Commentary

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Towards completing understanding of genome size characters in plants. A commentary on: 'Genome size and endopolyploidy evolution across the moss phylogeny'

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Major differences between moss and vascular plant genome sizes have major implications for stomatal biology whilst an absence of endopolyploidy in Sphagnum is most probably related to the unique development of the capitulum.

In contrast to the thousands of genome sizes known from angiosperms (Soltis *et al.*, 2018), including 1555 from the Asteraceae alone in 2018, the same information on bryophytes is patchy to say the least. To fill this lacuna, Bainard *et al.* (2020) present the most comprehensive information to date on genome sizes and endopolyploidy in mosses. Following a most useful critical analysis of previous methodologies and, with the inclusion of new genome size data for 33 mosses and endoreduplication indices for 20 species, the authors provide the first detailed evaluation of genome sizes within a phylogeny of 173 mosses.

On the one hand, the new data confirm small ancestral genome sizes with a high degree of endopolyploidy in bryophytes, while, on the other, they reveal marked differences from vascular plants which invite exciting further studies, especially on taxa not yet investigated. Indeed, this study will almost certainly become a keystone for furthering understanding of the organization of bryophyte nuclei in a variety of contexts.

Against the finding of small genomes in Andreaeales and Tetraphidaceae near the foot of the moss tree compared with the Sphagnales, top future priorities for genome data must now be *Takakia*, regarded as sister to all other mosses in some phylogenies, and *Oedipodium*, usually placed as sister to the Polytrichales on molecular grounds but vice versa on the basis of placental and water-conducting cell ultrastructure (Ligrone and Duckett, 2011). Much higher in the moss phylogeny, *Hookera lucens* with a genome size of 1.61 pg is the largest yet found in mosses, and immediately stands out since a noteable feature of this moss is that it has leaf cells so large as to be visible to the naked eye. Studies of further members of the Hookeriales are needed to confirm whether or not this is a signature of the order.

Mention of cell sizes immediately brings to mind the multiple correlations between stomatal and genome sizes in vascular plants. As with the paucity of genome size data, a detailed compilation of stomatal sizes does not exist for bryophytes, though limited information may be gleaned from the compilation of Paton and Pearce (1957). Examples of the range of stomatal sizes in four mosses with similar genome sizes are illustrated in Figs 1 and 2. Their highly disparate sizes suggest that the genome–stomata size relationships may not apply to bryophytes, a suggestion recalling the growing and still surprising evidence that these structures do not function in regulating gaseous exchange, but more probably are facilitators of sporophyte desiccation leading to spore discharge (Chater *et al.*, 2016). In addition to the absence of *Takakia* and *Oedipodium*, the former lacking stomata and the latter with numerous large stomata (Merced and Renzaglia, 2013), the present study does not include any really diminutive mosses such as *Ephemerum*, which has very small stomata like those in *Brachythecium* (Fig. 2). Although possible relationships between sporophyte and genome size await

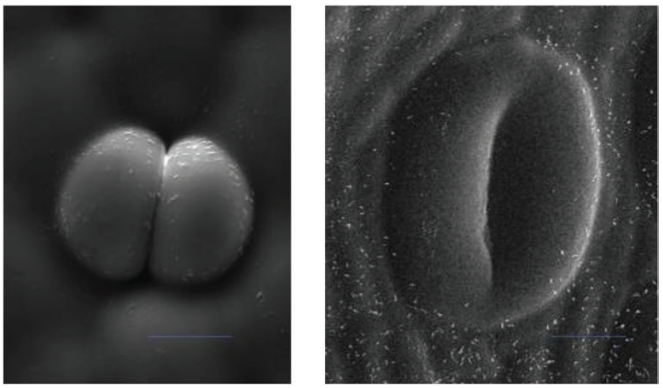

Fig. 1. Cryo-SEMs of a pseudostoma in *Sphagnum fimbriatum* (50 × 40 µm, IC 0.46) compared with *Polytrichiastrum formosum* (72 × 50 µm, IC 0.67) a species with one of the largest stomata found in mosses. The pseudostomata in *Sphagnum* are so called because they fail to develop open pores as illustrated here, and lack subtending intercellular spaces. Scale bars = 20 µm.

