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CIRCUMSCRIPTION AND PHYLOGENETIC TRENDS IN THE ORTHOTRICHALES (BRYOPSIDA)

by

Bernard Goffinet ©

A thesis submitted to the Faculty of Graduate Studies and research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Department of Botany

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled CIRCUMSCRIPTION AND PHYLOGENETIC TRENDS IN THE ORTHOTRICHALES (BRYOPSIDA) submitted by BERNARD GOFFINET in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Aux Louis,

à Anne,

et

à mes parents

Abstract

With over 500 species, the Orthotrichaceae (Bryopsida) are one of the largest families of mosses. Twenty-five genera are currently included in the Orthotrichaceae, with *Macromitrium* and *Orthotrichum* accounting for most of the taxonomic diversity. Together with the Erpodiaceae, Rhachitheciaceae, Microtheciellaceae and the Helicophyllaceae, they form the Orthotrichales. The limits and the relationships of the family and the order are here examined. The Microtheciellaceae are now excluded from the Orthotrichales on the basis of their pleurocarpy. The Helicophyllaceae are characterized by a unique combination of gametophytic characters, and are tentatively excluded, although with no clear affinities to other groups. Comparisons of nucleotide sequences of the chloroplast gene *rbc*L suggest that the Rhachitheciaceae and the Erpodiaceae belong to the Haplolepideae, and should therefore be excluded from the Orthotrichales. The genera *Kleioweisiopsis*, and *Trigonodictyon*, as well as *Octogonella* and *Uleastrum* are excluded from the Orthotrichaceae based on comparison of morphological characters, and transferred to the Ditrichaceae, Grimmiaceae, and Rhachitheciaceae, respectively. *Pleurozygodontopsis* is placed in synonymy with *Zygodon*. Cladistic analysis of 37 *rbc*L nucleotide sequences furthermore lead to the exclusion from the Orthotrichaceae of two gymnostomous genera, namely *Amphidium*, and *Drummondia*, both with affinities to the Haplolepideae. Twenty-two genera, including two new genera, *Bryomaltaea* and *Matteria*, as well as the reinstated genus *Codonoblepharon*, are now accepted within the Orthotrichaceae. These genera are distributed between four tribes belonging to two subfamilies. The sister-group to the Orthotrichales, now reduced to the Orthotrichaceae, remains somewhat ambiguous but is hypothesized, based on morphological characters to be the Bryales, rather than the Splachnales.

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Chapter one

Introduction

The Orthotrichaceae, with over 500 species, represent one of the largest families of mosses. The family is found in most major terrestrial biomes, from the arctic tundra to tropical rainforests, and from subantarctic sea shores to subalpine heaths in the tropics. Adaptation to xerophytism (see Vitt 1981) is thought to have been the major driving force in the diversification of the family, or at least of such speciose genera as *Macromitrium* (Vitt and Ramsay 1985), or *Orthotrichum* (Vitt 1971). Similar trends are also evident in two families considered only distantly related to the Orthotrichaceae (Vitt 1984), namely the Grimmiaceae (Churchill 1981), and the Pottiaceae (Zander 1993). Both families are mostly terricolous or saxicolous, whereas the Orthotrichaceae are predominantly epiphytic, and within the genus *Orthotrichum*, only the most derived species grow on rocks (Vitt 1971).

Twenty seven genera are currently included in the family, and of these, nineteen have 10 species or fewer (Table 1.1). The taxonomic diversity in the Orthotrichaceae is concentrated in three genera, *Orthotrichum* Hedw., *Macromitrium* Brid., and *Zygodon* Hook. et Tayl., that serve as type genera for three subfamilies. A fourth subfamily accommodates the small genus *Drummondia*. The current circumscription differs from Vitt's (1984) concept of the family, mainly by the inclusion of *Amphidium*, *Kleioweisiopsis*, and *Uleastrum*. Vitt (1973) argued against affinities of *Amphidium* with the Orthotrichaceae and transferred the genus to the Dicranales, whereas Lewinsky (1976) supported her argument in favor of an orthotrichaceous origin of *Amphidium* by similarities in the anatomy of the urn, particularly the anatomy of the trabeculae. Zander (1993) recently transferred the genus *Kleiweisiopsis* from the Pottiaceae to the Orthotrichaceae, based on the similarities between *K. denticulata* and *A. cyathicarpum*. Zander (1993) also excluded *Uleastrum* from the Pottiaceae, and placed it in the Orthotrichaceae, "a disposition making the least necessary emendation of recognized family limits". *Amphidium* and *Kleiweisiopsis* are gymnostomous (lack a peristome) whereas *Uleastrum* has a peristome that *a priori* is incompatible with any of the four major peristome-types. Addressing the familial relationships of these genera may thus rely on the analysis of an independent set of data, such as DNA nucleotide sequences.

Fleischer (1920), who was the first to recognize the distinctiveness of the Orthotrichaceae at higher ranks, included in the Orthotrichales besides the Orthotrichaceae, also the Erpodiaceae (Table 1.2). The Rhachitheciaceae were later segregated from the Orthotrichaceae (Robinson 1964) and the Microtheciellaceae were established by Miller and Harrington (1977) for the erpodiaceous taxon, *Microtheciella keerei*. The Helicophyllaceae, traditionally considered with affinities to *Racopilum* in the Bryales *sensu lato*, were transferred by Crosby (1980) to the Orthotrichaceae. In the most recent classification (Vitt 1984) the Orthotrichales are thus circumscribed by five families: the Orthotrichaceae, Erpodiaceae, Rhachitheciaceae, Microtheciellaceae, and Helicophyllaceae, the latter four of which are small families including fewer 20 species. The relationships among these families are obscured by the great variation in gametophytic and sporophytic characters, and this heterogeneity, for example in the peristomial architecture (see Edwards 1979, 1984) may be indicative of the polyphyly of the order.

Many of the early species now recognized in *Macromitrium*, *Schlotheimia*, and *Ulota*, were initially described as species of *Orthotrichum*. Arnott (1825) may not have recognized the great taxonomic heterogeneity of this genus *sensu* Hedwig, but he was the first to consider *Orthotrichum* sufficiently distinct to deserve its own family (as order "Orthotrichoideae"). Bridel (1826), in his extensive classification of mosses based on the distribution of the female gametangia and the extent of the peristome, recognized orders and families but included *Orthotrichum* and related genera in the large "order" *Amphistomi* including peristomate acrocarpous taxa. Müller (1851) recognized the Orthotrichaceae (as a subtribe) and placed it within the haplolepideous Pottiales (as tribe Pottioideae), between what is now considered the Pottiaceae and the Grimmiaceae. Schimper (1856) segregated the Zygodontaceae from the Orthotrichaceae, and placed both families between the Encalyptaceae (also haplolepideous) and the Grimmiaceae. Jaeger (1874) too, considered the Orthotrichaceae and the Grimmiaceae to be related, and Brotherus (1909) saw the Orthotrichaceae marking the transition from the Haplolepideae to the Diplolepideae. Fleischer (1920) based his classification primarily on the architecture of the peristome, and recognized that the Orthotrichaceae were more closely related to other diplolepideous mosses than to the haplolepideae. He placed the Orthotrichaceae, together with the Erpodiaceae in the Orthotrichineae, in the

Isobryales. Fleischer's (1920) classification was adopted by Brotherus (1924-1925) in his monumental treatise of the Bryopsida. Subsequently (Table 1.2.), the Orthotrichineae have mainly been recognized at the ordinal rank (Dixon 1932, Crosby 1980, Walther 1983, Vitt 1982a).

The most modern classification of mosses (Vitt 1984) divides the Bryopsida primarily on the basis of the architecture of the peristome following Fleischer's (1920) system, which in turn is inspired from Philibert's (1884-90) studies on the peristome. The arthrodontous peristome is composed of articulate teeth, and four distinct types can be recognized (Vitt 1981). Three of these typically have two rows of teeth (diplolepideous peristome), with the endostome either opposite (*Funaria*-type; Schwartz 1994, Shaw, Anderson and Mishler 1989) or alternate to the exostome. The Orthotrichales and the Bryales *sensu lato* share an alternate arrangement of teeth (Lewinsky 1989, Shaw 1985, Vitt 1981), but differ by the presence of cilia (appendages in between the segments of the endostome) in the Bryales (Shaw, Anderson and Mishler 1989). The fourth peristome-type (haplolepideous or *Dicranum*-type peristome; Shaw, Mishler, and Anderson 1989) is characterized by a single row of teeth with asymmetric divisions occurring in the innermost peristomial layer. The direction of peristome evolution is not agreed upon (Crosby 1980, Vitt 1981, Shaw and Rohrer 1985), although most recent evidence (see Vitt, Goffinet, and Hedderson 1997) suggest that the *Funaria*-type represents the ancestral type of peristome, and that the *Dicranum*-type diverged prior to the evolution of both the *Orthotrichum* and the *Bryum*-types. Whether the *Orthotrichum*-type and the *Bryum*-type actually define natural groups of equal rank is subject of debate: the uniqueness of the *Orthotrichum*-type peristome (Vitt 1981), may indeed not be sufficient to exclude a derivation from a *Bryum*-type peristome as suggested by Shaw (1985).

Objectives. The current circumscription of the Orthotrichales and the Orthotrichaceae serves convenience more than phylogenetic rationale. The purpose of this study is to examine the affinities of the genera of the Orthotrichaceae and the Orthotrichales based on comparative morphology and cladistic analyses of morphological and molecular data. This study will address the following questions: 1) are the Orthotrichaceae and the Orthotrichales monophyletic groups?, and 2) what are the major phylogenetic relationships among the taxa that compose the Orthotrichaceae.

Table 1.1. Current generic classification of the Orthotrichaceae (updated from Vitt 1982a) and the number of species included in each genus

Taxon	number of species
Zygodontoideae Brotherus	
Amphidium Schimp.	12
Kleioweisiopsis Dixon	1
Leptodontiopsis Broth.	4
Stenomitrium (Mitt.) Broth.	1
Zygodon Hook. & Tayl.	approx. 50
Pleurozygodontopsis Dixon	1
Orthotrichoideae Broth.	
Bryodixonia Sainsb.	1
Ceuthotheca Lewinsky	1
Muelleriella Dusén	4
Orthomitrium Lewinsky-Haapasaari & Crosby	1
Orthotrichum Hedw.	118
Pleurorthotrichum Broth.	1
Stoneobryum Norris & Robinson	2
Ulota Mohr	approx. 35
Drummondoideae Vitt	
Drummondia Hook.	5
Macromitrioideae Broth.	
Cardotiella Vitt	5
Desmotheca[1] Lindb.	2
Florschuetziella Vitt	2
Groutiella Steere	approx. 10
Leiomitrium Mitt.	1
Leratia Broth.	1
Macrocoma (C.Müll.) Grout	10
Macromitrium Brid.	approx. 250
Schlotheimia Brid.	approx. 50
Uncertain affinities	
Octogonella Dixon	1
Trigonodictyon Dixon & P de la Varde	1
Uleastrum Buck	4

[1] also placed in its own subfamily by Brotherus (1925), Walther (1983), and Crum (1987)

Table 1.2. Systematic position of the Orthotrichaceae and putative related families in major classification schemes (families included in the Orthotrichales by Vitt 1984 are in bold)

Jaeger (1874)	Brotherus (1909)	Fleischer (1920)	Brotherus (1924)	Dixon (1932)
Tribe Grimmiaceae	Grimmiaceae	Bryales	Isobryales	**Orthotrichales**
Zygodonteae	**Orthotrichaceae**	Isobryales	**Orthotrichineae**	**Erpodiaceae**
Orthotricheae	Funariaceae	**Orthotrichineae**	**Erpodiaceae**	Ptychomitriaceae
		Erpodiaceae	**Orthotrichaceae**	**Orthotrichaceae**
		Orthotrichaceae	Rhacopilineae	Eubryales
		Rhacopilineae	**Helicophyllaceae**	Rhacopilinae
		Helicophyllaceae		**Helicophyllaceae**

Robinson (1971)	Crosby (1981)	Walther (1983)	Vitt (1982b)	Vitt (1984)
Bryales	**Orthotrichales**	Grimmiales	Bryidae	Bryales
Rhachitheciaceae[1]	**Orthotrichaceae**	**Erpodiaceae**	**Orthotrichales**	**Orthotrichineae**
Erpodiaceae	**Erpodiaceae**	**Orthotrichales**	**Orthotrichaceae**	**Orthotrichaceae**
Helicophyllaceae	**Rhachitheciaceae**	**Orthotrichaceae**	**Erpodiaceae**	**Erpodiaceae**
Orthotrichaceae	**Microtheciellaceae**[2]	**Rhachitheciaceae**	**Rhachitheciaceae**	**Rhachitheciaceae**
...	**Helicophyllaceae**	**Helicophyllaceae**	**Microtheciellaceae**	**Microtheciellaceae**
		Hedwigiaceae	**Helicophyllaceae**	**Helicophyllaceae**
		Helicophyllaceae		
		Cryphaceae		
		Wardiaceae		

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[1] established by Robinson (1964)

[2] established by Harrington and Miller (1977)

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Chapter two

A reconsideration of the affinities of *Kleioweisiopsis* *Pleurozygodontopsis*, *Trigonodictyon*, and the Microtheciellaceae (Bryopsida, Orthotrichales)

The Orthotrichaceae is a cosmopolitan family, and with over 500 species is one of the most diverse families of arthrodontous mosses (Vitt 1982). The Orthotrichaceae are found in a great variety of habitats ranging from canopy branches in tropical upper montane forests (*Macromitrium* sp.; Vitt & Ramsay 1985) to rocks near sea level on subantarctic islands (*Muelleriella* sp.; Vitt 1976). Vitt (1982) listed 14 genera and characterized the family by a peristome of alternating endostomial segments and exostomial teeth, a thick OPL (accounting for the recurved teeth), an endostome lacking a basal membrane and cilia, costate leaves with nearly isodiametric, thick-walled, papillose upper cells, and no differentiated alar cells, and by terminal perichaetia with additional growth by lateral innovations. Vitt (1984) later added *Cardotiella* Vitt, *Octogonella* Dixon, *Pleurozygodontopsis* Dixon, *Trigonodictyon* Dixon & P de la Varde, and reinstated *Leptodontiopsis* Broth., *Leratia* Broth., *Leiomitrium* Mitt., and thus accepted 21 genera in the Orthotrichaceae. Recently Norris and Robinson (1987), Lewinsky (1994), and Lewinsky and Crosby (1996) established additional new genera *Stoneobryum*, *Ceuthotheca*, and *Orthomitrium*, respectively, whereas Zander (1993) transferred the genera *Uleastrum* Buck and *Kleioweisiopsis* Dixon from the Pottiaceae to the Orthotrichaceae. With the controversial inclusion of the gymnostomous genus *Amphidium* (Lewinsky 1976; see also Vitt 1982) the family currently includes 27 genera, of which 15 are composed of no more than three species. The Orthotrichales *sensu* Vitt (1984) include in addition to the type family, also the Erpodiaceae Broth., Helicophyllaceae Broth., Microtheciellaceae Miller & Harrington, and Rhachitheciaceae Robinson.

The current circumscription of both the order and the family serves convenience more than phylogenetic rationale, as no single autapomorphy or combination of unique characters states can *a priori* be found for defining either taxon. While morphological heterogeneity can result from severe reductionary trends with loss of typical character states (peristome features in gymnostomous taxa) or from reversal to plesiomorphic characters states within a monophyletic lineage, heterogeneity may also be indicative of the polyphyly of a taxon. Discriminating between these alternative sources of heterogeneity is not always obvious and therefore the monophyly of a given taxon should ideally be investigated using phylogenetic methods without any *a priori* judgment. In mosses, parallelism in gametophytic features can be severe even above the ordinal level (e.g., *Calomnion*; Vitt 1995; Waters et al. 1996) but for cladistic rationale to solve such cases of ambiguous affinities would require the inclusion of distantly related putative sister-taxa. In the case of the Orthotrichales, alternative affinities for some of the taxa may lie, as argued for below, with the Dicranales, Grimmiales, and Leucodontales, and maybe even the Seligeriales (see chapter 3). Including potential sister-groups from these orders, particularly if these are derived within their lineage (and thus with few plesiotypic characters) may introduce more phylogenetic noise and obscure relationships, rather than solve them. Taxa whose affinities clearly are outside the ingroup should be transferred whenever possible, prior to a cladistic analysis, as is common practice in taxonomic monographs where the phylogenetic reconstruction is preceded by the taxonomic treatment. This study examines the systematic affinities of *Kleioweisiopsis*, *Trigonodictyon*, and *Microtheciellaceae*, and the taxonomic status of *Pleurozygodontopsis*.

Kleioweisiopsis Dixon, Smithsonian Misc. Coll. 72(3): 18. 1920
Type: *Kleioweisiopsis denticulata* Dixon, Kenya, Aberdare Mts., *Allan 3951* (holotype: BM!; isotype: US). (Fig. 2.1)

In the protologue of *Kleioweisiopsis* Dixon (1920) suggested placing his new genus in the Pottiaceae based on overall similarity with *Astomum* and *Hymenostomum*. Zander (1993) in his thorough monograph of the Pottiaceae excluded *Kleioweisiopsis* and tentatively transferred the genus to the Orthotrichaceae, near *Amphidium*. *Kleioweisiopsis denticulata*, the sole species of the genus (Zander 1993), is characterized by its subulate perichaetial leaves, a very short seta seemingly caducous with the capsule, lack of stomata, and a differentiated, yet mostly persistent operculum (Fig. 2.1). At the base of the operculum the cells are weakly differentiated and may not be fully functional. The exothecium is composed of fragile cells that disintegrate allowing for the spores to be dispersed. The type specimen is annotated by Saito as a combination in *Pleuridium* Brid. in the Ditrichaceae. *Kleioweisiopsis* exhibits a combination of features indeed characteristic of the Ditrichaceae *sensu* Brotherus (1924; e.g., undifferentiated alar cells, costa with median guide cells and few ventral stereids, and mostly smooth laminal cells; Fig. 2.1) and should therefore be included in this family. Within the Ditrichaceae, immersed capsules are common to 8 genera, confined to the Ditrichoideae. This subfamily is divided in two groups based on the presence of a differentiated operculum (Brotherus 1924, Buck and Snider 1992). Because the operculum is not fully differentiated and functional, *Kleioweisiopsis* cannot be assigned to either group of taxa unambiguously. The first group, lacking a differentiated operculum, includes four genera: *Pleuridium*, *Cladostomum* C. Müll., *Crumuscus* Buck & Snider, and *Sporledera* Hampe. *Pleuridium*, *Cladostomum*, and *Crumuscus* differ from *Kleioweisiopsis* by the presence of a well developed cauline central strand, mitrate calyptrae (except *P. papillosum* Magill; Buck and Snider 1992). *Crumuscus* can furthermore be distinguished based on the partially bistratose lamina (Buck and Snider 1992). *Sporledera* lacks a central strand in the stem, but differs by the ovate to oblong leaf base, the presence of stomata, and the mamillate capsule. Compared to the taxa developing a dehiscent operculum on an immersed capsule, *Kleioweisiopsis* differs from *Pringleella* Card. by the lack of an annulus, and cucullate calyptrae, from *Garckea* C. Müll. by the gymnostomous and spheric capsule, from *Astomiopsis* C. Müll. by the flexuose leaves, the lack of an annulus, from *Eccremidium* Hook. f. & Wils. subg. *Eccremidium* by its flexuose leaves, and from subg. *Pseudo-Pleuridium* Broth. by its costate leaves. *Kleioweisiopsis* appears to share sufficient characters with the Ditrichaceae to be included in this family, where it should remain a distinct genus.

Kleioweisiopsis denticulata Dixon

Plants gregarious, to 5-6 mm high. Stems orthotropic, outer cortical cells weakly differentiated, central strand lacking. Leaves 2.0-2.5 mm long and 0.25-0.35 mm wide at base, erect to flexuose, lanceolate, entire, denticulate to serrulate toward apex. Costa ending within a few cells of apex, with median guide cells, and adaxial (sub-)stereids and seemingly a single abaxial stereid. Basal laminal cells hyaline, rectangular, thin to moderately thick-walled, 24-90 µm long, 8-24 µm wide. Upper laminal cells, short rectangular, quadrate to oblate, thick-walled, 10-24 µm long, 8-14 µm wide. Acrocarpous, autoicous. Perichaetia with paraphyses, archegonia 320 µm long. Perichaetial leaves to 4.5 mm long, erect and somewhat flexuose, linear-lanceolate, serrulate near apex. Perigonia subapical, paraphyses present, antheridia to 140 µm long. Perigonial leaves short, lanceolate. Setae 0.3 mm long, outer cells slightly thick-walled, inner cells thin-walled, mostly collapsed, central strand differentiated. Capsule spheric, exothecial cells very thin, disintegrating in old capsules, stomata absent. Operculum long, obliquely rostrate, rostrum to 0.4 mm long. Calyptrae cucullate, covering at least half the capsule, about 0.7 mm long. Spores 18-22 µm, granulose.

Key to the Ditrichaceae with immersed capsules (Ditrichoideae).

1. Operculum not differentiated 2
1. Operculum differentiated 6
  2. Stomata present 3
  2. Stomata absent 4
3. Cauline central strand present .... *Pleuridium*
3. Cauline central strand absent .... *Sporledera*
  4. Lamina partially bistratose .... *Crumuscus*
  4. Lamina unistratose 5
5. Leaves ovate, calyptra mitrate, cauline central strand present .... *Cladostomum*
5. Leaves lanceolate, calyptrae cucullate, cauline central strand absent ...*Kleioweisiopsis*
  6. Peristome present .... *Garckea*
  6. Peristome absent 7
7. Calyptrae mitrate .... *Pringleella*
7. Calyptrae cucullate or covering only the operculum 8
  8. Annulus not differentiated .... *Kleioweisiopsis*
  8. Annulus differentiated 9
9. Operculum with long oblique rostrum .... *Astomiopsis*
9. Operculum mamillate, or short erect rostrum .... *Eccremidium*

Zygodon Hook. & Tayl., Musc. Brit. 70. 1818.
Pleurozygodontopsis Dixon, Annales Bryologici 12: 51. 1939. **syn. nov.**
Type: *Pleurozygodontopsis decurrens* Dixon

Zygodon reinwardtii (Hornsch.) Braun in B.S.G.
Pleurozygodontopsis decurrens Dixon, Annales Bryologici 12: 51. 1939. **syn. nov.**
Type: Sumatra, Gunong Losir, Atjeh, Gajolanden, 2940 m, 5 Feb. 1937, *van Steenis 10159* (lectotype chosen here: BM-herb. Dixon 4044); ibidem, *van Steenis 10161* (syntype: BM-herb. Dixon 4041!). (Fig. 2.2)

Dixon (1939) proposed the new genus *Pleurozygodontopsis* to accommodate two collections similar in habit and foliation, to slender forms of *Leptodontium* (Pottiaceae) or more robust forms of *Zygodon*. Gametophytically these two genera are similar in habit but can be readily segregated by the costa anatomy (Zander & Vitt 1979). Dixon (1939) placed the new genus in the Orthotrichaceae, where "the position of the inflorescence, the decurrent leaves, and the narrowly cylindric, almost fusiform, plicate capsule" would distinguish the genus from related genera. Dixon interpreted the gametangia to be either basal or lateral on the autoicous individuals, yet on closer examination it is clear that the gametophyte produces terminal gametangia and resumes growth by subapical innovations. When a terminal perichaetium is produced, a subapical perigonium can be developed. Monoicy, decurrent leaves and cylindrical capsules are characters known from the genus *Zygodon* (Malta 1926). When compared to species of section *Zygodon* (i.e., species with papillose upper laminal cells) *P. decurrens* appears identical to the pantropical *Z. reinwardtii* (Hornsch.) Braun in B.S.G., except for the organization of the gametangia. Both species have broad leaves with undulate margins, apical marginal teeth, papillose (sometimes only weakly so) laminal cells covering the abaxial surface of the costa near the apex, and are monoicous (Fig. 2.2). *Zygodon reinwardtii* has been reported to be synoicous (Vitt 1993), "synoicous and synoicous or dioicous" (Fleischer 1904), or synoicous, but "pure male and female inflorescences present too" (Malta 1926). Both specimens of *P. decurrens* show no indication of any antheridia present in the perichaetia, but rather separate male and female gametangia, on a single individual.

In *P. decurrens* the costa ends below the apex. On a single stem, the apical cells of the leaves can be either papillose or more often smooth. The smooth cells are often somewhat elongate and may give the appearance of the costa being excurrent. In *Z. reinwardtii* the costa has been described as vanishing below the apex (Grout 1946, Vitt 1993), and percurrent (Malta 1926), excurrent (Lewinsky 1990), or shortly excurrent (Fleischer 1904). I have examined specimens of *Z. reinwardtii* from various parts of the neotropics and one specimen from New Guinea, and found the papillosity of the apical cells to be variable even among leaves from a single individual. In some leaves, where the costa distinctly vanishes below the apex, the unistratose apex can be composed distally by smooth and elongate cells and proximally by papillose cells. When these subapical papillose cells are lacking the elongate cells seem to represent the distal portion of the costa, yet because the apex always appears unistratose I feel that the costa of *Z. reinwardtii* cannot be described as excurrent, and is therefor similar to that of *P. decurrens*. With regards to the papillose cells on the abaxial surface of the apex of the costa of *Z. reinwardtii* (Vitt 1993), I found it to be variable too, ranging from virtually smooth to conspicuously papillose, even on a single stem of *Z. reinwardtii*. The costa in

Z. reinwardtii and *P. decurrens* can be either smooth all the way to the apex, or be covered ventrally in the apical region. None of the characters presented by Dixon (1939) to support the distinction of *P. decurrens*, withstand critical comparison with *Z. reinwardtii* and the two species should therefore be considered synonymous.

Trigonodictyon Dixon & P. de la Varde, Annales de Cryptogamie Exotique 1: 40. 1928.
Type: *Trigonodictyon indicum* Dixon & P. de la Varde (Fig. 2.3)

Dixon and P. de la Varde (in P. de la Varde 1928) characterized their new genus by the basal juxtacostal cells that form clear triangles like the cancellinae in the Calymperaceae. Because the abundant material of type and only collection lacks sporophytes systematic placement remained tentative. They decided to tentatively include *Trigonodictyon* in the Orthotrichaceae on the basis of the homogenous costa anatomy and the ventral position of the two guide cells. *Trigonodictyon* shares with some Orthotrichaceae, namely the Orthotrichoideae and the Zygodontoideae, terminal perichaetia (unlike the original authors I found some perichaetia; holotype BM) and the ventral guide cells in the costa. *Trigonodictyon* differs, however, from all Orthotrichaceae by the laminal cell architecture. The distal basal cells are distinctly sinuose to irregularly thick-walled (Fig. 2.3), a character distinctive for the Grimmiaceae. The Grimmiaceae *sensu* Churchill (1981) are composed of 11 genera distributed among three subfamilies. The generic and suprageneric taxonomy is mostly based on sporophytic characters. The only gametophytic characters, besides the sporeling type, are the shape of the leaf, the differentiation of basal and upper laminal cells, and the anatomy of the costa. *Rhabdogrimmia* and *Guembelia* differ from *Trigonodictyon* by the long acuminate apex of the leaf. The shape of the leaf and the differentiation of the laminal cells in two types, suggest affinities with the Coscinodontoideae. The costa of the Grimmiales is characterized by a type-C architecture (Churchill 1981), that is the adaxial, median and abaxial cells are all clearly distinct from one another (Kawai 1968). Transformations of this typical costa anatomy in the Grimmiales lead either to a loss of complexity (homogenous costa: type-A; or a costa with a differentiation of the adaxial cells only: type-B), or to an increased complexity, with the differentiation of guide cells in the median portion of the costa and ventral stereid cells (type-E; Churchill 1981). The dorsal or abaxial costal cells of *Trigonodictyon* have walls that are not strongly thickened (Fig. 2.3), unlike true stereids that have very incrassate walls and very narrow lumens. In a transverse section of the costa, the substereids of *Trigonodictyon* can hardly be differentiated from the surrounding cells, and the costa is thus of the type-A. Kawai (1968) defined the various types of costal anatomy based on transverse section only, and may in many cases have relied solely on observations by previous authors. Indeed, when examined in surface view, taxa considered with type-A costal anatomy (*Pleurorthotrichum*; Kawai 1966) can be interpreted as having a type-B costa (see chapter 6). Examination of the costa of *Trigonodictyon* in surface view reveals that the abaxial cells, except for the most proximal ones, are mostly short, and chlorophyllose, whereas the adaxial cells, are long, hyaline and with straight walls in the proximal portion of the costa, and chlorophyllose and with sinuose walls above. The median cells can also be examined in surface view, and they are mostly distinctly narrower than the adjacent cells, and hyaline. Similar patterns, particularly the sinuose adaxial cells have been seen in various representatives of the Grimmiales, but never in the Orthotrichales. The above characters seem to justify transferring *Trigonodictyon* from the Orthotrichales to the Grimmiales, a hypothesis that had already been raised by Dixon and P. de la Varde (1928), who had been misled by the costa anatomy as seen in transverse section. Based on Gangulee (1972), *Trigonodictyon* would key out as ***Racomitrium strictifolium*** (Mitt.) Jaeg., a species recently transferred to *Grimmia* by Deguchi (1980). *Trigonodictyon* differs from *G. strictifolia* by the unistratose margin, and the lack of a central strand in the stem. Until sporophytes are found, Trigonodictyon should be retained distinct within the Grimmiales, with uncertain systematic affinities. Considering my different interpretation of the costa anatomy and the discovery of the female gametangia, I am here providing a revised and updated description based on the only collection known, the holotype.

Trigonodictyon indicum Dixon & P. de la Varde (Fig. 2.3).

Type: India, Pambar Torrent, Kodaikanal, Pulney Hills, févr. 1927, *R.P. Foreau* (holotype, BM!; isotype, NY!).

Plants to 2.5 (-3.0) cm long. Stems prostrate (-decumbent ?), outer cortex composed of 2-3 layers of small, thick-walled, orange-red, cells, inner cortex of wide, moderately thick-walled, central strand lacking. Branches few (?) and mostly basitonous. Leaves 1.3-1.6 mm long and 0.3-0.6 mm wide, erect appressed, lanceolate to ovate-lanceolate, apex acute, margin entire, plane. Costa strong, ending a few cells below apex, with abaxial cells short rectangular to subquadrate chlorophyllose almost to the base, median substereids and adaxial cells hyaline and rectangular with straight walls in proximal portion of the costa, and chorophyllose and with sinuose walls above. Basal laminal cells rectangular, smooth, evenly thick-walled, walls straight, 12-60 µm long, 8-12 µm wide. Median cells, rectangular, smooth, with sinuose thick walls. Upper laminal cells, short quadrate but mostly irregular, smooth, thick walled, 10-24 µm long, 8-14 µm wide. Axillary hairs, with two quadrate, hyaline basal cells. Acrocarpous, dioicous. Perichaetia lacking paraphyses, archegonia 600 µm long, three to five per perichaetium. Perichaetial leaves to 2.2 mm long and 0.8 mm wide, erect, lanceolate to ovate-lanceolate, apex acute to acuminate, margin entire, reflexed in lower half. Perigonia and sporophyte unknown.

Microtheciella Dixon, J. Bot., Lond. 69: 1 & pl. 595, fig. 1, 1931.

Type: *Microtheciella kerrei* Dix., "On branches of *Rhabdia lycioides*, on open gravel bed in river, Ban Trang, Langsuan, Siam, c. 50 m alt.; 17 Feb. 1927, leg. *A.F. Kerr* (*195*)" (holotype-BM!).

This monotypic genus is known only from two collections, one from Thailand and the second one from Laos (Dixon 1931, 1936). Dixon placed his new genus in the Erpodiaceae where it remained until recently (Crum 1972). Miller and Harrington (1977) considered *Microtheciella* anomalous within the Erpodiaceae from which it differed by its costate leaves, differentiated marginal cells, and specialized motor cells, and therefore proposed a new family, the Microtheciellaceae, to accommodate it (see Miller & Harrington 1977, for excellent illustrations). Despite some parallels with the Neckeraceae or the Hookeriales, Miller & Harrington (1977) retained the Microtheciellaceae within the Orthotrichales. Its affinities within the order remained obscure (Vitt 1982).

Examination of the type specimen (BM) revealed that the perichaetia in *Microtheciella kerrei* are produced on short lateral innovations. Vegetative leaves similar to those found on sterile axis are not developed on these lateral innovations, instead only juvenile leaves are found below the perichaetium. The mode of pericheatium production is thus reminiscent of the pleurocarpous type but could also represent a "derived" type of cladocarpy with severe reduction of the sterile portion of the perichaetium-bearing axis, as in *Molendoa* (Pottiaceae; La Farge-England 1996). Both types can be distinguished based on the morphology of the juvenile leaves and on the width of the axis bearing the female gametangia (La Farge-England 1996). In *Microtheciella keerei* the juveniles leaves below the pericheatium are broader than those developed on sterile branches, but the width of the innovation appears similar to that of sterile axes. At present, and until more material becomes available I prefer to consider *Microtheciella keerei* as pleurocarpous, and should therefore be excluded from the Orthotrichaceae. The lack of pseudoparaphyllia in *Microtheciella keerei* (Miller & Harrington 1977) is not incompatible with affinities with pleurocarpous taxa, since pseudoparaphyllia have been lost repeatedly during the evolution of various pleurocarpous taxa (Buck and Vitt 1986, Hedenäs 1995), including in the Neckeraceae (*Homalodendron* Fleisch., Enroth 1993). Gametophytic features such as leaf shape, and cell areolation, are reminescent of the Neckeraceae (Miller & Harrington 1977), but the exostome in this family is never reduced (Enroth 1989) as it is in *Microtheciella* (Miller & Harrington 1977). Hedenäs (1995) recently demonstrated that the gametophytic characters are often less informative in addressing higher level relationships among pleurocarpous mosses. The systematic affinities of *Microtheciella* among pleurocarpous lineages will need to be further critically examined. For now the family should be retained distinct and placed near the Neckeraceae.

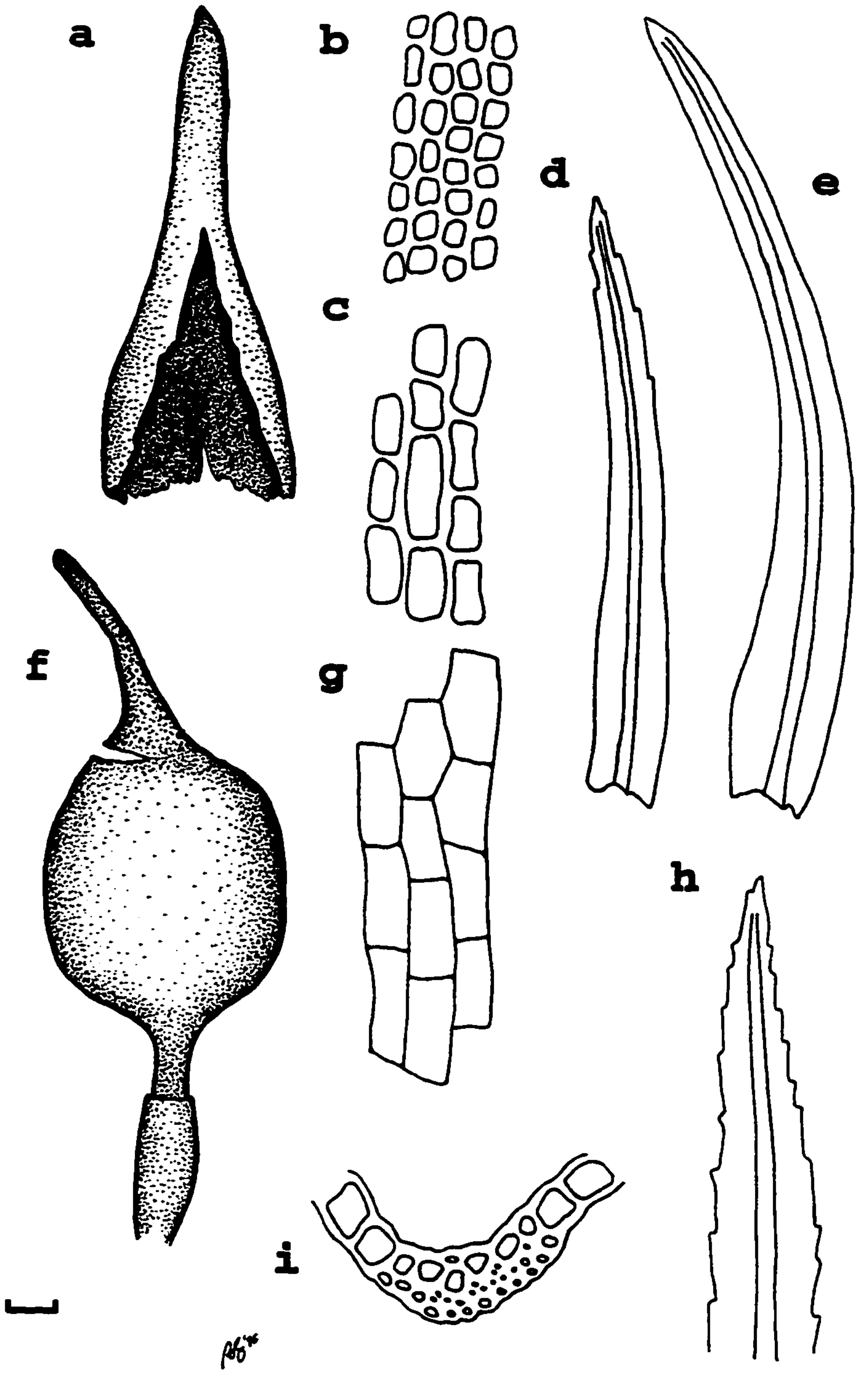

Figure 2.1. *Kleioweisiopsis denticulata* (holotype-BM). a. Calyptrae. - b. Upper laminal cells. - c. Median laminal cells. d. Vegetative leaf. - e. Perichaetial leaf. - f. Operculate capsule. - g. Basal laminal cells. - h. Apex of vegetative leaf. - I. Transverse section of the costa in median portion of the vegetative leaf. Scale bar = 0.2 mm (d, e), 81 µm (a, f, h), 20 µm (b, c, g, i).

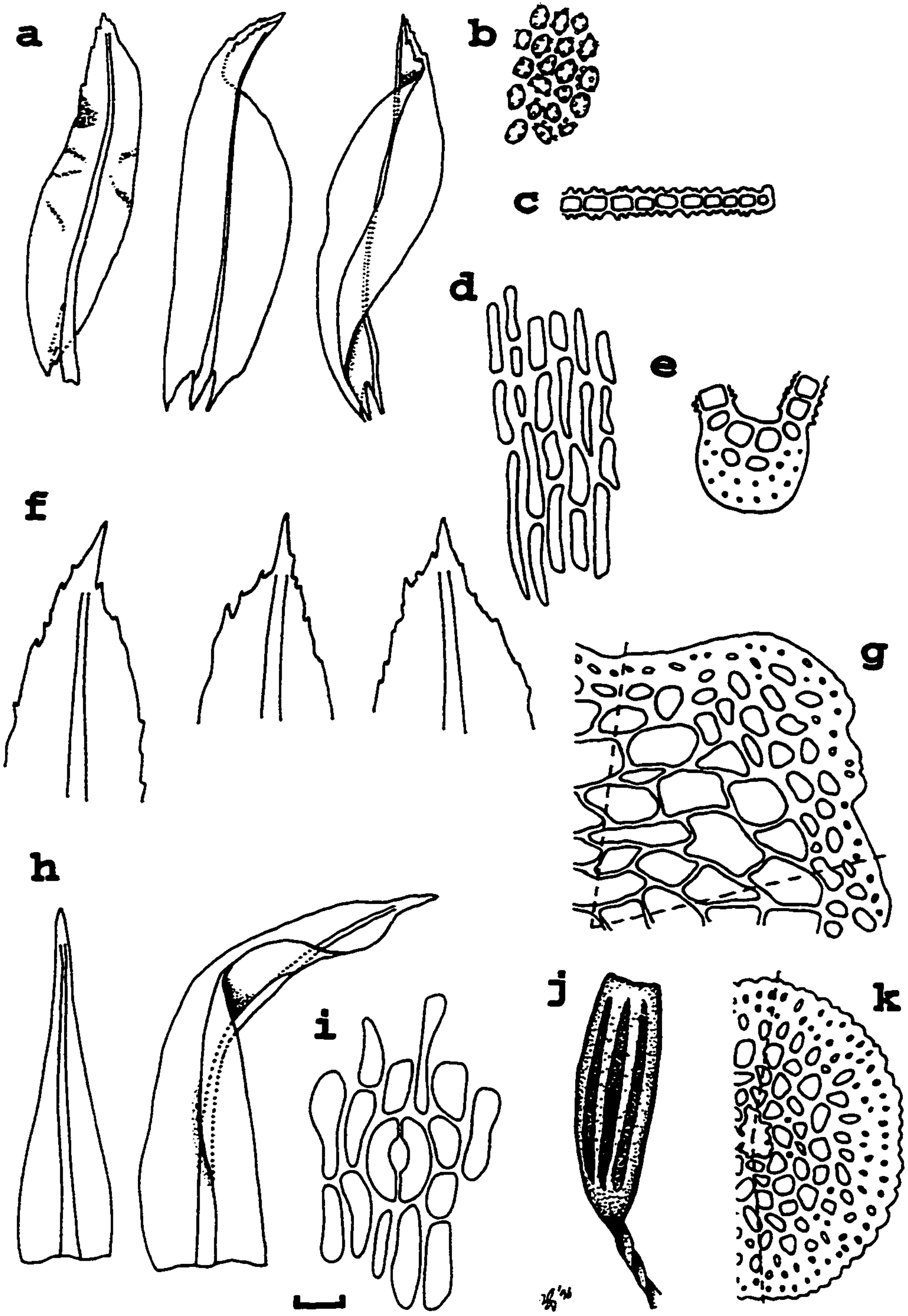

Figure 2.2. ***Pleurozygodontopsis decurrens*** (holotype-BM). a. Vegetative leaves. - b. Upper laminal cells. - c. Transverse section of upper lamina cells. - d. Basal laminal cells. - e. Transverse section of costa in median portion of vegetative leaf. f. - Apex of vegetative leaves. - g. Transverse section of stem. - h. Inner (left) and outer (right) perichaetial leaves. - I. Stomata. - j. Capsule habit. - k. Transverse section of the seta. Scale bar = 0.57 mm (j), 0.2 mm (a, h), 81µm (f), 20µm (b, c, d, e, g, i, k)

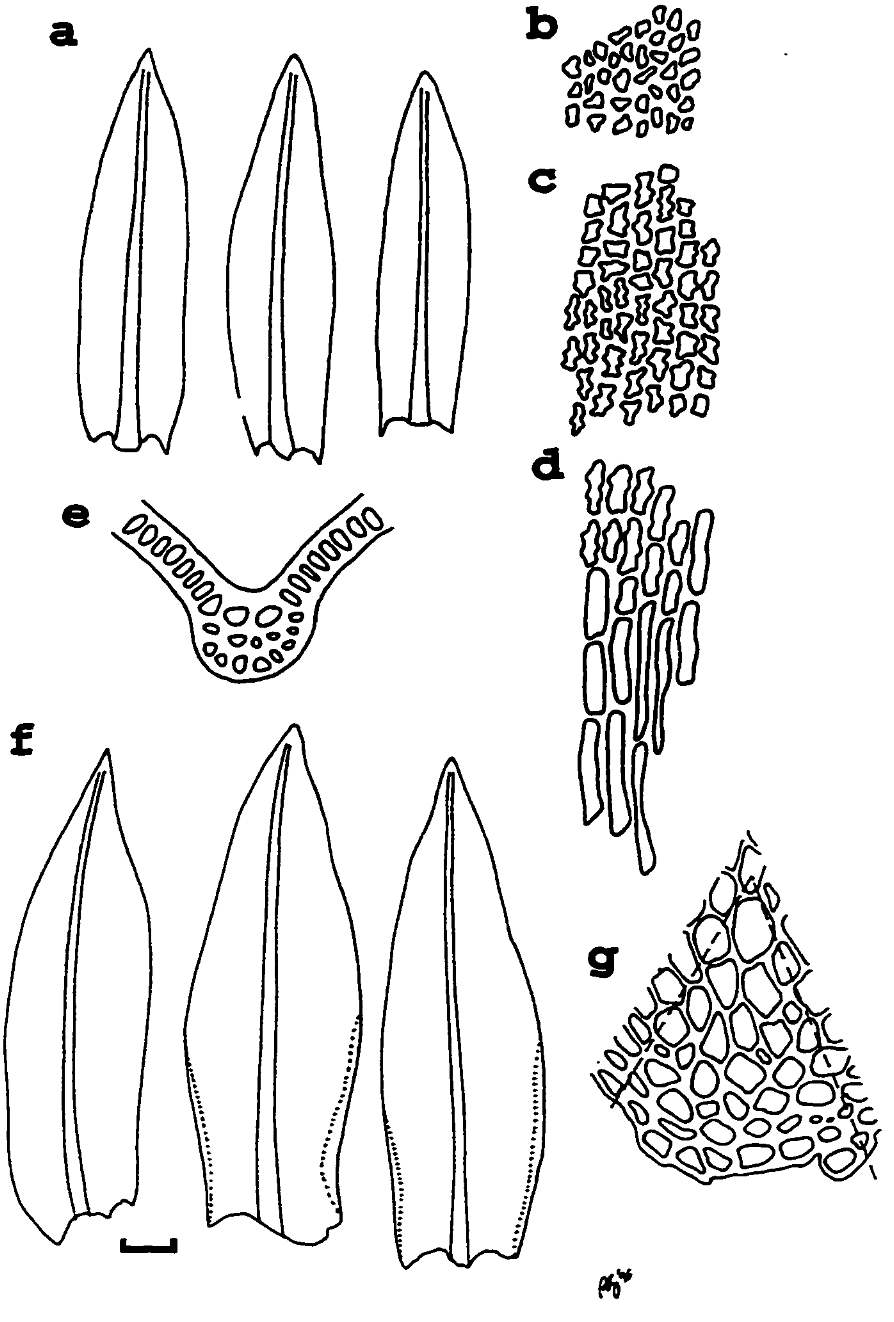

Figure 2.3. *Trigonodictyon indicum* (holotype-BM). a. Vegetative leaves. - b. Upper laminal cells. - c. Median laminal cells. - d. Basal laminal cells. - e. Transverse section of the costa in median portion of vegetative leaf. - f. Perichaetial leaves. - g. Transverse section of the stem. Scale bar = 0.2 mm (a, f), 20μm (b, c, d, e, g)

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Chapter three

The Rhachitheciaceae: revised generic circumscription and ordinal affinities

The Rhachitheciaceae is a small family established by Robinson (1964) to accommodate two former orthotrichaceous genera: *Rhachithecium* Le Jol. and *Hypnodontopsis* Iwatsuki & Noguchi. *Rhachitheciopsis* P. de la Varde, considered by Iwatsuki (1957) to be closely related to *Hypnodontopsis*, was reduced to a subgenus of *Rhachithecium* by Robinson (1964). Recently, Allen and Pursell (1991) transferred the genus *Jonesiobryum* Allen & Pursell from the Funariaceae to the Rhachitheciaceae, and Zander (1993) excluded the genus *Tisserantiella* P. de la Varde from the Pottiaceae and suggested that it too, "clearly belongs to the Rhachitheciaceae". All 13 species, except *Rhachithecium perpusillum sensu* Crum (1956), are narrowly distributed in tropical and subtropical regions of both hemispheres, where they grow on trees. The Rhachitheciaceae have been characterized by spathulate to lingulate, often apiculate vegetative leaves, differentiation of laminal cells into hyaline rectangular basal cells and chlorophyllose, isodiametric upper cells, a single costa extending to the upper portion of the leaf, the lack of a differentiated cauline epidermis, terminal perichaetia on the stem, a simple peristome composed of 16 teeth fused into eight pairs (Crum 1993; Zander 1993).

As part of a generic revision of the Orthotrichaceae, the genera *Octogonella* Dixon and *Uleastrum* Buck were studied. Both genera share several sporophytic features, that are *a priori* incompatible with typical Orthotrichaceae, but are instead reminiscent of the Rhachitheciaceae. The circumscription of this family is here revised and its systematic affinities to the Orthotrichaceae are discussed.

1. *RHACHITHECIOPSIS* P. de la Varde, Bull. Soc. bot. France 73: 74. 1926.

Potier de la Varde (1926) proposed this new genus to accommodate three *Rhachithecium*-like specimens from Africa, that differed from the symmetric *R. perpusillum* (as *R. transvaliense* C. Müll.) among others by the seta that is completely curved downward when young or moist and strongly curved into an "s"-like shape when dry, and poorly differentiated perichaetial leaves (Potier de la Varde 1926). Iwatsuki (1957) retained *Rhachitheciopsis* as distinct and suggested close affinities with

Hypnodontopsis based on the mitrate calyptrae. Potier de la Varde (1926) tentatively described the calyptra of *Rhachitheciopsis* as mitrate, and Iwatsuki (1957) interpreted this feature as an indication of close affinities between *Hypnodontopsis* and *Rhachitheciopsis*. I have seen several calyptrae in the type specimen, and although not fully developed, they appear clearly cucullate. Further, the genus *Hypnodontopsis* now includes a second species, *H. mexicana* (Thér.) Robinson, that differs from the type species, by several characters, including the cucullate calyptrae (Robinson 1964). The shape of the calyptrae thus fails to be informative in addressing the generic relationship of *Rhachitheciopsis*. Iwatsuki (1957) further emphasized that in both *Rhachitheciopsis* and *Hypnodontopsis* the anatomy of the seta, immediately below the capsule is strongly asymmetric, due to heavy excentric wall thickening on one side of the seta (Iwatzuki 1957; Fig. 3.1i). I have examined the anatomy of the seta immediately below the urn in *Rhachithecium perpusillum* (*Chang Jinkun 1748-3*—ALTA) and *R. papillosum* (holotype—NY) and in both cases the thickenings are also unilaterally heavier, suggesting that this character may be shared by taxa with strongly curved seta (see also under *Uleastrum*). The inner surface of the peristome teeth of *R. tisserantii* lacks the palisade-like markings typical of *Hypnodontopsis* (Figs. 3.2a & b and 3.3e & f). In their architecture and ornamentation the peristome teeth of *Rhachitheciopsis* (Figs. 3.2a & b) are very similar to those of *Rhachithecium* (Fig. 3.3c & d). Scattered additional divisions in the outer layer resulting in three or four cells (Fig. 3.2a) per tooth pair have also been observed in species of *Rhachithecium*, as well as in other taxa such as *Glyphomitrium* (Brotherus 1924), and do not seem to be taxonomically informative. Potier de la Varde (1926) described the teeth as minutely papillose. SEM observation, however, reveals that the teeth are smooth on the outer surface and at most minutely corrugate on the inner surface, as they are in *Rhachithecium* (Fig. 3.3c & d). Iwatsuki (1957) described the costa of *Hypnodontopsis apiculatus* as "in midleaf with two layers of stereid cells and 1 layer of large, thin-walled ventral cells, at the basal portion of the leaf with two layers of thick-walled cells, ..." I have seen only one specimen of *H. apiculatus* (Musci Japonici Exsiccati *1425*—ALTA). Here the costa definitely has adaxial substereids, as in *H. mexicana* (*Arsène 4793*—NY; Robinson 1964). The costa of *Rhachitheciopsis* lacks these ventral stereids and is more reminiscent of the costa of *Rhachithecium* (see below). The capsule of *Rhachitheciopsis* and *Rhachithecium* is globose to cup-shaped, whereas in *Hypnodontopsis* the capsule is more elongate and cylindrical. This suite of evidence thus supports Robinson's (1964) hypothesis that *Rhachitheciopsis* is more closely related to *Rhachithecium* than to *Hypnodontopsis*.

