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# Palaeogeographical controls on the Cambrian trilobite immigration and evolutionary patterns reported in the western Gondwana margin

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## Abstract

Southward drifting of the western Gondwanan margin during the Cambrian has been demonstrated by means of both palaeomagnetic methods and lithological indicators of climate (such as carbonates and evaporites). Recent improvements in biostratigraphical correlations permit an enhanced understanding of the climatic and palaeobiogeographical constraints that controlled the distribution of Cambrian benthic communities. Palaeogeographical and biogeographical reconstructions based on trilobites are reported in this paper in order to test interaction between migration, speciation and extinction rates. The variability of the documented biogeographical patterns is directly related to species diversity, in which wider distribution coincides with transgressive trends and subsequent connection of neighbouring platforms. Early Cambrian trilobite faunas show a high degree of both substrate control and endemism, although transgressions led to parallel shifts in faunal compositions. By contrast, Mid-Cambrian trilobite faunas are relatively uniform across western Gondwana, and latest Mid- and Late Cambrian associations document influence of an increased similarity with Asian trilobite faunas.

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## 1. Introduction

Four disciplines are the main sources for palaeogeographical reconstruction: palaeomagnetism, sedimentology, palaeoclimatology, and biogeography. The boundaries of the postulated plates and terranes (commonly discussed from the viewpoints of geophysics, tectonophysics and

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structural geologists) do not always match the biogeographical boundaries worked out by palaeontologists and biostratigraphers. However, do the biogeographical boundaries that prevented reproductive communication necessarily coincide with those of the tectonic plates? In some cases they do; many plate and terrane boundaries, however, do not correspond with biogeographical barriers and, on the contrary, a single continental margin can display barriers, particularly during regressive conditions, which separate different groups of organisms that are significant biogeographically. As a result, a biogeographical unit contains similar biotas, but may or may not show physical continuity.

One of the main projects of the *International Subcommission on Cambrian Stratigraphy* (ISCS) is the proposal of a global chronostratigraphical chart useful for international correlation (see Geyer and Shergold, 2000, for a recent statement of the problem). One of the major difficulties is the resolution of the drastic provincialism exhibited by the benthic fauna, such as the trilobites (Palmer, 1998). From the earliest occurrences of trilobite faunas there is clear evidence of biogeographical differentiation into two main provinces: the olenellid province, comprising much of Baltica, Laurentia, and Siberia, and the redlichiid province of Gondwana (Palmer, 1972). Subsequently, an overlapping bigotinid province was distinguished (Pillola, 1991a). For the Mid- and Late Cambrian, Palmer (1972) reported a more complicated scheme involving four provinces for the continental seas, and three other ones for exposed shorelines. In addition, conodont distribution in the Late Cambrian indicates the presence of two faunal realms (Bergström, 1990), a tropical Midcontinent region and a cool Atlantic region.

One geographical area where the biostratigraphical correlations are still strongly debated is the western Gondwana margin, which includes the Mediterranean area and much of western and central Europe. Geophysical data that would indicate Cambrian plate boundaries are scarce within this area. However, biogeographical disparities based on detailed and extensive trilobite studies reflect major palaeogeographical differences and relative sea-level fluctuations. Although theoretic-

ally the reproductive communication of trilobites was maintained by means of larvae, the Cambrian trilobite-based biogeographical patterns of the western Gondwanan margin, as it drifted towards the South Cambrian pole, are not homogeneous, and the changes in patterns of dispersal and evolution of some trilobite families remain uncertain. This paper offers an examination of the biogeographical patterns displayed by the Cambrian trilobites on the western margin of Gondwana, as a method of testing the established palaeogeographical models.

## 2. Basins and platforms: a nomenclatural approach

The Moroccan and European Hercynian (or Variscan) massifs, the latter located south of the Rheno–Hercynian zone and north of the Alpine realm (Fig. 1), contain a mosaic of Cambrian successions assigned to the western Gondwanan margin, namely Morocco, the Iberian and Armorican massifs, Montagne Noire, Sardinia, Saxo–Thuringia and Bohemia. Associated with the same margin are other small cratonic domains recognised in the southern British Isles; some of their boundaries are less well-defined (Cocks et al., 1997).

### 2.1. Morocco

The Neoproterozoic(?)–Cambrian successions of the Moroccan Atlas are located in the Anti-Atlas and central High Atlas mountains, although some disconnected outcrops occur in the Jbilet and Rehamna regions, and the Meseta plateau. The axis of the Late Proterozoic to Early Palaeozoic Souss Basin (Geyer, 1989) roughly coincides with the modern trend of the Anti-Atlas (SW–NE). Common west-to-east facies changes throughout the Cambrian successions reflect the eastern setting of proximal areas (Destombes et al., 1985; Geyer and Landing, 1995; Geyer et al., 1995).

### 2.2. The Iberian Massif

The Cambrian tectonosedimentary outcrops of the Iberian Massif were subdivided by Lotze

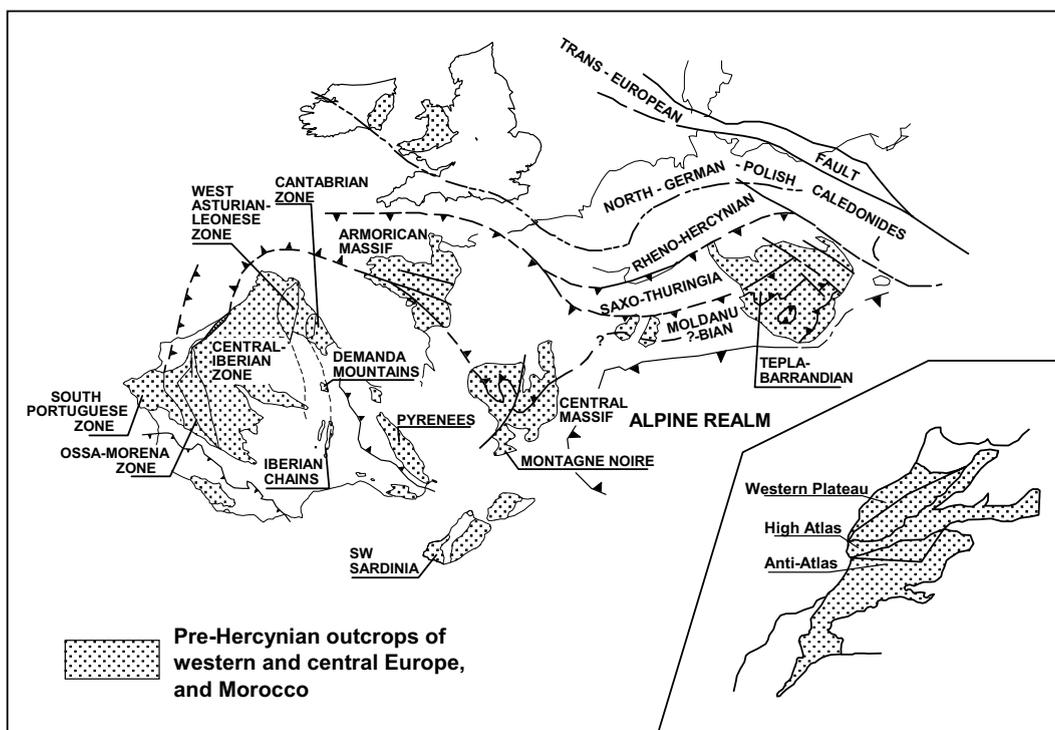


Fig. 1. Main tectonostratigraphical units of the Variscan Belt (modified after Franke, 2000), and northwestern Africa.

(1961) into zones, viz. the Cantabrian (CZ), Western Asturian–Leonese (WALZ), Central Iberian (CIZ) and Ossa–Morena (OMZ) zones. Their evolution has been interpreted in terms of two distinct troughs: the Cantabro–Iberian and the Andalusian basins, the latter including the OMZ. The Cantabro–Iberian Basin comprises the CZ, WALZ, northern CIZ, and their eastern prolongation into the Demanda Mountains (DM) and the Iberian Chains (IC). It was limited to the NE by the Cantabro–Ebroan Land area, which constituted the main source of sediments for both the Cantabro–Iberian and the Pyrenean basins (Carls, 1983), and in the SW by some uplifted areas (or median highs; Lotze, 1961), which episodically supplied sediments (Aramburu et al., 1992).

The geodynamic affinity of the OMZ is still controversial. One hypothesis supposes its accretion to the Iberian Autochthon (which would include the rest of northern zones) during the Cadomian orogeny (Quesada, 1991), whereas an-

other hypothesis considers the Iberian Massif as a complex tectonic mosaic constructed from two distinct plates that collided during the Early Devonian (Acadian orogeny; Martínez-García and Rolet, 1991). Because of this discussion, and the displacement of the OMZ from NW to SE along the Badajoz–Córdoba shear zone during the Hercynian orogeny, we will illustrate the OMZ as a neighbouring basin of the western Gondwanan margin.

### 2.3. The southern British Isles ('eastern Avalonia')

The main structural elements are the Midland Platform, bounded to the NW and NE by depositional troughs, and truncated to the south by the Hercynian front. The trough to the NE is the concealed 'Eastern England Caledonide Belt', in which Cambrian rocks of the Tornquist Sea may be present, but have not been proven. To the NW of the Midland Platform lies the Welsh Trough, an elongated ensialic basin that experienced sub-

sidence throughout much of the Cambrian Period. The Welsh Trough is limited to the NW by the tectonically active Monian Terranes that behaved as a positive area through the Cambrian, and which separate the Welsh Trough from the Leinster Basin of SE Ireland (Bluck et al., in Cope et al., 1992); the latter contains Cambrian rocks but has not yielded any trilobites. To the north, the Cambrian of Scotland is part of Laurentia, and is not discussed further here.

The Cambrian of England and Wales is developed in three main facies: (1) basinal clastic deposits of the Welsh Trough, exposed in two main areas in northern Wales (Harlech Dome and Arfon) and two in the south (St. David's and Llangynog areas); (2) outer-shelf clastics on the Midland Platform (Nuneaton); and (3) shallow-water clastics with very local limestones in the Welsh Borderland (Comley and Rushton areas), on the margin of the Midland Platform. The geology of these areas was reviewed by Rushton (1974) and Rushton et al. (1999), and the palaeogeography was summarised by Brasier et al. (in Cope et al., 1992). McKerrow et al. (1992) showed eastern Avalonia located close to Morocco at a latitude of about 40°S in the Early Cambrian, drifting south to about 60°S in the Late Cambrian (L.R.M. Cocks, pers. commun., 2002).

#### 2.4. *The Armorican Massif*

The Cambrian of the Armorican Massif consists dominantly of siliciclastic deposits. The facies strongly depends on the local position on the shelf and includes locally Lower Cambrian carbonates deposited in nearshore environments. Its apparent polar wander path can be superimposed across the Neoproterozoic–Early Palaeozoic interval on the Gondwana path. A counter-clockwise rotation of the massif has been proposed for Early Palaeozoic times (Young, 1990), based on sedimentological and palaeogeographical similarities with some Portuguese outcrops.

#### 2.5. *The Montagne Noire and southwestern Sardinia*

To the north of the Cantabro–Ebroan Land

area, a mosaic of platforms is represented in the Cambrian outcrops of the Pyrenees and Montagne Noire. The Cambrian stratigraphical and biogeographical patterns of southwestern Sardinia reveal a close similarity to the Montagne Noire so that this platform can be considered neighbouring the Montagne Noire segment at that time.

#### 2.6. *Saxo–Thuringia and Bohemia*

According to Havlíček et al. (1994), both the German and Barrandian (an area situated in the central part of the Bohemian Massif) Cambrian deposits belong to the ‘Perunica terrane’. This crustal segment was defined as a separate microplate occupying ‘the major part of the Bohemian Massif, and involving the Moldanubian, Barrandian and Saxothuringian (Saxothuringian–Lugian) Zones’ (Havlíček et al., 1994). This interpretation was based on biogeographical affinities of benthic faunas with those of Baltica and a northward drift of Perunica from high (57.9°S for the Lower Cambrian Paseky Shale) to lower latitudes (31.1°S for Middle Cambrian sediments and 28.6°S for Upper Cambrian andesites; Krs et al., 1987; Vrána and Štědrá, 1997). By contrast, Kukal (1971) assumed a semi-arid, rather warm climate of continental type for the Lower Cambrian. The Barrandian palaeolatitude setting has been widely debated. Recently, Linnemann et al. (2000) revised the concept of Perunica, eliminating the Saxo–Thuringia area; they distinguished the Brittany–Normandy, Perunica and Saxo–Thuringia terranes, which would form the so-called ‘Armorican Terrane collage’. Discussion about the existence of these microplates is beyond the aims of this paper. Nonetheless, two tectonostratigraphical areas are considered here: the Barrandian and Saxo–Thuringian areas. The latter comprises a fault-bounded crustal fragment that contains Cambrian outcrops in the Doberlug Syncline, Thuringia and the Franconian Forest area. The palaeogeographical affinity of the Görlitz Syncline offers some uncertainties but is here considered as a relic of an overlapping succession on the Cadomian basement of Saxo–Thuringia.

