Transient complex systems in the punctuated phyletic succession linking G. *pleisotumida* and G. *tumida*

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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 trippling in size over 2 Myr and directly appears to follow trends that accelerate and decelerate. Using a mathematical test of internal symmetry borrowed 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 sequence of growth phases bridging two steady states suggests a form of evolving complex system that would also satisfy the requirements for filling the typical gaps in the fossil record appearing at the speciation of more complex organisms. The possibility of environmentally driven change and the plausibility and requirements for transient growth systems to be the general causal mechanism of speciation are briefly discussed.

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

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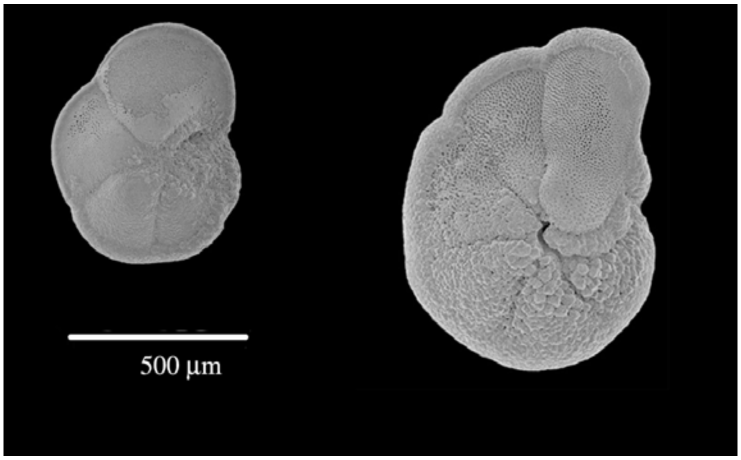

G. pleisotumida and G. tumida, electron micrographs taken by H.Hayashi (IGPS).

1. 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 the default hypothesis for the mechanism of genetic change. 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 all. (1983). His data shows an overall tripling in the size, following a succession of more and then less rapid change between 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 all. (1983) because it might have been 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.

2. Materials and Methods

2.1. 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 95 sediment samples spanning the last 7 million years, including the transition from the *G. pleisotumida* to *G. tumida* 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. 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.

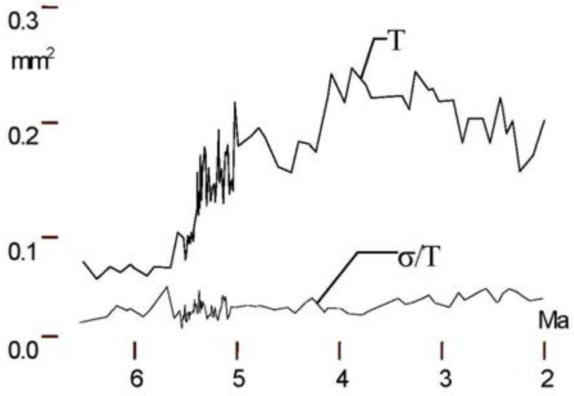

Figure 1. Mean Profile Area of G. tumida fossils from B. Malmgren et all. (1983) DSDP site 214. (T) The change in mean size of a common

plankton over six million years recorded in 95 samples of about 50 specimens each. (σ/T) The ratio of sample standard deviation divided by the mean.

Each of the samples taken 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 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, and so it is not immediately clear whether the increased variability seen during the transition is characteristic of only the transition period or present throughout. Still, sufficient numbers of specimens were recorded in each sample for reasonable estimates of each sample's standard deviation. On average the sample standard deviation is 32% of the mean, quite large, and has itself a standard deviation of 7%.

2.2. Analytical Methods

In order to qualify a data set for trend analysis it is necessary to first find it reasonable to describe the data as having rates of change, representing a continuous underlying process rather than a random walk (Bookstein 1987). In this case the nature of the underlying processes 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 (Henshaw 1999) it also fails to rule out random walk. 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).

2.3. *Step Variance Test-*

A direct test for the presence of random walk concerns whether the step variance is accumulative or not[1]. The idea is to measure whether the variance at any point is independent of prior steps (random walk) or tending to the opposite sign of the prior steps (either oscillation or symmetric noise about a norm).

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. This will be the case for sequences that reflect random variation about either a fixed or variable norm (an underlying continuity). For random walks the step variances for larger steps in the data will tend to increase. This test is a version of the Hurst exponent (Mandelbrot 1969; Hastings and Sugihara1993) and closely related to measures of fractal dimension.

