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Original article

Bryophyte phylogeny and lineages: a review paper

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ABSTRACT

Plants play a crucial role in supporting the existenceof life. Plants are regulators of ecosystem processes; establish complex relationships with other organisms; and possess interesting biodiversification. Regarded as the ancestors of plants, most bryophytes lack extensive tissue organization and show substantial variety in shape and ecology. The bryophytes, or nonvascular seedless plants, are divided into three groups: mosses *(Bryophyta)*, hornworts *(Anthocerotophyta)*, and liverworts *(Marchantiophyta)*. Anchored on extant works and relevant literature, this review paper intended to trace the phylogeny of bryophytes and the within relationships of its lineages. Understanding these patterns is vital in unlocking plant evolution and future direction. The review paper sought to identify the position of bryophytes in plant evolution. Though traditionally liverworts were basal of the bryophytes, recent studies and molecular analysis show hornworts to be the first of the bryophytes. Mosses form a link between bryophytes and tracheophytes, the ancestors of land plants

KEYWORDS: *bryophytes; hornworts; liverworts; mosses; phylogeny*

1 INTRODUCTION

All land plants share a life cycle composed of two multicellular phases: one bearing the sex organs (the haploid gametophyte) and the other producing the spores (the diploid sporophyte) (Goffinet & Buck, 2013). Shaw and Renzaglia (2004) stated that liverworts, mosses, and hornworts, the bryophytes, are the only terrestrial plants having a dominant gametophyte generation present, unifying and exclusive, and innovative structural and reproductive attributes. In addition to their pioneering role in the rehabilitation of waste residual sites, bryophytes serve a variety of ecological functions, including providing habitat for invertebrates, slowing water flow through systems and therefore reducing erosion, and serving as seedbeds that promote germination. They are also known as "the canaries in the coal mine" and have long been utilized as environmental indicators because of their sensitivity to pollutants in the air and water (Budke et al., 2018).

According to Goffinet and Buck (2013), to the evolutionary plant biologist, bryophytes are significant inthat: (1) phylogenetically, they mark the transition from the algal ancestor of land plants to the vascular plants, and thereby the seed and flowering plants; and (2) morphologically and developmentally they may represent a stage in the gradual transformation from a gametophyte-dominant to a gametophyte-subordinate life cycle, and hence are essential to our understanding of the evolution of a complex independent sporophyte.

Although found nearly everywhere, bryophytes are mostly ignored because they possess small stature, features that are not common, and because much of the year, they are dormant. However, bryophytes are exceptionally diverse, with nearly 25,000 named species. According to Mishler and Churchill (1984), it has been apparent that progress in understanding the phylogenetic relationships of the green plants is currently limited less by a lack of empirical data than by inadequacies of prevailing theoretical approaches. However, as Hedderson, Chapman, and Rootes (1996) stated, advances in nucleic acid sequencing techniques raised hopes that the historical information resident in gene sequences might solve many previously intractable phylogenetic problems. These techniques have recently been utilized in the study of bryophyte phylogeny.

2 MATERIALS AND METHODS

Establishing the phylogenetic relationship of the bryophytes is essential in understanding the evolutionaryhistory of plants, as they are considered the first land plants to transition into terrestrial life. Thus, this review explored the phylogenetic relationship of the bryophytes and the relationship among members of the three bryophyte lineages, namely the hornworts, liverworts, and mosses. To select relevant literature and related works, data was sourced by identifying published works that aimed to uncover the evolution and phylogeny of thebryophytes and their lineages. Based on the available literature, this review determined the

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position of the bryophytes within plants. In the later part of this paper, the relationship among members of the three lineages is also discussed.

