

Interrogation of distributional data for the End Ordovician crisis interval: *where did disaster strike?*

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The uppermost Ordovician–lowermost Silurian (Upper Katian–Rhuddanian) is surveyed with respect to the α - and β -diversity of rhynchonelliform brachiopods. The survey is based on new collections as well as existing literature, compiled in a large, georeferenced database. The brachiopod faunas are plotted using a Geographical Information System (GIS) and subjected to density analysis to display fluctuations within the different faunas through time. In addition, an analysis is performed on the preferred relative depth ranges of the brachiopod communities through the latest Ordovician–earliest Silurian crisis interval, following the concept of Benthic Assemblage zones. Both analyses support the view of a two-phased late Ordovician (Hirnantian) decline in diversity followed by a radiation in the early Silurian (Rhuddanian). These data show that the main taxonomic loss was geographically located on the peri-Laurentian terranes, in the Laurentian epicratonic seas and on the margins of the Ægir Ocean. Refuges during the survival interval were probably located in the shallow-water zones of especially Baltica, but also Gondwana, the peri-Laurentian terranes and the Kazakh Terranes. Except for Baltica, these refuges may to a large extent be obscured by the success of the *Hirnantia* fauna and, thus, may not contain many true survivor taxa. South China apparently operated as a refuge for the mid-shelf to deeper-water faunas. Avalonia, Baltica, Laurentia and South China experienced increased diversity in shallow-water settings in the recovery interval. Most regions experienced increased diversity among deeper-water faunas, although this appears to have been delayed until the late Rhuddanian on Laurentia. At this time the deeper-water faunas disappeared from the peri-Laurentian terranes (as did the terranes themselves) probably as a consequence of the progressively narrowing Iapetus Ocean. Copyright © 2011 John Wiley & Sons, Ltd.

Received 14 September 2010; accepted 26 April 2011

KEY WORDS End Ordovician crisis; brachiopods; α -, β - and γ -diversity; GIS

1. INTRODUCTION

The End Ordovician Extinction Event is recognized as one of the five main disaster intervals in the history of Phanerozoic life (Sepkoski, 1981). Almost 85% of all species were eradicated during a two-phased interval that had a duration of about 0.5–1.0 million years (Brenchley *et al.*, 1994; Sheehan, 2001). For rhynchonelliform brachiopods alone, up to 70% of all genera disappeared (Sheehan and Coorough, 1990; Rong *et al.*, 2006; Rasmussen, 2009). But, despite this colossal taxonomic loss, ecological niches were apparently not destroyed as they were rapidly reoccupied in the lowermost Silurian Rhuddanian Stage (Droser *et al.*, 1997), especially on Laurentia, where increased species origination, as well as

migration from Avalonia and Baltica, seem to have resulted in a quick rebound (Sheehan, 1975a; Krug and Patzkowsky, 2004, 2007; Rasmussen and Harper, in press). As sea level rose again within the Rhuddanian, some surviving groups of brachiopods, like the virgianids, became very large in size and dominated the near-shore carbonate platform environments. Other groups also radiated successfully during the early Silurian so that by the mid Llandovery, about 5 myr later, brachiopod diversity on Laurentia had rebounded to pre-Hirnantian levels. On a global scale this rebound may have taken as long as 15 million years (Krug and Patzkowsky, 2007; Rasmussen and Harper, in press).

Brenchley *et al.* (2001) demonstrated that, at least for brachiopods, all three measures of diversity (α , β , γ) fell sharply as a consequence of the crisis. This study focuses on this apparent enigma: how did the communities sustain their ecological structures despite catastrophic taxonomic losses?

First, with respect to γ or inter-provincial diversity, where geographically were the extinctions most severe? Previous

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research has indicated the shallow-water zone of the tropics was the primary focus of the crisis (Sheehan, 1973; Robertson *et al.*, 1991). This hypothesis can be tested. A global database of brachiopod occurrences within the latest Ordovician (uppermost Katian) through lowermost Silurian (Rhuddanian) interval has been compiled and plotted onto palaeoglobe reconstructions using GIS (Figures 1–5), thereby showing shifting trends in the density—here used as an indirect indicator of α -diversity—of brachiopod faunas through time. Second, with respect to β or inter-community diversity, the Benthic Assemblage zones (BA) of Boucot (1975) have been assigned to each lithological unit or brachiopod genus at each geographical location. This was implemented to assess water depths at which the extinction event was most severe. In combination with the density data, the information obtained from the BA survey forms a framework within which extinction, biodiversity hotspots, refuges and survival zones may be located both geographically and bathymetrically.

2. A CHANGING WORLD

The Great Ordovician Biodiversification Event (GOBE) was, until recently, believed to be at its peak during the greenhouse conditions of the Early Palaeozoic (Harper, 2006b). However, recent studies suggest that the initiation of the GOBE actually coincided with a climatic deterioration that was initiated during the early Mid Ordovician, but may have extended through the rest of the Ordovician (Rasmussen *et al.*, 2007, 2009; Trotter *et al.*, 2008; Vandenbroucke *et al.*, 2010). These climatic conditions were briefly interrupted by the end Ordovician ice age. Triggered by glaciations at the palaeo-South Pole, the buildup of ice caps on Gondwana caused an eustatic sea level draw-down and fundamental changes in ocean circulation (Sheehan, 1973, 1988; Brenchley *et al.*, 1994, 1995). Previously submerged cratons were drained and, as a result, the typical benthic faunas that had thrived in the shallow-water epicratonic seas, particularly characteristic of the Ordovician, were suddenly forced into new environments that were already pre-occupied by well adapted specialists (Sheehan, 1975a). The new situation was especially challenging—if not catastrophic—for the brachiopods. This group of marine invertebrates had dominated the Ordovician seafloor for some 40 myr (Sepkoski, 1981; Sepkoski and Sheehan, 1983; Harper, 2006b). Suddenly, their primary habitats disappeared simultaneously with the changes in ocean circulation and temperature.

The shallow-water, endemic faunas, predominantly existing in the tropics, thus became one of the main disaster zones (Robertson *et al.*, 1991), but deep-water clades were also severely hit by this extinction (Owen *et al.*, 1991; Harper and Rong, 1995). The deep sea suddenly became oxygenated, creating bottom currents and upwelling zones

that dramatically changed the Ordovician deep-water milieu (Brenchley *et al.*, 1994, 1995).

Although the main glaciation ended as rapidly as it began, the crisis itself continued throughout most of the Llandovery as the brachiopod faunas only slowly increased in diversity globally. This may be due to a narrowing of habitats caused by terrane accretion to the Laurentian craton, and thereby a loss of several peri-Laurentian terranes during the extinction and survival intervals. These had been the focal points of diversity prior to the extinctions, but near the end of the Llandovery were, if not amalgamated with, then in very close proximity to Laurentia (Rasmussen and Harper, in press). The recovery faunas were possibly further stressed by continued eustatic fluctuations in the lower part of the Llandovery Stage as more and more studies point to a prolonged series of glaciation events that continued throughout most of the Llandovery (Azmy *et al.*, 1998; Zhang and Barnes, 2002; Johnson, 2006; Díaz-Martínez and Grahn, 2007). The result was a taxonomic turnover that heralded the end of an Ecologic Evolutionary Unit (P2) and, before the new community structures were established by the end of the Llandovery, an interval of reorganization was initiated at the dawn of the Silurian (Boucot, 1983; Sheehan, 1996).

3. POSSIBLE SAMPLING BIAS

Global studies of biodiversity are subject to both random and systematic biases. Identification biases have been eliminated in this study, by careful scrutiny of both the literature and the unpublished data used. Apart from taphonomic biases that affect the preservation of all organisms, the upper Ordovician–lower Silurian interval was particularly susceptible to profound bathymetric fluctuations as the ice sheets on Gondwana waxed and waned, generating eustatic sea level changes. As a result, many regions of the world lack key biotas and strata through the extinction interval. Moreover, intense sampling is usually located near to areas that are accessible and highly-populated or with available labour. Thus, microcontinents and cratons such as Avalonia, Baltica and South China have relatively good coverage whereas the more remote regions, such as Antarctica and Greenland, are relatively poorly sampled. Rarefaction curves for some of the main areas show some contrasting patterns (Harper and Rong, 2008). Whereas relatively homogenous and well-sampled areas such as South China show that samples are adequate to assess the diversity of Hirnantian faunas, those from Laurentia and its margins are heterogenous and still require more intensive sampling. Brachiopods are commonly less well preserved in siliciclastic than in carbonate environments, and the minute size of the shells in, for instance, the *Foliomena* faunas is a hindrance to adequate discovery and sampling. During the Hirnantian regression there was

a switch in many places from carbonate to siliciclastic deposition and turbulent near-shore environments were prevalent; potential fossils are more fragmented and some faunas were reworked during the peak of the regression. The density plot for the upper Hirnantian (Figure 3) illustrates the main problem: relatively few faunas have been preserved even at localities that have been intensively sampled.

Studies of Lazarus taxa indicate that up to 30% more genera survived the extinctions than have actually been located in the Hirnantian (Rong *et al.*, 2006). Nevertheless, the event marked a major change in the Palaeozoic brachiopod fauna; many early Silurian faunas are very different from those of the Hirnantian with commonly monospecific, large-shelled incumbent brachiopod populations suddenly starting to dominate the most shallow-water zones of the Early Silurian. In contrast, during the Late Ordovician, faunas in near-shore environments were relatively diverse with high values for evenness and low for dominance. The following section presents some of the possible biases that should be mentioned when conducting this kind of large-scale survey.

4. METHODOLOGY AND COMPILATION OF DATA

In this study, geographic occurrences and stratigraphic ranges of rhynchonelliformean brachiopods have been recorded mainly from the literature and, to a lesser extent, from ongoing research. The database, though not exhaustive, is one of the largest compiled through the studied interval and thus the data are robust. Most data are from monographs or faunal analyses

that describe a large part of the brachiopod fauna at given localities. Papers dealing with particular genera have also been used mainly to avoid synonyms and double check their global distributions (both geographically and stratigraphically). However, despite all efforts, some synonyms probably still exist in the data matrix. Appendix A lists the references used in the database. The column 'No. of taxa' shows the number of unique taxa from that particular reference that was relevant for the database according to the principles listed above. The columns 'Age range' and 'Assigned BA range' show the age and bathymetric ranges of all taxa used from that particular reference; hence specific data on every single species in the data matrix have been omitted from this appendix due to space limitations. With respect to the BAs this range was often a subjective view based on the experience and interpretation of the authors.

Data have been compiled to the lowest possible taxonomic level, usually to species. If more than one species occurs at the same locality and one of them is listed as 'sp.', this has been counted as at least two species. Sub-species, though registered in the database, are omitted from this analysis. However, and not uncommonly, only generic lists are published and thus records at the specific level are not always possible.