In the Barrandian area, a distinct Cambrian sedimentary trough, the Příbram–Jince Basin, is

commonly recognised. It contains a thick Lower Cambrian continental succession covered by Middle Cambrian, transgressive marine fossiliferous shales (the Jince Formation), and Upper Cambrian volcanoclastic complexes. Laterally, the Jince Formation crops out in the Skryje–Tyřovice area. In the biogeographical discussions expressed below, the trilobites of the Skryje–Tyřovice area will be reported with those of the Příbram–Jince Basin.

### 3. Cambrian palaeogeographical evolution: an overview

Lack of uniformity in the successions of faunas and depositional environments in the western Gondwanan margin has led to the development of different regional biostratigraphies (Fig. 2). In order to avoid nomenclatural confusion in chronostratigraphical correlations, we here use a com-

bination of the Cambrian Moroccan and Iberian scales for the Lower Cambrian, and the Iberian–Montagne Noire scale for the Middle Cambrian. The sparse Upper Cambrian faunas are related to the Australian succession, though in Britain there are sufficient olenid trilobites to correlate with the Scandinavian succession. For Britain, the stratigraphical classification used in Cowie et al. (1972) is employed because it supplies a single standard for England and Wales and facilitates reference to Rushton’s (1974) stratigraphical summary. It is recognised that the lower two of the British regional series divisions – Comley and St. David’s series – do not correspond precisely with the usage of Lower and Middle Cambrian in use elsewhere, the inter-series boundary lying rather higher than the Lower–Middle Cambrian boundary in Morocco (Geyer, 1990a). The base of the Merioneth Series corresponds closely to that of the Upper Cambrian as generally understood and its top lies very close to the internationally

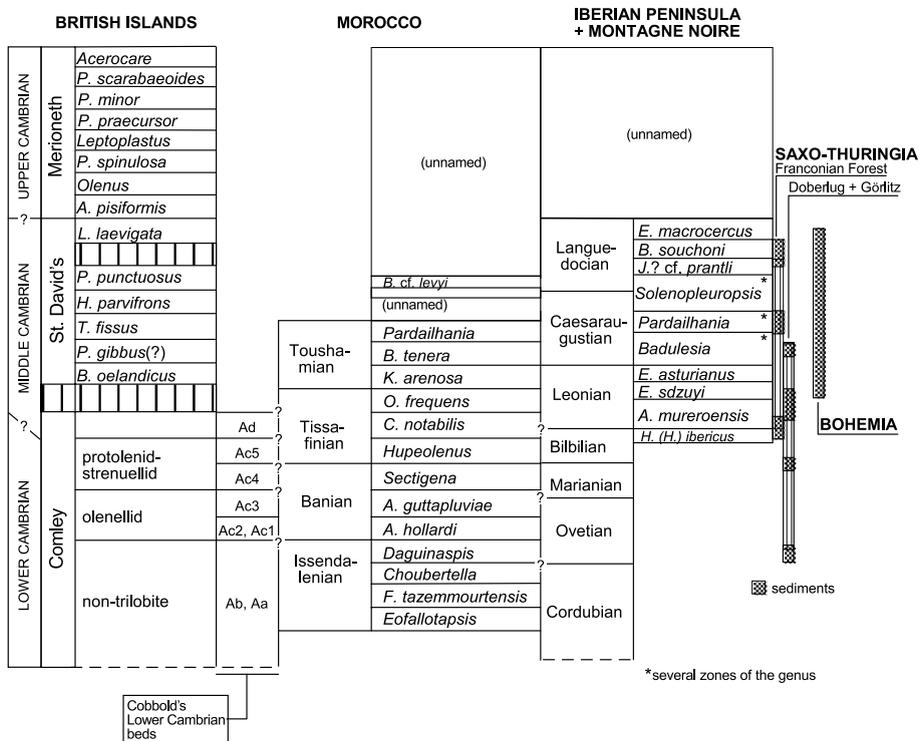


Fig. 2. Chronostratigraphic correlation of regional charts (based on Thomas et al., 1984; Geyer, 1990a; Álvaro and Vizcaïno, 1998; Szduy et al., 1999; Geyer and Shergold, 2000).

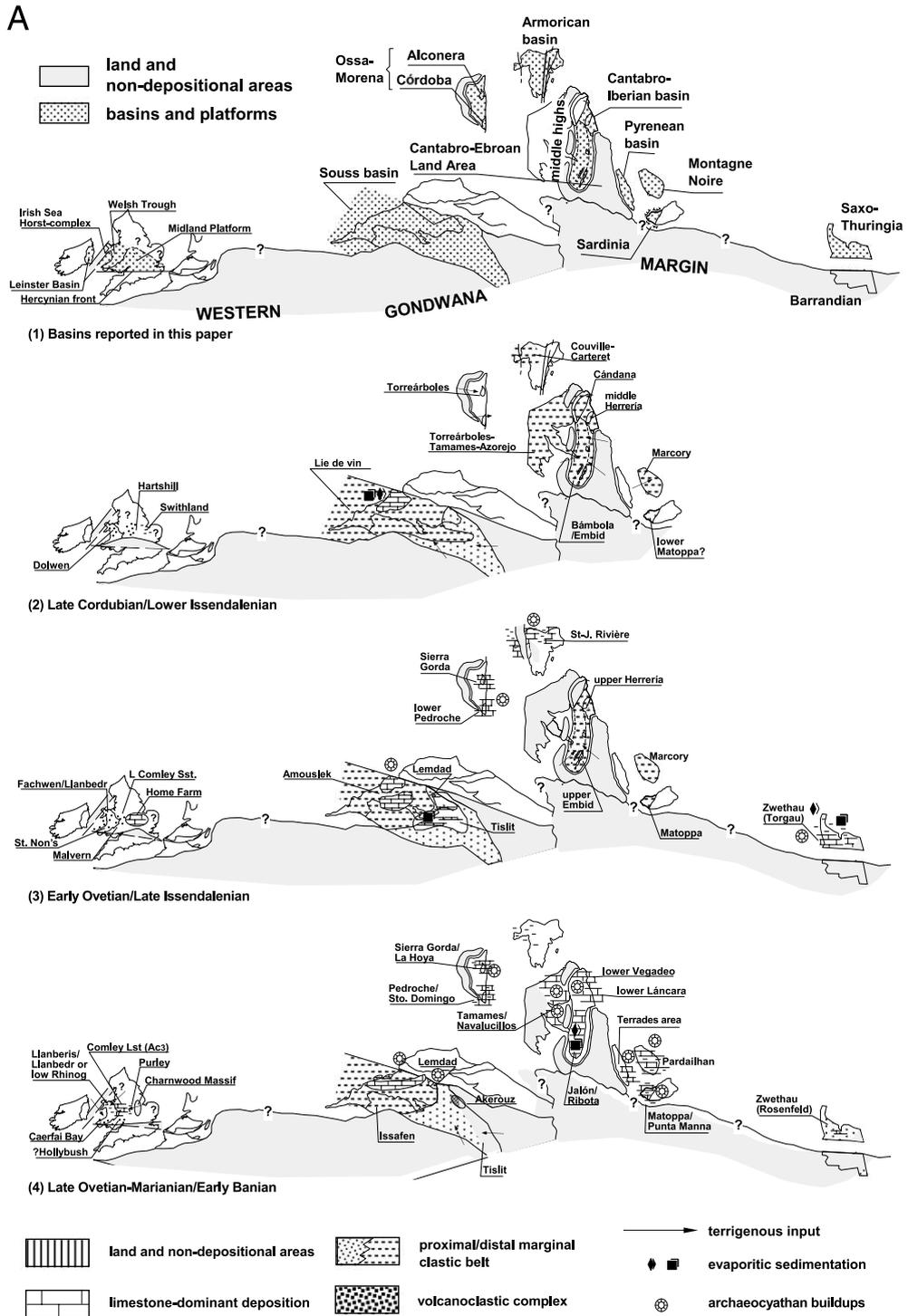


Fig. 3. Palaeogeographical evolution interpreted in the Cambrian basins and platforms of the western Gondwanan margin across eight intervals (not to scale).

B

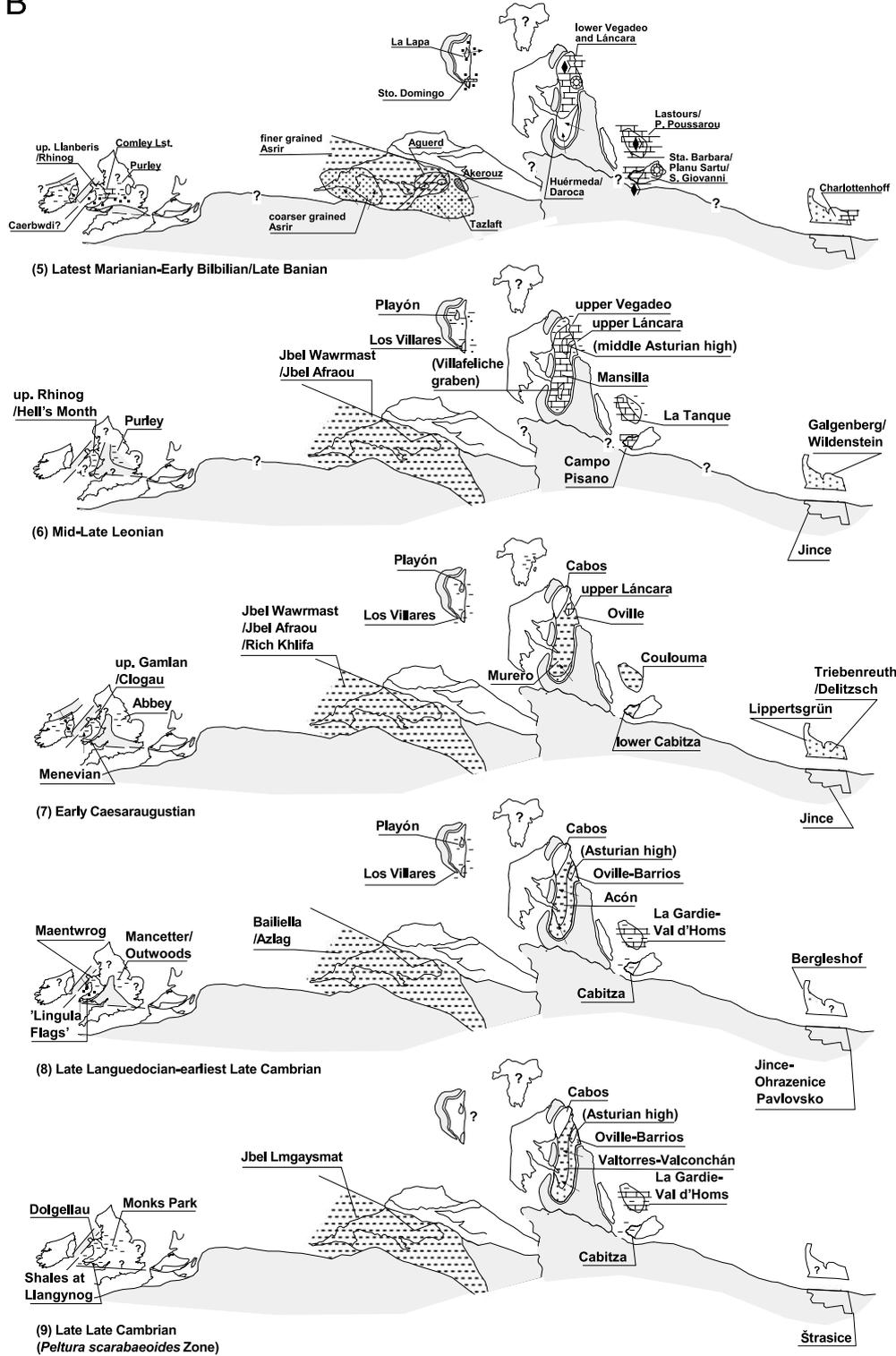


Fig. 3 (Continued).

agreed base of the Ordovician (Landing et al., 2000). Fig. 3A,B provides graphic representation of the changing palaeoenvironmental relationships discussed on the following pages.

