

REPLACEMENT EVENTS AMONG TETRAPODS: EXPANSION OR COMPETITION?

BENTON*, Michael J., Dept. of Geology, University of Bristol, Bristol, BS8 1RJ, U.K.; STORRS, Glenn W., Dept. of Geology, University of Bristol, Bristol, BS8 1RJ, U.K.

Many macroevolutionary patterns have been explained in the past on the basis of expectations and prejudice rather than quantitative testing. Large-scale ecological replacements have been a prime example, where expectations of progress and competitive advantage have coloured interpretations. Equally, no doubt, others have looked for, and found, evidence for entirely noncompetitive processes to explain major replacements (reviewed, Benton 1987).

A partially quantitative approach is presented, based on a study of tetrapod families, marine and nonmarine, through the interval from Devonian to the present day. New data bases of the history of tetrapod diversification have the advantage over older attempts of (1) a fully cladistic phylogeny, and hence monophyletic families; (2) a detailed overview of stratigraphy and improved range data; (3) palaeobiogeographic control; and, (4) definition of ecological categories in terms of mean body size categories, diet, main habitat types (fully marine; partially marine/ coastal; freshwater, aquatic/ terrestrial; lowland; upland; arboreal, aerial).

The bulk of the diversification of tetrapods is correlated with increases in the ranges both of habitats occupied and of diets (Benton 1990). However, tetrapod families came and went, and a large proportion of the diversification could have been driven by competition and progressive replacement of archaic families by competitively superior ones in ecological relays. In order to test this, the ranges of all tetrapod families were plotted against time and sorted into a variety of habitat, dietary, and palaeogeographic categories.

The results do not support a generalised view of competitive ecological relays. The majority of families appear to have arisen within new cells of the matrix, and did not apparently overlap in time with, or follow closely after, any potential competitors. This would be the minimum requirement for a postulate of competition. Only some 5% of cases could be open to a competitive explanation, and these include certain well known examples, such as multituberculates/ rodents, plesiadapiforms/ rodents, ichthyosaurs/ mosasaurs. The present study has narrowed the odds against large-scale competition as a significant motor of large-scale biotic replacements. Most new taxa of tetrapods appear to have arisen in response to the availability of empty adaptive space.

Environmental shifts may also be detected during the course of tetrapod evolution, with expansions offshore to ever more fully aquatic lifestyles among marine tetrapods (because they all arose from terrestrial ancestors!), and with expansions from lowland tropical zones to temperate belts, uplands, and marginal lifestyles (burrowing, climbing, flying) among nonmarine tetrapods.

Benton, M. J. 1987. Progress and competition in macroevolution. *Biological Reviews* 62: 305-338.

----- 1990. The causes of the diversification of life. *Systematics Association Special Volume* 42: 409-430.