Another source of bias is uncertainties concerning age ranges. The main problem with this kind of survey is the global correlation of lithostratigraphical units. This issue has been intensively studied for over two decades (see, for example, Cocks and Rickards, 1988). This study has relied on the most up-to-date correlation scheme from the literature. Stratigraphically, all data have been correlated

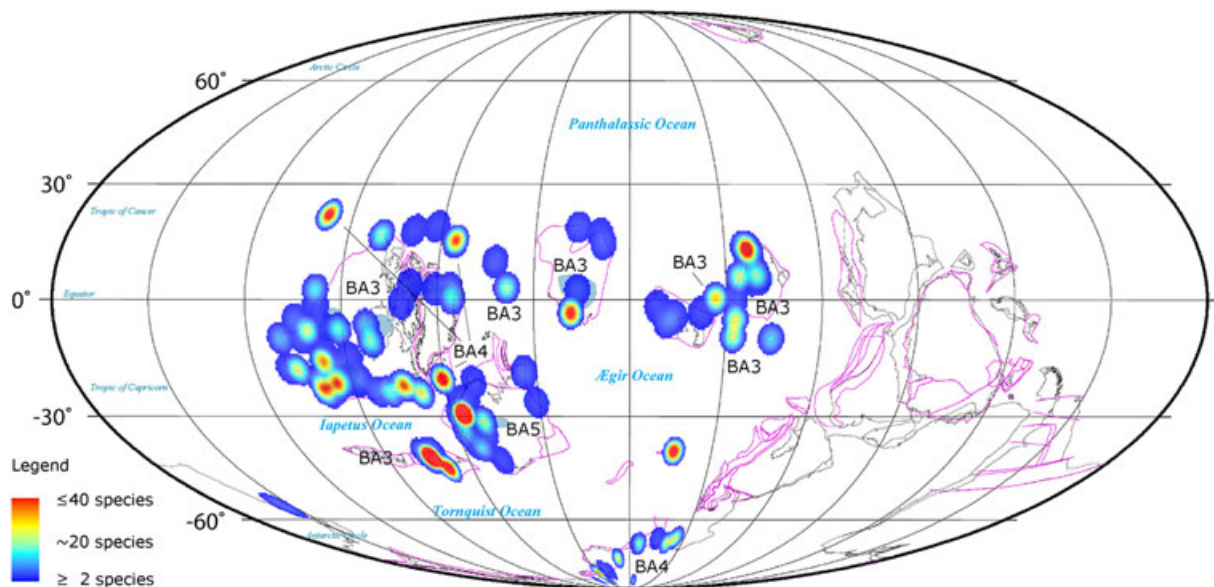


Figure 1. Mollweide palaeoprojection of the late Katian interval. Shallow-water epicratonic seas are indicated in light blue. Brachiopod faunas were plotted and run through a density analysis. Warm colours indicate high density (high α -diversity), cold colours low density. The most dominant Benthic Assemblage zone (BAs) for each geographic entity analysed for this study is shown (the BA that holds the largest amount of taxa relatively). For a projection of palaeogeographic names onto this map, see Rasmussen and Harper (in press).

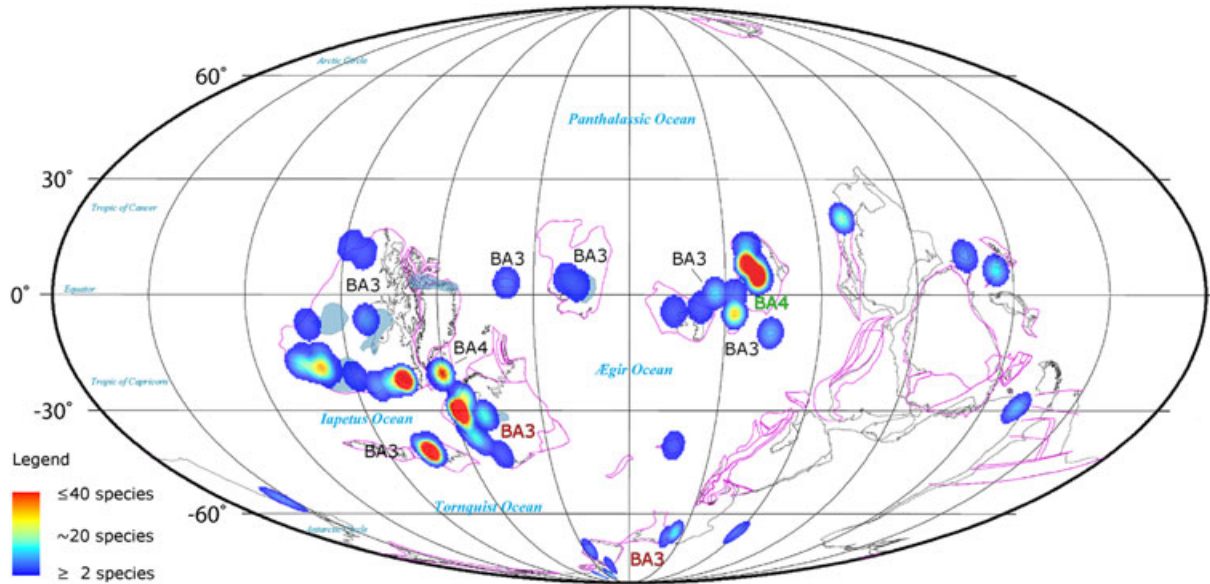


Figure 2. Mollweide palaeoprojection of the early–mid Hirnantian interval. Shallow-water epicratonic seas are indicated in light blue. Brachiopod faunas were plotted and run through a density analysis. Warm colours indicate high density (high α -diversity), cold colours low density. Moreover the Benthic Assemblage zone (BA) that most taxa prefer relatively, compared to that in the Late Katian (Figure 1), is also shown for each palaeogeographic region. If relatively more taxa have moved into a deeper BA compared to the late Katian, this has been indicated in green script. If instead there are relatively more taxa that have moved into a shallower BA zone compared to the late Katian, this has been indicated in red script. Black indicates no change compared to the previous map.

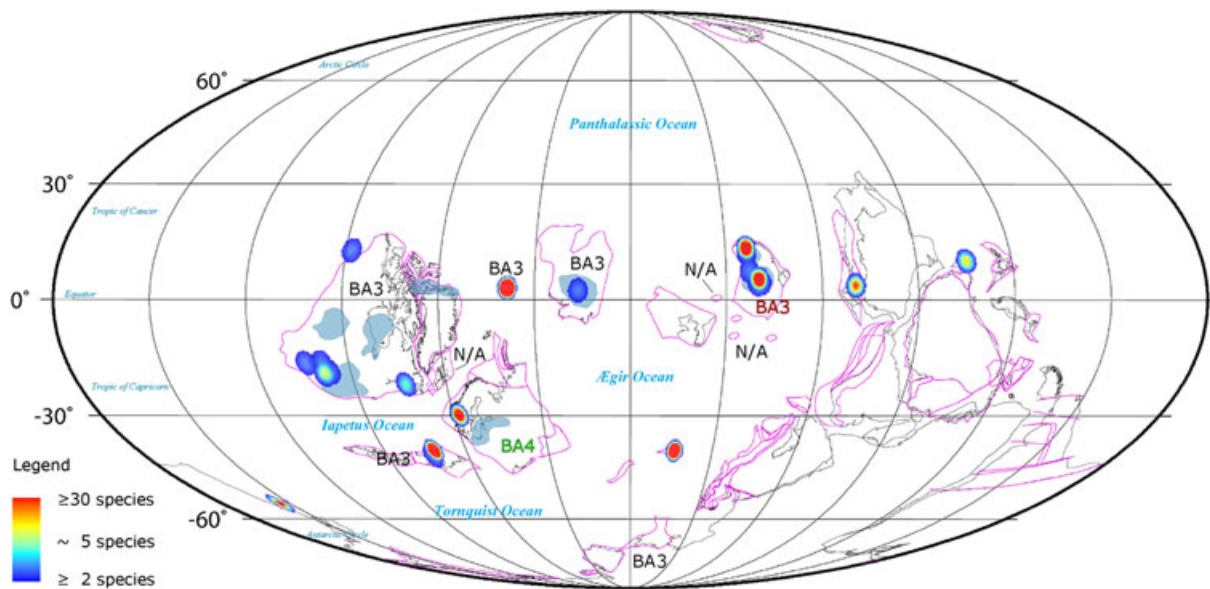


Figure 3. Mollweide palaeoprojection of the late Hirnantian interval. Shallow-water epicratonic seas are indicated in light blue. Brachiopod faunas were plotted and run through a density analysis. Warm colours indicate high density (high α -diversity), cold colours low density; note the scale is different from the other figures. Basinward or shoreward migrations of the BA with the highest number of taxa relatively within this time-slice compared to the early–mid Hirnantian interval (Figure 2) are also shown in green and red, respectively. Black indicates no change compared to the previous map.

with the British stage system using Bergström *et al.* (2009). All records were listed as precisely as possible, for example, early, mid or late Rawtheyan, forming narrow time-slices so

that fluctuations in diversity may be tracked with some precision. This, of course, may compromise some of the robustness of data analysed as discussed by other workers

WHERE DID DISASTER STRIKE DURING THE END ORDOVICIAN MASS EXTINCTIONS?

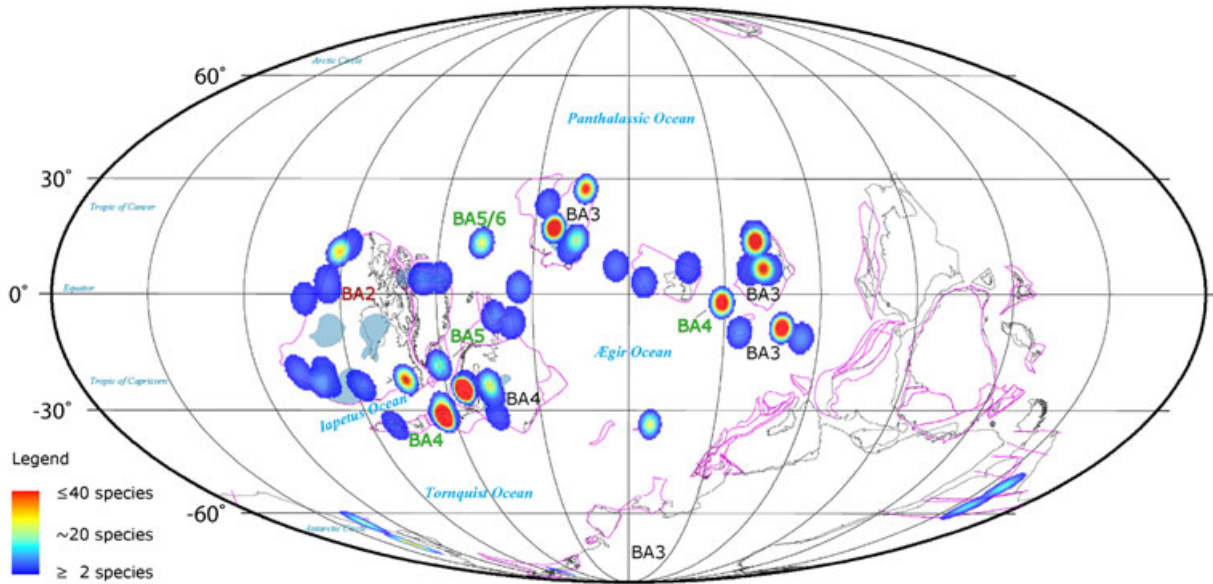


Figure 4. Mollweide palaeoprojection of the early Rhuddanian interval. Shallow-water epicratonic seas are indicated in light blue. Brachiopod faunas were plotted and run through a density analysis. Warm colours indicate high density (high α -diversity), cold colours low density. Basinward or shoreward migrations of the BA with the highest number of taxa relatively within this time-slice compared to the late Hirnantian interval (Figure 3) are also shown in green and red, respectively. Black indicates no change compared to the previous map.

