

BRACHYTHECIACEAE (BRYOPHYTA) –  
A FAMILY OF SIBLING GENERA

BRACHYTHECIACEAE (BRYOPHYTA) –  
СЕМЕЙСТВО РОДОВ–БЛИЗНЕЦОВ

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Abstract

The history of familial and infrafamilial circumscriptions of the Brachytheciaceae is briefly reviewed and a new classification of the family is proposed, based largely on a phylogenetic analysis of molecular and morphological characters. The family includes four subfamilies and 41 genera; the number of species is estimated to be 250-350. Some genera are established or re-established: *Brachytheciastrum* gen. nov. – for the group of species around *Brachythecium velutinum*; *Eurhynchiastrum* gen. nov. for *Eurhynchium pulchellum*; *Eurhynchiadelphus* gen. nov. for *Eurhynchium eustegium*; *Sciurohypnum* (Hampe) Hampe for the group of species around *Brachythecium oedipodium*, *B. reflexum*, *B. populeum*; *Oxyrrhynchium* (B. S. G.) Warnst., nom. conserv. prop. for the group of species around *Eurhynchium hians*; *Remyella* C. Müll. for a group of Malesian and Oceanian species, usually referred to *Rhynchostegiella*. *Camptothecium* and *Trachybryum* are not accepted and are placed in *Homalothecium*; *Steelecleus* and *Scleropodiopsis* are not accepted and are placed in *Rhynchostegium*. The Chinese endemic species known as *Platyhypnidium patulifolium* is transferred to *Donrichardsia*.

Abstract

Рассматривается история представлений об объеме семейства Brachytheciaceae и входящих в него родов и предлагается новая система семейства на основе анализа морфологических и молекулярных данных. Семейство включает четыре подсемейства, 41 род и 250-350 видов. Ряд родов описан в качестве новых и еще ряд родов восстановлен: *Brachytheciastrum* gen. nov. – для видов, близких к *Brachythecium velutinum*; *Eurhynchiastrum* gen. nov. для *Eurhynchium pulchellum*; *Eurhynchiadelphus* gen. nov. для *Eurhynchium eustegium*; *Sciurohypnum* (Hampe) Hampe для видов, близких к *Brachythecium oedipodium*, *B. reflexum*, *B. populeum*; *Oxyrrhynchium* (B. S. G.) Warnst., nom. conserv. prop. для видов, близких к *Eurhynchium hians*; *Remyella* C. Müll. для группы видов из Малазии и Океании, обычно относимых к *Rhynchostegiella*. *Camptothecium* и *Trachybryum* отнесены в синонимы к *Homalothecium*; *Steelecleus* и *Scleropodiopsis* – в синонимы к *Rhynchostegium*. Китайский эндемик *Platyhypnidium patulifolium* отнесен к роду *Donrichardsia*.

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The Brachytheciaceae is a family that is often considered taxonomically difficult. This paper gives a brief overview of the history of familial and generic concepts, and provides the nomenclatural consequences that are derived from phylogenetic inference based on molecular and morphological characters (Huttunen & Ignatov, 2003).

### 1. EARLY ATTEMPTS TO UNDERSTAND THE BRACHYTHECIACEAE (1812-1879)

The circumscriptions of many widespread boreal and temperate genera of pleurocarpous mosses, and of the Brachytheciaceae in particular, were established in “Bryologia Europaea...” (Bruch & al., 1851-1855). However, already in earlier publications of the XIXth century some groupings of species were proposed. One of the first classifications, wherein the Brachytheciaceae

are discernible, is that of Bridel (1812). In this second edition of “Muscologia Recentiorum...”, Bridel, who included most of the pleurocarps in the genus *Hypnum*, presented a rather elaborated subdivision of this genus, based on four characters of the branching pattern and foliage. Some sections of *Hypnum* that he established are similar to volume of modern genera (e. g. ‘*fissidentoidea*’ ~ *Plagiothecium*, and ‘*tamariscina*’ ~ *Thuidium*). The Brachytheciaceae in modern sense (except *Homalothecium* that was kept in *Leskea* due to the modified peristome) composed mostly<sup>1</sup> 6 of the 28 sections that Bridel recognized within *Hypnum*, namely [specific epithets are given here in modern nomenclature]:

Sect. ***Praelonga*** [foliis distichis, nudis, ramis vagis, ramulis subcompressis]: *hians*, *stokesii*, *speciosum*, *schleicheri*, *confertum*, *rotundifolium* (cf. the more commonly used concept of *Eurhynchium* s.l. and *Rhynchostegium*);

Sect. ***Illecebra*** [foliis spiralis imbricatis, appressis, ramis simpliciter pinnatis vel subpinnatis, ramulis teretibus obtusis]: *purum*, *touretii*, *cirrosum* (*Pseudoscleropodium*, *Scleropodium*, *Brachythecium*);

Sect. ***Muralia*** [foliis spiralis imbricatis, appressis, ramis confertis erectis]: *murale* (*Rhynchostegium*);

Sect. ***Velutina*** [foliis spiralis imbricatis, patentibus omnibus, ramis confertis erectis]: *velutinum*, *starkei*, *reflexum* (cf. small-sized species of *Brachythecium* s.l.);

Sect. ***Plumosa*** [foliis spiralis imbricatis, patentibus omnibus, ramis pinnatis vel subpinnatis]: *plumosum*, *salebrosum*, *lutescens*, *aureum*, *populeum* (cf. some narrow-leaved *Brachythecium* and *Homalothecium* species);

Sect. ***Rutabula*** [foliis spiralis imbricatis, patentibus omnibus, ramis vagis, ramulis subteretibus]: *rutabulum*, *rivulare*, *piliferum*, *touretii*, *megapolitanum*, *rusciforme* (cf. broad-leaved species of *Brachythecium*, *Cirriphyllum*, *Scleropodium*, *Rhynchostegium*, *Platyhypnidium*).

This classification is of certain interest for the following discussion, because one can see here the division of Brachytheciaceae into six more or less natural groups based on character states

1 – some placements, however, look odd from the current point of view, for example *Brachythecium acuminatum* (sub. *Hypnum oxycladon*) was in one section with *Orthothecium*, *Tomentypnum*, *Pleurozium*, *Calliergon*, and *Calliergonella*, obviously due to strongly appressed leaves.

Table 1. Number of species in the larger genera of Brachytheciaceae in four publications for Europe (Bruch & al., 1851-55) and the world. In Crosby & al. (1999) the species number given by two values: (recently revised and confirmed species, marked \*\*\*\* in Crosby & al., l.c.) / (all still not synonymized species) ) [roughly speaking: good species/ good plus dubious species].

	B.S.G. 1851-55	Jaeger & Sauerbeck 1876-79	Brotherus 1925	Crosby & al. 1999
<i>Homalothecium</i>	3	14	18	8/14
<i>Camptothecium</i>	3	9	17	(in <i>Homalothecium</i> )
<i>Brachythecium</i>	24	100	224	94/179
<i>Scleropodium</i>	2	3	8	5/9
<i>Eurhynchium</i>	17	62	31	25/54
<i>Rhynchostegium</i>	10	87	135	30/133

that are quite inappropriate in their application to certain taxa (e. g. *ramis vagis* is not the case of *Hypnum stokesii* and *H. piliferum*, and *ramis pinnatis* is quite a rare case in *H. lutescens*, etc.). Thus, this classification was essentially intuitive and the subsequent attempt to explain which morphological characters were involved was not very successful. The usage of these diagnostic characters to find a correct place for new species would be an impossible task.

Bruch, Schimper & Guembel in “Bryologia Europaea...” established several important genera of the Brachytheciaceae: *Homalothecium* 1851, *Rhynchostegium* 1852, *Brachythecium* 1853, *Camptothecium* 1853, *Scleropodium* 1853, and *Eurhynchium* 1854. Since the idea of the primary importance of peristome structure still dominated at that time, *Homalothecium* was placed in the tribe Orthothecieae (capsule usually straight, peristome intermediate between *Hypnum* and *Neckera*), whereas all other genera were in Hypneae (differs from Orthothecieae in gametophyte texture (“consistentia”), capsule and peristome). The diagnosis of genera was based mainly on sporophytic characters, though gametophytic ones were supplemented: *Rhynchostegium* (operculum longly rostrate), *Brachythecium* (differs from *Rhynchostegium* by its conic operculum), *Eurhynchium* (intermediate between *Rhynchostegium* and *Brachythecium* in operculum shape; differs from *Rhynchostegium* by shorter cells and leaf texture), *Camptothecium* (similar to *Homalothecium* in gametophytic characters, but its capsule is more like that in *Brachythecium*), *Scleropodium* (differs from *Brachythecium* by its narrow flexuose cells and julaceous foliage). The characters of branching and foliage (used by Bridel) were not mentioned.

The family Brachytheciaceae was established by Schimper in the second edition of “Synop-

sis Muscorum Europaeorum” (1876). Pleurocarps were divided into 6 tribes: Fontinaliaceae, Neckeraceae, Hookeriaceae, Fabroniaceae, Leskeaceae, Hypnaceae, and the latter included 5 families: 1. Pterigynandreae; 2. Orthothecieae (*Pylaisia*, *Entodon*, *Platygyrium*, *Isothecium*, etc., and *Homalothecium*); 3. Camptothecieae (*Camptothecium*); 4. Brachythecieae (*Brachythecium*, *Eurhynchium*, *Rhynchostegium*, *Scleropodium*, and also *Hyocomium*, *Ptychodium*, *Thamnum*, etc.); 5. Hypneae [names are in that day style]. The Brachytheciaceae, as we know them now, fell into 3 families, due to the differences in sporophytic characters. The family Hypneae was almost equal to the present volume of Hypnaceae + Amblystegiaceae + Plagiotheciaceae + Hylocomiaceae. The differences between Hypneae and Brachythecieae include characters of the seta (sometimes rough in Brachythecieae), capsule (longer in Hypneae) and areolation (cells often narrowly linear in Hypneae). It is obvious, that these differences are not enough to delimit these two groups. But it is no less obvious, that Schimper (1876) felt intuitively how to divide them very well – no species of the Brachytheciaceae (as we know it now) was placed in Hypneae (though some non-Brachytheciacean taxa fell into Brachythecieae). Two genera of the Brachytheciaceae were placed in two other families: *Homalothecium* – due to its reduced peristome, and *Camptothecium* – due to its transitional characters between *Homalothecium* and *Brachythecium*.

Lindberg (1879) in “Musci Scandinavici in Systemate novo naturali dispositi” did the next step towards improving the classification of the Brachytheciaceae. He used a nomenclature quite distinct from that of Schimper: *Hypnum* sensu Schimp. = *Stereodon* sensu Lindb., Orthothecieae pp. + Camptothecieae + Brachythecieae = *Hyp-*

Table 2. List of genera of Brachytheciaceae (\* – described as not a member of Brachytheciaceae)

- \**Helicodontium* Schwaegr., 1830 (gen. et sp. nov. / South America).  
 \**Clasmatodon* Hook. & Wils., 1842 (gen. et sp. nov. / North America).  
 \**Pleuropus* Griff., 1842, nom. illeg., later homonym (gen. et sp. nov. / Asia and Africa).  
 \**Eriodon* Mont., 1845 (gen. et sp. nov. / Patagonia and Chile).  
 \**Homalothecium* B. S. G., 1851 (segregated from *Leskea* / Europe & al.).  
 [\**Anisodon* B.S.G., 1852 (gen. et sp. nov. / Germany). – synonymized with *Clasmatodon*, but probably erroneously, see discussion under the latter genus below].  
*Rhynchostegium* B. S. G., 1852 (segregated from *Hypnum* / Europe & al.).  
*Brachythecium* B. S. G., 1853 (segregated from *Hypnum* / Europe & al.).  
*Camptothecium* B. S. G., 1853 (segregated from *Hypnum* / Europe & al.).  
*Scleropodium* B. S. G., 1853 (segregated from *Hypnum* / Europe & al.).  
*Eurhynchium* B. S. G., 1854 (segregated from *Hypnum* / Europe & al.).  
 \**Fiorinia* Schimp., 1865, nom. nud. et illeg., later homonym (gen. et sp. nov. / Italy).  
 \**Dubyella* Schimp., 1866 (replacing *Fiorinia*).  
 [\**Phlogostomum* Hampe, 1867, nom. illeg. (replacing *Anisodon*)].  
*Pancovia* Neck. ex J.J. Kickx, 1867, nom. illeg. (many groups of the family).  
*Sciuro-hypnum* (Hampe) Hampe, 1874 (*Hypnum* sect. *Sciuro-Hypnum* Hampe, 1867, segregated from *Brachythecium* and *Camptothecium*).  
*Scorpiurium* Schimp., 1876 (gen et sp. nov. / France and Algeria).  
*Rhynchohypnum* (Hampe) Hampe, 1878 (*Hypnum* subgen. *Rhynchohypnum* Hampe, 1852, various areas).  
*Oticodium* (C. Muell.) Kindb., 1888 (*Hypnum* sect. *Oticodium* C. Muell., 1875. Malesia).  
*Bryhnia* Kaurin, 1892 (gen. et sp. nov. / Norway).  
*Myuroclada* Besch., 1893 (segregated from *Hypnum* / Japan).  
*Rhynchostegiella* (B.S.G.) Limpr., 1896 (*Rhynchostegium* sect. *Rhynchostegiella* B.S.G., 1852).  
*Palamocladium* C. Muell., 1896 (replacing *Pleuropus*, nom. illeg.).  
*Remyella* C. Muell., 1896, nom. reject. (gen. et sp. nov. / Hawaii).  
*Cirriphyllum* Grout, 1898 (segregated from *Eurhynchium*).  
*Burnettia* Grout, 1903, nom. illeg., later homonym (segregated from *Pterigynandrum* / Japan).  
*Achrolepis* (Lindb.) Cardot, 1904, nom. illeg., based on the same type as earlier name [*Myuroclada*] (*Myurella* subgen. *Achrolepis* Lindb., 1872 / Japan).  
*Oxyrrhynchium* (B.S.G.) Warnst., 1905 (*Eurhynchium* subgen. *Oxyrrhynchium* B.S.G. 1854).  
*Paramyurium* (Limpr.) Warnst., 1905 (*Eurhynchium* subgen. *Paramyurium* Limpr. 1896).  
*Okamuraea* Broth., 1906 (gen. et sp. nov. / Japan).  
*Homalotheciella* (Card.) Broth., 1908 (*Homalothecium* sect. *Homalotheciella* Card., 1899).  
 \**Chionobryum* Glow., 1913 (segregated from *Bryum* (sic!) / Italy).  
*Flabellidium* Herzog, 1916 (gen. et sp. nov. / Bolivia).  
*Mandoniella* Herzog, 1916 (segregated from *Helicodontium*).  
*Eurhynchiella* Fleisch., 1923 (*Rhynchostegium* sect. *Leptorhynchostegium* C. Muell., 1899).  
*Pseudoscleropodium* (Limpr.) Fleisch., 1923 (*Scleropodium* sect. *Pseudoscleropodium* Limpr., 1896).  
 \**Platyhypnidium* Fleisch., 1923 (segregated from *Eurhynchium*, *Rhynchostegium*, and *Hygrohypnum*).  
*Schimperella* Thér., 1926 (gen. et sp. nov. / Madagascar).  
*Chamberlainia* Grout, 1928 (segregated from *Brachythecium*).  
 \**Rigodiopsis* Dix. et Thér., 1932. (gen. et sp. nov. / Japan).  
 \**Helicodontiadelphus* Dixon, 1936 (gen. et sp. nov. / Australia).  
*Bryoandersonia* H. Robinson, 1962 [1963] (segregated from *Cirriphyllum* / North America).  
*Cratoneurella* H. Robinson, 1962 [1963] (segregated from *Brachythecium*).  
*Stokesiella* H. Robinson, nom. illeg., later homonym, 1967 (segregated from *Bryhnia* or *Eurhynchium*).  
*Trachybryum* (Broth.) Schof., 1968 (*Camptothecium* sect. *Trachybryum* Broth., 1908).  
*Juratzkaeella* Buck, 1977 (segregated from *Juratzkaea*, a genus of *Stereophyllaceae* / China).  
 \**Donrichardsia* H. Crum et L. E. Anderson, 1979 (segregated from *Hygroamblystegium* or otherwise *Eurhynchium* / North America).  
*Kindbergia* Ochyra, 1982 [replacing *Stokesiella* H. Robinson, 1967].  
*Stereocleus* H. Robinson, 1987 (segregated from *Rhynchostegium*).  
*Nobregaea* Hedenaes, 1992 (gen. et sp. nov. / Madeira).  
*Scleropodiopsis* Ignatov, 1998 (gen. et sp. nov. / Altai).  
*Brachytheciella* Ignatov, 1999 (gen. et sp. nov. / Papua New Guinea).  
*Unclejackia* Ignatov, Norris et Koponen, 1999 (segregated from *Chaetomitrium*).

*num* sensu Lindb. The latter genus included five subgenera: 1. *Scleropodium*; 2. *Pankowia* (~*Eurhynchium* s. l.); 3. *Rhynchostegium*; 4. *Brachythecium*; 5. *Pleuropus* (species referred now to *Homalothecium*). This seems to be the first case wherein all the Brachytheciaceae were put together, in one “genus” (Lindbergs’ equivalent for familial level), and wherein genera described from the tropics were included in the classification (*Pleuropus*). This circumscription of the family was used with some relatively small modifications up to the recent time.

## 2. FURTHER ATTEMPTS TO UNDERSTAND BRACHYTHECIACEAE (LATE XIX<sup>TH</sup> CENT. – LATE XX<sup>TH</sup> CENT.)

The further studies of the Brachytheciaceae can be overviewed at three levels: specific, generic, and familial ones.

### 2A. STUDIES AT THE SPECIES LEVEL

Two main tendencies were important at this level. Since the second half of the XIX century and until the 1920s, exotic collections were actively studied, resulting in descriptions of many new species (Tabl. 1: note, that most of taxa were sorted into the three largest genera, established on European material). Since the second half of XXth century, a number of regional revisions of the family were undertaken, reducing the number of species, for example in Japan and its adjacent areas (Takaki, 1955ab, 1956; Noguchi, 1991), North America (Robinson, 1962), Fennoscandia (Nyholm, 1965), British Isles (Smith, 1978), East India and adjacent areas (Gangulee, 1978), Eastern North America (Crum & Anderson, 1981), Himalayas (Vohra, 1983), Madeira (Hedenäs, 1992), Latin America (McFarland, 1988), Altai Mts. (Ignatov, 1998), Papua New Guinea (Ignatov & al., 1999), West Indies (Buck, 1999), Australia (Hedenäs, 2002).

Though the exact number and the volume of many species remains obscure, it is clear now that the number of morphologically distinct species of the Brachytheciaceae in the world is between 250 and 350.

### 2B. STUDIES AT THE GENERIC LEVEL

At this level deviating taxa (especially those found outside Europe or rare in Europe) were recognized as separate genera, including some subgeneric units that were raised up to the generic level. This can be seen from the Table 2, which includes 50[-52] genera that are based on species of Brachytheciaceae, excluding in-

valid orthographic variants [*Anisodon* and *Phlogostomum* are included with questionmark, but see comments under *Clasmatodon* below]. Note, that Brachytheciacean genera started to appear before “Bryologia Europaea”, but many of them were attributed to the family later (those are marked with an asterisk).

Most of the genera, that appeared after “Bryologia Europaea”, were monospecific. Only six of them included more than 5 species (*Oxyrrhynchium*, *Rhynchostegiella*, *Bryhnia*, *Cirriphyllum*, *Chamberlainia*, *Stereocleus*) and all of them later were much disputed in regard to the position of some species within or outside their boundaries (i. e. none of six got a widely recognized reputation as a stable and clearly delimited group).

The discussions on three largest genera of the family, concerned the following:

(A) *Brachythecium* was claimed to be too heterogeneous and was subdivided into 4-8 sections, first introduced by Kindberg (1897), and then used with just a little alternations (Broth-erus, 1905-1909, 1925; Takaki, 1955b; Robinson, 1962; McFarland, 1988; Ignatov, 1998).

However, only one attempt was made to split it. Robinson (1962) transferred almost half of the North American species to *Chamberlainia*, a genus established originally for only one peculiar species, *Chamberlainia acuminata* [and two synonyms of this species]. Some years later, however, Robinson (1987), suggested that the previous broad concept of *Brachythecium* is better.

(B) *Rhynchostegium* was recognized as a separate genus by most authors. Robinson (1987) found that the group of tropical American species and the North American *R. serrulatus* are not related to the European *R. confertum*, the type of the genus, and segregated them to *Stereocleus*. McFarland (1994) and Buck (1999) however did not accept the latter genus. The aquatic species were placed in the genus *Platyhypnidium*, which was included by most of authors in *Rhynchostegium* and, by some, in *Eurhynchium*. The most recent revisions, however, kept it as a genus of its own (McFarland, 1994; Ignatov & al., 1999; Buck, 1999; Hedenäs, 2002).

(C) *Eurhynchium* in the original description included already two subgenera – *Eurhynchium* (in modern sense: *striatum*, *striatulum*, *circinatum*, *pulchellum*, etc.) and *Oxyrrhynchium* (*hians*, *praelongum*; and species traditionally re-

ferred to *Cirriphyllum*: *piliferum*, *cirrosum*, *crassinervium*, *flotowianum*, *tommasinii*). The latter subgenus was considered as a separate genus by Warnstorf (1905), Fleischer (1923) and Brotherus (1905-1909, 1925), mostly for species around *O. hians*. However almost all subsequent authors (cf. Takaki, 1956; Robinson, 1962; Buck, 1988) did not agree with this concept, and returned to the original broad concept of the genus. The group of species around *E. praelongum* was transferred by Robinson (1962) to the genus *Bryhnia*, but later he segregated them as a new genus *Stokesiella* (Robinson, 1967). The latter appeared to be illegitimate, and was replaced by *Kindbergia* (Ochyra, 1982). *Kindbergia* was accepted by Lawton (1971) and Crum & Anderson (1981), while most authors kept this group in *Eurhynchium* (cf. Noguchi, 1991; Buck, 1988, Hedenäs, 1992, 2002; Ignatov, 1998). Some authors united *Eurhynchium* (or part of it) and *Rhynchostegium* under the former (Grout, 1931, Koponen, 1987) or latter (McFarland, 1994) name.

Some species were moved from one genus to another many times: *Hypnum ornellanum* was placed in *Brachythecium*, *Cirriphyllum*, and *Scleropodium*; *Hypnum praelongum* in *Eurhynchium*, *Oxyrrhynchium*, *Bryhnia*, and *Kindbergia*, etc.

Summing up, despite various attempts to make the three biggest genera of Brachytheciaceae (*Brachythecium*, *Eurhynchium*, *Rhynchostegium*) smaller and more homogeneous, no attempt got a wide recognition, except for some cuttings off monotypic (*Myuroclada*, *Bryoandersonia*, etc.) or more rarely oligotypic genera. The reason for this is that the infraspecific variation in many species is very broad, with some extremes extending across generic boundaries. Thus, the affinities of some species remain ambiguous. Robinson (1962, p. 78) expressed the situation as follow: "Particularly important at the specific level are cases where no single specimen displays the full range of potential variation. Individual specimens of such highly variable species often show a very limited and distinctive morphology". This is quite applicable at the generic level as well.

## 2C. STUDIES AT THE FAMILIAL LEVEL

The attempts to circumscribe the family were many:

Brotherus (1905-1909) included into the Brachytheciaceae its core genera, *Homalothecium*, *Camptothecium*, *Brachythecium*, *Bryhnia*,

*Myuroclada*, *Cirriphyllum*, *Eurhynchium*, *Scorpiurium*, *Oxyrrhynchium*, *Rhynchostegium*, and *Rhynchostegiella*. He correctly added (as has turned out in this study) *Eridon*, *Okamuraea*, and *Homalotheciella*, and incorrectly (in the same sense) *Stenocarpidium*, *Ptychodium*, *Catagoniopsis*, and *Rigodium*.

Fleischer (1923) correctly excluded *Stenocarpidium*, *Rigodium*, and *Ptychodium* from the Brachytheciaceae and incorrectly excluded *Platyhypnidium* and *Okamuraea*.

Brotherus (1925) incorrectly included *Ishibaea*, *Sciuroleskea*, and *Lepyrodontopsis*; incorrectly retained *Tomentypnum* and *Catagoniopsis* in the Brachytheciaceae, and incorrectly retained *Okamuraea* outside the Brachytheciaceae.

Grout (1931) correctly included *Platyhypnidium* (within *Eurhynchium*), and incorrectly kept *Isothecium* and *Pseudoisothecium*.

Robinson (1962) incorrectly included *Conardia* and *Isothecium*.

Buck (1988) incorrectly included *Rozea*, *Stenocarpidiopsis*, and *Bryostreimannia*.

There is no need to comment all these transfers. They were numerous and arguments for them were short if any.

In the Northern Hemisphere the main problem was the border between Brachytheciaceae and Amblystegiaceae. Important steps forwards were taken by Hedenäs (1989a), who found [among others] a set of characters to separate the Brachytheciaceae+Hylocomiaceae+Ctenidiaceae from the Amblystegiaceae+Thuidiaceae+Hypnaceae (at least the main groups of these families). Among these characters are the appearance of the costa and the plicateness in perichaetial leaves, the shape of the stomata pore, the capsule shape, the pattern of exostome teeth border tapering, etc.

Thus, Hedenäs excluded from Brachytheciaceae *Isothecium* (Hedenäs, 1992), *Tomentypnum* (Hedenäs, 1987), *Conardia* (Hedenäs, 1989b), all correctly according to our studies. These publications of Hedenäs install the reliable and sharp border between Brachytheciaceae and Amblystegiaceae. Though recently Amblystegiaceae got a more definite and narrow circumscription (Vanderpoorten & al., 2002), the ideas of Hedenäs remain valid, because the pool of genera around Amblystegiaceae + Leskeaceae + Calliargonaceae + Rhytidiaceae + etc. is still a unit quite distant from the Brachytheciaceae.

Almost simultaneously with the resolution of the limits of the Brachytheciaceae in the boreal flora, the problem of its limits in the tropics was highlighted.

(1) In revisions of the genus *Lindigia* (Metetoriaceae) *L. capillacea* was transferred to Brachytheciaceae by Menzel (1991), to the new genus *Aerolindigia*, and by Visnadi & Allen (1991), to *Rhynchostegiella*.

(2) *Duthiella*, a genus commonly placed in Metetoriaceae or Trachypodaceae was placed in the Brachytheciaceae by Noguchi (1991).

(3) Buck (1994) re-evaluated the Metetoriaceae and found it very difficult to separate from Brachytheciaceae. Later Buck (1999) placed these families close to each other.

