



## A special issue of *Phytotaxa* dedicated to Bryophytes: The closest living relatives of early land plants

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The current issue of *Phytotaxa* is dedicated to a group of green land plants commonly referred to as bryophytes. A broad consensus confirms that bryophytes may not be monophyletic, but rather represent three paraphyletic lines, i.e., Marchantiophyta (liverworts, e.g., Fig. 1), Anthocerotophyta (hornworts, e.g., Fig. 2), and Bryophyta (mosses, e.g., Fig. 3) (e.g., Mishler & Churchill 1984, Kenrick & Crane 1997, Buck & Goffinet 2000, Crandall-Stotler & Stotler 2000, Shaw & Renzaglia 2004). Together, bryophytes are the second largest group of land plants after flowering plants, and are pivotal in our understanding of early land plant evolution (Garbary *et al.* 1993, Kenrick & Crane 1991, 1997, Shaw & Renzaglia 2004). A growing body of evidence is now supporting liverworts as the earliest diverging lineage of embryophytes, i.e., sister to all other groups of land plants (e.g., Mishler *et al.* 1994, Wellman *et al.* 2003, Qiu *et al.* 2006).

Bryophytes are important components of the vegetation in many regions of the world, constituting a major part of the biodiversity in moist forest, wetland, mountain and tundra ecosystems (Hallingbäck & Hodgetts 2000). Together, the three lineages, play a significant role in the global carbon budget (O'Neill 2000) and CO<sub>2</sub> exchange (De Lucia *et al.* 2003), plant succession (Cremer & Mount 1965), production and phytomass (Frahm 1990), nutrient cycling (Coxson *et al.* 1992) and water retention (Pócs 1980, Gradstein *et al.* 2001). Bryophyte communities offer microhabitats that are critical to the survival of a tremendous diversity of organisms such as single-celled eukaryotes, protozoa and numerous groups of invertebrates (Gerson 1980). These groups of plants are also important environmental indicators (Rao 1980, Gradstein *et al.* 2001, Pitcairn *et al.* 1995, Giordano *et al.* 2004) and have been used as predictors of past climate change, to validate climate models and as potential indicators of global warming (Gignac 2001).

The compilation of this volume can be attributed to a community effort and the high quality of papers is the product of all those who participated as reviewers, contributors and editorial support. In preparing for the volume, it became evident that the study of liverworts, hornworts, and mosses remains strong and has a healthy future as evidenced by contributions from senior scientists, post-doctoral researchers and doctoral students. We include 13 scientific papers from 35 authors. We hope the broad scope of papers will draw wide appeal and interest beyond the study of bryophytes. The papers include a broad array of disciplines and subjects, including biogeography, checklists and distribution, conservation, delimitation of species, fungal symbioses in bryophytes, molecular phylogenetics, species richness and systematics.

In this issue, we provide a rare collection of publications in a broad-based botanical journal that are solely dedicated to these remarkable plants. The first paper forges a new partnership between the Early Land Plants Today (ELPT) project and *Phytotaxa*. The ELPT project is a community-driven effort attempting to address the critical need to synthesize the vast nomenclatural, taxonomical and global distributional data for liverworts and hornworts. This effort is fundamental toward the development of a working list of all known plant species under the auspices of the Convention on Biological Diversity (CBD) and the Global Strategy for

Plant Conservation (GSPC). The paper outlines and discusses the methodology behind the major components of the ELPT project. The second paper illustrates the utility of the project in the form of a checklist of the hornworts and liverworts of Java by Söderström *et al.* (2010). Checklists are important tools in taxonomy, systematics and conservation, yet many biologically important regions of the world lack recent checklists. Two additional papers are devoted specifically to liverworts: i) a revised estimate of the number of liverwort species coupled with a discussion on potential problems and pitfalls of deriving estimates by von Konrat *et al.* (2010); ii) a systematic paper by Engel *et al.* (2010) on the family Lophocoleaceae with conclusions based on molecular and morphological evidence.



**FIGURE 1.** *Pleurozia purpurea* Lindberg (1877: 16), Fiji (Photo: Matt von Konrat). *Pleurozia* holds a pivotal position in liverwort classification and evolution. Traditionally, *Pleurozia* with its complicate-bilobed leaves, has been included in or near Porellales within the leafy liverworts. Recently, Crandall-Stotler *et al.* (2009) placed *Pleurozia* in its own order in the Metzgeriidae which is supported by most molecular analyses. *Pleurozia* has an interesting morphology with trap-like structures in the water sacs of their leaves. Experimental evidence provided by Hess *et al.* (2005) showed that the structures in the water sacs are able to trap individuals of *Blepharisma Americana* (Ciliata). This is only the second liverwort genus where evidence has been provided to indicate that the lobules function in zoophagy.

The sole paper on hornworts takes a new look at hornwort diversity and distribution. Despite their low species numbers, hornworts represent a key group for understanding the evolution of plant form because current phylogenies place them as sister to tracheophytes (Qiu *et al.* 2006). Villarreal *et al.* (2010) fill some important gaps in hornwort biology and biodiversity, providing estimates of hornwort species richness worldwide and identifying centers of diversity. The paper also includes some stunning plates illustrating the morphology and ultrastructure of this enigmatic group of plants. Villarreal *et al.* (2010) also point out that species-level work on hornwort systematics is sorely needed.

The first of two papers focusing on mosses (Bryophyta) uses the vast on-line database, TROPICOS, to provide a view of moss diversity based on moss nomenclature and associated natural history information that



is linked to species names. The paper also considers subsequent adjustments by monographic, floristic and molecular work. The second moss paper is certain to have a high impact on plant phylogenetics for years to come. Cox *et al.* (2010) present molecular phylogenetic analyses of moss taxa from 655 genera. As a peer reviewer stated, this is the most comprehensive phylogenetic analysis ever presented for mosses, providing a unique source of information to raise new questions and test new hypotheses.



