

Transient non-linear systems in the punctuated phyletic succession linking *G. pleisotumida* and *G. tumida*

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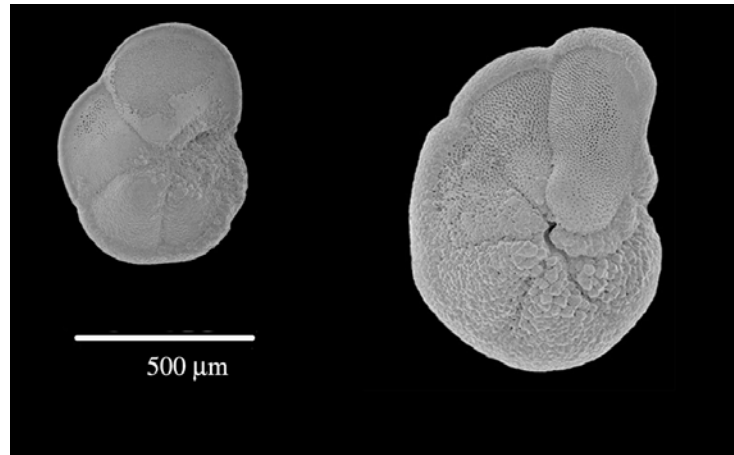
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Abstract. - The evolutionary transition from planktonic foraminifera *G. pleisotumida* to *G. tumida* provides an unusually detailed picture of a single speciation event. The transition is marked by an overall tripling in size over 2 Myr and directly appears to follow trends that accelerate and decelerate. Using a new mathematical test of internal symmetry adapted from fractal theory the prior interpretation of the data as a random walk is disproved, legitimizing the use of shape analysis to reveal the behavior of the underlying process. The classic progression of growth stages bridging from one steady state to another that appears is a classic form of evolving complex system. It suggests various specific mechanisms, and would also appear to well satisfy the requirements for filling the typical gaps in the fossil record appearing at speciation for more complex organisms. The possibility of environmentally driven change and the plausibility and requirements for transient growth systems to be considered as one of the normal causal mechanisms of speciation are briefly discussed.

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



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

Introduction

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 and needs to be ruled out. Accumulations of random steps are called random walks, and often appear to have regular shapes or directions even though

the underlying process has none. Whether random walks of biological characters actually occur is another question, but 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.

This study reexamines a classic example of evolutionary trends, the transition between the plankton species *Globorotalia pleisotumida* and *Globorotalia tumida* published by Bjorn Malmgren et al. (1983). His data shows an overall tripling in shell size, following a

sequence of more and then less rapid change connecting relative steady states. This was later reexamined 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 al. (1983) because he claimed it was probably produced by a random walk. This can now be ruled out with good confidence, using a more direct statistical test for the presence of random walk in the data, and confirming logic.

Materials and Methods

Preliminary Examination of the Data. -

Globorotalia tumida 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 95¹ sediment samples spanning the last 7 million years, including the transition from the *G. pleisotumida* to *G. tumida*

¹ To graphs show the first 86 of the 97 recorded data points to shorten the time axis and focus the graphics on the period of interest

beginning around 5.5 Ma. 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. The site is near the equator, in the present location of the south equatorial current of the Indian Ocean. 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 global 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.

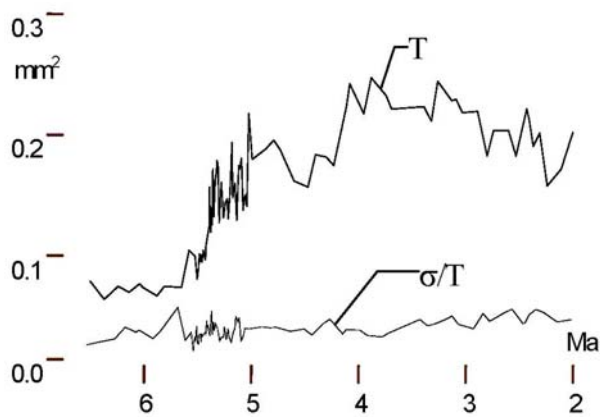


Figure 1. Mean Profile Area of *G. tumida* fossils from B. Malmgren et al. (1983) DSDP site 214. (T) The change in mean size of this common plankton over six million years showing 86 of the recorded 95 samples of about 50 specimens each. (σ/T) The ratio of standard deviation within each sample divided 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 unusually high sampling frequency during the period of transition. The higher rate of sampling during the transition period was not repeated at other times for 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, as seen in figure 1, 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 the

sequential record has a shape and what that shape might represent².

