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The palaeogeography of early Ordovician Iapetus terranes: an integration of faunal and palaeomagnetic constraints

D.A.T. Harper [a], C. Mac Niocaill [a], S.H. Williams [b]

[a] *Department of Geology, University College, Galway, Ireland*
[b] *Department of Earth Sciences, Memorial University, St. John's, Newfoundland, Canada*

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Abstract

New and existing fossil data from Ireland, Britain, Newfoundland and Scandinavia emphasize a significant degree of latitudinal variation in biogeographic patterns across the Ordovician Iapetus Ocean. Platform provinces together with marginal belts and island complexes can be recognised with increasing clarity on the basis of palaeontological information. Statistical analysis of the distribution patterns of about 70 early Ordovician brachiopod genera across some 25 sites, using both cladistic and phenetic methods, together with a critical analysis of their geological settings combined with current palaeogeographic and palaeomagnetic data, reaffirm the existence of the Celtic brachiopod province. During the early Ordovician, the majority of sites assigned to the Celtic province define a high-latitude, peri-Gondwanan belt shadowing the distribution of the low-latitude, circum-Laurentian Toquima-Table Head faunas. Rapidly changing Ordovician faunal signals across the Baltic province and Exploits Zone of central Newfoundland track the cross-latitude movement of these terranes from high temperate to near tropical belts during the period. New fossil information together with continuing statistical appraisal of an expanding database are providing more accurate and sophisticated models for the dynamics of the Iapetus ocean system.

1. Background

Since Tuzo Wilson's classic demonstration of the proto-Atlantic Ocean (1966), based to a large extent on palaeontological data, first, many new fossil assemblages have been documented from the Caledonian–Appalachian mountain belt and a wide range of statistical and graphical techniques are now available for their analysis; second, improved understanding of the geology of the circum-Atlantic area has helped define fragments of the Iapetus Ocean and its margins within the orogen; and third, a realistic and stable palaeomagnetic database has provided significant modifications to the palaeogeography of the North Atlantic area during the early Palaeozoic.

The facies and faunas of the platform realms of Laurentia, Baltica and Gondwana are now known in considerable detail. However initial attempts to assign faunas from the variety of accreted terranes, now amalgamated within the Caledonides, to these platform provinces have proved unsatisfactory. Firstly a further set of biogeographic units are required to describe faunas and floras developed seaward of the platform provinces. Secondly the demonstrable movement of terranes with time implies changing biogeographic signatures. The majority of fossil animals and plants, like their living counterparts, had a defined geographic range. Although the geographical ranges of some taxa are coincident and many overlap, in distribu-

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tions controlled by physical gradients, biogeographic units are best defined statistically. These analyses provide a facility for defining the latitude of terranes and their movements across Iapetus during the Ordovician.

The early Ordovician (Arenig) Toquima-Table Head faunal realm (Ross and Ingham, 1970) and the Celtic brachiopod biogeographic province (Williams, 1973) were erected because their brachiopod assemblages could not be readily accommodated within the Laurentian, Baltic and Mediterranean provinces. We now consider that these assemblages and the rocks that contain them characterize contrasting climatic realms: the Toquima-Table Head marks low-latitude, warm-water environments that surrounded transequatorial Laurentia, whereas those of the Celtic assemblage record the cooler waters of mid to high peri-Gondwanan latitudes (Neuman and Harper, 1992). The transequatorial position of Laurentia is supported by the symmetrical development of carbonate ooids and evaporite sediments on either side of the supposed track of the early Ordovician equator (Witzke, 1990, fig. 2). The presence of these distinctive fossil assemblages in crustal fragments (displaced terranes), now assembled in the collage of the Appalachian–Caledonide orogen assists in the determination of their Ordovician positions in the construction of palaeogeographic maps for the period.

Detailed knowledge of fossil assemblages has increased to the point that statistical comparison of coeval cratonic and peri-cratonic assemblages can be routinely applied. Brachiopods are particularly useful for palaeogeographic determinations since these animals were sessile, most of them lived in relatively shallow water, their shells accumulated in relatively large numbers and their taxonomy is reasonably stable (Rudwick, 1970); furthermore, and important in this context, many features that permit their generic identification are sufficiently robust to have survived considerable deformation and metamorphism. Other groups of benthic fossils have yielded comparable information (Fortey and Mellish, 1992) but are less abundant than brachiopods in displaced terranes. Graptolites and other planktonic organisms had habitats that were less sensitive to local climates; nevertheless statistical comparisons of assemblages have also demonstrated a palaeogeographic utility.

Nevertheless in a recent contribution to this discussion both Boucot (1993) and Cocks and McKerrow (1993) have raised concerns regarding the integrity and significance of the Celtic province; moreover Cocks and McKerrow (op. cit.) have explicitly criticised the use of biogeographical analysis in the reconstruction of the Ordovician Iapetus Ocean and its margins. Their construction of a single putative arc—the Bronson Hill-Tetagouche-Lushes Bight Island Arc (BHTL Arc) seaward of Laurentia (McKerrow et al., 1991) containing apparently both high latitude (Celtic) and low latitude (Toquima-Table Head) faunas (Cocks and McKerrow, 1993) requires detailed investigation and provides an opportunity to test this model with new and current palaeontological, geological and palaeomagnetic data.

To this end brachiopod distributional data from the Appalachians and the Caledonides are re-evaluated using a range of statistical and graphical techniques. The multivariate techniques of Cluster Analysis (CL), Correspondence Analysis (CA) and Principal Coordinate Analysis (PC) together with Cladistics are used to interrogate a binary matrix of presence and absence of brachiopod genera across the Caledonide area. Major biogeographic clusters identified statistically are plotted on a new palaeogeographic template, based on the currently available palaeomagnetic information, for the North Atlantic region. Finally the geological settings of these faunas in Newfoundland and along the Baltic and Avalonian margins are critically reassessed. The majority of the faunas investigated are of late Arenig to early Llanvirn age (mid Whiterock age). Nevertheless it proved impossible to find exact correlatives on the North American platform; the assemblages from the North American craton are older ranging from late Ibex to early Whiterock. These are specialized, low-diversity faunas that arguably continued through this early part of the Ordovician on the carbonate platform of North America. The biogeographic terms used in this study are defined in more detail by Williams et al. (1996); faunas and terranes developed at high latitudes and associated with the circumpolar supercontinent of Gondwana

are described as Gondwanan whereas those that evolved seaward of the supercontinent but, nevertheless, at high latitudes have been termed peri-Gondwanan.