The particular version of the Hurst exponent used here compares variances for sub-sequences (Henshaw 2000) rather than mean step sizes as more frequently used. The construction uses sub-sequences created by skipping fixed numbers of points in the data. If the sampling rate is **k** (the spacing of points read from a series), and **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

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[1] 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.

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 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 (H_σ) 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 S_j and S_k , with $\nu(S_j)$ and $\nu(S_k)$ 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 $H_\sigma = 0 \pm \varepsilon$.

By numerical experiment (see Figure 2) the standard deviation of H_σ for 95 point random walks is 27% (Henshaw 2000) of the mean so that with 95% confidence sequences with H_σ well outside the range of two standard deviations from the mean, values of H_σ between .47 and 1.53, can be firmly distinguished from random walks and probably represent some regular continuous process combined with noise.

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 derivative reconstruction (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.

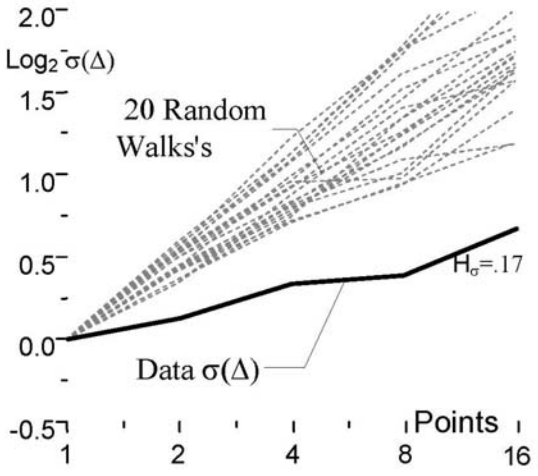

Figure 2. Step variance test for G. tumida size, and 20 random walks, normalized std deviation σ(Δ) for 2,4,8, & 16 point steps. The .17 value of the slope, H_{σ}: This demonstrates a dominance of white noise in the data rather than random walk.

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 lineages were random walks it would produce increasing variation in the population over time and an average that was constant.

2.4. *Noise Suppression-*

There is a random noise component present in any sequence of measures. A running average or center weighted average of points trades a loss of shape for reduction in noise. A smoothing 'kernel' is the mathematical rule used for the purpose, a distribution of factors 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 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.

2.5. *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 behavior 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).

2.6. Interpreting results.-

For most classes of behaviors there is a kind of taxonomy of familiar behavioral 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 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 some scale of smoothing of the data or its step differences (the equivalent of derivatives for sequences). 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 behavioral 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 matching underlying processes.

3. Results

3.1. Variance trend interpretation

The lower curve on Figure 1 shows the ratio of the standard deviation of each sample of about 50 specimens to the 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. 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 the independent variation of each lineage is if one lineage became dominant over and over and all others died out, so that all individuals are descended from the same ancestor a fixed number of generations before. Barring that the measure of size seems to be a corollary measure of non-neutral mutations and the different lines seem to share genetic material by some means.

3.2. 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, but 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 behavior, that it's just dots on a page. To use the step variance test sub-series of the 95 points (Malmgren et all. 1983) were prepared consisting of every 2nd, 4th, 8th and 16th points, and the variances of each 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_σ) 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.

3.3. *Trend analysis*

Having determined that the random noise in the series is largely symmetric, the G. *tumida* data was then treated as representing a continuous process with superimposed noise. Figure 3 shows the rapid transition section of the data enlarged, with very light smoothing, a 3 point center weighed average. There are only 5 double reversals in its 58 points, demonstrating a high degree of slope continuity.

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 maintain direction and change with progressions of small steps.

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 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.

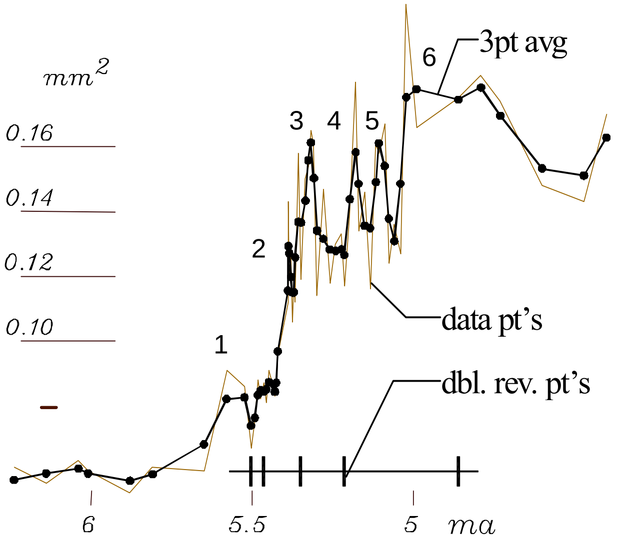

Figure 3. Enlarged view of the G *tumida* transition with a 3 point center weighted moving average. In 58 points the smoothed curve has only 5 consecutive reversals indicating a high degree of slope continuity.

