Building up the biota in novel environments: insights using the fossil record of epeiric seas

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The establishment of biota in epeiric seas provides a unique opportunity to observe long-term assembly and evolution in physically novel and originally vacant environments.

Here, I explore these dynamics using fossil ammonite distributions and body sizes from the Cretaceous Period (145-66 Mya).

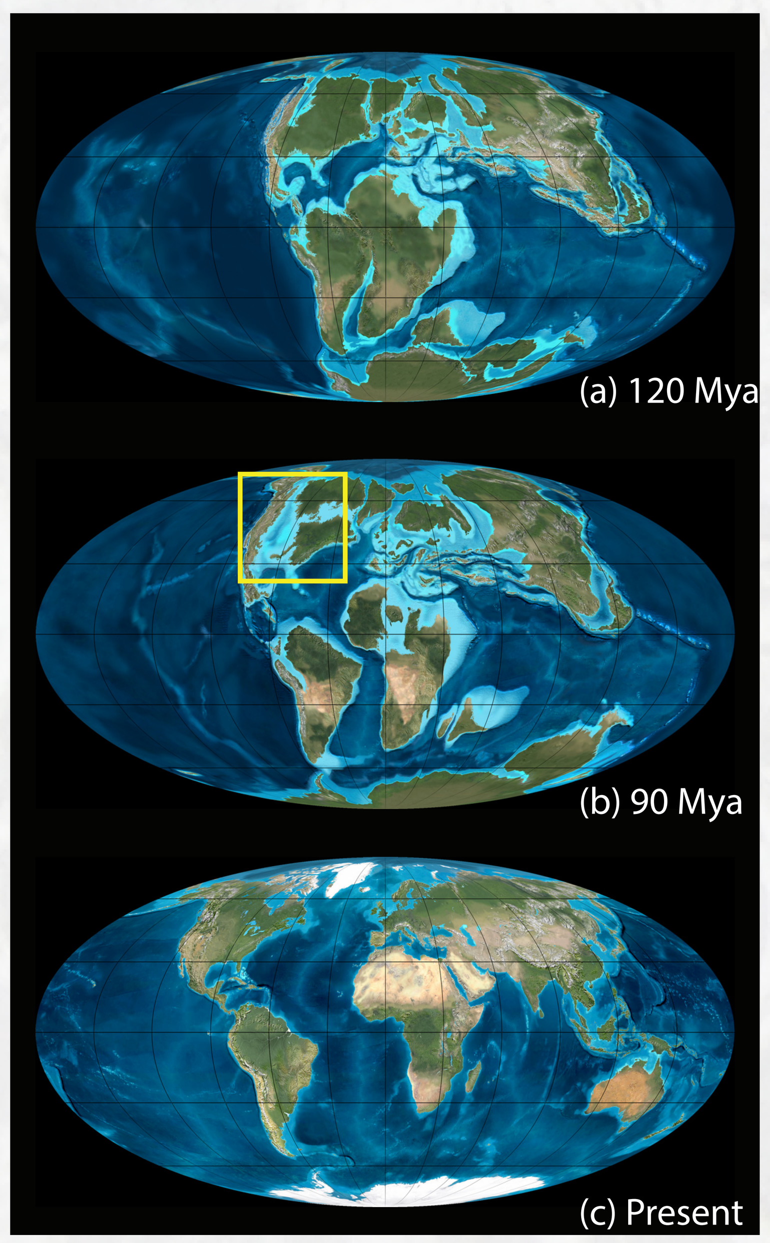


Fig. 1. Paleogeographic maps showing the extent of continental flooding during the (a) Early Cretaceous, 120 Mya, (b) Late Cretaceous, 90 Mya, and (c) present day. Yellow box indicates the Western Interior Seaway. (Ron Blakey, Colorado Plateau Geosystems, Inc.)

What are epeiric seas?

Epeiric seas are:
- Also known as epicontinental seas
- Physically distinct from open ocean environments
- Flooding of continental masses
- Typically associated with eustatic sea level rise
- Frequent throughout the Phanerozoic
- Evident on every continent
- Without a true modern analog

Previous Research

We are only beginning to quantitatively understand what's going on. Epeiric seas have lower origination but also lower extinction rates at mass extinctions. (Miller and Foote 2009) Epeiric seas have greater compositional heterogeneity as a function of area compared with open-ocean environments. (Lagomarcino and Miller 2012) The Western Interior Seaway possessed persistent high endemism regions. (Kauffman 1984) These and a few other studies have focused on faunal characteristics within the sea rather than understanding their establishment.