Robinson (1964) considered *Rhachitheciopsis* and *Rhachithecium* indistinguishable at the generic level, and rejected a distinction based on the shape of the operculum and the differentiation of the perichaetial leaves, two characters he considered "unusually subject to variation in this group". As a result he transferred *Rhachitheciopsis tisserantii* to *Rhachithecium*, where he placed it in its own subgenus distinct from subgenus *Rhachithecium* by the smooth calyptra, the "not noticeably differentiated" perichaetial leaves and the nearly flat operculum. I have seen three specimens of *Rhachitheciopsis* and in all three, the opercula were slightly convex and smooth (i.e., without a rostrum or a mammillae), and the perichaetial leaves were not sheathing the seta despite being as long as the seta. Furthermore the calyptra is definitely smooth in *Rhachitheciopsis* compared with a scabrous surface in *Rhachithecium* (Williams 1914; Crum 1956; Iwatzuki 1957). This study also revealed additional characters that separate *R. tisserantii* from species of *Rhachithecium sensu stricto*. The costa in *Rhachithecium* is weak, with only two bands of substereids, while in *Rhachitheciopsis tisserantii* the costa is strong due to the presence of several layers of substereid bands (Fig. 3.1d; see also Robinson 1964; Iwatzuki 1957). The annulus of *Rhachitheciopsis* is composed of two layers (and not one as described in the protologue; Fig. 3.1g), whereas in *Rhachithecium* the annulus is simple (Williams 1914; Iwatzuki 1957; Crum 1993; but see also under *R. welwitschii*) except maybe for *R. braziliense* (Brotherus 1924; synonymized with *R. perpusillum* by Crum 1956). Finally, the spore surface in *R. tisserantii* is conspicuously striate (Fig. 3.2c), while that in *R. perpusillum* and *R. papillosum* appears pitted (Fig. 3.2d), perhaps resulting from the proliferation of striation rather than from the formation of actual pits.

Considering the above differences in both the gametophyte (differentiation of perichaetial leaves, costa anatomy, surface of calyptra, spore wall ornamentation) and the sporophyte (shape of the operculum, complexity of the annulus; Tab. 3.1) I feel that *R. tisserantii* is best retained in its own genus. In the light of additional characters discovered since its original description I am here presenting a more complete description of the species.

Rhachitheciopsis tisserantii P. de la Varde. Bull. Soc. Bot. France 73: 74. 1926.(Figs. 3.1-2)

Type: Central African Republic: Plateau à 10 km d'Ippy, sur branches d'*Albizzia brownii*, 6.7.1929., *Tisserant 133* (Lectotype here designated—PC!, herb. *P. de Varde 2047*).

Rhachithecium tisserantii (P. de la Varde) Robins. The Bryologist 67: 449. 1964.

Plants to 3 mm high, green, orthotropic, acrocarpous. Stem sympodially branching, composed of wide lumened, thick-walled cells throughout, epidermal cells not differentiated, central strand lacking. Leaves spreading when moist, erect to spreading when dry, lingulate-spathulate, acute, to 1.4 mm long, 0.5 mm wide, margins plane, entire. Costa strong, ending 1/10 to 1/4 below apex, in transverse section with large, thin-walled, hyaline laminal cells, covering several abaxial layers of substereids. Basal cells differentiated in lower third or half of the leaf, hyaline, subquadrate to mostly long rectangular, 26-64 µm long, 16-26 µm wide, moderately thick-walled, smooth. Upper cells green, short, subquadrate to isodiametric, hexagonal, 10-40 µm long, 10-24 µm wide, rather thin-walled, flat, smooth. Gemmae not seen (but see Iwatsuki 1957). Autoicous, perichaetia terminal, paraphyses present. Perichaetial leaves weakly differentiated, lingulate to lanceolate, with incurved margins near apex, apiculate, with costa filling most of the apiculus, to 1.7 mm long. Basal cells rhomboid-elongate, smooth, hyaline. Upper cells differentiated only near apex, isodiametric, smooth, green. Perigonia axillary, gemmiform, paraphyses absent. Perigonial leaves differentiated, shortly ovate-oblong, strongly concave, to 0.5 mm long, costa lacking or weak. Seta twisted to right, curved downward when moist or capsule young, erect and kinked upward when dry, 1.5 mm long, composed of a cylinder of large, wide lumened, thick-walled cells, surrounded by small thick-walled epidermal cells arranged in a single row except below capsule, epidermal layers asymmetric, biseriate on one side and uniseriate on the opposite side; central strand present. Capsules 0.8 mm long, 0.7 mm wide, eight-ribbed, broadly cup-shaped, exothecial cells 2:1, those forming ribs, yellowish, with very thick longitudinal anticlinal walls, stomata phaneroporic, few, restricted to neck. Operculum slightly convex, lacking rostrum or mamilla. Peristome single, of 8-fused teeth; teeth lanceolate, 160 µm long, to 110 µm wide near base, incurved when moist, recurved when dry, yellowish, smooth on both sides, outer layer of a single tooth uniseriate dorsally, with some additional divisions occurring irregularly, trabeculae strong and projecting; base of tooth covered with thin, smooth biseriate membrane; inner surface of tooth smooth, composed of half a cell column. Calyptrae smooth, cucullate. Annulus bistratose, with both rows uniseriate, the outer row to ± 30 µm high, inner row ± 50 µm high, caducous to persistent. Spore 20-28 µm in diameter, papillose.

Specimens examined: Central African Republic: 6 km S d'Ippy, sur arbre dans les rochers du K. Lekpowa (?), 26 Fév. 1927, *Tisserant 247* (PC); 60 km N Bambari, rochers près Wamice, sur vieux bois, 27.7.1927, *Tisserant 392* (PC).

2. ***RHACHITHECIUM*** Le Jolis, Mém. Soc. Sc. Nat. Math. Cherbourg 29: 305. 1895.

a. ***Rhachithecium welwitschii*** (Duby) Zander, Bull. Buffalo Soc. Nat. Sci. 32: 277. 1993.

Zygodon welwitschii Duby, Mém. soc. Phys. Hist. Nat. Genève 21: 44, 1871. Type: "ad basin de Morro de Zopollo 5100 alt. in prov. Huilla regni Angol. det. cel. Welwitsch." (holotype—G!). *Ulea welwitschii* (Duby) Broth. in Par., In. Bryol. ed. 2, 5: 96. 1906.

Ulea welwitschii differs from other species of *Ulea* (now *Uleastrum* Buck) by the strongly ribbed capsule, the curved seta (except. *U. octoblepharis* (Jaeg.) Zander) and was therefore recently transferred to the genus *Rhachithecium* (Zander 1993). Zander (label annotation) hesitated to synonymize this species with the pantropical *R. perpusillum* from which he considered it "doubtfully different". The holotype consists only of a few, but complete (except for the calyptrae) individuals embedded between mica slides. The peristome teeth are identical to that of *Rhachitheciopsis* or *Rhachithecium*: the teeth are fused into eight pairs, and the dorsal surface of each tooth pair is biseriate and bears strong trabeculae, whereas the inner surface is uniseriate and smooth. Duby (1871) described the peristome as made of 16-32 teeth, and his drawing suggests that the paired teeth are split nearly to the base. The type does, however, clearly show 16 teeth fused into 8 pairs, split only in the upper portion, as in all peristomate species of *Rhachithecium* (see below). Duby also described the perichaetial leaves as "anguste lanceolatis enervis cellulis pellucidis elongato-parallelogrammicis", and thus differentiated from the vegetative leaves, and indicative of affinities with *Rhachithecium*. The operculum too, is reminiscent of that in *Rhachithecium*: it is distinctly conic and shortly rostrate. The annulus was described and illustrated by Duby as biseriate, suggesting a relationship with *Rhachitheciopsis*. In *Rhachithecium* the annulus is simple (Williams 1914; Iwatzuki 1957; Crum 1993) except maybe for *R. braziliense* (Broth.) Broth. I have not seen the type of the latter, but Brotherus' (1924) illustrations clearly show a compound annulus. Crum (1956) synonymized *R. braziliense* with the widespread *R. perpusillum*, a species he illustrates has having a single annulus (Crum 1956, 1993). One of the four slides of the type of *R. welwitschii* includes portions of an annulus, detached from the capsule. The cells are elongate and not inflated, as in *Rhachithecium perpusillum* (Crum 1993). The fragments of the annulus are clearly unistratose. In *Rhachitheciopsis* the annulus detaches from the capsule rim and both layers of the annulus separate when pressure is applied on the slide. Whether the annulus of

Rhachithecium welwitschii is actually bistratose as described by Duby, but has fragmented into separate layers during the preparation of the slide cannot be determined. The slide with the annulus holds all other portions of the deoperculate capsule, and one can assume that all portions of the annulus are present. Together all the fragments of the annulus only make up once the length of the circumference of the capsule mouth, suggesting that the annulus is composed of a single row of cells, and not two. The other capsules of the type are old and have lost their annulus. *Rhachithecium welwitschii* thus has clear affinities with *Rhachithecium* as suggested by Zander (1993). *Rhachithecium welwitschii* is currently known from only the type collected in Angola, whereas *Rhachithecium perpusillum* is reported for most of western Africa (O'Shea 1995). I agree with Zander (in litt.) that *R. welwitschii* is almost identical to *R. perpusillum* but unless the African material of *R. perpusillum* is revised, the differences in the shape of the annular cells should be taken as supporting the taxonomic distinction between both species.

b. ***Rhachithecium papillosum*** (Williams) Wijk & Marg., Taxon 9: 52. 1960.(Figs. 3.3c-d, 4)

Octogonella scabrifolia Dixon, J. Botany 74: 1 (+ plate 610). 1936, *syn. nov.* Type: "On tree, Kasauli, near Simla, India, *2929* (?); coll. P. *Tiwary*; comm. R.P. *Foreau* (*11b*)" (holotype—BM!)

Among the specimens of Indian mosses distributed by R. P. Foreau, Dixon found a collection of a few individuals "clearly allied to *Rhachithecium* but well marked in the coarsely tuberculate areolation" and the somewhat different peristome. When Dixon (1936) placed this new species in its own genus, *Octogonella*, *Rhachithecium* included only *R. perpusillum*, a species with smooth upper leaf cells and 16 peristome teeth fused into 8 pairs split near the apex. Robinson (1964) failed to include *Octogonella* in the Rhachitheciaceae and the genus remained in the Orthotrichaceae (Chopra 1975; Crum 1987).

As part of a generic revision of the Orthotrichaceae, I had the opportunity to examine the type of the only species of the genus, *Octogonella scabrifolia*. This species presents characters shared between the Rhachitheciaceae and two subfamilies of the Orthotrichaceae, namely the Orthotrichoideae and Zygodontoideae (e.g., the unicostate leaves, dimorphic proximal and distal cells, papillose upper leaf cells, and terminal perichaetia on stem) but its single peristome of smooth teeth with strong dorsal trabeculae is known, among orthotrichalean genera, only from the Rhachitheciaceae, namely *Rhachitheciopsis* and *Rhachithecium*. The strongly differentiated perichaetial leaves of *O. scabrifolia* suggest a relationship with *Rhachithecium*. The upper leaf cells of *Rhachithecium* can be either smooth (*R. perpusillum*, and *R. welwitschii*), mamillose (*R. nipponicum*) or unipapillose (*R. papillosum*). The strong papillae of upper leaf cells of *O. scabrifolia* are similar in shape and size to those of *R. papillosum* (Williams) Wijk & Marg. (Fig. 3.4; Williams 1914 and Iwatsuki & Sharp 1976 for illustrations of *R. papillosum*). Dixon (1936) also noticed that the peristome teeth in *Octogonella* are not split near the apex, and used this character to further support his new genus. *Rhachithecium perpusillum* and *R. welwitschii* have 16 peristome teeth that are fused in pairs except at tips (Crum 1956), but in *R. papillosum* the teeth appear to be either split (Williams 1914) or entire (Iwatsuki & Sharp 1976). The degree of fusion of the teeth thus fails to support both generic and specific distinction. Dixon (1936) also reported that "the ribs of the capsule are irregularly and minutely, but often quite markedly corrugate or papillose", yet, based on the only capsule I saw, the ribs appear to be smooth.

Octogonella scabrifolia is identical in gametophytic as well as sporophytic characters with *R. papillosum*. The latter was for long known only from the type locality in the Philippines until Iwatsuki and Sharp (1976) reported it from eastern India. The presence of this species is northern India (type of Octogonella) is thus not surprising even though it represents a noticeable range extension. This species is epiphytic and in the collection from northern India, the few stems of *R. papillosum* are found intermixed with a species of *Sematophyllum*.

3. *ULEASTRUM* Buck, Candollea 40: 203. 1985.

The genus *Uleastrum* Buck (=*Ulea* C. Müll.) was recently transferred by Zander (1993) from the Pottiaceae to the Orthotrichaceae. Chen (1941) had recommended excluding *Uleastrum* (then *Ulea* C. Müll.) from the Pottiaceae on the basis of its epiphytic habitat and peristome architecture, and further suggested placing it near *Rhachithecium* (then in the Orthotrichaceae). Gametophytic characters, such as leaf shape, lack of differentiated cauline epidermis, and differentiated perichaetial leaves point indeed toward a relationship with the Rhachitheciaceae, rather than the Orthotrichaceae, and I therefore propose removing *Uleastrum* from the Orthotrichaceae and include it in the Rhachitheciaceae. Robinson (1964) refrained from including *Uleastrum* (then *Ulea*) in the Rhachitheciaceae, because of the smooth capsule and the straight seta. With the inclusion in the Rhachitheciaceae of *Jonesiobryum* and *Tisserantiella* (Allen & Pursell 1991; Zander 1993), two genera with exclusively smooth capsules, ribbed urns no longer define the family. Furthermore, variation of this feature occurs within *Uleastrum*: *U. octoblepharis* has a curved seta, whereas the other species have a straight seta. *Uleastrum* is currently composed of four species distributed in two groups (Brotherus 1924): one including *Uleastrum nitidum* (Thér.) Zander, *U. palmicola* (C. Müll.) Zander, and *U. paraguense* (Besch.) Buck, and the other, restricted to *U. octoblephare* (Jaeg) Zander. Brotherus (1924) separated *U. octoblephare* on the basis of its dioicy, smooth laminal cells, obtuse leaves, curved seta, smooth calyptrae, undifferentiated annulus, smaller spores, split peristome teeth, and terricolous habitat. In addition, *U. octoblephare* differs from congeneric species by the presence of costal stereids, reddish-brown, isodiametric exothecial cells with strongly thickened distal periclinal walls, heavier thickening on the IPL than on the PPL, and 2:2 peristome formula (Tab. 3.2). All of these differences justify establishing a new genus for *U. octoblephare*. Since the generic type of *Uleastrum* is *U. paraguense* (Buck 1991), I propose the new genus *Zanderia* to accommodate *U. octoblephare*.

4. ***ZANDERIA*** Goffinet **gen. nov.**

Type: *Zanderia octoblepharis* (Spruce ex. Jaeg) Goffinet **comb. nov.**

Spruceella C. Müll., Gen. Musc. Fr. 396, 1900, hom. illeg. non Pierre, 1890. Type: *Spruceella octoblepharis* C. Müll.

Planta terricola, dioica, 3.0 mm alta. Folia lingulata ad spathulata. Cellulae basilares subquadratae ad rectangulae lucidae, superiores subquadratae, laevis. Capsulae exsertae, cylindricae, laeviae. Peristomium simplex. Cellulae exothecii rubrae, quadratae ad hexagonae, tenuis. Sporae 6-8 μm latae, granulosa.

Zanderia octoblepharis (Jaeg.) Goffinet **comb. nov.** (Figs. 3.5-6)

Pottia octoblepharis Jaeg., Ber. S. Gall. Naturw. Ges. 1871-1872: 343, 1873. *Ulea octoblepharis* (Jaeg) C. Müll,. Hedwigia 37: 234, 1898. Type: "Amerika austral. in terra arenosa rubra ad flora Amazonum p. Santarem in locis umbrosis, *Spruce 163*" (holotype—NY!; isotypes—NY!). *Uleastrum octoblephare* (Jaeg.) Zander, Bull. Buffalo. Soc. Nat. Sci. 32: 277, 1993.

Plants to 3 mm high, green, orthotropic, acrocarpous. Stem sympodially branched, composed of wide lumened, thick-walled cells throughout, epidermal cells not differentiated, central strand lacking. Leaves spreading when moist, erect to spreading, crisped when dry, lingulate-spathulate, acute to obtuse, 0.5-1.5 mm long, 0.2-0.6 mm wide, with largest leaves rosette-like at apex, smaller leaves below, margins incurved clasping in bottom third, plane above, entire. Costa ending 1/10 to 1/4 below apex, in transverse section with adaxial guide cells, median stereids, and abaxial substereids. Basal cells differentiated in lower third or half, hyaline, subquadrate to mostly long rectangular, 24-60 µm long, 15-28 µm wide, with thick-walls, smooth. Upper cells green, short, subquadrate to isodiametric, hexagonal, 8-16 µm long, 6-14 µm wide, thick-walled, flat, smooth. Dioicous, perichaetia terminal, paraphyses present, perichaetial leaves spathulate, to 1.5 mm long and 0.6 mm wide, erect crisped when dry and erect spreading when moist, the inner ones lanceolate, erect sheathing, to 0.7 mm long, cell architecture as in vegetative leaves. Perigonia not seen. Seta not twisted, curved downward when dry and erect when moist, 1.5 mm long, composed of a cylinder of wide lumened cells with evenly thickened walls, outer cells with eccentric thickening, lumen very narrow, confined in transverse section to proximal end of cell; central strand present. Capsules 0.8 mm long, 0.3 mm wide, smooth, cylindric; exothecial cells quadrate to hexagonal, with thin anticlinal walls and very thick outer periclinal wall; stomata superficial, few, restricted to the base of urn, neck not differentiated. Operculum conical, long and obliquely rostrate. Peristome single, of 16, lanceolate endostome teeth fused into eight pairs, split at apex, erect when moist, incurved when dry, yellowish, 160-180 µm long, to 50-60 µm wide near base, thickening heavier on the IPL than on the PPL, with arachnoid ornamentation on both surface, smooth and thin along median vertical walls on either side, IPL thickening further thinning in center of tooth, giving fenestrate appearance. Calyptrae smooth, cucullate. Differentiated annulus lacking. Spore 6-8 µm in diameter, finely granulose.

The new genus is named in honor of Dr. Richard Zander for suggesting the generic distinction of *Uleastrum octoblepharis* (Zander 1993).

The closest systematic affinities of *Zanderia* are not clear. Considering the number of differences with *Uleastrum*, the sister group of *Zanderia* may need to be sought for elsewhere in the Rhachitheciaceae. The subquadrate exothecial cells are known besides in *Zanderia* only from *Tisserantiella pulchella* (Thér. & Hilp.) Zander, which also lacks a differentiated annulus. This African species, however differs by its papillose laminal cells, a rather globose to cup-shaped urn, pale exothecial cells, and a gymnostomous capsule (holotype—PC!). A weak costa similar to that of *Zanderia* is also present in *Rhachithecium*, which also includes a species with smooth laminal cells. The latter differs however by the shape of the urn, of the exothecial cells, and peristome architecture. The excentric thickening of the outer cells of the seta separates *Zanderia* from *Uleastrum* and is further found in *Hypnodontopsis*, *Rhachitheciopsis*, *Rhachithecium* (see above). Frahm and Frey (1987) studied the twisting mechanism in the cygneous seta of the genus *Campylopus*, and concluded that the rotation of the seta upon moistening or during drying, was due to the presence of three distinct layers in the cell wall. The curved seta of *Zanderia* may similarly be correlated to the presence of epidermal cells with asymmetric thickening in the distal portion of the seta, considering that species of *Uleastrum*, that all have straight setae, have outer cells with evenly thickened walls. Whether the differential thickening of epidermal cells below the urn, common to the Rhachitheciaceae with curved seta, indicates common ancestry remains speculative. The genera of the Rhachitheciaceae express a wide range of gametophytic and sporophytic character transformations, and even within the genus *Tisserantiella sensu* Zander (1993), the divergence between species is such that the monophyly of the genus could be seriously questioned. Differentiating between patristic and homoplastic distances separating the genera, is furthermore hampered by the uncertainty regarding the sister-group of the Rhachitheciaceae. Except for *R. perpusillum*, all species currently known from the Rhachitheciaceae are narrow endemics, with little or no overlap in their ranges. The transatlantic (*Jonesiobryum*), transpacific (*Hypnodontopsis*), or pantropical (*Rhachithecium*) distribution of the genera, correlated with high phenetic distances between them, may be a strong indication of an ancient origin and early diversification of the family.

5. ***JONESIOBRYUM*** Bizot & Pócs *ex* Allen & Pursell, The Bryologist 94: 441 (1991)

Jonesiobryum sphaerocarpum Bizot *ex* Allen & Pursell

The genus *Jonesiobryum* comprises three species, of which *J. sphaerocarpum* is the only paleotropical species. The genus has recently been transferred from the Funariaceae to the Rhachitheciaceae (Allen & Pursell 1991). It is easily distinguished from related genera by immersed capsules. While studying specimens of *Rhachitheciopsis tisserantii*, I came across a collection with immersed capsules and scarcely differentiated perichaetial leaves, characters reminiscent of the genus *Jonesiobryum*. Based on Vital (1983) and Allen and Pursell (1991), the specimen keys to *J. sphaerocarpum*. This species was previously thought to be restricted to a single locality in Nigeria, West Africa. The present specimen was collected early this century from the Central African Republic, and represents only the second collection of this species. This major westward range extension across the continent may suggest that the species is actually more common across the west African plains. The habitat of this second collection agrees well with that of the type (Bizot et al. 1974): both specimens were collected on trees in savanna woodlands.

Specimen examined: Central African Republic, "s/arbre, savanne boisée, environs des Sabangas, 80 km N Bambari, 20 juin 1927. *Tisserant 334* (PC—herb. Potier de la Varde).

Artificial key to the seven genera of the Rhachitheciaceae.

1\. Capsule immersed, seta shorter than urn .... *Jonesiobryum*
1\. Capsule emergent or exserted, seta longer than urn 2
  2\. Peristome lacking .... *Tisserantiella*
  2\. Peristome present 3
3\. Peristome with dorsal trabeculae 4
3\. Peristome without trabeculae 5
  4\. Stem with central strand, perichaetial leaves conspicuously differentiated, sheathing, operculum short-rostrate, spores pitted .... *Rhachithecium*
  4\. Stem lacking central strand, perichaetial leaves undifferentiated, spreading, operculum flat, spores striate .... *Rhachitheciopsis*
5\. Longitudinal thickenings present on outer surface of peristome teeth .. *Hypnodontopsis*
5\. Longitudinal thickening lacking, outer surface smooth 6
  6\. Laminal cells smooth, dioicous, urn reddish-brown, and seta curved ....*Zanderia*
  6\. Laminal cells papillose, autoicous, urn pale, seta erect ....*Uleastrum*

Systematic affinities of the Rhachitheciaceae.

The Rhachitheciaceae have been placed historically in or near the Orthotrichaceae (Brotherus 1924; Robinson 1971; Crosby 1980; Vitt 1982, 1984; Walther 1983; Crum 1993). The peristome of the Rhachitheciaceae differs from the typical orthotrichaceous peristome (Shaw 1985; Lewinsky 1989) in that it is at the most, composed of a single row of teeth. Except in *Zanderia*, the inner layer of cells contributing to the teeth is composed of only eight cells, while 16 cells compose the outer layer. This 2:1 peristome is difficult to reconcile with a 4:2 exostome architecture found in all arthrodontous mosses (Edwards 1984; Shaw et 1989a; Schwartz 1994) including those species that lack an exostome at maturity (Edwards 1979; Shaw et al. 1989b). Alternatively, if the single peristome of the Rhachitheciaceae is an endostome, the outer layer composed of 16 cells would be consistent with the pattern observed for the PPL (Edwards 1979, 1984). In *Hypnodontopsis mexicana, Rhachitheciopsis tisserantii,* as well as *Uleastrum palmicola,* the basal portion of the outer surfaces of the teeth are covered by a smooth membrane (Figs. 3.2a; 3.3a, c) that is hardly visible under the light microscope. This outer membrane is composed of 4 cells per tooth pair. If the teeth are derived from the IPL and PPL, then the formula becomes 4:2:1, and the outer "membrane" represents a reduced OPL. Diplolepideous peristomes reduced to the endostome are known from other mosses (e.g., *Dichelodontium nitidum,* Magill 1987). Whether the endostome of the Rhachitheciaceae represents a reduced diplolepideous or haplolepideous peristome cannot be determined based on the peristome formula, because the 4:2:1 cell pattern would be atypical for either the diplolepideous or the haplolepideous peristome.

When Edwards (1979) critically examined cell patterns of haplolepideous peristome teeth, he found that "a number of haplolepideous species ..... possess a distinctive type of double peristome." The *Seligeria*-type peristome as he called it, is characterized by an endostome that has strong dorsal trabeculae, and an exostome that "adheres to the margins of these as a thin membrane." This endostome architecture is very similar to that found in *Rhachitheciopsis* and *Rhachithecium,* except that in the *Seligeria*-type peristome the IPL is composed of 24 cells, instead of 8. This haplolepideous peristome type is further defined by little or no thickening on the ventral layer, a situation also present in *Rhachitheciopsis, Rhachithecium,* and *Uleastrum,* where the horizontal divisions of the IPL appear very faint in light microscopy. Except for lacking the reduced OPL, the peristome architecture of *Zanderia* (i.e., a x:2:2 pattern) is similar to that of *Venturiella* (Erpodiaceae), a genus Edwards (1979) tentatively also linked to the group defined by the *Seligeria*-type peristome. This peristome type is further found in *Glyphomitrium* (Ptychomitriaceae), a genus (particularly the Asian species *G. humillimum* (Mitt.) Card., and *G. minutissimum* (Okam.) Broth.) with considerable resemblance to the Rhachitheciaceae (Robinson 1964). Robinson (1964) refrained to include *Glyphomitrium* in the Rhachitheciaceae because it lacks the "distinctive seta or plications in the capsule", an argument that no longer holds considering the current circumscription of the family (see above). Churchill (1981) excluded *Glyphomitrium* from the Grimmiaceae (including the Ptychomitriaceae), but was unable to ascertain an alternative systematic position.

Whether the *Seligeria*-type-peristome defines a natural group or not remains to be addressed. Peristome features alone may be misleading in addressing familial relationships (Buck 1991), but considering that the Rhachitheciaceae and the Seligeriaceae occupy very different habitats (trees versus rocks) it is unlikely that different selection pressures associated with these habitats would have resulted in nearly identical peristome architectures. The peristome of the Rhachitheciceae, which is atypical among diplolepideous mosses, is very similar to that of certain haplolepideous taxa may be seen as a strong indication of the haplolepideous nature of the Rhachitheciaceae. This hypothesis is currently being tested using molecular data.

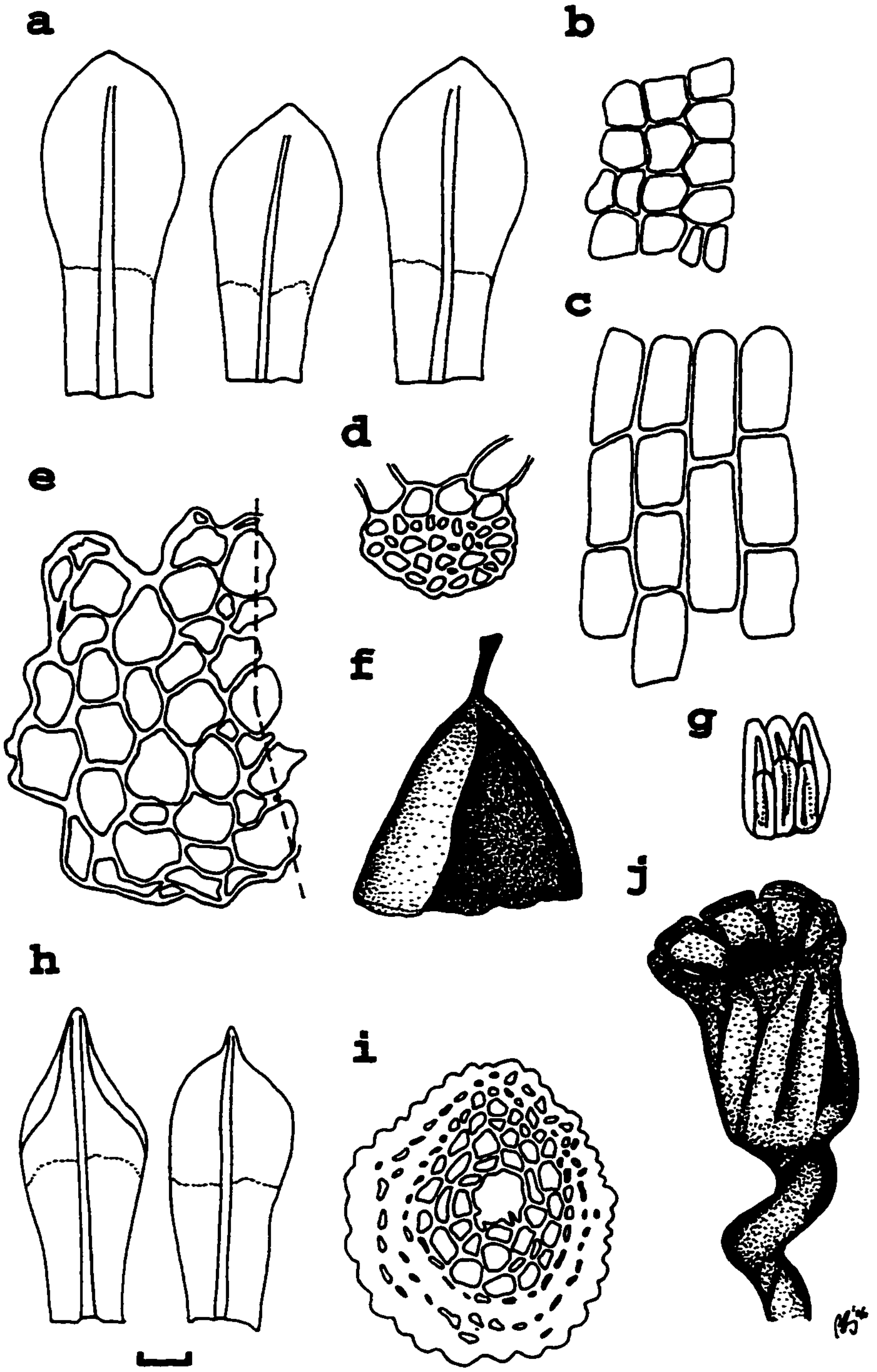

Figure 3.1a-j. *Rhachitheciopsis tisserantii.* a. Vegetative leaves. - b. Upper laminal cells. - c. Basal laminal cells. - d. Transverse section of costa at midleaf. -e. Transverse section of stem. - f. Calyptrae. - g. Annulus. - h. Perichaetial leaves. - i. Transverse section of seta immediately below the urn. - j. Capsule, habit when dry (Tisserant 247—PC). Scale bar = 0.2 mm (a, f, h), 20μm (b, c, d, e, g, i) and 70μm (j). (lectotype—PC unless otherwise noted)

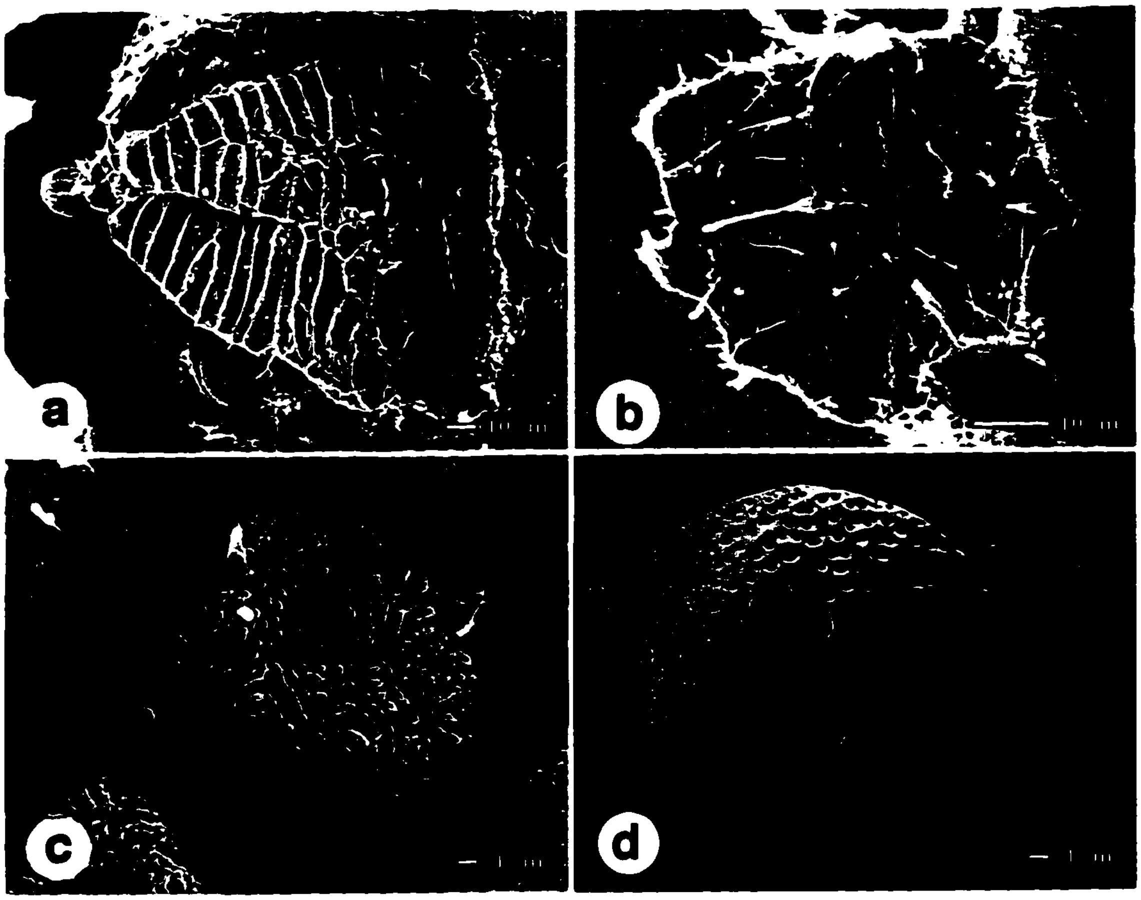

Figure 3.2. a-c. Morphology of *Rhachitheciopsis tisserantii* and *Rhachithecium perpusillum* a-c. *Rhachitheciopsis tisserantii* (lectotype-PC).
— a. Outer surface of tooth pair. — b. Inner surface of tooth pair. — c. Spore.
— d. *Rhachithecium perpusillum* (Chang Jinkun 1748-3—ALTA); spore.

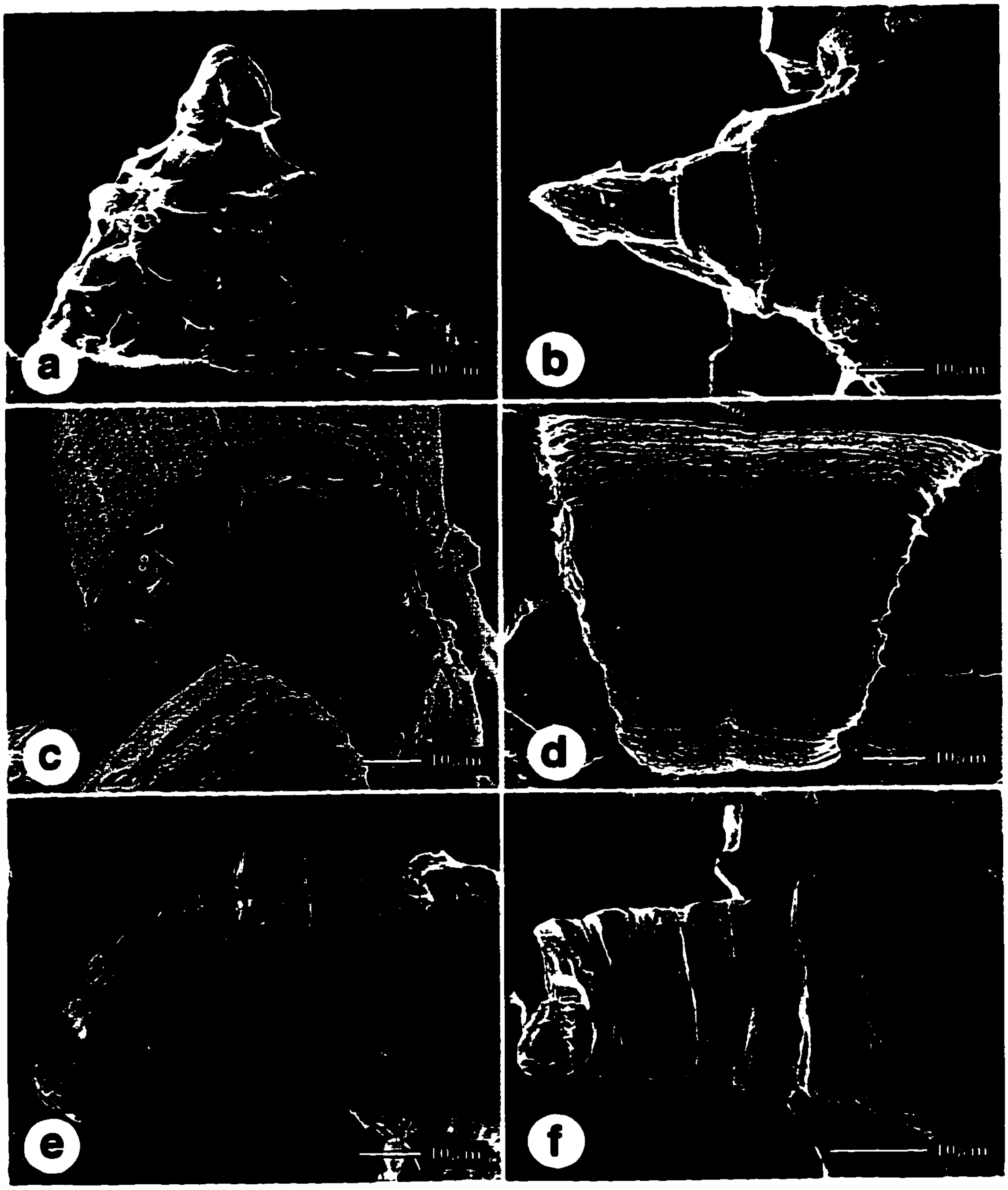

Figure 3.3. a-f. Morphology of peristome teeth in the Rhachitheciaceae. a-b. *Uleastrum palmicola* (Vitt 21162-ALTA). — a. Outer surface of tooth pair.
— b. Inner surface of tooth pair. c-d. *Rhachithecium papillosum* (holotype-NY)
— c. Lateral view of peristome tooth; arrow points to OPL membrane at base of tooth.
— d. Inner surface of tooth pair. e-f. *Hypnodontopsis mexicana* (Arsène 4793-NY)
— e. Outer surface of tooth pair; arrow points to OPL membrane at base of tooth.
— f. Inner surface of tooth pair.

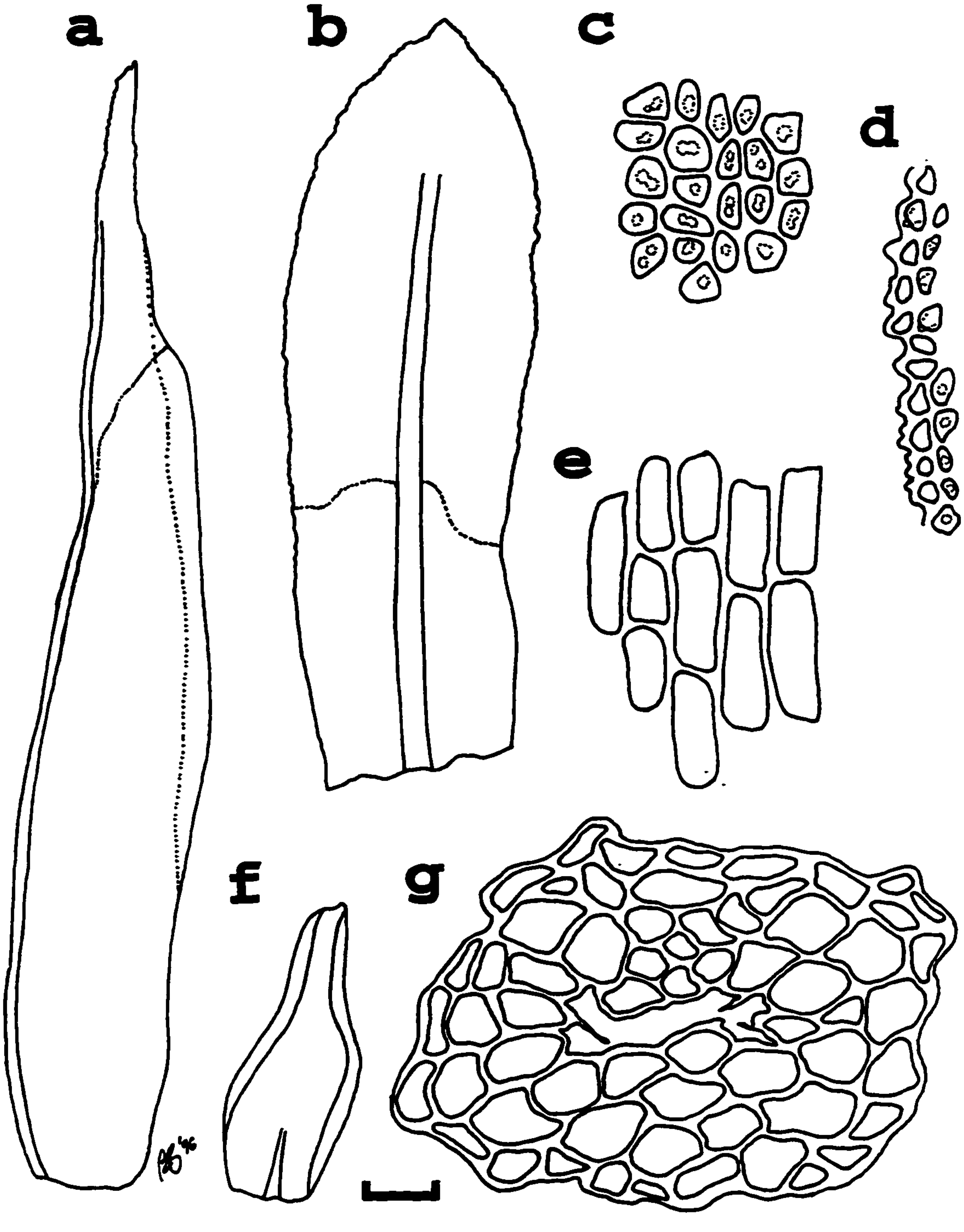

Figure 3.4. *Rhachithecium papillosum* (*Octogonella scabrifolia*: holotype—BM). - a. Vegetative leaf. - b. Upper laminal cells. - c. Basal laminal cells. - d. Longitudinal view of upper laminal cells. e. Innermost perichaetial leaf. - f. Perigonial leaf. - g. Transverse section through stem. Scale bar = 0.2 mm (a, e, f), and 20μm (b, c, d, g).

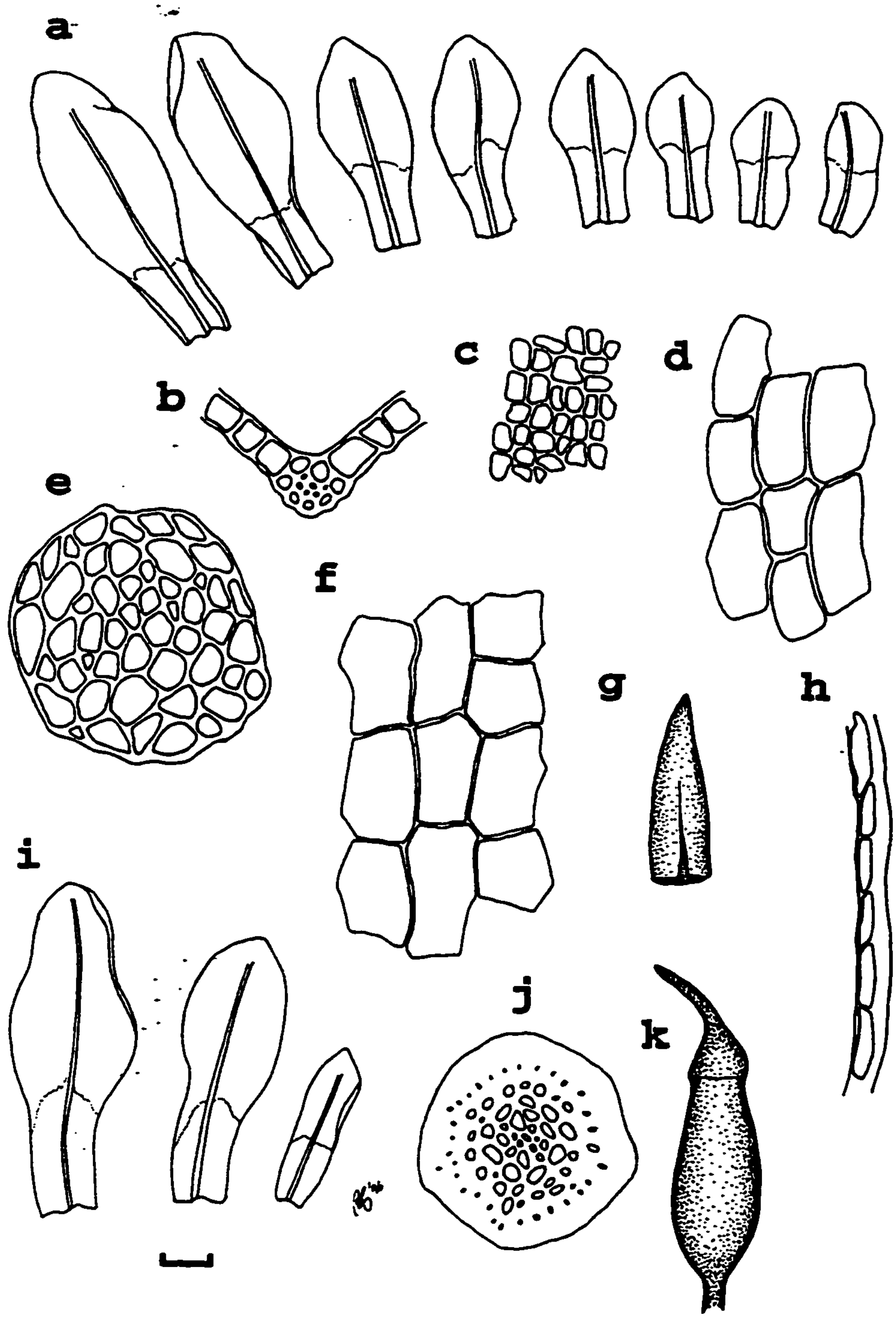

Figure 3.5. *Zanderia octoblepharis* (holotpye—NY). a. Vegetative leaves (left to right: from base to apex of stem). -b. Transverse section of the leaf. - c. Upper laminal cells, - d. Basal laminal cells. - e. Transverse section of the stem. - f. Exothecial cells. - g. Calyptrae. - h. Transverse section of exothecial cells (outer surface-right). - i. Perichaetial leaves. - j. Transverse section of seta. - h. Capsule, habit. Scale bar = 0.2 mm (a, g, i, k), and 20µm (b, c, d, e, f, h, j.).

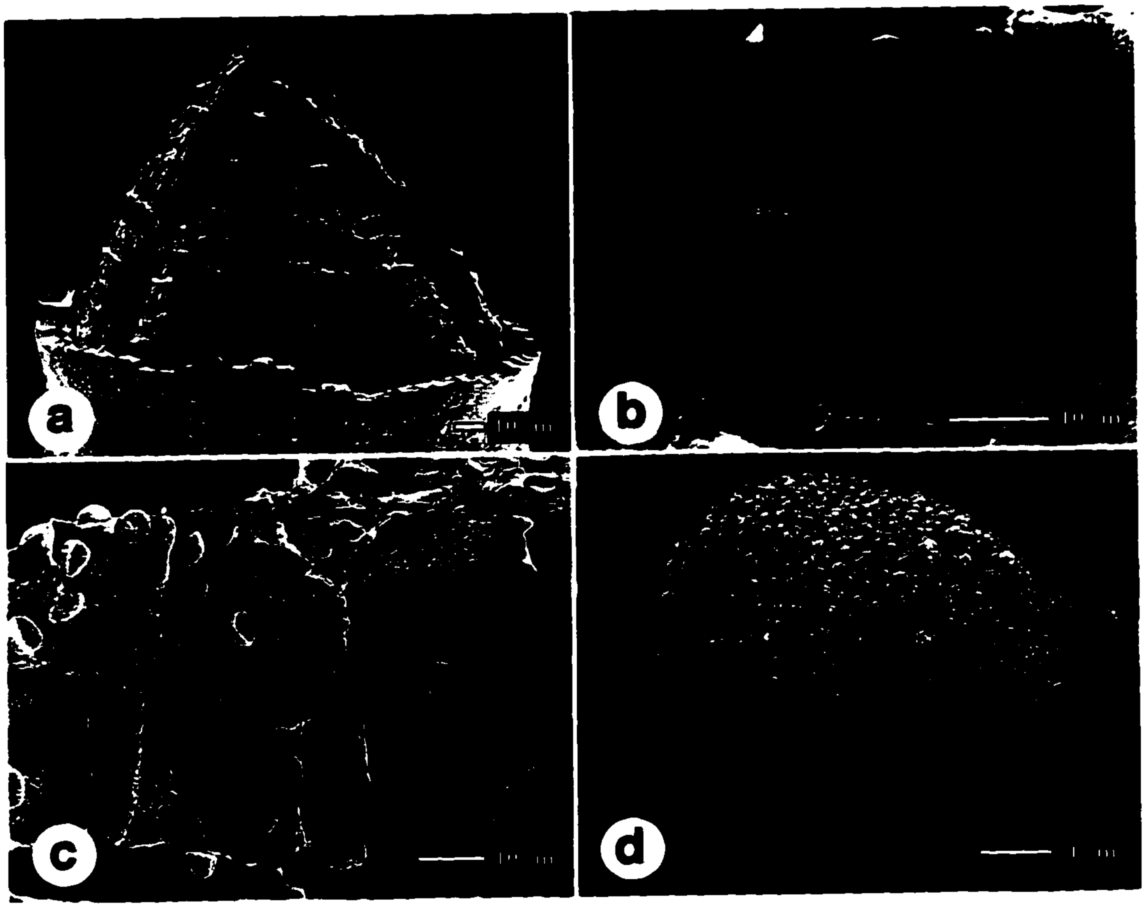

Figure 3.6. a-d. *Zanderia octoblepharis* (holotype—NY).
— a. Peristome, habit.
— b. Outer surface of tooth pair.
— c. Inner surface of tooth pair.
— d. Spore.

Table 3.1. Morphological characteristics separating the genera *Rhachitheciopsis* and *Rhachithecium*.

	Rhachitheciopsis	*Rhachithecium*
Cauline central strand	absent	present
Costal abaxial cells	to 5 layers	2 layers
Perichaetial leaves	erect-spreading	erect-sheathing
Calyptrae	smooth	papillose
Annulus	biseriate	uniseriate[1]
Spores	striate	pitted
Operculum	flat	short rostrate

[1] Except for *R. braziliense* which is illustrated by Brotherus (1925, p. 16) with a double annulus.

Table 3.2. Morphological characteristics separating the genera *Zanderia* and *Uleastrum*.

	Zanderia	*Uleastrum*
Upper laminal cells	smooth	papillose
Guide cells	adaxial	median
Costal stereid	median	not differentiated
Sexual condition	dioicous	autoicous
Exothecial cells: shape	irregular-isodiametric	rectangular
anticlinal walls	thin-walled	thick-walled
outer periclinal wall	evenly thickened	collenchymatous
colour	red-brown	pale brown
Peristome	2:2	2:1
	teeth splitting at apex	teeth fused to apex
	"fenestrate" due to thinner areas on IPL	thickening continuous
	IPL>PPL	IPL<PPL
Spore	<10 µm	>15µm
Seta	curved	erect
Epidermal cells of seta	thickening excentric	even all around
Annulus	absent	present
Habitat	terricolous	epiphytic

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Chapter four

Cardotiella elimbata (Thér.) Goffinet *comb. nov.*, and the significance of dorsally uniseriate endostome segments in the Orthotrichaceae[1]

The flora of Madagascar and the Mascarenes includes nearly 1100 moss taxa (Kis 1985) and includes many endemics. Among orthotrichaceous genera, three are particularly well represented: *Cardotiella* Vitt, *Macromitrium* Brid., and *Schlotheimia* Brid. While the latter two genera have diversified throughout the tropics, only one species of *Cardotiella* is known outside south-eastern Africa and East African Islands. The predominantly neotropical genus *Groutiella* Steere is represented on Madagascar by two species - *G. laxo-torquata* (Besch.) Wijk & Marg. and *G. elimbata* (Thér.) O'Shea (Crosby et al. 1983). The latter species was initially described in 1929 by Thériot as *Micromitrium elimbatum* and subsequently transferred to *Groutiella* (a new name for the illegitimate homonym *Micromitrium* Schimp.) by O'Shea (1995) as previously suggested by Crosby et al. (1983). Examination of the holotype, the only known collection of *Micromitrium elimbatum*, indicates that this species differs from congeneric taxa not only by the lack of a well developed border in the lower portion of the leaf, but also by the presence of conspicuous decurrencies of large, hyaline cells, small upper leaf cells, and non-plicate calyptrae (Fig. 4.1e, h, & l). All of these characters suggest an affinity with species of *Cardotiella*, a genus to which *M. elimbatum* Thér. is therefore transferred.

