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?

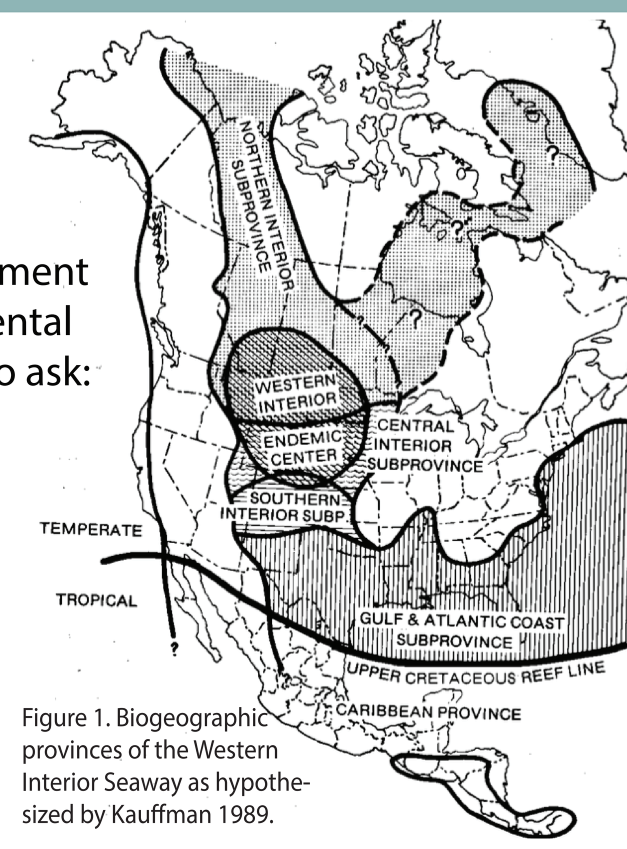


Figure 1. Biogeographic provinces of the Western Interior Seaway as hypothesized by Kauffman 1989.

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 Albian and Cenomanian (113 to 94 million years ago) North American planispiral ammonite occurrences compiled from the primary literature and the Paleobiology Database to identify genera with both "in" and "out" species for further analyses. (Fig. 2)