### 3.1. Morocco

The Late Proterozoic ('Panafrican') orogeny in Morocco and northwestern Africa was followed by deposition of a Neoproterozoic(?)–Cambrian cover succession that illustrates a long-term transition in lithofacies associations, and includes a thick interval (locally more than 2000 m) of carbonate-dominated rocks followed by siliciclastic-dominated rocks higher in the Cambrian in the western Anti-Atlas. The Neoproterozoic(?)–Cambrian transition in this region, viz the Adoudou, Lie de vin, and Igoudine Formations, is dominated by restricted marine platform limestones and dolostones, and is overlain by a long-term shale–carbonate cycle in the Lower Cambrian, the Amouslek Formation. Uppermost Lower Cambrian units include up to 200 m of fine-grained siliciclastics with relatively minor nodular and bedded limestones (Issafen Formation), overlain by the higher energy, shallow-marine, sandstone-dominated facies of the Asrir and Tazlaft Formations, which characterises the Lower–Middle Cambrian transition. This period reflects a significant change in sedimentation, related to an important phase of relative sea-level fluctuation which caused a major regression followed by an immediate transgressive event (Geyer, 1989; Geyer and Landing, 1995).

Limited carbonates also characterise the lower Middle Cambrian. Fossiliferous limestone beds are regularly encountered only in the 'Brèche à *Micmacca*' Member (lower part of the Jbel Wawrmast Formation, up to 300 m thick). Progressively stronger, higher-latitude influences are shown by the thick shallow-marine deposits that accumulated during most of the Mid- and Late Cambrian; they are a monotonous succession, up to 700 m thick, of siliciclastic sediments representing sandy shoals and tidal-flat environments as well as fluvial to deltaic environments prograding on distal muddy substrates (Jbel Afraou, Rich Khli-fa, *Bailiella*, Azlag, and Jbel Lmgaysmat Forma-

tions). The late Late Cambrian is unknown from the Moroccan Atlas but appears in part to be characterised by some 115 m of shallow-marine fine-grained siliciclastics (Dar Bou Azza Formation) in the Moroccan Meseta (Mergl et al., 1998). In this area this unit overlies a significant unit of 100 to 200 m of sandstones representing another important regressive unit of apparently earliest Late Cambrian shoreline deposits, the El Hank Formation.

### 3.2. The Iberian Massif

The Cambrian rocks rest unconformably on Neoproterozoic rocks in the whole massif except in the CIZ, where the Vendian–Cambrian transition is tentatively located in the Pusa Shales (Brasier et al., 1979). The transition contains megabreccias, conglomerates, quartzites, limestones and anoxic sediments deposited in a mixed shelf and slope apron (Valladares, 1995). The Cambrian commences with a dominantly terrigenous succession (or lower lithosome): the Herrería Formation, 900–1700 m thick, in the CZ, representing deltaic deposits with fluvial and intertidal episodes (Rodríguez Fernández et al., 1991); the Cándana Group, up to 2500 m, in the WALZ with shallow-water marine and continental facies (Crimes et al., 1977); the Tamames–Azorejo Formations in the CIZ, 500–600 m thick; the Torreárboles Formation, 0–350 m thick, in the OMZ with shallow subtidal and intertidal deposits; and the Bámbola and Embid Formations, 500–900 m thick, in the IC, interpreted as progradational deltaic systems and storm- and wave-dominated nearshore settings passing upward into tidally influenced subtidal and intertidal environments. During Early Cambrian times, the OMZ displayed the setting of rifting processes (Vegas, 1978; Mata and Munhá, 1990).

The second lithosome reflects the diachronous establishment of mixed carbonate–siliciclastic platforms, ranging from Ovetian to early Mid-Cambrian times: the lower member of the Lán-cara Formation (150–225 m thick) in the CZ, and the Vegadeo Formation (50–500 m) in the WALZ, displaying peritidal to shallow-water deposits with isolated microbial–archaeocyathan

buildups (Zamarreño, 1972; Russo and Bechstädt, 1994; Álvaro et al., 2000b). Mixed platforms were established across the late Ovetian–Marianian interval in the IC (the Jalón, Ribota and Huérmeda Formations; 300–500 m thick), Los Navalucillos and Tamames Limestones in the CIZ (120–600 m thick), and the Pedroche and Alconera Formations in the OMZ (350–900 m thick). These contain stromatolitic and archaeocyathan-microbial buildups, sandstones and variegated shales deposited in shallow subtidal to intertidal and supratidal environments; locally they bear anhydrite or gypsum pseudomorphs (see Álvaro et al., 2000a, and references therein). By contrast, the mixed sedimentation of the second lithosome was interrupted in the IC, CIZ and OMZ by early Bilbilian regressive siliciclastic sediments related to the Daroca regression (Álvarez and Vennin, 1998), lithostratigraphically recognised as the Daroca (IC), Los Cortijos–Endrinal (CIZ) and Castellar (OMZ) Formations (50–150 m thick). An early Bilbilian prograding shoreline is postulated in these areas, in which coastal and shoal complexes grew and migrated seawards during times of rapid sediment influx and regressive conditions.

The Lower–Middle Cambrian transition is characterised by a significant change in the style of sedimentation, related primarily to an important phase of tectonic activity. As a result, an irregular topography was widely developed on the platforms, which were differentiated into a mosaic of horsts and grabens. In situ carbonate production on relative topographic highs gave rise to the ‘griotte’ facies of the upper member of the Láncara (CZ) and Mansilla (IC) Formations.

The third lithosome reflects the disappearance of carbonate deposition in the whole Iberian Massif; it is interpreted as shallow platform deposits of intertidal and braid-plain deltaic environments in the Oville Formation (80–800 m) and the lower part of the Barrios Formation (300–400 m thick) in the CZ (Aramburu et al., 1992; Aramburu and García-Ramos, 1993), the shallow-marine deposits of the Cabos Series (up to 4000 m thick; Baldwin, 1977; Marcos and Pérez Estaún, 1981), and the Murero Formation, Acón Group and Valconchán Formation in the IC (600–1400 m thick)

representing storm-dominated offshore, prograding sandy shoals, and tidal-flat environments (Álvarez and Vennin, 2001).

### 3.3. *The southern British Isles*

In the southern British Isles, Cambrian rocks occur in England and Wales in scattered inliers, the largest of which are: (1) the Harlech Dome (and the St. Tudwal’s Peninsula), and the Arfon area of northern Wales; (2) Pembrokeshire in south Wales; (3) a number of small outcrops in Shropshire; (4) the Malvern Hills; and (5) the Nuneaton area in Warwickshire, British Midlands.

The lithostratigraphical successions of these areas differ greatly. The relatively thick and comparatively complete succession of northern Wales includes Lower Cambrian deposits consisting of >450 m of deltaic sandstones (Dolwen Grits) overlain by up to 200 m of prodeltaic shales (Llanbedr Slates), and a formation of up to 800 m of proximal turbiditic sandstones with shale intercalations (Rhinog Grits). Middle Cambrian deposits are generally basinal turbiditic sandstones and shales, together about 700 m thick, capped by 100 m of dark fossiliferous shales. Manganese-bearing rocks occur close to the base of the Middle Cambrian. The Upper Cambrian consists of 2000 m of fine-grained shales (or slates) and feldspathic flags, capped by a condensed unit of black mudstone, the Dolgellau Formation, about 100 m thick. The lower Upper Cambrian (Maentwrog Formation) is basinal, but the Festiniog and Dolgellau are open-shelf deposits.

The successions in Pembrokeshire show a comparable depositional sequence, commencing with the Lower Cambrian Caerfai Group, about 300 m thick, consisting of sandstones and shales overlying a transgressive basal conglomerate deposited in a shallow-marine, continuously subsiding basin. A depositional break testifies a regressive trend near the top of the group. The lower Middle Cambrian Solva Group consists of roughly 500 m of sandstones and shales deposited in relatively high-energy waters, whereas the upper Middle Cambrian, about 250 m of pyritous mudstones,

termed the Menevian Group, suggests quiet, oxygen-depleted environments. The Upper Cambrian ‘*Lingula* Flags’ (more than 600 m thick) are shallow-water storm-influenced deposits of a rapidly subsiding marine basin.

The shelf deposits in the English Midlands commence with Early Cambrian sandstones, the Hartshill Formation (260 m thick), which shows progressive deepening from a basal shoreface sand. There follow 600 m of outer-shelf mudstone, the Stockingford Shales, which extend from the higher Lower Cambrian to the top of the Upper Cambrian. The upper Middle Cambrian and the uppermost Upper Cambrian show strong lithological and palaeontological similarities to the correlative rocks in Wales, though the formations are thinner. The upper Middle Cambrian to Tremadoc succession is relatively complete. The successions in Shropshire, on the margin of the Midlands Platform, partly deposited in fault-bounded depocentres (Smith and Rushton, 1993), suggest the influence of shallow water almost throughout. At the top of the Comley Series are the condensed Comley Limestones that represent shallow-marine carbonates containing the best preserved and most important late Early Cambrian (in the traditional British sense) trilobite faunas of the British Isles.

In summary, the lowest Cambrian deposits were deposited unconformably on a variegated volcanic basement in both Wales and England, whereas younger Cambrian sediments in Wales formed in a subsiding ensialic basin, while their English equivalents formed on the subsiding Midland Platform.

### 3.4. *The Armorican Massif*

The Cambrian rocks of the Armorican Massif unconformably overlie the Cadomian basement. The most representative and complete Lower Cambrian succession is that of the North Contentin Syncline. A SW–NE-trending trough was filled by a succession ranging from 590 to 2100 m in thickness (Doré, 1994) with, from bottom to top: (1) the Couville Formation, up to 400 m thick, composed of conglomerates and sandstones interbedded with a volcanoclastic complex; (2) the

Carteret Formation, ca. 1000 m, consisting of littoral alternations of shales and silty sandstones rich in microfossils and ichnofossils of Cordubian age; and (3) the Saint-Jean-de-la-Rivière Formation, ca. 200 m thick, made up of peritidal alternations of limestones and siltstones, containing salt pseudomorphs, microbial–archaeocyathan buildups and oolitic shoals. Other Lower Cambrian successions are known in central and southern Normandy and Maine, and comprise small shelly fossils, brachiopods and ichnofossils. A post-orogenic volcanism took place along two volcano–tectonic structures: ignimbrite sequences underlying Lower Cambrian sediments, and the Maine graben interbedded with Lower Cambrian to Arenig? sediments. Other Cambrian fossiliferous rocks are incompletely known, such as a Middle Cambrian trilobite assemblage from the north-eastern Vendéan Massif and a suspected Late Cambrian brachiopod assemblage from the Chantonay synclinorium.

### 3.5. *The Montagne Noire and southwestern Sardinia*

Both areas display the same three-fold lithosome subdivision as that reported in the CZ and WALZ for Early to Mid-Cambrian times. The Neoproterozoic–Cambrian transition is not clearly identified in the former, where the lower terrigenously dominated lithosome begins with the Marcory (more than 1000 m thick) and Matoppa (300–600 m) Formations. The second, Ovetian–Bilbilian, lithosome represents the establishment of carbonate platforms; in the southern Montagne Noire these are subdivided into the Pardailhan, Lastours and Pont de Poussarou Formations (100–500 m thick), and in Sardinia the Punta Manna, Santa Barbara, Planu–Sartu and San Giovanni Formations (600–1200 m thick). These platforms were widely colonised by buildups of microbial–archaeocyathan communities, associated in Sardinia with a tensional tectonic activity reflecting the establishment of an isolated carbonate platform (see a summary in Perejón et al., 2000). In both areas the Lower–Middle Cambrian transition displays the tectonic instability already reported in the CZ and the IC, with de-

velopment of palaeotopographies and deposition of the ‘griotte’ facies (La Tanque and Campo Pisano Formations; up to 80 m thick). After drowning of the platforms and burial of the palaeotopography by offshore shaly sediments (Coulouma and lower Cabitza Formations; 30–80 m thick), the evolution in both areas differed drastically. The southern Montagne Noire exhibits the progradation of sandy shoals (Ferrals Formation; 130–200 m thick) and tidally induced systems (La Gardie Formation; 0–500 m thick), followed by important carbonate developments leading to deposition of new mixed carbonate–siliciclastic sediments on intra-shelf ramps (Val d’Homs Formation; 60–200 m thick). This episodic carbonate sedimentation is unique across the whole western Gondwanan margin for Late Cambrian times. By contrast, southwestern Sardinia shows a Middle–Upper Cambrian shale-dominated deposition (Cabitza Formation), distinctly condensed and remarkably uniform (ca. 190 m thick; [Loi et al., 1995](#)), which gradually passes into the Tremadocian.

