SYSTEMATICS OF THE BRYOPHYTA (MOSSES): FROM MOLECULES TO A REVISED CLASSIFICATION[1]

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Abstract

Two hundred years of bryological investigations of morphological, anatomical, and developmental characters form the foundation for systematics concepts in mosses, and hence for their classification. With the development of phylogenetic theory and more recently of techniques allowing the extraction of DNA and the amplification and sequencing of specific loci, a new source of characters has become available to test systematic hypotheses. In the last decade over 100 phylogenetic studies of mosses have been published. These have led to the revision of many supraspecific taxonomic circumscriptions. Indeed, many taxa, whether these are genera, families, or orders, have been shown to be paraphyletic or polyphyletic. The revised lineages may satisfy a criterion of monophyly, but in some cases they can no longer be diagnosed using traditional morphological characters. Although phylogenetic inferences are shaping our systematic concepts, the significance of the contributions remains to be tested by future studies. Indeed, several new hypotheses are only weakly supported. Only recently have inferences been made from multiple loci spanning all three genomic compartments, and structural constraints on the evolution of molecules are only beginning to be integrated in analytical assumptions. Here we review most studies that have addressed systematic hypotheses and, based on these results, have amended our recent classification of mosses. The following new taxa are proposed: Takakiopsida (Crand.-Stotl.) comb. et stat. nov., Andreaeaobryopsida (B. M. Murray) comb. et stat. nov., Oedipodiopsida (Schimp.) comb. et stat. nov., Oedipodiales (Schimp.) comb. et stat. nov., Tetraphidopsida (M. Fleisch.) comb. et stat. nov., Scouleriales (S. P. Churchill) comb. et stat. nov., Bryanae (Engl.) comb. et stat. nov., Rhizogonianae (M. Fleisch.) comb. et stat. nov., Rhizogoniales (M. Fleisch.) comb. et stat. nov., and Pylaisiadelphaceae fam. nov.

Key words: Bryophyta, classification, mosses, phylogeny.

The systematics of bryophytes s.l. has undergone a renaissance following the adoption of techniques extracting the phylogenetic signal carried by molecular characters. DNA extraction, RFLP analysis, and PCR-based amplification made their entry into bryological laboratories slowly, and only after the techniques had become routinely applied in mycological and vascular plant laboratories. The slow start may be explained by the difficulty in growing bryophytes in culture and the need, at least in early extraction protocols, for large amounts of material (e.g., one gram), a requirement not easily satisfied by most bryophytes. Now small quantities in the order of a few mg (e.g., a single operculate capsule, or even a section of fresh tissue) may suffice to yield enough DNA to serve as a template for a successful amplification. Although the first phylogenetic study including sequences of bryophytes was published in the mid 1980s (Hori et al., 1985), it took another seven years before the next such research projects were published (Mishler et al., 1992; Waters et al., 1992). Another period of latency followed, until the field of molecular phylogenetic systematics attracted the interest of various bryological laboratories (see Goffinet & Hax, 2001, and Goffinet, 2003, for bibliographies).

Following the annual meeting of the American Bryological and Lichenological Society in Montreal in 1997, research groups coordinated their efforts in addressing the major questions pertaining to the phylogeny of mosses, with the objective of providing a first summary of the potential and the contributions of sequence data to moss systematics at the International Botanical Congress in St. Louis in 1999. The initiative was sponsored by the Green Plant Research Coordination Group led in part by Brent Mishler (University of California, Berkeley). The proceedings of the symposium were published in *The Bryologist* the following year (Goffinet & Hedderson, 2000). All hypotheses that were tested pertained to ordinal or familial relationships. Indeed, few of these studies sampled DNA characters

[1] This study benefited from financial support from the National Science Foundation through a grant to BG (DEB-0089133). Constructive comments on an earlier version of the manuscript by Alain Vanderpoorten (University of Liège, Belgium) are gratefully acknowledged.

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to test phylogenetic hypotheses at the species (e.g., Shaw & Allen, 2000) or population level (Shaw, 2000a).

In the last three years researchers have broadened the scope of their studies, although the focus remains on elucidating the relationships among major lineages of bryophytes. Here we provide a review of the progress made in moss molecular systematics since the last botanical congress, the problems that have surfaced, and the perspectives that the field offers the bryological community. Although molecular markers have been critically explored for their signal to resolve the relationships among lineages of extant land plants, and in particular to test the monophyly of the Bryophyta (i.e., mosses) sensu Buck and Goffinet (2000), reviews of contributions to this field of study are available elsewhere and will not be repeated here (cf. Duff & Nickrent, 1999; Goffinet, 2000).

Molecules and Systematics

The objectives of systematics are to elucidate the relationships among taxa. Taxonomy deals with the recognition of taxa, with the main focus being on species. Two hundred years of bryological studies have led to the recognition of about 12,000 species of mosses (Crosby et al., 2000). Morphological characters have been central to our systematic hypotheses and have been the basis for the most widely adopted species concepts. These characters are the phenotypic expression of a genotype, and the phenotype may vary along an ecological gradient. Furthermore, most characters are continuous in nature rather than binary. Depending on the sample size, and one's knowledge of the group under consideration, the variation may be viewed as patterned or continuous and can determine the taxonomic concepts and consequently our phylogenetic predictions.

Genetic changes serve as another source of characters that can be used to test our hypotheses. The question is not whether they are better, more reliable, and hence more accurate than morphological characters. Indeed, if species are real and the product of evolution, there should be defined fixed changes in their genomes. Hence, the null hypothesis is that if our morphology-based hypotheses are correct, inferences from variation in molecular makers should strengthen them. The outcome of any test can be congruence or incongruence. The debate about the usefulness of molecular markers is fueled by cases of incongruence between the two sources of characters. Although the trend may be for molecular systematists to preferentially adopt the phylogenetic or genealogical pattern as the truth, and hence assume that inferences from morphological characters are misled by incorrect assumptions of homology (i.e., homoplasy), incongruence should, in fact, be the starting point for future research to elucidate the underlying nature of this incongruence. Few systematists engage in testing the stability of the traits under artificial conditions or their homology assumptions of morphological characters (typically based on levels of similarities of the end product of development) by seeking support from the ontogeny of these traits. Similarly, the constraints that shape the evolution of specific loci are often neglected, the orthology (and hence homology) of the sequences is often merely assumed, and the alignment itself may not be dictated by structural features of the gene product. Hence, incongruence can be accounted for by several sources of error. However, if we assume that all these a priori tests for homology were performed, inferences from morphological and molecular data sets may still lead to incongruence. The most likely sources for this may be caused by convergent evolution evident in morphological characters or lateral transfer of genetic material. Morphological reduction may lead to the loss of complex traits that are diagnostic (i.e., synapomorphies) of a lineage. Consequently, the reduced taxa display the symplesiomorphic state. Depending on the extent of the reduction, long branches may characterize these taxa in the true phylogenetic tree, and be pulled to the base in the reconstructed phylogeny. Morphological reduction is likely not paralleled by reversals to ancestral traits in DNA sequences, and hence it is in these cases that lay the potential and the contribution of molecular markers. Reduction may indeed be a common phenomenon in the evolution of bryophytes (Hyvönen et al., 2004). Character loss and neoteny are not the only sources of convergence. Parallel forward evolution (i.e., not reversals) characterize the independent acquisition of phyllodioicy in three subfamilies of the Brachytheciaceae (Huttunen & Ignatov, 2004), and within the Hookeriales a double costa has arisen at least six times and a laminal limbidium at least five times (Buck et al., 2004).

Lateral transfer of genetic material (i.e., hybridization) had been discounted as an evolutionary process shaping bryophyte diversification (Vitt, 1971). Several studies, in particular in *Sphagnum* (Såstad et al., 1999, 2000; Shaw & Goffinet, 2000), the Mniaceae (Wyatt et al., 1988), and the Polytrichaceae (Derda & Wyatt, 2000), have demonstrated the existence of several taxa of hybrid origin. Since hybrids retain discrete portions of their genome

from each parent, topological incongruence is not restricted to morphological versus molecular data, but also to loci from distinct genomic compartments, or maybe even between nuclear loci, if recombination took place following hybridization. The significance of hybridization as a process in bryophyte evolution is not clear, but evidence pointing to its widespread occurrence is growing (e.g., van der Velde & Bijlsma, 2004).

Molecular characters are thought to test homology assumptions made from morphological character states across systematic ranks and evolutionary lineages and, thereby, test morphology-based phylogenetic hypotheses. Here we review the studies aimed at testing the circumscription and relationships of supraspecific taxa of mosses, with a focus on families and orders.

Phylogenetic Reconstructions Among Mosses

early radiation of mosses

The early diversification of mosses is correlated with conspicuous transformations in the mode of sporangial dehiscence and, even more so, in spore dispersal mechanisms (Schofield, 1985). In most mosses the sporangium opens with the loss of an apical operculum, which forms a lid on the capsule. In *Takakia,* dehiscence follows a single spiral longitudinal line, and in the Andreaeopsida and Andreaeobryopsida, four (or sometimes more) straight lines stretch between the poles of the capsules. Among operculate mosses, *Sphagnum* lacks a peristome, whereas the vast majority of remaining mosses have teeth lining the mouth of the sporangium. The lack of a peristome among these derived mosses is considered the result of a reduction (i.e., loss) except maybe for *Oedipodium* (see below). Peristomate mosses and *Oedipodium* share a cylindric columella compared to the dome-shaped columella present in *Takakia,* the Sphagnales, and the Andreaeales, as well as the presence of protonematal side-branch initials (Newton et al., 2000).

Mishler and Churchill (1984) proposed the first formal phylogenetic hypothesis for the mosses. Their sampling did not include *Takakia,* whose affinities to the mosses were still unsubstantiated at the time, or *Andreaeobryum,* which had, however, already been described (Steere & Murray, 1976). Mishler and Churchill (1984) rooted their tree, in the absence of an explicit outgroup, with *Sphagnum.* Following their phylogeny, the following lineages arose sequentially through time: Andreaeales, Tetraphidales, Polytrichales, Buxbaumiales, and ultimately the Bryales. This hypothesis remained unchallenged for over a decade.

Based on variation in 18S (nrDNA), Hedderson et al. (1996, 1998) examined the relationships among the three main lineages of the Bryophyta s.l. Their sampling included nine mosses. They provided the first molecular evidence in support of *Takakia* belonging to the mosses, as suggested by gametangial and sporophytic characters (Smith & Davidson, 1993). Although the mosses were well supported as a monophyletic group, the relationships within this lineage lacked Bremer support. The hypothesis that *Takakia, Andreaea,* and the nematodontous mosses shared a unique common ancestor, and were sister to the arthrodontous mosses, remained tentative at best. Based on the mitochondrial locus *nad*5, Beckert et al. (1999) resolved *Sphagnum* as the most basal bryophyte. *Takakia* was missing from their taxon sampling. The peristomate mosses appeared as polyphyletic, as the Andreaeales were nested between the Polytrichales and the remainder of the peristome-forming mosses. However, the relationships among these major lineages also lacked support. Although Hyvönen et al. (1998) focused on the Polytrichales, they were the first to highlight the phylogenetic significance of *Oedipodium.* Rather than being allied to the Splachnaceae in the arthrodontous mosses as suggested by Vitt (1984), *Oedipodium* was resolved as sister to the Polytrichaceae (see also Hyvönen et al., 2004). This hypothesis has now been corroborated by other studies (Newton et al., 2000; Goffinet et al., 2001; Cox et al., 2004). Whether the absence of a peristome in *Oedipodium* is a true plesiomorphy or results from secondary loss remains unclear (Cox et al., 2004). The sister-group to *Oedipodium* cannot be defined by a single character except the presence of a peristome (Newton et al., 2000)

The first phylogenetic reconstruction to include an exhaustive sampling of ordinal exemplars (orders sensu Vitt, 1984) as well as *Takakia* and *Andreaeobryum* was presented by Newton et al. (2000). Their inferences from data combining sequences of the nuclear and chloroplast genomes and morphology led to an evolutionary scenario wherein *Takakia* and *Sphagnum* form a weakly supported basal lineage, followed by the Andreaeales (including *Andreaeobryum*), and finally those mosses with a cylindrical columella. The position of the Andreaeales between the *Takakia-Sphagnum* clade and the remaining mosses was well supported, but monophyly of the order received, by contrast, only weak support from the data. These hypotheses have most recently been tested by Cox et al. (2004), who inferred the succession of cladogenic events from variation in eight loci from all three genomes, using a set of representative taxa for each major lineage

of mosses sensu Vitt (1984). Their results concur with those of Newton et al. (2000), and, in fact, none of the ambiguities pertaining to the early diversification has been clarified despite this intensive character sampling and the application of distinct models of evolution to discrete partitions of the sequences. The failure to resolve the order of early cladogenic events is not inherent to the genetic data, as inferences from morphology alone also resulted in ambiguous affinities for *Takakia, Andreaea,* and *Andreaeobryum* (Newton et al., 2000). The reconstruction of ancient evolutionary events is problematic not only for mosses, but is a problem that plagues systematists working on flowering plants, invertebrates, and fungi. Much hope is being placed on the exploration of structural features of complete genomes to resolve these impasses (see, for example, Kelch et al., 2004).

EARLY RADIATION OF THE PERISTOMATE MOSSES

As mentioned above, one clear contribution of molecular data to our understanding of moss evolution has been the identification of *Oedipodium* as the sister-group to the peristomate mosses. Based on the primary architecture of the teeth, peristomes are either nematodontous (i.e., composed of whole cells) or arthrodontous (i.e., composed mainly of periclinal walls belonging to the cells of two or three [rarely more] concentric layers of cells of the amphithecium; Vitt, 1984; Schofield, 1985). The Tetraphidales and Polytrichales both have nematodontous peristomes. The two orders differ in the number and size of the teeth (four vs. 16, 32, 64, or more, respectively) and the ontogeny of the peristome. Based on the study by Wenderoth (1931), the development of the peristome of the Polytrichales is considered to be characterized by an early additional anticlinal division, which leads to a doubling of the number of cells in all amphithecial layers compared to other mosses. Furthermore, the divisions in the inner peristomial layer (IPL) all appear to be symmetric in *Polytrichum,* whereas in *Tetraphis* the critical division that leads to 16 cells in the IPL appears, albeit slightly, to be asymmetric (Goffinet et al., 1999; but see Shaw & Anderson, 1988, who argue for a symmetric division). Another sporangial character that distinguishes the two is the lack of air spaces in the Tetraphidales. This character state is shared with other basal lineages (*Takakia, Sphagnum,* and the Andreaeales; Goffinet et al., 2001).

The hypothesis that the nematodontous peristome defines a monophyletic lineage has never been explicitly tested, but instead has always been discussed in the context of moss evolution, and hence has never received the attention of taxon and character sampling that this important question deserves. Mishler and Churchill (1984) proposed that the nematodontous mosses were paraphyletic on the basis of the air space character mentioned above. Vitt (1984: 742–743) considered the peristome of the Polytrichales and Tetraphidales to be developmentally unrelated, and even raised the possibility that the Tetraphidaceae belong to the Bryales.

Inferences from *nad*2 and *nad*5 sequences suggest that the nematodontous mosses are monophyletic (Beckert et al., 2001). Paraphyly is supported by characters from the two other genomes (e.g., Hyvönen et al., 1998; Newton et al., 2000; Magombo, 2003a), although preliminary inferences by Hedderson et al. (in Vitt et al., 1998) from 18S sequences favored the common ancestry for the group. Support for monophyly of the nematodontous mosses (Beckert et al., 2001) seems stronger than that gathered in favor of paraphyly (e.g., Newton et al., 2000). The strength of the support may depend on the parameter chosen to measure it. Cox et al. (2004) showed that the clade comprising the Tetraphidales and the arthrodontous mosses received high posterior probabilities but low bootstrap percentages. This may be congruent with the relative short branches that unite these taxa. Within a paraphyletic scenario the order of evolution also remains ambiguous. Did the evolution of the Polytrichales precede that of the Tetraphidales or vice versa? Although most optimal reconstructions point to the former (except Magombo, 2003a), all the branches of interest are short and support values are virtually lacking. So far, taxon sampling within the Tetraphidales, which includes but five species (Crosby et al., 2000), has been limited to *Tetraphis pellucida* Hedw., and hence inferences are not considering the potential significance of *Tetrodontium.* The resolution of the relationships between the Tetraphidales and Polytrichales is essential for assessing the significance of the nematodontous peristome in the evolution of the arthrodontous teeth. Central to this question is also the position of the Buxbaumiales.

ORIGIN OF THE ARTHRODONTOUS MOSSES

The Buxbaumiaceae and the Diphysciaceae may be considered distinct families (e.g., Brotherus, 1925) or not (e.g., Vitt, 1982, 1984), but in either case they have traditionally been accommodated within a single lineage (e.g., Buxbaumiales by Brotherus, 1925, and Vitt, 1982, or Buxbaumiineae by Vitt, 1984). Although *Buxbaumia* and *Diphys-*

cium differ in a number of characters (see Magombo, 2003a), they share a unique peristomial architecture (Edwards, 1984). The inner peristome consists of a high, pleated membrane. In *Buxbaumia* the number of cells in each amphithecial layer is double that found in *Diphyscium* and most mosses (and is similar to the pattern found in *Polytrichum* (Wenderoth, 1931)), and hence *Buxbaumia* has 32 rather than 16 pleats. In *Diphyscium* the outer peristome is composed of a single row of teeth that is fused to the inner membrane. In *Buxbaumia* the cell walls of one or two outer peristomial layers of cells may be thickened and partially resorbed, and thus may form two rows of teeth, even if the outermost row is rudimentary and remains partially attached to the capsule wall (Edwards, 1984). Finally, in *Buxbaumia* the cells surrounding the outer peristome are entire and extremely thickened. Whether this peristome is homologous to the nematodontous peristome has been much discussed by early workers (see review in Edwards, 1984), and understandably so. Homology of these structures would suggest that the peristome of the Buxbaumiaceae is intermediate between the arthrodontous and nematodontous architectures and hence may mark the transition from one to the other. If the peristome of the Buxbaumiaceae shares anatomical features with the nematodontous teeth due to convergence then the affinities of the Buxbaumiaceae may not lay near the Polytrichales. Vitt (1982), for example, considered the Buxbaumiales to be arthrodontous and later even suggested that this lineage was ancestral to the haplolepideous mosses (Vitt, 1984). Most other workers treated the Buxbaumiales (as orders or suborders) as distinct from the arthrodontous mosses, with close ties to the Polytrichaceae (e.g., Brotherus, 1925) or in a truly intermediate position (e.g., Crosby, 1980; Mishler & Churchill, 1984).

