

Pathways and mechanisms of Late Ordovician (Katian) faunal migrations of Laurentia and Baltica

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Abstract. Late Ordovician strata within the Cincinnati Basin record a mass faunal migration event during the C4 and C5 depositional sequences. The geographic source region for the invaders and the paleoceanographic conditions that facilitated dispersal into the Cincinnati Basin has previously been poorly understood. Using Parsimony Analysis of Endemicity, biogeographic relationships among Laurentian and Baltic basins were analyzed for each of the C1–C5 depositional sequences to identify dispersal paths. The results support multiple dispersal pathways, including three separate dispersal events between Baltica and Laurentia. Within Laurentia, results support dispersal pathways between areas north of the Transcontinental Arch into the western Midcontinent, between the Upper Mississippi Valley into the Cincinnati Basin, and between the peri-cratonic Scoto-Appalachian Basin and the Cincinnati Basin. These results support the hypothesis that invasive taxa entered the Cincinnati Basin via multiple dispersal pathways and that the equatorial Iapetus current facilitated dispersal of organisms from Baltica to Laurentia. Within Laurentia, surface currents and large storms moving from northeast to southwest likely influenced the dispersal of organisms. Larval states were characterized for the Richmondian invaders, and most invaders were found to have had planktotrophic planktic larvae. These self-feeding larvae have high dispersal potential, which – in conjunction with oceanographic and climatic conditions – enabled long-distance dispersal and interbasinal species migrations.

Key words: Parsimony Analysis of Endemicity, dispersal, Cincinnati, Richmondian Invasion, biogeography, larvae, paleoceanography.

INTRODUCTION

The Richmondian Invasion, a regional invasion event that introduced over 60 genera from five phyla into the Cincinnati, Ohio, USA region, occurred during the early Richmondian (late Katian) Age. Several competing hypotheses exist regarding the geographic source of the invaders. The “Arctic” hypothesis (e.g. Foerste 1912; Holland 1997) postulated that invasive taxa originated in equatorial regions within Laurentia, in what today is Canada and Wyoming. Contrastingly, Jin (2001) proposed that at least some invaders originated in cool-water marginal basins around Laurentia and immigrated into the Cincinnati region as part of the broader *Hiscobeccus* expansion. Wright & Stigall’s (2013) phylogenetic analyses of brachiopods that participated in the Richmondian Invasion identified multiple geographic source regions within Laurentia, including both a marginal basin and western epicontinental basin. Bauer & Stigall (2014) reported support for the Arctic pathway as well as the pathways of Wright & Stigall (2014). Other authors (e.g. Anstey 1986; Webby et al. 2004; Congreve & Lieberman 2010) have supported

dispersal between Laurentia and Baltica or proposed Baltica as a source area for some Richmondian taxa (e.g. *Leptaena*, *Streptelasma*).

Many of these proposed migration pathways have received little explicit testing. Thus, in this contribution, we use the historical biogeographic method of Parsimony Analysis of Endemicity (PAE) to examine patterns of endemism and dispersal within Laurentia and between Laurentia and Baltica before and during the Richmondian Invasion. Recovered dispersal pathways and inferred larval ecology of Richmondian invaders are compared to paleoclimate and paleoceanographic conditions within Laurentia to determine dispersal mechanisms and test feasibility of hypothesized dispersal routes.

METHODS

Parsimony Analysis of Endemicity

Biogeographic patterns and dispersal pathways were analyzed using PAE, a quantitative biogeographic method used for reconstructing hierarchical area relationships in the absence of phylogenetic information (Rosen

& Smith 1988). Presence/absence matrices for 63 genera that participated in the Richmondian Invasion were constructed for five intervals within nine geographic areas (Fig. 1) (see Supplementary Materials archive: <http://dx.doi.org/10.6084/m9.figshare.1194963>). Occurrence data were obtained from online catalogs of natural history museums, online public databases (e.g. Paleobiology Database: www.fossilworks.org) and published literature. Formations within each geographic area were correlated to the C1–C5 depositional sequences of Holland & Patzkowsky (1996) using published chemostratigraphic and biostratigraphic data (e.g. Young et al. 2008; Bergström et al. 2010) and adjusted in consult with Dr Stig Bergström (pers. comm. 2014). For each depositional sequence (C1–C5) PAE areagrams were generated to determine changes in area associations between depositional sequences using the parsimony tool in PAST 2.17c (Hammer et al. 2001). Strict consensus trees were computed for analysis. Raup–Crick similarity indices were also calculated between each pair of basins in each depositional sequence (see Supplementary Materials archive: <http://dx.doi.org/10.6084/m9.figshare.1194963>).

