New evidence of feedback animated process in genetic evolution, an analysis of transient flow in the phyletic succession linking G. *pleisotumida* and G. *tumida*

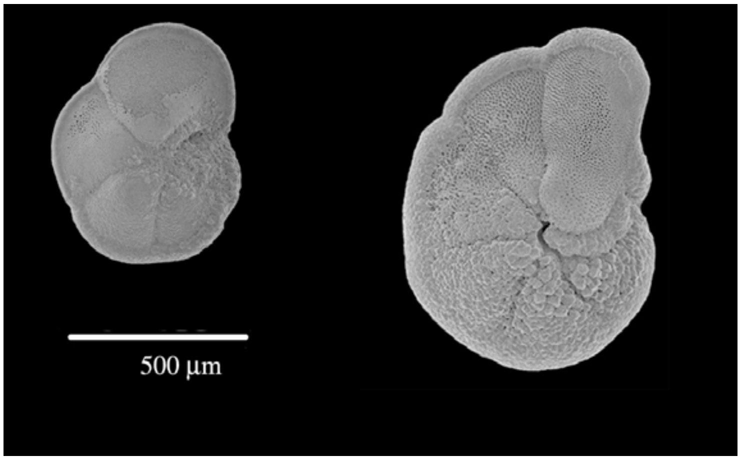
Philip F. Henshaw

680 Ft Washington Ave., New York NY 10040.

E-mail: id@synapse9.com

Abstract. - The evolutionary transition from planktonic foraminifera G. *pleisotumida* to G. *tumida* provides an unusually detailed picture of a single speciation event. The transition is marked by a complex change in shape and an overall tripling in size of the organism over 2 Myr and directly appears to follow trends that accelerate and decelerate. Mathematical tests for internal symmetry of variation, for flowing shape in the succession of slopes and the physical mechanisms involved rule out random walk as an explanation. Both light and strong smoothing display the clear dynamic shapes common in feedback animated systems exhibiting fluctuation on multiple scales, typical of natural systems. A way to explain the presence of classic growth and climax phases of developmental processes bridging steady states seems required, even if still speculative for lack of any identifiable mechanism. Some of the requirements for such mechanisms are discussed, along with how ordinary emergent feedback animated systems seem necessary to explain the typical gaps between stable states, the punctuated equilibria, in the general fossil record. Some of the other possible causes for rapidly fluctuating and transitional flowing shapes in the trends of changing biological forms are also briefly discussed.

Keywords: planktonic foraminifera, G. *tumida.,* pattern recognition, evolution, punctuated equilibrium, random walk, growth, complex systems, feedback animation



G. pleisotumida and G. tumida, electron micrographs taken by H.Hayashi (IGPS).

The shapes of things generally reflect their underlying structures, with a few notable exceptions. What appear to be trends in the fossil record might or might not reflect the underlying causes of genetic variation and selective pressures. Trends in evolution might also be considered to reflect nothing more than accumulating random variation, since that is frequently considered as a default hypothesis for the mechanisms of genetic change. Roopnarene (2003) reviews the literature on the subject finding that the study of rates of evolutionary change have generally not been fruitful, with little clear correlation between rates and behavior except that the longer the time span is considered the less behavior is apparent. The shorter period events in the fossil record are often assumed to be random walks, the accumulations of random steps that often visually appear to have rough shapes or directions like the changes seen in the fossil record, even though the underlying process of random accumulations of change has none. Whether random walks of biological characters actually occur is another question, however, is weakly supported except by assumption. Theoretically, characteristics of an organism that have no effect on survival could randomly wander, appearing to represent trends in evolution that actually aren't meaningful. The most interesting 'rate events', though, are the gaps in the fossil record, the events that can not be studied since there no data. Those of the shortest period, the common gaps in the fossil record at speciation, imply rates of change that are infinite and were first described as 'punctuated equilibrium' by Eldredge and Gould (1972) .

This study reexamines a classic example of evolutionary trends, the transition between the plankton species Globorotalia <u>*pleisotumida*</u> and Globorotalia <u>*tumida*</u> published by Bjorn Malmgren et all. (1983). The data shows an overall tripling in shell size, following a variable transition of variable rapid change connecting relative starting and ending steady states. Malmgren's data was later examined by Bookstein (1987), and various others. As Bookstein saw it, the appearance of a succession of trends could not be read as reflecting the punctuated gradualism claimed by Malmgren et all. (1983) because an accumulative range test did not rule out the possibility the data could have been produced by a random walk. This conclusion can now be reversed with good confidence using more direct statistical tests for the properties of random walks and the mathematical opposite of random walks, continuous flows, and also by considering the physical mechanisms available.

MATERIALS AND METHODS

Preliminary examination of the data. - Globorotalia <u>tumida</u> is a predominantly warm water planktonic foraminifera first identified by Brady in 1877. The data published by Malmgren et al. (1983), (Figure 1), shows the average size of the shells (oriented silhouette area) from 95 sediment samples spanning the last 7 million years, including the transition from the G. <u>*pleisotumida*</u> to G. <u>*tumida*</u> beginning around 5.5 Ma. The graphs show the first 86 of the 95 recorded data points to shorten the time axis and focus the graphics on the period of interest. The samples of about 50 specimens each were gathered from a single 140 m Indian Ocean sediment core from site 214 of the Deep Sea Drilling Project. It provides a particularly high quality source for measures based on the fossil record, an all but perfectly continuous record of a single lineage over a long period from a single stable environment. The source is not prone to the worst normal defects of the fossil record, that fossilization is usually a rare and scattered occurrence, containing information strongly biased toward the present (Raup 1987). The dating of the layers of the core seems reasonably reliable as well, estimated by the magnetic guidepost method of Ness et al. (1980). The species appears to have been readily identifiable, abundant in every sample, to represent a single global species freely circulating in ocean currents and to display only lineal morphological succession without lineal branching (Malmgren et al. 1983). The drilling site is believed to have been geologically stable over the period.

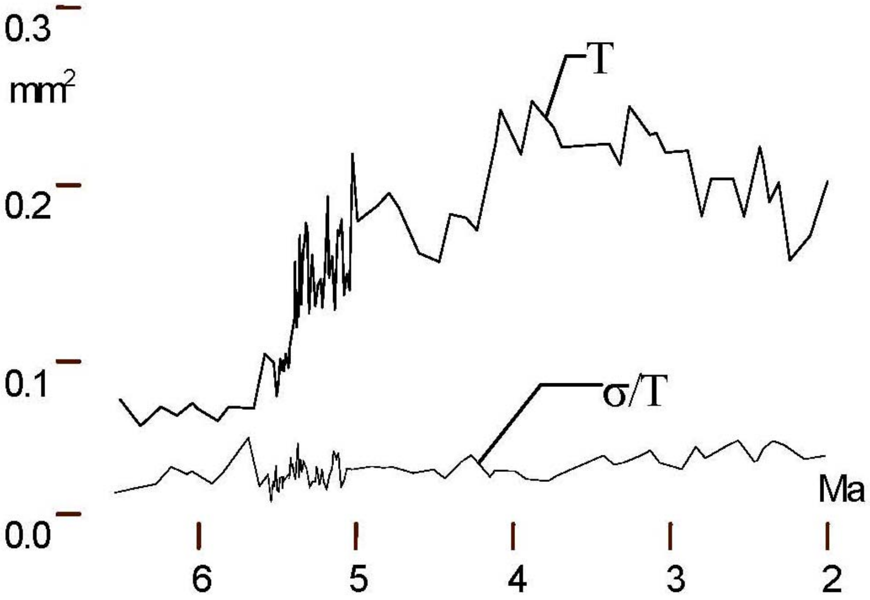


Figure 1. Mean Profile Area of G. *tumida* fossils from B. Malmgren et all. (1983) DSDP site 214. (T) The change in mean size of this common plankton over six million years showing 86 of the recorded 95 samples1 of about 50 specimens each. (σ/T) The ratio of standard deviation within each sample divided by the mean.

