

# Global earlier Ordovician transgressions and regressions and their biological implications

By RICHARD A. FORTEY

Global marine transgressions and regressions serve to define the original Series into which the earlier part of the Ordovician System was divided. The biological effects of these cycles are variously, but simultaneously expressed on what were independent continental blocks at the time. The faunal changes which occur at Series boundaries are as much a product of environmental shift as of evolutionary novelty. Scarcity of recoverable deep water facies from tectonic causes and partly from lack of searching) during regressive phases has meant that "ancestral" faunas have been generally overlooked, but they can be found in the correct sites in areas peripheral to former continents. Thus some of the "Llanvirn faunas" (transgressive) of Ordovician Gondwanaland can be identified in Arenig off-shelf occurrences in peripheral sites, and the "Middle Ordovician" North American fauna has a progenitor in what is believed were earlier rocks in Spitsbergen. Conversely, times of regression exposed offshore islands, and many (but not all) of these island faunas correspond with regressive intervals on the platform. Faunal interchange in relatively uniform deep water faunas may have proceeded in advance of major changes in provinciality, which are manifest when these faunas move shelfwards during transgression. These ideas are discussed in relation to trilobite and graptolite biofacies during the Tremadoc to Llandeilo. The eustatic changes could have been caused by fluctuations of a Gondwanan Ice Sheet.

*R. A. Fortey, Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW 7 5BD, England.*

In recent years a number of authors have drawn attention to the broad geological effects of transgressions and regressions during the Ordovician (Vail *et al.* 1977; Leggett 1978; Leggett *et al.* 1981). Major sea level changes of this type have been implicated in faunal changes which occurred during the Ordovician (Shaw & Fortey 1977; Jaanusson & Bergström 1980; Ludvigsen 1982). In this paper I attempt a brief overview of the biological effects of transgressions and regressions during the earlier part of the Ordovician. In a review of this length it is not possible to give detailed documentation of all the assertions; I have concentrated on a number of critical instances which may be used in support of the general picture.

Recognition of global as opposed to local events

Regressive-transgressive events can operate on

various scales; those which are addressed here are believed to have been major eustatic events independent of local tectonic circumstances. Especially in mobile sites at active continental margins during the Ordovician, there may be complex regional transgressions or local unconformities which may seem locally more significant than the more general eustatic events, and which may operate to enhance or oppose such events. Criteria which may be used to distinguish eustatic events of more than local significance are judged to be particularly:

1. That simultaneous regressions or transgressions occur on what were separate continental blocks (i.e. belonging to separate lithospheric plates), thus minimising regional influence.
2. That the events will be regionally correlatable in a consistent way. A transgressive event, for example, may be expected to in-

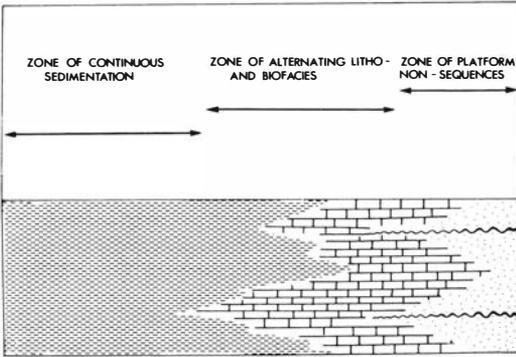


Fig. 1 – The simplest type of facies distribution patterns connected with transgressive and regressive cycles. Platform sandstones to right grading through limestones to deeper water shales. During regressive phase unconformities should coincide with exterior migration of limestone facies.

produce sediments onto cratonic areas for the first time since the last transgression, and this should be directly correlatable with events such as facies changes in peripheral cratonic sites where sedimentation is otherwise continuous. (Fig. 1.)

3. Only truly off-shelf sites, which are generally developed in graptolite facies in the Ordovician, are relatively immune from the effects of transgressive-regressive cycles. These are to be taken as the standard when assessing what might be "missing" in platform regions.

Both correlation between open-ocean facies and shelf faunas, and between widely separated cratonic areas – especially if they were at different palaeolatitudes – pose particular stratigraphic problems, a product of the more-or-less patchy distribution of the biostratigraphic indices. It is important to avoid circular arguments (for example, making an *a priori* assumption that two approximately coeval regressive

