



Did the amalgamation of continents drive the end Ordovician mass extinctions?

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ABSTRACT

Global biodiversity has been punctuated throughout the Phanerozoic by extinction events that vary in their degree of intensity and devastation. The mass extinction event that occurred at the end of the Ordovician Period rapidly removed a wide range of species. Because taxonomic loss occurred during an ice age, this is believed to have initiated the extinctions and thus, these extinctions have often been viewed as a deep time analogue to the loss in species diversity during the present day glacial interval. The current study, however, indicates that temperature – though arguably being a trigger – was not the sole reason for the crisis. Based on a large, bibliographic database of rhyntonelliform brachiopods that specifically operates within very narrow time-slices where every locality has been precisely georeferenced for the Upper Ordovician–Lower Silurian interval, we show that the extinctions were not uniformly distributed, nor was the succeeding recovery. Here we argue that changing plate tectonic configurations during the Ordovician–Silurian interval may have exerted a primary control on biotic extinction and recovery. In particular the proximity and ultimate loss of microcontinents and associated smaller terranes around Laurentia may have restricted shelf and slope habitats during the latest Ordovician but, nevertheless, in a contracted Iapetus Ocean, provided migration routes to help drive a diachronous early Silurian recovery. The conclusion that plate tectonics was a primary factor controlling the extent of the extinctions and the subsequent diversity rebound, demonstrates that a reduction in γ -diversity was perhaps the most important manifestation of the end Ordovician crisis and further raises the question whether this could be applied to other large Phanerozoic perturbations in biodiversity levels.

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1. Introduction

With an estimated taxonomic loss of species diversity at about 85%, the end Ordovician mass extinction event is widely recognized as the second largest of the five big Phanerozoic mass extinction events (Sepkoski, 1981; Jablonski, 1991). In contrast to species loss, the ecological impact was much less severe (Droser et al., 2000; McGhee et al., 2004), though it still marked the end of an Ecological Evolutionary Unit (Boucot, 1983). Apparently the taxonomic loss was not accompanied by major changes in community structures as permanent ecosystem damage or reorganization is not observed in the wake of the extinctions; additionally no higher taxa were replaced or became extinct during the crisis interval. Instead the crisis particularly targeted the lower taxonomic levels. Although the

recovery interval seems to vary from 5 to 15 myr from palaeocontinent to palaeocontinent (Krug and Patzkowsky, 2004), the faunas regrouped relatively quickly, thereby possibly accelerating evolution within the major taxonomic clades. This resulted in a wealth of new species that appeared after the crisis interval (Sheehan, 1996). Within the brachiopods, for example, a pentameroid genus such as *Brevilamnulella* was restricted to deeper-water communities during the Late Katian, prior to extinction in the latest Ordovician stage, the Hirnantian (Rasmussen et al., 2010). Once into the Rhuddanian, the lowermost Silurian stage, the pentameroids had evolved a series of morphological adaptations, permitting the group to successfully inhabit and dominate the most shallow-water, inner-shelf settings with genera such as *Viridita* and *Virgiana* exemplifying pioneer-taxa on and around Laurentia (Jin and Copper, 2010).

Against the background of these minor ecological disturbances, the catastrophic loss in species richness is striking. The present study presents new distributional data based on high resolution stratigraphical ranges and precise geographical occurrences of rhyntonelliform brachiopods through the Ordovician–Silurian interface to track fluctuations in brachiopod diversity in space and time, globally. Surprisingly, this analysis suggests that although the physical environment may well have triggered a massive loss in species

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richness, a major factor in exacerbating the crisis interval may in fact have been the loss of habitats around the congested Iapetus region as a result of terrane accretion to the palaeocontinent Laurentia. However, once into the recovery interval the very same palaeogeographic configuration may well have contributed to the rebound in diversity. Thus, the current study focusses on one key parameter that so far has largely been ignored in the literature: the configuration of the palaeoplates at the Ordovician–Silurian boundary and their impact on global biodiversity.

2. Brachiopod response to a climatically induced crisis interval

Several studies have discussed the diversity of rhynchonelliform brachiopods across the Ordovician–Silurian boundary. Following almost a decade of research (Berry and Boucot, 1973; Sheehan, 1973, 1975), Sepkoski (1981) was the first to actually quantify the taxonomic loss in some detail at the Ordovician–Silurian boundary. This was followed by a study that focussed in greater detail on each of the larger groups of fossils, particularly within the Ordovician (Sepkoski and Sheehan, 1983). They noted that during the period Sepkoski's Paleozoic Evolutionary Fauna increased its collective diversity by some 700% and that this implied a tripling of family diversity. As rhynchonelliform brachiopods were the main constituent of the Paleozoic Evolutionary Fauna, these have been studied intensively (Harper et al., 2004). Harper et al. (2004) discussed the diversity within each brachiopod superfamily during the Ordovician Period. By and large these curves show the same trends: a rapid increase in diversity from the Middle Ordovician (Darriwilian) onwards extending to the uppermost Katian, then a sharp decline from the uppermost Katian into the Hirnantian. The timing of the rebound within the early Silurian is more debatable, especially since data from Laurentia indicate a very rapid rebound (Krug and Patzkowsky, 2004, 2007). The current study questions this rapid rebound; instead we document in detail a delayed rebound that was probably influenced by invasion and subsequent higher origination rates in Laurentia, compared to other regions of the World.

2.1. The end Ordovician mass extinction event

It is now generally accepted that the initial end Ordovician mass extinctions were triggered by glaciations at the palaeo south pole (Berry and Boucot, 1973; Sheehan, 1973; Brenchley et al., 2001), perhaps instigated by increased volcanism (Buggisch et al., 2010). The peak of the glaciations most likely occurred within the course of just half a million years in the Hirnantian (Brenchley et al., 1994). Therefore, as opposed to the Quaternary glaciations, the Hirnantian glaciations rapidly modified several parameters such as oxygen content in the deep-water realm as well as lowered eustatic sea level, before a similarly swift return to greenhouse conditions. Thus, this was a two-phased crisis event. Contrary to the present glaciations, faunas did not have time to adapt to either the rapid deterioration of climate or, for that matter, the succeeding return to more normal conditions (Sheehan, 2001), although recent research has demonstrated a much more complex climatic situation during the later parts of the Ordovician and into the Silurian (Johnson, 2006; Trotter et al., 2008; Rasmussen et al., 2009; Johnson, 2010; Munnecke et al., 2010; Vandenbroucke et al., 2010; Finnegan et al., 2011). Some faunas, like the brachiopod *Hirnantia* fauna (Rong and Harper, 1988), successfully evolved and dominated cool-water environments during the crisis interval. However, as the climate normalized, this fauna became extinct.

The current study argues that an unfortunate configuration of palaeocontinents dramatically increased the effect that this fluctuating climate had on the benthos.

2.2. The importance of microcontinents in the Ordovician sea

The Ordovician Period was characterized by an exceptionally high degree of plate tectonic activity. This resulted in a rapid movement of the large palaeocontinents as well as a whole suite of microcontinents. The high plate tectonic activity resulted in a Phanerozoic sea-level maximum that, among other things, drowned the continents creating so-called epicontinental seas that lack modern analogues (Hallam, 1992; Nielsen, 2004). The combination of these two factors meant that this period was characterized by a high degree of provinciality (γ -diversity) that contributed immensely to the rapid increase in species diversity within the Ordovician Period (Harper, 2010). This radiation is now known as 'the Great Ordovician Biodiversification Event' (Harper, 2006a). Though brachiopods were particularly common in shallow-water settings, much of this diversity was also distributed within the deep-water faunas of foreland basins and on the slopes of microcontinents and island arcs – hereafter abbreviated to terranes. The Ordovician radiation has previously been linked to these orogenic centers that likely contained a greater suite of niches than the epicontinental seas, especially in deeper-water settings (Miller and Mao, 1995; Harper and Mac Niocail, 2002). Thus, an increased interval of terrane accretion to the larger continents probably had catastrophic consequences in terms of loss of γ -diversity.

