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Previews

How Plants Conquered Land

Stefan A. Rensing[1,2,3,*]
[1]Department of Biology, University of Marburg, Marburg, Germany
[2]Centre for Biological Signaling Studies (BIOSS), University of Freiburg, Freiburg, Germany
[3]SYNMIKRO Center for Synthetic Microbiology, University of Marburg, Marburg, Germany
*Correspondence: stefan.rensing@biologie.uni-marburg.de
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Approximately 500 Ma ago, freshwater algae adapted to live on Earth's surface, subsequently enabling animal life to pursue. Over the last decade, genomes of non-seed plants enabled us to infer trait evolution of early land plants. In this issue of *Cell*, Jiao et al. uncovered another genome, of the streptophyte algae Penium, enhancing our understanding of the water-to-land transition.

The green plants (Viridiplantae) live in very diverse habitats such as seawater, freshwater, soil, rock, and snow. They encompass organisms of very different anatomy, such as single-cell algae (e.g., the model organism *Chlamydomonas*), multicellular green seaweeds such as *Ulva* (sea lettuce), morphologically complex freshwater algae such as *Chara*, mosses such as the small-in-stature evo-devo model organism *P. patens*, and giant trees such as the iconic sequoia. Traits such as multicellularity or the adaptation to diverse habitats evolved several times within the green plants. However, the transition to the terrestrial habitat that eventually led to the stunning diversity of land plants (Embryophyta) most likely occurred only once. The Zygnematophyceae (conjugating algae) are the sister lineage to the land plants (One Thousand Plant Transcriptomes, 2019) and thus are of key importance to determine how molecular adaptation of plant life to land occurred. The genome of one of these algae (*Penium*) is published in this issue of *Cell* (Jiao et al., 2020) and shows that carbohydrate-active enzymes (CAZymes) are expanded in this species, probably involved in the generation of mucilage that acts as a protective sheet against drought, one of the prime abiotic stress factors that land plants have to cope with.

The Zygnematales belong to the Zygnematophyceae and are filamentous algae with peculiar properties. Their elaborately structured plastids have been subject of study in countless courses around the world, e.g., *Mougeotia* with its plate-shaped plastid exhibiting light-stimulated movement and *Spirogyra* with its iconic spiral-shaped plastid, name-inspiring of at least two bands. The Zygnematales went through evolutionary reduction of morphological features; for example, they secondarily lost flagellated sperm and sexually reproduce via conjugation, a process involving the fusion of male and female cells via bridges formed between filaments.

Inference of the ancestral traits that the most recent common ancestor (MRCA) of land plants and Zygnematophyceae possessed thus needs to take into account the different evolutionary trajectories that the lineages went through over the past ca. 550 Ma. Interestingly, Jiao et al. (2020) find that desiccation, but not other abiotic stresses, lead to differential expression of transcription factors (TFs) of the GRAS and DREB families that are expanded in *Penium*. Recent sequencing of two other subaerial Zygnematophyceae genomes found that GRAS genes might have been horizontally transferred into the ancestral algal genome from bacteria (Cheng et al., 2019). The ability to resist drought (the absence of an ambient water supply) is a hallmark of land plants. The successful conquest of the terrestrial habitat required the molecular adaptation to drought. Given that key features of this particular abiotic stress resistance most likely evolved in the MRCA of Zygnematophyceae and Embryophyta, they might be considered "Anydrophyta" (Figure 1), i.e., plants that can cope without water.

Genomes for five of the six lineages of streptophyte algae have been published in the past few years (Figure 1). Besides the namesake "twisted" appearance of the sperm cells, the MRCA of Streptophyta already featured a phytochrome (red-light sensor) and a plant-like cell wall and was on its way to adapting to subaerial/terrestrial habitats (Wang et al., 2020). The comparative analyses of streptophyte algae genomes suggest that on the trajectory toward Anydrophyta phytohormone biosynthesis and signaling gradually evolved into what is known in extant land plants (Nishiyama et al., 2018). For example, some parts of the biosynthesis and signaling toolkit of abscisic acid (ABA), a key phytohormone involved in abiotic stress signaling, are present in most streptophyte algae, but a "canonical" (plant-like) ABA receptor of the PYRABACTIN RESISTANCE (PYR/PYL/RCAR) family can only be detected in Anydrophyta (de Vries et al., 2018). Similarly, components of the auxin synthesis and signaling pathway are evolutionarily old, whereas the auxin repressors Aux/IAA of, e.g., *Chara* are part of a clade of non-canonical proteins (lacking domains I and II). The *Penium* proteins are part of the clade that includes land plant (canonical) Aux/IAAs, and the same is true for plant-like A/B type auxin response factor (ARF) TFs (Jiao et al., 2020). That the other two published Zygnematales genomes lack the genes encoding Aux/IAA underlines the need to further sample species diversity among streptophyte algae and non-seed plants in order to truly understand plant evolution.

