

Parallelism as the pattern and process of mesoevolution

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Over the last decade, evolutionary developmental biologists have increased the phylogenetic resolution of their studies from “coarse” comparisons between phyla and other distantly related taxa to “fine” comparisons between closely related species (Pennisi 2002; Wilkins 2002). This increase in phylogenetic resolution has led to illuminating discoveries about the developmental genetic basis of parallelism (Wray 2007). Parallelism is most often defined as the convergent or independent evolution of similar morphological characters *that share a common developmental basis* (Futuyma 1998; Hall 2003; Stearns and Hoekstra 2005). Several elegant studies (Gompel and Carroll 2003; Sucena et al. 2003; Shapiro et al. 2004, 2006; Prud'homme et al. 2006; McGregor et al. 2007) have recently shown that the independent gain or loss of similar morphologies can be accounted for by the gain or loss of expression of a single gene of “major” effect. The study by Prud'homme et al. (2006) is especially interesting. These authors have shown that the independent gain or loss of pigmentation spots on the wings of male drosophilid flies can be accounted for by the expression of the *yellow* gene. They were also able to identify the regulatory basis of the acquisition or loss of *yellow* expression. In two independent gains of the pigmentation spots, expression of *yellow* was reactivated using different *cis*-regulatory elements, but in two independent losses of the pigmentation spot, *yellow* expression was lost using the same *cis*-regulatory element.

These discoveries have fundamental implications for evolutionary biology. To focus discussions on the role of parallelism in the evolutionary process, we must first establish the view that parallelism represents a continuum or gray zone between homology and convergence (Meyer 1999; Wake 1999; Gould 2002; Hall 2003, 2007). Although parallelism is considered to be a form of convergent evolution, and can be recognized as such (homoplasy) in phylogenetic analyses (Desutter-Grandcolas et al. 2005), it is often distinguished from “true” convergence (analogy) by the fact that in parallel evolution independently evolved characters share a common developmental basis, whereas truly convergent characters do not (Hall 2003, 2007). This distinction, however, is arbitrary and is only a matter of degree. We know of many cases where truly convergent morphologies, such as fly and mouse eyes,

are also derived from a common developmental pathway, the *eyeless/Pax 6* pathway (Quiring et al. 1994; Halder et al. 1995). The difference between the independent gain of eyes in flies and mice, and of pigmentation spots on the wings of males in different drosophilid species is only a matter of degree of similarity in the morphology and underlying developmental pathway. The *eyeless/Pax 6* pathway has diverged (in regulation and downstream targets) to a greater degree between flies and vertebrates (Treisman 1999) than has the *yellow* pathway in which different *cis*-elements activate *yellow* expression in two independent gains of the spot (Prud'homme et al. 2006).

The distinction between parallelism and homology (characters derived from a similar character present in the most immediate common ancestor) is also not strictly dichotomous (Meyer 1999; Wake 1999; Hall 2003, 2007). Some authors have even classified parallelism as a form of homology (Fitch 2000). Even though the trait may not be expressed in the immediate common ancestor of all taxa within a group, it is clear that in some cases the genetic and developmental potential for the production of the trait has been retained from a recently shared but not immediate common ancestor (Meyer 1999; Wake 1999). In this way, there is continuity of the trait even if it is not expressed in all taxa within the group (Hall 2007). Thus, we can view parallelism as a transition between truly homologous and truly convergent characters.

If we accept this view, then parallelism, the flickering on or off of characters between closely related species through time, should be considered a special phase in evolution. This special phase is a transition between microevolution, the gradual divergence of homologous features within and between populations; and macroevolution, which includes adaptive convergence of characters between clades. This special phase is not just a pattern, but is driven by distinct mechanisms that are particularly relevant to this phase. The flickering on and off of characters is driven by a combination of two mechanisms: (1) The allowable accumulation of regulatory changes in genes of “major” effect that cause these genes to preferentially respond to similar selective regimes (Sucena et al. 2003; Prud'homme et al. 2006), thus creating a developmental

bias or constraint (Gould 2002), or genetic path of least resistance (Philippe et al. 2007). (2) At this point, developmental plasticity through genetic accommodation (West-Eberhard 2003) may further promote parallel evolution among species.

I propose that we term this special phase “mesoevolution” to represent both the patterns of parallel evolution and the distinct mechanisms relevant to it. Although I always hesitate to introduce new terminology, I am comforted that the term mesoevolution is not new (Dobzhansky 1954; Wray 2000; Moore and Woods 2006), and has been used in various contexts as shorthand for comparisons between closely related species, or specific time scales (10^5 – 10^6 years). Here, mesoevolution takes on a new and more important meaning. It is defined as a specific pattern and process in evolution that represents a transition between true homology and true convergence, as well as between micro and macroevolution. Microevolutionary forces within populations gradually form novel associations between regulatory genes of major effect, their networks, and adaptation of their corresponding phenotype to its environment. Once these novel associations are made, developmental bias or constraint through the activation of the same regulatory genes of major effect in similar environments is established and the conditions for mesoevolution are set. The constraints that have arisen during this transition to parallelism/mesoevolution will be reinforced, and will influence the evolution of truly convergent morphologies during macroevolution through the co-option of the same genes of major effect in response to similar selective regimes.

The study of mesoevolutionary processes requires that we continue to explore the developmental and genetic basis of parallel structures (Prud’homme et al. 2007), as well as to understand the microevolutionary forces that set up the developmental biases or constraints for mesoevolution to take place (Philippe et al. 2007; Tishkoff et al. 2007). We should be cautious, however, and adopt a hierarchical approach (Abouheif 1997; Abouheif et al. 1997) when studying mesoevolutionary patterns and processes. Independent gains and losses in morphology, embryology, and genes should be considered as separate levels when analyzing parallel features on a phylogeny. This permits a more open and rigorous analysis by allowing the possibility of alternative scenarios for the origin of parallel morphologies. Just as we allow for the possibility that homologous traits in closely related groups can be specified by different genes within a conserved network (Abouheif and Wray 2002), we should allow for the possibility that parallel morphologies be derived from the acquisition or loss of expression of similar or different genes. Evolutionary developmental biologists are at important crossroads in understanding the developmental and genetic basis of morphological evolution. A focus on patterns and processes of mesoevolution will help to break down the gap between micro

and macroevolution, and thus pave the way for a new evolutionary synthesis.

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