Brachiopods: Cambrian-Tremadoc precursors to Ordovician radiation events

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Notes

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Abstract: Brachiopod-dominated palaeocommunities incorporating a structure typical of faunal groups within the Palaeozoic Evolutionary Fauna were already present in North and East Gondwana and associated terranes as early as the mid-Cambrian, confined exclusively to shallow marine, inshore environments. The late Cambrian and Tremadoc record of these faunas is incomplete, because of pronounced global sea-level lowstand and subsequent break-up and destruction of the Cambrian Gondwanan margin. It is likely, however, that those groups later forming the core of the Palaeozoic Evolutionary Fauna evolved originally in shallow-water environments of low-latitude peri-Gondwana, and dispersed widely when favourable ecological conditions developed. Conspicuous sea-level rise through the early to mid-Arenig provided newly available habitats in the expanding epeiric seas, where the new faunas evolved and diversified by the mid-Ordovician, when rapid drift separated the early Palaeozoic continents. Relatively short-lived precursor and transitional brachiopod assemblages can be identified on most of the main palaeocontinents prior to the Ordovician radiation of the Palaeozoic Evolutionary Fauna.
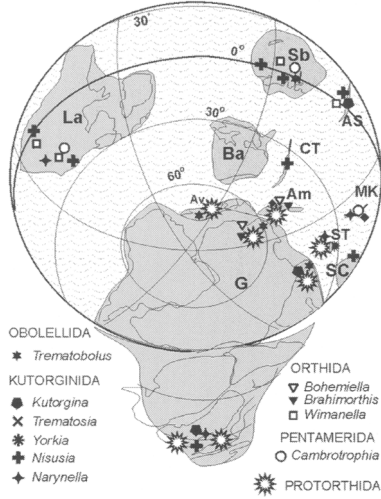
The Ordovician evolutionary radiation of marine metazoans was the second significant biodiversification event in Phanerozoic biotic history, following the origin and explosive radiation of skeletonized faunas at the beginning of the Cambrian. Ordovician events resulted not only in a significant global increase of taxonomic diversity, but also in substantial changes of benthic community structure on marine shelves, where the dominant trilobite–lingulate brachiopod associations of the Cambrian Evolutionary Fauna were replaced mainly by more advanced and structured benthic assemblages of the Palaeozoic Evolutionary Fauna, dominated by filter-feeders and especially by rhynchonelliformean brachiopods, bryozoans and pelmatozoan echinoderms (Sepkoski 1981, 1995). There was substantial overlap between these two biotopes in the earlier Ordovician, but generally on some major Lower Palaeozoic plates, including Laurentia, Baltica and Siberia, fully developed communities of the Palaeozoic Evolutionary Fauna have little in common with transitional faunas in which direct descendants of local Cambrian lineages predominate, or where transformation of the assemblages occurred almost abruptly so that newly emerging benthic faunas had little evident linkage with their Cambrian and early Ordovician predecessors (Sokolov 1982; Sepkoski & Sheehan 1983;

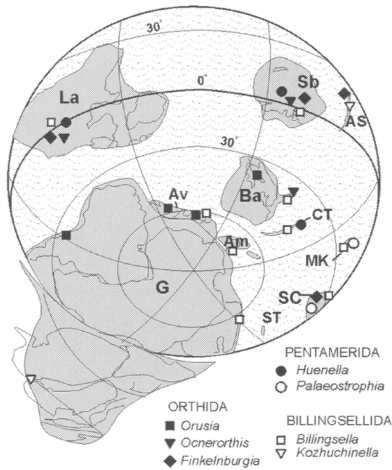Popov 1993; Patzkowsky 1995).

Rhynchonelliformean brachiopod assemblages that we identify and name below as transitional to the Palaeozoic Evolutionary Fauna (e.g. *Clarkella* Fauna and various syntrophinidine and *Tritoechia–Protambonites* associations) require particular discussion and definition. They already formed trophic structures (dominance of suspension-feeders) and tiering (presence of at least two levels) characteristic of the Palaeozoic Fauna, but the taxonomic composition of brachiopod genera and families retains distinct links to the ancestral Cambrian faunas, whereas their relationship with succeeding brachiopod faunas is less evident. These transitional assemblages also lack ostracodes and bryozoans, which are usually important components of Ordovician biotopes.

