phylogeny debated

Last August in Lawrence, Kan., scientists gathered for the North American Paleontological Convention. Perhaps the most-argued issue came up in the opening session, and the first 2 speakers have restated their views for Geotimes:

During the last decade the challenge of new theory and methodology has infused new vigor into systematics, that discipline of biology most concerned with the history of life. Nowhere, perhaps, is change going to be felt more than in paleontology.

If a general theory of phylogenetic analysis is to be developed it must encompass 2 fundamental issues. First is the model one might propose to explain the origin and diversification of evolutionary taxonomic units, which most systematists call species. The second issue is the theory and method one chooses for reconstructing the geometry of phylogeny, *i.e.*, the pattern of relationships among taxa, both extant and extinct.

The origins of current paleontological thinking about the evolutionary process can be understood only against the background of the development of modern science itself. The writings of Aristotle, Plato, and others initiated the belief that nature's objects, including living organisms, were arranged in a hierarchical order of perfection, with imperceptible differences among the objects. Physical science in the 16th a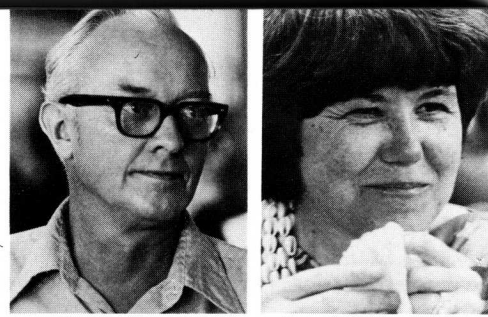nd 17th centuries contributed to the replacement of the Aristotelean idea of a stable, fixed universe with a view of constant change and motion governed by a few fundamental natural laws. The introduction in the 18th century of **1** the notion that change of the earth's surface was slow, and **2** uniformitarianism contributed to the necessity for vast amounts of time. The idea of gradual change thus was derived from geological observations but also from the replacement of the philosophical doctrine of essentialism by a nominalistic view of the *scala naturae*. The essentialist view was that species—as all objects of nature—were fixed, immutable entities; nominalism perceived species as nondiscrete, and nature was a chain of insensible gradations among forms.

Darwin assimilated the view that change must be slow and gradual and thus inferred that species are merely segments of an evolutionary continuum. His evidence did little to support these expectations, and he rationalized this by appeal to an incomplete geological record. Furthermore, to accept discrete, real species would seem to require belief in creationism.

The acceptance of slow, gradual change of one species into another has dominated the post-Darwinian paleontological perspective. Recently, some paleontologists, Niles Eldredge and Stephen Jay Gould in particular, have advocated the adoption of a neontological conception of species in which the latter are taken to be discrete, real entities, originating via geographically isolated populations. The species concept of paleontology and that of most neontology are not compatible philosophically, the former reflecting a nominalistic point of view, the latter an essentialist one.

What model of the evolutionary process should paleontologists adopt? I support the allopatric speciation model because **1** it unifies paleontology and neontology in terms of the conceptual framework predominating within modern evolutionary biology, **2** it will provide the conceptual foundation for an explosion of theory and methodology within paleontology, and **3** it will facilitate the incorporation within paleontology of a scientifically more rigorous methodology for reconstructing the history of life. This support should not be taken as a denial that phyletic evolution or gradualism occurs, but allopatric speciation seems to be more generally applica-

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A phylogeny is an outline of the evolutionary history of a group of animals. Traditionally, the study of phylogeny has been almost exclusively the domain of paleontology. Time is the principal dimension of history, as it is of phylogeny, and time on an evolutionary scale is a unique attribute and contribution of the fossil record. Hence it is not surprising that establishment of organic evolution in the 19th century was made by geologists and paleontologists: Lamarck, Cuvier, William Smith, Lyell, and Darwin all had first-hand experience working with fossils. Evolution as a general empirical fact was established a century ago, but there remains today a very active discussion of competing evolutionary models.

