be studied further. If both parents in a family are homozygous, it cannot provide useful information about the inheritance pattern of RFLP in the progeny.

Once the inheritance pattern of an RFLP has been traced in all the appropriate families, the data must be sent to Dausset at CEPH. The computer there can compare the results with the inheritance patterns of different RFLP markers that were determined in other laboratories to determine which markers are linked and how closely. "We hope to accelerate in this way the mapping of the human genome," Dausset says. "If many laboratories use the same families, it will be much easier."

The experiment has been arranged, Botstein points out, to obviate a consideration that might otherwise have been a problem. It requires the sharing of data, but not of the probes themselves, which investigators might have been much more reluctant to do. "What Dausset has done," Botstein explains, "is to make it possible for people to work together. He has reduced the competition problem."

How long it will take to complete the map is uncertain. This depends on the length of time required to cover the human genome with markers of suitable quality. The minimum required for future studies aimed at detecting linkages with disease loci is probably in the range of 100 to 150 evenly spaced markers.

Many additional RFLP's may actually have to be mapped to obtain markers of the desired quality, which will largely be determined by how many variants they have. Although in excess of 200 probes that detect RFLP's have been reported, perhaps only 10 to 20 percent have sufficient numbers of variants to be highly informative in gene linkage studies of human genetic diseases. In this context, more is definitely better.

Markers with many variants can provide more information because the variation helps to ensure that many members of the population will be heterozygous at the marker locus. This is a requirement for linkage studies. High polymorphism is especially important for showing linkages with genetic disease loci, a situation in which the families of interest are likely to be much smaller than those available for making the human genome map.

—JEAN L. MARX

Additional Reading

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2. G. M. Lathrop, J. M. Lalouel, C. Julier, J. Ott, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 3443 (1984).
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Pattern and Process in Life's History

Higher level selection processes are becoming acknowledged as important influences that shape the history of life

There are patterns in the history of life, of that there is no doubt. The question for evolutionary biologists is, how are these patterns to be interpreted? Specifically, if the perceived patterns are true deviations from chance clusterings, what is their configuration; and what processes might be responsible for shaping them?

The past several years has witnessed a good deal of public debate on some of these matters, which has ranged from proclamations of the supposed imminent demise of neo-Darwinism to suggestions that life on Earth is periodically assaulted by extraterrestrial bolides. Although the content of the public utterances has sometimes diverged startlingly from the exchanges between scholars of the subject, the razzmatazz accurately reflected the degree of intellectual foment.

Responding to the excitment of the times, the Dahlem Konferenzen, in West Berlin, last month held a workshop* that attempted to draw together some of the disparate approaches and viewpoints relating to these issues.

In common with Dahlem conference tradition, participants at this one were divided into four groups, each set the task of examining one major approach to the overall problem. The first group looked at some of the most obvious apparent patterns, such as the increase in complexity of life forms through time, the increase in body size within taxa through time, and so on, and discussed ways of testing their significance. The second concentrated on the causes and consequences of extinction, a very lively topic just now. The task of the third group, which included a mix of population geneticists and paleontologists, was to investigate the relationship between genomic and organismic evolution. And the fourth group concentrated on the evolution of communities, both living and fossilized. The overall goal was to see how far biological and paleobiological approaches could be integrated in a move "towards a new understanding of large-scale evolutionary change."

As ambitious a project as this was certain to lead to frustrations, not least because the languages and concepts employed by population geneticists, paleontologists, and ecologists are so disparate as to militate against ready communication. Moreover, the tone of disputation between population geneticists and paleontologists during the past decade has at times been harsh. In spite of these difficulties, however, the Dahlem meeting scored certain notable advances that mark an important turning point in the further development of evolutionary biology. There still are gaps between different intellectual approaches, to be sure, but there has been clear enhancement in mutual understanding, in addition to some very striking agreements.

