

The description and classification of evolutionary mode: a computational approach

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Abstract.—The incorporation of the random walk model into stratophenetic analysis marked a turning point by presenting a potential null model for microevolutionary patterns. Random walks are derived from a family of statistical fractals, and their statistics can be reconstructed using appropriate techniques. This paper lays the foundation for the explicit and uniform description of evolutionary mode in stratophenetic series using random walk null models and the information contained within incompletely preserved time series.

The method relies upon the iterative analysis of subseries of an original stratophenetic series by measuring the presence of deviations from statistical randomness as the lineage evolves. This measure, and its probability of significance (evaluated using a randomization test), forms the dimensions of a descriptive space for microevolutionary modes. Each stratophenetic series can then be viewed as a journey through this space. Computer simulation of various evolutionary modes demonstrates that different modes, for example stasis and gradualism, have differing trajectories and occupy different regions of the microevolutionary space. The method is applied to two published foraminiferal stratophenetic series, the Mio-Pliocene *Globorotalia plesiotumida-tumida* punctuated transition and an anagenetic trend in the Late Cretaceous *Contusotruncana fornicata-contusa* lineage. An anagenetic trend is strongly supported in the latter example, whereas transformation of the *Globorotalia* species seems to result from the fluctuating effectiveness of constraining processes.

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Introduction

Our understanding of the tempo and mode of species evolution has received considerable study for over 25 years. Few studies, however, have been dedicated to constructing a suitable and uniform methodology within a formal framework for the discussion of long-term microevolutionary processes (Raup 1977; Raup and Crick 1981; Charlesworth 1984; Bookstein 1987, 1988; Gingerich 1993; Roopnarine et al. 1999). A database of evolutionary patterns would allow us to address such important and largely unanswered questions as (1) What are the relative frequencies of various modes and patterns of evolutionary change, for example, gradualistic versus punctuated? The empirical evidence gathered since Eldredge and Gould's (1972) seminal paper suggests that we are dealing with a range of microevolutionary modes rather than a single phenomenon (Erwin and Anstey 1995). (2) How comparable are the temporal distributions of evolutionary patterns and rates among closely related and distantly related species, subjected to similar environmental conditions (Kauffman 1977)?

(3) Is the boundary between micro- and macroevolutionary processes simply quantitative and arbitrary (to paraphrase Dobzhansky [1970])? It remains unclear whether the observed gap between microevolutionary processes and macroevolutionary patterns results from a discontinuity of observational scales, or whether there is no simple extrapolation of process from the micro- to the macroscale (Rieppel and Grande 1994).

The traditional approach to the study of evolutionary pattern over geological time uses the description of one or more characters within a lineage through a stratigraphic interval. This approach was formalized by Gingerich (1974), who termed the procedure "stratophenetics." Studies using the stratophenetic approach generally focus on the categorization of the resulting temporal patterns of character evolution, for example as fitting either the model of morphological stasis and punctuated equilibrium or a model of gradual continuous change (Gingerich 1974). Bookstein (1987, 1988), however, revealed the statistical difficulty involved in recognizing and cate-