The fossil record is imperfect, and frustration with its imperfection has caused repeated attempts to reconstruct animal history without historical records. Elaborate systems have been built up, the current one being 'cladistics', to try to reconstruct phylogeny from comparisons of living animals. This is rather like trying to understand the growth and development of American railroads by watching trains. A cladistic approach to phylogeny is perhaps defensible when that is all that is possible, but many animal groups have an excellent fossil record, and any real understanding of patterns and processes of evolution must be based on these groups.

Current disagreements regarding speciation can be traced in large part to differences in one's approach to phylogeny reconstruction and to the quality of the fossil record supporting the phylogeny. Development of the latest saltational model of speciation, 'Punctuated equilibria' (see Stephen Jay Gould and Niles Eldredge, 1977, *Paleobiology*, 3:115-151), can be traced to Eldredge's cladistic study of the Devonian trilobite *Phacops* (*Evolution*, 25:156-167). Cladistics is a method based purely on morphology; species are diagnosed only on morphology, and it is not surprising that transitions between species are not preserved. Using a strictly morphological method, intermediate samples are artificially divided and placed in one or another of predetermined morphological 'species'. The point of this digression is to emphasize that our approach to phylogeny has a direct effect on how we perceive species and their evolution.

How does one reconstruct evolutionary history from the fossil record? Morphology is important to be sure, but it must be studied and interpreted in a temporal context. This temporal context is provided by stratigraphy, giving fossils their unique importance for phylogeny. If one studies all of the fossils from a given geologic stratum, they can be
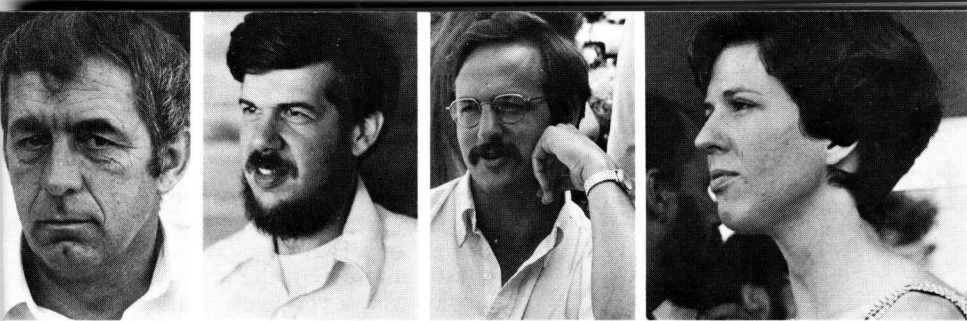
Left to right:
Norman F. Sohl, U.S. Geological Survey, Washington, D.C.
Jane Gray, Oregon State University, Corvallis.
Stanley S. Beus, Northern Arizona University, Flagstaff.
Stephen Jay Gould, Harvard University.
Philip D. Gingerich, University of Michigan, Ann Arbor.
Patti Swan, U.S. Geological Survey, Menlo Park.

ble to the analysis of the evolutionary process itself.

The second major component of phylogenetic analysis is the research strategy one adopts to reconstruct the *pattern* of phylogeny. Traditional paleontology would have us search the rocks for ancestors; this tradition, viewing fossils as 'directly historical data', has demanded the necessity of fossils if phylogenetic reconstruction is to be undertaken. An alternative methodology was first formulated precisely by the German entomologist Willi Hennig and is gaining wide acceptance within neontology but only recently has been introduced into paleontology. The basic premises of phylogenetic systematics, as it is called, follow.