Each of the samples consisted of approximately 50 micro-fossils taken from about 6-8 cc of mixed ocean sediment from 2-3 cm of the ~7 cm dia. core, representing approximately 1000 year accumulations. Each sample was washed and filtered and the specimens carefully picked at random by hand from the residue. The Samples were taken at 10 to 30 cm (~20 Kyr) intervals at the Miocene/Pliocene boundary (the period of rapid transition) and at about 2 m (~200 Kyr) intervals elsewhere. Measurements were made of both specimen size and shape. Only the data on specimen size are examined here though there was a similar trend in the measure of shape (Malmgren et al. 1983).

The trend in the data is readily visible, an appearance of a non-trending steady state at beginning and end connected with a significant time period of transition with progressively changing rates. The statistical analysis is complicated by the amount of variation and by the variable rate of sampling, much more frequent during the period of transition. The higher rate of sampling during the transition period was not repeated at other times for statistical comparison, so it is not immediately clear whether the same variability seen during the transition is present throughout. Still, sufficient numbers of specimens were recorded in each sample for reasonable estimates of each sample's standard deviation, and the ratio of standard deviation to the mean is fairly constant. On average the sample standard deviation is 32% of the mean, quite large, and has itself a standard deviation of 7%. The question is how to treat the data to determine whether there are real shapes in the record and what those shapes might represent. The analytical work for this study was done with a collection of lisp programs in AutoCAD by Autodesk, the JMP statistical package by the SAS Institute and MS Excel. The routines used for each are available on the internet as http://www.synapse9.com/ as file names as Curve.zip, StepVar.zip and PaleoDoubleR1.xls respectively.

Analytical methods. - In order to qualify a time-series data set for trend analysis it is necessary to first find it plausible that the data represents a continuous underlying process and that its shapes of change would likely correspond to the underlying mechanism of change. If it were statistically likely that the variation in the data was produced by a random walk, and no other evidence is available to establish the continuity of the underlying processes, it may not be worth speculating about the shapes in the data as there is no demonstrated basis for that (Bookstein 1987). In the case of the G.tumida transition, little is known about the underlying process of change and the data's irregularity makes random walk seem at least initially plausible. A method developed by Bookstein (1987) provides a range test to determine if a random walk could produce the extrema of a given data set and the test fails to rule out random walk when applied to the G. *tumida* data. A test for random walk developed by Gingerich (1993) determines whether the distribution of step rates is within the limits expected for a random walk. When applied in a test application, the method also failed to rule out random walk for the G. *tumida* data. A review of these methods by Roopnarine et all (1999) finds a high inherent likelihood of type II errors (incorrect failure to reject a null hypothesis) indicating the low confidence that either test identifies random walks, but simply fails to exclude them.

Step variance test. - A direct test for the presence of random walk concerns whether the step variance in the data is accumulative or not (Henshaw 2000). The idea is to measure whether the next change at any point is actually independent of prior steps (indicating random walk) or tending in the opposite direction of prior steps (indicating either complex fluctuation or symmetric noise about a norm).

The test is whether the variances of the steps in the data is the same for different size steps (stable variation) or is larger for larger steps (accumulating variation). It measures the degree to which successive changes in direction are locally symmetric and cancel each other out. What it brings out is the clear statistical difference between an accumulation of random changes and the natural behaviors with multiple scales of fluctuation like many natural homeostatic systems. These are sequences that reflect complex variation about either a fixed or variable norm. The analytical method uses a version of the Hurst exponent (Mandelbrot 1969; Hastings and Sugihara1993) and is closely related to measures of fractal dimension in data.

The particular version of the Hurst exponent used here compares variances of the step sizes rather than the mean of the step sizes which was chosen for having slightly more consistent results. The sub-sequences for the test are created by skipping fixed numbers of points in the data. If the sampling rate is k (the distance between points in the subset), and v is the step variance (variance of their sequential differences), the step variances for random walk data will increase at an average rate of k*v, showing the effect of having accumulative variance. If the step variances do not increase with increasing k, the statistically abnormal shapes in the data were not produced by accumulative variation. It indicates that noise suppression can then be used to potentially reveal meaningful shapes.

A theoretical random walk is a sum of independent copies of a random variable with variance v. The larger the steps through the sequence, the larger the variance (since it's additive). As such, a sub-sampling of a random walk is also a random walk, but with a variance of k*v. In contrast, a sequence with variation about a constant norm will tend to have the same absolute step variance at whatever rate it is sampled, a constant. This relation is displayed in the slope of a log/log plot comparing step sizes and variances, giving the Hurst exponent (Hσ) as the slope:

$$H_\sigma \cdot \ln \frac{k}{j} = \ln \frac{v(S_k)}{v(S_j)} \qquad (1)$$

where j and k are the number of points, or time periods, for re-sampling used to make sub-sequences Sj and Sk , with ν(Sj) and ν(Sk) their step variances. For a random walk Hσ =1 ± ε where ε is the tolerance allowed in any given case for not having an infinite number of points. For a sequence with only normal random variation Hσ = 0 ± ε.

By numerical experiment with 20 random walks (see Figure 2) the spread that occurs is a rough measure of the 95% confidence interval for the range of random walks, and displays the close clustering of random walks under this test. Sequences with Hσ well outside this interval (values of Hσ well outside .33 and .65) can be confidently distinguished from random walks and probably represent some regular continuous process combined with noise. The test can be somewhat loose for ruling out a presumption of random walk, since the object is only to find a reasonable doubt that the shapes are purely a product of noise. A strong indication that the data is not a random walk then just adds interest, still leaving the validation of any shape analysis to whether its implications are well supported otherwise.

If a random walk can be ruled out, and not just brought into question, it just increases the presumption that the shapes in the curve represent corresponding physical processes which can be validly explored by noise and shape suppression using iterative methods like Gaussian smoothing, or shape reconstruction by estimating missing derivatives (Henshaw 2000). To validate any results it remains, of course, to account for the sources of noise and correlate the suggested behavior with theory and independent evidence.

