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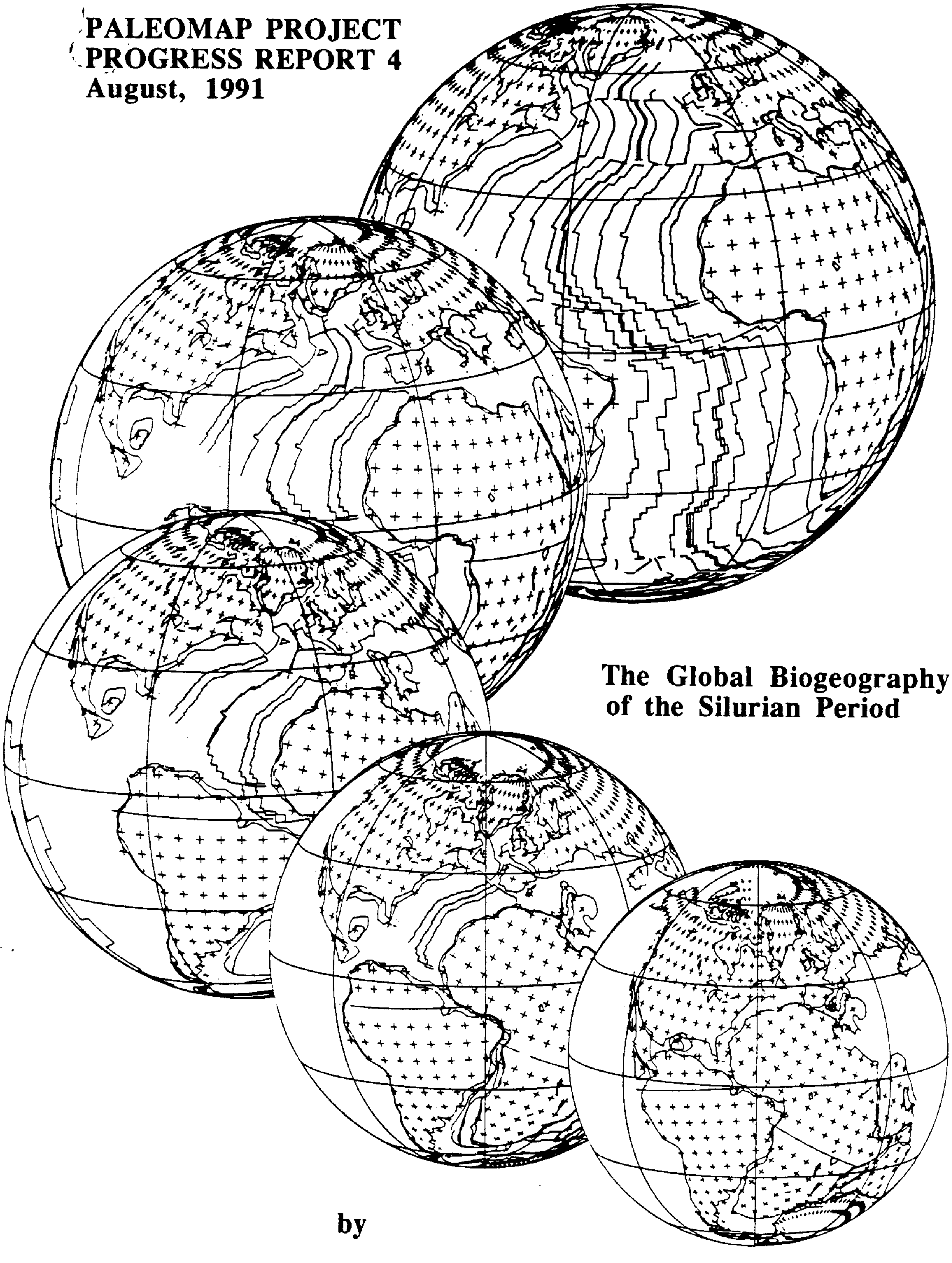

The Global Biogeography of the Silurian Period

by

L. R. M. Cocks and Christopher R. Scotese

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Abstract: During the 23 million years of the Silurian the palaeogeography was dominated by the large Gondwanan plate, which probably carried more than half the world's land areas. As this drifted over the then South Pole (which was probably in southern Africa or southern South America during the period) the area of what is now southern Europe gradually decreased in palaeolatitude and increased in ambient temperature. This was mirrored by an increase in the palaeolatitude of the Antarctic and Australian end of the continent. New maps show the general disposition of the palaeocontinents. The Silurian opened with relatively cool conditions and low-diversity faunas following the end-Ordovician ice age but by the end of Llandovery time global temperatures had increased, with large equatorial evaporitic deposits laid down during the mid and late Silurian. There was a corresponding increase in the faunal diversity and abundance.

Apart from the low-diversity *Clarkeia* fauna, the subpolar precursor of the Malvinokaffric faunas, which chiefly inhabitated South America and parts of Africa, the Llandovery and early Wenlock shelly faunas displayed considerable cosmopolitanism. In the latter part of the Silurian the precursors of the much more distinct and separate early Devonian faunal provinces were evolving as dispersal between the various geographical areas became more difficult. Laurentian conodont faunas, however,

remained in faunal continuity with part of Gondwana (southern Europe). Deeper-water deposits of the period are characterised by the remains of the graptolites which flourished in the overlying water columns. Large areas of continental as well as oceanic sea floor at higher latitudes must have been relatively anoxic, as witnessed by the occurrence of only limited but abundant and distinctive faunas such as the cardiolid bivalves of southern Europe and North Africa. These faunas occurred at a variety of depths right up to the shore-face without the contemporary common brachiopods, bryozoa, corals and crinoids.

The great leap forward from the era before the implications of plate tectonics became apparent on Palaeozoic continental distributions came with the short paper by Wilson (1966) who first postulated the existence of the ocean now known as Iapetus, and the next substantial step was the publication of continental distribution maps sequentially through the Phanerozoic (Smith *et al.* 1973). On these first maps some faunal distributions were plotted for the Silurian (Cocks & McKerrow 1973). Subsequently an excellent paper was published on Silurian continental distributions and palaeobiogeography by Ziegler *et al.* (1977) and later maps have mostly been refinements of their maps, which have been accepted by most workers in the field, but not all, e.g. Boucot & Gray (1983) who favoured a Pangeic reconstruction. Ziegler *et al.* (1977) justified the position of the various sutures identified, and these are not repeated here except when some modifications have been necessary.