The nature of faunal patterns and replacement was especially significant on the shallow shelves of Gondwana and its closely associated marginal terranes, where the development of distinctive trophic and taxonomic community structures was rooted deep in the Cambrian. This suggests that increased faunal exchange between palaeoplates at the beginning of the Ordovician could have been an important factor in triggering subsequent changes in community structure more widely across marine shelves,
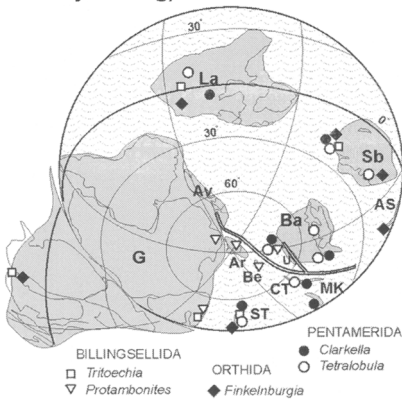
A. early Middle Cambrian (Amgaian)

OBOLELLIDA
* Trematobolus

KUTORGINIDA
● Kutorgina
✕ Trematosia
✳ Yorkia
✚ Nisusia
✚ Narynella

ORTHIDA
▽ Bohemiella
▼ Brahimorthis
□ Wimanella

PENTAMERIDA
○ Cambrotrophia

✺ PROTORTHIDA

B. late Cambrian

PENTAMERIDA
● Huenella
○ Palaeostrophia

ORTHIDA
■ Orusia
▼ Ocnerorthis
◆ Finkelnburgia

BILLINGSELLIDA
□ Billingsella
▽ Kozhuchinella

C. early Ordovician (late Tremadoc-early Arenig)

BILLINGSELLIDA
□ Tritoechia
▽ Protambonites

ORTHIDA
◆ Finkelnburgia

PENTAMERIDA
● Clarkella
○ Tetralobula

resulting in the significant increases in bio-diversity that characterize the Ordovician Period.

This chapter traces major steps in the construction of Cambrian rhynchonelliformean (organocalcitic shelled) brachiopod assemblages and their environmental settings, and identifies their main biogeographical patterns (Fig. 1) together with the possible causes of change that resulted in their subsequent geographical and environmental expansion. We have elsewhere (Bassett *et al.* 1999*a*) documented patterns of evolutionary origins and extinctions in organophosphatic shelled 'inarticulated' linguliformean brachiopods through the Cambrian–Ordovician, so an additional aim here is to add comparative data and interpretations for the whole phylum. In identifying these distinctive pre-Palaeozoic Evolutionary Fauna precursor and transitional assemblages, we use the term 'Fauna' to embrace biotas containing several closely related brachiopod assemblages in a particular region, and the term 'Association' to include low-diversity biotas generally in a particular environmental setting (Fig. 2).

Cambrian brachiopod-dominated faunas

Several short-lived rhynchonelliformean groups, such as the Obolellata and Kutorginata, were distinctive components of the Cambrian Evolutionary Fauna, and were among the first

Fig. 1. Biogeographical distribution of characteristic rhynchonelliformean brachiopods through the Cambrian to early Ordovician interval. Palaeogeographical reconstructions modified after Torsvik (1998). During the mid-Cambrian, protorthides had a peri-Gondwanan distribution (**A**). In the late Cambrian (**B**) and early Ordovician (**C**), pentameride distribution was confined mainly to low and mid-latitudes, whereas North Gondwana was characterized by an abundance of billingselloideans and polytoechioideans. The reconstruction for the early Ordovician (**C**) shows the possible position of a newly initiated spreading zone (double line) resulting from the separation of the Uralian margin of Baltica and the separation of Avalonia. Am, Armorica; AS, Altay–Sayany island arc systems; Av, Avalonia; Ba, Baltica; Be, Bohemia (Perunica); CT, Chingiz–Tarbagatay island arc (now eastern Kazakhstan, presumably active margin of Baltica in the Cambrian–early Ordovician); G, Gondwana; La, Laurentia; MK, Malyi Karatau (Aisha-Bibi) terrane; S, Siberia; ST, South Tien Shan island arc systems; SC, South China; U, East Uralian (Mugodzhary) microcontinent.

