Geological Society, London, Special Publications

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Geological Society, London, Special Publications 2000; v. 179; p. 9-20
doi:10.1144/GSL.SP.2000.179.01.03

Notes

The Late Palaeozoic relations between Gondwana and Laurussia

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Abstract: Reconstructions based on biogeography, palaeomagnetism and facies distributions indicate that, in later Palaeozoic time, there were no wide oceans separating the major continents. During the Silurian and Early Devonian time, many oceans became narrower so that only the less mobile animals and plants remained distinct. There were several continental collisions: the Tornquist Sea (between Baltica and Avalonia) closed in Late Ordovician time, the Iapetus Ocean (between Laurentia and the newly merged continents of Baltica and Avalonia) closed in Silurian time, and the Rheic Ocean (between Avalonia and Gondwana and the separate parts of the Armorican Terrane Assemblage) closed (at least partially) towards the end of Early Devonian time. Each of these closures was reflected by migrations of non-marine plants and animals as well as by contemporary deformation. New maps, based on palaeomagnetic and faunal data, indicate that Gondwana was close to Laurussia during the Devonian and Carboniferous periods, with fragments of Bohemia and other parts of the Armorican Terrane Assemblage interspersed between. It follows that, after Early Devonian time, the Variscan oceans of central Europe can never have been very wide. The tectonic evolution of Europe during Devonian and Carboniferous time was thus more comparable with the present-day Mediterranean Sea than with the Pacific Ocean.

Palaeozoic palaeocontinents

During the Palaeozoic era, there were several events when major continents rifted apart and others when they collided. No continent remained as a distinct entity throughout this era; so each palaeocontinent can only be defined after consideration of its history. The major Palaeozoic continents that are represented in Europe are Laurentia, Baltica, Avalonia and Gondwana, with smaller continental fragments of the Armorican Terrane Assemblage, including Bohemia and Armorica.

Laurentia, the Palaeozoic continent based on North America, did not include the Mesozoic and Cenozoic additions to the Western Cordillera, nor is it defined (Scotese & McKerrow 1990) as including the terranes accreted to the east coast in the Devonian and Carboniferous periods. Much of the northern Appalachians (eastern Newfoundland, New Brunswick, Nova Scotia and coastal New England) were parts of Avalonia until Silurian time. The Piedmont and Florida were parts of Gondwana until Carboniferous time. But Laurentia did include (as indicated by their Cambrian and Early Ordovician faunas) north-west Ireland, Scotland, Greenland, much of Svalbard, the North Slope of Alaska and the Chukotsk Peninsula of eastern Siberia (Scotese & McKerrow 1990). Palaeomagnetic data (Mac Niocaill & Smethurst 1994) and the prevalence of warm-water carbonate facies show that Laurentia remained close to the Equator throughout Palaeozoic time.

Baltica consists of Scandinavia and the East European Platform, as far east as the Urals. Its southern margin extends from the North Sea to the Black Sea along the Trans-European Suture, a line much complicated by later deformation. In

From: FRANKE, W., HAAK, V., ONCKEN, O. & TANNER, D. (eds).
Orogenic Processes: Quantification and Modelling in the Variscan Belt.
Geological Society, London, Special Publications, **179**, 9–20. 0305-8719/00/$15.00

Cambrian time, Baltica was at high southern latitudes (Torsvik *et al.* 1996); its trilobite faunas were similar to those of Laurentia but less diverse. The faunas were also similar to those of Avalonia, which were even less diverse, thus indicating that, before Ordovician time, Baltica was situated close to Avalonia in a position off the Florida or Venezuelan margins of Gondwana (McKerrow *et al.* 1992). Subsequently, Baltica moved slowly northwards; eventually warm-water carbonates appear in Late Ordovician time, and Baltica straddles the equator in Silurian and Devonian time.

Avalonia, consists of the eastern parts of the Northern Appalachians (from Connecticut to the Avalon Peninsula in Newfoundland), southern Ireland, Wales, England, Belgium and the Rheno-Hercynian belt of northern Germany (Cocks *et al.* 1997). In eastern Germany, Avalonian crust extends across the Elbe Line (Finger & Steyrer 1995; contra Cocks *et al.* 1997); an isolated fragment may also be present east of Bohemia in the Moravo-Silesian terrane.

During Cambrian time, Avalonia was attached to Gondwana not far from the South Pole. At this time it had clastic sedimentary facies, which suggest it was attached to the northern margin of South America rather than to Morocco where different Cambrian faunas are present in carbonates (McKerrow *et al.* 1992; Torsvik *et al.* 1996). Avalonia shows evidence of latest Precambrian arc rocks assigned to Cadomian time; its basement is thus not distinguishable from those parts of northern Gondwana now seen in the Armorican Terrane Assemblage of central and southern Europe; similar arc rocks also occur in Morocco (Piqué 1981). Avalonia became detached from Gondwana in Early Ordovician time and moved rapidly northwards to collide with Baltica in latest Ordovician time and with Laurentia in Silurian time (Cocks & Fortey 1982; McKerrow *et al.* 1991; Trench *et al.* 1992).

