PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Late Silurian-Early Devonian Biogeography, Provincialism, Evolution and Extinction [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1985 **309**, 323-339
doi: 10.1098/rstb.1985.0089

Phil. Trans. R. Soc. Lond. B **309**, 323–339 (1985) [323]
Printed in Great Britain

Late Silurian–early Devonian biogeography, provincialism, evolution and extinction

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There is increasing marine to continental regression from the latest Silurian until the latter half of the early Devonian, when a major transgressive trend is initiated which achieves its maximum in the later middle Devonian and late Devonian. Data suggest a relatively high climatic gradient, but no evidence favouring continental, sea-level glaciation during the late Silurian–early Devonian. Arid climate evidence (marine evaporites, calcretes) shows a well-developed arid belt. Coal deposits are lacking before the late Devonian. Palaeogeography of the time interval is disputed, largely owing to the use of different classes of data – remanent magnetic, lithological, biogeographical. I employ a pangaeic reconstruction because it fits the available lithological and biogeographical data comfortably, but I am under no illusions about its being the 'correct' palaeogeography.

Rate of phyletic evolution of marine benthos speeds up during the time interval owing to a steadily increasing level of provincialism, that is, cutting up biogeographical entities into smaller entities with consequent smaller populations. There are no major marine adaptive radiations, nor evidence for any marked extinction events during the interval. Few family level and higher taxa become extinct during this time interval; such units as the halysitid corals, pentamerinid brachiopods, and graptoloid graptolites are exceptional. Few adaptive radiations, such as those of the ammonoids and terebratuloids occur during the interval. The absence of other major biotic events during the interval is consistent with its position well within ecologic–evolutionary unit VI (A. J. Boucot, *J. Paleont.* **57**, 1–30, 1983).

Regression–transgression

An earlier global transgression, culminating in the Ludlovian, was followed by a major regression, culminating in the later Gedinnian,† followed in turn by a major transgression taking place in the Emsian.

The distribution of marine and non-marine strata of appropriate ages makes the above conclusions clear. Within the Malvinokaffric Realm there are widespread later Silurian marine beds (Berry & Boucot 1972, 1973), but virtually none of latest Silurian, Gedinnian, or Siegenian age, followed by very widespread Emsian and younger marine strata (Boucot 1975). The Emsian was a time of rapid transgression.

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† Invertebrate palaeontologists, possibly the majority, prefer the Bohemian time terms for the early Devonian (from oldest to youngest – Lochkovian, Pragian). However, because of the difficulty of correlating the non-marine, particularly the higher land plants and vertebrates, early Devonian sequences which tend to be interlayered with the Rhenish sequence (Gedinnian, Siegenian, Emsian), with the Bohemian sequence, as well as the as yet largely unexplored possibility for providing better correlations between Bohemian and Rhenish with acritarchs and chitinozoans, I will still adhere here to the Rhenish terms. The early Devonian is a particularly difficult interval in which to set up a global sequence of series because of the unusually high level of provincialism (three major realms), which makes correlation intrinsically far more difficult than in most, more cosmopolitan time intervals.

In North America the picture is little different from that seen in the Malvinokaffric Realm (figures 1 and 2), except that the area of non-marine sedimentation is smaller in North America. Marine rocks of Wenlockian, and especially Ludlovian age are widespread, whereas those of the Přídolían are far more restricted (Berry & Boucot 1970), as is true for the Gedinnian and not much less so for the Siegenian, following which there is a considerable Emsian transgression (Boucot 1975). In North America the Emsian transgression does not, however, reach anything like the limits of the far broader, later Devonian transgressive events.

In North Africa there is an overall interval of regression, which peaks in the Ludlovian–Siegenian, from the earlier Llandoverian transgression, followed by a widespread Emsian transgression (Boucot *et al.* 1983, summary and references). North Africa, in part, therefore, does not agree with the global, pre-Emsian trends.

In Europe there is widespread Wenlockian and Ludlovian transgression, followed by extensive late Ludlovian–Přídolían regression, followed by a brief, earlier Gedinnian, minor transgression, followed by a later Gedinnian–earlier Siegenian, minor regression, followed by a later Siegenian transgression, and then a much longer interval of widespread Emsian transgression.

In northern Asia there is widespread late Silurian regression, beginning within the Wenlockian, which continues through much of the early Devonian. In southern Asia there is a similar story of widespread regression during the late Silurian–early Devonian interval, but with an Emsian transgressive pulse.

In Australia (Talent *et al.* 1975) there is fairly widespread, although admittedly only marginal to the continent, Wenlockian–Ludlovian transgression, followed by Přídolían–Gedinnian regression, which in turn is followed by Siegenian–Emsian transgression.

In Antarctica there is no evidence for marine Silurian rocks, and marine Devonian only during the Emsian interval in two restricted parts of the Transantarctic Mountains.

Climatic gradients

The presence of a well-defined, moderately high, global climatic gradient during the late Silurian–early Devonian is well established (Boucot 1975). The southern, high latitude Malvinokaffric Realm of the time is characterized by physical and biological characters consistent with cool to cold water depositional environments, whereas the extra-Malvinokaffric environments yield warm to hot water environmental clues. The Malvinokaffric Realm during the Devonian (figure 1) appears to be substantially smaller than in the Silurian (figure 2), particularly in North Africa and northeastern South America plus Florida.

A south latitude, broad, arid belt is suggested by the distribution of arid climate indicators (figures 1 and 2) such as marine evaporites and calcretes. It must be noted, though, that the high global climatic gradient of the late Silurian–early Devonian declines rapidly during the latter parts of the Devonian to become very low by the late Devonian (Boucot & Gray 1983).

The lower latitude arid belt is part of a much wider warm belt characterized by such facies as red beds, widespread marine limestone and dolomite, and reef bodies.

The occurrence of the minerals celestite ($SrSO_4$) and strontianite ($SrCO_3$) in marine sedimentary sequences may be used as an indicator of arid conditions in areas otherwise devoid of evaporite minerals (Smirnov 1977; West 1973; Olaussen 1981; Frazier 1974). Celestite is precipitated in very small amounts under arid conditions (Skinner 1963; Evans & Shearman