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 examining its measures for rates of change might be productive. To determine the details of any underlying process one needs many kinds of information to make the slopes and dynamics of sequential data useful, but initially one should rule out random walk (Bookstein 1987). In this case the nature of the underlying process is unknown and random walk seems 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 to the G. *tumida* data a test application also failed to rule out random walk. A review of these methods by Roopnarine et al (1999) finds a high inherent likelihood of type II errors (incorrect failure to reject a null hypothesis).

Step Variance Test. - A direct test for the presence of random walk concerns whether the step variance is accumulative or not (Henshaw 2000). The idea is to measure whether the variation at any point is independent of prior steps (random walk) or tending to the opposite sign of the prior steps (exhibiting either fluctuation or symmetric noise about a norm).

² The analytical work for this study was done with a collection of lisp programs in AutoCAD by Autodesk and the tools of the JMP statistical package by the SAS Institute. The routines used for each are available on the internet as <http://www.synapse9.com/Curve.zip> and <http://www.synapse9.com/StepVar.zip> respectively.

The test is whether the step variances for sub-series created by sampling with different point spacing remain constant or increase. It measures the degree to which successive changes in direction are locally symmetric and cancel each other out, implying that larger scale changes follow from some continuous underlying condition or process. It's a clear

statistical difference between random accumulation and the data of systems with multiple scales of fluctuation like many homeostatic natural systems. These are sequences that reflect complex variation about either a fixed or variable norm (reflecting both superficial and underlying continuities). For random walks the step variances for larger steps in the data will, instead, tend to increase without bound. The structure of the test is a version of the Hurst exponent (Mandelbrot 1969; Hastings and Sugihara 1993) and closely related to measures of fractal dimension.

The particular version of the Hurst exponent used here compares variances for sub-sequences rather than mean step sizes. Either construction uses sub-sequences created by skipping fixed numbers of points in the data. If the sampling rate is \mathbf{k} (the spacing of points picked out from a series), and \mathbf{v} is the step variance of all the points in the sequence (variance of the first differences of the sequence), the sub sequence step variances for random walks will increase at an average rate of $\mathbf{k}*\mathbf{v}$, showing the effect of having accumulative variance. If the step variances do not increase with increasing \mathbf{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 \mathbf{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 $\mathbf{k}*\mathbf{v}$. 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 (H_σ) as the slope:

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

where j and k are the number of points, or time periods, for re-sampling used to make sub-sequences S_j and S_k , with $v(S_j)$ and $v(S_k)$ their step variances. For a random walk $H_\sigma = 1 \pm \varepsilon$ 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 $H_\sigma = 0 \pm \epsilon$.

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 H_σ well outside this confidence interval (values of H_σ 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, since the objective is only to spoil confidence in the opposite conclusion, that the test sequence is a random walk and shape analysis would be meaningless.

If a random walk can be ruled out there is then a valid basis for attempting to reconstruct the behavior by curve fitting with functions or iterative methods like Gaussian smoothing, or shape reconstruction by estimating the minimal underlying derivative rates required (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.

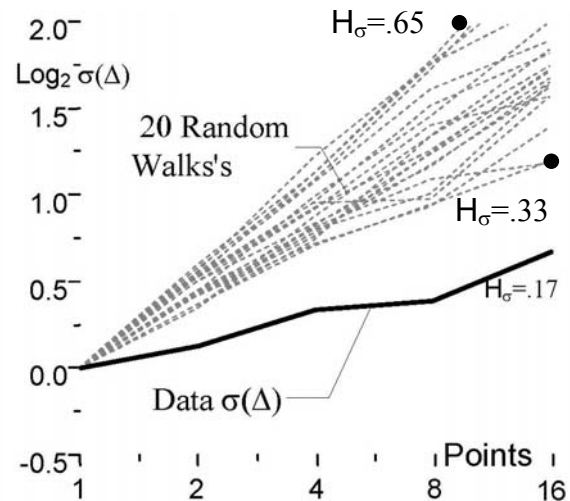


Figure 2. Step variance test for *G. tumida* size, and 20 random walks, normalized std deviation $\sigma(\Delta)$ for 2,4,8, & 16 point steps. The .17 value of the slope, H_σ . This demonstrates a dominance of white noise in the data rather than random walk.

