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PATTERNS AND PROCESSES OF VERTEBRATE EVOLUTION, by R.L. Carroll, 1997, Cambridge University Press, Cambridge, $85.00 (cloth), $39.95 (paper)

A century ago, vertebrate paleontologists such as Edward Drinker Cope and Henry Fairfield Osborn actively promoted their own, somewhat idiosyncratic ideas of evolution, based on their knowledge of the vertebrate fossil record. Fifty-five years ago, George Gaylord Simpson published *Tempo and Mode in Evolution*, which tried to show that the vertebrate record was consistent with the newly emerging Neo-Darwinian synthesis. Since that time, however, vertebrate paleontologists have not been major players in paleontologically-inspired debates over evolution (especially macroevolution and the punctuated equilibrium-species sorting debates). Although the vertebrate fossil record is not as dense and continuous as that of many invertebrates, our superior understanding of many living vertebrate groups would seem to be a solid foundation for important insights into evolutionary principles. When vertebrate paleontologists have been participants in the evolution debates in recent years, they have mostly played a reactive role, defending

Simpson and Neo-Darwinism against the challengers.

Thus, it is an important (and long overdue) event when a prominent vertebrate paleontologist such as Robert L. Carroll (whose 1988 tome, *Vertebrate Paleontology and Evolution*, is considered the successor to A.S. Romer's definitive text) examines the vertebrate record for its implications for evolution. As the dedication to Simpson indicates, however, Carroll's background and biases are on the conservative side, with a skeptical bias against many of the newer developments in evolutionary theory. This is particularly apparent in his criticisms of the punctuated equilibrium/macroevolution debate. In his first chapter, he introduces basic ideas about macroevolution, and points out that Darwin was wrong "in extrapolating the pattern of long-term evolution from that observed within populations and species" (p.8). In the next chapter, he concedes that "species that show little variability were obviously both common and long lived. Fossils showing transition between species are rare and confined to short stratigraphic intervals. Few well-studied examples from the record of fossil invertebrates show a pattern of evolution such as that predicted by Darwin, with gradual and progressive change within and between species over long periods of time" (p. 26). It would seem from these statements that he has just agreed with the basic ideas of punctuated equilibrium. Yet later in the chapter, he trots out the tired old arguments about incompleteness of the fossil record (ignoring the fact that stasis can be detected even in an incomplete record), the difficulty in assessing the relative prevalence of punctuation and gradualism (ignoring many recent examples that survey entire faunas), and the complaint that there is no mechanism to explain the long-term stability of species (which is not a liability, but a major challenge suggested by the macroevolutionary debate - conventional mechanisms of homeostasis, such as balanced polymorphism, or environmental stability, are insufficient to explain the stability of species over millions of years through well-documented climate changes).

He devotes the entire third chapter to reviewing examples of microevolutionary changes documented in living species (especially the Galapagos finches). Finally, in the fifth and sixth chapters, he discusses the patterns of evolution in the vertebrate record. Unfortunately, he confines his discussion primarily to late Cenozoic mammals, citing the summaries of Barnosky (1987, *Current Mammalogy* **1**:109-147), Martin and Barnosky (1993, editors, *Morphological Change in Quaternary Mammals of North America*, Cambridge University Press) and Barnosky *et al.* (1996, in *Paleoecology and Palaeoenvironments of Late Cenozoic Mammals*, edited by K.M. Stewart, University of Toronto Press). Carroll focuses on the few examples of gradual, anagenetic changes documented in these studies, while the clear message from their surveys is that the majority of Pleistocene mammals that have been studied show either stasis or random non-directional changes that result in no net change or new species. When these cases are added together, non-directional change or stasis far outweighs gradual change in Pleistocene mammals. More importantly, the classic Neo-Darwinian studies he cites in Chapter 3 are about gradual change in direct response to climatic changes. What Carroll fails to notice is that even the directional changes in Pleistocene mammals are not correlated with the frequent climate changes through the Ice Ages, and most species show no directional change through multiple climatic cycles. As Barnosky (1994, *Historical Biology* **8**:173-190) put it, " climatic oscillations on the multi-millennial scale may not stimulate speciation much."

Nor is it true that the Pleistocene is the only densely continuous, high-resolution mammalian record that could be studied in the macroevolution debate. The Eocene-Oligocene White River Group of the High Plains is equally dense and continuous on a timescale of less that tens of thousands of years, and can also be correlated with well known global climatic changes. Prothero and Heaton (1996, *Palaeogeogr. Palaeoclim. Palaeoec.* **127**:239-256) surveyed the entire White River Chronofauna over a 20 million year span of strata and found only a handful of gradual changes, and stasis in over 170 lineages. More importantly, those few gradual changes, and almost all the episodes of speciation and extinction documented in this interval do not coincide with known climatic events. In fact, during the largest climatic event of the Cenozoic (as documented by plants, soils, snails, reptiles and amphibians), 62 out of 70 lineages of mammals continue unchanged, clearly demonstrating that climatic change does not drive evolution or speciation in mammals.