CARDOTIELLA ELIMBATA (Thér.) Goffinet, *comb. nov.* (Figs. 4.1-3)

Micromitrium elimbatum Thér., Recueil. Publ. Soc. Havraise Études Diverses. 1929-1930: 113. 1929. Type: "Madagascar, Province de Farafangana, Ifandana, sur souche d'arbre, en forêt. leg. R. Decary," 8.9.1926 (holotype, PC!; isotype, S).

Groutiella elimbata (Thér.) O'Shea, Trop. Bryol. 10: 95. 1995.

Plants reddish brown, plagiotropic, cladocarpous. Stem monopodially branching, pentagonal in transverse section, composed of a cylinder of wide, thick-walled cells surrounded by a bi- to tristratose epidermis of narrow thick-walled cells, central strand lacking. Rhizoids orange-red, smooth, abundantly branched, commonly originating from the abaxial surface of costa of both stem and branch leaves. Stem leaves ovate-

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[1] A modified version of this chapter has been accepted for publication in The Bryologist 99 (4), 1996.

lanceolate, widest just above insertion, 1.00-1.45 mm long, 0.40-0.65 mm wide, flexuose when dry, widely spreading when moist, decurrent, weakly apiculate, costa with an adaxial row of guide cells and several abaxial rows of stereids, prominent, orange-red, ending below apex, margin recurved in lower half, plane above. Upper and median laminal cells subquadrate, pentagonal, or slightly elongate, smooth except for scattered unipapillose juxtacostal cells, thick-walled, in irregular rows. Basal laminal cells isodiametric to elongate, smooth except for a few marginal unipapillose cells above decurrency, thick-walled. Decurrencies composed of up to six rows of hyaline, moderately thick-walled cells, with outer ones strongly bulging. Branch leaves ovate-lanceolate, widest above insertion, 1.30-1.75 mm long, 0.40-0.50 mm wide, flexuose-contorted when dry, widely spreading when moist, decurrent, weakly apiculate, costa with adaxial row of guide cells and several abaxial rows of stereids, prominent, reddish, ending well below apex, margin narrowly recurved at least in lower half, plane above. Upper and median laminal cells subquadrate, pentagonal, or slightly elongate throughout except for ± oblate cells near base, 5-10 µm in diameter, smooth except for some, mostly adaxially, unipapillose cells particularly along costa, evenly thick-walled, mostly in irregular rows. Upper marginal cells forming discontinuous and indistinct border of elongate cells twice as long as wide. Basal laminal cells rectangular to elongate, 10-45 µm long, 6-10 µm wide, smooth except for a few marginal unipapillose cells above decurrency, thick-walled. Decurrencies composed of up to six rows of hyaline, quadrate, rectangular, or elongate, moderately thick-walled cells, outer ones strongly bulging. Axillary hairs two per leaf axil, to 170 µm long, basal cells quadrate, brown, smooth; upper 2-5 cells rectangular, hyaline, smooth to verrucose. Dioicous? Perichaetia terminal on erect, lateral branches, perichaetial leaves narrowly lanceolate, 1.4-2.0 mm long, 0.30-0.35 mm wide, flexuose from erect base. Seta to 11 mm long, erect, slightly twisted to the left, composed of narrow epidermal cells grading into wider central cells, walls yellow, thick throughout except near center, thin-walled cells often collapsed; differentiation of central strand seemingly absent at the level of vaginula. Vaginula naked or with few paraphyses and archegonia in upper half, composed of bistratose layer of narrow, thick-walled epidermal cells surrounding a multistratose layer of thick-walled wide lumened cells. Operculum conic, long rostrate, to 1.3 mm long. Capsule erect, eight-ribbed, yellow to brown; urn ovoid, to 2 mm long; neck well differentiated, to 1 mm long. Exothecial cells thick-walled, more or less rectangular, to 3 times longer than wide except for oblate cells forming rim and elongate cells along the edges of ribs. Stomata superficial, few, restricted to neck. Peristome double (4:2:4); exostome consisting of 8, long, lanceolate teeth splitting near apex, often truncate, yellow, to 400 µm long, strongly recurved when dry, erect when moist, OPL thick, densely papillose proximally and striate distally, PPL thin, horizontally striate-papillose proximally and vertically striate-papillose distally; endostome of 16, slender, linear, hyaline segments, these to 400 µm long and 40 µm wide near base, erect, inflexed, IPL horizontally striate on the contiguous basal cells, vertically striate above, PPL thin, smooth throughout, wall remnants shortly protruding or embedded in the PPL thickening. Spores isomorphic, 14-18 µm in diameter, irregularly-striate papillose. Calyptra smooth, lobed, to 2.8 mm long, naked or sparsely hairy; hairs erect, uni- or biseriate, smooth, composed of rectangular, thick-walled cells.

The genus *Cardotiella* now includes six species of which four are endemic to the East African islands (Crosby et al. 1983; Vitt 1981). *Cardotiella* is well marked from other orthotrichaceous genera by the leaf decurrencies composed of "inflated, bulging, tuberculate, hyaline cells" and the lobate, non-plicate calyptrae (Vitt 1981) with the latter characters suggesting a close relationship to *Schlotheimia* (Vitt et al. 1995). Additionally, all species have papillose upper leaf cells except for *C. renauldii* (Broth.) Vitt, a narrow endemic known from only the type specimen collected on Madagascar. Overall, *Cardotiella elimbata* is similar to *C. renauldii*, particularly in the predominantly smooth laminal cells, the indistinct border in the upper part of the leaf, and the flexuose rather than secund branch leaves, but differs in at least two gametophytic characters - scattered papillae on both surfaces of the upper lamina, and naked vaginulae. In *C. renauldii*, the laminal cells are smooth throughout the leaf (except for the basal marginal cells) while scattered cells with a single papillae, mostly on their adaxial surface only, are consistently found along the costa and across the lamina in the upper portion of the leaf in *C. elimbata* (Fig. 4.1c, f). *Cardotiella renauldii* further differs from *C. elimbata* by the abundant multiseriate hairs on the vaginula. The type collection of *C. elimbata* is abundantly fruiting and the vaginulae are naked, except for the presence of a few paraphyses and archegonia in the upper half. *Cardotiella elimbata* also resembles *C. subappendiculata*, which can however, be distinguished by its uniformly unipapillose cells, plane margin, larger spores, and distinctly biseriate dorsal surface of the endostome (see below).

When Vitt (1981) proposed the genus *Cardotiella*, the sporophyte was known for only a single species, *C. subappendiculata* (Broth.) Vitt. In this species, the peristome is composed of eight teeth and eight segments. Recently, Van Rooy and Van Wyk (1992) described the peristome for another species, *C. secunda* (C. Müll.) Vitt, and confirmed the peristomial architecture for the genus, except that in that species the endostome is composed of 8 to 16 segments. In both species the segments alternate with the teeth and possess on their PPL surface the median vertical wall characteristic of diplolepidous alternate peristomes. In *C. elimbata*, the presence of the median vertical wall as well as the horizontal walls can be demonstrated only with the use of the SEM. The PPL layer is thinner than the IPL and the anticlinal wall remnants of the PPL hardly emerge above the general surface of the PPL and are even most often not protruding at all (Figs. 4.2e, 3a, b).

Segments with a smooth PPL surface lacking anticlinal wall remnants have also been reported in *Florschuetziella* Vitt (Vitt 1979, 1981) and *Pleurorthotrichum* Broth. (Lewinsky 1994; Shaw 1986). In *Florschuetziella scaberrima* (Broth.) Vitt, the presence of "partial outer vertical and horizontal walls" on the lowermost portions only, of the outer surface of the some segments suggests "a reduction in the outer layer" in the median and upper portions of the segments (Vitt 1981). In *F. steerei* Vitt, light microscopical observation suggests the complete absence of anticlinal wall remnants on the dorsal surface of the segments, while SEM reveals the presence of a median vertical line and alternating horizontal lines (Fig. 4.3c). These lines are not apparent throughout the dorsal surface of the segment. Walls associated with these lines hardly protrude above the surface; the lack of lines in some portions of the segments is interpreted as a strong resorption of the wall remnants and their embedding in the PPL thickening. A lateral view of the segments clearly reveals the presence of a PPL thickening, that is much thinner than that of the IPL (Fig. 4.3d). Shaw (1986) interpreted the endostomial architecture in *Pleurorthotrichum chilense* Broth. as possibly resulting from "a reduced number of divisions in the primary peristomial layer, or a displacement of the anticlinal wall that forms the vertical line". The first explanation would require the loss of every PPL division since none of the 16 segments has a median vertical wall on the dorsal surface. The loss of anticlinal divisions matching the plane of division of the OPL would have to be compensated by the presence of other divisions. Examination of the ventral surface of the exostome teeth of the holotype (H-Broth!) reveals the presence of 16 divisions in PPL. The plane of each division is aligned with the vertical plane of the division of the OPL that separates two consecutive teeth. For the PPL divisions to be displaced, yet still be alined with the marginal vertical walls of each tooth, would require the breakdown between two teeth to be displaced by one cell. While these modifications would result in the lack of a median vertical wall on the dorsal surface of the segments, they would also lead to an opposite placement of the segment, which is clearly not the case. My own observations, based on a well developed peristome on half a capsule still attached to the gametophyte, suggest that a vertical wall is present on the PPL surface of the segment. The walls, however, appear as faint lines under light microscopy and the use of the SEM reveals that they do not, or only scarcely, extend above the thin PPL thickening of the dorsal surface of the segment (Figs. 4.3e, f).

In orthotrichaceous taxa with well developed endostomes, the endostomial PPL thickening is typically thinner than the IPL one. A strong resorption of anticlinal wall remnants to or below the surface of the PPL could result in the walls being undetected in light microscopy, but not in SEM. In *C. elimbata*, *F. steerei*, and *P. chilense* the dorsal surface of the segments appears uniseriate unless they are examined in SEM. I therefore conclude that endostome segments in *C. elimbata*, *F. steerei*, and *P. chilense* are characterized by a strong resorption of anticlinal PPL walls, leaving these remnants to slightly emerge from the PPL thickening or even be completely immersed in it.

The endostome of *C. elimbatum* has some occasional aberrations in that certain segments are forked from a uniseriate base (Y-shaped) or fused and ending in a uniseriate portion (inverted Y-shape). These observations do not seem to have any taxonomic or developmental significance. The vertical anticlinal divisions on the IPL surface of the basal membrane are somewhat displaced and are not aligned with the PPL or the OPL planes of division. The segments are supported by either a single cell or are raised, straddling above two cells of the basal membrane. Apparently the cells between the segments are somewhat narrower than cells supporting the segments. Such asymmetry is well documented for several species of *Orthotrichum* (Lewinsky 1993) and is found in other Orthotrichaceous genera as well. The spores of *C. elimbata* are similar to those of *C. secunda* and *C. subappendiculata*: they are isomorphic, and irregularly-striate papillose (Fig. 4.2d). They are smaller than those of *C. subappendiculata* (14-18 µm vs 20-25 µm, Vitt 1981) and within the range of those of *C. secunda*, the spores of which are about 15-23 µm in diameter (Van Rooy 1990).

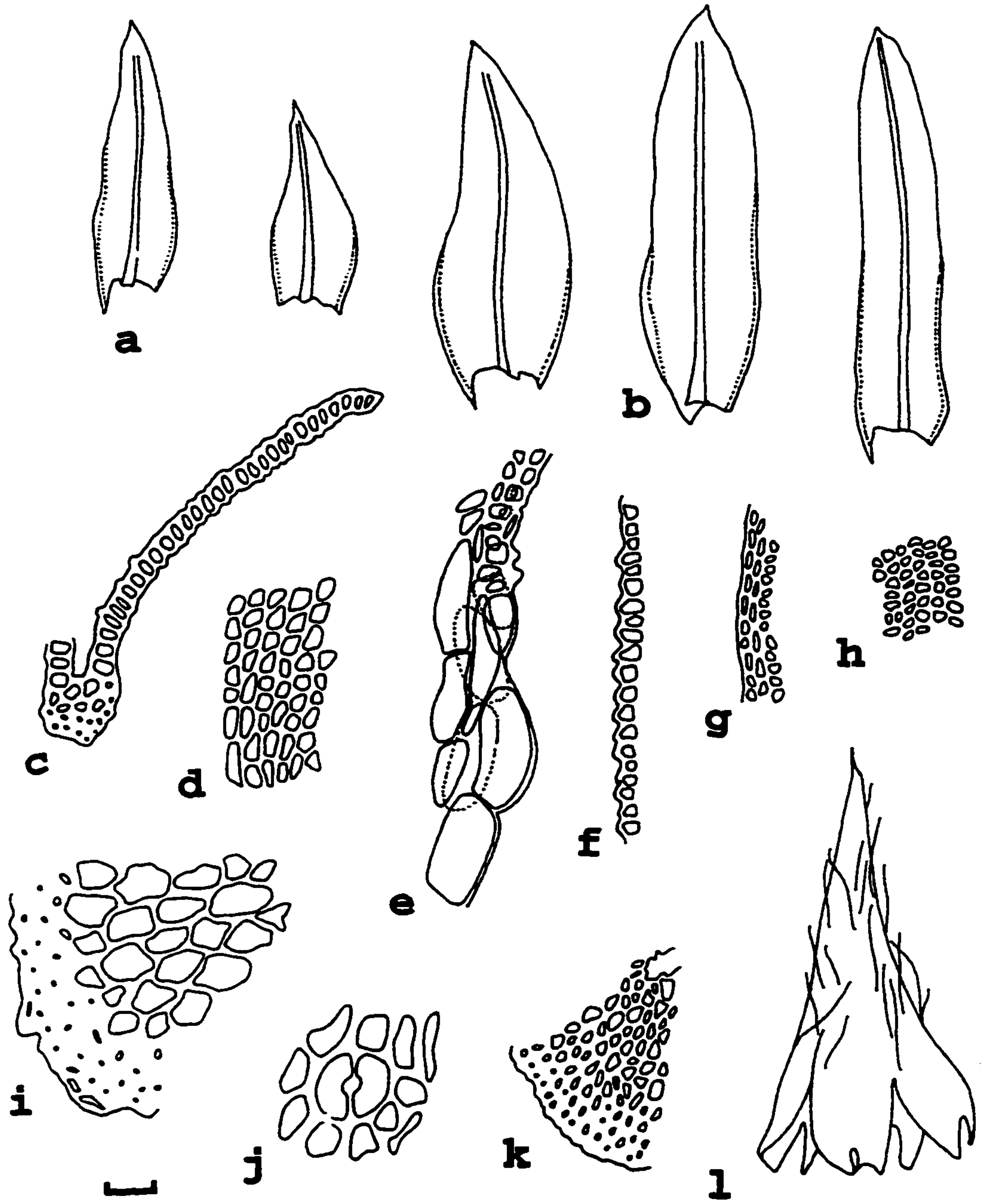

Figure 4.1. *Cardotiella elimbata* (holotype-PC). — a. Stem leaves. — b. Branch leaves. — c. Partial transverse section of branch leaf.— d. Basal cells of branch leaf. — e. Decurrent cells of branch leaf. — f. Longitudinal view of upper juxta costal cells of branch leaf. — g. Upper marginal cells of branch leaf. — h. Median upper laminal cells of branch leaf. — i. Partial transverse section of stem. — j. Stomata. —. k. Partial transverse section of seta. — l. Calyptra. (scale for a & b: .2 mm; for c-k: 20 μm; for l: .3 mm).

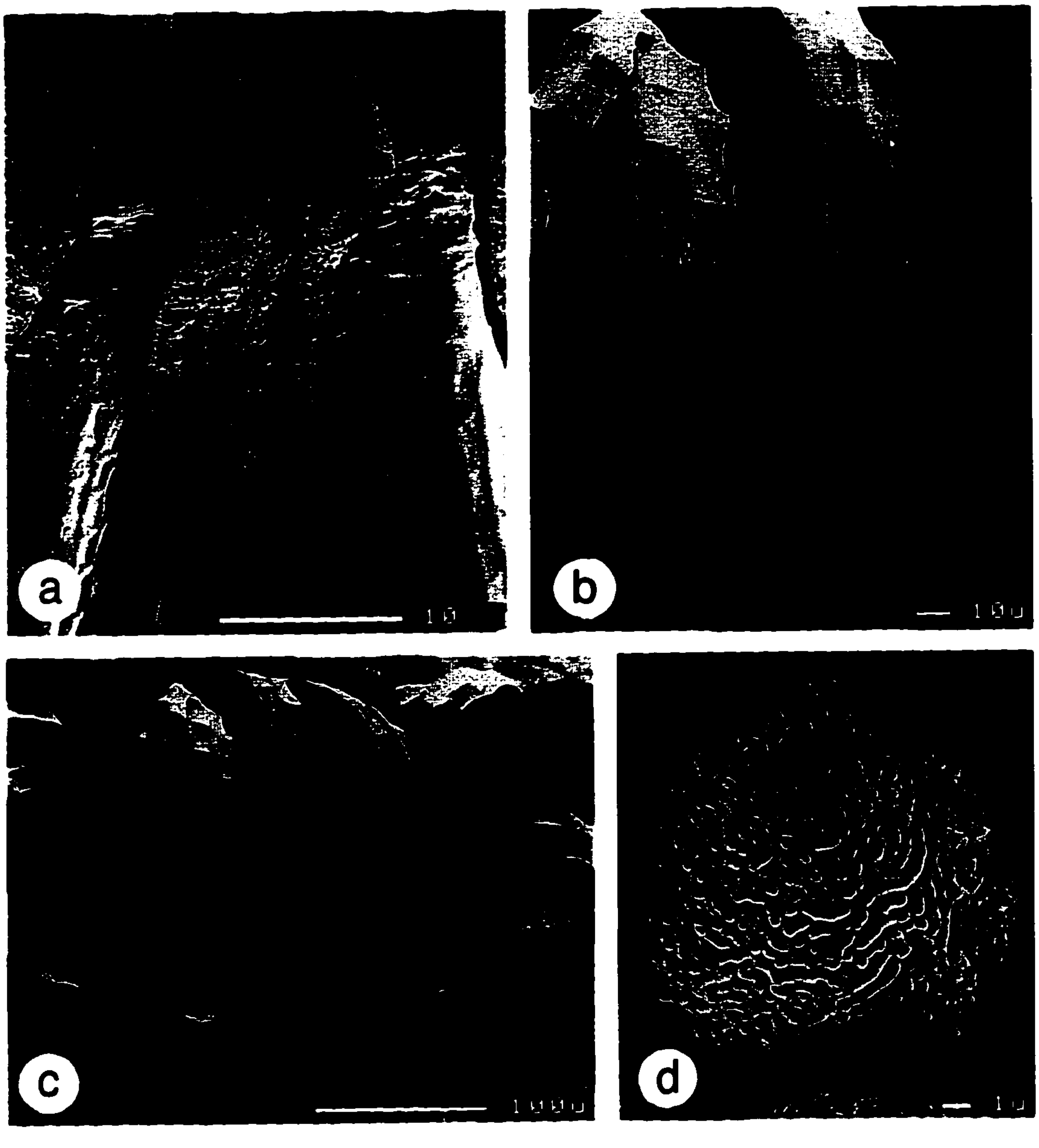

Figure 4.2. *Cardotiella elimbata* (holotype-PC).
— a. Ventral surface of exostome tooth.
— b. Dorsal surface of endostome segments.
— c. Outer view of endostome segments.
— d. Spore.

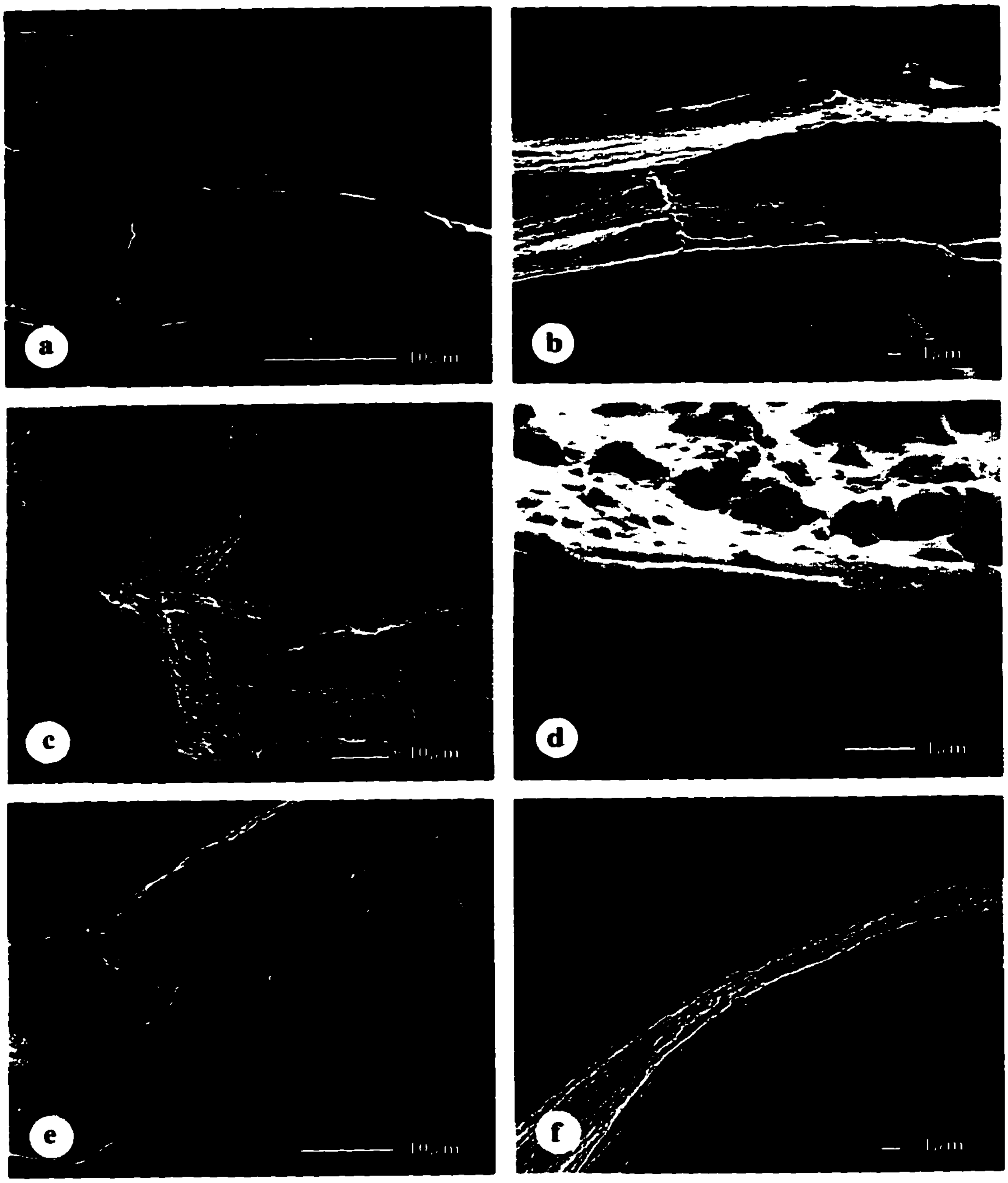

Figure 4.3. Architecture of endostome segments in *Cardotiella elimbata* (holotype, PC), *Florschuetziella steerei* (holotype, ALTA), and *Pleurorthotrichum chilense* ("part of the holotype used by Thériot when preparing the illustration for the original publication", label annotation by Lewinsky; H-Broth.). *C. elimbata* — a. Dorsal surface of endostome segment. — b. Oblique view of dorsal surface of endostome segment. *F. steerei* — c. Dorsal surface of endostome segment (the horizontal walls in the PPL are truly alternating, even though this pattern is less obvious toward the base of the segment). — d. Lateral view of endostome segment, PPL on top. *P. chilense* — e. Dorsal surface of endostome segment. — f. Lateral view of endostome segment, PPL on top.

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Chapter five

Circumscription and Phylogeny of the Orthotrichales inferred from *rbc*L sequence analyses

In arthrodontous mosses, the peristome teeth that line the mouth of the capsule and regulate spore dispersal, are made of cell wall remnants. Three concentric layers, namely the outer (OPL), the primary (PPL) and the inner (IPL) peristomial layer contribute to the teeth (Blomquist and Robertson, 1941). The number and the pattern of cell divisions occurring in these layers, particularly in the IPL, are central to the classification of arthrodontous mosses. Vitt (1984) recognized five types of articulate peristomes; four of these are diplolepideous and one is haplolepideous. The latter (or dicranaceous peristome type) is characterized by 1) a single row of teeth made from the proximal walls of the PPL and the distal walls of the IPL, and 2) by a strongly asymmetric "first-late" (sensu Schwartz, 1994) division in the IPL leading to a (4):2:3 cell pattern per eight of the peristome circumference (OPL:PPL:IPL; Edwards, 1979; Shaw, Mishler, and Anderson, 1989). The typical diplolepideous peristome consists of an additional row of teeth composed of proximal OPL walls and distal PPL walls. The flanged (or heterolepideous) peristome, partly composed of whole cells, and of additional intermediate exostome teeth (Edwards, 1984), characterizes the Encalyptineae, and is considered of diplolepideous affinities by Vitt (1984). In the *Funaria*-type peristome all divisions are aligned and the peristome formula is 4:2:4 (Shaw, Anderson, and Mishler, 1989; Schwartz, 1994). The bryaceous type is characterized by additional divisions in the IPL leading to the development of cilia in between the segments, the latter of which lie alternate to the exostome teeth (Shaw, Anderson, and Mishler, 1989). In the orthotrichaceous peristome, the thickening on the outer surface (OPL) of the exostome teeth is much heavier than on the inner surface (PPL), resulting in the teeth being recurved when dry. The divisions are typically aligned but the segments alternate with the teeth; the peristome formula is 4:2:4 (Lewinsky, 1989; Vitt, 1981a).

Crosby (1980) and Vitt (1981a) were the first to suggest that the haplolepideous peristome derived from a diplolepideous ancestor, but they disagreed with respect to the identity of this primitive diplolepideous peristome. Crosby (1980) and later Shaw and Rohrer (1984) suggested that the ancestral peristome was of the *Bryum*-type. The orthotrichaceous peristome, was consequently derived through reduction, a hypothesis also supported by Hedenäs (1994). Vitt (1984) argued that "the evolution of the peristome has not been uni-directional" and that the bryaceous peristome "is a totally separate evolutionary line than either the orthotrichaceous or haplolepideous divergences" from an ancestral funariaceous type (see also Vitt 1981a). More recently, Lewinsky (1989) argued in favor of a distinct orthotrichaceous peristome type that is "most likely to have evolved from a peristome with a formula of 4:2:4 with complete alignment of the cells in the IPL" - thus the funariaceous type - but unlike Vitt (1984) she considers the orthotrichaceous peristome as possibly pivotal to the evolution of the dicranaceous and the bryaceous types. Vitt , Goffinet, and Hedderson (1997) recently argued that morphological characters, used to define these major peristome types, are not phylogenetically informative, and that phylogenetic reconstruction of the Bryopsida at the ordinal (or subordinal) level will rely on independent sources of data such as ontogeny and gene sequences. The development of the funariaceous, bryaceous, and dicranaceous peristome types have been studied recently (Shaw, Mishler, and Anderson, 1989; Shaw, Anderson, and Mishler, 1989; Schwartz 1994), but unless similar data are available for the orthotrichaceous peristome, polarizing the developmental pathways, and thus defining homologies and monophyletic groups based on peristome architecture remains impossible.

The Orthotrichales include in addition to the Orthotrichaceae *sensu lato*, the Erpodiaceae Broth., Helicophyllaceae Broth., and Rhachitheciaceae Robinson. The Microtheciellaceae Harrington & Miller were recently excluded by Goffinet (chapter two) on the basis of the pleurocarpous distribution of the female gametangia, and placed in the Isobryales. The Rhachitheciaceae are reminiscent in their gametophytic characters of the Zygodontoideae (Orthotrichaceae). The peristome is always single and except for *Uleastrum octoblepharis*, each tooth pair is biseriate dorsally and uniseriate ventrally; the peristome formula is thus 2:1 (chapter three). The Erpodiaceae have traditionally been placed in the Orthotrichales (Fleischer; 1920; Brotherus, 1925; Dixon, 1932; Reimers, 1954; Robinson, 1971; Crosby, 1980; Vitt 1982a, 1984). Among erpodiaceous taxa, only species *Venturiella* and *Wildia* are peristomate. As in *U. octoblephare* of the Rhachitheciaceae, the teeth are uniseriate on both surfaces (Crum, 1972; Edwards, 1979), and the peristome architecture follows a 2:2 pattern (chapter three). These peristome formulas would be atypical for either an exostome or an endostome of any major peristome type, and are therefore uninformative in determining the ordinal affinities of these taxa. Edwards (1979) studied the peristome of *Venturiella* and reported a "rudimentary unthickened basal exostome" reminiscent of that found in the Seligeriaceae. Similar thickenings were also observed in the Rhachitheciaceae (chapter three). Walther (1983) consequently transferred the Erpodiaceae to the Haplolepideae. The affinities *Helicophyllum torquatum*, the sole species of the Helicophyllaceae, remain dubious too, due to the absence of a peristome and the unique gametophyte with reduced ventral and dorsal leaves, and lateral leaves that are inrolled when dry. Buck and Vitt (1986) argued in favor of a close relationship with the Racopilaceae (ciliate diplolepideae), as suggested by earlier authors (Brotherus, 1909, 1925; Fleischer, 1920; Dixon, 1932; Reimers, 1954). The perichaetia are, however, produced terminally on the main axis (De Luna, 1995), a condition that is *a priori* incompatible with a placement in a pleurocarpous lineage (La Farge-England, 1996). Walther (1983) had by far the broadest concept for the Orthotrichales, including in addition to the Orthotrichaceae, Hedwigiaceae, and Rhachitheciaceae, the Cryphaceae, and the monotypic Wardiaceae, two families traditionally considered pleurocarpous (Vitt, 1984; but see also La Farge-England, 1996). The circumscription of the Orthotrichales, based on morphological characters, may thus range from a single to seven families.

The Orthotrichaceae *sensu* Vitt (1984; and not *sensu* Churchill and Linares 1995) is among the most diverse families of mosses including over 500 species, distributed among 22 genera (see chapter two, and three), with *Orthotrichum*, and *Macromitrium* accounting for more than two thirds of the species richness (Vitt, 1982b). The family is cosmopolitan in distribution and is particularly prevalent in tropical montane forests. The Orthotrichaceae are traditionally characterized by "small, papillose upper leaf cells; no differentiated alar cells; large, usually mitriform calyptrae; terminal perichaetia with additional growth by lateral innovations; and sporophyte with a diplolepideous peristome having the following features - an endostome with segments which alternate with exostome teeth; lack of basal membrane and with segments, which are not or are rarely keeled; and an exostome which has a thick, outer layer and a thin, inner layer" (Vitt, 1982b; but see also Vitt 1981b). Investigations into the evolutionary history of the family have been hampered by the lack of monographic revisions for large genera (except *Orthotrichum* Lewinsky 1993) and unstable familial circumscription. The controversy focused particularly on the haplolepideous versus the diplolepideous affinity of gymnostomous taxa (*Amphidium*: Brotherus, 1909 versus 1925; Vitt, 1973 versus Lewinsky, 1976), or of taxa whose peristome is reduced (*Drummondia*: Shaw, 1985 versus Vitt, 1972). The current infrafamilial classification (Vitt, 1982b) reflects the four possible combinations of two characters - position of the female gametangia and "shape" of the calyptrae - and deviates little from Brotherus' concept early this century (Brotherus, 1925). In Vitt's (1982b) phylogenetic arrangement, the Zygodontoideae (Schimp.) Broth. (acrocarpous and cucullate calyptrae) are basal, followed by the Drummondioideae Vitt (cladocarpous and cucullate calyptrae) which are sister to a clade composed of the Orthotrichoideae Broth. and the Macromitrioideae Broth. (acrocarpous and cladocarpous respectively, and both with mitrate calyptrae). This phylogenetic arrangement is based upon a *Funaria*-type ancestor that is acrocarpous and has a cucullate calyptra. *Zygodon* sect. *Bryoides* Malta further shares smooth laminal cells with the Funariaceae, and may thus represent the most primitive taxon in the family. The monotypic Desmothecoideae accepted by Brotherus (1925 as Pseudo-Macromitrioideae), Walthers (1983) and Crum (1987), were synonymized with the Macromitrioideae by Vitt (1990) who felt that *Desmotheca* may be patristically distantly related to *Macromitrium* but because it shares "several basic features that characterize the Macromitrioideae....the genus is best kept in *this* subfamily".

The monophyly of the Orthotrichaceae and the Orthotrichales has recently been questioned by De Luna (1995) while examining the systematic affinities of the Hedwigiaceae. Based on a phylogenetic analysis using morphological characters, De Luna (1995) concluded that the Orthotrichales merely represent an evolutionary grade, suggesting that a clade of predominantly cladocarpous Orthotrichales (Macromitrioideae, Drummondioideae, Erpodiaceae, Microtheciellaceae, and Helicophyllaceae) was sister to the pleurocarpous mosses, and separated from the more primitive acrocarpous taxa of the order (acrocarpous Orthotrichaceae and Rhachitheciaceae) by the Hedwigiaceae. Affinities between the Hedwigiaceae and the Orthotrichaceae have been proposed by other authors (Walther, 1983; Frey et al., 1995). Because of the gymnostomous nature of the Hedwigiaceae and a unique combination of gametophytic characters (acrocarpy, lack of costa, and presence of pseudoparaphyllia), the affinities of *Hedwigia* are unlikely to be resolved with traditional morphological characters.

The central concept in the Hennigian phylogenetic approach is the use of appropriate outgroups, that allows adequate polarization of character state transformation in the ingroup. A reconstruction of the evolutionary history of the Orthotrichaceae based on morphology has been hampered by the lack of a peristome in certain taxa, the absence of gametophytic characters that are informative at higher taxonomic levels, and consequently the absence of a consensus regarding the putative sister-group and other outgroups to the order. Within the Bryophyta *sensu* Vitt (1984), phylogenetic reconstructions using nucleotide sequence data have focused exclusively on the monophyly and the relationships of the division and its classes (e.g., Mishler et al., 1992 and 1994; Waters et al., 1992; Capesius, 1995; Hedderson, Chapman, and Rootes 1996) rather than on the evolutionary history of arthrodontous mosses. Variation in the nucleotide sequence of the chloroplast gene *rbc*L, encoding for the ribulose 1,5 biphosphate carboxylase, has found a wide application in reconstructing the evolutionary histories within suprageneric taxa of vascular plants (Chase et al, 1993; Hasebe et al., 1995). The present study aims at setting the foundations for reconstructing the phylogeny of all orthotrichaceous genera based on morphology and for addressing the character evolution in this taxonomically and morphologically diverse family. Thus, the objectives are to use *rbc*L sequence data 1) to test the monophyly of the Orthotrichales and the Orthotrichaceae; 2) to determine the phylogenetic position of the Orthotrichales within the arthrodonteae, and thus identify its putative sister-group; and 3) to test the monophyly and the phylogenetic relationships of the subfamilies proposed by Vitt (1982).

Material and Methods

Taxon sampling. Following the exclusion of five genera from the Orthotrichaceae (chapter two and three) the family now consists of 22 genera. While material has been seen for all taxa except for the recently described *Orthomitrium* (Lewinsky-Haapasaari and Crosby 1996), extractions were not attempted for taxa known only from the type specimen (*Ceuthotheca* Lewinsky-Haapasaari, *Leiomitrium* Mitt., *Leratia* Broth.), or for which only very little material was available (*Stoneobryum* Norris and Robinson). DNA extractions were attempted for the remaining 17 genera, and for the most diverse genera such as *Macromitrium* and *Orthotrichum*, several species belonging to morphologically distinct infrageneric taxa were tentatively included. DNA extractions were also attempted for representatives of all related families in the Orthotrichales. Furthermore ten outgroup taxa were chosen, representing the Funariaceae, Splachnaceae, Encalyptaceae, Hedwigiaceae, the Haplolepideae (Ptychomitriaceae and Rhabdoweisiaceae), and the ciliate alternate peristomate mosses (Mniaceae, and Thuidiaceae).

DNA extraction and PCR-DNA amplification. DNA was extracted following a modification of Doyle and Doyle (1987; see Goffinet and Bayer, unpubl. for full protocol). The *rbcL* gene was amplified via the polymerase chain reaction (PCR) using Taq Polymerase (Promega). The amplification reaction was performed in 50 µL volume including 50 mM KCl, 10 mM Tris-HCl, 0.1% Triton, 5% glycerol, 2.5 mM $MgCl_2$, 20 mM of each dNTP, 0.2 mM of primers Z_1 and 1351R (Wolf, Soltis, and Soltis, 1994) and 0.2 to 30.0 ng of template DNA. This solution was overlaid with 30 µL of mineral oil. The samples were exposed to the following temperature profiles using a Grant thermal cycler: one cycle of 94°C for 3 min and 85°C for 4 min during which 1 unit of Taq DNA Polymerase (Promega) would be added to each tube, and 30 cycles of 94°C for one min, 52°C for one min, 72°C for two min, and finally one segment of 72°C for ten min. The double-stranded product subsequently served as the template for the amplification of single-stranded target DNA. This second PCR followed the same profiles as before but the reactions solution included only one of the two PCR primers: Z_1 for amplification of the forward strand and 1351R for the reverse strand. The single stranded product was precipitated with 20% PEG/2.5 M NaCl, washed first with 70% EtOH, then with 95% EtOH before being suspended in 7mL of TE (Morgan and Soltis, 1993).

Sequencing and alignment. Sequencing the single-stranded template followed the dideoxy chain termination method (Sanger, Nicklen, and Coulson, 1977) using the Sequenase® Version 2.0 T7 DNA Polymerase following the manufacturers instructions (Amersham, Canada). The sequence of the primers used are given in Table 5.1. The sequencing products were electrophoresed on a 6 % polyacrylamide gel (0.4 mm thickness; 1X TBE buffer), at 2400 V for four hours. The gels were fixed in 10% acetic acid, washed with distilled water, and dried in an oven at 65°C for 30 min. and autoradiographed for 36-48 hours. The sequences were entered in MacClade (version 3.03) and aligned against available sequences of *Sphagnum palustre* and *Andreaea rupestris* (GenBank acc. no. L13485 and L13473, respectively; Manhart 1994). The first and last 30 nucleotide sites, corresponding to the sequences of the PCR primers, were excluded from parsimony analyses.

Sequence and Phylogenetic analysis. RbcL sequence variation was analyzed by Neighbor-Joining (NJ; Saitou & Nei, 1987), and Maximum Parsimony (MP; Fitch 1971). Neighbor-joining analyses were performed using MEGA v. 1.0 (Kumar, Tamura, and Nei, 1993) using Tamura's distance parameter, following the authors' "Guidelines for choosing distance measures", and including both transitions and transversions. A "bootstrap confidence level" for the NJ tree was calculated over 100 replicates. Fitch parsimony analyses of nucleotide data were performed with PAUP v. 3.1 (Swofford, 1993) on a MacIntosh PowerPC 7200/90 using the heuristic search with the following options in effect: keep all characters, multistate taxa interpreted as uncertainties, tree-bisection-reconnection branch swapping, steepest descent, collapse zero-length branches, and addition sequence "as is". In an attempt to locate additional islands of shortest trees

(Maddison, 1991), the search strategy further followed the steps recommended in Pryer, Smith, and Skog (1995) except that the search was only replicated 100 times. Bootstrap analysis (Felsenstein, 1985; Hillis and Bull, 1993) were performed with 100 bootstrap replicates of the heuristic search with the same set of options in effect. Relative support for branches was further determined by the decay analysis (Bremer 1988; Donoghue et al. 1992) following the converse constraint method developed by Baum, Sytsma, and Hoch (1994). The ACCTRAN (accelerated transformation optimization) option of PAUP was applied for calculations of branch lengths. The phylogenetic signal present in the *rbc*L sequence data was estimated by calculating the g_1 statistic of the distribution of tree length of 500.000 random trees produced with PAUP using the "random tree" option (Hillis and Huelsenbeck, 1992). Consistency (CI) and retention indexes (RI), and f-values are calculated for all MPTs using PAUP. PAUP was also used to generate a matrix of absolute and mean distance between sequences. Average unit character consistencies (AUCC) are calculated for competing phylogenies in an attempt to select the tree with the strongest asymmetric distribution of homoplastic characters in the matrix (Sang, 1995). Costs in terms of number of additional steps required for alternative phylogenies were explored using the enforce constraint command during heuristic searches (Swofford, 1993). The same set of options as in the unconstrained searches was applied.

Results

The *rbc*L gene was successfully sequenced for 22 taxa of the Orthotrichaceae distributed among 10 genera, for representatives of 2 of the related families as well as for all selected outgroup taxa (Table 5.2; Appendix 1). Amplification products were not obtained for *Helicophyllum*. The sequences obtained from PCR fragments generated using the PCR primers Z_1 and 1351R, were as expected 1320 bases long (approximately 90% of the total length of the gene). Alignment of the sequences with known sequences of *Sphagnum palustre* and *Andreaea rupestris* did not require the inclusion of gaps. Phylogenetically informative characters are preponderant at the third codon position followed by the first and the second codon site (Table 5. 3). *Rbc*L sequence variation yield 108 sites that are potentially phylogenetically informative within the Orthotrichaceae. Informative characters are distributed fairly evenly across the sequence (Fig. 5.1). The distribution of 500.000 random trees using all characters had a skewness index g_1 of -0.55; excluding the first and second codon position yielded a similar index

(g_1 = -0.54), while trees generated solely from characters of these two first codon sites had a higher skewness index (g_1 = -0.39).

Using the maximum parsimony criterion with *Sphagnum* and *Andreaea* as the outgroup yields 39 most parsimonious trees (MPT) distributed among three islands of size 21, 6 and 12 respectively (Fig. 5.3). The MPTs are 964 steps long, and have a CI of 0.390 and a RI of 0.624. The f-value of the trees varies between 13306 and 19198. Both methods of analysis agree on the polyphyly of the Orthotrichales and place the Erpodiaceae and the Rhachitheciaceae as well as the orthotrichaceous genera *Amphidium* and *Drummondia* in a monophyletic clade with *Ptychomitrium* and *Rhabdoweisia* (Figs. 5.2-4). Constraining the search for the inclusion of the Erpodiaceae and Rhachitheciaceae in the Orthotrichales results in trees that are 17 and 15 steps longer than the shortest unconstrained trees. Including *Amphidium* and *Drummondia* in the Orthotrichaceae also increases the length of the most parsimonious topology (+ 25 steps), and furthermore these two genera remain more closely related to each other than they are to any other genus of the Orthotrichaceae. The NJ tree agrees with the strict consensus tree over all MPTs in the following relationships (Figs. 5.2 & 4): 1) *Funaria* occupies a basal position among arthrodontous mosses; 2) the Orthotrichales and the Splachnales form a monophyletic clade sister to the ciliate mosses; and 3) the haplolepideae, including *Amphidium*, *Drummondia*, *Venturiella* and *Uleastrum*, form a monophyletic group sister to derived Diplolepideae. *Hedwigia* is sister to the two ciliate mosses in 36 MPTs (Fig. 5.3) as well as in the NJ-tree (Fig. 5.2), and basal in the diplolepideous clade (excluding the Funariaceae) in the remaining three trees (Fig. 5.3). Compared to MP, NJ provides similar or slightly higher bootstrap values for major lineages (Haplolepideae, combined Splachnales and Orthotrichales, Orthotrichaceae, and ciliate mosses), but like MP, NJ fails to yield strong support for their relationships (Figs. 5.2 & 4).

The remaining genera of the Orthotrichaceae (thus excluding *Amphidium* and *Drummondia*) form a strongly supported monophyletic family in the phylogenetic reconstruction using Tamura's distance parameter (Fig. 5.2). Among the 39 MPTs found in the cladistic analysis (Fig. 5.3), 15 trees (38%), distributed between island 1 and 3 (each with 9 and 6 trees respectively), support the monophyly of the family. The trees of these two islands differ mainly by the position of *Encalypta* (Fig. 5.3). In island 3 (mean f-values: 13943), *Encalypta* is included in the haplolepideae (Fig. 5.3-B), while in islands 1 and 2 it occupies a position basal to the dichotomy between haplolepideae and the derived diplolepideae (Fig. 5.3-C; mean f-value overall: 16634). Comparison of the distribution of homoplasy among characters from two selected trees contrasted mainly by the position of *Encalypta* (island 1 versus island 3), yield an AUCC value of 0.71 for both, suggesting no difference in the distribution of homoplastic characters (Sang, 1995). All other indexes being equal, the tree with the lowest f-value (see Farris 1972) is shown (Fig. 5.4). The Orthotrichaceae are composed of two major lineages: one including all Macromitrioideae (*Cardotiella, Desmotheca, Groutiella, Macrocoma, Macromitrium,* and *Schlotheimia*) as well as *Zygodon obtusifolius*, and one uniting the remaining species of *Zygodon* with the Orthotrichoideae (*Bryodixonia, Orthotrichum,* and *Ulota*). Large genera such as *Macromitrium, Orthotrichum,* and *Zygodon* appear paraphyletic, independent of the method of analysis. In the NJ-analysis, as well as in all MPT of island 2, *Desmotheca* is basal in a clade centered around *Macromitrium*, while the other MPT suggest a derived position, sister to *Macromitrium richardii*.

Discussion

RbcL sequence data. *Rbc*L sequence data are routinely used to reconstruct evolutionary histories among (Chase et al. 1993; Hasebe et al. 1995) or more rarely within (Haufler and Ranker, 1995) genera of vascular plants. With 30% variable sites, including 12% of sites with changes that may be phylogenetically informative, the variation in the nucleotide sequences of the *rbc*L gene among moss taxa may yield sufficient characters for reconstructing the evolutionary history of the taxa included in this study. The distribution of informative characters appears rather uniform (Fig. 1), and is similar to that observed in vascular plants, that is with no obvious hot-spot detectable (Olmstead and Sweere, 1994). The distribution of randomly generated trees has a left-hand skewness with a g_1 value(-0.55) significantly smaller than the critical value (-0.10 or -0.08 for 100 or 250 characters respectively; p=0.01) furnished by Hillis and Huelsenbeck (1992), suggesting that our *rbc*L data set is more structured than a random data set of equal size and that it may contain significant phylogenetic signal (Hillis and Huelsenbeck 1992). Unlike Conti, Fischbach, and Sytsma's (1993) observation that the third codon position introduces "noise", a lower g_1 value is observed when the matrix is restricted to the third codon position (-0.54 vs -0.39) suggesting that the changes at the third codon position are more structured. Analyses of a data set restricted to the third codon positions only, yield topologies congruent with those obtained with the complete data set, whereas a search excluding changes at the third codon position results in a consensus tree incongruent with monophyletic concepts of either the ciliate mosses, or the haplolepideae (results not shown). This observation would suggest that the first two codon sites carry more homoplasies than the third position, which may thus be more informative. Alternatively, the taxon sample may be too disparate for variability at the more conserved positions one and two to be mostly phylogenetically informative. The significance of the difference between the g_1 value based on our data set and that of a random matrix may as a result be due to differences in the frequency of character states rather than in the congruence among characters in both data sets (Källersjö et al., 1992). This second hypothesis most likely applies to our data since our restricted taxon sample represents major lineages of arthrodontous mosses with a long evolutionary history (Frey, 1977, 1990).

Comparison of the variation in the nucleotide sequence against the secondary structure of the protein (as commonly done with nrDNA genes) is not possible, but an indication for the accuracy of our sequences may be obtained from the preservation of active sites in the enzyme. All amino acid residues of the active site found in spinach by crystallography (Andersson et al., 1989) are conserved among studied bryophyte taxa, except for position 404 (amino acid numbering) which is scored as polymorphic (Arg in addition to the conserved Gly) for six taxa, and thus excluded from phylogenetic analyses in MP. This observation may provide some preliminary support for the accuracy of the sequences obtained.

Circumscriptions of the Orthotrichales. *Rbc*L sequence data analyzed using either the neighbor-joining or the maximum parsimony criterion indicates that the Orthotrichales sensu Vitt (1984) are a polyphyletic taxon. Both the Erpodiaceae (*Venturiella sinensis*) and the Rhachitheciaceae (*Uleastrum palmicola*), as well as the orthotrichaceous genera *Amphidium* and *Drummondia* are indeed placed in a clade with haplolepideous taxa (Figs. 2 & 4). The monophyly of this haplolepideous clade is strongly supported (MP: decay index [DI] of 4, bootstrap value [BV] of 77%; NJ: BV=94%). Constraining these taxa to a relationship within a monophyletic Orthotrichales is furthermore very costly in terms of parsimony, requiring up to 25 additional steps. Variation in the nucleotide sequence of the *rbc*L gene is thus congruent with earlier hypotheses based on morphology and cytology, suggesting haplolepideous affinities of these taxa (Anderson and Crum, 1958; Vitt, 1970 and 1973; Edwards, 1979; Shaw, 1985; Goffinet chapter three). More extensive sampling of haplolepideous taxa would be needed before ordinal affinities are addressed further (see also affinities of excluded taxa).

De Luna (1995) recently argued that the Orthotrichales represented an evolutionary grade, reached by two lineages. The cladocarpous lineage (including, e.g., Erpodiaceae, Macromitrioideae) was sister to the Leucodontales and separated from the acrocarpous line (e.g., Rhachitheciaceae, Orthotrichoideae) by the Hedwigiaceae. Constraining the heuristic search to include ***Hedwigia ciliata*** in the Orthotrichaceae (as defined in Fig.5.2 & 5.4, and with no further relationships specified within this clade) yielded 12 trees that not only are 16 steps longer than the MPTs in the unconstrained search, but also share a monophyletic Orthotrichaceae. The incongruence between De Luna's morphological study (De Luna 1995) and the present molecular analysis may be due to inconsistent and inadequate taxon sampling with the absence of representatives of the Leucodontineae from the molecular analysis and of bryalean taxa from the morphological analysis. The latter analysis further includes taxa that are here shown to be unrelated to the diplolepideae (i.e., Erpodiaceae, Rhachitheciaceae) and might be affected by the subsequent misinterpretations of the nature of the peristome of these families (scored as an exostome instead of an endostome). A closer relationship between the Hedwigiaceae and the Orthotrichaceae cannot be excluded, but if the Hedwigiaceae were closely related to the Orthotrichaceae, *rbc*L data suggest that the Orthotrichaceae would most likely remain a natural group. The branch that supports the Hedwigiaceae-cladocarpous Orthotrichales-Leucodontales lineage is supported in De Luna's analysis (1995) by 3 synapomorphies, namely: plagiotropic growth, presence of pseudoparaphyllia, and differentiated perichaetial leaves. Two of these characters are reversed in the cladocarpous Orthotrichales, leaving a single character that actually supports a relationship of these taxa with the Hedwigiaceae and Leucodontales, namely plagiotropic growth. This character is, however, homoplastic among many families and genera of mosses (Meusel, 1935) and may thus not be truly informative at the ordinal level.

Analysis using the distance method yields a single tree (Fig. 5.2) that shows strong support for the monophyly of the Orthotrichaceae, a phylogeny congruent with that of 15 of the 39 MPTs found in the cladistic analysis. Käss and Wink (1995) and Barker, Linder, and Harley (1995) also used both methods (MP, and NJ) for phylogenetic reconstructions based on *rbc*L sequence data, and the results of both analyses were fairly congruent. Kim, Rohlf, and Sokal (1993) critically examined the accuracy of the NJ method under different constraints on a random data set, and found that this method "has the highest accuracy overall". Russo, Takezaki, and Nei (1996) recently compared the efficiency of various tree-building methods in recovering a known phylogeny, and concluded that NJ "gives as good a result as the more time consuming...methods". The congruence between the NJ tree and 15 MPTs is therefore here interpreted as supporting the monphyly of the Orthotrichaceae.

