

RESEARCH UPDATE

Punctuated equilibria (evolutionary theory)

The term “punctuated equilibria” refers to Stephen Jay Gould and Niles Eldredge's 1972 proposal regarding the nature of biological data as preserved in the fossil record and the implications that those data have for evolutionary theory. Eldredge and Gould proposed that the history of life was not characterized by morphologically “connecting together all the extinct and existing forms of life by the finest of graduated steps,” as hypothesized by Darwin in 1859 and subsequently portrayed by mid-twentieth-century textbooks (**Fig. 1**). Rather, Gould and Eldredge envisioned evolutionary history as a network characterized by long periods of morphologic stability (stasis mode) punctuated here and there by rapid events of speciation (punctuation mode) [**Fig. 2**]. When first proposed, the concept of punctuated equilibria caused considerable controversy because aspects of the punctuated-mode pattern were promoted as falsifying some long-held beliefs about Neo-Darwinian evolutionary theory—termed “phyletic gradualism” by Gould and Eldredge. Later, punctuated equilibria also came to be used by creationists (incorrectly) to throw doubt on the entire theory of evolution. Today, the punctuated equilibria model is regarded as a valid characterization of a number of fossil lineages, but is no longer regarded as challenging contemporary evolutionary theory.

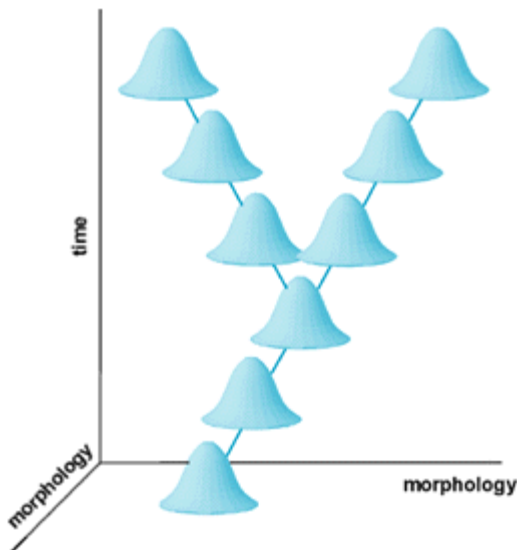


Fig. 1 Gradualist model of morphological change through time. In this conceptualization a series of fossil populations are represented as morphological frequency distributions moving to the right across a morphological change field (bottom of diagram) at a uniform rate. The speciation event occurs in the middle of the diagram when a branch of the original population splits off from the main lineage and begins moving off on a new trajectory (to the left), once again at a uniform rate. Note that consistent trends in morphological change are present within species as well as between species under the gradualist model. This figure, which is similar to the illustrations produced in paleontological textbooks of the 1950s and 1960s, was criticized by N. Eldredge and S. J. Gould because it implies substantial levels of morphological change within species (between speciation events). Defenders of the gradualist model, however, argue that such illustrations are grossly oversimplified caricatures of Neo-Darwinian evolutionary theory.

