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The Circumscription and Phylogenetic Relationships of the Hedwigiaceae (Musci)

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ABSTRACT. The Hedwigiaceae are a group of plagiotropic mosses of uncertain relationships either with the Orthotrichales or the Isobryales. A total of 41 morphological characters was studied in nine species of six genera in the Hedwigiaceae, 12 species of five families in the Orthotrichales, and 12 species of five families in the Leucodontineae (Isobryales). Two additional species represented the Hypnales, and *Funaria hygrometrica* (Funariales) was used as the outgroup. Based on cladistic analyses, *Rhacocarpus* and *Bryowijkia* are excluded from the family. The Hedwigiaceae are here circumscribed to include only the genera *Braunia*, *Hedwigia*, *Hedwigidium*, and *Pseudobraunia*. This monophyletic group is supported by two unique synapomorphies: papillose pseudo-paraphyllia and a globular protonemal development. Other synapomorphies for the Hedwigiaceae are: sinuous leaf cell walls, flagelliform branches, ecostate leaves, yellow paraphyses, and peristomate capsules. The sister group of the Hedwigiaceae is a large clade that includes the cladocarpous representatives of the Orthotrichales, plus the Leucodontineae, and the Hypnales. This relationship is supported by three synapomorphies: plagiotropic shoots, presence of pseudoparaphyllia, and differentiated perichaetial leaves. The Orthotrichales appear to be paraphyletic: cladocarpous taxa (such as *Erpodium* and *Groutiella*) are more related to the Leucodontineae than to the acrocarpous taxa (such as *Orthotrichum*).

The formulation of hypotheses about monophyletic groups and their relationships involves a search for putative synapomorphies. Fundamental in this search is the use of outgroups for hypotheses of character polarization (Watrous and Wheeler 1981; Farris 1982; Donoghue and Cantino 1984; Maddison et al. 1984; Clark and Curran 1986). The present study of the taxonomic problems in the Hedwigiaceae Schimper illustrates some of the common problems and necessary assumptions in outgroup analysis. These include, for example, unknown outgroups and higher level relationships, uncertain monophyly of outgroups, and unclear character homologies and polarity due to widely divergent outgroups (Kraus 1988; Wheeler 1990).

The choice of outgroups for the Hedwigiaceae is indeed problematic. First, relationships among moss families are poorly understood in current ordinal classifications (Robinson 1971a; Miller 1979; Crosby 1980; Vitt 1982a; Walther 1983; Vitt 1984; Buck and Vitt 1986). Particularly, the classifications of the Isobryales (Fleisch.) Fleisch. and the Orthotrichales (Fleisch.) Dixon are unsatisfactory as hypotheses of phylogenetic relationships since their

character support has not been evaluated. Second, important characters, such as those of the peristome, often indicative of the ordinal relationships of a family, are missing in the Hedwigiaceae. Crum (1976) stated: "since it lacks a peristome one can only guess at its true relationship, whether to the Haplolepidae or to the Diplolepidae." Consequently, this family has been variously classified within either of these two main groups of true mosses. Bruch et al. (1855), Jones (1933), Crum (1976), and Crosby (1980) classified the Hedwigiaceae in the Haplolepidae close to the Grimmiaceae Arnott. (Grimmiales Fleisch.). In contrast, Fleischer (1920), Brotherus (1925), and Buck and Vitt (1986) placed this family in the Diplolepidae, close to the Leucodontaceae Schimp. (Isobryales). Nyholm (1960) and Smith (1978) also classified the Hedwigiaceae in the Diplolepidae, but close to the Orthotrichaceae Arnott. (Orthotrichales).

The circumscription of the Hedwigiaceae has also been problematic. According to Brotherus (1909, 1925), the Hedwigiaceae include 46 species in the genera *Braunia* Bruch. & Schimp., *Hedwigia* P. Beauv., *Hedwigidium* Bruch. & Schimp., *Pseudobraunia* (Lesq. & James) Broth., *Rhacocarpus* Lindb., and *Bryowijkia* Nog. (as

Cleistostoma Brid.). This taxonomic concept of the family has been widely used in current floristic and taxonomic works (e.g., Walther 1983). However, this circumscription of the family has been questioned (Crum and Anderson 1981; Vitt 1982a) and several authors have proposed more homogeneous groupings. First, Vitt and Buck (1984) excluded *Bryowijkia* from the Hedwigiaceae, since its leaves have a costa, and its capsules have a peristome, contrary to all other species in the family. They suggested that *Bryowijkia* belongs to the Trachypodaceae Fleisch. Later, *Rhacocarpus* was excluded from the family (Buck and Vitt 1986), although debate remains over whether it should be left in the Hedwigiaceae (Barthlott and Schultze-Motel 1981; Koponen and Norris 1986). None of these competing circumscriptions of the family has been previously analyzed in detail using cladistic methods.

The questions addressed in this cladistic study were: 1) What are the ordinal relationships and most feasible outgroups of the family? 2) Is there a monophyletic group to which the name Hedwigiaceae can be applied? 3) What genera should be included? To develop phylogenetic hypotheses about the relationships and circumscription of the Hedwigiaceae many characters of potential use were studied in the gametophyte and sporophyte. Also, it was necessary to evaluate characters used by previous authors. This involved the collection of morphological data through examination of herbarium specimens and relevant literature. Additionally, developmental studies of gametophytes and sporophytes were conducted on selected species of the Hedwigiaceae, namely, protonemal development (De Luna 1990a), branching pattern (De Luna 1990b), and capsule development (De Luna, in mss.). Cladistic analyses of all available data are presented and discussed in this paper.

Summary of Previous Research on the Hedwigiaceae. The first species currently placed in the Hedwigiaceae was originally described as *Anictangium ciliatum* Hedw. [= *Hedwigia ciliata* (Hedw.) P. Beauv.], and it was included in the Grimmiaceae (Hedwig 1801). Shortly afterwards the generic name *Hedwigia* was first used by Palisot de Beauvois (1804). *Hedwigidium* and *Braunia* were established later (Bruch et al. 1846). Finally Brotherus (1909) included *Rhacocarpus*, *Cleistostoma* (= *Bryowijkia*) and *Pseudobraunia*. Most species now have several nomenclatural

combinations among *Hedwigia*, *Hedwigidium*, and *Braunia* (Wijk et al. 1959-1969).

Besides Brotherus' (1909, 1925) important worldwide synopsis of the Hedwigiaceae, only limited treatments of the family are available for restricted areas. Regional floras, such as those of Bartram (1949), Chopra (1975), and others (cf. Scott and Stone 1976), made important contributions to the taxonomy of the Hedwigiaceae on a regional basis.

Previous morphological and developmental investigations of the Hedwigiaceae have also been limited and only a few details have been examined. For example, Nishida (1972), Noguchi and Mizuno (1959), and Nehira (1983) described an unusual globular protonema in *Hedwigia ciliata*. Additionally, De Luna (1990a) reported the same type of globular protonema in three other genera within the Hedwigiaceae. The unicellular spores of *Hedwigia ciliata* were studied under the Scanning Electron Microscope (SEM) by Miyoshi (1969), and De Luna (1992) described multicellular spores in *Bryowijkia ambigua* (Hook.) Noguchi. Leaf surfaces have been studied using the SEM. Robinson (1971b) described leaves of *Braunia secunda* (Hook.) Bruch. & Schimp. and *Rhacocarpus purpurascens* (Brid.) Par. Also Sharp et al. (1978) studied leaf surfaces of *Braunia secunda*, *B. squarrosula* (Hampe) C. Muell. and *Hedwigidium integrifolium* (P. Beauv.) Dix. Barthlott and Schultze-Motel (1981) studied leaf surfaces in *Hedwigia ciliata*, *Hedwigidium integrifolium*, *Braunia secunda*, *Pseudobraunia californica* (Lesq.) Broth., and *Rhacocarpus purpurascens*, and Delgadillo (1982) described the alar cells in *Rhacocarpus purpurascens*. Leaf papillae of *Hedwigia ciliata* also have been studied in relation to the external conduction of water (Proctor 1979). The capsule, peristome and leaf surfaces in *Bryowijkia ambigua* were studied by Vitt and Buck (1984) using SEM. Recently, branching patterns in *Hedwigia ciliata* were studied developmentally by De Luna (1990b).

Chromosome numbers are known for two species of the Hedwigiaceae. Vaarama (1950, 1954, 1968) counted $n = 22$ and $n = 21$ in various populations of *Hedwigia ciliata* in Europe. However, the number $n = 10$ or $n = 11$ has been reported in populations from Great Britain (Smith and Newton 1968), North America (Steere et al. 1954; Al-Aish and Anderson 1961), and Japan (Inoue 1979). In *Pseudobraunia californica* the number of chromosomes is also $n =$

11 (Steere et al. 1954). A cytological feature shared by these two species is the presence of m-chromosomes that are also known in several other mosses of diverse relationships (Anderson 1980).

MATERIALS AND METHODS

Selection of Outgroups. Each procedure for applying the outgroup method employs different assumptions about monophyly of the ingroup, outgroups, and upper level relationships (Kluge and Farris 1969; Lundberg 1972; Watrous and Wheeler 1981; Maddison et al. 1984). In cases such as the present analysis where outgroups are not known, and monophyly of the ingroup is uncertain, a particular implementation of the outgroup method is necessary (Farris 1982; Donoghue and Cantino 1984; Maddison et al. 1984). A global parsimony approach was used for analyses of the Hedwigiaceae, in which several outgroups were included simultaneously in the analysis (Maddison et al. 1984) as opposed to the substitution approach of Donoghue and Cantino (1984), in which candidate outgroups are included singly in a series of analyses.

The choice of potential outgroups for the Hedwigiaceae in the present study explores only the hypothesis of relationships in the Diplolepididae. As stated above, this family has been classified either with the haplolepidous (Grimmiales) or diplolepidous (Isobryales, Orthotrichales) groups of mosses. The later hypothesis is evaluated first in view of recent developmental data from capsules in the Hedwigiaceae. Although mature capsules lack a peristome, developmental anatomy of the annular region of the capsules of *Hedwigia ciliata* and *Braunia secunda* has revealed a cellular pattern comparable with the diplolepidous peristome types (De Luna, et al. in mss.). These patterns suggest that the Hedwigiaceae belong among the "isobryalean" diplolepidous orders, particularly the Orthotrichales or Isobryales. Therefore, selected families in these two orders (as classified by Crosby 1980, and Buck and Vitt 1986) were studied.

Since the relationships among candidate outgroups in the Orthotrichales and Isobryales are unknown, the Hedwigiaceae and all its potential outgroups were tentatively rooted using *Funaria hygrometrica* Hedw. (Funariaceae) as a more

distant outgroup. Although relationships among the major diplolepidous groups of mosses have not been cladistically evaluated, a general hypothesis suggests the Funariales as the sister group for mosses with arthrodontous peristomes, such as the Bryales, Orthotrichales, Isobryales, and Hypnales (Vitt 1984; Schwartz 1989).

The Orthotrichales according to Crosby (1980) and Vitt (1984) include five families (Orthotrichaceae, Erpodiaceae Broth., Rhachiteciaceae Robins., Microtheciellaceae Miller and Harrington, and Helicophyllaceae Broth.). The rank of this group of families has varied from order (Orthotrichales, sensu Smith 1978), to suborder (Orthotrichineae Fleisch., sensu Vitt 1984). This group was circumscribed by "an exostome consisting of a thick outer layer and a thin inner layer," leaf aerolation, leaf papillae, and a plicate calyptra (Vitt 1984). However, according to other authors, such as Robinson (1971a), this group does not constitute a separate order and thus the five families are better classified with the rest of the Isobryales.

A relationship of the Hedwigiaceae to the Orthotrichales has been suspected because of the shape of upper leaf cells, leaf papillae, and acrocarpous branching system (De Luna 1990b; Smith 1978, Walther 1983). The mature plants of *Hedwigia ciliata* are plagiotropic. However, the main axis of this moss is a chain of sympodial innovations rather than one shoot of indeterminate growth as in pleurocarpous mosses. Anatomical evidence indicated that archegonia are terminal on sympodial shoots (De Luna 1990b). Among the diplolepidous mosses, this developmental pattern is similar to the archegonial position and branching in most taxa in the Orthotrichales.

The circumscriptions and relationships among the approximately 20 families within the Isobryales are also poorly understood. Recently, Buck and Vitt (1986) proposed a classification of four suborders within the Isobryales. Only one of these suborders (the Leucodontineae) is of interest here. They suggested that six families (Leucodontaceae, Cryphaeaceae Schimp., Anomodontaceae Kindb., Leptodontaceae Schimp., Cyrtopodaceae Fleisch., and Hedwigiaceae) make up the suborder Leucodontineae Fleisch. A truly pleurocarpous branching system, "mostly isodiametric" upper leaf cells, "oval" cells in the alar region, and a white papillose

peristome are the characters used to define their suborder Leucodontineae (Buck and Vitt 1986). Inclusion of the Hedwigiaceae in this group was based on a branching system interpreted by them as pleurocarpous (but see De Luna 1990b), ecostate leaves, shape of leaf cells, and a xerophytic habitat (Vitt 1982a; Buck and Vitt 1986).