With the exclusion of the Erpodiaceae, Rhachitheciaceae, and Hedwigiaceae from the Orthotrichales, the order is now reduced to the Orthotrichaceae and the Helicophyllaceae. In the absence of molecular data, the phylogenetic relationship between these two families remains dubious due to the unique combination of morphological characters of *Helicophyllum* (Vitt 1982a), and will most likely need to be resolved using molecular characters. A phylogenetic relationship between the Orthotrichaceae and the Cryphaeaceae and the monotypic Wardiaceae was not examined in the present study. *Wardia hygrometrica* should be excluded from the Orthotrichales based on well differentiated alar cells and its prosenchymateous cells. Combined with the acrocarpous condition (Welch, 1943), these characters may indicate a bryalean origin, a hypothesis recently confirmed using 18S gene sequences (Hedderson et al. unpubl.). The Cryphaeaceae have traditionally been placed among the Leucodontineae (Vitt 1984; Buck and Vitt, 1986). A relationship of this family to the Hedwigiaceae, and thus the Orthotrichales, has been considered and rejected (De Luna 1995), but may need to be reexamined in the light of the discovery of cladocarpous species of *Cryphaea sensu lato* (La Farge-England, 1996).

Ordinal relationship of the Orthotrichales--The affinities of the Orthotrichales - here restricted to the Orthotrichaceae - as indicated by comparisons of the *rbc*L sequences, are within a diplolepideous lineage including the Splachnales and the ciliate mosses. This clade shares a common ancestor with the Haplolepideae, and together they form a sister group to the Funariales (Figs. 5.2-4). This topology is congruent with Vitt's hypothesis (Vitt, 1981a) that the opposite diplolepideous peristome is primitive among arthrodontous mosses, and that the haplolepideous peristome is derived from such an ancestral type (Vitt, 1984). Alternative hypotheses proposed by Lewinsky (1989; Orthotrichales basal to dichotomy between haplolepideae and ciliate diplolepideae) or by Shaw and Rohrer (1984) and Crosby (1980; ciliate diplolepideae are the most primitive mosses) both require 5 additional steps.

The phylogeny obtained by either NJ or MP analysis (Figs. 2 & 4) also agrees with Vitt (1984) with regard to the monophyly of a lineage composed of the Splachnales, Orthotrichales and the ciliate mosses. The relationships among these lineages remain however, ambiguous (Fig. 5.3). The most parsimonious scenario points toward the Splachnales and the Orthotrichales being sister-groups. Vitt (1984) by contrast proposed that the Orthotrichales are sister to the ciliate mosses, a topology that would only require one additional step based on our *rbc*L data set. Koponen (1977, 1983) considered the genus ***Brachymitrium*** to be the most primitive extant member of the Splachnaceae. Unlike in related genera, the thickening on the PPL is heavier than on the OPL, and the PPL also has strong trabeculae (Koponen, 1977, 1982). Both these features are shared with the ***Funaria*** and the ***Bryum*** peristome type (Shaw and Rohrer, 1984). If the Orthotrichales and the Splachnales formed a monophyletic group, both orders would most likely remain natural orders, with the Orthotrichales defined by thick-walled laminal cells. The heavier thickening on the OPL would have arisen independently in both lineages. In terms of peristome evolution, these lineages would form a plesiomorphic sister group to the ciliate mosses, the latter one being defined by the asymmetric division of the IPL leading to the development of cilia. If we consider the alternative scenario where the Splachnales are sister to a clade composed of the Orthotrichales and the ciliate mosses, the most parsimonious topology based on our data suggests that within the latter, the ciliate mosses remain monophyletic. An extensive taxon sampling in the Bryales is, however, needed before their evolutionary relationship can be addressed more critically. Both the *Orthotrichales* and the *Bryales sensu lato* taxa share one plesomorphic state with the Splachnales: either completely aligned cell divisions (Orthotrichales; Lewinsky, 1989) or heavier thickening of the PPL and ventral exostomial trabeculae (typical ciliate mosses). The ciliate mosses have traditionally been defined by a strongly asymmetric division in IPL leading to the development of cilia. While some "ciliate" mosses actually lack cilia (Buck and Vitt, 1986), have a thickened OPL (*Eucamptodontopsis*, A. Newton pers. com.), and others even have opposite peristomes (*Garovaglia* div. sp. During 1977, Nishimura and Watanabe, 1992), none has yet been found to have a first-late symmetric division in the IPL. An asymmetric division is elsewhere found only among haplolepideous taxa. Considering that the Rhachitheciaceae are here shown to be of haplolepideous affinity, their peristome with a 2:1 formula most likely results from reduction, through the loss of the asymmetric first-late division. The asymmetric division of the ciliate mosses may not be homologous to that of the haplolepideae (Shaw, Mishler, and Anderson, 1989). Assuming that the genetic complexity behind the asymmetric division in both group is similar, we cannot exclude the possibility that a loss of it or a reversal to a symmetric division may be possible among ciliate mosses and may even occur in such genera as *Mielichhoferia* with a peristome formula of 4:2:4 (Shaw and Rohrer, 1984; Shaw and Crum, 1984). Since the possibility of a reversal to a symmetric division cannot be excluded, a bryalean origin of the Orthotrichaceae will need to be further examined in comparison with a broad sample of ciliate taxa.

Hedenäs (1994) considered *Schlotheimia* to be pleurocarpous, and based on this interpretation suggested that the Orthotrichaceae "are rather close to the clade where most pleurocarpous mosses belong". He further hypothesized that "the transition to pleurocarpy must have been gradual", and in this scenario the Orthotrichaceae would occupy an intermediate position. The Macromitrioideae differ however from typical pleurocarps by several characters and should rather be considered cladocarpous (La Farge-England, 1996). In genera where both cladocarpy and acrocarpy occur, the former seems to be restricted to terminal taxa suggesting that the trend is from acrocarpy to cladocarpy with no obvious cases of reversals (La Farge-England, 1996). Such a general trend may suggest that in the Orthotrichaceae too, the primitive condition is acrocarpy. Thus if the Orthotrichales are indeed reduced ciliate mosses, their putative sister group would most likely belong to a group of acrocarpous Eubryales.

Subfamilial phylogenetic relationships. The ten orthotrichaceous genera remaining in the present analysis are distributed among two clades that are moderately to strongly supported by either method of analysis, with bootstrap values (BV) ranging from 77 to 94% and decay indexes (DI) of 2 and 3. The orthotrichoid-clade combines the Zygodontoideae (*Zygodon* sections *Zygodon* and *Bryoides*) and the Orthotrichoideae (*Bryodixonia*, *Orthotrichum*, *Ulota*), while the macromitrioid-clade includes all the Macromitrioideae (*Cardotiella*, *Desmotheca*, *Groutiella*, *Macrocoma*, *Macromitrium*, and *Schlotheimia*) as well as *Zygodon obtusifolius* (*Zygodon* sect. *obtusifolii*). *Zygodon obtusifolius* has retained several characters considered here plesiomorphic, such as acrocarpy, smooth, cucullate calyptrae, but exhibits also some features reminiscent of the Macromitrioideae (strongly bulging cells, coarse papillae, undifferentiated basal cells, etc.; see chapter six). If *Z. obtusifolius* is to be retained within the Zygodontoideae, the unexpected relationship with the Macromitrioideae as proposed by *rbc*L sequence data may be an artifact due to a long branch attraction (Hendy and Penny, 1989) or an indication of hybridization involving chloroplast capture from a macromitrioid taxon (Soltis and Kuzoff, 1995). In the latter case, the topology obtained here may represent the "correct" gene tree, but deviate from the true phylogeny of the taxa (Doyle, 1992). This hypothesis is currently being tested by comparing sequence data of the nuclear gene 18S.

With the exclusion of the Drummondioideae, Vitt's (1982b) phylogenetic arrangement of subfamilies would have the Zygodontoideae (cucullate calyptrae) basal to a dichotomy between the Orthotrichoideae and the Macromitrioideae (both typically or exclusively have large mitrate calyptrae). The sister-group relationship between the orthotrichoid and the macromitrioid-clades proposed here deviates from Vitt's (1982b) phylogenetic concept of the family by the inclusion of the Zygodontoideae in the former clade, and parsimony would need to be relaxed by 6 steps for his concept to be satisfied (without constraining the affinities of *Z. obtusifolius*). The monophyly of *Zygodon* and thus Zygodontoideae is not supported by *rbc*L sequence data either, but the relationship of sections *Zygodon* and *Bryoides* to the Orthotrichoideae remain unresolved. If *Zygodon* is indeed paraphyletic, section *Zygodon* would most likely be the most primitive taxon, given that it shares the plesiomorphic state "smooth laminal cells" with either a splachnaceous or a bryaceous ancestor. The two sections of *Zygodon* differ on average by 40 mutations, while only 28 changes separate section *Zygodon* from the Orthotrichoideae, compared to 43 changes between section *Bryoides* and the Orthotrichoideae. Such divergences may be indicative of the monophyly of a clade composed of section *Zygodon* and the Orthotrichoideae, and support a single origin of papillae that would define this clade.

With regards to the Macromitrioideae, both methods of analysis yield two strongly supported monophyletic clades (Fig. 5.2 & 4): one composed of all three species of *Schlotheimia*, the other including all remaining Macromitrioideae (i.e., *Desmotheca*, *Groutiella*, *Macrocoma*, and *Macromitrium*). Vitt, Koponen, and Norris (1995) suggested that *Schlotheimia* and *Cardotiella* should be placed in a separate subfamily, and even if they did not explicitly state it, this hypothesis was based on the distinct lobate calyptra. *Rbc*L data do not support such relationship as 10 more steps are needed to unite *Schlotheimia* and *Cardotiella* into a monophyletic clade. The species of *Schlotheimia* differ on average from other Macromitrioideae (including *Cardotiella*) by 47 bases. By contrast, the average distance between these other macromitrioid genera is only 23 bases. If rates of molecular evolution are assumed to be similar among these taxa (a reasonable assumption considering both clades are predominantly phyllodioicous, and epiphytic in tropical montane forests; see Britten 1986), differences in nucleotide sequence may indicate a relative ancient divergence between *Schlotheimia* and the other Macromitrioideae. *Schlotheimia* differs from other Macromitrioideae also by several morphological characters, most of which are unique within the Orthotrichaceae (multistratose calyptrae, color of leaves, diagonal arrangement of cells; Goffinet unpubl.), and thus not informative phylogenetically. The pleisiomorphic state "smooth laminal cells" may, as was argued in the case of *Zygodon* sect. *Bryoides*, be indicative of the primitive position of *Schlotheimia* in the evolution of the Macromitrioideae. Considering both the morphological and molecular divergences between *Schlotheimia* and the remaining Macromitrioideae, and the strong support for the monophyly of both clades on molecular grounds, accommodating *Schlotheimia* in its own subfamily, as suggested by Vitt, Koponen, and Norris (1993), may better reflect the evolutionary relationship between these clades.

Brotherus (1925, as Pseudo-Macromitrioideae), Walther (1983) and Crum (1987) isolated *Desmotheca* from other Macromitrioideae on the basis of its dimorphic sterile and fertile branches. Vitt (1990) however argued that excluding *Desmotheca* from the Macromitrioideae would most certainly result in the paraphyly of the later subfamily. Based on variation in the *rbc*L sequences, the phylogenetic affinities of *Desmotheca* clearly lay with *Macromitrium sensu lato*, but remain ambiguous with regard to its sister group within this clade. Whether *Desmotheca* should be retained in its own subfamily, and placed sister to the Macromitrioideae (excluding *Schlotheimia*), or be inserted within the latter, is not clear. In 33 MPTs (including the 15 that share a monophyletic Orthotrichaceae) *Desmotheca* occupies a derived position (Fig. 5.4), nested between two *Macromitrium* species. In the remaining 6 MPTs as well as in the NJ tree (Figs. 5.4 & 2), *Desmotheca* is sister to the Macromitrioideae (*Schlotheimia* excluded). The phenetic distance between *Desmotheca* and other macromitrioid genera (Table 5.4; excluding *Schlotheimia*) are on average similar to those between *Orthotrichum* and *Ulota* (20 bases), in the Orthotrichoideae, suggesting that placing *Desmotheca* in a distinct subfamily may not be appropriate.

Based on our phylogenetic analyses of the *rbc*L sequence variation, the Orthotrichaceae could be regarded as composed of two subfamilies, the Orthotrichoideae and the Macromitrioideae with the latter further divided into two tribes "Macromitriae" and "Schlotheimiae". Alternatively, the two subfamilies may deserve recognition at the family level as suggested by Churchill and Linares (1995) and the Macromitriaceae would then be composed of two subfamilies, the Macromitrioideae and the "Schlotheimioideae". The status of the Zygodontoideae, and thus the relationship of the two main subgenera to the Orthotrichoideae needs further study.

Phylogenetic relationships of Orthotrichaceous genera. Analysis of *rbc*L sequence using either the MP or the NJ method suggests that four of the five larger genera, namely *Macromitrium*, *Orthotrichum*, *Ulota*, and *Zygodon*, are paraphyletic. The paraphyly of *Zygodon* has been addressed earlier. *Bryodixonia* is a monotypic genus endemic to New Zealand. Sainsbury (1945) argued for a generic distinction from *Ulota* on the basis of "the highly differentiated and conspicuous perichaetial bracts and the diminutive calyptra" and the immersed capsule. In addition, the perichaetial leaves have prorate basal laminal cells (Goffinet unpubl.), a feature otherwise unknown from the Orthotrichoideae. *Bryodixonia* does, however, share many of the characters found in the genus *Ulota*, such as very thick-walled cauline cells, the differentiated marginal cells of the lamina, the flexuose to crisped leaves. *Bryodixonia* may thus be patristically very derived; however, in cladistic terms it may not deserve taxonomic recognition at the generic level. *Rbc*L sequences of *Ulota lutea* and *Bryodixonia perichaetialis* differ only by 6 mutations, a degree of divergence that is similar to that found between species of *Groutiella* (4) or *Schlotheimia* (8-16) but moreover, it is less than the divergence recorded between the two species of *Ulota* (14; Table 5.4). Immersed capsules are characteristic of many mosses that are taxonomically unrelated but share a xerophytic habitat (Vitt, 1981a). Within the Orthotrichaceae completely immersed capsules are characteristic for *Schlotheimia* sect. *Stegotheca*, and a shortening of the setae leading ultimately to an immersed capsule occurs in *Orthotrichum* subg. *Gymnoporus* sect. *Leiocarpa*, subg. *Pulchella* sect. *Rivularia* and sect. *Diaphana*, as well as in subg. *Orthotrichum* (Lewinsky, 1993). Considering the low degree of morphological and molecular divergence of *Bryodixonia*, segregation at the generic level does not seem appropriate.

The monophyly of *Ulota* (including *B. perichaetialis*) is compromised by *O. lyellii* in the NJ tree and in 13 MPT (in 13 other MPTs their relationship is not resolved). Strong affinities of *O. lyellii* for *Ulota* (MP: 99% BV and DI of 5) and *U. obtusiuscula* in particular (13 MPTs) may indicate that among the different lineages of *Orthotrichum*, subg. *Gymnoporus* (Braithw.) Limpr. is the most closely related to *Ulota*. Among the characters that subg. *Gymnoporus* sect *Leiocarpa* (see description in Lewinsky, 1993) shares with *Ulota*, only the long flexuose vegetative leaves may be derived within the Orthotrichoideae and thus be indicative of common ancestry. The genus *Ulota* (even if including *Bryodixonia*) is morphologically well defined from *Orthotrichum*, suggesting that the paraphyly of the *Orthotrichum*, if confirmed, would need to be resolved by dividing the genus into discrete entities rather than broadening the concept of Orthotrichum by including *Ulota*. The relationships of the subg. *Orthophyllum* Delogn. (*O. obtusifolium*) and subg. *Orthotrichum* (*O. anomalum*) are not unambiguously resolved either: they form sister taxa in 13 MPTs as well as the NJ tree, while in 13 other MPTs, *O. obtusifolium* is sister to a clade composed of the remaining Orthotrichoideae. *Orthotrichum obtusifolium* had been placed together with the related *O. gymnostomum* Brid. in the genus, *Nyholmiella* (see Lewinsky 1993 for history), based on "the obtuse leaves with plane or incurved leaf margin and incrassate leaf-cells with a stout central papillae on each side" (Lewinsky 1993). Patterns in peristome ornamentation are similar to those observed elsewhere in the genus (Lewinsky 1993) and it may therefore be more parsimonious to retain subg. *Orthophyllum* in *Orthotrichum*.

Within the macromitrioid-clade (Fig. 5.4) the relationships remain ambiguous too (except for *Schlotheimia* see above), either because *Macromitrium* and *Macrocoma* truly are paraphyletic, or because of an insufficient taxon sample. The genus *Macromitrium* is, with over 250 species (Vitt 1982) by far the most speciose genus of the Orthotrichaceae (Vitt 1982). Mitten (1869) divided the genus in four sections, to which Buck (1991) recently added sect. *Reverberatum*. Two of these have recently been raised to the genus level, namely *Micromitrium* (now *Groutiella* Steere) and *Macrocoma* Grout. The genus *Macromitrium* remains however morphologically extremely diverse in terms of size of the plant, degree of differentiation of the basal cells, shape of the urn, laminal cell shape, orientation and ornamentation. The relatively high cost in terms of parsimony, for a monophyletic *Macromitrium* (9 steps) may be seen as just one other indication that the genus as currently defined is still a heterogeneous assemblage. *Groutiella* differs from *Macromitrium* by the marginal limbidium of hyaline elongate cells, and a short calyptra covering only the upper portion of the urn. Except for *G. tomentosa*, *Groutiella* is restricted to the Neotropics, where 10 species occur. The sister species in all shortest trees is *Macromitrium longifolium*, a neotropical endemic, rather than any of two paleotropical taxa (*M. richardii* is known from Africa and the Americas [van Rooy and van Wyk, 1992; Vitt 1993] and belongs to *M. ligulare*-group of the Old World; *M. incurvifolium* occurs throughout the Pacific Ocean [Vitt & Ramsay, 1985]). Whether these putative affinities of *Groutiella* for neotropical *Macromitria* indicates a common ancestry with a distinct neotropical lineage of *Macromitrium*, needs to be further investigated.

The genus *Macrocoma* is composed of two subgenera, subg. *Trachyphyllum* (*M. papillosa*) and subg. *Macrocoma* (*M. tenuis*), that differ by a series of characters, but particularly by the well developed peristome of the former (Vitt 1980). Our molecular data suggest that these two taxa too, form an artificial group; three additional steps are needed to restore the monophyly of *Macrocoma*. *Macrocoma papillosa* is found in a basal position among macromitrioid taxa (excluding *Schlotheimia*) in 33 MPTs (Fig. 5.4), while in the remaining 6 it is found in a more derived position with both species of *Groutiella* and *Macromitrium longifolium* and *Macrocoma tenuis.* While the Macromitrioideae are typically cladocarpous (i.e., with their perichaetia terminal on lateral branches) and have dimorphic leaves between stem and branches, *M. papillosa* is clado- and acrocarpous (i.e, with perichaetia terminal on lateral branches and on the stem; Goffinet unpubl.) and the leaves are not differentiated into stem and branch leaves. True acrocarpy also occurs in subg. *Macrocoma* (e.g., *M. braziliensis* [Mitt] Vitt), while other taxa of this subgenus are strictly cladocarpous (e.g. *M. tenuis* [Hook. & Grev.] Vitt). Acrocarpy and cladocarpy have not been reported before from the same taxon, not to mention from the same individual (see La Farge-England, 1996). The combination of plesiomorphies such as undifferentiated stem and branch leaves, terminal cauline gametangia and the complete double peristome may be a strong indication that subg. *Trachyphyllum* is a primitive clade not only when compared to subg. *Macrocoma* (Vitt 1982), but maybe even with regard to the evolution of the Macromitrioideae.

Affinities of excluded taxa. Critically addressing the relationships of the taxa here excluded from the Orthotrichaceae is beyond the scope of the present study, and would need a broader sampling of haplolepideous taxa. A suite of unique characters combined with the lack of characters that are phylogenetically crucial may always hamper determining sister group relationships based on morphology only. Crum (1987) already suggested that gametophytic characters may not suffice to resolve the phylogenetic relationship of *Drummondia.* The same opinion prevails with regards to *Amphidium.* Brotherus (1925), Anderson and Crum (1958), and Vitt (1973, 1982a, 1984) placed *Amphidium* near *Rhabdoweisia.* Our results, though preliminary, do not suggest that these genera are closely related and future study may need to consider alternative relationships, as for example with *Glyphomitrium,* due to the overall similarity of *Amphidium lapponicum-Glyphomitrium daviesii.*

Presence of a peristome allows for a more explicit hypothesis to be made regarding the systematic position of the Erpodiaceae and the Rhachitheciaceae. Edwards (1979), as part of a review of the haplolepideous peristome, examined the peristome architecture of *Venturiella,* and concluded that the teeth are "strongly dorsally trabeculate, and also have a rudimentary unthickened basal exostome", and that "these characters are of a haplolepideous peristome although not of the dicranaceous type" but of a distinct type, the *Seligeria*-type. This peristome type is characterized by little ventral thickening, strong dorsal trabeculae, and an exostome reduced to a thin, smooth membrane adhering to the trabeculae. This combination of characters has also been observed in the Rhachitheciaceae, and has been interpreted as a possible indication of haplolepideous affinities of the family (Goffinet unpubl.). Molecular data thus tend to confirm these hypotheses, and consequently the peristome of the Rhachitheciaceae and the Erpodiaceae should be regarded as derived, through reduction, from a typical haplolepideous peristome. Though the monophyly of a group of taxa sharing the *Seligeria*-type peristome has not been critically examined, the nearly identical peristomes of *Rhachithecium*, *Glyphomitrium* (Ptychomitriaceae), and *Blindia* (Seligeriaceae), may be seen as an indication of close phylogenetic relationships, despite gametophytic differences. Alternatively, the Rhachitheciaceae may be more closely related to *Rhabdoweisia* in the Dicranales, considering the similarities in the overall habit, leaf shape, and cell shape and differentiation.

Phylogenetic conclusions--Sequence data of the chloroplast gene *rbc*L are useful in circumscribing the Orthotrichales, particularly with regard to the systematic position of taxa lacking peristome features that are central to the classification of mosses. Analyses of the variation in the nucleotide sequence using either the parsimony or the distance method strongly suggests that the Orthotrichales are polyphyletic, and that the Erpodiaceae and the Rhachitheciaceae are of haplolepideous affinities as suggested by their *Seligeria*-type peristome. The Orthotrichaceae too, are shown to be an artificial assemblage due to the current inclusion of *Amphidium* and *Drummondia*, two genera better placed among the Haplolepideae. The Orthotrichaceae are only distantly related to the latter clade and should rather be considered a member of a derived diplolepideous clade. The relationship to the Splachnales and the ciliate mosses remain unsettled, but at present all three lineages are best considered monophyletic. Molecular data do not support Vitt's (1982b) subfamilial phylogeny, and instead suggest that the Orthotrichaceae are composed of two lineages. The first consists of the Zygodontoideae, and the Orthotrichoideae, while the second includes all Macromitrioideae. The monophyly of the Zygodontoideae remains ambiguous, and it is proposed that if the paraphyly suggested by *rbc*L sequence data is confirmed by future studies that *Zygodon* sect. *Bryoides*, including the taxa with smooth laminal cell and often well-developed peristome, may represent the most primitive clade within this predominantly acrocarpous clade. *Schlotheimia* would occupy a similar position in the evolutionary history of the Macromitrioideae.

The Orthotrichaceae are now composed of 20 genera: *Bryodixonia*, *Cardotiella*, *Ceuthotheca*, *Desmotheca*, *Florschuetziella*, *Groutiella*, *Leiomitrium*, *Leptodontiopsis*, *Leratia*, *Macrocoma*, *Macromitrium*, *Muelleriella*, *Orthomitrium*, *Orthotrichum*, *Pleurorthotrichum*, *Schlotheimia*, *Stenomitrium*, *Stoneobryum*, *Ulota*, and *Zygodon*. Examination of cladistic relationships and associated phenetic distances suggests that the monotypic genus *Bryodixonia* may be better regarded as a patristically derived species of *Ulota*. Our molecular data furthermore reveal that larger genera such as *Macromitrium* and *Zygodon* may merely represent evolutionary grades. Gene data obviously have proven to provide a significant contribution in resolving the circumscription of the Orthotrichaceae, and the relationship of the main lineages. Above all, however, this molecular study has laid the foundation for critically reexamining the morphological characters that are central to the generic concept used in the Orthotrichaceae.

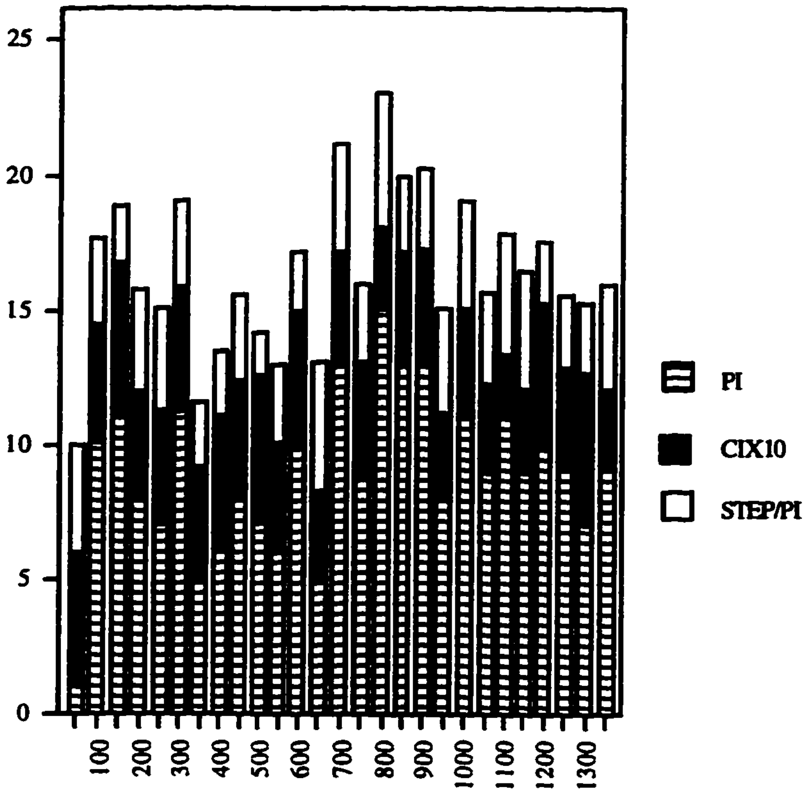

Figure 5.1: Distribution of phylogenetically informative characters, the average consistency index, and the average number of steps per phylogenetically informative character along the *rbc*L sequence.
Each class contains 50 sites, except the first one which includes sites 31-50.
▤: total number of phylogenetic informative characters (PI).
■: average CI value multiplied by 10
□: Total number of steps per total number of phylogenetically informative characters

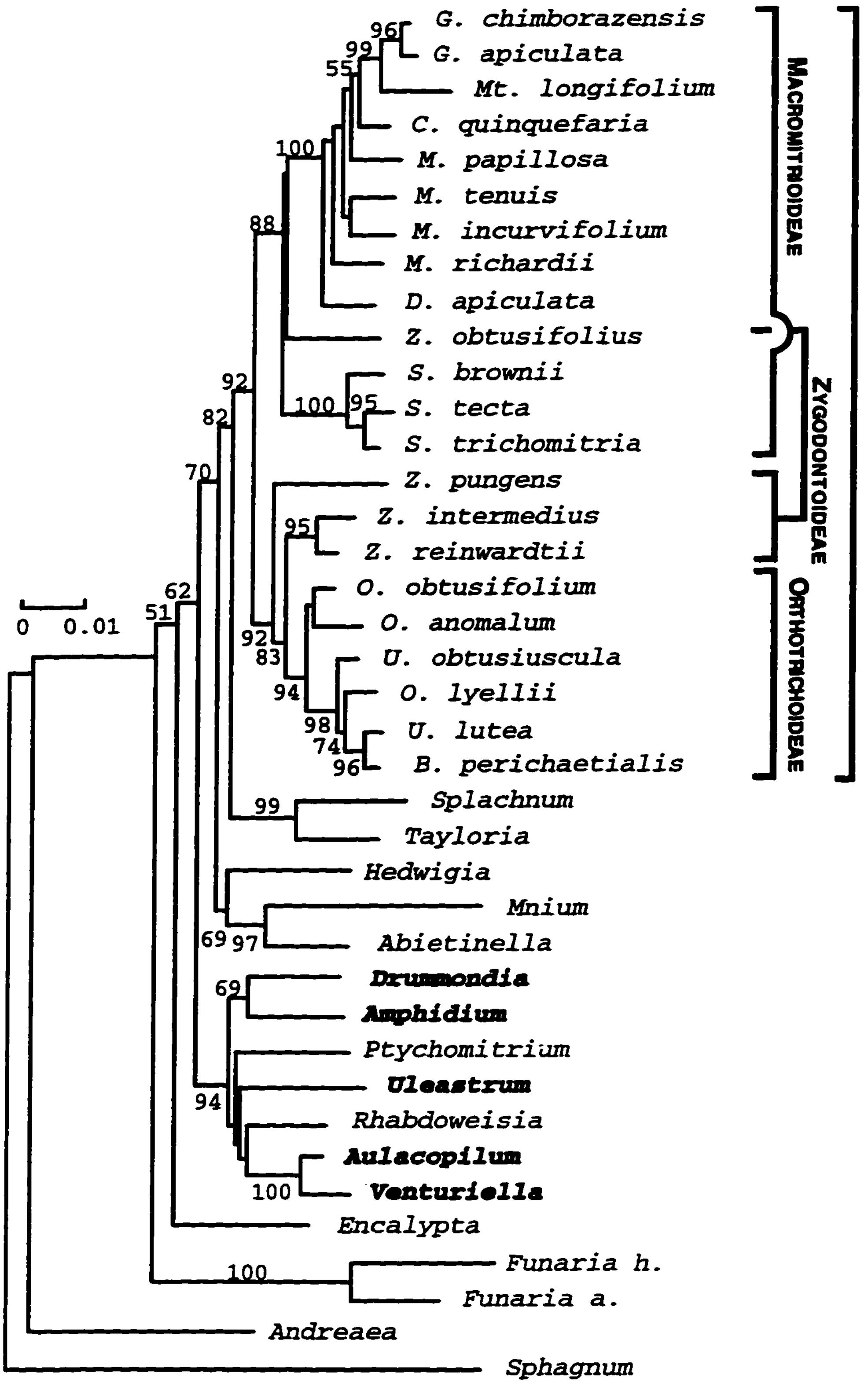

Figure 5.2. Phylogenetic tree reconstructed using the neighbor-joining method. with Tamura's distance parameter including both transitions and transversions. Bootstrap values (100 replicates) 50% or higher are plotted on the tree. Taxa excluded from the Orthotrichales are in bold.

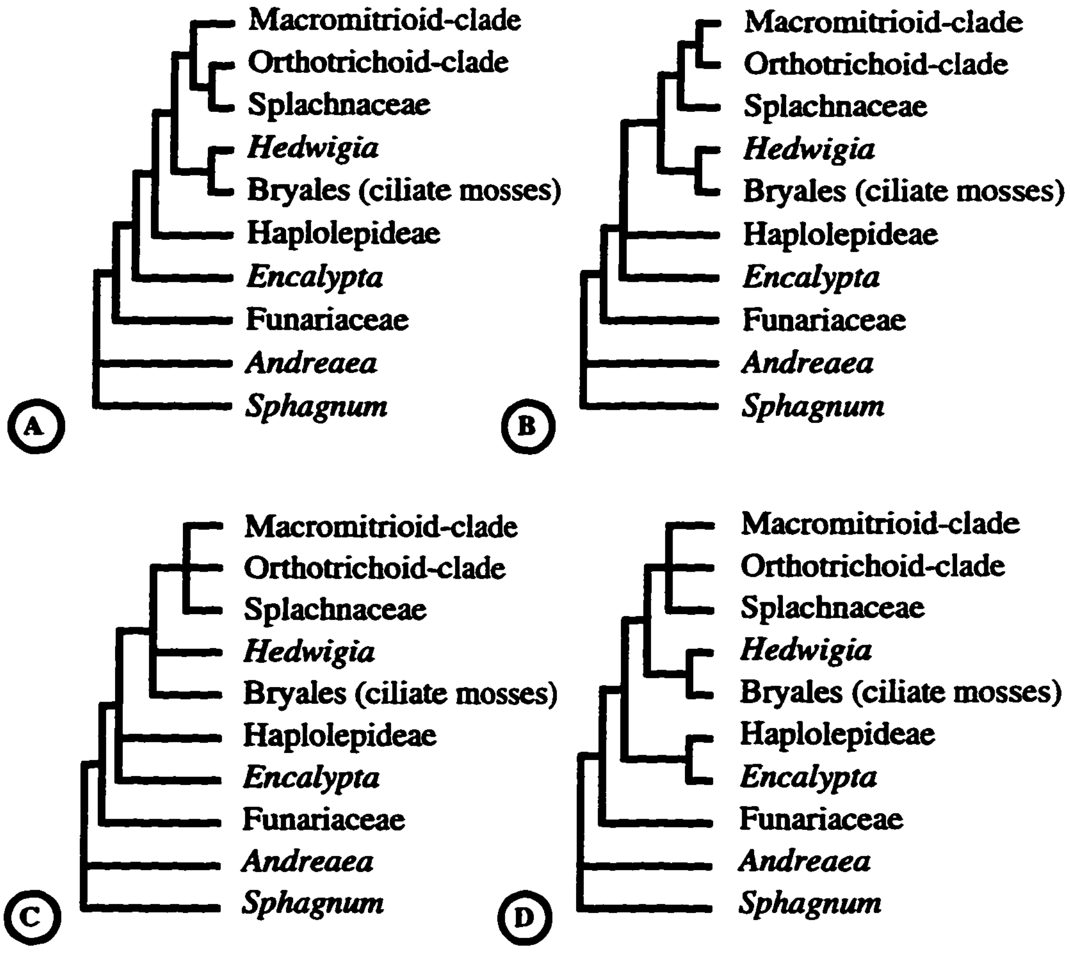

Figure 5.3. Summary consensus trees of most parsimonious Fitch trees found in a heuristic search using *rbc*L sequence data with *Sphagnum palustre* and *Andreaea rupestris* as designated outgroups.
A: strict consensus tree of all 3 islands (39MPTs; trees 964 steps; CI: 0.390; RI: 0.624);
B: 50% majority rule tree of island 3 (12MPT) (mean f-value: 13943 ± 656);
C: 50% majority rule tree of islands 1-2 (27MPTs) (mean f-value: 16633 ± 1308);
D: 50% majority rule tree of all 15 trees showing the Orthotrichaceae monophyletic (mean f-value: 16722 ± 2015)

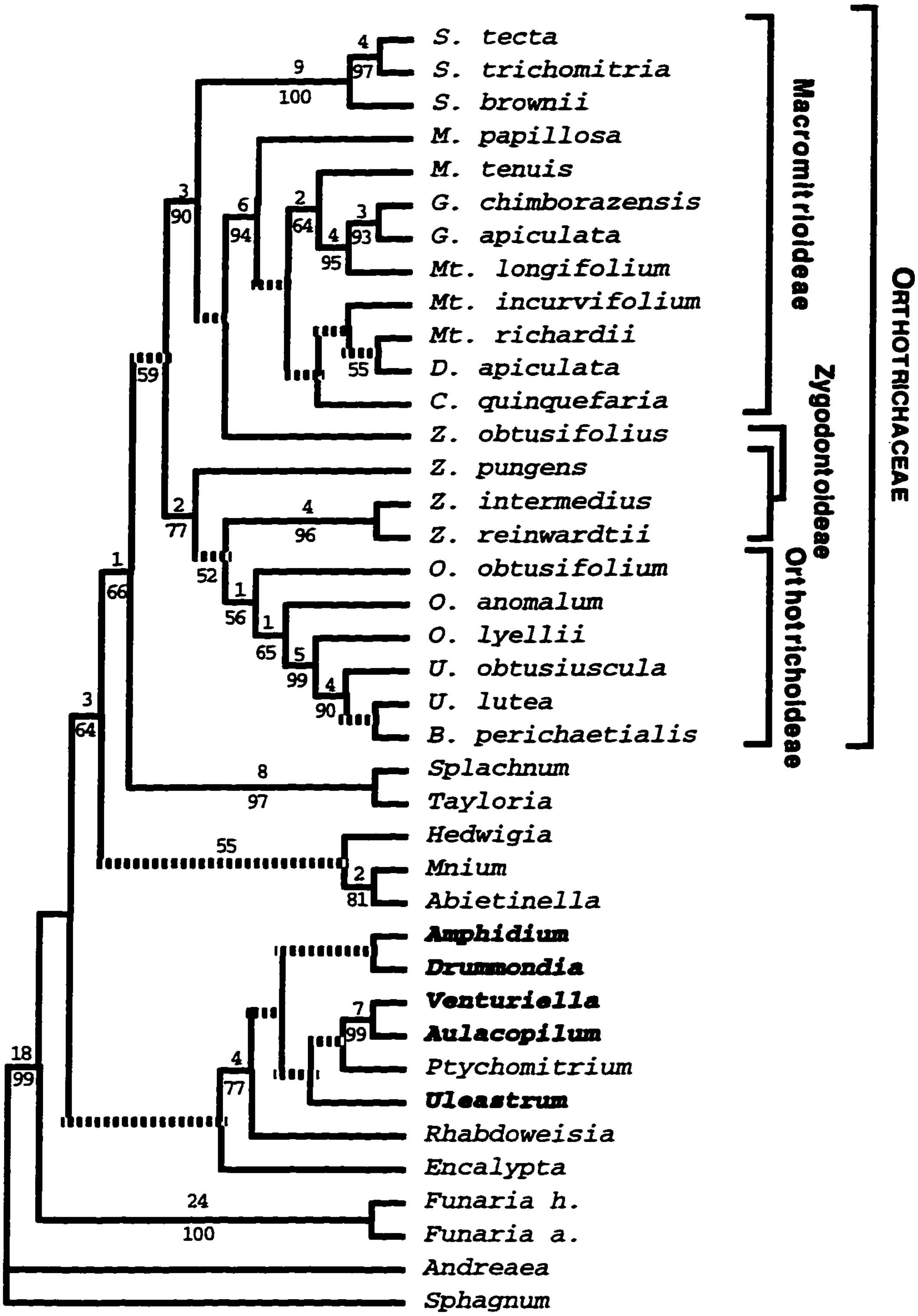

Figure 5.4. One of 39 most parsimonious Fitch trees found based on *rbc*L sequence data and using *Sphagnum* and Andreaea as outgroup. The dotted lines identify branches not present in the strict consensus tree. Bootstrap values (% of 100 replicates) higher than 50% are given below the branch, and decay indexes are presented above the branch. Taxa excluded from the Orthotrichales are in bold. (Abbreviations for the Orthotrichaceae follow those of table 5.4)

Table 5.1. Synthetic primers (5'–3') used for sequencing the *rbc*L gene in mosses (* marks primers designed and provided by G. Zurawski; others designed by authors).

Forward primers	
427*	GCTTATTCAAAAACTTTCCAAGGCCCGCC
997	GGTAAACTTGAAGGAGAACG
Reverse primers	
295R	CTAATGGGTAAGCAACATAAGC
515R	CATCCTAATAATGGACGACC
678R*	GATTTCGCCTGTTTCGGCTTGTGCTTTATAAA
895R*	ACCATGATTCTTCTGCCTATCAATAACTGC
1081R	CCCAGTCTTGAGTGAAGTAAATACC

Table 5.2. Taxa for which the *rbc*L gene sequence was obtained in this study (all vouchers deposited in ALTA unless otherwise noted).

Taxon	Voucher
ORTHOTRICHACEAE	
Zygodontoideae	
Zygodon pungens[1] C. Müll.	*La Farge-England* 8097
Zygodon obtusifolius Hook.	*Vitt* 38301
Zygodon intermedius B.S.G.	*Vitt* 29262.
Zygodon reinwardtii (Hornsch.)Braun	*Goffinet* 636.
Amphidium lapponicum (Hedw.) Schimp.	*Vitt* 33854.
Orthotrichoideae	
Orthotrichum obtusifolium Brid.	*Vitt* 33870.
Orthotrichum anomalum Hedw.	*Goffinet* 4115.
Orthotrichum lyellii Hook. & Tayl.	*Goffinet* 3162.
Ulota lutea (Hook. f. & Wils.) Mitt.	*Fife* 8042.
Ulota obtusiuscula C. Müll. & Kindb.	*Goffinet* 3161.
Bryodixonia perichaetialis Sainsb.	*Fife* 8083.
Drummondioideae	
Drummondia prorepens (Hedw.) Britt.	*Vitt* 26711.
Macromitrioideae	
Schlotheimia brownii Schwaegr.	*Vitt* 27485.
Schlotheimia tecta Hook. f. & Wils.	*Schäfer-Verwimp* 9686.
Schlotheimia trichomitria Schwaegr.	*Schäfer-Verwimp* 6902.
Cardotiella quinquefaria (Hornsch.) Vitt	*Buck* 26230.
Groutiella apiculata (Hook.) Crum & Steere	*Goffinet* 2764.
Groutiella chimborazense (Mitt.) Florsch.	*Goffinet* 1173.
Macrocoma papillosa (Thér.) Vitt	*Matteri* 6521.
Macrocoma tenuis (Hook. & Grev.) Vitt subsp. *sullivantii* (C. Müll.) Vitt	*Breedlove* 69342.
Macromitrium incurvifolium.	*Streimann* 49345.
Macromitrium longifolium (Hook.) Brid.	*Goffinet* 656.
Macromitrium richardii Schwaegr.	*Goffinet* 2648.
Desmotheca apiculata (Dozy & Molk.) Lindb.	*Vinas* 96-4

[1] This specimen is tentatively identified as *Zygodon pungens* C. Müll. a species hitherto not known from Africa (Malta 1926); but may represent a new species.

Table 5.2 (cont.). Taxa for which the *rbc*L gene sequence was obtained in this study (all vouchers deposited in ALTA unless otherwise noted).

Taxon	Voucher
ENCALYPTACEAE	
Encalypta procera Bruch	*Vitt* 37966.
ERPODIACEAE	
Aulacopilum hodgkinsoniae (C. Müll.) Broth.	*Vitt* 28261.
FUNARIACEAE	
Funaria apophysata (Tayl.) Broth.	*Vitt* 27234
Funaria hygrometrica Hedw.	*Priddle* 1408.
HEDWIGIACEAE	
Hedwigia ciliata (Hedw.) P. Beauv.	*Goffinet* 3324.
MNIACEAE	
Mnium thomsonii Schimp.	*Vitt* 35884.
PTYCHOMITRIACEAE	
Ptychomitrium gardneri Lesq.	*Ireland* 7038 (PMAE).
RHABDOWEISIACEAE	
Rhabdoweisia crenulata (Mitt.) Jameson	*Vitt* 36707.
RHACHITHECIACEAE	
Uleastrum palmicola (C. Müll.) Zander	*Vitt* 21162.
SPLACHNACEAE	
Tayloria lingulata (Dicks.) Lindb.	*Schofield* 98443.
Splachnum sphaericum Hedw.	*Goward* 95-1470.
THUIDIACEAE	
Abietinella abietina (Hedw.) Fleisch.	*Goffinet* 4106.

Table 5.3. Distribution and frequency (%) of constant and phylogenetically informative sites over all taxa and over the Orthotrichaceae only; characters with ambiguous or missing data are included.

	ALL TAXA				ORTHOTRICHACEAE
	first	second	third	total	total
	codon position				
Constant	368 (83.6)	407 (92.5)	148 (33.6)	923 (69.9)	1158 (87.8)
Phylogenetically informative	30 (6.1).	18 (4.1)	109 (24.7)	157 (11.9)	108 (8.2)

Table 5.4. Pairwise comparison of *rbc*L nucleotide sequence within the Orthotrichaceae Below diagonal: absolute distance; above diagonal: average distance. Distance values used for intrageneric comparisons (see text) are in bold.[1]

		1	2	3	4	5	6	7	8	9	10	11
1	*S. tecta*	-	0.006	0.012	0.035	0.036	0.035	0.040	0.040	0.036	0.049	0.033
2	*S. trichomitria*	8	-	0.012	0.036	0.036	0.033	0.040	0.040	0.038	0.047	0.036
3	*S. brownii*	16	16	-	0.030	0.031	0.030	0.033	0.033	0.033	0.041	0.031
4	*C. quinquefaria*	**46**	**48**	**39**	-	0.014	0.015	0.017	0.017	0.017	0.025	0.016
5	*M. tenue*	**48**	**47**	**41**	**19**	-	0.012	0.011	0.013	0.015	0.020	0.015
6	*M. papillosa*	**46**	**44**	**39**	**20**	16	-	0.016	0.017	0.018	0.024	0.020
7	*G. chimborazense*	**53**	**53**	**44**	**22**	**15**	21	-	0.003	0.014	0.016	0.019
8	*G. apiculata*	**53**	**53**	**44**	**22**	**17**	23	4	-	0.017	0.016	0.022
9	*Mt. incurvifolium*	**48**	**50**	**43**	**23**	**20**	24	**19**	23	-	0.023	0.014
10	*Mt. longifolium*	**64**	**62**	**54**	**33**	**26**	31	**21**	21	30	-	0.030
11	*Mt. richardii*	**44**	**47**	**41**	**21**	**20**	26	**25**	29	18	40	-
12	*D. apiculata*	**41**	**43**	**38**	**24**	**23**	27	**26**	26	**23**	**38**	**17**
13	*Z. intermedius*	**42**	**42**	**46**	**50**	**48**	47	**55**	59	**48**	**64**	**43**
14	*Z. reinwardii*	**46**	**44**	**46**	**47**	**49**	48	**56**	58	**45**	**65**	**46**
15	*Z. pungens*	**60**	**54**	**54**	**60**	**56**	56	**59**	59	**58**	**66**	**59**
16	*Z. obtusifolius*	44	40	41	46	41	40	45	49	42	55	42
17	*O. lyellii*	**60**	**54**	**54**	**63**	**58**	58	**65**	67	**62**	**72**	**64**
18	*O. obtusifolium*	**51**	**45**	**45**	**52**	**44**	47	**53**	55	**50**	**60**	**49**
19	*O. anomalum*	**56**	**50**	**50**	**57**	**52**	54	**56**	58	**58**	**63**	**60**
20	*U. obtusiuscula*	**54**	**48**	**50**	**59**	**52**	52	**59**	61	**56**	**66**	**60**
21	*U. lutea*	**62**	**56**	**56**	**65**	**58**	58	**65**	65	**62**	**70**	**66**
22	*B. perichaetialis*	**62**	**56**	**56**	**65**	**58**	58	**65**	67	**62**	**72**	**66**

[1] (B = *Bryodixonia*; C = *Cardotiella*; D = *Desmotheca*; G = *Groutiella*; M = *Macrocoma*; Mt = *Macromitrium*; S = *Schlotheimia*; O = *Orthotrichum*; U = *Ulota*; Z = *Zygodon*)

Table 5.4 (cont.). Pairwise comparison of *rbc*L nucleotide sequence within the Orthotrichaceae Below diagonal: absolute distance; above diagonal: average distance. Distance values used for intrageneric comparisons (see text) are in bold.[1]

	1	2	3	4	5	6	7	8	9	10	11
	12	13	14	15	16	17	18	19	20	21	22
1 *S. tecta*	0.031	0.032	0.035	0.045	0.033	0.045	0.039	0.042	0.041	0.047	0.047
2 *S. trichomitria*	0.033	0.032	0.033	0.041	0.030	0.041	0.034	0.038	0.036	0.042	0.042
3 *S. brownii*	0.029	0.035	0.035	0.041	0.031	0.041	0.034	0.038	0.038	0.043	0.043
4 *C. quinquefaria*	0.018	0.038	0.036	0.045	0.035	0.048	0.039	0.043	0.045	0.049	0.049
5 *M. tenue*	0.017	0.036	0.037	0.042	0.031	0.044	0.033	0.039	0.039	0.044	0.044
6 *M. papillosa*	0.020	0.036	0.036	0.042	0.030	0.044	0.036	0.041	0.039	0.044	0.044
7 *G. chimborazense*	0.020	0.042	0.042	0.045	0.034	0.049	0.040	0.042	0.045	0.049	0.049
8 *G. apiculata*	0.020	0.045	0.044	0.045	0.037	0.051	0.042	0.044	0.046	0.049	0.051
9 *Mt. incurvifolium*	0.017	0.036	0.034	0.044	0.032	0.047	0.038	0.044	0.042	0.047	0.047
10 *Mt. longifolium*	0.029	0.048	0.049	0.050	0.042	0.055	0.045	0.048	0.050	0.053	0.055
11 *Mt. richardii*	0.013	0.033	0.035	0.045	0.032	0.048	0.037	0.045	0.045	0.050	0.050
12 *D. apiculata*	-	0.037	0.035	0.045	0.030	0.045	0.036	0.042	0.041	0.046	0.046
13 *Z. intermedius*	**49**	-	0.009	0.031	0.034	0.024	0.018	0.023	0.023	0.026	0.026
14 *Z. reinwardii*	**46**	12	-	0.030	0.036	0.021	0.014	0.019	0.020	0.023	0.021
15 *Z. pungens*	**59**	41	39	-	0.037	0.036	0.027	0.032	0.033	0.036	0.035
16 *Z. obtusifolius*	39	45	47	49	-	0.042	0.035	0.037	0.037	0.042	0.042
17 *O. lyellii*	**60**	**32**	**28**	**47**	55	-	0.015	0.017	0.009	0.012	0.009
18 *O. obtusifolium*	**47**	**24**	**18**	**35**	46	20	-	0.011	0.017	0.020	0.017
19 *O. anomalum*	**56**	**31**	**25**	**42**	49	22	15	-	0.017	0.018	0.017
20 *U. obtusiuscula*	**54**	**30**	**26**	**43**	49	**12**	**22**	**22**	-	0.011	0.009
21 *U. lutea*	**60**	**34**	**30**	**47**	55	**16**	**26**	**24**	14	-	0.005
22 *B. perichaetialis*	**60**	**34**	**28**	**46**	55	**12**	**22**	**22**	12	6	-

[1] (B = *Bryodixonia*; C = *Cardotiella*; D = *Desmotheca*; G = *Groutiella*; M = *Macrocoma*; Mt = *Macromitrium*; S = *Schlotheimia*; O = *Orthotrichum*; U = *Ulota*; Z = *Zygodon*)

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Chapter six

Circumscription, and phylogenetic trends in the subfamilies of the Orthotrichaceae inferred from morphology

The Orthotrichaceae are a cosmopolitan family, with nearly 600 species (Vitt 1982a). Typical peristomate Orthotrichaceae share 1) a double peristome of alternating exostome teeth and endostome segments, 2) the lack of cilia as well as additional divisions in the IPL, and 3) a heavily thickened exostomial OPL (Lewinsky 1989, Shaw 1985, Vitt 1982a). Gametophytic features alone can be misleading in addressing systematic affinities of gymnostomous taxa or those taxa with a reduced peristome (e.g., *Amphidium* and *Drummondia*, see chapter 5), but most if not all Orthotrichaceae can nevertheless be characterized by the following combination of gametophytic characters: cauline central strand lacking, upper laminal cells isodiametric and papillose, alar cells not differentiated from inner basal cells, and perichaetia terminal on stem or lateral branches. The family now includes 20 genera (chapter two, three, and five) that are distributed among three subfamilies: the Orthotrichoideae, the Zygodontoideae (Schimp.) Broth., and the Macromitrioideae Broth. These subfamilies have traditionally been defined based on the position of the female gametangia (acrocarpy versus cladocarpy) and the shape of the calyptrae (cucullate versus mitrate; Brotherus 1925, Vitt 1972). Acrocarpous taxa with mitrate and typically plicate calyptrae, namely *Bryodixonia* Sainsb., *Muelleriella* Dusén, *Orthotrichum* Hedw., *Orthomitrium* Lewinsky-Haapasaari & Crosby, *Stoneobryum* Norris & Robinson, and *Ulota* Mohr., as well as *Pleurorthotrichum* with its smooth cucullate calyptrae, have traditionally been included in the Orthotrichoideae (Brotherus 1925, Vitt 1982a, Lewinsky 1994, Lewinsky-Haapasaari and Crosby 1996). The Macromitrioideae (i.e., *Cardotiella* Vitt, *Ceuthotheca* Lewinsky, *Florschuetziella* Vitt, *Groutiella* Crum & Steere, *Leiomitrium* Mitt., *Leratia* Broth., *Macrocoma* [C. Müll.] Grout, *Macromitrium* Brid., and *Schlotheimia* Brid.) share features of the calyptrae with the former subfamily, but differ from the Orthotrichoideae in their gametangia that develop from the apical meristem of lateral branches (except *Leratia*, see Crum 1987). *Desmotheca* Lindb. was segregated in its own subfamily by Brotherus (1925) and Crum (1987), but retained within the Macromitrioideae by Vitt (1990). The Zygodontoideae (*Leptodontiopsis* Broth., *Stenomitrium* (Mitt.) Broth., *Zygodon* Hook. & Tayl.) differ from the other subfamilies (except *Pleurorthotrichum*, and *Macromitrium* sect. *Reverbatum* Buck) by their invariably smooth and cucullate calyptrae.

