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TAXONOMIC STUDIES OF THE BARTRAMIACEAE Bryopsida

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Academic dissertation

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The thesis consists of this summary and the following articles, which are referred to by their Roman numerals:

I. Virtanen, V. 1996. Bryophyte flora of the Huon Peninsula, Papua New Guinea. LIX. *Breutelia* (Bartramiaceae, Musci). Acta Botanica Fennica 156: 49-62.

II. Virtanen, V. 1997. The genus *Breutelia* (Bartramiaceae, Musci) in Southeast Asia and Oceania. The Bryologist 100: 324-348.

III. Virtanen, V. 1999. Bryophyte flora of the Huan Peninsula, Papua New Guinea. LX. *Bartramia, Conostomum* and *Leiomela* (Bartramiaceae, Musci). Acta Botanica Fennica 165: 1-15.

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INTRODUCTION

The Bartramiaceae is a moss family with 386 species (Crosby et al. 1999) that grow in diverse habitats. The family has a worldwide distribution, with its greatest diversity in South America. Previous studies of the Bartramiaceae lack phylogenetic analyses (Griffin & Buck 1989). Study of the generic relationships of the Bartramiaceae is based on representatives from 11 genera and 2 datasets, one morphological and one molecular (IV). The focus of the research was to clarify the evolutionary history of the genera of Bartramiaceae, using cladistic analysis of morphological characters along with sequence data of the chloroplast-encoded gene for the large subunit of rubisco (ribulose-1,5-biphosphate carboxylase = *rbc*L).

Regional revisions of the genera in the Bartramiaceae (I-III) with species descriptions and illustrations clarify the taxonomy of each genus in the area. The Asian and Oceanian species of *Breutelia* had not been recently revised prior to my study (II). Taxonomic studies of *Bartramia*, *Breutelia*, *Conostomum*, and *Leiomela* (I, III) are included in the project dealing with the bryophyte flora of Western Melanesia (West Irian, Papua New Guinea, Solomon Islands). The project is based on studies of the 17 000 specimens collected by Professors D. H. Norris and T. Koponen during their field trips to New Guinea in 1981 (Koponen 1990, Koponen & Norris 1983, Norris & Koponen 1985). Five new genera and 75 new species have been described in 71 published papers, including 67 in the Huon Peninsula and 4 in the Frieda River series (Koponen 2000). In each paper keys to the genera and species plus specific descriptions are presented.

The aim of the present research was 1) to clarify the taxonomy of *Breutelia* in Southeast Asia, 2) to clarify the taxonomy of *Bartramia*, *Breutelia*, *Conostomum*, and *Leiomela* in Western Melanesia, 3) to test the monophyly of the subfamilies proposed by Griffin and Buck (1989), using cladistic analysis, and 4) to test the relationships of the genera included in the Bartramiaceae by Griffin and Buck (1989).

TAXONOMIC BACKGROUND AND KEY TO THE GENERA

BARTRAMIACEAE Schwägr. 1830

The Bartramiaceae is included in the Bryineae, based on its bryaceous, diplolepidious peristome (Vitt 1984). This classification closely follows those of Fleischer (1904-1923, 1920) and Brotherus (1924). In Vitt's classification a monophyletic group comprising the Bartramiaceae, Aulacomniaceae, Meesiaceae, and Catoscopiaceae forms a sister group to the Timmiaceae. These 4 families are a distinct group among the Bryineae based on spore morphology and chromosome numbers (Koponen 1977, Sorsa 1976). Vitt (1984) stated that this group of families has adapted to dry, or seasonally dry habitats with many resultant poikilohydric features. Axillary hair features allowed Griffin and Buck (1989) to propose the Timmiaceae as the nearest relative of the Bartramiaceae. Cox and Hedderson (1999) proposed a quite different hypothesis on the relationships of the Bryineae. According to their analysis, based on molecular characters with chloroplast and nuclear DNA sequences, the Bryineae appeared to be a polyphyletic group. The monophyletic clade of the Bartramiaceae was well supported, but neither *Timmia* nor *Meesia* proved to be sister groups to the Bartramiaceae. Instead, the sister groups of the Bartramiaceae are found among other Bryineae or a quite unresolved group including the acrocarpous Leucodontiineae, Orthotrichineae, or Hypnineae. The result of Cox and Hedderson (1999) agree

with Vitt's view (1984) that the Bartramiineae, as stated by Frey (1977), are not the basal group within the Bryineae.

Brotherus (1924) included eight genera in the Bartramiaceae: *Anacolia* Schimp., *Bartamia* Hedw., *Breutelia* (Bruch & Schimp.) Schimp., *Conostomum* Sw., *Exodokidium* Cardot, *Leiomela* (Mitt.) Broth., *Philonotis* Brid., and *Plagiopus* Brid. Later (1926) he added *Fleischerobryum* Loeske, after which Newton (1973, 1974) synonymized *Exodokidium* with *Bartramia*, and Magill (1987) described *Quathlamba* Magill. In their taxonomic treatment of the Bartramiaceae Griffin and Buck (1989) included 11 genera in the family: *Anacolia*, *Bartramia, Breutelia*, *Catoscopium* Brid., *Conostomum*, *Fleischerobryum*, *Flowersia*, *Leiomela*, *Philonotis*, *Plagiopus*, and *Quathlamba.* In agreement with Brotherus (1924), they treated *Bartramidula* Bruch & Schimp. as a section *Leiocarpus* Broth. of *Philonotis.* They included *Catoscopium* in the family, as did Flowers (1935) and Lindberg (1879). Griffin and Buck (1989) also created a new genus *Flowersia* to accommodate several anomalous species of *Anacolia*.

The majority of the 386 species of the family (Crosby et al. 1999) are included in the genera *Bartramia, Breutelia,* and *Philonotis. Catoscopium, Plagiopus,* and *Quathlamba* are monotypic. The species number in each genus is given in Table 1 (IV). Regional treatments of the entire family have been compiled for the genera of Eastearn Asia (Kabiersch 1937, Ochi 1962, 1963), Malaysia (Manuel 1981), Tierra del Fuego (Matteri 1985), Mexico (Griffin 1994), and Western Melanesia (Koponen & Norris 1996; I, III). The species richness appears to be highest in South and Central America; Churchill and Linares (1995) reported 111 species in 8 genera for the tropical Andes.

Griffin and Buck (1989) divided the Bartramiaceae into three subfamilies, based mainly on axillary hair morphology. Other characters they emphasized are stem anatomy (Kawai 1982, 1991), rhizoid ornamentation (Hirohama & Iwatsuki 1980), spore morphology (Griffin 1982, Hirohama 1977), and chromosome numbers (Fritsch 1972). *Breutelia, Philonotis, Anacolia, Fleischerobryum,* and *Quathlamba* were placed in the subfamily *Breutelioideae* Griffin & Buck, and *Bartramia, Catoscopium, Leiomela, Flowersia,* and *Plagiopus* in the *Bartramioideae* Griffin & Buck. *Conostomoideae* Griffin & Buck was erected to accommodate the single genus *Conostomum.* Akiyama and Nishimura (1993) separated *Catoscopium* into a family of its own based on the different branch development type present in *Catoscopium* in contrast to the other genera in the Bartramiaceae.

The Bartramiaceae, in general, have globose (to oblong-cylindrical) capsules, with the neck absent or inconspicuous, and a dense, often reddish tomentum on the stems. Branch primordia are naked (*Bryum*-type). In many genera the leaf cells are papillose or prorate.

KEY TO THE GENERA OF THE BARTRAMIACEAE

Catoscopium excluded based on Akiyama and Nishimura (1993) and the present study (IV).

