



Universiteit
Leiden
The Netherlands

Contributions to the phylogeny of the haplolepidaceous mosses

Bonfim Santos, M.

Citation

Bonfim Santos, M. (2024, January 23). *Contributions to the phylogeny of the haplolepidaceous mosses*. Retrieved from <https://hdl.handle.net/1887/3714301>

Version: Publisher's Version

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/3714301>

Note: To cite this publication please use the final published version (if applicable).

Chapter 1

General Introduction

What are mosses?

Bryophytes comprise three lineages: hornworts, liverworts, and mosses. Although the monophyly of bryophytes is still debated (Puttick et al., 2018; Wickett et al., 2014), they share a unique trait among the land plants: in all bryophytes the life cycle differs from the other land plants (the vascular plants) in having a dominant, branched gametophyte and short-lived sporophyte (Vanderpoorten & Goffinet, 2009). Among the bryophytes, the mosses, classified as division Bryophyta Schimp. (Frey & Stech, 2009; Goffinet et al., 2009; Goffinet & Buck, 2004; Vanderpoorten & Goffinet, 2009) or subdivision Bryophytina Engl. (Kadereit et al., 2014) can be recognised by their leafy gametophyte, seta (sporangial stalk) elongation prior to spore maturation, and capsules (sporangia) with a columella (see Figure 1) (Frey & Stech, 2009; Vanderpoorten & Goffinet, 2009). Due to these unifying morphological traits the mosses were long recognised as a natural group, which was later confirmed by phylogenetic analyses of molecular data (Qiu et al., 2006). As a species-rich group with ca. 12500 species in ca. 120 families and ca. 860 genera, mosses are morphologically diverse in both their gametophytic and sporophytic characters (Frey & Stech, 2009).

A brief overview of moss classifications

The mosses are currently arranged in eight classes and, within their most speciose class, Bryopsida Pax, seven subclasses (Figure 2; Goffinet & Buck, 2020; Liu et al., 2019), according to morphological features and to the results of molecular phylogenetics (D. Bell et al., 2020; Chang & Graham, 2014; Cox et al., 2004, 2010; Frey & Stech, 2009; Goffinet et al., 2009; Goffinet & Buck, 2020; Liu et al., 2019; One Thousand Plant Transcriptomes Initiative et al., 2019). Moss relationships, as resolved with molecular phylogenetic methods, are largely congruent with some of the sporophyte characters initially adopted to classify mosses. The mode of dehiscence of the capsule for spore release, and the presence or absence and characteristics of one or two rings of filaments or teeth around the opening of the capsule (the peristome, which controls the spore release) were the main characters used in the early moss classification systems (e.g. by Brotherus and Fleischer; cf. Vitt, 1984). In contrast, gametophyte characters used in early classifications seem to be much less congruent with the moss relationships as inferred by molecular phylogenetics. The position of the perichaetia (i.e., archegonia and modified leaves around them), for instance, was used to define major divisions in some classifications (see Vitt, 1984), however only one character state, pleurocarpy (perichaetia produced on lateral, differentiated branches), corresponds to a synapomorphy. In contrast, acrocarpy (perichaetia produced terminally in the main stem) is a plesiomorphic condition and the posteriorly defined cladocarpy (perichaetia produced terminally in lateral

branches) arose multiple times in moss evolution (Goffinet et al., 2009; La Farge-England, 1996; Vanderpoorten & Goffinet, 2009).