(4) Ignatov, Koponen & Norris (1999) found similar Brachytheciaceae/Metetoriaceae problems in New Guinea, around species of *Unclejackia*, *Brachytheciella*, and *Rhynchostegiella*.

(5) Ignatov (1999) found that members of both the Brachytheciaceae and the Metetoriaceae have similar pseudoparaphyllia pattern, which separate these two families from all other pleurocarps. Ignatov (l. c.) confirmed the exclusion from the Brachytheciaceae of *Isothecium*, *Conardia*, and *Tomentypnum*, and did not confirm the position in this family of *Rozea*, *Sciuroleskea*, *Stenocarpidiopsis*, *Catagoniopsis*, and *Lepyrodontopsis*. The position of *Trachypus* in Metetoriaceae was not confirmed [which however, appeared to be an exceptional case – the genus fell well within Metetoriaceae, both in molecular and overall morphological studies (Quandt & al., 2003a; Huttunen & Ignatov, 2003; also Figs. 1,2)].

However due to the limited number of genera studied, Ignatov (1999) failed to find any genera outside Brachytheciaceae+Metetoriaceae that can be included in this group of two families based on pseudoparaphyllia pattern.

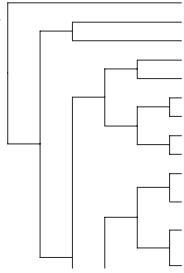
Soon afterwards, however, molecular data showed that Brachytheciaceae includes also *Clasmatodon* (Buck & Goffinet, 2000), *Helicodontium* (Buck & al., 2000), *Okamuraea* (Tsubota & al., 2002), and *Donrichardsia* (Stech & Frahm, 1999; Vanderpoorten & al., 2002). All these rather unexpected transfers were supported by our subsequent pseudoparaphyllia studies. This high congruence of molecular and morphological data is especially pleasant, raising the trust to molecular data by morphologists and perhaps vice versa.

The few exceptions were, however, found. The genus *Trachypus*, which clearly belongs to the Metetoriaceae clade on the basis of phylogenetic inference and also overall morphology (Buck, 1994, 1999), has pseudoparaphyllia that differ from the Brachytheciacean+Metetoriacean type. *Lindigia debilis* and *Neobarbella comes* have this type of pseudoparaphyllia, but the former was found outside the group of these two families in the present phylogenetic analysis, while the latter – in analysis of Quandt & al. (2003b).

While a close relationship between Brachytheciaceae and Metetoriaceae was found, the border between them appeared problematic. Since they were not considered closely related and were placed even in different orders (the first author who placed them closely was Buck, 1999) – their relationship has not been a subject for a comparative studies. Metetoriaceae were understood by having pendent growth (almost never so in Brachytheciaceae in a traditional sense), often papillose laminal cells (smooth in the Brachytheciaceae), seta often short (long in Brachytheciaceae), calyptra often hairy (very rarely so in Brachytheciaceae); a modified hygrocastic peristomes (Brachytheciaceae have usually more or less complete xerocastic peristomes with exostome teeth striolate below and an endostome with a high basal membrane, broad and broadly perforated segments, and long cilia). However, these characters are not consistent across taxa.

The single special study of Brachytheciaceae based on sequence data (Stech & Frahm, 1999), included eight species, mostly of the *Eurhynchium* group. It was found that *Eurhynchium pumilum* is more closely related to *Rhynchostegiella jacquinii*, whereas *Eurhynchium striatum* is neither related to *E. (Oxyrrhynchium) hians*, nor to *E. (Kindbergia) praelongum*. A number of species were included also in the analyses of Buck & al. (2000), Goffinet & al., (2001), Stech & Frahm (2001) and Tsubota & al. (2002).

Our analysis of sequence and morphological data is published separately (Huttunen & Ignatov, 2003). Consensus of three most parsimonious trees based on combined analysis of molecular and morphological data is presented in Fig. 1. This result is obtained using direct optimization method as implemented in phylogenetic software POY (Gladstein & Wheeler, 2001,



*Leskea polycarpa*  
*Rozea andrieuxii*  
*Rozea subjulacea*  
*Hypnum cupressiforme*  
*Ctenidium molluscum*  
*Isothecium alopecuroides*  
*Lembophyllum clandestinum*  
*Bestia longipes*  
*Dolichomitriopsis diversiformis*  
*Meteoriella soluta*  
*Hylocomium splendens*  
*Rhytidiadelphus triquetrus*  
*Lindigia debilis*  
*Leucodon sciuroides*  
*Plagiothecium denticulatum*  
*Amblystegium serpens*  
*Campylium stellatum*  
*Trachypus bicolor*  
*Chrysocladium retrorsum*  
*Meteorium polytrichum*  
*Duthiella wallichii*  
*Aerobryidium filamentosum*  
*Pseudospiridentopsis horrida*  
*Floribundaria floribunda*  
*Barbella flagellifera*  
*Trachycladiella aurea*  
*Scorpiurium circinatum*  
*Scorpiurium deflexifolium*  
*Plasteurhynchium striatulum*  
*Aerobryum speciosum*  
*Pseudoscleropodium purum*  
*Eurhynchium angustirete*  
*Eurhynchium striatum*  
*Palamocladium euchloron*  
*Palamocladium leskeoides*  
*Rhynchostegium psilopodium*  
*Platyhypnidium riparioides*  
*Rhynchostegium confertum*  
*Rhynchostegium pallidifolium*  
*Rhynchostegium serrulatum*  
*Rhynchostegium rotundifolium*  
*Rhynchostegium murale* (North Urals)  
*Rhynchostegium murale* (China)  
*Rhynchostegium murale* (South Urals)  
*Meteoridium remotifolium*  
*Squamidium brasiliense*  
*Zelometeorium patulum*  
*Bryoandersonia illecebra*  
*Rhynchostegiella tenella*  
*Rhynchostegiella teneriffae*  
*Rhynchostegiella macilenta*  
*Platyhypnidium austrinum*  
*Okamuraea brachydictyon*  
*Brachythecium kopenenii*  
*Cirriphyllum crassinervium*  
*Cirriphyllum piliferum*  
*Aerolindigia capillacea*  
*Rhynchostegiella brachypodia*  
*Clasmatodon parvulus*  
*Helicodontium capillare*  
*Homalotheciella subcapillata*  
*Eurhynchium pumilum*  
*Eurhynchium vagans* (China)  
*Donrichardsia macroneuron*  
*Platyhypnidium patulifolium*  
*Eurhynchium savatieri*  
*Eurhynchium hians*  
*Eurhynchium vagans* var. *bergmaniae*

METEORACEAE

RHYNCHOSTEGIOIDEAE

BRACHYTHECIOIDEAE

RHYNCHOSTEGIELLOIDEAE

BRACHYTHECIOIDEAE, HOMALOTHECIOIDEAE (see next page)



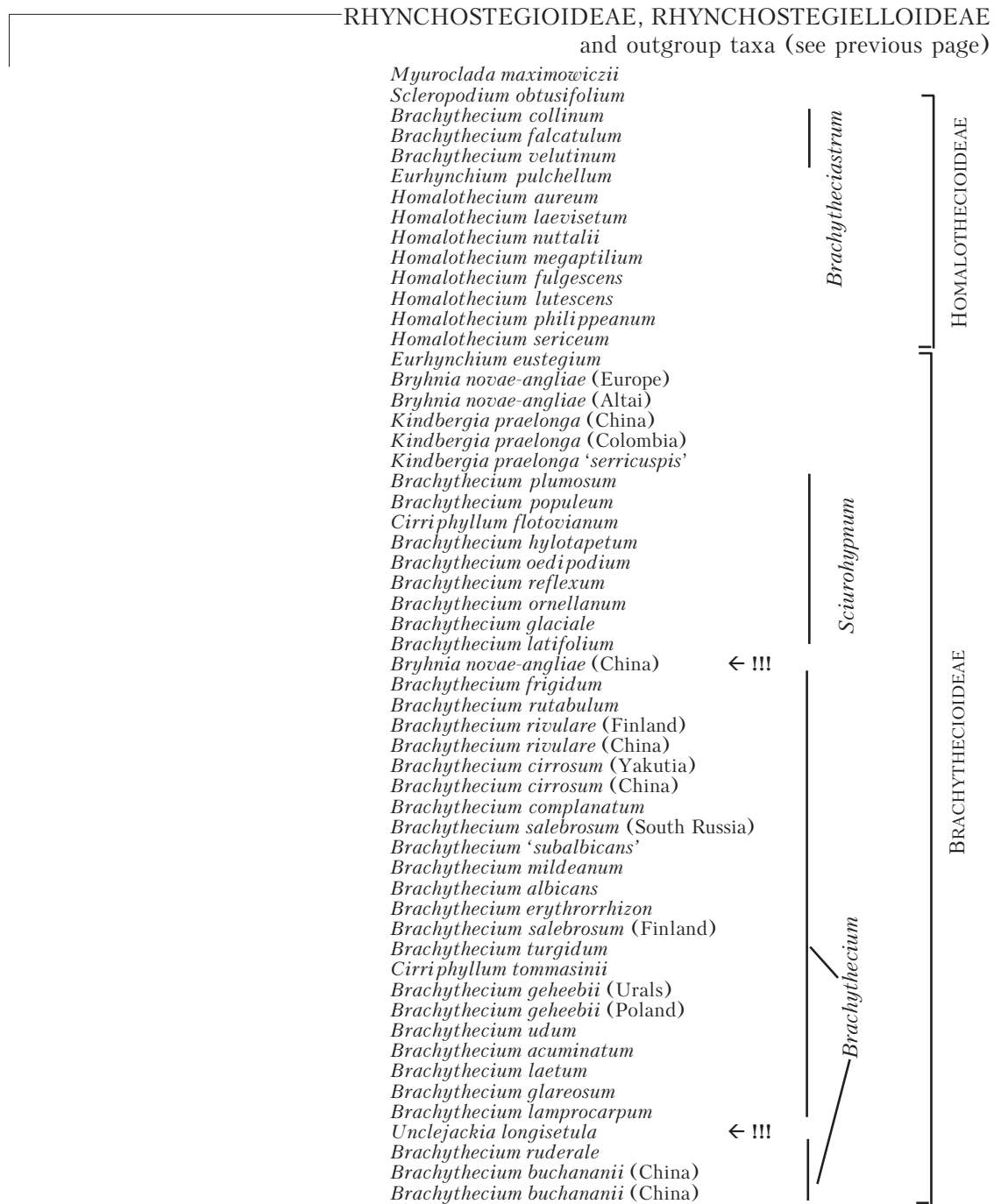


Fig. 1 (both this and opposite pages). Strict consensus tree of 3 most parsimonious trees (L=3546; CI=14; RI=88) from POY analysis of combined morphological and sequence data with gap cost 1. [*Brachythecium* 'subalbicans' = *Brachythecium* cf. *salebrosum* from China, similar to the type of *B. subalbicans* Broth., nom. illeg. (its holotype described and illustrated by Wang & Hu, 1998); *Kindbergia praelonga* 'serricuspis' – very thin phenotype of the species, earlier considered as an independent species *Eurhynchium serricuspis* C. Muell. See comments on *Bryhnia novae-angliae* and *Unclejackingia longisetula* (marked with !!!) under those genera.

<i>Leskea polycarpa</i>			
<i>Rozea andrieuxii</i>			
<i>Rozea subjulacea</i>			
<i>Leucodon sciuroides</i>			
<i>Lindigia debilis</i>			
<i>Bestia longipes</i>			
<i>Dolichomitriopsis diversiformis</i>			
<i>Isothecium alopecuroides</i>			
<i>Lembophyllum clandestinum</i>			
<i>Hypnum cupressiforme</i>			
<i>Ctenidium molluscum</i>			
<i>Plagiothecium denticulatum</i>			
<i>Amblystegium serpens</i>			
<i>Campylium stellatum</i>			
<i>Meteoriella soluta</i>			
<i>Hylocomium splendens</i>			
<i>Rhytidiadelphus triquetrus</i>			
<i>Trachypus bicolor</i>			
<i>Chrysocladium retrorsum</i>			
<i>Meteorium polytrichum</i>			
<i>Duthiella wallichii</i>			
<i>Aerobryidium filamentosum</i>			
<i>Pseudospiridentopsis horrida</i>			
<i>Floribundaria floribunda</i>			
<i>Barbella flagellifera</i>			
<i>Trachycladiella aurea</i>			
<i>Bryoandersonia illecebra</i>			
<i>Pseudoscleropodium purum</i>			
<i>Scorpiurium circinatum</i>			
<i>Scorpiurium deflexifolium</i>			
<i>Plasteurhynchium striatulum</i>			
<i>Palamocladium euchloron</i>			
<i>Palamocladium leskeoides</i>			
<i>Eurhynchium angustirete</i>			
<i>Eurhynchium striatum</i>			
<i>Aerobryum speciosum</i>			
<i>Platyhypnidium riparioides</i>			
<i>Rhynchostegium confertum</i>			
<i>Rhynchostegium psilopodium</i>			
<i>Rhynchostegium rotundifolium</i>			
<i>Rhynchostegium pallidifolium</i>			
<i>Rhynchostegium serrulatum</i>			
<i>Rhynchostegium murale</i> (China)			
<i>Rhynchostegium murale</i> (North Urals)			
<i>Rhynchostegium murale</i> (South Urals)			
<i>Myuroclada maximowiczii</i>			
<i>Meteoridium remotifolium</i>			
<i>Squamidium brasiliense</i>			
<i>Zelometeorium patulum</i>			
<i>Donrichardsia macroneuron</i>			
<i>Platyhypnidium patulifolium</i>			
<i>Eurhynchium hians</i>			
<i>Eurhynchium pumilum</i>			
<i>Eurhynchium savatieri</i>			
<i>Eurhynchium vagans</i> var. <i>bergmaniae</i>			
<i>Eurhynchium vagans</i> (China)			
<i>Platyhypnidium austrinum</i>			
<i>Rhynchostegiella tenella</i>			
<i>Rhynchostegiella teneriffae</i>			
<i>Rhynchostegiella macilenta</i>			
<i>Okamuraea brachydictyon</i>			
<i>Cirriphyllum crassinervium</i>			
<i>Brachythecium koponenii</i>			
<i>Cirriphyllum piliferum</i>			
<i>Aerolindigia capillacea</i>			
<i>Rhynchostegiella brachypodia</i>			
<i>Clasmatodon parvulus</i>			
<i>Helicodontium capillare</i>			
<i>Homalotheciella subcapillata</i>			

METEORACEAE

RHYNCHOSTEGIOIDEAE

BRACHYTHECIAEAE

Oxyrrhynchium

RHYNCHOSTEGIELLOIDEAE

BRACHYTHECIOIDEAE, HOMALOTHECIOIDEAE (see next page)

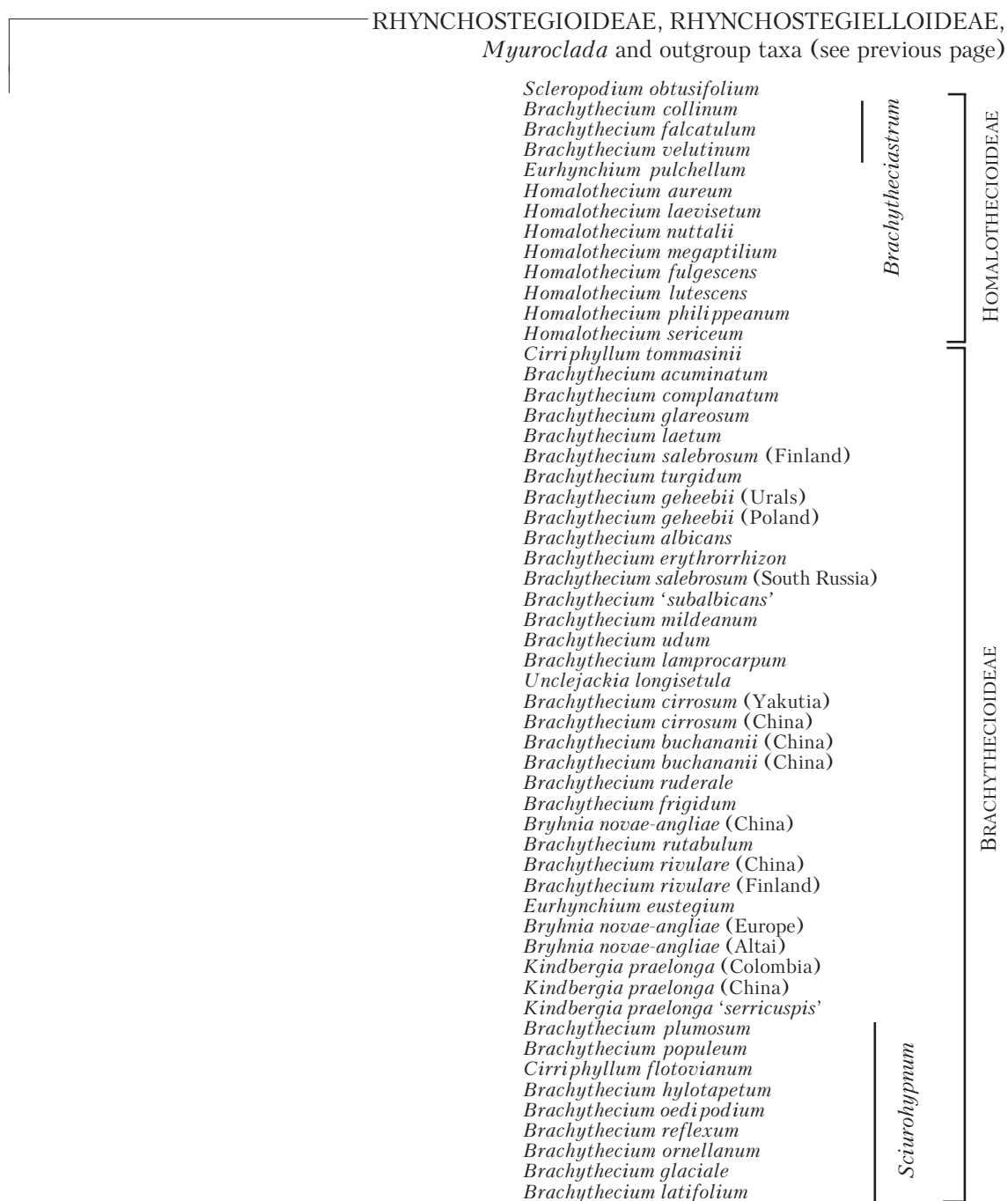


Fig. 2 (both this and opposite pages). Strict consensus tree of 779 most parsimonious trees (L=2436; CI=29; RI=67) from Nona analysis based on POY character optimization on combined morphological and sequence data with gap cost 1. Jackknife values for clades are presented above and bremer support below branches. See also comments to Fig. 1.

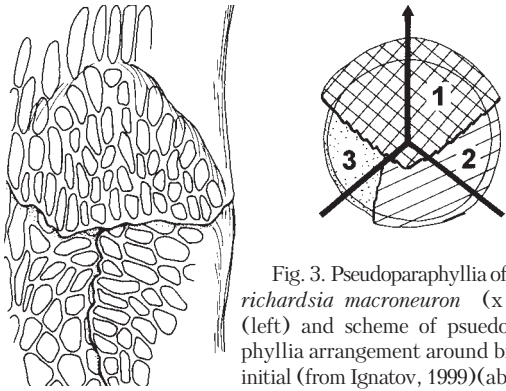


Fig. 3. Pseudoparaphyllia of *Donrichardsia macroneuron* (x 350) (left) and scheme of pseudoparaphyllia arrangement around branch initial (from Ignatov, 1999)(above).

for details see Huttunen & Ignatov, 2003). Due to difficulties to calculate branch support values in POY, jackknife and bremer support for clades were obtained from Nona analysis of the POY alignment (Fig. 2). This Nona tree is the main used for the subsequent discussion. However, clades lacking support are collapsed in Nona tree (Fig. 2), but not in the optimal tree resulting from the POY analysis (Fig. 1). Hence our discussion will refer to the results from POY analyses (Fig. 1) when addressing the affinities and circumscription of clades that are poorly resolved in Nona topology (Fig. 2).

### 3. CURRENT ATTEMPT TO UNDERSTAND BRACHYTHECIACEAE (2002)

#### 3A. THE CIRCUMSCRIPTION OF THE BRACHYTHECIACEAE

The Meteoriaceae and Brachytheciaceae form a monophyletic group in POY analysis (Fig. 1), but support for a shared ancestry in Nona analysis is lacking (Fig. 2). There are only two species, *Lindigia debilis* (Mitt.) Jaeg. and *Neobarbella comes* (Griff.) Noguchi (the latter not shown in the present analysis, but see Quandt & al., 2003b), with the pseudoparaphyllia pattern of the Brachytheciaceae and Meteoriaceae, which do not appear within the Brachytheciaceae + Meteoriaceae clade. These exceptions will be discussed elsewhere. Because both *Lindigia* and *Neobarbella* are not regarded as members of the Brachytheciaceae, they are not discussed in the present paper.

The Brachytheciaceae-Meteoriaceae clade (Fig. 1) includes two independent lineages. The first clade consists of typical Meteoriaceae sensu lato including former Trachypodiaceae (Buck, 1994, Quandt & al., 2003a). The other one includes Brachytheciaceae taxa together with a few genera, such as *Aerobryum*, *Aerolindigia*,

*Meteoridium*, *Zelometeorium*, and *Squamidium*, that have been traditionally placed into Meteoriaceae. Their position in the Meteoriaceae is, however, somewhat odd due to their smooth laminal cells, which make them different from most of the taxa in this family. According to Buck & Goffinet (2000) and also our results, they should be included in the Brachytheciaceae. Thus, the Meteoriaceae are quite nicely separated from Brachytheciaceae by having papillose laminal cells. Problems with the classification of the Meteoriaceae are discussed by Quandt & al. (2003a) and Huttunen (in prep.).

As defined here, the family Brachytheciaceae is monophyletic and can be surprisingly easily delimited by only two morphological characters: *Brachythecium*-like pseudoparaphyllia pattern (Fig. 3) and laminal cells without papillae (with two exceptions of *Neobarbella* and *Lindigia*, which otherwise share this definition, but according to the present results do not belong to the family). Some Brachytheciaceae have papilla-like prorae in cell corners, which are totally different from round "true" papillae above cell luminae or cell walls in Meteoriaceae. Delimited in this way, the Brachytheciaceae includes 41 genera with 250-400 species.

\* \* \*

Crosby & al. (1999) included in the Brachytheciaceae seven genera which do not belong neither to Brachytheciaceae, nor to Meteoriaceae according to morphological data (and in some cases also molecular data – those marked by asterisk): *Bestia*\*, *Bryostreimannia*, *Isothecium*\*, *Pseudopleuropus*, *Puiggariopsis*, *Rozea*\*, *Stenocarpidiopsis*. Ignatov's (1999) statement that *Squamidium* does not have pseudoparaphyllia of the Brachytheciacean type was based on misidentified material. Also the hypothesis that *Meteoriella soluta* is a member of the Brachytheciaceae (Ignatov l. c.) is currently being reexamined and the results will be discussed separately.

Goffinet & al. (2001) found *Hildenbrandtiella pachyclada* Besch. in the most basal position of the Brachytheciaceae clade (in analysis of rps4 data). However, this species has narrowly lanceolate pseudoparaphyllia, suggesting [among other morphological data] that its previous position within Pterobryaceae (cf. Buck & Goffinet, 2000) is likely to be correct.

## 3B. INFRAFAMILIAL CLASSIFICATION

Previous authors usually did not subdivide the family into subfamilies or tribes. Limpricht (1896) sorted European taxa into Brachystegiaceae (with short operculum) and Eustegiaceae (with rostrate operculum), and some subsequent authors followed him (e. g. Roth, 1905). The application of such descriptive names is allowed by the ICBN for taxa above the family level, without comments on what to do with such taxa at familial and infrafamilial levels. We suggest to ignore these Limpricht' subfamilies, as they do not refer to any generic name.

The present analysis of Brachytheciaceae reveals four well-supported clades, which are centered by *Homalothecium*, *Brachythecium*, *Oxyrrhynchium* + *Rhynchostegiella*, and *Rhynchostegium*. Of 98 specimens of ca. 90 species from 33 genera of Brachytheciaceae, two species were found in rather indefinite position, *Myuroclada maximowiczii* and *Scleropodium obtusifolium*. They are preliminary placed and discussed within the Brachythecioideae. Eight genera (*Brachytheciella*, *Nobregaea*, *Eurhynchiella*, *Flagelledium*, *Mandoniella*, *Schimperella*, *Juratzkaeella*, *Eriodon*), very rare and mostly monospecific and known mostly from the holotypes of type species, were not included in molecular studies; their placements are based on morphology and are considered as preliminary.

## 3C. A NEW GENERIC SYSTEM OF BRACHYTHECIACEAE

The genera as circumscribed below are supplemented with lists of species; the “species included” sections are based on specimens checked by ourselves. These lists of species serve to illustrate our concepts of genera and must not be considered as complete and taxonomically and nomenclaturally verified. They are based largely on Crosby & al. (1999) list, which summarized data from revisions, check-lists, and old publications.

Generic descriptions and distribution are based only on species from “species included”, not from problematic species (exception of *Bryhnia* specially discussed under that genus).

## NOTES ON TERMINOLOGY:

Axillary hairs – number of cells refers to whole axillary hair, not only to upper cells.

Paraphyllia – there is no big similarity between paraphyllia of the Amblystegiaceae or the Leskeaceae and that of the *Kindbergia* (Fig. 4). However, seems there is no better term for longitudinal ridges,

1 to 6 cells high, below the leaf insertion and around branch primordia (outside of pseudoparaphyllia).

Smooth laminal cells – since the evaluation of a smooth vs. a slightly prorate state, as we believe, depends much on microscope quality, we do not separate them. Only the cases where projections are high, tooth-like, and rather common, they are contrasted to former condition. Defined in this way, all genera have smooth cells except *Bryhnia*, *Kindbergia*, *Eurhynchiadelphus*, and *Plasteurhynchium*.

Spore size is categorized in two states: “spores large” means that at least a few spores are 25 µm or larger; otherwise spores are called small. Most species have spores ranging between 14 and 22 µm. The presence of very small spores (10–14 µm) in some taxa is specifically underlined.

Subalar cells. The highest differentiation among laminal basal cells in the Brachytheciaceae occurs in the area where the line of the leaf insertion makes maximal turn to the decurrency. Cell differentiation starts from this point and sometimes differentiated cells reach the leaf margin, thus allowing to use the term “alar cells” (=cells of basal leaf angles). However, in many cases (*Eurhynchium*, *Bryhnia*, etc.) the group of differentiated cells remains quite far from leaf angle. We suggest to call them “subalar cells”.