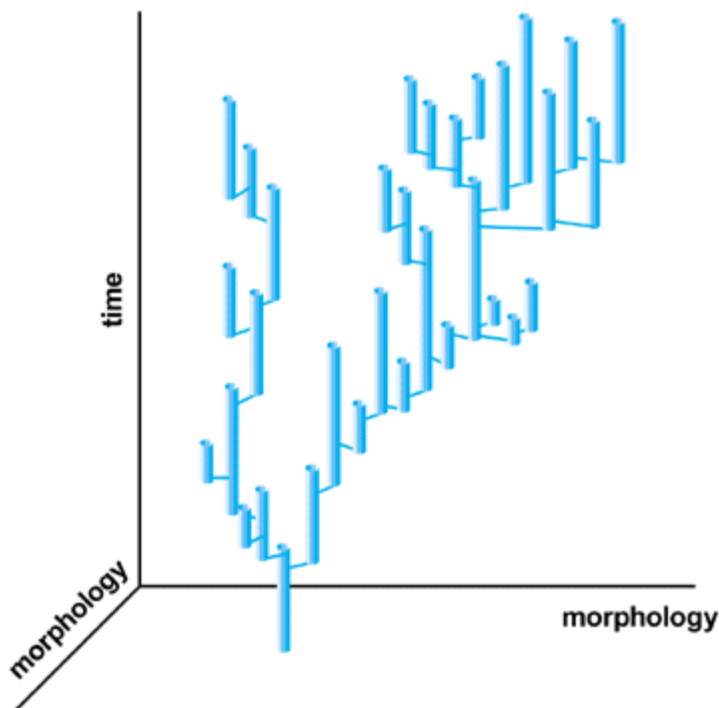


Fig. 2 Punctuated equilibria model of morphological change through time (after S. J. Gould and N. Eldredge, 1972). In this conceptualization of evolutionary change, species are represented as straight rods (symbolizing that morphological change within species is limited to random variation about a static average) and their pattern of ancestor-descendent relations is represented by short, horizontal ties (symbolizing rapid morphological changes occurring in small, isolated populations).

Punctuation mode: allopatric speciation

Drawing on the work of scientists from the mid-1800s to the mid-1900s, most evolutionary biologists and paleontologists had come to regard the speciation process as reflecting the accumulation of a number of small, progressive changes in organismal populations. The progressive nature of this transformation was thought to allow these populations to acquire novel attributes while retaining their overall fitness. This model, in turn, led to the concept of large-scale evolutionary change arising as a direct extrapolation of these small-scale modifications.

In conjunction with this work, it was realized that small populations characterized by limited inter-breeding with other populations and located on the periphery of a species' geographical range (where they might be subjected to unusual environmental conditions) would be favorable candidates within which morphological variations might spread and become established, producing new species. Such populations are termed allopatric. Many evolutionary theorists, including Eldredge and Gould, believe allopatric speciation is a dominant mode of species production.

Although Eldredge and Gould accepted the Darwinian mode of species transition by finely graduated steps within allopatric populations, they were the first to document examples of the punctuated speciation pattern—drawn from their own paleontological research (on snails and trilobites, respectively)—and argue that such a pattern was the expected signature of allopatric speciation in the fossil record. Two factors are thought to be responsible for this. First, the small size and isolated nature of the allopatric population reduces the probability that it will be preserved in the fossil record. This means that for many (if not most) species direct evidence of the gradual morphological transition is simply not there to be found. New species seem to appear suddenly in the fossil record because these appearances record the migration of fully formed

species into local areas, not evolutionary transformation in situ. Second, the short duration of such speciation events (approximately 5000–10,000 years) relative to the long intervals over which species exist (approximately 5 million to 10 million years) means that, even if a paleontologist was fortunate enough to happen upon the fossil record of an isolated population in which a new species was formed, the speciation event would be compressed into a very small physical interval, perhaps as small as a single depositional layer or bed. Given the realities of sampling the fossil record, this entire transition could easily be subsumed within a single rock sample and appear as a single point on a graph or table. Thus, the punctuation-mode aspect of punctuated equilibria theory does not conflict with the speciation mechanism of standard Neo-Darwinian evolutionary theory. Instead, it adjusts scientists' expectations of what an allopatric speciation event would look like in the fossil record.

Equilibrium mode

Theoretical justification for Gould and Eldredge's second pattern—the stasis or equilibrium mode of morphological change—has proven more controversial. From the beginning, both authors were struck by the manner in which many fossil species' morphologies remained more or less constant throughout their stratigraphic ranges, from the oldest to the youngest, in the rock layers where they are found. The fact that these time intervals often coincided with evidence of substantial environmental change (such as sea-level rises and falls, cooling and warming events, glaciations, even asteroid impacts) suggested that species may not be as responsive to external changes as some formulations of evolutionary theory implied. In addition, both authors (but especially Gould) developed an interest in accounting for the long-term trends in morphological change that appeared to characterize many lineages, with each new species carrying the trend forward (Figs. 1 and 2).

In order to address these issues within the punctuated equilibria model, Eldredge and Gould suggested that organismal morphologies were not as thoroughly adapted to local environments as had been thought previously. Instead, they viewed organisms as intricate systems whose complex biochemical and developmental structures gave them only limited capacities to respond to changes in external conditions. For example, Gould and Harvard geneticist Richard Lewontin have argued that the branching rib patterns that decorate the shells of many fossil mollusk and brachiopod species may represent nonfunctional by-products of these organisms' peculiar method of secreting their shells. Any such by-product would not necessarily be maintained directly by selection and so may be unalterable by environmental change without affecting some more basic component of the organism's organization. In another possible instance, the striking repetition of the same generalized shell geometries that characterize the evolutionary histories of many planktonic foraminiferal lineages may represent small variations in the gene sequences that create these organisms' shells, as opposed to opportunistic morphological solutions to specific environmental challenges. Such organizational constraints were proposed by Gould and Eldredge as being responsible for the morphological stasis they saw as being a dominant feature of the fossil record. Even more importantly, they saw the neglect of this aspect of organismal systems as being a flaw in evolutionary theory.

