

Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review

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Abstract: Very different palaeogeographical reconstructions have been produced by a combination of palaeomagnetic and faunal data, which are re-evaluated on a global basis for the period from 500 to 400 Ma, and are presented with appropriate confidence (or lack of it) on six maps at 20 Ma intervals. The palaeomagnetic results are the most reliable for establishing the changing palaeolatitudes of Baltica, Laurentia and Siberia. However, global palaeomagnetic reliability dwindles over the 100 Ma, and more evidence for relative continental positioning can be gleaned from study of the distribution of the faunas in the later parts of the interval. The new maps were generated initially from palaeomagnetic data when available, but sometimes modified, and terranes were positioned in longitude to take account of key faunal data derived from the occurrences of selected trilobites, brachiopods and fish. Kinematic continuity over the long period is maintained. The many terranes without reliable palaeomagnetic data are placed according to the affinities of their contained fauna. The changing positions of the vast palaeocontinent of Gondwana (which has hitherto been poorly constrained) as it drifted over the South Pole during the interval have been revised and are now more confidently shown following analysis of both faunal and palaeomagnetic data in combination, as well as by the glacial and periglacial sediments in the latest Ordovician. In contrast, the peri-Gondwanan and other terranes of the Middle and Far East, Central Asia and Central America are poorly constrained.

Keywords: Lower Palaeozoic, palaeogeography, palaeomagnetism, trilobites, brachiopods, fish.

Ocean-floor magnetic anomalies and the effects of the movements of terranes over the relatively stationary mantle plumes are essential tools for deciphering the positions of continents and terranes in Mesozoic to Recent times. Unfortunately, both these key methods are not available for understanding Palaeozoic and earlier times because of the continuing processes of subduction and obduction at oceanic, terrane and continental margins. Thus we are left with the inputs of palaeontological and palaeomagnetic studies, with supporting evidence from sedimentology, to determine where the continents (Fig. 1) and oceans were in more ancient times. Many such faunal (e.g. Cocks 2001) and palaeomagnetic (e.g. Torsvik 1998) studies have been published over the past 30 years, but very often without appropriate consideration for the results generated by those with specialities other than the authors of those studies, and often over restricted time intervals. In this paper we combine our expertise and experience in both faunas and palaeomagnetism to make a critical review of the period from 500 Ma, the late Cambrian, to 400 Ma, the early Devonian. We have indicated the current variability in our knowledge of palaeomagnetism by differential shading (Fig. 2) to indicate where our data are strong, weak or entirely lacking, and have only been able to include a few faunal data (Figs. 3–9) from the great quantity available, but we hope this review will indicate both significant progress and also challenging programmes for future research.

Principles

In this paper we combine faunal, palaeomagnetic and, to a lesser extent, sedimentological data. But the principles underlying these

approaches to palaeogeographical reconstruction are very different and worth reiterating here. The faunal principles have not changed since they were first set out by Cocks & Fortey (1982, fig. 1). Before any animal can be used, both its age and its individual ecology must be assessed correctly.

The distribution of those animals with a planktonic, pelagic or nektonic (swimming) lifestyle is controlled by oceanic currents and temperature and thus, although the deposits in which their fossils are found usually form part of one or more of the terranes that we recognize as separate, these occurrences are of no significance when assessing the closeness or individuality of such terranes. Because the great majority of such animals are dependent on temperature, their occurrence may only be generally correlated with the latitude in which the animals lived (Cocks & Verniers 2000). In the Lower Palaeozoic, these planktonic groups are best represented by graptolites, a minority of the trilobites such as the pelagic *Carolinites*, cephalopods, chitinozoa, acritarchs and apparently conodonts (the detailed ecology of which is still poorly understood). As the dispersal of these animals was very often rapid, the quickly evolving members of these groups include most of the best fossils for international correlation.

In contrast, there are those animals with a benthic lifestyle, which were and are confined to the sea floor for their adult life, such as brachiopods, most trilobites, bivalves, gastropods and most ostracodes, and which were also temperature dependent. These may be divided into two groups: the majority, which lived in shallower-water seas on the continental margins, and which were therefore both latitudinally related and also confined to

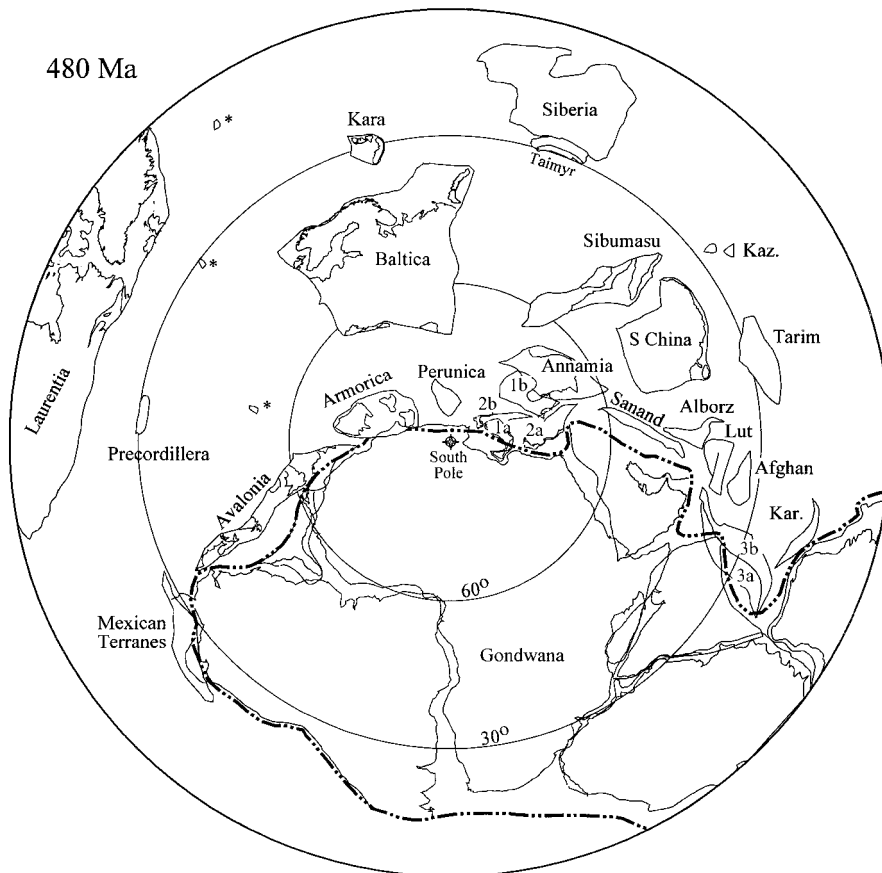


Fig. 1. The southern hemisphere at 480 Ma, showing the names of the major terranes. 1a, Apulia; 1b, Hellenic; 2a, Taurides; 2b, Pontides; 3a, south Tibet; 3b, Qiangtang; Kaz., Chu-Ili and North Tien-Shan; Kar., Karaku. Asterisks indicate islands within the Iapetus Ocean for which there are palaeomagnetic data (Table 1). The North China Terrane was entirely within the northern hemisphere at that time and is thus not shown. Figures 1 and 3–6 are Schmidt's Equal Area projection, with projection centre at the South Pole.

particular terranes; and a smaller number that lived below the thermocline and were thus independent of palaeolatitude, and were distributed on the deeper parts of continental shelves and on the ocean floors. It is the former, larger, group of benthic animals upon which we rely most strongly to provide the faunal support for the terrane reconstructions presented here. Cladistic analysis has been used to support some of the faunal distributions (e.g. Young 1990a, for early Devonian fish), but the development of robust enough trees for palaeobiogeographical use are as yet developed for only a very small number of fossil groups, and there are few such data from the Lower Palaeozoic.

Despite the fact that the adult brachiopods and most trilobites were confined to relatively small sites, their larval stage was planktonic for shorter or longer periods and thus the genera dispersed as time progressed. As a working rule of thumb, although different animals have and had very different dispersal rates (McKerrow & Cocks 1986), many faunas appear to be separable if the oceanic width is above 1000 km. If two terranes are at the same latitude, then the composition of the benthos will be largely the same if the terranes are close to one another. However, if the terranes drift apart, then the larvae of the descendant species of the original benthos will not cross the intervening deeper ocean after a certain period of time; the discriminating palaeontologist will thus be able to identify the two terranes as different and separate. Comparably, if two terranes at the same latitude but with different benthos drift towards each other, then the two terranes recognized by the palaeontologist in the earlier period will merge into a single faunal province in the later period, but without providing any certain evidence that the two terranes actually collided. In

addition, the largest palaeocontinents, such as Gondwana in our time period, are so substantial that they covered many degrees of latitude, and thus the benthos at the northern and southern extremes of the continent can be very different. However, between these two palaeolatitudinal extremes the faunas at intermediate latitude should show a gradation or cline, comparable with the cline seen today in the benthic molluscan faunas along the western seaboard of North America, which stretches from the tropics of Panama to the high latitudes of Alaska. This is allied to another principle: that the lower the latitude, the larger the number of different species and genera that will be found; that is, the biodiversity is generally greater (in equivalent ecological situations) the closer one approaches the Equator.