What are ammonites?

- Phylum: Mollusca
  - Class: Cephalopoda
    - Subclass: Ammonoidea
- Often coiled with complex suture patterns
- Persisted from the Devonian (419 Mya) until the Cretaceous-Paleogene boundary (66 Mya).


Fig. 2. Fossil ammonite specimen from the Cretaceous Western Interior Seaway.

Why use them?

Ammonites:
- Are abundant and globally distributed
- Are diverse: over 2300 genera
- Are fast-evolving: often used for biostratigraphy
- Have discernable ecologies: track environment
- Preserve well

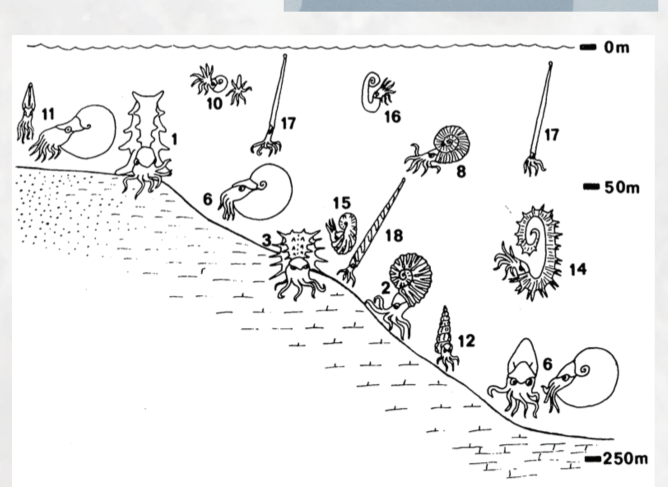


Fig. 3. Hypothesized habitat and depth preferences of ammonite morphotypes from the Western Interior Seaway during the Late Cretaceous Greenhorn Cyclothem. (Batt 1989)

The System

During the Late Cretaceous (100.5-66 Mya), marine flooding onto continents produced widespread shallow seas across Europe, northern Africa, northern South America. The Western Interior Seaway, connecting the Gulf of Mexico to the Arctic Ocean across North America, is one of the better-studied systems of this time, reaching depths of over 2,500 feet. Intermittent oceanic anoxic events (OAE) during this time reduced habitability of deeper ocean environments.

Methods

Species and genera were classified into categories based on the percentage of their total known fossil occurrences found in grid cells designated as shallow seas.

Occurrence data for all Cretaceous ammonites was downloaded from the Paleobiology Database (paleodb.org, latest download Oct. 24, 2012). Species are assumed to temporally range through and genera are considered present in a time period only if one of its constituent species is considered present at that time.

Geographic extent of epeiric seas was determined using a 5 by 5 degree grid system superimposed on maps depicting global paleogeography of the Cretaceous. Grid cells were considered to be epeiric if they were shallow and spatially separated from open oceans by one grid cell (see Miller and Foote 2009).

Size data was collected from the Treatise on Invertebrate Paleontology (Arkell et al. 1957) by a team led by Jonathan Payne at Stanford University. The Treatise features detailed descriptions of exemplar specimens representing every ammonite genus.

Fig. 4. Raw ammonite diversity counts across the Cretaceous based on occurrence data for a) species and b) genera. Red shading represents epeiric diveristy. Gray shading along the x-axis roughly indicates times when epeiric seas were present.

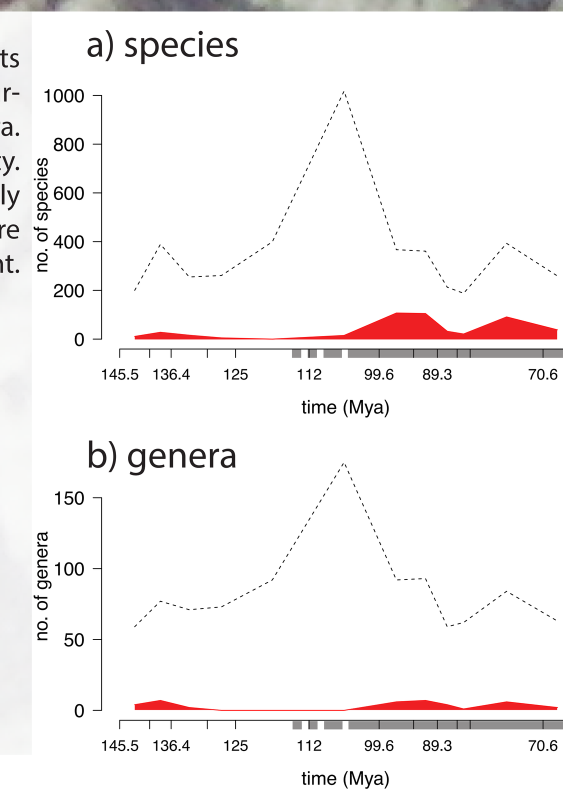


Table of Epeiricness:

	color	% occurrences found in shallow seas
EPEIRIC	red	>90%
SEMI-EPEIRIC	orange	≥10% and ≤90%
NON-EPEIRIC	purple	>0% and <10%
OPEN OCEAN	blue	0%