Since the Hedwigiaceae and the ten families included in present cladistic analyses can not be presumed as monophyletic, this raised questions about representation of large terminal taxa:

1) what type of terminal entities should be used to represent large taxa in cladistic analyses?, and 2) how to code character variation within such large taxa? If cladistic analyses for the internal relationships of terminal taxa are available, there would be at least two options to code character distributions. One is to use the reconstructed ancestral states for the family to be represented by a single terminal entity (Operational Taxonomic Unit, OTU). However, the often employed option of selecting combinations of common character states, or reconstructed ancestral states, to represent a polymorphic family as a single OTU is not advisable here. A second option is to represent a large terminal taxon by few phylogenetically important genera as OTU's. The absence of a cladistic hypothesis of relationships among genera within families for this study makes difficult the selection of OTU's to adequately represent phylogenetic structure within terminal taxa. This option was not possible except for families analysed cladistically such as the Anomodontaceae and Cyrtopodaceae, and for monotypic families such as the Microtheciellaceae and Helicophyllaceae.

The option adopted in this study was to represent phylogenetic diversity within large families as terminal taxa. Diversity within families was represented by selecting single species from as many different genera as possible. Selection of species, as the basic OTU's, as exemplars to represent large taxa (families in this case), ensures that character states assigned are real conditions. These character states assigned to species are less likely to change than those states that might be assigned as a generalized condition to a potentially not monophyletic family as a whole. Even with incomplete representation of a family, several OTU's provide explicit

statements about real combinations of character states as given by selected species. This approach does not eliminate the problem of non-monophyly and polymorphism within terminal taxa, but it establishes phylogenetically diverse and concrete samples that can be later complemented by more OTU's to represent better the variation within families.

The five families in the Orthotrichales and five in the Leucodontineae included in this study were represented by 24 species, one each from selected genera in those families. Among families studied, the most difficult to represent was the large and polymorphic family Orthotrichaceae. Previous ideas about evolutionary relationships within this family were used to guide selection of six representative genera. However, the use of a single species as OTU's for representation of these genera follows pragmatic concerns about character states (as explained above) rather than a hypothesis of internal relationships available for some genera (Vitt and Ramsay 1985). The following paragraphs contain general discussions of the diversity and taxonomy within the families represented in this analysis. Classification and nomenclature follow recent taxonomic treatments cited for each family. Brief comments are given of the systematic problems, characters, and genera within each family. Species selected from each family and selected specimens are presented in Table 1.

HEDWIGIACEAE. The approximately 46 species traditionally classified in this family generally have a capsule without peristome, leaves without costa, and leaf cells papillose. Brotherton (1925) based his generic distinctions on length of seta, shape of leaf cells, and types of papillae. The presence of a reduced peristome and a costa distinguished *Bryowijkia*. Elongated to vermiform leaf cells separated *Rhacocarpus*. The presence of one papilla per cell differentiated *Pseudobraunia* from *Braunia*. A short seta distinguished *Hedwigia* and *Hedwigidium* from all other genera. However, a generic distinction between *Hedwigia* and *Hedwigidium*, based on the ciliate perichaetial leaves and tall branched papillae of the former, is not always accepted (Scott and Stone 1976; Smith 1978). Nine species selected from all six genera were included in present analyses to test their inclusion in the Hedwigiaceae.

TABLE 1. List of representative specimens examined in the Hedwigiaceae and potential outgroups. Specimens are deposited at DUKE except where noted.

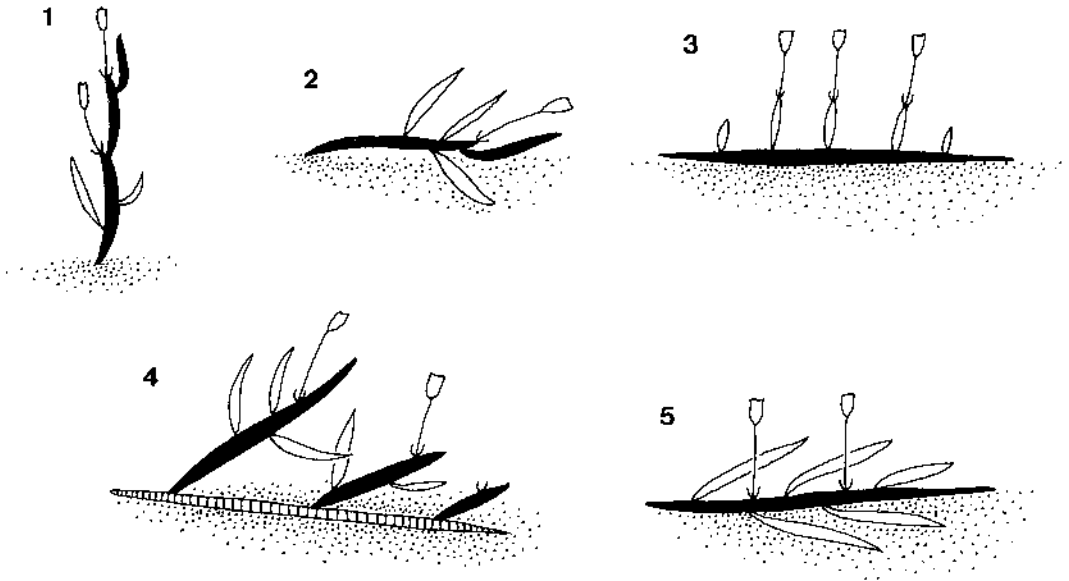
Family and species	Representative specimens
Hedwigiaceae	
<i>Pseudobraunia californica</i>	Schofield 37981
<i>Braunia squarrulosa</i>	De Luna 1772
<i>Braunia secunda</i>	De Luna 1437
<i>Braunia alopecura</i>	Frahm s.n., 1974 (JE)
<i>Braunia exserta</i>	Steere 60-233 (NY)
<i>Hedwigidium integrifolium</i>	Hermann 26448
<i>Hedwigia ciliata</i>	De Luna 1882
<i>Rhacocarpus purpurascens</i>	Hermann 26177
<i>Bryowijkia ambigua</i>	Touw 9124 (MO)
Orthotrichaceae	
<i>Orthotrichum alpestre</i>	Anderson 24108
<i>Zygodon conoideus</i>	Drummond 149
<i>Macromitrium richardii</i>	Sharp 2340
<i>Groutiella tumidula</i>	Sharp 4471
<i>Schlotheimia lancifolia</i>	Sharp 151
<i>Drummondia prorepens</i>	Sharp & Patrick 1177
Erpodiaceae	
<i>Erpodium domingense</i>	Cárdenas 3790a
<i>Venturiella sinensis</i>	Noguchi s.n., 1949
Rhachithecaceae	
<i>Hypnodontopsis apiculatus</i>	Crum 1141
Microtheciellaceae	
<i>Microtheciella kerrii</i>	No specimens seen; Characters based on Miller and Har- rington (1977)
Helicophyllaceae	
<i>Helicophyllum torquatum</i>	Santos 3731
Leucodontaceae	
<i>Leucodon julaceus</i>	Anderson 25216
<i>Dozya japonica</i>	Mituzutani 13730
<i>Felipponea montevicensis</i>	Landrum 3861
Cryphaeaceae	
<i>Cryphaea glomerata</i>	Anderson 5508
<i>Sphaerotherciella pinnata</i>	Delgadillo 2714
Anomodontaceae	
<i>Anomodon attenuatus</i>	Anderson 24170
<i>Haplomyenium triste</i>	Sharp 7591
Leptodontaceae	
<i>Leptodon smithii</i>	De Sloover 18596
<i>Forsstroemia producta</i>	Anderson 25220
<i>Pseudocryphaea flagellifera</i>	Reese 15567

TABLE 1. Continued.

Family and species	Representative specimens
Cyrtopodaceae	
<i>Cyrtopus setosus</i>	Schofield 49425
<i>Bescherellia cryphaeoides</i>	Schofield 51502
Hypnales	
<i>Hypnum cupressiforme</i>	Anderson 24126
<i>Brachythecium plumosum</i>	MacFadden s.n., 1927

ORTHOTRICHACEAE. This large family of acrocarpous mosses includes more than 500 species in 14 genera (Vitt 1982b). It is characterized by small, papillose, upper leaf cells, a large, usually mitriform calyptra, and an exostome with a thick, outer layer and a thin, inner layer (Vitt 1973, 1982b). Generic distinctions are based on characters such as the orientation of the branching system (which can be from completely prostrate to erect), differentiation of a central strand in the stem, presence of ventral guide cells and dorsal stereids in the costa, differentiation of perichaetial leaves, shape of calyptra, and others (Lewinsky 1977; Vitt 1979, 1982b). Only exemplar species from *Drummondia* Hook. in Drum., *Groutiella* Steere ex Crum & Steere, *Macromitrium* Brid., *Orthotrichum* Hedw., *Schlotheimia* Brid., and *Zygodon* Hook. & Tayl. were included in the present analyses. These six genera were selected here to represent the Orthotrichaceae because of their phylogenetic importance within the family. According to Vitt (1982b), the Zygodontoideae (Limpr. in Rabenh.) Broth. and Drummondoideae Vitt are basal to a group that includes the Macromitrioideae (Fleisch.) Broth. and the Orthotrichoideae (Limpr. in Rabenh.) Broth.

ERPODIACEAE. This family, according to Crum (1972), includes 26 species of small prostrate mosses classified in five genera. Other authors, such as Vitt (1983), have followed the suggestion of Miller and Harrington (1977) to segregate *Microtheciella* Dix. into its own family. According to Vitt (1984) the Erpodiaceae include only *Erpodium* (Brid.) Brid., *Venturiella* C. Muell., *Aulacopilum* Wils., and *Wildia* C. Muell. Species in this family generally share a creeping, pleurocarpous branching system, somewhat complanate leaves, undifferentiated costa, oblate-hexagonal leaf cells, and a mitrate calyptra. Two



FIGS. 1-5. Archegonial position and orientation of branching system in the Hedwigiaceae and its potential outgroups in the Orthotrichales and Leucodontineae (Isobryales). 1. Acrocarpous and orthotropic shoots as in *Orthotrichum*. 2. Acrocarpous and plagiotropic shoots as in *Braunia*. 3. Cladocarpous and plagiotropic shoots as in *Macromitrium*. 4. Pleurocarpous and plagiotropic shoots as in *Leucodon*. 5. Pleurocarpous and plagiotropic shoots as in *Hypnum*.

species representing *Erpodium* and *Venturiella* were included in the present analysis.

RHACHITHECIACEAE. The circumscription of this family has been questioned (Crum 1956; Iwatsuki 1957; Robinson 1964). The consensus is that *Hypnodontopsis* Iwats. & Nog. and *Rhachithecium* Broth. ex Le Jol. (which includes *Hypnodon* C. Muell. and *Rhachytheciopsis* P. de la Varde) are the only genera in the family. The perigonal leaves and the shapes of calyptrae are among the characters used for generic distinctions. The perigonal leaves are costate in *Hypnodontopsis* and ecostate in *Rhachithecium*. The calyptra is mitrate in *Hypnodontopsis* and cucullate in *Rhachithecium*. Two species representing both genera were included in the present analyses.

MICROTHECIELLACEAE. This is a monotypic family known only from a few specimens collected in Thailand (Miller and Harrington 1977). In *Microtheciella kerrii* Dix., the only species known, the gametophytic shoots are prostrate and complanate, but it is not clear whether branching development is sympodial but prostrate (pseudo-pleurocarpous, Fig. 2), such as in some Orthotrichaceae, or monopodial (truly pleurocarpous, Fig. 3). Features of the peristome

are not completely known either. A suboral membranaceous row 3-4 cells high has been interpreted as a reduced diplolepidous peristome (Miller and Harrington 1977). When more material becomes available, the branching system and the "peristome" should be studied developmentally to help clarify homologies.

HELICOPHYLLACEAE. This is also a monotypic family, but frequently collected in the Neotropics (Crum and Steere 1957). The only species known, *Helicophyllum torquatum* (Hook.) Brid., develops a prostrate, strongly complanate habit. The leaves are dimorphic, and the underside of the stem is densely covered with freely branched rhizoids. The branching system has been interpreted as pleurocarpous (Buck and Vitt 1986; Koponen 1988), but my observations suggest that it develops as an acrocarpous moss, with terminal archegonia on sympodially derived branches.

