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Diversification and speciation among Laurentian brachiopods during the GOBE: insights from basinal and regional analyses

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ABSTRACT

Full understanding of diversity dynamics during the Great Ordovician Biodiversification Event (GOBE) requires analyses that investigate regional and species-level data and patterns. In this study, we combine bedding-plane scale data on brachiopod species counts and shell size collected from the Simpson Group of Oklahoma, USA, with species-level phylogenetic biogeography for three articulated brachiopod lineages that occurred throughout Laurentia. From these data, we ascertain that the primary influences of brachiopod shell size and diversity in the Simpson Group reflect global drivers, notably temporal position and paleotemperature. Similarly, the primary speciation pattern observed within *Hesperorthis, Mimella,* and *Oepikina* is the oscillation in speciation mode between dispersal and vicariance, which reflect the connection and disconnection of geographic areas, respectively. Processes that facilitate cyclical connectivity are global to regional in scale such as oceanographic changes, glacial cycles, or tectonic pulses. Therefore, both regional and continental scale analyses reinforce the importance of global factors in driving diversification during the GOBE.

Introduction

The Ordovician Period is a key interval of diversification and differentiation in the history of marine life. In particular, the Middle Ordovician was a time of accelerated diversification of shelly taxa (e.g., Harper et al. 2013; Wright and Toom 2017; Stigall et al. 2019; Lam et al. 2021). The main pulse of the Great Ordovician Biodiversification Event (GOBE) occurs as an interval of statistically elevated diversification and increase in generic richness during the Dapingian and Darriwilian stages (Kröger et al. 2019; Rasmussen et al. 2019). It is increasingly important to understand how components of global diversity are generated (Stigall 2018), including how processes at local to regional scales influence broader patterns of diversification.

Herein, we examine diversity patterns and reconstruct speciation modes for a group of articulated brachiopods from the Middle Ordovician of Laurentia. Specifically, we combine outcrop-based analyses of diversification in the Southern Oklahoma Aulacogen of the Laurentian mid-continent with a broader multi-basinal phylogenetic biogeographic analysis of select clades. The primary research questions addressed are: (1) to what degree do regional patterns of diversity match patterns from global datasets; and (2) whether speciation in Laurentian brachiopods matches the anticipated patterns of alternating episodes of vicariance and dispersal proposed by Stigall et al. (2017). The first question is assessed using outcrop-level analyses of diversity and shell size, whereas the second question is addressed using phylogenetic biogeography. Combined, these analyses provide insight into diversification patterns and processes operating within Laurentia during the main pulse of the GOBE.

Materials and methods

Regional diversity and disparity patterns were assessed via bed-by-bed analysis of articulated brachiopods of the Simpson Group strata of south-central Oklahoma. This succession comprises one of the most complete (biostratigraphically) and best sampled (geochemically) Laurentian sections spanning the GOBE. Specifically, outcrops of the Joins, Oil Creek, McLish, Tulip Creek, and Bromide formations exposed along Interstate 35 and US-77 were targeted for analysis. Each bedding surface was examined and all identifiable brachiopods were counted. Shell width and depth were measured for all specimens with reasonably entire margins. Lithology was also recorded. For diversity analyses, data were aggregated into 10 temporal bins and rarefied diversity was calculated as specified in Trubovitz and Stigall (2016). Trends and variance in shell size through time were analysed using the R package PaleoTS (Hunt 2019) as specified in Hennessey (2023). To test for the impact of local, regional, and global controls on diversity and disparity patterns, a Boosted Regression Model (BRM) was developed using the R package "gbm" (Ridgeway et al. 2020). The BRM incorporated shell size as the independent variable relative to the contributions of lithology, temporal position, diversity (from Trubovitz and Stigall 2016), Δ^{13}C from Simpson Group strata from Edwards and Saltzman (2015) as a proxy for carbon cycle and nutrient conditions, δ^{18}O data from Avila et al. (2022) as a proxy for paleotemperature/salinity, and ^{87}Sr/^{86}Sr data from Avila et al. (2022) as a proxy for tectonic activity as specified in Hennessey (2023).

