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Dispersal in the Ordovician: Speciation patterns and paleobiogeographic analyses of brachiopods and trilobites

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ABSTRACT

The Middle to Late Ordovician was a time of profound biotic diversification, paleoecological change, and major climate shifts. Yet studies examining speciation mechanisms and drivers of dispersal are lacking. In this study, we use Bayesian phylogenetics and maximum likelihood analyses in the R package BioGeoBEARS to reanalyze ten published data matrices of brachiopods and trilobites and produce time-calibrated species-level phylogenetic hypotheses with estimated biogeographic histories. Recovered speciation and biogeographic patterns were examined within four time slices to test for changes in speciation type across major tectonic and paleoclimatic events. Statistical model comparison showed that biogeographic models that incorporate long-distance founder-event speciation best fit the data for most clades, which indicates that this speciation type, along with vicariance and traditional dispersal, were important for Paleozoic benthic invertebrates. Speciation by dispersal was common throughout the study interval, but notably elevated during times of climate change. Vicariance events occurred synchronously among brachiopod and trilobite lineages, indicating that tectonic, climate, and ocean processes affected benthic and planktotrophic larvae similarly. Middle Ordovician inter-oceanic dispersal in trilobite lineages was influenced by surface currents along with volcanic island arcs acting as "stepping stones" between areas, indicating most trilobite species may have had a planktic protaspid stage. These factors also influenced brachiopod dispersal across oceanic basins among Laurentia, Avalonia, and Baltica. These results indicate that gyre spin-up and intensification of surface currents were important dispersal mechanisms during this time. Within Laurentia, surface currents, hurricane tracks, and upwelling zones controlled dispersal among basins. Increased speciation during the Middle Ordovician provides support for climatic facilitators for diversification during the Great Ordovician Biodiversification Event. Similarly, increased speciation in Laurentian brachiopod lineages during the Hirnantian indicates that some taxa experienced speciation in relation to major climate changes. Overall, this study demonstrates the substantial power and potential for likelihood-based methods for elucidating biotic patterns during the history of life.

1. Introduction

The Middle to Late Ordovician (∼470 to 444 Ma) was a time of profound diversification and paleoecological change. This interval began with the Great Ordovician Biodiversification Event (GOBE), the greatest increase in marine families and genera in the Phanerozoic (Harper, 2006). Associated with this dramatic biodiversity increase, marine ecosystems became considerably more complex, and widespread metazoan reefs appeared for the first time (Sheehan, 1996; Servais et al., 2010). Contrastingly, the Ordovician ended with the Late Ordovician (Hirnantian) Mass Extinction, the second largest of Earth's mass extinctions in terms of taxonomic loss (Bambach et al., 2004). These biotic changes were coincident with and ultimately driven by a series of changes within the Earth system such as shifting oceanographic conditions and climate regimes, increased volcanic activity, and widespread carbonate platforms (Algeo and Seslavinsky, 1995; Miller and Mao, 1995; Young et al., 2010; Pohl et al., 2016a; Rasmussen et al., 2016; Young A.L. et al., 2016; Young S.A. et al., 2016). Biogeographic processes have long been considered critical for facilitating both biodiversity accumulation and ecosystem changes during the Middle to Late Ordovician interval (e.g. Miller, 1997; Harper et al., 2013; Wright and Stigall, 2013a; Trubovitz and Stigall, 2016; Stigall et al., 2017). However, empirical analyses of dispersal pressures and pathways constrained by evolutionary data have been limited to date.

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In this study, we utilize a suite of cutting-edge techniques to estimate biogeographic histories and analyze dispersal processes within the Middle to Late Ordovician shallow marine faunas of Laurentia, with additional data obtained from Baltica, Avalonia, Gondwana, and the intervening Iapetus Ocean. To reconstruct the pattern of dispersal events for the region, species-level phylogenetic hypotheses of rhynchonelliformean brachiopod and trilobite clades were employed in a time-stratigraphic framework across four temporal intervals during the Middle to Late Ordovician, each characterized by a different combination of tectonic and paleoclimatic conditions.

Tremendous methodological developments over the past few decades have provided rigorous analytical tools for examining evolutionary changes within a biogeographic context. Specifically, phylogenetic paleobiogeography has been used to interpret vicariance patterns and dispersal pathways, discern changes in area relationships, and identify areas of origination for both fossil and extant invasive taxa (e.g., Lieberman and Eldredge, 1996; Lieberman, 2003; Folinsbee and Brooks, 2007; Wright and Stigall, 2013a; Bauer and Stigall, 2014). Traditionally, most phylogenetically-informed biogeographic analyses have utilized parsimony-based approaches (e.g., Ladiges et al., 1987; Stigall, 2010; Wojcicki and Brooks, 2005; Escalante et al., 2007). Such approaches have produced novel and insightful results, but typically require assumptions of parsimony and congruence of biogeographic patterns among clades, which may not be valid in all circumstances. Recent developments have expanded the accessibility of maximum likelihood and Bayesian modeling approaches in phylogenetic biogeography (e.g., Sanmartin et al., 2001; Costa, 2010; Litsios et al., 2014; Sorenson et al., 2014; Wood et al., 2014). These methods provide a more robust exploration of probabilistic processes and idiosyncratic patterns. The full suite of phylogenetic biogeographic methods can be utilized with extant taxa; however, the requirement of contemporaneous terminal taxa curtailed the applicability of model-based methods (e.g., LAGRANGE, Ree and Smith, 2008) with fossil data. A newer method, BioGeoBEARS (Matzke, 2013; R Core Team, 2016), removes that limitation, and is thus fully compatible with extinct taxa.

