Estonian Journal of Earth Sciences, 2014, **63**, 4, 189–194 doi: 10.3176/earth.2014.17

Phylogenetic paleobiogeography of Late Ordovician Laurentian brachiopods

Jennifer E. Bauer[a*] and Alycia L. Stigall[a,b]

[a] Department of Geological Sciences, Ohio University, Athens 45701, Ohio, USA; jbauer5@vols.utk.edu
[b] OHIO Center for Ecology and Evolutionary Studies, Ohio University, Athens 45701, Ohio, USA; stigall@ohio.edu
* Current address: Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee 37996, USA.

Received 30 June 2014, accepted 11 September 2014

Abstract. Phylogenetic biogeographic analysis of four brachiopod genera was used to uncover large-scale geologic drivers of Late Ordovician biogeographic differentiation in Laurentia. Previously generated phylogenetic hypotheses were converted into area cladograms, ancestral geographic ranges were optimized and speciation events characterized as via dispersal or vicariance, when possible. Area relationships were reconstructed using Lieberman-modified Brooks Parsimony Analysis. The resulting area cladograms indicate tectonic and oceanographic changes were the primary geologic drivers of biogeographic patterns within the focal taxa. The Taconic tectophase contributed to the separation of the Appalachian and Central basins as well as the two midcontinent basins, whereas sea level rise following the Boda Event promoted interbasinal dispersal. Three migration pathways into the Cincinnati Basin were recognized, which supports the multiple pathway hypothesis for the Richmondian Invasion.

Key words: Lieberman-modified Brooks Parsimony Analysis, macroevolution, speciation, Katian, dispersal, vicariance, invasion.

INTRODUCTION

Species immigration and dispersal events are common in the fossil record. Reconstructing species migration pathways can provide insight into Earth system events that facilitated species dispersal. Thus, analyses that constrain both timing and directionality of large-scale species migration events are important for identifying feedbacks between biodiversity, tectonics and oceanographic events (Lieberman 2000). In this study, we examine a specific episode of interbasinal species invasion, the Richmondian Invasion, which is recorded in the Katian age strata of the Cincinnatian Series in the Cincinnati, USA region.

The Richmondian Invasion records an immigration of over 60 genera into the Cincinnati region, including members of orders which had been absent from the region for at least 5 million years (Holland 1997; Stigall 2010). The invasion was cross-faunal; immigrant taxa included arthropod, brachiopod, mollusk, echinoderm, cnidarian and bryozoan genera. Invasive taxa also included members of all trophic levels from pelagic predators to sessile benthos. The introduction of these new taxa caused a fundamental rearrangement of the community structure which had been stable for nearly 5 million years before the invasion (Patzkowsky & Holland 2007) and resulted in niche evolution among both native and incumbent species (Brame & Stigall 2014). The Richmondian Invasion occurred via multiple pulses in the C4 and C5 depositional sequences (Fig. 1A) and has previously been examined as a case study for analyzing the long-term impacts of modern species invasions (Stigall 2012). However, the migration pathways utilized by taxa that immigrated into the Cincinnati Basin are less clear. Early authors suggested that all invaders taxa immigrated from the paleoequator (e.g. Nelson 1959; Holland 1997), whereas later authors supported multiple invasion pathways (e.g. Jin 2001; Wright & Stigall 2013a) (Fig. 1B). The goal of this study is to determine whether the multiple pathway hypothesis is supported, contradicted or expanded by addition of the invasive brachiopod genus, *Eochonetes*, into a previously developed dataset (e.g. Wright & Stigall 2013a) and to identify which Earth system factors controlled biogeographic relationships between areas.

MATERIAL AND METHODS

Phylogenetic biogeographic methods were used to assess invasion pathways and biogeographic relationships. This analytical approach provides a framework to examine biogeographic evolution and speciation patterns within individual lineages as well as to assess hierarchical patterns in biogeographic area relationships when three or more clades are analyzed together (Lieberman 2000).