Vitt (1982a) proposed a speculative phylogenetic arrangement in which the Zygodontoideae are basal to a dichotomy between the Orthotrichoideae and the Macromitrioideae. Such an evolutionary scenario is based, even though this is not explicitly stated, upon a acrocarpous ancestor with cucullate calyptrae. Molecular data (chapter five), support the hypothesis of an acrocarpous ancestor rather than pleurocarpous affinities of the family (or portion thereof) as suggested by Hedenäs (1994). Furthermore, interpretation of the gene-based phylogeny, leads to the hypothesis that this ancestor to the Orthotrichaceae, as well as the primitive taxa within the family, had smooth laminal cells. Alternative hypotheses to Vitt's (1972) classification have emerged with ongoing taxonomic studies, but were never formally proposed. In 1979, Vitt suggested that *Florschuetziella*, *Macrocoma* and *Leiomitrium* (then including species now placed in *Cardotiella*) may be closely related and represent a distinct taxon. More recently, Vitt, Koponen and Norris (1993) considered a separation of *Schlotheimia* and *Cardotiella* from the Macromitrioideae on the basis of the lobate versus the entire to lacerate calyptrae (see Vitt 1981a). In contrast to these hypotheses which share a monophyletic concept of the Orthotrichaceae, Churchill and Linares (1995) felt that the Orthotrichaceae *sensu* Vitt (1984) were defined only by plesiomorphic character-states and that the acrocarpous (Orthotrichoideae and Zygodontoideae) and the cladocarpous (Macromitrioideae) lineages did not share a common evolutionary history. They therefore proposed recognizing the Macromitrioideae as a distinct family, the Macromitriaceae S.P. Churchill. De Luna (1995), too, considered the Orthotrichaceae to represent an evolutionary grade, with the Macromitrioideae being more closely related to the Leucodontales, but his study did not include many peristome characters, which may prove critical when addressing the monophyly of the Orthotrichaceae or the Orthotrichales. A phylogenetic reconstruction of arthrodontous mosses based on 18S gene sequences (Hedderson et al. unpubl.), however, suggests that the acrocarpous and cladocarpous lineages of the Orthotrichaceae are closely related and form a monophyletic family. *Rbc*L sequence data are congruent with a monophyletic concept of the family, albeit the most parsimonious trees should be lengthened by one step (see discussion chapter five). The molecular phylogeny based on the chloroplast gene does, however, agree with Churchill and Linares' (1995) hypothesis regarding the monophyly of a combined Zygodontoideae and Orthotrichoideae clade, sister to the Macromitrioideae.

Only a few phylogenetic relationships hypothesized within the Bryopsida have been proposed or tested using modern phylogenetic approaches with morphological data (e.g., Koponen 1968, Vitt 1971, Churchill 1981), and only recently has cladistic rationale become of common practice in morphology-based evolutionary studies of mosses (De Luna 1995, Hedenäs 1994, 1995, Zander 1993, Vitt 1995). This study is the first attempt to circumscribe suprageneric taxa in the Orthotrichaceae and identify their phylogenetic relationships based on a cladistic analysis of morphological characters. The Orthotrichaceae are a large family and, except for *Orthotrichum* (Lewinsky 1993) and *Zygodon* (Malta 1926), speciose genera such as *Macromitrium*, *Schlotheimia*, and *Ulota* have not yet been critically monographed and the evolutionary history of their species remains obscure. Although generic relationships will be addressed, this study does not pretend to solve the phylogeny within the Orthotrichaceae. Instead it should be viewed as 1) a study examining the suitability of the characters and the states commonly used when addressing systematic relationships in the Orthotrichaceae, and 2) an attempt at defining broad phylogenetic relationships that may serve as a basis for future phylogenetic reconstructions within genera or groups of putatively related genera.

Material and Methods

Selection of taxa. Following the amended circumscription proposed in chapters two, three and five, 20 genera, now considered the terminal taxa of the Orthotrichaceae, are included in this study (Table 6.1). The monophyly of some genera, such as *Macromitrium* and *Zygodon*, has been questioned on molecular grounds (chapter five). Instead of compartmentalizing such taxa for the present analysis (Mishler 1994), several species thought to represent distinct infrageneric evolutionary trends have been included for *Macrocoma*, *Macromitrium*, *Orthotrichum*, *Schlotheimia*, *Ulota*, and *Zygodon* (Table 6.1). The range of taxa used for the present analysis was aligned further with that included in the molecular analysis (chapter five) in order to have overlapping taxon samples. Because sporophytes are unknown for *C. quinquefaria* (Vitt 1981a), a second species of *Cardotiella*, *C. elimbata* (Thér.) Goffinet (see chapter three) was added. In total, 34 taxa representing 20 orthotrichaceous genera are included in the analysis. Character states were determined by direct examination of herbarium material, except when available material was incomplete, in which case character-states were identified based on published descriptions. The one collection of the recently described monotypic genus *Orthomitrium* was not studied and all entries are based on the protologue (Lewinsky-Haapassari & Crosby 1996).

The systematic relationships of the Orthotrichales within the diplolepideous mosses, and particularly with regard to the Bryales *sensu lato*, remain unresolved (chapter five). Analyses of molecular data from either the chloroplast gene *rbc*L (chapter five) or the nuclear gene encoding for the 18S rRNA (Hedderson et al. unpubl.), have provided evidence for the basal position of the Funariales among arthrodontous mosses (Vitt, Goffinet, and Hedderson 1997). The Orthotrichales belong to a clade also including the Splachnales and the Bryales *sensu lato*. Sequence data of the 18S gene strongly suggest that the Orthotrichales are closely related to the Bryales *sensu lato*. Whether the ciliate mosses form an evolutionary grade or a natural group, and whether the Orthotrichales are sister to all Bryales or only a portion of these, needs to be further addressed critically. In either case, molecular evidence (particularly from the 18S; Heddersson et al. unpubl.) combined with general evolutionary trends in morphological characters such as branching pattern and distribution of perichaetia (La Farge-England 1996) suggest that the Orthotrichaceae are derived from an acrocarpous (see discussion in chapter 5) and not a pleurocarpous ancestor (as suggested by Hedenäs 1994). A single representative of the Funariales, Splachnales, and Bryales has been included in the present analysis (Table 6.1).

The Orthotrichales are composed of two families, the Orthotrichaceae and the Helicophyllaceae. The Helicophyllaceae are monotypic, and have dubiu uncertain affinities with the Orthotrichaceae: both families share *a priori* only one apotypic character, namely papillose laminal cells. *Helicophyllum* is gymnostomous, and addressing phylogenetic relationships of aperistomate taxa based on gametophytic characters only can be misleading (see De Luna 1995). The strongly dimorphic, if not trimorphic, leaves found on a single axis (or module) are in sharp contrast with isomorphic leaves in the Orthotrichaceae (in the Orthotrichaceae, leaf dimorphism applies to leaves of distinct modules; see character 5 below). At present the Helicophyllaceae are best considered outside the Orthotrichaceae, and should therefore not be included in the present analysis.

Representatives of the haplolepideae, a group sister to the Splachnales-Orthotrichales-Bryales clade, were not included in the present analysis. The peristome of the haplolepideae is an opposite peristome (Vitt, Goffinet & Hedderson 1997): the exostome is typically missing in the haplolepideae, but if developmental data were extrapolated to a mature state, the exostome teeth would indeed be opposite the endostomial segments.

Such peristome architecture is indicative of an early derivation in the evolution of arthrodontous mosses (Vitt, Goffinet, and Hedderson 1997), a hypothesis supported by analyses of nucleotide sequences of both the nuclear 18S (Hedderson et al. unpubl.) and the plastid gene *rbc*L (chapter five). Both studies suggest that the haplolepideae are derived from a *Funaria*-type ancestor and are sister to a clade composed of the Splachnales, Orthotrichales, and Bryales *sensu lato*. The relationships within the haplolepideae are poorly understood, and none of the taxa exhibits clear gametophytic plesiomorphies similar to those found in the Funariales and the Splachnales. Instead many taxa (e.g., Grimmiaceae and Pottiaceae) are clearly homoplastic with the Orthotrichaceae in gametophytic features such as thick-walled cells, and large mitrate and plicate calyptrae. Although all putative sister groups should ideally be included in a phylogenetic analysis, the haplolepideae were expected to introduce phylogenetic noise, rather than contribute to polarizing character-states, and were not considered in this study.

Data analysis. Fitch parsimony analyses were performed with PAUP (version 3.1, Swofford 1993) on a Power MacIntosh 7200/90 using the heuristic search with the following options in effect: keep all characters, multistate taxa interpreted as polymorphic, steepest decent, and collapse zero length branches. *Funaria hygrometrica*, *Brachymitrium jamesonii*, and *Mnium thomsonii* were used simultaneously in the analysis, but the trees were rooted via the outgroup method (Watrous and Wheeler 1981) with *Funaria* as the sole outgroup. None of the outgroups included exhibits plesiomorphic states (*sensu* Miller 1979 and Vitt 1984; see also Shaw and Rohrer 1984) for all characters. Character transformations were therefore left reversible, multistate characters unordered, and polyphyletic origins of derived character states allowed. Furthermore, character-states of binary or multistate characters were given the same weight. A preliminary search was performed with 100 random additions, followed by a second analysis of 500 random replicates but with swapping restricted to trees at the most one step longer than the most parsimonious trees (of length 'X') found in the preliminary search and on a maximum of 25 trees that are X+2 steps long (see Maddison 1991, Pryer et al. 1995). A strict and a 50% majority rule tree were constructed using PAUP. Consistency and retention indexes, as well as f-value (Farris 1972) were calculated for all most parsimonious trees using PAUP. Character evolution was reconstructed using the accelerated transformation criterion in MacClade version 3 (Maddison and Maddison 1992). Relative support for branches was determined by decay analysis (Bremer 1988, Donoghue et al. 1992) following the method developed by Baum, Sytsma, and Hoch

(1994) and using 100 replicates in the heuristic search. Enforcing topological constraints in heuristic searches, using the same set of options as in the above analysis, allowed for the costs of alternative hypotheses to be determined.

Results

Character definition and coding.

Sixty-eight characters were initially examined for all taxa, and are reviewed below. Invariable, and autapomorphic characters were retained for the analysis, but 14 characters were excluded because of the difficulty in either observing the actual character or defining distinct character-states. The matrix is presented in Table 6.2.

1. **Stem orientation**: orthotropic (0), plagiotropic (1). The life form of a moss results from the cumulative effect of its growth form, branching pattern and the position of the female gametangia (La Farge-England 1996). General trends observed among mosses suggest that certain combinations of character states of these three characters appear more commonly than others, and therefore that these characters may not be totally independent. Closer examination reveals however that all 12 possible combinations of characters states are found in mosses (La Farge-England 1996), and therefore all three characters should be considered independent and be included in the analysis (see characters 22 and 23). In the Orthotrichaceae, the stems are either orthotropic (e.g., *Zygodon*) or plagiotropic (e.g., *Macromitrium*). The basal portion of the stems of *O. lyellii* or *P. chilense*, become prostrate as the stem grows, but the distal portion of this main axis still grows upright. *Orthotrichum lyellii* is therefore considered orthotropic.

2. **Anatomy of axial cauline cells**: cells differentiated into a cluster of narrow, thin-walled cells that are often collapsed, leaving a central cavity in the stem (0), or cells not differentiated (1). In all three outgroup taxa, *Funaria*, *Brachymitrium*, and *Mnium*, the central cells are well differentiated from the surrounding parenchymatous cells, whereas in the Orthotrichaceae no such differentiation has been observed (Hébant 1977; but see Lewinsky [1977]).

3. **Anatomy of outermost cells of the stem**: cells thin-walled, forming a distinct hyalodermis (0), or hyalodermis not differentiated (1). In *Funaria* and *Brachymitrium*, the outer cells are dimorphic: cells immediately adjacent to the parenchyma cells have thick, red cell walls; the cells outside to this differentiated cortex have clear and thin walls, and form a unistratose layer called a hyalodermis. Such differentiation is known from a variety of mosses but is lacking in the Orthotrichaceae.

4. **Anatomy of inner cortical cells**: thin-walled (0), thick-walled (1) or multilayered (2). The parenchyma cells of the stems are thin-walled in *Funaria*, *Brachymitrium*, and *Mnium*. In most Orthotriochaceae, the walls are thick, i.e., in light microscopy, the middle lamellae separating two adjacent cells is clearly visible. In some taxa, such as in many species of *Ulota*, the cell wall appears to be composed of many, concentric layers.

5. **Leaf morphology**: stem and branch leaves identical (0), or stem and branch leaves dimorphic. In taxa with orthotropic, and sympodially branching stems, the leaves of the branches are identical to those of the preceding module (except for the juvenile leaves; Mishler & De Luna 1991, and La Farge-England 1996). In taxa with monopodially branching stems, the branch leaves may be identical to (*Florschuetziella*) or differ from the stem leaves (*Macromitrium*). In the latter case, the stem leaves are always smaller than the branch leaves. The branch leaves of taxa with dimorphic leaves, such as *Macromitrium*, are similar to the stem leaves of orthotropic, sympodially branching taxa with monomorphic leaves, such as *Orthotrichum*. Dimorphism is here considered to be the derived condition, suggesting that the stem leaves differentiated from leaves that were similar if not identical to the branch leaves. Consequently comparisons of cell shapes, ornamentations, etc., between species with monomorphic and dimorphic leaves are based on stem and branch leaves, respectively.

6. **Leaf base morphology**: lower half of leaf more or less as wide as upper half (0), or leaf base wide and contracted into the linear upper lamina (1). The vegetative leaves of *Bryodixonia*, and many species of *Ulota*, are unique within the Orthotrichaceae by their ovate leaf base, that is narrowed into an acuminate upper lamina.

7. **Leaf attachment**: base of leaf not decurrent or decurrencies composed of chlorophyllose cells (0), or decurrencies conspicuous, composed of inflated hyaline cells (1). Whereas many taxa of the Orthotrichaceae can have decurrent leaves (e.g., *Zygodon*, Malta 1926), decurrencies composed of several rows of hyaline, bulging, and sometimes papillose to tuberculate cells, are only known from the genus *Cardotiella*.

8. **Anatomy of costa**: guide cells differentiated (0) or not differentiated (1), unknown (?). Kawai (1968) recognized three basic layers in the anatomy of the costa: the adaxial (a), abaxial (b), and the median (c) layer. Based on the degree of differentiation of three cell layers and the presence of additional layers, Kawai (1968) distinguished between five types of costal anatomy. Kawai (1968) examined several taxa of the Orthotrichaceae. He interpreted the costa of *Leratia*, *Orthotrichum*, and *Pleurorthotrichum* as homogenous, thus with no obvious differentiation between the layers (type-A), whereas in *Macromitrium* he considered the adaxial cells to be clearly distinct (type-B). Lewinsky

(1994) and Malta (1926) too described the costa of *Orthotrichum* and *Zygodon*, respectively, as homogenous. In transverse section the differentiation of the costa is often ambiguous: all cells are thick-walled and while the width of the cells appears to decrease from the adaxial to the abaxial surface of the costa, the demarcation of distinct layers is often impossible. In surface view however, the adaxial and the abaxial cells are often of distinctive shapes. Adaxial cells (excluding chlorophyllose cells, e.g., *Muelleriella*) are always (except for *Leratia*) broadly rectangular, hyaline, and with moderately incrassate walls, and the end walls are always flat. By contrast the abaxial cells (again excluding chlorophyllose cells) are typically linear and pointed (e.g., *Macromitrium*), and rarely irregularly rectangular with flat ends (*Orthotrichum*; see character 10). The rectangular adaxial cells are here interpreted as guide cells. This character is not scored for *Orthomitrium*. In the protologue the anatomy is not described except for the absence of stereids (Lewinsky-Haapasaari and Crosby 1996).

9. **Laminal cells covering the adaxial surface of the costa**: present (0) or absent (1). Laminal cells (morphologically similar to the cells of the lamina, and thus chlorophyllose) covering the ventral surface of the costa have been found in all three outgroups. Within the Orthotrichaceae, chlorophyllose cells covering the ventral surface of the costa, are known only from two taxa of *Muelleriella*, including the putative primitive taxon *M. crassifolia* (Vitt 1982b).

10. **Shape of abaxial costal cells:** with flat ends (0), or pointed ends (1), unknown (?). In all the Orthotrichaceae examined, with the exception of the genus *Orthotrichum*, the abaxial cells are rather elongate to linear, with pointed ends. These cells are best considered substereids. In *Orthotrichum*, the abaxial cells are irregularly rectangular, with flat ends, and are hereinterpreted as distinct from substereids. In *Orthomitrium*, a monotypic genus with potential affinities with either the Orthotrichoideae or the Macromitrioideae, the costa is described as lacking stereids (Lewinsky-Haapasaari and Crosby 1996). This character-state would be congruent with that found in the Orthotrichum (but not all other genra of the subfamily), but is incompatible with the anatomy of the costa in the Macromitrioideae. Since no material was seen, this character is better scored "unknown".

11. **Abaxial surface of the costa** not or only partly covered by laminal cells (0), or laminal cells covering the abaxial surface of the costa almost to the base (1), unknown (?). In some taxa the abaxial layer of the costa is composed of chlorophyllose cells, often similar in shape and ornamentation to the adjacent laminal cells (e.g., *Florschuetziella*). Laminal cells covering the costa are known from various taxa in the Orthotrichaceae,

particularly in *Zygodon* (Malta 1926, Vitt 1993). In *Z. reinwardtii*, the laminal cells are reported to cover the apical portion of the costa, but the extent of this laminal sheet is variable within a population (chapter two), but is always restricted to the upper half of the leaf. In *Leratia* and *Florschuetziella* these laminal cells extend almost invariably to the base. In species of *Orthotrichum*, the abaxial layer of the costa is also composed of chlorophyllose cells, albeit not as conspicuously as in the former genera. *Orthomitrium* is scored as unknown.

12. **Upper laminal cell surface**: flat (0), or bulging (1). Both periclinal walls of upper laminal cells in many Macromitrioideae are distinctly bent outward whereas in most taxa these walls are plane.

13. **Ornamentation of upper laminal cell**: smooth (0), papillose (1), not applicable (-). The Orthotrichaceae have traditionally been characterized by their papillose laminal cells, but some taxa such as *Schlotheimia* or *Zygodon* sect. *Bryoides* are exclusively composed of smooth celled species. In *Muelleriella* the laminal are smooth, but the lamina is also bistratose. Because a link between the two characters could not be excluded, the ornamentation is, for now, scored as "not applicable" in *Muelleriella*.

14. **Morphology of papillae** "single" (0), or in pairs and apparently shortly bifid, or c-shaped (1), not applicable (-). The papillae in *Zygodon* sect. *Zygodon* appear scattered, whereas in *Zygodon obtusifolius*, as well as in species of the Macromitrioideae *sensu lato*, the papillae appear in pairs (not all of them), and may appear branched or narrowly c-shaped (see also Malta 1926). Unlike the branched papillae found in *Orthotrichum* however, they never are distinctly stalked and bifurcated.

15. **Anatomy of basal laminal cells**: cells with equally thickened anti- and periclinal walls (0), or cells with periclinal walls thicker than anticlinal walls (1), or "not applicable" (-). In transverse section, the cells of *Stenomitrium* and *Pleurorthotrichum* differ from other taxa in the Orthotrichaceae by their cells having periclinal walls that are much thicker than the longitudinal anticlinal walls. All other taxa examined have evenly thickened walls. This character was scored as "not applicable" for taxa with smooth cells.

16. **Anatomy of upper laminal cells**: cells-wall thin (0), or thick (1). Upper laminal cells of the Orthotrichaceae are typically thick-walled (middle lamellae visible in light microscopy), whereas *Funaria* and *Brachymitrium* have thin-walled cells.

17. **Shape of basal cells**: cells isodiametric (0), oblate (1), or elongate-rectangular (2). The laminal cells of the Orthotrichaceae are typically differentiated into rectangular basal cells and isodiametric upper cells (e.g., *Macromitrium*). In some taxa this

differentiation is not obvious and the lamina appears to be uniformly composed of isodiametric cells, except for the most proximal cells (e.g., *Macrocoma*). In *Groutiella* and *Cardotiella*, the basal cells are not strictly isodiametric, but are rather oblate (with transversely elongate lumens).

18. **Thickness of lamina**: unistratose (0), or bistratose (1). In the Orthotrichaceae, bistratose laminas are typical only for *Muelleriella* (Vitt 1976), but also occur scattered in other genera (*Orthotrichum hallii* [Vitt 1973], *Macromitrium diaphanum* [Vitt and Ramsay 1985]).

19. **Morphology of basal cells**: cells monomorphic (0), or cells dimorphic. Whereas in most Orthotrichaceae, the basal cells are rather uniform, except for larger juxtacostal cells in some taxa (e.g., *Groutiella*), in *Leptodontiopsis*, and particularly in *Pleurorthotrichum* and *Stenomitrium*, the basal cells are of two types with some cells having very incrassate walls forming distinct yellowish longitudinal bands alternating with hyaline, moderately thick-walled cells.

20. **Morphology of basal margin of the leaf**: composed of undifferentiated cells (0), or cells differentiated forming a mostly uniseriate band of hyaline cells that are larger than the adjacent inner cells, and have thinner and bulging outer periclinal walls (1). These differentiated cells occur in many Macromitrioideae.

21. **Morphology of basal marginal cells of the lamina**: cells not differentiated from inner laminal cells (0), or cells hyaline and rhombic (1), cells, hyaline, and quadrate, with their anticlinal walls much thicker than the periclinal walls (2), or cells hyaline, linear (3). Subquadrate marginal cells are typical of *Ulota* and *Bryodixonia*. Linear, hyaline (intra-) marginal cells extending from the base upward, are known only from the genus *Groutiella*. Other species have elongate to linear marginal cells, but these are always chlorophyllose and restricted to the upper portion of the lamina (e.g., *Macromitrium ulophyllum*, Goffinet 1993). These linear cells typical of *Groutiella* are different from the basal hyaline marginal cells referred to in character 20: in *Groutiella* the outer most basal marginal cells are rectangular to elongate, and with thin, outer periclinal walls, whereas the inner cells adjacent to this basal margin are linear and form a band that extends beyond the uniseriate basal margin of large cells.

22. **Position of perichaetia**: terminal on main axis (0), or terminal on lateral branches (1). The variation in distribution of perichaetial position has been examined extensively by La Farge-England (1996). Within the Orthotrichaceae, female gametangia (the perichaetia) are terminal either on the main axis (acrocarpy) or on lateral branches (cladocarpy). The main axis of acrocarpous taxa such as *O. anomalum* may resume

growth by producing 1 or 2 subapical innovations. These innovations are considered to be modules of the same hierarchial levels as the module from which they originated, thus these branches are considered "new" stems, and the plant is therefore an acrocarp. In *Macromitrium*, the stem produces lateral innovations even though the apical meristem is still growing. These lateral branches are generally terminated by a gametangium; the apical cauline meristem does not produce terminal perichaetia and the plant is considered cladocarpous. In *Macrocoma papillosa*, the stem produces lateral innovations, which produce terminal gametangia, but the main axis, too, produces terminal gametangia; *M. papillosa* is thus considered polymorphic - both acrocarpous and cladocarpous.

23. **Branching of the main axis**: sympodial (0) or monopodial (1), not applicable (?). The branching mode is independent from the distribution of perichaetia on the axes (Mishler and De Luna 1991; La Farge-England 1996). Sympodial branching refers to a succession of modules of the same hierarchial level by subapical innovation; whereas monopodial branching implies the connection of modules of different ranks; a stem, module of the first degree, produces lateral branches, modules of the second degree. Strictly acrocarpous Orthotrichaceae always branch sympodially, whereas cladocarps have monopodially branching stems. In cladocarpous taxa, the secondary branches that are terminated by a gametangium may resume growth by subapical innovations, and thus branch sympodially. Orthotropic branches may become prostrate and function as a stem, and thus branch monopodially. Clearly the "homology" of these axes needs to be addressed further, but in the present study, the branching pattern was compared between functional stems, regardless of whether the stem is a modified branch or not (see also Allen and Crosby 1986 for similar ambiguities in the Pterobryaceae). In *Brachymitrium* no branch development has been observed and this characters is scored as "unknown".

24. **Sexual condition**: monoicous (0), dioicous (1), or phyllodioicous (2). Individual plants can bear either both sexes (archegonia and antheridia) or only one. In dioicous taxa, male plants can be monomorphic with the female plants, or be reduced to dwarf plants that seemingly grow exclusively on the female plant. Such sexual dimorphism is called phyllodioicy, and is known within the Orthotrichaceae from only the Macromitrioideae. Ramsay and Vitt (1986) hypothesized, based on cytological data, that within *Macromitrium*, monoicy is derived through polyploidization of haploid dioicous taxa, and that the sexual conditions further evolved to phyllodioicy through aneuploidy.

25. **Morphology of paraphyses**: paraphyses - partly - composed of inflated to globose cells (0), or of rectangular cells (1). Paraphyses in *Funaria* and *Brachymitrium* are composed of inflated, rather thin-walled hyaline cells, whereas in all the

Orthotrichaceae studied, the paraphyses are made of rectangular, rather thick-walled cells.

26. **Spore morphology**: unicellular (0), or multicellular (1), unknown (?). Except for *Orthotrichum steerei* (Lewinsky 1993), multicellular spores are known only from *Macrocoma* subg. *Trachyphyllum* (this study), *Muelleriella* (Vitt 1976), and *Orthomitrium* (Lewinsky and Crosby 1996). The sporophyte of *Cardotiella quinquefaria* is unknown, and all the remaining characters were scored as "unknown".

27. **Calyptra surface**: smooth (0), or plicate (1), unknown (?). The calyptra of mosses is generally smooth. In many Orthotrichaceae, however, the calyptra is distinctly plicate, with the plication composed of two cells at the base and a uniseriate crest. Calyptrae of *Brachymitrium* were not seen, and characters pertaining to the calyptrae are scored as unknown (except character 28).

28. **Calyptra shape**: cucullate (0), or mitrate (1), unknown (?). Cucullate calyptrae are defined by a long single slit. In the Orthotrichaceae, both types occur, and the shape of the calyptrae is conserved within most genera. All outgroup taxa have a cucullate calyptra.

29. **Calyptra outgrowth**: absent (0), or present (1), unknown (?). The calyptrae of the Orthotrichaceae are typically ornamented with hairs. In taxa with plicate calyptrae the hairs originated from the plicae (Janzen 1917). The ontogeny of hairs in taxa with smooth calyptrae (e.g., *Pleurorthotrichum chilense*, and *Schlotheimia trichomitria*) has not been investigated, but is tentatively considered homologous to the former.

30. **Outline of surface cells of calyptrae in transverse section**: rectangular (0), isodiametric (1), unknown (?). In *Macromitrium* and *Orthotrichum*, amongst others, the calyptra is composed of a single layer of thick-walled cylindrical cells. In *Zygodon* and *Schlotheimia*, the outer cells are rectangular in transverse section. In *Funaria* and *Mnium*, the calyptrae is unistratose and composed of broadly rectangular cells.

31. **Thickness of calyptra**: unistratose (0), uni- to bistratose (*Zygodon*-type), (uni-) bistratose to tristratose (*Schlotheimia*-type), unknown (?). In *Zygodon* the calyptrae are composed of one to two layers. The outer layer is composed of rather narrow cells, and the inner cells are broader. In *Schlothemia*, the inner cells tend to be broader than the outer cells too, but the outer cells are mostly isodiametric rather than rectangular in transverse scetion. In the other taxa, the calyptrae are mostly unistratose (except for the plication) and composed of narrow - in transverse section isodiametric - cells.

32. **Outline of base of calyptra**: entire or at most slightly dissected (0), lobate (1), or fringed and lacerate (2), or deeply lobate (3), unknown (?). The genus *Schlotheimia* has

traditionally been characterized by its distinctly lobate calyptrae. The lobes, typically five of them, are trapezoidal in shape, and the sinuses do not extend beyond the unistratose base of the calpytrae. In *Ulota*, the base is also lobate, but the lobes are rather irregular, and the sinuses extend to the median portion of the calyptrae; this situation is considered a distinct state.

33. **Calyptra size**: covering the urn completely (0), only the upper half of the urn (1), or only the operculum (2), unknown (?). The size of the calyptra, in comparison with the length of the urn, is variable within the Orthotrichaceae. In most taxa the calyptrae reach the base of the urn whereas in others, particularly in *Groutiella* they cover only the upper half of the urn. In taxa with immersed capsules, the calyptra may only cover the operculum (*Desmotheca*).

34. **Calyptra apex smooth** (0), or scabrose due to projecting cell ends (1), unknown (?). The apex of the calyptra in *Zygodon obtusifolius*, *Leratia neocaledonica* (and others), is roughened by prorate cells. This situation differs from papillose calyptrae found in *Orthotrichum obtusifolium* or *Florschuetziella steerei*, where the cells produce papillae over their lumen.

35. **Operculum shape**: flat (0), or conical (1), unknown (?). In the Orthotrichaceae, the operculum is either flat or nearly so (*Desmotheca*), or conspicuously convex, and conic. Opercula were lacking in all the material of *Pleurorthotrichum* examined, consequently characters 35 to 38 are scored as unknown for this taxon.

36. **Rostrum: absent** (0), present (1), unknown (?). *Stoneobryum* is the only Orthotrichaceous taxon where the operculum is not terminated by a rostrum.

37. **Rostrum length**: long (0) or short (1), unknown (?). The length of the rostrum is here considered with regard to the width of the operculum. Short rostra, i.e., rostra shorter then the width of the base of the operculum, occur in various taxa of the Orthotrichaceae (e.g., *Orthotrichum*, *Florschuetziella*).

38. **Rostrum orientation**: perpendicular to the base of the operculum (0), or oblique or curved (1), unknown (?). The rostrum in *Orthotrichum* is always straight, whereas in *Zygodon*, the rostrum is oblique.

39. **Urn surface**: smooth (0), or ribbed (1), unknown (?). The exothecial cells in many Orthotrichaceae are differentiated into longitudinal bands. The cells forming the ribs differ from those betwen the ribs by the heavily thickened outer periclinal and axial anticlinal walls. The ribs alternate with the exostome teeth, and the differentiation of ribs may be correlated, at least in some taxa with a well developed peristome. This needs to be further studied.

40. **Width of the mouth of the urn**: mouth not constricted (0), mouth constricted when dry (1), unknown (?). In some Orthotrichaceae the mouth of the capsule is constricted even in the moist state, and thus is independent of the presence of ribs extending to the mouth. Malta (1926) hypothesized a correlation of the constriction at the mouth and the reduction of the peristome in *Zygodon*. Similar trends are obvious in *Macrocoma*. More study is needed to assess this phenomenon.

41. **Stomata**: absent (0), or present (1), unknown (?). Stomata are present in most mosses. In the Orthotrichaceae, they have been lost in *Schlotheimia tecta* and *S. trichomitria*. The loss of stomata is considered derived in mosses (Miller 1979).

42. **Number of guard cells**: 1 (0), or two (1), unknown (?). Except for *Funaria hygrometrica*, which has a single "donut"-shaped guard cell per stomata, all other taxa examined have two guard cells.

43. **Stomatal exposure**: phaneropore (0), or cryptopore (1), unknown (?). Stomata with their guard cells immersed and partly or nearly covered by subsidiary cells occur in various unrelated taxa of mosses (Vitt 1981). Within *Orthotrichum sensu lato*, Lewinsky (1977) hypothesized that immersed stomata had arisen only once, whereas Vitt (1976) argued for a polyphyletic origin of cryptoporic stomata and thus for the generic distinction of *Muelleriella*.

44. **Stomata distribution**: confined to the neck or the lowermost portion of the urn (0), to the lower half and median portion of the urn (1), or the upper half of the urn (2), unknown (?).

45. **Anatomy of the axial cells of the seta**: cells differentiated into a central strand (0), or not differentiated (1). All taxa examined, except *Muelleriella* and *Stoneobryum*, have the axial cells of the seta differentiated: their walls are thinner and often collapse, resulting in an axial cavity.

46. **Anatomy of the cells surrounding the central strand in the seta**: cells not differentiated from other cortical cells (0), or differentiated and forming a distinct ring around the central strand (1). In *Funaria*, as well as in some Orthotrichaceae (*Orthotrichum lyellii*; see drawings in Lewinsky 1994) the cells surrounding the central strand are differentiated from the adjacent cortical cells and form a more or less distinct ring around the central strand.

47. **Twisting of the distal portion of the seta**: dextrorse (0), or sinistrorse (1), unknown (?). These character-states are defined based on a view from the inside of the spiral. In many taxa the twisting in the distal portion of the seta differs from that in the basal portion. Here only the distal portion of the seta, including the neck of the capsule is

considered. This character was not scored for taxa with immersed or emergent capsules (e.g., *Stoneobryum mirum*)

48. **Preperistome (prostome)**: absent (0), or present (1). A preperistome (i.e., a thickened layer composed of the outer OPLwalls and adjacent walls-Outer Peristomial Layer, Blomquist and Robertson 1941-) was thought to be restricted to the Orthotrichoideae, and particularly *Orthotrichum sensu lato* (Lewinsky 1977), but have recently been reported also from *Florschuetziella* (Vitt 1979) and *Leratia* (this study).

49. **Degree of fusion of exostome teeth**: teeth free (0), fused into 8 free pairs (1), or joined all around (2). In many Orthotrichaceae the exostome teeth are fused into eight pairs. Lack of fusion is known from various taxa (e.g., *Leratia, Schlotheimia*), whereas reduction of the exostome leading to a continuous "membrane" has occurred only within the Macromitrioideae (e.g., *Groutiella, Macrocoma, Macromitrium*).

50. **Thickness of the exostomial OPL**: OPL as thick (0), thinner (1), or thicker (2) than the exostomial PPL. The orthotrichaceous peristome differs from other diplolepideous peristome types in the exostomial OPL-thickening being heavier than the PPL-thickening of the exostome tooth. For taxa with the exostome reduced to a membrane, this character was considered as "not applicable": The exostome in these taxa has equally thick outer peristomial and primary peristomial layers, and this reduction in the thickening is considered linked to the reduction in size.

51. **Morphology of exostomial PPL**: PPL with strong trabeculae (0), or trabeculae absent (1). Trabeculae correspond to the thickened anticlinal wall remnants of the exostomial PPL. Such thickenings are missing from all orthotrichaceous taxa examined, but are present in *Funaria, Brachymitrium*, and *Mnium*.

52. **Morphology of endostomial PPL**: PPL without (0), or with a median vertical wall, not applicable (-). In the opposite diplolepideous peristome, the outer layer of the endostome segments is composed of a single row of PPL cells, whereas in the alternate peristomes (Orthotrichaceae and *Mnium*, in this study) the segments are made of two half cells on their PPL surface. The endostome is reduced or missing in various taxa, and this character is treated as not applicable.

53. **Width of endostome segments**: segments as wide as exostomial teeth (0), or narrower (1). Peristome reduction has taken place in many orthotrichaceous taxa that have adapted to xeric habitats (Vitt 1981b). In *Zygodon reinwardtii*, the mouth of the urn is constricted, and the peristome is reduced to a rudimentary exostome and short endostome segments. The segments, though reduced, are still almost connected at their

base, and therefore the endostome segments are considered to be as wide as the teeth, since they are as wide as they could be, given the constriction of the mouth.

54. **Endostomial cilia**: present (0), or not (1). In the diplolepideous alternate Bryum-type peristome the IPL undergoes additional divisions leading to a 4:2:8 pattern. Breakdown along the longitudinal walls of these cells leads to the formation of narrow appendages, the cilia. Cilia are never developed in the Orthotrichaceae, and additional divisions in the IPL where not found in any of the taxa studied.

Characters excluded

1. Anatomy of outer cortical cauline cells. The outer cells of the stem are typically smaller than the parenchyma cells and colored (yellowish to deep orange rather than hyaline). In some taxa, this differentiation affects several layers of cells, instead of just the outermost cells. By contrast in *Z. pungens*, the superficial cells are poorly differentiated. In most taxa, the differentiation may affect only the color of the walls, whereas in others, the walls of adjacent parenchyma cells are also colored. This character needs further study.

2. Axillary hairs. Axillary hairs were found of taxonomic use in the Pottiaceae (Saito 1975) and within pleurocarpous lineages (Hedenäs 1989). Within the Orthotrichaceae these hairs seems to be caducous as they can only be found with certainty in the apical region of either the stem or branches. All orthotrichaceous taxa examined have axillary hairs with at a least a single brown and quadrate cell, that is well differentiated from the remaining cells that are hyaline and rectangular. In some taxa, most hairs have been found with two such basal cells (*Pleurorthotrichum chilense*; *Cardotiella quinquefaria*) and in *Leratia*, both cells that compose the hairs are short, and brownish. The hairs can be very short and composed of only two cells (*Bryodixonia*) to very long and with many cells (*Stenomitrium*). I have found variation within the number of cells in several taxa, and on single stem the number of cells can be variable. This character is best excluded until the variation is more critically examined.

3. Perichaetial leaves. All the Orthotrichaceous taxa have differentiated perichaetial leaves. The degree of differentiation however varies considerably. Perichaetial leaves that differ in shape and size from the vegetative leaves are known from various taxa (e.g., *Pleurorthotrichum*, *Ceuthotheca*, *Schlotheimia* subg. *Stegotheca*). In general, however, the differentiation is less conspicuous, and is often restricted to the cell areolation and ornamentation. In *Bryodixonia*, for example the basal cells of the perichaetial leaves are prorate, whereas those of the vegetative leaves are smooth. In *Groutiella* all leaves are

similar in shape, but the perichetial leaves have basal cells that are more lax, elongate, rhomboid, hyaline, and the differentiation into chlorophyllose, isodiametric or oblate cells is restricted to the distal portion of the leaf. The differentiation of the perichaetial leaves needs to be examined critically before discrete character states can be defined, and before this character can yield significant phylogenetic information.

5. Outline of stem transverse section and ranking of leaves. In *Stenomitrium* and *Pleurorthotrichum* the vegetative leaves are distinctly ranked in five rows. In *Florschuetziella* too the leaves are five-ranked, but less conspicuously. Examining the outline of the transverse section of the stem, revealed that in those taxa the section is distinctly pentagonal. In most other taxa however, the transverse section is also pentagonal, or nearly so, and rarely round. The character was excluded from the analysis, because it could not be broken down into discrete character states.

6. Leaf habit and shape: The habit of the leaf has been used to distinguish between most species of *Orthotrichum* and *Ulota*. The habit of the leaf seems to be correlated with the size and shape of the leaves, and perhaps even to the anatomy of the costa and cell areolation. The lack of stereids, for example, seems correlated to erect leaves, in taxa with short, or broadly oblong leaves (*Orthotrichum obtusifolium*, or *Zygodon obtusifolius*). In *Orthotrichum lyellii*, the leaves are flexuose, yet their costa lacks stereids, too. In this case the twisting of the leaf may be made possible because the leaves are much longer, and rather linear-lanceolate, as well as by a weakening of the costa in the upper lamina. These characters have to be considered with great caution, particularly if possibly linked characters are included. Furthermore, the shape of the leaves is variable within genera (see illustrations in Malta [1926, for *Zygodon*], Malta [1927, 1933, for *Ulota*], or Lewinsky [1993] and Vitt [1973] for variation in Orthotrichum), and identification of discrete states is not readily obvious. These characters are therefore better excluded from phylogenetic analyses, at least at the generic level and above.

7. Peristome features. The ornamentation of the peristome in the Orthotrichaceae has been studied by Lewinsky (1977) and Shaw (1985). Though definite trends may be apparent within genera (towards a more elaborate ornamentation in *Orthotrichum*, Lewinsky 1977), the ornamentation appears very much linked to the degree of reduction of the peristome. Taxa with well developed peristomes (e.g., *Schlotheimia brownii*, *Macromitrium longifolium*, or *Stenomitrium pentastichum*) have strongly striate-reticulate and even lamellate OPL surfaces, whereas reduced teeth in *Macrocoma* or *Groutiella*, are covered with low, scattered papillae. Taxa with intermediate types of peristome

(moderately reduced) have teeth that are papillose, striate-papillose, with the striation changing orientation upward along the teeth. The use of this character in phylogenetic analyses, may have to await further study.

The number of IPL divisions is another character that may prove significant in identifying primitive taxa within the family. Within the genus *Orthotrichum*, Lewinsky (1993) argued that the primitive taxa have 32 cells composing the IPL. Subsequent evolution led to a reduction and a displacement of the IPL, resulting in only 16 cells in the IPL, with their anticlinal walls not aligned with the planes of divisions in the outer layer (Lewinsky 1993). The number of cells in the IPL can be determined either from the segments alone or from the basal connecting membrane. In many taxa, however, half or all segments as well as the basal membrane are lost, and the pertinent characters are consequently missing. Using this character with a reduced taxon sample covering such a large family as the Orthotrichaceae, and including several taxa with reduced endostomes, may fail to yield an accurate phylogenetic signal and lead to excessive homoplasy. It is therefore excluded from the present analysis.

8. Alignment of the proximal cells of the operculum. Hedenäs (1994, 1995) considered this character in the phylogenetic reconstruction of pleurocarpous taxa. In the Orthotrichaceae, the cells of the proximal rows of the operculum, are aligned in more or less distinct vertical rows. In *Funaria hygrometrica*, these cells form lines that are spirally twisted around the axis of the operculum, an observation that led to the hypothesis that the position of the cell of the operculum may be correlated to the ontogeny of the peristome. The peristome is formed from three layers of cells, below the presumptive zone of the operculum. In *Funaria hygrometrica* the peristome teeth are strongly sinuose, similar to the pattern of cells of the operculum. It is thus possible that the orientation of the cells of the operculum is dependent on the habit of the peristome. Within the Orthotrichaceae, the strong reductionary trends in the evolution of the peristome (as hypothesized in *Orthotrichum*; Vitt 1971, Lewinsky 1993) may result in the loss of alignment of the cells of the operculum. Such correlations need to be tested before the character is used in a phylogenetic analysis.

9. Chromosome numbers. Though the number of chromosomes is known for representatives of several genera of the Orthotrichaceae (see summary in Fritsch 1991, Ramsay 1993, Ramsay, Streimann, and Vitt 1995), no counts have been made for the smaller genera. Furthermore, the number of chromosomes varies within genera (Fritsch 1991, Ramsay and Vitt 1984, 1986). Ramsay and Vitt (1986) hypothesized that polyploidy ($X=6$ to $X=12$) is followed by aneuploid reduction through chromosome loss

or fusion. It is however impossible to ascertain the origin of aneuploids (fusion or loss of chromosome). Assuming homology for a given chromosome number shared between taxa may result in false synapomorphies, and therefore this characters has been excluded from the analysis.

Phylogenetic relationships. The heuristic search, using *Funaria hygrometrica* as the outgroup, found a single island composed of 56 equally parsimonious trees. The trees are 191 steps long and have a consistency and a retention index of 0.414 and 0.685, respectively. The f-value varies between 3720 (tree three) and 4568 (trees 18-20). A strict consensus as well as a 50% majority rule tree are presented (Figs. 6.1 and 6.2). Furthermore, the tree with the lowest f-value (tree three) is chosen for examining character transformations in the evolution of the Orthotrichaceae (Figs. 6.3-6). In all trees *Brachymitrium* is sister to a dichotomy between *Mnium* and the Orthotrichaceae (Fig. 6.1). The orthotrichaceous taxa are distributed among three major clades, except for *Leratia* which is basal within the family (Fig. 6.1). The 56 most parsimonious trees are congruent with regard to the monophyly of a zygodontoid-clade (*Leptodontiopsis, Pleurorthotrichum, Stenomitrium, Zygodon*), an orthotrichoid-clade (*Bryodixonia, Muelleriella, Orthomitrium, Orthotrichum, Stoneobryum*, and *Ulota*), and a macromitrioid-clade (*Cardotiella, Ceuthotheca, Desmotheca, Florschuetziella, Groutiella, Leiomitrium, Macrocoma, Macromitrium, Schlotheimia*). This analysis confirms strong affinities of *Ceuthotheca* for the Macromitrioideae, and *Orthomitrium* for the Orthotrichoideae, as well as only a distant relationship between Orthotrichoideae and *Pleurorthotrichum*, which is here placed in the Zygodontoideae. Within the latter clade, *Zygodon* appears paraphyletic, with species of section *Zygodon* more closely related to a derived clade composed of *Leptodontiopsis, Pleurorthotrichum*, and *Stenomitrium*, than to the other sections of *Zygodon* (Fig.6.4). The monophyly of *Orthotrichum* and *Ulota* within the Orthotrichoideae is not supported by any tree. The paraphyly of *Ulota* results from *U. obtusiuscula* and *U. lutea* being more closely related to *Bryodixonia* than to *U. magellanica*. *Orthotrichum* appears either paraphyletic (e.g., tree 1, not shown) or polyphyletic (tree 3, Fig. 6.5), due to *Muelleriella* which is nested within *Orthotrichum*, or to closer affinities of *O. lyellii* with the clade composed of *Ulota, Stoneobryum*, and *Orthomitrium*. Within the Macromitrioideae, too, not all currently accepted genera appear monophyletic. Both *Macrocoma* and *Macromitrium* are represented as paraphyletic or polyphyletic assemblages (Fig. 6.6). The relationships within the Macromitrioideae remain ambiguous for many taxa as shown in the strict consensus tree

(Fig. 6.1). All most parsimonious trees, however, agree on most taxa with short basal cells being less derived, forming a paraphyletic sister group to the clade composed of taxa with long rectangular basal cells.

Discussion

The Orthotrichaceae: morphological characterization and infrafamilial relationships. A cladistic analysis using 54 morphological characters yields a strongly supported monophyletic Orthotrichaceae. Among the seven characters that support the monophyly of the Orthotrichaceae (Fig. 6.4) four can be considered invariable within the family: the lack of cauline central strand (character 2), thick-walled upper laminal cells (16), OPL thickening heavier than PPL thickening (50) and absence of trabeculae on the exostomial PPL (51). The latter two character states are invariable among taxa with well developed peristomes only. The absence of a cauline central strand is considered derived within mosses (Miller 1979) and so are cells with incrassate walls (Vitt 1984), a thick OPL and a lack of dorsal exostomial trabeculae (Vitt, Goffinet, Hedderson 1997.; chapter five). The costa is always composed, in the plane of the laminal cells, by two ventral guide cells. The abaxial cells are always clearly differentiated into substereids (e.g., *Zygodon*), except in some taxa, mostly those with weak costae (e.g., *Orthotrichum*). In *Orthotrichum*, the anatomy of the costa has been interpreted as homogenous (Lewinsky 1994), yet the abaxial cells differ clearly from the the adaxial guide cells, although their differentiation into substereids is not complete, and the cells are irregular in shape. The Orthotrichaceae, except for two species of *Muelleriella*, can be defined further by the absence of chlorophyllose cells on the adaxial surface of the costa (9). The remaining character-states, namely papillose laminal cells (13), and outer cells of the calyptrae with a short rectangular outline in transverse section (30) are not constant within the family (Figs. 6.4-6), but are here suggested the plesiotypic character-states of the family. The fusion of the exostome teeth into eight pairs defines the monophyletic group sister to *Leratia*, that is all three major lineages within the Orthotrichaceae (Fig.6.1). If a more derived position is considered for *Leratia* (see below), the fusion of teeth would then become pleisiotypic, and synapomorphic for the Orthotrichaceae. The parenchyma cells of the stem, are thin-walled in all three outgroups, whereas in the Orthotrichaceae (except for *Stoneobrym*) the walls are thick or even very incrassate (e.g., *Ulota*). The transformation of this character is considered ambiguous by MacClade, because of the basal position of *Leratia* which has very thick-walled parenchyma cells. Considering that all outgroup taxa have thin-walled cells, a transformation from thin to thick-, to very thick-walled cells appears more likely than having very thick-walled cells arising from thin-walled cells, and later evolving to moderately thick-walled cells.

In summary, the Orthotrichaceae *sensu* Vitt (1984; and considering amendments in chapters two, three, and five) are thus phylogenetically clearly defined by apotypic character-states such as: lack of a cauline central strand, moderately thick-walled cauline parenchyma cells, thick-walled and papillose upper laminal cells, exostome teeth fused into eight pairs and with an OPL thicker than the PPL, lack of trabeculae on the exostomial PPL. Whether all of these character-states would remain synapomorphic in a broader phylogenetic context is difficult to ascertain since the true sister-group to the Orthotrichaceae is not known. Thick-walled upper laminal cells are known among acrocarpous Bryales (the putative sister-group to the Orthotrichaceae; chapter five) from the Bartramiaceae, a group considered by some authors a distinct order, sister to the remaining Bryales *sensu lato* (e.g., Koponen 1982). Comparisons of 18S gene sequences, however, suggests that the Bartramiaceae are nested within the Bryales (Hedderson et al. unpubl.). The possibility for the incrassate upper cells to be plesiotypic in the evolution of the Orthotrichaceae, due a shared ancestry with the Bartramiaceae, can therefore be rejected, and thick-walled upper laminal cells remains a good apomorphy for the Orthotrichaceae. Churchill and Linares (1995) considered the Orthotrichaceae to be defined by plesiotypic character-states only, and to represent an evolutionary grade reached by two distinct lineages: one composed of the acrocarpous taxa (Zygodontoideae and Orthotrichoideae) and the second one, restricted to the Macromitrioideae. A polyphyly of the family would necessitate parallellism in six character-states defining the Orthotrichaceae, as well as in three additional characters pertaining to the calyptrae, that defined a combined Orthotrichoideae-Macromitrioideae clade (see below). Incrassate cells have evolved, and cauline central strand been lost in various clades (e.g., Bartramiaceae, Orthotrichaceae, Pottiaceae) and calyptrae sharing same shape, ornamentation, etc., have arisen independently in distantly related taxa (e.g., Orthotrichaceae, Grimmiaceae; Janzen 1917). The possibility for a polyphyletic origin of the Orthotrichaceae thus rests on the likelihood of parallelism (versus shared ancestry) in peristomial features among putatively distantly related taxa. Thick OPL and loss of dorsal exostomial trabeculae are known from the Pterobryaceae Kindb. (Nishimura and Watanabe 1992) and the Hookeriaceae Schimp. (Vitt 1981a), two pleurocarpous, but otherwise unrelated taxa (Vitt 1984). Hedenäs (1994) included *Schlotheimia* in his phylogenetic analysis of pleurocarpous mosses. He argued for a rather close relationship between the Orthotrichaceae and "a clade where most pleurocarps belong". The various types of distribution of female gametangia in mosses have been critically reexamined by La Farge-England (1996) who considered *Schlotheimia* cladocarpous and not pleurocarpous as Hedenäs did (1994). Molecular data, both from the chloroplast gene *rbc*L (chapter five) and the nuclear gene 18S (Hedderson et al. unpubl.) converge with respect to the monophyly of the Orthotrichaceae, and based on morphological data available, this systematic hypothesis still represents the most parsimonious evolutionary scenario (Vitt, Goffinet & Hedderson 1997).

