1. Punctuated equilibrium or phyletic gradualism?

Shortly after Eldredge and Gould (1972) published their classic paper outlining the characteristics of punctuated equilibrium and phyletic gradualism, Gingerich (1976) presented a well documented example from among fossil mammals. The condylarth *Hyopsodus* is common over North America and Europe in the early Eocene, and especially in the Big Horn Basin of Wyoming. *Hyopsodus* was about rat-sized and lived in trees, feeding on small prey – a far cry from its distant living relatives such as horses and cattle.

Gingerich (1976) argued that *Hyopsodus* showed phyletic gradualism. In the diagram below, rock thickness, equivalent to time (y-axis), is plotted against measurements of the variable first molar tooth (x-axis), a standard measure used by mammal paleontologists in characterizing species. A year later, Gould and Eldredge (1977) suggested that the diagram really showed stasis, minor variation about a mean, for the evolution of a single variable species lineage.



- (a) Explain why Gingerich interpreted this as an example of phyletic gradualism.
- (b) What would be the main criticisms given by a punctuated equilibrist?

(c) Check this idea by plotting the mean values for the tooth measure against thickness. Calculate the mean (= average) value for all samples within time intervals of 200 feet. Remember to scale your calculations of global means to the numbers of specimens in each sample (small number at right-hand end of line), and calculate (or estimate) a regression line. Plot the graph by hand, and calculate the regression line on a scientific calculator if you have one, or estimate the regression line by eye. How well do the data fit the regression line? Work out the equation of the line, using a statistics program or a scientific calculator.

The equation for a regression line is written in the form,

y = mx + c,

where c is the intercept on the y axis, and m is the gradient.

- (d) Assuming that 200 ft = 10.000 yr, calculate the total rate of species origination and extinction from bottom to top of the succession. [Remember, total rates are given by $\Delta E = E/\Delta t$, $\Delta O = O/\Delta t$.]
- (e) What do your results show? Explain the fit, or lack of fit, of the regression line to the recalculated points. Is this a single variable lineage showing stasis, or not?

2. Patterns of punctuated species evolution

The diagram shows the pattern of evolution among species of the bryozoan *Metrarabdotos* in the Caribbean (Cheetham 1986). Today, there are three species of this genus, but there have been many more in the past. Careful collecting throughout the Caribbean has shown how the lineages exhibited stasis for long intervals, and then underwent phases of rapid species splitting, especially in the time from 8-4 Ma, the Dominican Sampling Interval (DSI) where records are particularly good. (Image Courtesy of Alan Cheetham.)



- (a) How many species are represented in all? How many are extinct? The overall time span shown is 25 myr, so what is the overall total rate of origination of species, O/δt?
- (b) The Dominican Sampling Interval (DSI) represents a time of heightened evolution. How long did this interval last? How many species originated in the DSI, and what is the total rate of origination of species then? How does this compare with the overall rate? What might have stimulated the appearance of such intense speciation over this span?
- (c) How many speciation events are anagenetic (within-lineage) and cladogenetic (splitting lineages)? Of the cladogenetic speciation events, how many represent new lineages and how many represent budding from a pre-existing species, which survives after the speciation event?
- (d) Why have paleontologists been happy to accept this study as evidence for punctuated equilibrium? Identify both geometric reasons (from the diagram) as well as broader issues about quality of data, sampling, and knowledge of modern species.

3. Patterns of gradual species evolution

The diagram shows evolution of the two modern species of the planktonic diatom *Rhizosolenia*, *R. bergonii* and *R. praebergonii*. These two species do not interbreed, and they differ in the height of the hyaline area. The plot shows samples taken from deep sea boreholes in the central Pacific, and each measurement of the height of the hyaline area is based on a large sample of hundreds of individuals; the means and 95% error bars for each sample are shown. The rock succession is dated by reference to the magnetostratigraphic scheme of normal (black) and reversed (white) polarity. (Image courtesy of Ulf Sorhannus.)



- (a) How closely sampled is this succession? Count the number of points for each species from left to right, and divide into the total duration: what is the mean time spacing of samples?
- (b) How long did it take for these two species to separate? To work this out, you must think about the error bars: why do you think the error bars vary in height for different samples? How many samples show an overlap of error bars, and over how long a time span?
- (c) For *R. praebergonii*, what is the rate of change in height of the hyaline area? Calculate the rate of change from 3.2 to 1.6 Ma, and then in two segments, from 3.2 to 2.7 and 2.7 to 1.6 Ma. You can express the rate of change as microns per 100,000 years. What happened 2.7 Ma, and what would you call the phenomenon in the interval from 2.7 to 1.6 Ma?

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