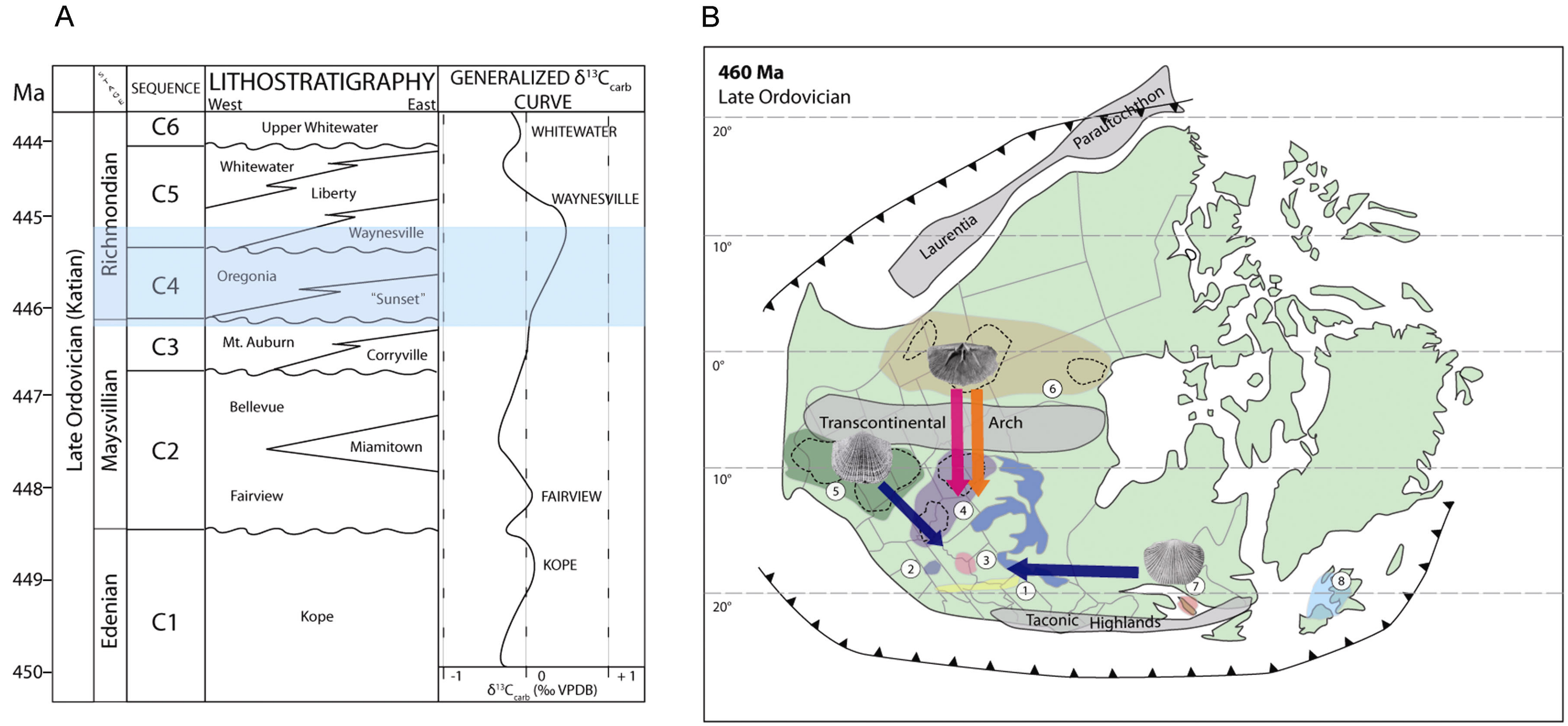

Fig. 1. Geologic setting. **A**, sequence stratigraphic framework of the Cincinnatian Series (modified from Holland 2008) with the corresponding generalized carbon isotope curve (modified from Bergström et al. 2009). The Richmondian Invasion occurred during the interval indicated by the blue bar. **B**, paleogeographic reconstruction of Laurentia (after Cocks & Torsvik 2011). With areas defined as: (1) Appalachian Basin, (2) Central Basin (= Nashville Dome), (3) Cincinnati Basin, (4) Eastern Midcontinent (= Illinois, Iowa, Missouri), (5) Western Midcontinent (= Texas, Oklahoma), (6) North of the Transcontinental Arch (= Bighorn, Williston, Hudson Bay basins), (7) Anticosti Island, (8) Scoto-Appalachian Basin (= Scotland, Northwest Ireland). Laurentia was primarily composed of landmasses within modern North America and Greenland but also included peri-Laurentian terranes from modern Europe, notably parts of Scotland and Ireland. The collision of an intra-Iapetus island arc with the Laurentian paleocontinent caused the contemporaneous Taconic and Grampian tectophases of the Taconic–Caledonian orogeny, producing structural elements including many domes and arches (Root & Onasch 1999; Cocks & Torsvik 2011) within Laurentia. Proposed invasion pathways are indicated by arrows. The orange arrow indicates the paleoequatorial ("Arctic") pathway, whereas the two dark blue arrows indicate pathways determined by Wright & Stigall (2013a). The pink arrow indicates the pathway utilized by *Eochonetes clarksvillensis*.

Phylogenetic and distribution data

Four clades of rhynchonelliform brachiopods are examined herein. Brachiopods have been widely used in paleobiogeographic analyses and provide a good indicator of oceanographic connectivity (Harper et al. 2013). Because a well-resolved species-level phylogeny is required for phylogenetic biogeography, only four genera were available for inclusion: *Hebertella* Hall & Clarke, 1892, *Plaesiomys* Hall & Clarke, 1892, *Glyptorthis* Foerste, 1914 and *Eochonetes* Reed, 1917. Species of these genera are typically common to abundant