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Flowing processes in a punctuated species change
G. pleisotumida to *G. tumida*
displaying feedback driven evolution

Jessie Lydia Henshaw

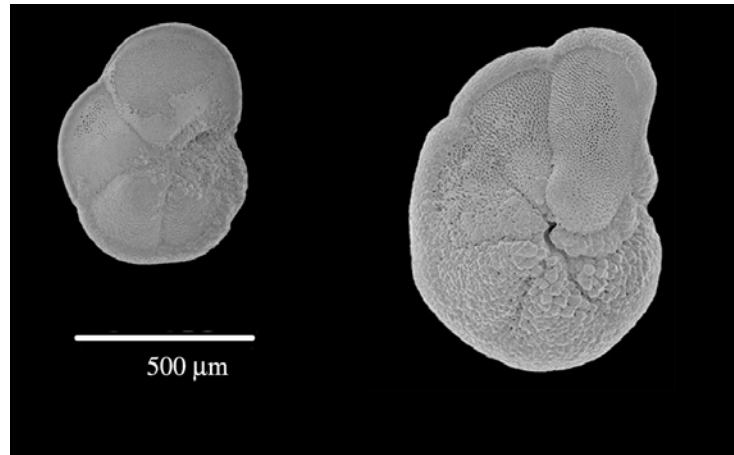
HDS Research / Proprietor

680 Ft Washington Ave., New York NY 10040.

E-mail: jd@synapse9.com

Abstract. - New analytic methods show that the step change in size that accompanied the species change from the plankton *G. pleisotumida* to *G. tumida* 5.5 Myr ago was produced by a transient flowing process that accelerated and decelerated. The evolutionary mechanisms needed to explain that could also explain the general pattern of gaps in the fossil record. Mathematical tests for internal symmetry and continuity and the physical mechanisms rule out random walk. Light and strong smoothing display the clear shapes of growth and complex fluctuation in a continuous process indicating process animation by feedback typical of natural growth systems. An evolutionary mode of branching in the organism's growth limits with 'facilitated variation' in the genome reported by others would permit an organism's developmental control system to actively explore local fitness landscapes with feedback. Ways of searching for other examples of transient flowing change in the fossil record are discussed.

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



electron micrographs taken by H.Hayashi (IGPS).

The evolutionary transition from *G. pleisotumida* (small) to *G. tumida* (large) displays either a step change between steady states taking about a million years, or a continual random walk as first presented by Malmgren et. al. 1983 (1). The possibility of step change was ruled out using a null hypothesis of random walk by Bookstein in 1983 (2), which was re-affirmed by Gingrich in 1993 (3) but then questioned by Roopnarene in 1999 (4). Then in a general review of the literature of evolutionary rates in 2003 Roopnarene finds the Malmgren data to fit the general model that little significant evolutionary information is provided by rates, since the longer the time span considered the less evidence of rates there is (5). A new analysis of the same data, looking for the mathematical signatures of complex fluctuation rather than uniform trends, requires a very different conclusion.

Globorotalia tumida is a predominantly warm water planktonic foraminifera first identified by Brady in 1877. The data published by Malmgren et al. (1)(Fig 1), shows the average size of the shells (oriented silhouette area) from the 95 samples spanning the past 7 million years, including the transition from *G. pleisotumida* beginning around

5.5 Ma. Samples of about 50 specimens each were gathered from a 140 m Indian Ocean sediment core, site 214 of the Deep Sea Drilling Project. It provides a particularly high quality fossil record, an all but perfectly continuous history of a single lineage in a 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 (6). The dating of the layers of the core uses the magnetic guidepost method of Ness et al. (7). The species appears to have been readily identified, 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 (1).

