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Plant Evolution: Phylogenetic Relationships between the Earliest Land Plants

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<https://doi.org/10.1016/j.cub.2018.01.034>

The key structures and functions of land plants are most often studied in flowering plant models. However, the evolution of these traits (character states) is often difficult to infer, because we lack an accurate phylogenetic frame of reference. The potential branching order of the earliest land plants has now been further condensed, narrowing down potential reference frameworks for comparative studies.

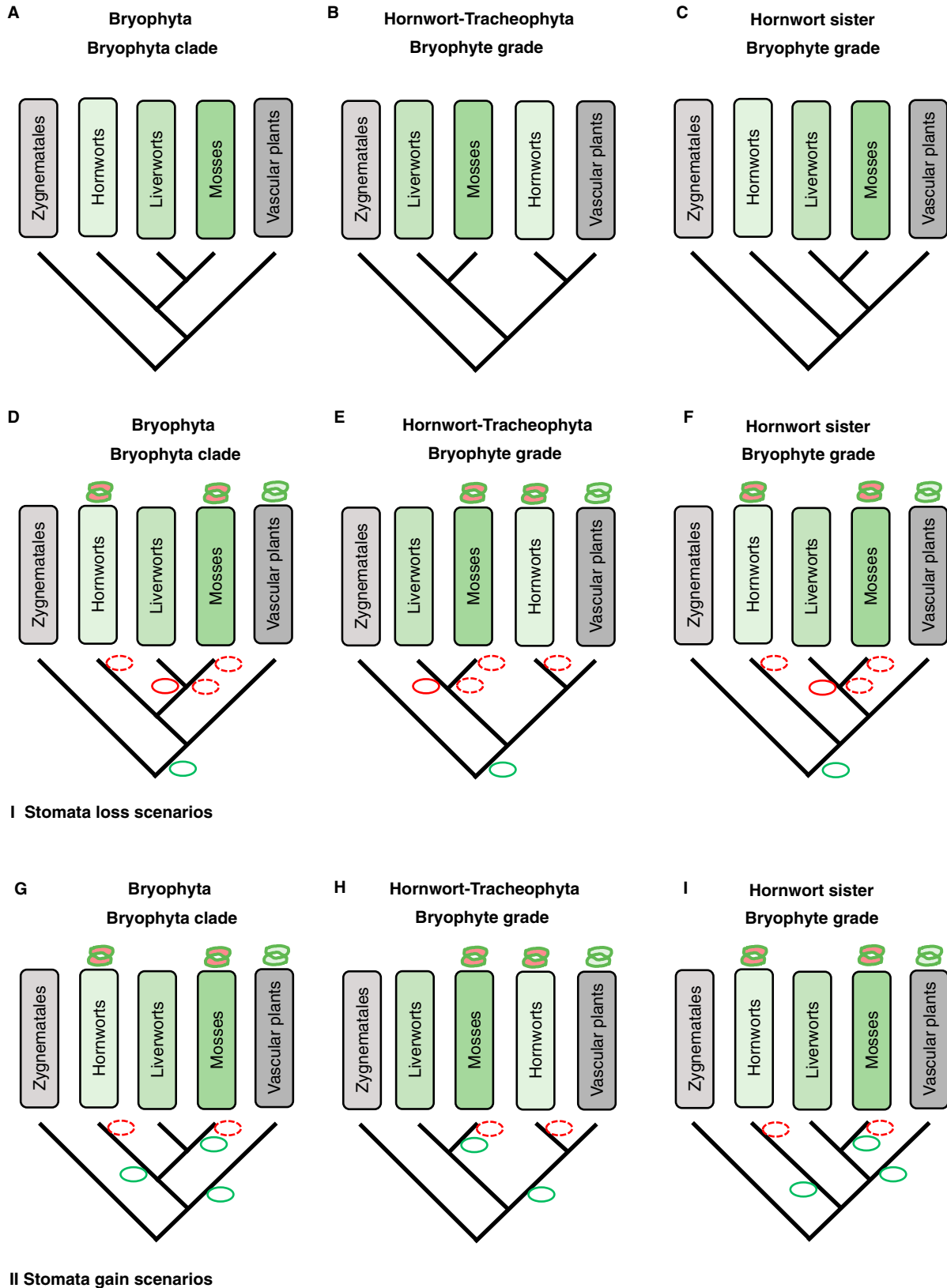
To resolve the topology of the earliest branches in the land plant tree of life is of crucial importance for interpretation of trait (i.e., character state) evolution, for instance for plant evolutionary developmental studies. In a new study in this issue of *Current Biology* [1], the authors have re-analysed the transcriptomic data of a previous paper [2], accounting for considerations like site heterogeneity (i.e., varying evolutionary rates), testing the fit to proposed topologies, and using a ‘supertree’ approach. The authors were using seven previously discussed potential topologies that relate bryophytes (comprising mosses, liverworts and hornworts) to Tracheophyta (vascular plants). These topologies differ in the branching order of the lineages, with one of the principal problems being whether mosses, liverworts and hornworts constitute a paralogous grade (‘bryophytes’), or a

monophyletic clade (‘Bryophyta’, Figure 1A–C).