### 3.6. Saxo–Thuringia

Lower and Middle Cambrian successions occur in the Doberlug–Delitzsch and Görlitz synclines, the Franconian Forest and Thuringia (Berga Anticline). Early Cambrian relationships between them are controversial because they are of different ages and the limited occurrence of fossils. Upper Cambrian successions are generally not preserved, as a result of uplift combined with denudation and weathering ([Linnemann and Buschmann, 1995](#)). The incomplete Early Cambrian succession of the Doberlug Syncline represents a carbonate ramp with archaeocyathan-microbial buildups (Zwethau Formation, more than 700 m thick) developed during early Ovetian times on the Cadomian basement of Saxo–Thuringia ([Elicki, 1999](#)). The Lower–Middle Cambrian transition is unknown because of the scarcity of outcrops and structural difficulties. The Middle Cambrian of the Doberlug area (Tröbitz and Delitzsch Formations, ca. 600 m thick), early Leonian–Caesaraugustian in age, is relatively fossiliferous ([Sdzuy, 1972](#)). The sediments were

deposited on an open siliciclastic platform. The Middle Cambrian of the Franconian Forest consists of isolated outcrops that represent at least five different formations, in ascending order the Galgenberg, Wildenstein, Triebenreuth, Lippertsgrün and Bergleshof Formations, of unknown thickness, all characterised by significant trilobite faunas.

The Early Cambrian of the Görlitz Syncline is very incomplete, but has yielded important trilobites. The Charlottenhof Formation is a fragment of a carbonate platform and represents the transition from rather shallow to deep subtidal conditions (Ludwigsdorf Member) and subsequently to deeper platform environments (*Lusatia* Member). The age of the formation is late Marianian or late Banian ([Elicki, 1994](#); [Geyer and Elicki, 1995](#)). Finally, the Cambrian (s.l.) of Thuringia (Berga Anticline) is known only from two boreholes: it is a slightly metamorphosed carbonate succession that has yielded a poorly preserved microfauna, with siliciclastic deposits at the base ([Elicki, 1997](#)).

### 3.7. Bohemia

The Příbram–Jince Basin of the Barrandian area contains about 2000 m of Lower Cambrian continental conglomerates and sandstones, punctuated by the deposition of sediments in a brackish environment (the Paseky Shale) containing endemic merostome(?) arthropods and possibly phyllocarids ([Chlupáč, 1995](#)). Deposition of Middle Cambrian transgressive marine fossiliferous shales was accompanied by two major palaeogeographical changes: (1) an eastward shift of the area of maximum subsidence, and (2) a change in orientation of the main structural directions and longitudinal basin axis from a NE–SW to a NW–SE trend ([Havlíček, in Chlupáč et al., 1998](#)). The Jince Formation (up to 400 m thick) consists of shales and fine-grained sandstones containing a rich and diverse fossil fauna of trilobites, brachiopods and echinoderms. The unfossiliferous Upper Cambrian deposits consist of volcanic complexes with rhyolitic effusions and pyroclastic layers. In the Skryje–Tyřovice area, the Cambrian succession consists only of the lower part of the Jince

Formation, which rests unconformably on Upper Proterozoic rocks. These outcrops reflect a Middle Cambrian deposition in a ‘channel-like’ trough affected by synsedimentary deformation and partly eroded during Upper Cambrian regressive conditions. The thickness of the Middle Cambrian decreases from about 200 m in Skryje to several tens of metres towards the northeast.

#### 4. Palaeoceanographic and palaeoclimatic constraints

The western Gondwanan margin during the Cambrian is commonly portrayed as oriented approximately SW–NE in a position on the Southern Hemisphere (McKerrow et al., 1992). As a consequence of this orientation, the shape of the tropical zones was affected by the course of major ocean currents transporting cool waters towards the tropics (Fig. 4). This would have caused the tropics to occupy a narrower latitudinal area on this western margin compared with the eastern margins (Briggs, 1995). This inferred palaeogeographical situation may be compared with that of the western Australian margin during the Eocene (McGowran et al., 1997), when Australia and Antarctica were close enough to prevent the development of a circum-Antarctica circulation. As a result, two main surface circulation patterns took place: a South Equatorial Current flowing (up to the Recent) as a low-salinity surface component of the global thermocline system, and a

western Australian Current (parallel to the western face of Australia) that disappeared with the Eocene opening of a gap between both continents. Apparently a similar western Gondwanan SW–NE current rising in latitude from polar areas operated during Cambrian times, which obviously affected faunal migrations and the palaeoclimates.

The lack of extensive carbonate deposition across the Precambrian–Cambrian transition in the western Gondwanan margin, except the Adoudou and Lie-de-vin Formations in Morocco, can be explained by a combination of active Cadomian orogenic phases, and active source regions, which supplied coarse-grained siliciclastics and inhibited carbonate production. Much of our understanding of the Lower Cambrian palaeoclimate evolution on the western Gondwanan margin comes exclusively from lithological indicators of climate, such as limestone (mainly reefal) and evaporite precipitation (Álvaro et al., 2000a). Lower Cambrian salinities seem to have been episodically and locally high enough to generate widespread deposition of evaporates, suggesting a generally subtropical arid climate. Although an Early Cambrian warm period has been claimed, global warming does not necessarily imply a poleward shifting of isotherms but might reflect their spacing when thermal gradients became flatter.

During Early and earliest Mid-Cambrian times, the western Gondwanan margin was rimmed by enormously extensive shallow-water subtropical platforms, where carbonate deposition was some-

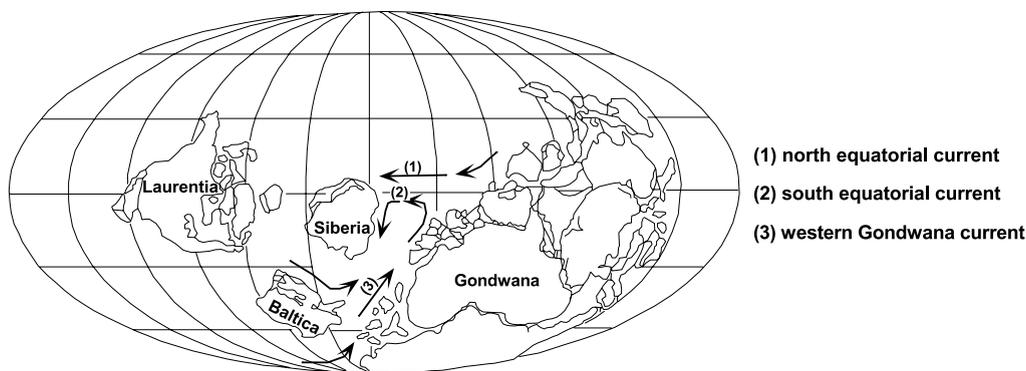


Fig. 4. Global Cambrian palaeogeography (modified after McKerrow et al., 1992) and proposal of palaeocurrents discussed in the text.

times outpaced by local, craton-derived terrigenous clastic sediments. As a result, the proportion of carbonate and siliciclastic rocks varies both regionally and stratigraphically. Incursions of shale onto the platforms is commonly related to sea-level rises, when the remobilisation and transport seaward of fine-grained siliciclastic sediments outpaced carbonate production. By contrast, regressive trends are represented by basinward shifts of peritidal deposits in carbonate and mixed platforms, and deltaic and coastal plain dilution related to terrigenous influx on platforms close to continental sources. For instance, the siliciclastic deposition related to the Daroca regression during the earliest Tissafrican or early Bilbilian age, affected the Souss Basin, the OMZ, CIZ and IC platforms, but was absent in the CIZ, WALZ, Montagne Noire and southwestern Sardinia platforms.

Despite the lack of lithological indicators for the climate during the Mid- to Late Cambrian, a transition from carbonate-dominated rimmed platforms to siliciclastic temperate- to cool-water platforms is attributed to changing oceanographic conditions across the Lower–Middle Cambrian transition. The southward-moving warm tropical waters of western Gondwana progressively invaded cold seas; as a result, Middle Cambrian sediments reflect a transition to temperate-water platform sediments. In a study of the Cambrian Iberian platform (IC), Álvaro and Vennin (2001) described a succession of benthic communities interpreted to have developed during a cooling period. This cooling trend, from subtropical to temperate waters, was marked by the successive decline and disappearance of: (1) ooids, evaporite relics and microbial carbonates; (2) eocrinoid-sponge meadows; (3) hydrodynamic bioclastic carbonates related to the contraction of carbonate factories into increasingly narrow belts ('griotte' facies); and there are trends to (4) an increase of trilobite-dominant communities on muddy bottoms; and (5) to decreasingly fossiliferous communities, then dominated by linguliform brachiopods in sandy shoals. The Languedocian–Late Cambrian interval seems to mark the culmination of the cooling trend as shown by the pervasive decrease in diversity, associated with the drastic

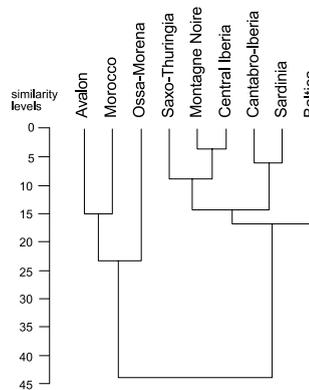
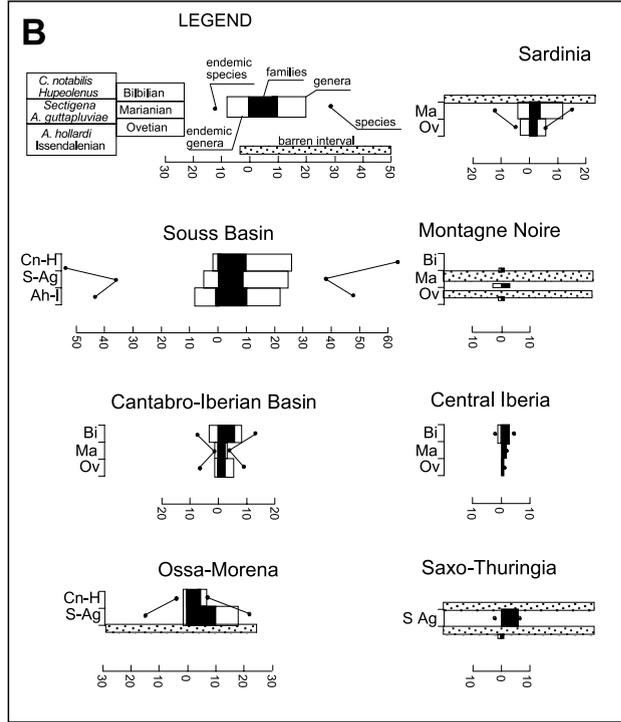
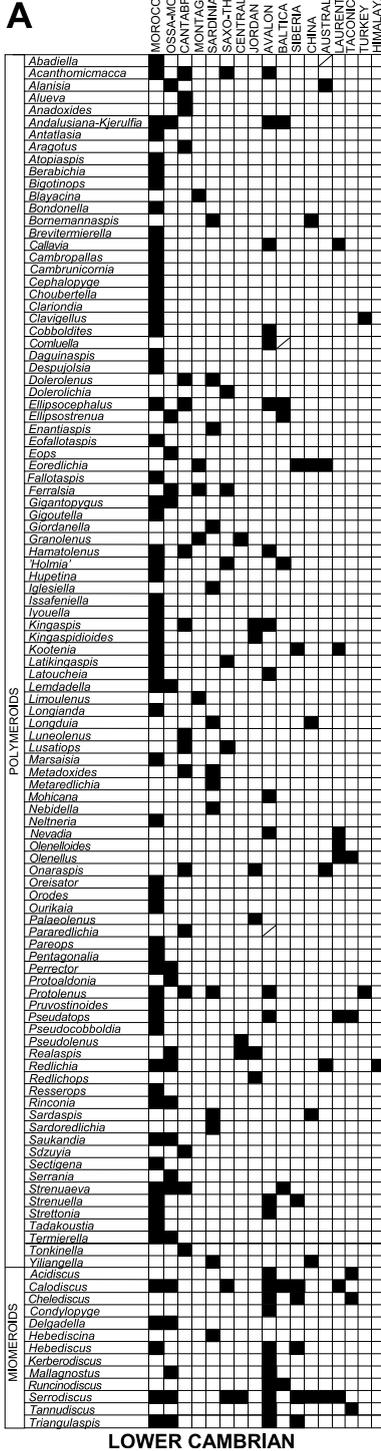
disappearance of bioclastic carbonates. On the other hand, the development of Late Cambrian isolated carbonate platforms within temperate-water settings of the southern Montagne Noire (Val d'Homs Formation) signals short-lived warming episodes in meridional parts of the western Gondwana margin extending into Tremadocian times.