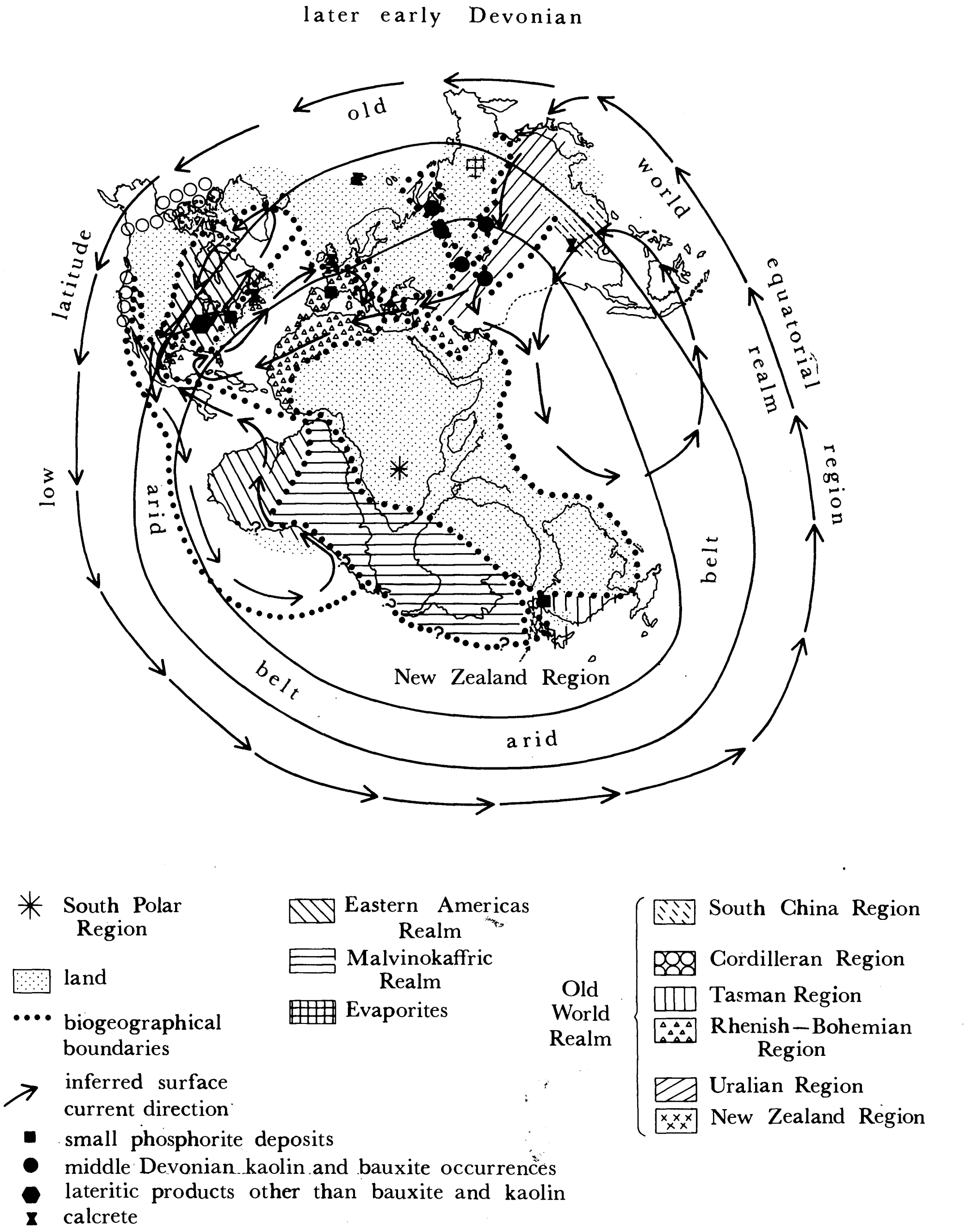

Figure 1. Pangaeic reconstruction indicating surface current circulation pattern, and biogeographical units (from Boucot & Gray 1983). The large area of Old Red Continent shown between Greenland and Spitsbergen is speculative, although consistent with presently available data.

1964; Kinsman 1969), but strontium is released from the anhydrite lattice during alteration to gypsum (Holliday 1970; Carlson 1983), and then celestite is secondarily precipitated in the same as well as in associated rocks (even including significantly older rocks if closely subjacent; Nickless *et al.* 1976). Celestite and strontianite are significantly less soluble than the other abundant evaporite minerals, and thus may form the last, only positive evidence for the existence of former, 'lost' evaporitic bodies. Olaussen (1981) reports celestite in associated

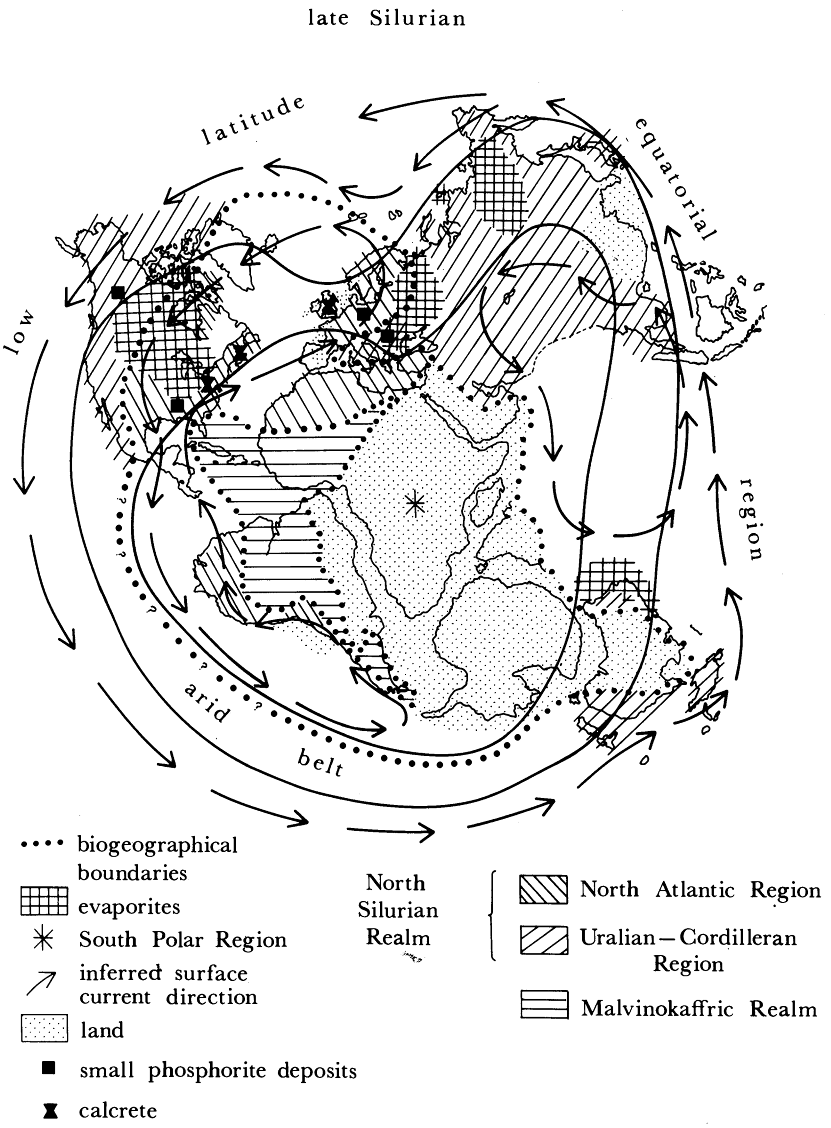

FIGURE 2. Pangaeic reconstruction indicating surface current circulation pattern, and biogeographical units. Note Arid Belt position, including location of known evaporites and calcretes.

supratidal carbonate rocks in the Wenlockian of the Oslo region. Celestite, and less commonly strontianite, have long been known in the Ludlovian and Přídolían strata of the Michigan Basin and adjacent areas of eastern North America: (Bellwood, Blair County, Pennsylvania is the 18th century type locality for celestite). (Ontario (Awald 1969); New York (Thibault 1935; Awald 1969; Jensen 1942; Monahan 1928; Grabau 1906; Kraus 1904, 1905); Ohio (Green 1971; Kessen *et al.* 1981; Roedder 1969; Morrison 1935; White 1975; Carlson 1983, unpublished; Pennsylvania (Pratt 1881; Young 1875; Hamilton 1950; Smith 1978; Geyer *et al.* 1976; Chamberlain & Dossert 1979); Michigan (Kraus & Hunt 1906; Kraus 1906; Roedder 1969; Carlson 1983); West Virginia (Williams 1890; Martens 1964; Frazier 1974)).

