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# ORDOVICIAN-SILURIAN DISTRIBUTION OF ORTHIDA (PALAEOZOIC BRACHIOPODA) IN THE GREATER IAPETUS OCEAN REGION

# Anders Tychsen and David A.T. Harper

# ABSTRACT

Analysis of Orthida (Brachiopoda) spatio-temporal data from a new database indicates that five major developments controlled the faunal provincialism of the Orthida in the Greater lapetus Ocean during the Ordovician-Silurian. These developments include: 1) A diversification during the Early Ordovician; 2) a diversity reduction during the Middle Ordovician, followed by; 3) renewed diversification during the early Caradoc; 4) the Hirnantian glaciation; and 5) a gradual homogenization of the faunas during the Silurian, despite some increasing endemism. The orthides of the peri-Gondwanan European massifs may have formed a faunal association, distinct from the faunas of the lapetan central area, whereas the general pattern of faunal associations appears to be related to palaeolatitude and the relative positions of the palaeoplates. The observed faunal patterns generally support recent plate tectonic reconstructions.

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# INTRODUCTION

Computerized databases of palaeontological information provide the only practical means for investigating large-scale palaeobiological patterns and processes over long time intervals (Benton 1999; Markwick and Lupia 2002). Furthermore, large palaeobiogeographical databases comprise a complementary method for the reconstructions of palaeoplate positions and movements, especially for the early Palaeozoic where continental palaeomagnetic evidence is less secure (Lees et al. 2002). Such models also allow for the comparison of biofacies and the relationship between faunal associations and physical factors, such as water depth and substrate type (Cocks and McKerrow

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1984; Bernasconi and Stanley 1994) across two or more margins. The use of large databases to analyze palaeodiversity, extinction and survival trends is, however, problematic because it assumes a number of conditions. For example it assumes that taxonomic and spatial errors are random (Benton 1999) and that sampling intensity is constant and independent of rock-volume variations (Smith 2001). If errors in taxonomic databases are random, this means that faunal signals cannot be created by the errors, however, they can be degraded due to the random noise the errors generate in the dataset (Raup 1991).

Brachiopods are ideal for palaeobiogeographical studies, because the animals were sessile, because most of them lived in relatively shallow water, because their shells accumulated in large numbers, and because they are commonly robust, with features that can survive transport, burial and diagenesis. Furthermore, their taxonomy is relatively stable (Rudwick 1970; Williams and Harper 2000).

Brachiopods were especially important elements of the benthic fauna during the early-middle Palaeozoic. The orthide (Order Orthida: Schuchert and Cooper, 1932) brachiopods were, together with the strophomenides, the first important rhynchonelliformean groups to diversify in great numbers. During the Ordovician, the diversity and fossil abundance of the orthide and strophomenide brachiopods dominated benthic assemblages. The orthides were particularly abundant during the Middle-Late Ordovician, however, the order ranged through the entire Palaeozoic (Williams and Harper 2000; Harper and Gallagher 2001). More than two hundred localities distributed globally have yielded orthide brachiopods, especially sites in North America, Europe, North Africa and China.

High orthide diversities were maintained through most of the Ordovician, following an initial rapid diversification during the Early Ordovician. After a dramatic, approximately 50%, reduction in global orthide diversity during the Late Ordovician extinction event, a steady decline in orthide diversity continued throughout the Silurian. The order briefly peaked during the Early Devonian, but gradually died out during the rest of the Palaeozoic. The last orthide is reported from around the Permian-Triassic boundary.

A general overview of the orthides from all the major terranes of the Ordovician-Silurian Palaeozoic Greater lapetus Ocean Region (GIOR) (including both the Rheic and Tornquist oceans and adjacent plates) (Mac Niocaill et al. 1997) in time and space is presented here based on data from a new global database. Data are recorded at the generic level of taxonomic resolution.