Gondwana was a large continent that originated in latest Precambrian time by amalgamation of parts of Africa, South America, India, Antarctica and Australia (Torsvik *et al.* 1996). In Cambrian time, it included all of Europe south of Avalonia and Baltica. In Late Ordovician time the South Pole was in North Africa and, although the terranes of southern Europe had separated from Gondwana, they were still far enough south to carry periglacial deposits (Havlíček 1989). Palaeomagnetic data show that, while Gondwana moved northwards during Silurian time, several south European terranes (including parts of Bohemia and Armorica) moved more rapidly (Tait *et al.* 1995; Torsvik *et al.* 1996).

The narrowing oceans

As two continents approach, it becomes progressively more difficult to use palaeomagnetic or sedimentological data to distinguish between them, but there are some organisms that remain useful until there is a continuous shallow-water or terrestrial connection (McKerrow & Cocks 1976; McKerrow 1978).

Marine organisms can be classified, according to their mode of life, into the following groups: (a) free-swimming and floating (or pelagic) nekton and plankton, such as the Early Palaeozoic graptolites and the Late Palaeozoic ammonoids and some fishes (including some Palaeozoic sharks). (b) Bottom-dwellers (benthos) that had a pelagic larval stage, and that include most marine invertebrates (e.g. trilobites and brachiopods). Some fishes (including placoderms and primitive lungfish) appear to have been benthic in coastal waters (Janvier 1996), but as it is not known whether they had pelagic larvae, they may or may not fall into this category. (c) A few marine organisms, such as some ostracodes, which hatch out from eggs on the sea floor and have no pelagic growth stage. Benthic ostracodes cannot cross deep water. (d) Aquatic organisms that are restricted to non-marine (rivers and lakes) or brackish environments. Many Devonian fish (for example, holoptychiids, phyllolepids and the more advanced lungfishes) are known only from Old Red Sandstone sediments, which are either non-marine or which have a limited marine influence. They appear to have been unable to cross narrow stretches of open sea. (e) Terrestrial organisms (plants with large seeds; post-Devonian tetrapods) that could only spasmodically cross open water, and thus are normally restricted in range until after (sometimes long after) continental collision.

In Cambrian and Early Ordovician time, when many continents were isolated by wide oceans, only the plankton (and a very few other forms) could cross all oceans (Cocks & Fortey 1990; Scotese & McKerrow 1990; McKerrow & Cocks 1995). Plankton normally show a geographical distribution related to climate, whereas most other organisms serve to distinguish individual continents (or groups of adjacent continents). In Late Ordovician time, many brachiopods and trilobites (benthos with pelagic larvae) start to have global distributions as the major continents become closer; until in Silurian time the only common fossils to distinguish many continents are ostracodes and fish. By the end of Early Devonian time, many ostracodes became widely distributed (Berdan 1990). The Devonian fish faunas show parallel changes: the fish of Laurussia (the continent resulting from the fusion of Laurentia, Avalonia and Baltica) started to merge with those of Gondwana and became increasingly similar through Mid- and Late Devonian time (Young 1990). There is no indication of any permanent barrier to migration across the Variscan orogen after Early Devonian time.

European suture zones

In central Europe sutures of five Palaeozoic oceans have been recognized (Fig. 1).

The Iapetus suture

The Iapetus suture in the British Isles extends from the Shannon estuary in western Ireland to the mouth of the River Tweed in northeast England. The Iapetus Ocean opened between Laurentia and Baltica at around 600 Ma. Closure between Laurentia and Laurussia (the fused Baltica–Avalonia) occurred in Mid-Silurian time (McKerrow *et al.* 1991; van Staal *et al.* 1998), when turbidites derived from Laurentia were deposited in a rapidly depressed foreland basin covering central Ireland in Wenlock time (Hutton & Murphy 1987) and the English Lake District in Ludlow time (Leggett *et al.* 1983). This foreland basin developed along the northwest margin of Avalonia as the continent was subducted below the active margin of Laurentia. It was persistent and continuous enough to prevent the migration of ostracodes across the Iapetus suture until Devonian time (Berdan 1990).

The Tornquist suture

The Tornquist suture (equivalent to the Trans-European Suture Zone of some workers) extends eastwards from the mouth of the Tweed, to the north of Hamburg, and passes east of the Görlitz area (in easternmost Germany) and Silesia (in southern Poland) not far from the course of the River Odra (Oder). It lies distinctly south of the Tornquist Line, after which it was named (Cocks & Fortey 1982).

