Detecting consistent morphological shifts across biogeographic boundaries in the fossil record

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Introduction
The formation of the Cretaceous Western Interior Seaway provides a natural experiment to test faunal response to rapid environmental change and invasion. We use this system to ask:

Is range expansion into the same environment associated with consistent morphological shifts?

Figure 1. Biogeographic provinces of the Western Interior Seaway as hypothesized by Kaufman (1994).

Framework
We focus on comparing the morphologies of congeneric species for genera that span the boundary between the "Southern Interior" and "Gulf and Atlantic Coast" subprovinces. (Fig. 1)

We used a dataset of Albion and Conacarian ammonite occurrences from the primary literature and the PaleoDB database to identify genera with both "in" and "out" species for further analyses. (Fig. 2)

Figure 2. Map of Albion and Conacarian North American ammonite occurrences in dataset. Color designates genera and solid points show occurrences for genera included in the remainder of this study.

Ammonite morphospace
Ammonite morphology, as captured through features such as aperture shape, is thought to broadly reflect mode of life. (Fig. 3)

Figure 3. Range of morphologies found by biogeographic analysis. Corresponding ecologies shown in brackets. (Gall, et al. 1996)

The Morphospace

Conclusions
- PC1 axis primarily captures variation in the degree of compression of the shell. PC2 axis primarily captures variation in the degree of involution (overlap of the whorls with growth) of the shell.
- Genera occupy relatively unique regions of morphospace.
- There is no apparent difference between morphospace occupied by those taxa that are in the seaway versus those that are out (Hotelling's T-squared statistic, p-value = 0.19).

Methods
Using photographs of museum specimens, we collected one aperture outline for each of 42 species (Figs. 4 and 5), representing eight genera that fit the biogeographic criteria for this study. The outlines were quantified using elliptical Fourier analysis (EFA). (Fig. 6) The morphospace was generated using a principal component analysis of coefficients for the first seven harmonics (28 total variables capturing 99% of shape variation) from the EFA.

Figure 4. Anagnostoceras belangeri (USNM 523053) as an example. Orange shows half-outlined aperture.

Figure 5. Outlines of each specimen included in this study colored by genus.

Figure 6. First two EFA harmonics used to quantify shape of A. belangeri aperture.

Morphological response to biogeographic shifts

The Models
We use a series of generalized linear mixed models to predict biogeographic status using aspects of morphospace. This allows for between-genus variation in modeled response, and thus comparisons of "in" and "out" species within each genus.

Conclusions
- Best models include PC2 (degree of involution) and are significant improvements over the null Model 1 (ANOVA, p-value = 0.04).
- Species that are present in the seaway appear to be consistently more invovled than their non-seaway counterparts, suggesting evolutionary response to invasion into novel habitats (e.g. a deepening seaway).

Acknowledgments
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