Figures 1 to 3 illustrate our palaeogeography of the Silurian and Early Devonian. The positions of the continental blocks are modified after McKerrow and Scotese (1990), and are substantially different from the Siluro-Devonian reconstructions previously published by (Scotese *et al.*, (1979; 1985), and Scotese, (1986). Major changes include a more southerly position for Laurentia and Baltica during the Early Devonian, the recognition that Kazakhstan is not a separate continent, but rather an aglomeration of island arcs and far-travelled terranes that accreted to the southwestern margin of Siberia, and an orientation for Gondwana that places the South Pole in southern Brazil and north-central Argentina during the Siluro-Devonian, With the Silurian now determined as a mere 23 million years long, as compared with the 75 Ma of the Ordovician and the 58 Ma of the Devonian (McKerrow et al. 1985), it is not surprising that the palaeobiogeography of the period appears to be less dynamic than its earlier and later neighbours. There is now a fair consensus on the relative positions of some of the larger palaeocontinents, in particular the large masses of Gondwana (which included Africa, South America, Australia, Antarctica, India and some adjacent parts of Asia and Europe - Cocks & Fortey 1988), Siberia and Laurentia (North America). However, there is not yet agreement on the extent to which the Iapetus Ocean had completed its closure and hence the extent to which Baltica had collided with Laurentia. Of the other substantial palaeocontinents, such as Kazakhstan, South China and North China, as well as the smaller continents and microcontinents, there is little substantial information on their position, although in some cases their approximate palaeolatitudes may be deduced from their contained faunas.

Needed Lecture

An obvious point, but one that has nevertheless been overlooked by some scientists who have worked mostly on particular narrow time slices, is that correct palaeogeography must be consistent with those in the previous and succeeding periods. , Even the fastest-moving palaeocontinent is unlikely to have moved towards or away from its neighbour by more than 15 cms a year, and there is every reason to suppose from the Mesozoic to Recent rates of plate motion that a more usual speed was in the 2-10 cms per year range.

rather than central Africa (Scotese & Barrett, 1990). These revised maps are similar in many respects to the Devonian reconstruction published by Heckel & Witzke (1979).

These changes have been made in light of new palaeomagnetic, palaeoclimatic, and biogeographic data that was presented at the symposium on Palaeozoic Biogeography and Palaeogeography convened in Oxford in August 1988 (McKerrow & Scotese, 1990). New palaeomagnetic data from North America places the Appalachian margin at 40° south during the Early Devonian (Miller & Kent, 1988). This new pole is consistent with palaeomagnetic results from Britain, which indicate palaeolatitudes of 20° - 25° south for parts of southern Scotland (Kent & Van der Voo, 1990). The more southerly position for North America also allows Siberia to occupy more subtropical latitudes. A more subtropical position better explains the occurrence of coral reefs and evaporites in Siberia and Mongolia during the Devonian. The more southerly position of North America and Baltica requires that contact between these continents and Gondwana occurred earlier than previously supposed. It now seems likely that there was not a wide ocean between Euramerica (North America and Baltica) and Gondwana during the Devonian. We prefer the scenario outlined by Neugebauer (1988) which suggests that Euramerica and Gondwana were in contact, but not in collision, during the Devonian, and that the Variscan orogeny was due to the clockwise rotation of Gondwana relative to Northern Europe during the Carboniferous. Central and Southern Europe were "caught in the vice" between these two supercontinents and were deformed in a transpressive shear zone resulting from the collision and rotation.

Figures 1 - 3 also show the approximate distribution of land, sea, and mountains (>2000m) and active plate boundaries during the Silurian and Early Devonian. The palaeogeography for the Silurian is modified after Ziegler *et al.* (1977, 1979). The Early Devonian palaeogeography is based on the compilation of Scotese and Barrett (1990). Ronov *et al.*, (1984) and Hongzhen (1985) also served as useful sources of palaeogeographical information.

The various palaeocontinents will now be reviewed in turn, followed by a section on faunal distributions and provinces.

Laurentia

The whole of what is today the United States, Canada and Greenland formed a single coherent block in Silurian times, apart from Florida, which formed part of Gondwana (as can be deduced from the Cambrian and Lower Ordovician facies and fauna) and eastern Newfoundland and the eastern parts of the Maritime Provinces of Canada, which formed part of the Avalonia-Baltic area. This large continental plate is termed Laurentia and it also included what ~~is~~ are now north-west Ireland, Scotland and the upper nappes in western Norway. This plate, as can be seen from the diversity of the faunas and the sedimentological facies, which include many warm-water carbonates and evaporites, sat squarely over the palaeoequator for most of Cambrian to Devonian times but appears to have drifted into the southern tropics during the Silurian. However, any lateral movement along the equator would be difficult to detect since both its faunas and its palaeomagnetic position would have been little affected.

The formations and ages of Laurentia have been summarised by Berry & Boucot (1970). Much of the continent appears to have been flooded by warm cratonic seas which have left a "layer-cake" stratigraphy of relatively thin deposits, best known from the classic works ~~in~~ of the last century in New York State, Ohio and Ontario. Much dolomitisation occurred. Nearer the margins the sediments are thicker, for example at Anticosti Island, Canada, where the Llandovery succession alone, although not quite complete at the top, attains a thickness of 1200m. Both macrofaunas, which are as usual dominated by brachiopods, and the microfaunas, of which the most common are ostracods (e.g. Copeland 1974) and conodonts (McCracken & Barnes 1981, Bergström 1990), are in general well-known and exhibit the expected tropical high diversity. In the early Silurian the community bands known from the Welsh Borderland in clastic rocks have been recognized in the mid-western United States in carbonate facies (Johnson 1980) apart from the shallowest community, which is dominated by algae.

