



Notes on Early Land Plants Today. 37. Towards a stable, informative classification of the Lepidoziaceae (Marchantiophyta)

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Abstract

Recent molecular phylogenies of the Lepidoziaceae indicate that the current classification is incongruent with the phylogeny. Although substantial uncertainties remain, an interim classification is needed. The classification proposed includes a broader definition of the Lembidioideae, reinstatement of *Neolepidozia* and *Tricholepidozia* and the recognition of the new genus *Ceramanus*. While the Zoopsidoideae are unlikely to represent a monophyletic group, it is not yet possible to provide a phylogenetically accurate revision of this subfamily.

Introduction

The Lepidoziaceae are a species-rich cosmopolitan family of leafy liverworts. Although estimates of total species number for liverworts are notoriously variable (von Konrat *et al.* 2010), the number of accepted species is c. 860 (ELPT database), perhaps as much as 9–10% of the total liverwort species diversity. Taxonomic diversity is highest in cool, wet areas of post-gondwanan land fragments, but the family is cosmopolitan in distribution. In addition to being species-rich and exceptionally widespread, the family also encompasses a large portion of the total morphological range covered by the liverworts. As well as the typical leafy morphology of the type genus, *Lepidozia*, the family accommodates such disparate morphotypes as, for example, *Pteropsiella*, which is remarkably similar to the simple thalloid morphology of the Metzgeriales, and *Protocephalozia*, which resembles a charophycean alga with its branched filamentous protonema giving rise directly to the gynoeceal and androeceal branches. Unsurprisingly, the Lepidoziaceae have presented a serious challenge to students of liverwort classification.

Since the advent of molecular phylogenetics, liverwort classification has been changing rapidly (Crandall-Stotler & Stotler 2000, Crandall-Stotler *et al.* 2009, Vilnet *et al.* 2009). Molecular phylogenetics provides a means of deriving robust hypotheses of relationship where ambiguous morphological characters, convergent and parallel morphological evolution, and overall structural simplicity combine to make estimating phylogeny from morphology difficult if not impossible (Renner *et al.* 2011). The value of morphological phylogenetics, be it speculative or intuitive (e.g. Evans 1939, Fulford 1965, Schuster 1972, 1984a) or be it explicitly analytical (e.g. Engel & Smith Merrill 2004, Renner *et al.* 2006), in providing an informative and useful set of hypotheses is beyond doubt, but a truly phylogenetic classification of liverworts can only be achieved by making use of molecular phylogenies. However, the rate at which novel molecular phylogenetic hypotheses are appearing is currently faster than the rate at which novel classifications are being proposed. This is presumably a result of the widely held belief in biological systematics that classifications, which are simply an aid to communication, derive their utility in part from their information content and in part through stability. In some cases, however, an emphasis on stability might be counter-productive in encouraging systematists to

publish only those classifications they consider final, where, in fact, the lack of an interim classification provides a greater taxonomic impediment and leads to less stability overall. The Lepidoziaceae are one such case, where an attempt to embody a literal reading of recent molecular phylogenies in a revised classification is impossible, but where molecular phylogenetics clearly indicates that the current classification is wholly inadequate.