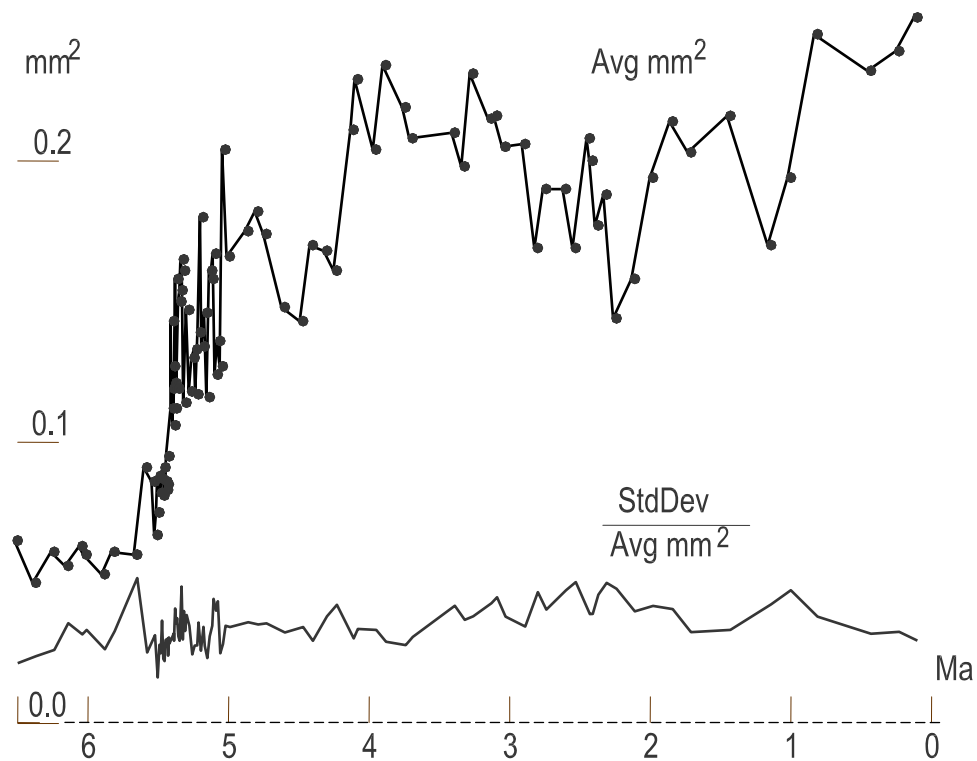


Figure 1. Mean Profile Area of *G. tumida* fossils and The ratio of standard deviation within each sample to the mean.

Each of the samples were washed and filtered from about 6-8 cc of mixed ocean sediment from 2-3 cm of the ~7 cm dia. core, representing approximately 1000 year

accumulations, and individual specimens were picked at random by hand from the residue. The Samples were taken at about 20 Kyr intervals at the Miocene/Pliocene boundary (the period of rapid transition) and at about 200 Kyr intervals elsewhere. Measurements were made of both specimen size and shape. Only the data on specimen size is examined here though a similar trend was found in the measure of shape (1).

The statistical analysis is complicated by the amount of variation and by the greater rate of sampling during the period of transition. The higher rate of sampling was not repeated at other times for statistical comparison, so it is not immediately clear whether the same variability seen during the transition is present throughout. Still, sufficient numbers of specimens were recorded in each sample for a reasonable standard deviation, and the ratio of standard deviation to the mean is fairly constant. The question is how to determine whether any of the shapes can shed light on the underlying processes.

If a series of points originate from independent processes the shapes of the data will not reflect the mechanism that produced them. The null hypothesis for rates of change in the fossil record (2,4,5) is that shorter period variation is assumed to be by random walks, partly because random walk curves often visually appear to have shapes or directions even though the change at each point is independent. Whether random walks of biological characters actually occur, i.e. accumulative change without effect on reproduction, is another question, however, and to not be ruled out as infeasible requires a workable mechanism. Theoretically, characteristics of an organism that have no effect on survival could randomly wander, appearing to represent trends in adaptation that actually aren't real.

The other largely unexplained shape in fossil record trends are the notable gaps in succession with no samples to study called punctuated equilibria, first described by Eldredge and Gould in 1972 (8). These common gaps at speciation imply either discontinuity, or rates of change that increase and decrease while hidden from view. That gaps of this kind are common is now well accepted and the generally developed view is that it must be possible for the well accepted mechanisms of evolution to sometimes operate rapidly in local niches so that new species can evolve without leaving a trace of how it occurred (9,10,11). The evidence shown here requires a new explanation.

RESULTS

Malmgren and others did not look at the ratio of sample variation to the mean, the bottom curve in Figure 1. It is apparent that the ratio is largely constant. If the individual lineages represented were each varying as a random walk the variance of the population would increase linearly over time, but that is clearly not the case. Similarly, if the organism were reproducing as a clone without direct genetic mixing, as plankton of this type sometimes do, you'd expect that to cause continual increase in sample variation too. Clearly accumulative variation of independent inheritance is either constrained by the environment or not occurring, even during the rapid transition period, and so the changes seen are not independent. The one wild scenario that could disguise the increasing variation expected from random walk of traits not affecting reproduction is if only one lineage survived over and over, for some other reason, as all others died out, so all organisms were related to a common ancestor a fixed short number of generations in the past. That could produce a random walk of the

population as a whole with constant population variance. Barring that elaborate and unlikely scenario the measure of size seems to be a corollary measure of some non-neutral genetic change and the different lineages within the species seem to share genetic material by some means.

