently rather than being derived from a most recent ancestor.

Keywords: Homology; *Macrothamnium*; Monophyly; Ontogenetic transformations; Paraphyllia; Patterson's three tests; Phyllocladous.

Introduction

The genera *Macrothamnium*, *Leptocladia*, *Leptohyphenium*, and *Orontobryum* are distributed mainly in the montane regions of southeastern Asia, with one exception—*Leptohyphenium tenue* (Hook.) Schwaegr., which was reported in the New World (Mexico) (Rohrer, 1985b, 1986). According to the fossil record of a *Macrothamnium* sp. found in Poland, the origin of the taxa can be traced to the Miocene (Miller, 1984).

The close relationship of *Macrothamnium*, *Leptohyphenium*, and *Orontobryum* has been interpreted in Rohrer's cladistic study on the Hylocomiaceae (Rohrer, 1985a), based on eighteen morphological characters. He recognized *Leptocladia* as a genus more distantly related to the above taxa, although many other bryologists had synonymized it either to *Leptohyphenium* (Andrews, 1954) or to *Macrothamnium* (Noguchi, 1972a).

The taxonomic position of the taxa is a controversial issue. There has been conjecture about the familial position of *Macrothamnium*, *Leptocladia*, *Leptohyphenium*, and *Orontobryum*. Rohrer (1985b) recognized twelve genera, including the above four taxa, in the Hylocomiaceae,

defined by weft growth-form. In delimiting the genera of the Hypnaceae, Nishimura et al. (1984) adopted Andrews' and Noguchi's concepts, and classified *Macrothamnium*, *Leptocladia*, and *Leptohyphenium* as Hypnaceae and *Orontobryum* as Hylocomiaceae by using the presence or absence of paraphyllia to distinguish them.

Buck and Vitt (1986) criticized the sole use of paraphyllia in defining the Hylocomiaceae as illogical. In their so-called 'pseudo-cladistic analysis', which was performed by arbitrary and empirical interpretation of morphological characters and taxonomic relationships of pleurocarpous mosses, they characterized the Hylocomiaceae by serrate leaf-margins, amplified costa, and reticulate exostome ornamentation. They classified *Macrothamnium*, *Leptocladia*, *Leptohyphenium*, and *Orontobryum* as Hylocomiaceae.

Buck and Crum (1990), in an evaluation of familial limits of Thuidiaceae and Leskeaceae, re-emphasized paraphyllia in defining the Hylocomiaceae and transferred genera *Hylocomiopsis* and *Actinotuidium* into the Hylocomiaceae. This classification has increased the complexity of the circumscription of the Hylocomiaceae and related families.

Nishimura et al. (1984) and Buck and Crum (1990) suggest that paraphyllia in the Hylocomiaceae is homologous and useful for classification, but Buck and Vitt (1986) and Rohrer (1985a) describe the homology as false. In my opinion, the homology remains unproven. To test it, I studied the ontogeny of paraphyllia in this group and conducted a cladistic analysis.

In this paper, I focus on the phylogenetic reconstruction of *Macrothamnium*, *Leptohyemium*, *Orontobryum*, and *Leptocladia*. I adopt the character concept of Chiang and Larson (1995), in which the whole ontogenetic transformation is recognized, rather than just the instantaneous characters of the adult-stage. The monophyly of the taxa is tested by cladistic analysis and statistical tests.

Macrothamnium, *Leptocladia*, *Leptohyemium*, and *Orontobryum* share several morphological characters—they lack foliose pseudoparaphyllia and have branching patterns and serrate leaf-margins. Rohrer (1985b) recognized five species in *Macrothamnium*, two taxa in *Leptocladia*, two species in *Leptohyemium*, and one taxon in *Orontobryum*. Koponen and Norris (1985) published a new species of *Leptocladia*—*L. flagellaris*. Reviews of taxonomic history can be consulted in Noguchi (1972a, b) and Rohrer (1985b).

Phylogenetic Analyses

Ingroup and Outgroup

Three species of *Macrothamnium*, two species of *Leptohyemium*, two species of *Leptocladia*, and one species of *Orontobryum* were examined. To polarize the characters more precisely, *Hypnum lindbergii* and *Gollania ruginosa* of the Hypnaceae and *Hylocomium splendens* and *Loeskeobryum cavifolium* of the Hylocomiaceae were chosen as outgroups (Appendix 1).

The specimens deposited in the herbaria of Missouri Botanical Garden (MO), the British Museum (BM), Farlow Herbarium (FH), Hattori Botanical Laboratory (NICH),

Leiden (L), and Hiroshima University (HIRO) were examined.

Characters Examined

Twenty-six characters were included in this analysis. All possible characters were studied, except for peristomes, which can be observed only in culture. Not all characters transform; the characters for which developmental changes were described are paraphyllia, central strand, and axillary hairs. The ontogenetic transformations were studied and sequenced by observing different stages in individuals—from stem apices to mature parts with inflorescences. The initial ontogenetic stage (usually of a single cell) was examined at the apical, meristematic cells of young innovation. The series of transformations was interpreted based on the principle of ontogenetic change in structure from simple to complicated, in terms of cell number or branching pattern.

The concept of character used in this paper primarily follows that of Chiang and Larson (1995), in which the whole transformation, rather than individual stages (Mishler and de Luna, 1991) was recognized as characters. Character states were polarized by outgroup comparison (Maddison et al., 1984) based on the genera *Hypnum*, *Gollania*, *Hylocomium*, and *Loeskeobryum* (Table 1). One of the characters used in Rohrer's (1985a) analysis—life-form—is not included in this study, because it is a subjective classification by bryologists. For example, Crum and Anderson (1981) say that the plants of *Hylocomium splendens* grow in loose mats, and those of *Rhytidium ruginosa* grow in tufts, whereas Rohrer (1985a) describes the life-form of both taxa as wefts. According to my own observation, there is no clear-cut boundary between weft and mat life-forms. The characters included in this analysis and the polarization of character states follow:

1. Paraphyllia: Paraphyllia are absent (state 3) in most taxa of *Macrothamnium* complex and the Hypnaceae.

Table 1. Distribution and polarization of characters and character-state for *Macrothamnium* complex and outgroups in cladistic analyses.