## 5. Biogeographical patterns

### 5.1. Lower Cambrian

The Lower Cambrian has for a long time been based on the concept of being characterised by the earliest Phanerozoic fossils. Brögger (1886) and subsequently Walcott (1891) developed the idea of a Lower–Middle Cambrian boundary based on the first appearance of the trilobite genus *Paradoxides* (s.l.) in Baltica and the disappearance of *Olenellus* (s.l.) in Laurentia. The lower boundary of the Cambrian was not fixed with any precision but in early days was assumed to coincide roughly with the first appearance of trilobites. Since 1974 work by the *International Subcommission on Cambrian Stratigraphy* has changed this concept. Incorporation of strata with 'primitive' Metazoan sclerites of uncertain systematic affinities (the so-called small shelly fossils) pushed down the level of the Cambrian lower boundary considerably. In the present concept, the earliest Cambrian strata are characterised by rocks with the first diversified trace fossil assemblages that underly strata with small shelly fossils. As a result, the Lower Cambrian was extended dramatically and the trilobite-bearing strata represent less than half of Early Cambrian time as presently understood (Landing, 1994; Landing et al., 1998).

In the Lower Cambrian, the ideal of a global biostratigraphy and palaeobiogeography suffers from both a relatively limited diversity of trilobites and their pronounced endemism. Furthermore, the distribution of trilobites is, from the earliest times, strongly controlled by facies, so that even a precise interregional correlation is difficult. The most complete Early Cambrian trilo-



**C**

bite succession of western Gondwana, with relatively diverse trilobite faunas from various biofacies, comes from the Moroccan Atlas ranges (Fig. 5A), with more than 200 trilobite species described from Lower and lowermost Middle Cambrian strata. This area clearly is the key for our understanding of the Lower Cambrian palaeobiogeography of western Gondwana and the neighbouring regions. Historically, this is the region where the first elaborate Lower Cambrian biozonation was developed (Hupé, 1952). The Lower Cambrian to lowermost Middle Cambrian biostratigraphy of Morocco now comprises ten biozones assigned to three stages (Fig. 2), which are all characterised by significant trilobite faunas and separated by faunal turnovers (Geyer, 1990a; Geyer and Landing, 1995).

Recent correlations suggest that the earliest trilobites from the lowermost Issendalenian Stage pre-date other trilobite occurrences in western Gondwana and are among the first trilobites known so far on a global scale (Sdzuy and Geyer, 1988; Geyer and Landing, 1995). These faunas of the *Eofallotaspis* Zone include several species of the fallotaspidid genus *Eofallotaspis* and the bigotinid genera *Hupetina* and *Bigotinops*, all of which are endemic, as are most trilobites of the overlying *Fallotaspis tazemmourtenensis*, *Choubertella* and *Daguinaspis* Zones. The entire Issendalenian is characterised by fallotaspidid, redlichiid and bigotinid trilobites. Fallotaspidids (the genera *Choubertella*, *Daguinaspis*, *Eofallotaspis*, and *Fallotaspis*) appear to have preferred fine-grained siliciclastic substrates and are now found almost exclusively in shales; deposition took place on a slightly restricted carbonate platform with archaeocyathan-microbial buildups, apparently with limited connections to the open sea. Elsewhere fallotaspidids (in a broad sense) occur with certainty in the Lower Cambrian of the White–Inyo Mountains, California, adjacent Nevada, and Siberia. Redlichiid–saukiandid trilobites (such as *Marsai-*

*sia*, *Pararedlichia*, and *Resserops*) are also typical in fine-grained siliciclastics. They share characters with genera from other Cambrian regions such as the South China (or Yangtze) Platform (Nangaoian Stage) and are sometimes erroneously synonymised with *Eoredlichia* because of the limited set of characters.

*Lemdadella* and bigotinid trilobites are typical of well-bedded platform carbonates. They may be helpful for future correlations but are still imperfectly known because the past research concentrated largely on shale faunas. Similar bigotinids are known from the Lower Cambrian of the Armorican Massif and the Córdoba platform of the OMZ (*Bigotina*) but also from the Lower Cambrian *Pagetiellus anabarus* Zone (middle Atdabanian) of the Siberian Platform, in both areas also in platform carbonates. Finally, *Lemdadella* has been reported from the Lower Cambrian of the OMZ (Liñán and Sdzuy, 1978) and Antarctica (Palmer and Rowell, 1995).

In summary, the Issendalenian shows a moderate diversification of trilobite faunas with high preference for fine-grained siliciclastics and peritidal carbonate muds. Most species and the majority of the genera are endemic, which is probably due to a lack of knowledge of coeval faunas from other western Gondwanan areas.

The Issendalenian–Banian transition in Morocco is marked by a dramatic decrease of the fallotaspidids, whereas primordial ellipsocephaloids (the antatlasiiids) arise and increase impressively in number and diversity to form the most characteristic faunal element in the Banian. Fallotaspidids are replaced by neltneriids. The first eodiscoids (*Delgadella*, *Hebediscus*) occur in the lower Banian. All trilobites apparently have noticeable preferences for distinct lithofacies, but the framework is more complicated than the simple distinction between shale and carbonate facies in the Issendalenian. Banian rocks are dominated by fine-grained siliciclastics with relatively minor

Fig. 5. Global distribution chart illustrating presence (black) and absence (white) of Lower Cambrian trilobite genera reported in the western Gondwanan margin (A), biodiversity patterns (B), and analysis of hierarchical Phi–Pearson similarity (C). Some of the reported genera could occur in Fig. 6 as Middle Cambrian trilobites according to the considered horizon of the Lower–Middle Cambrian boundary.

nodular and bedded limestones deposited in a low-energy middle to upper platform environment.

During the Banian, for the first time, strong similarities of trilobite faunas can be detected between the Moroccan Atlas region and the OMZ. *Delgadella* is found in the lower, middle and even in the upper part of the Banian (*A. hollardi*, *A. guttapluyiae* and *Sectigena* Zones) and is also a frequent faunal element in the earliest assemblages of the OMZ. The *Sectigena* Zone of Morocco shares a number of genera and even species with the lower two assemblages of the OMZ, such as *Andalusiana cornuta*, *Gigantopygus*, *Rinconia*, *Saukianda andalusiae*, *Termierella* and *Triangulaspis*. This distinctive zone is represented in Morocco by several quite different local assemblages that portray a variety of coeval biofacies. Stratigraphical successions dominated by low-energy shales include the Ossa–Morena-type *Saukianda–Termierella* assemblage. Shales to fine-grained sandstones deposited in more agitated shallow-marine environments tend to yield a *Berabichia–Delgadella–Pentagonalia* fauna. Limestones and marls yield an assemblage with *Hebediscus* and *Sectigena*. Other trilobites are facies-independent and occur in different types of rocks. *Issafeniella* has been identified from the Marianian of the OMZ, which also shares a first and simple species (*Acanthomicmacca*) with the Moroccan *Sectigena* Zone. *Sectigena* itself, *Berabichia* and *Issafeniella*, have their counterparts, and obviously close relatives, in the Siberian genera *Charaulaspis* and *Chorbusulina*. Both occur in the latest Atdabanian and early Botoman of the northern Siberian Platform, where they are accompanied by *Hebediscus* spp. and *Triangulaspis*. Two additional species of *Chorbusulina* were described from the Lower Cambrian of Antarctica, but in fact could belong to *Berabichia*.

An important genus that has its first appearance in the *Sectigena* Zone is *Serrodiscus*. This genus has a long stratigraphical range, but it is remarkable that the same type of red shales of the Issafen Formation, in which *Serrodiscus* first occurs in the Anti-Atlas, also contains the first *Serrodiscus* species (*S. silesius* and other species) in the Marianian of the CIZ and OMZ, and in the

Charlottenhof Formation of the Görlitz area, Saxo–Thuringia (*S. silesius*). The German and Spanish Marianian assemblages also share the genera *Ferralsia* and *Lusatiops*. *Ferralsia* is known from the OMZ, but was originally described from the uppermost(?) Lower Cambrian of the Montagne Noire. An *Acanthomicmacca*, although difficult to judge in terms of precise ontogeny, is also known from the Charlottenhof Formation. A probable species of *Holmia* is also identified from the Charlottenhof Formation, and species tentatively assigned to *Holmia* and *Kjerulfia* were described from the lower? *Sectigena* Zone of the Anti-Atlas. Both genera are distinctive of the *Holmia kjerulfi* Zone of Baltica.

The faunas of the Moroccan *Sectigena* Zone and the coeval assemblages from Iberia, Saxo–Thuringia, the southern British Isles, southeastern Newfoundland and other areas are characterised by an assemblage that include relatively widespread eodiscoids. Typical species of this assemblage include *Calodiscus helena*, *C. lobatus* (in strict sense), *C. schucherti*, *Hebediscus* (or *Dipharius*) *attleborensis*, *Serrodiscus bellimarginatus*, *S. silesius*, *S. speciosus*, *Triangulaspis annio*, *T. vigilans*, and other species of *Triangulaspis* (Fletcher, 1972; Robison et al., 1977; Geyer, 1990b; Geyer and Palmer, 1995). Most of these species are relatively endemic, but their ranges show some regional overlap and associated taxa permit a subglobal recognition, for example in Baltica (Sweden), Avalonia (southeastern Newfoundland, New Brunswick, Welsh Borderlands), western Gondwana (Spain, Morocco), Siberia, the Altay–Sayan Mountains, and Kazakhstan. In western Gondwana, *Triangulaspis zirarii* of Morocco has its counterpart in the extremely similar *Triangulaspis fusca* from the OMZ, which is associated with *Calodiscus schucherti*, a species that also occurs in the Moroccan *Sectigena* Zone.

Such assemblages are the earliest to show clear faunal relationships between Avalonia and western Gondwana. The top of the *Callavia broeggeri* Zone in southeastern Newfoundland (regarded as a distinct *Serrodiscus bellimarginatus* Zone by Fletcher, 1972) includes not only *Serrodiscus bellimarginatus* and *Hebediscus attleborensis*, but also *Acanthomicmacca* species typical of the *Sectigena*

Zone, the Marianian of the IC, and the Charlottenhof Formation in Saxo–Thuringia. It also includes *Mallagnostus* (formerly *Ladadiscus*; see Whittington et al., 1997) *llarenai*, a species first described from the OMZ. Very similar trilobites, including *Acanthomicmacca*, *Calodiscus lobatus*, *Hebediscus attleborensis*, *Serrodiscus bellimarginatus*, and *Triangulaspis annio*, are known from various levels in the Comley Limestones in the Welsh Borderlands of England. Some eodiscoids, such as *Calodiscus*, *Hebediscus*, *Serrodiscus*, and *Triangulaspis*, are shared with assemblages from the top of the *Judomia* and *B. micmaciformis*–*Erbiella* Zones on the Siberian Platform.

The Lower Cambrian of southwestern Sardinia has yielded a relatively diverse trilobite fauna with a pre-*Sectigena* age. Most of the species and even genera are endemic, probably because they are largely from lithologies incompletely studied in supposedly coeval successions from other parts of western Gondwana. Particularly well known are the genera *Dolerolenus*, *Giordanella*, and *Metadoxides*. The few eodiscoids in these assemblages are of little help for either biostratigraphical or biogeographical correlations because they are also endemic. Another so-called *Dolerolenus* fauna has been described from the Ovetian of the IC (Sdzuy, 1987), an assemblage representing the oldest diverse trilobite fauna known from Spain. However, the trilobites are mostly described under open nomenclature because of their poor preservation. Nevertheless, the taxonomic affinities are sufficient to recognise that both areas share a similar trilobite fauna and obviously were biogeographically connected. Both may be regarded as faunas particularly adapted to relatively isolated, probably rimmed, carbonate platforms.

In a monographic reappraisal of the Sardinian trilobites, Pillola (1991a) described a number of new, endemic species and revised older species, mainly redlichioids. He assigned many of them to genera known almost exclusively from the South China Platform and proposed a strong palaeobiogeographical connection to that Cambrian continent. However, trilobite faunas of similar age and from similar facies are unknown from the platforms supposed to have been situated between those regions during the Lower Cambrian.

Pillola's (1991a) revision partly affected the nomenclature of trilobites from the Lower Cambrian of the Montagne Noire. *Galloredlichia noiri* was assigned to the 'Yangtze' genus *Eoredlichia*, a genus that occurs in relatively early trilobite assemblages on the South China Platform such as the famous Chengjiang Fauna. This assemblage can be correlated with the Uper Issendalenian and Upper Ovetian. In the Montagne Noire, *Galloredlichia* occurs together with *Granolenus midi*, a species also known from the Upper Ovetian of the CIZ.

A Banian–Tissafinian faunal turnover is marked by a relatively sharp change in the composition of benthic communities, exemplified by: (1) the appearance and massive increase of protolenine trilobites, (2) the sudden but apparently stacked appearance of other new trilobite groups, and (3) the relatively abrupt disappearance of ellipsocephaloid lineages. These strata with Lower–Middle Banian faunas are traditionally termed the 'Protolenus Zone' and regarded as of Early Cambrian age.