From palaeomagnetism we can determine palaeolatitude and the rotation of a terrane through time, but the palaeomagnetic data give no insight into palaeolongitude. Palaeomagnetic poles do not distinguish between the North and the South Pole, and thus there is no initial constraint on which hemisphere the terrane should be placed in unless a well-defined apparent polar wander path (APW) exists from that time until the present day. Thus for our time interval only the major terranes (such as Baltica and Laurentia) can be unambiguously defined in this way, and other terranes (such as North China, South China and Sibumasu) could be shown as facing either north or south. The error in palaeolatitudinal estimates is of the order of 3–5° (300–500 km) at the best and at worst there are no constraints at all! In all our reconstruction poles (Table 1), we assume that the Earth's magnetic field is a dipole, but this basic premise has been questioned and incorporation of non-dipole fields, as recently argued by Van der Voo & Torsvik (2001), would add further

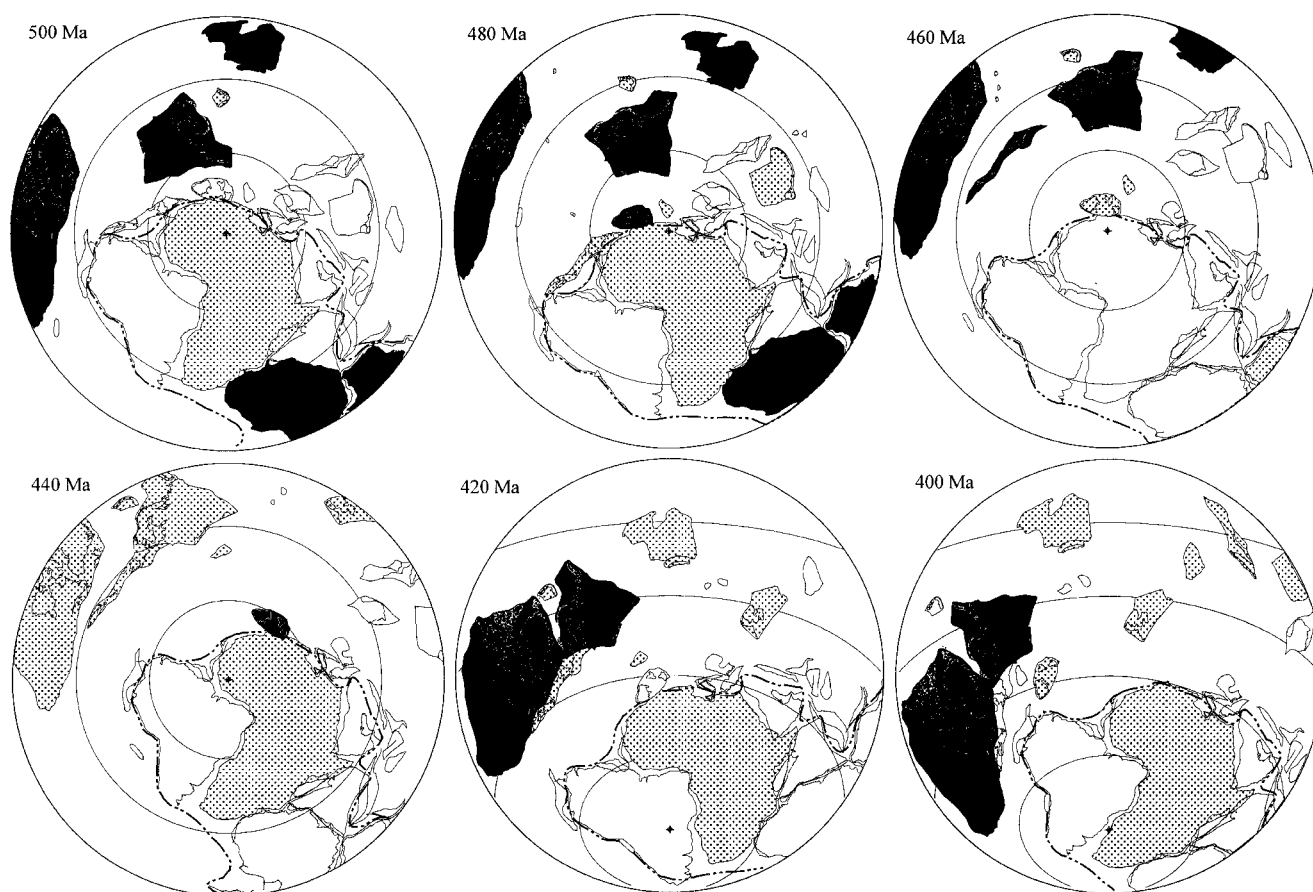


Fig. 2. Six successive time slices from 500 to 400 Ma showing our confidence in the palaeomagnetic data (Table 1) from the various terranes. Black is high confidence (well-defined APW or two or more consistent poles); stipple is some confidence; unshaded is little or no confidence.

errors of several hundred kilometres. Unfortunately, in the early years of palaeomagnetic investigations, workers had limited instrumentation and analytical insight, and therefore many data and APW paths published before 1980 should be considered with care and often rejected (unlike faunal studies, in which fossils described over 200 years ago can be incorporated appropriately).

The sedimentological criteria have been less important in determining our reconstructions; however, it is instructive to remember that, as a generality, carbonates, particularly in massive builds, are more common in lower latitudes, and that reefs today are also confined to lower latitudes, although there has not been space to include carbonate deposits on our maps. Evaporites too were always located in the desert belts, which were usually situated within 30° north and south of the Equator. In contrast, glacial features were formed at high latitudes, although some glaciogenic deposits, such as dropstones, can occur at the much lower latitudes to which larger icebergs have carried them, and these features are used in our latest Ordovician (440 Ma) map. However, clastic sediments, both on the continental shelves and in deeper waters, do not vary substantially with palaeolatitude, and comparable belts of sediments, in particular thick turbidites and olistostromes, occur around most of our terranes. We have not taken sedimentary provenance studies into account in the following reconstructions, as comparable signatures seem to occur on widely separated terranes.

Classic tectonic studies, particularly those on plate margins

and on the unravelling of fold belts, can indicate the timing and nature of terrane collisions and rifting; these fields of research are largely outside the scope of this paper.

Terrane margins

For this paper we have reviewed and partly revised the outline and margins of most of the major terranes as follows (their names and positions at 480 Ma are shown in Fig. 1). Of course, nearly all the continental margins shown are entirely the result of post-Palaeozoic tectonics and are thus very different from those actually present during our time periods. We omit the post-Devonian orogenic belts that today surround many of the terranes we show.

Baltica

This follows the traditional outline as used by many workers (e.g. Ziegler *et al.* 1977; Torsvik *et al.* 1990a), but is newly modified (1) to include both terranes, the southerly Malopolska and northerly Lysogory terranes, of the Holy Cross Mountains, Poland (Cocks & Fortey 1982, 1998); (2) to accept the southern extension of the area to the west of the Urals as far south as the northern part of the Caspian Sea (Cocks 2000, fig. 6); (3) with the exclusion of the highest nappes of the Trondheim area, Norway (Cocks & Fortey 1982); (4) with the exclusion of the

Table 1. Palaeomagnetic reconstruction poles used (south poles given as latitude/longitude), based on APW paths or individual poles with Q= 3 (Van der Voo 1993)

Continent	500 Ma	480 Ma	460 Ma	440 Ma	420 Ma	400 Ma
Baltica ¹	52/111	24/053	7/039	-5/007	-15/343	-2/325
Laurentia ¹	-4/345	-14/336	-13/329	-14/315	-14/305	-1/287
Siberia ²	40/300	43/302	27/312	9/288	0/280	3/279
Gondwana ³	25/005	32/007	29/357	12/351	-19/003	-22/013
Kara ⁴	26/079	20/059	12/040	3/023	-9/004	No data
Avalonia ⁵	PG	PG	5/016	As Baltica	As Baltica	As Baltica
Armorica ⁶	PG	PG	PG	19/001	-7/331	-13/331
Perunica ⁷	PG	PG	68/44	80/180	55/145	No data
North China ⁸	32/330	33/320	32/328	26/228	26/228	30/228
South China ⁹	No data	39/056	33/035	13/015	-26/023	-13/019
Tarim ¹⁰	No data	No data	No data	No data	No data	17/165
Sibumasu ¹¹	No data	No data	No data	No data	No data	67/134
Iapetus fragments ¹²						
Lawrence Head		-25/049				
Moreton's Harbour		-29/315				
Robert's Arm		-8/317				
Tetagouche		52/352				
Winterville			-26/328			
Bluffer Pond			-26/314			
Stacyville			14/008			

¹Upgraded from Torsvik *et al.* (1996) and Torsvik & Rehnström (2001a, b). Note that 420 and 400 Ma mean poles are based on a combination of Laurentia-Baltica poles in a Bullard *et al.* (1995) fit of the North Atlantic (closure of Iapetus Ocean – Scandian Orogeny).