Gondwana

Gondwana was by far the largest Silurian palaeocontinent, although rocks of that age are known only from its margins; Silurian deposits are unrecorded from the central core, Africa south of the equator, India, Madagascar, western Australia and Antarctica (apart from an unconfirmed record of two corals" Cocks 1989). The continent is presumed here to include Florida, southern Europe, Turkey, the Arabian Peninsula, Iran, South China, Tibet (Qiang Tong and Lhasa blocks) the Shan-Thai (or Sibumasu) block, New Guinea and New Zealand at its perimeters

(Fig. 4) and these all carry rocks of Silurian age, although they have been studied to very different levels (Cocks & Fortey 1988). Most of Southern Europe and North Africa were covered by anoxic deposts yielding chiefly graptolites, bivalves, and cephalopods during Llandovery and Wenlock time and these are known right up to the supposed shore-line deposits in Algeria, Tunisia and Libya. Later Silurian deposits of Ludlow and Přídolí age from these areas were clearly better aerated and carry a more substantial range of shelly faunas (Berry & Boucot 1973). In early Silurian times the South Pole was located in what is now North Africa (Fig. 1) and the vast Gondwanan mass drifted across it, so that by the beginning of the Devonian (Fig. 3) the South Pole was in southern Brazil. It therefore follows that what is now Southern Europe steadily decreased in latitude during the Silurian. This explains why the early Silurian deposits, in for example Bohemia, consist only of clastic materials, and why limestone deposits occurred sporadically in the Ludlow Kopanina Beds for the first time in the Lower Palaeozoic, and why carbonate deposits become more dominent in the Přídolí and Devonian, culminating in the famous Koneprusy reef deposits of late Lochkovian and Pragian age.

In South America, Silurian deposits are largely confined to the western half of the present-day continent, with the eastern half of these deposits consisting of the Malvinokaffric Profince with *Clarkeia* and other less diverse communities (Isaacson *et al.* 1976) and the western half, including Venezuela, carrying more diverse assemblages (Boucot *et al.* 1972, Laubacher *et al.* 1982). This distribution can be explained by the lower palaeolatitudes of what is now the western part of the continent (Figs 1-3). The *Clarkeia* faunas are also found in north-western Africa (Cocks 1972). Between them in Silurian times lay the Florida peninsula, from which Silurian rocks are known in the subsurface lying above Ordovician of undoubted Gondwanan rather than Laurentian affinities (Whittington 1953, Cocks & Fortey 1988).

In the Arabian peninsula, for example in Saudi Arabia, the early Silurian also exhibits glacial features (McClure 1988) and consists exclusively of clastic rocks, but the record from there to the Himalayas is poor (Berry & Boucot 1972b). Once again, though, the Ordovician deposits of these regions provide sensitive indications of both palaeolatitude and faunal affinities. However, in South China there are substantial deposits of Silurian age which have now been extensively documented in English, e.g. by Wang *et al.* (1984, 1987), and Mu *et al.* (1986) although the great bulk of the rocks are of Llandovery and early Wenlock age. The faunas are relatively cosmopolitan. From the disposition of the Lower Ordovician facies and faunas in South China it seems probable that at that time the South China area formed a marginal part of Gondwana (Figs 1-3), but whether or not it formed part of Gondwana in Silurian times is uncertain.

In the Shan-Thai or Sibumasu block, which stretches from the Shan States of Burma through much of Thailand and Malaysia down to Sumatra, the Silurian record is patchy. A variety of facies is represented, from the graptolitic deposits of the Shan States and the Langkawi Islands of north-western Malaysia to the shelf carbonates occasionally present, for example near Kuala Lumpur (Boucot *et al.* 1966). However, once again we follow the proposed reconstructions of Cocks & Fortey (1988) in placing this block on the margin of Gondwana (Figs 1-3).

In Australia, marine Silurian rocks are absent from the west of the country but the system is represented in Tasmania, Victoria, New South Wales and Queensland, although even there early Silurian rocks are relatively scarce and are confined to the graptolithic facies (Talent *et al.* 1975). Ludlow and Přidolí age rocks are more widespread and include the well-known and richly fossiliferous deposits of the Yass area, near Canberra. Near the margin of the Gondwanan palaeocontinent in New Zealand and New Guinea there has been much subsequent tectonic activity and Silurian rocks are only preserved fortuitously, for example the Llandovery age graptolites from the Kemoen Formation in New Guinea (Visser & Hermes 1962) and the Wenlock-Ludlow *Conchidium*-bearing beds at Hailes Knob, New Zealand (Cooper & Wright 1972).

Baltica and Avalonia

The time at which these two continents merged across the closing Tornquist's sea between them is still a matter for debate. Certainly there was good faunal contact between the two by mid-Caradoc times, but the actual collision may not have taken place until earliest Silurian times (Fig. 1), with the chain of buried igneous intrusions, many with Silurian radiometric dates, under the North Sea stretching across to the southern Baltic area representing the secondary phase of the union. The Silurian deposits of the area are amongst the best known of any, since they include the classic type Llandovery, Wenlock and Ludlow areas of Wales and the Welsh Borderland as well as the richly fossiliferous sequences exposed in Gotland and Estonia. Avalonia also includes much of the Maritime Provinces of Canada, with well-exposed and well-monographed successions such as at Arisaig, Nova Scotia (Harper 1973, Boucot _et_ _al._ 1974), as well as eastern Newfoundland, south-east Ireland and Belgium, and Baltica, the graptolite facies of southern Sweden and Denmark (e.g. Bjerreskov 1975) and the subsurface deposits of Latvia and Lithuania. In Poland most of the subsurface rocks and the outcrops in the Holy Cross Mountains at the southern edge of the palaeocontinent are in graptolitic facies, apart from the beds of Ludlow and Přídolí age which also contain some shelly fauna (e.g. Tomczykowa 1971). The palaeocontinent extends south-eastwards and includes flat-lying later Silurian rocks, which make up the Wenlock, Ludlow and Skala horizons of Podolia (Nikiforova 1977), and the eastern boundary coincides with the present-day Urals, extending northwards to include Novaya Zemlaya, from all of which extensive Silurian deposits are known (Nikiforova & Obut 1965).

Siberia

An enormous amount of data has been published on the Silurian rocks and faunas of this very large area, most of which falls within the USSR, but which also includes Mongolia and parts of northern China (Rong & Zhang 1982). However, although the Soviet literature was impressively summarized by Nikiforova & Obut (1965), for more than 20 years there has not been a succint summary of the area since its plate margins were recognised or any new review of its faunas during the Lower Palaeozoic.