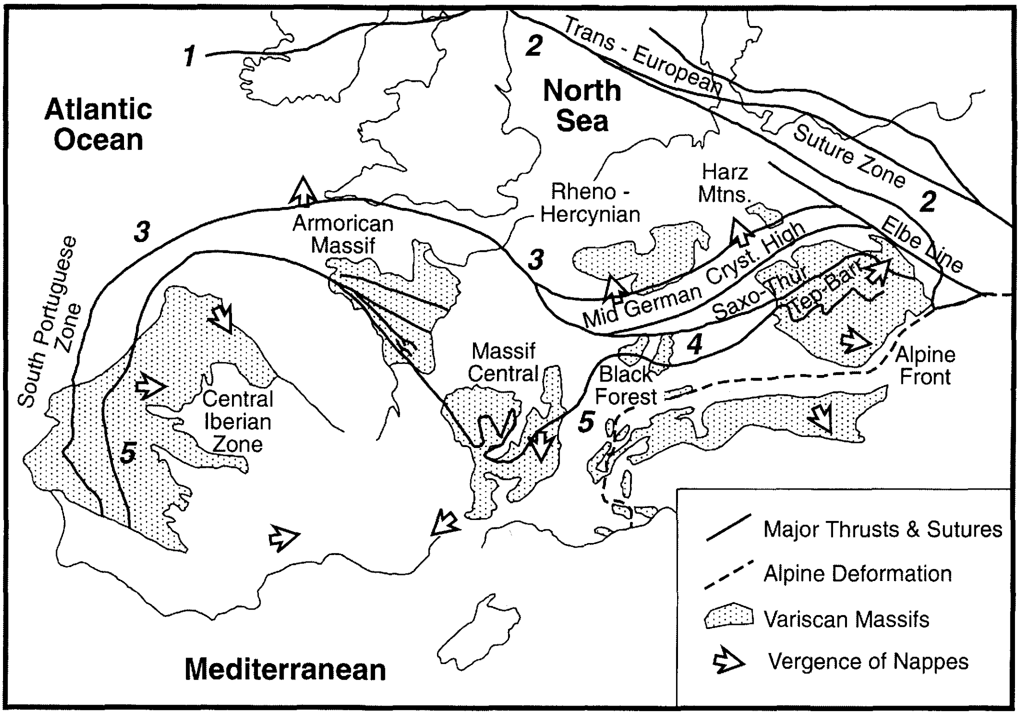

Fig. 1. Palaeozoic sutures in Europe (in part after Franke *et al.* (1995) and Matte *et al.* (1990)). 1, Iapetus Ocean; separating Avalonia from Laurentia. 2, Tornquist Sea; separating Avalonia from Baltica. 3, Rheic Ocean; separating Avalonia from the Armorican Terrane Assemblage. 4, Ophiolites south of the Saxo-Thuringian terrane. 5, Ligerian–Massif Centrale–Moldanubian ophiolites.

The Tornquist Sea (between Avalonia and Baltica) may have originated at the same time as the Iapetus Ocean (*c.* 600 Ma); Baltica was certainly separated from Gondwana (which included Avalonia until Early Ordovician time) throughout the Cambrian period (McKerrow *et al.* 1992). The Tornquist Sea probably closed in Late Ordovician time (Van Staal *et al.* 1998), at the time of the Shelveian Orogeny of western England (Toghill 1992); certainly the Early Silurian benthic ostracode distributions (Berdan 1990) show that there was no continuous deep water between Baltica and Avalonia.

The arc related to closure of the Tornquist Sea is seen in the Ordovician igneous rocks of the English Lake District (Kokelaar *et al.* 1984) and eastern England (Pharaoh *et al.* 1993). The Ordovician and Silurian volcanic series in eastern England (Pharaoh *et al.* 1993), the Ardennes and the Northern Phyllite Belt (Stillman 1988; Franke 1989) erupted between the Tornquist Sea and the Rheic Ocean; they may have been related to the subduction of either ocean (McKerrow et al., 1991; Franke et al., 1995).

The Rheic suture

The Rheic suture (Fig. 1) extends eastwards from southwest England to the south of the Ardennes and to the south of the Rheno-Hercynian terrane and the Harz Mountains of northern Germany (Franke *et al.* 1995; Cocks *et al.* 1997).

There is still some discussion about the position of the Rheic suture east of Dresden and in the Czech Republic and southern Poland (Belka *et al.* this volume; Finger *et al.* this volume). If the Mid-German Crystalline High and the Saxo-Thuringian terrane continue to the northeast of the Elbe line (Linnemann *et al.* 1998), then the Rheic suture (lying between Avalonia and Baltica to the north and Barrandia and other Armorican terranes to the south) may extend northeast to the vicinity of the Odra Fault, contrary to the conclusions of Cocks *et al.* (1997). The Rheic suture clearly may then merge with the Tornquist suture in Silesia. The eastward continuation of the Rheic suture is further complicated by the possible presence of an isolated remnant of Avalonia in Moravo-Silesia (Finger & Steyrer 1995). As Avalonia, Bohemia and Saxo-Thuringia were all originally parts of Gondwana, latest Precambrian (600–550 Ma) Cadomian arc rocks occur on many different terranes, and it is not possible to recognize the Rheic suture unless Palaeozoic sediments crop out.

The Rheic Ocean opened in Early Ordovician (Arenig) time, when Avalonia split off from the South American parts of Gondwana (Cocks & Fortey 1982; Scotese & McKerrow 1990), and closed (at least locally) in Emsian time (Van Staal *et al.* 1998). The closure of the Tornquist Sea (in Late Ordovician time) and of the Iapetus Ocean (in Wenlock time) left the Rheic Ocean, separating Bohemia and Armorica from Laurussia, as the principal surviving major long-lived ocean in Late Palaeozoic time (Fig. 2).

