

Early Ordovician rhynchonelliformean brachiopod biodiversity: comparing some platforms, margins and intra-oceanic sites around the Iapetus Ocean

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Abstract: During the Arenig–Llanvirn interval a series of radiations across all the major clades, established the Brachiopoda as a major component of the Palaeozoic benthos. Radiations on Baltica and Laurentia during the Arenig formed the basis for two distinct biogeographical provinces with contrasting articulated brachiopod faunas. These platform provinces were supplemented by the marginal Celtic and Toquima-Head provinces; the latter included both marginal and intra-oceanic island sites. These marginal and intra-oceanic sites may have served as both ‘cradles and museums’ alternately providing sources for radiations on the platforms and refugia for otherwise relict taxa. Such terranes also partitioned oceanic circulation patterns within the Iapetus Ocean and provided mosaics of rapidly changing, nearshore unstable environments. In contrast to later Ordovician brachiopod faunas, many early Ordovician genera are reported from only one or two sites in the Iapetus region; narrow geographical ranges are characteristic of many taxa. The strong biogeographic differentiation at the generic level is less marked at the familial and higher levels suggesting a series of late Cambrian and early Ordovician migrations prior to the more regional development of the Arenig–Llanvirn brachiopod biofacies across the Iapetus terranes. However, the origination of many brachiopod taxa apparently occurred outside the Iapetus region suggesting that the initial stages of the Ordovician radiations here were first spiked by a series of immigrations.

The Ordovician brachiopod faunas of the Greater Iapetus Region include arguably the best-documented assemblages of the period. The faunas are biostratigraphically and taxonomically well constrained while their palaeo-environmental and palaeogeographical settings have been significantly refined during the last 30 years. Recent reviews have emphasized the resolution of current palaeogeographical models (e.g. Cocks 2000, 2001) and the quality of faunal data available for the early Ordovician (e.g. Harper *et al.* 1996). Harper & Sandy (2001) have placed Ordovician provinciality within the context of the changing biogeographical patterns of the entire Palaeozoic. During the early Ordovician, brachiopod provinciality was marked in comparison with subsequent Silurian faunas (Boucot 1990); comparative provinciality was, however, re-established during the mid-Devonian (Boucot 1993, 1999). This enhanced biogeographical differentiation was associated with high diversities which together provided opportunities to test palaeogeographical models for the mid-Devonian (McKerrow *et al.* 2000), similar to those provided by early Ordovician faunas. But although

data for Lower Ordovician faunas are characteristically dispersed and uneven, current information is sufficient to frame and test various models for the early Ordovician radiation within the Iapetus region.

Ordovician radiation

The Ordovician radiation is now firmly recognized as one of the most significant events in metazoan history (Droser & Sheehan 1997). The detailed anatomy of the radiation is currently an area of intense investigation. New Bambachian megaguilds (Droser *et al.* 1997), associated with deep burrowing and complex tiering, are features of the radiation together with the establishment of new community types as well as the appearance of stromatoporoid reef structures (Bottjer *et al.* 2001). In addition, the capacity of each Bambachian megaguild was expanded to their Palaeozoic levels during a relatively short period of time.

Initial detailed research, mainly in the Great Basin of Laurentia (see Droser & Sheehan 1997 for summary), has indicated the importance of the faunal turnover at the base of the Whiterock

(equivalent to a level within the middle Arenig and close to the base of the Volkhov). Here shell beds are reported to have escalated in thickness with brachiopods rather than trilobites becoming the dominant components of such accumulations (Droser & Sheehan 1997) together with a shift from echinoderm to bryozoan-dominated hardground palaeocommunities; the diversification of echinoderms associated with soft substrates occurred later. Although trilobites were the major component of the Cambrian Evolutionary Fauna, a further group of families, the Whiterock Fauna, provided a mid-Ordovician expansion of the trilobite clade mainly at low latitudes (Adrain *et al.* 1998). Two diversification events within the Brachiopoda were signalled by Droser & Sheehan (1997, fig. 6): the continued diversification of 'early' brachiopods during the mid-Ibex (late Tremadoc) and a second diversification during the Llanvirn. Within the Great Basin the development of new orthid community types characterizes the radiation (Bottjer *et al.* 2001).