LEUCODONTACEAE. The circumscription of this family has undergone several recent changes. From the 11 genera Manuel (1974) included in the family, only *Leucodon* Schwaegr., *Dozya* Sande Lac. in Miq., and *Felipponea* Broth. in Felipp. are currently retained in the Leucodontaceae (Buck 1980; Akiyama 1986, 1988a;

Stark 1987). The costa is used for generic distinctions: it is single in *Dozya*, absent in *Felipponea*, and double or absent in *Leucodon*. A species representing each of these three genera was included in the present analyses, along with two genera (*Leptodon* Mohr and *Forsstroemia* Lindb.) that Buck and Vitt (1986) moved to the Leptodontaceae.

CRYPHAEACEAE. Manuel (1982) recognized eight genera in this heterogeneous family: *Cryphaea* Mohr in Web.; *Pilotrichopsis* Besch.; *Cyrtodontopsis* Dix.; *Sphaerotheciella* Fleisch.; *Dendrocryphaea* Par. & Schimp. ex Broth.; *Cyrtodon* (Broth.) Par. & Schimp. ex Fleisch.; *Schoenobryum* Dozy & Molk., and *Dendropogonella* Britt. According to Manuel (1982), generic distinctions are based on spore morphology, branching system, orientation of stems, and peristomes. *Cryphaea* and *Sphaerotheciella* were represented in the present analyses by one species each.

ANOMODONTACEAE. The systematic position of *Anomodon* is controversial. Initially, Vitt (1984) included this genus in the Leskeaceae Schimp., close to the Cyrtopodaceae and Cryphaeaceae. Later, Buck and Vitt (1986) recognized the Anomodontaceae to include six genera: *Anomodon* Hook. & Tayl.; *Haplohymenium* Dozy & Molk.; *Herpetineurum* (C. Muell.) Card.; *Thelia* Sull. in Sull. & Lesq.; *Myurella* Bruch. & Schimp., and *Lindbergia* Kindb. Initially, Granzow (1990) included the first four genera in his cladistic analysis of *Anomodon*, yet a recent study (Granzow 1992) did not include *Thelia* but included *Pterogonium gracile* (Hedw.) Sw. as distal outgroup. According to Granzow (1990), generic distinctions in the Anomodontaceae are based on the morphology of the endostome, branching system, leaf cell papillae, calyptra ornamentation, and costa morphology. One species each from *Anomodon* and *Haplohymenium* were included in the present analysis.

LEPTODONTACEAE. The validity of this family needs a careful evaluation. Buck (1980) included *Leptodon*, *Forsstroemia*, *Pseudocryphaea* Brid. ex Broth., and *Leucodontopsis* Ren. & Card. Stark (1987) provisionally accepted this circumscription, but warned about persisting taxonomic problems in the complex that includes the Cryphaeaceae, Leucodontaceae and Leptodontaceae. Generic distinctions in the Leptodontaceae are based on the sexual condition, paraphyllia presence, morphology of paraphyses, and exsertion of capsule (Stark 1987). One

species of each of the first three genera mentioned here were included in the present analyses.

CYRTOPODACEAE. According to Sastr-De Jesús (1987), this is a small family of only three species in two genera: *Bescherellia* Duby and *Cyrtopus* (Brid.) Hook. f. In her analysis, she concluded that a bistratose leaf subula is a synapomorphy for the family, compared to the completely unistratose leaves of the Cryphaeaceae and Leucodontaceae. Generic distinctions in the Cyrtopodaceae are based on the differentiation of the endostome, and seta length. One species from each genus was included in the present analysis.

Character Analyses. More than 200 herbarium specimens were examined from BM, DUKE, JE, NY, and MO. Selection of potential taxonomic characters was based on the extent of variation within and among the families studied. Given the wide scope of previously postulated relationships, a relatively large number of families was studied to estimate the circumscription and outgroup relationships of the Hedwigiaceae. Previous taxonomic treatments were consulted for potentially useful characters. However, most characters useful for familial relationships are not fully described in treatments of particular families or genera, since those characters are homogeneous at that level, for example, features of the vaginula, perichaetial paraphyses, and stomates. Thus, most characters used in the present analyses were derived directly from studies of herbarium specimens.

The selection of potentially useful characters is based on evaluations of relative levels of variation within and among the OTU's. In principle, a character should be considered if it shows at least two distinct character states among the groups studied. Although experience or intuition helps to anticipate which subsets of features might be more informative than others, characters should not be chosen on this basis alone. The selection of characters at a particular phylogenetic level should also not be guided by transferring judgments about the value (or lack thereof) of a character from another phylogenetic level or another group of organisms. Only an explicit examination of variation in each particular study can justify the inclusion or exclusion of a character.

Decisions about the number of states and ordering are discussed individually for all characters included here. Hypotheses of character

TABLE 2. Character state assignments for the taxa included in this study. Character numbers and character state codes are as in the text. Character states missing in a given taxon are coded as "?."

Taxa	Characters				
	10	20	30	40	
1 <i>Funaria hygrometrica</i>	00000000?0	0000000000	0000110000	0100000100	0
HEDWIGIACEAE					
2 <i>Pseudobraunia californica</i>	1011100111	0?10001000	0010110001	110112????	2
3 <i>Braunia squarrosula</i>	2011100211	0?10000100	1111110001	110112????	2
4 <i>Braunia secunda</i>	1011100211	0?10000100	1011110000	000112????	2
5 <i>Braunia alopecura</i>	1011100211	0?10000100	1011110000	000112????	2
6 <i>Braunia exserta</i>	2011100211	0?10000100	1111110011	010112????	2
7 <i>Hedwigidium integrifolium</i>	1011100211	0?10000100	1011010011	110112????	2
8 <i>Hedwigia ciliata</i>	1011100111	0?10001000	1010010011	111002????	2
9 <i>Rhacocarpus purpurascens</i>	0220100101	0?01220001	1210110002	111112????	2
10 <i>Bryowijkia ambigua</i>	22201000?0	000122010?	1020????12	10200??1??	2
ORTHOTRICHACEAE					
11 <i>Orthotrichum alpestre</i>	00001000?0	0000002000	0101101011	0111111100	1
12 <i>Zygodon conoideus</i>	00001000?0	0000002001	0100110000	0101112100	1
13 <i>Macromitrium richardii</i>	01101100?0	0000002010	0000101101	0000102100	2
14 <i>Groudiella tumidula</i>	01101100?0	0000000012	0000100111	10011??1??	2
15 <i>Schlotheimia lancifolia</i>	01101100?0	0000000002	0101100002	0001111100	1
16 <i>Drummondia prorepens</i>	21101100?0	0000000000	0100110002	0021002101	2
ERPODIACEAE					
17 <i>Erpodium domingense</i>	01101010?1	0?00002010	1020000112	000102????	2
18 <i>Venturiella sinensis</i>	01101000?1	0?00000000	1020100112	0001101100	2
RHACHITHECIACEAE					
19 <i>Rhachithecium perpupilum</i>	0?001010?0	0000000000	0220110011	1101112101	2
20 <i>Hypnodontopsis apiculatus</i>	0?001000?0	0000002000	0200000012	0100011?02	2
MICROTHECIELLACEAE					
21 <i>Microtheciella kerrii</i>	0?101010?0	0000000000	1?????0010	000????1?2	2
HELICOPHYLLACEAE					
22 <i>Helicophyllum torquatum</i>	00201010?0	0000002011	1020111012	000002????	2
LEUCODONTACEAE					
23 <i>Leucodon julaceus</i>	0211010101	0?01110021	12?0110002	0021100010	2
24 <i>Dozya japonica</i>	02110100?0	0101110001	1200110002	0101100011	2
25 <i>Felipponea montevidensis</i>	0211110201	0?01110001	1200110002	0101100010	2
CRYPHAEACEAE					
26 <i>Cryphaea glomerata</i>	0210110100	0101110020	10?0000012	0001100010	1
27 <i>Sphaerothereciella pinnata</i>	2210110200	0101110001	1000000012	000?0?010	?
ANOMODONTACEAE					
28 <i>Anomodon attenuatus</i>	02111110?0	0001112001	1000110002	0001100000	1
29 <i>Haplohymenium triste</i>	02101100?0	0001112001	1000111012	0021100000	2
LEPTODONTACEAE					
30 <i>Leptodon smithii</i>	0210110200	010111000?	1200111012	0021100010	1
31 <i>Forsstroemia producta</i>	0210110200	0101110001	1200111012	0021100011	1
32 <i>Pseudocryphaea flagellifera</i>	0210110200	0101110001	1200????02	0???10?000	?
CYRTOPODACEAE					
33 <i>Cyrtopus setosus</i>	0210010100	1101110001	1100110012	0001100010	0
34 <i>Bescherellia cryphaeoides</i>	0210010100	1101110001	1100110002	0001100010	2
HYPNALES					
35 <i>Hypnum cupressiforme</i>	0220101202	0001220001	1000110002	0001100102	0
36 <i>Brachithecium plumosum</i>	0220100100	0001220000	100011000?	0001100102	0

state order imply a relationship of adjacency (or transformational homology) among states. However, there is no directionality implied in hypotheses about ordering. Polarity of character state transformations should be established by outgroup analyses. In a two-state character there is only one possible relationship between the states. Among several possible order sequences in a multistate character, ontogenetic adjacency or a morphocline series can be used as criteria to select a particular ordering of states. Some multistate characters were left unordered because of unclear relationships among states and lack of information about their ontogenetic adjacency.

Cladistic Analyses. Cladistic analyses were performed with PAUP 3.0r (Swofford 1991). The data matrix (Table 2) consisted of 36 taxa and 41 informative characters (i.e., autapomorphies were not included). A heuristic search algorithm was used in all analyses. This type of search typically explores only a subset (an island) of all possible trees (Maddison 1991); therefore, to avoid exploring only one island and most-parsimonious trees derived from one starting tree, multiple searches were made with random addition of taxa (10 replications) in combination with the branch rearranger in PAUP. Three series of analyses were performed to find trees under different conditions to explore: 1) different branch swapping algorithms (tbr, spr, nni); 2) the exclusion of *Bryowijkia* and *Rhacocarpus*, and 3) the use of *Funaria hygrometrica* as distant outgroup. In this case, topologies were rooted with an outgroup and also with "Lundberg rooting" in which character states found in *Funaria hygrometrica* were used as ancestral states. Strict consensus trees were built to show monophyletic groups that are present in all equally most parsimonious trees found in the three series of analyses.

To evaluate the relative robustness of groups within a tree, "decay analyses" were made according to a method suggested by Bremer (1988), Graham et al. (1991), and Donoghue et al. (1992). Trees up to 3 steps longer than the most parsimonious were saved to estimate the decay index of particular clades. However, the decay indices presented are only estimates, since not all trees in the selected length range were examined (only 37,000 trees could be saved in 40 Mb of RAM). The number of character changes per branch was examined on one most parsimonious tree found in the first series of anal-

yses. Character state optimization was done using the ACCTRAN option in PAUP. The topology of this tree and the mapping of characters were simplified to focus on character support of main clades relevant to the circumscription and relationships of the Hedwigiaceae. Constraint trees were used to calculate lengths of competing hypotheses of relationships proposed in the literature.

RESULTS

Characters Included. The list of 41 characters presented below includes features of the gametophytes and sporophytes for which: 1) there was specific information about their taxonomic distribution in the species included; 2) it was possible to observe them from examination of herbarium specimens using compound and stereoscopic microscopes, and 3) classification of their variation into character states was readily obvious. Several additional features (observed or mentioned in the literature) require a better sampling of variation before they can be included in an analysis such as this (these are listed under Excluded Characters). The list of characters included in present analyses is therefore only a preliminary starting point. It is expected that future studies will clarify homologies, corroborate character distributions, and better circumscribe character states.

1. **Spores and protonema: 0 = spores unicellular and the protonema exosporic filamentous; 1 = spores unicellular but protonemal development exosporic and globular; 2 = spores multicellular [unordered].** In the majority of mosses the spores are unicellular (Mogensen 1983), and protonemal development is exosporic and filamentous. Genera in the Orthotrichaceae, *Rhacocarpus*, *Erpodium*, and the five families of the Leucodontineae are known to develop a exosporic filamentous protonema (the common *Macromitrium*-type; Nehira 1976; Nishida 1978). An exosporic globular protonema (which consists of a globular group of rounded cells, with a few later uniseriate filaments) has been described only in species of *Braunia*, *Hedwigia*, *Hedwigidium*, and *Pseudobraunia* (De Luna 1990a). In a few mosses, the protonema is endosporic (i.e., mitotic divisions start without breaking the spore wall; Nehira 1983; Nishida 1978) and therefore the spores are multicellular. In *Bryowijkia* initial cell divisions occur while

the spore is still inside the capsule. These multicellular spores are dispersed requiring rehydration to continue protonemal development (De Luna 1992). Endosporic protonemal development is also known in a few species of *Braunia*, *Drummondia*, and *Sphaerothereciella*.