The taxonomic history of the family begins in 1831 when Dumortier placed most of the, then known, species belonging to the Lepidoziaceae into his Tribe Jungermanniaceae under the genus *Pleuroschisma* sect. *Lepidozia* and sect. *Pleuroschismotypus* (Dumortier 1831). A few years later he erected the tribe Pleuroschismeae and elevated sect. *Lepidozia* (*Lepidozia* with 8 species) and sect. *Pleuroschismotypus* (*Pleuroschisma* with 9 species) to generic status (Dumortier 1835). A broader treatment of liverworts was given by Gottsche, Lindenberg and Nees in their pioneering work *Synopsis Hepaticarum* (Gottsche *et al.* 1844-1847). They divided the Hepaticae (=Marchantiophyta) into tribes Jungermannieae (approximately corresponding to the leafy and simple thalloid liverworts), Monocleae, Marchantieae, Riccieae (thalloid groups) and Anthocerotae (the hornworts). The Jungermannieae were subdivided into hemicyclum Foliosae (leafy) and hemicyclum Frondosae (simple thalloid). In the Foliosae they treated three genera currently assigned to the Lepidoziaceae, *Lepidozia* (38 species), *Mastigobryum* (=Bazzania, 54 species) and *Micropterygium* (2 species) under subtribus Trichomanoideae along with *Calypogeia* and *Physiotium* (=Pleurozia). These later two genera did not contain species currently placed in the Lepidoziaceae. A third genus now assigned to Lepidoziaceae, *Zoopsis* (one species), was included in the Frondosae. The family itself dates to 1877 when Limpricht, in Cohn's *Kryptogamen-Flora von Schlesien*, treated *Lepidozia* under the family Lepidoziaceae (=Lepidoziaceae) (Limpricht 1877). However, Stephani (1905-1909) who added greatly to the number of described species, did not use family level divisions.

Reviving family concepts, Evans (1939) provided a classification of liverworts that was based on intuitive phylogeny. The Lepidoziaceae included *Bazzania*, *Lepidozia*, *Microlepidozia* (=Kurzia), *Acromastigum*, *Micropterygium*, *Mytilopsis*, *Sprucella*, *Psiloclada*, *Mastigopelma* and *Telaranea*, whilst *Zoopsis*, *Arachniopsis*, *Lembidium* and *Pteropsiella* were placed in the Cephaloziaceae. Following Evans, Fulford (1965) also provided an explication of her intuitive phylogeny. Her treatment of the leafy hepaticae of Latin America (and associated work) included a review of the Lepidoziaceae in which the genera were assigned to five families (Fulford 1962, 1963a, b, 1966, 1968; Fulford and Taylor 1959a, b, 1961). Lepidoziaceae was comprised of 14 genera (*Bazzania*, *Acromastigum*, *Paracromastigum*, *Bonneria*, *Lepidozia*, *Sprucella*, *Neolepidozia*, *Micrisophylla*, *Microlepidozia*, *Telaranea*, *Psiloclada*, *Lembidium*, *Micropterygium* and *Mytilopsis*), the Regredicaulaceae with three genera (*Regredicaulis*, *Arachniopsis* and *Odontoseries*), the Zoopsidaceae with two genera (*Zoopsis* and *Pteropsiella*), the Hyalolepidoziaceae with one genus (*Hyalolepidozia*) and the Paracromastigaceae with two genera (*Paracromastigum* and *Leucosarmentum*).

The current classification of the family is largely based on the work of Rudolf Schuster who continued the tradition of using intuitive phylogenetic relationships to form classifications (for a statement of Schuster's phylogenetic system see Schuster 1972, 1984a). Schuster (1969a) dismissed Fulford's multifamily classification in a footnote and circumscribed the broad family we know today. Molecular phylogenies have universally supported Schuster's circumscription of the family (Heslewood & Brown 2007, He-Nygrén *et al.* 2006, Hendry *et al.* 2007, Cooper *et al.* 2011, 2012), but Schuster himself recognised the substantial challenge presented by subfamilial classification:

“...trying to find some way of splitting this large and admittedly complex family into two or more separate, natural units, I am convinced that any such attempt must fail.” [Schuster, 1972]

Had he anticipated the profound influence that chain terminating DNA sequencing (Sanger *et al.* 1977) would have in systematics, he would perhaps have been a little less pessimistic. The extent to which recent phylogenies are incongruent with the existing classification means that substantial changes to the classification will be required. Elsewhere I have expressed the opinion that changes to the classification would

be premature on the basis of the current phylogenetic data (Cooper *et al.* 2011, Cooper *et al.* 2012). Whilst this is certainly true for parts of the family, several lineages have sufficient support in the molecular phylogenies for changes to the classification to be proposed. In the interests of facilitating further phylogenetic, floristic and taxonomic study of the family, the present contribution aims to provide a workable, interim classification of the Lepidoziaceae. In doing so I emphasise that resolving the phylogeny of the Lepidoziaceae is a work in progress and that future changes to this classification are inevitable.

