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Advances and challenges in bryophyte biology after 50 years of International Association of Bryologists

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Research on bryophyte biology has made exciting advances during the last 10 to 15 years since the publications of Goffinet & Shaw (2008) and Frey & Stech (2009) that summarized the knowledge of the field. New fossils provided insights into past bryophyte diversity and integrative taxonomic approaches combine the ever increasing molecular data with thorough assessments of morphology and anatomy. Patterns of speciation, diversity at population level and geographic distributions are becoming better understood, and the interactions of bryophytes with their biotic and abiotic environment are increasingly being revealed. Nevertheless, important knowledge gaps remain, and anthropogenic threats such as habitat alterations and global climate change on bryophyte diversity increase the urgency of further research.

To mark the 50th anniversary of the International Association of Bryologists (IAB), this special issue of Bryophyte Diversity and Evolution presents a collection of 15 scientific papers that summarize the current state of knowledge, highlight new insights, and point out future directions of diverse aspects of bryophyte biology. The scientific papers are preceded by a flashback on 50 years of IAB activities pivotal to foster bryological knowledge, namely the organization of meetings, dissemination of bryological news, publication of scientific data, and awarding of prizes and grants (Gradstein 2021).

The first two scientific papers go back in evolutionary time and provide checklists of the fossil records of liverworts (Feldberg *et al.* 2021) and mosses (Ignatov & Maslova 2021), along with a discussion on the suitability of fossils as age constraints on molecular phylogenetic reconstructions. Numbers of fossils described have increased considerably in both liverworts and mosses, in particular from amber, but as discussed in both contributions, the identification of many older fossils in particular remains ambiguous. Nevertheless, the authors list several fossils suitable for calibrating molecular trees, which could be used for future evolutionary inferences from molecular data.

Discussing both the fossil and extant diversity, Bell *et al.* (2021) review the current knowledge on the phylogenetically isolated lineage of the "hair-cap mosses", class Polytrichopsida. They conclude that molecular phylogenetic analyses were able to resolve generic circumscriptions and relationships with fairly high confidence, and that the molecular relationships are, with few exceptions, supported by morphological characters and in line with the most developed classification from before the molecular era. However, future work is needed, ranging from taxonomic revisions to obtaining annotated genomes for selected species as a basis for physiological, developmental and comparative genomic studies. The latter aspect leads to the following contribution by Dong & Liu (2021), who compare mitochondrial genome diversity and evolution between liverworts, mosses, and hornworts. Bryophyte mitogenomes show lineage-specific characteristics and a conserved structure that might be maintained by different evolutionary mechanisms among these lineages. The authors acknowledge that high-throughput sequencing technologies offer new possibilities for in-depth studies of mitogenome evolution in bryophytes, including patterns and mechanisms of intron losses and gains, and the impact of RNA editing on phylogenetic reconstructions.

Leaving the field of macro-evolution and phylogeny, several papers of the special issue address karyology and biological processes involved in speciation in bryophytes. Sousa & Renner (2021) compare different protocols and

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provide step-by-step instructions to obtain meiotic or mitotic chromosome spreads from gametophytic (phyllids, antheridia) and sporophytic tissue of liverworts, tested on a number of species. These instructions should facilitate future cytogenetic studies in bryophytes. Carey *et al.* (2021) highlight the novel insights into genome evolution that can be gained by studying haploid U and V sex chromosomes in bryophytes. Although many of the processes shaping the evolution of haploid and diploid sex chromosomes are the same, the authors' observations demonstrate the potential for evolutionary genomic analyses of UV sex chromosome systems, combined with natural history studies, to understand how genetic conflict shapes sex chromosome gene content. Patel *et al.* (2021) reflect on karyotype diversity as a factor critical to catalyzing change in plant evolution. According to the authors, allopolyploidy receives more attention, while the prevalence and significance of autopolyploidy and aneuploidy in bryophytes is yet little understood. Based on comparative analysis of published ploidy levels in moss species, they conclude that cytological diversity likely underlies yet undescribed species diversity and emphasize the need of intensive karyological sampling to discover this diversity. Ostendorf *et al.* (2021) zoom in on the processes of polyploidization in the moss family Funariaceae. Based on phylogenetic and phylogenomic inferences from the model species *Physcomitrium* (*Physcomitrella*) *patens* (Hedwig 1801: 20) Mitten (1851: 363) and related species, they conclude that polyploidization, likely via hybridization, indeed gives rise to new species within the Funariaceae. Furthermore, the study highlights the potential impact of polyploidization on spore size and sporophyte architecture in the family. Expanding this topic to bryophytes in general again, Sawangproh & Cronberg (2021) conclude that hybridization is an important evolutionary phenomenon among bryophytes. Although the current molecular approaches support the prevalence of allopolyploidy, the authors, in line with Patel *et al.* (2021), anticipate that homoploid hybridization is more frequent than reported so far, and suggest directions for future studies of hybrid speciation among bryophytes.