2. Position of archegonium (or sporophyte) on gametophyte: ? = uncertain; 0 = acrocarpous, in which sporophytes (or archegonia) terminate a main module; 1 = cladocarpous, a special case of pleurocarpy in which archegonia terminate long lateral branches off a main module; 2 = pleurocarpous, in which archegonia terminate very short lateral branches off a main module [ordered]. Two fundamental types of sporophyte position are known in mosses: acrocarpous and pleurocarpous. A careful examination of the modular structure of the branching system, detected in part by the position of the heteroblastic leaf sequence, helps to determine the growth pattern (Mishler and De Luna 1991).

In acrocarpous mosses branching is sympodial. The main axis consists of a series of short determinate modules. Growth of the main axis is by sympodial innovations. Branching along this main axis is usually reduced to a few adventitious basal branches. Thus, the branching system often consists of only one order of branching. This character state occurs in some taxa of the Orthotrichaceae (e.g., *Orthotrichum*), some of the Hedwigiaceae (e.g., *Hedwigia*), and *Helicophyllum* (Figs. 1, 2).

In pleurocarpous mosses, branching is monopodial. The main axis is usually a long single module of indeterminate growth. Branching along this main axis is common. Lateral branches are often determinate, also often branched. Thus, the branching system can consist of one, two, or more orders of branching. Cladocarpus was observed in some taxa of the Orthotrichaceae (e.g., *Drummondia*) and the Erpodiaceae (*Erpodium* and *Venturiella*). All taxa studied in the Leucodontineae are pleurocarpous (Figs. 3–5). Branching in *Rhachithecium perpusillum* (Thwait. & Mitt.) Broth., *Hypnodontopsis apiculatus* Iwats. & Noguchi, and *Microtheciella kerrii* is uncertain and no character state is assigned to these taxa (coded as "?").

3. Orientation of branching system: 0 = orthotropic, main axis and branches erect, or more or less perpendicular to the substrate; 1 = main axis plagiotropic, but branches arcuate

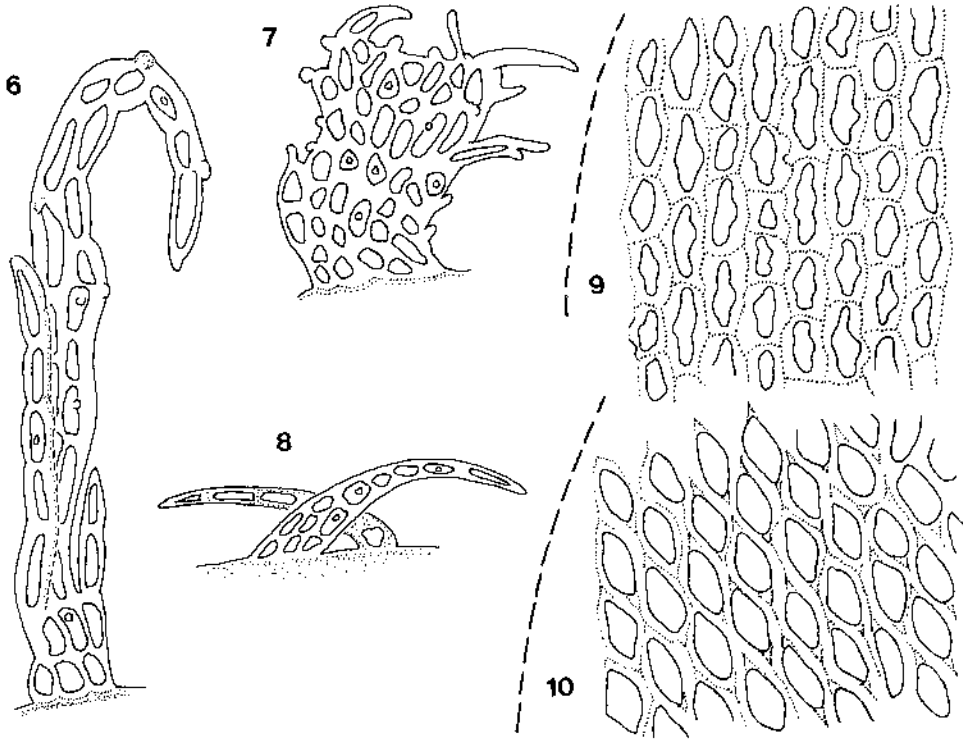
to erect; 2 = plagiotropic, main axis and branches prostrate [ordered]. The position of the main axis and branches of a moss on the substrate seems to be independent of sporophyte position and branching pattern. Although most erect mosses are acrocarpous and most plagiotropic mosses are pleurocarpous there are several cases where these two features do not correlate (Hagerup 1935; Meusel 1935). This justifies the treatment of branch orientation as a separate character.

Orthotropic shoots occur in *Funaria hygrometrica*, and some members of the Orthotrichaceae, such as *Orthotrichum* (Fig. 1). In the Hedwigiaceae the main axis is plagiotropic but the branches are arcuate to erect (Fig. 2). The same character state also occurs in a few taxa of the Orthotrichales (e.g., *Macromitrium*; Fig. 3) and in taxa of the Leucodontineae (e.g., *Leucodon* and *Cryphaea*; Fig. 4). It must be emphasized that only shoot orientation is similar among these taxa. This statement does not imply the interpretation that development of the branching system and the position of archegonia is also similar (see character 2).

4. Flagelliform branches: 0 = flagelliform branches absent; 1 = flagelliform branches differentiated. The occurrence of these modified branches has been reported in unrelated families of mosses. The leaves of flagelliform branches are smaller and narrower than those of the main stem and regular branches. Also, the tips of these branches are often terminated by clusters of rhizoids, which anchor the plant to the substrate. Flagelliform branches were observed in species of the Leucodontaceae, Anomodontaceae and Hedwigiaceae.

5. Central strand in stem: 0 = present; 1 = absent. The cells that make up the stem are sometimes differentiated, with a central strand of cells with thicker walls and smaller lumina. Kawai (1977) reported anatomical details of stem cross sections of fifty-two species of the Isobryales. He showed basic anatomical similarities among *Dozya japonica* Lac. in Miq., three species in *Leucodon* and *Hedwigia ciliata*. My observations and Kawai's (1977) excellent illustrations revealed wide variation in particular features of the cortical cells and the cells in the central tissue, but my interpretation is that distinct character states can be recognized only in the differentiation of a central strand.

6. Foliation on main axis: 0 = main axis and



FIGS. 6-10. Gametophyte features in the Hedwigiaceae and its potential outgroups. 6-8. Pseudoparaphyllia in the Hedwigiaceae. 6. *Pseudobraunia californica*. 7. *Braunia secunda*. 8. *Hedwigia ciliata*. 9-10. Alignment of leaf cells. 9. Longitudinal rows in *Braunia secunda*. 10. Oblique rows in *Felipponea montevidensis*.

branches are foliose; leaves dense; 1 = main axis without leaves, or with only a few very reduced leaves, secondary axes or branches densely foliose. The main axis generally has leaves, and the shape of these leaves is similar to those on the branches. This character state is present in *Funaria hygrometrica* and *Orthotrichum alpestre* Hornsch. ex B. S. G., among others. However, in some mosses, different degrees of leaf density occur between stem and branch leaves. This character state occurs in taxa of the Isobryales (e.g., *Cryphaea* and *Leucodon* among others; Fig. 4).

7. Leaf stance on stem: 0 = radial symmetry; 1 = bilateral symmetry, complanate leaves. The position of leaves is mostly spiral around the stem and branches. This character state occurs in the majority of taxa studied here. However, in the Erpodiaceae, Microtheciaceae, and Helicophyllaceae the leaves are complanate. Elsewhere, this character state occurs in a few unrelated genera in the Isobryales and in the Hypnales.

8. Pseudoparaphyllia: 0 = pseudoparaphyllia absent; 1 = pseudoparaphyllia filamentous, uni- or biseriate; 2 = pseudoparaphyllia foliose, very broad at the base [ordered]. Akiyama and Nishimura (1993) distinguished "pseudoparaphyllia" from "scaly-leaves." Ireland (1971) described these appendages mostly in pleurocarpous mosses, but he also observed pseudoparaphyllia in *Pseudobraunia californica*. Akiyama (1990) found also pseudoparaphyllia in *Hedwigia ciliata*. Similar uniseriate or leaf-like small appendages surrounding the branch buds and the base of branches have also been observed in a few of the acrocarpic genera included in this study (e.g., *Hedwigia* and *Braunia* among others; Figs. 6-8). Ordering is based on transformations observed during development in the Hedwigiaceae.

9. Surface of pseudoparaphyllia: ? = does not apply; 0 = surface smooth; 1 = surface papillose. Most pseudoparaphyllia have been described as having smooth surfaces. However, Akiyama (1990) recently described pseudopar-

aphyllia in *Hedwigia* as papillose. My studies confirm his observations. I also have observed this feature in additional species in *Braunia*, *Hedwigidium*, and *Pseudobraunia*. Besides these four genera in the Hedwigiaceae, papillose pseudoparaphyllia have not been reported in any other moss.

10. Leaf costa: 0 = costa single; 1 = costa absent; 2 = costa double [unordered]. When it is single, the costa varies from strong, such as in *Orthotrichum*, to weakly differentiated, as in *Microtheciella*. When the costa is double, it is weakly differentiated only in the basal half of the leaf.

11. Leaf subula: 0 = not differentiated; 1 = subulate leaves, subula bistratose. The shape of the leaf acumen varies greatly and continuously among species. It is gradually acuminate in several species in the Orthotrichales and mostly acute in the Leucodontineae, but no character states can be recognized. However, the differentiation of a bistratose leaf subula in the Cyrtopodaceae is clearly distinct from the leaves in all other species included here. Sastre-De Jesús (1987) discussed this character and interpreted it as a synapomorphy for the Cyrtopodaceae compared to Cryphaeaceae as outgroup.

12. Juxtacostal cells: ? = does not apply; 0 = juxtacostal cells not differentiated; 1 = juxtacostal cells differentiated. These are laminal cells located on both sides along the costa. Cells in this area are elongated compared to those in the middle part of the lamina. Sastre-De Jesús (1987) discussed this character in the Cyrtopodaceae and related families in the Leucodontineae. Among taxa studied here, this character state occurs in the species selected from families of the Leucodontineae (e.g., Cyrtopodaceae, Cryphaeaceae).

13. Longitudinal cell walls of upper leaf cells: 0 = straight or slightly undulate longitudinal cell walls; 1 = sinuous longitudinal cell walls. As seen in surface view, the longitudinal cell walls are those that run parallel to the leaf margins and these cell walls are straight. However, sinuous cell walls occur in species of the Hedwigiaceae such as *Braunia* (Fig. 9).

14. Alignment of leaf cells: 0 = cells aligned in longitudinal rows (i.e., parallel to the leaf margin); 1 = cells aligned in oblique rows (i.e., not parallel to leaf margin). The arrangement of cells during leaf development is in a network

with rows of cells generally aligned in the direction of the length of the leaf. In this type of network, leaf cells are commonly subquadrate to long oblong or broadly hexagonal and isodiametric. This pattern of cells in longitudinal rows occurs for example in *Funaria*, the Hedwigiaceae, and the Orthotrichaceae (Fig. 9). This cell alignment is well defined in early juvenile leaves of these taxa. On the other hand, taxa of the Leucodontineae, such as *Leucodon*, have cells aligned in oblique rows (Fig. 10). In these taxa the upper leaf cells are generally oval, elliptic or rhombic. This oblique cell alignment is also well defined in juvenile leaves.

15. Leaf marginal cells: 0 = marginal cells mostly quadrate to pentagonal; 1 = cells transversely oblate; 2 = cells long oblong to narrow vermiform [unordered]. Median marginal cells are sometimes differentiated from those in the middle of the leaf. Strongly differentiated cells occur in *Rhacocarpus* and *Bryowijkia*. In the former genus the marginal cells are linear and form a distinct marginal band. In *Bryowijkia* the cells are also very narrowly elongate. In the Leucodontineae, marginal cells are transversely rectangular, especially at the basal third of the leaf, as Sastre-De Jesús (1987) discussed and illustrated in the Cyrtopodaceae.

16. Alar cells: 0 = rectangular to quadrate; 1 = oval; 2 = inflated [ordered]. At the alar region of the branch leaves there is wide variation in the degree of differentiation of cells. In most species representing the Orthotrichales here these cells are rectangular but they gradually become quadrate. In contrast, in species representing the Leucodontineae the alar cells are mostly oval.