Whether the variance of the of the mean accumulates or not can also be directly measured. The step variance test (13) compares the variance for different sub-series of the 95 data points consisting of every 2nd, 4th, 8th and 16th points. These are graphed in Figure 4, along with the same measures for a group of 20 random walks of 95 points for comparison. The difference is clearly visible. The value of the slope ($H\sigma$) for G. tumida is .17, well outside the range for random walks, graphically estimated between .47 and 1.53. This indicates that the data varies about a norm rather than wandering freely like a random walk.

A flowing shape test, Figure 5 & 6, shows the variation in the means is composed largely of continuous complex fluctuation rather than noise. These are clearly visible in Figure 2, a close up view of the rapid transition section of the data superimposed with a very light 3 point centre weighed average smoothing. What's quite remarkable is that in these 58 points after light smoothing there are only 7 double reversals when more than 25 would be expected if the variation were random. You can clearly see long sequences of points with regular and progressive slope trends spread through the sequence. A fully analyzed mathematical test for derivative continuity in a data, flow, would be needed for less clear cases. Light smoothing exposes a continuous sequence of continuous processes, and so one needs to consider what types of processes could produce the evident behavior.

The prominent fluctuations labeled 1, 2, 3, 4, 5, 6 & 7 would be easily dismissible as noise, were it not for the fact that they are each traced by curves with progressively changing slopes, not randomly changing slopes. Whether the peaks on the curve represent elastic type fluctuations or independent eruptions is not clear, but as they are irregularly spaced and sized they appear to be independent. It would certainly be interesting to see if these same events, or different ones, are found in samples of the same plankton from other ocean cores.

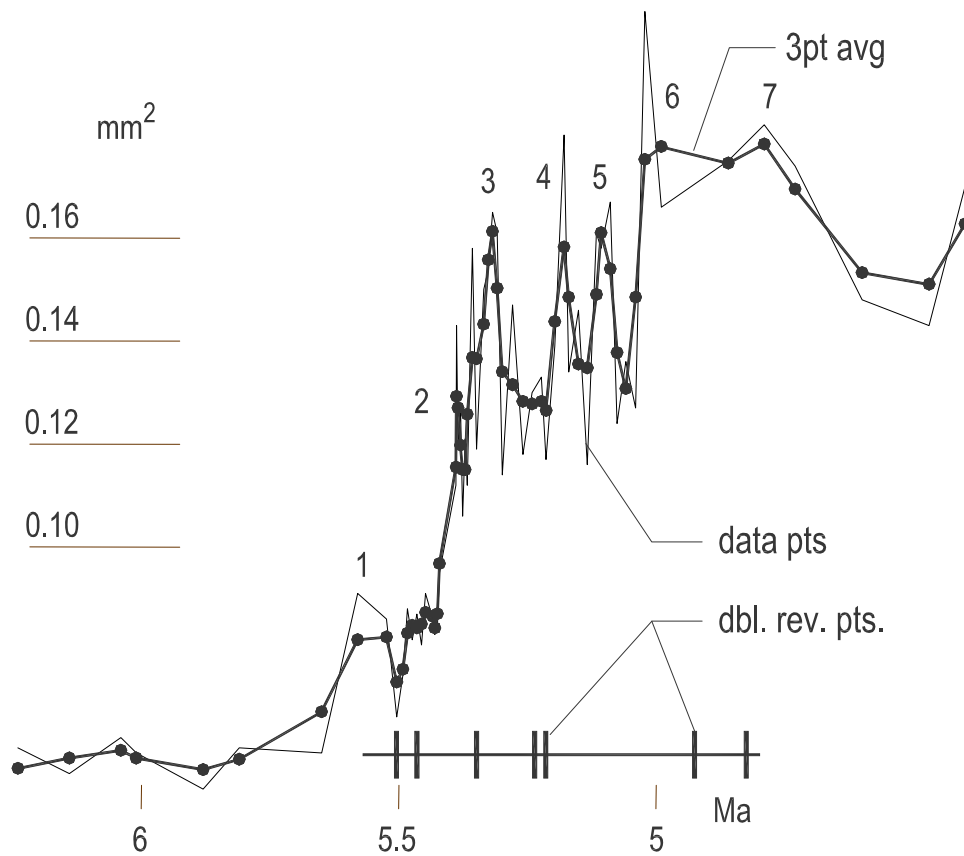


Figure 2. *G. tumida* transition with a 3 point centre weighted moving average. Continuous fluctuation demonstrated by the data's 29 double reversals reduced to 7 by light smoothing.

