A functional-morphospace analysis of allometrically growing ammonoids

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Theoretical morphology allows us to generalize the relationship between geometries and functional properties of biological form by constructing a functional landscape on a theoretical morphospace. Functional-morphospace analyses have been widely performed particularly for planispiral ammonoids using Raup’s theoretical morphologic model. However, such studies have largely omitted any exploration of the potential effects of allometry because Raup’s model is designed to simulate isometric growth. Here I propose a novel theoretical morphologic model which mimics allometric shell growth commonly observed in ammonoids to represent ontogenetic trajectories of morphological traits as well as shell shape itself. I tried to generalize the relationship between the shape change trajectories and hydrostatic and hydrodynamic properties using the newly introduced model.
The present model approximates shell shape by a planispiral conical tube with elliptic cross-section just as Raup’s model. However, the parameters are defined referring to a hypothetical spiral passing through the center of the elliptic generating curve unlike Raup’s parameters. They are defined using four dimensions, i.e., the lengths of a pair of radius vectors of the spiral parted by p (r_{q}, $r_{\mathrm{q-p}}$), and radii of the elliptic generating curve in the radial and bilateral directions (h_{q}, b_{q}), that are functions of the revolving angle of the generating curve around coiling axis. The present model is based on the allometric relations of $r_{\mathrm{q-p}}$, h_{q}, and b_{q} to r_{q}, and is defined by a total of six allometric coefficients (two for each allometry): degree of whorl involution, relative whorl height, relative whorl breadth, and their scaling exponents. A biometric analysis using more than 100 ammonoid species shows that ontogenetic change in shell shape can fairly be approximated by the present allometric model in most species examined.
A functional morphospace analysis was performed using the present allometric model. A time series of functional landscapes was constructed on a morphospace with reference axes representing the allometric coefficients. Hydrostatic inefficiency of shell shape was assessed by the specific surface area of the totally produced shell. Hydrodynamic inefficiency of shell shape at high Reynolds number was estimated by the projected area of the shell in the direction of movement per unit volume. Hydrodynamic inefficiency of shell shape at low Reynolds number was evaluated by the surface area of the exposed shell portion per unit volume. The results of the analyses revealed the followings: 1) Hydrostatic efficiency highly depends on allometry of whorl involution (or whorl expansion) rather than on allometry of whorl cross-sectional shape. 2) A positive allometry of whorl involution produces hydrostatically inefficient shell shape in a large individual. 3) Allometry of whorl cross-sectional shape dominantly influences hydrodynamic efficiency either at high or low Reynolds number. 4) When the whorl is depressed, a positive allometry of whorl height seems to compromise the three functional properties in a large individual, while a negative allometry of whorl height tends to minimize both hydrostatic and hydrodynamic efficiencies. The results suggest that a negative allometry of umbilical width commonly observed in many ammonoid lineages is advantageous for nektonic or nekton-benthic mode of life.

Keywords: theoretical morphology, allometry, functional-morphospace analysis