1. Stem in cross-section rounded-triangular, leaf cells verrucose ..... *Plagiopus*
1. Stem section not triangular but pentagonal to round, leaf cells smooth or papillose 2

2. Leaf cells without papillae, costa absent or rudimentary ..... *Quathlamba*
2. Leaf cells papillose, costa distinct 3

3. Leaves appressed, in 5 distinct rows, rhizoids smooth.....*Conostomum*
3. Leaves spreading or straight, not in 5 distinct rows, rhizoids papillose.....4

4. Leaves plicate, alar cells differentiated .....*Breutelia*
4. Leaves not plicate, alar cells not differentiated.....5

5. Whorl of subperichaetial branches distinct 6
5. Subperichaetial branches absent or few.....7

6. Capsule without neck, papillae distal or proximal (central in section *Catenularia*) ..... *Philonotis*
6. Capsule with neck, papillae central over lumina..... *Fleischerobryum*

7. Capsules furrowed when dry, mostly well-exserted, leaf bases differentiated .....*Bartramia*
7. Capsules smooth, or irregularly wrinkled or rugose when dry, mostly immersed or slightly exerted, leaf bases not differentiated.....8

8. Spore ornamentation reticulate, perichaetial leaves distinctly longer than vegetative leaves.....
.....*Leiomela*
8. Spores with robust papillae, perichaetial leaves shorter or similar to vegetative leaves.....9

9. Papillae distal on leaf cells ..... *Anacolia*
9. Papillae central on leaf cells .....*Flowersia*

Genus *Anacolia* Schimp. 1876
Generic type: *Anacolia webbii* (Mont.) Schimp., Syn. Musc. Eur. Ed. 2: 513. 1876. *Glyphocarpus webbii* Mont., Ann. Sc. Nat. II. Ser. 9: 56. 1838.
Type specimen: Canary Islands. ”Hab. Ad summam vallem Orotaviensem Insulae Teneriffae, in fissuris rupium quas incolae los Organos dicunt nec alibi, fructibus onustum huncce muscum detexit cl. *Webb*” (?).

Seven species are included in *Anacolia* (Crosby et al. 1999), four of which, *A. cameruniae* Dixon, *A. laevisphaera* (Taylor) Flowers, *A. menziesii* (Turner) Paris, and *A. webbii*, are treated in the monograph by Flowers (1952). Griffin and Buck (1989) segregated three species into a new genus *Flowersia* based on differences in axillary hair morphology, leaf papillosity, and position of the setae. Later, two *Bartramia* species were transferred into *Anacolia*: *A. aurescens* (Dixon) Z. Iwats. and *A. breutelii* (Schimp. ex Müll. Hal.) Magill. *Bartramia rosea* Herzog was considered to be synonymous with *A. laevisphaera* by Griffin (1990), based on axillary hair morphology. López-Sáez (1996) came to a similar conclusion when studying the flavonoid composition of these two species. *Anacolia scioana* (Brizi) Broth. was mentioned by Brotherus (1924) as a poorly known Abyssinian species, but the species was not treated by Flowers (1952). Norris and Shevock (Norris, pers. com.) will give species status to *A. baueri* (Hampe) Paris previously recognized as a subspecies of *A. menziesii*. Treatments of *Anacolia* have been compiled for Africa (De Sloover 1975b) and Mexico (Griffin 1994). Spore ornamentation studies were performed by Griffin and Acuña (1983).

Anacolia includes montane species with peculiar ranges. *Anacolia menziesii* is a North American species with a quite wide range in the mountains from Alaska to Colorado, southern California, and Mexico (Griffin 1994) and has a disjunct occurrence in Europe (Garcia-Zamora et al. 1998). *Anacolia laevisphaera* has a Cordilleran range from Alaska to South America (Griffin 1994),

Africa (De Sloover 1975b), and India (Gangulee 1974). *Anacolia aurescens* is an Asiatic species reported from Mt. Kinabalu in Borneo (Iwatsuki 1969). *Anacolia breutelii* and *A. cameruniae* are African endemics, the first reported from southern Africa (Magill 1987) and the second from Nigeria (Flowers 1952) and Tanzania (De Sloover 1975b). *Anacolia webbii* occurs in the Canary and Madeira Islands, Spain, Portugal, Corsica, Sicily, Algeria, and Morocco (Flowers 1952).

Genus *Bartramia* Hedw. 1801
Generic lectotype (Flowers 1935): *Bartramia halleriana* Hedw., Sp. Musc. Frond.: 164. 1801.
Type specimen: not selected.

This genus of 72 species (Crosby et al. 1999) lacks a modern taxonomic revision. Brotherus (1924) includes the only worldwide treatment. The taxonomic treatment of Fransén (1995) of the Neotropical taxa of section *Vaginella* Müll. Hal. with descriptions and figures of 10 species is the most recent and distinguished work. Regional studies with taxonomic results include Eastern Asia (Kabierch 1937), Japan (Ochi 1962), Colombia (Robinson 1967), South Georgia (Newton 1973, 1974), India (Chopra 1975), Juan Fernández (Robinson 1975), Patagonia (Matteri 1984, 1985), and South Africa (Magill 1987).

The genus has a worldwide distribution, but in the northern latitudes the species number is low. Five species occur in North America (Anderson et al. 1990) and Eurasia (Corley et al. 1981, Ignatov & Afonina 1992): *Bartramia halleriana*, *B. ithyphylla* Brid., *B. pomiformis* Hedw., *B. stricta* Brid., and *B. subulata* Bruch & Schimp., and these species can be considered more or less cosmopolitan. In addition, North America has *B. microstoma* Mitt., which also occurs in the Neotropics (Delgadillo et al. 1995). *Bartramia patens* Brid. is quite widely distributed in the Southern Hemisphere occurring in Australia, New Zealand, Antarctica, South America and on the islands between Antarctica and South America (Matteri 1984, 1985, Streimann & Curnow 1989). However, most of the taxa probably have quite limited ranges (Crosby & Magill 1994, Crosby et al. 1992, Wijk et al. 1959), or their taxonomy needs to be revised (Crosby et al. 1999). The greatest variation is found in the tropics, where the taxa are confined to high altitudes (Fransén 1995).

O'Shea (1995) reported 20 species and one variety from sub-Saharan Africa and adjacent islands with five species from South Africa (Magill 1987). Delgadillo et al. (1995) reported 37 species from the Neotropics. The geographical extent of their study area was from Mexico to the northern parts of Argentina, Chile, Paraguay, and Uruguay, and also included the West Indies and Galapagos Islands. Two of the four species from Antarctica to Patagonia studied by Matteri (1984, 1985) are also found in the Neotropics. Four species have been reported from China (Crosby et al. 1999, Redfearn et al. 1996), three from Japan (Noguchi 1989), and two from Oceania (Miller et al. 1978, III). Three species occur in Western Melanesia (III). Chopra (1975) recognized eight species from India. Streimann and Curnow (1989) reported nine species from continental Australia.

Bartramia has been divided into three sections: *Bartramia*, *Strictidium* (Müll. Hal.) Broth., and *Vaginella*. Brotherus (1924) included 11, 79, and 20 taxa, respectively, in these sections. Differences in leaf morphology are the important features for sectional distinctions. In section *Bartramia* the leaves are appressed but not tightly sheathing, and shoulders are not at all or only poorly differentiated. In section *Strictidium* the leaves are not sheathing but erect and lanceolate-acuminate. In section *Vaginella* the unistratose and hyaline sheathing leaf base is abruptly narrowed to the green, bi- to tristratose limb, with distinct shoulders in the transition zone. Müller

(1849) described section *Vaginella* with seven species including *Bartramia halleriana*, which was later chosen as the type species of the family by Flowers (1935). *Bartramia ithyphylla* was selected as the type species of section *Vaginella* in the revision of Fransén (1995).

Genus *Breutelia* (Bruch & Schimp.) Schimp. 1856
Basionym: *Bartramia* subg. *Breutelia* Bruch. & Schimp. 1851.
Generic type*: Breutelia arcuata* Schimp. 1856., nom. illeg. (*Mnium arcuatum* Dicks., Fasc. Quartus Pl. Crypt. Brit. Index: [3]. 1801., *Bartramia arcuata* Brid., Muscol. Recent. 2(3): 139. 1803, nom. illeg.) ≡ *Mnium chrysocomum* Dicks. ex Hedw., Sp. Musc. Frond.: 74. 1801. *Breutelia chrysocoma* (Dicks. ex Hedw.) Lindb., Öfv. Kongl. Svenska Vet.-Ak. Förh. 20: 389. 1863.
Type specimen: not seen.

