Identification of genes that regulate the complex life cycles of land plants helps to explain their evolutionary origins.

One Genome, Two Ontogenies

William E. Friedman¹·²

The fascination of humans with the notion of multiple personalities (and morphologies) is perhaps best captured in Robert Louis Stevenson’s 1886 tale of the Strange Case of Dr Jekyll and Mr Hyde. Land plants have been pulling off this trick for 475 million years, although perhaps to less acclaim. All of the roughly 300,000 extant species of land plants (¹) engage in a complex life cycle that alternates between sporophytes (spore-producing organisms) and gametophytes (gamete-producing organisms). Biologists have long pondered how each species of land plant can maintain separate developmental programs that produce fundamentally dissimilar ontogenies and morphologies. On page 1067 of this issue, Sakakibara et al. (²) provide insights into the developmental and evolutionary origins of this alternation of generations.

Today, the sporophyte generation dominates in most extant lineages of land plants (lycopods, ferns, horsetails, and seed plants), but this was not always the case (³). Among the earliest groups of land plants (liverworts, mosses, and hornworts), the gametophyte generation was and is the dominant component of the life cycle; the minute and nutritionally dependent sporophyte with its single spore-producing capsule grows upon the body of the larger and morphologically more complex gametophyte (see the figure).

But, which came first, the gametophyte or the sporophyte? The closest living relatives of land plants (⁴) are groups of green algae that lack an alternation of generations. Their only organismic generation is a haploid gametophyte; after fertilization and the formation of a diploid zygote, meiosis creates haploid propagules that reestablish new gametophytes. Thus, the only diploid phase in the life cycles of the ancestors of land plants was the single-celled zygote. The multicellular sporophyte as we know it (such as a leafy fern, pine tree, water lily, and buttercup) is a developmental innovation of land plants.

Sakakibara et al. now provide critical insight into the evolutionary developmental underpinnings of the diploid sporophyte generation in the first land plants. Working with the model moss species Physcomitrella patens, they show that the creation of the sporophyte and its ontogeny in the
life cycle of early land plants may have been facilitated by a mechanism that suppresses the expression of the ancestral gametophyte ontogeny brought onto land by green algal pioneers.

The authors show that KNOX2 genes, whose functions in land plants were previously poorly understood (3), are necessary for maintaining the sporophyte developmental program in P. patens. Mutant knockouts for the KNOX2 gene MKN6 unleash the expression of gametophyte ontogeny in diploid sporophytes. The data are compelling: The absence of MKN6 leads to a transition from the embryo/sporophyte ontogeny to the initiation of filamentous structures (protonema), whose morphology is characteristic of early gametophyte development in P. patens and many other mosses. Subsequent initiation of leafy shoot systems from protonema seals the case for the clear expression of the complete gametophyte ontogeny when sporophytes lack the proper expression of KNOX2 genes.

The discoveries of Sakakibara et al. complement the work of Okano et al. (6) and Mosquena et al. (7), who have shown that in P. patens, genes that encode subunits of the polycr comb repressive complex 2 (PRC2) are essential for the maintenance of gametophyte ontogeny. Gametophytes with deletions or mutations for these key components of the polycr comb complex have a Jekyll-and-Hyde-like habit of initiating sporophyte ontogeny. Thus, two central regulators of the contrasting gametophyte and sporophyte ontogenies of members of an ancient lineage of land plants are now known.

Genes encoding homeobox-containing transcription factors (homeoproteins), which include members of the KNOX family, are found in almost all major eukaryotic clades (8) and were probably present in the common ancestor of all eukaryotes (9). Evidence from the green alga Chlamydomonas indicates that two homeoproteins, Gsp1 and Gsm1, are essential for the transition from gametic fusion to proper zygote development (8). How far back and how often might homeoproteins have been involved in the evolution and regulation of complex life cycles? After all, land plants are not the only clade of eukaryotes to have made the transition from an ancestral simple life history with a single multicellular generation to a complex alternation of generations (see the figure).

Brown algae have isomorphic (sporophytes and gametophytes are morphologi-
cally similar) and heteromorphic (sporophytes and gametophytes are morphologi-
cally distinct) alternations of generations (10). Red algae have heteromorphic alter-
nations of generations that cycle between morphologically distinct gametophytes and sporophytes. Among the many lineages of green algae, most of which have gameto-
phyte-only life cycles (with the zygote as the only diploid phase), clades with isomor-
phic or heteromorphic alternations of generations have evolved several times.

Have photosynthetic eukaryotic lineages been rooting around in the same ancestral toolkit during the several separate evolu-
tionary origins of heteromorphic alternations of generations? Only time, a solid knowledge of algal diversity, and the proper phylogenetic choices for genome sequenc-
ing will tell. Long-sought answers to age-old questions of homoplasoy and evolution-
ary pattern await the study of future model systems that reflect the amazing diversity of photosynthetic life.

References