The continent is bounded to the west by the Urals, stretching northward to the Arctic Ocean, but Novaya Zemlaya is attributed entirely to Baltica (Fig. 1). The most substantial review of the Siberian brachiopods is still that by Nikiforova and Andreeva (1961) who described the Ordovician and Silurian faunas of the Siberian platform. The eastern slopes of the Urals also include widespread Silurian faunas, include some striking and dominant endemic pentamerid brachiopods (e.g. Sapelnikov 1972), however, most of the faunas of the palaeocontinent are essentially cosmopolitan in nature, for example, the brachiopods described by Lopushinskaya (1976), which consist of ten consecutive faunules of Llandovery to Ludlow age from the north of the Siberian Platform, and contain genera and even species also well-known from Baltica, Avalonia and Laurentia.

Kazakhstania

This palaeocontinent includes areas of the USSR and China east of the Urals, south-west of the Altai and north of the Pamirs and was separate since Precambrian times. The Silurian of the area has been the subject of numerous recent publications on specific aspects, e.g. the Ordovician-Silurian boundary (Apollonov *et al.* 1980, 1988), but the most comprehensive summary of the stratigraphy is still that by Bandaletov (1967). Extensive Silurian outcrops occur, ranging in age from Llandovery to Přídolí, and the dominance of tropical limestones and numerous corals at many horizons and localities testify that the continent must have lain not far from the Silurian palaeoequator.

Other palaeocontinents

This review has not included North China, from which no important Silurian faunas are known (Wang *et al.* 1984, 1987, Mu *et al.* 1986), although it is clear from the Ordovician facies and faunas that the area was subtropical, and Iran, from which sporadic Silurian faunas are known (e.g. Cocks 1979) and which also was unlikely to have been at a high palaeolatitude: both are shown here near Gondwana (Figs 1-3). In addition there were almost certainly some substantial areas now represented only as fragments in the Himalayas in which some Silurian rocks occur (Berry & Boucot 1972b); these are also shown here near Gondwana.

Palaeobiogeography

Changing developments in faunas through Silurian time will now be reviewed.

The Ordovician-Silurian boundary has been extensively described and discussed reviewed in recent papers (e.g. in Cocks & Rickards 1988). The melting of the late Ordovician ice-caps (Fig. 4) triggered eustatic sea level rises which were probably augmented by contemporary plate tectonic activity affecting the geometry of the ocean trenches. Thus the predominent expression is of Ordovician-Silurian unconformities in most places, overlain by transgressive rocks of Llandovery age. From studies in many places, for example the Welsh Borderland (Ziegler *et al.* 1968b), it can be seen that this transgression was not rapid, but progressed either steadily or in pulses through the whole spread of Llandovery time, perhaps 10 million years (McKerrow *et al.* 1985). There was a substantial faunal turnover near the Ordovician-Silurian in most groups of organisms but detailed analysis, e.g. Cocks (1988) for the brachiopods, demonstrates that the extinctions and new evolutionary groups by no means occurred simultaneously or at the boundary itself, but that the turnover progressed from Middle Ashgill to Early Llandovery times. Because of the better faunal communications, and therefore more cosmopolitanism in early Silurian times when compared with the Ordovician, there were fewer ecological niches available in the various areas and this alone would account for the smaller total diversity.

However, the most important questions to be posed for each slice of Silurian time are the possible existence and identification of faunal provinces, and the extent to which those provinces can exist in the determination and the verification of the palaeogeography.

Since first identified in the last century, a distinctive fauna dominated in many places by the rhynchonellide *Clarkeia* has been found (Fig. 5) in various parts of South America (Berry & Boucot 1972a), and elsewhere in Gondwana (Cocks 1972, Melou & Racheboeuf 1977). It is of low diversity, consisting of communities dominated by one or two species only of such genera as *Clarkeia*, *Australina* and *Harringtonina* and by the complete lack of corals, bryozoans and many other groups. Its dating is difficult, some of its earliest occurrences may be of Llandovery age, but there is no firm proof of that; some associated graptolites in Argentina are of lower Wenlock and early Ludlow age, and Copper et al. (1988) have suggested by interpolation that abundant Clarkeia-bearing beds in San José de Jachal in Argentina may be as young as Přidolí. Boucot (e.g. in Berry & Boucot 1972a) has termed these faunas as forming the Malvinokaffric Realm, and although this term is not truly appropriate until Devonian times (Cocks & Fortey 1988) it is used here.

However, apart from the Malvinokaffric Realm, most of the benthic faunas of late Llandovery to Wenlock age are in fact cosmopolitan. For instance, the five depth related benthic communities of Ziegler et al. 1968a, originally recognised from clastic rocks, viz the Lingula, Eocoelia, Pentamerus, Stricklandia, and Clorinda communities, are now known far from their original localities in the Welsh Borderland, for example in Scotland, the United States, Canada, Norway, Sweden, Estonia, Siberia, and China, which then spanned the palaeocontinents of Avalonia, Laurentia, Baltica, Siberia and Gondwana respectively. Indeed so impressive were the international communications that not just genera but also individual species, such as of the evolving lineages Stricklandia and Eocoelia, are identical and useful for dating round the globe at those and many other sites. In some areas, particularly those in the equatorial belts where bioherms and warm-water limestones were deposited, such as in Anticosti Island, Kazakhstan and the Urals, the diversity of shelly faunas was much increased, particularly amongst the spectacular and sometimes bizarre-looking pentamerides. This was confirmed by the report of several "Uralian" genera such as Virgianella and Pseudoconchidium from the Middle Llandovery of northern Greenland (Boucot & Hurst 1979). The molluscs parallel these distributions, for example the gastropods *Oriostoma*, and its close relative *Poleumita*, and *Euomphalopterus* have an extremely widespread distribution during the middle and late Silurian (Forney *et al.* 1981).

