The biostratigraphic origin of the theory of punctuated equilibria

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More than 40 years have passed since Niles Eldredge and Stephen Jay Gould introduced the theory of punctuated equilibria (hereafter PE) in their paper titled "Punctuated equilibria: An alternative to phyletic gradualism" (Eldredge and Gould, 1972). The theory sparked a bitter controversy regarding the nature of macroevolution.

The theory of PE includes several philosophical flavors (described below), but very few philosophers of science have published any analyses of the theory itself [1]. Rather, they have been interested in related ideas such as species selection and saltation. In the present paper, we focus on the theory of PE. We dissect the theory of PE into three parts: a pattern hypothesis, a process hypothesis, and a way of seeing the fossil record. We point out that Eldredge and Gould (probably unintentionally) transported a way of seeing the fossil record from biostratigraphy to evolutionary biology in 1972.

Biostratigraphy is the branch of geology that deals with the distribution of fossils throughout the stratigraphic record and organizes strata into units based on the fossils contained within them. Biostratigraphers usually define the boundaries of biostratigraphic units or biozones by the first appearances and last occurrences (or extinction levels) of fossil taxa (see the section titled "The biostratigraphic origin of the theory of PE").

Pattern hypothesis

The first component of the theory of PE is the "pattern hypothesis." Eldredge and Gould (1972) argued that the long-term stability and abrupt changes in morphology were prevalent pattern in the fossil record and that this pattern would accurately reflect actual evolutionary history. They developed this hypothesis as an alternative to "phyletic gradualism," which they considered to have originated from Darwin (1859). Figures 1 and 2 are adapted from Eldredge and Gould (1972). Figure 1 represents the pattern of phyletic gradualism, which is characterized by gradual changes in morphology. Figure 2 represents the pattern of PE, which is characterized by punctuation (namely, abrupt changes in morphology) and equilibria (namely, long-term stability of morphology). Paleontologists frequently observe these patterns in the fossil record (Figures 3 and 4).

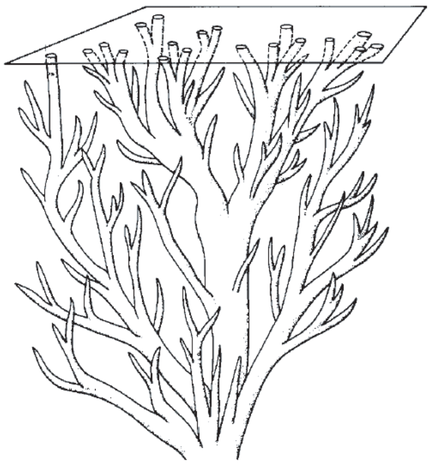

Figure 1. The pattern of phyletic gradualism (Eldredge and Gould, 1972).

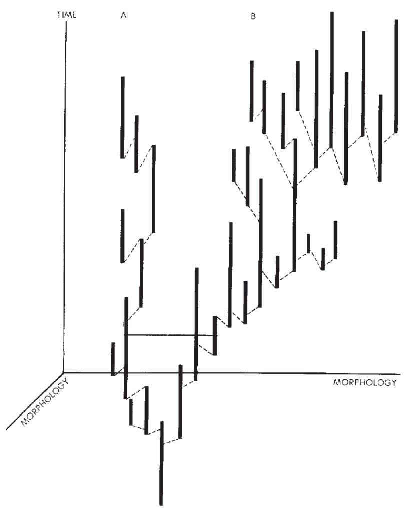

Figure 2. The pattern of PE (Eldredge and Gould, 1972).

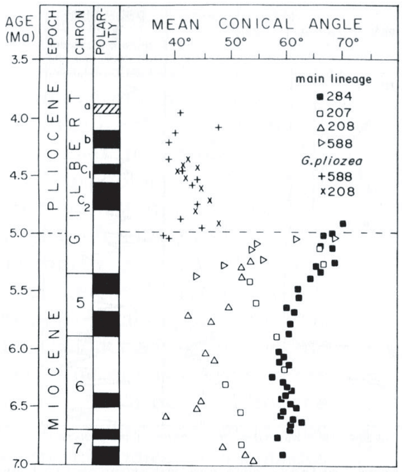

Figure 3. An example of the pattern of phyletic gradualism (Adapted from Wei and Kennett, 1988, with a slight modification). This figure shows historical change of the mean conical angle of the *Globoconella* (a kind of foraminifer) clade during the Late Miocene and Early Pliocene.