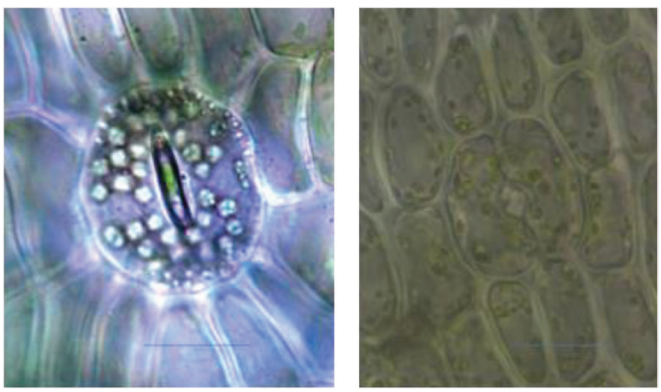

Fig. 2. Light micrographs of a long-pored stoma in *Funaria hygrometrica* with one guard cell (43 × 35 µm, IC 0.40) and a much smaller stoma in *Brachythecium rutabulum* (26 × 23 µm, IC 0.92) typical of taxa with round pores. Scale bars = 20 µm.

future investigation, the likely absence of any relationship between genome and stomatal sizes in mosses is yet one more feature that can be added to the growing list of differences between these in vascular plants (Field *et al.*, 2015). Nevertheless the two very different genome sizes found in *Sphagnum* clearly invite a simple comparative study of the pseudostomatal sizes. Sadly, a similar study on the Mniaceae, with likewise major differences in genome sizes, will be more problematic since the precise dimensions of their sunken stomata (Field *et al.*, 2015) are difficult to measure.

Given the knowledge that endoreduplication is a key feature of food-conducting cells and caulonemal/rhizoid differentiation, and is also an attribute of mucilage-secreting papillae, the finding that endoreduplication is prevalent across mosses is hardly surprising. Consideration of developmental processes perhaps provides an explanation as to why *Sphagnum* is the notable exception. In almost all mosses including the Polytrichales, food- and water-conducting cell and protonemal differentiation together with mucilage cell ontogeny are all strictly unidirectional processes producing cells incapable of regeneration. In contrast, capitulum differentiation in *Sphagnum* involves both apical and sub-apical meristematic activity, with the latter produced via a dedifferentiation process (Ligrone and Duckett, 1998). Thus endoreduplication in *Sphagnum* would seem unlikely on developmental grounds. Similarly, in contrast to the filamentous protonemal stages in most mosses, there is no evidence of endoreduplication in the thalloid protonema of S*phagnum*. Given its very small genome size together with the absence of conducting cells and a typical filamentous protonema, we now need endoreduplication data for *Andreaea*, not to mention *Takakia* which also lacks a protonemal phase but does have conducting cells.

Many years ago, at a time when phenetic classifications were very much in vogue and long before the advent of molecular data, the distinguished botanical polymath Michael Proctor, when asked about land plant phylogeny, almost invariably replied that this needed to be considered in the context that bryophytes which, being poikilohydric, do things very differently from vascular plants. Researchers should not, he said, expect the same experimental results as those with vascular plants. Nowhere is this axiom better expressed than in this study. The last half century has produced surprising revelations and even more unanswered questions from just about every new study into bryophyte biology and evolution. Prime examples are the total reorganization of the liverwort tree of life from the long-established phylogeny of the last century, and the resolution of the time scale of early land plant evolution (Morris *et al.*, 2018) set against the still problematic issue of the ordering of mosses, liverworts and hornworts at the base of extant land plants (Rensing, 2018). When more key taxa are added to the present study on genome sizes and endoreduplication, these will almost certainly be crucial new pieces in completing the jigsaw of land plant evolution.

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