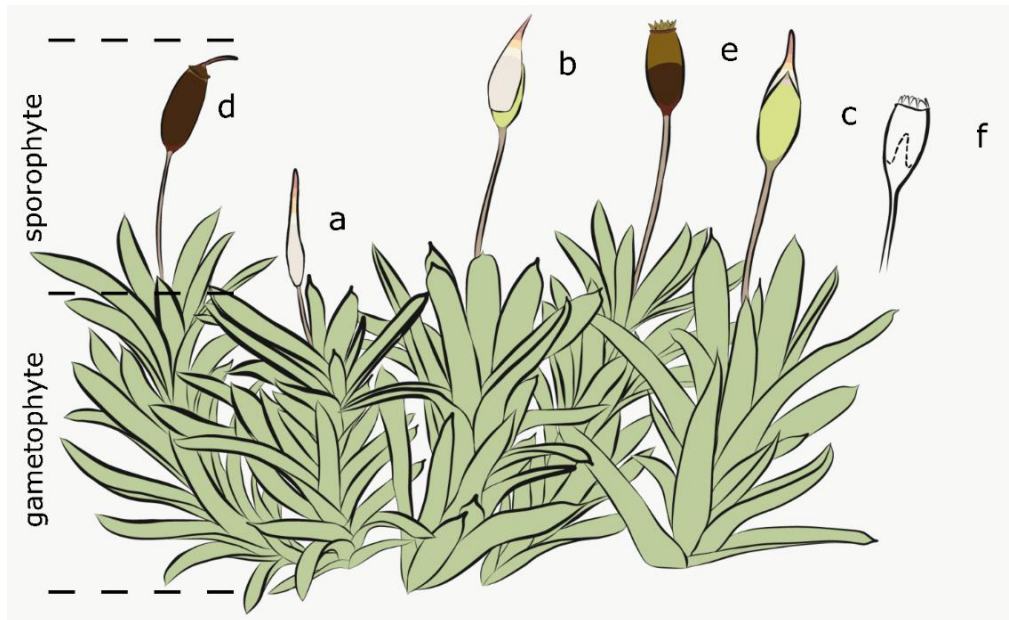


Figure 1. General morphology and diagnostic traits of mosses, as opposed to other lineages of land plants, exemplified by a drawing of *Octoblepharum Hedw.*: leafy gametophytes and the short-lived monosporangiate sporophytes in different stages of development: **a**: seta still elongating, capsule immature (before meiosis), covered by the calyptra*; **b**: seta elongated, capsule partially enlarged, covered by the calyptra*; **c**: capsule enlarged (after meiosis), with immature spores; **d**: capsule with mature spores and operculum visible after the calyptra* has fallen off; **e**: capsule open, half empty of spores, with peristome visible after the operculum has fallen off; **f**: outlines of the columella (central column of sterile tissue; dashed) and spore sac inside a capsule. *The calyptra, the protective cap that covers the capsule through its development, is not part of the sporophyte, but formed by gametophytic tissue derived from the archegonia.

Five classes of mosses characteristically do not have peristomes (i.e., are eperistomate or gymnostomous). Those classes differ from one another in the mode of dehiscence of their capsules, among other characters (Frey & Stech, 2009). In Takakiopsida Stech & W. Frey capsules open along a single, spiralled longitudinal slit, in Andreaeopsida J.H. Schaffn. and Andreaebryopsida Goffinet & W.R. Buck along four longitudinal slits, forming valves, and in Sphagnopsida Schimp. and Oedipodiopsida Goffinet & W.R. Buck via a differentiated lid (the operculum). Furthermore, Sphagnopsida and Andreaeopsida can be distinguished from other moss classes by the presence of a gametophytic stalk to elevate the sporangium (the pseudopodium) instead of the more common sporophytic seta.

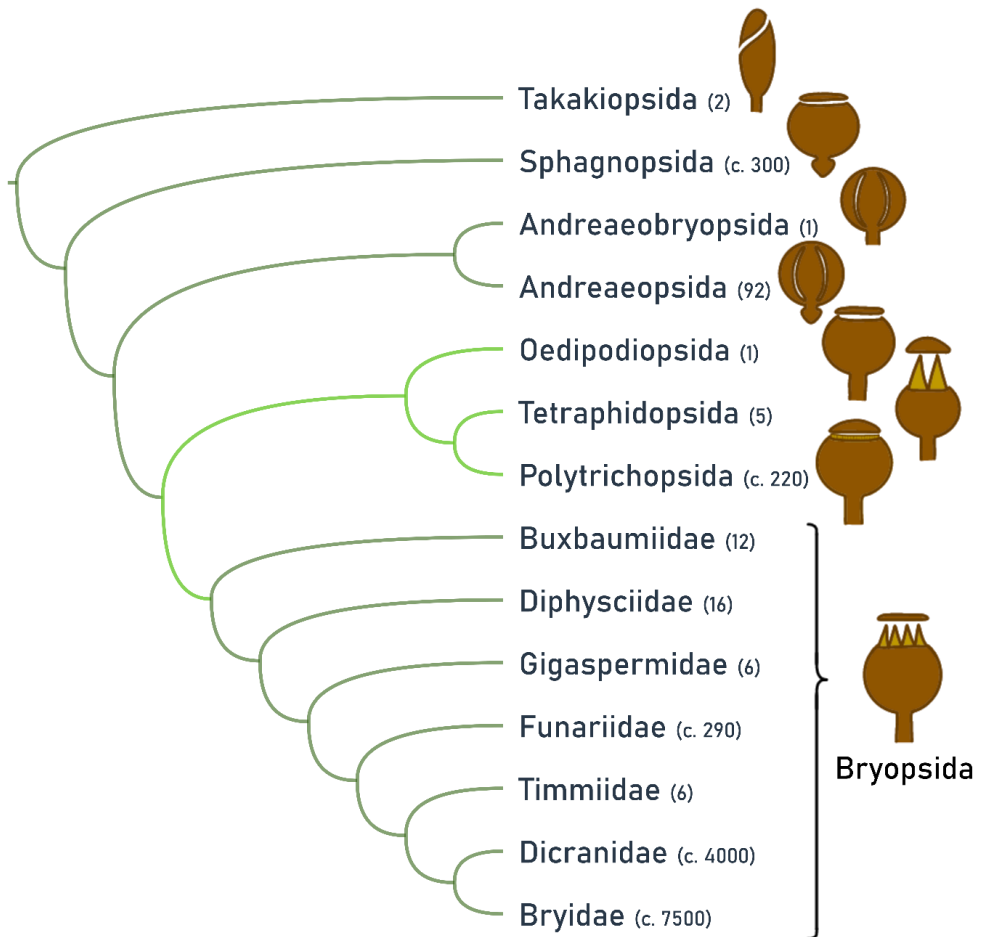


Figure 2. Major moss lineages: relationships, number of species and sporophyte characters for the eight classes. *Oedipodiopsida*, *Tetrachidopsida*, *Polytrichopsida* and *Bryopsida* form a well-supported clade, however the relationships between these four classes are not yet resolved with confidence (and are marked with light green branches to indicate that).