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 for looking at a trace of the slopes of a sequence, the first differences or derivative. They appear highly erratic if the smaller scale fluctuations are not eliminated. 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 major hazard of this approach is that the curve may represent the combined overlay of several different behavioral systems. 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. There are also several methods for separating fluctuations of different scale (Henshaw 2005). The ones used here treat the data as if the scales of fluctuation are constant, and careful noise suppression is followed by scale space analysis to display the character of irregularity in the scales of shape.

Figure 4 shows an initial strong smoothing (top curve), further smoothing after several repetitions (middle two curves), and the derivative of the second 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}).

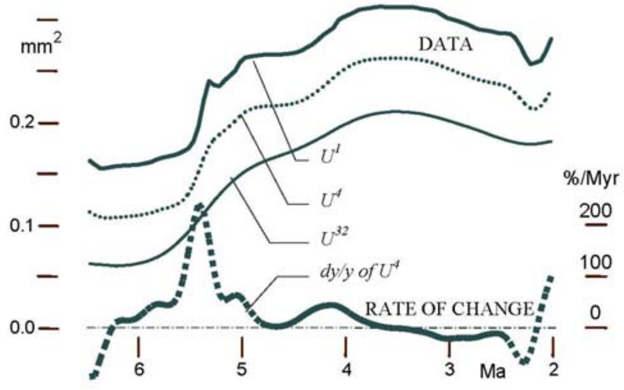

Figure 4. Revealing the behavioural shape with Gaussian Smoothing. Thee levels of smoothing U1, U4, U32 (each offset by .05 on the mm^2 scale for visual separation) and the first log derivative of U4. U1 is a 17point running average of fig 1 for noise suppression. After 0.05 Myr data point spacing equalization, 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 (Henshaw 2005) 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. Any curve trend analysis that uses a symmetric spread of points will have meaningless artefacts near the ends because of the asymmetry of adjacent points. This is evident in odd tails seen in all the smoothing curves of Figure 4, more pronounced in the derivative. The smoothing kernel had a .2 Myr spread on each side of any point, so that is the distance from the end of the curve where the shape begins to become more reliable.

To identifying the underlying physical processes one can compare a curve of one measure with others, 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 dynamic event that starts and stops. It directly suggests the progressively increasing and then decreasing positive rates of change of a growth system achieving climax. 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. 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.

3.4. 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 were the bump on the curve vanishes. The diagram demonstrates the endurance of each inflection point (whether originating with sampling noise or 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 $U^{1.5}$, $U^{4.5}$, U^{64}, and U^{1024} identify groups of successively more robust inflection points. Inflection point A remains through 512+ iterations of smoothing.