17. Luminal leaf-cell papillae: 0 = papillae absent; 1 = one or few papillae per cell; 2 = many papillae per cell [unordered]. The exposed cell walls on ventral and dorsal sides of the leaf are either smooth or develop papillae. These papillae are distributed over the lumen and are probably not homologous to papillae positioned marginally over the longitudinal cell walls. Luminal papillae are generally small, such as in *Zygodon* and *Braunia* among others.

18. Marginal leaf-cell papillae: 0 = papillae absent; 1 = papillae on longitudinal cell walls. Papillae generally project from the center of exposed cell walls and are erect or oblique, such as in the Orthotrichaceae. However, in *Braunia* and *Bryowijkia* papillae are marginal and project

from the adjoining longitudinal cell walls. These papillae are erect or curved towards center of cell lumen.

19. Leaf cell prorula: 0 = exposed cell walls flat, cells not inflated; 1 = exposed cell walls convex at center of cell, more or less equally on both leaf surfaces, lumen bulging; 2 = exposed cell walls flat at center of cell, but sharply convex at the end of each cell, with the lumen prorulose [unordered]. Prorulae and bulging cells are a type of cell ornamentation, but are not homologous to papillae. They are treated as a different character. As seen in cross section, the exposed cell walls on the ventral surface of the leaf are generally flat, and thus the exposed cell walls form a homogeneous leaf surface. However, in some of the species, the cells appear inflated in cross section, with cell walls bulging toward the dorsal or/and ventral leaf surfaces.

20. Distribution of gametangia: ? = uncertain; 0 = autoicous; 1 = dioicous; 2 = phyllo-dioicous [unordered]. In all species studied here, antheridia and archegonia develop on separate branches, either on the same or on different gametophores. All species in the Hedwigiaceae are autoicous. Species in the Orthotrichales and Leucodontineae are either autoicous or dioicous. All herbarium specimens examined of *Bryowijkia ambigua* contain only shoots with archegonia or sporophytes and reports of dwarf males (Ramsay 1979) remain unverified.

21. Perichaetial leaves: 0 = perichaetial leaves not or very little different from mature stem leaves; 1 = perichaetial leaves differentiated, oblong-lanceolate, broader than stem leaves (at least two times larger). In most selected species in the Leucodontineae and Hedwigiaceae the perichaetial leaves are strongly differentiated from vegetative leaves. On the other hand, most selected species in the Orthotrichales do not have differentiated perichaetial leaves.

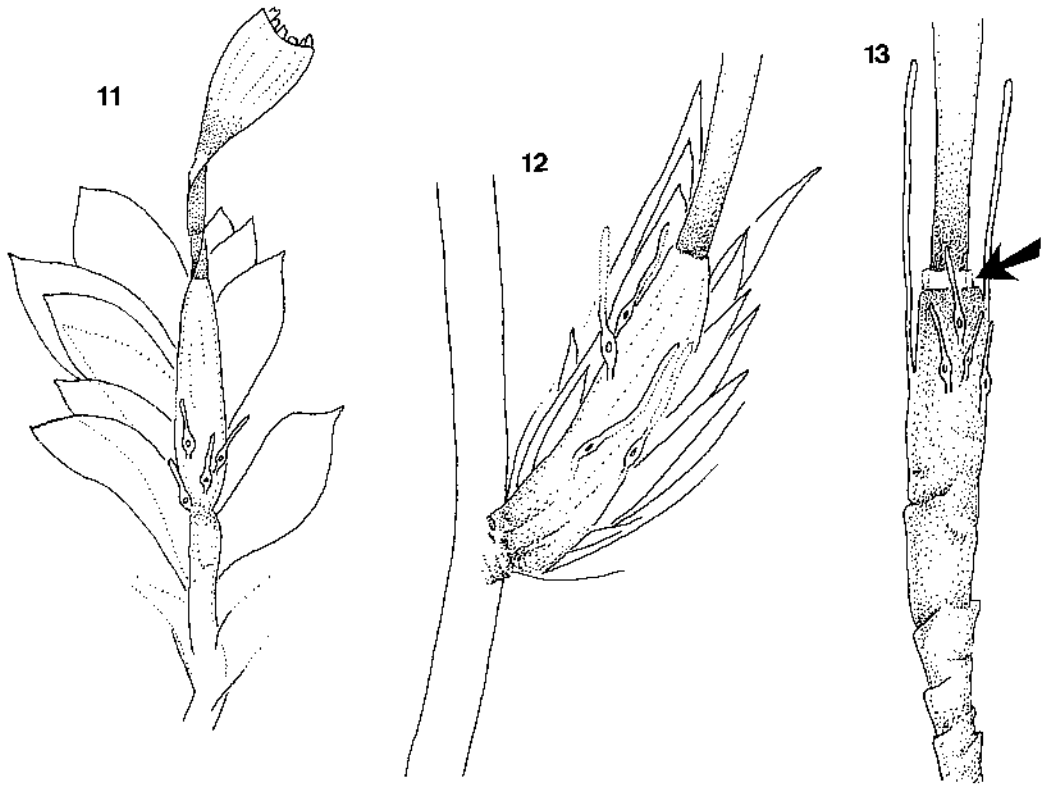
22. Position of archegonia on vaginula: ? = unknown; 0 = archegonia distal on vaginula; 1 = archegonia on medial portions of the vaginula; 2 = archegonia on proximal portion of vaginula. The distal portion of the stem that swells and surrounds the foot of the sporophyte is here designated the "vaginula," as defined by Nishimura (1981). It is generally assumed that the vaginula is derived from basal archegonial tissue (Magill 1990). Observations in this

study suggest that the vaginula may consist only of the swollen tip of the stem. The basal part of the archegonial wall developed into the calyptra (cf. character 25). A detailed study of the development of the vaginula is needed to corroborate its origin, whether stem or archegonial.

Within each perichaetium, several archegonia may be fertilized, but only one embryo develops to maturity. At maturation of the sporophyte, unfertilized archegonia and archegonia containing aborted sporophytes remain on the vaginula. In genera studied here, the vaginula is variously elongated but the final position of archegonia along the vaginula at sporophyte maturation it is not correlated with vaginula length. As done by Nishimura (1981), it is possible to find a pattern of vaginula distribution if the vaginula is divided into three segments. In some genera archegonia are attached at the basal $\frac{1}{3}$ of the vaginula, while in other genera archegonia are clustered at the middle portion. In *Braunia* the archegonia are positioned at the uppermost $\frac{1}{3}$ segment of the vaginula (Figs. 11-13).

23. Perichaetial paraphyses: ? = unknown; 0 = paraphyses present, short, hyaline; 1 = paraphyses present, long, becoming strongly yellowish after fertilization; 2 = paraphyses absent [ordered]. These are uniseriate, and occasionally multiseriate, filaments that occur in variable density within a moss perichaetium. Most genera in the Orthotrichales have very short hyaline paraphyses, while genera in the Leucodontineae and the Hedwigiaceae have long, sometimes yellow and exserted paraphyses. While studying phenology in genera of the Leucodontaceae, Leptodontaceae, and Cryphaeaceae, Stark (1985) noted a pattern of yellowish coloration in paraphyses after the archegonia are fertilized and the sporophyte develops. However, in those taxa scored as having hyaline paraphyses, color changes during maturation were not observed and have not been reported in the literature.

24. Ochrea: 0 = ochrea absent; 1 = ochrea present. This is a delicate, hyaline membrane that develops at the tip of the vaginula and loosely surrounds the seta at its point of insertion. According to observations made in this study, the ochrea is not made up of tissue. Rather, it seems to be composed of extracellular material, possibly derived from the basal part of



FIGS. 11-13. Ochrea and position of archegonia on vaginula. 11. Archegonia on proximal $\frac{1}{3}$ portion of vaginula in *Rhachithecium*. 12. Archegonia on the medial $\frac{1}{3}$ section of the vaginula in *Bescherellia*. 13. Archegonia on the distal $\frac{1}{3}$ of the vaginula in *Braunia*. This also illustrates the ochrea at the tip of vaginula (arrow).

the archegonial wall. This membrane is difficult to see and its taxonomic distribution is poorly known. It has been described in some species of the *Grimmiaceae*, but it is probably best known in several species of *Orthotrichum* (Flowers 1973). This membrane was found in some members of the Orthotrichaceae and in *Braunia* (Fig. 13).

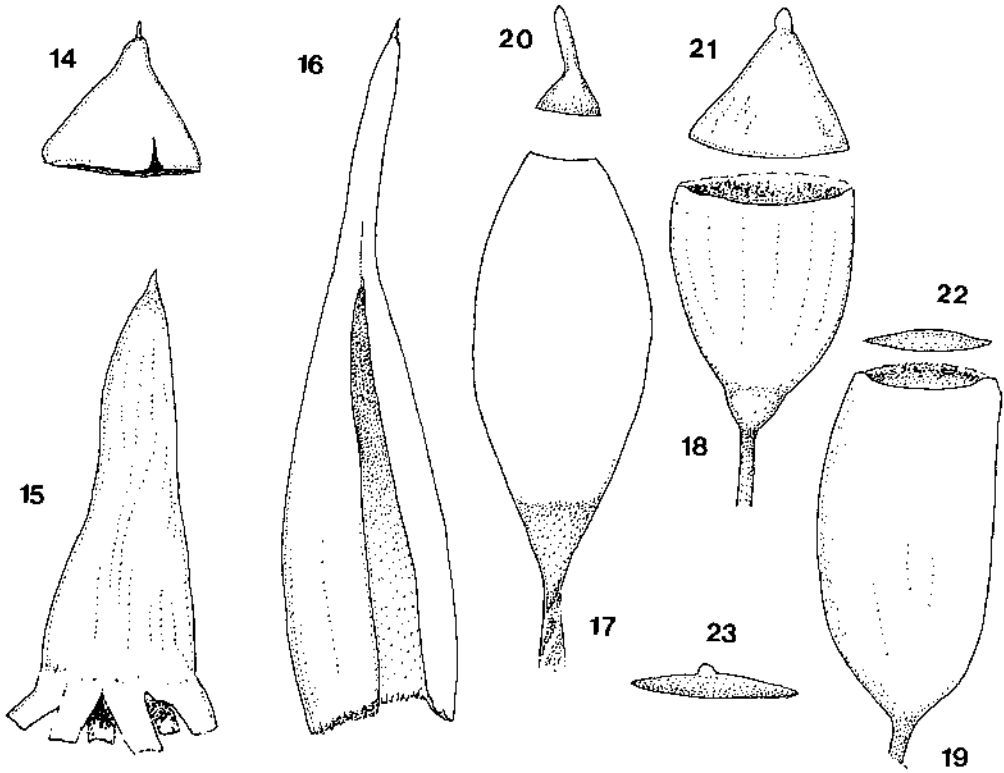
25. Calyptra size: ? = unknown; 0 = very small, covering only the operculum; 1 = large, covering most of the capsule. In most genera in the Orthotrichales and Leucodontineae the calyptra is large. Although there is considerable variation in size, large calyptrae consistently cover the operculum and part of the urn. This contrasts clearly with very small calyptra that covers only the operculum, as in *Hedwigia ciliata* (Figs. 14-16).

26. Calyptra shape: ? = unknown; 0 = mitrate; 1 = cucullate. The difference between these two states is clear. Cucullate calyptrae have only one long split (Figs. 14, 16). Mitrate calyp-

trae commonly have the base split at several sites (Fig. 15). In the Orthotrichales and Leucodontineae both types of calyptra occur. In the Hedwigiaceae all genera have cucullate calyptrae. The calyptra in *Bryowijkia* is still unknown.

27. Outgrowths on calyptra wall at maturity: 0 = no outgrowths; 1 = hairy. A variety of ornamentations may occur on the surface of the calyptra, ranging from small cell projections (prorulae) to long multicellular hairs. Prorulae on calyptrae are not considered homologous with multicellular hairs. Among species studied, prorulose calyptrae were found only in *Cryphaea glomerata* and thus are not informative for present analyses. Multicellular hairs were observed on the calyptrae of some species representing the Orthotrichales.

28. Plications on calyptra: 0 = calyptra smooth; 1 = calyptra plicate. In the Leucodontineae and in the Hedwigiaceae calyptrae are smooth, as in *Leucodon julaceus*. Calyptrae in



FIGS. 14-23. Calyptrae, operculae and capsules in the Hedwigiaceae and its potential outgroups. 14. Cucullate calyptra in *Hedwigia ciliata*. 15. Mitrated calyptra in *Schlotheimia lancifolia*. 16. Large cucullate calyptra in *Braunia secunda*. 17. Ellipsoid capsule, with long and gradually attenuate neck in *Braunia secunda*. 18. Urceolate capsule, with short and sharply ampullaceous neck in *Pseudobraunia californica*. This also illustrates the capsule surface longitudinally sulcate. 19. Capsule with neck not differentiated in *Helicophyllum torquatum*. 20. Operculum with a differentiated beak and a conic base in *Braunia secunda*. 21. Operculum with a beak consisting only of a small mammilla and a conic base in *Pseudobraunia californica*. 22. Operculum with no differentiated beak and a flat base in *Helicophyllum torquatum*. 23. Operculum with a small mammilla and a flat base in *Hedwigia ciliata*.

some species here representing the Orthotrichaceae develop longitudinal plications, as in *Macromitrium richardii*.

