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PHYLOGENY AND CLASSIFICATION OF THE MARCHANTIOPHYTA

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Input from molecular phylogenetics in the past five years has substantially altered concepts of systematic relationships among liverworts. While these studies have confirmed the monophyly of phylum Marchantiophyta, they have demonstrated that many previously recognised ranks within the hierarchy are unnatural and in need of modification. Changes in the ranks of suborder and above have been proposed by various workers, but modifications in the circumscription of genera and families are still required. A comprehensive, phylogenetic classification scheme that integrates morphological data with molecular hypotheses is presented. The scheme includes diagnoses and publication citations for all names above the rank of genus. All currently recognised genera are listed alphabetically in their respective families; subfamilies are not indicated. Major modifications and novel alignments of taxa are thoroughly discussed, with pertinent references provided. Jungermanniaceae is redefined and Solenostomataceae fam. nov. is formally described to accommodate some of the genera excluded from it.

Keywords. Classification scheme, family diagnoses, liverworts.

INTRODUCTION

Historically, classification schemes have been intuitively constructed to show relationships among organisms based upon degree of morphological similarity or difference. Major changes in classification generally reflected the addition of newly discovered organisms and new interpretations of anatomical characters. In *Species Plantarum*, the starting point for liverwort nomenclature, Linnaeus (1753) recognised the single genus *Jungermannia* to comprise both leafy and simple thalloid taxa, relegated the complex thalloid taxa to *Targionia*, *Marchantia* and *Riccia*, and associated *Blasia* with the complex thalloid group by placing it between *Marchantia* and *Riccia*. By the early 1800s, the 25 liverwort species treated by Linnaeus (1753) under *Jungermannia* [two additional *Jungermannia* species actually belonged to the moss *Andreaea*] had been partitioned independently by Raddi (1808, 1818), Gray (1821), Dumortier (1822, 1835), Corda (1829) and Nees von Esenbeck (1833) into 21 genera, with three different generic names sometimes applied to the same taxon.

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As botanical exploration expanded, new systems of classification were proposed to accommodate the increasing numbers of genera being described. Notable among these were the comprehensive classifications of Endlicher (1841), who adopted the de Jussieu (1789) natural order name Hepaticae (Latinised from the Greek ηπατοσ = hepatos) for the group; Gottsche *et al.* (1844–1847), who provided the first worldwide treatment of liverworts; and Schiffner (1893), who followed Leitgeb (1877) and divided the Jungermanniales into two subgroups, the akrogynae and the anakrogynae.

In addition to presenting a hierarchy of relatedness, natural systems of classification also reflect evolutionary assumptions. In the classifications of Endlicher (1841), Campbell (1891) and Cavers (1910–1911), taxa were arranged in an 'ascending' series, compatible with the theory that sporophytes evolved from simple to complex structures by progressive elaboration of sterile tissues (Bower, 1890). In such systems, *Riccia* and other complex thalloids were considered ancestral and erect, radially symmetric leafy liverworts with massive sporophytes, derived. In contrast, the classification schemes of Gottsche *et al.* (1844–1847), Evans (1939), Schljakov (1972, 1975), Schuster (1984) and Crandall-Stotler & Stotler (2000) assumed a model of reductive evolution of sporophytes (Church, 1919), sometimes accompanied by reduction in size and/or complexity of the gametophyte. As a consequence, in Crandall-Stotler & Stotler (2000), *Monoclea* was considered ancestral in the complex thalloids and *Riccia* derived; in simple thalloids, *Haplomitrium* was ancestral and *Metzgeria* derived; and in the Jungermanniidae, *Schistochila* was ancestral and *Cololejeunea* derived. Both the relationships among leafy, simple thalloid and complex thalloid lineages and the evolutionary trends hypothesised within each have been highly dependent upon which of these scenarios of sporophyte evolution has been applied.

In the past five years, the application of molecular methods to the unravelling of liverwort phylogeny has generated new insights into the evolutionary history of the group and revolutionised liverwort classification. For example, the long-held dogma that leafy, simple thalloid, and complex thalloid morphologies define three monophyletic groups is no longer acceptable. Of these, only the complex thalloid morphology is restricted to a single, monophyletic group. In all multi-locus reconstructions, taxa previously classified in the Metzgeriidae (Crandall-Stotler & Stotler, 2000) are resolved among four of the six backbone lineages (e.g. Forrest *et al.*, 2006; He-Nygrén *et al.*, 2006; Heinrichs *et al.*, 2007). Treubiales and Haplomitriales, which were traditionally considered only remotely related to each other (Schuster, 1984), are resolved as a monophyletic group that is sister to the rest of the liverworts; the Blasiales are sister to the Marchantiidae in a monophyletic Marchantiopsida; and the remaining simple thalloid taxa comprise two lineages, which have been designated as Pelliidae and Metzgeriidae (He-Nygrén *et al.*, 2006). The leafy liverworts, or Jungermanniidae, are monophyletic, with the exclusion of *Pleurozia*, which is resolved in the newly defined Metzgeriidae. This relationship, like many others resolved in molecular phylogenies, is incongruent with past phylogenetic interpretations of morphological data

(Crandall-Stotler & Stotler, 2000). Analyses of character evolution have demonstrated that many of the morphological characters previously used to define genera, families and even suborders are homoplastic (Crandall-Stotler *et al.*, 2005). In some groups (e.g. Pelliidae) more highly differentiated gametophytes are derived, and in others (e.g. Marchantiidae) there are trends towards gametophyte simplification. Sporophytes likewise have undergone reductive evolution in some groups (e.g. Jubulineae), but this is not the trend in all lineages (e.g. Lophocoleineae).

New insights provided by molecular phylogenetics have precipitated numerous modifications to the taxonomic hierarchy of liverworts (e.g. Frey & Stech, 2005, 2008; Heinrichs *et al.*, 2005; Forrest *et al.*, 2006; He-Nygrén *et al.*, 2006). With the exception of Frey & Stech (2005, 2008), all recently proposed schemes recognise the three major backbone lineages to correspond to classes, namely, the Haplomitriopsida, Marchantiopsida and Jungermanniopsida. Frey & Stech (2005: fig. 1) have applied class rank to later divergences and nested them within four superclasses. In their scheme, the jungermannioid lineage is divided between Superclass III (most simple thalloids) and Superclass IV (leafy liverworts and the Metzgeriidae), and there is an overall inflation of ranks throughout the hierarchy. We consider the three-class system to more accurately mirror the phylogenetic history of the Marchantiophyta and consequently, have built our hierarchy around that premise.

With but a few exceptions, recent classification schemes have considered only the ranks of suborder and above and have not addressed the modifications that must also be made in family level circumscriptions. The comprehensive classification scheme presented herein integrates morphology with current hypotheses generated from molecular analyses to circumscribe families as well as higher ranks, and to provide diagnoses of all taxa at all ranks above genus. In the diagnoses, morphological characters have been redefined to reflect current concepts of homology (Crandall-Stotler *et al.*, 2008). For example, gynoecial structures are defined as follows: pseudoperianth refers only to structures in Marchantiopsida that are derived from the archegonial stalk; perichaetial pseudoperianth, to perianth-like structures that form from the pre-fertilisation, inner perichaetium in Pelliidae; caulocalyx, to perianth-like structures that form from thallus tissue after fertilisation in Pelliidae; involucre, to enclosures of thalline origin in the Marchantiopsida; and perianth, to tubular enclosures of the inner perichaetium in *Pleurozia* and Jungermanniidae. In the past, the flask-shaped antheridial chambers with apical ostioles found in Pelliales and Sphaerocarpales have been termed ‘involucres’ and/or ‘antheridial ostioles’ (Schuster, 1992; Bischler, 1998). However, neither of these terms accurately reflects the homology of these elevated chambers to the sunken antheridial chambers of the Marchantiales (Crandall-Stotler & Stotler, 2000). Furthermore, ‘antheridial ostiole’ actually defines a pore-like opening in an antheridium through which sperm are released (Magill, 1990). Consequently, these structures are referred to as perigonial chambers, with notation as to whether they are embedded, partially emergent, or fully emergent on the thallus.

This treatment updates and expands upon the classification by Crandall-Stotler *et al.* (2008), with the addition of family level diagnoses, publication citations for all ranks above genus, and discussions of major modifications in taxon alignments. We recognise that families are sometimes morphologically heterogeneous, especially in the Jungermanniidae, and consequently, family diagnoses may not apply *in toto* to every genus in the family. This scheme reflects our current state of knowledge concerning genus level relationships. Both the arrangement of taxa and the homologies inferred will most certainly be subject to revision as new ontogenetic, ultrastructural and molecular data accumulate. Significant features, phylogenetic implications and justifications of this scheme are briefly discussed below.

DISCUSSION

1. Class Haplomitriopsida

The stem lineage of the Haplomitriopsida is estimated to have diverged from the rest of the liverworts in the Early Devonian (Heinrichs *et al.*, 2007). Despite their strikingly different habits, the relationship between Haplomitriaceae and Treubiaceae is robustly supported in all multi-locus molecular analyses. These taxa share a suite of morphological characters that have been reconstructed as plesiomorphies for hepatics (Crandall-Stotler *et al.*, 2005; Renzaglia *et al.*, 2007), including mucilage-secreting epidermal cells (Duckett *et al.*, 2006), tetrahedral apical cells, leaf development from a single primary initial, gametangia scattered in leaf axils, identical early ontogeny of antheridia and archegonia (Renzaglia *et al.*, 2007), multiseriate antheridial stalks, spermatids with massive blepharoplasts (Garbary *et al.*, 1993), anacrogynous gynoecia, and large sporophytes protected by massive shoot calyptrae or coelocaules. On the other hand, major differences in plant symmetry, leaf form and insertion, oil body morphology and distribution, and capsule anatomy and dehiscence properties justify placement of the two families into separate subclasses as proposed by He-Nygrén *et al.* (2006). In accordance with Rec. 16B of the International Code of Botanical Nomenclature (McNeill *et al.*, 2006), Calobryales is the preferred name for the single order comprising the Haplomitriidae (Stotler & Crandall-Stotler, 2008).

Haplomitriopsida is species poor as compared to the other two classes, with seven extant species in *Haplomitrium* (Bartholomew-Began, 1991), seven in *Treubia* and four in *Apotreubia*. Nonetheless, there is substantial molecular diversity within the class (Forrest *et al.*, 2005, 2006: fig. 2). In *Haplomitrium* relatively long branches separate three lineages that correspond to the infrageneric ranks recognised by Bartholomew-Began (1991), namely, *H.* subgen. *Haplomitrium* sect. *Archibryum*, *H.* subgen. *Haplomitrium* sect. *Haplomitrium*, and *H.* subgen. *Calobryum*. There is as much molecular distance separating each of these lineages as there is between *Treubia* and *Apotreubia*. Although the degree of lineage separation might justify recognition of separate genera, for the present, we choose to maintain a broad circumscription of *Haplomitrium*. An extremely high frequency of RNA editing of organellar genes, which could decrease mutational constraints, has been reported in *H. mnioides* (Lindb.) R.M.Schust. (Salone *et al.*, 2007), but whether a similar level of editing is universal in the class has not been tested. Broader sampling of both loci and taxa within Haplomitriopsida is needed to determine whether the divergences in both families should be recognised at generic or subgeneric ranks.

2. Class Marchantiopsida

Marchantiopsida, the second diverging lineage within liverworts (Forrest *et al.*, 2006), is estimated to have split from the Jungermanniopsida in the Late Devonian (Heinrichs *et al.*, 2007). Within the class, two subclasses are recognised, Blasiidae and Marchantiidae (He-Nygrén *et al.*, 2006). The Blasiidae display several jungermannioid characters, including simple thalloid gametophytes bearing only smooth rhizoids, and sporophytes bearing ellipsoidal capsules with multistratose walls, a large foot, a massive seta that elongates substantially prior to spore release, and 4-valved capsule dehiscence. At the same time, they share several fundamental characters with the marchantioids, including monoplastidic meiosis (Shimamura *et al.*, 2003), spermatids with a marchantioid locomotory apparatus (Carothers, 1973), gynoecia embedded in tubular involucres of thalline origin, cuneate apical cells, persistent rows of ventral scales and multicellular gemmae produced in receptacles. Within the Marchantiidae, hierarchial relationships are equivocal. The earliest divergences within the subclass include the Sphaerocarpales and recently named Neohodgsoniales and Lunulariales (Long, 2006), but the order of their divergences has not been resolved. There is also no resolution of relationships among the paraphyletic assemblage of families in the Marchantiales, the crown group of the subclass. Rates of molecular evolution in the organellar loci that have been widely used in molecular phylogenetics are much lower in the Marchantiopsida than in other liverworts (Forrest *et al.*, 2006), perhaps because mutation is constrained by a lack of RNA editing in this group (Salone *et al.*, 2007). In the absence of robust resolution of familial relationships, we have, therefore, chosen not to recognise the subordinal rankings recognised by Crandall-Stotler & Stotler (2000) in the Marchantiales.

As discussed by many authors (e.g. Wheeler, 2000; Boisselier-Dubayle *et al.*, 2002; Forrest *et al.*, 2006; Long, 2006), there is little congruence between past morphology-based classifications of the Marchantiidae (e.g. Bischler, 1998; Crandall-Stotler & Stotler, 2000) and the phylogenetic relationships resolved in recent multi-locus analyses. As a consequence, we have made major modifications in the classification of this subclass. The most significant changes include the following: the transfer of *Neohodgsonia* from the Marchantiaceae to its own family and order; the recognition of a monogeneric Lunulariales; the incorporation of Monocleales and Ricciales into the Marchantiales, with the Monocleaceae aligned near the Dumortieraceae and the Ricciaceae aligned close to Wiesnerellaceae; the transfer of *Peltolepis* from Monosoleniaceae to Cleveaceae; and the recognition of a monogeneric Dumortieraceae (Long, 2006).

The main evolutionary trend in the Marchantiidae leads to reduction and simplification of the gametophyte, as postulated by Goebel (1910, 1930) and expanded upon by Evans (1939). Elaborate air chambers and gametangiophores occur in many of the earliest diverging taxa (i.e. *Neohodgsonia*, *Lunularia* and Marchantiaceae), and various more simplified morphologies such as those of *Monoclea*, *Riccia*, *Targionia* and *Monosolenium* are distributed in several lineages of the crown group. Reduction in complexity is often displayed in one suite of characters, but not others. For example, *Targionia* has a complex thallus structure, but lacks gametangiophores, while *Monosolenium* has a simple thallus, without air pores or chambers, but retains archegoniophores. Genera with elaborate carpocephala are aligned with acarpocephalate taxa, as is the case with *Exormotheca* and *Corsinia*, *Wiesnerella* and *Targionia*, and *Dumortiera* and *Monoclea*. In addition, the following states that were reconstructed as derived by Bischler (1998) are now considered ancestral: compound air pores, single-layered air chambers with basement filaments, ventral scales in more than two rows, two or more rhizoid furrows in the carpocephalum stalk, and a spore:elater ratio greater than 4:1. Generating a scheme to explain the evolution and diversification of complex thalloid morphologies across this puzzling phylogeny requires additional input from ontogenetic studies of thallus and gynoecial anatomy.

3. Class Jungermanniopsida

Three subclasses are recognised in the Jungermanniopsida, corresponding to the three major lineages resolved in Forrest *et al.* (2006). The Pelliidae comprises the group designated Simple Thalloid I, the Metzgeriidae includes the Simple Thalloid II lineage and *Pleurozia*, and the Jungermanniidae consists of the leafy liverworts minus *Pleurozia* (He-Nygrén *et al.*, 2006). Pelliidae are the first diverging lineage within the class. Within the Pelliidae, the Pelliaceae are resolved as sister to the other lineages and the leafy Fossombroniaceae and Phyllothalliaceae, which have traditionally been considered primitive (Evans, 1939; Schuster, 1992; Crandall-Stotler & Stotler, 2000), are nested in the Fossombroniales and Pallaviciniales, respectively. Most genera of this subclass have a simple thalloid organisation and anacrogynous gynoecia, although there are exceptions to both. The subclass is morphologically heterogeneous. For example, all four types of apical cell geometries are expressed, with cuneate and lenticular types being of equal occurrence in the derived lineages (Shaw & Renzaglia, 2004). Androecial and gynoecial organisations vary from widely scattered, naked gametangia to tightly clustered perigonia and perichaetia, and sporophytes include both large, massive and small, reduced types. Strands of hydrolysed 'water-conducting' cells are restricted to Pallaviciniineae, a derived group in the subclass. Notable modifications in generic alignments from previous classifications (e.g. Schuster, 1992; Crandall-Stotler & Stotler, 2000) reflect the results of molecular phylogenetic analyses by Forrest *et al.* (2006), unless otherwise indicated, and include the following: (i) transfer of *Verdoornia* from Makinoaceae (Pelliidae) to the Aneuraceae (Metzgeriidae), (ii) realignment of the Makinoaceae with Fossombroniales, (iii) placement of Phyllothalliineae, previously aligned with Treubiineae based on capsule anatomy, into Pallaviciniales, (iv) transfer of Sandeothallaceae from Fossombroniales to Pallaviciniales, and (v) establishment of Moerckiaceae to include *Hattorianthus* and *Moerckia* (Crandall-Stotler & Stotler, 2007). On-going studies of relationships within the Fossombroniaceae by Forrest *et al.* (2003 & unpublished data) further confirm that *Austrofossombronia* is nested in *Fossombronia* and should be reduced to that genus. More detailed discussions of phylogenetic trends and intergeneric relationships in the Pelliidae are found in Forrest *et al.* (2006).