The three classes of peristomate mosses (with peristome; *Tetrachidopsida* Goffinet & W.R. Buck, *Polytrichopsida* Doweld, and *Bryopsida*) are operculate (with cases of secondary losses of peristome/operculum) (Frey & Stech, 2009; Goffinet et al., 2009). Their higher level classification is based on the peristome morphology (with support of molecular phylogenies; e.g. Chang & Graham, 2014; Liu et al., 2012). Peristome teeth are formed by the outer (OPL), primary (PPL), and inner (IPL) peristomial cell layers of the capsule amphithecium (i.e., the

outer one of two tissues in the embryonic capsule; the inner tissue is called endothecium) (Figure 3c, d), and differences in the ontogeny result in the broad variation observed (Edwards, 1979, 1984). The teeth vary in structure (i.e., formed by entire cells or by cell wall remnants, the peristome plates), number of rings or rows of peristome teeth (one or two, i.e., single or double peristomes), shape, and ornamentation (Goffinet et al., 2009).

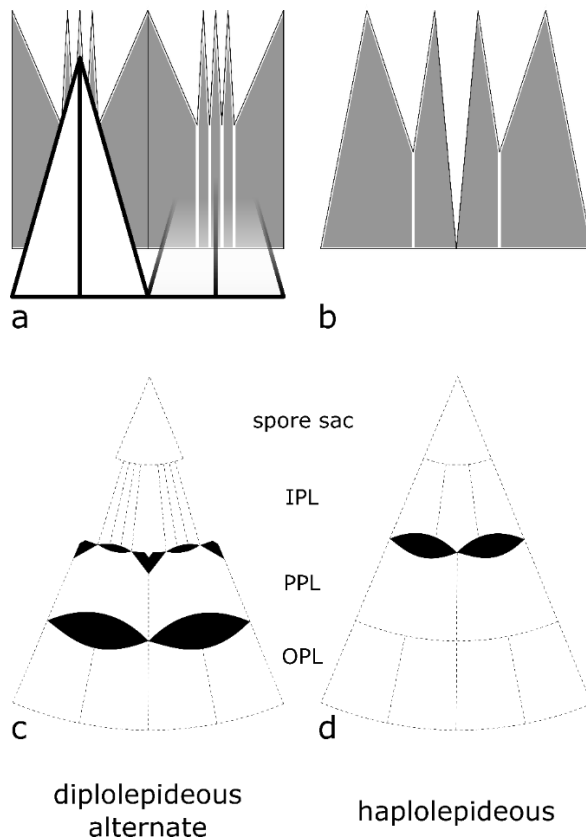


Figure 3. Two examples of arthrodontous peristomes and their cell layers. **a, b**: views from the outside. The plates forming the peristome teeth are represented with distinct outlines and filling according to which peristomial cell layer they originate from: outer layer (OPL) by thick black lines and white filling, primary layer (PPL) by thin black lines without filling, and inner layer (IPL) by thick white lines with grey filling. **c, d**: transverse section of the capsule at the height of the peristome teeth, showing the cell walls which are degraded during maturation of the peristome in dashed lines, and the remaining cell walls which form the plates of the peristome teeth highlighted in solid black. The capsule wall (exothecium) and the OPL, PPL, and IPL originate from the amphithecium, while the columella and spore sac originate from the endothecium. **a, c**. Diplolepidous alternate, Bryum-type peristome, 4:2:4–12, **b, d**. Haplolepidous, Dicranum-type peristome, 4:2:3. The peristomial formula OPL:PPL:IPL is derived from the number of cells in each layer in 1/8 of the capsule circumference. All schemes show 1/8 of the capsule circumference.

The species in Tetraphidopsida and Polytrichopsida have one ring of peristome teeth formed by bundles of entire, elongated cells (nematodontous peristome), the former with four massive, erect teeth, the latter with numerous short teeth and a thin membrane, the epiphragm, closing the mouth of the capsule (Frey & Stech, 2009; Goffinet et al., 2009). The species in Bryopsida have one or two rings of peristome teeth, which are formed by pairs of plates and most frequently are capable of hygroscopic movements (arthrodontous peristome; Figure 3) (Frey & Stech, 2009; Gallenmüller et al., 2018; Goffinet et al., 2009). Some characteristics of the arthrodontous peristome can be described by the peristomial formula, devised by Edwards (1979). It serves as a short descriptor of the number of cell columns in each of the peristomial layers that determine the number of plates which form the outer and inner surfaces of the peristome teeth in the peristome rings. The OPL and PPL contribute to the structure of the outer ring of teeth (the exostome), and the PPL and IPL contribute to the inner ring (the endostome) (see Figure 3).

