The environmental distribution of associations belonging to the *Hirnantia* fauna – Evidence from North Wales and Norway

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The differentation of the *Hirnantia* fauna into two or more associations has been possible in the Hirnantian of Wales and Norway. The *Hirnantia* fauna *s.l.* is shown to have occupied a rather wide bathymetric range on late Ordovician shelves. In North Wales, Rawtheyan shelly faunas are used as evidence indicating a palaeoslope dipping gently to the west in the vicinity of the Berwyn Hills; brachiopod dominated, plectambonitacean/dalmanellid faunas pass westward into sparse trilobite-dominated faunas. Slumped deposits indicate the shelf/basin transition was south-west of Bala. The *Hirnantia* fauna in the nearer shore environments of the east Berwyns is dominated by *Hindella* while the more offshore environments to the west have *Eostropheodonta* and *Hirnantia.* Palaeogeographical and sedimentological evidence from the Oslo–Asker district of Norway confirms the inner shelf position of *Hindella* dominated assemblages and the deeper shelf position of the *Hirnantia* association. A third, intermediate, *Dalmanella* association has also been recognised. The faunal associations which together comprise the *Hirnantia* fauna *s.l.* appear similar in nature to brachiopod-dominated associations of communities recognised at other horizons in the Lower Palaeozoic.

Nearly all the assemblages recorded in North Wales can be assigned to the *Hirnantia* fauna, but in the formerly more tropical area of Norway there were, in addition to the *Hirnantia* fauna, two offshore associations, the *Onniella* and *Holorhynchus* associations and two nearshore associations in carbonate facies, the *Brevilamnulella* and *Thebesia* associations. Sandy shoreface facies characteristically contain the trace fossil *Monocraterion.*

The distinctive features of the *Hirnantia* fauna are discussed, and it is concluded that the fauna was probably a cold water fauna.

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The *Hirnantia* fauna is a brachiopod-dominated fauna which is characteristically found in the uppermost part of the Ordovician (i.e. the Hirnantian Stage). The fauna has attracted special attention and a special designation because elements of the fauna are unusually widespread. Even when the continents are reassembled into a probable late Ordovician configuration, the *Hirnantia* fauna is still found at sites which were widely separated and ranged from circumpolar to near tropical positions, though it is more common in the former (Jaanusson 1979).

The core of the *Hirnantia* fauna is composed of several eurytopic genera, such as the brachiopods *Hirnantia, Eostropheodonta, Kinnella, Plectothyrella,* and the trilobites *Mucronaspis* and *Brongniartella,* which also have a wide geographical distribution. At any particular locality there may be, in addition, several endemic taxa (Lespérance 1974). The differing abundance of genera and species at different locations has been noted by Temple (1965), Bergström (1968), Wright (1968), Lespérance (1974), Cocks & Price (1975) and Harper (1981). A subdivision of the *Hirnantia* fauna into distinct associations has been made in China by Rong (1979), in Scotland by Harper (1981), and in Scandinavia by Brenchley & Cocks (1982). In some regions there are, in addition to the *Hirnantia* fauna, other distinct assemblages. For example, an association characterised by *Holorhynchus* is found at localities as separates as

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China (Rong 1979) and Scandinavia (Jaanusson 1979, Brenchley & Cocks 1982), while other associations confined mainly to carbonate facies are recorded by Amsden (1974) from the U.S.A. and Brenchley & Cocks (1982) from Scandinavia.

Although the variability of the *Hirnantia* fauna has been well described, there is still little information about how this variability is related to environmental parameters, or indeed about the environmental range of the fauna as a whole. Wright (1968) noted the presence of the fauna, in association with oolites at Bala, North Wales, and in association with reef limestones at Kildare, in Ireland, and concluded that the fauna lived in a shallow water environment. Further, the restricted diversity of some assemblages strongly suggested a lagoonal type of environment (Wright 1968). Reinvestigation of Hirnantian sediments in North Wales suggest that the oolites near Bala lie in channels and were probably allochthonous, while the late Ordovician bioherms, such as those at Kildare in Ireland, Keisley in northern England and Boda in Sweden are carbonate mud mounds and not organic framework reefs. The evidence that the *Hirnantia* fauna lived in a shallow water environment is therefore questionable. An alternative view is that of Sheehan (1979) who has suggested that the *Hirnantia* fauna in Västergötland, Sweden, can be assigned to benthic assemblage 4 (cf. Boucot 1975), implying a moderately deep shelf environment for the fauna.

The purpose of this paper is to assess the environmental range of the *Hirnantia* fauna in the Upper Ordovician of North Wales and southern Norway, and to show that the fauna in both areas can be sub-divided into associations which were depth related and similar in nature to palaeocommunities described from other levels in the Lower Palaeozoic. The distinctive features of the *Hirnantia* fauna are then discussed.

Faunal Associations in North Wales

The *Hirnantia* fauna is found at more than ten localities in the Hirnantian rocks of North Wales (Fig. 1) and faunal lists have been published for Bala (Bassett *et al.* 1966) and Glyn Ceiriog (Hiller 1981). The main elements of the fauna found at selected localities are shown in Table 1. Study of this shows that *Hirnantia, Eostropheodonta* and *Dalmanella* occur in most localities but *Eostropheodonta, Hirnantia, Bancroftina* and *Plectothyrella* are particularly common in the western localities, around Bala, whereas *Hindella* is the dominant brachiopod at the eastern localities, such as Meifod and Llanfyllin, where *Plectothyrella* is absent. We will refer to these western and eastern associations as the *Hirnantia* associations and *Hindella* associations respectively.