Progressively during the Ordovician, various palaeoplates moved northwards (Cocks and Torsvik, 2002). One by one they had rifted off the palaeocontinent of Gondwana, by far the largest continent at this point in geological time, stretching from the South Pole to the equator (Fortey and Cocks, 2003; Torsvik and Cocks, 2009). By the Late Ordovician, the large continents of Baltica and Avalonia had docked and were rapidly drifting towards Laurentia. Thus, as the initiation of glaciations caused the eustatic sea level to fall rapidly, the available shelf space narrowed considerably. But the Hirnantian icehouse conditions made the situation extreme. Suddenly shallow-water faunas of the epicontinental seas were forced out into deeper-water settings on the continental margins. Here, in the slope settings, specialized incumbent faunas already occupied the available ecological niches. Consequently, the typical shallow-water species could not adapt to the rapidly changing environments and thus largely became extinct. As noted by Sheehan (1975), this was especially the case with Laurentian shallow-water faunas. He further noted that this was in contrast to the Baltic faunas that were much better adapted to the changing environments. This is supported by new data that indicate Baltica acted as a refuge for shallow-water brachiopod faunas during the crisis interval (Rasmussen and Harper, 2011). Further evidence for this are the occurrences of relict Ordovician brachiopod faunas in the uppermost Hirnantian of South China and the lowermost Silurian of Avalonia (Harper and Williams, 2002) and Baltica (Baarli and Harper, 1986). Therefore, Baltic faunas could easily migrate and invade Laurentia once the crisis interval had ended and environments returned to pre-crisis conditions. In fact, as shown in Appendix A, it appears that invasive species may already have crossed the Iapetus Ocean and reached the margins of Laurentia during the crisis interval (Jin and Copper, 2008).

But not all deep-water faunas successfully moved into shallow water settings. The data presented in the current study reveal that some faunas probably were unable to evolve the required morphological adaptations, notably those faunas that were situated on the series of terranes within the ever narrowing Iapetus Ocean (Neuman and Harper, 1992; Harper et al., 1996, 2008). The importance of these terranes with respect to brachiopod γ -diversity was first recognized by Neuman (Neuman, 1972, 1984, 1988), who argued for the existence of island arc faunas within the Iapetus Ocean. The terranes acted as 'ferries' or 'mid-ocean refuges' between the large continents such as Laurentia, Baltica and Avalonia (Harper et al., 1996). Thus each terrane evolved its own distinct fauna, just as the large palaeocontinents evolved even more endemic counterparts. The present study

demonstrates, for the first time, the true importance of these mid-ocean refuges.

3. Methods

The database was constructed by extracting taxonomic, stratigraphical, lithological and geographical information from the known rhynchonelliform brachiopod literature spanning the Sandbian–Telychian interval (about 30 myr). Thus the database is collection based. In all 257 references were used (see Appendix B). The data matrix was constructed using range-through data to correct for Lazarus taxa. As the database primarily aims at describing fluctuations in α -diversity from an area, not all occurrences of a given taxa within the close proximity of a given locality have been entered. However multiple occurrences at the same locality were registered if the references listed different stratigraphical ranges. Also taxa were entered from nearby localities with contemporaneous beds if these were deposited in a different facies. This allowed subsequent analysis of β -diversity fluctuations (See Rasmussen and Harper, 2011).

Therefore the database is unique in operating to the lowest possible taxonomical level with very narrow time slices where every locality has been precisely georeferenced. In all 6276 occurrences of rhynchonelliform brachiopods have been entered into the database distributed across 110 families encompassing 602 genera (including sub genera). The current study operates with 16 geographical entities of varying sizes that consist of a large number of localities, that for the purpose of the Mollweide projection used for Fig. 1, were merged into 57 'regions' distributed across the 16 geographic entities. Of these, nine of the regions are in the Iapetus region.

The database records the sum of taxa in a given palaeogeographic entity through time. Fig. 1 shows the geographic position of these regions within each geographic entity. These generally follow Fortey and Cocks (2003), with a note that the Farewell terrane is here

regarded peri-Laurentian within the studied interval though new findings, based on a formal description of Late Ordovician brachiopod faunas from the White Mountain area, actually indicate that it may be peri-Siberian (Rasmussen et al., 2011). In addition, the extremely complex Kazakh terranes have only been split into three entities: Karaganda with only one datapoint, is contained within the Chinghiz terrane; the Selyty River fauna has been placed in the Chu-Ili terrane, with which it is most closely associated, geographically, according to Fortey and Cocks (2003) and all occurrences south and west of Tien-Shan, incl. Kyrgyzstan, are maintained within that terrane to simplify this complex region. However, in Table 1, the three Kazakh regions have been amalgamated into one for the purposes of the table.

Genera occurring in more than one of the regions used in this study have been counted once for every geographic entity used in Figs. 4 and 5. This 'double-counting' was conducted to compare the α -diversity in each region through time and not only the endemics. Therefore Figs. 4 and 5 are not based on cumulative data compared to Figs. 2 and 3.

Due to the large volume of literature that uses the British stage system all records were referred to this system as a first approximation by correlating contemporaneous graptolite zones from each of the geographic entities. Thus, the occurrences in the database have been subdivided into graptolite zones where possible to attain the highest possible stratigraphical resolution. This was done using primarily Bergström et al. (2009) as the standard reference for the Ordovician part of the database. Taxonomically, records were entered down to the species level, where possible. Every effort was made to avoid synonyms. However, for the global study presented here, species range data were too insufficient to be reliable, thus only generic and family data were used. All locality data were plotted at high accuracy for later treatment with GIS-software and lithological data were used together with faunal data to assess bathymetrical aspects of the faunas (see Rasmussen and Harper, 2011).