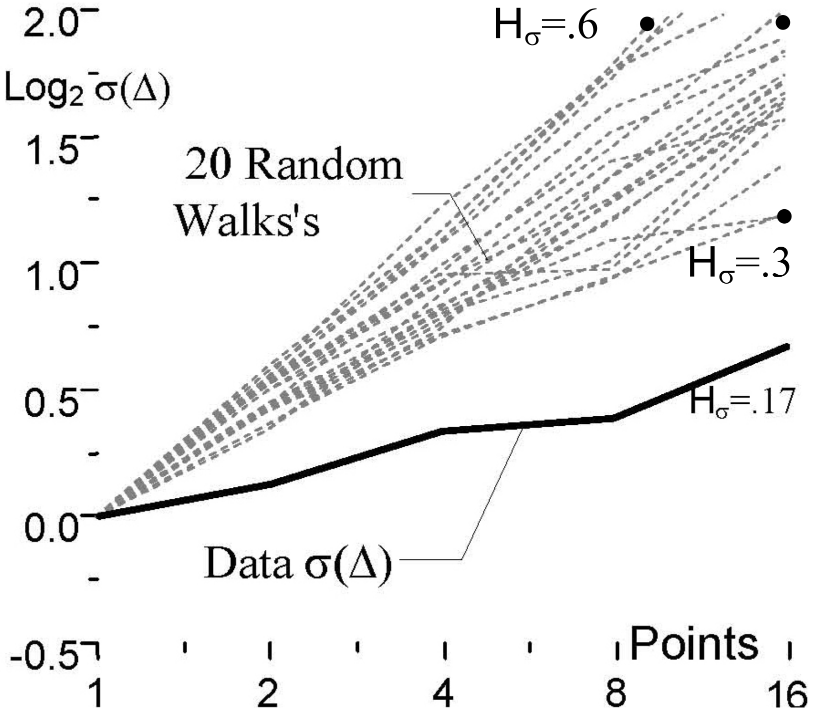


Figure 2. Step variance test for G. *tumida* size, and 20 random walks, showing the trend of std deviations σ(Δ) for the differences between 2,4,8, & 16 point steps in the data.

The Hσ=.17 value is the slope for G. tumida, showing a substantial departure from the norm of random walks.

Apart from the helpful evidence of the statistical test it is also apparent that there is a logical problem with postulating random walk of a whole population. If random walk in the characters of the whole population occurs, it must be the result of some pattern of change in the characters of individual organisms. Individuals within a population can not continually make matching ‘random’ neutral changes at the same time, and that is the only way the variation of individuals can produce a collective random walk. It appears that for populations there may be no functional basis for random walk. If the characters of individual lineages of a population exhibit independent (rather than matching) random walks, the resultant mean value for the population will be constant, with the variance within any sample continually increasing. Assuming one approaches analysis moving from general to specific, the issue would become one of the preferred order of considering statistical or physical possibilities, rather than one of natural behavior. Since random walks of individual traits would not produce random walks of population traits it would appear the ‘null hypothesis’ only states a preference to qualify ones later analysis based on the data alone before considering the feasible physical behavior of the system. The attempt to assure that statistical analysis will be purely value-free, using the posture of ‘naïve realism’ that all you have is your data with no knowledge of any connection between the points, that they’re just dots on a page, overstates the true case. In data there are lots of interesting and confusing effects, of course. That would include the interesting cases where random walks of neutral traits in individual lineages may occur, and could lead to accumulative changes that have large affects combined with other factors in later generations.

Flowing shape test. – Once it is clear that random walk would not explain irregular population data one can try to find out how much of the variation is due to sampling the inherent diversity in a population (noise), and how much is due to sampling complex fluctuations in the population's processes of change. Flow is the property of some physical systems that allows them to be approximated by mathematical functions. Having flowing shape is the physical system corollary to the mathematical property of the derivative, and a large part of what makes mathematics useful for describing nature. In both cases it means that the succession of changes will have no kinks or breaks, and so that the slope at a point when approached from either direction is the same. A simple test of a time series data set to see if the underlying system is likely to represent a process having continuous flows is to measure the number of sequences of three slopes that have sequentially opposite signs, the number of double slope reversals or zig zag's. It's surprising, but no mention of flow as a property of physical systems and the statistical indicators that might demonstrate its presence in time series data were found in several good statistical research handbooks (Hamilton 1994, Rice 1995 among them) and a web search. From experience it appears that the question does not come up because the continuity of natural processes is assumed to be mathematical, and their physical continuity a function of the equation to be used in describing them and not a physical property of the natural system.

The direct measure for flowing shape use here is to count how often the slope between points reverses twice in a row. In a curve with pure flowing shape and dense enough points to describe it, there will be none. In curves with only random fluctuation there will be on average nearly half the possible number of double reversals possible. In particular, light smoothing does not reduce the number of double reversals for curves with shapes produced by random fluctuation (compare figure 3a & figure 3b). Sometimes light smoothing will greatly reduce the number of double reversals, producing a curve with a much greater degree of flowing shape. The likelihood, then, is that the data recorded a continuous but fluctuating process as is common for natural systems, which will show clearly when the noise in the data is gently suppressed.

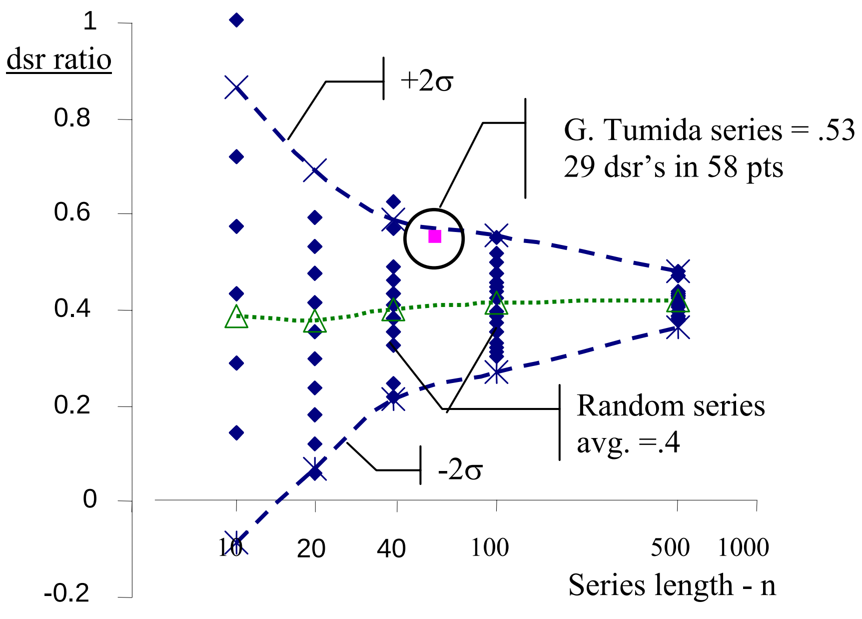


Figure 3a. Fraction of double slope reversals (dsr) [\/\ ] for 20 random series of varying length (10, 20, 40 & 100 points), w/curves for mean and 2 std. deviations above

and below, with value of .51 for the 58 point G. tumida data.

