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VERTEBRATE PALEONTOLOGY AND EVOLUTION, by Robert L. Carroll, 1988. W. H. Freeman and Company, New York. xiv + 698 pp., 682 figs.; \$52.95.

This is the updating, after more than twenty years, of A. S. Romer's (1966) *Vertebrate Paleontology*, probably the most widely used textbook in paleontology. Those who are most interested in large population samples closely spaced in time, either for evolutionary studies or for stratigraphy, generally gravitate towards invertebrate paleontology, micropaleontology, or palynology. The appeal of vertebrate paleontology is the opportunity it gives for following complex anatomical changes from early primitive forms to later, much modified forms, and the great detail that is often possible in knowledge of strange extinct animals. Romer's text gave a simple (I fear, oversimplified) history of the skeletal changes (particularly, in the general form of the skull) in vertebrates throughout their fossil record and an overview of vertebrate diversity in the past as revealed by the fossil record.

Carroll keeps Romer's general emphasis and has produced a similarly useful general text that undoubtedly will become the textbook for vertebrate paleontology courses. Because nearly every reader of this journal will (and should) buy this book and those who teach will adopt it as a text, the most useful function for a short review is to give the readers some warnings. This book is remarkably up-to-date, with most major reports through 1986 included; but this has come at a cost; there are many misprints, both in the text and in the Appendix, listing fossil genera, and several of the figures are mislabelled. For example, the figure showing the accessory vertebral articulations of snakes (p. 235) has the leader intended for the zygosphenon ending on the neural arch; the orbital series of foramina of the lateral view of an opossum skull (p. 405) are misidentified ("foramen ovale" should be *f. rotundum*, "foramen rotundum" should be combined optic *f.* and sphenorbital fissure, and "optic foramen" should be the vascular sinus canal foramen). Although the West Indian insectivores *Solenodon* and *Nesophontes* are figured and noted in the text, they are omitted from the Appendix, as are the West Indian rodents referred by some to a "Family Hep-taxodontidae". The Dromornithidae are listed (as Casuariiformes) in the Appendix as Recent (rather than Miocene to Pleistocene) and the Pleistocene Australian snake *Wonambi*, a remarkably late relative of *Madtsoia*, is attributed to South Africa. Errors such as this are unavoidable in any undertaking as enormous as the Appendix, but there is now a danger that theoreticians may use the Appendix for some calculation of extinction rates or faunal interchange rates to draw sweeping conclusions without checking.

The last three chapters of Romer (1966), reviewing the chronological history of vertebrates, have disappeared in Carroll's book—an unavoidable omission because Carroll's book is much longer than Romer's; and a chronological review today, including Chinese, Australian, and African vertebrate-bearing deposits, would now be a hefty tome in itself.

But as one who comes to paleontology as an anatomist, rather than as a geologist, I miss this summary at a time when it would be even more useful. It should be noted that zoology students may find Carroll's occasional use of Lias and Liassic for Lower Jurassic confusing. As did Romer, Carroll sometimes recognizes a "Middle Cretaceous", but not consistently. Cenomanian lizards are "Middle Cretaceous" but Cenomanian snakes are Upper Cretaceous.

Romer's book represented one man's opinion and the sources of bits of information were not cited. Carroll attempts to note at least the existence of conflicting opinions and to cite references for statements. For the most part, these references are to major reviews that have appeared in the last decade, to which the reader can go to trace the source of a discovery or of an interpretation. This third-hand summarizing seems necessary for keeping a general text to a reasonable size, but it can confuse a naive student about the history of the science, since it is the last author to state an interpretation who gets cited, rather than the originator. In some cases, Carroll further confuses the issue by misstating the history, as in his attribution to Huxley of the term "paleognathous" for ratite palates. Huxley used the term "dromognathous" for the palate of tinamous, to set them apart from other Carinatae. It was Pycraft (1901) who coined the term "paleognathous," with its implications of being ancient, and attempted to define the term to include all ratites (including the ostrich) and tinamous and to exclude other birds.

Some of Carroll's anatomical statements are also in need of correction. Carroll has greatly improved the account of the ear in tetrapods over Romer's simple assumptions that a tympanic cavity and membrane arose once in the tetrapods. Carroll notes the apparent multiple origins of a tympanum and of a slender stapes, but (p. 225) worries unnecessarily over why *Sphenodon* has a slender stapes but lacks a middle ear cavity. Versluys (1898) accurately described and figured the middle ear cavity of *Sphenodon*, in the large "quadrate foramen", with the quadratojugal bone lying in the position where one would expect a tympanic membrane (and probably serving a similar function, since the extracolumella reaches the dorsal quadratojugal-quadrate contact). A similarly large "quadrate foramen" with a slender stapes is seen in Saurischia. If this is the result of phylogeny, then Carroll's reference of the Sphenodontida to the Lepidosauriamorpha seems wrong and his entire classification of the Diapsida (mostly based on the sternum and ankle) is suspect.