Brachiopod diversifications

A number of step-wise radiations across the phylum Brachiopoda during the early to mid-Ordovician helped set the agenda for much of level-bottom life on the Palaeozoic seafloor (Harper *et al.* 2001). By the late Ordovician, with the exception of some of the more bizarre upper Palaeozoic taxa such as the lyttonioids and richthofenioids, the main ecogroups had evolved characterized by a variety of morphological adaptations (Harper & Wright 1996).

The organophosphatic linguliformeans had already diversified during the mid- and late Cambrian and represented an integral part of the Cambrian Evolutionary Fauna. During the Tremadoc–early Arenig, morphological and taxonomic diversity was restored following a marked decline in the latest Cambrian; during the early Ordovician the low-diversity lingulide communities retained a dominant position in nearshore environments on clastic shelves. The shallow-water epibenthic linguloideans were mainly replaced by infaunal linguloideans, discinoideans and bivalves during the Llanvirn. Radiation of the micromorphic acrotretides and siphonotretides, during the early and mid-Ordovician, provided the most significant additions to lingulate biodiversity at this time; moreover members of the group show a clear shift to more basal environments (Bassett *et al.* 1999a). Concomitantly the craniformean

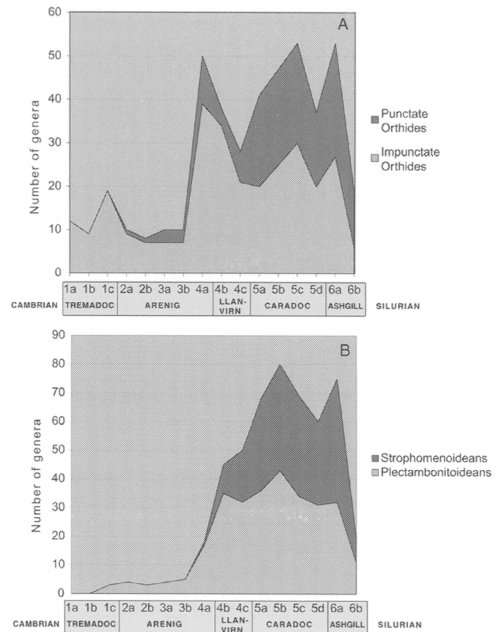


Fig. 1. Global biodiversity curves for the two main components of the early Ordovician brachiopod fauna: (A) Orthida (the two suborders Orthidina and Dalmanellidina are indicated); (B) Strophomenida (the two superfamilies Strophomenoidea and Plectambonitoidea are indicated). Data are from the revised *Treatise, Part H* (Williams *et al.* 2000).

brachiopods developed rapidly, with the morphological differentiation of the craniids and the trimerellides; both taxa significantly expanded their geographic ranges during the mid-Ordovician (Popov *et al.* 1999).

Rhynchonelliformean brachiopods represent one of the most important components of the developing Palaeozoic Evolutionary Fauna; distinctive community structures and a characteristic onshore–offshore biofacies distribution were established by the mid-Ordovician during late Arenig–early Llanvirn radiations. Among the deltidodont rhynchonelliformeans, the orthides and strophomenides (Fig. 1) diversified into deeper water environments during the mid-Ordovician, the latter occupying niches within a soft-substrate biota; the pentamerides evolved rapidly at low latitudes globally, often forming the core of communities associated with carbonate build-ups. The origin of the cyrtomatodont articulation in the rhynchonellides during the Llanvirn formed the basis for another series of step-wise, but more

restricted, radiations during the mid- to late Ordovician (Bassett *et al.* 1999b); ecological competition and displacement both within the cyrtomatodonts and between the deltidodonts and the Caradoc in the tropics, whereas the athyridides and the spiriferides were not numerically significant components of the Ordovician radiations. The pentamerides and spire-bearers were to form the basis of subsequent radiations during the early Silurian, commonly associated with carbonate environments (Rong & Harper 2000; Harper & Rong 2001).

During the early Ordovician the contrasting escalation of the pedunculate orthides and the recumbent strophomenides was the most marked amongst the rhynchonelliformeans. Global datasets suggest initial (late Arenig–early Llanvirn) radiations were dominated by the orthides whereas the strophomenides first diversified during the early Llanvirn but most markedly during the Caradoc (Harper *et al.* 1999a).