²Upgraded from Smethurst *et al.* (1998).

³This study and Torsvik & Van der Voo (2002).

⁴APW path based on Metoelkin *et al.* (2000).

⁵Torsvik *et al.* (1993). Avalonia is sutured to Baltica from 440 Ma (closure of Tornquist Sea).

⁶APW path based on Torsvik *et al.* (1990b), Tait (1999) and Schatz *et al.* (2002).

⁷Tait *et al.* (1994, 1995, 1996) and Nysæther, *et al.* (2002).

⁸APW path based on data by Zhao *et al.* (1992, 1993) and Huang *et al.* (1999).

⁹APW path based on data by Opdyke *et al.* (1987), Fang *et al.* (1989), Fang & Van der Voo (1990), Chen *et al.* (1996) and Huang *et al.* (2000).

¹⁰Li *et al.* (1990).

¹¹Fang *et al.* (1989).

¹²Poles listed in MacNiocaill *et al.* (1997).

PG, Peri-Gondwana; all palaeomagnetic data for Avalonia, Armorica and Perunica show high latitudes in the early Ordovician and we have positioned these elements as part of NW Gondwana. Avalonia rifted off first.

Taimyr Peninsula (see under 460 Ma below). We have restored Novaya Zemlya to its pre-Triassic position as a direct extension of the Urals (Torsvik & Andersen 2002).

Avalonia

The faunal integrity of what are today the North American and European parts of Avalonia precludes the possibility that they represented more than one terrane in Lower Palaeozoic times, particularly when the terrane's rapid movements over the latitudes during the Ordovician is considered. Thus 'West' and 'East' Avalonia for the two parts are not recognized as separate here and we do not recommend further use of these terms. The North American part of Avalonia (including Eastern Newfoundland, most of the Maritime Provinces of Canada and the eastern US seaboard as far south as Cape Cod, Massachusetts; Cocks *et al.* 1997) has been reconstructed to the European part using the fit originally proposed by Bullard *et al.* (1965) (see Van der Voo 1993).

Perunica

Often termed Bohemia. We have arbitrarily included the area today north of the Barrandian basin of Bohemia within this terrane, so that it has a northern boundary in post-Hercynian times to coincide with the southeastern boundary of Avalonia.

Armorica

This includes the Armorican Massif of Normandy and Brittany, the Massif Central and the Montagne Noire areas of France, together with the Iberian Peninsula (apart from the westernmost South Portuguese Zone; Cocks 2000) corrected for the Cretaceous Bay of Biscay opening, and Sardinia. Although some workers have shown differential movements within this terrane, we have no evidence to disperse its regions during our time slice and therefore show them together. In particular, the sedimentological and palaeontological analysis of Young (e.g. Young 1990b) has demonstrated that Brittany and western Iberia formed one unit. The oldest rocks from the South Portuguese Zone are of mid-Devonian age and the area is thus excluded from our maps: in any case its terrane affinities are uncertain; Cocks *et al.* (1997) showed it as part of Avalonia.

Laurentia

The margins of Laurentia have been modified: (1) to include Spitsbergen in a position near NE Greenland; although this archipelago represented two or even three separate terranes, the easternmost area of Spitsbergen can only be considered as having formed part of the margin of the Laurentian craton during early Ordovician times (Fortey 1975); (2) to show the margin near NE Greenland as based on the assumption of 50% stretching of the crust in post-Devonian times; (3) to accept the Ouachita Front as

the southern margin, following the line shown by Keppie & Dostal (1999); (4) to include the Arctic islands of Canada as shown by Natalin *et al.* (1999) but excluding the proposed Bennett–Barrovia Terrane; (5) with the British Isles north of the Iapetus Suture fitted to North America using the Bullard *et al.* (1965) fit. Laurentia, Avalonia and Baltica combined to form Laurussia in the late Silurian, as shown in our 420 and 400 Ma maps (Figs. 8 and 9).

Siberia

We follow the outline of Rundqvist & Mitrofanov (1993), which includes most of the Baikeralides, which accreted onto the main craton in late Precambrian times. Our reconstructions include south and central Taimyr as part of Siberia, although this has been controversial (see below under 460 Ma). Siberia collided with Baltica and the Kazakh terranes in Permo-Carboniferous times.

Kara

This terrane consists of northern Taimyr and Severnaya Zemlya (Metoelkin *et al.* 2000). Kara collided with central Taimyr (today part of the Siberian Plate) in late Carboniferous–Permian times (Vernikovskiy 1996).

North China

In general we follow the outline of Rong *et al.* (1995) and various other workers in the Palaeozoic divisions of China, with North China's southern boundary at the Qinling Line. The terrane includes the Palaeozoic of the Korean peninsula, but the northern margin is somewhat arbitrary because of the absence of known Palaeozoic rocks from much of Manchuria. Again arbitrarily, we take North China's modern western margin at the western boundary of the Huanghe Region.

South China

This outline also follows Rong *et al.* (1995) and previous workers and we include the modern southeastern coastline and the island of Hainan (which has only Mesozoic to Recent rocks) to aid recognition of the terrane in our reconstructions. The terrane collided with North China in the Permo-Triassic.

Tarim

We follow the boundaries shown by Zhou & Chen (1992), with the northern boundary delimited by the Tien-Shan fold belt. The neighbouring Qaidam Terrane to the south is entirely post-Lower Palaeozoic and is therefore omitted from our diagrams.

Sibumasu and Annamia

These terranes, sometimes termed the Shan–Thai and Indo-China terranes, respectively, largely follow the margins shown by Scotese & McKerrow (1990) and Fortey & Cocks (1998). Minor amendments, particularly at the northern boundary of Annamia, have been made so that that boundary is congruent with the southern boundary of South China, with which the terrane amalgamated in the late Jurassic. Unlike many other reconstructions (e.g. Scotese & McKerrow 1990; Van der Voo 1993), we do not place Sibumasu (for which the palaeomagnetic data are scanty) adjacent to Gondwana throughout our time period, but

prefer to link it to South China (which has better palaeomagnetic data) and with which it has strong faunal affinity at various times (Fortey & Cocks 1998).

Gondwana

The Gondwanan core (the bold dashed line in Figs 1–9) consists of Africa, Arabia, Madagascar, Greater India, most of Antarctica, most of Australia, New Guinea and most of South America. New Zealand is shown divided into North and South, following Lottes & Rowley (1990). Southernmost South America and much of western Antarctica are not shown, as they were post-Devonian accretions. Florida was also an integral part of Gondwana and is included using the fit of Lawver & Scotese (1987). Gondwana formed at around 550 Ma (Meert & Van der Voo 1997) and its early dispersal history commenced with the rifting off of Avalonia in Arenig–Llanvirn times (465 Ma).

Apulia and the Hellenic Terrane

We follow Stampfli *et al.* (1998) in the identification of Apulia (southern Italy: 1a in Fig. 1) and the Hellenic Terrane (largely Greece: 1b in Fig. 1) as separate terranes, but there is little evidence for their separate movements within peri-Gondwana during our time period and no terrane-diagnostic fossils.

Middle Eastern peri-Gondwanan terranes

The Taurides Terrane comprises most of central and southern Turkey (2a in Fig. 1). Although tectonically recognized as separate, the terrane was apparently situated in a position relative to Arabia comparable with that seen today. We take its boundaries from many workers. The Pontides of northern Turkey (2b in Fig. 1) are shown as a separate terrane to the west of the Taurides, following Dean *et al.* (2000). The Lut, Alborz and Sanand terranes (mostly today in Iran), which are separated by various workers (e.g. von Raumer *et al.* 2002), are grouped as one for this paper (Millson *et al.* 1996), as there are no good faunal or palaeomagnetic data for our time period that warrant their distinction or identify contemporary movement between them. The Afghanistan and Karaku terranes can also be treated in a similar way and are also shown as part of Greater Gondwana in our diagrams.

