BRACHIOPOD DISTRIBUTIONS AND FAUNAL PROVINCES IN THE SILURIAN AND LOWER DEVONIAN

by L. R. M. COCKS *and* W. S. MCKERROW

ABSTRACT. Silurian shelf faunas were cosmopolitan, except for two areas: (i) South America and west Africa yield the *Clarkeia* fauna from the Llandovery to the Ludlow; and (ii) north-western America, north Greenland, and the U.S.S.R. yield the *Atrypella* fauna in the Late Silurian. During the Lower Devonian several provinces gradually appeared, to reach five in number by Emsian time. The geographical extent and composition of these provinces varies with time, and the distribution of the faunas is related to palaeolatitude, presumably reflecting climatic zones.

Faunal links between northern North America and the U.S.S.R. east of the Urals suggest proximity between these land masses in the Late Silurian and Early Devonian.

WILLIAMS (this volume) has shown that the faunal provinces present in the Northern Hemisphere during the Cambrian and Ordovician disappeared slowly during Late Caradoc and Ashgill times, culminating in the world-wide distribution of the *Hirnantia* fauna. This situation continued throughout the Silurian and, apart from the *Clarkeia* and *Atrypella* faunas discussed below, no distinct faunal provinces appear to have existed between the Upper Ordovician and the Lower Devonian. Holland (1971) has reviewed the other animal groups which support this conclusion. Faunal provinces reappear in Gedinnian times.

Text-fig. 1 shows the distribution of the four main types of sedimentary regime in the Silurian (drafted on the symposium map for the Lower Devonian). Although the map shows in detail the situation at the end of the Llandovery, no major changes occurred in these regimes on a world-wide scale during the whole of the Silurian period.

Both the platform carbonates and the platform mudstones seldom attain more than a few hundred metres in thickness. While the carbonates usually have a varied bottom-dwelling fauna, the platform mudstones normally contain only pelagic or epiplanktonic forms, mainly graptolites, bivalves, orthocones, and ostracods, with only a few specialized examples of other groups. The 'variable clastic sediments' include slope and ocean deposits, which are often greywackes up to some thousands of metres thick, as well as bordering shelf sediments.

The sloping shelves in the latter areas contain assemblages reflecting bottom-dwelling animal communities which change with depth (Ziegler *et al.* 1968). The composition of these communities changed with time during the Silurian; text-fig. 2 shows the relative succession at different times. We are grateful to N. J. Hancock and C. E. Calef for information on Wenlock and Ludlow communities. Rubel (1970) has been able to recognize this same sequence of animal communities in the Llandovery carbonate deposits of Estonia. However, in the carbonate deposits of central North America, where the *Pentamerus* Community, for example, may be a thousand kilometres wide, the faunas are not completely uniform; that is, there are many local

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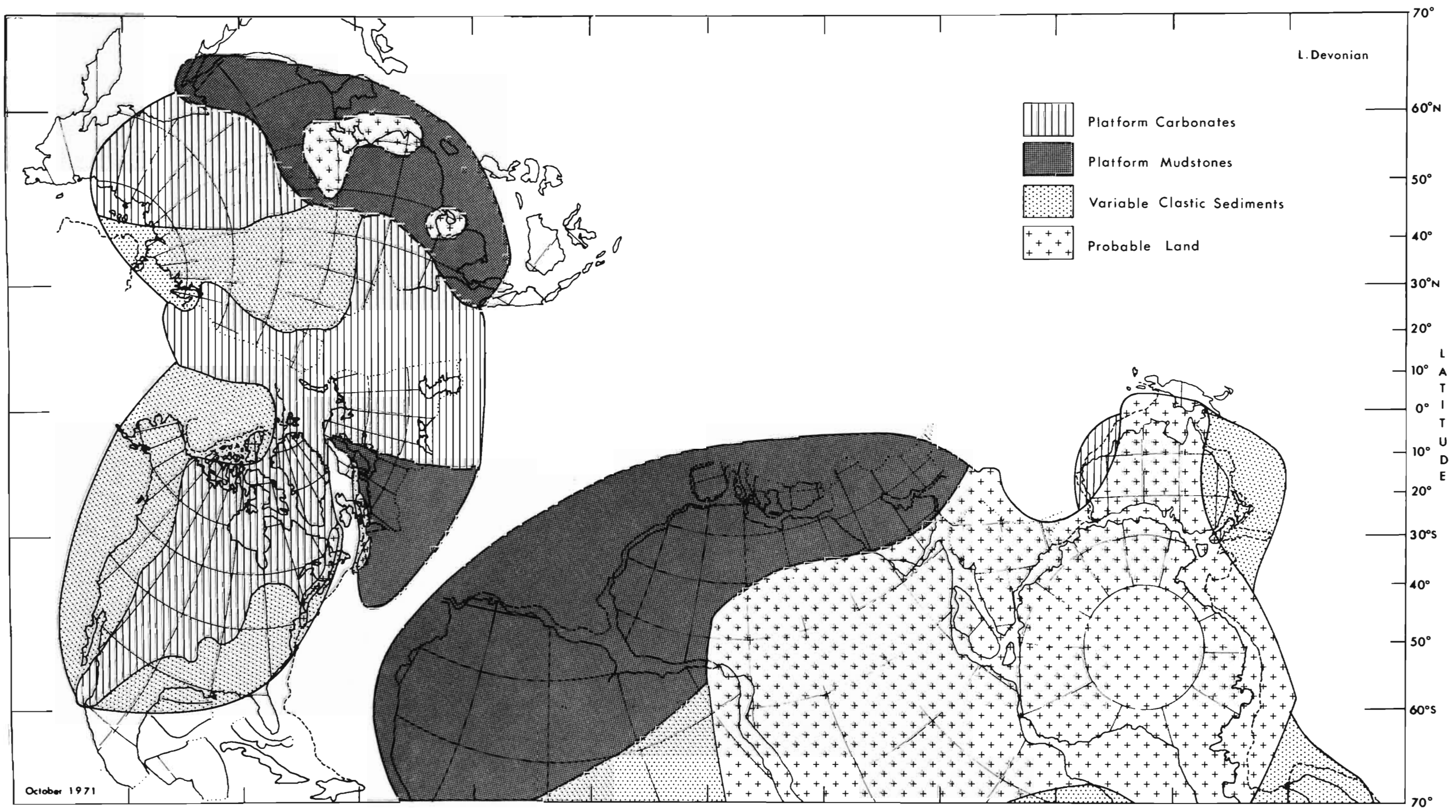


