

Extreme faunal endemism, super-island faunas, and the Late Ordovician mass extinction[☆]

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ARTICLE INFO

Editor: L Angiolini

Keywords:

Late Ordovician mass extinction event (LOME)
Brachiopods
Faunal endemism
Palaeobiogeography
Laurentia

ABSTRACT

The majority of studies on mass extinction events (MEEs) have focused on the various extrinsic or palaeoenvironmental killing mechanisms, most associated with habitat destruction and some of which remain hotly contested. The '*mass extinction by insularization and kill*' (MEIK) model of this study is proposed as a significant intrinsic cause of the Late Ordovician MEE based on palaeoecological and palaeobiogeographical analyses of Ordovician brachiopod faunas from Laurentia and its adjacent tectonic plates. During the Late Ordovician pulses of a first-order sea-level rise, the MEIK model reveals that biodiversity hotspots shifted from open ocean to epicontinental seas associated with a drastic increase in faunal endemism. Continental-sized 'island faunas', exemplified by the Laurentian intracratonic-sea brachiopods, were characterized by high abundance but relatively low diversity, but more critically the eventual loss of their inter-plate dispersal ability. The onset of mass extinction of these highly endemic 'super-island' faunas, specialized in living in shallow intracratonic seas for ~8 million years during the Katian, occurred at the start of the Hirnantian glaciation due to draining of epicontinental seas and loss of their specialized habitats. The data presented here suggest that during a major sea-level rise, global biodiversity epicentres migrated from the ocean to epicontinental seas, becoming genetically isolated, rendering marine shelly benthos intrinsically susceptible to rapid environmental change and subsequent mass extinction.

1. Introduction

In Darwinian evolution, its underlying intrinsic cause is genetic mutations, which are selected by myriads of extrinsic environmental controls, leading to the origin of new species. In addition, the intrinsic factor for the extinction of species is isolation and reduction of populations to destroy the viability of their gene pool, which may also be caused by various environmental constraints. In previous studies of mass extinction events (MEEs), much attention has been focused on extrinsic factors. This has led to numerous debates because extinctions tend to have multiple environmental causes. This approach can be likened to an attempt to determine an environmental factor as the cause of speciation, while ignoring genetic mutation as the singular underlying intrinsic cause.

The Late Ordovician Mass Extinction (LOME) was the first of the big five MEEs in Phanerozoic history (Raup and Sepkoski Jr, 1982), wiping out about an estimated 50 % of the marine invertebrate genera in double

pulses, one at the onset of the Hirnantian glaciation, and the other near its termination (Sheehan, 1973, 2001; Sepkoski Jr, 1981; Alroy et al., 2008; Rasmussen and Harper, 2011; Rasmussen et al., 2019; Harper, 2024), although the possibility of a continuous single-pulse scenario has also been proposed for the LOME (e.g., Wang et al., 2019). Previous work emphasized the spatiotemporal relationship and a cause-effect connection between the LOME and glaciation, supported by a wide range of palaeontological, sedimentological, and geochemical data (Sheehan, 2001; Brenchley et al., 1994; Delabroye and Vecoli, 2010; Finnegan et al., 2011, 2012; Harper et al., 2014; Ghienne et al., 2023; Kaiho, 2025). However, the Pleistocene glaciation, of similar magnitude to that of the Hirnantian, was not associated with a mass extinction event (Finnegan et al., 2011; McGhee Jr et al., 2012). Thus, in addition to the various extrinsic environmental factors associated with the Hirnantian glaciation, intrinsic biological factors most likely have played a significant role in the Hirnantian mass extinction.

The classic theory of island biogeography (MacArthur and Wilson,

* This article is part of a Special issue entitled: 'Brachiopods' published in Palaeogeography, Palaeoclimatology, Palaeoecology.

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1967) demonstrated that the isolation of a biota, due to either space limitation or reduced immigration, leads to increased extinction rates. Extreme isolation of an island biota, popularized as a process of insularization by Quammen (1996), reduces the genetic variability and population viability of species, eventually leading to their extinction. Geographically isolated or ‘perched faunas’ (Johnson, 1974; Stanley, 2010) have been proposed as an important biological cause for some MEEs although the previous hypotheses have never been tested by quantitative faunal data.

Brachiopods were the most dominant group of marine shelly benthos in the Palaeozoic, and as such they are critical to our understanding of the cause and processes of the Hirnantian mass extinction. During the Great Ordovician Biodiversification Event (Webby et al., 2004; Harper, 2006; Servais and Harper, 2018; Rasmussen et al., 2019; Harper et al., 2020; Servais et al., 2010, 2021), a fundamental brachiopod faunal turnover took place in the Middle Ordovician (middle Darriwilian), corresponding to the traditional Arenig–Llanvirn boundary (Harper et al., 2004). In this study, we focus on the changing biogeography in the post-turnover Ordovician, an interval of some 20 million years marked by drastic changes in global climate, palaeogeography, and eustatic sea level (Haq and Schutter, 2008; Scotese, 2023; Young et al., 2023). In this study, upper Darriwilian to Hirnantian brachiopod faunas from both pericratonic and intracratonic depositional settings of Laurentia are reviewed to determine their levels of endemism by comparison with other well-documented tropical brachiopod faunas from its adjacent tectonic plates (Fig. 1; Supplementary Material, Table S1). The traditional North American stratigraphic stages are used as time slices because the global stages (especially the Katian) are too long for

meaningful faunal divisions, although where possible these are correlated with the global stages for the system (see Bergström et al., 2008; updated in ISOS, 2025).

2. Material and methods

2.1. Middle–Upper Ordovician brachiopod faunal data and stratigraphic correlations used for calibration of faunal endemism

In compiling the Ordovician brachiopod faunal database for global biodiversity and biogeographic analyses, only the subphylum Rhynchonelliformea is considered because the other two subphyla, Linguliformea and Craniiformea, constitute only minor components of the faunas and their taxonomic study is extremely uneven for different regions due to the lack of experts in these groups or the strong collection bias introduced by the predominance of phosphatic micro-brachiopods etched out from limestones.

The selection of regions and their brachiopod faunas is based mainly on two criteria:

- (1) The brachiopod taxonomy should be up to date through reliable systematic descriptions. Most of the faunas used in this study have undergone recent taxonomic revisions or assessment, particularly in association with the recent internationally coordinated revision of the brachiopod volumes of the Treatise on Invertebrate Paleontology (Kaesler, 1997–2006; Selden, 2007). The faunal lists from the United Kingdom (both the Avalonian terrane of England and Wales and the peri-Laurentian terranes of

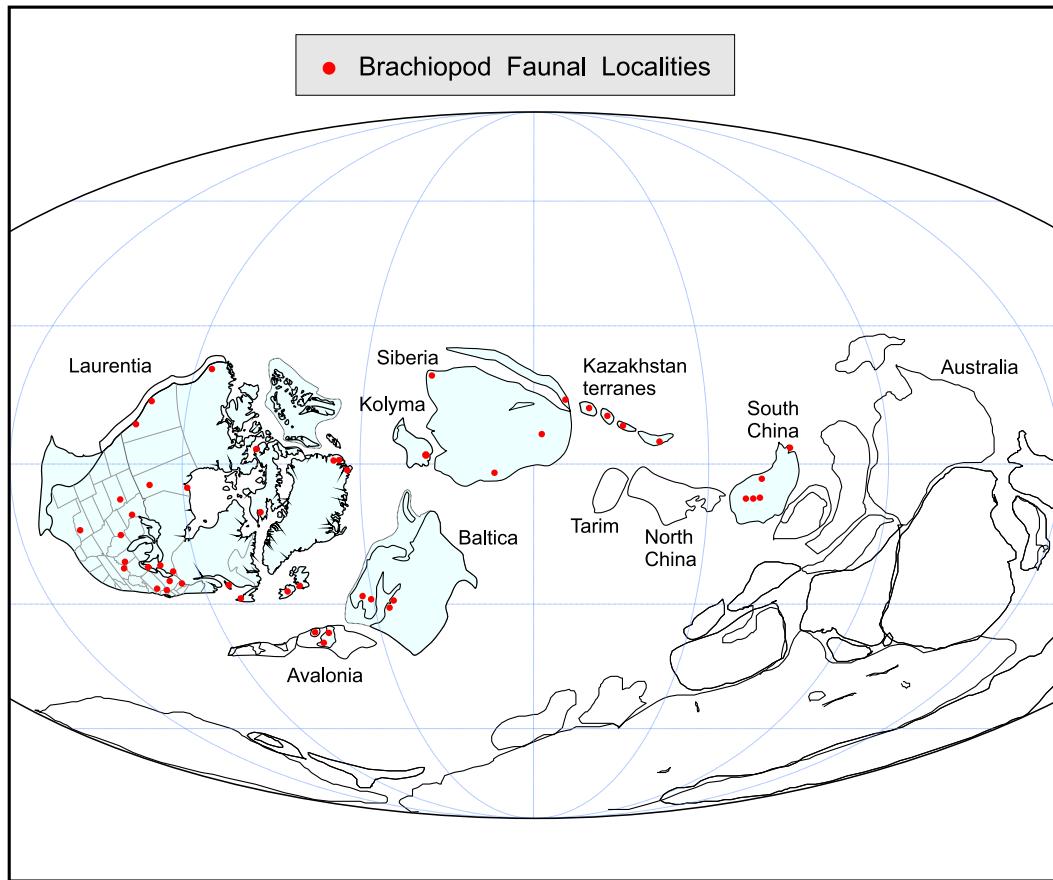


Fig. 1. Global palaeogeography during the Late Ordovician, with the late Katian (Richmondian) used as an example. For palaeo maps of other time slices, refer to Cocks and Torsvik (2021) and Scotese (2023). Brachiopod faunal localities (red dots) considered in this study are plotted on the base map modified from several sources (Rasmussen and Harper, 2011; Cocks and Torsvik, 2011, 2021; Scotese, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Scotland and Northern Ireland) are derived from the updated taxonomic compendium of [Cocks \(2008\)](#). The faunal data are based also on numerous recent monographs and other taxonomic studies for North America (e.g., [Cooper, 1956](#); [Jin et al., 1997, 2024](#); [Jin and Zhan, 2001, 2008](#)), Siberia (e.g., [Yadrenkina, 1989; Cocks and Modzalevskaya, 1997](#)), Baltica (e.g., [Bondarev, 1968; Hints and Harper, 2003, 2015; Rõõmusoks, 2004; Cocks, 2005; Hints et al., 2018](#)), Kazakhstan (e.g., [Popov et al., 2000, 2002; Nikitin et al., 2006; Nikitina et al., 2006](#)), and South China (e.g., [Zhan and Cocks, 1998; Zhan and Jin, 2005; Rong et al., 2020; Huang et al., 2020; Jin and Harper, 2024](#)). A comprehensive list of publications and faunal lists used for compiling the faunal database are too long to be presented here but are available from the first author.

