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THE SHAPE OF THINGS TO COME?[1]

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Review of *Evolution*, by Nicholas H. Barton, Derek E. G. Briggs, Jonathan A. Eisen, David B. Goldstein, and Nipam H. Patel. 2007. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY. xiv + 833 pp. Cloth. $100. ISBN 978-0-87969-684-9.

An evolutionary perspective now permeates the literature in all of biology, from ecology to molecular biology. Consequently, the scope of evolutionary biology is becoming increasingly broad. This trend presents a serious challenge for teachers of evolutionary biology. Although we can still justify a central role for evolution by citing Dobzhansky's claim that "nothing in biology makes sense except in the light of evolution," we can also turn things around and argue that nothing in evolution makes sense except in the light of [all of] biology. Dobzhansky's claim about the importance of evolutionary biology was based on his belief that structure and function (what things are and how they work) can be fully appreciated only in the context of understanding how they came to be the way they are. What he wrote in his provocatively titled essay (Dobzhansky 1973) was: "Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts, some of them interesting or curious but making no meaningful picture as a whole."

Today, the pile of sundry facts has grown very large, and many of these facts influence directly how we think about the evolutionary process. Dramatic growth in the breadth and depth of biological knowledge has uncovered an array of new structures, functions, and interactions that require explanations of how they came to be. At the same time, our increasingly sophisticated understanding of biological mechanisms allows more complete explanations of the process of evolutionary change. Learning (and teaching) evolutionary biology, therefore, must be an iterative process.

As teachers, we can present the broad outlines of variation, inheritance, descent with modification, and natural selection without relying on a detailed knowledge of ecology, behavior, physiology, genetics, or molecular biology. After all, Darwin had no clear understanding of the mechanisms of inheritance, let alone the molecular basis of heredity, and yet he was able to publish a compelling discourse on the fundamental principles of evolution, principles that have endured for 150 years. But to describe the detailed mechanisms that produce adaptation and diversification, we do need an intimate knowledge of all of biology.

For example, to explain variation in beak size and shape in Galapagos ground finches, we start with observations of phenotypic variation in natural populations (Lack 1947). We then show that the variation is heritable, demonstrate that patterns of variation depend on presence/absence of presumed competitors for food (seed) resources, record single generation changes in the proportions of birds of different sizes and correlate them with the size spectrum of seed resources, document that changes in beak shape also drive the evolution of song, and finally show that expression patterns of the genes *Bmp4* and *calmodulin* appear to determine aspects of beak shape and therefore may be targets of selection (Boag 1983; Gibbs and Grant 1987; Grant 1999; Podos 2001; Abzhanov et al. 2004, 2006). For a student to fully appreciate this story, which reveals the continuity of thought from Darwin to modern developmental genetics, she must have an appreciation of foraging ecology, competition for limiting resources, trait heritability, role of song in species recognition and mate choice, and how patterns of gene expression are responsible for the unfolding of developmental programs and determination of adult form and function. She would also do well to understand the geological history of the Galapagos Islands.

Historically evolutionary biology has been viewed as the "sister discipline" of ecology and behavior (most academic institutions in which the basic biological sciences have been carved up into multiple departments combine evolutionary biology with ecology, behavior, or "organismal biology"). Of course, evolutionary biology has intimate ties to all biological disciplines, and increasingly genetics, genomics, development, and molecular biology are providing insights into the detailed mechanisms of evolutionary change. The pace of discovery in these disciplines has quickened substantially in the past few decades. Molecular tools allow high resolution views of patterns of variation and patterns of descent. Knowing the details of genome structure, gene regulation, and protein structure and function imposes constraints on our models of evolutionary process and mechanism. The sophisticated student of evolutionary biology will need to learn these details to appreciate what is really meant by "descent with modification." Does new variation usually arise through base substitutions or are transposable elements significant players in generating new genotypes and phenotypes? How important for phenotypic evolution are "structural" changes in gene products versus changes in cis-regulatory elements that affect levels of gene expression and therefore the amounts of those products? What is the source of epigenetic modifications, how do they persist, and what consequences do they have for mapping of genotype to phenotype? Why are genomes apparently so much larger than they "need to be"—are they full of junk or selfish DNA or are we simply ignorant of the function of much of this excess DNA?

Given the increasing importance of molecular biology in resolving questions about evolution (and the increasing importance of evolutionary thinking in explaining observations at the molecular level), it is no surprise to see a new textbook that focuses on the interface between the two disciplines. *Evolution*, by Barton, Briggs, Eisen, Goldstein, and Patel, claims that it "is unique in integrating molecular biology with evolutionary biology." The claim is certainly true; this evolutionary biology text is unusual in its emphasis on molecular biology (including genomics and developmental genetics). Traditionalists will surely be surprised to discover that Chapter 2 deals with "The Origin of Molecular Biology," that the structure, expression, and phenotypic effects of *Hox* genes (and especially the Drosophila *Ubx* gene) occupy 20 pages of text whereas extinctions (including mass extinctions and their causes) are covered in 2 pages, that vulval development in *C. elegans* gets more space than punctuated equilibrium, and that biochemistry, but not biogeography, is in the index.

