An Incipient Synthesis

Patterns and Processes of Vertebrate Evolution. ROBERT L. CARROLL. Cambridge University Press, New York, 1997. xvi, 448 pp., illus. $85 or £70, ISBN 0-521-47232-6; paper, $39.95 or £24.95, ISBN 0-521-47809-x. Cambridge Paleobiology, 2.

In 1968, Alfred S. Romer, the dean of American vertebrate paleontologists, produced a slim volume called *Notes and Comments on Vertebrate Paleontology* to accompany the third edition of his classic textbook *Vertebrate Paleontology*, published in 1966. Romer used his supplement to provide background, examine controversies, and generally deepen the standard textbook presentation.

In 1987, Robert Carroll updated Romer with his own textbook, *Vertebrate Palaeontology and Evolution*, which has since become the standard of the field. Now he has followed it with a not so-slim volume that examines how the vertebrate fossil record tells us about the interplay between micro- and macroevolution. But Carroll's new book is to Romer's sequel as *Star Wars* is to *Flash Gordon*. To write this book, Carroll has plunged into several fields of biology that are (in recent tradition, at least) uncommon pursuits of vertebrate paleontologists, including genetics, development, and molecular biology. What ensues is a thoroughly integrated approach to understanding both the patterns of vertebrate morphology and to using those patterns, particularly as seen in the fossil record, to illuminate questions of how organisms actually evolve.

One reason this book should be valuable to nearly all vertebrate biologists is simply that extinct animals provide us with a broader spectrum of evolutionary possibilities than we can get from the living world alone. For example, Carroll examines Barnosky's microstratigraphic studies of sub-Recent rodent molars as a closely controlled time sequence of morphological change, its rates, and its wanderings over geologically short (but biologically long) intervals of time. He examines how Caldwell's studies of ontogenetic ossification sequences in ichthyosaur limbs might tell us about both the establishment of homological identifications of these elements and the pathways by which limb development evolves. And he compares the rapid evolution of species flocks in cichlid fishes of the African Great Lakes with those in semionotid fishes of the rift lakes of the Newark Supergroup during the Late Triassic and Early Jurassic.

Carroll uses these and many other examples to weave a tapestry with a particular warp and woof. He seems almost to return to the views of G. G. Simpson (to whom the book is appropriately dedicated) and others who forged the Modern Synthesis of evolution in the 1930s, that all large-scale patterns in the fossil record can be explained simply by upward extrapolation of genetic processes seen in living populations. But today's genetic processes are not limited to those known in the 1930s, and Carroll is making a much more sophisticated argument based on quantitative genetics, developmental genetics, Hox genes and homeoboxes, and a wealth of even more sophisticated studies of the vertebrate fossil record. He concludes that some major evolutionary transitions—the evolution of flight, the movement to land, the repeated returns to water—happened so quickly (on a geologic scale) that we may never fully resolve their timing and sequence of morphogenetic change. But our stratigraphic constraints on the amount of time that such major changes took are often becoming clearer, and the times are surprisingly short. Carroll sees this quite reasonably as testimony to the ability of the developmental program to respond quickly to evolutionary opportunities, given the plasticity of complex behavior shown by most vertebrates. These patterns are repeated so often in the fossil record that we must infer that they are basic to the evolution of vertebrates.

On the other hand, Carroll is not persuaded that morphological stasis, as argued by Eldredge and Gould's theory of punctuated equilibria, is predominant in the vertebrate fossil record, and he doubts that there is much in the way of true macroevolutionary processes, except perhaps those of plate tectonics, mass extinction, and other external forces operating on a scale of 105 years or greater. I would tend to demur. In most cases in the vertebrate fossil record, we simply do not have large enough samples with tight enough temporal and stratigraphic control to tell much about stasis, punctuation, and gradualism. Different characters change at different rates, and for different reasons. The size and shape of rodents and their molars may be as closely attuned to climate as are the same features in marine foraminifera. It is often difficult to get a clear reading from independent lines of evidence that may test these apparent patterns. And I do think that the patterns of clade diversifications, of selection and sorting at supraspecific levels, have pointed us to better insights about how certain groups of organisms may intrinsically evolve. Certainly these changes have their bases in genetic and populational processes, but there is much more to it than that, and the larger scale patterns could not be predicted solely from observations of populations and their genetics, as Carroll explains. Support for many of these insights has come from phylogenetic analyses, which are surprisingly rarely incorporated into Carroll's arguments.

This book marshals a tremendous amount of information integrated from many historically disparate fields that are just beginning to realize that they need each other. It is in my view the most important book in vertebrate evolution since Simpson's *Tempo and Mode in Evolution* (1944), because of what it offers as a summary, an integration, and above all a prospectus for vertebrate biologists of a new synthesis that is showing all signs of a very healthy infancy. Our next generation of scientists would do well to train themselves as Carroll has done in order to fulfill his vision of what integrative vertebrate biology can become.

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Vignette: An Official Duty

I received a visit from M. de Buffon this morning . . . . I like men who are very confident of their talents. He is the head of the Académie Française and, in that capacity, has the responsibility for three or four reception speeches, a cruel chore. What to say of a M. de Limoges? What to say of a M. Watelet? What to say of the dead and the living? Moreover, he is not allowed to offend them by scorn; he will have to praise them, and he said: "So be it! I will praise them, I will praise them well, and I will be applauded. Does an eloquent man find any subject sterile? Is there anything about which he does not know how to speak?"

—*Denis Diderot* (1760), as quoted by Jacques Roger in *Buffon: A Life in Natural History* (Cornell University Press)