

## But which morphospace to choose?

### Theoretical Morphology

by G.R. McGhee, Jr

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All palaeontologists, and most biologists, recognize Raup's<sup>1</sup> much-reproduced diagram of diverse molluscan shells plotted along three orthogonal axes. The axes represented the parameters of an isometric helicospiral, and the important observation was that some shapes of helicospiral have never evolved. This book defines theoretical morphology narrowly as a three-stage procedure based on Raup's approach: (1) a minimal number of parameters is used to generate a spectrum of biological shapes (not necessarily in a way related to their biological morphogenesis); (2) the parameter values that would generate real species are plotted in a 'theoretical morphospace' of all shapes allowed by the model; (3) this distribution is explained in terms of functional morphology or constraints. McGhee's definition excludes studies in which multivariate analyses of real shapes generate an 'empirical morphospace'. He also ignores many optimality models of morphology, even though such studies also postulate a range of theoretical forms and map species relative to the predicted optimum.

McGhee's book is a thorough survey of the numerous studies that have emulated Raup's approach – shells figure prominently, but far from exclusively. Each study is clearly and fairly described (with many illustrations, copied from the original publications). Although it is excellent to see these diverse studies linked into a logical framework, I found McGhee's opinions on the published work often rather uncritical, and the book attempts no advance in theory or methodology. The later chapters survey simulations of morphogenesis, but are biased strongly towards phenomenological models of gross shape, dealing only superficially with mechanistic models of how cell behaviour generates form.

McGhee is evangelical in his advocacy that Raup's approach should be followed through all three stages. However, many studies have not completed this procedure or have diverged from it, and it has seldom caught on with non-palaeontologists. The labour required to measure novel parameters on many species is one problem, and such measurements might feel unsatisfactory if the model fits schematically only.

Another potential problem is how to identify gaps within a morphospace statistically.

What is the null hypothesis? A uniform distribution of realized forms is not what we expect from a clade branching randomly in the morphospace<sup>2</sup>. In some morphospaces, hundreds of species have been plotted, but no allowance has been made for their phylogenetic non-independence.

A more fundamental problem is that the size of a gap, or the size of a shift in distribution, depends on the parameters chosen. For instance, a logarithmic transformation will disperse the scatter near what was the origin. No criteria specify the best transformation, and we can recombine parameters to generate an infinite number of new parameter sets. In this selection of axes I sense some loose argument behind criticisms of Raup's axes as being non-independent and non-orthogonal. To take an analogous example, a morphospace of triangles might be three axes describing the length of each side, or three axes describing two angles and the area. Fixing the length of two sides leaves the length of the third unconstrained, so these three axes are independent. However, the area of the triangle affects all three lengths, so we would view the lengths as non-orthogonal axes if area were seen as a more fundamental sort of variation. The problem is 'What is fundamental?'

Several authors have sought axes that parameterize plausible mechanisms for morphogenesis. One example, not included in the book, is the orb web of a spider<sup>3</sup>, where the mechanism of morphogenesis is observable directly (e.g. the capture spiral is spaced using a leg as a calliper). Clearly, parameters can be chosen that represent the spider's construction rules more directly than parameters based on artificial methods of generation. McGhee seems

neutral over whether such morphospaces are superior.

Another possibility would be to use features affecting performance as parameters; for instance, for a web – its silk requirements or symmetry. The most common procedure is to make axes represent aspects of shape that vary most between taxa. This is not theoretical morphology, but standard multivariate morphometrics. McGhee seems happy to see the dimensions of a theoretical morphospace reduced because species show little variation along certain axes; nevertheless, he strongly opposes empirical morphospaces, mainly because the axes change when new points are added. I see other more serious problems with multivariate morphometrics but, nevertheless, thoughtful interpretation of empirically derived axes can yield meaningful insights.

McGhee hopes that one day a theoretical morphospace encompassing all arthropods will answer whether morphological diversity has decreased since the Cambrian. I suspect that any such morphospace would be too arbitrary, schematic and multidimensional to be useful, and that theoretical morphology is best restricted to elegant models of simpler-shaped organisms.

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- 2 Kauffman, S.A. (1993) *The Origins of Order*, Oxford University Press
- 3 Krink, T. and Vollrath, F. (1997) *J. Theor. Biol.* 185, 321–331

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