The ‘Greater Iapetus Region’

The Iapetus Ocean was bordered by a number of platform provinces and punctuated by a variety of marginal and oceanic terranes. This sector of the Earth’s crust has provided a critical field area for the understanding of the dynamics and evolution of Early Palaeozoic brachiopod faunas. Terrane models for most parts of the region are relatively far advanced (Harper 1998) and the extent of most continents and their margins are now well defined. The margins of, for example, Avalonia (Cocks *et al.* 1997) and Baltica (Cocks & Fortey 1998) have been described in detail.

Perspectives on the development of the Iapetus Ocean system have changed markedly during the past three decades. The innovative orthogonal model for oceanic opening and closure (Wilson 1966), which has formed the basis for the Wilson Cycle, indicated the separation of North American and European brachiopod faunas during the Early Palaeozoic. Statistical analyses of a range of brachiopod faunas mainly associated with the Iapetus region (Williams 1969, 1973) suggested a number of provinces existed within the Greater Iapetus region. Nevertheless, as closure of the Iapetus Ocean progressed sequentially less mobile organisms were able to cross a narrowing seaway (McKerrow & Cocks 1976); for example, many brachiopod genera were present on both sides of the ocean by the Caradoc whereas

similar brachiopod species were present in both Europe and North America during the Ashgill (McKerrow & Cocks 1976). During the early to mid-1980s a series of more complex models was developed for the ocean emphasizing, for example, the role of decreasing endemicity with depth (Cocks & Fortey 1982) and the participation of a more complex system of continents, including Laurentia, Avalonia and Baltica, within the cycle (Cocks & Fortey 1982; Fortey & Cocks 1986). Each continent, and to a lesser extent its margins, contained a distinctive early Ordovician brachiopod fauna defining a province and suggesting oceanic separation from coeval continental areas; distinctions become less clear during and following the early Caradoc *gracilis* transgression.

Neuman, in a series of papers (Neuman 1972, 1984; Neuman & Harper 1992), added greater realism to these palaeogeographical reconstructions with the addition of islands and archipelagos into otherwise barren oceanic tracts, based on data initially from the Appalachians. The importance of marginal and oceanic sites was confirmed and developed, on the basis of data from Scandinavia, by Bruton & Harper (1981, 1985). More focused statistical analyses of the brachiopod faunas from around and within the Iapetus Ocean (Neuman & Harper 1992; Harper *et al.* 1996) confirmed the status of the platform provinces but also flagged groups of marginal and ocean biotas associated with islands composed of both basement and volcanic material. For example, the Toquima-Table Head faunas developed circumferal and seaward of Laurentia at low latitudes whereas the Celtic faunas formed a high-latitude belt marginal to Gondwana (Harper *et al.* 1996). These models have been tested by seriation, using simulated annealing (Ryan *et al.* 1999). This algorithm clearly recognized clusters of associated faunas but was less successful in clarifying the relationships between the groupings. Possibly many of the early Ordovician high-latitude faunas were more isolated from coeval faunas elsewhere having fewer widespread taxa and more endemics than those faunas from low latitudes. That situation contrasts with the pattern for the latest Ordovician, when a clearer latitudinal gradient across more cosmopolitan faunas is apparent (Ryan *et al.* 1999).

Palaeogeographical templates for the early Ordovician of the Iapetus region have increasingly emphasized the role of marginal and oceanic tracts now entrained as a variety of terranes within the Appalachian–Caledonian mountain belt. The biological importance of these sites has been specified in a number of