TEXT-FIG. 1. The four major sedimentary facies of the Silurian period (at an approximate time of Late Llandovery–Early Wenlock) drafted on the symposium palaeomagnetic map for the Lower Devonian.

divisions within the *Pentamerus* Community. Each of these subdivisions is composed of a selection of genera from the *Pentamerus* Community as a whole, and represents the same kind of clumping commonly found on the sea floor today. Even so, problems remain in the faunal interpretation of some carbonate deposits.

RHUDDANIAN	IDWIAN	FRONIAN	TELYCHIAN AND LOW WENLOCK	HIGH WENLOCK AND LUDLOW
Clorinda	Clorinda	Clorinda	Clorinda	Dicoelosia
Stricklandia	Stricklandia	Stricklandia	Costistricklandia	Isorthis
	Pentamerus	Pentamerus	Pentameroides	Sphaerirhynchia
Cryptothyrella		Eocoelia	Eocoelia	Salopina
Lingula	Lingula	Lingula	Lingula	Lingula

TEXT-FIG. 2. The sequence of animal communities at different times in the Silurian.

Over most of continental Europe, from south Britain to Podolia and from south Sweden to Morocco, the lower half of the Silurian is entirely within the platform mudstones. The absence of the common shelf benthos has been explained by Berry and Boucot (1967) by invoking water too cold for them. However, we suggest that the absence of brachiopods in any particular place may be due either to too great a depth of water (i.e. greater than that under which the *Clorinda* Community lived) or to foul bottom conditions, which may be at any depth. These latter may or may not have included low temperature conditions, but some brachiopods today thrive in the Arctic, and we reject cold water as a likely explanation of the central European Silurian.

A clue to the interpretation of this large central European sea is provided by Bohemia in the latter part of the Silurian, where there were volcanic outpourings in the Wenlock. These caused local shallowing of the sea, and the swells or islands thus formed were populated by sporadic shelly faunas, which in many cases consisted of endemic species often in carbonate facies. We consider that this phenomenon is too local to be termed a province in the Silurian. The only major change in the environment caused by the volcanics was the shallowing of the sea. Depth alone may thus explain the absence of brachiopods from most of the central European Silurian.

FALSE INDICATORS

Before examining the distribution and sequence of faunal provinces in the Silurian and Lower Devonian, we discuss some phenomena which have been taken for provincialization, but on what we consider to be spurious criteria.