Cocks and McKerrow (1994) contended that the early Ordovician Celtic-type faunas occur on parts of Laurentia, parts of Avalonia and on terranes accreted onto continents during the early Palaeozoic; if this is the case the palaeogeographic usefulness of the Celtic signature is severely limited. This hypothesis is tested.

2. The Celtic Province

The Celtic Province was established on the basis of Arenig brachiopod assemblages from Anglesey, north Wales (Williams, 1969, 1973, 1976; Bates, 1968, Neuman and Bates, 1978) and Tagoat, south-east Ireland (Bates in Brenchley et al., 1967; Harper and Bates, in review). Williams (1973) emphasised the strong links of the assemblages with those of Baltica; graphical and statistical analysis based on a similarity coefficient of association indicated their close similarity with his Anglo-French and Baltic groups and their marked contrast to those assigned to the NW American and Scoto-Appalachian assemblages.

The distinctiveness of Celtic assemblages of brachiopods and trilobites from five Appalachian–Caledonian sites (Maine, New Brunswick, Central Newfoundland, Tagoat and Anglesey) in contrast with those from three Norwegian sites (Otta, Smøla and Hølonda) was confirmed by semiquantitative studies (Bruton and Harper, 1981b, 1985). Whereas the Celtic assemblages had no clear links with any coeval platform faunas, the slightly younger Norwegian assemblages show some connections with the faunas of the North American platform. Nevertheless Cocks and Fortey (1982) excluded these data from their analysis of the Iapetus Ocean system (Fig. 1A).

Neuman (1984) in comprehensive review and analysis of the early Ordovician brachiopods of the North Atlantic area, consolidated his earlier (1972), then radical suggestion, that many of these faunas from the Caledonian mountain belt, often from volcanic and volcaniclastic facies, originated around islands within the Iapetus Ocean. Both Neuman (1972, 1984) and Bruton and Harper (1981a,b, 1985) have emphasised some of the peculiar characteristics of these faunas. Many have mixed biogeographic signatures, a high proportion of endemic taxa and may contain taxa that are more common in younger strata on the adjacent platforms. Moreover, Neuman's model (Fig. 1B) is supported by the configuration of modern oceans punctuated by islands of both volcanic and basement rocks. For example, the present North Atlantic area (Williams, 1984) is characterized by submarine rises of both basement and volcanic material.

New records of Celtic genera, far removed from the Iapetus area in a variety of facies, for example from carbonate rocks in Argentina (Herrera and Benedetto, 1991) and from siltstones in South China (Xu and Liu, 1984) required a reassessment of the distribution and status of the entire array of Celtic assemblages. Neuman and Harper (1992) in a global study of the distribution of early Ordovician brachiopods established, statistically, using Correspondence Analysis, the mutual integrity and contrast of the Celtic and Toquima-Table Head groups of faunas. The former demonstrated relationships with both Baltic and Gondwanan faunas but little or no similarity to the Toquima-Table Head set. Harper (1992) in a more focused analysis of the Ordovician brachiopod faunas within and around the Iapetus Ocean confirmed the statistical coherence of the Celtic group of faunas and its clear distinction from the Laurentian marginal, Toquima-Table Head, faunas.

In reply to Paris and Robardet's (1990) fundamentally different faunal and floral analysis of the Iapetus area (see also Fig. 1C), Fortey and Mellish (1992) together with Fortey and Cocks (1992) discussed the usefulness of different fossil groups in these conflicting continental reconstructions of the North Atlantic area. Both papers present identical sets of cladograms (fig. 2 of both papers) for ostracode, graptolite, trilobite, acritarch and brachiopod assemblages of early Ordovician faunas and floras from mainly in and around the Iapetus ocean system. Significantly both brachiopod cladograms associate Anglesey and Eastern Newfoundland (actually Central Newfoundland).