This argument is further reinforced by evidence for a whole genome duplication (WGD) event in *Spirogloea* (Cheng et al., 2019) but not in *Mesotaenium*, *Penium*, or any other studied streptophyte alga.

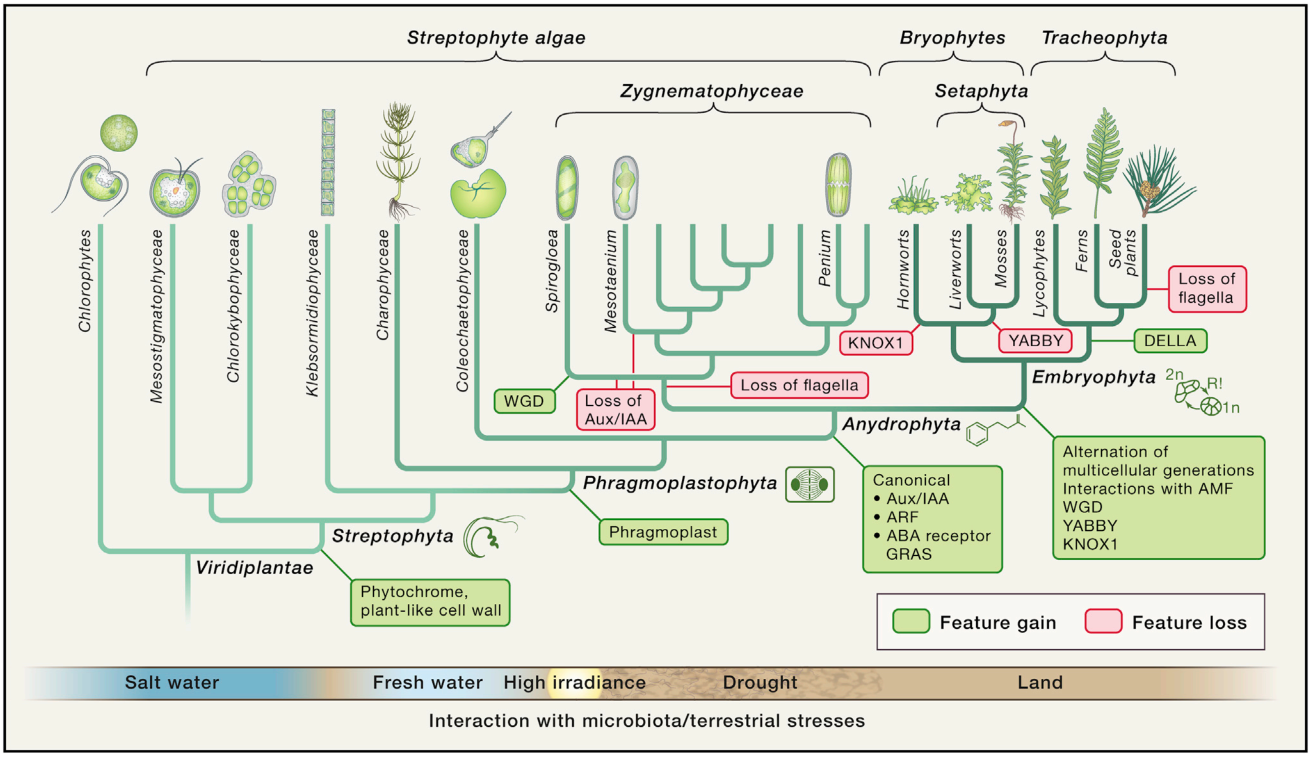

Figure 1. Dendrogram Depicting Important Steps of Early Plant Evolution

The dendrogram shows the lineages of Viridiplantae (green plants), comprising the nested monophyletic clades Streptophyta, Phragmoplastophyta, and Embryophyta (land plants). Though the Streptophyta are monophyletic, the streptophyte algae are a paraphyletic grade, because they cannot be united in a clade excluding the land plants. Among the latter, the bryophytes have recently been shown to be monophyletic and sister to vascular plants. Within the Phragmoplastophyta, the Zygnematophyceae are the sister lineage to land plants. Because the MRCA of Zygnematophyceae and land plants is inferred to have evolved molecular features to cope with drought, this clade is here called Anydrophyta, plants that are able to deal with lack of water (symbolized by a phenylpropanoid structure, representing a suite of protective substances that help plants to cope with stress). The blue/brown bar symbolizes the habitat transition from sea water to fresh water to land and the concomitant molecular adaptation. For some of the clades, icons are used to denote the namesake/defining properties: Streptophyta are named after the twisted appearance of their male, motile sperm cells, and Phragmoplastophyta are named after the phragmoplast, defining the plane of cell division. The Embryophyta are united by their peculiar life cycle (alternation of generations) that involves two multicellular phases (generations), the haploid (1n) gametophyte and the diploid (2n) sporophyte (from which haploid cells are generated via meiosis, R!). The green boxes show selected traits discussed in the text that are inferred to have evolved in the MRCA of the respective clade. The red boxes show traits inferred to have been secondarily lost in the respective lineage.

This is significant because the propensity for WGD, considered to provide an evolutionary playground for sub- and neofunctionalization of the resulting paralogs, is a hallmark of land plants. TF genes are often retained after WGD, and the expanded *Penium* GRAS family might have resulted from such an event. There are many ways in which the GRAS genes might be linked to the evolutionary success of the Anydrophyta. Not only are they linked to stress responses but they co-occur in species