

## DEVELOPMENTAL AND NON-DEVELOPMENTAL MORPHOSPACES IN EVOLUTIONARY PALEOBIOLOGY

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Morphospace studies are rich in pattern and process. Techniques for adequate description and mapping of morphologies have been increasingly refined and applied, the same being true of metrics for relevant parameters (like disparity). However, the testing of process hypotheses for specific patterns of morphospace occupation in time and space is less refined and demands more intensive scrutiny. The polarization of ecological and developmental explanations entails a need to properly tease apart their respective contributions. There are different ways to go about this problem. Here I describe one approach: the isolation of development as a target for testing via the construction of developmental morphospaces.

Comparison of differently constructed morphospaces (one reflecting development directly, the other indirectly) provides a way of consistently studying the impact of development in constraining or facilitating changes in diversity. Congruence of range and/or location on "developmental" and "non-developmental" morphospaces, when properly interpreted to account for possible stochastic effects, is powerful evidence for a controlling influence of ontogeny. Appropriate choices involve three kinds of contrasts (with qualifications): theoretical (generative) vs. empirical (descriptive), abnormal (teratological) vs. normal, and juvenile vs. adult morphospaces. Theoretical morphospaces encapsulate logically simple principles of form generation, mimicking the potential simplicity of epigenetic processes. Teratological morphospaces are based on unsuccessful experiments in evolution, but any regularities encountered must reflect internal constraints and opportunities. Juvenile morphospaces are likely to depict a range of pronounced allometries that can serve as raw material for evolution. I provide an extended example of juvenile vs. adult morphospace comparisons with a case study on the evolutionary history of the echinoid order Spatangoida.

Spatangoids constitute a monophyletic group that appears in the early Cretaceous (145 m.y. ago) and ranges to the Recent, experiencing substantial losses at both the end-Cretaceous and late Eocene extinction events, but rebounding to attain ever higher diversities. The broad pathways of morphospace occupation through geologic time for adults in the order are contrasted with the distribution of juveniles in a developmental morphospace constructed from post-metamorphic specimens. To ensure comparability, the same homologous landmarks are used for adults and juveniles. The expectation that constraints imposed by development should channel directions of adult evolution is tested: although early juveniles are more generalized (supporting Von Baer's second law, which states that more specific characters are developed from more general ones), the total distribution of juvenile morphologies matches several directions in adult morphospace. The general utility of the construction of explicitly developmental morphospaces as a complement to other approaches is underscored.