Paleobiology: Random Events over Geological Time

Patterns abound in the fossil record. Species emerge, diversify, change their shapes, and become extinct in ways that have been viewed as decidedly nonrandom. Traditionally, paleobiologists have focused on the individual histories of various species, endeavoring to understand how each evolved the way it did and to provide a basis for formulating general laws that would explain these individual histories. However, in almost no cases has this approach led to explanations or predictions of the patterns of evolution.

In August 1972, a small group of investigators met at Woods Hole to devise a new way to study the fossil record. This group, which consisted of Thomas Schopf of the University of Chicago, Stephen Jay Gould of Harvard University, Daniel Simberloff of Florida State University, and David Raup of the University of Rochester, developed models that treated evolution as a random process. Their aim was to see whether random events are sufficient to generate patterns that are qualitatively similar to those found in the fossil record. Those patterns that could not be generated by random processes would then be prime candidates for detailed studies and deterministic explanations. Thus, these investigators hoped to use models based on random events to pick out significant phenomena from the vast and bewildering array of paleontological data.

Schopf likens the models that he and his colleagues developed to those used to study the behavior of gases. In such models, each gas molecule is treated like every other gas molecule. And, although the behavior of each molecule can be described by Newton's laws of motion, the overall behavior of the gas can be more easily described when the molecules are treated as statistical entities. For example, this statistical point of view leads to an understanding of why a gas changes its pressure and temperature when its volume is altered. Such an understanding would be very hard to come by on the basis of Newton's laws alone. Schopf believes that, over geological time, individual species might be treated somewhat like gas molecules. Their emergences and extinctions may have particular causes but the overall patterns of paleobiology may only become clear when the species are treated as statistical entities.

By developing statistical models of the evolutionary process, Schopf, Gould, Raup, Simberloff, and others have obtained results that, they believe, lead to a new understanding of the fossil record. They recently have drawn on these results to propose solutions to some outstanding problems involving patterns of phylogeny, evolution of particular morphological forms, rates of evolution, and causes of faunal extinction. Although somewhat controversial, their methods and conclusions are arousing a great deal of interest among paleobiologists.

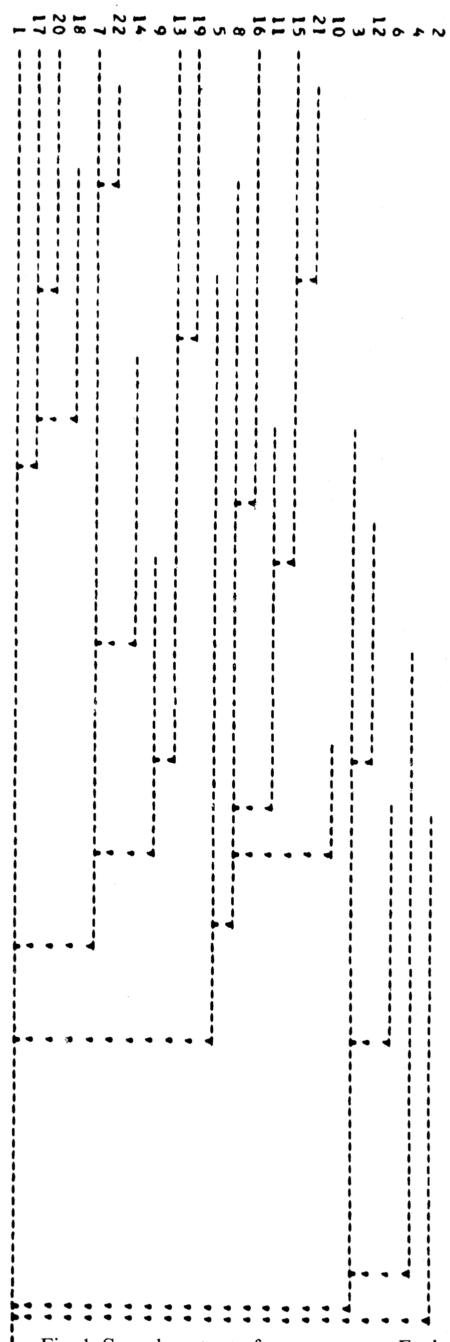

Fig. 1. Sample output of computer run. Each vertical dash represents one time unit. [Courtesy of Thomas Schopf]

Different phyla, or genetically related groups of organisms, have evolved in different ways. Some groups, such as the dinosaurs, gradually increased in species diversity and then rapidly became extinct. Other groups, such as the trilobites, diverged quickly into a large collection of species and then slowly died out. Raup, Gould, Schopf, and Simberloff modeled these patterns of phylogeny with a computer simulation based on random, or stochastic, events assumed to affect all species in the same ways.