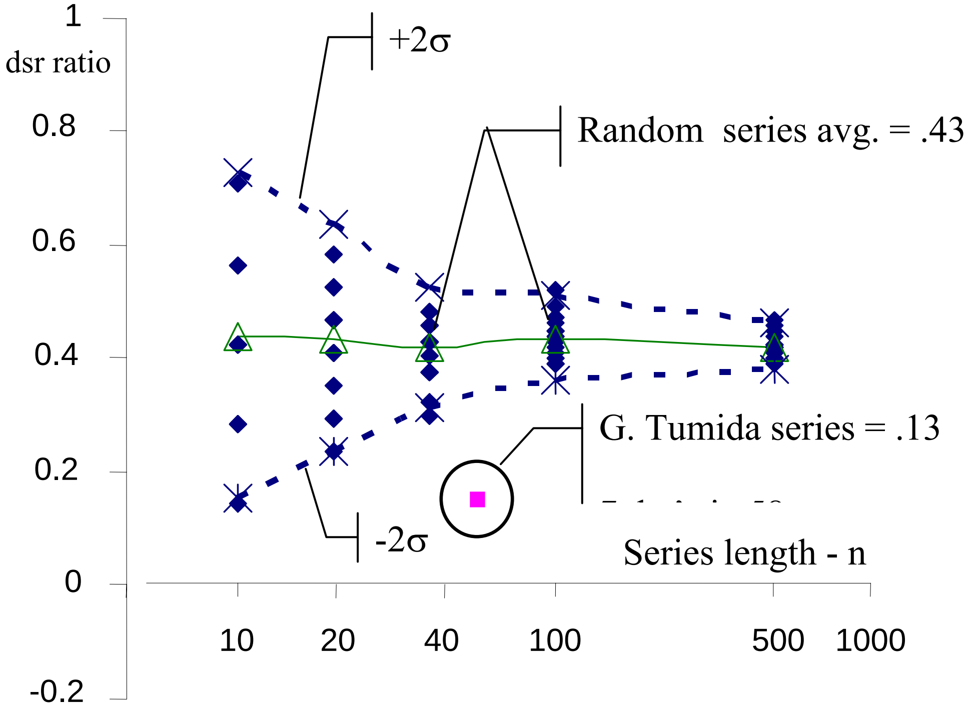


Figure 3b. Fraction of double slope reversals (dsr) [╲╱╲] for lightly smoothed random series w/ mean & 2 std. dev. curves, and value for 58 pt G. tumida data. Smoothing is by a 3 point center weighted kernel (1,2,1). Shows that light smoothing does not change the mean frequency of slope inconsistency for noisy data, and conversely that the irregularity of the G. tumida data originates from complex fluctuation of larger period than the data in an underlying process with a flowing shape.

Noise suppression. - There is a noise component present in any sequence of measures. A running average or centre weighted average of points trades a loss of shape for a distribution of the noise making the underlying shapes more visible. A smoothing 'kernel' is the mathematical rule to be applied sequentially to clusters of points for the purpose. It's usually a simple distribution of 'weights' with a sum of one, such as:

$$\text{for } -a < n < a \quad k(n) = \frac{e^{-|n|/2}}{\sum_n e^{-|n|/2}} \qquad (2)$$

giving a Gaussian (bell curve) distribution of weights to a group of 2a+1 points, used to calculate contributions from neighboring points in smoothing a sequence. Smoothing suppresses all variation in a sequence while giving previously invisible turning points in the data clear definition, making the series approximately differentiable.

Scale space analysis. - With repeated smoothing of a curve the smaller scale turning points are successively suppressed leaving only the principle turning points of the data. In most data sets there are several distinct scales of variation present, representing several scales of underlying processes (like ripples on waves on swells, etc.). A chart (see Figure 6) tracing the migration and disappearance of inflection points provides traceable shape landmarks for different scales of noise and different types of underlying behaviour present. These landmarks can serve as a fingerprint for making matches between different shapes and for identifying different scales of underlying behavior. The fact that all shapes can be deconstructed and compared in this way is now commonly exploited in computer vision (Lindberg 1994).

Interpreting results.- For most classes of behaviors there is a kind of taxonomy of familiar dynamical shapes associated with familiar behavioral processes. One of the available general taxonomies of shape is provided by the common forms of equations, distinguished by relationships of their derivatives (representing the classic types of physical systems). For example, the difference between a simple polynomial (having only one, two or three exponents for example, and thus higher derivatives flattening to 0) and an exponential (infinite series of exponents and all higher derivatives present and of the same sign) may be clearly visible in the shapes in a curve. Those revealing shapes may be enhanced at one scale of smoothing of the data or its step differences and not at others (the curves of the ‘step differences’ in sequential data display the slopes of the data similar to the way derivatives display the slopes of functions). One may also use specialized techniques to avoid the shape distortion of Gaussian smoothing such as derivative reconstruction (Henshaw 2000).

For each recognizable mathematical shape there are a set of possible corresponding behavioural processes. It is the goal of curve interpretation to identify them. For example, it is a primary interest to distinguish between the shapes of transient developmental processes (endogenous or self-organizing system events) and the effects of some secondary processes (exogenous effects). An ‘S’ curve, for example, could equally represent a diffusion of effects from some remote cause or evidence of a local self-organizing cascade directly involving the measured quantity. This difference often can not be determined from examining the data alone, and sometimes a full examination of many plausible mechanisms and correlation with other data is required to determine whether the apparent shapes in a curve do in fact correspond to plausible underlying processes.

RESULTS

Direct inspection. - The upper curve on Figure 1 shows the mean of each of 58 samples. The lower curve the ratio of the standard deviation of each sample to its mean. If the individual lineages represented were each varying as a random walk the variance of the population would increase linearly over time, whether there were trends in the average or not, but that is clearly not the case. One of the other interesting issues is that the organism may be reproducing as a clone, as plankton of this type sometimes do, and the models of evolution depending on genetic mixing through sex or other mechanism might not apply. If that were the case every lineage would varying independently, however, so you would also expect a substantial increase in population variance over time for many reasons. That is clearly not happening. If any thing, the population variance declines a little in the period of most rapid change. The one wild scenario that could disguise independent random variation of each lineage as a separate species is if only one lineage survived over and over, as all others died out, so that all individuals remained descended from the same ancestor a fixed number of generations before. Barring that unlikely scenario the measure of size seems to be a corollary measure of non-neutral genetic change and the different lines seem to share genetic material by some means.

Step variance test. - Though it does not seem reasonable that a whole population could perform a random walk, with all lineages making the same accumulating neutral changes, it's the required presumption under a widely accepted null hypothesis (Bookstein 1987). To use the step variance test, various sub-series of the 95 data points (Malmgren et all. 1983) were prepared consisting of every 2nd, 4th, 8th and 16th points, and the variances of each these new series plotted. These are graphed in Figure 2, along with the same measures for a group of 20 random walks of 95 points for comparison. The difference is visible. The value of the slope (Hσ) for the G. _tumida_ data is .17, a fraction of the mean for random walks of 1.0 and well outside the range of two standard deviations from the mean for random walks, by graphic estimate, between

.47 and 1.53. This indicates that the structure of the variance is locally symmetric and that the G. _tumida_ data is not an accumulation of random variation, with a better than .05 level of confidence.

