Book Reviews

Paleontologists Confronting Macroevolution

Patterns of Evolution as Illustrated by the Fossil Record. A. Hallam, Ed. Elsevier, New York, 1977. xiv, 592 pp., illus. $69.50. Developments in Palaeontology and Stratigraphy, 5.

The tradition of paleontology has been to describe taxonomic and morphological change revealed by fossils. From time to time, beginning with Charles Darwin, individuals have used the findings of paleontology to elucidate evolutionary mechanisms. Among the finest contributions of the neo-Darwinian revolution of the late 1930's and 1940's was G. G. Simpson's synthesis of evolutionary theory and the fossil record. Recently, acceptance of continental drift, improvements in dating and stratigraphy, increasing study of contemporary species to interpret ancient life, and widespread recognition of advances in molecular evolution and community ecology have stimulated a new intellectual revival in paleontology. *Patterns of Evolution as Illustrated by the Fossil Record* heralds this revival and promises an assessment of "the evolutionary patterns that can be discerned from the fossil record, interpreted in the light of evolutionary theory and our present knowledge of the changing environment of our planet." I review this volume from my perspective as an evolutionary ecologist.

In the introductory chapter, S. J. Gould places three contemporary controversies in a historical context as the "eternal metaphors" of paleontology. First, do the results of evolution, including morphology and diversity, exhibit directional change or are they steady-state variations on established themes? Second, is evolutionary change caused by external factors acting on a malleable genotype or do internal factors constrain or even direct the course of evolution? Third, does evolution occur by gradual change or by episodes of rapid change interspersed with periods of stasis (punctuational evolution)? Gould correctly argues that evolutionary biologists and ecologists have steady-state, externalistic, gradualistic leanings whereas paleontologists espouse directional, internalistic, and episodic views. The fossil record and contemporary processes lend support to both sides of each controversy. I had hoped to see a reconciliation of these controversies and a new synthesis of evolution and paleontology. But, rather than search for ties between microevolutionary processes and macroevolutionary patterns, Gould believes that the two are "decoupled" and exhorts, "There can scarcely be a more important task for paleontologists than defining the ways in which macroevolution depends on processes not observed in ecological time."

In the last chapter of the book, T. J. M. Schopf summarizes the views of the authors on each of the major issues. He finds that most are steady-state on diversity and believes that ecological factors limit the number of coexisting species. Most of the authors are progressive on morphological change. Those who are steady-state on diversity also believe that external factors exercise control. Curiously, those who are explicitly progressive on morphological change have little to say about the cause of progress. Even S. M. Stanley's theory of "species selection" does not resolve whether progressive adaptations are selected by a changing environment (externalist) or by the evolving diversity of life itself (internalist).

With respect to the tempo of evolution, the contributors to this volume are split between gradualist and episodic viewpoints. Presenting the episodic extreme, N. Eldredge states that "the origin of taxa—species and populations—is the only context in which evolution is actually known to act." Several authors—Schopf, Kennedy, Doyle, and, especially, Gingerich—defend the view that morphological change occurs gradually within a phylogenetic line against the "punctuated equilibrium" hypothesis that change occurs only during speciation events.

Most of the 15 chapters between Gould's introduction and Schopf's summary describe patterns of evolution within particular phylogenetic groups. Many of the chapters are comprehensive, sensible, and clearly written, and they make the volume a valuable source for all students of evolution. Among the highlights for me: S. J. Gould lucidly describes the historical context of modern controversies in macroevolution. D. M. Raup cautions us that many "patterns" in evolution can be obtained by stochastic, Monte Carlo simulations in which rates of speciation, extinction, and morphological change are random (nondirectional, time-independent) variables. In a thorough and somewhat technical discussion, C. R. C. Paul presents convincing evidence for the progressive evolution among primitive echinoderms of adaptations for increased protection from predators, increased efficiency of the feeding apparatus, and increased efficiency of respiration. S. M. Stanley summarizes the evolution of bivalves and provides a sound functional interpretation of morphological trends. A convinced punctuationalist, he contrasts bivalves and mammals to support (unconvincingly, I believe) the hypothesis that rate of evolution is determined by rate of speciation. In his account of ammonites, W. J. Kennedy finds no morphological grounds for the concept of racial senescence, although K. S. Thomson argues that, for fish and other vertebrates, patterns of diversification and extinction are so periodic as to indicate internally regulated cycles. A. Seilacher uses trace fossils to show that the efficiency of searching patterns among benthic invertebrates has increased throughout geologic time. By emphasizing the gaps in the fossil record of amphibians, R. L. Carroll contributes an important perspective to the volume. R. T. Bakker comes closest to reconciling evolutionary patterns with contemporary processes. He places fossil beds in their proper geographical context as deposition basins that narrowly sample the total diversity of life. He then relates extinctions of Mesozoic tetrapods to regressions of the shallow seas that covered large areas of the continents. P. D. Gingerich claims that when the major orders of mammals arose they differed from each other much less than they do at present. J. W. Valentine in a discussion of early metazoan evolution makes the same point about phyla. These comments raise many questions, unanswered in this volume, about biases incurred through taxonomic practices.