The computer simulation is used to generate a family tree of species (Fig. 1). At each unit of computer time, each species in the tree can diverge to form two species, go extinct, or remain the same. What each species does at each time is decided by a process equivalent to rolling a weighted die. The probabilities of extinction, branching, and remaining the same are decided before the computer run begins. Then, computer-generated random numbers are used to determine which events take place at each time.

Raup, Gould, Schopf, and Simberloff assumed in their computer simulation of phylogeny that species diversity would increase only until it reached a predetermined equilibrium value. When the computer run begins, the probability of species branching is set higher than the probability of extinction so that the number of species increases. This corresponds to a period soon after life originated when there were few species and many available niches. Species, presumably, quickly diversified as they evolved to utilize different resources. After a while, species diversity leveled off as ecological niches were filled. This situation is simulated in the computer model. When species diversity reaches the equilibrium value, the probability of branching is set equal to the probability of extinction so that species diversity levels off and, from then on, oscillates about the equilibrium value.

In order to interpret the computer-generated lineages of species in terms of the taxonomic groups studied by paleobiologists, Raup and his associates divided the lineages into subunits, called clades, which they consider to be equivalent to higher taxonomic groups. These clades, they found, evolved in patterns very similar to patterns of phylogenies deduced from the phylogenetic record (Fig. 2). For example, one clade pattern looked like the pattern of the dinosaurs and another looked like that

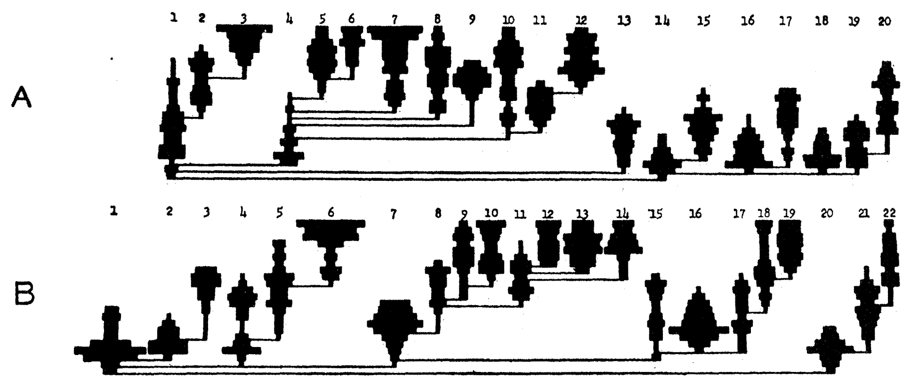

Fig. 2. Clades produced by two computer runs. Clade A-16 rapidly increased in diversity and then gradually died out, similar to the trilobites. Clade B-3 gradually increased in diversity and then rapidly died out, similar to the dinosaurs. [Courtesy of Thomas Schopf]

of the trilobites. This result, according to these investigators, means that variations in evolutionary patterns are not necessarily the result of inherent biological differences between species.

A second result of the computer model provides what Raup and his colleagues call "a new perspective on evolution." In one computer run, 20 percent of the clades, by chance, became extinct at the same time. When such events occur in real life, these investigators claim, deterministic explanations are sought. However, the computer simulation provides evidence that different groups of species can die out for totally unrelated reasons and yet, by chance, they can die out simultaneously.

Raup and Gould extended the computer model of phylogeny to study the evolution of morphology. Often during the course of evolution, species will change in form according to what looks like irreversible trends. For example, around the time of the dinosaurs there was a widespread evolution toward gigantism. Species evolved, becoming bigger and bigger until they eventually became extinct. Once started on such a path, species did not regress to smaller size. Such phenomena have been the subject of a great deal of speculation. Evolutionists named the phenomena directional or unidirectional selection and explained them by evoking selection pressures that force species to evolve along certain paths. Raup and Gould, however, speculated that seemingly directed patterns of morphological evolution could be produced by random events.

In their computer simulation of the evolution of morphology, Raup and Gould assigned the ancestral species a "morphology" that consisted of ten characters, all of which were arbitrarily set at 0 when the computer run began. The morphology of the ancestral species was, then, (0,0,0,0,0,0,0,0,0,0). At each unit of computer time, each character of the morphology could change by increasing or decreasing one unit. Whether a character of the morphology changed was decided by chance. Thus, in the computer model, morphologies evolved as species evolved and, like speciation, morphological change was a random event.

The computer-simulated evolution of morphology, Raup and Gould found, displays patterns like those attributed to unidirectional selection. They conclude that undirected, rather than directed, selection may predominate during the course of evolution.

