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IN BRIEF

Plastid Genes That Were Lost along the Road to Parasitism

Some plants rely on others to do their photosynthesis for them. For example, most plants in the broomrape family (Orobanchaceae; see figure) are parasitic, meaning they rely on a host plant for inorganic and organic nutrients as well as water. In most land plants, the selective pressure on photosynthesis-related elements causes plastid chromosomes to be conserved in terms of structure, gene content, and nucleotide substitution rate (Wicke et al., 2011). However, in parasitic plants, photosynthesis-associated genes are no longer required, so they may become pseudogenized and (eventually) deleted, resulting in a functional and physical reduction of the plastid genome (Krause, 2011). While some broomrapes are holoparasites, relying completely on the host plant for water and nutrients, others are hemiparasites, still carrying out photosynthesis to some extent, and a few are autotrophs. Broomrapes are therefore perfect for studying the course, tempo, and mechanisms of plastome evolution after the loss of photosynthesis, as such a study requires comparative analyses of closely related nonparasitic and parasitic species with different degrees of trophic specialization.

Wicke et al. (pages 3711–3725) compared the complete plastome sequences of 11 members of the broomrape family, including one nonparasitic species, one hemiparasite from the earliest diverging parasitic branch of the family, and nine holoparasites from an exclusively nonphotosynthetic clade. By sampling the broomrape family in this manner, the authors were able to infer the modes and mechanisms of plastome reduction that occurred after the transition to holoparasitism. They found that the autotroph's plastome is similar to that of tobacco (*Nicotiana tabacum*), and no genes were physically lost in the hemiparasite (but several photosynthesis-related genes were pseudogenized), while most of these genes were pseudogenized in the holoparasites. The holoparasites' plastomes are quite variable, as the reduced functional constraints on photosynthesis lead to the accumulation of mutagenic factors, such as microsatellites, long homopolymer stretches, forward or palindromic repeats of various lengths, and low GC content. Such elements increase the instance of illegitimate recombination, sometimes leading to deletions of dispensable plastome fragments. By reconstructing the ancestral set of protein-coding genes, rRNA genes, and tRNA genes of the holoparasites, the authors determined that the loss of photosynthesis coincided with the pseudogenization of 31 out of 49 plastid genes for photosystems and photosynthetic electron transport. In addition, several housekeeping genes became pseudogenes during or shortly after the transition to holoparasitism. Interestingly, not all changes to plastid gene content were initiated by the loss of photosynthesis, as some of these changes occurred in the hemiparasite, which is still in the process of transitioning to a parasitic lifestyle. Losses of most ribosomal protein genes, tRNA isoacceptors, and others represent independent and repeated functional losses, occurring later in holoparasitic evolution, which points to increased transfer of functional plastid DNA to the nuclear genome in parasites. While some photosynthesis-related genes were quickly lost in all of the holoparasites, some were retained, such as all six ATP synthase complex genes. These genes may play an alternate role in the parasitic lifestyle unrelated to photosynthesis. Moreover, some dispensable genes or pseudogenes may have been retained because of their proximity to an essential element or operon, as determined by multiple regression analyses. However, gene length and strandedness do not appear to play a role in gene retention.

Orobanche gracilis, a holoparasitic broomrape, parasitizes a wide range of legumes and occasionally attacks crops. It robs its hosts of water and nutrients before emerging aboveground for reproduction, where it can grow up to 1.5 feet tall. *O. gracilis* possesses a remarkably reduced chloroplast genome attributable to massive gene loss and reconfiguration of the plastome structure. (*Figure courtesy of K.F. Müller, University of Münster*.)

Indeed, the road to parasitism is an interesting one.

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REFERENCES

Krause, K. (2011). Piecing together the puzzle of parasitic plant plastome evolution. Planta **234:** 647–656.

Wicke, S., Müller, K.F., de Pamphilis, C.W., Quandt, D., Wickett, N.J., Zhang, Y., Renner, S.S., and Schneeweiss, G.M. (2013). Mechanisms of functional and physical genome reduction in photosynthetic and nonphotosynthetic parasitic plants of the broomrape family. Plant Cell **25:** 3711–3725.

Wicke, S., Schneeweiss, G.M., dePamphilis, C.W., Müller, K.F., and Quandt, D. (2011). The evolution of the plastid chromosome in land plants: Gene content, gene order, gene function. Plant Mol. Biol. **76:** 273–297.

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