Stasis is also prevalent in other areas where dense, continuous records of mammals have been documented, such as the early Eocene Bighorn Basin of Wyoming. Detailed monographs by Bown (1979, *Mem. Geol. Surv. Wyoming* **2**:151 p.), Schankler (1980, *Univ. Michigan Pap. Paleont.* **24**:99-114), and Gingerich (1989, *Univ. Michigan. Pap. Paleont.* **28**:97 p.) have shown that stasis is prevalent among most of the taxa during this interval (despite papers which feature the few apparent examples of gradualism). Although not that many complete faunas have been adequately surveyed, some exceptionally well sampled lineages, such as horses, are replete with examples of stasis and bushy, branching speciation (MacFadden, 1992, *Fossil Horses*, Cambridge Univ. Press). Instead, Carroll focuses on the gaps between lineages, and the few examples of anagenetic changes within lineages (p. 69).

In the next chapter, Carroll reviews the record of Pleistocene reptiles and amphibians, and must concede that they showed enormous stasis through the Ice Ages. But then he tries to dismiss this fact with the *ad hoc* statement that "this, however, can be seen as but one end of a spectrum of rates of changes, with certain mammalian groups on the other. It in no way supports Gould and Eldredge's assumption that most species are incapable of phyletic evolution" (p. 118). But if gradualism is rarer than Carroll admits, and reptiles and amphibians show nothing but stasis, then the spectrum is clearly weighted heavily toward stasis. This is exactly what Gould and Eldredge predicted.

Once these contentious issues have been covered, Carroll does an excellent job of reviewing many of the newer developments of evolution as exhibited in the vertebrates. Chapters 8 and 10 examine the issue of evolutionary constraints, but Carroll does not connect this to the issue of stasis in species. Chapter 9 summarizes conventional population genetics, which seems somewhat out of place in a book which focuses on mostly macroevolutionary issues. Carroll is at his best when he discusses the many exciting discoveries in development and embryology (Chapter 10), including the revolutionary implications of homeotic genes. Yet he fails to make the connection behind many of

these studies - that large-scale homeotic changes are just the kind of macroevolutionary, "hopeful monster", leaps in morphology that would lead to new species without gradual change. Such macromutations would explain the major changes in evolutionary *Baupläne* without intermediates, and their long-term stability since the major phyla and classes first appeared. He writes (p. 263) "it is not possible to demonstrate that changes brought about by mutation in developmental systems have never produced significant jumps from one phenotype to another. Many large gaps are known between the morphology of ancestral and descendant lineages, but most can be attributed to the absence of appropriate fossil-bearing beds in the intervening period". That's an *ad hoc* way to explain it, but such large homeotic changes would occur so rapidly (possibly even in a single generation) that not even the best fossil record would ever sample them. In this case, the support for the homeotic mutant-hopeful monster model would not come from the fossil record directly, but is supported by the prevalence of rapid changes followed by periods of stasis, and also by arguments about the prevalence of such changes in the living fauna, and the inviability of many intermediate forms (Frazzetta, 1975, *Complex Adaptations in Evolving Populations*, Sinauer).

The book concludes with reviews of the many excellent examples of evolutionary transitions now becoming better documented in the vertebrate record (particularly the origin of tetrapods, birds, mosasaurs and whales). The final chapter discusses major examples of evolutionary radiation in the vertebrate record, and briefly summarizes (but does not critique) research on plate-tectonic effects on evolution, and the mass-extinction debates. Unfortunately, the latest data on mass extinctions change so fast that this section has become dated already.

In summary, Carroll has written a provocative book that would be valuable for evolutionary biologists and paleontologists who wish to review the current understanding of vertebrate evolution. However, the reader should be aware that Carroll approaches the more contentious issues with Simpson-colored glasses, and sees very little merit in most of the evolution debates, because he misses the central points of the arguments, or sees only the cases that support his biases. A book such as this demonstrates that vertebrate paleontologists have too long been away from the "high table" and have been relegated to a role as minor players in the macroevolution controversy. Yet the quality of their fossil record is sufficient that vertebrates should have a much greater say in how we view evolution in the future. Hopefully, future vertebrate paleontologists will take up this challenge.

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