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Punctuated Equilibria—Where is the Evidence?

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Eldredge and Gould (1972) presented "punctuated equilibria" as an alternative to phyletic gradualism. Recently, they have again defended its originality (Gould and Eldredge, 1983), noting that Darwin never wavered in his support of gradualism. A gradual process is one that advances by steps rather than jumps—moving, changing, developing by degrees. Intermediates are present as evidence of transition. Included is the idea, implicit in a step-by-step procedure, that the process advances slowly—slowly enough to make the intermediates recognizable at some appropriate scale of resolution. Why was Darwin committed to gradualism, and how does this commitment relate to punctuated equilibria? What evidence might distinguish these competing hypotheses?

Darwin (1859:189) wrote in the *Origin of Species*: "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down." In the *Origin* he further characterized gradualism as slow: "We see nothing of these slow changes . . . until the hand of time has marked the long lapse of ages" (Darwin, 1859:84). Change that appears slow to us in ecological time may, of course, represent almost any rate over geological time.

Two fundamental questions remain in the debate over gradualism and punctuated equilibria. First, Darwin viewed evolution as a process of *continuous* change (change involving an uninterrupted se-

quence of intermediates), but did he see evolution as a process of *continual* change (perpetual, constant change)? Second, why was Darwin committed to gradualism when those around him, including the influential Thomas Huxley, considered saltation a viable possibility?

In the original paper on punctuated equilibria, Eldredge and Gould (1972:97) equated Darwin's gradualism not only with continuous change, but also with continual change:

Although phyletic gradualism prevails as a picture for the origin of new species in paleontology, very few "classic" examples purport to document it. . . . [We] usually explain the paucity of cases by a nearly-ritualized invocation of the inadequacy of the fossil record. It is valid to point out the rarity of thick, undisturbed, highly fossiliferous rock sections in which one or more species occur continuously throughout the sequence. Nevertheless, if most species evolved according to the tenets of phyletic gradualism, then, *no matter how discontinuous a species' occurrence in thick sections, there should be a shift in one or more variables from sample to sample up the section* [italics added].

Gould (1982:383) sustained this interpretation in equating gradualism with a "world . . . of constant change."

My reading of the *Origin of Species* indicates that such a narrow view of gradualism cannot be attributed to Darwin. As Rhodes (1983) noted, Darwin's gradualistic model embraced a large component of stasis. Darwin wrote of "only a few species . . . undergoing change at any one period" (1859:463), and later that "a number of species . . . might remain for a long period unchanged" (1859:488). The following comparative analysis of Eldredge and Gould's (1972) diagrammatic representation of punctuated equilibria and Darwin's (1859) diagrammatic portrayal of gradualism confirms that stasis is an integral part of both punctuated equilibria and Darwinian gradualism.

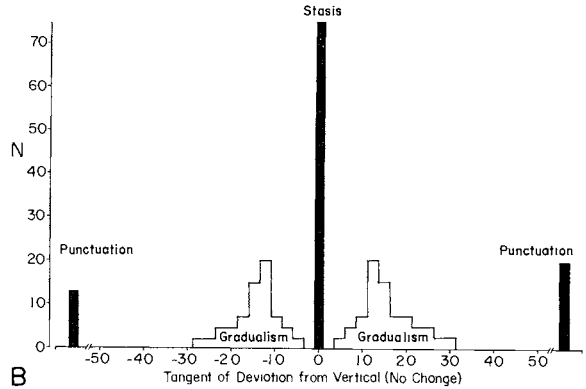
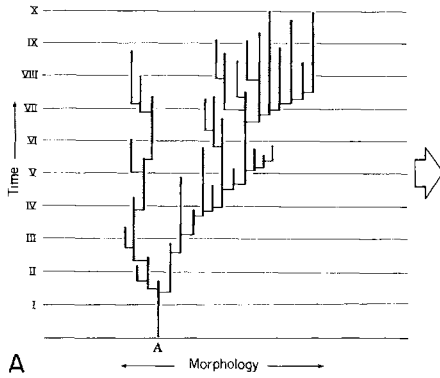
The Eldredge-Gould model of punctuated equilibria, illustrated in Figure 1A, features morphological stasis in a central role, long intervals of "equilibrium" being disrupted occasionally by rapid (geologically instantaneous) "punctuation" events equated with speciation. The Eldredge-

Gould model is unscaled, but, whatever the scale, the magnitude of the angle of any morphological deviation from a vertical axis (representing time) must be proportional to the rate of any given morphological change. In this context, stasis (or equilibrium), involving no deviation, is appropriately portrayed as change at zero rate. Punctuated speciation events, involving high angles of positive or negative deviation from vertical, are associated with very high rates of positive or negative change. According to the Eldredge-Gould model, one should expect to find predominantly stasis, with some very high rates of change distributed randomly among lineages, through the course of evolution. Stasis and punctuation are represented by shaded columns in the rate distribution of Figure 1B. According to Eldredge and Gould (1972), gradualism, if present at all, would be confined to intervals of the rate distribution (here shown as unshaded histograms) between stasis and the positive and negative punctuation modes.

Darwin's model of gradualism, also expressed in diagrammatic form, is reproduced in Figure 1C. Here again, the morphological axis is unscaled, precluding calculation of absolute rates. As in the Eldredge-Gould model, the magnitude of the angle of any morphological deviation from vertical (time) must be proportional to the rate of any morphological change. Stasis, involving no deviation, again corresponds to change at zero rate, and positive or negative angles of deviation from vertical reflect rates of change in a positive or negative direction. According to Darwin's model, one should expect to find predominantly stasis, with progressively higher rates of change in a positive or negative direction occurring with decreasing frequency (shaded distribution in Fig. 1D).

