4. Reiff, T., Jacobson, J., Cognigni, P., Antonello, Z., Ballesta, E., Tan, K.J., Yew, J.Y., Dominguez, M., and Miguel-Aliaga, I. (2015). Endocrine remodelling of the adult intestine sustains reproduction in *Drosophila*. eLife *4*, e06930.

5. Schwenke, R.A., and Lazzaro, B.P. (2017). Juvenile hormone suppresses resistance to infection in mated female *Drosophila melanogaster*. Curr. Biol. *27*, 596–601.

6. Santos, C.G., Humann, F.C., and Hartfelder, K. (2019). Juvenile hormone signaling in insect oogenesis. Curr. Opin. Insect Sci. *31*, 43–48.

7. Kurogi, Y., Mizuno, Y., Imura, E., and Niwa, R. (2021). Neuroendocrine regulation of reproductive dormancy in the fruit fly *Drosophila melanogaster*: a review of juvenile hormone-dependent regulation. Front. Ecol. Evol. *9*, 715029.

8. Fernandez-Nicolas, A., and Belles, X. (2017). Juvenile hormone signaling in short germ-band hemimetabolan embryos. Development *144*, 4637–4644.

9. Naruse, S., Washidu, Y., Miura, K., Shinoda, T., and Minakuchi, C. (2020). Methoprene-tolerant is essential for embryonic development of the red flour beetle *Tribolium castaneum*. J. Insect Physiol. *121*, 104017.

10. Truman, J.W., Riddiford, L.M., Konopová, B., Nouzova, M., Noriega, F., and Herko, M. (2023). The embryonic role of juvenile hormone in the firebrat, *Thermobia domestica*, reveals its function before its involvement in metamorphosis. eLife *12*, e92643. https://doi.org/10.7554/eLife.92643.

11. Barton, L.J., Sanny, J., Dawson, E.P., Nouzova, M., Noriega, F.G., Stadtfeld, M., and Lehmann, R. (2024). Juvenile hormones direct primordial germ cell migration to the embryonic gonad. Curr. Biol. *34*, 505–518.

12. Richardson, B.E., and Lehmann, R. (2010). Mechanisms guiding primordial germ cell migration: strategies from different organisms. Nat. Rev. Mol. Cell Biol. *11*, 37–49.

13. Barton, L.J., LeBlanc, M.G., and Lehmann, R. (2016). Finding their way: themes in germ cell migration. Curr. Opin. Cell Biol. *42*, 128–137.

14. Van Doren, M., Broihier, H.T., Moore, L.A., and Lehmann, R. (1998). HMG-CoA reductase guides migrating primordial germ cells. Nature *396*, 466–469.

15. Santos, A.C., and Lehmann, R. (2004). Isoprenoids control germ cell migration downstream of HMGCoA reductase. Dev. Cell *6*, 283–293.

16. Niwa, R., Niimi, T., Honda, N., Yoshiyama, M., Itoyama, K., Kataoka, H., and Shinoda, T. (2008). Juvenile hormone acid O-methyltransferase in *Drosophila melanogaster*. Insect Biochem. Mol. Biol. *38*, 714–720.

17. Jindra, M., Bellés, X., and Shinoda, T. (2015). Molecular basis of juvenile hormone signaling. Curr. Opin. Insect Sci. *11*, 39–46.

18. Liu, P., Peng, H.J., and Zhu, J. (2015). Juvenile hormone-activated phospholipase C pathway enhances transcriptional activation by the ethoprene-tolerant protein. Proc. Natl. Acad. Sci. USA *112*, E1871–E1879.

19. Zheng, H., Wang, N., Yun, J., Xu, H., Yang, J., and Zhou, S. (2022). Juvenile hormone promotes paracellular transport of yolk proteins by remodeling zonula adherens at tricellular junctions in the follicular epithelium. PLoS Genet. *18*, e1010292.