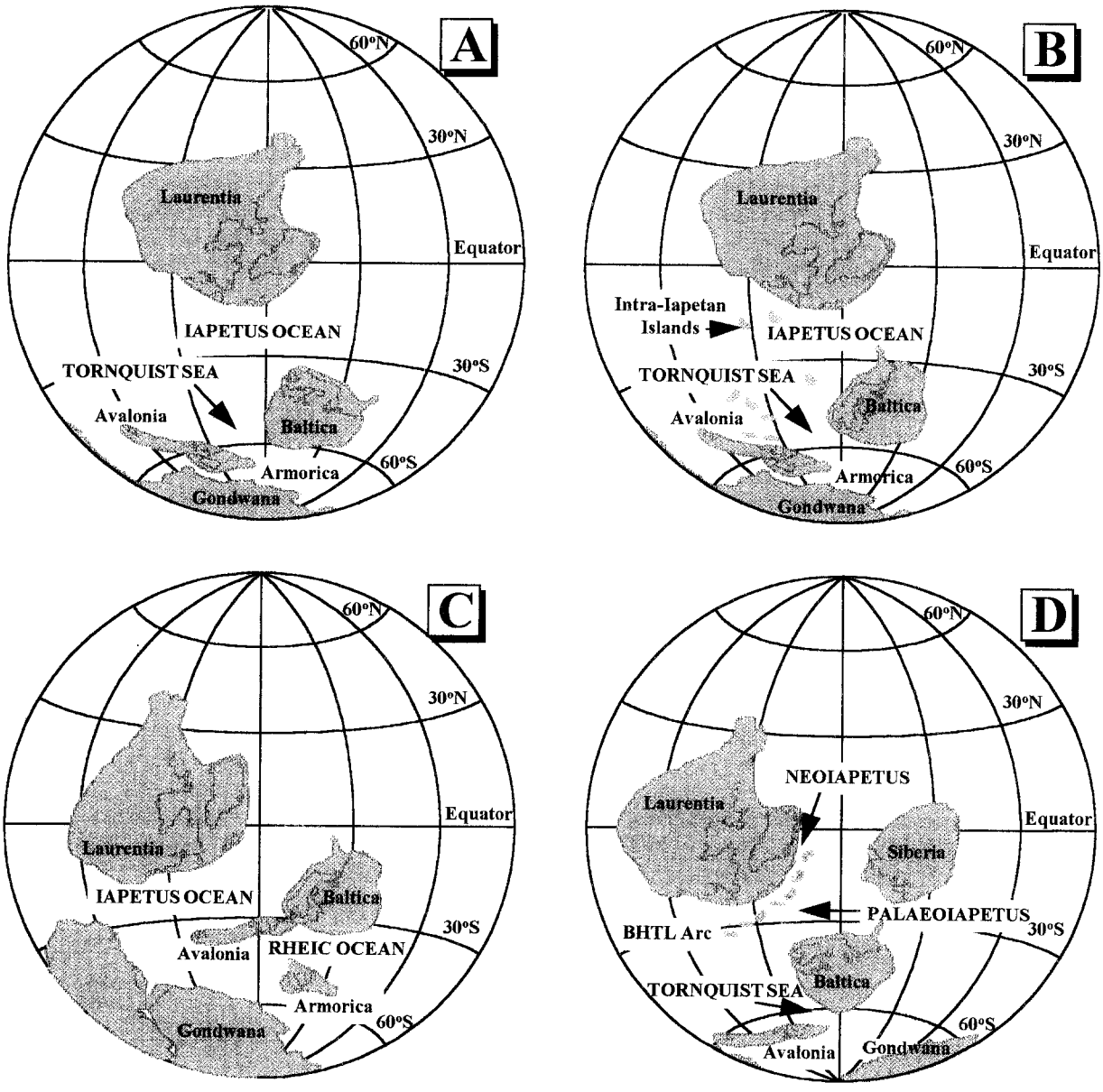


Fig. 1. Four published scenarios of the Early Ordovician palaeogeography of the Iapetus region. A. The simple three continent system (after Cocks and Fortey, 1982 but with Baltica rotated after Torsvik and Trench, 1991). B. A similar reconstruction but with the addition of oceanic islands (after Neuman, 1984). C. The fundamentally different reconstruction of Paris and Robardet (1990) based on palynomorphs. D. The recent reconstruction by Cocks and McKerrow (1993) with a single Bronson Hill-Tetagouche-Lushes Bight Island Arc located marginal to Laurentia.

In fact the brachiopod faunas cited, in both papers, from E Newfoundland are from Virgin Arm (Neuman, 1976) within the Exploits Subzone of the Dunnage Terrane, more correctly referred to Central Newfoundland, and thus together with the Anglesey faunas would constitute the Celtic set.

Cocks and McKerrow's (1993) more recent contribution to the debate (Fig. 1D) has elaborated

on the evolution of a single major arc system seaward of Laurentia and extending SSW from Greenland to the southern Appalachians (McKerrow et al., 1991). Since various parts of the arc system have different rocks and biogeographic signatures both the geological settings of each of the now dismembered parts of the arc together with the provinciality of their faunas must be reassessed. These faunas and their geological and palaeolatitudinal settings are thus reappraised herein.

3. Palaeogeographical template

A reliable palaeogeographical template on which faunal distributions can be plotted is of crucial importance to any assessment of the biogeography of the early Ordovician circum and intra Iapetan faunas. In this study a number of recent palaeomagnetic data compilations are used for Laurentia (Mac Niocaill and Smethurst, 1994), Baltica (Torsvik et al., 1992), Gondwana (Bachtadse and Briden, 1990) and Avalonia (Torsvik et al., 1993). These studies have employed stringent reliability assessments of the palaeomagnetic data. Using these as a base all the available palaeomagnetic data from the marginal areas of Iapetus pertinent to this discussion have been plotted, including Central Newfoundland and New Brunswick (Van der Pluijm et al., 1990; Van der Voo et al., 1991, Johnson et al., 1991; Liss et al., 1993). It must be emphasised that no longitudinal constraints are provided by palaeomagnetic data and thus separations between continents are described in terms of latitude only.

The early Ordovician palaeogeography of the Iapetus Ocean, as constrained by the palaeomagnetic data, is shown in Fig. 4. Laurentia occupied equatorial latitudes, whereas Avalonia lay some 3000–4000 km south at latitudes of 40–50°S. No significant latitudinal separation can be inferred for western and eastern Avalonia (see for example the list of Van der Pluijm et al., 1990 for western Avalonia and Torsvik et al., 1993 for eastern Avalonia) and accordingly they are plotted together. Baltica was located at similar latitudes to Avalonia (Torsvik et al., 1992) but given the clear faunal differences between the two continents (Fortey and Mellish, 1992; Fortey and Cocks, 1992) there must have been a degree of longitudinal separation.

Of the fossiliferous intra-Iapetan terranes used in this study only three have palaeomagnetically constrained palaeolatitudes; western Ireland (Morris et al., 1973; 15°S), the Summerford Group, the Robert's Arm and Chanceport groups (Van der Voo et al., 1991; 31°S), of the Exploits subzone (Johnson et al., 1991) and the Tetagouche Group of the Mirimichi terrane in New Brunswick, a lateral extension of the Exploits subzone of the central Mobile Belt (Liss et al., 1993; 53°S). However, these palaeolatitudes are supported by additional palaeomagnetic data from other non-fossiliferous terranes. These include the Moreton's Harbour Group (Johnson et al., 1991; 11°S) from the Notre Dame subzone and the Pennington Mountain terrane of Maine (Potts et al., 1995; 11°S). These studies point to clear latitudinal separation between the Notre Dame subzone and the Exploits subzone in the early Ordovician, with the Notre Dame subzone lying at latitudes of circa 11°S, near the Laurentian margin, and the Exploits subzone lying at higher latitudes: circa 31–53°S, in an intra-Iapetan setting. This is in contrast to the recent interpretation of Cocks and McKerrow (1993) which places a single arc, the BHTL arc, on the northern margin of Iapetus. However their analysis ignores critical data from the Moreton's Harbour Group (Johnson et al., 1991) and the Tetagouche Group (Liss et al., 1993) and includes low latitude Toquima-Table Head faunas in the arc by orienting the Laurentian margin in a NE–SW direction. The palaeomagnetic data imply a more E–W orientation of the Laurentian margin during the early Ordovician (Mac Niocaill and Smethurst, 1994), rotating to a NE–SW orientation during the late Ordovician (Van der Voo, 1988; Kent and Van der Voo, 1990; Mac Niocaill and Smethurst, 1994).