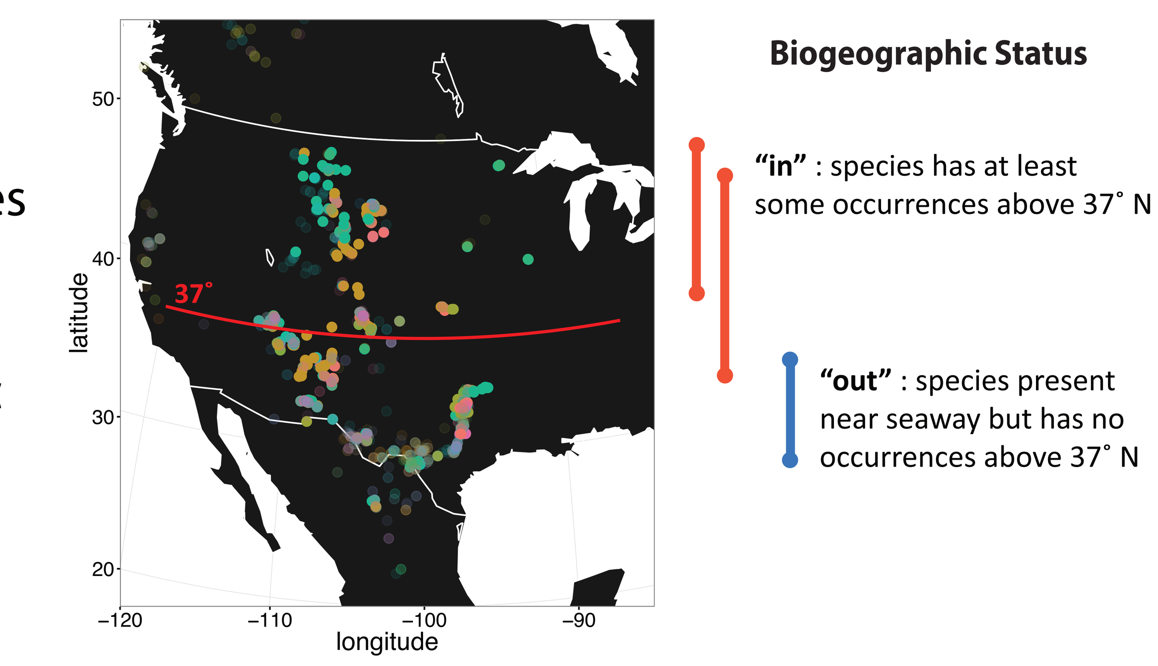


Figure 2. Map of Albian and Cenomanian North American ammonite occurrences in dataset. Colors designate genera and solid points show occurrences for genera included in the remainder of this study.

Ammonite morphospace

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

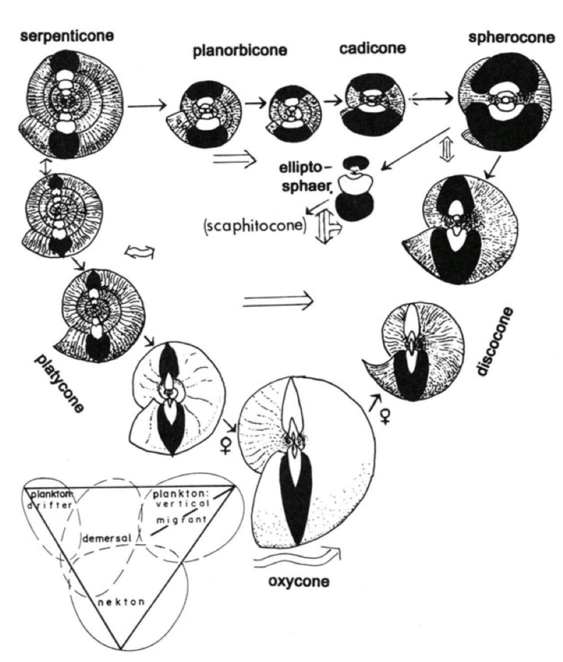
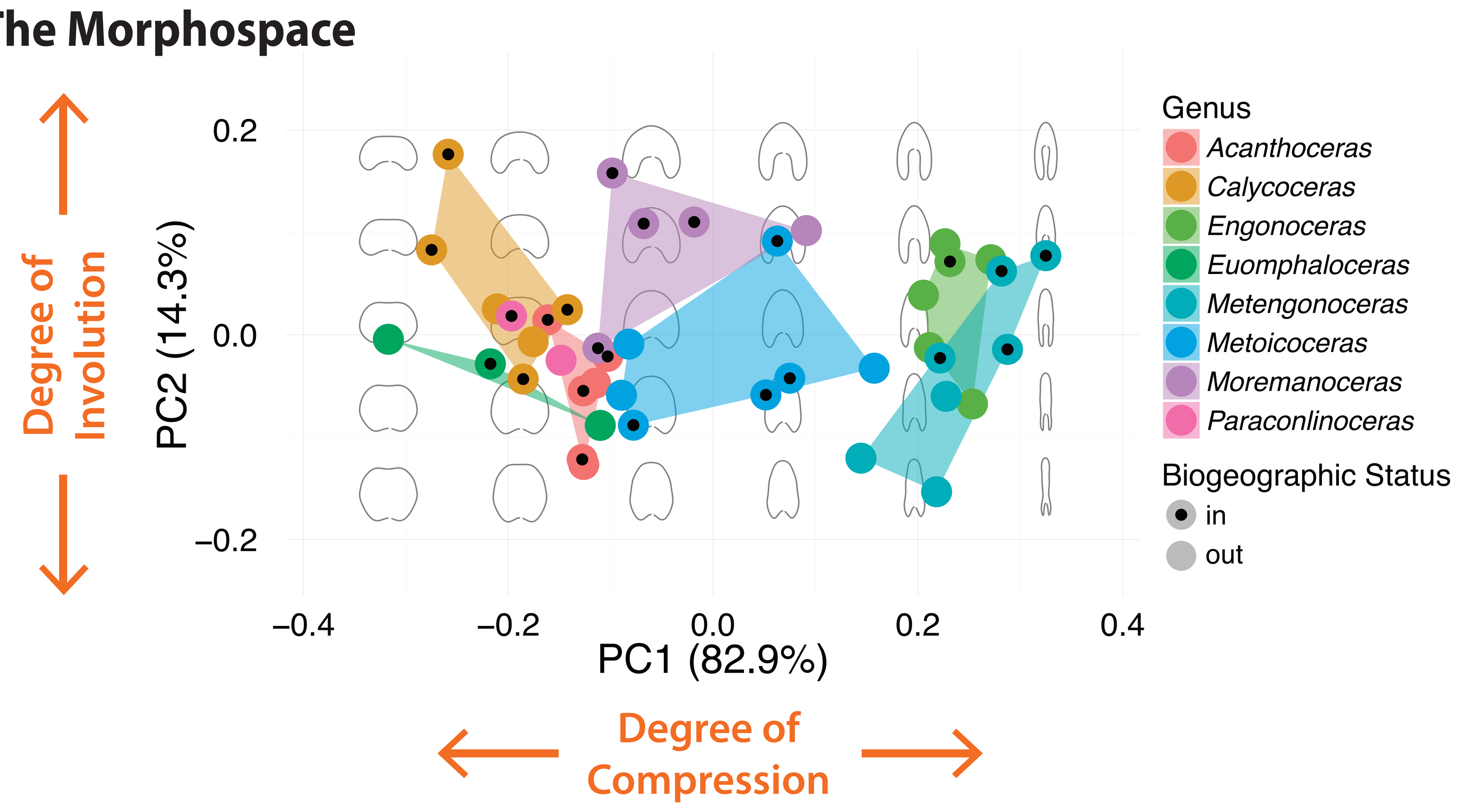


