Late Ordovician environmental changes and their effect on faunas

By PATRICK J. BRENCHLEY and the late GEOFFREY NEWALL

It is estimated that the late Ordovician glaciation extended to 40° latitude from the southern pole, but that there was no glaciation in the northern hemisphere. There was a related < 100 m lowering of sea-level. The lowering of sea-level produced profound changes in palaeogeography, notably (1) disconformities in shelf areas with widespread karst surfaces in carbonate environments and channels on terrigenoclastic shelves, (2) deep erosion at shelf margins to produce marked disconformities, (3) a variety of syn-sedimentary deformation structures on shelves and slopes, (4) mass flow deposits and fans at the base of the slopes. The ensuing transgression flooded platform areas to produce a mantle of argillaceous sediment, often carbonaceous, which extended down the slopes and across the basin floors. These environmental changes, recorded from outgrop geology, confirm and expand previous models of transgressive/regressive sequences.

Contemporaneous with these late Ordovician environmental changes was a striking extinction of both benthonic and planktonic faunas. However, major taxonomic groups were differently affected and the timing of the extinction was also variable. The extinction of trilobites and graptolites occurred close to the Rawtheyan-Hirnantian boundary and preceeded the main drop in sea-level. Evidence suggests that the initial wave of extinction was related to global cooling while reduction in habitable area may have been important in later extinctions.

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Although there have been several glaciations during the history of the earth, the glaciation at the end of the Ordovician is of particular interest because the glacial maximum was pronounced but relatively brief and the resultant facies changes can often be precisely identified in the stratigraphical record. There is widespread evidence of continental glacial deposits on those continents which formerly composed Gondwanaland, and those in Saharan Africa, have been particularly well described by Beuf *et al.* (1971). The related glacio-eustatic sea-level changes caused environmental changes which can be recognised on separate continents and plates (Berry & Boucot 1973). Coincident in time and almost certainly causually related was an extinction of a substantial part of the late Ordovician biota (Berry & Boucot 1973; Sheehan 1973).

Because it is possible to identify the environmental changes related to the Gondwana glaciation in many stratigraphic sequences in a wide variety of environments, late Ordovician rocks are used as evidence in this paper to test both models of environmental change, resulting from eustatic sea-level change (Vail *et al.* 1977), and hypotheses concerning the causes of extinction. Furthermore, since the environmental changes caused by the rise and fall in sea-level were synchronous around the globe, and as they occurred close to the Ordovician-Silurian boundary, an understanding of these changes might influence decisions as to which is the best position to place the boundary between to two systems.

The Late Ordovician Glaciation

Glacial Deposits

Continental glacial deposits of approximately late Ordovician age are known from widely se-

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parated localities on the Gondwana continental plate. They are known from several sites in and around Saharan Africa, from South Africa, South America (see Spjeldnæs 1981 and references) and have been reported from Saudi Arabia (McClure 1978). Well preserved striated pavements provide convincing evidence of land-based ice and the variety of glacial geomorphological features, glacial and fluvio-glacial sediments and ice deformation structures are consistent with the former presence of a major ice-cap based on a generally flat continental shield area (Beuf *et al.* 1971; Allen 1975; Spjeldnæs 1981).

Tilloids, typically composed of mudstones containing dispersed angular or sub-angular carbonate clasts, together sometimes with well rounded quartz grains, are found at many localities in northern France and Iberia. Clasts with well preserved ice scratches have been described by Doré & Le Gall (1972) from the "Tillite de Fueguerolles" in Normandy which convincingly demonstrate the glacial origin of these tilloid beds. The similarity of texture and stratigraphic position of tilloids elsewhere in western Europe suggests that they have the same origin, though ice scratches have not been identified. However, the presence of "drop-stones" which have deformed delicate laminae in the Schistes du Cosquer in Brittany (Hamoumi 1981) also attests to the former presence of floating ice in the region. Tilloids of probably glacial origin are now known from localities in Normandy (e.g. Dangeard & Doré 1971; Robardet 1973), and Brittany (Hamoumi *et al.* 1980) in France; Celtiberia (Carls 1975), Montes de Toledo (Robardet 1982), and Sierra Morena (personal observation) in Spain; Valongo in northern Portugal (Romano & Diggens 1973–1974), and many localities in central Portugal (personal observation). The Ledershiefer in the German Democratic Republic (Greiling 1967) may also be of glacial origin.

Although the tilloids at most of these localities are rather similar in appearance, many of the vertical sequences differ in detail because there are variable amounts of intercalated laminated mudstones and bedded sandstones, commonly showing soft sediment deformation. Not only are the vertical sequences varied, but lateral facies changes can occur over a few kilometres. This variability was used by Greiling 1967) as evidence against a glacio-marine origin for the tilloids. However, there is no reason to expect uniformity of lithology under ice floating across a relatively shallow platform, particularly towards the distal margin of ice influence. This is confirmed by samples of Recent bottom sediments around the Antartic which show considerable heterogeneity (Anderson 1972; Anderson *et al.* 1977).

On the Gondwana continent the distribution of continental glacial deposits of late Ordovician age shows that land-based ice extended outwards across at least 40 degress of latitude from the south pole and that floating ice may have extended a further 10 degrees (Fig. 1). This is comparable to the spreads of ice at glacial maxima during the Pleistocene (Flint 1971). However, whereas the Pleistocene glaciation was bi-polar, the configuration of the continents in the late Ordovician (Smith *et al.* 1973; Ziegler *et al.* 1977) makes it unlikely that there was a north polar ice-cap during the Ordovician because open oceanic circulation apparently prevailed there.

