# The evo-devo comet

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In his inspiring book *Ontogeny and Phylogeny* (1977), the late Stephen J. Gould explained why developmental biology and evolution, two essential domains of the life sciences, had diverged during the course of the twentieth century; both disciplines had to reach independently a platform of mutual understanding, a theoretical framework wherein concepts are understood and accepted by both parties. A step towards this goal was achieved in the 1980s with the discovery that animals not only share similar 'developmental genes', but also more integrated structural and functional aspects of their ontogenies (McGinnis *et al*, 1984; Akam, 1989). While these advances opened the door towards a molecular understanding of development, the analyses of gene expression in various species also allowed for the establishment of correlations between genetic activities and evolving forms.

This comparative approach triggered the emergence of novel animal models and generated a portfolio of concepts, which nowadays form the basis of a discipline sometimes referred to as 'evo-devo' (Wallace, 2002; Carroll, 2005; de Robertis, 2008). The frontiers of this field, however, are not clearly defined. Evo-devo research extends from simply 'PCRing' a trendy gene from a weird animal, up to the most sophisticated molecular genetic approaches dealing with the evolution of gene function and regulation. Yet the experiments are always within the general context of homology, as understood by using either morphological, functional or regulatory criteria, indiscriminately.

With our improved knowledge of the mechanisms underlying animal development, we can now address the question of natural variation; we have learnt, for instance, that rather limited sets of genes and signalling pathways are used over and over again, hence the development of most organs or structures relies on comparable rules. This, in turn, implies that developing systems have highly constrained roadmaps, the modifications of which lead generally to pleiotropic effects (Duboule & Wilkins 1998; Kirschner & Gerhart, 2005). This natural parsimony in the use of genetic tools makes it sometimes difficult to infer a conservation in function from the mere conservation of gene expression patterns—for instance, between two evolutionary distant animals—and thus calls for a deeper level of conservation to ascertain such phylogenetic relationships.

This issue can be addressed either by a thorough understanding of those regulations at work, assuming that a conservation of regulatory circuits demonstrates a common phylogenetic history, or by a large survey of various species, should we accept that a robust association between gene expression and a particular trait bears an evolutionary meaning. The latter point raises the paradox of model systems: that is, whether general conclusions can be extracted from given biological items, which themselves were often chosen for study owing to particularly well-adapted features, rather than for their elusive paradigmatic value. In other words, will we ever understand the full set of core principles by working exclusively with adaptive traits that intrinsically tend to distract from these rules? While this issue is somewhat theoretical, the popular idea that some species can display advantages over others, in terms of experimental benefit, indicates clearly that such questions have not yet been discussed in sufficient depth.

The lack of a clear definition of what evo-devo covers as a discipline is echoed by the difficulty to elaborate a commonly accepted set of guidelines, mostly owing to the conflicting *ménage* between developmental geneticists on the one hand, with their mindset inherited from T. Morgan and H. Spemann, and population (evolutionary) geneticists on the other hand, the direct descents of the new synthesis. In fact, we face a modern version of the classical dichotomy between variation—the 'how' question—and selection—the 'why' question—and we may wonder how long this productive relationship will last. While it might consolidate itself and lead to an integrated theory of evolution that includes the emerging mechanistic side, it could well split again into divergent trajectories, like a comet that returns closer to a planet every hundred years to fill itself with concepts and energy before leaving again for yet another journey.

Evo-devo is arguably a transitory discipline. We are witnessing the emergence of a new developmental biology, relying on high-throughput approaches, systems analyses and modelling to use gene (information) clusters, or even full genomes, as we currently use single genes. The accompanying shift in the required competencies—for example, bioinformatics, physics and maths—although of great interest mechanistically speaking, does not necessarily strengthen the link with the genetic framework of evolution. Also, we should remember that evolution and development are disciplines built on different epistemological grounds, which bring to their fusion an unstable equilibrium. Development is a science of recurrence; based on the assumption that the same process will happen again, in each generation, leading to results that we can predict. As such, it has a fixed timeframe. Evolution relies on the exact opposite premises; it is by definition a linear process, wherefrom recurrence is impossible. It has no clear timeframe and (so far) no predictable result. The former discipline explains how things happen, the latter how things most likely happened.

This theoretical antagonism might nevertheless become obsolete once the mechanisms of development are fully understood and once the computation of various ontogenetic roadmaps will discriminate the possible from the impossible, thus telling us which form could evolve out of a given species. This will primarily concern macroevolution, as micro-evolutionary phenomena are probably less constrained and, as such, more difficult to anticipate. If this were true, one should be able to predict with some accuracy the few alternative solutions offered to one particular species for the next million years, especially if environmental conditions can also be predicted. In such a scenario, the next *rendezvous* with the comet will turn evolution into a predictive science. This may indeed take another century.

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