Shaw et al. (1987) demonstrated that the inner peristome in *Diphyscium* is homologous in position to the endostome of arthrodontous mosses and that the development of this membrane follows a pattern identical to that observed in haplolepideous mosses. In fact, these authors concluded that based on morphological and ontogenetic data, *D. foliosum* is fundamentally haplolepideous.

Clearly, ambiguous homologies and overall phenetic isolation have fueled much of the controversy regarding the systematic position of the Buxbaumiales and their phylogenetic significance over the last century and more. Inferences from mitochondrial loci (Beckert et al., 1999, 2001), chloroplast loci (Goffinet et al., 2001), or combined nuclear and cytoplasmic loci (Newton et al., 2000; Cox et al., 2004) suggest that *Diphyscium* is the closest extant relative to the arthrodontous mosses. Hence, the Buxbaumiaceae sensu Vitt (1984) are consistently resolved as a paraphyletic entity, with *Buxbaumia* having evolved prior to the differentiation of arthrodontous mosses from *Diphyscium* (Magombo, 2003a). Goffinet et al. (2001) suggested, on the basis of inferences from the plastid gene *rps*4, that *Buxbaumia* may be closely related to the Tetraphidaceae, but this hypothesis has subsequently been refuted. *Buxbaumia, Diphyscium,* and the arthrodontous mosses share a significant deletion in the *rps*4-*trn*S_{UGU} intergenic spacer (Cox et al., 2004).

The resolution of the sister-group to the arthrodontous mosses could have significant implications regarding the evolution of peristome types in mosses. However, given the paraphyly of the Buxbaumiaceae sensu Vitt (1984), *Diphyscium* can no longer serve as an exemplar for the family. Furthermore, it is impossible on the basis of the phylogeny alone to argue for or against the homology of the peristome and the nematodontous architecture. It is imperative that the ontogeny of the peristome of *Buxbaumia* be described to complete the survey of peristome development.

EARLY DIVERSIFICATION OF THE ARTHRODONTOUS MOSSES

Shaw et al. (1987) argued that the development of the peristome of *Diphyscium* follows a pattern consistent with that of haplolepideous mosses: the division in the inner peristomial layer (IPL) that results in 16 cells is clearly asymmetric, and this division is typically followed by one or, rarely, two more cytokinetic events, resulting in typically 24 cells in the IPL. The peristomial formula (after Edwards, 1984) is 4:2:3, and prior to cell-wall thickening and resorption, the amphithecium of *Diphyscium* and that of the haplolepideous mosses is identical. We now know that this similarity is not indicative of close affinities between these taxa but should instead be viewed as evidence that the 4:2:3 pattern and the asymmetry of the IPL division is plesiomorphic in mosses. If so, is the haplolepideous condition basal among the arthrodontous mosses?

The Bryopsida sensu Buck and Goffinet (2000) accommodate nearly 12,000 species, which can be arranged into three groups based on their peristomial architecture (Philibert, 1884–1890, and translated by Taylor, 1962). The haplolepideous peristome or *Dicranum*-type peristome is defined by the endostome segments being composed of a single column of cell plates on their outer surface. The

division in the IPL that leads to the 16-cell stage is asymmetric (Shaw et al., 1989b). The exostome is highly reduced and most often completely lacking. By contrast, the exostome is characteristic of the diplolepideous mosses, but the term "diplolepideous" refers not to the two rings of teeth, but to the two columns of dorsal plates on the outer teeth. Two main types of diplolepideous peristomes can be recognized, and these are typified by the peristomes of *Funaria* and *Bryum*. In the former, the endostome segments are positioned opposite the exostome teeth (diplolepideous opposite peristome), whereas in the latter, the teeth and segments alternate (diplolepideous alternate peristome). Furthermore, the IPL undergoes a symmetric division in *Funaria* (Shaw et al., 1989a; Schwartz, 1994), whereas in *Bryum* that division is clearly asymmetric (Shaw et al., 1989a). The *Bryum*-type peristome differs further by the presence of cilia between the segments and hence positioned opposite the outer teeth (Vitt, 1981).

The relationships among the haplolepideous, diplolepideous alternate, and diplolepideous opposite mosses have been inferred implicitly on the basis of these peristomial features (e.g., Vitt, 1981, 1984). However, as pointed out by Vitt et al. (1998), these characters alone fail to yield a robust hypothesis because (1) there are too few characters, (2) lineages are defined by character combinations and not individual characters, and, hence, (3) individual characters are incongruent among themselves. Thus, it is not surprising that the relationships within the Bryopsida remained unresolved.

Most inferences from cytoplasmic genome-encoded protein loci suggest that the diplolepideous mosses are paraphyletic, with the haplolepideous mosses forming a sister-group to those species with a *Funaria*-type peristomial architecture and the Encalyptaceae (hypothesis I; e.g., Beckert et al., 1999, 2001; Goffinet & Cox, 2000; Goffinet et al., 2001). Under this scenario, the haplolepideous mosses and the *Funaria*-type peristomate mosses would share an opposite arrangement of their peristomes (Vitt et al., 1998; Goffinet et al., 2001). By contrast, inferences from nuclear-encoded genes (Hedderson et al., 1996; Capesius & Stech, 1997) resolve the haplolepideous mosses as sharing a common ancestor with the diplolepideous alternate mosses (i.e., those with a *Bryum*-type peristome; hypothesis II); here the asymmetric division in the IPL serves as a synapomorphy linking the haplolepideous mosses to a group of mosses with diplolepideous peristomes. When the data are combined the overall signal is ambiguous and may favor the first (Goffinet & Cox, 2000) or the second hypothesis (Cox et al., 2000, 2004; Newton et al., 2000).

Paralleling the ambiguity of the relationships among these main lineages of the Bryopsida is the uncertainty regarding the affinities of *Timmia*. The peristome of *Timmia* is double, and its architecture is clearly that of a diplolepideous moss as the dorsal surface of each exostome tooth is derived from two columns of cells (Murphy, 1988). However, its endostome differs from the typical *Funaria*-type or *Bryum*-type in that it is divided into 64 segments, which are reminiscent of cilia. Vitt (1984) and others must have considered this peristome to be derived from a *Bryum*-type situation because *Timmia* is historically included in the Bryales or Bryineae, depending on the classification scheme. The hypothesis that *Timmia* is a member of the Bryales sensu Vitt (1982) or Crosby (1980) is refuted by all phylogenetic analyses of DNA sequences. Hypotheses regarding its precise affinities are, however, incongruent among the various studies. *Timmia* has been reconstructed as basal among arthrodontous mosses (Goffinet & Cox, 2000 [their combined data set]; Tsubota et al., 2003 [*rbc*L]), as sister to the Dicranales-Funariales-Encalyptales clade or sister to only the Funariales based solely on cytoplasmic DNA (Beckert et al., 1999, 2001; Goffinet & Cox, 2000; Goffinet et al., 2001), or as marking the transition between the Funariales and the remaining arthrodontous mosses when the phylogenetic signal of genomic markers is combined (Cox et al., 2000; Newton et al., 2000).

Although it is evident that a formal reconstruction of peristome transformations should not be done in the absence of a robust phylogeny, it is not clear to what extent *Timmia* will be informative toward elucidating the evolution of peristome types. Indeed, the interpretation of evolutionary trends will be biased by the a priori homology assumptions that are made. Are the "cilia" of *Timmia* homologous to those of *Bryum*? Are the segments of *Funaria* and *Bryum* analogous and derived independently through fusion of the "cilia" of *Timmia*? Cox et al. (2004) considered the peristome of *Timmia* to be of the opposite diplolepideous type and concluded, given the basal position of the genus, that this peristome type was plesiotypic and hence ancestral to the diplolepideous alternate type. The underlying assumption of this hypothesis needs to be substantiated.

Molecular data may be essential for providing the underlying phylogenetic hypothesis, but developmental characters are imperative, although not sufficient, to clarify homology assumptions between the peristome of *Timmia* and other arthrodontous

mosses. The early radiation of arthrodontous mosses remains basically unresolved. The incongruence among studies may be caused by (1) inconsistencies in the taxon sampling, and hence be an artifact of the analyses, (2) lack of a strong phylogenetic signal in one or more data partitions, (3) inappropriate assumptions regarding the models of evolution of the partitions, or (4) reflect true incongruence between genomes due to lateral gene transfer. This final hypothesis (the fourth) seems likely considering the congruence among cytoplasmic genomes, and their incongruence with nuclear DNA. To test for ancient hybridization, inferences from nuclear, mitochondrial, chloroplast, and combined loci must be compared for identical sets of taxa. So far, such analyses are lacking.

SYSTEMATICS OF MAJOR LINEAGES OF MOSSES

Reconstruction of the backbone phylogeny of mosses has only consumed a portion of the efforts invested in inferring phylogenies from molecular data. Many studies focus on individual lineages and, increasingly, on the relationships within orders and families. Although the taxonomic spectrum covered continues to expand, notable gaps exists, such as the lack of investigation in the Andreaeales sensu Vitt (1984).

The following review aims at being comprehensive but will not include an in-depth discussion of the implications in terms of morphological evolution for all aspects of the phylogenies that have been proposed. Except for the Sphagnaceae and Polytrichaceae, generic or infrageneric relationships will not be addressed, unless genera are identified as polyphyletic based on DNA data.

The Sphagnaceae

The peatmosses comprise two genera, *Sphagnum* and *Ambuchanania*. The latter is monospecific and is based on *S. leucobryoides* Yamaguchi, Seppelt & Z. Iwats. (Yamaguchi et al., 1990), for which the original authors erected the section *Buchanania* within *Sphagnum*. This species is morphologically isolated within the genus, and Crum and Seppelt (1999) subsequently established a new genus, family, and even order within the Sphagnopsida (Crum, 2001). Whether the elevation of *S. leucobryoides* to the rank of genus or above results in *Sphagnum* being paraphyletic has been tested only once: Shaw (2000b) obtained partial sequences for the 26S gene (nrDNA) for *Ambuchanania*. His inferences resolve *Ambuchanania* as sister to the remainder of *Sphagnum* and thereby are congruent with the systematic concept of Crum and Seppelt (1999).

Given that some sequences (e.g., *psb*T and 26S) yielded insufficient variation to yield either resolution or support of the infrageneric phylogeny of *Sphagnum*, the sampling of molecular characters was extended and more taxa were included (Shaw, 2000b). In an unrooted tree four main clusters could be recognized. The cores of these groups correspond to the sections *Acutifolia*, *Cuspidata*, *Sphagnum*, and *Subsecunda* within *Sphagnum*. Smaller sections (e.g., sects. *Squarrosa* and *Rigida*) were synonymized, although their position in the combined tree did not violate the monophyly of larger sections (sects. *Acutifolia* and *Sphagnum*, respectively). Shaw et al. (2003a) subsequently focused on the backbone phylogeny of *Sphagnum* in order to polarize morphological character transformations, and to identify the sister group to section *Acutifolia*, which is the focus of their current research. Unfortunately, due to the scarcity and maybe the age of the original material (pre 1990), Shaw et al. (2003a) were not able to use *Ambuchanania* to root their reconstruction of *Sphagnum*. Their inferences were based on an unprecedented 16 loci composing a matrix with nearly 16,000 characters (yielding 712 parsimony informative characters) sampled for 24 species. Based on a preliminary analysis, constructed with approximately 10,000 characters and using *Takakia* and *Andreaea* as the outgroups, they identified *S. sericeum* Müll. Hal. and *S. lapazense* H. A. Crum as basal taxa in *Sphagnum*. In the rooted tree, these two species form a grade. They are consistently (i.e., for every locus) well differentiated from other Sphagna, and at least *S. sericeum* had been considered a potential candidate for an ancestral position in the genus. However, in his previous study Shaw (2000b) tentatively concluded that *S. sericeum* was a member of section *Acutifolia*. His caution, which proved justified (Shaw et al., 2003a), was based on the fact that only one locus (i.e., ITS) had been sequenced for this species and that hybridization, although not verified for this taxon, has been demonstrated as an evolutionary process within the genus (Shaw & Goffinet, 2000).

The relationships among the main sections of *Sphagnum* could not be resolved or well supported due to the paucity of characters in the data set (see fig. 1 in Shaw et al., 2003a). The inclusion of additional and more variable regions whose alignment is less unambiguous within the ingroup, and rooting the tree with *S. sericeum* and *S. lapazense*, the remainder of the Sphagna compose two major lineages that were well supported by posterior probabilities but lack bootstrap support (see fig. 2 in Shaw et al., 2003a). The first lineage comprises the

sections *Sphagnum*, *Rigida*, and *Cuspidata*. Their monophyly is well supported but their relationships are not. Similarly the relationships among three sections in *Sphagnum* (i.e., *Acutifolia*, *Squarrosa*, and *Subsecunda*) composing the second lineage are ambiguous, and the affinities of *S. wulfianum* Girg. (sect. *Polyclada*) within this clade are unresolved. Whether the basal branches can be characterized by transformations in morphological characters, and hence whether the suprasectional clades can be defined by synapomorphies, remains to be addressed. The various studies by Shaw and colleagues have laid the foundation for future in-depth work on discrete sections of *Sphagnum*, and also have set what may soon or should become a standard in character sampling.

The Polytrichaceae

The Polytrichaceae share "a well developed conducting system, differentiated above-ground and below-ground portions and a complex leaf structure" (Vitt, 1982: 308), and to these could be added thigmotropism (Newton et al., 2000). All these characters, however, may not represent synapomorphies.

The complex leaf structure mentioned by Vitt (1982) likely refers to the presence of photosynthetic lamellae on the adaxial surface of the leaves. The sole comprehensive phylogenetic reconstruction of the family by Hyvönen et al. (1998) suggests that these structures evolved after the early diversification of the group, and hence serves to unite a clade within the family rather than characterize the family as a whole. Hyvönen et al. (1998) based their inferences on variation in a nuclear locus (18S), a chloroplast gene (*rbc*L), and morphological characters. Support for the monophyly of the family is drawn primarily from *rbc*L data. The 18S data set comprises few parsimony informative sites, and the morphological characters appear highly homoplastic and their analysis yields no resolution from other peristomate mosses used as outgroups. Similarly, support is lacking for relationships within the ingroup, except after successively weighting transformations, and then only for generic monophyly or a sister-group association between *Bartramiopsis* and *Lyellia*. Hence, no informative evolutionary interpretation could be made from their analyses. Broadening the character sampling to the *trn*L-*trn*F region (cpDNA) and partial sequences of the *nad*5 locus (mtDNA) and including more taxa led the total evidence analyses to converge on two most parsimonious trees (Hyvönen et al., 2004). Although the hypotheses of monophyly must be rejected for several genera (i.e., *Oligotrichum*, *Polytrichastrum*, *Pogonatum*, and *Polytrichum*), based on the criterion of maximum parsimony, the incongruence among characters seems significant considering the overall low bootstrap values characterizing most nodes. Moderate support characterizes the branch that separates the core of the Polytrichales from a basal grade composed of *Alophozia*, *Atrichopsis*, *Bartramiopsis*, and *Lyellia*. *Alophozia* and *Atrichopsis* compose a lineage sister to the remainder of the order. They lack the ventral lamellae that are typically seen as diagnostic of the Polytrichales. Thus, it is hypothesized that these structures were acquired after the early diversification of the Polytrichales, and hence cannot serve as a synapmorphy for the lineage.

The Diphysciaceae/Buxbaumiaceae

The Buxbaumiaceae as defined by Vitt (1984) are clearly paraphyletic, and *Diphyscium* appears as the sister-group to the arthrodontous mosses (Magombo, 2003a). The Buxbaumiaceae s. str. are monogeneric, whereas the Diphysciaceae traditionally included three genera. *Muscoflorschuetzia* and *Theriotia*, however, are resolved in a nested position within *Diphyscium*. The former is gymnostomous, and multistratose leaves distinguished the latter. Both these conditions must be interpreted as of late derivation. Hence, recognition of these genera as distinct taxonomic entities should be abandoned as proposed by Magombo (2003b; cf. Appendix 1 herein).

Phylogeny of the Funariales

Within the Funariales, Vitt (1982; or suborder in Vitt, 1984) included the Funariaceae, Disceliaceae, Pseudoditrichaceae, Gigaspermaceae, and Ephemeraceae. A single study (Goffinet & Cox, 2000) focused on the circumscription and phylogeny of this lineage. The affinities of the Pseudoditrichaceae have not yet been tested using DNA sequences, but Shaw (1984) interpreted the peristome as of the *Bryum*-type and hence transferred the family to the Bryales. *Goniomitrium* and *Ephemerum* have been transferred to the Pottiales by Goffinet and Cox (2000), and should be considered members of the Pottiaceae (cf. Appendix 1 herein). Neither of these taxa shares a deletion of one codon in the *rps*4 gene that is characteristic of the Funariaceae (Goffinet & Cox, 2000). The Funariales are best defined by the architecture of the leaf, and although *Discelium*, the Gigaspermaceae, and several Funariaceae are gymnostomous, all these taxa may share with peristomate Funariaceae a pattern of cell division in

the amphithecial layer wherein the divisions that lead to a 16-celled IPL are symmetric (Rushing & Snider, 1980; Shaw & Allen, 1985; Shaw et al., 1989a; Schwartz, 1994; Goffinet et al., 1999).

The Funariales may be most closely related to the Encalyptales. Morphological support for a shared ancestry is lacking given the highly divergent gametophytic and sporophytic architecture (Vitt, 1982, 1984), but may be found in the development of the amphithecium. Goffinet et al. (1999) considered the division in the IPL in *Encalypta* to be symmetric as in the Funariales, but ontogenetic evidence for this hypothesis has not been published.