- (2) The stratigraphic position of each brachiopod fauna is now relatively well established. During the last three International Geoscience Programme projects (IGCP 410, 503, and 591) that focused on the Ordovician biodiversification, palaeoclimate and palaeobiogeography, the global correlation of Ordovician strata has been vastly refined as a result of international collaboration. The most recently formalized global stages, especially those for the Middle and Late Ordovician (e.g. Darriwilian, Sandbian, and Katian) are, however, too broad to be used as the primary time slices for the biogeographic analysis in this study. Instead, the North American stages are used as the time units partly because of their finer division, and partly because North America (Laurentia) is treated as a central reference point for palaeobiogeographical analysis and determination of various levels of faunal provincialism and endemism. Inter-region stratigraphic correlations are based on the most recent recommendations of International Subcommission on Ordovician Stratigraphy ([ISOS, 2025; Cohen et al., 2025](#)).

Within Laurentia, [Cooper's \(1956\)](#) classic monographic study "Chazyan and related brachiopods" includes the main part of the upper Darriwilian–lowermost Katian (Chazyan–Sandbian) brachiopod faunas of Laurentia. His stratigraphic scheme, however, has been problematic. When incorporating [Cooper's \(1956\)](#) brachiopod data and converting his stages (e.g., Marmorian, Ashbyan, Porterfieldian, Wildernessian) and associated stratigraphic units to the modern North American regional stages, this study follows the recalibrated stratigraphic scheme by Bergström et al. (1988) based on conodont data. In addition, [Cooper's \(1956\)](#) brachiopod ranges were double checked against their associated geological formation. For example, the brachiopod genera that occur in his Marmorian Stage include those from the Lenoir, Day Point, Crown Point, Valcour, and Mingan formations of eastern Laurentia, which are considered correlatives to the British Llanvirn Stage (Bergström et al., 1988), equivalent to the upper Chazy (upper Darriwilian) in modern chronostratigraphy. Most of Cooper's other stages (e.g., Ashbyan, Porterfieldian, Wildernessian, etc.) have been broadly correlated with the British Caradoc Series (Bergström et al., 2008, p. 30) and can be considered equivalent to the modern global Sandbian Stage because these stages as used by [Cooper \(1956\)](#) are pre-Chatfieldian (pre-Katian).

2.2. Faunal similarity analysis

Based on selection criteria outlined above, the global faunal database is divided into seven time slices for the Chazyan, Turonian, Chatfieldian, Edenian, Mayillian, Richmondian, and Hirnantian (Supplementary Material, Tables S2–S8). For each time slice, the binary dataset is analyzed using the PAST software package ([Hammer et al., 2001; Hammer and Harper, 2024](#)) to calculate Simpson similarity coefficient values among the brachiopod faunas of nine palaeogeographical regions (Scotland, Northern Ireland, Avalonia, Baltica, Siberia, Kazakhstan, and South China). The Simpson similarity coefficient is used as a proxy for

the palaeobiogeographic affinities of Laurentia with other regions because this coefficient values tend to be more evenly distributed between 0 and 1 (Supplementary Material, Table S1). Some other similarity coefficients (e.g., Raup-Crick) may have accentuated values towards the two ends of the spectrum and obscure some details — for example, Simpson coefficient values lower than 0.1 may be lumped into 0.

In the PAST program, the Simpson similarity coefficient for paleobiogeographic affinity is

$$S_s = \frac{M}{N_{min}}$$

where S_s = Simpson similarity coefficient; M = number of taxa shared by two faunas (number of positive matches); N_{min} = the smaller of the numbers of presences in the two faunas.

To generate plots of cluster analysis (CA) for these faunas, the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on the Raup-Crick similarity coefficient is used to accentuate the clustering patterns and make them easier to visualize, although other similarity measures resulted in similar but less clearly delineated patterns of clusters. The CA dendrogram based on the Raup-Crick index ([Raup and Crick, 1979](#)) has the best scaling for visual presentation, as plots based other coefficients tend to have a scaling pattern less suitable for visual presentation (e.g. the cluster linkage points become concentrated near the bottom of the plot if the similarity formula, such as the Simpson coefficient, generates proportionally lower values, although the cluster groupings are similar). The Raup & Crick index uses a randomization ("Monte Carlo") procedure, comparing the observed number of species occurring in both associations with the distribution of co-occurrences from 200 random replicates ([Hammer and Harper, 2024](#)). It is based on probability theory and thus obviating need for error estimates, and at the same time emphasizing the significance of relatively rare, shared taxa for palaeobiogeographic affinities.

The CA plots for the Chazyan and Hirnantian brachiopod faunas are provided as examples of semi-cosmopolitanism ([Fig. 2A, D](#)); whereas the plots for the Chatfieldian and Richmondian faunas as examples of the onset and peak endemism associated with the origin and evolution of the epicontinentalsea shelly fauna of Laurentia ([Fig. 2B, C](#)). Details of palaeobiogeographic similarities among various faunas can be found in the Supplementary Material (Table S1).

2.3. NMDS and network analyses

To complement the cluster analysis of the four key time slices as discussed above, Non-metric Multidimensional Scaling (NMDS) and network analyses were performed to provide more visually intuitive plots of the size of faunas and numbers of endemic or cosmopolitan taxa for each palaeogeographical region ([Figs. 3, 4](#)), based on the same binary dataset used for the cluster analysis (see Supplementary Data).

Non-metric Multidimensional Scaling (NMDS) analysis was performed using PAST ([Hammer et al., 2001; Hammer and Harper, 2024](#)) to detect palaeobiogeographical affinities among the faunas of Laurentia, peri-Laurentia (e.g., Scotland, Northern Ireland), Baltica, Siberia (including peri-Siberian blocks, such as Kolyma), and South China. By treating faunal localities as cases and brachiopod genera as variables, the Raup-Crick similarity coefficient is used to map out the faunal affinities. This coefficient has the advantage of generating more clearly differentiated clusters by enforcing the significance of shared genera, based on the concept that the probability for two regions to share a rare genus is lower than to share a common (e.g., cosmopolitan or long-ranging) genus. In other words, a shared rare genus carries more weight than a shared common genus for indicating a close palaeobiogeographical affinity between two regions. In this sense, the Raup-Crick coefficient shares a certain degree of similarity to palaeobiogeographic analysis using a cladistic (parsimony) approach, such that used

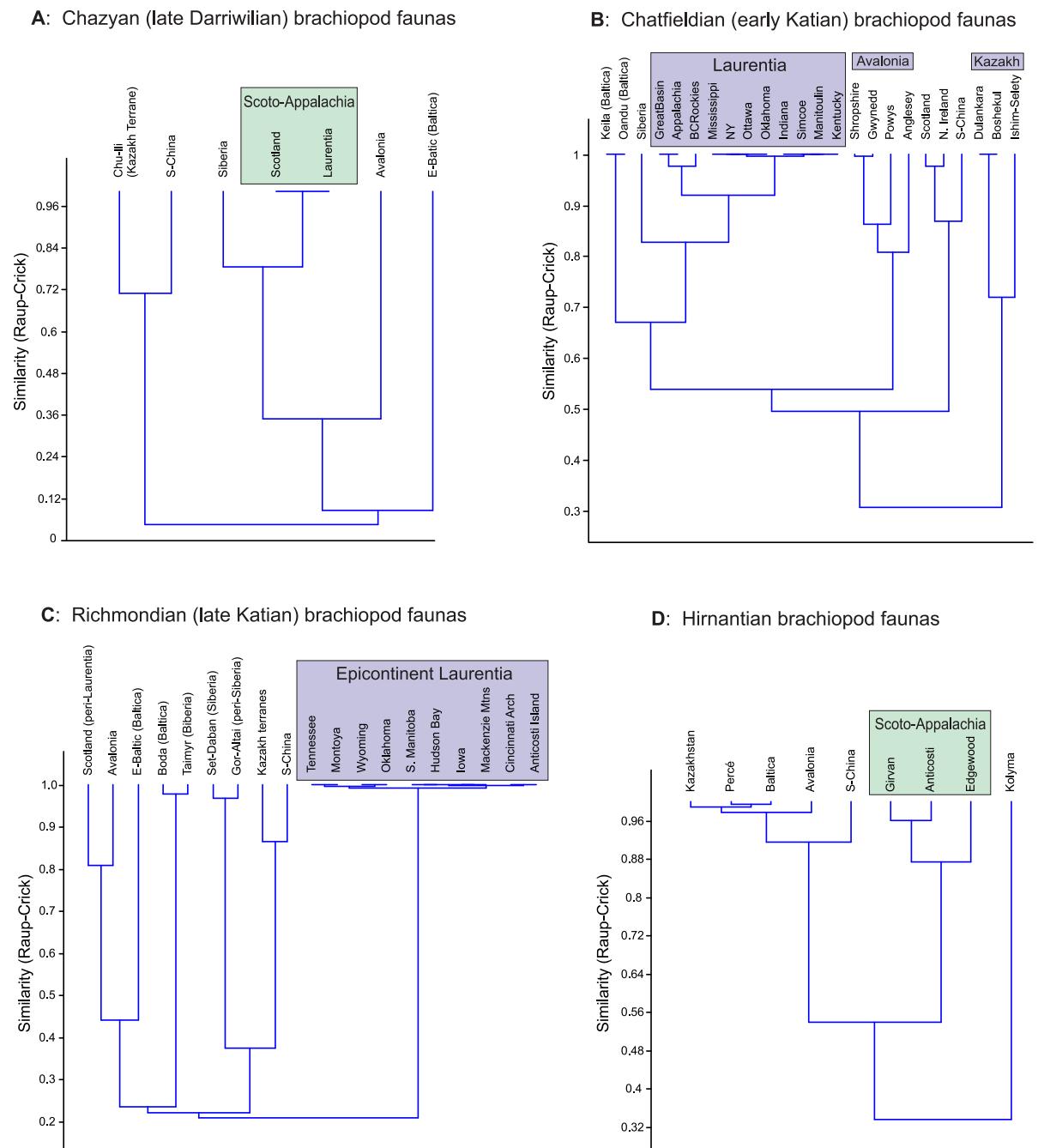


Fig. 2. Cluster analysis of brachiopod faunas. A, B) Semi-cosmopolitan, pericratonic Scoto-Appalachian fauna persisted from Chazyan to Chatfieldian (late Darriwilian–early Katian). C) extremely endemic epicontinent Laurentia during the Richmondian, in keeping with the broad trend of Katian marine transgression related to a first-order sea-level highstand (Haq and Schutter, 2008; Scotese, 2023). D) Return of the semi-cosmopolitan pericratonic brachiopod fauna during the Hirnantian sea-level lowstand.

for the study of Devonian biogeography (e.g., Lieberman, 2003; Stigall Rode and Lieberman, 2005). Similar to the mapping of synapomorphic characters shared between two taxa, cladistic biostratigraphic analysis tends to emphasize the presence of “unique taxa” shared between two geographic areas and hence their significance for determining palaeobiogeographic affinity.

