

Emergence of Shape

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Published online: 17 July 2013
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Although the comparative study of morphology has for centuries been a viable intellectual pursuit, inquiry into the emergence of the form or shape of structures under scrutiny still often remains a disconnected endeavor. For example, during the 1970s and especially 1980s the guiding principle was Lewis Wolpert's (1980) "pattern formation" model, in which the focus was on positional information and variation in what William Bateson (1894) referred to as "repeated parts." For developmental biology, the notion of naïve cells being imbued with the potential to generate topology (i.e., three-dimensional structure and form, not to be confused with bacterial envelopes) from an extrinsic morphogenetic source (e.g., for teeth see Butler 1939, 1978) was challenged by the perspective that the emergence of structure and form was at least as much due to properties intrinsic to cells and between cells in time and space (e.g., Osborn 1978; Lumsden 1979).

Later in the 1980s and into the 1990s, the discovery in animals and then plants of homeobox genes and their roles in both generating positional information and affecting the development of repeated parts seemingly opened new vistas for understanding morphology and its use in systematics and phylogenetic reconstruction. For example, with the identification in insects (*Drosophila*) of the gene Antennapedia and its vertebrate orthologue, the HOX-gene family (Quiring et al. 1994; Halder et al. 1995; Mathers et al. 1997; Gehring 2002), comparative morphologists and developmental geneticists sought to produce diagrams of nested sets of clades on which ancestors with hypothesized regulatory gene activity producing different types of

appendages could be represented (e.g., Shubin et al. 1997). Although seen as generating theories of relatedness, these "analyses" and those thereafter (e.g., Shubin et al. 2009) first assume a phylogeny upon which developmental data are overlain and from which scenarios of "evolution" are then constructed.

The belief still persists that one can understand the emergence of structural and organismal shape from increasingly more detailed comparisons between entire genomes of different individuals of the same species and between different but presumably very closely related species (Krings et al. 1997; Noonan et al. 2006). The underlying assumption is that there are specific "genes for" specific structure and that a mere "tweaking" of a gene will easily convert one morphological configuration into another, even if the "gene" is developmentally regulated (Noonan et al. 2006). This, of course, is a false impression reminiscent of the lack and even dismissal by early 20th-century population geneticists of developmental biology in general and the nascent field of developmental genetics in particular (Morgan 1925, 1935; Dobzhansky 1941; Mayr 1942, 1965; Simpson 1952). Consequently, it was not only sufficient, but also reasonable to infer the existence of (unspecified) genetic factors underlying adult morphology from adult phenotypes alone. Yet we should recall Gavin de Beer's (1930) criticism of this notion in *Embryology and Evolution*. To paraphrase, while population genetics focuses on only two cell divisions, most important is the sequence of developmental events that leads to adult form. Clearly, especially in light of advances in developmental biology and the considerations of EvoDevo, de Beer's sentiment is remarkably sentient. Just because one can identify genes or molecular sequences as a result of advances in technology, this endeavor can no longer be embraced as adequate to understand the emergence of

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three-dimensional structure. Further, this myopia also overlooks entirely myriad aspects of, and constraints imposed by, the physical world that not only affect, but also profoundly impact development.

In this regard, we can turn, for example, to D'Arcy Thompson's (1917) suggestion in *On Growth and Form* that cell symmetry versus asymmetry as well as physical forces such as gravity might play crucial roles in shaping structure. To Conrad Waddington's (1940) hint in *Organisers and Genes* and Søren Løvtrup's (1974) recognition in *Epigenetics: A Treatise on Theoretical Biology* that breaking cell-symmetry coincident with gastrulation can lead at least in metazoans to a diversity of three-dimensional adult shapes. To George Oster and Pere Alberch's (1982) argument in the journal *Evolution* that differential effects of hydration on cells in conjunction with cell shape can profoundly alter developmental topographies and ultimately structure. And to various contributions, including those of the editors Gerd Müller and Stuart Newman (2003), in *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*, in which physical factors such as cell packing, adhesive interactions, and self-organization are centrally situated in theories of development.

In the spirit of these precedent-setting works, and with the generous financial, organizational, and structural support of the Konrad Lorenz Institute for Evolution and Cognition Research (KLI), I organized the 24th Altenberg Workshop in Theoretical Biology, which was held at the KLI September 23–26, 2010. The theme was “Emergence of Shape in Plants and Animals.” The articles in this issue, which derive from this workshop, capture the excitement of that coming together and, I believe, make clear the importance of keeping alive an intellectual environment that promotes and protects alternative thinking, especially in evolutionary biology.

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