**BRACHYTHECIACEAE** Schimp., Syn. Musc. Eur., ed. 2. XCV sic [CXV], 637. 1876, “Brachytheciae”. Type: *Brachythecium* B. S. G.

Camptotheciaceae Schimp., Syn. Musc. Eur., ed. 2. XCV, 635. 1876, “Camptotheciae”. Type: *Camptothecium* B. S. G.

Donrichardsiaceae Ochyra, Lindbergia 11: 7. 1985. Type: *Donrichardsia* Crum et Anderson.

Diagnostic characters: first (earliest in differentiation) pseudoparaphyllium [=juvenile branch leaf, scaly leaf] faced downward, second and third – at the angle 120° to the first. Laminal cells without papillae above central part of lumina. Stomatal pore round.

Besides these character states there are no morphological features that consistently characterize members of Brachytheciaceae, and at the same time excluding members of other families. Hence the family description is rather lowly informative: Stem creeping, ascending to erect or pendent, sometimes with stolons; differentiation into primary and secondary stems absent or present; central strand present or absent; branching irregular to pinnate. Foliage julaceous or complanate, very dense to very lax; stem leaves commonly ovate-lanceolate, sometimes orbicular, sometimes narrowly linear; costa present, rarely ab-

sent; laminal cells linear, elongate, rhombic, ovate or round, thin- or thick-walled; alar cells not differentiated, or small and opaque, or large and inflated. Branch leaves similar to stem leaves or differentiated. Autoicous, dioicous, polyoicous, synoicous, or phyllodioicous. Perichaetial leaves smooth or plicate, costate or ecostate. Seta short (capsule immersed to emergent) or long, smooth or rough. Capsule erect, inclined, horizontal, or pendent. Operculum conic to longly, obliquely rostrate. Annulus separating by fragments, of 2-3 rows of large cells, or absent. Peristome xerocastique or hygrocastique, in latter case variously reduced; exostome present to reduced (*Clasmatodon*), when developed proximally cross-striolate, papillose or smooth. Endostome completely developed (with 3-4 shortly appendiculate cilia) to reduced to short basal membrane (free segments lacking, some segment material adherent to teeth, cilia none). Spores small or large. Calyptra cucullate to somewhat mitrate, naked to hairy.

**SUBFAM. HOMALOTHECIOIDEAE**

**SUBFAM. NOV.**

*Plantae minutae vel robustae. Folia caulina ovata vel anguste lanceolata, acuta vel acuminata; folia ramulina acuta, acuminata vel obtusa; costa crassa vel tenuis; cellulae elongatae vel lineares. Autoica, dioica, synoica, polyoica vel phyllodioica. Seta scabra vel laevissima. Capsula erectis vel horizontalis. Peristomium perfectum vel imperfectum. Operculum rostratum vel conicum.*

Type species: *Homalothecium* B. S. G.

Plants often rather rigid, rich green to rich golden, more rarely pale. Leaf margin toothed to the base, more rarely subentire; costa frequently ending in spine; laminal cells narrowly linear; basal cells frequently small, thick-walled; alar cells small, subquadrate, in subquadrate group. Autoicous, dioicous, synoicous, polyoicous, phyllodioicous. Seta rough or smooth. Operculum conic or rostrate. Peristome complete to strongly modified. Calyptra smooth, rarely hairy. Xeromesophytic.

Genera included: *Homalothecium*, *Brachytheciastrum*, *Eurhynchiastrum*.

1. **Homalothecium** B. S. G., Bryol. Eur. 5: 91. 1851. Type: *H. sericeum* (Hedw.) B. S. G. (= *Leskea sericea* Hedw.).

*Camptothecium* B. S. G., Bryol. Eur. 6: 31. 1853. Type: *C. lutescens* (Hedw.) B. S. G. (= *Hypnum lutescens* Hedw.).

*Trachybryum* (Broth.) W. B. Schofield, J. Hattori Bot. Lab. 31: 222. 1968. – *Camptothecium* sect. *Trachybryum* Broth., Nat. Pfl. 1(3): 1140. 1908. Type: *Camptothecium megaptilum* Sull. (= *T. megaptilum* (Sull.) W. B. Schofield.)

*Oticodium* (C. Müll.) Kindb., Enum. Bryin. Exot. 27. 1888. – *Hypnum* sect. *Oticodium* C. Müll., Linnaea 39: 469. 1875. Type: *Hypnum celebesiae* C. Müll. (= *O. celebesiae* (C. Müll.) Kindb.) = *Homalothecium laevisetum* Sande Lac.

Plants large to medium-sized, green to golden or pale yellow. Stem prostrate to ascending, with central strand, densely foliate, irregularly to regularly pinnately branched, branches straight or curved, densely foliate. Axillary hairs 3-6-celled, upper cells often relatively short. Pseudoparaphyllia acute or acuminate. Stem leaves erect-appressed when dry, erect to erecto-patent when wet, lanceolate or narrowly triangular, being widest just above leaf base, acuminate, strongly longitudinally plicate; margin serrulate to subentire, sometimes with sharp backward recurved teeth in alar region; costa ending above mid-leaf to percurrent, at end smooth or toothed; laminal cells elongate to linear, thick-walled; basal cells short, small and thick-walled, forming opaque area across the base; alar cells isodiametric, forming more or less well delimited group. Branch leaves not differentiated or somewhat narrower and with a more serrate margin and frequently larger than stem leaves. Dioicous or phyllodioicous. Perichaetial leaves with straight or more rarely reflexed acumina. Seta rough or smooth. Capsule erect, symmetric or more or less curved to inclined. Annulus separating by fragments. Operculum highly conic and gradually tapered to rostrum or more rarely conic. Peristome hygrocastique, rarely xerocastique, perfect to modified; exostome teeth below cross striolate, papillose, or smooth; endostome perfect (with high basal membrane, broad segments and cilia more than half of segment length) to strongly reduced (low basal membrane with rudimentary segments). Spores small. Calyptra naked or rarely hairy. Xeromesophytic.

Distribution: Eurasia and North America.

(a) *Homalothecium* is monophyletic and well supported if the species sometimes considered in *Camptothecium* and *Trachybryum* are included.

(b) The genus *Camptothecium* was segregated from *Homalothecium* based principally on the better developed to almost complete peristome.

However, the type of *Homalothecium*, *H. sericeum*, appears in phylogenetic analysis more closely related to *Camptothecium* (*Homalothecium*) *lutescens*, the type of *Camptothecium*, than to the American species with modified peristome, like *H. nuttallii*. The results of our analysis show that species with rather well-developed peristome are basal in the *Homalothecium* clade, and that taxa with modified peristomes are grouped by their geographic distribution. This supports the conclusion of Ignatov & al. (1998) based on SEM studies, that there are at least two independent lineages of peristome modification in the genus. Note, that the North American pattern of peristome modification is different from that in Eurasian species.

(c) The only species of *Trachybryum*, *T. megaptilum* appears well nested within *Homalothecium* in all analyses. This species is peculiar in its large size and quite regular pinnate branching. However, pinnate branching is not a unique case in the genus. For example, the North American *H. nuttallii* and *H. pinnatifidum* are always very regularly pinnate, although sometimes not conspicuously so because of curved branches.

(d) *Homalothecium laevisetum* is found together with the rest of the genus in most of the analyses, although the chloroplast genes suggest a position within a *Rhynchostegium*-clade, close to *Palamocladium leskeoides*. The problem needs additional studies. However, it is worth to notice that this species is probably the most isolated in the genus based on morphology – it has a strongly reduced peristome, and the shoots (in southern populations) are sometimes attenuate, becoming stoloniferous. If further studies support the isolated position of this species, *Oticodium* would be the correct generic name for this segregate.

(e) *Brachythecium geheebii* was transferred to *Homalothecium* by Wigh (1973). This species is commented under *Brachythecium*.

Species included:

*Homalothecium aeneum* (Mitt.) Lawt.

*H. arenarium* (Lesq.) Lawt.

*H. aureum* (Spruce) H. Robinson

*H. fulgescens* (Mitt.) Lawt.

*H. laevisetum* Sande Lac.

*H. lutescens* (Hedw.) H. Robinson

*H. megaptilum* (Sull.) H. Robinson

*H. nevadense* (Lesq.) Ren. et Card.

*H. nuttallii* (Wils.) Jaeg.

*H. philippeanum* (Spruce) B. S. G.

*H. pinnatifidum* (Sull. et Lesq.) Lawt.

*H. sericeum* (Hedw.) B. S. G.

Hofmann (1998) published a world-wide revision of the genus, wherein she discusses eight more species, which she excludes from the circumscription, but without offering alternative systematic placements (mostly in *Brachythecium*). The affinities of one species, *Camptothecium subhumile* Broth., remain unclear, as the type was not found in H-BR.

2. **Brachytheciastrum** gen. nov. Type: *B. velutinum* (Hedw.) Ignatov et Huttunen (= *Hypnum velutinum* Hedw.).

*Plantae minutae vel mediocres. Folia erecta vel falcata, lanceolata vel lanceolata-ovata, margine toto serrulata vel serrata; costa ad medium vel ultra evanida vel percurrenta; cellulae lineares, cellulae alares subquadrates, crassiuscules. Autoica, synoica vel polyoica. Seta scabra vel laevissima. Capsula horizontalis, subventricosis. Peristomium perfectum. Operculum conicum.*

Plants small to medium-sized, green to golden, more rarely pale yellow. Stem prostrate, with central strand, densely or loosely foliate, irregularly to at places regularly pinnately branched, branches straight, densely or loosely, julaceous or complanately foliate. Axillary hairs 2-3(-4)-celled, upper cells relatively short and blunt. Pseudoparaphyllia acute. Stem leaves erecto-patent, erect, imbricate or falcate-secund, lanceolate to ovate, acuminate, slightly longitudinally plicate to smooth; margin serrulate to subentire, costa ending above mid-leaf to percurrent, at end smooth or toothed; laminal cells elongate to linear, thick-walled; alar cells isodiametric, forming more or less well delimited subquadrate group. Branch leaves somewhat narrower, with more serrate margin and back of costa, and usually smaller than stem leaves. Autoicous, more rarely synoicous to polygamous. Perichaetial leaves with reflexed acumina. Seta rough or smooth. Capsule inclined to horizontal, often ventricose, remains greenish until almost mature. Annulus separating by fragments. Operculum conic. Peristome xerocastique, perfect. Spores small, mostly, ca. 10-13 µm. Calyptra naked. Xeromesophytic or mesophytic.

Distribution: subcosmopolite.

(a) This group of species was recognized by Brotherus (1925) and many other authors as the subgenus or section *Velutina*. In the optimal trees

presented here (Figs. 1, 2) *Brachytheciastrum* is resolved as a paraphyletic group, although this result is highly dependent on minor variation in alignment of sequence data and hence also on gap cost used in POY analysis as well as treatment of 9 bp inversion region on psbT-N spacer region (Huttunen & Ignatov, 2003). In the analyses with higher gap costs than one and in those analyses where inversion region is omitted or altered, the three species of *Brachytheciastrum* involved in the present analysis appear as a clade. Although more detailed studies are needed to understand the relationships between species, the isolated position of this group with regard to *Brachythecium*, even in its broadest sense, is clear. Thus, it is with only a little hesitation that we propose to recognize it as a separate genus. Our decision is also supported by several earlier classifications where this group has been recognized as an own entity (e.g. Brotherus, 1925, Ignatov, 1998).

(b) The close relationship of the *Brachythecium velutinum* group to *Homalothecium* has never been suggested earlier. These taxa share only a few character states, which are, however, not present in all species: plants often quite rich golden, cells of axillary hairs uniformly short, leaves rather rigid, margin sharply serrulate almost to the base, costa often ending in spine and sometimes toothed near its end; laminal cells narrowly linear, alar cells thick-walled, subquadrate, in subquadrate group.

(c) Most species of *Brachytheciastrum* have small plants, but a few Central Asian and Himalayan species (e. g., *B. falcatulum* and *B. kashmirensis*) are of about the same size as *Brachythecium salebrosum*.

Species included:

***B. collinum*** (Schleich. ex C. Müll.) comb. nov. – *Hypnum collinum* Schleich. ex C. Müll., Syn. Musc. Frond. 2: 429. 1851.

***B. dieckei*** (Roell) comb. nov. – *Brachythecium dieckei* Roell, Hedwigia 36 Beibl. 2: 41. 1897.

***B. falcatulum*** (Broth.) comb. nov. – *Hypnum falcatulum* Broth., Acta Soc. Sci. Fenn.: 24(7): 34. 1899.

***B. kashmirensis*** (Broth.) comb. nov. – *Hypnum kashmirensis* Broth., Acta Soc. Sci. Fenn.: 24(2): 37. 1898.

***B. leibergii*** (Grout) comb. nov. – *Brachythecium leibergii* Grout, Mem. Torrey Bot. Club 6: 197. 1897.

***B. microcollinum*** (E. B. Bartram) comb. nov. – *Brachythecium microcollinum* E. B. Bartram, Farlowia 2(3): 318. 1946.

***B. paradoxum*** (Hook. et Wils.) comb. nov. – *Hypnum paradoxum* Hook. et Wils., London J. Bot. 3: 554. 1844.

***B. trachypodium*** (Funck ex Brid.) comb. nov. – *Isothecium trachypodium* Funck ex Brid., Bryol. Univ. 2: 766. 1827.

***B. velutinum*** (Hedw.) comb. nov. – *Hypnum velutinum* Hedw., Sp. Musc. Frond. 272. 1801.

Species referred to the genus based on literature descriptions [new combinations are not done, as we did not studied specimens]: *Brachythecium appleyardiae* McAdam et A. J. E. Smith (McAdam & Smith, 1981), *B. bellicum* Buck, W. R., J. A. Jiménez, R. M. Ros et M. J. Cano (Buck & al., 2001), *B. bolanderi* (Lesq.) Jaeg. (Lawton, 1971); *B. curvatum* (Broth.) Par. (Gangulee, 1978; Vohra, 1983); *B. fendleri* (Sull.) Jaeg. (McFarland, 1994), *B. occidentale* (Hampe) Jaeg. (McFarland, 1994), *B. percurrens* Hedenäs (Hedenäs, 1992), *B. praelongum* Schimp. ex C. Müll. (McFarland, 1988), *B. saporense* (Besch.) Takaki (Takaki, 1955b).

Species of *Brachytheciastrum* which status needs to be confirmed [new combinations are not done, as these taxa might be proofed to be just a synonyms]:

*Brachythecium leiopodium* Broth. (~ *falcatulum*)

*B. olympicum* Jur. (~ *velutinum*)

*B. venustum* De Not. (~ *velutinum*)

**3. *Eurhynchiastrum*** gen. nov. Type: *E. pulchellum* (Hedw.) Ignatov et Huttunen (= *Hypnum pulchellum* Hedw.).

*Plantae minutae vel mediocres. Folia caulina ovata-triangularata vel ovata-lanceolata, margine serrata vel subintegra; costa ultra medium evanida; cellulae lineares, cellulae alares subquadrates, crassiuscules; folia ramulina ovata-lanceolata, obtusa. Phyllodioica vel dioica. Seta laevissima. Capsula horizontalis. Peristomium perfectum. Operculum rostratum.*

Plants small to medium-sized, green to brownish-green. Stem prostrate, with central strand, densely or loosely foliate, irregularly densely branched, branches straight to often curved, densely julaceously foliate. Axillary hairs 3(-4)-celled. Pseudoparaphyllia acute. Stem leaves erect to erecto-patent, ovate-triangular to ovate-lanceolate,



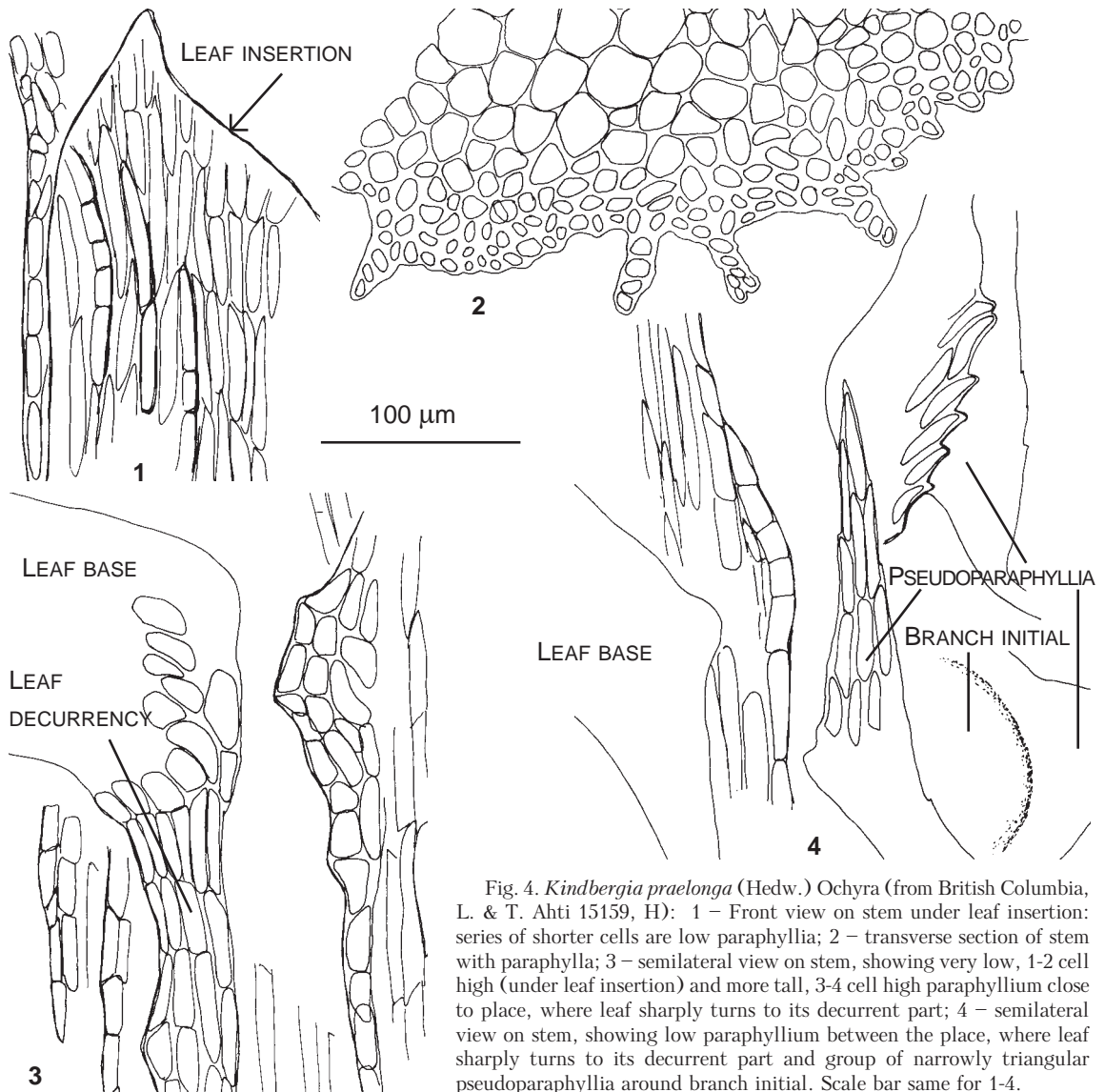


Fig. 4. *Kindbergia praelonga* (Hedw.) Ochyra (from British Columbia, L. & T. Ahti 15159, H): 1 – Front view on stem under leaf insertion: series of shorter cells are low paraphyllia; 2 – transverse section of stem with paraphyllia; 3 – semilateral view on stem, showing very low, 1-2 cell high (under leaf insertion) and more tall, 3-4 cell high paraphyllium close to place, where leaf sharply turns to its decurrent part; 4 – semilateral view on stem, showing low paraphyllium between the place, where leaf sharply turns to its decurrent part and group of narrowly triangular pseudoparaphyllia around branch initial. Scale bar same for 1-4.

acuminate, not plicate; margin serrulate to subentire, costa ending above mid-leaf in spine; laminal cells linear, moderately thick-walled; alar cells isodiametric, thick-walled, forming a more or less well delimited subquadrate group. Branch leaves blunt, and smaller and narrower than stem leaves; costa with prominent spine. Dioicous or phyllodioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small, 17-23 µm. Calyptra naked. Xerome-sophytic or mesophytic.

Distribution: Holarctic and Central America.

(a) The nested position of *Eurhynchium pul-*

*chellum* in the Homalothecioideae clade strongly supports excluding it from *Eurhynchium*, a genus based on *E. striatum*, a member of the Rhynchostegioideae clade. Although our data offer little support for either *Eurhynchiastrum* or *Brachytheciastrum*, these two genera are quite distinct morphologically. Among others, the former has smooth seta (rough in most species of *Brachytheciastrum*), and rostrate operculum (conic in *Brachytheciastrum*), etc. We consider that such differentiation warrants taxonomic recognition, and therefore establish the new genus *Eurhynchiastrum*.

(b) In the present treatment *Eurhynchiella* (South Africa and probably also South Ameri-

ca; not included in our molecular studies), was tentatively put in Rhynchostegielloideae (Ignatov & al., 1999). However this genus is similar with *Eurhynchiastrum* in appearance, size, and smooth seta (so it can not be excluded, that in future studies its position will be reconsidered).

Species included:

***E. pulchellum*** (Hedw.) comb. nov. – *Hypnum pulchellum* Hedw., Sp. Musc. Frond. 265. 68: f. 1-4. 1801.

Species of *Eurhynchiastrum*, which status has to be confirmed:

*Eurhynchium yezoanum* Okam. (~ *E. pulchellum*).

#### SUBFAM. BRACHYTHECIOIDEAE

Type species: *Brachythecium* B. S. G.

Plants rigid to soft in texture, rich green, yellowish to very pale stramineous. Leaf margin toothed to base or not; costa ending in spine or without spine; laminal cells ovate, hexagonal, or elongate to linear, thin- or thick-walled, often strongly tooth-like prorate on upper dorsal lamina (in *Bryhnia* and *Kindbergia*); alar cells small, subquadrate, relatively thick-walled, or large, inflated, thin-walled, in subquadrate or elongate group. Autoicous, dioicous, rarely phylloidioicous. Seta rough or smooth. Operculum conic to rostrate. Peristome perfect to modified (in *Unclejackia*). Hygromesophytic, mesophytic, or xeromesophytic.

Genera included: *Kindbergia*, *Eurhynchiadelphus*, *Bryhnia*, *Brachythecium*, *Sciurohypnum*, *Unclejackia*.

Genera included with questionmark: *Myuroclada*, *Scleropodium*, *Brachytheciella*.

4. ***Kindbergia*** Ochyra, *Lindbergia* 8: 53. 1982. Type: *Hypnum stokesii* Turn. = *K. praelonga* (Hedw.) Ochyra.

*Stokesiella* H. Robinson, *Bryologist* 70: 39. 1967, nom. illeg., later homonym.

Plants medium-sized to robust, green to brownish-green. Stem prostrate, ascending to erect, with central strand, usually very loosely foliate, quite regularly pinnately branched, branches straight, densely or moderately densely, julaceously foliate. Axillary hairs 4-5-celled. Pseudoparaphyllia acuminate. Paraphyllia sometimes present (see Fig. 4 and discussion below). Stem leaves erecto-patent to squarrose, broadly triangular and tapered to lanceolate acumen, at base cordate and

longly, broadly decurrent, rarely slightly so; margin serrate above, serrulate below; costa ending in acumen, sometimes subpercurrent, with or without spine; laminal cells elongate, moderately thick-walled, sometimes forming tooth-like projections on dorsal surface; subalar cells isodiametric, relatively large and thin-walled, forming indistinctly delimited group. Branch leaves smaller, narrower, acuminate, with more strongly serrate margin and back of costa and more toothed dorsal lamina, than in stem leaves. Dioicous. Perichaetial leaves with reflexed acumina. Seta rough. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small or more rarely large. Calyptra naked. Mesophytic to hygromesophytic.

Distribution: Holarctic, Africa and South America.

(a) The species of this genus have typically broadly decurrent leaves. There are, however, two exceptions: *Kindbergia altaica* and *K. squarriifolia*, both known from a single collection well outside the range on *K. praelonga*, in Altai and Japan respectively.

(b) *Kindbergia* has many similarities with *Bryhnia* and *Eurhynchiadelphus*. These genera have sometimes strongly prorate laminal cells, forming dorsal tooth-like projections. Robinson (1962) considered *Kindbergia* species within *Bryhnia*, before he separated them in their own genus (Robinson, 1967).

(c) Stem on *Kindbergia* has longitudinal ridges, which we call paraphyllia. They are lower than in other genera, where they are taller and therefore look "foliose". However otherwise they seem to be similar, at least to what we call paraphyllia in *Palustriella*, *Leskea* and similar groups.

Species included:

*K. africanua* (Herz.) Ochyra

***K. altaica*** (Ignatov) comb. nov. – *Eurhynchium altaicum* Ignatov, *Arctoa* 7: 141. 37-38. 1998.

*K. arbuscula* (Broth.) Ochyra

***K. dumosa*** (Mitt.) comb. nov. – *Hypnum dumosum* Mitt., *J. Linn. Soc. Bot. Suppl.* 1: 80. 1859.

*K. kenyae* (Dix. ex Tosco & Piovano) O'Shea et Ochyra

*K. oedogonium* (C. Müll.) Ochyra

*K. oregana* (Sull.) Ochyra

*K. praelonga* (Hedw.) Ochyra

***K. squarriifolia*** (Broth. ex Iishiba) comb. nov.  
– *Eurhynchium squarriifolium* Broth. ex Iishiba, Bot. Mag. (Tokyo) 49: 602. 1935.

5. ***Bryhnia*** Kaur., Bot. Not. 1892: 61. 1892.  
Type: *Bryhnia scabrida* (Lindb.) Kaur. (= *Hypnum scabridum* Lindb.).

Plants small to rather robust, green, yellowish to brownish-green. Stem prostrate, with central strand, unevenly foliate, alternating cochleariform parts with moderately loose foliage or moderately dense with very loose, irregularly to regularly pinnately branched, branches straight, moderately densely, subcomplanately foliate. Axillary hairs 3-4-celled. Pseudoparaphyllia acute. Stem leaves imbricate-appressed, erect to patent, suborbicular or broadly triangular and broadly acute to ovate-lanceolate and then tapered to long acumen, decurrent; margin serrate above, serrulate below; costa ending in upper part of leaf, often with spine; laminal cells elongate-flexuose, moderately thick-walled, sometimes forming tooth-like projections on dorsal surface; alar cells (or sometimes only subalar cells) isodiametric, rather large and thin-walled, forming indistinctly delimited group. Branch leaves narrower and smaller than stem leaves (sometimes strongly and abruptly so), acute to acuminate (sharper than stem leaves), with margin and back of costa more strongly serrate and dorsal lamina more toothed. Dioicous. Perichaetial leaves with reflexed acumina. Seta rough. Capsule inclined to horizontal. Annulus separating by fragments. Operculum high-conic, tapered to broad beak. Peristome xerocastique, perfect. Spores small or more rarely large. Calyptra naked to hairy. Mesophytic to hygromesophytic.