Network Analysis is an ordination method that generates a network diagram indicating the relationships between localities and taxa together with their relative generic richness (indicated by the diameter of the circle for each locality), as well as the number of localities where each genus occurs (the number of occurrences per genus is also indicated by the circle size). The analysis utilised the Gephi software package

(Bastian et al., 2009) and the bipartite network, showing both localities and genera accordingly. A locality node is connected to a genus node if the genus is found in that locality. In this plot, nodes are repelled from each other but attracted by edges using the ForceAtlas2 algorithm.

2.4. Diversity of faunas

For a global-scale comparison of faunal similarities among tectonic plates, a binary dataset (presence 1, absence 0) is used. In this study, all our reference to “diversity” implies the number of genera per time slice per plate. At this scale of study, it would be highly impractical to calculate true alpha and beta diversities, where abundance data per

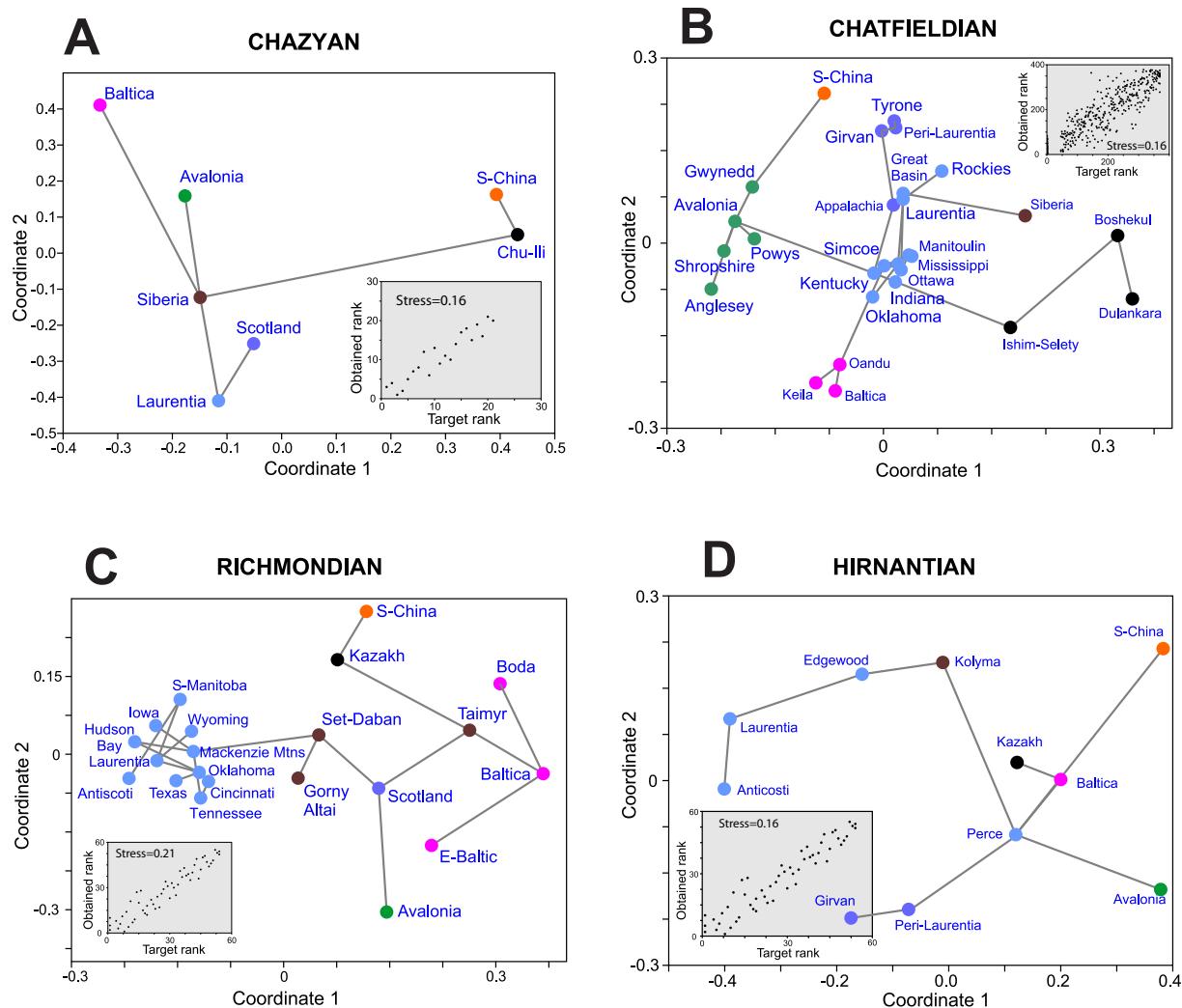


Fig. 3. Non-metric Multidimensional Scaling (NMDS) Ordination of brachiopod faunas. A, B) Semi-cosmopolitan, pericratonic Scoto-Appalachian fauna persisted from Chazyan to Chatfieldian (late Darriwilian–early Katian). Coordinates ranging from –0.4 to 0.5 along the X-axis and –0.4 to 0.5 along the Y for the Chazyan and –0.3 to 0.45 along the X-axis and –0.3 to 0.3 along the Y for Chatfieldian. C) Highly endemic epicontinental fauna of Laurentia during the Richmondian (left), in keeping with the broad trend of Katian marine transgression related to a first-order sea-level highstand (Haq and Schutter, 2008; Scotes, 2023). D) Return of the semi-cosmopolitan pericratonic brachiopod fauna during the Hirnantian sea-level lowstand; coordinates ranging from –0.3 to 0.4 along the X-axis and –0.3 to 0.3 along the Y.

taxon (e.g. number of specimens per species per sample) would be needed. Such studies are not suitable for a study at the global scale as designed for this study, since each study area within a tectonic plate would be the subject of an individual investigation, out of the scope of the present analyses. Where abundance data are available for the Ordovician faunas dealt with in this study, such detailed studies of alpha or beta diversities have been already carried out (e.g., Zhan et al., 2002, 2006; Jin and Copper, 2008; Sproat and Jin, 2017).

3. Results of quantitative faunal analyses

The results of the cluster, NMDS and network analyses, as well as the spatiotemporal trends of endemism and diversity, are summarized in Figs. 2–5, with the faunal data provided in the Supplementary material. From the plots, it can be observed that the brachiopod faunas in Laurentia exhibited stepwise trends in their palaeoecological and palaeogeographical transformations, leading to pronounced endemism and an overall reduction in diversity compared to the Scoto-Appalachian fauna that thrived in continental-margin, pericratonic seas, as is discussed in detail below.

4. Discussion — development of brachiopod faunal endemism in intracratonic seas

During the Late Ordovician major sea-level rise, brachiopod faunas underwent progressive faunal insularization and intra-continental regional invasions (Stigall, 2023) as they radiated rapidly to evolve into strongly endemic ‘super-island’ faunas. By the late Katian, they occupied the vast epicontinental seas of Laurentia, prior to the onset of the Hirnantian glaciation.

4.1. The Laurentian brachiopod fauna in the Middle–Late Ordovician transition: from semi-cosmopolitan to endemic

After the Middle Ordovician faunal turnover (Harper et al., 2004), the brachiopod faunas of Laurentia evolved initially during a sea-level lowstand in the late Darriwilian (Chazyan, Llanvirn), confined mostly to pericratonic marine shelves (Fig. 1). In marginal Laurentia (e.g., eastern New York and Pennsylvania, and eastern Quebec) and peri-Laurentia (e.g., Scotland, and Northern Ireland), a Scoto-Appalachian fauna (Jaanusson, 1979) thrived, sharing a large number of brachiopod genera with Avalonia, Baltica, and Siberia (Figs. 2A, 3A, 4A).