Taxa characters	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
<i>Gollania ruginosa</i>	3	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	1	0	0	0
<i>Hypnum lindbergii</i>	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	1	0	1
<i>Hylocomium splendens</i>	1	2	2	1	0	0	1	0	0	0	0	2	0	0	1	0	2	0	1	1	0	0	0	0	0	1
<i>Loeskeobryum cavifolium</i>	0	2	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1
<i>Macrothamnium macrocarpum</i>	3	2	0	1	0	0	0	1	0	0	0	1	0	0	2	2	3	0	2	1	1	0	1	1	0	1
<i>M. javense</i>	3	2	0	1	0	0	0	1	0	0	0	1	0	0	2	2	3	1	2	1	1	0	1	1	0	1
<i>M. leptohyemnioides</i>	3	2	0	1	1	1	0	1	1	2	0	1	0	0	2	2	3	0	2	1	1	0	1	1	1	1
<i>Leptohyemium tenue</i>	3	2	0	1	1	1	1	2	2	2	1	1	0	0	2	2	3	0	0	1	0	0	1	1	1	1
<i>L. hokinense</i>	3	2	0	1	1	1	*	2	2	2	1	0	0	0	2	2	3	0	1	1	0	0	1	1	1	1
<i>Orontobryum hookeri</i>	2	1	0	0	1	1	0	1	2	2	1	1	0	0	0	2	1	0	2	1	1	0	1	1	2	1
<i>Leptocladia psilura</i>	3	2	2	1	0	1	1	1	0	1	0	0	1	1	3	2	0	0	0	1	0	1	1	1	0	1
<i>L. delicatula</i>	3	2	1	1	0	1	1	1	0	1	0	0	0	1	3	2	3	0	0	1	0	1	1	1	0	1

(* data not available).

Three types of paraphyllia—ox-horn type (state **0**), deer-horn type (state **1**), and foliose type (state **2**)—are present in *Loeskeobryum*, *Hylocomium*, and *Orontobryum* respectively.

2. Pseudoparaphyllia: Pseudoparaphyllia are not differentiated (state **2**) in most taxa of *Macrothamnium* complex and the Hylocomiaceae. A foliose type (state **0**) occurs in the Hypnaceae, i.e. *Hypnum* and *Gollania*. *Orontobryum* has pseudoparaphyllia of ‘curious leaf’ type (Noguchi, 1972b) (state **1**).

3. Central strand of stems and branches: Central strands are absent (state **2**) in *Hylocomium* and *Leptocladiaella psilura*. According to the timing of differentiation in the stem, two types can be observed: early type (state **0**) in the Hypnaceae and most taxa of *Macrothamnium* complex and late type (state **1**) in *Loeskeobryum* and *Leptocladiaella delicatula*.

4. Growth form: *Orontobryum*, *Hypnum*, and *Gollania* have monopodial (state **0**) growth-form. In contrast, other taxa in this study have sympodial (state **1**) growth-form.

5. Capsule inclination: Capsules are inclined or subinclined (state **0**) in most taxa and the outgroup. Erect capsules (state **1**) were observed in *Macrothamnium leptohymenioides*, *Leptohymenium*, and *Orontobryum*.

6. Annulus: Annulus are absent (state **1**) in *Leptocladiaella*, *Leptohymenium*, *Orontobryum*, and *Macrothamnium leptohymenioides*, and are differentiated (state **0**) in other taxa.

7. Operculum: Conic operculum (state **0**) was observed in *Macrothamnium*, *Orontobryum*, and the Hypnaceae. Rostrate operculum (state **1**) occurs in *Leptohymenium*, *Leptocladiaella*, and the Hylocomiaceae.

8. Exostome ornamentation: Three types of ornamentation on exostome were observed: reticulate type (state **0**) in *Hylocomium*; cross-striate type (state **1**) in *Gollania*, *Hypnum*, *Loeskeobryum*, *Macrothamnium*, *Leptocladiaella*, and *Orontobryum*; and smooth type (state **2**) in *Leptohymenium*.

9. Segments of endostome: Broad segments with perforations (state **0**) were observed in *Macrothamnium macrocarpum*, *M. javense*, *Leptocladiaella*, and four outgroup taxa; linear segments with perforations (state **1**) occur in *M. leptohymenioides*; and imperforate segments (state **2**), often poorly developed, were observed in *Leptohymenium* and *Orontobryum*.

10. Cilia: In most taxa, endostome are well differentiated, with more than three cilia (state **0**) in each capsule. One or two cilia (state **1**) were observed in *Leptocladiaella*. Cilia are not differentiated in *Orontobryum* and *Leptohymenium* (state **2**).

11. Stem- and branch-leaves: Stem- and branch-leaves are differentiated (state **0**) in most ingroup taxa and four outgroup taxa, and are not differentiated (state **1**) in *Leptohymenium* and *Orontobryum*.

12. Apex of stem-leaf: Apex of stem-leaf is tapering (state **0**) in *Gollania*, *Hypnum*, *Loeskeobryum*,

Leptocladiaella, and *Leptohymenium hokinense*. Apiculate apices (state **1**) of stem-leaves were observed in *Macrothamnium*, *Orontobryum*, and *Leptohymenium tenue*. In contrast, crimped apices (state **2**) of stem-leaves occur in *Hylocomium*.

13. Costa number of branch-leaf: Most taxa have double costae (state **0**) in branch-leaf. In *Leptocladiaella psilura*, costae are forked (state **1**).

14. Costal spine: Costal spines were observed (state **1**) on leaves of *Leptocladiaella*. In most taxa, costal spines are not differentiated (state **0**).

15. Cell papillosity: Cell walls are smooth (state **0**) in *Hypnum*, *Loeskeobryum*, and *Orontobryum*. In *Gollania*, *Macrothamnium*, and *Leptohymenium*, cell ends project slightly (state **2**). In *Hylocomium*, cell ends project strongly (state **1**). Regular-sized cell ends mixed with some enlarged papilla at the corner of cells (state **3**) were observed in *Leptocladiaella*.

16. Leaf-base: Three types of leaf-base were observed: **0**, not decurrent (in *Hylocomium*); **1**, auriculate (in *Loeskeobryum*); **2**, decurrent (in most other taxa).

17. Branching pattern of plants: Four types are coded: **0**, 1' irregularly pinnate; **1**, 1' regularly pinnate; **2**, 2'-3' regularly pinnate; **3**, 2'-3' irregularly pinnate.

18. Dwarf males: Dwarf males occur (state **1**) in *Macrothamnium javense*, and are absent (state **0**) in other taxa.

19. Costa length: Three types of costa length were observed: **0**, shorter than half; **1**, longer than half; **2**, variable.

20. Leaf shape: In *Hypnum lindbergii* and *Gollania ruginosa*, leaves are falcate (state **0**). In the ingroup taxa and the Hylocomiaceae, leaves are erected (state **1**).

21. Leaf margins: In *Macrothamnium* and *Orontobryum*, leaf margins are serrate (tooth consisting of more than one cell, state **1**). In other taxa, leaf margins are serrulate (tooth consisting of one cell, state **0**).

