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Plant Evolution: When Arabidopsis is more ancestral than Marchantia

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Summary

The quest for determining how looked like the plants that first lived on lands 450 million years ago is among the most exciting challenges in evolutionary biology. Recent works indicate that they displayed angiosperm-like stomata.

Text:

The ancestor of extant land plants diverged from the lineage leading to the Zygnematophyceae algae and gradually adapted to the terrestrial environment. Fossils of 450-475 million years old spore dyads and tetrads, which are structures associated only with land plant, are the first evidence of the changes in this branch of the green lineage [1]. Well-preserved fossil specimens tell us that less than 50 million years later the plant lineage had already diversified, with plants displaying subaerial and underground axes, and vasculature [2]. Between these two milestones: a gap of 50 million years devoid of known macrofossils, leaving a gap even wider in our understanding of plant evolution. The morphology, physiology and overall biology of the first land plants remain an absolute mystery.

Although the hunt for fossils of the first land plants is ongoing, an alternative approach would be to infer, to *predict*, their morphology and physiology based on extant land plant species. For such an inference, an accurate understanding of the plant phylogeny and the precise description of the traits of interest across this phylogeny are needed [3].

In this issue of *Current Biology* Harris *et al.* (XXX) combined a consolidated plant phylogeny with the phylogenetic analysis of genes linked to stomata development to determine whether stomata were present in the most recent common ancestor (MRCA) of land plants.

The monophyly of Bryophytes supported once again

Resolving the deep nodes of the land-plant phylogeny, the ones close to their origin more than 450 million years ago, has been a major goal in evolutionary biology for decades. Over the last five years, the availability of newly sequenced genomes and transcriptomes combined with a wide array of molecular phylogenetic methods allowed two hypotheses to

stand out. Harris *et al.* conducted yet another phylogenetic analysis on a carefully curated gene set. Although the debate is likely not over yet, this work, together with a number of other very recent studies [4–6], brings even more support to one of the two hypotheses: the monophyly of the Bryophytes that encompasses liverworts, mosses and hornworts. In other words, the bryophyte and the tracheophytes (vascular plants) have independently evolved for over 400 million years.

One essential consequence of the Bryophyte monophyly, highlighted elsewhere [7], is that any trait present only in the tracheophytes or the Bryophytes might be either ancestral (*i.e.* was present in the MRCA of the land plants) and lost in one of the two lineages, or derived in the lineage where it occurs.

Ambiguously, Bryophytes are often described as *lower* plants or even *primitive* by contrast with *higher* plants referring to angiosperms. This is not appropriate as, obviously, vascular plants, that encompass angiosperms, and Bryophytes have evolved for the exact same time since they diverged from their MRCA. Therefore, both lineages should display a mix of derived and ancestral traits. In their study, Harris *et al.* perfectly illustrate this concept, referred to as heterobathmy, by studying the evolution of stomata.

Tracking gene losses consolidates the model of stomata evolution

Stomata are present in the sporophytes of most vascular plants in many mosses and hornworts. Most importantly, stomata are absent from all known liverworts.

With the ever increasing body of proof in favour of vascular plants and Bryophytes as sister monophyletic clades, the parsimonious scenario for the evolution of stomata is a single gain in the extant embryophyte ancestor and multiple losses in the Bryophytes. This single gain hypothesis is supported first by the homology of molecular mechanisms found between *Physcomitrella patens* and *Arabidopsis thaliana* by the analysis of mutants of orthologous genes [8]. In addition, the phylogenetic analyses of the entire genetic toolkit of stomata development and function such as in Harris *et al.* and in recent other studies [6,9] further consolidate the conservation between angiosperms, mosses and hornworts.

Apart from gene conservation, gene loss is another powerful way of inferring the evolutionary history of a trait. The principle in which a gene linked to a specific trait is lost following the loss of the trait is called co-elimination. In plants, this principle had been for instance used to validate the multiple losses of the nitrogen fixing symbiosis in the Fabales, Fagales, Cucurbitales, and Rosales over a previous theory of predisposition and multiple gains [10,11]. In the study by Harris *et al.*, the sampling includes several species that do not display stomata including liverworts, some mosses and hornworts the lycophyte *Isoetes tegetiformans* and the marine angiosperm *Zostera marina*. Those last two plants are vascular plants that adapted to an aquatic environment and for which the absence of stomata is

unambiguously the result of secondary losses. Both *Z. marina* and *I. tegetiformans* have lost two genes from the stomata toolkit: TMM and EPF1/2, as a likely result of co-elimination. In the stomata-less bryophyte species, similar losses were observed indicating that, as in vascular plants, the selection pressure to maintain TMM and EPF1/2 was linked to the ability to form stomata. Therefore, the most parsimonious scenario of a single gain of stomata in Embryophytes followed by multiple independent losses is fully supported. Having determined the evolution of the trait, Harris *et al.* went on to infer the ancestral stomata toolkit based on gene gains, losses and duplications and the mechanistic knowledges acquired in angiosperms and mosses. One outstanding result of the proposed inference is that the genetic toolkit found in stomata-bearing Bryophytes is very different from the ancestral one. Reversely, the one known in angiosperms overlaps significantly with the predicted ancestral stomatal genetic toolkit. This indicates that vascular plants, including angiosperms, retain part of the ancestral toolkit that has derived – and even be lost – in extant Bryophytes.

The stomata of the first land plants

All the recent data, and the comprehensive study by Harris *et al.*, infer that the MRCA of land plants had stomata on the sporophytic generation which were controlled by a more complex gene network than the one observed in extant Bryophytes, allowing to conclude that "... bryophyte stomata underwent reductive evolution". In other words this exemplifies the concept of heterobathmy and shows that, yes, Arabidopsis can be genetically *more ancestral* than Bryophytes.

In extant Bryophytes, stomata are restricted to the sporophyte where they contribute to its dehiscence and have been maintained only in part of the moss and hornwort lineages [9,12,13]. In extant vascular plants, besides the losses in aquatic species, stomata are extremely conserved and involved in respiration and evapotranspiration, a trait linked to a functional vasculature in the sporophyte. Given that the function of the stomata, and the selection to maintain them, differs so strongly between the two sister-lineages of extant land plants, inferring their function in the MRCA of land plants becomes extremely difficult.

One can hypothesize that such a complex structure is more likely to have arisen from selective pressure for increased air intake and had been *exapted* for sporophyte maturation in Bryophytes than the other way around. In this scenario, the MRCA of land plants had stomata that would improve its CO₂ intake in the sporophyte. While what would later become vascular plants became gradually larger with a proper vasculature and megaphylls, the Bryophytes took the reverse route by favouring smallness which in turn released the need for elaborate air exchange and transpiration. So, as for the genetic pathway regulating their development, the stomata function in bryophyte may represent a derived state.

Fossils from 400 million years ago are remarkably diverse with some displaying stomata in both the sporophyte and the gametophyte, a state not found in extant land plants. With the bryophyte monophyletic, the affinity of these fossils with the tracheophyte or pro-tracheophyte lineages remains even more elusive than earlier. Being very speculative, we build on the data presented in Harris *et al.* and propose that these fossils may reflect the diversity of the land plants before the split between bryophytes and tracheophytes. This would result in a most parsimonious scenario for the evolution of stomata involving a single gain in relatively isomorphic gametophytes and sporophytes, followed by a single loss of stomata in the gametophytic generation before the divergence of the Bryophyte and tracheophyte lineages and the exaptation toward a non-essential role in sporophyte dehiscence in bryophytes (Figure 1).

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