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Problems in the measurement of morphological rates of change

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The quantification of morphological change plays a major role in the study of the pattern and process of evolution. Here we present a short history of the quantification of evolutionary rates and a review of the problem.

1. Introduction

The analysis and interpretation of morphological change over long time spans are within the domain of paleontology. One of the first to recognize the importance of these type of data for evolutionary studies was Björn Kurtén (1958, 1960), who also recognized the significance of studying the organism as an integrated unit and not merely as a series of unassociated single characters. He used the fossil record of mammals to empirically study evolution in the context of three-dimensions, with the developmental implications of allometry and morphological rates.

The rate of evolution can be considered as the amount and direction of change, if any, in one or more variables relative to a standard; thus, rate is a quantitative feature. However, in the literature, there are many subjective (qualitative) references to rates, and such are more accurately termed descriptions.

Evolutionary rates are useful in the interpretation of the pattern and process of evolution. Given a phylogenetic framework, rates can be construed as one of three broadly defined patterns: (l) a fairly constant rate through time; (2) a pattern in which long periods of stasis are interrupted by periods of change which are rapid on the geological time scale; and (3) variation in rate through time.

The purpose of this paper is to present a brief history and a short review of problems related to the measurement of morphological rates.

2. Historical background

Most approaches to the study of morphological rates of change can be traced to Simpson (1944, 1953). Studies following Simpson's books, T*empo and Mode In Evolution* and *The Major Features of Evolution*, either apply methods proposed in them or develop methods based on suggestions made in them. In 1944 Simpson defined the morphological rate of evolution as "... [the] amount of morphological change relative to a standard," thereby imparting the historical meaning of evolutionary rate as an average rate distinct from the definition of an instantaneous rate (cf. Bookstein 1987, 1988). Several different means of measuring morphological rates of evolution were introduced by Simpson in 1944 and elaborated upon in 1953. These techniques were in terms of single characters, character complexes, and allometric ccefficients. The use of each of these techniques has subsequently been developed by other workers (e.g. Haldane (1949) for single characters, Westoll (1949) for character complexes, and Kurtén (1958) for allometry). Simpson also suggested that these measures can be expressed in terms of absolute time, relative time, or biological time. Each of these scales can be found in subsequent work, e.g. Van Valen (1974) for absolute time, Gingerich (1976) for relative time, and Wood (1949) for a biological scale.

Simpson (1944) introduced three terms to describe rates of evolution: horotelic, bradytelic, and tachytelic. Horotelic rates describe a "standard" rate distribution within a group; bradytelic refers to a low-rate distribution; and tachytelic describes a high-rate distribution. These terms involve a mixing of taxonomic and morphological rates of evolution; the assumption being that high rates of taxonomic evolution are tied to high rates of morphological evolution, low to low, and standard to standard. Stanley (1984) and Gilinsky (1988) have questioned the validity of Simpson's definitions. Gilinsky (1988) claiming that there is a greater probability of a long-lived taxa surviving to the Recent than of a short-lived taxa surviving to the Recent; thereby creating differences in rate distributions as an artifact, and that these rate distributions were determined on the basis of genera within the pelecypods. Such pooling of data within supraspecific and suprapopulational levels can easily bias the data and lead to spurious conclusions.

Both in 1944 and in 1953 Simpson expressed that perhaps the best measure of evolutionary rate would be the measurement of change in genetic terms. Lande's work on quantitative genetic theory and its subsequent application to the fossil record by both himself and Reyment (Lande 1979, 1980a, b, Lande & Arnold 1983, Reyment 1982a, b, 1983, 1985a) indicates that we are approaching this objective. These methods have been used to provide important estimates of the intensity of selection and the importance of selection relative to genetic drift in accounting for the observed morphological change (Lande 1976, Turelli et al. 1988, Bookstein 1989). Haldane (1949) was the first to introduce a standardized measure of the rate of evolution of a single character. These suggestions included quantification of the rate of morphological evolution as: (l) the time required for the character to move one standard deviation, (2) change in percent per million years, and (3) the darwin. Lerman (1965a, b) used measures based on Mahalanobis' D^2 statistic as a multivariate measure of the distance between populations and then converted this to a rate by dividing by time. Based on Lerman's suggestions, Bilsborough (1973, 1976) introduced the use of canonical variates analysis into the study of morphological rates (cf. Niklas 1978). Currently there exists a great diversity of methods for the calculation of evolutionary rates, none of which is clearly superior.