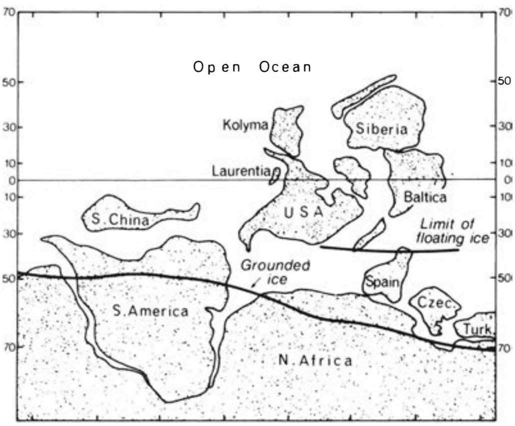

Figure 1 – Estimated limits of the late Ordovician ice-cap and of floating ice. The distribution of continents is based on the early Silurian palaeogeographical reconstruction by Ziegler et al. (1977).

Timing of the glaciation

Continental glacial deposits are notoriously difficult to date stratigraphically because they generally lack fossils. This is true both of Pleistocene deposits and more ancient tills where estimates of age are usually made by using well dated fossiliferous beds above and below. The late Ordovician glacial deposits are best dated in Morocco where an upper Ashgill, *Hirnantia* fauna is intercalated with them (Destombes 1968). In South Africa the main tillites lie above an upper Ordovician fauna and are overlain by sediments which have not been dated (Cocks *et al.* 1970). Elsewhere, all that is known is that the beds above the tillites are generally Silurian and the beds below are of rather variable Ordovician age.

An alternative approach to the dating of glacial periods is to monitor sea-level changes. The growth and decay of an ice-sheet requires that water be withdrawn and subsequently returned to the oceans and that these changes are reflected in glacio-eustatic sea-level changes and in the isotopic composition of sea water (e.g. Shackleton 1977).

In order to establish that eustatic sea-level changes have occurred it must be demonstrated that there were synchronous sea-level changes on several unconnected plates. It is more difficult to establish whether the changes were glacio-eustatic or were tectono-eustatic, i.e. the result of changes in the configuration of ocean basins. However, it does appear likely that there was a substantial difference in the rates of sea-level change associated with glacio-eustatic and tectono-eustatic events (Pitman 1978). Evidence from the Pleistocene indicates that whilst the growth of an ice-cap may take several million years, the cyclic changes of climate within the major glacial period last tens of thousand of years and cause large glacio-eustatic sea-level changes over the same time scale (Shackleton 1977). The decay of an ice-cap and the related rise in sea-level are apparently particularly rapid. In contrast tectono-eustatic changes usually operate over millions of years. In favourable circumstances it should be possible to discriminate between transgressive deposits formed by rapid glacio-eustatic sea-level and those deposits which were formed during the slower tectono-eustatic changes.

Throughout Ordovician times Gondwanaland apparently occupied a polar position so there existed the potential for a land based, polar icecap. The strong climatic zoning demonstrated by Spjeldnæs (1961, 1981) supports the existence of cold polar climates. Within the Ordovician there were several Ordovician transgressions at least one of which appears to have been eustatic (McKerrow 1979), but the evidence for eustatic regression is not strong, except at the end of the Ashgill. It is therefore uncertain whether there was any substantial growth or decay of ice-caps before the Hirnantian.

The late Ordovician sedimentary changes are, in contrast to those earlier in the Ordovician, particularly distinctive because in many sections there is an abrupt change from deep to shallow water deposits, and a subsequent abrupt reverse change to deeper water facies, reflecting a rapid rise in sea-level. These particular changes are widely recognised (Berry & Boucot 1973) on plates which were separate in Ordovician times, and fulfill the criteria for glacially controlled sea-level changes. Furthermore, these events correlate very well with the Moroccan evidence for the glaciation being late Ashgill.

Using this evidence of sea-level changes, it is possible to identify quite precisely the time at which the ice caps grew. The first evidence of regional shallowing occurs at the base of the Hirnantian, where in the type Ashgill sequence in England, for example, the Cautley Mudstones with a fauna generally dominated by trilobites give way upwards to mudstones with a sparse brachiopod fauna (Ingham 1966). A similar change occurs at the same stratigraphic level in the Oslo region of Norway (Brenchley & Cocks 1982). However, in both these places shelf mudstones persist through the lower part of the Hirnantian and the first influx of sandstones marking a strong regressive phase is higher in the sequence. It therefore appears that the drop in sea-level which drained many of the continental shelves did not reach completion until sometime well within the Hirnantian Stage (see bathymetric curve, Fig. 7). The reverse change from shallow to deeper water deposits is a sharp one in most sections and is at the top of the Hirnantian. It apparently occurred either within the *G. persculptus* Zone (lowest Zone of the Silurian) or at the base of the zone, but the exact position is still a matter for debate (Ingham & Williams 1982). If the late Ordovician glaciation spanned only the Hirnantian Stage and the glacial maximum occupied only a part of the stage it is likely to have lasted for less than 2 m.y. (Brenchley & Newall 1980).

Oscillations of sea-level within the glacial period

Pleistocene oceanic sequences preserve a record of $0^{16}/0^{18}$ isotopic composition in planktonic and benthonic foraminifera which shows that oceanic temperatures have changes through cycles of approximately 20,000, 40,000 and 100,000 years duration (Hays *et al.* 1976). The 20,000 and 40,000 year cycles are similar to those predicted by Milankovich (1938) on astronomical grounds and are believed to be related to changes in the orientation and obliquity of the earth's axis. The 100,000 year cycle appears to be related to the eccentricity of the earth's orbit, but why it should have a dominant influence is obscure because its likely effect on insolation appears to have been too small to have been a major climatic influence.

Similar climatic cycles might be expected to have taken place during earlier glacial periods, so we have looked for evidence, both in the field and from existing literature, for oscillations in sea-level within the span of the late Ordovician ice age. The evidence is unfortunately scattered and equivocal.