within local community assemblages. *Eochonetes* species occupy deeper shelf settings than the other focal taxa, thus, this set of four genera provides a broad coverage of moderately deep to shallow depositional environments. Phylogenetic hypotheses for these genera are published in Wright & Stigall (2013b, 2014) and Bauer (2014). Wright & Stigall (2013a) divided cladogenetic events in these taxa into two temporal bins. Herein, we include only species and speciation events present in their Time Slice 2, which is effectively equivalent to the Katian Stage of the Late Ordovician. Taxa analyzed were widely distributed within Laurentia. Eight biogeographic areas were utilized for this study: the Appalachian, Central, Cincinnati, Scoto-Appalachia, Western and Eastern Midcontinent basins, Anticosti Island and North of the Transcontinental Arch (Fig. 1B). The geographic distribution of each terminal taxon was coded based on the full distribution of each species with the focal regions using detailed locality data published in Wright & Stigall (2013a) and Bauer (2014).

Analyses

Biogeographic patterns were analyzed using the Lieberman-modified Brooks Parsimony approach detailed in Lieberman (2000). First, geographic ranges of ancestral nodes were optimized using a modified Fitch parsimony algorithm. The optimization was then examined to identify episodes of speciation by vicariance (splitting of ancestral range) or dispersal (colonizing areas additional to or different from the ancestral range) (Fig. 2). Vicariance and geodispersal matrices were coded from the resulting data set of 36 species and 68 cladogenic events (see Supplementary Materials archive: http://dx.doi.org/10.6084/m9.figshare.1151584). Matrices were subjected to maximum parsimony analysis using the Exhaustive search method in PAUP 4.0b (Swofford 2002). Node support was constrained via jackknife and bootstrap analyses. Jackknife values were recovered using 100 replicates of a full-heuristic search method with 5% character deletion. Bootstrap values were determined by resampling 68 individuals with a set value of 100 maximum trees saved.