Distribution: Holarctic.

Species included:

*Bryhnia scabrida* (Lindb.) Kaurin.

The circumscription of this genus needs a complete re-evaluation with DNA markers. The morphology seems to be especially misleading in this genus. In Japan and its adjacent areas, Takaki (1956) first split the genus into 15 species, but only 6 of them survived the revision by Noguchi (1991), all others were synonymized, mostly with *B. novae-angliae*. Of the remaining ones, three species show transitions to *B. novae-angliae* s. l., whereas the two last ones are quite distinct. However, their position in this genus is not obvious.

In Central China plants referred to this genus have narrower and more distant leaves (cf. Ignatov & al., 2003), but since these phenotypes occur also in North China and Japan, forming a continuous transition to the typical *B. novae-angliae* phenotype, we considered them conspecific with the latter (Koponen & al, 2000). The present investigation showed that the Chinese plants are very different from European and Siberian material. Is then American *B. novae-angliae* closer to European material (described as *B. scabrida*) or to Chinese population? In the latter case, our data suggest that American "*Bryhnia novae-angliae*" might be not even congeneric with the European *B. scabrida*. Very preliminary comparisons of our *Bryhnia* *trnL-F* sequences and American one available in Genebank (sequence AF143029/AF161122) show that this is not unlikely. Further studies are needed. However, the above generic diagnosis is retained here for *Bryhnia* in its traditional sense; Siberian and European populations, used in the present study, were described and illustrated by Ignatov (1998) and Popov & al. (2000). The Siberian material used for molecular studies was chosen to be as similar to American specimens as possible, with rather numerous branches and strongly prorate laminal cells.

6. ***Eurhynchiadelphus*** Ignatov, Huttunen et T. Kop., gen. nov. Type: *E. eustegia* (Besch.) Ignatov et Huttunen (= *Brachythecium eustegium* Besch.).

*Plantae mediocres vel robustae. Folia variabiles, oblongo-lanceolatae, ovato-triangularatae vel suborbiculatae; cellulae folii medianae breves, cellulae alares subquadrates. Phyllodioica vel dioica. Seta laevissima. Capsula horizontelis. Peristomium perfectum. Operculum lato rostratum.*

Plants rather robust, yellowish-green, not or slightly glossy. Stem creeping, with central strand, rather densely foliate, foliage of proximal and distal parts of shoots sometimes different; remotely pinnate-branched. Axillary hairs 3-4-celled, 1-2 basal cells colored. Pseudoparaphyllia triangular. Stem leaves erect to spreading, slightly to strongly concave, broadly oblong-lanceolate to ovate, acuminate or acute, twisted at apex, broadly and shortly decurrent; margin serrulate to serrate throughout; costa ending above mid-leaf, with spine; laminal cells irregularly elongate-polygonal, mod-

erately thick-walled, sometimes forming tooth-like projections on dorsal surface of upper leaf, towards base shorter and wider; alar cells subquadrate to rectangular, with incrassate cell walls, forming a moderately delimited opaque group; subalar cells sometimes enlarged and thin-walled. Branch leaves slightly smaller and relatively narrower than stem leaves, otherwise undifferentiated. Proximal (fairly developed) branch leaves similar to distal or sometimes differentiated and then short triangular, rounded above, very concave, forming cochleariform zones in both male and female shoots. Phyllocladous or dioicous. Perichaetial leaves with long, reflexed acumina. Seta long, smooth. Capsules inclined to horizontal. Annulus separating by fragments. Operculum conic with broad, distinctly or indistinctly delimited beak. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: East Asia.

(a) This East Asian species was transferred many times from *Brachythecium* (due to gametophytic characters) to *Eurhynchium* (due to beaked operculum) and back. Molecular data nicely confirmed the conclusion of a close relationship between this genus and *Bryhnia*, which was originally suggested based on morphology (Ignatov & al., 2003). Especially important for the latter conclusion was the finding of enormous variation in leaf shape along individual shoots in some Chinese populations.

(b) For discussion and illustration see Takaki (1956) and Ignatov & al. (2003).

Species included:

***Eurhynchiadelphus eustegia*** (Besch.) comb. nov. – *Brachythecium eustegium* Besch., Ann. Sci. Nat., sér. 7, 17: 375. 1893.

7. ***Myuroclada*** Besch., Ann. Sci. Nat., Bot., ser. 7, 17: 379. 1893. Type: *Myuroclada concinna* (Wils.) Besch. (= *Hypnum concinnum* Wils.) = *M. maximowiczii* (Borszcz.) Steere et Schof. *Achrolepis* (Lindb.) Card., Beih. Bot. Centralbl. 17: 34. 1904, *nom. illeg.*, type of earlier name included. – *Myurella* subgen. *Achrolepis* Lindb., Act. Soc. Sci. Fenn. 275, 276. 1872. Type: *Hypnum concinnum* Wils.

Plants rather robust, green to brownish-green. Stem prostrate to ascending, especially in dense growth, with central strand, julaceous, irregularly branched, branches straight, foliage simi-

lar. Axillary hairs 2-4-celled. Pseudoparaphyllia orbicular-triangular. Stem leaves tightly imbricate, orbicular or broadly ovate, very broadly acute and shortly apiculate, shortly decurrent, strongly concave; margin serrate except near base; costa ending in upper half of leaf without spine; laminal cells short rhombic to rhombic, moderately thick-walled, towards base wider and longer; alar cells subquadrate, forming indistinctly delimited area extending up along margin; subalar cells rather large and thin-walled, forming indistinctly delimited group. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum high-conic, gradually tapered to broad beak. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: East Asia and North America (introduced in Europe).

(a) Bescherelle (1893) considered this species to be close to *Scleropodium*, due to its cochleariform foliage, but Robinson (1962) found it to be close to *Bryhnia*. *Myuroclada* differs from *Bryhnia* in having smooth seta, and invariably suborbicular leaves. Another genus, closely related to *Bryhnia* and also having smooth seta is *Eurhynchiadelphus*. The latter, however, strongly differs from *Myuroclada* in leaf characters and branching pattern.

(b) Analysis of chloroplast sequence data alone (Huttunen & Ignatov, 2003) places *Myuroclada* in the same clade with *Bryhnia* and *Eurhynchiadelphus*. However, the inclusion of nuclear ITS2 data and morphological data resolve *Myuroclada* quite far from this position (Figs. 1, 2). The situation needs further investigation. Temporarily we keep *Myuroclada* close to *Bryhnia* and *Eurhynchiadelphus*.

Species included:

*M. maximowiczii* (Borszcz.) Steere et Schof.

Species excluded: *M. rotundifolia* (H. Arnell) A. L. Abramova et I. I. Abramov – ~ *Myrinia*.

8. ***Scleropodium*** B. S. G., Bryol. Eur. 6: 27. 1953. Type: *Scleropodium illecebrum* B. S. G. = *Scleropodium touretii* (Brid.) L. F. Koch.

Plants large to medium-sized, rigid, green to yellowish or brownish. Stem prostrate, with cen-

tral strand, densely foliate to cochleariform, irregularly and mostly sympodially branched. Axillary hairs 2-4-celled. Pseudoparaphyllia triangular. Stem leaves ovate to ovate-lanceolate, obtuse, acute to shortly acuminate, strongly concave; margin serrulate; costa ending in upper half of leaf, laminal cells unistratose, flexuose-linear, thick-walled; basal cells very thick-walled, making leaf difficult to detach, alar cells isodiametric, larger, thin- to thick-walled. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves with reflexed acumina. Seta strongly rough, rarely almost smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum conic. Peristome xerocastique, perfect. Spores small. Calyptra naked. Hygrophytic to xeromesophytic.

Distribution: Holarctic and maybe Australia.

(a) The present analysis (Figs. 2) supports a close relationship of *Scleropodium obtusifolium* to the Brachythecioideae and Homalothecioideae, but more detailed studies are needed to confirm this hypothesis.

Species included:

*S. obtusifolium* (Mitt.) Kindb.

*S. touretii* (Brid.) L. F. Koch

Species referred to the genus by Hedenäs (1996):

*S. australe* Hedenäs

Species referred to the genus by Lawton (1967):

*S. californicum* (Lesq.) Kindb., *S. cespitans* (Wils. ex C. Müll.) L. F. Koch, *S. julaceum* Lawt.

These four latter species have never been placed outside the genus and morphologically are similar to the type species. However surprises from *Platyhypnidium* (see below) call for more detailed studies using molecular data (one or two species are subaquatic; seta strongly rough to smooth, or in some species unknown).

Problematic species:

*S. coreense* Card. and *S. brachyphyllum* Card.

– We were unable to locate types or any material of two latter species in PC, BM, H, NICH, KYO.

**9. Brachythecium** B. S. G., Bryol. Eur. 6: 5. 1853. Type: *B. rivulare* B. S. G. (selected by Robinson, 1962).

*Paramyurium* (Limpr.) Warnst., Krypt. Fl. Brandenburg 2: 763. 1905. – *Eurhynchium* subgen. *Paramyurium* Limpr. 1896, Laubm. Deutsch. 3: 173. 1896. Lectotype: *Eurhynchium tomassinii* (Sendtn. ex Boulay) Mol. (= *Hypnum tomassinii* Sendtn. ex Boulay), selected here. Comment: four species were included in the original description: *Eurhynchium flotowianum* (sub *velutinoides*), *E. tomassinii*, *E. cirrosum*, *E. crassinervium*. No one of them has obvious advantages for to be selected as the generitype. We choose one that has a higher probability (very low, however) for separation of a genus of its own.

*Chamberlainia* Grout, Moss. Fl. N. Am. 3: 27. 1928. Lectotype: *C. acuminata* (Hedw.) Grout (= *Leskea acuminata* Hedw.), selected by Robinson (1962).

Plants small to large, green to yellowish green and often pale stramineous with age. Stem prostrate to ascending, with central strand, densely, rarely more loosely, julaceously to rarely complanately foliate, irregularly or at a certain distance regularly pinnately branched, branches usually straight, densely or loosely, julaceous or rarely complanately foliate. Axillary hairs 2-3-celled, uppermost cell relatively long and often gradually tapered to distal end. Pseudoparaphyllia acute to acuminate. Stem leaves erect, imbricate, patent or falcate-secund, lanceolate to broadly ovate, acuminate or acute, deeply longitudinally plicate to smooth; margin serrate to subentire, costa ending above mid-leaf to percurrent, without spine or sometimes with; laminal cells elongate to linear, thin to moderately thick-walled; alar cells subquadrate to shortly rectangular, large thin-walled or small thick-walled, distinctly or indistinctly delimited, alar group quadrate or extending up along margin or sometimes only subalar cells differentiated. Branch leaves narrower, with margin and back of costa more strongly serrate, usually smaller than stem leaves. Autoicous, dioicous, more rarely polygamous. Perichaetial leaves with reflexed acumina. Seta long, rough or smooth. Capsule inclined to horizontal, more rarely erect. Annulus separating by fragments, not separating, or totally indiscernible. Operculum conic, very rarely rostrate. Peristome xerocastique, perfect, very rarely hygrocastique. Spores small. Calyptra naked, very rarely hairy. Hygrophytic to xeromesophytic.

Distribution: subcosmopolite.

(a) General classification of *Brachythecium*:

The genus *Brachythecium*, in a traditional sense, was split only once by Robinson (1962), who sorted the species around two core taxa: *B. rivulare* (alar cells large, seta rough, leaves straight)

and *B. salebrosum* (alar cells small, seta smooth, leaves often falcate). The latter group was segregated as the genus *Chamberlainia*. This genus was first established for *C. acuminata* and two more species, which were found conspecific with it, but later much expanded by Robinson (1962). The distinction between the two groups, however, appeared fairly unclear when all the species are taken into consideration, hence later Robinson (1987) refrained from this idea. Although, as we believe, the separation of *Sciurohypnum* and *Brachytheciastrum* makes *Brachythecium* more natural, it still remains quite heterogeneous.

Since the sequence variation is not very high within the *Brachythecium*, many of the clades have no support (Fig. 2). The topology based on POY analyses (Fig. 1) is better resolved than strict consensus from Nona analyses. But since a similar topology to Fig. 1 was obtained from POY analysis despite of the gap cost, we believe, that the principal grouping of species in Fig. 1 is more or less reliable.

*Brachythecium rivulare* and related species with rough seta are basal in the *Brachythecium* clade. The more advanced species are more *B. salebrosum*-like, mostly with smooth seta, but including also several species with the rough seta, which precludes the segregation of *Chamberlainia* (*B. cirrosum*, *B. complanatum*, *B. gehlbii*, *B. tommasinii*). The most apical portion of the clade includes southern and tropical species, such as *B. buehneri* (East Asia), *B. ruderales* [well known as *B. stereopoma* in tropical America and as *B. implicatum* in tropical Africa], and *B. lamprocarpum* (Malesia, Oceania). This group was segregated into a separate section by McFarland (1994), but since he obviously did not validate it, we will call it the *B. stereopoma*-group sensu McFarland. *Brachythecium laetum* also belongs to this group, as it is similar to the tropical species of this group in the absence of an annulus. This clade includes also *B. acuminatum*, the type of the genus *Chamberlainia*. And finally this clade also includes *Unclejackia*, the curious moss with almost ecostate leaves, recently transferred from *Chaetomitrium* (Symphyodontaceae) to Brachytheciaceae (Ignatov & al., 1999).

(b) The position of *Unclejackia* and *Brachytheciella*: In accordance with a monophyletic

taxon concept, the nested position of *Unclejackia* in *Brachythecium* requires that either *Unclejackia* is synonymized with *Brachythecium*, or that *Brachythecium* is divided into several smaller units. The second alternative seems inappropriate, because in this case distinct phenotypes of what we now call *Brachythecium salebrosum* would be in different genera. The inclusion of *Unclejackia* in *Brachythecium* makes the morphological definition of the latter genus, however, extremely broad. *Unclejackia* is a large golden-lustrous moss with strongly concave leaves, a very flexuose leaf acumen, with very short (0.1-0.2 of leaf length) to absent costa, and a strongly modified peristome; it occurs in the subalpine savannah in New Guinean mountains (at about 3500 m elev.), where it grows always on trunks of the tree fern *Cyathea*. The placement of *Unclejackia* in the Brachytheciaceae has been disputed both in personal correspondence and by Tan (2000) who believed that *Unclejackia* is better to be placed with *Chaetomitrium* in a separate family.

Based on morphological, molecular and phytogeographic data, the origin of *Unclejackia* is more or less clear. Its closest relative is probably *Brachythecium lamprocarpum*, which is similar to *Unclejackia* in some rare character states, like, for example, the peculiar "border" of pellucid cells at the leaf base, etc. (Ignatov & al., 1999). However, this species has a smooth seta, while it is rough is *Unclejackia*. *Brachythecium lamprocarpum* is the only widespread similar species of *Brachythecium* of that area. In our analyses (cf. Figs. 1-2) *Unclejackia* is resolved as closely related to *B. lamprocarpum*, though with only low support. Thus, it is more or less clear that *Unclejackia* is close to the group of southern *Brachythecium* taxa, and has most likely evolved rapidly from them in a limited area and under an unusual environment, which lead to a differentiation of several morphological characters compared to its sister taxa. Concerning the taxonomy, however, we see no better choice than to retain *Unclejackia* in a genus of its own, at least until the evolution within the *Brachythecium*-subgroup is resolved in greater detail. It seems like the problem with the rank of *Unclejackia* is similar to the acceptance of birds as a class of vertebrates, which makes the class of reptiles paraphyletic (cf. for example, Forey, 2002).

Almost the same discussion can be repeated for *Brachytheciella*, another New Guinean endemic genus, for which molecular data were not available in this study.

(c) Basal species with rough seta. The sister clade to the rest of the *Brachythecium* clade includes *Brachythecium rivulare*, *B. rutabulum*, *B. frigidum* + South Chinese *Bryhnia* (cf. Fig. 1). The curious position of the latter taxa calls for further extensive studies of this group. This position of the South Chinese *Bryhnia* can hardly be considered an analytical artifact, as despite of excluding all the possibilities for contamination, this specimen was never resolved close to *Bryhnia*, but always close to *Brachythecium frigidum* (in analyses of chloroplast sequence data set alone, and chloroplast plus nuclear set, and combined molecular and morphological sets with different gap costs, etc.).

(d) *Brachythecium tommasinii* differs from the rest of *Brachythecium* in its rostrate operculum. This offers important new insight of the value of this character. Though it is rather stable within two other subfamilies (invariably rostrate in Rhynchostegielloideae; almost always rostrate in Rhynchostegioideae, with the only exception of *Pseudoscleropodium*), it is rather freely variable in the Brachythecioideae. The situation parallel to *B. tommasinii* was found also in *Sciurohypnum*, where *S. flotowianum* has been found close to *S. populeum* (see below). Both *B. tommasinii* and *Sciurohypnum flotowianum* are characterized by a rostrate operculum and short laminal cells. Such combination can also be recognized in the basal part of the *Brachythecium*-clade, if *Bryhnia* and *Kindbergia* are considered as derivatives from a *Brachythecium rivulare*-like ancestor.

(e) Wigh (1973) suggested to transfer *Brachythecium geheebii*, a rare Western Palearctic species, to *Homalothecium*, based partly on chromosome numbers. *B. geheebii* has  $n=10$ , a number known (that time!) in *Brachythecium* only in morphologically very distinct species with smooth seta. However,  $n=10$  or  $11$  is known in *B. tommasinii* and the East Asian *B. (Campthothecium) auriculatum* and *B. coreanum*; all three species have rough seta (see also Appendix 1). *Brachythecium geheebii* has very deeply plicate leaves in combination with rough seta, which in Europe is known only in *Homalothecium*, never

in *Brachythecium*. In Asia, however, this combination is known in *B. coreanum*, *B. coarctum*, and some phenotypes of *B. auriculatum*. The latter species was incorrectly synonymized with *Palamocladium leskeoides* by Hofmann (1998), who oversaw the rough seta in this species.

(f) This new circumscription of *Brachythecium* opens an opportunity for the placement of one peculiar Chinese endemic, *B. (Eurhynchium) coarctum*. This species has medium-sized to large plants, long plicate leaves with a non-*Homalothecium* base, laminal cells with length:width ratio ca. 5-8:1, rough seta and a rostrate operculum. Based on this character state combination we believe that it is close to *B. tommasinii*.

Species included: (+ – not listed in Crosby & al., 1999)

- B. acuminatum* (Hedw.) Aust.
- B. albicans* (Hedw.) B. S. G.
- B. afroglareosum* (Broth.) Par.
- +*B. auriculatum* Jaeg.
- B. austroglareosum* (C. Müll.) Kindb.
- B. austrosalebrosum* (C. Müll.) Kindb.
- B. bellii* (Mitt. ex Broth.) Par.
- B. buchananii* (Hook.) Jaeg.
- B. campestre* (C. Müll.) B. S. G.
- +***B. coarctum*** (C. Müll.) *comb. nov.* – *Eurhynchium coarctum* C. Müll., Nuov. Giorn. Bot. Ital., n. ser. 5: 198. 1898.
- B. complanatum* Broth.
- B. coreanum* Card.
- B. coruscum* I. Hag.
- B. digastrum* C. Müll. ex Kindb.
- B. erythrorrhizon* B. S. G.
- B. frigidum* (C. Müll.) Besch.
- B. garovaglioides* C. Müll.
- B. geheebii* Milde
- B. glareosum* (Bruch ex Spruce) B. S. G.
- B. helminthocladum* Broth. et Par.
- B. kamounense* (Harvey) Jaeg.
- B. kuroishicum* Besch.
- +*B. laetum* (Brid.) B. S. G.
- B. lamprocarpum* (C. Müll.) Jaeg.
- B. longicuspidatum* (Mitt.) Jaeg.
- B. mildeanum* (Schimp.) Schimp. in Milde
- +*B. papuense* Ignatov
- B. pinnirameum* C. Müll.
- B. podadelphus* C. Müll.
- B. procumbens* (Mitt.) Jaeg.
- B. rivulare* B. S. G.

*B. rotaeanum* De Not.

*B. ruderale* (Brid.) Buck [= *B. stereopoma*, *B. implicatum*]

*B. rutabulum* (Hedw.) B. S. G.

*B. salebrosum* (Web. et Mohr) B. S. G.

*B. subplicatum* (Hampe) Jaeg.

*B. spectabile* Broth.

+***B. tommasinii*** (Sendtn. ex Boulay) comb. nov. – *Hypnum tommasinii* Sendtn. ex Boulay, Fl. Crypt. Est, Muscin. 225. 1872.

*B. turgidum* (C. Hartm.) Kindb.

*B. udum* I. Hag.

*B. velleureum* (Mitt.) Jaeg.

Species referred to the genus based on literature descriptions:

McFarland, 1994a: *Brachythecium chocayae* Herzog, *B. conostomum* (Taylor) Jaeg., *B. polyoicum* (Thér.) McFarland, *B. zanonii* Buck.

Hedenäs, 2002: *B. latinervium* Hedenäs

Buck, 1993: *B. gloriosum* (C. Müll.) Par.

(3) Species excluded from the genus (see also all species under *Brachytheciastrum* and *Sciurohypnum* [there are no heterotypic species epithet]):

*B. kopenonii* Ignatov – *Cirriphyllum*

*B. weinmannii* (Nees) Par. = *Callicladium haldanianum* (type in LE!).

10. ***Unclejackia*** Ignatov, T. Kop. et D. Norris, Acta Bot. Fennica 165: 37. 1999. Type: *Unclejackia longisetula* (E. B. Bartram) Ignatov, T. Kop. et D. Norris (= *Chaetomitrium longisetulum* E. B. Bartram).

Plants robust, golden-green to rich golden. Stem creeping, with central strand, julaceously foliate, irregularly branched, branches straight, branch foliage similar to that in stem. Axillary hairs 2-3-celled, upper cells hyaline. Pseudoparaphyllia longly acuminate. Stem leaves loosely imbricate, from ovate or elliptic, very concave basal part abruptly contracted into filiform, moderately to strongly flexuose (in both dry and wet condition) acumen, not decurrent; margin serrulate to subentire; costa reaching 0.1(0.2) of leaf length or totally absent, ending smoothly; laminal cells linear, moderately thick-walled, towards leaf base wider; alar cells larger, in few rows along margin, extending shortly up along margin. Branch leaves smaller than stem leaves, otherwise similar. Autoicous (or sometimes dioicous?). Perichaetial leaves with

long, reflexed acumina. Seta strongly rough. Capsule erect to slightly inclined, cylindrical. Annulus not differentiated. Operculum high-conic. Peristome xerocastique, modified; exostome teeth red-brown, gradually tapered above, papillose above, cross-striolate below; endostome with basal membrane about 1/4 of endostome height, segments narrow, narrowly perforated along keel, cilia very short. Spores large. Calyptra naked. Mesophytic (on trunks of fern-trees in subalpine savannah).

Distribution: New Guinea.

(a) See discussion under *Brachythecium*, also Ignatov & al. (1999).

Species included:

*U. crispifolia* (E. B. Bartram) Ignatov, T. Kop. et D. Norris

*U. longisetula* (E. B. Bartram) Ignatov, T. Kop. et D. Norris.

11. ***Brachytheciella*** Ignatov in Ignatov, T. Kop. et D. Norris, Acta Bot. Fennica 165: 35. 1999. Type: *B. stolonifera* Ignatov.

Plants medium-sized to moderately robust, very fragile, golden-green to rich golden. Stem creeping, with central strand, julaceously foliate, irregularly branched, branches straight, foliage similar. Axillary hairs 2-3-celled, upper cells hyaline. Pseudoparaphyllia longly acuminate. Stem leaves erect-appressed, from ovate, concave basal part gradually contracted into filiform acumen, not decurrent; margin subentire; costa absent; laminal cells linear, moderately thick-walled, towards leaf base wider; alar cells larger in few rows along margin and this group extending shortly up along margin. Branch leaves similar to stem leaves. Dioicous? Perichaetial leaves erect, acuminate. Seta slightly rough below capsule, otherwise smooth. Capsule inclined, ovate-cylindrical, constricted below mouth. Annulus, peristome and calyptra unknown. Operculum high-conic. Spores small (16-22 µm). Mesophytic (on trunks of fern-trees in subalpine savannah).

Distribution: New Guinea.

(a) This genus is similar in many respects to *Unclejackia* (see discussion on this genus under *Brachythecium*, and also Ignatov & al., 1999).

Species included:

*B. stolonifera* Ignatov.



12. **Sciurohypnum** (Hampe) Hampe, *Linnaea* 38: 220. 1874. – *Hypnum* subg. *Sciurohypnum* Hampe, *Flora* 50: 76. 1867, ‘*Sciuro-hypnum*’. Lectotype: *Hypnum plumosum* Hedw. = *S. plumosum* (Hedw.) Ignatov et Huttunen, selected here.

*Chionobryum* Glow., *Oesterr. Bot. Z.* 63: 279. 1913, *syn. nov.* Type: *C. venturii* (De Not.) Glow. (= *Bryum venturii* De Not.) = *Sciurohypnum glaciale* (B. S. G.) Ignatov et Huttunen, *comb. nov.* (fide Loeske in Mönkemeyer, 1927, as *Brachythecium glaciale*), *syn. nov.*

*Cratoneurella* H. Robinson, *Bryologist* 65: 140. 1962, *syn. nov.* Type: *C. uncinifolia* (Broth. et Par.) H. Robinson, *syn. nov.* (= *Brachythecium uncinifolium* Broth. et Par.)

Plants small to large, light to deep green, becoming brownish or rarely whitish with age. Stem prostrate, with central strand, loosely, rarely more densely, julaceously or rarely complanately foliate, irregularly to at places regularly pinnately branched, branches straight or curved, foliage somewhat denser than that of stem and more often complanate. Axillary hairs 2-3(-5)-celled, uppermost cell obtuse, rarely indistinctly tapered to distal end. Pseudoparaphyllia acute. Stem leaves erecto-patent, patent, reflexed, imbricate, ovate to ovate-lanceolate, acuminate or acute, indistinctly plicate to smooth; margin serrate to subentire; costa ending above mid-leaf to percurrent, without spine; laminal cells ovate to linear, thin- to moderately thick-walled; alar cells isodiametric, large and thin-walled or small and thick-walled, alar group isodiametric, usually poorly delimited. Branch leaves narrower than stem leaves, with more strongly serrate margins and costa more often ending in a spine. Autoicous, very rarely dioicous (but some autoicous species rare with sporophytes). Perichaetial leaves with reflexed acumina. Seta rough or very rarely smooth. Capsule inclined to horizontal, more rarely erect. Annulus separating by fragments, not separating, or totally indiscernible. Operculum conic, more rarely rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Hygromesophytic to xeromesophytic.