Analyses of molecular, as well as morphological, data sets (Crandall-Stotler *et al.*, 2005) have consistently resolved Metzgeriidae as the sister group of the Jungermanniidae and the second divergence within Jungermanniopsida. Our placement of *Pleurozia* in its own order in the Metzgeriidae is supported by most molecular analyses (e.g. Davis, 2004; Crandall-Stotler *et al.*, 2005; Heinrichs *et al.*, 2005, 2007; Forrest *et al.*, 2006), but is in contrast to its placement as the earliest divergence of the Jungermanniidae by He-Nygrén *et al.* (2006). Although the relationship between Pleuroziales and Metzgeriales is difficult to explain morphologically (Crandall-Stotler *et al.*, 2005), it remains strongly supported even with increased taxon sampling and under different analytical models (Forrest *et al.*, 2006). Recently, the presence of lenticular apical cells and bilateral symmetry in both the leafy shoots and cylindrical rhizomes of all four subgenera of *Pleurozia* and all taxa of the Metzgeriales has been confirmed (O'Hearn & Crandall-Stotler, 2007). The ancestral link between *Pleurozia*, a taxon long considered to be an isolated lineage of the Jungermanniidae, and the Metzgeriales is further supported by these findings.

The taxonomic position of *Mizutania* is problematic. Tsubota & Deguchi (2004) proposed the transfer of this simple thalloid plant from the Metzgeriales to the Jungermanniidae, based on its resolution within the *Calypogeia* clade in a one-locus *rbc*L analysis. This transfer was formalised by He-Nygrén *et al.* (2006). A relationship between *Mizutania* and *Calypogeia* is not supported by any morphological evidence (Crandall-Stotler *et al.*, 1994). In addition to its simple thalloid morphology, which is unknown even in sporelings of *Calypogeia*, *Mizutania* possesses large, *Riccardia*-like oil bodies (Crandall-Stotler *et al.*, 1994: fig. 2) that are quite unlike the botryoidal oil bodies of *Calypogeia*, and has archegonia with six, rather than five, rows of neck cells, as is typical of the Metzgeriidae. The anomalous placement of this taxon in the analysis might be explained by contamination of the *Mizutania* accession by gemmae from *Calypogeia* since the DNA from even a few gemmae within a DNA sample can be preferentially amplified, leading to spurious results as discussed in Forrest *et al.* (2006). However, a preliminary analysis of *rbc*L sequences from a new accession of *Mizutania* also suggests affinities with the Jungermanniidae, although not a close association with *Calypogeia* (L. Forrest, pers. comm.). *Mizutania* may be a neotenic taxon of the Jungermanniidae, but until its position is confirmed in a broad, multi-locus analysis we prefer to retain the taxon in the Metzgeriidae.

Definition of genera within the Metzgeriaceae remains problematic, but current evidence lends support to the reduction of the segregate genera *Apometzgeria* and *Austrometzgeria* (Kuwahara, 1966) to *Metzgeria* as proposed, respectively, by

Schuster (1992) and So (2002). In the multi-locus analyses of Forrest *et al.* (2006: fig. 7), *Apometzgeria* is nested in *Metzgeria*, and So (2002) has shown that *Austrometzgeria saccata* is morphologically identical to *Metzgeria francana*, a species that Kuwahara (1978) himself recognises as belonging to *Metzgeria*. Although Schuster (1992) also proposes reduction of *Steereella* to *Metzgeria*, this taxon differs enough in morphology to warrant recognition until its status can be tested with molecular data. The transfer of *Vandiemenia* to the Metzgeriaceae is supported by the morphological studies of Furuki & Dalton (2008), and the reduction of *Cryptothallus* to *Aneura* is based on the molecular analyses of Wickett & Goffinet (2008).

The Jungermanniidae are estimated to have diverged from the Metzgeriidae in the Late Carboniferous (Heinrichs *et al.*, 2007) and are today the most speciose subclass of liverworts. As discussed in several publications (Davis, 2004; Heinrichs *et al.*, 2005, 2007; Forrest *et al.*, 2006; He-Nygrén *et al.*, 2006), Jungermanniidae are generally resolved to comprise two major lineages, designated as Porellales and Jungermanniales by Heinrichs *et al.* (2005). The majority of taxa that have been included in various analyses clearly distribute between these two groups, an exception being those of Ptilidiineae. In some analyses (He-Nygrén *et al.*, 2004, 2006; Heinrichs *et al.*, 2005, 2007), Ptilidiineae is aligned with Porellales, and in others (Davis, 2004; Forrest *et al.*, 2006), it resolves as the first divergence of Jungermanniales, but neither placement is robustly supported. Recognising the unique assemblage of porelloid and jungermannioid characters displayed by the taxa currently resolved in this lineage, we have relegated Ptilidiineae to its own order, the Ptilidiales. Although backbone relationships of the Jungermanniidae are fairly well established, many generic and family level relationships are yet to be tested, since molecular analyses have included slightly less than 25% of the genera comprising this subclass. Consequently, we have relied heavily on morphology for placement of genera in families, with molecular evidence primarily influencing the arrangement of families in suborders.

Three suborders are recognised in the Porellales. This arrangement is compatible with the analyses of Forrest *et al.* (2006) and is supported by morphological evidence. As herein defined, all taxa of the Jubulineae are characterised by sporophytes borne in stalked, true calyptrae and have beaked perianths, spheroidal capsules, and vertically aligned elaters that are attached to the capsule valve apices. The Radulineae lack underleaves, produce only *Radula*-type vegetative branches and form stem perigynia below their flattened, truncate perianths. The Porellineae is more heterogeneous, due primarily to the inclusion of the Lepidolaenaceae in the suborder. This grouping is, nonetheless, supported by several molecular analyses (Heinrichs *et al.*, 2005, 2007; Forrest *et al.*, 2006).

Generic level delineations in the Porellaceae, including the reduction of *Macvicaria* to *Porella*, are based on the studies of Hentschel *et al.* (2007a), and the classification of the Lejeuneaceae incorporates the molecular analyses of Wilson *et al.* (2007a). As first suggested by Mizutani (1961) and later supported by several molecular studies (Ahonen *et al.*, 2003; Ahonen, 2004; Wilson *et al.*, 2004, 2007a, 2007b), *Nipponolejeunea*, which shares several features of sporophyte anatomy with *Jubula*, is placed in the Jubulaceae and the Jubulaceae is recognised as distinct from both the Frullaniaceae and the Lejeuneaceae, whereupon Lejeuneaceae Cavers becomes the correct name for this taxon. Lejeuneaceae was nomenclaturally superfluous when published by Cavers (1910–1911) because it included the type genus of the older legitimate Jubulaceae H.Klinggr. (Klinggräff, 1858). Grolle (1973) proposed to conserve Lejeuneaceae Casares-Gil, Fl. Ibér. Brióf.: 703 (1919), which was accepted and afterwards included in Appendix II (Nomina Familiarum Conservanda) of the Leningrad Code (Stafleu *et al.*, 1978). That entry can be found in all subsequent Codes until the recent Vienna Code (McNeill *et al.*, 2006) where it was replaced by the earlier published Lejeuneaceae Rostovzev, Morfol. Sist. Pechen. Mkhov: 94 (1913). However, according to Art. 52.3 of the Code (McNeill *et al.*, 2006) since Lejeuneaceae no longer includes the genus *Jubula*, Lejeuneaceae Cavers 1910 becomes correct since it is based on the name-bringing stem of a legitimate generic name, *Lejeunea* Lib. (see Art. 52.3 and 52.3 Ex. 16). Within the Lejeuneaceae, the reductions of *Macrolejeunea*, *Taxilejeunea* and *Neopotamolejeunea* to *Lejeunea*, and *Aphanolejeunea* to *Cololejeunea*, are fairly well supported by both molecular and morphological data (Wilson *et al.*, 2007a), but the reductions proposed within the *Cheilolejeunea–Leucolejeunea* complex by Wilson *et al.* (2004, 2007a) are problematic and are, therefore, not incorporated in the current scheme. As discussed by Evans (1906), *Cheilolejeunea* comprises a heterogeneous assemblage of taxa, as is also reflected in the multiple lineages resolved in molecular analyses. The type species of *Cheilolejeunea*, *C. aneogyna* (Spruce) A.Evans, has not been included in any molecular studies so it is not possible to determine which of the lineages actually define the genus. In 2004, Wilson *et al.* reduced *Cystolejeunea* to *Cheilolejeunea*, but with increased sampling this taxon is resolved as sister to a paraphyletic *Cheilolejeunea* clade rather than being nested within it (Wilson *et al.*, 2007a). As a consequence, *Cystolejeunea* is still recognised in our classification. Additional generic reductions that have been incorporated are supported by morphology-based, revisionary studies by Reiner-Drehwald & Goda (2000), Zhu & Grolle (2003), Ilkiu-Borges (2005), Reiner-Drehwald (2005), Pócs (2006) and Zhu & Cheng (2008), and are yet to be tested in molecular studies.

The phylogenetic position of the Ptilidiales has not yet been firmly determined, despite an increase in the number of loci being analysed and the application of additional analytical models (J. Shaw, pers. comm.). Placement of the Neotrichocoleaceae in this order, as proposed by He-Nygrén *et al.* (2006), is supported by several molecular analyses (Davis, 2004; Forrest *et al.*, 2006; Hendry *et al.*, 2007; Liu *et al.*, 2008; J. Shaw, unpublished data), all of which resolve a sister relationship between *Ptilidium* and *Neotrichocolea*. In addition, the multi-locus analysis of Liu *et al.* (2008) verifies that *Trichocoleopsis* and *Neotrichocolea* form a monophyletic group, despite their strikingly different water sac morphologies. The inclusion of the newly described, monogeneric Herzogianthaceae in the order (Crandall-Stotler *et al.*, 2008) is based on the studies of Hendry *et al.* (2007), in which *Herzogianthus* is resolved in a position close to *Ptilidium*, but *Chaetophyllopsis*, the genus with which it had been previously aligned in the Chaetophyllopsidaceae (Schuster, 1960, 1974a), is resolved with strong support as a member of the Scapaniaceae (Jungermanniales), a placement also recognised by He-Nygrén *et al.* (2006). *Herzogianthus* approaches other elements of the Ptilidiales in having a highly branched, pinnate habit; asymmetrically 3-lobed leaves; fundamentally 3-keeled perianths; a thick, multistratose capsule wall, bearing few localised thickenings on the inner walls; coarsely papillate to verrucate spores; and unbranched, bispiral elaters. Although this genus is superficially similar to *Ptilidium*, molecular evidence coupled with differences in leaf insertion, stem anatomy and branch morphology precluded the inclusion of *Herzogianthus* in the Ptilidiaceae (Schuster, 1960, 1974a), and necessitated the naming of a new family for this taxon (Crandall-Stotler *et al.*, 2008). Additional molecular and morphological data, including details of spore germination, leaf ontogeny, and sporophyte anatomy, are needed to resolve robustly the phylogenetic relationships of this order.

The Jungermanniales is the largest order of hepatics, consisting of about 2600 species in 220 genera. As proposed by He-Nygrén *et al.* (2006), we recognise four suborders in the order – Personiellineae, which is sister to all other lineages in the order, and Lophocoleineae, Cephaloziineae and Jungermanniineae, which equate, respectively, to Clades A, B and C in Forrest *et al.* (2006). These four major lineages have been consistently resolved in molecular analyses and there is general agreement as to their composition. However, circumscription of both families and genera remains in a state of flux. As demonstrated in several studies focused on single families or generic complexes (e.g. He-Nygrén & Piippo, 2003; Yatsentyuk *et al.*, 2004; Hentschel *et al.*, 2006a, 2006b, 2007b, 2007c; De Roo *et al.*, 2007; Wilson *et al.*, 2007a), many taxa that had been defined on the basis of morphological similarity are paraphyletic, and characters once considered reliable indicators of relationship are homoplastic. As a consequence, several large families have been redefined and previously named segregates of broadly circumscribed genera like *Jungermannia* and *Lophozia* are now recognised as distinct. For example, the Scapaniaceae now includes most elements previously placed in Jungermanniaceae subfam. Lophozioideae (Schill *et al.*, 2004; De Roo *et al.*, 2007; Heinrichs *et al.*, 2007), Jungermanniaceae subfam. Jamesonielloideae Inoue has been elevated to family rank (He-Nygrén *et al.*, 2006) and Lophocoleaceae is reinstated to include numerous genera previously placed in Geocalycaceae (Hentschel *et al.*, 2006a). The segregate genera *Liochlaena* and *Solenostoma* are recognised as distinct from *Jungermannia*, as proposed by Hentschel *et al.* (2007b), and Jungermanniaceae is modified to include a much smaller suite of taxa than traditionally placed there. Many of the taxon arrangements proposed in our classification of the Jungermanniales have also been suggested by other workers, but a few novel and/or controversial placements require further discussion.

We do not accept the placement of *Blepharostoma* in a monogeneric Blepharostomataceae, as proposed by Frey & Stech (2008), but continue to regard it as an element of the Pseudolepicoleaceae (Crandall-Stotler & Stotler, 2000). In the multi-locus analysis of He-Nygrén *et al.* (2006) *Blepharostoma* and *Temnoma* form a monophyletic lineage that is sister to the Trichocoleaceae, lending support to their inclusion in a single family. The other five genera of the Pseudolepicoleaceae that bridge the morphological distance between *Blepharostoma* and *Temnoma* have yet to be included in molecular analyses and it seems, therefore, premature to modify the circumscription of this family. Current molecular analyses that include sampling from both families do not support the suggested erection of separate orders by Frey & Stech (2008) for the Trichocoleaceae and Pseudolepicoleaceae. As discussed by Engel & Glenny (2007), *Castanoclobos*, a newly described genus of the Trichocoleaceae, in fact combines morphological features of the two families, further supporting their close affinity.

Delineation of genera in the Lepidoziaceae has changed little in recent years. Although preliminary molecular studies of Heslewood & Brown (2007) suggest that several genera, including *Kurzia*, *Telaranea* and *Zoopsis*, are paraphyletic, broader sampling within the family is needed before modifications in the classification of this family are undertaken.

We have relied on the molecular analyses of Hentschel *et al.* (2006a, 2006b, 2007c) for circumscription of the Lophocoleaceae, but we have not incorporated all of their proposed reductions in the *Chiloscyphus* complex. Initially, molecular studies seemed to support the reduction of *Lophocolea* to the earlier named *Chiloscyphus*, as proposed by Engel & Schuster (1984), since *Chiloscyphus polyanthos* (L.) Corda, the type species of *Chiloscyphus*, was nested in *Lophocolea* (He-Nygrén & Piippo, 2003; Hentschel *et al.*, 2006a, 2006b). With increased taxon sampling, however, other morphologically distinct genera are resolved within a broadly defined, paraphyletic *Chiloscyphus*, including *Pachyglossa*, *Clasmatocolea* and *Leptoscyphus* (Hentschel *et al.*, 2007c). Instead of reducing all of these genera to *Chiloscyphus*, well-supported monophyletic lineages that have been recognised as subgenera by Hentschel *et al.* (2007c) can be recognised as genera. The fairly large clade that includes *Lophocolea bidentata* (L.) Dumort. (= *Chiloscyphus latifolius* (Nees) J.J.Engel & R.M.Schust.), the type species of *Lophocolea*, excludes the type species of *Chiloscyphus*, and is herein recognised as comprising the genus *Lophocolea*. *Campanocolea* (accommodating *Lophocolea fragmentissima* R.M.Schust.) is nested in this clade and is justifiably reduced to *Lophocolea*. Like *Lophocolea*, *Leptoscyphus* is strongly supported as a monophyletic lineage that can be recognised as a genus. Evidence for the reduction of *Pachyglossa* to *Chiloscyphus* (Hentschel *et al.*, 2007c) is weak, with only 65% bootstrap support in maximum likelihood analysis for its resolution as a sister taxon to *Chiloscyphus* subgen. *Notholophocolea* and we therefore continue to recognise this genus. The reduction of *Invisocaulis* to *Pachyglossa* is based on the morphological studies of Váňa & Gremmen (2005). Species of *Clasmatocolea* are resolved in three lineages, suggesting that this problematic genus is in need of further study before decisions regarding its status are made. Indeed, rather than reducing many genera to *Chiloscyphus*, the problem of its paraphyly could be solved by revising the genus to exclude those elements that are not resolved in the lineage of the type species; for example, establish a new genus for *Chiloscyphus* subgen. *Connati* (Hentschel *et al.*, 2007c). Although the status of *Tetracymbaliella* has not been tested in molecular studies, we agree with Engel & Schuster (1984) that it is best regarded as a subgenus of *Heteroscyphus*. Obviously, expanded studies that incorporate both morphological and molecular data are needed to resolve unambiguously the genera of this complex family.