Fig. 2. Succession and environmental distribution of distinctive Cambrian–early Ordovician rhynchonelliformean brachiopod assemblages across different palaeoplates.

animals to form distinctive communities with essentially the same trophic and environmental characteristics as brachiopod-dominated communities of the Palaeozoic Evolutionary Fauna. The kutorginides *Kutorgina* and *Trematosia* and the obolellide *Trematobolus* formed the oldest known rhynchonelliformean brachiopod-dominated assemblages (Figs 1, 2). These assemblages were almost invariably of low taxonomic diversity, generally comprising or dominated by a single species, living in low-energy, shallow shelf environments affected by storm events, on low-latitude carbonate platforms usually in or adjacent to areas of hypersaline carbonate accumulation. Two illustrative examples are the marginal part of the Turukhansk–Irkutsk facies belt on the Siberian Plate, characterized by deposition of evaporites (Pelman 1992), and the Burj Formation on the eastern Dead Sea coast of Jordan together with the closely adjacent and coeval Nimra Formation of the southern Negev desert, Israel (Cooper 1976; and our unpublished studies), deposited on northern peri-Gondwana. These successions also contain the oldest known brachiopod coquinoid concentrations, usually in storm beds, which in some cases are of remarkable abundance and extent (Powell 1989). With the extinction of obolellides and kutorginides at the end of the early Cambrian, rhynchonelliformean brachiopod-dominated assemblages and shell bed accumulations declined during the mid-Cambrian in Siberia and Laurentia, but they remained a characteristic feature of shallow shelf environments across Gondwana and peri-Gondwanan regions, as discussed below.

By mid-Cambrian times, benthic palaeocommunities with a structure and dominant taxonomic composition typical of the Palaeozoic Evolutionary Fauna occurred widely across Gondwana (Middle East, Australia) and neighbouring areas, where they were confined exclusively to shallow, inshore marine environments (e.g. Cooper 1976; Roberts & Jell 1990). Two characteristic assemblages can be recognized.

The first is named here as the Protorthide Fauna (Fig. 2), comprising a medium-diversity association of archaic orthidines and protorthides and often including some obolellide, kutorginide and linguliformean taxa (Fig. 1A). We interpret protorthides as a stem group to pentamerides and clitambonitoideans (unpublished studies; see also Williams *et al.* 1996). This fauna embraced a wide variety of mid-Cambrian brachiopod associations containing characteristic protorthide components (e.g. *Protorthis* in New Brunswuck; *Jamesella* in Bohemia, Spain and North Africa; *Glyptoria* and *Psiloria* in

Israel and Kyrgizstan; *Arctochedra* in Kyrgizstan and Australia, etc.). Nearly all known protorthide occurrences (Fig. 1A) except Kyrgizstan and Alaska were parts of Gondwana through the Cambrian (Dalziel 1997; Torsvik & Rehnström 2001). Lower to Middle Cambrian deposits of South Tien Shan in Kyrgizstan probably originated in an adjacent peri-Gondwanan island arc (Fig. 1A; Holmer *et al.* 2000). The occurrence of the protorthide *Arctochedra* in Alaska (Cooper 1936) does not seemingly indicate expansion of the group to Laurentia, but in our view was probably related to an exotic terrane of uncertain origin.

The second assemblage is defined here as the *Billingsella* Association (Fig. 2). It is a low-diversity association dominated by *Billingsella* itself or by related billingsellid genera (e.g. *Cymbithyris*), and shows patterns characteristic of opportunistic life strategies (Alexander 1977), e.g. limited areal distribution, high density clustering in thin, widespread isochronous horizons, overwhelming numerical dominance in the assemblage and remarkable abundance in atypical facies, mostly related to nearshore depositional environments. Billingsellids often formed inshore coquinoid accumulations. The most spectacular examples known to us are extensive shell beds in the Upper Cambrian Kyjandy Formation of north-central Kazakhstan (Nikitin 1956) and in the Middle to Upper Cambrian Derenjal Formation of east-central Iran (Fig. 3a). We interpret billingsellides as the ancestral stock of the Strophomenata including strophomenides, orthotetides and polytoechioideans (see also Williams *et al.* 1996). The *Diraphora* Association is a generally monospecific assemblage which immediately precedes the *Billingsella* Association in regions such as Novaya Zemlya (Fig. 2; Popov 1984); the ecological setting of both these associations appears to be very similar.

The Protorthide Fauna was confined exclusively to the mid-Cambrian of peri-Gondwana, whereas the *Billingsella* Association became almost cosmopolitan in the late Cambrian (Fig. 1). The rhynchonelliformean taxa in both assemblages can be traced phylogenetically into Ordovician descendants, and both the Protorthide Fauna and *Billingsella* Association probably represent nuclei that gave rise to stocks characteristic of the Palaeozoic Evolutionary Fauna.