29. Seta length: 0 = seta long, capsule exserted; 1 = seta very short, capsule immersed, or emergent. In most species representing the Orthotrichales and Leucodontineae, seta length is very variable although consistently long and with the capsules always exserted (e.g., *Schlotheimia lancifolia* Bartr.). This contrasts clearly with a very short seta with capsules immersed or scarcely emergent found in other taxa (e.g., *Lepidotodon smithii*).

30. Capsule neck: 0 = neck long, gradually attenuate; 1 = neck short, sharply ampullaceous; 2 = neck not differentiated [unordered].

In a few of the species representing the Orthotrichaceae and Hedwigiaceae capsules have a long, gradually attenuate neck. In the species representing the Leucodontineae capsules do not differentiate a neck (Figs. 17-19).

31. Capsule shape: 0 = capsules cylindrical to ellipsoid, mouth narrower than widest part of capsule; 1 = capsules urceolate to subglobose, mouth wider than the width at middle of capsule. In species representing the Orthotrichales and Leucodontineae capsules are very variable in size, but their shape ranges between cylindrical (as in *Bescherellia cryphaeoides*) to ellipsoid (as in *Leucodon julaceus*). This variation is here interpreted as a single character state. The other character state occurs in a few species, such as

Hedwigia ciliata and *Bryowijkia ambigua* in which the capsules are urceolate to globose (Figs. 17–19).

32. Capsule surface: 0 = smooth or irregularly wrinkled; 1 = longitudinally sulcate. The surface texture of the capsule varies from smooth or wrinkled, as in *Cryphaea glomerata*, to distinctly grooved as in *Orthotrichum alpestre*. In sulcate capsules, exothelial cells along the ridges are often differentiated, forming distinct rows of elongated cells (Figs. 17–19).

33. Stomata: 0 = stomata superficial; 1 = stomata immersed; 2 = stomata not present [unordered]. Stomata (when present) are usually located at the base of the urn and in the neck of the capsule. Stomata in most species studied here are in the same plane as the exothelial cells, but in few species stomata are in a lower plane forming a small stomatal chamber.

34. Operculum beak: 0 = only a small mammilla, or not differentiated; 1 = rostrum differentiated, short to long, slender. The operculum is here considered to consist of two independent parts: the base and the beak (Figs. 20–23). The degree of differentiation of the beak varies from a small mammilla (as in *Hypnodontopsis apiculatus*) to a long slender rostrum (as in *Rhacocarpus purpurascens*). There is much variation in the length and inclination of the rostrum and no further character states can be recognized.

35. Operculum base: 0 = flat, or convex; 1 = conic. The base of the operculum varies from nearly flat (as in *Drummondia prorepens*), to high conic (as in *Pseudobraunia californica*). Most genera in the Leucodontineae and the Hedwigiaceae have the base of the operculum conic (Figs. 20–23).

36. Differentiation of exostome: ? = uncertain; 0 = present, 16 separate teeth; 1 = present, teeth fused into eight pairs; 2 = absent [unordered]. Capsules in the Hedwigiaceae lack a peristome and most genera in the Leucodontineae and Orthotrichales have capsules with a peristome. Although all exostomes have 16 teeth as a basic number, the teeth are sometimes joined in pairs, as in *Schlotheimia lancifolia*. The membrane found in *Groutiella tumidula* and the rudimentary peristome in *Bryowijkia ambigua* were coded as "uncertain" since their homology with either exostome or endostome has not been clarified.

37. Shape of exostome tooth: ? = does not apply; 0 = teeth long, slenderly lanceolate, 1

= teeth short, broadly acuminate, 2 = teeth short, truncated [unordered]. Most species representing the Leucodontineae have long, slenderly lanceolate teeth (such as in *Cryphaea glomerata*). However, in some species representing the Orthotrichales the teeth are short, broad, and appear truncated (such as in *Drummondia prorepens*). A different character state occurs in other taxa of the Orthotrichales (e.g., *Orthotrichum alpestre*) in which the teeth are also short and broad, but acuminate.

38. Color of exostome: ? = does not apply; 0 = whitish; 1 = yellowish. Typically the color of peristomes is yellowish, deep orange, or reddish. However, species representing the Leucodontineae share a whitish peristome.

39. Movement of peristome: ? = does not apply; 0 = teeth xerocastique; 1 = teeth hydrocastique. Most mosses show hygroscopic movement of the exostome teeth such that the teeth arch over the mouth when wet (xerocastique). In a few cases, the teeth are reflexed when wet (hydrocastique). Stark (1987) reported hydrocastique peristomes in several genera of the Leucodontineae, and Akiyama (1988a) further discussed the systematic value of this character. It seems that these peristome movements are correlated with particular ultrastructural features of the teeth (Newmann and Mueller 1987).

40. Surface of exostome: ? = does not apply; 0 = papillose; 1 = smooth; 2 = striate [unordered]. Ornamentation of the outer surface of exostome has been considered a source of reliable characters. Extensive surveys using the SEM have revealed that papillae and striations are responsible for most of the ornamentation patterns known (Shaw 1986; Akiyama 1987, 1988a; Stark 1987; Lewinsky 1989). Most species here representing the Orthotrichales have papillose peristomes. In contrast, among species studied here, most representatives of the Leucodontineae have smooth peristomes, except *Cryphaea glomerata* and two species of the Cyrtopodaceae, which Sastre-De Jesús (1987) described as having the exostome teeth "spiculate."

41. Segments of the endostome: 0 = segments tall, well differentiated; 1 = segments short, poorly developed; 2 = segments not present [ordered]. Few mosses in this study develop the endostome common in other diplolepideous mosses. The poor development of the endostome, among other characters, has been a

justification for recognizing the Isobryales (Crosby 1980; Buck and Vitt 1986).

Characters Excluded. The following characters were not included in present cladistic analyses because incomplete information on character variation and character state distribution among taxa examined. Characters not clearly discrete were also excluded.

1. Stem anatomy. In cross section, most mosses have an outer layer of thicker, smaller cells, and delicate, larger cells to the inside (Kawai 1977). Variation in these anatomical features, particularly those in the outer layer, could not be partitioned into discrete states. In a continuous range of variation, a few taxa have scarcely differentiated cells to the outside and other taxa have strongly differentiated outer cells.

2. Axillary hairs. Recent taxonomic studies in diverse moss groups have included features of the hairs in leaf axils (Akiyama 1988b). These structures were studied in more than 150 species belonging to the Hypnales (Hedenäs 1989), but such study included only a few of the Leucodontineae. My limited observations in the Leucodontineae suggest that there might be a useful pattern of variation, for example, in the number of hairs per leaf axil, the number of cells that make up the hair, and the differentiation of the basal cell. However, there are multiple levels of developmental variation and a possible heteroblastic series that have not been evaluated.

3. Leaf cell pits. These perforations presumably connecting leaf cells are another potential source of characters (Newton, pers. comm.). There seem to be two types of perforations: those whose edges are sharp at both ends and those that become narrowly attenuate. Although some of the taxa in the present study have one or the other of these two types of pits, without more sampling the extent of variation within taxa could not be evaluated.

4. Cells of the capsule wall. A number of potential characters can be found in the shape of exothecial cells as seen in surface view, as well as in cross section. The number of cell layers that make up the capsule wall at the middle part of the capsule and at the mouth varies from very few cell layers (2-3) to multiple cell layers (7-10). This character variation seems especially useful in the group of families close to the Pterobryaceae (Newton, pers. comm.). The shape and alignment of the exothecial cells also

vary from narrowly rectangular to broadly polygonal. This variation is specially informative within the Hedwigiaceae. These characters need to be studied in more detail in the Orthotrichales and the Leucodontineae.

5. Annulus. This row of cells is not differentiated in the Hedwigiaceae. In the species representing the Leucodontineae and the Orthotrichales both character states occur. However, closed capsules are not always available to verify the annulus before shedding the operculum. This character was excluded from analyses because character state distribution is uncertain in several species included here.

6. Anatomy of the seta. Few characters have been traditionally recognized from the seta. However, the anatomy as seen in cross sections may provide features of systematic value at the level of the Isobryales. For example, in some of the species studied here there is a variable degree of differentiation of the cortical cells and the cells of the central strand. This character was excluded because of incomplete observations in several species studied.

7. Anatomy of calyptra. Janzen (1916) described and illustrated variation in the anatomy of calyptrae in *Braunia*, *Hedwigia*, *Orthotrichum*, and *Leucodon*. His report and a few personal observations suggest that the number of cell layers in cross section, and the thickness of cells, are another potential source of characters in the Isobryales. It was not possible to observe this character for most taxa in this study because the lack of material.

8. Shape of stomatal pores. Surveys of the morphology of the stomata suggest that there may be two shapes of pores: round and elongate (Egunyomi 1982; Paton and Pearce 1957). These two stomatal shapes were observed in some of the taxa for this study, but some capsules seem to have a mixture of the two pore shapes. The extent of the variation of this character is unclear.

9. Thickness of outer and inner layers of exostome teeth. Generally, diplolepidous peristomes have the inner and outer layer homogeneously thickened. However, according to Vitt (1973, 1984), the orthotrichaceous peristome is characterized by having an exostome with thickened outer plates. This peristome type presumably is known in all the Orthotrichaceae. However, the precise taxonomic distribution of this character has not been reported in the literature for all the species included here.

10. Ecological and other characters. Other characters were excluded, although they were used by previous bryologists studying the same taxa in the Leucodontineae (Buck and Vitt 1986), such as ecological features (xerophytic vs. mesophytic habitats) and substrates (saxicolous, epiphytic, etc.). Characters like these were excluded in the present study because of problems in applying basic principles of character analysis (e.g., homology).

Phylogenetic Relationships. Topologies found in the first series of heuristic analyses (using different branch swapping algorithms) are summarized in the strict consensus tree shown in Fig. 24. A total of 288 equally most parsimonious trees of 185 steps was found, with a consistency index (CI) of 0.319. Taxa traditionally classified in the Leucodontineae (Isobryales) are paraphyletic compared to a group including *Brachythecium* and *Hypnum*, representing the Hypnales. Taxa traditionally classified in the Orthotrichales are also paraphyletic, compared to the Leucodontineae plus Hypnales. Part of the traditional Hedwigiaceae (*Braunia*, *Hedwigia*, *Hedwigidium*, and *Pseudobraunia*) is monophyletic and nested within the Orthotrichales. The other two genera of the traditional Hedwigiaceae, *Bryowijkia* and *Rhacocarpus* are placed as a sister group of the Hypnales (Fig. 24).

The second series of analyses (excluding *Bryowijkia* and *Rhacocarpus*) resulted in 144 equally most parsimonious trees of 170 steps (CI = 0.347). The strict consensus tree (not shown) gives the same topology as the consensus tree from the first series of analyses that included all taxa (Fig. 24). A third series of analyses with all taxa but using "Lundberg rooting" (to explore the effect of choosing *Funaria hygrometrica* as outgroup) resulted in 1,176 equally most parsimonious trees of 178 steps (CI = 0.331). The strict consensus tree (not shown) allows the recognition of only two main clades: 1) *Bryowijkia* plus *Rhacocarpus* plus Leucodontoideae plus Hypnales, and 2) Hedwigiaceae. Both clades are the same as found in the first series of analyses using outgroup rooting with *Funaria hygrometrica*. In the consensus tree, the relationships among all other taxa in the Orthotrichales and these two main clades are unresolved.

Branch support as estimated by decay analyses (Fig. 24) is robust for a clade that includes

the genera *Braunia*, *Hedwigia*, *Hedwigidium* and *Pseudobraunia*. The clade formed with the Hedwigiaceae plus the cladocarpous Orthotrichales plus the Isobryales and Hypnales is also robust. Most other clades collapse in the consensus of trees that are two steps longer than the most parsimonious.

Character support is shown only for main clades relevant to the circumscription and relationships of the Hedwigiaceae (Fig. 25). Since relationships among terminal branches are not robust, the cladogram in Fig. 25 shows only characters supporting relationships among major clades but not among genera. Character changes per branch are presented based on one most parsimonious tree selected among those found in the first series of analyses.

