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## Plant Evolution: Assembling Land Plants

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Traditional evolutionary scenarios posit that land plants emerged from land plant-like relatives, the charophytes. New phylogenies suggest a closer affinity to simpler pond scum relatives, and evidence the gradual assembly of the land plant genome, revealing a phenotypic simplification from the complex ancestors envisaged by traditional scenarios.

The emergence of land plants (Embryophyta) is unquestionably one of the most formative episodes in the evolution of the Earth System; increasing the energy budget of life on Earth through photosynthesis on land, altering the albedo of the continents, increasing weathering rates, and increasing the complexity of global biogeochemical cycles [1]. It also constitutes the earliest step in the evolution of this great kingdom of multicellular organisms and led to the establishment of terrestrial habitats ripe for exploitation by animal lineages.

When and how this revolution was brought about is a central question in the evolution of terrestrial systems. Evolutionary scenarios for evolution of land plants from within the streptophytes (Figure 1; the clade including land plants) have been built around plant-like relatives of the land plants, especially the Charophyceae and Coleochaetophyceae lineages of charophyte algae which, like land plants, exhibit branching, tissue-grade organization, cell walls with plasmodesmata, apical meristems, asymmetric cell division and zygotes

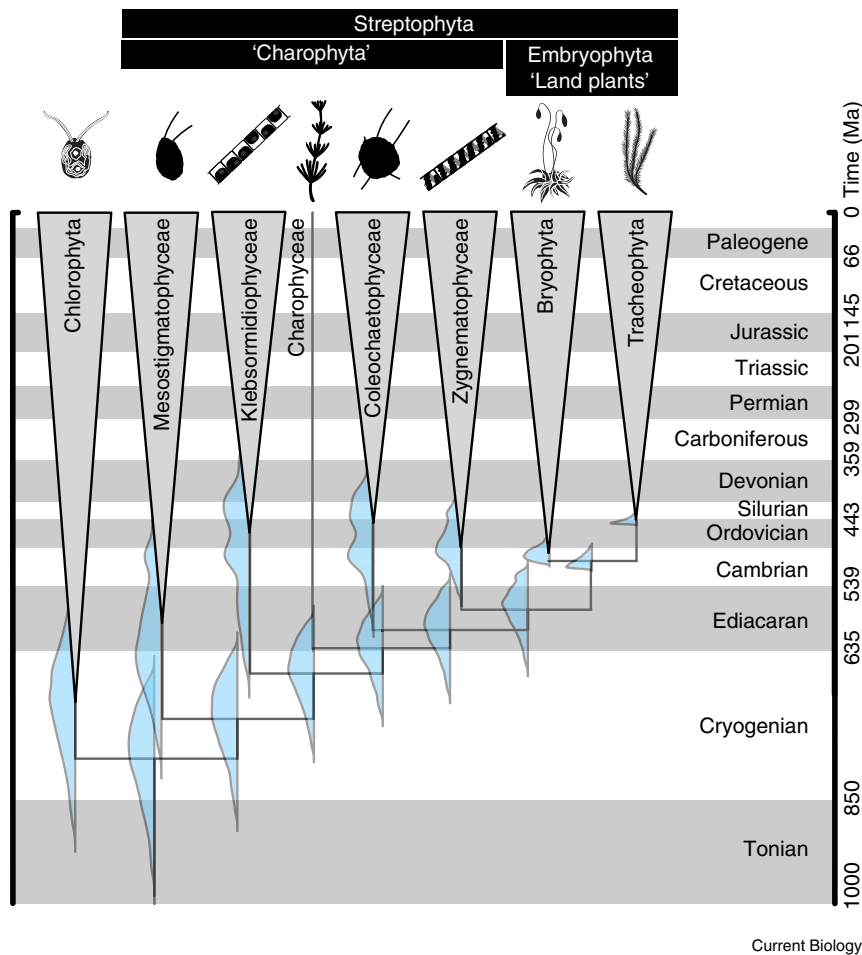
that produce sporopollenin [2,3]. Embryophytes are envisaged to have emerged through the evolution of a multicellular sporophyte that featured a protective cuticular layer, stomata, seta (stalks) to support sporangia, and spore-forming tissues and spores. However, phylogenomic analyses now indicate convincingly that the Zygnematophyceae, hitherto perceived as an outgroup of Charophyceae, Coleochaetophyceae and land plants, are instead the closest relatives of the land plants (for example [4]; Figure 1). Although some lineages of Zygnematophyceae exhibit multicellular branching, many are unicellular, casting doubt on long-standing evolutionary scenarios for the origin of land plants and increasing the phenotypic and ecological gulf between land plants and their immediate charophyte relatives.

In a new study, Cheng and colleagues [5] attempt to bridge that gap, describing genome assemblies for *Spirogloea muscicola* and *Mesotaenium endlicherianum*. These two species are among the earliest-branching lineages of Zygnematophyceae, strategically positioned in streptophyte phylogeny to

provide insight into the evolutionary assembly of land plant genomes. The study reveals that the emergence of zygnematophycean algae and land plants is associated with the origin of new transcription factors, phytohormone signalling genes, and factors involved in the synthesis of the plant cell wall. Ancestry of Zygnematophyceae and land plants is also associated with gene families that, in extant land-plant model systems, are associated with responses to biotic and abiotic stressors, such as desiccation, essential adaptations to a life on land and in ephemeral water bodies.