The book has many strengths. The prose is crisp and explanations are rigorous but clear. The authors do not hesitate to discuss complex ideas or to provide appropriate caveats about the certainty of our knowledge. The Figures are useful and abundant (although I wished that references for the data presented in figures were included in the captions, rather than in notes at the end of the book). The expertise of the authors in quantitative, population, and developmental genetics is obvious; explanations are often less formal than in other texts, but at the same time are more sophisticated and more intuitive. The chapters on diversity include a detailed but engaging introduction to the genetics and genomics of bacterial and archaeal diversity, the origins of multicellularity, and the evolution of novelty inferred from both fossil data and from developmental biology. Although I had assured myself that I would not read the text word-for-word, I found myself deeply immersed in many chapters and read them from beginning to end. The material was not new (for me), but the descriptions and explanations seemed fresher and more compelling than in other current evolution texts. The explicit focus on questions at the molecular level determines the use of examples throughout the text, but these examples come from basic biology, not biomedical science. This book will be particularly attractive to molecular biologists who want to learn the details of evolutionary pattern and process. It may also be the book of choice for evolutionary biology graduate students with interests in population genetics, "evo-devo," and molecular evolution. Introductory undergraduate evolutionary biology courses (in the United States) will find the book too demanding, although advanced courses and dedicated students should certainly consider it.

The book also has some limitations (all books do). Perhaps most obvious to me are issues surrounding what material is included in the book and where certain topics are introduced. There are many ways to teach an evolutionary biology course; some instructors begin with the details of evolutionary process, and then proceed to discuss patterns at the micro and macro scales. Others (and I include myself in this group) prefer to begin by introducing students to the evidence for change over time (earth history, fossils, and phylogenies) and only then discuss process and mechanism. Although the basic structure of *Evolution* reflects the second approach, the emphasis on molecular biology gives the book a unique character. For example, Chapter 2 provides an excellent introduction to molecular biology and its history, but there is no corresponding introduction to ecology or behavior, disciplines that traditionally have been closely linked with evolutionary biology.

Part II is a lengthy discussion of biological diversity, beginning with the origin of life, tracing diversification within bacteria and archaea, and then examining the origin and diversification of eukaryotes. The second chapter in Part II introduces some very basic concepts, e.g., descent with modification, evolutionary trees, homology, convergent and parallel evolution. These essentials may not get the attention they deserve, given that they are embedded in a larger section that focuses more on "molecular facts" (bacterial and archaeal genetics and genomics, origin and evolution of the nuclear genome, origin of multicellularity, evolution of developmental programs). Chapter 10 ("Diversification of Plants and Animals") departs from the molecular focus and traces the history of the fossil record and what we learn from it. It is very well done, but personally I wished for a more substantial treatment of these issues. There is minimal discussion of earth history, and no introduction to stratigraphy. Fossils (and what we know of them) are essential elements in evolutionary explanations, and if molecular biologists are to become educated evolutionary biologists, then they should learn more about interpreting and dating fossil material. As alluded to above, "macroevolutionary" topics in this chapter (e.g., extinctions, punctuated equilibrium) are treated only briefly, perhaps because the authors assume that molecular biologists do not need to or want to think about these issues.

Part III focuses on the genetics of the evolutionary process, on mutation, recombination, patterns of variation, random drift, and natural selection. Again, the emphasis on molecular biology is evident, but this emphasis does not distort the presentation of evolutionary process or compromise the clarity of the explanations. Examples tend to come more often from genetic model organisms (flies, worms, bacteria) and less from natural history. This contrasts with most other evolution texts and may generate angst in some teachers and students.

Finally, I take issue with the authors' claim that "remarkable developments [in molecular biology] are scarcely reflected in the way that evolutionary biology is taught" (p. xi). Many of us who currently teach evolutionary biology highlight the impact of recent and dramatic advances in molecular biology. And other texts, although not exclusively dedicated to the integration of molecular and evolutionary biology, have included major sections on gene and genome evolution and developmental genetics. Most evolutionary biologists will acknowledge that the details uncovered by molecular biologists are contributing to more refined explanations of evolutionary pattern and process. But in our excitement to uncover these details, let us not lose sight of the fact that observations of change over time, diversity in form and function, and differential survival and reproductive success in natural environments, remain the starting points for integrating a "pile of sundry facts" into a coherent and meaningful whole.

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