

Modularity in Animal Development and Evolution: Elements of a Conceptual Framework for EvoDevo

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ABSTRACT For at least a century biologists have been talking, mostly in a black-box sense, about developmental mechanisms. Only recently have biologists succeeded broadly in fishing out the contents of these black boxes. Unfortunately the view from inside the black box is almost as obscure as that from without, and developmental biologists increasingly confront the need to synthesize known facts about developmental phenomena into mechanistic descriptions of complex systems. To evolutionary biologists, the emerging understanding of developmental mechanisms is an opportunity to understand the origins of variation not just in the selective milieu but also in the variability of the developmental process, the substrate for morphological change. Ultimately, evolutionary developmental biology (EvoDevo) expects to articulate how the diversity of organic form results from adaptive variation in development. This ambition demands a shift in the way biologists describe causality, and the central problem of EvoDevo is to understand how the architecture of development confers evolvability. We argue in this essay that it makes little sense to think of this question in terms of individual gene function or isolated morphometrics, but rather in terms of higher-order modules such as gene networks and homologous characters. We outline the conceptual challenges raised by this shift in perspective, then present a selection of case studies we believe to be paradigmatic for how biologists think about modularity in development and evolution. *J. Exp. Zool. (Mol. Dev. Evol.)* 285:307–325, 1999. © 1999 Wiley-Liss, Inc.

Biologists have long recognized that the evolvability of development is the key to morphological evolution. However, only recently has molecular genetics produced substantial characterizations of developmental regulatory processes and thus made it possible to analyze them comparatively. This has fueled resurgent interest in the evolution of development, but evolutionary developmental biology (EvoDevo) lacks a clear conceptual framework. Blithe attempts to apply classical comparative concepts to development lead more often than not to confusing or contradictory results. Furthermore the idea that one should focus on developmental mechanisms as units of evolutionary change begs the question, what constitutes a developmental mechanism?¹

Classical accounts of animal form concentrate on identifying morphological characters and on tracing their phylogenetic modification. The dichotomous notions of homology and analogy are implicitly predicated on a modular view of animal design; their ease of use is proportional to the ease with which one can identify the modules. Embryogenesis, too, consists of logically separable processes—gastrulation, establishment of body axes or morphogenesis of individual organs or appendages—and we take

for granted that logical separability reflects underlying modularity: the experimental study of development assumes that one may meaningfully isolate (physically or conceptually) and study individual processes independent from one another. Functional decomposability is thus a necessary presumption to considering developmental mechanisms either as units of explanation within de-

¹This essay arose from a workshop on modularity in development and evolution organized by the authors and Dr. Evelyn Fox Keller, held in September 1997 at the Friday Harbor Laboratories. In addition to the authors, the participants were Drs. Jessica Bolker, Richard Burian, Marie-Anne Félix, Scott Gilbert, Jason Hodin, Evelyn Fox Keller, Eli Moeir, Jay Mittleenthal, Lisa Nagy, Garrett Odell, Jarmila Kukalova-Peck, Louise Roth, Günter Wagner, and William Wimsatt. To the workshop proceedings and participants we owe much of the development of our thinking on the topics discussed in this essay and several of the examples discussed, and we are forever grateful to the participants for sharing their thoughts and collegiality both during the workshop and after. We express our appreciation to the Friday Harbor Laboratories, its staff, and director for a wonderful environment for a meeting. We are also especially grateful to Dr. Evelyn Fox Keller for encouraging us in these directions, for the idea of a workshop on modularity, and for providing the bulk of the funding for that workshop out of her own pocket.

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