It appears increasingly clear that many of the essential elements of a land plant genome have a much deeper evolutionary origin within Streptophyta and beyond. For example, many of the genes required for fungal symbiosis were acquired prior to the last common ancestor of Zygnematophyceae and land plants [6]; genes implicated in cell wall biosynthesis evolved deep within Charophyta [7], whereas key land-plant hormones, signalling-pathway components, as well as drought- and light-stress-response factors all





**Figure 1. Time-scaled phylogeny of Streptophyta and the outgroup Chlorophyta.** Timescale from [16]; blue curves represent varying probability of the age of the respective clade. 'Charophyta' is paraphyletic with respect to Embryophyta. (Images of Klebsormidiophyceae and Coleochaetophyceae from [phylopic.org](http://phylopic.org).)

evolved prior to emergence of the charophyte–embryophyte clade [8]. This apparent disconnect between land-plant genomic and phenotypic evolution mirrors the pattern revealed through phylogenetic dissection of the animal 'developmental toolkit'. Mining the genomes of single-celled relatives of animals revealed that its components were assembled stepwise over geologic time, some with an origin so ancient that they were present in eukaryotic ancestors shared with land plants [9]. Also like animals, this forensic phylogenetic investigation of the assembly of the land-plant genome and body plan reveals that these genes often have a deeper origin, because they are associated with a more ancient origin of innovations that might be erroneously

associated with the origin of land plants. Thus, though there is debate over whether the charophyte ancestor of land plants was terrestrial or freshwater, or whether land plants were pre-adapted to life on land [3,10,11], this perhaps misses the point that the adaptations required of life on land versus shallow and ephemeral water bodies are much the same.

Although the ancient charophyte origin of many key land-plant genes may not be a great surprise, the means by which they were acquired by charophyte lineages most certainly is. In particular, Cheng and colleagues [4] present evidence that the stress-response genes GRAS and PYL were incorporated into an ancestor of Zygnematophyceae and land plants by horizontal gene transfer from soil bacteria.

Claims of horizontal gene transfer between prokaryotes and eukaryotes are not uncontroversial [12,13], not least because these events are often so ancient that the resolution of gene trees from which they can be diagnosed is limited by both the small size of gene sequences as well as the challenge of rooting [14]. Alternative explanations for the origin of GRAS and PYL are perhaps less palatable — they might be very ancient but were then lost in very many lineages, or they are present in the clade of Zygnematophyceae and land plants because they were inherited from a much older lineage, and a concomitantly older horizontal gene transfer event. Furthermore, there is abundant evidence of horizontal gene transfer within land plants and between plants and fungi [15]. Nevertheless, the scenario of horizontal gene transfer from soil bacteria, in particular, is perhaps tenuous since the nature of early abiotic and microbial soils, and their microbiomes, would have been very different from those of the later embryophyte world.

The pattern of genome evolution revealed is not all gain. Genes related to flagella and immunity seem to have been lost in these algae, supporting the idea that the body plans of Zygnematophyceae are simplified relative to the ancestor they shared with land plants and, indeed, their shared ancestor with the more distantly related, but phenotypically more plant-like charophytes, Charophyceae and Coleochaetophyceae. Hence, there remains much truth in those old evolutionary scenarios rooted in outdated phylogenies that envisaged Charophyceae and Coleochaetophyceae as the closest relatives of the land plants. Though the comparatively simple Zygnematophyceae may be the immediate relatives of the land plants, they are descended through simplification from more complex and, ultimately, more embryophyte-like ancestors whose body plans and genomes were assembled in deeper charophyte ancestors. Consequently, the phenotypic and ecological gulf between the ancestral embryophyte and its charophyte forebears might be much less than it may otherwise appear.

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# Cell Biology: Tight Junctions as Biomolecular Condensates

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Two recent studies report that ZO proteins, the main scaffolding proteins of tight junctions, undergo liquid phase separation. This new concept provides understanding at the mechanistic level of how tight junctions are formed and how they participate in mechanochemical signaling in early development.

In multicellular organisms, most cells interact with neighboring cells through specialized sites of cell–cell contact. In epithelia, adherens junctions (AJs) and tight junctions (TJs, also known as *zonulae occludentes* (ZOs)) are involved in adhesion and permeability barrier functions, as well as organization of the cytoskeleton, signaling, mechanotransduction and morphogenesis [1–4]. To guarantee a leakproof semipermeable seal for solutes and pathogens, TJs must form continuous interconnecting belts along the apical boundaries of cells (Figure 1A,B), and they do so by spatially and functionally associating with the

circumferential *zonula adhaerens* (ZA) and its submembrane actomyosin ring. The ZA is an apical specialization of cadherin-based AJs that contains PLEKHA7 (Figure 1C) and afadin [5]. The TJ barrier is formed by claudins, transmembrane proteins that polymerize into strands which are visualized by freeze–fracture electron microscopy [3]. ZO proteins (ZO-1, ZO-2, and ZO-3) are critically required to form cytoplasmic scaffolds for claudins and other TJ membrane proteins [1,6,7] (Figures 1D and 2). Two papers recently published in *Cell* now report that ZO proteins self-organize into biomolecular condensates, indicating that ZO-protein phase separation drives

TJ formation [8] and is involved in the mechanochemical signaling required for proper epiboly movements of the enveloping layer (EVL) in zebrafish development [9].

ZO-1, the most evolutionarily conserved of the ZO proteins, regulates tensile forces applied to apical junctions (reviewed in [10]). Schwayer *et al.* [9] have revealed a new role for ZO-1b and ZO-3 during zebrafish gastrulation. These authors detected ZO-1 in non-junctional, phase-separated clusters in the cytoplasm of the yolk syncytial layer (YSL) and showed that these clusters progressively accumulate at the region of contact between the YSL and the EVL and