22. Epidermal cells of stem: Two states were coded: **0**, not enlarged (in most taxa); **1**, enlarged (in *Hypnum* and *Leptocladiaella*).

23. Neck of leaf: Neck of leaf is present (state **0**) in *Hylocomium* and *Loeskeobryum*, and is absent (state **1**) in most other taxa.

24. Axillary hairs: Three apical cells (state **1**) were observed on axillary hairs in the ingroup taxa, *Loeskeobryum*, and *Hypnum*. In *Gollania* and *Hylocomium*, five apical cells (state **0**) were observed at terminal stage.

25. Spore size: Most taxa have spores approximately 20 μm in diameter (state **0**). *Leptohymenium* and *Macrothamnium leptohymenioides* have larger spores (20–30 μm) (state **1**). The diameter of spores in *Orontobryum* is larger than 30 μm (state **2**) (Rohrer, 1985).

26. Leaf orientation: The leaves of *Gollania ruginosa* are falcate-secund (state **0**). Other taxa have heteromallously oriented leaves (state **1**).

Cladistic Analysis

Cladistic analyses of the ontogenetic data and other morphological characters were conducted using the exhaustive searches of the PAUP computer program (Version 3.1.1, Swofford, 1993). A strict consensus tree and a 50% majority-rule consensus tree rooted at outgroups were identified. All characters were unweighted.

The reliability and accuracy of clades in cladograms was tested using bootstrap resampling with 400 replicates (Felsenstein, 1985). A *gI* test (Huelsenbeck, 1991) of skewed tree-length distribution was calculated from 1,000 random trees generated by the PAUP program to evaluate the phylogenetic information content of the data. Critical values of *gI* are given in Hillis and Huelsenbeck (1992). The fit of character data to phylogenetic hypotheses was evaluated using consistency index (CI) (Kluge and Farris, 1969) and retention index (RI) (Farris, 1989). The statistical significance of CI was determined according to Klassen et al. (1991).

Based on inferred phylogeny, the morphological evolution was analyzed using the MacClade computer program (Maddison and Maddison, 1992). The homology of characters, such as paraphyllia and peristomes, was tested following Patterson's methodology (Patterson, 1982), i.e. similarity, conjunction, and congruence tests.

Results and Discussion

Ontogenetic Transformations of Morphological Characters

A) Paraphyllia: Paraphyllia are differentiated in only three of the species examined. Three types of adult-stage paraphyllia were observed: ox-horn type (*Loeskeobryum cavifolium*, Figure 1A: a-f), deer-horn type (*Hylocomium splendens*, Figure 1A: a-g), and foliose type (*Orontobryum*, Figure 1B: a-g) (cf. Noguchi, 1972a, b; Rohrer, 1985a). The first two types are more similar than either is to the third type.

All developmental transformations initiate with a single, lanceolate cell (Figure 1A: a and 1B: a) followed by a two- or three-cell 'hair-like' stage which develops via an elongation process (Figure 1A: b-c; 1B: b-c). In ox-horn and deer-horn types, branching is the next process, in which 'hairs' transform into a 'forked' stage (Figure 1A: d). The basal cells of 'forked' paraphyllia then divide into two rows (Figure 1A: e). The development of the ox-horn type ends at this stage. In deer-horn paraphyllia, the basal cells continue dividing into three or four rows (Figure 1A: f), and the paraphyllia keep branching and develop three or four 'arms' (Figure 1A: g).

In foliose paraphyllia, the branching process is absent. The basal cells of the hair-like structure divide into two rows (Figure 1B: d). By a series of divisions, the paraphyllia arrive at a 'foliose' terminal stage (Figure 1B: e-g).

B) Central strands: central strands are conducting tissue originating from the apical cells of stems or branches, and if present, can be classified into two types, early and late, according to the timing of differentiation.

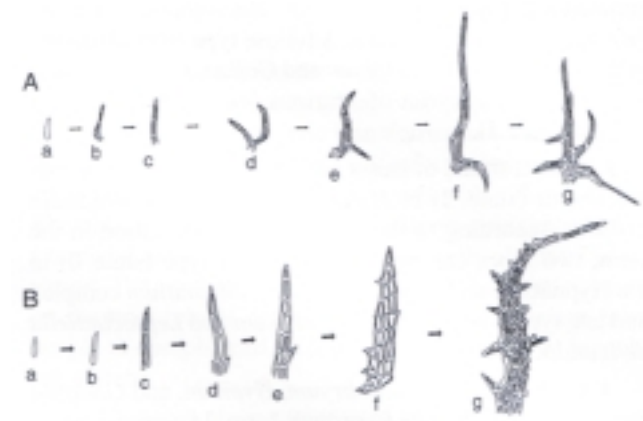


Figure 1. Ontogenetic transformations of paraphyllia: **A)** horn-type a, paraphyllia initial; b and c, elongating; d-f, branching, ox-horn type (*Loeskeobryum*); g, broadening basal portion, deer-horn type (*Hylocomium*); **B)** foliose-type (*Orontobryum*): a, paraphyllia initial; b-d, elongating; e-g, foliating. [all $\times 250$, drawn from Koponen 19258 (*Loeskeobryum cavifolium*), Redfearn & Su 745 (*Hylocomium splendens*), and Griffith s. n. (*Orontobryum hookeri*)].

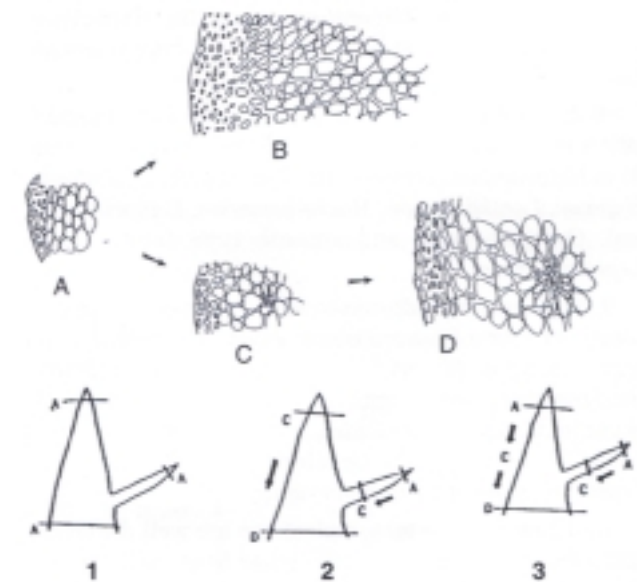


Figure 2. Ontogenetic transformations of central strands: **A** and **B)** central strands absent; **A, C,** and **D)** differentiation of central strands; 1-3 (on bottom): states of ontogeny of central strands: 1, absent (*Hylocomium splendens*, drawn from Redfearn & Su 745); 2, early central strand (*Macrothamnium macrocarpum*, drawn from Chiang 20318); and 3, late central strand (*Leptocodiella delicatula*, drawn from Zhang 467). (A-D. $\times 250$).

a. 'Early' type (Figure 2-2): The central strands of stems are differentiated from the tip of apical cells. No transformations are observed in this type. Early central strands occur in most taxa.

b. 'Late' type (Figure 2-3): The central strands are not differentiated at stem apices. This type occurs in *Loeskeobryum cavifolium* and *Leptoclatiella delicatula*.

c. Absent (Figure 2-1): In *Hylocomium splendens* and *Leptoclatiella psilura*, central strands are not differentiated.

