Thinking about Developmental Evolution

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Source: BioScience, 52(11) : 1043-1044

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2002)052[1043:TADE]2.0.CO;2

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The Evolution of Developmental Pathways. Adam S. Wilkins. Sinauer Associates, Sunderland, MA, 2002. 603 pp., illus. $54.95 (ISBN 0878939164 cloth).

Adam Wilkins, the longtime editor of *BioEssays* and a geneticist by training, approaches the thriving field of evolutionary developmental biology (EDB, or "evo-devo") from the standpoint of molecular developmental genetics, a perspective shared by Carroll and colleagues (2001) and Davidson (2001). The genetic pathway, that is, the sequence of requisite genetic and molecular activities that underlie a developmental process, is Wilkins's organizing concept and proposed general framework for thinking about developmental evolution. His focus is specifically on "the nature of the genetic changes that underlie evolutionary alterations in developmental processes and on how those changes first translate into developmental ones, then spread in populations to create genuine evolutionary change" (p. xiv). Few authors have attempted to describe the connection between speciation and developmental evolution; Wilkins's exploration of this topic in chapter 12 is well done.

After a brief and well-referenced history of the disconnect between developmental biology and evolutionary biology, population biology and ecology, Wilkins sets the stage for integration in the first section of his book. Two chapters have as major titles "Information Sources for Reconstructing Developmental Evolution." The subtitle of chapter 2 is "I. Fossils" and of chapter 3, "II. Comparative Molecular Studies." A later edition of this book should provide a missing chapter: "III. Comparative Morphological Studies." A wealth of comparative morphological data formed the basis of many well-corroborated phylogenetic studies on both extinct and extant taxa. Hypotheses of specific changes in morphology at specific points and nodes in the history of a lineage are the legacy of this work; the nature and polarity of these changes form *the* starting point for comparative developmental molecular studies. Wilkins clearly appreciates morphology, however, and as is obvious from his expert use of phylogenetic logic and language throughout (e.g., discussion of basal vs. "ancestral" conditions), the context for all of his evo-devo considerations is phylogenetic.

I particularly enjoyed Wilkins' perspective (chapter 4) on the history and conventions of genetic pathway thinking and the conceptual evolution from pathways to networks. While a pathway is characterized by a single input and a single output, networks have multiple inputs and, frequently, multiple outputs. He points out that "in effect, pathway schemes tend to evolve into network models as more information is acquired" (p. 119). Understanding this data-generated shift in thinking in developmental biology, from strict linear and hierarchical terms to conception of developmental processes in terms of interactive networks, is fundamental, he notes, to developing a useful and predictive analytical framework for evolutionary developmental biology. From this perspective, evolutionary questions concern the nature of the genetic, molecular, and selectional events that shape and alter genetic pathways and networks.

Wilkins's aim is to demonstrate that the concept of the genetic pathway provides a useful framework for interpreting developmental evolution, and he is successful in this. The complexity, individuality, and generalities of genetic control in pathways and networks are illustrated by three highly detailed, molecular genetic case studies of evolving developmental pathways: sex determination in mammals and insects (chapter 6), segmental patterning in insects (largely *Drosophila,* with comparisons to other insects; chapter 7), and organ formation (nematode vulva and tetrapod limb; chapter 8). Although understanding such "baseline" molecular detail is requisite for evolutionary comparisons, these case studies are dense and lengthy (approximately 150 pp.).

The modular basis of developmental evolution has been a focus of EDB books (Raff 1996), symposia (Babbitt et al. 2002), and research (Mabee et al. 2002). Although Wilkins's emphasis on modules is not as central as Raff's (1996) or even Carroll and colleagues' (2001), the concept of modularity is extended to the promoter and enhancer elements in a readable and interesting chapter (chapter 9). Wilkins grapples with the paradox of conserved regulatory genes and diverse developmental outcomes, concluding that most of the highly conserved patterning genes act at intermediate steps in genetic pathways. Evolution of development pathways in large groups such as the Metazoa may be to a large extent a matter of evolved differences in pathway components surrounding conserved regulators. Chapter 10 discusses the process of gene recruitment and the way in which evolutionary forces that act on recruitment events may be rate limiting for developmental evolution.

In his chapter on morphogenesis, Wilkins points out the roles of gene products (extracellular matrix), cells, and the cell cycle in determining the products of morphogenesis, growth, and pattern formation. In this way, he links molecular genetics to much of the previous top-down, evo-devo thinking and developmental biology done at a primarily cellular level. Though Wilkins addresses the Cambrian explosion and the controversy surrounding the rapid evolution of the diversity of metazoan body plans (chapter 13), he does not focus on this issue. The final chapter, "The Coming Evolution of Evolutionary Developmental Biology," addresses the technological advances that continue to drive the field of molecular genetics and now evo-devo. The new

"quasi-genetic" tools are of particular revelance to those of us who are most interested in the development and evolution of nonmodel systems.

Wilkins characterizes EDB as a field that still lacks an analytical framework, that is, an interpretive structure, although it possesses key ideas (e.g., about functional conservation and gene recruitment) and is immensely rich in observations and data. He proposes the concept of genetic pathways and networks as a useful framework for interpreting all evo-devo changes.

One immediate question that is raised concerns the nature of ancestral pathways and networks. Ancestral character state reconstruction or "optimization" of homologous modules in gene networks (i.e., methods that hypothesize the condition of the ancestor) may be addressed using phylogenetic methods, but these are not discussed. Reconstruction of the sequence of ancestral and descendant gene regulatory networks is, however, the ultimate goal of EDB. The pathway framework is potentially a powerful one for representing the universe of developmental genetic changes that have occurred in animal and plant evolution. The widespread adoption of pathway and network representation as a form of universal pictorial language for mapping evolutionary changes in development would permit much readier comparisons—and ultimately generalizations—than are possible without it. Nevertheless, these too must be optimized for a given phylogeny for an explicit and predictive view of the evolution of development.

Wilkins takes a relatively comprehensive look at the lively field of evo-devo. His molecular developmental perspective is extended and connected more successfully to the fields of population genetics and evolution than perhaps are any previous attempts. This well-referenced (1500 references) book is accessible to researchers in the fields of population biology, ecology, paleontology, systematics, and evolution who are seriously interested in broadening and updating their understanding of molecular developmental biology. It is appropriate for a graduate seminar course, but it is most likely beyond the grasp of most undergraduates.

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