In the Hirnantian of the Oslo Region there are locally developed successions showing three tidal channel sequences stacked vertically one above the other (Brenchley & Newall 1980). These could reflect oscillation in sea-level, but equally well they might have been formed by three episodes of tidal channel migrations across the area in conditions of constant subsidence. Possibly more significant are the karstic surfaces, one within and one at the top of a Hirnantian carbonate sequence, in the Oslo Region (Hanken 1974). Further suggestive evidence comes from Iberia where, in Celtiberia an Ashgill limestone formation (the Urbana Limestone) has a karstic top reflecting emergence (Carls 1975) and is succeeded by glacio-marine tilloids (Orea Shales) indicating an episode of marine transgression. Quartzites above suggest a later regressive phase, whilst a further trangression is indicated by dark graptolitic shales of Silurian age. A rather similar sequence is developed in clastic rocks in the Dornes area of Central Portugal where shales pass upwards into quartzites in a regressive sequence. These are succeeded by tilloids, more quartzites and finally by shales of Silurian age (Cooper 1980). Although the stratigraphic control is poor at these horizons the sequences might reflect an early Hirnantian regression followed by a rise in sea level associated with floating ice, then a further period of emergence and finally the drowning of the region at the start of the Silurian.

In conclusion, although at least one oscillation in sea-level is tentatively recognised, there is no clearly preserved record of climatic cycles comparable with those of the Pleistocene. However, the Pleistocene record on the continental shelves is very incomplete, and without the foraminiferal and $0^{16}/o^{18}$ record in oceanic cores, the long and complex climatic history of the Pleistocene would not have been recognised. It seems unlikely that there was a long succession of late Ordovician glacials and interglacials, but the matter has not yet been proved.

Late Ordovician Environmental Changes

The evidence for world-wide development of regressive facies or disconformities and their relationship to glacio-eustatic sea-level changes has been reviewed bu Berry & Boucot (1973). The following account describes the environmental changes in stable platform to deep basin areas of Europe which in Ordovician times were situated in peri-Arctic to tropical latitudes.

Rawtheyan high standard of sea-level

While sea-level stood at a relatively high level during the Ashgill the continental shelves and platforms were covered by sea and blanketed by rather uniform terrigenous muds or carbonates (Fig. 2). The basin also received mainly muddy sediment while turbidite deposition was limited to tectonically active regions.

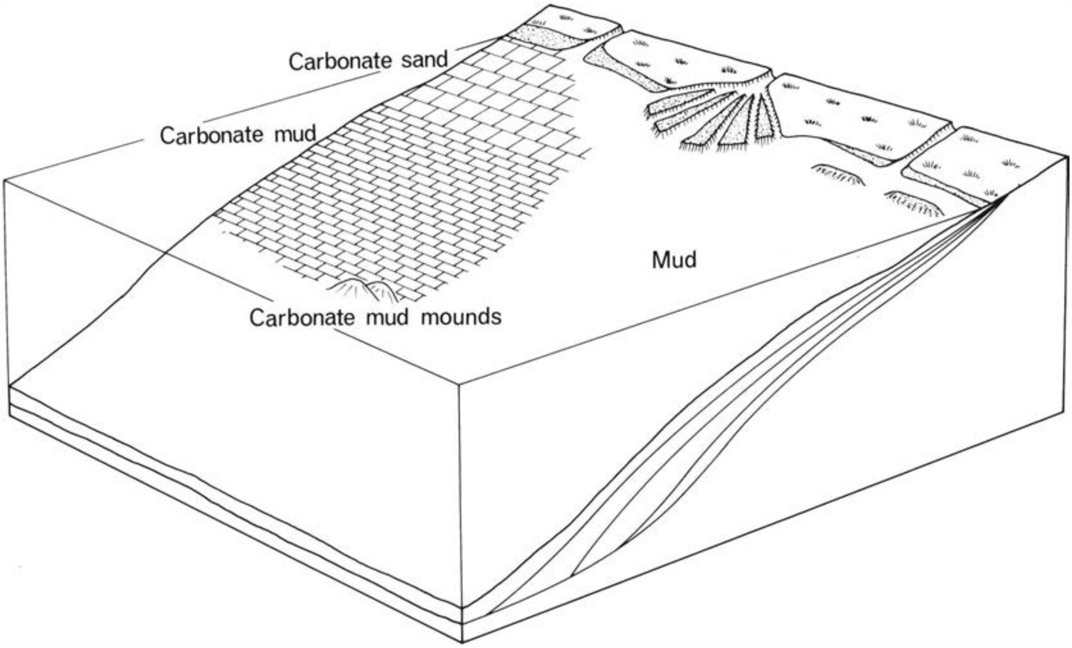

Figure 2 – Reconstruction of generalised facies distribution during Rawtheyan high stand of sea-level.

Hirnantian low stand of sea-level

The glacio-eustatic lowering of sea-level during the Hirnantian produced radical environmental changes both on shelves and in basins, which left a clear imprint on the stratigraphic record.

1) On clastic shelves in areas where sand was generally scarce, there was little or no aggradation of sediment during the period when sea-level dropped. Shales of Rawtheyan age were commonly cut by channels which subsequently filled with silts and sands, so that the sequences show Hirnantian sandstones lying on Rawtheyan mudstones with a sharp erosional contact (Brenchley & Newall 1980). Many of the sandstones filling the channels contain an *Hirnantia* fauna and may exhibit large-scale cross-stratification, but are more commonly massive, so that deposition within the channels appears to have been generally rapid. The exact timing of the filling is uncertain, but they might have been filled either during the initial regressive phase, during an intra-ice-age rising in sea-level, or during the rise in sea-level at the end of the glaciation.

2) On clastic shelves where there was a sufficient supply of sand to maintain continuous deposition during the early Hirnantian regression, there was shoreline progradation (Fig. 3), forming regressive, upward coarsening sequences (e.g. Oslo Region, Norway; Brenchley & Newall 1980; and Central Portugal, Cooper 1980). The shoreface sandstones associated with these sequences commonly have ball-and-pillow structures and other syn-sedimentary deformation structures suggesting that the rate of sedimentation of at least some of the beds was particularly rapid (i.e. centimetres per day).