The classification

The phylogeny of the Lepidoziaceae is summarised in figure 1 and a revised classification is proposed below. The Early Land Plants Today project has identified a range of nomenclatural changes and these changes as well as the outstanding combinations required by the classification proposed below are made in an accompanying paper (Cooper *et al.* 2013). A global checklist of liverworts is in preparation (von Konrat, Söderström and Hagborg pers. comm.) and will include a complete checklist of Lepidoziaceae arranged according to the classification below.

Lepidoziaceae Limpr., *Krypt.-Fl. Schlesien* 1: 310, 1877 (Limpricht 1877), “Lepidoziae”. Type:—*Lepidozia* (Dumort.) Dumort.

Zoopsidaceae Nakai, *Ord. Fam. Trib. Gen. Sect. nov. ed.* 199, 1943 (Nakai 1943). Bazzaniaceae Nakai, *Ord. Fam. Trib. Gen. Sect. nov. ed.* 200, 1943 (Nakai 1943). Hyalolepidoziaceae Fulford, *Mem. New York Bot. Gard.* 11: 376, 1968 (Fulford 1968). Regredicaulaceae Fulford, *Mem. New York Bot. Gard.* 11: 358, 1968 (Fulford 1968). Paracromastigaceae Fulford, *Mem. New York Bot. Gard.* 11: 384, 1968 (Fulford 1968). Neogrolleaceae J.J.Engel & Braggins, *J. Hattori Bot. Lab.* 91: 195, 2001 (Engel & Braggins 2001).

Genera incertae sedis

Meinungeria Frank Müll., *Bryologist* 110: 494, 2007 (Müller 2007).

subfam. Bazzanioideae Rodway, *Tasman. Bryoph.* 2: 23, 1916 (Rodway 1916).

Acromastigum A.Evans, *Bull. Torrey Bot. Club* 27: 103, 1900 (Evans 1900). *Bazzania* Gray, *Nat. Arr. Brit. Pl.* 1: 704, 1821 (Gray 1821). *Mastigopelma* Mitt., *Seemann, Fl. Vit.*: 406, 1871 [1873] (Mitten 1873).

subfam. Drucelloideae R.M.Schust., *Phytologia* 56: 69, 1984 (Schuster 1984b).

Drucella E.A.Hodgs., *Trans. & Proc. Roy. Soc. New Zealand, Bot.* 2: 45, 1962 (Hodgson 1962).

subfam. Lembidioideae R.M.Schust., *Hep. Anthocerotae N. Amer.* 2: 11, 1969 (Schuster 1969a).

Dendrolembidium Herzog, *Ark. Bot. n.s.* 1: 497, 1951 (Herzog 1951). *Hygrolembidium* R.M.Schust., *J. Hattori Bot. Lab.* 26: 277, 1963 (Schuster 1963). *Isolembidium* R.M.Schust., *Nova Hedwigia* 15: 466, 1968 (Schuster 1968). *Kurzia* Mart., *Flora* 53: 417, 1870 (Martens 1870). *Lembidium* Mitt., *Handb. N. Zeal. Flora* 2: 751, 754, 1867 (Hooker 1867). *Megalembidium* R.M.Schust., *J. Hattori Bot. Lab.* 26: 258, 1963 (Schuster 1963). *Pseudocephalozia* R.M.Schust., *Nova Hedwigia* 10: 21, 1965 (Schuster 1965).

subfam. Lepidozioideae Müll.Frib., *Rabenh. Krypt.-Fl., ed.* 2, 6 (15): 6, 1912 (Müller 1912).