C) Axillary hairs: The transformations of axillary hairs (Figure 3) began with a basal, colored cell (Figure 3: a).

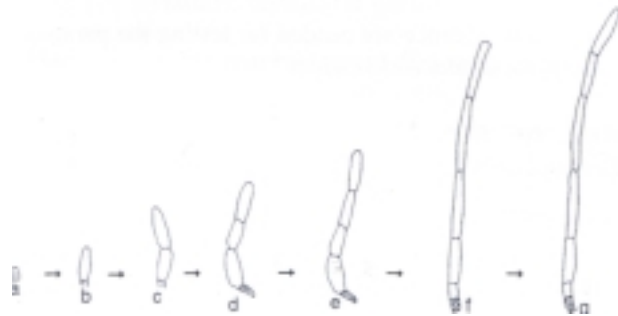


Figure 3. Ontogenetic transformations of axillary hairs: a, Basal cells; b–d, 1- to 3-cell stage; e, 4-cell stage; f, 5-cell stage. (drawn from Redfearn & Su 745, *Hylocomium splendens*).

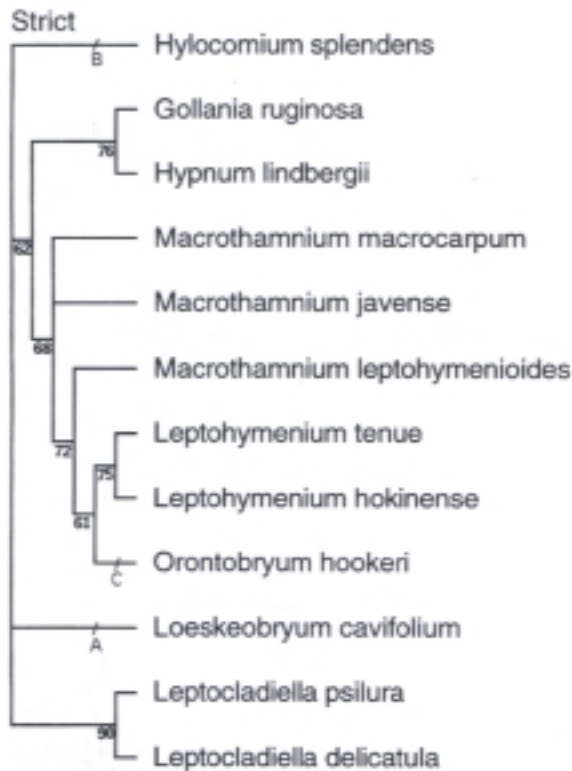


Figure 4. The strict consensus tree of *Macrothamnium* and related taxa rooted at Hylocomiaceae and Hypnaceae. /: paraphyllia. A) ox-horn type; B) deer type; C) foliose type). Numbers at nodes are bootstrapping values.

The basal cell may divide into a two-cell stage and give rise to apical cells (Figure 3: a-e). Most taxa examined had three apical cells, except for *Gollania ruginosa* and *Hylocomium splendens*, which had five apical cells.

Phylogenetic Inference

A strict consensus of three equally most-parsimonious trees (Figure 4), with a length of 56 steps, a consistency index (CI) of 0.732 ($p < 0.01$), and a retention index (RI) of 0.727, was identified rooted at *Hylocomium*, *Loeskeobryum*, *Hypnum*, and *Gollania*. A *gi* statistic of -0.591 indicated a significant amount of phylogenetic signal in the ontogenetic and morphological data.

The monophyly of *Macrothamnium*, *Leptohymenium*, and *Orontobryum*—a sister clade to *Hypnum* and *Gollania*—is significantly supported by a bootstrap value of 96% (Figure 5). That is, these three genera are more closely related to the Hypnaceae than to Hylocomiaceae. This clade is characterized by sharing regularly pinnate branching pattern and amplified costa, and by lacking foliose pseudoparaphyllia. Genus *Macrothamnium*, however, is revealed to be a paraphyletic group, in which *M. leptohymenioides* is more related to *Leptohymenium* and *Orontobryum* than it is to other taxa of *Macrothamnium* because of a lack of shared derived characters. The clade of *Leptohymenium* and *Orontobryum* is characterized by having erect capsules with reduced endostomes. Within this clade, the most parsimonious tree shows that

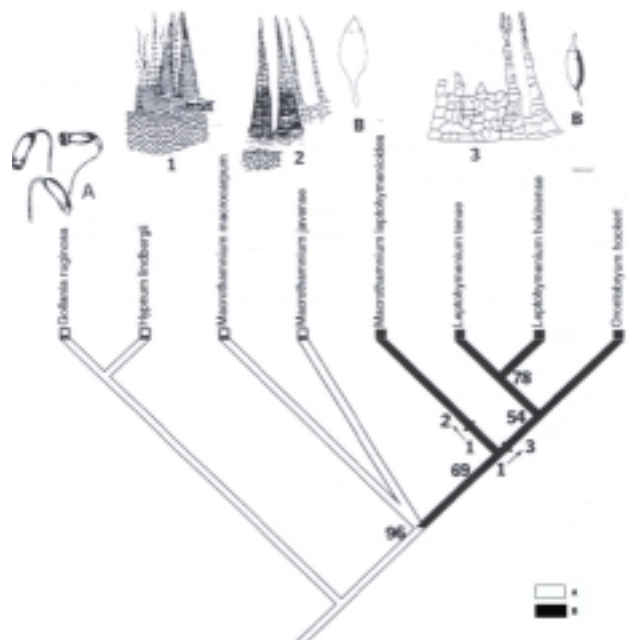


Figure 5. The strict consensus tree of *Macrothamnium*, *Leptohymenium*, and *Orontobryum* rooted at *Hypnum* and *Gollania*: A) inclined capsules with well-differentiated cilia; B) erect capsules, cilia absent; 1, endostome well-differentiated; 2, endostome incomplete; 3, endostome residual. Numbers at nodes are bootstrapping values.