The *Hindella* association has, in addition to the core genera *Hindella, Dalmanella, Hirnantia* and *Eostropheodonta,* a large number of corals, bryozoa and molluscs, together with a relatively large number of other brachiopod genera. This association is therefore considerably more diverse than the *Hirnantia* association.

In the most easterly area, near Glyn Feiriog, faunal assemblages are found which are similar to the *Hindella* association in having large numbers of solitary corals and bryozoans although they lack *Hindella* itself. Instead, *Hesperorthis* and *Nicolella* are particularly common, and since these rather variable and undoubtedly near-shore assemblages cannot be assigned to the *Hindella* association they are termed orthid-coral assemblages.

Assemblages in the west Berwyns are geographically intermediate between the eastern and western regions and have some similarities with both the *Hindella* and *Hirnantia* associations. Although *Hindella* is common it does not dominate the fauna to the same extent as at Meifod or Llanfyllin, and the number of genera making up the brachiopod fauna increases to a maximum of 12 with poorly preserved ?*Platymena* being the dominant member of the fauna.

The *Hirnantia* association as seen in the type area for the Hirnantian Stage, Bala, consists almost wholly of the brachiopods *Hirnantia, Eostropheodonta, Bancroftina* and *Plectothyrella* (Temple 1965; Wright 1968; Cocks & Price 1975), although bivalves also occur in conjunction with the *Hirnantia* fauna at a few localities.

One of the most notable features of the *Hirnantia* association is the almost complete absence of corals and bryozoans which are so common in the more easterly faunas. The association has a low diversity even though the

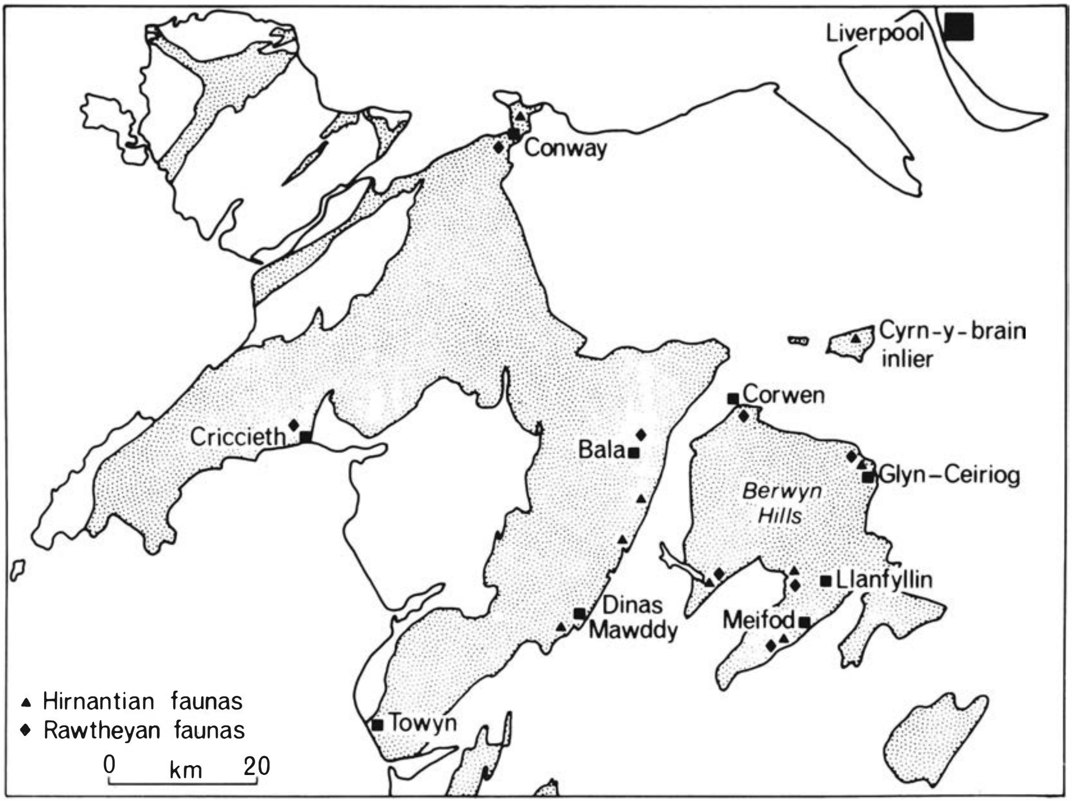

Fig. 1. Location of selected localities for Rawtheyan and Hirnantian faunas in North Wales. Outcrop of Ordovician rocks shaded.

number of specimens found at Bala is large.

Beyond the areas where the brachiopod-dominated *Hirnantia* fauna occurs there are sections where Hirnantian faunas are trilobite-dominated. Usually only the single genus, *Dalmanitina* is present although it is often represented by specimens of unusually large size. Lesperance (1974) refers to a *Mucronaspis (Dalmanitina)-Hirnantia* fauna as a combination of the trilobite and brachiopod-dominated *Hirnantia* faunas. The Welsh localitites have mainly yielded *Dalmanitina* on its own and it appears that in Wales the *Hirnantia* fauna (s.s.) and the *Dalmanitina* bearing assemblages are separate entities.