Ceramanus E.D.Cooper, *Phytotaxa* 97 (2): 52, 2013 (Cooper *et al.* 2013). *Lepidozia* (Dumort.) Dumort., *Receuil Observ. Jungerm.*: 19, 1835 (Dumortier 1835). Basionym:—*Pleuroschisma* sect. *Lepidozia* Dumort., *Syll. Jungerm. Europ.*: 69, 1831 (Dumortier 1831). *Neolepidozia* Fulford *et J.Taylor*, *Brittonia* 11: 81, 1959 (Fulford & Taylor 1959b). *Tricholepidozia* (R.M.Schust.) E.D.Cooper, *Phytotaxa* 97 (2): 57, 2013 (Cooper *et al.* 2013). Basionym:—*Telaranea* subgen. *Tricholepidozia* R.M.Schust., *J. Hattori Bot. Lab.* 26: 256, 1963 (Schuster 1963).

subfam. Micropterygioideae Grolle, *Rev. Bryol. Lichénol.* 33: 226, 1964 [1965] (Grolle 1965).

Micropterygium Gottsche, Lindenb. *et Nees, Syn. Hepat.* 2: 233, 1845 (Gottsche *et al.* 1845). *Mytilopsis* Spruce, *Cephalozia*: 90, 1882 (Spruce 1882).

subfam. Protocephalozioidae R.M.Schust., *Hepat. Anthocerotae N. Amer.* 3: 649, 1974 (Schuster 1974)
Protocephalozia (Spruce) K.I.Goebel, *Flora* 77: 83, 1893 (Goebel 1893).

subfam. Zoopsidoideae R.M.Schust., *Hepat. Anthocerotae N. Amer.* 2: 12, 1969 (Schuster 1969a).

Amazoopsis J.J.Engel et G.L.Merr., *Fieldiana, Bot., n.s.* 44: 242, 2004 (Engel & Smith Merrill 2004).
Hyalolepidozia S.W.Arnell ex Grolle, *Rev. Bryol. Lichénol.* 32: 179, 1963 [1964] (Grolle 1964). *Neogrollea*
 E.A.Hodgs., *Trans. & Proc. Roy. Soc. New Zealand, Bot.* 3: 70, 1965 (Hodgson 1965). *Odontoseris* Fulford, *Mem.*
New York Bot. Gard. 11: 364, 1968 (Fulford 1968). *Paracromastigum* Fulford et J.Taylor, *Brittonia* 13: 336, 1961
 (Fulford & Taylor 1961). *Psiloclada* Mitt., *Hooker, Bot. Antarct. Voy. II (Fl. Nov.-Zel. 2)*: 143, 1854 (Mitten 1854).
Pteropsiella Spruce, *J. Bot.* 14: 161, 1876 (Spruce 1876). *Telaranea* Spruce ex Schiffn., *Nat. Pflanzenfam. [Engler*
& Prantl]: 103, 1893 (Schiffner 1893). *Zoopsidella* R.M.Schust., *Nova Hedwigia* 10: 24, 1965 (Schuster 1965).
Zoopsis Hook.f. ex Gottsche, *Lindenb. et Nees, Syn. Hepat.* 4: 473, 1846 (Gottsche *et al.* 1846).