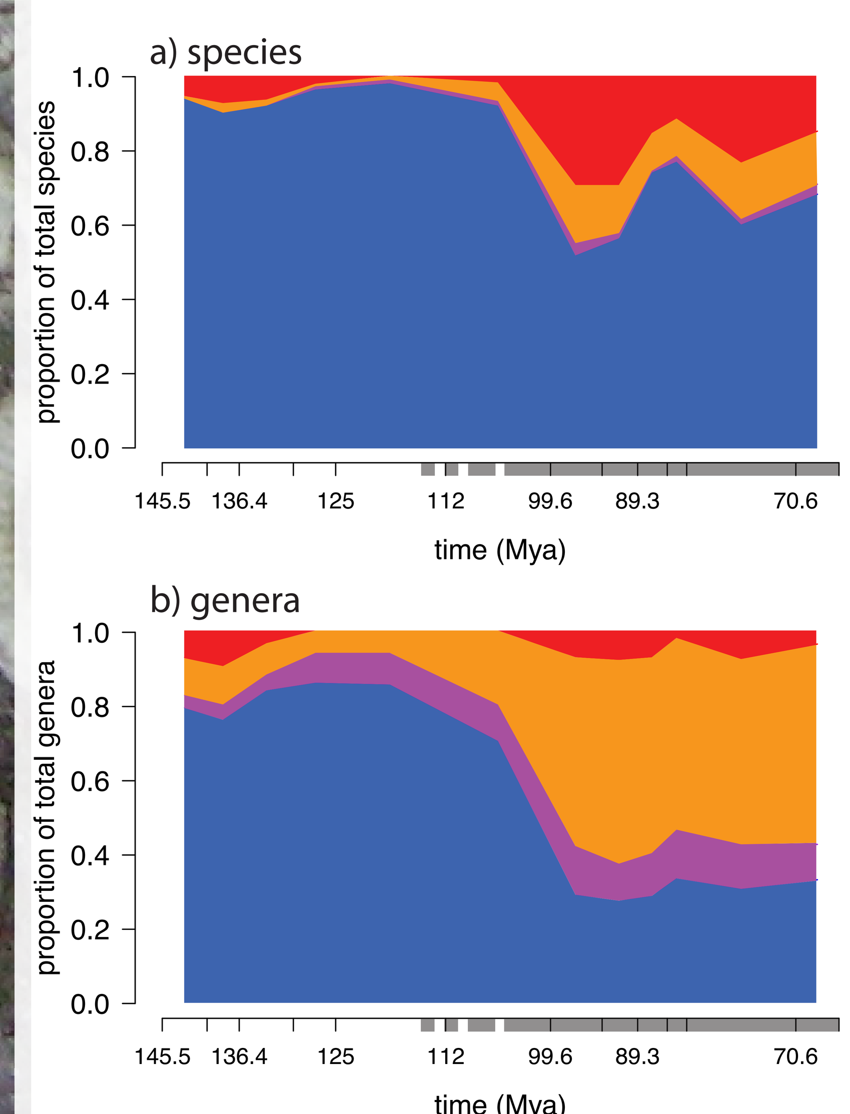
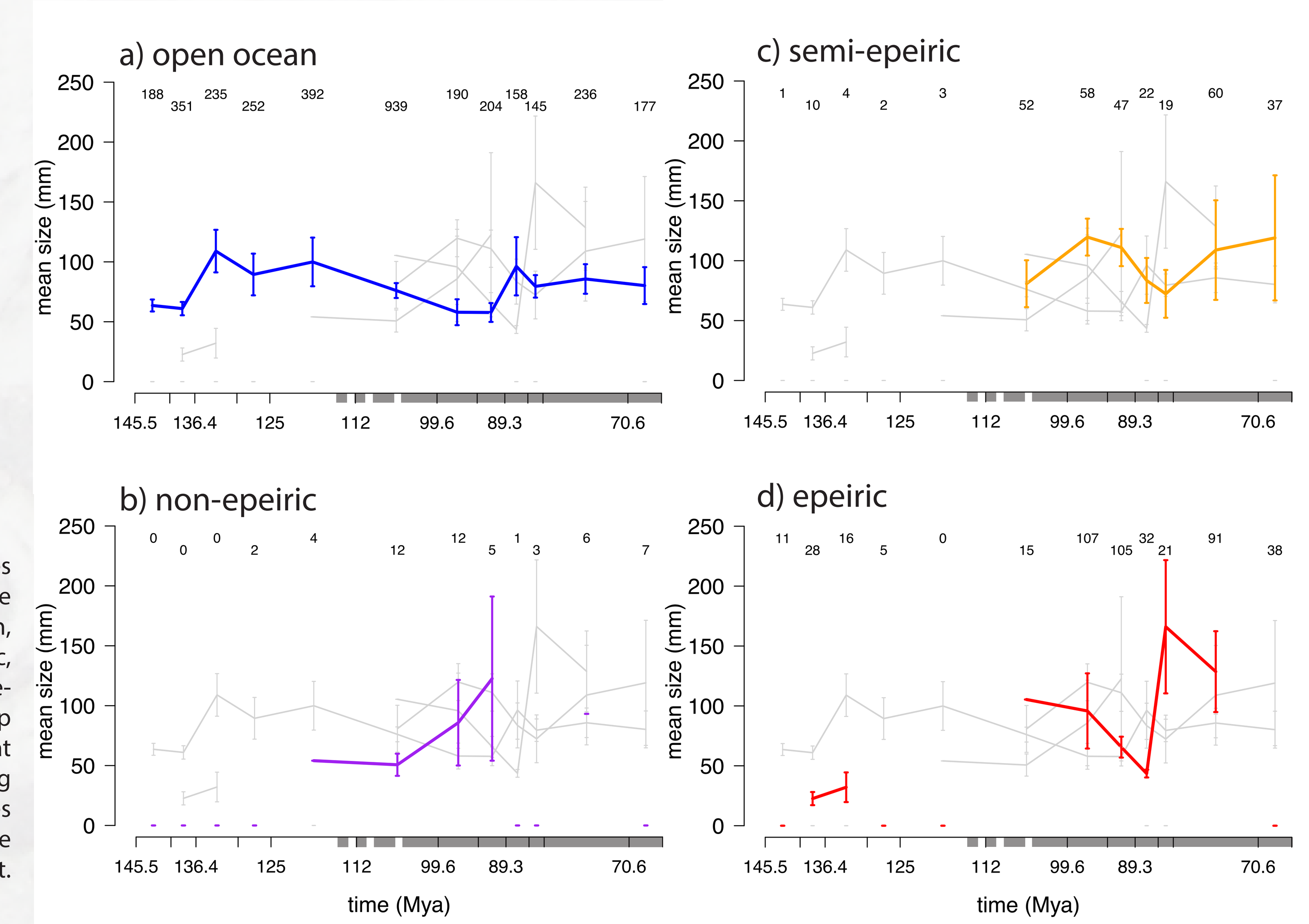