The Giessen, Harz and Lizard ophiolites are overlain in some sections by thin, condensed Emsian–Eifelian cherts and shales. This Rheno-Hercynian basin appears to have opened in late Emsian time, very close to the line of the Rheic suture (Franke, this volume). These sequences have been thrust over the southern margins of Avalonia in the Lizard (of SW England), Giessen (north of Frankfurt) and the Harz Mountains (Franke 1989, p. 72, and this volume); they appear to have originated from a line very close to the Rheic suture. If the Rheic Ocean closed in Emsian time, these ophiolites appear to have developed in a recently opened ocean nearby.

The suture south of the Saxo-Thuringian terrane

This suture has been inferred from allochthonous Lower Palaeozoic mid-ocean ridge basalt (MORB) type rocks, which are now present between the Saxo-Thuringian terrane and the Teplá–Barrandian of Bohemia (Franke *et al.* 1995, pp. 581–582; Linnemann *et al.* this volume), and from palaeomagnetic data showing that Saxo-Thuringia and Bohemia rotated independently during Silurian and Devonian time (Tait *et al.* 1995, this volume). The Saxo-Thuringian basin has thick clastic deposits and bimodal volcanic rocks which indicate a Cambro-Ordovician rift basin (Franke *et al.* 1995, p. 581); it is thus possible that the Saxo-Thuringian terrane separated from Gondwana around this time. Allochthonous latest Cambrian (500 Ma) eclogites derived from MORB-type rocks south of the Saxo-Thuringian terrane may represent fragments of an ocean, which, although long-lived, does not appear to have ever been a barrier of biogeographical significance.

As the Saxo-Thuringian terrane dies out towards the Rhine Valley, this suture merges west with the Rheic suture (Fig. 1).

The Ligerian (south Brittany), Massif Central, Moldanubian (south Bohemia) suture

This suture marks the separation of several distinct microcontinents (including Bohemia and Brittany) from Gondwana during Ordovician

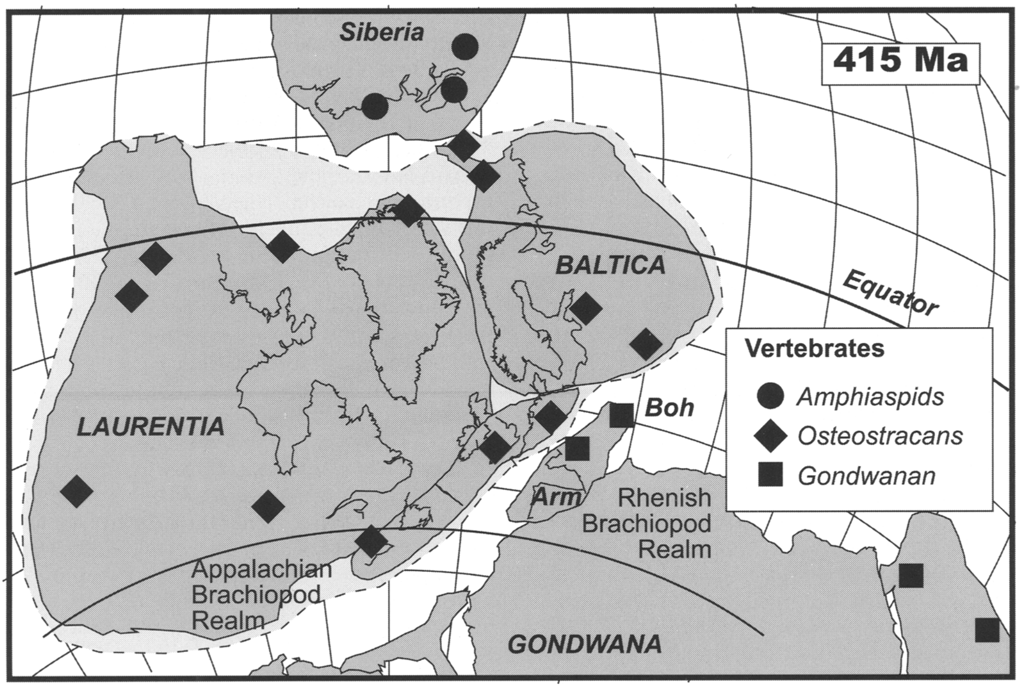

Fig. 2. Continental dispositions in Early Devonian time (Lochkovian, 415 Ma) showing distribution of non-marine (and ?coastal) fish (after Young 1990). It should be noted that different families occurred in Siberia, Laurussia and in Gondwana, and that Armorica and Bohemia appear to be attached to Gondwana. The boundary of the Appalachian and Rhenish (marine) brachiopod realms during Emsian time (after Boucot *et al.* 1969) is also shown; this now appears to be related to climate, as it lies parallel to latitude. Its position helps to align Gondwana with the northern continents.

time. It should perhaps be distinguished as several distinct sutures, but until we know just how many different terranes are present in central and southern Europe, it is convenient to consider them together (Matte *et al.* 1990; Franke *et al.* 1995).