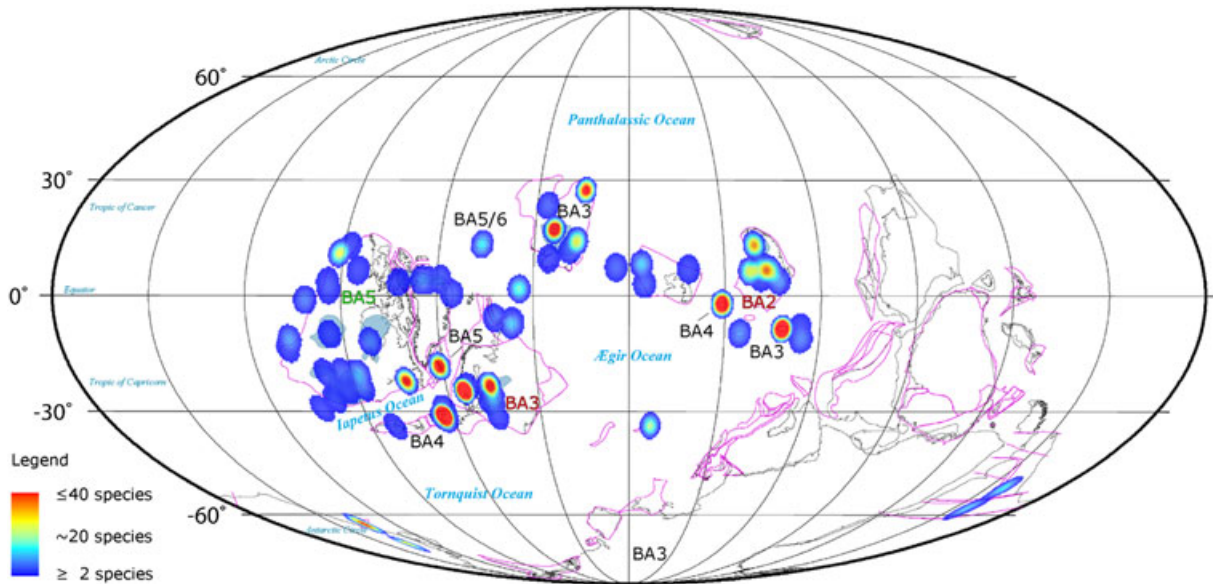


Figure 5. Mollweide palaeoprojection of the late Rhuddanian interval. Shallow-water epicratonic seas are indicated in light blue. Brachiopod faunas were plotted and run through a density analysis. Warm colours indicate high density (high α -diversity), cold colours low density. Basinward or shoreward migrations of the BA with the highest number of taxa relatively within this time-slice compared to the late Hirnantian interval (Figure 4) are also shown in green and red, respectively. Black indicates no change compared to the previous map.

(Sheehan and Coorough, 1990). Therefore, for this particular study, the tri-partite division of the Rawtheyan Stage used in the database was abandoned to secure a more robust signal from the pre-crisis interval. However, in some

instances only 'Ashgill' designations were given and thus had to be applied in the database. Such ranges have been included in the upper Katian and early-mid Hirnantian intervals. If 'Hirnantian' was listed in the literature the data were used in

the lower-middle Hirnantian matrix (*extraordinarius* Zone) in this investigation. Upper Hirnantian (*persculptus* Zone) is exclusively based on literature that states this.

Where listed, BAs have been assigned according to the literature. However, as these data seldom were available, the zones are based primarily on lithological characters and, secondly, if no lithological data were available, on a subjective assessment based on the genera occurring in the assemblage. For this specific exercise it is worth noting that the current data matrix is part of a much larger database spanning the Early Sandbian–Late Telychian interval (Rasmussen, 2009; Rasmussen and Harper, in press). In this way more generic occurrences form the basis for the BA assignment, though clearly many show changes in environmental occurrence throughout the interval covered by the database.

Finally, small biases may occur when positioning data points (localities) on the GIS base map. Localities have been placed as precisely as possible. However, in some instances records were very imprecise—for example, a record from ‘eastern USA’ is difficult to plot accurately. In these instances, if original literature is not available, data points have been placed within the eastern USA. But this is not considered a major bias as the numbers of these are quite small.

5. DATA ANALYSIS

5.1. Density plots

The locality data with its different taxa—usually species—are distributed geographically using GIS software. The distribution data have been plotted on five different time-slices (Figures 1–5): upper Katian, lower–middle Hirnantian, upper Hirnantian, and lower and upper Rhuddanian. The upper Ordovician time-slices are based on a Mollweide palaeoglobe projection from ~450 Ma, whereas the Silurian time-slices are based on a ~440 Ma projection. The palaeoglobes were provided by Trond Torsvik, Geological Survey of Norway. The position of smaller terranes, such as Farewell, Northern Precordillera, Kolyma, Altai and the Kazakh terranes, however, have been placed by the authors.

The distribution data have been processed by a density analysis using the Kernel method. This method statistically predicts how densities will affect neighbouring regions (cells) that do not contain any data. Thus, Figures 1–5 give a tentative impression of where regions with high α -diversity occurred, as these density measures compare the mutual diversities of different localities. Warm colours (red and yellow) indicate high densities and cold colours (blue) low densities.

The upper Katian time-slice (Figure 1) shows a high density in the Iapetus region with highest densities in Avalonia and Baltica in the south and east in addition to high, although more moderate densities, in the eastern Laurentian margin (Anticosti Island and Maine), and Girvan in the west and north. Like

Girvan, other peri-Laurentian terranes show moderate to high densities. These are the Klamath Mountains and the Farewell Terrane (west-central Alaska). In the current study these regions are often referred to as ‘peri-Laurentian terranes’. Thus, they are not the margins of the Laurentian craton itself, but rather terranes positioned relatively close to that continental block, although in the case of the Farewell Terrane its position is more questionable as the shared faunal links are mostly deep-water species that may prove to be cosmopolitan in extent (Rasmussen *et al.*, 2011). On cratonic Laurentia, the Jones Ridge area (that is, the Alaska–Yukon border) appears more diverse than many other contemporaneous faunas on Laurentia. This is because Jones Ridge has some rather poor age constraints (‘pre-Hirnantian Ashgill’) so in reality this fauna may not be upper Katian at all (Ross and Dutro, 1966; Potter and Boucot, 1992). The ‘Great American Bank’ region shows the highest densities on cratonic Laurentia. Adjacent to Laurentia, the Kolyma Terrane also show a moderately high density, as does the Taimyr Peninsula in Siberia, but, again, this latter terrane is only constrained to the Mid Ashgill (Cocks and Modzalevskaya, 1997).

Another province with high density is the northern Ægir Ocean of Torsvik and Rehnström (2001) and Fortey and Cocks (2003). This includes South China, the Kazakh terranes and Altai. Within the Kazakh Terranes, Tien-Shan has been regarded as peri-Gondwanan by several workers, which we follow here (Fortey and Cocks, 2003). Other Gondwanan and peri-Gondwanan regions with moderate to high densities are Perunica, Armorica, the Carnic Alps, Sardinia and Iberia (see Appendix A for references). These faunas are also only constrained to Rawtheyan at best.

In the Lower–Middle Hirnantian (Figure 2), during the first phase of the extinctions, the Iapetus region still exhibited high levels of density. Of the peri-Laurentian terranes, only Girvan exhibited high density. The Quebec area and northeastern USA showed high densities on the Laurentian cratonic margin, whereas the Laurentian epicratonic seas (the southwestern parts of the ‘Great American Bank’) showed moderately high densities. Outside the Iapetus region South China and the Chu-Ili Terrane still had high density. The other Kazakh terranes and Altai lack data. On and around Gondwana the highest density spots apparently migrated to the equatorial region at northern Sibumasu and southern New Zealand. Farther south, the Northern Precordillera and the Carnic Alps were the only areas with moderate densities, but their geographical extent has been narrowed considerably. In general, it appears that the faunas are not as geographically dispersed as in the upper Katian.

Only a few brachiopod faunas have been described from the upper Hirnantian *persculptus* Zone (Figure 3). Therefore, especially at this level, one must take into account sampling bias. The high density areas have shrunk to the margins of Baltica (Oslo Region) and Avalonia. The peri-Laurentian

terrane appear non-existent. Within the previously high density spot of eastern Laurentia, only Anticosti Island shows a moderate density level. On Laurentia the westernmost part of the 'Great American Bank' shows the highest density on the palaeocontinent, although it is only of moderate levels. The Mackenzie Mountains in northwestern Canada have a low density level. Outside the Iapetus region, Kolyma show high density, as does South China, though the density areas are considerably narrower. Siberia indicates a small increase in density compared to that of the *extraordinarius* Zone; however, it only has a small geographical extent. On the peri-Gondwanan terranes high densities are apparent in southern Sibumasu, Tasmania, Perunica and the Northern Precordillera (the last of these is difficult to see in Figure 3 due to the Mollweide projection).

In the early Silurian the picture changed dramatically. The narrowing Iapetus region was re-established as a high density province in the early Rhuddanian, as was South China and Altai (Figure 4). In the Iapetus region the deep-water Oslo Region showed the highest density with the shallow-water East Baltic faunas exhibiting moderately high density. Avalonia, Girvan and Anticosti Island also showed moderate to high densities. Thus, density was high in both shallow and deep water on both sides of the Iapetus Ocean. On Laurentia the highest density was seen in the Mackenzie Mountains, northwestern Canada, that were situated on the Laurentian margin. The Great Basin and the Franklinian Basin (North Greenland) showed low levels of diversity. Kolyma remained characterized by rather high density and now Siberia had three areas with moderate to high density. In Kazakhstan, Tien-Shan showed high density, but it is only moderate at Chinghiz and no data is available from Chu-Ili. Although more moderate levels than Tien-Shan, other peri-Gondwanan (or Gondwanan) areas also showed increased density. There are several places in present day South America including the Northern Precordillera (these are difficult to see in Figure 4 due to the projection).