By far the most notable of these agreements was the acceptance by the population geneticists that certain major evolutionary trends revealed in the fossil record might be the result of selection between species, a process that is analagous to selection between individual organisms within a species. This formulation, known as species selection, casts evolution as a hierarchical process and extends, but not replaces, conventional neo-Darwinism, which traditionally has focused on natural selection within species. The notion of species selection emerged from the development of the punctuated equilibrium hypothesis, initially advanced by Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University, in 1972. Important developments of the theory's implications have been made by Steven Stanley of Johns Hopkins University and Elisabeth Vrba of the Transvaal Museum, Pretoria.

Until last month's Dahlem meeting most population geneticists strenuously

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*The Dahlem Workshop on Phanerozoic, Life: Pattern and Processes, was held in Berlin from 16–21 June, 1985. The proceedings will be published by Springer-Verlag, Berlin/Heidelberg/New York/Tokyo.

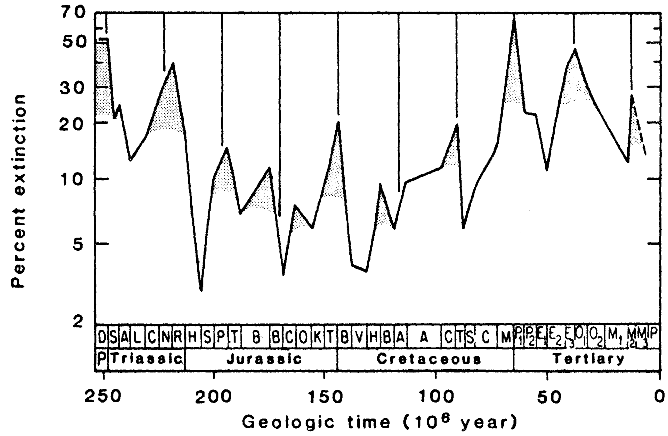
supported the conventional neo-Darwinian explanation of evolutionary trends: no higher levels of selection were required, they said. John Turner, a population geneticist at Leeds University, England, played a key role in persuading his colleagues of the importance of a hierarchical view of evolution. The rapprochement on this point is certain to provide solid foundation on which to build further synthesis.

Much of the intellectual conflict within evolutionary biology in recent times has centered on the punctuated equilibrium hypothesis and its unfavorable reception among population geneticists. Eldredge and Gould put forward the hypothesis as an alternative to the neo-Darwinian explanation of evolutionary change.

In strict neo-Darwinism, species track shifts in their environment through the selection of heritable adaptations: at its simplest, four-toed *Eohippus* became single-toed *Equus* through a series of equally adapted intermediates, each merging gradually, imperceptibly into the other. Eldredge and Gould said that the fossil record does not look like that. Instead, once they arise, species appear to track a more or less unvarying course, at some point to give rise to clearly related but distinctly different descendants. The origin of a new species is too rapid an event to be traced in the fossil record, except in unusual situations.

Key elements of the hypothesis, therefore, are the putative stasis of species through most of their history and the concentration of morphological change at the branching point at which a new species arises. How well have these elements stood up to scrutiny?

The population genetics group at the Dahlem meeting appeared to be ambivalent about stasis, at one point noting that invariance is a common theme of evolution, which needs to be understood, and at another stating that there is no evidence that stasis is common in the fossil record. By contrast many paleontologists do see stasis as a common feature of the fossil record.



Periodic extinction

Raup and Sepkoski's original extinction chart based on marine families. [Proc. Natl. Acad. Sci. U.S.A. **81**, 801 (1984)]

Generally, stasis has emerged as "a phenomenon that calls for an explanation," as John Maynard Smith, an avowed neo-Darwinian at the University of Sussex, England, noted recently. One interpretation, which is within the neo-Darwinian tradition, is that it is the result of normalizing or stabilizing selection. A second notion, related to the first, is that stasis might be the result of the tight packing of niche space, which is loosened by extinction: surviving species then "rush" to fill the newly available ecological opportunities, changing morphologically as they go. The ecologists were not much impressed with this idea, as there is little evidence that niche space is ever tightly packed in any important manner.