Trend analysis. - Having determined that the random noise in the series is largely symmetric, the G. _tumida_ data was then treated as possibly representing a continuous process superimposed with fluctuation and noise. Figure 4 shows a close up view of the rapid transition section of the data, with very light smoothing, a 3 point centre weighed average. There are only 5 double reversals in the gentle smoothing of this sub-sequence of 58 points, demonstrating a high degree of slope continuity. A sophisticated mathematical test for derivative continuity in a data set is what is needed, but unknown, even if clearly visible in the flowing shape, visually demonstrating what the step variance test demonstrated was likely.

The step variance test showed that the data varied about a moving norm, and the slope continuity after light smoothing shows both how closely the data follows that norm, and that the norm tends to change direction with flowing shape composed of progressions of small steps as in derivative continuity for mathematical functions.

The prominent fluctuations labeled 1, 2, 3, 4, 5 & 6 would be easily dismissible as noise, were it not for the fact that they are each traced by curves with progressively changing slope, not randomly changing slopes. These fine scale fluctuations have durations of about 150, 25, 140, 80, 80 and 600 thousand years, respectively. The way I measured the duration was between the midpoints of fluctuation pairs in the moving average. Fluctuation number 6 is treated as the long regular wave shown, though the longer sampling rate at that time might well disguise rapid flowing fluctuation of the type seen in the earlier periods.

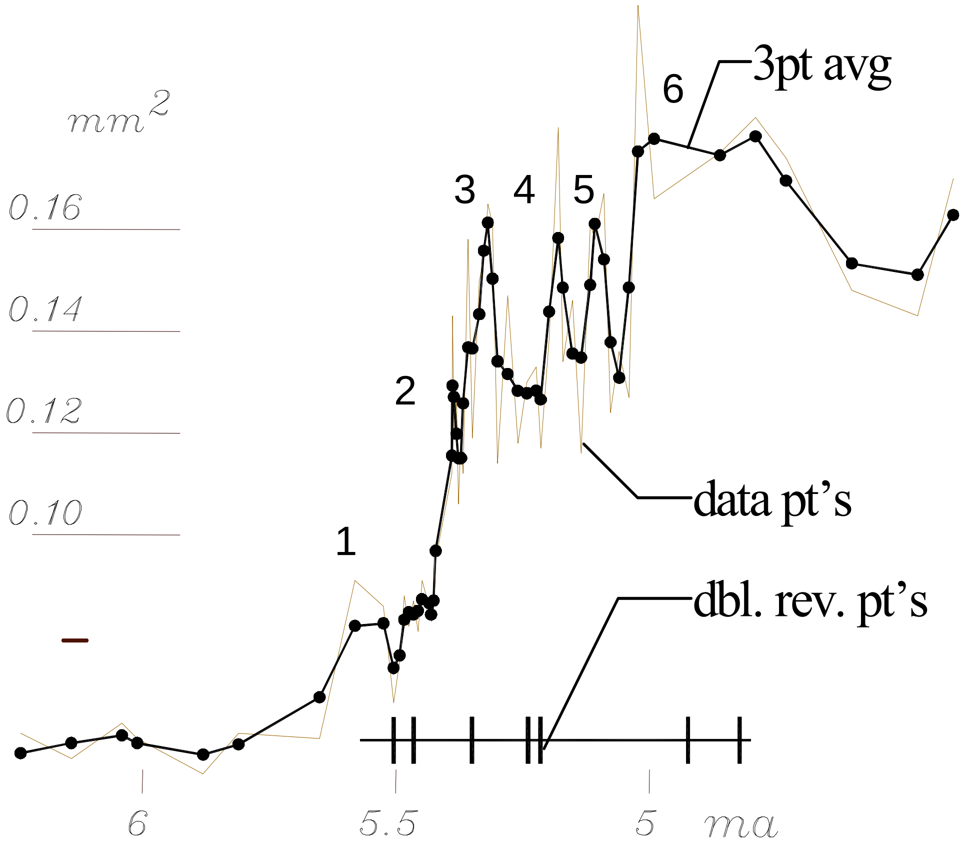


Figure 4. Enlarged view of the G *tumida* transition with a 3 point centre weighted moving average. In 58 points the smoothed curve has only 7 consecutive reversals indicating a high degree of slope continuity.

It is typical of continuous systems to have fluctuations of large and small scale superimposed so that the underlying trends, and long duration fluctuations are easily recognized only after suppressing the smaller ones. That is particularly true for looking at a trace of the point to point slopes of a sequence, the first differences. They tend to look highly erratic if the smaller scale fluctuations are not eliminated first. When the smaller scale fluctuations are suppressed enough, progressive rates of changing slope show the dynamics of the underlying system. It's a matter of glossing over the ripples so you can see the waves. The 'ripples' in this case, the several short lived peaks, are apparently real individual events, but superimposed as fluctuations on a larger event.

One major hazard of this approach to interpreting data is that any sequence of measures might reasonably represent overlapping information from several different behavioral systems happening at the same time. In this case, because the species was easily identified and branching was not apparent (Malmgren 1983) and the variance has no evident trends, it appears the measure is a consistent indicator of only one thing. A more thorough examination of the individual specimen data might help prove the case in either direction, though. That said, the further display of the character of variation in the sequence assumes that there is one process with various scales of fluctuation and stripping them away will expose a central behavior. Successive shape suppression reveals a simple shape with a recognizable derivative, and is followed by scale space analysis to display the different levels of irregularity in the scales of the shape.

Figure 5 shows an initial strong Gaussian smoothing (top curve), further smoothing after 4 and then 32 more repetitions (middle two curves), and the derivative of the middle smoothing curve (bottom). The curve scales are shifted so the curves can be seen separately. The top curve in Figure 5 was produced using a Gaussian smoothing kernel with a 17 data point spread (Henshaw 2000). The degree of initial smoothing was arrived at experimentally, intended to represent the least suppressed good representation of the overall shape. The point spacing of the data was then regularized at .05 Myr, by periodic integration, (converting to a sequence with equally spaced points). This is required so repeated smoothing will have a uniform effect. Then the further smoothing was done with a 9 point (.4 Myr) Gaussian kernel, first with 4 iterations (U4) and then 32 iterations (U32).