The orthide data have been evaluated using a range of statistical and graphical techniques. The multivariate methods (Jongman et al. 1995; Etter 1999) include Principal Coordinates Analysis (PCO or PCoA, MDS) (Davis 1986), Non-Metric Multi Dimensional Scaling (NMDS) and UPGMA (paired linkage) cluster analysis (Krebs 1989), based on the Dice similarity coefficients. Diversity curves as well as the endemic properties of the orthide genera are also considered. The results have been validated using similarity indices, which are calculated differently than the Dice index, in order to assess the strengths of the faunal signals apparent from the analyses. The two validation indices were the Simpson and the Raup-Crick indices (Raup and Crick 1979). These results are compared with plate tectonic models for the region (e.g., McKerrow et al. 1991; Cocks and Torsvik 2002; Torsvik and Rehnström 2003). Analyses were performed using the statistical package Palaeontological Statistics (PAST<sup>©</sup>, Ø. Hammer and D.A.T. Harper; Hammer et al. 2001) and Microsoft EXCEL (©Microsoft). Taken together, the results provide a broad overview of the history of the lapetan orthides and their associated plates and terranes.

#### DATA

The data for this study are derived from The Orthida Database, which contains information on the more than 300 Orthida genera, recently revised by Williams and Harper (2000). The database also contains information on other brachiopod orders, however, these are not used here. The data are collected from published sources only and are of varying quality in their spatial and temporal resolution.

The records of The Orthida Database that are precise to a specific area such as a site, formation, country or a single plate which is well defined, and which have a temporal precision of epoch level or stage level, comprise a truncated dataset amounting to about 40% of the total dataset. The truncated data are used here. Of these records, European and North American data comprise about 67%, which indicates that there is a skewed distribution in the geographical distribution of orthide data, which should, however, not be relevant to this study which primarily deals with areas of consistent high sampling intensity. The dataset does not utilize the range-through assumption, including only genera actually reported from the particular stage or epoch. The data quality and related problems are discussed in further detail below.

With respect to the temporal resolution of the data, clearly older publications contain less precise temporal data. This is primarily due to updates in the chronostratigraphic framework since their publication. This is also true for the age of rock formations: For the Cambrian, only approximately 35% of the total dataset is at Epoch or better temporal resolution, while for the Devonian this proportion is over 50%.

The data used in this study are drawn from the Ordovician-Silurian sections of the truncated dataset from the GIOR plates. Using this focused dataset allows a better temporal resolution than would have been possible with the total dataset. Although the total dataset results in higher total diversities, tests during construction of The Orthida Database showed only minor changes in the overall biogeographical patterns between the two datasets (see also Sepkoski 1993).

### METHODS

The use of ordination (Legendre and Legendre 1998) and cluster (classification) analysis (Krebs 1989) based on similarity index analysis to quantify faunal data originally stems from ecology (e.g., Lichstein et al. 2002). The methods have been applied to palaeontological data for some time (Etter 1999). Ordination methods attempt to order the sampled faunal data in a continuum according to a given set of guidelines. In the ordination techniques applied here, the ordering is calculated based on values of the similarity between faunas, which are in turn calculated using simple algorithms (Jongman et al. 1995). In contrast to cluster analysis, ordination seeks to accentuate the intergradational aspects of the sample data (Etter 1999). The dimensions of the multivariate taxa space are therefore reduced meaningfully, graphically displaying relationships between the sampled units. Ordination provides a method of modelling the pattern of the index value, and the results can be compared to e.g., palaeomagnetic data to aid plate reconstructions.

Clustering or classification is a straightforward method of visualizing association data, however, the confidence of the nodes are highly dependent on data quality, and levels of similarity for cluster nodes is dependent on the similarity index used. The mean linkage (UPGMA) method is chosen here, because clusters are joined based on the average distance between all members in the two groups. Krebs (1989) noted that mean linkage is superior to single and complete linkage methods for ecological purposes because the other two are extremes, either producing long or tight, compact clusters respectively. There are, however, no guidelines as to which mean-linkage method is the best (Swan and Sandilands 2001).

Mean-linkage and ordination (PCO and NMDS) analysis was performed on brachiopod data from all Ordovician and Silurian epochs and stages. Irrespective of the specific choice of ordination and cluster methods and the different way these calculate faunal associations or taxon-space organization of samples, using several methods allows for consistent cross-validation of results (Harper et al. 1996). As a further check on results, analyses were performed at both epoch and stage levels of temporal resolution. Here some examples of the cluster analysis results in the form of dendrograms are presented at epoch level of resolution. Likewise presented are examples of the ordination diagrams at stage level of resolution.