DISCUSSION

Relationships among genera in the Leucodontineae and Orthotrichales implied by topologies found in the present analyses must be regarded with caution. Representation of terminal taxa and sampling of characters were not meant to address those phylogenetic problems. The cladogram in Fig. 24 is offered as an initial phylogenetic framework for further systematic research, both at the species level within the Hedwigiaceae, and at the family level in the Orthotrichales and Isobryales. As more taxa and different types of characters are added to the analyses, some aspects of this hypothesis of relationships will undoubtedly change, but other aspects (e.g., circumscription of the Hedwigiaceae) seem relatively well supported by the data at hand.

Circumscription of Hedwigiaceae. Results from the three series of cladistic analyses strongly suggest that the Hedwigiaceae as a monophyletic group should include only *Braunia*, *Hedwigia*, *Hedwigidium*, and *Pseudobraunia* and that *Rhacocarpus* and *Bryowijkia* do not belong to the Hedwigiaceae. The Hedwigiaceae, as circumscribed here, are supported by eight synapomorphies (Fig. 25). Two are unique synapomorphies: globular protonemal development (character 1) and papillose pseudoparaphyllia (9). The other six synapomorphies are not unique, but they are interpreted as independently derived in the Hedwigiaceae. They are: development of flagelliform branches (4), ecos-

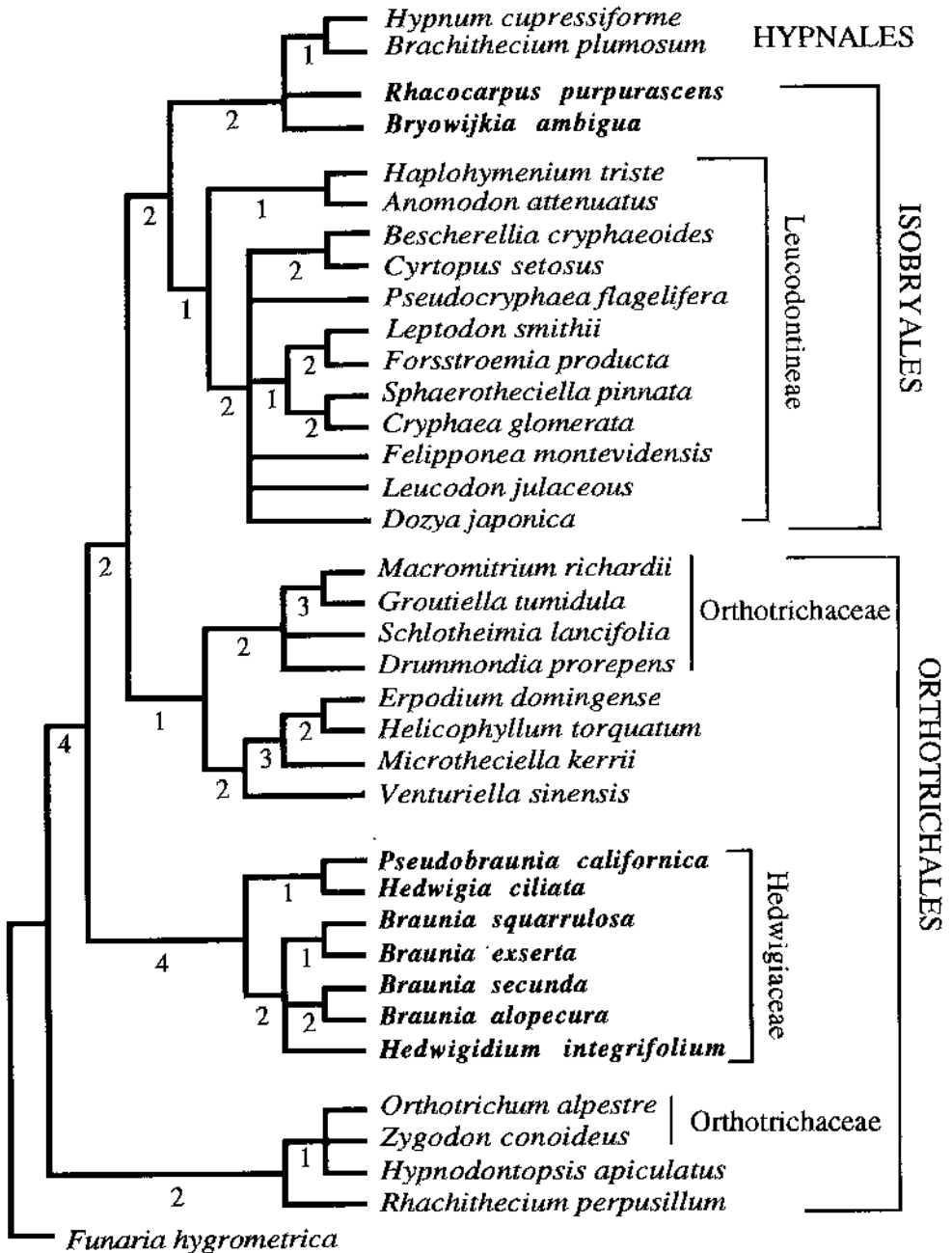


FIG. 24. Phylogenetic relationships of the Hedwigiaceae. Strict consensus tree of 288 equally most parsimonious trees (185 steps, CI = 0.319) found in a heuristic search based on 41 characters in 36 OTU's representing selected families in the Orthotrichales and Leucodontideae (Isobryales). *Funaria hygrometrica* was used as the outgroup and *Brachythecium* and *Hypnum* were included to represent the Hypnales in the ingroup. Genera traditionally placed in the Hedwigiaceae are in bold. Numbers below the branches are estimated values of the "decay index."

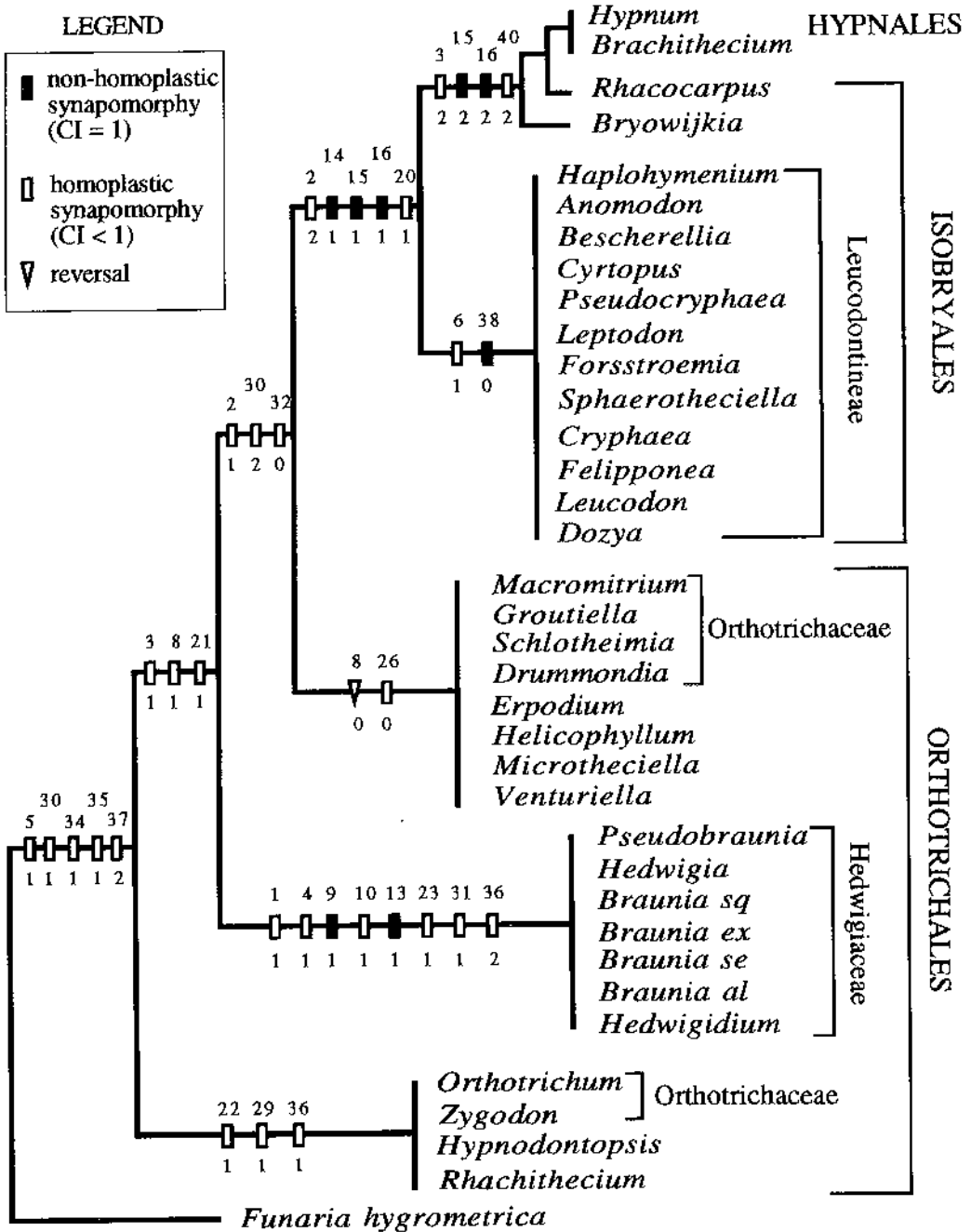


FIG. 25. Synapomorphies that support phylogenetic relationships of the Hedwigiaceae. This is one tree selected at random from the set of 288 equally most parsimonious trees found in a heuristic search. This tree shows only the basic clades relevant to the problem of relationships of the Hedwigiaceae. It was simplified to show character changes only on main branches by deleting terminal branches and deleting species names. Character numbers (above the line) and states (below the lines) correspond to those in the text and in Table 2.

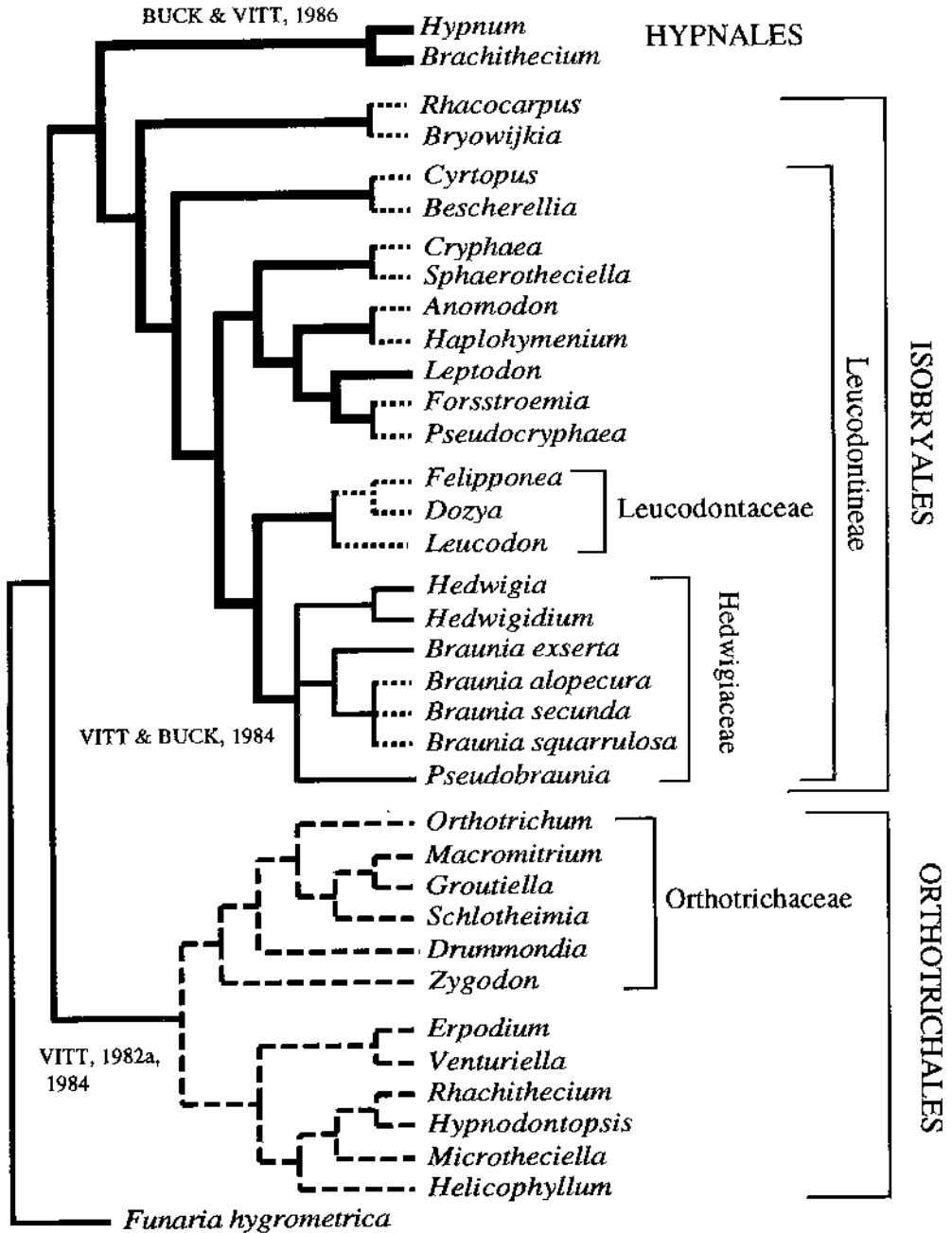


FIG. 26. Phylogenetic relationships of the Hedwigiaceae according to previous reports in the literature. This is a combined tree built from various sources. The clade showing relationships in the Isobryales and Hypnales (heavy black lines) was taken from Buck and Vitt (1986). They suggested a sister group relationship between the Hedwigiaceae and the Leucodontaceae. Relationships within the Hedwigiaceae (normal black lines) were taken from the classification in Vitt and Buck (1984). The clade depicting the relationships within the Orthotrichales (dashed black lines) was taken from Vitt (1982a, 1984). According to him, the Orthotrichaceae and Orthotrichales are monophyletic. This combined tree topology was input to PAUP to evaluate its level of parsimony using the data matrix in Table 2. This tree has a length of 219 steps (CI = 0.269).

tate leaves (10), sinuous cell walls (13), yellow perichaetial paraphyses (23), broad capsules (31), and eperistomate capsules (36).

