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Streptophyte multicellularity, ecology, and the acclimatisation of plants to life on land

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Land plants are celebrated as one of the three great instances of complex multicellularity, but new phylogenomic and phenotypic analyses are revealing deep evolutionary roots of multicellularity among algal relatives, prompting questions about the causal basis of this major evolutionary transition

The origin of land plants has long been perceived as the fundamental step change in the evolutionary history of life on land predicated on a number of fundamental innovations (e.g. thick waxy cuticle, stomata, spores, rooting systems and vascular systems) that distinguish land plants from their algal relatives and allowed them to colonise the land surface ¹. The fossil record demonstrates that there was life on land before land plants ² and the evolutionary achievements of the earliest land plants were predicated on innovations that arose much earlier in streptophyte evolutionary history ³. However, resolving this formative phase in the deep evolutionary history of land plants has been challenging because of a paucity of genome data from species representative of streptophyte phylogeny. A new study by Bierenbroodspot and colleagues ⁴ provides fresh new insight into this formative evolutionary episode based on a wealth of new genome scale data from one of the earliest branching lineages of streptophytes.

Land plants are a derived lineage of streptophytes which, together with chlorophytes, comprise the green plants. The residual streptophyte rump, often referred to as the 'charophytes', are a paraphyletic grouping of largely filamentous and single-celled green algae that thrive in freshwater and terrestrial environments. The evolutionary relationships and, therefore, the systematic classification of streptophytes have long been in a state of flux but, increasingly, phylogenetic order is being imposed on this morass of diversity due to the adoption of streptophyte algae as model organism systems to inform understanding of land plant evolution, such as *Chara* ⁵ and *Penium* ⁶, as well as large scale sequencing projects like the One Thousand Plant Genomes Project ⁷. This has yielded the genome scale sequence data required to build phylogenies, from which evolutionary history can be inferred.

For decades, insights into the antecedents of land plants have been sought in the multicellular and land plant-like Charophyceae and Coleochaetophyceae ⁸, but it is the largely unicellular Zygnematophyceae that phylogenomic analyses have resolved as the sister lineage to land plants ⁹ with which they comprise the clade 'Anhydrophyta' (Figure 1). Zygnematophytes are primitively unicellular but multicellular filaments have evolved multiple times independently within the group ¹⁰. Coleochaetophyceae and Charophyceae combine with anhydrophytes to comprise 'Phragmoplastophyta', named after the phragmoplast, a microtubule-formed structure involved in cell wall development during cell division. While the

plant-like characteristics of these complex multicellular organisms are clearly convergent ¹¹, phragmoplastophytes have generally been interpreted as primitively multicellular, suggesting that the unicellular zygnematophytes have evolved from multicellular ancestors. The deeper branches of streptophyte phylogeny are much more uncertain, comprising three fundamental lineages, Klebsormidiophyceae, Mesostigmatophyceae and Chlorokybophyceae, the relationships among which have not been clear – until now.

In their new study, Bierenbroodspot and colleagues ⁴ delve into the depths of streptophyte phylogeny to resolve these remaining uncertainties. They focus their efforts on imposing systematic order on Klebsormidiophyceae but, in so doing, resolve the fundamental relationships of this clade to Mesostigmatophyceae, Chlorokybophyceae and the phragmoplastophytes. To do this, they more than doubled the number of klebsormid species for which transcriptomic data are available (increasing from 14 to 38), analysed phylogenetically using a complex substitution model which accommodates the biases in amino acid composition among sites that often confound phylogenetic studies. The team then dated the phylogeny using molecular clock methodology though, in the absence of fossil klebsormids, the resulting timescale is inevitably very uncertain. Nevertheless, these analyses reveal a fundamental split among klebsormids during the late Mesoproterozoic - early Neoproterozoic (1147-702 Ma) and then each lineage splits again sometime between the early and late Neoproterozoic (977-565 Ma), with the largest majority of sampled species belonging to *Klebsormidium*, diverging in the Palaeozoic. These analyses also resolve Mesostigmatophyceae and Chlorokybophyceae as a natural group, sister to all other streptophytes and diverging at about the same time as Klebsormidiophyceae. Overall, Bierenbroodspot and colleagues estimate streptophytes to have originated deep in the Mesoproterozoic (Figure 1), but with uncertainties extending down into the Palaeoproterozoic and up into the Neoproterozoic.