As demonstrated in Figure 5, many new faunas appeared in the late Rhuddanian, but the regions with high density remained the same. Small differences included a new high density area in Baltica and modest increases in the northern Urals, and the islands of Novaya and Severnaya Zemlya. On Laurentia there were now, for the first time since the pre-crisis interval, faunas on the entire craton with highest densities—though only moderate levels—in the 'Great American Bank'. Only the Mackenzie Mountains and Anticosti Island, both situated at the margins of Laurentia, reached moderate levels in density on Laurentia. Other marginal settings, such as Nevada and the Franklinian Basin, exhibited modest levels in densities that were slightly higher than the Laurentian average. North China also exhibited modest levels of density. On Gondwana, the Northern Precordillera and other areas of mid-South America showed high density. Again, the Mollweide projection makes these difficult to see.

5.2. Benthic assemblage zones

Table 1 show the relative distribution of taxa along the BA depth transect through the crisis interval from ten different palaeogeographic regions. In addition, their relative global distribution is shown.

Table 1 was calculated by assigning BAs to all lithological units and occurrences of taxa in the entire database. Thus, two datasets of assigned BAs were developed, one based on lithology and one based on taxa. The dataset based on taxon occurrences was used to fill in the gaps where no lithological data were available. This was preferred as the lithological dataset is much more coherent, whereas BAs based solely on taxa will fluctuate a lot (i.e. a lithological unit may be assigned a BA4–5 depth, but have an associated fauna with taxa that has varying ranges, such as BA1–4 or 3–6). Hereafter, the data were split into the ten different regions and separated by time-slices that vary in length depending on the regional stratigraphical resolution. Subsequently, each time-slice was normalized so that the occurrences of taxa in a given BA within each time-slice could be compared relative to the other BAs in the same time-slice. The column 'Total' list the number of total occurrences in each time-slice. As a given taxon may occur in more than one BA and in more than one locality within each geographic entity, this column lists the sum of total occurrences from BA 1–6, not the actual total number of taxa. Nevertheless, this column clearly illustrates two phases of decline in the Hirnantian and a sharp rise in the lower Rhuddanian. This corresponds well with previous studies that showed that these declines coincide with the beginning of the *extraordinarius* and *persculptus* Zones respectively (Brenchley *et al.*, 2001; Rong *et al.*, 2006).

For ease of reading, Table 1 has been given three colour codes. Yellow indicates the maximum concentration of taxa in a BA within a given time-slice (the BA where most species could occur relative to the contemporaneous BAs); green indicates the initiation of relative increases in taxa in a particular BA zone compared to the same BA in the preceding time-slice; and red indicates the onset of a decline in possible taxa in a particular BA, relative to the same BA in the preceding time-slice. In addition, the same increases and decreases in preferred BAs are shown with the same colour codes in Figures 1–5 indicating whether faunas preferentially moved into shallower or deeper BAs through the crisis interval.

Arguably, this distribution of taxa along the BA depth transect depicted in Table 1 represent shifts and fluctuations in β -diversity, as it indicates the number of species that may occur at several localities within each geographical unit, and the total number of taxa that were able to occupy a specific BA zone within a specific time-slice. It is not, strictly speaking, a measure of α -diversity, since the analysis includes different communities within the same geographic entity. Instead, it can be regarded as a proxy for β -diversity.

Global %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian	1	11	32	41	14	1	1975
Lower Hirnantian	6	23	35	25	11		631
Middle Hirnantian	5	20	40	27	9		746
Upper Hirnantian		17	52	24	7	1	227
Lower Rhuddanian	2	17	33	23	22	3	910
Mid.-Upper Rhud.	2	17	31	29	20	1	1373

Altai %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Ashgill		19	40	27	10		62
Llandovery	1	8	24	39	27		65

Avalonia %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian		24	29	28	13	7	257
Low.-Mid. Hirnantian		23	34	29	15		110
Upper Hirnantian		3	50	47			38
Lower Rhuddanian		7	17	43	33		149
Mid.-Upper Rhud.		5	11	44	40		185

Baltica %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian	1	2	13	39	42	3	256
Low.-Mid. Hirnantian	17	21	32	16	16		206
U Hirnantian			14	86			14
Low Rhuddanian		5	30	41	24		143
Mid.-Upper Rhud.		6	50	32	12		173

China %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian	3	15	37	24	15	6	194
Lower Hirnantian		6	39	43	13		101
Middle Hirnantian		3	46	46	6		178
Upper Hirnantian		4	42	28	26		50
Lower Rhuddanian	7	27	31	21	12	1	121
Mid.-Upper Rhud.	13	34	25	15	13	1	119

Gondwana %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian		2	29	34	29	6	284
Low.-Mid. Hirnantian		33	37	22	7		81
Upper Hirnantian		41	51	6	3		69
Lower-Upper Rhud.		21	32	27	14	6	182

Kazakhstan %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian		6	63	21	11		72
Low.-Mid. Hirnantian		42	47	6	6		36
Rhuddanian	2	26	34	27	12		184

Kolyma %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian		14	68	14	5		22
Upper Hirnantian			83	6	6	6	36
Rhuddanian		3	13	10	37	37	30

Peri-Laurentian terranes %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian		3	5	48	44		167
Low.-Mid. Hirnantian		38	43	9	9	2	47
Mid.-Upper Rhud.		23	23	25	27	1	91

Laurentia %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Katian	1	14	38	31	12	3	640
Low.-Up. Hirnantian	2	20	43	26	8		178
Lower Rhuddanian		30	26	26	21	1	77
Mid.-Upper Rhud.	1	22	22	27	29	1	158

Siberia %	BA 1	BA 2	BA 3	BA 4	BA 5	BA 6	total
Upper Ashgill		1	49	46	3		91
Llandovery	3	17	40	24	15		182

Table 1. Relative depth ranges of brachiopods through the investigated interval separated into each of the geographic entities analysed by the current study. As a given taxon may occur in more than one BA, the column 'Total' list the sum of total occurrences within each interval. Thus, not the total number of taxa. Yellow boxes indicate the BA maximum, that is, the BA that contains the largest number of taxa in a given BA relatively within that particular time-slice. Green boxes indicate the beginning of sharp increases in the number of taxa within a BA in a time-slice compared to the same BA in the preceding time-slice; red boxes indicate the beginning of sharp decreases in the amount of taxa in a BA within a time-slice compared to the previous time-slice. This table is available in colour online at wileyonlinelibrary.com/journal/gj

In the 'Global' section (top left in Table 1) most taxa in the uppermost Katian are concentrated in BA zones 3–5, with the highest concentration in BA4 (indicated by a yellow box in Table 1). Once into the lower Hirnantian there is a marked change in preferred BAs with a large increase in percentage in zones 1–3. Farther off-shore, there is now a decrease in the number of possible species occurrences compared with those in the Upper Katian, though there is a similar abundance of communities in BA2 and BA4. There are no longer any species in the BA6 zone. An almost identical pattern is seen in the middle Hirnantian. The upper Hirnantian *persculptus* Zone is characterized by a very large decrease in total occurrences (the 'Total' column). There are no longer species in the BA1 zone and there are small declines in occurrences in BA2, 4 and 5. However, it is not known if there are species that could extend into the BA6 zone. The BA3 zone seems to have been the most preferred habitat throughout the Hirnantian and also in the succeeding Rhuddanian Stage, but there are also noticeable changes

with increases in the percentage of possible occurrences in the BA5–6 zones in the Lower Rhuddanian and an increase in BA4 in the Middle–Upper Rhuddanian.

These new data are based on a much more robust dataset than previously compiled and confirm the results of Brenchley *et al.* (2001), closely reflecting the eustatic sea level signal, that is, a regression followed by two pulses of sea level rise. However, to discover where the extinction was most severe, a similar investigation was carried out for ten different regions.

Partitioned region-by-region, the shift from dominance of deeper water BA4 communities in the upper Katian to shallower BA3 dominated communities in the Hirnantian is demonstrably widespread, as is a sharp increase in communities preferring deeper water in the Rhuddanian. However, there are some discrepancies that require explanation.

The data for China, which is an amalgamation of North and South China together with Sibumasu, show a different trend. Here it is the BA3 zone that is most diverse in the upper

Katian, whereas the BA4 zone becomes more diverse in the lower Hirnantian. There is also a sharp drop in β -diversity in the BA2 zone. In the middle Hirnantian the BA3 and 4 zones are equally diverse. Then, in the upper Hirnantian, the BA3 zone is more diverse than BA4. Thus, overall the distribution of Chinese taxa in the upper Ordovician is almost completely opposite to the global data trend. In the Rhuddanian, communities in the BA3–4 zones continue to dominate, but with increased diversity in most shallow water zones. The Rhuddanian distribution, however, is more similar to the global data except for the relatively high number of near-shore communities that is particularly marked in the Middle–Upper Rhuddanian.

It is interesting that in the upper Katian, Baltica, Gondwana and the peri-Laurentian terranes have a high percentage of communities in BA4–5 compared to those of the other geographic units. The Hirnantian communities, however, apparently preferred the same depth as those globally. Thus, there is a very sharp drop in preferred BAs to zones 1–3. The pattern in Baltica is particularly striking as it has a very high percentage of taxa in BA1.

In the lower Rhuddanian, Baltica, together with Altai and Avalonia, are the only regions where there are a higher percentage of taxa in the BA4 zone and, thus, the faunas of this zone are more diverse than those in the BA3 zone. In Baltica, however, the BA3 zone is more diverse in the upper Rhuddanian. In Kolyma and the peri-Laurentian terranes, the deeper-water communities became successful at the beginning of the recovery interval, despite having had more successful shallow-water communities in the Hirnantian.

6. DISCUSSION

The α - and β -diversity data and analyses presented in the current study show some important aspects with respect to survivorship and recovery through the crisis interval. Both diversity measures illustrate clearly the two-phased taxonomic loss succeeded by a radiation in the Rhuddanian that have been described by previous workers (Brenchley *et al.*, 1994; Rong *et al.*, 2006).

From the α -diversity analysis it is clear that the main taxonomic loss from the upper Katian to the Lower–Middle Hirnantian is situated on Laurentia, the peri-Laurentian terranes and the margins of the \AA gir Ocean. One could argue that, in particular, the Kazakh Terranes experienced a great loss in α -diversity. However, this is an artefact since there are no relevant data from this region. The β -diversity analysis of the preferred depth range of the brachiopod communities shows, as demonstrated by Brenchley *et al.* (2001), that the deepest communities, such as the *Foliomena* fauna, disappeared by the end of the Katian. In the Hirnantian

no BA6 range brachiopods have been found and the BA4–5 zones were severely affected by the first phase of the extinctions. During the late Katian, the *Foliomena* fauna also occurred on Gondwana as well as on the peri-Gondwanan terranes of Perunica and Armorica (Havlíček *et al.*, 1994; Villas *et al.*, 2002; Zhan and Jin, 2005). These terranes formed part of the Mediterranean Province (Harper and Rong, 1995). These faunal distinctions disappeared after the Katian, and, instead, the typical and atypical *Hirnantia* faunas took over and defined the high- and mid-latitude Bani and Kosov provinces, respectively (Rong and Harper, 1988). These faunas disappeared during the *persculptus* Zone as indirectly seen in the present BA survey (Table 1) where only Gondwana exhibited an increase in the BA2 zone. This may explain the drop in α -diversity at the margins of the \AA gir Ocean (compare Figures 1 and 2). As was also recognized by Brenchley *et al.* (2001), no apparent decline in zones 1–3 is observed. The sudden dominance of the *Hirnantia* fauna may have compensated for this loss from the onset of the Hirnantian glaciations (Brenchley *et al.*, 2001). Thus, this explains why the current analysis cannot clearly resolve the dilemma of previous studies (Sheehan, 1973; Sheehan and Coorough, 1990), which noted that faunas prior to the crisis that thrived in the shallow-water epicontinental seas were most severely targeted by the extinctions. However, a separate γ -diversity analysis of an extended version of the current database demonstrates that the faunal turnover was very high at the Katian–Hirnantian boundary (Rasmussen and Harper, in press). This was largely due to the loss of taxa belonging to the shallow-water zones in the upper Katian and the subsequent success of the shallow-water Edgewood and *Hirnantia* faunas in the Hirnantian.