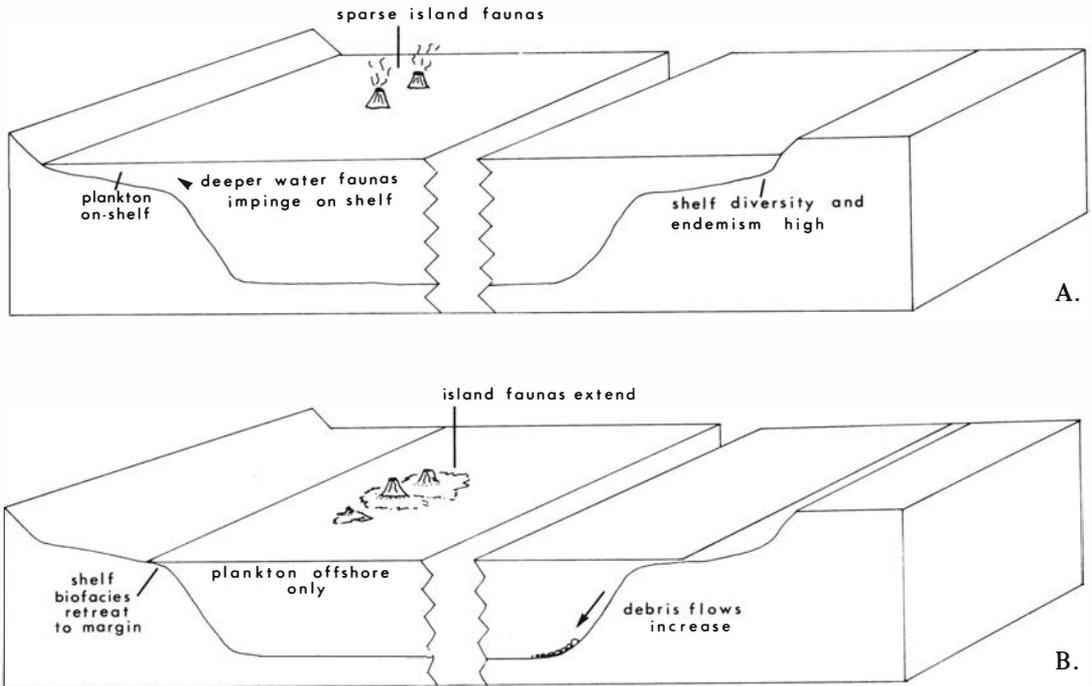


Fig. 2 – Cartoon representing some of the effects predicted during times of transgression (A) and regression (B) on opposing continental blocks.

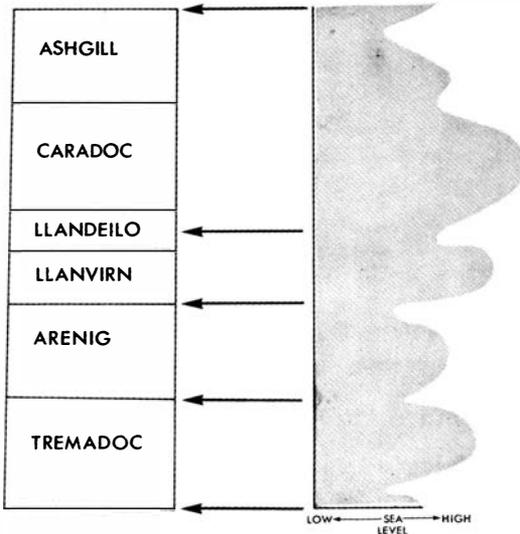


Fig. 3 – Times of proposed maximum regression (arrowed) with hypothetical sea-level curve to right.

cycles are exactly contemporary just *because* they are regressive) by treating faunal evidence on its own merits, and separately. The correlations used here are, naturally, my own, and it would be surprising if there were not areas of disagreement with other specialists. I have chosen to treat the Tremadoc to Llanvirn in detail because it is best known to me; there have been numerous recent studies on the regression associated with the late Ordovician glaciation (Sheehan 1973, 1975; Brenchley & Cocks, 1982) and further comment here would be nugatory.

### Biological effects of transgressive-regressive cycles

As a basis for considering the effects of transgressive-regressive cycles on marine organisms, assumptions are made concerning the distribution of biofacies in a profile running from the interior of cratonic areas to the open ocean (Fig. 2). This is developed from the trilobite-based biofacies/community-type analyses of Fortey (1975, 1980), Ludvigsen (1975) and Cocks & Fortey (1982). Inner shelf-to-slope transects are interrupted in tropical latitudes by a carbonate mound facies which does not have a counterpart at higher latitudes. Volcanic islands are introduced on the assumption that

continental edges were active margins in many places.

### A. Transgression

During a relatively transgressive phase the following biological effects are predicted: (Fig. 2)

1. Flooding of cratonic areas will produce widespread shallow epicontinental seas. Spatial heterogeneity (Eldredge 1974) and the "species area" effect (Ludvigsen 1982) will play a part in inducing high speciation rates in epicontinental areas. Cratonic areas separated – especially by latitude – from their neighbours will generate endemic taxa.
2. As transgression proceeds, and especially in more exterior sites, previously extra-cratonic biofacies will be brought on to the shelf. Such changes will be more or less diachronous according to the rapidity of transgression (below). In some cases this may entail displacement shelf-wards of faunas usually living below the thermocline, and may produce extinctions of shelf forms.
3. Because deep water faunas are more independent of continental boundaries, times of transgression may *appear* as times of provincial breakdown.
4. In tropical areas mound faunas will migrate on-shelf.
5. Island faunas will be generally rarer as offshore 'highs' are immersed. This will apply only in the broadest sense, because active vulcanicity will overtake transgressive events in some circumstances.

### B. Regression

During a relatively regressive phase the following biological effects are proposed:

1. Interior cratonic sites will either have stratigraphic gaps, or, seawards, super- or infratidal deposits poor in fossils. These might be dolomites in the tropical regions or Grès Armorica facies (Dean 1976) at high latitudes.
2. On the cratonic interior, across such a regressive phase, faunas will appear to change

with a taxonomic jump, which will not be so apparent in off-shelf faunas.

3. Retreat of biofacies seawards will mean that the "ancestors" of the faunas which are found on-shelf during transgressive phases must be sought in peripheral sites. Because such sites are narrow, and often involved in subsequent tectonism, or over-ridden by nappes, they will be uncommon.
4. Conversely, regressive phases will tend to *increase* the incidence of island faunas (or faunas fringing microcontinents) by a greater extension of surrounding productive shelves, and by bringing formerly submerged volcanic islands to shallow sub-littoral depths. These faunas will thus tend to belong in the cratonic "gaps"; exceptions are noted above.
5. Mound faunas in the tropics will be near the edge of shelf areas. Regressive phases will coincide with times when allochthonous debris-slides from such sites were at a maximum, as in the Cow Head Group, western Newfoundland (James *et al.* 1979).
6. Both mounds and islands may provide sites of retreat for shelf forms, and, if new taxa also originate there, may appear to anticipate the younger faunas of ensuing transgressive phases.