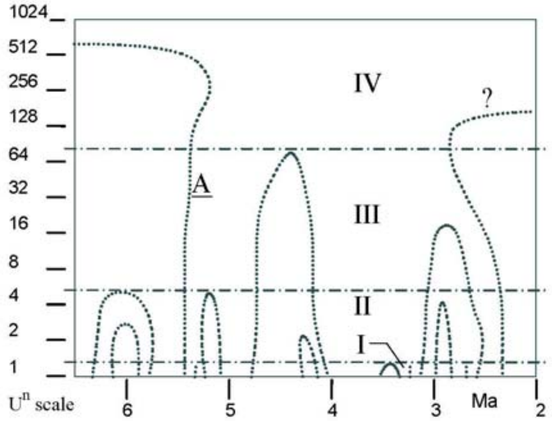

Figure 5. Scale space diagram. Tracing the location of inflection points through 1024 iterations of 9 point (0.4 Myr) Gaussian smoothing. General shape scale levels I, II, III, IV representing four general scales of inflection point persistence with line A coinciding with the prominence in the derivative curve in Figure 4.
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The first shape scale regions (I & II) might represent real shapes in the underlying process, or residual statistical noise. There might be no statistical noise represented at all, though considering the surprising slope continuity of the very lightly smoothed data shown in Figure 3. Otherwise it would be surprising if there were no residual effects of sampling noise in the smoothed shapes of a data set with high standard deviations. That five pairs of inflection point traces in drop out in region II seem to indicate a true scale of secondary fluctuation in the underlying behavior, and suggests a causal connection. That might be due to internal or external behaviors, but look as if they are somehow related. The two pairs of inflection points that drop out in period III are of a different scale and probably reflect some different cause. 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 at the very end where the data is cut off during a period of rapid change. That leaves an artefact in the smoothing curves because the smoothing kernels run out of points to interpolate at the end. The smoothing kernel used always 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. There are always defects in analytical methods and instead of hiding them my preference is to minimize them but let them remain visible.

4. Discussion

What Malmgren (1983) first found in this same data he called it “punctuated gradualism”, because it appeared to display a period of increased random variation and selection. It was then interpreted as a random walk (Bookstein 1987), indicating a complete absence of underlying rates or processes for 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, or similarly, a species taking on a symbiotic partner (ecology evolution). These and others could potentially produce significant short term change by themselves, or several together, with only a minor contribution 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 ±.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) provide a comprehensive global survey of ocean temperature and plankton size relationships, including a review of the G. tumida transition data. The data show a clear regular global trend producing in a 25% change in plankton size from about 10 ma to the present. Adjusting for different drawing scales the ½ Myr G. tumida rate of change at the transition is 200%, about 160 times as fast as the average for other plankton. The steepest sustained rate of change for G. tumida, 12 data points over 110 kyr, was 550 times as fast. That's different in kind, not just 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 other things 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 does tend to increase the species size, and that a similar transition is visible in Atlantic Ocean G. *tumida* though the little G. *pleisotumida* appear to stay around a little longer.

In summarizing the debate over punctuated equilibrium (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 protistans 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 G. *tumida* transition perfectly fits the missing piece of the punctuated equilibrium puzzle in that it shows a definite transition between distinct stable species in a short time by a continuous incremental process. There seems to be little missing but the need to explain why there's no data. Considering the wealth of information that dense and voluminous data sets can be encouraged to produce about underlying continuous processes it seems possible that the random drift consensus for plankton is more of an assumption than a conclusion. Testing irregular data for behavioral fluctuation rather than assuming it represents statistical noise would probably turn up a great deal more clear behavior.

The central problem of punctuated equilibrium (Gould & Eldridge 1972) is that the higher species tend to appear abruptly in the fossil record and remain unchanged for long periods, implying that speciation occurs relatively rapidly, in relatively small localized populations, and represents relatively stable structures that don't continually change with shifting environmental pressures. After twenty years of research and debate that view has been broadly confirmed (Prothero 1992), based on the abrupt appearance of species in the fossil record, their increasingly evident stability and a complete lack of evidence for how they are created. 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. There'd no way to trace how it happens no matter how or where it occurs.

One logical way for larger jumps to occur in evolution is for an accumulated random walk of neutral genetic changes to later be found to aid or hinder reproduction in combination with 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 is for stasis to give way to rapid change and back to stasis by a sequence of small steps. One mechanism that would do that, is if the success of one mutation produced others of similar kinds. I know of no branching structure in the genome, but something having that effect it is implied and might be observed statistically. While open to change a branching chain of mutations would get both expanded and pruned, and end with filling the gaps leaving no openings for new branches.

If genetic comparisons were done of separate lineages of any species and they showed any clustering in the location or kinds of genetic differences, the potential case for that mode of genetic feedback would be demonstrated. One piece of common evidence seeming to support a model of this kind is the seeming impossibly close fit between unusual special traits of different species. That suggests that successful accidents can sometimes multiply similar variations (reinforcing feedback) between different species and lead to major coordinated change.

It may seem as uncomfortable as Darwin's origin of the species was at first, but I think it is just as logically necessary, and that that can direct attention to where the evidence will be found. What is clearly implied by the evidence is short periods of rapid reorganization in complex distributed systems that proceed by progressively larger and then smaller steps. A growth system is always just that. What is evolving is a living growth system after all, the process of an organism's biological development. Why shouldn't the same organizational process be involved in how it changes? Punctuated equilibria are also found in complex systems of all kinds (Bak & Boettcher 1997), including storm systems and politics, and we hardly give it a thought. They all develop complex distributed organization through a growth process without any recorded code to past experiments to follow.