Palaeogeographic distribution of the *Hirnantia* faunas in North Wales

The Hirnantian faunas under discussion all occur at localities which lay within the Welsh basin. This was a fault-bounded trough in which a large volume of sediment accumulated, although during the Ordovician the faults did not always mark the topographic divide between shelf and basin. In mid-Caradoc times, for example, a shallow shelf extended fully across the northern part of the basin. Further south the transition from shelf to basin lay near Bala, some 40 km west of the Church Stretton Fault (Brenchley & Pickerill 1980) and the topographic basin occupied only the medial part of the overall fault-bounded trough.

The Ashgill palaeogeography was apparently broadly similar to that of the middle Caradoc as shown by the occurrence of varied brachiopod and trilobite shelf faunas across the northern part of North Wales as far west as Bala, whereas graptolitic or unfossiliferous mudstones occur beyond Bala (Fig. 2 & 3). It is possible to determine a more detailed palaeogeography for Rawtheyan times based on the

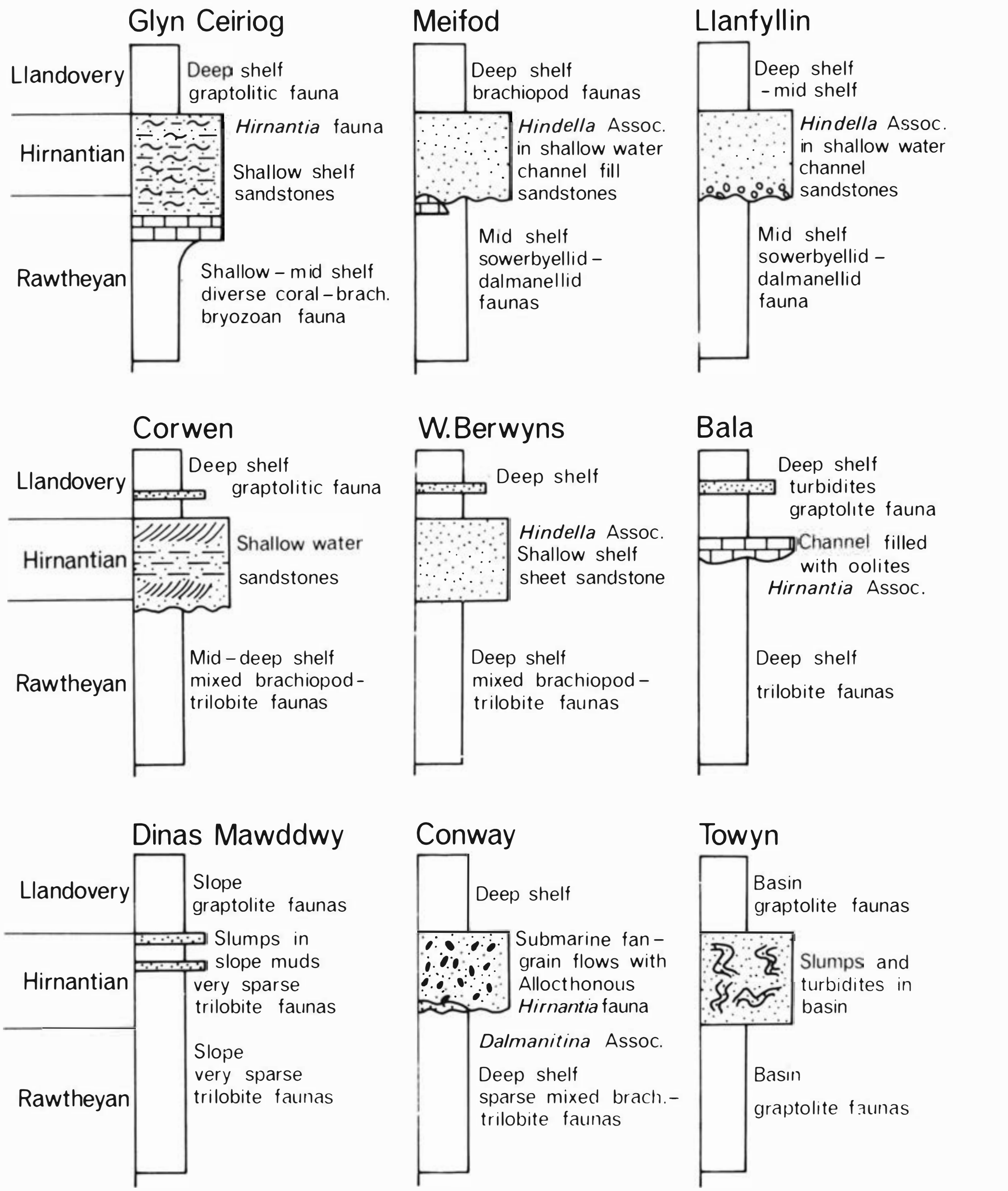

Fig. 2. Simplified stratigraphical columns and environmental interpretations for sections through the Upper Ordovician and lowermost Silurian in North Wales.

