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NEW HIGHER TAXA OF COMPLEX THALLOID LIVERWORTS (*MARCHANTIOPHYTA – MARCHANTIOPSIDA*)

D. G. Long

Recent studies on molecular phylogeny of complex thalloid liverworts (*Marchantiopsida*) have revealed the need to recognize four new higher taxa: Family *Neohodgsoniaceae*, Order *Neohodgsoniales*, Order *Lunulariales* and Family *Dumortieraceae*. These are formally described along with notes on their differences from other complex thalloid liverworts.

Keywords. Complex thalloids, *Dumortiera*, liverworts, *Lunularia*, *Neohodgsonia*.

Introduction

Great advances have been made in the past few years in understanding the evolution of the three major bryophyte lineages (liverworts, hornworts and mosses), primarily due to rapid advances in molecular systematics. Studies on liverworts (*Marchantiophyta*) have been fewer than those on mosses (*Bryophyta*) but this is now rapidly changing. Recent studies on liverwort phylogeny have made significant progress and have confirmed earlier views that two major lineages of liverworts exist: the complex thalloid (Class *Marchantiopsida*) and the leafy/simple thalloid (Class *Jungermanniopsida*), as well as a small third lineage, the Class *Haplomitriopsida*. However, within these lineages many new and at times unexpected results have been obtained, some of which will, when more fully researched, greatly change the classification of liverworts at the levels of subclass, order and family. However, sampling throughout the liverworts, especially in the *Jungermanniopsida*, is still very incomplete and future studies must both greatly increase the sampling and also incorporate a broader range of markers to attempt to achieve better resolution of the molecular trees.

Amongst the *Marchantiopsida* the sampling level has been higher than in the *Jungermanniopsida* but several key families and genera remain to be investigated. The main studies to date focusing on phylogeny of the *Marchantiopsida* have been those by Wheeler (2000), Long *et al.* (2000), and Boisselier-Dubayle *et al.* (2002), with more limited sampling in broader liverwort studies such as Heinrichs *et al.* (2005) and He-Nygrén *et al.* (2006). The three studies on the *Marchantiopsida*, however, were limited by both sampling and markers used. The most recent study on liverwort phylogeny (Forrest *et al.*, 2006) has utilized three chloroplast genes, one

Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK. E-mail: d.long@rbge.ac.uk

nuclear gene and one mitochondrial gene, and sampled 173 species in 117 genera of liverworts, including seven of the eight orders of *Marchantiopsida* (49 species in 27 genera) – a much better sampling of complex thalloid liverworts than achieved before. This study has clarified and reinforced some of the conclusions from earlier molecular studies, for example that the genus *Monoclea* Hook. cannot be sustained as a separate Order *Monocleales*; it has also confirmed the basal position of *Blasiales* and the nesting of *Sphaerocarpales* within the *Marchantiopsida* previously found by He-Nygrén *et al.* (2006). This study has also shown that the recent classification of liverworts by Crandall-Stotler & Stotler (2000) requires considerable amendment, particularly due to the irreconcilable incongruences between their morphological cladistic analysis and new molecular studies. A forthcoming new edition of this work will include a new classification of liverworts, and for this reason four new higher taxa of *Marchantiopsida* require now to be described formally. For each of these a description and explanatory notes are included below, but for the full results and discussion of the molecular study see Forrest *et al.* (2006).

New Higher Taxa and Taxonomic Notes

1. Family Neohodgsoniaceae D.G.Long, **fam. nov.**
Frons stratosa; stomata complexa; squamae ventrales biseriales exappendiculatae; rhizoidea omnia laevia; cellulae oleiferae adsunt; organa specialia asexualia (scyphuli) adsunt; monoicae; antheridia in receptaculo simplici stipitato; archegonia et sporophytum juvenile in perianthio campanulato inclusa; sporophyta in receptaculo stipitato ramoso; involucrum bivalve; seta non elongata; elateres adsunt; capsula per valvas 4–5 irregulares dehiscens. – Type: *Neohodgsonia* Perss., the only genus.

