Ecological drivers of body size evolution in brachiopods and trilobites across the Late Ordovician mass extinction

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Background

The Late Ordovician mass extinction was first of the “Big Five” mass extinctions in Earth’s history. Biodiversity losses were likely driven by a number of coincident factors, including cooling, glaciation, eustatic sea level fall, and changes in ocean chemistry, resulting in a complex two-pulse extinction[5].

Previous studies of the Late Ordovician mass extinction have found evidence for selective extinction of brachiopods across bathymetric gradients and of trilobites by larval type (i.e., benthic vs. pelagic). Further, there is some evidence for a Late Ordovician “Lilliput Effect,” a general reduction in the body size of organisms after a mass extinction due to environmental stressors and/or selective extinction of larger taxa.

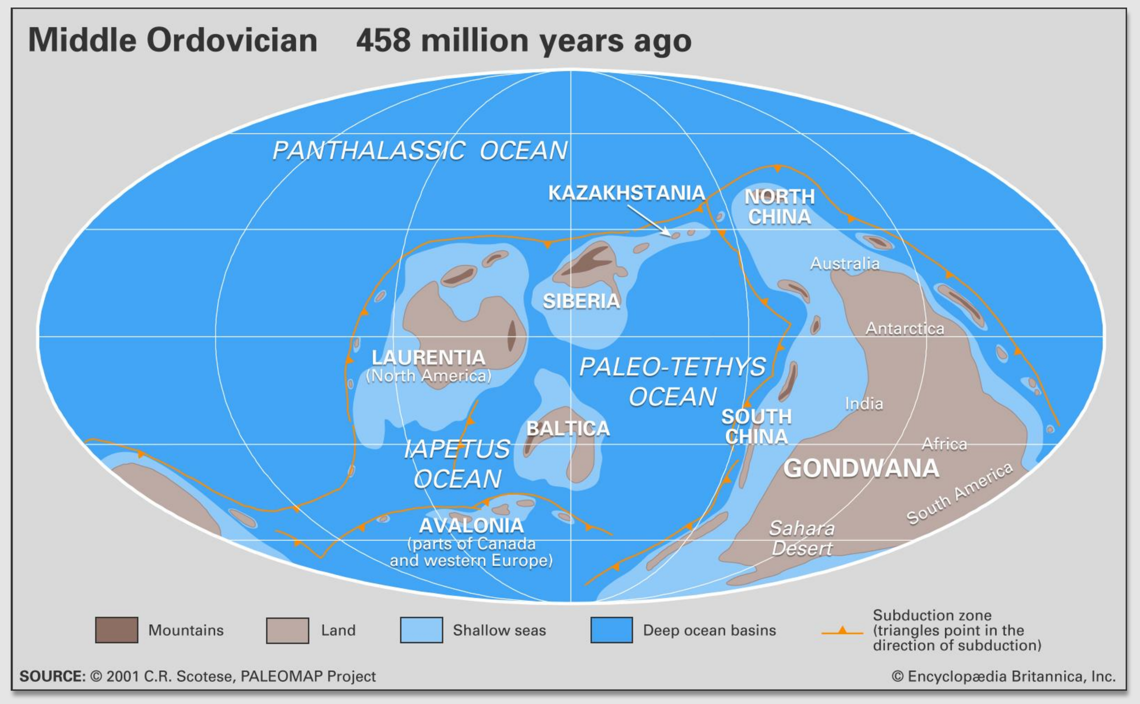


Figure 1. Reconstruction of Earth in the Middle Ordovician[6]. Notably, continents are very diffuse along the equator, with lots of margin for marine habitat, and the largest continent, Gondwana, extends over the South Pole, allowing glaciers to form.