3 RESULTS AND DISCUSSION

Body of Review

BRYOPHYTE LINEAGES AND EVOLUTIONARY POSITION

Phylogenetic relationships of the bryophytes, defined traditionally to comprise the hornworts *(Anthoceropsida)*, liverworts *(Hepatopsida)*, and mosses *(Bryopsida),* are pivotal in understanding the evolutionary transition to a land flora. Remaining to be a significant unresolved matter in plant evolutionary biology is the question of the relationships among the three bryophyte lineages (Goffinet, Cox, Shaw, & Hedderson, 2001). Because bryophytes are small plants with limited and often changeable physical features, identifying and delimiting species can be difficult. Molecular data has helped determine evolutionary links between taxa and species diversity (Dantas, Valente, Carvalho-Silva & Camara, 2018).

Although many details of bryophyte genealogy remain unresolved, numerous recent analyses, using diverse data sources, show that the bryophytes occupy a phylogenetic position between the tracheophytes and the green algal ancestors of land plants (Hedderson, Chapman & Rootes, 1996). This is supported by Shaw and Renzaglia (2004), who stated that a factual inference from many current investigations on the phylogeny of streptophytes shows bryophytes as the first green plants to occupy land niches successfully. Sequence data from chloroplast-encoded rRNA genes supported the sister group relationship between tracheophytes and mosses and the placement of the hepatics basal to this clade (hornworts were not included); the support for these nodes was generally weak, however, as indicated by decay indices (Mishler & Churchill, 1984). Preliminary analyses of nuclear-encoded rRNA gene sequences (Waters et al., 1992) placed a hornwort + moss clade as sister to the tracheophytes with the liverworts remaining basal to other land plants. Still, the moss + hornwort node was weakly supported, and forcing the topology of Mishler and Churchill (1984) onto the rRNA tree required only one extra step.

Commonly, bryophytes are viewed as three monophyletic lineages, with a pending branching order (Mishler & Churchill, 1984). Qiu, Li, and Wang (2006) stated that bryophyte relationships remain unsettled although extant bryophytes are grouped into three lineages. Existing bryophytes are categorized into liverworts *(Marchantiophyta)*, hornworts *(Anthocerotophyta)*, and mosses *(Bryophyta)*. In addition, Murphy, Rost, and Barbour (2015) inferred that studies of bryophytes had provided a great deal of support for the following hypotheses: (1) land plants evolved only once from a single algal ancestor, specifically a charophyte; (2) the first land plants were bryophytes and appeared no later than the Ordovician period, about 475 million years ago; (3) the bryophytes form a non-monophyletic group (that is, the bryophytes gave rise to vascular plants); and (4) each of the three living bryophyte lineages--the hornworts, liverworts, and mosses--is monophyletic.

Figure 1 is a cladogram of relationships between the bryophytes and vascular plants. Hornworts are the basal-most lineage of land plants, although other hypotheses place liverworts in that position. Mosses are almost certainly the sister group to vascular plants.

In a study by Stech and Quandt (2014), it was concluded that within all three bryophyte groupings, higher-level phylogenetic relationships were resolved with high confidence to a large extent. This is especially true in mosses, where the numerous documented phylogenetic tree (Cox et al. 2004; Shaw et al. 2005; Stech & Quandt 2006; Goffinet et al. 2007; Quandt et al. 2007; Stech & Frey 2008) all seem to agree on a single explanation for the moss phylogeny's 'backbone' links. Although the trnL intron may still be considered a prime option, along with one or two other variable plastid or even nuclear markers, the best mix of markers may differ among all bryophytes (Liu, Yan, Cao & Ge, 2010). Furthermore, because plastid G2 introns (trnG, trnV, rpl16, trnK) and fast-evolving plastid genes like matK or ndhB are relatively long in comparison to sections of the plastid intergenic spacers but exhibit a lot of diversity, an increase in their use is expected.