# PLATE TECTONIC SETTING

A total of 11 plates from the entire GIOR were included in the study. These were the Gondwanan South America and Africa (there are no Ordovician orthide data from Antarctica), the peri-Gondwanan European massifs: Bohemia (Perunica), Apulia, Iberia and Armorica and the core lapetus Ocean terranes of Laurentia, Siberia, Baltica and Avalonia. Additionally the Precordillera was included (see below). We generally have used the newest data available (e.g., Cocks and Torsvik 2002; Stampfli and Borel 2002) to outline the borders of these terranes with respect to the placement of orthide data on the various plates.

Most of these did not entail problems, however, it is important to note that this study is based on data from a global database, applied to a regional scale area. This means that some problems such as the tectonic history of the "exotic" blocks of the Holy Cross Mountains (HCM) of Poland have not been resolved in this study (Belka et al. 2002; Cocks 2002). In such cases, the choice of which plate to assign the orthide data to was based on a mixture of literature searches, the similarity of the orthide data from the area in question to the faunas of the possible host plates and lastly the reconstruction software used (PALEOMAP). Fortunately the problematic data usually accounts for only a minor part of the total diversity, which means that the analyses of the data were only slightly affected by their precise placement. In the case of the HCM, orthide data include Baltic endemics, however, also included are genera indicative of a Celtic influence. The data have here been placed within Baltica.

In some cases, the spatial resolution of the data was not good enough to place them on a definite plate, however, as noted above these were not included. Most of the problematic data are related to the greater spatial and temporal uncertainties of Cambrian and Early Ordovician data compared to later Ordovician and Silurian data.

Ireland posed another problem due to the exotic or suspect nature of some of the terranes of the island. The Central Terrane with the two smaller eastern Grangegeeth and Bellewstown terranes encompass most of the uncertainty. The northern terranes of Ireland and the southern Leinster Terrane (Fortey et al. 2000) are, however, firmly established as belonging to Laurentia and Avalonia, respectively, during the Ordovician-Silurian. Data from the northern Irish terranes and the southern Leinster Terrane were included in the analysis. Data from the Central Terrane, Grangegeeth and Bellewstown terranes were excluded on the grounds that the history of especially the two minor terranes remains uncertain (Fortey et al. 2000).

As a final example of currently debated issues in present palaeoreconstructions, the Precordilleran microcontinent (Fortey and Cocks 2003) of Argentina is somewhat of a roque phenomenon. The microcontinent includes the fossil faunas of the San Juan Formation and Las Aquaditas Formation, from which much of the faunal data involved in reconstructing the wandering path of the terrane was taken. The Precordilleran terrane may originally have been derived from southeastern Laurentia (Thomas 1991; Astini et al. 1995), more specifically the Ouachita embayment of the southeastern USA (Gerbi 1999; Davis et al. 1997) and is recorded immediately south of the central lapetus suture during the Late Cambrian-Early Ordovician between Gondwana and Laurentia (Cocks and Torsvik 2002). During the Ordovician-Silurian the microcontinent moved southward and docked to the eastern bend of the South American plate (Fortey and Cocks 2003). This history is tested with the limited orthide data available.

#### RESULTS

As noted previously, the data used here vary from temporal resolutions at stage to epoch level. This variance causes some temporal smearing, i.e., artificially high diversities for some stages. The effect is presumed random and the majority of the records have a stage-level temporal precision. However, for the Early Ordovician temporal smearing is more serious. Especially for Baltica and Laurentia, diversity counts are problematic because the records detailing these faunas often have a temporal resolution at the epoch level. Furthermore records detailing the faunal developments of the Early Ordovician are often old, meaning that the original correlations are uncertain. This has the effect that some genera belonging to the Arenig are also reported for the Tremadoc and vice versa, artificially increasing the diversity. A more detailed study of these data is planned, however, this problem is the primary reason why the Early Ordovician data are only briefly described here.

There are common trends in all the diversity curves for the plates of the greater lapetus region (Figure 1) despite the latitudinal difference in position from a lower latitude (Laurentia, Siberia), midlatitude (Baltica, Avalonia depending on the time), higher latitude (European massifs) and polar (Gondwanan terranes, however, note that South America reached fairly far north [Cocks and Torsvik 2002]). The curves display a rapid diversity increase from approximately the Tremadoc-Abereiddian, followed by a diversity drop that lasted until the Costonian, where renewed diversification is rapid, especially on Avalonia Major and the European massifs (Figure 1).