Breutelia, with 93 species (Crosby et al. 1999), occurs mainly in temperate and tropical areas in the Southern Hemisphere. Its distinct group of alar cells and plicate leaves easily distinguishes it from the other genera. The regional revisions of the genus cover the whole world quite well, except Australia, although monographic work could clarify the total species number and distribution of the taxa. Species richness is highest in Central and South America with about 65 species (Griffin 1984a). Twenty species are reported from sub-Saharan Africa and adjacent islands (O'Shea 1995), one species from Europe and North America, and 11 from Australia (Streimann & Curnow 1989). Species numbers recorded in regional generic revisions are given in Table 1. Griffin (e.g. 1984b, 1988, 1989) dealt with the taxonomy of the American taxa in several papers.

Table 1. Number of *Breutelia* species recorded in regional generic revisions.

Area	No. of taxa	Reference
Africa	16	De Sloover 1975a
Africa, south	5	Magill 1987
Brazil	5	Griffin 1984a
Patagonia	7	Matteri 1973, 1985
Southeast Asia, Oceania	12	II
South Georgia	1	Newton 1973

The name *Bartramia arcuata* has been generally ascribed to Swartz (1801: 182). However, under Art. 33.1 of the Code (Greuter et al. 2000), his mention of *Mnium arcuatum*, with reference to Dickson's (1793) exsiccate, does not constitute acceptable publication of *Bartramia arcuata*. Moreover, Swartz's contribution must have been published after September 1, 1801, the date of an anonymously published letter in the same journal (p. 440-442). This letter states that the fourth fascicle of Dickson's exsiccate (Dickson 1801) has recently appeared, and in the index annexed to that fascicle, *Mnium arcuatum* is validly published. However, due to inclusion of *Mnium chrysocomum*, Dickson's name is illegitimate and, under Art. 7.5, automatically homotypic with that older name.

Brotherus (1924) recognized five sections in *Breutelia*, and Griffin and Buck (1989) typified these. The taxonomic status of the sections was discussed and doubt expressed concerning the validity of *Acoleus* (Müll. Hal.) Broth. and *Anacoliopsis* (Müll. Hal.) Broth. (II). The characteristics for the sections include the following: in *Acoleus* plants are shiny with spreading, rather than erect-appressed

leaves. *Anacoliopsis* shares these characteristics with *Acoleus*, but the plants are not shiny. In *Polyptychium* (Müll. Hal.) Broth. plants are not shiny with erect-appressed leaves. The robust plants belong to two other sections: in section *Breutelia*, plants are shiny with erect-appressed leaves. The other section with robust plants is *Lycopodiobryum* (Müll. Hal.) Broth. with axillary hairs different from those of the other members of the genus and with obtuse to rounded-retuse, apiculate leaf apices (Griffin & Buck 1989).

Genus *Conostomum* Sw. ex F. Weber & D. Mohr 1804
Generic type: *C. arcticum* Sw. ex F. Weber & D. Mohr, Naturh. Reise Schweden: 122. 1804, nom. illeg. ≡ *Mnium tetragonum* Dicks. ex Hedw., Sp. Musc. Frond.: 73. 1801. *Conostomum tetragonum* (Dicks. ex Hedw.) Lindb. Öfv. Kongl. Svenska Vet.-Ak. Förh. 20: 392. 1863.
Holotype specimen: Great Britain. ''in alpibus scoticis, Ben Lomond, *Dickson*" (BM!).

Conostomum, with the characteristics of tightly appressed leaves in five rows and a rostellate lid in capsules, an unusual feature for the family, has been well distinguished from the other genera. The 5-ranked leaves of *Conostomum* are not unique but are also found in *Philonotis falcata* (Hook.) Mitt. Brotherus (1904) recognized eight species in two sections: a monotypic section *Pseudo-Bartramidula* Broth. without peristome and section *Conostomum* Sw. including seven species with a single peristome. Recently, *Conostomum* was revised by Frahm et al. (1996), and the species number was reduced from 15 to seven and no sections were recognized.

The generic name has usually been cited as *Conostomum* Sw. in F. Web. & Mohr, apparently incorrectly so under Art. 46.2 of the Code. The validating description provided by Weber and Mohr (1804: 121-122) was scarcely contributed by Swartz. It is even controversial whether the publishing author's statement "eine Neue Gattung, die Swartz *Conostomum* nennt" does constitute an ascription in the sense of the current Art. 46.3 (in fact, under Art. 46.4 the attribution "Sw. ex" is optional and might thus be omitted as well). Concerning the citation of *Mnium tetragonum* Dicks. ex Hedw., Hedwig (1801: 73, 349) clearly ascribed this name to Dickson.

Conostomum is mainly a southern hemispheric genus with only one species present in the Northern Hemisphere. The ranges reported here follow those of Frahm et al. (1996). Two of the species are Australasian: *C. curvirostre* (Mitt.) Mitt. is reported from a narrow range of southeastern Australia, and *C. giganteum* E. B. Bartram & Dixon is widely dispersed in Australia and New Zealand. In South or Central America and on the islands near Antarctica four species are found: *C. cleistocarpum* Herzog and *C. macrotheca* Herzog are reported only from Bolivia, *C. magellanicum* Sull. from the South Orkney Islands, South Shetland Islands, Falkland Islands, and South Georgia, and *C. perpusillum* Cardot & Broth. from the Falkland Islands and Tierra del Fuego (Matteri 1985). *Conostomum tetragonum*, previously known only from the Northern Hemisphere, has been combined with five species with South American and Australian ranges (Frahm et al. 1996). The combination with *C. pentastichum* (Brid.) Lindb., a species with a wide range in the Southern Hemisphere, was not accepted by either Fife (1998) or Virtanen (1999; III).

Genus *Fleischerobryum* Loeske 1910
Generic type: not selected.

This Asiatic genus of two species (Crosby et al. 1999) was segregated from *Philonotis* section *Pseudo-Philonotis* M. Fleisch. (Fleischer 1904-1923) by Loeske (1910) with *Fleischerobryum longicolle* and *F. wallisii* (Müll. Hal.) Loeske. Later, *Fleischerobryum wallisii* was synonymized

with *Philonotis hastata* (Duby) Wijk & Margad. by Bartram (1939). Fleischer (1904-1923) added *F. eurybrochis* (Renauld & Cardot) M. Fleisch., but that was synonymized with *Philonotis vescoana* (Besch.) Paris by Koponen and Norris (1996). *Fleischerobryum macrophyllum* Broth. was added by Brotherus (1926). Loeske (1910) did not indicate the type species for the genus. *Fleischerobryum longicolle* will probably be selected as the type species of the genus *Fleischerobryum*, because it is the only of the two species included by Loeske (1910) that is retained in the genus (Crosby et al. 1999).

Fleischerobryum is distinguished from *Philonotis* (Loeske 1910), based on the presence of long cylindrical or slightly asymmetric capsules, which are horizontal or pendulous with a long neck. The gametophytic features are closest to *Philonotis*. Koponen (1996) discussed the characters useful in the taxonomy of *Philonotis*, and the taxonomy of *Fleischerobryum* was discussed by Koponen and Virtanen (1998). The significance of the distribution of mammillae/papillae on leaf cells in different parts of the leaves and the morphology of the exothecial cells of the capsule was emphasized. In *Fleischerobrym* the combination of leaf cell areolation and distribution of mammillae/papillae differ from that of *Philonotis*: the area of wide thin-walled cells fills nearly the entire basal half of the leaf, and the leaf cells in the narrow apex are narrow with firm walls. Basal cells with proximal mammillae, midleaf cells with central papillae, and upper cells with distal papillae are unique characteristics of *Fleischerobryum*, and are distinct from any species of *Philonotis*. However, the size and height of the papillae in *Fleischerobryum* are especially variable, and leaf cells may be practically smooth.

Fleischerobryum longicolle has been reported from Japan (Noguchi 1989), China (Koponen et al. 2000, Redfearn et al. 1996), Western Himalaya (Gangulee 1974), Malesia (Eddy 1996), and Papua New Guinea (Koponen & Norris 1996). *Fleischerobryum macrophyllum* is known from the Philippines (Bartram 1939, Tan & Iwatsuki 1991), Taiwan (Redfearn et al. 1996), and the Himalayas (Gangulee 1974).