3. Discussion of problems

Gingerich (1982) found three major biases in the measure of evolutionary rates: (l) the tendency to ignore zero rates, i.e. "stasis is data" (Gould & Eldredge 1977); (2) the misinterpretation of stratigraphic data; and (3) the inverse correlation of rate with time interval (cf. Kurtén 1960, Ginzburg & Rost 1982, Gingerich 1983, 1984, Gould 1984, Bell et al. 1985, Williams 1987). In addition, there are problems regarding consideration of phylogeny, ontogeny, random sequences, and mathematical difficulties in the calculation of rates. These questions will be discussed in the sections that follow.

3.1. Phylogenetic and systematic considerations

As pointed out by Hecht (1965) a major problem in the study of evolutionary rates is the accuracy of the phylogenetic scheme and the recognition of a lineage (Niklas 1978, Bell & Haglund 1982). These difficulties include distinguishing the polarity of a transformation series, recognition of homoplasy (Hecht 1965, Boucot 1983), determination of the boundaries of groups, and the unresolved question of the recognition of species in asexually reproducing organisms (cf. Sorhannus & Fenster 1989).

Identifying organisms found sequentially in the fossil record as having an ancestral-descendant relationship is difficult, if not impossible (Schaeffer et al. 1972), and as pointed out by Cracraft (1984), it is inappropriate to measure rates across the terminal nodes of a cladogram. The confounding nature of this problem is easily overlooked in studies that consider rates and patterns of evolution since it is quite easy to treat a fossiliferous sequence as a succession of ancestral-descendant relationship. In such instances terminal nodes of a cladogram are treated as a continuous morphological sequence on a direct ancestral-descendant line. However, in their discussion of the deep-sea microfossil record, Prothero & Lazarus (1980) presented a scenario by which ancestral-descendant relationships may be recognized. To identify such a relationship it must be assumed that the direct ancestor has been preserved, will be included in the samples, and that the morphological data are appropriate for phylogenetic analysis. In general, these assumptions are difficult to meet. The deep sea microfossil record with which Prothero & Lazarus (1980) were concerned is especially suitable to meeting such assumptions because of its availability of closely-spaced temporal samples from a wide geographic area.

The measurement of rates concerns morphological change within a single phyletic lineage (anagenetic rates), or comparison across diverging lineages. Without the assumption of ancestral-descendant relationship in anagenesis the significance of morphological rates is reduced. This assumption of linearity of the relationship restrict the study of rates to the phyletic lineage in the sense of Bock (1986). A further problem encountered here is exemplified by Bader's (1955) work on evolution in oreodonts in which morphological change was studied at the level of the subfamily, rather than the populational level. If the character under study varies among the members of the higher taxonomic level (above the population or species) at a given point in time then it is not valid to use this character to quantify morphological rates at this higher level; since the higher level metrics are not representative of all the taxa comprising it. In addition, those who have pooled higher level taxa have not made it clear as to whether the means they are evaluating are means of individuals or grand means (in the case of the genus the mean of the species means).

