REVIEW

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Missing Links: Evolutionary Concepts and Transitions through Time. Robert A. Martin. Jones and Bartlett, Sudbury, Massachusetts. 303 + xvi p.

Reading this compact, well written, and informative little book, I found myself frequently checking the title. Is the main subject here really evolutionary transitions? It seems instead to be a broad and very good introduction to paleontological evidence and inference in general, with a strong emphasis on modern evolutionary biology that includes insights from speciation, population biology, genetics, and even evo-devo. Of course, Martin focuses heavily on some of the ''big changes'' in vertebrate history, such as the origins of mammals, birds, tetrapods, whales, horses, and hominids, and provides some great first-hand explanation of his specialty, arvicoline rodents. But any general reader might pick it up as a good place to start learning about paleontology as a science—including some of the important questions and examples involved in the problem of the evolution of major adaptations.

To begin with, let's consider the targeted audience for this book. Jones and Bartlett have been developing a nice little list of what we might call ''anti-textbooks'': books for the general reader and the classroom that are briefer, hipper, and better written than many of the mass-produced, committee-designed tomes that students are forced to buy and lug around in their knapsacks. Martin's book fits the former category. His audience is the students who don't already know a lot about paleontology and biology, but are interested. Some might even have a background that leaves them suspicious of or even hostile to evolutionary concepts. Many of those students, if they are open-minded, however, should be won over by his engaging prose and frank explanations. With a few reservations, noted below, this book would be excellent for freshman courses and seminars and to recommend to people who just want to know what evolutionary biology, particularly paleontology, is all about.

For the benefit of these potential readers, it seems particularly useful that Martin gives extensive attention to the various hierarchical levels of evolution (micro, macro, and speciation), even though he concentrates on paleontology. As most American colleagues know, anti-evolutionists in this country object less to changes in gene frequencies and populational components (elements of microevolution they regard simply as noise in the system), than to evolution in the long run, which can only be studied in the fossil record. So it is good that someone knowledgeable in the field has written an accessible book that will give these readers a competent introduction.

The entire first third of the book, in fact, covers the basics of microevolution, speciation, ecology, and classification. The rest of the book is about specific evolutionary transitions (noted above). The prose is clear and the examples are laid out well. Fans of fossil invertebrates (excepting a brief discussion of the Burgess Shale fauna) and plants are sadly out of luck with this book, however: it's pretty much vertebrates all the way down. On the bright side, if students can get into the vertebrate examples discussed here, maybe some will plumb deeper into other phyla and kingdoms. That would be good for a number of reasons, only one of which is taxonomic breadth.

A more important reason, perhaps, is that the vertebrate record is far poorer than the invertebrate record. Among vertebrates, we may see abrupt transitions more often than among invertebrates, because fossiliferous sections frequently preserve many invertebrate specimens situated in precise stratigraphic position. As a result, changes in lineages, whether directional or wobbly, tend to be better documented. And the much greater diversity of fossil invertebrates makes them amenable to better quantification of evolutionary trends and events.

Where does that leave us with the vertebrate record? One reason why cladistics took hold sooner among vertebrate than invertebrate workers may be that the vertebrate record is more incomplete. It made sense to look for synapomorphies to link taxa that have relatively different morphologies. Long, relatively complete series of transitional vertebrate forms were elusive, especially at lower taxonomic scales. More often, invertebrate workers could see related species (even whole communities) succeeding each other through time; so it might have seemed less necessary to try to construct cladograms when the actual evolution was seen so well in the rocks. (In recent years this view seems to have changed, however.)

This brings us to a very important distinction in tracing lineages. The title of this book is *Missing Links.* I have seldom, if ever, heard a professional paleontologist refer to any specimen as a ''missing link.'' In most respects, paleontology largely gave up the literal search for ''missing links'' decades ago. (Here, by ''missing links'' I mean transitional forms, direct ancestors, specific critters that fill gaps in lineages.) So, in a book intended for students who don't know much about the subject, why focus on an outmoded concept?

Yet this focus may not be outmoded. Paleontologists constantly discover organisms that are nothing like those alive today, with mosaic features that help us understand how life evolved piece by piece. They are ''missing'' from the living world and provide great insight into evolution's past. But how do we analyze this evidence?

When anthropologists discuss ancestors, they separate them into *direct* ancestors, such as parents and great-great-great-grandparents, and *collateral* ancestors, such as uncles, great-aunts, and cousins twice removed on the mother's side. When the concept of ''missing links'' is broached, many people get the idea that paleontologists are looking for *direct* ancestors, a concept that can seldom be realized. (The specimens of *Archaeopteryx* seem to have no features that bar the taxon from direct ancestry of more derived birds. But did they contribute to the gene pool of today's robins and nuthatches?) A fifteenth-century cemetery in Jutland, or the bodies of the ''Bog People'' that are so beautifully preserved, need not include the direct ancestors of today's Scandinavians in order to give us a good idea of the characteristics of those past populations. And so it is with fossils. Paleontologists are not looking for transitional *forms*; we're looking for transitional *features.*

And here's where cladistics comes in. (Those colleagues who eschew phylogenetic systematics may wish to skip the next paragraphs.) Cladistics is all about transitional features, because phylogenetic analysis identifies newly evolved characters that are shared by the descendants of a common ancestor. We may not know that ancestor, but we find its traces in its descendants who share the features inherited from it. At some point, feathers evolved, teeth became only deciduous, lungs functioned in respiration, hooves struck hard ground. These are derived changes. We use them to understand the sequence by which the parts of complex adaptations are assembled in macroevolution.

