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Land Plant Model Systems Branch Out

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The genome of the liverwort *Marchantia polymorpha* is an important step toward development of a new plant model system (Bowman et al., 2017). Liverworts may be the sister taxon to all other land plants, and the genome shows features that illuminate the ancestor of all land plants and give insights into how plant systems function and evolved.

In this issue of *Cell*, Bowman et al. (2017) present the genome of *Marchantia polymorpha*. Many readers may ask, "what the heck is *Marchantia*?" It is a thalloid liverwort, an inconspicuous organism that is part of a lineage often lumped together with mosses and hornworts as "bryophytes". *Marchantia* is easy to grow in the laboratory, can be readily transformed, and is amenable to other forms of genetic manipulation, including gene editing (Ishizaki et al., 2016). Consequently, *Marchantia* is emerging as a promising plant model system.

What most distinguishes *Marchantia* as a model system is its phylogenetic position because it can serve as a landmark for the emergence of key plant traits (Figure 1). It joins two other well-established model systems that are phylogenetically distant to angiosperms (flowering plants): the chlorophyte green alga *Chlamydomonas reinhardtii* and the moss *Physcomitrella patens* (Chang et al., 2016). Liverworts are among the earliest diverging lineages of plants, but the thalloid morphology of *Marchantia* is almost certainly a derived condition; there are also "leafy" liverworts that have a much more familiar plant morphology, with a stem and leaf-like extensions. It is tempting to think of *Marchantia* as a "primitive" organism, but, like all living things, it is a mosaic of traits, and its genome displays some properties that are shared with green algae (the broader group to which all land plants belong), others that are shared with vascular plants to the exclusion of green algae, and still others that are uniquely its own. Perhaps the most important characters are those that help illuminate the properties of the common ancestor of all land plants, giving insight into the circumstances by which plants colonized dry land and in so doing created the opportunity for the success of all terrestrial life (Delwiche and Cooper, 2015). Thus, study of *Marchantia* can provide insights into some of the most foundational events in the history of life on earth.

The *Marchantia* genome proves to be moderately small (~226 Mb) and of low genetic redundancy but with some expanded gene families in tandem arrays. It shows no evidence of ancestral polyploidy or whole-genome duplications, which is helpful in a model system because of the overall simplicity of gene families. Angiosperms, including *Arabidopsis thaliana*, seem to have undergone several sequential whole-genome duplications, the number depending upon the lineage (del Pozo and Ramirez-Parra, 2015). Whole-genome duplication has also been documented in *Physcomitrella* (Rensing et al., 2008), but not in the vascular plant *Selaginella moellendorffii* (Banks et al., 2011), which also has received attention as a potential model system.

Analysis of the *Marchantia* genome provides significant insight into the origin of a number of fundamental plant properties. For example, there is marked expansion of diversity within transcription factor families. This may have allowed for increased diversification of developmental and environmental responses, presumably because life on land involves more varied environmental conditions than life in the water. The genome also shows the emergence of components for the angiosperm-like machinery of several plant hormone signaling pathways, suggesting that these pathways were assembled largely in the common ancestor of land plants after the colonization of land; included are the signaling pathways of auxin, jasmonic acid, abscisic acid, and salicylic acid, which are critical for the regulation of key processes in land plants, such as growth, differentiation, tropic responses, dormancy, desiccation tolerance, and plant defense. Interestingly, *Marchantia* has a set of signaling components for gibberellic acid (GA) but lacks the GA receptor known in angiosperms, whereas the pathways for ethylene and cytokinin are known in charophyte algae and thus are considered to be more ancient. Also appearing in *Marchantia* are genes encoding "new" biochemical pathways, including certain photoreceptors and phenylpropanoids for adaptation to photooxidative stress and components for cuticle and wax biosynthesis to prevent water loss and protect against insects, again consistent with the evolutionary transition to land.

The genome shows evidence of substantial gene transfer from fungi and bacteria, such as the genes involved in the biosynthesis of terpenes that contribute to oil bodies, which are defensive organelles unique to liverworts. Strikingly, the majority of genes involved in terpene biosynthesis appear to be the product of horizontal gene transfer from fungi, suggesting that the evolution of oil bodies relied critically upon transferred genes. Perhaps the growth habit of thalloid liverworts, being in intimate contact with the soil, facilitated this transfer, although the transfer does not seem to have been from symbiotic mycorrhizal fungi.