composition of the benthic faunas which can be divided into a number of broad faunal assemblages. The more easterly faunas, as illustrated by sections near Glyn Ceiriog (Fig. 2), consist of brachiopods, corals, trilobites, bryozoans and molluscs (Table 2) found in fine sandstones which were deposited in a shallow shelf environment. There is also some localised development of carbonates in this area and the substrate is generally coarser than in the more western areas. The most striking feature of these inshore assemblages is the high proportion of solitary corals and molluscs which only occur rarely in the more offshore assemblages. Table 2 shows that a number of eurytopic brachiopod genera, particularly *Sowerbyella* and *Dalmanella,* occur in most of the areas investigated in North Wales. However these two brachiopod genera are particularly dominant in the brachiopod assemblages at Meifod and Llanfyllin where they account for more than 50% of the total preserved biota. These assemblages are assigned to a *Sowerbylla-Dalmanella* association. Trilobites are present in the association at some localities but the number of trilobite genera is relatively small and the fauna is generally dominated by brachiopods.

Further west near Lake Vrynwy in the western Berwyns there is a more varied fauna which includes brachiopods, trilobites and abundant bryozoa. The high proportion of articulated brachiopod valves and associated unbroken bryozoans probably reflect quiet water conditions. It is suggested that the mixed brachiopod assemblages lived in the outer part of the midshelf. The faunas from areas further west are often very variable but may be placed into two main types, namely diverse trilobite-dominated faunas such as those at Llanystumdwy, near Criccieth (Price 1981) and in the Rhiwlas Limestone at Bala (Bassett *et al.* 1966), and sparse mixed brachiopod-trilobite faunas such as those at Conway. In the Bodeidda mudstones (Cautleyan-Rawtheyan) at Conway only a few genera of brachiopod are present (see Table 2) and these are generally small and thin-shelled. *Christiania* is the dominant brachopod and is locally abundant at Conway but is rare at all other localities. There are in addition several genera of trilobites notably *Tretaspis,* in greater abundance than in most other western localities. One striking feature of the sparse mixed fauna is the almost total lack of any fauna other than brachiopods and trilobites.

In the basinal areas such as Dinas Mawddwy only a very sparse fauna is found in the Rawtheyan sediments. The fauna is most usually graptolitic and trilobites are only rarely found.

It is believed that the faunal associations found in the Rawtheyan are similar in nature to the depth-related associations described from other horizons in the Ordovician. A *Dalmanella-Sowerbyella* association is generally regarded as being an inner shelf association (Pickerill & Brenchley 1979; Hurst 1979; Lockley 1983), while assemblages with genera such as *Eoplectodonta* and *Christiania* are regarded as indicating a deep shelf environment (Williams & Wright 1981; Brenchley & Cocks 1982). Trilobite-dominated assemblages which pass laterally into graptolitic faunas would be consistent with an environmental range from slope to basin.

The rather monotonous Rawtheyan mudstones which mantle large parts of both the shelf and basin were succeeded by a varied suite of Hirnantian sediments deposited during a period of low stand sea level (Fig. 2). The eastern areas are characterised by sheet sandstones and thin lenses of conglomerates which were deposited in channels eroded into the Rawtheyan mudstones.

The orthid-coral assemblages dominated by *Hesperorthis* or *Nicolella* occur in thin ripple-laminated fine sandstones of the Glyn Formation (Rawtheyan-Hirnantian) near Glyn Ceirog (Fig. 2). These assemblages may have been transported from further east and may therefore be representatives of faunas which lived inshore of the *Hindella* association. The overall character of the Glyn Formation is strongly suggestive of deposition within a wide channel developed near the shoreface.

The *Hindella* association also occurs within similar channel-fill sandstones and there was probably some transport of fossils, which makes it difficult to determine the exact environmental position of the fauna. However, the ratio of opposing valves for the brachiopods is very close to unity and no large net transport is indicated. The *Hindella* association probably inhabited a shallow shelf environment and may have lived in or close to the channels in which the association is commonly found. The *Hirnantia* association as seen at Bala (Fig. 2) is almost certainly autochthonous and occurs in mudstone in an outer shelf position although water depth was probably not great. The *Hirnantia* association also occurs in sandy facies and in oolitic limestones (Hirnant Limestone). The ooids of the Hirnant Limestone are almost certainly allochthonous but the fauna collected from the limestone and the surrounding mudstones is not significantly different and the fossils in the limestone do not show any evidence of being transported over a great distance, since they are mainly unbroken and opposing valves occur in similar numbers. The fauna