The Catascopiaceae, a monospecific family traditionally placed in the Bryales (Vitt, 1984), was resolved within the Funariales-haplolepideous clade based on *rps*4 data (Goffinet et al., 2001). The diplolepideous peristome of *Catoscopium* is composed of an endostome that is reduced to a low hyaline membrane. The architecture of the peristome is, therefore, not informative to assess the ordinal affinities of *Catoscopium*. Virtanen (2003) further demonstrated that *Catoscopium* did not belong to the Bartramiaceae (Griffin & Buck, 1989). Inferences from three combined chloroplast loci resolved the genus as sister to the Bryales s.l., but analyses of the *rbc*L or the *trn*L-*trn*F sequences place it in the diplolepideous alternate mosses (Virtanen, 2003). None of these hypotheses is, however, well supported.

No study has yet focused on the infrafamilial relationships within the Funariaceae. Based on a limited sampling, the results by Goffinet and Cox (2000) suggest that, within the Funariaceae, *Funaria* and *Entosthodon* are polyphyletic, and that *Physcomitrella* may not warrant segregation from *Aphanorhegma*. That this family has escaped the attention of molecular systematists is surprising. Indeed, the taxa are easily grown in culture, the complete genome of *Physcomitrella* is being sequenced (Rensing et al., 2002), and the peristome evolution is characterized by severe, but maybe gradual reduction, leading to multiple gymnostomous taxa. Hence, the Funariaceae may be a model system for testing hypotheses on peristome evolution within the diplolepideous mosses, such as the untested assumption that peristome loss may be irreversible.

The circumscription of the Funarialean lineage is still tentative, and the affinities of the Encalyptales and Timmiales are in need of more critical studies. Since increasing the character sampling has not settled the ambiguity (Cox et al., 2004), efforts should perhaps be directed at broadening the species representation, especially in recognition of the phylogenetic significance of gymnostomous taxa (e.g., *Oedipodium* basal to all peristomate mosses).

Phylogeny of the haplolepideous mosses

Mosses with a haplolepideous peristome compose a monophyletic lineage that is well supported by molecular data (La Farge et al., 2000; Newton et al., 2000; Beckert et al., 2001; Tsubota et al., 2003; Werner et al., 2004). The circumscription of this lineage has been extended to accommodate several taxa with reduced peristomes that were previously considered of diplolepideous affinities based on gametophytic features. Goffinet et al. (1998) provided evidence from *rbc*L data that *Drummondia,* the Erpodiaceae, and the Rhachitheciaceae belong to the Dicranineae sensu Vitt (1984) rather than the Orthotrichineae. Their study also led to the transfer of *Amphidium* to the haplolepideous mosses, a hypothesis later supported by Stech (1999a). *Ephemerum, Goniomitrium,* and *Splachnobryum* were also resolved within the haplolepideous clade rather than with the Funarineae based on nuclear or cpDNA data (Goffinet & Cox, 2000). Heddersen et al. (2004) excluded *Bryobartramia* from the Dicranales and suggested that it may be a derived member of the Encalyptaceae. Inferences from nuclear and chloroplast sequences revealed that *Wardia* and *Schistostega* should be aligned within the haplolepideous mosses rather than with the Leucodontineae or Bryineae among the diplolepideous alternate mosses (Cox & Hedderson, 1999; Hedderson et al., 1999; Tsubota et al., 2002). Similarly, *Archidium,* which Vitt (1982, 1984) considered as the basalmost lineage among arthrodontous mosses, has been shown to be instead nested within the haplolepideous mosses (Goffinet & Cox, 2000), although its affinities remain ambiguous (Goffinet et al., 2001). Vitt's (1984) hypotheses that the Buxbaumiaceae and Encalyptaceae are basal lineages within the haplolepideous mosses have been refuted (see discussion above). Similarly, Stech et al. (2003b) inferred the ordinal affinities of *Pulchrinodus* based on cpDNA data and transferred the genus to the diplolepideous mosses, where its relationships remain obscure.

The significance of molecular data resides in its ability to test systematic hypotheses pertaining to the affinities of taxa that are patristically distant from most typical lineages. All phylogenetic reconstructions resolve a group of three genera at the base of the evolutionary tree of the haplolepideous mosses: *Drummondia, Scouleria,* and *Bryoxiphium.* Not only had *Drummondia* been placed by Vitt

(1984) and others in the Orthotrichales, but affinities to neither of the two other genera had ever been proposed. This is hardly surprising considering their highly divergent gametophytes, sporophytes, and even habitats (Vitt, 1982). The precise relationships among the three genera and the remainder of the haplolepideous mosses remain ambiguous (Hax & Goffinet, unpublished), although *Drummondia* and *Scouleria* are often resolved as sister-taxa (e.g., Tsubota et al., 2003). No morphological synapomorphy is readily obvious for any association that involves these genera. It is likely that much of the morphological transformation occurred well after the origin of the taxa and that the synapomorphies have been lost. Although these genera may not be very informative in terms of polarization of morphological character transformations at the base of the haplolepideous mosses, they may be essential for the proper rooting of the core of this lineage.

Six studies have focused exclusively on the phylogeny of the haplolepideous mosses: Stech (1999b), La Farge et al. (2000, 2002), Tsubota et al. (2003), Hedderson et al. (2004), and Werner et al. (2004). In all cases, inferences were made from variation in cpDNA loci. Stech (1999b) reconstructed the relationships based on *trn*L-*trn*F sequences only. Support for the relationships was poor and lacking for the ingroup (i.e., Dicranaceae), subfamilies, and shallower nodes. The remaining studies differ mainly in their taxon sampling because, except for Tsubota et al. (2003), inferences were made at least in part from *rps*4. La Farge et al. inferred the phylogeny also from *trn*L (2000, 2002) and *rbc*L (2000), whereas Tsubota et al. (2003) relied exclusively on the phylogenetic signal contained in the *rbc*L sequences. The relationships among the major lineages are consistently poorly supported, and thus, although these may be correct, further evidence is needed to corroborate the observed phylogenetic pattern. However, these studies resolve three major clades within the haplolepideous mosses. The first one is composed of the core families Dicranaceae, Leucobryaceae, and Calymperaceae, whereas the second includes the Pottiaceae as a crown group, subtended by the Erpodiaceae, and maybe also the Rhachitheciaceae, Ditrichaceae, and Rhabdoweisiaceae. The third lineage comprises the Grimmiales and Seligeriales. The monophyly of the first two main lineages remains to be asserted. In all cases the Seligeriales are sister to the Grimmiales. This hypothesis, which was also proposed by Vitt (1984), is particularly well supported by inferences from *rbc*L sequences (Tsubota et al., 2003). A shared ancestry for the Calymperaceae and Pottiaceae, as proposed by Vitt (1984), is thus not supported by these studies. The phylogenetic significance of the Fissidentaceae within the Dicranales is ambiguous.

Phylogenetic relationships among orders of haplolepideous mosses have never been inferred from morphological characters alone, and the implicit hypothesis proposed by Vitt (1984) is not supported by synapomorphies for sister-groups. Similarly, none of the studies based on molecular data offered morphological transformations that correlate with early cladogenic events. It is likely that major lineages of haplolepideous mosses, and hence of all mosses, have a relative ancient origin that may date back a couple of hundred million years, and any synapomorphies have been erased by subsequent modifications. Considering that mosses are of a rather simple morphology, neither the gametophyte nor the sporophyte offers many characters that could be targeted by selection, and hence adaptive pressures act on a small set of features. However, there is hope that ontogenetic data, such as the protonematal developmental studies carried out by Duckett and his collaborators (see Duckett et al., 2004), may yield characters to support the phylogenetic hypotheses derived from molecular studies for the arthrodontous mosses, similar to those scored by Newton et al. (2000) to complement the sequence data used to reconstruct the phylogeny of all mosses.

The chloroplast loci used by La Farge, Hedderson, and their coauthors provide strong support for several lineages that correspond to families as defined by Vitt (1984), but whose circumscription requires nevertheless some significant amendments. Most notably is the polyphyly of the Dicranaceae sensu Vitt (1984). Following La Farge et al. (2002), the family should include *Wardia* and the Dicnemonaceae, but exclude several other taxa, such as *Campylopus,* which is transferred to the Leucobryaceae, as well as many genera characterized by smaller gametophytes, most of which are best accommodated within the Rhabdoweisiaceae. The circumscription of the Pottiaceae, the only other family specifically targeted (Werner et al., 2002, 2004), underwent fewer changes. The genera included by Vitt (1984) or Zander (1993), except for *Timmiella,* share a common ancestor, but Werner et al. (2004) confirmed that to satisfy a criterion of monophyly, the family must also include the genera transferred earlier by Goffinet and Cox (2000), namely, *Ephemerum, Goniomitrium,* and *Splachnobryum.* Affinity of *Ephemerum* with the Pottiaceae is supported by their shared mode of protonematal development (Duckett et al., 2004). The Seligeriaceae and the

Grimmiaceae appear as monophyletic, whereas the Ptychomitriaceae are resolved by Tsubota et al. (2003) as a polyphyletic group. Based on *rbc*L data, *Glyphomitrium* appears nested within the Rhabdoweisiaceae (Tsubota et al., 2003). Whether *Campylostelium* belongs to the Ptychomitriaceae or Grimmiaceae is not clear (Tsubota et al., 2003).

All the above hypotheses are derived from analyses of chloroplast data. Given that all phylogenetic hypotheses may reflect the evolution of this genome rather than the species sampled, independent testing using nuclear loci is imperative. Spagnuolo et al. (1999) inferred phylogenetic relationships among pottiaceous taxa from variation in the ITS1 (nrDNA) locus, but other ribosomal RNA-encoding genes, which may be better suited for testing hypotheses at suprageneric and familial levels, have not yet been used. Extending the sampling to other loci and genomes may yield the level of variation needed for obtaining robust support for the series of cladogenic events. The speciose families Fissidentaceae and Grimmiaceae have not yet received any attention from molecular systematists.

Phylogeny of the diplolepideous alternate mosses

The diplolepideous alternate peristome is shared by those acrocarpous mosses traditionally defined as the Bryales (Vitt, 1982) or Bryineae (Vitt, 1984), as well as all pleurocarpous lineages (i.e., Hypnidae). Acrocarpous lineages consistently fail to compose a monophyletic lineage that is sister to the pleurocarpous mosses, and one question that has driven much of the interest on this group is to resolve the origin of the pleurocarps (e.g., De Luna et al., 1999, 2000).

The circumscription of the Bryineae sensu Vitt (1982) underwent some revisions in recognition of phylogenetic inferences. The Splachnaceae were considered by Vitt (1984) and earlier workers as allied to the Funariineae or intermediate between it and the Bryineae. Inferences from chloroplast and nuclear data suggest that the Splachnaceae compose a lineage of derived bryalean mosses. The endostome is retained only in the genus *Splachnum*: it lacks cilia, and the segments lay opposite the exostome teeth to which they are fused. This opposite arrangement prompted Vitt (1982, 1984) to consider an early origin of this family. The development of the amphithecial layers is, however, congruent with a bryalean origin (see Goffinet et al., 1999, for an interpretation of the developmental data provided by Schwartz, 1994). The Splachnaceae appear indeed most closely related to the Meesiaceae, including *Leptobryum* based on molecular characters (Cox & Hedderson, 1999; Goffinet et al., 2001).

The Orthotrichaceae sensu Goffinet and Vitt (1998) share a distinct architecture of the peristome wherein the outer peristomial layer is highly thickened and the endostome lacks cilia. These characters formed the basis for Vitt's (1981, 1984) argument to retain the Orthotrichaceae outside of the Bryineae. Phylogenetic evidence for this hypothesis is lacking, as the Orthotrichaceae are consistently resolved in a somewhat nested position near the base of the Bryineae (Cox & Hedderson, 1999; Cox et al., 2000; Newton et al., 2000; Goffinet et al., 2001). Hence, the peristome is better considered as derived from the *Bryum* peristome, as suggested by developmental data (Goffinet et al., 1999). The circumscription of the family has been revised (Goffinet & Vitt, 1998) following the phylogenetic study by Goffinet et al. (1998), which led to the exclusion of several taxa, now accommodated within the haplolepideous or pleurocarpous mosses (Goffinet, 1998; Goffinet & Vitt, 1998).

The Hedwigiaceae contain few species (Crosby et al., 2000). The lack of a peristome precludes an unambiguous supraordinal assignment. The perichaetia can be terminal on stems or branches (Vitt, 1982). Vitt (1982, 1984) placed the family among the pleurocarpous mosses, probably because the leaves are ecostate, a feature extremely rare among acrocarpous arthrodontous mosses. Note that *Bryowijkia,* which has a short costa and a poorly developed peristome, may not belong to this family (Cox, pers. comm.). Inferences for *Hedwigia* support the hypothesis that the family belongs to the diplolepideous alternate mosses, with stronger affinities to the acrocarpous lineages (Goffinet et al., 1998; Cox et al., 2000, 2004; Newton et al., 2000). A nested position within the Orthotrichaceae (De Luna, 1995) is, however, not supported by molecular data (Goffinet et al., 1998; Cox & Hedderson, 1999). The Rhacocarpaceae seem to be closely allied to the Hedwigiaceae (Frahm et al., 1997).

The familial relationships within the Bryineae remain ambiguous. Inferences from one nuclear (18S) and two chloroplast loci (*trn*L-*trn*F, *rps*4) provide strong support for main lineages, some of which corresponded to families, but not for their affinities (Cox & Hedderson, 1999). Broadening the character (*rbc*L) and taxon sampling did not improve the level of confidence with regard to individual nodes (Cox et al., 2000). From these studies *Orthodontium* emerges as the acrocarpous Bryalean moss most closely related to the pleurocarps. Multigenomic inferences, based on eight loci for a restricted sampling of taxa, yielded little support for

this hypothesis (Cox et al., 2004), but this may be due to (1) low taxon sampling among Bryalean mosses, and (2) exclusion of potential informative regions due to ambiguous homology of DNA regions across all mosses.

Although the Bryineae are characterized by their acrocarpous development of perichaetia, several families exhibit perichaetia produced on short lateral branches. The Spiridentaceae, Hypnodendraceae, Pterobryellaceae, Cyrtopodaceae, Hypopterygiaceae, and Racopilaceae all have creeping stems and lateral sporophytes (Vitt, 1982), yet their position in classifications is inconsistent. Vitt (1982, 1984) and Buck and Vitt (1986) regarded the Spiridentaceae as a member of the Bryineae or its equivalent taxon. The Hypnodendraceae were placed in the Bryineae or Bryales by Vitt (1984) and Vitt (1982), respectively, but then moved to the Hypnales (Buck & Vitt, 1986). The Pterobryellaceae were treated as Leucodontalean taxa by Vitt (1982, 1984), but with Hypnalean affinities by Buck and Vitt (1986). The Cyrtopodaceae were also considered pleurocarpous mosses and placed in the Leucodontales (or its equivalent; Vitt 1982, 1984; Buck & Vitt, 1986). Vitt (1982, 1984) placed the Racopilaceae in the Hypnales, but Buck and Vitt (1986) regarded the family to have a Bryalean origin and to be closely related to the Hypopterygiaceae. The latter was placed in the Hookeriales by Vitt (1982, 1984) before being transferred to the Bryales by Buck and Vitt (1986). Inferences from chloroplast loci have shown that all these families, with the exception of the Hypopterygiaceae, are not nested within the main lineage of pleurocarps and are instead of Bryalean origin (Withey, 1996; De Luna et al., 1999; Buck et al., 2000; Goffinet et al., 2001). Whether this lineage of Bryalean pleurocarps may be a sister-group to the true pleurocarps and hence share a common ancestor and thus be regarded as an early derivation within the pleurocarps is not fully resolved (Buck et al., 2000; De Luna et al., 2000; Tsubota et al., 2002). Inference from *rbc*L sequences are incongruent with that hypothesis unless they are combined with morphological data (De Luna et al., 1999). The Hypopterygiaceae are consistently resolved as a sister to the Hookeriales by these studies (Buck et al., 2000), and this hypothesis is corroborated by nuclear and mitochondrial data (Buck et al., 2004). The affinities of the other families to the Bryales raise the question about possible multiple origins of pleurocarpy. La Farge-England (1996) considered all these families (except the Pterobryellaceae, which she did not study) to be pleurocarpous based on her stringent definition of pleurocarpy. Pleurocarpy would thereby have arisen twice. In neither clade is there evidence of reverse evolution and pleurocarpy appears to result from an irreversible transformation.

DNA sequence data have also provided the basis to test generic circumscription and relationships within the Bryineae sensu Vitt (1982) or Bryales (cf. Appendix 1). The Splachnaceae are best known for some of its species that occur on substrates of animal origin and that rely on insects to disperse their spores. Much of the classification of the family was based on sporophytic characters, of which many could be considered linked to the dispersal strategy. Inferences from cpDNA suggest that several supraspecific concepts did not satisfy a criterion of monophyly (Goffinet & Shaw, 2002; Goffinet et al., 2004a). *Brachymitrion* Taylor was placed in synonymy with *Tayloria*, and the Voitioideae were transferred to the Splachnoideae within the Splachnaceae. Lineages resolved as monophyletic based on DNA evidence do, however, lack any non-homoplasious morphological synapomorphy.

Within the core clade of Bryalean mosses, Cox and Hedderson (1999) have further shown that the Bryaceae are polyphyletic, and that the genera around *Pohlia* form a monophyletic lineage within the Mniaceae. This and other studies (Cox & Hedderson, 2003; Pederson & Hedenäs, 2003; Pedersen et al., 2003) have further shown that the speciose genus *Bryum* is polyphyletic if some of its segregates are considered distinct at the generic level. Modifications of the peristome may define monophyletic entities, but the taxa with the ancestral state compose a grade in the Bryaceae. Hence, peristomial architecture is not a reliable phylogenetic indicator. *Orthodontium* is consistently resolved outside of the Bryaceae and seems to be more closely related to the immediate ancestor to the pleurocarps (Cox & Hedderson, 1999; Cox et al., 2000; Goffinet et al., 2001), although its precise affinities remain ambiguous (Cox et al., 2004).