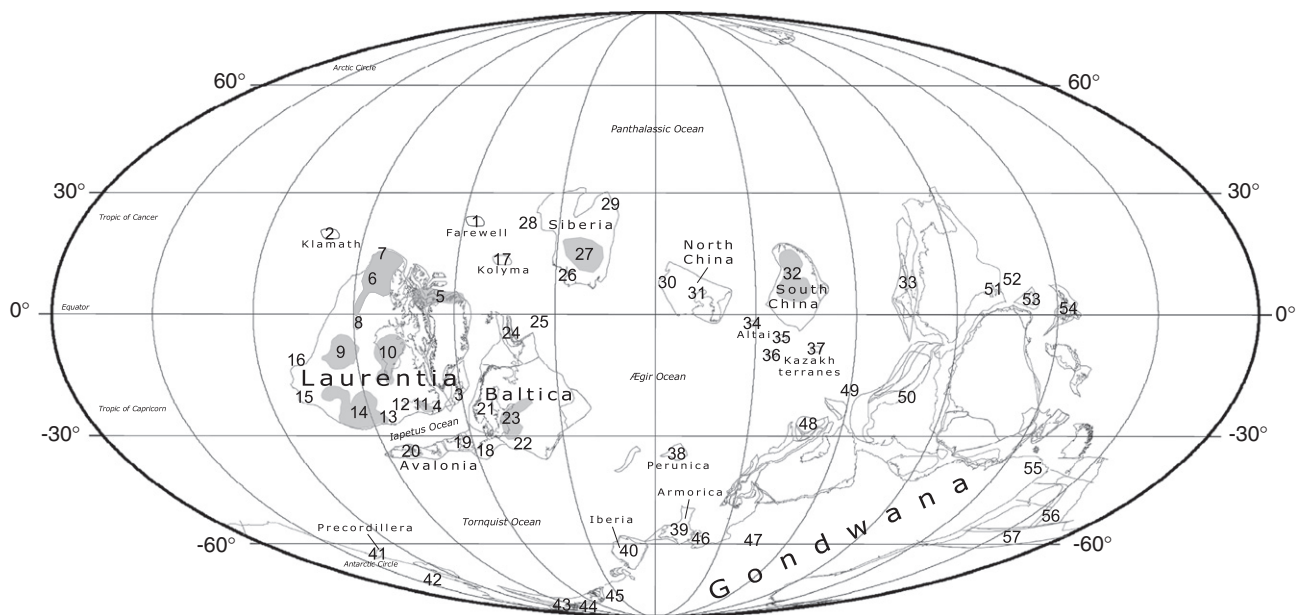


Fig. 1. Palaeogeographic projection for the latest Ordovician (~450 Ma). Grey shades indicate shallow-water carbonate basins. Numbers refer to 'regions' within the larger geographical entities used in Figs. 4–7. Peri-Laurentian terranes: 1, Farewell Terrane (here including Baird Mountain of the Arctic Alaska Terrane); 2, Eastern Klamath Mountains; 3, Midland Valley Terrane (Girvan, Kibbucho, W. Ireland and Pomeroy); 4, Newfoundland. Laurentia: 5, Franklinian Basin; 6, Selwyn Basin with Jones Ridge (7); 8, Columbia Basin; 9, Williston Basin; 10, Hudson Basin; 11, Anticosti Basin; 12, Quebec and New Brunswick; 13, Maine and New York; 14, 'Great American Carbonate Bank'; 15, Oklahoma, Texas, New Mexico and Mexico; 16, California, Nevada, Utah and Wyoming. Kolyma: 17. Avalonia: 18, Belgium; 19, U.K. and Ireland; 20, Appalachians (Nova Scotia). Baltica: 21, Scandinavia; 22, Poland, Belarus and Ukraine; 23, Moscow Basin. Novaya and Severnaya Zemlya: 24, 25. Siberia: 26, Taimyr; 27, Siberian Platform incl. Salair; 28, Siberian Margin; 29, Tuva and Mongolia. North China: 30, Alxa Block; 31, Shaanxi Province. South China: 32, Yangtze Platform; Sibumasu: 33, Altai: 34. Kazakh Terranes: 35, Chu-Ili; 36, Chinghiz; 37, Tien-Shan. Perunica: 38. Armorica: 39. Iberia: 40. Northern Precordillera: 41. Gondwana: 42, Venezuela; 43, Sardinia; 44, Morocco; 45, Algeria; 46, Carnic Alps; 47, Libya; 48, Iran; 49, Tarim; 50, India; 51, Victoria; 52, New South Wales; 53, Tasmania; 54, New Zealand; 55, South Africa; 56, West Argentina (Cordillera Oriental); 57, Paraguay. Mollweide projection provided by Trond Torsvik, Norwegian Geological Survey.

3.1. A biased survey?

Global studies of Palaeozoic biodiversity are subject to both random and systematic biases. Taxonomic biases, however, have been eliminated in this study, by using the most up to date literature, quality controlled by the authors. Of more concern in the upper Ordovician–lower Silurian interval is taphonomy, a particularly challenging bias, as the interval is characterized by large eustatic fluctuations in sea-level, controlling the magnitude and style of deposition. The lowered Hirnantian sea-level caused a shift from carbonate to siliciclastic deposition in many regions, which does not always favour the preservation of brachiopod shells. In addition the more turbulent near-shore environments that became dominant further fragmented potential fossil assemblages and thus some faunas were reworked during the peak of the regression. Another taphonomic bias is that many regions lack strata through the crisis interval, due to the early Hirnantian regression. Hence no faunas are recorded from such regions. Moreover, the best sampled localities are often situated close to easily accessible areas. Consequently the palaeocontinents Avalonia, Baltica and South China are relatively well sampled as compared to many regions of Gondwana. Harper and Rong (2008) showed some rarefaction curves for the Hirnantian of the larger palaeocontinents based on 95 brachiopod genera distributed on some 50 localities. These show some contrasting patterns. South China proved relatively homogenous and adequately sampled to assess the diversity of Hirnantian faunas, whereas those from Laurentia and its margins are heterogeneous and still require more intensive sampling.

The importance of sampling intensity is also demonstrated by the large monographic work of Cooper (1956). Fig. 7 illustrates the effect on the diversity curve that the Sandbian part of his data has on the database (blue line). At the end of this well sampled interval, there appears to have been a drop in diversity on Laurentia. However, this is solely ascribed to this monumental work.

In the current study, facies have not been differentiated, as this study aims at showing the total diversity of a given geographic entity. Thus, bathymetrical differences in diversity from marginal to epicontinental settings or along environmental gradients are not considered here (see instead Rasmussen and Harper (2011) for discussion). However, these still represent a likely bias, as particular depth-related faunas may not have been preserved and thus represent an artificial drop in diversity. However, this has somewhat been accounted for by using range through data that extends to 15 myr after the extinction event to capture possible Lazarus taxa from these environments. But as many of these Lazarus taxa originated in one geographic entity only to show up in the post-extinction faunas of another geographic entity, one cannot ascertain where these taxa originated or became extinct. Thus the data matrix constructed for Figs. 4 and 5 may have different ranges of the same taxa going from one geographic entity to another. For the same reason it is difficult to assess geographic range sizes for genera through the investigated interval, although it would be highly relevant to pursue this in the future.

To sum up, the main dilemma is that relatively few faunas have been preserved in the Hirnantian rock record even at localities that have been intensively sampled (see also Rong et al., 2006). But is this a true diversity signal? Or could it be that the drop in diversity only reflects variations in regional sampling intensity or uneven sampling within a region through time? This could potentially just mean that the extinction event basically reflects unsampled environments. A problem that previous authors have addressed by using sub-standardization of samples (i.e. Krug and Patzkowsky, 2004, 2007) or by assessing the number of Lazarus taxa through the interval (Rong et al., 2006). There are obvious advantages in using sub-samples, because this may artificially compensate for these biases. However, in order to use sub-standards larger sample sizes are needed from each interval, thus forcing one to use larger time slices. Krug and Patzkowsky (2007), for instance, used five million year bins; far too

low a resolution, when trying to resolve faunal fluctuations that may have occurred within half a million years. With respect to Lazarus taxa, studies have shown that up to 30% of the fauna go through the crisis interval without being detected in the Hirnantian fossil record (Rong et al., 2006). In the current data matrix, this has been compensated for by using range-through occurrences. Furthermore, Table 1 shows the percentage diversity loss through the extinctions for each of the regions; intervals that appear taphonomically-biased have been indicated. But we have chosen not to use sub-standards as this study operates with the highest possible stratigraphical resolution in order to detect when and where fluctuations in brachiopod diversity occur.

4. Analysis and discussion of the database

Section 2 described diversity estimates that are complemented by the database constructed for this study. This is demonstrated in Figs. 2 and 3, which show the global standing diversity through the studied interval at different taxonomic levels. Fig. 2 records the total diversity of families in the database, using range through data. The diversity curve is endpoint corrected to correct for singletons. Here, the Katian peak in diversity and the Upper Hirnantian trough in diversity are clear. As the curve is endpoint corrected, the Sandbian and Telychian troughs are overemphasized because this method counts a first appearance datum (FAD) or last appearance datum (LAD) in a sample as 0.5 and singletons as 0.33 instead of 1 (Hammer and Harper, 2006). We have used the endpoint correction method to strengthen the data matrix in the extinction interval. When not accounting for FADs and LADs (without endpoint correction) there is a slight increase in diversity from the Sandbian into the Katian and a weaker decline in numbers of Telychian families. Also it is evident that there is a two-phased extinction event from the uppermost Katian through the Hirnantian and that this is followed by a large origination phase in the lowest Rhuddanian.