3) In deep shelf areas there was continuous deposition of mainly argillaceous sediments from the Rawtheyan through the Hirnantian and these areas were never emergent. However, the beginning of a fall in sea-level at the Rawtheyan/Hirnantian boundary is indicated by a change from mainly trilobite-dominated faunas in the Rawtheyan to the brachiopod-dominated faunas of the Hirnantian (e.g. at Cautley in Northern England; Ingham 1966; near Bala in North Wales, Bassett *et al.* 1966).

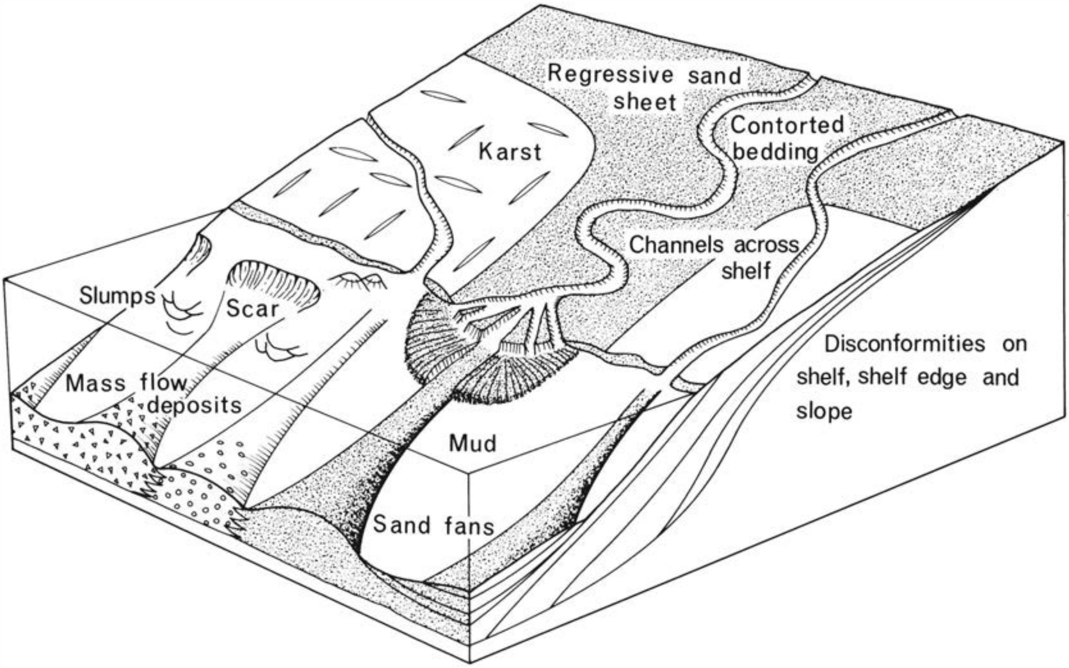

Figure 3 – Reconstruction of generalised facies distribution during Hirnantian low stand of sea-level.

Later in the Hirnantian there were times when channels were formed in these areas and filled with sediment derived from near the shoreline. The fill of these channels, which cut the deeper part of the shelf, is very variable and includes ooids at Bala (Bassett *et al.* 1966), and a variety of ill-sorted breccias suggesting rapid deposition (Cautley) and possible mass flows such as the breccias in the Coniston Limestone in Northern England (the latter were described as fault breccias by Mitchell 1956) and breccias at Portrane, Ireland (Lamont 1941).

4) Carbonate shelves were generally emergent during the Hirnantian and have karst surfaces (Fig. 3). In some areas there is relief of several metres on the erosional surface (e.g. Celtiberia, Spain; Carls 1975) but elsewhere the karst surface may only have a relief of tens of centimetres and the upper surface of the limestone is planar for tens or hundreds of metres (e.g. Cystoid Limestone, central Spain; Hafenrichter 1979). The carbonate mud mounds of central Sweden became exposed during the Hirnantian and have well developed microkarst surface on the crown and upper flanks (Brenchley & Newall 1980).

5) The shelf edge, never an extensive area, is not easily recognised in ancient rocks. However there is some evidence to suggest that the shelf margin might have been deeply notched during the Hirnantian low stand of sea-level (Fig. 3). At two places in Wales close to the shelf-slope break there is evidence of deep, late Rawtheyan or early Hirnantian erosion. At Bala, nearly 500 m of Moelfryn Mudstones (Rawtheyan age) could be missing locally (Bassett *et al.* 1966) and at Garth on the Towy anticline nearly 100 m of Rawtheyan mudstones are missing (Williams & Wright 1981). The stratigraphical relationships have been interpreted as unconformities of tectonic origin but an alternative explanation is that the erosion was caused by channelling of the shelf margin comparable to the notching of the shelf margin by canyon formation during the Pleistocene. The erosion surface at Bala is covered by a thin veneer of Hirnantian sandstones, whereas Garth there is a lenticular sandstone fill as

