Second To The Right, Straight On 'Til Morning

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I thank Michael Ruse (2007) for his follow-up letter on evolution, selection, and development. This helps greatly in lessening the area of perceived differences between us. Of course, seeing one's ideas referred to in print as “hogwash” (Ruse 2006) is likely to get one “riled up.” While I do confess to a tree-of-life metaphor wherein the majority of the trunk, branches and buds are the products of development (as they are in the corporeal tree) and where natural selection is primarily the pruner and shaper of the tree, I have no desire to see the role of selection taken over by developmental biology. Natural selection works. It selects from the variants those that are the most fit for the environment and is critical for the origin and especially the maintenance of biodiversity. What I did say was that developmental biology (and especially developmental genetics) is also critical for the origin and maintenance of biodiversity and deserves at least as much a place in evolutionary theory as population genetics. In the origin of selectable variation, development should be the predominant mode of explanation. In the maintenance of variation, natural selection should dominate the discussions. However, both are needed. Moreover, because of the substantial role of development in the origin of variations, I also predicted (Gilbert et al. 1996) that population genetics was going to have to change its foci, if it were to remain relevant to studying important areas of evolution.

Recent studies are confirming this contention. As Mary Jane West-Eberhard (2005: 6549) wrote in her appreciation of Ernst Mayr, “Lack of attention to developmental phenomena in relation to speciation promises to change, because genomic studies of speciation can now contemplate gene expression as well as gene frequency data.” This change is being seen in research investigating speciation in sticklebacks (reviewed in Foster and Baker 2004) and Drosophila (Michalak and Noor 2003), but the new findings concerning primate evolution are probably the most relevant. By comparing genomic regions between humans and chimps, the fastest diverging areas are not found in protein-coding sequences, but in the “dark matter” of the genome that can regulate the expression of such genes. (This pattern was predicted2 by Mary-Claire King and Allan C. Wilson in 1975, one of the papers that prompted the approaches mentioned in the Gilbert et al. article of 1996.) Specifically, several “human accelerated regions” distinguishing human from chimp appear to consist of DNA elements near the genes expressed in developing cortical neurons (Pollard et al. 2006; Prabhakar et al. 2006; reviewed by Pointing and Lunter 2006). This variation is not in the alleles normally studied by population geneticists. Nor is it in the alleles encoding developmental regulatory proteins that have roles in forming embryonic organs (such as FOXP2, which is involved in speech production, or ASPM, which is involved in brain growth). Rather, this variation is at yet another level—in the alleles of regulatory regions controlling the synthesis of developmental proteins. These DNA sequences determine the amount, location, and duration of developmental gene expression and may contain enhancers or encode regulatory RNAs. If these are indeed the important loci for species differences, the traditional focus of population genetics is very likely to change. The comparative genomics of developmental regulation may be able to tell us what actually happened in speciation. So, I will stand by my original contention.

The continental biologists of the late 19th century, who tried to combine embryology and Darwinism, failed. They failed for several reasons—their lack of a criterion for homology, the influence of Romantic Naturphilosophie, and the adherence to a notion of the Great Chain of Being, among them. While many of their ideas were flawed (as were many of the genetic ideas proposed after them), these embryologists did have some proposals that were very good; among these
was the notion that evolution consists of inherited changes in development. This allowed them to look beyond the species level and into the more profound levels of phylogeny, not only at the twigs, but at the trunks and branches of the evolutionary tree. I think that to investigate how alterations of development can cause speciation as well as the major anatomical changes associated with classes and phyla, we need a “deep” population genetics, one based on the expression of developmental genes. The combination of comparative genomics and developmental genetics may be presenting evolutionary biology with exactly this type of genetics.

To be called Peter Pan at age 57 is sheer flattery; but I hope that I am pointing not to an imaginary Neverland, but to the deep time of our own planet.

**Notes**

1. Because it favors the buffering of environmental effects in some circumstances, selection can enable the accumulation of unexpressed variation, enabling systematic phenotypic change to occur rather suddenly. But, this accomplishment can also be seen as a product of the developmental system. Indeed, I cannot resist mentioning the *bon mot* that evolutionary developmental biologist Jukka Jernvall (2006) made in his talk at the European Evolutionary Developmental Biology Meeting in Prague. Showing the ways by which changing the synthesis and diffusion characteristics of paracrine factors can generate the dentition of the mammalian radiation, he proclaimed: “Nothing in variation makes sense except in the light of development.”

2. Specifically, the King and Wilson (1975, p. 114) paper says, “The organismal differences between chimpanzees and humans would then result chiefly from genetic changes in a few regulatory systems, while amino acid substitutions in general would rarely be a key factor in major adaptive shifts.”

**References**