Leptohyemenium is a monophyletic group characterized by cell papillosity pattern and crenulate leaf-margins; a close relationship between *Leptocladia* and the other genera treated in this paper is not supported. Based on a cladistic analysis of morphological and ontogenetic characters, *Leptocladia* is a genus of Hylocomiaceae.

Homology of Paraphyllia

Horn-type and foliose-type paraphyllia share similar ontogenetic transformations. No two individuals or species had both horn-type and foliose-type paraphyllia, and thus they passed Patterson's (1982) similarity and conjunction tests.

No exclusive clade (of *Hylocomium*, *Loeskeobryum* and *Orontobryum*), however, is characterized by paraphyllia. The reconstructed phylogeny suggests that *Orontobryum* is more related to *Macrothamnium* than it is to other taxa with paraphyllia. Patterson's congruence tests of the homology hypothesis failed. In conclusion, the hypothesis of homology of the paraphyllia in Hylocomiaceae and *Orontobryum* is false. The paraphyllia in *Orontobryum* are likely to have evolved independently from those of other taxa.

Reductive Evolution of Sporophytic Characters in the *Macrothamnium* Complex

The sporophytic structures in *Macrothamnium* complex are homologous according to Patterson's three tests. A nested hierarchical relationship of capsule inclination, endostomes, and cilia is supported (Figure 5). A transformation is observed from inclined and well-differentiated capsules in *Macrothamnium*, through erect capsules with incomplete endostomes in *M. leptohymenioides*, to erect capsules with residual endostomes in *Leptohyemenium* and *Orontobryum*. It has been hypothesized that the erect capsules correlate with corticolous (Grout, 1903) or xerophytic habitats (Vitt, 1981). Since these taxa are elements of temperate forests, the association with xerophytic habitats does not hold. In addition, the literature (e.g. Rohrer, 1985b) and collection records of herbarium specimens do not support the hypothesis of obligatory epiphytes for this group.

From the ontogenetic sequence, erect capsules are a stage prior to the curvation of capsules. Phylogenetically erect capsules are a derived state, but retain juvenile morphology by truncating development (paedomorphosis). The change in inclination of capsules may be an adaptation associated with the function of spore dispersal. On the other hand, the erect capsules may constrain the development of peristomes.

Taxonomic Treatment

Three species of *Macrothamnium*, two species of *Leptohyemenium*, two species of *Leptocladia*, and one species of *Orontobryum* are recognized. *Leptocladia flagellaris* T. J. Kop. and D. H. Norris is synonymized to *Hypnum*.

Macrothamnium appears to be a paraphyletic group according to the above analysis since no derived characters are able to differentiate *M. macrocarpum* and *M. javense* from other taxa (*M. leptohymenioides*, *Leptohyemenium*, and *Orontobryum*). To transfer *Leptohyemenium* and *Orontobryum* to *Macrothamnium* nomenclaturally is one of the possible ways to resolve the taxonomy of this complex. Nevertheless, the main purpose of this paper is to generate a testable phylogenetic hypothesis, which appears to agree with Rohrer's (1985a) analysis at generic level. Before more biological evidence of this complex is accumulated, such as the molecular systematics and biology of adaptation, it is not valid to make any nomenclatural change. I would leave *Macrothamnium* to be a paraphyletic group in the following taxonomic treatment. Further research and evidence are needed for testing the paraphyly hypothesis of *Macrothamnium*.

Key to the Species of *Macrothamnium*, *Leptocladia*, *Leptohyemenium*, and *Orontobryum*

1. Paraphyllia present; plants monopodial.....
.....*Orontobryum hookeri*
1. Paraphyllia absent; plants sympodial..... 2
 2. Capsule suberect, horizontal, or inclined; endostomal cilia present 3
 3. Males dwarf.....*Macrothamnium javense*
 3. Males normal-sized 4
 4. Spinous projection of laminal cells absent.....
.....*Macrothamnium macrocarpum*
 4. Spinous projection present at ends of laminal cells..... 5
 5. Central strands absent throughout ontogenetic transformations, branch leaves lanceolate.....*Leptocladia psilura*
 5. Central strands present at adult stage only, branch leaves ovate.....
.....*Leptocladia delicatula*
 2. Capsule erect; endostomal cilia absent 6
 6. Exostome ornamentation cross-striate.....
.....*Macrothamnium leptohymenioides*
 6. Exostome ornamentation smooth 7
 7. Leaves broad-ovate.....
.....*Leptohyemenium tenue*
 7. Leaves lanceolate.
.....*Leptohyemenium hokinense*

I. MACROTHAMNIUM M. Fleisch., Hedwigia 44: 307. 1905. Type species: *Hypnum macrocarpum* Reinw. & Hornsch.

1. *Macrothamnium leptohymenioides* Nog., Kumamoto J. Sci. Biol. 11: 6. 1972.—TYPE: Nepal, *Tokyo Univ. Exped. n. 237772* (holotype: NICH).

Orontobryum recurvulum Gangulee, Mosses E. India 6: 1506. f. 754. 1977.—TYPE: Bhutan, *Griffith 130* (holotype: BM; isotype: FH).

This species is gametophytically identical to *Macrothamnium macrocarpum*, but it lacks endostomal cilia, a feature that links it to *Leptohymenium tenue* (Hook.) Schwaegr. *Macrothamnium leptohymenioides* is placed in *Macrothamnium* on the basis of its stem central strand and irregularly cross-striolated peristome teeth. This species is especially close to the 'submacrocarpum' expression of *M. macrocarpum*.

Distribution. Myanmar, Nepal, Bhutan and China (Tibet).

Additional specimens examined. **BHUTAN:** Griffith 735 (MO, BM, FH), 756, 144 (BM), 736 (FH); Iwatsuki 1844 (FH); Mills *et al.* *s.n.* (FH). **BIRMA:** Sheriff & Taylor 3846b (BM). **TIBET:** Dixon 3847 (BM).

2. *Macrothamnium macrocarpum* (Reinw. & Hornsch.) M. Fleisch., *Hedwigia* 44: 308. 1905.

Hypnum macrocarpum Reinw. & Hornsch., *Nov. Act. Acad. Caes. Leop.* 14, Suppl.: 725. 1829.—**SYNTYPE:** Java, Malabaria, Mt. Gede, *Reinwart s.n.* (L).

Microthamnium submacrocarpon A. Jaeger ex Renauld & Cardot, *Bull. Soc. R. Bot. Belg.* 41: 99. 1905.