It is typical of measures of natural systems, as for ripples on waves on swells, to have fluctuations of large and small scale superimposed. Long duration fluctuations may be only recognized after suppressing the smaller scales of variation. That is

particularly true tracing the slopes of a sequence, the first derivative (first differences). When the smaller scale fluctuations are suppressed enough, the derivative shows the non-linear dynamics of the underlying larger scale clearly.

Successive shape suppression as shown in Figure 5 using Gaussian smoothing reveals a simple and unambiguous singular rate spike event in the 1st derivative. That's the clear signature of a step change. The top curve shows one iteration of 17 point linear smoothing (shifted up by $.1\text{mm}^2$ to separate the curves). The second curve shows moderate Gaussian smoothing (shifted up $.05\text{mm}^2$) and the third curve heavy Gaussian smoothing. The derivative is of the second curve drawn to the scale on the right. The initial degree of 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 (13), making a sequence with equally spaced points as required for repeated Gaussian smoothing to have a uniform effect. Then the further smoothing was done with a 9 point (.4 Myr) Gaussian kernel, first with 4 iterations (U4) and then 32 iterations (U32).

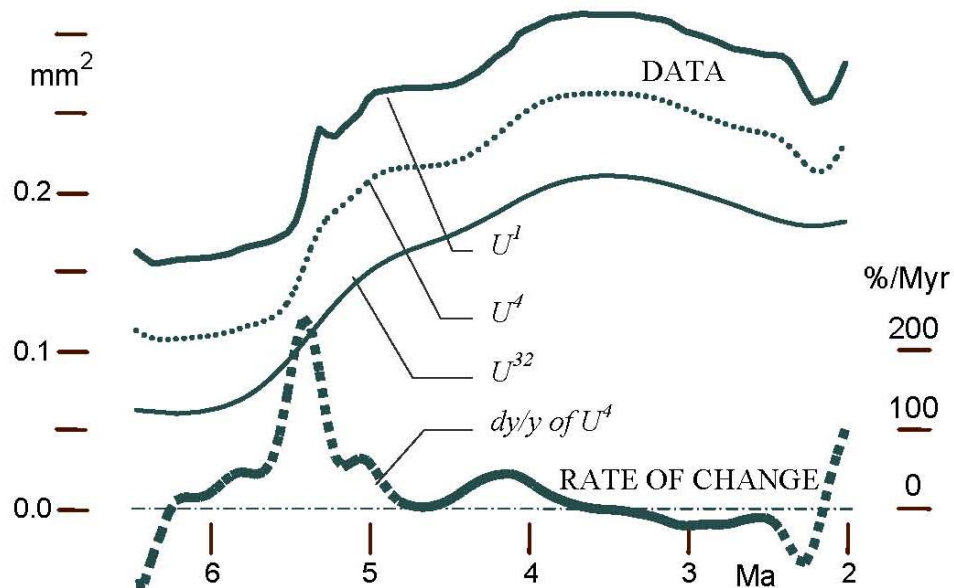


Figure 3. Behavioral shape using Gaussian smoothing. U_1 is a 17point running average regularized to a .05 Myr point spacing. U_4 & U_{32} show smoothing 4 and 32 times with a 9 point (.4 Myr) Gaussian kernel, plus the first log derivative of U_4

Whether this is useful depends on whether the underlying shapes are recognizable and can be associated with particular underlying mechanisms. One very recognizable shape in all the smoothing curves is an artefact of the way they were calculated, the odd jogs at their ends. These are shapes of the original data that can't be altered by smoothing because any symmetric smoothing kernel is shortened as it approaches the end of the curve, unless you create imaginary points beyond the end of the curve by some scheme. My preference is to simply let the artefact show. One could hide this by doing smoothing on a longer data set and cutting off the ends for presentation, but data is scarce and it's valuable to be reminded of the effect of one's own tools, so I just leave them as they come. There are also a variety of other kinds of analysis one can do to investigate the detailed structures of a sequence's continuity, including the use of scale space diagrams as used in pattern recognition (13).

The case of events that appear to begin and end with continuity is both problematic and a clear indicator of one of the broadest and most common typical types of causal mechanisms. In most cases it would directly imply the presence of accumulative change that goes to completion involving a temporary and locally self-organizing growth process. It directly suggests the progressively increasing and then decreasing rates of change of an ordinary emergent change of state.

