

torily accounts for why the transitions for one species to another are not seen in the fossil record, why gaps are biologically meaningful, and why there are so few unbroken sequences of chronospecies known. Stanley follows Eldredge and Gould in recognizing that phyletic gradualism is too slow to account for the diversity of life, and his view of macroevolution is in the punctuational mode.

It is now generally agreed that speciation is the raw material of macroevolution. Stanley takes the position that only quantum speciation (Verne Grant's term for rapid and radically divergent speciation, and a catchall phrase according to M. J. D. White) will account for the pulses in life revealed in the fossil record. He describes numerous examples of divergent evolution at the specific (cichlids in African lakes), generic (rhinos and polar bears), and subfamilial (giant panda) levels. He speculates on the role of regulatory genes and minor chromosomal rearrangements as underlying agents of these transformations, but the discussion only underscores our continued ignorance in these matters. At the other end of the rate spectrum, he discusses those taxa that have persisted virtually unchanged through time: Darwin's "living fossils." A notostracan crustacean genus that evolved 300 million years ago and two of its member species that have apparently survived nearly 200 million years to the present day are tributes to phyletic gradualism.

A chapter on sex in a book concerned primarily with fossils?! Stanley's argument, that sexual reproduction prevails because speciation and macroevolution are virtually impossible without it, represents something of a departure from the conventional wisdom. Perhaps it accounts for why the asexual bdelloid rotifers have produced only 200 species in 400 million years of evolution.

Stanley concludes that microevolutionary agents are inadequate to account for macroevolution. He sees the two processes as being decoupled, one involving primarily phyletic gradualism and the other quantum speciation. He postulates a series of processes to account for large-scale trends: species selection, phyletic drift, and directed speciation. Species selection or lineage selection is the most important of these and is held to operate on differential rates of speciation and extinction. Its agents are competition, predation, and habitat alteration. Like its analog, natural selection, it is a tautology since it provides no criteria of fitness independent of mere survival.

Stanley has been wise not to attempt a synthesis like Simpson's *Major Features of Evolution*; paleobiology is in its infancy and there is now too much uncertainty. It is unfortunate therefore that some of the major controversies are not developed more fully. Although Stanley is careful to cite his fellow workers he has a tendency to attemper their contributions. The reader may be interested to know, for example, that P. H. Greenwood's interpretation of the 170 species of cichlids that evolved in Lake Victoria during the last 1 million years is rather different from Stanley's. In his recent presidential address to the Linnean Society (*Biol. J. Linn. Soc.* **12**, 293 [1979]) Greenwood argued that macroevolution is a myth in that it is simply speciation, nothing more. In the case of the cichlids he thinks that opportunities for rapid speciation rather than quantum speciation are responsible. Again, our ignorance of the mechanisms underlying speciation hinders profitable discussion of these alternative interpretations. A second controversy involves the phenomenon of "nonadaptive" characters. Stanley, who has studied the functional morphology of bivalves, is a selectionist. Allegedly nonadaptive features, like some features of the giant panda, are explained as the result of pleiotropic effects. This is too convenient; it may be that macroevolutionary trends, to a greater extent than microevolutionary ones, are limited by genetically regulated developmental pathways and architectural constraints.

The new paleobiological view of evolution, based on the application of theoretical ecology to the fossil record by Gould, Raup, Schopf, Sepkoski, Stanley, Valentine, Van Valen, and others, is intuitively appealing. So far the modelers have avoided two of the pitfalls that initially retarded progress among their neontological colleagues: an infatuation with the way numbers interact with one another and a denial of the role of environmental trends and spatial heterogeneity. The latter phenomena are obviously of major significance to macroevolution; without them monsters would have no hope. Evolutionary biologists can no longer ignore the fossil record on the ground that it is imperfect. As Stanley shows, it is highly relevant to the elucidation of Darwin's mystery of mysteries—the origin of species and the diversification of life.

