CURRENT ISSUES IN EVOLUTION: PUNCTUATED EQUILIBRIUM

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I. INTRODUCTION

A. What is punctuated equilibrium?

Punctuated equilibrium (PE) is a theory about evolutionary change. PE was originally proposed (Eldredge and Gould 1972) as the expected outcome of the process of allopatric speciation. Allopatric speciation occurs when a small semi-isolated peripheral population of a species become differentiated into a new species. Since the speciation process involves a small population and probably occurs relatively rapidly, the chances are small that any members of the transitional population will be preserved as fossils. This makes it highly unlikely that fossil links between species would be discovered. Lack of transitions between species is a well-known phenomenon in the fossil record, and can also be observed in living faunas. PE offers a possible explanation of why species are usually found to be separated by morphological gaps without intermediates.

PE theory makes two claims about the fossil record: stasis and abrupt appearance. According to PE, most species remain relatively unchanged for long periods of time. This resistance to change is called "stasis". Stasis is interrupted by speciation events, which occur relatively rapidly and in small populations. During the process of speciation, morphological change is rapid, until a new stable morphology is produced, and a new species is established. Since the morphological change was concentrated in a relatively short time and involves relatively few individuals, it is unlikely to leave any evidence. This is why most fossil species appear abruptly in the fossil record. Both of these concepts have been tested in the fossil record, with controversial results.

B. Why is it significant to evolutionists?

The discussion about PE is basically a discussion over the process of speciation and relative rates of morphological change. PE is contrasted with gradualism, the theory that species change gradually, due to the accumulation of very small changes. If this is the way in which species change, one would expect to find a morphological continuum among species in a given lineage, each species grading into the next species in the lineage.

In both PE and gradualism natural selection is considered to be the driving force behind morphological change. According to gradualism, the changes occur in very small steps which are more or less continuous. Missing transitional links between species are attributed to the incompleteness of the fossil record. According to PE, changes in species occur in larger and more rapid steps, and primarily during the process of speciation. In the latter case, morphological changes rarely occur, but when they do, they take place so rapidly that one would not expect to find fossil intermediates. Thus the discussion of PE may include differing views on the completeness of the fossil record.

The suggestion that a new theory was needed to replace evolutionary gradualism generated considerable discussion. It is a common observation that one species often replaces another species in the fossil record with no evidence of connecting links. Yet according to the theory of evolution, all species are connected in a single tree of life. The theory of PE, if true, might help to explain why the connecting links between species were missing. (However it would not help explain why the gaps are larger between higher categories than between lower categories.) On the other hand, if most species are connected by intermediate morphologies, PE theory would be shown to be unnecessary.

PE also has controversial implications about the process of speciation. Evolutionary theory holds that changes in species are the result of changes in the environment. If species remain unchanged over millions of years despite environmental changes, what causes them to change? If changes occur rapidly,

why don't we observe such changes in nature? Because of its importance to evolutionary theory, several studies have been conducted to determine whether morphological change is concentrated in short "spurts" in the fossil record, or whether it is distributed more-or-less evenly across many stratigraphic levels.

II. EVIDENCE BEARING ON PE

A. Difficulty of testing PE

The basic claims of PE are that species remain unchanged for long periods of time, then change abruptly without leaving evidence of transitional forms. Since speciation seems to be a slow process, it is difficult to adequately test PE by observations of living species. Because of this, most of the discussion about PE has centered around the fossil record. Evolutionists assume the fossil record was accumulated over long ages of time and shows sequences of species in various lineages. If this is so, one could test the accuracy of PE by analyzing series of fossils. Numerous examples have been proposed, claiming to show either punctuation or gradualism. Reading these reports and the criticisms given in response gives one a good illustration of how difficult it is to prove or disprove a hypothesis. For example, there is disagreement on how complete the fossil record is, the role of the environment in speciation, and what is needed to provide a valid test of PE vs gradualism.

B. Stasis

The first issue in PE theory is stasis. Do species actually remain static for long periods of time, despite changes in the environment? This question can be answered from paleontology if long ages of time are assumed for the fossil record. The answer often seems to be yes.

Of the species of mammals living in Europe, about 85% are found as fossils in deposits interpreted to be 400,000 years old (Stanley 1982). To those who accept this age, stasis seems to be widespread. Stasis over a supposed four million years has been reported among the Eocene mammal fauna of the Willwood Formation in Wyoming (Bakker 1985). The abrupt appearance of new species is explained as due to immigration rather than in situ evolution.

Study of living species may also contribute to the discussion of stasis. Does morphology remain constant for a species, regardless of differences in environmental conditions? Here the answer is one of degree. Minor morphological differences can be seen among populations living under different environmental conditions, but members of a species are remarkably uniform morphologically, regardless of their local environments. This suggests that environmental factors have only limited ability to effect morphological changes. This conclusion is well-supported experimentally by the stability of species despite attempts to produce changes through selective breeding programs.