Both models are unscaled. The Eldredge-Gould model could possibly be altered to make it more gradual by shortening temporal intervals until they approach generation lengths and decreasing morphological differences between segments until they approach differences between individual organisms. However,

ELDREDGE-GOULD MODEL



DARWIN'S MODEL

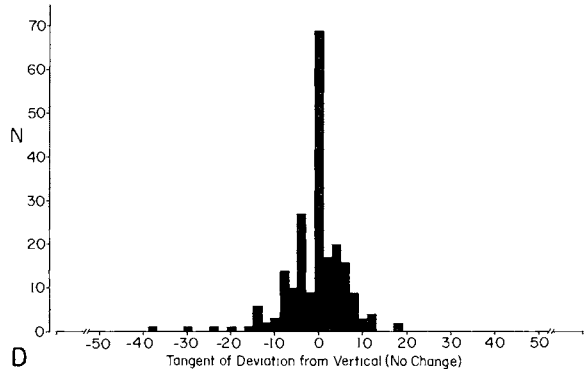
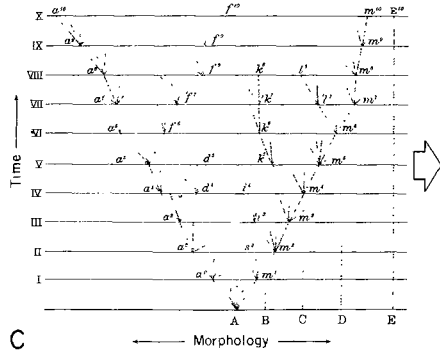


FIG. 1. Comparison of the distribution of rates of evolution implicit in the Eldredge-Gould punctuated equilibria model with the distribution inherent in Darwin's gradualism model. (A) Eldredge-Gould model, redrawn from figure 10 of Eldredge and Gould (1972) with morphology compressed to a single axis (abscissa) and time intervals I-X superimposed (ordinate) for comparison with Darwin's model. This diagram is unscaled, but proportional rates of morphological change can be measured as the tangent of the angle of deviation of each line segment from vertical (time). (B) Distribution of evolutionary rates, compiled interval by interval, corresponding to Eldredge-Gould model. (C) Darwin's model, copied from the *Origin of Species* (right half of Darwin's [1859] figure, included in rate compilation, is omitted here to conserve space). Again, morphology is portrayed on the abscissa and time is shown on the ordinate. (D) Distribution of evolutionary rates, compiled interval by interval, corresponding to Darwin's model. The Eldredge-Gould model predicts most evolution at zero rate (stasis or equilibrium, shaded central column), with morphological change occurring rapidly at very high positive or negative rates ("punctuation," shaded peripheral columns). According to Eldredge and Gould (1972; see also Gould, 1982), gradualism involves relatively slow constant change (shown diagrammatically by open distributions). Eldredge and Gould's narrow view of "gradualism" might better be labelled orthogenesis. Darwin's model predicts that stasis will predominate (shaded central column; differences of scale will not alter this), with morphological change taking place at slow to moderate rates (shaded distribution about central column). Stasis is an integral part of both models, and stasis does not distinguish punctuated equilibria from Darwinian gradualism.

transformation of Darwin's model would not make it "punctuated," nor could manipulation remove stasis as a dominant mode in the associated distribution of rates.

Eldredge and Gould's gradualism, ex-

cluding morphological stasis, is not the gradualism advocated by Darwin. Comparing the rate distribution implicit in the Eldredge-Gould model with that inherent in Darwin's model (Fig. 1), it is clear that

stasis is an integral component of both. It is a misrepresentation of Darwin to equate Darwinian gradualism with continual, constant change. Darwin's gradualism was not orthogenesis (Penny, 1983).

Why was Darwin so committed to gradualism, while at the same time Huxley advocated saltation? This commitment cannot be dismissed as political rhetoric, nor can it be written off as a cultural artifact that "translated Victorian society into biology" (Gould and Eldredge, 1977:145; Victoria was, after all, queen to both Huxley and Darwin). Absence of evidence is absence of evidence, not evidence of absence as Eldredge and Gould suggest with respect to gaps in the evolutionary record. Any form of saltation or punctuation based on gaps, any theory that advocates evolutionary change without intermediates because the intermediates are unknown, is a theory based on negative evidence. The geological record *is* imperfect; stratigraphic resolution *is* often poor; animals and plants *do* expand and contract geographic ranges as environments change. The effect in each instance is a gap in the fossil record. It may be true that paleontological gaps are caused by punctuation, but this is not demonstrated by mere existence of gaps themselves. Hypotheses of saltation or punctuation that depend on gaps, negative evidence, can never be tested. In this context, it appears that Darwin's commitment to gradualism reflects, above all, commitment to empiricism and dedication to the principal of testability in science.

Punctuated equilibria as an alternative to gradualism is not supported by stasis in

the fossil record: connected series of forms showing no change over time are a common element of gradualism. Stasis can be viewed, in this instance, as gradualism at zero rate. Further, punctuated equilibria as an alternative to gradualism is not supported by gaps in the fossil record: gaps are gaps, providing no evidence of transition. Without positive empirical evidence, punctuated equilibria, like saltation, cannot be sustained as an alternative to gradualism. Perhaps the time has come to end this false debate and concentrate instead on study of the rates and patterns we can observe.

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