The shape of the process, now clearly depicted, could possibly be due to changes in ocean temperature, perhaps, or shifts in nutrient currents, or involve ecosystem co-evolution, such as one species taking on a symbiotic partner without species evolution (ecophenotypic change). These and other mechanisms were investigated and the temperature, symbiot and eco-system change possibilities seemingly ruled out. The response of plankton size to ocean temperature is well known and even commonly used as a measure of ocean temperature (14, 15,16). Smolka (14) reported summer and winter temperatures from measurements taken from the same sediment core (DSDP 214) that the G. tumida samples were taken from. His data showed a $4.0 \pm .3^\circ$ C dip and recovery in summer temperature in the 1 Myr before the G. tumida transition but otherwise no significant change in the period. Schmidt et. all. (15, 16) provide a comprehensive global survey of ocean temperature and plankton size relationships, finding a general 25% change in plankton size over 10 Myr, quite unlike the 200% change in size in a half Myr for G. tumida.

One expert on the subject, Richard Norris of Woods Hole (17) reported that G. tumida has never hosted 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. In any case these ecophenotypic mechanisms would all rely on causing change in the phenotype without change in the genotype, and a quick inspection of the images of G. pleisotumida and G. tumida shells clearly discredit that hypothesis. It's easy to see that the forms of the shells are related, but quite different, and so clearly represent genetic change. It would be helpful to compare the behavior found in this ocean core with others. Knowing that there is complex flowing change in the transition, and plentiful specimens, suggests scanning the specimen images to view them in sequence, to watch progressions of the individual bumps on the creature's shell like an animated movie and see what shapes on the curve their changes correspond to.

What Malmgren (1) first found in this same data he called 'punctuated gradualism', because it appeared to display a period of increased random variation and directed selection. There is no known extended process of evolution that abruptly starts and stops, so a new mode is suggested to explain the kind of single rate event demonstrated. If there is clearly more than one mode of speciation, there may also be more than two as well, of course. Perhaps the assumption that there is only one has been preventing an open search for what various modes there might be.

DISCUSSION

The appearance of an evolutionary step change by a continuous process seems to neatly satisfy the main requirements for the previously unobserved mechanism of punctuated equilibrium, that the mechanism start and stop. Prothero (11) summarizing the

discussion in 1992 provides 15 citations including Gould's later views (10) and those of Stanley (18) for what still seems to be the consensus. Most evolution for larger species occurs by a hidden process during the gaps in the fossil record at speciation with long periods of little change between, and that evolution for microscopic protists including foraminifera like *G. tumida* gradual random drift prevails. Using this new method to study the *G. tumida* transition, though, clearly demonstrates temporary flowing evolutionary change, completely unlike any kind of random drift. It opens the possibility that all punctuated evolution occurs by events of this same kind.

Because this finding results from using a different mode of data analysis, looking for complex flow rather than for rates, means all the old data on rates of evolution may potentially be hiding a kind of information that was not looked for before. The traditional approach to irregular data automatically treats the variation as noise, using regression to fit simple mathematical shapes. By being overly conservative in looking for shape, the method actually erases the information in the data about its complex shapes.

Better analysis can not make up for missing data, of course. The fossil record may provide specimens for one out of a few thousand generations and speciation may occur in a few hundred, so there would be no way to trace the shape of the process. Other data sources or types of measures might be explored. There are various modern collections of fauna and flora in the drawers of century old naturalist collections for various locales that might accidentally capture a flowing step pattern of change. It might be rare but worth considering as a standard part of longitudinal studies.

It remains to consider if any modes of genetic change for this behavior are feasible. What's needed for complex developmental change in short periods is for structural stasis to give way to rapid change and then go back to stasis again, by a sequence of small steps. That very precisely calls for some kind of process feedback. What you'd be looking for is the success of one mutation to both aid reproduction and also increase the frequency of mutations *of similar kinds*. That way the new variations would serve to 'explore' the viability of local paths in the same region of fitness potentials. The literature on this possible mode of variation is yet to be collected, but includes the proposal by Kirschner and Gerhart (19) that they call 'facilitated variation', proposing a specific developmental biochemical process for it. They call it 'resolving Darwin's dilemma', because it finally provides a positive way to address the problem that genuinely random mutation would seem more likely to be destructive. This general idea of 'variation at the fringe' (while protecting the core) is the same change in design needed to produce process feedback, though Kirschner and Gerhart (19) don't discuss that potential. One might also think of it as suggested by the fact that the growth of an individual organism is itself a branching tree of growth events and that evolution is precisely a stepwise modification of that tree's branches. One does not need a particular branching structure to observe that organisms clearly develop along branching pathways, with their starting, turning and stopping points clearly included in the design of species. That design would necessarily need to evolve by the successive adjustment of those developmental pathways.