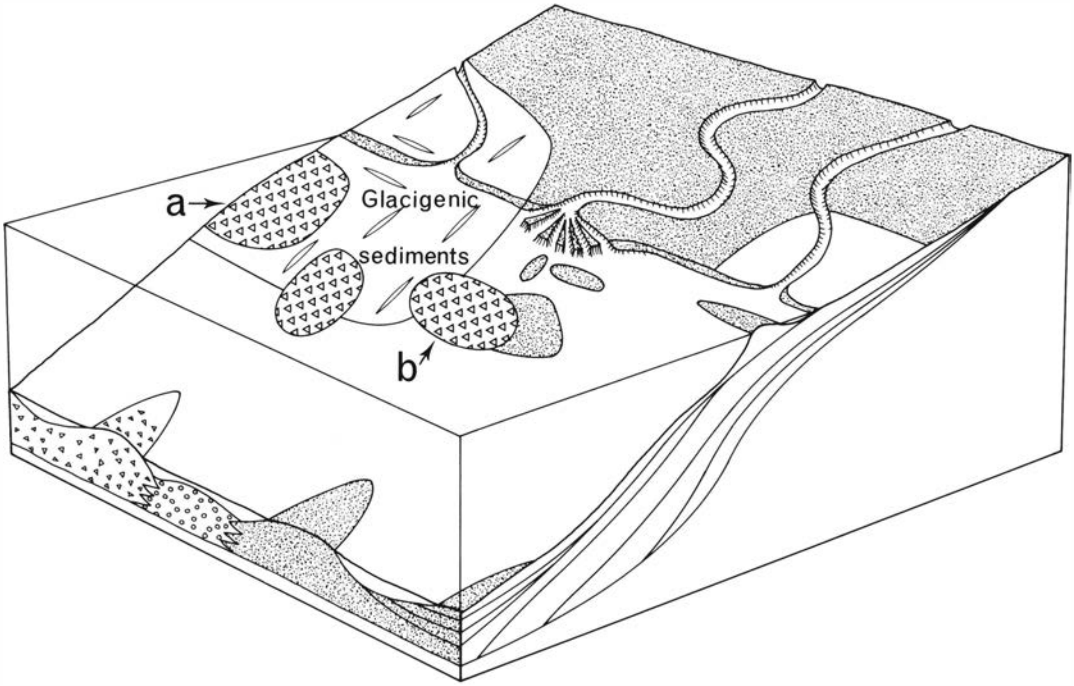

Figure 4 – Reconstruction of generalised facies distribution during minor rise of sea-level in late Hirnantian times, with deposition of glacio-marine tilloids. "a" indicates localities with tilloids over limestone with karst, "b" shows tilloids on a regressive sandy sequence.

much as 50 m thick.

6) On slope environments the Hirnantian is marked by a phase of sediment instability and the formation of large slump sheets (for example in the Towyn-Abergynolwyn District in Wales; James 1971). In stratigraphic sequences the monotonous mid-Ashgill shales are succeeded by shales and turbidites with slumps on a variety of scales.

7) In basin areas the Hirnantian was marked by an influx of gravity flow sediments, ranging from mass flow deposits to turbidites (Fig. 3). Major deep sea fans have been recognised in Wales at Plynlymmon (James 1972), Llangranog and Corris (James & James 1969). A base of slope fan, developed in much shallower water and containing bioclastic and shelf carbonates, was formed near Conway, North Wales (James & James 1969). The widespread evidence of sediment instability and accumulation of thick gravity flow deposits, suggests that sedimentation rates on the basin slopes and floor were unusually high during the Hirnantian. Comparably high rates of sedimentation, an order of magnitude higher than normal, are known from Pleistocene deep sea sediments (Davies *et al.* 1977). The late Ordovician glacio-eustatic sea level changes are reflected in basin areas such as the Welsh Basin by stratigraphic sequences with Ashgill mudstone overlain by gravity-flow deposits. The exact age of the change in sedimentation cannot always be determined but it is close to the Rawtheyan/Hirnantian boundary.

Hirnantian glacio-marine deposition

Many localities in Iberia have sequences with tilloids which usually succeed either a regressive sandy sequence or lie on a karstic limestone surface. The presence of karst with only a shallow erosion surface at several localities suggest that the climate may have been cold and dry and chemical weathering was consequent-

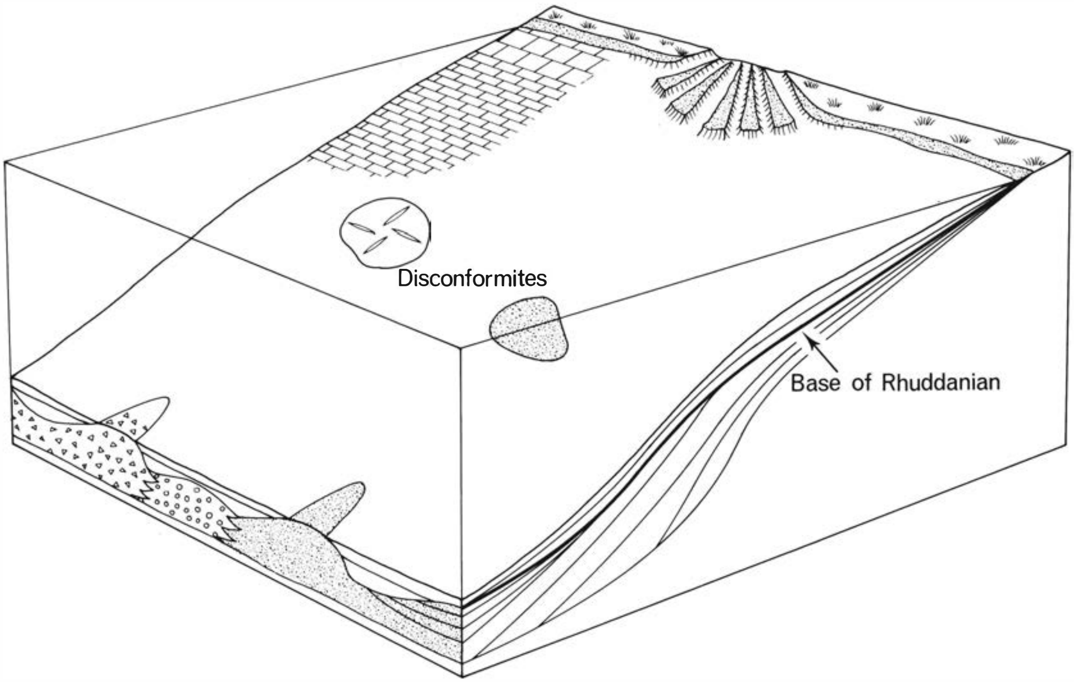

Figure 5 – Reconstruction of generalised facies distribution during Rhuddanian high stand of sea-level.

ly restricted. The presence of limestone clasts (of Ashgill age) in the tilloids indicates that ice was at least locally grounded on a limestone surface and that, although some mechanical erosion occurred, the ice cover may have prevented deep chemical erosion. Figure 4 shows a generalised reconstruction of the kind of palaeogeography which would have produced the Hirnantian sequences containing tilloids.