Three large subfamilies have been recognized traditionally within the Orthotrichaceae based on the shape of the calyptrae and the distribution of the female gametangia: the Orthotrichoideae, Macromitrioideae and the Zygodontoideae (e.g., Brotherus 1924, Vitt 1982a). The distinction of these three major lineages within the Orthotrichaceae is supported by all 56 most parsimonious trees, but suppon for their monophyly is weak (Fig. 6.1). The relationships among these lineages is further congruent with Vitt's (1982a) hypothesis that the Zygodontoideae are sister to a clade combining the Orthotrichoideae and the Macromitrioideae (Fig. 6.1). The Zygodontoideae, as well as its sister-group are defined by three putative synapomorphies all pertaining to the calyptrae. Vitt (1984) considered the mitrate calyptrae, as found in the Orthotrichoideae and the Macromitroideae, the plesiotypic state in mosses. The cucullate calyptrae of the Zygodontoideae is invariably smooth, whereas in the Orthotrichoideae and the Macromitroideae the calyptrae are plicate, a state *a priori* considered derived in mosses. The polarization of the transformations of the shape (cucullate versus mitrate) and the surface of the calyptrae (smooth versus plicate) in the Orthotrichaceae is ambiguous, and cannot be solved without a better understanding of its potential sister-group. The narrowly rectangular cells composing the outer layer of the calyptrae in this subfamily may be seen as a reduction of the broadly rectangular cells in the outgroups, with further reduction leading to the in transverse section, isodiametric cells found in the Orthotrichoideae and Macromitrioideae. The oblique orientation of the rostrum may be an adaptation to facilitate shedding of the cucullate calyptrae or alternatively the calyptrae may have become be cucullate under the constraint of an oblique rostrum. In either case, the oblique orientation of the rostrum seems linked to the cucullate shape of the calyptrae, and may thus be considered plesiotypic, too. As a result, the Orthotrichoideae-Macromitrioideae clade appears more derived than the Zygodontoideae. The shape and number of papillae per cell were seen by Vitt (1972, 1982a) as discrimantory characters for the Zygodontoideae, many of which have up to six, small, clavate papillae per cell. The number and size of the papillae is, however, variable (Malta 1926, Zander & Vitt 1979, Vitt 1972, 1982a) and some Macromitrioideae have numerous small papillae (e.g., *M. incurvifolium*), too. Vitt (1983) and later Vitt and Ramsay (1985) argued that the primitive Australasian Macromitria have smooth laminal cells and that papillosity has arisen independently in several groups. The small papillae in the Macromitrioideae are most likely not strictly homologous to those of the Zygodontoideae. A distinction of papilla types between these taxa is difficult to rationalize based on morphology alone, and may have to await studies of their ontogeny. Considering that papillae in the Macromitrioideae are most often if not always associated, with bulging rather than flat cells, as in most Zygodontoideae, papillae may actually undergo a different developmental sequence in the Macromitrioideae and the Zygodontoideae.

The relationships between the three subfamilies as obtained from morphological data are weakly supported (Fig. 6.1) and differ from the nucleotide based phylogeny (chapter five), by the Orthotrichoideae being sister to the Macromitrioideae rather than forming a monophyletic group with the Zygodontoideae. Transferring the Orthotrichoideae to a sister-group position with the Zygodontoideae, a relationship congruent with the molecular phylogeny, and keeping all internal topologies to the subfamilies identical to those obtained in the most parsimonious tree, not only requires three additional steps, but also results in the Orthotrichoideae-Zygodontoideae clade being defined strictly by plesiomorphic character states. Olmstead (1995) recently argued in favor of "plesiospecies", i.e., species that lack uniquely derived characters. Extending this concept, should allow for "plesiosubfamilies" to be, at least tentatively accepted as well, as resulting from the diversification of an ancestral plesiospecies. Plesiotaxa may actually lack autapomorphies only at the time of the actual speciation event of the sister apotaxon. Ultimately, however, genetic change may occur in the plesiotaxon (gradual evolution), and lead to autapomorphic character-states. A plesiotaxon may thus only be an artifact of a particular study based on a given set of characters available. Future studies may reveal morphological or molecular character-states unique to a "Zygodontoideae+Orthotrichoideae" clade. Therefore the absence of synapomorphic characters for this combined clade may not represent an obstacle for accepting the monophyly of this lineage. Considering that most branches collapse when the most parsimonious scenario is relaxed by a single step, the alternative phylogeny, though it necessitates 3 additional steps, cannot be rejected based on the data presented here.

Circumscription and relationships within the Zygodontoideae. When Brotherus (1924) proposed the Zygodontoideae he included next to the type genus, also *Rhachithecium* Le Jolis, a genus later placed in its own family (Robinson 1964) and recently excluded from the Orthotrichales (chapter three and five). Malta (1926) arranged the nearly 70 species of *Zygodon* into four sections. Section *Bryoides* included all taxa with smooth laminal cells. Papillose taxa were distributed among three sections. Sections *Obtusifolii* and *Stenomitrium* are both monotypic and are defined by obtuse and five-ranked leaves, respectively. The type section, the largest of all four, included all remaining papillose taxa. Malta (1926) considered section *Zygodon*, and particularly the synoicous species, the *Z. reinwardtii*-group to represent the most primitive members of the genus. *Leptodontiopsis fragilifolia* was initially placed by Brotherus (1911) in the Pottiaceae (see also Brotherus 1924), and later described as *Zygodon fragilifolius* Broth. (in Malta 1926) and included in section *Zygodon*. Zander & Vitt (1979) too, suggested that *Leptodontiopsis* "is probably best considered as a synonym of *Zygodon*" (see also Vitt 1982a). *Leptodontiopsis* currently includes four species all endemic to high mountains in East Africa or Borneo (Brotherus 1910, Dixon 1934, 1938). The monotypic genus *Stenomitrium*, which is endemic to western South America (Robinson 1975), was segregated from *Zygodon* by Brotherus (1909) whereas Mitten (1869), and Malta (1926) considered it synonymous with *Zygodon*. Vitt (1984) tentatively retained *Leptodontiopsis* and the monotypic *Stenomitrium* distinct from *Zygodon*.

The relationships among the Zygodontoideae are well resolved and consistent in all trees, but support is weak (Fig. 6.1). *Stenomitrium* and *Leptodontiopsis* have clear affinities with *Zygodon*, particularly section *Zygodon*, resulting in the paraphyly of the genus *Zygodon sensu stricto*, in all most parsimonious trees (Fig. 6.4). The paraphyly seems even more accentuated by the inclusion of *Pleurorthotrichum*, a monotypic genus endemic to central Chile (Lewinsky 1994) and its close relationship with *Stenomitrium* and *Leptodontiopsis* (Fig. 6.4). Lewinsky (1994) recently argued that the affinities of *Pleurorthotrichum* could be with either the Macromitrioideae or the Orthotrichoideae, and that some characters are even incompatible with either placement. *Pleurorthotrichum chilense*, easily distinguished within the Orthotrichaceae by the narrowly lanceolate and long acuminate perichaetial leaves (Lewinsky 1994), actually shares several character-states (including plesiomorphic ones) with the Zygodontoideae, and particularly *Stenomitrium*. The perichaetia are terminal on the stem, and not on short lateral branches as suggested by Lewinsky (1994). The stem resumes growth through a single lateral innovation to a centimeter below the apex. This axis is clearly identifiable as a branch by the presence of juvenile leaves at its base (see La Farge-England 1996). Not all branches are developed following the perichaetium formation on the main axis, but these appear to be basitonous, rather than acrotonous as in the Macromitrioideae. Male gametangia were unknown for *Pleurorthotrichum* and phyllodioicy (a character state hitherto known only from the Macromitrioideae) was suspected (Lewinsky 1994). Perigonia were found however in at least two collections (*Carl & Inga Skottsberg 211*—H-Br.; *Mahu 10119*—H), on plants monomorphic with the perichaetium bearing plants. The calyptra is cucullate and in transverse section reveals a similar cell outline as in other species of the Zygodontoideae. The hairy calyptrae, reminiscent of the Orthotrichoideae or Macromitrioideae, are not incompatible with the Zygodontoideae, since they occur also in the African species, *Z. trichomitrius* Hook. & Wils., a species which also has differentiated perichaetial leaves (Malta 1926). The chlorophyllose cells are distinctly papillose, and whereas the upper laminal cells bear only one or two papillae (see Lewinsky 1994) the proximal chlorophyllose cells are ornamented by up to six, albeit small, papillae, similar to most species of section *Zygodon*. The transfer of *Pleurorthotrichum* from the Orthotrichoideae to the Zygodontoideae is thus well justified based on morphological characters.

Pleurorthotrichum forms with *Stenomitrium* and *Leptodontiopsis* a monophyletic group seemingly distinct from *Zygodon sensu stricto* by dimorphic basal cells. The proximal portion of the leaf is composed of alternating bands of clear, evenly thick-walled cells and cells with strongly incrassate, nodose to porose, yellow walls. Malta (1926) reports yellow-colored basal cell walls from various andean species of *Zygodon* (e.g., *Z. nivalis* Hampe), and nodose walls from a southern South American species, *Z. bartramioides* (Dusén) Malta. *Zygodon bartramioides* had been included in (section) *Stenomitrium* by Brotherus (1925), but excluded by Malta (1926). Both authors may have disagreed with regard to the affinities of *Z. bartramioides*, but both rejected recognizing *Stenomitrium* at the generic level because *Z. bartramioides* was seen as the obvious link between *Stenomitrium* and *Zygodon*, since it shared five ranked leaves with the former and acrocarpy with the latter (Brotherus 1925, Malta 1926). Griffin (1990), also placed *Stenomitrium pentastichum* in *Zygodon*, but unlike previous authors, described *Z. bartramioides* as having creeping stems with erect branches. Material of *Z. bartramioides* was not available for study, but may be crucial in understanding the affinities of *Stenomitrium*. *Leptodontiopsis*, *Pleurorthotrichum*, and *Stenomitrium* each exhibit at least one unique character that is *a priori* difficult to reconcile with the genus

Zygodon or even only with section *Zygodon*. *Leptodontiopsis* is the only taxon in the Zygodontoideae to have smooth urns. *Pleurorthotrichum* has differentiated cells surrounding the central strand in the seta, a uniquely reduced peristome (within the Zygodontoideae; chapter four) and by far the tallest plants in the subfamily, with a height of up to ten centimeters (Lewinsky 1994). *Stenomitrium* is easily distinguished by its cladocarpy and prostrate growth. The last two taxa further differ from section *Zygodon* by the seta which is twisted to the left in the distal portion. Whether *Leptodontiopsis*, *Pleurorthotrichum*, and *Stenomitrium* warrant generic status based on these patristic distances, depends,within a phylogenetic framework, more on the monophyly of its immediate sister-groups (i.e., section *Zygodon*) than on the character-states themselves.

Section *Zygodon* is composed of two major groups, distinguished by their sexual condition. Malta (1926) considered the dioicous taxa derived and the monoicous species composing the *Zygodon reinwardtii* group the most primitive within the genus. This hypothesis is supported by the present data but comes within a paraphyletic concept of the section, with *Z. intermedius* sister to the dioicous genera *Leptodontiopsis*, *Pleurorthotrichum*, and *Stenomitrium*. Constraining *Z. intermedius* and *Z. reinwardtii* to be sister-taxa, requires only one additional step. To satisfy the monophyly of the genus *Zygodon*, parsimony would need only to be relaxed by two steps. Obviously the relationships among sections of *Zygodon* are not robust. Expanding the current concept of *Zygodon* to accomodate *Stenomitrium*, *Leptodontiopsis* and *Pleurorthotrichum*, to solve the paraphyly of *Zygodon* may not be appropriate, and would *a priori* obscure evolutionary trends within the Zygodontoideae, as it would result in a highly variable and ill-defined genus.

The remaining papillose taxon in *Zygodon*, namely *Z. obtusifolius*, is sister to a clade combining both sections *Bryoides* and *Zygodon*, as well as the *Stenomitrium*-clade. *Zygodon obtusifolius*, the sole species in section *Obtusifolii* (Malta 1926) differs from congeneric taxa by its short, obtuse, erect-appressed leaves, bulging laminal cells, short basal cells, chlorophyllose cells covering most of the abaxial surface of the costa, prorate cells at the apex of the calyptrae (also seen in *Z. pungens*), and "bifid to c-shaped" papillae (Malta 1926, and pers. obs.) Of these characters, only the latter four were considered in the present analysis (see "results"), and only two of these, namely the laminal cells covering the costa and the rather isodiametric basal cells of the leaf phylogenetically define *Z. obtusifolius*. The prorate apical cells of the calyptrae are interpreted as a plesiotypic state, due to the "basal" position of *Leratia*, which also has these differentiated cells. Furthermore, all taxa with "bifid" papillae also have simple papillae, and all these taxa were scored polymorphic. Since *Florschuetziella*, *Z. obtusifolius*, and *Leratia* which all share this polymorphism, are "basal" in their respective clade or in the family, the character transformation is left ambiguous, and thus not phylogenetically informative. *Leratia* has been traditionally placed in the Macromitrioideae (Brotherus 1925 [as *Leratiella* Broth. & Syd.]; Crum 1987, Vitt 1982a) a relationship based on a "*Macromitrium*-like peristome" with deep-set endostome and a short, and irregularly dissected membrane (Crum 1987). While a relationship with the Orthotrichoideae has been argued against by Crum (1987), affinites to the Zygodontoideae have never been hypothesized, even though *Leratia* has a non-plicate cucullate calyptrae. *Leratia* may indeed be better considered closely related to *Z. obtusifolius*. The only character that is *a priori* in conflict with an inclusion in the Zygodontoideae, is the presence of a preperistome (Goffinet unpubl.). This additional outer reduced peristome has not been hitherto reliably reported from the Zygodontoideae (Lewinsky 1977). *Zygodon obtusifolius* is a widespread species known from Asia, Africa, South America, and Australasia (Lewinsky 1990, Vitt 1993). In Australasia, it is known from several localities in New Zealand, but only one from Australia (Tasmania; Lewinsky 1990). Section *Obtusifolii* is currently considered monotypic (Malta 1926), but examination of populations from Thailand, Mexico, and Australasia reveals variation in peristome ornamentation (results not shown) that may be indicative of cladogenesis. The Australasian populations are considered conspecific (Lewinsky 1990), and their disjunct distribution between New Zealand and Tasmania as well as their overall scattered distribution in New Zealand may suggest poor dispersal capabilities. Within such scenario and considering that *Leratia* is endemic to New Caledonia, from where *Z. obtusifolius* has not been reported yet (Pursell and Reese 1982), it is easily conceivable that *Leratia* was derived from *Z. obtusifolius* through long distance dispersal or represents a vicariant of the latter. A basal position of *Leratia* within the Orthotrichoideae appears anomalous, as it leads to an early loss -reversal- of features indicative of adaptations to xeric environments (bulging cell-walls and "bifid" papillae; see Schofield 1981) in a family where major evolutionary trends are considered to lead to increased drought tolerance (Vitt 1972, 1982a, 1983, Vitt and Ramsay 1985). *Leratia* is thus best considered a member of the Zygodontoideae, with close affinities with *Z. obtusifolius*. Section *Obtusifolii* may now again be characterized by its distinct papillae, as suggested by Malta (1926) as well as by the bulging cells, both unique features within the Zygodontoideae.

With both sections *Obtusifolii* and *Zygodon*, now derived through the acquisition of papillae, section *Bryoides*, defined by smooth laminal cells, may be regarded as the most primitive member of the Zygodontoideae. Such a scenario would be against Malta's (1926) hypothesis, but be more congruent with general trends in mosses (see Miller 1979, and Vitt 1984) as well as with the molecular based hypothesis that the Orthotrichaceae would be derived from an acrocarpous ancestor with a cucullate calyptrae and smooth laminal cells.

Circumscription and relationships within the Orthotrichoideae. The Orthotrichoideae have been traditionally defined by terminal cauline gametangia and a large mitrate calyptra (Brotherus 1925, Vitt 1972). Neither of these character-states is however apomorphic for the subfamily in the present phylogenetic scenario: acrocarpy is the plesiotypic state to the family, and mitrate calyptrae evolved in the ancestor to the Orthotrichoideae and the Macromitrioideae. Derived character-states distinguishing the Orthotrichoideae from the Macromitrioideae (and also from the Zygodontoideae) can instead be found in the sporophyte: the stomata are found in the lower portion of the urn, above the neck (41) and the distal portion of the seta is sinistrorse (47; Fig. 6.5). Six genera share this set of characters and compose the Orthotrichoideae (Fig. 6.5): *Bryodixonia*, *Muelleriella*, *Orthomitrium*, *Orthotrichum*, *Stoneobryum*, and *Ulota* (the position of the stomata is however variable within the latter; Malta 1927, 1933). The adaxial cells of the costa are either well differentiated from the adaxial guide cells, into substereids (*Ulota* spp., *Muelleriella*, *Stoneobryum*) or only weakly so and the costa appears homogenous in transverse section (e.g., *Orthotrichum*). The absence of distinct substereids in *Orthotrichum*, may be interpreted as a result on heterochrony, with the differentiation of the dorsal cells prematurely stopped.

The paraphyly of the two most speciose genera, *Orthotrichum* and *Ulota* as suggested based on *rbc*L sequence comparisons (chapter five), is supported by morphological data.

A molecular comparison of *Bryodixonia perichaetialis* with two species of *Ulota* revealed that *Ulota lutea* is more closely related to *Bryodixonia* than to *U. obtusiuscula* (*U. magellanica* not included in molecular analysis) suggesting that a generic distinction of *Bryodixonia* is not appropriate. Close affinities between *Ulota* and *Bryodixonia* are very much apparent from the morphological analysis: both genera share well differentiated basal marginal cells with their thicker anticlinal walls (21/2), inner cortical cauline cells with very thick (and deeply colored) walls (4/2; except in *U. magellanica*), and a deeply lobed but not lacerate calyptrae (32/3). *Bryodixonia* differs from *Ulota* by the "highly differentiated and conpicuous perichaetial bracts and the diminutive calyptrae" (Sainsbury 1945) as well as prorate basal cells in the perichaetial leaves (unique within the Orthotrichaceae, results not shown), and a flat operculum. The taxonomy of the European species of *Ulota* has been well established (see Frey et al. 1995) and the genus has been revised for Australia (Malta 1927), South-America (Malta 1933), and recently for North America (Vitt 1972) and Japan (Iwatsuki 1959). Despite this good taxonomic framework, evolutionary trends within the genus appear obscure and no infrageneric classification of the approximately 50 taxa (Vitt, Koponen, and Norris 1993) has ever been proposed. This apparent homogeneity within the genus may suggest that the monophyly of *Ulota* should be restored by including *Bryodixonia* rather than splitting *Ulota* into several, *a priori* ill defined genera.

The genus *Orthotrichum* is, with 118 species (Lewinsky 1993, 1995, 1996) by far the most speciose genus of the Orthotrichoideae. The species are currently distributed among seven subgenera (Lewinsky 1993), of which three are represented in this study: subg. *Orthophyllum* (*O. obtusifolium*), subg. *Orthotrichum* (*O. anomalum*) and subg. *Gymnoporus* (*O. lyellii*). The genus appears para- or even polyphyletic in all most parsimonious trees, due to the inclusion of *Muelleriella* or to the stronger affinities of *O. lyellii* for the clade composed of *Orthomitrium*, *Stoneobryum*, and *Ulota sensu lato*. *Muelleriella*, *Stoneobryum*, and *Orthomitrium*, are all recent segregates of *Orthotrichum*, and are composed of four, two, and one species, respectively (Vitt 1976, Norris and Robinson 1981, Lewinsky-Haapasaari and Crosby 1996). The most parsimonious scenario restoring the monophyly of the *Orthotrichum* complex is only one step longer than the unconstrained tree, but retains the paraphyly of *Orthotrichum sensu stricto*. *Orthotrichum obtusifolium* and *O. anomalum* (the type of the genus) are closely related (Fig. 6.5) and together form a sister-group to *Muelleriella*, a relationship defined by the flat operculum and the presence of a preperistome. *Muelleriella* differs from typical *Orthotrichum* species by a bistratose lamina, a more "complex" costal anatomy, lack of a central strand in the diminutive seta (capsule immersed), multicellular spores, exothecial cells with strongly thickened axial anticlinal walls (thickening increases towards the outer surface where the thickening of both walls meet, resulting in a V-shape pattern in transverse section), and smooth capsules (Vitt 1976, this study). Such high patristic distance may indicate high evolutionary rates in *Muelleriella* or an early divergence from *Orthotrichum*. Lewinsky (1977) argued against a segregation of *Muelleriella* from *Orthotrichum* as both taxa share cryptoporic stomata and a preperistome, two states previously known, within the Orthotrichaceae, only from *Orthotrichum*. Cryptoporic stomata occur however also in another segregate, *Stoneobryum*, which does not appear closely related to *Orthotrichum*, and preperistomes have been described recently from *Florschuetziella* (Macromitrioideae; Vitt 1979) and *Leratia* (Zygodontoideae; this study). *Muelleriella* is composed of four species; three of these are narrow high elevation island endemics that are thought to have been derived from a widespread lowland species, *M. crassifolia* (Vitt 1976). The multicellular spores may *a priori* be seen as an argument against long distance dispersal (van Zanten and Pócs 1981) and thus recent speciation within the genus. Morphometric analysis of *M. crassifolia* over its range reveals little variation in all characters studied (Vitt 1976). If strong selective pressure prevent morphological divergence between long isolated populations of this species (Vitt 1982b), the "significant" morphological differences between *Orthotrichum* and *Muelleriella* may be indicative of an ancient divergence from a common ancestor shared with *Orthotrichum* (*sensu* Vitt 1984), rather than a recent split from a derived (*sensu* Lewinsky 1994) group of *Orthotrichum* (i.e., with cryptoporic stomata). The extent of morphological divergence may of course vary with the mode of cladogenesis, and *Muelleriella* may have accumulated all the above changes rapidly after speciation, and have remained rather static in its morphology ever since then.

Retaining *Muelleriella* as a distinct genus, may necessitate redefining *Orthotrichum*, and consider additional segregate genera. If *Orthotrichum* represents an evolutionary grade rather than a natural group, distinct evolutionary lineages may only be identified if their potential sister taxon (e.g., *Ulota*) is included in the analysis. The affinities between *Orthomitrium* and *Stoneobryum* (Fig. 6.5) are most likely an artifact of the data, as both taxa are patristically only very distantly related (11 states separates these two taxa in tree three, Fig. 6.2) and should be reconsidered more specifically when addressing the evolution of the *Orthotrichum*-complex. A phylogenetic reconstruction of the genus *Orthotrichum* is in progress (Lewinsky pers.com.), and should allow for the circumscription of *Orthotrichum* and its relationships to its "satelitte" genera to be addressed more critically.

Circumscription and relationships within the Macromitrioideae. The Macromitroideae are composed of over 300 species distributed among nine genera, all restricted to south temperate, montane tropical or subtropical climates (Vitt 1982a). The subfamily has been defined traditionally by large mitrate calyptrae, creeping stems, and gametangia terminal on lateral branches (Vitt 1972, 1982a). In the present phylogenetic scenario (Figs. 6.5-6) mitrate calyptrae are shared with the Orthotrichoideae.

Florschuetziella is sister to all remaining taxa of the subfamily in all most parsimonious trees (Fig. 6.1). Because *Florschuetziella* is polymorphic with regard to the position of the perichaetia (a single gametophyte can bear terminal perichaetia on stems or branches), the origin of cladocarpy in the subfamily is ambiguous: is cladocarpy plesiotypic in the Macromitrioideae or has it arisen independently in *Florschuetziella* and in the ancestor to the remaining members of the subfamily? If the distribution of the perichaetia is controlled by a single gene, polymorphism may be indicative of gene duplication or autopolyploidy with subsequent mutations or allopolyploidy. Genome duplication can be suspected early in the evolution of *Macromitrium* (Ramsay and Vitt 1984, 1986) and may have even occurred in the ancestor to the subfamily. Genetic change required for the character transformation to cladocarpy may be "minimal", since cladocarpy occurs in Orthotrichoideae and the Zygodontoideae, too. Though autopolyploidy seems likely, allopolyploidy has recently been demonstrated in mosses, and may actually be a common mechanism of speciation in bryophytes (Boisselier-Dubayle and Bischler 1996, Wyatt et al. 1988, 1993). *Florschuetziella* shares several character-states with *Z. obtusifolius* (and *Leratia*), and species of *Macromitrium*, and may have originated through hybridization between distantly related progenitor species (e.g., belonging to distinct subfamilies). If hybridization is confirmed for this species, the basal position of *Florschuetziella* within the Macromitrioideae may reflect more its mode of speciation than its actual phylogenetic relationships with other species of the Macromitrioideae (MacDade 1992). Until the systematic affinities of *Florschuetziella* are elucidated, cladocarpy should be regarded as synapomorphic for the Macromitrioideae.

Within the Orthotrichaceae, the stem branches either sympodially, through subapical innovations, or monopodially, involving *quasi* continuous acrotonous development of lateral branches along a growing stem (see La Farge-England 1996). The genetic basis or proximal causation for a switch to monopodial growth in the Macromitrioideae or other Orthotrichaceae (see above), is not known. The ultimate causation for changing the mode of branching is however most likely to be sought for in the parallel occurrence of cladocarpy, where perichaetia are produced at the apex of lateral branches. Consequently, monopodial branching should, like cladocarpy (see above) be regarded as a synapomorphy for the Macromitroideae. The occurrence of polymorphism may have genetic causes similar to those advanced for polymorphism in the distribution of the perichaetia, and needs to be investigated further.

Constraining the character transformation to satisfy the parsimony criterion further results in the plesiotypic state for the shape of the basal cells to be isodiametric (character 17/2) rather than rectangular (17/0) as in *Schlotheimia*, or most species of *Macromitrium* (Fig. 6.6). Short basal cells are characteristic of several genera (i.e., *Cardotiella*, *Florschuetziella*, *Groutiella*, *Leiomitrium*, *Macrocoma*) as well as *Macromitrium* sect. *Cometium* Mitt. (Brotherus 1925). These cells, except the most proximal rows, are always chlorophyllose, and thus very similar to the isodiametric upper laminal cells. The basal cells of most Macromitria are isodiametric and chlorophyllose in the juvenile leaves, and later undergo elongation and lose the chlorophyll. The short cells found at maturity in *Groutiella* and other taxa, may have arisen through heterochrony (paedomorphosis *sensu* McNamara 1986). The ecological significance of short chlorophyllose basal cells, is difficult to ascertain in the absence of empirical data. Based on field observations and herbarium label information, species with uniform, chlorophyllose cells in the lamina appear to grow predominantly in xerophytic (micro-)habitats, whereas taxa with long basal cells seem to have broader amplitudes along a moist to dry gradient. The genus *Groutiella*, for example, which is geographically sympatric with *Macromitrium*, shares with the latter an epiphytic habitat in tropical forests. *Groutiella* is however restricted, in Central America and the West Indies, to lower montane forests, or to disturbed habitats in montane forests (trees on road sides and in pastures), but is virtually absent from the moss flora of the upper montane and elfin forests, whereas *Macromitrium* is often a dominant component of epiphytic communities at these higher elevations. *Groutiella* differs superficially from *Macromitrium* only by the differentiated hyaline margin (character 21; Fig. 6.6) and has most likely evolved from a *Macromitrium*-like ancestor (Fig. 6.6). If such correlation between basal cell shape and habitat can be confirmed and demonstrated for *Florschuetziella*, *Cardotiella*, *Leiomitrium*, and *Macrocoma* (both *M. papillosa* and *M. tenuis*), then short basal cells may not be plesiotypic in the family (as suggested in Fig. 6.6), and are better considered to have evolved independently from an ancestor which retained the plesiotypic state to the family, namely rectangular basal cells.

All Macromitrioideae are characterized by prostrate growth (Fig. 6.6), with stems growing parallel to the surface of the substratum. This change in the direction of growth of the stem, from orthotropic to plagiotropic, is most easily interpreted, in the Macromitrioideae as well as in the cladocarpous Zygodontoideae and Orthotrichoideae, as a consequence of monopodial growth. Unlike in the latter two subfamilies, the functional differentiation of stem and branches, has been accompanied in most

Macromitrioideae by the development of dimorphic leaves (Fig. 6.6, character 5). The stem leaves in *Macromitrium* and *Schlotheimia* for example are typically acuminate from an ovate base, and much smaller than the branch leaves, with the latter being similar in cell areolation, outline, size, etc., to the stem leaves of the Orthotrichoideae. Such leaf dimorphism is thus most likely due to changes in the stem rather than the branch leaves. The plesiotypic condition where stems and branches bear identical leaves, may not be identical to the situation in the acrocarpous ancestor shared with the Orthotrichoideae. In an acrocarpous plant, the stem is terminated by a perichaetium, and so will the subsequent subapical innovations. From a functional point of view, these modules are identical, yet from a developmental standpoint, the first axis of the plant is the stem and the lateral innovation is a branch. If acrocarpy and cladocarpy are homologous (and thus exclusive in a haploid organism, see above), the cladocarpous ancestor to the Macromitrioideae, would have lost the ability to produce a terminal perichaetium on the stem. In a cladocarpous individual, the stem and the branch assume different functions: the stem insures continuous growth, whereas the branch develops the perichaetium. A perichaetium bearing branch, may "resume" growth by means of a subapical innovation, which in turn will assume the function of perichaetium production. The leaves of this subapical branch are identical to those of the branch below. Thus if we compare two consecutive modules of the same order, thus with the same function (production of the perichaetium) in *Orthotrichum* and *Macromitrium*, the leaves would be interpreted as isomorphic in both taxa; yet if modules were defined based on ontogeny (primary stems verus primary branches) a comparison within the same two taxa would lead to the leaves found in *Macromitrium* to be considered dimorphic. If modules sharing an identical function should be compared, the stem of most Macromitrioideae could not be compared to any module in the acrocarpous Orthotrichaceae, since the stems of the latter always produce a terminal perichaetium. Bryophyte systematics is based on comparisons of functional modules (e.g., stolon, stem, branch, and flagella in *Squamidium*, Pterobryaceae; Allan & Crosby 1986). If such a criterion is acceptable for reconstructing the phylogeny of modular organism, than the weight of alternative functions remains to be determined. Attributing more significance to the function of perichaetia production rather than perenniality of the plant, may *a priori* appear justified, since the former may contribute more to the perenniality of the species rather than just the individual. Applied to the Orthotrichaceae, this would lead to the consideration of a distinct character, morphology of the leaves of sterile stems. This character would only be applicable to cladocarpous taxa, since stems in acrocarps are ultimately fertile (produce a perichaetium), rather than sterile . The phylogenetic consequences of such strategy may be that it would allow for a derived position of taxa with isomorphic leaves within the Macromitrioideae, since this transformation would be influenced no longer by the character-state in the sister-group, the acrocarpous Orthotrichaceae.

The phylogenetic relationships among the various genera composing the Macromitrioideae are obviously very much dependent on the early character transformations. Including additional characters, such as peristomial features, may contribute to solving generic affinities. The genus *Schlotheimia* is the only large genus whose monophyly has withstood both the morphological and molecular analyses. Its siter-group relationship to the remaining Macromitrioideae, though strongly supported in the latter analyses (chapter five), is absent from all most parsimonious scenarios. Species of *Schlotheimia* all have a well developped peristome, including an endostomial connecting that may be synplesiomorphic for the family (Lewinsky 1993). Furthermore, all Schlotheimiae have smooth laminal cells, and smooth calyptrae, both features that would link it to what has been argued above to be the least derived acrocarpous taxon in the family, namely *Zygodon* sect. *Bryoides*. A basal position of this large genus is therefore not to be dismissed. The polyphyletic origins suggested for *Macrocoma* and *Macromitrium*, are likely to withstand future analysis. *Macrocoma* is a small genus including 11 species, arranged in two subgenera, subg. *Macrocoma* and subg. *Trachyphyllum* (Broth.) Vitt (Vitt 1980). In addition to the differences described by Vitt (1980), the bitypic subg. *Trachyphyllum* is also distinct by its multicellular spores, short and oblique rostrum, and given the oblique rostrum, the calyptra which is campanulate as in congeneric species, but has a major slit on one side, may be best considered cucullate. These differences may be regarded as sufficient to regard subg. *Trachyphyllum* as a distinct genus. Whether the polymorphism in the branching pattern and the distribution of the perichaetia, is indicative of a hybrid origin of the ancestor to the subgenus, needs to be investigated further. *Macromitrium* is the largest genus in the Orthotrichaceae with approximately 250 species (Vitt 1982a) and is suggested to be, based on morphological and molecular data, of polyphyletic origin. The species taxonomy has been revised in many parts of the world (van Rooy and Wijk 1992, Vitt 1983, 1993, Vitt and Ramsay 1985, Vitt et al. 1995), but still has to withstand critical study for most of South America, the center of diversity of *Macromitrium* (Vitt 1982a). Completion of the world monograph of *Macromitrium* should allow for examplar taxa of major evolutionary trends to be identified and for the here presented phylogenetic hypotheses of this morphologically diverse species complex to be addressed further.

Phylogenetic conclusion A phylogenetic analysis of 54 morphological characters supports the recognition of the three subfamilies traditionally accepted within the Orthotrichaceae: the Zygodontoideae, Orthotrichoideae, and Macromitroideae. The relationships among these subfamilies are defined by features of the calyptrae and on the distribution of the perichaetia, and are congruent with Vitt's (1982a) tentative phylogenetic arrangement. Five genera are currently accepted within the Zygodontoideae (i.e., *Leptodontiopsis*, *Pleurorthotrichum*, *Stenomitrium*, *Zygodon*, as well as *Leratia*), and the recognition of the sections of *Zygodon* at the generic level appears more appropriate than broadening the generic concept of *Zygodon* to accommodate all of the variation in the subfamily. Within the Zygodontoideae, section *Bryoides*, including taxa with smooth laminal cells, is argued to be the least derived. The Orthotrichoideae are composed of *Muelleriella*, *Orthomitrium*, *Orthotrichum*, *Stoneobryum*, and *Ulota*. The monotypic genus *Bryodixonia* is best considered synonymous with *Ulota*. The recent segregate genera of *Orthotrichum* (*Muelleriella*, *Orthomitrium*, and *Stoneobryum*) are retained at the generic level, until the possible polyphyly of *Orthotrichum* is further examined. Nine genera compose the largest of the three subfamilies, the Macromitrioideae: *Cardotiella*, *Ceuthotheca*, *Desmotheca*, *Florschuetziella*, *Groutiella*, *Leiomitrium*, *Macrocoma*, *Macromitrium*, and *Schlotheimia*. The relationships among these taxa remain obscure, possibly as a result of hybridization, or analogous character-states.

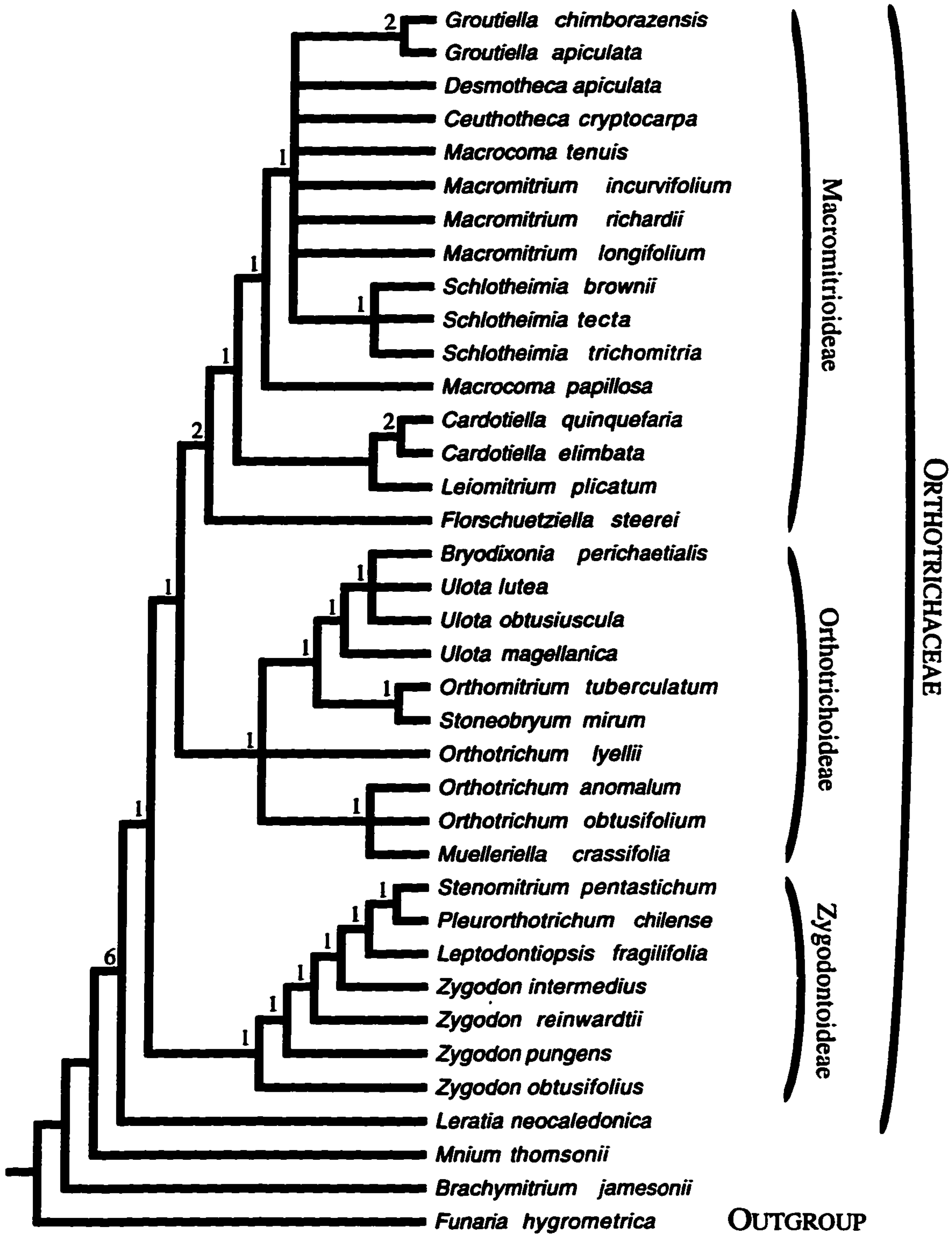

Figure 6.1. Strict consensus tree of 56 most parsimonious trees (MPT) obtained from a cladistic analysis including 54 morphological characters. MPTs 191 steps long, CI= 0.414; values above branch indicate the number of steps needed for the branch to collapse.

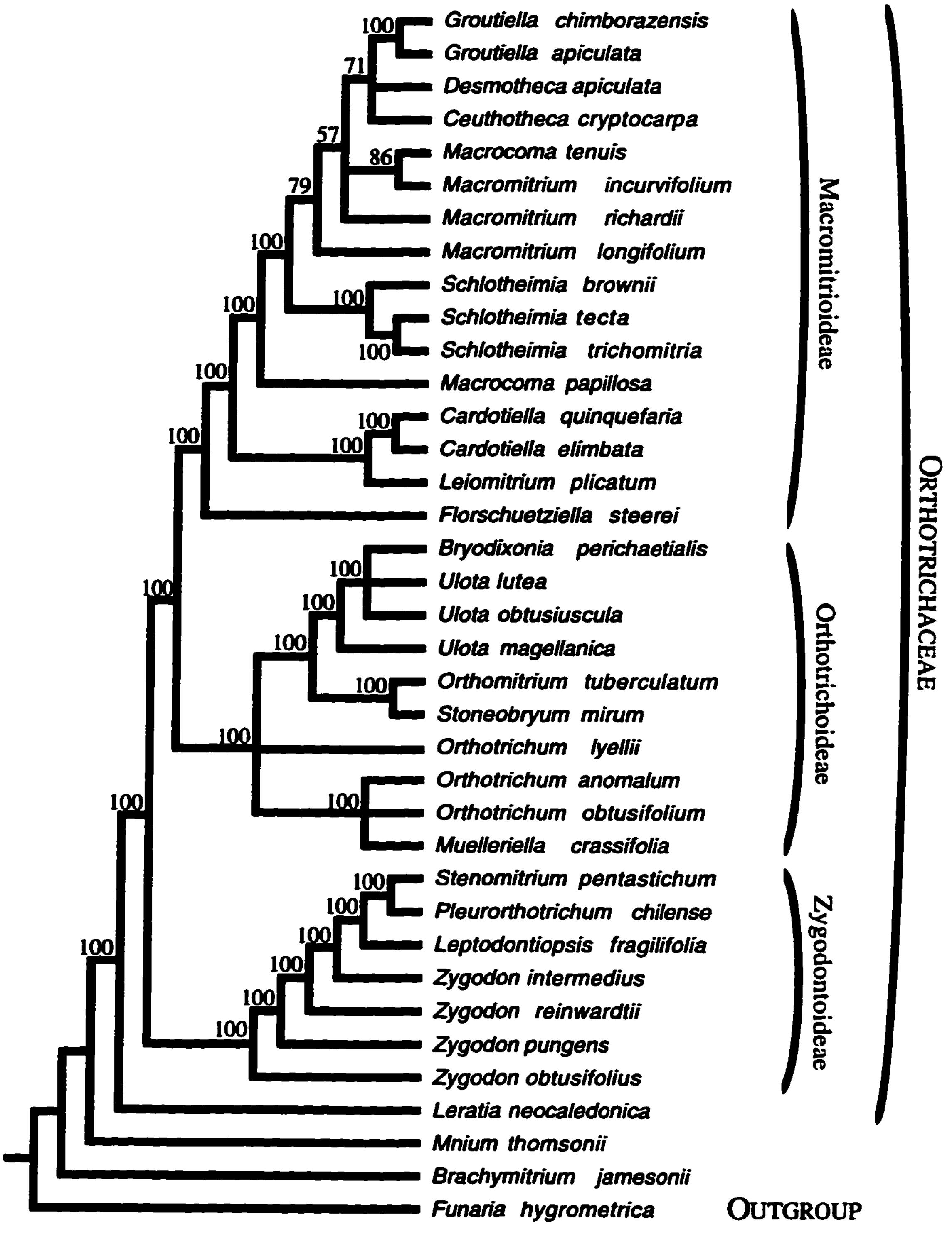

Figure 6.2. 50% majority rule consensus tree of 56 most parsimonious trees (MPT) obtained from a cladistic analysis including 54 morphological characters. MPTs 191 steps long, CI= 0.414; values above branch indicate the percentage of most parsimonious trees that share the topology.

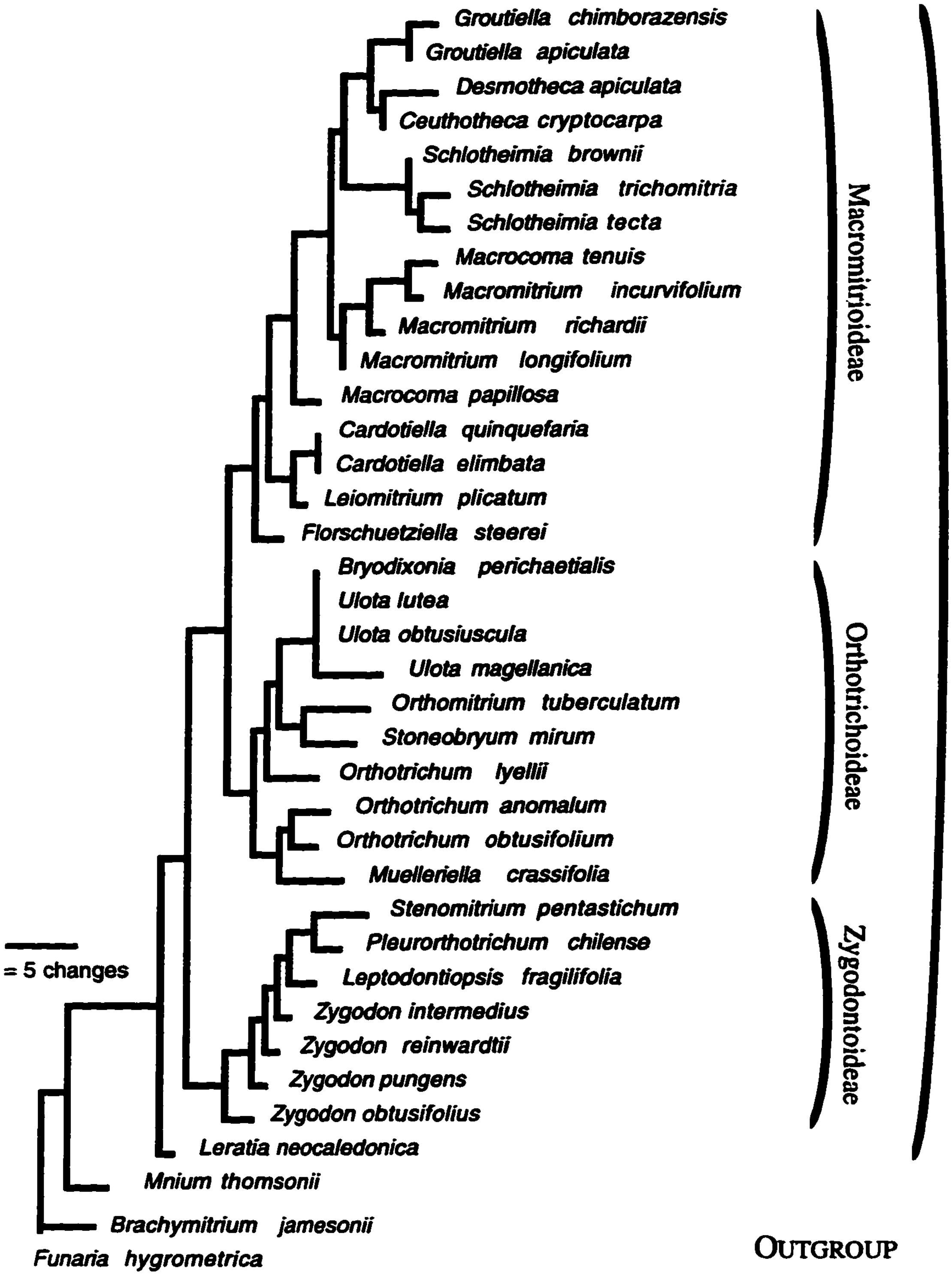

Figure 6.3. Phylogram of tree number three; tree with lowest f-value among all most parsimonious trees obtained from a cladistic analysis including 54 morphological characters. Tree 191 steps long, CI= 0.414.

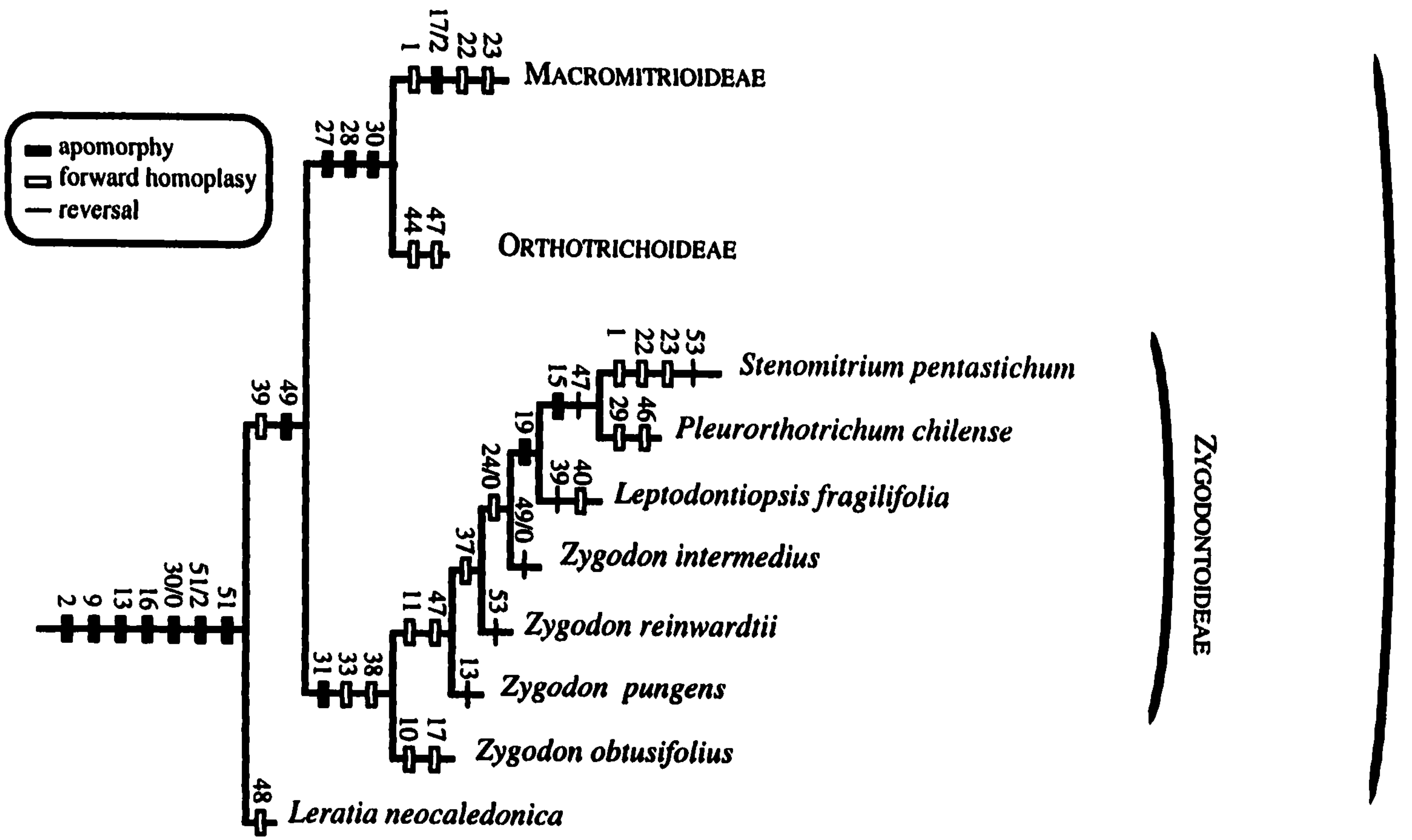

Figure 6.4. Phylogram of tree number three showing the character transformations supporting the monophyly of the Orthotrichaceae, as well as the relationships between subfamilies and the genera within the Zygodontoideae. For character numbers see text.

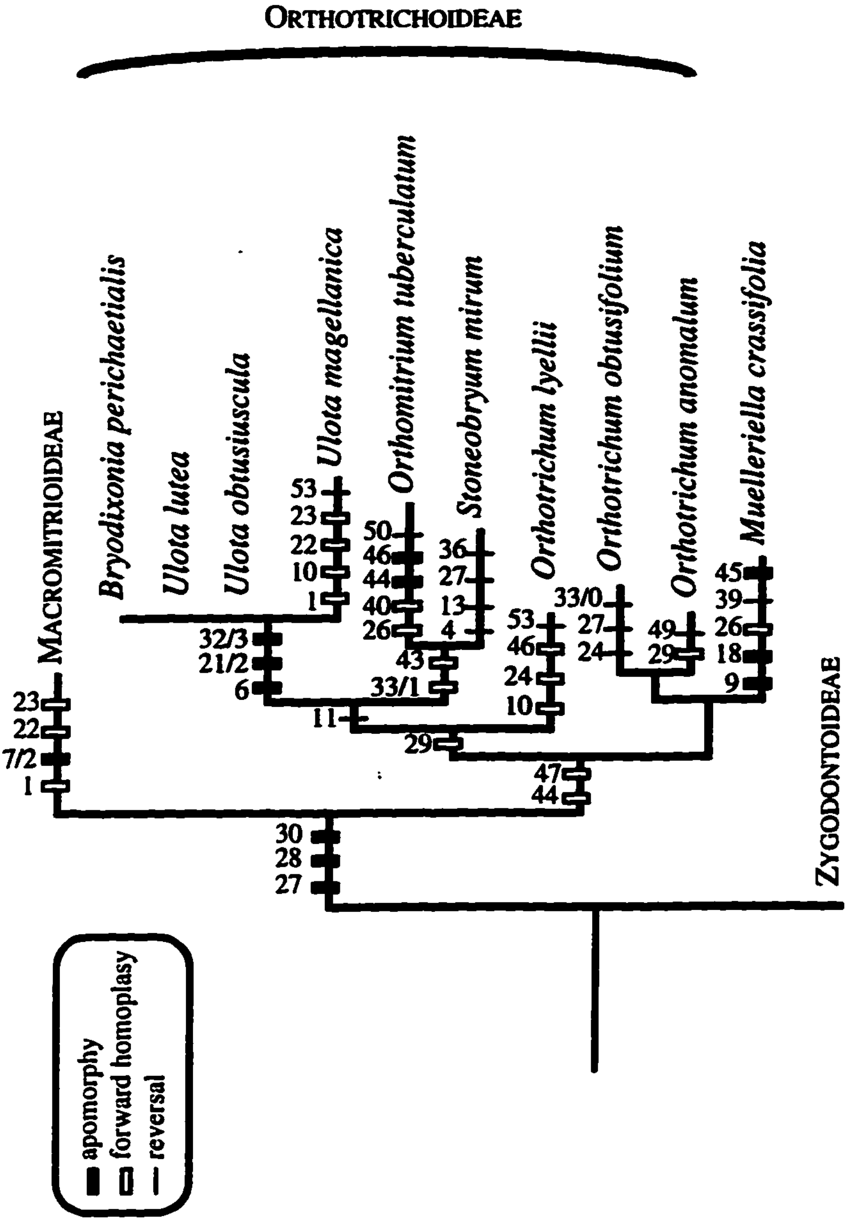

Figure 6.5. Phylogram of tree number three showing the character transformations supporting the monophyly of the Orthotrichoideae, and the relationships within the subfamily For character numbers see text.

