



A synthesis of hornwort diversity: Patterns, causes and future work

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Abstract

Hornworts are the least species-rich bryophyte group, with around 200–250 species worldwide. Despite their low species numbers, hornworts represent a key group for understanding the evolution of plant form because the best-sampled current phylogenies place them as sister to the tracheophytes. Despite their low taxonomic diversity, the group has not been monographed worldwide. There are few well-documented hornwort floras for temperate or tropical areas. Moreover, no species level phylogenies or population studies are available for hornworts. Here we aim at filling some important gaps in hornwort biology and biodiversity. We provide estimates of hornwort species richness worldwide, identifying centers of diversity. We also present two examples of the impact of recent work in elucidating the composition and circumscription of the genera *Megaceros* and *Nothoceros*. Important areas for further research are highlighted, particularly at taxonomic, ultrastructural, phylogenetic and genomic levels.

Keywords: Hornworts, biodiversity, diversification times, taxonomy, *Megaceros*, *Nothoceros*

Introduction

The eukaryote Tree of Life is sprinkled with lineages of Paleozoic origin that have little extant diversity [Cycads (ca. 250 spp., Hill *et al.* 2003), Ginkgophyte (1 sp.), Gnetophytes (95 sp., (Carmichael & Friedman 1996), Sphenopsids (15 spp., Rothwell 1996)]. With distinct morphologies, these lineages are of paramount importance in understanding character transformations and the evolution of body form (Carmichael & Friedman 1996). Low extant diversity is often explained by an ancient radiation that was followed by multiple and massive extinctions through geological time (Kenrick & Crane 1997). For example, the sphenopsids are known from an extensive fossil record that first appeared in the Devonian. The group flourished in diversity with many genera and species in the Carboniferous, and through extinction events in the eons that followed are represented today by a single genus, *Equisetum* Linnaeus (1753: 1061–1062), with 15 species (Rothwell 1996; Smith *et al.* 2006). The fossil record, however, is extremely fragmentary for bryophytes, the first colonizing land plants, and does little in the way of resolving the earliest divergences and radiations among embryophytes.

Hornworts are the most species depauperate of all seedless plant phyla. Current hornwort diversity is estimated at 200–250 species, a small number in comparison to mosses (11000–13000 spp., Magill 2010), liverworts (7000–9000 spp., von Konrat *et al.* 2010), lycophytes (1285 spp., Frey & Stech 2009) and ferns (11000 spp., Smith *et al.* 2006). Despite low numbers of species, hornworts represent a key group in the