Himalayan terranes

A number of terranes within today's Himalayas were discrete elements in Palaeozoic times and include the Lhasa Terrane (south Tibet: 3a in Fig. 1) and the Qiangtang Terrane (north Tibet: 3b in Fig. 1). However, in the absence of independent palaeomagnetic or faunal criteria, these are tied to Gondwana in our reconstructions. Their outlines follow Watson *et al.* (1987) but the modern sutures and other evidence indicate that they did not accrete to Greater India until the early Tertiary.

Precordillera

This small terrane, which is today in western South America (northwestern Argentina), is shown here with an arbitrary outline.

Mexican terranes

At least three, and probably more, terranes today occupy the area between the Ouachita Front of the USA and northwestern South America; the most important is the Oaxaquia Terrane. We show

these terranes together and linked to Gondwana in our reconstructions, in a similar way to Florida: they did not accrete to Laurentia until Permo-Carboniferous and later times (Keppie & Dostal 1999).

Minor terranes

There are a number of areas with Lower Palaeozoic rocks and fossils apart from those listed above, notably in Kazakhstan and adjacent areas, Tuva, Mongolia, the margins of the North Atlantic area and the Arctic. These were caught up in and often formed part of the island arcs that lay between many of the major terranes. Kazakhstan is represented diagrammatically on our maps by two small terranes; a recent analysis of Cambrian and early Ordovician brachiopods by Holmer *et al.* (2001) has demonstrated at least four separate terranes, but there are no palaeomagnetic constraints from the region.

Methods

We have assembled our maps with both palaeomagnetic and faunal data in mind, and to a lesser extent sedimentary evidence, and the final results conflate those originally independent data sources. However, so that both we and our readers can understand in every case whether both, one or none of our inputs were used for any one terrane in any one time slice, we present each of these sources separately here. We have tried to include on our maps all the terranes of any magnitude (when projected on a global scale) that we think existed within our time interval. The palaeomagnetic data are shown in Fig. 2 with one of three types of shading: black for those terranes where the data are good; grey stipple where there are some data; unshaded in those terranes from which there are few or no data that we accept as valid. Each terrane is treated as a single entity, apart from Gondwana and Laurussia, in which each modern major sector is shown with the appropriate shading. The faunal data are presented in Figs 3–9 as individual symbols on the site from which they have been recorded. As there are often many fossil localities too close together to be shown separately on global maps of this scale, a single faunal symbol may represent any number from one to many localities. We show only those fossils that have given a terrane-linked faunal signal that we can interpret, but we could have presented many more faunal distribution diagrams than those included here. When a particular terrane has no faunal or palaeomagnetic data to aid our positioning of it in any particular time slice, then we have interpolated its position from older or younger data gleaned from that same terrane; in a comparable way we have made sure that the six time-slice maps present a kinematic continuity through time, each one taking into account those maps that both precede and follow it. The radiometric dates for the various geological periods follow McKerrow & van Staal (2000).

We have omitted the various island arcs, because their individual constituents are too small to evaluate properly; however, three island arc segments in the present-day North Atlantic area, from which good palaeomagnetic data are known, have been indicated by asterisks in Fig. 1 and listed under Iapetus Fragments in Table 1.

Earth geography from 500 to 400 Ma

In the following sections we trace the developing situation by presenting maps (Figs 3–9) and commentary at 20 Ma intervals over a 100 Ma time period. The palaeomagnetic data are often

merged to within ± 10 Ma within our various maps, but, during each 10–20 Ma interval, animal evolution proceeded apace and we have been careful not to misleadingly compare particular fossils with others of substantially different ages from within such large time slices, and thus the faunas shown are restricted to intervals of about 2 Ma in each case.

Geography at 500 Ma (latest Cambrian)

The Cambro-Ordovician boundary is now radiometrically dated at 490 Ma and so only rocks and fossils of late Cambrian age are included in this part of our survey. Gondwana stretched from the South Pole (in northern Africa) to the Equator (Australia) and included the high-latitude Avalonia, Armorica, Perunica and Florida terranes as well as many fringing middle- to lower-latitude terranes now forming much of the Middle East, SE Asia and Central and South America. We show Laurentia in low latitudes and separated from Gondwana (South America) and the present SE margin of Baltica by the Iapetus Ocean. The opening of the Iapetus Ocean in this sector took place in Vendian–early Cambrian times when Laurentia rifted off South America (Torsvik *et al.* 1996; Carwood *et al.* 2001). Laurentia moved from high southerly latitudes to the equator, where it essentially remained from late Cambrian to early Silurian times (compare our 500 Ma and 440 Ma reconstructions). Siberia also stayed in low to equatorial latitudes during the first half of our study interval and was separated from both Laurentia and Baltica. Kara was probably positioned between Baltica and Siberia in the late Cambrian.

Baltica was 180° geographically inverted and the present NE margin faced NW Gondwana. The Iapetus-facing part of Baltica was a passive margin: dextral strike-slip probably took place along the Gondwana-facing margin whilst subduction occurred in the Ægir Sea (Torsvik & Rehnström 2001). Eclogites dated to about 505 Ma indicate deep subduction (50–70 km) along the Caledonide margin of Baltica in the late Cambrian. This subduction must have taken place beneath an arc or a microcontinent, as the Siberia-facing margin was a passive margin until late Carboniferous times. The Kara Terrane might be this previously unidentified micro-continent (or part of it); the Cambrian–Ordovician unconformity within Kara on October Revolution Island (Severnaya Zemlya) attests to tectonic disturbance at this time, although late Cambrian faunas underlying the unconformity indicate isolation from Baltica before then (Rushton *et al.* 2002). Collision between Baltica and Kara (and potentially other terranes and arcs) led to a rapid counter-clockwise rotation of Baltica (55° within 20 Ma; see references given by Torsvik & Rehnström 2001).

The late Cambrian is a frustrating time to study faunas for several reasons. First, there are no late Cambrian rocks in many areas: they are represented by unconformities. Second, some large terranes, particularly Baltica, carry little or no distinctive benthos as the shallow cratons and their sediments were partially dysaerobic, allowing only specialized trilobites such as olenids to thrive. Third, although agnostid trilobites are common in late Cambrian rocks, they too must be disregarded as palaeogeographical indicators as they were pelagic and thus not tied to specific terranes. Shergold (1988) recognized Baltica, North China, South China, Laurentia and possibly Siberia as four or five trilobite-defined faunal ‘provinces’; however, we recognize only Laurentia, Siberia and peri-Gondwana as separate on faunal criteria and we have included South China within peri-Gondwana. The Mexican (Oaxaquia) terranes carry Gondwanan trilobites (Robison & Pantoja-Alor 1968), as does Florida. Some distinc-

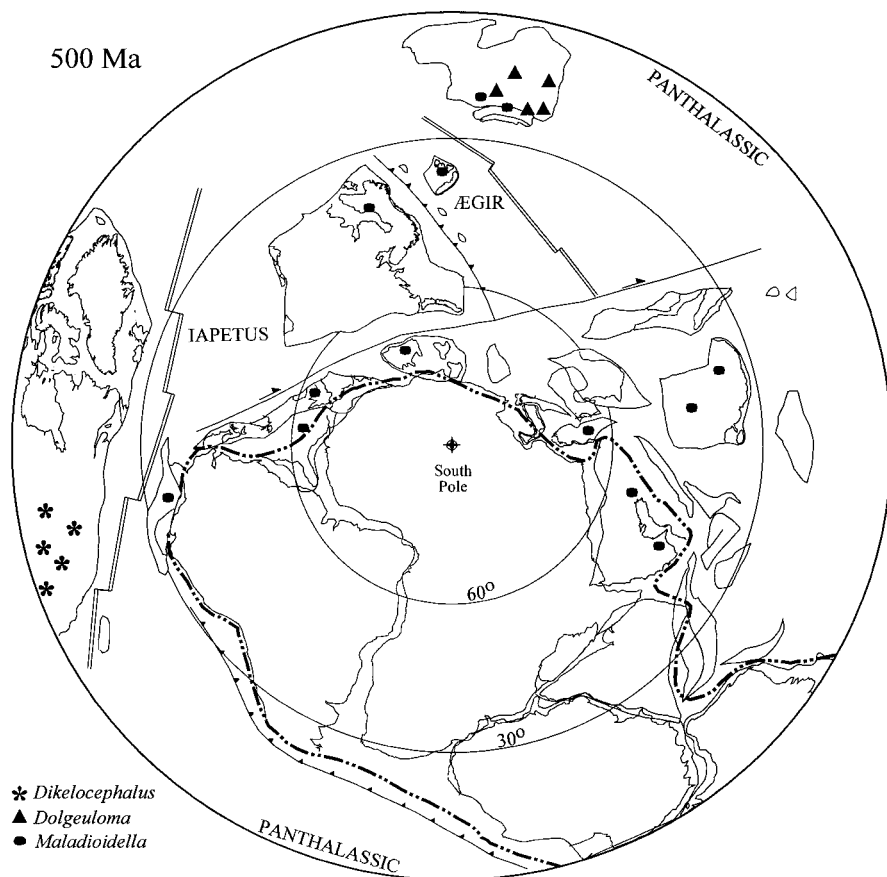


Fig. 3. Reconstruction for late Cambrian (500 Ma) times, with some key trilobite genera. In this and subsequent maps we have included some tentative spreading centres and subduction zones. North China was in the northern hemisphere.

