Constructional linkages among morphological characters in ammonoids

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Since Raup's (1967) pioneering work, large collections of morphological data have been used to explore functional morphology, macroevolutionary trend, and/or disparity of normally coiled ammonoids. However, previous analyses were based on data sets measured in adult stages and did not deal with ontogenetic change of shell shape, although allometry is common in ammonoids. Ontogenetic and morphogenetic aspects have been incorporated tenuously in terms of the models that simply specify the manner of shell coiling and aperture shape.

In the present study, a new theoretical morphologic model is proposed for the analysis of growth, form and evolutionary history of ammonoid shells. In this model, the shape of a radial cross section through the shell is simulated by 'piggybacking' of successive whorls. The 'piggyback whorls model' is designed to simulate allometric growth, and is based on the geometric balance between perimeter and area of the cross-sectioned whorl. The balance determines degree of compression and involution of whorls, and none of the parameters used in this model directly defines the shape of the aperture and the manner of shell coiling. Each model is defined in terms of the enlarging rate of the perimeter and the proportion of the dorsal wall to the whorl periphery. Allometric coefficients on these growth parameters determine how compressed and evolute shells are formed.

Theoretical forms generated by using the piggyback whorls model do not fully occupy the theoretical morphospace derived from conventional Raup's model. The occupation patterns of morphospace were analyzed in more than 100 Devonian to Cretaceous ammonoid species to verify the appropriation of the model. The present model successfully reproduced some correlations among purely geometric variables that were observed in our biometric analyses and partly have been previously reported. This model yields a hypothesis of 'constructional linkages' between aperture shape and coiling manner that might provide a functional coupling between hydrostatic and hydrodynamic characters. These linkages can be regarded as adaptive developmental constraints in ammonoid evolution. The model may partly explain Buckman's Law of Covariation between rib features and shell shapes, i.e., strongly ornamented ammonoids tend to have an evolute conch and circular whorls.