To assess speciation mode and connections between marine basins within Laurentia, species-level phylogenies were developed for three common clades of Middle Ordovician brachiopods: orthids *Hesperorthis* and *Mimella*, and the strophomenid *Oepikina.* A total of 65 species were examined among the three clades and scored for 30, 31, and 32 discrete morphological characters among *Hesperorthis, Mimella,* and *Oepikina* species, respectively. Character matrices were analysed using a Bayesian tip-dated phylogenetic analysis conducted using Markov chain Monte Carlo (MCMC) analysis in MrBayes 3.2.7 (Wright 1997; Ronquist et al. 2012). Consensus topologies were timescaled using the R package "paleotree" (Bapst 2012) and biogeographic analysis was conducted in "BioGeoBEARS" (Matzke 2013). Dispersal events were identified when descendent species inhabited additional geographic ranges relative to their ancestors. Vicariance events were identified when descendent species inhabited fewer geographic ranges relative to their ancestors (e.g., Lieberman 2000; Lam et al. 2018, 2021). Data and methods for the phylogenetic and biogeographic analyses are detailed in Censullo (2020).

Results and discussion

Results of field-based analyses of the Simpson Group brachiopods indicate a rapid increase in species diversity coincident with increased shell volume. Significantly, these increases are statistically identifiable as related to rapid state changes, rather than long-term directional trends occurring over a million years or more. These coordinated increases are recorded within the lower portion of the Oil Creek Formation, which is correlative with the *Histiodella sinuosa* and *H. holodentata* conodont biozones. Notably, diversity increases on other paleocontinents, including Baltica and Gondwana, are coincident with the observed diversity increase in Oklahoma (Trubovitz and Stigall 2016; Stigall et al. 2019). The results of boosted regression analysis further indicate that the primary factors influencing shell volume are age (=position in time), paleotemperatures/salinity, and overall diversity. Each of these factors are globally influential. Conversely, local factors such as lithology and basin-specific carbon cycle changes have limited impact on shell volume. Thus, the general picture that emerges is that diversification and ecosystem change was rapid, coincident with similar changes on other paleocontinents, and was primarily influenced by global (age, δ^{18}O, diversity) rather than local (Δ^{13}C, lithology) factors. These results from regional analysis of one of the best preserved Middle Ordovician sections in Laurentia indicate the importance of global environmental changes for driving evolutionary patterns at the regional/local scale within Laurentia during the GOBE.

To investigate processes of diversification, we examined how connections vs separations among multiple basins within Laurentia impacted speciation patterns and what environmental factors exerted strong influence on these processes. Diversification rates of *Hesperorthis*, *Mimella*, and *Oepikina* lineages were greatest during the Darriwilian and tapered off during the Late Ordovician. In fact, 89% of observed speciation events occurred during the Early to Middle Ordovician. This pattern of increased diversification, spiking during the Middle Ordovician, is consistent with other marine clades, such as crinoids, graptolites, and bryozoans, which also experienced rapid radiation during this time (Wright and Toom 2017; Stigall et al. 2019).

Speciation within *Hesperorthis, Mimella,* and *Oepikina* reflects alternating episodes of speciation via dispersal followed by vicariance events (Figs 1–3), although the frequency of dispersal events vs vicariant events varied among the lineages. A dispersal event followed by a vicariant event, or vice versa, occurred approximately 80% of the time within the genus *Hesperorthis*, 71% within the genus *Mimella*, and 58% of the time in *Oepikina*. Thus, alternation of dispersal and vicariance is a common motif observed within these clades. This alternation supports the BIME (Biotic Immigration Event) biodiversity accumulation model proposed by Stigall et al. (2017), in which alternation between dispersal and vicariance events facilitates speciation through a cyclical process.

Reconstructed dispersal events between basins are consistent with potential dispersal pathways facilitated by ocean currents surrounding Laurentia during the Middle to Late Ordovician (Pohl et al. 2016; Lam et al. 2018). The best fit biogeographic models indicate that founder-event speciation (denoted by the +*J* added within each model) was an important biogeographic process driving evolution. Basins which