In addition, this survey supports Owen *et al.* (1991) and Harper and Rong (1995) who suggested that the mid-deep shelf biotas were least affected by the extinctions. Partitioned region-by-region, it is striking that the peri-Laurentian terranes, Gondwana and, particularly, Baltica apparently had higher BA2–3 β -diversity values in the *extraordinarius* Zone than in the upper Katian. This may be because these faunas were better pre-adapted to changing conditions, and thus more survivors co-existed together with the *Hirnantia* fauna in these regions despite the fact that eustatic lowering of sea level increased competition for space by the restriction of shelf areas. Sheehan (1975a) suggested that the Rhuddanian newcomers on the Laurentian craton were, in fact, hold-over taxa from the North European Province (Avalonia and Baltica); these faunas had survived because they were better adapted to these conditions compared to the endemic shallow-water Laurentian genera such as *Hiscobeccus*, *Hypsiptycha*, *Lepidocyclus* and *Rostricellula* that were part of the *Hypsiptycha*–*Lepidocyclus* fauna in the late Katian. This has recently been supported by more detailed studies using standardized databases (Krug and Patzkowsky, 2004, 2007),

and by individual taxonomic studies that have tracked the origination and migration routes of *Brevilamnulella* and *Clorinda* (Rasmussen *et al.*, 2010). Jin and Copper (2008) found that some immigrants already appeared in unusually diverse faunas within the Hirnantian part of the Ellis Bay Formation on Anticosti Island. This is further supported by Rasmussen and Harper (*in press*), who demonstrated that most newcomers on Laurentia within the *extraordinarius* Zone appear to have been invaders originating from both Baltica and Avalonia or (to a lesser extent) from the peri-Laurentian terranes, if not originating from the Laurentian craton itself. Within the lower Rhuddanian, most newcomers are Laurentian endemics, but still with invaders from Baltica and Avalonia. In the upper Rhuddanian the origination of Laurentian endemics is still high, but the interval is characterized particularly by increased invasion, now especially from Kolyma and Siberia, but also from the peri-Laurentian terranes and with a smaller portion arriving from Baltica and Avalonia. However, from the Aeronian onwards invasion almost completely halts. Instead, the Laurentian newcomers are now almost exclusively Laurentian endemics. Thus, within the Early Silurian, the primary invasion of newcomers in Laurentia may have occurred in the late Rhuddanian. This may suggest that the eustatic transgressive pulse was delayed in the epicontinental seas of this craton. This is supported by several sea-level curves constructed for the Lower Silurian of Anticosti Island (Dewing, 1999; Jin and Copper, 1999; Zhang and Barnes, 2002) and, moreover, seems to match global data (Johnson, 2006).

Because only very few taxa from the *persculptus* Zone have been recorded from Laurentia, the second extinction phase can only be seen indirectly, as the lower Rhuddanian values have already declined in BA zone 3 compared to the *extraordinarius* Zone. This suggests that the so-called warm-water Edgewood fauna was particularly successful in Laurentia before the *persculptus* Zone. But there is also an increase in diversity in BA zones 2 and 5, the former now holding the largest number of possible occurrences. Both could be ascribed to the arrival of newcomers (see above). Within the shallow-water BA2 zone, *Dalmanella*, *Eospirigerina*, *Eostropheodonta* and *Hindella* dominated. All were remnants of the *Hirnantia* fauna, but now developed as part of the new communities such as the *Hindella* Community. These taxa may have originated on peri-Laurentian terranes with some Baltic affinities, as the *Hirnantia* fauna probably did not reach the Laurentian shores during the cooling period (Rong and Harper, 1988). The deep-water BA5 was characterized by genera such as *Brevilamnulella*, *Cyclospira*, *Dicoelosia*, *Epitomyonia*, *Levenea* and *Stricklandia*. At least some of these genera are known from the *Dicoelosia*–*Skenidioides* and *Stricklandia* communities.

By the upper Rhuddanian, the Laurentian data appear more similar to global patterns, as there is a drop in communities in BA zones 2–3 and an increase in zones 4–5. This may suggest that

the arrival of many newcomers was delayed on Laurentia, and that once genera such as *Coolinia*, *Cyclospira*, *Skenidioides* and *Stricklandia* were established they were particularly successful in deeper waters. Some genera, such as *Brevilamnulella* and *Dicoelosia*, were able to move into more shallow-water zones on Laurentia in the recovery interval as shallow-water habitats had become available (Sheehan, 2008a). The introduction of *Brevilamnulella* into more shallow-water zones seems to have been particularly important, as this genus appears to have been ancestral to the *Viridita*–*Virgiana* lineage (Jin and Copper, 2010). There were, nevertheless, still endemics such as *Rhynchotrema* in the deeper benthic zones, but endemics were much more successful in the near-shore environments, with the almost monospecific *Virgiana* communities accounting for the drop in α - and β -diversity. The *Virgiana* communities included a few slightly deeper-water elements such as *Stegerhynchus*, a genus that dominated Laurentian faunas later in the Llandovery, whereas the *Virgiana* Community thrived on much of Laurentia in the late Rhuddanian (Jin *et al.*, 1996, 1999; Jin and Copper, 2000, 2004). This is reflected here by the low density colours seen throughout Laurentia in the upper Rhuddanian density plot in Figure 5 (compare with Figure 4, the lower Rhuddanian, where no part of interior Laurentia was populated) and also the Upper Rhuddanian drop in the number of occurrences in the BA2–3 zones on Laurentia. Moreover, recent investigations that found the macrofauna of western Laurentia to have a long delay in recovery from the extinctions, support the present study (Sheehan, 2008b). Sheehan speculated that this delay may have been caused by unfavourable oceanic currents or anomalous physical conditions off the margin of Laurentia.

However, a delayed immigration on Laurentia is in direct contrast to the very quick rebound of recovery faunas found by Krug and Patzkowsky (2004, 2007). There are probably two explanations for this. One could be that their database was at a lower temporal resolution than that of the present study and used time-slices of 5 million year intervals, that are, longer than the duration of for example the Rhuddanian. However, as the same quick rebound on Laurentia was found by Rasmussen and Harper (*in press*), based on the same database that was used for the current study, the stratigraphical resolution does not explain the contrasting results regarding the Laurentian diversity rebound. Instead, as another explanation, it seems more likely that, as the current study to a large extent shows trends on the species level, as compared to the generic level, this will yield stronger fluctuations in diversity. Thus, the quick generic rebound on Laurentia may actually cover over a delayed, but even quicker and faster rebound at the species level, possibly caused by the immigration of new species as a result of the large transgressive pulses that occurred within the upper Rhuddanian.

China, and in particular South China, seems to be quite unique. The Rhuddanian β -diversity fluctuations are somewhat different from the global data in that there is a substantial increase in near-shore communities and a concomitant drop in

BA3–5, although the highest diversity is still within BA3. In China this pattern is further amplified in the upper Rhuddanian, now with the highest number of possible species occurrences in the BA2 zone. This marked transition with the large increase in shallow water β -diversity in China from the upper Hirnantian *persculptus* Zone to the upper Rhuddanian is explained by the appearance of relict genera of the typical *Hirnantia* fauna, such as *Dalmanella*, *Eostropheodonta* and *Hindella*, that are referred to the *Alispira* fauna in the Rhuddanian. In addition, the *Eospirifer*–*Nalivkinia* fauna dominated the shallow-water Rhuddanian seas of South China. These differences between the Chinese and global data may be ascribed to the unusually high provinciality seen in South China during the lower Silurian (Wang *et al.*, 1984). Thus, there may be an aspect of γ -diversity hidden within these α - and β -diversity signals.

The brachiopod faunas of South China have been well studied during the crisis interval through numerous investigations. Previous reports have also suggested that this palaeocontinent is anomalous compared to global data (Wang *et al.*, 1984). For instance, the *Foliomena* and *Hirnantia* faunas both have their earliest appearances here (lower Sandbian and uppermost Katian, respectively) (Rong, 1979, 1984; Rong *et al.*, 1999). Though with respect to the *Hirnantia* fauna it may only be some early precursors of the fauna that existed in the uppermost Katian. Moreover, South China was one of the relatively few places where the *Hirnantia* fauna survived into the *persculptus* Zone (Rong and Harper, 1999; Harper and Williams, 2002). This diachroneity of both the *Foliomena* and *Hirnantia* faunas has been explained by them tracking cool or warm water masses (Rong *et al.*, 1999; Sheehan, 2001). Earlier in the Ordovician, South China also apparently initiated at least part of the Great Ordovician Biodiversification Event with high values in α -diversity that pre-date those from other palaeocontinents (Harper *et al.*, 2004; Zhan and Harper, 2006; Rasmussen *et al.*, 2007). For some reason this geographic unit was apparently a good ‘mega-habitat’ for the Brachiopoda. It is likely that this isolated, very large, shallow-water, epicontinental craton was positioned ideally at relatively low latitudes, probably combined with deep cold water currents from Gondwana, maybe as an Ordovician equivalent to the present day South American Pacific coast where both warm surface waters and cold deep water currents meet. However, this is speculative, as it would suggest some extent of eutrophic conditions in the oceans before the Hirnantian. This is in contrast to the view of Branchley *et al.* (1995).

7. CONCLUSIONS

The current study indicates that fluctuations in α -diversity are not geographically uniform through the investigated crisis interval. Though much more uniform, the bathymetrical β -diversity trends also show some discrepancies.

Both analyses support previous investigations and indicate a two-phased crisis interval followed by a radiation. The first wave of extinctions primarily targeted the shallow-water epicratonic seas, but also removed the deeper-water *Foliomena* faunas. The mid-shelf faunas were least affected, probably due to a combination of the success of the *Hirnantia* fauna, and better pre-adapted faunas from Baltica, Gondwana and the peri-Laurentian terranes that were able to inhabit more shallow water. This resulted in a relative increase of taxa that could survive in the BA1–3 zones in these regions as the eustatic lowering of sea level caused ever narrowing habitats. However, the near-shore faunas, and especially the *Hirnantia* fauna, were the primary victims of the second wave of extinctions.