Figure 3. Range of morphologies found in planispiral ammonites. Corresponding ecologies shown in bottom-left triangle. (Westermann 1996)

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 outlineswere 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. *Acanthoceras bellense* (USNM 388098) in apertural view. Orange shows half-outlined aperture.

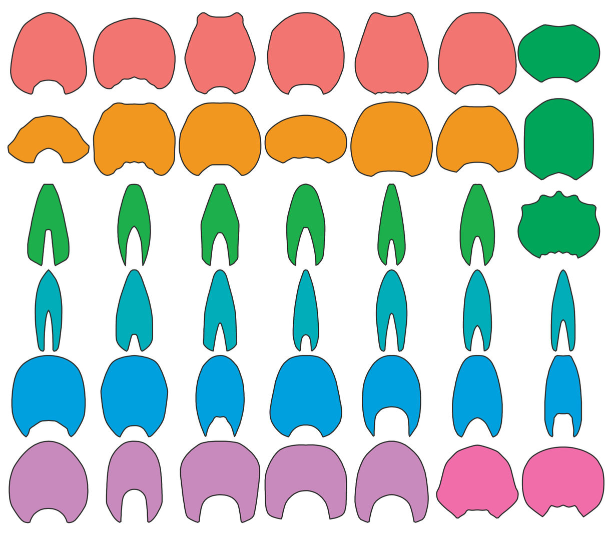


Figure 5. Outlines of each specimen included in this study colored by genus.

