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Anagenetic evolution, stratophenetic patterns, and random walk models

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Abstract.—Previous studies have suggested that unbiased random walks may serve as appropriate null hypotheses for the detection of pattern in stratophenetic series. While numerous processes that influence the perceived temporal morphological evolution of a species may yield stratophenetic patterns that conform to the model of a random walk, use of the model as a null hypothesis raises several concerns. First, unbiased random walks are only a subset of a much larger set of random motions, including biased and fractional random walks. Some of these motions could also serve as appropriate null models for stratophenetic patterns. Second, due in part to the fractal nature of random walks, many types of time series begin to resemble random walks statistically as sampling resolution decreases. Therefore, indiscriminate support for unbiased random walks as null hypotheses of stratophenetic pattern leads inevitably to the commitment of Type II errors (incorrect failure to reject a null hypothesis). In this paper we simulate different hypothetical patterns of microevolution using various random walk models and apply the test of the null hypothesis. The frequency of Type II errors increases as stratigraphic completeness decreases, but at a currently unknown rate. Moreover, the test is insensitive to nongradual patterns of anagenesis.

We also demonstrate that a previously published approach is closely related to a standard method of fractal time series analysis and represents a good qualitative test of evolutionary pattern. The statistical variation underlying this method, however, is currently unknown, and further work is required to make it a robust quantitative test.

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Introduction

The traditional approach to the study of microevolution over geological time uses the description of one or more characters within a lineage through a stratigraphic interval. The resulting stratophenetic series frequently form the basis for quantitative assessments of fossil morphology through geological time, yet few studies have actually been dedicated to constructing a methodology capable of providing a strong formal framework for discussion of long-term microevolutionary processes (exceptions exist, for example Raup and Crick 1981; Bookstein 1988; Gingerich 1993). Understanding the patterns generated by stratophenetic analysis remains problematic for two reasons: (1) the lack of general statistical methods designed to address irregularly sampled time series, and (2) the inability to reify patterns without associated measurement of causative factors. Bookstein (1987, 1988) argued that in the absence of independently measured, covarying factors, the interpretation of stratophenetic series runs the risk of attaching meaningless explanations to such series. He was able to demonstrate this by simulating stratophenetic series using unbiased (symmetric) random walks, many of which can appear on first inspection to have deterministic underlying mechanisms. The disturbing fact for paleontology is that series generated randomly can have all of the visual appeal of stratophenetic patterns, such as stabilizing or directional selection, punctuation, or gradualism, which have been interpreted as reflections of deterministic mechanisms. This has led many paleontologists to accept the necessity of eliminating the "null possibility before searching for a 'cause of consequence'" (McKinney 1990: p. 55). Nevertheless, failure to reject the null hypothesis, an indication of apparent randomness, should be an admis-

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