The current study indicates that the main taxonomic loss was situated at the peri-Laurentian terranes, Laurentia and the margins of the *Ægir* Ocean. High-latitude faunas also experienced large taxonomic losses. Although arguably experiencing a greater taxonomic loss, the extinctions do not seem to have specifically targeted the low-latitude tropical faunas, as otherwise previously postulated, yet various biases, such as sampling intensity and taphonomy, must be considered.

It appears that Baltica hosted a large relative increase in near-shore taxa in the survival interval. Thus, Baltica could be viewed as a shallow-water refuge during the crisis. Other regions that may have also acted as shallow-water refuges are Gondwana, Kazakhstan and the peri-Laurentian terranes. But the success of these refuges, in biodiversity terms, may to a large extent be explained by the diversity of the *Hirnantia* fauna.

South China, in particular, seems to have been a good habitat for the mid-deep shelf faunas through the survival interval, but from the Rhuddanian onwards it was mainly the shallow-water forms that were successful. These differences between the global and the Chinese data may be explained by an unusually high provinciality in the latter region during the early Silurian. Therefore, an aspect of γ -diversity probably is concealed within the α - and β -diversity signals.

In the recovery interval, the *persculptus* Zone and the lower Rhuddanian of Laurentia experienced an increase in BA2 taxa. This may be explained by the development of the *Hindella* Community, whose taxa all were remnants of the *Hirnantia* fauna. In addition, the lower Rhuddanian exhibits an increase in diversity in BA5, but a decline in BA 3–4. This may indicate some early invaders from the Iapetus Region into the deep-water environments.

By the late Rhuddanian, only Laurentia appears to show a decrease in shallow-water taxa and an increase in the deeper-water forms. This is explained by the monospecific virganiid faunas that began to dominate in near-shore environments, whereas the main pulse of newcomers may

have arrived at this time in the deeper-water environments. Thus, the primary invasion by newcomers in Laurentia may have arrived in the Late Rhuddanian. This may suggest that the eustatic transgressive pulse was delayed in the epicontinental seas on this craton. At the same time, the peri-Laurentian terranes experienced a decline in the deeper-water faunas. This may be ascribed to the ever-closing Iapetus Ocean and other terranes that by the late Rhuddanian had accreted onto Laurentia.

ACKNOWLEDGEMENTS

We thank Trond Torsvik, Oslo, for providing the palaeoglobes, Rong Jia-yu for providing us with his assessment of Benthic Assemblage zones in the Chinese sections and Niels Jákup Korsgaard for his assistance with the GIS-software. Further, we thank Steve Donovan, Leiden, and Alan Owen, Glasgow, for their constructive reviews. This paper is a contribution to IGCP 503 'Ordovician palaeogeography and palaeoclimate'. CMØR acknowledges the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate, as well as support to the Nordic Center for Earth Evolution. DATH acknowledges support from the Danish Council for Independent Research (FNU). We both acknowledge Pat Brenchley's formidable contributions to the recognition and understanding of the end-Ordovician extinctions.

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APPENDIX A

List of references used to construct the database that forms the basis for the current study. Though the primary literature source was preferred this was not always possible to obtain and thus the references listed are often secondary sources. The column 'Number of taxa' is the number of taxa from that particular reference that was relevant for this database. The same taxa may occur in more than one of the references, even though it only occurs once in the database. The column 'Assigned BA range' is the range of all taxa within a given reference.

WHERE DID DISASTER STRIKE DURING THE END ORDOVICIAN MASS EXTINCTIONS?

References used to construct the database.

Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
Altai				
	12	Rawtheyan	BA 2–4	Chen <i>et al.</i> (2008)
	10	U Pusgillian–Rawtheyan	BA 2–4	Severgina (1978)
	12	U Rhuddanian	BA 4–5	Kulkov and Severgina (1987)
	12	Rawtheyan	BA 2–4	Kulkov and Severgina (1989)
	30	Llandovery	BA 1–5	Rong <i>et al.</i> (1995)
	1	Rawtheyan	BA 2–5	Cocks and Modzalevskaya (1997)
	1	Rawtheyan	BA 2–3	Copper (2004)
	1	Llandovery	BA 3–4	Jin and Copper (1997)
	2	U Rhuddanian	BA 4–5	Jin and Zhan (2001)
	1	Rawtheyan	BA 3	Rong <i>et al.</i> (2004)
	2	Llandovery	BA 3	Modzalevskaya (2003)
	2	Llandovery	BA 3	Ivanovsky and Kulkov (1974)
	9	Rawtheyan–M Hirnantian	BA 3–4	Sennikov <i>et al.</i> (2008)
Avalonia				
	44	Rawtheyan	BA 4	Sheehan (1988)
	7	Rawtheyan	BA 2–6	Cocks and Rong (1988)
	1	Pre-Hirnantian Ashgill	BA 3–4	Cocks (1978)
	79	Hirnantian–L Rhuddanian	BA 2–5	Cocks (1988)
	1	L Rhuddanian	BA 4–5	Cocks and Price (1975)
	2	U Rhuddanian	BA 4–5	Cocks <i>et al.</i> (1984)
	2	Rhuddanian	BA 3–5	Copper (1982)
	3	U Cautleyan–U Hirnantian	BA 2–4	Copper (1986)
	1	L Rhuddanian	BA 4–5	Copper (1995)
	2	Rhuddanian	BA 3–5	Copper (2004)
	2	Rawtheyan	BA 5–6	Zhan and Jin (2005)
	7	Rawtheyan	BA 2–5	Boucot <i>et al.</i> (2003)
	3	U Rhuddanian	BA 2–5	Baarli and Harper (1986)
	1	Rhuddanian	BA 3–4	Baarli (1995)
	3	Rawtheyan	BA 2–4	Cocks and Modzalevskaya (1997)
	8	Rawtheyan–Aeronian	BA 4–5	Cocks and Rong (1989)
	39	Rhuddanian–L Aeronian	BA 2–5	Cocks and Rong (2007)
	8	Rawtheyan–U Rhuddanian	BA 2–5	Cocks (2005)
	6	Llandovery	BA 3–5	Cocks (2008)
	2	Pusgillian–Rawtheyan	BA 2–5	Hansen (2008)
	10	L Rhuddanian	BA 3–4	Harper and Williams (2002)
	61	U Cautleyan–Rhuddanian	BA 2–5	Hiller (1980)
	1	Rawtheyan	BA 4	Jin and Copper (1997)
	1	U Rhuddanian	BA 3–4	Jin and Copper (2004)
	2	Llandovery	BA 2–5	Musteikis and Cocks (2004)
	1	Rawtheyan	BA 5–6	Neuman (1994)
	1	Rawtheyan	BA 3–4	Nikitin <i>et al.</i> (2003)
	3	Hirnantian	BA 3–4	Rong <i>et al.</i> (2006)
	1	Rhuddanian	BA 2–3	Sheehan (1975b)
	2	Rhuddanian	BA 2–5	Li and Copper (2006)
	17	U Hirnantian	BA 3–4	Temple (1968)
	34	U Rhuddanian–L Aeronian	BA 4–5	Temple (1970)
	37	U Rhuddanian	BA 2–5	Temple (1987)
	1	Rawtheyan	BA 3–5	Villas <i>et al.</i> (1989)
	2	U Rhuddanian–L Aeronian	BA 3–5	Williams and Wright (1981)
	14	Rawtheyan	BA 5–6	Zhan and Jin (2005)
	2	Hirnantian–Rhuddanian	BA 4	Zhang and Boucot (1988)
Baltica				
	18	L–M Hirnantian	BA 4–5	Bergström (1968)
	5	Rhuddanian	BA 2–3	Beznosova (1994)
	5	Rhuddanian	BA 2–3	Beznosova (1996)
	6	U Rhuddanian	BA 2–3	Cocks and Rong (2007)

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Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
	1	Rawtheyan	BA 5–6	Boucot <i>et al.</i> (2003)
	45	U Hirnantian–U Aeronian	BA 3–4	Baarli and Harper (1986)
	10	U Hirnantian–M Aeronian	BA 3–4	Baarli (1988)
	7	U Hirnantian–L Aeronian	BA 3–4	Baarli (1995)
	3	L–M Hirnantian	BA 2–3	Chen <i>et al.</i> (2000)
	10	U Cautleyan–Raw. 3 ‘U Ordo.’)	BA 3–5	Cocks and Modzalevskaya (1997)
	7	Rawtheyan–Aeronian 2 ‘U Ordo.’)	BA 2–5	Cocks and Rong (1989)
	68	Hirnantian–L Rhuddanian	BA 1–5	Cocks (1988)
	45	U Cautleyan – Hirnantian	BA 1–5	Cocks (2005)
	1	Ashgill	BA 2–3	Copper (1977)
	2	Llandovery	BA 3	Copper (1982)
	2	Rhuddanian	BA 3–5	Copper (2004)
	10	L–M Hirnantian	BA 3	Dahlqvist <i>et al.</i> (2010)
	1	U Caradoc–Rawtheyan	BA 2–5	Hints (1975)
	1	U Rhuddanian	BA 3	Jin and Copper (1997)
	1	Ashgill	BA 4–5	Jin and Copper (1999)
	1	Rhuddanian–L Aeronian	BA 3	Modzalevskaya (2003)
	10	Rhuddanian–Pridoli	BA 2–5	Musteikis and Cocks (2004)
	1	U Rawtheyan	BA 5	Popov and Cocks (2006)
	1	L–M Hirnantian	BA 4–5	Poulsen (1976)
	4	U Rawtheyan–Hirnantian	BA 3–5	Rasmussen <i>et al.</i> (2010)
	8	Rawtheyan	BA 3–5	Rong and Boucot (1998)
	2	Rawtheyan	BA 3–4	Rong <i>et al.</i> (1989)
	3	Llandovery	BA 2–4	Rong <i>et al.</i> (1995)
	5	U Cautleyan–Rawtheyan	BA 3–5	Rong <i>et al.</i> (2004)
	1	Hirnantian	BA 3–4	Rong <i>et al.</i> (2008b)
	13	U Caradoc–M Hirnantian	BA 3–4	Röömusoks (2004)
	18	U Rhuddanian	BA 3	Rubel (1970)
	1	Ashgill	BA 2–5	Sheehan (1975b)
	33	U Cautleyan–Rawtheyan	BA 3–5	Sheehan (1979)
	3	Rhuddanian	BA 3	Thomsen <i>et al.</i> (2006)
	1	U Cautleyan–Rawtheyan	BA 4–5	Wright and Rong (2007)
	1	Rawtheyan	BA 3–5	Wright and Jannusson (1993)
	17	Rawtheyan	BA 4–6	Zhan and Jin (2005)
	2	U Cautleyan–Rhuddanian	BA 4–5	Zhang and Boucot (1988)
	1	Cautleyan–Hirnantian	BA 2–5	Zuykov and Harper (2007)
Novaya Zemlya				
	1	Rhuddanian	BA 2–4	Jin <i>et al.</i> (1996)
	2	Rhuddanian (1 ‘Llandovery’)	BA 2–5	Musteikis and Cocks (2004)
Severnaya Zemlya				
	9	L Rhuddanian–U Aeronian	BA 3	Modzalevskaya (2003)
Kazakhstan				
Chinghiz				
	6	Pre-Hirnantian Ashgill	BA 3–5	Cocks and Rong (1989)
	2	Rawtheyan?	BA 3	Cocks and Rong (2007)
	1	U Rhuddanian	BA 3	Oradovskaya (1983)
	1	Rhuddanian	BA 2–3	Popov <i>et al.</i> (2000)
	10	Rawtheyan–L Aeronian	BA 3	Rong and Boucot (1998)
	1	Rawtheyan	BA 3	Rong <i>et al.</i> (1989)
	1	L Rhuddanian–U Aeronian	BA 1–3	Rong <i>et al.</i> (1994)
Chu-Ili				
	1	Hirnantian	BA 2–3	Cocks and Rong (1989)
	13	Hirnantian	BA 2–3	Cocks (1988)
	12	U Rhuddanian	BA 1–5	Modzalevskaya and Popov (1995)
	1	M Ashgill	BA 2–3	Popov <i>et al.</i> (1999)
	1	Rawtheyan	BA 3–5	Popov and Cocks (2006)
	10	Rawtheyan	BA 3–4	Rong and Boucot (1998)

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WHERE DID DISASTER STRIKE DURING THE END ORDOVICIAN MASS EXTINCTIONS?