The vast majority of moss species belong to Bryopsida (ca. 98%), and its seven subclasses can also be recognised based on peristome variation (Frey & Stech, 2009). Buxbaumiidae Doweld, Diphysciidae Ochyra, and Timmiidae Ochyra, some of the least speciose lineages, comprise quite particular peristome types. Their peristomes may be considered evolutionary intermediate stages between nematodontous and arthrodontous peristomes: thus not typically arthrodontous, and resembling in some features the nematodontous peristomes (Edwards, 1984). The Gigaspermidae Stech & W. Frey, the fourth of the least species-rich subclasses of Bryopsida, have either gymnostomous or cleistocarpous (i.e., without a differentiated operculum) capsules.

The remaining subclasses have either haplolepidous or diplolepidous peristome types, patterns which were first described by Philibert (Philibert, 1884; Taylor, 1962). Philibert classified the peristome as haplolepidous or diplolepidous based on the number of columns of plates on the outer surface of each of the outer (or single ring of) peristome teeth: one column of plates in the haplolepidous peristomes and two columns in the diplolepidous peristomes (Goffinet et al., 2009; Taylor, 1962). Philibert remarked that (according to his observations and interpretation) haplolepidous peristomes never had a second ring of teeth, while a second ring of teeth occurred in nearly all diplolepidous moss families (cf. Taylor, 1962). That led to the simplified and incorrect notion that haplolepidous and diplolepidous peristomes differ by the number of rings of peristome teeth and not by the structure of the peristome teeth in terms of peristome plates as defined by Philibert (cf. Taylor, 1962) and later refined by other authors (e.g. Edwards, 1979, 1984).

The Funariidae Ochyra have diplolepidous opposite peristomes (with exostome and endostome teeth opposite to each other), the Bryidae Engl. have diplolepidous alternate peristomes (with the exostome teeth alternate with the endostome teeth), and the Dicranidae Doweld, the study group of this thesis, have haplolepidous (or double-haplolepidous) peristomes (Edwards, 1984; Fedosov et al., 2016a).

The backbone evolutionary relationships of mosses are resolved with high support, based on phylogenetic analyses of different (sets of) molecular markers (Chang & Graham, 2011, 2014; Cox et al., 2004, 2010; Liu et al., 2012, 2019; Magombo, 2003; Newton et al., 2000; Wahrmund et al., 2010). The monophyly of each of the classes and subclasses and their relationships as depicted in Figure 2 are a consensus among the mentioned studies.

The haploleptideous mosses

The haploleptideous mosses (Dicranidae) comprise ca. 30% of the moss diversity, with about 4000 species (Figure 2; Frey & Stech, 2009). Since their characterization by Philibert (1884; cf. Taylor, 1962), the haploleptideous mosses have been considered a natural group, and their monophyly was strongly supported by molecular phylogenetic studies (e.g. Chang & Graham, 2014; Cox et al., 2010; Goffinet & Cox, 2000; Tsubota et al., 2003). Haploleptideous peristomes can be recognised by their peristomial formula 4:2:3 (modified in some taxa), the number 3 in the IPL being caused by an asymmetric pattern of cell divisions (Edwards, 1979). In typical haploleptideous peristomes with 16 (endostome) teeth each tooth has two ventral peristomes plate columns of uneven width, correspondent to one and a half cells of the IPL per tooth (Figure 3; Edwards, 1979; Hedderson et al., 2004; La Farge et al., 2000).

As expected for a group of this size, the haploleptideous mosses comprise a wide range of sporophytic and gametophytic morphological traits (Frey & Stech, 2009; Goffinet et al., 2009; Vitt, 1984). The sporophyte variation is associated with life strategies and optimization of spore dispersal (Goffinet et al., 2011; Vitt, 1984), for example, with a trend of peristome reduction in epiphytic bryophyte groups (Olsson et al., 2009) also observed among the haploleptideous mosses (e.g. in the Calymperaceae Kindb. s.l. clade; Fisher et al., 2007). Some taxa with modified peristomes (i.e., with a fully developed exostome and rudimentary endostome, double peristomes with a fully developed exostome, or reduced to absent forms) were for that reason not at first recognised as belonging in this group (e.g. *Catoscopium* Brid., *Ephemerum* Hampe, *Pseudoditrichum* Steere & Z. Iwats.; Fedosov et al., 2016a; Goffinet et al., 2011; Ignatov et al., 2015; H. A. Miller, 1979; Vitt, 1984). Number and shape of the peristome teeth, their patterns of ornamentation, and thickening of the peristome plates all vary, and were traditionally used to characterise the haploleptideous moss orders (Edwards, 1979; Fedosov et al., 2016a; Frey & Stech, 2009; Shaw, 1985). The capsules vary in shape, orientation, and mode of dehiscence (some are cleistocarpous; Frey & Stech, 2009). The seta varies in length, bending, and even torsion (e.g. in the Leucobryaceae Schimp.; Frahm, 1991).