Macrothamnium submacrocarpum (Renauld & Cardot) M. Fleisch., *Hedwigia* 44: 308. 1905.—**TYPE:** Bhutan, inter Maria Basti & Labar, *Durel s.n.* (lectotype: BM), Sikkim-Himalaya, *Decoly & Schaul s.n.*; Sikkim, *Kurz s.n.* (all syntypes: BM), *syn. nov.*

Macrothamnium longirostre Dix., *Rev. Bryol. Lichen.* 13: 19. 1942.—**TYPE:** Japan, *Sasaoka 4748* (holotype: BM).

Bryologists have over-emphasized the extreme forms of this variable species, and as a result, there has been a proliferation of names that are usually based on the examination of only a few specimens. In this species, leaf-shape is unreliable as a taxonomic character, since it varies greatly even within a single specimen. No clear-cut boundary can be drawn that separates these taxa. Even growth form varies greatly among specimens from different areas. The plants may branch either monopodially or sympodially, the leaf margins vary from serrulate to serrate, and the leaf-bases can be weakly to strongly decurrent. The capsules vary from suberect to inclined.

Distribution. Java, Philippines, Taiwan, Japan, China, Thailand, Nepal, Bhutan, India and Sri Lanka.

Additional specimens examined. **JAVA:** Fleischer *s.n.* (FH); Nyman 433. (MO); Schiffner 3896 (MO); Fleischer 349 (BM); Kurz 807 (BM); Junghuh *s.n.* (BM); Fleischer 349 (FH); Nyman 453 (FH); Warburg *s.n.* (FH). **BORNEO:** *Kirthales s.n.* (BM); *Svihla 3377, 3610, 3429, 3423, 2797, 2777* (FH); *Meijer 12700* (FH). **PHILIPPINES:** *Tan & Aguila 81-28, Tan 74-214* (MO); *Robinson 6596* (BM); *Ramos 5966* (BM); *Merrill 4878* (BM); *Hadan 153, 158* (FM); *Williams 81709* (FH). **TAIWAN:** *Chiang 20318, 2500, 25324, 18951, 20609* (MO); *Chuang s.n.* (MO); *Chiang s.n.* (MO); *Shimada,*

s.n. (MO); *Chuang & Schofield 597* (MO); *Chuang 1390* (MO), 411, 396, 6217, 2038, 597, 4117, 5098, 5088 (FH); *Sasaoka 3811* (BM). **CHINA:** *Handel-Mazzetti 394c* (BM); *Chung 4081* (FH); *Merrill 10415* (FH); *Redfearn, He & Su 516, 657, 198, 884a, 688, 806a* (SMS). **MALESIA:** *Henderson 23611* (BM); *Clemens 33890* (FH). **BIRMA:** *Dickason 8531, 8773, 7497, 7701, 8647, 9076, 9646, 9087, 9076, 9646, 9082, 8773, 8531, 8102, 7258, 8647* (FH); *Egerod 25* (FH). **THAILAND:** *Touw 9194, 8836, 10701, 9680, 9165* (MO, FH), *Hansen & Smitinand 13125* (MO); *Kerr 18, 47* (BM); *Smitinemd 8854* (FH); *Wahdge & Carpenter 1500* (FH); *Touw 9194, 8719, 8836, 11098* (FH). **NEPAL:** *Iwatsuki 38* (MO); *Dixon s.n.* (BM); *Norkett 6594, 6157* (BM); *Stewart 14473* (FH); *Falconer 737, 739* (FH); *Duthie s.n.* (FH); *Kurz 2513* (FH); *Weber 99341, 99443, 99408* (FH). **INDIA:** *Fleischer 3228, 3230, 3074, 3073* (MO); *Weir 5* (BM); *Brotherus 3183* (BM); *Oliver 1896* (BM); *Berroter 407* (BM); *Gough 72 12, 12, 7* (BM); *Burkill 36533, 36544* (BM); *Fischer s.n.* (BM); *Griffith 754* (BM); *Shepherd 4* (BM); *Norkett 11866* (BM); *Bahadru s.n., 54* (BM); *Dixon s.n.* (BM); *Hook 1057, 1059, 949* (BM); *Gollan 2403* (BM); *Brotherus s.n.* (BM); *Kurz 2150* (FH); *Hiangulu 4973* (FH); *Walker 453, 513, 489* (FH); *Mitten s.n.* (FH); *Hooker s.n.* (FH); *Chopra & Abrul 456* (FH). **BHUTAN:** *Griffiths s.n.* (MO); *Bartholomew 152* (MO); *Falconer 737* (MO); *Bobert s.n.* (BM); *Mecbold 16628, 16630* (BM); *Levier s.n.* (BM); *Kurz 2406, 2418, 2397, s.n.* (FH); *Hooker 952, 981* (FH); *Xavier 126* (FH). **CEYLON:** *Thwaites 209* (MO, BM); *Fleischer 448* (BM). **HAWAII:** *Baldwin 138, 252* (FH).

3. *Macrothamnium javense* M. Fleisch., *Hedwigia* 44: 311. 1905.—**TYPE:** Java, *Fleischer 348* (holotype: FH).

Macrothamnium hylocomioides M. Fleisch., *Nova Guinea* 12(2): 125. 1914. *syn. nov.*—**TYPE:** New Guinea, Niederl. Sudwest-Neu-Guinea: Am Goliath-Gebirge 1950-3000 m, *Dekock 14* (lectotype: FH). *Dekock 29* p.p. 33 p.p. (syntype: FH).

Chaetomitriopsis diversifolia Zanten, *Nova Guinea Bot.* 10: 316. 1964. *syn. nov.*—**TYPE:** New Guinea, Mt. Antares, *Zanten 382* (holotype: L); Orion Mts., Tenmasigin, *Vervoort 306* (paratype: MO).

Macrothamnium hylocomioides was separated from *M. javense* based on leaf-shape and inclination of capsules, but the characters are variable even within populations. No significant difference can be found that differentiates them as two species.

One of the most distinguishing characteristics of this species is its sexuality. *Macrothamnium javense* and *M. hylocomioides* were distinguished from other cladodioecious species by their phylloodioecious condition (Fleischer, 1905; Noguchi, 1972a). In this condition, the bud-like androecious plants are epiphytic on the leaves of normal-sized gynoecious plants (Wyatt, 1985). The presence of large and small spores was described in *M. javense* by Fleischer (1905). Noguchi (1972a) excluded the pos-

sibility of large spores in *M. javense*, arguing that they were nothing more than reproductive bodies of fungi. Some mosses, however, are amphispory (Mogensen, 1981; 1983)—a condition in which the ratio of large spores to small spores is variable. This condition has been reported in *Pleurozium schreberi* (Longton and Greene, 1979) and *Plagiomnium medium* (Newton, 1972). Small spores are believed to be abortive in the amphisporeal condition. Unlike anisospory, in which the ratio of large spores to small spores is approximately 1, amphispory in *Macrothamnium javense* seems to be a character sensitive to ecological factors.