The rest of the Caradoc and the Ashgill is generally marked by high diversities, with indications of a decline in diversity beginning in Ashgill on Laurentia Major and the Core Gondwanan terranes. This pattern is expressed to a lesser degree on Siberia and Avalonia Major. The European massifs and Baltica appear unaffected during this interval. At the Hirnantian-Rhuddanian transition, all plate groups except Baltica and Avalonia experienced dramatic reductions in diversity.

The European massifs suffered the worst, dropping from about 50 to only 10 genera. Avalonia experienced only a minor diversity decrease within this interval, however, displayed a similar reduction during the Rhuddanian-Aeronian (Figure 1). Baltica deviates further from this pattern - similar to Avalonia there is a small diversity decrease in the Hirnantian-Rhuddanian, but the dramatic reduction does not occur until the Telychian-Sheinwoodian. This is coeval with a facies change in the Scandinavian area from marine to terrestrial facies (Worslev et al. 1983). The orthides of Baltica did experience a reduction in diversity during the Ordovician-Silurian transition, however, already by the Rhuddanian new diversifications were characterizing the emptied niches, so that the net result was a faunal turnover, not a permanent reduction in diversity.

The development after the extinction event shows the most contrasts. Laurentia experienced renewed diversity increases from the Shein-



**Figure 1.** Orthide diversity curves for the six major plate/terrane groups and the Precordillera. Baltica Major = Baltica + Scania, Laurentia Major = Core Laurentia + Greenland plate + Svalbard + Cordilleran accreted terranes, - Mexican Terrane, Avalonia Major = American and European Avalonian sections, European massifs = Armorica, Bohemia, Apulia and Iberia, Siberia = Siberia including the Kolyma Block and Taimyr but excluding the Kazakh terranes, Core Gondwana = South America and Africa.

woodian-Gleedonian, but this is not seen on the other plate systems. Siberia, the European massifs and Baltica do not record the rising diversity seen on Laurentia, however, at the end of the Silurian diversity in the European massifs was increasing. The core Gondwanan terranes and Avalonia Major generally follow a declining pattern, the major diminution in diversity occurring together with the diversity drop in Laurentia during the Gleedonian-Gorstian.

#### Endemism

The geographical range definition is used for endemism. Genera indigenous to certain plates or plate groups such as the peri-Gondwanan terranes or Avalonia Major are here termed endemic. How endemism is defined naturally affects levels of endemism. With the limits on the range of an endemic genera being defined as stated, the orthides of the GIOR display a high degree of endemism (Figure 2). During most of the Ordovician the total endemic rate at the generic level was around 50%. In the Late Cambrian there was about 75% endemic genera (not included in Figure 2), however, this dropped to about 46% in the Tremadoc, signifying a geographical expansion of taxa. This was coupled with a 344% increase (25 to 86 genera) in total diversity from the Late Cambrian to the Early Ordovician.

The Late Abereiddian-Llandeilian increase in endemicity is correlated with a significant diversity decrease for all terranes except the tropically placed (Cocks and Torsvik 2002) Laurentia and Siberia. In the Late Abereiddian, the global orthide diversity experienced a minor reduction, followed by an interval of high endemism and low diversity rates. Globally orthide diversity was about 25% lower than that in the time after the early Caradoc, and about 20% below Abereiddian diversity values. The situation persisted until sometime around the late Velfreyan-Costonian, where there was a drop in the degree of endemism corresponding with a surge in diversity for all plates. This increase, however, was relatively limited for Laurentia. Baltica appear to have experienced a more gradual diversity buildup, lacking the period of low diversity fol-



Trans-Iapetan Region generic endemic rates

**Figure 2.** Rates of endemic orthide genera in percent correlated with time for the Ordovician-Silurian for the GIOR (Laurentia Major, Baltica Major, Avalonia Major, Siberia, European massifs [Bohemia, Armorica, Iberia and Apulia] and Core Gondwana [South America and Africa]). The results are summed to 100%. Note that the term plate group refers to the fact that e.g., Laurentia Major was composed of several components, as were the European massifs.

lowing the Llandeilian reduction. Globally the diversity increased about 25% from the late Vel-freyan to the Costonian.

During the Late Ordovician Extinction Event, the proportion of endemic genera was markedly reduced. The reduction affected most genera with restricted geographical distributions (one to three plate groups in Figure 2). The relative proportion of genera with representative species on all the GIOR plates increased, while the actual generic diversity dropped dramatically in the Hirnantian-Rhuddanian.