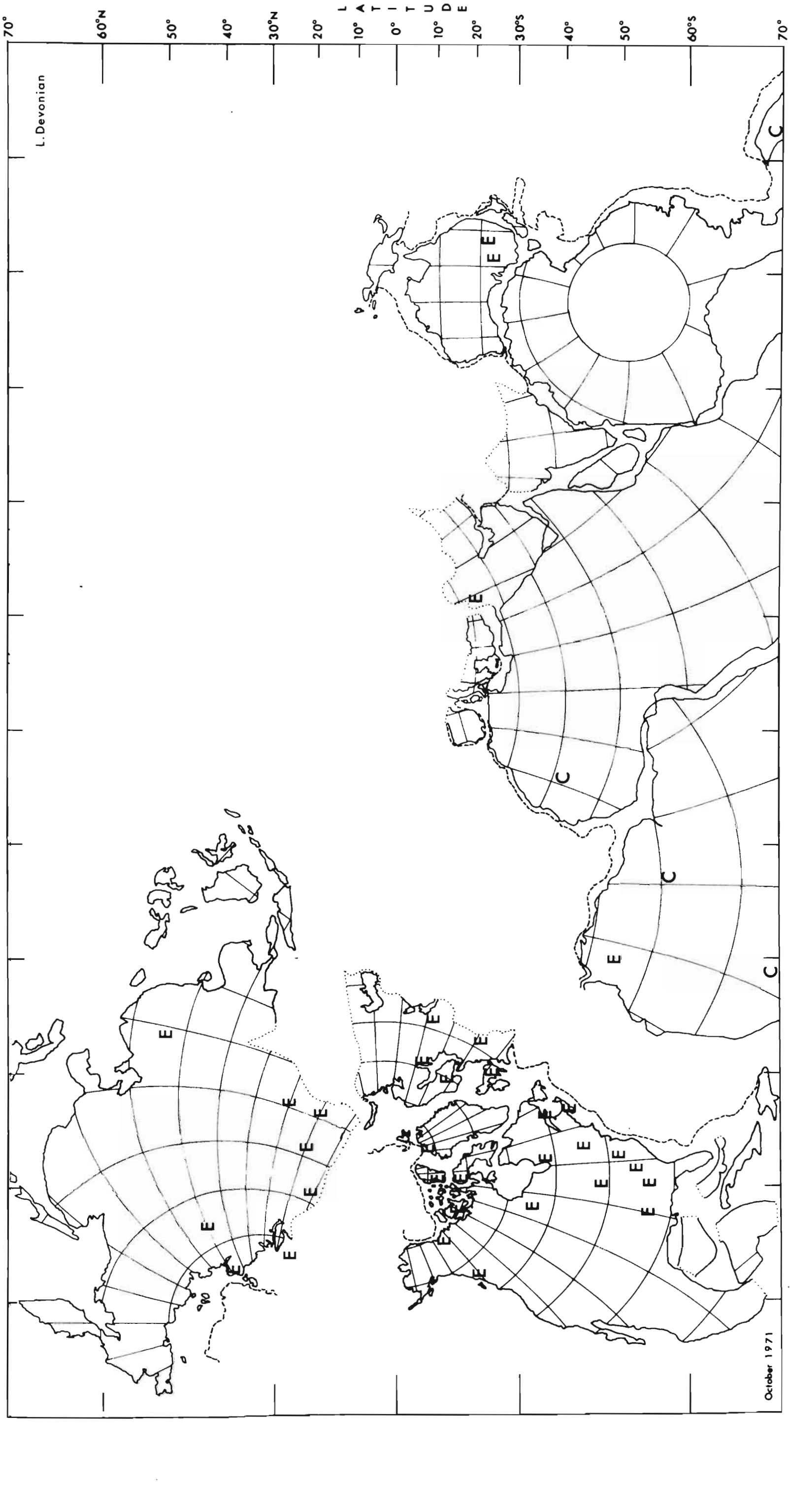
(*a*) *Confusion with animal communities.* Similar problems also arise in areas where the depth of the sea has remained roughly constant through large periods of time, and the number of communities is severely restricted. One such area is at Arisaig, Nova Scotia (Boucot *et al.*, in press), where the *Eoccelia* Community and its depth equivalents persist with few interruptions from Middle Llandovery until Gedinnian times. In some instances this restriction of communities has led to confusion, and been mistaken for faunal provinces. For example, the absence of the *Pentamerus* Community from Pembrokeshire and the southern Welsh Borderland in the Upper Llandovery led O. T. Jones to postulate two geographically distinct 'sub-facies', one there and the other at Llandovery and in Shropshire. A study of animal distribution within different environments is thus an essential preliminary to the certain recognition of faunal provinces.

(*b*) *Local environmental effects*. In Europe, the platform mudstones have already been discussed. Over most of North America, from Baffin Island to Mexico and from British Columbia to Quebec, masses of the ribbed pentamerid *Virgiana* are found in rocks of Middle Llandovery age (Berry and Boucot 1970, fig. 8). This and its very close (if not congeneric) relative *Platymerella* were long thought to be confined to this area, but *Virgiana* is now known from many localities in the northern U.S.S.R., notably Novaya Zemlya, the Pai Khoe area, the north and east slopes of the Urals, the Taimir region, and the Siberian Platform (Nikiforova and Andreeva 1961). However, *Virgiana* is still not known from Europe west of the Urals or Gondwanaland, despite many localities, at least in Europe, with ostensibly suitable ecological niches of the right age. That this is an ecological, rather than a provincial, problem is suggested by the associates of *Virgiana*, which do occur in Europe with *Pentamerus* in the Middle Llandovery. In North America the *Virgiana* and *Platymerella* Communities occur offshore of the *Cryptothyrella* Community. In the U.S.S.R., although the community situation has not yet been fully evaluated, beds with *Stricklandia* and others with *Clorinda* occur near by, and we suggest that *Virgiana* is the ecological equivalent of the European *Pentamerus* at this time. Since only two genera are involved in this odd distribution pattern, we do not feel that the phenomenon may properly be termed provincialization in this case.

(*c*) *Abnormal salinity*. Salinity reduced or increased from normal leads to a decrease in animal diversity. For example the Upper Silurian Salina Group of the eastern United States, with its evaporite deposits, yields a very sparse fauna. This is due to the local environment, and is quite independent of our concept of faunal provinces. Articulate brachiopods appear to be even more susceptible to salinity changes than most other macrofauna.

LLANDOVERY TO LUDLOW TIMES

Apart from the *Clarkeia* and *Atrypella* faunas discussed below, there is no hint of faunal provinces during most of Silurian time. Text-fig. 3 shows the distribution of faunas which are common in the *Salopina*, *Sphaerirhynchia*, *Isorthis*, and *Dicoelosia* Communities of Britain during Late Wenlock and Early Ludlow times. It will be seen that these faunas occur in North America and Venezuela, Europe, Asia, and Australia. We follow Boucot (1969) in postulating a now-eroded series of platform carbonates across the Russian Platform west of the Urals in a similar manner to that in North America. The bulk of the information for Asia comes from Niki-



TEXT-FIG. 3. The distribution of the *Clarkeia* Province (C) and the cosmopolitan shelly fauna (E) during Late Wenlock and Early Ludlow time.