**FIGURE 2.** *Leiosporoceros dussii* (Stephani 1893: 142) Hässel (1986: 255), Panama (Photo: Juan Carlos Villarreal). *Leiosporoceros* is monotypic genus sister to all other hornworts. In the past decade the number of well-recognized hornwort genera has increased from 6 to 14. *Phaeomegaceros* is one of the newly-erected genera and as the name implies, this genus has features that are diagnostic of *Megaceros* (no pyrenoid and single antheridia per cavity) and others shared with *Phaeoceros* (especially the presence of stomata). Despite the delineation of new genera, hornworts have low species numbers and, alarmingly, this distinct and small group has not been monographed worldwide. Because current phylogenies place them as sister to tracheophytes, hornworts are a critical group for understanding the evolution of plant form (Villarreal *et al.* 2010). Hornworts have a unique combination of morphological and developmental traits that have long fascinated scientists. Most hornworts have an algal-like chloroplast and exhibit a carbon concentration mechanism not seen in other land plants (e.g., Hanson *et al.* 2002, Meyer *et al.* 2008). Interestingly, a cyanobacterial association is ubiquitous in hornwort gametophytes.

The issue also includes papers that are broad in scope and of wide appeal. Stech & Quandt (2010) provide an indispensable resource for bryologists engaged in phylogenetic research using DNA markers. Their paper reviews the history of the use of molecular markers (with an emphasis on DNA sequence data) in the reconstruction of bryophyte relationships. The compilation of citations alone makes the paper a useful resource for those researchers who are at the stage of marker choice. The commentary paper by Vanderpoorten & Shaw (2010) presents a valuable and noteworthy discussion on the application of molecular data to the phylogenetic delimitation of species in bryophytes. In their paper, they suggest that if species delimitation, and species differentiation, are the primary goals in a research program, nucleotide sequence



data should be complemented with approaches that focus on larger numbers of unlinked loci that are more variable.



**FIGURE 3.** *Sphagnum pulchrum* (Lindberg 1880: 25) Warnstorf (1900: 42), Alaska (Photo: Blanka Shaw). *Sphagnum* comprises a speciose clade of mosses that dominates many wetland ecosystems, especially in the boreal zone of the Northern Hemisphere (Shaw et al. 2003). In particular, *Sphagnum* is an important and conspicuous component in peatlands, which perform a significant global function in regulating the Earth's atmospheric chemistry as well as providing valuable economic commodities (Rocheftort 2000). *Sphagnum* holds an interesting position amongst mosses, with Cox et al. (2004) indicating that *Sphagnum* and *Takakia* form a clade sister to all remaining mosses.

The paper by Pressel *et al.* (2010) is a comprehensive and fascinating review of fungal symbioses in bryophytes. Fungal symbioses are one of the key attributes of land plants and are widespread in liverworts and hornworts but absent in mosses. This review is unique in that it considers phylogenetic data from both the bryophyte and fungal symbionts. Liverworts and hornworts harbor fungi with highly distinctive morphologies embracing short-lived intracellular fungal lumps, intercellular hyphae and thick-walled spores. The paper includes an important first report of *Treubia* and *Haplomitrium*, the sister taxa to other liverworts, forming a symbiosis with a more ancient group of fungi than the glomeromycetes, previously assumed to be the most primitive mycorrhizal fungi in land plants.

The biogeography paper by Desamore *et al.* (2010) summarize the hypotheses that have been proposed to account for the evolution of the unique biota in the Pantepui area—an area of northern South America comprising about 50 terrestrial islands above a lowland rainforest matrix. In doing so, they discuss several explanations for differences observed in the patterning of diversity between bryophytes and angiosperms. Importantly, the authors contend that bryophytes offer a unique model to revisit hypotheses regarding the origin and evolution of endemism among the Pantepui biota.

The volume ends with two papers on conservation, reflecting the strong commitment bryologists have to this important endeavour. Hallingback & Tan (2010) provide a review of past and present progress in

bryophyte conservation worldwide. The strategy and action programs in bryophyte conservation in the future are also presented. The final paper on the conservation efforts of threatened bryophytes in New Zealand/Aotearoa—an area of remarkable species richness for bryophytes, particularly liverworts, provides a model template in evaluating threatened taxa. The effort is particularly noteworthy because it involves local and international participants from universities, museums, research institutes and government departments.

CONCLUDING REMARKS: In this important Year of Biodiversity, 2010, the reflections and syntheses presented in this special issue are of particular importance. The papers published herein provide the most up-to-date interpretations and analyses on the biological, ecological, and environmental significance of bryophytes. Experts from around the world have contributed new insights and data to the burgeoning bryological literature. We anticipate the issue will provide the foundation for further research as well as to foster more students to study and enjoy these intriguing plants. The vast morphological diversity, phylogenetic importance, and key roles in the ecosystems of the world, lend bryophytes to many interesting and new avenues of study.

## Standards

Many papers follow the *Phytotaxa* standard for the citation of authorities for plant names. However, due to the scope and breadth of the papers we had to allow for some flexibility in departing from this standard. All remaining papers follow the on-line version of Authors of Plant Names at the Royal Botanical Gardens, Kew Website ([www.ipni.org](http://www.ipni.org)). The full citation and reference for plant names used can be obtained at MOSs TROPICOS (<http://www.mobot.org/MOBOT/tropicos/most/iom.shtml>); and the Botany Taxon Pages project of the Field Museum (see [http://emuweb.fieldmuseum.org/botany/botany\\_taxon.php](http://emuweb.fieldmuseum.org/botany/botany_taxon.php))

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