VOLCANISM AND OROGENY

I have earlier (1975) reviewed the evidence regarding orogeny for the late Silurian–early Devonian. There is little evidence for orogeny during the late Silurian in the world, but a limited amount from near the Silurian–Devonian boundary to the early Devonian. There are a few places, such as the Tasman Geosyncline, where there was major orogeny near the Silurian–Devonian boundary, but in most regions of the world the final, major Caledonian Orogeny movements are within the middle Devonian – including such events as the Tabberabberan Orogeny of the Tasman region, and the Acadian Orogeny of eastern North America, as well as many of the major Old Red Sandstone angular unconformities within the North Atlantic Region – parts of eastern Greenland and Britain. In most parts of the world where fossiliferous evidence for the Silurian–Devonian boundary is available, we have evidence for conformity. Included here are such regions as most of eastern North America, western and Arctic North America, South America in many places, Africa, both north and south, continental Europe, much of China and Asiatic Russia. The many discussions in the literature that try to determine the position of the Silurian–Devonian boundary from region to region by means of fossils make this very clear. Volcanism is largely restricted, except for some bentonites, to the geosynclinal regions of the interval, but is not notably higher or lower in volume or areal distribution than earlier in the Silurian or later in the Devonian. Correlation of orogeny and volcanism with biotic factors in this time interval is poor.

LEVELS OF PROVINCIALISM

Changing levels of provincialism may be measured by noting the changing numbers of biogeographical units present through time, at the varied unit ranks (realm, region, province, subprovince), and by counting the numbers of taxa (commonly genera or species; less commonly, families and higher taxa) present for each time interval within each biogeographical unit. The definition of Silurian and Devonian biogeographical units has been dealt with elsewhere (Boucot 1975; Wang *et al.* 1984).

For the interval late Silurian–early Devonian there is a definite, measurable increase in level of provincialism for marine benthos (Boucot (1975) table III, pp. 156–158, makes it clear that the number of articulate brachiopod genera increases from the Wenlockian through the Emsian). Figures 1 and 2 here show that there are far more biogeographical units for the later early Devonian than for the late Silurian (Malvinokaffric Realm: North Silurian Realm, Uralian–Cordilleran Region, North Atlantic Region, European Province, American Province in the late Silurian, and Malvinokaffric Realm: Eastern Americas Realm, Appohimchi Subprovince, Amazon–Colombian Subprovince, Nevada Subprovince: Old World Realm, Rhenish–Bohemian Region, Uralian Region, South China Region, Tasman Region, New Zealand Region, Cordilleran Region, in the later early Devonian; see also Savage *et al.* (1979)).

Young (1982) has compiled data on Devonian vertebrate provincialism which is permissively in accord with the marine invertebrate record of changing levels of provincialism.

Late Silurian–early Devonian biogeography

During the entire time there existed a pronounced, southern Hemisphere, cool or cold region, the Malvinokaffric Realm (Boucot (1975) synthesis of data). The Malvinokaffric Realm is distinguished by beds lacking the features common to warm or hot climate regions (red beds, bauxites, calcretes, evaporites, reefs, abundant limestone and dolomite, etc.). Faunally, the virtual absence of corals (tetracorals and tabulates, except for one rare genus of Devonian tetracoral), and the absence of bryozoans, stromatoporoids, nowakiid dacryoconarids, and conodonts, combined with the abundance of conulariids and hyolithids, plus the relatively small number of shelly genera/community type when contrasted with warm region communities, the overall larger size and thicker shells of the Malvinokaffric genera, and the absence of many other widespread orders, superfamilies, and families of shelly fossils such as articulate brachiopods (Boucot 1975, table VI, p. 301) combined with the overall small number of genera present in the realm serve to distinguish it readily from the other realms of this time interval.

The warm to hot regions are the North Silurian Realm of the late Silurian, and the Eastern Americas plus Old World Realms of the early Devonian, the latter being derived from the North Silurian Realm.

It is worth mentioning that the Silurian faunas of the Malvinokaffric Realm become largely extinct near the end of the Silurian, to be replaced in the later early Devonian by new Malvinokaffric Realm faunas largely derived from earlier early Devonian antecedents of the Eastern Americas Realm.

The North Silurian Realm is divided into a North Atlantic Region and a Uralian–Cordilleran Region (figure 2). The distribution of certain genera can be used to provide low level biogeographical subdivisions. For example, the brachiopod *Dayia* is known from the western part of the Old World in some abundance (Podolia, Baltic States, Turkey, Sweden, Britain, Czechoslovakia, France), but is unknown in North or South America within this region. Witzke *et al.* (1979) point out that the pelmatozoan faunas of Europe and North America within the North Atlantic Region exhibit a high level of endemism, indicating that this group shows a higher level of provincialism than is the case with the brachiopods and some other groups, although paralleling the ostracodes. It is unfortunate that the pelmatozoans are so uncommon and poorly known in most places. By using their data, plus the limited supporting data provided by the brachiopods and ostracodes, it is reasonable to recognize European and American Provinces of the North Atlantic Region from the late Llandovery through the late Silurian – data for the earlier Llandovery provide an inadequate basis for making such a division at this time.

The Eastern Americas Realm of the early Devonian has no region-level biogeographical units, but may be divided into three subprovinces if one uses the precentage of endemic species as a criterion (Boucot 1975). The Old World Realm is currently subdivided into six regions (Boucot 1975; Wang *et al.* 1984). The Eastern Americas Realm, although definitely a warm water unit, is probably intermediate in environmental terms between the Malvinokaffric and Old World Realms (Koch & Boucot 1981), particularly in terms of temperature; this conclusion accords well with the Eastern Americas Realm derivation of many of the Malvinokaffric genera.

There is clearly a gradual increase in level of provincialism from the Wenlockian through the Emsian. For example, the late Silurian, Přídolían precursor of the Appohimchi Subprovince of the Eastern Americas Realm appears to include the *Eccentricosta* Community and related units in eastern North America (from Alabama to Gaspé; Berdan *et al.* 1985; Boucot 1975). Within the Eastern Americas Realm there is a steady increase in level of generic endemism from the Gedinnian through the Emsian (see tables and text in Savage *et al.* 1979).

A similar increase in level of endemism is shown by Savage *et al.* (1979) within the Rhenish–Bohemian, Cordilleran, and Tasman Regions of the Old World Realm for the early Devonian. Parallel increases in level of endemism are also present in the Uralian Region, and have recently been documented for the South China Region by Wang *et al.* (1984). We lack enough data for the New Zealand region to arrive at a solid conclusion, but the available data are permissively in agreement.

One cannot discuss late Silurian–early Devonian levels of provincialism without mentioning that late Silurian levels were little different from those of the early Silurian (Wang *et al.* 1984), whereas beginning in the middle Devonian there is a steady, global decline in levels of provincialism, which culminates in the high cosmopolitanism of the late Devonian (Boucot 1975; Young 1982, for the vertebrates). The cause or causes of these global changes in level of provincialism are hard to evaluate. The global lowering of climatic gradient from moderately high in the Silurian through earlier middle Devonian to very low in the late Devonian may be an important factor, but biogeographically significant changes in palaeogeography may also have been important, although presently difficult to evaluate. These are far from the only factors worthy of consideration.