Generic reductions in the Plagiochilaceae agree with the findings of Groth & Heinrichs (2003), Groth (2005) and Heinrichs *et al.* (2004, 2006), with the older name *Dinckleria* replacing *Proskauera* (Engel & Heinrichs, 2008). According to Groth (2005), the placement of *Acrochila* in the family is equivocal, with *rps*4 data placing it with Plagiochilaceae, but *rbc*L data placing it with Jamesoniellaceae. *Pedinophyllum* appears to be paraphyletic, with *P. truncatum* (Steph.) Inoue from Japan nested in the Jamesoniellaceae and *P. interruptum* (Nees) Kaal., which is the type species of *Pedinophyllum*, resolved in the Plagiochilaceae (Groth, 2005). Although He-Nygrén *et al.* (2006) included only *Pedinophyllum truncatum* in their studies, they concluded that *Pedinophyllum* is an element of the Jamesoniellaceae. It is notable that these two elements, which were once considered subspecies of a single species (Inoue, 1958), have been consistently resolved in two different suborders. It is possible that the single accession of *Pedinophyllum truncatum* that provided the sequences used by all authors (e.g. Groth, 2005; Heinrichs *et al.*, 2005; He-Nygrén *et al.*, 2006; Hentschel *et al.*, 2007b) was misidentified and actually is *Jamesoniella*, but Groth (2005) has indicated that an additional unpublished sequence of *P. truncatum* also places it in the Jamesoniellaceae. Such findings definitely underscore the importance of including the type species in molecular studies before translating the resultant phylogeny into a classification scheme.

The unexpected placement of Jamesoniellaceae, once considered a subfamily of Jungermanniaceae (e.g. Crandall-Stotler & Stotler, 2000; Schuster, 2002), in the Cephaloziineae has been confirmed in several studies (e.g. He-Nygrén *et al.*, 2006; De Roo *et al.*, 2007; Hentschel *et al.*, 2007b). Genera currently included in the family follow Schuster's interpretation of the subfamily, as delineated in 2002. This includes *Roivainenia*, which Schuster (2002) initially placed in Jungermanniaceae subfam. Lophozioideae, but on review, transferred to the subfamily Jamesonielloideae based on similarities in gynoecial structure (Schuster, 2002: 345). Unpublished molecular data (J. Shaw *et al.*) further support this transfer. Groth & Heinrichs (2005) suggested that *Syzygiella* is 'loosely related to Lophoziaceae and Scapaniaceae', but inclusion of species of *Jamesoniella* in the molecular data set clearly shows its alignment with the Jamesoniellaceae (Heinrichs *et al.*, 2005; He-Nygrén *et al.*, 2006) as proposed by Schuster (2002). Placement of *Vanaea* in this family follows the recommendation of Schuster (2002).

Crandall-Stotler *et al.* (2008) recognised *Apotomanthus* as a genus of the Cephaloziaceae, in contrast to Váňa (1976) and Engel (1988), who regarded it as a subgenus of *Nardia* (Jungermanniaceae). In the analyses of Heinrichs *et al.* (2005), Hentschel *et al.* (2006a) and He-Nygrén *et al.* (2006), *Nardia assamica* (Mitt.) Amak., a species of *N.* subgen. *Apotomanthus* (Engel, 1988), is nested, with strong support, in the Cephaloziaceae, while *Nardia compressa* (Hook.) Gray and *N. scalaris* Gray are resolved in a clade with *Jungermannia* (Hentschel *et al.*, 2006a) and/or *Gymnomitrion* (He-Nygrén *et al.*, 2006). However, new molecular studies that include *Nardia succulenta* (A.Rich. ex Lehm. & Lindenb.) Spruce (the type species of *Apotomanthus*) and additional species of *Nardia* now support the reduction of *Apotomanthus* to *Nardia* (Hentschel *et al.*, 2007b; J. Shaw *et al.*, unpublished data) in the Solenostomataceae. In the absence of molecular evidence, the suggestion in the abstract by Engel & Braggins (2005) that *Trabacellula* be recognised in its own family and included with Myliaceae in the suborder Myliineae J.J.Engel & Braggins (2005: 665, nom. inval.) is not accepted. It must be noted that although these suggestions are included in the abstract, *Trabacellula* is still classified in the Cephaloziaceae in the body of the paper (Engel & Braggins, 2005: 673).

Cephaloziellaceae is strongly supported as a monophyletic lineage that is sister to the Scapaniaceae in most molecular analyses (e.g. Forrest *et al.*, 2006; Heinrichs *et al.*, 2007; Hentschel *et al.*, 2007b) and is, therefore, still recognised. This treatment is in contrast to the suggestion of De Roo *et al.* (2007) that Cephaloziellaceae is nested, albeit with weak support, within a broadly defined Scapaniaceae. Our transfer of *Gymnocoleopsis* to Cephaloziellaceae is based on its resolution as a sister taxon to *Cephaloziella* (De Roo *et al.*, 2007), which suggests that its affinities are with the Cephaloziellaceae rather than *Gymnocolea* as originally proposed (Schuster, 1967). Morphological characters that further support this alignment include the following: small plant size, ellipsoidal 2-celled gemmae, reduced 8 + 4 seta anatomy, and bistratose capsule wall. The reduction of *Stenorrhipis* to *Kymatocalyx* is based on the morphological studies of Gradstein & Váňa (1999), and remains to be tested with molecular data.

In 2004, Schill *et al.* demonstrated that Scapaniaceae is nested in the Lophoziaceae (= Jungermanniaceae subfam. Lophozioideae). Molecular studies since then (e.g. Heinrichs *et al.*, 2005, 2007; Forrest *et al.*, 2006; He-Nygrén *et al.*, 2006; De Roo *et al.*, 2007) have consistently confirmed that Scapaniaceae and Lophoziaceae should comprise a single family, which by rules of priority must bear the name Scapaniaceae. They also support the familial status of Blepharidophyllaceae and Delavayellaceae, as proposed by Schuster (1999). In all cases, *Diplophyllum* is resolved sister to the *Scapania* clade, and there is no support for recognising the Diplophyllaceae, as circumscribed by Potemkin (1999). The reduction of *Macrodiplophyllum* to either *Diplophyllum* (Schuster, 1974b) or *Scapania* (Potemkin, 1999, 2002) is also not supported by available molecular data. In Yatsentyuk *et al.* (2004), *Macrodiplophyllum microdontum* (Mitt.) Perss. is nested in *Scapania*, but *M. plicatum* (Lindb.) Perss., the type species of the genus, is resolved sister to *Douinia* in a clade that is sister to *Diplophyllum*. The reduction of *Krunodiplophyllum* to *Diplophyllum* (Engel & Merrill, 1998) is equivocal and has not been tested with molecular data. It has been suggested that *Krunodiplophyllum squarrosum* (Steph.) Grolle, the type species of *Krunodiplophyllum*, is closely related to *Blepharidophyllum* (Grolle, 1965; Schuster, 1971, 2002; Engel & Merrill, 1998), a genus which, on the basis of molecular data, now appears to be a lineage of the Jungermanniineae and unrelated to the Scapaniaceae (De Roo *et al.*, 2007). Consequently, we prefer to retain *Krunodiplophyllum* as a genus until its status is tested. Decisions regarding the circumscription of other genera placed in the family have been strongly influenced by the studies of De Roo *et al.* (2007). This includes the recognition of *Isopaches* and *Schistochilopsis* as distinct from *Lophozia*, of *Sphenolobus* as distinct from *Anastrophyllum*, and the transfer of *Gottschelia* and *Chaetophyllopsis* to the family. As shown in several studies (e.g. Yatsentyuk *et al.*, 2004; Forrest *et al.*, 2006; De Roo *et al.*, 2007; Hentschel *et al.*, 2007b), *Leiocolea* is not only distinct from *Lophozia*, to which it was reduced by Schuster (1969), but in fact is closely allied to *Mesoptychia* as indicated by its placement in the Mesoptychiaceae by Crandall-Stotler *et al.* (2008). Additional data provided by the analyses of Hentschel *et al.* (2007b) now suggest expansion of this family to include *Eremonotus* and a narrowly defined *Jungermannia*, necessitating the replacement of Mesoptychiaceae by Jungermanniaceae.

Deciphering relationships within the Jungermanniineae that are supported by both morphological and molecular evidence has resulted in numerous modifications in family circumscriptions. Molecular studies have demonstrated repeatedly that Jungermanniaceae, as defined by Schuster (1984) and Crandall-Stotler & Stotler (2000), is polyphyletic (Hentschel *et al.*, 2007b). As a consequence, subfamily Lophozioideae has been transferred to the Scapaniaceae and subfamily Jamesonielloideae has been elevated to family rank in the Cephaloziineae, as previously discussed. Additional segregates within the Jungermanniineae include the Myliaceae and Solenostomataceae, rendering the Jungermanniaceae a small family with but six genera. Because of differences in cell wall structure, Engel & Braggins (2005) segregated *Mylia anomala* (Hook.) Gray into the new genus *Leiomylia*, which they retained in the Jungermanniaceae, and proposed that *Mylia* be removed to its own family and be placed with *Trabacellula* in a new suborder, the Myliineae (Engel & Braggins, 2005: 665, nom. inval.). In De Roo *et al.* (2007), *Leiomylia* and *Mylia* are resolved as sister taxa in a strongly supported clade that is sister either to the remaining Jungermanniineae (maximum likelihood) or to all Jungermanniales (maximum parsimony). He-Nygrén (2007) reports a similar placement for the family, but includes only *Mylia taylorii* (Hook.) Gray. In other studies (e.g. Schill *et al.*, 2004; Heinrichs *et al.*, 2007; Hentschel *et al.*, 2007b) Myliaceae are the first divergence of the Jungermanniineae, as recognised in our classification. In contrast to He-Nygrén (2007), we do not recognise this lineage as comprising a separate suborder nor do we accept the suggestion by De Roo *et al.* (2007) that *Leiomylia* should be reduced to *Mylia*.

Our inclusion of *Stephaniella* and *Stephaniellidium* in Arnelliaceae is based on De Roo *et al.* (2007) in which *Stephaniella* is nested in this family. In previous classifications (e.g. Schuster, 1984; Crandall-Stotler & Stotler, 2000), these genera were aligned with the Gymnomitriaceae, but were separated from that family to form the Stephaniellaceae R.M.Schust. by Schuster (2002), who noted that the characters they share with Gymnomitriaceae are largely adaptive features. Although the position of *Stephaniella* in Arnelliaceae is ambiguous, its inclusion in this clade is strongly supported; its transfer to this family is further supported by the shared occurrence of a *Calypogeia*-type marsupium, and long cylindric capsule, with bistratose wall (Winkler, 1969).

Analyses by De Roo *et al.* (2007) have shown, as suggested by Schuster (1999), the Blepharidophyllaceae and Delavayellaceae to be remote from the Scapaniaceae, where they were placed by Crandall-Stotler & Stotler (2000). He-Nygrén *et al.* (2006), De Roo *et al.* (2007), Heinrichs *et al.* (2007) and Hentschel *et al.* (2007b) have further demonstrated that *Delavayella* is closely allied to *Liochlaena*. In Hentschel *et al.* (2007b) the Delavayellaceae clade is sister to a clade that includes *Eremonotus*, *Leiocolea* and *Jungermannia*, while *Solenostoma*, which was considered a subgenus of *Jungermannia* by Váňa (1996), Grolle & Long (2000) and Crandall-Stotler & Stotler (2000) among others, is resolved in a different lineage. Hentschel *et al.* (2007b: fig. 2) proposed combining Delavayellaceae with Jungermanniaceae, but suggested no family placement for *Solenostoma* or *Nardia*. In contrast, we recognise three families to resolve the paraphyly of *Jungermannia* and accommodate the complex of 'jungermannioid' genera in these clades. Delavayellaceae includes *Delavayella* and *Liochlaena* [= *Jungermannia* subgen. *Liochlaena* (Nees) S.W.Arnell] and Jungermanniaceae includes *Jungermannia* [= *Jungermannia* subgen. *Jungermannia*] and *Eremonotus* as well as the genera included in Mesoptychiaceae by Crandall-Stotler *et al.* (2008). A new family, Solenostomataceae, is erected to accommodate *Solenostoma* [*Jungermannia* subgen. *Solenostoma* (Mitt.) Amakawa and *Jungermannia* subgen. *Plectocolea* (Mitt.) Amakawa], *Nardia* and other taxa placed in Jungermanniaceae subfam. Jungermannioideae by Váňa (1973) and Schuster (2002). These families are morphologically similar, with differences most apparent in reproductive organisations. Both Delavayellaceae and Jungermanniaceae have sporophytes enclosed by a shoot calyptra and long, emergent perianth, without perigynial development, but the Solenostomataceae characteristically show reduction in perianth size with formation of perigynia. Special, erect gemmiparous shoots with scale-like leaves are formed only in Delavayellaceae, while gemmae are rarely produced in Jungermanniaceae and Solenostomataceae. Our transfer of *Notoscyphus* from the jungermannioid complex to the Geocalycaceae is based on Schuster (2002) and is tentatively supported by the analyses of Hentschel *et al.* (2007b).

Gymnomitriaceae are typically resolved as the monophyletic sister group of Solenostomataceae (e.g. Forrest *et al.*, 2006; Hentschel *et al.*, 2007b; He-Nygrén, 2007), but in most studies only *Marsupella* and *Gymnomitrion* have been sampled. Analyses of Davis (2004) and Forrest *et al.* (2006) align *Herzogobryum teres* (Carrington & Pearson) Grolle with the Cephaloziellaceae–Scapaniaceae lineage. Since this is not the type species of *Herzogobryum*, however, we continue to recognise *Herzogobryum* as an element of the Gymnomitriaceae. The recognition of *Poeltia* in the family is also problematic, as discussed by Váňa (1999). *Poeltia* was reduced to *Marsupella* by Schuster (1996), but the study of additional specimens with more mature sporophytes has demonstrated that it is quite distinct from *Marsupella* and may not even belong to the Gymnomitriaceae (Váňa, 1999). Although its relationship to other genera of the family is unclear, it is retained here until its affinities can be tested with molecular data. As in the Solenostomataceae, taxa of Gymnomitriaceae have perianths that are usually reduced and associated with a perigynium, and it might be argued that the two families should be combined. Gymnomitriaceae are, however, unambiguously differentiated as a family by leaf insertions that are dorsally interlocking and by spheroidal capsules with quadrate inner wall cells that bear nodular thickenings. So, although these families are related, we prefer to recognise Solenostomataceae as distinct from Gymnomitriaceae.

Although the majority of genera in the Jungermanniidae are yet to be included in phylogenetic analyses, some trends in the evolution of morphological characters within the subclass have emerged. Radial symmetry is a homoplastic expression of several lineages and does not represent the ancestral state of the Jungermanniidae. The ability to form ventral branches is also derived, but only within some lineages of the Jungermanniales. The formation of gynoecia and androecia on a main axis is ancestral, while restriction of either or both to abbreviated branches is derived. In both Porellales and Jungermanniales, coelocaules are reconstructed as plesiomorphic and perianths and stem perigynia are apomorphic (He-Nygrén *et al.*, 2006). Although sporophyte reduction characterises Jubulineae, it is not an overall trend of the subclass. Furthermore, some characters traditionally considered advanced, like water sacs and endosporous germination (Schuster, 1966), characterise all of the Porellales, which are estimated to have diverged from the Jungermanniales in the Early Permian, approximately 280 million years BP (Heinrichs *et al.*, 2007). This ancient dichotomy suggests that many of the characters associated with the epiphytic habit are ancestral in this lineage, rather than derived (He-Nygrén *et al.*, 2006). Expanded analyses within lineages are necessary to unravel many of the trends in character evolution in this large and diverse group of hepatics.

Concluding Remarks

As is obvious in the classification scheme herein proposed, concepts of liverwort phylogeny have changed dramatically since Crandall-Stotler & Stotler (2000), due primarily to insights provided by molecular phylogenetic studies. We recognise that molecular data can provide valuable clues to the phylogenetic history of an organism, but we are also aware of problems that are inherent in molecular studies. In addition to problems of specimen misidentification, mixed collections (especially of gemma-producing taxa) and erroneous GenBank sequences (as cited in Forrest *et al.*, 2006), inadequate taxon sampling and heterogeneous mutation rates across the phylogeny can also generate spurious results. Unexpected relationships resolved in molecular analyses should be compatible with intrinsic morphological characters; that is, there should be morphological markers that also support the relationship, such as comparable apical cell organisation, oil body form, branch position and/or ontogeny, gametangial anatomy, or capsule wall thickening pattern. Ideally, questionable taxon placements, especially those that appear unsupported by morphology, should be strongly supported by multiple DNA accessions and analyses. Seeing a relationship appear in several different papers does not necessarily reinforce its placement since a single GenBank accession has often been used in all of the papers, as in the case of *Pedinophyllum truncatum*. The judgements made in constructing this classification have been tempered by these concerns.

Reconstructing the phylogenetic history of the Marchantiophyta continues to be an arduous task. Many small families have not been sampled, and many of the large families and genera that have been sampled appear to be either polyphyletic or paraphyletic. Although progress has been made, much more intensive taxon sampling that incorporates both morphological and molecular markers across the phylogeny is needed. Just as past classifications have been modified by new discoveries, so also will this one. Nonetheless, it can serve as a framework for future investigations.

The Classification Scheme

Note that genera treated in Crandall-Stotler & Stotler (2000) or other recent classifications that are not now recognised are indicated in brackets following the taxon to which they are now referred.