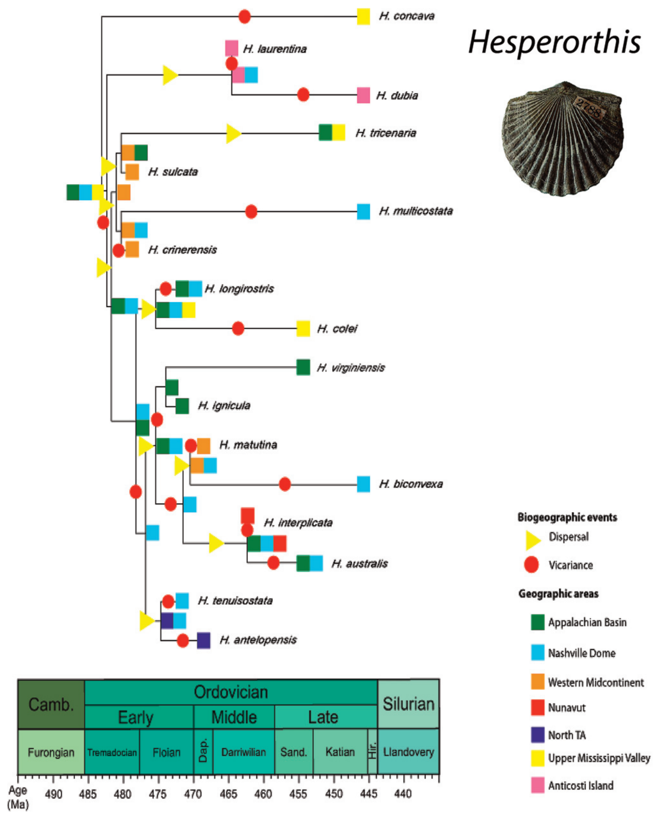

Fig. 1. Paleobiogeographic reconstruction of *Hesperorthis* from the BioGeoBEARS analysis. The DIVALIKE+*J* model, shown here, was the most likely model for the biogeographic evolution of the species of *Hesperorthis* (AIC = 86.44). Dispersal events are indicated by a yellow triangle and variance events by a red circle. Abbreviations: TA – Transcontinental Arch, Camb. – Cambrian, Dap. – Dapingian, Sand. – Sandbian, Hir. – Hirnantian. Modified from Censullo (2020).

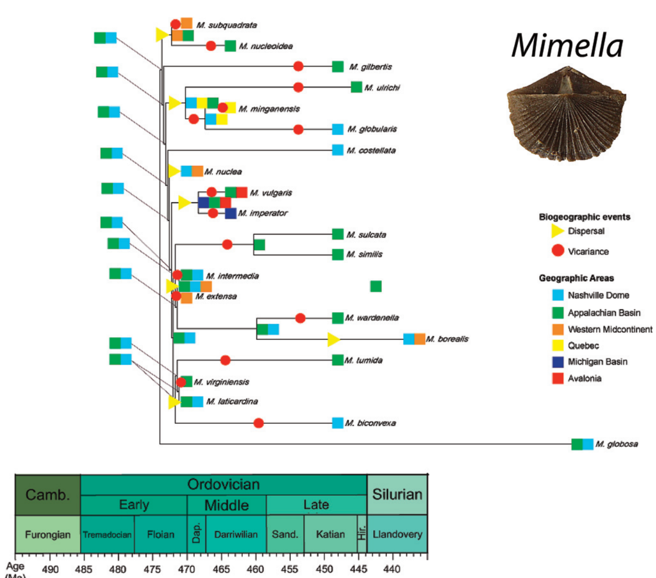

Fig. 2. Paleobiogeographic reconstruction of *Mimella* from the BioGeoBEARS analysis. The DEC+*J* model, shown here, was the most likely model for the biogeographic evolution of the species of *Mimella* (AIC = 95.01). Abbreviations: Dap. – Dapingian, Camb. – Cambrian, Sand. – Sandbian, and Hir. – Hirnantian. Modified from Censullo (2020).

