

MADS-BOX FAMILY

Enabling the water-to-land transition

A major transitional step in Earth's history was the conquest of land by plants, which fundamentally changed carbon cycling and elevated oxygen levels. In a moss model of early land plants, three out of six MIKC^C-type MADS-box transcription factors ensure external water conduction and the function of motile sperm.

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The invasion of plants onto land occurred approximately 500 million years ago, a time when the ancestors of humans were water-borne animals of about 1–2 mm in size with a big mouth and no anus¹. To evolve into complex land animals, atmospheric oxygen levels had to rise above a critical level. It has become clear from experiments with the moss *Physcomitrella patens* and from climate modelling that the first land plants triggered an ice age by decreasing carbon dioxide levels² and that the photosynthetic action of these plants was sufficient to create modern levels of atmospheric oxygen³, thereby paving the way to animal evolution on land. The fundamental question here is what plant innovations are the basis for the transformation of filamentous haploid freshwater algae to land-dwelling complex plants with their characteristic alternation of a haploid gametophyte and a diploid sporophyte (Fig. 1). Recently it became clear that a specific P450 enzyme created a phenol-enriched cuticle that protects against desiccation, provides stiffness for erect growth and allows complex plant organs to unfold⁴. Subsequently, the homeobox transcription factor BELL1, after dimerization with a KNOTTED1-like homeobox (KNOX) transcription factor, led to zygote retention and the development of a diploid embryo, which gave rise to the diploid complex sporophyte as the alternating generation⁵. Later on, these complex sporophytes evolved the dimerization of the basic helix–loop–helix transcription factors FAMA and SCREAM to reprogram epidermal cells into stomata, microscopic valves that facilitate gas exchange and dehydration of the spores after meiosis⁶. These innovations predated the evolution of roots, leaves and flowers and helped the earliest plants to spread relatively quickly. However, they still exhibited an amphibian lifestyle, as extant bryophytes still do, because they had to rely on water for growth and for fertilization. Now, in a paper published in *Nature Plants*, Koshimizu