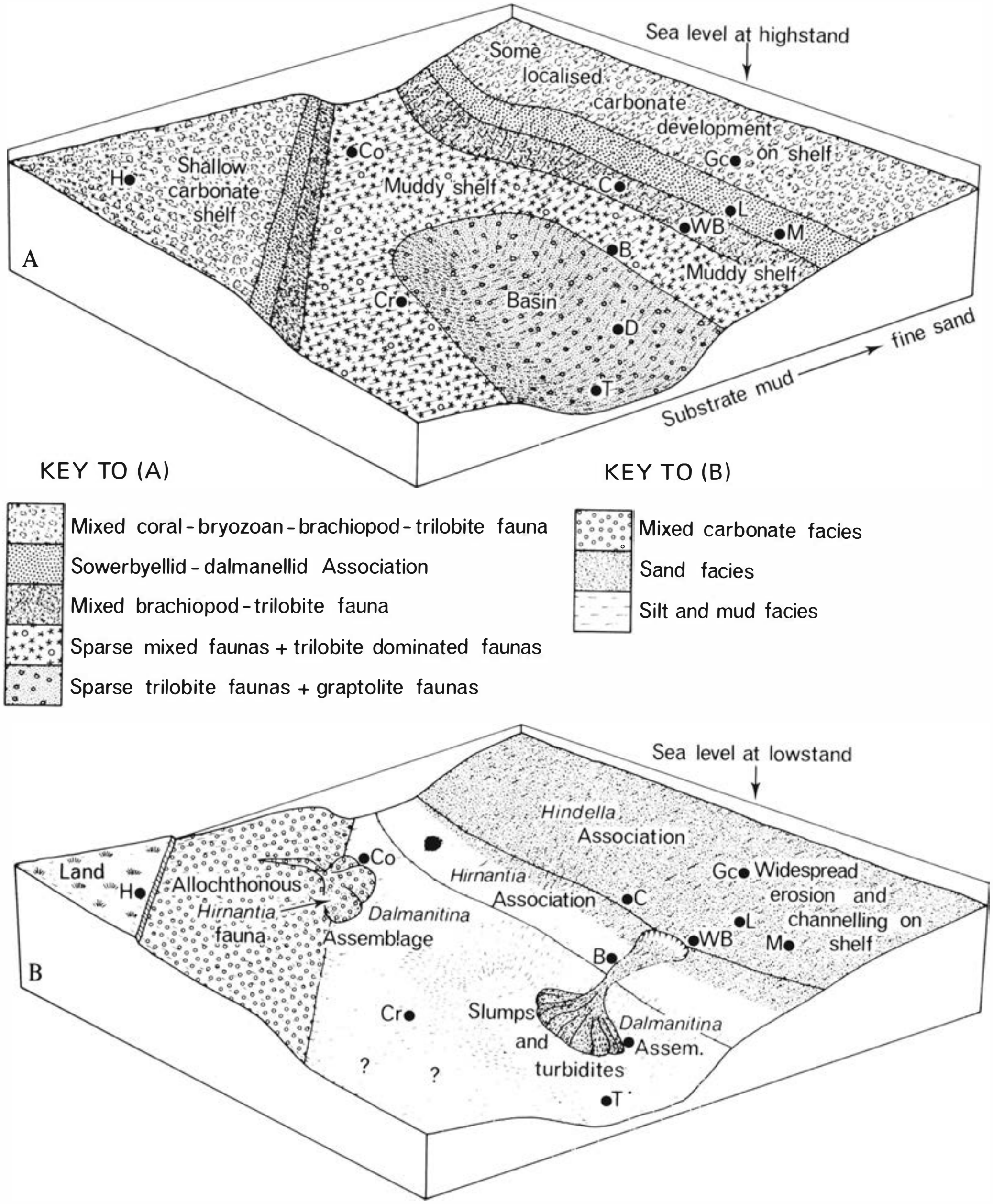

Fig. 3. Palaeogeographic reconstruction of the Northern part of the Welsh Basin during the Rawtheyan (A) and Hirnantian (B) stages, showing distribution of the faunal associations.
Locations: B = Bala, C = Corwen, Co = Conway, Cr = Criccieth, D = Dinas Mawddwy, Gc = Glyn Ceiriog, H = Holyhead, L = Llanfyllin, M = Meifod, T = Towyn, WB = Western Berwyns.

was probably derived from the adjacent muds and swept into the channel during the deposition of the ooids.

The *Dalmanitina* assemblage occurs at Conway 1.2 m below the base of the Conway Castle Grits (Fig. 2) which are a series of calcarenitic proximal turbidites containing an allochthonous *Hirnantia* fauna transported from the

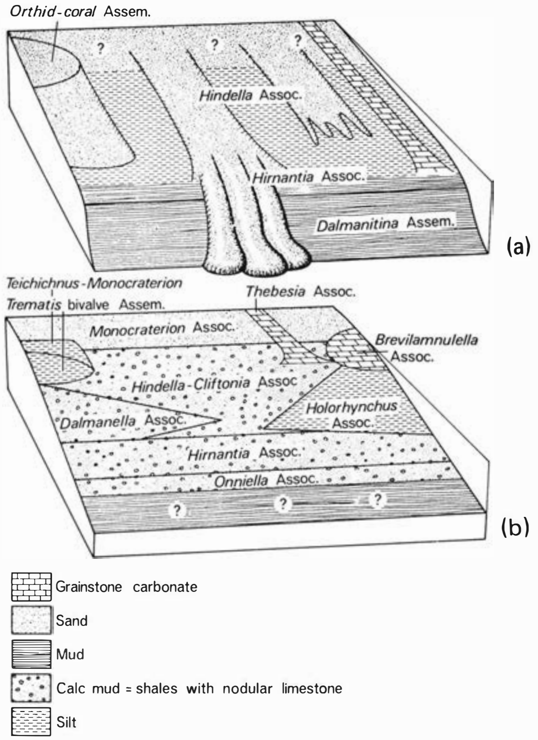

Fig. 4. Reconstructions of the environmental distribution of Hirnantian faunal associations in (a) North Wales and (b) Oslo–Asker district, Norway.

west. These turbidites accumulated in a submarine fan when sea-level fell in Hirnantian times. The *Dalmanitina* assemblage would have been the local autochthonous fauna occurring in mudstones of the deep shelf. The *Dalmanitina* assemblage also occurs in the Foel-y-Ddinas Mudstones (Hirnantian) at Dinas Mawddwy (Fig. 2) but the same formation when traced laterally contains the *Hirnantia* association 18 km to the north east at Bala. The *Dalmanitina* assemblage appears to have occupied a position further down the palaeoslope that the *Hirnantia* association. The environmental distribution of the *Hirnantia* fauna in North Wales is summarised in Fig. 3.