Distribution: subcosmopolite.

Nomenclatural notes:

(a) The name *Sciurohypnum*, as a subdivision of *Hypnum*, first appeared in Hampe’s (1852) publication without description, with the simple listing of species. The Brachytheciaceae were represented

in that list by two species of *Palamocladium*. Hence it is considered as a *nomen nudum* and not used further. Moreover its concept differs greatly from the subsequent one. The first publication with a description (also as a subdivision of *Hypnum*, Hampe, 1867), included two species, *Hypnum plumosum* and *H. velutinum*, which were taken as examples, whereas the circumscription of the group was extended to include all the *Brachythecium* and *Camptothecium* sensu “Bryologia Europaea”. In subsequent publications Hampe (1871, 1873) included in this section *H. campestre*, *H. lutescens*, *H. populeum*, *H. rutabulum*, *H. salebrosum*, etc. Later Hampe (1874) described a new species from Madagascar, calling it *Sciuro-hypnum borgenii* (the only member of Brachytheciaceae in his publication). Since that species was considered a relative of *Hypnum albicans*, and also according to the species description, it is clear that the concept of this new genus was simply taken from the concept of subgenus. According to Art. 33.2 of the Saint Louis Code the generic name must be treated as a transfer from *Hypnum* subgen. *Sciuro-hypnum* 1867. Thus, *Sciuro-hypnum borgenii* Hampe (indicated in Index Muscorum as the type) is not the correct type of the generic name and the lectotype must be chosen from the two elements definitely included in the 1867 protologue, namely *H. plumosum* or *H. velutinum*. We prefer *H. plumosum*. The reason is just etymological. If *H. velutinum* would be chosen as a type, then the earliest generic name for this group of species would be *Chionobryum* (“snow-moss”). However, the species of the genus are common in boreal, temperate, and subtropical forests. In addition, most species of the *Brachythecium velutinum* group (that should be called *Sciurohypnum* in this case) have a rather loose foliage and are not “sciureous” at all.

(b) *Chionobryum* Glow. was described for one species, *C. venturii* (De Not.) Glowacki = *Bryum venturii* De Not. When describing the latter, De Notaris compared it with *Bryum funkii* (!), but Mönkemeyer (1927) stated that according to Loeske the only collection of this species belongs to *Brachythecium glaciale*. We were able to study an isotype: “Auctor cot C. Müll. ex auct. De Not., Bryum Venturii De Not., Epilogo p. 408. Hochalpe Seant in Ratti. August 74. Venturi”. (H-SOL 516001), and confirm Loeske’s opinion.

(c) *Cratoneurella* was established by Robinson (1962) based on *Brachythecium uncinifolium*, a very rare species from Japan. Japanese authors placed this species next to *B. reflexum* (Takaki, 1955b; Noguchi, 1991), and Takaki (l. c.) commented that they are closely related. It seems like the important reason for the separation of this genus was that Robinson considered the leaf falcateness as a very important character separating *Brachythecium* s. str. and *Chamberlainia* s. lat. No species of *Brachythecium* sensu Robinson had falcate leaves, so the inclusion of this species into *Brachythecium* would reduce the number of differential characters between the two genera seriously (because they are few). Our observations on species morphology confirm Takaki's opinion that *B. uncinifolium* and *B. reflexum* are very close, if not conspecific.

Systematic notes:

(d) This group existed in most previous treatments of *Brachythecium* s. l. as sections *Cirriphyllopsis* and *Reflexa*. Its relative homogeneity is easy to see by retrieving keys for the *Brachythecium* in different handbooks: contrast, such as {plants small to medium-sized, leaves plus minus smooth} vs. {plants large, leaves usually plicate} is commonly found at the beginning of long keys to *Brachythecium* sensu B. S. G. Large-sized plants are known in *Sciurohypnum* only in polyploid *S. oedipodium* and putative polyploid *S. hylotapetum* (cf. Appendix 1). Our analysis resolved *Sciurohypnum* with high jackknife and bremer support (Fig. 2), and actually its species form one of the most stable clades in various analyses of different sets with different parameter (Huttunen & Ignatov, 2003).

(e) The most unexpected novelty in this group is the close relationship of *Sciurohypnum* (*Cirriphyllum*, *Eurhynchium*) *floto-wianum* to *S.* (*Brachythecium*) *populeum*, which also got high jackknife and bremer support (Fig. 2). These two species have similar appearances and leaf shapes, and a percurrent costa is not rare in *S. floto-wianum*, at least in the branch leaves. However *S. floto-wianum* differs from *S. populeum*, as well as from all other species of the genus, in having rostrate operculum and rather short laminal cells. It seems like these two characters often evolve together in a parallel way; cf. the case of

*Brachythecium tommasinii* (above).

Species included:

***S. brotheri*** (Par.) comb. nov. – *Brachythecium brotheri* Par., Index Bryol. (ed. 2) 2: 139. 1904.

***S. floto-wianum*** (Sendtn.) comb. nov. – *Hypnum floto-wianum* Sendtn., Denkschr. Bayer. Bot. Ges. Regensburg 3: 146. 1841, '*floto-wianum*'.

***S. glaciale*** (B. S. G.) comb. nov. – *Brachythecium glaciale* B. S. G., Bryol. Eur. 6: 15. 542. 1853.

***S. hylotapetum*** (N. Higinbotham et B. Higinbotham) comb. nov. – *Brachythecium hylotapetum* N. Higinbotham et B. Higinbotham, Bryologist 61: 339. 1958.

***S. latifolium*** (Kindb.) comb. nov. – *Brachythecium latifolium* Kindb., Forh. Vidensk.-Selsk. Kristiania 1888 (6): 8. 1888.

***S. majusculum*** (Newton) comb. nov. – *Brachythecium majusculum* Newton, Brit. Ant. arct. Surv. Bull. 39: 45. f. 1. 1974.

***S. oedipodium*** (Mitt.) comb. nov. – *Hypnum oedipodium* Mitt., J. Proc. Linn. Soc., Bot. 8: 32. 1865.

***S. ornellanum*** (Molendo) comb. nov. – *Hypnum ornellanum* Mol., Ber. Naturhist. Vereins Augsburg 18: 185. 1865.

***S. plumosum*** (Hedw.) comb. nov. – *Hypnum plumosum* Hedw., Sp. Musc. Frond. 257. 1801.

***S. populeum*** (Hedw.) comb. nov. – *Hypnum populeum* Hedw., Sp. Musc. Frond. 270. 70 f. 1-6. 1801.

***S. reflexum*** (Starke) comb. nov. – *Hypnum reflexum* Starke, Bot. Taschenb. 306. 1807.

***S. starkii*** (Brid.) comb. nov. – *Hypnum starkei* [starkii] Brid., Muscol. Recent. 2(2): 107. 1801.

Species belonging to *Sciurohypnum* as deduced from McFarland's (1988) descriptions: *Brachythecium filirepens* Dusen, *B. cirriphylloides* McFarland.

Species of *Sciurohypnum* which status is to be confirmed:

*Brachythecium uncinifolium* Broth. et Par. (~*reflexum*).

*B. dovensis* (Limpricht) Amann (~*glaciale*)

*B. nelsonii* Grout (~*latifolium*)

*B. uematsui* Broth. (~*plumosum*)

*B. pulchellum* Broth. et Par. (~*plumosum*)

*B. spuriopopuleum* (Broth.) Par. (~*populeum*)

*B. pseudouematsui* Noguchi (~*plumosum*)

**SUBFAM. RHYNCHOSTEGIELLOIDAE****SUBFAM. NOV.**

*Plantae minutae vel robustae. Folia lato ovata vel anguste lineares, acuta, acuminata vel obtusa; costa crassa vel tenuis; cellulae angusto lineares vel brevi ovaes. Autoica, dioica vel polyoica. Seta scabra vel laevissima. Capsula erecta vel horizontalis. Peristomium perfectum vel imperfectum. Operculum rostratum.*

Type species: *Rhynchostegiella* (B. S. G.) Limpr.

Plants minute to robust. Leaves broadly ovate to narrowly linear, acute, acuminate, or obtuse; costa very strong to thin; cells narrowly linear to shortly ovate. Autoicous, dioicous, or polyoicous (never phylloidioicous). Seta rough or more rarely smooth, long to very short. Capsule inclined to erect. Peristome perfect to variously reduced. Operculum rostrate (never conic).

This is the largest subfamily in term of number of genera, 19 [with some more to be described]; the following groups are well-supported within it (? – species attributed to group based on morphology only):

(1) *Cirriphyllum* + *Okamuraea*; (2) *Oxyrrhynchium* + *Donrichardsia* + *?Nobregaea* + *?Eurhynchiella*; (3) *Rhynchostegiella* (European and partly African taxa); (4) *Clasmatodon* + *Helicodontium* + *?Rhynchostegiella* p. p. (see note “a” under that genus) + *Homalotheciella* + *?Flabellidium* + *?Mandoniella* + *?Juratzkaeella* + *?Schimperella*; (5) *Aerolindigia* + *Remyella*; (6) *Meteoridium* + *Zelometeorium* + *Squamidium*.

13. ***Cirriphyllum*** Grout, Bull. Torrey Bot. Cl. 25: 222. 1898. Type: *C. piliferum* (Hedw.) Grout (= *Hypnum piliferum* Hedw.).

Plants large to medium-sized, slender to moderately rigid, light green to golden or brownish green. Stem prostrate to ascending, with central strand, densely to moderately densely, julaceous foliate, irregularly to rather regularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 3-5-celled, often with 3 short lower cells. Pseudoparaphyllia orbicular-triangular to acuminate. Stem leaves loosely to closely imbricate to erecto-patent, from ovate or elliptic base more or less abruptly contracted into long to short, filiform or lanceolate acuminate, or gradually acuminate apex, longly or moderately decurrent, moderately to strong-

ly concave, plicate or not; margin serrate to serrulate; costa ending without spine; laminal cells linear, elongate or rhombic-elongate, moderately thick-walled; alar cells subquadrate, small or large, forming isodiametric group or extending up along margin. Branch leaves rather different from stem leaves in being narrower, less abruptly tapering or contracting to acumen, not decurrent, more strongly serrate. Dioicous. Perichaetial leaves abruptly contracted to long, reflexed acumina. Seta long, rough. Capsule inclined to horizontal, ovate. Annulus separating by fragments. Operculum longly rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: Holarctic and Malesia.

(a) *Cirriphyllum* is one of the most troublesome genera to describe based on morphology. A change in the cell length to width ratio seems to have evolved in parallel with an elongation of the rostrum of the operculum in many groups of Brachytheciaceae. The group close to *C. piliferum* can be understood as a series from the long-celled *C. piliferum* via the moderately short-celled *C. crassinervium* to the short-celled *Okamuraea*. Interestingly, the axillary hairs in these two genera have usually many short cells proximally.

Species included:

+ *C. crassinervium* (Tayl.) Loeske et Fleisch. (listed Crosby & al., 1999 under *Eurhynchiium*).

+ ***Cirriphyllum kopenhagenii*** (Ignatov) comb. nov. – *Brachythecium kopenhagenii* Ignatov, Acta Bot. Fenn. 165: 29. 2. 1999.

*C. piliferum* (Hedw.) Grout

Species transferred to other genera:

*C. cirrosum* (Schwägr.) Grout – *Brachythecium*

*C. flotozianum* (Sendtn.) Ochyra – *Sciuohypnum*

*C. germanicum* (Greb.) Loeske et Fleisch. – not a Brachytheciaceae

*C. tommasinii* (Sendtn. ex Boulay) Grout – *Brachythecium*.

14. ***Okamuraea*** Broth., Oefvers. Foerh. Finska Vetensk.-Soc. 49: 2. 1906. Type: *O. cristata* Broth. = *O. hakoniensis* (Mitt.) Broth.

Plants medium-sized, rather rigid, yellowish green. Stem creeping, with central strand and 4-6-stratose sclerodermis, densely to moderate-

ly densely foliate, irregularly pinnately branched, branch foliage similar to that in stem, sometimes branches attenuate. Axillary hairs 3-6-celled, blunt, composed of short cells throughout or at least in the lower part. Pseudoparaphyllia triangular. Stem leaves erect to erect appressed when dry, spreading when wet, ovate to ovate-lanceolate, longly acuminate, not decurrent, more or less concave, plicate or not plicate; margin serrulate; costa ending above mid-leaf, without spine; laminal cells rhombic-ovate, very thick-walled; at leaf base cells shorter, alar cells subquadrate, moderately thick-walled, forming extensive opaque area extending up along margin. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves straight, abruptly longly acuminate, costate, costa reaching  $1/2$ – $1/4$  of leaf length. Seta long, smooth. Capsule suberect to inclined, shortly ovate to cylindrical. Annulus not differentiated. Operculum moderately to longly rostrate. Peristome hygrocastic, strongly modified; exostome red-brown, teeth massive, with numerous dense trabeculae, on the outer surface with small papillae to the base, inner surface not papillose; endostome with basal membrane to about  $1/3$  of tooth length, but without segments and cilia. Spores large. Calyptra hairy. Brood branches in clusters in axils of upper leaves present in one species. Mesophytic to xeromesophytic.

Distribution: East Asia.

(a) In the original description *Okamuraea* was compared with *Forsstroemia*, Cryphaeaceae. Later, in 1908, Brotherus (1905-1909) placed it in the Brachytheciaceae, Fleischer (1923) and Brotherus (1925) in the Rhytidiaceae, Noguchi (1953) in the Brachytheciaceae, and Iwatsuki & Noguchi (1973) and Noguchi (1991) in the Leskeaceae. In almost all publications of the last decades of the XX<sup>th</sup> Century it was placed in the latter family. Based on molecular data, Tsubota & al. (2002) placed it in the Brachytheciaceae. Studies of the pseudoparaphyllia support this, as well as the results of our analysis of combined molecular and morphological data.

(b) In our analysis, *Okamuraea* was found to be closely related to *Cirriphyllum*. Note, that in *C. crassinerviium* the cells are considerably shorter than in *C. piliferum*, and it can hence be interpreted as a transitional morphotype (Figs. 1-2).

Noguchi's (1953, 1991) publications include all known species of the genus.

Species included:

*O. brachydictyon* (Card.) Noguchi

*O. brevipes* Broth. ex S. Okamura

*O. hakoniensis* (Mitt.) Broth.

*O. plicata* Card.

15. **Oxyrrhynchium** (B. S. G.) Warnst., Krypt. Fl. Brandenburg 2: 781. 1905, nom. cons. prop. – *Eurhynchium* subgen. *Oxyrrhynchium* B. S. G., Bryol. Eur. 5: 224. 1854. Type: *Eurhynchium hians* (Hedw.) Sande Lac. (= *Hypnum hians* Hedw., *Oxyrrhynchium hians* (Hedw.) Loeske), typ. cons. prop. (Ignatov & Isoviita, 2003).

Plants medium-sized, moderately rigid, green to brownish green. Stem creeping, with central strand, very loosely or at places more densely julaceously foliate, at places rather regularly branched, branch foliage julaceous, subcomplanate to sometimes distinctly complanate. Axillary hairs 2-3-celled, often 2-celled with upper cell vesiculate inflated, hyaline or pale brownish. Pseudoparaphyllia triangular, acute. Stem leaves erecto-patent to patent, ovate, longly or shortly acuminate, slightly concave, smooth; margin serrate to serrulate; costa ending in spine; laminal cells elongate to linear, moderately thick-walled; alar cells weakly differentiated (sometimes only subalar cells differentiated), short rectangular, thin-walled, forming an indistinctly delimited group. Branch leaves different from stem leaves in being more elliptic in overall shape, shortly acuminate to acute, asymmetric at base, twisted in mid-leaf and more strongly serrate and with costa sometimes toothed distally, ending in a more stout spine. Dioicous or more rarely synoicous or polyoicous. Perichaetial leaves abruptly contracted to long, reflexed acumina. Paraphyses often conspicuously exerted. Seta long, rough, more rarely smooth. Capsule inclined to horizontal, ovate. Annulus separating by fragments. Operculum longly rostrate. Peristome xerocastic, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: subcosmopolite.

(a) This genus includes most of the species formerly placed in *Eurhynchium*. They have smooth leaves, often twisted in the middle, branch leaves tending to be elliptic; axillary hairs short, 2-3-celled, and in many species upper cells much broadened to almost vesiculate.

Most species of the genus have a rough seta, but *O. vagans*, widely distributed from Himalayas to Malesia, and several South Hemispheran species have a smooth seta. The very loose foliage with remote, subcomplanate leaves often allow immediate recognition of the genus. However, almost all species become subdendroid in dense growth, then lacking the complanate foliage as leaves tend to be more rigid and subcarinate. This polymorphism causes problems with the identification of species, because without special experience it is difficult to believe that these contrasting phenotypes belong to the same species. The taxonomy in regions where 2-3 species of *Oxyrrhynchium* occur (Europe: *hians-schleicheri*), China (*hians-savatieri-vagans*) is especially troublesome.

(b) *Oxyrrhynchium* was found monophyletic with moderate support in Nona analysis (Fig. 2), while POY analysis resolved it as paraphyletic group with *Donrichardsia* nested within it (Fig. 1).

Species included:

*O. asperisetum* (C. Müll.) Broth.

*O. clinocarpum* (Taylor) Broth.

*O. hians* (Hedw.) Loeske

***Oxyrrhynchium laevisetum*** (Geheeb) comb. nov. – *Eurhynchium laevisetum* Geheeb, Rev. Bryol. 3: 4. 1876.

*O. protractum* (C. Müll.) Broth.

*O. pumilum* (Wils.) Loeske

*O. remotifolium* (Grev.) Broth.

*O. rugosipes* (Besch.) Broth.

*O. savatieri* (Schimp. ex Besch.) Broth.

*O. schleicheri* (Hedw. f.) Roell

***Oxyrrhynchium trichocladoides*** (Ignatov) comb. nov. – *E. trichocladoides* Ignatov, Acta Bot. Fennica 165: 58. 1999.

***Oxyrrhynchium vagans*** (Jaeg.) comb. nov. – *Rhynchostegium vagans* Jaeg., Ber. Thätigk. St. Gallischen. Naturwiss. Ges. 1876-77: 369. 1878. (Ad. 2: 435).

Problematic species:

*O. speciosum* (Brid.) Warnst. – the overall morphology of this species is rather similar to other species of the genus, but it has exceptionally long (often 5-celled) and brownish axillary hairs, quite different from those of other members of the genus. Since many subaquatic species often have long axillary hairs, one might hypothesize, that the growth in this environments, exceptional for the genus, is resulted in

this exceptional morphology. An alternative hypothesis is that the overall similarity of *O. speciosum* and other *Oxyrrhynchium* species is superficial. This dilemma needs a more detailed study. Note that chromosome number in *O. speciosum* is  $n=15$  (versus  $n=7, 8, 10$  in other taxa, cf. Appendix 1), suggesting that it is of a polyploid (e.g., allopolyploid) origin.

16. ***Donrichardsia*** Crum et Anderson, Fieldiana, Bot., n. s. 1: 7. 1979. Type: *D. macroneuron* (Grout) Crum et Anderson (= *Hygroamblystegium macroneuron* Grout).

Plants robust, rigid, in dense mats, dark-green to brownish-green. Stem prostrate, occasionally curved at end, central strand present, cortical cells in (1–)2 rows of small, thick-walled cells, densely to moderately densely foliate, foliage julaceous to homomallous, irregularly loosely branched, branches prostrate to ascending, rather densely imbricately foliate, subjulaceous to homomallous. Axillary hairs 2-4-celled, colored throughout. Pseudoparaphyllia orbicular-triangular. Stem leaves erect to appressed, suborbicular to ovate-lanceolate, broadly acute, sometimes abruptly cuspidate or shortly apiculate; strongly concave, shallowly longitudinally plicate; margin serrulate to serrate throughout with small acute or blunt teeth; costa strong, shortly excurrent, percurrent, or ending at (0.7–)0.8–0.95 of leaf length; laminal cells unistratose or partly 2-4-stratose, elongate to linear, moderately thick-walled; basal cells shorter, thick-walled, alar cells not differentiated, but subalar cells often enlarged and forming an indistinct group. Branch leaves erect to patent, differing from stem leaves in often being slightly asymmetric, slightly longer and narrower, and in having somewhat longer laminal cells. Dioicous? Perichaetial leaves with slightly reflexed acuminate. Seta long, rough. Capsule inclined to horizontal. Operculum rostrate. Peristome xerocastique, perfect. Spores and calyptra unknown. Hydrophytic or hygrophytic.

Distribution: desjunctive between East Asia and Eastern North America.

(a) *Donrichardsia macroneuron*, a curious aquatic species was originally described in *Hygroamblystegium*, but later placed in *Eurhynchium* (considering its affinities to *Platyhypnidium*, which was that time included in *Eurhynchium*) and then segregated in a monotypic genus

of Amblystegiaceae (Crum & Anderson, 1979). Vanderpoorten & al. (2002) in their analysis of Amblystegiaceae s. lat. suggested to accommodate *Donrichardsia* in *Platyhypnidium*, which is not surprising, because their study included only two genera of the Brachytheciaceae. We appreciate their decision to put *Donrichardsia* in the Brachytheciaceae, but according to the present results it belongs to another subfamily than *Platyhypnidium*. The morphology of *Platyhypnidium* seems to be no more than a running-water habitat syndrome, shared by different aquatic Brachytheciaceae and Amblystegiaceae s. lat. (see also comments on *Platyhypnidium*).

(b) In our study the closest relative of *Donrichardsia macroneuron* was found among East Asian species (cf. classical “*Liriodendron*” disjunction, known also in mosses, cf. Iwatsuki, 1958). *Platyhypnidium patulifolium* is an interesting plant from China originally described from a very poor collection in the genus *Rhynchostegium*, and later accepted by some authors in *Platyhypnidium*. A second collection by Koponen in China allowed for a more thorough description (Ignatov & al., 2003). Recent studies of specimens in PE allow to discover also sporophytes (PE#062123; Yunnan, co. Gongsham, 28.IX.1935 coll. [?] # 6462(391)). The operculum is rostrate, peristome is complete and the seta is rough (sporophytes either immature, or old, with considerably broken peristome). The essential characters of this species include concave leaves and a costa that reaches almost to the apex. The axillary hairs are wide, but relatively short for this group of aquatic plants. In contrast to *D. macroneuron* it does not have an especially broad costa and the lamina is never bistratose. These characters are, however, variable in some other genera of Brachytheciaceae: the bi- or unistratose lamina is known in *Platyhypnidium* (Ochyra & Vanderpoorten, 1999) and the costa varies from very narrow to 3/4 of leaf width in *Rhynchostegiella*. Taking into consideration the very high support (Fig. 2), we suggest to transfer *Platyhypnidium patulifolium* to *Donrichardsia*.

(c) The *Donrichardsia* is certainly closely related to *Oxyrrhynchium*, being resolved as a sister group (Fig. 2) or sometimes as an ingroup (Fig. 1). This affinity is in a nice agreement with the character state of rough seta, a characteristic of most of the *Oxyrrhynchium* species.

(d) Further studies are needed to understand the correct position of the species known as “*Platyhypnidium austrinum*”. It seems to be an another derivative of the *Oxyrrhynchium* lineage.

Species included:

*D. macroneuron* (Grout) Crum et Anderson.

***Donrichardsia patulifolia*** (Card. et Thér.) comb. nov. – *Rhynchostegium patulifolium* Card. et Thér. in Thér., Bull. Acad. Int. Géogr. Bot. 21: 272. 1911. – *Platyhypnidium patulifolium* (Card. et Thér.) Broth., Nat. Pfl. ed. 2, 11: 347. 1925.

17. **Nobregaea** Hedenäs, Bryophyt. Biblioth. 44: 124. 1992. Type: *N. latinervis* Hedenäs.

Plants small. Stem prostrate, with central strand, loosely foliate, irregularly branched. Axillary hairs 2-4-celled. Pseudoparaphyllia triangular. Stem leaves patent, ovate-lanceolate to lanceolate, narrowly acute; margin serrate; costa very broad, indistinctly separated from lamina; laminal cells at places bistratose, elongate, rather irregular in shape, thick-walled; alar cells rectangular, forming indistinctly delimited elongate group. Branch leaves similar to stem leaves or smaller and narrower. Gametangia and sporophyte unknown. Hygro- or hydrophytic.

Distribution: Madeira.

(a) The only species of the genus is known from only one place in Madeira, where it grows on rock near a waterfall. The broad costa, small size and habit suggest a relationship with *Rhynchostegiella*, which, however, never has an as distinctly serrate margin and axillary hairs as long as those in *Nobregaea*. Besides *Rhynchostegiella*, the broad costa is known in Brachytheciaceae only in *Donrichardsia*, which belongs to the same subfamily. The latter genus is also similar to *Nobregaea* in having a multistratous lamina.

Species included: *N. latinervis* Hedenäs.

18. **Eurhynchiella** Fleisch., Musci Buitenzorg 4: 1566. 1923. Lectotype: *E. zeycheri* (C. Müll.) Fleisch. (= *Hypnum zeycheri* C. Müll.), selected by Ignatov & al. (1999).

Plants small, yellowish or sordid green, glossy. Stem prostrate, with weak central strand, moderately densely, julaceously foliate, irregularly or at places regularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 3-celled, pellucid, upper cell pellucid, somewhat

broader than cells below. Pseudoparaphyllia orbicular-triangular. Stem leaves rigidly erect-spreading, ovate-lanceolate, broadly to narrowly acuminate or somewhat attenuate; margin serrate to serrulate throughout; costa ending above mid-leaf in a stout spine; laminal cells linear, thick-walled, smooth, towards base short in about 2 rows, alar cells not differentiated. Autoicous. Perichaetial leaves erect, acuminate. Seta smooth, rather short. Capsule inclined, oblong, contracted below mouth. Annulus separating by fragments. Operculum obliquely rostrate. Peristome xerocastique, perfect; exostome red/brown, with incrassate dorsal trabeculae; endostome complete, cilia 1-2, nodose. Spores small. Calyptra naked. Mesophytic (tree base in shaded place).

Distribution: South Africa +?South America.

(a) The selection of the lectotype of the genus was not commented on by Ignatov & al. (1999). Our argument was that the genus is based on *Rhynchostegiella* sect. *Leptorhynchostegium* Broth., to which six South-African species were referred (without description) by Carl Müller (1899). Later five of these six species were synonymized by Dixon & Gepp (1923) and by Sims (1926 [cited in Index Muscorum]) with the sixth species, *Rhynchostegiella* (*Eurhynchiella*) *zeyheri*. Thus, the only one South African species is a good candidate for lectotype.

