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PUNCTUATED EQUILIBRIUM VERSUS CONTINUOUS EVOLUTION

Type of life science: Evolutionary biology
Other fields of study: Genetics and systematics (taxonomy)

According to classical evolutionary theory, new species arise by gradual transformation of ancestral ones. Speciation theory of the 1950's and 1960's, however, predicted that new species arise from small populations isolated from the main population, where they diverge rapidly. In 1972, Niles Eldredge and Stephen Jay Gould applied this concept to the fossil record, predicting that species should arise suddenly ("punctuated" by a speciation event) rather than gradually, and then persist virtually unchanged for millions of years in "equilibrium" before becoming extinct or speciating again.

Principal terms

ALLOPATRIC: refers to populations of organisms living in different places and separated by a barrier that prevents interbreeding

GRADUALISM: the idea that transformation from ancestor to descendant species is a slow, gradual process spanning millions of years

MACROEVOLUTION: large-scale evolutionary processes that result in major changes in organisms and allow them to change rapidly, occupy new adaptive niches, or develop novel body plans

MICROEVOLUTION: small-scale evolutionary processes resulting from gradual substitution of genes and resulting in very subtle changes in organisms

PUNCTUATED EQUILIBRIUM: the idea that new species form during relatively short (a few generations) speciation events and then persist for millions of years unchanged until they go extinct

SPECIATION: the process by which new species arise from old species, either by splitting off from their ancestor or by the transforming of the ancestor into the descendant

SPECIES SELECTION: the idea that species are independent entities with their own properties, such as birth (speciation) and death (extinction); a higher level of selection above that of natural selection is postulated to take place on the species level

STASIS: the long-term stability and lack of change in fossil species, often spanning millions of years of geologic time

SYMPATRIC: refers to populations of organisms living in the same place, not separated by a barrier that would prevent interbreeding

Summary of the Phenomenon

Although Charles Darwin's most influential work was entitled *On the Origin of Species* (1859), in fact it did not address the problem in the title. Darwin was

concerned with showing that evolution had occurred and that species could change, but he did not deal with the problem of how new species formed. For nearly a century, no other biologists addressed this problem either. Darwin (and many of his successors) believed that species formed by gradual transformation of existing ancestral species, and this viewpoint ("gradualism") was deeply entrenched in the biology and paleontology books for a century. In this view, species are not real entities but merely arbitrary segments of continuously evolving lineages that are always in the process of change through time. Paleontologists tried to document examples of this kind of gradual evolution in fossils, but remarkably few examples were found.

By the 1950's and 1960's, however, systematists (led by Ernst Mayr) began to study species in the wild and therefore saw them in a different light. They noticed that most species do not gradually transform into new ones in the wild but instead have fairly sharp boundaries. These limits are established by their ability and willingness to interbreed with each other. Those individuals that can interbreed are members of the same species, and those that cannot are of different species. When a population is divided and separated so that formerly interbreeding individuals develop differences that prevent interbreeding, then a new species is formed. Mayr showed that, in nature, large populations of individuals living together ("sympatric" conditions) interbreed freely, so that evolutionary novelties are swamped out and new species cannot arise. When a large population becomes split by some sort of barrier so that there are two different populations ("allopatric" conditions), however, the smaller populations become isolated from interbreeding with the main population. If these allopatric, isolated populations have some sort of unusual gene, their numbers may be small enough that this gene can spread through the whole population in a few generations, giving rise to a new species. Then, when the isolated population is reintroduced to the main population, it has developed a barrier to interbreeding, and a new species becomes established. This concept is known as the allopatric speciation model.

The allopatric speciation model was well known and accepted by most biologists by the 1960's. It predicted that species arise in a few generations from small populations on the fringe of the range of the species, not in the main body of the population. It also predicted that the new species, once it arises on the periphery, will appear suddenly in the main area as a new species in competition with its ancestor. These models of speciation also treated species as "real" entities, which recognize one another in nature and are stable over long periods of time once they become established. Yet, these ideas did not penetrate the thought of paleontologists for more than a decade after biologists had accepted them. In 1972, Niles Eldredge and Stephen J. Gould proposed that the allopatric speciation model would make very different predictions about species in the fossil record than the prevailing dogma that they must change gradually and continuously through time. In their paper, they described a model of "punctuated equilibrium." Species should arise suddenly in the fossil record ("punctuation"), followed by long periods of no change ("equilibrium," or "stasis") until they went extinct or speciated again. They challenged paleontologists to examine their biases about the fossil record and to see if in fact most fossils evolved gradually or rapidly, followed by long periods of stasis.

In the years since that paper, hundreds of studies have been done on many different groups of fossil organisms. Although some of the data were inadequate to test the hypotheses, many good studies have shown quite clearly that punctuated equilibrium describes the evolution of many multicellular organisms. The few exceptions are in the gradual evolution of size (which was specifically exempted by Eldredge and Gould) and in unicellular organisms, which have both sexual and asexual modes of reproduction. Many of the classic studies of gradualism in oysters, heart urchins, horses, and even humans have even been shown to support a model of stasis punctuated by rapid change. The model is still controversial, however, and there are still many who dispute both the model and the data that support it.