Genus *Flowersia* D. G. Griffin & W. R. Buck 1989
Generic type: *F. campylopus* (Schimp.) D. G. Griffin & W. R. Buck, Bryologist 92: 372. 1989. *Bartramia campylopus* Schimp. in Müll. Hal., Syn. Mus. Frond. 2: 619. 1851.
Lectotype (Fransén 1988): Mexico. Orizaba auf 12 000' Höhe, *Liebmann 17* (BM!).

Flowersia was distinguished from *Anacolia* by Griffin and Buck (1989). It includes four species: *F. abyssinica* (Müll. Hal.) D. G. Griffin & W. R. Buck, *F. campylopus*, *F. setifolia* (Hook. et Arn.) D. G. Griffin & W. R. Buck, and *F. sinensis* (Broth.) D. G. Griffin & W. R. Buck. Fransén (1988) clarified the nomenclature and selected type specimens for *F. setifolia* and *F. campylopus*. Griffin and Buck (1989) based the segregation of *Flowersia* from *Anacolia* on the following features: the terminal cell in axillary hairs is thickened, not elongated as in *Anacolia*, leaf cells are papillose over the lumen, not from the distal part of the cell ends as in *Anacolia*, and the setae are arcuate to curved, rather than straight as in *Anacolia*.

The ranges and figures of the taxa are well presented in Flowers (1952), except *F. setifolia*. This taxon was transferred to *Leiomela* by Flowers (1952) and to *Bartramidula* by Fransén (1988). Griffin and Buck (1989) included it in *Flowersia*, proposing it to represent a primitive member of this genus. *Flowersia campylopus* has been reported from Mexico, Central America, and in South America from Colombia to Peru (Flowers 1952 as *Anacolia intertexta*, Griffin 1994). *Flowersia abyssinica* is an African endemic reported from Eritrea (Flowers 1952), and *F. sinensis* occurs in China (Flowers 1952) and eastern Nepal (Gangulee 1974). Flowers (1952) noted the similarity of

these three species and questioned their identity. *Flowersia setifolia* is a South American species reported from Peru, Ecuador (Fransén 1988, Griffin & Hegevald 1986) and Bolivia (Hermann 1976).

Genus *Leiomela* (Mitt.) Broth. 1904
Basionym: *Bartramia* subsect. *Leiomela* Mitt. 1869.
Generic type: not selected.

All 13 species of *Leiomela* (Crosby et al. 1999) are neotropical with *L. bartramioides* (Hook.) Paris reported from Africa and Indonesia in addition to the Neotropics (Delgadillo et al. 1995, Matteri 1997; III). The distribution for the other species is quite scattered (Table 2); however, modern revision should clarify the true ranges and possibly the number of taxa will be reduced.

Table 2. Number of *Leiomela* species in the Neotropical countries.

Area	No. taxa	Reference
Bolivia	2	Hermann 1976
Brasilia	4	Sehnem 1976, Yano 1981
Colombia	5	Churchill and Linares 1995
Ecuador	3	Robinson 1977
Guyana	1	Delgadillo et al. 1995
Peru	2	Menzel 1992
Venezuela	3	Pursell 1973
Cuba	1	Duarte-Bello 1997

Neither Brotherus (1904) nor Mitten (1869) selected a type species for the genus. Probably, the proper type species would be *Leiomela lutescens* (Hamp.) Broth., as it was among the five species that Mitten (1869) included in the subsection *Leiomela* of section *Eubartramia* in the Bartramineae, but under the name *Bartramia lutescens* Hamp. It is the only of those five species, which was included in the genus *Leiomela* by Brotherus (1904). *Leiomela lutescens* was synonymized with *L. bartramioides* by Churchill and Linares (1995).

In gametophytic features *Leiomela* is most similar to *Bartramia*. Plants with elongate linear leaves are present in both genera. The extremely long perichaetial and perigonial leaves are typical for *Leiomela* but some species of *Bartramia* also have this feature, e.g. *B. mathewsii* Mitt. Reticulate spore ornamentation is unique for *Leiomela* within the family (Griffin 1981) and provides a characteristic by which to distinguish problematic taxa.

Genus *Philonotis* Brid. 1827
Generic type (Flowers 1935): *P. fontana* (Hedw.) Brid., Bryol. Univ. 2: 18. 1827. *Mnium fontanum* Hedw., Sp. Musc. Frond. 195. 1801.
Type specimen: not selected.

Crosby et al. (1999) included 169 species in *Philonotis*, but the actual number will not be known until a modern revision of the genus is produced. *Philonotis* includes species with highly variable characteristics, and species identification is difficult (Koponen 1999). Koponen and Norris (1996) discussed the division of the genus by different authors and the confusion existing among them. In

their revision of *Philonotis* in Western Melanesia and adjacent areas, 17 names were reduced as synonyms involving the six species of the area. Species numbers reported in a few references are given in Table 3.

Brotherus (1924) recognized six sections: *Philonotula* Hampe, *Catenularia* Müll. Hal., *Euphilonotis* Limpr. (*Philonotis* Brid.), *Pseudo-Mniobryum* Broth., *Leiocarpus* Broth., and *Pseudo-Philonotis* M. Fleisch. Section *Leiocarpus* accounts for *Bartramidula* Bruch & Schimp., which has been ranked as a genus (Kabierch 1937, Ochi 1962) or a section of *Philonotis* (Griffin & Buck 1989). *Pseudo-Philonotis* was separated as the genus *Fleischerobryum* by Loeske 1910 - an opinion later accepted by Brotherus (1926). Most of the species are included in sections *Philonotis* and *Philonotula*.

Koponen (1996) discussed characteristics useful in the taxonomy of *Philonotis*. He emphasized the significance of the distribution of mammillae/papillae on leaf cells in different parts of the leaves and the morphology of the exothecial cells of the capsule. Vegetative propagules could be useful in distinguishing certain taxa; however, the taxa occurring in the Boreal and Temperate Zones usually lack this feature (Koponen 1999).

Table 3. Number of *Philonotis* species reported for the geographical areas.

Area	No. taxa	Reference
Africa	66	O'Shea 1995
Africa, South	6	Magill 1987
Australia, New Zealand	11	Beever et al. 1992
		Streimann and Curnow 1989
Eurasia	9	Corley et al. 1981
		Ignatov and Afonina 1992
China	20	Redfearn et al. 1996
Japan	9	Noguchi 1989
Nepal and India	12	Gangulee 1974
Neotropics	55	Delgadillo et al. 1995
North America	9	Crum et al. 1973
Western Melanesia	6	Koponen and Norris 1996

Genus *Plagiopus* Brid. 1826
Generic type: *P. oederianus* (Sw.) H. A. Crum & L. E. Anderson, Mosses of Eastern North America 1: 636. 1981. *Bartramia oederiana* Sw., J. Bot. 1800 (2): 180. 1801.
Type specimen: not selected.

This monotypic genus is well distinguished from the other genera of the Bartramiaceae. Distinguishing features include the triangular stem and the finely papillose-striate leaf cells. The species is widely found in the Northern Hemisphere: Eurasia (Corley et al. 1981, Ignatov & Afonina 1992), North America (Anderson et al. 1990), Japan (Noguchi 1989), China (Redfearn et al. 1996), Nepal and India (Gangulee 1974), plus Hawaii (Bartram 1933).

Genus *Quathlamba* Magill 1987
Generic type*: Q. debilicostata* Magill, Fl. S. Africa, Bryophyta, Mosses 2: 421. F. 120. 1987.
Holotype: Africa. Lesotho, top of Sani Pass, on soil of rock crevices along northern cliff face just E of Mountain Lodge, 2860 m, *Magill 4512* (MO!).

Quathlamba is a monotypic African genus. By its gametophytic features it does not resemble any other genus of the family. It has ovate leaves with weak costae and smooth leaf cells, in contrast to more or less linear-lanceolate leaves with single and often strong costae. The smooth cells are seldom seen in other members of the family. Magill (1987) placed the genus in the Bartramiaceae based on its sporophytic features.

Genus *Catoscopium* Brid. 1826 (Catoscopiaceae)
Generic type: *C. nigritum* (Hedw.) Brid., Bryol. Univ. 1: 368. 1826. *Weissia nigrita* Hedw., Sp. Musc. Frond.: 72. 1801.
Type specimen: not selected.

