

Book Reviews

The Evolution of Developmental Pathways

By Adam S. Wilkins. Sinauer Associates, Sunderland, Massachusetts. 2002.

Adam Wilkins's new book *The Evolution of Developmental Pathways* is a very timely and monumental guide to the rapidly growing field of evolutionary developmental biology. The principal thesis of the book is the notion that genetic pathways and networks provide a much-needed framework for an analytical approach to evolutionary developmental biology. The book begins with an extremely useful and sobering historical account of the fields of embryology and the strong mutual neglect between embryology and mainstream evolutionary biology. It then introduces the foundations of the field by discussing the types of data available and presenting prevailing ideas about animal development.

Wilkins captures our attention by provoking combinations of topics or case examples throughout the book. Developmental evolution in sea urchins and frogs (especially the skipping of larval stages in some lineages) is discussed side by side with the origin of the craniate head, as well as sex determination systems across phyla with segmental patterning in insects, and the development of nematode vulva (22 cells total) with that of very diverse tetrapod limbs. Throughout the book the combination of classical embryology, fossil data, and comparative molecular analyses clearly demonstrates that the time for evolutionary developmental biology has come. The goal of integrating genes, molecules, growth, and form within a single developmental system seems finally achievable. Students and researchers in need of an inspiring break from their highly focused research,

be it biased toward whole organism or intracellular signal transduction, will welcome the panoramic view provided by Wilkins.

Wilkins defines a genetic pathway as "the underlying causal chain of gene activities that propels a particular developmental process." The book is really about the paradox between conserved regulatory genes and diverse developmental outcomes. One proposed solution to this paradox is the modularity of many pathways, and especially certain of their elements, such as upstream enhancers. Many enhancers are semi-independent in function, which allows them to be used for large numbers of genes and genetic pathways. As such, these form perfect material for evolutionary tinkering (or "bricolage"). The modularity of regulatory genes such as *HOX* genes likely explains why these genes play such major, yet different, roles in the development of insects as well as vertebrates. Wilkins argues convincingly for their dual role of patterning and control of cell proliferation. The generation of new enhancer elements allows the recruitment of genes to existing pathways; such recruitments also depend on the "capture" of transcription factors by the new enhancers. The multiplicity of controlling elements upstream of expressed genes and the delicate balance between activating and inhibiting transcription factors represent a situation rife with evolutionary potential. Even a slight tweaking of one of the elements in such systems is likely to lead to different outcomes for the organism.

Examples for such expanding pathways are discussed. Some involve upstream recruitment, others mainly the downstream addition of steps. Yet other pathways may evolve by intercalating new elements, leading to genetic networks, whenever the newly recruited

gene also happens to be part of another preexisting pathway. The importance of gene duplication in generating families of diversifying genes from which such gene recruitments become possible is thoroughly discussed. Such gene families also provide substantial functional redundancy, which may be crucial in both increased precision for gene dosage and lowering the cost of novel gene recruitment.

Wilkins's new book instills a tremendous sense of wonder in the reader. Refreshingly, the author keeps stressing the unknowns, and rather tellingly he devotes more than one third of the book to "conundrums." These include the nature and degree of genetic variation necessary for allowing developmental evolution, the nature and extent of constraints on such evolution, and the respective roles of physical forces and genes in producing morphology. The genetic changes underlying speciation remain poorly characterized, but there are a few candidates, such as the transcription factor "bric-a-brac" in *Drosophila melanogaster*, which is known to affect mate choice by the regulation of sexual dimorphism in females. The book ends with three open questions: How do novelties arise? How do microevolutionary processes differ from macroevolutionary processes? What are the factors determining rates of developmental evolution?

Wilkins convincingly does away with the simplistic view of genetic pathways as linear hierarchical sequences under the control of "master genes." He also wisely warns against simplification and does an excellent job elaborating on the complexity underlying the development of even relatively simple structures such as the nematode vulva. Among the few omissions from this book is the absence of a discussion of post-translational

modification. Despite the brief mention of glycosyltransferases of the *fringe* family and the mention that the cell adhesion molecule NCAM is heavily glycosylated, there is no discussion of the large additional complexity created by glycosylation and other posttranslational modification such as sulfation of glycosaminoglycan chains. Many posttranslational modifications involve genetic pathways of their own, and different animal phyla differ in the kind of posttranslational modifications they carry, such as the high prevalence of sialic acids in deuterostomes contrasted with their virtual absence in all other bilateria. A discussion of the potential of proteomic studies accompanying the promises of DNA array approaches would have been helpful. Similarly, considering the crucial importance of enhancer evolution, I looked in vain for a discussion of the role of transposable elements (TE) and endogenous retroviruses for shuffling enhancer sequences toward novel target genes.

Apart from said omissions and minor errors such as the feminization of Cuvier's book *Le Règne Animal* and the recurrent point mutation in Susumu Ohno's name, the book is simply fantastic.

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