DAVID S. WOODRUFF

Department of Biology,  
University of California at San Diego,  
La Jolla 92093

## Invertebrate Phylogeny

**The Origin of Major Invertebrate Groups.** Proceedings of a symposium, Kingston upon Hull, England, April 1978. M. R. HOUSE, Ed. Published for the Systematics Association by Academic Press, New York, 1979. x, 518 pp., illus. \$82.50. Systematics Association Special Volume No. 12.

For biologists, the chief use of this book will be for access to accurate paleontological information about times of origination of several major invertebrate taxa and discussions of their early phylogeny. Eighty percent of the text is by specialists who present up-to-date summaries of the origins of major groups. (Cnidarians are treated by Scrutton, bryozoans by Larwood and Taylor, brachiopods by Wright, arthropods by Whittington and by Manton and Anderson, mollusks by Yochelson, by Graham, by Holland, and by Morris, echinoderms by Paul, graptolites by Rickards, and chordates by Jeffries. The chapters by Scrutton and Whittington are especially thoroughly done.) The remaining 20 percent of the book consists of broader-ranging papers—discussions of life of the later Precambrian (by the late P. C. Sylvester-Bradley, to whom the volume is dedicated, and by Ford), reviews of current thinking on early eukaryotic and metazoan radiations (by Sleight and by Clark), and a very thorough paleontological summary of distributions of microfossils and invertebrate fossils—stage by stage!—across the Precambrian–Cambrian boundary (by Brasier).

Most of the discussions of originations and phylogenetic relations are limited to morphological evidence, especially size, shape, and skeletal composition but also including data on embryological fate maps (Manton and Anderson) for arthropods and functional morphology for several groups. This last approach is used very effectively by Clark in his continuing investigation of the origin of the coelom vis-à-vis the evolution of a hydrostatic skeleton. Perhaps owing to the large amount of material already in hand, the authors do not attempt to relate their phylogenetic ideas to data on protein or DNA sequences or other pertinent biochemical information. Thus the book can be seen as setting the stage for what must be done during the 1980's in order to bring the level of argumentation beyond conventional data. Sleight strongly endorses the symbiosis theory of the origin of eukaryotes. His chapter shows the continuing need for paleontologists to learn all they can about cell biology so that they may evaluate his reliance on

different patterns of evolution of the mitotic spindle ("closed" versus "open" mitosis) in light of paleontological evidence on the time of occurrence of different taxa.

Perhaps what emerges most strikingly from these essays is the reaffirmation that a very large number of classes and phyla appear in the fossil record within the approximately 70-million-year interval from the late Precambrian (Upper Vendian) through the Lower Cambrian (Tomotian and after). Brasier's summary should be considered together with tabulations presented by Sepkoski in *Paleobiology* (4, 223 [1978] and 5, 222 [1979]) and by various authors in Part A of the *Treatise on Invertebrate Paleontology* (R. A. Robison and C. Teichert, Eds., Geological Society of America, 1979). The change in diversity is spread over millions of years, but still only about 10 percent of Phanerozoic time, and the total effect is astounding. In part on the basis of data in this book, Sepkoski (in preparation) documents that two-thirds of the 90 metazoan classes with a marine fossil record originated in the Vendian-Cambrian interval; for contrast, he finds that during the later half of the Phanerozoic (essentially from the Permian to today) only 5 percent of the classes originated. The sometimes-heard suggestion that there is a long Precambrian fossil record for the metazoa (if we would but be diligent enough to find it) is not substantiated in these most recent summaries.

The desire for a mechanistically acceptable genetic explanation for this enormous radiation in biologic diversity has led some of the contributors (most notably Yochelson) to espouse one form or other of the currently popular developmental macromutation line of thought. Perhaps molecular biology with its recent focus on split genes and insertion sequences (transposons, for example) may yet make the major macroevolutionary question of "how the Cambrian radiation could have occurred" comprehensible from a genetic point of view.