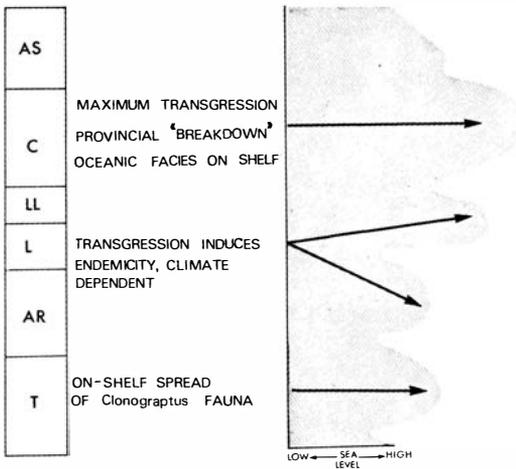


Fig. 4 – Some of the important events in Ordovician faunal dynamics related to the sea-level curve.

## Times of regression and transgression

Using the criteria for recognition of worldwide transgressive-regressive events listed above, the following times are suggested for the climaxes of cycles (Fig. 3).

### Basal Tremadoc

This is a time of regression; its world-wide character was suggested by Miller (1978), and reiterated on different evidence by Leggett *et al.* (1981). In this paper, evidence of its effects can be deduced from what happens around several independent continental areas at the time.

(a) On the Gondwanan margin of Iapetus, in the Anglo-Welsh area, which embraces a craton-to margin profile, sedimentation across the Cambro-Ordovician boundary is complete only in the peripheral area in North Wales recently documented by Rushton (1982). Elsewhere in North Wales the *Acerocare* Zone is missing, or represented in a phosphate horizon. At the edge of the craton, in Shropshire, there is a considerable non-sequence, with a shallowing-upward Cambrian sequence (glaucinitic shales) doubtfully as young as *Peltura* Zone, overlain by Tremadoc beds with *Dictyonema flabelliforme*, but excluding the oldest subspecies of this species group.

(b) On the North American craton the interval embraced by the *Corbinia apopsis* Subzone of Upper Cambrian age, the *Missisquoia* Zone, and the early *Symphysurina* Zone (Ordovician) marks the maximum regression and the beginnings of the ensuing transgression (Miller 1978; Ludvigsen 1982; Fortey *et al.* 1982). It has recently been shown that the base of the Tremadoc can be correlated with an horizon, either in the upper part of the *Missisquoia* Zone or more probably, early in the *Symphysurina* Zone. The regression in North America is therefore coincident with the regressive event in the type Tremadoc area.

(c) In platformal Australia (Queensland), the Upper Cambrian terminates with a typical shallowing-upwards sequence of regressive sandstones, overlying fossiliferous limestones. As Miller (1978) pointed out, the

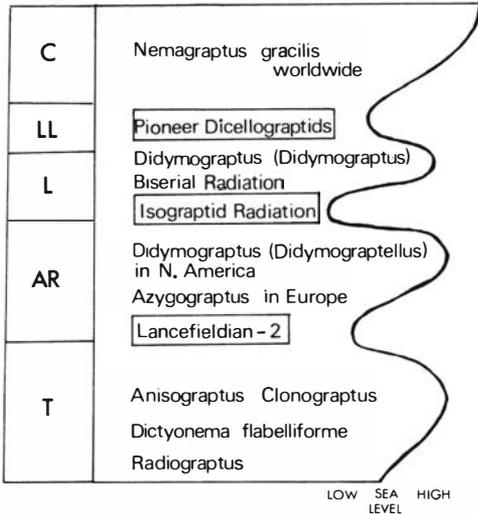


Fig. 5 – Taxonomic and geographical events in graptolite history (see text) related to sea level curve for Tremadoc to Caradoc. Times of regressive maxima shown in boxes.

following Tremadoc transgression, which re-introduces limestone deposition of the Ninmaroo Formation, correlates closely with the "Cambrian-Ordovician" boundary in North America. Miller also notes that the same "event" is recorded in platformal NE Siberia.

- (d) In Scandinavia the regression at the level of the *Acerocare* Zone is well-known (Martinson 1974; Rushton 1982). The Zone is present in the peripheral facies of the Oslo Region (Bruton *et al.* 1982) and Bornholm, for example, but is absent over much of central Sweden and eastwards on to the Russian Platform.

There is thus evidence for a regression at this time in four widely separated (and presumably tectonically independent) regions.

The ensuing transgression brought Tremadoc graptolite faunas more and more on-craton (Fig. 5), with progressively younger "*Dictyonema*" *flabelliforme* subspecies achieving wider dispersal, and culminating in the anisograptid fauna which alone penetrates into peripheral platform deposits in North America (Erdtmann & Comeau 1980). Endemic speciation of on-shelf trilobite faunas paralleled the transgressive phase, laying the foundations of the bathy-

urid faunas of North America, endemic asaphids in Baltoscandia, and such "Gondwanan" elements as Dikelocephalinidae, Orometopidae and Taihungshandiidae.

### Basal Arenig

The possibility of a similar regressive-transgressive event near the base of the Arenig was noted by Fortey (1979); however, correlation between different faunal provinces is especially difficult at this stratigraphic level.