In the Tremadoc–early Arenig, the *Billingsella* Association *sensu stricto* was replaced across the shallow clastic shelves of North Gondwana (Fig. 2; Iran, North Africa, Armorica) by low-diversity assemblages
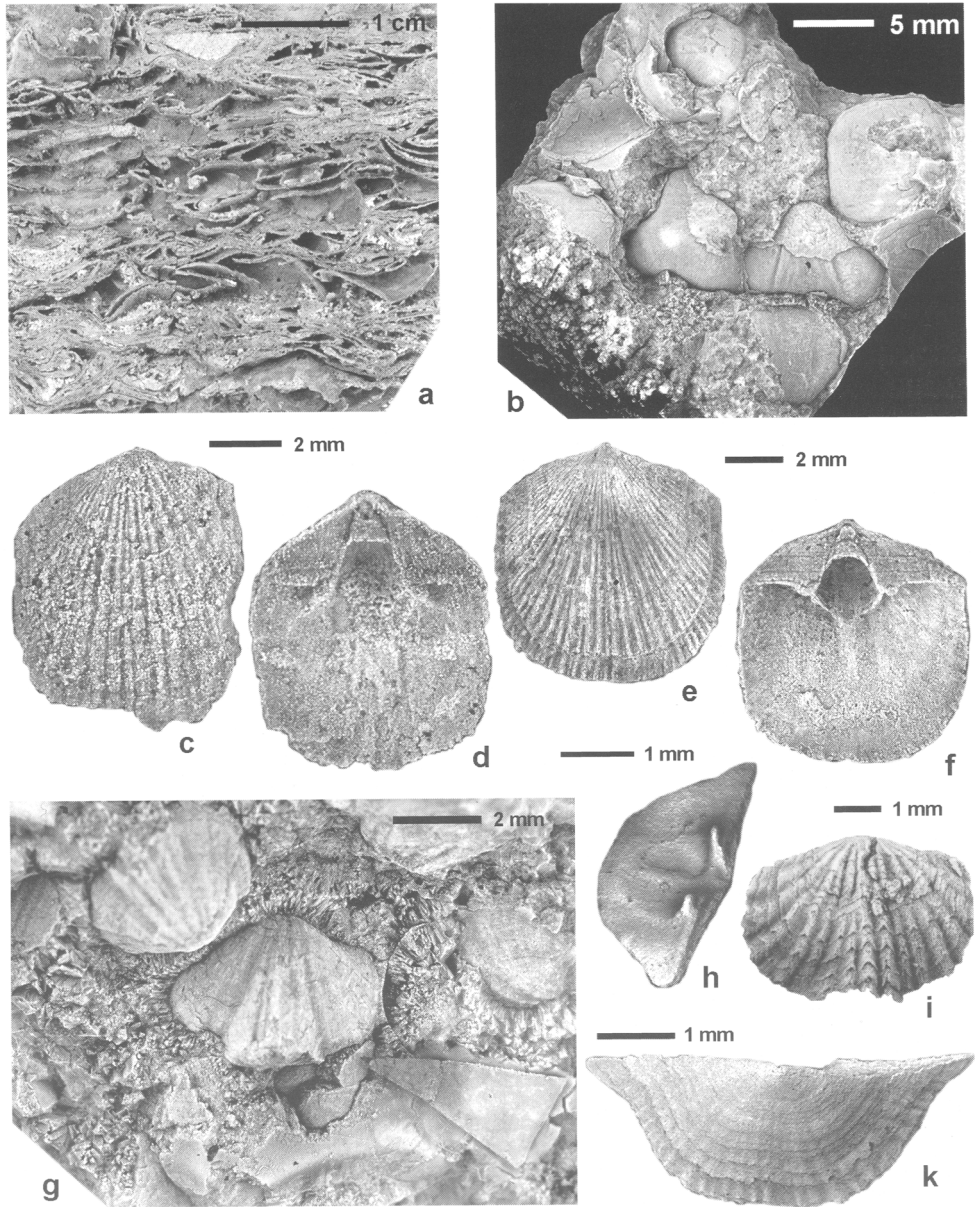
Fig. 3. Examples of late Cambrian–early Ordovician brachiopods that occur typically as coquinoid accumulations. (**a**) Storm bed formed by the accumulation of *Billingsella* sp., NMW 2001.45G.1, Upper Cambrian, Derenjal Formation, Shirgesht, Tabas Region, East Central Iran. (**b**) Shell bed comprising the syntrophioidean *Clarkella supina* Nikitin, NMW 98.67G.95, Lower Ordovician, Koagash Formation, Koagash River, South Urals, Kazakhstan. (**c, d**) *Billingsella* sp., NMW 2001.45G.2, interior and exterior of ventral valve, horizon and locality as in (**a**). (**e, f**) *Protambonites* sp. NMW 2001.45G.3, Lower Ordovician, Shirgesht Formation, Shirgesht, Tabas Region, East Central Iran. (**g**) Bedding surface with accumulation of *Huenella texana* (Walcott), USNM 52494, Upper Cambrian, Packsaddle Mountain, Llano County, Texas, USA. (**h, k**) Characteristic protorthide taxa from coquina accumulations in the Middle Cambrian, Amgaian, Arpatektyr Mountains, South Kyrgizstan: (**h, k**) NMW 98.69G.22, dorsal valve interior and NMW 98.69G.24 ventral valve of *Arctohedra pyramidalis* Aksarina; (**i**) CNIGR Museum 22/12761, dorsal valve exterior of *Glyptoria gulchensis* Popov and Tikhonov. NMW, National Museum of Wales, Cardiff; USNM, United States National Museum, Washington DC; CNIGR, Central Geological Research and Exploration Museum, St Petersburg.