that mutualistically interact with arbuscular mycorrhiza fungi (AMF). Loss of symbiotic status, as well as secondary adaptation to aquatic habitats, coincides with loss of GRAS genes (Cheng et al., 2019). After the water-to-land transition, plants evolved a subfamily of GRAS proteins harboring a DELLA domain. Acting initially as transcriptional co-activators, DELLA proteins evolved as interactors of the gibberellic acid (another phytohormone) receptor GID1 in vascular plants (Hernández-García et al., 2019).

Many species of Streptophyta follow the trend that the number of TFs encoded by their genome correlates with their morphological complexity, especially given that many of these TFs evolved in the streptophyte algae (Wilhelmsson et al., 2017). However, there are exceptions, like the high number of TFs in *Penium* (potentially because of the WGD and expansion of a few families) or the low numbers in bryophytes *Marchantia* and *Anthoceros*, that probably went through a secondary evolutionary reduction (Puttick et al., 2018; Li et al., 2020). The *Anthoceros* (hornwort) genomes are one of the most recent additions to the repository of non-seed plant genomes (Figure 1) and show secondary loss of TFs, such as KNOX1, but also the presence of YABBY TF—suggesting that the land plant MRCA already possessed YABBY, which has since been lost in the other bryophyte lineages, so far represented mainly by *Marchantia* and *Physcomitrella* (Li et al., 2020). Extended species sampling of these interesting organisms will further inform our understanding of plant evolution.

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REFERENCES

Cheng, S., Xian, W., Fu, Y., Marin, B., Keller, J., Wu, T., Sun, W., Li, X., Xu, Y., Zhang, Y., et al. (2019). Genomes of Subaerial Zygnematophyceae Provide Insights into Land Plant Evolution. Cell *179*, 1057–1067.e14.

de Vries, J., Curtis, B.A., Gould, S.B., and Archibald, J.M. (2018). Embryophyte stress signaling evolved in the algal progenitors of land plants. Proc. Natl. Acad. Sci. USA *115*, E3471–E3480.

Hernández-García, J., Briones-Moreno, A., Dumas, R., and Blázquez, M.A. (2019). Origin of Gibberellin-Dependent Transcriptional Regulation by Molecular Exploitation of a Transactivation Domain in DELLA Proteins. Mol. Biol. Evol. *36*, 908–918.

Jiao, C., Sørensen, I., Sun, X., Sun, H., Behar, H., Alseekh, S., Philippe, G., Lopez, K.P., Sun, L., Reed, R., et al. (2020). The *Penium margaritaceum* Genome: Hallmarks of the Origins of Land Plants. Cell *181*, this issue, 1097–1111.