Some of the best gathered evidence for evolutionary extension and branching are the patterns of proportional relationships in the shapes of organisms first carefully documented by D'Arcy Thompson (20). That work was not rigorous in every way, and

the shape of body form is a difficult subject for analysis, but the work is of both enduring popular and professional interest, seeming to substantiate the idea that change by proportional geometry and making a mutually responsive comfortable fit in a succession of forms is something nearly everyone recognizes. It apparently addresses something real that is not yet well explained.

One way for body parts to vary independently but in relation to each other is for there to be coordinated endpoints of development. That there might to be a coordinated set of growth limits for different parts follows from the appearance is that organism growth does not end by either internal or external exhaustion or conflict. The growth of organisms ends at a point of comfortable balance between parts and the environment. That suggests there must be some specific means of coordinating the stopping points for development's branching process.

The question here is less how these structures work, but that a network of some kind performing the function must exist, and if one limit changes it would have a ripple affect on the others. One familiar 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 variations in that version of an unstable network multiplied. That describes a mechanism for an organism to destabilize its growth limits, follow a branching path of variation and restabilize.

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 processes as a possible mode of evolution. Chaotic variation in an organism's growth limit control system would not by itself lead to change in many features at once, just change in many 'pressures' at once. You would still need a mechanism like 'facilitated variation' (19) to provide the biochemical mechanism.

The idea of development in evolution it turns out is not a new idea at all, but a long discredited one that may have been mistakenly discarded. That Lamarck may have been wrong about everything except his concept may seem as different and difficult today as Darwin's proposal was originally. The various bits of new evidence make considering a kind of evolution more like Lamarck's than Darwin's seem logically necessary though, and there may be others as well. What Gould clearly showed is that most evolution happens during short periods, a branching reorganization of a complex branching system of growth that starts and stops. Locally self-organizing growth systems of all kinds and shapes throughout nature 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's that it's 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, a moving end point in the growth of individual organisms. It seems reasonable that changes in the those end points might themselves sometimes develop by growth.

CONCLUSION

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

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

The result has been to reveal the underlying behavioral shape of the phyletic succession from G. *pleisotumida* to G. *tumida*. The shape found is a rather familiar one, even if unfamiliar in this context, that of rapid complex organizational change by growth. Malmgren's (1) conclusion of punctuated gradualism and Bookstein's (2) interpretation of random walk have both been updated.

MATERIALS AND METHODS

The Step Variance Test measures whether increasing steps in the data have increasing variance or not (13). The idea is to measure whether the next change at any point is actually independent of prior steps (indicating random walk) or tending in the opposite direction of prior steps (indicating either complex fluctuation or symmetric noise about a norm). The analytical method uses a version of the Hurst exponent (22, 23) and is closely related to measures of fractal dimension in data.

By numerical experiment with 20 random walks (Figure 4) the spread that occurs estimates the 95% confidence interval for random walks and displays their close clustering. Sequences with $H\sigma$ well outside this interval (.33 to .65) are distinguished from random walks and probably represent some regular continuous process combined with fluctuation or noise. The test can be somewhat loose for ruling out a presumption

of random walk, since the object is to find a reasonable doubt that the data is purely a product of noise.