The special volume continues with two contributions dealing with specific geographic aspects of bryophyte diversity and evolution. Patiño & Vanderpoorten (2021) provide an updated account on the impact of bryology in island biogeography, in the framework of the 50 most fundamental questions for present and future island biology research identified by Patiño *et al.* (2017). According to their assessment, only about 50% of the key current questions in island biogeography have been addressed for bryophytes, and especially species and community phylogenetics, biotic interactions, and invasion biology of island bryophytes need to be further explored. Câmara *et al.* (2021) review the current state and discuss future directions of Antarctic bryophyte research, following up on a similar account on Arctic bryophytes (Lewis *et al.* 2017). While molecular data provide new insights into species delimitations, population diversity, origin of bipolar distribution patterns and dispersal pathways to and within Antarctica, especially liverworts are understudied and the impact of climate change on Antarctic bryophytes remains to be assessed.

Ecological topics are addressed by two following papers of the special issue. Stanton & Coe (2021) discuss three core aspects of functional ecological traits in bryophytes, namely dynamic water content (including poikilohydry and desiccation tolerance), multiple scales of interaction with the environment, and reproduction and life history. The authors furthermore highlight how bryophytes influence ecosystem processes, including primary productivity, nutrient cycling, hydrology, and ecological interactions with other species, and indicate knowledge gaps for future studies. Vitt & House (2021) emphasize the role of bryophytes as key indicators of ecosystem functioning and structure of northern peatlands, focusing on mechanisms of resistance to decay in ecological groups that are dominant in bogs and poor fens *versus* rich fens. Furthermore, the authors point out the importance of bryophyte species and their abundances across different gradients as indicators for classifying wetland site-types.

Hornworts, the smallest, yet highly characteristic bryophyte lineage, have so far only been addressed in this special issue in the contributions on mitogenomes (Dong & Liu 2021) and hybridization (with no record of hybridization in hornworts found; Sawangproh & Cronberg 2021). The second last paper by Henry *et al.* (2021), in contrast, specifically focuses on the biochemistry and development of the unique placenta of hornworts. After the recent study on cell wall polymers in the placenta of the liverwort *Marchantia* Linnaeus (1753: 1137–1138) by Henry *et al.* (2020), the present study of two species of the hornwort genus *Phaeoceros* Proskauer (1951: 346–347) allows the first detailed comparison of placental cell wall organization in bryophytes.

Last but not least, Pressel *et al.* (2021) address interactions between bryophytes and fungi in their review on mycorrhizal-like associations. They highlight that early divergent liverwort clades and some hornworts engage with a wider repertoire of fungal symbionts than previously thought, and that Mucoromycotina symbionts, together with Glomeromycota, are widespread in thalloid liverworts and hornworts, confirming that these associations are mycorrhizal-like in liverworts. Furthermore, the study reports a higher diversity of ascomycete symbionts of leafy liverworts than previously known.

The abovementioned papers clearly demonstrate the progress that has been made in diverse fields of bryophyte biology, while at the same time pointing out important knowledge gaps. We hope that this special issue of Bryophyte

Diversity and Evolution will stimulate, and serve as a reference for, future research that aims to fill these gaps and further advance our understanding of the fascinating world of bryophytes.

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