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An Algal Greening of Land

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Photosynthetic eukaryotes arose ~1.5 billion years ago by endosymbiosis with a cyanobacterium. Algae then evolved for a billion years before one lineage finally colonized land. Why the wait? The *Chara braunii* genome details a decisive step linking plant origins with Earth's history.

In this issue of *Cell*, Nishiyama et al. (2018) present the genome of *Chara braunii*, a simple freshwater alga that enriches our understanding of life's eventual conquest of land. The fossil record tells us that the first land plants appeared about 450 million years ago (Kenrick et al., 2012). Before life on land, all photosynthesis took place in aquatic environments, either marine or freshwater. In order to go ashore, plants had to obtain the tools necessary for life in thin air. Adaptation involves expressing suites of evolutionary innovations that arise blindly through mutation but prove useful (selectable) in new environments—provided they are expressed at the right time. For instance, photosynthetic tissue in air required stomatopores that opened to allow in atmospheric CO_2 but also closed to limit water loss by evaporation. The *Chara* genome is rich with information about the evolutionary inventions that enabled life on land.

Chara does not represent the first lineage of land plants; it represents their precursors, the lineages of freshwater algae from which land plants emerged (Delwiche and Cooper 2015) (Figure 1). Plotted onto phylogeny, the *Chara* genome pinpoints the evolutionary timing of key innovations (Nishiyama et al., 2018), giving insights into life on Earth's last frontier.

Algae faced numerous hurdles as they risked the first steps onto the shoreline. They had to protect themselves against water loss with a cuticle. They had to support their own weight, requiring rigid cell walls with cellulose fibers. They required new tools to master photosynthesis using CO_2 from the atmosphere while sensing an environment—life in air—to which their water-borne cousins were oblivious. The algal forebears of land plants also had to establish co-evolutionary links with bacterial and fungal partners for assimilation of nitrogen and phosphorus.

Chara sheds light on the origin of environmental signaling via plant hormones and via the plastid. Plants regulate many aspects of organ development, growth timing, and stress response by producing hormones that act individually and in concert to elicit specific molecular, cellular, and organismal responses. The *Chara* genome uncovers important pieces in the stepwise evolutionary origin of plant signaling by means of auxins, cytokinins, ethylene, and abscisic acid (Nishiyama et al., 2018). The plastid of a land plant is heavily involved in environmental signaling because it has to integrate light and nutrient inputs for photosynthesis without generating reactive oxygen species (ROS) that cause damage to the cell. Several pathways of both internal plastid and plastid-to-nucleus signaling in plants and algae make cytoplasmic and nuclear transcriptional machinery responsive to environmental change (Puthiyaveetil et al., 2013). While the *Chara* chloroplast has only a plastid-encoded RNA polymerase, the *Chara* nuclear genome encodes a set of components of the plastid-to-nucleus, or "retrograde," signaling pathway found in higher plants. These features, together with hormones for long-distance signaling across cells and organs, reveal steps in the emergence of plant signal transduction.

Chara's plastids points to a further, crucial aspect of land plant origin. All green algal ancestors of land plants have only one—usually very large—chloroplast in each cell (de Vries and Gould 2018). Only on land do green plants start to exhibit many plastids per cell. As early land plants faced new challenges in water budget, gas exchange, and waste disposal (vacuoles instead of the medium), plastids became smaller in size and larger in number, increasing plastid surface area for gas and metabolite exchange with the cytosol. The *Chara* genome highlights reactions involving gasses at the core of plant biology. Photorespiration, for example, is a consequence of O_2 competing with CO_2 as a substrate for the enzyme Rubisco in the Calvin cycle, thus limiting photosynthetic carbon assimilation. In common with plants but few other algae, *Chara* has glycollate oxidase and other enzymes of the photorespiratory pathway, reflecting a physiological innovation that could become beneficial, thus selected, at higher oxygen levels.

A key cellular trait that maps to the origin of the lineages that include *Chara* and land plants is the phragmoplast, a structure that becomes the cell wall between daughter cells during mitosis. The phragmoplast underlies multicellularity in the land plant lineage and in *Chara*, a simpler multicellular form. This trait is coupled with the organization of cellulose synthase complexes into rosettes, which produce the cellulose fibrils we recognize as the tough, fibrous substance of plant cells and wood. The phragmoplast and cellulose synthase rosettes were present in the algal ancestors of land plants and were selected for more intense use during the conquest of land—classical evolutionary innovation.