The question is how to test the hypothesis. A single record of speciation by a transient growth process 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 structure to the 95 points of the Malmgren (1983) data and simply analyzing the individual specimen records instead of 50 specimen averages would probably show a grain of clustering that would be instructive. Better mathematical tests for implied derivative continuity underlying time series data would help to identify other places to look for the same type of evidence.

Another approach is to look for evidence of what is logically necessary. If fossilized genetic material can be found, comparisons of G. *tumida* through the transition could isolate progressive changes, and hint at what sort of influences would produce them. It's possible that there are unseen coordinating structures between genes or that the genotype is not entirely represented by genetic structure itself, perhaps requiring the living part of the cell for completion.

5. 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 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 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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References

Bak, Per and Boettcher, Stefan, 1997 Self-organized criticality and punctuated equilibria, Physica D 107, 143 (1997)

Bookstein, F. L., 1987. Random walk and the existence of evolutionary rates. *Paleobiology*. 13(4):446-464

Eldredge, N. & Gould, S.J. 1972. "Punctuated equilibria: an alternative to phyletic gradualism, in Models in Paleobiology. T.J.M. Schopf (ed.) San Francisco: Freeman, Cooper. Pp 82-115

Gingerich, P. D., 1993. Quantification and comparison of evolutionary rates. *American Journal of Science* V293-A p453-478

Gould, S. J., & Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology*, 3, 115-151.

Gould, S. J.1992. "Punctuated equilibrium in fact and theory," in *The Dynamics of Evolution.* A. Somit and S.A. Peterson (ed.), Ithaca, New York: Cornell University Press pp. 85-102.

Hastings, H. and Sugihara, G., 1993. *Fractiles, a User's Guide for the Natural Sciences*. Oxford Science Publications

Henshaw, P. F., 2000. Features of Derivative Continuity in Shape. Chapter 6 pp.101-120 *in* M. A. Rodrigues ed., *Invariants for Pattern Recognition and Classification*, World Scientific Pub.

Henshaw, P. F., 2005. Notes and preparatory studies

Lindberg, T., 1994. Scale Space Theory in Computer Vision. Kluwer Academic Publishers

Malmgren, B. A., W. A. Berggren, and G. P. Lohmann, 1983. Evidence for punctuated gradualism in the Late Neogene Globorotalia *tumida* lineage of planktonic foraminifera. *Paleobiology* 9:377-389

Mandelbrot, B., 1969. Some long run properties of geophysical records. *Water Resources Res*. 5 Pp321-340

Mokhtrian, F. and A. K. Mackworth, 1992. A theory of multi-scale curvature-based shape representation for planar curves, *Transactions in Pattern Analysis and Machine Intelligence*, 14, 8 Pp 789-805

Ness, G., S. Levi and R. Couch., 1980. Marine magnetic anomaly time scales time-scales for the Cenozoic and Late Cretaceous: a précis, critique, and synthesis; *Review of Geophys. Space Phys.* 18:753-770

Norris, Richard D. 1996. conversation, Department of Geology and Geophysics, Woods Hole, MA 02543

Prothero, Donald R., 1992. Punctuated Equilibrium at Twenty, *Skeptic* vol. 1, **no. 3**, Fall 1992, pp. 38-47.

Raup, D. M., 1987. Major features of the fossil record and their implications for evolutionary rate studies. in Campbell, K. S. W. & contrib. *Rates of Evolution*. Allen & Unwin, London

Roopnarine, P. , Byars, G., Fitzgerald, P., 1999. Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* **25(1**) (1999) 41-57

Schmidt, Daniela N., Thierstein, Hans R., Bollmann, J., 2004. The evolutionary history of size variation of planktic foraminiferal assemblages in the Cenozoic, Palaeogeography, Palaeoclimatology, Palaeoecology 212 (2004) 159– 180

Smolka, P., 1991, Neogene Oceans Data. IGBP PAGES/World Data Center-A for Paleoclimatology ;ftp://ftp.ngdc.noaa.gov/paleo/contributions_by_author/smolka1991/welt.gs1 & readme_smolka1991.txt; Data Contribution Series # 92-003. NOAA/NGDC Paleoclimatology Program, Boulder CO, USA.

Stanley, S. M. 1992. “The empirical case for the punctuational model of evolution,” in *The Dynamics of Evolution*. A. Somit and S.A. Peterson (ed.), Ithaca, New York: Cornell University Press pp. 85-102.