One of the more surprising implications of the model is that long periods of stasis are not predicted by classical evolutionary theory. In neo-Darwinian theory, species are highly flexible, capable of changing in response to environmental changes. Yet, the fossil record clearly shows that most species persist unchanged for millions of years, even when other evidence clearly shows climatic changes taking place. Instead of passively changing in response to the environment, most species stubbornly persist unchanged until they either go extinct, disappear locally, or change rapidly to some new species. They are not infinitely flexible, and no adequate mechanism has yet been proposed to explain the ability of species to maintain themselves in homeostasis in spite of environmental changes and apparent strong natural selection. Naturally, this idea intrigues paleontologists, since it suggests processes that can only be observed in the fossil record and were not predicted from studies of living organisms.

The punctuated equilibrium model has led to even more interesting ideas. If species are real, stable entities that form by speciation events and split into multiple lineages, then multiple species will be formed and compete with one another. Perhaps some species have properties (such as the ability to speciate rapidly, disperse widely, or survive extinction events) that give them advantages over other species. In this case, there might be competition and selection between species, which was called "species selection" by Steven Stanley in 1975. Some evolutionary biologists are convinced that species selection is a fundamentally different process from that of simple natural selection that operates on individuals. In species selection, the fundamental unit is the species; in natural selection, the fundamental unit is the individual. In species selection, new diversity is created by speciation and pruned by extinction; in natural selection, new diversity is created by mutation and eliminated by death of individuals. There are many other such parallels, but many evolutionary biologists believe that the processes are distinct. Indeed, since species are composed of populations of individuals, species selection operates on a higher level than natural selection.

If species selection is a valid description of processes occurring in nature, then it may be one of the most important elements of evolution. Most evolutionary studies in the past have concentrated on small-scale, or microevolutionary, change, such as the gradual, minute changes in fruit flies or bacteria after generations of breeding. Many evolutionary biologists are convinced, however, that microevolutionary processes are insufficient to explain the large-scale, or macroevolutionary, processes in the evolution of entirely new body plans, such as birds evolving from dinosaurs. In other words, traditional neo-Darwinism says that all evolution is merely microevolution on a larger scale, whereas some evolutionary biologists consider some changes too large for microevolution. They require different kinds of processes for macroevolution to take place. If there is a difference between natural selection (a microevolutionary process) and species selection (a macroevolutionary process), then species selection might be a mechanism for the large-scale changes in the earth's history, such as great adaptive radiations or mass extinctions. Naturally, such radical ideas are still controversial, but they are taken seriously by a growing number of paleontologists and evolutionary biologists. If they are supported by further research, then there may be some radical changes in evolutionary biology.

Methods of Study

Determining patterns of evolution requires a very careful, detailed study of the fossil record. To establish whether organisms evolve in a punctuated or gradual mode, many criteria must be met. The taxonomy of the fossils must be well understood, and there must be large enough samples at many successive stratigraphic levels. To estimate the time spanned by the study, there must be some form of dating that allows the numerical age of each sample to be estimated. It is also important to have multiple sequences of these fossils in a number of different areas to rule out the effects of migration of different animals across a given study area. Once the appropriate samples have been selected, then the investigator should measure as many different features as possible. Too many studies in the past have looked at only one feature and therefore established very little. In particular, changes in size alone are not sufficient to establish gradualism, since these phenomena can be explained by many other means. Finally, many studies in the past have failed because they picked one particular lineage or group and selectively ignored all the rest of the fossils in a given area. The question is no longer whether one or more cases of gradualism or punctuation occurs (they both do) but which is predominant among all the organisms in a given study area. Thus, the best studies look at the entire assemblage of fossils in a given area over a long stratigraphic interval before they try to answer the question of which tempo and mode of evolution is prevalent.

Context

Since the 1940's, evolutionary biology has been dominated by the neo-Darwinian "synthesis" of genetics, systematics, and paleontology. In more recent years, many of the accepted neo-Darwinian mechanisms of evolution have been challenged from many sides. Punctuated equilibrium and species selection represent the challenge of the fossil record to neo-Darwinian gradualism and overemphasis on the power of natural selection. If fossils show rapid change and long-term stasis over millions of years, then there is no currently understood evolutionary mechanism for this sort of stability in the face of environmental selection. A more general theory of evolution may be called for, and, in more recent years, paleontologists, molecular biologists, and systematists have all been indicating that such a radical rethinking of evolutionary biology is on the way. Evolutionary biology as it has been presented in textbooks and popular books in the second half of the twentieth century may be completely revamped by the end of that century.

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__________. *The New Evolutionary Timetable: Fossils, Genes, and the Origin of Species*. New York: Basic Books, 1979. Along with Eldredge's *Time Frames*, one of the best introductions to the subject for the nontechnical reader. Stanley gives a good background on evolutionary biology before punctuated equilibria and illustrates his points with many well-chosen examples.

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Cross-References

Evolution: A Historical Perspective, 903; Convergent and Divergent Evolution, 910; Extinction, 953; Gene Flow, 1097; Isolating Mechanisms in Evolution, 1493; Natural Selection, 1870; Speciation and the Species Concept, 2521.