Reconstructions within the Orthotrichaceae (Goffinet al., 1998) revealed the polyphyly or paraphyly of several taxa (e.g., the Zygodontoideae, *Zygodon* and *Orthotrichum*) and some of these observations have been integrated into a new classification (Goffinet & Vitt, 1998). Analyses of nuclear and mitochondrial loci have corroborated the earlier conclusions and further systematic changes have been made (Goffinet et al., 2004b). From these it appears, as is the case of the Amblystegiaceae (see section on pleurocarp phylogeny), that neither sporophytic nor gametophytic characters are consistently informative about relationships across the family. The phylogeny inferred from molecular data

is consistent with the gametophytic differentiation of *Codonoblepharon* and *Leratia* and supports the rejection of segregate genera solely on the basis of sporophytic characters (e.g., *Bryodixonia* Sainsbury, *Muelleriella* Dusén, and *Leptodontiopsis* Broth.). Furthermore, the morphological similarities between *Orthotrichum exiguum* Sull., *Bryomaltaea* Goffinet, and *Leratia* are shown to result from shared ancestry rather than convergent evolution; hence, all three taxa are now accommodated within *Leratia* (Goffinet et al., 2004b).

Among the diplolepideous mosses, the Bartramiales sensu Vitt (1982) appears as a somewhat isolated lineage due to its globose capsules and the typically prorulose cells. The Bartramiaceae are the only family whose circumscription has remained stable following phylogenetic investigations (Virtanen, 2003), although she confirmed that *Catoscopium*, which had been transferred to the Bartramiaceae by Griffin and Buck (1989), should be excluded from the family as suggested by the results of Goffinet et al. (2001). The genera *Bartramia* and *Philonotis* appear paraphyletic, but overall support is weak to moderate, even if morphological data are added to the sequences (Virtanen, 2003).

The contribution of molecular data to the systematics of the Bryineae sensu Vitt (1984) lay particularly in the recognition that the acrocarpous mosses with a diplolepideous alternate peristome compose a paraphyletic assemblage that includes the Splachnineae, Orthotrichineae, and all the so-called Bryalean pleurocarps, and that the evolution of this grade leads to the pleurocarpous mosses. Although the loci sampled so far help define the circumscription of the families and hence to identify natural lineages, much further work is needed to determine the sequence of cladogenesis within this grade, and in particular the sister-group to the pleurocarps.

Circumscription of pleurocarpous mosses

Perichaetia arising from lateral buds rather than at the apex of differentiated branches and stems characterize the pleurocarps. As discussed above, pleurocarpy per se does not suffice to define this clade. Hedenäs (1994) suggested that this clade may be better diagnosed by a homogeneous costal anatomy. However, this character too may not be unique to pleurocarps, and perhaps the clade is best defined by a combination of both characters.

Although long seen as a natural lineage, this clade lacked a name until Buck et al. (2000) erected the Hypnidae to accommodate them. The monophyly of the Hypnidae is well supported by molecular data (e.g., Tsubota et al., 2002). Three main lineages of pleurocarpous mosses have traditionally been recognized based among other characters on peristomial architecture and type of modular growth or branching (Buck & Vitt, 1986): the Hypnineae (or Hypnobryales sensu Vitt, 1982), the Leucodontineae (or Isobryales sensu Vitt, 1982), and the Hookeriineae (or Hookeriales sensu Vitt, 1982). The Hypnineae were defined by "specialized sporophytic features" (Buck & Vitt, 1986: 39), including asymmetric, horizontal capsules whose mouth is lined by a distinctly ornamented peristome characterized by the abruptly tapered exostome teeth (see Buck & Vitt, 1986, for details). This lineage is predominant in north temperate climates. The Leucodontineae were diagnosed by their creeping, sympodially branching stems and by erect capsules with gradually acuminate and poorly ornamented teeth. The Hookeriales also have similar sporophytes but their exothecial cells are collenchymatous, and their endostome segments have a bamboo-like architecture (Buck, 1998). Whether these morphological characters serve to identify monophyletic groups was first investigated by Buck et al. (2000) and De Luna et al. (2000). Both of these studies clearly showed that the pleurocarps compose two main lineages, equivalent to the Hookeriales and the Hypnales (including the Leucodontales). Indeed, neither the Hypnales nor the Leucodontales sensu Vitt (1982) are monophyletic. Instead the two orders are intimately mixed as is shown also by inferences from *rbc*L sequences alone (Tsubota et al., 2002). Consequently, none of the characters seen as diagnostic of the two orders is a good phylogenetic indicator. Reduction of the peristome and a shift to a sympodial mode of branching have occurred multiple times and likely parallel a transition to epiphytism (Buck et al., 2000), a hypothesis formulated earlier by Buck (1991).

The Hookeriales are monophyletic if the Hypopterygiaceae are included. Blöcher and Capesius (2002) refuted an affinity of the Hypopterygiaceae to the Hookeriales based on *rps*4 sequences (which were also used by Buck et al., 2000). Support for an exclusion of this family from the Hookeriales-Hypnales clades was, however, lacking. The Ptychomniaceae and Garovagliaceae have traditionally been placed in the Leucodontineae (Vitt, 1982 [as "Leucodontales"], 1984), but rather the group has been resolved as a sister-group to the combined Hookeriales-Hypnales by nuclear and mitochondrial data (Buck et al., 2004). The later authors have now synonymized the two families and accommo-

dated the Ptychomniaceae within its own order the Ptychomniales, sole order of the Ptychomnianae.

The Hookeriales are now interpreted as consisting of seven families (Buck et al., 2004). The order may have undergone a constant rate of diversification, and although it is much less diverse than its sister group, the Hypnales, the Hookeriales contain much larger amounts of phylogenetic diversity (Shaw et al., 2003b).

Although much effort has been invested in resolving the relationships among pleurocarpous families, only those involving the Hookeriales are well supported (Buck et al., 2004). Within the Hypnales, phylogenetic inferences have relied mostly on cpDNA sequences (i.e., *rbc*L, *rps*4, and *trn*L-*trn*F), except for the studies on the Amblystegiaceae (Vanderpoorten et al., 2001, 2002a) or Lembophyllaceae (Quandt et al., 2000). Families often receive moderate support (except in Goffinet et al., 2001, where it is virtually lacking), but inferences regarding their mutual relationships are rarely robust (e.g., Tsubota et al., 1999, 2002; Buck et al., 2000; Maeda et al., 2000; Arikawa & Higuchi, 2002). Evolutionary histories have been reconstructed based on DNA sequences for the following families: Amblystegiaceae (Vanderpoorten et al., 2001, 2002a, b), Fontinalaceae (Shaw & Allen, 2000), Hylocomiaceae (Chiang & Schaal 1999a, b, 2000a, b), Hypnaceae (Tsubota et al., 1999; Arikawa & Higuchi, 2003), Lembophyllaceae (Quandt et al., 2000), Plagiotheciaceae (Arikawa & Higuchi, 1999, 2002), and Sematophyllaceae (Tsubota et al., 2000, 2001a; Akiyama & Tsubota, 2001).

The Hypnaceae are consistently resolved as a polyphyletic entity (Tsubota et al., 1999, 2002; Buck et al., 2000). For example, *Platygyrium* is resolved within the Sematophyllaceae based on *rbc*L data (Arikawa & Higuchi, 2003). The inferences based on multiple genomic sequences also suggest that a shift from a single to a double costa has occurred multiple times (Tsubota et al., 1999; Buck et al., 2004) and hence that a reduction of the single costa is not a reliable phylogenetic indicator as proposed by Buck and Vitt (1986). The polyphyly of the Hypnaceae is also accounted for by the polyphyly of *Hypnum* itself. Tsubota et al. (1999, 2002) confirmed the hypothesis proposed by Hedenäs (1990) based on morphological characters that *H. lindbergii* Mitt. is more closely related to *Calliergonella* (Amblystegiaceae) than to other species of *Hypnum* (note, however, that *Calliergonella* is excluded by Vanderpoorten et al. (2002b) from the Amblystegiaceae). *Hypnum tristo-viride* (Broth.) Paris is, by contrast, closely related to *Brotherella* (Sematophyllaceae for Tsubota), whereas *H. cupressiforme* Hedw., the type of the genus, perhaps is sister to the Entodontaceae–Sematophyllaceae clade (Tsubota et al., 2000), but this relationship remains dubious (Tsubota et al., 2001a, b).

Several studies have focused on the circumscription of the Sematophyllaceae (Tsubota et al., 2000, 2001a, 2001b). Tsubota et al. (2000) confirmed the inclusion of *Brotherella* and related genera in this family rather than in the Hypnaceae. Similarly, *Isopterygium* was regarded as a member of the Sematophyllaceae based on *rbc*L data (Tsubota et al., 2001a). By contrast, *Glossadelphus* was excluded from the family and considered a possible member of the Hypnaceae (Tsubota et al., 2001a). The affinities of *Taxithelium* remained unresolved (Tsubota et al., 2001a, b), although when a smaller set of hypnoid taxa was analyzed the genus fell within the Sematophyllaceae (Akiyama & Tsubota, 2001). The unstable circumscription of the Hypnaceae and Sematophyllaceae reveals that none of the characters used historically serves as a diagnostic feature of either family, or that these characters (e.g., strongly shouldered exostome for the Sematophyllaceae (Buck & Vitt, 1986)) have undergone further modifications during the evolution of the family. Hedenäs and Buck (1999) reconstructed the phylogeny of the Sematophyllaceae from variation in morphological characters. Constraining their inferences to the phylogenetic hypothesis inferred from *rbc*L sequences may yield the synapomorphies needed to diagnose the Sematophyllaceae as redefined by Tsubota et al. (2001a). The value of morphological characters for defining genera within the family has also been questioned since several genera (i.e., *Trismegistia*, *Mastopoma*, and *Wijkia*) may compose polyphyletic entities (Akiyama & Tsubota, 2001; Tsubota et al., 2001b). In the classification system presented below, we have made an initial attempt to help resolve the problems with a polyphyletic Sematophyllaceae by describing the new family Pylaisiadelphaceae for a number of these more Hypnoid-like genera.

The brown mosses or Amblystegiaceae typically grow in wet habitats. A phylogenetic reconstruction of pleurocaprous mosses based on two chloroplast markers led Buck et al. (2000) to suggest that *Anacamptodon* should be included in this family rather than the Fabroniaceae (Vitt, 1984), a hypothesis corroborated by inferences from ITS, *trn*L-*trn*F, and *atp*B-*rbc*L intergenic spacer and morphology (Vanderpoorten et al., 2002a). The latter study also indicated that the Amblystegiaceae, as defined by Vitt (1984) and older classifications, are polyphyletic. The genera form two main lineages and Vanderpoorten et al. (2002b) treat these as two families:

the Amblystegiaceae, accommodating 14 genera, and the Calliergonaceae, which are defined by inflated alar cells, comprising 5 genera. The families do not share a most recent common ancestor, but their respective sister group is still unknown. *Donrichardsia* and *Platyhypnidium* are transferred to the Brachytheciaceae (Stech & Frahm, 1999), and *Platylomella* is also consistently resolved outside the family, but remains of uncertain affinities (Arikawa & Higuchi, 1999; Tsubota et al., 2002). Similarly, the affinities of *Conardia, Campylophyllum,* and several species of *Hygrohypnum* (other than the type species) remained uncertain, except that they clearly appeared unrelated to the Amblystegiaceae s. str. (Vanderpoorten et al., 2002b). The former two genera may be best accommodated in the Hypnaceae (cf. Appendix 1). Ancestral character reconstructions based on their optimal phylogeny reveal that (1) transformations in both sporophytic and gametophytic characters are correlated to shifts in habitat (unless these characters are genetically linked to characters that are adaptive to the habitat), and (2) that these characters are more labile than previously thought (Vanderpoorten et al., 2002a). Broad pseudoparaphyllia, for example, have likely arisen four times in taxa that were previously treated as members of the Amblystegiaceae sensu Vitt (1984), but are now considered unrelated (Vanderpoorten et al., 2002a). Although the lability of the characters has not decreased following the phylogenetic studies by Vanderpoorten et al. (2002a), they tend to be more stable within the new defined clades (Vanderpoorten et al., 2002a, 2002b). The circumscription of the Amblystegiaceae, as amended by these authors, leaves their Amblystegiaceae without a single morphological synapomorphy.

The Hylocomiaceae are among the most conspicuous mosses in boreal to subarctic regions. The delimitation of the family and its separation from the Rhytidiaceae is controversial. Buck (1980) excluded *Rhytidium* but included *Pleurozium.* Based on inferences from ITS2 and *atp*B-*rbc*L spacer sequences (Chiang & Schaal, 2000a, 2000b), *Rhytidium* appears to be nested within the Hylocomiaceae, whereas *Pleurozium* is sister to it. However, it is not clear whether *Pleurozium* should be included or not in the Hylocomiaceae, since it is drawn to the single outgroup species (i.e., *Entodon seductrix* (Hedw.) Müll. Hal., Entodontaceae). Additional outgroup taxa are needed to test whether the 94% bootstrap value given based on ITS2 (Chiang & Schaal, 2000b) characterizes a sister-group association of *Entodon* and *Pleurozium* versus a shared ancestry of *Pleurozium* and the remaining Hylocomiaceae. An unusual peristome ornamentation in *Pleurozium* seems to be found otherwise only within the Hylocomiaceae, and similarly the chromosome number of $n = 4$ is strongly indicative of a relationship to that family (Buck, 1980). The studies by Chiang and Schaal (2000a, b) also resolve the monogeneric Theliaceae as a member of the Hylocomiaceae. Such phylogenetic affinities for the Theliaceae have not been proposed previously. Although this hypothesis is well supported by both sources of molecular characters, it remains to be tested within a broader context of pleurocarp phylogeny to determine whether this association is an artifact due to the limited sampling. *Rps*4 data do not resolve the Hylocomiaceae as monophyletic (based on two genera only; De Luna et al., 2000; Goffinet et al., 2001). Support for the monophyly is provided by *rbc*L (Tsubota et al., 2002), but the former locus has not been sequenced for *Thelia,* and hence the affinities of this genus, and thus of the Theliaceae to the Hylocomiaceae, remain ambiguous. The study by Tsubota et al. (2002) also resolves *Ctenidium,* a genus traditionally aligned with the Hypnaceae, as a member of the Hylocomiaceae, based on *rbc*L data. This hypothesis, too, remains to be critically tested.

The circumscription of the Lembophyllaceae has been revised based on variation in cpDNA and nrDNA sequences (Quandt et al., 2000). The phylogenetic inferences support the retention of *Weymouthia* in the Lembophyllaceae rather than in the Meteoriaceae, and indicate further that the definition of the later is in need of further research, considering the ambiguous affinity of *Pilotrichella* to either of these families based on *trn*L and ITS data. Akiyama and Tsubota (2004) also argued for the polyphyly of the Lembophyllaceae. Their study lends support to Buck's (1980) hypothesis that *Dixonia* should be excluded from this family, but the alternative affinities of this genus remain unclear. The genus might be better accommodated within the Neckeraceae.

The Brachytheciaceae are one of the most speciose families of pleurocarpous mosses (cf. 43 genera, Appendix 1), and also one exhibiting the widest range of morphological variation. Hence, it is not surprising that generic circumscriptions and relationships have been controversial (Ignatov & Huttunen, 2002). Huttunen and Ignatov (2004) tested phylogenetic hypotheses within this family by combining sequence data from two chloroplast regions (*trn*L-*trn*F and *psb*T-*psb*N-*psb*H regions) and one nuclear locus (ITS2) with morphological characters. Their inferences resolved the Brachytheciaceae as essentially defined by Buck and Goffinet (2000) as

monophyletic (with minor generic alterations), and sister to the Meteoriaceae. The phylogenetic hypotheses served as a basis for the subsequent systematic interpretation and a new classification of the Brachytheciaceae (Ignatov & Huttunen, 2002). The chloroplast loci exhibit little variation to resolve infrageneric relationships, whereas the nuclear ITS2 region may, in some cases, be too variable to even resolve species as monophyletic entities. Independent analyses of the four character partitions yielded different topologies, but the incongruence was not significant enough and character sources were combined. To what extend the optimal topologies retrieved from the combined data set are shaped by the morphological data is not clear, although it was noted that the total-evidence phylogeny mostly resembled the topologies obtained from analyzing the ITS2 data alone.

The monophyly of the Brachytheciaceae sensu Ignatov (1999) is well supported. The family is now best defined by the arrangement and shape of the pseudoparaphyllia and the smooth laminal cells, although exceptions within and outside the family defy this generalization. Four main lineages are now recognized as subfamilies within the Brachytheciaceae (Ignatov & Huttunen, 2002). Support for the monophyly of these clades varies (Huttunen & Ignatov, 2004): it is high for the Homalothecioideae but low to absent for the other three subfamilies. In the case of the Rhynchostegioideae monophyly is dependent on the equal weighting of the morphological data, and, even then, support values are virtually lacking. Several speciose genera (e.g., *Eurhynchium* s.l.) are revealed as polyphyletic, and others are resolved only as monophyletic lineages if morphological characters are included in the analyses (e.g., *Kindbergia*). Peristome reduction is shown to have occurred in all clades. Except for the Rhynchostegioideae, the subfamilies are shown to be polymorphic for the roughness of the seta (smooth vs. rough), and all but the Rhynchostegielloideae are variable with regard to the shape of the operculum. These and other characters have traditionally been used to define supraspecific taxa within the family, and are shown to be broadly homoplasic. Hence, as has been the case in other families (e.g., Splachnaceae), many clades resolved within the Brachytheciaceae by the phylogenetic analyses cannot be diagnosed by "known morphological characters" (Huttunen & Ignatov, 2004: 175). Much remains to be done to elucidate the generic definitions and relationships within the Brachytheciaceae, but this study offers a sound basis for further research.

The Plagiotheciaceae sensu Vitt (1984) are resolved as a polyphyletic entity with *Entodontopsis* and *Stereophyllum* forming a monophyletic lineage distantly, but also ambiguously related to the *Plagiothecium* as suggested by Buck and Ireland (1985), who erected the Stereophyllaceae to accommodate *Entodontopsis* and *Stereophyllum* as well as other genera. The inclusion of *Herzogiella* in the Plagiotheciaceae as proposed by Pedersen and Hedenäs (2001) is not well supported (Arikawa & Higuchi, 2003), but neither is its exclusion (Arikawa & Higuchi, 2002).