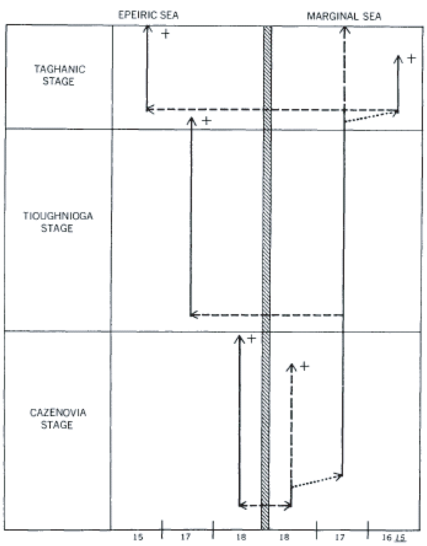

Figure 4. An example of the pattern of PE (Eldredge, 1971). This figure shows phylogeny of the *Phacops rana* (a species of trilobite) stock in the Middle Devonian of North America. This figure is included in Eldredge's paper published in 1971. Then, he had already presented an essential idea of the theory of PE. Hence this is the first figure of the pattern of PE drawn by Eldredge.

Both patterns of phyletic gradualism and PE are cladogenesis, or the branching of species from a common ancestor. However, additional types of macroevolutionary patterns exist in the fossil record. Paleontologists have observed patterns of gradual anagenesis, punctuated anagenesis, and punctuated gradualism (Figure 5). The pattern of gradual anagenesis is gradual morphological change without branching into divergent lineages. The pattern of punctuated anagenesis is long-term stability punctuated by abrupt morphological changes without branching. The pattern of punctuated gradualism is a combination of gradual and abrupt changes (Figures 6–8).

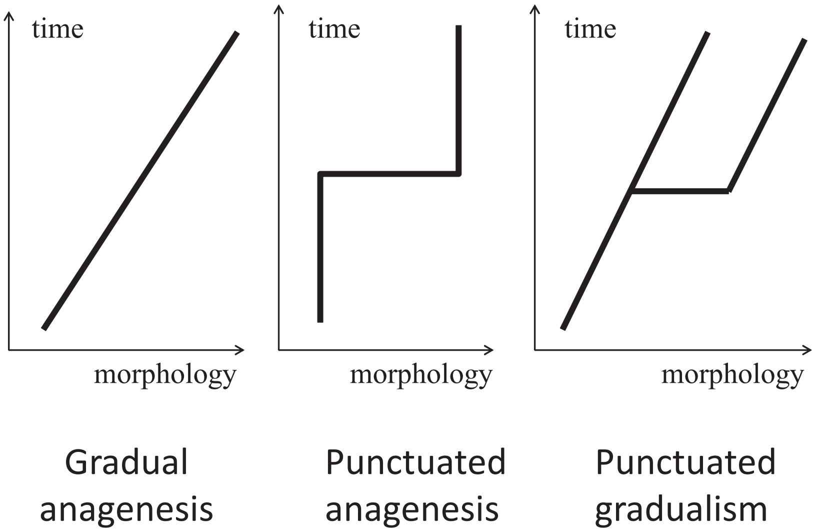

Figure 5. Gradual anagenesis, punctuated anagenesis, and punctuated gradualism.

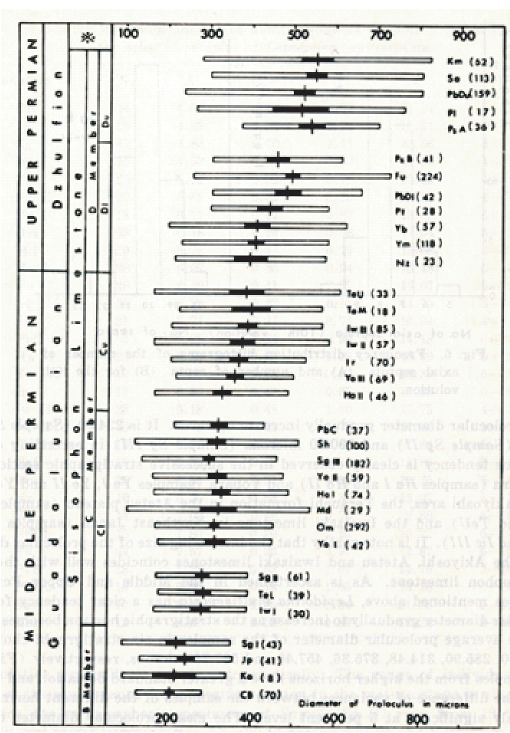

Figure 6. An example of the pattern of gradual anagenesis (Ozawa, 1975). This figure shows historical change of prolocular diameter (in microns) in a Permian foraminifer, *Lepidolina multiseptata*, from Eastern Asia.

