Palaeontologia Electronica
http://palaeo-electronica.org

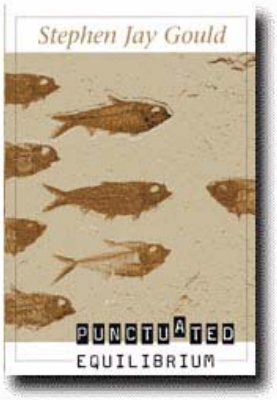
PUNCTUATED EQUILIBRIUM

Reviewed by Philip D. Gingerich

Stephen Jay Gould
Harvard University Press 2007
ISBN 0-674-02444-3, $18.95

Punctuated Equilibrium is a theory about how the evolutionary process works, based on patterns of first appearances and subsequent histories of species in the fossil record. The theory holds that species originate too rapidly to enable their origins to be traced by paleontologists (punctuation), and then persist unchanged through geological time in stasis (equilibrium). All is due to a mysterious shared homeostasis that is postulated to regulate the collective morphology of individuals. When species-level homeostasis is working, species persist unchanged; when species-level homeostasis breaks down, speciation results. It is difficult to imagine a construct more antithetical to Darwinian natural selection.

The late Stephen Jay Gould was obsessed with punctuated equilibrium from the time it was invented, and the obsession comes through so clearly in *Punctuated Equilibrium* that a reader would think he invented it all. The book itself is a 396 page extract from Gould's 1433 page *Structure of Evolutionary Theory* (Harvard University Press, 2002). The introduction here (pp. 1-13) reprints pages 37 to 48 in chapter 1 of *Structure of Evolutionary Theory,* and the remainder of the text (pp. 14-361) reprints Chapter 9 of *Structure of Evolutionary Theory.* If you succeeded in reading the 2002 book you probably do not need to read this again. If you never made it through all 1433 pages of the original *Structure of Evolutionary Theory,* then you might want to buy this 396 page version and try again.



Development of the theory of punctuated equilibrium was initiated by Niles Eldredge in a study titled 'The allopatric model and phylogeny in Paleozoic invertebrates,' which appeared in *Evolution* in 1971. Here Eldredge described the appearances and subsequent histories of three subspecies of *Phacops rana* trilobites that characterize successive geological stages of the middle Devonian. As described, each subspecies had a fixed number of dorsoventral columns of eye lenses, 18, 17, and 16-15, respectively. These did not change through Cazenovia, Tioghnioga, and Taghanic stages spanning 6-7 million years of Middle Devonian time. Eldredge interpreted this stepped change to be the pattern expected from an allopatric model of speciation where morphological change is postulated to occur rapidly in peripheral isolates.

The same year, Gould and Eldredge published a meeting abstract titled 'Speciation and punctuated equilibria: an alternative to phyletic gradualism' (Geological Society of America Abstracts with Programs, 1971: 584-585). Here they proposed that evolution is not a process of slow transformation, but a process, in their words, of 'homeostatic equilibria, rarely disturbed by rapid events of speciation.' Homeostasis is a property of organisms with cells linked by nerves, blood, and

Ginatedgerich, Philip D., 2007. [Review of *Punctuated Equilibrium*]. *Palaeontologia Electronica* Vol. 10, Issue 3, R6; 2pp. 129KB;
http://palaeo-electronica.org/paleo/2007_3/books/equal.htm

endocrine signaling that enables them to regulate their physiology and activity to maintain a stable internal environment. Gould and Eldredge's postulation was that the average morphology of species is regulated similarly to the average physiology of organisms, and by implication species are functionally organisms at some higher scale. Homeostasis, equilibrium, punctuation, and even allopatric speciation are theories to explain what cannot be seen and studied.

This view was more fully articulated in a book chapter by Eldredge and Gould titled 'Punctuated equilibria: an alternative to phyletic gradualism' (in *Models in Paleobiology* edited by T. J. M. Schopf; Freeman Cooper, 1972). Introducing the chapter, Schopf wrote:

> The significance of 'gaps' in the fossil record has been a recurrent 'difficulty,' used on the one hand to show that spontaneous generation is a 'fact,' and on the other hand to illustrate the incompleteness of the fossil record ... The interpretation supported by Eldredge and Gould is that allopatric speciation in small, peripheral populations *automatically* results in 'gaps' in the fossil record.

Curious company, spontaneous generation, and punctuated equilibria.

An innovation in the 1972 Eldredge and Gould chapter is the claim that speciation takes place randomly through time, and randomly in terms of direction of change. Hence trends, if there are any, must result from differential survival of species much as a Darwinian would view selection in a population of individual organisms. The idea that speciation takes place randomly through time has been tested by Vrba, Brett, Ivany, and others, who found pulses of turnover and coordinated stasis when faunas were studied through time. Rather than being random, speciations, like gaps in the fossil record and boundaries of geological formations, are often coincident, and further correlate with times of environmental change.

Punctuated equilibria [*sic*] as *patterns of stasis and episodic turnover* are important generalizations about the fossil record that have been represented in the lexicon of paleontology over the years in many different ways. In contrast, Gould's punctuated equilibrium [*sic*] as a p*rocess explaining punctuated equilibria* has serious competition. A pattern of rapid evolution leading to stasis is the logical expectation of Darwinian gradualism when evolution is fast, geological time is long, and major events of environmental change are widely spaced in time. This is the world we live in, and rapid evolution leading to stasis is the essence of an important article on coevolution written by Stenseth and Maynard Smith and published in *Evolution* in 1984. Surprisingly the article is not discussed or even cited here. It explains punctuated equilibria with natural selection—no homeostasis required. I have written about this too, based on quantification of rates of evolution, again not cited here.

The fossil record is only as good as the stratigraphic record, which often has gaps in local sections. An alternative to glorifying the gaps, by basing a theory of speciation on such absences of evidence, is to search more widely for places where the stratigraphic record is complete for an interval of interest. My sense as a paleontologist is that we could learn much about species origins from the fossil record if we studied better sections more intensively and if we measured more.

Punctuated equilibrum developed hand-in-hand with cladistics as an approach to systematics. In cladistics, time and variation are ignored, and morphology is viewed as something that can be discretely coded. Punctuated equilibrium is a theory used to justify coding, but time and variation won't go away. It is a point in Darwin's favor that the *Origin of Species* and natural selection both featured time and variation. What are paleontology and evolution without them?

I once won a bet with Steve Gould concerning the number of figures in the *Origin of Species* (there is one; Gould said two), and in a day when more words are published than a person can read, I am increasingly drawn to figures as a way to absorb information efficiently. My recommendation to readers of *Punctuated Equilibrium* is to start with the figures: what do they show, how are they scaled, and are they scaled appropriately for what they claim to show? How do you recognize 'punctuation'? How do you recognize stasis? Can these be quantified in terms of rate for comparison to change on the generation-to-generation scale of the evolutionary process? Has this been done? If not, why not?

The publisher, promoting *Punctuated Equilibrium,* suggests "we may now be living within a punctuation, and our awareness of what this means may be the enduring legacy of one of America's best-loved scientists." When you finish the book, ask yourself whether we are living in a punctuation? One of America's best-loved scientists—yes. Living in a punctuation—who knows what this might mean?