Analysis of larval type, paleoceanography and paleoclimate

The larval type and time spent in the larval phase were characterized for invasive genera using published data (e.g. Valentine & Jablonski 1983; Chatterton & Speyer 1989). Due to poor preservation in Late Ordovician strata, the larval type was indeterminable for most molluscan taxa. Controversy exists in the literature over rhynchonelliform brachiopod larval type and when planktotrophy evolved within the clade (e.g. Freeman & Lundelius 2005; Peterson 2005; Popov et al. 2011). This study follows the views of Freeman & Lundelius (2005) in which they concluded that planktotrophy evolved within the Rhynchonellata by the Early Ordovician. Paleoclimatological data for the Late Ordovician Iapetus Ocean were obtained from published ocean modeling studies by Poussart et al. (1999) and Herrmann et al. (2004). Paleoclimate data were interpreted from the literature (e.g. Holland & Patzkowsky 1996; Jin et al. 2013).

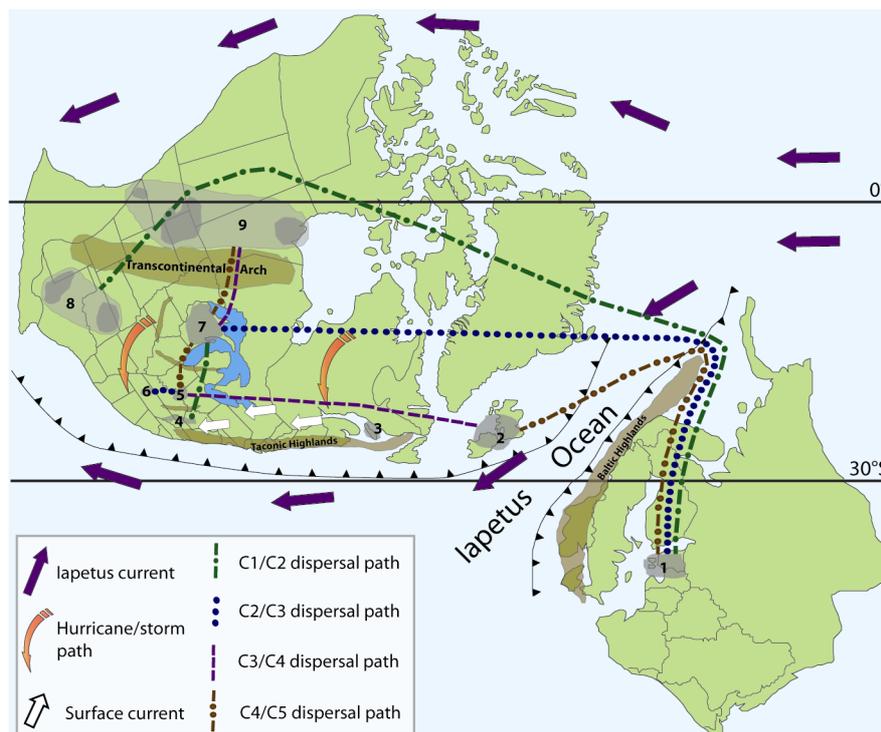


Fig. 1. Paleogeography map of Laurentia and Baltica during the Late Ordovician with inferred dispersal pathways and major paleoclimate and oceanographic influences on larval dispersal labeled. Biogeographic areas analyzed are: 1, Baltic Basin; 2, Scoto-Appalachian Basin; 3, Anticosti Island; 4, Appalachian Basin; 5, Cincinnati Basin; 6, Nashville Dome; 7, Upper Mississippi Valley; 8, Western Midcontinent (Texas and Oklahoma basins); 9, North of the Transcontinental Arch (Hudson, Williston and Bighorn basins). Paleoclimatology after Cocks & Torsvik (2011); current direction and storm tracks after Poussart et al. (1999), Herrmann et al. (2004) and Etensohn (2010).

RESULTS AND INTERPRETATION

Larval type

Richmondian invaders with an identifiable larval type are predominantly planktotrophic (self-feeding) planktic larvae (67.8%). Genera included in this group are members of Crinoidea, Strophomenata and Rhynchonellata. Planktic planula (self-feeding) larvae, representing the class Anthozoa, are also common (28.6%). Lecithotrophic benthic larvae, which gain energy exclusively from yolk sacs during a relatively brief larval stage, comprise only 3.6% of invasive genera. Thus, most Richmondian invaders had long-lived larval phases with the potential for long-distance transport.

Paleobiogeography

Within PAE analyses, dispersal events are identified by changes in biogeographic area relationships on subsequent areagrams. Areagrams resulting from this analysis (Fig. 2), include many such occurrences between multiple and shifting regions. Between the C1 and C2 sequences, there is evidence for dispersal among the

western Midcontinent region, north of the Transcontinental Arch and the Baltic Basin, as well as between the Appalachian Basin and the Upper Mississippi Valley (Fig. 2). Similarity indices for the C2 sequence support close area relationships between the western Midcontinent and north of the Transcontinental Arch (RC index = 0.93) but lower overall similarity between these areas and the Baltic Basin (0.30 and 0.63, respectively). The overall similarity between the Appalachian Basin and Upper Mississippi Valley is 0.55. Thus, we interpret that dispersal occurred primarily between the southern Midcontinent and north of the Transcontinental Arch with some influence from the Baltic Basin during the C1 and C2 sequences.