Early Cambrian (Comley Series) trilobites are known from Comley and the Rushton area in the Welsh Borderland and at Nuneaton on the Midland Platform, together with a very few, including *Hamatolenus* and *Pseudatops*, from northern Wales. There has been little recent revision of British Early Cambrian trilobites, and in view of significant recent work in Morocco, Spain and Germany, the generic placement of certain British taxa, particularly of ellipsocephaloids, is now open to question. Thomas et al. (1984) listed some 36 taxa from the Comley Series. If we accept the names currently applied, their affinities lie most strongly with trilobites from elsewhere in Avalonia. About 12 species are common to western Avalonia, including some eight of eodiscoids and species of *Protolenus*, *Strenuella* and possibly of *Callavia*; and a further 12 represent genera known from Avalonia and the Taconic Belt of New York. In contrast, only two species and three or four genera can be compared with Baltic faunas. The affinities with marginal Gondwana appear to be restricted to three species known from the OMZ – *Calodiscus schucherti*, *Mallagnostus llarenai* and possibly *Serrodiscus serratus* – and

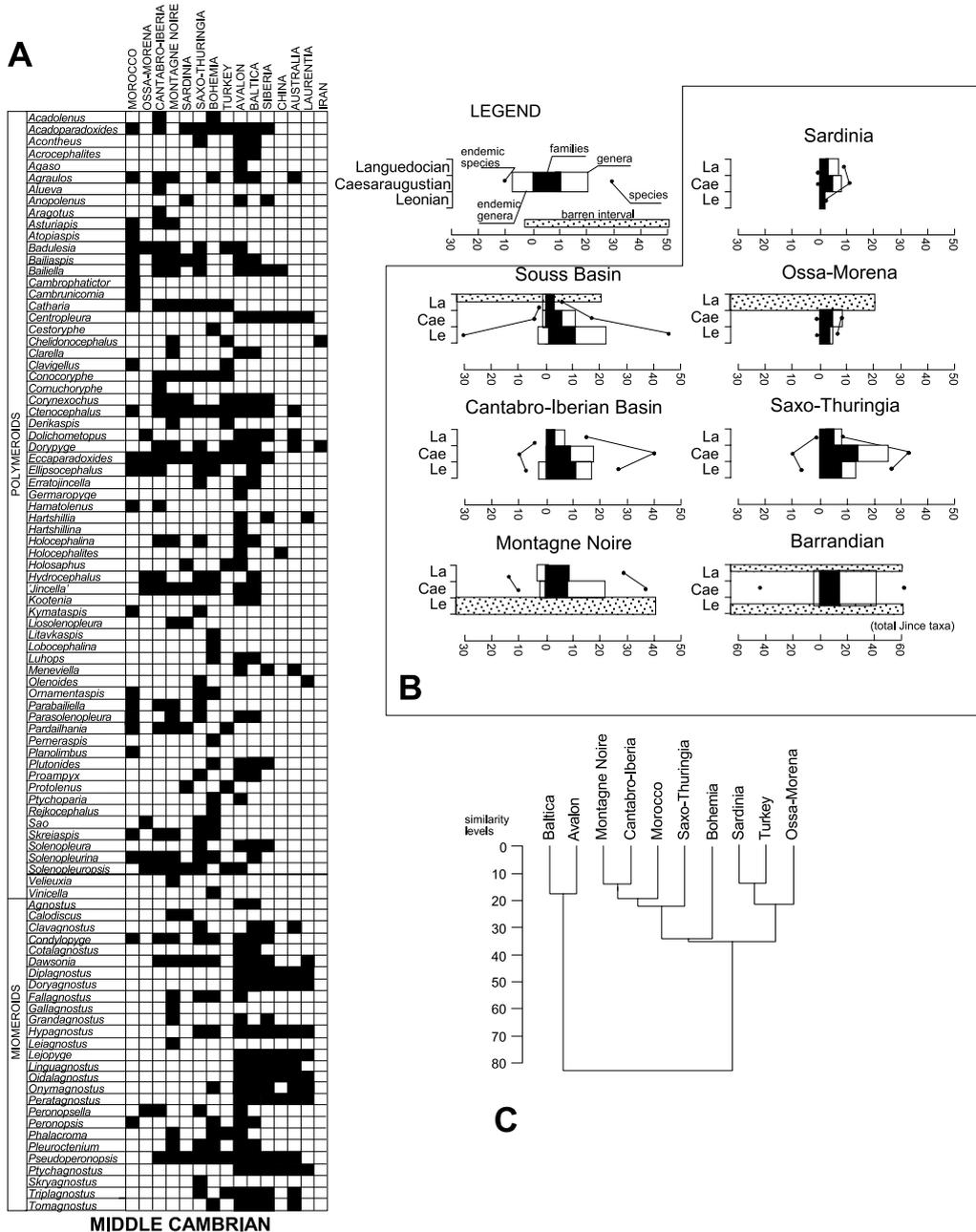


Fig. 6. Global distribution chart illustrating presence (black) and absence (white) of Middle Cambrian trilobite genera reported in the western Gondwanan margin (A), biodiversity patterns (B), and analysis of hierarchical Phi–Pearson similarity (C).

there are another 12 genera in common. The British representatives of these genera are: *Callavia callavei* and other species, *Cobboldites comleyensis*, *Comluella platycephala* (Morris, 1988, has

*Strenuella* (*Comluella*)), *Condylopyge amitina*, *Ellipsocephalus* (or *Ourikaia*?) *heyi* (see Geyer, 1990b), *Hamatolenus douglasi*, *Hebediscus attlebornensis*, *Latoucheia latouchei*, *Micmacca* spp.,

*Protolenus paradoxoides*, *Serrodiscus bellimarginatus* and other spp., and *Triangulaspis annio*. According to Sdzuy (1961), possibly *Andalusiana?* (or *Kjerulfia?*) *granulata* should also be included. The greatest resemblance is shown by faunas from the ‘Brèche à *Micmacca*’ in the basal Middle Cambrian in Morocco. Geyer and Malinky (1997) correlated this unit with the *Protolenus* Limestone of Comley, Shropshire (Cobbold’s unit Ac5; see Rushton et al., 1999), which in Britain was treated hitherto as late Early Cambrian.

## 5.2. Middle Cambrian

As discussed above for the Lower Cambrian trilobites of the western Gondwana margin, the database from which the following analysis is made is heterogeneous. This is due to the existence of barren intervals, across the Leonian in the Montagne Noire and the Middle–Late Languedocian in Morocco and the OMZ, which prevent complete correlations (Fig. 6A). The Lower–Middle Cambrian boundary is not uniform over the whole area, because it has been characterised by different bioevents based on trilobite and acritarch appearances. The Lower–Middle Cambrian transition contains numerous barren stratigraphical intervals and unconformities, so that the transition (and not its boundary) will be described below in two key areas with continuous sedimentation and fossil wealth: Morocco and the IC. In the present state of knowledge, two different biodiversity patterns are recognised during Mid-Cambrian times: (1) a progressive decrease in diversity in Morocco, and (2) a composite increase–decrease trend in the whole of southwestern Europe. Consequently, during Early to Middle Cambrian times, the area of maximum diversity migrated northeastwards; a result that may be related to the southwestward drifting of the western Gondwana margin.

In general, two Middle Cambrian trilobite diversifications are recognised (Fig. 6B): (1) a major migratory radiation of trilobites during the Tissafrican/Upper Bilbilian to Caesaraugustian when most families appeared without obvious ancestors in the fossil record; and (2) a Late Languedocian trilobite diversification connected with transgres-

sive episodes and representing new migratory inputs of recurrent trilobite genera. Both episodes were punctuated by distinct faunal turnovers.

Several lines of evidence have been put forward that imply extinction events towards the end of the Early Cambrian. They point to the concept of a widespread latest Early Cambrian biocrisis, as the culmination of a worldwide decline of trilobites and other taxa that commenced earlier in the Early Cambrian and led to a global diachronous extinction (Debrenne, 1991; Brasier, 1995; Zhuravlev, 1995; Álvaro et al., 1999). The terminal Lower Cambrian strata display a succession of extinction events related to the disappearance in the western Gondwana margin of microbial–archaeocyathan buildups and the establishment of regressive conditions. A local event has been identified in the IC at the end of this tendency, termed the ‘Valdemiedes event’. Data from the trilobites do not necessarily support a catastrophic extinction at this horizon, their record being imperfect on account of barren intervals prior to that event. The event represents the end of the relatively endemic, inner-platform survivors of the area, followed by an inshore migration of more pandemic, outer-platform faunas.

It should be noted that during the Lower–Middle Cambrian transition the Moroccan succession shows a different pattern from that portrayed by southwestern Europe. In the Atlas ranges, the terminal Lower Cambrian–basal Middle Cambrian regressive–transgressive trends are represented by a marked coarse clastic input, regionally overprinted by volcanoclastic deposits. Two distinct unconformities exist, one within the sandstone–volcanoclastic unit (which is accordingly divided into the Tazlaft and Tatelt Formations), and another one at its top. The fossil record, however, is rich across both formations and suggests that a punctuated extinction did not take place. Although the faunal turnover reported across the Banian–Tissafinian transition signals a strongly depauperate fauna in the basal Tissafinian *Hupeolenus* Zone, some species range across the boundary; this turnover pre-dates the ‘Valdemiedes event’ of the IC, which roughly coincides with the base of the *Cephalopyge notabilis* Zone. The fossil poverty of the *Hupeolenus* Zone fauna can

largely be attributed to unfavourable living conditions during the pronounced input of terrigenous clastics and volcanogenic components. By contrast, the *C. notabilis* Zone includes one of the most diverse trilobite assemblages in the world known from this time. Its base is regionally placed within the clastic blanket so that the diversification can be proved to be a true radiation rather than merely created by a favourable diversity of ecological niches. Nevertheless, the peak diversity was not reached until the establishment of a number of diverse facies conditions on the basal Middle Cambrian platforms. As noted above, the strata with Lower–Middle Cambrian faunas are correlated with the ‘*Protolenus* Zone’ in areas such as eastern Avalonia (England and Wales), western Avalonia (southeastern Newfoundland and New Brunswick) and Baltica, and are regarded as of Early Cambrian age.

The earliest Mid-Cambrian faunal recovery can be regarded as an adaptative radiation of an immigrant trilobite community that progressively invaded the western Gondwanan margin from deeper-water environments. The Tiszafrican/Leonian immigration is characterised by the stepwise appearance of relatively cosmopolitan trilobites, such as the acrocephalitids, agraulids, corynexochids, conocoryphids, paradoxidids, solenopleurids and agnostoids (condylopygids, phalacromids and spinagnostids). The observed pattern of diversification was not facies-controlled because trilobites appeared in a wide diversity of facies and environments. Some trilobite families crossed the Lower–Middle Cambrian transition, although decreasing sharply in diversity, such as the ellipsocephaline and protolenine trilobites. Subsequently, the western Mediterranean area apparently operated as a centre of evolutionary radiation (or a site of speciation), from which the species were able to spread outward into adjacent platforms, in some cases by sympatric speciation (Álvarez and Vizcaíno, 2001). As a result, a relative biogeographical concordance of evolutionary patterns is virtually complete for some trilobite families, and there are no apparent extrinsic barriers separating the sibling species. Some Caesaraugustian benthic species evolved in this area and proved capable of migrating to colonise areas

from Newfoundland and Rhode Island to Turkey (e.g. *Badulesia tenera*). There were no physical barriers preventing trilobite dispersal, which was favoured by uniform seafloor conditions (open-platform, muddy offshore substrates), and low temperature-gradients. Diversity increased and species proliferated during Caesaraugustian times. The acme is associated with transgressive conditions and subsequent connection of platforms, and represents the peak in diversity of trilobite families, genera and species during the Middle Cambrian.

A major reduction in the number of trilobite genera occurred across the Caesaraugustian–Languedocian transition, at a time of widespread coarse-grained terrigenous input associated with a well-documented regressive trend. The disappearance of trilobite taxa is related to the disappearance of their habitats. This diachronous decline was catastrophic for some previously successful trilobites, such as the solenopleurinae (except the genus *Sao*). This biocrisis is not a major extinction at familial level for trilobites, but represents a significant generic turnover. The faunal turnover coincides with a rapid prograding and shoaling that produced widespread areas of coarse-grained sandstones and, therefore, seems to reflect geographically extensive environmental changes. In Baltica there is a regression at the level of the late Middle Cambrian Andrarum Limestone (Nielsen, 1996), and this is recognised in the southern British Isles and Newfoundland as an ‘Andrarum Limestone regression’, with the *laevigata* Zone above. It is unlikely that the last Languedocian fauna is as young as the *L. laevigata* Zone (see Fig. 2); paradoxidids appear to be extinct by then in Baltica and a new fauna occurs with trilobites of Upper Cambrian aspect, such as *Agnostus*, *Andrarina*, and *Proceratopyge*.

