

## Early introduction of major morphological innovations

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The origin of major morphological innovations poses a major problem for macroevolutionary biologists. Such innovations appear to be overwhelmingly concentrated early in the history of major clades: subsequent evolution involves elaboration and variation on these early themes. Although confirmation of this pattern requires morphometric techniques only now being developed, it seems too firmly established to be an illusion. A variety of explanations have been advanced for the extensive morphologic innovation during the Cambrian radiation, including the ecospace hypothesis which relies on more extensive ecospace, and a variety of genomic hypotheses ranging from a more rapid rate of real or apparent mutation, to novel types of genetic change, or novel effects within a more plastic developmental system. Recently some theorists have suggested the inherent properties of complex dynamic systems are a sufficient explanation. However, most discussions have emphasized the ecosystem and genomic hypotheses. These have proven difficult to disentangle because no unique predictions about expected patterns have been proposed, but I suggest here phylogenetic tests which do discriminate between these possibilities. There is a curious distinction between the empty ecospace hypothesis and one variant of the developmental hypothesis: Under the former, extensive morphologic innovation should be possible whenever extensive ecospace becomes available. The constraints on innovation are atemporal and extrinsic. In contrast, under the second scenario the formation of developmental systems itself constrains further innovation. Thus the concentration of innovation early in the history of clades may stem from irreversible changes associated with the origin, rather than subsequent modification, of development.

**Key words:** innovation, metazoan radiation, evolutionary theory, evolutionary radiations.

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