vast area full of ancient problems. But by being selective he was able to provide an elegant analysis of the empiricistic doctrine, which has dominated the discipline all through its history.

The success of the book can be attributed to several factors, including careful planning, diligent editing (I saw no errors), the action of some hidden force that induced all of the contributors to minimize their own contributions, the use of a whole army of sympathetic reviewers, and the inclusion of 84 portraits of historically important persons.

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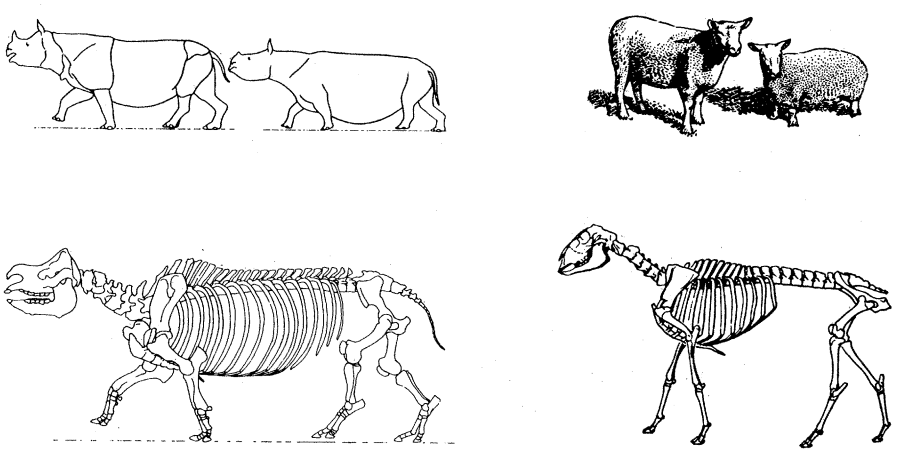
Evolution: The Paleobiological View

Macroevolution. Pattern and Process. STEVEN M. STANLEY. Freeman, San Francisco, 1979. xii, 332 pp., illus. $20.

Macroevolution is concerned with the origin and extinction of species and the diversification of lineages, or, turning the problem around, with how key morphological and functional features of a lineage evolve. One of the major debates in biology concerns the role of microevolutionary forces (natural selection, genetic drift and mutation) at the transspecific level: Are the major changes in the history of life attributable to speciation or to the gradual transformation of lineages within established species by microevolutionary forces? Stanley's exploration of this problem from a paleontological viewpoint is a welcome addition to the literature of evolutionary biology. Paleontology is currently undergoing an exciting rejuvenation, and Stanley and his fellow paleobiologists (as they are now called) have introduced some scientific rigor into a traditionally descriptive field. Now, in place of inspired speculation, we see attempts to test hypotheses derived from theoretical population ecology against the extensive fossil record. Although this volume is in large part an amalgamation of the author's previous publications, his ideas deserve the wider readership they will now receive. He documents and discusses a wide range of interesting topics, and biologists unfamiliar with the recent progress in paleobiology will find this a useful reference. (More than half of the 400 reference citations are to works published since 1969.) Because much of the discussion is controversial the book should also be considered for use in advanced classes and seminars on evolution.

Stanley's contributions to biology include the development of techniques for the estimation of rates of evolution in the fossil record at the level of the species. This volume contains the results of his analyses, a wealth of well-illustrated data on rates of speciation, extinction, and the diversification of higher taxonomic categories. He discerns a *scala naturae* in the average duration of species in different groups: mammals, ammonites, and trilobites, 1 to 2 million years; echinoderms, 5 million years; marine mollusks, 10 to 15 million years; and planktonic forams, 25 million years. In marked contrast to the relative longevity of species is the speed with which adaptive radiations occur; the diversification of the angiosperms (Darwin's "abominable mystery") in 10 million years, 20 orders of mammals in 12 million years, and 20 families of ammonites in 8 million years. This inconsistency has created a major problem for evolutionary biologists. Darwin and most subsequent authors including G. G. Simpson have held that most evolutionary transitions occur within established lineages by phyletic gradualism guided by natural selection. But fossil species remain unchanged throughout most of their history and the record fails to contain a single example of a significant transition. Similarly, it is difficult to account for the greatly accelerated pace of evolution during periods of adaptive radiation. An alternative model of evolution, that of punctuated equilibria, introduced by Niles Eldredge and Stephen Jay Gould in the early 1970's, more fully accounts for these same observations. According to this major conceptual breakthrough, rapid evolution is typically associated with speciation events that occur cryptically in small isolated populations, often at the edge of a species's geographic range. (This model does not require macromutations of the type that characterized earlier punctuational schemes.) It satisfac-



Effects of achondroplasia. (Left) The living Indian rhino, *Rhinoceros unicorni*, and the Late Miocene achondroplastic dwarf rhino, *Teleoceras fossiger*. (Right) Normal domestic sheep and member of the achondroplastic Ancon strain. Among the phenomena "strongly suggestive of rapid evolutionary transition is the origin by single mutations in domestic animals of certain distinctive morphologic features . . . that closely resemble traits of species that appear suddenly in the fossil record as the earliest members of discrete higher taxa. . . . At least twice during the last 200 years, achondroplastic sheep have arisen by single mutations under domestic conditions, and dwarf populations have been maintained by artificial inbreeding. . . . It is much easier to imagine that *Teleoceras* evolved by the rapid fixation of achondroplasia in a small, inbreeding population than by the dwarfing of an entire species." [From *Macroevolution*; drawings at left by Gregory S. Paul, at right from H. Grüneberg, *The Pathology of Development* (Wiley, 1963)] 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.

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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 Sleigh 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. Sleigh 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