The crisis becomes much more evident at the generic level (Fig. 3), using the same statistical methods that were used to produce Fig. 2. Following a plateau in the Sandbian–middle Katian interval, diversity sharply increased until the uppermost Katian (middle Rawtheyan). Then a sharp decrease continued through the upper Rawtheyan into the lower Hirnantian. This is succeeded by a slight increase in

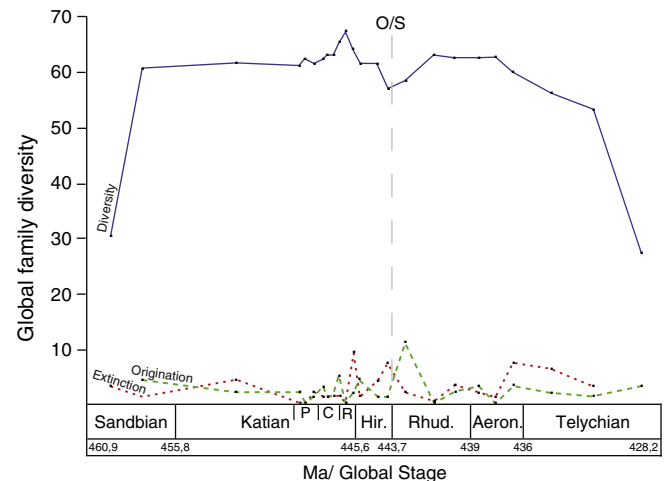


Fig. 2. Global family diversity (blue), origination (green) and extinction (red) through the time interval considered by the database. A taxonomic drop is clearly seen at the Ordovician–Silurian boundary. The curves are endpoint corrected and based on range-through data. Black points along the lines depict the binning of the data. Abbreviations: O/S – Ordovician–Silurian boundary, P – Purgillian, C – Cautleyan, R – Rawtheyan, Hir. – Hirnantian, Rhud. – Rhuddanian, Aeron. – Aeronian.

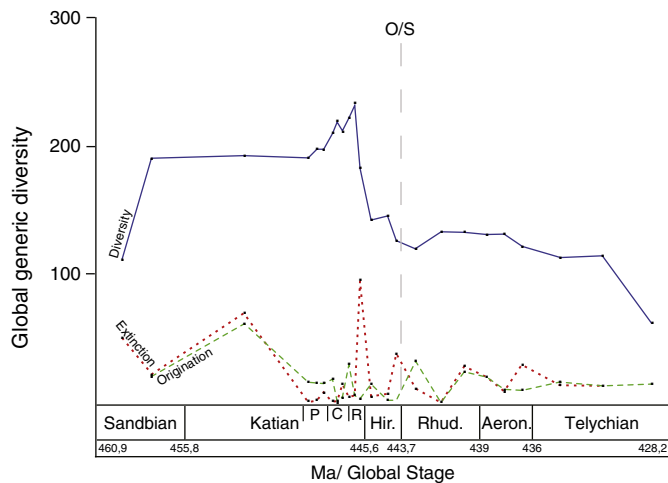


Fig. 3. Global generic diversity (blue), origination (green) and extinction (red) based on the database. A drastic drop in diversity is evident. Contrary to Laurentian studies (Krug and Patzkowsky, 2004, 2007), this global database does not clearly indicate a quick rebound following the crisis interval. When the geographic entities are treated separately, the Laurentian diversity data show a markedly delayed recovery interval compared to other regions (Figs. 4, 5 and 7). Curves are endpoint corrected and based on range-through data. Black points along the lines depict the binning of the data. Abbreviations as in Fig. 2.

diversity before yet another sharp decrease in diversity is seen in the upper Hirnantian through to the lower Rhuddanian. Hereafter follows a slight increase where diversity appears to reach a more stable level. This is in line with previous studies that also showed that only few higher taxa disappeared, whereas the catastrophe particularly targeted the generic (and specific) level (Sheehan and Coorough, 1990; Rong et al., 2006). But contrary to studies on Laurentian faunas (Krug and Patzkowsky, 2004, 2007), this global database does not show a rapid rebound in diversity.

But was the extinction together with the succeeding recovery uniform across the different palaeocontinents and terranes?

4.1. A peri-Laurentian diversity hot-spot revealed

According to this database the extinctions were not uniform from region to region. This is clearly illustrated in Figs. 4–7, as well as in Table 1. It must be stressed, though, as discussed in Section 3, that neither is the sampling uniform, neither regionally nor up through the time interval considered and thus these potential biases should be noted. Still, the most robust data, the family diagram, show very little diversity decrease on the largest or best sampled palaeocontinents (Avalonia, Baltica, Laurentia and South China) when crossing the Ordovician–Silurian boundary. This is no surprise as we have just seen that at the family level the extinctions only caused minor taxonomic disturbance (Fig. 2). However, at the generic level it becomes more apparent that there is a greater taxonomic loss. Especially Laurentia, Siberia and South China indicate some decrease, whereas this is less obvious for Baltica. Avalonia, on the other hand, appears relatively unaffected by the extinctions, but instead experienced a drastic decrease from the Aeronian onwards.

But the areas that contain the greatest number of victims are those that here are termed the peri-Laurentian terranes. These include the Farewell Terrane, the Midland Valley Terrane (Girvan, Kilbucho, Western Ireland and Pomeroy), the Eastern Klamath Terrane, and Newfoundland. These terranes are all situated close to Laurentia, and mostly within the Iapetus Ocean. This drastic taxonomic drop is surprising as these are characterized by deeper-water faunas that usually are believed to have been those that were best adapted to survive the extinctions.

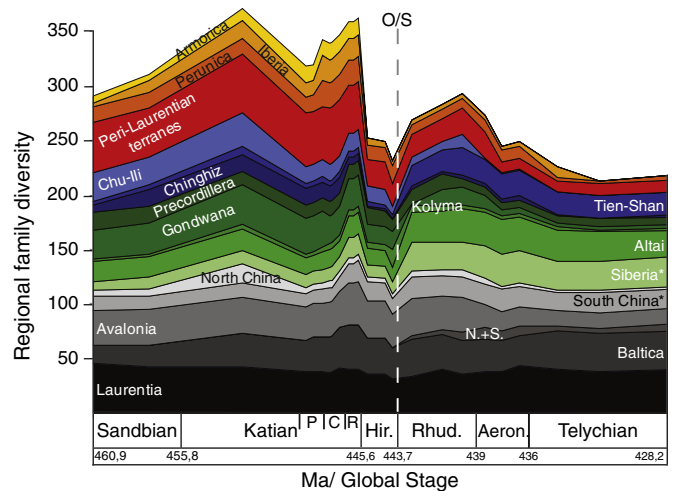


Fig. 4. Diversity at the family level split into separate geographic entities. Note that virtually no drop in diversity is seen for the large, well sampled continents (dark colours at bottom of diagram), whereas smaller terranes exhibit a large taxonomic loss (warm colours at top of diagram). The diagram is based on range-through data. Abbreviations: N.+S. – Novaya+Severnaya Zemlya, South China* means including Sibumasu, Siberia* means including Mongolia, Taimyr and Tuva. Other abbreviations as in Fig. 2.