3.2. Ontogeny and morphological rates

Most paleontological studies of morphological change have been comparisons of the adult character states of the different taxa. In many forms, particularly those species with complex life histories involving some type of metamorphosis, the various adult forms show little variability in morphology across taxa. Whereas, the earlier stages (e.g. larvae) show marked variation in ontogenetic trajectory across taxa. For example, among the live bearing frogs (e.g. *Nectophrynoides*) and the marsupial frogs (*Gastrotheca*) the adult skeleton remains characteristically anuran clearly demonstrating their familial relationships. However, in *Gastrotheca*, there is a complete reorganization of the egg (Elinson 1987) and morphological changes in the tadpole (Del Pino 1989), which often obliterate old larval morphologies. Furthermore, the ontogenetic trajectory of the tadpole can be altered to the point of eliminating these stages. The end form of the these processes, the adult, shows stasis in geological time. Therefore, it is clear that without consideration of ontogeny, the adult morphology can present a false impression of stasis.

McNamara (1988) has reviewed the problem of heterochrony in the fossil record and its dependance upon the assumption of ancestral-descendant relationship. Making such an assumption, or the establishment of such a relationship, enables one to distinguish between the most common processes (neoteny, progenesis, acceleration) leading to patterns of paedomorposis or peramorphosis. In extant taxa, such as frogs and salamanders, the genetic determining factors of neoteny and progenesis are often simple, involving a minimum of loci, but the morphological results can be profound. Thus, illustrating a dislinkage of morphological and genetic rates of evolution. Anderson (1987) presented evidence of a linkage between developmental and morphological rates of evolution; this linkage is attributed to the complexity of developmental programs. The alteration of a developmental program (e.g. the tetrapod limb, notochord-neural tube induction system) is complex and thus by necessity occurs in small steps and may give the appearance of stasis. In the development of the tetrapod limb similar morphologies as in the carpus of frogs and salamanders are attained by different ontogenetic patterns of fusion and deletion under the influence of common morphogens and their effects (Hecht 1989). Anderson (1987) also states that developmental constraints, in addition to limiting the rate of evolution, also plays a role in limiting the direction of evolution. For example, the trend towards increasing neoteny in euryceoid plethodontid salamanders in central-western Texas is associated with increasing aridity and troglobitic life (Hecht 1983).

Developmental biology, while being an additional complexity in the analysis of morphological change, elucidates process and pattern of morphological change. Therefore, we suggest that when studying the morphological history of lineages the proper consideration is one that includes comparison of ontogenetic trajectories (Hecht 1989).

3.3. Random walk

As pointed out by Bookstein (1987, 1988) instantaneous rates do not exist for random walks and this has implications for the study of evolution. Studies by Charlesworth (1984) and Bookstein (1987, 1988) pointed out that from a statistical perspective the null hypothesis of a random walk must be examined before rates can be quantified. As mentioned earlier, Lande (1976) and Turelli et al. (1988) provided a test for random genetic drift which is based upon estimates of population size, population structure, heredity, and mutation rates. Such estimates are difficult to make for fossil populations.

Instantaneous evolutionary rates are derivatives of some quantitative feature with respect to time; such derivatives are not meaningful estimates of rate for symmetric random walks (Bookstein 1987, 1988). Since a random walk may imitate trends, saltations, and stasis, we are always faced with this null hypothesis as an alternative explanation for a sequence of morphological points. In their papers, Charlesworth (1984) and Bookstein (1987, 1988) developed tests for the null hypothesis of a random walk. Charlesworth's method involves autocorrelation and Bookstein's method (Range Test) is derived from the mathematics of Brownian motion.

Questions beyond testing for randomness of a given morphological series need to be considered. For example, the acceptance of the null hypothesis does not rule out the possibility that the situation is not one of drift but one of deterministic change in which the causal factor appears to follow a random walk (Charlesworth 1984). Thus, if the null model is not rejected the question still remains as to whether the observed pattern has been generated by random or deterministic processes (Fisher 1986). Therefore, a random walk with respect to time loses much of its significance if the changes in the observed characters can be related to a (paleoecological) variable. In addition, a given single species time series should be compared to overlapping time series of related and ecologically similar species as an aid in interpretation of the results of testing the hypothesis of a random walk. Moreover, the null hypothesis of a random walk may be inappropriate for biological systems. Does this null hypothesis ignore the biology of a living system? The results of such statistical analyses need to be interpreted within a biological framework. Raup & Crick (1981) discussed a model in which a random walk occurs within selective boundaries and we suggest that a random walk can occur within developmental boundaries. Moreover, while a random walk is generally attributed to genetic drift, anagenesis to directional selection, and stasis to stabilizing selection, it must be understood that a given pattern (or lack of pattern in the case of a random walk) makes no statement with regard to underlying causality. It is possible to imagine a situation in which randomly varying causal factors produce stasis. It is also possible that two or more concurrent sequences of morphological points may yield conflicting results concerning the question of a random walk while still exhibiting the same gross pattern. In his study of iterative patterns of evolution in Neogene diatoms Sorhannus (1990) found sequences of essentially identical morphologies, some of which conformed to a random walk and some of which conformed to anagenetic change.

