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Horizontal Gene Transfer: Accidental Inheritance Drives Adaptation

Few facts in biology are more certain than offspring inheriting genetic material from their parents, but not all genes are acquired this way. A new report documents the horizontal transfer of a potentially adaptive gene between distantly related plants.

Endymion D. Cooper

It is common knowledge that individuals inherit features from their parents. For example, children are frequently described as having “his mother’s eyes” or “her father’s nose”. Introductory courses in biology teach students that mutations produce genetic diversity and that sorting of genetic diversity in populations produces fixed genetic differences and biological diversity. But are these processes enough to explain the level of diversity we see in the living world? Perhaps not. Pioneering studies implicating DNA in inheritance also revealed a different mechanism through which organisms can acquire genes [1]. This process, known as horizontal gene transfer (HGT), is receiving increased recognition for its important role in evolution, particularly in prokaryotes.

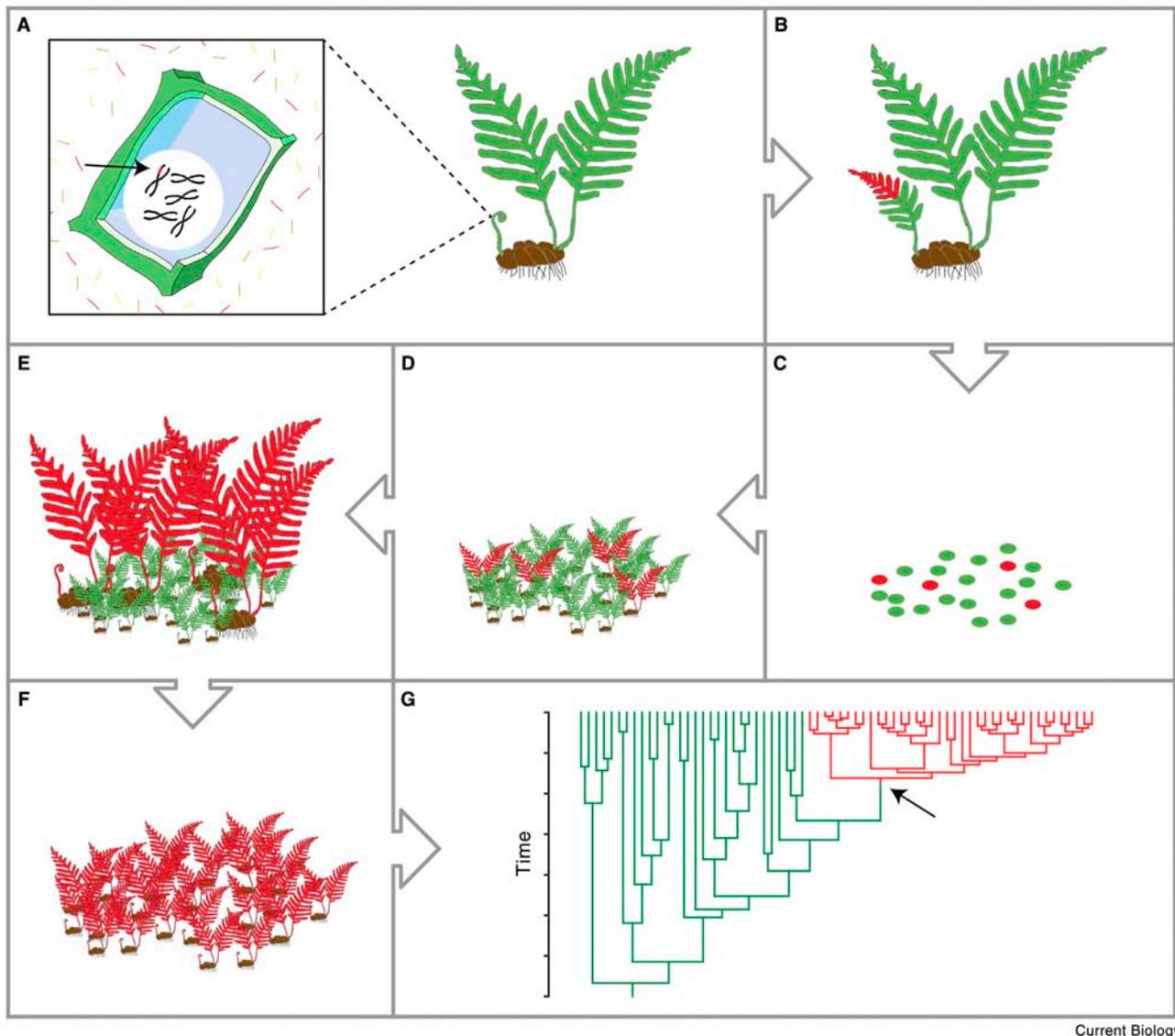
A new study by Fay-Wei Li and colleagues, published recently in