4. Geological settings of the Celtic faunas

Neuman (1984) provided a detailed analysis of the geological settings of the main Celtic and

Toquima-Head faunas. We review here further geological data relevant to the settings of Celtic type faunas (Fig. 2). Toquima-Table Head faunas are restricted to terranes located at low latitudes, usually marginal to Laurentia (Neuman and Harper, 1992). In contrast Celtic faunas are located on a variety of terranes which originated at high latitudes during the early Ordovician; some such as the Exploits subzone moved rapidly to low latitudes during the Ordovician.

4.1. Central Newfoundland

Williams et al. (1996) summarized Lower Palaeozoic fossil data from Newfoundland and their biogeographical significance whereas Neuman et al. (1989) reviewed palaeontological data from the Appalachian belt in the United States. In Central Newfoundland the Dunnage Zone consists of two main parts with contrasting geological histories: the Notre Dame and Exploits subzones. The boundary between the two is the Red Indian Line which probably represents a major suture (Williams et al., 1988). Although fossiliferous rocks are rare in the Notre Dame subzone, Arenig–Llanvirn graptolites have been recorded at three localities and conodonts have been extracted from carbonate clasts in a volcaniclastic breccia. Both groups have strong Laurentian affinities (Nowlan and Thurlow, 1984;

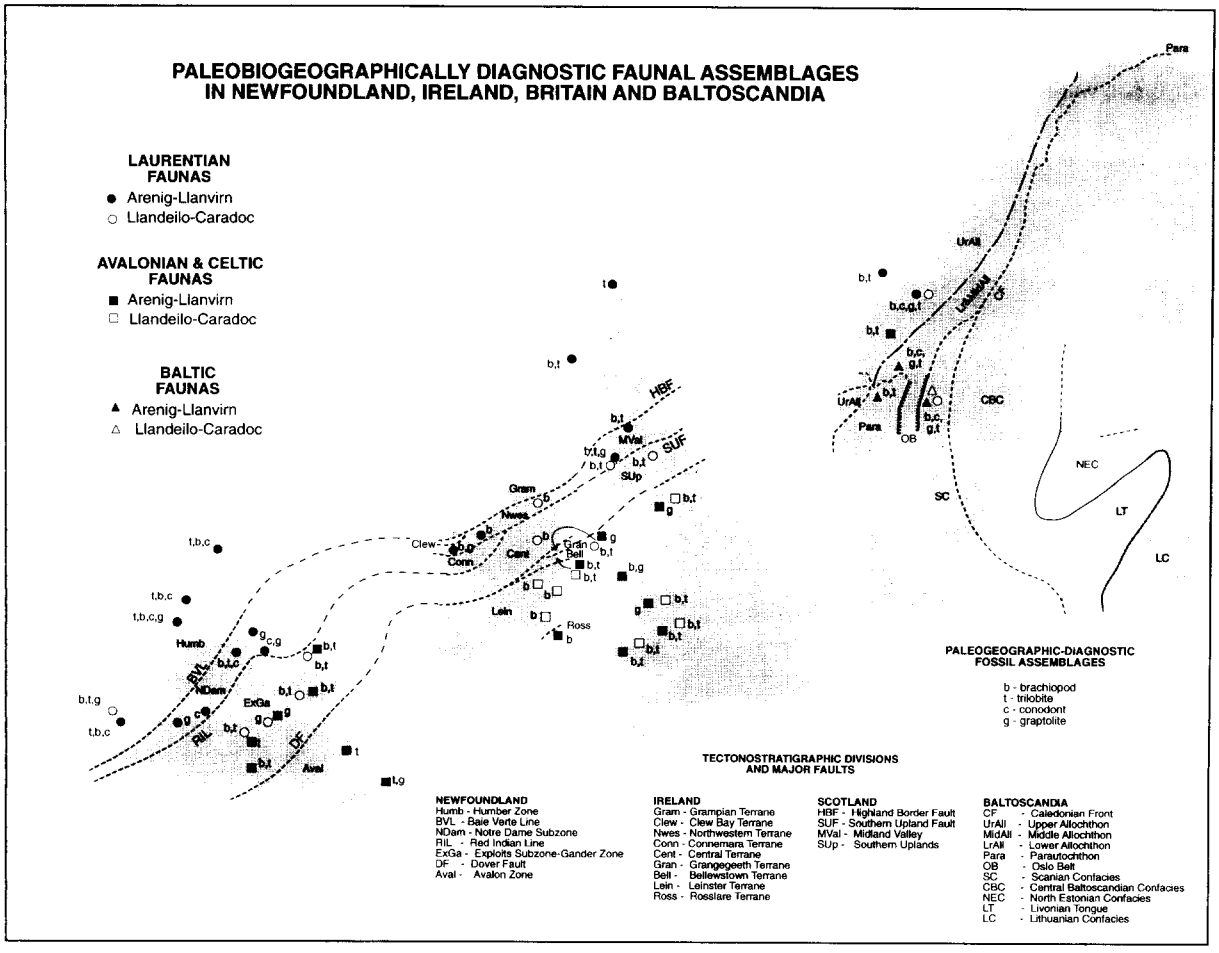


Fig. 2. Along-strike correlations of tectonostratigraphic units currently recognised in the northern Appalachians, Ireland and Britain together with similar units in Scandinavia. The palaeobiogeographic affinities of key faunas, through Ordovician time, are indicated.

Williams, 1990; Williams et al., 1992, 1995). Lower Ordovician fossiliferous rocks are more abundant in the Exploits subzone although faunal data are still sparse in contrast to information from middle Ordovician–lower Silurian strata. In addition to the six occurrences of Celtic assemblage brachiopods (C1–C6 of Neuman and Harper, 1992; see also Harper, 1992 and Cocks and McKerrow, 1993) early Ordovician Gondwanan trilobites (*Cyclopyge*) together with graptolites (*Undulograptus*) were recorded from Central Newfoundland (Williams et al., 1992) adjacent to Celtic brachiopods (C5 of Neuman and Harper, 1992). Furthermore, a newly discovered locality to the southwest of Gander Lake yielded late Arenig–early Llanvirn graptolites including *Aulograptus* cf. *cucullus* (Bulman) and a possible specimen of *Azygograptus*. Servais and Maletz (1992, p. 274) noted that *A. cucullus* has been widely recorded from the Gondwanan margin; there appears to be, however, only one record of the genus from north America (Lenz and Jackson, 1986, fig. 6h) from the upper part of the *P. tentaculatus* Zone of northwest Canada. *Azygograptus* has previously been recorded only from Gondwana (Atlantic province) regions and appears to be diagnostic of early Ordovician, high latitudes (Cooper et al., 1991; Rigby and Rushton, 1991, p. 35). The single specimen described by Williams and Tallman (submitted) was unfortunately insufficient for positive identification of the genus. The combination of these forms does, however, support a Gondwanan affinity for the Exploits subzone during the early Ordovician. The striking faunal contrast between the marginal Gondwanan (Celtic) aspect of the lower Ordovician faunas and assemblages of Laurentian affinities in middle and upper Ordovician rocks within the subzone was ignored by Cocks and McKerrow (1993; see for example Neuman et al., 1994); this contrast is an essential component in the understanding of the Celtic province both in Newfoundland and palaeogeographically equivalent regions elsewhere.