This study is the first to use the maximum likelihood models implemented within the R package BioGeoBEARS to examine evolutionary biogeographic patterns among Paleozoic taxa. Specifically, ten published species-level data matrices of Middle through Late Ordovician rhynchonelliformean brachiopods and trilobites are re-analyzed using Bayesian methods to develop time-calibrated fossil phylogenies ("tip-dating"; Matzke and Wright, 2016; Bapst et al., 2016). These phylogenies are then used in BioGeoBEARS analyses to estimate biogeographic history. The results are interpreted in a paleogeographic and paleoceanographic context through the Middle and Late Ordovician epochs to 1) reconstruct dispersal pathways and identify speciation mode through time, 2) compare shifting biogeographic patterns with paleoceanographic and tectonic reconstructions for the Middle to Late Ordovician, and 3) identify the impact of different environmental factors on biodiversity during the study interval.

1.1. Middle - Late Ordovician biogeography, tectonics, and paleoceanography

1.1.1. Geologic context

Tectonic and paleoceanographic conditions of Laurentia, Baltica, Avalonia, and Gondwana influenced biogeographic patterns of Paleozoic brachiopods and trilobites throughout the Middle to Late Ordovician. The entire study interval was associated with active tectonism and high rates of seafloor spreading (Servais et al., 2010), leading to widely dispersed continents and terranes surrounded by active volcanic island arcs that deposited massive K-bentonite beds in North America, Europe, South America, and China (Cocks and Torsvik, 2002; Huff et al., 1992, 2010; Rasmussen and Harper, 2011). The constriction of the Iapetus Ocean between Laurentia and Baltica and the Tornquist Ocean between Avalonia and Baltica produced volcanic island arcs and led to the eventual collision of these paleocontinents in the latest Ordovician through middle Silurian (Cocks and Torsvik, 2011).

Global climate transitioned from greenhouse to icehouse conditions during the study interval. The Cambrian through Early Ordovician was characterized by very warm global temperatures and high sea-level (Trotter et al., 2008). The Middle Ordovician was an interval of cooling, and continental glaciation may have occurred as early as the Darriwilian Age as hypothesized by high-resolution geochemical, paleoecological, and backstripping studies (Vandenbroucke et al., 2009; Dabard et al., 2015; Amberg et al., 2016; Pohl et al., 2016a; Rasmussen et al., 2016), with some studies indicating glaciation may have taken place as early as the Early Ordovician (e.g., Turner et al., 2011). Continental

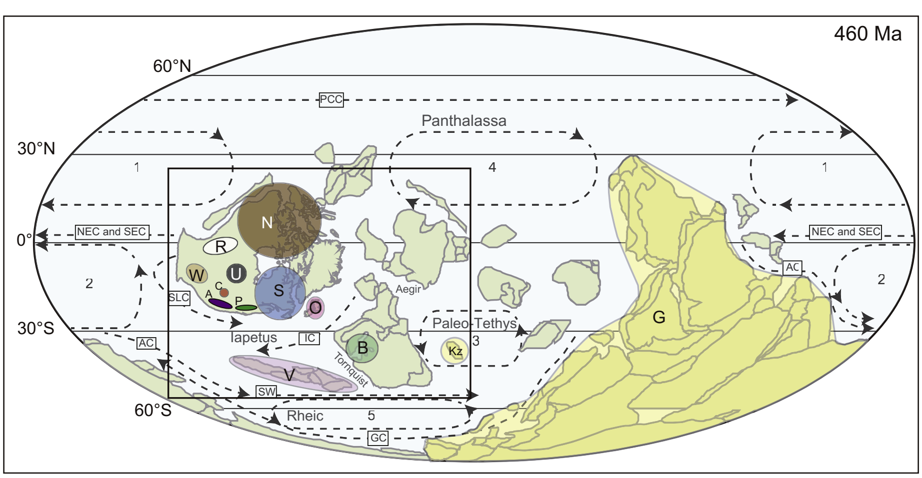

Fig. 1. Paleogeographic reconstruction of the latest Middle Ordovician Darriwilian Age with oceanic basins and major ocean gyres (numbered) and currents (dotted lines). Geographic areas considered in this study are lettered: N, Northern Laurentia (Northwest Territories, Nunavut, British Columbia); R, North of the Transcontinental Arch; W, Western Midcontinent; U, Upper Mississippi Valley; C, Cincinnati basin; A, Southern Appalachian basin; P, Northern Appalachian basin; S, Southern Laurentia (Newfoundland, Quebec, Anticosti Island); O, Scoto-Appalachia; V, Avalonia; B, Baltica; G, Gondwana (Kazakh terranes (Kz), Australia, Japan, Arabia, Turkey, Bohemia, Spain, France). Ocean gyres are as follows: 1, North Panthalassic convergence; 2, South Panthalassic convergence; 3, South Paleo-Tethys convergence; 4, North Paleo-Tethys convergence; and 5, the Rheic convergence. Black boxes denote the names of major ocean currents: PCC, Panthalassic Circumpolar Current; IC, Iapetus Current; SLC, Southern Laurentia Current; NEC and SEC, North and South Equatorial Currents; AC, Antarctic Current; SW, South Westerlies; and GC, Gondwana Current. Large black box around Laurentia, Avalonia, and Baltica denotes the area represented in Fig. 5. Map modified from Torsvik and Cocks (2013); ocean currents and gyres from Pohl et al. (2016b). The paleogeographic maps of the Late Ordovician Sandbian Age from Torsvik and Cocks (2013) are used throughout the text across all four time slices for illustrative purposes, although paleogeography was changing through the study interval.