BOOKS: MORPHOLOGY

Spatial in Formation

Jon R. Stone

Shells of animals in the molluscan classes gastropoda (including snails, slugs, and sea hares) and pelecypoda (including cockles, clams, mussels, oysters, and scallops) have traditionally been considered homologous. According to this view, the single shell of snails might have evolved into one of the two valves characteristic of cockles—or vice versa. Such transformations can be quantitatively analyzed by the formulation of a theoretical model of organic growth or form, and the use of such a model to construct a mathematical space (a "theoretical morphospace") in which to evaluate morphological evolution. This two-component method of analysis constitutes the discipline that George McGhee examines in *Theoretical Morphology*.

Theoretical Morphology
The Concept and Its Applications
by George R. McGhee Jr.
Columbia University Press, New York, 1999. 328 pp. $60, £48. ISBN 0-231-10666-1. Paper, $26.50, £13.95. ISBN 0-231-10667-X.

Although it includes concepts that can be traced back to antiquity, modern theoretical morphology originated with David Raup's research in the 1960s. Raup formulated a four-parameter model that enabled computer-graphics simulations of univalved coiled shells (*1*). Considering only shells with circular apertures, Raup constructed a mathematical space with axes delimited by the remaining three parameters. He identified regions within this space that represented forms of shells that are, were, or never have been occupied by organisms. Raup noted that the distribution of forms representing actual shells is nonrandom, and he considered possible explanations for the distribution of realized and unobserved morphologies.

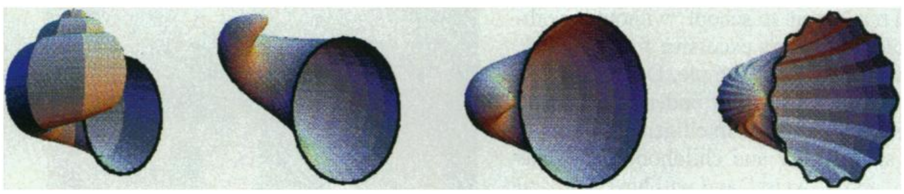
McGhee suggests that Raup's three-phase approach characterizes the use of theoretical morphospaces, but he acknowledges that the explanatory phase is sometimes omitted. This last phase often consists of scenarios in which adaptation is subject to functional constraint. For example, McGhee uses a theoretical morphospace of bivalved shells to show that the approximately spherical shells of biconvex brachiopods maximize the ratio of internal volume to surface area (V/A) while still maintaining articulation of the two valves. He concludes that such forms enhance the efficiency of filter-feeding by the internal lophophore. He also applies his scenario to other brachiopods, in particular to the nonbiconvex forms having flattened or concave valves. Because these occupy regions of the morphospace remote from the shapes that maximize V/A, McGhee suggests that extinct nonbiconvex forms used a feeding system very different from that found in extant brachiopods.

This plausible extrapolation demonstrates the powerful insight that can come from analyses of theoretical morphology. But it also reveals a serious shortcoming of much research in the field. Functional explanations for the observed distributions of actual organisms in theoretical morphospaces could be complemented or superseded by considerations of developmental or phylogenetic constraints. These constraints, however, have rarely been discussed in theoretical morphological analyses; consequently, they receive little attention in the book.

Since Raup's revolutionary work, shells have been the subjects of the majority of theoretical morphology studies. Thus McGhee gives ample attention to morphospaces for univalved and bivalved shells and to the accretionary growth systems that produce them. But he also discusses branching growth systems, which produce such disparate organic forms as bryozoans and trees. And his survey of discrete growth systems, in which parts are added episodically, introduces an extensive set of theoretical morphospaces including foraminiferal tests (shells), silicoflagellate skeletons, stromatoporoid colonies, and shark scales. McGhee notes that creating a theoretical morphospace for arthropods, with their "segments and sections" skeletons and molting, remains a monumental challenge.

Sometimes missing entities can induce interesting insights. As disproving the existence of the ether enlightened physicists' understanding of electromagnetic radiation, nonexistent morphologies might modify biologists' interpretations of morphological evolution. Voids in theoretical morphospace can result from functional, developmental, or phylogenetic constraints (forms that are nonviable or have been diverted or precluded from evolving). Voids also can represent the result of structural constraint (forms prohibited by geometry or properties of materials) or temporal constraint (forms that never evolved because lineages that would have led to the production of such morphologies became extinct or have existed for insufficient periods of time). Analyses of occupation and emptiness of theoretical morphospace through time can quantify historical patterns of morphological disparity and their differences from taxonomic diversity (during evolutionary radiations or mass extinctions, for example), and are allotted an entire chapter in the book.

Although minor aspects of the book might wrinkle a few foreheads, McGhee lucidly conveys the main concepts and applications of theoretical morphology. He also dispels the misconception that the construction of theoretical morphospaces requires complicated mathematics and sophisticated computer graphics. Most of the book's many illustrations are reproduced from the primary literature, and the variation in their styles reflects the charming diversity of this discipline.



From snail to cockle. Using forms generated by a simple model of snail shell morphology, the coiled spiral of a snail can be transformed to a cockle valve by reducing the number of whorls, decreasing the vertical translation of the generating curve, and corrugating the resulting planispiral form.

Theoretical Morphology surveys an under-utilized approach to understanding evolution that has enormous potential. McGhee has written specifically for graduate students and morphologists hunting for research topics, and throughout the book he indicates promising areas (and volumes) for future investigation. Readers desiring more "spatial information" of the sort discussed here are encouraged to peruse this extensive and entertaining encapsulation of the discipline.

The author is at the Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794–5245, USA. E-mail: stone@life.bio.sunysb.edu

References

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