PHYLUM: MARCHANTIOPHYTA Stotler & Crand.-Stotl. in A.J.Shaw & B.Goffinet, Bryoph. Biol.: 63 (2000).

CLASS: HAPLOMITRIOPSIDA Stotler & Crand.-Stotl., Bryologist 80: 425 (1977) [includes Treubiopsida M.Stech, J.-P.Frahm, Hilger & W.Frey, Nova Hedwigia 71: 207 (2000)].

Plants with leaf-like appendages at nodes; stems secreting copious mucilage from epidermal cells, with interior cells containing unique associations of glomeromycotean fungi; apical cells tetrahedral; androecia and gynoecia loosely organised (apical discs in some species of *Haplomitrium*); 1 primary androgonial initial in early ontogeny; spermatids with a massive spline; anacrogynous (acrogynous in *Haplomitrium* subgen. *Calobryum*); sporophytes large, enclosed by a fleshy shoot calyptra or coelocaule.

SUBCLASS: TREUBIIDAE Stotler & Crand.-Stotl., Taxon 57: 290 (2008).

Plants prostrate; leaves in 2 rows, unequally divided into a small dorsal lobule and large ventral lobe, with the lobe fleshy, confluent with the stem, longitudinal or slightly succubous, polystratose except near the margins; rhizoids scattered on the ventral side of the stem; oil bodies large, in idioblastic cells; gametangia protected by dorsal lobules; capsules ovoid, wall 3- to 5-stratose, dehiscence 4-valved; gemmae multicellular, scattered on the dorsal side of the stem, not in receptacles.

ORDER: TREUBIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 499 (1972).

Treubiaceae Verd., Man. Bryol.: 427 (1932). *Apotreubia* S.Hatt. & Mizut., *Treubia* K.I.Goebel

SUBCLASS: HAPLOMITRIIDAE Stotler & Crand.-Stotl., Taxon 57: 290 (2008).

Plants with leafless, subterranean stolons and erect leafy shoots; leaves in 3 rows with the third row of leaves dorsal, isophyllous or anisophyllous, transverse or weakly succubous, undivided, mostly unistratose, but polystratose at the base; stems parenchymatous, with a central strand of thin-walled, hydrolysed cells, bearing small perforations; rhizoids absent; oil bodies small, homogeneous, in all cells; antheridia and archegonia in leaf axils, or on apical discs; capsules cylindric, wall unistratose, dehiscence along 1, 2 or 4 sutures, nonvalvate; gemmae absent.

ORDER: CALOBRYALES Hamlin, Rec. Domin. Mus. 7: 315 (1972).
Haplomitriaceae Dědeček, Arch. Naturwiss. Landesdurchf. Böhmen 5(4): 71 (1884). *Haplomitrium* Nees nom. cons.

CLASS: MARCHANTIOPSIDA Cronquist, Takht. & W.Zimm., Taxon 15: 132–133 (1966). ('Marchantiatae').

Plants thalloid, rarely leafy; apical cell cuneate with four cutting faces; thallus typically differentiated into assimilatory and storage tissues, generally with persistent ventral scales bearing appendages; rhizoids usually dimorphic (occasionally only smooth); oil bodies large, single in idioblastic cells (rarely absent); gametangia on specialised branches or dorsal on the thallus; antheridia enclosed singly in perigonial chambers, with 4 primary androgonial initials in early ontogeny; embryos often octamerous; sporophytes usually enclosed by an involucre of thallus origin, rarely only by a pseudoperianth, or embedded in the thallus; sporophyte seta usually elongating only slightly (sometimes absent); capsule wall usually unistratose; sporocytes unlobed, spores usually polar and highly ornamented; gemmae, when present, multicellular, typically contained in specialised receptacles (gemma cups).

SUBCLASS: BLASIIDAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Thallus lacking dorsiventral differentiation; wing margins scarcely (*Cavicularia*) to deeply lobed (*Blasia*); midrib bearing a strand of calcium oxalate deposits (*Blasia*) or with 3 strands of elongate, hydrolysed cells (*Cavicularia*); ventral scales in 2 rows, lacking appendages, with a row of *Nostoc*-containing auricles (domatia) to the outside of each row of scales; rhizoids only smooth; idioblastic oil cells absent; oil bodies absent (*Blasia*) or few per cell, homogeneous (*Cavicularia*); perigonial chambers partially sunken along the midrib, irregularly dispersed (*Blasia*), or in 2 or 3 rows (*Cavicularia*); gynoecia at thallus apices; involucre tubular; seta highly elongated prior to spore release; capsule ellipsoidal, with the wall 2- to 4-stratose, dehiscing by 4 valves; gemmae of two types, a stellate form borne in clusters on the dorsal surface of the thallus (*Blasia*) and an ovoid form borne in flask-shaped receptacles (*Blasia*) or crescent-shaped cups (*Cavicularia*).

ORDER: BLASIALES Stotler & Crand.-Stotl. in A.J.Shaw & B.Goffinet, Bryoph. Biol.: 63 (2000).
Blasiaceae H.Klinggr., Höh. Crypt. Preuss.: 14 (1858). *Blasia* L., *Cavicularia* Steph.

SUBCLASS: MARCHANTIIDAE Engl. [Unterklasse 'Marchantiales'] in Engl. & Prantl, Nat. Pflanzenfam. I(3): 1 (1893).

Plants thalloid, rarely leafy; thallus usually with dorsiventral differentiation (undifferentiated in a few taxa); air chambers and air pores usually present; ventral scales usually present, appendaged or not; rhizoids usually dimorphic, sometimes only smooth; idioblastic oil cells usually present; perigonial chambers scattered on the dorsal surface of the thallus or aggregated in cushions on the main thallus or ventral branches, or on stalked receptacles (antheridiophores); gynoecia dorsal or terminal on the thallus, or short ventral branches, or on stalked receptacles (archegoniophores); sporophyte seta usually remaining very short, rarely elongate, absent in a few taxa; capsules usually spheroidal, with the wall unistratose, dehiscence by longitudinal valves or slits, or by a lid, sometimes cleistocarpous.

ORDER: SPHAEROCARPALES Cavers, New Phytol. 9: 81 (1910).
Plants leafy; stems bearing 2 rows of longitudinally inserted lateral leaves (Sphaerocarpaceae) or small lateral and ventral scale-like leaves and one (rarely two) large dorsal wing(s) (Riellaceae); leaves and dorsal wing(s) unistratose; rhizoids smooth; idioblastic oil cells absent or present (*Riella*); perigonial chambers scattered dorsally on the stem or near the margin of the dorsal wing(s); each archegonium and sporophyte enclosed only by a pseudoperianth; involucres absent; seta very short; capsules cleistocarpous; elaters absent; spores shed singly or in tetrads.

Sphaerocarpaceae Heeg, Verh. K. K. Zool.-Bot. Ges. Wien 41: 573 (1891). Plants terrestrial, dioicous, strongly dimorphic, with the male plants minute, often reddish, and the female plants much larger and green (only slightly dimorphic in *Geothallus*); ventral slime papillae present at plant apices; idioblastic oil cells absent; oil bodies absent; perigonial chambers emergent, pyriform to bottle-shaped; pseudoperianths cylindrical to flask-shaped, covering the dorsal surface of the stem; spores shed singly or in tetrads; gemmae absent. *Geothallus* Campb., *Sphaerocarpos* Boehm.

Riellaceae Engl., Syllabus, Grosse Ausgabe: 45 (1892). Plants aquatic, submerged to emergent, dioicous, rarely monoicous, when dioicous with male and female plants of similar size; ventral scales present, in 2 rows, without appendages; idioblastic oil cells present; perigonial chambers embedded in the dorsal wing, opening along the margin; pseudoperianths pyriform to flask-shaped, in a row to either side of the dorsal wing (or between the two wings in *Riella bialata* Trab.); spores shed singly; gemmae, when present, intermixed with the ventral scales. *Riella* Mont.

ORDER: NEOHODGSONIALES D.G.Long, Edinburgh J. Bot. 63: 258 (2006).
Thallus differentiated, with compound air pores; ventral scales in 2 rows, lacking appendages; rhizoids all smooth; idioblastic oil cells present; monoicous; perigonial chambers aggregated on unbranched, stalked receptacles, with the receptacles bearing compound air pores and the stalk with 1 rhizoid furrow; sporophytes on branched, stalked receptacles, with the receptacles bearing compound air pores and the stalk with 1 rhizoid furrow; involucres bivalved; pseudoperianths present, campanulate; seta not elongated; elaters present; capsule dehiscence by irregular valves; gemmae in cup-shaped receptacles.

Neohodgsoniaceae D.G.Long, Edinburgh J. Bot. 63: 258 (2006). *Neohodgsonia* Perss.

ORDER: LUNULARIALES D.G.Long, Edinburgh J. Bot. 63: 259 (2006).
Thallus differentiated, with simple air pores; ventral scales in 2 rows, with a single appendage; rhizoids dimorphic; idioblastic oil cells present; dioicous; perigonial chambers aggregated in terminal cushions on the thallus; sporophytes on stalked, deeply 4-lobed receptacles, with the receptacles lacking air pores and the stalk without rhizoid furrows; involucres tubular; pseudoperianths absent; seta massive, elongating prior to spore dispersal; elaters present; capsule dehiscence by a lid and 4 valves; gemmae in crescent-shaped receptacles.

Lunulariaceae H.Klinggr., Höh. Crypt. Preuss.: 9 (1858). *Lunularia* Adans.

ORDER: MARCHANTIALES Limpr. in Cohn, Krypt.-Fl. Schlesien 1: 239, 336 (1877).

Thallus usually differentiated; epidermis with either simple or compound air pores (rarely absent); ventral scales in 2 to 10 rows, sometimes absent, usually with 1 to 3(to 6) appendages; rhizoids usually dimorphic, sometimes only smooth; idioblastic oil cells usually present; monoicous or dioicous; perigonial chamber positions variable; sporophyte positions variable; involucres bivalved, cup-shaped, scale- or flap-like, or tubular, sometimes absent; pseudoperianths absent or present; seta usually short or absent; elaters usually present; capsule dehiscence by longitudinal valves, longitudinal slit or lid, sometimes cleistocarpous; gemmae present in a few taxa.

Marchantiaceae Lindl., Nat. Syst. Bot., ed. 2: 412 (1836). Thallus differentiated, with compound air pores; ventral scales in 2 to 10 rows, with 1 to 3 appendages; perigonial chambers aggregated on stalked receptacles, with the receptacles bearing compound pores and the stalk with 2 to 4 rhizoid furrows; sporophytes on stalked receptacles, with the receptacles bearing compound air pores and the stalk with 2 to 4 rhizoid furrows; involucre bivalved or cup-shaped; pseudoperianths present, campanulate; seta remaining short; capsule dehiscence by irregular valves; gemmae absent, or present in cup-shaped receptacles (*Marchantia*). *Bucegia* Radian, *Marchantia* L., *Preissia* Corda

Aytoniaceae Cavers, New Phytol. 10: 42 (1911). Thallus differentiated, with simple air pores; ventral scales in 2 rows, with 1 to 4 appendages; perigonial chambers embedded in ill-defined groups dorsally in the thallus or aggregated in cushions on the thallus; sporophytes on stalked receptacles, with the receptacles bearing compound air pores and the stalk with 1 rhizoid furrow; involucres bivalved, cup-shaped or flap-like; pseudoperianths absent, but present in *Asterella*, splitting into linear segments when present; seta remaining short; capsule dehiscence by a lid; specialised asexual structures absent. *Asterella* P.Beauv., *Cryptomitrium* Austin ex Underw., *Mannia* Opiz nom. cons., *Plagiochasma* Lehm. & Lindenb. nom. cons., *Reboulia* Raddi nom. cons.

Cleveaceae Cavers, New Phytol. 10: 42 (1911). Thallus differentiated, with simple air pores; ventral scales in several irregular rows, with 1 to 3 appendages; perigonial chambers embedded in ill-defined groups dorsally in the thallus or aggregated in cushions on the thallus; sporophytes on stalked receptacles, with the receptacles lacking air pores or with simple air pores and the stalk with 0, 1 or 2 rhizoid furrows; involucres bivalved; pseudoperianths absent; seta remaining short; capsule dehiscence by irregular valves; specialised asexual structures absent. *Athalamia* Falconer, *Peltolepis* Lindb., *Sauteria* Nees

Monosoleniaceae Inoue, Bull. Natl. Sci. Mus. Tokyo 9: 117 (1966). Thallus undifferentiated, without air pores; ventral scales in 2 rows, with or without 1 small appendage; perigonial chambers aggregated in dorsal cushions on the thallus; sporophytes on stalked receptacles, with the receptacles lacking air pores and the stalk with 2 rhizoid furrows; involucres bivalved; pseudoperianths absent; seta remaining short; capsule dehiscence by irregular valves; specialised asexual structures absent. *Monosolenium* Griff.

Conocephalaceae Müll.Frib. ex Grolle, J. Bryol. 7: 207 (1972). Thallus differentiated, with simple air pores; ventral scales in 2 rows, with 1 appendage; perigonial chambers aggregated in terminal cushions on the thallus; sporophytes on stalked receptacles, with the receptacles bearing compound air pores and the stalk with 1 rhizoid furrow; involucres tubular; pseudoperianths absent; seta remaining short; capsule dehiscence by irregular valves; asexual reproduction by fragmenting thallus tips or ventral bulbils. *Conocephalum* Hill nom. cons.

Cyathodiaceae Stotler & Crand.-Stotl. in A.J.Shaw & B.Goffinet, Bryoph. Biol.: 63 (2000). Thallus differentiated, with simple air pores; ventral scales in 2 rows, minute, without appendages; rhizoids mostly smooth, a few pegged; perigonial chambers embedded dorsally on ventral or apical thallus branches; sporophytes ventral at the thallus apex; involucres bivalved; pseudoperianths absent; seta remaining short;

elaters few per capsule; capsule dehiscence by a lid and irregular valves; asexual reproduction by fragmentation of the thallus margin. *Cyathodium* Kunze

Exormothecaceae Müll.Frib. ex Grolle, J. Bryol. 7: 208 (1972). Thallus differentiated, with highly elevated, simple air pores; ventral scales in 2 rows, with 1 to 3 appendages or with appendages sometimes lacking; perigonial chambers embedded in the dorsal groove of the thallus, or forming irregular rows on the thallus; sporophytes on stalked receptacles, with the receptacles bearing simple pores and the stalk with 1 rhizoid furrow; involucres tubular; pseudoperianths absent; seta remaining short; elaters present; capsule dehiscence by irregular valves or irregular lid and valves; specialised asexual structures absent. *Aitchisoniella* Kashyap, *Exormotheca* Mitt., *Stephensoniella* Kashyap

Corsiniaceae Engl., Syllabus, Grosse Ausgabe: 44 (1892). Thallus differentiated, with simple air pores; ventral scales in 2 or several ill-defined rows, with 1 to 6 appendages; perigonial chambers embedded in the dorsal groove of the thallus; sporophytes dorsal on the thallus; involucres scale-like; pseudoperianths absent; seta very reduced; elaters absent (*Corsinia*) or reduced (*Cronisia*); capsules cleistocarpous; specialised asexual structures absent. *Corsinia* Raddi, *Cronisia* Berk.

Monocarpaceae D.J.Carr ex Schelpe, J. S. African Bot. 35: 110 (1969). Thallus differentiated, with large open air chambers, with the epidermis and air pores lacking; ventral scales absent; rhizoids all smooth; idioblastic oil cells absent; antheridia borne on the floor of open air chambers; sporophytes borne within open air chambers, each closely enclosed within a short-stalked globose receptacle with an apical orifice and air chambers with compound pores; involucres absent; pseudoperianths absent; seta very short; elaters absent; capsules cleistocarpous; specialised asexual structures absent. *Monocarpus* D.J.Carr

Oxymitraceae Müll.Frib. ex Grolle, J. Bryol. 7: 215 (1972). Thallus differentiated, with simple air pores; ventral scales in 2 rows, with 1 appendage; idioblastic oil cells absent; perigonial chambers embedded in the dorsal groove of the thallus; sporophytes in a dorsal depression of the thallus; involucres pyriform, sometimes fused to form a crest; pseudoperianths absent; seta absent; elaters absent; capsules cleistocarpous; specialised asexual structures absent. *Oxymitra* Bisch. ex Lindenb.

Ricciaceae Rchb., Bot. Damen: 255 (1828). Thallus differentiated, with simple air pores or with air pores absent; ventral scales in 2 or several rows, appendages absent or small; idioblastic oil cells absent (present in *Ricciocarpos*); perigonial chambers embedded dorsally in the thallus, scattered; sporophytes embedded singly in the thallus; involucres absent; pseudoperianths absent; seta absent; elaters absent; capsules cleistocarpous; specialised asexual structures absent. *Riccia* L., *Ricciocarpos* Corda

Wiesnerellaceae Inoue, Ill. Jap. Hepat. 2: 192 (1976). Thallus differentiated, with simple air pores; ventral scales in 2 rows, with 1 appendage; perigonial chambers aggregated in terminal cushions on the thallus; sporophytes on stalked receptacles, with the receptacles bearing compound air pores and the stalk with 2 rhizoid furrows; involucres bivalved; pseudoperianths absent; seta remaining short; capsule dehiscence by 4 to 6 irregular valves; specialised asexual structures absent. *Wiesnerella* Schiffn.