With respect to the theory of classification, only Jeffries uses cladistic procedures to reconstruct phylogenetic relationships, and this he does for the deuterostome wing of the metazoa. (In contrast, the three or four phyla of the arthropod grade of development [Chelicerata, Crustacea, Uniramia, and possibly Trilobita] are not explicitly differentiated in a cladistic fashion.) The cladistic procedure has the advantage of spelling out the basis for a decision on classification at each branch point so that it is immediately clear to others. Whether or not Jeffries's resulting pattern is

any more likely to be correct in its linking of "carpoids" with chordates (instead of with echinoderms) of course cannot be resolved by a methodological procedure and remains open to question.

In sum, this is an excellent book to which neontologists and paleontologists engaged in phylogenetic studies should have ready access. The final chapter records some of the discussion from the meeting that gave rise to the book, and the remarks of several persons were

worth including. Hessler, for example, ponders whether the arthropod diversity in the Burgess Shale is really any greater than that of a modern crustacean fauna—and hence he questions the tendency to assign these admittedly strange ancient beasts to a high taxonomic rank. A good index closes the book.

THOMAS J. M. SCHOPF  
*Committee on Evolutionary Biology,*  
*University of Chicago,*  
*Chicago, Illinois 60637*

## Mammals in the Age of Dinosaurs

**Mesozoic Mammals.** The First Two-Thirds of Mammalian History. JASON A. LILLEGRAVEN, ZOFIA KIELAN-JAWOROWSKA, and WILLIAM A. CLEMENS, Eds. University of California Press, Berkeley, 1980. x, 312 pp., illus. Cloth, \$35; paper, \$9.75.

This beautifully conceived and executed book covers a subject that after a long period of stasis has undergone rapid advances during the 1960's and '70's. The editors and authors literally have left few stones unturned in their search for and summary of available knowledge about Mesozoic mammals. The range of their own background of fieldwork and original scientific contributions to the subject is outstanding. One of the authors, George Gaylord Simpson, published two monographs in 1928 and 1929 that served for many years as the starting point for most students interested in these furred but unspectacular players in a drama dominated by large reptiles. In the last 20 years a flood of information has been published about early and primitive extinct mammals, but the information is widely scattered and many of the publications are already out of print. This mass of data had not been summarized adequately by anyone until Lillegraven and his well-organized co-workers took up the task. They have done it admirably well. The book has a generally lively style, is well illustrated (some reprinted figures have suffered in the process, however), and is almost completely free of typographical errors.

Lillegraven's introduction (chapter 1) lays down important ground rules, which I appreciate although I do not entirely agree with all of them: (i) a cutoff date of 1 January 1978 for inclusion of new information; (ii) no new taxa (this results in a coy circumlocution for a family based upon *Gypsonictops*); (iii) taxonomic

chapters have the same format; and (iv) classification remains eclectic and arbitrary rather than phylogenetic. A conscious effort is thus made to avoid new, higher-order taxonomic formulations on the grounds that they might be unfamiliar, unstable, or somehow hinder communication!

The second chapter, entitled "Where, when, and what—a survey of known Mesozoic mammal distribution," offers a thorough review of the provenience of the known specimens of Mesozoic mammals. Its authors are Clemens, Lillegraven, E. H. Lindsay, and Simpson. Profound successes in field exploration have been realized for the Mongolian Cretaceous, the Portuguese Jurassic, and the late Triassic or early Jurassic of a number of areas in Eurasia and Africa, but it is pleasant to note that the vast former gaps in the Mesozoic mammalian fossil record are gradually being filled for other areas of the world as well, as in the case of the late Jurassic and Cretaceous of North America, the early Jurassic of Andhra Pradesh, India, and the latest Cretaceous of the Peruvian Andes. This chapter is highly useful, both as a summary of what we know and as a guide to where future exploration should be concentrated. I only wish that the authors had gone on and told a little of the "who and how" that have been responsible for the "where, when, and what."

In another stage-setting chapter, A. W. Crompton and F. A. Jenkins, Jr., discuss the origin of mammals, at least as the term Mammalia is currently defined. The familiar story of the evolution of the mammalian jaw joint is told and a commitment is made to a model involving parallel or convergent evolution of the three-boned middle ear separately in monotremes and therians.

After these beginnings, separate chap-