The gametophyte variation is also sometimes associated with physiological or ecological adaptation (Goffinet et al., 2009; Vanderpoorten & Goffinet, 2009; Vitt, 1984). Most haploleptideous mosses are acrocarpous (Frey & Stech, 2009; Goffinet et al., 2009), however, some groups developed the cladocarpous gametophyte architecture, as *Bryowijkia* Nog. (Cox et al., 2010; Touw, 1993). There are also examples of neoteny within Dicranidae, as in *Micromitrium* Austin and *Ephemerum*, which have gametophytes characteristically little developed and minute (Goffinet et al., 2011). Among other characters, leaf shape, structure of

the leaf costa (the multilayered median part of the leaf), and cell shape, size and wall ornamentation in the leaf lamina (the single layered part of the leaf) vary as well (Frey & Stech, 2009; Goffinet et al., 2009; Vanderpoorten & Goffinet, 2009).

The most common types of costa structure in the haplolepidous mosses (namely the *Dicranum*-type, the *Pottia*-type, and a less specialised one with a homogeneous costa) are characterised by a predominance of chlorophyllose cells (Frey & Stech, 2009). They vary in the specialization of the costa cell layers, which can be differentiated in guide cells, stereids, and epidermal cells, arranged in several ways. Figure 4 (left) shows an example of such costa structure, the genus *Dicranella* (Müll.Hal.) Schimp. A remarkably contrasting pattern is the so-called leucobryoid costa, named after the genus *Leucobryum* Hampe, which is possibly an adaptation to enhance gas exchange (Robinson, 1985, 1990; Vanderpoorten & Goffinet, 2009). Most of the costa cells are enlarged and hyaline (hyalocysts), interconnected by pores, except for 1(-3) layer(s) of small chlorophyllose cells (chlorocysts), which causes these plants to have their characteristic glaucous aspect (Figure 4, right; Goffinet et al., 2008). According to Robinson (1985), large air bubbles extending through the web of hyalocysts would provide the conditions for appropriate gas exchange for the photosynthesis in the chlorocysts, which are enclosed by the leucocysts and thus not directly exposed to air. Furthermore, in the plants with a leucobryoid costa (leucobryoid mosses) the leaf lamina is narrow, sometimes restricted to the leaf base, and the costa occupies most of the leaf width. This highly specialised morphology is so distinct from the morphology of the other haplolepidous mosses that these plants were at first classified together in a single family (Leucobryaceae; Schimper, 1856), despite the differences in their sporophyte characteristics. Earlier molecular phylogenies already indicated that the leucobryoid mosses are polyphyletic, with the exact number of lineages yet to be determined (Cox et al., 2010; Inoue & Tsubota, 2014), and thus have shown that the gametophytic similarities of the leucobryoid lineages are a very curious case of evolutionary convergence.



Figure 4. Two costa types of the haplolepidous mosses. Left: *Dicranella varia* (Hedw.) Schimp., with a *Dicranum*-type costa. Left, above: habit; below: leaf in cross section showing a structure formed by different types of chlorophyllose cells, without hyalocysts. Right: *Leucobryum juniperoideum* (Brid.) Müll.Hal., with a leucobryoid costa. Right, above: habit, showing glaucous aspect of the plants; below: leaf in cross section showing a broad costa with layers of enlarged, porous hyalocysts above and below a single layer of small, diamond-shaped chlorocysts. Pictures by Michael Lüth reproduced with permission of the author (from Lüth, 2020).

Systematics of the haplolepidous mosses

The orders in the Dicranidae were defined mainly by peristome features, especially the patterns of thickening and ornamentation of the peristome plates (e.g. Fleischer, 1900-1923; Vitt, 1984). However, detailed studies of the peristome demonstrated that the existing variability did not fully correspond to the ordinal classification (Edwards, 1979) and the introduction of molecular phylogenetic analyses to moss systematics additionally demonstrated the limited correspondence between the ordinal and family level classification and phylogenetic relationships. In the classification by Goffinet & Buck (2021) there are eight main groups of haplolepidous mosses: the unranked group Protohaplolepidae (Hedderson et al., 2004) plus seven orders (Archidiales Limpr., Bryoxiphiales H.A. Crum & L.E. Anderson,

Dicranales M. Fleisch., Grimmiales M. Fleisch., Pottiales M. Fleisch., Pseudoditrichales Ignatov & Fedosov, and Scouleriales Goffinet & W.R. Buck). A simplified classification for the Dicranidae with only three orders (one of them a broadly circumscribed Dicranales including most protohaplolepidous lineages and Pottiaceae Schimp., among others) was also recently adopted in the literature (Hodgetts et al., 2020).