- (a) Again, the type area presents a profile running from relatively inshore facies in Shropshire to peripheral cratonic facies in West and North Wales, and open oceanic in the Lake District. In western and northern Wales (Lynas 1973), the top of the Tremadoc is often a series of regressive sandstones, while the base of the Arenig is everywhere a coarsely arenaceous unit which is probably diachronous eastwards. It is difficult to assess exactly how much of the Tremadoc/Arenig interval is missing, or represented by these shallow-water deposits. Certainly there is as yet no evidence of the Zone of *Tetragraptus approximatus* in the type area, a Zone which is widespread in truly oceanic facies (condition 3 above) and frequently adopted as the arbitrary base for the Series in continuous graptolitic sequences. It seems likely that the equivalents of the Lancefieldian and possibly the early Bendigonian (Australian oceanic standard) are present in regressive facies in most of England and Wales. As might be expected, in Shropshire the gap is even larger; work in progress by myself and R. M. Owens suggests that here the "basal" transgressive sandstone is middle Arenig.

- (b) On the North American platform shallow water carbonate deposition is predominant through this interval. In western Newfoundland, the St. George Group is generally poor in shelly fossils, but in the Catoche Formation a rich trilobite fauna appears relatively suddenly, including a number of oceanic trilobites and rare graptolites, a response to a sudden "deepening event" (Fortey 1979), which we would associate with the early Arenig transgression. This may be of *T. approximatus* Zone age or slightly younger and

zone H in terms of the sheily North American zones (Ross 1951). Beneath this interval there is some evidence (W. D. Boyce pers. comm.) of missing trilobite zones in the early upper Canadian. Elsewhere along the eastern seaboard of North America where sparse trilobite faunas appear in the Beekmantown (Midcontinent) facies, they also seem to be of Catoche type. In the Basin Ranges of Utah and Nevada, the regressive interval may be represented in the thick intraformational conglomerates at the base of the Fillmore Limestone (Hintze 1973) – here in basinal facies, and overlain by earliest Arenig graptolites (Braithwaite 1976). Intraformational conglomerates are widespread in the Zone F – Zone G interval in the Garden City Formation (Ross 1951). Even in the Marathon region, Texas, a presumably off-shelf graptolitic sequence, the regressive interval may be represented by the Monument Spring Dolomite Member, which Berry (1960) comments "lies completely within Zone 3" (*T. approximatus*). A trilobite from Zone 4, presumably at the early stage of the transgression, is identical to one from the Catoche Formation in Newfoundland mentioned above. Even allowing for the correlation problems involved, it does seem reasonable to assume a regressive event at the Tremadoc-Arenig boundary over the North American platform.

- (c) In central Australia (western Queensland) there is a stratigraphic gap between the Kelly Creek and Nora formations, with an intraformational conglomerate at the base. Unpublished work by myself and J. Shergold suggests that the transgression does not reach the continental interior here until probably Middle Arenig times. In a more peripheral site in the Canning Basin (Legg 1976), so-called Fauna 2 of probably earliest Arenig age is transgressive over ?Precambrian. The evidence is still incomplete on how much late Tremadoc is "missing" in platform Australia, but does support the notion of the early Arenig transgression. The graptolitic facies of Victoria is, of course, unaffected by the regression, and may be the most complete anywhere across this interval.
- (d) Over the Scandinavian platform the dia-

chronous early Arenig transgression has been documented in detail by Tjernvik (1956) and details need not be repeated here. Even progressing from South to North on the island of Öland (Tjernvik 1956, fig. 19) the earlier Tremadoc zones of *Apatokephalus serratus* to *Plesiomegalaspis planilimbata* are cut out – that of *A. serratus* first. This is presumably the time at which the regression was at a maximum. In the more off-shelf facies of the Oslo Region Norway the event is marked by the sudden appearance of the correlative *Ceratopyge* Limestone within the otherwise deeper-water sequence.

The evidence for a world-wide regression again seems persuasive. Since the *Ceratopyge* Limestone is overlain by *T. approximatus*-bearing beds, the time at which the regression was at a maximum may have been Lancefieldian Stage 2 in terms of the complete oceanic sequence of Victoria, Australia (see condition 3 above). This may well account for the extreme scarcity of graptolite faunas of this age. In any case, the transgression probably commenced within the range zone of *T. approximatus*, but may not have reached interior cratonic sites until much later.

During the subsequent Arenig transgression graptolites again appeared in cratonic sequences. In former low latitudes endemic speciation produced a variety of pendent didymograptids, which were absent from cratonic facies at former high latitudes at that time; here, the genera which apparently penetrated into epicratonic deposits were *Azygograptus* and *Corymbo-graptus*, the former entirely absent from the "Pacific" province. These genera presumably constitute the epiplanktonic graptolite fauna, and as such were strongly under latitudinal control for their distribution, but able to penetrate into relatively shallow-water sediments (Fig. 6). The more oceanic graptolitic facies (here termed the isograptid biofacies) is characterised by a richer fauna, including *Isograptus* and *Pseudisograptus*, slender, many-branched sigma-graptines such as *Sigmagraptus* and *Laxograptus*, and probably *Pseudotrigranograptus*. Unlike the epiplanktonic species these were capable of crossing latitudinal barriers but are only found in the most exterior sites. Among trilobite faunas, the Arenig transgression accom-