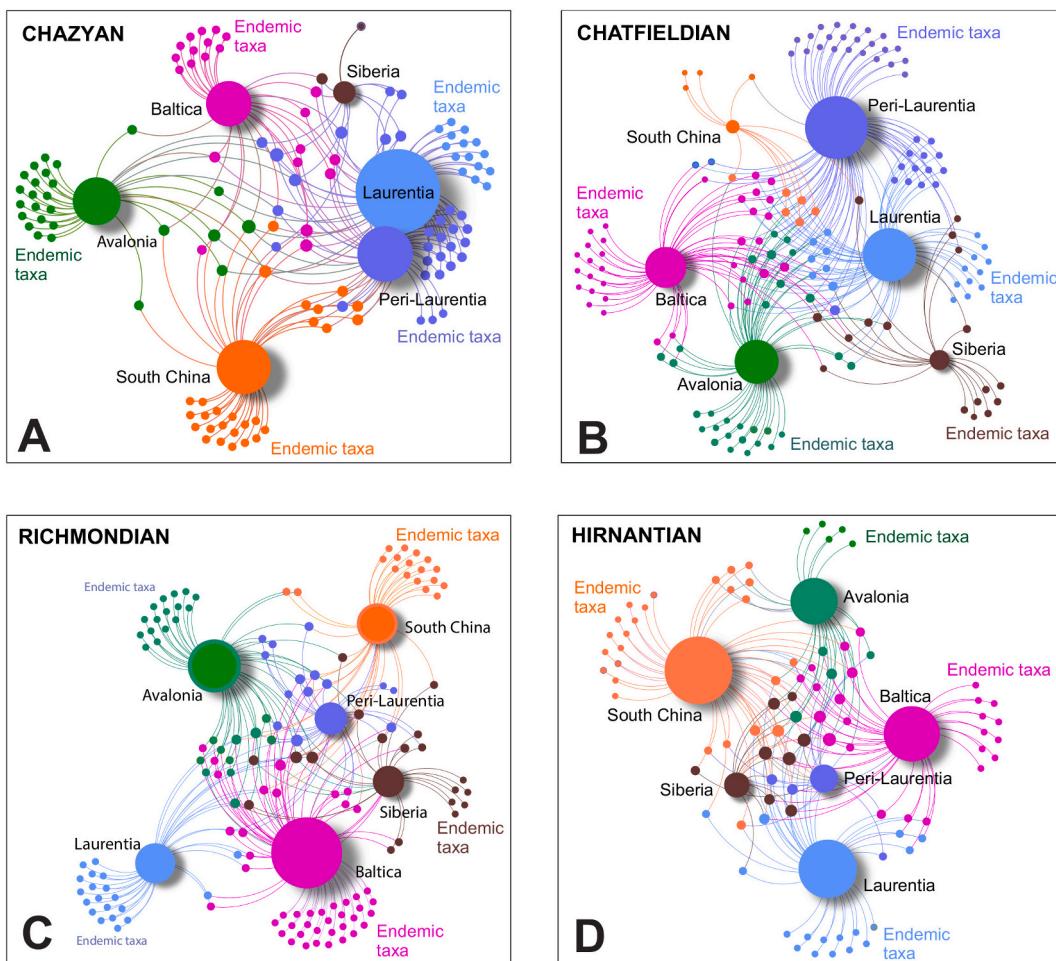


Fig. 4. Network analysis of brachiopod faunas, corresponding to the four plots of cluster analysis in Fig. 2. Note that the size of a locality circle (shadow-bearing) is positively related to the number of genera it contains. A, B) Semi-cosmopolitan, pericratonic Scoto-Appalachian fauna from Chazyan to Chatfieldian (late Darriwilian–early Katian). C) Strongly endemic fauna of Laurentia during the Richmondian, represented by a reduced total number of genera but relatively large proportion of endemic genera. D) Semi-cosmopolitan, pericratonic brachiopod fauna during the Hirnantian.

The highest brachiopod diversity was centered along the southeast passive margin of Laurentia before the initiation of the Taconic (Appalachian) Orogeny. The pericratonic brachiopod fauna along the southeast margin of Laurentia comprised 63 rhynchonelliform genera (Figs. 5, 6A), scoring a Simpson similarity coefficient value of 0.84 with the fauna in peri-Laurentia terranes (mainly Scotland), and 0.77 with Siberia (coefficient scale 0–1). The similarity scores are also relatively high with those in higher-latitude terranes (e.g., Avalonia) or farther away plates (e.g., South China), in the range of 0.38–0.39. This implies a high degree of faunal exchange between Laurentia and other mid-latitude to tropical plates and a period of semi-cosmopolitanism of the predominant marine shelly benthos, with characteristic taxa (e.g., *Christiana*, *Hesperorthis*, *Leptellina*, *Nothorthis*, *Palaeostrophia*, *Rostricellula*) spanning four to five of the tectonic regions considered in this study. Scotland was a peri-Laurentia terrane during the Ordovician, and its close faunal affinity with cratonic Laurentia supports the concept of a Scoto-Appalachian fauna (Williams, 1973; Jaanusson, 1979; Jaanusson and Bergström, 1980; Jin, 2001; Harper et al., 2013; Candela, 2014) on continental-margin shelves before the onset of the Taconic Orogeny. The high-abundance and high-diversity Scoto-Appalachian fauna was symbolized by *Christiana* (and closely related *Nubialba*, *Christianella*) and *Bimuria* (and *Bilobia*, *Craspedelia*) in the Chazyan–Turinian (upper Darriwilian–Sandbian) strata of pericratonic marine shelf settings in Laurentia and the peri-Laurentia terranes of Scotland, and Northern Ireland, and continued into the Katian (Chatfieldian–Richmondian; Fig. 7P–U).

The relatively high level of cosmopolitanism of the Scoto-Appalachian fauna was also characterized by the global distribution of *Christiana* and *Bimuria* during their early occurrences in the Chazyan–Sandbian interval, reported from palaeogeographical regions ranging from tropical to temperate palaeolatitudes, such as Laurentia and the peri-Laurentia terranes of Scotland and Northern Ireland (Cooper, 1956; Williams, 1962), Baltica (Spjeldnæs, 1957; Jaanusson, 1962; Bondalev, 1968; Mitchell, 1977); Siberia and peri-Siberian terrane of Gorni Altai (Kulkov and Severgina, 1989), Avalonia (Lockley and Williams, 1981; Cocks, 2008), Kazakh terranes (Rukavishnikova, 1956; Nikitin and Popov, 1984) and South China (Zeng, 1987; Liang et al., 2014).

Brachiopod semi-cosmopolitanism persisted into the Turinian (Sandbian) and the early Chatfieldian (earliest Katian), with a sustained increase in overall diversity in Laurentia and its adjacent regions. Cluster and NMDS analyses (Fig. 2B, 3B) show that the epicratonic brachiopod fauna of Laurentia became clearly defined during the Chatfieldian, with a close biogeographic link with the fauna of Baltica, although network analysis (Fig. 4B) demonstrates that both cosmopolitan and endemic taxa were similarly numerous at that time. Despite a relatively high Simpson similarity values between Laurentia and peri-Laurentia from Turinian to early Chatfieldian (0.61 and 0.61), the network analysis indicates that the two faunas became somewhat more isolated by Chatfieldian than in the Chazyan (compare Fig. 4A with 4B). Globally, the Chatfieldian brachiopod fauna of Laurentia maintained a relatively high level of biogeographic affinity to other regions, as indicated by

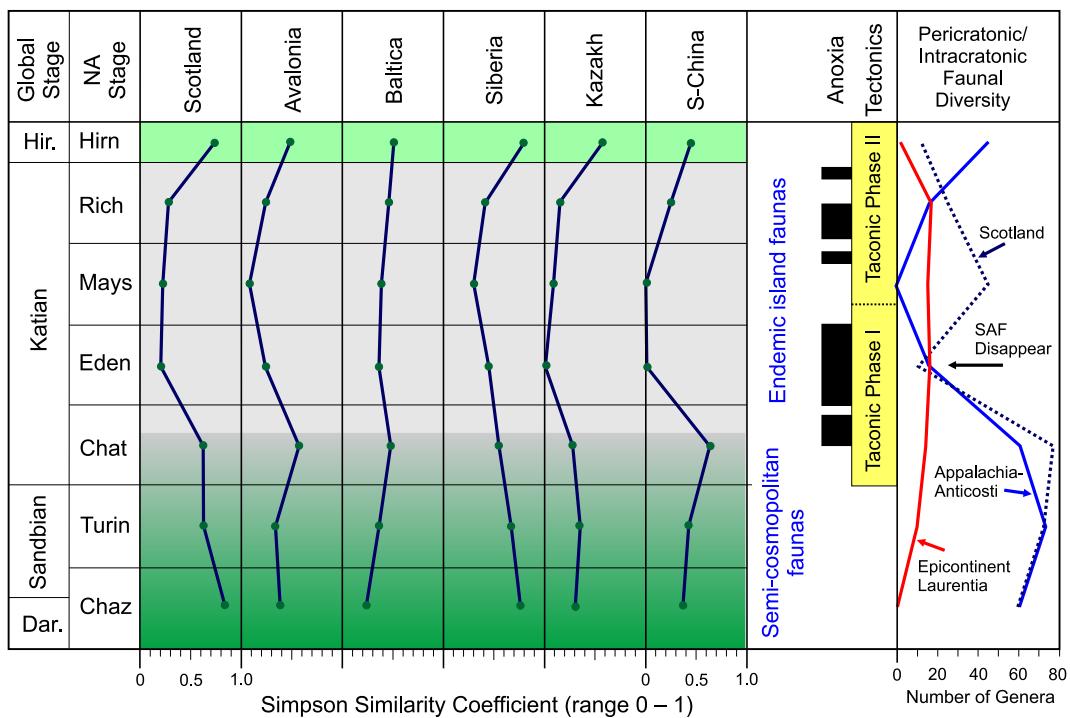


Fig. 5. Brachiopod faunal affinities between Laurentia and other tropically located tectonic plates from Llanvirn to Richmondian (late Darriwilian–late Katian). Note sharp declines of Simpson similarity values from Llanvirn to Chatfieldian and disappearance of the pericratonic Scoto-Appalachian fauna by Edenian (mid-Katian) when the biodiversity epicenter shifted to epicontinentals seas to form a highly endemic ‘super-island fauna’. The intervals of anoxia during the peak of a first-order sea-level rise (Haq and Schutter, 2008; Scotese, 2023) are based mainly on the following black shale deposits in Laurentia: Utica-Collingwood-Blue Mountain formations (up to 700 m thick, 1,000,000 km²), Macasty Formation (150 m, 600,000 km²), Boas River, and Road River formations (800 m, 250,000 km²) as summarized in Thériault (2012) and Desrochers et al. (2023). SAF, Scoto-Appalachian fauna. Simpson Similarity Coefficient 0 = completely dissimilar, 1 = completely similar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Simpson similarity values 0.68–0.55 for Laurentia-Siberia, and even relatively high similarity coefficients with far removed regions like South China (0.41–0.62). The Scoto-Appalachian fauna was best defined and most diverse in the Turonian and earliest Katian, reaching 80 genera in the Appalachian region, 79 in Scotland, 66 in Northern Ireland, and 67 in Balto-Scandia (Figs. 5, 6A–C; also, Supplementary Material, Tables S1–S8).

In contrast, endemism became relatively strong in the Edenian and continued to intensify until the late Richmondian (late Katian), indicated by an accelerated drop in Simpson coefficient values between Laurentia and other regions from the Edenian to the Maysvillian (Fig. 5).

The high level of endemism in the Edenian, however, was partly related to a widespread diversity “crash” at this time, which was particularly pronounced in the brachiopod faunas of Laurentia, peri-Laurentia, Baltica, Avalonia, and South China (Fig. 6A–C, F). For example, the pericratonic fauna of Laurentia dropped from 80 genera in the Chatfieldian to 34 in the Edenian, the peri-Laurentia (Scotland and Northern Ireland) fauna from 79 to 10, in Baltica from 67 to 26, and in South China from 13 to 0. As will be discussed in the sections below, this diversity crash coincided with Taconic Orogeny Phase I of Ganis and Wise (2008) and an episode of widespread marine anoxia and accumulation of organic-rich marlstone and black shale, such as the Utica Formation and correlative strata in eastern Laurentia (Lavoie, 1994; Thériault, 2012; Ritzer et al., 2024; Atasiei et al., 2025).

