

Punctuated Equilibrium: Come of Age?

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ABSTRACT

The concept of punctuated equilibrium (PE) is explained. The development of the idea since its inception by Stephen Gould and Niles Eldredge is traced, as well as some of the controversies.

PE consists of two aspects:

- (1) an observation — that the fossil record is characterised by
 - (a) abrupt appearance of species, and*
 - (b) stasis, or lack of substantial change, throughout a species' range in the fossil record; and**
- (2) a theoretical attempt to explain how this pattern can fit an evolutionary (naturalistic) model for the origin of species.*

Gould and Eldredge claimed that the abrupt appearance of species could be explained by the transition occurring quickly, geologically speaking, in small, isolated populations such that the transitional forms would be highly unlikely to be preserved. They claimed that this theory arose out of biology, but there is no empirical biological basis for such speciation events. It seems that the 'mechanism' was adopted because it 'explained' their observation of the fossils (they are both palaeontologists). Gould gave air to ideas of macromutational change to explain major transitions and fuelled perceptions that PE's rapid speciation was a form of 'hopeful monsters' evolution. Gould and Eldredge denied that this is what they meant.

The debate over PE has given publicity to stasis as a serious problem for evolution (how can you believe in evolution, or change, when the fossils testify to stasis, or lack of change?). The recognition of the reality of abrupt appearance and stasis corroborates what creationists have been saying since Darwin — that the evidence fits special creation combined with the results of a worldwide Flood. In this context, Wise's 'punc eq creation style' is also discussed.

THE CONCEPT OF PUNCTUATED EQUILIBRIUM

Niles Eldredge (now curator of invertebrates at the American Museum of Natural History, New York City) and Stephen Jay Gould (Professor of Geology, Museum of Comparative Zoology, Harvard University) gave birth to the idea of 'Punctuated Equilibria' at a symposium on models in palaeontology in 1970 at the University of Chicago, with a paper being published in 1972.^{1,2} The idea

grew out of their recognition of stasis (lack of gradual change) in the fossil record. That is, that species remain remarkably stable throughout their 'history', showing little change from when they appear in the fossil record to when they disappear. Eldredge in particular had spent much effort trying to find evidence for gradual evolutionary changes linking trilobite species in Devonian strata in the United States and Canada, without success. For example, the number of lens elements in the eye should have, according to neo-Darwinian theory, changed gradually from

one species of trilobite to another. But it did not. There was little variation over long periods of time and ‘species’ seemed to just appear and disappear.

Eldredge and Gould recognized, as palaeontologists, that this pattern, of little change over long periods of time (in the evolutionary interpretation of the record), and lack of evidence for gradual transformation of one species into another, was a general characteristic of the fossil record; it was not peculiar to Devonian trilobites. New species ‘appear’ in strata without indication of gradual change from a different form. The fossil record is characterised by long periods of stasis, or equilibrium, where species are clearly identifiable and stable, punctuated on occasions by the sudden, or ‘rapid’, appearance of new species. Hence — ‘punctuated equilibria’.

Palaeontologists had generally blamed the gaps in the fossil record (lack of evidence for gradual change and Phylogeny) on incompleteness of study, as did Darwin; Eldredge and Gould faced up to the truth that gaps characterised the fossil record. Palaeontologists also ignored stasis as ‘non-data’, as of no interest; Gould and Eldredge recognized ‘*stasis is data*’.

Gould and Eldredge saw species as discrete entities with an identifiable beginning (at speciation) and end (at extinction), in contrast to the neo-Darwinian concept of species as continually transforming, without a clear identity. Eldredge and Gould spoke of species as ‘individuals’. ‘Speciation’ is for species what mutation is for individuals. Speciation is viewed as random, just as mutations are for individuals. Natural selection operates on the new species to weed out the non-viable ones.