Associations of the Hirnantia fauna in the Oslo region

Three associations belonging to the *Hirnantia* fauna have been recognised at the very base of the Hirnantian in the Oslo–Asker district of southeastern Norway (Brenchley & Cocks 1982). They are the *Hirnantia* association *s.s.*, the *Dalmanella* association and the *Hindella-Cliftonia* association. Several genera are common to the three associations but they are present in very different proportions.

In addition to the three associations of the *Hirnantia* fauna there are four other associations present in Hirnantian rocks of the Oslo–Asker district. An *Onniella* association persisted from the Rawtheyan into rocks probably belonging to the lower part of the Hirnantian, a *Holorhynchus* association is locally present in the area in the middle part of the Hirnantian, and two associations, the *Thebesia* association and the *Brevilamnulella* association, are found in shallow marine facies as the top of the Hirnantian stage (Brenchley & Cocks 1982).

Palaeogeographical distribution of the *Hirnantia* fauna in the Oslo region

In Ordovician times an extensive, relatively shallow marine platform occupied the Baltic region and extended about 1500 km from western Norway to eastern Estonia. The western margin of the platform was raised to form a palaeoslope which dipped gently eastwards toward the central part of the platform. The Oslo–Asker district lay on this gentle palaeoslope which influenced the nature of the sediments. In the west of the district these were more richly fossiliferous and calcareous than those in the east (Kiær 1902; Størmer 1967; Brenchley & Newall 1980). A broadly similar palaeogeography persisted into early Hirnantian times when block faulting of the basement coupled with a probable glacio-eustatic lowering of sea level radically changed the distribution of facies.

The three associations of the *Hirnantia* fauna known from the Oslo–Asker district are all found in bioturbated shelf mudstones which lie in a regressive sequence below sandy shoreface sediments.

The *Hindella-Cliftonia* association is found in an up-slope position, in relatively calcareous mudstones (Fig. 4b), the *Hirnantia* association is found downslope in more argillaceous sediments to the east and the *Dalmanella* association occurs in an intermediate position (Fig. 4b). The presence of many articulated valves of *Cliftonia* and *Hindella,* and a well preserved life assemblage of the latter indicate that the *Hindella-Cliftonia* association probably lived below wavebase, while the other associations presumably lived in somewhat deeper parts of the shelf. Some elements of the *Hirnantia* fauna are found stratigraphically higher in the sequence where shelf mudstones pass upwards into shoreface sandstones. *Hirnantia, Eostropheodonta, Hindella* and *Plectothyrella* are found associated with *Trematis,* corals and bivalves in silty and sandy sediments reflecting an environment near the bottom of the shoreface (Brenchley & Cocks 1982). The shoreface, and associated sediments deposited in tidal channels, have trace fossils such as *Monocraterion,* but most lack body fossils, except for the local presence of the *Thebesia* and *Brevilamnulella* associations. Both of these associations are found in coquinas formed of locally transported valves deposited in channels (Fig. 4b).

The *Onniella* and *Holorhynchus* associations are both found in bioturbated shelf mudstones. The former is believed to have occupied a deep shelf environment while the latter may have lived in an inner shelf environment comparable to that occupied by *Pentamerus* in the succeeding Silurian (Brenchley & Cocks 1982).

In conclusion, the position of the *Hirnantian* fauna in a regressive sequence, below shoreface sediments, provides convincing evidence of a shelf environment for the fauna. Although some elements of the fauna probably lived close to the shoreface, the shallowest of the well-defined associations, the *Hindella-Cliftonia* association, typically occurred below wave base and the other two associations in positions slightly further down the palaeoslope. Co-existing with the *Hirnantia* fauna but living in other parts of the shelf were the *Onniella* and *Holorhynchus* associations. Sediments of the shoreface generally only supported a fauna recorded as trace fossils but two low diversity and locally restricted associations, the *Thebesia* and *Brevilamnulella* associations, colonised shallow maine, channel environments.

Discussion

The eight associations in the Hirnantian of the Oslo–Asker district are believed to have been eight distinct biofacies representing eight biotic communities. This degree of partitioning of the shelf biota into associations appears comparable with that found lower in the Ordovician where about six associations, excluding ichnofacies, are typical of the Caradoc (Lockley 1983). Similarly, about five brachiopod associations are typically found in Lower Silurian shelf sediments (Ziegler 1965). The presence of oolites and reefs in the Upper Ordovician of the Oslo region, Norway, supports the limited palaeomagnetic data in placing Baltoscandia in or near the southern tropics (cf. Ziegler *et al.* 1977). The variety of associations could therefore be a feature of the Ordovician tropics.