Another important feature related to the abrupt rise of brachiopod faunal endemism in the Edenian is that the onset of endemism can be traced back to the Chatfieldian, although the highly endemic taxa was overshadowed by the overwhelming diversity of the Chatfieldian fauna, which contained a large number of holdover genera from earlier time intervals. During the Chatfieldian, marine transgression still had not reached its maximum extent compared to the Richmondian, and the brachiopod faunas not yet established in such large intracratonic seas as

the Hudson Bay and Williston basins of Laurentia (Zhang, 2011; Desrochers et al., 2023). In Laurentia, the Chatfieldian was marked by the rise of the pioneer epicontinentals fauna of Laurentia, characterized by the origin of the largely Laurentia-confined *Hiscobeccus* lineage (Jin and Norford, 1996; Sohrabi and Jin, 2013) and the diversification and intercontinental dispersal of the *Rhynchotrema* and *Cincinnatina-Paucicura* lineages (Jin, 2012; Sproat and Jin, 2017). In Laurentia, the oldest well-documented *Rhynchotrema*, such as *R. wisconsinense*, is reported in the Turonian (Sandbian) Platteville Formation of Minnesota (Fig. 7A–E); see also Sohrabi and Jin, 2013). It became extremely abundant and ubiquitous in the marine basins of Laurentia by the Chatfieldian, with the increased development of shell wrinkling (imbricating growth lamellae) leading to the origin of *Hiscobeccus* in the early Katian (Fig. 7F–J). The brachiopod faunas of the pericratonic settings, as well as in epicontinentals seas close to the continental margin (e.g., Michigan Basin, Mississippi Valley, Ottawa Graben), began to form a fairly well-defined Chatfieldian fauna that showed a notable level of endemism, although they still maintained a relatively strongly biogeographic affinity with the brachiopod faunas across the tropical seas worldwide, from Baltica to South China.

By the Maysvillian and Richmondian, the brachiopods in the epicontinentals seas of Laurentia had evolved into a homogeneous and nearly ubiquitous ‘super-island fauna’ (Fig. 2; see also Jin et al., 2014), which had a drastically reduced faunal affinity with any of the faunas associated with the other tectonic plates, or even compared with the peri-Laurentian terranes of Scotland and Northern Ireland, or the adjacent Avalonia (Simpson coefficient mostly below 0.2; Figs. 2C, 5). Whereas the NMDS analysis revealed a clearly isolated cluster of brachiopod fauna in epicontinentals-sea settings (Fig. 3C), the network analysis (Fig. 4C) showed that brachiopod faunas of both Laurentia and peri-Laurentia became notably less diverse (in number of genera) during the Richmondian (compared to their Chatfieldian counterparts as well as

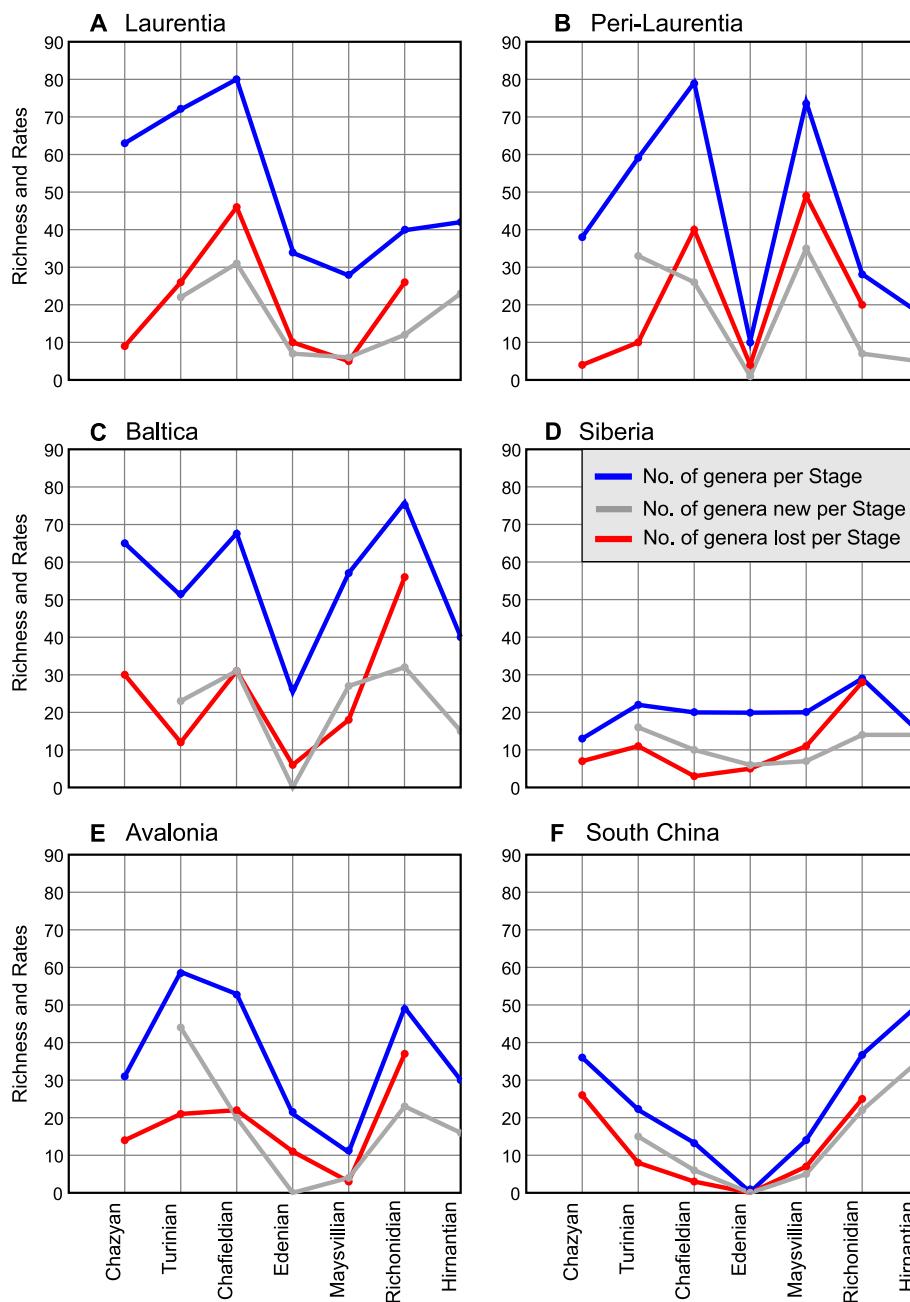


Fig. 6. Brachiopod diversity, extinction and origination rates (measured by number of genera present, lost, or new, per Stage) for six palaeogeographical regions and seven stages from the late Darriwilian to Hirnantian. The dataset used for the plots are in Supplementary Material (Table S1). Software package: PAST ver. 5.2.1 (Hammer et al., 2001; Hammer and Harper, 2024).

to their contemporaneous late Katian faunas in the adjacent, smaller tectonic plates of Avalonia and Baltica). Concomitant with a reduced faunal diversity, the epicontinental fauna of Laurentia had a very high proportion of endemic taxa, although the prominence of endemic taxa was also manifest in adjacent tectonic plates (Baltica, Siberia, and Avalonia), with newly evolved taxa (e.g. the distinctive *Hiscobeccus* fauna of Laurentia) being virtually absent elsewhere (for summary see Jin et al., 2014). This implies that, by the late Katian, the entire marine shelly benthos of cratonic Laurentia had effectively become a highly endemic but internally homogeneous ‘super-island fauna’ through frequent inter-regional dispersal and invasions (Stigall, 2023). During the Richmondian, the specialization of brachiopods in epicontinental-sea environments was manifest in several trends of shell transformations that evolved in phylogenetically unrelated groups, such as

the orthoids, dalmanelloids, strophomenoids, and rhynchonellides. These trends were all likely a reflection of extravagant calcification of epicontinental tropical seas that were supersaturated with respect to CaCO₃ precipitation, characterized by drastic increase in overall shell size and globosity, thickening of the shell wall, enlarged muscle attachment structures, and excessive growth of shell rugae and imbricated growth lamellae (for a summary see Jin, 2001, 2012), as represented by the Richmondian forms of *Hiscobeccus* and closely allied *Hypsiptycha* and *Lepidocyclus* (Fig. 7K–O; see also Sohrabi and Jin, 2013).