PNAS, demonstrates a remarkable case of HGT between distantly related plants [2]. Most ferns possess an unusual photoreceptor, neochrome, which consists of red-sensing phytochrome fused to blue-sensing cryptochrome. How ferns came to have this photoreceptor had remained an unsolved mystery until, using data from a large transcriptome sequencing initiative, Li *et al.* found neochrome in another group of plants, the hornworts. More striking, however, was the discovery that fern neochrome was acquired from hornworts more than 200 million years after the vascular plants, which include ferns, and hornworts diverged from their common ancestor.

Three pieces of evidence suggest that acquisition of neochrome from hornworts drove an adaptive radiation in ferns. First, transfer of hornwort neochrome to ferns occurred close to the origin of the angiosperms. Subsequent diversification of the

angiosperms had a profound influence on the structural complexity of forests and, not surprisingly, the diversification rate of shade-loving ferns accelerated in response [3]. Second, neochrome is not found in early-diverging, species-poor, fern lineages [4], suggesting a relationship between neochrome and species richness. Third, ferns that possess neochrome have enhanced phototropic responses [4]. Together, these three points support the hypothesis that HGT of neochrome enhanced the photo-sensing ability of ferns and enabled them to adapt and diversify in angiosperm-shaded environments.

What makes this HGT event so interesting is that it happened despite being fundamentally improbable. Much like the origin of life itself, HGT-stimulated adaptive radiation of ferns could only have occurred at the intersection of several individually unlikely events and circumstances. First, exogenous DNA must have made its way into a cell and from there, into its genome (Figure 1A). As a protein-coding gene, the full open reading frame must have been incorporated into the genome in such a way as to be successfully transcribed and translated. The translated protein had to be able to interact with existing cellular networks to produce a phenotypic outcome. Next, the mutant



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Figure 1. Horizontal gene transfer of a selectively advantageous gene drives an adaptive radiation.

(A) Extracellular DNA is incorporated into a plant cell and (B) creates a mutant cell line. (C, D) Reproductive organs produced by the mutant cell line pass the HGT gene to the next generation. (E) The HGT gene confers a selective advantage (F) and over time becomes fixed in the population. (G) The fixed HGT gene stimulates an adaptive radiation.

cell must have continued to grow and divide, eventually producing reproductive organs and thereby passing the newly acquired gene to the next generation (Figure 1B–D). The presence of the new gene would have conferred a competitive advantage and, over many generations, it became fixed in the population (Figure 1E–F). Acquired in this way, neochrome allowed ferns to diversify rapidly (Figure 1G) into the range of newly created niches in angiosperm-dominated forests.

Several recent reviews and perspectives have examined how exogenous DNA might enter eukaryote

cells [5] and the potential impact of HGT on adaptive evolution in eukaryotes [6,7]. However, fern neochrome and other recent examples such as C_4 photosynthesis genes in grasses [8] are reminders that we currently know very little about the process of HGT in eukaryotes. Considering each step of the fern neochrome HGT example provides an opportunity to generate predictive hypotheses for further investigation.

