

Introduction to the Symposium

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There has been an unprecedented amount of introspection among systematists in recent years. As especially reflected in the pages of *Systematic Zoology*, systematists have been examining the theoretical basis of their science. The pursuit has been relentless and, at times, merciless as old shibboleths are put aside and new ones proposed in their stead.

It would be natural to assume that paleontologists have been in the thick of things as the debate on how to reconstruct life's history rages on. Nothing could be further from the truth. Paradoxically, the working days of most paleontologists, whatever they might be filled with, are not devoted to drawing cladograms, phylogenetic trees, or any other similar diagrams depicting their views of phylogenetic relationships among taxa. The prime goal of paleontology is not the reconstruction of life's history—at least judging from the activities of the vast majority of its practitioners. Contrary to the remarks of a reviewer of an early version of the present book, the entire multivolumed work *Treatise on Invertebrate Paleontology* contains relatively little about phylogenetic relationships—in many cases absolutely nothing (e.g., the volume of trilobites)—and this can be taken as a fairly accurate reflection of the way paleontologists typically order their priorities.

Despite this state of affairs, the myth persists among paleontologists (and also quite a few of our neontological colleagues) that fossils somehow afford the best, if not the only, means of reconstructing phylogenetic history. This

view has been challenged persistently since Darwin's day. Haeckel, for example, never believed it. It stands to reason that if paleontology affords a special, privileged means of insight into evolutionary history, its practitioners have an obligation to specify their method. But, with few exceptions, they have been collectively silent during most of the recent discussion about method and theory in phylogenetic reconstruction.

The above perception of paleontological practice provided the rationale for the present symposium, which was held as part of the North American Paleontological Convention II, convened at the University of Kansas in Lawrence, Kansas, on August 7-10, 1977. All participants were chosen for their conviction that phylogenetic analysis is important in paleontology and that attempts to systematize fossil species should be based on an analysis of phylogenetic history.¹ All appear also to believe that good systematics underlies all but the most purely theoretical work done in paleontology. Hence the reconstruction of phylogeny assumes a position of central importance as the basis for subsequent research on fossils—after all, how can we do anything with a fossil unless we know what it is? The participants in this symposium appear to agree that "What it is" in the last analysis boils down to "What are its relationships?" It is our collective intention in this symposium to underscore our conviction that phylogenetic research has been badly neglected in paleontology and that such research of the highest caliber is necessary for further progress in our understanding of the nature of life's history. We test hypotheses of process with corroborated hypotheses of pattern, but we do not yet have more than a rather dim and confused notion of that pattern.

A second, more specific aim of this symposium is to expose and elucidate the contemporary controversy regarding the methodology of phylogenetic reconstruction. All of the participants have a strong paleontological back-

¹ Numerical taxonomy is conspicuous in its absence in this symposium—all the more surprising, perhaps, because the symposium was held in Lawrence, Kansas, long the North American center of numerical taxonomy. The decision to omit numerical taxonomy from the symposium reflects the disinterest in phylogenetic reconstruction expressly stated by the leading theoreticians of numerical taxonomy. However, numerical techniques are of course germane to phylogenetic reconstruction, and more importantly, a considerable segment of systematists believe that phenetics—the ordering of the biota in terms of overall phenotypic similarity—is important for the estimation of overall genetic similarity and hence crucial to phylogenetic reconstruction. Thus phenetics, the theoretical basis of numerical taxonomy, is represented in several contributions to this symposium.

ground and were invited on the basis of their recent contributions to the debate on these and related topics within paleontology. The plan of the book follows the organization of the symposium; there are five papers (which comprised the formal session) followed by two shorter papers commenting on the formal ones. The five formal papers were organized as a sort of debate. The first paper, by J. Cracraft, presents an overview of phylogenetic research in paleontology—its history, relationship to evolutionary theory, current status, and proper place within the discipline. The remaining four papers are organized to illustrate the diversity of opinion within vertebrate paleontology (P. D. Gingerich and E. S. Gaffney) and invertebrate paleontology (S. S. Bretsky and N. Eldredge). Each of the latter four speakers was given a list of questions (devised by Cracraft and Eldredge, organizers of the symposium) which he or she was asked to consider during preparation of the manuscript: What, exactly, is a phylogeny? What is the relationship between evolutionary theory, on the one hand, and ideas about the nature of phylogenetic reconstruction, on the other? What are ancestors and how might they be recognized? What is character analysis? Is there any point in recognizing a formal distinction between primitive and derived character states? And if so, how do we determine what is primitive and what is derived? In connection with character analysis, how do we utilize intrinsic data (i.e., comparative anatomical and morphogenetic information) and how do we handle extrinsic data (i.e., information on the distribution of organisms in space and time)? and finally, how do we string all of this information together into a phylogeny?