The Late Languedocian trilobite diversification is well documented in the southern Montagne Noire, Sardinia, and Saxo–Thuringia, where it is characterised by an abrupt increase in genera and families. The appearance of this new assemblage of trilobites represents an immigration event related to transgressive pulses. Episodically, off-platform trilobite taxa migrated towards the inner platform, leading to a strict facies control on the

lithofacies differentiation, and coinciding with the establishment of suitable muddy offshore substrates. However, the diversity of the new groups is less than in the previous radiation. Dispersal took place to some extent, but the presence of some provincialism suggests that species exchange was selective, and that the oceanic areas may have served as partial barriers to migration. Late Languedocian trilobites include typical genera of the Leonian–Caesaraugustian diversification (such as the conocoryphids and paradoxidids) and new Asian invaders, such as the genera *Abharella*, *Chelidonocephalus*, *Derikaspis* and *Dorypyge* (see Álvaro et al., 1999, and references therein). This influence illustrates the immigration of faunas from the northern Gondwanan margin, which went on during Late Cambrian times (see below). However, the percentage of pandemic species decreased across the Languedocian, and geographic distribution also decreased because of successive regressive pulses.

The Middle Cambrian of the British Isles (St. David's Series) is in the lower part generally developed as arenaceous clastic deposits, and in Shropshire (and possibly elsewhere also, though the evidence is not so clear) they overlie a break in the succession. These deposits contain a restricted fauna of agnostoids, paradoxidids and a few other taxa such as *Bailiella*. Higher up, dark mudstones (the classical 'Menevian Beds') are widespread. They contain a richer fauna of agnostoids, paradoxidids and various polymerid trilobites, commonly including blind genera. These dark beds are overlain by a hiatus that in most places is evinced by erosion during the marine low-stand corresponding to the *Solenopleura* (now *Erratojincella*) *brachymetopa* Zone (Rushton, 1978; Nielsen, 1996). Thomas et al. (1984) listed 106 named St. David's taxa, and more recent work has added a few more: in St. Tudwal's Peninsula, northern Wales, Young et al. (1994) figured forms derived from the *brachymetopa* Zone, namely *Bailiaspis glabrata* (as a senior synonym of *B. nicholasi*), *Dolichometopus* cf. *svecicus*, *Linguagnostus aristatus*, and fragments of *Acrocephalites*, *Dorypyge* and *Centropheura*, whilst Bridge et al. (1998) have figured *Luhops expect-*

*ans*, *L.?* *pugnax* (*Clarella* in Morris, 1988) and *Paradoxides abenacus*. The faunas are most closely related to those of Baltica, with which 40 species are in common, and a further 14 at generic level, and with western Avalonia (mainly Newfoundland), with which 34 species are in common and a further fourteen at the generic level. Resemblance with the Gondwanan margin is considerably lower: there are eight species in common with Bohemia and Saxo–Thuringia, namely *Condylopyge rex*, *Eccaparadoxides pusillus*, *Luhops expectans*, *Peronopsis integra*(?), *Phalacroma bibullatum*, *Phalagnostus nudus*, *Pleuroctenium granulatum granulatum*, and *Plutonides* (*Hydrocephalus*) *hicksii*. Further genera in common appear to include *Acadoparadoxides*, *Agraulos*, *Ctenocephalus*, *Dawsonia*? (if *Metadiscus* is a synonym), *Holocephalina*, *Hypagnostus*, *Paradoxides*, *Ptychagnostus*, and *Ptychoparia*? There are about six species in common with the Iberian Peninsula, namely *Agraulos longicephalus*, *Condylopyge carinata*, *C. rex*, *Paradoxides davidis*?, *Peronopsis fallax*?, *Plutonides hicksii*, and, from Sardinia, *Anopolenus henrici*? (Loi et al., 1995). The only British member of the important peri-Gondwanan family Solenopleuropsidae is *Solenopleuropsis* (*Manublesia*) *variolaris*, which occurs in the *punctuosus* Zone. This assessment shows once again that the agnostoid trilobites are the most widely dispersed of taxa, with *Condylopyge rex* being recorded from each of the regions considered here. The resemblance of the British (eastern Avalonia), Newfoundland (western Avalonia) and Baltic faunas rests largely on the similarity of their agnostoids, and doubtless the relative paucity of peri-Gondwanan agnostoids is a hindrance to inter-regional correlation. Avalonia and Baltica show agnostid faunas intermediate between those of Laurentia and parts of the Gondwanan margin (Conway Morris and Rushton, 1988). Some species of paradoxidids are also relatively widely distributed, although their larger size and commonly fragmentary preservation sometimes makes for difficulties in collection and identification. The polymerid trilobites such as conocoryphids and ptychopariids appear much more frequently to be endemic.

### 5.3. Upper Cambrian

Upper Cambrian trilobites are very rare in the western Gondwanan margin, compared with the wealth recorded in the Lower and Middle Cambrian, and occur in a variety of lithofacies associations ranging from inner platform sandstones and shales to outer platform and slope carbonates. Temperate-water faunas were less diverse and more impoverished than Lower–Middle Cambrian ones. In contrast, British faunas contain around 100 taxa that represent the whole Upper Cambrian.

#### 5.3.1. The Iberian Massif

Late Cambrian trilobites occur in the WALZ, DM and IC. The occurrence of Late Cambrian trilobites in the DM was first reported by Colchen (1967) who determined the presence of *Chuangia* and *Prochuangia* in the lower member of the Najerilla Formation. These trilobites were subsequently described and revised by Shergold et al. (1983), who recognised two trilobite associations: (1) an oldest one comprising four taxa (aphelaspine, leiostegiid?, *Maladioidella colcheni*, and *Langyashania felixi*); and (2) a younger assemblage, from the second member of the Najerilla Formation, containing only two taxa (pagodiine and a solenopleuroidean? aff. *Lajishanaspis*). These determinations support Colchen's contentions of an Asian influence, e.g. *Maladioidella* has a distribution that extends from Spain to northern China (Rushton and Hughes, 1996; Jago, in Brock et al., 2000).

In the IC, the first Late Cambrian trilobites were determined by Sdzuy (in Josopait, 1972), and subsequently described by Shergold and Sdzuy (1991). These occur both in the middle part of the Valtorres Formation and the lower part of the overlying Valconchán Formation. The faunal association includes agnostoid, aphelaspine aff. *Aphelaspis rara* (Orłowski) sensu Żylińska (2001), *Elegantaspis* cf. *beta*, *Parachangshania* sp., *Pseudagnostus* sp., *Punctaspis?* *schmitzi*, solenopleuroidean, and *Valtorresia volkeri*. The Upper Cambrian assemblage is overlain in the uppermost Valconchán Formation by a sandstone bed containing *Pagodia* (*Wittekindtia*) *alarbaensis*

and olenid fragments now thought to represent a species of *Jujuyaspis* that would indicate an earliest Ordovician age. It is possible that the occurrence of *P. (Wittekindtia)* in the DM is also of this age. Both there and in the IC, this subgenus is associated with the echinoderm-like *Oryctocoelus lobatus* Colchen and Ubaghs, 1969. By virtue of the aphelaspine morphologies in the IC, and *Maladioidella* in the DM, the trilobites of northern Spain are considered to have an Iberian age according to the Australian standard and a Sunwaptan age on the Laurentian timescale.

#### 5.3.2. Montagne Noire

Late Cambrian trilobites occur in the Val d'Homs Formation (Ferrals-les-Montagnes). They were first described by Feist and Courtesole (1984), who recognised two species referred to *Prochuangia gallica* and *Bergeronites latifalcatus*. Subsequent collecting from a limestone lens close to the base of the formation has revealed the presence of further taxa (Shergold et al., 2000): *Abharella* sp., *Ammagnostus* (A.) aff. *sinensis*, *Kormagnostus?* sp., *Olentella* cf. *africana*, *Palaeadotes latefalcata*, *Paraacidaspis ultima*, *Proceratopyge* (P.) spp., *Prochuangia gallica*, *Shengia* cf. *spinosa*, and *Stigmatia courtessolei*. The age of this fauna is judged to be similar to, but slightly older than, that characterised by *Maladioidella* in the DM. Many of its elements have a widespread distribution along the Gondwanan margin (Shergold et al., 2000), and the agnostoids and *Proceratopyge* extend even to Laurentia. However, the Ferrals association shows greatest relationship with southern and central China, Australia and Antarctica.

Elsewhere in the Montagne Noire, an assemblage containing species of *Maladioidella*, *Onchonotellus*, *Probilacunaspis*, *Proceratopyge*, *Prochuangia*, and a pseudagnostinid occurs in carbonates of the Val d'Homs Formation to the southwest of Coulouma. Once more, its composition is dominated by Chinese genera. This assemblage is the youngest Cambrian fauna found so far in the Montagne Noire. The earliest Ordovician is marked traditionally by the appearance of *Proteuloma geinitzi* described by Sdzuy (1958) from reddish limestones just below the base of

the La Dentelle Quartzite in the vicinity of Combes de Barroubio.

### 5.3.3. Sardinia

Although they have not been systematically documented, Late Cambrian trilobites have been noted and illustrated in the upper part of the Cabitza Formation in the Cabitza area and north of Domusnova (Loi et al., 1995, 1996). They occur in fine sandstones and siltstones probably representing a tide-dominated deltaic environment. Illustrated trilobites (Loi et al., 1995, 1996) are from faunal assemblage CAB 5b, which contains *Macropyge* sp., *Maladioidella* cf. *colcheni*, *Micragnostus* cf. *haudei*, *Niobella* cf. *primaeva*, *Onchonotellus?* *amsassensis*, *Proceratopyge* sp., a leiostegiid aff. *Pagodia*, a eulomid, and a calymenid. At Monte Cani this assemblage is succeeded by green siltstones containing (CAB 6) *Rhabdinopora flabelliformis* (Pillola and Gutiérrez-Marco, 1988; Pillola and Leone, 1993), *Proteuloma geinitzi* (Pillola, 1991b) and *Oryctoconus* cf. *lobatus*. The younger assemblage is clearly of earliest Tremadocian age.

### 5.3.4. Morocco

Two Late Cambrian trilobite taxa have been documented from the upper member of the Jbel Lmgaysmat Formation, in the Foum Zguid region (Destombes and Feist, 1987). *Olentella africana* and *Seletella latigena* represent the first Upper Cambrian occurrence in North Africa. Both genera occur in the Sakian, *Aphelaspis*–*Kujandaspis* Zone, in central Kazakhstan (Ivshin, 1955, 1956, 1962). *Olentella* cf. *africana* has also been described from Ferrals-les-Montagnes in the Montagne Noire (Shergold et al., 2000). The fossiliferous Upper Cambrian is overlain by a discordance followed by shales containing *Rhabdinopora flabelliformis*.

### 5.3.5. British Isles

The Late Cambrian (Merioneth Series) trilobites have been found in England and Wales wherever rocks of that age are exposed, and all the main zones are proved. In the lower Merioneth Series there are commonly muddy, silty and sandy beds with *Homagnostus* and a few species

of *Olenus*. The higher Merioneth is developed everywhere as black mudstones related to the olenid biofacies and contains a considerable variety of olenids, admixed with a small number of agnostoid and other non-olenid genera. A number of new records have appeared since the publication of Thomas et al. (1984): Allen and Jackson (1985) recorded the presence of *Niobella homfrayi* *preciosa*, *Parabolina acanthura*, *P.* cf. *angusta*, and *Parabolinella contracta*; Hughes and Rushton (1990) transferred '*Dikelocephalus*' *discoidalis* to the ceratopygid genus *Cermatops*; Cope and Rushton (1992) described previously unknown faunas from Llangynog, south Wales, that include *Ctenopyge* (*C.*) *linnarssoni*; Howells and Smith (1997) recorded the presence of *Loganellus* sp., *Maladioidella abdita* ('*Conokephalina*' in Morris, 1988), *Olenus* cf. *solitarius*, *Parabolina* aff. *mobergi* and *P.* (*Neoparabolina*) *lobata praecurrens*; Bridge et al. (1998) noted *Ctenopyge* (*C.*) *pecten tenuis* from a borehole.

Of these trilobites, the olenids are widely distributed where the appropriate dysaerobic facies is present, and some others, such as agnostoids (especially *Glyptagnostus reticulatus*), *Proceratopyge* and other ceratopygoids, *Irvingella* and *Maladioidella* (Rushton and Hughes, 1996) are widely distributed in a variety of shelf environments. In Britain other rare non-olenid, non-agnostoid taxa include species of *Acanthopleurella*, *Aphelaspis* (Żylińska, 2001), *Araiopleura*, *Conophrys*, *Cyclolorenzella*, *Eoasaphus*, *Loganellus*, *Modocia*, *Niobella*, *Parabolinoidea*, *Proteuloma*, *Richardsonella*, and *Schmalenseeia*.