dominated by the polytoechioideans *Protambonites* (Fig. 3e–f) or *Tritoechia* (e.g. Serre de los Cabos area of NW Spain, Shirgesht Formation of central Iran; Villas *et al.* 1995; Bassett *et al.* 1999*b*). These assemblages also spread to the Uralian margin of Baltica near the Tremadoc–Arenig boundary (Popov *et al.* 2001). Polytoechioideans were probably derived directly from the *Billingsella* Association (Popov *et al.* 2001) and demonstrate similar environmental requirements (Figs 1C, 2). In Iran and the South Urals they co-occur with a *Thysanotos–Leptembolon* Association of linguliformean brachiopods (Fig. 2; Popov & Holmer 1994, 1995; Bassett *et al.* 1999*b*).

Another distinctive group of late Cambrian–Tremadoc rhynchonelliformean assemblages was formed by syntrophioideans. These early pentamerides were most typical of low-latitude carbonate platforms on microcontinents and island arcs associated with Gondwana (e.g. South and North China, Central Asia, etc.) and Laurentia (Figs 1B, 2). The core of these assemblages was generally formed by a single taxon, usually *Huenella* (Fig. 3g) or *Palaeostrophia*. Associated brachiopods were mostly orthides (e.g. *Apheoorthis, Eoorthis,* etc.) and less abundant *Billingsella*. The co-occurrence of these faunas with pelmatozoan echinoderms such as eocrinoids is fairly typical, suggesting a relatively complex trophic structure involving at least two tiering levels. By the end of the Tremadoc (lower *Paroistodus proteus* Biozone), the syntrophioidean-dominated faunas were transformed to medium-diversity associations typified by the co-occurrence of the pentamerides *Clarkella, Diaphelasma, Glyptotrophia, Tetralobula,* etc. Here we identify this as the *Clarkella* Fauna (Figs 1C, 2, 3b). Brachiopods from the Lower Ordovician Olenty Formation of north-central Kazakhstan described by Nikitin (1956) include a good example of this newly emerging fauna. The *Clarkella* Fauna is unknown in West Gondwana, which by then had drifted to a high latitude (Fig. 1C), but it is characteristic of low latitude Laurentia and of the numerous terranes now incorporated into the complex tectonic collage of Central Asia and Kazakhstan, and is also recorded in South China and the Uralian margin of Baltica, located at that time in temperate latitudes. In all these regions, assemblages of the *Clarkella* Fauna occur in shallow-water carbonate depositional environments; they also incorporate descendants of local late Cambrian lineages (e.g. *Finkelnburgia, Apheoorthis, Eoorthis,* etc.) and polytoechioideans, but show little in common with succeeding Ordovician brachiopod associations.