A series of studies have dealt with the status of species-poor or often monospecific genera erected for aquatic mosses that are characterized by a pluristratose lamina and/or leaf border and a broad costa. These features are otherwise very rare among pleurocarpous mosses. Furthermore, most of these taxa are sterile (except *Hypnobartlettia* and *Platyhypnidium mutatum* Ochyra & Vanderpoorten), and hence their generic or familial affinities are ambiguous. Molecular data have proven essential to settle the controversy regarding the systematic status of these aquatic mosses. *Donrichardsia, Platyhypnidium riparioides* (Hedw.) Dixon, and *P. mutatum* are now considered members of the Brachytheciaceae (Stech & Frahm, 1999); *Gradsteinia* and *Ochyraea* were transferred to the Amblystegiaceae (Stech & Frahm, 2000, 2001). Affinities of *Ochyraea* to the Amblystegiaceae were based on its relationships to *Calliergonella* and *Hygrohypnum*, which were subsequently excluded from the family (Vanderpoorten et al. 2002b). *Ochyraea* is now accommodated in the Hypnaceae (Vanderpoorten et al., 2002b). The Hypnobartlettiaceae and Vittiaceae were merged with the Amblystegiaceae (Vanderpoorten et al., 2002b, 2003). These inferences have provided the first molecular evidence of convergent evolution in gametophytic characters in mosses in response to shifts in habitats. Whether these modifications are genetically fixed or phenotypic expressions has not been formally tested. In other taxa, morphological characters appear to be very much shaped by environmental parameters. For example, all morphological species centered around *Amblystegium tenax* (Hedw.) C. E. O. Jensen are now considered to merely represent phenotypic variants (Vanderpoorten, 2004). A similar situation may occur in *Fontinalis*. Shaw and Allen (2000) sampled 13 taxa within *Fontinalis*, and several were represented by multiple populations distributed across their transatlantic ranges. Inferences from ITS and *trn*L-*trn*F sequences revealed that all but one of the morphological species for which two or more samples were included are not monophyletic, and the only one representing a natural

lineage (i.e., *F. squamosa* Hedw.) is nested in a clade of *F. antipyretica* Hedw. Hence, characters of the leaves used to define species of *Fontinalis* appear particularly labile in this group of aquatic mosses.

Testing systematic concepts developed by Vitt (1984) or Buck and Vitt (1986) against phylogenetic inferences based on morphological characters revealed that many suprageneric taxa did not satisfy a monophyly criterion (e.g., Hedenäs, 1995; Hedenäs & Buck, 1999). The contribution of molecular data has been particularly significant in addressing the affinities of taxa with reduced morphologies and taxa that have undergone severe morphological transformations in response to a shift in habitat. The phylogenetic association of taxa occupying different habitats, and hence with distinct morphological adaptations, has not solved the problem of the morphological heterogeneity of families. Hence, some families cannot be diagnosed by a single morphological synapomorphy that is conserved by all its taxa.

Although analyses of DNA sequence data have led to a revision of most familial circumscriptions and have offered moderate to strong support for the monophyly of these clades, the relationships among families of pleurocarpous mosses remain, for the most part, ambiguous. The difficulty in resolving the evolutionary history of the Hypnidae may be a direct consequence of their rapid radiation (Shaw et al., 2003b) and hence the paucity of fixed changes in the ancestor to diverging families. The problem is compounded by the fact that many exemplars may not be representative of their family (since many are shown to be polyphyletic) or even their genus. Studies need to include a broad systematic spectrum because many taxa may not be monophyletic, but, of course, by doing so and by focusing on a single locus, homoplasy is potentially rampant and the prospect of resolving the relationships rapidly vanishes. De Luna et al. (2000) showed that for a limited number of pleurocarps resolution is dramatically increased as the number of characters increases. However, the combination of three chloroplast loci failed to offer much support for the nodes of the better resolved consensus tree obtained for hypnobryalean mosses.

Most inferences rely on variation in chloroplast loci, and few have included sequences of the nuclear genome. Variation in the 18S locus is minimal (Capesius & Stech, 1997). Buck et al. (2004) inferred relationships in the Hookeriales in part from the 26S locus. Whether phylogenetic informative variation could be retrieved for the Hypnales from this locus is not clear, especially in the light of the evidence of a rapid radiation of this lineage (Shaw et al., 2003b). The ITS region has been used to assess relationships among species of the liverwort genus *Plagiochila* (Dumort.) Dumort., as well as among populations (e.g., *Mielichhoferia*; Shaw, 2000a), species (e.g., *Fontinalis*; Shaw & Allen, 2000), and genera of acrocarpous (e.g., Pottiaceae; Spagnuolo et al., 1996, 1999) and pleurocarpous mosses (Brachytheciaceae; Huttunen & Igantov, 2004). Among pleurocarpous mosses, this region may be useful to reconstruct the relationships among genera (e.g., Quandt et al., 2000; Vanderpoorten et al., 2001; Huttunen & Ignatov, 2004). Whether the ITS region can contribute to resolving the ambiguity characterizing the relationships among most families of pleurocarpous mosses remains to be tested.

Perspectives

Phylogenetic inferences based on DNA sequence data have shed light on the circumscription of and relationships among various taxa of mosses, from orders to genera and species. Molecular phylogenetics has corroborated many core familial concepts, but the circumscription of virtually all families examined so far must be revised. In many cases, these revisions implicate taxa that are heterogeneous, and hence for which diagnostic characters (i.e., synapomorphies) cannot be defined. Considering that the molecular tools have only been applied recently to bryophyte systematics, it is not surprising that many basic hypotheses remain to be tested in addition to the many that have been raised by recent investigations. Efforts invested in resolving either the supraordinal phylogeny of mosses or the relationships among lineages within the Hypnidae have remained poorly rewarded, as little progress has been made at these levels.

Most inferences rely on variation in chloroplast loci, with fewer studies sampling the nuclear or mitochondrial genome. Few chloroplast loci have been sampled beyond the traditional ones (*trn*L-*trn*F, *rps*4, *rbc*L, and, to a lesser extent, the *atp*B-*rbc*L spacer), but these may merit more attention. Shaw et al. (2003a) and Pedersen and Hedenäs (2003) sequenced *psb*A, and the former study also included *psb*T. Variation in *psb*A among major lineages of Sphagnaceae and Bryaceae was higher than that found for *rps*4 in both studies and similar to those observed for *rbc*L. *Psb*T was more conserved than either of these loci (Shaw et al., 2003a). *Rpl*16 is a protein-coding gene that is slightly more variable than the *psb*A locus (Pedersen & Hedenäs, 2003). The *mat*K region, which has been used extensively

by phanerogamists (Hilu & Liang, 1997; Hilu et al., 2003), has not yet been sampled for bryophytes, although it is currently being screened for addressing the phylogeny of the Pottiaceae (Quandt, pers. comm.). The divergence in the *chl*B sequences among land plants is higher than that of the *rbc*L gene, as well as in mosses and liverworts (two taxa of each sampled; Boivin et al., 1996), and suggests that this locus may be informative at ordinal or higher levels. Primers for the *trn*G locus were developed by Pacak and Szweykowska-Kulinska (2000) and used by Pedersen and Hedenäs (2003). The level of variation exceeded that of several chloroplast loci and hence appears promising as a source of characters.

Following the pioneering work by Beckert et al. (1999), the *nad*5 locus has been used to reconstruct the relationships among major lineages of mosses (Cox et al., 2004) as well as orders among pleurocarpous orders (Buck et al., 2004). *Nad*2 exhibits a similar level of variation (Beckert et al., 2001). Cox et al. (2004) also used *nad*7. *Nad*5 and *nad*7 were sampled by Shaw et al. (2003a) for the Sphagnaceae, which showed about 10% phylogenetically informative sites. By contrast, the level of divergence in the *cox*3 gene between *Ceratodon* and *Physcomitrella* is low (Malek et al., 1996), which may explain why systematists have not yet targeted this locus.

The nuclear genome has offered the least number of loci used so far for phylogenetic reconstruction in bryophytes. The nrDNA repeat is the most widely used nuclear character source for inferring phylogenies of angiosperms (Hershkovitz et al., 1999), as well as for bryophytes. Besides the rRNA encoding genes and the spacers present in the repeat units, few loci have been sequenced. Wall (2002) inferred relationships within *Mitthyridium* (Calymperaceae) based on glyceraldehyde 3-phosphate dehydrogenase sequences. Although the primers developed for this study are presented as being universal, at least within mosses, no other study has used this locus, and our own attempts with these primers have failed to yield any PCR product. Vanderpoorten et al. (2004) targeted the gene for the adenosine kinase enzyme for the *Amblystegium* complex, but obtained multiple amplicons due to the presence of paralogous loci. Similarly, several genes may be present in *Ceratodon* (Shaw et al., 2002), whereas in *Physcomitrella* a single locus occurs (von Schwartzenberg et al., 1998). Shaw et al. (2002) also reported on two other nuclear loci (Δ^6-fatty acyl acetylenase/desaturase (Sperling et al., 2000), and a phytochrome (Pasentsis et al., 1998); all three loci are being sequenced for populations of *Ceratodon purpureus* (Hedw.) Brid. The results of these studies are not yet published, and it is not clear whether the signal is suitable for phylogenetic as well as phylogeographic studies. Sequences of the RNA polymerase II (Denton et al., 1998) and a phytochrome (Kolukisaoglu et al., 1993) have been published and examined for their levels of variation among land plants, but have not been surveyed further within the context of bryophyte phylogeny. Similarly, a family of cytosolic small heat-shock proteins has been characterized for mosses (Waters & Vierling, 1999), but not explored for its potential in phylogenetic inferences.

Shaw et al. (2003a) searched for new sources of phylogenetic characters by exploring the suitability of randomly amplified loci. They found two regions, of unknown genomic homology, whose level of variation was adequate for resolving the sectional phylogeny within *Sphagnum*. Bailey et al. (2004) applied a similar strategy for uncovering loci that display mutations between closely related angiosperm species (i.e., species of *Leucaena*, Fabaceae). The two RAPD loci they ultimately selected exhibited levels of variation that were higher than those observed for cpDNA restriction sites or the ITS region, and led to greater phylogenetic resolution and higher bootstrap values. Screening of amplicons obtained by using RAPD primers may thus offer access to the vast portions of the genome that have remained largely untouched by systematists.

In the past, phylogenetic inferences were based on a single locus (e.g., Goffinet et al., 1998), but increasingly the trend is to combine data from several loci (e.g., Pedersen & Hedenäs, 2003) and ultimately from several genomic compartments (e.g., Shaw et al., 2003a; Buck et al., 2004). Inferences from single loci should be avoided, in part because the level of resolution and support may be low (i.e., Goffinet et al., 2001), or because lateral gene transfer (e.g., hybridization) is potentially more common in mosses than previously thought (e.g., Shaw & Goffinet, 2000; Såstad et al., 2001). Of course, the debate over more taxa (e.g., Tsubota et al., 2002) or more characters (e.g., Cox et al., 2004) is unsettled. If the ambiguity must be settled, one has to choose a criterion upon which to favor one approach over the other. Most often support values are taken as an indicator of accurateness of the phylogeny (as is done throughout this review). However, low bootstrap percentages or low posterior probabilities reveal only that the support is lacking, but not that the hypothesis is incorrect. A hypothesis can only be rejected if an alternative scenario can be significantly favored. For example, the relationships inferred from the small *rps*4 gene based

on 225 species of mosses (Goffinet et al., 2001) are mostly not well supported, but many of the unsupported branches are likely correct (e.g., monophyly of the Splachnaceae, monophyly of the pleurocarps). Long branch attraction (Felsenstein, 1978) has often been invoked to account for results that are in conflict with morphology (e.g., Hyvönen et al., 2004). When mutations yield the same nucleotide in several positions in unrelated taxa, phylogenetic inferences may lead to these taxa being attracted to each other. Thus, the convergence outweighs the true synapomorphies that would place these taxa in their respective clades. It seems clear, without much demonstration, that this can be avoided when species allied to the taxa in question are added, as they would break down the attraction caused by convergence in other sites. Thus, single locus phylogeny for a large taxon sampling may be acceptable, but not desirable. What must be avoided are inferences on a small set of taxa for which a single gene is targeted. Similarly, studies testing the circumscription of an ingroup should include more than one outgroup to avoid the pitfall of a priori bias.

The underlying causes to the phylogenetic ambiguity lay not only with the paucity of the loci sampled. In some cases, the incongruence between studies could be traced to a misidentified herbarium collection (e.g., *Mittenia* in Goffinet et al., 2001; see Bell & Newton, 2004) or culture collection (Arikawa & Higuchi, 2003). A lack of care also resulted in Goffinet (in Goffinet et al., 2001) moving *Pleurophascum* to the Bryales (Buck & Goffinet, 2000), when a closer look at the matrix should have revealed that the *rps*4 sequence for *Pleurophascum* was incomplete. Fortunately, the vast majority of studies are rigorous in confirming the identity of the exemplars that are sampled.

The incongruence between the phylogenetic signals of morphological and molecular data is often implicitly attributed to erroneous homology assumptions of morphological characters. Although the homology of individual sequence characters can also be questioned, especially for non-coding regions that vary in length, a more fundamental assumption, namely, the orthology of the sequences compared between taxa is often implicitly made but rarely tested. Vanderpoorten et al. (2004) revealed extensive duplication of the locus encoding the adenokinase gene in *Hygroamblystegium*. Similarly, the ITS region, which is widely used for its variation among species or populations, occurs in numerous copies (Hillis & Dixon, 1991), and some of these may be pseudogenes (Bailey et al., 2003), which may have their own phylogenetic utility (Razafimandimbison et al., 2004). Clearly, great care must be taken to assert the homology of the loci targeted for phylogenetic reconstructions.

The phylogenetic signal contained in a set of sequences can be retrieved under different assumptions. The sequences of most loci, including those that do not code for a protein or an RNA molecule, may only vary within a space constrained by the secondary structure of either the transcribed product or the ultimate translated product. Many analyses under maximum parsimony treat all characters and all transformations within them as equally probable and equally costly. Inferences under maximum likelihood tend to integrate different rates of evolution for discrete character partitions, as well as different costs for particular nucleotide substitutions. It is beyond the scope of this review to enter the debate regarding the pros and cons of various optimality criteria. However, Cox et al. (2004) showed that, at least at deep levels of the phylogenetic tree (toward the root), saturation of the protein-coding genes may lead to long branch attraction. This problem is alleviated by replacing the third codon position bases by a binary character (purine-pyrimidine) which downweighs transitions or by invoking a model of sequence evolution for the partitions (i.e., 1st, 2nd, and 3rd codon positions; Cox et al., 2004). The secondary structure of non-coding regions should also be taken into account when defining the character homology assumptions (i.e., aligning the sequences; An et al., 1999; Gottschling et al., 2001). Although several studies have relied on ITS sequences to yield the information necessary to reconstruct the phylogeny, none of the studies focusing on mosses have aligned their sequences based on structural constraints on the molecule. The two Internal Transcribed Spacers (ITS1 and ITS2) may not code for RNA molecules but play a role in the maturation of the rRNA subunits, and both spacers have a primary sequence from which a secondary structure can be derived (e.g., Goertzen et al., 2003), and this structure seems highly conserved among plants (Coleman, 2003). Similarly, the alignment of the *trn*L intron, which is widely used in moss phylogenetics, should also be didacted by models of the secondary structure (e.g., Borsch et al., 2003; Stech et al., 2003a). Quandt et al. (2003) described a dyad symmetrical element in the *psb*N-*psb*H spacer (cpDNA) and small inversions that occurred in the loop of the hair-pin structure. If no effort had been made to test for, and hence predict, a secondary structural model, then the inversions would have remained unnoticed, and homology assumptions flawed. Indeed, Quandt et al. (2003) demonstrated that these

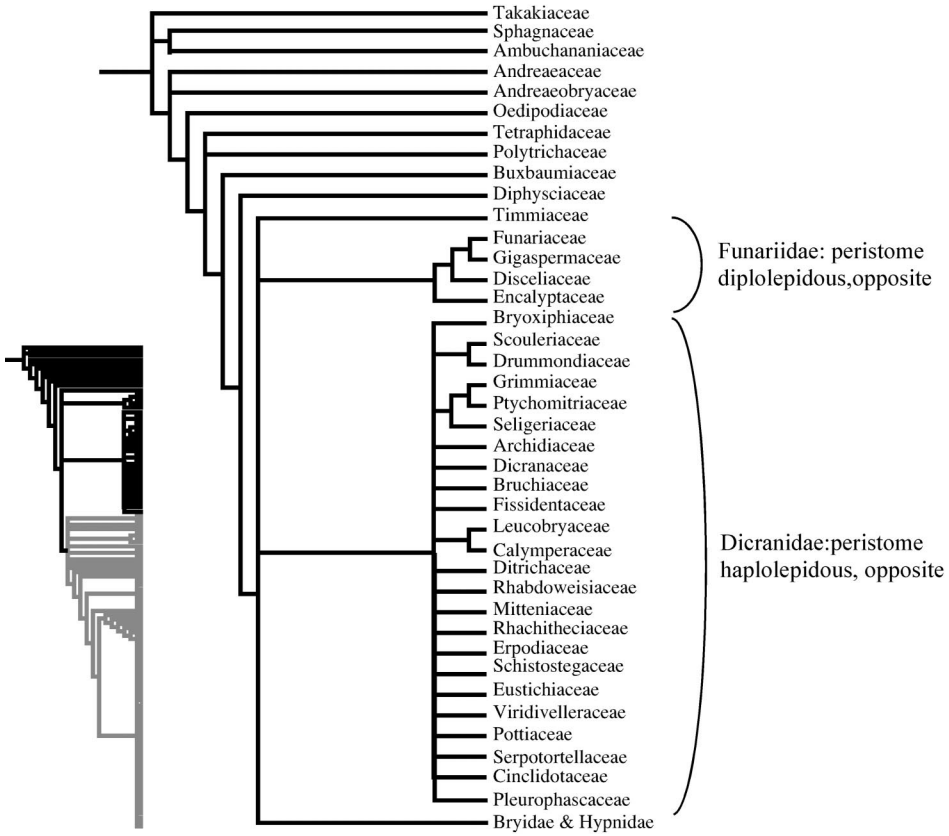

Figure 1. Summary of current state of phylogenetic resolution for families of mosses, based on inferences from DNA sequence data (see text review). Taxa of ambiguous affinities are retained in a conservative position.

mutations are highly homoplasic even among genera of pleurocarpous mosses, and also suggested that the inclusion of the loop in the analyses significantly decreased the robustness of the results. It, thus, appears imperative to explore secondary structure models for primary sequence data in order to extract a robust and accurate signal.

