

BOOK REVIEWS

PALAEOECOLOGY AND PALAEOENVIRONMENTS OF LATE CENOZOIC MAMMALS. TRIBUTES TO THE CAREER OF C. S. (RUFUS) CHURCHER, edited by Kathlyn M. Stewart and Kevin L. Seymour, 1996. University of Toronto Press, Toronto, 675 pp. ISBN 0-002-0072-87. Price US \$75.

In an age of proliferating scientific publications, one of the most problematic media is the scientific festschrift or memorial volume. Patched together from the contributions of scientists who happen to have been influenced by the person to whom the work is dedicated, such volumes are usually less than satisfactory. They tend to be hodge-podges of unrelated papers of variable quality and significance, frequently without much peer review. These weighty, expensive tomes sell very few copies, because most scientists do not find enough useful papers in them to justify the high cost. Publishers hate to print volumes of this type, since they almost never break even, let alone turn a profit. A lot of good science is ignored when it is published in a festschrift or memorial volume.

Fortunately, this book, organized on the occasion of the retirement of C. S. "Rufus" Churcher from the University of Toronto, is an exception. The editors and many of the 53 contributors were students of Churcher or they were strongly influenced by him, so their work tends to reflect his longstanding interests. Of the 30 papers in the book, 21 concern Pleistocene mammals. There are so many important and original contributions here that specialists in this field will definitely want to own the volume. Nine chapters relate to late Cenozoic mammals of Africa. These will be of interest to those who work on the homeland of hominids. Most papers in the book are highly technical studies of Pleistocene mammalian faunas, or the systematics of specific groups of Pleistocene mammals. A number of papers yield more general conclusions that will interest paleontologists outside this field. Since there is not space here for a detailed discussion of all 30 contributions, I will focus on a few papers with wider implications.

In recent years, a number of paleontologists have used the excellent data base of Pleistocene mammals to assess the evolutionary roles of punctuated equilibria and phyletic gradualism. Pleistocene mammals occur in large sample sizes over large geographic areas, with stratigraphic detail that offers better than 100,000 year resolution, all during a period of rapid climatic fluctuation between glacial and interglacial cycles. Under such conditions, it should be possible to see whether or not climatic fluctuations cause gradual phyletic evolution, as Neo-Darwinism has long predicted. The results of such studies have been mixed at best. Barnosky (1987) documented a few cases of phyletic gradualism, but also many cases of stasis and punctuation. Similar results were obtained by the studies published in a recent book edited by Martin and Barnosky (1993). In the volume under review, Barnosky et al. conclude that the response of mammalian faunas to the glacial-interglacial transition that occurred 425,000 years ago was a complex one. It does not follow simple models of response to climate change, or even resemble the last glacial-interglacial transition, 10,000 years ago. Martin describes what he calls a "stepped anagenetic pedomorphocline" in late Pleistocene muskrat evolution. Carroll reviews several recent studies, conceding that stasis has been documented in a majority of Pleistocene mammalian lineages, and even more so in Pleistocene amphibians and reptiles. Nevertheless, he feels that the hard-line Neo-Darwinian position has not been challenged. Apparently, Carroll has missed the point of much of the debate. The argument is no longer over whether punctuation or gradualism occurs (they both do), but rather over which is more prevalent (stasis and punctuation, counter to Carroll's gradualistic bias). More importantly, the prevalence of stasis during well-documented Pleistocene climatic changes challenges a fundamental Neo-Darwinian assumption: that species are infinitely flexible, changing in response to selective pressures of their environments. Such flexibility may be true of Darwin's finches or fruit-flies in a bottle, but the overwhelming conclusion of studies of the fossil record, over the past 20 years, shows that most fossil species are static through millions of years and remarkably unresponsive to environmental changes. Nowhere is this more dramatically demonstrated than in the Pleistocene. If species were "rolling balls" on an "adaptive landscape" (to use popular metaphors), they should change with every major glacial-interglacial cycle. *But they don't!* Instead, they are static through climatic changes, responding (if at all) by migrating with their preferred climatic zones, not by speciating or changing their morphologies. If ever there were strong evidence that something is wrong with the prevailing Neo-Darwinian view of micro evolution and macroevolution, the mammals of the Pleistocene provide it.

Akersten examines another interesting evolutionary phenomenon: the few surviving members of a once-diverse clade tend to be very specialized and

atypical of the history of the group. These are what Akersten calls "oddball survivors." Tree sloths are atypical of the long history of mostly ground-dwelling sloths. The living coelacanth is very aberrant compared to the extinct coelacanths. Living monoplacophorans and *Nautilus* have many characteristics that are atypical of their lineages, making them poor analogues for their extinct relatives. Akersten concludes that if groups go through "diversity bottlenecks," the odds are good that survivors will be oddballs, because they are less vulnerable to key environmental factors that controlled more typical members of the group during their heyday. Such an hypothesis seems reasonable, but another comes to mind: oddballs may seem that way only because survivors come in such small samples, and their survival could be due to chance. Before we take the phenomenon of "oddball survivors" seriously, looking for deterministic, causal explanations, a quantitative study is required. How many "living fossils" are there, and how many of them qualify as "oddball survivors"? It may turn out that the few striking "oddball survivors" are not representative of the totality of living organisms representing once diverse but now nearly extinct groups. If so, this "phenomenon" may rest on our biased perception of the outcome of a series of random accidents.