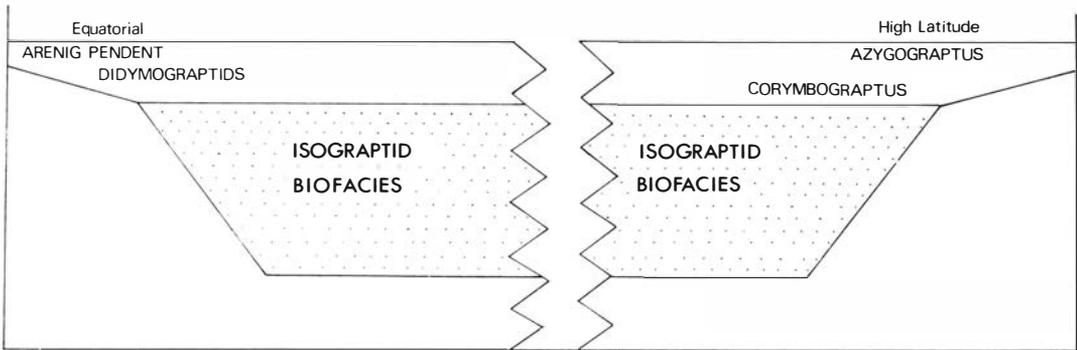


Fig. 6 – Biogeography of isograptid biofacies between North America and Gondwanaland in the early Ordovician. Some epiplanktic forms with restricted distribution are indicated.

panied what was probably the climax of bathy-urid evolution in North America and endemic asaphid evolution in Sweden (Tjernvik 1956), and is associated with the appearance of bizarre endemics in the Nora Formation, central Australia.

#### Arenig-Llanvirn boundary

I believe that this was another time at which an important regressive-transgressive event occurred, although it does not figure on the sea-level curve of Leggett *et al.* (1981). The time of maximum regression is considered to be in the upper Arenig, equivalent to the *Didymograptus hirundo* Zone of the British standard and equating with the Castlemainian stages 2–3 and (possibly) Yapeenian Stage of Australia (Cooper & Fortey 1982). This affects both shelf and graptolitic facies worldwide, and local causes seem improbable.

(a) I have reviewed the evidence for a stratigraphic gap in shelly facies over platform North America below the Middle Ordovician (Fortey 1980). Briefly, there is a missing series of shelly faunas between the Canadian and Whiterock in sections spanning this interval. There may be regressive dolomites, with a low diversity mid-continent conodont fauna. The gap varies from place to place; it appears to be at the least in the Basin Ranges of the western United States. Shelly faunas of this age are present in only a few shelf-edge or off-shelf localities: in the Cow Head

Group, western Newfoundland, Glenogle shales, British Columbia (Norford & Ross 1978), and, most prolifically, in the Valhalla Formation northern Spitsbergen. The interval has been termed the Valhallan Stage, and is the youngest subdivision of the Canadian Series. The ensuing Whiterock to Chazyan transgression is diachronous, and corresponds to the Llanvirn of Europe.

(b) In southern Wales the upper part of the Arenig Series is developed in a relatively deep-water graptolitic facies of black mudstones with huge-eyed bathypelagic and blind benthic trilobites. Below the Arenig-Llanvirn boundary there is a distinct facies change: light coloured shales appear with a different fauna of normal-eyed trilobites (*Ectilaelenus*, *Barrandia*, *Ormathops*, abundant *Placoparia*) known from the Tankerville Flags, Shropshire. The Llanvirn boundary is marked by a dramatic influx of pendent didymograptids, which are absent in the Arenig beds here. The succession deepens upwards again into a thick, graptolitic Llanvirn turbidite-shale sequence, or, westwards, into euxinic black shales. The interruption of the deeper water sedimentation at the Arenig-Llanvirn boundary is remarkable, and it is tempting to associate the appearance of the pendent didymograptids with the onset of the ensuing transgression. What happens in North Wales is not fully known, but preliminary work suggests that the upper Arenig is absent in the type area.

(c) On the Australian platform the Nora For-

mation (western Queensland) is capped by a regressive sandstone facies which passes up into the Carlo sandstone. The succeeding Mithaka Formation is probably transgressive, and may be Llanvirn in age. In the more marginal Canning basin, Fortey & Cooper (1982) summarise evidence that the regression serves to remove the latest Arenig graptolite faunas, and that the Llanvirn again introduces graptolitic shales. Elsewhere on platform Gondwanaland, the Llanvirn marks a general transgression over often shallow-water Arenig facies. This applies over the Armorican-Iberian region, North Africa, and even over platform Saudi Arabia, where the *Neseuretus* trilobite fauna, and pendent didymograptids, appear in the Hanadir Shale above the Saq Sandstone (Fortey & Morris 1982). Unfortunately, the faunal control is insufficient to say how much of the Arenig Series may, or may not be missing beneath the Llanvirn transgression.