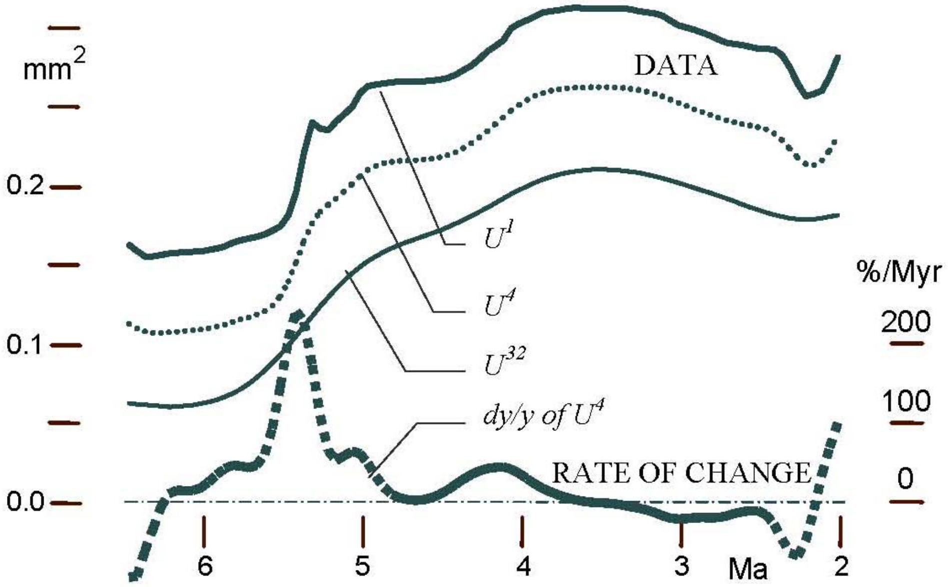


Figure 5. Revealing the behavioral shape with Gaussian smoothing. Thee levels of smoothing U1, U4, U32 (each offset by .05 on the mm2 scale for visual separation) and the first log derivative of U4. U1 is a 17point running average of the raw data for noise suppression. After 0.05 Myr data point spacing equalization, repeated smoothing is performed with a 9 point (.4 Myr) Gaussian kernel.

One secondary technical issue concerns the order of these steps. The initial smoothing kernel used a set number of points from the original data set (rather than a set time interval) to define the range for the initial smoothing. After that the point spacing was changed using the interpolated values of the initial smoothing curve at regular time intervals. The reason is partly that Gaussian smoothing produces distorted results when the point spacing is not constant. Another is that the initial smoothing is for the purpose of noise and fluctuation suppression, and noise and fluctuation in data is on the scale of the actual point spacing, whether regular or not. Once the initial smoothing is done further smoothing is not for noise suppression, but shape suppression, to make the rate of change curves more readable and to suppress inflection points to see which are the most robust. Experiments were also done with regularizing the point spacing first and found to produce greater distortion of the more detailed portions of the curve.

Whether the smoothing was ultimately useful depends on whether the underlying shape is recognizable and can be associated with some particular underlying mechanism. Getting to that determination is the reason for allowing an initially weak hypothesis, to try looking for something hoping to confirm the details later. Another note is that any curve trend analysis that uses a symmetric spreads of points to smooth data will develop meaningless shape artefacts near the beginning and end because of the asymmetry of the end conditions. This is evident in odd tails seen in all the smoothing curves of Figure 5, especially pronounced in the derivative. One could hide this by doing smoothing on a longer data set and cutting off the ends, but data is scarce and it's valuable to be reminded of the effect of one's own tools so I just leave them as they come. In this case the normal smoothing kernel had a .2 Myr spread on each side of any point. To adjust, at that distance from the end of the curve the smoothing kernel starts loosing points and at the very end is reduced to 1 point so as the shape of the rest of the curve is suppressed the end point never moves.

To identify the underlying physical processes from a curve shape one can compare a curve based on one kind of measure with others, perhaps to see if their turning points line up, for example, or use curve fitting with a model equation to investigate the possibility that the underlying system has a consistent mathematical structure. Sometimes derivative progressions can be directly identified by their shape. Here, one may recognize in the derivative (Figure 5, dy/y of U4) the classic shape of an isolated positive rate spike bounded by relative steady states, identifying it as some dynamic event that starts and stops. It directly suggests the progressively increasing and then decreasing positive rates of change of a growth system change of state. The singular spike in the derivative is reinforced by the progressive slopes evident both in the smoothing curves and seen through the noise and smaller scale fluctuations in the original data (figure 1) and the light smoothing (Figure 4). In most cases these would be clear indicators of a dynamic change in an internally organized complex local system guided by positive and negative feedbacks. What those might be in this case and whether it is reasonable to consider that possibility for speciation events, of course, remains entirely open.

Scale Space Display. - Figure 6 is a map of the movement and suppression of the inflection (curvature reversal) points resulting from extended repetitions of Gaussian smoothing. Each bump on the curve is represented by a pair of inflection points, one on either side. These serve as landmarks in the curve shape. As a bump is slowly smoothed out with higher repetitions of smoothing the scale space chart will show two lines from the bottom of the chart coming together and joining at the point were the bump on the curve vanishes. The diagram demonstrates the endurance of each inflection point (whether representing some source of noise or some kind of behavioural fluctuation). The curves shown were drawn by plotting the location of each inflection point for each smoothing level and then manually fitting a b-spline curve to pass through those points to show the implied continuous path. More sophisticated methods are available (Lindberg 1994, Mokhtrian and Mackworth 1992). The apparent shape scale boundaries at approximately U1.5, U4.5, U64, and U1024 identify groups of successively more robust inflection points. Inflection point A remains through 512+ iterations of smoothing.

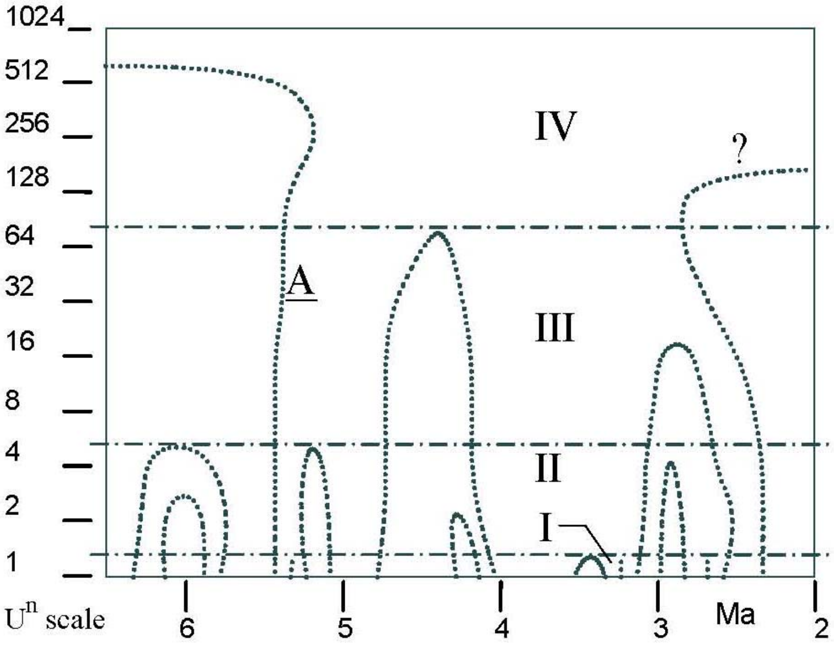


Figure 6. Scale space diagram. Tracing the location of inflection points through 1024 iterations of 9 point (0.4 Myr) Gaussian smoothing. General shape scale levels I, II, III, IV representing four general scales of inflection point persistence with line A coinciding with the prominence in the derivative curve in Figure 5. .