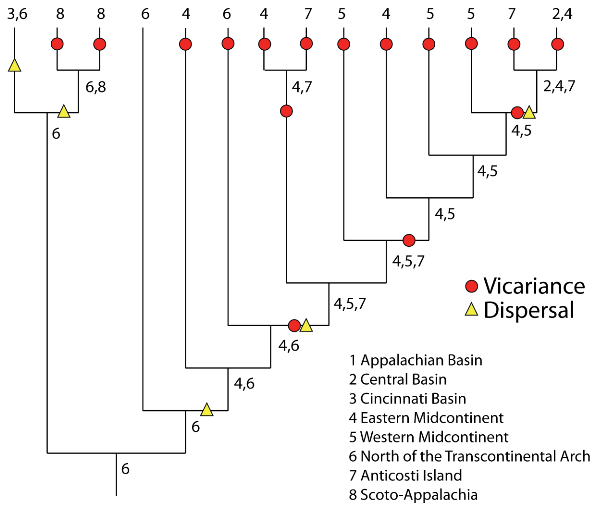

Fig. 2. Cladogram of evolutionary and biogeographic relationships for species in *Eochonetes*. Phylogenetic topology and geographic distributions from Bauer (2014). Biogeographic states for ancestral nodes were optimized using Fitch Parsimony as described in Lieberman (2000).

RESULTS

Biogeographic patterns within clades

Of the 68 cladogenetic events, 40 speciation events exhibit a biogeographic shift indicating speciation by dispersal (= 37.5%) or vicariance (= 62.5%) (see Supplementary Materials archive: http://dx.doi.org/10.6084/m9.figshare.1151584). The three focal species that invaded the Cincinnati Basin during the Richmondian Invasion each followed a different migration route. *Eochonetes clarksvillensis* (Foerste, 1912) originated north of the Transcontinental Arch, *Glyptorthis insculpta* (Hall, 1847) migrated from the Western Midcontinent and *Plaesiomys subquadratus* Hall, 1847 migrated from the Anticosti Island region.

Relationships among geographic areas

The strict consensus trees produced from the recovered general area cladograms are presented in Fig. 3. Tree scores, indicated in the figure caption, demonstrate a significant biogeographic signal within the dataset. The vicariance tree is partially resolved and indicates recent fragmentation between the area pairs of Central +

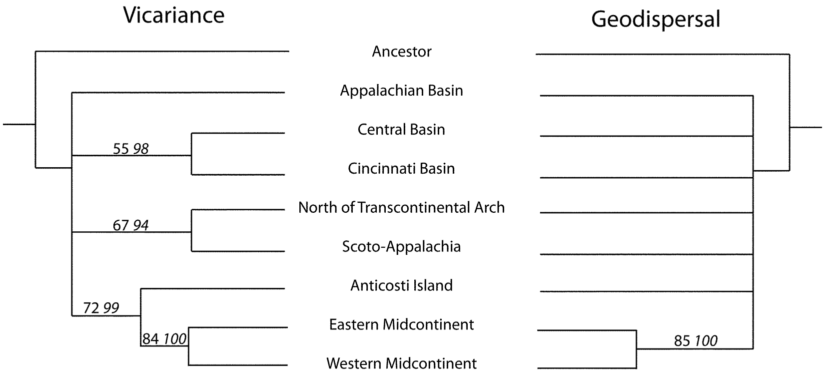

Fig. 3. Vicariance and geodispersal general area cladograms. The vicariance tree indicates the relative order that areas became separated from each other due to barrier formation (intracratonic arch, water mass changes, etc.). The geodispersal tree indicates the relative order in which regions were joined. Congruence between tree topologies indicates that geographic barriers rose and fell in the same relative order, indicating the importance of cyclical geologic processes (e.g. oscillating sea levels), whereas incongruence indicates that singular events (e.g. tectonic pulses) were more influential in biogeographic evolution of the clades (Lieberman 2000). The vicariance area cladogram is the strict consensus of two most parsimonious trees (length of 103 steps, retention index (RI) 0.515, consistency index (CI) 0.845) and the dispersal area cladogram is the strict consensus of eleven most parsimonious trees (91 steps, RI 0.500, CI 0.923). Numerical values indicate bootstrap (plain text) and jackknife (italicized) support for the nodes.

Cincinnati Basins, North of the Trancontinental Arch + Scoto-Applachian Basin and Anticosti Island + (Eastern and Western Midcontinent Basins). The strict consensus tree of geodispersal relationships is almost entirely unresolved, but the sister area relationship between the Eastern and Western Midcontinent regions indicates faunal exchange between these regions.