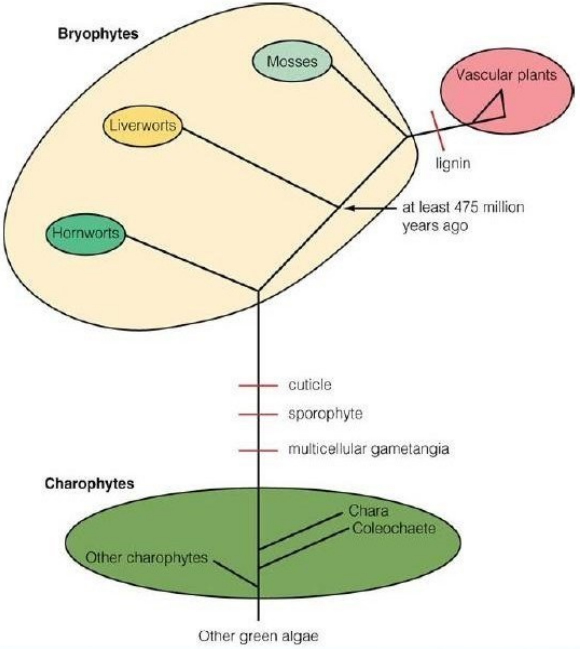

Figure 1. A cladogram adapted from Murphy, Rost and Barbour (2015)

HORNWORTS (Anthocerotophyta)

With about 200–250 species worldwide, Hornworts represent a crucial group for understanding plant diversification and evolution (Qiu, Li & Wang., 2006). The hornworts (Anthocerotophyta) are a small, isolated, and presumably ancient group of land plants, comprising 11(-12) genera with probably 100-150 species after generic revisions that are still due for the larger genera. According to Stotler and Crandall-Stotler (2005), such a small and homogeneous assembly comprises 100-150 inadequately delineated species. Studies on the interrelationships of hornworts based on morphology and the resulting classification scheme reveal no consensus at the genera, familial or order levels.

Distinct to hornworts is the extension of each sporophyte that involves a continuous seemingly indeterminate basipetal growth of an elongated sporangium. In one single hornwort, all stages of the spore development can be found, that is, from undifferentiated cells to mature spores. A continual spore production ensures dispersal throughout as long as the gametophyte persists. This method of sporophyte is not found in any other green plants, therefore, concealing the position of hornworts among other plant groups (Shaw & Renzaglia, 2004).

As cited by Stech, Quandt, and Frey (2003), apart from their symbiosis with cyanobacteria (Nostoc), which, however, occurs also in the liverwort family Blasiaceae (Blasio, Cavicularia) and in some mosses (e.g. Pleurozium schreberi), the hornworts differ from other bryophytes by several morphological and developmental characters, e.g. sex organ ontogeny, the unique intercalary meristem of the sporophyte, occurrence of pseudo-elaters in the sporangia, primary vertical division of the zygote (Mishler & Churchill 1984), and the gametophyte–sporophyte junction (Frey & Stech, 2005).

Monophyly of the Anthocerotophyta, as already widely accepted based on non-molecular characters, has so far been supported by all analyses based on coding DNA sequences that included more than one hornwort species (Hedderson, Chapman & Rootes, 1996), except for the 18S rDNA analysis of Soltis et al. (1999). The study results by Stech, Quandt, and Frey (2003), inferred from trnL intron sequences, are in concordance with the former results and show that monophyly of the hornworts is also observed at the molecular level if the number of species is increased. The trnL intron sequences distinguish hornworts, liverworts, mosses, and tracheophytes, which are all resolved as monophyletic (Stech, Quandt, & Frey (2003). However, relationships between these groups cannot be inferred from the trnL intron data alone.

There are twelve genera of hornworts that have been identified. The following genera are widely recognized (Shaw & Renzaglia, 2004): Megaceros, Anthoceros, Folioceros. Dendroceros, Notothylas, Phaeoceros. The other genera are named as follows, Aspiromitus, Hattorioceros, Leiosporoceros, Nothoceros, Mesoceros, and Sphaerosporoceros.

Supporting morphological inferences, molecular evidence indicates that the hornworts are monophyletic. Named because of its irregularly small and monolete smooth spores produced in isobilateral tetrads, the genus *Leiosporoceros* is sister to the remaining hornworts. A more detailed assessment of *Leiosporoceros dussii* shows both morphological and molecular features that haven't been identified nor described in any hornwort. Additionally, gene sequences of *Leiosporoceros* have deficient levels of RNA editing, implying differences from other hornworts who, in contrast, show extensive editing (Yoshida et al., 2010).