Higher level molecular phylogenetic studies of (or including) the haplolepidous mosses have been performed since the late 1990s (e.g. N. E. Bell & Newton, 2004; Cox et al., 2010; Fedosov et al., 2015; Fedosov et al., 2016a, 2016b; Goffinet et al., 1998, 2001, 2011; Hedderson et al., 1999, 2004; Hernández-Maqueda, Quandt, Werner, et al., 2008; Ignatov et al., 2015; Inoue & Tsubota, 2014; La Farge et al., 2000, 2002; Newton et al., 2000; O'Brien, 2007; Stech, 1999a, 1999b; Stech et al., 2012; Stech & Frey, 2008; Tsubota et al., 2003, 2004; Wahrmund et al., 2010; Werner et al., 2004, 2007a, 2013), using in their analyses a range of molecular markers from all three genomes – the most widely used being the chloroplast *rbcl* gene and *trnS-trnF* region and the mitochondrial *nad5* intron. These studies resolved a tree of the haplolepidous mosses with two major groups: the protohaplolepidous grade and the core haplolepidous clade (Figure 5). The protohaplolepidous grade comprises a series of species-poor clades which were resolved at the base of the haplolepidous moss tree, including families which previously were either not considered to be haplolepidous mosses (Catoscopiaceae Broth., Drummondaceae Goffinet, Pseudoditrichaceae Steere & Z. Iwats.), considered to be part of core haplolepidous families (Chrysoblastellaceae Ignatov & Fedosov, Distichiaceae Schimp., Flexitrichaceae Ignatov & Fedosov, Hymenolomataceae Ignatov & Fedosov, Scouleriaceae S.P. Churchill, Timmiellaceae Y. Inoue & H. Tsubota), or (only one case) considered as isolated lineages of uncertain placement within Dicranidae (Bryoxiphiaceae Besch.). Four of these clades were classified in their own orders, existing (Bryoxiphiales) or newly described (Catoscopiales Ignatov & Ignatova, accepted by Frey & Stech (2009), Pseudoditrichales, and Scouleriales), and three others were described as new families, but without a discussion on their ordinal placement (Distichiaceae, Flexitrichaceae, Timmiellaceae).