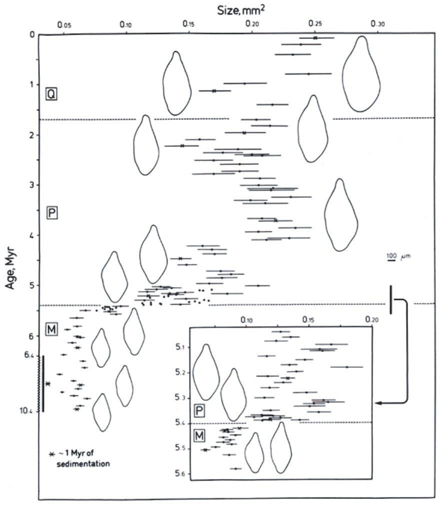

Figure 7. An example of the pattern of punctuated anagenesis (Malmgren et al., 1983). This figure shows an abrupt increase in size of planktonic foraminifers across the Miocene/Pliocene boundary.

Figure 8. An example of the pattern of punctuated gradualism (Fortey, 1988). Part of the *Gryphaea* (the Jurassic oyster) lineage shows both punctuation and gradual change.

Facing these various types of macroevolutionary patterns, we ask how prevalent the patterns of PE are in the fossil record. Answering the question requires an enormous amount of work. Initially, we surveyed 93 articles describing various macroevolutionary patterns, and classified these into 5 categories.

Table 1 summarizes the result of our survey. We identified only one example of the pattern of punctuated gradualism (Fortey, 1988). Therefore, we replaced this pattern with "stasis," or long-term morphological stability. Notably, patterns of phyletic gradualism comprised only a small minority of the articles (6/93), whereas the majority of patterns involved long-term stability and abrupt changes (punctuated anagenesis + PE + stasis = 54/93 and punctuated anagenesis + PE = 48/93, respectively) [2] .

Table 1. Taxonomic relative frequency of morphological macroevolutionary patterns.

Taxa	Gradual anagenesis	Phyletic gradualism	Punctuated anagenesis	Punctuated equilibria	Stasis
○Bivalves	4	2	3	4	2
Gastropods (Snails)	2			6	
○Ammonoids	4		2	2	
○Foraminifers	8		1		
○Radiolarians	3	1	2	2	
○Diatoms			2		
Ostracods	1		3		1
○Trilobites	1			5	3
Urchins	1		2	2	
Bryozoans	2			2	
Brachiopods	2		2	1	
Coral	1		1		
Stromatoporoids				1	
○Conodonts				1	
Fishes	1				
Mammals	3	3	3	1	
Total	33	6	21	27	6

* ○: Taxa frequently used as the index fossils   Grand total = 93

We suggest that paleontologists question why there are so many types of macroevolutionary patterns in the fossil record and why the result of our survey shows such a relative frequency. The morphological, developmental, and genetic hallmarks of a taxon are most likely related to evolutionary patterns that the taxon exhibits. Therefore, paleontological studies of macroevolution should involve genetics and developmental biology.

Process hypothesis

The theory of PE concerns not only macroevolutionary patterns but also macroevolutionary processes, which are described by the "process hypothesis." According to Eldredge and Gould (1972), Ernst Mayr's theory of allopatric speciation could explain abrupt evolutionary changes or punctuation (Mayr, 1942, 1963). We argue that the third component of the theory of PE (a way of seeing the fossil record) was transported from biostratigraphy to evolutionary biology. Given this, it is noteworthy that Eldredge and Gould (1972) proposed their theory as an application to paleontology of Mayr's theory of allopatric speciation.

An exhaustive discussion of process hypotheses is beyond the scope of the present paper. Table 2 summarizes the different process hypotheses (see Takahashi and Tanaka, in prep., for explanation).

Table 2. Process hypotheses about the pattern of PE.