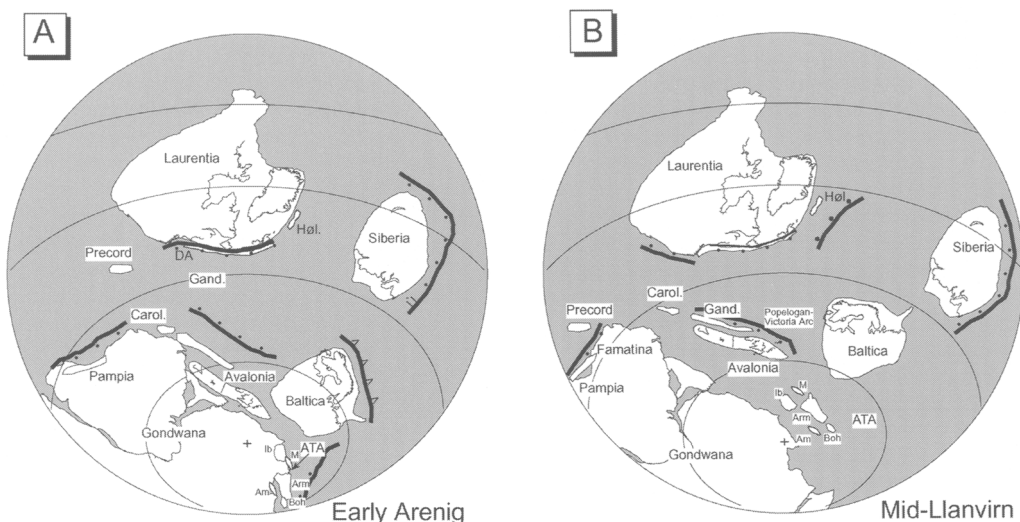


Fig. 2. Palaeogeographical reconstructions for (A) early Arenig and (B) the mid-Llanvirn. The early Arenig to mid-Llanvirn interval highlights the development of a series of peri-Gondwanan terranes, many forming the basis for the Celtic Province. Laurentia has been positioned according to the palaeomagnetic compilation of Mac Niocaill & Smethurst (1994); Baltica and Gondwana after Torsvik *et al.* (1996); Siberia after Smethurst *et al.* (1998); Avalonia has been palaeolatitudinally positioned after Mac Niocaill (2000). The locations of intra-Iapetus arcs are based on Mac Niocaill *et al.* (1997) and van Staal *et al.* (1998). Abbreviations used are as follows: Høl, Hølonða; DA, Dashwoods block; Precord, Precordillera; Gand, Gander terrane; Carol, Carolina terrane; ATA, Armorican Terrane Assemblage, the individual elements being as follows; Ib, Iberia; M, Meguma; Am, Armorica; Boh, Bohemia [= Perunica]; Am, Alpine Massifs.

contributions (Neuman 1972, 1976; Bruton & Harper 1981, 1985; Harper *et al.* 1996); roles as centres for speciation, refugia during regression and stepping stones along migrational routes have been proposed. A number of islands clearly changed their faunal affinities during cross-latitude movement (Owen *et al.* 1992).

The addition of realistic ocean-circulation patterns (Christiansen & Stouge 1999) has enhanced understanding of the mechanics of the Iapetus oceanic system. Predicted warm- and cool-water gyres may have also provided a partition between the low-latitude Laurentian and Toquima-Table Head faunas and those at high latitudes associated with Avalonia, Gondwana and the Celtic group of faunas. The presence of island chains within the Iapetus Ocean may have helped develop the interface between the two current systems.

Platforms, margins and intra-oceanic sites

The early Ordovician Iapetus region contains a spectrum of continental and ocean terranes in a variety of tectonic settings (Fig. 2). The larger platform areas of Laurentia, Baltica and

Gondwana are supplemented by marginal sites such as the Oslo region and Western Newfoundland and microcontinents such as Avalonia and Perunica. Although there are abundant brachiopod data from many of these sites there are few regional databases. Preliminary databases, at the generic level, have been established here as an initial test for a number of hypotheses regarding the early Ordovician brachiopod radiation. The East Baltic (Harper & Hints 2001), Morocco (Havlíček 1971), Welsh Basin (Lockley 1983) and the Prague Basin (Havlíček 1976, 1998) have been used as proxies for the Baltic, Gondwanan, Avalonian and Bohemian biogeographic units. Nevertheless such areas, for example Baltica, contain a range of facies, and initial studies (e.g. Jaanusson 1973, 1976; Harper 1986) have emphasized that the various facies belts reacted in different ways to changing latitude and waves of immigrants.

Critical to the early Ordovician radiations is the development of marginal and intra-oceanic terranes and their roles in the development, dispersal and survival of taxa, the partition of oceanic circulation patterns within the Iapetus Ocean and the provision of mosaics of rapidly changing, nearshore unstable environments.

Harper *et al.* (1996) identified nearly 20 early Ordovician intra-oceanic and marginal sites within the Iapetus region. A range of multivariate analyses confirmed the coherence of the Toquima-Table Head (low latitude) and Celtic (high latitude) groups of faunas. A number of authors have emphasized the biological importance of these sites (Neuman 1972, 1984; Bruton & Harper 1981, 1985; Fortey 1984; Harper 1992; Harper *et al.* 1996). These marginal and intra-oceanic sites may have served as both 'cradles' and 'museums' alternately providing sources for radiations on the platforms and refugia for otherwise relict taxa.