tive trilobites are shown in Fig. 3; for example, *Maladioidella* was widely distributed (Rushton & Hughes 1996) within peri-Gondwana, northern Siberia and South China, with single occurrences in Baltica (Västergötland) and Kara (Severnaya Zemlya) (Rushton *et al.* 2002). *Chuangia* (not shown in Fig. 3) is also characteristic of the lower-latitude parts of peri-Gondwana. Laurentia certainly had a distinctive fauna, including, for example, *Dikelocephalus* (Hughes 1994). Siberia (A.W.A. Rushton, pers. comm.) also had many endemics: from several possibilities we show *Dolgeuloma*, which is an abundant and widespread Siberian endemic genus; for example, at the Rivers Kulyumbe and Chopko, and the Irgark and Norilsk areas. Faunal differentiation does not allow easy distinction between the various Gondwanan and peri-Gondwanan terranes. Articulated brachiopods show relatively little diversity in the late Cambrian, although *Orusia* occurs only in Gondwana (Avalonia and Argentina) and Baltica, and *Huenella* only in Laurentia and Siberia.

Geography at 480 Ma (Tremadoc and early Arenig)

This interval includes the Tremadoc (beginning at 490 Ma) and early Arenig (beginning at 480 Ma, ending at 471 Ma) during which the major oceans, particularly in today's North Atlantic area, were at their widest. Partly because of the width of the oceans and partly because of the large numbers of both faunal and palaeomagnetic studies that have been undertaken on rocks of that age, it is the time slice in which we have the most confidence in our reconstructions. The well-known bathyrid, ptychopygine–megalaspid, calymenacean–dalmanitacean and dikelocephalinid faunas shown (Fig. 4) follow Cocks & Fortey

(1990) with additional records, and demonstrate the separation of Baltica at this time from any of the other large terranes. The Precordillera was within faunal contact of Laurentia, as shown by bathyrid trilobites and brachiopods (Benedetto 1998).

During late Cambrian and early Ordovician times the Iapetus Ocean widened (Torsvik & Trench 1991) and the distance across the British sector (between England and Scotland) was 5000 km in our reconstruction. We show the Lawrence Head, and other formations of Newfoundland and New Brunswick, with the palaeomagnetic positions summarized by Mac Niocaill *et al.* (1997), which indicate their situations as part of an island arc off Laurentia. Sea-floor spreading took place between Baltica and NW Gondwana and the width of the Tornquist ocean there was *c.* 1300 km. Baltica rotated very rapidly counter-clockwise from late Cambrian to early Ordovician times, but throughout the later Ordovician this rotation continued at a slower pace. In late Cambrian and early Ordovician times, Avalonia was part of the NW margin of Gondwana but rifted off sometime before the Llanvirn. Armorica and Perunica were both attached to, and formed part of, Gondwana at 480 Ma.

Geography at 460 Ma (late Arenig to Caradoc)

The interval includes the late Arenig (Fennian, beginning at 471 Ma), the Llanvirn (beginning at 465 Ma) and the Caradoc (beginning at 459 Ma, ending at 449 Ma). This was the time of greatest diversification within the most common brachiopods, for example, the Strophomenoidea increased from one to 37 and the Plectambonitoidea from 17 to 43 genera within the 470–450 Ma period. Williams (1973) was the first to group brachiopod

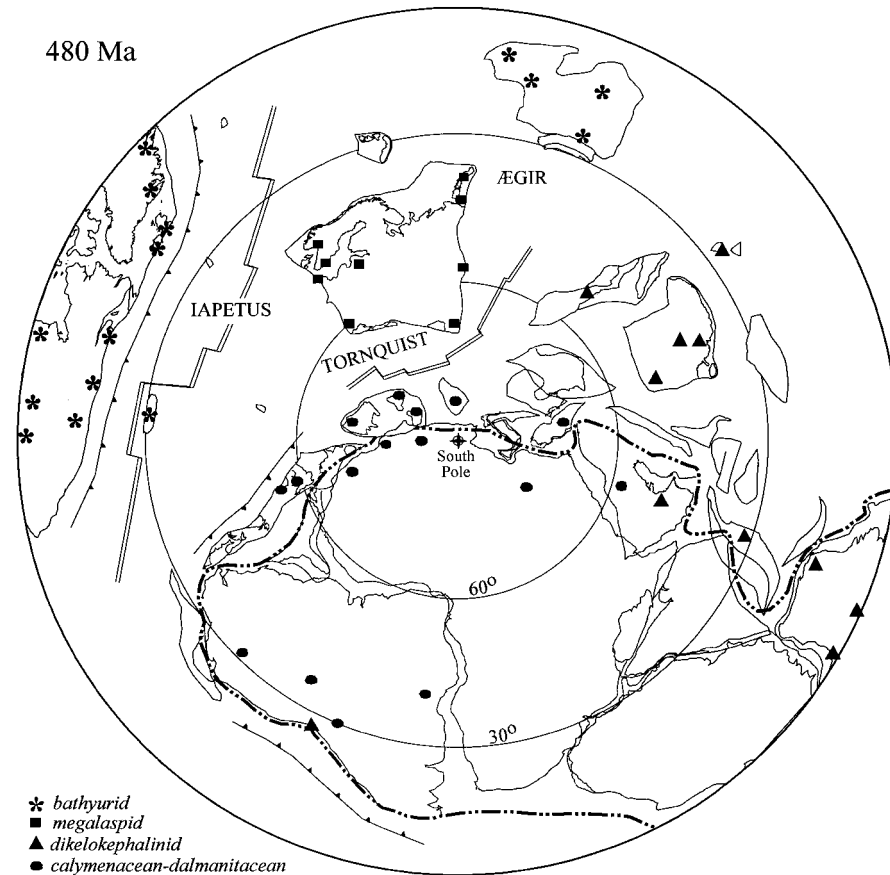


Fig. 4. Reconstruction for early Ordovician (480 Ma) times, with some key Arenig–Llanvirn trilobite faunas. North China was in the northern hemisphere.

assemblages of the period into several clusters, which have been identified as faunal provinces, but much more is now known, particularly from Asia, Australia and South America. The trilobites too are very diverse. This is the last time slice with benthic faunal data from Tarim (Zhou & Chen 1992). The Precordillera carried endemic Caradoc faunas, suggesting contemporary distancing from both Laurentia and Gondwana (Benedetto 1998). Reassessment of Llandeilo and early Caradoc trilobites of southern Taimyr indicates the presence there of several genera of the distinctive family Monorakidae (Balashova 1960), a family known only from the Siberian craton, and providing a much stronger faunal signal than the suggestion put forward by Cocks & Modzalevskaya (1997), based on Ashgill brachiopods, that central and south Taimyr were related to Baltica. Hence south Taimyr has wrongly been shown within Baltica in various reconstructions (e.g. Cocks & Fortey 1998; Torsvik 1998), and it is here placed with confidence as part of Siberia. Northern Taimyr formed part of the Kara Terrane.