Table 1 shows the percentage of generic loss and recovery relative to the Late Katian for the different regions shown in Figs. 4 and 5. To obtain a more coherent matrix for study of the recovery interval, Novaya and Severnaya Zemlya have been included in the Baltic region, the three Kazakh terranes are here included as one and the Cordillera Oriental and the Northern Precordillera have here been included in the Gondwanan region. The table is divided in two; the top part, which is sub-divided into three sections, shows regions with adequate data to assess the rate of recovery, whereas the lower part shows regions with inadequate data to study the recovery rate.

The three sub-divisions in the upper part of the table highlight different survival and recovery rates. They are all arranged according to percentage survival in the Upper Hirnantian. The top part (Baltica–South China) contains the regions where more than 50% of the fauna

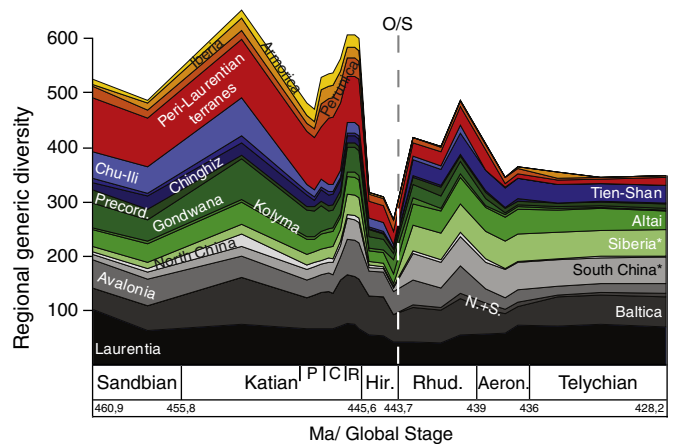


Fig. 5. Generic diversity split into separate geographic entities. Same trends are observed as in Fig. 4, but with a much larger drop in diversity at the smaller terranes, notably the peri-Laurentian terranes. In the recovery interval Laurentia show a delayed rebound not reaching pre-extinction levels in diversity before the Late Aeronian. Avalonia, on the other hand, appears to be less affected by the Hirnantian extinctions, but instead exhibits a drop in diversity from the Aeronian onwards. The diagram is based on range-through data. Abbreviations are as in previous figures.

Table 1

Percentage of regional loss in generic diversity relative to the latest Katian. Numbers indicate in percent how much of the diversity remained relative to pre-extinction levels. Colours indicate peak extinctions (grey), more than 90% recovery (green), more than 50% recovery (yellow), less than 50% recovery (pink). In addition, regions that are likely to be affected by taphonomic biases are indicated (orange). The table is further divided in two parts, where the bottom one shows regions with inadequate data to assess the recovery rates. The top part is further sub-divided into three sections, all arranged according to percent survival in the Upper Hirnantian. Top section (Baltica–South China) holds the regions where more than 50% of the fauna had recovered by the lower Rhuddanian. Middle section (Avalonia and Gondwana), the same success rate in recovery, but with a subsequent sharp Aeronian decrease in diversity that did not rebound during the remaining part of the Llandovery and finally, the lower section are the regions where faunas never recovered from the Hirnantian mass extinctions (Iberia, Peri-Laurentia and Perunica). Asterisks are the same as for Figs. 4 and 5, although here Novaya and Severnaya Zemlya have been amalgamated with Baltica and the Cordillera Oriental and the Northern Precordillera have been added to the Gondwana matrix. Further, the three Kazakh terranes used in the text have been summed to one entity for this analysis.

	Upper Katian	Lower Hirnantian	Middle Hirnantian	Upper Hirnantian	Lower Rhuddanian	Middle Rhuddanian	Upper Rhuddanian	Lower Aeronian	Middle Aeronian	Upper Aeronian	Lower Telychian	Middle Telychian	Upper Telychian
Baltica*	100	80	80	58	73	70	81	57	44	43	64	66	69
Laurentia	100	74	70	55	58	55	72	76	79	97	93	97	92
Altai	100	63	63	53	122	128	150	138	138	144	128	125	109
Kazakh terranes	100	68	68	29	110	113	148	129	123	129	113	110	113
Siberia*	100	18	18	16	126	126	139	132	134	132	126	126	126
South China*	100	18	18	16	126	126	139	132	134	132	126	126	126
Avalonia	100	67	67	63	67	52	76	37	33	33	24	24	27
Gondwana*	100	62	54	37	63	60	58	42	21	21	19	19	19
Perunica	100	36	36	64	27	27	27	33	33	33	9	9	12
Peri-Laurentia	100	38	38	28	29	31	41	42	8	8	9	9	16
Iberia	100	20	20	5	5	5	5	5	5	10	55	0	0
Regions with inadequate data:													
Kolyma	110	50	40	270	110	50	60	40	40	40	30	20	20
North China*	100	57	43	43	71	71	114	86	29	29	29	29	29
Armorica	100	0	0	0	0	0	0	0	0	0	0	0	0

Note that whereas diversity ultimately was fully restored on Laurentia by the Late Aeronian, it never rebounded on the peri-Laurentian terranes. Further note that Avalonia – the least affected region by the extinctions – suffered a great taxonomic loss from the Aeronian onwards. This suggests that the combination of terrane accretion and glaciations likely continued to affect the rebound in γ -diversity at least through the Rhuddanian–Aeronian intervals.

had recovered by the lower Rhuddanian and with a sustained high level of recovery in the Llandovery.

The middle part also shows more than 50% success rate in recovery in the lower Rhuddanian, but with a subsequent, sharp Aeronian decrease in diversity that did not rebound during the remaining part of the Llandovery. Finally, the lower part shows, the regions where faunas never recovered from the Hirnantian mass extinctions. In addition, the table is colour coded to simplify the main points; green indicates more than 90% recovery, yellow more than 50% recovery and pink, less than 50% recovery. Furthermore, intervals with an unusually high recovery rate in one time-slice are shown in orange to indicate regions that may be particularly prone to taphonomic biases. Such a sudden increase reflects more genera at this interval which again is likely to indicate that a large part of the regional fauna is missing.

Table 1 shows that Avalonia and Baltica are the regions which contained most survivors in the Upper Hirnantian. This is in line with Rasmussen and Harper (2011), who found both regions to have high α -diversity levels throughout the Hirnantian Stage and further that Baltica was a particularly good refuge for shallow-water species. However, Table 1 also shows that Laurentia was apparently one of the regions that best survived the crisis. This is contrary to previous reports (Sheehan, 1975; Sheehan and Coorough, 1990), as well as the current study, as Fig. 7 clearly shows a high turn-over rate during the Hirnantian Stage. In addition, as described below, the Laurentian margins were already occupied by some Baltic invaders during the crisis interval. Thus, it is more probable that this apparent high Laurentian recovery rate noted in Table 1 reflects a combination of the successful Edgewood-fauna, as well as the introduction of new invasive genera, primarily from Baltica.

With respect to recovery, Table 1 clearly demonstrates that the peri-Laurentian terranes, along with Iberia and Perunica, did not rebound from the Hirnantian mass extinctions during the Llandovery. In addition, it is evident that although Laurentia regained some of its diversity during the Late Rhuddanian, it was not until the Late Aeronian it had recovered to pre-extinction levels. Whereas Altai, the Kazakh terranes, Siberia and South China quickly rebounded and exceeded their pre-extinction levels in diversity, Baltica, Avalonia and Gondwana, did not reach Katian levels in diversity during the

Llandovery. Interestingly, Avalonia appears to have been the region least affected by the Hirnantian extinctions and suffered a sharp decrease in diversity that commenced from the beginning of the Aeronian. As this coincides with an Aeronian drop in diversity on Baltica, one might speculate that this is related to the amalgamation of Avalonia and Baltica with Laurentia at this point in the Llandovery.

