BOOK REVIEW

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A review of *From DNA to diversity: molecular genetics and the evolution of animal design* by Sean B. Carroll, Jennifer K. Grenier, and Scott D. Weatherbee

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From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design. Carroll, S. B., Grenier, J. K., Weatherbee, S. D. 2001. Blackwell Science, Malden, MA. 214 pp., color illustrations, bibliography, index. $44.95. ISBN 0-632-04511-6.

> Finally, it may even be possible that, freed from the trammels and fetters of the theory of recapitulation which have so long confined thought, the whole of the animal kingdom may appear in a new light, more homogeneous and compact than had been imagined, and with gaps between its major groups less formidable and perhaps even bridgeable. *Embryos and Ancestors* (de Beer 1951)

It is half a century ago this year that Sir Gavin de Beer closed his book, *Embryos and Ancestors*, with the above prediction. Today we find ourselves knowing more about what makes animals similar than what makes them different. Why is the anatomy of a mouse different from that of a rat, a frog, or a mollusc? The realization that the answer can be found in embryonic development is not new. Darwin knew that embryos harbor clues to the evolutionary history of species, and Bateson suggested that a genetic approach would uncover the source of morphological variation. Naturally, both were correct. Today evolutionary developmental biologists are betting that the latest revival of the evolutionary-embryological-genetic synthesis will unearth the causes of evolutionary novelties. Thus far, comparative studies of the genetic control of embryonic development have thrown up far more examples of conservation than innovation. Examples of evolutionary conservation are so commonplace that we are no longer surprised by reports of orthologous genes controlling development of fly and mouse organs. So, wherein lie the differences?

This question is at the heart of the evolutionary developmental biology. Armed with molecular biology and new technology, evolutionary developmental biologists are revisiting ancient zoological questions and getting answers in the form of mechanisms. With the revolution in full swing, a new generation of biology students wants to train in the integrative field of "evo-devo." Just in time for next semester comes a textbook designed with these students in mind. In *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*, Sean Carroll, Jennifer Grenier, and Scott Weatherbee take us on an exciting tour of the field, beginning with the evolutionary history of animals and ending with a discussion of regulatory evolution as the "creative force underlying morphological diversity." Along the way, the authors cover the molecular genetics of animal development (neatly split into two chapters entitled "The Genetic Toolkit for Development" and "Building Animals"), molecular evolution, developmental evolution, and mechanisms for evolving morphological novelties. I had high hopes for this book and it did not disappoint. The authors have produced an outstanding text in which the complexities and logic of molecular development reveal the pathways by which evolutionary change may be generated.

The concept of a genetic toolkit is central to this book. The biggest surprise in comparative developmental biology has been the discovery that the bodies of distantly related animals, often with radically different forms, are constructed using the same sets of genes. These genes comprise the genetic toolkit. The toolkit is introduced early (Chapter Two) and becomes a pervasive theme. It is an elegant device for explaining the molecular mechanisms of development and developmental evolution. The logic of *Drosophila* is used to develop the genetic toolkit concept, and the "tools" are classified according to their function in building the fly body. Homeotic genes get the most attention (deservedly), and the description of their structure, expression, organization, and function is excellent. Maternal, pair-rule, and segment polarity genes are given clear, simple introductions, which set the stage for a discussion of gene expression.

This book overflows with colorful and striking images of the primary data (much of it from Carroll's own lab), which illustrate the beauty of embryonic development. The inclusion of actual data (rather than over-simplified schematics) wherever possible should also smooth the students' transition from textbooks to the primary literature. Shaded boxes are used to demonstrate how data are generated at a practical level. For example, one box describes the process by which toolkit genes are isolated and identified in different animals (URLs are listed for several major databases). Another describes gene regulation, and the tests used to define terms such as *necessity* and *sufficiency*. Throughout the text, important new terminology is highlighted and defined in a brief but effective glossary at the back.

With the nuts and bolts of animal development described in Chapter Three, the authors move on to the evolution of developmental mechanisms (Chapter Four). Here again the toolkit takes center stage, as the evolutionary history of gene families is covered. The bilaterian toolkit is the product of gene duplication followed by functional divergence, in which new functions are acquired and/or existing functions are divided among larger numbers of genes (subfunctionalization). When these events are mapped onto a phylogeny, a historical picture of genome evolution emerges. In a clear "case study," the *Hox* complex serves as an exemplar of gene duplication and divergence followed by large-scale gene and genome duplications. These illustrations of dynamic genomes reveal the processes that lead to chromosomal synteny and functional diversification.

Molecular evolution is brought to bear on development in the chapters on anatomical diversification (Chapter Five) and evolution of novelties (Chapter Six). Big questions abound as the discussion covers exciting recent discoveries, such as how evolving developmental programs resulted in the vertebrate brain, the limbless abdomen of insects, the butterfly eyespot, and the chordate notochord. This discussion, with its emphasis on *how* one goes about addressing evolutionary developmental questions, should lead students to ponder not only the specific questions covered here but also the uncharted territory in animal evolution. This highlights one of the most important contributions of this book; it is not just a catalog of facts and discoveries, but a guide to the practice of evolutionary developmental biology.

In the final chapter, entitled "The Primacy of Regulatory Evolution," the reader is treated to a rich discussion of the mechanisms by which developmental programs evolve. Carroll, Grenier, and Weatherbee explore the relationship between molecular evolution and phenotypic variation, and they make a good case for regulatory evolution as the business-end of developmental evolution. *Cis*-regulatory elements are therefore revisted, this time within the context of regulatory DNA sequence evolution and its effect on developmental control genes. A growing body of evidence indicates that changes to the regulatory elements that direct spatial and temporal dynamics of gene expression are a real mode of morphological evolution. Although toolkit genes are widely distributed throughout the animal kingdom, the regulatory control of toolkit genes is highly specific. Important phenotypic differences among metazoa can indeed be accounted for by differential regulation of toolkit genes and their targets. Regulatory evolution underlies the modular control of developmental fields and has allowed single genes to be differentially expressed in, for example, fore- and hind limbs. Regulatory evolution is clearly a powerful mechanism of phenotypic evolution. Several potential pathways for *cis*-regulatory sequence evolution are discussed, giving the reader a sense of how developmental evolution can occur.

As in the preceding chapters, case studies feature prominently here, and, importantly, microevolution is not overshadowed by macroevolutionary examples. Some of the nicest work in this area has been carried out on the *cis*-regulatory element that controls the second of seven stripes of *even-skipped* (*eve*) expression in *Drosophila*. In different species of *Drosophila,* variation exists in the sequence of the *eve* stripe two element, but the function of the element has been conserved, illustrating how stabilizing selection can act to conserve function in the face of sequence evolution. Lessons such as this emphasize another major strength of this book; with such a broad and multidisciplinary field to cover, depth and detail have not been sacrificed.

Carroll, Weatherbee, and Grenier have produced a wonderful and exciting introduction to the field of evolutionary developmental biology. Their account of the field is lucid and rich with examples, and they avoid the pitfalls of so many introductory texts, which tend to provide an overview without getting into the juicy biology. Newcomers and aficionados will find this a compelling read. These are early days for the molecular rebirth of evolutionary development, but the molecular bases for the "gaps between (the) major groups" are already becoming "less formidable and perhaps even bridgeable." Gavin de Beer would be pleased.

REFERENCES

deBeer, Gavin R. 1951. *Embryos and Ancestors*, revised edition. Oxford University Press, London.