(Continued)

Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
Tien-Shan	9	Rawtheyan	BA 3–4	Rong <i>et al.</i> (1994)
	1	U Rhuddanian	BA 2–5	Rong <i>et al.</i> (1995)
	1	L Rhuddanian–U Aeronian	BA 3	Rong <i>et al.</i> (2004)
	7	U Rhuddanian–Aeronian	BA 2–4	Babayeva <i>et al.</i> (1991)
	2	Ashgill	BA 2–5	Cocks and Modzalevskaya (1997)
	1	Pre-Hirnantian Ashgill	BA 3–5	Cocks and Rong (1989)
	10	U Rhuddanian	BA 2–5	Cocks (1988)
	2	Rhuddanian	BA 2–3	Jin <i>et al.</i> (1996)
	3	Pusgillian–M Hirnantian	BA 2–3	Popov and Cocks (2006)
	4	Rawtheyan–L Telychian	BA 2–5	Rong and Boucot (1998)
Peri-Laurentian terranes Girvan (Midland Valley Terrane)	1	Rawtheyan?	BA 3	Rong <i>et al.</i> (1989)
	2	U Rhuddanian–Wenlock	BA 1–3	Rong <i>et al.</i> (1994)
	28	Llandovery	BA 1–5	Rong <i>et al.</i> (1995)
	4	M Cautleyan–M Hirnantian	BA 2–5	Harper (1988)
	11	U Rhuddanian	BA 2–5	Baarli and Harper (1986)
	5	U Rhuddanian	BA 4–5	Baarli (1995)
	1	Rawtheyan	BA 4–5	Cocks and Modzalevskaya (1997)
	6	Rawtheyan–U Rhud. (1 ‘Ashgill’)	BA 2–5	Cocks and Rong (1989)
	11	L–U Rhuddanian	BA 2–5	Cocks and Toghil (1973)
	11	Hirnantian–L Rhuddanian	BA 2–5	Cocks (1988)
Pomeroy (Midland Valley Terrane)	5	Rhuddanian–Aeronian	BA 2–5	Cocks (2008)
	1	Rawtheyan	BA 5	Harper (2006a)
	1	L–M Hirnantian	BA 2–3	Harper (1989)
	13	U Cautleyan–M Hirnantian	BA 2–5	Harper (2000)
	30	Cautleyan–M Hirnantian	BA 2–5	Harper (2006a)
	1	Rhuddanian	BA 5–6	Musteikis and Cocks (2004)
	1	M Rhuddanian	BA 2–3	Thomsen <i>et al.</i> (2006)
	1	U Rhuddanian	BA 4–5	Cocks (2008)
	1	Pusgillian–Rawtheyan	BA 4–5	Cocks and Rong (1989)
	1	L–M Hirnantian	BA 3–6	Mitchell (1977)
Klamath	37	Pusgillian–Rawtheyan	BA 4	Potter (1990a, b)
	20	Pre-Hirnantian Ashgill	BA 4–5	McKerrow and Cocks (1981)
Arctic Alaska Terrane	1	Rawtheyan	BA 3	Blodgett <i>et al.</i> (2002)
	18	Pusgillian–Rawtheyan	BA 4–5	Rasmussen <i>et al.</i> (2011)
Farewell Terrane	2	Pusgillian–Rawtheyan	BA 3	Rong and Boucot (1998)
	1	‘Ashgill’	BA 3	Rong <i>et al.</i> (2004)
Livengood Terrane	20	Pre-Hirnantian Ashgill	BA 2–5	Hammann <i>et al.</i> (1982)
	1	Cautleyan–Rawtheyan	BA 4–6	Mélou (1971)
	12	Pre-Hirnantian Ashgill	BA 3–4	Mélou (1990)
	1	Pre-Hirnantian Ashgill	BA 4–6	Cocks and Rong (1989)
	1	Pre-Hirnantian Ashgill	BA 5–6	Zhan and Jin (2005)
Paraguay	6	Rhuddanian–U Aeronian	BA 2–5	Benedetto and Cocks (2009)
	3	Rhuddanian	BA 2–4	Benedetto and Sánchez (1990)
Argentina	4	Rhuddanian	BA 2–4	Isaacson <i>et al.</i> (1976)

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Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
Venezuela	17	Rhuddanian–L Aeronian	BA 2–5	Boucot <i>et al.</i> (1991)
Carnic Alps	17	Rawtheyan?	BA 3–4	Havlíček <i>et al.</i> (1987)
	6	L–M Hirnantian	BA 2–3	Schönlaub (1988)
Liberia	2	L–M Hirnantian	BA 2–4	Sutcliffe <i>et al.</i> (2001)
Morocco	2	L Rhuddanian	BA 5	Cocks and Rong (2007)
	6	Pusgillian–Rawtheyan	BA 3–4	Havlíček (1971)
	10	U Rawtheyan–M Hirnantian	BA 2–3	Sutcliffe <i>et al.</i> (2001)
	5	L–M Hirnantian	BA 2–3	Villas <i>et al.</i> (2006)
Sardinia	15	Rawtheyan	BA 4	Leone <i>et al.</i> (1991)
	12	Rawtheyan	BA 5–6	Villas <i>et al.</i> (2002)
	1	Rawtheyan	BA 5–6	Zhan and Jin (2005)
Tasmania	6	L Hirnantian–L Rhuddanian	BA 3	Cocks and Cooper (2004)
	7	U Hirnantian	BA 3	Laurie (1991)
	2	U Hirnantian	BA 3	Rong <i>et al.</i> (1994)
	1	U Hirnantian	BA 3	Sheehan and Baillie (1981)
New Zealand	6	L–M Hirnantian	BA 4	Cocks and Cooper (2004)
Iberia	22	U Pusgillian–Raw. (3 ‘Ashgill’)	BA 2–5	Boucot <i>et al.</i> (2003)
	2	L–M Hirnantian	BA 2–3	Chen <i>et al.</i> (2000)
Northern Precordillera	9	L–M Rhuddanian	BA 3–4	Benedetto and Cocks (2009)
	14	M Rhuddanian–Telychian	BA 2–4	Benedetto (1995)
	13	Cautleyan–U Hirnantian	BA 2–5	Benedetto (2002)
Perunica	23	U Pusgillian–U Hirnantian	BA 2–5	Cocks (1988)
	5	U Pusgillian–U Hirnantian	BA 2–5	Cocks and Rong (1989)
	1	Pusgillian–Rawtheyan	BA 3–6	Copper (1986)
	1	Pusgillian–Rawtheyan	BA 3–6	Cooper (1930)
	20	U Pusgillian–U Hirnantian	BA 2–5	Havlíček (1967)
	12	U Pusgillian–Rawtheyan	BA 5	Havlíček (1982)
	13	U Pusgillian–Rawtheyan	BA 5	Havlíček <i>et al.</i> (1994)
	24	U Pusgillian–Aeronian	BA 2–6	Havlíček (1977)
	1	U Pusgillian–Rawtheyan	BA 5	Cocks (2005)
	1	Rhuddanian–Aeronian	BA 2–6	Li and Copper (2006)
	2	U Pusgillian–Rawtheyan	BA 5	Neuman (1994)
	1	U Pusgillian–Rawtheyan	BA 5	Villas <i>et al.</i> (2002)
	1	U Pusgillian–Rawtheyan	BA 5	Zhang and Boucot (1988)
South Africa	1	Hirnantian	BA 2–4	Bassett <i>et al.</i> (2009)
	2	Hirnantian	BA 2–4	Cocks <i>et al.</i> (1969)
Kolyma	1	U Ordovician	BA 3–6	Cocks and Modzalevskaya (1997)
	5	Rhuddanian	BA 2–6	Cocks and Rong (2007)
	2	Ashgill	BA 3–4	Cocks and Rong (1989)
	36	U Hirnantian–L Rhuddanian	BA 3–6	Cocks (1988)
	1	U Rhuddanian	BA 5–6	Copper (2004)
	1	U Ordovician	BA 2–3	Copper (1977)
	1	U Hirnantian–L Rhuddanian	BA 2–3	Jin and Copper (1997)
	2	U Rawtheyan–Hirnantian U	BA 3	Jin and Popov (2008)
	1	Rhuddanian	BA 5–6	Jin <i>et al.</i> (1996)