The northern edge of Gondwana extended from South America (with Avalonia attached before Ordovician time), through Florida, West Africa and southern Europe to Turkey, Afghanistan to South China (McKerrow *et al.* 1992). This margin was active until the completion of Cadomian arc-related igneous activity around 550 Ma, close to the start of the Cambrian period (Tucker & McKerrow 1995; Landing *et al.* 1998). Extension on this margin is recorded by Cambrian subsidence in Wales, central Armorica, Saxo-Thuringia and Bohemia, but the earliest evidence of separation from Gondwana is seen in Avalonia, which probably rifted in Early Ordovician time (Cocks & Fortey 1982; Van Staal *et al.* 1998); subsequently there is palaeomagnetic evidence that Bohemia had separated from Gondwana by Late Ordovician time (Tait *et al.* 1995, this volume).

Biogeography

Ordovician and Silurian time

During Early Ordovician time, wide oceans separated Laurentia, Baltica and Gondwana so that the distribution of most benthic faunas reflected geographical isolation (Cocks & Fortey 1990); it was only the pelagic forms (such as graptolites and some conodont animals) that were able to migrate freely around the world (Berry & Wilde 1990). In the Early Palaeozoic era, we estimate that the majority of animals with pelagic larvae (such as trilobites and brachiopods) could traverse oceans up to 1000 km wide (McKerrow & Cocks 1986). In Late Ordovician time, trilobites and brachiopods have widespread geographical distributions related to latitude (Cocks & Fortey 1990). We conclude that, by this time, there were no oceans wider than 1000 km that separated the major continents without intermediate island stop-overs, such as, for example, the various components of the Armorican Terrane Assemblage situated between Gondwana and Laurussia.

During Silurian time, benthic animals with pelagic larval stages (such as like brachiopods and trilobites), could migrate freely between the major continents such that only climatic factors, rather than isolation, played a major role in their biogeography (Cocks & Fortey 1990). Less diverse high-latitude assemblages can be recognized in some benthos. Geographical isolation was present in only two groups of less mobile animals, which remained distinct: benthic ostracodes, which had (and have) no pelagic larval stage, and certain fish taxa, which were mainly restricted to non-marine and coastal environments (Berdan 1990; Young, 1990). These less mobile forms permit recognition of the Rheic Ocean through much of Early Devonian time.

Early and Mid-Devonian time

The biogeographical evidence for a narrow Rheic Ocean during Early Devonian time (Fig. 2) is reinforced by palaeoclimatic and lithological data (Scotese & Barrett 1990) and by palaeomagnetic data (Van der Voo 1993). Available palaeomagnetic poles from Gondwana for Late Silurian and Early Devonian time fall in South America, and reconstruction of Gondwana places the northern margins (north Africa and Arabia) in the tropics. Hence the Rheic Ocean cannot have been more than a few hundred kilometres wide.

The situation is made more complicated by the fact that several oceanic sutures are present between Gondwana and Baltica (Fig. 1). In Early Devonian time (Lochkovian and Pragian time) the ostracodes (which were marine but had no pelagic larval stages) crossed from Laurussia to Bohemia and Armorica, but did not reach Africa (Berdan 1990). This palaeontological evidence supports palaeomagnetic data (Tait *et al.* 1994, 1995) indicating that these microcontinents had rifted from Gondwana before Silurian time and were close to Laurussia at the start of Devonian time.

Our new reconstruction, which incorporates palaeomagnetic data with climatic, lithological and biogeographical data, now permits orientation of the the major continents so that new explanations can now be postulated for certain biogeographical observations. In particular, the Emsian brachiopod distributions first described 30 years ago (Boucot *et al.* 1969) are now seen to be related to latitude (Fig. 2). The Rhenish province of North Africa and Europe (with a few sporadic occurrences in Nova Scotia, Quebec and Nevada) developed in low latitudes, whereas the Appalachian province of the USA lies more than 40° south of the Equator. The boundaries between the two provinces on opposing margins of Gondwana with Laurussia allow the two continents to be matched with some confidence, and suggest that Morocco was opposed to Nova Scotia as the ocean closed.

Before Emsian or Givetian time, the Rheic Ocean affected the distribution of only non-marine (and coastal?) fish (Young 1990); after this time, the main factors governing biogeographical distributions were increasingly related to climate and to the disposition of suitable local environments (lakes, rivers, deltas, etc.) rather than to isolation by wide oceans.

Late Devonian time

In Late Devonian time, many non-marine and marginal marine fishes developed world-wide distributions (Fig. 3). Among the placoderm fishes, for example, the antiarchs *Bothriolepis* (mostly restricted to the Old Red Sandstone, but with some marine occurrences) and *Remigolepis* (entirely restricted to the Old Red Sandstone) both originated in Gondwana, but spread across Laurussia (Greenland, Scotland and Russia) during Late Devonian time (Young 1984). Similarly, the phyllolepid arthrodires first appeared in Givetian time in Australia and occur throughout much of Laurussia in Famennian time (Long 1984).