The rifting between Avalonia and Gondwana in the Arenig was the first breakaway of peri-Gondwana terranes, and Avalonia drifted rapidly northward between 480 and 460 Ma to reach palaeolatitudes comparable with Baltica during the Caradoc. We show that terrane *c.* 1000 km west of Baltica at 460 Ma and the width of the Iapetus Ocean at 2000 km across the British sector (between the North of England and Scotland). The intermediate positions of Avalonia during its transit across the closing Iapetus Ocean are well characterized by the changing affinities of its brachiopods from Gondwanan to a mixture of genera with ancestors from both Baltica and Laurentia as the Ordovician progressed. Tornquist oceanic crust was being subducted beneath Avalonia as witnessed by calc-alkaline magmatism in SE Eng-

land (Pharaoh *et al.* 1993). Armorica was still attached to NW Gondwana at 460 Ma, as shown by palaeomagnetic data from the Massif Central and faunal data from Brittany and Spain. This was the period of maximum provinciality for the trilobites and brachiopods of Perunica (Havlicek *et al.* 1994), although that terrane still carried much of the Gondwanan ‘Mediterranean’ fauna, and suggests a lower latitude for Perunica than Armorica at this time, indicating that the former had already become detached from Gondwana. The ocean to the south of Avalonia was the Rheic, and we have also tentatively shown its spreading centre as extending eastward to separate South China, Annamia and Sibumasu from Gondwana.

Our map (Fig. 5) has on it a few selected brachiopod genera from the early Caradoc. It should be emphasized that the selection of only five genera from over 200 articulated brachiopods known from this period is very subjective, but they have been chosen to demonstrate links between some of the terranes. Many Caradoc genera were very widespread, and some, such as *Howellites*, *Rafinesquina* and *Rostricellula*, were virtually cosmopolitan, indicating some faunal communication between most of the terranes as well as relatively uniform global temperatures. Despite some reports of Caradoc glaciation, these have not been confirmed and appear unfounded, following examination of the relevant sections in Morocco by one of us (L.R.M.C.) with other colleagues. Of the genera shown in Fig. 5, *Tafilaltia* and *Tissintia* are very characteristic of the high-latitude Mediterranean Province of western Gondwana and neighbouring peri-Gondwanan terranes (references given by Havlicek *et al.* 1994), but is also known from Wales (Avalonia). *Estlandia* was endemic to Baltica, as were several members of its family, the Gonambonitidae. *Saucrorthis* is known only from South China and Burma

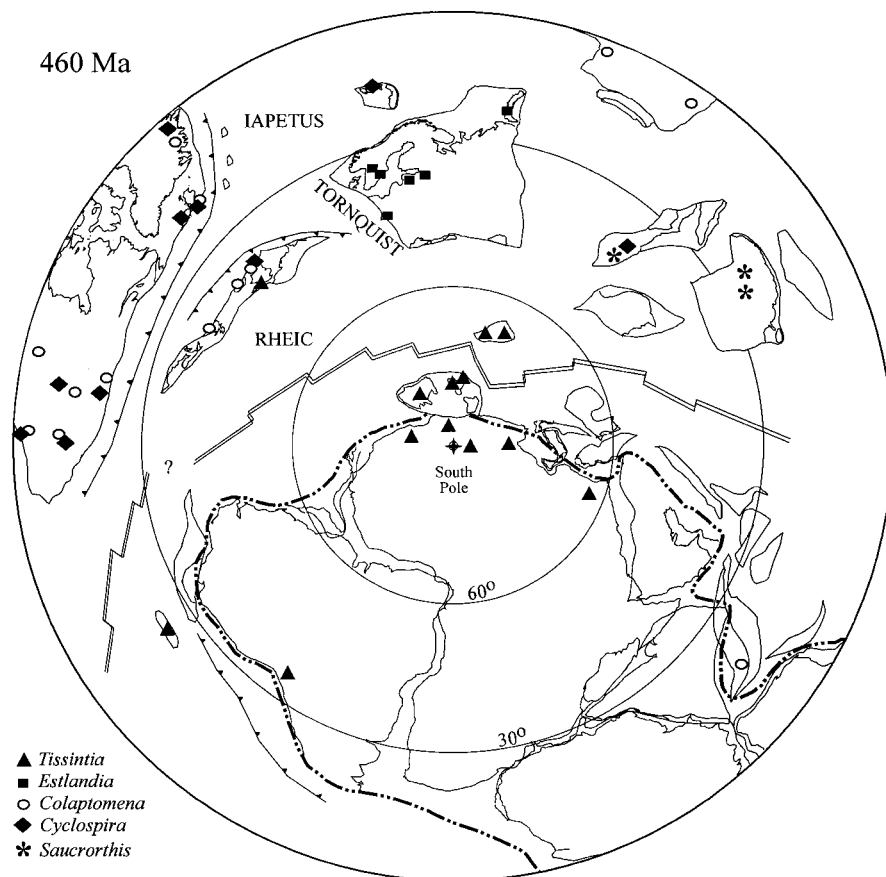


Fig. 5. Reconstruction for mid-Ordovician (460 Ma) times, with some key Caradoc brachiopod genera. North China was in the northern hemisphere.

(Sibumasu). *Colaptomena* (now known to be a senior synonym of *Macrocoelia*) is recorded from the then tropical belt of Laurentia, Siberia and Tasmania, but also again from Avalonia, whereas *Cyclospira* had a slightly wider distribution. Many other distributions are relevant; for example, Jin (1996) noted that the differentiation of rhynchonelloid faunas of Laurentia from those of Siberia, Kazakhstan and North China began in Caradoc time, a distancing that increased progressively until at least the end of the Silurian.

Geography at 440 Ma (Ashgill and Llandovery)

This interval includes the Ashgill (beginning at 449 Ma) and the Llandovery (beginning at 443 Ma, ending at 429 Ma). Although Siberia and Tarim were entirely within the northern hemisphere (Fig. 7), the major oceans had narrowed sufficiently to allow the interchange of the larvae of most benthic animals, and thus the faunas by the end of this time had become very cosmopolitan over a wide range of palaeolatitudes, even though the ocean closures and consequent reduction in endemism were gradual. The brachiopods and trilobites of Baltica and Avalonia became progressively similar (Cocks & Fortey 1982). There was a comparable reduction in the numbers of endemic brachiopod and trilobite genera in Perunica during the Ashgill (Havlicek *et al.* 1994). In contrast, the progressive isolation of North China encouraged the development of endemic rhynchonelloid brachiopods there (Jin 1996). However, global climates deteriorated from about 445 Ma, culminating in an outstanding event at the very end of the Ordovician (443 Ma): the Hirnantian glacial episode. The peak of the glaciation, represented by a very

noticeable oxygen isotope excursion, lasted about half a million years (Brenchley *et al.* 1994), and glacial pavements and other features are well exposed within Gondwana at that time (Fig. 6). These climatic factors, as well as changes in ocean circulation patterns and other parameters, led to a very substantial series of faunal turnovers during the glacial period (although not a relatively instantaneous mass extinction such as that postulated by some at the Cretaceous–Tertiary boundary).

Avalonia collided with Baltica during the Ashgill, as documented by palaeomagnetic, tectonic and isotope data, all supported by the earlier evidence of progressive faunal integration. SW Baltica (Scania) records a Caledonian thermal event (Ashgill) that is broadly comparable with the Shelveian event in Avalonia (Torsvik & Rehnström 2002). This event is also synchronous with Caledonian low-grade metamorphism in the North Sea and was probably related to Avalonia–Baltica collision. Within the Iapetus Ocean, subduction mostly took place beneath Laurentia and the oceanic width across the British sector was reduced to *c.* 1300 km. Perunica probably rifted off NW Gondwana before 460 Ma, whereas Armorica did not start its journey toward lower latitudes until just before 420 Ma. At 440 Ma the Rheic Ocean was at its widest at nearly 5000 km, and Perunica was 500 km to the south of Baltica. Siberia had been located in low southerly latitudes during Cambrian and early Ordovician times, but by 440 Ma it had started its journey across the Equator and into intermediate northerly latitudes.