Rates of Evolution

Paleobiologists and zoologists have long sought an explanation for what has been termed different rates of evolution (*Science*, 8 August, p. 446). The claim has been made that different groups of organisms evolve at very different rates. Mammals, for example, are said to have evolved an order of magnitude faster than clams. However, the existence of different rates of evolution contradicts a fundamental hypothesis of the computer simulation of evolution: namely, that all species can be treated alike.

Schopf, Raup, Gould, and Simberloff considered the possibility that these so-called variations in rates of evolution may be an artifact of the way those rates were measured. They studied the taxonomic literature to see how many descriptive characters are used to categorize different organisms. Organisms, such as clams, that are said to evolve slowly are characterized with far fewer descriptors than organisms, such as mammals, said to evolve rapidly. With more descriptors that can be used to detect morphological changes, more complex organisms could appear to evolve more rapidly. Schopf and his associates find that, when rates of evolution are normalized to take into account the number of descriptors of morphological change, different organisms evolve at similar rates.

Although many patterns of the fossil record can be generated by random events, some phenomena do not fit this model. For example, random processes are not sufficient to explain the mass extinctions that took place several times during geological history. One of the most dramatic of these extinctions took place during the Permian period—from 275 to 170 million years ago. During this time, the total number of shallow water marine invertebrate species decreased by 50 percent. Species diversity increased again after the Permian (during the Triassic period), but it never again reached the abundance of the early Permian period. Schopf and Simberloff propose that the Permian extinctions can be explained by means of an equilibrium model from theoretical ecology.

The model from theoretical ecology is based on the hypothesis that species diversity is a function of habitable area. An island, for example, will support fewer species than a large landmass of the same ecological complexity. If all species are removed from an island (after a volcanic eruption, for example), new species will colonize the island and species diversity will increase until it reaches an equilibrium value characteristic of the island's area.

Schopf and Simberloff suggest that species diversity decreased dramatically during the Permian period because the area habitable by shallow water marine invertebrates decreased. Schopf analyzed published paleontological data to show that, when continents coalesced during the Permian, the areas of shallow marine seas decreased by about 70 percent. He then collated data on shallow marine sea area and species diversity of marine invertebrates at various times during the Permian. Simberloff showed that these data are in agreement with the curves predicted from the model from theoretical ecology relating species diversity to habitable area.

The statistical models advanced by Raup, Gould, Schopf, and Simberloff to generate the overall patterns of the fossil record are based on the assumption that some sort of species equilibrium was reached long ago. Fluctuations in species diversity then would reflect changes in proportions of various habitats, such as marine versus terrestrial. Although it is difficult to test this hypothesis of species equilibrium, Raup and Gould have recently obtained evidence indicating that the hypothesis may be correct.

Raup statistically analyzed the size, shape, and duration of clades that arose from the computer simulation of phylogeny. This analysis provided Gould with a standard for comparing real clades in order to see whether differences exist be-

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tween real and randomly generated systems. He discovered that real clades of shallow water marine invertebrates that originated in the Cambrian and Ordovician periods differ from randomly generated clades. These clades fill up more quickly with species and die out more slowly than the random clades. However, during these periods, which occurred early in geological history, the earth was filling up with species. After the Ordovician, during the Silurian period, all major taxonomic groups were established and no new phyla originated. At this time, presumably, species diversity could have reached equilibrium. Gould found that the clade shapes for shallow water marine invertebrates during and after the Silurian resembled those of the randomly generated clades.

Not all investigators accept the models and conclusions drawn by Raup, Gould, Schopf, and Simberloff. Arthur Boucot of Oregon State University, for example, thinks the models are too simple. They are "clever, polished, but of limited use," he says. Randomness in evolution is not unexpected, Boucot points out. And major geological events, such as climactic changes, are correlated with major evolutionary events, such as massive species diversifications and extinctions. However, such correlations are not considered in the models that treat all species and all geological times alike.

Another criticism of the stochastic models of evolution is voiced by Karl Flessa and Jeffrey Levinton of the State University of New York at Stony Brook. These investigators used the independent statistical techniques of factor analysis and the runs test to argue that the originations of various taxa in the real world did not occur at random and that there are nonrandom patterns of taxonomic diversity in the fossil record. In other words, they believe that many of the patterns in the fossil record could not have been randomly generated. Gould and Schopf, however, are not convinced that Flessa and Levinton have demonstrated patterns above and beyond those that could be derived from random processes.

Although equilibrium models in paleobiology are still a new concept, Schopf believes that they are leading to a revitalization of that field. Investigators devoted the past century to studying the histories of individual species, but were unable to solve some major problems. Now that a new conceptual framework has been introduced, says Schopf, "it will be fun to see where things go."—GINA BARI KOLATA

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