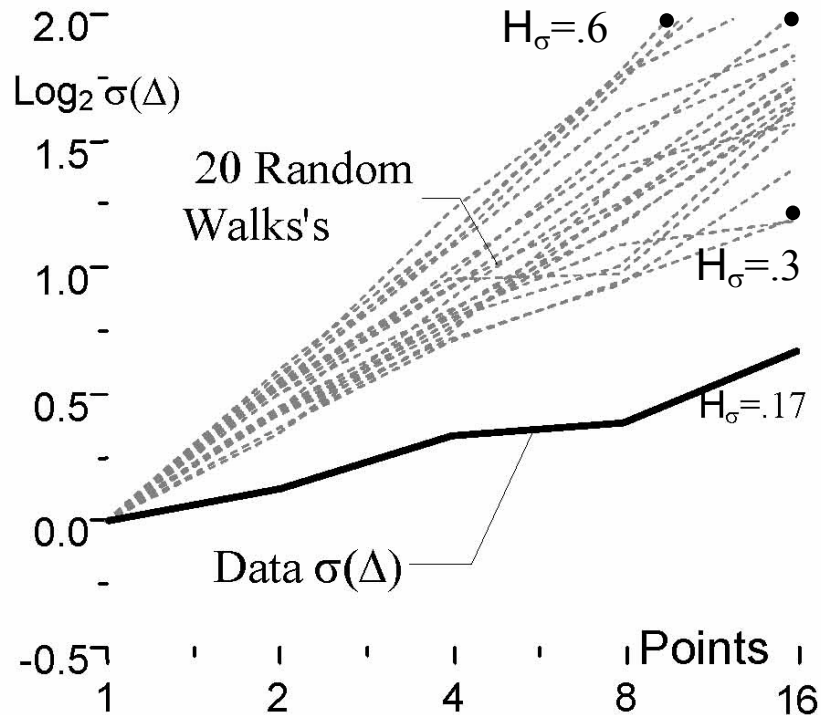


Figure 4. Step variance test for *G. tumida* size, and 20 random walks, the slopes ($H\sigma$) of std deviations and step size for subsequences of 2,4,8, & 16 point steps for each data set. The $H\sigma=.17$ for *G. tumida*, showing a substantial departure.

Apart from the statistical test it is apparent there is a logical problem with postulating random walk of a whole population. If random walk in the characters of the whole population occurs, it must be the result of some pattern of change in the characters of individual organisms. Individuals within a population can not continually make matching 'random' neutral changes at the same time, and that appears to be the only way the variation of individuals can physically produce a collective random walk. Consequently it appears that for populations there may be no functional basis for random walk, and the 'null hypothesis' is not for a physical, but a statistical

mechanism of evolution. If the characters of individual lineages of a population exhibit independent (rather than matching) random walks, the resultant mean value for the population will be constant, with the variance within any sample continually increasing. This is clearly the opposite of the pattern seen in the data and extremely unlikely to be found in the diversity of any species. If a random walk can be either ruled out, or brought into question it supports the use of shape analysis to look for meaningful shapes that can be substantiated by other means, perhaps further explored with scale space analysis or derivative reconstruction to give more form to identifiable continuous processes (13).

The Flowing Shape Test measures the property of rates of change in continuous physical systems that makes it useful to approximate them with mathematical functions that have derivative continuity. The successions of rates of change have no abrupt breaks or shifts, so that the slope at a point when approached from either direction is the same. A simple test of a time series data to see if the underlying system is likely to represent a process having continuous flows is to measure the sensitivity of its 'jaggedness' to smoothing. Neither this or any other indicator of flow in measures of physical systems were not found in the statistical research handbooks (24, 25) or a web search. From experience it appears that the question does not come up because the continuity of natural processes is assumed to be a function of the equation to be used in describing them rather than in the structure of their behaviors.

One measure of 'jaggedness' is the count of three slope segments that reverse sign twice, the consecutive double reversals of slope. In curves with only random fluctuation there will be, on average, nearly half the number of double reversals

possible. Light smoothing does not significantly reduce the number of double reversals as seen in comparing Figure 5 & 6. Sometimes light smoothing will greatly reduce the number of double reversals, producing a curve with a much greater degree of flowing shape. That then is an indicator of complex fluctuation rather than noise as the source of data variation, and that the proper curve fitting is one that fits the fluctuations rather than cuts through them. For The G. tumida data light smoothing reduces the number of double reversals from 29 to 7 instead or remaining constant as shown in figure 6. The indication of flowing shape it visually confirmed in Figure 2 which clearly shows the flowing shapes revealed.

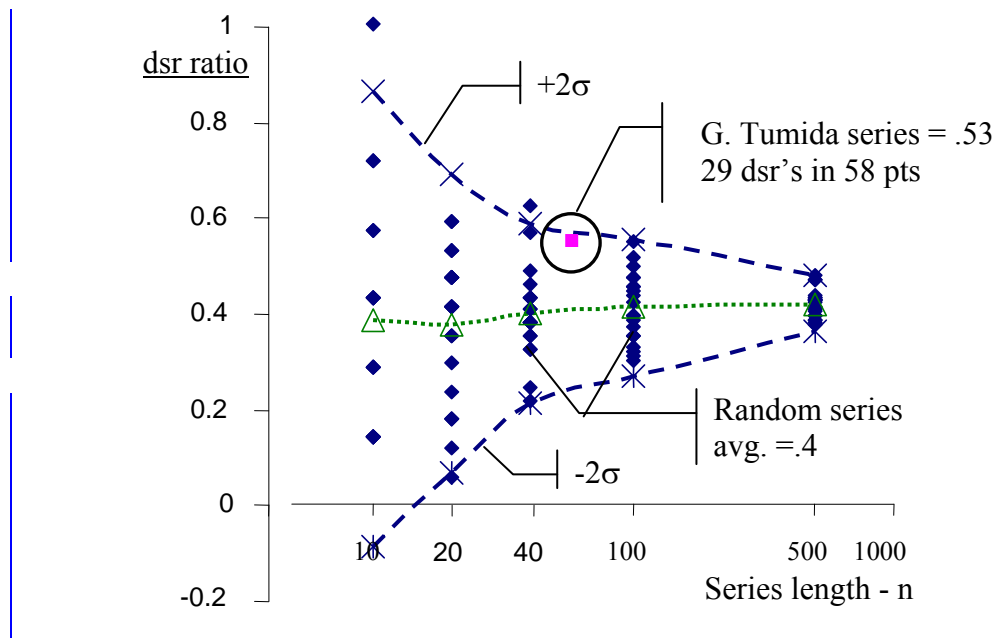
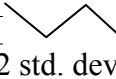