Finally, Reyment (pers. comm.) suggests use of the mode rather than the mean in the analysis of morphology since the mode exhibits greater stability than the mean (and thus tends to show stasis more often?) and is representative of the most common morph in a population.

3.4. Stratigraphy and geography

Problems regarding stratigraphy and geography concern the presence of gaps in the sedimentological record, rates of sedimentation, geographic variation in these parameters and in populations, and differences in preservational probabilities among environments.

Early methods for the measurement of the rate of evolution primarily involved the plotting of a variable against either time or stratigraphic level, such as was done by Colbert (1948). Similar studies are those of Simpson (1944), Gingerich (1976), and Bookstein et al. (1978). In general the methods employed in these papers involved plotting of a character versus stratigraphic level rather than time. The conclusions regarding evolutionary patterns and rates were thus based on the assumption of a constant rate of sedimentation. Raup & Crick (1981) have recognized this and consider consider it an absurd (but unavoidable) assumption. Further, recall our preceeding discussion concerning the importance of testing the hypothesis of a random walk and consider that time may not necessarily be, and is likely not to be, an appropriate causal variable. Thus, it remains to find an appropriate extraneous variable against which to plot morphology.

Sadler (1981) and Dingus & Sadler (1982) pointed out that when interpolating between known points in time it is not appropriate to assume constant rates of sedimentation. If gaps are seen in the fossil record the question as to the cause of the gaps arise. Are the gaps a result of periods of non-deposition of sediment, migrational events, or to exceptionally rapid periods of evolution? Gaps in the stratigraphic record are an unavoidable result of the sedimentation process (Schindel 1982). If neontological concepts are to be applied to the biostratigraphic record it would be best to use organisms with dense fossil records, long generation times, and sections that are both fairly recent and have high rates of sedimentary accumulation (Dingus & Sadler 1982).

Several workers have discussed problems involved in the interpretation of stratigraphic data. McKinney (1985), for example, discussed how different patterns of deposition in shallow-water versus deep-water marine environments can bias the apparent pattern of evolution, and raised questions concerning the validity of stratigraphic data (Bell & Haglund 1982). Benson (1983) demonstrated that both punctuational and gradualistic patterns of evolution can appear within the same lineage during roughly the same period of time depending on the localities from which the samples were taken. This is analogous to the finding of both random and non-random sequences within the same lineage as was discussed earlier (Sorhannus 1990). In his study, Benson (1983) found that the ostracode *Poseidonamicus riograndensis* was replaced in a punctuated fashion by *P. miocenicus* in the western part of its range whereas in the eastern part of its range the same transition was gradual. This may be due to migration of *P. miocenicus* or, instead, may be a result of the relative completeness of the stratigraphic record in these sections (Dingus & Sadler 1982). Bookstein et al. (1978) also expressed concern over the possibility of stratigraphy related misinterpretion of the fossil record. They pointed out that gaps in the fossil record, especially where specimens are missing for several continuous stratigraphic sequences, suggest that a punctuational event has occurred (cf. Rensch 1959, Levinton & Simon 1980). In their analysis of single characters in *Kosmoceras*, Raup & Crick (1982) found that morphological gaps are associated with sedimentary breaks more often than expected by chance, but that the majority of sedimentary breaks are not associated with morphological gaps. Some gaps may be due to missing sediments, and thus may be viewed in terms of stratigraphic completeness. Often gaps are a result of non-preservation or non-deposition of fossil material. Rensch (1959) noted the example of the crossopterygian *Latimeria* being re-discovered in 1938: yet this lineage left no fossil evidence throughout the Tertiary (approximately 63 million years), but has a relatively complete record in the Paleozoic and Mesozoic. Furthermore, when, in small populations, evolution proceeds at a very rapid rate the expectation is of a poorly preserved fossil record.