Targioniaceae Dumort., Anal. Fam. Pl.: 68, 70 (1829). Thallus differentiated, with simple air pores; ventral scales in 2 rows, with 1 appendage; perigonial chambers embedded in irregular groups dorsally on the thallus or on short ventral branches; sporophytes ventral at the thallus apex; involucres bivalved; pseudoperianths absent; seta remaining short; capsule dehiscence by an irregular lid and valves; specialised asexual structures absent. *Targionia* L.

Monocleaceae A.B.Frank in Leunis, Syn. Pflanzenk., ed. 2: 1556 (1877). Thallus not differentiated, air chambers and air pores absent; ventral scales absent, but with stalked mucilage papillae ventrally; rhizoids all smooth; perigonial chambers aggregated in dorsal cushions on the thallus; sporophytes along the thallus margin; involucres tubular; pseudoperianths absent; seta massive, highly elongated prior to spore release; capsule dehiscence by a single longitudinal slit; specialised asexual structures absent. *Monoclea* Hook.

Dumortieraceae D.G.Long, Edinburgh J. Bot. 63: 260 (2006). Thallus weakly differentiated into layers, with vestigial air chambers and air pores absent or few near the thallus apex, simple when present; ventral scales in 2 rows, without appendages; rhizoids dimorphic, sometimes modified as bristles; idioblastic oil cells few; perigonial chambers on stalked receptacles, with the receptacles lacking air pores and the stalk with 2 rhizoid furrows; sporophytes on stalked receptacles, with the receptacles bearing a few open air chambers and the stalk with 2 rhizoid furrows; involucres tubular, bristly, opening by a slit; pseudoperianths absent; seta remaining short; capsule dehiscence by irregular valves; specialised asexual structures absent. *Dumortiera* Nees

CLASS: JUNGERMANNIOPSIDA Stotler & Crand.-Stotl., Bryologist 80: 425 (1977).

Plants thalloid or leafy; oil bodies usually present in all cells (absent in a few taxa), usually more than one per cell; rhizoids monomorphic, smooth-walled; antheridia with 2 primary androgonial initials in early ontogeny; embryos filamentous; seta elongation pronounced; capsule wall 2- or more stratose; sporocytes lobed, spores cryptopolar to apolar, rarely polar.

SUBCLASS: PELLIIDAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Plants mostly thalloid, without air chambers; if leafy, leaves developing from 1 initial, never lobed, arranged in 2 rows, succubous in insertion; branches exogenous in origin, terminal or intercalary, lateral or ventral; antheridia on the dorsal surface of the midrib or stem, with or without perigonia (on abbreviated ventral branches in *Hymenophyton*); gynoecia usually anacrogynous, on the dorsal surface of the midrib or stem (acrogynous in *Pellia*, on abbreviated branches in *Hymenophyton* and *Podomitrium*).

ORDER: PELLIALES He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006). Plants thalloid or leafy with the leaves succubous; apical cell tetrahedral, cuneate, or hemidiscoid; ventral appendages stalked papillae or uniseriate hairs, dispersed or in 2 rows; rhizoids hyaline or brownish to pale reddish brown; ventral branches rare; antheridia arranged in 2 rows, or scattered or weakly clustered on the thallus, each in a conical or flask-shaped chamber with an apical ostiole; archegonia naked and arranged in 2 rows along the midrib (*Noteroclada*), or in an acrogynous cluster, protected by a perichaetial flap or sheath (*Pellia*); sporophytes enclosed by a shoot calyptra and caulocalyx (*Noteroclada*) or perichaetial pseudoperianth (*Pellia*); capsules spheroidal, with conspicuous basal elaterophore, dehiscing into 4 valves; spore germination precocious and endosporic.

Pelliaceae H.Klinggr., Höh. Crypt. Preuss.: 13 (1858). *Noteroclada* Taylor ex Hook. & Wilson, *Pellia* Raddi nom. cons.

ORDER: FOSSOMBRONIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 500 (1972).

Plants thalloid or leafy; ventral appendages foliose scales, uniseriate hairs, or stalked papillae, arranged in 2 rows; oil bodies of the *Massula*-type; ventral branches rare; gynoecia anacrogynous; capsules usually spheroidal (cylindrical in *Makinoa*); dehiscence not valvate, irregular (by a single slit in *Makinoa*); spore germination exosporic.

SUBORDER: CALYCULARIINEAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Plants thalloid with a well-defined midrib; apical cell hemidiscoid; ventral appendages foliose scales; rhizoids hyaline; antheridia in several rows on the midrib, with laciniate perigonial scales; gynoecia anacrogynous, with archegonia and perichaetial scales clustered; sporophytes enclosed by a shoot calyptra and caulocalyx; capsules spheroidal, with a basal elaterophore, dehiscing irregularly into 5 to 7 unequal segments.

Calyculariaceae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).
Calycularia Mitt.

SUBORDER: MAKINOIINEAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Plants thalloid with an inconspicuous midrib; apical cell cuneate; ventral appendages 3- to 6-celled, uniseriate hairs; rhizoids reddish brown; androecia large, up to 80 antheridia sunken in thallus depressions, protected by a posterior lunulate ridge of thallus tissue; archegonia in small dorsal clusters protected by a posterior flap of thallus tissue; sporophytes enclosed by a coelocaule; capsules cylindrical, with a rudimentary basal elaterophore, dehiscing along one slit.

Makinoaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 201 (1943).
Makinoa Miyake

SUBORDER: FOSSOMBRONIINEAE R.M.Schust. ex Stotler & Crand.-Stotl. in A.J.Shaw & B.Goffinet, Bryoph. Biol.: 63 (2000).

Plants thalloid or leafy; apical cell tetrahedral, lenticular or cuneate; ventral appendages foliose scales, filamentous hairs, or stalked slime papillae; rhizoids purplish, brownish or hyaline; antheridia scattered or in clusters on the midrib, with or without perigonial scales; archegonia scattered or clustered, with or without perichaetial scales; sporophytes protected by a shoot calyptra and either a caulocalyx or perichaetial pseudoperianth (except *Allisonia*); capsules spheroidal, lacking an elaterophore, with dehiscence irregular or the capsule breaking into 5 to 7 unequal segments.

Petalophyllaceae Stotler & Crand.-Stotl., Novon 12: 335 (2002). Plants thalloid, thallus wings unistratose, usually with unistratose dorsal lamellae (absent in *Sewardiella*); apical cell tetrahedral; ventral appendages foliose scales; rhizoids hyaline or brownish; antheridia in 2 or 3 rows, protected by extensions of the thallus lamellae or by perigonial scales; archegonia clustered with perichaetial scales and a perichaetial pseudoperianth; sporophytes enclosed by a shoot calyptra and perichaetial pseudoperianth; capsule wall multistratose, with cell wall thickenings in all wall layers. *Petalophyllum* Nees & Gottsche ex Lehm., *Sewardiella* Kashyap

Allisoniaceae Schljakov, Pecenocnye Mchi, Morfol. Filog. Klassif. [Liverwort morphology, phylogeny, classification]: 119 (1975). Plants thalloid; midrib well defined and projecting ventrally; apical cell cuneate; ventral appendages filamentous hairs; rhizoids brown to purplish; antheridia clustered to dispersed, with perigonial scales laciniate; archegonia in an elongate cluster, surrounded by laciniate, connate scales; sporophytes enclosed in a true calyptra; capsule wall multistratose, with cell wall thickenings in all wall layers. *Allisonia* Herzog

Fossombroniaceae Hazsl. nom. cons., Magyar Bir, Moh.-Fl.: 20, 36 (1885). Plants leafy; leaves succubous; apical cell lenticular; ventral appendages variable, foliose scales or very short filamentous hairs or stalked papillae; rhizoids normally purplish; antheridia dispersed along the stem, naked or protected by a scale; archegonia dispersed along the stem, naked; sporophytes enclosed by a shoot calyptra and a caulocalyx; capsule wall bistratose, with epidermal cells lacking wall thickenings. *Fossombronia* Raddi [includes *Austrofossombronia* R.M.Schust.]

ORDER: PALLAVICINIALES W.Frey & M.Stech, Nova Hedwigia 81: 64 (2005).
Plants thalloid (except *Phyllothallia*), midrib usually well defined; apical cells cuneate, lenticular or hemidiscoid; ventral appendages stalked papillae or hairs, dispersed or in 2 rows; ventral branches common; antheridia associated with perigonial scales, aggregated or in rows on the midrib; archegonia associated with perichaetial scales, aggregated; sporophytes enclosed by a coelocaule or by a shoot calyptra and perichaetial pseudoperianth or caulocalyx; capsules usually ellipsoidal to cylindrical, with a multistratose apical cap (except *Phyllothallia*) and dehiscence usually 2- or 4-valved, with the valves often apically coherent.

SUBORDER: PHYLLOTHALLIINEAE R.M.Schust., Trans. Brit. Bryol. Soc. 5: 283 (1967).
Plants leafy, with the leaves opposite, distant to contiguous, with well-defined internodes; apical cell cuneate; ventral appendages stalked papillae, dispersed; antheridia and perigonial scales in clusters at the nodes; archegonia and perichaetial scales in clusters at the nodes; sporophytes enclosed by a coelocaule; capsules subspheroidal to ovoidal, with the wall multistratose and dehiscence 4-valved, with the valves usually splitting into 2 or more additional segments.

Phyllothalliaceae E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 2: 247 (1964). *Phyllothallia* E.A.Hodgs.

SUBORDER: PALLAVICINIINEAE R.M.Schust., Phytologia 56: 65 (1984).
Plants thalloid, with the wings sometimes deeply lobed, midrib with 1 or 2(or 4) strands of elongate, hydrolysed cells (strands lacking in *Sandeothallus* and some species of *Moerckia*).

Sandeothallaceae R.M.Schust., New Man. Bryol.: 951 (1984). Thallus wings flaccid, midrib homogeneous, without strands; apical cell hemidiscoid; ventral appendages short hairs, reddish, in 2 rows; rhizoids deep red to purple; perichaetium a single, large, lacerate scale, posterior to the archegonial cluster; sporophytes enclosed by a shoot calyptra and caulocalyx; capsules ellipsoidal, with the wall multistratose, with nodular thickenings in both outer and inner wall cells and dehiscence 2-valved, with the valves apically coherent. *Sandeothallus* R.M.Schust.

Moerckiaceae Stotler & Crand.-Stotl., Nova Hedwigia Beih. 131: 54 (2007). Thallus often stipitate; midrib with 2 strands of hydrolysed cells with unpitted walls, or lacking strands; apical cell cuneate or lenticular; ventral appendages uniseriate, 2- to 5-celled hairs, in 2 rows; sporophytes enclosed by a shoot calyptra and perichaetial pseudoperianth; capsules ellipsoidal, with the wall multistratose (bistratose in *Moerckia hibernica* (Hook.) Gottsche), with the radial walls of the epidermal cells evenly thickened and the inner wall cells without thickenings and dehiscence mostly 4-valved, with the valves free. *Hattorianthus* R.M.Schust. & Inoue, *Moerckia* Gottsche

Hymenophytaceae R.M.Schust., J. Hattori Bot. Lab. 26: 296 (1963). Plants dendroid, stipitate, with 3- to 5-furcate thalli arising from rhizomatous axes; thallus midrib and rhizomes with 1 strand of hydrolysed cells with thick, pitted walls; apical cell lenticular; ventral appendages stalked papillae, in 2 rows; androecia and gynoecia on abbreviated ventral branches; gynoecia acrogynous; sporophytes enclosed by a shoot calyptra and caulocalyx; capsules cylindrical, with an apical elaterophore, with the wall bistratose, with the radial walls of the epidermal cells with uneven, nodulose thickenings and the inner wall cells without thickenings and dehiscence 4-valved, with the valves free. *Hymenophyton* Dumort.

Pallaviciniaceae Mig., Krypt.-Fl. Deutschl., Moose: 423 (1904). Thalli prostrate or erect, with or without a stipe, sometimes dendroid; thallus wing margin often bearing short teeth and/or slime papillae, midrib with 1 or more strands of hydrolysed cells with thick, pitted walls; apical cell lenticular or cuneate; ventral appendages stalked papillae or short hairs, dispersed; androecia in discrete clusters or in elongate rows over the thallus midrib; gynoecia anacrogynous on the dorsal surface of the thallus (acrogynous on ventral branches in *Podomitrium*); sporophytes enclosed by a shoot calyptra and perichaetial pseudoperianth, or by a coelocaule; capsules cylindrical, with the wall 2-stratose, with the radial walls of the epidermal cells evenly thickened and the inner wall cells without thickenings and dehiscence 2- or 4-valved, with the valves apically coherent. *Greeneothallus* Hässel, *Jensenia* Lindb., *Pallavicinia* Gray nom. cons., *Podomitrium* Mitt., *Seppeltia* Grolle, *Symphyogyna* Nees & Mont., *Symphyogynopsis* Grolle, *Xenothallus* R.M.Schust.

SUBCLASS: METZGERIIDAE Barthol.-Began, Phytologia 69: 465 (1991 ['1990']).

Plants mostly thalloid, without air chambers, if leafy, leaves developing from 3 initials, arranged in 2 rows; apical cells lenticular; branches exogenous or endogenous in origin, terminal or intercalary, lateral or ventral; androecia on abbreviated lateral or ventral branches (except *Verdoornia*); gynoecia acrogynous, on abbreviated lateral or ventral branches (except *Verdoornia*); capsule dehiscence 4-valved.

ORDER: PLEUROZIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 505 (1972).

Plants leafy; leaves succubous, unequally complicate-bilobed, with the larger lobe shallowly bifid and the small lobule usually forming a complex, valvate water sac [leaves simple in *Pleurozia paradoxa* (J.B.Jack) Schiffn.]; underleaves and ventral slime papillae lacking; branches endogenous, lateral (*Plagiochila*-type); antheridia solitary in the axils of reduced perigonial leaves; archegonia enclosed by a perianth and 2 to 5 series of modified perichaetial leaves; sporophytes enclosed by a shoot calyptra and perianth; capsules ovoid to subspheroidal, with the wall 8- to 10-stratose, with the epidermal cells having 2-phase development and the walls of the inner cells bearing complex fenestrate thickenings; spore germination endosporic.

Pleuroziaceae Müll.Frib., Lebermoose 1: 404 (1909). *Pleurozia* Dumort. [includes *Eopleurozia* R.M.Schust.]

ORDER: METZGERIALES Chalaud, Ann. Bryol. 3: 41 (1930).

Plants thalloid; ventral appendages 1- or 2-celled slime papillae, dispersed or in 2 rows; archegonial neck highly reduced, only weakly differentiated from the venter; sporophytes enclosed by a fleshy shoot calyptra or coelocaule; capsules ovoid, ellipsoid or cylindric, with an apical elaterophore, with the wall 2-stratose, with the cells in both layers bearing wall thickenings; spore germination exosporic; asexual reproduction by gemmae common.

Metzgeriaceae H.Klinggr., Höh. Crypt. Preuss.: 10 (1858). Thallus differentiated into a distinct midrib and unistratose wing, with unicellular setose hairs on the thallus margin and/or ventral surface of the midrib; ventral slime papillae 1-celled, in 2 rows; vegetative branching furcate or ventral endogenous; oil bodies lacking; antheridia in 2 rows on abbreviated ventral exogenous branches, without perigonial scales; archegonia on abbreviated ventral endogenous branches, without perichaetial scales; sporophytes enclosed by a hairy coelocaule; capsules ovoid to oblong; gemmae multicellular, exogenous. *Metzgeria* Raddi [includes *Apometzgeria* Kuwah. and *Austrometzgeria* Kuwah.], *Steereella* Kuwah., *Vandiemenia* Hewson

Aneuraceae H.Klinggr., Höh. Crypt. Preuss.: 11 (1858). Thallus fleshy, lacking a strongly differentiated midrib; ventral slime papillae 2-celled, in 2 rows or dispersed; vegetative branching monopodial; oil bodies present; antheridia sunken in chambers on abbreviated lateral branches (on the main thallus in *Verdoornia*); archegonia in clusters, with paraphyses, on abbreviated lateral branches (on the main thallus in *Verdoornia*); sporophytes enclosed by a fleshy shoot calyptra or coelocaule; capsules ellipsoid to cylindric; gemmae usually endogenous (exogenous, but rare in *Aneura*). *Aneura* Dumort. [includes *Cryptothallus* Malmb.], *Lobatiriccardia* (Mizut. & S.Hatt.) Furuki, *Riccardia* Gray nom. cons., *Verdoornia* R.M.Schust.

Mizutaniaceae Furuki & Z.Iwats., J. Hattori Bot. Lab. 67: 291 (1989). Thallus unistratose throughout; ventral slime papillae absent; oil bodies present; gynoecia on highly reduced lateral branches, appearing sessile on the thallus margin; gemmae multicellular, exogenous. *Mizutania* Furuki & Z.Iwats.

SUBCLASS: JUNGERMANNIIDAE Engl. [Unterklasse 'Jungermanniales'] in Engl. & Prantl, Nat. Pflanzenfam. I(3): 1 (1893).