The pattern of phylogeny is one of branching and divergence, and this branching implies a hierarchical structure to that pattern. *Cladograms* are hypotheses about the structure of nature's hierarchy. Cladograms are not in themselves phylogenies for they do not incorporate decisions about the 2 kinds of relationships ancestral-descendant and common ancestry. Rather, cladograms are branching diagrams of nested sets of taxa manifesting a nested pattern of shared similarities. *Trees* are exten-

sions of cladograms in that decisions about the recognition of ancestors have been made. Cladograms are more general statements than trees because a branch point of the former includes the possibility of either a common ancestry of the 2 taxa involved or, when species-level taxa are being considered, an ancestral-descendant relationship between the 2 species.

How are cladograms constructed? There are only 2 kinds of similarity: nonevolutionary (nonhomologous, convergent) and evolutionary (homologous). Of the latter, 2 or more taxa may share similarities that were inherited from ancestors more distant than their immediate common ancestor (primitive similarities) or they may share similarities inherited only from their immediate common ancestor and not shared with more distantly related taxa (derived similarities). Homologous similarities can always be considered derived at one level of the hierarchy and primitive at all more inclusive levels. Hence, the structure of the hierarchy is defined in terms of shared derived similarities. The latter can be hypothesized after extensive comparative analysis of all pertinent taxa; similarities present within the group in question

and also common to taxa presumably closely related can be assumed to be primitive. The expectation of a cladogram which truly reflects the hierarchical structure of nature is that the nested patterns of shared derived similarities will be congruent.

To summarize, evolutionary paleontology currently operates within a tradition defined more by the supposed empirical observation of life's history rather than by its inference. It is also clear, with respect to theory and method, that paleontology has been isolated from neontology. Neontologists have given to paleontology the responsibility of interpreting life's history upon the misunderstanding, on both sides, that the dimension of time is somehow the key to that history. I claim this has prevented a unified theory of comparative biology applicable to neontology and paleontology alike. The adoption of both the allopatric speciation model and the methods of phylogenetic systematics will go far in solving these critical problems of evolutionary paleontology.

Joel Cracraft
Department of Anatomy
University of Illinois
at the Medical Center
Chicago, 60680

clustered into discrete groups of very similar individuals representing the different basic kinds present, just as one identifies species of birds in the backyard by grouping them into clusters of similar individuals. The advantage of the fossil record is that one can follow this with study of the next higher stratum and identify clusters as before. Doing this for a long series of superposed strata, it is possible to trace the same basic kinds of animals up through the geological column and link them into lineages—some lineages change through time while others may stay the same. A lineage that does not change significantly is retained in a single species, while a lineage that changes markedly can often be subdivided into several successive species by choosing arbitrary strata as cut-off levels, rather as one chooses the vertical position of the minute hand on a clock as the cut-off point between hours. From such studies one perceives species as

units of evolutionary lineages. Transitions from one species to another are usually continuous and gradual. Even the division of one lineage into two often appears gradual. I described several examples of this in fossil mammals last year (*American journal of science*, 276:1-28). Although mammals cannot adequately represent the entire animal kingdom, this study does illustrate the detailed stratigraphic approach that must be taken if we are to gain an unbiased view of species and their origin.

The discussion above has been limited to evolution at the species level. What about evolution at higher levels? What can we say about the relationships of major groups of animals? We can take the same stratigraphic approach just outlined, albeit usually proceeding stage by stage, or epoch by epoch rather than stratum by stratum. For example, tracing cats and dogs backward in the fossil record we see them converge in the

Eocene into a single group, the miacid carnivores. This convergence is strong empirical evidence documenting the close relationship of cats and dogs, and permitting one to date their time of divergence.

As a final question, are evolutionary hypotheses constructed in this way 'scientific'—are they testable? Some measure of the reliability of a phylogeny can be gained by examining the density and continuity of the fossil record on which it is based, but the real test of any hypothesis is the extent to which new data fit into it. Fortunately, new paleontological discoveries are made every day, and they test stratigraphically based phylogenies as rigorously as any hypothesis is tested in other branches of science.

Philip D. Gingerich
Museum of Paleontology
University of Michigan
Ann Arbor, 48109