During the Silurian, the number of endemic genera gradually increased to and even above the Ordovician average in the Gorstian-Ludfordian, where about 52.5% of the genera were endemic to one plate system. This level of endemism was the highest since the Velfreyan. There were, however, fewer orthide genera around (Figure 1). These two intervals of increasing endemicity correspond to the Early-Middle and Middle-Late Silurian boundaries (Figure 2). Only a very few genera were spread across the entire GIOR (total average approximately 3.3 genera for the Silurian versus 5.9 for the Ordovician (Appendix), however, these comprise a larger proportion of the total generic diversity following the diversity reduction at the Hirnantian-Rhuddanian boundary.

#### **Cluster Analysis**

As noted above, Early Ordovician data are somewhat uncertain in their spatio-temporal precision. However, a few general patterns are obvious from the association analyses performed on the separate and combined Tremadoc and Arenig datasets (Figure 3, top left). The three European massifs that include orthide data form a separate faunal group, while the remainder of the analyzed plates form an undifferentiated cluster, whose internal organization is not very well resolved and varied between the indices used (Dice, Raup-Crick and Simpson) for generating the dendrograms. The supercluster was consistent, and the Early Ordovician orthides appear fairly widespread in their distribution within the GIOR.



**Figure 3.** Dice index dendrograms at epoch level of temporal resolution. Early Ordovician (top left), Llanvirn (top right), Caradoc (mid left), Ashgill (mid right), Llandovery (bottom left) and Ludlow (bottom right).

During the Arenig-Llanvirn, a gradual shift in the organization of the faunal associations occurred. At the same time data quality increases markedly. Up to and including the Llanvirn (Figure 3, top right), Avalonia still groups with the core Gondwanan terranes for all three indices, however, with the onset of the Late Ordovician (Figure 3, mid left), the microcontinent changes association to associate with Baltica and Laurentia. Baltica and Laurentia differentiate by the Llanvirn, suggesting that Baltica had then drifted enough northwards to attain a faunal composition different from the Gondwanan. The peri-Gondwanan terranes of Iberia, Armorica and Bohemia retained their individual faunal composition. Siberia appears oddly placed in the Llanvirnian dendrogram, however, analysis of the orthide data indicates that Siberia shared faunal elements with both Laurentia and the Gondwanan terranes, which gives the placement in the dendrogram.

By the Caradoc (Figure 3, mid left), a clear differentiation into three faunal associations had emerged, largely defined by latitudinal placement. The peri-Gondwanan terranes retain their independent status, and the core lapetan terranes of Baltica, Avalonia and Laurentia have separated from South America and Africa. This pattern is essentially the same for the Ashgill (Figure 3, mid right).

Siberia is grouped somewhat differently depending on the index used, either with the Gondwanan core or with the Laurentia-Baltica-Avalonia group. The position of the Precordillera in the cluster and ordination analysis is tentative because of the small amount of genera available for analysis.

By the Llandovery (Figure 3, bottom left), the associations have been altered. The core lapetan terranes now form part of a well-isolated cluster with the core Gondwanan terranes. The European massifs association is retained, however, marked diversity reductions have severely diminished orthide stock on Apulia and Iberia. This pattern is retained later into the Silurian (Figure 3, bottom right). Siberia continues its intermittent placement. Siberia branches off the larger associations near the base of the dendrograms, and the affinities of the Precordillera are somewhat uncertain during this interval. However, it is clearly not Laurentiarelated.

#### **Ordination Analysis**

While there are differences between the NMDS and PCO results, these are mostly in the detail. The differences are fairly well correlated with the signal strength in the faunal data, i.e., the differences were largest in the diagrams for the temporal intervals of the lowest diversity, e.g., the Tremadoc. The individual PCO-eigenvectors (PCO can be expressed as a distance-based method like NMDS or as an eigenanalysis) generally did not account for much of the variance in the datasets, typically around 20-40% of the variance was accounted for by the 1<sup>st</sup> axis, while the 2<sup>nd</sup> accounted for about half of the first axis. This suggests that there is no single gradient that fully

explains the variation of the dataset. The Late Ordovician plots were the best resolved, corresponding with the largest amount of data available. The ordination diagrams generally display the same dramatic change in overall faunal patterns from the Hirnantian to the Rhuddanian as the classification diagrams. The faunas change from being divided into relatively well-defined groups to a single large association with some more or less detached faunal elements (Figure 4).