Consider, for example, the conditions that must be met for a horizontally transferred gene to confer a selective advantage. Beyond the requirement for a transcribable and

translatable reading frame, the gene product must either be directly advantageous (e.g. a herbivore toxin) or must be capable of interacting with pre-existing cellular networks to improve some aspect of cell or organism function. The horizontally transferred neochrome is similar to pre-existing fern photoreceptors and would have been capable of interacting with the existing light-signalling network. Similarly, the C_4 photosynthesis genes transferred between grasses are homologous to photosynthesis genes conserved in all plants [8] and could be directly incorporated into the existing

metabolic pathway. More generally, to have an impact on cell or organism function, a gene product involved in metabolism needs a substrate, a transcription regulator needs a target, and a protein involved in signal transduction needs interacting partners. If these conditions are not met, a transferred gene might have no, or only negligible, impact on the recipient organism. Even if these conditions are met, the impact of a transferred gene might be selectively neutral or deleterious.

So what happens to products of HGT? It is reasonable to expect standard population genetic principles to apply. At one end of the spectrum, strongly deleterious genes will be eliminated from populations through purifying selection. While at the other extreme, advantageous genes will become fixed through positive selection. Neutral and nearly neutral genes occupy the middle ground and will have a probability of fixation or elimination determined by genetic drift. The frequency with which HGT occurs, and where transferred genes fall on the spectrum of potential adaptive impact, remains an open question. However, examples of adaptive HGT suggest the likely occurrence of a larger number of non-adaptive HGT events. Furthermore, this suggests the hypothesis that eukaryote genomes are littered with horizontally transferred DNA. This hypothesis is being actively investigated and genome-scale analyses are already finding support for relatively frequent HGT into eukaryotes (e.g. [9,10]).

The remarkable impact that HGT appears to have had on the evolutionary trajectory of ferns suggests an exciting, albeit highly speculative, solution to a classic problem in evolutionary biology. Sister lineages often have significantly different numbers of species. Commonly referred to as the phylogenetic imbalance problem, this enigmatic pattern was famously highlighted by the geneticist J.B.S. Haldane, who suggested that, a creator, if one exists, must have had “an inordinate fondness for beetles” [11]. Indeed, why are there so many species of beetles (Coleoptera) and so few of, for example, velvet worms (Onychophora). Or amongst plants, why are there so many daisies (Asteraceae) and only one *Ginkgo*? Could it be that the acquisition of

adaptive genes via HGT is responsible for accelerating diversification in some lineages?

The Li *et al.* report is likely to inspire biologists to search for further cases. But I would like to offer a small word of caution: in seeking evidence for HGT, it is important to recognise that the assumptions of standard phylogenetic methods will often be violated in cases of suspected HGT. For an accessible discussion of phylogenetic models and their assumptions, see [12]. The severity of such violations will vary, and in many cases will not produce incorrect results, but it is important to realise that phylogenetic analysis will not necessarily yield reliable trees. The reliability of phylogenetic methods in identifying the correct origin of horizontally transferred genes will decrease with increasing age of the putative HGT event and different approaches can produce dramatically different results for ancient HGT (e.g. [13,14]). Nevertheless, with increased interest in HGT we can expect additional cases to be identified, and the impact of HGT in macroevolution will become better known.

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Evolution: How a Barnacle Came to Parasitise a Shark

A new study on a parasitic barnacle that lives on a deep sea shark found that its closest living relatives are rocky shore barnacles. The findings provide insight into barnacle phylogeny and raise new questions about the evolution of parasitism.

Tommy L.F. Leung

Parasitism is one of the most common modes of life on this planet [1]. It has independently evolved several times in

all domains of life, and many animal phyla have parasitic species [2]. But for most parasite groups, very little is known about how they made the evolutionary transition from a