The original paper³ began with a philosophical treatment of the reluctance of mainstream evolutionists to admit the lack of fossil evidence for gradualism. That is, the pre-eminence of theory over ‘facts’. Eldredge and Gould recognized, like other commentators on the scientific method, that facts only ‘speak’ when theory accommodates them; otherwise they are explained away. They claimed they were proposing a new theory which would allow the facts of stasis and abrupt appearance in the fossil record to be accommodated in an evolutionary (that is, naturalistic) framework. Previously, stasis had been ignored and the gaps were explained as due to incomplete knowledge.

At one level punctuated equilibrium (PE) is merely a description of the fossil record (assuming geologic time, of course). At another level, it is a process of evolution which Eldredge and Gould claimed could account for the pattern in the fossil record. They claimed that major changes occurred in small, isolated populations removed from the major population (allopatric speciation via peripheral isolates). Furthermore, they claimed these changes happened rather quickly (geologically speaking). This was the supposed ‘mechanism’ which accounted for the stasis and ‘gappiness’ of the fossil record. They said:

‘Since speciation occurs rapidly in small populations

occupying small areas far from the center of ancestral abundance, we will rarely discover the actual event in the fossil record.’⁴

They did not define ‘rapidly’, except to say the changes happened

‘in a short period of time relative to the total duration of a species’.⁵

The other main proponent of PE has been Steven Stanley, who claimed that:

‘Gradual evolutionary change by natural selection operates so slowly within established species that it cannot account for the major features of evolution’,⁶

thus agreeing that changes which produced new species occurred relatively quickly.

THE PEDIGREE OF PUNCTUATED EQUILIBRIUM

Others had recognized that the fossil record did not show gradual transitions between taxa. For example, in 1940 Richard Goldschmidt⁷ argued that transitions must have occurred quickly, in jumps, such that there were no intermediate forms to be fossilised because they never existed. Goldschmidt’s ideas were ridiculed by the establishment of the 1940s and 1950s, because mainstream palaeontologists still believed that the transitional fossils would be found with further study. Furthermore, there was no biological basis for understanding how new species could arise as quickly as Goldschmidt suggested.

The basic ‘mechanism’ of speciation proposed by Eldredge and Gould was borrowed from others. The concept of allopatric (geographic) speciation had been recognized as a mechanism of evolutionary change, albeit in a gradualistic manner. Mayr⁸ in particular had elaborated on this. Eldredge⁹ acknowledged that allopatric speciation can be traced even to pre-Darwinian biology. Eldredge and Gould made one controversial addition, that:

‘Most evolutionary changes in morphology occur in a short period of time relative to the total duration of a species’¹⁰

and argued that it was a logical deduction from the peripheral isolate theory of allopatric speciation. Although they acknowledged that:

‘No new theory of evolutionary mechanisms can be

PUNCTUATED EQUILIBRIA OR PUNCTUATED EQUILIBRIUM?

In their 1972 paper, Eldredge and Gould used the term ‘punctuated equilibria’ to refer to their concept. Eldredge used this term in his writings, whereas Gould used ‘punctuated equilibrium’ (compare the titles of references 9 and 28, for example). Their review paper of 1993 used ‘punctuated equilibrium’, so it appears that this term has come to prevail.

generated directly from paleontological data,¹¹

one suspects that the concept of rapid speciation came from their reading of the fossil record rather than from any new understanding of allopatric speciation. Even this concept of rapid speciation was not really new. Other than Goldschmidt, Soviet workers had proposed in the 1960s that change tends to be concentrated in rapid speciation events and that species remain remarkably stable after becoming established.¹²

'PUNC EQ CREATION STYLE'

Kurt Wise,* a creationist palaeontologist, suggested an alternative explanation for the fossil evidence of abrupt appearance of species and stasis that Gould and Eldredge recognized. Gould and Eldredge assume the conventional interpretation of the stratigraphic column as resulting from deposition over a long period of time, such that each layer represents a sample of the earth's life forms at that time. The fossil record is then a bit like a time-lapse movie of the history of life on earth (albeit with variable time-lapses). Wise pointed out that if most of the stratigraphic record resulted from a single catastrophe, such as the Great Flood and its aftermath, this would account for the pattern of abrupt appearance and stasis in the fossil record. Each species would be sampled in a moment of time by such an event and would thus show stasis. Rare exceptions to stasis, that is, consistent vertical gradients of change, such as increasing size upwards (a common observation called Cope's Law), could be accounted for by sorting processes. Trends could also reflect original geographic or altitudinal gradients in morphology. Additionally, a vertical gradient in form could possibly result from an actual transition during the catastrophe, but this could only occur in a species resistant to the conditions of the catastrophe and with a generation time substantially shorter than that of the duration of the catastrophe (a year for the Flood). Wise suggested that exceptions to stasis would be marine organisms with short generation times. The best possible exception to stasis that Wise knew of was a Permian foraminifer, which is a marine organism with a short generation time, consistent with a catastrophic Flood model.