But a classification based on the anatomical details of the individual fossils seems far better to me than Romer's (1966) definition of the Archosauria on the basis of the evolutionary destiny of the earlier forms, a mystical concept that I cannot pretend to understand. Probably everyone will differ with many of Carroll's interpretations and wish for inclusion of

many aspects that Carroll has omitted. But a great deal of precise information has been added to vertebrate paleontology in the last twenty years. A more detailed statement of what happened, based on real specimens, is now possible. Because it reflects this progress and the contributions of many workers, Carroll's book is better than the book it replaces.

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It has been 22 years since publication of the third edition of Romer's influential *Vertebrate Paleontology*. Since 1966, several texts on vertebrate history have appeared, including the third edition of Edwin Colbert's classic *Evolution of the Vertebrates*. But until now, no one has attempted the comprehensive technical synthesis that Romer assembled in one of the great works of our profession. With the rapid growth of the discipline in recent years, the publication of many new journals and symposia, and the enormous diversity of Vertebrata, this comes as no surprise.

Coincidentally, it has also been 22 years since publication of the English translation of Hennig's *Phylogenetic Systematics*, another work of enormous impact that played a central role in accelerating development of its field. Although some paleontologists still debate how Hennig's influence should be manifested, few will deny the benefit to paleontology of the philosophical awareness and sophistication he prompted. As Alfred North Whitehead (1925:23) said, "If science is not to degenerate into a medley of *ad hoc* hypotheses, it must become philosophical and must enter upon a thorough criticism of its own foundations." Synthesis of the huge body of new data in light of the immense growth of systematics poses a formidable task indeed.

Robert Carroll, a preeminent paleontologist and one of Romer's last students, has attempted such a synthesis in *Vertebrate Paleontology and Evolution*. This book endeavors to up-date the technical information and methodology of Romer's third edition, while preserving its aim as a serious undergraduate text with sufficient depth of concept and detail (698 pages) to serve as a prime reference for graduates and professionals. The book has been beautifully and abundantly illustrated by Pamela Gaskill, although the abundance of illustrations—many redrawn from the literature—has come with some cost to detail, accuracy and utility. By the time this review appears most readers will probably already own a copy—a testimonial to the book's instant and deserved celebrity.

The opening chapter, "Fossils and Relationships," deals chiefly with Hennigian systematics, synopsisizing Carroll's views on modern systematic theory and methods, and sets

out the basic perspective of the book. Paleontologists secure in the systematic traditions embodied by Romer's great text will find satisfaction in this chapter and good service from the rest of the book. Although the vocabulary has changed a bit, its philosophic outlook is basically the same as Romer's. But those wishing to view vertebrate history from a perspective afforded by modern systematic theory will find less of merit. Carroll describes an eccentric, contradictory amalgamation of methods, with predictable results. His view of monophyly, for example, which determines the organization and content of the book, first recognizes that "A major objective of classification is to unite species sharing a common ancestry" (p. 6), but then contradicts, "In this text the term monophyletic will be used to refer to the origin of groups without consideration of their descendants" (p. 13). What this means is made clear by the recognition of an abundance of paraphyletic groups, including Agnatha (excluding gnathostomes), Osteichthyes (excluding tetrapods), Lacertilia (excluding snakes), Reptilia (ancestral to but excluding birds and mammals), Anapsida (including only captorhinids, procolophonids, pareiasaurs, and mesosaurs), Thecodontia (excluding Crocodylia, Pterosauria, Dinosauria), and the list goes on and on.

To a degree, recognition of paraphyletic taxa accurately reflects even the most current literature, which has yet to see reanalysis of the full range of taxa covered in this huge book. Nevertheless, many of the groups Carroll recognizes at all hierarchical levels have been challenged in literature published in or before 1986. Although debate is often mentioned, dissent to Carroll's views is usually dismissed in a word. A number of important recent references are conspicuously absent, and the reader is offered little useful information on currently problematic aspects of vertebrate history, or even much awareness of the extent and kinds of problems many authorities believe to exist.

Confusing taxonomic contradictions also frustrate the reader. In discussing dinosaurs, for instance, Carroll argues that "there is no fossil evidence to support the long-held assumption . . . that saurischians and ornithischians had separate origins from distinct groups of thecodonts" (p. 289), seeming to imply that Dinosauria is monophyletic. But in the appended classification, Saurischia (lacking Aves) and Ornithischia are not united, instead being listed as two of five separate orders in the superorder Archosauria. Then, on page 621, appears the enigmatic category "Dinosauria incertae sedis"—the only place where the word Dinosauria occurs in the classification—which contains only Segnosauridae. Dinosaurs are characterized in chapter 14 using mostly characters that admittedly occur in "thecodonts" and birds as well as many ornithischians and extinct saurischians. One can only wonder what the terms "dinosaur" and "Dinosauria" purport to represent, and similar ambiguity beleaguers many other groups in the book.