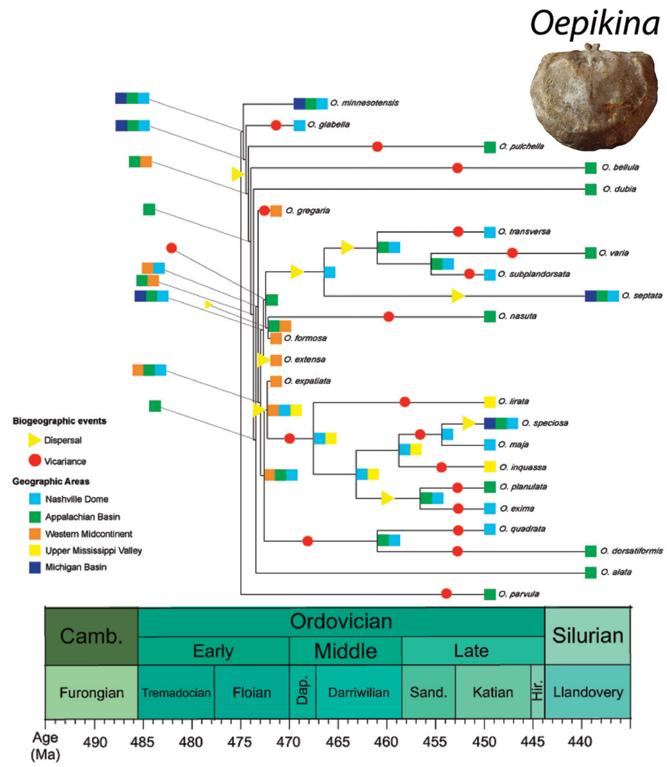

Fig. 3. Paleobiogeographic reconstruction of *Oepikina* from the BioGeoBEARS analysis. The DEC+*J* model, shown here, was the most likely model for the biogeographic evolution of the species of *Oepikina* (AIC = 108). Abbreviations: Camb. – Cambrian, Dap. – Dapingian, Sand. – Sandbian, and Hir. – Hirnantian. Modified from Censullo (2020).

are geographically close would have been connected during intervals of sea-level rise but disconnected following a sea-level fall. Another pattern prevalent through the evolution of these clades is the dispersal to and from the Nashville Dome or Appalachian Basin and the western Midcontinent. Dispersal between these basins, and subsequent dispersal events from the western Midcontinent to northwestern basins, correlates with intracontinental surface currents from prevailing winds (Lam et al. 2018). Reversed dispersal events which brought species from the western Midcontinent east to the Appalachian Basin and the Nashville Dome correlate with larger ocean gyres, such as the Southern Laurentia Current, and the Iapetus Current, which operated around the continent of Laurentia, within the Iapteus Ocean (Pohl et al. 2016).

Sea level fluctuated often during these critical times of speciation during the Ordovician (Pohl et al. 2016; Lam et al. 2018), which would have facilitated the observed pattern of alternating dispersal and vicariance. Sea-level cyclicity has been linked to glaciation potentially as early as the Middle Ordovician (Rasmussen et al. 2016). Cooling ocean temperatures and the formation of glaciers at high latitudes in the Southern Hemisphere caused declining sea level during the Middle Ordovician (Rasmussen et al. 2016). Each genus in this study expanded its range during this time, which may reflect greater potential for brachiopods to occupy previously unavailable niches and regions due to cooling oceans paired with changing surface ocean circulation patterns. Rapidly changing sea-levels would have connected and disconnected adjacent basins, facilitating the alternation of dispersal and vicariance events, such as the oscillations evident within the lineages of *Hesperorthis, Mimella,* and *Oepikina* during the Middle Ordovician. Similarly to the diversification analyses of the Oklahoma basin, these multi-basin scale analyses indicate that global factors, such as climatic cooling and changes in ocean circulation, exerted core influences on regional diversification processes within Laurentia during the GOBE.

Conclusions

Combining a single-basin, stratigraphically constrained analysis with a multi-basin evolutionarily constrained analysis provides a framework to examine regional vs global diversity dynamics. Within the Southern Oklahoma Aulacogen, diversity and shell volume increased rapidly during the early Darriwilian Stage. This paired increase was primarily influenced by global factors, including temporal position and paleotemperature/salinity, but was not strongly influenced by local factors such as lithology. Notably, speciation events within the *Mimella*, *Hesperorthis*, and *Oepikina* lineages alternated between dispersal (due to connections among geographic areas) and vicariance (due to isolation of geographic regions). Factors capable of producing oscillations in connectivity among basins primarily reflect global influences related to cooling oceans, ice expansion in the Southern Hemisphere, and/or regional tectonics. By integrating these analyses, it is clear that large-scale drivers are important for facilitating local speciation, and thus diversification, within Laurentia during the GOBE.

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