DISCUSSION

Migration routes during the Richmondian Invasion

Of the focal clades examined in this chapter, three species migrated into the Cincinnati Basin during the Richmondian Invasion from three different ancestral areas: the paleoequatorial region north of the Transcontinental Arch, the midcontinent region and a peripheral basin (Fig. 1B). Surface water currents with a southwestern trajectory across the southern portion of Laurentia (Herrmann et al. 2004) likely facilitated the movement of *Plaesiomys subquadratus* from the Anticosti region to the Cincinnati Basin. Newly developed coastal upwelling along the margin of the Western Midcontinent Basin have previously been hypothesized to facilitate a northward migration of cool-water benthic faunas across eastern Laurentia (Pope 2004) and could have facilitated the transport of *Glyptorthis insculpta* into the Cincinnati region. Trade winds facilitated the transport of warm tropical water onto the paleocontinents, into the basins to the north of the Transcontinental Arch (Pope 2004), and presumably further towards the midcontinent region. *Eochonetes clarksvillensis* originated in the area north of the Transcontinental Arch and utilized the previously documented “Arctic” pathway (Holland 1997 and references therein). These dispersal vectors indicate that multiple pathways, including the previously proposed Arctic (= paleoequatorial) pathway and those described by Wright & Stigall (2013a) were operational during the Richmondian Invasion and that the Cincinnati Basin exchanged fauna with both intracratonic and marginal basins.

These results indicate that the classic Cincinnatian fauna was assembled in a piecemeal fashion: different elements arrive from different places at different times. This pattern matches that observed by Lieberman (1994) for the Middle Devonian Hamilton Fauna of the Appalachian Basin, the classic fauna on which coordinated stasis was defined (Brett et al. 1996). Furthermore, the dominance of speciation by vicariance at the basin-scale observed during this time of overall invasion at the continent-scale provides further evidence that vicariance is an extremely important process in the history of life (cf. Stigall 2013).

Biogeographic area relationships

The vicariance area cladogram reveals the relative timing that barriers formed between areas: areas closer together on the tree were more recently separated from each other than from areas farther away (Rode & Lieberman 2005). Separation between these marine basins was primarily due to exposure of intracratonic arches due to either tectonic uplift or sea level fall. The Taconic tectophase of the Taconic orogeny produced loading on the continental margin that uplifted these arches (Root & Onasch 1999) and reduced connectivity between the marine basins. Repeated intervals of sea level rise and fall are also documented for this interval (e.g. Holland 2008), which could have isolated the Cincinnati and Central basins, the two midcontinent basins and Anticosti Island.

The geodispersal area cladogram indicates the relative timing in which barriers were removed facilitating faunal exchange (Rode & Lieberman 2005). The lack of resolution in the geodispersal area cladogram is due to conflicting dispersal routes among the focal taxa, such as the three discrete dispersal pathways into the Cincinnati Basin described above. The Cincinnati Basin exhibits a sister group relationship with the area north of the Transcontinental Arch in several of the most parsimonious topologies, but pairs with the two midcontinent basins and the Central Basin in other equally parsimonious reconstructions. The influx of invasive species to the Cincinnati basin during the C5 sequence corresponds to the most extensive transgressive event in the Katian (Holland 1997). This transgressive event was a response to a global temperature rise, termed the Boda Event (Fortey & Cocks 2005). During intervals of global warming, taxa which were primarily equatorial could expand their ranges southward as environmental conditions changed. The associated sea level increase would have flooded intracratonic arches (Root & Onasch 1999), thereby removing barriers to species migration and allowing dispersal between multiple basins across Laurentia simultaneously.

Both vicariance and geodispersal analyses recovered a sister area relationship between the Eastern and Western midcontinent basins. This congruence indicates that the midcontinent basins experienced alternating separation and connection signifying that cyclical processes, such as oscillating sea level, were influential in the biogeographic evolution of these areas. Cyclical changes in sea level have been reported and correlated (i.e. Pope 2004) using conodont data between the Appalachian Basin, midcontinent basins and Anticosti Island during this interval, which is consistent with this interpretation.