Based on the visual indication of fine grain behaviour (Figure 4) the first shape scale regions (I & II) where 5 pairs of fairly robust inflection point traces drop out represent a consistent level of fluctuation in the underlying process. Perhaps with if started with a lighter smoothing the shape scale analysis would be able to separate what is apparently a very low level of actual noise in the data from the strong fine scale fluctuation. Whether that level of fluctuation represents variation in a central process or transient side processes is not clear. It is also not clear whether these fluctuations are endogenous or exogenous in origin. The do look enough alike as if they are related though.

The two pairs of inflection points that drop out in period III are of a different scale and probably reflect some different cause than those of smaller scale. Any growth system will trigger both rapidly and slowly changing environmental responses and in looking to associate causes with affects one would look for processes with matching response times.

The last inflection point to the right, starting from about 2.3 ma at U1 appears to be a false positive. If you look carefully at the data shape at 2.3 Ma (Figure 1), for example, you'll see a large fluctuation largely the result of one exceptional point at the very end of the sequence where the data. That leaves an artefact in the smoothing curves because the smoothing kernels run out of points to interpolate at the end. As usual, the smoothing kernel leaves the end point unchanged, reducing the point range of the kernel from the normal 9 to 7 to 5 to 3 to 0 points, so that shape suppression declines at the ends. As a result, the retention of shapes near the ends is less significant.

DISCUSSION

What Malmgren (1983) first found in this same data he called 'punctuated gradualism', because it appeared to display a period of increased random variation and directed selection. It was then interpreted as a random walk (Bookstein 1987), indicating a complete absence of underlying rates or processes based on a failure to rule out the null hypothesis, and the matter was treated as closed. What the curve shape now visible shows is different and the question has to be revisited whether it has anything to do with evolution at all, and what that could mean.

Changes in the profile area of a plankton species could conceivably be due to a simple matter such as a change in ocean temperature, or shifts in nutrient currents (ecophenotypic change). It could also result from ecosystem change, where a community of species develops a mutual support and reliance, such as a species taking on a symbiotic partner (ecosystem evolution without species evolution). These and other mechanisms could potentially produce significant changes in phenotypes by themselves, or together with several factors having enhanced combined effects. There's no necessity to conclude from the shapes of the curve that the dynamic event visible here originated from genetic evolution.

The response of plankton to ocean temperature without genetic change is well known and even commonly used as a measure of ocean temperature (Smolka 1991, Schmidt et. all. 2004, 2005). Smolka (1991) reported summer and winter temperatures from measurements taken from the same sediment core (DSDP 214) that the G. *tumida* samples were taken from. His samples were taken about a ½ Myr apart and, except for a 4.0 ±.3° C dip and recovery in summer temperature in the 1 Myr before the G. *tumida* transition, show fairly constant summer and winter temperatures during the period. Schmidt et. all. (2004, 2005) provide a comprehensive global survey of ocean temperatures and plankton size relationships, including a review of the G. *tumida* transition data. The combined data show a clear and fairly steady global increase in plankton size of about 25% over the past 10 million years. Schmidt & Kucera (2005) recently updated this assessment with the observation that the general size increase trend observed was not actually unidirectional, but also perhaps responsive to macro-ecologic events, though none of those listed appear to coincide with either the timing or degree of the 5.5ma transition of G. *tumida*. The different drawing scales used by Schmidt et all. (2004) give the G. *tumida* transition the appearance of having a similar slope to the general trend. The actual average rate of change during the G. *tumida* transition is 200% in ½ Myr, about 160 times as fast as the global average plankton size trend, however. The steepest sustained rate of change for G. *tumida*, 12 data points over 110 kyr, was 550 times as fast. That reads as a difference in kind, not just in degree and is inconsistent with the general temperature influence demonstrated.

No hard evidence was found of other environmental or ecological changes, though it would seem unlikely that any one global species would change dramatically without other things changing at the same time. One expert on the subject, Richard Norris (1996) has reported that G. *tumida* has never hosted a symbiot organism, though that is fairly common in similar plankton species and when it occurs it does tend to increase the species size. He also confirmed that a similar transition is visible in Atlantic Ocean G. *tumida* lineage samples, though reportedly, the little G. *pleisotumida* appear to linger somewhat longer.

Punctuated Equilibrium. - In summarizing the debate over punctuated equilibrium begun by Eldredge & Gould (1977), Prothero (1992) provides 15 citations including Gould (1992) and Stanley (1992) for what still seems to be the consensus, that gradual random genetic drift prevails for microscopic protestants including foraminifera like G. *tumida*. The G. *tumida* transition does not fit that description though, and may well be unique or rare. On the surface, though, the unusual G. *tumida* transition pattern could be taken to neatly fit the shape of the fossil record gaps that give rise to the punctuated equilibrium puzzle. It shows a definite transition between distinct stable species in a relatively short time by a continuous incremental process. This would seem to be a testable hypothesis perhaps, except that the gaps needing explanation arise directly from a distinct lack of data in the fossil record. A direct test using this approach requires a fairly large number of samples. This analytical approach does draw out a wealth of new kinds of information from unspectacular data, however, so revisiting old data my be productive, and tell another story than has been assumed as the G. *tumida* data does. Testing sequential data for the presence of behavioural fluctuation hidden in minor noise, rather than assuming that irregularity is entirely noise or random walk, would probably turn up a great deal more clear behavior.

The central problem of punctuated equilibrium (Gould & Eldridge 1972) is that the more complex species tend to appear abruptly in the fossil record and remain unchanged for long periods, implying that speciation occurs relatively rapidly, in relatively small and localized populations, and produces relatively stable new organisms that don't continually change with shifting environmental pressures. After twenty years of research and debate a consensus agreement was generally reached (Prothero 1992) which remains commonly reaffirmed (Geary 2003), based largely on the abrupt appearance of species in the fossil record, their usual structural stability and a complete lack of evidence for how they are created for lack of evidence.

The data collection problem for the higher species is that the fossil record may provide an example of one out of a few thousand generations and speciation may occur in a few hundred. Given that sampling pattern there would be no way to trace the shape of how it happens no matter how or where it occurs. The direct approach to answering the question might be closed, but there may be others. There are various modern collections of fauna and flora in the drawers of century old naturalist collections for various locales that might accidentally capture a sequence of generations displaying the necessary pattern kind of change . How frequently that would be found is hard to estimate, but transient flowing shapes in characters may never been looked for before and if one were looking with the right analysis tools, it seems likely one would come across more examples.

Potential modes of feedback. - One logical way for larger jumps of genetic change to occur in evolution is for an accumulated random walk of neutral genetic changes to later be found to aid or hinder reproduction. That might occur by itself, or in combination with and amplify some other genetic or ecological change, Prothero (2000). That mechanism could produce a sudden multiplication of population numbers for one lineage, but not a progressive or coordinated pattern of mutations for a whole population. What's needed to fit the pattern of large complex change in short periods of time is for structural stasis to give way to rapid change and then go back to stasis again, by a sequence of small steps. That very precisely calls for feedback.