Apart from the helpful evidence of the statistical test is also apparent that there is a logical problem with postulating random walk of a whole population. If random walk occurs it must be of characters of actual successive organisms, not whole populations. For populations there is no functional basis for random walk of the whole, surprising change yes, but not regularly additive random walk. The genomes of whole populations don't change all at once. If all individual lineages were separate random walks it would a) produce increasing variation in the population over time, and b) an average for the population that was constant.

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 apparent reduction in noise. 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:

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

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 5) 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 behaviours there is a kind of taxonomy of familiar dynamical shapes associated with familiar behavioural 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, a simple polynomial has only one, two or three exponents, for example, and thus higher derivatives flattening to 0. An exponential has an infinite series of exponents and all higher derivatives present and of the same sign. These classic shapes may be clearly visible in the

curve, and more pronounced at one scale of smoothing of the data or its step differences³ and not at others. Exploring a data set to discover the different kinds of information found with aggregations of the data is usually fruitful. 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 local 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 or indirectly

³ 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.

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 apparently matching underlying processes.

Results

Direct inspection. - The lower curve on Figure 1 shows the ratio of the standard deviation of each sample of about 50 specimens to its mean. If the individual lineages represented were each varying as a random walk the variance of the population would increase over time, whether there were trends in the average or not, but that is clearly not the case. One of the other interesting possibilities is that the organism reproduces as a clone and the models of evolution depending on genetic mixing through sex or other mechanism would not apply. If that were the case, and every lineage is varying independently, you would also expect a substantial increase in population variance over time, since whether random or not, they would be varying independently. That is clearly not

happening either. If any thing, the population variance declined a little in the period of most rapid change. The one wild scenario that could disguise independent random variation of each lineage is if separate lineages became dominant 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 with constant uncertainty, it's the required presumption under a widely accepted null hypothesis (Bookstein 1987). In an attempt to assure that statistical analysis will be purely value-free a posture of 'naïve realism' is taken, that there is initially presumed to be no connection between any data set and any physical behavior, that it's just dots on a page. To use the step variance test, various sub-series of the 95 data points (Malmgren et al. 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 (H_0) for the G. *tumida* data is .17, a fraction of the mean for random walks of 1.0 and well outside the range of twenty random walks, falling between .33 and .65. 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 3 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 more sophisticated mathematical test for derivative continuity in a data set is needed to provide a less subjective test for what is clearly

visible in this case. Still, the clearly visible dynamic behavior closely following the original points visually demonstrates the strong underlying process continuity present which the step variance indicated 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, following 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 in the original data. In Figure 3 it's clear they are each traced by line segments 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.

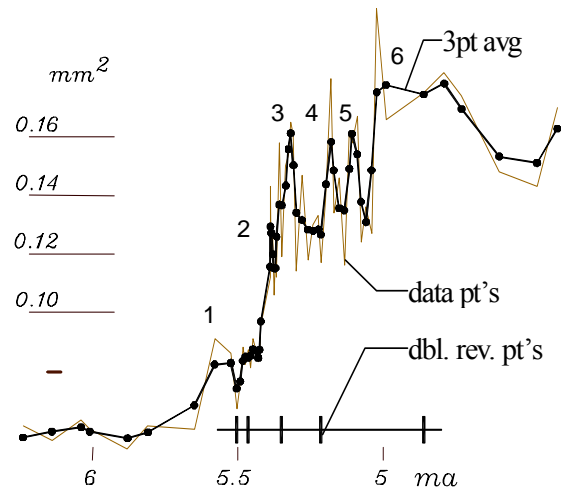


Figure 3. Enlarged view of the G *tumida* transition with a 3 point centre weighted moving average. In 58 points the smoothed curve has only 5 consecutive reversals indicating a high degree of slope continuity.

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 when you trace the slopes of a sequence (the first differences or derivative). They tend to look much more erratic than the data if the smaller scale fluctuations are not eliminated first. When the smaller scale fluctuations are suppressed enough derivative rates of change showing the dynamics of the underlying system become visible. 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 the 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 4 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 4 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 (U^4) and then 32 iterations (U^{32}).