Difficulty also besets consistent interpretation of the diverse graphic devices labeled as "phylogenies." There are balloon diagrams that may be entirely closed or open at one or both ends, parallel lines drawn on a time chart, cladograms taken from cladistic literature, bushes, tree-trunks, and other devices. Some higher taxa pinch out, becoming "extinct" just as they "give rise" to descendent higher taxa, while others simply don't connect anywhere (surely he doesn't mean to imply their independent creation!). No graphic "phylogeny" of any sort is presented for several major segments of Vertebrata, including Aves, Saurischia, and Archosauria, taxa that account for nearly one-fourth of vertebrate species. The

graphic confusion and oversights are not mitigated by the text.

In both the text and illustrations, vertebrate history is depicted as a potpourri of disjunct entities and events, and such fundamental concepts as homology, phylogeny, and classification are applied so inconsistently as to appear virtually without meaning. The resulting 'evolutionary' pattern reflects as much human predilection as natural history, and it defies logical interpretation. As Wyss and de Queiroz (1984) asked, how can one say that a group such as "Protorothyridae" became extinct while at the same time maintaining that it was the direct ancestor of living amniotes? What does it mean to label this group "conservative" if its lineage includes organisms as different as whales, turtles, snakes, and birds? Can groups like "Protorothyridae" honestly be said to possess *any* evolutionary properties when they can be defined only by what they are not?

One can only stand in awe of the scope of Carroll's undertaking. He has succeeded in assembling a huge body of data, but it only dimly reflects the enormous development of systematics in recent decades. As Whitehead predicted,

without a critical philosophical outlook this view of vertebrate evolution is largely ad hoc. To students using this as a text, vertebrate history must appear utterly bewildering. Despite these objections, the sheer volume of data between its covers offers considerable utility and everyone with serious interest in vertebrate history will want to own this book. Its mammoth dimensions and controversial content will insure its prominence in paleontological discussion and debate for years to come.

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REVIEW

SYSTEMATICS, FUNCTIONAL MORPHOLOGY AND MACROEVOLUTION OF THE EXTINCT MAMMALIAN ORDER TAENIODONTA, by Robert M. Schoch, 1986. Yale University Peabody Museum of Natural History Bulletin No. 42, 307 pp., 60 figs., 65 pls. ISBN 0-912532-04, paper.

The taeniodonts, a distinctive order of Puercan (early Paleocene) to Uintan (medial Eocene) North American mammals, have long been a neglected group. Until 1980 the most extensive studies of taeniodonts were those of Wortman (1897), Matthew (1937), and Patterson (1949). Wortman was the first to understand the basic interrelationships among taeniodonts, but many aspects of his study have long been outdated. Matthew's work focused on taeniodonts of the San Juan Basin, while Patterson was interested in general evolutionary trends and rates of change. Schoch's monograph makes available for the first time a detailed, integrated and updated picture of taeniodont taxonomy, function, and evolution. It is based, with few alterations, on Schoch's 1983 Ph.D. dissertation at Yale.

The first and longest part of the monograph is a detailed systematic revision of the Taeniodonta. The two families (Conoryctidae and Stylinodontidae), eight genera, and 12 species of taeniodonts accepted by Schoch are all rediagnosed, synonymies of taxa from earlier literature are listed, and complete lists of referred specimens, with geographic and geologic distributions, are provided. Schoch also gives detailed descriptions of known skeletal and dental remains for each species. The descriptions are supplemented by drawings, 21 tables of measurements, and 65 plates illustrating virtually all important taeniodont specimens. The plates are a particularly valuable part of the monograph and will be used actively by anyone seeking to identify specimens. Un-

fortunately, some of the photographs of teeth are rather small, but this deficiency is at least partly offset by the enlarged composite drawings of the dentitions of each genus.

Noting the small number of specimens available, one can easily see why taeniodonts have been neglected for so long. There are no complete skeletons, and only three genera (*Onychodectes*, *Psittacotherium*, and *Stylinodon*) are known from relatively complete skeletal material. Many of the remains are scrappy, and the cheek teeth are often worn flat. Schoch does an admirable job of synthesizing the available information and differentiating the taxa in a coherent way. Nonetheless, some of his conclusions might easily change if additional material were available. For example, he separates the stylinodontid genus *Ectoganus* into two species based primarily on size; he then divides both species into subspecies which differ in the degree of dental hypsodonty. The pattern of variation in size and hypsodonty might become clearer if more remains were available and particularly if there were quarry samples which could be analyzed statistically. However, taeniodont remains are virtually always surface finds, and no quarry samples are available for any species.

Schoch successfully weeds out and synonymizes a number of typological old species names. Two former species are retained as subspecies (*Onychodectes tisonensis rarus* and *Ectoganus gliriformis lobdelli*). The distinguishing characters of these subspecies vary along a continuum but appear to be valid for differentiating 75% of the known specimens (the