Looking forward, broader lineage sampling will enrich genomic resources for better understanding the algal progenitors of land plants, early land plant

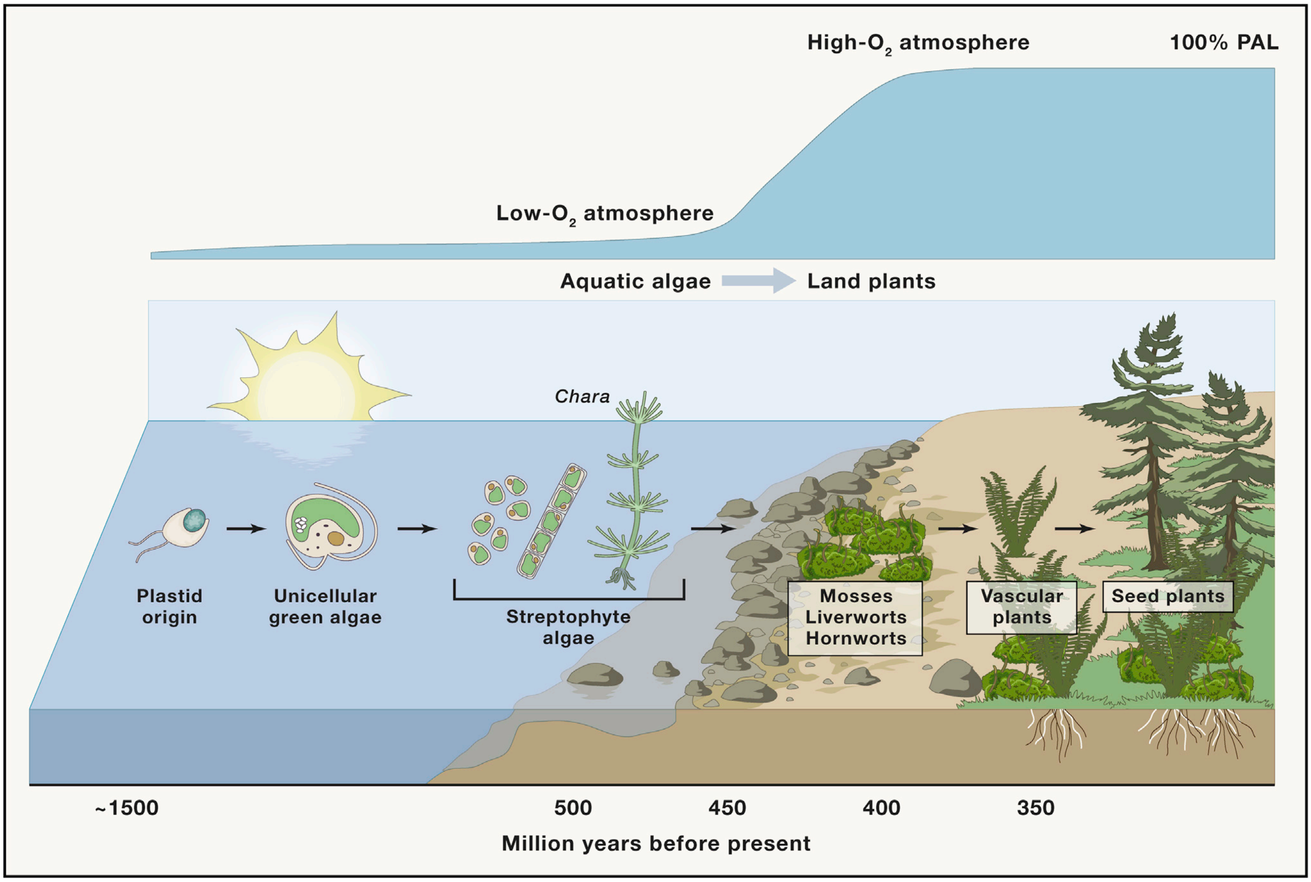

Figure 1. Streptophyte Algae and the Rise of Atmospheric Oxygen

The complex and multicellular green alga *Chara* is aquatic. Superficially, *Chara* species, with the common name stoneworts, resemble a land plant in morphology, being branched and anchored to a solid substrate by rhizoids. The complete genome sequence of *C. braunii* now shows that its plant-like appearance is more than skin deep, with molecular, cellular, and biochemical properties consistent with phylogenetic evidence that something like a modern *Chara* species gave rise to the earliest land plants. From the deep endosymbiosis that gave plastids and the chloroplasts of photosynthetic eukaryotes, modern representative species can be assembled into a sequence (left to right) consistent with phylogeny. The success of the earliest land plants caused a major increase in atmospheric oxygen content beginning in the early Phanerozoic Eon. The step up in oxygen content (upper panel) leading to 100% of present atmospheric level (PAL) may have originated from the advent of terrestrial photosynthesis and biomass production accompanied by carbon burial (see text).