In North Wales, an area which was probably more temperate, there were no clearly defined associations in addition to the *Hirnantia* fauna, but the fauna itself, can be sub-divided into two associations. Other nearshore assemblages appear distinctive in being coral-bivalve rich and may represent a separate association. In deep shelf or slope environments assemblages generally lack brachiopods and are characterised by the trilobite *Dalmanitina.* There were therefore only two brachiopods associations in the Hirnantian which contrasts with the six in the Caradoc of the same region. Elsewhere in the world there is insufficient information on the environmental distribution of late Ordovician faunas to determine whether or not there were several co-existent biofacies in any particular area. However, the lack of evidence may in itself be significant and might suggest that the differentiation of the Hirnantian biota into associations was not pronounced outside the Ordovician tropics.

The associations of the *Hirnantia* fauna apparently occupied an environment which ranged from the inner to the deep shelf, and could be assigned to benthic assemblages three, four and possibly five according to the scheme proposed by Boucot (1975).

Several of the species of the *Hirnantia* fauna are eurytopic and are present in all the associations. Eurytopic species are not unique to the *Hirnantia* fauna but are found in earlier Ordovician associations. For example, *Howellites antiquior* and *Sowerbyella sericea* are found in at least three associations in the Caradoc of North Wales (Pickerill & Benchley 1979; Lockley 1980) and the inarticulate brachiopod, *Paracraniops doyleae* is found in as many as eight associations in the Caradoc of Shropshire (Hurst 1979). However, in both these areas there are no species, except *Paracraniops doyleae,* which have a range across most of the shelf, as is the case for several species of the *Hirnantia* fauna.

The characteristic genera and species of the *Hirnantia* fauna are not only eurytopic, as noted above, but are also cosmopolitan (Lespérance 1974; Rong 1979; Jaanusson 1979). Brachiopod faunas in general became progressively more cosmopolitan during the late Ordovician and though there were still local, endemic species in Hirnantian times, faunal provinces were no longer clearly differentiated (Jaanusson 1979). The existence of this cosmopolitan fauna at a time when there was a large polar ice cap, and therefore probably well developed climatic belts, is unexpected (Lespérance 1974). It does not apparently conform with the models of Valentine (1973), which predict that faunas should be particularly well differentiated when global climates are most strongly contrasted. One possible explanation of this apparent anomaly is that the *Hirnantia* fauna was a cold water fauna as suggested by Sheehan (1979) and that during the late Ordovician glaciation the temperate climatic belts contracted to such an extent that cool oceanic waters extended from the poles to areas which were formerly tropical (Skevington 1974, Sheehan 1979).

The evidence for the *Hirnantia* fauna being a cold water fauna is:

1. It characteristically occurs in areas which were previously occupied by faunas of the Mediterranean Province, and is composed of some genera which have Mediterranean origins (Jaanusson 1979; Sheehan 1979). The Mediterranean fauna probably occupied a temperate or circum-polar position (Spjeldnæs 1961, 1981; Havlíček & Vaněk1966).. However the evidence is not conclusive. There had been a progressive breakdown of provincial barriers from mid-Ordovician times onwards, probably related to changes in the geography of the continental plates, so that by the late Ashgill there was a general increase in the number of pandemic genera (Williams 1973). The *Hirnantia* fauna is found in areas well outside the former Mediterranean province and in addition to cosmopolitan genera of Mediterranean origin (e.g. *Hirnantia, Drabovia*) there are several new pandemic genera (e.g. *Plectothyrella, Eostropheodonta*) and other pandemic genera persisting from earlier times (e.g. *Dalmanella, Bancroftina* c.f. Havlíček 1976). The Hirnantian was thus a time when cosmopolitan genera flourished, some of which were of Mediterranean origin.

2. The *Hirnantia* fauna shows, in common with the Mediterranean fauna (except in the mid-Ashgill) a rather low diversity of brachiopod species, but a eurytopism of these species. It is likely that the cool water faunas in the Ordovician were generally poorly differentiated into associations and were geographically widespread. This is consistent with many colder water faunas at the present day which tend to have generalist species and fewer associations (Valentine 1973; 261, 365).

The evidence against the *Hirnantia* fauna being a cold water fauna is that it is found in a few sequences, such as those in the Oslo region, with characteristically tropical facies, including oolites. However, in these sequences the *Hirnantia* fauna is confined to clastic facies and is not found in the warm water carbonates, so the fauna could have colonised the shelf area during the colder phases of the Hirnantian.

Although the evidence is inconclusive we believe it favours a cold water environment for the *Hirnantia* fauna. It might therefore be significant that at the end of the Hirnantian, when the ice cap melted and a warmer regime was probably initiated, there was an extinction of most of the remaining remnants of the Mediterranean trilobite fauna and the early Silurian diversification of the brachiopods came not from Mediterranean stocks, but from the more tropical, Hiberno-Salairian faunas (Jaanusson 1979). It therefore appears that the cold water cosmopolitan *Hirnantian* fauna of the late Ordovician might have been replaced by cosmopolitan, but warm water faunas in the Silurian.

Table 1. Composition of the Hirnantian faunal associations based on assemblages at selected localities in North Wales, percentages refer to percentages of total fauna. Diversity is measured by the number of taxa in an assemblage. Locations refer to those marked on Figure 1.