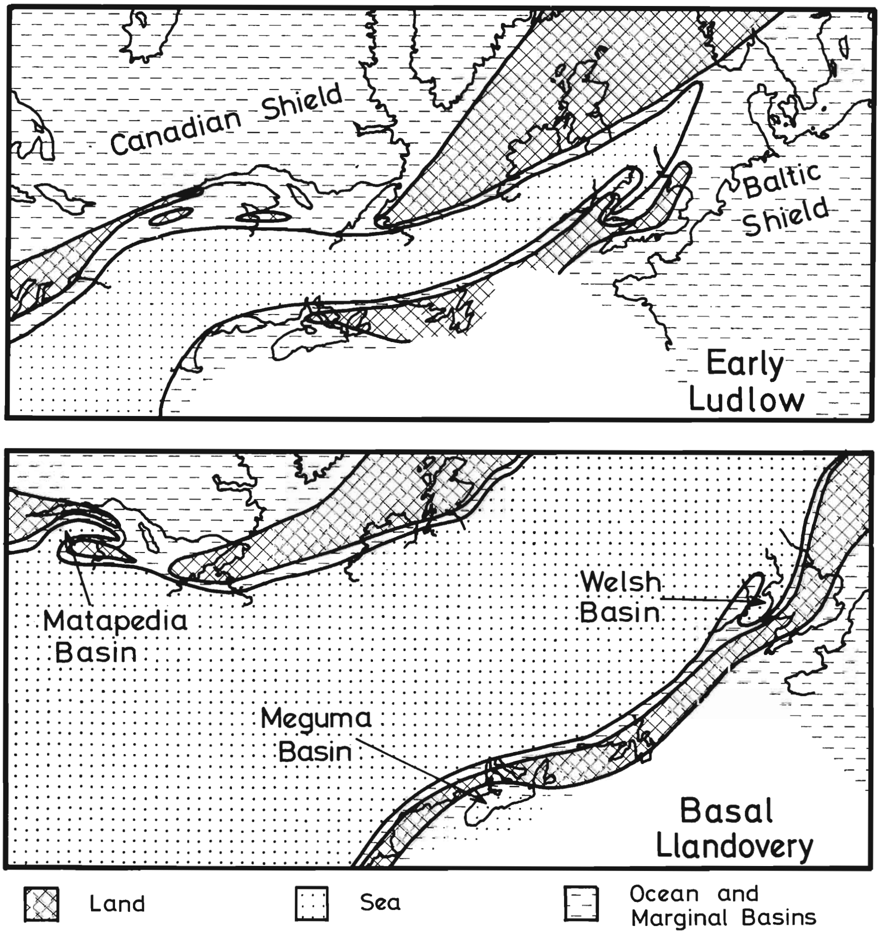
forova and Obut (1965) and Yin Tsan-Hsun (1966). There are no known Silurian deposits in Antarctica, but a shelly fauna including *Conchidium* has recently been reported for the first time from New Zealand (Cooper and Wright 1970). In north Africa few of the Silurian deposits contain brachiopods, but cosmopolitan Ludlow shelly faunas are present in the Upper Silurian of Morocco, Algeria, and Tunisia. South of the Sahara there are no known Silurian faunas, although part of the Table Mountain Group of South Africa is almost certainly of Silurian age; a Late Ashgill fauna and an Emsian fauna both occur in this thick sedimentary sequence (Cocks *et al.* 1970).

The Clarkeia *fauna*. The only example of provincialization shown in text-fig. 3 is the *Clarkeia* fauna. Over the whole of South America south of Venezuela the only shelly fauna found in the entire Silurian is one consisting of articulate brachiopods, a few homalonotid trilobites, inarticulate brachiopods, and a few molluscs. The articulate brachiopods are most abundant but only seven species are present: *Clarkeia antisiensis*, which occurs in rock-building swarms in places, together with lesser quantities of *Heterorthella freitana*, *Leptocoelia acutiplicata*, *Eostropheodonta fascifer*, *Australina jachalensis*, *Strophochonetes fuetensis*, and *Leptaena argentina*. This fauna has recently been recognized in Mauretania, West Africa (Cocks 1972), which would have been adjacent to Brazil in the Silurian. All these brachiopod species and the genera *Clarkeia* and *Australina* are endemic, and in addition *L. acutiplicata* and *S. fuertensis* may also represent undescribed endemic genera. The fauna has a rather low diversity and probably occupied a parallel ecological niche to the *Cryptothyrella*, *Eocoelia*, and *Salopina* Communities (which have similar low diversities). The *Clarkeia* fauna probably originated from the Late Ashgill fauna in the Table Mountain Group of South Africa. It is a question of definition whether this *Clarkeia* fauna is considered an example of provincialization in the Silurian (it is difficult to date precisely, but probably extended from Llandovery to Early Ludlow time), or whether it is simply to be considered a cold-water fauna. The palaeomagnetic base-map suggests that the area was nearly polar at the time, and there is much evidence of Late Ordovician and Early Silurian glaciations in South America, South Africa, and North Africa (Beuf *et al.* 1971). The *Clarkeia* fauna was thus confined to high latitudes.