The data in Fig. 6 are entirely confined to the last 1 Ma of the Ordovician, and show the substantial peri-Gondwanan and Gondwanan glacial deposits, which are known particularly from North Africa (Beuf *et al.* 1971), but also from South America,

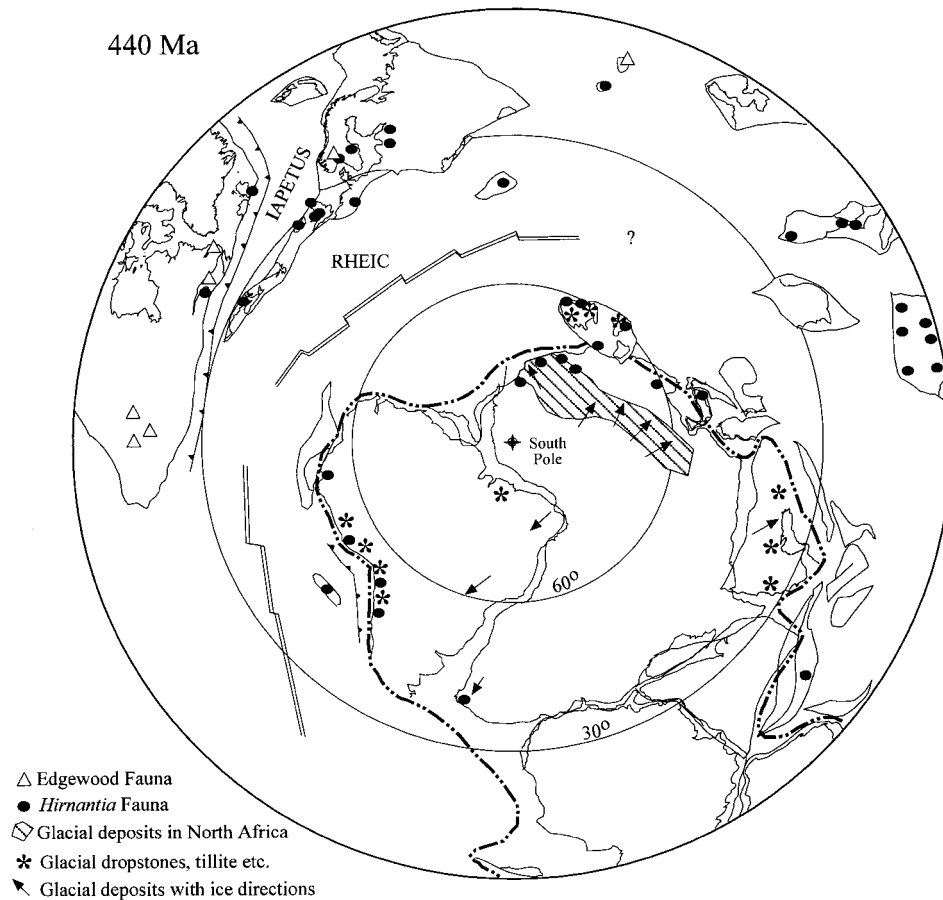


Fig. 6. Reconstruction for latest Ordovician–earliest Silurian times (440 Ma) with Hirnantian ice sheets and other glacial features, together with the distribution of the *Hirnantia* and Edgewood brachiopod faunas. Tarim and Siberia were in the northern hemisphere.

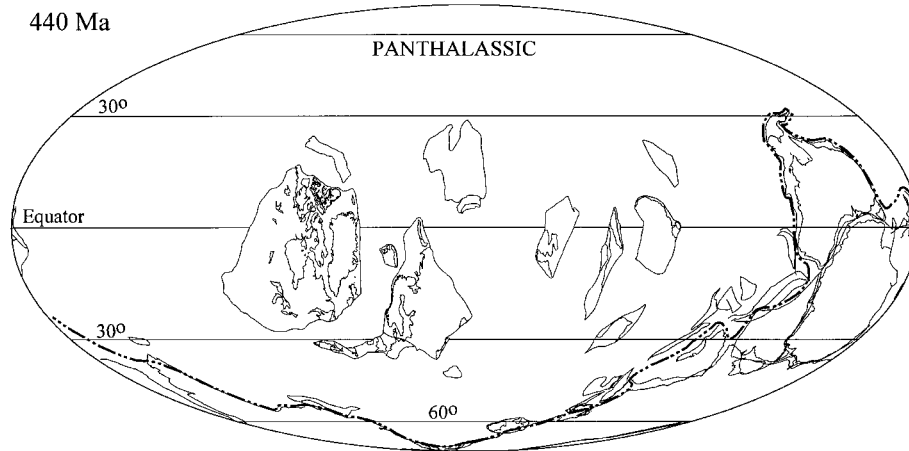


Fig. 7. Global reconstruction for latest Ordovician–earliest Silurian times (440 Ma), Mollweide projection, showing all the major areas absent from Fig. 6 and the extensive Panthalassic Ocean.

Arabia and South Africa. The known ice-flow directions are shown, as are the positions of tilloids, dropstones and other periglacial features; the latter are known from a much wider spread of palaeolatitudes than occupied by the core of Gondwana, including Armorica, and dropstones from even as far north as Avalonia (Wales). The distribution of all these glacial features correlates very satisfactorily with our proposed South Pole position within Gondwana. Also plotted in Fig. 6 are the contemporary Hirnantian brachiopod faunas: the very widespread cool to tropical *Hirnantia* fauna, and the Edgewood fauna, which is also tropical but much more diverse (Rong & Harper 1988, 1999; Cocks 2001). Figure 7 shows the entire Earth at this time and demonstrates the positions of Siberia and Tarim and the

substantial extent of both Laurentia and Gondwana, and also the large size of the Panthalassic Ocean, which was mostly in the northern hemisphere and comparable in size with the Pacific today.

Geography at 420 Ma (late Silurian and earliest Devonian)

This interval includes the Wenlock (beginning at 429 Ma), the Ludlow (beginning at 424 Ma), the Prídolí (beginning at 420 Ma), the Lochkovian (beginning at 418 Ma) and the Pragian (beginning at 414 Ma, ending at 410 Ma). In contrast to the period preceding it, although a broad band of almost cosmopoli-

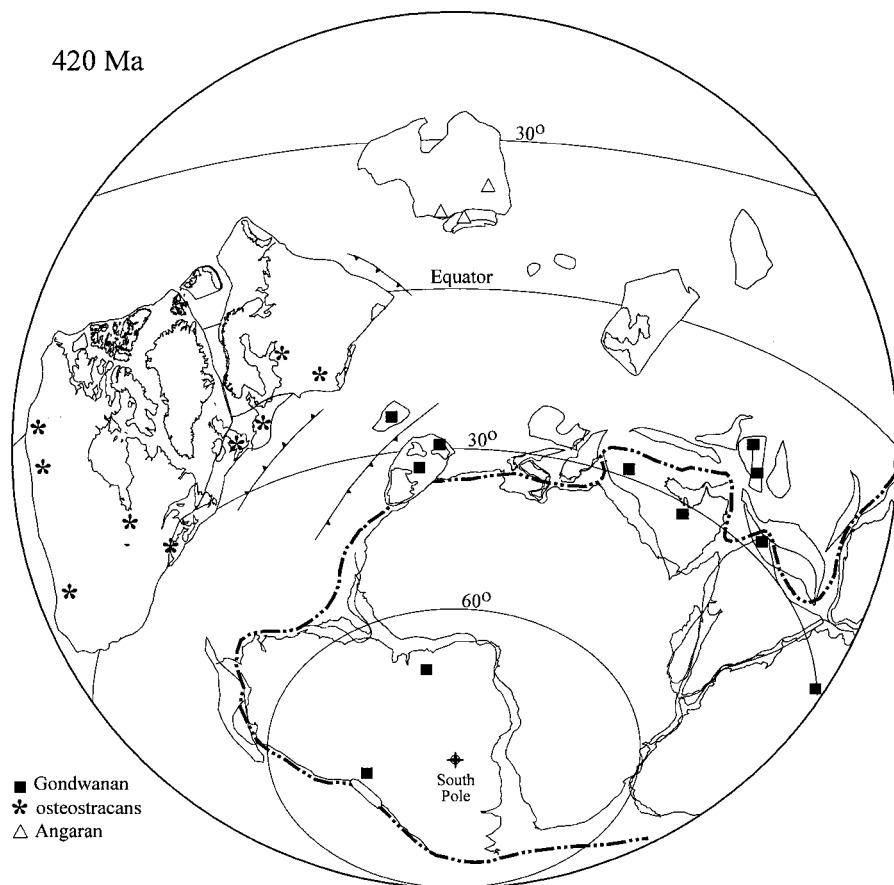


Fig. 8. Reconstruction for late Silurian and early Devonian (420 Ma) times, with some key Lochkovian and Pragian fish faunas. Figures 8 and 9 are Schmidt's Equal Area projection, with projection centre at 30°S. No sea-floor spreading centres are known with confidence from this period. The different Galeaspid fauna is also known, chiefly in South China, which was at tropical to northern intermediate latitudes and to the east of Tarim, as were Sibumasu and Annamia: all three terranes are thus absent from this figure.

tan benthic faunas existed at low and intermediate palaeolatitudes, there were also distinctive high-latitude faunas in both hemispheres. Although not figured here, the brachiopod-based *Clarkeia* fauna was confined to southern hemisphere higher latitudes in southern Gondwana and the *Tuvaella* fauna to northern hemisphere high-latitude localities in northern (today's southern) Siberia and North China (Cocks & Scotese 1991; Rong *et al.* 1995; Cocks 2001). The global climate ameliorated slowly during the early Silurian, with the last known glacial sediments before the Carboniferous being found in the Wenlock of Brazil (Caputo 1998). The Precordillera had docked with Gondwana (Argentina) before this time (Benedetto 1998).

