

## **Piggyback whorls: A new theoretical morphologic model reveals constructional linkages among morphological characters in ammonoids**

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*Acta Palaeontologica Polonica* 53 (1), 2008: 113-128 doi:<http://dx.doi.org/10.4202/app.2008.0108>

A new theoretical morphological model is proposed for the analysis of growth, form and morphospace 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 defined in terms of the enlarging rate of the perimeter and the proportion of the dorsal wall to the whorl periphery, if an isometric relationship is assumed between perimeter and area of the cross-sectioned whorl. Allometric coefficients on these growth parameters determine how compressed and evolute shells are formed. The present model successfully reproduced some correlations among purely geometric variables that have been reported in previous works and were also observed in our biometric analyses. This model yields a hypothesis of 'constructional linkages' between aperture shape and coiling geometry that might provide a functional coupling between hydrostatic and hydrodynamic characters. The model may partly explain Buckman's Law of Covariation between rib features and shell shapes.

**Key words:** Key words: Theoretical morphology, ammonoids, cross-sectional shape, morphospace, constructional linkage, morphological diversity.

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