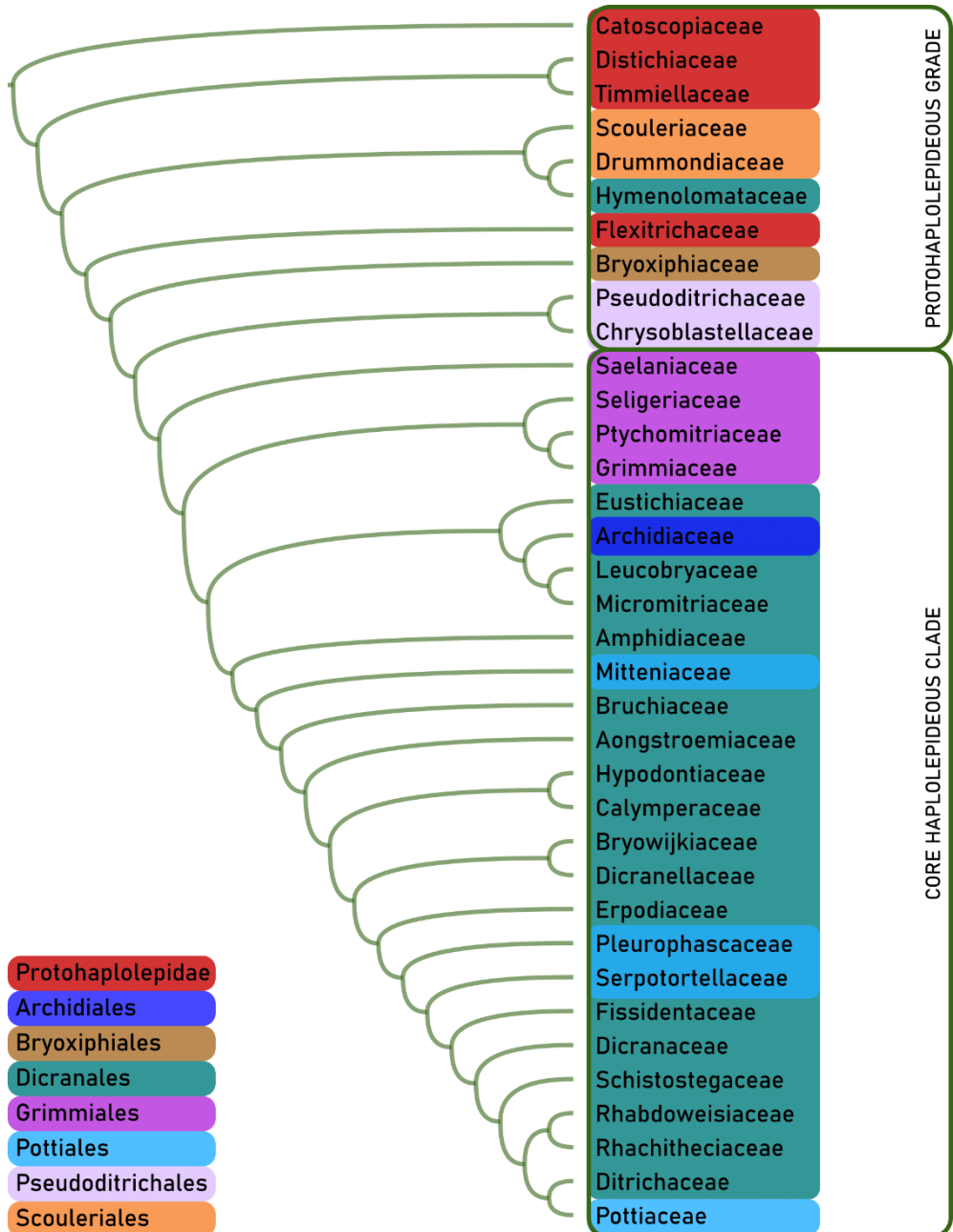


Figure 5. A summary of the supported relationships between haplolepidous moss families.

The core haplolepeidous clade (e.g. Cox et al., 2010; Fedosov et al., 2016a; Stech et al., 2012) comprises the majority of the haplolepeidous moss species. The traditional orders (Dicranales, Grimmiiales, Pottiiales, Syrrhopodontales Dixon) are part of this group, as well as some taxa previously not known to belong to the haplolepeidous mosses (e.g., *Archidium* Brid., *Ephemerum*, *Mittenia* Lindb.). Most of the new additions were transferred to existing haplolepeidous moss orders, except *Archidium* and *Mittenia*, which were placed in Dicranidae in their own previously described orders (in Frey & Stech, 2009; the Mitteniaceae Broth. were placed in Pottiiales in Goffinet et al., 2008). Among the three traditional haplolepeidous moss orders still accepted in current classifications, Grimmiiales was the only monophyletic one, after some changes in its circumscription (Fedosov et al., 2016a; Goffinet & Buck, 2004; Tsubota et al., 2003). The monophyly of Pottiiales as presently circumscribed was not supported, since *Hypodontium* Müll.Hal. and *Serpotortella* Dixon were resolved in a clade with the Dicranaceae Schimp. and other Dicranales families (Cox et al., 2010; Fedosov et al., 2016a; Stech et al., 2012). Finally, Dicranales has the most problematic circumscription since its families were scattered all over the haplolepeidous tree, and due to the difficulty to characterise it morphologically, given the variation it comprises. As currently circumscribed (Frey & Stech, 2009; Goffinet et al., 2009; Goffinet & Buck, 2021), the orders do not correspond to the haplolepeidous peristome types as traditionally defined (cf. Edwards, 1979). While Edwards (1979) described six main peristome types largely correspondent to the haplolepeidous moss ordinal classification at that time (one of each Dicranales, Fissidentales M. Fleisch., Grimmiiales, Pottiiales and Syrrhopodontales, plus the seligerioid type), the same orders (those still accepted in the present) nowadays comprise mixed peristome types (e.g. Dicranales, comprising plants with dicranoid, fissidentoid and syrrhopodontoid peristomes). Moreover, further anatomical and morphological studies of the peristome, in some cases coupled with phylogenetic analyses, revealed that the diversity of the haplolepeidous peristome is even greater than as described by Edwards (1979, 1984), for instance with modified peristomes as that of *Pseudoditrichum* (Fedosov et al., 2016a; Shaw, 1984).

Molecular phylogenetic studies also contributed to improving the lower-level classification of the haplolepeidous mosses. The largest family, Pottiaceae, was resolved as monophyletic, and except for some rather small additions (e.g. *Ephemerum*; Goffinet & Cox, 2000) and exclusions (e.g. *Luisierella* Thér. & P. de la Varde and *Timmiella* (De Not.) Limpr.; Inoue & Tsubota, 2014), its circumscription remained largely unchanged (Goffinet & Buck, 2004). In contrast, one of the main changes resulting from molecular phylogenies was probably the re-circumscription of the Dicranaceae. The family was historically broadly defined based on a widespread character, the dicranoid haplolepeidous peristome, coupled with a rather little specialised gametophyte morphology, with few exceptions (Schimper, 1856). Phylogenetic analyses have shown that the family actually comprised a few clades that are not closely related, which were described/resurrected as separate families (e.g. Aongstroemiaceae De Not., Dicranellaceae Stech; Frey & Stech, 2009; La Farge et al., 2000, 2002; Stech, 1999a; Stech & Frey, 2008).