The Ordovician/Silurian rise in sea-level

In most areas in both shelf and basin successions there is an abrupt upward transition from the heterogeneous Hirnantian facies to the uniform, dark grey and generally carbonaceous shales of the Silurian (Fig. 5). In shelf regions the transgressive sea did not substantially rework and remould the underlying clastics (e.g. Oslo Region, Brenchley & Newall 1980), and the rise in sea level was apparently as fast as the Recent post-glacial rise (i.e. it spanned only a few thousand years). Only in the channels, which were incised across the shelves could there have been substantial deposition of sand during the post Ordovician rise in sea level, and even some of these were incompletely filled. In deep shelf, slope and basin successions, dark grey graptolitic shales usually lie with a sharp contact on the Hirnantian grey mudstones and turbidites.

The oldest graptolitic shales contain a fauna of the *G. persculptus* Zone, but at many localities, both in shelf and the basin sequences several zones are missing at this level and the lowest Silurian faunas may be as young as Wenlock age. Such disconformities in deep marine areas are becoming well known from D.S.D.P. cores, and apparently reflect a balance between rates of sedimentation and erosion by oceanic currents (Kennett 1982: 93). Experience of Tertiary to Recent sequences has shown that, although there were vigorous bottom currents and associated erosion during the Pleistocene, the high sedimentation rates nevertheless produced a substantial net accumulation. The periods for which the Tertiary record is most incomplete (Moore *et al.* 1978) are earlier in the Tertiary when although bottom currents were probably more sluggish, sedimentation rates were even more reduced. The early Silurian disconformity might therefore reflect a rise in sea-level which flooded the shelves and reduced sedimentation rates to a minimum.

The environmental changes outlined above are believed to have been the result of sea-level changes of 50–100 m (Brenchley & Newall 1980). The exposure of shelves during low-stand of sea-level with resultant formation of channels and disconformities, the development of submarine fans in deep water, and rapid coastal onlap during the major episode of sea-level rise are all predicted by the models of Vail *et al.* (1977) based on a knowledge of Pleistocene to Recent changes and evidence from seismic profiles.

The models we have outlined apply to a "usual" range of sedimentation rates and vertical tectonic movements and would be modified by a) unusually high sedimentation rates, or b) very active tectonics. High sedimentation rates would have particularly affected sequences developed during the earliest Silurian transgression. In extreme cases, instead of there having been coastal retreat at this time, unusually high rates of sedimentation could have caused coastal progradation even in the face of rapid sea-level rise (Vail *et al.* 1977; Heward 1981: 233). In such situations the Ordovician/Silurian boundary could lie within an unbroken sandstone sequence, as for example in the Queenston delta of the Eastern North American (Dennison 1976).

Active vertical tectonics with the same sense of movement as the sea-level changes could have effectively masked the glacio-eustatic effects. If, however, the sea-level changes were as rapid as we have suggested, tectonic movements of a comparable rate are likely to have been uncommon.

Because glacio-eustatic sea-level changes are synchronous, and because they leave a distinctive mark on the stratigraphic record, they have considerable chronostratigraphic significance, as in the final choice of level at which the Ordovician/Silurian boundary should be drawn. The widespread development of a disconformity at the top of the Hirnantian, both in shelf and basin areas suggests that if the boundary is placed either at the base of the *persculptus* zone or the base of succeeding *acuminatus* zone it will lie within a depositional hiatus in many sections throughout the world.

The late Ordovician extinction

An extinction episode of late Ordovician age was one of several such events recognised by Newell (1967) in his review of the Phanerozoic fossil record. More recently Raup & Sepkoski (1982) have identified a late Ordovician peak of family extinction, which is significantly above background extinction levels (Raup & Sepkoski 1982, Fig. 1) and is one of four mass extinctions which they identify in the fossil record.

The late Ordovician extinction peak is, however, almost certainly a composite peak composed of a late Caradoc to early Ashgill reduction in species diversity and a separate late Ashgill episode of extinction. The first wave of extinction resulted from plate movements which reduced the width of the Iapetus Ocean and allowed interchange of benthic faunas. Separate trilobite faunal provinces on either side of the Iapetus Ocean had lost their distinctive character before the middle Caradoc (Whittington & Hughes 1972) and brachiopod provinces had essentially merged by early Ashgill times (Williams 1976). The unification of these separate provinces into one single province almost certainly accounts for the reduced late Caradoc early Ashgill diversity in some groups. The second wave of extinction is stratigraphically quite distinct from the earlier one, and was confined to the late Rawtheyan and Hirnantian stages.

The magnitude of the extinction was considerable but different groups were affected to a different degree. Most data on changes in taxonomic abundance are plotted for series and not stages, so the following account initially refers to extinctions within the Ashgill Series. Later, data will be used to demonstrate specifically Hirnantian extinctions.

