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Homoplasy: from detecting pattern to determining process in evolution, but with a secondary role for morphology?

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David Wake and colleagues provided a thought-provoking review of the concept of homoplasy through the integration, within a phylogenetic framework, of genetic and developmental data (Wake *et al.* 2011). According to them (p. 1032) "Molecular sequence data have greatly increased our ability to identify homoplastic traits." This is made clear, for example, in their flow chart for homoplasy detection (Figure 2, p. 1034), wherein homoplasy is discovered through the mapping of "traits of interest" onto a phylogram, a practice common in the molecular phylogenetic paradigm. The "mapping" is usually of morphological characters that are employed to support the chosen (molecular) topology, but which, as a consequence, do not themselves contribute to the formation of those topologies (Assis & Carvalho 2010).

Considering that the reason we study homology, homoplasy, and indeed phylogeny, is largely to understand the origin and transformation of morphological characters and their complexity, it is questionable to turn solely to a molecular phylogenetic analysis and exclude morphology from a more central role. We welcome all data relevant to uncovering hypotheses of homoplasy, including molecular. However, we do disagree with the secondary role in that process ascribed to morphology by Wake *et al.* Their perspective may lead to problems relative to the use of different kinds of data in support of hypotheses of relationship and character evolution. Once the main focus is restricted to genetics and developmental biology, morphological data (classical anatomy) may be interpreted as irrelevant for evolutionary studies. Furthermore, by stating that molecular sequences have greatly improved our understanding of the evolution of homoplastic traits, the authors appear to imply that molecular phylogenetic inferences are the best way of discovering morphological homoplasies and homologies solely through the mapping of traits of interest.

Our fears are well founded. A recent review showed that analyses of molecular data have, for most groups, supplanted morphological data in modern phylogenetic studies (Bybee *et al.* 2010). Nevertheless, morphologists cannot accept molecular phylogenetics as a solution to their problems; rather, it is a new problem to be tackled through morphological analysis itself. The study of the evolution of development is a promising approach supporting a deeper understanding of phenotypic evolution (Laubichler 2000, West-Eberhard 2003, Holland 2004). Indeed, a great deal of potential exists in *returning* our attention to the analysis of individual morphological characters and character systems rather than producing phylogenies, based on molecules, only to subsequently map morphological characters (Holland 2004, Nelson 2004, Rieppel 2004). It is in the context of analyzing individual characters that molecular genetics and developmental genetics stand to make their greatest contributions, possibly much greater than the role of molecular genetics in phylogeny reconstruction. In addition, to do justice to an integrative approach between developmental (morphological) evolution and phylogenetic systematics, data resulting from genetic and developmental studies, as well as those from classical anatomy, need to be appropriately incorporated in phylogenetic analyses. Only then can we assess their impact on the formulation of hypotheses of character evolution and phylogenetic relationships (Wheeler 2008, Assis & Carvalho 2010). In either context, morphology is both the beginning (the greatest questions to be answered) and the end (the interpretation of phylogeny).