During the Costonian (Figure 4, top left), Laurentia, Avalonia and Baltica formed an individual association. Avalonia held an intermediate position between the core Gondwanan terranes and Laurentia/Baltica, suggesting shared faunal elements. Likewise, the position of Laurentia and South America possibly indicate some shared faunal elements. These relationships are well known (Fortey and Cocks 2003) and documented, and it is, therefore, not surprising. Baltica appears to be the most faunally isolated of the three core lapetan plates. The core Gondwanan terranes are positioned together, as are the peri-Gondwanan terranes. By the Hirnantian (Figure 4, top right), Bohemia is indicated close to Avalonia and Baltica, perhaps indicating an intermittent position between these and the peri-Gondwanan terranes.

Siberia is in a rogue position between the three plate groups. Siberia and Avalonia probably retained some of their common Gondwanan elements, which explain the faunal similarity. The two core Gondwanan terranes still appear to form a separate group.

In the Rhuddanian (Figure 4, bottom left), half the plates form a closely knit group consisting of the core Gondwanan terranes as well as Laurentia, Avalonia and Baltica, however, apparently Siberia retained a different faunal composition. This might, however, be an artifact of low diversity from the craton during the Rhuddanian, not a true pattern. The terranes separated from this group are Apulia-Armorica, which have almost identical faunas. Bohemia retains a position somewhere between this plate pair and the large group. The Precordillera remains unattached to any of the groups. This pattern is retained in the Telychian. For the Gorstian (Figure 4, bottom right), the same pattern is basically retained; however, there is some separation into subgroups. Most of the peri-Gondwanan terranes remain marginal to the large group, and Siberia appears separate also. The two Gondwanan core elements remain tightly connected, and the old Baltica-Laurentia-Avalonia group is also well constrained. Bohemia shared faunal elements with all three groups, however, as indicated by the classification analysis, the terrane is now



**Figure 4.** Selected Ordovician and Silurian NMDS diagrams at stage level of resolution using the Dice coefficient as the similarity indicator: Costonian (top left) (Shepard plot stress = 0.1688); Hirnantian (top right) (Shepard plot stress = 0.1418), Rhuddanian (bottom left) (Shepard plot stress = 0.08995) and Gorstian (bottom right) (Shepard plot stress = 0.1641). Red circles include Gondwanan terranes, purple circles include peri-Gondwanan terranes and blue circles include the core lapetan terranes of Laurentia, Baltica and Avalonia. Green circles include Siberia. The Precordillera is not included in either of these groups, further note that the Precordillera plots very far from the rest of the plates in the Costonian diagram and therefore is not included. This is probably related to the small amount of data available from the terrane during this time.

firmly placed with the Gondwanan and core lapetan faunas.

#### DISCUSSION

The general history of the Orthida in the GIOR is in accordance with the general tectonic and faunal history of the region established by earlier authors (Cocks and Torsvik 2002). Even though endemic rates and ordination analysis targets two different aspects of the faunal data they can be compared and support each other – or conversely indicate that the results of the analyses are uncertain.

The faunal data can be divided into three segments based on the overall association trends of the analyses: The 1<sup>st</sup> segment includes the Early-



**Figure 5.** The world at 460 Ma (Caradoc) near the boundary between the 1<sup>st</sup> and 2<sup>nd</sup> segments (source: Scotese 2001).

Middle Ordovician, where the old Gondwana marginal terranes of Baltica and later Avalonia changed faunal content to develop a more mixed composition between the equatorial terranes and the polar to high latitude Gondwanan terranes. At the same time there was a dramatic diversification and geographical expansion among the orthides (Harper and Gallagher 2001; Harper and Mac Niocaill 2002), which was truncated by an Abereiddian-Llandeilian diversity reduction and an increase in endemism. This diversity reduction may have been the result of a contraction in available living space caused by a regression during the Arenig (Barnes et al. 1996). From the Early Ordovician, the European massifs formed their own faunal association, with Armorica and Iberia forming a tight link, which is in accordance with the conclusions of Cocks and Torsvik (2002); these authors included Iberia with Armorica, except the South Portuguese Zone where the oldest rocks are of Middle Devonian age (Cocks 2000). Note that the faunal association of the European massifs may not be restricted to these, as the analysis presented here does not include all the plates in the neighborhood of the European massifs.