The geographical distribution is another interesting phenomenon in *Macrothamnium*. *Macrothamnium macrocarpum* is widely distributed in Japan, Taiwan, China, Indo-China, the Himalayas, India, Sri Lanka, Malesia, the Philippines, Borneo, and West Java. The distribution of *M. javense* is almost east of that of *M. macrocarpum*. The species overlap in the Philippines, Borneo, and Java. No significant difference of sporophytic and gametophytic characters, except sexuality, can be found in *M. macrocarpum* and *M. javense*. Dwarf males epiphytic on female plants is unique to *M. javense*. In the type specimen of *M. javense*, a detached branch with normal males was marked by Fleischer, although it was not reported in the original description of this species. Misplacement of that branch could explain the mix of sexualities in the same collection. On the other hand, *M. macrocarpum* might be sexually polymorphic among populations. The physiological and ecological adaptation of dwarf males to ecological factors has been studied in other mosses. Une (1985) showed that male dwarfness in anisoporous species such as *Macromitrium* is genetically determined, whereas in isoporous species, dwarfness is regulated by phytohormones from female plants. Furthermore, the male spores of isoporous *Macromitrium* have the potential to develop into either normal or dwarf males. The mechanism of expression of dwarf males in amphisporous species remains unknown.

According to the specimen records, the distribution of *M. javense* in Java is restricted to the eastern portion. It can be explained that there is a sympatric region of the two taxa in central Java. No other specimens with mixed sexualities have been found in Java. More evidence from field surveys and population genetics is needed to test the hypothesis of identity of *M. macrocarpum* and *M. javense*.

Chaetomitriopsis diversifolia was found in New Guinea. Zanten (1964) claimed that this species is related to *Chaetomitrium*, a genus of the Hookeriaceae. *Chaetomitriopsis diversifolia* is distinguished from *Chaetomitrium* by having paraphysis. The differentiation of stem- and branch-leaves, sympodial growth-form, and irregular branching pattern in *C. diversifolia* were not observed in other species of *Chaetomitriopsis*. *Chaetomitriopsis diversifolia* is a species of *Macrothamnium* and is synonymous with *M. javense*.

Distribution. Java, Borneo, Celebes, Philippines, and New Guinea.

Additional specimens examined. **NEW GUINEA:** *Koponen 32955, Norris 59911* (MO); *Carr 15215* (MO); *de Sloover 42739* (MO); *Weber & McVean 32180* (MO); *Hoogland 9579* (FH); *Hoogland & Schodde 6930* (FH); *Robbins 3414, 3152, 3032, 3044, 219, 217, 2770, 2776* (FH); *Carr 15214* (FH); *Nils & Gyldenstolpe s. n.* (FH); *Koponen 29846, 32800, 29934, 33881, 60886, 30165, 33910* (FH); *Norris 64551, 63376, 63285* (FH); *Brass 9385, 10942, 10956, 9699, 9698, 9870, 9389, 10024, 10942, 10956, 22621, 22543* (FH); *Creek 720, 719* (FH); *Clemens 11296* (FH); *Sloover 42, 981* (FH); *Fleischer 14* (FH); *Thiers 3398, 3663, 3714* (FH); *Morris 60205, 66517* (FH); *Wade 8110* (FH); *Weber & McVean 32214* (FH); *Mundua 33* (FH); *Toia 115* (FH). **JAVA:** *Fleischer 348, 1300* (FH); *Seifrig s. n.* (FH); *Moller s. n.* (FH); *Schiffner 3896, 13024* (FH). **CELEBES:** *Everett s. n.* (FH); *Dixon s. n.* (FH). **PHILIPPINES:** *Copeland 827, s. n.* (FH); *Robinson 6596* (FH). **BORNEO:** *Korthals s. n.* (MO); *Clemens 33122, 40289* (FH).

II. LEPTOCLADIELLA M. Fleisch., Musci Fl. Buitenzorg 4: 1476. 1923.—TYPE: *Stereodon psilura* (Mitt.) M. Fleisch.

1. Leptocladiella psilura (Mitt.) M. Fleisch., Musc. Fl. Buitenzorg 4: 1205. 1923.

Stereodon psilurus Mitt., J. Proc. Linn. Soc. Suppl. Bot. 1: 112. 1859.—TYPE: India, *Hooker 754* (holotype: BM; isotype: FH); Himalaya, *Bahadru 1* (paratype: FH).

The costae of branch-leaves are variable within individuals. The costa can be forked or single. The other unique characters are the costal spine and the lack of central strand.

Distribution. China, the Himalayas, India, Thailand.

Additional specimens examined. **NEPAL:** *Norkett 7559A* (BM); *Wallich s. n.* (BM); *Polunin et al. 5418a, 5421a* (BM); *Higuchi 18108, 16292* (HIRO). **CHINA:** *Redfearn et al. 516* (FH, SMS, MO); *Brotheros 6661* (BM). **TIBET:** *Chen 256* (MO). **INDIA:** *Mills et al. 754, s. n.* (FH). **THAILAND:** *Ogawa 67836* (FH).

2. Leptocladiella delicatula (Broth.) J. R. Rohrer, J. Hattori Bot. Lab. 59: 266. 1985.

Macrothamnium delicatulum Broth., Symb. Sin. 4: 131. 1929.—TYPE: China, Setschwan, *Handel-Mazzetti 1486* (holotype: H).

Distribution. This species has rarely been reported or collected. The distribution of this species is restricted to southwestern China.

Additional specimens examined. **TIBET:** *Chen 245a* (MO); *Zhang 467* (MO).

III. LEPTOHYMENIUM Schwaegr., Sp. Musc. Suppl. 3(1): plate 246c. 1828.—TYPE: *Neckera tenue* Hook.

This genus is gametophytically similar to *Macrothamnium macrocarpum* or *M. leptohymenioides*. The weak differentiation of stem- and branch-leaves can be used to distinguish the sterile specimens of *Leptohymenium* from those of *Macrothamnium*. The erect capsules are different from the inclined ones of *M. macrocarpum* and *M. javense*. *Macrothamnium leptohymenioides*, however, has sporophytes similar to those of *M. macrocarpum*, except for having cross-striate exostome ornamentation.

1. *Leptohymenium tenue* (Hook.) Schwaegr., Sp. Musc. Suppl. 3(1): plate 246c. 1828.

Distribution. The Himalayas, China, Indo-China, India, the Philippines, and Mexico. The geographical distribution of the species is unique. A disjunct distribution pattern has been described based on the populations of Asia and Mexico (Rohrer, 1986).