The early Ordovician rhynchonelliformean brachiopod fauna is dominated by billingsellides (including the clitambonitidines) and orthides. Analysis of the distribution of these taxa across the Celtic and Toquima-Table Head belts, targeting the marginal and intra-oceanic sites, suggests that 32% ($N = 45$) of the brachiopods at these sites were endemic to either a single locality or to a group of adjacent localities (Fig. 3). Moreover 30% of the taxa represent the first occurrence of a genus and 25% the last. Only 13% of the occurrences represent within-range spikes. The available data tend to confirm the role of these sites as the locus for endemics and possible roles as cradles and refugia within the Iapetus Ocean system.

Early to mid-Ordovician development of the Iapetus brachiopod fauna

The initial break-up of the northern margins of Gondwana and the arcs around Laurentia created a diversity of terranes (Fig. 2). This disparate array of terranes formed an ideal environment for the development of gamma diversity (inter-province) across the Iapetus Ocean. The isolation of these terranes was enhanced by the late Arenig regression, when there was a concentration of island biotas (Fortey 1984). Many islands and archipelagos may have been emergent, with narrow shelf areas with relatively small populations. The majority of brachiopod faunas inhabited shallow-water, nearshore environments, probably no deeper than Benthic Assemblage zones 3–4 (Cocks 1996). By comparison with the non-articulates, dispersion of the rhynchonelliformeans was relatively limited; the latter probably possessed relatively short, nektobenthic larval stages restricting the rapid spread of many articulated groups (Harper & Sandy 2001).

Subsequent transgressions promoted migration and the subsequent colonization of the shelf

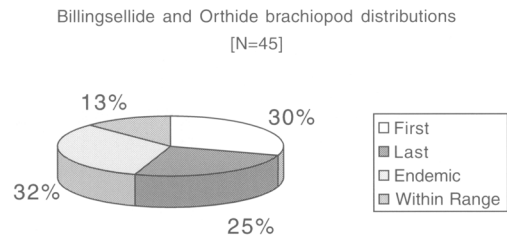


Fig. 3. Proportions of endemics, first, last and mid-range occurrences of billingsellide and orthide genera across the marginal Celtic and Table Head faunas. Data are modified from Harper *et al.* (1996).

areas of the platform provinces (Figs 4 and 5). These mechanisms provided for the escalation of alpha diversity (within-community) as established regional palaeocommunities were supplemented by immigrants. These diversifications were most marked in shallow-water palaeocommunities, for example in the inner, nearshore facies of Avalonia and the Baltic province (Harper & Hints 2001). This diversity spike is most obvious along the margins of Baltica, for example in the Oslo Region (Harper 1986). The faunas were dominated by larger pedunculate orthidine brachiopods. In addition to sea-level changes the approach of terranes, particularly from the peri-Gondwanan region, may have provided additional taxa to participate in these radiations (Holmer *et al.* 2000). This process of integration has also been suggested for the development of the Celtic terranes (Bruton & Harper 1985).

The most marked radiations, however, occurred during the Caradoc (Figs 4 and 5). This diversity spike is clear in global databases but is also obvious in the regional datasets for Avalonia, Baltica, Gondwana and Perunica. These later diversifications may have been associated with beta diversity changes as a variety of new palaeocommunities inhabited deep-water environments with a greater dominance of the recumbent strophomenides (Harper *et al.* 1999b; Rong *et al.* 1999).

Comparison of early and late Ordovician brachiopod biofacies

In contrast to later Ordovician brachiopod faunas, a large number of early Ordovician genera are reported from only one or two sites in the Iapetus region; narrow geographical ranges are characteristic of many early Ordovician taxa (Fig. 6). The distribution patterns of these taxa show a positive skewness, suggesting