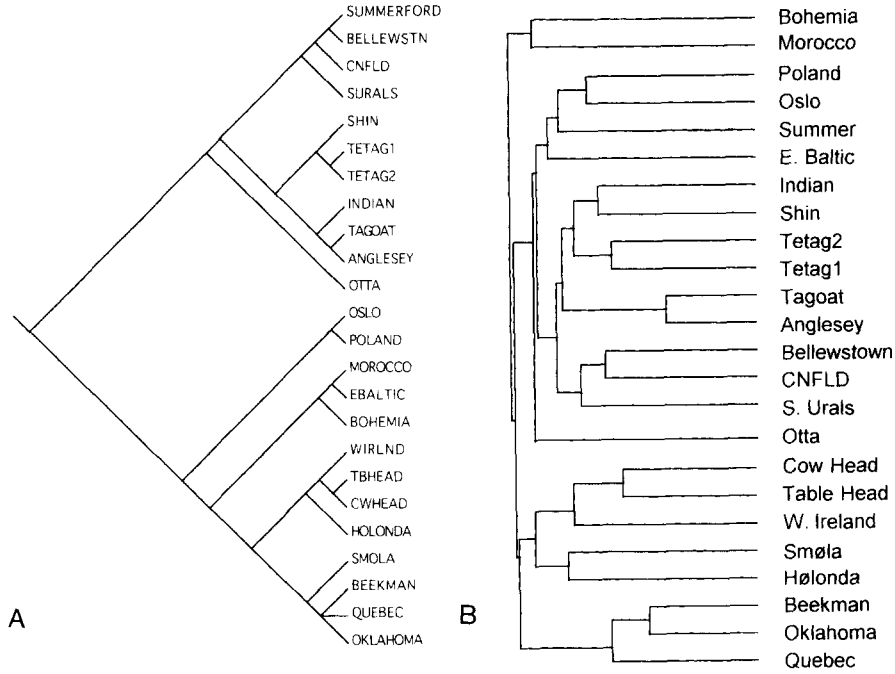
4.2. Avalonian margins

The early Ordovician brachiopod faunas from Anglesey together with those from Tagoat, SE Ireland, form the standard reference of the Celtic province (Williams, 1973; Neuman and Bates, 1978). Despite some discussion regarding the exact position of Anglesey with respect to North Wales during the early part of the Ordovician (Gibbons, 1983), most recent studies agree that Anglesey formed part of the northern margin of the microcontinent of Avalonia. Fortey and Cocks (1986) critically assessed the early Ordovician faunas of Anglesey, strongly supporting the high latitude stamp of these Celtic assemblages. Bassett (in Fortey and Cocks, 1986, p. 157) identified the following genera in the Arenig rocks of Dyfed, south Wales: *Hesperonomiella*, *Rhynchorthis*, *Skenidioides*, *Progonambonites*, "*Orthambonites*" [*Paralenorthis*], *Platystrophia* and possibly *Toquimia*. The Dyfed fauna was not included in the statistical analyses presented here since monographic work in still in progress; nevertheless on the basis of the data available the Dyfed fauna plots within the Celtic cluster. The fauna is not highly correlated with cratonic Gondwanan faunas such as those from Morocco and Bohemia (Havlíček, 1971, 1989; Cocks and Fortey, 1988).

In eastern Newfoundland diagnostic Gondwanan graptolites, including *Didymograptus* (s.l.) *simulans* Elles and Wood occur in the middle Arenig prodeltaic siliciclastics and oolitic ironstones on Bell Island (Williams, 1990) confirming the faunal links between Anglesey and the Avalon Peninsula during the early Ordovician.