During the later half of the Silurian, from mid Wenlock times onwards into the Ludlow and Přidolí, whilst the Malvinokaffric Realm faunas still remained distinct, the remainder of these previously worldwide cosmopolitan faunas began to be progressively more compartmentalised, a process which commenced with species differences across some widening oceans, e.g. the contrast between *Protomegastrophia walmstedti*, *Eoplectodonta duvalii* and *Leangella segmentum* in the Wenlock of England (in Avalonia), on the one hand and *Protomegastrophia miranda*, *Eoplectodonta decorata* and *Leangella tufogena* in beds of the same age in Bohemia (NW Gondwana) on the other, both on opposite sides of the Rheic Ocean (Cocks & Fortey 1988). Boucot (1970) was the first to list the variety of shallow-water brachiopod dominated level-bottom communities in the middle Silurian niche equivalent to the *Eocoelia* community. These communities are the *Salopina* community of Europe, northern Siberia, the United States and southern parts of Canada, Venezuela, China and elsewhere, the *Nalivkinia* community of Kazakhstan, the *Tuvaella* fauna of southern Siberia, North China and Mongolia, and the *Atrypella* fauna of northern Europe, much of northern Canada including the Arctic Islands, Greenland and Novaya Zemlya and the northern Urals. Replotting of the distribution of the *Tuvaella* fauna given by Rong & Zhang (1982) on one of our new maps (Fig. 5) indicates that that fauna was at the northern edge of the Siberian palaeocontinent, and that this distinctive fauna which was dominated by the endemic genera *Tuvaella* and *Tannuspirifer* favoured a more temperate climate, although, unlike the contemporary *Clarkeia* fauna, it also had more cosmopolitan associates such as *Leptostrophia*, *Meristina*, *Leptaena*, *Strophonella* and *Isorthis* as quantitatively less significant parts of the fauna, indicating that faunal connections between the *Tuvaella* fauna and its warmer-water and more diverse southern neighbours had by no means been completely severed.

Most conodont faunas have been recovered from shallow-water carbonates, and although they also occur in deep-water carbonates and even dark shales, the difficulties of extraction make the latter poorly represented in the literature. A survey of Palaeozoic conodont provinciality by Bergström (1990) has demonstrated that in late Caradoc and early Ashgill times there were many provinces, viz the Red River and Ohio provinces in North America, the Baltic Province, the British Province, the Mediterranean Province and the Siberian Province. Particularly striking are the minimal faunal similarities between Laurentia and Siberia, both then on the palaeoequator. However, near the Ordovician-Silurian boundary a large faunal turnover occurred and these provinces had virtually disappeared by early Llandovery time, except perhaps from Australia (Bischoff 1986), and this cosmopolitan pattern continued through the Wenlock and Ludlow into the Přidoli. No conodont faunas have been reported and in fact may not have existed in the Malvinokaffric area - in fact the most southerly palaeolatitudes from which they have been described are from France in the Llandovery and Wenlock and from

Spain and Mauretania in the Přídolí, none of which sites would have been greater than 50°S on our new reconstructions in Figs 1-3 (although some of the late Ordovician sites in North Africa were perhaps at latitudes of over 60°S - Bergström 1990 Fig. 4). It is particularly striking that in Llandovery time virtually all of the conodonts known came from within the palaeolatitudes 40°S and 40°N (Sweet 1985) and this may perhaps be interpreted to indicate colder polar temperatures on average in the Silurian than in the Ordovician, an impression strengthened by the distribution and nature of the various sedimentary facies. It is also important to note that all conodont faunas of Přídolí age reported to date are of relatively low diversity - even the most varied include only 15 species of eight genera. There is also little conodont provincialism in the early Devonian, in contrast to the brachiopods and molluscs.

Silurian graptolites show very little endemism (Berry 1979) and this is also apparently true of the chitinizoa (Laufeld 1979). However, the acritarchs were obviously much affected by palaeolatitude; Cramer (1971) established this in pioneer work in the Atlantic area which was followed up by Richardson et al. (1981) who were able to chart global distributions in the Ludlow and Přídolí which ran subparallel with the palaeolatitudes suggested in the present paper.

Thus much is now known of Silurian times and agreement on faunas, palaeobiology and the position of continents is becoming closer over much of the world. However, the relative positions of North China, Kazakhstan and the various areas which today run between Turkey through the Himalayas to south-east Asia are all poorly known, and there appears to be much scope in the future for the finding and description of new faunas and revision of the palaeogeography.

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Figure Captions

Fig. 1. Early Silurian palaeogeography (Llandovery). Shallow seas (light stipple), land (medium stipple), and highlands (dark stipple). Bold lines with teeth indicate possible subduction zones. Direction of sea floor spreading is shown by medium lines and arrows.

Fig. 2. Middle Silurian palaeogeography (Wenlock). Same legend as Fig. 1.

Fig. 3. Earliest Devonian palaeogeography (Lochkovian). Same legend as Fig. 1.

Fig. 4. The latest Ordovician (Hirnantian) deposits. The arrows and shaded areas represent the known ice sheets, the stars other glacial deposits (e.g. dropstones). The black dots and open circles show the distribution of the Hirnantia fauna and the trilobite *Mucronaspis* respectively (data from Cocks & Fortey 1988 redrafted on new base map).

Fig. 5. Late Silurian faunal distributions. The open triangles are the Malvinokaffric *Clarkeia* fauna, the solid black triangles are clastic deposits with *Salopina*, the open squares are carbonate deposits with diverse *Salopina* communities and the solid black dots the *Tuvaella* fauna.

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L.R.M. Cocks,
Department of Palaeontology,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