The re-circumscription of the Dicranaceae also influenced the classification of the leucobryoid mosses. Their classification was revised even before the supporting results of molecular

phylogenetic studies which showed this morphological pattern had multiple origins, however the relationships of the leucobryoid taxa remain to be further investigated. The genus *Octoblepharum* Hedw., most frequently classified in the Calymperaceae, is yet undersampled, and its closest relationships unclear. Further studies are also necessary for the morphologically heterogeneous but molecularly strongly supported Leucobryaceae, which presently comprise both leucobryoid and dicranoid plants, but within which the phylogenetic relationships between the plants with the two morphological patterns were not yet established with confidence.

The monophyly of other (weakly) morphologically circumscribed haplolepidous moss taxa also remains to be tested. Some of these taxa are species-rich and display great gametophytic and sporophytic variability, but remain very little studied, both in terms of taxonomical revisions and molecular phylogenetic studies. One of them is the family Ditrichaceae Limpr., which was resolved as highly polyphyletic in recent studies (Fedosov et al., 2015; Fedosov et al., 2016a). Part of its newly discovered phylogenetic diversity, which extends across the proto- and core haplolepidous mosses, was described as new or resurrected families (e.g., Distichiaceae, Saelaniaceae Ignatov & Fedosov), resulting in a more refined classification also in terms of the morphological diversity of the Ditrichaceae s.l. Nevertheless, the still unresolved/unsupported relationships in the Ditrichaceae s.s. demand further studies and will likely require further taxonomic changes. But there are taxa in an even worse state, as the genus *Dicranella* (Dicranellaceae). With more than 150 species and great morphological variation, the genus has so far been represented in molecular phylogenetic studies by only three species, one of which was found to belong in a different family, the Aongstroemiaceae (Stech, 1999c; Stech et al., 2012).

Aims and outline of the thesis

This thesis aims to infer relationships and clarify circumscriptions of selected haplolepidous mosses, focusing on the taxa formerly classified in the family Dicranaceae and on plants with a leucobryoid leaf morphology. The chosen study cases illustrate potential conflicts between the (morphological) circumscription of taxa and their supposed evolutionary relationships. The phylogenetic analyses presented in this manuscript were based on molecular markers of the three genomes: the nuclear ribosomal ITS1-5.8S-ITS2 region, the mitochondrial *nad5* G1 intron, and the chloroplast regions *trnS-trnF* and *atpB-rbcL* spacer. The results of the molecular phylogenetic analyses served as a framework for the interpretation of the morphology of the study taxa, allowing the re-evaluation of their circumscriptions in an integrative taxonomic approach.

Chapter 2 focuses on the relationships and circumscription of the leucobryoid genus *Octoblepharum*. The genus was most often placed within the family Calymperaceae, however an alternative taxonomic position in its own family, Octoblepharaceae (Cardot) A. Eddy ex M. Menzel, was proposed. In this thesis, the phylogenetic position of *Octoblepharum* was studied based on its largest sampling so far, to address whether there is morphological and molecular

data support to the classification of the genus in its own family, and to contribute to the understanding of the circumscriptions of its species.

The origin of the leucobryoid morphology within the morphologically heterogeneous family Leucobryaceae remains unclear since relationships within the family were not yet resolved with high support. No study so far targeted the relationships on this level in the Leucobryaceae, and in other studies where the family was represented the sampling of its genera was limited and few molecular markers were applied. In **Chapter 3** phylogenetic analyses were performed to infer the suprageneric relationships within the Leucobryaceae, based on a sampling representing 11 out of its 14 genera (excluded only the rare genera which were never sampled for molecular data), and including ancestral state reconstruction analyses for selected morphological characters. The goal was to evaluate and improve morpho-molecular circumscriptions of the family and its genera. Hypotheses for the evolution of important taxonomic characters were applied to help clarifying the usefulness of such characters in the classification of the family.

Chapter 4 focuses on widespread, morphologically diverse, and yet little studied dicranoid taxa. Families Aongstroemiaceae and Dicranellaceae have been accepted in the latest moss classifications as segregates of the Dicranaceae, but their circumscriptions remain poorly defined. The families and most of their genera, including the type genera *Aongstroemia* Bruch & Schimp. and *Dicranella*, lack thorough taxonomic studies and are little represented in molecular phylogenetic studies. Moreover, the small sampling overlap for the families between different molecular phylogenetic studies greatly restricts the understanding about the phylogenetic relationships in these diverse groups of plants. The sampling for these families was extended with newly sequenced species, especially representing the genus *Dicranella*, and combined all available sequences from other studies to maximise the taxon sampling. This data was analyzed in the context of an alignment containing representatives of 37 out of the 38 haplolepideous families (sensu Frey & Stech, 2009; except the family Viridivelleraceae I.G. Stone which was never sampled for molecular data). Are changes needed to the circumscriptions of Aongstroemiaceae, Dicranellaceae and their genera?