The record of a cosmopolitan fauna in the Ludlow of Venezuela shows that the *Clarkeia* fauna was not completely isolated geographically. It is probable that the Venezuelan assemblages represent the *Sphaerirhynchia*, *Isorthis*, and perhaps *Dicoelosia* Communities, which perhaps preferred water too deep for the *Clarkeia* fauna. In addition to these environmental distinctions, the two faunas had different histories: the *Clarkeia* fauna being endemic to the Silurian polar regions; while the *Sphaerirhynchia*, *Isorthis*, and *Dicoelosia* Communities evolved during the Wenlock in North America and Eurasia. We consider that the *Clarkeia* fauna did represent a true faunal province in the Llandovery and Wenlock. It is not clear, however, what the position was in the Ludlow. The cosmopolitan faunas of Venezuela and north Africa may have been separated from the *Clarkeia* faunas of Brazil and Mauretania either by land barriers or by environmental differences, for example deep waters or climate.

The Proto-Atlantic Ocean. The two sides of the North Atlantic yield virtually identical faunas during the Silurian period. The width of ocean necessary to separate two provinces depends on the distribution of currents and oceanic islands. Williams (1969) has made a reconstruction of what the Ordovician current system might have been like in this area, and concluded that the currents flowed sub-parallel with the ocean margins. Assuming this to be true, a relatively narrow ocean basin would have been sufficient to prevent migration. All that can really be inferred is that the Proto-Atlantic Ocean ceased to be a barrier towards the end of the Ordovician, though it was still many hundreds of kilometres in width. The closure of the Proto-Atlantic throughout the Silurian (text-fig. 4) can also be inferred from the type of vulcanicity along its margins (Dewey 1969).

The palaeomagnetic evidence suggests that, during the Cambrian and Ordovician, the equator passed through North America: the areas on either side of the Proto-Atlantic Ocean would thus have had different climates from each other. This evidence is supported by the fact that limestones are much more abundant in the Cambrian



TEXT-FIG. 4. The closing Proto-Atlantic Ocean during the Silurian Period (after McKerrow and Ziegler 1972).

and Ordovician to the north-east of the Proto-Atlantic than to the south-west. The difference in climate would have helped to maintain the isolation of the pre-Silurian faunal provinces; for if some forms managed to get across (as they did to a small extent in New York and western Newfoundland) they would not be so well adapted for survival as the endemic forms. In the Silurian, the equator may have been closer to the narrowing Proto-Atlantic; and by the Upper Silurian there is evidence of warm-water faunas building limestones on both sides. It is thus possible that, as well as the narrowing of the ocean, a more uniform climate played a part in the loss of the faunal provinces in the Late Ordovician.

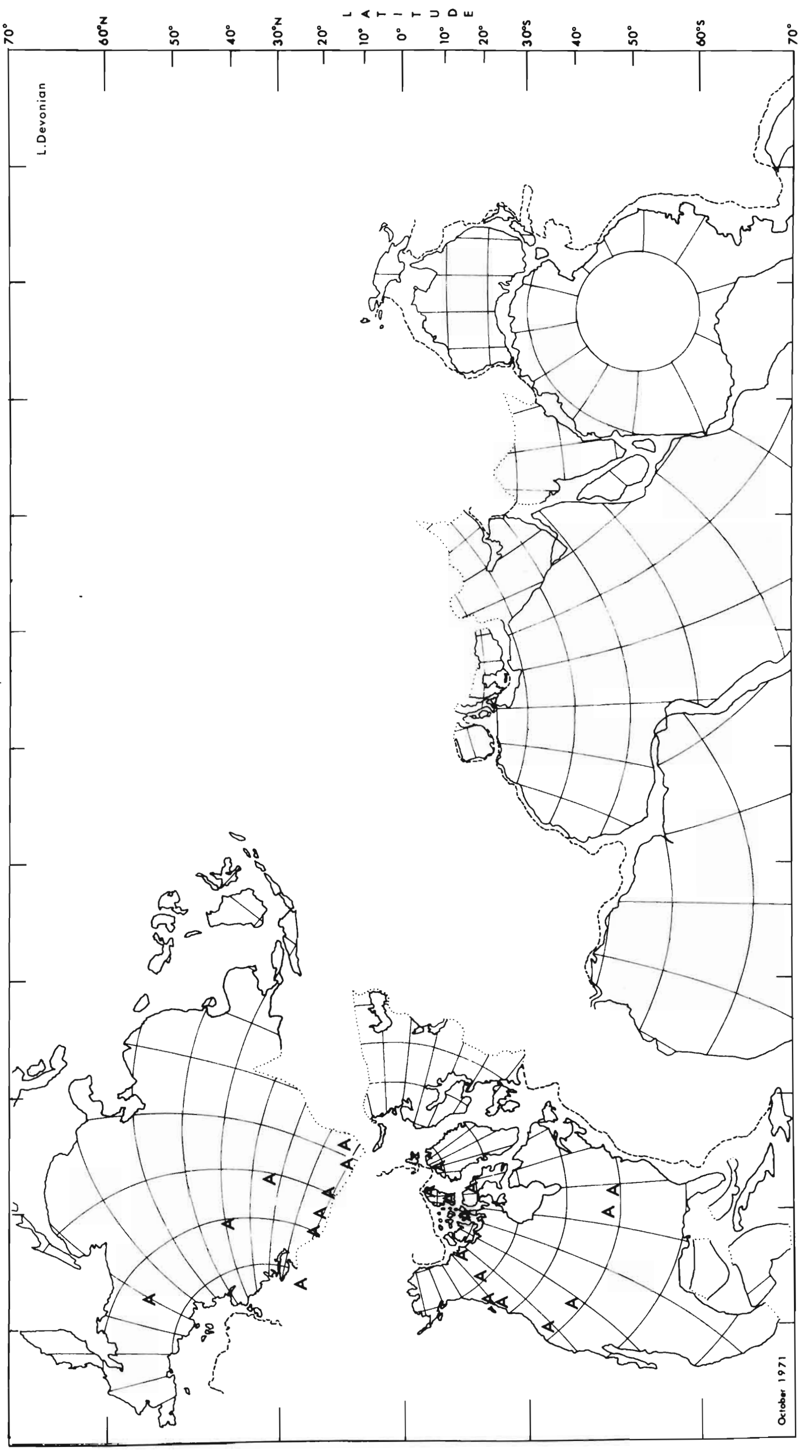
The main conclusion to be drawn from the geographical studies of Silurian faunas is that none of the continents are likely to have been widely separated. The occurrences of similar brachiopod assemblages in North America, Venezuela, Europe, north Africa, Asia, and Australia show that parts of Gondwanaland were within range of brachiopod spatfall from the other continents. Likewise, Asia east of the Urals was within similar range of North America, Europe, or Australia (text-fig. 3).