Li, F.W., Nishiyama, T., Waller, M., Frangedakis, E., Keller, J., Li, Z., Fernandez-Pozo, N., Barker, M.S., Bennett, T., Blázquez, M.A., et al. (2020). Anthoceros genomes illuminate the origin of land plants and the unique biology of hornworts. Nat. Plants *6*, 259–272.

Nishiyama, T., Sakayama, H., de Vries, J., Buschmann, H., Saint-Marcoux, D., Ullrich, K.K., Haas, F.B., Vanderstraeten, L., Becker, D., Lang, D., et al. (2018). The Chara Genome: Secondary Complexity and Implications for Plant Terrestrialization. Cell *174*, 448–464.24.

One Thousand Plant Transcriptomes Initiative (2019). One thousand plant transcriptomes and the phylogenomics of green plants. Nature *574*, 679–685.

Puttick, M.N., Morris, J.L., Williams, T.A., Cox, C.J., Edwards, D., Kenrick, P., Pressel, S., Wellman, C.H., Schneider, H., Pisani, D., et al. (2018). The Interrelationships of Land Plants and the Nature of the Ancestral Embryophyte. Curr Biol *28*, 733–745.e2.

Wang, S., Li, L., Li, H., Sahu, S.K., Wang, H., Xu, Y., Xian, W., Song, B., Liang, H., Cheng, S., et al. (2020). Genomes of early-diverging streptophyte algae shed light on plant terrestrialization. Nat. Plants *6*, 95–106.

Wilhelmsson, P.K.I., Mühlich, C., Ullrich, K.K., and Rensing, S.A. (2017). Comprehensive Genome-Wide Classification Reveals That Many Plant-Specific Transcription Factors Evolved in Streptophyte Algae. Genome Biol. Evol. *9*, 3384–3397.

Filling Important Gaps in the Genomic History of Southwest Asia

Ludovic Orlando[1,2,*]
[1]Laboratoire d'Anthropobiologie Moléculaire et d'Imagerie de Synthèse, CNRS UMR 5288, Université de Toulouse, Université Paul Sabatier, 31000 Toulouse, France
[2]Globe Institute, Lundbeck Foundation GeoGenetics Centre, University of Copenhagen, 1350K Copenhagen, Denmark
*Correspondence: ludovic.orlando@univ-tlse3.fr
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Many crucial developments in human prehistory occurred in Southwest Asia, including the transition to agriculture as well as the emergence of writing and of the earliest civilization. Two new studies in this issue of *Cell* map the genetic composition of human groups inhabiting the region during the sixth and first millennia Before Common Era (BCE) and uncover periods of significant population turnover.

The region of Southwest Asia that extends from the Levantine and Anatolian shores to the southern foothills of the Caucasus and the Zagros mountains of Iran hosted many major turning points in human history (Mills and Fowles, 2017). It saw the first developments of crop farming and animal herding in the Fertile Crescent some 10,000 years Before Common Era (BCE), initiating the Neolithic era, in which human populations could produce and store their own food resources and grow exponentially. Southwest Asia is also where the first written language emerged, where many city-states and empires (such as the Akkadian, Assyrian, and Babylonian) rose and collapsed, and where the Christian and Jewish religions take their roots. In this issue of *Cell*, Skourtanioti et al. and Agranat-Tamir et al. make use of state-of-the-art techniques in ancient genomics to map whether some of the major civilization changes in the region also translated into major changes in the genetic composition of the underlying human groups (Skourtanioti et al., 2020; Agranat-Tamir et al., 2020).

Previous work established that the genetic composition of early Neolithic groups in Iran, Central Anatolia, and the Levant largely matches that of previous local hunter-gatherer groups (Lazaridis et al., 2016; Feldman et al., 2019a). This suggested that little migration accompanied the transition to agriculture along the Fertile Crescent; thus, that ideas and technologies spread, rather than people. With time, the initially highly genetically differentiated Neolithic populations present in Southwest Asia came into contact and mixed, judging from the genetic affinities of a limited number of individuals scattered across the region and dating to the following millennia (Figure 1).

The exact time and dynamics of this latter phase remained, however, unmapped in the absence of key samples connecting those different areas prior to the fifth millennium BCE. This gap was filled by Skourtanioti et al. describing the genomic ancestry profiles of eight