There is little evidence of a late Ordovician extinction of orders, but several phyla show evidence of reduction in the number of families and genera present (Fig. 6). Thirty eight families of trilobites in the Ashgill were reduced to fourteen in the early Silurian (Jaanusson 1979)

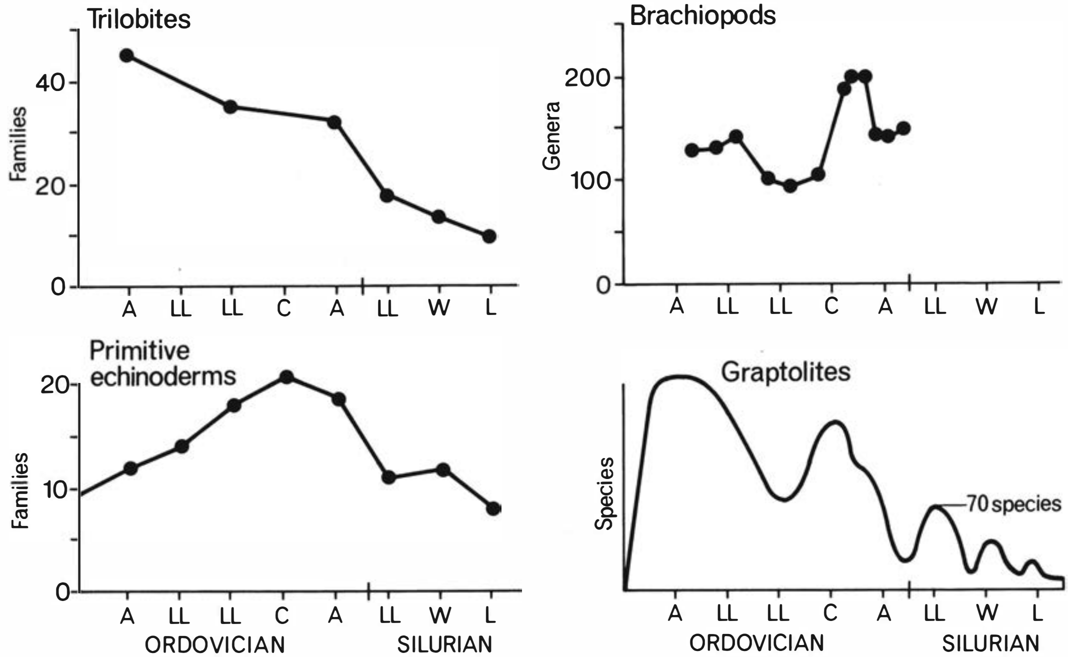

Figure 6 – Changes in taxonomic abundance through the Ordovician and Lower Silurian of (a) trilobites (data from Harrington 1959), (b) brachiopods (after Fig. 151, Williams 1965), (c) Cystoidea, Cyclocystoidea and Edrioasteroidea, unpublished data C. R. C. Paul) and (d) graptolites (after Fig. 3, Koren & Rickards 1979).

and cystoids too show a substantial drop in family diversity (Paul 1980). Generic and species diversity was substantially reduced in groups such as the brachiopoda (Williams 1965) and graptolites (Koren & Rickards 1979). Other elements of the plankton such as acritarchs (C. Downie, pers. comm.) and conodonts (cf. Orchard 1980) were apparently reduced in specific diversity in Hirnantian rocks though this stratigraphic interval still remains to be studied in detail. The diverse tabulate and heliolitid coral faunas of the late Ordovician, which are represented by about 70 genera were drastically reduced by the loss of about 50 genera prior to the Silurian (Kaljo & Klaaman 1973).

From the above discussion it is clear that the late Ordovician extinction affected most elements of the biota, including the sessile, filter feeding, shelled benthos, the vagile benthos, the phytoplankton and zooplankton.

The following data suggest that the time of extinction was slightly different for different groups, and ranged from late Rawtheyan or early Hirnantian times to late Hirnantian times. At least 10 of the trilobite families that became extinct, did so in the Rawtheyan and especially towards the end of the stage. At the generic level they show there was a high percentage of survival from stage to stage through the Ashgill until the end of the Rawtheyan, when only about 15% survived into the Hirnantian (Fig. 7). These figures are drawn from European localities which would have ranged from mid-latitudes to the southern tropics in late Ordovician times, but the data appear to be valid for all the climatic zones.

The timing of graptolite extinction relative to that of benthonic groups is difficult to determine because the late Ordovician graptolite zones are not precisely correlated with the Ash-