Thus, to sum up, it seems that the greatest taxonomic losses were among deep-water taxa located on relatively isolated terranes, primarily situated in the Iapetus Ocean. To some extent these faunas may have replaced the shallow-water forms of Laurentia, as suggested by Sheehan (1975). However, the diversity loss on the peri-Laurentian terranes at different taxonomic levels, recorded by the current study, does not seem to be compensated by a corresponding increase in Laurentian diversity (Figs. 6 and 7). Thus, though some taxa were replaced, it appears that the greater majority became extinct. Instead,

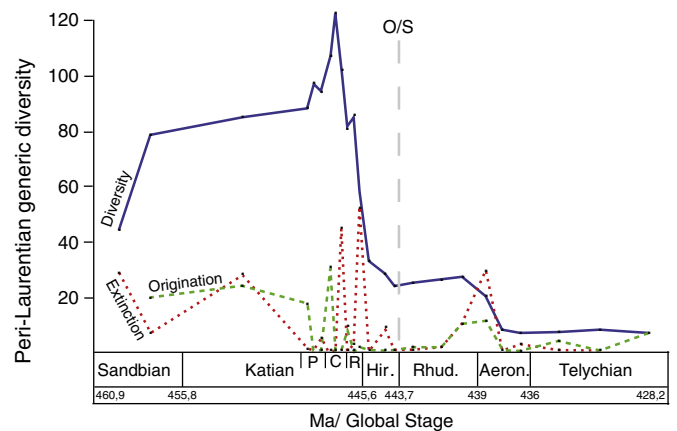


Fig. 6. Generic diversity for the peri-Laurentian terranes. The catastrophic consequences of the end Ordovician crisis event are evident. For a detailed list of the invasive and endemic genera constituting the origination curve during the survival and recovery interval, see Appendix A. Curves are endpoint corrected and based on range-through data. Black points along the lines depict the binning of the data. Abbreviations are as in Fig. 2.

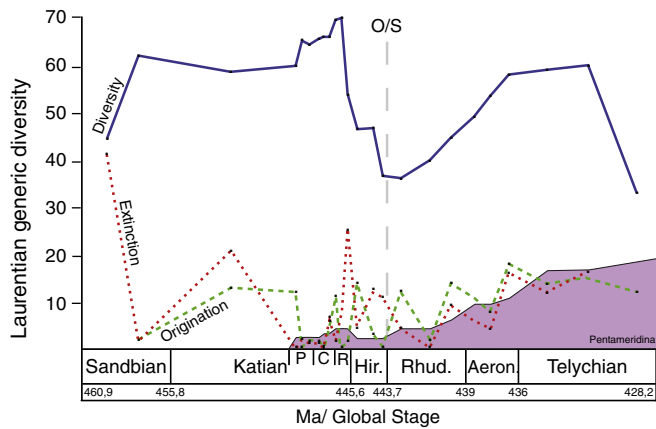


Fig. 7. Generic diversity for Laurentia. In blue is the total diversity estimate based on all occurrences in the database. Note that diversity is almost fully restored by the end of the Aeronian. In addition, the generic diversity within the Pentameridina is shown (purple), illustrating their importance with respect to the delayed diversity rebound on Laurentia. For a detailed list of the invasive and endemic genera constituting the origination curve during the survival and recovery interval, see Appendix A. Curves are endpoint corrected and based on range-through data. Black points along the lines depict the binning of the data. Abbreviations are as in Fig. 2.

as will be discussed in Section 4.2. below (and shown in Appendix A), the main post-extinction increase in Laurentian diversity did not occur until the Aeronian and this appears to be primarily driven by the origination of new endemic species that had evolved from successful invaders, not directly by invasion itself.

4.2. A diachronous early Silurian recovery interval

With respect to the duration of the recovery interval on the larger palaeoplates, brachiopods on Laurentia appear to increase in diversity from the Late Rhuddanian onwards (Figs. 5, 7 and Table 1). By the Late Aeronian diversity was restored to pre-extinction levels; much later than that seen on most of the other large palaeoplates, thus, in contrast to the observations of Krug and Patzkowsky (2007). In conducting a β -diversity analysis based on the current database, Rasmussen and Harper (2011) found that restoration of diversity on Laurentia appeared to be delayed until the Late Rhuddanian, whereas other large palaeoplates have higher diversity values already by the Early Rhuddanian. They mainly ascribed this phenomenon to the very low diversity *Virgiana*-communities on Laurentia. But as these pentameroid brachiopods became hugely successful and rapidly diversified within the Aeronian and Telychian one could argue that this time lag may have yielded longer term benefits. Once the group gained dominance, it evolved into virtually every available niche in shallow to mid shelf settings in the tropical environment, boosting α - and β -diversity values dramatically to reach pre-extinction diversity levels by the Late Aeronian. The Late Rhuddanian increase in diversity on Laurentia could instead coincide with an increased appearance of atrypids, and as shown below, an increased invasion of exotic taxa, at this interval. These may have entered into marginal settings on Laurentia, which was otherwise dominated by monospecific virgianid communities in the shallow-water interior seaways. The invasion was probably due to a large transgression event occurring across Laurentia at this time (Zhang and Barnes, 2002; Rasmussen and Harper, 2011).

It may be that much the same occurred on the terranes of Armorica, Perunica and Iberia where only a few species survived into the early Rhuddanian. By that time these terranes probably had amalgamated with Baltica (Fortey and Cocks, 2003). However, this should be tested in detail. If this is true it also implies that there will be

few Silurian faunas to sample from these areas. Therefore, it is difficult to compare the Ordovician and Silurian faunas.

One region that, according to the database, seems to contain both Ordovician and Silurian faunas, is Siberia. According to the diagrams, as well as Table 1, this palaeo-plate experienced a crisis interval spanning the Hirnantian Stage. The faunas of this palaeo-plate have proven to be quite diverse during the Katian and again in the Llandovery (Cocks and Modzalevskaia, 1997; Modzalevskaia, 2003). But Hirnantian faunas have not been reported. However, it should be stressed that most records from Siberia are not precisely constrained. The same is the case with the terrane of Altai that was probably positioned close to Siberia during the crisis interval (Fortey and Cocks, 2003; Cocks and Torsvik, 2007).

5. Origin and migration of brachiopod genera on Laurentia and peri-Laurentia during the crisis interval

To test the theory of continental amalgamation, origination and migration data was extracted from the database (see Appendix A) to analyze in greater detail from where invasive genera entered Laurentia in the recovery interval and to what extent newcomers were related to speciation on the peri-Laurentian terranes and Laurentia. To get a more complete overview of the intervals of main invasion, the latest Katian (Rawtheyan) has been included in the analysis to study whether trends that occurred prior to the crisis interval continued despite the extinctions.

5.1. Katian

During the latest Katian, eight genera enter the peri-Laurentian terranes. Of these, seven may have originated here and only four are later found on Laurentia. Of the 11 genera that originate on Laurentia in the same interval, eight were invaders. These are more or less cosmopolitan deep-water taxa, except for the relatively widespread *Tcherskidium*, which probably can be assigned to a more shallow-water facies.

5.2. Hirnantian

There appear to have been no newcomers on the peri-Laurentian terranes within the Hirnantian. On Laurentia, on the other hand, 17 newcomers arrive during the extinction interval in the *extraordinarius* Zone. Of these, up to five genera may have originated on Laurentia during this interval, indicating the success of largely the warm-water Edgewood fauna. The invasive species appear mostly to have entered from peri-Laurentia, Baltica and to some degree Avalonia. Significantly only four genera – *Eostrophonella*, *Homoeospira*, *Leptoskelidion* and *Biparetis* – migrated from Laurentia in the same interval.