A number of the chapters focus on particular stratigraphic units or faunas. Pinosof examines the poorly understood Sangamonian interglacial (75 to 125 ka) and summarizes its known fauna from all over North America. Karrow et al. conduct an integrated stratigraphic study of the Fort Thompson Formation, near Tampa, Florida. Starting with the biostratigraphy of 63 taxa of fish, amphibians, reptiles, birds and mammals, as well as 46 taxa of marine and freshwater mollusks and ostracodes, they also employed U/Th and amino acid dating to place the sequence in isotopic stages 5 to 7, or middle Pleistocene (early Rancholabrean, about 300-130 ka in age). The entire study is an elegant example of an analysis in which the biostratigraphy of marine and terrestrial organisms is combined with isotopic data to give highly resolved chronostratigraphy. Anderson summarizes the large carnivoran fauna from the late Irvingtonian Porcupine Cave in south-central Colorado. Harington describes the middle Wisconsin Dublin Gulch fauna, from the Yukon Territory of Canada.

Several chapters analyze large quarry samples of mammals to determine their population structures. McDonald examined *Equus simplicidens* from the Hagerman Horse Quarry, in Hagerman Fossil Beds National Monument, in Idaho. He finds a ratio of few males to many females, and an abundance of juveniles, suggesting a polygynous harem structure with a seasonal breeding season. This is typical of most zebras and wild horses. Daeschler examined the sample of mastodons (*Mammot americanum*) from the Irvingtonian Port Kennedy Cave, Pennsylvania. He finds that 90% of the individuals were

juveniles, less than 10 years old at death. Such a high proportion of juveniles suggests that they were the prey of carnivores, dragged into the cave after they had been killed. Cooke examines sexual dimorphism in the antelope *Antidorcas recki* from Bolt's Farm, near the famous hominid site of Sterkfontein, in South Africa. He finds a striking difference in horn shape that seems consistent with sexual dimorphism, and very similar to that found in the living relative, *Antidorcas marsupialis*. Klein and Cruz-Urbe wrestle with the problem of recognition of *Equus* species and subspecies from skulls alone. Using discriminant analysis, they conclude that there are clear distinctions in the skull, which do not conform to criteria proposed by earlier authors. They use their methods to resolve the long-controversial question as to whether the recently extinct quagga was related to plains zebras, or to other equids. They conclude that the quagga is actually more similar to mountain zebras and horses.

Several authors contributed studies in functional morphology, long an interest of Churcher's. Bryant wrestles with the controversial problem as to how sabertoothed cats killed their prey. He concludes that the jaw adductor muscles alone were inadequate to produce sufficient bite force, so they must have used their head depressor muscles to drive the saber-like canines into the prey, before they bit down. Laub compares the functional morphology of the teeth and jaws of mastodons and mammoths. He concludes that mastodons ate with a side-to-side jaw motion (much like that of tapirs, as their lophodont teeth suggest), while mammoths employed a specialized front-to-back grinding motion like that of living elephants.

Colbert discusses the pattern of development of antlers in North American cervids and of ossicones in African giraffids. Unfortunately, this paper demonstrates a common problem with festschrift/symposia volumes, where some invited authors have little original to say. This paper is a derivative and superficial gloss on more thoughtful work by Janis, Gentry, Jarman, and others.

Fortunately, no such complaint can be made about most of the papers in this book. In general, the authors have original ideas and important data to contribute. Thanks to the focus on Pleistocene mammals, the book has remarkable coherence and consistency. Most of the papers are too specialized for those who do not have a special interest in late Cenozoic mammals of North America or Africa, but several of those featured above deserve to be read by any paleobiologist who is concerned with the general issues they address. In short, the book will be a standard reference on the shelves of many paleomammalogists, and the well-rounded paleontologist should definitely give it a look.

References

- Barnosky, A. D. (1987) Punctuated equilibrium and phyletic gradualism: some facts from the Quaternary mammalian record. *Current Mammalogy* 1, 109-147.
- Martin, R. A. and Barnosky, A. D., editors, (1993) *Morphological Changes in Quaternary Mammals of North America*, Cambridge: Cambridge University Press, 415 pp.

DONALD R. PROTHERO

Department of Geology

Occidental College

Los Angeles, CA 90047