Catoscopium is a monotypic genus with one circumpolar species in temperate and boreal areas in the Northern Hemisphere (Corley et al. 1981, Crum et al. 1973, Redfearn at al. 1996). The affinity of the genus can be considered uncertain, as it has been included in the Bartramiaceae (Griffin & Buck 1989, Flowers 1935, Lindberg 1879), but also in the Meesiaceae (Limpricht 1893, Schimper 1855), and distinguished as a family of its own (Brotherus 1924). Griffin and Buck (1989) proposed *Catoscopium* to be closest to *Plagiopus* on the basis of similar axillary hairs, as well as the 3-ranked leaves and nonpapillose leaf cells. Akiyama and Nishimura (1993) excluded it from the family, based on the different branch development pattern.

MATERIAL AND METHODS

MATERIAL

Herbarium specimens were used both for the morphological studies and DNA extraction. The herbaria are mentioned in the Material and Methods chapters (I-IV). Fresh material for DNA extraction was stored in plastic bags with silica gel until used (1 week - 2 months). Whenever possible, studied specimens were compared with type specimens of the species to confirm identifications. Voucher specimens are deposited in the herbaria indicated in the text (I-III) and Table 1 (IV). Studies in the Huon Peninsula series (I, III) were based mainly on the collections of Koponen and Norris from the Huon Peninsula, Papua New Guinea deposited in the herbarium in Botanical Museum in Helsinki (H). Material from other herbaria was also studied, and the specimens are cited in the text (I, III). Twenty-four taxa representing 11 genera of the Bartramiaceae (Griffin & Buck 1989) and three outgroup species were included in the cladistic analyses (Table 1 in IV). The type species of each genus was used, in addition to the type species of the sections of the large genera *Bartramia*, *Breutelia*, and *Philonotis*. Three outgroup taxa were selected from the Aulacomniaceae, Meesiaceae, and Timmiaceae. These families have been classified next to the Bartramiaceae based on morphological characters (Brotherus 1924, Griffin & Buck 1989, Vitt 1984). Character states for morphological characteristics included in the analyses are given in Appendix 1 and the sequences of *rbc*L used in the phylogenetic analysis for the 16 taxa representing the ingroup and outgroup are given in Appendix 2 (IV). The characters

chosen for cladistic analyses are discussed in Chapter 4 and references for representative figures of each taxon are given in Table 1 (IV).

MORPHOLOGICAL STUDIES

The specimens were examined using dissecting and compound microscopes. To examine the cells the specimens were soaked first in ethanol, then in a dilute solution of potassium hydroxide (KOH), and finally in water prior to preparing the slides. About 20 cells in each of 10 leaves in each specimen were studied for measuring the leaf cell dimensions. For laminal cells, those in the middle of the leaf in the area between the costa and border were used. For spore measurements about 20 spores from each capsule were studied. The position of the stomata relative to the exothecial cells was studied with microtome sections of paraffin-embedded material. The number of samples for each species varied between 1-20.

MOLECULAR TECHNIQUES

A gene from the chloroplast DNA coding for *rbc*L was sequenced, since it has been well surveyed for green plants and varies at level shown to be useful for reconstruction of phylogenies on the family and generic levels for vascular plants (e.g. Hoot et al. 1999, Olmstead et al. 1992, Qui et al. 1998, Soltis et al. 1990, Soltis & Soltis 1997, Williams et al. 1994) and bryophytes (Cox & Hedderson 1999, De Luna et. al. 1999, Hyvönen et al. 1998). The availability of specific sequencing primers for mosses (IV) also made it easy to use in this study. Sequencing followed the procedure outlined in IV.

PHYLOGENETIC ANALYSIS

Cladistic analyses (IV) were performed with PAUP versions 4.02d (Swofford 1998) and 4.0b3a (Swofford 2000). Six different analyses were performed: 1) Simultaneous analysis (Nixon & Carpenter 1996) by combining molecular and morphological datasets providing a total of 1385 characters, 2) An analysis of the moprhological dataset of 44 characters (Appendix 1 in IV), 3) An analysis of the molecular dataset of 1341 characters (Appendix 2 in IV), 4) An analysis of the morphological and molecular datasets excluding those taxa without molecular characters, 5) Simultaneous analysis of combined datasets of molecular and morphological data with 1387 characters including the chromosome number (Fritsch 1972) and branch primordia type (Akiyama & Nishimura 1993), and 6) Simultaneous analysis of the combined datasets of molecular and morphological data with 1386 characters including the chromosome number (Fritsch 1972) and branch primordia type (Akiyama & Nishimura 1993) and excluding the peristome type. The first simultaneous analysis was also performed with program NONA (Goloboff 1993a) with the options hold*;hold/100;mult*200, which signifies a heuristic search with random addition of taxa saving 100 starting trees for TBR (tree bisection-reconnection) branch swapping of each of the 200 replicates.

The analyses were performed as described in the article IV. Polymorphic characters were included in the analyses, although they have often been excluded. However, Wiens (1995, 1998) concluded that although polymorphic characters are less reliable in inferring phylogeny than fixed characters, in most datasets analyzed they contained significant phylogenetic signal. The strict

consensus trees were used for summarizing the most parsimonious trees (see e.g. Kitching et al. 1998).

Branch support

The clade support was evaluated by the total support index = ti (Bremer support), which quantifies the branch support as the extra length needed to lose a branch in the consensus of near most-parsimonious trees (MPTs; Bremer 1994). It operates solely on the original data. A branch present in one of the MPTs is more strongly supported by the data if a large increase in the length of additional trees is required before that branch is lost in the consensus (Källersjö et al. 1992). The total support indices (ti) were gathered by heuristic analyses performed with PAUP (Swofford 1998, 2000) with saving trees up to 4 steps longer than the MPTs. However, Kluge (1997a) criticized the measures of tree stability, since the stability *per se* is not one of the goals of cladistics.

The two other indices used here are based on permutation and randomization of the data. The jackknife and the bootstrap were used for testing branch support, both with 10 000 replicates. Bootstrap analysis (Felsenstein 1985) was performed using PAUP versions 4.02d (Swofford 1998) and 4.0b3a (Swofford 2000). Jackknife values were calculated with the Parsimony Jackknifer Jac version 4.22 (Farris 1995). Kluge and Wolf (1993) challenged the use of both bootstrapping and jackknifing, because their underlying assumptions are violated and they are sensitive to character frequencies. In bootstrapping (Felsenstein 1985, Sanderson 1989) the original dataset is randomly resampled so that entire characters are replaced by other characters. A new dataset will be of the same size as the original with some data excluded and some characters present more than once. Bootstrapping values are not based on parsimonious trees, and the MPTs are not found in the search at all. It gives the frequency of clades found in the analysis. As Chavarría and Carpenter (1994) pointed out, the assumption that characters are randomly sampled from independent, identically distributed populations is clearly wrong, and bootstrapping has been much criticized (e.g. Carpenter 1992, Kluge & Wolf 1993, Farris in Werdelin 1989). The validity of bootstrapping has also been criticized because inclusion of uninformative characters (autapomorphies) commonly leads to a loss of 'significance' (Carpenter 1996). Hillis and Bull (1993) tested bootstrapping results as measures of repeatability and accuracy by simulations, and they concluded that bootstrap proportions are not good estimates of the repeatability of a given phylogenetic analysis and that bootstrapping provides a biased but highly conservative estimate of accuracy. However, according to Felsenstein and Kishino (1993) the phenomena that Hillis and Bull (1993) determined were not a result using bootstrap but of summarizing the evidence for a group by using a *P* value. Overall, criticism of bootsrapping has been quite strong and the values are not interpreted here as a measure of probability of the true phylogeny. In jacknife sampling the pseudoreplicate datasets are smaller than the original. According to Farris et al. (1996) parsimony jackknifing is an efficient procedure for identifying well-supported monophyletic groups, since a branch is retained only if it shows a change under every parsimonious construction. A resampled matrix is formed by deleting characters randomly and independently from the original matrix. Group frequencies can be intepreted safely only if obtained by a method that gives high frequences only to those groups with high support, e.g. to total elimination of zero-length branches.