Reefs and bioherms

Reefs in the broad sense within this time interval may include many rock units that lacked a wave resistant organic framework. Therefore, it might be better to refer to bioherms, some of which apparently were reefs. With this caveat in mind it is clear that there are widespread Wenlockian to Přídolían 'reefs' in the warm water regions: none, of course, within the cool to cold water Malvinokaffric Realm. The early Devonian, on the other hand, is largely distinguished by rarity of 'reefs', particularly when contrasted with the middle Devonian. Reasons for this anomaly do not spring easily to mind. There has been no careful study of the community ecology of late Silurian–early Devonian reefs that might tell us whether the early Devonian reefs in large part sprang from a distinctive group of level-bottom precursors after extinction of the Silurian reefs, or whether we are merely recognizing a massive decrease in early Devonian 'reef' abundance. One might speculate that early Devonian regressions correlated with higher levels of near-shore turbidity and fresh water influx that were inimical to 'reef' organisms although not to the more eurytopic level-bottom organisms.

In this same vein it is well to warn non-palaeontologists that there has been virtually no attention given yet to the definition of specific non-level-bottom community complexes, such as crinoid thickets and sponge forests, during this time interval, nor to their stratigraphic ranges. It is possible that the overall impression of relatively little major change within the marine environment should be rephrased in the future to state little major change in the level-bottom environment. Keep in mind that the level-bottom environment has always dominated the fossil record in terms of area and numbers of specimens, just as it does today, and that this inevitably prejudices us when trying to arrive at generalizations.

FAUNAL CHANGES: ADAPTIVE RADIATIONS AND EXTINCTIONS

By and large the late Silurian–early Devonian interval is one in which few major changes occurred in the marine realm: this is not the Triassic–Jurassic boundary 'revolution', the Permian–Triassic 'event', or the lower Ordovician–middle Ordovician major change (Arenigian–Llanvirnian). We do, of course, have the initial adaptive radiation of the ammonoid cephalopods, and the terminal extinction of the graptoloid graptolites within the later early Devonian, the terminal extinction of the massive, shelled Pentameridae in the late Silurian, the radiation of the terebratuloid and ambocoeliid brachiopods during the early Devonian, and so forth, but this is dominantly an interval of relatively gradual change: species to species, among a host of long ranging genera.

The most notable extinction event in many ways is the disappearance of some of the Malvinokaffric Silurian groups near the end of the Silurian (*Clarkeia* and *Heterorthella* in particular), but the number of taxa involved is very small despite the prior abundance of the taxa cited.

For many animal groups our knowledge is still too limited to enable any significant comments to be made about either adaptive radiations or extinctions, mainly because of the lack of basic taxonomic and biostratigraphic knowledge of the groups. Included here are such groups as the benthic Foraminifera, scolecodonts, holothurians, radiolaria, inarticulate brachiopods, the minor molluscan groups (chitons, monoplacophorans, scaphopods, rostroconchs).

For the non-marine groups our information is very limited indeed. There is, of course, the major radiation of the woody plants within the early Devonian (Edwards, this symposium). For the non-marine animals data are very limited; this is particularly true for the invertebrates. There is certainly good evidence for some important early Devonian radiations among the vertebrates as discussed by Halstead (this symposium) and Janvier (this symposium). It is easy to interpret the woody plant and vertebrate radiations as largely decoupled (Boucot 1983) from what was happening in the marine environment.

For a few groups there were major changes. For example, the eurypterids changed from inhabiting both fully marine, including hypersaline, and non-marine waters during the late Silurian to only non-marine during the early Devonian, with a consequent loss of many fully marine and hypersaline taxa.

The gradual nature of the faunal changes present during the Wenlockian–Emsian interval is indicated by the uncertainty in determination of the Llandoverian–Wenlockian, Wenlockian–Ludlovian, Ludlovian–Přídolían, Přídolían–Gedinnian, Siegenian–Emsian, and Emsian–Eifelian boundaries in the absence of truly rich and varied faunas. Even with a rich and varied fauna there are numerous instances where precise location of these boundaries is uncertain. For example, with the exception of the graptolitic facies it is clear that recognition of the Llandoverian–Wenlockian boundary in the marine facies is virtually impossible. Group after group of genera and species have a C_6, latest Llandoverian to early Wenlockian range, that is, the actual Llandoverian–Wenlockian boundary within the shelly facies is virtually impossible to recognize away from the type areas where the determination is made on lithology. However, microfossils such as acritarchs and chitinozoans may rectify this situation in the future.

CHANGES IN MAJOR MARINE ANIMAL GROUPS ACROSS THE SILURIAN–DEVONIAN BOUNDARY

Articulate brachiopods

Little major change is seen in the articulate brachiopods during the interval. The Pentameridae do become extinct by the end of the Přídolían, as do the Subrianidae. In the Gedinnian we see the beginnings of the terebratuloid and ambocoeliid radiations. A compilation for the Silurian–Devonian boundary (Boucot 1977) indicates how many genera cross the Přídolían–Gedinnian boundary, and another (Boucot 1975, figure 27) the ranges of the genera during this interval. A few families become extinct during the late Silurian, and a few new ones appear during the early Devonian, but most go sailing right through. The character of the varied earlier, pre-Silurian–Devonian boundary, and later, post-Silurian–Devonian boundary time units is little different from the Přídolían–Gedinnian. For example, one lineage of stricklandiids becomes extinct in the early Wenlockian, a second in the later Wenlockian, but the varied contemporary, related pentameroid brachiopods continue right through the Wenlockian. I have previously mentioned the terminal Silurian extinction of numerically important Malvinokaffric Silurian brachiopods, but these are merely two genera, despite their numerical importance within the Realm.

Bryozoans

N. Spjeldnaes (personal communication) suggests that there were probably no great extinctions or diversity explosions among the bryozoans during the Wenlockian–Emsian interval. 'The situation seems to be a slow decrease in generic, and possibly familial diversity, which picks up in the Emsian–Eifelian, first in specific diversity, later at the generic and familial levels.' This 'slump', Spjeldnaes thinks, may be due to lack of knowledge of the group rather than to a real decrease.

Cephalopoda

C. Teichert points out (personal communication) that the initial phase of the adaptive radiation of the ammonoids occurred in the Emsian (Alberti (1983) for the age of the Hunsrückschiefer from which the specimens have been obtained; Erben (1964, 1965, 1966) for the details of the radiation; Chlupac & Turek (1983) for excellent description of many of the taxa), as did that of the coleoids (Bandel *et al.* 1983)). However, the coleoids did not become abundant until long after the Devonian. C. Teichert (1967, figure 20) suggested that most nautiloid families present in the Wenlockian–Emsian interval extend throughout the interval, but he emphasizes (personal communication) that the group is poorly known during this interval. There are some generic extinctions and radiations, but nothing like a well-coordinated, major nautiloid event.

Chitinozoa

S. Laufeld (personal communication) concludes that there is no evidence for any major chitinozoan adaptive radiation or extinction during the interval, and cites Paris (1981) as additional evidence.

Conodonts

References (Harris *et al.* 1983; Jeppsson 1974) provided for me by G. Klapper (personal communication) suggest that the conodonts show no evidence during the Wenlockian–Emsian interval for anything other than an orderly progression of taxa (genera, species, and subspecies) with some appearing for the first time, and others dropping out from time to time. There does not appear to be any evidence favouring the presence of either adaptive radiations or notable extinction events at any taxonomic level.