The 2<sup>nd</sup> segment (Figure 5) was initiated during the Costonian with the singularly largest diversity increase for most of the plate groups investigated. During the 2<sup>nd</sup> segment, Baltica, Ava-Ionia and Laurentia consolidated as a coherent faunal association independent of the peri-Gondwanan European massifs and core Gondwanan terranes, creating a gradient that correlates roughly with palaeolatitude (Torsvik 1998; Cocks and Torsvik 2002). Three distinct faunal associations formed, however, note that neither analytical method presented here provides a measure of the physical distance between the plates. The 3rd seqment (Figure 6) covers the Silurian, during which the overall faunal association pattern changed rapidly as a result of the Late Ordovician extinction event, forming a more or less homogenous faunal association during the early parts of the Llandovery.

This homogenous association gradually differentiated, however, perhaps as a result of the core lapetan plates moving towards Gondwana during the Silurian, the same degree of faunal provincialism as evidenced during the Middle-Late Ordovician was never re-established. At the Lower-Middle Silurian boundary, two distinct faunal associations



**Figure 6.** The world at 440 Ma (Llandovery), near the boundary between the 2<sup>nd</sup> and 3<sup>rd</sup> segments (source: Scotese 2001).

emerged from the supergroup, forming a (within the region) cosmopolitan low-mid latitude fauna and a high latitude fauna (*Clarkeia* fauna, see Fortey and Cocks 2003). Furthermore, the apparent isolation of Siberia indicates a separate faunal association of this plate.

During this interval the European massifs retained their faunal integrity, however, Bohemia changed from being associated with the massifs to the larger Gondwanan-lapetan association, indicating movement of this terrane. These conclusions are tentative however, being hampered by very low Silurian diversities, which add uncertainty to the results of the analyses.

#### Siberia

Siberia is highly mobile throughout the analyses, which is partly the result of low diversities during the earlier and later temporal intervals analyzed. The Siberian orthides appear to be of a mixed association, including both Gondwanan and Laurentian elements, which causes the spurious placement in the dendrograms (Figure 3). The relationship of Siberia with the other GIOR plates is clearer in the NMDS diagrams (Figure 4), where it is initially shown with a placement near Laurentia and South America, however, during the Late Ordovician Siberia became progressively more affiliated with the core lapetan plates, retaining, however, a distinct faunal signal. The Late Ordovician extinction event possibly affected the Siberian faunas differently than the Laurentian as seen in the placement of Siberia in the Rhuddanian NMDS diagram (Figure 4, bottom left). A tentative link with the Silurian Gondwanan-lapetan faunal association was, however, retained during the entire Silurian. This pattern is consistent with other faunal data (Nikiforova and Andreeva 1961) and is repeated for groups like trilobites (Chugaeva 1973). These faunal data suggest that Siberia was at least in partial faunal contact with Laurentia during the Silurian, this distance being smaller than the distance to the North China Plate, whose influence was apparently less; during the Early and Early-Middle Silurian the fauna remained a tropical pandemic (Fortey and Cocks 2003).

#### The Precordillera

This terrane is also highly mobile in the cluster and ordination diagrams presented here, owing both to changing compositions in the faunal data and low diversities. Orthide data support a Laurentian origin for the Precordillera. During the Arenig, 15 genera are reported from the Precordillera. With the exception of Monorthis, the Precordilleran genera were all found on Laurentia. Monorthis is reported from the Early Ordovician only from Wales (Avalonia) and Argentina (the Precordillera). This is in accordance with Fortey and Cocks (2003), who noted an Avalonian influence in the faunas. Apart from Argentina, orthides are reported from Bolivia, Brazil and Colombia within South America. These records are unfortunately much more fragmented than those from Argentina. There are five genera recorded from Arenig deposits of these countries, and none of these is found on the Precordillera, however, for example Acanthorthis and Orthidium are shared between the Precordillera and Laurentia. This lends to support for Precordillera origin within Laurentia as proposed by Thomas (1991); Astini et al. (1995); Davis et al. (1997) and Gerbi (1999).

The orthides of the Middle-Late Ordovician from the Precordillera are commonly widespread to cosmopolitan. The orthide data, therefore, cannot be safely used to delineate the position in time and space of this terrane during the Late Ordovician – faunal data from other groups needs to be employed.