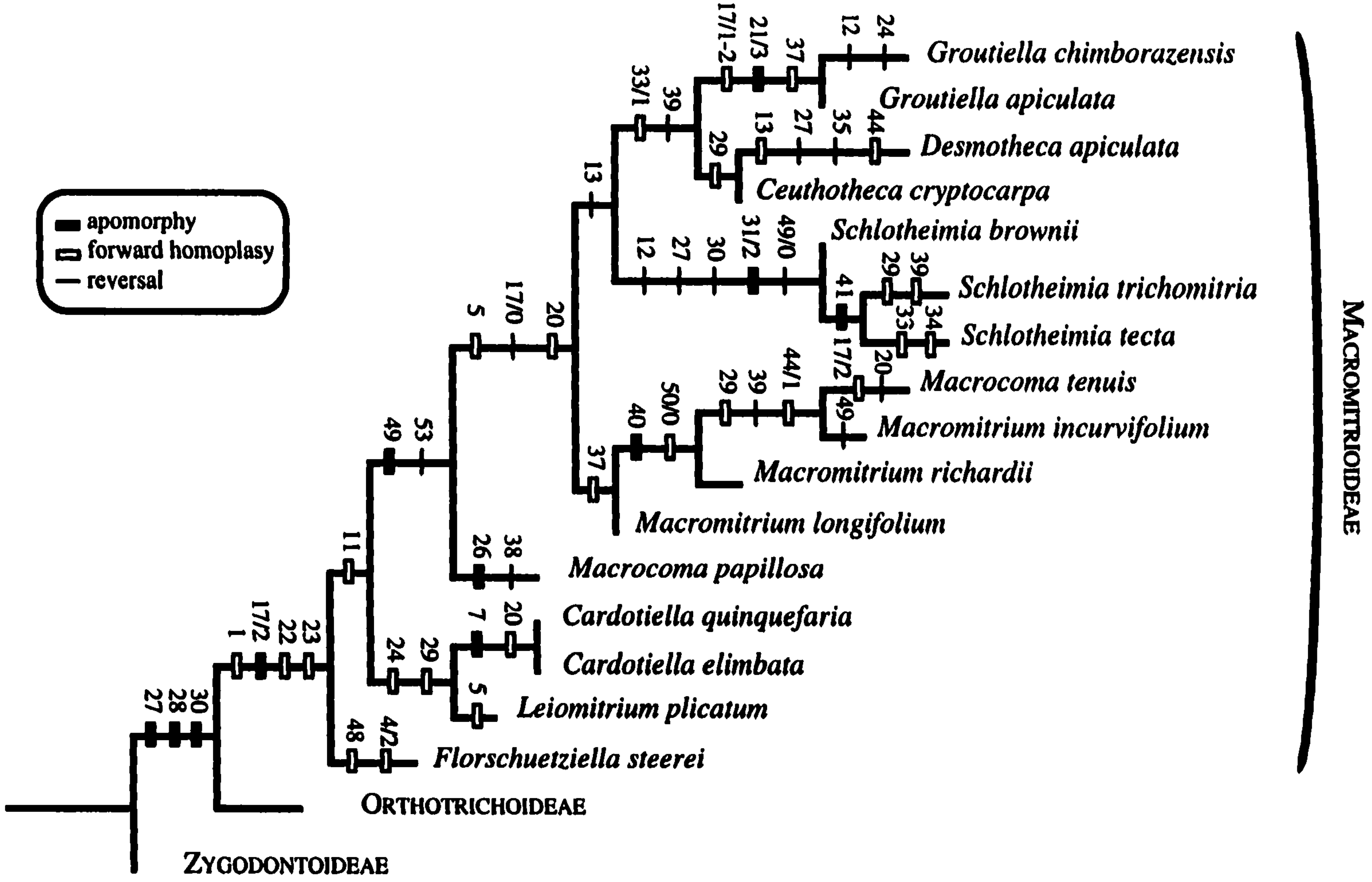

Figure 6.6. Phylogram of tree number three showing the character transformations supporting the monophyly of the Macromitroideae, and the relationships within the subfamily. For character numbers see text.

Table 6.1. List of representative specimens examined (all deposited in ALTA unless otherwise noted) * refers to taxa for which entries are based on publishing descriptions.

OUTGROUP	
Funaria hygrometrica Hedw.	*Priddle* 1408
Brachymitrium jamesonii Tayl.	*Griffin* 955
Mnium thomsonii Schimp.	*Schofield* 94579 *& Hedderson*
ORTHOTRICHACEAE	
Zygodontoideae	
Leptodontiopsis fragilifolia Broth.	Lectotype (H-Broth.)
Stenomitrium pentastichum (Mont.) Broth.	*Mahu* 10685
Zygodon intermedius B.S.G.	*Vitt* 29362
Zygodon obtusifolius Hook.	*Vitt* 38301
Zygodon pungens[1] C. Muell.	*La Farge-England* 8097
Zygodon reinwardtii (Hornsch.) B.S.G.	*Goffinet* 636
Orthotrichoideae	
Bryodixonia perichaetialis Sainsb.	*Vitt* 29862
Muelleriella crassifolia (Hook. f. & Wils.) Dusén subsp. *acuta* (C.Müll.) Vitt	*Engel* 7718
Orthomitrium tuberculatum Lewinsky-Haapasaari & Crosby	* *Lewinsky-Haapasaari* and *Crosby* (1996)
Orthotrichum anomalum Hedw.	*Goffinet* 4115
Orthotrichum lyellii Hook. & Tayl.	*Goffinet* 3162
Orthotrichum obtusifolium Brid.	*Goffinet* 4137
Pleurorthotrichum chilense Broth.	Holotype (H-Broth.)
Stoneobryum mirum (Lewinsky) Norris & Robinson	*Magill* 7054 (MO)
Ulota lutea Mitt.	*Fife* 8042
Ulota magellanica (Mont.) Jaeg.	*Schäfer-Verwimp & Verwimp* 7970
Ulota obtusiuscula Mac. & Kindb.	*Goffinet* 3161
Macromitrioideae	
Cardotiella elimbata (Thér.) Goffinet	Holotype (PC; *Goffinet* 1996)
Cardotiella quinquefaria (Hornsch.) Vitt	*Vital & Buck* 11836
Ceuthotheca cryptocarpa (Bart.) Lewinsky-Haapasaari	Holotype (FH)
Desmotheca apiculata (Dozy & Molk.) Lindb.	*Vinas* 96-4
Florschuetziella steerei Vitt	Holotype
Groutiella apiculata (Hook.) Crum & Steere	*Goffinet* 2764
Groutiella chimborazensis (Mitt.) Florsch.	*Goffinet* 1173
Leiomitrium plicatum Mitt.	Holotype (NY)
Leratia neocaledonica Broth.	Lectotype (H-Broth.)
Macrocoma papillosa (Thér.) Vitt	Syntype (Hickens 1921—J)
Macrocoma tenuis (Hook. & Grev.) Vitt subsp. *sullivantii* (C.Müll.) Vitt	*Schäfer-Verwimp* 8150
Macromitrium incurvifolium (Hook. & Grev.) Schwaegr.	*Streimann* 42622
Macromitrium longifolium Hook.	*Goffinet* 656
Macromitrium richardii Schwaegr.	*Goffinet* 1689
Schlotheimia brownii Schwaegr.	*Vitt* 27485
Schlotheimia tecta Hook. & Wils.	*Schäfer-Verwimp* 9686
Schlotheimia trichomitria Mitt.	*Schäfer-Verwimp* 6902

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[1] This specimen is tentatively identified as *Zygodon pungens* C.Müll., but this neotropical species is hitherto not known from Africa (Malta 1926).

Table 6.2: Morphological characters scored[1] for 37 species representing three outgroup taxa and 34 Orthotrichaceae

	1	1111111111	2222222222	3333333333	4444444444	5555
	1234567890	1234567890	1234567890	1234567890	1234567890	1234
OUTGROUPS						
Funaria hygrometrica	0110000111	100-000000	0001000003	001000--10	1010110001	1000
Brachymitrium jamesonii	0110000111	100-000000	10?100?1??	???111100	1100101101	1--0
Mnium thomsonii	0100000111	100-000000	0000100003	0000110000	111010?001	1111
ORTHOTRICHACEAE						
Zygodontoideae						
Leptodontiopsis fragilifolia	0001000101	0010010010	0000100000	1000111001	1100101---	----
Stenomitrium pentastichum	1001000101	0010110010	0110100000	1010111010	1100100012	0100
Zygodon obtusifolius	0001000100	111P012000	0001100000	1011110010	1100100012	0110
Zygodon pungens	0001000101	000-010000	0001100000	1011110010	1100101012	0110
Zygodon reinwardtii	0001000101	0010010000	0001100000	1010111010	11001010--	-100
Zygodon intermedius	0001000101	0010010000	0000100000	1010111010	1100101002	0110
Orthotrichoideae						
Bryodixonia perichaetialis	0002010101	0010010000	2001101111	0310010110	110110-012	0---
Muelleriella crassifolia	0001000111	10?-010100	0001111101	0000010100	111100-112	0---
Orthotrichum obtusifolium	0001000100	1010010000	0000100101	0010010110	110110-112	0110
Orthotrichum anomalum	0001000100	1010010000	0001101111	0000010110	1111101102	0---
Orthotrichum lyellii	0001000100	1010010000	0000101111	0000110110	1101111012	0100
Orthomitrium tuberculatum	0001000?0?	?010010000	0001111111	0010110111	111211?0P0	0---
Pleurorthotrichum chilense	0001000101	0010110010	0000100010	1000???10	1100110012	0110
Stoneobryum mirum	0000000101	000-010000	0001100111	001010--10	111110-012	0110
Ulota obtusiuscula	0002010101	0010010000	2001101111	0300110110	1101111012	0110
Ulota lutea	0002010101	0010010000	2001101111	0300110110	1101101012	0110
Ulota magellanica	1001010100	0010010000	2111101111	0300110110	1101101012	0100

[1] P=0&1; V=0&2

Table 6.2 (cont.): Morphological characters scored for 37 species representing three outgroup taxa and 34 Orthotrichaceae

	1	1111111111	2222222222	3333333333	4444444444	5555
	1234567890	1234567890	1234567890	1234567890	1234567890	1234
Macromitrioideae						
Cardotiella elimbata	1001001101	011001V001	0110100110	2110111110	1100100012	0110
Cardotiella quinquefaria	1001001101	011001V001	01101-----	----------	----------	----
Ceuthotheca cryptocarpa	1001100101	010-010001	0112101111	0210110100	1100?0-02-	-100
Desmotheca apiculata	1001100101	011P010001	0112100111	0210010100	1101------	----
Florschuetziella steerei	1002000101	111P012000	0PP1101?01	0?00110110	110P100112	0110
Groutiella chimborazensis	1001100101	000-01V001	3110101101	0210111100	110010002-	----
Groutiella apiculata	1001100101	010001V001	3112101101	0210111100	110010002-	----
Leiomitrium plicatum	1001100101	011P012000	0110101111	0??0????10	110010?0?2	0110
Leratia neocaledonica	0002000101	111P010000	0001100000	0001110100	1100100102	0110
Macrocoma papillosa	1001000101	0110012000	0PP1111101	0?00110010	1100100022	0100
Macrocoma tenuis	1001100101	0110012000	0111101111	0200111101	110110002-	0---
Macromitrium incurvifolium	1001100101	011P010001	0112101111	0200111101	1101100010	0---
Macromitrium longifolium	1001100101	0110010001	0112101101	0200111110	1100100022	0100
Macromitrium richardii	1001100101	0110010001	0111101101	0200111111	1100100000	----
Schlotheimia brownii	1001100101	000-010001	0112100100	2100110110	1100100002	0100
Schlotheimia tecta	1001100101	000-010001	0112100100	2111110110	0---10-002	0100
Schlotheimia trichomitria	1001100101	000-010001	0112100110	2100110100	0---100002	0100

[1] P=0&1; V=0&2

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Chapter seven

Revised generic classification of the Orthotrichaceae.

The goal of phylogenetic studies is to elucidate trends in character evolution, in order to better understand the relationships among taxa sharing particular characters. Since characters, morphological or others, form the basis for arranging taxa in groups of higher ranks, classification should reflect the evolutionary history of the organisms under consideration (Donoghue and Cantino 1988). Classifications, and particularly classification of the Bryopsida, have until recently predominantly relied on comparative morphological studies (see Vitt 1984). With the advent of molecular techniques (see Hillis and Moritz 1990), new sets of characters, *a priori* thought to occur in large numbers (but see Doyle 1992), and for which homology in more easily established (see Wägele 1995), have become available. Their use in phylogenetic reconstructions often yield phylogenies conflicting with those obtained from morphology (Hillis 1987), but these discrepancies are often just as striking as the incongruencies between different morphology-based phylogenies or different gene trees (Patterson, Williams, and Humphries 1993). Two approaches have been proposed for retrieving phylogenetic information from such incongruent data sets (see de Queiroz, Donoghue, and Kim 1995, for review). The first method, taxonomic congruence, is based on the comparison of alternative trees by constructing a consensus tree (Adams 1972) of all alternative trees. This method has been criticized 1) because incongruence may often result from procedural problems (taxon sample, errors in assessing homology, etc.; Patterson, Williams, and Humphries 1993) 2) because of unequal rates of evolution (Bull et al. 1993), 3) because it is subjective and not testable (Tehler 1995), and 4) because the consensus tree itself is not a phylogeny, but only a summary of congruence of alternative trees (Swofford 1991). Hillis (1987) also argued that a character set is never informative at all systematic levels, and therefore suggested that data sets should be combined in an attempt to resolve the phylogeny based on "total evidence". Combining data sets may however yield strongly unresolved phylogenies if the data sets combined are of different size (e.g., uneven taxon sample), and the final matrix includes many missing data (see Wilkinson 1995). In the present study, the generic representation of the Orthotrichaceae is complete in the morphological analysis, whereas only 10 of the 19 genera were included in the molecular study due to difficulties in obtaining good quality DNA, if any, for many of the small, often monotypic genera known only from the type collection. A combined analysis was therefore considered premature, and will have to await obtaining *rbc*L sequences for at least some of the missing taxa.

The most parsimonious phylogenies obtained from both data sets are partly incongruent with regards to the subfamilial and generic circumscriptions within the Orthotrichaceae. Presenting a revised classification of the family based on conflicting trees may *a priori* appear subjective and thus not scientific (Tehler 1995), but is not less objective than the initial choice of the taxa or the characters used to infer the phylogenies. Neither phylogeny is *a priori* better than the other. Molecular characters, single nucleotides in the sequence, suffer from their lack of complexity and thus a higher likelihood of homoplasy (Wägele 1995). Furthermore, characters retrieved from a single gene may not satisfy the criterion of independence, because not all changes may be equally probable at a particular site (e.g., in a case of base composition bias) or along the sequence (functional constraints) and therefore yield trees incongruent with the actual taxon phylogeny (Doyle 1992). Compared to molecular characters, establishing the homology of morphological characters may be more difficult (see discussion chapter six). Furthermore, the high level of homoplasy found in the most parsimonious scenario (chapter six) may simply be indicative of the inadequacy of the characters included. The subfamilial classification adopted here is based on the molecular phylogeny (chapter five), whereas the hypotheses derived from the analysis of morphological characters serve as a framework for circumscribing the genera and tribes. The Orthotrichaceae are here divided into two subfamilies, the Orthotrichoideae (including the Zygodontoideae) and the Macromitroideae. Morphological characters suggest that the Zygodontoideae are basal to the dichotomy between the Macromitrioideae and the Orthotrichoideae *sensu stricto*. The distinction between the Zygodontoideae and its sister-group is based solely on characters of the calyptrae (shape, and anatomy). Though the calyptra of the Zygodontoideae is clearly distinct from that found in other orthotrichaceous taxa, the genetic complexity of this character may not be very high, since smooth calyptrae do occur in some species of*Orthotrichum* (Lewinsky 1993), and cucullate calyptrae are known from *Macromitrium leprieurii* (Goffinet 1993). Complex characters may be given more weight in phylogenetic analysis (Wägele 1995, see also Kadereit 1994), but given the rather simple anatomy and morphology of mosses, establishing a gradient of complexity of characters, particularly gametophytic characters is hazardous, at present. A combined Zygodontoideae-Orthotrichoideae would in the most parsimonious scenario lack any synapomorphies (see chapter six), and be characterized by such synplesiomorphies as acrocarpy, orthotropic sympodially branching stems, whereas the Macromitroideae include mostly taxa with apotypic traits such as plagiotropic, monopodially branched stems with perichaetia terminal on lateral branches. The phylogenetic signal carried by two of these three characters is compromised by the presence, within the Macromitrioideae, of "basal" taxa that are polymorphic for the latter two characters. A possible hybrid nature of these taxa may be at the base of the incongruence regarding the subfamilial affinities between the two trees (McDade 1992). This hypothesis is expected to be addressed soon.

The generic circumscription follows the discussion presented in chapter six. It is hypothesized that most speciose genera of the Orthotrichaceae (i.e., *Macromitrium*, *Orthotrichum*, *Zygodon*), as well as the small genus *Macrocoma*, are currently representing evolutionary grades. The first systematic implications of this study are proposed here, with the recognition at the generic level of all four sections composing the genus *Zygodon sensu* Malta (1926), as well as the two subgenera of *Macrocoma* (Vitt 1980). The remaining two putative paraphyletic assemblages, *Macromitrium* and *Orthotrichum*, are retained in a conservative sense, pending further study.

ORTHOTRICHACEAE Arnott,

Disp. Méth. esp. mousses: 13. 1825 (1826?, fide Margadant 1968)

Zygodontaceae Schimp., Coroll. Bryol. Eur. 39. 1856; Type: *Zygodon* Hook. & Tayl.

Macromitriaceae S.P. Churchill, Bibl. J.J. Triana 12: 588. 1995, **syn. nov.** Type: *Macromitrium* Brid.

Plants pale or dark green to rusty brown, 1 to 10cm tall. Stems erect or plagiotropic, branched sympodially or monopodially; outer cortical cells typically with very thick and colored walls, parenchyma cells thick-walled and hyaline to yellowish, to rarely very thick-walled and orange-red in color, central strand lacking. Rhizoids, red, thick-walled, smooth to papillose, sparsely to abundantly branched. Axillary hiars with one or two differentiated basal brown cells, and no to several; hyaline, rectangular, thick-walled cells. Leaves erect, appressed or variously flexuose when dry, spreading when moist, spirally inserted or in five ranks, plane, rugose to undulate, flat or keeled, ovate, oblong, lanceolate, to linear, apex acute, acuminate or obtuse, rarely retuse. Costa always present, single, reaching apex, to excurrent, composed of two ventral guide cells, dorsal cells typically differentiated into substereids, rarely undifferentiated and chlorophyllose; chlorophyllose cells covering the adaxial surface of the guide cells typically absent. Basal laminal cells differentiated, rectangular and hyaline to isodiametric and chlorophyllose, thick-walled, rarely nodose or porose, flat, smooth to papillose or tuberculate. Upper laminal cells thick-walled, isodiametric to short rectangular, rarely long rectangular, flat to bulging, smooth, unipapillose to pluripapillose, papillae clavate to conical, simple, bifid. Dioicous, monoicous (autoicous, rarely synoicous or paroicous), or phyllodioicous. Perichaetia terminal on stem or branches, paraphyses always present, long, linear, cells rectangular, apical cell pointed. Perichetial leaves weakly to strongly differentiated, oblong-lanceolate to linear-lanceolate; costa percurrent to strongly excurrent and forming arista; basal cells differentiated and often extending to the upper lamina, rectangular to rhombic, hyaline, smooth, tuberculate or prorate, upper cells chlorophyllose, isodiametric, smooth to papillose. Perigonia axillary or terminal, bud-like. Perigonial leaves strongly differentiated, short, concave; costa often weakly differentiated, ending well below the apex; basal cells rhombic, rather thin to moderately thick-walled, hyaline to yellowish; chlorophyllose cells, restricted to apex. Monosetous, seta short or long, sinistrorse to dextrorse at the apex, outer cortical cells thick-walled, parenchyma cells thick-walled, central strand present to rarely lacking. Vaginula glabrous to hairy, ochrea well developed or absent. Capsule immersed, emergent, to exserted, neck well differentiated to almost lacking. Stomata with two guard cells, in neck, lower or rarely upper portion of the urn, pore elongate, phaneroporic to cryptoporic, and subsidiary cells weakly to strongly covering guard cells. Exothecial cells, rectangular, anticlinal and outer periclinal walls moderately to very thick, rarely strongly collenchymateous, inner periclinal wall moderately thick, cells often differentiated into longitudinal bands, forming ribs, cells at mouth short, isodiametric to oblate. Annulus typically absent or poorly differentiated. Urn cylindric to globose, mouth wide or constricted. Peristome double, simple or lacking. Prostome of 64 cells present or absent, reduced to base of tooth, if well developed, caducous and peeling. Exostome teeth, 16, free or fused into eight pairs, or continous membrane, long acuminate to truncate, or even absent, erect, reflexed or recurved; OPL of 32 symmetric cells, heavily thickened, papillose, striate, reticulate or lamellate; PLL of 16 symmetric cells, moderately thickened on the exostome, here smooth, papillose, striate, rarely reticulate. Endostome segments, 16, 8 or lacking, inflexed, flat or keeled, lanceolate to linear, or truncate, free or fused into continous membrane, connecting membrane one to three cells high, or lacking, cilia absent; PPL smooth, thin to very thin; IPL of 16 to 32 symmetric to strongly asymmetric cells, papillose to striate papillose, moderately thick. Calyptrae cucullate or mitrate, narrowly cylindric, broadly campanulate, to conic, covering the urn competly or only the operculum, smooth to plicate, entire, lobate or moderately to deeply lacerate, thick-walled cells unistratose to tristratose, isodiametric to rectangular, smooth, papillose or prorate, hairs lacking or present, uniseriate to foliose, cells thick-walled, smooth, papillose or prorate. Operculum flat to mostly conic, rostrum short to long, rarely absent, erect or curved, straight or oblique. Exosporic or endosporic, spores granulose, reticulate or pitted, isomorphic to strongly dimorphic.

I. Orthotrichoideae

Zygodontoideae Broth., Nat. Pfl. 11(2): 11. 1925. **syn. nov.**[1 (see annotation p. 154)]

Plants pale to deep green. Stem typically orthotropic, and sympodially branched, rarely plagiotropic and monopodially branched. Leaves erect appressed, twisted, flexuose or crisped, plane. Abaxial costal substereids well or poorly differentiated, chlorophyllose cells covering adaxial surface typically absent. Laminal cells flat, rarely bulging, smooth, uni- or pluripapillose, papillae clavate, conical, simple to bifid, small or coarse. Dioicous, monoicous (autoicous, rarely synoicous or paroicous), acrocarpous, rarely cladocarpous. Seta dextrose or sinistrose. Peristome, double, simple or lacking. Exostome teeth free or fused, never reduced to membrane. Endostome free, connecting membrane present or absent, never reduced to a continuous membrane. Calyptrae cucullate or mitrate.

A. *Zygodonteae* (Broth.) Goffinet[2]

Basal laminal cells mono- or dimorphic, evenly thick-walled, rarely nodose, or porose. Chlorophyllose laminal cells flat, rarely bulging, smooth to papillose, papillae one to six, small clavate to coarse, simple to bifid at base, never bifid from a stalk. Seta dextrorse or sinistrorse. Calyptrae cucullate, entire, smooth, covering upper half of urn, thick-walled cells cells rectangular, and bistratose.

1.*Codonoblepharon* Schimp.[3], Spec. Musc. Suppl. 2(1): 142. 1824.

2. *Bryomaltaea* Goffinet[4]

3. *Leratia* Broth., Öfvers. Finska Vetensk.-Soc. Förh. 51A(17): 14. 1909.
4. *Zygodon* Hooker & Taylor, Musc. Brit. 70. 1818.
5. *Leptodontiopsis* Broth. in Mildbr.[5], Wiss. Ergebn. Deutsch. Zentr. Arf. Exp. 2: 146. 1910.
6. *Pleurorthotrichum* Broth., Öfvers. Finska Vetensk.-Akad. Handl. 47: 1. 1905.
7. *Stenomitrium* (Mitt.) Broth., Nat. Pfl. 1(3) 464. 1902.

B. *Orthotricheae* Goffinet[6]

Basal cells monomorphic, even thick-walled to nodose, never porose. Chlorophyllose laminal cells flat, never bulging, smooth to papillose, papillae 1 or two, rarely more, conical, rarely small and clavate, simple to branched from a stalk. Seta sinistrose. Calyptrae mitrate, entire to deeply lobate, plicate, rarely smooth, covering urn completely or only operculum, thick-walled cells cells isodiametric, and unistratose.

1. *Orthotrichum* Hedw., Spec. Musc.: 162, 1801.
2. *Muelleriella* Dusén, Bot. Not. 1905: 304. 1905.
3. *Orthomitrium* Lewinsky-Haapasaari & Crosby, Novon 6: 2, 1996.
4. *Stoneobryum* Norris & Robinson, The Bryologist 84: 96. 1981.
5. *Ulota* Mohr[7], Ann. Bot. 2: 540. 1806.

II. Macromitrioideae Broth., Nat. Pfl. 11(2): 25. 1925
Pseudo-Macromitrioideae Broth., Nat. Pfl. 11(2): 49. 1925.
Desmothecoideae Crum, Mem. New Yrok Bot. Grad. 45: 603. 1987.

Plants pale to deep green, to rusty brown. Stem plagiotropic, creepng to rarely pendulous, monopodially, rarely also sympodially branched. Branches erect, sympodially branched. Leaves erect appressed, twisted, flexuose or crisped, plane to rugose or undulate. Abaxial costal substereids well differentiated, chlorophyllose cells covering adaxial surface absent. Laminal cells flat, bulging, smooth, uni- or pluripapillose, or tuberculate, papillae conical, or cylindric, simple to bifid, small or coarse, basal cells porose or not. Dioicous, monoicous (autoicous), mostly phyllodioicous, cladocarpous, rarely also acrocarpous. Seta dextrorse. Peristome, double, simple or lacking. Exostome teeth free, fused into pairs, basal margin contiguous, or teeth reduced to membrane. Endostome free, connecting membrane present or absent, well developed to trunctae of reduced to a continuous membrane. Calyptrae mitrate, rarely cucullate.

A. *Schlotheimieae* Goffinet[8]

Plants deep green to rusty brown. Basal laminal cells, smooth or prorate. Upper laminal cells always flat and smooth. Cladocarpous. Calyptrae mitrate, smooth, cylindric to conic, lobate base unistratose, bi to tristratose above.

1. *Schlotheimia* Brid. Sp. Musc. 2: 16. 1812.

B. *Macromitrieae* Goffinet[9]

Plants green to deep green. Basal laminal cells, smooth or tuberculate, not prorate. Upper laminal cells flat or bulging, smooth, uni- to pluripapillose, papillae simple or bifid at base. Cladocarpous, rarely also acrocarpous. Calyptrae mitrate, rarely cucullate, plicate, rarely smooth, campanulate to conic, entire to deeply lacerate, unistratose, thick-walled cells isodiametric.

1. *Macromitrium* Brid. Mant. Musc.: 132. 1819.
2. *Leiomitrium* Mitt., Phil. Trans. Roy. Soc. Lond. 168: 390, 1879.
3. *Cardotiella* Vitt, J Hattori Bot. Lab. 49: 101, 1981.
4. *Macrocoma* (C. Müll.) Grout, The Bryologist 47: 4, 1944.
5. *Matteria* Goffinet[10]
6. *Florschuetziella* Vitt, The Bryologist 82: 16. 1979.
7. *Groutiella* Steere, The Bryologist 53: 145. 1950.
8. *Ceuthotheca* Lewinsky-Haapasaari, Lindbergia, 19: 18, 1994
9. *Desmotheca* Lindb. J. Lin. Soc. Bot. 13: 184. 1872.

Annotations and nomenclatural changes

1. The subfamilies Orthotrichoideae and Zygodontoideae were described by Brotherus in the same publication, with the Zygodontoideae preceding the Orthotrichoideae (Brotherus 1925). According to article 19.4 of the International Code of Botanical Nomenclature (Greuter 1994), the name Orthotrichoideae is to be preferred

over Zygodontoideae because the Orthotrichoideae contains the type of the family: *Orthotrichum* Hedw.

2. **Zygodonteae** (Broth.) Goffinet **comb. nov.**
Zygodontoideae Broth., Nat. Pfl. 11(2): 11. 1925.
Type: *Zygodon* Hook. & Tayl.

3. **Codonoblepharon** Schwaegr. Spec. Musc. Suppl. 2(1): 142, 1824.
Type: *C. menziesii* Schwaegr. Spec. Mus. Suppl. 2(1): 142, 1824.
Zygodon Hook. & Tayl. sect. *Codonoblepharum* (Schwaegr.) C. Müll. Linnea 18: 669, 1845.
Thyridium Mitt. sect. *Codonoblepharum* (Schwaegr.) C. Müll. in Jaeg. Ber. S.Gall. Naturw. Ges. 1877-1878: 414, 1880 (Ad. 2: 678).
Zygodon sect. *Bryoides* Malta, Acta Univers. Latv. 6: 281. 1923. **syn. nov.**

Schwaegerichen (1824) included a single species in *Codonoblepharon* and defined the genus by the double peristome, composed of 16, paired, reflexed exostome teeth, and erect arcuate segments, unisexual plants with terminal capitulate gametangia, and cucullate calyptrae. Müller (1845, 1848) regarded *Codonoblepharon* as a section of *Zygodon*, and included four taxa. Jaeger (1874) added two new species and transferred 7 more from *Zygodon*. Should *Codonoblepharon* be later retained at the sectional level, the name *Zygodon* sect. *Codonoblephron* (Schwaegr.) C.Müll. (1845) has priority over *Zygodon* sect. *Bryoides* Malta (1926). Though the name *Codonoblepharon* was first used by Schwaegrichen (1824), the concept used here for the genus follows that of Malta for Zygodon sect. Bryoidese. *Codonoblepharon* thus includes only species with smooth laminal cells.

Only one species formerly placed in *Codonoblepharon* is retained here, in addition to *C. menziesii*: *Codonoblepharon pungens* (C.Müll.) Jaeg. (Ber. St. Gall. Naturw. Ges. 1872-1873: 119. 1874). The type material of the following taxa has not been studied but it is presumed that these too, belong to *Codonoblepharum*:

Zygodon corralensis Lorentz, Bot. Zeit. 24: 187, 1866.
Z. gracillimus Fleisch., Musci Flo. Buitz. 2: 392, 1902-1904.
Z. humilis Thw. & Mitt., J. Lin. Soc. 13: 304, 1873.
Z. menziesii var. *angustifolius* Malta, Acta Univers. Latv. 10: 317, 1924.
Z. microtheca Dixon ex Malta, Acta Univers. Latv. 10: 315, 1924.

Z. minutus C. Müll. & Hampe, Linnea 28: 209, 1856.

Z. parvulus Geheeb & Hampe, Enumer. Muscorum brasiliens. 23, 1897.

Zygodon forsteri (Dicks.) Mitt. (Ann. Mag. of natur. hist. 2. ser. 8: 321, 1851) included by Malta (1926) in *Z.* sect. *Bryoides*, may however not belong to *Codonoblepharon*. *Zygodon forsteri* is the only species of this group to occur in the northern temperate zone, whereas all other species are mostly distributed in subtropical to tropical regions or in the southern temperate zone (Malta 1924). Thus, *Z. forsteri* could have derived from an ancestor belonging to *Zygodon sensu stricto*, and have lost the papillae. Kindberg (1897; Eur. N. Am. Bryin. 2: 314, 315) placed *Z. forsteri* in own infrageneric taxon (rank not clear). Material of *Z. forsteri* was not readily available for study. The group, sect. *Bryoides sensu* Malta (1926) is in critical need of revision.

4. **Bryomaltaea** Goffinet **gen. nov.**

Zygodon Hook. et Tayl. affinis. Planta epiphytica, acrocarpa, autoica. Folia ligulata, ovata-lanceolata, obtusa, erecta-appressifolia. Cellulare superiores subquadratae, papillosae. Calyptrae cucullatae, laevis, glabrae. Peristomium duplex.

Type: **Bryomaltaea obtusifolia** (Hook.) Goffinet **comb. nov.**

Zygodon obtusifolius Hook. Musci Exo.: 159. 1820. Type: New Zealand; *Knight* (lectotype: BM; isotype: H)

Plants small, to 1.5 cm tall. Stems orthotropic, sympodially branched. Leaves erect-appressed, ovate-oblong, obtuse. Costa ending below apex, with two ventral guide cells, covered on the abaxial surface by rather short to isodiametric chlorophyllose cells. Basal cells weakly or not differentiated from upper laminal cells. Upper laminal cells isodiametric, thick-walled, strongly bulging, coarsely papillose, papillae two or three, corase, bifid (or in pairs). Acrocarpous, Autoicous, or dioicous. Perichaetial leaves weakly differentiated. Capsule exserted, urn ribbed, stomata phaneroporic, in neck. Peristome double, alternate. Exostome of 16 teeth fused into eight pairs. Endostome of 8 segments. Annulus none. Operculum conic, with a short oblique, rostrum. Calyptrae cucullate, smooth, with prorate cells at apex.

Bryomaltaea is easily distinguished from *Zygodon* by its erect appressed and obtuse leaves. One specimen from Thailand (*Touw 8473*, ALTA) differs from typical *B. obtusifolia* by being dioicous. Whether *Bryomaltaea* is indeed monotypic as suggested by Malta (as Z. sect. *obtusifolius*, 1926) needs to be critically reexamined (see Lewinsky 1990).

5. **Leptodontiopsis** Broth.

Leptodontiopsis was described by Brotherus for *L. fragilifolia* Broth., a species endemic to the high elevations in East Africa (Brotherus 1911). *Leptodontiopsis* differs from *Zygodon* sect. *Zygodon* mainly by the smooth capsule, and dimorphic basal cells. *Leptodontiopsis* may *a priori* not deserve generic distinction but considering a possible a common evolutionary history with *Stenomitrium*, and *Pleurorthotrichum* (chapter 6) it should tentatively be retained as a distinct genus. Malta (1926) described *Zygodon fragilifolius* based on two collections from Mount Kilimanjaro and attributed the species to Brotherus. His description fits that of the type of *Leptodontiopsis fragilifolia* by Brotherus (1911): both have fragile leaf apices, and dimorphic basal cells. I have not yet seen the type of *Z. fragilifolius* Broth. ex Malta, but if this specimen is identical to *Leptodontiopsis fragilifolia* Broth., the latter name would have priority, if *Leptodontiopsis* should be synonymized with *Zygodon*.

6. **Orthotricheae** Goffinet **trib. nov.**

Planta acrocarpa. Calyptrae mitriformae.

Type: *Orthotrichum* Hedw.

7. **Ulota** Mohr

Bryodixonia Sainsb. Trans. Roy. Soc. New Zealand 75: 177. 1945. **syn. nov.**

Ulota perichaetialis (Sainsb.) Goffinet **comb. nov.**

Bryodixonia perichaetialis Sainsb., Trans. Roy. Soc. New Zealand 75: 177. 1945. Type: New Zealand, "on bark of subalpine scrub, Mount Egmont, ca. 4000 feet; coll. *G.O.K. Sainsbury*, January 1945, no. *6005*".

I have not yet seen the type of this species, but have however examined the collections kept in ALTA. This species is very distinctive, by its *Ulota*-like habit, immersed capsules and well differentiated perichaetial leaves.

8. **Schlotheimieae** Goffinet **trib. nov.**

Planta cladocarpa. Calyptrae mitriformae, laevis.

Type: *Schlothemia* Brid.

A sister group relationship of *Schlotheimia* with regard to the other Macromitrioideae was strongly supported based on analyses of *rbc*L sequence data. Though this relationship was not supported in the most parsimonious scenario using morphological characters, *Schlotheimia* was the only large genus the monophyly of which withstood both analyses. Morphologically the genus is well differentiated from the *Macromitrium*-complex, and the invariably well developped peristome suggests that *Schlotheimia* is the least derived in the Macromitroideae.

9. **Macromitrieae** Goffinet **trib. nov.**

Planta cladocarpa vel clado- et acrocarpa. Calyptrae mitriformae, plicatis.

Type: *Macromitrium* Brid.

10. **Matteria** Goffinet **gen. nov.**

Macrocoma (Broth.) Grout affinis. Planta epiphytica, autoica, acro- et cladocarpa. Folia patula (patens) y squarrosa. Cellulae costalis adaxialis elongata. Peristomii duplex. Sporae multicellulae.

Type: *Matteria gracillima* (Besch.) Goffinet

Macromitrium subg. *Trachyphyllum* Broth. in Engl. & Pr., Nat. Pfl. 1(3): 478, 1902.

Macrocoma (Hornsch. ex. C. Müll.) Grout subg. *Trachyphyllum* (Broth.) Vitt, The Bryologist 83: 433, 1980.

a. *Matteria gracillima* (Besch.) Goffinet **comb. nov.**

Schlotheimia gracillima Besch., Bull. Soc. Bot. France 32: LXI. 1885. Type: "Patagonie occidentale, île Wellington: Port Eden, 24 janvier 1879 (*Dr. Savatier*, no. *1838* e. p.)" (holotype—BM-Besch.).

Macromitrium gracillimum (Besch.) Broth. in Engl. & Pr., Nat. Pfl. 1(3): 478, 1902.

Macrocoma gracillima (Besch.) Vitt, The Bryologist 83 (4): 433, 1980.

Specimen examined: Chile: Llanquihue: Volcan Osorno, 10.5 km from junction of road Ensenada Yerbas Buenas, on road to ski slopes, ± 940 m, 41°05'S, 72°33' W, on fallen branch, *James* and *Andrea Solomon 4602* (ALTA); Valvidia: Bog of Astelia, Donatia and Gaimardia with scattered patches of *Sphagnum* at summit of El Mirador, ca. 100 m. southwest of refugio, Cordillera Pelada, near road between LA Union and Punta Hueicolla, alt. 1000 m., 40°07'S, 73°33'W, on tree in *Fitzroya* dominated woods, 19

January 1976, *Crosby 12874* (ALTA); Crumao, Cordillera Pelada, 1000 m, 29.I.1934, *P. A. Hollermayer* (J); Cordillera Pelada (S. Juan), 1000 m, 30.I.35, *P. Ath. Hollemayer* (J); Isla Magdalena; Grenzfluss., 13.12.39, *G.H. Schwabe* no. 33/c (J); Cordillere Pelado, Februar 1935, *A. Hollermayer* (S).

b. *Matteria papillosa* (Thér.) Goffinet **comb. nov.**

Macromitrium papillosum Thér. in Herz., Arch. Esc. Farm. Fac., Cienc. Med. Cordoba 7: 50, 1939. Type: "Prov. Chiloé, Dep. Llanquihé: Pétrohué, leg. *C.C. Hosseus* (n. *521*)" (lectotype—PC-Thér.; isotype—J!).

Macrocoma papillosa (Thér.) Vitt, The Bryologist 83 (4): 433, 1980.

Specimen examined: Chile: Parque Nac. Nahuel Huapi. Neuquén. Puerto Cántaros. Bosque costero bordeando el brazo Blest con *Nothofagus dombeyii, Saxegothaea conspicua, Laurelia philippiana, Azara lanceolata*, etc. 41°04'S,71°49'W. 750 msm, 13/3/95, on small branches of Saxegothaea, *Matteri 6521*, Schiavone (Musci Patagonici Exsiccati-ALTA); Puerto Moutt, Saltos de Petrohue on Guerina auellana, bark, shaded, 150 m, January 1979, *O. van Zanten 7-901143* (ALTA); IX. Region, Nationalpark Villarrica, Nothofaguswald, on *Nothofagus*; 920 msm, 9. Januar 1987, *Schäfer-Verwimp & Verwimp 8144* (ALTA).

In addition to the characters presented by Vitt (1980), *Matteria* (as *M.* subg. *Trachyphyllum*) is easily distinguished from *Macrocoma* (as *M.* subg. *Macrocoma*) by the multicellular spores. The calyptra of *Matteria* is subentire (i.e., laceration along the plications, are restricted to the basal portion of the calyptra) but has one major slit expanding beyond the middle. This situation has also been observed in species of *Macrocoma* (e.g., *M. orthotrichoides Pedersen 13393*—ALTA). Whether the calyptrae are actually cucullate is difficult to ascertain, and more material may be needed to clarify this. The cucullate nature of the calyptrae may however not be surprising considering that the rostrum is somewhat oblique and that in other genera of the Orthotrichaceae, a cucullate calyptra is often found in species with oblique rostra.

Key to the genera of the Orthotrichaceae

1. Stems orthotropic, sympodially branched 2
1. Stems plagiotropic, monopodially branched, rarely also sympodially branched 13

2. Laminal cells smooth 3
2. Laminal cells papillose 6
3. Calyptrae cucullate, seta dextrorse below urn, capsule exserted .... *Codonoblepharon*
3. Calyptrae mitrate, seta sinistrorse or capsule immersed .... 4.
4. Lamina bitratose, urn smooth, spores multicellular .... *Muelleriella*
4. Lamina unistratose, if bistratose, urn ribbed and spores unicellular 4
5. Dorsal cells of costa linear, with pointed ends, leaves flexuose .... *Stoneobryum*
5. Dorsal cells of costa irregularly rectangular, not linear, leaves erect appressed, rarely flexuose .... *Orthotrichum*
6. Basal marginal cells differentiated from inner cells, hyaline, quadrate, with strongly thickened, horizontal anticlinal walls .... *Ulota*
6. Basal marginal cells not differentiated from inner cells 7
7. Basal cells dimorphic, strongly incrassate, nodose or porose, yellowish cells alternating with evenly thickened, hyaline cells 8
7. Basal cells monomorphic, if nodose, then cells not forming alternating bands of yellowish and hyaline cells 9
8. Urn smooth, long exserted, gymnostomous, perichaetial leaves weakly differentiated, endemic to high elevations in East Africa and Borneo .... *Leptodontiopsis*
8. Urn ribbed, emergent, peristome double, perichaetial leaves strongly differentiated, endemic to Central Chile .... *Pleurorthotrichum*
9. Laminal cells strongly bulging 10
9. Laminal cells flat 11
10. Leaves green, short, ovate oblong, broadly obtuse, urn ribbed .... *Bryomaltaea*
10. Leaves orange-brown to green, ovate lanceolate, narrowly obtuse, urn smooth .... *Leratia*
11. Dorsal cells of costa linear, with pointed ends, leaves flexuose, calyptrae cucullate, seta dextrorse .... *Zygodon*
11. Dorsal cells of costa irregularly rectangular, not linear, leaves erect appressed, rarely flexuose, calyptrae mitrate, seta sinistrorse.. 12
12. Capsule globose, constricted at mouth, stomata cryptoporic, restricted to upper half of urn .... *Orthomitrium*
12 Capsule cylindric to ovate, if globose, than not contricted at mouth, stomata phaneroporic or cryptoporic, restricted to the lower half of the urn .... *Orthotrichum*
13. Calyptrae lobate at base 14

13. **Calyptrae entire to lacerate** **16**

  14. **Basal marginal cells hyaline, quadrate, with strongly thickened, horizontal anticlinal walls, forming multiseriate margin, calyptrae unistratose** .... ***Ulota***

  14. **Basal marginal cells not differentiated, or if differentiated, than not quadrate and not in several rows, calyptrae bi- to tristratose** **15**

15. **Leaves decurrent, decurrencies composed of two to three rows of large, inflated hyaline, papillose to tuberculate cells, dioicous** .... ***Cardotiella***

15. **Leaves not decurrent, and hyaline basal marginal cells not papillose or tuberculate, phyllodioicous** .... ***Schlotheimia***

  16. **Stem and branch leaves monomorphic (only shape is considered not the size)** **17**

  16. **Stem and branch leaves conspicuously dimorphic** **21**

17. **Basal marginal cells hyaline, quadrate, with strongly thickened, horizontal anticlinal walls, forming multiseriate margin, calyptrae unistratose** .... ***Ulota***

17. **Basal marginal cells not differentiated, or if differentiated, then not quadrate and not in several rows, calyptrae bi- to tristratose** **18**

  18. **Abaxial layer of the costa composed of strongly bulging, papillose, isodiametric cells almost to the base** .... ***Florschuteziella***

  18. **Abaxial layer of costa composed of substereids (i.e, flat, smooth, linear cells)** **19**

19. **Basal cells rectangular, dimorphic, strongly incrassate, nodose, porose, yellowish cells alternating with evenly thickened hyaline cells, calyptrae cucullate** .... ***Stenomitrium***

19. **Basal cells, except for the most proximal ones, isodiametric, monomorphic** **20**

  20. **Leaves squarrose-recurved, to widely spreading, abaxial surface of costa composed of elongate cells into apex, spores multicellular** .... ***Matteria***

  20. **Leaves erect-appressed, abaxial surface of costa covered with isodiametric cells, spores unicellular** .... ***Macrocoma***

21. **Marginal cells linear and hyaline, forming a distinct border at least in the lower third of the leaf** .... ***Groutiella***

21. **Marginal cells not differentiated into a border of linear, hyaline cells** **22**

  22. **Laminal cells smooth** **23**

  22. **Laminal cells papillose** **26**

23. **Laminal cells flat** .... ***Schlotheimia***

23. **Laminal cells bulging** **24**

  24. **Perichaetial leaves aristate, capsule immersed** .... ***Ceuthotheca***

  24. **Perichaetial leaves not with long excurrent costa, if aristate, capsule exserted** **25**

25. Leaves decurrent, decurrencies composed of two to three rows of large, inflated hyaline, papillose to tuberculate cells, basal cells not differentiated, short, isodiametric, oblate, chlorophyllose .... *Cardotiella*

25. Leaves not decurrent, if decurrent then cells linear and chlorophyllose, or decurrency composed of a single row of hyaline, bulging cells, basal cells differentiated from upper cells, rectangular, hyaline ....*Macromitrium*

26. Branch leaves of sterile and perichaetium bearing branches dimorphic ....*Desmotheca*

26. Branch leaves monomorphic 27

 27. Basal laminal cells long rectangular, hyaline ....*Macromitrium*

 27. Basal laminal cells, except the most proximal ones, short, isodiametric to oblate, chlorophyllose 28

28. Leaves decurrent, decurrencies composed of two to three rows of large, inflated hyaline, papillose to tuberculate cells, basal cells not differentiated, short, isodiametric, oblate, chlorophyllose ....*Cardotiella*

28. Leaves not decurrent, if decurrent then cells linear and chlorophyllose, or decurrency composed of a single row of hyaline, bulging cells, basal cells differentiated from upper cells, rectangular, hyaline 29

29. Capsule ribbed, dioicous ....*Leiomitrium*

29. Capsule smooth , phyllodioicous ....*Macromitrium* subg. *Cometium* Mitt.

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Chapter eight

Conclusion

The Bryopsida (*sensu* Vitt 1984) with over 9000 species (Schofield 1985), are as diverse as the Filicopsida (*sensu* Mickel 1982) and form the third largest class of land plants after the Magnoliopsida and Lilicopsida (*sensu* Cronquist 1982). Although the relationships of mosses to other green plants have been the focus of many studies over the last decade (e.g., Capesius, 1995; Hedderson, Chapman, and Rootes 1996; Krantz et al. 1995, Manhart 1994; Mishler and Churchill 1984, 1985; Mishler et al. 1992, 1994; Waters et al. 1992), the monophyly and the phylogeny of the Bryopsida has drawn little attention since the advent of molecular techniques. Addressing the evolution of mosses at the ordinal and familial level, necessitates the identification of major monophyletic groups and the selection of appropriate exemplar taxa (Mishler 1994). The Bryopsida are currently divided into 16 orders (Vitt 1982; 14 of these as suborders in Vitt 1984), of which 14 share an arthrodontous peristome. Vitt (1981) recognized four major types of arthrodontous peristomes: the *Funaria*-type, *Orthotrichum*-type, *Bryum*-type, and the *Dicranum*-type. The direction of peristomial character transformations among these types is not agreed upon (Crosby 1980, Lewinsky 1989, Shaw and Rohrer 1984, Vitt 1984,). The Orthotrichales as currently defined (Vitt 1984) are heterogeneous with regards to the architecture of the peristome (see Edwards 1979, 1984, Vitt 1981, Shaw 1985, Lewinsky 1989), and their monophyly needs to be critically reexamined before the order and its type family can be adequately represented in any higher level phylogenetic study.

Circumscription of the Orthotrichales. The Orthotrichales *sensu* Vitt are composed of five families: the Erpodiaceae, Helicophyllaceae, Microtheciellaceae, Orthotrichaceae, and Rhachitheciaceae. Except for the Orthotrichaceae, these families are composed of gymnostomous taxa or taxa with a peristome that *a priori* is incompatible with any of the four main types. The family is shown to be of polyphyletic origin (chapters three and five). The Microtheciellaceae are excluded based on morphology: the only species, *M. kerrei*, is clearly pleurocarpous. The family may be related to the Neckeraceae, and is therefore transferred to the Leucodontales. Critical examination of the peristome of the Erpodiaceae (Edwards 1979; pers. observations) and of the Rhachitheciaceae (chapter three), suggests that these families may be only distantly related to the Orthotrichaceae. These hypotheses were subsequently supported by comparisons of nucleotide sequences of the chloroplast gene, *rbc*L, and these families, the Rhachitheciaceae and the Erpodiaceae, are transferred to the haplolepideae, with affinities to the Seligeriales (chapter three and five). The monotypic and gymnostomous Helicophyllaceae are characterized by a unique combination of morphological characters, and are considered only distantly related to the Orthotrichaceae. Though molecular data are not yet available for this taxon, the family is tentatively excluded from the order. The Orthotrichales are thus here considered restricted to the Orthotrichaceae *sensu* Vitt (1984).

Circumscription of the Orthotrichaceae. The Orthotrichaceae, one of the largest families of arthrodontous mosses, were prior to this study, composed of 26 genera (Lewinsky 1976, Lewinsky 1994, Lewinsky-Haapasaari and Crosby 1996, Vitt 1984, Zander 1993) distributed among four subfamilies (Vitt 1972). The heterogeneity of the family, as expressed by the great variation in morphological characters, is best explained by its polyphyletic circumscription (chapters two and three). Critical examination of morphological characters based on type material leads to 1) the synonymy of the monotypic *Pleurozygodontopsis* with *Zygodon* (*Z. reinwardtii*, chapter two), and 2) the exclusion from the Orthotrichaceae of *Kleioweisiopsis* (Ditrichaceae, chapter two), *Trigonodictyon* (Grimmiaceae, chapter two), *Octogonella* and *Uleastrum* (Rhachitheciaceae, chapter three). The systematic affinities of gymnostomous taxa such as *Amphidium* and *Drummondia* were addressed using molecular techniques. Based on a cladistic analysis of *rbc*L nucleotide sequences, both genera are shown to be of haplolepideous origin and only distantly related to the Orthotrichaceae (chapter five). The Orthotrichaceae are thus restricted to 19 of the original genera.

Major phylogenetic relationships. Cladistic analyses using either molecular or morphological characters provide strong support for the monophyly of the amended Orthotrichaceae, rather than for a polyphyletic origin of the family (Churchill and Linares 1995, De Luna 1995). The relationships among the 19 genera are, however obscure. Based on *rbc*L sequence data, the Zygodontoideae and the Orthotrichoideae form a monophyletic clade sister to the Macromitrioideae, whereas morphological characters support a close relationship between the latter two subfamilies with the Zygodontoideae sister to this combined clade. It is argued that uncertainties about the homology of certain morphological character-states may be at the origin of the discrepancies between both analyses. The subfamilial classification of the Orthotrichaceae therefore follows the gene phylogeny, and the family is divided in two subfamilies, the Orthotrichoideae and the Macromitrioideae (chapter seven).