C. Punctuation

A second issue in PE is punctuational change. This is more difficult to test than one might expect. Determining the relationship between morphological change and the speciation process requires the accurate identification of the fossil specimens and the ancestor-descendant relationship of the species. These are difficult problems when dealing with fossils. One problem in testing PE and gradualism is that of recognizing species limits in the fossil record. It is difficult to distinguish between two species with their transitional forms and a single polymorphic species. Since breeding cannot be studied using fossils, the only criteria for determining fossil species is morphology. The question then becomes one of determining whether morphological changes occur gradually or whether such changes are abrupt. Another difficulty in trying to answer questions about PE is the problem of identifying a species lineage. A "new" species may not have evolved from an old species in the same region, but may have migrated into the area and replaced the old species. In this case the series of fossil species would not represent a lineage, and the data could not answer the question.

One example that has been used to support both PE and gradualism is the Eocene mammal *Hyopsodus* (a condylarth). Using the size of the 1st lower molar, a gradualist (Gingrich 1974) claimed to show that *Hyopsodus* changed gradually over the section he studied. Later a punctuationalist (Bakker 1985) claimed he had looked at the strata more carefully and found that punctuational changes occurred between the species. Numerous other examples have been proposed, but there seems to be no consensus as to the relative importance of punctuation and gradualism.

The issue of whether morphological change occurs mostly during the process of speciation is still controversial. Many living species are known which are nearly indistinguishable morphologically from other living species. This is good evidence that speciation can occur without morphological change. But it does not eliminate the possibility that morphological change may usually occur in short rapid spurts during speciation events. Another point demonstrated in living species is that minor morphological change may occur in small steps. Gradual changes in characters within a species can be seen geographically, where one race grades into another as one moves across an ecological gradient. Species within a genus may differ from each other in the same traits as distinguish local populations of a species, and may even overlap in characteristics. These observations indicate that punctuation is not required to produce a new species, and tend to favor gradualism. But this still does not answer the question as to whether PE or gradualism is more important in evolutionary history.

III. SIGNIFICANCE OF PE TO CREATIONISM

A. Continuity and speciation

A creationist might wonder whether PE theory is helpful to creation theory. Using PE to explain the existence of gaps between similar species in the fossil record is of little significance to creation. Creation theory includes changes in species, regardless of the details. PE does not address the effectiveness of such changes in explaining the larger gaps between higher taxa, which is a major concern of creationists. PE's emphasis on morphological gaps has been helpful, it seems to me that PE is wrong in explaining the gaps by linking morphological change and speciation events. The existence of "sibling species" demonstrates that speciation and morphological change are not necessarily linked. I suggest the presence of morphological gaps between closely related species in the fossil record is because the respective species are sister species rather than a species lineage. The ancestral species no longer existed at the time of burial, leaving no evidence of morphological intermediates.

B. Stability of species

On the other hand, some of the questions raised by PE might be very helpful to creationism. The observations of stasis in fossil species and the morphological stasis of living species suggest that evolutionary change is limited. This is in harmony with creationist assertions that changes in species are not sufficient to account for organic diversity.

C. Rapid change

One area where PE has been especially interesting is in raising the possibility of rapid morphological change. Creationists have accepted that species can change, but the time creationists believe to have been available for change is much less than traditional neo-darwinian theory proposed was necessary. PE has stimulated discussion on rates of change, resulting in research that has shown that change may occur much more rapidly than was once thought. One can now read statements that changes in species can take place in a relatively few generations.

D. Determining a possible flood boundary

Another way in which PE theory could be helpful to creationists is in determining which fossil series may show gradual changes and which show discontinuity. There may be two reasons why a series of

"species" might grade into a continuum. A series of species might represent a lineage of species over time. Alternatively, the species might have lived in environments representing an ecological continuum. Thus continuity between species could indicate either ancestral-descendant relationship or responses to intergrading environmental conditions. By contrast, discontinuity between species probably indicates they are not members of a single lineage. Such species might have been contemporaries, their ancestors having died out before the fossils were buried.

This could be used by creationists in studying possible flood boundaries (Wise 1989). If a fossiliferous deposit is characterized primarily by species which are not linked to other species by transitional forms, a creationist might postulate they represent populations that lived at the same time and do not have an ancestor-descendent relationship. Any ancestral species could have become extinct before the fossils were buried. Such deposits could indicate deposition by the flood. On the other hand, if a deposit is characterized by species that are linked to other species by intermediate morphological characteristics, and if the lineage extends continuously to living species, a creationist could propose that such deposits represent speciation and deposition after the flood. Examples of gradual change in species in the fossil record tend to be most common in groups with short generation times that survived through the flood, such as forams (Wise 1989) or that probably lived after the flood (e.g. microtine rodents; Chaline 1987).

IV. SUMMARY

PE is a theory about speciation. It makes two claims about the fossil record: stasis and abrupt appearance. Both claims have been tested in the fossil record, with controversial results. Living species suggest that PE theory is flawed in that speciation may occur without morphological change, and that morphological change may be accomplished in small steps. However, PE's claims of stasis and abrupt appearance in the fossil record appear to be largely correct. This seeming contradiction might be explained by creationists as indicating that changes in species do occur gradually, but that species are too stable for major changes to occur. Abrupt morphological changes in the fossil record are evidence that the species are sister species rather than members of a species lineage. Fossil faunas with a predominance of abrupt morphological change may indicate deposition by the flood. Faunas showing morphological gradation between species may represent a pre-flood ecological gradient or a post-flood succession of species.

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