- (d) Tjernvik (1972) and Tjernvik & Johansson (1980) have presented a detailed discussion of the correlation of the beds near the Arenig-Llanvirn boundary in Sweden. The correlation problems at this level are evidently highly complicated and contentious. It may be that the introduction of the concept of a regression and subsequent transgression at this level will help to solve some of these problems. Several remarks made by Tjernvik & Johansson (1980) are suggestive of a regression: for example, they observe that in Scania (presumably relatively marginal) there are beds "which may perhaps occupy a hiatus between the Zone of *Megistaspis limbata* and that of *Asaphus expansus*", and an environmental control at this horizon may be responsible for regional absence of the *Lepidurus* Limestone they claim for much of Sweden. In more marginal facies the situation may be clearer. The appearance of the "Orthoceras" Limestone and correlative units in the Oslo Region between the Lower and Upper *Didymograptus* Shale is exactly where it would be expected. I am indebted to Dr S. Stouge for pointing out to me that the Komstad Limestone of Bornholm and adjacent Scania occupies a comparable stratigraphic position, and Dr Stouge has recognised a succession of conodont

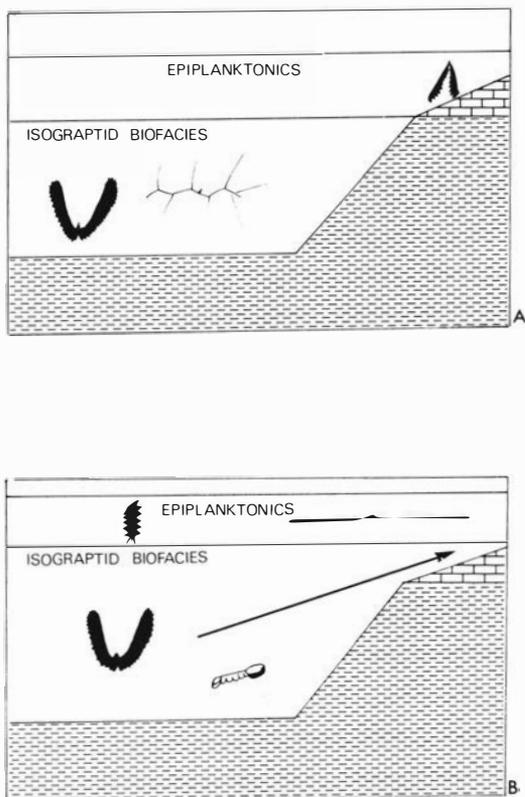


Fig. 7 – Shelfward encroachment of the isograptid biofacies in the Llanvirn transgression (B) brings this fauna onto the platform for the first time in North America. Compare this with the Arenig (A).

"Iso-communities" recording the shallowing sequence.

The evidence seems to be very good for a simultaneous regressive-transgressive event the world over – and a eustatic cause is again probable.

The Llanvirn transgression brought a flood of pendent didymograptids of the subgenus *Didymograptus* into cratonic successions around Ordovician Gondwanaland – Shropshire, England; Bohemia; France; Spain; Saudi-Arabia. The same transgression caused an onstep of the isograptid biofacies on to the edge of the North American craton (Finney & Skevington 1979). It is perhaps not surprising that the wide dispersal of "oceanic" graptoloids at this time permits relatively sound correlation in graptolitic facies (Fig. 7). The

same transgression accompanied the endemic radiation of dalmanitacean trilobites in Eastern Gondwanaland, the Chazy "reefs" in North America, and later megalaspid evolution in Scandinavia.

### Llandeilo and Caradoc

I do not propose to examine the evidence for the later Ordovician in detail, but for the sake of completeness it is noted that the Llandeilo and Caradoc also appear to be defined by eustatic events. It has been recognised for some time that the Llandeilo represents a relatively short interval compared with the other standard divisions of the Ordovician; in the type area the Llandeilo limestone with its characteristic fauna is the expression of a regression and subsequent transgression (Wilcox & Lockley 1981) similar to that which terminated the Arenig. Comparable facies changes occur elsewhere in Britain – for example in Shropshire. The evidence for its world-wide extent is perhaps less convincing than for the examples discussed above, but it might be noted that in platform successions on Gondwanaland (e.g. Saudi-Arabia, SE China) Llanvirn graptolitic deposits are succeeded by regressive sandstones, which in

turn underlie fossiliferous Caradoc rocks. It may also be significant that a series of extra-cratonic island deposits (see condition 5, p. 40) of supposed Llandeilo age, occur across the mobile belt in Newfoundland. The transgressive nature of the Caradoc is well known, and needs no elaboration here. It was probably of greater extent than any that preceded it, judging from the widespread introduction of facies of oceanic aspect over equatorial areas which had previously only had platform carbonate deposition. This is shown, for example, by the relatively wide geographical spread of the trilobite family Cyclopygidae during the upper compared with the early Ordovician (Fig. 8). Cyclopygidae are invariably associated with exterior facies, and may well have had bathypelagic habits. Only during the Caradoc did they penetrate over former cratonic areas and for the first time, into North America. When rare exterior sites can be recognised through a long interval of time as they have been in Kazakhstan, their associated cyclopygid faunas show very little morphological change (Apollonov 1975, 1976).

In summary, all the major divisions of the earlier part of the Ordovician are represented by regressive-transgressive events at their



Fig. 8 – Distribution of cyclopygid trilobites (left) in the early Ordovician and (right) the later Ordovician. Based on various sources. Map after Whittington & Hughes 1972.