Avalonia and Baltica collided at about 440 Ma, but from 425 to 420 Ma these combined landmasses collided with Laurentia to produce the Scandian Orogeny. Shortly after collision, these amalgamated landmasses (Laurussia) appear from palaeomagnetic data to have drifted rapidly southward whilst undergoing counter-clockwise rotation (compare Figs 8 and 9). This rapid departure to southerly latitudes following collision is remarkable but might possibly be explained as artificial and caused by tilting of the Earth's rotation axis (true polar wander; Van der Voo 1994; Torsvik *et al.* 1996).

Most previous reconstructions show Armorica as detached from Gondwana, but we do not agree, and with our revised Gondwana mean pole (Table 1), it is appropriate to keep the two together and this is supported by the similar faunas on both areas. On our map (Fig. 8) are plotted data for Early Devonian (Lochkovian and Pragian) fish: it may be compared with a map given by McKerrow *et al.* (2000, fig. 2). Despite much literature

to the contrary, Blicek & Janvier (1999) have made a convincing case that these fish lived in essentially marine conditions, although often in reduced salinity, rather than in fresh water. Young (1990a) described the pattern of provinciality, with the very endemic amphiaspid faunas of Siberia, the osteostracan cephalaspid province of Laurussia and the wattagoonaspid–phyllolepid province of Gondwana and (by then detached) Armorica and Perunica. Young grouped both South and North China within a single galeaspid–yuanolepid province, but Blicek & Janvier (1999, p. 93) believe that the latter province was endemic only to the South China plate in the early Devonian, and we follow them here. However, in contrast to the fish, the Lochkovian and Pragian ostracodes (whose spat usually found it notoriously difficult to cross oceans) were the same in Laurussia, Perunica and Armorica, indicating that the Rheic Ocean between Gondwana and Laurussia was unlikely to have been of substantial width.

Geography at 400 Ma (early Devonian)

This time slice includes the slightly shorter interval of the Emsian (beginning at 410 Ma, ending at 394 Ma). Different brachiopod distributions in this time have been recognized for many years, and the Emsian was the highest level of brachiopod provincialism between the late Ordovician and the Famennian. The faunas shown on our map (Fig. 9) were well identified by Boucot *et al.* (1969), partly updated by Boucot & Blodgett (2001), but differentiating only between the Rhenish–Bohemian (or Old World) Realm, the Appalachian Realm and the high-

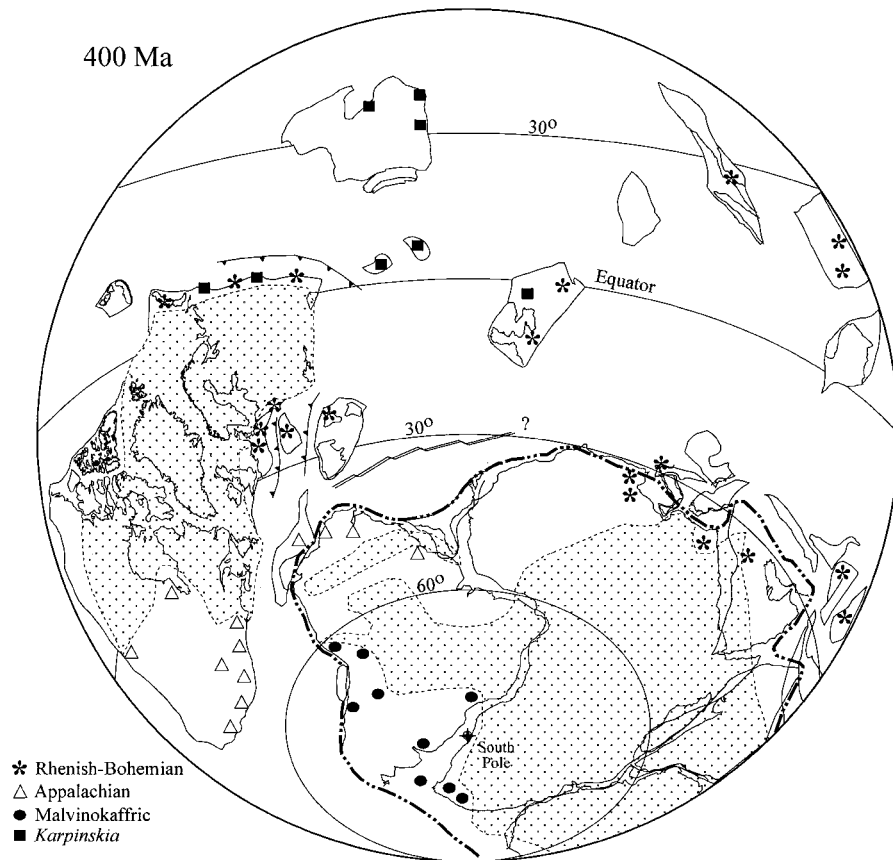


Fig. 9. Reconstruction for early mid-Devonian (400 Ma) times, with Emsian brachiopod provinces. Also shown are the major continental land areas (shaded).

latitude Malvinokaffric Realm. Although the Talacasto Formation of the Argentinian Precordillera has been assigned to the Malvinokaffric Realm in the past, Herrera & Racheboeuf (1997) described it as carrying a brachiopod fauna representing a zone of mixing between the Malvinokaffric Realm and more temperate faunas. In addition, we show some of the localities in which the brachiopod *Karpinskia* has been found (data from many sources), and this distinctive and locally abundant genus appears to have had a distribution linking the Urals, Siberia, North China and some of the smaller terranes now forming part of Kazakhstan: a distribution reinforcing the reconstruction we have made. Thanh *et al.* (1996) have identified the same yunnanolepiform fish fauna as endemic to both South China and Annamia at this time, suggesting the closeness of those two terranes. We also show the more substantial landmasses (modified from Young 1990a), including the Old Red Sandstone continent, which covered much of the large Laurussia plate in Europe and North America.

Between 420 and 400 Ma Gondwana approached Laurussia rapidly and the Rheic Ocean dwindled. At 400 Ma it is possible to maintain the close links between Armorica and Gondwana, as shown in our previous maps, but we have shown Armorica as detached because in later Devonian and Carboniferous times the Hercynian Orogeny demonstrates its collision with Perunica and other elements of northern and central Europe.

Conclusions

(1) The combined constraints and use of data from both fauna and palaeomagnetic studies have produced very different global

palaeogeographical reconstructions from those previously published, especially outside the present-day North Atlantic area. In particular, the relative positions of the four major continents of Gondwana, Laurentia, Siberia and Baltica are now more confidently known.

(2) The availability of good palaeomagnetic data (Fig. 2) dwindles as our time interval progressed, with the exception of those from Laurentia, Baltica and Avalonia, which terranes had, however, all combined to form Laurussia by the late Silurian–early Devonian. Thus our later reconstructions rely more heavily upon the faunas and (from the Ashgill to the Wenlock) on the locations of the glacial deposits. Gondwana is shown moving across the South Pole during our period in a manner similar to that originally postulated by Cocks & Fortey (1988), deduced from the faunas, and Scotese & Barrett (1990), deduced from the lithologies.

(3) Following reassessment of both Gondwana palaeomagnetism and also the faunas, we show Armorica as attached to Gondwana during nearly all of our time period: we only show it detached in our 400 Ma reconstruction.

(4) Our study confirms the well-known early Ordovician maximum width of the Iapetus Ocean, and its narrowing during the Ordovician and the subsequent collision of Laurentia with Avalonia and Baltica; and the changing palaeolatitude positions of Siberia have become clearer by our combined analysis.

(5) The identification and relative positions of the various peri-Gondwanan terranes are still very provisional, particularly those in SE Asia, and their elucidation remains a major challenge for future work on both palaeomagnetism and faunas. In addition, the collage that today makes up Kazakhstan, the Altai and

surrounding areas in Central Asia is still very problematic, with poor palaeomagnetic constraints and complex signals from the faunas. However, we show South China and Sibumasu as further away from Gondwana than in previous reconstructions because of palaeomagnetic data from South China, and strong links between the faunas, and at times even sequences, of South China and Sibumasu.

We have benefited much from stimulating discussions with many colleagues, particularly R. A. Fortey, A. W. A. Rushton and A. Blicek on the faunas, and E. A. Eide and J. Mosar on the terrane positioning. We thank VISTA and NGU for financial support, and The Natural History Museum for the provision of facilities.

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Received 24 August 2001; revised typescript accepted 10 May 2002.

Scientific editing by Jane Francis