Wise wrote:

'The rarity of exceptions to PE sensu stricto [that is, stasis and abrupt appearance of species] indicates that a model of catastrophic deposition of the earth's rocks could be invoked as a mechanism to account for the paleontological observation of PE theory.'

* Wise, K. P., 1989. Punc eq creation style. *Origins (USA)*, 16:11–24.

THE FIRST TEN YEARS

In the 1970s, following the publication of the original paper, Gould was quite assertive about the lack of gradualism in the fossil record and the rapidity of the evolutionary 'spurts'.

In their original 1972 paper, Eldredge and Gould argued that the fossil record is characterised by stasis and gaps, and candidly admitted that this could not be due to incomplete study. Gould in particular made a number of strong statements in the 1970s about the lack of evidence in the fossils for the gradual transformation of one species into another. For example, in 1977 Gould wrote:

*'The extreme rarity of transitional forms in the fossil record persists as the trade secret of paleontology. ... to preserve our favored account of evolution by natural selection we view our data as so bad that we never see the very process we profess to study.'*¹³

In their 1972 paper Eldredge and Gould did not define what they meant by rapid change, or what biological mechanism could be responsible for such change. In a joint paper published in 1977, Gould and Eldredge reiterated their claim of 'rapid' speciation saying

*'most evolutionary change . . . is concentrated in rapid (often geologically instantaneous) events . . .'*¹⁴

What does 'geologically instantaneous' mean? Gould wrote of speciation occurring over

'thousands of years at most compared with millions for the duration of most species.'

He also wrote of

' . . . a host of alternatives that yield new species rapidly even in ecological time' (my emphasis).¹⁶

Notice that Gould here switches from 'geological time' to 'ecological time' — he is emphasizing the rapidity of change.

GOULD AND 'HOPEFUL MONSTERS'

Although PE was initially restricted to 'conventional speciation in sexually reproducing Metazoa',¹⁷ Gould and Eldredge suggested the concept could be applied with benefit at higher taxa than species, indeed even as a general principle in palaeontology. In this context, Gould and Eldredge wrote of

'Speciation, the source of macroevolutionary variation . . .'

and

*'Smoother intermediates between Baupläne are almost impossible to construct, even in thought experiments . . . We believe that a coherent, punctuational theory . . . will be forged . . .'*¹⁸

Although PE strictly applies to speciation, Gould and Eldredge recognized that the fossil record fitted the same pattern at higher taxonomic levels.

In a paper published in 1977 titled 'The Return of Hopeful Monsters', Gould wrote:

*'All paleontologists know that the fossil record contains precious little in the way of intermediate forms; transitions between major groups are characteristically abrupt.'*¹⁹

He agreed with Goldschmidt, that small changes in genes controlling rates of early embryo development could result in the production of an adult differing significantly from its parents — a 'hopeful monster', although Gould distanced himself from the more extreme changes, such as a reptile egg hatching a bird. He wrote:

*'Indeed, if we do not invoke discontinuous change by small alteration in rates of development, I do not see how most major evolutionary transitions can be accomplished at all'*²⁰

and

*'I . . . predict that during the next decade Goldschmidt will be largely vindicated in the world of evolutionary biology.'*²¹

In 1980 Gould re-iterated the problems in the fossil record for gradualism:—

*'The absence of fossil evidence for intermediary stages between major transitions in organic design, indeed our inability, even in our imagination, to construct functional intermediates in many cases, has been a persistent and nagging problem for gradualistic accounts of evolution.'*²²