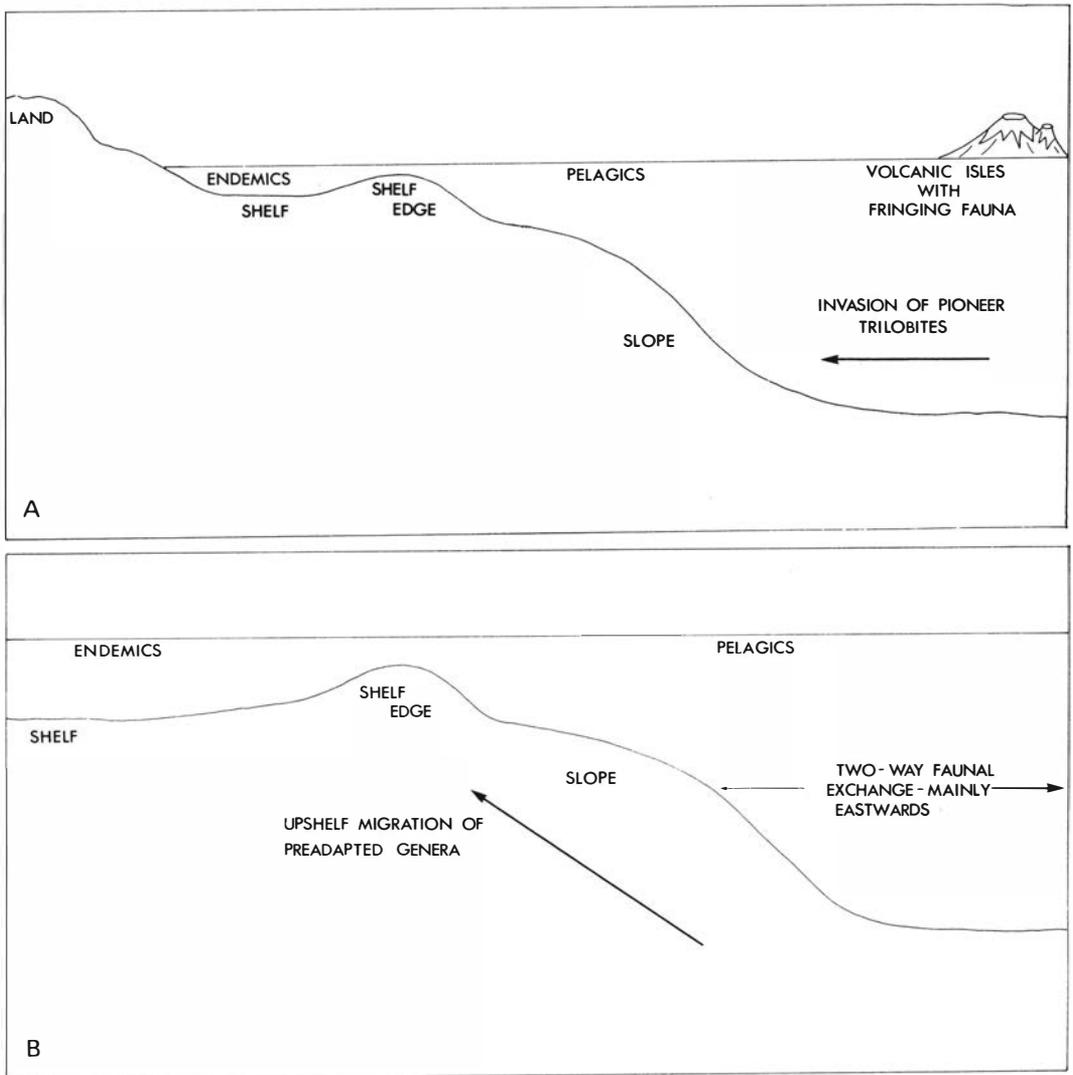


Fig. 9 – Contribution of a transgression to the Caradoc 'provincial breakdown' (A). Pre-Caradoc faunal exchange via islands or deep water facies, becomes manifest over a wider area (B) as transgression proceeds.

boundaries. The Llandeilo may be unique in that it probably consists of the regressive and only part of the transgressive event *alone*, which possibly accounts for the difficulties in its precise definition. This coincidence is not surprising, because the shifts in biofacies, lithofacies, and local unconformities at these times introduce precisely the kind of "natural" divisions which were astutely recognised by geologists unravelling the complexities of Ordovician correlation. Ironically, it is precisely the natural-

ness of the divisions that makes the recognition of their boundaries – not least the Cambrian-Ordovician boundary – so fraught with difficulties.

#### Provincial breakdown (Fig. 9)

Much is made of the breakdown of the faunal "provinces" during the Caradoc, which is usually attributed to tectonic causes such as the

impending closure of Iapetus. In the present context it is worth asking how much of this breakdown may be attributable to the Caradoc transgression itself. We have already seen how the extracratonic biofacies overstep the North American continent at this time, and are widely distributed elsewhere (Whittington 1963; Whittington & Hughes 1972, 1974). Could the replacement of the earlier trilobite "provinces" by a unified "Remopleuridid Province" (except for a relict *Selenopeltis* Province surrounding the pole) simply be greater spread of an outer shelf or upper slope biofacies? It does seem likely that the trinucleids, for example, were a group with an origin around Gondwanaland, and that they spread into outer shelf or slope benthic faunas in the Arenig, whence they may have been free to disperse to similar sites around other continental blocks. They appear in abundance in North America as the Caradoc transgression proceeds, but they *are* known from earlier marginal occurrences (Shaw & Fortey 1977). Other elements of the "unified" fauna (e.g. calymenids, raphiophorids) may have crossed Iapetus early on in the same fashion. Conversely, *Remopleurides* and dimeropygids probably had North American origins, occurring in the faunas of the Tremadoc transgression. By the Llanvirn, however, they can be found in exterior facies, whence they were free to disperse in the opposite direction to the trinucleids.