20. Markov, G.V., and Laudet, V. (2022). Small molecules as products of evolution. Curr. Biol. *32*, R100–R105.

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

Philip C.J. Donoghue[1,*] and James W. Clark[2]
[1]Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Bristol BS8 1TQ, UK
[2]Milner Centre for Evolution, Department of Life Sciences, University of Bath, Bath BA2 7AZ, UK
*Correspondence: Phil.Donoghue@bristol.ac.uk
https://doi.org/10.1016/j.cub.2023.12.036

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 relied 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, Darienko and colleagues[4], published in this issue of *Current Biology*, 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 'Anydrophyta' (Figure 1). Zygnematophytes are primitively unicellular, but multicellular filaments have evolved multiple times independently within the group[10]. Coleochaetophyceae and Charophyceae combine with anydrophytes 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, Darienko 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, the authors 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
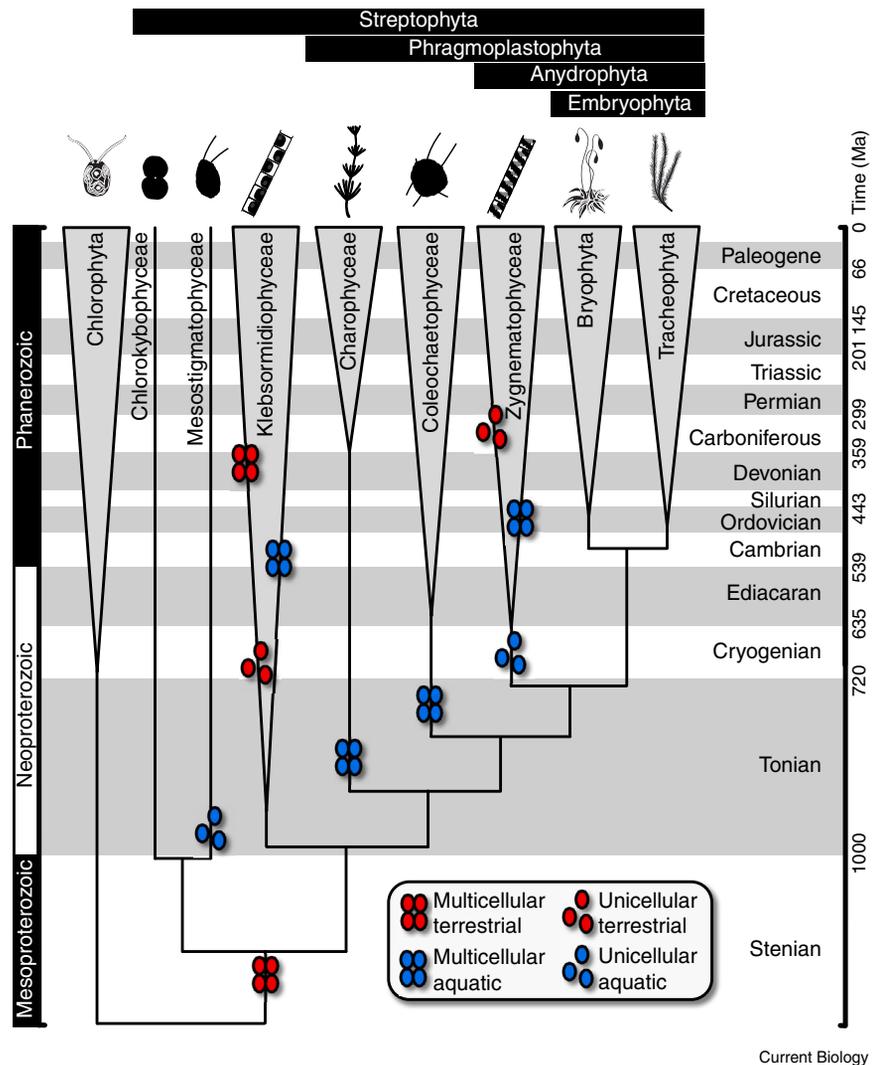

Figure 1. Time-scaled phylogeny of Streptophyta and the outgroup Chlorophyta after Bierenbroodspot, Darienko et al.[4].
Summary timescale and inferred evolution of multicellularity and ecology. (Images of Chlorokybophyceae, Mesostigmatophyceae, Klebsormidophyceae, Charophyceae, Coleochaetophyceae and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

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 Neoproteozoic (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, Darienko and colleagues estimate streptophytes to have originated deep in the Mesoproteorozoic (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 uniseriate filaments, and three dimensional sarcinoid multicellular packets. Bierenbroodspot, Darienko 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 streptophytes[14]. These comparative genomic 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, Darienko and colleagues[4] 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 Zygnematophyceae[15]. Bacterially derived UV-tolerance genes acquired independently by both land plants and Klebsormidiophyceae demonstrate the important role that horizontal gene transfer has played during the process of terrestrialisation[16]. The genomes of *Chlorokybus* (Chlorokybophyceae) and *Mesostigma* (Mesostigmatophyceae) include many gene families associated with terrestrial ecology, suggesting that *Mesostigma* may be secondarily aquatic[17]. 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 fossils[18] of their sister-lineage, the chlorophytes — the absence of fossil streptophytes from contemporary terrestrial and freshwater ecosystems[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 Mestostigmatophyceae[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 by Bierenbroodspot, Darienko and colleagues[4], 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.