4.2. Displacement of biodiversity center from pericratonic shelves to intracratonic seas during sea-level rise

Concomitant with the onset of endemism, there was a shift of the

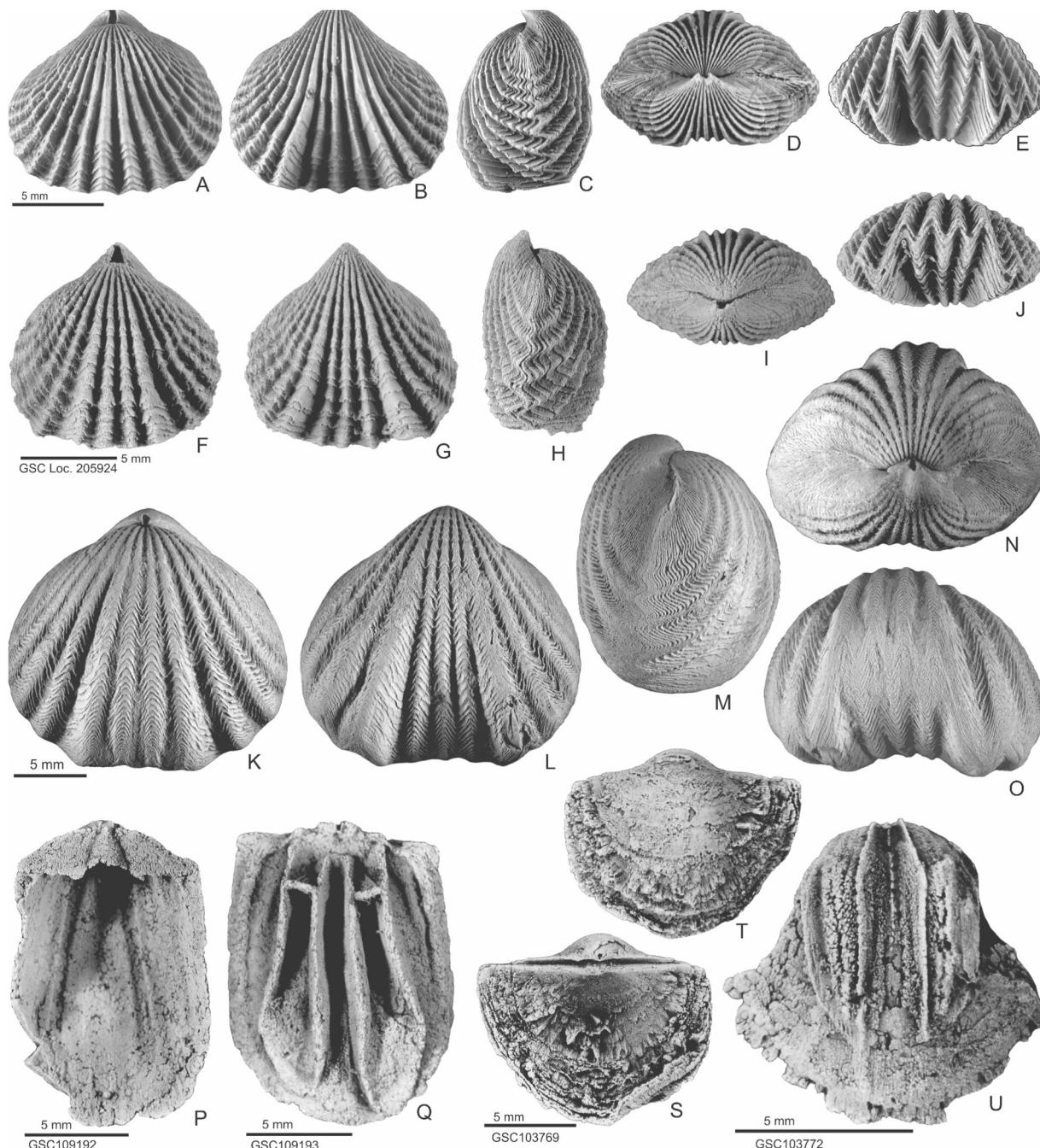


Fig. 7. Diagnostic brachiopods of relatively cosmopolitan Scoto-Appalachian fauna of late Chazyan–early Chatfieldian age, and increasingly endemic fauna of late Chatfieldian–Richmondian age in epicontinental seas of Laurentia. A–E, *Rhynchotrema wisconsinense*, dorsal, ventral, lateral, posterior, and anterior views of anteriorly ‘wrinkled’ shell, locality Mn10–1, McGregor Member (Turonian), Platteville Formation, Minnesota, USA. F–J, *Hiscobeccus mackensiensis*, dorsal, ventral, lateral, posterior, and anterior views of relatively small shell, with anterior four-fifth of surface bearing wrinkles; specimen from lower Advance Formation (lower Katian), GSC locality 205924, northern Rocky Mountains, British Columbia, Canada. K–O, *Hiscobeccus capax*, dorsal, ventral, lateral, posterior, and anterior views of large, strongly biconvex shell, with entire surface bearing wrinkles; shell from Waynesville Formation (middle Richmondian), Cincinnati region, USA. P–Q, *Christiania subquadra*, ventral and dorsal interiors, specimens GSC109192 and GSC109193, respectively, basal Advance Formation (basal Katian), British Columbia. S–U, *Bimuria* cf. *superba*, dorsal and ventral views of conjoined shell (S, T, GSC103769) and dorsal interior (U, GSC103772), same sample as above (see Jin and Norford, 1996 for more details). *Christiania* and *Bimuria* were most common in Chazyan–Turonian (upper Darriwilian–Sandbian) strata of peri-Laurentia. GSC, Geological Survey of Canada.

biodiversity epicenter from the continental margin to inland (epicontinental) seas, in step with the general rise in relative sea level and extensive flooding of the intracratonic Laurentia in the Katian. This was indicated by several features of faunal evolution, as summarized below.

4.2.1. Decline of the Scoto-Appalachian brachiopod fauna

The pericratonic brachiopod faunas in the Appalachian region underwent a sharp drop from the Chazyan to the Edenian, with a reduction of genera from a maximum of 79 to 10 (Fig. 5, 6A, B; Table S1). This is demonstrated also by the relatively high extinction rates during the Chatfieldian interval in Laurentia, peri-Laurentia, and Baltica

(Fig. 6A–C, 8), which were major palaeobioregions of the Scoto-Appalachian fauna. In the numbers of genera lost per stage, the extinction of the Scoto-Appalachian brachiopod fauna rivals the first pulse of LOME in Laurentia (Fig. 8).

4.2.2. Establishment of brachiopod fauna in intracratonic seas

Concomitant with the decline of the Scoto-Appalachian brachiopod fauna in peri-cratic seas, the intracratonic brachiopod fauna experienced a corresponding increase in the total number of genera from 0 (before marine inundation) to a plateau of 15–17 genera by the Edenian. The newly established epicratonic-sea faunas persisted successfully from Edenian to Richmonidian, with relatively low extinction rates (Figs. 6A, 8). It is notable that, despite the generally high abundance and widespread distribution of brachiopod faunas in intracratonic seas of Laurentia during the late Katian, the overall diversity (in terms of total number of genera) of these faunas is rather low compared to the Scoto-Appalachian fauna that thrived in continental-margin seas during the Sandbian, as clearly shown in the diversity ‘saddle’ in epicratonic seas of Laurentia during the Edenian–Richmonidian interval (Figs. 5, 6A). This suggests that the vast area of epicontinental seas actually had a lower ‘carrying capacity’ of brachiopod diversity than pericratonic seas along the continental margin. For example, the total number of brachiopod genera in the vast intracratonic seas of Laurentia during the Richmonidian (late Katian) was 40, which was notably lower than the 80 genera that concentrated along pericratonic seas during the Chatfieldian (early Katian) when much of the Laurentia interior was not yet inundated by marine transgression (Table S1). This trend is corroborated by the higher generic diversity of the *Hirnantia* fauna of Anticosti basin (as part of the Appalachian foreland basin along the southeast margin of Laurentia) during the LOME in comparison to the Richmonidian brachiopod fauna that occupied a far greater palaeogeographical area of intracratonic seas (Figs. 5, 6A, B). The *Hirnantia* fauna of eastern Canada (Anticosti Island and Percé, Quebec) contained numerous taxa that are diagnostic of the ‘typical’ *Hirnantia* fauna (sensu Rong et al., 2020) of the

Kosov Province, such as *Cliftonia*, *Eospirigerina*, *Eostropheodonta*, *Hindella* (Anticosti Island being the type locality of the type species of *Hindella*), and *Hirnantia* (Fig. 9), all ranging from the base to the top of the Ellis Bay Formation (Jin and Zhan, 2008; Copper et al., 2013; Copper and Jin, 2014; Zimmt and Jin, 2024; Jin and Harper, 2024). Another well-known fauna of the Hirnantian age, the Edgewood fauna, occurs also widely in Laurentia, from eastern USA to the Mackenzie Mountains in north-western Canada and northern Greenland (Amsden, 1974; Jin and Harper, 2024; Jin et al., 2024). Both faunas of Hirnantian age attained a relatively high level of cosmopolitanism during global cooling and sea-level lowstand, similar to the conditions in the late Chazyan and Turonian.

4.2.3. Demise of brachiopod fauna in anoxic pericratonic-seas of eastern Laurentia

By the Edenian, the Simpson coefficient values between the epicontinental-sea brachiopod fauna and the remnant Scoto-Appalachian fauna dropped to as low as 0.2, notably lower than in the Chazyan–Chatfieldian interval (Fig. 5; Table S1). The brachiopod fauna nearly disappeared from the Appalachian foreland basin itself, due to a rise in relative sea level and change of the shallow-water pericratonic shelf to an anoxic basin, where thick sequences of black shale (the Utica and Macasty formations) accumulated (Fig. 3; anoxia column; see also Thériault, 2012 and Desrochers et al., 2023). This change was associated with widespread anoxia around Laurentia as well as the downwarp of the Appalachian foreland basin during the Taconic Orogeny (Ganis and Wise, 2008). During episodic peaks of ocean anoxia in the Edenian and Maysvillian, black shale deposits even spilled over from the Appalachian foreland basin (represented by a massive sequence of the Utica shale up to ~700 m thick; Lavoie, 1994; Thériault, 2012) into shallow-water epicontinental seas adjacent to the southeast margin of Laurentia, such as the Collingwood black shale in the Michigan Basin (Atasiei et al., 2025), the widespread organic-rich mudrock of the Kope Formation in the American midcontinent, and Boas River oil shale in the intracratonic Hudson Bay Basin (Goldman and Bergström, 1997; Brett et al., 2006; Zhang, 2011; Banas, 2012). A striking feature of those black shale deposits is the paucity of graptolites except in occasional beds, indicating intense anoxia probably coupled with sulphidic conditions. Such an anoxic and toxic water mass would have acted as an effective barrier for larval dispersal, hence insularize the epicontinental shelly benthos generating a ‘super-island fauna’.

Several episodes of anoxia marked by transgressive black shale have been documented through the Katian on pericratonic settings worldwide (Page et al., 2007; Melchin et al., 2013). The onset of black shale accumulation has been interpreted to coincide with the Guttenberg positive carbon isotope excursion (GICE) and considered by some as the initiation of a general trend of global cooling and eutrophication (Saltzman and Young, 2005; Page et al., 2007; Finnegan et al., 2012; Ritter et al., 2024; Atasiei et al., 2025). In Laurentia, however, the episodes of anoxia were correlated with pulses of major sea-level rise and massive flooding of the continental interior (Zhang, 2011), which are best explained by pulses of a greenhouse climate, when warmer polar sea temperature probably reduced thermohaline downwelling and psychrospheric flow, resulting in sluggish ocean circulation and oxygen starvation in deep sea (Fig. 10). For example, within a broad trend towards a positive $\delta^{13}\text{C}$ excursion indicating cooling climate in the Late Ordovician, two significant negative $\delta^{13}\text{C}$ excursions are recorded in the Katian, one in the Edenian, and the other in the Richmonidian (Young et al., 2010; Zhang et al., 2025). In particular, a recent high-resolution study of late Katian–Hirnantian climate changes based on radioisotopically dated sections in South China (Zhang et al., 2025) shows a significant late Katian warming episode, with sea-surface temperatures of 32–38 °C, thus confirming the presence of the Boda warming event of Fortey and Cocks (2005). Similarly, $\delta^{18}\text{O}$ data based on global average values derived from bulk carbonate (Goldberg et al., 2021) and conodonts from South China (Luan et al., 2025) revealed at least two major

