

ANALYSIS OF RATES OF MORPHOLOGIC EVOLUTION

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■ **Abstract** Rates of morphological evolution exist at several hierarchical levels. The most fundamental rate, termed instantaneous or intrinsic, is a measure of evolutionary change between consecutive generations. Comparisons of these rates between different characters or taxa are best done by measuring change proportionally or logarithmically. The variation of instantaneous rates over geological time, or between taxa, is a reflection of differing intrinsic factors (e.g., mutation rates) or environmental conditions, and may explain rates at higher levels of the hierarchy such as apparent variable rates of evolution and diversification. Such long-term rates, termed here microevolutionary rates, have been measured variously as factors of exponential change over time (the “darwin”), or have been scaled for comparison according to sample standard deviations (the “haldane”). The relationship between these long-term measures and instantaneous rates, however, is not constant, nor measurable, unless evolution is monotonic and directional or static. Those modes produce an inverse relationship between microevolutionary rates and the interval of time over which they are measured. Any introduction of apparent randomness into the morphological evolutionary series of a taxon, however, likewise produces an inverse relationship between rate and timescale. This latter result is largely a mathematical artifact predictable on the basis of the behavior of random walks. Failure to reject a null hypothesis of random walk for an evolutionary series therefore precludes the interpretation of microevolutionary rates as products of real evolutionary processes. Methods developed to use random walk statistics and microevolutionary rates as sources of information about evolutionary mode and instantaneous rates are problematic because they (*a*) depend on a nonlinear relationship between microevolutionary rates and elapsed time, and (*b*) are prone to spurious correlation.

Rates of evolution may be measured above the level of species, for example as rates of origination within monophyletic clades. Taxonomic rates of evolution assume genealogical information that is generally not available for the groups under consideration. Likewise, many classic examples of rates of evolution comprise taxa of unknown