REFERENCES

1. Donoghue, P.C.J., Harrison, C.J., Paps, J., and Schneider, H. (2021). The evolutionary emergence of land plants. Curr. Biol. 31, R1281–R1298. https://doi.org/10.1016/j.cub.2021.07.038.

2. Wellman, C.H., and Strother, P.K. (2015). The terrestrial biota prior to the origin of land plants (embryophytes): a review of the evidence. Palaeontology 58, 601–627. https://doi.org/10.1111/pala.12172.

3. Bowles, A.M.C., Williamson, C.J., Williams, T.A., Lenton, T.M., and Donoghue, P.C.J. (2022). The origin and early evolution of plants. Trends Plant Sci. 28, 312–329. https://doi.org/10.1016/j.tplants.2022.09.009.

4. Bierenbroodspot, M.J., Darienko, T., de Vries, S., Fürst-Jansen, J.M.R., Buschmann, H., Pröschold, T., Irisarri, I., and de Vries, J. (2024). Phylogenomics insights into the first multcellular streptophyte. Curr. Biol. 34, 670–681.

5. 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.e24. https://doi.org/10.1016/j.cell.2018.06.033.

6. Jiao, C., Sorensen, I., Sun, X., Sun, H., Behar, H., Alseekh, S., Philippe, G., Palacio Lopez, K., Sun, L., Reed, R., et al. (2020). The Penium margaritaceum genome: hallmarks of the origins of land plants. Cell 181, 1097–1111.e12. https://doi.org/10.1016/j.cell.2020.04.019.

7. Wong, G.K., Soltis, D.E., Leebens-Mack, J., Wickett, N.J., Barker, M.S., Van de Peer, Y., Graham, S.W., and Melkonian, M. (2020). Sequencing and analyzing the transcriptomes of a thousand species across the tree of life for green plants. Annu. Rev. Plant Biol. 71, 741–765. https://doi.org/10.1146/annurev-arplant-042916-041040.

8. Graham, L.E. (1985). The origin of the life-cycle of land plants. Am. Sci. 73, 178–186.

9. Wickett, N.J., Mirarab, S., Nguyen, N., Warnow, T., Carpenter, E., Matasci, N., Ayyampalayam, S., Barker, M.S., Burleigh, J.G., Gitzendanner, M.A., *et al*. (2014). Phylotranscriptomic analysis of the origin and early diversification of land plants. Proc. Natl. Acad. Sci. USA *111*, E4859–4868. https://doi.org/10.1073/pnas.1323926111.

10. Hess, S., Williams, S.K., Busch, A., Irisarri, I., Delwiche, C.F., de Vries, S., Darienko, T., Roger, A.J., Archibald, J.M., Buschmann, H., *et al*. (2022). A phylogenomically informed five-order system for the closest relatives of land plants. Curr. Biol. *32*, 4473–4482.e7. https://doi.org/10.1016/j.cub.2022.08.022.

11. Clark, J.W. (2023). Genome evolution in plants and the origins of innovation. New Phytol. *240*, 2204–2209. https://doi.org/10.1111/nph.19242.

12. Harris, B.J., Clark, J.W., Schrempf, D., Szöllősi, G.J., Donoghue, P.C.J., Hetherington, A.M., and Williams, T.A. (2022). Divergent evolutionary trajectories of bryophytes and tracheophytes from a complex common ancestor of land plants. Nat. Ecol. Evol. *6*, 1634–1643. https://doi.org/10.1038/s41559-022-01885-x.

13. Bowles, A.M.C., Bechtold, U., and Paps, J. (2020). The origin of land plants Is rooted in two bursts of genomic novelty. Curr. Biol. *30*, 530–536. https://doi.org/10.1016/j.cub.2019.11.090.