C.R. Scotese
4425 Betty Street,
Bellaire,
Texas 77401,
USA

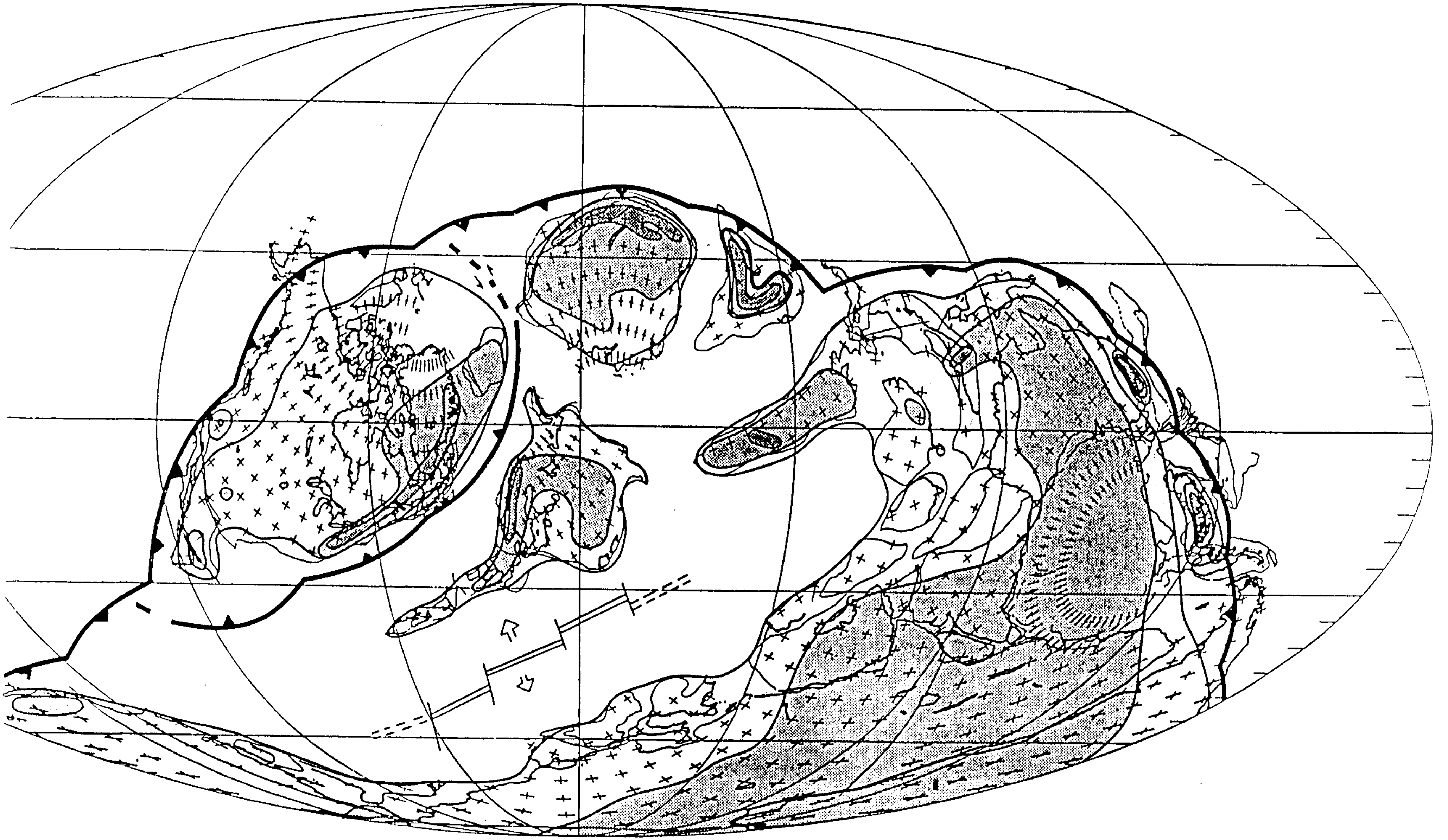

Figure 1