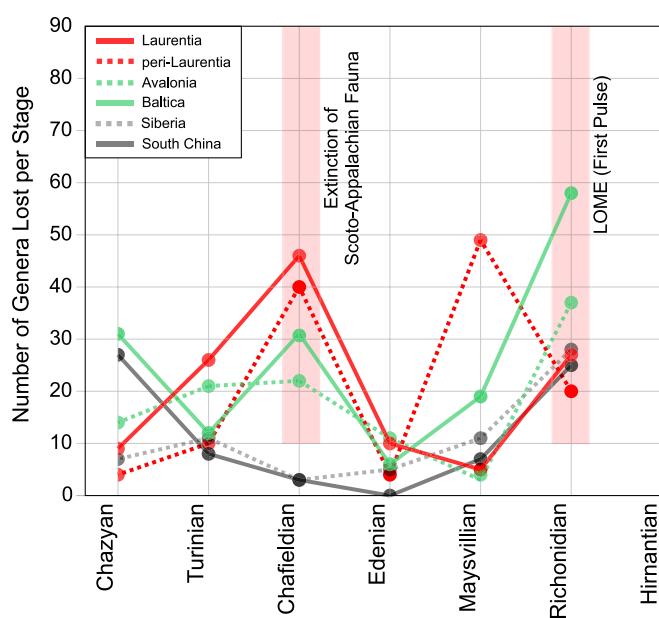


Fig. 8. Examples of regional brachiopod extinction rates for the seven Middle–Late Ordovician time intervals (late Chazyan, Turonian, Chatfieldian, Edenian, Maysvillian, Richmonidian, and Hirnantian). Note that the high extinction rate in the Chatfieldian interval coincided with the beginning of a major pulse of sea-level rise, and with a transition from continental-margin to epicontinental-sea benthic shelly faunas. The low extinction rates during the Edenian–Richmonidian interval coincided with the persistence of a high-abundance, moderate-diversity, incumbent epicontinental-sea fauna until the first pulse of LOME at the Richmonidian–Hirnantian transition.

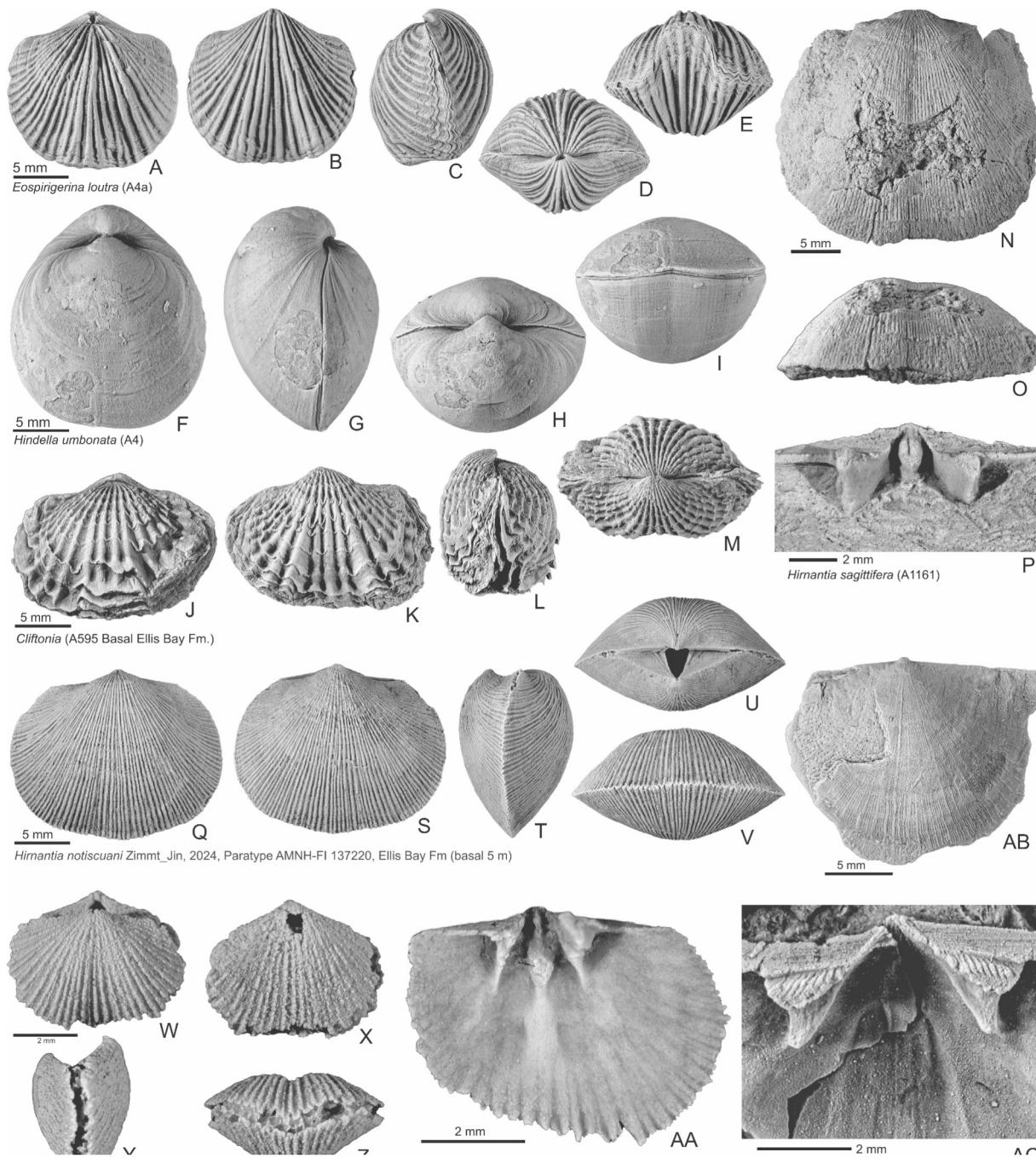


Fig. 9. Representative genera of *Hirnantia* fauna of eastern Laurentia, all from Anticosti Island except for *Kinnella*. A–E, *Eospirigerina* sp., dorsal, ventral, lateral, posterior, and anterior views of strong biconvex shell, upper Fraise–lower Juncliff members (lower Hirnantian), lower Ellis Bay Formation (locality A4a). F–I, *Hindella umbonata*, dorsal, lateral, posterior, and anterior views of average-sized shell for species; note fine ribbing in anterior part of shell, upper Fraise Member (locality A4). J–M, *Cliftonia psittacina*, dorsal, ventral, lateral, and posterior views strong lamellose shell, aulacerid beds within basal 5 m of Ellis Bay Formation, Anse Mauvaise (locality A595). N–P, *Hirnantia sagittifera*, exterior, and external anterior, and interior views of dorsal valve, reefal facies of Laframboise Member (middle-upper Hirnantian), top Ellis Bay Formation, Naticotek road (= sentier Baie La Tour; locality A1161). Q–V, *Hirnantia notiskuani*, dorsal, ventral, lateral, posterior, and anterior views of average-size shell for species, paratype AMHM-FI 137220, from basal 5 m of Ellis Bay Formation, Ruisseau Macaire. W–AA, *Kinnella laurentina*, dorsal, ventral, lateral, anterior views of conjoined, silicified shell (GSC 117900), and interior of dorsal valve (GSC 117908), Katian–Hirnantian boundary beds, Karawong West, Manitoulin Island (see Stott and Jin, 2007). AB–AC, *Eostropheodonta planoconvexa* (reported as *Aphanomena* in Dewing, 1999, with hinge denticles), ventral view of conjoined shell (AB) and apical view of another specimen (AC), Fraise Member, basal Ellis Bay Formation, Chemin 4 (locality A1504).

warming episodes during the Katian. During episodes of climate warming, a heated and sluggish ocean would lead to a reduced level of dissolved oxygen, increased phosphate release from organic-rich sediments coupled to increased sulphate reduction and sulphide release, which would have contributed to widespread and intense anoxia and sulphidic euxinia (Meyer and Kump, 2008; Li et al., 2019). In North

America, the global ocean anoxia was further intensified by such regional factors as the Taconic Orogeny and a large part of its epicontinental seas being located within the hurricane-free palaeoequatorial zone (Fig. 1). Along the north and western margins of Laurentia, the thick black shales of the Road River Formation (upper Sandbian–upper Katian) were also widespread (Reershemius and Planavsky, 2021; Lyons

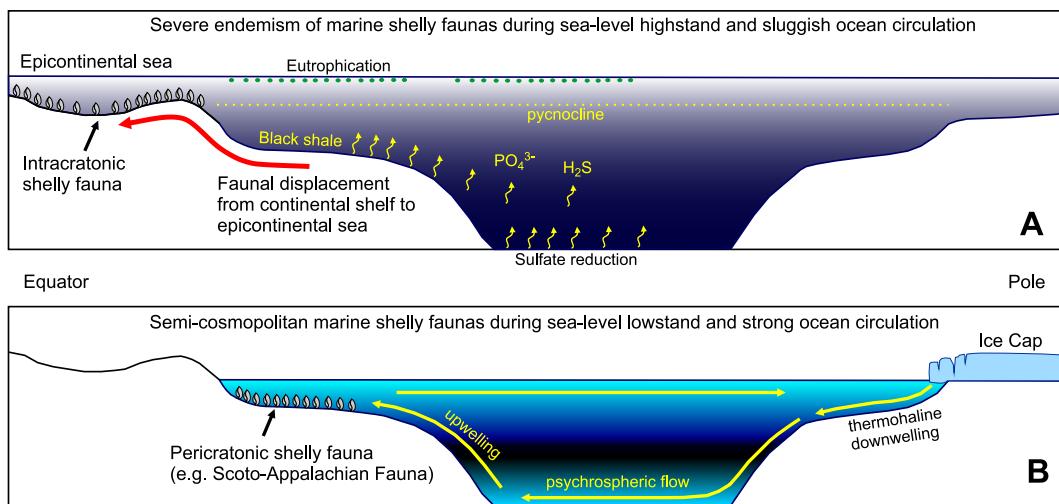


Fig. 10. The MEIK (mass extinction by insularization and kill) model for the Late Ordovician mass extinction. A) Faunal cosmopolitanism during icehouse climate and sea-level lowstand. B) Displacement of biodiversity epicenter from continental shelf to inland seas, and development of endemic ‘island fauna’ during greenhouse climate and sea-level rise. Such island faunas were extremely prone to extinction during the Hirnantian glaciation when the epicontinental seas were drained by rapid sea-level fall.

and Young, 2022; Ritzer et al., 2024).