Eldredge and Gould suggested that stasis indicated that morphological change was perhaps more circumscribed than had been allowed by conventional population genetics theory, particularly through the constraints of development. Limitations of this sort had once been part of the perceptions of evolutionary biologists—to wit, C. H. Waddington's canalization—but had slipped into oblivion somewhat, partly because the whole business of development appeared so mystical. Judging from recent literature of evolutionary biology, and from exchanges at the Dahlem meeting, neo-Darwinists have welcomed back the notion into their purview.

The population geneticists' criticism of stasis at the Dahlem meeting was as naught compared with their assessment of the putative link between speciation and morphological change. The assertion, they argued, is untestable in the fossil record. It is true that work on living organisms shows that many closely related pairs of species can be virtually indistinguishable morphologically, so much so that a paleontologist would probably classify them as a single species if they were to be found in the fossil record. The only kind of speciation that would be identifiable in the record, therefore, would be one that was accompanied by morphological change. Hence, the argument runs, this aspect of the hypothesis is untestable.

Gould's reply was that yes, speciation clearly can occur in the absence of morphological change. What the hypothesis addresses, however, is the location of morphological change, when it does occur: first look for the event where morphological change is concentrated, and then ask if it coincides with speciation.

The hypothesis is vulnerable to evidence such as that of Anthony Hallam of the University of Birmingham, England. He traces the history of certain bivalves in the record and sees long periods of stasis, which, although interrupted by concentrated bursts of morphological change, does not seem to be accompanied by splitting of the lineage, or speciation. In addition, Turner described significant pigment change within the butterfly species, *Heliconius*.

Both of these examples appear to demonstrate morphological change without associated speciation, which, if repeatedly shown to be the dominant pattern, would indeed sink this aspect of the punctuated equilibrium hypothesis.

One of the most striking patterns in the history of life is the very rapid evolution of the different body plans—bauplane—once multicellular organisms became established in the late pre-Cambrian, 600 million years or so ago. Virtually all existing phyla, and many that have since been extinguished, originated within a period of 20 million years. The Cambrian therefore was a time of great elaboration of bauplane, each of which showed relatively few variations. Throughout the Phanerozoic—the Cambrian to the Present—there has been a considerable pruning out of major body forms, but a great proliferation of variation on those remaining.

This pattern has been termed, somewhat misleadingly, early experimentation and later standardization. A more reasonable interpretation is that the loss of individual bauplane does not indicate bad adaptation, but merely bad luck: the expected outcome for some lineages in a stochastic world. Once lost, that particular body form is unlikely to reemerge, especially if, as group two concluded, "internal constraints must influence the direction of evolution to some degree." Internal constraints, the group argued, was likely to have been very important in the persistence of surviving bauplane. In other words, the pattern is one of historical accident and architectural limitation.

Perhaps the most striking pattern of all, to modern eyes at least, is the repeated interruption of Phanerozoic life by dramatic drops in diversity, the result of major extinction events. These rapid declines in diversity are followed by somewhat slower rebounds, which typically are dominated by fauna different from those that were most prevalent previously. The pattern and nature of extinction represent a very hot topic in evolutionary biology just now, not least because it offers many hypotheses for relatively reliable test. This is the more remarkable because as little as 15 years ago the subject was virtually unrecognized, except by one or two notable workers, and excited no general interest: the ghosts of Cuvier's catastrophism and Lyell's uniformitarianism loomed large.

Of the tremendous amount of data on extinctions that has been produced in the past 5 years, those most in the headlines have, of course, been related to the notion that the Earth is the periodic—26 million year period to be precise—target of extraterrestrial bolides, specifically comets, which repeatedly extinguish a substantial proportion of the planet's biota. The idea was inspired in part by the very thorough analysis of the last 250 million years of the marine fossil record at the family level by Jack Sepkoski and David Raup of the University of Chicago, which indicated that extinction rates rose substantially above background levels every 26 million years or so.