In the stratigraphic record aggregations of fossils, particularly marine microfossils, may include up to several thousand generations and as a result will tend to obscure the presence of short-term trends in the fossil record. Directional trends through these aggregations may represent either a gradualistic trend or a series of punctuational events with intervening periods of stasis (Levinton & Simon 1980). Moreover, such trends must be examined in light of the points raised in our discussion of importance of testing data against the hypothesis of a random walk and relating these data to independent variables. Random inter-generational changes within these aggregations can lead to misinterpretation of the sequences. There is a need to determine if the changes seen within a lineage at the populational level are attributable to local evolution, migration of geographic variants, ecophenotypic variation, or some combination of these factors. To account for these factors populational samples from sites in several distinct geographic regions are necessary. Gould & Eldredge (1977) pointed out that ecophenotypic variation needs to be considered (Bell & Haglund 1982, Boucot 1982) before making a claim for either phyletic gradualism or punctuated equilibrium. A false impression of gradualism or punctuation can result from the immigration of geographic or ecophenotypic variants into the stratigraphic section being studied (Sorhannus 1990). Migration of geographic or ecophenotypic variants can also result in a false pattern of stasis (Bookstein et al. 1978), as in the instance of an interaction between clinal and temporal gradients in morphology. Such migration may likewise account for a significant fraction of the variation in the rate of evolution (Charlesworth 1984). If the evolutionary patterns at different sites are in conflict, such as those observed by Benson (1983) and Sorhannus (1990), then these conflicts need to be examined; especially in terms of stratigraphic completeness, depositional rate, and temporal resolution.

3.5. Temporal scaling

In 1983–1984 three papers (Gingerich 1983, 1984, Gould 1984) appeared in Sci*ence* concerning the inverse relationship between time interval and evolutionary rate. Gingerich (1983) found that the average amount of evolutionary change in the studies he surveyed was: $\ln X_2 - \ln X_1 = 0.15$. The plot of the natural log of the rate of change in darwins (the natural log of the natural log) against time (in millions of years) results in a smooth curve with a slope of –1.0. Both Gould (1984) and Gingerich noted that the effects of the chosen time interval and of scaling for differences in time interval will lead to incorrect conclusions regarding relative rates of evolution. Gould (1984) considered the ratio of $X_2/X_1 = 1.2$ to be a result of human perception; whereas Gingerich (1984) considered the range of proportional differences between the initial and final state, with an average of 1.2, to be of biological significance. Gould (1984) pointed out that Gingerich's (1983, 1984) conclusion that the rate of evolution is inversely related to the time interval over which the rate is measured is based on a statistical artifact of plotting the inverse of time (rate) against time. Gingerich (1983) used the data in Van Valen (1974); data we question since it involved calculation of rates at taxonomic levels above that of the species and across hierarchial levels.

3.6. The major univariate method

A problem with the univariate measure of morphology is that it tends to atomize the organism; whereas the organism is actually a coherent unit with its many parts functioning in an integrated fashion.

As mentioned earlier, Haldane (1949) suggested three measures of morphological rates of evolution. Of these measures the darwin has captured the imagination of most investigators.