Taking into account the folding of the molecule allows also the detection of any compensatory changes that occur on complementary portions of the sequence (Álvarez & Wendel, 2003; Coleman, 2003; Quandt et al., 2003). In the case of the *trn*L intron, Quandt et al. (2004) argue that these base changes contribute significant phylogenetic signal only when deep nodes of the evolutionary tree of land plants are considered, but that they may have little effect if apical clades such as the pleurocarpous mosses are considered. However, considering that pleurocarpous mosses are of fairly recent origin and have undergone a rapid diversification (Shaw et al., 2003b), it is not clear if Quandt et al.'s observation will apply to other groups of mosses.

During the last ten years, bryologists have overcome the difficulties of extracting, amplifying, and sequencing DNA from fresh as well as older herbarium material to test phylogenetic hypotheses. The data derived from DNA sequencing have permitted new insights into moss phylogeny. Inferences from DNA sequences may corroborate the hypothesis drawn from morphological characters (e.g., monophyly of the Splachnaceae: Goffinet et al., 2004a), resolve relationships that were left ambiguous based on morphology (e.g., affinities of the Encalyptaceae: Goffinet & Cox, 2000), or lead to a reevaluation of homology assumptions of morphological characters in cases of severe conflict (e.g., circumscription of the Bryaceae and Mniaceae: Cox & Hedderson, 1999; 2003). Morphological characters define the null hypotheses that are being tested using sequence data, and they remain central to our interpretations of phylogenetic hypotheses. However, as is evident from the present review, most morphological characters traditionally used to defined taxonomic entities of bryophytes are poor phylogenetic indicators, although others may be revealed to hold the signal that marks the origin of a

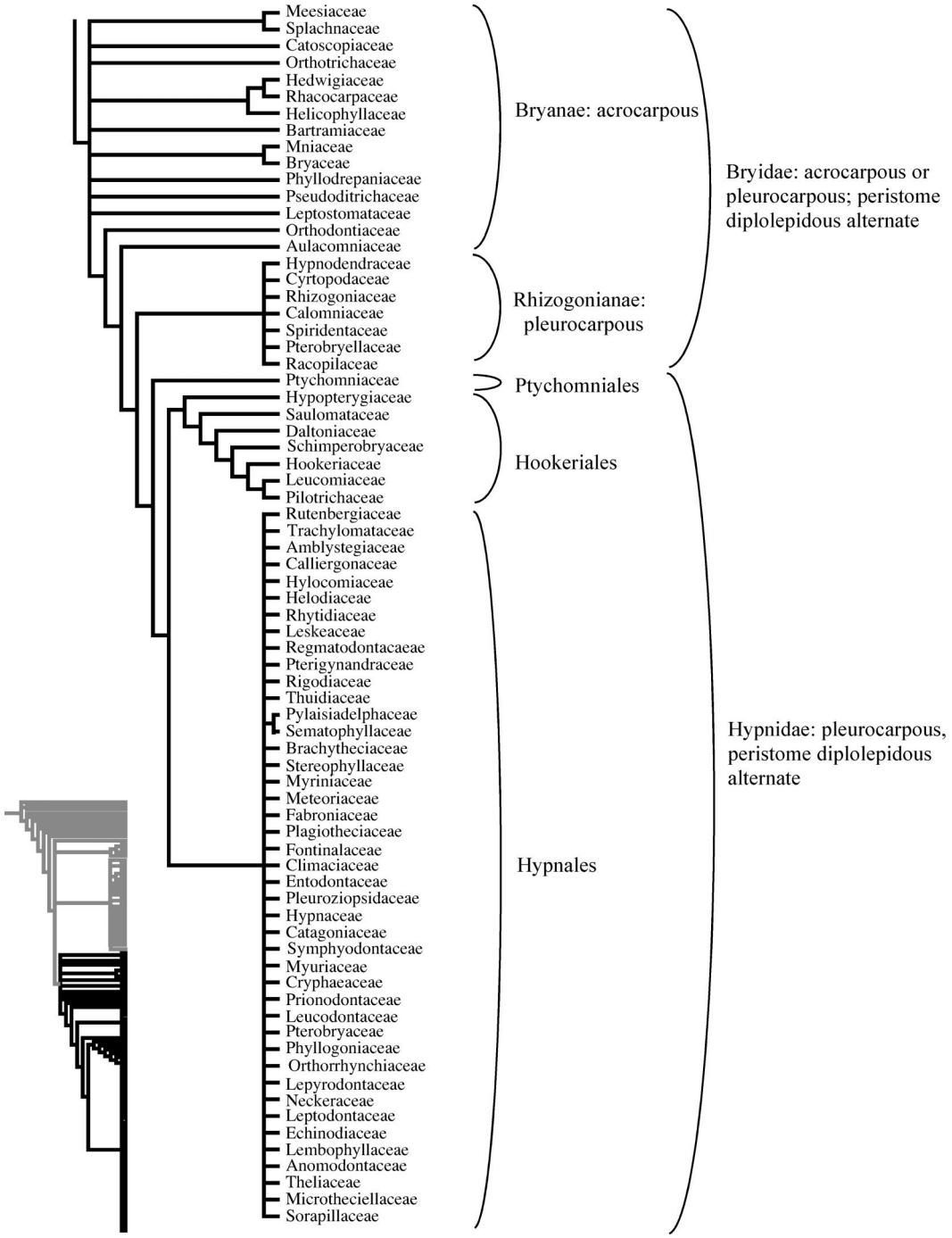

Figure 1. Continued.

clade. As bryologists move into the 21st century, all sources of data that allow for a better resolution of phylogenetic relationships are needed, and molecular sequences offer the best hope for understanding not only familial circumscriptions and phylogeny, but ultimately also the evolution of morphological characters. It is, indeed, the history of morphological transformations that define taxa or of the distribution ranges of the species that justify the investment into phylogenetic approaches. A re-

vival of critical morphological and anatomical studies is, however, imperative if major clades of mosses are to be diagnosed by characters other than their genomes.

Classification of the Bryophyta

From the preceding review it is clear that inferences from molecular data contribute significantly to our understanding of the evolutionary relationships among mosses. Molecules have been essential to resolve the affinities of taxa with reduced morphologies (e.g., *Ephemerum*, *Oedipodium*), and to reveal that similarities in morphological characters may result from convergence rather than shared ancestry (e.g., Leucodontales). As a consequence, several taxa appear to be polyphyletic (e.g., *Bryum*, Bryaceae). Monophyly of the ingroup is an essential assumption to the reconstruction of the phylogeny and its interpretation in terms of character evolution. Monophyly may be violated if taxa of distant relationship are included in the ingroup and if others, currently accommodated in distinct lineages, are omitted from the ingroup. To test whether any taxa are missing from the ingroup is an impossible task, as exemplars of all outgroup taxa must be sampled. However, testing the shared ancestry of taxa assumed to be members of the ingroup is more readily done, especially as the number of available sequences to include in the outgroup is growing. Goffinet et al. (2001) argued that the *rps*4 gene of all ingroup taxa (or their exemplars) should be sequenced and inserted in the large matrix, simply to provide a preliminary test of the monophyly of the group. Although it is not a robust test, the *rps*4 data set is currently the largest available one covering a broad systematic spectrum of mosses. The affinities of monospecific genera or monogeneric families in the Bryophyta could be easily addressed using this broad character sample.

Novel hypotheses drawn from the analyses of molecular data (see Fig. 1 for summary) are integrated here (Appendix 1) into the classification of mosses recently revised by Buck and Goffinet (2000). These amendments to the circumscription of taxa are complemented by several studies based on patterns emerging from the variation of morphological characters. The classification proposed here represents only our best interpretation of the available evidence. In cases of incongruence, we have favored morphology when alternative hypotheses seem poorly supported by molecular data. Many studies have revealed the polyphyly of large genera, but failed to offer new systematic concepts; hence, these moss taxa are retained here in their traditional sense.

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Appendix 1. Classification of the mosses.

BRYOPHYTA Schimp.:

Superclass I

Class Takakiopsida (Crand.-Stotl.) Goffinet & W. R. Buck, comb. et stat. nov. Takakiophyta Crandall-Stotler, J. Bryol. 14: 17. 1986.

Order Takakiales S. Hatt. & H. Inoue

Takakiaceae S. Hatt. & Inoue Type: *Takakia* S. Hatt. & Inoue

Superclass II

Class Sphagnopsida (Engl.) Ochyra

Order Sphagnales Limpr.

Sphagnaceae Dumort. Type: *Sphagnum* L.

Order Ambuchananiales Seppelt & H. A. Crum

Ambuchananiaceae Seppelt & H. A. Crum Type: *Ambuchanania* Seppelt & H. A. Crum

Superclass III

Class Andreaeopsida (Limpr.) Rothm.

Order Andreaeales Limpr.

Andreaeaceae Dumort. Type: *Andreaea* Hedw.

Acroschisma Lindl., *Andreaea* Hedw.

Superclass IV

Class Andreaeobryopsida (B. M. Murray) Goffinet & W. R. Buck, comb. et stat. nov. Andreaeobryales B. M. Murray, Beih. Nova Hedwigia 90: 299. 1988.

Order Andreaeobryales B. M. Murray

Andreaeobryaceae Steere & B. M. Murray Type: *Andreaeobryum* Steere & B. M. Murray

Superclass V

Class Oedipodiopsida (Schimp.) Goffinet & W. R. Buck, comb. et stat. nov. Oedipodiaceae Schimp., Syn. Musc. Eur. ed. 2, XCVIII, 354. 1876.

Order Oedipodiales (Schimp.) Goffinet & W. R. Buck, comb. et stat. nov. Oedipodiaceae Schimp., Syn. Musc. Eur. ed. 2, XCVIII, 354. 1876.

Oedipodiaceae Schimp. Type: *Oedipodium* Schwägr.

Class Polytrichopsida Ochyra, Zarnowiec & Bednarek-Ochyra

Order Polytrichales M. Fleisch.

Polytrichaceae Schwägr. Type: *Polytrichum* Hedw.

Alophozia Card., *Atrichopsis* Card., *Atrichum* P. Beauv., *Bartramiopsis* Kindb., *Dawsonia* R. Br., *Dendroligotrichum* (Müll. Hal.) Broth., *Hebantia* G. L. S. Merr., *Itatiella* G. L. Sm., *Lyellia* R. Br., *Meiotrichum* (G. L. Sm.) G. L. S. Merr., *Notoligotrichum* G. L. Sm., *Oligotrichum* Lam. & DC., *Plagioracelopus* G. L. S. Merr., *Pogonatum* P. Beauv., *Polytrichadelphus* (Müll. Hal.) Mitt., *Polytrichastrum* G. L. Sm., *Polytrichum* Hedw., *Pseudatrichum* Reimers, *Pseudoracelopus* Broth., *Psilopilum* Brid., *Racelopodopsis* Thér., *Racelopus* Dozy & Molk., *Steereobryon* G. L. Sm.

Class Tetraphidopsida (M. Fleisch.) Goffinet & W. R. Buck, comb. et stat. nov. Bryales subordo Tetraphidiineae M. Fleisch., Musci Fl. Buitenzorg 3: xvi. 1908.

Order Tetraphidales M. Fleisch.

Tetraphidaceae Schimp. Type: *Tetraphis* Hedw.

Tetraphis Hedw., *Tetrodontium* Schwägr.

Class Bryopsida (Limpr.) Rothm.

Subclass Buxbaumiidae (M. Fleisch.) Ochyra

Order Buxbaumiales M. Fleisch.

Buxbaumiaceae Schimp. Type: *Buxbaumia* Hedw.

Subclass Diphysciidae (M. Fleisch.) Ochyra

Order Diphysciales M. Fleisch.

Diphysciaceae M. Fleisch. Type: *Diphyscium* D. Mohr

Subclass Funariidae (W. Frey) Ochyra

Order Timmiales (M. Fleisch.) Ochyra

Timmiaceae Schimp. Type: *Timmia* Hedw.

Order Encalyptales Dixon

Encalyptaceae Schimp. Type: *Encalypta* Hedw.

Bryobartramia Sainsb., *Bryobrittonia* R. S. Williams, *Encalypta* Hedw.

Order Funariales M. Fleisch.

Funariaceae Schwägr. Type: *Funaria* Hedw.

APPENDIX 1. Continued.

Aphanorhegma Sull., *Brachymeniopsis* Broth., *Bryobeckettia* Fife, *Corynotheca* Ochyra, *Cygnicollum* Fife & Magill, *Entosthodon* Schwägr., *Funaria* Hedw., *Funariella* Sérgio, ×*Funariophyscomitrella* Wettst., *Loiseaubryum* Bizot, *Nanomitriella* E. B. Bartram, *Physcomitrella* Bruch & Schimp., *Physcomitrellopsis* Broth. & Wager, *Physcomitrium* (Brid.) Brid., *Pyramidula* Brid.

Disceliaceae Schimp. Type: *Discelium* Brid.

Gigaspermaceae Lindb. Type: *Gigaspermum* Lindb.
Chamaeobryum Thér. & Dixon, *Costesia* Thér., *Gigaspermum* Lindb., *Lorentziella* Müll. Hal., *Oedipodiella* Dixon

SUBCLAS DICRANIDAE (W. Frey) Ochyra

ORDER SCOULERIALES (S. P. Churchill) Goffinet & W. R. Buck, comb. et stat. nov. Scouleriaceae S. P. Churchill in Funk & D. R. Brooks, Advances Cladistics 143. 1981.

Scouleriaceae S. P. Churchill Type: *Scouleria* Hook.
Scouleria Hook., *Tridontium* Hook. f.

Drummondiaceae (Vitt) Goffinet Type: *Drummondia* Hook.

ORDER BRYOXIPHIALES H. A. Crum & L. E. Anderson

Bryoxiphiaceae Besch. Type: *Bryoxiphium* Mitt.

ORDER GRIMMIALES M. Fleisch.

Grimmiaceae Arn. Type: *Grimmia* Hedw.
Aligrimmia R. S. Williams, *Bucklandiella* Roiv., *Codriophorus* P. Beauv., *Coscinodon* Spreng., *Coscinodontella* R. S. Williams, *Dryptodon* Brid., *Grimmia* Hedw., *Guembelia* Hampe, *Hydrogrimmia* (I. Hagen) Loeske, *Indusiella* Broth. & Müll. Hal., *Jaffueliobryum* Thér., *Leucoperichaetium* Magill, *Niphotrichum* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *Orthogrimmia* (Schimp.) Ochyra & Zarnowiec, *Racomitrium* Brid., *Schistidium* Bruch & Schimp., *Streptocolea* (I. Hagen) Ochyra & Zarnowiec

Ptychomitriaceae Schimp. Type: *Ptychomitrium* Fürnr.
Campylostelium Bruch & Schimp., *Ptychomitriopsis* Dixon, *Ptychomitrium* Fürnr.

Seligeriaceae Schimp. Type: *Seligeria* Bruch & Schimp.
Blindia Bruch & Schimp., *Brachydontium* Fürnr., *Hymenolomopsis* Thér., *Seligeria* Bruch & Schimp., *Trochobryum* Breidl. & Beck

ORDER ARCHIDIALES Limpr.

Archidiaceae Schimp. Type: *Archidium* Brid.

ORDER DICRANALES H. Philib. ex M. Fleisch.

Fissidentaceae Schimp. Type: *Fissidens* Hedw.

Eustichiaceae Broth. Type: *Eustichia* (Brid.) Brid.

Ditrichaceae Limpr. Type: *Ditrichum* Hampe
Astomiopsis Müll. Hal., *Austrophilibertiella* Ochyra, *Bryomanginia* Thér., *Ceratodon* Brid., *Cheilothela* Broth., *Chrysoblastella* R. S. Williams, *Cladastomum* Müll. Hal., *Cleistocarpidium* Ochyra & Bednarek-Ochyra, *Crumuscus* W. R. Buck & Snider, *Cygniella* H. A. Crum, *Distichium* Bruch & Schimp., *Ditrichopsis* Broth., *Ditrichum* Hampe, *Eccremidium* Hook. f. & Wilson, *Garckea* Müll. Hal., *Kleioweisopsis* Dixon, ×*Pleuriditrichum* A. L. Andrews & F. J. Herm., *Pleuridium* Rabenh., *Rhamphidium* Mitt., *Saelania* Lindb., *Skottsbergia* Cardot, *Strombulidens* W. R. Buck, *Trichodon* Schimp., *Tristichium* Müll. Hal., *Wilsoniella* Müll. Hal.

Bruchiaceae Schimp. Type: *Bruchia* Schwägr.
Bruchia Schwägr., *Cladophascum* Sim, *Eobruchia* W. R. Buck, *Pringleella* Cardot, *Trematodon* Michx.

Rhabdoweisiaceae Limpr. Type: *Rhabdoweisia* Bruch & Schimp.
Amphidium Schimp., *Arctoa* Bruch & Schimp., *Cynodontium* Schimp., *Dichodontium* Schimp., *Dicranoweisia* Milde, *Glyphomitrium* Brid., *Holodontium* (Mitt.) Broth., *Hymenoloma* Dusén, *Kiaeria* I. Hagen, *Oncophorus* (Brid.) Brid., *Oreas* Brid., *Oreoweisia* (Bruch & Schimp.) De Not., *Pseudohyophila* Hilp., *Rhabdoweisia* Bruch & Schimp., *Symblepharis* Mont., *Verrucidens* Cardot

Rhachitheciaceae H. Rob. Type: *Rhachithecium* Le Jolis
Hypnodontopsis Z. Iwats. & Nog., *Jonesiobryum* B. H. Allen & Pursell, *Rhachitheciopsis* P. de la Varde, *Rhachithecium* Le Jolis, *Tisserantiella* P. de la Varde, *Uleastrum* W. R. Buck, *Zanderia* Goffinet

Erpodiaceae Broth. Type: *Erpodium* (Brid.) Brid.
Aulacopilum Wilson, *Erpodium* (Brid.) Brid., *Solmsiella* Müll. Hal., *Venturiella* Müll. Hal., *Wildia* Müll. Hal. & Broth.

Mitteniaceae Broth. Type: *Mittenia* Lindb.