Weighting the characters

Weighting the characters has been performed for selecting a tree among many equally parsimonious trees to increase the congruence among characters within the dataset. *A posteriori* successive weighting was developed by Farris (1969) and further discussed in detail by Carpenter (1988). In successive weighting the weight is given for the characters with best fit to a tree, and Farris (1989) suggested the that rescaled consistency index (rc) should be used for this purpose. Goloboff (1993b) suggested that the characters should already be weighted during the search, with those characters showing less homoplasy being weighted more. Kluge (1997a, b) has criticized all weighting schemes, because the phylogeny displays a unique history and the homoplasious characters have evolved independently.

A priori differential weighting has been commonly used in the analyses of molecular data. Rapidly evolving nucleotide sites of protein-encoding genes have been regarded as less reliable than the more slowly evolving ones in resolving the phylogeny. Based on this hypothesis, third positions have usually been downweighted. However, the results of Källersjö et al. (1999) and Björklund (1999) showed exactly the opposite. In the analysis of 2538 *rbc*L sequences Källersjö et al. (1999) found that the third positions contained most of the phylogenetic structure of the data, while Björklund's (1999) results also rejected the hypothesis that second positions provide better phylogenetic signal than third positions. Wenzel and Siddall (1999) concluded that differential weighting, e.g. downweighting of third positions, is not well advised for reducing the influence of noise, nor are more noisy datasets likely to degrade signals found in less noisy datasets. Allard and Carpenter (1996) tested whether congruence was improved by weighting the characters using the incongruence length difference test. They viewed the use of differential weighting as an outcome of insufficient taxonomic sampling and character information, and did not find weighting to improve the results. Since weighting the characters has not been proved to add to the accuracy of any hypothesis, neither *a priori* nor *a posteriori* weighting was used here.

RESULTS

THE GENUS *BREUTELIA* IN SE ASIA AND OCEANIA

The genus *Breutelia* is represented by the following 12 species in Southeast Asia. The total range of each taxon is given in the parentheses.

1. *B. affinis* (Hook.) Mitt. (Australia, Tasmania, New Zealand, Hawaii, Chile).
2. *B. aristifolia* Zanten (New Guinea).
3. *B. arundinifolia* (Duby) M. Fleisch. (Japan, Taiwan, China, Indonesia, Malaysia, Philippines, Papua New Guinea, Hawaii).
4. *B. crassicaulis* (Müll. Hal.) Paris (New Guinea, Hawaii).
5. *B. dicranacea* (Müll. Hal.) Mitt. (Sri Lanka, India).
6. *B. eugeniae* Ångstr. (Society Islands).
7. *B. kinabaluensis* Dixon (Malaysia, New Guinea).
8. *B. longicapsularis* Dixon (New Guinea).
9. *B. microdonta* (Mitt.) Broth. (India, Philippines, Brazil, Madagascar, South Africa).
10. *B. papuensis* Virtanen (New Guinea).
11. *B. roemeri* M. Fleisch. (New Guinea).
12. *B. yunnanensis* Besch. (India, Nepal, Bhutan, China).

Three names were reduced to synonymy. *Breutelia sclerodictya* Cardot was synonymized with *B. microdonta,* and *B. setscwanica* Broth. and *B. subdeflexa* Broth. with *B. yunnanensis.* Sporophyte was reported for the first time and the neotype proposed for *B. dicranacea*. The key to the taxa with species descriptions and illustrations are given in II. Until this revision, a total of 15 species had been recognized in Asia (As 2, 3, 4) and Oceania (Crosby & Magill 1994,, Crosby et al. 1992, Wijk et al. 1959).

THE FAMILY BARTRAMIACEAE IN WESTERN MELANESIA

The family Bartramiaceae includes 18 species in six genera in Western Melanesia. A key to the Western Melanesian genera is given in III. Species descriptions and illustrations of *Bartramia*, *Conostomum,* and *Leiomela* are given in III and those of *Breutelia* in I. Western Melanesian *Philonotis* and *Fleischerobryum* were revised by Koponen and Norris (1996). The four genera dealt with in this thesis include the following taxa in Western Melanesia:
1. Genus *Bartramia* Hedw. 1801
B. conica E. B. Bartr., *B. halleriana* Hedw., *B. ithyphylla* Brid.
2. Genus *Breutelia* (Bruch & Schimp.) Schimp. 1856
B. arundinifolia (Duby) M. Fleisch., *B. crassicaulis* (Müll. Hal) Paris, *B. aristifolia* Zanten, *B. longicapsularis* Dixon, *B. roemeri* Fleisch., *B. papuensis* Virtanen.
3. Genus *Conostomum* Sw. 1804
C. pentastichum (Brid.) Lindb.
4. Genus *Leiomela (*Mitt.) Broth. 1904
L. bartramioides (Hook.) Paris.

Breutelia papuensis was described as a new species (I). *Leiomela africana* Thér. & Naveau and *L. javanica* (Renauld & Cardot) Broth. were synonymized with *L. bartramioides,* and *Conostomum pentastichum* was not considered conspecific with *C. tetragonum* (II) as has been stated by Frahm et al. (1996). In addition to the six species of *Breutelia* reported for Western Melanesia (I, III), Eddy (1996) reported one collection of *B. kinabaluenis* Dixon from New Guinea, but I have not seen the specimen. The lectotype selected for *Breutelia crassicaulis* (*Baldwin 24* H, FH) is not valid as the lectotype specimen should be selected from among the specimens cited in the protologue. The original material is probably destroyd, and the specimen I proposed for a new type would be suitable for a neotype. The name will be neotypified and a neotype specimen will be selected in a separate paper.

GENERIC TAXONOMY OF BARTRAMIACEAE

The molecular data included 1341 characters, of which 80 were informative. The latter were used together with the 46 morphological characters in the analyses (Appendices 1, 2 in IV). The results are represented here (Fig. 1) by the strict consensus tree based on the results obtained by simultaneous analysis of combined molecular and morphological datasets with 126 informative characters including the chromosome number (Fritsch 1972) and branch primordia type (Akiyama & Nishimura 1993) and excluding the peristome type. The differences among the results shown by the analyses performed are discussed below.

The Bartramiaceae was supported as a monophyletic group containing nine genera: *Anacolia, Bartramia, Breutelia, Fleischerobryum, Flowersia, Leiomela, Philonotis, Plagiopus,* and *Quathlamba.* This clade was supported in five of the six analyses performed (Figs. 2-6 in IV).

Catoscopium was included in the Bartramiaceae in the simultaneous analysis of 1385 characters (Fig. 1 in IV) but excluded in all the others. The family Catoscopiaceae was proposed to include the genus *Catoscopium* with one species *Catoscopium nigritum*, in accordance with Brotherus (1924), Vitt (1984), and Akiyama and Nishimura (1993).