Corals

W. Oliver (personal communication) comments as follows: 'the corals don't pay much attention to the Silurian–Devonian boundary. The halysitids come to a very ragged end – late Ludlovian to early Lochkovian in different places. Most changes are very subtle and at the species level, if indeed there are changes. In general, where the facies cross the boundary the species do also. The significant coral change is in the Upper Pragian or Lower Emsian. Emsian corals are largely new, with genera and even families coming in. Lochkovian and Pragian corals are basically Silurian types. The new Treatise does not distinguish between earlier and later Lower Devonian taxa – all are lumped together into the lower Devonian'. In view of the above, and of the fact that there do not appear to have been any profound extinction or adaptive radiation events in the Wenlockian–Přídolían interval which affected the corals, it would seem that this is a time of relative quiescence for the group.

Gastropods

D. Rohr and E. Yochelson (personal communications) are comfortable with the conclusion that there are few major changes during the interval. A few families drop out in the late Silurian, and a few more come in during the early Devonian, but most persist. It is commonly difficult, for example, to be certain whether one is dealing with late Silurian or early Devonian faunas when only gastropods are available. This may reflect, in part, the need for more morphological and taxonomic attention for the group rather than any inherent evolutionary torpor. Gastropods are not of much service in zoning the late Silurian–early Devonian interval at the moment.

Graptolites

The existing graptolites (see Rickards *et al.* (1977) for a summary) have generally gradational relations with each other at the Llandoverian–Wenlockian boundary, radiate in post-*M. riccartonensis* time, then show a major extinction at the end of the Wenlockian (during the *dubius-nassa* interregnum), then have a burst in the earlier Ludlovian, followed by an additional radiation in the later Ludlovian, and finally the ultimate extinction event near the end of the early Devonian. In general the graptoloids of the interval show a more or less orderly progression of eliminations and replacements at the generic level – most of the appearances and extinctions are at the generic and specific levels. Not enough is known about the dendroid graptolites to be able to say anything of consequence.

Ostracodes

J. M. Berdan (personal communication) finds that ostracode ranges during the Wenlockian–Emsian interval do not provide strong evidence for either notable extinction events or adaptive radiations. Known ranges of genera may vary from one biogeographical unit to another. One could conclude that ostracode evolution during the interval proceded steadily, with some taxa appearing while others disappeared, but without notable 'events'.

Pelecypoda

J. Pojeta (personal communication) concludes that there are no major extinction events or adaptive radiations within the Wenlockian–Emsian interval, and cites as an example Pojeta *et al.* (1976). However, the Pelecypoda are a group deserving a great deal more taxonomic attention and collecting before one can be certain of such conclusions.

Pelmatozoans

Witzke *et al.* (1979) make it very clear that there are a number of significant changes, including extinctions and the introduction of new families, near the Silurian-Devonian boundary. Most of the data come from North America and Europe. Witzke & Strimple (1981) indicate that the North American Upper Silurian pelmatozoans may be easily derived from local Upper Llandoverian taxa. There is (C. Brett, personal communication) a major increase in diversity in the late Llandoverian, and also a marked appearance of specialized 'reef-dwellers' at about C_6 (uppermost Llandoverian). The big change apparently occurs in the earlier late Llandoverian, as is also the case for many other groups of benthic megafossils (see Wang *et al.* 1984). There is no evidence of major changes within the Silurian. Neither is there evidence for major changes within the Lower Devonian. Marked changes in North American echinoderm faunas occur in the Eifelian–Givetian, reflecting an influx of European forms (McIntosh 1983), but this is clearly a biogeographical rather than an evolutionary event (dispersal), and also occurs in other important benthic groups (Boucot 1975) at this time and place. McIntosh & Macurda (1979) confirm and expand a bit on the views expressed by Witzke *et al.* (1979) about the distinction between Silurian and Devonian echinoderm faunas. C. Brett (personal communication) agrees with the conclusions arrived at by these authors. However, the general rarity of well-preserved pelmatozoans in late Silurian strata makes it impossible to give more than tentative statements at this time. There is a notable lack of data from South America, Asia, Africa, and Australia.

Sponges

K. Rigby (personal communication) comments 'most of the lineages present in the Silurian continue on into the Devonian. There is not a major break in sponge history near the boundary, particularly now that we have found the Devonian lithistid assemblages from Australia. Principal mid-Palaeozoic changes in sponge assemblages appear to take place near the end of the Devonian. Mississippian suites contrast sharply. The record of sponges is intermittent, however, so it is a bit difficult to evaluate'. It is clear that present knowledge of the Porifera does not suggest any major extinction or adaptive radiation events during the interval.

Stromatoporoids

Stearn (1979, 1982) and Stock (1983) review varied aspects of stromatoporoid history. Neither provides any basis for recognizing either major extinction events or adaptive radiations within the Wenlockian–Emsian interval. However, C. W. Stearn (personal communication) raises the question concerning whether the significantly lower number of early Devonian stromatoporoid species may not be an artefact, seriously influencing our interpretation of this group for this time interval, owing to greater rarity of pre-Emsian reef bodies, as well as lack of taxonomic attention. Stearn comments: 'there are quite a few Emsian reefs and it appears likely to me that the Eifelian radiation started with Emsian transgression'. Stearn comments that the Eifelian radiation probably started with the spread of reef growth in Emsian time. Documenting this radiation from the literature is difficult owing to lack of agreement on correlation of the Emsian–Eifelian boundary in the reefal facies.

Tentaculitids

The bottom-dwelling tentaculitids proper show little evidence of any major terminal extinction events or adaptive radiations during the interval (Larsson 1979; Lardeaux 1969). The planktonic nowakiids become suddenly abundant during the Devonian, beginning with the Gedinnian, after being virtually unknown during the Silurian (Tunnicliff 1983), and persist until much later in the Devonian. Generic and specific diversity of both groups is low at all times.

Trilobites

B. Chatterton (personal communication) writes that '...my view would be that trilobites were under environmental stress near the end of the Silurian and during the Devonian. As a result of this, important groups disappeared periodically. The frequently reef-associated Illaenidae disappeared near the end of the Silurian; the rare Raphiophoridae also disappeared at about the same time; and most of the Encrinuridae disappeared at the end of the Silurian, except in the Tasman region where they lingered on into the Devonian. The trilobite disappearances do not appear to have been particularly sudden, and there is little evidence for mass extinction. No explosion of new taxa took place, although proetid and phacopine trilobites became more numerous and diverse so as to dominate most trilobite faunas by the middle Devonian.'

CONCLUSIONS

The available evidence, imperfect as it is, does indicate the presence of minor adaptive radiations in a few groups near the Přídolían–Gedinnian and Siegenian–Emsian boundaries. A few articulate brachiopod families radiate near the Přídolían–Gedinnian boundary, the Ammonoidea and Coleoidea radiate in the beginning of the Emsian, there is a tetracoral radiation of sorts near the Siegenian–Emsian boundary as may have been the case with some stromatoporoids; a number of pelmatozoan families become extinct while others radiate near the Přídolían–Gedinnian boundary; the nowakiids become abundant near the Přídolían–Gedinnian boundary; the marine eurypterids disappear near the end of the Přídolían; and the graptolites become extinct within the Emsian. The abrupt appearance in the Malvinokaffric Realm, near the beginning of the Emsian, of many new genera and species largely of Appohimchi Subprovince derivation, together with abundant *Australocoelia* (which may be of Malvinokaffric Realm origin) is notable, although a purely local matter on a global scale. These changes are not nearly enough to require the presence of additional 'ecologic–evolutionary units', but do indicate the possibility for employing subunits of one type or another.