So it was disappointing to find only one cladogram in the whole book (and even sadder, it was from my own work). By a cladogram (and not a tree or phylogeny) I mean a diagram that links taxa by the possession of synapomorphies that are graphically represented. These diagrams have been tremendously useful in

providing and testing hypotheses of evolutionary change in lineages. The book's narrative explains some transitions among vertebrate groups, but there are no other graphic representations of them, so students will have to memorize evolutionary details without seeing their hierarchical distribution on trees, or the frequent coincidence of many lines of evidence that test and support explanations of change. The use of phylogenetics generally does not get high priority in this book; cladistics is contrasted with ''phenetics'' (by which the author conflates two schools: the ''evolutionary school'' of Ernst Mayr and his colleagues, who stressed the use of both genealogy and similarities; and numerical taxonomy, which used mensurable, similar features with no emphasis on genealogy), but there is no sense that the advances in understanding the relationships of organisms in the past two decades and more have come almost entirely from cladistics. I regard this as a disservice to students, because at some point the public will have to learn how systematic biologists actually do their work, and it has long been through cladistics. Why shouldn't they learn from books like this one?

This brings us to another missed opportunity. In the beginning of the book the author provides an excellent discussion of what science is, how it differs from other kinds of human endeavors, and how it depends on method. But from that point, there is no sense of how scientists use systematic methods to resolve questions about the origins of major groups that involve hypotheses with very different predictions. So, for example, in this book dissenters from the generally accepted and very well-documented view that birds evolved from theropod dinosaurs are permitted simply to disagree that the characters used in these phylogenetic analyses are good ones, and that pretty much neutralizes the argument for Martin's readers. There is no sense of the fact that said dissenters have never produced a single cladogram supporting any other result than the fact that birds are theropods, nor that they seem in their works to deny all testable methods for reconstructing phylogenies. There are other such examples in the book. After all that has been written on this topic, this is a shame. Also disappointing is that there is no attempt to distinguish two very different sorts of problems that are approached in different ways and that, when kept separate, are critically useful in cross-testing hypotheses. Those problems are the origins of taxa and the origins of adaptations, a distinction made by George Lauder and others over two decades ago. In this book, whether the discussion concerns basal tetrapod relationships (vs. the emergence from water), the origin of mammals (vs. the transformation of jaws and ears), or the evolution of whales (vs. changes in skull, backbone, hips, and environments of deposition), questions of phylogenetic relationships and ecological transitions are conflated. The result is a good paleontological narrative, but not an instruction in paleontological methods that would convince a skeptical student that we are not just making up stories—if that student learned from the beginning of the book that methods (not just interpretable evidence) are the heart of science.

This book is bound to do a great deal of good, and I very much look forward to a second edition that could bring students up to date with the methods of our field, and not only their narrative results. The phylogenetic diagrams of amniotes, tetrapods, and other taxa are misleading in parts (to take one example [p. 54], the amniotes are represented as an unresolved pentatomy, and half the diapsid groups are not included in Diapsida), and it would be good to have consistent, nonparaphyletic use of taxonomic names. Other small points could be discussed. There is considerable evidence for clade selection (p. 59); parsimony does not allow you to conclude that the simplest classification is most likely to be the most biologically ''real'' (p. 78); Van Valen's second law does not say that extinction rates are constant, but that the probability of extinction within a clade is stochastically constant regardless of the age of the taxon (p. 95); *Longisquama* is not a theropod (p. 158); *Rahonavis* is not a composite (p. 160); *Presbyornis* is not a transition between shorebird and duck (p. 161); definitions are not diagnoses (p. 167); ''early'' and ''late'' are not the same as ''basal'' and ''derived'' (p. 169 *et passim*); and there is no evidence that the premaxillary glands of *Eusthenopteron* secreted poison, as far as the Extant Phylogenetic Bracket or any independent evidence indicates. Finally, the text needs much more stringent definitions of terms such as ''fish,'' ''tetrapod,'' ''reptile,'' ''mammal,'' and so on. Whereas it is true that these words have been used in different senses by various authors, some senses are clearly more useful or accepted than others, and nonspecialists may be excused for being easily confused by variation in professional practice, especially when they may be asked to explain these concepts on exams.

Not all colleagues will find the issues discussed here problematic, and students will benefit very much from having this book in their hands. I expect to refer students to it often, because it contains a lot of information (though few references) that nearly any scientist and student will find new and useful. However, some colleagues may wish for a more up-to-date synthesis of methods and evidence, which the author is certainly well qualified to provide in a second edition if demand warrants. The reality is that an increasing proportion of trained professionals in our field—and most others in comparative biology—begin asking questions about evolutionary events by using the methods of phylogenetic systematics. More of these professionals—especially younger colleagues—will find a book useful if it integrates cladistic methods and results with evolutionary narratives.

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