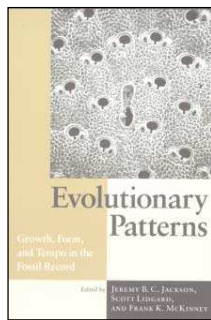


## Book Review

## Empiricism at all levels

### Evolutionary Patterns. Growth, Form and Tempo in the Fossil Record

edited by Jeremy B.C. Jackson, Scott Lidgard and Frank K. McKinney.  
The University of Chicago Press, 2001.  
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Do species evolve directionally along anagenetic pathways? Or are they constrained until the time of speciation? How rapidly does speciation proceed? Is the incremental evolution of a species at all

relevant to the pattern of macroevolution of its clade? These questions lie at the heart of studies concerning the tempo and mode of evolution, and *Evolutionary Patterns* is the latest publication to address these issues. Although the title promises a description of rates and patterns of evolution inferred from the fossil record, the book wisely does not deliver on that promise. Rather, it takes a synthetic approach comprising a diverse array of topics and delivers far more than the usual discussion of punctuated equilibrium versus gradualism, or comparisons of evolutionary rates.

The volume is dedicated to Alan Cheetham, and its tribute lies in the diverse, quantitatively oriented, empirically based approaches taken by most of the chapters. The book is arranged somewhat hierarchically, and builds itself from the nuts and bolts of organismal organization and growth, to the analysis and interpretation of large-scale patterns.

The first section is a rather eclectic collection of papers with a common neontological basis: Buss discusses growth patterns of hydractinoid colonies; McShea attempts to construct a hierarchical framework for changes in the number of components and modularity at various levels of organismal complexity; and Okamura *et al.* present a possibly classic study in biological fluid mechanics. On their own, none of these papers addresses tempo and mode over geological

time, but each one provides hypotheses for testing them. Okamura *et al.*'s contribution is particularly valuable, because it uses morphologies that are well represented in the fossil record, and is a direct test of competition for space as a driving agent of trends in bryozoan evolution.

The remaining chapters can be divided into studies dealing with macroevolutionary patterns that are rooted firmly in organismal-level processes and interactions, and those that emerge from such processes or are imposed extrinsically upon the organismal level. For example, Nehm addresses several fundamental questions, such as: are features of morphological evolution similar within and among clades? Do similar developmental processes lead to morphological similarities? And, how does development influence morphological disparity? His study is outstanding, because it combines morphometric description with an independently derived phylogeny. Nehm concludes that, at least for two Neogene gastropods, morphological change during speciation far exceeds variation exhibited by any single lineage during its lifetime. Gould follows with a review of a palaeobiologist's perception of species concepts, species recognition and speciation processes in the fossil record. The treatments here of morphospecies, stasis and punctuated equilibrium are well developed and broadly inclusive. Gould's statement, however, that '...the punctuation pattern exists at high relative frequencies, and that few gradualistic and anagenetic continua have been documented...' is based largely on compilations that are of necessity cursory (e.g. [1]), comprising studies that generally fail to appreciate the difficulties inherent in evolutionary pattern recognition. Increased confidence in such compilations depends upon the continued development of methods for analysing fossil and morphological distributions. Hayek and Bura's chapter is an excellent step in this direction, presenting a new approach for calculating confidence intervals for stratigraphic occurrences. They make the key observation that the derivation of confidence intervals should incorporate sampling beyond the first and last observed occurrences of a taxon, because absences can have multiple

causes. This is the most utilitarian chapter, and an interesting follow-up would be the use of appropriate simulations to test its effectiveness and make comparisons to others (e.g. [2–4]).

The hierarchical arrangement of *Evolutionary Pattern* continues with a consideration of processes that might operate above the species level. Foote takes up the challenge of deconvoluting biological turnover into rates of origination and extinction. This chapter is a wonderful abstraction of organismal-level happenings and requires little biological information for exploration of the underlying model. However, readers should be aware of the abstraction before interpreting the model. For example, rates of change in diversity do not necessarily represent rates of evolution. This is done only by the origination rate, and then only at the species level, because higher taxa do not evolve. Foote's observation of the symmetry and time reversibility of his equations is a point worth noting. Translating this empirically, one can ask whether the processes that cause extinction within a taxon are likely to be the same ones that promote origination.

Perhaps this challenge is taken up by most of the remaining chapters. Pandolfi *et al.* and Budd and Johnson examine diversity changes in late Cenozoic corals, focusing on rapid extinction and biotic turnover respectively. These are both excellent chapters and lead to questions that bridge evolutionary biology and palaeoecology; do ecological relationships at lower taxonomic levels scale up taxonomically and temporally? Do ultimate causes of extinction [5] operate most effectively at the level of geographical range, whilst proximal causes interact most strongly with rarity? When and why are rare species never widespread geographically (geographically widespread does not imply numerically abundant)?

The last chapters take the final hierarchical steps. Håkansson and Thomsen examine the macroevolutionary trend toward asexual reproduction in cheilostome bryozoans. McKinney *et al.* take an almost meta-analytic approach to the relationship between macroevolution and macroecology, emphasizing the importance of abundance data, and the danger of reliance on species lists in studies at these highest of Phanerozoic