He again wrote approvingly of Goldschmidt's ideas — he wrote of the 'Goldschmidt break' in reference to a qualitative difference between adaptive change within populations and the origin of new species. (In arguing for PE Gould and Eldredge had argued that speciation was different to adaptation within populations.) Gould here down-played the importance of allopatric speciation, (that is, via geographic isolation of groups on the periphery of the main population) compared to sympatric speciation (whole population, in place), arguing that isolation could occur in a small group in the centre of the population by genetic means such as 'chromosomal speciation' (Goldschmidt's ideas again).

In 1980 Gould discussed macromutations in the context of a mechanism for rapid speciation:—

*'The most exciting entry among **punctuational models for speciation** in ecological time is the emphasis . . . on chromosomal speciation'* (my emphasis).²³

This paper was written in the context of **punctuational models for speciation**. He also said:

*'We [Gould and Eldredge] regard stasis and discontinuity as an expression of how evolution works . . .'*²⁴

Is not stasis and discontinuity the essence of PE? He also discussed the inadequacy of the 'modern synthesis', or gradualism, to explain the origin of new species, as well as other levels in the hierarchical scheme of life (genera, families, orders, classes, phyla). Their joint papers, and Eldredge's, on PE omitted to suggest a 'genetic process' to account for 'rapid speciation events', or the 'punctuations' in punctuated equilibria, but Gould made

plenty of saltationist suggestions. John Maynard Smith²⁵ understood that Gould was proposing that speciation is decoupled from microevolution, involving non-adaptive change. It is not surprising that many evolutionists and creationists (such as Parker²⁶) have understood PE as a saltational (macromutational) model because that is surely how Gould often wrote of punctuational speciation in the 1970s. Gould probably has himself to blame for

*'the misunderstandings of colleagues who . . . interpreted punctuated equilibrium as a saltational theory.'*²⁷

SINCE 1981

As we have seen above, before 1981 Gould was dogmatic about the lack of fossil evidence for gradual (neo-Darwinian, or 'modern synthesis') evolution bringing about species transitions. In the 1980s he seemed to soften his stand markedly. In 1982 he wrote:

'I am not saying that punctuated equilibrium is the only mode of speciation'

and

*'Gradual, phyletic transformation can and does occur.'*²⁸

Previously, PE was **the** explanation for the fossil record; now it complements gradualism, although it is still more important. The 1980s saw a marked lack of clear statements about the lack of transitional fossils, or criticism of claimed fossil series. Maybe it's just that he had said it all before, but I suggest there may have been a change in Gould's attitude following the Arkansas creation/evolution trial in 1981.

Gould testified at the Arkansas creation/evolution trial, where he criticised creationists for supposedly misusing his statements about the fossil record and punctuated equilibrium. Eldredge weighed in by writing a book criticising creationist views.²⁹ In their recent review of punctuated equilibrium, they wrote with pride of these actions, speaking of Creationism as *'this philistine scourge'*.³⁰

Gould in particular was annoyed by creationists' use of his admissions about the lack of evidence for phylogeny in the fossils and his sympathy for Goldschmidt's 'hopeful monsters' mode of speciation. Gould's statements in the 1970s had been widely quoted by creationists. A recent paper³¹ shows that Gould seems to have 'come full circle'. He has abandoned his earlier position that there are no indisputable examples of transitional fossil series, either inter-specific or between major designs, and has embraced the 'walking whale' story as evidence for transformation of one species into another. The evidence for this transition is scant, but Gould uncritically accepts the fanciful description of how *Ambulocetus natans* walked and swam, as given by Thewissen *et al.*³² In the 1970s, a number of examples of gradualism in the fossils were proposed by others as refutation of the concept of punctuated equilibria (that is, as evidence for gradualism). Gould and Eldredge

dismissed these claims arguing

‘that virtually none of the examples brought forward to refute our model can stand as support for phyletic gradualism.’³³

Claimed examples of transitional series and intermediate forms received an incisive critique from Gould in the 1970s, but now he describes the very flimsy story of whale evolution as

‘the sweetest series of transitional fossils an evolutionist could ever hope to find.’³⁴

One only has to read Gould’s paper to see how uncritically he accepts the whole story. The paper also reveals Gould’s almost obsessive concern for countering creationist claims that the fossil record does not show evolution; that there are no indisputable intermediate forms — a claim that Gould made a number of times in the 1970s when he was pushing stasis and punctationalism, and when creationists were apparently not such a consideration.