5.3. Rhuddanian

Within the Rhuddanian none of the 12 newcomers originated on the peri-Laurentian terranes. *Palaeoleptostrophia* and *Saughina* occur in several regions at the same time as their peri-Laurentian records, and thus the present study cannot exclude that they originated elsewhere. Most genera appear to have migrated from either Avalonia or Baltica to peri-Laurentia.

On cratonic Laurentia, the same interval is characterized by the early radiation of new virgianid genera, such as *Viridita* and *Virgiana*. These became hugely successful in shallow-water environments in this interval. Based on species richness these two can with some confidence be viewed as having originated on Laurentia, though contemporary occurrences from other regions could challenge this statement. Within the Early–Mid Rhuddanian six of 13 newcomers originated on Laurentia. Significantly it is likely that all of them subsequently were able to migrate from Laurentia primarily

towards Baltica, Avalonia and Siberia, but also to more exotic regions such as the Kazakh terranes. At the same time, Laurentia was colonized by invaders mainly from Baltica and Kolyma, but also peri-Laurentia and maybe even Gondwana (*Ovaella*). Particularly *Stegerhynchus*, originating from Baltica, was to become dominant on Laurentia.

In the Late Rhuddanian only five of 14 genera originated on Laurentia and only two of them migrated from the craton to Baltica (*Eomegastrophia*) and Iberia (*Fenestrirostra*). More interestingly most newcomers were invaders from Kolyma, Siberia, Baltica or peri-Laurentia and possibly also more exotic regions, indicating faunal exchange between palaeoplates during the Late Rhuddanian. This corresponds well with a global transgression in the Late Rhuddanian (Zhang and Barnes, 2002) and further corresponds well with the earliest post-extinction major radiation event on Laurentia in the Late Rhuddanian (Rasmussen and Harper, 2011). Sheehan (2008) found that this part of the Rhuddanian had an anomalous fauna on the west coast of Laurentia. This could be related to that transgression.

5.4. Aeronian

The Early Aeronian interval records the origination of five genera out of 11 newcomers on peri-Laurentia. Whereas most of these remained confined to peri-Laurentia or only migrated to neighbouring palaeoplates, *Gracianella* appeared later on the South China plate. The remaining newcomers in this interval, the invaders, were almost cosmopolitan in distribution and this trend continued in the Late Aeronian where only one newcomer, the cosmopolitan *Aegiria*, is recorded.

The Early–Mid Aeronian of Laurentia is characterized by the continued radiation of pentamerid brachiopods such as *Apopentamerus*, *Clorinda*, *Harpidium*, *Kulumbella*, *Microcardinalia*, *Nondia*, *Pentamerus* and *Sulcpentamerus*. These genera originated almost exclusively on Laurentia and subsequently, with great success, migrated to remote palaeoplates, such as South China as in the case of *Sulcpentamerus* (Jin et al., 2009). Of the 19 newcomers occurring in the interval, only four are likely to have been invaders, all from the nearby palaeoplates of Avalonia and Baltica. This enormous radiation among endemic genera continued in the Late Aeronian with at least eight out of 18 newcomers originating on Laurentia. This radiation no longer involved only the pentameroids, now other groups also began to rapidly diversify. Many of the newcomers (six) remained endemic to Laurentia, but a few were able to migrate all the way to South China. The invaders, on the other hand, were widespread or near-cosmopolitan taxa.

5.5. Telychian

In the last interval analyzed, the Telychian, the trend developed in the Aeronian is reinforced. Only nine new genera appear on peri-Laurentia, two of which, *Erinostrophia* and *Oglupes*, arrived in the Late Telychian and may or may not have originated here. The rest are invasive genera from Avalonia, Baltica, Laurentia, or, less likely, Siberia. By the Late Telychian most newcomers probably arrived from either Laurentia or Avalonia/Baltica.

The opposite happened on Laurentia. The radiation continued with at least five out of 11 newcomers originating on Laurentia in the Early Telychian. Invaders appear not to have migrated long distances and Laurentian endemics did not migrate at all. In the succeeding Mid–Late Telychian this development continued with a massive diversification of new, endemic genera. Of 15 newcomers in the Mid Telychian and 12 in the Late Telychian, only one genus in the Mid Telychian and three in the Late Telychian interval were invaders from the neighbouring palaeoplates.

5.6. Could high sea-level and the invasion of key taxa have caused a delayed Laurentian recovery?

The analyses described in Sections 5.1 through 5.5 clearly illustrate that the crisis faunas on the peri-Laurentian terranes slowly vanished within the Llandovery. With only moderate origination in the Rhuddanian that subsequently diminished through the rest of the Llandovery, high generic diversity could not be sustained due to the restriction of habitats. This is linked to the disappearance of terranes that one by one accreted to the Laurentian craton.

It is clear from this analysis, that the delayed diversity rebound seen on Laurentia, can be ascribed to a wealth of new, successful genera that originated particularly from the Late Aeronian onwards. These remained endemic to Laurentia at least within the Llandovery Series. But the origin of this radiation is likely to have been spawned by important newcomers originating within the Early Rhuddanian and the subsequent major transgression in the Late Rhuddanian. Because of the proximity to other palaeoplates, Laurentia experienced increased invasion during the Late Rhuddanian. This could indicate that succeeding the devastating extinction interval and a prolonged recovery interval that lasted until the Late Rhuddanian, life in the seas of Laurentia in the recovery interval were favoured, first by free faunal exchange between palaeoplates and then by taxa that explored and diversified vacant niches very rapidly in the Late Aeronian and Telychian. In particular, the shallow-water interior seaways were successfully invaded by shallow-water virgianid faunas, such as *Viridita* and *Virgiana*.

Thus, although the destruction of habitats may have been forced by the coincident configuration of palaeoplates, this may well also have contributed directly in shortening what could otherwise have become an even longer recovery interval on Laurentia as key taxa were able to invade at least the margins of Laurentia during the crisis and initial recovery interval due to the mutual proximity of the various continents. These taxa, with great success, utilized newly available niches driving a major radiation in the later part of the Llandovery.

6. An ice age at an unfortunate time

The amalgamation of the palaeoplates facilitated a large drop in γ -diversity that may well have been the most devastating factor with respect to global diversity. In addition the destruction of habitats prolonged the recovery interval considerably on a global scale, although regionally it may ultimately have helped Laurentia to regain its diverse faunas.

By the earliest Silurian a considerable number of terranes were virtually amalgamated primarily to Laurentia, but also to Baltica. Therefore the total area of available habitats on the continental margins remained smaller and less isolated than prior to the extinctions. This caused a major habitat loss and thereby a drastic decrease in α - and β -diversity. Plate tectonics, therefore, not only provides a further primary reason for the great taxonomic loss just prior to the Ordovician–Silurian boundary, but also a significant reason for the diachronous recovery interval.

Previous studies have considered the link between marine diversity and the dispersal of continents throughout the various periods of the Phanerozoic (Valentine, 1970; Valentine et al., 1978; Miller et al., 2009). Miller and co-workers found no indication of an increased disparity of faunas as a function of geographical dispersion up through the Phanerozoic. However, they did find it possible that significant terrane accretion to larger continents could have contributed to a loss in γ -diversity in the Palaeozoic.

Within the Upper Ordovician, a narrowing Iapetus Ocean was also believed to have caused a drop in diversity at the lower–middle Katian interval (Caradoc–Ashgill boundary) (Williams, 1973; McKerrow and Cocks, 1976), however, that drop in diversity is possibly a sampling

artifact that has been diminished with a better constrained global stratigraphy.