The taxonomic housekeeping is welcome, not least because it is based on a robustly tested phylogeny. Perhaps more interestingly, however, the authors use this framework to infer the evolution of multicellularity within Klebsormidiophyceae. Klebsormids manifest different grades of multicellularity, from filaments that disintegrate into unicells, through obligate uniserial filaments, and three dimensional sarcinoid multicellular packets. Bierenbroodspot and colleagues analyse the evolution of these states on their phylogeny using a number of different approaches, revealing that the ancestor of Klebsormidiophyceae was multicellular and potentially terrestrial. The nature of their multicellularity remains equivocal, with the diversity and distribution of growth forms precluding a decisive reconstruction. However, these results support a complex pattern of cellular evolution among streptophytes (Figure 1). Unlike in land plants, multicellularity among other streptophyte algae appears labile, with multiple independent reversions to unicellularity across Klebsormidiophyceae and Zygnematophyceae. Reductive evolution via gene loss has been proposed as a means of explaining the relatively simple body plans among other streptophytes (e.g. bryophytes and Zygnematophyceae ¹⁰⁻¹²). Instead, the team argue that the frequent transitions between uni- and multicellularity suggest the required regulators are likely maintained across lineages ⁴. By mapping the transitions between uni- and multicellularity, they present an excellent opportunity to understand the genomic basis of complexity among plants. Multicellularity is often viewed from a land plant perspective, yet gene families characterised in land plants typically have a deeper origin within streptophytes ¹³. Here again, the origin of signalling pathway genes implicated in multicellular development can be identified as having evolved in

the ancestor of Klebsormidiophyceae and Phragmoplastophyta, coincident with the first instances of filamentous growth among streptophytes¹⁴. These comparative genomics analyses reconcile well with an early origin of multicellularity and complexity in streptophytes, around a billion years ago according to the new timescale.

The evolution of ancestral ecologies revealed by Bierenbroodspot and colleagues⁴ follows a similarly convoluted path, again without a decisive conclusion on the habitat of the ancestral streptophyte. However, genomic evidence is pointing increasingly towards a multicellular ancestor that was capable of life on land (Figure 1). Klebsormidiophyceae appears to harbour a similar diversity of physiological adaptations as Zygnematophyceae¹⁵. Bacterially-derived UV-tolerance genes acquired independently by both land plants and Klebsormidiophyceae demonstrates the important role that horizontal gene transfer has played during the process of terrestrialisation¹⁶. The genomes of *Chlorokybus* (Chlorokybophyceae) and *Mesostigma* (Mesostigmatophyceae) include many gene families associated with terrestrial ecology, suggesting that *Mesostigma* may be secondarily aquatic¹⁷. All of this points to there having been a rich diversity of multicellular streptophytes in terrestrial and freshwater environments deep within the Proterozoic. This should have been predicted based on billion year old fossils¹⁸ of their sister-lineage, the chlorophytes; the absence of fossil streptophytes from contemporary terrestrial and freshwater ecosystems (e.g.¹⁹) perhaps reflects only that sporopollenin spore walls, an innovation of embryophytes, had not yet evolved.

Genome data representative of Coleochaetophyceae are long overdue and the next targets for diverse genome sampling must surely be Chlorokybophyceae and Mesostigmatophyceae (e.g.²⁰), helping to resolve the ancestral nature and ecology of Streptophyta. The importance of outgroup sampling in unravelling the origin of the ancestral land plant genome has long been recognised. However, diverse sampling of the streptophyte relatives of embryophytes, like that undertaken Bierenbroodspot and colleagues⁴, shows the limitations of sampling single lineages from among diverse clades. This approach, facilitated by the falling costs of sequencing, provides for a much richer understanding of the origin of evolutionary innovations. The origin of land plants remains distinctive in terms of both the evolution of organismal grade multicellularity and terrestrialization. In some way, embryophytes were imbued with greater evolutionary potential than their streptophyte cousins and there are no comparable evolutionary experiments from which general insights into this singularity may be obtained. Nevertheless, the repeated patterns of aquatic acclimation and terrestrialization, uni- and multicellularity, provide some explanation for why many of the genes implicated in embryophyte developmental, anatomical and stress-response innovations have proven to have a much deeper evolutionary history among streptophytes^{13,15,17}. This may indicate that, rather than being preadapted (or exapted) to a landlubber's life, ancestral embryophytes were already acclimated to life on land because they are descended from a lineage with a long and rich history of living a multicellular life within the terrestrial realm.

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Figure 1. Time-scaled phylogeny of Streptophyta and the outgroup Chlorophyta after ⁴. Summary timescale and inferred evolution of multicellularity and ecology. (Images of Chlorokybophyceae, Mesostigmatophyceae, Klebsormidophyceae, Charophyceae, Coleochaetophyceae and Zygnematophyceae from phylopic.org.)