It would, however, be an over-simplification to attribute too much to the effects of the transgression alone. It would indeed be responsible for the wider spread of more cosmopolitan biofacies, and in a statistical sense for a greater appearance of faunal uniformity. North American endemic shelf trilobite faunas retreated during the Caradoc, but survived with the last bathyurids at least until the early Caradoc in the Decorah of the Upper Mississippi Valley. On the other hand the equator-wards movement of the Baltic-Welsh continent would have brought shelf environments into latitudes where compatible environments existed on both sides of Iapetus; at this stage migration could have been more or less direct. Thus, the establishment of carbonate "mound" faunas in the Ashgill of Sweden, Kazakhstan, Salair, Ireland, and northern England includes many genera with an ultimately North American pedigree

(e.g. *Isbergia*, *Toernquistia*, *Heliomera*, *glaphurids*) together with other of Gondwanan origins (*Prionocheilus*, *Tretaspis* etc.). This fauna is genuinely an amalgamation of biogeographically separate earlier genera, and the mixing that occurs cannot be explained by transgression alone; the relative convergence of climatic belts during oceanic closure is reasonably invoked in this case. Note that the widespread occurrence of "mound" faunas is in accordance with the prediction (5, above) that they will occupy shelf positions in times of transgression.

### Island faunas

If regressive phases expose islands (volcanic, or microcontinents), or increase the length of shorelines about them, we might expect a concentration of records of island faunas at about the times of regression. Since vulcanicity can happen at any time this will not be an invariable rule; it will better apply to "dead" volcanoes and microcontinents. One example of the latter has very recently come to light in the Scottish Caledonides. Curry et al. (1982) report an early Arenig fauna from the Highland Border rocks, a shallow-water fauna of platform North American bathyurid biofacies which may have related to an island beneath the present Midland Valley. Previous evidence of this island consisted of a derived boulder of very early Canadian age (Rushton & Tripp 1979). It is coincidence that both these occurrences correspond with, or immediately postdate, our regressive climaxes at the first two Series boundaries of the Ordovician? Similarly, it is striking how many of the "Celtic Province" island faunas lie near the Arenig-Llanvirn boundary, and hence close to, or immediately after, the climax of the late Arenig regression. The most recently described of these is that from the Otta Conglomerate, south Central Norway (Bruton & Harper 1981); this was suggested as of "late Arenig-early Llanvirn age" on the basis of brachiopods, and early Llanvirn age on the trilobites. Faunas of similar age have been described from elsewhere in the Caledonides (Neuman & Bruton 1974; Bruton & Bockelie 1980) and in the Appalachians (Neuman 1972). Island faunas approximating to the Llandeilo regression are known from several sites in the mobile belt of Newfoundland. The "Celtic Province" is a

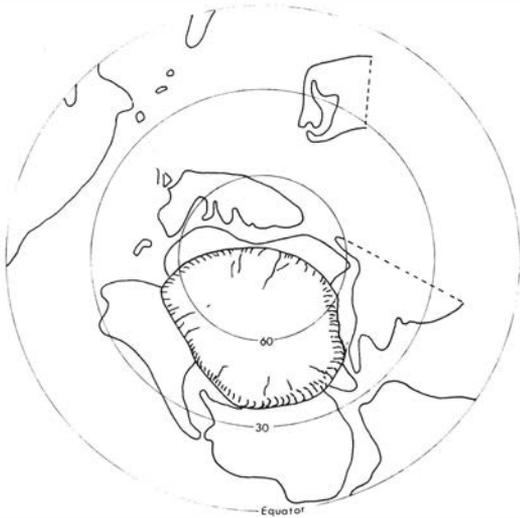


Fig. 10 – Possible extent of early Ordovician ice sheet. Its limits are taken inside the distribution of the inshore *Neseuretus* facies over Gondwanaland (from Fortey & Morris 1982).

rather loose term to describe opportunistic biotas that fringe such islands: they often seem to be derived from shallow-water sites, but I can see no reason in principle why they should not be derived from several depth associations. It is not surprising to find that they are a taxonomic/provincial mixture in terms of platform faunas. The islands may, however, be important havens during regressive phases, and if their isolation stimulated allopatric speciation, they may be implicated in the evolution of forms which acquire importance in the ensuing transgressions. They may account for the "precocious" appearance of some of the brachiopod genera (Neuman 1972) in these island faunas.

#### Causes of regressive-transgressive cycles

The major causes of eustatic cycles (Hallam 1981) include the effects of retreating and advancing polar ice sheets, or fluctuations in the rate of sea-floor spreading (Hays & Pitman 1973). Because there were large continental masses in the south polar region in the earlier Ordovician, the conditions were appropriate for the establishment of major ice sheets long

before the well-known Ashgill glaciation. If it is assumed that the ice sheet occupied an area in the Arenig-Llanvirn, and polewards of the *Neseuretus* biofacies (Fortey & Morris 1982), which is the most inshore, we would have a possible ice sheet approximately twice the area of that in the Antarctic today (Fig. 10). It has been estimated that melting of the Antarctic icecap would induce a sea-level rise of about 50 metres; if a major advance-retreat cycle occurred in the earlier Ordovician it could have produced a transgression of even greater magnitude. Given the virtually peneplaned topography of the epicontinental areas at this time this could be sufficient to account for the biofacies and lithofacies shifts outlined in this paper, without invoking tectonic causes. However, the Caradoc transgression appears to be of greater magnitude, with the displacement of truly oceanic biofacies over the shelf edge in some places. Since the same period has been identified as one where subduction (and presumably concomitant ocean floor spreading) was particularly active, it seems possible that tectonic and glacial causes were operating together at this time. It is interesting to observe that the reconstructions of Scotese *et al.* (1979) show Gondwanaland having drifted off the pole at this period.

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