In 1982 Gould distanced himself from ‘hopeful monsters’:

‘Punctuated equilibrium is not a theory of macromutation, it is not a theory of any genetic process.’³⁵

Gould admits to having supported

‘certain forms of macromutational theory . . . though not in the context of punctuated equilibrium.’³⁶

In 1986, Eldredge published **Time Frames: the Rethinking of Darwinian Evolution and the Theory of Punctuated Equilibria**. He wrote:

‘This book is my version of the story of ‘punctuated equilibria’. . .’ (my emphasis),³⁷

suggesting that he would like to distance himself from other versions. Eldredge was less dogmatic than Gould had been in the 1970s about the lack of gradual change in the fossil record. He wrote:

‘gradual change remains a theoretical possibility’³⁸

and

‘. . . there is some gradual change . . . But it doesn’t tell us, really, about the advent of the truly new. It never really gets us anywhere.’³⁹

He emphasized the importance of allopatric (geographic) speciation in explaining gaps in the fossil record. That is, Eldredge saw major changes as occurring somewhere else, away from the main population, in small, isolated populations, so they are not (usually) preserved, especially *in situ* with the parent species. He emphasized the peripheral isolate theory of allopatric speciation.

Eldredge objected to the ‘hopeful monster’ characterisation of PE:

‘The assertion that punctuated equilibria represents a resurrection of Goldschmidt’s “macromutations” and “hopeful monsters” remains the most serious and irksome misconstrual of our ideas.’⁴⁰

He also wrote about

‘The most common misconception about “punctuated equilibria” — that Gould and I proposed a saltationist

model of overnight change supposedly based on sudden mutations with large-scale effects (macromutations à la Richard Goldschmidt) . . .’⁴¹

Eldredge said,

‘selective change will ordinarily be rapid. But rapid in the context of millions of years’ (my emphasis).⁴²

IS EVOLUTION BY PUNCTUATED EQUILIBRIUM A LOGICAL ABSURDITY?

Gould and Eldredge say,

‘Stasis, as palpable and observable in virtually all cases (whereas rapid punctuations are usually, but not always, elusive), becomes the major empirical ground for studying punctuated equilibrium’

and

‘. . . stasis, inevitably read as absence of evolution, had always been treated as a non-subject. How odd though to define the most common of all palaeontological phenomena as beyond interest or notice!’^a

What are Gould and Eldredge ultimately saying? What is PE? Ultimately, PE is a proposed mode of evolution. What is evolution? Is it not **change**? PE is supposed to be a mode of change and yet the evidence for it is stasis. But what is ‘stasis’? Is it not lack of change? So then lack of change (stasis) is the evidence for change (evolution via PE)!

As a matter of amusement, the tautological nature of ‘survival of the fittest’ as a definition of natural selection in neo-Darwinian evolution is wonderfully preserved in Gould and Eldredge’s extrapolation of the concept to species:

‘. . . the geological record features episodes of high dying, during which extinction-prone groups are more likely to disappear, leaving extinction-resistant groups as life’s legacy.’^b

ReMine^c has shown how evolutionary theory is commonly formulated in a way that is either tautological, or in other ways untestable. The addition of PE to neo-Darwinian ‘theory’ effectively renders the very concept of evolution itself untestable. That is, even more than before, whatever the fossils show, ‘evolution’ can account for it! If lineages can be found, that is evidence for gradualistic evolution; if lineages cannot be found, then that is evidence for punctational evolution. ‘Heads we (evolutionists) win; tails you (creationists) lose’!

a. Gould, S. J. and Eldredge, N., 1993. Punctuated equilibrium comes of age. *Nature*, **366**:223–227 (p. 223).

b. Gould and Eldredge, Ref. a, p. 225.

c. ReMine, W., 1993. **The Biotic Message**, St Paul Press, St Paul, Minnesota.