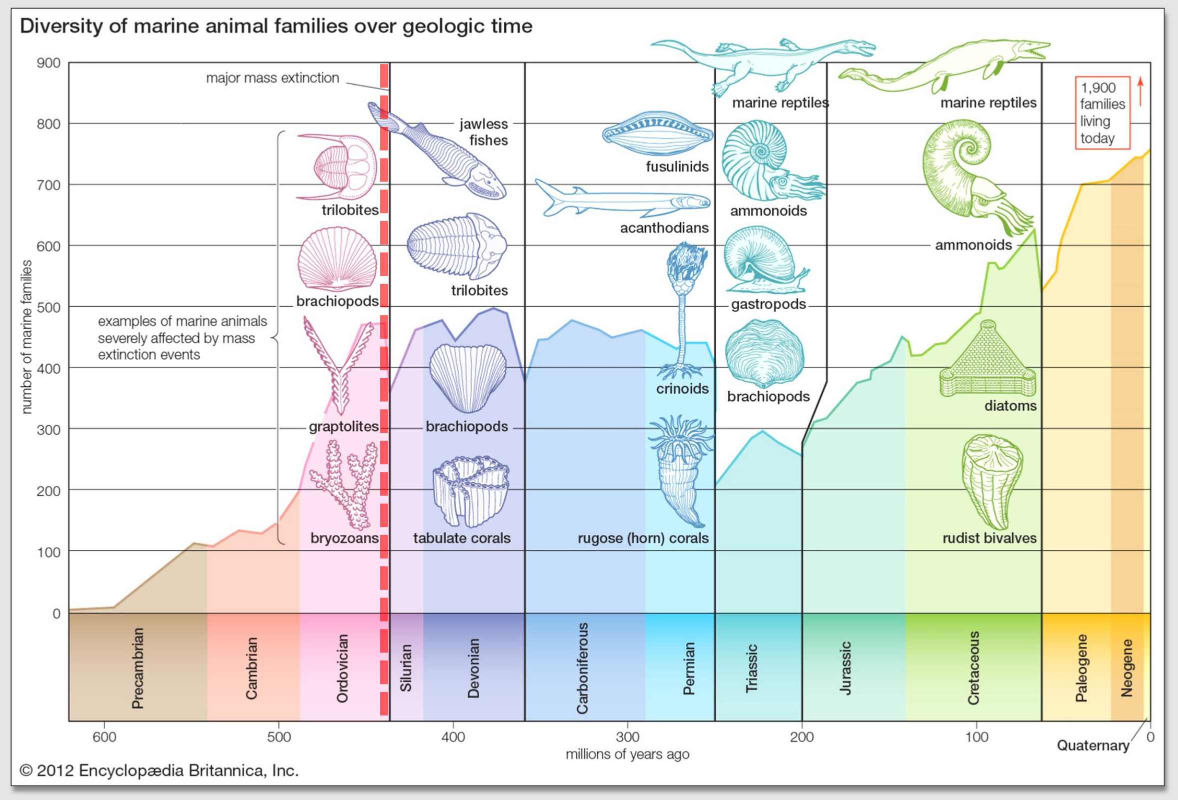


Figure 2. Marine faunal diversity over geologic time, at the family level[3]. Dashed red line at ~450 Ma denotes the Late Ordovician mass extinction.

The “Lilliput Effect” has been observed over the Late Ordovician extinction in several major groups of marine invertebrates, including brachiopods, trilobites, and crinoids. However, the timing, geographic extent, and taxonomic scope of these changes in body size are not well-understood, and their potential relationship with heterogeneity in extinction intensity has not yet been explored.

Key Questions

Do differences in extinction intensity based on ecological factors also correspond to changes in body size across the Late Ordovician extinction?

Controlling ecological factors:

Brachiopods – water depth

Strophomenids – inhabited deeper, muddier habitats

Orthids – inhabited shallower, rockier habitats

Previous evidence shows selective extinction of:
- deep water taxa in first extinction pulse (Katian—Hirnantian)
- shallow water taxa in second extinction pulse (Hirnantian—Llandovery)

Trilobites – larval ecology

Planktonic – spend part of their life in the water column

Benthic – spend their entire life around the sea floor

Previous evidence shows selective extinction of:
- trilobites with a planktonic life stage

Methods

Body size was estimated using log area calculated from length and width measurements for Middle Ordovician to middle Silurian brachiopods (n=2,906) and trilobites (n=783) using a combination of museum collections and published literature. Median size for each genus was then calculated from specimen measurements.