Process hypotheses about punctuation	Process hypotheses about equilibria
• Allopatric speciation (Mayr, 1942, 1963; Eldredge and Gould, 1972) • Quantum evolution (Simpson, 1944, 1953) • Abrupt and strong directional selection (Kimura, 1983) • Intraspecific substitution of polymorphic phenotypes (Hayami, 1973, 1984) • Physical constraints (Okamoto, 1988, 1989) • Adaptive radiation (Gould, 1989; Davidson and Erwin, 2006) • Species selection (Gould and Eldredge, 1993; Gould, 2002)	• Developmental and genetic constraints (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1979) • Homeostasis (Eldredge and Gould, 1972; Hayami, 2009) • Stabilizing selection (Kimura, 1983) • Habitat tracking (Eldredge, 1995) • Genetic flow (Mayr, 1954, 1963; Dobzhansky, 1950)

A way of seeing the fossil record

The third component of the theory of PE is a way of seeing the fossil record. The pattern hypothesis of PE is based on the recognition of long-term stability and abrupt morphological changes in the fossil record. According to Eldredge and Gould (1972), phyletic gradualists claim that the fossil record provides us an incomplete depiction of the history of life. However, Eldredge and Gould (1972) argued that the fossil record can provide a nearly complete history of life. Thus, their way of seeing the fossil record is opposed to that of phyletic gradualists.

The biostratigraphic origin of the theory of PE

We suggest that Eldredge and Gould (1972) (probably unintentionally) transported a way of seeing the fossil record from biostratigraphy to evolutionary biology. We use the terms "probably unintentionally" because these researchers rarely referred to the methods of biostratigraphy in their papers, and this lack of reference is not a mystery. Their objectives in 1972 were the application of Mayr's theory of allopatric speciation to paleontology and the demonstration that paleontological observations were not contradictory to modern evolutionary thinking.

In general, the theory of PE is regarded as a combination of a pattern hypothesis and a process hypothesis (Mayr's theory of allopatric speciation). We interpret the theory from a different perspective and suggest that recognition of the biostratigraphic origin of the theory of PE will lead to a new way of evaluating this theory.

We postulate that the theory of PE has biostratigraphic origins and validate this interpretation by citing Eldredge and Gould's statements from 1977 in their paper titled "Evolutionary models and biostratigraphic strategies," which was published in *Concepts and Methods of Biostratigraphy* (a text unlikely to attract evolutionary biologists or philosophers of biology):

> Biostratigraphers have known for years that morphological stability, particularly in characters that allow us to recognize species-level taxa, is the rule, not the exception. (Eldredge and Gould, 1977, p. 29)

> [B]iostratigraphers have always treated their data as if species do not change much during their [residence in any local section], are tolerably distinguishable from their nearest relatives, and do not grade insensibly into their closest relatives in adjacent stratigraphic horizons. (Ibid., p. 40)

Before detailing our interpretation, we should introduce the first paleontologist in Japan to support the theory of PE. Itaru Hayami, Professor Emeritus at the University of Tokyo, focused on the biostratigraphic origin of the theory of PE even earlier than Eldredge and Gould. The following remark by Hayami (1973), published in the *Journal of the Geological Society of Japan*, is relevant to our argument. Again, this journal is unlikely to garner the attention of evolutionary biologists or philosophers of biology.

> The method of biostratigraphy has been purely empirical and influenced little by the development of evolutionary theory and the change of species concept, notwithstanding the fact that it depends entirely upon the past evolving organisms. Among various kinds of biostratigraphic units, lineage-zones (or phylozones) recognized within a single evolutionary lineage are especially interesting and significant not only in stratigraphy but also from the standpoint of evolutionary biology. (Hayami, 1973, p. 235)

Next, we explain biostratigraphy in detail. Biostratigraphy is the branch of geology that considers the distribution of fossils in the stratigraphic record and organizes strata into units on the basis of their contained fossils. The distribution of fossils in the stratigraphic record is the basic data of biostratigraphy. Figure 9 is an example of the data.