The major biotic 'events' on land, such as the adaptive radiation and diversification of the woody plants, as well as those affecting the vertebrates present in fresh water, were clearly decoupled from the relatively uneventful history of the marine fauna during this time interval. However, the term 'marine fauna' used here refers almost exclusively to low trophic level benthos from which most of our data has been derived. The factor or factors responsible for the non-marine 'events' is not apparent from the data of the fossil record. However, the fact of the decoupling suggests that extraterrestrial events capable of affecting both the marine and the non-marine environments were probably not involved.

I am grateful for advice concerning the presence and absence of both extinction events and adaptive radiations in varied animal groups to the following: Ellis Yochelson, Keith Rigby, Colin Stearn, Carlton Brett, William Oliver, Curt Teichert, John Pojeta, William Berry, Gilbert Klapper, Jean Berdan, Nils Spjeldnaes, Brian Chatterton, Sven Laufeld, David Rohr, Richard Boardman, Jess Johnson; and to Pierre-André Bourque for advice concerning the nature of Silurian-Devonian reefs.

REFERENCES

Alberti, G. K. B. 1983 Unterdevonische Nowakiidae (Dacryoconarida) aus dem Rheinischen Schiefergebirge, aus Oberfranken und aus N-Afrika (Algerien, Marokko). *Senck. Leth.* **64**, 295–313.

Awald, C. J. 1969 Minerals of the Niagara Frontier Region. *Science on the march* **49**, 48–51, 57–59.

Bandel, K., Reitner, J. & Stürmer, W. 1983 Coleoids from the Lower Devonian Black Slate ('Hunsrück–Schiefer') of the Hunsrück (West Germany). *N. Jahrb. Geol. Pal., Abh.* **165**, 327–507.

Berdan, J. M. 1983 Biostratigraphy of Upper Silurian and Lower Devonian Ostracodes in the United States. In *Applications of Ostracodes* (ed. R. F. Maddocks), pp. 313–337. Univ. Houston Geosc.

Berdan, J. M., Boucot, A. J. & Ferrill, B. A. 1985 The first fossiliferous Pridolian beds from the Southern Appalachians in northern Alabama, and the age of the uppermost Red Mountain Formation. *J. Paleont.* (In the press.)

Berry, W. B. N. & Boucot, A. J. (ed.) 1970 Correlation of the North American Silurian Rocks. Spec. Paper 102, Geol. Soc. America, 289 pp.

Berry, W. B. N. & Boucot, A. J. (ed.) 1972 Correlation of the South American Silurian Rocks: Spec. Paper 133, Geol. Soc. America, 59 pp.

Berry, W. B. N. & Boucot, A. J. (ed.) 1973 Correlation of the African Silurian Rocks: Spec. Paper 147, Geol. Soc. America, 83 pp.

Boucot, A. J. 1975 Evolution and extinction rate controls. New York, Amsterdam: Elsevier.

Boucot, A. J. 1977 Brachiopods. In *The Silurian–Devonian boundary* (ed. A. Martinsson), pp. 306–314. I.U.G.S. Series A, no. 5 E. Stuttgart: Schweizerbart'sche.

Boucot, A. J. 1983 *Does evolution take place in an ecological vacuum? II. J. Paleont.* **57**, 1–30.

Boucot, A. J. & Gray, J. 1983 *A Paleozoic Pangaea. Science, Wash.* **222**, 571–581.

Boucot, A. J., Massa, D. & Perry, D. G. 1983 Stratigraphy, biogeography and taxonomy of some Lower and Middle Devonian brachiopod-bearing beds of Libya and northern Niger: *Palaeontographica*, Abt. A, Bd. **180**, 91–125.

Carlson, E. H. 1983 The occurrence of Mississippi Valley-type mineralization in northwestern Ohio. In *Int. Conf. Mississippi Valley-type lead–zinc deposits* (ed. G. Kisvarsanyi, S. K. Grant, W. P. Pratt & J. W. Koenig), pp. 424–435. University Misouri-Rolla.

Chamberlain, S. C. & Dossert, W. P. 1979 Faylor–Middlecreek Quarry, Winfield, Pennsylvania. *Rocks and Minerals* **54**, 104–107.

Chlupáč, I. & Turek, V. 1983 Devonian goniatites from the Barrandian area, Czechoslovakia. *Rozpravy Ust. ust. geol.*, Sv. **46**, 159 pages.

Erben, H. K. 1964 Die Evolution der ältesten Ammonoidea. I. *N. Jahrb. Geol. Pal., Abh.*, **120**, 107–212.

Erben, H. K. 1965 Die Evolution der ältesten Ammonoidea. II. *N. Jahrb. Geol. Pal., Abh.*, **122**, 275–312.

Erben, H. K. 1966 Ueber den Ursprung der Ammonoidea. *Biol. Rev.* **41**, 641–658.

Evans, G. & Shearman, D. J. 1964 Recent celestine from sediments of the Trucial Coast of the Persian Gulf. *Nature, Lond.* **202**, 385–386.

Frazier, W. J. 1974 The paleoenvironmental significance of celestite. *Ann. Mtg. Abst., Am. Assoc. Petrol. Geologist* vol. 1, p. 37. Society of Economic Paleontologists and Mineralogists.

Geyer, A. K., Smith, R. C., II & Barnes, J. H. 1976 Mineral collecting in Pennsylvania: General Geol. Rpt 33, Environmental Resources, Penna., 260 pages.

Grabau, A. W. 1906 Guide to the geology and paleontology of the Schoharie Valley in eastern New York. *N.Y. State Mus. Bull.* **92**, 386 pages.

Green, R. 1971 Ohio Lime, Woodville. *Rocks Minerals* **46**, 280–281.

Hamilton, H. V. 1950 Notes on the occurrence of celestite in Pennsylvania. *Rocks Minerals* **25**, 348–350.

Harris, A. G., Hatch, N. L., Jr & Dutro, J. T., Jr 1983 Late Silurian conodonts update the metamorphosed Fitch Formation, Littleton Area, New Hampshire. *Am. J. Sci.* **283**, 722–738.

Holliday, D. W. 1970 The petrology of secondary gypsum rocks: a review. *J. sed. Pet.* **40**, 734–744.

Jensen, D. E. 1942 Minerals of the Lockport Dolomite in the vicinity of Rochester, N.Y. *Rocks Minerals* **17**, 199–203.

Jeppsson, L. 1974 Aspects of Late Silurian conodonts. *Fossils and Strata* no. 6, 54 pages.

Kessen, K. M., Woodruff, M. S. & Grant, N. K. 1981 Gangue mineral ^{87}Sr/^{86}Sr ratios and the origin of Mississippi Valley-type mineralization. *Econ. Geol.* **76**, 913–920.

Kinsman, D. J. 1969 Modes of formation, sedimentary associations and diagenetic features of shallow-water and supra-tidal evaporites. *Bull. Am. Ass. Petrol. Geol.* **53**, 830–840.

Koch, W. F., II & Boucot, A. J. 1981 Temperature fluctuations in the Devonian Eastern Americas Realm. *J. Paleont.* **56**, 240–243.

Kraus, E. H. 1904 The occurrence of celestite near Syracuse, N.Y. *Am. J. Sci.* **18**, 30–39.

Kraus, E. H. 1905 On the origin of the caves of the island of Put-in-Bay, Lake Erie. *Am. Geol.* **35**, 167–171.