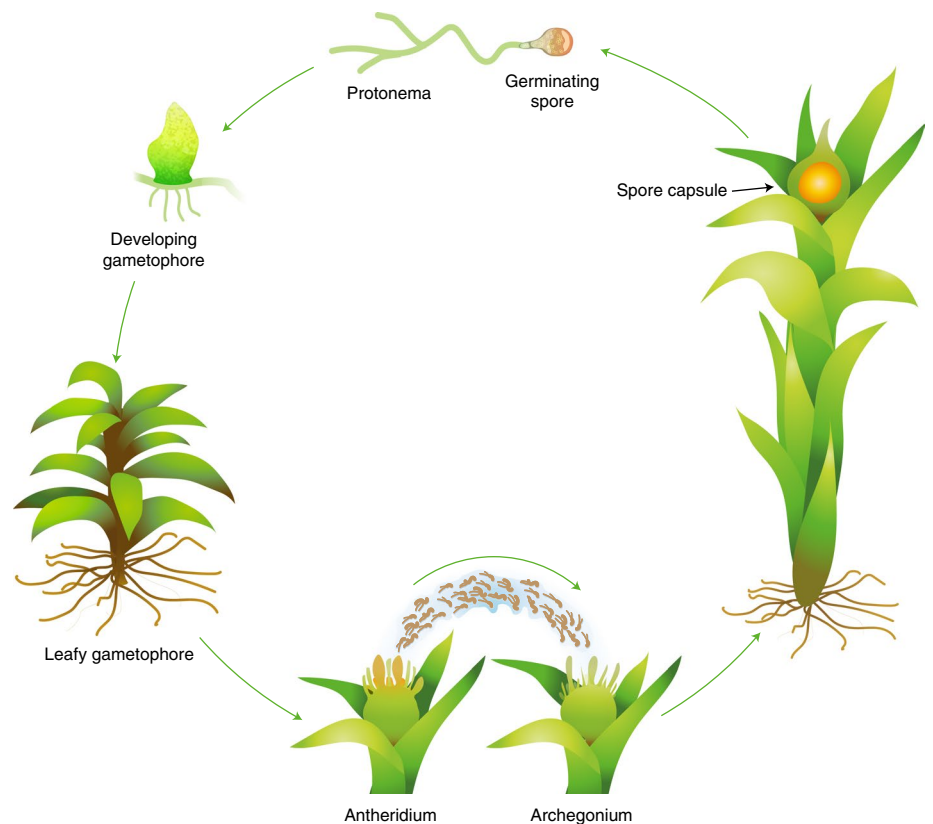


Fig. 1 | The lifecycle of the moss *P. patens* is an alternation of heterophasic and heteromorphic generations. Haploid spores germinate under the influence of light and water to give rise to the filamentous haploid protonema. Some protonema cells give rise to buds (developing gametophores), which proliferate via three-faced apical cells to give rise to the haploid rhizoids, stems and leaves (phyllids), the adult gametophyte, which is also called the leafy gametophyte. It carries the male (antheridium) and female (archegonium) sexual organs (gametangium). Buds, stems and leaves are covered by a phenol-enriched cuticle that reduces water loss and enables erect growth. Antheridium generates bi-flagellated sperm that actively swim in a film of water to the archegonium for fertilization. The diploid zygote is the stem cell that gives rise to the embryo, the sporophyte. Embryo and sporophyte grow via two-faced apical cells. The spore capsule (sporangium) is covered by an epidermis that contains, after reprogramming of the epidermal cells, stomata that facilitate gas exchange and provide a fitness advantage. The spore capsules contain spore mother cells, which after meiosis give rise to the haploid spores that are covered by sporopollenin. *P. patens* spore capsules do not have specific structures for spore release but simply break open under suitable environmental conditions to release the spores.

and colleagues⁷ report the identification of transcription factors that regulate water supply and movement of the flagellated sperms of the model moss *P. patens*.

The *P. patens* genome encodes six MIKC classic (MIKC^C)-type MADS-box transcription factors, whose functions remained elusive. Koshimizu *et al.* analysed

the protein localization and the phenotypes of loss-of-function as well as overexpression mutants of all six genes⁷. They found that three of these six regulate cell division and stem growth for appropriate water conduction, as well as the function of the bi-flagellated sperm cells. According to reporter lines all six genes are expressed in nearly all tissues, but with varying patterns; some of them seem to have a sex-biased expression, that is, are not expressed in male or in female cells. Interestingly, only sextuple loss-of-function mutants displayed the full phenotype: the stems were taller and the internodes longer due to a greater number of cell divisions rather than larger cells, for example. These longer stems were not able to conduct water supply for the leaves and the sex organs properly, leading to reduced fertility. In addition, sperm cells of the sextuple mutants were significantly less mobile than wild-type sperms. Similar phenotypes occur in respective triple mutants, identifying three out of the six MIKC^C-type MADS-box proteins as responsible for controlling stem cell division and sperm motility.

First and most important, this paper is the first to reveal a role of transcription factors in flagellum formation of a plant.

Second, it is now clear that the well-known roles of the homeotic MADS-box proteins in floral organ development^{8,9} evolved only after the evolutionary divergence of the vascular plants from the mosses. It is most likely that these basal functions described by Koshimizu *et al.* predate the invention of the stomata and follow the invention of the sporophyte. However, some additional experiments are needed to provide a more precise timing of the events. Likewise, the current study was not able to pinpoint a specific function to any one of the MIKC^C-type MADS-box proteins. It is unlikely that they have completely redundant functions. MIKC^C-type transcription factors have, besides the MADS-domain, additional domains for protein–protein interactions, making it likely that these proteins need interaction partners to exert their function. These interaction partners may have a more restricted expression pattern and thus ensure the precise spatiotemporal control of these protein heterodimers. The down-stream genes represent another open question. The current study identified a number of differentially expressed genes between wild type, overexpressors and sextuple mutants, some of which share homology with

Arabidopsis genes and some others may have functions in flagellum formation. Future research on these genes may hold the key to a better understanding of the timing of this developmental innovation as well as the precise role that these transcription factors play in flagellum formation in *P. patens*. □

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Competing interests

The author declares no competing financial interests.