Laurentia, Baltica and Siberia: general patterns of faunal replacement in the early Ordovician

The general characters of faunal replacement prior to the early Ordovician radiation are well documented and analysed only for Laurentia (Sepkoski & Sheehan 1983; Droser & Sheehan 1997), where the transition from benthic community types of the Cambrian Evolutionary Fauna to those characteristic of the Palaeozoic Evolutionary Fauna occurred in the Ibexian–early Whiterockian. Notable diversification of echinoderms (e.g. Sprinkle 1995) in the Ibexian represents the earliest indication of the Ordovician radiation in Laurentia (Guensberg & Sprinkle 1992), whereas the diversity of rhynchonelliformean brachiopods remained relatively low, represented mostly by families transitional from the Cambrian (Patzkowsky 1995). The abundance of polytoechiides and syntrophiidines diagnostic of the *Clarkella* Fauna is also characteristic. Typical Ordovician rhynchonelliformeans (e.g. camerelloideans and plectambonitoideans) together with bryozoans became increasingly abundant during the Whiterockian (Wilson *et al.* 1992), which was the interval when benthic assemblages with a structure and composition characteristic of the Palaeozoic Evolutionary Fauna became fully formed and widespread across Laurentia (Patzkowsky 1995; Sepkoski & Sheehan 1983; Droser & Sheehan 1997).

Available data from Baltica demonstrate that a benthic structure typical of the Palaeozoic Evolutionary Fauna arose there as early as the Billingenian (mid-Arenig, *Prioniodus elegans* Biozone), including the earliest representatives of plectambonitoideans, camerelloideans, endopunctate orthides and clitambonitidines among brachiopods, plus bryozoans, ostracodes, pelmatozoan echinoderms and asaphide trilobites (Fig. 2; Popov 1993; Pushkin & Popov 1999). This newly emergent fauna had no obvious origins in the low-diversity obolid-dominated assemblages of shallow shelf environments or in the predominantly dysoxic outer shelf olenid trilobite faunas characteristic of Baltica in the late Cambrian–Tremadoc. The sharp nature of faunal replacement in Baltoscandia suggests regional extinction and subsequent fairly rapid immigration of new taxa, concomitant with significant environmental changes including the onset of continuous carbonate sedimentation and the development of numerous hardground surfaces (Dronov *et al.* 1996).

In Siberia, early Ordovician (Tremadoc to

early Arenig) benthic assemblages retained major characters of the Cambrian Evolutionary Fauna, with abundant trilobites and with low-diversity orthide brachiopod assemblages represented by families transitional from the late Cambrian, accompanied by syntrophioideans (Sokolov 1982). The transitional interval through the late Arenig–Llanvirn was characterized by the presence of an essentially endemic low-diversity fauna of trilobites and rhynchonelliformeans, the problematical molluscs *Angarella* and *Moyeronia*, gastropods, locally abundant ostracodes, and the rare tabulate coral *Cryptolichenaria* (Kanygin *et al.* 1984). Other distinctive components of the Palaeozoic Evolutionary Fauna, such as rhynchonelliformean brachiopods of the orders Strophomenida, Triplesiida and Rhynchonellida, bryozoans and crinoids were introduced into Siberia only during the late Llanvirn–Llandeilo, where their sudden appearance suggests a major immigration from Laurentia (Rozman 1977).

Brachiopod radiation and palaeogeography

Within the newly emergent Ordovician faunas, rhynchonelliformean brachiopods were among the most important components, which in significant part defined the structure of benthic communities. Characters of faunal turnover and replacement in the early Ordovician of Laurentia, Baltica and Siberia – the three major early Palaeozoic plates outside Gondwana – suggest the importance of large-scale immigration of new brachiopod taxa, such as strophomenides, endopunctate orthides, clitambonitidines, triplesiides, and possibly camerelloideans, often of uncertain geographical and evolutionary origin, which comprise a significant component of the new faunas. Present-day rhynchonelliformeans and many bryozoans have a very low dispersal potential because of the very short free-swimming duration of their lecithotrophic larvae (Hyman 1959). Recent phylogenetic studies suggest that lecithotrophic larvae evolved early in ancestors of craniiformean and rhynchonelliformean brachiopods (Williams *et al.* 1996), and data from Palaeozoic rhynchonelliformean brachiopod biogeography also point to a relatively low ability for migration across oceans (Boucot 1975; Williams 1973, 1976). Their rapid expansion across the shelves of all major palaeoplates in the early to mid-Ordovician may therefore reflect a unique combination of environmental, geographical and tectonic factors that allowed them to cross oceanic divides separating major continents and

then to settle, replace or integrate successfully into previously aboriginal benthic assemblages.