Raup and Sepkoski had previously demonstrated the reality of mass extinctions—the "big five," Late Ordovician, Devonian, Permian, Triassic, and Cretaceous—each of which was generally assumed to be the result of a different constellation of causes. When they discovered more, albeit of somewhat lesser magnitude, which appeared to fit into a regular periodic pattern, the obvious inference was that a single, common cause was operating. Shortly before this, Luis Alvarez and his colleagues at Berkeley discovered a putative chemical signature of asteroid impact at one of the most notorious of mass extinction, that at the Late Cretaceous, which included the last days of the dinosaurs. Put the two together and the asteroid impact hypothesis was born as a general explanation for all major extinction events.

Extinction has often been viewed as failure of a species to adapt, specifically in competition with others. The falling by the wayside of species during the "progress" of life to greater and greater "complexity," both of which terms are highly loaded and almost certainly contain a greater stochastic element that generally imagined, was therefore considered to be the result of bad genes. The demonstration of occasional mass extinctions overturns this most simplistic of views, forcing it to accommodate the disruptive effect of repeated major perturbations.

Nevertheless, as long as mass extinctions could be seen as simply magnifying the natural process of weeding out the less fit taxa, the traditional view of the world could remain more or less intact. That this might not be the case is becoming one of the most intriguing questions in the current research on extinctions.

If . . . major extinction events are selective in a qualitatively different way from background extinction, then they will have a profound influence on the history of life.

First, the evidence for periodicity is extremely damaging to the conventional view, because it puts the emphasis on external rather than internal causes for mass extinction. Second, preliminary evidence is beginning to accumulate that identifies different taxon characteristics as being important in vulnerability to background extinction as against mass extinction.

The Dahlem meeting heard evidence that appears to add support to the proposed periodicity of major extinction events. For instance, Sepokoski is repeating the analysis, this time at the generic level and extending it back through the Paleozoic, 250 million to 500 million years ago. He detects the same type of pattern as previously obtained, though the results are still incomplete. And Edward Connor, of the University of Virginia, using an independent time series analysis of Raup and Sepkoski's original data, supports the general conclusion. Raup and Sepkoski now state their position more cautiously than before, saying that statistical analysis rejects the model that extinction events are randomly distributed and that periodicity emerges as the hypothesis to test.

In reviewing the potential ultimate, as opposed to proximal, causes of major extinctions, the meeting was divided on the impact hypothesis. Sea level changes, perhaps in combination with other events, remains a popular alternative.

Glimpses of a possible qualitative, as well as quantitative, difference between major extinction events and background extinction come from two principal sources, both very preliminary. First, David Jablonski of the University of Arizona, Tucson, has found in an investigation of gastropod taxa around the Late Cretaceous extinction boundary that broad geographic range at the species level and high species richness of a clade enhanced survivorship during times of background extinction. During major extinction events, however, these properties were of no account. Instead, those clades with broad geographic ranges, regardless of the geographic range of constituent species, were those more likely to survive.

Second, Richard Bambach of Virginia Polytechnic Institute and State University sees that orders early in their history are more resilient to major extinction events than those late in their history. If orders early in their history are geographically widespread, and later become more provincial, then this observation and Jablonski's might coincide. If not, and both results stand up to further examination, then other explanations will have to be sought.

If it is true that major extinction events are selective in a qualitatively different way from background extinction, then they will have a profound influence on the history of life. Each radiation after such an event depends completely on who survived. A focus on the features that enhance survival through major perturbations and give an edge in the subsequent radiation will give important insights into the patterns in the history of life.

There is a pervasive belief that the mammals are "better" than the reptiles, which in turn were "better" than the mammal-like reptiles, each of which group expanded on the decline of the previous one. This may in some sense be correct, but there is likely to have been a great deal more luck and as yet unrecognized, high level bias in determining which groups come to dominate different periods of Earth history than has previously been accepted.

The untangling of pattern and process is often an invitation to confusion and false inference. The Dahlem meeting was acknowledged to be an important advance in the rational untangling of one of the most complex patterns of all, the history of Phanerozoic life.

—Roger Lewin