Plants leafy, isophyllous or anisophyllous with the ventral leaves (underleaves or amphigastria) smaller and/or morphologically different from the lateral leaves, very rarely thalloid (e.g. *Pteropsiella*); leaves in 2 or 3 rows, with the third row ventral, developing from 2 primary leaf initials, frequently divided into 2 or more lobes; apical cell tetrahedral; antheridia in the axils of modified leaves, rarely underleaves (male bracts and bracteoles); archegonia acrogynous, usually surrounded by a perianth and modified leaves and underleaves (female bracts and bracteoles); capsules variable in shape, with the wall 2- to 10-stratose and dehiscence 4-valved.

ORDER: PORELLALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 505 (1972).

Leaves incubous, complicate, unequally 2- or 3-lobed, with the smaller lobe(s) or lobules ventral; lobule commonly forming an inflated water sac; underleaves present or absent, sometimes with water sacs; rhizoids fascicled, from the underleaf base; branches exogenous, lateral; spore germination precocious and endosporic (unknown in *Goebeliella*).

SUBORDER: PORELLINEAE R.M.Schust., J. Hattori Bot. Lab. 26: 229 (1963).

Plants robust, highly branched, pinnate or bipinnate; branches lateral, of the *Frullania*-type; underleaves present; gynoecia with multiple archegonia and several series of bracts and bracteoles; elaters free and randomly dispersed in the capsule.

Porellaceae Cavers nom. cons., New Phytol. 9: 292 (1910). Leaves 2-lobed, with the dorsal lobe entire or toothed, and the ventral lobule explanate (auricles at the base of the lobe and lobule inflated to form *Lejeunea*-type water sacs in *Ascidiota*); underleaves undivided (with basal water sacs in *Ascidiota*); androecia and gynoecia on abbreviated branches; sporophytes enclosed by a shoot calyptra and perianth; perianths 3-keeled, with the mouth contracted (rarely beaked); capsules spheroidal, with the wall 3- to 6-stratose, with both epidermal and inner cells bearing wall thickenings. *Ascidiota* C.Massal., *Porella* L. [includes *Macvicaria* W.E.Nicholson]

Goebeliellaceae Verd., Man. Bryol.: 425 (1932). Leaves 3-lobed, with the large dorsal lobe entire, and the two ventral lobules forming horn-like, *Frullania*-type water sacs; underleaves reniform, undivided; androecia terminal or intercalary on leading axes; gynoecia on long branches; sporophytes enclosed by a true calyptra and perianth; perianths 3-keeled, with the mouth truncate; capsules ellipsoidal, with the wall 3- or

4-stratose, with both epidermal and inner cells bearing wall thickenings; spores unicellular at dehiscence; sporeling unknown. *Goebeliella* Steph.

Lepidolaenaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 200 (1943). Leaves 3-lobed, with the large dorsal lobe variously toothed, the median lobule forming a *Frullania*-type water sac, and the ventral-most lobule forming a foliose stylus; underleaves bifid or quadrifid, with the segments forming *Frullania*-type water sacs on the branches; androecia and gynoecia on leading axes; sporophytes enclosed by a coelocaule; perianths absent or rudimentary; capsules ellipsoidal to cylindric, with an apical cap, with the wall 2-stratose, with the epidermal cells lacking thickenings (except *Jubulopsis*), with the valves apically coherent. *Gackstroemia* Trevis., *Jubulopsis* R.M.Schust., *Lepidogyna* R.M.Schust., *Lepidolaena* Dumort.

SUBORDER: RADULINEAE R.M.Schust., J. Hattori Bot. Lab. 26: 229 (1963).

Plants irregularly pinnate to bipinnate, with branches of the *Radula*-type; leaves 2-lobed, with the ventral lobule slightly inflated near the keel; underleaves absent; rhizoids in fascicles from the leaf lobules; androecia amentiferous, on lateral branches, rarely intercalary on the leading axis; gynoecia terminating a leading axis, rarely on a lateral branch, with 2 to 4 archegonia; bracts in a single series; bracteoles absent; sporophytes enclosed by a shoot calyptra or stem perigynium and perianth; perianths 2-keeled, dorsiventrally compressed, with the mouth truncate; capsules cylindric, with the wall 2-stratose, with both epidermal and inner cells bearing wall thickenings; multicellular discoid gemmae in some species.

Radulaceae Müll.Frib., Lebermoose 1: 404 (1909). *Radula* Dumort. nom. cons.

SUBORDER: JUBULINEAE Müll.Frib., Lebermoose 1: 403 (1909).

Plants usually with underleaves (absent in a few Lejeuneaceae); rhizoids fascicled from the underleaf base; sporophytes enclosed by a stalked, true calyptra and perianth; perianths beaked; capsules spheroidal, with the wall 2-stratose; elaters vertically aligned, attached to the valve apices; spores with rosette markings in the exine (absent in *Jubula*).

Frullaniaceae Lorch in G.Lindau, Krypt.-Fl. Anf. 6: 174 (1914). Leaves 3-lobed, with the dorsal lobe usually entire, the median lobule forming a *Frullania*-type water sac, and the ventral-most segment forming a uniseriate or laminar stylus; underleaves bifid; vegetative branches mostly of the *Frullania*-type (*Bryopteris*-type on decapitated shoots); androecia on elongate to capitate *Frullania*-type branches, occasionally becoming intercalary; gynoecia on leading axes, with multiple archegonia; bracts and bracteoles in 3 or 4 series, without subfloral innovations; seta up to 12 cells in diameter, nonarticulate; gemmae absent. *Frullania* Raddi [includes *Amphijubula* R.M.Schust., *Neohattoria* Kamim., *Schusterella* S.Hatt., Sharp & Mizut., and *Steerea* S.Hatt. & Kamim.]

Jubulaceae H.Klinggr., Höh. Crypt. Preuss.: 40 (1858). Leaves 2-lobed, with the dorsal lobe margin spinose, rarely entire, ventral lobule forming water sacs of the *Frullania*-type (*Jubula*) or *Lejeunea*-type (*Nipponolejeunea*), with a stalked slime papilla at the postical insertion of the lobe in *Jubula*; underleaves bifid; vegetative branches mostly of the *Frullania*-type; androecia spicate, on collared, *Bryopteris*-type branches, or intercalary on a leading axis; gynoecia on leading axes, with 1 or 2 archegonia; bracts and bracteoles in 1 to 3 series, with 1 or 2 *Radula*-type subfloral innovations; seta 4 cells in diameter, cruciate, nonarticulate; gemmae absent. *Jubula* Dumort. nom. cons., *Nipponolejeunea* S.Hatt.

Lejeuneaceae Cavers, New Phytol. 9: 291 (1910). Leaves 2(or 3)-lobed, with the dorsal lobe entire or toothed and the ventral lobule forming a *Lejeunea*-type water sac, sometimes with a small stylus ventral to the lobule (e.g. *Cololejeunea*); vegetative branches of the *Lejeunea*-type, less frequently of the *Frullania*-type, rarely of the *Bryopteris*-type; underleaves undivided, bifid, or absent; androecia and gynoecia on abbreviated branches of the *Lejeunea*-type, or on leading axes; gynoecia with 1 archegonium and a single series of bracts and bracteoles; subfloral innovations, when present, of the *Radula*-type; seta 4 cells in diameter, cruciate, commonly articulate or tiered, but nonarticulate in some taxa; discoid gemmae formed in some taxa. *Acanthocoleus* R.M.Schust., *Acantholejeunea* (R.M.Schust.) R.M.Schust., *Acrolejeunea* (Spruce) Schiffn. nom. cons., *Anoplolejeunea* (Spruce) Schiffn., *Aphanotropis* Herzog, *Archilejeunea* (Spruce) Schiffn., *Aureolejeunea* R.M.Schust., *Austrolejeunea* (R.M.Schust.) R.M.Schust. [includes *Nephelolejeunea* Grolle], *Blepharolejeunea* S.W.Arnell, *Brachiolejeunea* (Spruce) Schiffn., *Bromeliophila* R.M.Schust., *Bryopteris* (Nees) Lindenb., *Calatholejeunea* K.I.Goebel, *Caudalejeunea* (Steph.) Schiffn., *Cephalantholejeunea* (R.M.Schust. & Kachroo) R.M.Schust., *Cephalolejeunea* Mizut., *Ceratolejeunea* (Spruce) J.B.Jack & Steph., *Cheilolejeunea* (Spruce) Schiffn. [includes *Cyrtolejeunea* A.Evans], *Chondriolejeunea* (Benedix) Kis & Pócs, *Cladolejeunea* Zwick., *Cololejeunea* (Spruce) Schiffn. [includes *Aphanolejeunea* A.Evans and *Metzgeriopsis* K.I.Goebel], *Colura* (Dumort.) Dumort., *Cyclolejeunea* A.Evans, *Cystolejeunea* A.Evans, *Dactylophorella* R.M.Schust., *Dendrolejeunea* (Spruce) Lacout., *Dicranolejeunea* (Spruce) Schiffn., *Diplasiolejeunea* (Spruce) Schiffn., *Drepanolejeunea* (Spruce) Schiffn. [includes *Capillolejeunea* S.W.Arnell and *Rhaphidolejeunea* Herzog], *Echinolejeunea* R.M.Schust., *Evansiolejeunea* Vanden Berghen, *Frullanoides* Raddi, *Fulfordianthus* Gradst., *Haplolejeunea* Grolle, *Harpalejeunea* (Spruce) Schiffn., *Hattoriolejeunea* Mizut., *Kymatolejeunea* Grolle, *Leiolejeunea* A.Evans, *Lejeunea* Lib. nom. cons. [includes *Amblyolejeunea* Ast, *Amphilejeunea* R.M.Schust., *Crossotolejeunea* (Spruce) Schiffn., *Cryptogynolejeunea* R.M.Schust., *Dactylolejeunea* R.M.Schust., *Dicladolejeunea* R.M.Schust., *Echinocolea* R.M.Schust., *Macrolejeunea* (Spruce) Schiffn., *Neopotamolejeunea* E.Reiner and *Taxilejeunea* (Spruce) Schiffn. nom. cons.], *Lepidolejeunea* R.M.Schust., *Leptolejeunea* (Spruce) Schiffn., *Leucolejeunea* A.Evans, *Lindigianthus* Kruijt & Gradst., *Lopholejeunea* (Spruce) Schiffn. nom. cons., *Luteolejeunea* Piippo, *Macrocolura* R.M.Schust., *Marchesinia* Gray nom. cons., *Mastigolejeunea* (Spruce) Schiffn., *Metalejeunea* Grolle, *Microlejeunea* Steph., *Myriocolea* Spruce, *Myriocoleopsis* Schiffn., *Neurolejeunea* (Spruce) Schiffn., *Odontolejeunea* (Spruce) Schiffn., *Omphalanthus* Lindenb. & Nees, *Oryzolejeunea* (R.M.Schust.) R.M.Schust., *Otolejeunea* Grolle & Tixier, *Phaeolejeunea* Mizut., *Physantholejeunea* R.M.Schust., *Pictolejeunea* Grolle, *Pluvianthus* R.M.Schust. & Schäf.-Verw., *Prionolejeunea* (Spruce) Schiffn., *Ptychanthus* Nees, *Pycnolejeunea* (Spruce) Schiffn., *Rectolejeunea* A.Evans, *Schiffneriolejeunea* Verd., *Schusterolejeunea* Grolle, *Siphonolejeunea* Herzog, *Sphaerolejeunea* Herzog, *Spruceanthus* Verd., *Stenolejeunea* R.M.Schust., *Stictolejeunea* (Spruce) Schiffn., *Symbiezidium* Trevis., *Thysananthus* Lindenb., *Trachylejeunea* (Spruce) Schiffn. nom. cons. [includes *Potamolejeunea* (Spruce) Lacout.], *Trocholejeunea* Schiffn., *Tuyamaella* S.Hatt., *Tuzibeanthus* S.Hatt., *Verdoornianthus* Gradst., *Vitalianthus* R.M.Schust. & Giancotti, *Xylolejeunea* X-L.He & Grolle

ORDER: PTILIDIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 501 (1972).
Plants regularly pinnate to bipinnate; leaves asymmetrically 3-lobed, with the dorsal lobe the largest; lobes with marginal cilia, plane, or with the ventral-most lobe forming a water sac of either the *Frullania*-type (*Neotrichocolea*, branch leaves only) or the *Lejeunea*-type (*Trichocoleopsis*); leaf insertion transverse to weakly incubous, or succubous (*Herzogianthus*); underleaves bifid (sometimes quadrifid in *Herzogianthus*); rhizoids in fascicles from the underleaf

base; branches of the *Frullania*-type; androecia becoming intercalary on leading axes or on short lateral branches (*Herzogianthus*); gynoecia on leading axes, becoming pseudolateral with the growth of subfloral branches; capsules ovoid to ellipsoidal, with the walls 4- to 7-stratose; spore germination exosporic (*Ptilidium*) or endosporic (*Trichocoleopsis*); gemmae absent.

Ptilidiaceae H.Klinggr., Höh. Crypt. Preuss.: 37 (1858). Leaves transverse to weakly incubous; underleaves large, bifid, with the margins ciliate like the leaves; subfloral innovations lacking; sporophytes enclosed in a shoot calyptra and perianth; capsules ovoid; capsule wall 3- to 5-stratose; spores small, < 35 μm; spore germination exosporic. *Ptilidium* Nees

Neotrichocoleaceae Inoue, Ill. Jap. Hepat. 1: 176 (1974). Leaves transverse, with the ventral-most lobules forming water sacs; water sacs of the *Frullania*-type, formed only on branches in *Neotrichocolea*, or of the *Lejeunea*-type on all leaves in *Trichocoleopsis*; underleaves bifid, with numerous long cilia obscuring the lobes in *Trichocoleopsis*; sporophytes enclosed in a coelocaule; capsules ellipsoidal, with the wall 3- or 4-stratose; spore germination endosporic. *Neotrichocolea* S.Hatt., *Trichocoleopsis* S.Okamura

Herzogianthaceae Stotler & Crand.-Stotl. in B.Goffinet & A.J.Shaw, Bryoph. Biol., ed. 2: 54 (2008 ['2009']). Leaves dimorphic, with those of the main axis succubous, large and distant, and those of the branches reduced, subtransverse, vaginate and dorsally connate; underleaves bifid, or quadrifid on robust stems; rhizoids purple; sporophytes enclosed in a shoot calyptra and perianth; capsules ovoid, with the wall fleshy, 6- or 7-stratose; spores large, > 60 μm. *Herzogianthus* R.M.Schust.

ORDER: JUNGERMANNIALES H.Klinggr., Höh. Crypt. Preuss.: 16 (1858).

Leaves succubous, incubous, or transverse, undivided or variously lobed, sometimes complicate, but then usually with the smaller lobe(s), or lobules, dorsal, rarely with inflated water sacs of the *Lejeunea*-type; underleaves present or absent; rhizoids fascicled from the underleaf base or scattered along the ventral side of the stem; branches exogenous or endogenous, lateral or ventral; spore germination usually exosporic.

SUBORDER: PERSSONIELLINEAE R.M.Schust., J. Hattori Bot. Lab. 26: 229–230 (1963).

Plants large, anisophyllous or distichous (isophyllous in *Pleurocladopsis*); leaves complicate-bilobed, with the lobes symmetric or if unequal, usually with the smaller lobe dorsal, with the keel often winged; leaf insertion transverse, but with dorsal lobes incubously shingled; rhizoids scattered (fascicled in *Pachyschistochila*), magenta to purple (colourless in *Pachyschistochila*), with the apices highly branched and sometimes septate; branches lateral, of the *Plagiochila*-, *Frullania*- and *Radula*-type; androecia dispersed on leading axes, with the bracts scarcely differentiated, with the antheridia long-stalked; perianths absent; sporophytes enclosed in a coelocaule; spore germination exosporic, sporeling filamentous; gemmae absent.

Perssoniellaceae R.M.Schust. ex Grolle, J. Bryol. 7: 216 (1972). Plants distichous; leaf lobes subequal, with the slightly smaller lobe ventral, with the keel not winged; underleaves absent; capsules ellipsoidal, with the wall 2-stratose. *Perssoniella* Herzog

Schistochilaceae H.Buch, Commentat. Biol. 3(1): 9 (1928). Plants isophyllous or anisophyllous (rarely distichous); leaf lobes subequal to unequal, with the smaller lobe dorsal, with the lobe apices acute to acuminate and the margins usually dentate to ciliate, with the keel bearing 1 or 2 wings; underleaves bifid or quadrifid (absent in *Gottschea*); capsules ellipsoidal to cylindric, sometimes with an apical cap, with the wall 3- or 4-stratose. *Gottschea* Nees ex Mont. [includes *Paraschistochila* R.M.Schust.], *Pachyschistochila* R.M.Schust. & J.J.Engel, *Pleurocladopsis* R.M.Schust., *Schistochila* Dumort.

SUBORDER: LOPHOCOLEINEAE Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 504 (1972) [syn.: Geocalycineae R.M.Schust., J. Hattori Bot. Lab. 36: 397 (1973 ['1972'])].

Leaves transverse, succubous, or incubous, divided into 2 to 4 lobes, or undivided; underleaves usually present; perianths, when present, usually with 3 broad keels; capsule walls polystratose, only rarely 2-stratose; spore germination exosporic, mostly of the *Nardia*-type; gemmae rare.