Thomas et al. (1984) listed 86 named taxa and the above-mentioned works added nine more. Of these, 61 are identified with, or compared with, species from Baltica, and a further 10 are comparable at the generic level. The Upper Cambrian faunas of western Avalonia appear to be less fully known, but, out of a total of about 20 species recorded by Martin and Dean (1988), there are 13 species in common with British faunas and four or five additional shared genera.

The Upper Cambrian in the peri-Gondwanan region contains a number of faunas (discussed above), but, presumably because the prolific olenid biofacies is not well developed, there are rel-

atively few taxa in common with Britain. For example, there is nothing in British faunas to match the oriental genera recorded from the Montagne Noire, and with the transfer of *Olentella rara* of Rushton (in Allen and Jackson, 1985) to *Aphelaspis* (Żylińska, 2001), there is no genus in common with the Moroccan fauna. Upper Cambrian outcrops from Spain (Shergold et al., 1983) have only yielded *Maladioidella*, and possibly an undetermined aphelaspidine that can be compared with taxa in British faunas, while a fauna from Sardinia only has a few more comparable taxa, namely *Maladioidella*, *Proceratopyge*, an early form of *Niobella* and some unspecified olenids (Loi et al., 1995).

#### 5.3.6. Turkey

Late Cambrian trilobites have been recorded from the Taurus and Amanos Mountains in south-central Turkey. In the northeast, they occur in the Seydişehir Formation of the Sultan Dağ (Shergold and Sdzuy, 1984; Dean et al., 1993), on the Tülüce Tepe section. Trilobites described by Shergold and Sdzuy (1984) include *Homagnostus?* sp., *Maladioidella kelteri*, *Pseudagnostus* cf. *cyclopyge*, *Pseudagnostus* sp., and undetermined ptychoparioids and solenopleuroideans. Dean et al. (1993) also illustrated specimens of *Homagnostus* and *M. kelteri*. All these assemblages are Late Cambrian in age, which may well correlate with the *Maladioidella*-bearing horizons of Sardinia, Montagne Noire, and northeastern Spain.

In the Sultan Dağ, this fauna is succeeded by a younger association (Shergold and Sdzuy, 1984) containing *Koldinioidia* (*K.*) cf. *sulcata*, *Macropyge* cf. *taurina*, *Micragnostus haudei*, *Niobella* cf. *primaeva*, *Onchonotellus* aff. *amsassensis*, *Parakoldinioidia* cf. *gibbosa*, *Proteuloma* cf. *geinitzi*, and *Rhaptagnostus?* sp. This was assumed by Shergold and Sdzuy (1984) to indicate an Early Tremadocian age since elements of the association are traditionally considered to be of this age and have a wide distribution in the Franconian Forest area (Germany), the Montagne Noire, the Czech Republic, southern Kazakhstan, southern Siberia, and the Xinjiang Province in China. However, all of the generic taxa have latest Cambrian origins, except perhaps *Macropyge* (although the genus is

noted to occur in the Sardinian CAB 6 fauna, though not illustrated). *Micragnostus*, *Niobella* and *Parakoldinioidia*, for example, are related to taxa described from the *Acerocare* Zone (Rushton, 1982), which Landing et al. (1978) regard as correlatable with the *Cordylodus proavus* conodont Zone. Given the current acceptance of the position of the Cambrian–Ordovician boundary (Cooper and Nowlan, 1999) at the first appearance of the conodont *Iapetognathus fluctivagus* Nicoll et al., 1999, associations correlated with the *C. proavus* Zone are terminal Cambrian age, or Datsonian in the Australian standard (see also the discussion of the Sardinian CAB 6 assemblage by Loi et al., 1995; and the correlations proposed by Geyer and Shergold, 2000). Accordingly, it may be necessary to reassess the Sultan Dağ ‘Tremadocian’.

Finally, in southeastern Turkey, Late Cambrian trilobites have been reported by Dean et al. (1981) and Dean and Monod (1997) from the Seydişehir Formation of the Samur Dağ area, on the Yayla Tepe section. Trilobites reported from here include species of *Chuangia*, *Drepanura*, and *Prochuangia*, overlain by younger assemblages characterised by *Alborsella*, *Niobella*, *Pagodia* (*Wittekindtia*), and *Saukia*, all indicating affinities with northern Iran.

## 6. Biogeographical cluster analyses

A matrix tabulating all genera and species known from the Lower and Middle Cambrian of Morocco, Ossa–Morena, the Cantabro–Iberian Basin, Montagne Noire, Sardinia, Saxo–Thuringia, the Barrandian area and Turkey (the latter only for the Middle Cambrian) has provided significant information (Figs. 5C and 6C). Phylogenetic biogeography (Lieberman, 2002) is not available for the Cambrian trilobites of the western Gondwanan margin due to the scarcity of cladistic analyses. However, the data reported here (114 genera and 249 species for the Lower Cambrian, and 113 genera and 442 species for the Middle Cambrian) were analysed using a standard method of linkage cluster analysis, namely analysis of hierarchical Phi–Pearson similarity,

which produces dichotomising patterns that are easier to interpret than multivariate analyses. Percentage similarity in a single linkage cluster analysis provides an approximate key to robustness of branching nodes within the constraints of parametric analysis. Trilobite faunas from the different basins and platforms are associated in terms of their shared genera and species. The analysis of similarity produces bifurcating dendrograms readily interpreted in terms of biogeography. The disadvantage of this method is that biofacies patterns are not considered, and that the total diversity of each platform strongly affects the percentage of shared taxa. Endemic taxa were eliminated from the database before they were entered in the data matrix because they may represent local ecological conditions, lack of marine connections to neighbouring platforms, or sampling biases. Further research might extend the known biogeographical distribution of some taxa but it seems unlikely that such new data would seriously modify the basic patterns discussed in this paper.

### 6.1. Lower Cambrian

The Lower Cambrian shallow subtropical marine biota exhibits the greatest diversity patterns in the whole Cambrian. One of the most interesting features of the Lower Cambrian is the widespread development of endemic species. The Lower Cambrian palaeogeographical complexities of the carbonate and mixed platforms, episodically related to the development of microbial–archaeocyathan reefal complexes, offered various opportunities for the isolation of populations and subsequent allopatric speciation. Many subtropical endemic trilobites assemblages are essentially related to reef communities. Trilobite similarity exhibits two major clusters (Fig. 5C): (1) the southern British Isles, Morocco, and the OMZ; and (2) Saxo–Thuringia, Montagne Noire, the CIZ, the Cantabro–Iberian Basin, and Sardinia. The close relationship of the OMZ with the entity ‘eastern Avalonia–Morocco’ is significant because it could reflect easier reproductive communication in the southwesternmost part of the area studied due to open oceanographic conditions and a possible setting of the OMZ closer to Morocco than that

illustrated in palaeogeographical maps. Trilobite faunas show a marked change in distribution patterns across the Lower–Middle Cambrian transition; this is attributed to a major palaeogeographical reorganisation, in which the endemic patterns displayed by the Lower Cambrian trilobite fauna ended diachronously and were followed by a period of relative sedimentary homogeneity, with an open connection of platforms that allowed immigration of trilobites.

### 6.2. Middle Cambrian

Trilobite similarity shows two main clusters (Fig. 6C): (1) Baltica–eastern Avalonia, and (2) the rest of the basins discussed here. This also shows strong support for the presence of two Mid-Cambrian biogeographical entities within the Mediterranean subprovince of Sdzuy (1972), distinctly differentiated from eastern Avalonia and Baltica. Therefore the relative Baltic affinity of the Middle Cambrian faunas from the Příbram–Jince Basin (Havlíček, 1999) does not support differentiation of a Middle Cambrian Perunica terrane. Another important biogeographical relationship with Bohemia is indicated by a Middle Cambrian trilobite assemblage found in the *Ptychagnostus atavus* Zone of the Carolina Slate belt (eastern United States). The latter is considered as an exotic terrane likely accreted to North America during the Early or Middle Palaeozoic, although an alternative possibility has been proposed placing this fauna in cool-water environments along the periphery of Laurentia (Samson et al., 1990).

The variability of the biogeographical distribution documented in the studied populations is directly related to species diversity. Decreasing provinciality of trilobites during the Caesaraugustian appears to have been accompanied by an increase in total diversity. The development of regional regressions induced habitat differences on a local and regional scale favouring ‘microallopatric’ speciation.

Regarding the British Cambrian faunas, they have their closest affinity to those of the Gondwanan margin at the end of the Early Cambrian (or earliest Mid-Cambrian in Morocco) and this

affinity declines through the Middle and Late Cambrian. Through the same period the British Cambrian faunas retain considerable similarities with western Avalonian faunas (those of east maritime Canada and eastern United States, e.g. Massachusetts, New Brunswick, Newfoundland, etc.) and become progressively more similar to Baltic faunas.

### 6.3. Upper Cambrian

A cluster analysis of the Upper Cambrian trilobite faunas is not significant because of their low diversity patterns in areas other than Britain. In addition, trilobite biofacies possibly occur at only three stratigraphical levels: (1) the Idamean or Steptoean (IC, Montagne Noire, Morocco), characterised by aphelaspoid morphologies; (2) the Iverian or Sunwaptan (DM, Montagne Noire, Sardinia, western Turkey), characterised by the occurrence of *Maladioidella*; and (3) the Datsonian, of *Cordylodus proavus* Zone age. If the age of strata with *Niobella*, *Macropyge*, *Pagodia* (*Wittekindtia*), and *Parakoldinioidia* can be firmly established as of *Cordylodus proavus* Zone age, then that biofacies becomes the third of latest Cambrian age. Some support for this assumption comes from conodonts recovered by Özgül and Gedik (1973) from the Seydişehir Formation in the central Taurus Mountains, which by Australian standards are terminal Cambrian. Strata with *Oryctoconus* also support this assignment, since they occur in association with the *Acerocare* Regressive Event (Erdtmann, 1986; Nicoll et al., 1992; Loi et al., 1995, 1996), a global sea-level fluctuation close to the currently adopted Cambrian–Ordovician boundary. Most of the Upper Cambrian faunas described from western Gondwana contain elements interpreted as of central and southeastern Asian provenance.

## 7. Conclusions and further questions

One process can be considered primarily responsible for the northeastward migration of the biodiversity centre (based on trilobites) on the western Gondwanan margin during the Cambri-

an: the cooling associated with the southwestward drift of the continental margin. Diverse Lower Cambrian trilobite assemblages are found in the shallow waters of subtropical areas, as studied in the Souss Basin of Morocco. The progressive change from relatively endemic to cosmopolitan trilobite assemblages across the Lower–Middle Cambrian transition can be related to three main events: (1) the disappearance of microbial–archaeocyathan buildups and neighbouring perireefal environments, (2) the relative uniformity of muddy offshore substrates related to a regional (eustatic?) early Mid-Cambrian transgression, and (3) the disappearance of significant temperature gradients on the Southern Hemisphere. The peak of Middle Cambrian trilobite diversity progressively migrated from Morocco to southwestern Europe (Cantabro–Iberian, Montagne Noire, Saxo–Thuringia and Barrandian areas), although these subtropical- to temperate-water platforms did not reach the richness reported in the Lower Cambrian of the Souss Basin. Finally, Upper Cambrian temperate-water faunas are dramatically impoverished compared with the previous wealth, except in the southern British Isles, where the prolific olenid biofacies developed, exhibiting a strong biogeographical relationship with Baltica.

Ocean currents played a significant role in the regional distribution of benthic communities. Two Cambrian unidirectional circulation trends seem to have been in operation: (1) in the Early to Mid-Cambrian, a western peri-Gondwanan current with a SW–NE trend extended from polar areas to lower latitudes and favoured interchange with benthic communities of Baltic affinity; (2) in the Late Cambrian a NE–SW longshore current flowed towards higher latitudes and seem to have involved organisms of Asian affinity. However, it remains a question whether the dispersal of subtropical, Australo–Sinian trilobites into temperate or cold seas of the Southern Hemisphere can be attributed to transport of southward-drifting currents? Or did the migration take place in a direction opposite to that of the main northeastward flow of surface waters?

Numerous questions are still open for future discussion that will benefit from a multidisciplinary

nary approach. This paper constitutes only one new step in the establishment of Cambrian palaeobiogeographical models. The palaeobiogeographical maps and biogeographical interpretations expressed here are intended to stimulate critical remarks from specialists of other fossil groups and geological disciplines, and to be tested further in the light of new data.

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