The darwin is defined (Haldane 1949:55) as "...an increase or decrease of size by a factor of *e* per million years, or, what is practically equivalent, an increase or decrease of 1/1000 per 1000 years." The incorporation of *e* in the definition is viewed by Simpson (1953) as being an unnecessary complication. Gould (1984) also found fault with the darwin as a measure of evolutionary rate. He stated that its use to compare organisms is valid regardless of time interval, only if the rate of change is exponential; otherwise measurements must be taken over equal time intervals. Haldane's measure of evolutionary rate expressed as percent change per million years has been criticized by Lerman (1965a) for not considering changes in the variance of a character through time. Such a failure can result in changes well within the variance of a character being mistaken for significant evolutionary change. This problem remains, however, regardless of the chosen measure since due to preservational problems the observed variance of a fossil population may not be reflective of its variance when it was an extant population.

3.7. Multivariate methods

Multivariate methods permit the study of the organism as an integrated unit. Such measures allow for viewing the changing organism as a coherent unit (Simpson 1949, 1953), not as a collection of independent characters. This is not to deny the importance of the study of single characters, nor to deny that a single character may accurately reflect the evolutionary pattern of a taxon (cf. Sorhannus et al. 1988). Many recent studies (e.g. Lazarus 1986, Cheetham 1986, Chaline & Laurin 1986, Sorhannus et al. 1988, Fenster et al. 1989) have attempted the use of multivariate measures in their quantification of morphological change through time. Such studies have primarily treated multivariate rates of evolution as a scalar quantity, whereas Bookstein (pers. comm.) suggests expressing multivariate rates of change as a vector. There are a number of additional mathematical issues related to the use of multivariate methodology. An example of the need to view the organism as a whole is provided by Malmgren & Kennett (1981) who studied the evolution of the foraminiferan lineage leading from *Globorotalia (Globoconella) conoidea* to *G. inflata*. They concluded that the patterns of evolution in the characters studied bear little similarity to each other. All but one of the characters exhibited a gradual rather than punctuational pattern. This may be construed as evidence that both gradualistic and punctuational trends involving different characters can occur within a single population during a particular time interval, thus showing that several characters need to be considered in an analysis of evolutionary rates and patterns, and that different characters are subject to different constraints and/or selection.

Almost all studies that have presented a multivariate rate of evolution have presented such a value as a scalar quantity. In addition, all such studies have only considered the first discriminant function which, while accounting for the greatest amount of variation, does not account for all variation in the direction of among-group difference. Bookstein (1988) discussed some of the problems inherent in multivariate measures of evolutionary rate when the null hypothesis of a random walk has not been rejected. These problems concern interpretation of the within-group and between-group covariance matrices in view of a random walk across the inevitable pooling of generations within a given sample. Further, Reyment (1985b) emphasized the ability of outlyers to distort the covariance matrix and the desirability of homogeneous covariance matrices. Bookstein (1988) provided a multicharacter extension of the Range Test, distributed as chi-square, to test the hypotheses of anagenesis, random walk, and stasis; which, however fails to take inter-character correlation into consideration.

4. Conclusions

The major problems involved in the quantification of evolution are: the recognition of ancestral-descendant sequences, the role of ontogeny, stratigraphic uncertainty, the inverse correlation of rate with time interval, the existence of random walks, detection of patterns of migration and clinal translocation, and biases in preservation. Presently there is no superior method for the measurement of evolutionary rate. We find it to be of dubious value to calculate morphological rates of change above the population level or across terminal nodes of a cladogram.

Modern hypotheses of evolutionary mode are qualtitative in nature. Thus, it is very difficult to distinguish among these modes, and the same data can be used to support competing hypotheses. Of the available methods we favor the application of Bookstein's (1987, 1988) Range Test which allows for two-tailed testing of the null hypothesis of a random walk and the calculation of reduced speeds. However, we do acknowledge the limitations of the multivariate Range Test in its failure to consider character correlations. A random walk must be rejected in order to justify the calculation of instantaneous rates. If a sequence is shown to be non-random then a lineage can be classified with regard to evolutionary pattern by hierarchical linear modeling. It is at this point that evolutionary rates will be useful in the comparison of the patterns.

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