4.3. Baltic margins

The structure of the Scandinavian Caledonides is now known in considerable detail (Gee et al., 1985; Furnes et al., 1985; Roberts and Gee, 1985). The early Llanvirn shelly fauna of the Otta serpentinite conglomerate has provided a considerable challenge to models for the development of this part of the Caledonian orogen (Bruton and Harper, 1981a, 1988). The Otta conglomerate is part of the lower unit of the Upper Allochthon associated with terranes that developed seaward of the miogeoclinal rocks of the Middle Allochthon. Adjacent parautochthonous rocks to the south at Hardangervidda contain a Baltic fauna (Bruton et al., 1984). The Lower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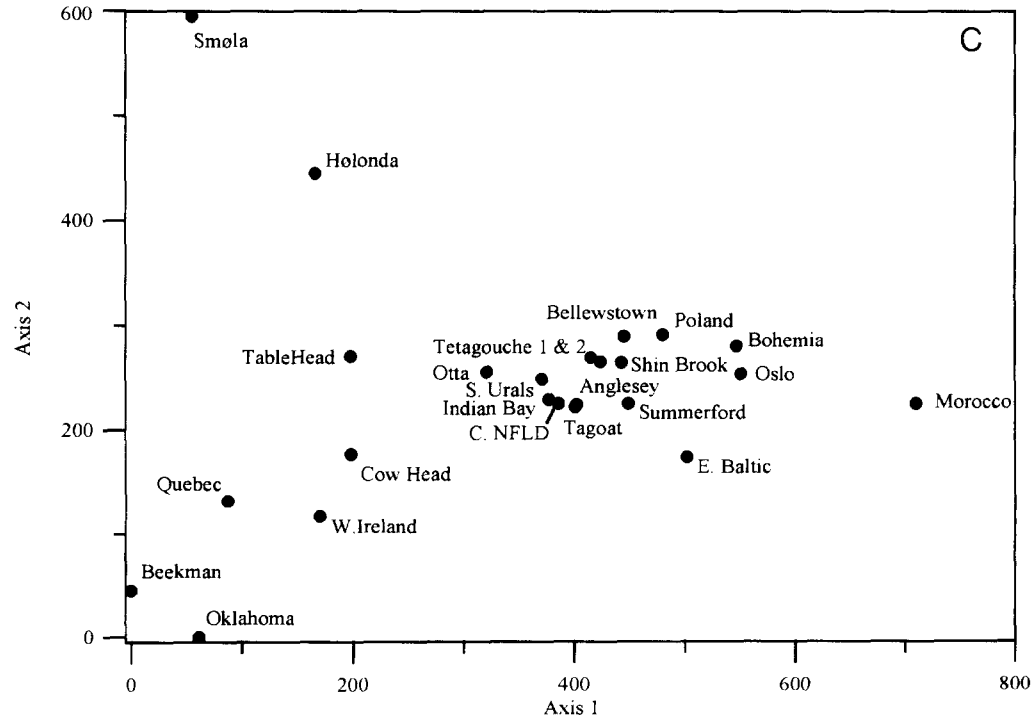
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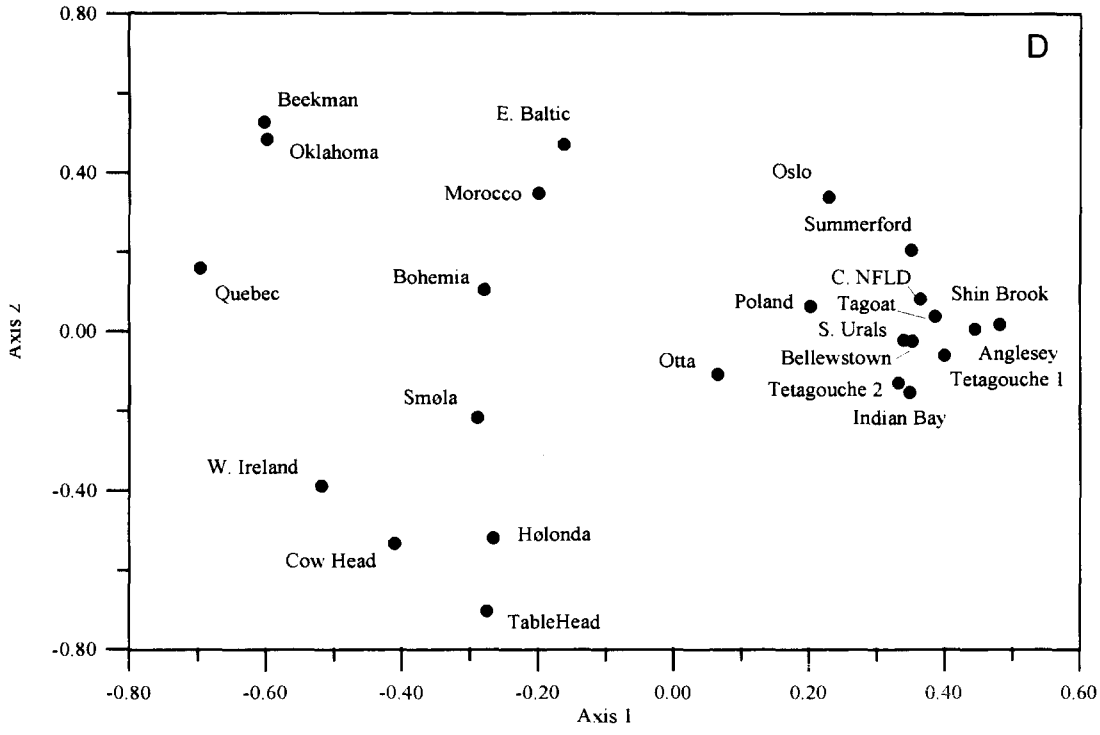

Fig. 3. Statistical treatment of the Iapetus data set: sources are listed in Neuman and Harper (1992) and the original labels have been retained on Fig. 4 for cross reference. It is difficult to locate comparable early Ordovician (Arenig–Llanvirn) brachiopod faunas from cratonic North America. However the Beekmantown-type facies ranges in age from Tremadoc to Arenig and additional, essentially similar, faunas from Oklahoma and Quebec have been added to the Beekmantown assemblage from Maryland to underpin cratonic Laurentia. A. Cladogram generated by PAUP 3.1 and manipulated by MacClade 3: note the clear differentiation of the Laurentian and Laurentian marginal clades from those of the Celtic province characterized by synapomorphic taxa. B. Cluster analysis of a matrix based on the Jaccard Coefficient by average pair linkage: note the three main parts to the dendrogram representing Gondwanan, high and low latitude faunas. C. Correspondence analysis of a matrix of conditional probabilities: note central cluster of Celtic sites, to the right of the Toquima-Table Head and North American faunas and to the left of the Baltic and Gondwanan faunas. D. Principal coordinate analysis executed on a nonparametric similarity matrix based on Spearman's Rho: note the relatively tight cluster of Celtic sites on the right of the plot.

Allochthons were deposited in a series of encratonic basins on the margin of Baltica and are characterised by Baltoscandian faunas (Bruton and Harper, 1988).

Sturt et al. (1991) favoured a setting for the Otta Conglomerate at the base of a cover sequence overlying an obducted ophiolite. The Vågåmo Ophiolite was deformed and obducted onto Baltica during the early Ordovician Finnmarkian events; the rising Finnmarkian land mass provided both shelf area and a selective faunal barrier (Sturt et al., 1991; Bøe et al., 1993). Alternatively, the Otta fauna may have developed on the shelf of a serpentine seamount within an intra-oceanic setting (Pedersen et al., 1992) and arrived much later, during the late Silurian Scandian phase of the Caledonian orogeny, on the Baltic craton.

In the Trondheim Region, outcrop of the higher parts of the Upper Allochthon is characterised by North American amphicratonic faunas; comparable faunas are known from the west of Ireland (Williams, 1972; Harper et al., 1985). The late Arenig–early Llanvirn graptolite fauna of the Bogo Shale is one of a number of marginal Laurentian assemblages (Blake, 1962). The fauna is essentially identical to that from the Cow Head Group and contrasts markedly with coeval assemblages from both Gondwana and Baltica (Schmidt, 1984).