Bryophyte evolution is probably highly convoluted by multiple convergent losses and gains of key features [3]. Bryophytes are united by life cycles comprising dominant haploid gametophytes and nutritionally dependent, diploid sporophytes. Many key features of land plants evolved in the gametophyte and were later co-opted (recruited), in the most recent common ancestor (MRCA) of vascular plants, for the dominant sporophyte [4,5]. An exception is possibly stomata, which evolved in the sporophyte and were combined with gametophyte-derived vasculature and rooting structures (rhizoids) in the MRCA of vascular plants, which was potentially a basis for its evolutionary success [4].

Let us take a look at stomata as an example to illustrate how the

topology of the land plant tree of life influences inference of character state evolution. Control of stomata by ABA, certain transcription factors and ion channels appears to be evolutionarily conserved between *Physcomitrella* and *Arabidopsis* [6–8], and stomata were classically argued to have evolved in the MRCA of land plants (Embryophyta). Indeed, stomata are principally present in all land plant lineages except liverworts, which might have lost stomata because their sporophytes mature surrounded by protective tissue [3]. Also, some hornworts have secondarily lost stomata [3,9] and some early divergent moss taxa either lack stomata or they are anatomically different and do not function in gas exchange, while derived moss lineages have secondarily lost them [3]. Thus, the presence/absence pattern of



stomata, depicted in Figure 1D–I, cannot easily be explained.

Moss and hornwort stomata have been argued to be potentially involved in transpiration-controlled flow from gametophyte to sporophyte and in drying of spores [10]. The finding that moss stomata are not responsive to CO₂ suggests that the primary and ancestral function of stomata was desiccation of the sporophyte for spore release [11]. Recent evidence suggests that stomata might have evolved several times independently, because aeration of intercellular spaces in moss sporophytes does not rely on stomata, while it does in hornworts [11]. If we consider the presence/absence pattern of stomata as outlined above and in Figure 1D–I, we find that the assumed presence of stomata in the MRCA of land plants requires one gain and at least four losses to explain the extant situation, independent of the topology of the earliest branches (Figure 1D–F). If, however, we assume that stomata were independently gained during land plant evolution, we require two or three gains and two losses, with topology B requiring one change less than A or C (Figure 1G–I).

In the new paper by Puttick and colleagues [1], among other findings, a statistical test showed that only 148 of 852 genes previously analysed do not display compositional heterogeneity. Interestingly, when restricting the dataset to the least heterogeneous genes (148), mosses and liverworts are resolved as a sister lineage to all other embryophytes, and Charales as sister to the embryophytes. Since there is overwhelming evidence that at least the latter is not true, but that Zygnematales are the sister lineage to land plants [2,12–14], one should also regard the idea of the moss–liverwort group as sister to all other embryophytes topology with a grain of salt.

The authors, similar to previous results [2], find good support for the monophyly of mosses and liverworts, and somewhat less support for the monophyly of Bryophyta. The support for the monophyly of the Bryophyta clade (Figure 1A) mainly stems from testing which gene trees fit the seven *a priori* topologies selected by the authors. Hence, if previously discussed topologies are presented to select from, monophyly of Bryophyta is achieved.

When considering site heterogeneity, the two most abundant positions of the hornworts reflect either the now more traditional view [15] of hornworts sister to tracheophytes ('Hornwort–Tracheophyta', Figure 1B; this topology is also supported when considering across-branch heterogeneity), or the position suggested in the original work by Wickett and colleagues [2], with hornworts as a sister group to all other embryophytes ('hornwort-sister'; Figure 1C).

In summary, most of the analyses support Bryophyta monophyly and the authors argue that conflicting topologies might be caused by incomplete lineage sorting and lineage-specific heterogeneity. From the seven topologies that have previously been suggested for early land plants, the present data allow us to reject four, but it cannot yet be resolved which of the remaining three (Figure 1A–C) is correct. More data from so far neglected lineages might resolve the issue in future.