Between the C2 and C3 sequences there is evidence for dispersal between the Upper Mississippi Valley and the Baltic Basin and between the Cincinnati Basin and the Nashville Dome (Fig. 2). General similarity between the Upper Mississippi Valley and the Baltic Basin, however, is low (0.03) for the C3 sequence, indicating extremely limited faunal interchange. High general similarity (0.81) between the Cincinnati Basin and Nashville Dome indicates substantial faunal mixing, which supports the interpretation of an active dispersal pathway during this time.

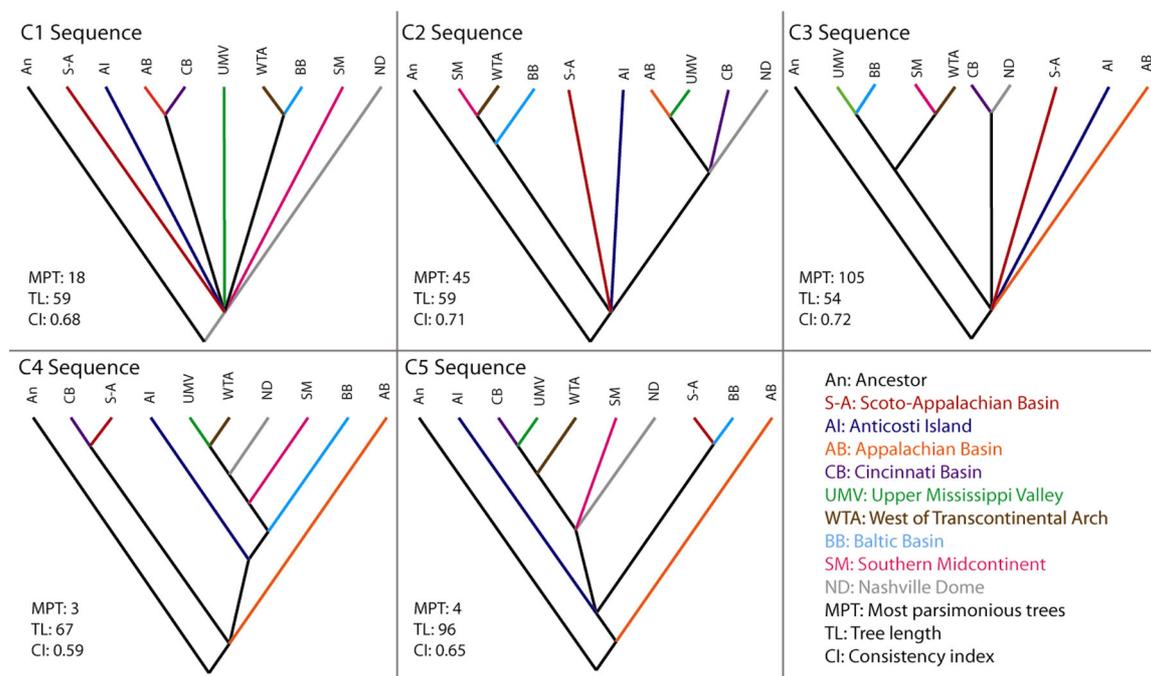


Fig. 2. Parsimony Analysis of Endemicity areagrams. Areas group together in sister-area relationships based on the number of shared endemic taxa; the nested patterns present indicate hierarchical relationships of shared endemic taxa, which is a different metric than overall similarity (similarity values in supplementary materials archive: <http://dx.doi.org/10.6084/m9.figshare.1194963>). Shifts in area relationships between time slices indicate dispersal between those basins.

Between the C3 and C4 sequences, there is evidence for dispersal between the Cincinnati and Scoto-Appalachian basins, and among the Upper Mississippi Valley, north of the Transcontinental Arch, Nashville Dome, western Midcontinent region and the Baltic Basin (Fig. 2). Overall similarity is high for the Nashville Dome and western Midcontinent basins (0.99), and the Baltic Basin and Anticosti Island (0.87), which supports faunal connections between each pair of areas. The lower similarity (0.41) between the Cincinnati and Scoto-Appalachian basins indicates selectivity along this dispersal route.