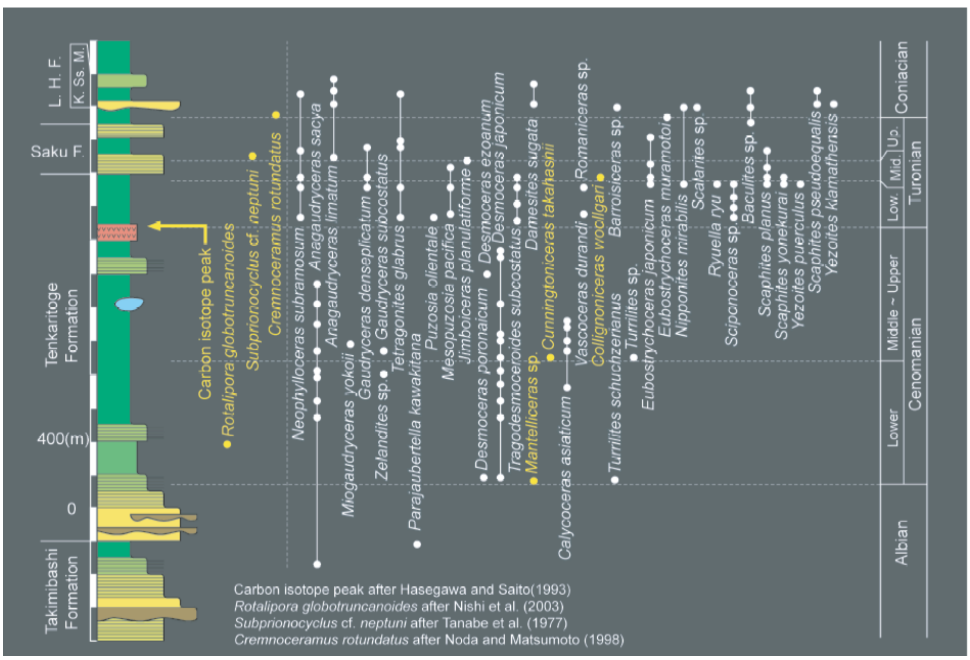

Figure 9. An example of stratigraphic distribution of mid-Cretaceous ammonoids.

The methodology of biostratigraphy is constituted from two steps. First, biostratigraphers attempt to find evidence in the fossil record of long-term stability and abrupt changes in strata without sedimentary gaps (without stratigraphic incompleteness). Subsequently, they "correlate" or demonstrate the correspondence in their fossil content of fossil-bearing beds. Figure 10 describes several stratigraphic correlation methods. Biostratigraphers usually define boundaries of biostratigraphic units or biozones by the first appearances and last occurrences (or extinction levels) of fossil taxa. Of the various types of biostratigraphic units, we focused on "lineage zones," which Hayami (1973) emphasized as the most important from an evolutionary viewpoint.

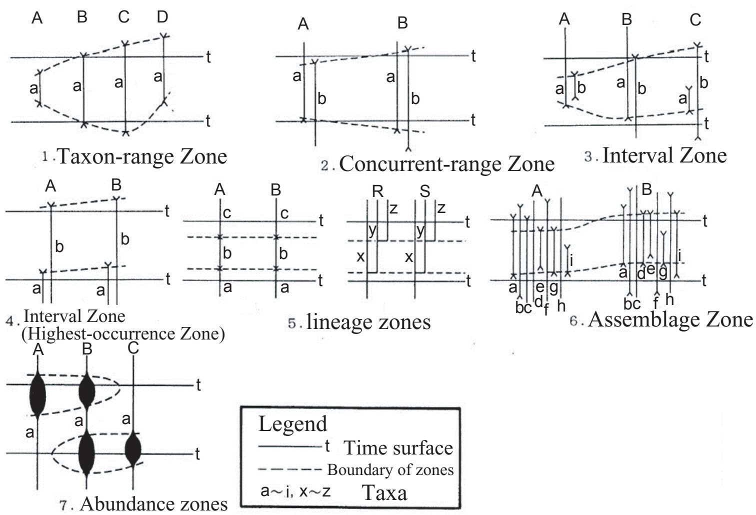

Figure 10. A variety of kinds of the biostratigraphic units.
Revised after Salvador ed. (1994).

A lineage zone is a body of strata containing fossils that represent a specific segment of an evolutionary lineage. In Figure 10.5, fossil taxa are represented by x, y, and z. Assume that two stratigraphic sections (R and S; Figure 10.5) exist in different places and that lineage zones observed in both sections represent the pattern of PE. We then can correlate based on the pattern. Whenever the lowest appearance of successive segments in an evolutionary lineage over the area of their distribution can be considered basically synchronous, the lineage zones have strong time significance, i.e., they make correlation possible.