Following the early Cambrian radiation, when the trilobite and lingulate brachiopod-dominated Cambrian Evolutionary Fauna was established and diversified, the mid-Cambrian to Tremadoc interval was a time of relative evolutionary and environmental conservatism. By comparison with the succeeding Ordovician, this interval was characterized by pronounced global sea-level lowstand with insignificant sea-level fluctuations, as indicated recently by the analysis of almost continuous shallow marine deposition in the East Baltic (Artyushkov *et al.* 2000), accompanied by minimal volcanic activity, while the expansion of Iapetus led to increasing separation of Baltica from Laurentia. By contrast, the Arenig–Llanvirn was a period of remarkable tectonic activity, which included the break-up of the Gondwanan margin, resulting in particular in the origin of Avalonia as a separate microplate (Torsvik 1998) and separation of the East Uralian microcontinent from Baltica (Şengör & Natal'in 1996). Onset of arc volcanism in the Tremadoc of Eastern Avalonia (e.g. Kokelaar *et al.* 1984) and the late Cambrian to early Tremadoc rapid subsidence of the Welsh basin (Prigmore *et al.* 1997) possibly suggest initial development of rifting of Avalonia from Gondwana at about that time. Prigmore *et al.* (1997) supposed that the wider separation of Avalonia from Gondwana possibly coincided with a second phase of subsidence in the Arenig–early Llanvirn, although only by the late Llanvirn had evident biogeographical differences developed between Avalonian and Gondwanan shallow-shelf benthic faunas (Cocks 1999). Available data for the Uralian margin of Baltica are less focused, but they suggest initiation of late Cambrian to early Ordovician rifting of the Uralian margin of Baltica (Zonenshain *et al.* 1984), and possibly the detachment of island arc systems east of Baltica related to backarc spreading (Şengör and Natal'in 1996).

The possible position of Baltica in relation to North Gondwana (Fig. 1C) suggests that this chain of events may have resulted in the formation of a new spreading zone comparable with that of the present-day North Atlantic oceanic ridge, followed by a tectonically induced sea-level rise and a change of direction in the rotation of Baltica, leading to initiation of the closure of Iapetus. Volcanism commenced in Avalonia by at least the late Tremadoc (Kokelaar *et al.* 1984), and the presence of an active volcanic arc in the proximity of the Caledonian margin of Baltica at about that time

became evident (Sturt & Roberts 1991). Evidence of increased early Ordovician island arc volcanism in the orogenic belts of Central and East Asia (Nikitin *et al.* 1991; Apollonov 2000) also suggests that the relatively narrow oceanic divide between the eastern margin of Baltica and equatorial Gondwana was occupied by chains of volcanic island arcs and microcontinents acting possibly as faunal 'bridges' between these two continents.

There is little doubt that the Ordovician Period mainly documents an interval of substantial sea-level rise, with a maximum in the Caradoc when most palaeoplates were flooded (Barnes *et al.* 1996). Superimposed second-order eustatic cycles corresponding approximately to the Tremadoc, Arenig and Llanvirn also can be recognized (Fortey 1984). The first episode of sea-level rise, corresponding to the transgressive phase of the Black Mountain eustatic event (mid-Tremadoc) of Miller (1984), is recorded on nearly all early Palaeozoic continents. This and the second transgressive phase in the Arenig reduced the influx of siliciclastic sediments into the large epeiric basins and provided good conditions for carbonate deposition, both in low (Laurentia, Siberia, North China) and temperate (Baltica, South China) latitudes. Areas of shallow marine carbonate deposition with numerous hardgrounds provided environments in which the earliest rhynchonelliformean brachiopod-dominated associations evolved.