Between the C4 and C5 sequences, PAE results indicate dispersal among the Cincinnati Basin, the Upper Mississippi Valley and areas north of the Transcontinental Arch, and between Scoto-Appalachia and the Baltic Basin. Overall similarity indices indicate substantial faunal exchange between the Baltic Basin and Scoto-Appalachia (0.96), and between the Upper Mississippi Valley and north of the Transcontinental Arch (0.90), whereas overall similarity between the Cincinnati Basin and north of the Transcontinental Arch was lower (0.40). Combined, these results suggest that the Upper Mississippi Valley region could have operated as an intermediate in the dispersal pathway between areas north of the Transcontinental Arch and the Cincinnati Basin.

Paleoceanography and paleoclimate

Ocean circulation models for the Late Ordovician (e.g. Poussart et al. 1999; Hermann et al. 2004) indicate the equatorial Iapetus Current flowed around Laurentia from the east, splitting around the paleocontinent to the north and south (Fig. 1). Trans-Iapetus dispersal was likely accomplished by “island hopping” among volcanic arcs surrounding Laurentia, as the majority of Richmondian invaders had planktotrophic planktic larvae with the potential to disperse over 100 km during one generation (Tremblay et al. 2008).

Intercontinental currents likely facilitated dispersal among Laurentian basins. The recovered dispersal pathways between the Cincinnati Basin and surrounding areas suggest that earlier (C1 through early C2 sequence) species migrations were likely influenced by the funneling of oceanic waters into Laurentia by the Sebree Trough (Ettensohn 2010). However, subsequent weathering and erosion of the Taconic highlands produced heavy sedimentation and the Sebree Trough was infilled by the beginning of the C2 sequence, restricting contact with the open ocean (Ettensohn 2010). A surface current, developed from the interaction of prevailing trade

winds and the Coriolis Effect, has been proposed to have flowed from northeast to southwest across Laurentia (Fig. 1; Ettensohn 2010). Dispersal from Scoto-Appalachia and Anticosti Island to the Cincinnati Basin could have been facilitated by this southwesterly oriented current.

Furthermore, storms swept across Laurentia from the northeast during the Late Ordovician (Fig. 1). Tempestite beds in the Cincinnati region indicate the area was subjected to strong seasonal storms (Holland & Patzkowsky 1996). Modern studies of coral larval transport have demonstrated that similar storm activity can greatly increase the dispersal distance (Radford et al. 2014). Therefore, storms tracking from the northeast could have transported organisms across geographic barriers that would not normally be breached, aiding in the dispersal of taxa into surrounding basins from the Upper Mississippi Valley and north of the Transcontinental Arch.

In addition, a substantial transgression occurred at the onset of the C5 sequence, which has been linked to global warming from the short-lived Boda Event (Fortey & Cocks 2005). This transgression could have flooded intracratonic arches and facilitated dispersal between geographically separated areas (Wright & Stigall 2013), such as the basins in Cincinnati, the Upper Mississippi Valley and north of the Transcontinental Arch regions.

DISCUSSION

Results of PAE support multiple dispersal pathways per timeslice and similarity analyses indicate the degree of faunal exchange along these connections. These data support three separate dispersal events between Laurentia and Baltica. Within Laurentia, the basins of the western Midcontinent and north of the Transcontinental Arch exhibit close area relationships and high similarity in all intervals, which indicates substantial dispersal between these areas throughout the study interval. For the Cincinnati Basin, the primary dispersal routes involved the Nashville Dome (C2–C3 sequences), Scoto-Appalachian Basin (C3–C4 sequences) and the Upper Mississippi Valley and north of the Transcontinental Arch (C4–C5 sequences).

The recovered pattern supports the multiple pathway hypothesis for the Richmondian Invasion (cf. Wright & Stigall 2013) and the idea that separate pulses of the Richmondian Invasion had distinct source areas. Specifically, PAE results indicate a counter-clockwise shift in migration routes between the C2 and C5 sequences. The primary invasion pulses occurred in the

C4 and C5 sequences. The C4 sequence invasion sourced taxa from peripheral basins east of the Cincinnati region, such as the Scoto-Appalachian Basin and Anticosti Island, which is consistent with the dispersal path previously reconstructed for the brachiopod *Plaesiomys* (Wright & Stigall 2013). The second phase of the Richmondian Invasion, in which over 50 new genera appeared in the Cincinnati Basin, occurred in the early C5 sequence (Holland 1997). This phase involved taxa immigrating from basins northwest of the Cincinnati Region (Fig. 2), which accords with dispersal paths reconstructed for brachiopods *Eochonetes* and *Glyptorthis* and solitary corals (Elias 1983; Bauer & Stigall 2014; Wright & Stigall 2014). This shift in continental dispersal pathways coincides with a large transgression and a shift from temperate-style to tropical-style carbonate deposition throughout Laurentia, thought to be the result of global warming from the short-lived Boda Event (Fortey & Cocks 2005), or termination of cool-water upwelling due to basinal infilling (Holland & Patzkowsky 1996).

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