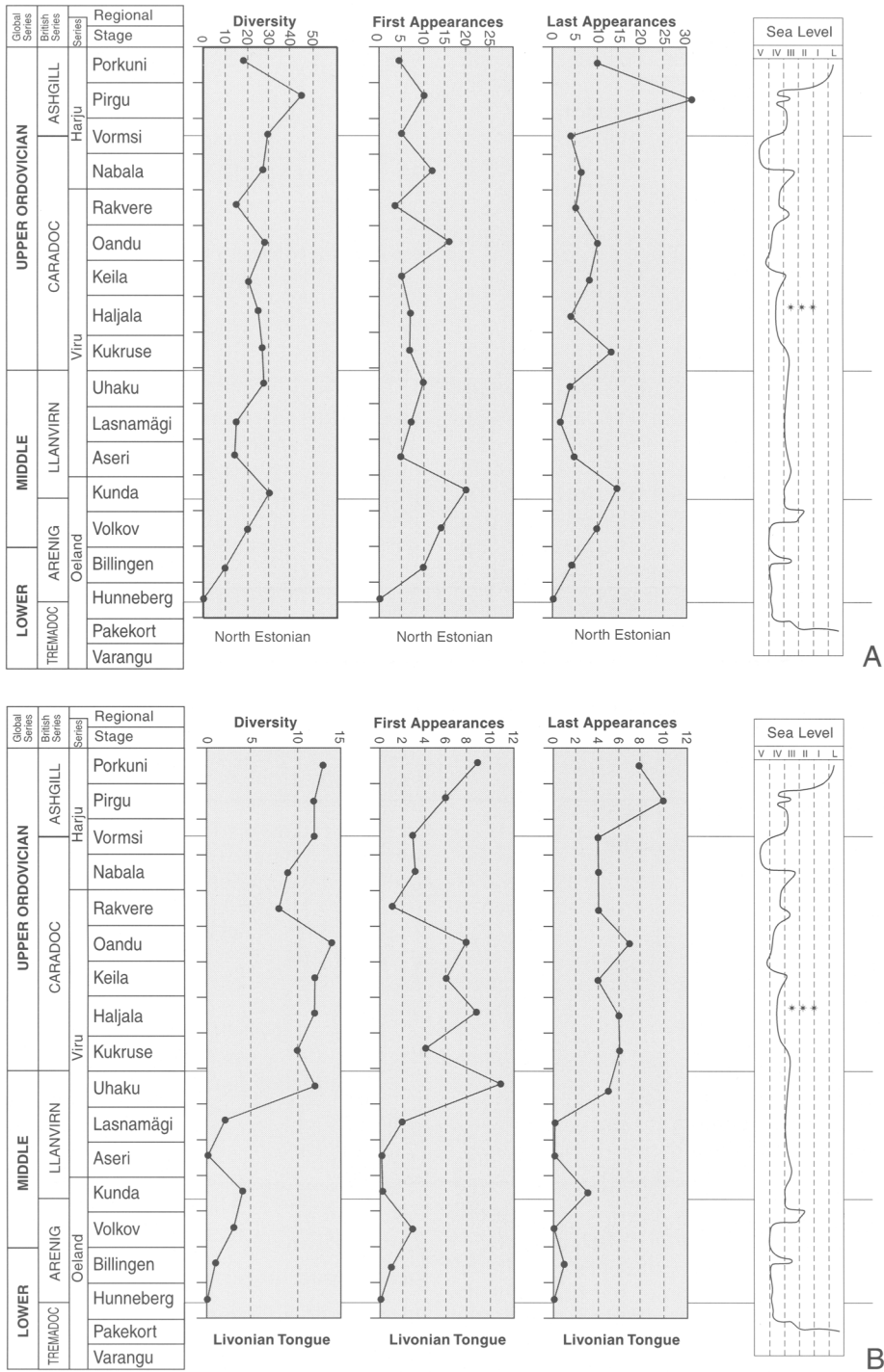


Fig. 4. Diversity profiles (unstandardized numbers of genera) through (A) the shallow-water North Estonian confacies belt and (B) the deeper-water Livonian Tongue (equivalent to the Central Baltoscandian confacies belt of Jaanusson 1976). Sea-level stands are calibrated in terms of Benthic Assemblage zones. Data are modified from Harper & Hints (2001).

