Fossils and Phylogeny

Phylogenetic Analysis and Paleontology. Proceedings of a symposium, Lawrence, Kans., Aug. 1977. JOEL CRACRAFT and NILES ELDREDGE, Eds. Columbia University Press, New York, 1979. x, 234 pp., illus. Cloth, $22.50; paper, $9.

Issues concerning the role of fossils in the reconstruction of phylogeny are old but far from settled. Darwin recognized the potential significance of fossils as evidence for pathways of descent, but he was not impressed with the smattering of data provided by the then-available fossil record. That record has improved enormously since Darwin's time. Nevertheless, controversy over the relationship between fossils and phylogeny persists because the ongoing debate concerning theory and practice in systematic biology brings under scrutiny many of the assumptions and methods that characterize paleontological research.

Joel Cracraft and Niles Eldredge are active paleontologists who believe that many of their colleagues would profit from a greater appreciation of phylogenetic issues. As editors of *Phylogenetic Analysis and Paleontology*, they provide an interesting exposition of contrasting views on these topics. The book reproduces five formal papers and two invited commentaries presented in a symposium held as part of the North American Paleontological Convention II. The papers were presented and organized in the spirit of a debate, but explicit criticisms of the opposing viewpoint are generally confined to the commentaries. Four of the authors (Cracraft, Eldredge, Eugene Gaffney, and E. O. Wiley) can be identified as advocates of "phylogenetic systematics" (also known as "cladism" or "cladistics"), an approach emphasizing branching relationships of taxa based on the distribution of shared advanced characters. The remaining authors (A. J. Boucot, Sara S. Bretsky, and Philip Gingerich) subscribe to methods that emphasize, among other things, phenetic similarity, stratigraphic occurrence, and ancestor-descendant relationships in phylogenetic reconstruction (an approach frequently labeled "evolutionary" or "eclectic" systematics).

The papers in *Phylogenetic Analysis and Paleontology* focus, with varying degrees of emphasis, on four closely related topics: the effects of different models of speciation on interpretations of the fossil record, the bearing of fossil data on hypotheses concerning ancestor-descendant relationships, the logic and testability of phylogenetic hypotheses, and the role of intrinsic data (comparative anatomy and ontogeny) and extrinsic data (spatial and temporal distribution) in phylogenetic analysis. The first topic is the subject of a paper by Cracraft, who briefly reviews the history of views, from ancient Greek philosophy to 20th-century evolutionary biology, on speciation. Much of the paper concerns the eight-year-old competition between "punctuated equilibrium" and "phyletic gradualism" for recognition as the speciation model most compatible with patterns observed in the fossil record. Cracraft does not compare these models at length; rather, he expresses his preference for the punctuated-equilibrium model and considers its favorable implications for paleontological research. In developing his arguments, Cracraft makes several interesting, but contestable, points. For example, he contends (p. 26) that the punctuated-equilibrium model is set apart from neontological theories of allopatric speciation in assuming that speciation is a "geologically instantaneous phenomenon." The matter of tests for such a phenomenon immediately comes to mind. Cracraft suggests the adoption of the concept of "methodological time" because "in the vast majority of cases, our ability to resolve time in the fossil record only allows for 'instantaneous' species formation." This qualification weakens Cracraft's assertion that acceptance of the punctuated-equilibrium model will rescue paleontologists from the pervasive recognition of "gaps" (of either a morphologic or a distributional nature) in the fossil record as imperfections.

One might indeed wonder what minimum standards fossil data must meet in order that punctuated equilibrium, phyletic gradualism, or other evolutionary models be tested. Cracraft states (p. 27) that such tests will require a "very good fossil record" but does not elaborate. Gingerich, who contributes a chapter on his "stratophenetic" approach to phylogeny reconstruction, is more explicit on this matter. He provides several examples from his studies of fossil mammals that he believes illustrate gradual evolutionary change between ancestral and descendant species. Given a "reasonably dense and continuous" fossil record, Gingerich outlines a procedure wherein species or "phenetic clusters" in stratigraphic intervals are recognized, stratigraphic levels are arranged in chronological order, and species at a chosen stratigraphic level are linked to other species in adjacent levels on the basis of overall similarity. He maintains that the spatial and temporal distribution of fossils provides a means of reading phylogeny directly without recourse to a priori hypotheses concerning character evolution. Gingerich's presentation is lucid, and his detailed work on the fossil record is praiseworthy. Nevertheless, his stratophenetic approach has been criticized on several counts. Although older fossils may generally show more primitive traits than younger fossils, there is no guarantee that that is always the case; it is possible that a fossil sequence may actually represent the reverse of the true evolutionary trend (if the older taxon is divergently specialized), and it is extremely difficult to determine whether or not the record is "dense and continuous" enough to preclude this possibility. Moreover, the linking of stratigraphically adjacent taxa on the basis of phenetic resemblance allows more assumptions concerning ancestor-descendant relationships than many systematists are willing to accept, a matter that Gaffney considers in his contribution to the volume. Given this diversity of opinion, independent analysis of the examples cited by Gingerich based on alternative procedures (for example, cladistics) would be illuminating.