Diverse and abundant shelly faunas have been known from the Trondheim Region for over 60 years. Monographic revision of the brachiopods and trilobites (Bruton and Bockelie, 1980; Neuman and Bruton, 1974, 1989) confirmed their affinities with those of the Toquima-Table Head province of marginal North America. Carbonate facies and faunas on the island of Smøla have similarities with platformal sequences on Laurentia (Bruton and Bockelie, 1979).

5. Statistical analysis and discussion

The techniques available for the statistical and graphical analysis of biogeographical data have been summarized in recent publications (Newton, 1990; Smith, 1990); the technical and operational details of many of these are discussed by Davis (1986). We present here statistical analyses of early Ordovician brachiopod assemblages from the allochthonous terranes of the Appalachian–Caledonide orogen and its bordering cratons and cratonic margins. A sample of 69 genera (not including single-site endemics) of articulate brachiopods from 24 sites (or localities) in and around the Iapetus Ocean has been assembled for the current analysis. The original data set used in this study has been deposited as an Excel File in the James Mitchell Museum, University College Galway.

A large database for early Ordovician brachiopod distributions has been assembled over the last 25 years. Nevertheless there have been relatively few scientific analyses of these data. For the Arenig, Williams (1973) analyzed a data matrix of 18 assemblages with a total of 125 genera, generating five main clusters and three outlying assemblages. His fourth cluster, the Celtic province, contained the Anglesey and Tagoat faunas characterised by the endemic *Rhynchorthis*; this province had strong links with the Baltic cluster of assemblages. More recently Harper (1992) and Neuman and Harper (1992) favoured the phenetic technique of Correspondence Analysis whereas Fortey and Cocks (1992) and Fortey and Mellish (1992) pursued a cladistic methodology. As noted above both phenetic and cladistic strategies yielded broadly similar results.

Four statistical techniques, three phenetic and one cladistic, were selected for this analysis. Cluster Analysis (CL), Correspondence Analysis (CA) and Principal Coordinate Analysis (PCL) were processed by MVSP (Kovach 1990–1993). Although the data set is heterogeneous (Harper, 1992), the analyses provide frameworks for more scientific investigation of distributional data rather than the subjective approaches employed so often in the past. Modifications of the data set by taxonomic reassessments of already-documented faunas, addition of new occurrences to existing assemblages and the description of entirely new faunas can be input and the analyses rerun.

The cladogram (Fig. 3A) was first generated with PAUP 3.1 software (Swofford, 1993) and, within the constraints of the search strategy, the shortest tree was produced by a heuristic search using branch swapping and assuming the binary character states are unordered. This tree was imported into MacClade 3 (Maddison and Maddison, 1992) and manipulated further while retaining the original tree length. Despite the large number of absences, a number of distinct clades are identified; less certain is where a few of these clades should be rooted. A Celtic clade may be split into two groups—the Shin Brook, Tetagouche, Indian Bay, Tagoat and Anglesey sites characterizing the typical Celtic province whereas Summerford, Bellewstown, Central Newfoundland and the Southern Urals are related but perhaps developed both at slightly different latitudes and in different facies. Currently the documented diversity of the Bellewstown (Harper et al., 1990) and Urals (Andreeva, 1972) faunas are low. A Laurentian clade includes Oklahoma, Quebec, Beekmantown and Smøla whereas the adjacent marginal Laurentian clade includes western Ireland, Table Head, Cow Head and Holønda, sites typical of the Toquima-Table Head province. Oslo together with Poland and Morocco, East Baltic and Bohemia form two separate clades.

The dendrogram presented (Fig. 3B) was generated through the cluster analysis of a similarity matrix based on the Jaccard Coefficient by average pair linkage. Clusters comparable to the clades

generated by PAUP and MacClade were defined by MVSP87. Beekmantown, Oklahoma and Quebec form a Laurentian cluster associated with the Toquima-Table Head sites of Cow Head, Table Head, western Ireland and Holønda; Smøla however is combined with the Laurentian marginal sites rather than with the platform itself. A Celtic cluster includes Indian Bay, Shin Brook, Tetagouche, Tagoat and Anglesey associated with a cluster containing Bellewstown, Central Newfoundland and the southern Urals.

Two further phenetic analyses were run using MVSP87. Correspondence Analysis is an eigen technique based on the analysis of a matrix of conditional probabilities. Only the scores of sites on the first and second eigenvectors, holding most of the sample variation, were plotted. Groups of genera combine together to load each axis and thus the scores of the sites reflect the relative presence or absence of the these generic combinations across inter-site space. The most informative spread is evident along the first eigenvector or axis 1 (Fig. 3C). A relatively dense central cluster contains the Celtic sites whereas Otta plots to the left and Poland, Bohemia, Oslo and the east Baltic all plot to the right. The Laurentian sites have low scores on both eigenvectors whereas Holønda, Table Head, Cow Head and western Ireland plot between the Laurentian sites and the Celtic cluster. Morocco has an isolated position with the largest score on axis 1. The loadings of genera on the first eigenvector correspond to the control of site scores on that axis. Thus high-latitude genera associated with cratonic Gondwana have high scores on this axis, for example *Euorthisina*, *Prantliina*, *Ranorthis* and *Tarfaya*. The Celtic set of genera, for example, *Ffynnonia*, *Platytoechia*, *Rhynchorthis*, *Treioria* and *Tritoechia* have moderately high scores reflecting the position of the well-defined Celtic cloud of data points. However, the lowest scores are associated with cratonic Laurentian genera such as *Polytoechia* and *Syntrophopsis*; Toquima-Table Head genera, for example *Eremotoechia*, *Rhysostrophia*, *Toquimia* and *Vehnia* have higher scores corresponding to the position of that cluster between Laurentian sites and the Celtic sites.

Principal Coordinate Analysis was executed on a nonparametric similarity matrix based on Spearman's Rho. Again only the scores on the first and second eigenvectors were plotted. Similar clusters were however generated although in different positions. The Celtic sites form a relatively tight cluster on the right of the first eigenvector (Fig. 3D).

6. Palaeogeographic implications

Palaeogeographic maps of the Iapetus Ocean basin and related features, now incorporated in the Appalachian–Caledonide orogen, have evolved as new geological, palaeontological, palaeomagnetic and other information has become available. Recognition of contrasting faunal assemblages across now-adjacent terranes within the orogen has proved critical in both suggesting and testing Lower Palaeozoic palaeogeographic reconstructions (Williams et al., 1996). Pioneering early palaeogeographic maps charted the orthogonal movements of major continental blocks (Wilson, 1966) while more recent studies have incorporated strike-slip movements and continental rotations (Torsvik et al., 1991). Most of these maps and their contemporaries, however, lack any features within their broad oceanic tracts and are thus unrealistic when compared with modern oceans that are littered with islands and archipelagos. Cocks and Fortey (1982, p. 466, see also 1990) dismissed the role of islands, noting that they were of little importance in the reconstruction of continental configurations. We consider that major sources of significant information are stored in accreted or displaced terranes that developed seaward of miogeoclines and are now included within the Appalachian–Caledonide collages.