LATE SILURIAN TIMES

A distinctive fauna, dominated by *Atrypella* associated with the pentamerids *Kirkidium*, *Brooksina*, *Cymbidium*, and *Harpidium*, occurred in Late Ludlow and Pridoli times. This *Atrypella* fauna is found in much of the Canadian Arctic, Greenland, south-east Alaska, northern Indiana, Ohio, northern California, Nevada, Novaya Zemlya, the Urals, and Turkestan. The most widespread element of this fauna is *Atrypella phoca*, by far the most common Silurian brachiopod of the present-day Arctic regions (though it should be noted that *Kirkidium* and other species of *Atrypella*, including the type species *A. prunum*, occur in many parts of the world quite apart from this *Atrypella* fauna). The interpretation of the *Atrypella* fauna is difficult; the ecology and faunas of the Late Ludlow and Pridoli are as yet poorly known compared with those earlier in the Silurian and later in the Lower Devonian. The fauna has a relatively low diversity, which is unexpected in view of its supposedly equatorial position in the Silurian. The low diversity could be explained by a shallow-water origin, but large pentamerids are usually found elsewhere in a rather deeper position.

Towards the end of the Silurian period, folding took place in parts of Scotland and Norway which, together with other evidence (McKerrow and Ziegler 1972) suggests that continental collision took place in the Ludlow or Pridoli or earlier times. This folding was appreciably earlier than the equivalent Middle Devonian Acadian orogeny of the northern Appalachians; thus during Pridoli times the Proto-Atlantic Ocean may not have been completely closed in the Appalachians. The mountain range that extended from Scotland northwards through Norway appears to have acted as a barrier between the European faunas and the *Atrypella* fauna. However, the eastern boundary of the *Atrypella* faunal province probably passes to the east of Quebec; but Appalachia had not yet been uplifted, so if there was a land barrier it must therefore have been formed by raised parts of the Canadian shield.

The *Atrypella* fauna is also present in the U.S.S.R. east of the Urals. It would thus seem probable that the Asian continent was closer to Canada during the Late Silurian than it was to western Europe (text-fig. 5). The palaeomagnetic data upon



TEXT-FIG. 5. The distribution of the *Atrypella* fauna during Late Silurian time (Late Ludlow and Pridoli).

which these base-maps have been constructed gives an estimate of the latitude and angular position of each continental mass, but not the longitude. The distribution of the *Atrypella* fauna in the Late Silurian is the first reason why we have shown the main Asian block adjacent to Canada in our maps.

LOWER DEVONIAN TIMES

Much of this section is based on the comprehensive account of the distribution of Lower Devonian brachiopods given by Boucot *et al.* (1969), where detailed lists of genera may be found.