Figure 2, provided by Duff, Cargill, Villareal, and Renzaglia (2004), represents a widely accepted tree of the phylogeny of hornworts. It is one of the most parsimonious trees based on rbcL sequences from seven of the 11 named genera of hornworts *(Anthocerophyta).* Bootstrap percentages are shown below branches.

A feature found only in *Anthoceros* and *Folioceros* is the number of antheridia per cavity greater than 20 (Duff, Cargill, Villareal, & Renzaglia, 2004). However, unlike other hornworts where Nostoc is in discrete spherical colonies within the ventral thallus, *Leiosporoceros, Nostoc* is in branching strands that longitudinally run and are sequestered in the mid-region of the thallus. Likewise, in other taxa, ventral mucilage clefts that allow Nostoc entry and create colonies are absent in *Leiosporoceros.*

Leiosporoceros chloroplasts can also be distinguished from those of other hornworts. Starch is neatly collected around the organelle's periphery, with a center elaboration of photosynthetic membranes; there are no pyrenoids in chloroplasts. The similarities betweenLeiosporoceros and other hornworts reveal plesiomorphies within the group (Shaw & Renzaglia, 2004).

Anthoceros and *Folioceros* form a clade after *Leiosporoceros,* sister to other hornworts. Anthoceros, Folioceros, and Phaeoceros have rosette-like habits, big solitary chloroplasts with well-developed pyrenoids, and similar sporophyte morphology. However, dorsal lamellae, schizogenous mucilage cavities, and antheridia in vast groups of up to 50 per cavity separate Anthoceros and Folioceros from other hornworts, as opposed to 1–4 (–6) antheridia per cavity in other hornworts. RbcL data well support close affinities between Folioceros and Anthoceros, and most current classifications reflect this (Hyvonen, Kosinen, Smith Merrill, Hedderson, & Stenroos, 2004). The remaining hornworts are divided into two monophyletic groups: *Phaeoceros laevis sensu lato* plus *Notothylas* and *Megaceros* plus *Dendroceros*. Spiraled pseudoelater, absence of stomata, and solitary antheridia are morphological features that show a close relationship between *Megaceros* and *Dendroceros.*

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Dendroceros, the only epiphytic hornwort, features a thicker midrib with perforated wings, massive center pyrenoids in each plastid, and multicellular spores (Renzaglia & Vaughn, 2000).

Stomata are critical adaptations in the diversificationof terrestrial plants because they are structures that promote gas exchange. Their appearance in hornworts has been interpreted as either a synapomorphy with mosses and tracheophytes or a homoplastic acquisition within hornworts (Renzaglia & Vaugh, 2000). Stomata are found in *Leiosporoceros, Anthoceros*, and *Folioceros*, implying that they are plesiomorphic in hornworts and may be analogous to those found in mosses and tracheophytes. The loss of stomata in three or four hornwort lineages: *Notothylas, Dendroceros*, and *Megaceros,* is an actual occurrence of homoplasy (Shaw & Renzaglia, 2004).

Extant members of *Anthoceros, Leiosporoceros*, and *Phaeoceros* have a habit that may represent the ancestral condition in hornworts and be related to their joint presence on exposed soil. Other taxa's morphological variety is most likely the result of radiationand adaptation to specialized settings (Shaw & Renzaglia,2004).