Marchantia also presents an opportunity for the study of the evolution of sex chromosomes. *Marchantia* is dioecious (has separate male and female gametophytes),

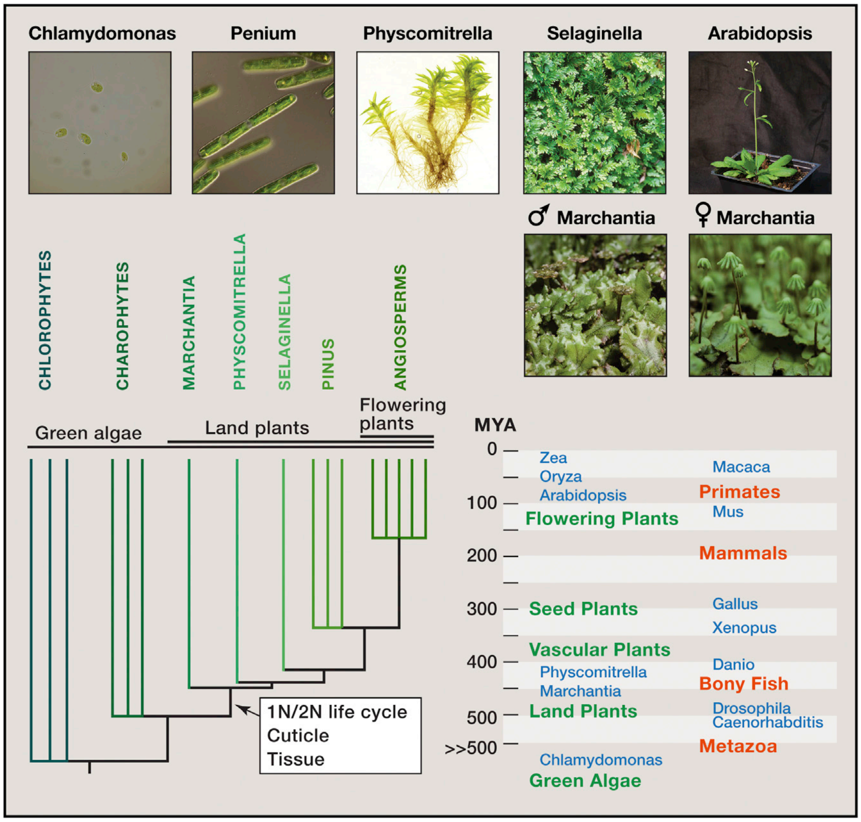

Figure 1. Key Plant Lineages

Images of representative organisms that are in use or show promise as model systems for plants, along with a phylogenetic tree showing the relationships among these organisms and their approximate divergence times from *Arabidopsis thaliana*. Shown are *Chlamydomonas* (a chlorophyte green alga), *Penium* (a charophyte green alga), *Physcomitrella* (a moss), *Selaginella* (a vascular non-seed plant), and *Arabidopsis* (a flowering plant), along with both male and female gametophytes of *Marchantia* showing antheridiophores (male) and archegoniophores (female). The timescale applies to both the phylogenetic tree and the taxa listed to the right and shows the approximate ages of key groups of plants (green) and animals (red), along with the approximate divergence times for each model system (blue) (Herendeen et al., 2017; Kumar et al., 2017). All images by C.F.D.

and development of the two sexes is regulated by X and Y chromosomes. The sex chromosomes appear to be non-recombining, with no discernable synteny, and silent sites in codons of protein-coding genes are saturated. This implies that liverwort sex chromosomes are an ancient innovation in the liverwort lineage. Most plants do not have sex chromosomes, although they have evolved independently in several plant lineages (Charlesworth, 2016).

Model systems have been one of the great successes of modern biology. Application of a panoply of forward- and reverse-genetic techniques in well-characterized systems has made it possible to characterize specific mechanisms and processes for a wide range of long-standing biological questions. In most cases, the model systems are not important in and of themselves; rather, they are important when the insights they provide can be extended to fundamental biology or to less-tractable organisms. In the context of model systems biology, the unique, derived features that are characteristic of individual lineages are a form of noise. They distract from the underlying shared biology and make it more difficult to extrapolate from the model system to other species. Consequently, the study of animal biology has benefitted greatly from the development of model systems that span a range of divergence times from a few tens of millions to many hundreds of millions of years (Figure 1). By contrast, models in plant biology have been developed primarily within the relatively young group of angiosperms (Chang et al., 2016), a group that diversified less than 140 million years ago. Plant model systems are neither as numerous nor as phylogenetically dispersed as those for animals, and the publication of the *Marchantia* genome is a major step forward for plant biology.

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