With respect to the end Ordovician crisis interval, [Brenchley \(1984\)](#) argued for a restricted habitat model that in many ways concurs with the current findings. However, contrary to Brenchley, the current study points directly to the configuration of large scale palaeoplates and the coincidental accretion of terranes as the main causal factor for this habitat restriction. Further, this study demonstrates that it was specifically the terranes situated within the Iapetus Ocean and along the margins of Laurentia that were the most severely affected regions. The sudden strike of an ice age with its changes in ocean water chemistry and sea level lowering had a catastrophic impact on the benthic faunas at various depths. We argue that the continents relatively proximal position to each other in the Iapetus region may have exacerbated the extinctions.

6.1. Terrane amalgamation during an Early Silurian icehouse?

The velocity that continents drift relative to one another control 1st order cyclicity in eustatic sea level. A decrease in the global spreading rates, for instance, would result in a eustatic sea level lowering that could exaggerate the glacially induced sea level lowering at the Hirnantian glacial maximum. As the peak glaciations may only have lasted half a million years, even with a rapid spreading rate of ~30 cm/year, the continents would have become only some 150 km closer to each other during that interval. So far, there are no estimates of how fast peri-Laurentian terranes, such as Girvan, drifted towards Laurentia. But [Torsvik et al. \(1992\)](#) reported that the Baltic plate increased its speed towards the end of the Ordovician, so that it moved towards Laurentia at 8 cm/year. Hence, not fast enough to drift long distances during the glacial maximum and further, as the plate appears to speed up rather than slow down, there is no indication of additional sea level draw-down caused by 1st order cyclicity (of course this would depend on the overall global signal).

However, it may be that it was not only the Hirnantian glacial maximum that controlled the extent of the crisis interval. Recent evidence supports the theory of continued existence of smaller Gondwanan glaciations at least through to the Aeronian ([Azmy et al., 1998](#); [Zhang and Barnes, 2002](#); [Johnson, 2006](#); [Díaz-Martínez and Grahn, 2007](#); [Jin, 2008](#); [Munnecke et al., 2010](#); [Johnson, 2010](#); [Finnegan et al., 2011](#)) that may have begun in the Darriwilian ([Rasmussen et al., 2009](#)). This would have prolonged the interval where recovery faunas, in the wake of the extinctions, would be continuously stressed by eustatic sea-level fluctuations by up to 10 million years. Consequently, during the Hirnantian–Aeronian interval, the peri-Laurentian terranes could have drifted almost 800 km, if we assume the Baltic data could be applied to Girvan. This is much farther than required to amalgamate with Laurentia in the early Llandovery. Thus, their species-rich diverse habitats were continuously restricted within this time interval, before simply disappearing.

[Table 1](#) further shows that both Baltica, and especially Avalonia, experienced a large taxonomic loss in the Aeronian. This is probably related to the amalgamation of Avalonia/Baltica with Laurentia and thus, this further illustrates the great impact on γ -diversity plate tectonics had during the long recovery phase after the End Ordovician mass extinctions.

Continued climatic fluctuations would further have stressed a fauna already in crisis, slowing down the global rebound in diversity. Ironically, on Laurentia, where the extinctions had been most sweeping, the tropical conditions, as well as the proximity of adjacent palaeoplates, may have been optimal for a diversity rebound that, although being delayed for millions of years, paved the way for a full recovery in the later parts of the Llandovery. In particular when compared to other regions of the World, such as Avalonia and Baltica, that did not rebound to their pre-extinction diversity levels.

In the earliest Silurian, the pentamerids were the most successful group within the Brachiopoda to re-adapt to the new, now vacant, shallow-water equatorial habitats. This most emphatically occurred on the Laurentian margin, with probably the most diverse pentamerid faunas known found in present day North Greenland ([Rasmussen, 2009](#)). Continued eustatic sea level draw-downs in the Llandovery could have been to their considerable advantage, as they were now specialists in the mid-shelf to most shallow-water settings. Those groups that did not re-adapt, notably groups like the strophomenides and orthides, were in some respects dead clades walking ([Jablonski, 2002](#)) as their niches were never fully restored after the Hirnantian extinctions. And so it may be that it was in fact Baltic invaders, such as the early pentameroid genus *Brevilamnulella* that made possible the rapid recovery of Laurentian faunas ([Rasmussen et al., 2010](#)).

7. Conclusions

Based on a large bibliographic database, this study suggests that a key factor controlling the duration and magnitude of the drop in species diversity during the end Ordovician crisis interval was the configuration of the palaeoplates. Analysis of the database shows a major regional disparity in the distribution of brachiopod diversity at the Ordovician–Silurian interface and further that the disparity continues through diachronous recovery intervals from one palaeogeographic entity to the next. Especially within the peri-Laurentian terranes the extinction event proved to be catastrophic. Laurentia appeared to have a delayed recovery interval, compared to other regions. Thus, on Laurentia, the crisis interval seems to have extended at least until the Late Rhuddanian. These observations suggest that the diverse habitats of the island arcs of the Iapetus Ocean – that had been one of the focal points in diversity prior to the extinctions – could not be sustained during the survival and recovery intervals. The most obvious reason for this, in our view, is that these terranes accreted to the Laurentian craton. If not during the Hirnantian, then in the succeeding lower part of the Llandovery stage where continued glacially induced sea level fluctuations made it difficult to adapt to the changing environments. On a global scale, the loss of habitats considerably extended the recovery interval as survivors were forced to re-adapt to continuously changing environments that they had not inhabited prior to the crisis. Regionally, Laurentia, benefitted from the terrane accretion, by ‘adopting’ exotic taxa during the crisis and initial recovery interval. Although, the recovery interval was delayed millions of years, compared to other regions of the world, these invaders evolved into a wealth of new taxa that caused a successful radiation so that by the end of the Llandovery, Laurentia was populated by much more diverse brachiopod faunas than those on, for instance, Avalonia and Baltica.

Paradoxically, the coincident palaeogeographic configuration that may have contributed to a global decline in diversity, at the same time, from a regional perspective, contributed greatly to the recovery on one of the main disaster zones, Laurentia. The extent and duration of the extinctions in these regions are probably related to the closing of the Iapetus Ocean. Implicit is that climatic change, although being the trigger that changed important physical conditions, the ‘unfortunate’ palaeogeographic configuration at the end of the Ordovician Period considerably exacerbated the magnitude of the extinctions; habitats narrowed and further prolonged the changed settings initiated by the sudden ice house conditions. This, again, caused a global reduction in brachiopod γ -diversity.

This extinction process may provide an insight into why one of the most major taxonomic extinctions ([Bambach, 2006](#)) did not ignite an ecological catastrophe. The amalgamation of terranes together with a global cooling and regression significantly restricted habitats and triggered major diversity loss. It is possible that no habitats were actually completely destroyed and biotas were free to migrate across latitudes.

The Earth has witnessed many drastic climatic fluctuations through geological time that did not have a severe affect on life. However, the timing of this particular rapid cooling at the close of the Ordovician Period coincided with a particular configuration of the palaeoplates that may have forced very specialized species to compete with each other. Those that were pre-adapted would stand a better chance of survival. However, to survive, they were required to rapidly re-adapt and adjust their mode of life, possibly several times, to occupy old, but by now vacant niches. In short, it was not enough to be incumbent and pre-adapted to succeed. The evolution of the pentamerid brachiopods illustrates this point.

Fortunately, for the subsequent success of the Brachiopoda, the end Ordovician mass extinctions succeeded the Great Ordovician Biodiversification Event, probably the most important interval within the Phanerozoic with respect to the radiation of life. It facilitated the filling of a range of newly available niches. Had life not become so highly diverse by the end of the Ordovician, this particular mass extinction event could very possibly have had an even more severe outcome that could have seriously influenced the subsequent overall structure of Palaeozoic ecosystems.

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