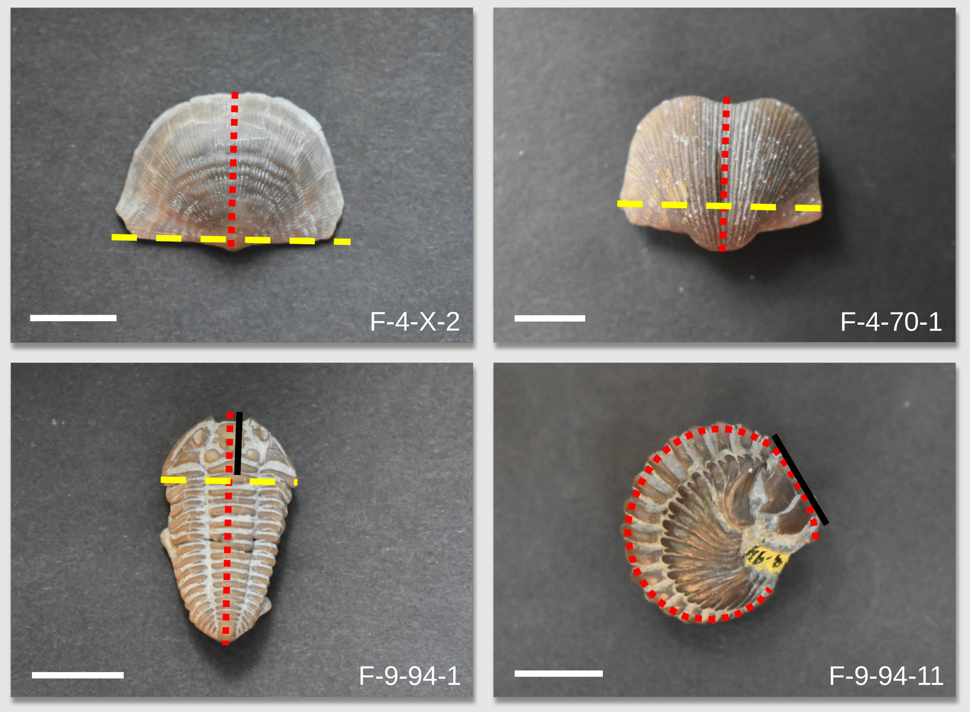


Figure 3. Measured specimens from Earlham College Department of Geology. Top left: strophomenid brachiopod *Leptaena richmondensis,* Top right: orthid brachiopod *Hebertella sp*., Bottom left: trilobite *Flexicalymene meeki*, Bottom right: enrolled *Flexicalymene*. Dotted red line is length, dashed yellow line is width, and solid black line is head length (trilobites). Scale bar = 10 mm.