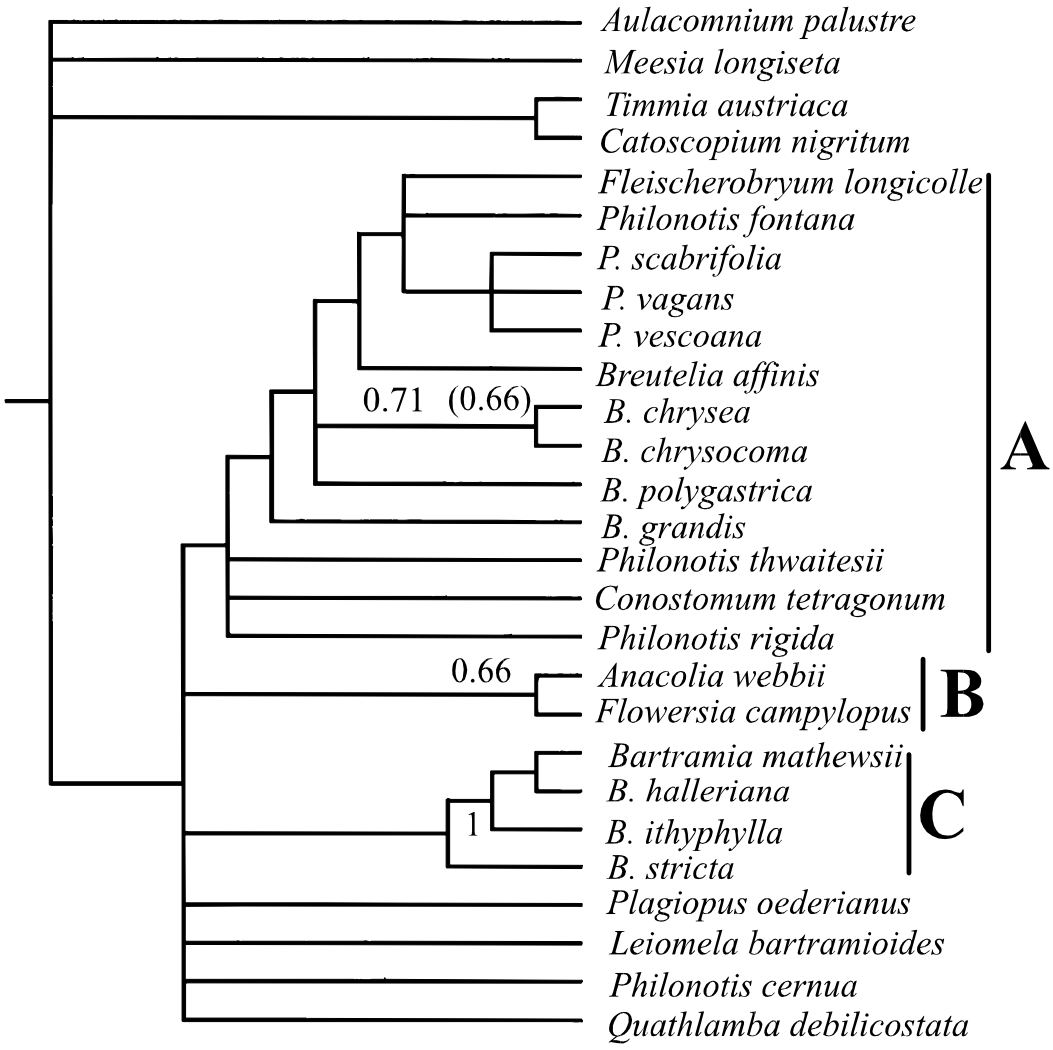

Figure 1. Strict consensus of 10 MPTs (length 639, CI = 0.6604, RI = 0.5303) from parsimonious analysis of 125 informative characters of morphological (45 char.) and *rbc*L sequence data including two additional morphological characters, chromosome number (Fritch 1981) and branch primordia type (Akiyama & Nishimura 1993), and excluding the peristome type. Numbers above the branch are bootstrap values, and numbers below total support values. MPT=most parsimonious tree, CI=ensemble consistency index, RI= ensemble retention index.

The close relationship of the genera *Conostomum, Philonotis, Breutelia,* and *Fleischerobryum* was shown in most of the analyses (Figs. 1-6 in IV). In all the analyses (Figs. 1-6 in IV) the genus *Bartramia* forms a distinct monophyletic group. The closer relationship of the taxa representing 2 different sections, *Bartramia mathewsii* and *B. halleriana*, is probably only due to lack of sequence data for *B. ithyphylla*. In the simultaneous analysis excluding the peristome type the clade representing the genus *Bartramia* was placed in a basal position within the family (Fig. 6 in IV).

The relationships of *Anacolia, Flowersia, Leiomela, Quathlamba, Plagiopus* and *Philonotis cernua* remained more or less unresolved. Among these unresolved taxa, however, the close relationship of *Anacolia* and *Flowersia* was evident (Figs. 1-3, 5-6 in IV), and the separation of *Anacolia* and *Flowersia* into different subfamilies by Griffin and Buck (1989) was not supported. The clade containing *Anacolia* and *Flowersia* was among the few that obtained support by branch support indeces. Branch support, as bootstrapping, jackknife, and total support values, for various branches are given in IV.

The consistency indices (CI) based on informative characters on morphological data and molecular data were 0.4252 and 0.4428, respectively (Figs. 1-2 in IV). The consistency indices were somewhat higher in analyses three to six, 0.8554, 0.7238, 0.6579, and 0.6604, respectively (Figs. 3-6 in IV). The relationship between the consistency index and the number of taxa in cladistic analyses is shown by Hedenäs (1998). The values in my analyses are rather close to what can be expected for the number of terminal taxa that were studied.

DISCUSSION

PHYTOGEOGRAPHY OF THE SE ASIAN *BREUTELIA*

Most of the Asian species of *Breutelia* have fairly restricted distributions (Figs. 13 and 14 in III) resembling the Neotropical and African taxa (Delgadillo et al. 1995, De Sloover 1975). Using the distribution types presented in Hyvönen (1989), 6 species of the Asian *Breutelia* are Malesian endemics, one species represents the Australasian – Oceanian flora, and one species is included in the Asian – Oceanian flora. One species has disjuncts in South America, continental Asia, and Malesia. In addition, three species are restricted to SE Asia. Only two species of these 12 occurring in Southeast Asia have wider ranges. Similar ranges within SE Asia are found, e.g. in *Orthomnion* (Mniaceae); two of the nine species have fairly wide ranges in SE Asia and the rest are rather local endemics in SE Asia or Australasia (Koponen 1980).

The genus *Breutelia* may represent a Gondwanaland element. One can hardly make any conclusion based on the distribution patterns of the sister groups of *Breutelia*, since the group including taxa in *Breutelia, Conostomum, Fleischerobryum*, and *Philonotis* was highly unresolved in the cladistic analyses (Figs. 1-6 in IV). In addition, the number of taxa representing each genus in the analyses was low. However, only a few members of *Breutelia* occur in areas of Laurasian origin, and a consensus has emerged that much of Southeast Asia was rifted from the eastern margin of Gondwanaland (e.g. Hallam 1994). The fragmentation of Gondwanaland was completed between about 80 mya and 50 mya BP, with India and Madagascar drifting apart and India migrating northward. Africa separated from Gondwanaland even earlier, beginning in the Jurassic (about 200 mya BP). In the study of the Garovaglioideae, During (1977) favored the hypothesis that the group inhabiting SE Asia and Oceania originated on the eastern margin of Gondwanaland, then migrated with the Australian - New Guinea landmass, or with India, to the

north and spread over Malaysia and Indonesia. As with the Garovaglioideae, *Breutelia* also occurs in tropical montane areas and it may have a similar distributional history. With the disjuncts of *Breutelia microdonta* in Madagascar and India as well as in Africa and Philippines, it can be hypothesized that this species already evolved prior to the fragmentation and ranged widely over Gondwanaland.

PHYTOGEOGRAPHY OF THE WESTERN MELANESIAN BARTRAMIACEAE

The distribution types present in the Western Melanesian Bartramiaceae are quite similar to those presented by Hyvönen (1989) for the Western Melanesian mosses, in general. The pantropical and widely distributed species are the minor groups, and the Western Melanesian and Malesian endemics, as well as species restricted to SE Asia or the Asia - Oceania – Australia area form majority.

Most of the Western Melanesian taxa are species restricted to the Southern Hemisphere. Only two species are widely distributed, occurring in both the Northern and Southern Hemispheres, and can be considered to be cosmopolitan (III). In addition, one species of *Philonotis* is widely distributed in the Southern Hemisphere, with a disjunct occurrence in Europe (Koponen & Norris 1996). The largest portion of the Bartramiaceae taxa belong to the Asian – Oceanian species group, many species are also Western Melanesian and Malaysian endemics (I, III). In general, Western Melanesian endemics are the largest group of phytogeographical elements in mosses and hepatics in that area (Hyvönen 1989, Piippo 1994), but in the Bartramiaceae the species showing this type of distribution pattern are present only in the genus *Breutelia*. Some species (Koponen & Norris 1996, I) are restricted to SE Asia. The only *Conostomum* species occurring in Western Melanesia is rather widely distributed in the Southern Hemisphere representing the Asian – Oceanian – Australian element (Hyvönen 1989). This species, *Conostomum pentastichum*, was synonymized with the northern hemispheric *C. tetragonum* by Frahm et al. (1996), but in my opinion these two are distinct and should be recognized as two separate species (III). The genus *Leiomela* is mainly neotropical, including species with scattered distribution. The only Western Melanesian representative of this genus can be considered to be pantropical, since it occurs in Indonesia, Africa, and the Neotropics.