Pseudolepicoleaceae Fulford & J.Taylor, Nova Hedwigia 1: 411 (1960). Leaves transverse or succubous, deeply divided into 3 or 4 (rarely more) lobes, sometimes bisbifid; underleaves morphologically like the leaves, but sometimes smaller; branches terminal of the *Frullania*-, *Microlepidozia*- and *Acromastigum*-type, and ventral endogenous (*Bazzania*-type); rhizoids fascicled; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and perianth, with the foot and seta deeply embedded in stem tissue; perianths cylindric, broadly 3-plicate, with the third keel ventral; capsules ovoid to ellipsoidal, with the wall 2- to 4-stratose. *Archeophylla* R.M.Schust., *Blepharostoma* (Dumort.) Dumort., *Chaetocolea* Spruce, *Herzogiaria* Fulford ex Hässel, *Isophyllaria* E.A.Hodgs. & Allison, *Pseudolepicolea* Fulford & J.Taylor [includes *Archeochaete* R.M.Schust. and *Lophochaete* R.M.Schust.], *Temnoma* Mitt.

Trichocoleaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 201 (1943). Leaves succubous, asymmetrically 4-lobed, with the lobes often further divided and ciliate; underleaves smaller than the leaves, 4-lobed, with the margins ciliate; branches of the *Frullania*-type, rarely of the ventral *Acromastigum*-type; sporophytes enclosed by a fleshy shoot calyptra, coelocaule, or stem perigynium; perianths usually absent (present in *Castanoclobus*); capsules spheroidal or ellipsoidal, with the wall 6- to 8-stratose. *Castanoclobus* J.J.Engel & Glenny, *Eotrichocolea* R.M.Schust., *Leiomitra* Lindb., *Trichocolea* Dumort. nom. cons.

Grolleaceae Solari ex R.M.Schust., Phytologia 56: 66 (1984). Leaves transverse, bilobed, with the margins entire; underleaves like the leaves; rhizoids red-violet, in fascicles between underleaves; branching endogenous, of the *Bazzania*- and *Plagiochila*-type; sporophyte enclosed by a calyptra and the terminal series of bracts and bracteoles; perianths absent; capsules spheroidal, with the wall 2-stratose. *Grollea* R.M.Schust.

Mastigophoraceae R.M.Schust., J. Hattori Bot. Lab. 36: 345 (1973 ['1972']). Leaves transverse to incubous, 3- or 4-lobed; underleaves smaller than the leaves, bifid or quadrifid; branches lateral, of the *Frullania*-type; androecia with bracteolar antheridia; gynoecia on abbreviated lateral branches; sporophytes enclosed by a shoot calyptra and deeply divided perianth; capsules spheroidal, with the wall 4- to 6-stratose. *Dendromastigophora* R.M.Schust., *Mastigophora* Nees nom. cons.

Herbertaceae Müll.Frib. ex Fulford & Hatcher, Bryologist 61: 284 (1958). Plants with primary rhizomatous axes; leafy shoots with leaves transverse to weakly incubous, 2-, 3- or 4-lobed, with the lobes entire; isophyllous; branches endogenous, of the *Bazzania*- and *Plagiochila*-type; androecia with bracteolar antheridia; gynoecia on leading axes; sporophytes enclosed by a calyptra and perianth; perianths 3-keeled, with the third keel dorsal, with the mouth deeply 6-lobed; capsules spheroidal, with the wall 7- to 10-stratose. *Herbertus* Gray, *Olgantha* R.M.Schust., *Triandrophyllum* Fulford & Hatcher

Vetaformataceae Fulford & J.Taylor, Mem. New York Bot. Gard. 11: 27 (1963). Leaves transverse, bisbifid; underleaves like the leaves; branches terminal of the *Frullania*- and *Acromastigum*-type, and axillary endogenous, of the *Bazzania*- and *Plagiochila*-type; androecia scarcely differentiated, with bracteolar antheridia; sporophytes enclosed by a coelocaule; perianths absent; mature sporophytes unknown. *Vetaforma* Fulford & J.Taylor

Lepicoleaceae R.M.Schust., Nova Hedwigia 5: 27 (1963). Leaves weakly incubous, bisbifid; underleaves like the leaves; branches lateral, of the *Frullania*-type, often flexuous and attenuate; androecia with bracteolar antheridia; sporophytes enclosed by a coelocaule; perianths absent; capsules spheroidal, with the wall 5- or 6-stratose. *Lepicolea* Dumort.

Phycolepidoziaceae R.M.Schust., Bull. Torrey Bot. Club 93: 442 (1967). Vegetative axes reduced to 1 central and 5 epidermal cells, with the leaves reduced to stalked slime papillae; underleaves absent; branches ventral, endogenous (*Bazzania*-type); androecia terminating leafless axes, with bifid bracts but no bracteoles; gynoecia on abbreviated branches, with bracts and bracteoles bifid; sporophytes enclosed by a calyptra and perianth; perianths with the mouth deeply lobed; seta reduced, with a 4 + 4-seriate morphology; capsules ellipsoidal, with the wall 2-stratose, with the epidermal cells tiered, with 1-phase ontogeny. *Phycolepidozia* R.M.Schust.

Lepidoziaceae Limpr. in Cohn, Krypt.-Fl. Schlesien 1: 310 (1877). Leaves incubous or succubous, rarely transverse, 2-, 3- or 4-lobed, rarely 5- or 6-lobed, lobes conduplicate in some genera; underleaves lobed like the leaves, but smaller; rhizoids fascicled; branches terminal, of the *Frullania*-, *Microlepidozia*- and *Acromastigum*-type, and ventral endogenous *Bazzania*-type, with the ventral branches often flagelliform or stoloniferous; androecia and gynoecia on abbreviated *Bazzania*-type branches; gynoecium with isomorphic bracts and bracteoles; sporophytes enclosed by a shoot calyptra and perianth; perianths 3-keeled, with the third keel ventral; seta of 8 to 16 epidermal cells and numerous smaller internal cells; capsules ovoid to ellipsoidal, with the wall 3- to 5-stratose, with the epidermal cells with 2-phase ontogeny. *Acromastigum* A.Evans, *Amazoopsis* J.J.Engel & G.L.S.Merr., *Arachniopsis* Spruce, *Bazzania* Gray nom. cons., *Chloranthelia* R.M.Schust., *Dendrobazzania* R.M.Schust. & W.B.Schofield, *Drucella* E.A.Hodgs., *Hyalolepidozia* S.W.Arnell ex Grolle, *Hygrolembidium* R.M.Schust., *Isolembidium* R.M.Schust., *Kurzia* G.Martens, *Lembidium* Mitt. nom. cons., *Lepidozia* (Dumort.) Dumort. nom. cons., *Mastigopelma* Mitt., *Megalembidium* R.M.Schust., *Micropterygium* Lindenb., Nees & Gottsche, *Monodactylopsis* (R.M.Schust.) R.M.Schust., *Mytilopsis* Spruce, *Neogrollea* E.A.Hodgs., *Odontoseries* Fulford, *Paracromastigum* Fulford & J.Taylor, *Protocephalozia* (Spruce) K.I.Goebel, *Pseudocephalozia* R.M.Schust., *Psiloclada* Mitt., *Pteropsiella* Spruce, *Sprucella* Steph., *Telaranea* Spruce ex Schiffn., *Zoopsidella* R.M.Schust., *Zoopsis* Hook.f. ex Gottsche, Lindenb. & Nees

Lophocoleaceae Vanden Berghen in Robyns, Fl. Gén. Belgique, Bryoph. 1: 208 (1956). Leaves succubous, 2-lobed or undivided; anisophyllous (isophyllous in *Pachyglossa*); underleaves bifid, frequently with marginal teeth, often connate with the leaves; rhizoids fascicled; lateral branches of the *Frullania*- and *Plagiochila*-type (*Anomoclada*-type in *Evansianthus*), ventral branches of the *Bazzania*-type; stolons usually absent; androecia usually on leading axes (sometimes on abbreviated lateral or ventral endogenous branches); gynoecia usually on leading axes (sometimes on abbreviated lateral or ventral endogenous branches); sporophytes enclosed by a shoot calyptra and perianth; perianths 3-keeled with the third keel dorsal, sometimes laterally compressed with the ventral side reduced; capsules ovoid to ellipsoid, with the wall 4- or 5-stratose and the epidermal cells with 1-phase ontogeny; gemmae present in a few taxa. *Amphilophocolea* R.M.Schust., *Chiloscyphus* Corda, *Clasmatocolea* Spruce, *Conoscyphus* Mitt., *Cyanolophocolea* R.M.Schust., *Evansianthus* R.M.Schust. & J.J.Engel [includes *Austrolembidium* Hässel], *Hepatostolonophora* J.J.Engel & R.M.Schust., *Heteroscyphus* Schiffn. nom. cons. [includes *Tetracymbaliella* Grolle], *Lamellocolea* J.J.Engel, *Leptophyllopsis* R.M.Schust., *Leptoscyphopsis*

R.M.Schust., *Leptoscyphus* Mitt., *Lophocolea* (Dumort.) Dumort. [includes *Campanocolea* R.M.Schust.], *Pachyglossa* Herzog & Grolle [includes *Invisocaulis* R.M.Schust. nom. inval.], *Perdusenia* Hässel, *Physotheca* J.J.Engel & Gradst., *Pigafettoa* C.Massal., *Platycaulis* R.M.Schust., *Pseudolophocolea* R.M.Schust. & J.J.Engel, *Stolonivector* J.J.Engel, *Xenocephalozia* R.M.Schust.

Brevianthaceae J.J.Engel & R.M.Schust., Phytologia 47: 317 (1981). Leaves undivided, succubous; underleaves lacking; rhizoids scattered; branches of the *Plagiochila*-type; androecia on very small, capitate branches; gynoecia on abbreviated branches; sporophytes enclosed by a vestigial stem perigynium, true calyptra and perianth; perianths ovoid, broadly plicate, with the mouth 3-lobed; capsules spheroidal, with the wall 3- or 4-stratose and the epidermal cells with 1-phase ontogeny; gemmae absent. *Brevianthus* J.J.Engel & R.M.Schust.

Chonecoleaceae R.M.Schust. ex Grolle, J. Bryol. 7: 206 (1972). Leaves bifid, succubous; underleaves reduced, subulate or short filaments; rhizoids scattered; branches of the *Plagiochila*-type; androecia and gynoecia on leading axes; sporophytes enclosed by a calyptra and perianth; perianths campanulate, with the mouth 4-lobed; seta reduced, with an 8 + 4-seriate morphology; capsules spheroidal, with the wall 2-stratose. *Chonecolea* Grolle

Plagiochilaceae Müll.Frib. & Herzog in Müller, Leberm. Eur.: 877 (1956). Leaves succubous, undivided, with the margins entire or toothed to ciliate and the dorsal margin often reflexed; underleaves reduced or absent; rhizoids scattered or restricted to leaf bases; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and perianth; perianths laterally compressed, bilabiate, with the mouth truncate, not contracted; capsules ovoid to ellipsoidal, with the wall 4- to 10-stratose. *Acrochila* R.M.Schust., *Chiastocaulon* Carl, *Dinckleria* Trevis. [≡ *Proskauera* Heinrichs & J.J.Engel], *Pedinophyllopsis* R.M.Schust. & Inoue, *Pedinophyllum* (Lindb.) Lindb., *Plagiochila* (Dumort.) Dumort. nom. cons. [includes *Rhodoplagiochila* R.M.Schust., *Steereochila* Inoue, and *Szweykowskia* Gradst. & E.Reiner], *Plagiochilidium* Herzog, *Plagiochilion* S.Hatt., *Xenochila* R.M.Schust.

SUBORDER: CEPHALOZIINEAE Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 503 (1972) [syn.: Cephaloziineae R.M.Schust., J. Hattori Bot. Lab. 36: 391 (1973 ['1972'])].

Leaves usually succubous (transverse in Cephaloziellaceae), undivided or 2-lobed, with the margins entire or with small teeth; underleaves absent or very small; rhizoids scattered; ventral *Bazzania*-type branches common; sporophytes usually enclosed by a calyptra and perianth; gemmae common.

Adelanthaceae Grolle, J. Hattori Bot. Lab. 35: 327 (1972). Plants differentiated into a highly branched system of microphyllous, geotropic shoots and unbranched leafy shoots with cernuous apices; leaves succubous, entire or with small marginal teeth; underleaves absent, or vestigial papillae; rhizoids absent on leafy shoots; branches mostly endogenous, of the *Bazzania*- and *Plagiochila*-type, rarely *Frullania*-type; androecia and gynoecia on highly abbreviated branches at the base of leafy shoots; sporophytes enclosed by a firm, green shoot calyptra and perianth (some species of *Adelanthus*), or only by a very fleshy, green shoot calyptra; perianths, when present, 3-keeled; seta massive, to 12 cells in diameter; capsules ellipsoidal, with the wall 4- to 7-stratose; gemmae present in *Calyptrocolea*. *Adelanthus* Mitt. nom. cons. [includes *Pseudomarsupidium* Herzog], *Calyptrocolea* R.M.Schust., *Wettsteinia* Schiffn.

Jamesoniellaceae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006). Plants sparingly branched, rhizomatous system lacking; leaves succubous, entire (subapically toothed in *Anomacaulis*); underleaves usually reduced (large in *Roivainenia*), subulate to lanceolate; rhizoids scattered; branches of the *Frullania*- and *Bazzania*-type, not forming stolons; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and perianth; perianths pluriplicate, sometimes twisted, with the mouth contracted; capsules ovoid-ellipsoidal, with the wall 4- to 7-stratose; gemmae absent. *Anomacaulis* (R.M.Schust.) Grolle, *Cryptochila* R.M.Schust., *Cuspidatula* Steph., *Denotarisia* Grolle, *Jamesoniella* (Spruce) F.Lees, *Nothostrepta* R.M.Schust., *Pisanoa* Hässel, *Protosyzygiella* (Inoue) R.M.Schust., *Roivainenia* Perss., *Syzygiella* Spruce, *Vanaea* (Inoue & Gradst.) Inoue & Gradst.

Cephaloziaceae Mig., Krypt.-Fl. Deutschl., Moose: 465 (1904). Plants small and soft-textured; leaves succubous to nearly longitudinal, 2-lobed or undivided (e.g. *Odontoschisma*); underleaves small and bilobed, or absent; rhizoids scattered; branches of the *Bazzania*-type common, sometimes microphyllous, rarely lateral *Frullania*- or *Plagiochila*-type also present; androecia and gynoecia on ventral branches (on leading axes in *Metahygrobiella*); antheridial jacket cells in tiers; sporophytes enclosed by a thin calyptra and perianth; perianths 3-keeled, with the third keel ventral; seta reduced, 8 + 4-seriate morphology; capsules ovoid-ellipsoidal, with the wall 2-stratose; the epidermal cells with 2-phase ontogeny; sporelings filamentous; gemmae common. *Alobiella* (Spruce) Schiffn., *Alobiellopsis* R.M.Schust., *Anomoclada* Spruce, *Cephalozia* (Dumort.) Dumort., *Cladopodiella* H.Buch, *Fuscocephaloziopsis* Fulford, *Haesselia* Grolle & Gradst., *Hygrobiella* Spruce, *Iwatsukia* N.Kitag., *Metahygrobiella* R.M.Schust., *Nowellia* Mitt., *Odontoschisma* (Dumort.) Dumort., *Pleurocladula* Grolle, *Schiffneria* Steph., *Schofieldia* J.D.Godfrey, *Trabacellula* Fulford

Cephaloziellaceae Douin, Bull. Soc. Bot. France, Mém. 29: 1, 5, 13 (1920). Plants very small, often with microphyllous, geotropic axes; leaves transverse to weakly succubous (incubous in *Cephalojonesia*), 2-lobed (undivided in *Kymatocalyx*); underleaves absent or very reduced; rhizoids scattered; branches mostly endogenous *Bazzania*-type, but *Frullania*-, *Acromastigum*- and *Plagiochila*-type also rarely present; androecia and gynoecia usually on leading axes; sporophytes enclosed by a calyptra and perianth; perianths (3-)4- or 5-plicate, with the mouth broad, not contracted; seta reduced, 4 + 4-seriate morphology (8 + 4 to 12 inner cells in some taxa); capsules ovoid to ellipsoidal, with the wall 2- or 3-(4-)stratose and the epidermal cells with 1-phase ontogeny; gemmae common. *Allisoniella* E.A.Hodgs. [includes *Protomarsupella* R.M.Schust.], *Amphicephalozia* R.M.Schust., *Cephalojonesia* Grolle, *Cephalomitrion* R.M.Schust., *Cephaloziella* (Spruce) Schiffn. nom. cons., *Cephaloziopsis* (Spruce) Schiffn., *Cylindrocolea* R.M.Schust., *Gymnocoleopsis* (R.M.Schust.) R.M.Schust., *Kymatocalyx* Herzog [includes *Stenorrhipis* Herzog]

Scapaniaceae Mig., Krypt.-Fl. Deutschl., Moose: 479 (1904) [includes the Chaetophyllopsidaceae R.M.Schust., J. Hattori Bot. Lab. 23: 68 (1961 ['1960']), the Diplophyllaceae Potemk., Ann. Bot. Fenn. 36: 281 (1999), and the Lophoziaceae Cavers, New Phytol. 9: 293 (1910)]. Leaves transverse to succubous, complicate-bilobed with the dorsal segment smaller, or 2-, 3- or 4-lobed (unlobed in *Gottschelia*), flat to concave or conduplicate, margins toothed to long ciliate (entire); underleaves usually absent (large, bifid); rhizoids usually scattered; androecia and gynoecia on leading axes; perigonia usually with paraphyses; sporophytes enclosed by a shoot calyptra and perianth; perianths cylindric or dorsiventrally flattened, with the mouth broad, or plicate and contracted; capsules ovoid (spheroidal or ellipsoidal), with the wall 2- to 8-layered; gemmae common, usually stellate. *Anastrepta* (Lindb.) Schiffn., *Anastrophyllum* (Spruce) Steph., *Andrewsianthus* R.M.Schust. [includes *Cephalolobus*

R.M.Schust.], *Barbilophozia* Loeske, *Chaetophyllopsis* R.M.Schust., *Chandonanthus* Mitt., *Diplophyllum* (Dumort.) Dumort. nom. cons., *Douinia* (C.N.Jensen) H.Buch, *Gerhildiella* Grolle, *Gottschelia* Grolle, *Gymnocolea* (Dumort.) Dumort., *Hamatostrepta* Váňa & D.G.Long, *Hattoria* R.M.Schust., *Isopaches* H.Buch, *Krunodiplophyllum* Grolle, *Lophozia* (Dumort.) Dumort., *Macrodiplophyllum* (H.Buch) Perss., *Plicanthus* R.M.Schust., *Pseudocephaloziella* R.M.Schust., *Scapania* (Dumort.) Dumort. nom. cons., *Scapaniella* H.Buch, *Schistochilopsis* (N.Kitag.) Konst., *Sphenolobopsis* R.M.Schust. & N.Kitag., *Sphenolobus* (Lindb.) Berggr., *Tetralophozia* (R.M.Schust.) Schljakov, *Tritomaria* Schiffn. ex Loeske

SUBORDER: JUNGERMANNIINEAE R.M.Schust. ex Stotler & Crand.-Stotl. in A.J.Shaw & B.Goffinet, Bryoph. Biol.: 64 (2000).