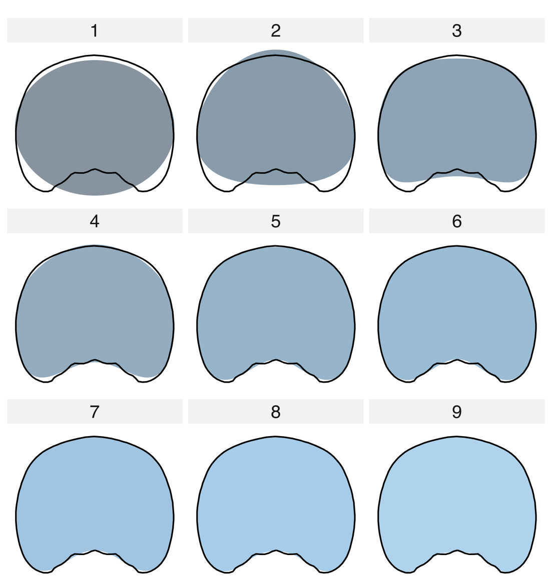


Figure 6. First nine EFA harmonics used to quantify shape of *A. bellense* aperture.

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.

	formula	df	ΔAIC	AIC weight
1. Are we better off without these predictors?	(1|gen)	2	2.03	0.16
2. Is it simply how compressed a species is?	PC1 + (1|gen)	3	2.91	0.10
3. Is it simply how involute a species is?	PC2 + (1|gen)	3	0.00	0.43
4. Is it some combination of the two? (Random intercept)	PC1 + PC2 + (1|gen)	4	0.72	0.30
5. Is it some combination of the two? (Random intercept and slopes)	PC1 + PC2 + (1+PC1+PC2|gen)	9	9.26	0.00

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 involute than their non-seaway counterparts, suggesting evolutionary response to invasion into novel habitats (e.g. a deepening seaway).

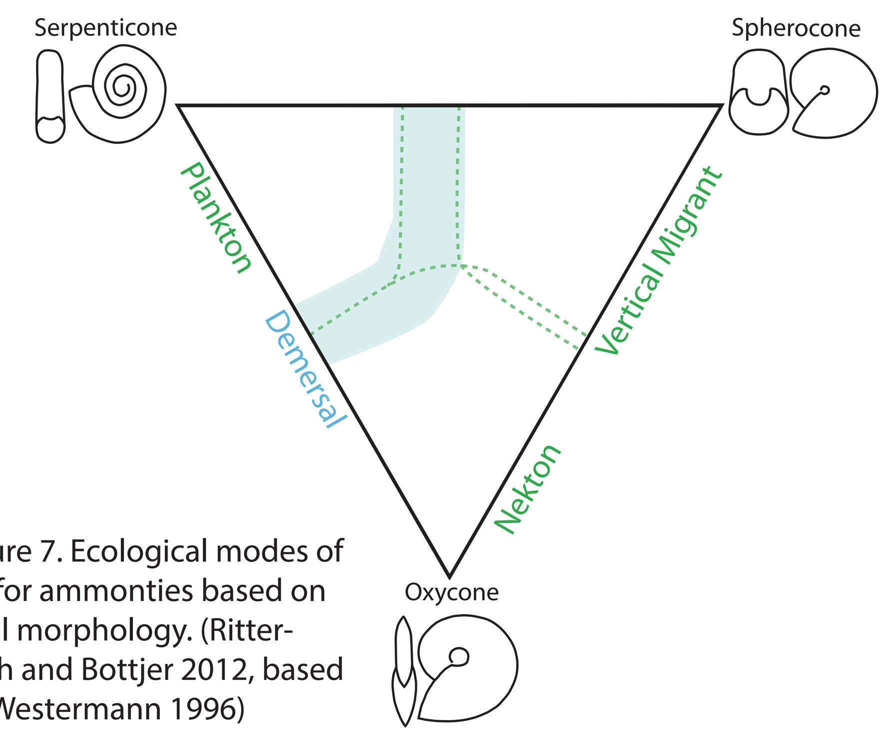
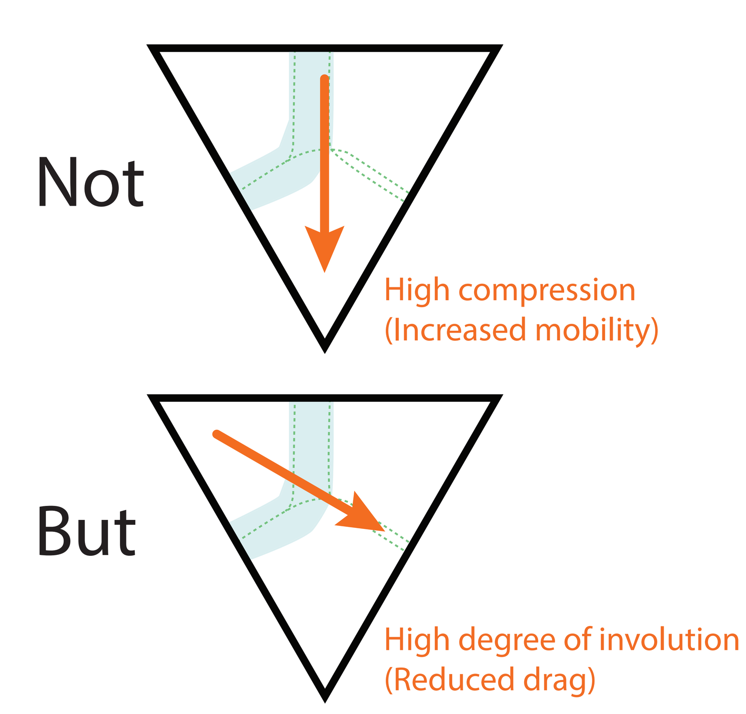