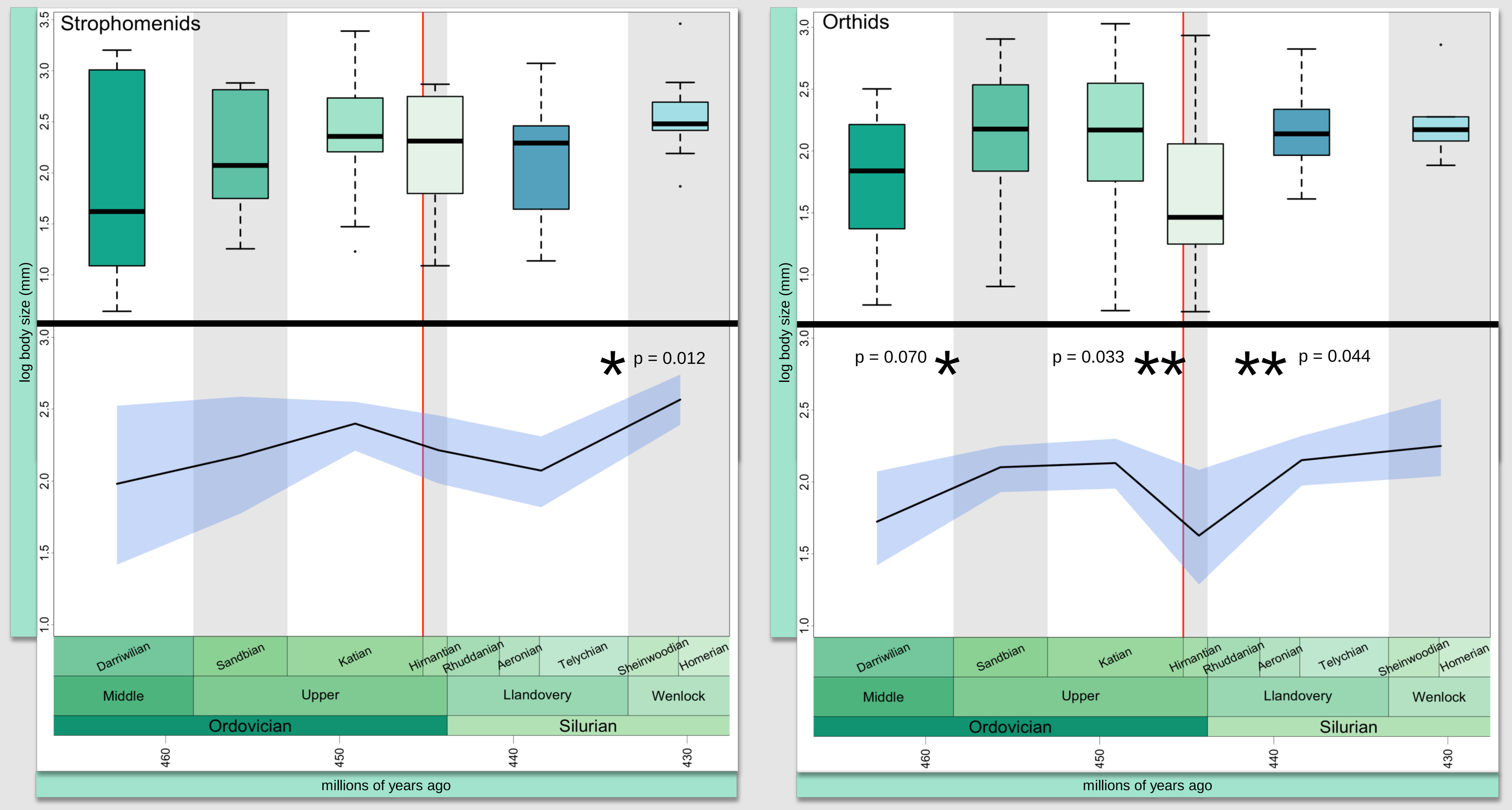
Unique genera sampled

- Strophomenids (n = 1,015): 67
- Orthids (n = 1,891): 72
- Benthic trilobites (n = 371): 49
- Planktonic trilobites (n = 379): 34

Based on existing compendiums, depth preferences in terms of benthic assemblage zones[1] were assigned to brachiopod genera[4], and planktonic vs. benthic larval types were assigned to trilobite genera[2]. The resulting dataset includes taxa from all major paleogeographic regions to capture global trends in body size across the Ordovician extinction.

Brachiopods

Strophomenid brachiopods exhibited no significant change in body size across the extinction, with only a late, marginal increase in the Silurian. Orthids, however, show a distinct drop after the first extinction pulse, with a quick rebound directly after. Little evidence was found for selectivity in either group based on depth, with the exception of a steep drop in orthids of benthic zone 3.



Figures 4 and 5. Paired plots showing body size of brachiopods during each stage of the Middle Ordovician to middle Silurian, split between strophomenids (left) and orthids (right) Red line at the start of the Hirnantian stage denotes first pulse of the extinction. 2 stars denote statistical significance using the Wilcoxon rank sum test, 1 star denotes marginal significance.
Upper panels: Boxplots of genus body size; horizontal lines are medians, vertical lines are 95% confidence intervals.
Lower panels: Bootstrap resampling plots of genus body size; solid lines are genus body size from 100 bootstrap resampling replicates, shaded areas represent 95% confidence intervals.