Testing punctuated equilibria

Since 1972, researchers have documented many paleontological examples of the morphological succession of species within local fossil records. In some cases, these met the expectations of the traditional, gradualist model (**Fig. 3 a**). In others, Gould and Eldredge's punctuated pattern was evident (**Fig. 3b**). There are even examples that are claimed by both groups (**Fig. 3c**). Interestingly, the most detailed examples of morphological evolution have been obtained from microfossils (the fossils of microscopic marine protists, algae, arthropods, and other groups), and these tend to conform to the gradualist model.

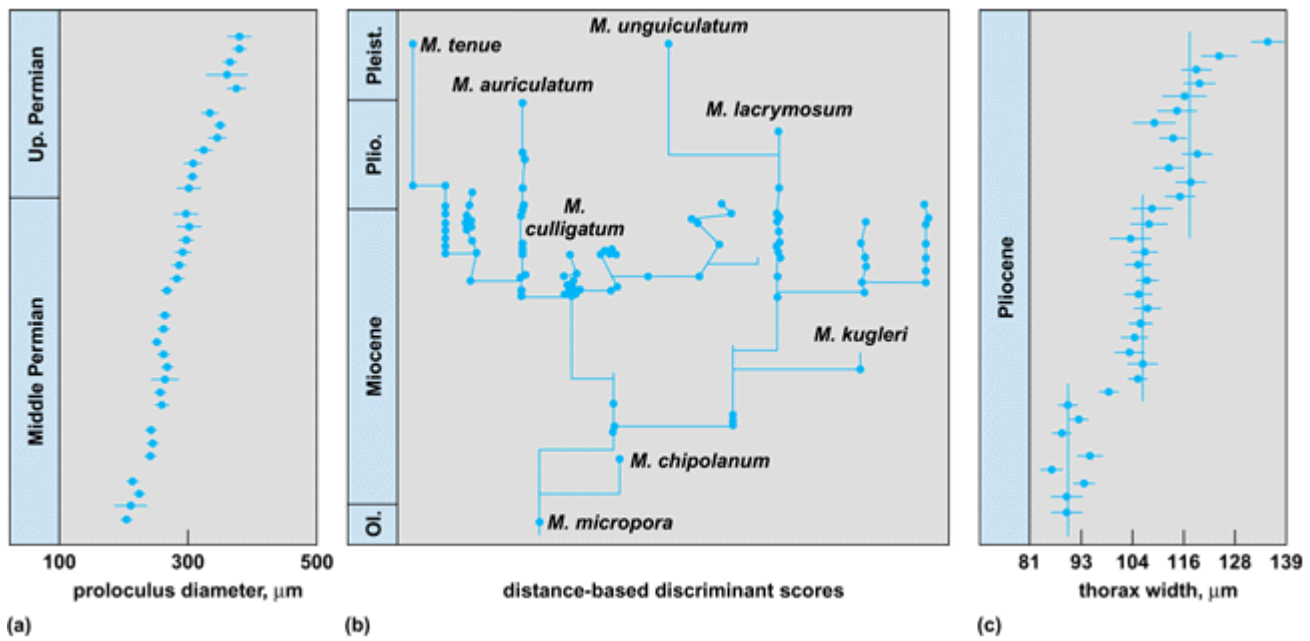


Fig. 3 Empirical data from the fossil record exhibiting both gradualist and punctualist patterns of evolutionary change. (a) Gradual change in the diameter of the first chamber (proloculus) of the benthic foraminiferal species *Lepidolina multiseptata* through a long middle-upper Permian time interval (approx. 10 million years). Circles represent sample averages; horizontal bars represent 95% confidence intervals (after T. Ozawa, 1975). (b) Punctuated change in a series of Caribbean bryozoan species belonging to the genus *Metrarabdotos* through a 24-million-year interval. All unlabeled lineages represent new species (after A. H. Cheetham, 1986). (c) Morphological change in thorax width of Antarctic populations of the radiolarian species *Pseudocubus vema* over a 3.5-million-year interval. Circles represent sample averages; horizontal bars represent 95% confidence intervals. Although adherents of the gradualist model regard this pattern as supporting a model of continuous, within-species morphological change, adherents of the punctualist model point to the fact that morphological variation within this species seems to be organized around three discrete steps (vertical lines) connected by rapid between-step transitions (after D. E. Kellogg 1975).