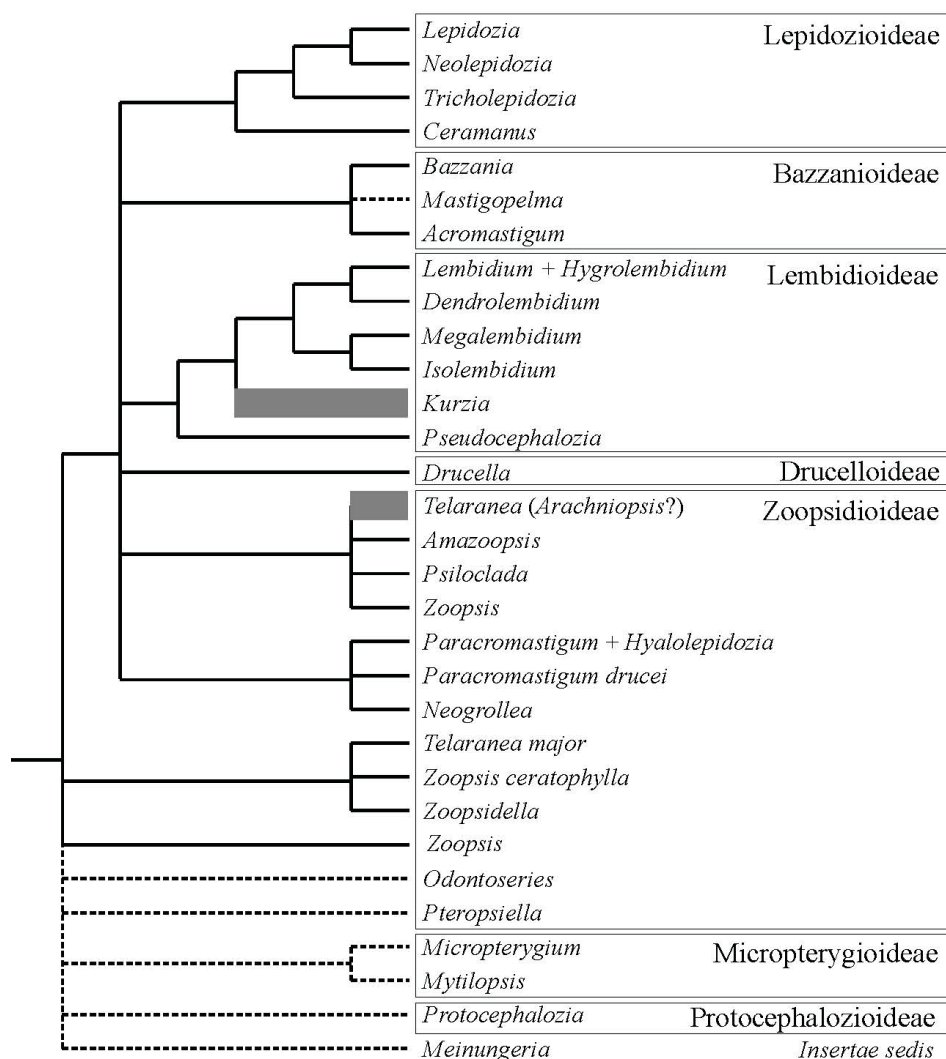


FIGURE 1. Summary of phylogenetic relationships in the Lepidoziaceae. Only those groups strongly supported by molecular phylogenetic analyses are shown (Cooper *et al.* 2011, 2012) and all other relationships are collapsed to polytomies. Taxa that have not yet been included in a molecular phylogenetic study are indicated by dotted lines. Only *Mastigopelma* can be inserted in the phylogeny with any confidence. Thick grey bars indicate those groups whose representatives in the molecular phylogeny did not form supported monophyletic groups. Boxes are drawn around groups recognised in the interim classification. The uncertain status of *Arachniopsis* is indicated by placing it in parentheses alongside *Telaranea*. *Telaranea* and *Arachniopsis* have been considered synonyms, with *Telaranea* the conserved name (Engel & Smith Merrill 2002), but the types have not been included in phylogenetic analyses and it is unclear whether one or more genera will be necessary to accommodate the species here retained in *Telaranea*.