Thallus differentiated into layers, with upper layer containing air chambers; air pores present in epidermis, compound; ventral scales in 2 rows, without appendages; rhizoids all smooth; oil cells present containing single oil body; specialized asexual structures (gemma cups) present; monoecious; antheridia on terminal unbranched stalked receptacle; archegonia and young sporophyte enclosed in campanulate pseudoperianth; sporophytes on terminal 1–3-branched stalked receptacle; involucre bivalved; seta not elongated; elaters present; capsule dehiscence by 4–5 irregular valves; spores with trilete scar and irregular pits.

For discussion see below.

2. Order Neohodgsoniales D.G.Long, **ord. nov.**
Frons stratosa; stomata complexa; squamae ventrales exappendiculatae; rhizoidea omnia laevia; cellulae oleiferae adsunt; organa specialia asexualia (scyphuli) adsunt; antheridia in receptaculo simplici stipitato; archegonia et sporophytum juvenile in perianthio campanulato inclusa; sporophyta in receptaculo stipitato ramoso; seta

non elongata; elateres adsunt; capsula per valvas 4–5 irregulares dehiscens. – Type: Automatically typified (Art. 16.1) by *Neohodgsoniaceae* D.G.Long, the only family.

Thallus differentiated into layers; air pores present in epidermis, compound; ventral scales without appendages; rhizoids all smooth; oil cells present; specialized asexual structures (gemma cups) present; antheridia on terminal unbranched stalked receptacle; sporophytes on terminal branched stalked receptacle; seta not elongated; elaters present; capsule dehiscence by 4–5 irregular valves.

For a more detailed description of the genus *Neohodgsonia* see Bischler-Causse *et al.* (1995).

Taxonomic notes. The genus *Neohodgsonia* was formerly placed in Order *Marchantiales* family *Marchantiaceae* (Persson, 1954; Bischler, 1998). It is similar to *Marchantiaceae* (as now restricted to *Marchantia* L., *Preissia* Corda and *Bucegia* Radian) in its differentiated thallus with compound air pores, dorsal gemma cups (only in *Marchantia*, though the gemmae of *Neohodgsonia* differ from those of *Marchantia* in having only one growing point in contrast to two in *Marchantia*), archegonia and young sporophyte enclosed in a pseudoperianth and a very short seta. It differs from most *Marchantiales*, including *Marchantiaceae*, in its ventral scales which always lack appendages and (except *Monocarpus* D.J.Carr and *Monoclea*) in the absence of pegged rhizoids (although the rhizoids are weakly dimorphic in that some are sinuose) and in its spores which lack elaborate ornamentation. It differs from all other complex thalloid liverworts (Orders *Blasiales*, *Sphaerocarpales*, *Lunulariales* and *Marchantiales*) in having branched archegoniophore stalks.

From Order *Blasiales* it also differs in its differentiated thallus layers, presence of air pores in the thallus, presence of specialized oil cells, cup-shaped gemma cups, stalked male and female receptacles, bivalved involucres, pseudoperianth and very short seta. From Order *Sphaerocarpales* it also differs in its differentiated thallus layers, presence of air pores in the thallus, presence of specialized oil cells (except *Riella* Mont.), stalked male and female receptacles, bivalved involucres, pseudoperianth, spirally thickened elaters and valved capsules. From Order *Lunulariales* it also differs in its compound air pores in the thallus, lack of pegged rhizoids, cup-shaped gemma cups, stalked male receptacles, bivalved involucres, pseudoperianth, very short seta and irregularly-valved capsule.

Ordinal and family rank for *Neohodgsonia* are supported by the molecular data (Forrest *et al.*, 2006) and the unique combination of morphological features.