(b) The genus was not included in our analyses of molecular data and its affinities are unclear and need further studies. Morphology gives controversial evidences. The plants are small, with smooth setae reminiscent of *Eurhynchiastrum pulchellum*. Actually, one of the synonyms of *Eurhynchiella zeyheri* is called *Rhynchostegium afro-strigosum* C. Müll. (*Eurhynchium strigosum* is a well-known synonym of *E. pulchellum*). However, the uppermost cell of the axillary hairs is broad in *Eurhynchiella*, sometimes almost inflated, thus suggesting a relationship between this genus and *Oxyrrhynchium*. Somewhat less direct evidence on the close position of *Eurhynchiella* relative to *Oxyrrhynchium* is the fact, that leaves of *E. zeyheri* are sometimes attenuate and similarly attenuate leaves are known from South American and New Zealandian *O. remotifolium*, a species with a rough seta. Though most species of *Oxyrrhynchium* (and Rhynchostegielloideae as a whole) have a rough seta, few

exceptions are known: for example, seta is smooth in *Oxyrrhynchium vagans* and *Rhynchostegiella tenella*.

Species included:

*E. zeyheri* (C. Müll.) Fleisch.

Species included based on Brotherus (1925): *E. acanthophylla* (Mont.) Fleisch., *E. semitorta* (Jaeg.) Broth., *E. tenuinervis* Herzog, *E. toncolensis* (Broth.) Broth. (all from South America).

Species excluded from *Eurhynchiella*:

*E. decurrens* P. Varde – *Kindbergia africana* (fide Ochyra, 1997)

19. **Rhynchostegiella** (B. S. G.) Limpr., Laubm. Deustsch. 3: 207. 1896, *nom. cons.* – *Rhynchostegium* subgen. *Rhynchostegiella* B. S. G., Bryol. Eur. 5: 201. 1852. Type: *Rhynchostegium tenellum* (Dicks.) B. S. G. (= *Hypnum tenellum* Dicks., *Rhynchostegiella tenella* (Dicks.) Limpr.).

(*Rhynchostegiella* is conserved against *Remyella* C. Müll., which, however is considered here as a distinct genus)

Plants small, soft to very rigid, yellowish to deep green or brownish. Stem prostrate, with weak and discontinuous lacking central strand, loosely to moderately densely foliate, remotely to rather regularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 2-3-celled. Pseudoparaphyllia acuminate or acute. Stem leaves erect to spreading, in dry state slightly different or with somewhat incurved margins, lanceolate to narrowly lanceolate, acuminate, not or hardly concave in basal portion; margin wavy-crenulate to subentire; costa thin and ending below mid-leaf to broader than half leaf and excurrent, without spine, laminal cells elongate to linear, firm-walled; towards base somewhat shorter, alar cells not differentiated or a few cells in leaf corner subquadrate. Branch leaves similar to stem leaves or smaller and narrower. Autoicous. Perichaetial leaves acuminate, straight or with slightly reflexed acumina. Seta long, rough to smooth. Capsule inclined to horizontal, ovate. Annulus separating by fragments. Operculum longly obliquely rostrate. Peristome xerocastique or hygrocastique, moderately modified; exostome teeth red-brown, papillose above, cross striolate below, striae smooth to moderately papillose; endostome with high basal membrane, segments

moderately broad, non- or slightly perforated along keel, cilia long. Spores small. Calyptra naked. Xeromesophytic to hygromesophytic.

Distribution: Western Palearctic + ?East Africa.

(a) Ignatov & al. (2003) discussed the species of the genus in East Asia and found that most of them can be classified into two groups in that area. The first group comprises delicate plants, usually growing on twigs, that have spiculate leaves when dry. This group is treated here as *Remyella* (see below). The second group ("*Rhynchostegiella sinensis*"-group) includes small, dull plants, with lanceolate to ovate-lanceolate leaves, short, thick-walled laminal cells, often with a collapsed cytoplasm pattern, subquadrate alar cells extending up along the margin, a slightly rough seta, a weakly inclined short capsule, and small spores. This group includes *R. sinensis* Broth. et Par., *R. santaiensis* Broth. et Par., *R. mindorensis* (Broth.) Broth., *R. opacifolia* Dix., and *R. papuensis* E. B. Bartram. The Australian *R. cucullata* (Mitt.) Broth. ex Par. also seems to fit this group very well. The latter species was placed in *Scorpiurium* by Hedenäs (1996), due to the similarity in leaf structure. However *Scorpiurium* species have a smooth seta. It seems like this group of South-East Asian, Malesian and Australian *Rhynchostegiella* is closer to South American *Helicodontium* or maybe *Flabellidium*. Although with some hesitation we add to this group one more Australian species, *R. muriculata* (Hook. et Wils.) Broth.: it has unusually long laminal cells for this group, but is otherwise very similar. The final decision has to be confirmed by molecular studies.

(b) We were able to study the isotype of *Cirriphyllum germanicum* (H), which has been synonymized with *Rhynchostegiella tenuicaulis* by Karttunen (1990), and found that the pseudoparaphyllia are not of the Brachytheciacean pattern.

(c) The revision of Dirkse & Bouman (1995) for Canary Islands covers most taxa of the genus in strict sense.

Species included:

*R. curviseta* (Brid.) Limpr.

*R. litorea* (De Not.) Limpr.

*R. macilenta* (Ren. et Card.) Card.

*R. tenella* (Dicks.) Limpr.

*R. teneriffae* (Mont.) Dirkse et Bouman

Species, probably belonging to *Rhynchostegiella*:

*R. holstii* (Broth.) Broth.

Species excluded to other genera:

*R. brachypodia* Fleisch. – *Remyella*

*R. cucullata* (Mitt.) Broth. ex Par. – see note "a" ("*R. sinensis*"-group)

*R. hawaica* (C. Müll.) Broth. – *Remyella*

*R. laeviseta* Broth. – *Rhynchostegium psilopodium*.

*R. leptoneura* Dix. et Thér. – ?*Remyella*

*R. menadensis* (Sande Lac.) E. B. Bartram – ?*Remyella*

*R. mindorensis* (Broth.) Broth. – see note "a" ("*R. sinensis*"-group)

*R. muriculata* (Hook. et Wils.) Broth. – see note "a" ("*R. sinensis*"-group)

*R. opacifolia* Dix. – see note "a" ("*R. sinensis*"-group)

*R. papuensis* E. B. Bartram – see note "a" ("*R. sinensis*"-group)

*R. ramicola* (Broth.) Broth. – *Remyella*

*R. sakuraii* Takaki – *Brachythecium* cf. *plumosum* (see Ignatov & al., 2003).

*R. santaiensis* Broth. & Par. – see note "a" ("*R. sinensis*"-group)

*R. santosii* E. B. Bartram – *Remyella*

*R. sinensis* Broth. et Par. – see note "a" ("*R. sinensis*"-group)

*R. sumatrana* Fleisch. – *Remyella*

*R. tenuicaulis* (Spruce) Karttunen – not Brachytheciaceae, see note "b"

*R. vriesei* (Dozy et Molk.) Broth. – *Remyella*

*R. zeyheri* (Spreng. ex C. Müll.) Broth. – *Eurhynchiella*

20. **Helicodontium** Schwägr., Sp. Musc. Frond., Suppl. 3(2): 293. 1830. Type: *H. tenuirostre* Schwägr. = *H. capillare* (Hedw.) Jaeg.

?*Dubyella* Schimp., Musci Europaei Novi, fasc 3-4. 1866. Type: *D. italica* Schimp.

Plants small, slender, sordid green to brownish, dull. Stem creeping, with central strand, moderately densely foliate, irregularly branched, branches moderately densely foliate. Axillary hairs 2-3-celled, pellucid. Pseudoparaphyllia orbicular-triangular. Stem leaves appressed when dry, more or less spreading when wet, ovate to lanceolate, gradually tapering to blunt apex, slightly concave; margin crenulate almost



throughout, narrowly recurved in lower half; costa ending at 0.6-0.7(0.8) of leaf length, without spine; laminal cells rhombic to rhombic-ovate, thick-walled, cell walls sometimes sinuous; alar cells oblate to subquadrate, extending up along margin. Branch leaves similar to stem leaves. Autoicous. Perichaetial leaves erect, rather broadly acuminate. Seta relatively long, slightly rough to smooth. Capsule erect, ovate. Annulus separating by fragments. Operculum obliquely rostrate. Peristome xerocastique, moderately modified; exostome teeth red-brown, cross-striolate below; endostome with moderately high basal membrane, segments moderately broad, perforated, cilia absent. Spores small. Calyptra naked. Xeromesophytic.

Distribution: South and Central America and Mexico + ?.

(a) This genus was for a long time placed in the Fabroniaceae and then in the Myriniaceae, until molecular analysis resolved it as a member of Brachytheciaceae (Buck & al., 2000). This placement is in agreement with the pseudoparaphyllia pattern in the genus.

(b) The close relationship between *Helicodontium* and *Clasmatodon* and *Homalotheciella* was strongly supported by the present analysis (Figs. 1-2), and the same topology has also been found by Buck & al. (2000). However each of these three genera has unique morphological characteristics, so we prefer to retain them distinct at the generic level, until the delimitation of *Helicodontium* from the large group of *Rhynchostegiella* species centered around *R. sinensis* has been critically addressed (Ignatov & al., 2003, see also discussion under *Rhynchostegiella* above).

(c) Other relatives of this genus have to be searched among “short-celled *Rhynchostegiella*” of East Asia, Malesia, and neighbouring areas (group 2 in discussion under *Rhynchostegiella*).

Species included:

*H. capillare* (Hedw.) Jaeg.

Buck (1980a) synonymized a number of species described from South America with *H. capillare*, the only species on that continent. Species from other regions need to be revised. *Helicodontium italicum* (Schimp.) Fleisch., the only species from Europe, is known only from the type collection. Its description agrees with *Helicodontium* in all important points.

*codontium* in all important points.

21. **Clasmatodon** Hook. et Wils., J. Bot. (Hooker) 4: 421. 1842. Type: *C. pusillus* Hook. et Wils. = *C. parvulus* (Hampe) Sull.

?*Anisodon* B. S. G., Bryol. Eur. 5: 75. 1852. Type: *Anisodon perpusillus* B. S. G.

?*Phlogostomum* Hampe, Flora 50: 74. 1867, *nom. illeg.*

Plants small, slender, sordid green to brownish, dull. Stem creeping, with central strand, densely foliate, irregularly branched, branches densely foliate. Axillary hairs 2-celled, pellucid, upper cell sometimes vesiculate-inflated. Pseudoparaphyllia orbicular-triangular. Leaves closely imbricate when dry, more or less spreading when wet, ovate to suborbicular, shortly acuminate or acute, slightly to strongly concave; margin serrulate to subentire; costa ending in mid-leaf without spine; laminal cells rhombic to rhombic-ovate, thick-walled, lumina with round ends; alar cells oblate to subquadrate, extending up along margin. Branch leaves similar to stem leaves. Autoicous. Perichaetial leaves erect, rather broadly acuminate. Seta relatively long, smooth. Capsule erect, ovate. Annulus of 3 rows of cells, separating by fragments. Operculum obliquely rostrate. Peristome strongly modified; exostome teeth pale, very short, hardly exceeding mouth level; endostome with very low basal membrane, filiform, much spaced segments, cilia absent. Spores small. Calyptra naked. Xeromesophytic.

Distribution: temperate Eastern North America.

(a) Similarly to *Helicodontium*, this genus was for a long time placed in the Fabroniaceae and then in the Myriniaceae, until molecular analysis suggested close relationship with the Brachytheciaceae (Buck in Crosby & al., 1999, Buck & al., 2000). This placement is in agreement with the pseudoparaphyllia pattern in the genus.

(b) Morphologically *Clasmatodon* is one of the most unusual representatives of Brachytheciaceae due to the strong reduction of the exostome. Only thin, cilia-like segments can slightly affect the spore dissemination. The plants are also very small and the leaf laminal cells are shortly ovate or rhombic. Phylogenetic inferences from sequence data suggest close affinities to other New World taxa, namely *Homalotheciella* and *Helicodontium capillare*.

(c) *Anisodon perpusillus* B. S. G., the type of *Anisodon*, was described from a single collection from Germany. The description in "Bryologia Europaea" referred, to our mind, to *Habrodon perpusillus*. We have no explanation why Schimper (1860) especially underlined that his *Anisodon* is not the same as *Habrodon*, and accepted Sullivant's opinion (cited in Schimper, l. c.), that *Anisodon* is the same as the North American *Clasmatodon*. Surprisingly, the description and illustration of *Clasmatodon* in Limpricht (1896) are correct. We however suspect that they were based on non-European material: Duell (1994) reported no proofed materials from Germany. Hence, *Anisodon* is probably a earlier synonym of *Habrodon*. However, a final decision can only be made once the expanded search of the original collections of *Anisodon* would give no results.

(d) The name *Phlogostomum* was suggested by Hampe to replace *Anisodon*, since he thought that this name was already used in the Solanaceae. He obviously confused it with *Anisodus* (Solanaceae).

Species included:

*Clasmatodon parvulus* (Hampe) Sull.

22. **Flabellidium** Herz., Biblioth. Bot. 87: 163. 1916. Type: *F. spinosum* Herz.

Plants small, rather rigid, sordid to yellowish green. Pseudoparaphyllia triangular. Stem creeping to ascending, with central strand and 2-3-stratose sclerodermis, densely foliate, irregularly pinnately branched, branches slightly arcuate, foliage same as that of stem. Stem leaves erect to imbricate, ovate, gradually tapered above, acute, more or less concave, not plicate; margin serrate throughout; costa ending above mid-leaf in sharp spine, distally toothed; laminal cells rhombic-ovate to shortly elongate-flexuose, thick-walled; in alar area subquadrate, forming extensive opaque area extending up along margin. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves straight, abruptly broadly acuminate, costa reaching above mid-leaf. Seta smooth. Calyptra naked. Mesophytic? (on tree roots in forest). Other sporophytic characters unknown.

Distribution: Bolivia.

(a) The genus is only known from the holotype collected in Bolivia. Enroth (1995), who monographed *Flabellidium*, agreed with Broth-

erus' (1925) view that it is closely related to *Scorpiurium*. The two genera differ by the frondose branching and thick-walled but not opaque alar cells of *Flabellidium*. These characters would also be congruent with a relationship with *Helicodontium* that is widespread in the South America. The size of plants of *Helicodontium* is the same as of *Flabellidium*, while Mediterranean *Scorpiurium* species are usually larger. *Helicodontium capillare*, the only species of the genus retained for Latin America by Buck (1980a), differs from *Flabellidium* in having a somewhat rounded leaf, blunt marginal teeth, and a costa that is not or only very slightly projecting. A similar morphology is characteristic for some East Asian species traditionally referred to *Rhynchostegiella* (see discussion under that genus).

Species included:

*Flabellidium spinosum* Herz.

23. **Homalotheciella** (Card.) Broth., Nat. Pfl. 1(3): 1133. 1908. – *Homalothecium* sect. *Homalotheciella* Card., Bull. Herb. Boissier 7: 374. 1899. Type: *Homalothecium subcapillatum* (Hedw.) Sull. (= *Pterigynandrum subcapillatum* Hedw.) = *Homalotheciella subcapillata* (Hedw.) Broth.

Plants small, soft, pale yellowish-green. Stem prostrate to ascending, with weak and at places lacking central strand, densely foliate, densely, but irregularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 2-celled. Pseudoparaphyllia orbicular-triangular, blunt. Stem leaves erect, from narrowly elliptic or obovate base acuminate, concave; margin serrate to serrulate to alar group; costa thin, ending shortly above mid-leaf without spine; laminal cells elongate to linear, thick-walled, flexuose; towards base cells shorter to short rectangular in 2-3 rows, alar cells subquadrate, in rather well delimited group, well extending up along margin. Branch leaves similar to stem leaves. Autoicous. Perichaetial leaves acuminate, more or less straight. Seta long, rough. Capsule erect to slightly inclined, ovate to oblong. Annulus separating by fragments. Operculum moderately longly rostrate. Peristome hygrocastique, strongly modified; exostome teeth pale, papillose almost to base; endostome with low basal membrane, rather strongly papillose segments, segments free or adherent to exostome teeth, cilia absent. Spores large. Calyptra hairy. Mesophytic to xeromesophytic.

Distribution: temperate Eastern North America.

(a) This genus has a strongly modified peristome with the endostome mostly adherent to the exostome. In the Brachytheciaceae a similar case is found only in *Homalothecium philippianum* and *H. laevisetum*, which explains why *Homalotheciella subcapillata* was first placed in *Homalothecium*, where it was accommodated in a distinct section. In all published systematic arrangements *Homalotheciella* has been considered close to *Homalothecium*.

(b) The phylogenetic inferences made from our data are congruent with those of Buck & al. (2000) in that *Homalotheciella* appears only distantly related to *Homalothecium*, but with close affinities to *Helicodontium capillare* and *Clasmatodon*. The latter are also epiphytes in the New World, and share with *Homalotheciella* strongly modified peristomes (though in different manners), and subquadrate alar cells extending up the margin in an elongate group, but differ by their shorter laminal cells, smaller and blunt leaves and subentire to bluntly crenulate margins. Another possible affinity of *Homalotheciella* is with three genera that were not included in our phylogenetic analyses, *Schimperella*, *Mandoniella*, and *Juratzkaeella*.

Species included:

*H. subcapillata* (Hedw.) Broth.

Problematic species:

*H. sinensis* Card. et Thér.

*H. tenerrima* (C. Müll.) E. B. Bartram

24. **Mandoniella** Herzog, Biblioth. Bot. 87: 165. 1916. Type: *M. spicatinervia* (R. S. Williams) Herzog (= *Helicodontium spicatinervium* R. S. Williams).

Plants moderately small, soft, yellowish. Stem creeping, with central strand, loosely to moderately densely foliate, remotely branched, branches moderately densely to densely foliate. Axillary hairs on branches 2-celled (not found on stem), upper cells blunt. Pseudoparaphyllia triangular. Stem leaves erecto-patent, ovate-lanceolate, acuminate, not or hardly concave, sometimes with 1-2 sharp, but shallow plicae; margin sharply serrate above, serrate to serrulate to base; costa ending above mid-leaf in long spine, sometimes with additional spine a little below; laminal cells elongate to linear, with narrowly acute ends, moderately thick-walled, highly re-

fracting; basal cells shorter, irregular in shape, more strongly thick-walled in few rows across base or only in alar area. Branch leaves smaller than stem leaves and acuminate to acute. Autoicous. Perichaetial leaves gradually tapered to reflexed acumina. Seta long, smooth. Capsule erect, ovate. Annulus of 1-2 rows of large cells, hardly separated. Operculum obliquely rostrate. Peristome hygrocastique, modified; exostome teeth red-brown, not spaced at mouth level, on outer surface papillose above and cross striolate below; endostome with low basal membrane, narrow segments, split along keel, and very short or absent cilia. Spores small. Mesophytic or xeromesophytic (on tree at high elevation).

Distribution: Bolivia.

(a) When describing this species, Herzog (Bibl. Bot. 87: 165. 1916) provided a rather detailed illustration of it. The shape of the operculum is described by Williams (1910), we did not see any. The genus is known by only one collection.

(b) Gametophytically this species is somewhat similar to *Brachythecium acuminatum* or *Homalotheciella*, but the costa is excurrent and the seta is smooth. A position near the latter genus is most probable.

Species included:

*M. spicatinervia* (R. S. Williams) Herz.

25. **Schimperella** Thér., Recueil Publ. Soc. Havraise Études Diverses 1925: 26. 1926. Type: *S. rhynchostegioides* Thér.

*Rhynchocarpidium* P. Varde et Leroy, Bull. Jard. Bot. État 18: 188. 1947. Type: *R. katalense* P. Varde et Leroy.

Plants small to medium-sized, golden-green. Stem creeping, with central strand, moderately densely, terete foliate, irregularly branched, branch and stem foliage similar. Stem leaves erecto-patent, ovate, acute to broadly acuminate, twisted just below apex, not or slightly concave, not plicate; margin sharply serrate above, serrulate below; costa ending above mid-leaf in small spine, sometimes with additional spine a little below; laminal cells long-hexagonal or elongate to linear, thin-walled, alar cells short-rectangular, thick-walled across base and extending up along margin. Branch leaves narrower and with longer costa, otherwise similar to stem leaves. Autoicous. Perichaetial leaves erect, with recurved apices. Seta long, smooth, becoming very dark with age. Capsule erect or suberect. Annulus of

1-2 rows of large separating cells. Operculum longly, obliquely rostrate. Peristome modified; exostome teeth on outer surface papillose above and cross-striolate below; endostome with low basal membrane, narrow segments, split along keel, and very short or no cilia. Spores small. Calyptra naked. Mesophytic.

Distribution: East Africa and Madagascar.

(a) We did not see any material of this genus. The above description is compiled from Buck (1985, 1993) and Thériot (1926).

Species included by Buck (1985, 1993):

*S. bello-intricata* (Broth.) Buck

*S. rhynchostegioides* Thér.

26. **Juratzkaella** Buck, Rev. Bryol. Lichénol. 43: 312. 1977. Type: *J. sinensis* (Fleisch. ex Broth.) Buck (= *Juratzkaea sinensis* Fleisch. ex Broth.).

Plants moderately small, soft, yellowish. Stem creeping, thin, with central strand, 2-3-stratose sclerodermis and only 1-2-stratose medullary zone, densely foliate, subpinnately branched, branches densely foliate. Axillary hairs 2-3-celled, pellucid. Pseudoparaphyllia triangular. Stem leaves erect-appressed to slightly homomallous, lanceolate, acuminate, plane to slightly concave; margin serrulate above, bluntly serrulate below; costa narrow, ending above mid-leaf, without spine; laminal cells elongate-rhomboidal, with narrowly acute ends, thick-walled, highly refracting; alar cells subquadrate, often reaching costa, and extending far up along margin. Branch leaves similar to stem leaves. Autoicous. Perichaetial leaves erect, longly acuminate. Seta long, smooth, strongly twisted. Capsule erect or suberect, short-cylindrical. Annulus of one row of large cells, hardly separating. Operculum obliquely rostrate. Peristome xerocastique, slightly modified; exostome teeth reddish, not spaced at mouth level, on outer surface papillose above and cross-striolate below; endostome with high basal membrane (about 1/3 of endostome height), moderately broad segments, split along keel, and without cilia. Spores small. Habitat unknown, but probably not epiphytic (stem covered with sand).

Distribution: China.

(a) The genus is described, illustrated and discussed by Buck (1977). It is similar to *Homalotheciella* in its gametophytic characters, but has a smooth seta and rather completely developed peristome.

Species included:

*J. sinensis* (Fleisch. ex Broth.) Buck

27. **Aerolindigia** Menzel, Nova Hedwigia 52: 321. 1991. Type: *A. capillacea* (Hornsch.) Menzel (= *Pilotrichum capillaceum* Hornsch.).

Plants small, soft, pale green to yellowish. Stem mostly creeping, sometimes pendent, with weak central strand, loosely to moderately densely foliate, remotely branched, branch foliage similar to that in stem. Axillary hairs 2-celled. Pseudoparaphyllia longly acuminate. Stem leaves erecto-patent to slightly reflexed, ovate-lanceolate, acuminate, not or hardly concave; margin serrate to serrulate; costa ending in mid-leaf or often shortly below, without spine; laminal cells elongate to rhombic-elongate, firm-walled; towards base considerably wider, alar cells not differentiated. Branch leaves similar to stem leaves. Autoicous. Perichaetial leaves straight. Seta relatively short, 2-5 times longer than urn, rough. Capsule straight, ovate. Annulus separating by fragments. Operculum shortly rostrate. Peristome xerocastique, moderately modified; exostome teeth narrow, cross-striolate below; endostome with high basal membrane, moderately broad segments, and no cilia. Spores large. Calyptra naked. Xeromesophytic, tolerant to desiccation.

Distribution: tropical America and Africa.

(a) The genus was revised and illustrated by Menzel (1991). Ignatov & al. (1999) discussed the possible relationship of *Aerolindigia* to the group of East Asian, Malesian and Oceanian species, which were uncomfortably placed in *Rhynchostegiella*. They argued that based on morphology the latter seem more similar to *Aerolindigia* than to the European *Rhynchostegiella* species. The results of our phylogenetic analyses based on morphological and molecular data (Figs. 1-2) support the close relationship between *Aerolindigia* and at least one *Rhynchostegiella* species of this group, the Malesian *R. brachypodia*. At the same time, some important morphological differences (long and very strongly rough seta, large spores, golden color) support keeping *Aerolindigia* as a separate genus. Fortunately this group of Malesian and Oceanian *Rhynchostegiella* has an existing generic name, *Remyella* (see below).

Species included:

*A. capillacea* (Hornsch.) Menzel

28. **Remyella** C. Müll., Flora 82: 477. 1896. Type: *R. hawaica* C. Müll.

Plants small, soft to somewhat rigid, yellowish to rich golden. Stem mostly creeping, sometimes pendent, with weak central strand, loosely to densely foliate, remotely to rather regularly pinnately branched, branch foliage more dense. Axillary hairs 2-celled. Pseudoparaphyllia longly acuminate. Stem leaves spreading to reflexed, in dry state with similar orientation, but in some species becoming tubulose-spiculose due to incurved to inrolled margins, ovate-lanceolate, acuminate, not or hardly concave in basal portion; margin serrate to serrulate; costa ending in mid-leaf or below, without spine, laminal cells elongate to rhombic-elongate, firm-walled; towards base considerably wider, alar cells not differentiated. Branch leaves smaller and narrower, otherwise similar to stem leaves. Autoicous. Perichaetial leaves with reflexed acumina. Seta long, very rough. Capsule erect, cylindrical. Annulus not separating. Operculum with long beak. Peristome xerocastique, moderately modified; exostome teeth red-brown, strongly papillose above, cross-striolate below, strioles papillose, inner surface incrassate; endostome with high or rather low basal membrane, segments moderately broad, non- or slightly perforated along keel, cilia short to slightly above half of segment length. Spores large. Calyptra naked. Xeromesophytic, tolerant to desiccation.

Distribution: East Asia, Malesia, Oceania, and ?Australia.

(a) This group was briefly commented under *Rhynchostegiella* (see above) and also by Ignatov & al. (1999, 2003).

Species included:

***R. brachypodia*** (Fleisch.) comb. nov. – *Rhynchostegiella brachypodia* Fleisch., Musci Buitenzorg 4: 1564. 246. 1923.

*R. hawaica* C. Müll.

***R. ramicola*** (Broth.) comb. nov. – *Rhynchostegium ramicola* Broth., Bull. Soc. Roy. Bot. Belgique 41(1): 91. 1905.

***R. santosii*** (E. B. Bartram) comb. nov. – *Rhynchostegiella santosii* E. B. Bartram, Philipp. J. Sci. 87: 279. 1958.