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Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
	7	Cautleyan–Hirnantian U	BA 2–3	Oradovskaya (1983)
	3	Ashgill	BA 3	Rong and Boucot (1998)
	4	Rawtheyan	BA 3	Rong <i>et al.</i> (1989)
	1	M–U Rawtheyan	BA 3	Rong <i>et al.</i> (2004)
Laurentia				
	11	M Cautleyan–M Rawtheyan	BA 2–5	Alberstadt (1973)
	6	M Cautleyan–M Rawtheyan	BA 2–5	Amsden and Sweet (1983)
	35	Hirnantian–L Rhud. (1 ‘Sil.’)	BA 2–3	Amsden (1974)
	1	U Rhuddanian–L Aeronian	BA 3	Boucot and Chiang (1974)
	6	Rawtheyan–Llandoverly	BA 2–4	Rasmussen (2009)
	14	Rawtheyan–U Rhuddanian	BA 2–5	Rasmussen and Harper (2010)
	5	U Ordovician	BA 3–5	Cocks and Rong (1989)
	17	Hirnantian–L Rhuddanian	BA 2–5	Cocks (1988)
	6	Ashgill	BA 3–6	Cocks (2005)
	2	Hirnantian–Rhuddanian	BA 3	Cocks and Modzalevskaya (1997)
	2	Hirnantian	BA 2–4	Cocks (2008)
	1	Ashgill	BA 2–5	Cooper (1930)
	9	‘Pre-Hirnantian Ashgill’	BA 4–5	Copper (1977)
	3	U Rhuddanian	BA 2–3	Copper (1982)
	2	‘Pre-Hirnantian Ashgill’	BA 3–6	Copper (1986)
	7	L Rhud.–L Aeronian (1 ‘Lland’.)	BA 2–5	Copper (1995)
	1	Rawtheyan	BA 4	Dewing (1999)
	22	Rawtheyan–Telychian	BA 2–5	Dewing (2001)
	1	U Rhuddanian–Telychian	BA 2–5	Hansen (2008)
	3	Pusgillian–Rawtheyan	BA 2–3	Howe and Reso (1967)
	3	Pusgillian–Rawtheyan	BA 2–4	Howe (1965)
	3	M Cautleyan–Rawtheyan	BA 2–4	Howe (1966)
	6	‘Pre-Hirnantian Ashgill’	BA 3	Howe (1967)
	5	U Cautleyan–M Rawtheyan	BA 2–5	Howe (1969)
	68	Pusgillian–Rawtheyan	BA 2–5	Howe (1988)
	1	Rhuddanian	BA 2–4	Hurst (1980)
	15	Hirnantian–Rhuddanian	BA 4–5	Jin and Chatterton (1997)
	9	L Rhuddanian–M Telychian	BA 2–5	Jin and Copper (2004)
	5	Hirnantian–L Rhuddanian	BA 2–5	Jin and Copper (1997)
	2	Ashgill–U Rhuddanian	BA 4–5	Jin and Copper (1999)
	3	L Rhuddanian–L Aeronian	BA 2–5	Jin and Copper (2000)
	1	L Rhuddanian	BA 2	Jin and Copper (2010)
	6	L–U Hirnantian	BA 2–5	Jin and Zhan (2000)
	26	Pusgillian–Rawtheyan	BA 4	Jin and Zhan (2001)
	8	Rawtheyan–U Rhuddanian	BA 2–4	Jin and Zhan (2008)
	2	U Rhuddanian–Telychian	BA 4–5	Jin (2002)
	3	U Rhuddanian–L Telychian	BA 1–4	Jin (2005)
	2	U Rhuddanian–L Aeronian	BA 2–4	Jin <i>et al.</i> (1996)
	3	U Rhuddanian	BA 2–3	Jin (2008)
	11	Cautleyan–M Rawtheyan	BA 2–3	Jin <i>et al.</i> (1989)
	1	Rhuddanian–L Aeronian	BA 2–3	Jin <i>et al.</i> (1999)
	24	Pusgillian–L Hirnantian	BA 3	Jin <i>et al.</i> (1997)
	3	M Rhuddanian–L Aeronian	BA 2–5	Jin <i>et al.</i> (2006)
	10	Hirnantian–L Aeronian	BA 2–5	Li and Copper (2006)
	12	M Cautleyan–Rawtheyan	BA 3–4	Macomber (1970)
	1	U Rhuddanian–Aeronian	BA 3	Poulsen (1934)
	1	Silurian	BA 3	Poulsen (1943)
	12	Rawtheyan	BA 5–6	Neuman (1994)
	18	L Pusgillian–M Rawtheyan	BA 2–5	Patzkowsky and Holland (1997)
	3	Ashgill	BA 1–2	Pollock <i>et al.</i> (1994)
	1	M Cautleyan–M Rawtheyan	BA 2–5	Popov <i>et al.</i> (2000)
	1	Hirnantian	BA 4	Potter (1990a, 1990b)

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Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
	1	Pre-Hirnantian Ashgill	BA 4	Potter (1991)
	3	Rawtheyan–L Telychian	BA 2–5	Rong and Boucot (1998)
	1	Rawtheyan	BA 3	Hurst and Sheehan (1982)
	4	Ashgill–L Aeronian	BA 2–5	Rong <i>et al.</i> (1989)
	1	Ashgill	BA 3	Rong <i>et al.</i> (2004)
	8	Hirnantian	BA 2–4	Rong <i>et al.</i> (2006)
	1	U Rhuddanian	BA 2–3	Rong <i>et al.</i> (2007)
	13	Pre-Hirnantian Ashgill	BA 1–5	Ross and Dutro (1966)
	1	Rhuddanian	BA 2–3	Sheehan (1975b)
	4	U Rhuddanian–Aeronian	BA 2–3	Sheehan (1980)
	2	Rawtheyan–U Rhuddanian	BA 2–5	Thomsen <i>et al.</i> (2006)
	2	Pre-Hirnantian Ashgill	BA 4	Troedsson (1928)
	16	Cautleyan–Rawtheyan	BA 3–4	Wang (1949)
	2	Ashgill	BA 2–6	Zhan and Jin (2005)
	3	Hirnantian–Llandovery	BA 3–6	Zhang and Boucot (1988)
	1	M Cautleyan–M Rawtheyan	BA 3–5	Villas <i>et al.</i> (1989)
	1	U Rhuddanian	BA 2–3	Zuykov and Harper (2007)
Siberia				
	1	Llandovery	BA 1–3	Copper (1977)
	1	L–U Rhuddanian	BA 3–4	Copper (1982)
	3	Llandovery	BA 2–5	Copper (1995)
	7	Llandovery	BA 3–5	Copper (2004)
	1	Pusgillian–Rawtheyan	BA 2–4	Jin <i>et al.</i> (1999)
	1	U Rhuddanian	BA 2–4	Jin <i>et al.</i> (1996)
	1	L–U Rhuddanian	BA 3	Rong <i>et al.</i> (1995)
	6	L Rhuddanian–Aeronian	BA 3–5	Tesakov <i>et al.</i> (2003)
	29	Hirnantian–Llandovery	BA 3	Modzalevskaya (2003)
	24	Llandovery	BA 1–5	Rong <i>et al.</i> (1995)
	1	Rhuddanian	BA 2–5	Sheehan (1975b)
Mongolia				
	1	Ashgill	BA 3–4	Jin and Copper (1997)
	1	Pusgillian–Rawtheyan	BA 3–4	Jin and Popov (2008)
	2	Llandovery	BA 3–5	Copper (1982)
Taimyr				
	1	Rawtheyan	BA 3–5	Cocks (2005)
	37	Rawtheyan	BA 3–4	Cocks and Modzalevskaya (1997)
Tarim				
	3	Rhuddanian	BA 1–3	Rong <i>et al.</i> (2003)
Terranes off the coast of Siberia (Shublik Mts, NE Alaska)				
	2	M Cautleyan–Rawtheyan	BA 3	Blodgett <i>et al.</i> (1987)
Tuva				
	1	Rhuddanian?	BA 3–4	Copper (2004)
	1	Ashgill	BA 3–4	Kulkov <i>et al.</i> (1985)
	3	Rhuddanian–Aeronian	BA 2–3	Rong <i>et al.</i> (1994)
	19	Llandovery	BA 1–5	Rong <i>et al.</i> (1995)
China				
North China incl. Alxa Block				
	2	Llandovery	BA 2–5	Copper (2004)
	2	Rhuddanian–L Aeronian	BA 2–3	Rong and Boucot (1998)
	4	U Rhuddanian–L Aeronian	BA 2–3	Rong and Chen (2003)
	1	U Rhuddanian	BA 2–3	Rong <i>et al.</i> (1994)
	1	Rawtheyan	BA 3	Rong <i>et al.</i> (2004)
	4	M Ashgill–Ashgill (pre-Hirnantian?)	BA 2–5	Popov <i>et al.</i> (1999)
	1	Pre-Hirnantian Ashgill	BA 3–5	Cocks and Modzalevskaya (1997)
	2	Rawtheyan–L Hirnantian + U Ordo.	BA 2–5	Cocks and Rong (1989)
Sibumasu				
	3	Hirnantian	BA 2–5	Cocks and Cooper (2004)

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WHERE DID DISASTER STRIKE DURING THE END ORDOVICIAN MASS EXTINCTIONS?

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Geographic entity	No. of taxa	Age range	Assigned BA range	Reference
South China	12	Hirnantian (7 'U Hirnantian')	BA 3–4	Cocks and Fortey (1997)
	35	U Rawtheyan–L Rhuddanian	BA 2–5	Chen <i>et al.</i> (2000)
	3	Hirnantian	BA 2–5	Cocks and Cooper (2004)
	2	M Hirnantian	BA 3–4	Cocks and Fortey (1997)
	6	Rawtheyan–M Hirnantian, 1 'Ashgill'	BA 3–5	Cocks and Rong (1989)
	26	L–U Rhuddanian	BA 1–3	Cocks and Rong (2007)
	9	Hirnantian	BA 3–4	Cocks (1988)
	1	Rawtheyan	BA 3–5	Cocks (2005)
	2	Llandovery	BA 2–5	Copper (2004)
	3	U Rawtheyan–M Hirnantian	BA 3–4	Harper and Williams (2002)
	2	Rawtheyan	BA 3	Jin <i>et al.</i> (2006)
	1	Rawtheyan	BA 1–3	Jin <i>et al.</i> (2007)
	1	Rawtheyan	BA 2–3	Nikitin <i>et al.</i> (2003)
	2	U Pusgillian–Rawtheyan	BA 2–3	Popov and Cocks (2006)
	3	Rawtheyan	BA 3–4	Popov <i>et al.</i> (1999)
	1	Rawtheyan	BA 2–3	Popov <i>et al.</i> (2000)
	1	Rawtheyan–Hirnantian	BA 3–4	Rong and Harper (1988)
	2	Rawtheyan–L Aeronian	BA 3–4	Rong and Boucot (1998)
	1	L Rhuddanian	BA 2–3	Rong and Harper (1999)
	5	L Hirnantian–L Rhuddanian	BA 3–4	Rong and Li (1999)
	1	Rawtheyan	BA 3	Rong and Zhan (1996)
	11	L Rhuddanian	BA 2–3	Rong and Zhan (2006)
	1	Rawtheyan	BA 5–6	Rong <i>et al.</i> (1989)
	11	Rhuddanian–L Aeronian	BA 1–4	Rong <i>et al.</i> (1994)
	22	Llandovery	BA 2–5	Rong <i>et al.</i> (1995)
	14	Rawtheyan	BA 2–6	Rong <i>et al.</i> (1999)
	37	L–U Hirnantian	BA 2–4	Rong <i>et al.</i> (2002)
	1	M Hirnantian	BA 2	Rong <i>et al.</i> (2006)
	13	U Hirnantian	BA 5	Rong <i>et al.</i> (2008a)
	1	Ashgill	BA 2–5	Rong <i>et al.</i> (2008b)
	17	Rawtheyan	BA 1–3	Xu (1996)
	3	Rawtheyan	BA 3–5	Zhan and Cocks (1998)
6	Rawtheyan	BA 2–4	Zhan and Jin (2005)	
5	Rawtheyan	BA 2–5	Zhan <i>et al.</i> (2002)	
22	Pusgillian–Rhuddanian	BA 3–6	Zhan <i>et al.</i> (2008)	