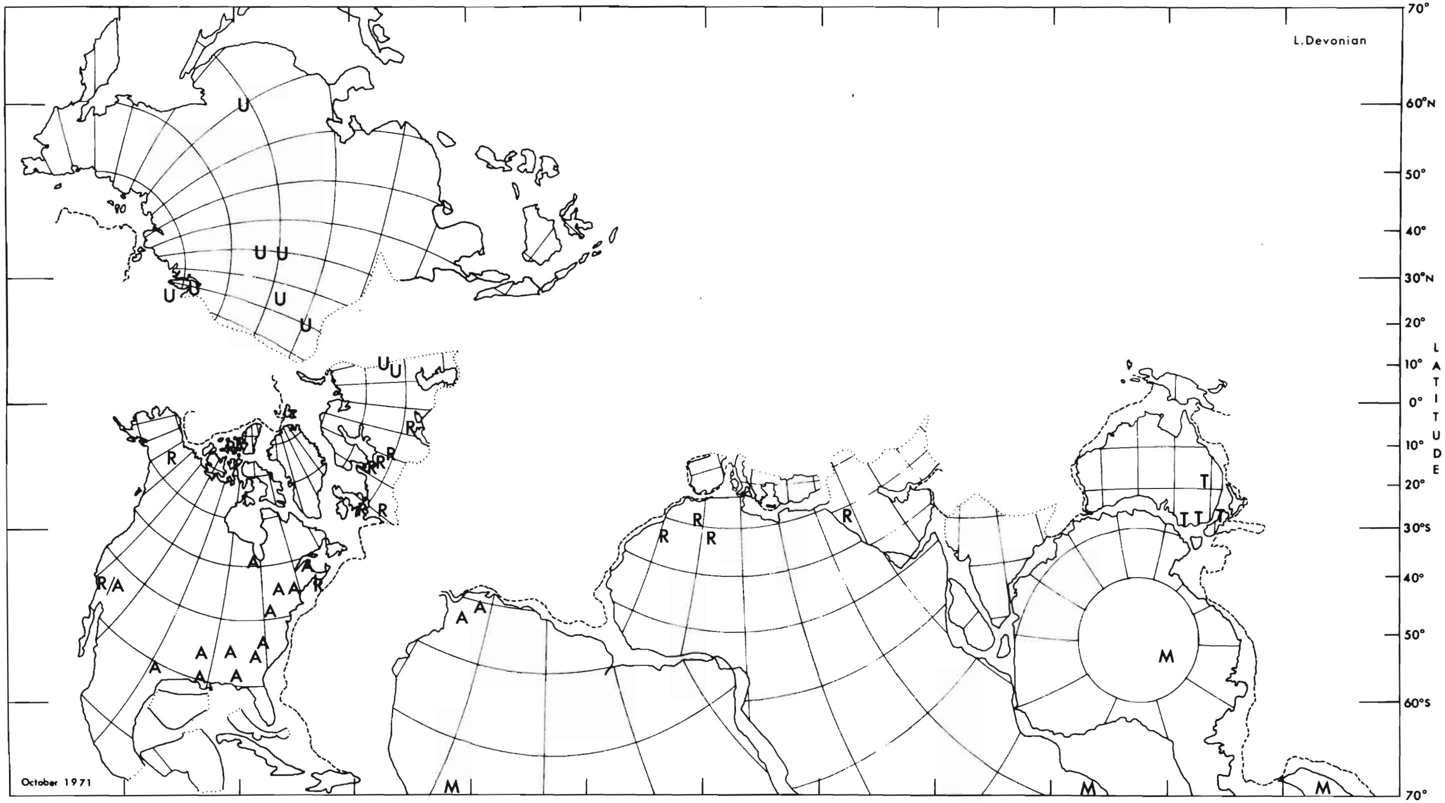
In contrast to the Silurian, many continents ceased to be covered by extensive shelf seas in the Lower Devonian. They thus became potential barriers to the migration of shelf sea faunas, but nevertheless, except in the Appalachians, faunal provinces developed only slowly. During the Gedinnian and Siegenian, provincialism was mainly at the species level, but no province was completely isolated.

The Lower Devonian shelf sea to the west of the Appalachians was isolated from California and Nevada by the southward extension of the Old Red Sandstone land mass which covered the Canadian shield. However, an old-world Rhenish fauna of Siegenian age occurs in the Annapolis valley of south-western Nova Scotia; but, as the Acadian orogeny had not yet taken place, there cannot have been a mountain belt acting as a barrier between Nova Scotia and Quebec. Contemporary non-marine fish faunas at Arisaig suggest that there may have been some small land area isolating Nova Scotia from the shelf areas north of the Fredericton Trough (McKerrow and Ziegler 1971).

No Gedinnian or Siegenian faunas are known from South America or the Antarctic. But Gondwanaland could not have been isolated from the other continents because during Gedinnian and Siegenian times European faunas are present in north-west Africa. The Tasman Province appeared for the first time in the Late Gedinnian in eastern Australia and New Zealand; this was an equatorial fauna (text-fig. 6), perhaps isolated by continental land masses from North Africa.

The Emsian has been considered the peak time of provinciality in the Devonian. When the data for the Early Emsian are plotted on a base-map with the continents arranged according to the latest palaeomagnetic evidence, with the Asian block transferred to the same position as in text-fig. 5 (based on the distribution of the *Atrypella* fauna in the Late Silurian) the distributions become clearer. There are five main provinces: Rhenish and Tasmanian near the palaeoequator; Uralian north of the equator; and Appalachian and Malvinokaffric south of the equator, the latter extending over the South pole (text-fig. 6). We group the 'Cordilleran Province' recognized by some authors with the Rhenish Province, their faunas are closely overlapping both in composition and geographical distribution.

The Rhenish Province extended from California around the northern margin of the Old Red Sandstone continent to central Europe and Nova Scotia. The Rhenish fauna also occurred in North Africa, which on text-fig. 6 is separated from Europe by some 50 degrees of palaeolongitude. It is possible that these two continents may have been closer together in the Lower Devonian than is shown on this map. The other equatorial province was the Tasman Province of eastern Australia. It was



TEXT-FIG. 6. Faunal provinces in Early Emsian time. Data has been taken from Boucot *et al.* 1969, and drafted on to the symposium palaeomagnetic map for the Lower Devonian (with the Asian plate shifted to the west).

separated from the Rhenish Province of Arabia by some 85 degrees of palaeolongitude, and from the Rhenish Province of California by some 70 degrees of palaeolongitude. The gap between California and Australia was ocean, but why there was no mixing between Arabia and Australia is not clear; there must have been some barrier along the northern Gondwanaland coast. Whether this was some land barrier jutting northwards into harsher climates or whether the barrier was defined by some other parameters is not known.