The pluses and minuses of each chapter aside, *Patterns of Evolution* fails to provide the cogent exposition of evolutionary paleontology that it promises.

First, the book lacks a discussion of the adequacy of the fossil record. Paleontologists may have resolved this problem to their own satisfaction, but others will wonder about the potential biases of widespread gaps in time, distribution, and habitat sampling and the degree to which interpretations depend on the taxonomic level considered. Second, the book lacks a much-needed statement about the geologic context of fossils: the positions of continents and deposition basins, the nature and distribution of sediment types and their meanings, and climate patterns during each geologic age. Several chapters hint at great variation in climate and conditions of sediment deposition. How much these physical conditions color our perception of evolutionary patterns is not resolved for the nonpaleontologist. Third, many new theories about macroevolution have appeared in the paleontological literature, but, with the exception of Stanley's exposition of species selection and Raup's discussion of Monte Carlo models, none of these is adequately explained in *Patterns of Evolution*. To understand the theory of punctuated equilibria—that most morphological change occurs as a result of speciation events—I had to read Eldredge and Gould's original articles. The fossil record clearly is inadequate for many purposes. To be sure, one can discern general trends in morphology and diversity within phylogenetic groups. At the family to class levels of taxonomy, most paleontologists agree that adaptive radiations occur in brief bursts, often after the decline of ecologically related groups, and are followed by long periods of evolutionary quiet. And most agree that higher taxonomic groups usually disappear suddenly in conjunction with pronounced environmental or geologic change. But fossils do not reveal the details of speciation or extinction at the population level. More often than not, they fail to record morphological transitions between higher taxonomic groups. The time scale of these events may be too brief, the geographic setting too fine, or the fossil sample too poor. Several chapters in *Patterns of Evolution* left me with the strong impression that "episodes" in the history of life are caused partly by geologic rather than biological revolutions. Mass appearances are as evident as mass extinctions, but their similar time courses are unlikely to have resulted from inherent properties of biological systems. I cannot speculate about the degree to which the suddenness of macroevolutionary events is an artifact of the geologic record, but I was not convinced that paleontologists have squarely confronted this difficulty.

As one might expect, paleontologists agree about patterns of evolution that are best preserved—progressive evolution, for example. They are split over phenomena, such as speciation and its role in evolution, about which fossils reveal little information. In *Patterns of Evolution* little is written, in comparison with the pages devoted to rate of evolution and its relationship to speciation, about how progressive changes are selected. With few exceptions paleontologists are either silent or uninformed on matters that involve genetics, ecology, and statistics (including sampling).

Paleontologists have liberally, uncritically, and inappropriately applied neontological concepts to patterns of macroevolution: *r*- and *K*-selection (selection for weediness versus demographic conservatism, used by Schopf as a context for evolutionary patterns in Bryozoa), species-area relationships and speciation-extinction equilibria (borrowed from island biogeography to elucidate mass extinction), competitive exclusion (Stanley's species selection, a mechanism to explain macroevolutionary trends), regulatory genes (mentioned by Valentine to account for rapid evolution), and allopatric speciation (the basis of Eldredge and Gould's model for episodic morphological change).