Some groups of sarcopterygian fish also became widespread in Late Devonian time. The tristichopterids appeared first in Givetian time in Laurussia, and soon spread to Gondwana, but generic differences between the two continents indicate that they did not migrate freely (Ahlberg & Johanson 1997); they appear to have been largely non-marine, although a marine occurrence is recorded in Morocco (Lelièvre *et al.* 1993). The Late Devonian holoptychiid *Holoptychius* was widespread in Laurussia throughout Frasnian and Famennian time, but crossed to Gondwana (Australia) during Famennian time (Young 1993). The earliest rhizodont sarcopterygians occurred in Gondwana in Late Devonian time (Johanson & Ahlberg 1998) and reached North America in Famennian time (Andrews & Westoll 1970); they spread to Europe in the Early Carboniferous period. The proximity of Laurentia and Gondwana during Late Devonian time is further illustrated by the lungfish *Soederberghia*, which had skeletal adaptations for air-breathing (cranial ribs, stalked parasphenoid) and which is represented by a single species in the Famennian succession of Greenland, North America and Australia (Ahlberg *et al.* 2000).

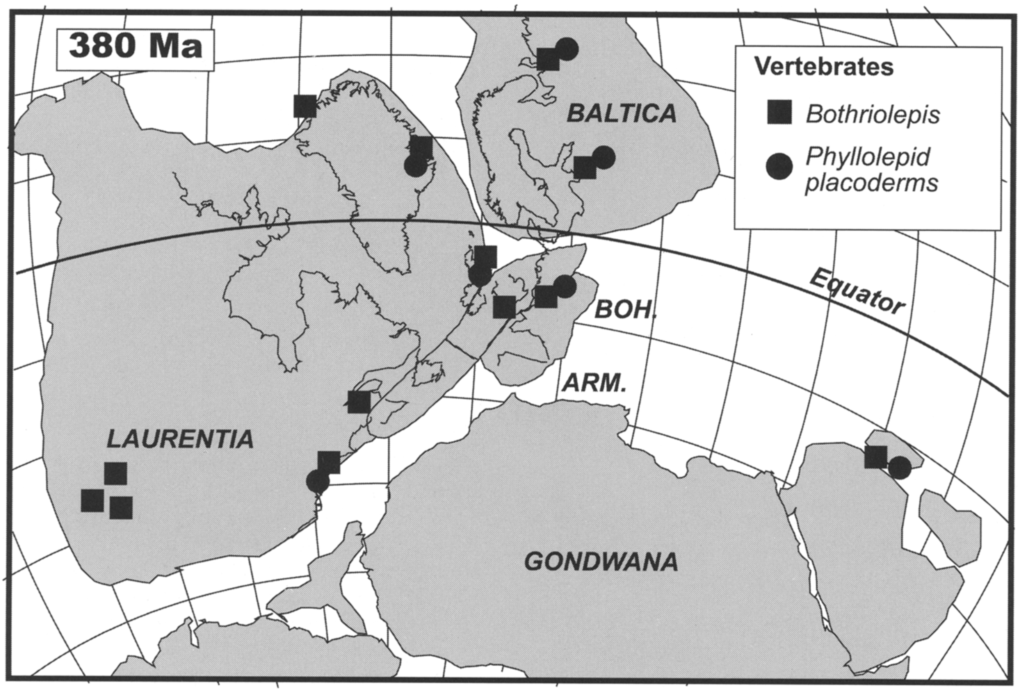

Fig. 3. Continental dispositions in Late Devonian time (Frasnian, 380 Ma) showing distribution of some non-marine (?coastal) fish (after Young 1990). By this time many fish families freely cross the suture of the Rheic Ocean, which was thus closed in places.

Tetrapods, which were initially more or less aquatic and tied to Old Red Sandstone environments, appear to have originated in late Frasnian time in Laurussia, where closely related (Givetian–early Frasnian) fish are also present (Ahlberg & Clack 1998). These animals crossed to Gondwana in Famennian time, when they reached Australia (Campbell & Bell 1977; Young 1993; Ahlberg & Clack 1998).

Devonian vegetation consisted mainly of spore-producing plants and shows little global provincialism (Meyen 1987; Edwards & Berry, in Cleal 1991). For example, the Devonian floras of northern Venezuela (Berry *et al.* 1993) are broadly similar to those of New York State (Banks *et al.* 1985); and the tree *Calloxylon*, previously known from the Late Devonian rocks of North America, also occurs in Morocco (Meyer-Berthaud *et al.* 1977) These examples support the evidence for no great separation across the Rheic suture.

Early Carboniferous time

In Early Carboniferous time, many plant distributions were dominated by climate (Fig. 4), but some floras in Venezuela (Pfefferkorn 1977) and Morocco and Algeria (Lejal-Nicol, in Wagner *et al.* 1985, p. 387) include lycophytes (e.g. *Lepidodendron*, *Lepidodendropsis*) and some seed plants (*Triphyllopteris*, *Sphenopteridium*) characteristic of the European Palaeoarea floras (*sensu* Cleal & Thomas, in Cleal 1991). Such floras are well known throughout southern Laurentia and Avalonia; they include the classic floras of the Price, Pocono and Mauch Chunk Formations in the central Appalachians (Read 1955), the Horton Group in Nova Scotia (Bell 1960), Teilia in North Wales and the oil shales of southern Scotland (Kidston 1923–1925). The other European records of these floras (in northern and eastern Germany and Silesia) were reviewed by Meyen in Vakhrameev *et al.* (1978).