Uralian Province faunas are known from the plate margins on both sides of the present-day Ural Mountains. These two margins appear to have formed a belt lying between the equator and 60 degrees north in Emsian time. This supports the evidence of the Silurian *Atrypella* faunal province as to the relative positions of Asia and North America in the Middle Palaeozoic. House (1971, p. 93) gives more data which also supports these relative positions in Upper Devonian times.

The relationship between the Appalachian and the Malvinokaffric Provinces was not so simple. Although text-fig. 6 shows the situation in Early Emsian time, the Malvinokaffric Province had disappeared by the Late Emsian (Boucot *et al.* 1969, fig. 4). The Malvinokaffric Province yields a distinctive suite of largely endemic genera, yet distributions became mixed at the province margins. For example, in the Early Emsian of Bolivia (Kozlowski 1923) four 'Malvinokaffric' genera, *Australocoelia*, *Notiochonetes*, *Scaphiocoelia*, and *Pleurothyrella*, are found together with three 'Appalachian' genera, *Meristella*, *Plicoplasia*, and *Pustulatia*. Rather later in the same area *Pustulatia* and another Appalachian genus *Tropidoleptus* are found together, but by this time the typical Malvinokaffric genera had largely become extinct. Similarly, in New Zealand, 'Tasman' and 'Malvinokaffric' genera occur together. These facts, and the polar position of the Malvinokaffric Province, lead us to postulate that the Malvinokaffric Province may have been no more than a colder-water equivalent of the Appalachian Province. Certainly no province in Emsian time was completely isolated by wide ocean barriers.

CONCLUSIONS

The Silurian and Lower Devonian faunal provinces illustrate the three main factors which we consider essential to the development of faunal provinces based on shelf sea benthos. These are: (i) Isolation, (ii) Different climates, and (iii) The previous geological history of an area.

Isolation is the key factor in the development of a faunal province; without isolation faunal provinces could not originate. Wide oceans and continents can both form barriers, but it is only the oceans that are seen to provide barriers that persist through long periods of geological time; for example, the Proto-Atlantic separates provinces throughout the whole of the Cambrian and most of the Ordovician.

Climates can provide faunal provinces without much isolation, but these provinces tend to be short-lived, for example the Malvinokaffric Province in Lower Emsian time. But when areas with different climates are also isolated, for example the Lower Ordovician on either side of the Proto-Atlantic, then climate can reinforce the effects of isolation to produce the distinctive endemic genera characteristic of a long-lived faunal province.

The previous geological history of the *Clarkeia* Province illustrates our third factor. Arising from an isolated Ashgill fauna in South Africa, the *Clarkeia* fauna colonized the Silurian polar regions of South America and west Africa in Llandovery times, and remained there until the Ludlow.

One of the main palaeogeographical differences between the Silurian and the Lower Devonian is the extent of the shelf seas over the continents. In the Silurian much of Asia, Europe, and North America was covered by shelf sea; these seas were so extensive that none of these continents acted as barriers to the migration of shelf faunas. This, together with the lack of wide oceans between the continents, is the dominant reason for the cosmopolitan nature of Silurian shelf faunas. In the Lower Devonian, on the other hand, major parts of the Canadian and Baltic Shields were above sea level; it is probable that the same is true for much of Siberia and Gondwanaland.

In addition to the larger land masses, some narrow mountain belts were also present in the Pridoli and Lower Devonian, for example the Caledonides between Scotland and Spitsbergen provided a barrier during earlier Pridoli times between the *Atrypella* fauna of northern Greenland and the 'normal' Late Silurian faunas of Europe. Continental land barriers are less effective as barriers than wide oceans; the faunas on either side tend to overlap in composition and to persist as recognizable provincial entities for relatively short periods of time. Narrow mountain belts like the Caledonides would have formed even more temporary barriers than did continental masses.

Isolation and climate are each alone sufficient to create a faunal province, but a combination of these two factors is much more effective. Even with a wide ocean, there will always be sporadic larval migration between provinces, so that long-lived provinces are constantly subject to occasional foreign invasions. These invasions will succeed only if a suitable environment exists in the new area. If the environment is not nearly perfect, then the invader can seldom compete with the well-adapted endemic species of a province with a long history. Isolated continents with different climates and different endemic faunas will thus provide the most distinct and the most enduring faunal provinces.

There were no endemic provinces at the start of the Devonian. Of the only two Silurian provinces, the *Clarkeia* Province persisted no later than the Ludlow and the *Atrypella* fauna did not give rise directly to any of the Devonian provincial faunas. As a result the Lower Devonian provinces were all short-lived, and the boundaries between successive provinces often fluctuated rapidly: the Devonian provinces tended to move their boundaries and even merge or break up over short periods of time. Because there had been no previous history of provincialization, the faunal diversification did not proceed far enough to establish the separate provinces on a permanent basis. In addition, apart from the isolation of the Tasman Province by Gondwanaland, there seems to have been no large barriers to provide isolation. Thus in the Lower Devonian the main cause of the provinces appears to have been climate alone.

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L. R. M. COCKS
Department of Palaeontology
British Museum (Natural History)
London SW7 5BD

W. S. MCKERROW
Department of Geology and Mineralogy
Oxford OX1 3PR