CONCLUSIONS

The biogeographic patterns documented in this study were produced by oceanographic changes, facilitated by tectonic and climatic events. Vicariance was promoted by uplift of intracratonic arches due to the Taconic tectophase and the regional sea level fall, whereas dispersal was facilitated by the eustatic rise following the Boda Event. This study provides evidence for three distinct migration routes into the Cincinnati Basin during the Late Ordovician Richmondian Invasion. The shared history between the basins of Laurentia is complex and extensive, supporting the multiple pathway hypothesis for the Richmondian Invasion including sources from both intracratonic basins as well as marginal basins.

Acknowledgements. We thank Robin Cocks and Bruce Lieberman for constructive comments that helped us improve this paper. This study was supported by NSF (EF-1206750, EAR-0922067 A. L. Stigall) and the Yale Peabody Museum's Schuchert and Dunbar Grants-in-Aid Award, the Dry Dredgers Paleontological Research Award, Geological Society of America Student Research Grant and an Ohio University Geological Sciences Alumni Grant to J. E. Bauer. This paper is a contribution to IGCP Project 591 "The Early to Middle Paleozoic Revolution." Supplementary materials for this paper are archived at: http://dx.doi.org/10.6084/m9.figshare.1151584.

REFERENCES

Bauer, J. E. 2014. *A Phylogenetic and Paleogeographic Analysis of the Ordovician Brachiopod Eochonetes*. MS thesis, Ohio University, Athens, Ohio, USA, 154 pp. https://etd.ohiolink.edu/!etd.send_file?accession=ohiou1397486053&disposition=inline [accessed 10 Sept. 2014].

Bergström, S. M., Chen, X., Gutiérrez-Marco, J. C. & Dronov, A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ^{13}C chemostratigraphy. *Lethaia*, **42**, 97–107.

Brame, H. M. R. & Stigall, A. L. 2014. Controls on niche stability in geologic time: congruent responses to biotic and abiotic environmental changes among Cincinnatian (Late Ordovician) marine invertebrates. *Paleobiology*, **40**, 70–90.

Brett, C. E., Ivany, L. C. & Schopf, K. M. 1996. Coordinated stasis: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **127**, 1–20.

Cocks, L. R. M. & Torsvik, T. H. 2011. The Palaeozoic geography of Laurentia and western Laurussia: a stable craton with mobile margins. *Earth-Science Reviews*, **106**, 1–51.

Foerste, A. F. 1912. The Arnheim Formation within the areas traversed by the Cincinnati Geanticline. *The Ohio Naturalist*, **12**, 429–456.

Foerste, A. F. 1914. Notes of the Lorraine faunas of New York and the province of Quebec. *Bulletin of the Denison University Science Laboratory of Denison University*, **17**, 247–328.

Fortey, R. A. & Cocks, L. R. M. 2005. Late Ordovician global warming – The Boda event. *Geology*, **33**, 405–408.

Hall, J. 1847. Descriptions of the organic remains of the lower division of the New York System. *Palaeontology of New York, Vol. 1*. New York State Geological Survey, 338 pp.

Hall, J. & Clarke, J. M. 1892. An introduction to the study of the genera of Palaeozoic Brachiopoda. *Palaeontology of New-York, Vol. 8, Part 1*. New York State Geological Survey, 367 pp.

Harper, D. A. T., Rasmussen, C. M. Ø., Liljeroth, M., Blodgett, R. B., Candela, Y., Jin, J., Percival, I. G., Rong, J.-Y., Villas, E. & Zhan, R.-B. 2013. Biodiversity, biogeography, and phylogeography of Ordovician rhynchonelliform brachiopods. *Geological Society, London, Memoirs*, **38**, 127–144.