The Eldredge-Gould concept of punctuated equilibria has gained wide acceptance among paleontologists. It attempts to account for the following paradox: Within continuously sampled lineages, one rarely finds the gradual morphological trends predicted by Darwinian evolution; rather, change occurs with the sudden appearance of new, well-differentiated species. Eldredge and Gould equate such appearances with speciation, although the details of these events are not preserved. They suggest that change occurs rapidly, by geologic standards, in small, peripheral populations. They believe that evolution is accelerated in such populations because they contain a small, random sample of the gene pool of the parent population (founder effect) and therefore can diverge rapidly just by chance and because they can respond to local selection pressures that may differ from those encountered by the parent population. Eventually some of these divergent, peripheral populations are favored by changed environmental conditions (species selection) and so they increase and spread rapidly into fossil assemblages.

The punctuated equilibrium model has been widely accepted, not because it has a compelling theoretical basis but because it appears to resolve a dilemma. Apart from the obvious sampling problems inherent to the observations that stimulated the model, and apart from its intrinsic circularity (one could argue that speciation can occur only when phyletic change is rapid, not vice versa), the model is more ad hoc explanation than theory, and it rests on shaky ground. Paleontologists seem to be enthralled by small populations. Indeed Valentine, discussing the invasion of new adaptive zones and the establishment of higher taxa, says, "While crossing the adaptive threshold, the population size of the invading lineage may be small indeed (perhaps only tens or hundreds) and evolution rapid." The notion that small populations can evolve rapidly is based largely on such laboratory experiments as Dobzhansky's in which small "founder" populations of *Drosophila* maintained widely divergent frequencies of chromosome arrangements—genetic reorganization, perhaps, but hardly macroevolution. Weighing against the findings of these experiments, genetic diversity and opportunity to accumulate mutations are reduced in small populations. Even though Eldredge and Gould may be proved right, their model, and other recent models in paleontology, should not be accorded the status of a major synthesis.

Speculation about punctuated equilibria is symptomatic of paleontology as a whole. The neo-Darwinian revolution came about because paleontologists, taxonomists, and biogeographers became geneticists or evolutionary biologists to resolve problems in their respective fields. They published their work in such journals as *Evolution* and *Genetics* and revolutionized their adopted disciplines with their broad perspectives. The paleontologists represented in this volume have not yet taken this step; they are applying neontological theory to evolutionary patterns rather than creating new genetic, microevolutionary, and ecological theory from their unique perspective. I hasten to point out that ecologists and geneticists have not elucidated macroevolutionary patterns; the gap has not been bridged from either side.

In their search for a reconciliation and synthesis of macroevolutionary patterns and microevolutionary processes, biologists have been frustrated by obstacles common to a number of disciplines. The problem is partly one of scale in time and space. More important, however, it is one of level of biological organization. It is the same problem that confronts the ecologist who seeks to explain patterns of community organization in terms of population processes, or the evolutionary biologist who seeks to interpret the genetic differences between species in terms of one- or two-locus models. The patterns we observe in biological communities and evolutionary radiations are the sum of many lower-order processes and interactions. Such systems are so complex, and their structure results from so many factors, as to appear randomly assembled. Indeed, the success of Monte Carlo simulations of evolutionary patterns and R. H. MacArthur's "broken-stick" model of the relative abundances of species point out the similarities between natural patterns and randomly generated systems. It is not clear that an understanding of deterministic processes and both internally and externally imposed constraints will necessarily elucidate macroevolution.

Patterns of Evolution reveals both awakening interest in an evolutionary synthesis and entrenchment of old ideas and uncritical approaches. It also reveals both the richness and the limitations of the fossil record. It is difficult to predict whether the time for interchange between paleontologists and evolutionary biologists has come, but the attraction of an evolutionary synthesis may now be strong enough for a new beginning.

ROBERT E. RICKLEFS
Department of Biology, University of Pennsylvania, Philadelphia 19104

Plate Tectonics

The Evolving Continents. BRIAN F. WINDLEY. Wiley, New York, 1977. xviii, 386 pp., illus. Cloth, $29.95; paper, $11.95.

It is now 12 years since Tuzo Wilson outlined the basic ideas of plate tectonics in his transform fault paper and only about seven years since geologists began to apply seriously the qualitative aspects of plate tectonics to rock assemblages. In view of the now enormous literature of plate tectonics and its geologic corollaries it is surprising that so few serious books have been written on the subject, but the scarcity is perhaps a reflection of our ignorance of how the geology of plate tectonics works in detail. *The Evolving Continents* is a bold attempt to fill the gap; it is the first and only fairly advanced textbook in physical-historical geology at the senior undergraduate and beginning graduate student level that is largely based on the plate tectonic paradigm.

