Animal Evolution: Genomes, Fossils, and Trees

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contemporary genetic differentiation, common garden data to estimate adaptive differences, and theoretical simulations to investigate the impact of evolutionary factors influencing adaptive differentiation (Q_{ST}). Nichols and Neale give a general introduction to the molecular genetic approaches used to map genes of adaptive significance (QTL or quantitative trait loci), and then summarize all the known studies that have identified these genes in relevant animals and plants. In a similar vein, Zamudio and Harrison discuss the evolutionary consequences of hybridization in endangered species, summarize all the studies of hybridization in endangered and nonendangered species, and then discuss the implications. Finally, Ivy and Lacy provide a useful introduction to the genetic management of captive breeding programs and then demonstrate how molecular data can be incorporated into them.

Several of the examples deserve mention. In particular, Schall and her coauthors present research on the origin of weedy rice in Thailand; Devlin and Sundström discuss the impact of transgenes on growth in Pacific salmon; Ritland discusses the "Spirit bear," a rare white black bear; and Busch, McCreight, and Waser discuss their long-term studies on the banner-tailed kangaroo rat.

Molecular Approaches in Natural Resource Conservation and Management should provide readers with a good introduction to a number of topics in conservation genetics. As the editors suggest, this volume could be useful to "academics interested in conservation genetics, molecular ecology, and the quantitative genetics of wild organisms." The editors also state that the book could serve as a "text for graduate ecology/genetics courses but also, perhaps, in advanced undergraduate courses." In my opinion, however, a more thorough introduction to conservation genetics can be found in the coordinated and comprehensive treatments of the field from several textbooks now available, namely *Conservation and the Genetics of Populations* (Allendorf and Luikart 2007) and *Introduction to Conservation Genetics, 2nd ed.* (Frankham et al. 2010). On the other hand, some of the chapters present detailed information and examples that would not be found in a textbook and provide more advanced coverage of specific topics. In other words, I generally liked the book and the diversity of topics, but it is not a textbook and it is also not largely composed of "original" articles. Only in specific reviews that bring together summaries of research does it provide articles that are likely to be cited and later used.

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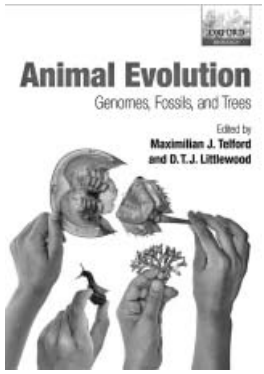
A BIRDS-EYE VIEW OF ANIMAL EVOLUTION

Animal Evolution: Genomes, Fossils, and Trees. Maximilian J. Telford and D. T. J. Littlewood, eds. Oxford University Press, 2009. 264 pp., illus. $80.00 (ISBN 9780199570300 paper).

Animal Evolution: Genomes, Fossils, and Trees is the latest synthesis of data assembled from paleontology, molecular systematics, and developmental biology to help readers answer the big questions of metazoan evolution. The book falls into a long and distinguished line of past volumes emphasizing one or another aspect of the big picture of animal evolution and development: books such as *Genome Evolution* (edited by Gaby Dover and Richard Flavell, 1980), Stephen Jay Gould's *Wonderful Life* (1989), Claus Nielsen's *Animal Evolution* (1995), and Sean Carroll's *From DNA to Diversity* (2001). In a very real sense, Maximilian J. Telford and D. T. J. Littlewood's *Animal Evolution* is a mix of all of these. In 18 chapters the book surveys the latest discoveries and controversies surrounding the relationships among metazoan lineages, when they diversified, and what this can tell us about the evolution of morphology and development. Or, as the summary more succinctly states, "Arguably, there is one underlying common quest that unites the goals of individual researchers [of animal evolution]: the search for homology—recognizing it, defining it, and using it."



Animal Evolution is one of the best recent examples of integrative biology I've read. The book's major methodological approaches—paleontology, phylogenomics, and morphogenetic studies of animal development—emerge not only from the diversity of individual chapters and researchers but often as a dialogue within individual chapters. A high degree of collaboration is evident: 13 of 18 chapters are multiauthored and the chapters often include researchers from departments of molecular

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biology alongside museum curators. There is an earnestness to the book; this new incarnation of the field seems not yet comfortable ruminating about cosmic issues such as macroevolution and punctuation. Instead, each chapter focuses on the nuts and bolts of animal evolution, mapping out the tree of life for metazoans and explaining the implications for morphological evolution. One senses here that the first applications of genome-scale data sets and gene expression patterns to metazoan phylogenetics are combining fruitfully with the foundation that continues to be laid by paleontology. A high value is placed throughout the book on hypothesis testing and on the weight of evidence for or against competing ideas. To be sure, for every clarification of an ancient controversy that the field has experienced in recent years, several new controversies have sprung up. Such are the hallmarks of a field brimming with new data and creative energy.