Herrmann, A. D., Haupt, B. J., Patzkowsky, M. E., Seidov, D. & Slingerland, R. L. 2004. Response of Late Ordovician paleoceanography to changes in sea level, continental drift, and atmospheric $p\mathrm{CO}_2$: potential causes for long-term cooling and glaciation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**, 385–401.

Holland, S. M. 1997. Using time/environment analysis to recognize faunal events in the Upper Ordovician of the Cincinnati Arch. In *Paleontological Events: Stratigraphic, Ecological, and Evolutionary Implications* (Brett, C. E. & Baird, G. C., eds), pp. 309–334. Columbia University Press, New York.

Holland, S. M. 2008. The type Cincinnatian Series: an overview. In *Stratigraphic Renaissance in the Cincinnati Arch: Implications for Upper Ordovician Paleontology and Paleoecology* (McLaughlin, P. I., Brett, C. E., Holland, S. M. & Storrs, G. W., eds), *Cincinnati Museum Center Scientific Contributions*, **2**, 174–184.

Jin, J. 2001. Evolution and extinction of the North American *Hiscobeccus* brachiopod fauna during the Late Ordovician. *Canadian Journal of Earth Sciences*, **38**, 143–151.

Lieberman, B. S. 1994. Evolution of the trilobite subfamily Proetinae and the origin, evolutionary affinity, and extinction of the Middle Devonian proetid fauna of Eastern North America. *Bulletin of the American Museum of Natural History*, **223**, 1–176.

Lieberman, B. S. 2000. *Paleobiogeography: Using Fossils to Study Global Change, Plate Tectonics, and Evolution*. Kluwer Academic Press/Plenum Publishing, New York, 208 pp.

Nelson, S. J. 1959. Arctic Ordovician fauna: an equatorial assemblage? *Journal of Alberta Society of Petroleum Geologists*, **7**, 45–53.

Patzkowsky, M. E. & Holland, S. M. 2007. Diversity partitioning of a Late Ordovician marine biotic invasion: controls on diversity in regional ecosystems. *Paleobiology*, **32**, 295–309.

Pope, M. C. 2004. Cherty carbonate facies of the Montoya Group, southern New Mexico and western Texas and its regional correlatives: a record of Late Ordovician paleoceanography on southern Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**, 367–384.

Reed, F. R. C. 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. *Royal Society of Edinburgh, Transactions*, **51**, 795–998, pls 24.

Rode, A. L. & Lieberman, B. S. 2005. Paleobiogeographic patterns in the Middle and Late Devonian emphasizing Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **222**, 272–284.

Root, S. & Onasch, C. M. 1999. Structure and tectonic evolution of the transitional region between the central Appalachian foreland and interior cratonic basins. *Tectonophysics*, **305**, 205–223.

Stigall, A. L. 2010. Using GIS to assess the biogeographic impact of species invasions on native brachiopods during the Richmondian Invasion in the Type-Cincinnatian (Late Ordovician, Cincinnati region). *Palaeontologia Electronica*, **13**, 5A. Stigall, A. L. 2012. Using ecological niche modeling to evaluate niche stability in deep time. *Journal of Biogeography*, **39**, 772–781.

Stigall, A. L. 2013. Analysing links between biogeography, niche stability and speciation: the impact of complex feedbacks on macroevolutionary patterns. *Palaeontology*, **56**, 1225–1238.

Swofford, D. L. 2002. *PAUP**. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, Massachusetts.

Wright, D. F. & Stigall, A. L. 2013a. Geologic drivers of Late Ordovician faunal change in Laurentia: investigating links between tectonics, speciation, and biotic invasions. *PLoS ONE*, **8**, e68353. DOI: 10.1371/journal.pone.0068353.

Wright, D. F. & Stigall, A. L. 2013b. Phylogenetic revision of the Late Ordovician orthid brachiopod genera *Plaesiomys* and *Hebertella* from Laurentia. *Journal of Paleontology*, **87**, 1107–1128.

Wright, D. F. & Stigall, A. L. 2014. Species-level phylogenetic revision of the Ordovician orthide brachiopod *Glyptorthis* from North America. *Journal of Systematic Palaeontology*, **12,** 893–906.