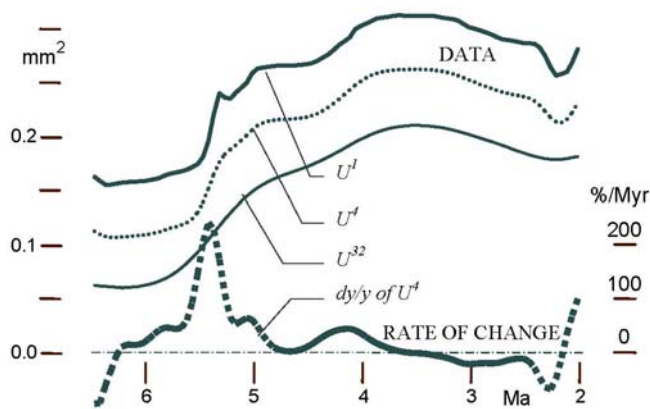


Figure 4. Revealing the behavioural shape with Gaussian Smoothing. Three levels of smoothing U^1 , U^4 , U^{32} (each offset by .05 on the mm^2 scale for visual separation) and the first log derivative of U^4 . U^1 is a 17point running average of fig 1 for noise suppression. After 0.05 Myr data point 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 look for hidden patterns to be confirmed by other means later. Another note is that any curve trend analysis that uses a symmetric spread of points to smooth data will develop meaningless shape artefacts near the beginning and end, because of the rule being used becomes asymmetric there. This is evident in the odd tails seen in all the smoothing curves of Figure 4, especially pronounced in the derivative. One could partly hide this, say by guessing extra points to make the data set longer and then cutting off the ends, but that hides

rather than eliminates the problem, 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 losing 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. In reading them you just discount the significance of shapes cut off at the ends.

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 4, dy/y of U^4) the classic shape of an isolated positive rate spike bounded by relative steady states, identifying it as some non-linear 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 directly visible through the noise and smaller scale fluctuations in the original data (figure 1) and the light smoothing (figure 3). 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 5 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 where 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, Mokhtarian and Mackworth 1992). The apparent shape scale boundaries at approximately $U^{1.5}$, $U^{4.5}$, U^{64} , and U^{1024} identify groups of successively more robust inflection points. Inflection point A remains through 512+ iterations of smoothing.

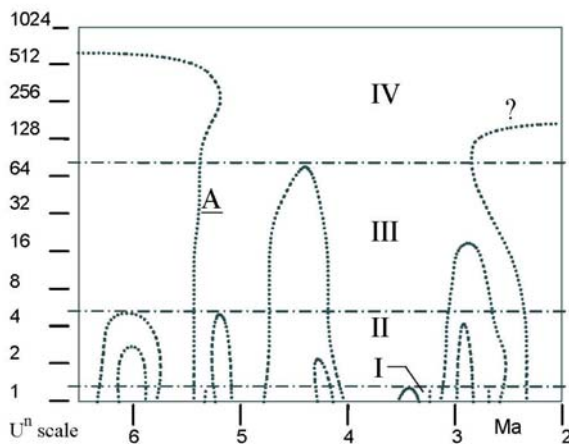


Figure 5. Scale space diagram. Tracing the location of inflection points through 1024 iterations of 9 point (0.4 Myr) Gaussian smoothing. General shape scale levels I, II, III, IV representing four general scales of inflection point persistence with line A coinciding with the prominence in the derivative curve in Figure 4.

Based on the visual indication of fine grain behavior (figure 3) 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 U^1 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 is 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 speciation). These and other mechanisms could potentially produce significant short term system changes by themselves, or with several factors having enhanced effects together. There's no necessity to conclude from the shapes of curves that the non-linear change event that is 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). 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 $4.0 \pm 3^\circ$ 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) 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 somewhat responsive to macro-ecologic events. None of the atypical tendencies or events listed appear to coincide with either the timing or degree of the 5.5ma body shape transition of G. *tumida*. The different drawing scales for sizes of different species 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 steep as the average plankton size trend. The steepest sustained rate of change for G. *tumida*, 12 data points over 110 kyr, was 550 times as great. That reads as a difference in kind, not just in degree.

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 something else changing at the same time. One expert on the subject, Richard Norris (1996) has reported that G. *tumida* does not have a symbiot, 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 seems to remain 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, 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. 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. Perhaps other available sequential data can be explored to see if it tells another story than has been assumed. Testing sequential data for behavioural fluctuation or changes of state hidden by noise, would probably turn up numerous examples clear non-linear behaviors.