lineages, and microbial interactions in the rhizosphere. This knowledge will help uncover how nature solved problems like desiccation tolerance, nutrient acquisition, signaling, light management during photosynthesis, creation of fertile soil, and the physiological interplay between CO_2 and O_2. Evolutionary insights into how plants naturally adapted as the food chain reached land could impact modern agriculture, particularly where water is scarce.

Land plants brought new biomass to Earth—and lots of it. Current estimates have it that land plants comprise 80% of the Earth's current biomass (Bar-On et al., 2018), a proportion that may have been reached rapidly soon after plants colonized land, a niche which at first was without competitors. The accumulation of biomass on land had consequences of extraordinary significance for Earth history, a recognition that is only now coming into focus. The story of land plant origin is a story of the oxygen we breathe.

When cyanobacteria started producing oxygen 2.5 billion years ago, they did not immediately oxygenate either the atmosphere or the oceans (Fischer et al., 2016). It took almost 2 billion years for O_2 to begin to reach modern levels. Independent lines of evidence now indicate that the big jump in Earth oxygen levels took place a mere 430 million years ago (Lenton et al., 2016; Stolper and Keller 2018) (Figure 1). Early land plants are now implicated as causal agents behind increased O_2 levels through a process called carbon burial. The first land plants buried so much carbon that O_2 accumulated in the atmosphere to roughly present levels (Lenton et al., 2016).

In the bigger picture of Earth history, the late accumulation of O_2 helps to explain why Earth's oceans remained anoxic for so long (Stolper and Keller 2018). It also explains why all major eukaryotic lineages retained pathways for anaerobic energy metabolism (Müller et al., 2012): land plants and land animals in their wake were the first eukaryotes to adapt to today's high oxygen conditions. The *Chara* genome helps us to understand how land plants came ashore, how they brought plentiful oxygen to air, and how a few evolutionary innovations can have consequences of planetary scale.

REFERENCES

Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. Proc. Natl. Acad. Sci. USA. Published online May 21, 2018. https://doi.org/10.1073/pnas.1711842115.

de Vries, J., and Gould, S.B. (2018). The monoplastidic bottleneck in algae and plant evolution. J. Cell Sci. *131*, jcs203414.

Delwiche, C.F., and Cooper, E.D. (2015). The evolutionary origin of a terrestrial flora. Curr. Biol. *25*, R899–R910.

Fischer, W.W., Hemp, J., and Johnson, J.E. (2016). Evolution of oxygenic photosynthesis. Annu. Rev. Earth Planet. Sci. *44*, 647–683.

Kenrick, P., Wellman, C.H., Schneider, H., and Edgecombe, G.D. (2012). A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. Philos. Trans. R. Soc. Lond. B Biol. Sci. *367*, 519–536.

Lenton, T.M., Dahl, T.W., Daines, S.J., Mills, B.J.W., Ozaki, K., Saltzman, M.R., and Porada, P. (2016). Earliest land plants created modern levels of atmospheric oxygen. Proc. Natl. Acad. Sci. USA *113*, 9704–9709.

Müller, M., Mentel, M., van Hellemond, J.J., Henze, K., Woehle, C., Gould, S.B., Yu, R.-Y., van der Giezen, M., Tielens, A.G.M., and Martin, W.F. (2012). Biochemistry and evolution of anaerobic energy metabolism in eukaryotes. Microbiol. Mol. Biol. Rev. *76*, 444–495.

Nishiyama, T., Hidetoshi, S., 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*, this issue, 448–464.

Puthiyaveetil, S., Ibrahim, I.M., and Allen, J.F. (2013). Evolutionary rewiring: a modified prokaryotic gene-regulatory pathway in chloroplasts. Philos. Trans. R. Soc. Lond. B Biol. Sci. *368*, 20120260.

Stolper, D.A., and Keller, C.B. (2018). A record of deep-ocean dissolved O_2 from the oxidation state of iron in submarine basalts. Nature *553*, 323–327.