Since the late eighteenth century, biostratigraphers have conducted and assembled an international correlation to reconstruct the geological history of Earth. This is akin to solving an enormous jigsaw puzzle. Figure 11 represents the biozones of the Late Cretaceous marine strata in the Northwest Pacific. This figure was prepared using the methods of biostratigraphy.

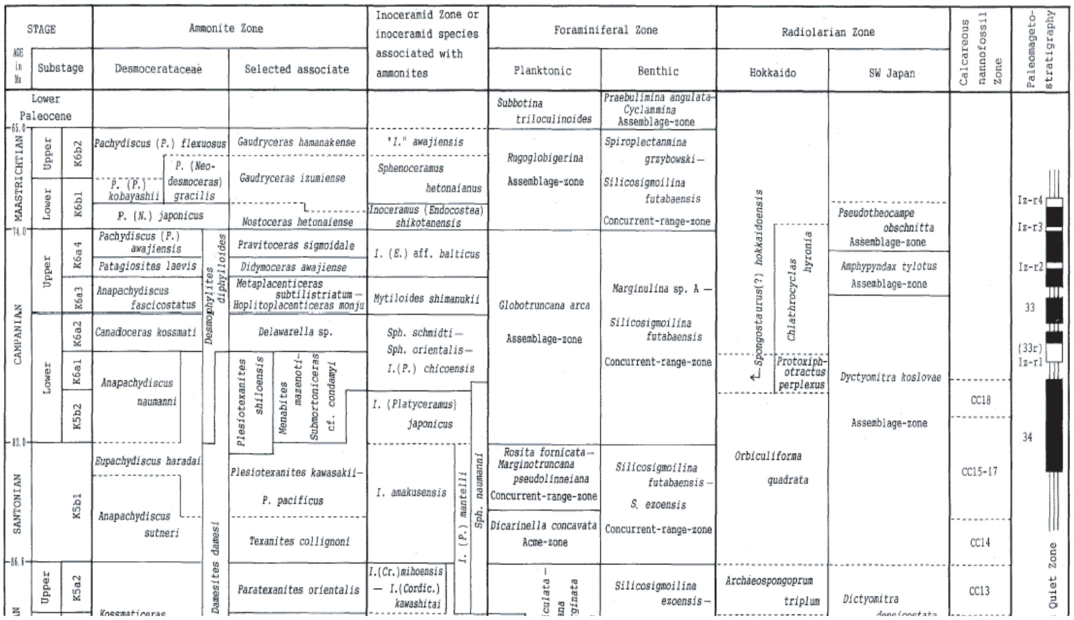

Figure 11. An example of the biozones of the Late Cretaceous marine strata in the Northwest Pacific (Toshimitsu et al., 1995).

Figure 11 corresponds to a portion of the International Chronostratigraphic Chart (Figure 12), which represents the entire geological history of Earth. The main tool that geologists have used to construct this chart is biostratigraphy.

The central claim of the present paper is that if long-term periods of stability and abrupt changes were merely illusions or artifacts in the fossil record owing to its incompleteness, then biostratigraphers could not have internationally correlated, let alone reconstructed, the geological history of Earth. Thus, we argue that the patterns of PE are real and sufficiently prevalent for biostratigraphers to detect empirically and to apply in the reconstruction of Earth's geological history.