# Bohemia (Perunica)

A greater amount of orthide data are known from the Ordovician-Silurian of Bohemia, than from any other peri-Gondwanan terrane, due to the studies of the Bohemian successions in the Prague Basin, especially by authors such as Barrande in the 19th century and more recently by Havlícek (Havlícek 1977; Havlícek et al. 1994). During the Early-Middle Ordovician. Bohemia obviously formed part of the European massif association, supporting the conclusions of Fortey and Cocks (2003). As indicated by the cluster analysis, the European massifs remain more closely related to each other than any other plate or plates during the entire Ordovician, and only by the Middle Silurian does Bohemia switch association (Figure 3, bottom right). During the Caradoc, ordination plots indicate, however, that Bohemia was that of the European massifs most closely associated with the lapetan and Gondwanan plates (Figure 4), a situation which developed during the Caradoc-Ashgill.

The orthide data confirm the conclusions of Fortey and Cocks (2003), who summarized trilobite and brachiopod data from Bohemia, and noted that the terrane was probably close to, however, perhaps tectonically separate from West Gondwana by the Tremadoc. Greatest oceanic separation was achieved during the Caradoc, followed by an interval when Bohemia drifted progressively closer to Baltica.

### CONCLUSIONS

This study indicates that five important developments affected faunal organization of the orthides of the greater lapetus region: 1) the diversification of the Early Ordovician, 2) the Middle Ordovician diversity reduction, 3) renewed diversification of the early Caradoc, 4) the Hirnantian glaciation and 5) the following gradual homogenization of the faunas during the Silurian. The conclusions agree with the general plate tectonic history presented for the GIOR presented in recent reconstructions such as those of Cocks and Torsvik (2002) and Torsvik and Rehnström (2003).

The high degree of correspondence between the palaeogeographic maps for the greater lapetus region and the results of the ordination/cluster analysis presented here lends credibility to the use of these methods in palaeobiogeography. However, it remains unresolved which similarity/distance measures that should be used for the calculations and if and how these should be modified to accommodate differences across environmental gradients.

This study indicates that a combination of indices is necessary to find the strongest faunal signals. Plates such as Siberia and the Precordillera will remain problematic because their faunal signals are mixed, however, this can perhaps be resolved with the appliance of data from other groups (Fortey and Cocks 2003). Moving from the type of generalized study presented here, the next logical step would be to distinguish between intracratonal/marginal locations or even individual biofacies. Furthermore, the important intra-oceanic terranes and islands of the Celtic province should be separated (Harper and Mac Niocaill 2002). This separation would add a further level of precision to the analyses presented here.

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#### APPENDIX

Average generic orthide diversities and total percentages for the Ordovician-Silurian of the Greater lapetus Ocean Region (Table 1). The columns "average number of genera" contain the average number of genera according to geographic range, e.g. orthide genera found on three plates groups during each stage of the investigated temporal interval comprise 10.4% of the total dataset, corresponding to an average generic diversity of 7.23 genera for every stage of the Ordovician and Silurian. The Min % and Max % are the minimal and maximal values encountered for a single stage during the temporal interval (either the Ordovician-Silurian, only the Ordovician or only the Silurian). The averages are calculated based on diversity and distribution values from each stage of the temporal interval in question, with separate calculations for the Ordovician and the Silurian also provided. Note the difference in average generic diversity between the two periods (again at stage level of resolution), which however is not greatly reflected in the spatial distribution (degree of endemicity) of the surviving genera, barring a decrease in the amount of endemic genera.

					Ordovician				Silurian			
	Average number of genera	Average of total in %	Min %	Max %	Average number of genera	Average of total in %	Min %	Max %	Average number of genera	Average of total in %	Min %	Max %
1 plate group	35.23	50.68	33.96	75	45.75	52.18	35.82	75	18.75	44.51	33.96	68.75
2 plate groups	13.05	18.77	4.17	31.25	16.83	19.2	4.17	30.77	7.38	17.52	6.25	31.25
3 plate groups	7.23	10.4	0	16	9.17	10.46	0	13.33	4.38	10.4	6.25	16
4 plate groups	6.33	9.11	0	22.64	6.79	7.74	0	16.07	5.75	13.65	0	22.64
5 plate groups	3.59	5.16	0	15.38	4.38	5	1.87	15.38	2.63	6.24	0	9.3
6 plate groups	4.08	5.87	0	12.5	4.75	5.42	0	11.94	3.31	7.86	0	12.5
Average generic diversity	69.51				87.67				42.13			

Table 1. Faunal Indices.

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