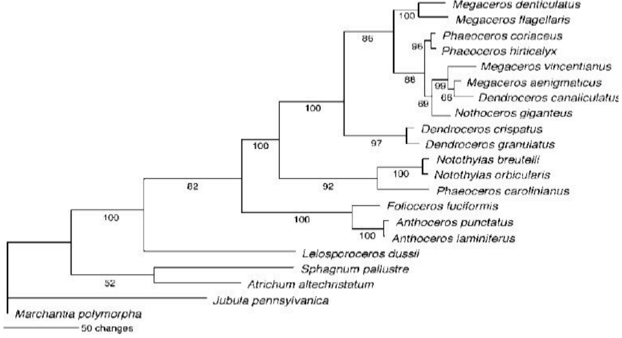

Figure 2. "Backbone" phylogeny of hornworts

LIVERWORTS (*Marchantiophyta*)

Liverworts, or *marchantiophyta*, with an extant diversity of about 6,000 species in about 350 genera, were separated from other lineages in the earliest diversification of plants on land (Heinrichs et al., 2007). Approximately liverworts comprise an order of 4500–5000 in 376 genera and 74 families (Stotler & Crandall-Stotler, 2008). The large majority of species belong to the *Jungermanniopsida* sub cl. *Jungermanniidae* or leafy liverwort group. According to Forrest et al. (2006), although the leafy liverworts contain most of the taxonomic diversity of the phylum, the most significant morphological diversity is expressed within the thalloid liverwort groups. Thalloid currently comprises around 500 species of simple thalloid *(Jungermanniopsida subcl. Metzgeriidae)* and 350 species of complex thalloid *(Marchantiopsida).*

Shaw and Renzaglia (2004) stated that the presenceof oil bodies, unique organelles in which terpenoids collect, distinguishes liverworts from hornworts and mosses. Mosses and hornworts, for example, create cytoplasmic oil droplets (typically triglycerides), but they are not sequestered in specialized organelles.

DNA sequence data and other molecular-level evidence have been used in the evolutionary reconstruction of liverworts over the last 20 years. A study by He-Nygren, Juslén, Ahonen, Glenny, and Piippo (2006) used three different methods of analysis: (1) direct optimization, (2) parsimony analysis with the program NONA, and (3) a Bayesian inference approach as implemented in the program MrBayes resolved liverworts as a monophyletic lineage. The study has offered strong support for several clades and new insights into the group's phylogenetic history with a broad representation of liverworts. Likewise, it also agrees with recently published studies (e.g., Forrest and Crandall-Stotler, 2004; Heinrichs et al., 2005) on the phylogenetic relationships of major liverwort groups.

Figure 3 illustrates the phylogenetic relationships of major liverwort clades. The topology is from a maximum likelihood analysis of 12 nuclear, plastid, and mitochondrial genes. Broken-bold branch indicates uncertainty in the placement of *Haplomitrium.*

Crandall-Stotler, Stotler, and Long (2009) anchoredon morphological characters to generate a cladistic analysis of liverworts. There were 34 taxa and 61 characters identified. As resolved by their analyses, complex thalloid *(Marchantiopsida)* and simple thalloid plus leafies *(Jungermanniopsida: Metzgeriidae, Jungermanniidae,* respectively) were the two main lineages. But the sampling of the analyses was not substantial enough to convey phylogenetic concerns, especially issues concerning the major clades.

Unlike other hepatic groupings, the complexthalloid liverworts have drought-resistant species. Although Marchantiopsida is monophyletic, molecular evidence does not always support traditional taxonomic relationships. Nucleotide sequence findings dispute the traditional morphological division of this liverwort class into three orders: Monocleales, Sphaerocarpales, and Marchantiales (Boisselier-Dubayle, Lambourdie, & Bischler, 2002). Additionally, parallel alterations in several lineages may explain the inconsistency between morphological and molecular trends.

Known as not a monophyletic group, Mezgeriidae conventionally comprises 30 highly varied genera of leafy and thalloid forms (Shaw & Renzaglia, 2004). Distinguished from leafy liverworts, the simple thalloid genera are anacrogynous. That is, they possess archegonia which are produced along the mod-thallus of either the central, lateral, or ventral shoots. The largest liverwort groups, the leafy liverworts, include 4000-6000 species. They thrive in diverse terrestrial and aquatic habitats and are specifically diversified in high-moisture environments (Shaw & Renzaglia, 2004).

