Bold yet austere

The Evolution of Developmental Pathways, (2002) Adam Wilkins. Sinauer Associates, Sunderland Massachusetts. 603 pp. Hardcover $54.95 ISBN 0878939164

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The field of Evolutionary Developmental Biology (EDB or Evo-Devo) has certainly accomplished a right of passage in the last year. With the publication of Carroll et al.'s *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*, Davidson's *Genomic Regulatory Systems—Development and Evolution*, and the subject of this review Adam Wilkins' *The Evolution of Developmental Pathways*, all written within a year or so of each other, the field of EDB has reached a defining moment. Is it good news or bad? In my opinion not since Lewontin's 1974 book *The Genetic Basis of Evolutionary Change* has there been such a clear and truly synthetic description of the limits and boundaries of a new field in evolutionary biology. While the three EDB books are quite different in head-to-head comparison, in combination they compliment each other much like the three seminal publications that defined the New Synthesis in the middle of the last century (Dobzhansky's *Genetics and the Origin of Species*, Mayr's *Systematics and the Origin of Species* and Simpsons's *Tempo and Mode in Evolution*). While the Carroll et al. book is for a broad audience and Davidson's volume is more for the technically advanced, Wilkin's book is in essence a textbook, written in a style that grabs the reader and keeps the attention. He builds from first principles in all chapters and the book is crafted to teach and to lead the reader through the fields of evolution and development. I intend to use this book as a text for evolution courses but it is also important to note that Wilkins has written a volume that adeptly synthesizes evolution and development as well as the Carroll et al., and Davidson volumes.

Wilkins has divided his book into three major parts. The first part gives the reader the context and foundation for examining evolution and development, a second part examines several now classic case studies in developmental pathway evolution and a third part called "Conundrums" discusses several unanswered evolutionary questions that Wilkins deems approachable through the synthesis of developmental biology and evolution. The book begins with a brief history of the study of embryology and evolution. In this chapter, the author describes the dichotomy that existed between evolution and development all through most of the twentieth century. The schism or "fracturing of the mirror" between the two fields is described and explained in detail and the early glimmers of the field of EDB are described. The final four chapters in the first part of the book describe how developmental and evolutionary information can be collected, manipulated and used in concert to examine problems in EDB. In particular, there are lengthy discussions of developmental model systems, techniques for the study of developmental pathways, the conservation of genes involved in development and, most importantly for this reviewer, phylogenetic or systematic approaches. Most EDB work to date with very few exceptions utilize phylogeny or an evolutionary context to guide the choice of interesting and important taxa or neat developmental questions or, in the case of fossils, to fill in gaps of our knowledge of the kinds of forms that are possible. In other words, most studies have approached the field and data of EDB so as to hang the ornamentation of development on the tree of life. As Wilkins discusses in the second chapter of the book—this is not enough. Wilkins has presented a detailed approach to understanding the history of life through phylogenetic analysis and the analysis of ancestral character states. The phylogenetic approach to understanding the history of life is well presented in this book, with an appendix included on cladistic methods for the totally uninitiated. However, the direct application of the phylogenetic approach of ancestral character state reconstruction to most studies that would call themselves EDB have not taken this approach, probably because it is still too early in the field's existence. The result of this early ontogenic stage of the field of EDB is that taxon sampling and the amount of character data needed to adequately test hypotheses using the phylogenetic approach are too few to really make it worth it. On the other hand, several examples of successful use of ancestral character state reconstruction are discussed in detail very nicely by Wilkins. Among these are Greg Wray's analysis of the evolution of direct development in sea urchins (which by the way occupies a prime position on the cover of the book), Paula Mabee's analysis of tetrapod limb evolution and Nipam Patel's examination of insect segmentation. While the number of studies like Wray's, Patel's and Mabee's will increase in the future, it is important to note that Wilkins has presented a clear and concise description of how the application of phylogenetic methods to the understanding of the evolution of developmental pathways might be done.

The second part of the book comprises three chapters, all of which look at specific case studies in developmental pathways and how these can be used in studies of evolution. The developmental pathways that were chosen as topics for this part of the book are now classic topics. Each has the

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similarity of having long and storied traditions in genetic and molecular background, with more recent forays into expanding taxon knowledge about the pathway. Sex determination, insect segmentation, nematode vulval formation and tetrapod limbs are all appropriate and great subjects for discussion in the classroom when the subject of EDB arises and Wilkins has clearly and concisely treated all four. This middle part of the book is a great example of Wilkins' ability to start with first principles and build from these to teach about development and evolution and their synthesis. The pathways involved are described in detail and, where necessary, techniques and background embryology are utilized to present a clear picture of the network. Next, the organismal sampling and comparative data are presented and this is followed by a synthesis of the information in an evolutionary context.

The third part of the book is about conundrums that exist in evolutionary biology that Wilkins feels can be approached by integrating evolution and development. Wilkins has indeed created a lineup of some of the most difficult and important questions in evolutionary biology, which include the origin of genetic source material for the evolution of novel systems, the concept of constraint, the developmental evolutionary genetics of morphogenesis, speciation in the context of development and the origin of complex body plans. The final chapter of the book centers around three questions critical to the future of EDB. (1) How do developmental novelties arise in evolution? (2) How do macroevolutionary processes differ from microevolutionary processes? (3) What factors determine rates of developmental evolution? More importantly Wilkins points to new methods of collecting data and what needs to be done in the future. The answer from Wilkins is simple but well made, and that is we need to collect more data, more rapidly and more directed to EDB questions in order to push the field forward. In this sense Wilkins brings us full circle with the last six chapters of the book. Remember that the first chapter of the book is a description of the ''cracking of the mirror'' or schism of evolution and development for most of the twentieth century. The final part of the book on conundrums makes it abundantly evident that evolution and development cannot exist separate of each other.

One final comment is appropriate for this review with respect to the historical approach of this book. About the only, even slightly irksome aspect of the historical version of evolution and development presented by Wilkins is his entirely positive depiction of Etienne Geoffroy Saint Hillaire. I mention this aspect of his historical treatment only because the Cuvier–Geoffroy debate has been resurrected by several scientists and historians as a potential lesson for modern EDB studies. While Wilkins makes it clear that Geoffroy's bold ideas about transmutation were more in line with evolutionary thinking than Georges Cuvier's hard line approach, I feel that neither Cuvier nor Geoffroy can be looked upon as guiding lights for this new field of EDB. To understand my sentiments here, we must realize that Geoffroy was criticized by Cuvier for straying from the ''school of facts'' as Toby Appel so clearly details in his 1987 book, *The Cuvier–Geoffroy Debate*. In essence, while Cuvier was guilty of being too austere, dogmatic and entrenched in an authoritarian approach to science, he criticized Geoffroy for having no real methodology to prove his bold ''school of ideas''. What is interesting here, and what Wilkins has clearly defined for the reader in this book is a way to be both bold and austere in our approach to EDB. The boldness comes from examining the important and unanswered questions in evolutionary biology from a developmental perspective. The austerity comes from transforming the developmental data into characters that can then be used to test hypotheses about the history of life in a phylogenetic context.