The four most speciose genera of the Orthotrichaceae, namely *Macromitrium*, *Orthotrichum*, *Ulota*, and *Zygodon*, as well as the small genus *Macrocoma* are suggested to merely represent evolutionary grades (chapter five and six). The monophyly of *Ulota* is restored with the inclusion of the monotypic genus *Bryodixonia* (chapter seven). The heterogeneity of *Orthotrichum* and *Macromitrium* needs further study, whereas new genera are proposed to accommodate the variation found in *Zygodon* and *Macrocoma* (chapter seven). The Orthotrichaceae are now considered to be composed of 22 genera. The relationships between the genera remain mostly ambiguous. Morphological stasis (see Williamson 1987, and Larson 1989) associated with decoupled molecular and morphological evolution may lead, in a classification system based solely on comparative morphology, to the recognition of grades rather than natural groups (e.g., Zygodontoideae and *Orthotrichum*). Similarly, the intrinsic nature of the molecular character, that is the simplest and thus least robust character available, may result in higher levels of homoplasy (Wägele 1995) and thus yield false phylogenies due to long branch effects (Hendy and Penny 1989). A revised classification of the Orthotrichaceae is presented (chapter seven). It incorporates relationships strongly supported by at least one of the data sets (e.g., sister-group relationship between *Schlotheimia* and the other Macromitrioideae) as well as "default" affinities (e.g., monophyly preferred to paraphyly of the *Zygodon*-complex as suggested by *rbc*L data). The Orthotrichaceae are thus considered composed of two subfamilies, each including two tribes: the Zygodonteae and the Orthotricheae (Orthotrichoideae) and the Schlotheimieae and the Macromitrieae (Macromitrioideae).

This study is the first attempt to examine the generic circumscription of an order and a large family of mosses, using molecular data. DNA sequences are shown to offer a unique opportunity to solve the systematic affinities of taxa lacking characters that are central to the classification of mosses. Careful morphological comparisons of taxa remains nevertheless essential to phylogenetic studies because molecules *a priori* tell us something about relationships but nothing about character evolution, and because most hypotheses are meaningful only if placed in a morphological context. The results presented here together with those obtained in a parallel study using 18S gene sequences (Hedderson et al. unpubl.) formed the basis for a revised classification of the Bryopsida (Vitt, Goffinet, and Hedderson 1997).

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Appendix 1. *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                   10>       20>       30>       40>       50>       60>       70>       80>
Funaria hygrometrica        ??????????????????????????????GCTGGATTTAAAGCTGGTGTTAAAGATTACCGATTAACTTATTACACTCC
Funaria apophysata          ??????????????????????????????.T............................A...................
Splachnum sphaericum        ??????????????????????????????.T...........................TA...................
Tayloria lingulata          ??????????????????????????????.T...........................TA...................
Hedwigia ciliata            ??????????????????????????????.T............................A...................
Mnium thomsonii             ??????????????????????????????.................G.....G......A...................
Abietinella abietiena       ??????????????????????????????.T............................A...................
Schlotheimia tecta          ??????????????????????????????.T............................A......A............
Schlotheimia trichomitria   ??????????????????????????????.T............................A...................
Schlotheimia brownii        ??????????????????????????????.T............................A...................
Cardotiella quinquefaria    ??????????????????????????????.T............................A...................
Macrocoma tenue             ??????????????????????????????.T............................A...................
Macrocoma papillosa         ??????????????????????????????.T............................A...................
Groutiella chimborazense    ??????????????????????????????.T............................A...................
Groutiella apiculata        ??????????????????????????????.T............................A...................
Macromitrium involutifolium ??????????????????????????????.T............................A...................
Macromitrium longifolium    ??????????????????????????????.T............................A...................
Macromitrium richardii      ??????????????????????????????.T............................A......A............
Desmotheca. apiculata       ??????????????????????????????.T............................A...................
Zygodon intermedius         ??????????????????????????????.T............................A......A............
Zygodon reinwardii          ??????????????????????????????.T............................A...................
Zygodon pungens             ??????????????????????????????.T............................A...................
Zygodon obtusifolium        ??????????????????????????????.T............................A...................
Orthotrichum lyellii        ??????????????????????????????..............................A...................
Orthotrichum obtusifolium   ??????????????????????????????.T............................A...................
Orthotrichum anomalum       ??????????????????????????????.T............................A...................
Ulota obtusiuscula          ??????????????????????????????.T............................A...................
Ulota lutea                 ??????????????????????????????.T............................A...................
Bryodixonia perichaetialis  ??????????????????????????????.T............................A...................
Drummondia prorepens        ??????????????????????????????.T............................A...................
Amphidium lapponicum        ??????????????????????????????.T............................A...................
Rhabdoweisia crenulata      ??????????????????????????????.T............................A...................
Aulacopilum hogdkinsoniae   ??????????????????????????????.T............................A...................
Venturiella sinensis        ??????????????????????????????.T............................A...................
Uleastrum palmicola         ??????????????????????????????.T............................A...................
Encalypta procera           ??????????????????????????????.T............................A...................
Ptychomitrium gardnerii     ??????????????????????????????.T............................A......A......T.....
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                     90>       100>       110>       120>       130>       140>       150>       160>
Funaria hygrometrica          AGATTATCAAACTAAAGATACTGACATTCTAGCAGCATTTCGTATGACTCCTCAGCCAGGTGTACCACCTGAAGAAGCAG
Funaria apophysata            ........................T..............................A.....A...............TGT.
Splachnum sphaericum          ..................A.....T...T.............A.................A......G............
Tayloria lingulata            ..................A.....T...T.............A.................A......G.......G....
Hedwigia ciliata              .........G........C.....T...T.............A...........A.....A......G....G..G....
Mnium thomsonii               .........G........A.....T...T.....G.......A.....C.....A..G..A......G.......G....
Abietinella abietiena         .........G........A.....T...T.............A...........A.....A.....CG.......G....
Schlotheimia tecta            ........................T...T.............A...........A.....A.....GG.......G....
Schlotheimia trichomitria     ........................T...T.............A...........A.....A.....GG.......G....
Schlotheimia brownii          ........................T...T.............A...........A.....A.....GG.......G....
Cardotiella quinquefaria      ...G..........TT........T...T.............A...........A.....A.....GG.......G..G.
Macrocoma tenue               .............TC...A.....T...T.............A...........A.....A.....GG.......G..G.
Macrocoma papillosa           ..................A.....T...T.............A...........A.....A.....GG.......G..G.
Groutiella chimborazense      .............TC.C.A.....T...T.............A...........A.....A.....GG.......G..G.
Groutiella apiculata          .............TC.C.A.....T...T.............A...........A.....A.....GG.......G..G.
Macromitrium involutifolium   ..............C.C.A.....T...T.............A...........A.....A.....GG.......G..G.
Macromitrium longifolium      .............TC.C.A.....T...T.............A...........A.....A.....GG.......G..G.
Macromitrium richardii        .............TC.........T...T.............A...........A.....A.....GG.......G..G.
Desmotheca. apiculata         .............TC...A.....T...T.............A...........A.....A......G..........G.
Zygodon intermedius           ........................T...T.............A...........A.....A.....GG.......G..T.
Zygodon reinwardii            ..................A.....T...T.............A...........A.....A......G.......G....
Zygodon pungens               ..................A.....T...T.............A...........A.....A......G.......G..T.
Zygodon obtusifolium          ..................A.....T...T.............A...........A.....A.....GG............
Orthotrichum lyellii          ........................T...T.............A...........A.....A......G............
Orthotrichum obtusifolium     ..................A.....T...T.............A...........A.....A..G...G.......G....
Orthotrichum anomalum         ..................A.....T...T.............A...........A.....A..G...G............
Ulota obtusiuscula            ..................A.....T...T.............A...........A.....A......G............
Ulota lutea                   ..................A.....T...T.............A...........A.....A......G............
Bryodixonia perichaetialis    ..................A.....T...T.............A...........A.....A......G............
Drummondia prorepens          .........G........A.....T...T.............A...........A.....A..G................
Amphidium lapponicum          ..................A.....T...T.............A...........A.....A...................
Rhabdoweisia crenulata        ..................A.....T...T.............A...........A.....A..G................
Aulacopilum hogdkinsoniae     ..................C.....T...T.............A...........A.....A...................
Venturiella sinensis          ...C...G..........A..C..T...T.............A...........A.....A...................
Uleastrum palmicola           .............TT...A.....T...T.............A...........A.....A.....TG............
Encalypta procera             .........G........A.....T...T...........A.A...........A..G..A...................
Ptychomitrium gardnerii       ..................A.....T...T.............A...........A.....A...................
```

Appendix 1 (cont.). *RbcL* gene sequences of 37 arthrodontous mosses.

```
                                   170>      180>      190>      200>      210>      220>      230>      240>
Funaria hygrometrica         GAGCTGCTGTAGCTGCAGAATCTTCTACTGGTACATGGACTACTGTTTGGACTGATGGACTTACTAGTCTTGACCGTTAC
Funaria apophysata           ................G........C..A............................................T......
Splachnum sphaericum         .C.......................................................................T..C..T
Tayloria lingulata           .........................................................................T.....T
Hedwigia ciliata             .......A........G........C..............C................................T.....T
Mnium thomsonii              ....G..A........G........C..........................C..C........C........T......
Abietinella abietiena        .......A........G........C..............C.......................C........T.....T
Schlotheimia tecta           .......A.................A........G.....C.................T..............T.....T
Schlotheimia trichomitria    .......A.................A........G.....C.................T..............T.....T
Schlotheimia brownii         .......A.................G........G.....C.................T..............T.....T
Cardotiella quinquefaria     .......A.....G...........G..............C.................T..............T.....T
Macrocoma tenue              .......A.....G...........G..............C.................T..............T.....T
Macrocoma papillosa          .......A.....S...........G..............A.................T..............T.....T
Groutiella chimborazense     .......A.....G...........G..............C.................T..............T.....T
Groutiella apiculata         .......A.....S...........G.............MC.M...............T..............T.....T
Macromitrium involutifolium  .......A.....G...........G..............C.................T..............T......
Macromitrium longifolium     .............G...........G..............C...........C.....T...........C..T.....T
Macromitrium richardii       .......A.....G...........G..............C.................T..............T.....T
Desmotheca. apiculata        .......A.....G...........G..............C.................T..............T.....T
Zygodon intermedius          .......A..................................................C..............T.....T
Zygodon reinwardii           .......A..................................................C..............T.....T
Zygodon pungens              .......A................................C.................C..............T.....T
Zygodon obtusifolium         .......G.................A..............C.................T..............T.....T
Orthotrichum lyellii         .......A..................................................C..............T.....T
Orthotrichum obtusifolium    .......A..................................................C..............T.....T
Orthotrichum anomalum        .......A..................................................C..............T.....T
Ulota obtusiuscula           .......A..................................................T..............T.....T
Ulota lutea                  .......A..................................................C..............T.....T
Bryodixonia perichaetialis   .......A..................................................C..............T.....T
Drummondia prorepens         .......A........G........C..............C................................T.....T
Amphidium lapponicum         .......A.................C..............C................................T.....T
Rhabdoweisia crenulata       .......A........G........C...............................................T.....T
Aulacopilum hogdkinsoniae    .......A........G........................................................T.....T
Venturiella sinensis         .......A........G........................................................T.....T
Uleastrum palmicola          .......A........G.......................C................................T.....T
Encalypta procera            .......A.................C.........................................C.....T......
Ptychomitrium gardnerii      .......A........G.......................C................................T.....T
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                   250>      260>      270>      280>      290>      300>      310>      320>
Funaria hygrometrica         AAAGGTCGTTGCTATGGAATTGAACCAGTTGCTGGAGAAGAAAATCAATTTATTGCTTATGTTGCTTATCCACTAGATTT
Funaria apophysata           ......A.A.......C.............C..................A......................T.......
Splachnum sphaericum         .....A..A.......ATC.....G.T...C..................A...............A..C...T.......
Tayloria lingulata           .....A..A.......ATC.....G.T...C..................A..................C..GT.......
Hedwigia ciliata             .....G..A.......A.......G................T.......A......G...........C...T.......
Mnium thomsonii              .....A..A........T......G.....C..........G.......A.......C..............T.......
Abietinella abietiena        .....A..A.......ATC.....G.....C..........G.......A..................C...T.....C.
Schlotheimia tecta           .....AA.A.......AT......G.....C..........T.......A............G.....C...T.......
Schlotheimia trichomitria    .....AA.A.......AT......G.....C..........T.......A............G.....C...T.......
Schlotheimia brownii         .....AA.A.......AT......G.....C..........T.......A............G.....C...T.......
Cardotiella quinquefaria     .....AA.A.......ATC.....G.....C..........T.......A..................C...T.......
Macrocoma tenue              .....AA.A.......AT......G.....C..........T.......A..................C...T.......
Macrocoma papillosa          .....AA.A.......AT......G.....C..........T.......A..................C...T.......
Groutiella chimborazense     .....AA.A.......AT......G................T.......A..................C...T.......
Groutiella apiculata         .....AA.A.......AT......G.....C..........T.......A..................C...T.......
Macromitrium involutifolium  .....AA.A.......AT......G................T.......A..................C...T.......
Macromitrium longifolium     .....AA.A.......AT......G.G...C..........T.......A..................C...T.......
Macromitrium richardii       .....AA.A.......AT......G................T.......A..................C...T.......
Desmotheca. apiculata        .....AA.A.......AT......G.....C..........T.......A..................C...T.......
Zygodon intermedius          .....A..A.......ATC.....G................T.......A..................C...T.......
Zygodon reinwardii           .....A..A.......ATC.....G................T.......A..................C...T.......
Zygodon pungens              .....A..A.......ATC.....G.....C..........T.......A..................C...T.......
Zygodon obtusifolium         .....AA.A.......AT......G................T.......A..................C...T.......
Orthotrichum lyellii         .....A..A.......ATC.....G.....C..........T..C....A..................C...T.......
Orthotrichum obtusifolium    .....A..A.......ATC.....G.....C..........T.......A..................C...T.......
Orthotrichum anomalum        .....A..A.......ATC.....G.....C..........T.......A..................C...T.......
Ulota obtusiuscula           .....A..A.......ATC.....G.....C..........T..C....A..................C...T.......
Ulota lutea                  .....A..A.......ATC.....G.....C..........T..C....A..................C...T.......
Bryodixonia perichaetialis   .....A..A.......ATC.....G.....C..........T..C....A..................C...T.......
Drummondia prorepens         ........A.......AT......G.....C..........G.......A...C..............C...T.....C.
Amphidium lapponicum         ........A..T....AT......G.....C..........G.......A...C..............C...T.......
Rhabdoweisia crenulata       ........A.......ATC.....G.....C..................A..................C...T.......
Aulacopilum hogdkinsoniae    ........A.......AT......G.....C..................A...C..............C...T.......
Venturiella sinensis         ........A.......AT......G.....C..................A...C..............C...T.......
Uleastrum palmicola          ........A.......AT......G........................A...C..............C...T.......
Encalypta procera            ........A.......AG......G.....C..................A..................C...T.......
Ptychomitrium gardnerii      ........A.......ATC.....G.....C..................A...C..............C...T.......
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                     330>      340>      350>      360>      370>      380>      390>      400>
Funaria hygrometrica           ATTTGAAGAAGGTTCTGTTACTAACTTATTTACTTCTATTGTTGGTAACGTTTTTGGATTTAAAGCTTTAAGAGCTTTAC
Funaria apophysata             ................................................................................
Splachnum sphaericum           .....................C..T.......................T.....C...............C.........
Tayloria lingulata             .....................C..T.....C.................T.....................C.........
Hedwigia ciliata               ........................T.................C.....T.....................C.........
Mnium thomsonii                .....................C..T.......................T.....C.....C.........C.........
Abietinella abietiena          .....................C..T.......................T.....................C.........
Schlotheimia tecta             ................................................T.....................C.........
Schlotheimia trichomitria      ................................................T.....................C.........
Schlotheimia brownii           ................................................T.....................C.........
Cardotiella quinquefaria       ........................T.......................T.....................C.........
Macrocoma tenue                ........................T.......................T.....................C.........
Macrocoma papillosa            ........................T.......................T.....................C.........
Groutiella chimborazense       ........................T.......................T.....................C.........
Groutiella apiculata           ........................T.......................T.....................C.........
Macromitrium involutifolium    ........................T.......................T.....................C.........
Macromitrium longifolium       ........................T.......................T.....................C.........
Macromitrium richardii         ........................T.......................T.....................C.........
Desmotheca. apiculata          ........................T.......................T.....................C.........
Zygodon intermedius            .....................C..T.......................T.....................C.........
Zygodon reinwardii             .....................C..T.......................T.....................C.........
Zygodon pungens                ........................T.......................T.....................C.........
Zygodon obtusifolium           ........................T.......................T.....................C.........
Orthotrichum lyellii           .....................C..T.......................T.....................C.........
Orthotrichum obtusifolium      .....................C..T.......................T.....................C.........
Orthotrichum anomalum          .....................C..T.......................T.....................C.........
Ulota obtusiuscula             .....................C..T.......................T.....................C.........
Ulota lutea                    .....................C..T.......................T...............................
Bryodixonia perichaetialis     .....................C..T.......................T.....................C.........
Drummondia prorepens           .....................C..T.......................T.....C...............C.........
Amphidium lapponicum           .....................C..T.......................T...........C.........C.......G.
Rhabdoweisia crenulata         ........................T.......................T.....................C.......G.
Aulacopilum hogdkinsoniae      .....................C..T.......................T.....................C.......G.
Venturiella sinensis           .....................C..T.......................T.....................C.......G.
Uleastrum palmicola            .....................C..T.......................T.....................C.........
Encalypta procera              .....................C..T.......................T.....................C....C....
Ptychomitrium gardnerii        .....................C..T.......................T.....................C.......G.
```

Appendix 1 (cont.). *RbcL* gene sequences of 37 arthrodontous mosses.

```
                                      410>      420>      430>      440>      450>      460>      470>      480>
Funaria hygrometrica         GTCTAGAAGATTTACGTATTCCTCCAGCTTACTCCAAAACTTTCCAAGGCCCACCTCACGGTATTCAAGTTGAAAGAGAT
Funaria apophysata           ...............................T.................................G..............
Splachnum sphaericum         ................C..............T...........T.....T..............C...............
Tayloria lingulata           ...............................T..T.....C........T..............................
Hedwigia ciliata             ...............................T...........T...........G..T.....................
Mnium thomsonii              ....G..........................T..........................T..............G......
Abietinella abietiena        ...............................T..........................T.....................
Schlotheimia tecta           ...............................T..........................T.....................
Schlotheimia trichomitria    ...............................T..........................T.....................
Schlotheimia brownii         ...............................T..........................T.....................
Cardotiella quinquefaria     ..........C....................T..........................T.....................
Macrocoma tenue              ..........C....................T.................T........T.....................
Macrocoma papillosa          ..........C....................T..........................T.....................
Groutiella chimborazense     ..........C....................T..........................T.....................
Groutiella apiculata         ..........C....................T..........................T.....................
Macromitrium involutifolium  ...............................T...........T..............T.....................
Macromitrium longifolium     ..........C....................T..........................T.....................
Macromitrium richardii       ...............................T..........................T.....................
Desmotheca. apiculata        ...............................T..........................T.....................
Zygodon intermedius          ...............................T.................T........T...............C.....
Zygodon reinwardii           ...............................T.................T........T...............C.....
Zygodon pungens              ...............................T.................T........T...............C.....
Zygodon obtusifolium         ...............................T.................G........T.....................
Orthotrichum lyellii         ..T............................T.................T........T...............C.....
Orthotrichum obtusifolium    ..T............................T.................T........T...............C.....
Orthotrichum anomalum        ...............................T.................T........T...............C.....
Ulota obtusiuscula           ..............A................T.................T........T...............C.....
Ulota lutea                  ...............................T..T..............T........T...............C.....
Bryodixonia perichaetialis   ...............................T..T..............T........T...............C.....
Drummondia prorepens         .............G.................T......................................C.........
Amphidium lapponicum         ..T..........G.................T..........................T...........C.........
Rhabdoweisia crenulata       .............G.................T..........................T.....................
Aulacopilum hogdkinsoniae    .............G.................T...........T..............T.....................
Venturiella sinensis         .............G.................T...........T..............T.....................
Uleastrum palmicola          .............G............T....TA....G....................T.....................
Encalypta procera            ..............?...........................................T.....................
Ptychomitrium gardnerii      .............G.................T...........T..............T.....................
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                   490>      500>      510>      520>      530>      540>      550>      560>
Funaria hygrometrica          AAATTAAACAAATATGGTCGTCCATTATTAGGATGTACTATTAAACCAAAATTAGGTTTATCTGCTAAAAACTATGGTAG
Funaria apophysata            ................................................................................
Splachnum sphaericum          ...........G...........G........C......................................T........
Tayloria lingulata            ............................................G..........................T..C.....
Hedwigia ciliata              ............................................G........G..........................
Mnium thomsonii               .....G........C.............................G........G..........................
Abietinella abietiena         ........T...................................G........G..........................
Schlotheimia tecta            ...................................C...................................T........
Schlotheimia trichomitria     ...................................C...................................T........
Schlotheimia brownii          ...................................C...................................T........
Cardotiella quinquefaria      .....................................................G.................T..C.....
Macrocoma tenue               .....................................................G.................T..C.....
Macrocoma papillosa           ...........................C.........................G.................T..C.....
Groutiella chimborazense      .....................................................G.................T..C.....
Groutiella apiculata          .....................................................G.................T..C.....
Macromitrium involutifolium   .....................................................G.................T........
Macromitrium longifolium      .....................................................G.................T..C.....
Macromitrium richardii        .....................................................G.................T........
Desmotheca. apiculata         .....................................................G.................T........
Zygodon intermedius           .......................................................................T........
Zygodon reinwardii            .......................................................................T........
Zygodon pungens               .......................................................................T........
Zygodon obtusifolium          .....................................................G.................T........
Orthotrichum lyellii          ................................G......................................T........
Orthotrichum obtusifolium     ................................G......................................T........
Orthotrichum anomalum         ................................G......................................T........
Ulota obtusiuscula            .......................................................................T........
Ulota lutea                   ................................G......................................T........
Bryodixonia perichaetialis    ................................G......................................T........
Drummondia prorepens          ................................................................S...............
Amphidium lapponicum          ...................................C.................G....................C.....
Rhabdoweisia crenulata        .....................................................G.....G..............C.....
Aulacopilum hogdkinsoniae     .....................................................G..........................
Venturiella sinensis          ..........................G........C.................G..........................
Uleastrum palmicola           .....................................................G.....G....................
Encalypta procera             .............................G...........?...........G..........................
Ptychomitrium gardnerii       .................G.................C.................G..........................
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                      570>      580>      590>      600>      610>      620>      630>      640>
Funaria hygrometrica          AGCTGTATACGAGTGTCTTCGTGGTGGACTTGATTTCACTAAAGATGATGAAAACGTAAACTCTCAACCTT?CATGCGTT
Funaria apophysata            .......................................A...............................T........
Splachnum sphaericum          ...G.....T..A..........................A....................T..........TT.......
Tayloria lingulata            ...G.....T..A..........................A....................T..........TT.......
Hedwigia ciliata              .........T..A..........................A...............................TT.......
Mnium thomsonii               .........T..A.................C..C.....A....................T.....G....TT.......
Abietinella abietiena         .........T..A..........................A....................T..........TT.......
Schlotheimia tecta            .........T..A..........................A.................C..T..........TT.......
Schlotheimia trichomitria     .........T..A..........................A.................C..T..........TT.......
Schlotheimia brownii          .........T..A..........................A.................T..T..........TT.......
Cardotiella quinquefaria      .........T..A..........................A..............T................TT.......
Macrocoma tenue               .........T..A..........................A..............T................TT.......
Macrocoma papillosa           .........T..A..........................A..............T................TT.......
Groutiella chimborazense      .........T..A..........................A..............T................TT.......
Groutiella apiculata          .........T..A..........................A..............T................TT.......
Macromitrium involutifolium   .........T..A..........................A..............T................TT.......
Macromitrium longifolium      .........T..A..........................A..............T................TT.......
Macromitrium richardii        .........T..A..........................A..............T................TT.......
Desmotheca. apiculata         .........T..A..........................A..............T.....T..........TT.......
Zygodon intermedius           .........T..A..............C...........A....................T..........TT.......
Zygodon reinwardii            .........T..A..............C...........A....................T..........TT.......
Zygodon pungens               .........T..A.......................T..A....................T..........TT.......
Zygodon obtusifolium          .........T..A..........................A....................T..........TT.......
Orthotrichum lyellii          .........T..A..........................A....................T..........TT.......
Orthotrichum obtusifolium     .........T..A..........................A..............T.....T..........TT.......
Orthotrichum anomalum         .........T..A..........................A....................T..........TT.......
Ulota obtusiuscula            .........T..A..........................A....................T..........TT.......
Ulota lutea                   .........T..A..........................A....................T..........TT.......
Bryodixonia perichaetialis    .........T..A..........................A....................T..........TT.......
Drummondia prorepens          .........T..A..........................A..............T.....T........G.TT.......
Amphidium lapponicum          ......G..T..A.......................T..A...............?....T........G.TT.......
Rhabdoweisia crenulata        .........T..A..........................A..............T.....T........G.TT.......
Aulacopilum hogdkinsoniae     ......G..T..A........................T.A....................T........A.TT.......
Venturiella sinensis          ......G..T..A..........................A....................T........G.TT.......
Uleastrum palmicola           ......T..T..A..........................A..............T.....T........G.TT.......
Encalypta procera             .........T..A..........................A..............T.....T..........TT.......
Ptychomitrium gardnerii       .........T..A..T.G.....................A....................T........A.TT.......
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                    650>      660>      670>      680>      690>      700>      710>      720>
Funaria hygrometrica         GGAGAGACCGTTTCTTATTTGTAGCAGAAGCTATTTACAAATCTCAAGCTGAAACAGGTGAAATTAAAGGGCATTATCTA
Funaria apophysata           ....................TGT........................T................................
Splachnum sphaericum         .........................T............................................A......T..
Tayloria lingulata           .......T.................T.....A.....T.....G..........................A......T..
Hedwigia ciliata             .......T............A....T...........T................................A......T..
Mnium thomsonii              .......T.................T.....CC.....................................A......TC.
Abietinella abietiena        .......T.................T............................................A......T..
Schlotheimia tecta           .......T.................T.....................T......................A......T..
Schlotheimia trichomitria    .......T.................T.....................T......................A......T..
Schlotheimia brownii         .......T.................T.....................T......................A......T..
Cardotiella quinquefaria     .......T.................T.................G...T......................A......T..
Macrocoma tenue              .......T........G...A....T.................G..........................A......T..
Macrocoma papillosa          .......T.................T.................G..........................A......T..
Groutiella chimborazense     .......T............A....T.................G..........................A......T..
Groutiella apiculata         .......T............A....T.................G...T......................A......T..
Macromitrium involutifolium  .......T............A....T.................G..........................A......T..
Macromitrium longifolium     .......T............A....T.................G..........................A......T..
Macromitrium richardii       .......T.................T.................G..........................A......T..
Desmotheca. apiculata        .......T.................T.................G...T......................A......T..
Zygodon intermedius          .........................T........C..T................................A.....CT..
Zygodon reinwardii           .........................T........C..T.........T......................A......T..
Zygodon pungens              .......T.................T...........T..........G.....................A......T..
Zygodon obtusifolium         .......T.................T...........T..........GA....................A......T..
Orthotrichum lyellii         ....................TGT..T........C..T................................A......T..
Orthotrichum obtusifolium    .........................T........C..T................................A......T..
Orthotrichum anomalum        ....................TGC..T........C..T.......................G........A......T..
Ulota obtusiuscula           ....................TGT..T........C..T..G.............................A......T..
Ulota lutea                  ....................TGT..T........C..T................................A......T..
Bryodixonia perichaetialis   ....................TGT..T........C..T................................A......T..
Drummondia prorepens         .........................G......C....T....................A...........A......T..
Amphidium lapponicum         .........................G......C.....................................A......T..
Rhabdoweisia crenulata       .........................G.....................T......................A.........
Aulacopilum hogdkinsoniae    .......T.....T...........G......................G.....................A.........
Venturiella sinensis         .......T.....T...........G......................G.....................A.........
Uleastrum palmicola          .......T............A....G.....................AA.......AA...G........A......T..
Encalypta procera            .............TC.................C....T.................G..G...........A.....CT..
Ptychomitrium gardnerii      .......T.................G......C.....................................A......T..
```

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                    730>      740>      750>      760>      770>      780>      790>      800>
Funaria hygrometrica          AATGCTACTGCAGGTACTTGTGAAGAAATGATGAAAAGAGCTCAATTTGCTAGAGAATTAGGTGTACCTATTGTAATGCA
Funaria apophysata            ...............................................................A.G........T.....
Splachnum sphaericum          .................A.............................................A.G........T.....
Tayloria lingulata            .................A.......................C.....................A.G........T.....
Hedwigia ciliata              ........C........A.......................................C....C..T........T.....
Mnium thomsonii               ........C........A........................T.C............C....C.CT........T.....
Abietinella abietiena         ........C........A.C........................G.................CA.G........C.....
Schlotheimia tecta            ........C........A.C.....................AGC..G.........GC....CA.G..............
Schlotheimia trichomitria     ........C........A.C.....................AGC..G.........GC....CA.G..............
Schlotheimia brownii          ........C........A.......................AGC..G.........GC....CA.G..............
Cardotiella quinquefaria      .................A.......................AGC..G...............CA.G..............
Macrocoma tenue               .................A.......................AGC..G...............CA.G..............
Macrocoma papillosa           .................A.......................AG...G...............CA.G..............
Groutiella chimborazense      .................A..C....................AGC..G................A.G..............
Groutiella apiculata          .................A..C.........C..........AGC..G................A.G..............
Macromitrium involutifolium   .................A.......................AGC..G...............CA.G..............
Macromitrium longifolium      .................A............C..........AGC..G................A.G..............
Macromitrium richardii        .................A.......................AGC..GC..............CA.G..............
Desmotheca. apiculata         .................A.C.....................AGC..GC..............CA.G..............
Zygodon intermedius           ........C........A.C.....................A....G...............CA.G..............
Zygodon reinwardii            ........C........A.......................A....................CA.G..............
Zygodon pungens               ........C........A..C.....................G...G...............CA.G..............
Zygodon obtusifolium          .................A.C......................GC..G.........G.....CA.G..............
Orthotrichum lyellii          ........C........A.......................AG...................CA.G..............
Orthotrichum obtusifolium     ........C........A.......................AGC..................CA.G..............
Orthotrichum anomalum         ........C........A.......................AGC.............C....AA.G..............
Ulota obtusiuscula            ........C........A.......................AG...G...............CA.G..............
Ulota lutea                   ........C........A............C.A........AG...G...............CA.G..............
Bryodixonia perichaetialis    ........C........A.......................AG...................CA.G..............
Drummondia prorepens          ........C........C............T.A.........................G..C.CT........T.....
Amphidium lapponicum          ........C.................G...C.A.........G..............C.G..C.CT........T.....
Rhabdoweisia crenulata        ........C........C.........................G................G..CA.G........T.....
Aulacopilum hogdkinsoniae     ........C........C............T.A.........GC..G............G..CA.G........T.....
Venturiella sinensis          ........C........C............T.A.............G............G..CA.G........T.....
Uleastrum palmicola           ........C........C............T.A.............................C..T........T.....
Encalypta procera             ........C........A............................................C.CT........T.....
Ptychomitrium gardnerii       ...........T.....C............T.A........AG...................C.CT........T.....
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                      810>      820>      830>      840>      850>      860>      870>      880>
Funaria hygrometrica           TGACTACTTAACTGGTGGTTTTACTGCAAACACTAGCTTGGCTCACTACTGCCGTGACAACGGTTTACTTCTTCACATTC
Funaria apophysata             ............C.......................T..A........T..T........T...................
Splachnum sphaericum           ...T..T.....A.................T.....T..A........T..T..C..T..T..C...........T....
Tayloria lingulata             ......T.....A.................T.....T..A.....T...........T..T..C...........T....
Hedwigia ciliata               ......T.....A..C............C.T.....T........T..T........T..T..C...........T....
Mnium thomsonii                ...T..TC....A.................T....CT........T...........T..T..C........C..T....
Abietinella abietiena          C.....T.....A.................T.....T.....C..T.....T.....T..T..C..G........T....
Schlotheimia tecta             ......T.....A.....G...........T.....T........T..T..T.....T..T............T.T....
Schlotheimia trichomitria      ......T.....A.....G.........?.T.....T........T..T..T.....T..T..............T....
Schlotheimia brownii           ......T.....A.................T.....T........T..T..T.....T..T..............T....
Cardotiella quinquefaria       ...T..T.....A..C..............T.....T........T..T........T..T..C...........T....
Macrocoma tenue                ...T..T.....A.................T.....T........T..T........T..T..C...........T....
Macrocoma papillosa            ...T..T.....A...........C.....T.....T........T..T...........T..C...........T....
Groutiella chimborazense       ...T..T.....A.................T.....T........T..T........T..T.CC...........T....
Groutiella apiculata           ...T..T.....A.................T.....T........T..T........T..T.CC...........T....
Macromitrium involutifolium    ...T..T.....A.................T.....T........T..T........T..T..C...........T....
Macromitrium longifolium       ...T..T.....A.................T.....T.....C..T..T........T..T..C...........T....
Macromitrium richardii         ...T..T.....A.................T.....T........T..T........T..T..C...........T....
Desmotheca. apiculata          ...T..T.....A.................T.....T........T..T........T..T..C...........T....
Zygodon intermedius            ......T.....A.................T.....T........T..T........T..T............T.T....
Zygodon reinwardii             ......T.....A.................T.....T........T..T........T..T............T.T....
Zygodon pungens                ......T.....A.................T.....T.....G..T..T.....C..T..T..............T....
Zygodon obtusifolium           ...T..T.....A.................T.....T........T...........T..T..C...........T....
Orthotrichum lyellii           ......T.....A.................T....CT........T..T........T..T..............T..C.
Orthotrichum obtusifolium      ......T.....A.................T....CT........T..T........T..T..............T....
Orthotrichum anomalum          ......T.....C.................T.....T........T..T........T..T..............T....
Ulota obtusiuscula             ......T.....A.................T....CT........T..T........T..T..............T....
Ulota lutea                    ......T.....A.................T.....T........T..T........T..T..............T....
Bryodixonia perichaetialis     ......T.....A.................T....CT........T..T........T..T..............T....
Drummondia prorepens           ......T.....A.................T.....T...........T........T..T..G.........?.T....
Amphidium lapponicum           ......T.....A.................T....CT..A.....T..T........T.....A...........T....
Rhabdoweisia crenulata         ......TC....A.................T.....T..A.....T..T........T.....G...........T....
Aulacopilum hogdkinsoniae      ......T.....A.................T.....T..A.....T..T........T.....A...........T....
Venturiella sinensis           ......T.....A.................T....CT..A.....T..T........T.....A...........T....
Uleastrum palmicola            ......T.....A.................T....CT..A....GT..T........T.....G...........T....
Encalypta procera              ......T.....A.................T.....T..A.....T..T........T..T..A................
Ptychomitrium gardnerii        ......T.....A.................T....CT..A.....T..T........T..T..G...........T....
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                  890>      900>      910>      920>      930>      940>      950>      960>
Funaria hygrometrica        ACCGTGCAATGCACGCAGTTATTGACCGTCAAAAAAACCACGGTATGCACTTCCGTGTATTAGCTAAAGCATTACGTTTA
Funaria apophysata          ................................................................................
Splachnum sphaericum        .T...........T......C.......A........T..T.....T..T..............................
Tayloria lingulata          .............T......C.......A...........T........T..............................
Hedwigia ciliata            ....C........T..............A.......T...T........T...............C............C..
Mnium thomsonii             .............T..............A........T..T........T.........C....................
Abietinella abietiena       .............T..............A........T..T........T..............................
Schlotheimia tecta          .............T..T...........A...........T........T..............................
Schlotheimia trichomitria   .............T..T...........A...........T........T..............................
Schlotheimia brownii        .............T..T...........A...........T........T..............................
Cardotiella quinquefaria    .T...........T..............A.......T...T........T....................G.........
Macrocoma tenue             .T...........T..............A...........T........T....................G.........
Macrocoma papillosa         .T...........T..............A...........T........T....................G.........
Groutiella chimborazense    .T...........T......C...................T........T....................G.........
Groutiella apiculata        .T...........T......C...................T........T....................G.........
Macromitrium involutifolium .T...........T..............A.......T...T........T....................G.........
Macromitrium longifolium    .T...........T..............A.....G.....T..A.....T....................G.........
Macromitrium richardii      .............T......C.......A.......T...T........T....................G.........
Desmotheca. apiculata       .............T......C.......A....................T..............................
Zygodon intermedius         .............T..............A...........T........T....................G.........
Zygodon reinwardii          .............T..............A.......T...T........T....................G.........
Zygodon pungens             .T...........T...........T..A.......TT..T........T....................G.........
Zygodon obtusifolium        .............T..............A........T..T........T..T...........A.....G.........
Orthotrichum lyellii        .T...........T..............A...........T........T..............................
Orthotrichum obtusifolium   .............T..............A...........T........T....................G.........
Orthotrichum anomalum       .............T..............A...........T........T....................G.........
Ulota obtusiuscula          .T...........T..............A...........T........T..............................
Ulota lutea                 .T...........T..............A...........T.....T..T..............................
Bryodixonia perichaetialis  .T...........T...........G..A...........T?....T..T..............................
Drummondia prorepens        .............T........C.....A........T..T........T............................C..
Amphidium lapponicum        .............T......G.......A...........T........T............................C..
Rhabdoweisia crenulata      .............T..............A...........T........T..............................
Aulacopilum hogdkinsoniae   .............T..............A........T...........T..............................
Venturiella sinensis        .............T..............A.......TT...........T..............................
Uleastrum palmicola         .............T..............A........T..T........T............................C..
Encalypta procera           ....C........T..............C...........T.....T..T..............................
Ptychomitrium gardnerii     .............T..............A........T..T........T............................C..
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                   970>      980>      990>     1000>     1010>     1020>     1030>     1040>
Funaria hygrometrica         TCTGGTGGTGACCACATTCACGCAGGTACTGTAGTAGGTAAACTTGAAGGGGAACGTGAAGTAACTCTAGGGTTTGTTGA
Funaria apophysata           .......................C.................................C......................
Splachnum sphaericum         ..C.....A.....T.......T.T..........................A......C........T.............
Tayloria lingulata           ..C.....A.....T........T..G..............G........A......C........T.............
Hedwigia ciliata             ........A.....T........T...........................A...............T.............
Mnium thomsonii              ..C.....A..T..T........T.....C.....................A...S..C........T.............
Abietinella abietiena        ..C.....A.....T........C...........................A.....CC........T.............
Schlotheimia tecta           ..A.....A.....T.....T..T...........................A......C........T.............
Schlotheimia trichomitria    ..A.....A.....T.....T..T...........................A......C........T.............
Schlotheimia brownii         ..A.....A.....T.....T..T...........................A......C........T.............
Cardotiella quinquefaria     ..A.....A.....T........T...........................A......C........T.............
Macrocoma tenue              ..A.....A.....T........T...........................A...............T.............
Macrocoma papillosa          ..A.....A.....T........T...........................A......C........T.............
Groutiella chimborazense     ..A.....A.....T........T...........................A...............T.............
Groutiella apiculata         ..A.....A.....T........T...........................A...............T.............
Macromitrium involutifolium  ..A.....A..T..T........T...........................A...............T.............
Macromitrium longifolium     ..A.....A..T..T........T...........................A...............T.............
Macromitrium richardii       ..A.....A.....TG.......T...........................A......C........T..........G..
Desmotheca. apiculata        ..A.....A.....T........T...........................A......C........T.............
Zygodon intermedius          ..A.....A..T..TG.......T.....G.....................A......C........T.............
Zygodon reinwardii           ..A.....A..T..T........T.....G.....................A......C........T.............
Zygodon pungens              ..A.....A..T..T.....T..T.....A.................G..A......C........T..........G..
Zygodon obtusifolium         ..A.....A.....T.....T..T...........T...............A......C........T.............
Orthotrichum lyellii         ..A.....A..T..T........T.....G.....................A......C........T....A........
Orthotrichum obtusifolium    ..A.....A..T..T........T.....A.....................A......C........T.............
Orthotrichum anomalum        ..A.....A..T..T........T.....A.....................A......C........T.............
Ulota obtusiuscula           ..A.....A..T..T........T.....G.....................A......C........T.............
Ulota lutea                  ..A.....A..T..T......T.T.....G.....................A......C........T.............
Bryodixonia perichaetialis   ..A.....A..T..T......T.T.....G.....................A......C........T.............
Drummondia prorepens         ..A.....A..T..T........T....................G.....A......C........T....A........
Amphidium lapponicum         ..A.....A..T........T..T...........................A......C........T....A.....G..
Rhabdoweisia crenulata       ..A.....A..T..T........T...........................A......C........T....A.....A..
Aulacopilum hogdkinsoniae    ..G.....A..T..T........T...........................A......C........T....A.....G..
Venturiella sinensis         ..A.....A..T..T........C...........................A......C........T....A.....G..
Uleastrum palmicola          ........A..T..T........T...........................A......C........T..........A..
Encalypta procera            ........A..T.......................................A......C........T.............
Ptychomitrium gardnerii      ..A.....A..T..T........T...........................A......C........T....A........
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

	1050> 1060> 1070> 1080> 1090> 1100> 1110> 1120>
Funaria hygrometrica	CTTACTTCGTGATGACTACATTGAAAAAGATAGAAGTCGTGGTATTTACTTTACTCAAGACTGGGTTTCTTTACCAGGTG
Funaria apophysata	..................T...T..............T....
Splachnum sphaericum	TC.............T....................C...
Tayloria lingulata	TC.............T....................C.......................T...................
Hedwigia ciliata	T..............T..T.................C..............C............................
Mnium thomsonii	T.C..C............T..C..............C...........T..C..C..G........C.....S.......
Abietinella abietiena	T.C............T..T.................C...........T..C..C.........................
Schlotheimia tecta	TC....G...........T..C..............C...
Schlotheimia trichomitria	TC....G...........T..C..............C..............C............................
Schlotheimia brownii	TC....G......A.T..T...T...................
Cardotiella quinquefaria	TC.............T................................T...............................
Macrocoma tenue	T..............T..
Macrocoma papillosa	TC.............T..
Groutiella chimborazense	TC.............T................................T..........T...................
Groutiella apiculata	TC.............T................................T..........T...................
Macromitrium involutifolium	TC.............T..T...
Macromitrium longifolium	TCC............T................................T..C..C.....T...................
Macromitrium richardii	T..............T..T...
Desmotheca. apiculata	T..............T..T...................................?.........................
Zygodon intermedius	TC.............T..T...............................C.............................
Zygodon reinwardii	TC.............T..T...............................C.............................
Zygodon pungens	T...T.G........T..T.....G..............C........T..C........T...................
Zygodon obtusifolium	TC.............T..T.....G.........................C.............................
Orthotrichum lyellii	TC.............T..T...............................C........T...................
Orthotrichum obtusifolium	T..............T..T...............................C........T...................
Orthotrichum anomalum	TC.............T................................T..C........T...................
Ulota obtusiuscula	TC.............T..T.................C..............C........T...................
Ulota lutea	TC.............T..T...............................C........T..................A
Bryodixonia perichaetialis	TC.............T..T...............................C........T..................A
Drummondia prorepens	T.................T..C..............C..............C............................
Amphidium lapponicum	T.................T..C..
Rhabdoweisia crenulata	T.................T.............................T..........T...................
Aulacopilum hogdkinsoniae	T.................T.............................T..C........T...................
Venturiella sinensis	T.................T.............................T..C........T...................
Uleastrum palmicola	T.................T.............................T..C............................
Encalypta procera	T.................T.....G..............C........T...........T...................
Ptychomitrium gardnerii	T.....G........T..T....................C........T...........T..............G....

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

	1130> 1140> 1150> 1160> 1170> 1180> 1190> 1200>
Funaria hygrometrica	TTCTACCAGTAGCTTCCGGTGGTATTCACGTTTGGCACATGCCTGCGTTAACTGAAATCTTCGGAGATGACTCTGTATTA
Funaria apophysata	..T..A....................................
Splachnum sphaericum	..T....T........T...........T........T.....A..A..............T........T..A......
Tayloria lingulata	..T....T........T..C........T........T.....A..A..............T..................
Hedwigia ciliata	..T....T....................T........T.....A..A..............T........T.........
Mnium thomsonii	..T....T........T..C.....C..T..C.....T..?..A..A..............T........T.........
Abietinella abietiena	..T....T........T...........T........T..?..A..A.....C........T........T.........
Schlotheimia tecta	..T....T........T...........T........T..?..A..A..............T........T.........
Schlotheimia trichomitria	..T....T...........C........T........T.....A..A..............T........T.........
Schlotheimia brownii	..T....T........T........?..T........T.....A..A..............T........T.........
Cardotiella quinquefaria	..T....T........T...........T........T.....A..A..............T........T.........
Macrocoma tenue	..T....T........T...........T........T.....A..A...........A..T........T.........
Macrocoma papillosa	..T.........................T........T..?..A..A..............T........T.........
Groutiella chimborazense	..T....T........T...........T........T..?..A..A..............T........T.........
Groutiella apiculata	..T....T........T....................T.....A..A..............T........T.........
Macromitrium involutifolium	..T....T........T.....C.....T........T..?..A..A..............T........T.........
Macromitrium longifolium	..T....C........T........C..T........T.....A..A..............T........T.......C.
Macromitrium richardii	..T....T........T.....C.....T........T.....A..A..............T........T.........
Desmotheca. apiculata	..T....T........T...........T........T.....A..A..............T........T.........
Zygodon intermedius	..T....T........T..C........T........T.....A..A...........T..T........T.........
Zygodon reinwardii	..T....T........T..C........T........T.....A..A...........T..T........T.........
Zygodon pungens	..T.............T..C.................T.....A..A...........T..T........T.....C...
Zygodon obtusifolium	..T....T........T..C........T........T..?..A..A..............T........T.........
Orthotrichum lyellii	..T....T........T..C........T........T.....A..A...........T...........T......C..
Orthotrichum obtusifolium	..T....T........T..C........T........T..?..A..A...........T..T........T.........
Orthotrichum anomalum	..T....T........T..C........T........T.....A..A...........T..T........T.........
Ulota obtusiuscula	..T....T........T..C........T........T..?..A..A...........T...........T......C..
Ulota lutea	..T....T........T..C........T........T..?..A..A...........T...........T......C..
Bryodixonia perichaetialis	..T....T........T..C........T........T.....A..A...........T...........T......C..
Drummondia prorepens	..T....T...........C........T........T.....A..A..............T........T.........
Amphidium lapponicum	.......T........T..C........T........T.....A..A..............T........T.........
Rhabdoweisia crenulata	..T....T........T..C........T........T.....A..AC.............T..................
Aulacopilum hogdkinsoniae	..T....T........T...........T........T.....A..A...........T..T..................
Venturiella sinensis	..T....T........T...........T........T.....A..A...........T..T..................
Uleastrum palmicola	..T....T........T..C........T........T.....A..A...........T..T..................
Encalypta procera	..T................C........T........T.....A..A..............T.....C..T.........
Ptychomitrium gardnerii	..T....T........T...........T........T..?..A..A...........T..T........T.........

Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

```
                                   1210>     1220>     1230>     1240>     1250>     1260>     1270>     1280>
Funaria hygrometrica          CAATTTGGTGGTGGAACTTTAGGTCACCCTTGGGGTAACGCACCTGGTGCAGTTGCTAACAGGGTTGCTTTAGAAGCTTG
Funaria apophysata            ................................................................................
Splachnum sphaericum          ..G........A...........A..T...........T....................T..A.................
Tayloria lingulata            ..G........A...........A..............T....................T..A.....C...........
Hedwigia ciliata              ...........A..........................T....................T..A.....C...........
Mnium thomsonii               ..G......S.A........G.................T........C...........T..A..C..A...........
Abietinella abietiena         ..G........A..........................T........A...........T..A.....C...........
Schlotheimia tecta            ..G......S.A..........................T.................G..T..A.................
Schlotheimia trichomitria     ..G......S.A..........................T....................T..A.................
Schlotheimia brownii          ..G.....C..?.....A....................T.................G..T..A.................
Cardotiella quinquefaria      ..G........A.....A........T...........T.................G..T..A......G..........
Macrocoma tenue               ..G........A.....A........T...........T.................A..T..A.................
Macrocoma papillosa           ..G......S.A.....A........T...........T.................G..T..A.................
Groutiella chimborazense      ..G........A.....A........T...........T.................G..T..A.................
Groutiella apiculata          ..G........A.....A........T...........T.................G..T..A.................
Macromitrium involutifolium   ..G........A.....A........T...........T.................G..T..A......GC.........
Macromitrium longifolium      ..G........A.....A........T...........T..G..............G..T..A.................
Macromitrium richardii        ..G........A.....A........T...........T.................A..T..A......G..........
Desmotheca. apiculata         ..G........A.....A........T...........T.................G..T..A......G..........
Zygodon intermedius           ..G........A..........................T....................T..A.................
Zygodon reinwardii            ..G........A..........................T....................T..A......G..........
Zygodon pungens               ..G........A..........................T....................T..A.................
Zygodon obtusifolium          ...........R.....A....................T.................G..T....................
Orthotrichum lyellii          ...........A..........................T....................T..A.................
Orthotrichum obtusifolium     ..G......S.A..........................T....................T..A.................
Orthotrichum anomalum         ...........A..........................T....................T..A.................
Ulota obtusiuscula            ...........A..........................T....................T..A.................
Ulota lutea                   ...........A..........................T....................T..A.................
Bryodixonia perichaetialis    ...........A..........................T....................T..A.................
Drummondia prorepens          ..G........A..........................T....................T..A.................
Amphidium lapponicum          ..G........A..........................T....................T..A.................
Rhabdoweisia crenulata        ..G........A...............................................T..A.................
Aulacopilum hogdkinsoniae     ..G........A..........................T....................T..A.................
Venturiella sinensis          ..G........A..........................T........?...........T..A.................
Uleastrum palmicola           ...........A..............T...........T....................T..A.....A...........
Encalypta procera             ...........A...............................................T..A.................
Ptychomitrium gardnerii       ..G........C..............T...........T........?...........T..A..............C..
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Appendix 1 (cont.). *Rbc*L gene sequences of 37 arthrodontous mosses.

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                                  1290>     1300>     1310>     1320>     1330>     1340>     1350>
Funaria hygrometrica         TGTACAAGCTCGTAACGAAGGACGTGACCTTGCTCGTGAAGGAAATGATGTTATTCGTGAAGCTACTAAA
Funaria apophysata           ...............T....................C.....T.....CA....................
Splachnum sphaericum         ...............T....................C.....T.....A.....................
Tayloria lingulata           ...............T...........T........C.....T.....A....................G
Hedwigia ciliata             ...............T...........T........C.....T.....A....................?
Mnium thomsonii              ...............T...........T........C.....T.....AA....................
Abietinella abietiena        ...............T...........T........C.....T.....AA....................
Schlotheimia tecta           .....T.........T...........T........C.....T.....AA....................
Schlotheimia trichomitria    ...............T...........T........C.....T.....A.....................
Schlotheimia brownii         ...............T...........T........C.....T.....A................G....
Cardotiella quinquefaria     ...............T.....G.....T........C.....T.....AA...............G....
Macrocoma tenue              ...............T...........T........C.....T.....A.....................
Macrocoma papillosa          ...............T...........T........C.....T.....A.....................
Groutiella chimborazense     ...............T...........T........C.....T.....A...............G.....
Groutiella apiculata         ...............T...........T........C.....T.....A...............G.....
Macromitrium involutifolium  ...............T...........T........C.....T.....AA..............G.....
Macromitrium longifolium     ...............T...........T........C.....T.....A...............G.....
Macromitrium richardii       ...............T...........T........C.....T.....AA....................
Desmotheca. apiculata        ...............T...........T........C.....T.....AA....C.........G.....
Zygodon intermedius          ...............T...........T........C.....T.....AA....................
Zygodon reinwardii           ...............T...........T........C...........AA....................
Zygodon pungens              ...............T...........T..............T.....A...............G.....
Zygodon obtusifolium         ...............T...........T..............T.....A.....................
Orthotrichum lyellii         ...............T...........T..........................................
Orthotrichum obtusifolium    ...............T...........T....................A.....................
Orthotrichum anomalum        ...............T...........T....................A.....................
Ulota obtusiuscula           ...............T...........T....................A.....................
Ulota lutea                  .........C.....T...........T....................A.....................
Bryodixonia perichaetialis   .........C.....T...........T....................A.....................
Drummondia prorepens         ...............T...........T........C.....T.....A....................G
Amphidium lapponicum         ...............T...........T........C.....T.....A....................G
Rhabdoweisia crenulata       ...............T...........T........C.....T.....AA...................G
Aulacopilum hogdkinsoniae    ...............T...........T........C.....T.....A...............G....G
Venturiella sinensis         ...............T...........T........C.....T.....A...............G....G
Uleastrum palmicola          ...............T...........T........C.....T.....AA...................G
Encalypta procera            ...............T........C..T........C.....T.....A....................G
Ptychomitrium gardnerii      ...............T........C..T........C.....T.....A....................G
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