While Latest Devonian miospores had cosmopolitan distributions, those in Early Carboniferous (Viséan) time show strong latitudinal correlation (Sullivan 1965, 1967; Clayton 1985, 1996). The *Monilospora* Microflora occurs in northwest Canada, Svalbard and the northern parts of Baltica. The *Grandispora* Microflora is well documented from the South Portuguese Zone, the British Isles, northern Germany (Rügen), northern Poland (Pomerania) and

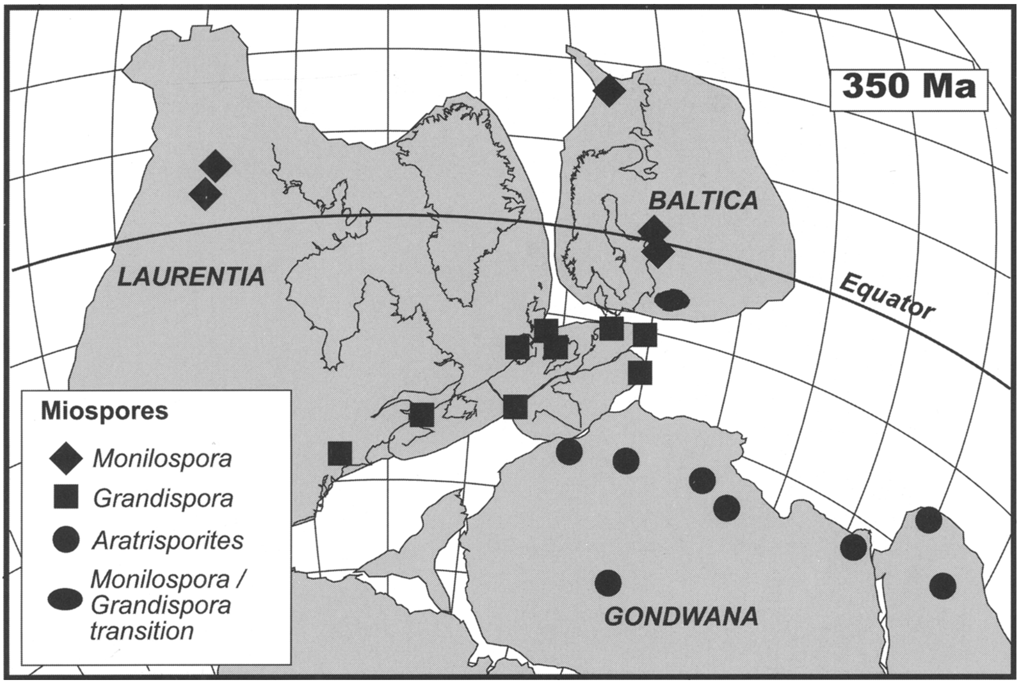

Fig. 4. Continental dispositions in Early Carboniferous time (Viséan, 350 Ma) showing distribution of three floral regions (after Sullivan 1965, 1967; Clayton 1985, 1996). They are associated with climatic belts. It should be noted that Avalonia and the Armorican Terrane Assemblage share the *Grandispora* Microflora.

Romania (Moesian Platform). A third microflora (*Aratrisporites saharaensis*) is known from North Africa (Morocco to Egypt), Niger, Syria and Saudi Arabia. Whereas the *Monilospora* and *Grandispora* Microfloras show some transitional associations, no such gradations have yet been described between these and the *Aratrisporites saharaensis* Microflora, except possibly in South America. During Early Carboniferous time, the northern margin of Africa was apparently a barrier to plant migration; perhaps some plants were more sensitive to minor changes in climate than others.

Carboniferous tetrapods are considerably more advanced than those in the Devonian period. They seem to be the product of a basal Carboniferous monophyletic radiation, which is widely represented in Laurussia, but only sporadically in Gondwana (Thulborn *et al.* 1996).

Late Carboniferous time

During Late Carboniferous time, paralic coalfields extended across Laurussia from North America across Britain and the Rheno-Hercynian region of Germany, and thence to Silesia and the Donetz area. This extensive region suffered several marine incursions, and clearly most of the Westphalian deposition (largely non-marine) occurred close to sea level (Paproth 1991) on the northern (passive margin) side of the Rheic suture; areas formerly composing Avalonia and Baltica (compare Fig. 1 with Trueman (1946, fig. 7)). By contrast, the Stephanian intermontane limnic basins developed mainly to the south of the suture on the various components of the Armorican Terrane Assemblage.