Little is known of the characteristics of faunal replacement during the late Cambrian to early Ordovician of Gondwana and its associated terranes. In part this is a result of the marked period of sea-level lowstand through the late Cambrian to early Tremadoc, and the subsequent destruction of the Cambrian Gondwanan margin through the Palaeozoic, when areas of Cambrian shallow marine deposition were separated and later obscured within tectonic collages of Western Europe, the Middle East, and Central and Southeast Asia. By the beginning of the Ordovician, the North African and Middle Eastern sectors of Gondwana drifted into high latitudes and brachiopod assemblages linked to areas of carbonate deposition mainly disappeared (Fig. 1C). However, the late Cambrian *Billingsella* Association and succeeding early Ordovician polytoechioidean associations remained characteristic of some regions, for example in Iran and Armorica (Fig. 2). It is likely that in the late Cambrian–Tremadoc, benthic assemblages transitional to the Palaeozoic Evolutionary Fauna persisted mainly in faunas of peri-Gondwanan terranes, such as the South and North China plates, or on island arcs

and microplates incorporated into the orogenic belts of Central Asia, where the *Clarkella* Fauna became widespread in the late Tremadoc–early Arenig (Nikitin 1956; Holmer *et al.* 2001) and also colonized the Uralian margin of Baltica (Bondarev 1968) before that plate began its rapid northwesterly drift away from Gondwana. The early Arenig brachiopod-dominated fauna of the Billingenian Regional Stage (mid-Arenig) in the East Baltic contains all the main features of the Palaeozoic Evolutionary Fauna, including such characteristic groups as bryozoans and ostracodes (Popov 1993; Pushkin & Popov 1999). Assemblages of similar character appeared in Laurentia somewhat later, in the mid-Whiterockian (Wilson *et al.* 1992). Similar faunas in Siberia, which was possibly the most isolated continent of that time, appeared only in the late Llanvirn–Llandeilo. The abrupt nature of the faunal replacement in Baltica and Siberia, together with the abundance of new groups of high taxonomic rank and of taxa unrooted in indigenous lineages, suggests that the newly appearing faunas were mature assemblages that had evolved and immigrated from elsewhere. By contrast, faunal replacement in Laurentia was passive and non-competitive in nature (Westrop & Adrain 1998), and newly appearing taxa of rhynchonelliformean brachiopods and bryozoans were incorporated into the transformed benthic assemblages together with locally evolved faunas of trilobites and echinoderms.

Synopsis

The pre-Arenig nuclei of benthic communities dominated by suspension-feeders with a structure and composition characteristic of the Palaeozoic Evolutionary Fauna most probably evolved on the Cambrian shallow carbonate shelves of equatorial Gondwana and peri-Gondwanan terranes. Dispersion of these faunas outside Gondwana is evident from the late Cambrian–Tremadoc, when syntrophioidean, *Billingsella* and polytoechiid associations reached Laurentia, Siberia and the Uralian margin of Baltica, but wider significant transformation of benthic shelf assemblages was delayed until the Arenig–Llanvirn and then occurred diachronously across the major palaeocontinents. Substantial sea-level rise from the Tremadoc to Caradoc, coupled with extensive carbonate deposition and the development of associated hardgrounds in the shallow epeiric seas of low and temperate latitudes, established increased ecospace for colonization by the newly emerging benthic assemblages of the Palaeozoic

Evolutionary Fauna. These faunas included new stocks of rhynchonelliformean brachiopods, and possibly bryozoans (Hu & Spjeldnæs 1991), which were preadapted to these environments. Thus the well known onshore–offshore pattern in ecological expansion of rhynchonelliformean brachiopod assemblages in the Ordovician (Sepkoski 1991) reflects the fact that areas of shallow carbonate deposition were the primary environments in which these brachiopods flourished in the Cambrian, and which they then occupied first in their geographical expansion in the early Ordovician.

As noted by Sepkoski & Sheehan (1983), 'there was no immediately obvious physical trigger for such a great burst of evolutionary activity' to drive the Ordovician biodiversification. However, significant intensification of plate tectonic activity at the beginning of the Ordovician, including rifting of the Gondwanan margin and the Uralian margin of Baltica, resulted in the origin of extensive new spreading zones and substantial increase of island arc volcanism and eustatic sea-level rise, which provided a physical background for the remarkable transformations of marine biodiversity.

Reconstructions of Baltica and Laurentia during the Tremadoc–early Arenig place them in the relative proximity of Gondwana (Dalziel 1997; Torsvik 1998; Torsvik & Rehnström 2001). Benthic faunal groups with low dispersal potential thus had enhanced opportunities to cross the intervening oceans; at the same time, newly emergent volcanic arcs formed 'island hopping bridges' between the major continents, to further develop the pathways for such migrations. Conspicuous sea-level rise at the beginning of the Ordovician led to the development of vast new shelves and platforms in the expanding epeiric seas, which the new faunas invaded, then evolved and diversified by mid-Ordovician times when rapid drift began the separation of the early Palaeozoic continents.

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