In their later writings Eldredge, and especially Gould (for example, Gould, 2002), accepted that “punctuated equilibrium may not be a dominant pattern in certain groups, particularly in asexual single-celled protists [including foraminifera and radiolaria]...where speciation cannot be defined in the traditional sense.” This statement represents an important reformulation of punctuated equilibria's scope by its cofounder and primary advocate. The fact that the organisms with the best fossil records (such as microfossils) tend to exhibit the gradual transitions between species expected under the allopatric speciation model is seen by some as providing evidence against the punctuated equilibria model. As has been noted, however, it was never Eldredge's or Gould's intention to deny that allopatric speciation events proceed through the accumulation of small changes in a population. A perspective that is increasingly popular among biologists and paleontologists is to view the microfossil studies as confirming Gould and Eldredge's basic contention that only exceptionally detailed fossil records (like those of microfossils) are likely to preserve the intermediate forms that document the speciation event itself. More typical fossil records do tend to exhibit the abrupt or punctuated pattern of trans-specific morphological change.

In terms of the second of punctuated equilibria's predictions, the existence of long periods of morphological stasis in fossil taxa—even microfossil taxa—is unquestionable (Fig. 3a and c). So too is the fact that such patterns often exist in stark contrast to unquestionable evidence for substantial environmental changes. It is important to appreciate, however, the nature of stasis as documented in the fossil record. Stasis does not assume the complete absence of within-species morphological variation. Instead it reflects a lack of overall

direction in such patterns. Careful measurements of morphological variation in successive fossil populations typically reveal complex shifts in virtually all continuously variable parameters (such as overall body size and overall body shape; Fig. 3a and c). In addition, local rates of morphological change are known to be inversely scale-dependent (the smaller the time interval between successive samples, the greater the rate). Such patterns are presumably driven by a combination of genuine response to local environmental change, genetic drift, the effect of migration and emigration, and sampling error. The attribution of stasis is applied when these data appear directionless, or at least statistically indistinguishable from a random pattern.

Do such patterns provide evidence for the operation of species-specific constraints on morphological evolution? Although genetic phenomena such as pleiotropy (a condition in which multiple morphological effects are produced by variation in a single gene) and canalization (a condition in which the expression of a gene complex is constrained to occur along discrete pathways leading to a specific range of morphological types irrespective of changes in environmental conditions) are well known, Gould and Eldredge's early writings are vague about the precise manner in which such phenomena—which themselves can be selected for or against—represent species-defining characteristics or how such factors might operate in an evolutionary context. Moreover, as pointed out by Richard Dawkins, evidence from laboratory populations is not encouraging. If such constraints were present, artificial selection experiments should detect their presence. Instead, the common observation is that laboratory populations seem almost infinitely malleable for continuous characteristics until such time as a lack of variation due to inbreeding (reflecting a lack of time for mutation to occur) terminates the experiment.

Resolution of dilemma

A resolution to the dilemma posed by punctuated equilibria's stasis mode was proposed in 1987 by Douglas Futuyama, and is now receiving increased attention from paleontologists as a result of its acceptance by Gould and Eldredge. Futuyama argues that the morphological stasis pointed to by Gould and Eldredge is exactly what it appears to be: a collection of directionless and temporary responses to local environmental change on the part of a large, heterogeneous population which, through time, becomes statistically overwhelmed by recombination coupled with stabilizing selection. The only way for lineages to surmount long-term stasis and preserve any component of localized adaptation, according to Futuyama's model, is through an allopatric speciation event, in which case back-crossing with the parent population is prevented. Futuyama's model provides a compelling resolution to the original controversy by its abandonment of attributions to ill-defined and experimentally unsupported organizational constraints, and by its shifting of the focus of the explanation for stasis back to the speciation event itself, which was always felt by all parties to fall squarely within the Neo-Darwinian paradigm.

See also: Organic evolution; Paleontology; Population genetics; Speciation

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