Kraus, E. H. 1906 Occurrence and distribution of celestite-bearing rocks. *Am. J. Sci.* **19**, 286–293.

Kraus, E. H. & Hunt, W. F. 1906 The occurrence of sulfur and celestite at Maybee, Michigan. *Am. J. Sci.* **21**, 237–244.

Lardeaux, H. 1969 Les tentaculites d'Europe Occidentale et d'Afrique du Nord. *Cahiers Paléontol.* Paris: C.N.R.S. 238 pages.

Larsson, K. 1979 Silurian tentaculitids from Gotland and Scania. *Fossils and Strata*, no. 11, 180 pages. Universitäts Verlag.

Martens, J. H. C. 1964 Minerals of West Virginia. W. Va. Geol. Econ. Survey, Educational Series, 41 pages.

McIntosh, G. C. 1983 Crinoid and blastoid biogeography in Middle Devonian (Givetian) of eastern North America. *Abst.*, *Geol. Soc. Am.*, **15**, 171.

McIntosh, G. C. & Macurda, D. B., Jr 1979 Devonian Echinoderm biostratigraphy. In *Special Papers in Palaeontology*, no. 23, pp. 331–334. London: Palaeontological Association.

Monahan, J. W. 1928 Minerals in eastern exposures of the Lockport in eastern New York State. *Am. Miner.* **13**, 70–71.

Morrison, R. B. 1935 The occurrence and origin of celestite and fluorite at Clay Center, Ohio. *Am. Miner.* **20**, 780–790.

Nickless, E. F. P., Booth, S. J. & Mosley, P. N. 1976 The celestite resources of the area northeast of Bristol. *Inst. Geol. Sci.*, Min. Assessment Rpt 25, 83 pages.

Olaussen, S. 1981 Formation of celestite in the Wenlock, Oslo Region, Norway-evidence for evaporitic depositional environments. *J. sed. Pet.* **51**, 37–46.

Paris, F. 1981 Les Chitinozoaires dans le Paléozoique du Sud-Ouest de l'Europe. *Mém. Soc. Géol. Min. Brétagne*, no. 26, 412 pages.

Platt, F. 1881 The geology of Blair County. Penna. Geol. Surv., 2nd series, 311 pages.

Pojeta, J., Jr, Kříž, J. & Berdan, J. M. 1976 Silurian–Devonian pelecypods and Paleozoic stratigraphy of subsurface rocks in Florida and Georgia and related Silurian pelecypods from Bolivia and Turkey. U.S.G.S. Prof. Paper 879, 29 pages.

Rickards, R. B., Hutt, J. E. & Berry, W. B. N. 1977 Evolution of the Silurian and Devonian Graptoloids. *Bull. Brit. Mus.* (*Nat. Hist.*), *Geology* **28**, 120 pages.

Roedder, E. 1969 Varvelike banding of possible annual origin in celestite crystals from Clay Center, Ohio, and in other minerals. *Am. Miner.* **54**, 796–810.

Savage, N. M., Perry, D. G. & Boucot, A. J. 1979 A quantitative analysis of Lower Devonian brachiopod distribution. In *Historical biogeography, plate tectonics, and the changing environment* (ed. J. Gray and A. J. Boucot), pp. 169–200. Oregon State University Press.

Skinner, H. C. W. 1963 Precipitation of calcian dolomites and magnesian calcites in the southeast of South Australia. *Am. J. Sci.* **261**, 449–472.

Smirnov, V. I. 1977 *Ore deposits of the USSR: III.* London: Pitman. 492 pages.

Smith, R. C., II 1978 *The mineralogy of Pennsylvania 1966–1975.* Spec. Publ. no. 1, Friends of Mineralogy, Pennsylvania Chapter, Inc. 304 pages.

Stearn, C. W. 1979 Biostratigraphy of Devonian stromatoporoids. *Special Papers in Palaeontology*, no. 23, pp. 229–232. London: Palaeontological Association.

Stearn, C. W. 1982 The unity of the Stromatoporoidea. *Proc. Third North American Paleo. Conv.*, pp. 511–516. Department of Geology, of University of Montreal and Geological Survey of Canada.

Stock, C. W. 1983 Stromatoporoids: geologic history. In *Sponges and spongiomorphs.* (ed. J. K. Rigby and C. W. Stearn), Univ. Tenn. Dept. Geol. Sci. Studies in Geol. **7**, 167–172.

Talent, J. A., Berry, W. B. N. & Boucot, A. J. 1975 *Correlation of the Silurian Rocks of Australia, New Zealand, and New Guinea.* Spec. Paper 150, Geol. Soc. America, 108 pages.

Teichert, C. 1967 Major features of cephalopod evolution: Univ. Kansas Dept. Geol. Spec. Publ. **2**, 162–210.

Thibault, N. W. 1935 Celestite from Chittenango Falls. *Am. Min.* **20**, 147–152.

Tunnicliff, S. P. 1983 The oldest known nowakiid (Tentaculoidea). *Palaeontology* **26**, 851–854.

Wang Yu, Boucot, A. J., Rong Jiayu & Yang Xuechang 1984 Silurian and Devonian biogeography of China. *Bull. geol. Soc. Am.* **95**, 265–279.

West, I. 1973 Vanished evaporites; significance of strontium minerals. *J. sed. Pet.* **43**, 278–279.

White, J. S., Jr 1975 What's new in minerals. *Mineral. Rec.* **6**, 38–40.

Williams, G. H. 1890 Celestite from Mineral County, West Virginia. *Am. J. Sci.* **39**, 183–188.

Witzke, B. J., Frest, T. J. & Strimple, H. L. 1979 Biogeography of the Silurian, Lower Devonian Echinoderms. In *Historical biogeography, plate tectonics, and the changing environment* (ed. J. Gray and A. J. Boucot), pp. 117–129. Oregon State University Press.

Witzke, B. J. & Strimple, H. L. 1981 Early Silurian camerate crinoids of eastern Iowa. *Proc. Iowa Acad. Sci.* **88**, 101–137.

Young, C. A. 1875 The occurrence of celestine in Blair County, Pennsylvania. *Proc. Acad. Nat. Sci. Phila.* **27**, 127–128.

Young, G. C. 1982 Biogeography of Devonian Vertebrates. *Alcheringa* **5**, 225–243.

Discussion

J. B. RICHARDSON (*British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.*). Regarding the age of the vascular macroplants from Libya described as late Llandovery–early Wenlock (Gray *et al.* 1982) I would like to see the evidence for the age of the plant material precisely stated and documented in detail. In my experience Libyan geology is complicated and may change rapidly from one part to another. Further, the spore sequences in north Africa do not differ very much from those in the British Isles for this interval of time and so it is surprising that along with the apparently more advanced macroplants in Libya there is no corresponding advance in the spores.

Reference

Gray, J., Massa, D. & Boucot, A. J. 1982 Caradocian land plant microfossils from Libya. *Geology* **10**, 197–201.