These questions were formulated, not to serve as an outline for each paper, but to give common points of reference on the more crucial issues currently debated, thus providing a common theme to each of the latter four papers. "Standard," or "traditional," paleontological approaches to phylogenetic reconstruction have been only occasionally, and in general incompletely, developed in the literature. Opinions differ, of course, as to exactly how this approach should be structured. In this symposium, P. D. Gingerich and S. S. Bretsky develop their own original formulations which, although they transcend "traditional" approaches in many respects, nonetheless appear to represent, in analytic form, prevailing and preferred views on the methodology of phylogenetic reconstruction in paleontology. E. S. Gaffney and N. Eldredge, on the other hand, discuss their views on the application of "phylogenetic systematics" (also known as "cladism") to the fossil record. No

two cladists agree with each other (or, for that matter, with Willi Hennig) on every point, and this "school" of systematics is no more a monolith than that of the more traditional "evolutionary taxonomy," or even the school of "numerical taxonomy." Thus the papers were organized as a sort of debate, with the essential difference being that there were no formal presentations explicitly criticizing the opposing point of view, in the expectation that the two invited critical commentaries and the open discussion would supply ample quantities of criticism.

The five formal papers were presented at the opening session of the North American Paleontological Convention II on August 8, 1977. The two invited commentaries, by A. J. Boucot and E. O. Wiley, were presented in the evening of August 8 and were followed by several hours of discussion. All seven manuscripts were prepared before the convention and circulated to the other participants; the commentaries by Boucot and Wiley were prepared in direct response to the drafts of the five papers presented formally. Final versions of all seven manuscripts were prepared in response to commentary from other symposium participants, persons in attendance at the symposium, and reviewers arranged for privately by the individual authors and Columbia University Press. On the whole, they are faithful renditions of the gist, if not the exact verbiage, of the symposium held in Lawrence.

Was the symposium a success? Judging from the attendance at both the formal session in the morning and the more informal evening session, it was. Our basic aim was to stimulate interest in the general subject of phylogenetic reconstruction in paleontology and to inform anyone interested as to what the issues, in fact, are. All of the participants received a great deal of commentary on the material they presented, and in some cases, the commentary was not very polite or flattering. But commentary it was—hence our conclusion that the desired stimulation was achieved.

The title of the symposium, "Phylogenetic Models," turned out to be, in a sense, a *double entendre*. Many people interpret "phylogenetic models" as sets of views pertaining to the nature of the evolutionary process. Nearly all of the invited participants discussed evolutionary theory, and many of the evening discussants seemed frankly more interested in such notions than in the nitty-gritty of phylogenetic reconstruction. We acknowledge the stronger appeal that evolutionary theory (i.e., the causal process itself) may have over the seemingly drier subject of methodology of phylogenetic reconstruction (i.e., analysis of historical pattern). But surely these subject areas

are related. Some of us think that notions of the evolutionary process logically imply which of the available approaches to phylogenetic reconstruction should be chosen. Some of us think that we can intelligently discuss evolutionary processes within paleontology only when we compare existing hypotheses about process with phylogenetic patterns and thus that the pattern must be worked out before statements on process can be made. Whatever the proper connection may be, evolutionary theory cannot progress much further without a better set of patterns of historical relationships among the elements of the biota, and it is to this subject that the book is specifically addressed. Perhaps by the time of North American Paleontological Convention III we shall be ready for a symposium on the relationship between paleontology and evolutionary theory *per se*. For now, we are pleased to present the proceedings from the symposium on phylogenetic reconstruction held in Lawrence in 1977.

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