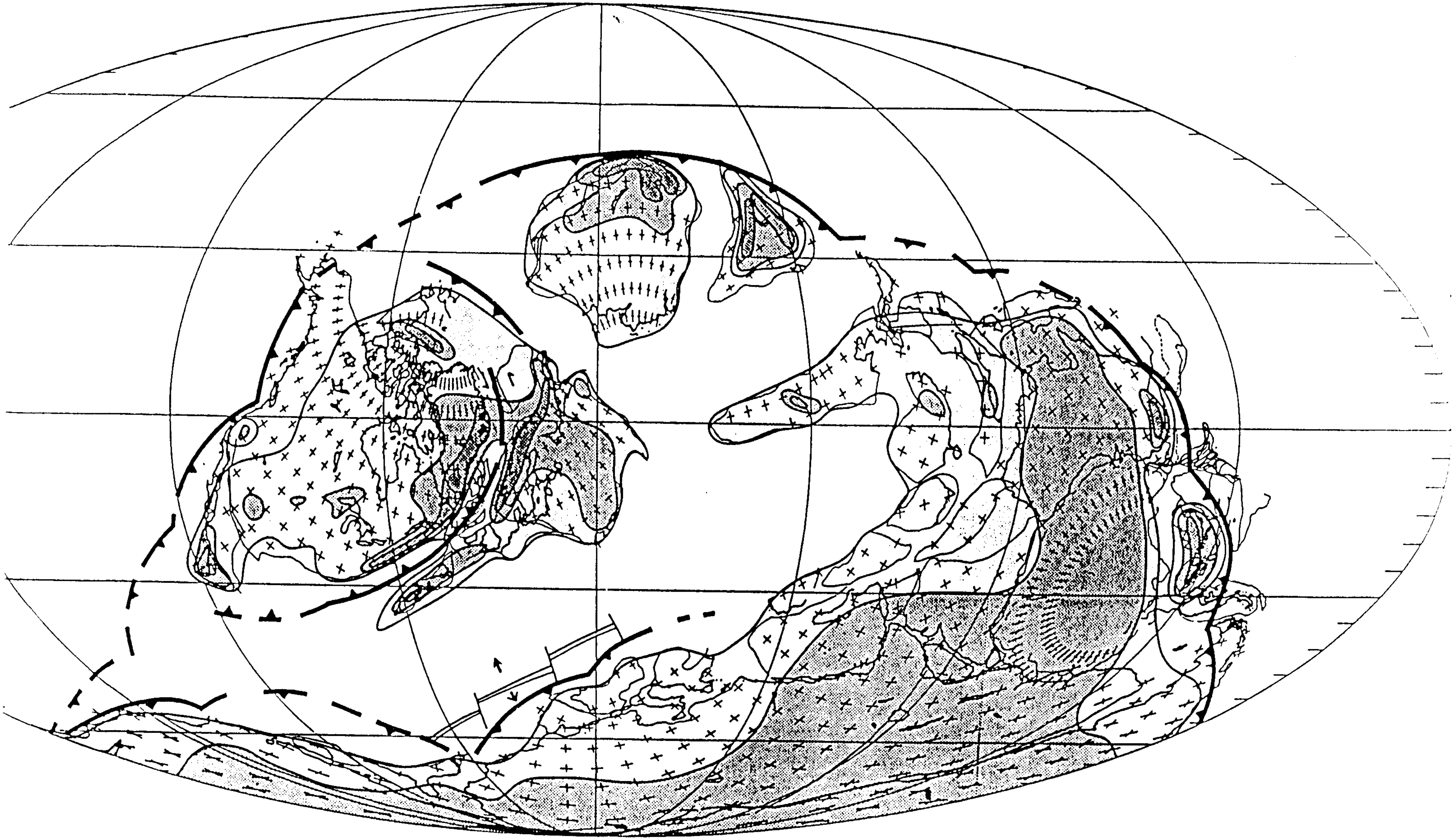

Figure 2

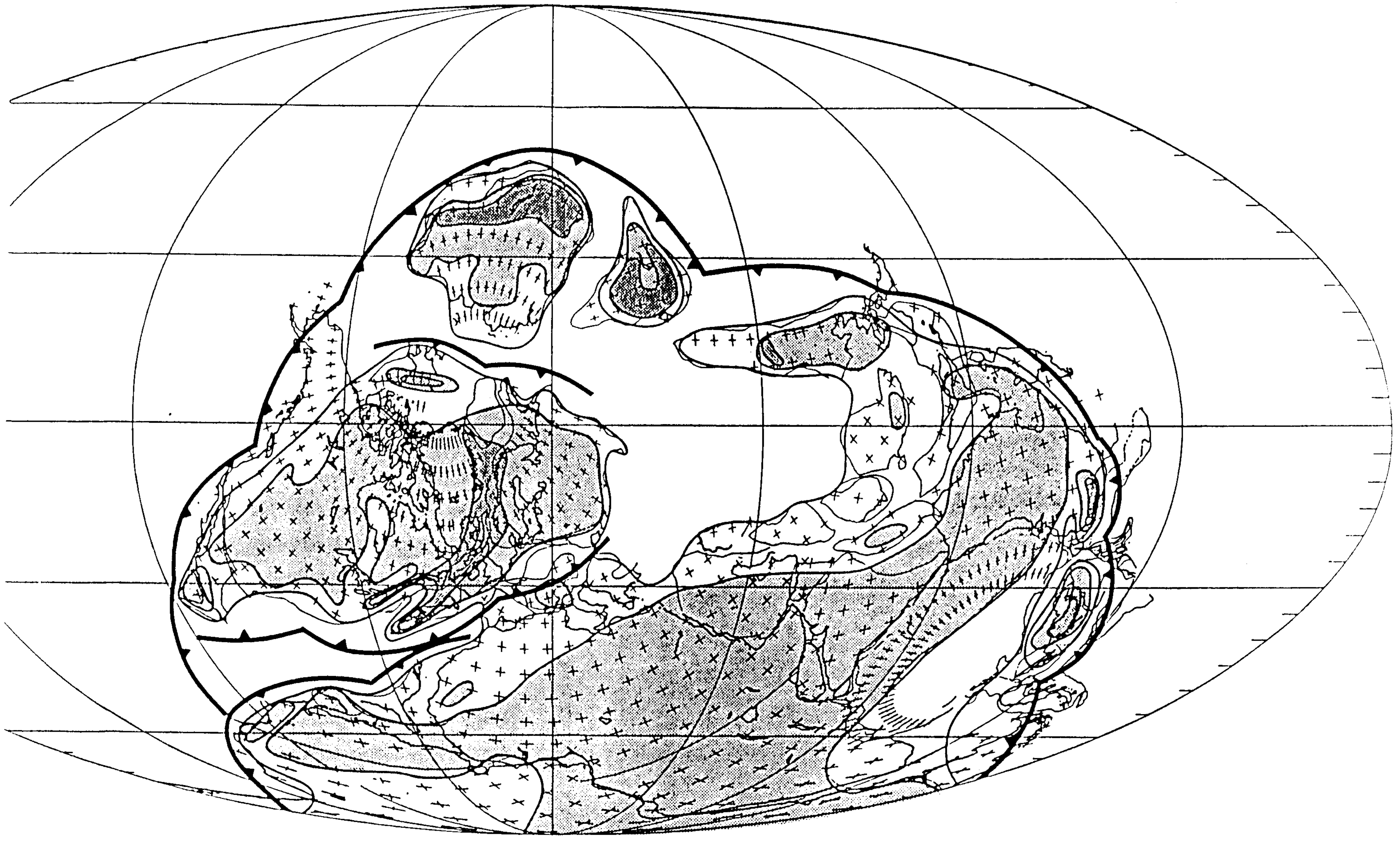

Figure 3

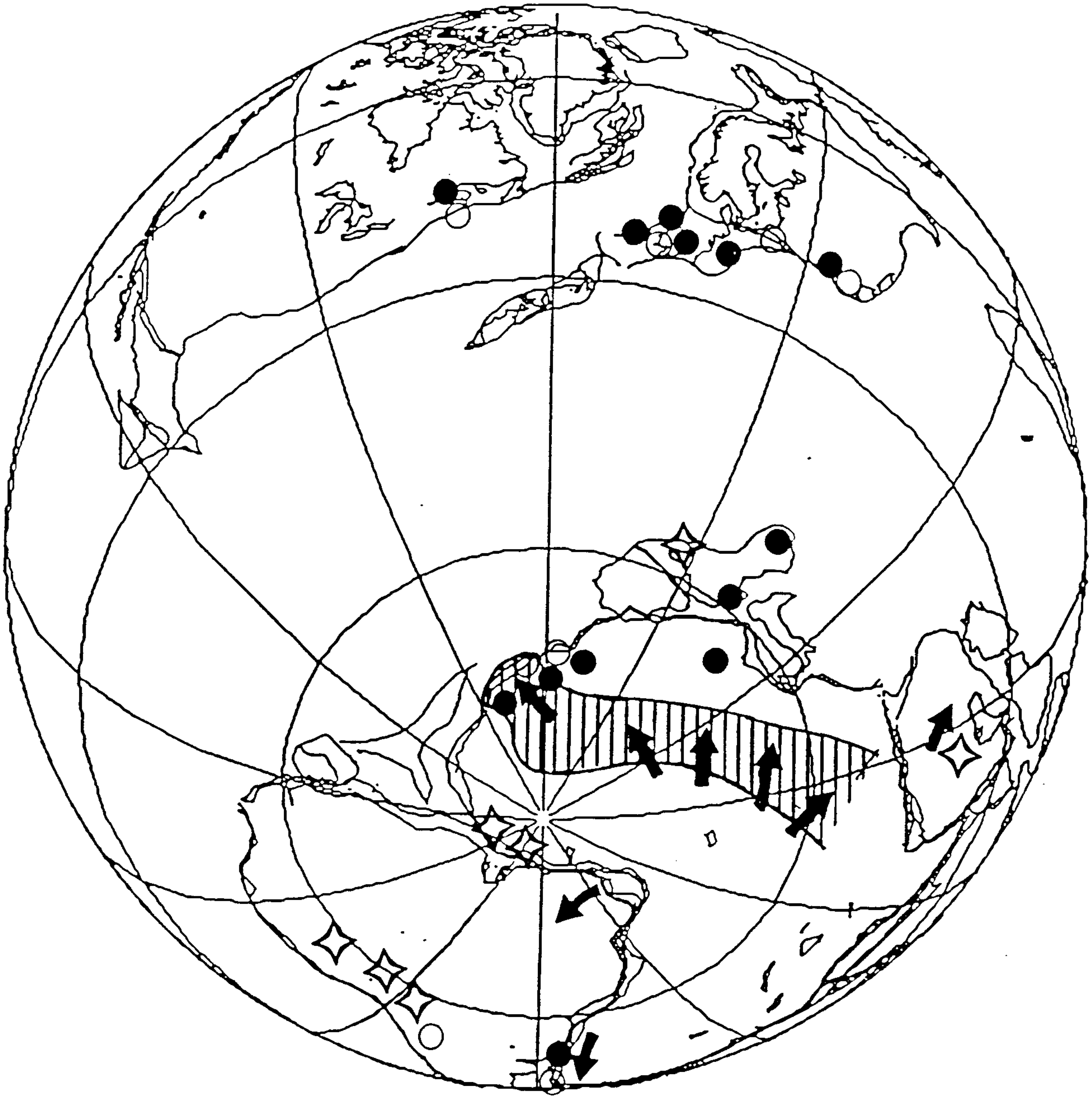