***R. sumatrana*** (Fleisch.) comb. nov. – *Rhynchostegiella sumatrana* Fleisch., Musci Buitenzorg 4: 1566. 1923.

***R. vriesei*** (Dozy et Molk.) comb. nov. –

*Rhynchostegiella vriesei* Dozy et Molk., Ann. Sci. Not. Bot., sér. 3, 2: 309. 1844, ['vriesei'].

Species probably belonging to *Remyella*:

*Rhynchostegiella menadensis* (Sande Lac.) E. B. Bartram, *R. leptoneura* Dix. et Thér., and *Rhynchostegium nano-pinnatum* (Broth.) Kindb. probably relate to this group, but the seta is smooth in these species, the spores are small, and the areolation is somewhat narrower, than in large-spored species of the genus. Hence the further studies are needed before nomenclatural transfers.

29. **Meteoridium** (C. Müll.) Manuel, Lindbergia 4: 47. 1977. – *Neckera* subsect. *Meteoridium* C. Müll., Syn. Musc. Frond. 2: 672. 1851. Type: *Neckera remotifolia* (C. Müll.) Hornsch. ex C. Müll. (= *Leskea remotifolia* C. Müll., *Meteoridium remotifolium* (C. Müll.) Manuel).

Plants large, soft, green to yellowish. Stem creeping to pendent, with weak and at places absent central strand, loosely foliate in creeping part, more densely foliate in pendent part, at places rather regularly remotely branched, branch foliage same as that of pendent part of stem. Axillary hairs 4-5-celled. Pseudoparaphyllia triangular. Stem leaves widely spreading, broadly ovate to ovate-lanceolate, longly acuminate to attenuate, not or hardly concave; margin serrulate; costa ending in mid-leaf or just above, without spine, laminal cells linear, thick-walled; alar cells scarcely differentiated, but a few subalar cells somewhat enlarged, shortly rectangular, rather thick-walled. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves with  $\pm$ erect to slightly reflexed acumina. Seta 1.5-2 times longer than urn, smooth. Capsule emergent from perichaetium, straight. Annulus separating by fragments. Operculum shortly rostrate. Peristome xerocastique, moderately modified; exostome teeth narrow, cross-striolate below; endostome with very low basal membrane, narrow filiform segments and no cilia. Spores large. Calyptra naked. Mesophytic, tolerant to desiccation.

Distribution: tropical America.

(a) This genus was segregated from *Meteoropsis* by Manuel (1977a), who recognized it for a single species. Originally the name was given to a monotypic section of *Neckera*.

(b) In our analysis *Meteoridium* was always

sister to *Squamidium* plus *Zelometeorium* (Figs. 1-2). *Meteoridium* differs from two latter genera in its xerocastique, relatively complete peristome and naked calyptra (we did not see any, information about calyptra is from Crum, 1994). This group of three pendent tropical, mainly American genera form a rather isolated clade, sister to the remainder of the subfamily Rhynchostegielloideae.

Species included:

*M. remotifolium* (C. Müll.) Manuel

Species included by Buck (1999):

*M. tenuissimum* (Hook. et Wils.) M. A. Lewis

30. **Squamidium** (C. Müll.) Broth., Nat. Pfl. 1(3): 807. 1906. – *Meteorium* sect. *Squamidium* C. Müll., Linnaea 42: 420. 1879. Type: *Meteorium lorentzii* C. Müll. ['i'] (= *Squamidium lorentzii* (C. Müll.) Broth.) = *S. brasiliense* (Hornsch.) Broth.

Plants large, soft, green to pale yellow, old parts tinged with black to totally black. Stem creeping to pendent, with weak and discontinuous central strand, rather densely foliate. Axillary hairs 3-7-celled. Pseudoparaphyllia triangular. Stem leaves strongly concave in basal part, resulting in terete foliage, broadly ovate to ovate, gradually or abruptly tapered into short or long and sometimes flexuose acumen; margin serrulate or subentire; costa ending in mid-leaf or above without spine, laminal cells linear, thick-walled; alar cells weakly differentiated, a few subalar cells enlarged, shortly rectangular, thick- or thin-walled. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves with  $\pm$ erect acumina. Seta smooth to slightly rough. Capsule immersed to emergent, straight. Annulus separating by fragments. Operculum shortly rostrate. Peristome hygrocasticque, modified; exostome teeth narrow, papillose to base; endostome with rather high basal membrane, narrow segments, and rudimentary cilia. Spores large. Calyptra hairy. Mesophytic, tolerant to desiccation.

Distribution: tropical America and Africa.

(a) *Squamidium* was segregated as a section of *Meteorium*, and since that time its concept remains almost the same. It has been revised recently by Allen & Crosby (1986), who accepted 7 species. Despite that the genus is not big, the species are grouped into two sections, and even this does not make the groups

very homogenous. At least in the type section one species has small and thick-walled alar cells (incl. *S. brasiliense*, used in the present analysis), whereas the other four species have inflated alar cells.

(b) Our analysis showed a very high support for a close relationship between *Zelometeorium* and *Squamidium*. This allows to hypothesize that an analysis of all species of *Squamidium* and *Zelometeorium* might show more complex interrelations among their species.

Species included:

*S. brasiliense* (Hornsch.) Broth.

Species included by Allen & Crosby (1986): *S. diversicoma* (Hampe) Broth., *S. isocladum* (Ren. et Card.) Broth., *S. leucotrichum* (Tayl.) Broth., *S. livens* (Schwägr.) Broth., *S. macrocarpum* (Spruce ex Mitt.) Broth., *S. nigricans* (Hook.) Broth.

31. **Zelometeorium** Manuel, J. Hattori Bot. Lab. 43: 110. 1977 [1978]. Type: *Z. patulum* (Hedw.) Manuel (= *Hypnum patulum* Hedw.).

Plants large, soft, green to yellowish, old parts tinged with black to totally black. Stem creeping to pendent, with weak and at places absent central strand, loosely foliate in creeping part, more densely foliate in pendent part, at places rather regularly remotely branched, branch foliage same as that of pendent part of stem. Axillary hairs 3-4-celled. Pseudoparaphyllia triangular. Stem leaves spreading to recurved from clasping base, broadly ovate and suborbicular to ovate-lanceolate, acute to acuminate, acumen sometimes attenuate-flexuose, margin serrulate; costa ending in mid-leaf or above without spine, laminal cells linear, relatively thin-walled; alar cells weakly differentiated, a few subalar cells enlarged, shortly rectangular, thick-walled. Branch leaves less longly acuminate. Dioicous. Perichaetial leaves with  $\pm$ erect acumina. Seta as long as urn, slightly rough to almost smooth. Capsule immersed to emergent, straight. Annulus separating by fragments. Operculum shortly rostrate. Peristome hygrocasticque, modified; exostome teeth narrow, papillose to base; endostome with low basal membrane, narrow segments, and rudimentary cilia. Spores large. Calyptra hairy. Mesophytic, tolerant to desiccation.

Distribution: tropical America.

(a) This genus was segregated from *Meteo-*

riopsis by Manuel (1977b), who included 5 species in it. See also note under *Squamidium*.

Species included:

*Z. patulum* (Hedw.) Manuel

Species included by Manuel (1977b): *Z. allionii* Manuel, *Z. ambiguum* (Hornsch.) Manuel, *Z. patens* (Hook.) Manuel, *Z. recurvifolium* (Hornsch.) Manuel

#### SUBFAM. RHYNCHOSTEGIOIDEAE

##### SUBFAM. NOV.

*Plantae mediocres vel robustae. Folia lato ovata vel anguste lanceolata; cellulae anguste lineares vel elongatae. Autoica, dioica vel phyllo dioica. Seta laevissima. Capsula horizontalis, raro erecta. Peristomium perfectum, raro imperfectum. Operculum rostratum, raro conicum.*

Type genus: *Rhynchostegium* B. S. G.

Plants commonly large, rich to pale green to yellowish-brown, often characteristically whitish and with silky (? oily) gloss. Axillary hairs frequently long and their upper cells more strongly colored than the basal cells. Autoicous, dioicous, phyllo dioicous. Seta always smooth. Operculum in most groups with sharply delimited beak (excepting only *Pseudoscleropodium*). Peristome perfect, very rarely modified (*Palamocladium*, *Eriodon*).

Genera included: *Rhynchostegium*, *Platyhypnidium*, *Scorpiurium*, *Eurhynchium* s. str. (= species of *E. striatum* group), *Plasteurhynchium*, *Palamocladium*, *Bryoandersonia*, *Pseudoscleropodium*, *Aerobryum*.

Genus included based in morphology only: *Eriodon*.

32. **Platyhypnidium** Fleisch., Musci Buitenzorg 4: 1536. 1923. Lectotype: *Platyhypnidium muelleri* (Jaeg.) Fleisch. (= *Rhynchostegium muelleri* Jaeg.), selected by Ignatov & al. (1999).

Plants large, deep green, becoming brownish with age. Stem prostrate, with central strand, moderately densely, julaceously foliate, old leafless stems often remaining for a long time, irregularly branched, branches straight, foliage similar to that of stem. Axillary hairs 4-7-celled, upper cell often brownish and verrucose. Pseudoparaphyllia triangular. Stem leaves erect or gradually reflexing from an erect base, in their middle often twisted, broadly ovate or suborbicular to ovate-lanceolate, ± broadly acute, with acute to blunt apex, smooth, more rarely

indistinctly plicate; margin serrate, costa ending above mid-leaf and often at 0.8-0.9 of leaf length, without spine; laminal cells linear, moderately thick-walled; alar (or sometimes only subalar) cells shortly rectangular, thin-walled, indistinctly delimited from neighbouring cells. Branch leaves smaller than stem leaves, otherwise similar. Autoicous. Perichaetial leaves with slightly reflexed, often rather stiff acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Hygrophytic, occasionally hydrophytic.

Distribution: Subcosmopolite.

(a) *Platyhypnidium riparioides* was found in our analysis (Fig. 1-2) to be not distinct from *Rhynchostegium*. However, this species was represented in our analysis by cpDNA only, thus we hesitate to use obtained data for certain judgements on relationships between *Rhynchostegium* and *Platyhypnidium*. However, their close relationship is very probable.

(b) *Platyhypnidium* was established for aquatic plants and thus placed in the Amblystegiaceae by Fleischer (1923) and Brotherus (1925). Subsequent authors usually included its species in *Rhynchostegium*, or more rarely *Eurhynchium*. The most recent revisions, however, accepted it as a genus of its own (McFarland, 1994; Ignatov & al., 1999; Buck, 1999). Hedenäs (2002) also recognized it and stated that the genus seems to be well circumscribed. Ironically, the only species recognized by him in Australia, *P. austrinum*, has never been found in our analysis close to *P. riparioides*. All the analyses put *P. austrinum* into the Rhynchostegielloideae, not Rhynchostegioideae. This position is well in agreement with the fact, that *P. austrinum* is different from all other members of *Platyhypnidium* (and also from all other members of the subfamily Rhynchostegioideae!) in having a rough seta. Another difference between *P. austrinum* and other species of *Platyhypnidium* with smooth setae is the rather short costa (0.6-0.8 vs. 0.7-0.9). Our analysis suggests the position of *Platyhypnidium austrinum* sister to the *Cirriphyllum*-clade or *Rhynchostegiella*-*Cirriphyllum*-*Homalotheciella* clade (Figs. 1-2), but more studies are needed to resolve its relationships and to define the taxonomic status. Al-

though such polyphyly of *Platyhypnidium* appeared rather unexpectedly, this is not the first case when taxa referred to this genus are found very distant. Loeske (1911), when segregating this group (under *Platyhypnum*), included in it besides *P. riparioides* also *Hygrohypnum dilatatum*, *H. molle*, and *H. alpinum* (now not in Brachytheciaceae). The aquatic environment seems to affect morphology strongly, resulting in convergent similarities.

(c) Chinese *Platyhypnidium patulifolium* was found very closely related with *Donrichardsia macroneuron*, and thus is discussed under *Donrichardsia*.

Species included:

*P. aquaticum* (Jaeg.) Fleisch.

*P. muelleri* (Jaeg.) Fleisch.

*P. pringlei* (Card.) Broth.

*P. riparioides* (Hedw.) Dix.

Species probably belonging to *Platyhypnidium*:  
*Eurhynchium fuegianum* Card.

Species excluded from *Platyhypnidium*:

*P. patulifolium* (Card. et Thér.) Broth. – *Donrichardsia*

*P. austrinum* (Hook. et Wils.) Fleisch. – unclear generic position within the Rhynchostegelloideae, maybe close to *Oxyrrhynchium*.

33. **Rhynchostegium** B. S. G., Bryol. Eur. 5: 197. 1852. Type: *R. confertum* (Dicks.) B. S. G. (= *Hypnum confertum* Dicks.).

*Steerecleus* H. Robinson, Mem. New York Bot. Gard. 45: 480. 1987. Type: *S. serrulatum* (Hedw.) H. Robinson (= *Hypnum serrulatum* Hedw.).

*Scleropodiopsis* Ignatov, Arctoa 7: 149. 1998. *syn. nov.* Type: *S. laxiretis* Ignatov = *Rhynchostegium arcticum* (I. Hag.) comb. nov., *syn. nov.*

Plants large or medium-sized, light green, becoming argentate-whitish with age. Stem prostrate, with central strand, loosely to densely, julaceous or complanately foliate, irregularly branched, branches straight, foliage similar. Axillary hairs 3-6-celled, upper cell often brownish and verrucose. Pseudoparaphyllia triangular. Stem leaves from erect to patent, more rarely imbricate, in middle often twisted, broadly ovate or lanceolate, acuminate or more rarely acute, not plicate; margin serrate to serrulate, occasionally subentire, costa ending shortly above mid-leaf, occasionally below mid-leaf, without or with spine; laminal cells linear, moderately thin- to

moderately thick-walled; alar cells very weakly to strongly differentiated, rectangular to isodiametric, thin-walled, in distinctly or indistinctly delimited group. Autoicous. Perichaetial leaves with slightly reflexed acumina or straight, longly acuminate. Seta smooth. Capsule inclined to horizontal, often relatively small (comparatively with that of *Brachythecium*), strongly contracted below mouth. Annulus separating by fragments. Operculum obliquely rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: Subcosmopolite (though absent in most of boreal zone in Holarctic).

(a) It is rather surprising, that this big and relatively diverse genus, which was thought to be heterogeneous, appears monophyletic [with the only exception of *Platyhypnidium riparioides*, whose position remains ambiguous due to the incomplete data set for this species]. We attempted to cover this genus both from the morphological and geographical points of view and included in the analysis both tropical species, "typical *Steerecleus*", such as *R. pallidifolium* and *R. serratum* (pale, large leaved, complanate), *R. murale* (imbricate, deeply green), *R. confertum* (usually green, often with costa ending in a spine), *R. psilopodium* (green, narrow leaved species, previously referred to *Rhynchostegella*), and *R. rotundifolium* (with exceptionally lax areolation, dark green to brownish).

(b) According to the present results, the status of *Steerecleus* as independent genus is not supported, though species of this segregate, namely *R. serrulatus* and *R. pallidifolius*, appear in the present analysis close to each other (Figs. 1-2).

(c) *Scleropodiopsis laxiretis* was found to be identical with *Rhynchostegium murale* var. *arcticum* Hagen, which, however seems to merit a species rank.

(d) Being widespread and variable, some *Rhynchostegium* species exhibit characters, which were considered as characteristic for *Eurhynchium* s. l. and moreover diagnostic for this genus versus *Rhynchostegium*. For example *R. confertum* often has its costa ending in a spine, the foliage is not complanate at all in narrow-leaved species, like *R. psilopodium*, etc. Thus it is not surprising, that authors failed to find stable characters to segregate these two genera and therefore considered them congeneric.



(d) The genus *Rhyncho-hypnum* Hampe is usually considered as established by Hampe based on his earlier (Hampe, 1852) subgenus of *Hypnum* subg. *Rhynchohypnum*. The latter included two species, *Hypnum confertum* and *H. murale* (here in *Rhynchostegium*), that, however, are not mentioned in the paper where *Rhyncho-hypnum* is validated as a genus. Seems, Hampe never transferred neither *Rhynchostegium confertum*, nor *R. murale* to *Rhyncho-hypnum*, where he classified mostly species now referred to the Sematophyllaceae. We retain the problem of lectotypification of *Rhynchohypnum* for future. Maybe this generic name can be used in the Sematophyllaceae.

Species included:

***Rhynchostegium arcticum*** (I. Hag.) comb. nov.  
– *R. murale* var. *arcticum* I. Hag., Tromsø Mus. Aarsh. 21-22 (3): 305. 1904. – *Scleropodiopsis laxiretis* Ignatov, Arctoa 7: 150. 1998. syn. nov.

*R. assumptionis* Besch.

*R. beskeanum* (C. Müll.) Jaeg.

*R. brachypterum* (Hornsch.) Jaeg.

*R. celebicum* (Sande Lac.) Jaeg.

*R. comorae* (C. Müll.) Jaeg.

*R. complanum* (Mitt.) Jaeg.

*R. compridense* (C. Müll. ex Broth.) Par.

*R. confertum* (Dicks.) B. S. G.

*R. contractum* Card.

*R. distratum* (Hampe) Jaeg.

*R. duthiei* C. Müll. ex Dix.

*R. herbaceum* (Mitt.) Jaeg.

*R. hookeri* Jaeg.

*R. inclinatum* (Mitt.) Jaeg.

*R. javanicum* (Bél.) Besch.

*R. laxatum* (Mitt.) Par.

*R. megapolitanum* (Bland. ex Web. et Mohr) B. S. G.

*R. murale* (Hedw.) B. S. G.

*R. ovalifolium* Okam.

*R. pallidifolium* (Mitt.) Jaeg.

***Rhynchostegium psilopodium*** nom. nov. – *Rhynchostegiella laeviseta* Broth., Symb. Sin. 4: 109. 1929.

*R. rotundifolium* (Brid.) B. S. G.

*R. scariosum* (Tayl.) Jaeg.

*R. sellowii* (Hornsch.) Jaeg.

*R. serrulatum* (Hedw.) Jaeg.

*R. tenuifolium* (Hedw.) Reichardt

A number of names are synonymized by Ignatov & al. (2003).

34. ***Eriodon*** Mont., Ann. Sci. Nat. Bot. ser. 3, 4: 98. 1845. Type: *E. conostomus* Mont.

?*Helicodontiadelphus* Dix., J. Bot. 74: 5. 1936. Type: *Helicontiadelphus australiensis* Dix. = *Eriodon cylindritheca* (Dix.) Dix. et Sainsb. (synonymized by Buck, 1981a).

Plants medium-sized, soft, light green, whitish with age. Stem creeping to pendent, without central strand, loosely to moderately densely foliate, remotely branched, branch foliage similar to that in stem. Axillary hairs 2-3-celled, very short. Pseudoparaphyllia triangular. Stem leaves widely spreading, ovate-lanceolate, longly acuminate, not or hardly concave; margin sharply serrate above, serrulate to base; costa ending above mid-leaf without spine, laminal cells linear, moderately thick-walled; at base cells wider, especially a few cells in submarginal area. Branch leaves smaller than stem leaves, otherwise similar. Autoicous. Perichaetial leaves straight, shortly acuminate. Seta very long, thin and smooth. Capsule erect, longly cylindrical or slightly curved (in *Leskea* manner). Annulus separating by fragments. Operculum very long, straight, gradually tapered to rostrum. Peristome hygrocastic, strongly modified; exostome teeth narrow, very evenly and longly tapered, pale yellowish, spaced at mouth level, on outer surface papillose to base, inner surface papillose to base; endostome colored stronger than exostome, lightly orangish, with low basal membrane, narrow filiform segments, rigidly standing and sometimes twisting distally (in *Tortula* manner), with long gaps along keel, cilia absent. Spores large. Calyptra naked. Mesophytic, tolerant to desiccation.

Distribution: Chile and Argentina.

(a) The above description is based on *Eriodon conostomus*, the only species undoubtedly referred to the genus.

(b) The genus is unique in having the longest peristome in the family. Leaf texture and areolation show certain similarities with *Rhynchostegium*, but differ from most of its species in a very short hyaline axillary hairs. See also below discussion under *E. cylindritheca*.

Species included:

*Eriodon conostomus* Mont.

Problematic species:

*Eriodon cylindritheca* (Dix.) Dix. et Sainsbury. Buck (1981b) retained this species in *Eri-*

*odon*, despite several differences in sporophytic characters. Hedenäs (2002) included it in *Rhynchostegium*, where it was originally placed. Hedenäs stated that this species is gametophytically very close to *Rhynchostegium*, as peristome specialization is known in many tropical groups. However, to our mind, *Eriodon conostomus* is also derived from *Rhynchostegium*, and shares with it several gametophytic characters [Brotherus' (1925) illustration and statement that laminal cells are strongly prorate in this species is misleading – we found, that cells are smooth or very slightly prorate, not differing in this respect from all other studied *Rhynchostegium* species]. Similarly to *E. conostomus*, *E. cylindritheca* grows on twigs and its sporophyte can be regarded as a grade toward the ultimate specialization of *E. conostomus*. It has slightly curved capsules, gradually tapered long and broad beaks, a pale exostome, and even an orangish endostome, which is, however, much less modified from the basic hypnoid type, than that of *E. conostomus*. Whether the South American *E. conostomus* and the Australasian *E. cylindritheca*, arose via reduction from distinct ancestors or a shared ancestor remains to be critically tested. Whether *Eriodon* should be retained as a distinct genus even though *Rhynchostegium* would thereby be paraphyletic [if the above written hypothesis on its affinity is true, of course], we can only repeat the same as for *Unklejackia* (cf. discussion on p. 266).

*Eriodon radicalis* Spruce ex Jaeg. This species has been referred to *Entodontopsis* (Stereophyllaceae) by Buck (1981b), who reported filamentose pseudoparaphyllia in this species (no specimens cited, but the drawing of leaf and areolation is called “from type, NY”). We were able to study an isotype in H-BR (1401. *Eriodon radicalis* Spruce. Andes Quitoensis. Leg. R. Spruce) and found that it has Brachytheciacean pattern of pseudoparaphyllia. The leaf characters are similar to those of *E. conostomus* (except that basal cells are larger and the costa ends in spine). The plants seem not to be pendent and are golden in color. Axillary hairs were not observed. The capsule is cylindrical. The exostome teeth are dark red-brown, strongly loop-like curved at base (similarly to *Leskea polycarpa*), and according to Brotherus (we hesitated to destroy the last capsule with teeth) at their base cross- to obliquely-striolate. The endostome is dark-pellucid, with a low basal

membrane and narrow segments (much shorter than in *E. conostomus*). Hence, the position of this species in *Eriodon* is unlikely.

35. **Aerobryum** Dozy et Molk., Ned. Kruidk. Arch. 2(4): 279. 1851. Type: *A. speciosum* (Dozy et Molk.) Dozy et Molk. (= *Meteorium speciosum* Dozy et Molk.).

Plants very large, light green to whitish and soon becoming dark brown to black. Stem creeping to pendent, with central strand, moderately densely, julaceously foliate, in creeping parts sometimes subcomplanate, very sparsely branched, branch foliage similar to that in stem. Axillary hairs 4-6-celled, uppermost cells pale brown. Pseudoparaphyllia triangular. Stem leaves spreading from erect base, sometimes with clasping base (due to U-shaped insertion on stem), very broadly ovate, rather shortly acuminate, not plicate, not concave, but somewhat conduplicate and twisted at mid-leaf; margin serrulate to subentire, costa ending shortly below mid-leaf without spine; laminal cells elongate to linear in upper leaf, firm-walled and often cell wall thickenings resulting in bone-shaped pattern; basal cells slightly larger, more strongly porose, alar cells undifferentiated; a few subalar cells sometimes slightly enlarged, short-rectangular, thick-walled. Branch leaves similar to stem leaves. Dioicous or phyllodioicous. Perichaetial leaves with reflexed acumina. Seta smooth, rather short, 2-4 times longer than urn. Capsule inclined to horizontal. Annulus separating by fragments. Operculum shortly rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: East Asia and Malesia.

(a) This genus was only recently transferred to the family (Buck & Goffinet, 2000). Thus, its relation to other genera of the Brachytheciaceae was never a subject for discussion. According to the results of our phylogenetic analyses it obviously belongs to the subfamily Rhynchostegioidae, but its position within the latter is not stable: Nona analysis resolve it more closely related to *Rhynchostegium*, while in POY topologies it is often resolved sister to *Pseudoscleropodium* (cf. Figs. 1 & 2). Morphologically *Aerobryum* is somewhat similar to the former genus in size, often whitish-argentate color, subcomplanate foliage in creeping shoots, smooth seta, etc. (we found no explanation of the statement of Norris & Koponen (1985), that the seta is rough

in New Guinean populations – we found it to be smooth in all studied collections from that area). *Aerobryum* has, however, many unique or rare character states in the Brachytheciaceae: the seta is short, in combination with an inclined-horizontal capsule; old parts of the plants are dark-brown to black; the growth is pendent in the main part of its geographical area; the laminal cells have strongly incrassate walls, resulting in some cases in a bone-shaped pattern [i. e. the longitudinal cell walls strongly incrassate and look like bones, due to two “pores” (=short thin-walled places) near each cell end.

Species included:

*A. speciosum* (Dozy et Molk.) Dozy et Molk.

36. **Pseudoscleropodium** (Limpr.) Fleisch., Musci Buitenzorg 4: 1542. 1923. – *Scleropodium* sect. *Pseudoscleropodium* Limpr., Laubm. Deutsch. 3: 142. 1896. Type: *Scleropodium purum* (Hedw.) Limpr. (= *Hypnum purum* Hedw., *Pseudoscleropodium purum* (Hedw.) Fleisch.).

Plants large, pale sordid green to yellowish or whitish. Stem prostrate or ascending, with central strand, densely, julaceously foliate, rather regularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 4-9-celled, uppermost cells pale brown. Pseudoparaphyllia orbicular-triangular. Stem leaves imbricate, broadly elliptic, broadly obtuse to rounded and apiculate, slightly plicate, strongly concave; margin subentire, costa ending in or shortly above mid-leaf without spine; laminal cells linear-flexuose, moderately thick-walled; basal cells wider, much incrassate, alar cells subquadrate, more or less inflated, thin- or thick-walled, forming poorly delimited group. Branch leaves smaller and narrower than stem leaves. Dioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum conic. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic to xeromesophytic.

Distribution: subcosmopolite (in some areas introduced?).