Relationships of the Hedwigiaceae. Previously proposed relationship of the Hedwigiaceae with the Leucodontaceae in the Isobryales (Buck and Vitt 1986) is not supported by the present analyses (Fig. 26). Such a relationship was based on a branching system and archegonial position in the Hedwigiaceae described as pleurocarpous, and on features of "capsules, basal cells, and leaf characters" (Vitt 1982a; Buck and Vitt 1986). Among the leaf characters used by Buck and Vitt (1986), the absence of a costa, thick walled and oval alar cells, thick walled leaf cells, and short narrow lumina were also mentioned as supporting such a relationship. However, additional study has revealed these conclusions to be either misinterpretations or based on a homoplastic occurrence of the character states.

A study of the archegonial position and branching system in the Hedwigiaceae shows that it is not pleurocarpous, but acrocarpous, even though it has a prostrate habit (De Luna 1990b). Furthermore, the alar cells in the Hedwigiaceae are quadrate to oblate, rather than oval, and thus different from those in the Leucodontaceae or related families in the Isobryales. Although the cells are indeed thick walled, this is a character shared by several families outside the Isobryales, and not particularly indicative of a close relationship between the Hedwigiaceae and the Leucodontaceae. There are several characters, such as the differentiated juxtacostal cells, leaf cells aligned in oblique rows, and a prostrate main axis without leaves, that are shared by the families in the Leucodontineae, but are absent in the Hedwigiaceae. All these characters strongly suggest that the Hedwigiaceae should not be classified in the Isobryales.

When competing hypotheses of relationships are available, as in this case, the criterion of parsimony is used to select a most acceptable alternative. The hypothesis of relationships of the Hedwigiaceae within the Leucodontineae (Isobryales), offered by Buck and Vitt (1986) was input to PAUP as a constraint tree to evaluate its feasibility. Within a monophyletic Leucodontineae (nested in the Isobryales), they proposed the Hedwigiaceae (excluding *Bryowijkia* and *Rhacocarpus*) as a sister group to the Leu-

codontaceae (Fig. 26). Resolution shown within the Hedwigiaceae was based on the generic classification presented in Vitt and Buck (1984). This tree for the Leucodontineae was complemented with combined information from two other published topologies. Species representing the Orthotrichales were nested in groups based on trees presented by Vitt (1982b, 1984). The combined constraint tree (Fig. 26) is 219 steps long as calculated by PAUP. It therefore requires at least 34 additional character state changes (C. I. = 0.269) with my data matrix and it is considerably less parsimonious than the hypothesis offered in this study (Fig. 24).

The topology of relationships offered by Buck and Vitt (1986) is one of many trees of the same level of parsimony. These authors did not explore other possible trees of same length or the consensus tree. It is obvious that many conflicting topologies exist in the length range between the two competing trees. In fact, the consensus of trees only five steps longer than the most parsimonious is completely unresolved. Since no explicit character state assignments were made for each terminal taxon included in Buck and Vitt's (1986) and Vitt's (1982b, 1984) papers, it was not possible to compare competing topologies using *their* data. However, one way of testing a phylogenetic hypothesis is by its congruence with other data sets. In this case, Buck and Vitt's (1986) hypothesis of relationships within the Leucodontineae is not supported by the data shown in Table 1.

The phylogenetic hypothesis presented here (Fig. 24) suggests that the Hedwigiaceae are nested within the Orthotrichales. The Hedwigiaceae are placed as sister group to a large clade that includes the cladocarpous species of the Orthotrichales (i.e., *Schlotheimia*, *Macromitrium*, *Erpodium*, etc.) plus the rest of the species studied representing the Isobryales and Hypnales (Figs. 24, 25). The decay analysis suggested that this sister group relationship is robust, since it is still present in the consensus of trees up to four steps longer than the most parsimonious (Fig. 24). Three synapomorphies support this relationship: plagiotropic shoots (character 3), presence of pseudoparaphyllia (8), and differentiated perichaetial leaves (21). The same sister group relationships are also obtained even if *Bryowijkia* and *Rhacocarpus* are excluded from cladistic analyses.

Previous authors have speculated on a rela-

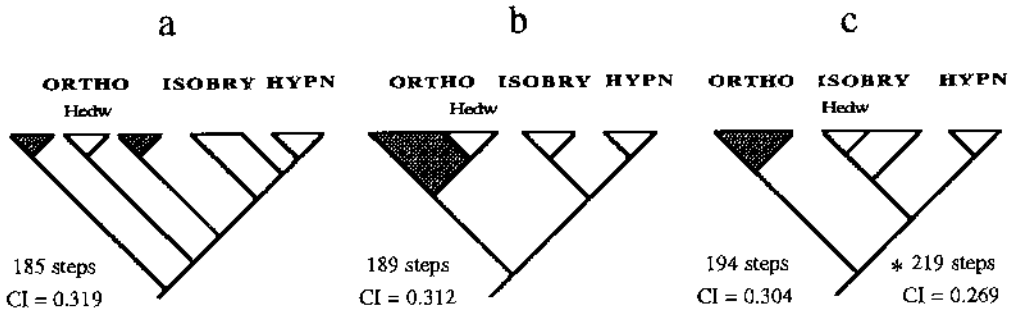


FIG. 27. Competing hypotheses of phylogenetic relationships of the Hedwigiaceae. a. Most parsimonious hypothesis proposed in the present study. The Hedwigiaceae are nested in the paraphyletic Orthotrichales (ORTHO). b. Most parsimonious hypothesis if the Hedwigiaceae belong in the Orthotrichales as a monophyletic order. c. Most parsimonious hypothesis if the Hedwigiaceae belong in the Isobryales (ISOBRY). Shorter tree under this constraint (nine steps longer than most parsimonious) is considerably shorter than the hypothesis proposed by previous authors (Vitt 1982a, 1984; Vitt and Buck 1984; Buck and Vitt 1986). The length of the tree by their hypothesis is indicated by the asterisk (cf. Fig. 26).

tionship of the Hedwigiaceae to the Orthotrichales. For example, Nyholm (1960) and Smith (1978) classified the Hedwigiaceae in the Orthotrichales, close to the Orthotrichaceae. Moreover, Walther (1983) interpreted the archegonial position as "acrocarp-pleurocarp," and he classified the Hedwigiaceae (including *Rhacocarpus* and *Bryowijkia*) in the Orthotrichales. Phenetic similarity of the Hedwigiaceae to the Orthotrichaceae is due to seemingly plesiomorphic character state changes of the branching system, leaf cell alignment and shape, papillae, and capsule neck. Other shared characters are homoplasies, for example, the ochrea is now best interpreted as independently derived in the Hedwigiaceae (*Braunia* and *Hedwigidium*) and in the Orthotrichaceae. It is possible that some of these character state changes might be assigned to different branches in the cladogram if additional characters and species are explored in the Orthotrichaceae.

Using PAUP's "constraints" option, the hypothesis of a relationship of the Hedwigiaceae within the Orthotrichales as a monophyletic group was compared with results of present study and the hypothesis of Vitt and Buck (1986). Two constraint trees defined three clades as shown in Fig. 27b, c. In each constraint statement, the three clades were left internally unresolved to allow PAUP to find the most parsimonious solution possible. Under the topological constraint that the Hedwigiaceae belongs in the Orthotrichales (Fig. 27b), the most parsimonious tree is 189 steps long, only four

additional steps compared to the hypothesis derived from the present study (Fig. 27a). In comparison, if the Hedwigiaceae belong in the Isobryales, the most parsimonious tree is 194 steps, twenty five steps shorter than the tree developed by Buck and Vitt (Fig. 27c). These results suggest that classification of the Hedwigiaceae in the Orthotrichales would be more acceptable than its classification in the Isobryales. Although no synapomorphies are evident that would support the Orthotrichales as a monophyletic group (Fig. 25), provisionally it is convenient to continue its recognition and to classify the Hedwigiaceae in that order.

The present study illustrates the need to use a further outgroup to root the set of potential outgroups and the ingroup when their monophyletic status and upper level relationships among them are unknown. The series of analyses excluding *Funaria hygrometrica*, but using the same string of character states as ancestral states for the "Lundberg rooting" option resulted in a consensus tree with unresolved relationships among potential outgroups of the Hedwigiaceae. The use of *Funaria hygrometrica* seems the best decision given present insights into moss relationships. This distant outgroup, besides revealing relationships of the Hedwigiaceae to other families, also offers insight on the relationships among the collection of potential outgroups, particularly the Orthotrichaceae and the Orthotrichales.

The hypothesis of phylogenetic relationships proposed in this study suggests that the Ortho-

trichaceae as currently circumscribed might not be a monophyletic group (Fig. 24). Cladocarpous taxa, such as *Drummondia*, and *Groutiella*, are not in the clade that includes acrocarpous taxa such as *Orthotrichum*; rather they are included in a monophyletic group basal to the Leucodontineae plus Hypnales. Present results may appear to be biased in view of the exclusion of a peristomial character (excluded character 9) previously interpreted as a potential synapomorphy for the Orthotrichaceae (Vitt, pers. comm.). An analysis was performed to test the effect of including this character, coding all taxa in the Orthotrichaceae with peristomes as having the outer layer of the peristome thickened. Results still support the same general topology shown in Fig. 25. The exostome with thickened outer plates would be interpreted as a parallel gain in the two clades that include genera of the Orthotrichaceae (Fig. 25). The possibly heterogeneous nature of such a large family as the Orthotrichaceae has been suggested before. Recently, Crum (1987) speculated on transferring the pleurocarpous genera into a different family, but refrained from doing so because of the lack of sufficient study. The results from the present analyses reinforce Crum's suggestion.

Also, the hypothesis of phylogenetic relationships proposed in this study suggests that the Orthotrichales are a paraphyletic order. In less explicit terms, other authors (e.g., Crosby 1980) have also recognized problems in the circumscription of the Orthotrichales. Although the present analyses did not include a full sample of characters and taxa thought to belong in the Orthotrichales, one clear result is that a clade composed of acrocarpous genera in this order, such as *Orthotrichum* and *Zygodon*, is placed as the sister group to the large clade that includes the Hedwigiaceae plus the cladocarpous genera of the Orthotrichales and the rest of Leucodontineae and Hypnales (Figs. 24, 25). Further research should include additional species and characters for detailed cladistic analyses within the Orthotrichaceae and the Orthotrichales as presently defined.

In conclusion, cladistic analyses reported here strongly suggest that *Rhacocarpus* and *Bryowijkia* should be excluded from the Hedwigiaceae. This family is here circumscribed to include only the genera *Braunia*, *Hedwigia*, *Hedwigidium*, and *Pseudobraunia*. This monophyletic group is supported by eight synapomorphies. However, the ordinal classification of the family in the Ortho-

trichales and most appropriate outgroups are still weakly supported. The sister group of the Hedwigiaceae appears to be a large clade that includes the cladocarpous representatives of the Orthotrichales, plus the Leucodontineae, and the Hypnales. Undoubtedly most families used as potential outgroups deserve a thorough phylogenetic analysis including more representative taxa. Particularly, the proposed phylogenetic relationships of the Hedwigiaceae help to point out that further comparative work in the Orthotrichaceae is crucial (Vitt, pers. comm.).

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