Discussion

Several lineages within the Lepidoziaceae are resolved with a high degree of confidence. The Bazzanioideae, a rare exception amongst Schuster's subfamilies, is a monophyletic group whose membership requires no revision in a phylogenetically accurate classification. *Bazzania* and *Acromastigum* are both well supported monophyletic genera. Only the status of *Mastigopelma* remains in doubt. Although it seems likely that the four species represent a group of diminutive *Bazzania* species that have lost the capacity to form terminal branches, there is currently no molecular support for any taxonomic change. Unlike the Bazzanioideae, phylogenetic study of the Lepidozioideae indicated that re-circumscription of this subfamily and its constituent genera was required (Cooper *et al.* 2012). These changes are reflected in the classification proposed here, in which the subfamily comprises four genera whose boundaries are supported by the phylogeny. Based on strong phylogenetic support, the circumscription of the Lembidioideae is here expanded to include *Kurzia* (previously included in the Lepidozioideae) and *Pseudocephalozia* (previously included in the Zoopsidoideae). The Megalembidioideae has already been placed in synonymy with the Lembidioideae (Cooper *et al.* 2011). The delimitation of genera in this subfamily requires additional study. *Kurzia*, a widespread and morphologically varied genus, was not recovered as a monophyletic group and a broader, more geographically representative, sampling will be required. The lembidioid clade, in addition to the more speciose *Hygrolembidium*, comprises a diverse group of several monotypic or diatypic genera. The paraphyly of *Lembidium*, here expanded to include *L. berggrenii* (previously a *Chloranthelia*), suggests that generic delimitation should be revisited in the group.

The proposed classification leaves the Zoopsidoideae largely unchanged. The subfamily is unlikely to represent a monophyletic group, but the depth of taxon sampling and the lack of resolution at the base of the phylogeny leaves a phylogenetic revision of the subfamily impossible at this time. Nevertheless, the phylogenetic relationships between several taxa provide interesting insights into morphological evolution in the Lepidoziaceae. For example, the leaf apical cells in *Telaranea major* (Herzog 1950) Engel & Smith Merrill (2004) are rounded and near isometric and the septa between the apical and penultimate cells is constricted. In *Zoopsidella caledonica* (Stephani 1922) Schuster (1969b) and *Z. ceratophylla* (Spruce 1882) Schuster (1969c) all cells of the lobes have this morphology and fragmentation of the lobes is believed to provide a mechanism for asexual reproduction. Although this has not been reported in *Telaranea major*, the close phylogenetic relationship between these species suggests that the unusual apical cell morphology is derived from a homologous reproductive strategy in this clade. Similarly, the narrow lobe apical cells in *Psiloclada* are perpendicular to the leaf disc and oriented towards the shoot apex. This character is shared with those species of *Zoopsis* that are resolved with *Psiloclada* on the molecular phylogeny (Cooper *et al.* 2011). It is likely that molecular phylogenetic analysis with dense taxon sampling and careful morphological study, in particular study of leaf ontogeny, will yield well supported clades whose morphological evolution supports revised subfamilial and generic groupings.

Several taxa are yet to be included in the molecular phylogeny; at the subfamily level *Micropterygioideae* and *Protocephalozioideae*, and at the generic level *Odontoseris*, *Pteropsiella*, *Meinungeria* and *Mastigopelma*. This group of unsampled taxa includes some of the more enigmatic elements of the Lepidoziaceae; *Meinungeria* is unusual in having a largely echlorophyllose stem and greatly reduced leaves, *Pteropsiella* has an extraordinarily broad, winged stem and retains only tiny vestigial leaves, and *Protocephalozia* shows extreme neoteny of the gametophyte in which the reproductive branches arise directly from the protonema. Any attempt to revise the position of these taxa without evidence from molecular phylogeny would be futile.

Acknowledgements

I gratefully acknowledge the contributions of Dr Elizabeth Brown (Royal Botanic Gardens, Sydney) in her

role as postgraduate mentor. Although we disagreed on the need for the present contribution, Dr Brown has played, and continues to play, an important role in resolving the phylogeny and revising the classification of the Lepidoziaceae. The early land plants today (ELPT) team provided the impetus for timely publication of this work and provided substantial nomenclatural support. The original research on which the proposed classification is primarily based was largely funded by the Australian Biological Resources Study, the Linnaean Society of New South Wales and a Commonwealth of Australia, Australian Postgraduate Award. The manuscript was prepared whilst I was a postdoctoral associate at the University of Maryland, College Park, supported by an NSF-AToL grant to Prof. Charles Delwiche (grant number DEB-1036506).

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