Figure 5. Double slope reversals ratio (dsr) [] for 20 random series of varying length (10, 20, 40 & 100 points), mean and 2 std. deviations above and below, with single point ratio of .51 for the 58 point G. tumida data.

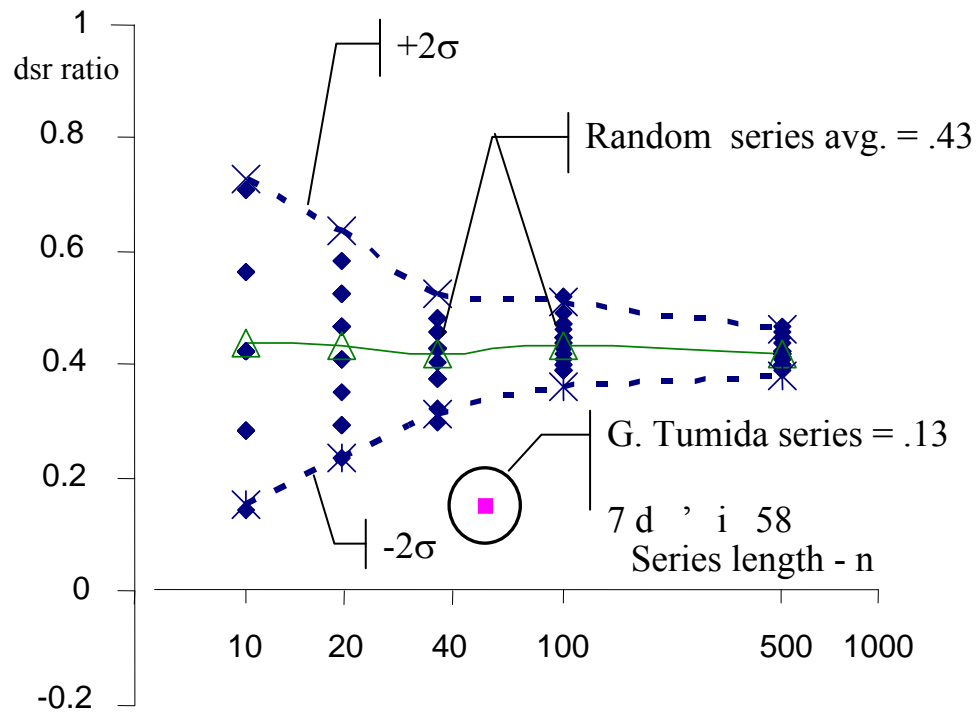



Figure 6. Double slope reversals (dsr) [] for 20 smoothed random series of varying length and dsr ratio of .13 for the *G. tumida* data. Smoothing is by a 3 point centered kernel (1,2,1). Light smoothing does not change the jaggedness for noisy data, and greatly reduces the jaggedness of the *G. tumida* data.

In complex fluctuation, with ripples on waves on swells, smaller scale reversals tend not to be symmetric about the next larger scale. There is also a noise component present in any sequence of measures, reflecting independent influences of various kinds. A running average suppresses both noise and smaller scale fluctuations trading a loss of small scale shape for making the larger scale shapes more visible. Another means of achieving the same thing is to strip fluctuations from a curve by connecting the inflection points (11), but the more common approach is Gaussian smoothing. 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:

$$\text{for } -a < n < a \quad k(n) = \frac{e^{-|n|/2}}{\sum_n e^{-|n|/2}} \quad (1)$$

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 exposing the more robust turning points in the data, making the series approximately differentiable, as shown in figure 3.

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