Two significant clades of subclass Jungermanniidae were resolved by Davis (2004) through a liverwort backbone tree based on 12 loci. One clade is composed of the taxa with complicated-bilobed or transverse leaves. This clade comprises *Porellaceae, Lejeuneaceae, Jubulaceae,* and *Radulaceae.* On the other hand, the other clade includes the other leafy liverworts families. Additionally, a more extensive taxon analysis (with 81 liverworts, two mosses, a hornwort based on 26S rDNA, two plastid loci, and mitochondrial nad5 sequences), the same two leafy liverwort clades were resolved.

In every significant hepatic group, leaves or leaflike lobes have been present. *Treubia* and *haplomoitrium* possess appendages that are leafy. Taxa within the marchantioid line, Sphaerocarpos, and Blasio evolved leafy habits. With leafy gametophytes, *Phyllothallia, Pleurozia*, and Noterolada are spread among simple thalloid taxa. These plants have leaves that are usually inserted transversely. These leaves are formed from either wedge-shaped, tetrahedral, or lenticular apical cell types. Produced from two leaf initials derived from a tetrahedral apical cell, bifid leaves are an autapomorphy of the Jungermanniidae.

In addition, according to Shaw and Renzaglia (2004), there remain critical unanswered questions in liverwort phylogenies, such as the placement of *Pleurozia*among the simple thalloid vs. leafy clades, the position of Haplomitrium (and Treubia), and the precise positions of *Sphaerocarpos* and *Lunularia* within the complex thalloid lineage.

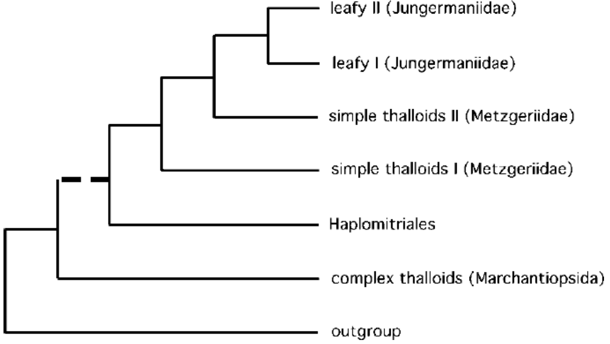

Figure 3. “Backbone” tree showing phylogenetic relationships among the major clades of liverworts, redrawn from Davis (2004).

MOSSES (Bryophyta)

Comprising the second largest of the major land plant lineages, Mosses include an estimated 12,800 species (Crosby, Magill, Allen, & He, 1999). Mosses are characterized by high ecological and morphological diversity. Conventionally, the bryophyte groups: mosses, hornworts, and liverworts, were categorized as classes of the Bryophyta division. They are the direct descendants of the earliest divisions in land-plant phylogeny and are functionally important in many terrestrial ecosystems (Rydin, 2009). The precise placement of mosses in plant phylogeny — i.e., their position relative to the two other bryophyte clades (liverworts and hornworts) and the vascular plants — has been controversial (Chang & Graham, 2011).

According to Stech and Frey (2008), molecular data confirmed that mosses comprise several isolated basal lineages, represented by morphologically and ecologically distinct extant taxa such as Takakia and Sphagnum Andreaea, Andreaeobryum, Oedipodium, Tetraphis, the Polytrichaceae and Buxbaumia, which probably have long independent phylogenetic histories. Takakia and Sphagnum are the earliest diverging moss taxa in molecular phylogenies (e.g., Newton et al. 2000, Cox et al. 2004, Qiu et al. 2006, Newton et al. 2007). That Takakia is a moss and not a liverwort was confirmed by analysis of DNA sequences and phylogenomic characters such as the distribution of mitochondrial introns. On the one hand, most molecular studies resolve Takakia and Sphagnum as sister genera, although only partly with high statistical support (Stech & Frey, 2008).

The Bayesian reconstruction by Cox, Goffinet, Shaw, and Boles (2004), which utilized sequences from four species of liverworts as the outgroup, presented that Takakia and Sphagnum are clade sisters to all remaining mosses (Shaw & Renzaglia , 2004). The most favored "backbone" for moss was derived from an analysis of eight genes representing the mitochondria, plastids, and nuclear genome of 30 samples representing significant strains, based on previous studies (Cox et al., 2004).