Figure 7. Ecological modes of life for ammonties based on shell morphology. (Ritterbush and Bottjer 2012, based on Westermann 1996)



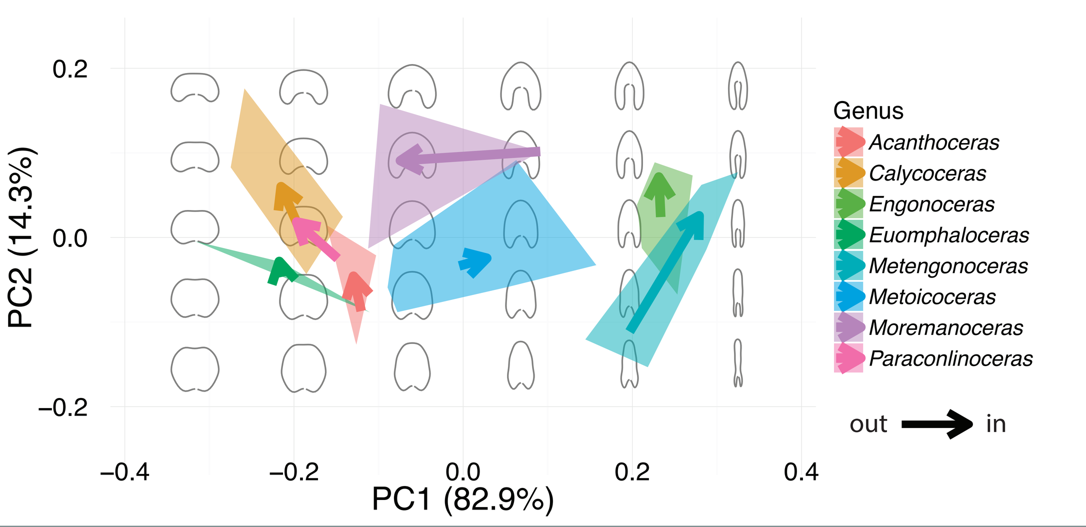


Figure 8. Morphospace of Albian and Cenomanian ammonites included in this study. Arrows point from the morphological centroid of species in the seaway to centroid of species out of the seaway for each genus.

Acknowledgments

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