Schistostegaceae Schimp. Type: *Schistotega* D. Mohr

Viridivelleraceae I. G. Stone Type: *Viridivellus* I. G. Stone

APPENDIX 1. Continued.

Dicranaceae Schimp. Type: *Dicranum* Hedw.
Anisothecium Mitt., *Aongstroemia* Bruch & Schimp., *Aongstroemiopsis* M. Fleisch., *Braunfelsia* Paris, *Brotherobryum* M. Fleisch., *Bryotestua* Thér. & P. de la Varde, *Camptodontium* Dusén, *Campylopodium* (Müll. Hal.) Besch., *Chorisodontium* (Mitt.) Broth., *Cnestrum* I. Hagen, *Cryptodicranum* E. B. Bartram, *Dicnemon* Schwägr., *Dicranella* (Müll. Hal.) Schimp., *Dicranoloma* (Renauld) Renauld, *Dicranum* Hedw., *Diobelonella* Ochyra, *Eucamptodon* Mont., *Eucamptodontopsis* Broth., *Holomitriopsis* H. Rob., *Holomitrium* Brid., *Hygrodicranum* Cardot, *Leptotrichella* (Müll. Hal.) Lindb., *Leucoloma* Brid., *Macrodictyum* (Broth.) E. H. Hegew., *Mesotus* Mitt., *Mitrobryum* H. Rob., *Muscoherzogia* Ochyra, *Orthodicranum* (Bruch & Schimp.) Loeske, *Paraleucobryum* (Limpr.) Loeske, *Parisia* Broth., *Platyneuron* (Cardot) Broth., *Pocsiella* Bizot, *Polymerodon* Herzog, *Pseudephemerum* (Lindb.) I. Hagen, *Pseudochorisodontium* (Broth.) C. H. Gao, Vitt, X. H. Fu & T. Cao, *Schliephackea* Müll. Hal., *Sclerodontium* Schwägr., *Sphaerothecium* Hampe, *Steyermarkiella* H. Rob., *Wardia* Harv. & Hook., *Werneriobryum* Herzog

Leucobryaceae Schimp. Type: *Leucobryum* Hampe
Atractylocarpus Mitt., *Brothera* Müll. Hal., *Bryohumbertia* P. de la Varde & Thér., *Campylopodiella* Cardot, *Campylopus* Brid., *Cladopodanthus* Dozy & Molk., *Dicranodontium* Bruch & Schimp., *Leucobryum* Hampe, *Microcampylopus* (Müll. Hal.) Fleisch., *Ochrobryum* Mitt., *Pilopogon* Brid., *Schistomitrium* Dozy & Molk.

Calymperaceae Kindb. Type: *Calymperes* Sw.
Arthrocormus Dozy & Molk., *Calymperes* Sw., *Exodictyon* Cardot, *Exostratum* L. T. Ellis, *Leucophanes* Brid., *Mitthyridium* H. Rob., *Octoblepharum* Hedw., *Syrrhopodon* Schwägr.

ORDER POTTIALES M. Fleisch.

Pottiaceae Schimp. Type: *Pottia* (Reichenbach) Fürnr.
Acaulon Müll. Hal., *Aloinia* Kindb., *Aloinella* Cardot, *Anoectangium* Schwägr., *Aschisma* Lindb., *Barbula* Hedw., *Bellibarbula* P. C. Chen, *Bryoceuthospora* H. A. Crum & L. E. Anderson, *Bryoerythrophyllum* P. C. Chen, *Calymperastrum* I. G. Stone, *Calyptopogon* (Mitt.) Broth., *Chenia* R. H. Zander, *Chionoloma* Dixon, *Crossidium* Jur., *Crumia* W. B. Schofield, *Dialytrichia* (Schimp.) Limpr., *Didymodon* Hedw., *Dolotortula* R. H. Zander, *Ephemerum* Schimp., *Erythrophyllastrum* R. H. Zander, *Erythrophyllopsis* Broth., *Eucladium* Bruch & Schimp., *Ganguleea* R. H. Zander, *Gertrudiella* Broth., *Globulinella* Steere, *Goniomitrium* Hook. f. & Wilson, *Gymnostomiella* M. Fleisch., *Gymnostomum* Nees & Hornsch., *Gyroweisia* Schimp., *Hennediella* Paris, *Hilpertia* R. H. Zander, *Hymenostyliella* E. B. Bartram, *Hymenostylium* Brid., *Hyophila* Brid., *Hyophiladelphus* (Müll. Hal.) R. H. Zander, *Hypodontium* Müll. Hal., *Leptobarbula* Schimp., *Leptodontiella* R. H. Zander & E. H. Hegew., *Leptodontium* (Müll. Hal.) Lindb., *Luisierella* Thér. & P. de la Varde, *Microbryum* Schimp., *Microcrossidium* J. Guerra & M. J. Cano, *Micromitrium* Austin, *Mironia* R. H. Zander, *Molendoa* Lindb., *Nanomitriopsis* Cardot, *Neophoenix* R. H. Zander & During, *Pachyneuropsis* H. Mill., *Phascopsis* I. G. Stone, *Plaubelia* Brid., *Pleurochaete* Lindb., *Pottiopsis* Blockeel & A. J. E. Sm., *Pseudocrossidium* R. S. Williams, *Pseudosymblepharis* Broth., *Pterygoneurum* Jur., *Quaesticula* R. H. Zander, *Reimersia* P. C. Chen, *Rhexophyllum* Herzog, *Sagenotortula* R. H. Zander, *Saitobryum* R. H. Zander, *Sarconeurum* Bryhn, *Scopelophila* (Mitt.) Lindb., *Splachnobryum* Müll. Hal., *Stegonia* Venturi, *Stonea* R. H. Zander, *Streptocalypta* Müll. Hal., *Streptopogon* Mitt., *Streptotrichum* Herzog, *Syntrichia* Brid., *Teniolophora* W. D. Reese, *Tetracoscinodon* R. Br., *Tetrapterum* A. Jaeger, *Timmiella* (De Not.) Schimp., *Tortella* (Lindb.) Limpr., *Tortula* Hedw., *Trachycarpidium* Broth., *Trachyodontium* Steere, *Trichostomum* Bruch, *Triquetrella* Müll. Hal., *Tuerckheimia* Broth., *Uleobryum* Broth., *Weisiopsis* Broth., *Weissia* Hedw., *Weissiodicranum* W. D. Reese, *Willia* Müll. Hal.

Pleurophascaceae Broth. Type: *Pleurophascum* Lindb.

Serpotortellaceae W. D. Reese & R. H. Zander Type: *Serpotortella* Dixon

Cinclidotaceae K. Saito Type: *Cinclidotus* P. Beauv.

SUBCLASS BRYIDAE Engl.

Superorder Bryanae (Engl.) Goffinet & W. R. Buck, comb. et stat. nov. Bryidae Engl. in Engl. & K. Prantl, Nat. Pflanzenfam. 1(3): 2. 1893.

ORDER SPLACHNALES (M. Fleisch.) Ochyra

Splachnaceae Grev. & Arn. Type: *Splachnum* Hedw.
Aplodon R. Br., *Moseniella* Broth., *Splachnum* Hedw., *Tayloria* Hook., *Tetraplodon* Bruch & Schimp., *Voitia* Hornsch.

Meesiaceae Schimp. Type: *Meesia* Hedw.
Amblyodon P. Beauv., *Leptobryum* (Bruch & Schimp.) Wilson, *Meesia* Hedw., *Neomeesia* Deguchi, *Paludella* Brid.

Appendix 1. Continued.

Order Orthotrichales Dixon
Orthotrichaceae Arn. Type: *Orthotrichum* Hedw.
Cardotiella Vitt, *Ceuthotheca* Lewinsky, *Codonoblepharon* Schwägr., *Desmotheca* Lindb., *Florschuetziella* Vitt, *Groutiella* Steere, *Leiomitrium* Mitt., *Leratia* Broth. & Paris, *Macrocoma* (Müll. Hal.) Grout, *Macromitrium* Brid., *Matteria* Goffinet, *Orthotrichum* Hedw., *Pentastichella* Müll. Hal., *Pleurorthotrichum* Broth., *Schlotheimia* Brid., *Sehnemobryum* Lewinsky-Haapasaari & Hedenäs, *Stoneobryum* D. H. Norris & H. Rob., *Ulota* D. Mohr, *Zygodon* Hook. & Taylor
Order Hedwigiales Ochyra
Hedwigiaceae Schimp. Type: *Hedwigia* P. Beauv.
Braunia Bruch & Schimp., *Bryowijkia* Nog., *Hedwigia* P. Beauv., *Hedwigidium* Bruch & Schimp., *Pseudobraunia* (Lesq. & James) Broth.
Helicophyllaceae Broth. Type: *Helicophyllum* Brid.
Rhacocarpaceae Kindb. Type: *Rhacocarpus* Lindb.
Pararhacocarpus Frahm, *Rhacocarpus* Lindb.
Order Bryales Limpr.
Catoscopiaceae Broth. Type: *Catoscopium* Brid.
Bartramiaceae Schwägr. Type: *Bartramia* Hedw.
Anacolia Schimp., *Bartramia* Hedw., *Breutelia* (Bruch & Schimp.) Schimp., *Conostomum* Sw., *Fleischerobryum* Loeske, *Flowersia* D. G. Griffin & W. R. Buck, *Leiomela* (Mitt.) Broth., *Neosharpiella* H. Rob. & Delgad., *Philonotis* Brid., *Plagiopus* Brid.
Bryaceae Schwägr. Type: *Bryum* Hedw.
Acidodontium Schwägr., *Anomobryum* Schimp., *Brachymenium* Schwägr., *Bryum* Hedw., *Leptostomopsis* (Müll. Hal.) J. R. Spence & H. P. Ramsay, *Mniobryoides* Hörmann, *Osculatia* De Not., *Perssonia* Bizot, *Plagiobryum* Lindb., *Rhodobryum* (Schimp.) Limpr., *Roellia* Kindb., *Rosulabryum* J. R. Spence
Phyllodrepaniaceae Crosby Type: *Phyllodrepanium* Crosby
Mniomalia Müll. Hal., *Phyllodrepanium* Crosby
Pseudoditrichaceae Steere & Z. Iwats. Type: *Pseudoditrichum* Steere & Z. Iwats.
Mniaceae Schwägr. Type: *Mnium* Hedw.
Cinclidium Sw., *Cyrtomnium* Holmen, *Epipterygium* Lindb., *Leucolepis* Lindb., *Mielichhoferia* Nees & Hornsch., *Mnium* Hedw., *Ochiobryum* J. R. Spence & H. P. Ramsay, *Orthomnion* Wilson, *Plagiomnium* T. J. Kop., *Pohlia* Hedw., *Pseudobryum* (Kindb.) T. J. Kop., *Pseudopohlia* R. S. Williams, *Rhizomnium* (Broth.) T. J. Kop., *Schizymenium* Harv., *Synthetodontium* Cardot, *Trachycystis* T. J. Kop.
Leptostomataceae Schwägr. Type: *Leptostomum* R. Br.
Aulacomniaceae Schimp. Type: *Aulacomnium* Schwägr.
Orthodontiaceae (Broth.) Goffinet Type: *Orthodontium* Wilson
Orthodontium Wilson, *Orthodontopsis* Ignatov & B. C. Tan
Superorder Rhizogonianae (M. Fleisch.) Goffinet & W. R. Buck, comb. et stat. nov. Bryales subordo Rhizogoniineae M. Fleisch., Musci Fl. Buitenzorg 4: xvi. 1923.
Order Rhizogoniales (M. Fleisch.) Goffinet & W. R. Buck, comb. et stat. nov. Bryales subordo Rhizogoniineae M. Fleisch., Musci Fl. Buitenzorg 4: xvi. 1923.
Rhizogoniaceae Broth. Type: *Rhizogonium* Brid.
Cryptopodium Brid., *Goniobryum* Lindb., *Hymenodon* Hook. f. & Wilson, *Hymenodontopsis* Herzog, *Leptotheca* Schwägr., *Mesochaete* Lindb., *Pyrrhobryum* Mitt., *Rhizogonium* Brid.
Calomniaceae Kindb. Type: *Calomnion* Hook. f. & Wilson
Hypnodendraceae Broth. Type: *Hypnodendron* (Müll. Hal.) Mitt.
Cyrtopodaceae M. Fleisch. Type: *Cyrtopus* (Brid.) Hook. f.
Bescherellia Duby, *Cyrtopodendron* M. Fleisch., *Cyrtopus* (Brid.) Hook. f.
Spiridentaceae Kindb. Type: *Spiridens* Nees
Franciella Thér., *Spiridens* Nees
Pterobryellaceae (Broth.) W. R. Buck & Vitt Type: *Pterobryella* (Müll. Hal.) A. Jaeger
Racopilaceae Kindb. Type: *Racopilum* P. Beauv.
Powellia Mitt., *Racopilum* P. Beauv.
Subclass Hypnidae W. R. Buck, Goffinet & A. J. Shaw
Superorder Ptychomnianae W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet
Order Ptychomniales W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet
Ptychomniaceae M. Fleisch. Type: *Ptychonion* (Hook. f. & Wilson) Mitt.

APPENDIX 1. Continued.

Cladomnion Hook. f. & Wilson, *Cladomniopsis* M. Fleisch., *Dichelodontium* Broth., *Endotrichellopsis* During, *Euptychium* Schimp., *Garovaglia* Endl., *Glyphothecium* Hampe, *Hampeella* Müll. Hal., *Ptychomniella* (Broth.) W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet, *Ptychomnion* (Hook. f. & Wilson) Mitt., *Tetraphidopsis* Broth. & Dixon

Superorder Hypnanae W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet

ORDER HOOKERIALES M. Fleisch.

Hypopterygiaceae Mitt. Type: *Hypopterygium* Brid.
Arbusculohypopterygium Stech, T. Pfeiffer & W. Frey, *Canalohypopterygium* W. Frey & Schaepe, *Catharomnion* Hook. f. & Wilson, *Cyathophorella* (Broth.) M. Fleisch., *Cyathophorum* P. Beauv., *Dendrocyathophorum* Dixon, *Dendrohypopterygium* Kruijer, *Hypopterygium* Brid., *Lopidium* Hook. f. & Wilson

Saulomataceae W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet Type: *Sauloma* (Hook. f. & Wils.) Mitt.
Ancistrodes Hampe, *Sauloma* (Hook. f. & Wilson) Mitt., *Vesiculariopsis* Broth.

Daltoniaceae Schimp. Type: *Daltonia* Hook. & Taylor
Achrophyllum Vitt & Crosby, *Adelothecium* Mitt., *Benitotania* H. Akiy., Yamaguchi & Suleiman, *Bryobrothera* Thér., *Calyptrochaeta* Desv., *Crosbya* Vitt, *Beeveria* Fife, *Daltonia* Hook. & Taylor, *Distichophyllidium* M. Fleisch., *Distichophyllum* Dozy & Molk., *Ephemeropsis* K. I. Goebel, *Leskeodon* Broth., *Leskeodontopsis* Zanten, *Metadistichophyllum* Nog. & Z. Iwats.

Schimperobryaceae W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet Type: *Schimperobryum* Margad.

Hookeriaceae Schimp. Type: *Hookeria* J. E. Sm.
Crossomitrium Müll. Hal., *Hookeria* J. E. Sm.

Leucomiaceae Broth. Type: *Leucomium* Mitt.
Leucomium Mitt., *Rhynchostegiopsis* Müll. Hal., *Tetrastichium* (Mitt.) Cardot

Pilotrichaceae Kindb. Type: *Pilotrichum* P. Beauv.
Actinodontium Schwägr., *Amblytropis* (Mitt.) Broth., *Brymela* Crosby & B. H. Allen, *Callicostella* (Müll. Hal.) Mitt., *Callicostellopsis* Broth., *Cyclodictyon* Mitt., *Diploneuron* E. B. Bartram, *Helicoblepharum* (Mitt.) Broth., *Hemiragis* (Brid.) Besch., *Hookeriopsis* (Besch.) A. Jaeger, *Hypnella* (Müll. Hal.) A. Jaeger, *Lepidopilidium* (Müll. Hal.) Broth., *Lepidopilum* (Brid.) Brid., *Neohypnella* E. B. Bartram, *Philophyllum* Müll. Hal., *Pilotrichidium* Besch., *Pilotrichum* P. Beauv., *Stenodesmus* (Mitt.) A. Jaeger, *Stenodictyon* (Mitt.) A. Jaeger, *Thamniopsis* (Mitt.) M. Fleisch., *Trachyxiphium* W. R. Buck

ORDER HYPNALES (M. Fleisch.) W. R. Buck & Vitt

Rutenbergiaceae (Broth.) M. Fleisch. Type: *Rutenbergia* Besch.
Neorutenbergia Bizot & Pócs, *Pseudocryphaea* Broth., *Rutenbergia* Besch.

Trachylomataceae (M. Fleisch.) W. R. Buck & Vitt Type: *Trachyloma* Brid.
Braithwaitea Lindb., *Trachyloma* Brid.

Fontinalaceae Schimp. Type: *Fontinalis* Hedw.
Brachelyma Cardot, *Dichelyma* Myrin, *Fontinalis* Hedw.

Climaciaceae Kindb.: *Climacium* F. Weber & D. Mohr

Pleuroziopsidaceae Ireland Type: *Pleuroziopsis* E. Britton

Amblystegiaceae G. Roth Type: *Amblystegium* Schimp.
Amblystegium Schimp., *Anacamptodon* Brid., *Bryostreimannia* Ochyra, *Campyliadelphus* (Kindb.) R. S. Chopra, *Campylium* (Sull.) Mitt., *Conardia* H. Rob., *Cratoneuron* (Sull.) Spruce, *Cratoneuropsis* (Broth.) M. Fleisch., *Drepanocladus* (Müll. Hal.) G. Roth, *Gradsteinia* Ochyra, *Hygroamblystegium* Loeske, *Hygrohypnum* Lindb., *Hypnobartlettia* Ochyra, *Koponenia* Ochyra, *Leptodictyum* (Schimp.) Warnst., *Limbella* (Müll. Hal.) Müll. Hal., *Palustriella* Ochyra, *Pictus* C. C. Towns., *Pseudo-calliergon* (Limpr.) Loeske, *Sanionia* Loeske, *Sasaokaea* Broth., *Sciaromiella* Ochyra, *Sciaromiopsis* Broth., *Scorpidium* (Schimp.) Limpr., *Sinocalliergon* Sakurai, *Serpoleskea* (Limpr.) Loeske, *Vittia* Ochyra

Calliergonaceae (Kanda) Vanderpoorten, Hedenäs, C. J. Cox & A. J. Shaw Type: *Calliergon* (Sull.) Kindb.
Calliergon (Sull.) Kindb., *Hamatocaulis* Hedenäs, *Loeskypnum* H. K. G. Paul, *Straminergon* Hedenäs, *Warnstorfia* Loeske

Helodiaceae (M. Fleisch.) Ochyra Type: *Helodium* Warnst.
Actinothuidium (Besch.) Broth., *Bryochenia* C. H. Gao & K. C. Chang, *Helodium* Warnst.