Figure 4 depicts the backbone phylogenetic tree of mosses and the relationship among its major clades which are characterized by different peristome types. This is the single optimal tree under maximum likelihood (Cox et al., 2004).

The gametophytes of sphagnum moss and Takakia are no more different. The gametophytes of sphagnum moss are small, simple in structure, and reminiscent of liverworts, while the gametophytes of sphagnum moss are large and feature a series of endemic traits. Two basic types of peristomes, nematodontous and arthrodontous, are distinguished by whether the tooth comprises whole dead cells or only the debris of the cell wall. Nematodontous peristome is heterogeneous in both developmental and mature structures. The so-called Polytrichum type consists of 32 or 64 teeth whose tips are connected by a membranous epigram. Arthrodontous peristomes encompass mainly mobileular wall material periclinal plates; maximum of the anticlinal partitions are resorbed before maturity. Arthrodontous peristomes may also have one or earrings of teeth. Diplolepideous peristomes normally encompass an outer ring of sixteen teeth, the exostome, and an internal extra sensitive ring, the endostome. Buxbaumiaceae and Diphysiaceaeperistomes are identified as intermediate between nematodontous and arthrodontous. Buxbaum is characterized as having other teeth derivative of whole cells while the inner teeth are arthrodontous. The diphyscium peristome is completely arthrodontous, however, it is a pleated cone, unlike any other

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arthrodontous peristome.

As stated by Shaw and Renzaglia (2004), additional work on the developmental anatomy of the peristome is also needed in conjunction with the ongoing phylogeny work. As with the development of the unique Timia peristome, the development of the peristoma cell layer of Ishizuchisou (lacking peristome) is important. Resolving moss, especially the closely related family-level relationships of the pleura, requires an extended dataset based on not only one or two genes but five, but perhaps 15 to 20 genes.

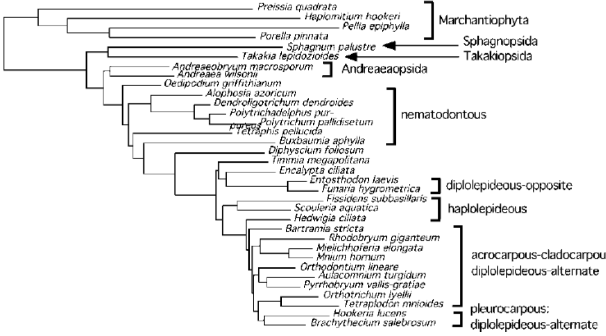

Figure 4. ‘‘Backbone’’ phylogenetic tree of mosses showing relationships among major clades. Adapted from Cox et al., (2004).

4 CONCLUSIONS AND RECOMMENDATION

Bryophytes are almost certainly not a monophyletic group because they gave rise to vascular plants. It is unclear which bryophyte lineage represents the first to diverge. However, numerous studies support bryophytes as a group and occupy a phylogenetic position between the tracheophytes and land plants, the green algal ancestors of land plants. Though there is an ambiguity as to which of the three bryophyte lineages first diverged, recent molecular and morphological analyses suggest it may have been the hornworts. Compared to liverworts and hornworts, relationships between large moss clades are relatively well resolved. With unique terrestrial adaptations such as sporophyte basal elongation and fragile tissue internalization, bryophytes continue to provide important information on the early evolution of terrestrial plants. Critical unanswered questions in liverwort phylogeny remain. Unresolved questions about moss phylogeny include the relationship between *Takakia,* sphagnum moss, *Andreaea*, the origin and evolution of the major peristome types, and the acrocalpic ancestral nature of the pleural calpic taxon. Undeniably, technology is dynamic, and it is constantly moving forward. Molecular technologies are improving at a rate that is unpredictable and incomprehensible.However, the relationship among members of each lineage is still vague; their resolution is not far from beingrealized.

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