(a) Buck (1980b) revised this monospecific genus, but did not discuss its affinity within the family. Originally it was segregated from *Scleropodium*. The position of the latter genus is fairly unresolved, but these two genera never appeared closely related. In our analyses *Pseudoscleropodium* always appears as a member of

the subfamily Rhynchostegioideae, but its position within the latter varies: it was found either in basal position within Rhynchostegioideae clade, or sister to *Aerobryum* (cf. Figs. 1-2). *Pseudoscleropodium* is unique in this subfamily in having a conic operculum.

Species included:

*P. purum* (Hedw.) Fleisch.

37. **Bryoandersonia** H. Robinson, Bryologist 65: 137. 1962. Type: *B. illecebra* (Hedw.) H. Robinson (= *Hypnum illecebrum* Hedw.).

Plants large, rigid, green to golden-brownish. Stem prostrate or more commonly ascending to erect in dense tufts, with central strand, moderately densely, julaceously foliate, irregularly pinnately branched or with sympodial shoots only, branch foliage similar to that in stem. Axillary hairs 4-6-celled, uppermost cell obtuse, pale brown. Pseudoparaphyllia acute. Stem leaves rigidly and loosely imbricate, broadly ovate-triangular to suborbicular, rather slightly plicate, strongly concave; margin serrate to serrulate, costa ending above mid-leaf without spine; laminal cells elongate-flexuose, moderately thick-walled; basal cells with much incrassate cell walls, subalar cells subquadrate, larger than neighbouring cells, thick-walled, forming opaque, poorly delimited group. Branch leaves similar to stem leaves. Dioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic to xeromesophytic.

Distribution: temperate Eastern North America.

(a) This genus was segregated from *Cirriphyllum* by Robinson (1962), without indication of its possible affinity. In Nona analysis it was resolved in a very basal position in Rhynchostegioideae, close to *Pseudoscleropodium* with a high support, while POY analysis resolved it to the basal position in Rhynchostegielloideae (cf. Figs. 1-2). Its position seems to be highly sensitive to small differences in sequence alignment.

Species included:

*Bryoandersonia illecebra* (Hedw.) H. Robinson

38. **Eurhynchium** B. S. G., Bryol. Eur. 5: 217. 1854. Type: *E. longirostre* B. S. G. = *E. striatum* (Hedw.) Schimp.

*Pancovia* Neck. ex J.J. Kickx, Flore Cryptogamique des Flandres 1: 75, 91. 1867. *nom. illeg.*

[originally this genus included species from many genera of Brachytheciaceae and *Isothecium*; Lindberg (1879) used it as a subdivision of *Hypnum* in the sense close to *Eurhynchium* of "Bryologia Europaea"].

Plants large, rigid, light green to somewhat whitish or brownish. Stem prostrate, with central strand, moderately densely, julaceously foliate, irregularly pinnately branched and with numerous erect and arching sympodial shoots, branch foliage similar to that in stem. Axillary hairs 2-4-celled, uppermost cell obtuse, hyaline to pale brown. Pseudoparaphyllia acute. Stem leaves rigidly erect-spreading to spreading, broadly ovate-triangular to ovate-lanceolate, acute to acuminate, plicate, concave in basal part; margin serrate to serrulate, costa ending far above mid-leaf, at 0.7-0.8(0.9) of leaf length, with spine; laminal cells elongate to linear, thin-walled; towards base shorter; alar cells differentiated or only subalar cells differentiated, large, thin-walled, forming indistinctly delimited group. Branch leaves somewhat narrower and smaller than stem leaves, otherwise similar. Dioicous or phyllodioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic.

Distribution: Palearctic.

(a) The new definition of the genus makes it very homogeneous, and the two species included in it are sometimes treated as subspecies. The closest relatives of this genus are *Plasteurhynchium* and *Palamocladium* (see comments under the latter genus).

Species included:

*E. angustirete* (Broth.) T. Kop.

*E. striatum* (Hedw.) Schimp.

Species transferred to other genera:

*E. africanum* Herz. – *Kindbergia*

*E. altaicum* Ignatov – *Kindbergia*

*E. arbuscula* Broth. – *Kindbergia*

*E. asperisetum* (C. Müll.) E. B. Bartram –

*Oxyrrhynchium*

*E. clinocarpum* (Tayl.) Par. – *Oxyrrhynchium*

*E. crassinervium* (Tayl.) B. S. G. – *Cirriphyllum*

*E. dumosum* (Mitt.) Jaeg. – *Kindbergia*

*E. eustegium* (Besch.) Dix. – *Eurhynchiadelphus*

*E. flotowianum* (Sendtn.) Karttunen – *Sciurohypnum*

*E. fuegianum* Card. – ?(probably *Platyhypnidium*)

*E. hians* (Hedw.) Sande Lac. – *Oxyrrhynchium*

*E. laevisetum* Geheeb – *Oxyrrhynchium*?

*E. meridionale* (B. S. G.) De Not. – *Plasteurhynchium*

*E. oreganum* (Sull.) Jaeg. – *Kindbergia*

*E. praelongum* (Hedw.) B. S. G. – *Kindbergia*

*E. pumilum* (Wils.) Schimp. – *Oxyrrhynchium*

*E. remotifolium* (Grev.) Jaeg. – *Oxyrrhynchium*?

*E. savatieri* Schimp. ex Besch. – *Oxyrrhynchium*

*E. schleicheri* (Hedw. f.) Milde – *Oxyrrhynchium*

*E. serricuspis* C. Müll. – *Kindbergia*

*E. speciosum* (Brid.) Jur. – ?(see discussion under *Oxyrrhynchium*)

*E. squarriifolium* Broth. ex Iishiba – *Kindbergia*

*E. striatulum* (Spruce) B. S. G. – *Plasteurhynchium*

*E. trichocladoides* Ignatov – *Oxyrrhynchium*

39. **Plasteurhynchium** Fleisch. ex Broth., Nat. Pfl. ed. 2, 11: 212. 1925. Lectotype: *P. striatulum* (Spruce) Fleisch. (= *Hypnum striatulum* Spruce), selected here.

Plants large, rigid, deep green to brownish or olive-green. Stem prostrate, with central strand, moderately densely, julaceously foliate, irregularly pinnately branched and with arching sympodial shoots, branch foliage similar to that in stem. Axillary hairs 3-5-celled, uppermost cell obtuse, pale brown. Pseudoparaphyllia acute. Stem leaves rigidly erect-spreading to erect-appressed, ovate-triangular to ovate, broadly acuminate, more or less plicate, concave in basal part; margin serrate to serrulate, costa ending in or above mid-leaf in spine; laminal cells elongate, moderately thick-walled; basal cells much shorter and with incrassate walls, forming opaque area across leaf base or alar group of short cells delimited. Branch leaves somewhat narrower and smaller than stem leaves, otherwise similar. Dioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to horizontal. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic to xeromesophytic.

Distribution: Western Palearctic.

(a) *Plasteurhynchium* was originally placed in the Lembophyllaceae to accommodate spe-

cies superficially rather similar to *Isothecium* (Brotherus, 1925). In recent publications it was included in the Brachytheciaceae as a genus (Ochyra & al., 1992), or more frequently its species were classified within *Eurhynchium* (Smith, 1978; Hedenäs, 1992, etc.). Molecular and morphological data confirmed this latter placement within the Brachytheciaceae and resolved the genus as a close relative of *Eurhynchium* s. str. and *Palamocladium*. *Plasteurhynchium* is somewhat similar to *Eurhynchium striatum* in its general appearance: robust plants with curved branches, plicate leaves, and a complete peristome. The morphological similarity with *Palamocladium* lays in the opaque basal areolation. However *Plasteurhynchium* differs from both these genera in having a prorate toothed dorsal lamina, and a more pronounced differentiation into primary and secondary stems. A phylloidioicous condition was never found in *Plasteurhynchium*, unlike in both *Eurhynchium* and *Palamocladium*.

Species included:

*P. meridionale* (B. S. G.) Fleisch.

*P. striatum* (Spruce) Fleisch.

40. **Palamocladium** C. Müll., Flora 82: 465. 1896. Type: *Pleuropus fenestratus* Griff. = *Palamocladium leskeoides* (Hook.) Britt.

*Pleuropus* Griff., Calcutta J. Nat. Hist. 2: 473. 1842. nom. illeg., later homonym.

Plants large, rigid, deep green to brownish or olive-green. Stem prostrate to ascending, with weak central strand, moderately to very densely, julaceous foliate, irregularly pinnately branched, branch foliage similar to that in stem. Axillary hairs 3-6-celled, uppermost cell obtuse, pale brown. Pseudoparaphyllia acute. Stem leaves rigidly erect, lanceolate-triangular to ovate-lanceolate or lanceolate, gradually and broadly acuminate, at base slightly auriculate, deeply plicate or in slender plants smooth; margin sharply serrate, with teeth partly recurved, costa ending above mid-leaf or almost reaching apex, without spine; laminal cells elongate, relatively short (in comparison with large size of leaf), moderately thick-walled; basal cells much shorter and wider, with incrassate cell walls; alar cells numerous, subquadrate, forming extensive opaque area, sometimes throughout auricles. Branch leaves somewhat narrower and smaller than stem leaves, other-

wise similar. Dioicous or phylloidioicous. Perichaetial leaves with reflexed acumina. Seta smooth. Capsule inclined to erect. Annulus separating by fragments. Operculum rostrate. Peristome hygrocastic, slightly to moderately modified; exostome teeth cross-striolate below, red-brown or pale yellow; endostome with basal membrane 1/2–1/4 of its length. Spores small or large. Calyptra naked. Mesophytic to xeromesophytic.

Distribution: pantropical, expanding to Eastern North America and East Asia.

(a) *Palamocladium* was considered as a relative of *Homalothecium* since Lindberg (1879), who united them in *Hypnum* subgen. *Pleuropus*. This opinion was supported by Brotherus (1925), Robinson (1962), Hofmann (1997) and almost all other authors. Our analysis does not confirm this. *Palamocladium* has been found in all analyses within the subfam. Rhynchostegioidae. The most closely related genera are probably *Eurhynchium* s. str. and *Plasteurhynchium* (Figs. 1, 2), however a support for this has not been obtained. *Palamocladium* differs from the latter genera by its narrow leaves and hygrocastic peristome that is more or less modified. *Palamocladium* is similar to *Eurhynchium* in its phylloidioicous sexual condition and to *Plasteurhynchium* in its opaque basal areolation.

(b) The genus was monographed by Hofmann (1997). She accepted the pantropical *P. leskeoides* in a very broad sense. Based on morphology, it would probably be impossible to consider this very variable species in another way. However, a confirmation of its genetic unity based on molecular data is desirable.

Species included:

*P. euchloron* (Bruch ex C. Müll.) Wijk et Marg.

*P. leskeoides* (Hook.) Britt.

*P. wilkesianum* (Sull.) C. Müll.

41. **Scorpiurium** Schimp., Syn. Musc. Europ. 2: 855. 1876. Type: *S. rivulare* Schimp. = *S. deflexifolium* (Solms) Fleisch. et Loeske.

Plants medium-sized to moderately small, somewhat rigid, green to yellowish or brownish green. Stem prostrate to ascending, with central strand, densely foliate, irregularly pinnately branched, branch curved, their foliage similar to that in stem, sometimes branches attenuate. Axillary hairs 4-6-celled, hyaline or brownish.

Pseudoparaphyllia triangular. Stem leaves appressed when dry, erect-spreading when moist, broadly ovate to ovate-lanceolate, acute or very broadly acuminate, more or less concave, not plicate; margin bluntly serrate to serrulate; costa ending above mid-leaf with spine, and often with several teeth near its end (especially in branch leaves); laminal cells rhombic-ovate to rhombic/elongate, thick-walled; at base cells shorter, forming opaque area across base, alar area subquadrate to oblate, forming extensive opaque area extending up along margin. Branch leaves smaller than stem leaves, otherwise similar. Dioicous. Perichaetial leaves with reflexed, relatively short acumina. Seta long, smooth. Capsule suberect to inclined, shortly ovate to cylindrical. Annulus separating by fragments. Operculum rostrate. Peristome xerocastique, perfect. Spores small. Calyptra naked. Mesophytic to xeromesophytic.

Distribution: Western Palearctic.

(a) This genus was united with *Eurhynchium* s. l. by some authors (Mönkemeyer, 1927, etc.), whereas Brotherrus (1925) placed *Scorpiurium* and *Eurhynchium* at opposite ends in his account of genera of the Brachytheciaceae. Brotherrus seems to have considered it especially isolated, though he did not express this explicitly. Our studies support this idea. *Scorpiurium* (with *Bryoandersonia*) appeared in the analyses in basal position in the Rhynchostegioideae (Fig. 1, 2), the most basal clade of the family.

(b) A key for all three European species was published by Matracchi (2001).

Species included:

*S. circinatum* (Brid.) Fleisch. et Loeske

*S. deflexifolium* (Solms) Fleisch. et Loeske

*S. sendtneri* (Schimp.) Fleisch.

Species not confirmed in the genus:

*S. cucullatum* (Hampe) Hedenäs. Many morphological character states of this Australian endemic species are similar to those of three Mediterranean species of *Scorpiurium*, but they also fit *Flabellidium*, *Helicodontium*, *Rhynchostegiella* (see note "a" under that genus), and we expect it must be in one of these genera. Especially, the rough seta in *S. cucullatum* is according to our phylogenetic analysis in conflict with a placement in *Scorpiurium*, since no one species of Rhynchostegioideae has this character state. Thus, we doubt its generic placement within this subfamily.

## EPILOGUE

The current grouping of genera of the Brachytheciaceae differs quite a lot from previous ones. The greatest changes are suggested for the genera *Eurhynchium*, in its traditional sense, *Cirriphyllum*, *Platyhypnidium*, and maybe also *Bryhnia*. All bryologists who dealt with *Eurhynchium* in the recent past included in it also *Oxyrrhynchium*, sometimes specifically underlining that they are not distinct (Takaki, 1956; Buck, 1988; Koponen, 1987; Robinson, 1962; Hedenäs, 1992; Ignatov, 1998; Matteri & Ochyra, 1989; Crum & Anderson, 1981). Our inferences based on molecular and morphological data strongly suggest that these two genera are not closely related, and following our systematic concept, they belong to different subfamilies. *Platyhypnidium* was re-established recently for the small group of aquatic species. Its homogeneity was underlined by Ignatov & al. (1999), and Hedenäs (2002). Phylogenetic inferences suggest that *Platyhypnidium* is polyphyletic with species scattered between different genera of different subfamilies. The situation with *Bryhnia novae-angliae* is even more contrasting with the traditional views. Different populations of this "species" were not resolved as a monophyletic entity, and may belong to more than one genus.

Seeing these sometimes confusing groupings, should we trust these results based mainly on molecular data? After careful evaluation of the results, one can notice that at least some of the newly revealed groups quite nicely correspond to some morphological characters, which were probably under-evaluated by earlier authors. For example, *Oxyrrhynchium* species often grow in loose mats (but in dense growth they become subdendroid), with subcomplanate branches in loose growth, the branch leaves have a tendency to be elliptic, and in loosely foliate parts of the branches they are often twisted from the middle. Such characters are difficult to use due to their rather inexact definition, and thus they were not taken into consideration or involved in earlier classifications.

Although species of *Platyhypnidium* resemble each other in leaf characters, the genus may be polyphyletic: our analysis suggests that *P. austrinum* may belong to the Rhynchostegielloideae whereas *P. riparioides* seems nested within the

Rhynchostegioideae. Note that *P. austrinum* has a rough seta, a state never present in the Rhynchostegioideae. This forces us to consider that their position in different subfamilies is not an artifact of the analysis. The aquatic environment obviously has a strong effect on morphology (especially leaf morphology), and for this reason the taxonomic position of aquatic taxa must be evaluated with the extreme caution. It is worth to remember that Loeske (1911) included in the genus *Platyhypnum* (later transformed to *Platyhypnidium*) also *Hygrohypnum dilatatum*, *H. molle*, and *H. alpinum*. These latter taxa were traditionally segregated in *Hygrohypnum*, Amblystegiaceae, but according to Vanderpoorten & al. (2002), *Hygrohypnum* is still more severely polyphyletic than *Platyhypnidium*, as its species are suggested to belong to at least three different families.

Another morphological character induced apparently by aquatic habitat is a bistratose lamina. It was considered as unique character, having high taxonomic value (Ochyra, 1985). However later Ochyra & Vanderpoorten (1999) found it had independently evolved within *Platyhypnidium*, and Stech & Frahm (2001) expanded this list further.

Before this study, a rostrate operculum was not known to occur in *Brachythecium* s. str., in fact, it was considered incompatible with the concept of the genus. The nested position of “*Cirriphyllum tommasinii*” in *Brachythecium* and that of “*Cirriphyllum flotowianum*” in *Sciurohypnum* (earlier included in *Brachythecium*), the latter with a high support, overturn this belief. When the value of this character is reconsidered, one might notice the overall similarity between *Sciurohypnum flotowianum* and *S. populeum* in appearance and in some leaf characters, which appear to be more important for delimiting this group than the shape of the operculum. In both cases trends towards a rostrate operculum were associated with a considerably decreasing of length:width ratio of leaf laminal cells. If we consider that these two character states often correlate (cooccur) with each other (especially in epiphytic groups), then the new placements of these former *Cirriphyllum* species do not look so odd.

This and similar minute parallels convince us, that the obtained results based largely on molecular data are able to improve the tradi-

tional classification to a certain extent. Then, after finding a new and presumable better grouping, we are coming to updated the circumscription of subfamilies and genera. However, do these new circumscriptions help to attribute the problematic species in certain group of the Brachytheciaceae? We found it is more or less easy for three big genera – in *Rhynchostegium*, *Homalothecium*, and *Brachythecium*, if we accept the latter in a relatively broad sense, as suggested here. Note, however, that attributing a species to one of four main infrageneric units of *Brachythecium*, groups {around *Brachythecium rivulare*}, {*B. tommasinii-geheebii-complanatum-cirrosium*}, {around *B. salebrosum*}, and {*B. buchananii-ruderae-laetum*} is not always easy. Sometimes we hesitate to refer species to *Brachythecium* vs. *Sciurohypnum* based on the morphological description only. In other genera the problems are much worse. *Cirriphyllum* seems to totally lack morphological synapomorphies. Genera with unusual combinations of character states, like *Mandoniella*, *Juratzkaella*, and *Schimperella* are difficult to link with certainty to one or another subfamily. Plants of the group of *Helicodontium*, *Scorpiurium*, *Flabellidium*, and the group of *Rhynchostegiella* species with short and thick-walled cells are very similar – but note, that they are in two subfamilies! The enumeration of cases where morphology is misleading in Brachytheciaceae can be continued further. But we believe that the reader who knows this family is convinced already, that it is not always possible to refer a species **with certainty** to any specific genus. In this situation we can probably speak about “sibling genera” using a parallel from “sibling species”. Actually, a similar situation started to become common at the genus level after molecular studies became a widely used tool of systematics. The situation at the level of family is even more dramatic: cf. Vanderpoorten & al. (2002), who suggested a new classification of Amblystegiaceae with “morphological synapomorphies unknown” for the family, some subfamilies and tribes.

So, are we far from Bridel, who circumscribed taxa, giving no key to identify them? After that, the authors of “Bryologia Europaea” did their best in selecting “recognizable” characters which could be used for identification of taxa. Some

groups have been delimited, so that we are able to use them in practical work now, but for example in the case of the rostrate operculum, this key character "helped" to place in the subgenus *Oxyrrhynchium* six species, which according to the present data belong to five genera of three subfamilies. Note also that Bridel put *Hypnum velutinum* (cf. our *Brachytheciastrum*), *H. reflexum*, and *H. starkei* (cf. our *Sciurohypnum*) in a separate section, different from the rest of *Brachythecium*. Bruch & al. (1851-55) combined them with the rest of *Brachythecium* based on the key character state of conic operculum, and now we are returning back to Bridel... And we are almost sure, that further authors will find no less drastic errors in the present paper too.

How can we then classify a species with an unusual combination of characters, if it is known only by old and imperfect collections? It seems like the best (if not the only) way is to sequence the living beings with the maximally similar phenotypes from the maximally close geographical area and then re-evaluate the morphological characters, testing their significance in this particular group, and only then make taxonomic decisions. At least in the Brachytheciaceae this might help.

#### APPENDIX 1.

#### CHROMOSOME NUMBERS IN BRACHYTHECIACEAE

The increasing of information on the chromosome numbers lead to slightly controversial results, making the whole amount of data difficult to discuss. However, if species with variable counts from few specimens are omitted, the catalogue of Fritsch (1991) can be generalized as follow [with addition of data of Uniyal, 1997]:

#### Homalothecioideae

**Homalothecium aureum** n=10 (more rarely 10+2m); *fulgescens* n=10+m, 16; *laevisetum* n=11; *lutescens* n=10 (more rarely 8, 10+m, 10+B, 10+1 acc., 11, 12, 14, 24); *philippeanum* n=8, 8+2m, 10, 16; *sericeum* n=8, 10 (more rarely 8+X/Y, 9, 10+m, 10+B, 10+1acc., 10+3 acc., 11, 11+m, 11+2m).

**Brachytheciastrum collinum** n=10+m; *paradoxum* n=22; *velutinum* n=10 (much more rarely 10+m, 10+1, 10+2 acc., 11, 12, 12+m, 18),

*trachypodium* n=10. [*Brachythecium appleyardi-ae* n=11]

**Eurhynchiastrum pulchellum** n=10, 11 (more rarely 7, 8+X/Y, 12, 20).

#### Brachythecioideae

**Kindbergia arbuscula** n=10, 11, *oregana* n=8, *praelonga* n=9 (more rarely 7, 8, 9+1 acc., 9+2 acc., 9+4 acc., 10, 10+m, 11).

**Bryhnia hultenii**, *noesica*, *novae-angliae*, *tenerrima*, *trichomitria* n=11 (more rarely 10), *decurvans*, *tokubuchii*, n=10; *tenerrima* n=8.

**Eurhynchiadelphus eustegium** n=11.

**Myuroclada maximowiczii** n=10, 11.

**Brachythecium rivulare-group**: *frigidum* n=6; *rivulare* n=6 (much more rarely 11, 12, 16), *rutabulum* n=12 (much more rarely 5, 6, 10, 10+m, 13, 20, 22, 24).

**Brachythecium** [basal species with rough seta]: *auriculatum* n=11; *coreanum* n=11; *geheebii* n=10; *tommasinii* n=10, 11;

**Brachythecium salebrosum-group**: *albicans* n=7 (more rarely 6, 9), *austroglareosum* n=13, *austrosalebrosum* n=10, 11, 13, 20; *campestre* n=16 (more rarely 17, 11, 12), *glareosum* n=9 (more rarely 6, 10), *mildeanum* n=13, 14; *salebrosum* n=13 (much more rarely 10+m, 12+m, 13+m); *turgidum* n=14.

**Brachythecium stereopoma-group** (sensu McFarland, 1988): *buchananii* n=10 (also 9+m, 10+m, 11, 14, 20+2m), *garovaglioides* n=10, *kamounense* n=10, 10+m, *kuroishicum* n=10.

**Sciurohypnum flotowianum** n=11; *glaciale* n=8, *oedipodium* n=20 (much more rarely 7, 10, 11), *populeum* n=10 (more rarely 9, 10+m, 11), *plumosum* n=10 (more rarely 9+m, 10+m, 11, 11+m), *reflexum* n=10 (more rarely 11, 12, 20), *starkei* n=10 (more rarely 20).

#### Rhynchostegielloideae

**Scleropodium obtusifolium** n=10+m, 22; *touretii* n=11.

**Rhynchostegiella curviseta** n=11; *tenella* n=11, 22; *R. tenerrifae* n=11.

**Cirriphyllum crassinervium** n=11; *piliferum* n=11.

**Clasmatodon parvulus** n=11, 10+m.

**Oxyrrhynchium hians** n=7 (very rare 7+2 acc., 11), *pumilum* n=10, 10+m; *savatieri* n=8; *schleicheri* n=11; *speciosum* n=15; *vagans* n=10.

**Okamuraea brachydiction** n=11, *hakkonien-sis* n=11.

**Homalotheciella subcapillata** 10+m.



**Rhynchostegioideae**

**Pseudoscleropodium purum** n=11 (Europe), more rarely 7 (Japan).

**Plasteurhynchium meridionale** n=11, *stiatulum* n=11.

**Palamocladium leskeoides** n=11.

**Eurhynchium angustirete** n=6, 11 (more rarely 6, 12, 12+1 acc.), *striatum* n=11 (more rarely 6, 12).

**Rhynchostegium cataractile** n=10, 22; *confertum* n=10, 11 (more rarely 10+m, 13+m, 12); *duthiei* n=10, 10+m; *herbaceum* n=10+m, 11; *inclinatum* n=22; *laxatum* n=20+m, 22; *megapolitanum* 10, 11 (more rarely 11+1m); *murale* n=10, 11 (more rarely 10+m, 11+m); *pallidifolium* n=11; *rotundifolium* n=10+m, 11; *serrulatum* n=9, 9+m, 11; *tenuifolium* n=22.

**Platyhypnidium riparioides** n=11 (more rarely 7, 8, 10, 12, 20); *muelleri* n=9.

**Bryoandersonia illecebra** n=12.

**Scorpiurium circinatum** n=11.

Thus, the most common numbers in the Rhynchostegielloideae and Rhynchostegioideae are n=10 and 11. The only genus that is strongly different is *Oxyrrhynchium*, where n=7, 8, and 15 are stable and found in many counts for more than the half species. Note that 7 is known as the most common number in only one more species, *Brachythecium albicans*, while 15 is unique among the Brachytheciaceae.

In the *Homalothecioideae* n=10 and 11 are also common, but some species have n=8 and more rarely 9.

The *Brachythecioideae* includes two large genera, which differ in chromosome numbers. *Sciurohypnum* has mostly n=10; only two species have n=8 and 11, both based on a single count, and also *S. oedipodium* has mostly n=20. The polyploid nature of the latter species can be supported from morphology, as it is much larger than other related species studied for

chromosomes. It can be hypothesized that *S. hylotapetum*, the largest species of the genus, is also a polyploid. Chromosome numbers in *Brachythecium* are more or less corresponding to the main groups of species: (1) the *B. rivulare*-group has n=6 and 12; (2) the *B. stereopoma*-group sensu McFarland has n=10 [however, many counts are reported so far for only one species, *B. buchananii*], and (3) *B. salebrosum* group is very variable (n= 7, 10, 13, 14, 16); note however, that the number is more or less stable within the individual species; (4) only two species have n=10, *B. tommasinii* and *B. geheebii* (both with a rough seta and in some analyses (cf. Fig. 1), they are closely related, though without support); *B. auriculatum* and *B. coreanum*, which we consider close to the latter group, have n=11 (they also have rough seta).

Hence some peculiar groups in Brachytheciaceae also have deviation in chromosome counts (i. e. others than n=10-11).

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