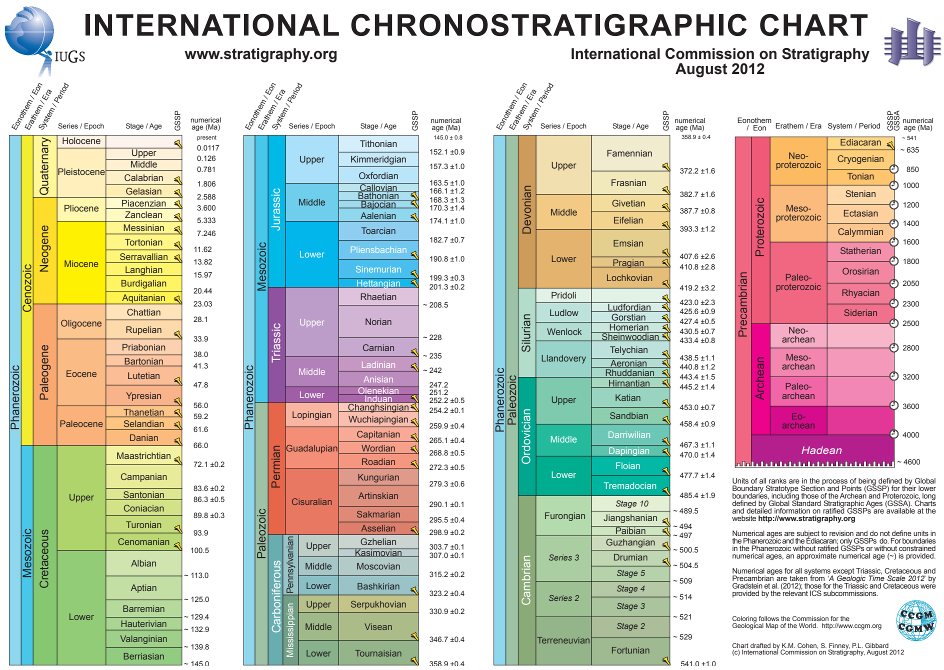

Figure 12. International Chronostratigraphic Chart
(International Commission on Stratigraphy, August 2012)

Theory-ladenness of data?

Surprisingly, philosophers of science have paid little attention to the fact that Eldredge and Gould (1972) were deeply influenced by Thomas Kuhn's *The Structure of Scientific Revolutions* [3] . From Eldredge and Gould (1972):

> The idea of *punctuated equilibria* is just as much a preconceived picture as that of phyletic gradualism. We readily admit our bias towards it…our interpretations are as colored by our preconceptions as are the claims of the champions of phyletic gradualism by theirs. (Eldredge and Gould, 1972, p. 98, italics original)

> [O]ne must have some picture of speciation in mind…the data of paleontology cannot decide which picture is more adequate…the picture of punctuated equilibria is more in accord with the process of speciation as understood by modern evolutionists. (Ibid., pp. 98–99)

In the above discussion, Eldredge and Gould clearly refer to the theory-ladenness of data. Thus, we must ask: are the data of paleontology theory-laden?

Recall that Eldredge and Gould (1972) transported a way of seeing the fossil record from biostratigraphy to evolutionary biology. Biostratigraphy is a branch of geology, which has been little influenced by the development of evolutionary theory, as Hayami (1973) emphasized. Notably, the history of biostratigraphy is older than the Darwinian theory of evolution and far predates the theory of PE. Thus, their way of seeing the fossil record must not be colored by any evolutionary theory, let alone Mayr's theory of allopatric speciation!

This point was emphasized by Richard Fortey (1988).

> [Biostratigraphers] appeared to approach the data without any particular *a priori* presumptions, if only because their main concern was the mundane business of correlation between rock sections, and maybe the accurate description and recognition of species. If we are able to accept such observations as *not* being theory-laden,…then there is a good chance that what is reported on phylogeny *does* accurately reflect what is actually going on in the rocks rather than a repetition of what the textbooks say ought to be going on in the rocks. (p. 5, italics original)

The statement, "what the textbooks say ought to be going on in the rocks," refers clearly to the pattern of phyletic gradualism.

As Fortey (1988) stated, biostratigraphers have focused on practical methods of study such as the correlation and reconstruction of the geological history of Earth. For almost all of biostratigraphers, the process of evolution is of no interest. In contrast, the works of biostratigraphers have been unlikely to draw the attention of evolutionary biologists. Thus, a gap exists between biostratigraphy and evolutionary biology, although the former applies the evolutionary patterns of organisms to their study.

It seems reasonable to conclude that biostratigraphers are unbiased observers with regard to the pattern(s) by which organisms evolved. Though they have reported various types of macroevolutionary patterns, biostratigraphers focus not on gradual changes but on abrupt, punctuated changes because they are useful to correlate.

Conclusion

We conclude the following: (1) Eldrege and Gould (1972) transported a way of seeing the fossil record from biostratigraphy to evolutionary biology; (2) Their way of seeing the fossil record must not be colored by any evolutionary theory of speciation; and (3) Patterns of PE are real and sufficiently prevalent evolutionary patterns for biostratigraphers to detect empirically and apply to their reconstruction of the geological history of Earth.

Notes

1. Sterelny (2007) and Turner (2011) are exceptions to this statement. However, we consider their papers unsatisfying because they did not mention biostratigraphy in any detail.
2. See Takahashi and Tanaka (in prep.) for a detailed analysis of Table 1.
3. Turner (2011) analyzes this point exceptionally.

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