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. It implies that speciation occurs relatively rapidly, in relatively small and localized populations, and is a distinct change of state producing stable structures 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 continues to be commonly reaffirmed (Geary 2003), based largely on the abrupt appearance of species in the fossil record, their usual structural stability and a general 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 ways. There are various modern collections of fauna and flora in the drawers of the naturalist collections for various locales that might accidentally capture a sequence of generations displaying the kind of change pattern necessary. How frequently that would be found is hard to estimate. If one were looking for non-linear change of state progressions of characters with analysis tools for investigating slope and derivative change continuity and their structural

shapes of change, there is some chance that one might stumble across it.

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 amplifying 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. What's needed to fit the pattern of complex changes of state in short periods is for structural stasis to give way to rapid change and go back to stasis again, by a sequence of small steps.

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. 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. There is a branching structure of genetic information evident in the branching

growth and development of any individual, though I know of no particular branching structure in the genome. Still something having that effect seems implied for opportunistic genetic progressions to occur. It requires some kind of genetic structure that allows an expansion and then contraction of possible changes. One could look for statistical evidence of it.

A clever analysis of the data for individual specimens from the G. *tumida* lineage might possibly show the cloud of variation around any given mean to be biased in the directions of future progressive change. Another avenue for finding evidence of genetic variation sensitive to feedback would be to look for variation clusters that change over time in the mutation background for any species. That approach might still be too difficult or unaffordable, however. Such hypothetical branching structures would begin by creating a succession of branching possibilities, and getting variable positive feedback. It would end in producing fewer and fewer branches, using up structural possibilities, resulting in a new stasis.

One pattern of evolution that might be explained by this mode of evolution is the quite common tight fit between special traits of different species. It superficially suggests that a genetically localized coevolution occurred, 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. A branching variation would potentially allow two species to travel a very narrow channel of reinforcement leading to a complexly coordinated narrow change.

One potential biological mechanism that could result in branching genetic 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, that nearly everyone recognizes. It apparently addresses something real that is not yet well explained. It's related to the similarly clear appearance that evolutionary change tends to involve the migration of the

endpoints, rather than the starting points, of biological growth (the branches rather than the trunks of development). Because the growth of organisms does not end by internal exhaustion or conflict, there must be some coordination of the stopping points for its separate growth centers. Organisms never seem to mature by starvation or organ over-crowding, so their growth must be turned 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 others. If there is some kind of interrelated proportional system for the set points for an organism's growth climaxes, change in one might have various kinds of ripple effects on others. 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 (random with respect to each other). The affect of a structure that coordinates growth limits could still work in that interpretation. By itself it would create a complex change in shape of the organism's potentials, it's 'fitness landscape', opening up and closing down a variety of new 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. Perhaps that and other mechanisms operate in different patterns.

The question is whether to add a new potential mode of evolution, not necessarily to negate any of those that can be substantiated by

other means. Environmental pressure is clearly implicated in producing great varieties of variation within a species, for example in the great diversity of heritable breeds of domestic animals like dogs and cattle, which don't seem to alter their species. There's no reason this kind of preferential selection in the environment wouldn't have at least as much influence anywhere else.

The question here is whether 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 new landscape stimulated by feedback. 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 control system might have lots of side effects, but more likely to be near than 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 complex distributed systems, and it would need to proceed by successively larger and then smaller steps. Growth systems of all kinds regularly do exactly that. That growth in complex systems has not been studied extensively is not because it has an unimportant role in events. It seems intimately involved with all kinds of events, but is a complex distributed change in order that is notoriously hard to study. 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., and we think nothing of it. The details are always all but too impossibly complicated to describe, unfortunately, but they do tend to display complex distributed organization and feedback regulated growth progressions, most often in the absence of any outside direction or aided by any 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 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 the 95 points 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 implied behavioral continuity underlying time series data 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 what sort of mechanisms might cause them.

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 to solve a stubborn problem of pattern recognition. It would seem likely that the same combination of techniques, distinguishing random walks and noise from continuous non-linear processes, 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 typical growth curve shape found is a rather familiar one, even if unfamiliar in this context of a change in species. Malmgren's (1983) conclusion of punctuated gradualism and Bookstein's (1987) interpretation of random walk have both been updated.

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