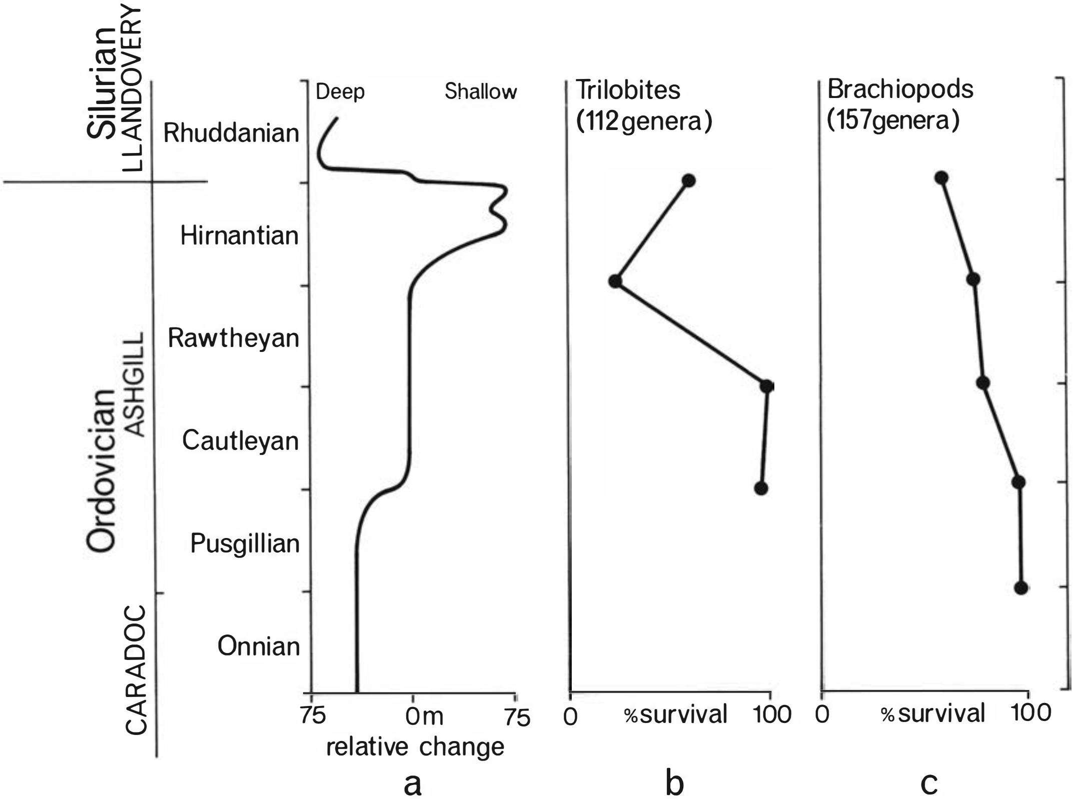

Figure 7 (a) Estimated relative changes in sea-level in the Upper Ordovician (Brenchley & Newall 1980), (b) Percentage survival of genera from stage to stage in the Upper Ordovician/Lower Silurian e.g. 93% of Pusgillian tilobite genera from selected localities in Europe, survived into the Cautleyan, (c) Percentage survival of brachiopod genera. The graphs are based on genera found in sequences with good stratigraphic control in Britain, Scandinavia and Poland.

(The data are drawn from twenty two references, including Bassett et al 1966; Bergström 1968; Brenchley & Cocks 1982; Dean 1959, 1971, 1974, 1977; Hiller 1981; Ingham 1966; McNamara 1979; Owen 1981; Price 1980; 1981; Temple 1965; Williams & Wright 1981, and Wright 1963, 1964). Data concerning total ranges of the genera are mainly from the Treatise of Invertebrate Palaeontology.

gillian stage boundaries based on shelly facies. The trough in graptolite diversity occurred in the *extraordinarius* Zone and though it may have extended into the *persculptus* Zone (Koren & Nikitin 1982) it certainly preceded the end of the Hirnantian and could thus have coincided with trilobite extinction at the Rawtheyan/Hirnantian boundary, but this has yet to be proved. The conodonts and acritarchs appear to have been reduced in numbers at the Rawtheyan/Hirnantian boundary within Europe but elsewhere assemblages persisted in more tropical regions and on Anticosti Island (Achab & Duffield 1982) are found nearly up to the Ordovician/Silurian boundary. There is however, a short length of section at the boundary which lacks chitinozoa and a significant change in the composition of the acritarch floras occurs here. Skevington (1974) has suggested that the low level of provinciality amongst graptolites in late Ordovician times reflects a reduction in the number of habitable climatic belts to a single tropical zone. This interpretation could be reasonably applied to the other planktonic groups.

In contrast to the trilobites, the brachiopods do not appear to have been nearly so severely affected at the Rawtheyan/Hirnantian boundary (Fig. 7), and the persistence of many genera from the Rawtheyan into the Hirnantian is reflected in some Hirnantian brachiopod faunas of considerable diversity (Bergström 1968; Williams & Wright 1981; Brenchley & Cocks 1982). There was, however, some reduction of diversity before the Hirnantian (Lespérance 1974) and a further reduction before the basal stage of the Silurian, implying a late Hirnantian extinction.

Two principle hypotheses have been proposed to account for the late Ordovician extinctions. One is a lowering in water temperature related to the Gondwana glaciation, and the second is exposure of the continental shelves following the glacio-eustatic fall in sea-level (Sheehan 1973, 1975, 1979; Jaanusson 1979).

The significance of the stratigraphic dating of the extinctions outlined above is the demonstration that the first wave of extinction commenced when sea-level started to fall but preceded the main rop in sea-level. This fall is unlikely to have caused extinction by reducing the area of the continental shelves. On the other hand, the second wave of extincttions which reduced the variety of shelly sessile benthos could have been related to lowered sea-level and the decrease of habitable areas.

The cause of the first wave of extinctions remains obscure, particularly because substantial changes of temperature during the Pleistocene glaciation did not produce such waves. Biotas were apparently able to move with the shifting climatic belts (Berger & Berger 1981; Ford 1982) and, given time, some appear to have been able to adapt to a temperature regime outside their accustomed range (Ford 1982: 29). It could be that the crucial effect was not temperature *per se* but the cooling of surface waters outwards from the polar region which contracted the plankton belts to such a degree that habitable areas was severely reduced, and extinction resulted. Moreover, the very extensive epicontinental seas of the mid-Ashgill may have had niche-specific, highly adapted faunas, which were ill-equipped to withstand rapid environmental changes. This was in marked contrast to the conditions in the Pleistocene. Furthermore it is likely that the rate at which the Ordovician ice cap developed was considerably faster than the Pleistocene. There appears to have been a gradual cooling of climate from the early Tertiary and ice probably began to develop in the Antarctic at least as early as the Miocene (Kennett 1982: 730). The build up of the polar ice caps was progressive, though step-like, over as much as 20 million years. The evidence for the Ordovician though less precise, suggests that, although polar climates may have been present throughout the Ordovician, there was a particularly rapid onset of glaciation at the beginning of Hirnantian times implying a rapid decrease in marine temperatures and a sharp contraction of the climatic belts in a matter of 1 million years. Temperature, and related climatic changes certainly have a profound affect on the distribution of fauna in the short term (Ford 1982) and if the decline in temperature was sufficiently rapid this might have been fatal to many species.

It appears likely that no single factor caused extinctions (cf. Jaanusson 1979), but that extinctions were caused by a complex combination of circumstances. Nevertheless we believed it is possible to isolate some of the major causes of extinction, and that contraction of the climatic belts in early Hirnantian times as envisaged by Skevington (1974) and Sheehan (1979) was initially a significant factor while contraction of habitable area in later Hirnantian times was a later contributory cause. It is also possible that there were even further extinctions, as Jaanusson (1979) has suggested, when the early Silurian rise in sea level flooded many shelf areas to considerable depths and there was an accumulation of black euxinic muds inimicable to a bottom living shelly benthos.

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