Rigodiaceae H. A. Crum Type: *Rigodium* Schwägr.

Leskeaceae Schimp. Type: *Leskea* Hedw.
Claopodium (Lesq. & James) Renauld & Cardot, *Fabronidium* Müll. Hal., *Haplocladium* (Müll. Hal.) Müll. Hal., *Hylocomiopsis* Cardot, *Leptocladium* Broth., *Leptopterigynandrum* Müll. Hal., *Lescuraea* Bruch & Schimp., *Leskea* Hedw., *Leskeadelphus* Herzog, *Leskeella* (Limpr.) Loeske, *Lindbergia* Kindb., *Mamillariella* Laz., *Miyabea* Broth., *Orthoamblystegium* Dixon & Sakurai, *Platylomella* A. L. Andrews, *Pseudoleskea* Bruch & Schimp., *Pseudoleskeella* Kindb., *Pseudoleskeopsis* Broth., *Ptychodium* Schimp., *Rigodiadelphus* Dixon, *Rozea* Besch., *Schwetschkea* Müll. Hal.

APPENDIX 1. Continued.

Thuidiaceae Schimp. Type: *Thuidium* Bruch & Schimp.
Abietinella Müll. Hal., *Boulaya* Cardot, *Cyrto-hypnum* (Hampe) Hampe & Lorentz, *Fauriella* Besch., *Pelekium* Mitt., *Rauiella* Reimers, *Thuidiopsis* (Broth.) M. Fleisch., *Thuidium* Bruch & Schimp.

Regmatodontaceae Broth. Type: *Regmatodon* Brid.

Stereophyllaceae (M. Fleisch.) W. R. Buck & Ireland Type: *Stereophyllum* Mitt.
Catagoniopsis Broth., *Entodontopsis* Broth., *Eulacophyllum* W. R. Buck & Ireland, *Juratzkaea* Lorentz, *Pilosium* (Müll. Hal.) M. Fleisch., *Sciuroleskea* Broth., *Stenocarpidium* Müll. Hal., *Stereophyllum* Mitt.

Brachytheciaceae G. Roth Type: *Brachythecium* Schimp.
Aerobryum Dozy & Molk., *Aerolindigia* M. Menzel, *Brachytheciastrum* Ignatov & Huttunen, *Brachythecium* Schimp., *Bryhnia* Kaurin, *Bryoandersonia* H. Rob., *Cirriphyllum* Grout, *Clasmatodon* Hook. f. & Wilson, *Donrichardsia* H. A. Crum & L. E. Anderson, *Eriodon* Mont., *Eurhynchiadelphus* Ignatov & Huttunen, *Eurhynchiastrum* Ignatov & Huttunen, *Eurhynchiella* M. Fleisch., *Eurhynchium* Bruch & Schimp., *Flabellidium* Herzog, *Helicodontium* Schwägr., *Homalotheciella* (Cardot) Broth., *Homalothecium* Schimp., *Juratzkaeella* W. R. Buck, *Kindbergia* Ochyra, *Lindigia* Hampe, *Mandoniella* Herzog, *Meteoridium* (Müll. Hal.) Manuel, *Myuroclada* Besch., *Nobregaea* Hedenäs, *Okamuraea* Broth., *Oxyrrhynchium* (Schimp.) Warnst., *Palamocladium* Müll. Hal., *Plasteurhynchium* Broth., *Platyhypnidium* M. Fleisch., *Pseudopleuropus* Takaki, *Pseudoscleropodium* (Limpr.) M. Fleisch., *Remyella* Müll. Hal., *Rhynchostegiella* (Schimp.) Limpr., *Rhynchostegium* Bruch & Schimp., *Schimperella* Thér., *Sciuro-hypnum* (Hampe) Hampe, *Scleropodium* Bruch & Schimp., *Scorpiurium* Schimp., *Squamidium* (Müll. Hal.) Broth., *Stenocarpidiopsis* M. Fleisch., *Tomentypnum* Loeske, *Zelometeorium* Manuel

Meteoriaceae Kindb. Type: *Meteorium* (Brid.) Dozy & Molk.
Aerobryidium M. Fleisch., *Aerobryopsis* M. Fleisch., *Barbella* M. Fleisch., *Barbellopsis* Broth., *Chrysocladium* M. Fleisch., *Cryphaeophilium* M. Fleisch., *Cryptopapillaria* M. Menzel, *Diaphanodon* Renauld & Cardot, *Duthiella* Renauld, *Floribundaria* M. Fleisch., *Lepyrodontopsis* Broth., *Meteoriopsis* Broth., *Meteorium* (Brid.) Dozy & Molk., *Neodicladiella* W. R. Buck, *Neonoguchia* S. H. Lin, *Pseudospiridentopsis* (Broth.) M. Fleisch., *Pseudotrachypus* P. de la Varde & Thér., *Sinskea* W. R. Buck, *Toloxis* W. R. Buck, *Trachycladiella* (M. Fleisch.) M. Menzel & W. Schultze-Motel, *Trachypodopsis* M. Fleisch., *Trachypus* Reinw. & Hornsch.

Myriniaceae Schimp. Type: *Myrinia* Schimp.
Austinia Müll. Hal., *Macgregorella* E. B. Bartram, *Merrilliobryum* Broth., *Myrinia* Schimp., *Nematocladia* W. R. Buck

Fabroniaceae Schimp. Type: *Fabronia* Raddi
Dimerodontium Mitt., *Fabronia* Raddi, *Ischyrodon* Müll. Hal., *Levierella* Müll. Hal., *Rhizofabronia* (Broth.) M. Fleisch.

Hypnaceae Schimp. Type: *Hypnum* Hedw.
Acritodon H. Rob., *Andoa* Ochyra, *Bardunovia* Ignatov & Ochyra, *Breidleria* Loeske, *Bryocrumia* L. E. Anderson, *Callicladium* H. A. Crum, *Calliergonella* Loeske, *Campylidium* (Kindb.) Ochyra, *Campylophyllum* (Schimp.) M. Fleisch., *Caribaeohypnum* Ando & Higuchi, *Chryso-hypnum* (Hampe) Hampe, *Crepidophyllum* Herzog, *Ctenidiadelphus* M. Fleisch., *Cyathothecium* Dixon, *Ectropotheciella* M. Fleisch., *Ectropotheciopsis* (Broth.) M. Fleisch., *Ectropothecium* Mitt., *Elharveya* H. A. Crum, *Elmeriobryum* Broth., *Entodontella* M. Fleisch., *Eurohypnum* Ando, *Foreauella* Dixon & P. de la Varde, *Gammiella* Broth., *Giraldiella* Müll. Hal., *Gollania* Broth., *Hageniella* Broth., *Herzogiella* Broth., *Homomallium* (Schimp.) Loeske, *Hondaella* Dixon & Sakurai, *Horridohypnum* W. R. Buck, *Hyocomium* Bruch & Schimp., *Hypnum* Hedw., *Irelandia* W. R. Buck, *Isopterygiopsis* Z. Iwats., *Leiodontium* Broth., *Leptoischyrodon* Dixon, *Macrothamniella* M. Fleisch., *Mahua* W. R. Buck, *Microctenidium* M. Fleisch., *Mittenothamnium* Henn., *Nanothecium* Dixon & P. de la Varde, *Ochyraea* Vána, *Orthothecium* Bruch & Schimp., *Phyllodon* Bruch & Schimp., *Plagiotheciopsis* Broth., *Platydictya* Berk., *Platygyriella* Cardot, *Podperaea* Z. Iwats. & Glime, *Pseudohypnella* (M. Fleisch.) Broth., *Pseudotaxiphyllum* Z. Iwats., *Ptilium* De Not., *Pylaisia* Schimp., *Pylaisiopsis* (Broth.) Broth., *Rhacopilopsis* Renauld & Cardot, *Rhizohypnella* M. Fleisch., *Sclerohypnum* Dixon, *Stenotheciopsis* Broth., *Stereodontopsis* R. S. Williams, *Syringothecium* Mitt., *Taxiphyllopsis* Higuchi & Deguchi, *Taxiphyllum* M. Fleisch., *Tripterocladium* (Müll. Hal.) A. Jaeger, *Vesicularia* (Müll. Hal.) Müll. Hal., *Wijkiella* Bizot & Lewinsky

Catagoniaceae W. R. Buck & Ireland Type: *Catagonium* Broth.

Pterigynandraceae Schimp. Type: *Pterigynandrum* Hedw.
Habrodon Schimp., *Heterocladium* Bruch & Schimp., *Iwatsukiella* W. R. Buck & H. A. Crum, *Myurella* Bruch & Schimp., *Pterigynandrum* Hedw., *Trachyphyllum* A. Gepp

APPENDIX 1. Continued.

Hylocomiaceae (Broth.) M. Fleisch. Type: *Hylocomium* Bruch & Schimp.
Ctenidium (Schimp.) Mitt., *Hylocomiastrum* Broth., *Hylocomium* Bruch & Schimp., *Leptocladiella* M. Fleisch., *Leptohymenium* Schwägr., *Loeskeobryum* Broth., *Macrothamnium* M. Fleisch., *Meteoriella* S. Okamura, *Neodolichomitra* Nog., *Orontobryum* M. Fleisch., *Pleurozium* Mitt., *Puiggariopsis* M. Menzel, *Rhytidiadelphus* (Limpr.) Warnst., *Rhytidiopsis* Broth., *Schofieldiella* W. R. Buck

Rhytidiaceae Broth. Type: *Rhytidium* (Sull.) Kindb.

Symphyodontaceae M. Fleisch. Type: *Symphyodon* Mont.
Chaetomitriopsis M. Fleisch., *Chaetomitrium* Dozy & Molk., *Dimorphocladon* Dixon, *Symphyodon* Mont., *Trachythecium* M. Fleisch., *Unclejackia* Ignatov, T. Kop. & D. Norris

Plagiotheciaceae (Broth.) M. Fleisch. Type: *Plagiothecium* Bruch & Schimp.
Buckiella Ireland, *Plagiothecium* Bruch & Schimp., *Struckia* Müll. Hal.

Entodontaceae Kindb. Type: *Entodon* Müll. Hal.
Entodon Müll. Hal., *Erythrodontium* Hampe, *Mesonodon* Hampe, *Pylaisiobryum* Broth.

Pylaisiadelphaceae fam. nov.
Sematophyllaceis affine, cellulis exothecii non collenchymatosis cellulis alaribus parviore plerumque non inflatis pseudoparaphylliis saepe filamentosis differt. Typus: *Pylaisiadelpha* Cardot, *Revue Bryologique* 39: 57. 1912.
Aptychella (Broth.) Herzog, *Brotherella* M. Fleisch., *Clastobryopsis* M. Fleisch., *Clastobryum* Dozy & Molk., *Heterophyllium* (Schimp.) Kindb., *Isocladiella* Dixon, *Isopterygium* Mitt., *Mastopoma* Cardot, *Platygyrium* Bruch & Schimp., *Pterogonidium* Broth., *Pseudotrismegistia* H. Akiy. & Tsubota, *Pylaisiadelpha* Cardot, *Taxitheliella* Dixon, *Taxithelium* Mitt., *Trismegistia* (Müll. Hal.) Müll. Hal., *Wijkia* H. A. Crum

Sematophyllaceae Broth. Type: *Sematophyllum* Mitt.
Acanthorrhynchium M. Fleisch., *Acroporium* Mitt., *Allionellopsis* Ochyra, *Aptychopsis* (Broth.) M. Fleisch., *Chinostomum* Müll. Hal., *Clastobryella* M. Fleisch., *Clastobryophilum* M. Fleisch., *Colobodontium* Herzog, *Donnellia* Austin, *Hydropogon* Brid., *Hydropogonella* Cardot, *Macrohymenium* Müll. Hal., *Meiotheciella* B. C. Tan, W. B. Schofield & H. P. Ramsay, *Meiothecium* Mitt., *Papillidiopsis* (Broth.) W. R. Buck & B. C. Tan, *Paranapiacabaea* W. R. Buck & Vital, *Potamium* Mitt., *Pterogoniopsis* Müll. Hal., *Piloecium* (Müll. Hal.) Broth., *Radulina* W. R. Buck & B. C. Tan, *Rhaphidostichum* M. Fleisch., *Schraderella* Müll. Hal., *Schroeterella* Herzog, *Sematophyllum* Mitt., *Timotimius* W. R. Buck, *Trichosteleum* Mitt., *Trolliella* Herzog, *Warburgiella* Müll. Hal.

Cryphaeaceae Schimp. Type: *Cryphaea* D. Mohr
Cryphaea D. Mohr, *Cryphidium* (Mitt.) A. Jaeger, *Cyptodon* (Broth.) M. Fleisch., *Cyptodontopsis* Dixon, *Dendroalsia* E. Britton, *Dendrocryphaea* Broth., *Dendropogonella* E. Britton, *Pilotrichopsis* Besch., *Schoenobryum* Dozy & Molk., *Sphaerotheciella* M. Fleisch.

Prionodontaceae Broth. Type: *Prionodon* Müll. Hal.

Leucodontaceae Schimp. Type: *Leucodon* Schwägr.
Antitrichia Brid., *Dozya* Sande Lac., *Eoleucodon* H. A. Mill. & H. Whittier, *Felipponea* Broth., *Leucodon* Schwägr., *Pterogonium* Sw., *Scabridens* E. B. Bartram

Pterobryaceae Kindb. Type: *Pterobryon* Hornsch.
Calyptothecium Mitt., *Cryptogonium* (Müll. Hal.) Hampe, *Henicodium* (Müll. Hal.) Kindb., *Hildebrandtiella* Müll. Hal., *Horikawaea* Nog., *Jaegerina* Müll. Hal., *Micralsopsis* W. R. Buck, *Muellerobryum* M. Fleisch., *Neolindbergia* M. Fleisch., *Orthorrhynchidium* Renauld & Cardot, *Orthostichidium* Dusén, *Orthostichopsis* Broth., *Osterwaldiella* Broth., *Penzigiella* M. Fleisch., *Pireella* Cardot, *Pseudopterobryum* Broth., *Pterobryidium* Broth. & Watts, *Pterobryon* Hornsch., *Pterobryopsis* M. Fleisch., *Pulchrinodus* B. H. Allen, *Renauldia* Müll. Hal., *Rhabdodontium* Broth., *Spriridentopsis* Broth., *Symphysodon* Dozy & Molk., *Symphysodontella* M. Fleisch.

Phyllogoniaceae Kindb. Type: *Phyllogonium* Brid.

Orthorrhynchiaceae S. H. Lin Type: *Orthorrhynchium* Reichardt

Lepyrodontaceae Broth. Type: *Lepyrodon* Hampe

Neckeraceae Schimp. Type: *Neckera* Hedw.
Baldwiniella M. Fleisch., *Bissetia* Broth., *Bryolawtonia* D. H. Norris & Enroth, *Caduciella* Enroth, *Crassiphyllum* Ochyra, *Cryptoleptodon* Renauld & Cardot, *Curvicladium* Enroth, *Dixonia* Horik. & Ando, *Dolichomitra* Broth., *Handeliobryum* Broth., *Himantocladium* (Mitt.) M. Fleisch., *Homalia* (Brid.) Bruch & Schimp., *Homaliadelphus* Dixon & P. de la Varde, *Homaliodendron* M. Fleisch., *Hydrocryphaea* Dixon, *Isodrepanium* (Mitt.) E. Britton, *Metaneckera* Steere, *Neckera* Hedw., *Neckeropsis* Reichardt, *Neomacounia* Ireland, *Noguchiodendron* Ninh & Pócs, *Pendulothecium* Enroth & S. He, *Pinnatella* M. Fleisch., *Porotrichodendron* M. Fleisch., *Porotrichopsis* Broth. & Herzog, *Porotrichum* (Brid.) Hampe, *Thamnobryum* Nieuwl., *Touwia* Ochyra

APPENDIX 1. Continued.

Echinodiaceae Broth. Type: *Echinodium* Jur.
Leptodontaceae Schimp. Type: *Leptodon* D. Mohr
Alsia Sull., *Forsstroemia* Lindb., *Leptodon* D. Mohr, *Taiwanobryum* Nog.
Lembophyllaceae Broth. Type: *Lembophyllum* Lindb.
Acrocladium Mitt., *Bestia* Broth., *Camptochaete* Reichardt, *Dolichomitriopsis* S. Okamura, *Fallaciella* H. A. Crum, *Fifea* H. A. Crum, *Isothecium* Brid., *Lembophyllum* Lindb., *Neobarbella* Nog., *Orthostichella* Müll. Hal., *Pilotrichella* (Müll. Hal.) Besch., *Weymouthia* Broth.
Myuriaceae M. Fleisch. Type: *Myurium* Schimp.
Eumyurium Nog., *Myurium* Schimp., *Oedicladium* Mitt., *Palisadula* Toyama
Anomodontaceae Kindb. Type: *Anomodon* Hook. & Taylor
Anomodon Hook. & Taylor, *Bryonorrisia* L. R. Stark & W. R. Buck, *Chileobryon* Enroth, *Curviramea* H. A. Crum, *Haplohymenium* Dozy & Molk., *Herpetineuron* (Müll. Hal.) Cardot, *Schwetschkeopsis* Broth.
Theliaceae (Broth.) M. Fleisch. Type: *Thelia* Sull.
Microtheciellaceae H. A. Mill. & A. J. Harr. Type: *Microtheciella* Dixon
Sorapillaceae M. Fleisch. Type: *Sorapilla* Spruce & Mitt.