4.3. Reduced faunal dispersal ability and mass extinction

The brachiopod faunal endemism in the Late Ordovician (Katian) was most likely related to the reduction or loss of inter-continental dispersal potential at several levels in Laurentia:

4.3.1. Loss of inter-plate dispersal ability at the faunal level

The limited dispersal ability of the epicratonic brachiopods of Laurentia between tectonic plates and even between major latitudinal climatic zones within Laurentia is demonstrated by the strong faunal homogeneity (at generic level) and high abundance within Laurentia and at the same time an extreme endemism in relation to other tectonic plates, especially during the post-Chatfieldian and pre-Hirnantian interval. For example, the widespread phenomenon of the Richmondian Invasion (Stigall, 2023) contributed greatly to inter-regional mixing of brachiopod taxa, with the very minor introduction of taxa that newly evolved on other tectonic plates during that age. This resulted in the widespread distribution of a large number of endemic taxa within Laurentia, defining an extremely tight cluster of its epicratonic fauna (Figs. 2C, 3C) and a relatively small network centre pulled sideways by a large number of endemic genera in comparison to its adjacent plate Baltica (Fig. 4C). Despite its virtually ubiquitous distribution within Laurentia, the *Hiscobeccus* brachiopod fauna in the Richmondian of Laurentia was largely absent from other tectonic plates (Jin, 2001; Jin et al., 2014).

4.3.2. Strong ecological and faunal gradients within Laurentia

Within many taxonomic groups, closely related genera or congeneric species became sharply segregated from palaeoequatorial to palaeosubtropical latitudes, and from continental margins to inland seas (e.g., Jin, 2012; Jin et al., 2014). This implies that, despite the high degree of homogeneity at the genus level, there was only limited species exchange between palaeoequatorial intracratonic and higher-tropical pericratonic seas; that is, the epicontinental brachiopods had lost their ability to migrate to the cool-water subtropical seas along the continental margin, let alone to other tectonic plates, due to an effect known as oceanic thermal barriers (Stanley, 2010). The effectiveness of such a thermal barrier during the late Katian was convincingly demonstrated by the contrasting distribution patterns of the “Red River” brachiopod fauna and its contemporaneous *Tcherskidium* fauna of Laurentia. Whereas the

“Red River” fauna typical of the southern paleo-tropics, represented by such diagnostic taxa as *Plaesiomys*, *Diceromyonia*, *Nasutimena*, *Hiscobeccus*, *Hypsipytha*, and *Lepidocyclus*, successively dispersed into the northern palaeotropics, the truly warm-water *Tcherskidium* Fauna was confined to the palaeoequatorial and lower palaeotropics of the northern hemisphere and completely absent from the otherwise high-abundance, moderate-diversity “Red River” brachiopod faunas in the southern-hemisphere Laurentia (Jin et al., 2022, 2024). The thermal barrier during the late Katian was created by a southern-hemisphere Laurentia severely impacted by frequent cold-water incursions from the ice-sheet-capped Gondwana, whereas northern-hemisphere Laurentia lacked any large landmasses north of the tropics and experienced minimal cold-water incursions (Jin et al., 2022). Fundamental genetic and physiological changes must have occurred in epicontinental brachiopods to cause their drastically reduced dispersal ability (Stanley, 2010), probably as a result of their ecological specialization in the epicontinental seas, especially in the relatively stable palaeoequatorial settings free of severe storms and seasonality. Similar reduction in genetic adaptability in incumbent tropical species is known also in other organisms, such as in modern tropical fruit flies as compared to their counterparts in higher latitudes, which has been explained by a revised *climatic variability hypothesis* in biodiversity and biogeography (Kellermann et al., 2009).

4.3.3. Loss of migration stepping stones

Periodic eutrophication and substrate oxygen starvation in pericratonic seas resulted in the loss of outer shelf habitats for some diverse benthic faunas worldwide. This process was demonstrated by the extinction of the Scoto-Appalachian brachiopod fauna along the southeast margin of Laurentia by the Edenian (Figs. 5, 8). That fauna originated during the late Middle Ordovician in subtropical oligotrophic environments and thrived as one of the most diverse brachiopod faunas until the early Katian, with a total duration of approximately 10 myr. Its disappearance during the Edenian marine transgression signalled the loss of a major ‘stepping stone’ for faunal migration between adjacent continents, in particular, between the warm-water brachiopod fauna of epicontinental Laurentia and the cool-water faunas of Avalonia and Baltica (Fig. 3).

5. Concluding remarks

5.1. The MEIK model for the LOME (first pulse of extinction)

The data presented in this paper demonstrate that a chain of environmentally and biologically linked events led to the insularization of the Upper Ordovician marine shelly benthos across the expansive epicontinental seas in Laurentia, making them vulnerable to drastic changes in extrinsic factors and consequent extinction. This process is referred to in this study as the '*mass extinction by insularization and kill*' (MEIK) model. We emphasize that the relatively long pre-extinction process of intensifying faunal endemism played a crucial role in the Hirnantian MEE (LOME), whereas the extrinsic factors of sea-level rise, ocean anoxia, and glacioeustatic sea-level fall constituted a chain of events which contributed to not only the initial dispersal and diversification but also the subsequent extinction of the brachiopod faunas. As noted by Harper et al. (2014), endemic taxa inhabiting shallow-water epicontinental seas were particularly prone to extinction when multiple adverse environmental factors coincided. By analogy with the Darwinian theory of speciation, faunal endemism can be likened to genetic mutation as the singular, unifying intrinsic factor, and the external environmental factors that forced faunal endemism are analogous to the various stressors of natural selection. For both speciation and MEE, the intrinsic factor is singular, whereas extrinsic factors are multiple. Once a fauna is segregated into highly endemic island faunas, they are exposed and any abrupt environmental perturbation can trigger an MEE, be it a large impactor, magmatic event, ocean anoxia, swings in greenhouse-icehouse climate or related sea-level fluctuations.

For the Late Ordovician MEE, the *MEIK hypothesis* and its process can be summarized as follows:

(a) During the late Darriwilian sea-level lowstand and relatively cool climate, the dominant marine shelly benthos, represented by brachiopods, formed a highly diverse and semi-cosmopolitan Scoto-Appalachian Fauna in the continental-margin seas of Laurentia (Fig. 10B).

(b) The global sea-level rise and marine transgression in the Sandbian (Caradoc) initiated a brachiopod invasion into the newly created epicontinental seas to evolve into new faunas (Fig. 10A).

(c) Several episodes of extensive anoxia in pericratonic seas during the middle-late Katian (Edenian–Richmondian) caused a decline and disappearance of the Scoto-Appalachian Fauna due to ecological deterioration, as indicated by the high extinction rate at Tournian–Chatfieldian and Chatfieldian–Edenian transition intervals and concomitant increase in faunal endemism for Laurentia and several other tropically located plates (Figs. 2–5). At the same time, the diversity epicenter of brachiopod faunas shifted to from continent-margin shelves to epicontinental inland seas (Fig. 10A).

(d) Drastic sea level fluctuations during the Katian (Page et al., 2007; Haq and Schutter, 2010; Finnegan et al., 2012; Scotese, 2023) exerted great environmental stress on the shelly faunas. During pulses of warmer climate, sluggish ocean and anoxic waters became dominant around Laurentia (and probably many other tectonic plates), causing isolation of the epicontinental-sea brachiopods, which were already becoming specialized in these habitats, into an extremely endemic, continent-sized "island fauna" that ultimately lost its ability for long-distance dispersal out of its specialized habitat.

(e) The rapid sea-level fall at the onset of the Hirnantian glaciation caused the massive drawdown of the epicontinental seas and, therefore, the habitats for the highly specialized epicontinental fauna were either lost or severely deteriorated, such as the intensified hypersaline conditions in the larger Williston and Hudson Bay basins of Laurentia from latest Katian to Hirnantian (see Desrochers et al., 2023 for a recent summary). As a result of this major glacio-eustatic sea-level drop, the highly specialized and insularized brachiopod faunas in epicontinental seas constituted the major casualties of the first pulse of LOME, with a steep rise in extinction rate at the Richmondian–Hirnantian transitional interval in Laurentia, as well in other palaeogeographical regions

(Figs. 5, 8). In the immediately ensuing Hirnantian, the ecological vacuum left by the initial Hirnantian extinction, in combination with cooler, and better circulated oceans, favoured a rapid dispersal the cool-water-adapted *Hirnantia* brachiopod fauna (Fig. 9), which evolved into one of most diverse and most cosmopolitan Ordovician brachiopod faunas. This is clearly demonstrated by the coordinated jump in extinction rate at the Richmondian–Hirnantian transitional interval (Figs. 5, 6A, B, 8) followed immediately by a sharp increase in faunal similarity coefficient across several tectonic plates (Fig. 5). Detailed investigations of the double-pulsed LOME and palaeobiogeographic relationships among major *Hirnantia* faunas worldwide have been summarized recently in Rong et al. (2020) and Jin and Harper (2024) and will not be repeated in this study.

5.2. Implications of the MEIK model for other mass extinction events

The process of environmental change described here for the diversification and extinction of Late Ordovician marine shelly benthos may be common for other MEEs. The Late Devonian (F/F) and Cretaceous-Palaeogene (K/Pg) mass extinctions, for example, were also proceeded by first- or second-order marine transgressions with intense pulses of ocean anoxia, followed by a rapid marine regression and MEE. The MEIK model proposed in this study, therefore, may have a much wider applicability. The intrinsic factor common to these MEEs is the radiation of highly endemic 'island faunas' associated with isolation of shallow marine habitats by oceanic anoxia or plate tectonics (e.g., the Tethys fauna related to Pangaea); whereas the extrinsic kill mechanism or trigger was different for each MEE, ranging from glaciation (Late Ordovician), magmatism (P/T, K/Pg), to impact (K/Pg), as summarized by Shen et al. (2011) and Schulte et al. (2010). Any of those large perturbations could have triggered a mass extinction at the peak of faunal endemism. Compared to this key intrinsic factor, these various extrinsic causes acted simply as triggers, thus playing a complementary (although significant) role in the Phanerozoic MEEs. This study suggests that future work on MEEs should focus more on biotic insularization as the underlying and unifying theme, although the search for diverse kill mechanisms remains important.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113222>.

CRediT authorship contribution statement

Jisuo Jin: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David A.T. Harper:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was funded by a Discovery Grant to Jin from the Natural Science and Engineering Research Council of Canada. We thank Leonid Popov, Peter Sheehan, and the late Robin Cocks for discussing and refining our fossil data from Kazakhstan, Siberia, Baltica, Laurentia, and Avalonia as well as providing insightful comments on global palaeogeography. The critical and constructive comments of two anonymous journal reviewers greatly helped improve our data presentation and the clarity of our discussions. Harper thanks the Leverhulme Trust (UK) for support.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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