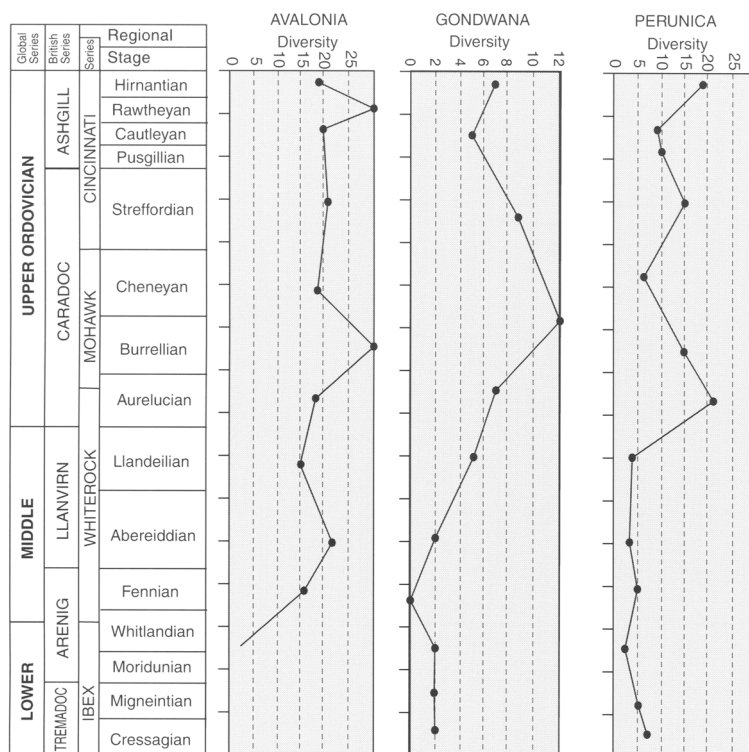


Fig. 5. Diversity profiles (unstandardized numbers of genera) from Avalonia (based on sources in Lockley (1983) and some additional data), part of the Gondwanan margin (based on Havlíček 1971) and Perunica (based on sources in Havlíček 1998).

that the majority of taxa are in fact reported from only one or two sites. This pattern contrasts with that for the late Ordovician where a less skewed distribution indicates fewer endemic taxa and more widespread genera. Seriation of these sites has emphasized these contrasting spatial patterns (Ryan *et al.* 1999). Early Ordovician faunas were successfully arranged into cohesive sets representing the main provincial groupings; the links between these groups were less clear. Faunal gradients are much clearer during the late Ordovician when a series of overlapping provinces can be recognized from the high-latitude Bani province, through the Kosov province to the low-latitude Edgewood province (Rong & Harper 1988; Owen *et al.* 1991; Ryan *et al.* 1999).

Conclusions

This study emphasizes the role of marginal and oceanic sites in the Ordovician radiation. Intra- and marginal Iapetus Ocean terranes acted as

both cradles and museums for brachiopod taxa during the early Ordovician (late Arenig to early Llanvirn) phases of the diversification. Terrane fragmentation, particularly at high latitudes, was essential for the generation of an initial gamma diversity. Diversification, however, was more pronounced when individual platform communities first expanded in size with the development of alpha diversity, during the Llanvirn. These diversifications may have helped propel the offshore movement of communities during the Caradoc as beta diversity intensified.

During the early Ordovician many brachiopod families were relatively widespread: biogeographical signals provided by generic distributions. This suggests that the origins of many Ordovician brachiopod families may be tracked back into the Cambrian outside the Iapetus region. The circum-Iapetus platforms and margins provided opportunities but not the origins for a mid-Arenig radiation. The early Ordovician dispersion of the continents and associated outboard terranes provided the

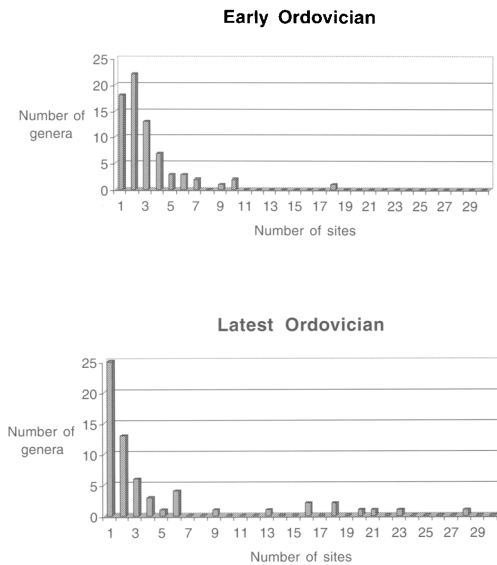


Fig. 6. Comparison of some of the distributional properties of early and late Ordovician brachiopod faunas. Data are modified from sources in Harper *et al.* (1996) and Owen *et al.* (1991).

conditions for geographic isolation and speciation. Migration of taxa onto the platforms during the early Llanvirn generated the first increases in within-community diversity that may have driven the development of new, particularly deeper-water, community types especially during the Caradoc.

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