The phylogenetic implications of stratigraphic information on fossils are also considered by Bretsky, who employs examples from the invertebrate fossil record to argue that some fossil data are sufficient as tests for theories about ancestor-descendant relationships. Rather than outlining a rigorous procedure for identifying such relationships, Bretsky advocates some flexibility in approach; her statements imply that the quality of the paleontological data will generally dictate the preferred methodology. Bretsky's discussion alights on numerous topics of paleontological interest. Unfortunately, several tantalizing ideas are passed before the reader too swiftly or are blunted by a complicated expository style. Where concepts are developed sufficiently, results are stimulating. For example, Bretsky adds an inter-

esting twist to the punctuated-equilibrium-versus-phyletic-gradualism controversy. She contends that the large-scale separation of populations represents cases where allopatric isolation might not lead to "geologically instantaneous" speciation if development of a geographic barrier were prolonged. Of course, this argument requires the assumptions that gene flow between the populations undergoing isolation was sufficiently damped to allow gradual divergence and that this divergence was not augmented dramatically with complete closure of the barrier. Bretsky also asserts that critics of those who investigate ancestor-descendant relationships rarely consider the problem of intraspecific variation. Her opinions on this issue warrant lively discussion, but are largely unanswered in the volume.

The two remaining papers are discussions of "phylogenetic systematics" or "cladism." Gaffney clearly presents his views on phylogenetic reconstruction and the hypothetico-deductive method in science, the recognition of shared advanced characters as evidence for relationships, and the parsimony procedure in testing phylogenetic hypotheses. In the course of his discussion, Gaffney exposes many of the assumptions tacitly accepted in formulations of phylogenetic hypotheses. These themes are extensively treated in other publications, particularly in articles that have appeared during the last five years in *Systematic Zoology*. Gaffney's contribution, however, is a very useful summary of the basic working principles of cladism, complemented by a lengthy bibliography with references by topic. The paper is not meant to represent a consensus view of cladists. For example, Gaffney concludes (p. 101) that "morphoclines" and "character phylogenies" "can only be deduced by tracing a pattern of structures through a preexistent phylogenetic hypothesis, and are a corollary of that hypothesis." He also claims that morphoclines are misused when more than two states are hypothesized because "even before the polarity of the morphoclines is sought, the statement of it precludes large numbers of alternative sequences." Rather than assuming such morphoclines, Gaffney recommends their subdivision and testing with hypothetico-deductive methods. He provides some logical insight into the problem of morphocline analysis, but his opinions are likely to raise eyebrows among systematists who regard the development of character phylogenies as an integral part of cladistic analysis.

The problem of recognizing assumptions in phylogenetic analysis is further considered in a paper by Eldredge aptly titled "Cladism and common sense." Eldredge distinguishes cladograms (branching diagrams based on distributions of shared advanced characters) from more highly inferential phylogenetic trees, which place branching relationships in a framework of geologic time and allow for the possibility of ancestor-descendant relationships. A third level of reconstruction, and one requiring additional assumptions, is the adaptive scenario, which Eldredge defines (p. 192) as "a phylogenetic tree with an overlay of adaptive narrative." Eldredge presents his arguments on these matters in a refreshingly undogmatic and lucid fashion; even readers not particularly sympathetic to the objectives of cladism may find his discourse heuristic. Examples taken from the author's detailed studies of trilobite evolution nicely complement his arguments.

The invited commentaries, by Boucot and Wiley, reveal radically different attitudes and emphases. Boucot, in a very informal and sometimes amusing fashion, assails the cladists for introducing too much jargon for old concepts and burdening systematists and paleontologists with excessive terminology. He also maintains that cladists have misrepresented the consensus view of paleontological theory and practice. This point seems appropriately aimed in some instances, but one wishes Boucot had elaborated on it. His views on the debate at hand seem aligned with those of Gingerich and, especially, Bretsky insofar as he believes that the methods of phylogenetic reconstruction are highly dependent on the quality of sampling and that this matter has not received due emphasis by cladists. One might counter that cladism does not deny the possibility that better samples (which can also be interpreted as more information about taxonomic characters) might yield "more reliable" phylogenies; it is merely offered as a single method for samples of varying quality.

Wiley's contribution is less an explicit commentary on various opinions raised in the book than an exposition of his own views on species concepts and his conclusions that supraspecific taxa cannot be ancestors and supraspecific ancestors should not be invoked in phylogenetic reconstruction. His ideas are of theoretical interest, but the volume as a whole could have benefited from a more detailed critique of essentially "noncladistic" views. The impression of the book as a record of debate is weakened by the lack of such a critique.

Phylogenetic Analysis and Paleontology is a deceptively short book on some very thought-provoking issues. It presents few major concepts for the first time, but it succeeds in bringing together a diversity of viewpoints, sometimes antithetical, on the relationship between fossil evidence and phylogenetic reconstruction. It is a strength of the book that the disagreement that exists on these issues is not camouflaged. Such conflicts in a science can be disturbing to some, but in retrospect they usually mark times of healthy change. Paleontology and systematics are in a phase of exemplary self-examination that mandates the attention of their own practitioners and those from other sciences.

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A Figure in Psychology

J. B. Watson. The Founder of Behaviorism. A Biography. DAVID COHEN. Routledge and Kegan Paul, Boston, 1979. vi, 298 pp. $20.

Right from the start, Darwinism tended to push psychology toward behaviorism, because it enlarged the scope of the subject to other creatures besides introspective *Homo sapiens*. Evolutionary doctrine said that monkeys and chickens ought to have some sort of protopsychology in them, but we could know about it only from how they acted. Well before 1913, when John B. Watson first declared himself a "behaviorist" in public, biological, psychological, and philosophical journals and monographs were increasingly full of behavior. Watson, however, made a virtue of necessity by arguing that the behavioral measures of comparative psychology were vastly preferable in a natural science, compared to the introspective methods of 19th-century psychology. His claim simply redefined psychology, which became, for him, the experimental science of behavior, rather than the reflective study of the mind.

Watson in 1913 was 35 years old, a handsome, successful, and influential professor of psychology at Johns Hopkins University. He had launched a career with ceaseless productivity as a comparative psychologist, but now he was confronting his contemporaries with something deeper than data. He had crystallized a school, "behaviorism," which psychologists had to accept or reject, for it became a fork in the road for