GENERIC TAXONOMY OF BARTRAMIACEAE

To combine separate datasets into one analysis (simultaneous/total evidence) or to combine trees after separate analyses (taxonomic congruence) is an area of disagreement in systematics (see reviews by de Queiroz et al. 1995, Huelsenbeck et al. 1996, Miyamoto & Fitch 1995, Nixon & Carpenter 1996). Both types of analyses were performed hee (IV). An argument against combining the datasets has been the assumption that different datasets may show distinctly different rates of evolution (Bull et al. 1993, Huelsenbeck et al. 1996), or that different genes may even have different phylogenetic histories (reviewed by Doyle 1992). As Bull et al. (1993) said, if the datasets are heterogeneous they should not be combined in an analysis, but combining the independent estimates by consensus is preferred. In their opinion the inclusion of many different characters may have the effect that support for the ”true” phylogenetic groupings coming from reliable characters may be swamped by random or systematic errors from unreliable characters. However, Wenzel and Siddall (1999) showed that noisier datasets are not likely to degrade signal, found in less noisy datasets. Nixon and Carpenter (1996) argued that simultaneous analysis of combined data better maximizes cladistic parsimony than separate analyses, provides the greatest

possible explanatory power, and should always be evaluated when possible. In my study both the combined dataset and the morphological dataset had quite similar values of the consistency indices (Figs. 1 and 2 in IV). This suggests the presence of similar levels of phylogenetic signal in molecular and morphological data (CI=0.4252 and 0.4428, respectively). Simultaneous analysis did not resolve the status of the Bartramiaceae as a monophyletic group (Fig. 1 in IV), which was a result of the analysis of morphological data (Fig. 2 in IV). On the other hand, a monophyletic group containing taxa in *Breutelia*, *Conostomum*, *Fleischerobryum* and *Philonotis* (clade A in Fig. 1 in IV) was resolved with the combined dataset, but not with morphological data. In a study including *rbc*L and morphological data of mosses, De Luna et al. (1999) also found similar levels of phylogenetic signal in the datasets, but the number of morphological characters in relation to number of taxa was distinctly higher in their study, and the trees were better resolved.

In my study better resolution was achieved based an analysis of sequence data with an ensemble CI of 0.8554 (Fig. 3 in IV), which is a higher value than would be expected based on the number of taxa (Hedenäs 1998). This analysis resolved the Bartramiaceae as a monophyletic group, and also a clade quite similar to that obtained in the analysis of combined datasets including *Breutelia*, *Conostomum*, and *Philonotis* (clade A in Figs. 1 and 3 in IV), was resolved. In addition, the close relationship of *Anacolia* and *Flowersia* was supported, as well as a clade containing species of *Bartramia*. Although the differences among the CI values are significant, it should be kept in mind that according to Sanderson and Donoghue (1989) homoplasy increases with the number of taxa, and the number of taxa was significantly lower in the analysis based on sequence data only.

The resolution in the analysis based on morphological data (Fig. 2 in IV) shows considerable conflict between different characters. The high level of homoplasy in morphological characters in mosses was also found by Hyvönen et al. (1998). On the other hand, resolution obtained with the simultaneous analyses including the chromosome number and the branch primordia type (Figs. 5 and 6 in IV) was not much lower than that of separate analysis based on sequence data only (Fig. 3 in IV). Besides, the consistency indeces of the analyses based on morphological and combined datasets, were rather close to what were to be expect with this number of terminal taxa (Hedenäs 1998). Some similarities were observed concerning the relationships resolved in the analyses (Figs. 1-6 in IV). Three groups were distinguished: one containing the taxa in *Breutelia*, *Conostomum*, *Fleischerobryum*, and *Philonotis* (clade A in Fig. 1), one with *Anacolia* and *Flowersia* (clade B in Fig. 1), and one with species of *Bartramia* (clade C in Fig. 1). The position of *Anacolia*, *Flowersia*, *Leiomela*, *Philonotis wilsonii*, and *Quathlamba* remained rather unresolved in the analyses (Figs. 1 – 6 in IV), although they formed a monophyletic group based on morphological data (clade B in Fig. 2 in IV)**.** However, very few synapomorphies exist for this clade other than the reduced peristome. The peristome character was excluded from the analysis (Fig. 1), because it is possible that the simplified peristomes present in many unrelated taxa is due to parallel evolution resulting from adaptation to xerophytic habitats or ephemeral life style (Vitt 1984), and the assumption of homology of reduced peristomes in different taxa (Hedenäs 1995, Newton & De Luna 1999) has been challenged. This analysis resolved *Philonotis cernua* among the other taxa of *Philonotis* and gave no support for distinguishing it as a separate genus *Bartramidula*, as proposed by Kabiersch (1937) and Ochi (1962).

The data analyzed included many missing values, because the molecular data were obtained for only 16 taxa out of a total of 27. In addition, I had difficulty in amplifying the total gene of *rbc*L with many species, although the results were better after amplification was done in two fragments. In general, amplification of the first fragment with primers M28 and M740r failed**.** Fresh material was lacking for *Quathlamba* and *Leiomela*, and the amplifications of the DNA from herbarium specimens were not successful. The missing data can result in resolutions that are not supported

by the data analyzed (Maddison 1993, Platnick et al. 1991), or the number of shortest trees may increase (Nixon & Davis 1991). I assume that the high proposition of missing values in the dataset was at least partly the reason, why the trees were not better resolved in the simultaneous analysis (Fig. 1 in IV)**.** Wiens and Reeder (1995) concluded that incompletely scored taxa may cause an incorrect tree to be chosen as the most parsimonious. In the present study, the taxa that remained more or less unresolved (*Anacolia, Flowersia, Leiomela, Plagiopus, Philonotis wilsonii, Quathlamba,* and some taxa in *Breutelia* and *Philonotis*) lacked the molecular data totally or only short partial sequences were obtained. However, these taxa were added to the analysis to derive a phylogenetic hypothesis for all the members of the group, as suggested by Wiens and Reeder (1995). Wiens (1998) used simulations and concluded that addition of a set of characters with missing data is generally more likely to increase phylogenetic accuracy than to decrease it, but the potential benefits of adding these characters quickly disappears as the proportion of missing data increases. The proportion of missing data was probably too high in the present material. Wilkinson (1995) offered a way to ameliorate the effect of missing entries under the rules of safe taxonomic reduction, which enables deletion of some taxa from the analysis. Unfortunately, these rules were not met here.

Based on the analyses presented here (IV), and the results of Akiyama and Nishimura (1993), I do not include *Catoscopium* in the Bartramiaceae. Five of the six different analyses performed here (IV) lend support for classification of the Bartramiaceae as a monophyletic group containing the genera *Anacolia, Bartramia, Breutelia, Fleischerobryum, Flowersia, Leiomela, Philonotis, Plagiopus,* and *Quathlamba* (Fig. 1). Division of the Bartramiaceae into 3 subfamilies (Griffin & Buck 1989) is not supported by the analysis. The subfamily *Conostomoideae* was erected by Griffin and Buck (1989) to contain a single genus *Conostomum*, but my results do not support this conclusion. The monophyletic group (clade A in Fig. 1) containing the genera *Conostomum, Philonotis, Breutelia,* and *Fleischerobryum* was obtained in most of the analyses. This monophyletic group is similar to that of Hirohama and Iwatsuki (1980), who divided the Bartramiaceae into 2 major subgroups according to papillosity of the rhizoids. Based on my analysis the smooth rhizoids of *Conostomum* appear to have evolved by reversal, and the finely papillose rhizoids are a synapomorphy for this group. According to Hirohama and Iwatsuki (1980) the papillosity of rhizoids could be an adaptation to habitat conditions, because species with smooth rhizoids or with low papillae live in wetter habitats than species with high papillae. The other group distinguished by Hirohama and Iwatsuki (1980) includes *Anacolia, Bartramia, Leiomela* and *Plagiopus,* but no support for such a clade was found here.

Adding molecular data for those taxa currently lacking it (e.g. *Leiomela, Quathlamba, Philonotis cernua*), as well as more complete data for *Anacolia* and *Flowersia,* would probably improve the resolution. The resolution could probably also be highly improved even with the current sampling simply by sequencing more genes.

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