Figure 4

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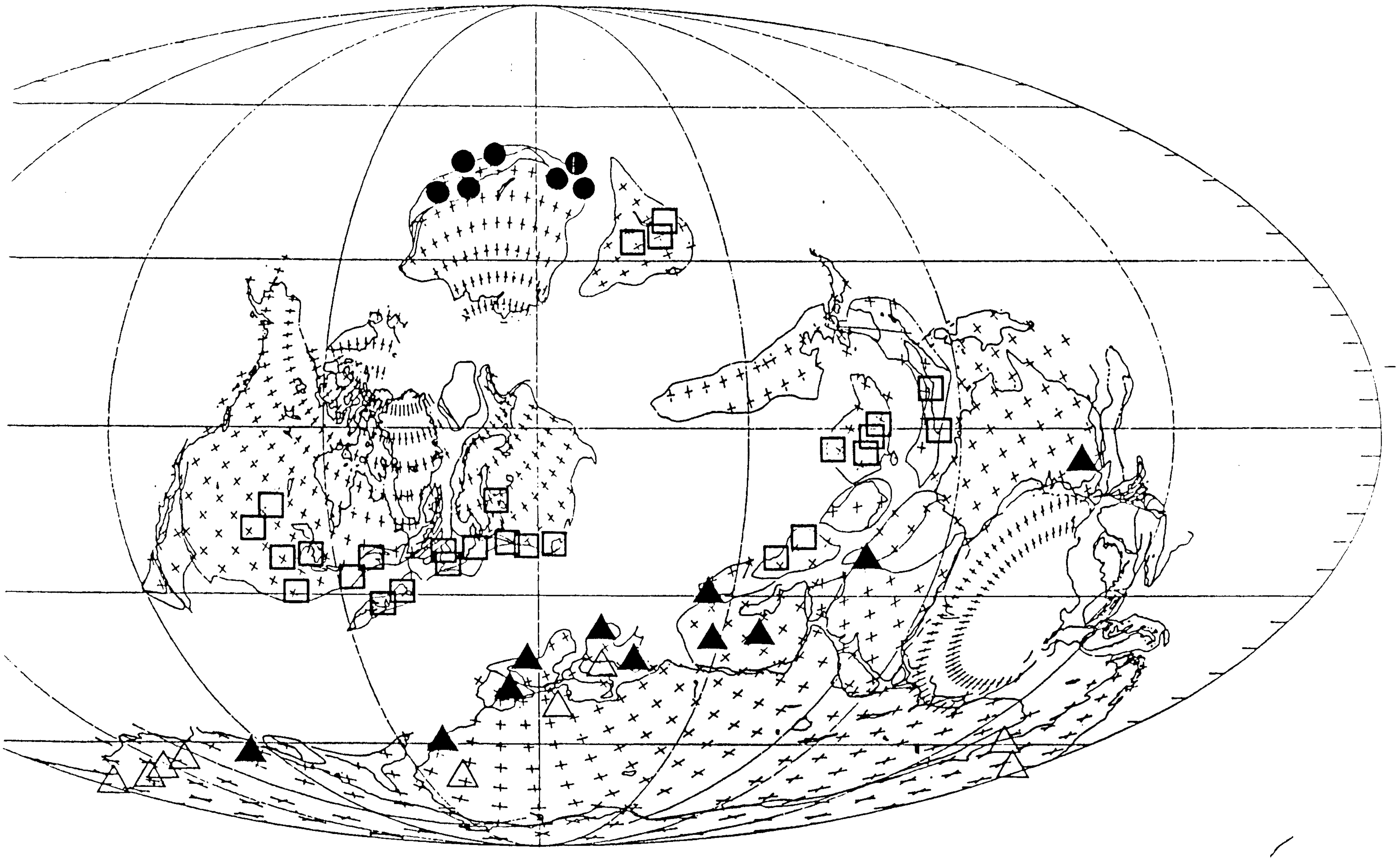

Figure 5