3. Order Lunulariales D.G.Long, **ord. nov.**

Frons stratosa; stomata simplicia; squamae ventrales biseriales appendiculo unico; rhizoidea dimorpha laevia paxillata; cellulae oleiferae adsunt; organa specialia asexualia (scyphuli lunati) adsunt; dioicae; antheridia in fronde in pulvinis terminalibus instructa; sporophyta in receptaculo stipitato profunde 4-lobato; involucrum tubulosum; seta elongata pergrandis; elateres adsunt; capsula per valvas

4 ad basim solutas dehiscens. – Type: Automatically typified (Art. 16.1) by *Lunulariaceae* Klinggr., the only family.

Thallus differentiated into layers, with upper layer containing air chambers; air pores present in epidermis, simple; ventral scales in 2 rows, with single appendage; rhizoids dimorphic, smooth and pegged; oil cells present with single oil body; specialized asexual structures present (crescent-shaped gemma cups); dioecious; antheridia in terminal cushions on thallus; sporophytes on terminal stalked deeply 4-lobed receptacle; involucre tubular; seta elongate, massive; elaters present; capsule dehiscence by 4 valves dividing to base; spores almost smooth.

For a full description of *Lunulariaceae* see Schuster (1992) and Perold (1993).

Taxonomic notes. The family *Lunulariaceae* with its single monospecific genus *Lunularia* Adans. was formerly treated as a member of Order *Marchantiales*. However, it differs from all other *Marchantiales* in its crescent-shaped gemma receptacles and (except *Monoclea*) in its elongate massive seta exserted from a tubular involucre. Ordinal rank for *Lunulariaceae* is well-supported by the molecular data (Forrest *et al.*, 2006).

4. Family Dumortieraceae D.G.Long, **fam. nov.**
Frons estratosa, cavernulis aeriis vestigialibus; stomata carentia vel pauca, simplicia, ad apicem frondis; squamae ventrales rudimentales biseriales exappendiculatae; rhizoidea dimorpha laevia paxillata et setae unicellulares (rhizoidea transformata) in pagina ventrali instructae; cellulae oleiferae paucae adsunt; organa specialia asexualia desunt; monoicae; antheridia in receptaculo brevistipitato; sporophyta in receptaculo stipitato; involucrum tubulosum per rimam dehiscens; seta brevis; elateres adsunt; capsula per valvas irregulares dehiscens. – Type: *Dumortiera* Nees, the only genus.

Thallus undifferentiated but with few vestigial air chambers; air pores absent or few, simple, at thallus apex; ventral scales rudimentary, in 2 rows, without appendage; rhizoids dimorphic, smooth and pegged, also with unicellular bristles (modified rhizoids) present on ventral surface; oil cells present (few), with single large oil body; specialized asexual structures absent; monoecious; antheridia in terminal short-stalked disciform receptacle; sporophytes on stalked receptacle; involucre tubular, bristly, opening by slit; seta present, shortly exserted; elaters present; capsule dehiscence by irregular valves; spores irregularly tuberculate.

For a full description of *Dumortiera* see Schuster (1992) and Perold (1993).

Taxonomic notes. The single genus *Dumortiera* has been traditionally placed in *Wiesnerellaceae* or *Marchantiaceae* but is not closely related to either; in the molecular trees (Forrest *et al.*, 2006) it is sister to *Monoclea*. It differs from all other *Marchantiales* in the presence of unique 'bristles' (in addition to rhizoids) on the ventral surface of the thallus and gametangiophores, and in its tubular bristly involucres opening by a slit. From *Wiesnerellaceae* it also differs in lacking a distinct

assimilatory layer in the thallus, in having no or only a few vestigial air pores and bearing its antheridia in stalked receptacles. From *Marchantiaceae* s.s. (*Marchantia*, *Preissia*, *Bucegia*) it also differs in lacking a distinct assimilatory layer in the thallus, in its air pores when present being simple not compound, unappendaged ventral scales, male receptacle without pores and sporophytes lacking pseudoperianths. Family rank for the genus *Dumortiera* is supported by the molecular data (Forrest *et al.*, 2006).

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