Specimens examined. **BHUTAN:** Kurz 89, 2525 (BM); Griffith 738, 739, 740 (BM); Siphara 563 (BM). **NEPAL:** Hooker 908, 947, 955, 1169, 1840 (BM); Wailich 160, 2096, s.n. (BM); King 56 (BM, FH); Sherrin 3 (BM); Buchanan s. n. (BM); Gardner s. n. (BM); King 1894 (FH); Man 828 (FH); Kharraddiu s. n. (FH); Hara et al. 200006 (FH); Iwatsuki 1367 (FH); Mills et al. s. n. (FH); Hooker 955, 958 (FH); Baesley s. n. (FH); Rana. s. n. (FH); Higuchi 15918 (HIRO). **INDIA:** Hooker 951 (BM); Ryley 14 (BM); Dixon 271, 325, 609 (BM); Kurz 2261 (BM); Fleischer 3255 (FH); Griffith 738, 740, 178, s. n. (FH); Mueller 1701 (FH); Miller 11 (FH); Parish 130 (FH); Beddome 145, 563 (FH); Strachey & Winterbottom 99, 908, 953, 961, 947, 946, 955, 959, 950, 948, 958 (FH). **CHINA:** Redfearn, He & Su 6126, 688 (SMS). **TIBET:** Su 2646 (MO). **BIRMA:** Kurz 2820, 3344 (BM); Dixon 685 (BM); Khairuddin s. n. (FH); Dickason 7501, 7292, 7427, 9446, 9642, 9644, 9429 (FH); Svihla 3747, 3427, 9429, 3580 (FH). **THAILAND:** Yoda 67719 (FH); Touw 9121, 9784 (FH). **PHILIPPINES:** Curran et al. 16425 (FH); Clemens 9316 (FH); Jacobs 567, 14 (FH); Tan 86291 (FH). **MEXICO:** Sharp 5629 (FH); Norris et al. 20667 (FH); Mueller 2268 (FH); Crum 1137, 811 (FH); Arsene 7998 (FH, MO).

2. *Leptohymenium hokinense* Besch.—TYPE: China, Yunnan, Delavay 4131 (lectotype: BM).

Lanceolate leaves are unique to this rare species.

Distribution: Restricted to southwestern China.

Specimens examined. **CHINA:** Delavay 4663 (FH, BM).

IV. ORONTOBRYUM Fleisch. ex Brother. in Engler & Prantl, Nat. Pfl. ed.2, 11: 261. 1925.—TYPE: *Stereodon hookeri* Mitt.

1. *Orontobryum hookeri* (Mitt.) M. Fleisch. ex Broth. in Engler & Prantl, Nat. Pfl. ed. 2, 11: 261. 1925.

Stereodon hookeri Mitt.—TYPE: India, Hooker 819 (holotype: FH).

This species is characterized by globular capsules, monopodial growth-form, and foliose paraphyllia.

Distribution. Himalayas, India, Birma.

Additional specimens examined. **HIMALAYAS:** Mill et al. s. n. (FH); Iwatsuki 753 (FH); Romos 66 (BM). **NEPAL:** Norkett 9317 (BM); Higuchi 17494 (HIRO). **INDIA:** Wood 2006a, 4220c (BM); Polunin M47 (BM). **BHUTAN:** Griffith s. n. (BM, MO). **BIRMA:** Kingdon Ward 21160h (BM).

Excluded Species

Hypnum flagellaris (T. J. Kop. & D. H. Norris) T.-Y. Chiang, comb. nov.

Basionym: *Leptocladia flagellaris* T. J. Kop. & D. H. Norris, Acta Bot. Fennica 131: 53-61. 1985.—TYPE: Papua New Guinea, Norris 63839 (holotype: HEL); Koponen 34317 (paratype: MO).

This species was recorded as new by Koponen and Norris (1985) from New Guinea. It is characterized by curved stem-leaves, ovate-lanceolate pseudoparaphyllia, early central strand, and well-differentiated alar cells of stem-leaves. It seems to be more related to *Hypnum* than it is to *Leptocladia*, which is characterized by having late central strands and enlarged epidermal cells, and by lacking pseudoparaphyllia.

Additional specimens examined. **NEW GUINEA:** Norris 61619 (MO), Sloover 42936 (MO).

Acknowledgments. I thank Drs. Bruce Allen and Robert E. Magill for their valuable comments on taxonomic treatment. I am grateful to the curators of BM, FH, HIRO, NICH, L, MO, and PE for access to cited specimens.

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Appendix 1. Examined specimens of outgroup taxa.

Loeskeobryum cavifolium (Lac.) M. Fleisch.

Japan: *Koponen 19258* (MO); *Mizutani 13899* (MO); *Higuchi s.n.* (MO).

Hylocomium splendens (Hedw.) B.S.G.

China: *Redfearn & Su 745, 757b* (SMS); *Redfearn, Allen & Wu 34625a, 34694, 34582, 35228, 35276, 35229c, 34605, 35232* (SMS); *Redfearn, He & Su 1295* (SMS).

Gollania ruginosa (Mitt.) Broth.

China: *Redfearn, He & Su 1035* (MO).

Leptocладиella flagellaris Norris & Koponen

New Guinea: *Norris 61619* (MO); *Sloover 42936* (MO).

大木蘚及相關屬種的親緣關係及形態演化

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本文對三種大木蘚，二種殘齒蘚，二種細枝蘚以及一種圓蒴蘚進行分類訂正。作者利用鱗毛，葉生毛及中央束的發生學序列以及其他的形態特徵重建大木蘚及相關屬種的親緣關係，爲了測驗這一群植物的分類地位，分別從灰蘚科及塔蘚科選取兩種作爲外群；由 PAUP 的分析顯示大木蘚，殘齒蘚及圓蒴蘚形成屬於灰蘚科自然的一群，其共同的特徵爲個體規則羽狀分枝，發達的中肋及缺乏分化的擬鱗毛；但是，大木蘚屬因缺乏共同的進化特徵形成一個 paraphyletic group，其中殘齒大木蘚更近緣於殘齒蘚及圓蒴蘚；相對的，細枝蘚屬的分類地位較近緣於塔蘚科。作者利用 Patterson (1982) 的三個測驗方式測試特徵的同源假說，顯示塔蘚科的牛角形鱗毛與圓蒴蘚的葉狀鱗毛並非同源，推論這兩類形的鱗毛並非來自近緣的共同祖先，而是對生育環境的平行演化。

關鍵詞：大木蘚屬；矮雄雌雄異株；發生序列；鱗毛；Patterson 測驗；同源。