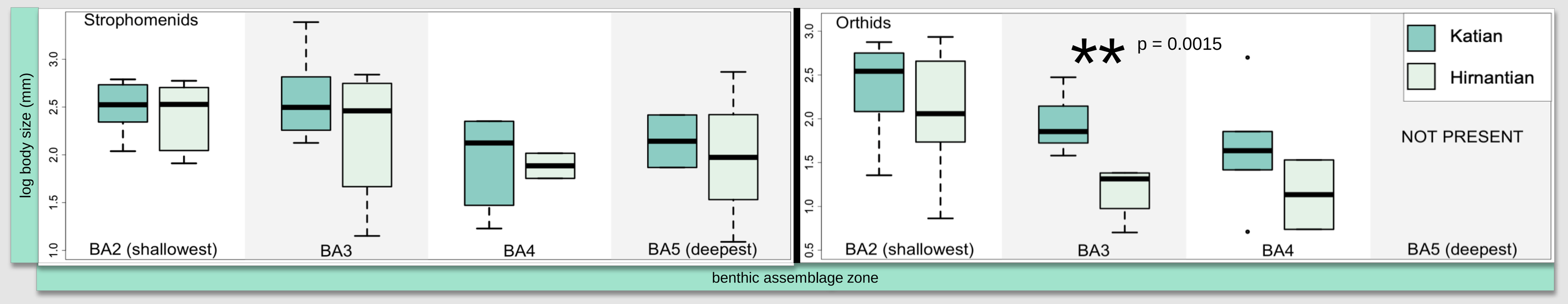
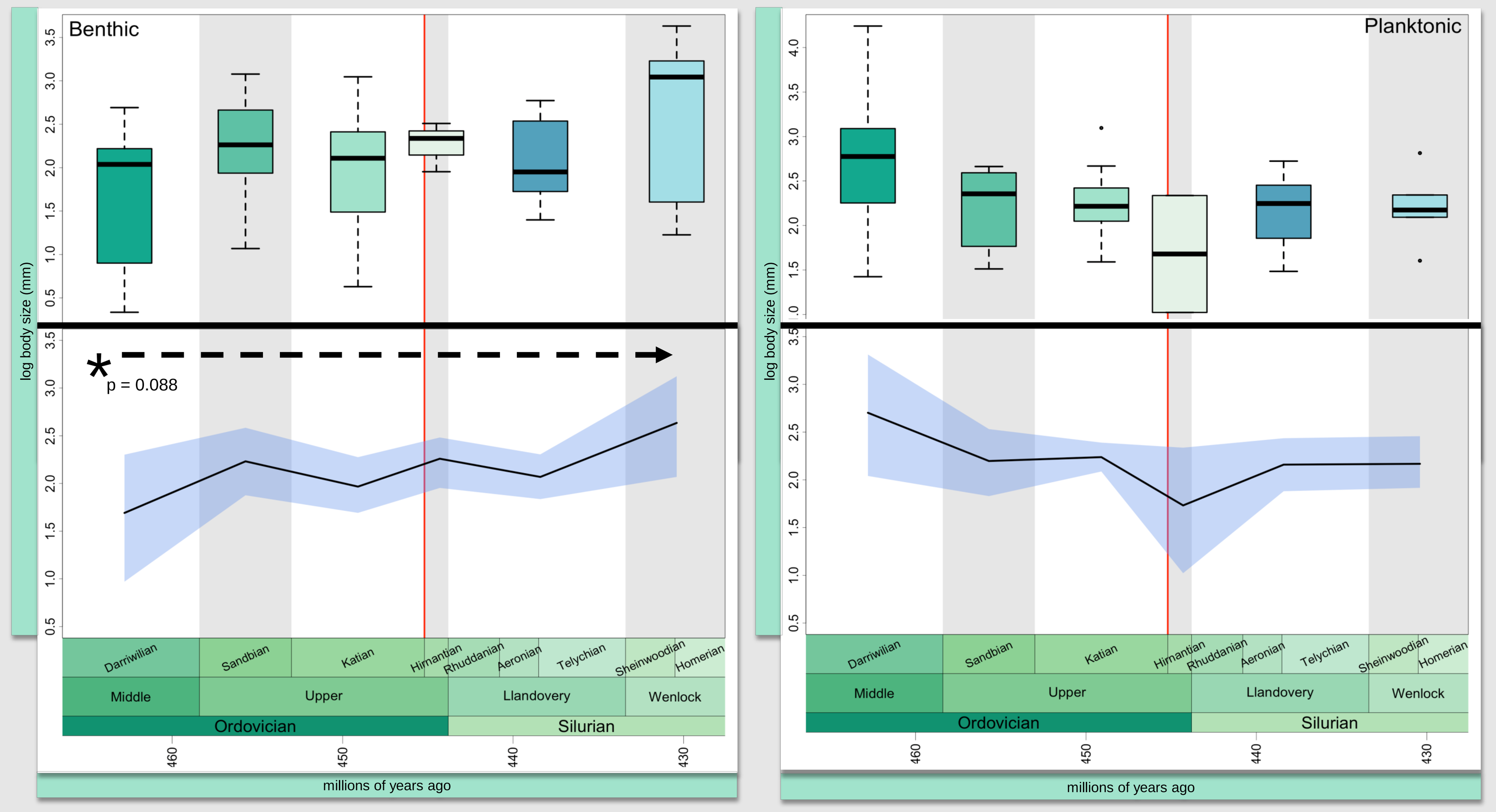


Figure 6. Boxplots showing body size change between the Katian and Hirnantian stages at 4 different depths, split between strophomenids (left) and orthids (right).

Trilobites

Neither benthic nor planktonic trilobites showed a significant change in size between any two stages of the extinction. However, it is worth noting the general drop in planktonic trilobites size, which we may predict from a selective extinction of this group.



Figures 7 and 8. Paired plots showing body size of trilobites during each stage of the Middle Ordovician to middle Silurian, split between benthic (left) and planktonic (right). Dashed arrow by star indicates marginal statistical significance between the Darriwilian and Wenlock. Panels and all other symbology are consistent with Figures 4 and 5.

Conclusions

These finding show evidence for a decrease in body size correlated with mass extinction intensity in orthid brachiopods, but not in strophomenids, regardless of depth, nor in benthic or planktonic ecological trilobite groupings.

Potential biases:

- Low sampling from the Hirnantian stage, during which the extinction takes place, due to its brevity and a large unconformity of over 100m in many places
- Poor time bin resolution in the Silurian due to most specimens only being labeled to the epoch

Future directions:

- Sample more Hirnantian taxa and correlate Silurian formations to stages
- Continue investigating whether the “Lilliput Effect” occurs in other Ordovician taxa

References

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