The most important argument of the study is that, given the present data, liverworts are not the sister lineage to all other embryophytes. Hence, given their reduced complexity, they have apparently undergone a series of losses, and do not represent the earliest land plants in terms of character states. This is a very important notion because it has recently

been argued that the liverwort model *Marchantia* is most similar of all bryophytes to the trait setup of the Embryophyta MRCA [16]. It is crucial to note that liverwort traits should be discussed with a secondary loss scenario in mind. Only through analyses of more models [17] with their genomes and transcriptomes and through further unravelling the topology of the embryophytes will we be able to accurately determine plant character state evolution.

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Figure 1. Cladograms of the three remaining plausible topologies after [1], and loss/gain scenarios for stomata.

(A–C) The position of the streptophyte algae sister lineage to land plants (Zygnematales), as well as of the vascular plants, is invariant. Topology A depicts the most highly supported branching order for Bryophyta monophyly, while topologies B and C depict the conflicting topologies for bryophyte grades, with hornworts sister to vascular plants (B) or to all other land plants (C). Note that mosses and liverworts are always monophyletic, and hence in none of the topologies liverworts are sister to all other land plants. (D–I) Symbols are added to the topologies shown in A–C (above the lineage boxes) showing the presence or absence of stomata. Green symbols denote presence in the full lineage, while red-filled symbols denote lineages in which not all species exhibit stomata. D–F display evolutionary loss scenarios under the assumption that stomata were originally gained in the MRCA of land plants (green ellipse), as well as in some basal mosses, and later in some derived mosses and hornworts (dashed red ellipses; see text for details). In all topologies (D–F) the number of required evolutionary changes (gains and losses) is five, thus independent of the topology. G–I display evolutionary gain scenarios for stomata, under the assumption that the MRCA of land plants did not possess them. Here, topology H requires only four changes, while G and I require five. Topology H thus offers the most parsimonious explanation for stomata character evolution. It should be noted that this is a simplified scenario for illustration purposes only.

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Brain Evolution: Intelligence without a Cortex

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<https://doi.org/10.1016/j.cub.2018.01.065>

Birds are capable of high level cognition even though their telencephalon is organized into nuclear groups rather than a six-layered cortex as in the mammalian brain. New data show that, despite their different macroscale organization, the circuitries of avian and mammalian telencephalon are fundamentally similar and may therefore carry out equivalent computations.

The crowning glory of the human brain is our cortex: a massive folded sheet (typically 2–3 mm thick) with sharp depressions (sulci) that separate prominent ridges (gyri) that completely cover the rest of the brain. The neurons within the mammalian cortex are organized into six layers, each of which contains highly specialized neuron types, receives different inputs and then sends its outputs to different targets. Sensory inputs from the thalamus, for example for vision, audition or touch, end mainly on excitatory cells in layer 4 (L4), while layers five (L5) and six (L6) contain excitatory neurons that send output back to lower brain centers that can, for example, directly control movement. Cortical layers 2 and 3 (L2/L3) and, to a lesser extent L5, contain excitatory neurons, the output of which remains confined to the telencephalon — either the cortex or basal ganglia. A key cell type within cortex is the excitatory pyramidal cell, the

dendrites of which can span different layers. One much-studied type of pyramidal cell has its soma and basal dendrites in L5, where they receive feedforward input, and a long apical dendrite that extends to L1 and can receive feedback input from other parts of cortex. The basal and apical dendrites have distinct biophysical properties and their complex nonlinear interactions determine the patterning of the pyramidal cell's action potential outputs. Experimental and theoretical studies have emphasized the importance of interacting feedforward and feedback inputs to pyramidal cells as contributing to cognitive functions.

All mammals have a cortex and the 'intelligence' of a mammalian species tends to be correlated to the size and differentiation of its cortex. The natural conclusion is that sophisticated cognition depends on the extent and differentiation of the intricate cortical neural networks. In

contrast, the equivalent highest level of the bird brain, the dorsal telencephalon, is not layered but rather organized into clusters of neurons (nuclei); layer-spanning pyramidal cells with highly differentiated dendrites have not been found. The natural conclusion reached by early comparative neurobiologists was that birds were lacking the morphological substrates required for advanced cognitive function. This conclusion is no longer tenable. Even birds that are not notably intelligent, such as pigeons, can learn to group patterned visual stimuli into distinct categories [1], while song birds can learn to discriminate acoustic patterns constructed to be as complex as those of human language [2]. Members of the crow family are especially clever: their short-term memory capacity rivals that of primates [3] and their capacious long-term memory enables planning for future actions and gauging the intentions of rivals [4].