The book is organized into three parts: the origin of animals, the Bilateria (which includes most animals), and "Themes and Perspectives." Nearly every chapter is written by one of the heavy hitters in the field, starting with an opener by Graham Budd outlining the paleontological and environmental setting for the earliest fossil animals. Budd concludes that "Cambrian life is different, but not alien," thereby subscribing to the view that most Cambrian fossils (including the famous Burgess Shale Lagerstatten) can, in fact, be assigned to modern phyla. Budd reviews the controversy surrounding the role of oxygen in the origin of metazoan life, expertly summarizing both the paleoenvironmental and biochemical pros and cons. He notes that some metazoans fare quite well in low-oxygen settings, making use of little known anaerobic pathways. According to Kevin Peterson and colleagues in another chapter, if the Ediacaran period gave rise to forms whose taxonomic affinities are difficult to pin down, we can nonetheless be more certain that this period served as the cradle of diversification of lineages giving rise to extant metazoan diversity. The authors update their molecular estimates of divergence times in the metazoan tree and conclude that the major period of diversification falls squarely in the Ediacaran, consistent with interpretations of at least some fossil taxa.

A major theme throughout *Animal Evolution* is the frequency of reversals, loss of traits, and convergence in animal evolution. We learn, for example, about the plausibility of multiple origins of the anus, a hypothesis that can help explain its high diversity of form in Bilaterians. Rudy Raff provides an authoritative review of the two hypotheses of the origin of larval forms: the Haeckellian idea that the earliest animal forms were planktonic and similar to modern larvae (probably not correct) versus the idea that the first animal forms were bilaterian and that larvae have evolved multiple times convergently (a hypothesis favored by recent phylogenetic and developmental studies). Loss and simplification of morphological structures also appear to characterize the evolution of tunicates; ditto for crown group echinoderms. I was surprised to learn that loss and simplification also characterize evolution at the molecular level throughout metazoans. Various lineages such as tunicates have lost *Hox* genes, for example. In another twist, the presence or absence of microRNAs (miRNAs) in a genome may comprise a very promising new type of phylogenetic character—one that can be easily characterized using next-generation sequencing approaches and that evolves quickly enough to provide much needed phylogenetic resolution. Nonetheless, occasional loss of miRNAs from a genome can complicate the picture. Thus, there are numerous points in animal phylogeny where the simple-to-complex progression that is often assumed is reversed or otherwise undermined.

The book does an excellent job of engaging the reader with the big phylogenetic controversies, of which there are many. An ongoing debate arises as to the validity of various clades. An example is the Ecdysozoa (including arthropods, nematodes, and many other groups), an important clade of molting animals defined in the late 1990s, which seems to be holding its ground with the onslaught of larger phylogenomic data sets. We learn that a slew of papers questioning this clade likely suffered from insufficient taxon sampling, leading to systematic errors.

A more tenable new hypothesis is the paraphyly of sponges, with some lineages being more closely related to eumetazoans than to other sponges. This arrangement could have serious implications for useful models for the origin of multicellularity, as we learn from the contribution by Nicole King and colleagues, who favor instead a tree with sponge monophyly and choanoflagellates as the closest outgroup. The paradigm of the "tree as roadmap" and the close connection between phylogeny and hypotheses of transformation have rarely been clearer. In another example, Andreas Hejnol and Mark Martindale discuss gastrulation and the origin of the anus and blastopore. Here, placement of acoel flatworms at the base of the Bilateria (just outside the nemertodermatids) is another possible, but as yet unconfirmed, hypothesis on which this and many other potentially novel morphological transformations rest.

If many of the terms of metazoan development and evolution mentioned in the book are baffling to you (e.g., amphistomy, homoscleromorph, enteropneust, and the list goes on), then you are among those who, like me, will lament the absence of a glossary. *Animal Evolution* is beautifully published with many fine illustrations, but its impact on the broader audience of biology will be compromised without a glossary (the omission of which is likely a casualty of swiftly publishing the proceedings of a conference as a book). Those of us whose working days are spent using a narrower or just different lexicon must be satisfied with the wonder conveyed by the mere sounds, imbued as they are with a depth and history to the field unmatched by few areas of evolutionary biology. Still, I

learned a lot from this book, and I look forward to the next decade of integration of genomics, paleontology, and development.

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