One plausible genetic mechanism that could do that, would be for the success of one mutation to increase the frequency of other mutations of similar kinds. That way the new variations would serve to 'explore' the region of positive phase space of the original. One might think of it as suggested by the fact that the growth of an organism is itself a branching tree of events and that evolution is a stepwise modification of that tree's branches. I know of no particular branching structure in the genome, but something having that effect is implied for opportunistic genetic progressions to occur. It requires some kind of genetic structure that allows an expansion and then contraction of possible changes, and that pattern should leave some kind of statistical evidence. A clever analysis of the data for individual specimens from the G. <u>*tumida*</u> lineage might possibly show the cloud of variation around any given mean to be biased in the directions of future progressive change, for example. Another avenue for finding evidence of genetic variation sensitive to feedback would be to look for variation clustering that changes over time in the background variation for any species.

One pattern of evolution that might be explained by a branching/feedback mode of evolution is the quite common tight fit between special traits of different species. It suggests that a genetically localized coevolution occurs, i.e. restricted to a limited cluster of features. Evolution by distributed variation throughout the genomes of interacting species would be more likely to develop a diversity of relationships instead. A branching variation would potentially allow two species to travel a very narrow channel of mutual reinforcement leading to a complexly coordinated narrow change.

One potential biological mechanism for producing a branching genetic structure and variation sensitive to feedback is suggested by the patterns of proportional relationships in the shapes of organisms first carefully documented by D'Arcy Thompson (1917 & 1942). That work was not rigorous in every way, but is a work of enduring popularity focusing on an aspect of body form, proportional geometry and comfortable fit, nearly everyone recognizes. It apparently addresses something real that is not yet well explained.

A similarly clear appearance in evolutionary change is that changes tend to involve the migration of the endpoints, rather than the starting points, of biological growth. Because evolution involves more change in the characters that develop late in individual organism growth the appearance is that change occurs more at the ends of the branching process of development. A second appearance is that the growth of organisms does not end by internal exhaustion or conflict, suggests there must be some coordination of the stopping points for development's branching process. The limits of growth for organisms never seem to be starvation or organ congestion and the taught stretching of skin, so the various branches of development in growth must turn themselves off from the inside.

The question here is less how growth is turned off from within and more whether the alteration of a set point for the end of growth for one thing might affect the endpoint of others. If there is some kind of interrelated proportional system for the set points for an organism's growth climaxes, a physical structure corresponding to the proportionalities we observe, change in one might have various kinds of ripple effects. One popular image of such ripple effects of small changes in complex systems is the idea of 'chaos'. Complex balances can begin to wobble or meander when slightly perturbed, until a new balance is found. Given environmental rewards and penalties some of these would be reinforced by enhanced reproduction and some constrained by failure.

The question is not whether such a mechanism actually exists, but whether that kind of mechanism is sufficiently plausible to suspend the usual dismissal of feedback regulated growth as a possible mode of evolution. No doubt chaotic variation in an organism's growth limit control system might lead to change in many features at once that might either help or hinder its life support and reproduction. In the normal interpretation of 'mutation and selection', the mutation and selection processes are strictly independent though. It's customary, but is it necessary? By itself the presence of a structure that coordinates growth limits would create a coordinated shape in the organism's potentials, it's 'fitness landscape', opening up and closing down a variety of new potential peaks and pathways. The usual interpretation is that uninfluenced random variation throughout the genome will tend to be reinforced if it moves an organism downhill in such a fitness landscape. The question here is whether such a complex change in an organism's 'fitness landscape' would be accompanied by related variation in the vicinity of the new paths, such as to constitute a kind of exploration, or probing of the landscape. Since this is really all an argument by speculation, looking for what to look for, it seems reasonable to conclude by suggesting that instability in a system's developmental climax control system might have lots of side effects, allowing small increments to move the system either near and far from its present state.

The context of complex systems. - It may seem as different and difficult as Darwin's proposal for the origin of species was at first, but the various bits of confounding evidence for evolution really make some new idea logically necessary. What is clearly implied by the evidence is that most evolution happens during short periods, by rapid reorganization of a complex distributed system of growth, and that it is logically necessary that it proceed by successively larger and then smaller steps. Growth systems of all kinds and shapes regularly do exactly that. That growth in complex systems has not been studied extensively is not because it has an unimportant role in events. Feedback animated step changes in development are found extensively in all kinds of events, but it's notoriously hard to study, and ultimately requires considering the behavior as developing inside the system exhibiting it. The one thing we know with little doubt is that evolution is a sequential change in the kind of growth climax individuals of a species come to in their own biological development. Perhaps it's reasonable that changes in the form of that growth climax might themselves sometimes develop by growth.

'Punctuated equilibria', fit the general model of complex system organizational shifts generally known as 'changes of state'. All of these generally proceed by a growth process and are found in great variety in complex evolving systems (Bak & Boettcher 1997). Some disciplines have even demonstrated limited success in modelling them by computer. (Lewin 1999). Complex system level shifts are found in climate & weather systems, politics & social systems, animal behavior, ecologies, electrical discharge, thermal changes of state, etc. We don't understand quite how, but we think nothing of it. The details are always hugely complicated to describe, unfortunately, displaying complex distributed organization most often in the absence of any outside direction or internal record of past experiments to follow.

Possible tests. - The question is how to test the hypothesis. A single record of speciation by a transient growth process arguably demonstrated here is a small but significant piece of evidence. Where there is one example there may be others. There does seem to be very fine grain behavioral fluctuation behind the irregularity of Malmgren's (1983) data set. Since it's apparently a global species and the fossils are plentiful in hundreds of cataloged ocean sediment cores, it would seem practical to look to see which if any of the same fluctuation events appeared elsewhere. Better mathematical tests for filtering data sets for those displaying behavioral flow and transient dynamics would help to identify other places to look for the same type of evidence. It should also be asked whether fossilized plankton contain some genetic material. Searches for genetic patterns that change progressively, in step with fluctuations in body structure, could possibly hint at the discrete mechanisms involved.

CONCLUSION

For some time it has been understood that most adaptation and invention in evolution occurs at speciation, appearing as gaps in the fossil record that need to be filled by some relatively rapid process of stepwise change.

What has been demonstrated is the use of mathematical techniques borrowed from fractal theory and computer vision and new statistical tests for underlying process flow to solve a stubborn problem of pattern recognition. It would seem likely that the same combination of techniques, distinguishing statistical variation from behavioral variation, followed by curve recognition, could be put to good use elsewhere as well.

The result has been to reveal the underlying behavioral shape of the phyletic succession from G. *pleisotumida* to G. *tumida*. The shape found is a rather familiar one, even if unfamiliar in this context, that of rapid complex organizational change by growth. Malmgren's (1983) conclusion of punctuated gradualism and Bookstein's (1987) interpretation of random walk have both been updated.

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