A. J. BOUCOT. The age of the vascular macroplants referred to above by Dr Richardson is a problem, but not a very serious one for the stratigrapher familiar with problems of Libyan mid-Palaeozoic biostratigraphy and lithostratigraphy. The material (Klitzsch *et al.* 1973) was collected from the top of the Acacus Sandstone in the Djebel Fezzan (see figure D1 for location of the Djebel Fezzan), beneath the major, regional disconformity overlain by the Siegenian–Emsian age Tadrart Sandstone (see Boucot *et al.* (1983) for the age of the Tadrart). This regional disconformity may be traced from central Arabia (figure D1), across to western Egypt, through Libya, across northern Africa to Ghana, and thence across Brazil – south of the Amazon and Parnaiba Basins – turning southwesterly between Bolivia and Paraguay. The regional disconformity places Emsian-age beds dated by means of marine fossils, above a southerly and southeasterly older sequence ultimately terminating in Precambrian age rocks. The Djebel Fezzan locale is more than midway south in this disconformable transect. The youngest fossiliferous beds beneath the Djebel Fezzan plant macrofossils are graptolites of about Lower Llandovery–Middle Llandovery (zone 19) boundary age. The graptolitic beds are gradationally overlain in turn by coarse sandstones of the Acacus Formation, including some cross-bedded strata, which total about 100 m or so, and include in their top the plant fossils. From the stratigraphers point of view the question resolves itself into puzzling over whether about 100 m of coarse, cross-bedded sandstone of the Acacus Formation can extend in age far into the later Llandovery, or even into the Wenlock. In the disconformable belt to which the Djebel Fezzan locality belongs no post-Llandovery Wenlock, Ludlow or Přídolí age Silurian marine fossils have been reported from Arabia to Brazil. The presence of any post-Llandovery age erosional

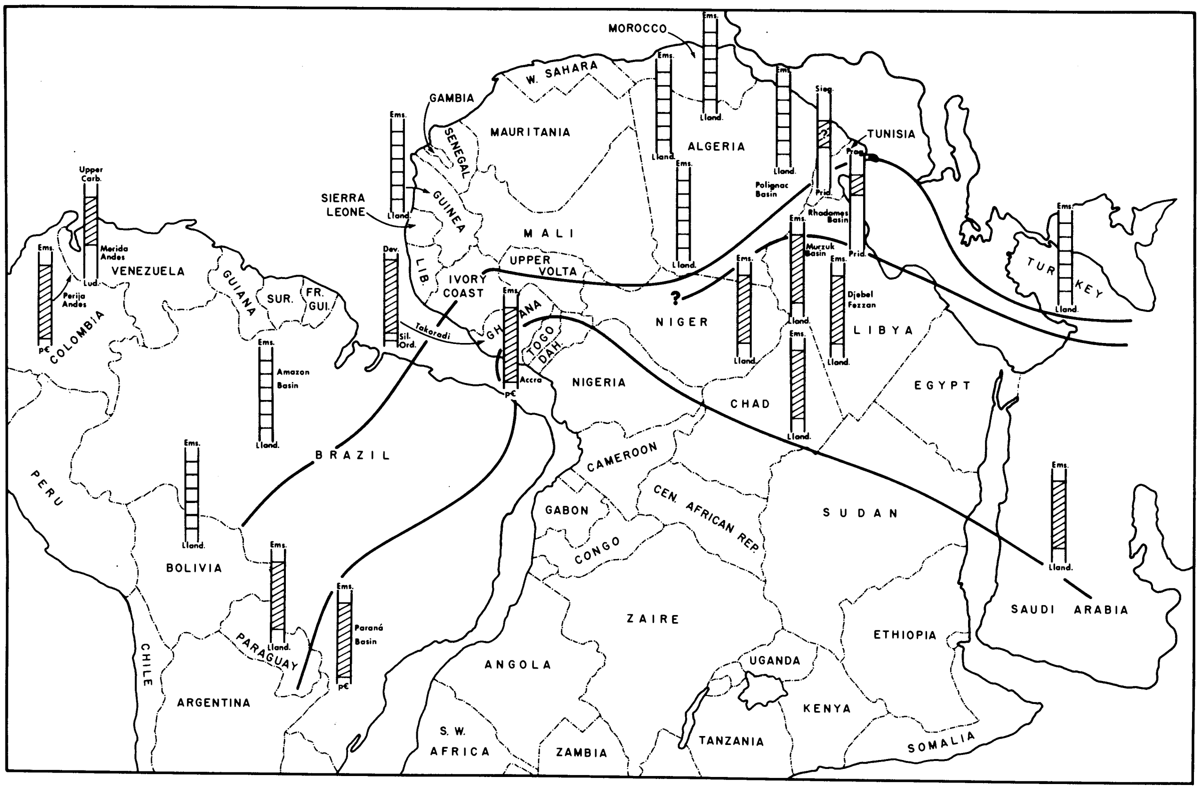

FIGURE D1. Diagram, with Africa and South America shown in what may be a reasonable mid-Palaeozoic relation, indicating the position of the major, pre-Emsian disconformity affecting large parts of Arabia, northern Africa, and eastern South America. North of the upper line the available stratigraphic columns indicate that there was continuous marine or non-marine sedimentation from the earlier Silurian (Llandovery) through at least the Emsian: except in the Merida Andes of Venezuela and the Perija Andes of Colombia and Venezuela. The Andean situations referred to here are, however, far removed from the problem being discussed by Richardson, and probably reflect a purely local rather than regional situation. The second line down, terminating in a question mark in Niger, includes a region where only strata of Přídolían age are absent. South of the lowermost line beds of Emsian age rest directly on Precambrian age strata. Note that in the Saudi Arabian, Libyan (including the Djebel Fezzan), Chad, and Niger columns the Emsian rests directly on Llandovery age beds. Data in support of these relations is available in varied works on the regional geology of North Africa, as well as in the Silurian correlation charts for South America and Africa published by the Geological Society of America as Special Papers.

remnants in this belt would not be expected. I conclude that it is unlikely that the Djebel Fezzan locality is of post-Llandovery age, and certainly not of later Wenlock, Ludlow or Přídolí age. Although neither Richardson nor I have actually carried out any field studies, or collected fossils in Libya (we both would like to visit and carefully recollect this critical locality), it is apparent from the published work of other geologists that the Libyan Silurian–Devonian is part of a platform sequence characterized by a relatively normal, layer-cake, easily worked out stratigraphic sequence. There are some faults of post-Devonian age, as well as some very broad structural domes and basins, but the overall story is very simple and straightforward. Libya is not a structurally complex region as far as the Palaeozoic rocks are concerned. The Silurian–Devonian lithofacies changes are both broad and gradual, and are summarized by Bellini & Massa (1980). I find no unusual complications in the Silurian–Devonian geology of Libya.

We (Boucot & Gray 1982) have previously discussed the evolutionary implications inherent in the apparent discrepancy between the Libyan macrofossils of putative later Llandovery age and contemporary spore floras. The ecological or evolutionary, or both, explanations for this apparent anomaly remain to be worked out.

References

Bellini, E. & Massa, D. 1980 A stratigraphic contribution to the Palaeozoic of the southern basins of Libya. In *The geology of Libya*, vol. 1, (ed. M. J. Salem and M. T. Busrewil), pp. 3–56. Academic Press.

Boucot, A. J. & Gray, J. 1982 Geologic correlates of early land plant evolution. *Proc. third N. Am. Paleontol. Conf.* **1**, 61–66.

Boucot, A. J., Massa, D. & Perry, D. G. 1983 Stratigraphy, biogeography and taxonomy of some Lower and Middle Devonian brachiopod-bearing beds of Libya and northern Niger. *Palaeontographica* A **180**, 91–125.

Klitzsch, E., Lejal-Nicol, A. & Massa, D. 1973 Le Siluro-Dévonien à Psilophytes du Bassin de Mourzouk (Libye). *C.r. hebd. Séanc. Acad. Sci., Paris*, D **277**, 2465–2467.