The dominant merits of the book are the extraordinary quantity of well-synthesized information, the cohesive, integrated way in which the data are presented, and the informal, succinct style. Here, in one book, are really careful summaries of a range of Precambrian and Phanerozoic tectonic provinces and orogens and their evolution in an unashamedly plate tectonic framework with bets sensibly hedged for the Archean and early Proterozoic.

A peculiar and difficult aspect of the work is that the first half or thereabouts is a fairly exhaustive treatment of the Precambrian; such basic tools as the elements of plate tectonics, paleoclimatology, and paleomagnetism are introduced in dribs and drabs as the Precambrian description and discussion progresses, and a full treatment of plate tectonics appears only in chapter 15. The book could have been rearranged in almost reverse order to great effect, at least for the student, who should be taken from the most well known and least problematic, that is Quaternary, geology back to the dawn of the rock record in the Archean.

JOHN F. DEWEY
Department of Geological Sciences, State University of New York, Albany 12222

Cancer Research

Genetics of Human Cancer. Papers from a conference. JOHN J. MULVIHILL, ROBERT W. MILLER, and JOSEPH F. FRAUMENI, JR., Eds. Raven, New York, 1977. xxii, 520 pp., illus. $20. Progress in Cancer Research and Therapy, vol. 3.

This volume is the proceedings of a conference at which 58 contributors and 20 discussants brought their knowledge and foresight to bear on one of the critical problems in oncology: what part do genetic changes, in both germ and somatic cells, play in neoplastic transformation?

A large number of constitutional anomalies that predispose to neoplasia have now been documented; J. J. Mulvihill lists some two hundred single gene traits, many of which are discussed in detail by other contributors. But these, as well as congenital chromosome anomalies, which likewise carry a risk of leukemia or solid tumors, are on the whole rare, and, although their study may illuminate mechanisms of oncogenesis, their impact on the sum total of human malignancy is quite small.

Perhaps of greater importance, therefore, is the evaluation of the respective roles of constitutional and environmental factors (many of the latter being known mutagens) in bringing about the forms of cancer common in the population at large. In this connection, R. W. Miller remarks that "it is as important to know who gets cancer and why as it is to know what environmental agents induce neoplasia in man," and M. Swift points out that heterozygous carriers of genes for rare autosomal recessive syndromes predisposing to malignancy may be relatively common and may themselves be predisposed. (The risks of malignancy in such carriers have yet to be evaluated, however.) The usefulness of epidemiologic studies in tackling these broader problems is affirmed by several of the contributors, particularly those describing special situations such as are presented by "cancer families," cancer in twins, and the genealogically and medically well-documented Mormon population in Utah. It is salutary, however, that some of these contributors give as much space to a discussion of the potential value of a study and the difficulties involved as to the presentation of results so far achieved.

Cancer risk may be associated with the presence of genetic markers, defined by M.-C. King and N. L. Petrakis as proteins or other phenotypes determined by single loci with two or more alleles present at significant frequencies in the population of interest; several contributors discuss the usefulness of genetic markers in epidemiologic studies. P. J. Fialkow summarizes results obtained from the study of the glucose-6-phosphate dehydrogenase marker as they pertain to the question whether the origin of neoplasms is unicellular or multicellular. Limited coverage is given to several other topics, including chromosome abnormalities in cancer cells, immunosurveillance, the use of somatic cell hybrids in the genetic analysis of malignancy, and the place of oncogenic viruses in the order of things.

As is not unexpected in view of the large number of contributors, there is a degree of overlap on some of the topics. This is hardly a disadvantage, however, since different authors frequently present different points of view. For example, on the topic of mutations and cancer, there are separate contributions by A. G. Knudson, Jr., and L. C. Strong relating to the former's model of two mutational steps in carcinogenesis (one either inherited or acquired, the other always acquired), while different approaches are presented by J. Herrmann and D. E. Comings.

N. B. ATKIN
Department of Cancer Research, Mount Vernon Hospital, Northwood HA6 2RN, England