	BALA	*W. BERWYNS*	*LLANFYLLIN*	*MEIFOD*	*GLYNCEIRIOG*
Brachiopods					
Hirnantia	21.1%	11.2%	13.8%	19.8%	5.9%
Eostropheodonta	32.1%	11.2%		8.9%	2.0%
Dalmanella	6.8%	5.2%	5.1%	5.5%	13.7%
Plectothyrella	5.0%	2.2%			
Hindella		9.0%	25.1%	20.3%	
Kinnella	3.6%	4.5%		0.5%	
Bancroftina	23.3%	0.7%			
Sowerbyella	0.4%	2.2%	3.1%		3.9%
Christiania			1.6%		
Diambonia			1.0%		
Leangella				0.5%	
Rhychotrema		0.7%	1.5%	2.0%	
Plaesiomys		0.7%			
Leptaena					2.0%
Hesperorthis					21.5%
Dolerorthis					7.8%
Sampo					2.0%
Platymena		20.8%			
Epitomyonia		0.7%			
Orthambonites					3.9%
rhynchonellids	5.2%				
Cnidarians					
streptelasmatids			34.4%	11.9%	15.6%
favositids			12.8%		2.0%
conulariids	0.7%				
Bryozoa					
Hallopora	6.1%	20.9%	abundant	27.7%	3.9%
trepostome	1.1%				
dendroid bryozoans				0.5%	3.9%
Molluscs					
bivalves		1.5%	0.5%		2.0%
gastropods			0.5%	0.5%	
Others		2.4%	0.5%	2.3%	10.2%
TOTAL	100.2%	99.1%	99.9%	99.9%	100.3%
Diversity	11	18	14	15	17
Sample size (number of individuals)	280	134	206	202	55

Table 2. Occurrence of the commoner elements of the Rawtheyan faunas at localities in North Wales shown in Figure 1.

	Glyn Ceirog	*Meifod*	*Llanfyllin*	*W. Berwyns*	*Corwen*	*Conway*
Brachiopods						
Dalmanella	9.3%	49.5%	11.4%	12.9%	10.9%	10.9%
Sowerbyella	0.8%	2.8%	59.6%	5.8%	31.3%	17.4%
Anisopleurella		7.3%	1.2%	2.3%		2.2%
Dolerorthis	2.3%		0.8%		3.1%	
Christiania		2.8%				37.0%
Saukrodictya	0.8%	1.8%	0.4%	1.2%		
Skenidioides	1.6%		0.4%	7.0%	0.8%	
Orthambonites		6.4%	3.1%	1.2%		
Glyptorthis			2.4%	10.5%	3.9%	
Schizophorella	2.3%					
Triplesia		2.8%			4.7%	
Rhynchotrema		2.8%			0.8%	
Nicolella	7.0%				0.8%	
Schizonema		3.7%				
Leangella			0.4%			8.7%
Sampo					3.1%	
Orbiculoidea		0.9%		7.0%	0.8%	2.2%
other brachiopods	3.9%	13.8%	2.8%	9.3%	6.4%	4.4%
Trilobites						
Gravicalymene	0.4%	0.9%		0.1%		
Encrinurus	0.4%	0.3%			0.2%	
Prionocheilus	0.1%					
Remopleurides		0.1%		0.1%		
Paracybeloides		0.1%				
Tretaspis				0.1%	0.3%	3.3%
Octillaenus				0.1%		
Stenopareia					0.4%	
Phillipsinella						0.2%
Trinodus						0.4%
Lonchodomas						0.4%
other trilobites	0.4%					2.1%
Bryozoa						
stick bryozoans	17.8%	3.2%	12.9%	22.2%	26.6%	
trepostomes	8.5%			15.2%	2.3%	2.2%
"dendroid"	2.3%				2.3%	
Corals						
streptelasmatids	25.6%	0.9%				
Molluscs						
Bivalves	4.7%		0.4%			
Gastropods	10.9%			1.2%		
Echinoderms						
Cystoids			1.4%	1.2%	0.8%	
crinoid collumnals	common	common	common	abundant	present	rare
conulariids				2.3%		2.2%
TOTAL	99.1%	100.1%	99.2%	99.7%	99.5%	100.1%
Diversity	20	19	19	20	21	17
Sample size (number of individuals)	130	110	255	90	140	46

Table 3. Occurrence of the commoner taxa in the three associations of the Hirnantia *fauna in the Oslo–Asker district, shown as a percentage of the total fauna, and a percentage of the brachiopod fauna (in brackets). Diversity is measured by the number of taxa in an assemblage. (Data showing the variation between localities is given in Brenchley & Cocks 1982.)*

	Hirnantia Association	*Dalmanella* Association	*Hindella/Cliftonia* Association
Hirnantia sagittifera	23% (41%)	< 1%	< 1%
Dalmanella testudinaria	15% (24%)	69% (81%)	4% (9%)
Eostropheodonta hirnantensis	6% (10%)	- -	2% (4%)
Hindella cassidea	2% (3%)	2% (2%)	25% (32%)
Cliftonia aff. psittacina	6% (3%)	2% (3%)	25% (32%)
	6% (13%)	2% (3%)	34% (49%)
Mucronaspis mucronata	4%	< 1%	< 1%
Mean total diversity	14.3	5.3	11.6
Mean brachiopod diversity	6.5	4.0	6.3
Mean sample size	97.5	30.8	63.7

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