By the time of their 21st anniversary review of PE,⁴³ Gould and Eldredge had retracted to proposing PE as ‘a complement to phyletic gradualism’. This is a rather major backdown on the brashness of their claims in 1972, and especially Gould’s claims up to 1980, as recognized by Levinton in a response to the review.⁴⁴

SIGNIFICANCE AND ACCEPTANCE OF PUNCTUATED EQUILIBRIUM

In 1993 Gould and Eldredge wrote that they ‘believe . . . that punctuated equilibrium has been accepted by most of our colleagues . . . as a valuable addition to evolutionary theory.’⁴⁵

Many palaeontologists do indeed support the concept of PE. For example, Stanley⁴⁶ and Vrba.⁴⁷

However, PE has received less acceptance amongst evolutionary biologists or geneticists. For example, Maynard Smith’s overall view

‘. . . is that we can forget about new paradigms and the death of neodarwinism.’⁴⁸

In regard to species selection, he said

‘there never was much sense in the idea anyway.’

Others such as Clarke⁴⁹ refuse to acknowledge any significant contribution from Gould and Eldredge, claiming that Simpson and Mayr had proposed everything worthwhile that PE contained.

Undoubtedly the PE debate has heightened appreciation for the true nature of the fossil record — that of stasis. Gould and Eldredge said,

‘. . . palaeontologists never wrote papers on the absence of change in lineages before punctuated equilibrium granted the subject some theoretical space’

and

‘Many leading evolutionary theorists . . . have been persuaded that maintenance of stability within species must be considered as a major evolutionary problem.’⁵⁰

Mayr seems to have come to agree with them on the reality of stasis.⁵¹

Even opponents of PE seem to have accepted the concept of stasis, and even brief periods of rapid change, but they reject the anti-neo-Darwinian concept of non-adaptive, random origin of new species and species selection as the mode of macroevolution. John Maynard Smith, for example, said:

‘It would be quite possible, however, to accept the claim that the typical pattern of change is one of long periods of stasis interrupted by brief periods of rapid change, without accepting the ideas of non-adaptive change, species selection, and the uncoupling of macro- and micro-evolution. This is a question for palaeontologists to settle.’⁵²

It is interesting that in their 1993 review paper, Gould and Eldredge define macroevolution in terms of ‘species sorting’ and somewhat softly assert that

‘darwinian extrapolation cannot fully explain large-scale change in the history of life.’⁵³

But what does explain large-scale change? They once again claim

‘that punctuated equilibrium was never meant as a saltational theory’.⁵⁴

They offer no suggestion of a biological basis for large-scale change. Indeed,

‘continuing unhappiness, justified this time, focuses upon claims that speciation causes significant morphological change, for no validation of such has emerged’

and

‘Moreover, reasonable arguments for potential change throughout the history of lineages have been advanced, although the empirics of stasis throws the efficacy of such processes into doubt.’⁵⁵

In other words, theoretical processes for change exist, but the fossil data show stasis, thus bringing into question the reality of processes which could bring about change (evolution). As they said,

‘stability within species must be considered as a major evolutionary problem’.⁵⁶

Undoubtedly Gould and Eldredge have done palaeontology a great service by giving the real data of palaeontology, that is, stasis and abrupt appearance, theoretical breathing space. One can only hope that there will be similar frankness amongst evolutionary biologists about the lack of any observed biological mechanism for producing abrupt appearance.

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QUOTABLE QUOTE: A Major Evolutionary Problem

‘Many leading evolutionary theorists, while not accepting our preference for viewing stasis in the context of habitat tracking or developmental constraint, have been persuaded by punctuated equilibrium that maintenance of stability within species must be considered as a major evolutionary problem.’

— Stephen Jay Gould and Niles Eldredge, 1993. Punctuated equilibrium comes of age. **Nature**, **366**, pp. 223–224.