Leaves succubous, transverse or incubous, undivided or 2(to 4)-lobed; anisophyllous or distichous, rarely isophyllous; sporophytes frequently enclosed by structures derived from the stem, including stem perigynia, hollow marsupia of the *Calypogeia*-type, or solid marsupia of the *Tylimanthus*-type; perianths sometimes absent; capsules spheroidal, ovoidal, or ellipsoidal to cylindric, with the wall often 2-stratose; gemmae present in some taxa.

Myliaceae Schljakov, Novosti Sist. Nizsh. Rast. 12: 308 (1975). Leaves succubous, undivided, with the leaf surface fissured and divided into irregular plates and fibril-filled grids (*Mylia*) or smooth (*Leiomylia*); underleaves smaller than the leaves, lanceolate, undivided; rhizoids scattered; branches lateral of the *Frullania*-type; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and perianth; perianths laterally compressed above, with the mouth broad, bilabiate, dentate or ciliate; capsules ovoid, with the wall 3- to 5-stratose; gemmae 1- or 2-celled, on leaf tips. *Leiomylia* J.J.Engel & Braggins, *Mylia* Gray

Trichotemnomataceae R.M.Schust., J. Hattori Bot. Lab. 36: 340 (1973 ['1972']). Leaves succubous, undulate-crispate, asymmetrically 4-lobed, with the dorsal lobes somewhat smaller than the ventral, with the margins recurved and armed with pairs of stout cilia; underleaves half as large as the leaves, 2-lobed, with the margins ciliate to laciniate; rhizoids in fascicles at the underleaf base, with the tips digitate; branches mostly ventral, of the *Bazzania*-type, rarely lateral *Frullania*-type; androecia and gynoecia on abbreviated ventral branches; sporophytes enclosed by a calyptra and hollow marsupium of the *Calypogeia*-type; perianths absent; capsules ellipsoidal, with the wall 2-stratose; gemmae absent. *Trichotemnoma* R.M.Schust.

Balantiopsidaceae H.Buch, Mitt. Thüring. Bot. Ges. 1(2–3): 23 (1955). Leaves succubous, rarely transverse or incubous (e.g. *Isotachis*), 2-lobed or bisbifid (unlobed), with the margins dentate to ciliate, with the lobes subequal or the dorsal lobe smaller than the ventral (dorsal lobe larger than the ventral in *Isotachis*), complicate in *Balantiopsis*; underleaves bifid, with the margins entire, dentate or ciliate (truncate-entire); rhizoids in fascicles from the underleaf base; branches lateral of the *Frullania*-type, or ventral *Bazzania*-type; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and a stem perigynium, with or without a perianth, or a hollow marsupium of the *Calypogeia*-type (*Balantiopsis*); perianths, when present, tubular, often reduced at the apex of the stem perigynium; capsules cylindric (spheroidal in *Ruizanthus*), with the wall 2- to 5-stratose, with the valves spirally twisted (straight in *Ruizanthus*); gemmae absent. *Acroscyphella* N.Kitag. & Grolle [≡ *Austroscyphus* R.M.Schust. nom. illeg.], *Anisotachis* R.M.Schust., *Balantiopsis* Mitt., *Eoisotachis* R.M.Schust., *Hypoisotachis* (R.M.Schust.) J.J.Engel & G.L.S.Merr., *Isotachis* Mitt., *Neesioscyphus* Grolle, *Ruizanthus* R.M.Schust.

Acrobolbaceae E.A.Hodgs., Rec. Domin. Mus. 4: 177 (1962). Leaves succubous, undivided to 2(to 3 to 5)-lobed, with the margins entire or toothed or ciliate; underleaves absent or vestigial; rhizoids in fascicles at the leaf base or scattered; branches lateral of the *Plagiochila*-type, or sometimes ventral *Bazzania*-type; androecia and gynoecia on leading axes (except on abbreviated ventral branches in *Marsupidium*); gynoecium bilateral, with the innermost bracts very reduced; sporophytes enclosed by a solid marsupium of the *Tylimanthus*-type (by a shoot calyptra and hollow marsupium of the *Calypogeia*-type in *Lethocolea* and *Goebelobryum*); perianths absent; capsules ellipsoidal to cylindric, with an apical cap, with the wall 5- to 9-stratose; gemmae present in *Austrolophozia* and *Lethocolea*. *Acrobolbus* Nees, *Austrolophozia* R.M.Schust., *Enigmella* G.A.M.Scott & K.G.Beckm., *Goebelobryum* Grolle, *Lethocolea* Mitt. nom. cons. [includes *Neoprasanthus* S.Winkl.], *Marsupidium* Mitt., *Tylimanthus* Mitt.

Blepharidophyllaceae R.M.Schust., Nova Hedwigia Beih. 119: 491 (2002). Leaves distichous, transverse to obliquely succubous, complicate bisbifid with the lobes subequal or with the 2 dorsal lobes somewhat smaller, with the margins dentate to ciliate; underleaves absent except on gemmiparous shoots; rhizoids in fascicles from the leaf base; branches usually of the *Frullania*-type, rarely ventral *Bazzania*-type; androecia becoming intercalary on leafy stems; gynoecia terminal, lacking innovations; sporophytes enclosed by a calyptra and perianth; perianths fusiform, dorsiventrally flattened, narrowed and plicate apically, with the mouth ciliate and somewhat bilabiate; capsules long ovoid to cylindric, with the wall 5- to 6-stratose; gemmae absent (*Clandarium*) or 2-celled (*Bleparidophyllum*), formed on tristichous gemmiparous shoots. *Blepharidophyllum* Ångstr., *Clandarium* (Grolle) R.M.Schust.

Arnelliaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 200 (1943). Leaves succubous, opposite, dorsally connate (alternate, densely imbricate in *Stephaniella* and *Stephaniellidium*), undivided, with the margins entire; filamentous to lanceolate stem paraphyllia enclosed by echlorophyllose leaves in *Stephaniella* and *Stephaniellidium*; underleaves absent or minute and lanceolate; rhizoids scattered; branches lateral of the *Plagiochila*- or *Frullania*-type; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and hollow marsupium of the *Calypogeia*-type; perianths at the top of the marsupium, bilabiate, hidden by the inner bracts, or absent; capsules ellipsoidal to long cylindric, with the wall 2-stratose; gemmae formed from the abaxial surface of the leaves, 1- to 2-celled. *Arnellia* Lindb., *Gongylanthus* Nees, *Southbya* Spruce, *Stephaniella* J.B.Jack, *Stephaniellidium* S.Winkl. ex Grolle

Jackiellaceae R.M.Schust., J. Hattori Bot. Lab. 36: 395 (1973 ['1972']). Leaves succubous, undivided, with the margins entire; underleaves vestigial to absent; rhizoids fascicled; branches of the ventral *Bazzania*-type; androecia and gynoecia on abbreviated ventral branches; antheridial jacket cells tiered; sporophytes enclosed by a solid marsupium of the *Tylimanthus*-type; perianths absent; capsules ellipsoidal-cylindric, with the wall 2-stratose; gemmae common. *Jackiella* Schiffn.

Calypogeiaceae Arnell in Holmberg, Skand. Fl. 2a.: 189 (1928). Leaves incubous, undivided, with the margins entire or bidentate; underleaves 2-lobed or entire and retuse; rhizoids in fascicles from the underleaf base; branches ventral of the *Bazzania*-type (rarely *Acromastigum*-type) or lateral of the *Frullania*-type, forming an extensive stolon system in *Mnioloma*; androecia and gynoecia on very abbreviated ventral branches (except *Eocalypogeia*); sporophytes enclosed by a shoot calyptra and hollow marsupium of the *Calypogeia*-type; perianths absent; capsules ellipsoidal to cylindric, with the wall 2-stratose and the epidermal cells with 2-phase ontogeny, with the valves spirally twisted; gemmae produced in clusters on ascending shoot tips. *Calypogeia* Raddi nom. cons., *Eocalypogeia* (R.M.Schust.) R.M.Schust., *Metacalypogeia* (S.Hatt.) Inoue, *Mnioloma* Herzog

Delavayellaceae R.M.Schust., Bryologist 64: 202 (1961). Leaves strongly succubous, with a long line of insertion, either shallowly 2-lobed, with the ventral lobe slightly smaller than the dorsal and forming a *Lejeunea*-type water sac at the postical base (*Delavayella*) or undivided to retuse (*Liochlaena*), with the margins entire; underleaves absent; rhizoids scattered; branches lateral, of the *Plagiochila*-type; androecia and gynoecia on leading axes; perichaetial bracts like the leaves; bracteoles absent; sporophytes enclosed by a shoot calyptra and perianth; perianths long cylindric, smooth, with the mouth narrowed or constricted to a beak, dentate; capsules ovoid to ellipsoidal, with the wall 2-stratose; gemmae formed singly from marginal cells of scale-like leaves on erect branches, globose and pluricellular (*Delavayella*) or 2-celled, ellipsoidal (*Liochlaena*). *Delavayella* Steph., *Liochlaena* Nees

Jungermanniaceae Rchb., Bot. Damen: 256 (1828) [includes Mesoptychiaceae Inoue & Steere, Bull. Natl. Sci. Mus. Tokyo, B 1: 62 (1975)]. Leaves succubous (transverse in *Eremonotus*), shallowly 2(or 3)-lobed or undivided; underleaves absent or vestigial (large, bifid, with ciliate margins in *Mesoptychia*); rhizoids scattered, forming dense mats; branches lateral, usually of the *Plagiochila*-type, sometimes of the *Frullania*-type; androecia and gynoecia on leading axes; sporophytes usually enclosed by a shoot calyptra and perianth (a hollow marsupium formed beneath the perianth in *Mesoptychia*); perianths terete, smooth, often plicate near the mouth, with the mouth contracted or beaked; capsules subspheroidal to shortly ellipsoidal, with the wall 2-stratose; gemmae absent (present in *Leiocolea heterocolpos* (Thed.) H.Buch). *Eremonotus* Lindb. & Kaal. ex Pearson [includes *Anomomarsupella* R.M.Schust.], *Hattoriella* (Inoue) Inoue, *Jungermannia* L., *Leiocolea* (Müll.Frib.) H.Buch, *Mesoptychia* (Lindb.) A.Evans

Solenostomataceae Stotler & Crand.-Stotl., **fam. nov.** Plantae foliis succubis, simplicibus (vel bilobatis breviter), amphigastris nullis vel parvis; perianthiis subtentis caulibus-perigyniis; parietibus capsulis 2(4)-stratosis, cellulis intimis rectangularibus, praeditis fasciis semiannularis. Type: *Solenostoma* Mitt. Leaves succubous, undivided or shallowly bilobed, with the margins entire; underleaves usually absent (small and lanceolate in *Nardia*); rhizoids scattered; branches lateral, of the *Frullania*- or *Plagiochila*-type; androecia and gynoecia on leading axes; sporophytes enclosed by a shoot calyptra and stem perigynium–perianth complex, sometimes with incipient marsupium development; perianths often reduced, terete below, pluriplicate above, with the mouth gradually contracted, rarely beaked; capsules subspheroidal to ovoid or shortly ellipsoidal, with the wall 2(to 4)-stratose, with the innermost wall cells rectangular, with semiannular thickenings; gemmae absent (present in *Solenostoma caespiticium* (Lindenb.) Steph.). *Arctoscyphus* Hässel, *Bragginsella* R.M.Schust., *Cryptocolea* R.M.Schust., *Cryptocoleopsis* Amak., *Cryptostipula* R.M.Schust., *Diplocolea* Amak., *Horikawaella* S.Hatt. & Amakawa, *Nardia* Gray nom. cons. [includes *Apotomanthus* (Spruce) Schiffn.], *Scaphophyllum* Inoue, *Solenostoma* Mitt. [includes *Plectocolea* (Mitt.) Mitt.]

Geocalycaceae H.Klinggr., Höh. Crypt. Preuss.: 34 (1858). Leaves succubous, undivided or 2-lobed, with the margins entire; underleaves bifid, with the margins entire or toothed (undivided, lanceolate in *Harpanthus*), frequently connate with the leaves; rhizoids scattered, but more abundant near the underleaves; branches ventral, of the *Bazzania*-type; androecia and gynoecia on abbreviated ventral branches; sporophytes enclosed by a shoot calyptra and hollow marsupium of the *Calypogeia*-type;

perianths absent or present at the top of the marsupium, 3-keeled with the third keel ventral; capsules ovoid to cylindric, with the wall 2-stratose (4- to 6-stratose in *Saccogynidium*) and the epidermal cells with 1-phase ontogeny; gemmae sometimes present. *Geocalyx* Nees, *Harpanthus* Nees, *Notoscyphus* Mitt., *Saccogyna* Dumort. nom. cons., *Saccogynidium* Grolle

Gyrothyraceae R.M.Schust., Trans. Brit. Bryol. Soc. 6: 87 (1970). Leaves succubous, undivided, entire; underleaves small, bifid, with large, purple cushions of rhizoid initials at the base of each underleaf; rhizoids formed at the periphery of the cushions; branches lateral, of the *Plagiochila*-type; androecia and gynoecia on leading axes; sporophytes enclosed by an incipient solid marsupium and perianth; perianths short and tubular; capsules cylindric, with the wall 2-stratose, without wall thickenings in either strata, with the valves spirally twisted; gemmae in dense clusters on ascending microphyllous apices. *Gyrothyra* M.Howe

Antheliaceae R.M.Schust., J. Hattori Bot. Lab. 26: 236 (1963). Leaves transverse to weakly succubous, 2-lobed, with the lobes entire; underleaves like the leaves; rhizoids in fascicles at the underleaf base; branches lateral, of the *Frullania*-type, or sporadically ventral of the *Bazzania*-type; androecia and gynoecia on leading axes; sporophytes enclosed by an incipient coelocaule and short, scarcely emergent perianth; perianths pluriplicate, with the mouth wide, deeply 3- to 6-lobed; capsules spheroidal, with the wall 2-stratose; gemmae absent. *Anthelia* (Dumort.) Dumort.

Gymnomitriaceae H.Klinggr., Höh. Crypt. Preuss.: 16 (1858). Leaves transverse to weakly succubous, interlocking dorsally, with insertions extending across the stem midline, 2-lobed (rarely undivided), with the apices and margins often hyaline; underleaves absent or vestigial; rhizoids scattered; branches lateral, of the *Plagiochila*-type, rarely *Frullania*-type; androecia and gynoecia on leading axes; androecia scarcely differentiated from vegetative regions; sporophytes enclosed by either a true or a shoot calyptra and a perianth or stem perigynium–perianth complex (or incipient hollow marsupium in *Prasanthus*); perianths short, nonemergent, or lacking (replaced by large bracts in *Gymnomitrion*); capsules spheroidal, with the wall 2-stratose, with the inner wall cells quadrate, with nodular thickenings; gemmae absent. *Acrolophozia* R.M.Schust., *Apomarsupella* R.M.Schust., *Gymnomitrion* Corda nom. cons., *Herzogobryum* Grolle, *Lophonardia* R.M.Schust., *Marsupella* Dumort., *Nanomarsupella* (R.M.Schust.) R.M.Schust., *Nothogymnomitrion* R.M.Schust., *Paramomitrion* R.M.Schust., *Poeltia* Grolle, *Prasanthus* Lindb.

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