Subduction zones on the opposite sides of the Iapetan region were shown in the Middle–Late Ordovician map of Scotese and McKerrow (1991, fig. 5) but their slightly earlier revised and updated set of maps (Scotese and McKerrow, 1990) showed a chain of islands only on the southern margin of Laurentia, and this island arc was portrayed through three intervals of geological time: Tremadoc, Arenig and Llandeilo–Caradoc (op. cit. fig. 6). No points on this chain were constrained by palaeomagnetic data and the chain itself had

disappeared by the late Ordovician. Subduction complexes on the opposite side of the Iapetus basin were apparently devoid of islands (see also McKerrow et al., 1991). Similarly Cocks and McKerrow (1993) appended an arcuate island chain to marginal North America; this is the basis for their unified Bronson Hill-Tetagouche-Lushes Bight Island Arc. Neuman (1984) provided a more realistic model of the Iapetus ocean basin punctuated by islands similar to modern ocean configurations such as the present Atlantic (Williams, 1984).

The four statistical analyses presented reveal valuable and broadly consistent palaeogeographic data. The statistical analyses emphasize that the disparate Celtic sites have many genera in common and confirm the integrity of the Celtic group of faunas; nevertheless many of the Celtic assemblages also differ from the platform faunas in having relatively high proportions of endemic genera restricted to single sites. The geological settings together with available palaeomagnetic information for the Celtic sites confirm positions in a high-mid latitude belt seaward of Gondwana (Fig. 4). Some Celtic sites also have apparently mixed faunal affinities; but this effect is not only restricted to Caledonian faunas (see Newton, 1988 for similar problems in Mesozoic faunas from the Western Cordillera of North America).

Several Caledonian terranes with early Ordovician Celtic faunas are characterized by Scoto-Appalachian (Laurentian marginal) faunas during the mid and late Ordovician. For example on Newfoundland, the late Arenig New World Island sequences in the Exploits subzone of the Dunnage terrane, contain diverse Celtic-type faunas. The upper Llandeilo Cobbs Arm Limestone, however, contains elements of the Scoto-Appalachian fauna (McKerrow and Cocks, 1986). Similarly in the Irish Iapetus suture zone the Grangegeeth terrane is characterised by early Ordovician Gondwanan graptolite faunas but the Caradoc brachiopod and trilobite faunas are more typical of Scoto-Appalachian assemblages (Harper and Parkes, 1989; Owen et al., 1992).

Several recent palaeodrift models have discussed the rapid movement of Laurentia from high to low latitudes during the late Precambrian and early Palaeozoic. These models involve a late

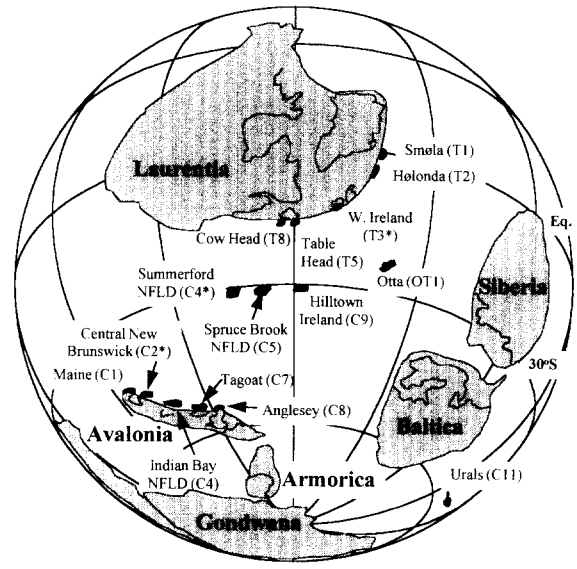

Fig. 4. Early–mid Ordovician palaeogeographic reconstruction based on both faunal and palaeomagnetic data. The positions of the major Iapetus-bordering continents are based on palaeomagnetic compilations of Van der Voo (1988), Torsvik and Trench (1991), Torsvik et al. (1992) and Mac Niocaill and Smethurst (1994). Intra-Iapetan terranes marked with asterisks are those where palaeolatitudes have been obtained in palaeomagnetic studies and include results from Morris et al. (1973), Van der Voo et al. (1991) and Liss et al. (1993).

Precambrian Laurentian breakout from Rodinia leaving a rump Gondwana (Dalziel, 1991; Dalziel et al., 1994; Dalla Salda et al., 1992). Rapid movement of Laurentia from near polar to equatorial latitudes occurred during the latest Precambrian and early–mid Cambrian, when the continent migrated from high to equatorial latitudes. High velocities, averaged at 16 cm yr^{-1} have been calculated over an interval of 50 Ma for this rapid northward drift of Laurentia (Meert et al., 1994). Similarly, Baltica moved at rates of over 10 cm yr^{-1} during its migration from high to low latitudes during the Ordovician (Torsvik et al., 1992). During the mid Ordovician, Scoto-Appalachian faunas entered the Oslo Region and Central Baltoscandian confacies belt (Harper, 1986). Although the movements of smaller intra-Iapetus terranes have yet to be tracked by palaeomagnetic methods, the simplest scenario involves similar relatively rapid northward migrations

during the Ordovician; cross-latitude movements were indicated by changing provincial signals.

In conclusion, during the early Ordovician, Celtic faunas occupied two main types of terrane: (1) islands and microcontinents associated with Avalonia, probably derived from Gondwana in the late Cambrian and early Ordovician and (2) a variety of arc settings originating both within and marginal to the southern part of the Iapetus Ocean but accreted to Laurentia later in the Ordovician. Contrary to Cocks and McKerrow (1994) there is no evidence to suggest that the Celtic brachiopod faunas ever colonized Laurentian or Laurentian-derived terranes during the early Ordovician. Celtic faunas have useful biogeographic signatures of considerable relevance to the reconstruction the Iapetus Ocean and its ancient margins.

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