Coal-forming environments were present south of the Rheic suture in the Saar–Lorraine basin during late Westphalian time (possibly earlier) and continued until early Stephanian time (Weingart 1976); then after a short hiatus, they returned in mid-Stephanian time (Germer *et al.* 1968; Cleal 1984). In France, intermontane basins appeared in early Stephanian time (Bouroz *et al.* 1990), whereas in Spain, some coalfields originated in early Westphalian time, though they did not become widespread until late Westphalian time (Wagner & Alvarez-Vázquez 1991). Some of these internal basins yield non-marine bivalves that include species known in the Appalachians and northern Europe (Eagar 1983, 1984, 1985, 1994). It is thus evident that, by latest

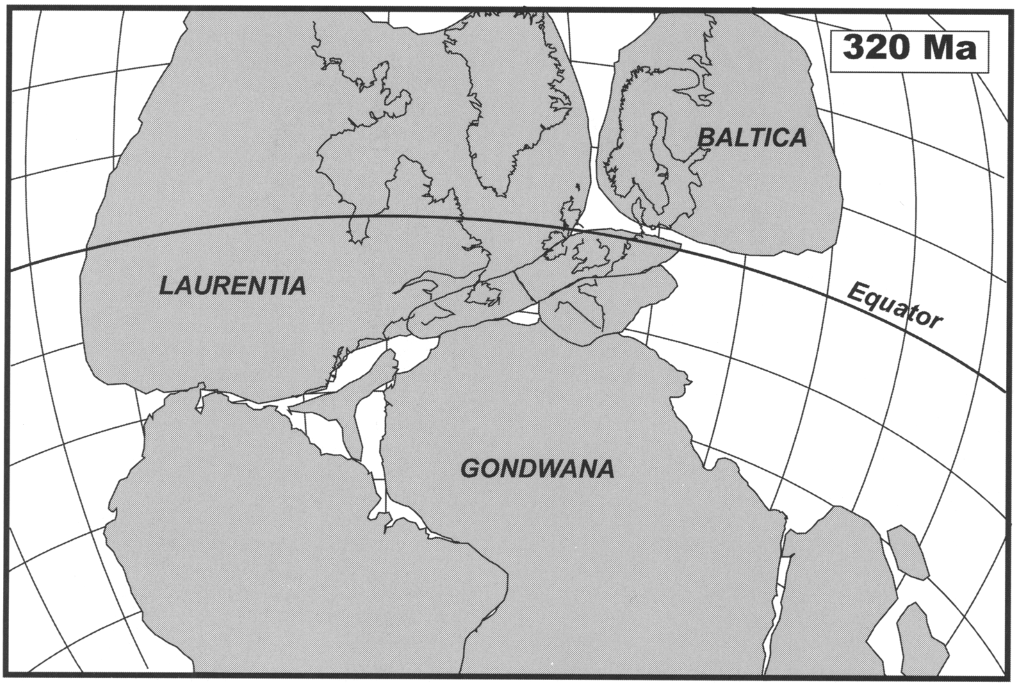

Fig. 5. Continental dispositions in Late Carboniferous time (Westphalian, 320 Ma). Apart from climatic influences, all the non-marine floras and faunas crossed freely from Gondwana to the northern continents.

Carboniferous time, non-marine mollusc faunas had crossed all the Variscan sutures in central Europe.

The Variscan orogen south of the Rheic suture (Fig. 1) was sufficiently uplifted before Westphalian D times, so that no Namurian or early Westphalian plant remains are known. However, well-documented late Westphalian floras occur in the Djerada Basin of Morocco (Jongmans 1952) and the Bechar Basin of Algeria (Jongmans & Deleau 1951; Migier 1982), which are very similar to the floras of the paralic basins in Britain and the Ruhr; they include *Paripteris pseudogiganta*, which Laveine *et al.* (1993) used to argue for strong links between North Africa and Europe during later Westphalian time. Further west, in northern Venezuela, Odreman & Wagner (1979) reported a fossil flora that is very similar to Westphalian D floras of Laurussia; these include material from the Upper Allegheny Formation of the Appalachians (Wagner & Lyons 1997), the Sydney coalfield of Nova Scotia (Zodrow 1986) and the Pennant Formation of Wales (Cleal 1997).

Late Carboniferous palynological data are not as definite as those of the Early Carboniferous period, but there is close similarity between Westphalian miospore assemblages from Europe and Africa, suggesting absence of the barrier to migration postulated in Viséan time.

The Westphalian plant distributions indicate that northern Gondwana was close to Laurasia (Fig. 5). Some of the best indicators of this proximity are the medullosalean pteridosperms, whose seeds could reach lengths of 100 mm (Gastaldo & Marten 1978) and can be transported by wind over only a few metres (Laveine *et al.* 1999). Postulating a wide ocean between these continents would require seed dispersal mechanisms that are unknown in Palaeozoic gymnosperms.

Conclusions

It can be demonstrated from both palaeontological and palaeomagnetic evidence that, after the Rheic Ocean closed in Emsian time, there were no wide oceans associated with the sutures in the European Variscides. In particular, the distributions of plants and freshwater faunas appear to be controlled by climate rather than by isolation. We conclude that the Variscides of Europe were more analogous to the present-day Mediterranean Sea than to the modern western Pacific.

We thank R. Feist and another referee for comments.

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