14. Mulvey, H., and Dolan, L. (2023). RHO of plant signaling was established early in streptophyte evolution. Curr. Biol. *33*, 5515–5525.e4. https://doi.org/10.1016/j.cub.2023.11.007.

15. Dadras, A., Furst-Jansen, J.M.R., Darienko, T., Krone, D., Scholz, P., Sun, S., Herrfurth, C., Rieseberg, T.P., Irisarri, I., Steinkamp, R., *et al*. (2023). Environmental gradients reveal stress hubs pre-dating plant terrestrialization. Nat. Plants *9*, 1419–1438. https://doi.org/10.1038/s41477-023-01491-0.

16. Ma, J., Wang, S., Zhu, X., Sun, G., Chang, G., Li, L., Hu, X., Zhang, S., Zhou, Y., Song, C.P., and Huang, J. (2022). Major episodes of horizontal gene transfer drove the evolution of land plants. Mol. Plant *15*, 857–871. https://doi.org/10.1016/j.molp.2022.02.001.

17. 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. https://doi.org/10.1038/s41477-019-0560-3.

18. Li, D., Luo, G., Tang, Q., She, Z., and Xiao, S. (2023). New record of the green algal fossil Proterocladus and coexisting microfossils from the Meso-Neoproterozoic Diaoyutai Formation in southern Liaoning, North China. Precambrian Res. *393*, 107104. https://doi.org/10.1016/j.precamres.2023.107104.

19. Slotznick, S.P., Swanson-Hysell, N.L., Zhang, Y., Clayton, K.E., Wellman, C.H., Tosca, N.J., and Strother, P.K. (2023). Reconstructing the paleoenvironment of an oxygenated Mesoproterozoic shoreline and its record of life. Geol. Soc. Am. Bull. https://doi.org/10.1130/b36634.1.

20. Irisarri, I., Darienko, T., Proschold, T., Furst-Jansen, J.M.R., Jamy, M., and de Vries, J. (2021). Unexpected cryptic species among streptophyte algae most distant to land plants. Proc. R. Soc. B *288*, 20212168. https://doi.org/10.1098/rspb.2021.2168.

Vision: A prolonged and colorless experience

Geoffrey K. Aguirre

Department of Neurology, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA 19104, USA
Correspondence: aguirreg@upenn.edu
https://doi.org/10.1016/j.cub.2023.12.052

The discovery of melanopsin cells in the retina might render the standard model of human color perception incomplete. Measurements made with a technically advanced visual display address this question and point to a new role for the melanopsin system.

Human color perception is well explained by the properties of the cells of the eye, which project the continuous, natural spectrum of light onto signals from three classes of cones. Over the last 20 years, it has become clear that there is an additional cell in the retina that is active under daylight conditions and is capable of supplying signals for conscious visual perception — the melanopsin-containing retinal ganglion cell. This finding has raised the possibility that the standard model of color perception must be expanded to account for this cell. A new study by Woelders and colleagues[1] reported in a recent issue of *Current Biology* resolves a disputed role for melanopsin in human vision, and identifies a new function for this system in sustaining percepts over time.

If you are reading these words (and with apologies to Braille readers), they are being conveyed to your eyes within the framing assumption of trichromatic vision. If by digital screen, then varying intensities of three color light sources, or 'primaries' (e.g., red, green, and blue), have been additively combined to produce the images you see. And if by print, then varying combinations of three pigments were 'subtractively' combined to render the page (leaving aside the K of CMYK). These approaches reflect a core assumption that the combination of three primaries is necessary, and in principle sufficient, for a display to fully reproduce the appearance of the visual world. Expressed formally, there should exist for a standard human observer a combination of three primaries that is perceptually

indistinguishable from any natural spectrum of light composed of an arbitrary mixture of power at different wavelengths.

This principle is rooted in the biology of the human retina, which contains three classes of cone cells that support vision under daylight conditions. The different cone cells express photosensitive proteins (opsins) that tend to capture short (S), medium (M), and long (L) wavelength photons. The spectral sensitivity of the cone cells has been meticulously characterized, as has the influence of other light-absorbing structures in the eye such as the crystalline lens and macular pigment. As the properties of color perception are essential to the design of modern environments, an international organization (the Commission