

# Functional morphospace analysis of molluscan shells

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Morphospace is a powerful tool for large-scale comparison of morphology across a number of species. Morphospaces are geometric spaces in which a particular organic form can be plotted with reference axes chosen to represent morphological parameters. Abstraction of essential morphological traits allows us to summarize complex morphological variation into a few dimensional morphospace. If a functional performance can be assessed for a set of organic shapes accommodated in the morphospace, the relationship between the functional performance and morphological traits can be visualized as a surface on the morphospace which mimics an adaptive landscape. The functional morphospace allows us to predict which shape is common or rare from the view point of functional morphology. Such a prediction can be readily tested for paleontologists by referring actual fossil records. The present talk introduces a couple of case studies on evolutionary morphology of fossil and extant molluscan shells using morphospaces based on theoretical morphologic models.

In the first topic on bivalve shell morphology, geometric constraints of bivalve shell form derived from space conflict between umbones of both valves are discussed. A functional morphospace analysis of bivalve shells using a theoretical morphologic model revealed that the space conflict between umbones restricts morphological diversity of bivalve shell of each group depending on hinge morphology. A characteristic type of ligament evolved in a heteroconch bivalve in the late Mesozoic may have allowed the clams to develop an adaptive shell shape for burrowing through their macroevolution.

The second topic on shell form of gastropod snails focuses on a functional trade-off between postural stability and efficiency of shell construction. The result of a functional morphospace analysis of gastropod shells revealed that mechanical stability of a snail while creeping and the amount of shell material necessary for shell construction both depend on shell shape and are hardly compatible with each other. The aperture of snail is often inclined to the coiling axis particularly in the species living in the environment with less buoyancy and calcium carbonate. The results

suggest that the aperture inclination downward relaxes the functional trade-off between postural stability and efficiency of shell construction.

The subject of the third topic on cephalopods focuses on the functional properties for their nektonic mode of life. The functional morphospaces constructed using a theoretical model representing planispiral cephalopod shells clearly shows a functional trade-off between hydrostatic and hydrodynamic efficiencies: a shell form which minimizes a form drag acting on the shell while swimming readily maximizes the density of the totally produced shell. The results of morphometric analyses indicates the followings. Nautilids tend to be optimized for hydrostatics in comparison with other groups. Some ammonoid groups seem to be optimized for hydrodynamic efficiency. Tarphycerid cephalopods tend to have high scores of postural stability. The results suggest that the macroevolutionary pattern is clearly different among cephalopod phylogenies.

Morphospaces constructed through geometric morphometric and multivariate analyses appear to be potentially useful for a functional morphospace analysis. Evolutionary morphology based on morphospace analysis can be facilitated by big-data analyses using morphological databases. Combining the conventional functional morphospace analyses and their potentially relevant techniques is an interesting subject of future research.