Fig. 5. (left) Relative proportion of total taxa in each epeiricness category for a) species and b) genera. Gray shading along the x-axis roughly indicates times when epeiric seas were present.

Fig. 6. (right) Mean body sizes and standard errors across the Cretaceous for a) open ocean, b) non-epeiric, c) semi-epeiric, and d) epeiric ammonite species. Numbers along the top indicate raw diversity for that data point. Gray shading along the x-axis roughly indicates times when epeiric seas were present.



Conclusions

- If you're somewhat epeiric, you're likely **very epeiric**. (Fig. 5a)
- Despite similar diversity dynamics (Fig. 4), discrepancy between trajectories in relative proportions of epeiricness between species and genus levels (Fig. 5) suggests **little discrimination of immigrant species at the taxonomic/phylogenetic level**.
  - In other words, many genera have epeiric representation, but few genera are primarily epeiric.
- Body size of epeiric ammonites exhibit **greater range and mean size** than do open ocean ammonites, despite lower diversity. They also appear to **fluctuate more** temporally. (Fig. 6)

Future Directions and Feedback

- Environmental and biotic factors contributing to body size trends
- Phylogenetic context
- Comparison with modern systems (eg. Mediterranean Sea, Red Sea)
- Ecology, geography, and spatial extent of completely non-epeiric taxa

Acknowledgments

Charles Marshall

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